THE PALAEOBIOLOGY OF LATE CAMBRIAN PROTOCONODONTS, PARACONODONTS AND EUCONODONTS

by

KAREN DAWN COCHRANE

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ABSTRACT

Late Cambrian protoconodonts, paraconodonts and euconodonts from Laurentia and Baltoscandia have been investigated in terms of their apparatus composition and histology. Protoconodonts are considered to be members of the phylum Chaetognatha in accordance with the views of previous authors. The apparatus compositions of some primitive euconodonts are more complex than previously thought, with *Eoconodontus notchpeakensis* being assigned a septimembrate apparatus that has been described using nomenclature formerly applied to *Panderodus*. The histology of primitive and more derived euconodonts is homologous, with the exception that 'true' white matter is replaced by 'pseudo'-white matter in the enamel crown. Globular calcified cartilage and atubular dentine are present in the basal bodies of species from the *Proconodontus* complex. Similarities in apparatus composition and histology between primitive euconodonts suggest that they form a monophyletic group. Paraconodonts possess multielement apparatuses, and a suprageneric classification has been erected on the basis of new apparatus descriptions. Finally, a histological comparison of the inner core in the paraconodont *Proonoeotodus* and the basal body in several euconodont genera, leads to the conclusion that certain paraconodonts are related to euconodonts, and that the history of the vertebrate mineralised dermal skeleton can be extended into the Middle Cambrian.

This work is dedicated to my family and friends.

When you are a Bear of Very Little Brain, and you Think of Things, you find sometimes that a Thing which seemed very Thingish inside you is quite different when it gets out into the open and has other people looking at it.

A. A. Milne (1882-1956), *The House at Pooh Corner* (1928).

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My parents have offered unrelenting support and love during the last four years for which I cannot express enough gratitude. Friends have always been there in times of need and also in times when beer wasn't needed. Those who deserve a special mention are: (in alphabetical order as a matter of diplomacy) Andy, Ben, Bryan, Eithne, Jo, Louise, Nick, Rich, Simon and Steve and last, but most definitely not least Jack and Vern, my best friends in the world to whom I owe my gratitude, my love and my apologies for being such a pain in the posterior for the past 12 months.

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CHAPTER 1

INTRODUCTION

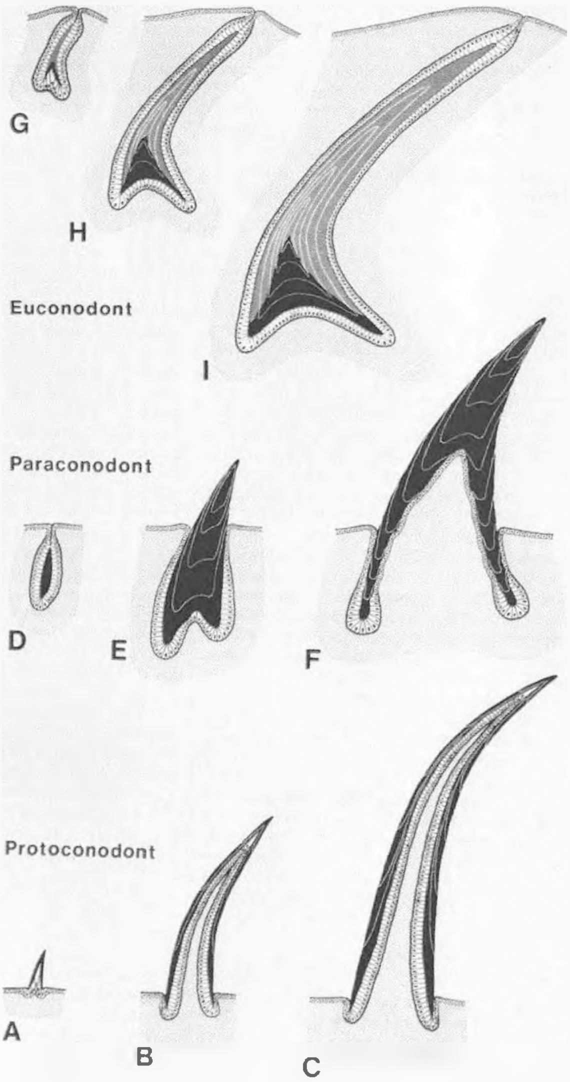
1.1 Background to the study

Sansom *et al.* (1992) recognised that euconodont hard tissues were closely comparable to those in the mineralised dermal skeleton of early vertebrates and, shortly afterwards, Aldridge *et al.* (1993) re-described the soft-anatomy of euconodonts according to a chordate bauplan. Studies following these investigations have elucidated the histology of a number of post-Cambrian euconodont elements and, in the most recent summary of euconodont biology, Donoghue *et al.* (2000) have included the euconodonts as agnathan members of the gnathostome stem-group. Most authors currently agree that euconodonts represent some of the earliest vertebrates with mineralised skeletons, and with soft-bodied vertebrates now recognised in the Lower Cambrian (Shu *et al.* 1999), the origin of the euconodonts has become a subject of increasing importance (Smith *et al.* in press).

Bengtson (1976) formulated an hypothesis concerning the origin of euconodonts, suggesting that euconodonts evolved from the protoconodonts via the paraconodonts during the Late Cambrian (Text-figure 1.1). Subsequent work by Szaniawski (1982, 1983, 1987) has shown the protoconodonts to be ancient members of the Recent phylum Chaetognatha and, since euconodonts are vertebrates and are unlikely to be closely related to chaetognaths (Nielsen 1995), Bengtson's hypothesis has been rendered untenable. However, although it is unlikely that protoconodonts and euconodonts are related, the paraconodonts have remained enigmatic and potentially hold key solutions to the problem of the origin of euconodonts.

Additionally, the interrelationships within the each group of Late Cambrian conodonts (proto-, para- and euconodonts) are poorly understood, and some current hypotheses (Miller 1980, 1984; Sweet 1988; Ji and Barnes 1990; 1994a; Donoghue *et al.* 2000) suggest that the euconodonts form a polyphyletic group, with two distinct groups of euconodonts appearing in the Late Cambrian. These were termed 'lineages' by Miller (1980) who named them after the first occurring genus in each group, giving the *Proconodontus* and *Teridontus* lineages, but these 'lineages' have been modified to 'complexes' by Ji and Barnes (1990, 1994a) since the evolution of these early euconodont groups cannot be considered to be 'linear'.

A paucity of soft-part, fused cluster and bedding plane assemblage data determines that potential relationships between proto-, para- and euconodonts must be investigated using discrete element collections. Methods that can be employed to infer relationships are twofold – comparisons between apparatus composition and architecture and comparisons between the histology of different elements. A systematic re-description of some Late Cambrian proto-, para- and euconodonts, including attempts at more comprehensive multi-element taxonomy, has been compiled to provide valuable insights into the relationships within and between the various euconodont and paraconodont groups. The histological investigation also contributes further evidence that enables Bengtson's hypothesis to be tested in order to resolve the systematic position of the paraconodonts, and also sheds light on the question of euconodont monophyly or polyphyly.



Text-figure 1.1. Bengston's growth hypothesis describing how protoconodonts could have evolved via paraconodonts to euconodonts during the Late Cambrian. (From Bengtson 1976).

1.2 Material

Samples from the Bighorn Mountains, Wyoming were collected by Dr M. P. Smith and Dr I. J. Sansom during a field season in 1996, and additional comparative material from the same area has been loaned by Dr J. E. Repetski (USGS, Washington D. C.). Most of the material from the Swedish Alum Shale used in this study was collected by Dr M. P. Smith and Dr I. J. Sansom during a field-trip to the area in 1993. Additional material was collected by Dr M. Y. Huselbee in 1994, and has been donated by Prof. E. N. K. Clarkson (Edinburgh). Comparative material was also kindly donated by Prof. R. E. Ethington (University of Columbia, Missouri) and Prof. J. F. Miller (Southwest Missouri State University) during a visit to the USA in the spring of 1998 following the Pander Society AGM in Columbus, Ohio. Inspection of Late Cambrian conodont collections at the United States Geological Survey (Reston) were also conducted with the help of Dr. J. E. Repetski and Dr. A. G. Harris. Prof. S. Conway Morris (Cambridge) allowed inspection of protoconodont material from China.

1.3 Techniques

1.3.1 Processing. Limestone samples from the Snowy Range Formation of the Bighorn Mountains, Wyoming and from the Alum Shale Formation of Västergötland and Öland, Sweden weighing approximately 3 kg were processed using acetic acid techniques. The samples were mechanically broken into fragments of less than 5 cm to increase the surface area to volume ratio and to therefore speed up the acid etching process, and were placed in buckets of 8 per cent acetic acid buffered with powdered calcium carbonate. Samples were then washed through a sieve stack (smallest mesh size 63 µm), with material coarser than 1 mm being replaced in a bucket of fresh acetic acid. The <1 mm residue was then dried in an oven before being separated using heavy liquids.

The Alum Shale proved particularly difficult to dissolve, being very rich in organic matter and usually containing some oil. In this case, the dissolved residue remained on the surface of the mechanically broken rock pieces and had to be scraped off by hand, piece by piece, since washing under a water stream with slightly increased pressure was not sufficient to dislodge the organic-rich residual material. Rubber gloves were used to prevent skin irritation and discolouration.

Sodium polytungstate with a specific gravity of 2.9 would have been the preferred heavy liquid for the separation of the dense conodont-containing fraction since it is non-toxic and its use is not restricted to fume cabinets, however, the viscosity of the sodium polytungstate caused the organic-rich Alum Shale residues to form large clumps at the top of the separating flasks, and no conodonts were recovered by this method. Bromoform with a specific gravity of 2.9 was therefore used to recover conodonts from both the Alum Shale and the Wyoming samples, since the conodont elements were able to settle out through this medium. Both acetone and industrial methylated spirits (IMS) were used to wash the bromoform out of the samples following separation, but IMS proved to be the more successful and least expensive method. The Alum Shale samples once again posed problems by discolouring the bromoform from an original pale pink colour to a dark brown-black liquid after only two or three separations. Used bromoform was collected and washed following each separation to remove the acetone or IMS and was re-used as many times as possible. The acetone and IMS could not be recovered.

The heavy fractions were then hand picked under a light microscope onto black or white backed slides and then sorted. Material with the best preservational quality was reserved for use in thin sectioning.

1.3.2 Thin sectioning techniques. Specimens were embedded in a transparent cold-curing polyester resin (Struerrs Resin) in a precise orientation so that a thin-section can be cut in a preferred direction. A circle of dark coloured ink was drawn around each specimen to make location of the element easier during the later stages of the process. Unwanted resin was removed from one side of the disc-shaped block using a circular saw, or a rotating diamond grinder until the specimen was very close to the surface. Coarse carborundum powder (800 μm) on a glass plate was then used to grind away the remaining resin, to expose the conodont at the surface. The side of the slide to which the block was to be adhered was also ground with 800 μm powder to improved the bonding strength. The surface of the resin was then polished on a rotating felt lap using 0.1 μm alumina powder until the desired level within the conodont element was reached. The element was then impregnated with a blob of 'Epotec' glue overnight, which was then removed using carborundum and alumina powders as before. The resin block was glued to the prepared slide using Epotec glue and left for 24 hours to bond. Following this, the remaining resin block was removed from the slide using a 'Petro-thin' thin-section machine to a level of about 100 μm. Sections made thinner than 100 μm using the mechanical grinder were often shattered or destroyed. Specimens were then impregnated once again with Epotec glue overnight and then ground and polished as before. For inspection under the SEM, sections were etched with 0.5% orthophosphoric acid for seven and a half minutes, but sections that were only intended for observation under the light microscope were left un-etched. Etched specimens can be re-polished if necessary.

1.3.3 Scanning electron microscopy. For morphological investigation under the SEM, specimens were fixed to stubs using PVA glue since double-sided sticky-tape proved to be too strong an adhesive and elements could not be turned or removed once stuck down, even if the stickiness had been reduced by touching the surface of the tape with a finger. The elements were then sputter coated with gold before observation under the SEM. Various scanning electron microscopes were used during the course of the study, but the majority of the photographs used in this study were taken on a JEOL JSM-5200 SEM housed in the Centre for Electron Microscopy at the School of Metallurgy and Materials at the University of Birmingham. Thin sections were stuck to larger SEM stubs using carbon pads or double-sided sticky-tape, of which the latter proved more successful since the slides were easier to remove from the stubs without the use of scalpel or razor blades.

1.3.4 Light microscopy. Thin sections were investigated in transmitted light using a Zeiss microscope with Nomarski Interference Contrast Optics. This improves and gives a three-dimensional aspect to the images produced. Specimens were also viewed in cross-polarised light, and were also photographed with a gypsum plate inserted to improve the contrast between histological features. Some elements were also viewed under immersion oil (clove oil), which has a refractive index close to that of apatite but no images used in this report were produced using this method.

1.3.5 Photography. Illustrations in this thesis have been produced digitally using a flat-bed scanner to acquire the diagrams and a slide scanner to acquire most of the photographic images. Adobe® Photoshop® version 5.5 has been used to manipulate these digital images.

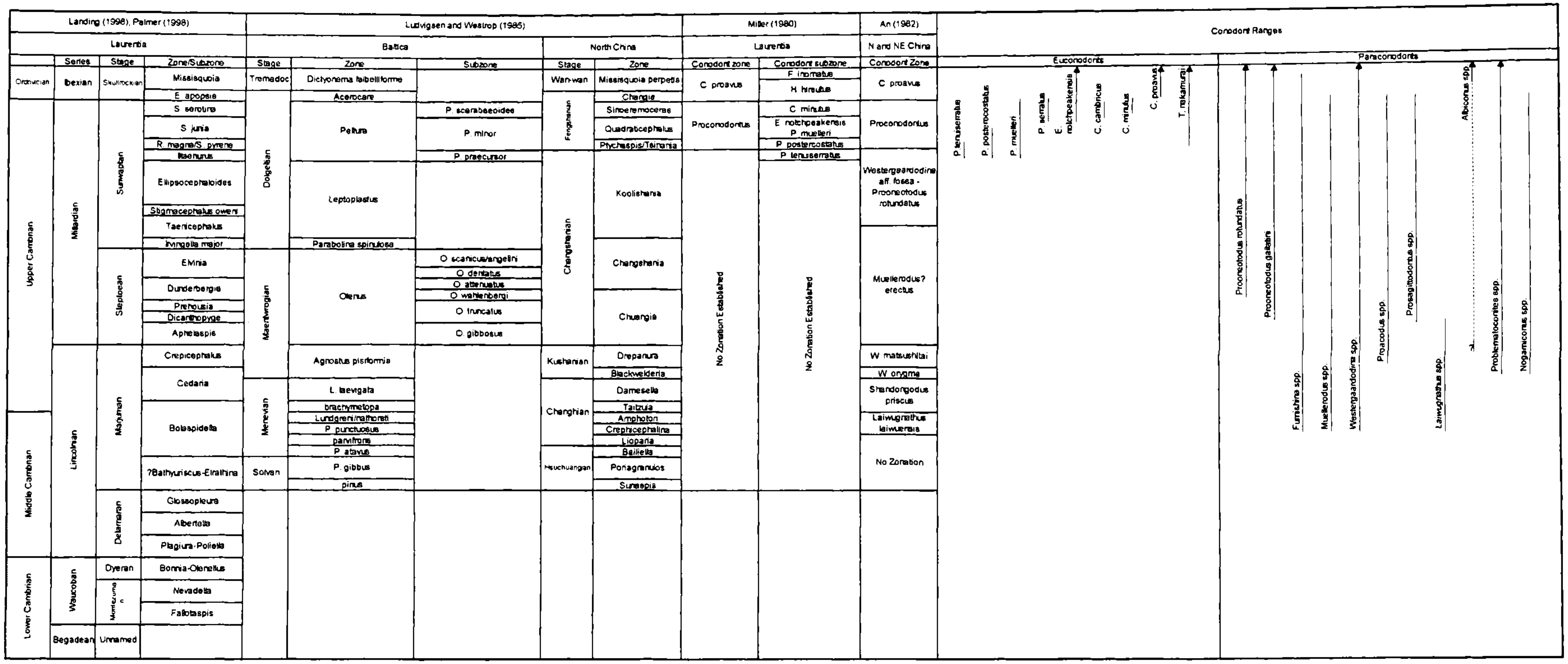
1.3.6 Systematic palaeontology. Synonymy lists have been annotated using the symbols outlined by Matthews (1973). Taxa left in open nomenclature have been named using the terminology described by Bengtson (1988).

CHAPTER 2

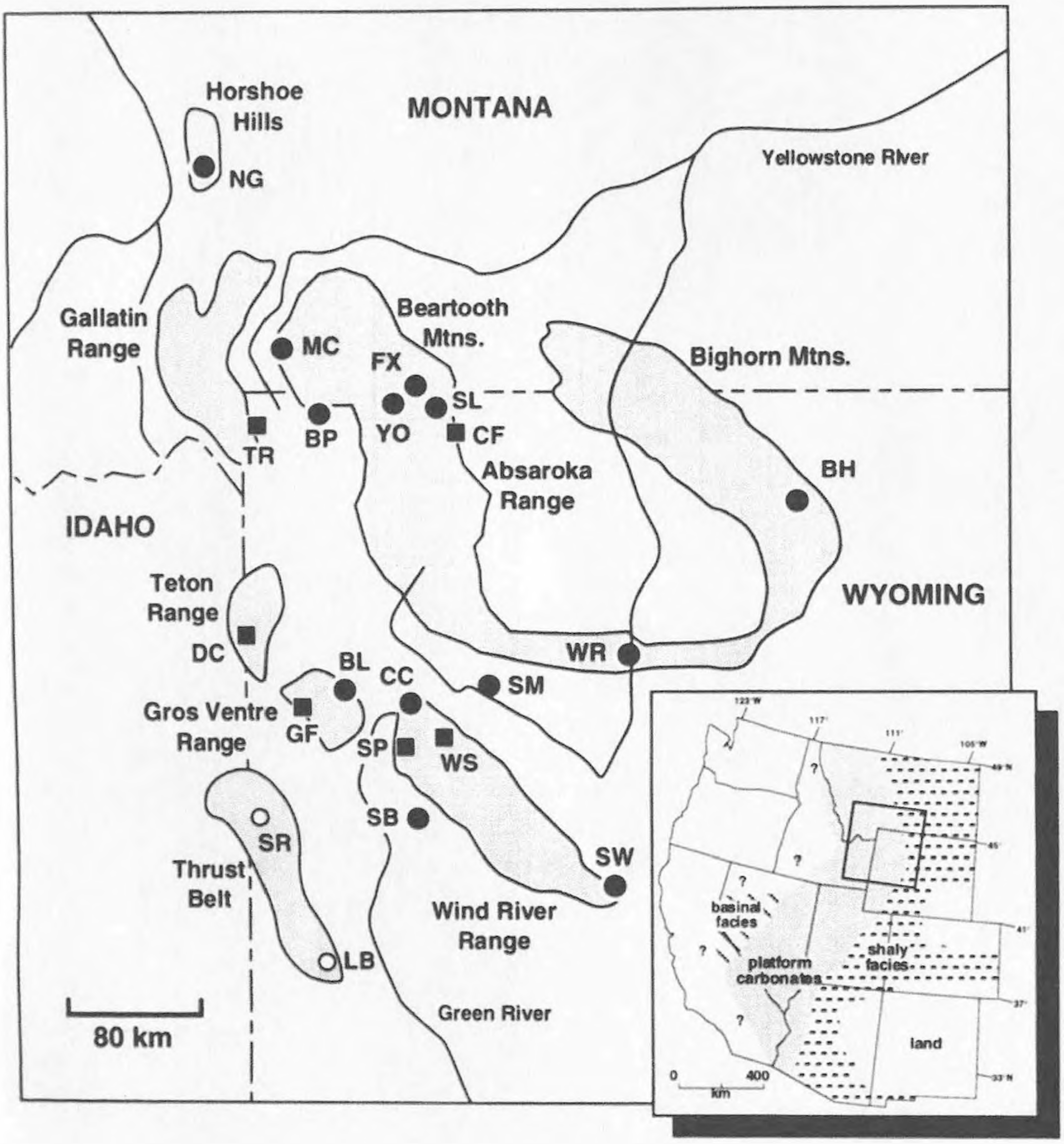
THE BIGHORN MOUNTAINS – PREVIOUS CONODONT STUDIES, DEPOSITIONAL SETTING AND REGIONAL STRATIGRAPHY

2.1 Previous Cambrian conodont studies in the Bighorn Mountains

Branson and Branson (1941) were the first authors to report the presence of euconodonts in successions from the Bighorn Mountains, Wyoming, although Cambrian conodont faunas from the area were not described until the work of Müller (1959). Müller's study comprised two distinct conodont assemblages, one containing only paraconodont elements and a second consisting entirely of Ordovician euconodonts. As euconodont faunas are only known from rocks of mid-Sunwaptan (Text-figure 2.1) and younger age, the paraconodont fauna reported by Müller (1959) is probably early Sunwaptan age or older. Koucky *et al.* (1961), Stone and Furnish (1959) and Goodwin (1961, 1964) reported similar faunas, with paraconodont assemblages from the upper Gros Ventre Formation, and Lower Ordovician euconodont faunas from the upper Gallatin Limestone. However, a fauna that included paraconodonts such as *Furnishina*, together with euconodont elements of 'transitional' morphology between typical Cambrian and Ordovician forms, including laterally compressed elements that approached '*Drepanodus*' in form, was described by Koucky *et al.* (1967). It is likely that the transitional elements mentioned by Koucky *et al.* represent forms from the *Proconodontus* lineage, rather than the Ordovician species that had been described previously. An unambiguous Sunwaptan mixed paraconodont-euconodont fauna from the Bighorn Mountains was identified and documented by Kurtz (1976, 1978), who demonstrated that this fauna was similar to others found in rocks of similar age from other parts of the American Midcontinent Province.



Text-figure 2.1. A summary table illustrating the stratigraphical nomenclature that is currently in use, and the ranges of selected Late Cambrian paraconodonts and euconodonts.



Text-figure 2.2. Map showing the location of the Bighorn Mountains in north-central Wyoming, BH = Bighorn Locality. (from Saltzman 1999).

Saltzman (1999), (Lochman-Balk 1971), Sansom and Smith (in prep.)	Darton (1906a,b)	Amsden and Miller (1942)	Hose (1955)	Stone and Furnish (1959)	Koucky et al. (1961)	Cygan and Koucky (1963)	Miller (1930)	Branson and Branson (1941)	Miller (1936)	Foster (1947)	Mapel (1959)	Miller (1936)	Miller (1936)	Miller (1936)	Wanless (1955)
Bighorn Mountains	Bighorn Mountains	Bighorn Mountains	Bighorn Mountains	Bighorn Mountains	Bighorn Mountains	Bighorn Mountains	Wind River Canyon, Wy.	Wind River Mountains, Wy	Warm Springs Creek, Wy	Gros Ventre Mountains, Wy	Johnson Creek, Wy	Dry Creek, Wy	Crow Creek Canyon, Wy.	Death Canyon, Wy	Teton, Hoback, Grps Ventre, Wy
Bighorn Dolomite	Bighorn Dolomite	Bighorn Dolomite	Bighorn Dolomite	Bighorn Dolomite	Bighorn Dolomite	Bighorn Dolomite	Bighorn Dolomite	Bighorn Dolomite	Bighorn Dolomite	Bighorn Dolomite	Bighorn Dolomite	Bighorn Dolomite	Bighorn Dolomite	Bighorn Dolomite	Bighorn Dolomite
Lander Sst		Sst and shales	Sandstone	Lander Sst	Lander Sst	Lander Sst		Lander Sst.			Basal sandstone				
Winnipeg Formation				Harding Sst	Harding Sst	Harding Sst.									
Snowy Range Formation	Deadwood Formation	Deadwood Formation	Gallatin and Gros Ventre Formations (undivided)	Gallatin Formation	Gallatin Formation	Gallatin Formation	Upper Limestone	Gallatin Formation	Upper Limestone	Boysen Limestone	Gallatin and Gros Ventre Formations (undivided)	Gallatin Formation	Upper Limestone	Upper Limestone	Boysen Limestone
							Middle Shale		Middle Shale				Middle Shale	Middle Shale	
							Du Noir Member		Du Noir Member				Du Noir Member	Du Noir Member	
Depass Formation					Gros Ventre Formation	Gros Ventre Formation	Depass Formation	Gros Ventre Formation	Upper Shale	Gros Ventre Formation		Depass Formation	Upper Shale	Upper Shale	Park Shale
									Death Canyon Member				Death Canyon Member	Death Canyon Member	Death Canyon Limestone
									Lower Shale				Lower Shale	Lower Shale	Wolsey Shale
Flathead Sandstone			Flathead Formation			Flathead Formation	Flathead Formation	Flathead Formation	Flathead Formation	Flathead Formation	Flathead Formation	Flathead Formation	Flathead Formation	Flathead Formation	Flathead Formation
Precambrian	Precambrian	Precambrian	Precambrian			Precambrian	Precambrian	Precambrian	Precambrian	Precambrian	Precambrian	Precambrian	Precambrian	Precambrian	Precambrian

Text-figure 2.3. Summary table illustrating the various terminology used during the last century to describe the Lower Palaeozoic stratigraphy of the Bighorn Mountains, Wyoming.

2.2 Geological Setting

The Bighorn Mountains are situated on the eastern flank of the Rocky Mountains, in north-central Wyoming (Text-figure 2.2), the Bighorn Uplift forming at the same time as the main Rocky Mountain chain, during the Laramide Orogeny (Cretaceous – Eocene). To the north and east of the Bighorn Uplift lies the Williston Basin, which gradually evolved through Phanerozoic time (Gerhard and Anderson 1988), and to the west lies the Bighorn Basin which formed contemporaneously with the Bighorn Uplift, although the Laramide tectonics in the basin overprint less dominant Mesozoic and Palaeozoic structures (Love 1988). Archaean granites form the core of the mountain range, with Palaeozoic and younger sediments occurring around the margins.

2.3 Stratigraphical Framework

Stratigraphical terminology used to describe the Cambrian units of northwestern Wyoming and southwestern Montana has been in a state of flux since the early work of Darton (1904, 1906). A summary of the names given by various authors to the parts of the succession in different areas is presented in Text-figure 2.3. Three main units have been consistently recognised, a basal sandstone overlying Precambrian granitic basement, an intermediate succession of green limestone-shales and sandstones and an upper member of slabby limestones and flat-pebble conglomerates. Sandstones overlying the Cambrian succession are of Ordovician age, with an unconformity separating the uppermost Cambrian unit from the lowermost Ordovician unit. Sansom and Smith (in prep.) reviewed the Ordovician stratigraphy of the area and highlighted the presence of a second unconformity between the top of the first Ordovician sandstone and the overlying basal sandy member of the massive dolomite unit.

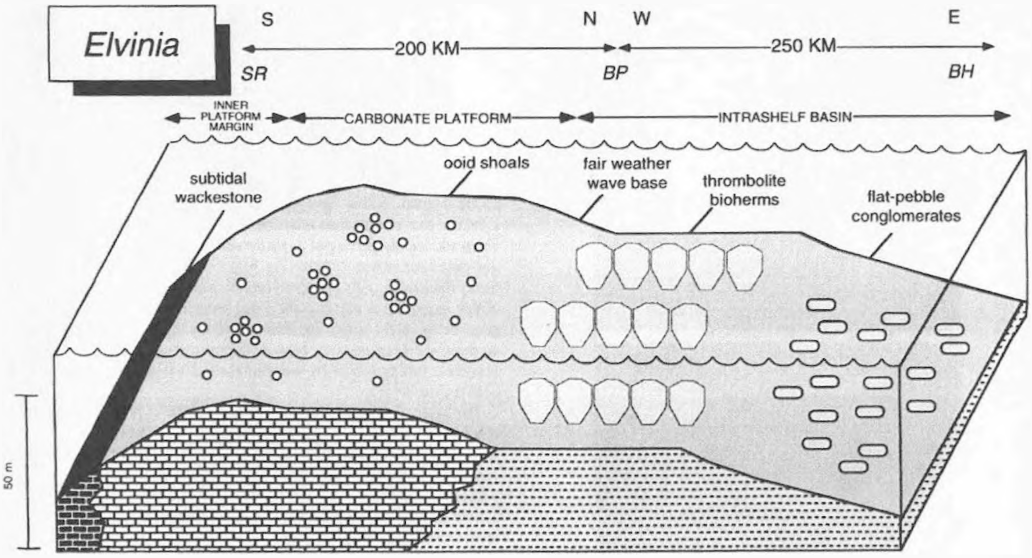
The most recent study of the Cambrian succession in northwestern Wyoming (Saltzman 1999) adopts the stratigraphical nomenclature outlined by Lochman-Balk (1971). In the Bighorn Mountains, the basal transgressive Flathead Sandstone lies directly on granitic basement and is conformably overlain by the shaley limestones of the Depass Formation. At the top of the Cambrian succession is the Snowy Range Formation, comprising flat-pebble conglomerates and glauconitic limestones. The basal Ordovician sandstone is the South Piney Member of the Winnipeg Formation, which is unconformably overlain by the Lander Sandstone Member of the Bighorn Dolomite. However, the Cambrian facies in the Bighorn Mountains differs somewhat to that found to the west of the region and there is still a degree of uncertainty concerning the naming of successions in this area (Saltzman, pers. comm.). Traditionally the terms Gros Ventre Formation and Gallatin Formation have been used to describe the upper two Cambrian units in the Bighorn Mountains, but it is evident from the work of Saltzman (1999) that this needs to be reviewed. Terms used to describe the two dominant Upper Cambrian facies (Open Door Formation = outer-shelf facies, and the Snowy Range Formation = intrashelf basin facies) are applied to the sequence found in the Bighorn Mountains, to replace the various poorly workable schemes of stratigraphical nomenclature that are currently in use.

2.4 Depositional environment

During the Cambrian, North America formed part of the Laurentian supercontinent, with Wyoming occupying a position on the western continental shelf of the landmass in an approximately equatorial location (Scotese *et al.* 1979; Scotese and McKerrow 1990; Ziegler *et al.* 1979). Lochman-Balk (1971) and Lochman (1972) reviewed the changing palaeogeography and palaeoenvironments of North America during Upper Cambrian time, showing the gradual transgression of different lithofacies onto the Laurentian continent. Changes in relative sea-level during this time (Palmer 1981; Montañez *et al.* 1986; Saltzman *et al.* 1995, 1998; Perfetta *et al.* 1999) were relatively minor because northwestern Wyoming formed part of a very stable continental shelf area controlled by E-W trending structural blocks of Archaean terrane (Tonnsen 1986, p. 27, figs 4, 5, 6), and constituted the major sedimentary depocentre between the less stable blocks of Montana to the north and Colorado to the south.

The phosphatic microfaunas of the Bighorn Mountains of Wyoming detailed in this study were obtained from flat-pebble conglomerate units from the upper part of the Snowy Range Formation (Plate 19. Figure B). Limestone pebbles within the units are coarse-grained, laminated, and tabular but rounded in shape; they are generally smaller than 6 cm in diameter and 1 cm deep, supported in a silty matrix. Lochman (1957) would have placed these in her 'Type 2' category of flat-pebble conglomerates, deposited at a variable distance from the shoreline, in a water depth of less than 30 m. A study of Cambrian flat-pebble conglomerates from Montana, Wyoming and South Dakota, conducted by Sepkoski (1982), concluded that the most likely depositional environment of these units was a lagoonal setting, where partially lithified, laminated limestones were broken up and redeposited during storm events. Sepkoski dismissed an intertidal setting for the deposition of these units because of a lack of other features typical of this type of environment such as stromatolites, flaser bedding and channel structures (Sepkoski 1982, p. 379), together with an absence of characters indicative of subaerial weathering. Attention was drawn to this last point by Sepkoski, as it implies that the formation of the limestone clasts was not due to subaerial desiccation, but to the break up of limestone beds that had undergone early cementation under submarine conditions. Hardground lithologies have been recognised in flat-pebble conglomerates from the Upper Cambrian Snowy Range

Formation of Montana and Wyoming by Brett *et al.* (1983), with evidence for early lithification including the truncation of intraclasts, pitting and etching of upper surfaces of clasts, and the presence of encrusting fossils, including pelmatozoan echinoderm holdfasts and spongiomorph algae, on clast surfaces (Brett *et al.* 1983, p. 283). Mount and Kidder (1993) recognised hardground formation in the intraclast conglomerates of the Lower Cambrian Sellick Hill Formation of South Australia, and stated that the units were likely to have been deposited on a broad carbonate ramp, where low sedimentation rates prevailed, with high phosphate accumulation rates and generally low energy conditions. It is implied by Mount and Kidder that the flat-pebble conglomerates formed from a combined flow origin, as a result of intense storm activity, with currents largely moving the pebbles by traction. A storm-generated origin was also suggested for the flat-pebble conglomerates of the Upper Cambrian Nolichucky Formation of southwest Virginia by Markello and Read (1981). Osleger and Read (1991, 1993) stated that flat-pebble conglomerates were deposited in a shaley deep ramp/intrashelf basin setting, under water depths of between 10 and 40 m, in agreement with Lochman (1957). In the most recent study of some Upper Cambrian successions from northwestern Wyoming, Saltzman (1999) included flat-pebble conglomerates in the 'Intrashelf-Basin Facies Association' of the Snowy Range Formation, in accordance with the views of earlier authors.



Text-figure 2.4. Palaeoenvironments of northwest Wyoming during the Late Cambrian *Elvinia* Zone. SR = Snake River Range, BP = Buffalo Plateau, BH = Bighorn Mountains (from Saltzman 1999).

The conodont faunas found in the flat-pebble conglomerates of the Snowy Range Formation in the Bighorn Mountains were therefore likely to have inhabited a generally low energy shelf environment, with water depths of less than 40 m and a relatively low background sedimentation rate (Text-figure 2.4). Early lithification of the sea-floor sediments was common, and the environment was often interrupted by intense storm activity, that lead to the formation of the flat-pebble conglomerate units.

CHAPTER 3

SWEDISH ALUM SHALE – PREVIOUS CONODONT STUDIES, DEPOSITIONAL SETTING AND REGIONAL STRATIGRAPHY

3.1 Previous Cambrian conodont studies in Sweden

Conodonts from the Cambrian of Sweden were first mentioned by Wiman (1893), but it was not until the 1950s that the faunas became the focus of major investigations. Westergård (1953) illustrated and described elements as 'Problematicum I', which were later included in the paraconodont genus *Westergaardodina* by Müller (1959). Müller (1956, 1959) was the first author to fully document Upper Cambrian conodont faunas from Sweden and has continued to play a major role in the description of the Alum Shale microfaunas including conodonts (Müller 1962, 1971; Müller and Nogami 1971, 1972a, b; Müller and Andres 1976; Müller and Hinz 1991, 1998), together with other exceptionally preserved phosphatic organisms possessing intact soft-parts (Müller 1964, 1979, 1981, 1983; Müller and Walossek 1985). Several authors have used the exceptionally well-preserved Alum Shale faunas to demonstrate the histological development of conodont elements (Müller and Nogami 1971, 1972a, b; Andres 1981, 1988; Szaniawski and Bengtson 1993, 1998; Müller and Hinz-Schallreuter 1998), including the important work of Bengtson (1976, 1983) who used these faunas to subdivide the conodonts into proto-, para- and euconodont categories based on differences in their mode of growth.

Much of the Alum Shale has not yet been biostratigraphically zoned using conodonts due to the condensed nature of the sequence and the typically long-ranging occurrence of many of the conodont species found there. Szaniawski and Bengtson (1998) have attempted to establish a conodont zonation scheme for the Swedish Cambrian and have correlated this with the North American (Laurentian) scheme based on euconodonts, developed over some years by Miller (1969, 1980, 1984, 1988). However, the new scheme of Szaniawski and Bengtson (1998) adds only one conodont subzone to the known stratigraphy, defined by, and named after, their newly erected euconodont species, *Proconodontus transitans*. This species is not recognised in the samples from Sweden and USA used during the course of this study, and in general euconodont elements are rare or absent in the majority of the Swedish samples. Trilobites remain the group most suited to establishing a biostratigraphical zonation, and the schemes proposed by Westergård (1947) and Henningsmoen (1957) are referred to (Text-figure 3.1). The Upper Cambrian conodont faunas used in the current study are dominated by proto- and paraconodonts, with only very rare occurrences of euconodont species. This faunal composition is typical of other studies in the area.

Stage/Age		Zone Number	Zones	Subzones	Stratigraphy
Tremadoc		8 Ceratopyge Beds	*Apatokephalus serratus/ T. phyllograptoides*		Alum Shale
			Shumardia pusilla/ Clonograptus heres		
		7	*Dictyonema flabelliforme*	*D. flab. anglicum / Anisograptus*	
				D. flab. norvegicum / Bryogr. kjerfulfi	
				C. tenellus / Adelogr. hunnebergensis	
				D. flab. flabelliforme	
				D. flab. sociale	
				D. flab. desmograptoides	
Upper Cambrian		6	*Acerocare*	*d. Aercare ecorne*	
				c. Westergaardia spp.	
				b. Acreocarina	
				a. Parabolina heres group	
		5c	*Peltura scarabaeoides*	*f. Parabolina megalops*	
				e. Parabolina lobata	
				d. Peltura scarabaeoides	
		5b	*Peltura minor*	*c. Peltura minor and P. aeutidents*	
				c. C. angusta and C. flagellifera	
		5a	*Protopeltura praecursor*	*a. L. neglectus*	
		4	*Leptoplastus*	*e. L. stenotus*	
				d. L. angustatus	
				c. L. ovatus and Eurycare latum	
				b. L. raphidophorus	
				a. L. paucisegmentatus	
		3	*Parabolina spinulosa*	*b. Parabolina spinulosa*	Great Stinkstone
				a. P. aciculata / Par. brevispina	
		2	*Olenus and Agnostus obesus*	*f. Olenus scanicus*	
				e. Olenus dentatus	
				d. Olenus attenuatus	
				c. Olenus wahlenbergi	
				b. Olenus truncatus	
				a. Olenus gibbosus	
		1	*Agnostus pisiformis*	*Agnostus pisiformis*	
Middle Cambrian	*Paradoxides forschammeri*	C3	*Lejopyge laevigata*		Alum Shale
		C2	*Solenopleura brachymetopa*		Exporrecta Limestone
		C1	*P. lundgreni / P. nathorsti*		Alum Shale
	Paradoxides paradoxissimus	B4	*Ptychagn. punctuosus*		
		B3	*Hypagnostus parvifrons*		
		B2	*T. fissus / Ptychagn. atavus*		
		B1	*Ptychagnostus gibbus*		Exultans Limestone
	Eccaparadoxides oelandius	A2	*E. oelandicus f. pinus*		Alum Shale
		A1	*Eccaparadoxides insularis*		

Text-figure 3.1. Biostratigraphy of the Swedish Alum Shale (After Bergström and Gee 1985, based on Westergård 1922, 1957).

3.2 *Geological setting*

Cambrian sediments are found in various areas throughout Sweden and Scandinavia, but can be divided into three main categories, autochthonous sediments (occurring in Västergötland, Ostergötland, Öland, Scania, Närke, Bornholm and in the sub-surface trending from Kalmar-

Öland to Estonia and in the Gulf of Bothnia), allochthonous sediments (occurring in the Caledonian Mountains from the Digermul Peninsular in Finnmark in the north to Fen and Oslo in the south) and parautochthonous occurrences in lower tectonic levels to the west of the main thrust front, for which the amount of displacement is uncertain (Text-figure 3.2). In the allochthon, the Middle and Upper Cambrian Alum Shales are strongly compressed and folded (Thorslund *in* Thorslund and Jaanusson 1960) and often form the detachment plane of many of the NW dipping thrusts in the area, formed during the closure of the Iapetus Ocean, causing tectonic thinning and repetition of the sequence (Andersson *et al.* 1985). Often the sediments have been metamorphosed, with Ordovician conodonts in Jämtland having CAI values of between 3 and 5, which show heating in the temperature range of 110-300°C (S. M. Bergström 1980). Further east, CAI values are much lower (CAI<2 = 90°C), but elevated in the vicinity of the Permo-Carboniferous dolerite sills that have intruded into the Lower Palaeozoic succession.

Text-figure 3.2. Map showing the location and outcrops of the Alum Shale Formation in southeast Baltoscandia (from Andersson *et al.* 1985).

Material used in the present study (collected by I. J. Sansom and M. P. Smith during the summer of 1993, in addition to material donated by E. N. K. Clarkson) is from two areas of the autochthon, Västergötland and the Isle of Öland. In Västergötland, Cambrian sediments are preserved in a series of outliers which form several hills in the district. Six main outliers are recognised (Billingen, Falbygden, Lugnåsberget, Kinnekulle, Hunneberg and Halleberg) in which Cambrian sediments overlie Precambrian basement (Text-figure 3.2). Each hill, apart from Lugnåsberget is capped by a Permo-Carboniferous dolerite sill (Thorslund *in* Thorslund and Jaanusson 1960; Martinsson 1974; Bergström and Gee 1985). On Öland, Cambrian sediments are preserved along the westernmost part of the island, thinning markedly and disappearing towards the north (Westergård 1922). Throughout the area, Lower Cambrian sandstones and siltstones lie unconformably on Precambrian granite-gneiss basement, or are occasionally underlain by ?Vendian tillites (Andersson *et al.* 1985). In turn, the Lower Cambrian succession is overlain by the Middle and Upper Cambrian Alum Shale Formation and a Lower Ordovician series of limestones with variable content of sand, glauconite and phosphate.

3.3 Regional stratigraphy

The basement rock in Scandinavia is granitic-gneiss of Svecokarelian (1800 Ma) to Dalslandian (1000 Ma) age (Andersson *et al.* 1985). A major unconformity separates the basement from the overlying sediments, which in the west are ?Vendian tillites and Late Palaeozoic glacial deposits, and in the east are Lower Cambrian sandstones (Andersson *et al.* 1985). In Västergötland, the Lower Cambrian File Haidar Formation is approximately 30 m in thickness and is composed of two sandstone horizons, the lowermost clayey, thin-bedded Mickwitzia Sandstone Member which is conformably overlain by the massively-bedded, almost pure quartz Lingulid Sandstone Member (Thorslund *in* Thorslund and Jaanusson 1960; Bergström and Gee 1985). At the top of the Lingulid Sandstone is a conglomerate and a phosphatic sandstone, occasionally overlain by green silts and shales, showing a transition into Middle Cambrian Alum Shale deposition (Thickpenny 1984). Lower Cambrian sandstones in Öland are lithologically similar to those in Västergötland, but are thought to be stratigraphically older and are equivalent in age to the Kalmarsund Sandstone (*Platysolenites* Zone of Martinsson 1974).

Middle and Upper Cambrian successions are almost entirely developed as Alum Shales. Contained within the Alum Shales are a series of beds, lenses and nodules of bituminous limestones, locally termed 'orsten', and often called 'stinkstones' due to the strong smell of petroleum released when they are split open. On average, the Alum Shales form a condensed sequence, only 22-23 m thick in Västergötland, thinning eastwards to the Baltic, thickening to 100 m in the southernmost region near Oslo and Scania (Thorslund *in* Thorslund and Jaanusson 1960; Thickpenny 1984).

Three limestone layers within the Alum Shale are sufficiently laterally extensive to be of stratigraphical use. The lowest of these limestones is the Exulsans Limestone Member (locally developed as the Acrothele granulata Conglomerate) which occurs in the *Ptychagnostus gibbus* Zone (Bergström and Gee 1985). Above this lies the Exporrecta Limestone (also known as the Andrarum Limestone (Martinsson 1974)), which lies in the *Forchammeri* Stage of Thorslund (*in* Thorslund and Jaanusson 1960) and in the *Solenopleura brachymetopa* Zone C_5 according to Martinsson (1974), Bergström and Gee (1985) and Berg-Madsen and Malinky (1999). The uppermost bituminous limestone horizon is the 'Great Stinkstone' which extends in some areas from the *Agnostus pisiformis* Zone at the base to the *Parabolina spinulosa* Zone at the top. Mostly the unit is found within the *Olenus* Zone (Bergström and Gee 1985).

The Alum Shale thins dramatically northwards on the Isle of Öland, from 24 m at the southern margin of the island where shale sequences are more common, to less than 2 m in the north, where limestone is the dominant lithology (Andersson *et al.* 1985). Black shale lithologies are developed higher through the stratigraphical succession in Öland than elsewhere in Sweden, extending as far as the Tremadoc *Ceratopyge* Zone (Andersson *et al.* 1985). In Västergötland the Lower and Middle Ordovician is limestone-rich, with the sequence becoming dominated by muds and shales in the upper part (Thorslund *in* Thorslund and Jaanusson 1960). At Kinnekulle, the Ordovician sequence is 115 m thick, overlain by 55 m of Silurian (Llandovery) strata comprising dark muds and shales with occasional limestone beds and lenses (Thorslund *in* Thorslund and Jaanusson 1960). Throughout the Alum Shale, fossils occur mainly in the limestone horizons, occasionally in rock-forming numbers, with the shale layers being largely unfossiliferous.

3.4 Depositional environment

During the Late Cambrian and Early Ordovician, Sweden was part of the Baltic continent, occupying mid-latitudes south of the equator (30-60°S) and was inverted relative to present-day geography (Torsvik *et al.* 1991). Iapetus separated Baltica and Avalonia from Laurentia, as demonstrated by the different Lower Palaeozoic faunas found in those provinces (Cocks and Fortey 1982; Scotese and McKerrow 1990). In contrast to the warm, relatively high energy conditions inhabited by the Late Cambrian conodonts from the margins of Laurentia, conodonts recovered from Sweden occupied deeper water, with lower temperatures (cold faunal realm of Miller (1984)) where current activity and ventilation were very much reduced.

3.4.1 Lower Cambrian transgression. Lower Cambrian sandstones in Västergötland are arkosic and contain dreikanters, implying that the sediment from which they are formed was of terrestrial origin. Trilobite trackways found in the same horizons are, however, indicative of deposition in a marine environment (Thorslund *in* Thorslund *et al.* 1960). Mudcracks and ripples in the Mickwitzia Sandstone constrain the depositional environment to one of very shallow water, but fucoids in the overlying Lingulid Sandstone replace the typical *Mickwitzia* ichnofauna and suggest that deposition occurred in a deeper environment further from the shore (Martinsson 1974). J. Bergström (1980) noted that the sub-Cambrian planation surface was a relatively flat, uniform platform and that minor changes in sea-level could produce major changes in the position of the shoreline. Basal sandstones in Öland may be older than those in Västergötland, but the presence of a bioturbated 'kråksten' horizon implies that they were deposited in a similar environment to the Mickwitzia and Lingulid sandstones (Martinsson 1974).

3.4.2 Middle and Upper Cambrian Alum Shale Formation. The transition from the Lower Cambrian to the Middle Cambrian was accompanied by a lateral facies change from shallow, intertidal conditions (sands and shales) to stagnant, basinal environments (Alum Shales) (Andersson *et al.* 1985). In general, authors agree that the entire Middle Cambrian to Lower Ordovician Alum Shale sequence was deposited on a stable platform, in relatively shallow water depths, although there has been discussion concerning the formation of the bituminous limestone horizons (Martinsson 1974; Hallam 1981; Thickpenny 1984; Andersson *et al.* 1985; Bergström and Gee 1985; Nicoll *et al.* 1992; Clarkson and Taylor 1995; Clarkson *et al.* 1998), the high concentrations of organic matter, radioactive elements and heavy metals in the sequence, and the presence or absence of adequate oxygen levels in the sediment and overlying water column.

3.4.3 Limestone development. Two hypothesis exist concerning the broader environmental conditions associated with limestone emplacement. Firstly, Hallam (1981) described the stagnant conditions that could occur on a relatively flat, stable shelf, with large-scale topographical undulations of the seafloor over distances of tens of kilometres, amplitudes of only tens of metres and in water depths of less than 200 m. Thickpenny (1984) and Andersson *et al.* (1985) noted that limestone formation may have been associated with times when seafloor highs emerged above an hypothetical fluctuating anoxic layer, giving periods of oxygenated, habitable conditions followed by sudden and perhaps prolonged periods of anoxia. Clarkson and Taylor (1995) and Clarkson *et al.* (1998) have commented on the relative oxygenation of the Alum Shale seafloor, using the presence of the benthic trilobite *Olenus* as evidence of times when O_2 levels were elevated, with the presence of the bradoriid *Cyclotron* being indicative of times of severe O_2 depletion.

Nicoll *et al.* (1992) expressed the second hypothesis concerning the environmental conditions of bituminous limestone formation, stating that each limestone horizon was associated with a eustatic regressive event which, in some cases, could be correlated with Late Cambrian successions in Australia and the United States. Nicoll *et al.* (1992) suggested that trilobite remains provided a seed for carbonate precipitation, and that layers with abundant trilobite exoskeletons were deposited during more clement intervals associated with shallower sea-levels, i.e. nodular levels are products of low-stands. However, some limestone horizons do not contain fossils, and the ecology of some trilobites is insufficiently known to provide accurate water-depths, so sea-levels could only be estimated as a function of the spatial distribution of the Alum Shale Formation during any given time period. Bergström and Gee (1985) and Martinsson (1974) have also related limestone formation to regressive events.

3.4.4 Shale deposition. The shale lithologies often have elevated total organic carbon (TOC) contents, with TOC values occasionally reaching 25% (Bergström and Gee 1985). High TOC levels are often associated with O_2 depleted conditions, where the organic content of the sediment cannot be oxidised or destroyed. Clarkson and Taylor (1995) suggested that bacterial mats occupied the seafloor and were responsible for the concentration of heavy metals, uranium and vanadium that are common in the Alum Shale, comparing the formation of the organic-rich shales to the conditions on the seafloor beneath the present-day upwelling zones of NW Africa and South America. However, sedimentation rates below upwelling systems are often high, suggesting that this may not be a perfect example of a modern analogy for Alum Shale deposition. Thickpenny (1984) also predicted that conditions at the seafloor were predominantly anoxic, and that sedimentation rates of 3-8 mm/1000 years are similar to that of modern-day pelagic oozes. Quaternary sapropels in the Mediterranean are known to have high TOC values and to be sites of concentration of uranium (Mangini and Dominik 1979) and may represent a better modern-day analogue for Alum Shale deposition (Andersson *et al.* 1985). Laminations within the shales are preserved, which supports the idea of the stagnant seafloor being inhospitable to burrowing organisms. No evidence of current activity in the form of scours or ripple marks is known from the shale horizons and therefore ventilation of the seafloor is thought to have been restricted to times of limestone formation.

During the Upper Cambrian the shale lithology becomes increasingly dominant, suggesting that the platform became more stable, however an influx of siltstones and sandstones during the Tremadoc indicates that the platform returned to unstable conditions in the Early Ordovician.

CHAPTER 4

PROTOCONODONT SYSTEMATIC PALAEONTOLOGY

4.1 *Introduction*

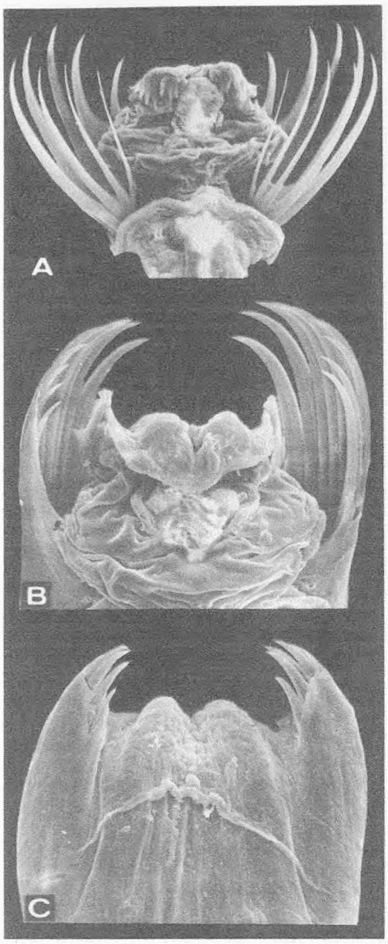
Bengtson (1976) introduced the informal term 'protoconodont' for the group of conodont elements which possessed deep basal cavities and in which the growth lamellae were only added on the inner surface, usually towards the basal margin. Included in this category by Bengtson (1976) were only three species, *Hertzina*? *bisulcata* (= *Gapparodus bisulcatus*), *Amphigeisina danica* and *Proconodontus* sp., a form that must belong in a different genus since *Proconodontus* is a euconodont. The number of true protoconodont species remains uncertain, because not all of the forms reported as protoconodonts have been histologically investigated.

In the Treatise volume, Clark (1981) did not distinguish between protoconodonts and paraconodonts, including elements with both types of internal structure within the Paraconodontida Müller, 1962. This tradition was also followed by Müller and Hinz (1991) who grouped protoconodonts and paraconodonts together on the grounds that both types of elements grow by accretion of material at the base. Szaniawski (1982, 1983, 1987) however, demonstrated that protoconodonts have a three-layered internal structure and, after also considering the apparatus composition and architecture of *Prooneotodus*? *tenuis* (= *Phakelodus tenuis*), concluded that protoconodonts were closely related to the Recent chaetognaths (see Chapters 7 and 8 for a review). Since euconodonts, and at least some of the paraconodonts (Chapter 9), are now considered to be of vertebrate affinity (*inter alia* Sansom *et al.* 1992; Aldridge *et al.* 1993; Donoghue *et al.* 2000), protoconodonts must be excluded from the Paraconodontida and tentatively included as Precambrian – Middle Ordovician members of the phylum Chaetognatha.

4.2 *Protoconodont clusters*

Fused clusters and bedding plane assemblages of protoconodont elements are relatively common occurrences in comparison to fused clusters of para- or euconodonts. The most numerous clusters are of elements of the genus *Phakelodus* Miller, 1984, and these have proved useful in determining that protoconodont apparatuses are unimembrate, and have also demonstrated that *P. tenuis* and *P. elongatus* (two elements that could easily have been grouped into a bimembrate apparatus) are clearly distinct species. Studies that have described fused clusters of bedding plane assemblages of protoconodonts include Miller and Rushton (1973), Müller and Andres (1976), Landing (1977, 1983), Landing *et al.* (1980), Andres (1981, 1988), Fortey *et al.* (1982), Bergström and Orchard (1985), Buggisch and Repetski (1987), Heredia and Bordonaro (1988), Müller and Hinz (1991), Hinz (1992), Dong (1993) and, most recently, a Lower Cambrian bedding plane assemblage reported by McIlroy and Szaniawski (2000). In addition, Aldridge (pers. comm. 2000) has reported finding protoconodont bedding plane assemblages associated with possible soft part remains. These specimens await formal description, and will probably prove to be particularly pertinent to the hypothesis that protoconodonts are of chaetognath affinity.

The architecture of protoconodont apparatuses has been reconstructed using the grasping spines of Recent chaetognaths as a template (Müller and Andres 1976; Szaniawski 1982, 1983, 1987). Very often elements are found in close association in contact along their lateral margins, usually in an arc or crescent-shaped arrangement with the largest elements in the centre of the apparatus. On the basis of such evidence, Landing (1977) formulated the 'super-tooth model', in which the elements functioned together as a single grasping or biting element, however, other authors (Müller and Andres 1976; Andres 1981; Szaniawski 1982) noted that the elements were more likely to function individually as component parts of a grasping apparatus. The grasping spines of the Recent chaetognaths are withdrawn into the hood-part of their head region during times of non-function, extending into a fan-like grasping array when in use (Text-figure 4.1). Clusters of protoconodonts, such as the one illustrated in Plate 7, Fig. 7, are assumed to be preserved remains of elements in their non-functional positions, because during times of use the elements are not in such close contact along their lateral margins, and are far more likely, therefore, to become dissociated by post-mortem processes.



Text-figure 4.1. SEM photograph of a chaetognath with grasping spines (A) fully extended from the head in a fan-like arrangement during function, (B) elements partially retracted into the hood and (C) fully retracted into the hood in a non-functional position. (from Szaniawski 1982).

4.3 PROTOCONODONT SYSTEMATIC PALAEONTOLOGY

?Phylum CHAETOGNATHA Slabber 1778

Genus GAPPARODUS Abaimova, 1978

1978 *Gapparodus*, Abaimova, p. 496.
1991 *Gumella*, Müller and Hinz, p. 26.

Type species. *Hertzina*? *bisulcata* Müller, 1959, p. 456, Upper Cambrian Zone 1, Gudhem am Mösseberg, Västergötland, Sweden.

Diagnosis. Long, proclined protoconodont elements possessing a furrow or indentation on both lateral margins. Elements may be narrowly tapering from tip to base, or may be widely flaring in the basal region.

Description. Long, slender, coniform protoconodont elements possessing a longitudinal furrow on each lateral face. Anterior margin broadly curved from base to tip, rounded, with or without slightly elevated, transverse ribs, spaced evenly along the margin. Ribs, if present, extend from tip to base of the element, but do not meet the furrows on the lateral faces, being restricted to the areas immediately surrounding the anterior margin. Posterior margin broadly curved, rounded, unornamented or bearing a shallow longitudinal groove along the entire length of the central part of the margin. Posterior margin may be markedly shorter than the anterior margin in some forms. Lateral faces bear a furrow of variable depth and width, which reaches almost to the tip of the element, and becomes more prominent towards the base. Furrow usually situated towards the posterior of the element. Basal cavity very deep, extending almost to the tip of the element. Some forms possess a secondary tip of the basal cavity situated in early growth stages towards the tip of the element. Transverse cross-section at the tip is circular, becoming more differentiated by the lateral and posterior furrows towards the base. Elements usually symmetrical or slightly subsymmetrical due to very slight lateral deflection of the tip of the element towards the inner face. Right and left forms present and distinguished by lateral deflection of the tip or by the differential development of the lateral faces of the elements, one being larger than the other.

Remarks. *Gapparodus bisulcatus*, the type species of the genus, was originally assigned tentatively to the genus *Hertzina* by Müller (1959). However, the diagnosis for *Hertzina* (Müller 1959, p. 454) states that two carinae must be present towards the posterior margin of the element, a feature that is not present in *G. bisulcatus*. In addition, elements belonging to *Hertzina* do not possess lateral furrows, and tend to have a more flattened posterior margin in comparison to elements assigned to *Gapparodus*. Abaimova (1978) erected the genus *Gapparodus*, and included five species in the new genus. These have since been synonymised by Müller and Hinz (1991) under the species *G. bisulcatus*, as they are thought to represent intraspecific morphological variations.

Gumella, the monospecific genus erected by Müller and Hinz, 1991, which also possesses longitudinal lateral furrows, but has a more widely flaring basal region, is here included for the first time in *Gapparodus* even though in some elements, as noted by Müller and Hinz (1991), there is a secondary basal opening (basal canal) in posterior parts of early growth stages in elements of *G. cuneatus*, towards the tip. This feature has not been observed in the other species assigned to *Gapparodus* (*G. bisulcatus*). *Gapparodus bisulcatus* and *G. cuneatus* were not found together in samples from Sweden, and for this reason they are unlikely to belong together in one apparatus as morphotypes of a single species.

Gapparodus bisulcatus (Müller, 1959)

Plate 7, figure 12.

*p	1959	*Hertzina*? *bisulcata* Müller, p. 456, pl. 13, figs 22-23, 27 (*non* pl. 13, fig. 24 [= *H. elongata*]).
	1966	*Hertzina*? *bisulcata* Müller; Poulsen, p. 8, pl. 1, fig. 9; text-fig. 3.
	1969	*Hertzina bisulcata* Müller; Clark and Miller, p. 125, text-fig. 1, figs 2-4.
	1969	*Hertzina bisulcata* Müller; Clark and Robison, p. 1045, text-fig. 1d.
	1971	*Hertzina bisulcata* Müller; Müller, p. 8, pl. 1, fig. 7.
	1974	*Hertzina bisulcata* Müller; Landing, p. 1246, text-fig. 1c.
	1974	*Hertzina bisulcata* var. 1 Müller; Landing, p. 1246, text-fig. 1d, e.
	1974	*Hertzina bisulcata* var. 2 Müller; Landing, p. 1246, text-fig. 1f.
	1974	*Hertzina bokonoi* Landing, p. 1246, text-fig. 1h, i.
?	1975	*Hertzina*? *bisulcata* Müller; Lee, p. 80, pl. 1, fig. 3; text-fig. 2c.
	1976	*Hertzina*? *bisulcata* Müller; Bengtson, p. 191, text-figs 5-9.
	1978	*Gapparodus bellus* Abaimova, p. 497, pl. 7, figs 6, 7.

1978 *Gapparodus bisulcatus* (Müller); Abaimova, p. 497, pl. 7, fig. 8.

1978 *Gapparodus heckeri* Abaimova, p. 496, pl. 7, figs 3, 4, 10.

1978 *Gapparodus porrectus* Abaimova, p. 497, pl. 7, fig. 5.

? 1979 *Gapparodus* cf. *bisulcatus* (Müller); Bednarczyk, p. 428, pl. 3, fig. 2.

? 1981 *Hertzina* cf. *H. bisulcata* Müller; An, p. 218, pl. 1, fig. 17.

p 1987 *Gapparodus bisulcatus* (Müller); An, p. 106, pl. 1, figs 6, 8, 9, 26 (*non* pl. 1, fig. 10 [= *G. cuneatus*]).

1990 *Gapparodus bisulcatus* (Müller); An and Zhang, p. 159, pl. 1, figs 2, 8.

1991 *Gapparodus bisulcatus* (Müller); Müller and Hinz, p. 25, pl. 3, figs 1-42.

1992 *Gapparodus bisulcatus* (Müller); Hinz, p. 254, pl. 1, fig. 6.

1993 *Gapparodus bisulcatus* (Müller); Dong, p. 361, pl. 6, figs 1, 3, 9, 12.

1994 *Gapparodus bisulcatus* (Müller); An and Mei, p. 543, pl. 1, fig. 30.

Holotype. SMF 10 346, Müller (1959), pl. 13, fig. 22, Upper Cambrian Zone 1, Gudhem am Mösseberg, Västergötland, Sweden.

Material. 12 elements.

Diagnosis. Unimembrate apparatus of slender *Gapparodus* elements in which the posterior and anterior margins are of the same length, and the furrows are equally developed and found towards the centre of each lateral face.

Description. Slightly subsymmetrical, slender, elongate, coniform protoconodont elements characterised by the presence of a distinctive longitudinal furrow on each lateral side of the element. Anterior margin convex, evenly curved from base to tip, rounded, occasionally bearing prominent transverse ridges. Ridges flat, elevated, generally moderately wide and evenly spaced along the margin. Only in rare cases do the ridges reach around the element as far as the lateral furrows. Posterior margin concave, curved evenly from tip to base, rounded and unornamented. Lateral faces both bear a longitudinal furrow, formed by the indentation of the lateral face. In some cases the furrow is a narrow groove, but in others the posterior margin of the furrow is recurved towards the anterior, forming a more distinct, deeper and narrower indentation. Depth and width of the furrow are both variable characters. In general, the furrow is absent from the tip of the element, becoming deeper and more prominent towards the base, and is usually situated towards the posterior margin of the element. Cross-section of the tip of the element is circular, but towards the base the rounded nature of the cross-section becomes differentiated by the lateral indentations. Basal cavity very deep, extending to the tip of the element.

Remarks. Müller (1959) only tentatively assigned *H. bisulcata* to the genus *Hertzina*, because the two additional species assigned to *Hertzina*, *H. americana* and *H. elongata*, did not possess longitudinal furrows on the lateral faces of the elements. Poulsen (1966) proposed a relationship between *H*? *bisulcata* and the new species *Hertzina danica*. However, *H. danica* has since been reassigned as the type species of the monospecific genus *Amphigeisina* by Bengtson (1976) which comprises protoconodont elements in which the concave posterior margin is flanked by two sharp posterior carinae. Clark and Miller (1969) stated that *H. bisulcata* was the oldest reliably dated conodont that had been reported, and noted that the age of *H. danica* could not be conclusively determined.

Landing (1974) divided the elements of *H. bisulcata* into two varieties which he termed 'A' and 'B'. Variety A possesses a deep, prominent furrow that is situated very close to the posterior margin, whereas the furrow in variety B is not as well-developed, and is represented by a shallow indentation that lies in a position somewhat further towards the centre of the element in comparison to that observed in variety A. A new species of *Hertzina*, *H. bokonoi*, was also described by Landing (1974), but here this is included in the synonymy of *H. bisulcata* because the element (Landing 1974, text-fig. 1, figs h, i) possesses lateral furrows, and the posterior margin is not concave as it might be if this element bore a closer relationship to *A. danica* Poulsen. Overall no significant differences occur between the element of *H. bokonoi* and elements of *H. bisulcata*. Subsequent authors, who have commented on *H. bisulcata*, have not referred to the distinction of elements into two morphotypes as proposed by Landing (1974).

A single element of *H*? *bisulcata* was described by Lee (1975), but this is only tentatively included in the synonymy, because the longitudinal furrow appears to lie towards the anterior margin of the element, unlike other elements referred to *H. bisulcata* in which the furrow is situated posteriorly. Bengtson (1976), in an investigation of the histology of various Middle Cambrian conodonts, maintained the tentative assignment of *H*? *bisulcata* to the genus *Hertzina*, stating that, without further knowledge of the microstructure, the relationship of *H*? *bisulcata* with the type species of *Hertzina*, *H. americana*, was not clearly understood.

Abaimova (1978) assigned *H*? *bisulcata* as the type species of the new genus *Gapparodus*, distinguished from *Hertzina* by the presence of two longitudinal lateral furrows, and by the lack of sharp junctions between the posterior margin and the lateral faces. Three other species of *Gapparodus* (*G. bellus*, *G. heckeri* and *G. porrectus*) were erected by Abaimova (1978), who believed that the minor differences in the position of the longitudinal furrows relative to the posterior margin constituted interspecific variation. However, the differences between the species erected by Abaimova are considered to be intraspecific (rather than interspecific) variations typical of elements of *G. bisulcatus*, since the position of the lateral furrows in relation to the anterior and posterior margins is a variable feature. Additionally, Abaimova reassigned *H. bokonoi* Landing to *Gapparodus*.

A single element assigned to *Gapparodus* cf. *bisulcatus* by Bednarczyk (1979) is tentatively included in the synonymy because, although the figured element (Bednarczyk 1979, pl. 3, fig. 2) appears not to possess the longitudinal furrows typical of *G. bisulcata*, the description (p. 429) does state that they are present. An (1981) illustrated an element which he assigned to *Hertzina* cf. *H. bisulcata*, but this is only tentatively included in the synonymy because the figured specimen (An 1981, pl. 1, fig. 17) is poorly preserved and longitudinal furrows cannot be clearly distinguished.

Of the five elements of *G. bisulcatus* illustrated by An (1987), one (pl. 1, fig. 10) is removed to *G. cuneatus* due to its flaring basal region, which is not typical of elements of *G. bisulcatus* in general. Müller and Hinz (1991) illustrated a range of element morphologies of *G. bisulcatus*, and included a number of figures showing the transverse cross-section at various levels in the elements. Dong (1993) figured elements of *G. bisulcatus*, together with elements of a new species of *Gapparodus* (*Gapparodus* Sp. A) which strongly resemble *G. bisulcatus*, except that a narrow, longitudinal furrow is present along the posterior margin of the elements, as well as on the lateral faces.

Occurrence. Sample ENKC, Upper Cambrian Alum Shale, Sweden.

Gapparodus cuneatus (Müller and Hinz, 1991)

Plate 7, figure 8-11; Plate 16, figures A-D, F.

1971 *Hertzina elongata* Müller; Müller, p. 8, pl. 1, figs 2, 3.
?p 1987 *Gapparodus bisulcatus* (Müller); An, p. 106, pl. 1, fig. 10 (*non* pl. 1, figs 6, 8, 9, 26 [= *G. bisulcatus*]).
* 1991 *Gumella cuneata* Müller and Hinz, p. 26, pl. 4, figs 1-25; pl. 5, figs 1-28.
1992 *Gumella cuneata* Müller and Hinz; Hinz, p. 254, pl. 1, fig. 1.

Holotype. UB 980, Müller and Hinz (1991), pl. 4, figs 1-5, Upper Cambrian Zone 1, Gum Quarry, Kinnekulle, Västergötland, Sweden.

Material. 176 elements.

Diagnosis. *Gapparodus* elements in which the posterior margin is markedly shorter than the anterior margin, and in which the basal part of the element is flared.

Description. Elongate, relatively broad, coniform protoconodont elements characterised by a widely flaring base and the presence of longitudinal lateral furrows. Anterior side curved from base to tip, broadly rounded, convex. Posterior side also curving, with the curvature increasing towards the tip, shorter, narrower and more flattened that the anterior margin. Lateral margins bear a distinct furrow which runs sub-parallel with and close to the posterior margin, becoming more distal to the margin and also more pronounced towards the base. Furrows usually deep, with the lateral margins of the posterior part of the element often being bent to face towards the anterior. Furrows extend almost to the tip of the element. Anterior parts of the element are often ornamented with oblique annulations that are higher close to the anterior of the element, tending to lower parts towards the posterior. Posterior margin shorter than the anterior margin, making the basal cavity opening flare widely towards the posterior, often being broadly triangular in shape. Basal cavity deep, extending to the tip of the element. A secondary tip or canal is sometimes developed in the posterior part of the element, confined to early growth stages of the tip. Element cross-section circular at the tip, becoming more differentiated towards the base due to the presence of increasingly prominent lateral furrows. In basal regions of the elements, where the posterior margin is lacking, the lateral margins of the anterior part of the element curved outwards, even being slightly recurved towards the anterior in some cases, so that the lateral furrow is a continuous feature to the base. Left and right forms distinguished by the presence of one slightly concave and one slightly convex lateral face.

Remarks. Müller (1971) illustrated two elements (pl. 1, figs 2, 3) which he assigned to *Hertzina elongata*, however, both specimens bear longitudinal furrows and are relatively broadly tapering from tip to base, unlike the more slender elements of *Gapparodus bisulcatus*, and are thus included in the above synonymy. A single element of *G. bisulcatus*, figured by An (1987, pl. 1, fig. 10), is referred to *G. cuneatus* because of its short posterior margin and widely flaring basal opening.

Müller and Hinz (1991) erected the new species *Gumella cuneata*, and divided the elements into two morphotypes (Alpha and Beta). Alpha elements possess a secondary canal in the posterior of early growth stages, towards the tip of the element due to the more severe indentation of the lateral furrows. The secondary canal merges with the main basal opening when the flanks of the element begin to diverge more steeply. Beta morphotypes do not possess a secondary canal, and are evenly tapering from tip to base. Hinz (1992) also commented on the presence of two morphotypes of *G. cuneatus*. The differences between the two morphotypes are considered here to be subtle, and secondary basal canals have only been recognised in specimens with broken tips (Plate16, Figs A-D, F). For this reason, the division of the elements into two morphotypes has not been followed.

Occurrence. Samples VG93-13, VG93-14 VG93-15, VG93-16, Upper Cambrian Alum Shale, Västergötland, Sweden

Genus HERTZINA Müller, 1959

1959 *Hertzina*, Müller, p. 454.

Description. Gently curved, coniform protoconodont elements bearing two postero-lateral carinae. Length of element varies between species, with some elements being relatively short and squat and others being very long and slender. Anterior margin weakly but evenly curved, convex, rounded. Posterior margin curved, usually bounded by postero-lateral carinae, one of which forms the posterior margin, and the other being developed on one of the lateral faces. Right and left forms can be distinguished according to the face on which of the lateral faces bears a carina, and by the curvature of the element towards the inner (carinate) face. The sharp to narrowly rounded carinae extend from base to tip of the element. Posterior flank flattened, anterior and lateral flanks flat to weakly concave. Faint traces of growth lines may be present on the outer surfaces of the elements. Basal cavity very deep, extending to the tip of the element. Cross-section broadly triangular from tip to base due to the development of the postero-lateral carinae.

Remarks. In his original description of *Hertzina*, Müller (1959) stated that two carinae were present towards the posterior margin of the elements, and compared the genus with the paraconodont *Furnishina*. However, Müller (1959) noted that the carinate margins that form the boundary of a flat face lie towards the anterior in *Furnishina*, but towards the posterior in

Hertzina. *Hertzina* can be distinguished from *Phakelodus* Miller, because of the presence of postero-lateral carinae and flattened faces, which are absent in the rounded, ovate to tear-shaped *Phakelodus* elements. *Gapparodus* Abaimova possesses lateral furrows, which are absent from *Hertzina*.

Hertzina elongata Müller, 1959

Plate 7, figures 5, 6.

*	1959	*Hertzina elongata* Müller, p. 455, pl. 13, fig. 28.
p	1959	*Hertzina*? *bisulcata* Müller, p. 456, pl. 13, fig. 24 (*non* pl. 13, figs 22, 23, 27 [= *Gapparodus bisulcatus*]).
non	1971	*Hertzina elongata* Müller; Müller, p. 8, pl. 1, figs 2, 3 [= *G. cuneatus*].
	1975	*Hertzina* sp., Matthews and Missarzhevsky, p. 299, pl. 3, fig. 7.
	1979	*Hertzina elongata* Müller; Bednarczyk, p. 429, pl. 3, figs 1, 4, 8, 11, 13.
p	1979	*Prooneotodus tenuis* (Müller); Bednarczyk, p. 433, pl. 3, fig. 6 (*non* pl. 3, figs 3, 5, 7 [= *P. tenuis*]).
?	1982	*Hertzina elongata* Müller; An, p. 134, pl. 10, fig. 10.
	1984	*Hertzina elongata* Müller; Brasier, p. 235, text-fig. 1o, p, q.
	1985	*Hertzina elongata* Müller; Bergström and Orchard, p. 33, pl. 2.1, figs 2-5.
?	1987	*Hertzina* cf. *H. elongata* Müller; Buggisch and Repetski, p. 156, pl. 8, fig. 4.
	1987	*Hertzina elongata* Müller; Hinz, p. 62, pl. 14, fig. 8; text-fig. 2A, B.
	1991	*Hertzina elongata* Müller; Müller and Hinz, p. 26, text-fig. 9A-K.

Holotype. HUB ct. 229, Müller (1959), p. 455, pl. 13, fig. 28, Blatt Sagard, Rügen.

Material. 814 elements

Description. Asymmetrical, slender, elongate coniform protoconodont elements, in which the posterior margin is sharp with a carina developed on one lateral face so that a flat surface is present towards the posterior of the element. Anterior margin very gently curved, narrowly rounded, convex. Posterior margin narrowly rounded or sharp, gently and evenly curved from base to tip, concave. A narrowly rounded carina is developed on one lateral flank, extending from the tip to the base and usually situated towards the posterior of the element so that a flat face is developed in the postero-lateral region of the element. The opposite flank is flattened and unornamented. Basal cavity very deep, extending to the tip of the element. Cross-section triangular at both the tip and the base of the element. Right and left forms present.

Remarks. Hertzina elongata differs from the type species, *Hertzina americana* by being longer and more slender, and by possessing a more rounded carina. Müller (1959) erected the new species *H. elongata,* and noted that certain similarities with *Oneotodus tenuis* (= *Phakelodus tenuis*) could be observed. However, *P. tenuis* lacks a lateral carina and has an ovate, not triangular, cross-section and is quite easily distinguished from *H. elongata* even though both species tend to be long, slender and gently curved from tip to base. One of the elements assigned to *Hertzina*? *bisulcata* by Müller (1959, pl. 13, fig. 24) is referred to *H. elongata* because of the presence of a distinct postero-lateral carina. The anterior flank of the specimen is slightly concave, and it is for this reason that the element may have been misidentified.

Neither of the specimens of *H. elongata* illustrated by Müller (1971, pl. 1, figs 2, 3) are retained in the synonymy and are referred instead to *Gapparodus cuneatus* because both have longitudinal furrows on their lateral faces, and are too widely tapering to belong to *G. bisulcatus.* Together with elements of *H. elongata,* Bednarczyk (1979, pl. 3, fig. 6) figured a single element of *P. tenuis* that is now referred to *H. elongata* due to the presence of a distinct longitudinal carina on one of its lateral faces. The lateral carina of the element of *H. elongata* figured by An (1982, pl. 10, fig. 10) is poorly developed, and therefore the specimen is only tentatively included in the above synonymy.

Although stratigraphically older than most specimens of *H. elongata* figured by other authors, the elements illustrated by Brasier (1984) do agree with the description and diagnosis given for the species by Müller (1959). Buggisch and Repetski (1987) illustrated a single specimen which they compared to *H. elongata,* because the specimen bears two carinae, but is broken at both the tip and the base, therefore precluding a definitive assignment of the specimen. The presence of two carinate margins towards the posterior side of the element is indicative of the species, and the element is thus very tentatively included in the synonymy. Müller and Hinz (1991) noted that *H. elongata* demonstrated intraspecific variability in the development of the lateral flanks and the posterior face, together with the height : width ratio of the basal opening, resulting in different degrees of asymmetry. Also of importance is the presence of basally directed growth lines on the outer surface of the elements (Müller and Hinz 1991, text-fig 9C, D) which demonstrate the protoconodont nature of these elements.

Occurrence. Samples O93-1, O93-2, O93-4, O93-5, O93-6; O93-7c, O93-7d, VG93-8, VG93-10, VG93-14, VG93-16, VG93-17, Upper Cambrian Alum Shale, Öland and Västergötland, Sweden.

Genus PHAKELODUS Miller, 1984

1984 *Phakelodus*, Miller, p. 65.

Type species. Oneotodus tenuis Müller, 1959, p. 457, Deadwood Formation, Little Elk Creek, Black Hills, South Dakota.

Description. Thin walled, slender, gently curved, usually laterally compressed protoconodont elements. Posterior margin may be sharp or narrowly rounded, broadly curving to tip. Anterior margin rounded, gently curving. Faces either smooth and unornamented, or with one or two sets of faint oblique annulations or striations. In some forms the annulations run parallel to the basal margin. Cross-section remains consistent in shape along the entire length of the element, usually ovate to rounded, tear-shaped in forms with sharp posterior margins. Basal cavity very deep, extending almost to tip of element.

Remarks. Species now assigned to the genus *Phakelodus* were previously included in the genera *Prooneotodus* Müller and Nogami, 1971, and *Oneotodus* Lindström, 1954. The original description of *Oneotodus* was very broad, including all coniform elements with well-defined basal cavities and circular to sub-circular cross-sections. The type species of *Oneotodus*, *Distacodus? simplex* Furnish, 1938 is a relatively simple coniform euconodont, with no external ornament, a sub-circular basal cross-section and, in comparison to *Phakelodus*, a shallow basal cavity. Müller and Nogami (1971) erected the new genus *Prooneotodus* to include those specimens of *Oneotodus* that had a paraconodont style of growth. However, the histological work of Bengtson (1976), reported by Landing (1977), concluded that some species assigned to *Prooneotodus* were of protoconodont affinity, and could no longer be classified under the paraconodont genus *Prooneotodus*. Miller (1984) erected the genus *Phakelodus* to include those *Prooneotodus* species that were found to be of protoconodont affinity.

Fused clusters of *Phakelodus* elements are relatively common and have been described and illustrated by many authors (Miller and Rushton 1973; Müller and Andres 1976; Landing 1977, 1983; Landing *et al.* 1980; Andres 1981, 1988; Fortey *et al.* 1982; Bergström and Orchard 1985; Buggisch and Repetski 1987; Heredia and Bordonaro 1988; Müller and Hinz 1991; Hinz 1992; Dong 1993). Landing (1977) formulated the "Supertooth" model, whereby the elements of each half-apparatus functioned together as one integrated unit to overcome the supposed weakness of the individual elements. Most authors, however, tend to support the hypothesis proposed by Andres (1981, 1988) and Szaniawski (1982, 1983) that suggests that *Phakelodus* elements functioned in a similar way to the grasping spines of recent chaetognaths, and that their three-layered histology implies that the grasping spines and the protoconodont elements are homologous structures (Szaniawski 1982; Bengtson 1983). Fused clusters of *Phakelodus* elements often form half-apparatuses, and are occasionally found as complete units. Half-apparatuses are usually composed of a number of elements (between 2 and 13) arranged in an arched sequence with the lateral margins juxtaposed and the tips in close association. In other examples, two half-apparatuses are present in one cluster, with the two components being diametrically opposed and the tips facing the central part of the apparatus (e.g. Müller and Hinz 1991, plate 1, figs 2-4, 8, 13; plate 2, figs 15, 16, 23). Several examples are preserved with elements joined along their lateral margins, but with the elements in opposing orientation so that the tips of one or more elements are found next to the bases of the elements in the opposing part of the apparatus.

Phakelodus elongatus (Zhang *in* An *et al.*, 1983)

Plate 7, figures 3, 4; Plate 16, figure E.

p	1959	*Oneotodus tenuis* Müller, p. 457, pl. 13, fig. 11 (*non* pl. 13, figs 13, 14, 20 [= *Phakelodus tenuis*]).
?	1969	?*Oneotodus tenuis* Müller; Miller, p. 436, pl. 64, figs 43-45; text-fig. 5c.
?p	1973	*Prooneotodus tenuis* (Müller); Müller, p. 45, pl. 1, fig. 2 (*non* pl. 1, figs 1, 3 [= *Phakelodus tenuis*]).
?	1978	*Proconodontus savitsky* Abaimova, p. 499, pl. 7, figs 13, 14; pl. 8, fig. 1.
	1982	*Prooneotodus* aff. *tenuis* (Müller); An, p. 145, pl. 1, figs 2-6; pl. 2, figs 1, 5.
*	1983	*Proconodontus elongatus* Zhang *in* An *et al.*, p. 125, pl. 5, figs 4, 5; text-fig. 9, fig. 16.
p	1986	*Phakelodus tenuis* (Müller); Chen and Gong, p. 157, pl. 23, figs 4-6, 15; pl. 24, fig. 3; text-fig. 59 (*non* pl. 22, figs 7, 8, 12, 14, 19, 21; pl. 23, figs 8, 13, 21 [= *Phakelodus tenuis*]).
	1986	*Proconodontus elongaus* [*sic*] Zhang; Jiang *et al.*, pl. 3, fig. 6.
?	1987	*Prooneotodus* aff. *tenuis* (Müller); An, pl. 1, fig. 5.

1991 *Phakelodus elongatus* (An) [*sic*]; Müller and Hinz, p. 32, pl. 1, figs 1-5, 7-9, 12-14, 22.

1992 *Phakelodus elongatus* (Zhang *in* An *et al*.,); Hinz, p. 256, pl. 2, fig. 2.

? 1993 *Phakelodus elongatus* (An) [*sic*]; Dong, pl. 4, figs 10, 11; pl. 5, figs 6, 7.

1994 *Phakelodus elongatus* (An) [*sic*]; Repetski *et al*., p. 21, text-fig. 18Z.

1995 *Phakelodus* cf. *P. elongatus* An [*sic*]; Harris *et al*., pl. 1, fig. V.

1998 *Phakelodus elongatus* (Zhang *in* An *et al*.); Müller and Hinz-Schallreuter, p. 99, text-figs 6.3-6.5.

Holotype. SB0088, An *et al*. 1983, pl. 5, fig. 5, Gushan Formation, Mongying County, Shandong Province, China.

Material. 239 elements from Wyoming, 451 from Sweden.

Description. Erect, slender, elongate elements of *Phakelodus*. Anterior margin rounded, curved into a broad arc from base to tip. Posterior margin sharp, also curved and of equal length to the anterior margin. Lateral flanks flattened to slightly convex. Transverse cross-section through element tear-shaped. Elements are usually sub-symmetrical, with the outer lateral flank being very slightly wider than the inner, and with minor bending of the element towards the inner margin. Outer surface usually unornamented but, in rare cases, the external surface bears oblique, closely spaced annulations.

Remarks. Elements of *Phakelodus elongatus* follow the generic description, being long, slender protoconodonts with a rounded anterior margin, a sharp posterior margin and a tear-shaped cross-section. The original description of the species *Oneotodus tenuis* (= *Phakelodus tenuis*) by Müller (1959) included broadly curved, slender, elongate coniform sclerites, both with and without a keel or carina present on the posterior margin. Subsequently, a division has been made so that forms without a sharp posterior margin (i.e. an oval cross-section) fall under *Phakelodus tenuis*, and those with a sharp posterior margin (i.e. a tear-shaped cross-section) fall under *Phakelodus elongatus*. Miller (1969) was the first author to imply that a division of *Oneotodus tenuis* should be made, noting that all of his specimens possessed sharp posterior margins, rather than just a proportion of them as would have been likely according to Müller's original description. Müller (1973) reassigned the elements to the new genus *Prooneotodus* Müller and Nogami, 1971, after realising that the growth style of the elements was not similar to that of the "true conodonts".

Abaimova (1978) described the new species *Proconodontus savitskyi*, but it is evident from the figures therein (Abaimova 1978, pl. 7, figs 13, 14, pl. 8, fig.1) that the elements are too long, curved and slender to fall within the diagnosis of *Proconodontus* and, more importantly, crown-material is absent and striations are well developed on the element surfaces. The posterior margins of these elements appear to be sharp, and it is for this reason that they are included under *P. elongatus* rather than *P. tenuis*. An (1982) recognised a distinction between elements with and without a sharp posterior margins, and noted this by assigning elements with the former character to *P.* aff. *P. tenuis*, implying a close relationship between the two types of element.

Zhang (*in* An *et al.* 1983) erected a new species name (*P. elongatus*) for the forms closely resembling *P. tenuis*, with sharp posterior margins, but assigned the new species to *Proconodontus* because he believed that the development of a sharp or keeled posterior margin was indicative of a close relationship between *P. elongatus* and other species of *Proconodontus*. A translation of the original manuscript (dictated by Chen Jun-yuan to J. F. Miller in 1983) states that Zhang believed *P. elongatus* to be a transitional form between *Prooneotodus* and *Proconodontus*. An additional note by Miller, included in the translation, explained his belief that *P. elongatus*, as described by Zhang, is of protoconodont affinity, and therefore cannot be closely related to *Proconodontus*. Miller also noted that *P. elongatus* could not be assigned to the genus *Prooneotodus* due to its protoconodont, not paraconodont, affinity, and expressed his opinion that both *P. elongatus* and *P. tenuis* should be united at generic, if not specific, level. The following year Miller (1984) erected the genus *Phakelodus* to incorporate protoconodont species that had previously been assigned to the paraconodont genus *Prooneotodus*. Chen and Gong (1986) reverted to the use of Müller's original description of the species, including elements with or without a sharp posterior margin under the one species name. However, evidence from fused clusters (e.g. Müller and Hinz, plate 1) has demonstrated that *Phakelodus elongatus* apparatuses are entirely unimembrate, consisting only of elements in which the posterior margin is sharp, and in which the transverse cross-section is tear-shaped.

Subsequent to the work of Müller and Hinz (1991), the species concept of *Phakelodus elongatus* has stabilised, although confusion as to the authorship of the species has arisen. Müller and Hinz (1991), Dong (1993), Repetski *et al.* (1994) and Harris *et al.* (1995) all attributed the species to An (1983). The species was first described by Zhang in a multi-authored paper (An *et al.* 1983), and so the correct binomen should be *Phakelodus elongatus* (Zhang *in* An *et al.*, 1983).

Occurrence. WY96-17, WY96-18, Gallatin Formation, Bighorn Mountains, Wyoming, USA. Samples O93-1, O93-2, O93-4, O93-5, O93-6, O93-7d, VG93-7, VG93-8, VG93-10, VG93-13, VG93-14, VG93-15, VG93-16, VG93-17, Upper Cambrian Alum Shale, Öland and Västergötland, Sweden.

Phakelodus tenuis (Müller, 1959)

Plate 7, figures 1, 2, 7; Plate 16, figure G.

*p 1959 *Oneotodus tenuis* Müller, p. 457, pl. 13, figs 13, 14, 20 (*non* pl. 13, fig. 11 [= *Phakelodus elongatus*]).
1966 *Oneotodus tenuis* Müller; Nogami, p. 356, pl. 9, figs 11, 12.
? 1969 *Oneotodus tenuis* Müller; Clark and Robison, text-fig. 1a.
? 1971 *Oneotodus tenuis* Müller; Druce and Jones, p. 83.
1971 *Oneotodus tenuis* Müller; Müller, p. 8, pl. 1, figs 1, 4-6.
p 1973 *Prooneotodus tenuis* (Müller); Müller, p. 45, pl. 1, figs 1, 3 (*non* pl. 1, fig. 2 [= *Phakelodus elongatus*]).
1975 *Prooneotodus tenuis* (Müller); Lee, p. 83, pl. 1, figs 14-17; text-fig. 2K, L.
1976 *Prooneotodus tenuis* (Müller); Müller and Andres, text-fig. 2; pl. 22.
1976 *Prooneotodus tenuis* (Müller); Miller and Paden, p. 596, pl. 1, figs 20-23.
1977 "*Prooneotodus*" *tenuis* (Müller); Landing, pl. 1, figs 1-9; pl. 2, figs 1-11.
? 1978 *Prooneotodus tenuis* (Müller); Abaimova, p. 499, pl. 8, figs 2, 4, 9.
? 1978 "*Prooneotodus*" *tenuis* (Müller); Landing *et al.*, p. 76, text-fig. 2b.
1978 *Prooneotodus tenuis* (Müller); Tipnis, Chatterton and Ludvigsen, pl. 1, text-fig. 6.
1979 *Prooneotodus tenuis* (Müller); Bednarczyk, p. 433, pl. 3, figs 3, 5-7.
1979 "*Prooneotodus*" *tenuis* (Müller); Tipnis and Chatterton, p. 259, pl. 29.1, figs 1-9.
1980 "*Prooneotodus*" *tenuis* (Müller); Landing, Ludvigsen and von Bitter, p. 34, text-fig. 8m, n.
1980 *Prooneotodus tenuis* (Müller); Lee, pl. 1, fig. 5.
1980a *Prooneotodus tenuis* (Müller); Szaniawski, p. 115, pl. 18, figs 5, 6.
1981 *Prooneotodus tenuis* (Müller); An, p. 218, pl. 1, fig. 16.
1981 *Prooneotodus* (Müller); Andres, text-figs 1-7.
1981 *Prooneotodus tenuis* (Müller); Azmi *et al.*, pl. 1, fig. 3.
? 1981 '*Prooneotodus*' *tenuis* (Müller); Miller *et al.*, p. 192, text-fig. 4p-t.
1981 *Prooneotodus tenuis* (Müller); Wang and Wang, pl. 1, fig. 1.
1982 *Prooneotodus tenuis* (Müller); An, p. 145, pl. 1, fig. 1.

non 1982 *Prooneotodus* aff. *tenuis* (Müller); An, p. 145, pl. 1, figs 2-6; pl. 2, figs 1, 5 [= *Phakelodus elongatus*].

1982 "*Prooneotodus*" *tenuis* (Müller); Fortey, Landing and Skevington, text-fig. 8w.

1982 *Prooneotodus*? *tenuis* (Müller); Szaniawski, text-fig. 1a-h.

1983 *Prooneotodus tenuis* (Müller); An *et al.*, p. 130, pl. 5, figs 2, 3.

1983 *"Prooneotodus" tenuis* (Müller); Landing, p. 1180, text-fig. 10n.

1984 "*Prooneotodus*" *tenuis* (Müller); Burrett and Findlay, p. 724, text-fig. 3D.

1985 "*Prooneotodus*" *tenuis* (Müller); Bergström and Orchard, p. 54, pl. 2.1, figs 1, 7.

1985 *Prooneotodus tenuis* (Müller); Wang, p. 236, pl. 3, fig. 11; pl. 7, fig. 9; pl. 12, fig. 10.

?p 1986 *Phakelodus tenuis* (Müller); Chen and Gong, p. 157, pl. 22, figs 7, 8, 12, 14, 19, 21; pl. 23, figs 8, 13, 21 (*non* pl. 23, figs 4-6, 15; pl. 24, fig. 3; text-fig. 59 [= *Phakelodus elongatus*]).

? 1986 *Phakelodus tenuis* (Müller); Chen *et al.*, p. 368, pl. 2, figs 1-3.

1986 *Prooneotodus tenuis* (Müller); Jiang *et al.*, pl. 3, fig. 5.

1987 *Prooneotodus tenuis* (Müller); An, p. 112, pl. 1, fig. 4.

1987 *Phakelodus tenuis* (Müller); Buggisch and Repetski, p. 158, pl. 7, figs a-k.

? 1987 *Prooneotodus tenuis* (Müller); Dong, p. 169, pl. 1, fig. 12.

1988 *Phakelodus tenuis* (Müller); Andres, p. 110, pl. 1, figs 1-8; pl. 2, figs 1-8; text-figs 2, 5, 6.

1988 *Phakelodus tenuis* (Müller); Heredia and Bordonaro, p. 192, pl. 3, figs 1, 2.

? 1989 *Phakelodus tenuis* (Müller); Popov *et al.*, p. 144, pl. 17, figs 6-10.

1990 *Prooneotodus tenuis* (Müller); An and Zhang, p. 160, pl. 1, figs 1, 6, 7.

1991 *Phakelodus tenuis* (Müller); Müller and Hinz, p. 33, pl. 1, figs 6, 10, 11, 15-21, 23; pl. 2, figs 1-24.

1992 *Phakelodus tenuis* (Müller); Buggisch *et al.*, p. 172, pl. 2, figs 19, 20, 22.

1992 *Phakelodus tenuis* (Müller); Hinz, p. 256, pl. 2, fig. 1.

1993 *Phakelodus tenuis* (Müller); Dong, pl. 4, figs 12, 13; pl. 6, figs 2, 8, 17.

1993 *Phakelodus tenuis* (Müller); Landing, text-fig. 4.1.

1994 *Phakelodus tenuis* (Müller); Lehnert, p. 255, pl. 1, figs 14a, b.

1994 *Phakelodus tenuis* (Müller); An and Mei, pl. 1, fig. 23.

1994 *Phakelodus tenuis* (Müller); Repetski *et al.*, p. 21, fig. 18Y.

Holotype. SUI 10299, Müller (1959), pl. 13, fig. 14, Upper Cambrian Deadwood Formation Member 4, Little Elk Creek, Black Hills, South Dakota, USA.

Material. 1599 elements.

Description. Erect, slender, elongate elements of *Phakelodus*. Anterior and posterior margins rounded, curving evenly from base to tip. Lateral margins flattened to slightly convex. Transverse cross-section ovate, rounded anteriorly and posteriorly and slightly flattened in the lateral parts. Outer surface of the elements either smooth, or bearing closely spaced, oblique annulations.

Remarks. Elongate, slender *Phakelodus* elements with rounded anterior and posterior margins and an ovate to rounded cross-section are assigned to *P. tenuis*. Since the original description of *Oneotodus tenuis* (= *P. tenuis*) by Müller (1959), the specific concept has remained mostly unaltered, except for the generic assignment which has changed according to the histological investigations that have been carried out (Müller and Nogami 1971; Szaniawski 1982; Miller 1984). A clear distinction between *P. tenuis* and *P. elongatus* was made by Zhang (*in* An *et al.* 1983) who noted that the presence or absence of a sharp posterior margin was not an intraspecific variation as had been suggested by Müller (1959). Previously this character had been remarked upon by other authors (Nogami 1966; Lee 1975; Abaimova 1978) who continued to follow the convention established by Müller. An (1982) had also made this observation, and assigned elements with a sharp posterior margin to *P* aff. *tenuis* maintaining those with a rounded posterior margin in *P. tenuis*. Miller (1984), in his description of the new protoconodont genus *Phakelodus*, described only forms in which the posterior margin was drawn out into a keel, and mentioned only the type species *P. tenuis*, however, it is more likely that Miller was describing elements of *P. elongatus* and not *P. tenuis*.

Occurrence. Samples O93-1, O93-2, O93-4, O93-5, O93-6; O93-7c, O93-7d, VG93-7, VG93-8, VG93-10, VG93-13, VG93-14, VG93-15, VG93-16, VG93-17, ENKC, Upper Cambrian Alum Shale, Öland and Västergötland, Sweden.

CHAPTER 5

PARACONODONT SYSTEMATIC PALAEONTOLOGY

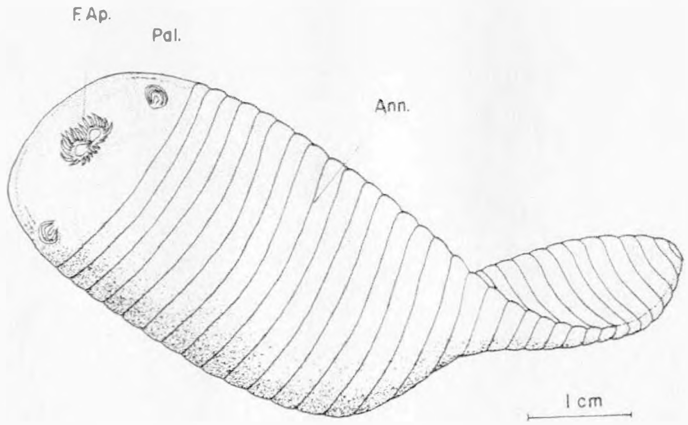
5.1 Introduction

In the majority of studies of paraconodonts the elements have been classified according to form taxonomy, although symmetrical and asymmetrical elements displaying the same overall morphological characteristics are often grouped together into a bimembrate apparatus. Reconstructions of multielement paraconodont apparatuses have been hampered by the restricted range of element morphologies and the paucity of evidence from fused clusters and bedding plane assemblages of elements.

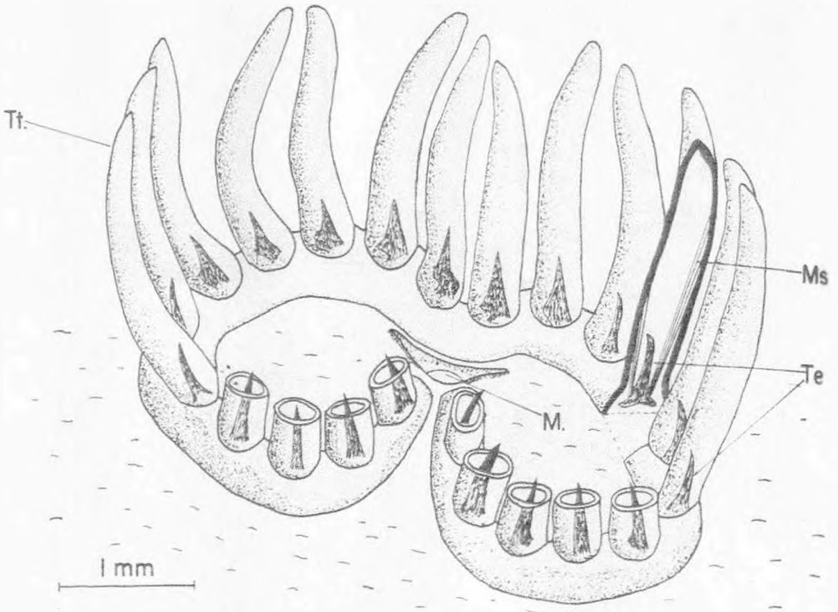
5.2 Odontogriphus omalus *– a questionable paraconodont bedding plane assemblage*

Odontogriphus omalus was described by Conway Morris (1976) from the part and counterpart of a single preserved specimen from the Phyllopod Bed of the Middle Cambrian Burgess Shale of British Columbia, Canada. From the remains, Conway Morris reconstructed a dorso-ventrally compressed animal, about 6 cm long and 2.5 cm in maximum width, with an annulated body that is poorly-differentiated from the head. Towards the anterior, within the head region, is a double-looped lophophoral apparatus bearing the conical tooth-like elements. Other features include a straight gut, a terminal anus and lateral musculature on either side of the trunk (Conway Morris 1976, p 200, Text-fig. 5.1). The tooth-like elements in the lophophoral apparatus are preserved as external moulds or thin reflective films, and are arranged around the double-looped structure, with an almost symmetrical element closest to the midline of the animal. Conway Morris (1976) suggested that, during life, the elements would have functioned as tentacular supports in the feeding apparatus, in which the mouth was located in the centre of the double-looped structure (Text-fig. 5.2). He used the probable morphological similarity of the elements with Cambrian coniform conodonts such as *Scandodus* to imply a conodont affinity, but could not determine whether the affinity lay closer to the paraconodonts or the euconodonts, since the quality of preservation of the specimen precluded a histological investigation. If the elements are indeed mouldically preserved paraconodonts, then it is more likely that they belong to the genus *Furnishina*. Further support was added to this hypothesis by Conway Morris, who noted that the lophophoral apparatus was similar to the hypothesis of conodont element function proposed by

Lindström (1974), but Conway Morris acknowledged that the two ideas were not totally concordant, as Lindström's reconstruction was of an animal completely covered in tentacles.



Text-figure 5.1. Reconstruction of *Odontogriphus omalus* from the Burgess Shale of British Columbia. Ann. = annulations, F. Ap. = feeding apparatus, Pal. = Palps. (From Conway Morris 1976).



Text-figure 5.2. Reconstruction of the anterior feeding apparatus showing the position of the putative paraconodont elements as supports of the tentacles surrounding the mouth. Ms. = muscle, M. = mouth, Te. = 'teeth', Tt. = tentacles. (from Conway Morris 1976).

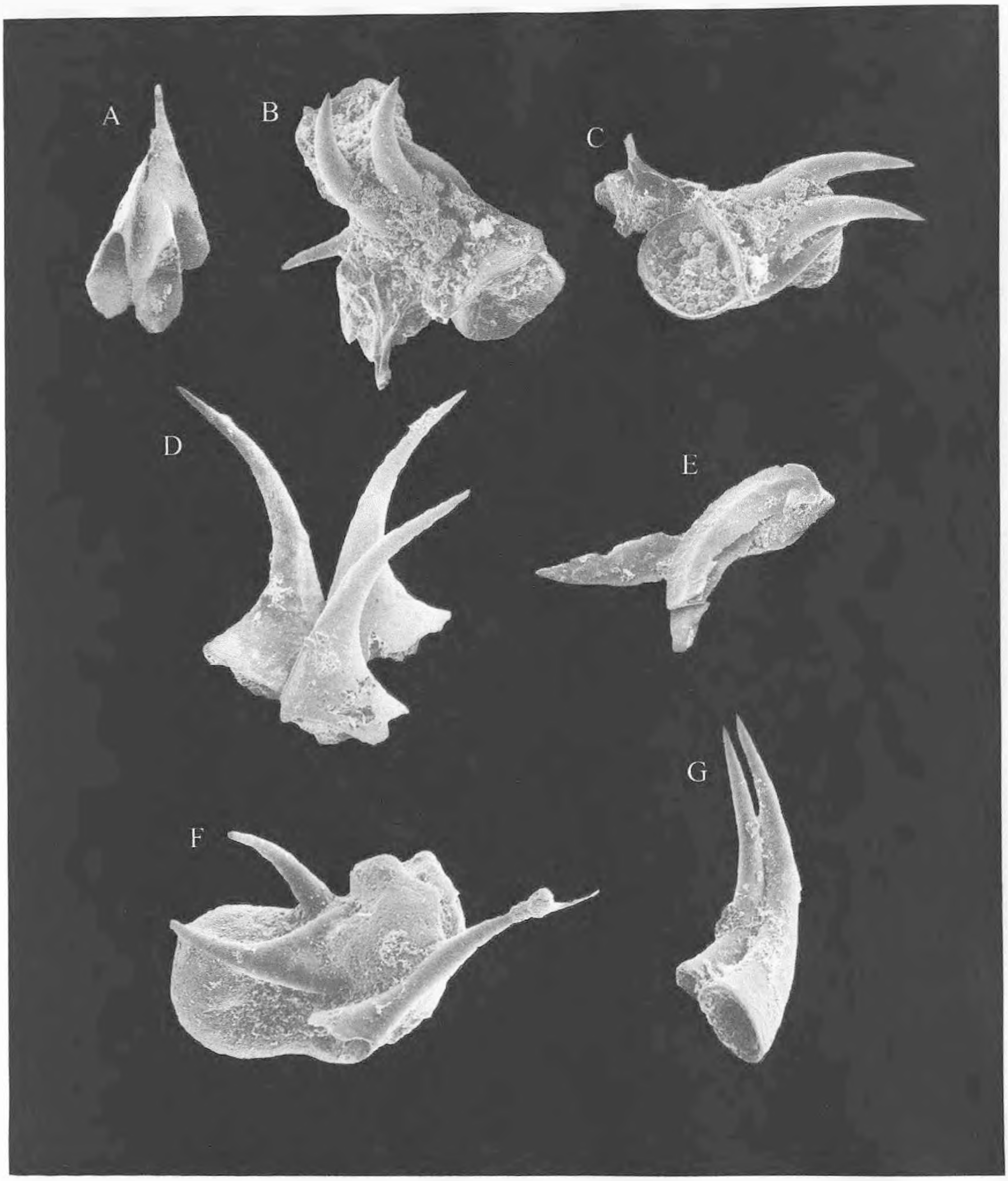
On the basis of his description of *Odontogriphus omalus*, Conway Morris (1976) assigned the Conodontophorida to the superphylum Lophophorata, but the current assignment of the euconodonts, and probably the paraconodonts, to the phylum Vertebrata negates this assignment, or calls into question the conodont affinity of this organism. Since no uniquely vertebrate characters have been recognised in the soft-part remains of *O. omalus* it appears that either the original interpretation is incorrect, or *Odontogriphus omalus* is not of conodont affinity. In either case, further work on *O. omalus* is required in the future, in order to resolve this problem.

5.3 Fused clusters of paraconodonts

On the rare occasions when paraconodont elements are found in fused clusters, they often represent juvenile stages in ontogeny (Szaniawski 1980b, 1987; Andres 1981, 1988). Andres (1988) attributed this rarity to the morphological differentiation between juvenile and adult elements, particularly in the genus *Furnishina*, whereby the basal region becomes expanded in relation to the cusp in adult forms (Szaniawski 1971, p. 404, text-fig. 1). In juvenile forms it is therefore possible for the margins of the elements to remain in contact, whereas in adult specimens the widely-flaring nature of the base precludes this arrangement. This situation has also been recognised by Müller and Hinz (1991) who figured fused cluster of paraconodonts including *Furnishina furnishi*, *Muellerodus subsymmetricus*, *Nogamiconus falcifer*, *Prooneotodus gallatini* and *Trolmenia acies* (= *Proacodus acies*). Since no fused cluster of paraconodont elements have been recovered from the material used in the current study, and because Müller and Hinz (1991) did not describe the clusters they illustrated in any great detail, it is pertinent to give a brief review of their illustrations, to provide a sounder basis for the multielement descriptions which follow.

5.3.1 Furnishina furnishi *(Müller and Hinz 1991, pl. 13, fig. 11).*

This specimen comprises a cluster of three small elements (Text-fig. 5.3A). The cluster is viewed from the posterior and shows that the elements are connected along their lateral margins. All three elements are of similar size, two are aligned with their tips and bases in close association, but the third element is raised slightly by comparison, with its basal margin approximately level with a point a third of the way up the other two elements. The basal opening is not as distinct as in the other two, perhaps because the third element has been compressed, or because the specimens are juveniles and the basal opening has yet to form properly (compare Müller and Hinz, pl. 13, fig. 6). All these elements would fall into the 'gamma' element category as established in this report (Section 5.6), and appear to be in what must be assumed to be their original positions.



Text-figure 5.3. Illustrations extracted from Müller and Hinz (1991) and put together into a single figure using Adobe Photoshop. A, *Furnishina furnishi*; B, C, *Muellerodus subsymmetricus*; D, *Proacodus acies*; E, *Nogamiconus falcifer*; F, G, *Prooneotodus gallatini*. The original plate and figure numbers in Müller and Hinz's publication are given in the text.

5.3.2 Muellerodus subsymmetricus *(Muller and Hinz 1991, pl. 19, figs 13, 14).*

This is a poorly-organised cluster of four similarly sized elements, possible not in their original arrangement (Text-fig. 5.3B, C). Two elements of the cluster are illustrated with both their cusps and their basal openings in view, however the remaining two elements are recognised only by their cusps because the specimen has not been photographed from the reverse, where the bases of these elements are presumed to lie. The elements that are recognised only from their cusps appear to be aligned sub-parallel to one another, because the tips of the cusps point in the same direction but diverge slightly. If the part of the specimen that is illustrated is assumed to be posterior, the tips of these two elements point towards the anterior, with their anterior margins facing the top left hand corner of the figure. The element in the foreground of Text-fig. 5.3C (Müller and Hinz 1991, pl. 19, fig. 14) is the most completely visible, with its base opening towards the posterior and the tip of its cusp twisted slightly towards the centre of the specimen, also pointing in a posterior direction. The fourth element has its base visible in Text-fig. 5.3C but the specimen has to be rotated (Text-fig. 5.3B; Müller and Hinz 1991, pl. 19, fig. 13) in order for its cusp to come into view. This element is possibly broken, as its cusp and base are not in strict alignment, however, if this is the case, the breakage is obscured by material that adhered to the specimen. Once again, all the elements in this cluster appear to be of similar morphology, with no marked differences in shape or size. An explanation for this is that the cluster represents only a part of the total apparatus and that, in this part-apparatus, elements of similar size and morphology existed alongside one another, with elements of a different morphology occurring in a separate part of the apparatus. The poor organisation of the elements in the *M. subsymmetricus* cluster may have resulted from taphonomic disturbance, or it may be that this cluster is a coprolitic assemblage of elements.

5.3.3 Nogamiconus falcifer *(Müller and Hinz 1991, pl. 21, fig. 16)*

This fused cluster comprises three elements, all of exactly the same size, with two aligned parallel to one another with their lateral margins in contact and a third in an opposing position with its lateral margin in contact with the central element in the cluster. The elements in the foreground of the illustration (Text-fig. 5.3E) have their anterior margin to the right, curving so that the posterior corners of the element are pointing downwards and the basal cavities of the elements open towards the bottom-right of the figure. The opposing element is inverted with its basal cavity opening towards the top-left of the illustration, and its anterior part aligned adjacent to the anterior of the other two elements. Its posterior corner points towards the left. This arrangement could have been achieved by the horizontal flipping of the element at the rear of the cluster so that it became inverted relative to the other two elements. Alternatively, the third element may have been in an opposing part of the apparatus and has been rotated anticlockwise around a point located in the anterior part of the elements, so that it became inverted relative to its original position, with its anterior part remaining relatively stationary and the posterior of the element moving in an arc to face in the opposite direction to its initial alignment. In comparison to the *Muellerodus* cluster, this assemblage of elements has undergone a relatively small amount of post-mortem disturbance although it is still likely that the complete apparatus would have been composed of a larger number of elements. All the elements in the *Nogamiconus* cluster were assigned to the 'alpha' morphotype of Müller and Hinz (1991, p. 104), and so it is possible that the 'beta' elements were found in a different part of the apparatus that became separated after the death of the animal. The terms 'alpha' and 'beta' as used by Müller and Hinz (1991) to denote element morphotypes in certain apparatuses do not correspond to the new terminology involving the terms 'alpha', 'beta', 'gamma' and 'delta', which is outlined below (Section 5.6).

5.3.4 Prooneotodus gallatini *(Müller and Hinz 1991, pl. 24, figs 10, 26)*

Two clusters of *P. gallatini* elements were illustrated by Müller and Hinz (1991; Text-fig. 5.3F, G). One consists of three similarly-sized elements in a random arrangement (Text-fig. 5.3F; Müller and Hinz 1991, pl. 25, fig. 10). The cusp of one element points in the opposite direction to the other two elements and none of the anterior or posterior margins of the elements are in alignment with any of the others. Each of the elements can be assigned to the 'gamma' morphotype category outlined in the following section. The poorly-organised nature of this specimen implies that the elements are not in their original positions and that this assemblage is either coprolitic, as suggested by Müller and Hinz (1991) or was severely disrupted by post-mortem taphonomic processes.

The second cluster (Text-fig. 5.3G; Müller and Hinz 1991, pl. 24, fig. 26) contains only two elements. It is viewed from the posterior and the element on the right (foreground) is slightly larger than the element on the left. Both elements are of the gamma morphotype. In contrast to the former cluster, these elements are aligned parallel to one another, and are in contact along their lateral margins from the base to about three-quarters of the way up the element. The tips of the elements are not in contact, partly because of the tapering of the element towards the tip and the difference in size, and partly because each element is slightly twisted in relation to the other, towards the centre of the specimen. It is likely that these elements have not been disturbed by post-mortem processes and that they are in their original position.

A third specimen (Müller and Hinz 1991, pl. 24, fig. 25) shows a situation where two apparently discrete elements are joined together at the base, with one being found posterior to the other.

Müller and Hinz (1991, p. 110) suggested that these elements were pathologically united, and termed them 'Siamese twins'. No similar elements were recovered during the present study and it is assumed that this cluster is a rare example of a mutated form.

5.3.5 Trolmenia acies (= Proacodus acies) *(Müller and Hinz 1991, pl. 26, fig. 11)*

This fused cluster consists of three elements, all of similar size and morphology (Text-fig. 5.3D). The sharp, lateral margin of each of the elements faces towards the centre of the specimen, and all three elements possess the same degree of twisting of the cusp so that if the sharp margin is to the dextral side of the element, the cusp points towards the posterior. The cusps of the elements are radially organised pointing away from the centre of the specimen, and the tips and bases are all on a similar level, with no element significantly out of alignment. By rotating the element on the left of the specimen clockwise around the centre, it would be brought into alignment with the other two elements, and would place the three elements in an array similar to that seen in the second example of a fused cluster of *P. gallatini* (Müller and Hinz 1991, pl. 24, fig. 26; see above). It is likely that only a small amount of post-mortem disruption occurred to rotate the third element out of its natural position, and to dislodge elements one and two so that their anterior and posterior margins respectively were no longer in close association.

5.4 Discussion of fused cluster evidence

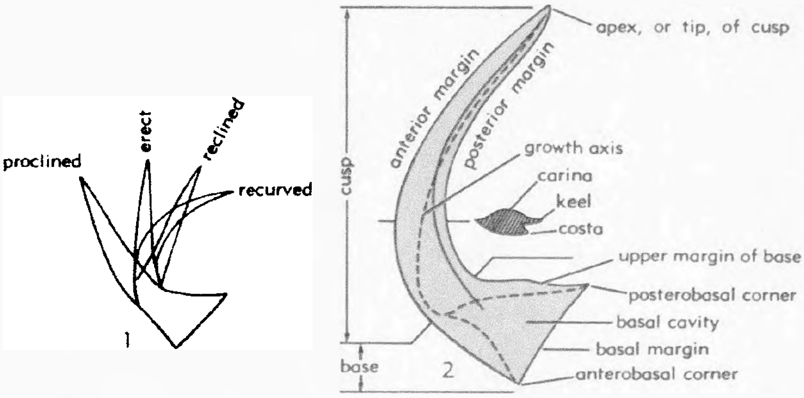
Examples of fused clusters of paraconodont elements are still exceptionally scarce and, for this reason, multielement taxonomy and descriptions of apparatuses are rarely used in paraconodont systematics. Even with the small amount of data outlined above, it is possible to suggest the type of arrangement of elements that is likely to occur at least in the morphologically 'simple' coniform paraconodonts, if not in the more complex westergaardodinids and prosagittodontids. In a comparable manner to the arrangement of elements in the protoconodonts and in the coniform euconodont *Panderodus*, it seems likely that most coniform paraconodont elements were found in bilaterally opposed arrays, in which the elements of each array were aligned approximately parallel to one another. One of the clusters of *P. gallatini* suggests that there may be a certain amount of variation in the size of the elements within an array, an observation that has previously been noted in protoconodont clusters (Müller and Nogami 1972a; Szaniawski 1982; amongst others). Coniform euconodont apparatuses however, possess elements that are morphologically differentiated, even in the stratigraphically oldest, more primitive forms and, since paraconodonts are closely related to euconodonts (Chapter 9), it seems likely that their apparatuses are more complex than those of the unrelated protoconodonts. None of the clusters of paraconodonts illustrated by Müller and Hinz (1991) represents a complete apparatus, or possesses any significant variation in the morphology of the component elements, but the range of morphological variation found in discrete element collections is large and implies that paraconodont apparatuses are probably more complex than these clusters suggest. As with the primitive euconodonts, it is likely that the apparatuses of paraconodonts will remain a subject of much speculation, pending the discovery of bedding plane assemblages or more complete fused clusters in the future.

5.5 *Current paraconodont multielement taxonomy and notation*

In their monograph of Upper Cambrian conodonts from Sweden, Müller and Hinz (1991) tended to strictly constrain their descriptions of the morphology of paraconodont elements and, as a result of this, erected a large number of new genera and species. One of the objectives of the current study was to broaden these descriptions, and to break away from the use of form taxonomy, in order to encompass different element morphologies into single paraconodont species' and, therefore, to initiate a multielement approach to systematic description of paraconodont apparatuses.

Multielement taxonomy was applied to the apparatuses of *F. furnishi* and *P. gallatini* by Hinz (1992, p. 250, text-figs 6C and 6B respectively), using specimens illustrated by Müller and Hinz (1991). Hinz had, as the junior author in the Müller and Hinz (1991) publication, considered paraconodonts to possess transition series of elements, and therefore believed that paraconodont elements could not be separated into discrete categories (excepting occasional variations in morphotype in certain species). To describe the reconstructed apparatuses of *F. furnishi* and *P. gallatini*, Hinz (1992) utilised the notation scheme of Armstrong (1990), uniting elements of *F. furnishi*, *F. curvata* and *F. gossmannae* in the *F. furnishi* apparatus of sym.p, ap, aq, sq and r elements. The *P. gallatini* apparatus also comprised sym.p, ap, aq, sq and r elements according to Hinz (1992), but these were already assigned to *P. gallatini* and the new apparatus did not contain elements from any other species. Briefly, the terms used by Hinz (1992) correspond to a curvature series, p elements being erect, q elements being slightly recurved with wider bases and r elements having very broad bases and being strongly recurved and markedly asymmetrical. The prefixes sym (s) and a refer to the symmetry of the elements (symmetrical and asymmetrical respectively). Apart from these two apparatus reconstructions, Hinz (1992) described the remainder of her paraconodont fauna using form taxonomy. Use of the Armstrong notation scheme by Hinz for the description of paraconodonts is considered to be slightly premature because, although a potential homology has now been recognised that unites at least some of the paraconodonts with the euconodonts, there is still a limited amount of data concerning the exact relationships between the two groups.

Since the Armstrong notation scheme was erected specifically for use with coniform euconodonts, a new scheme has been employed that is entirely separate to all former schemes used to describe proto-, para- or euconodont apparatuses. The new scheme is relatively simple, has no basis in any previous scheme which might imply homology with other apparatuses and is entirely based on morphological characteristics of coniform paraconodont elements. The apparatus architecture can only be speculated upon and it is therefore inappropriate to attempt to place the elements within a locational framework. Too few specimens of non-coniform paraconodonts (westergaardodinids) were recovered to attempt a rigorous apparatus reconstruction, but it is possible that these species also possess more complex apparatuses than is currently believed.



Text-figure 5.4. Diagram to show the terms used in the description of paraconodont elements. Note that they are the same as those used in the description of euconodonts. (From Sweet *in* Robison 1981, after Lindström 1954).

5.6 *New notation*

For the purposes of this study, the traditional terms have been used in relation to the orientation of the elements (Text-fig. 5.4), and the new scheme of Purnell *et al.* (2000) has not been adopted, since there is no direct evidence to support the use of the terms rostral, caudal, dorsal, ventral, adaxial or abaxial, because the apparatus architecture of paraconodonts is, as yet, unknown. The new notation takes the form of the erection of generalised element categories, or morphotypes, into which all the coniform paraconodont elements in the current study can be placed.

Unfortunately, multielement apparatuses were not found for all the paraconodont species investigated, since many elements were relatively scarce in the samples. This may be rectified with further work on more abundant material.

The new terms used are letters from the Greek alphabet, to avoid confusion with the notation schemes that are currently employed which use letters from the English alphabet to describe element morphologies and locations. Müller and Hinz (1991) have previously used the terms 'alpha' and 'beta' to refer to the different element morphotypes in *Gumella cuneata* (= *Gapparodus cuneatus*) and *Nogamiconus*, but herein the terms 'alpha', 'beta', 'gamma' and 'delta' will be used to denote specific morphological categories of elements in more than one apparatus. Brief descriptions of these categories are outlined in Text-figure 5.5.

Element Category	Description
Alpha	Erect elements, sometimes with narrowly tapering margins, usually asymmetrical. In some cases these elements are flattened either laterally or antero-posteriorly.
Beta	Symmetrical elements, usually slightly recurved.
Gamma	Asymmetrical elements, slightly recurved and often with a relatively broad base.
Delta	Strongly asymmetrical, markedly recurved elements, with an antero-posteriorly extended base.

Text-figure 5.5. Table describing the key morphological characteristics of each of the new element categories which can be applied to paraconodont apparatuses.

5.7 PARACONODONT SYSTEMATIC PALAEONTOLOGY

Phylum CHORDATA Bateson, 1886
Subphylum VERTEBRATA Linnaeus, 1758
Class CONODONTA Eichenberg, 1930; *sensu* Clark, 1981

Remarks. Following the classification of Aldridge and Smith (1993) and the phylogeny of Donoghue *et al.* (2000) the euconodonts are recognised as a group of vertebrates. Multielement apparatus reconstructions together with histological evidence presented herein (Chapter 9) indicate that the paraconodonts also share this position. Accordingly, the Paraconodontida is here included within the Conodonta. Although some protoconodonts have previously been included in the Paraconodontida by Clark (1981) in the *Treatise* volume and by Müller and Hinz (1991) in their monograph of Late Cambrian conodonts from Sweden, they are now tentatively removed to the phylum Chaetognatha because of the similarity in histology and apparatus composition and architecture that the protoconodonts and chaetognaths share (Szaniawski 1982, 1983, 1987). It is recognised that, with further investigations of the histology of a larger number of paraconodont genera and species, and possibly the use of cladistics to test relationships between them, that the Paraconodontida may prove to be a paraphyletic group. However, this is true of many euconodont orders and, therefore, the inclusion of the Paraconodontida within the Conodonta is found to be a more satisfactory and natural interim classification. This taxonomic reassessment has significant stratigraphical implications, and extends the known history of the vertebrate mineralised skeleton into the Middle Cambrian.

Subclass PARACONODONTA Nov.

Order PARACONODONTIDA Müller, 1962

Remarks. Müller (1959) originally assigned all the coniform elements in his study of Cambrian conodonts to the Family Distacodidae Ulrich and Bassler, 1925, including *Distacodus* (= *Muellerodus*), *Furnishina*, *Hertzina*, *Oneotodus* (= *Prooneotodus* or *Phakelodus*), *Proacodus*, *Sagittodontus* (= *Prosagittodontus*) and *Scandodus* (= *Furnishina*). Müller (1962) erected the new Order Paraconodontida, but none of these forms were included, *Furnishina*, *Hertzina*, *Proacodus* and *Scandodus* were left in the Distacodidae, *Sagittodontus* was considered to be of unknown family affinity, and *Oneotodus* was included in the Distacodidae as a junior synonym of

Drepanodus Pander, 1856. Of the three genera assigned to the Paraconodontida (*Problematoconites* Müller, 1959, *Pygodus* Lamont and Lindström, 1957 and *Rhombocorniculum* Walliser, 1958), only *Problematoconites* is still regarded as a paraconodont. Lindström (1970) included all coniform, bi- and tricuspidate Cambrian elements, i.e. *Furnishina*, *Hertzina* and *Proacodus*, together with *Westergaardodina*, in the Family Westergaardodinidae, and did not use the Order Paraconodontida, as established by Müller (1962) to unify these taxa.

Müller and Nogami (1971) elevated the Paraconodontida to the taxonomic rank of suborder and formalised the description to include elements which possess a higher organic content than later conodonts, a thick outer layer of organic material, initial stages of growth in which the lamellae are fully enclosed succeeded by lamellae which are open to the outer surface of the elements, no basal body or white matter, and growth lamellae that are larger and fewer in number than are typical in conodonts of similar shape and size. The suborder was divided into two families, the Furnishinidae Müller and Nogami, 1971 and the Westergaardodinidae Müller, 1959, with *Furnishina*, *Proacodus*, *Problematoconites*, *Hertzina*, *Proscandodus* (= *Furnishina*), *Prosagittodontus* and *Prooneotodus* assigned to the former and *Westergaardodina* and *Chosonodina* to the latter. *Chosonodina* is now regarded as a euconodont (Ethington and Clark 1981; Aldridge and Smith 1993).

According to the evolutionary scheme established by Bengtson (1976) elements of three informal groupings are included in the above list. Bengtson erected a three-fold division of the conodonts into proto-, para- and euconodont categories according to their mode of growth. Paraconodonts formed the intermediate stage in the evolution between protoconodont grade (basal internal growth) and euconodont grade (outer centrifugal growth) by the addition of growth lamellae on both the inner and outer parts of the basal margin (Page 1, Text-figure 1.1). It is this informal classification that has become most popular in recent years, although Bengtson's hypothesis concerning the evolutionary development of the conodonts has been cast into doubt by the discovery that euconodonts are vertebrates (see for example Sansom *et al.* 1992; Aldridge *et al.* 1993; Janvier 1995; Donoghue 1998) and protoconodonts probably represent the mineralised remains of chaetognath grasping spines (Szaniawski 1982, 1983) (Chapters 7 and 8). It is generally accepted that chordates and chaetognaths do not share a close relationship, with chordates belonging in the deuterostomes, and chaetognaths in the protostomes (Nielsen 1995; Nielsen *et al.* 1996), although some authors have suggested that there is a closer link and that chaetognaths should be placed alongside the chordates within the deuterostomes (Christoffersen and Araújo-de-Almeida 1994).

In the *Treatise* volume, Miller (*in* Robison 1981) divided the Paraconodontida into two superfamilies (Amphigeisinacea Miller and Furnishinacea Müller and Nogami 1971), with the Amphigeisinacea containing one monogeneric family, the Amphigeisinidae Miller. The Furnishinacea were divided into the Furnishinidae Müller and Nogami, 1971, and the Westergaardodinidae Müller, 1959, with two genera, *Westergaardodina* and *Chosonodina* being included in the latter. Twelve genera were assigned to the Furnishinidae by Miller (*in* Clark 1981) including the protoconodonts *Gapparodus*, *Hertzina* and *Protohertzina* and the paraconodonts *Furnishina*, *Albiconus*, *Muellerodus*, *Nogamiconus*, *Proacodus*, *Problematoconites*, *Prooneotodus*, *Prosagittodontus* and *Proscandodus* (= *Furnishina*). *Prooneotodus* Müller and Nogami, 1971, originally included both paraconodont and protoconodont species until *P. tenuis* Müller, 1959, was confirmed as a protoconodont by Bengtson (*in* Landing 1977) and was subsequently referred to the new genus *Phakelodus* by Miller (1984). Müller and Hinz (1991) followed the *Treatise* classification scheme of Miller (*in* Clark 1981) and united forms with proto- and paraconodont histology in the Order Paraconodontida, using the different styles of growth to distinguish the protoconodonts as a subset of the paraconodont order.

An and Mei (1994) suggested that three paraconodont lineages exist; *Laiwugnathus* – *Westergaardodina*, *Dolabrodus* – *Furnishina* and *Prooneotodus* (including *Prosagittodontus*). This hypothesis could not be tested on the basis of the material used in this study because of the absence of key genera (*Laiwugnathus* and *Dolabrodus*), although it may be pertinent in future paraconodont studies. As part of their hypothesis, An and Mei (1994) suggested that the protoconodont *Gapparodus* was the ancestor of the *Laiwugnathus* – *Westergaardodina* lineage, with the *Prooneotodus* lineage stemming from the protoconodont *Phakelodus*. No protoconodont predecessor was suggested for the *Dolabrodus* – *Furnishina* lineage, with the paraconodont *Dolabrodus* aff. *plicatus* being named as the oldest member of the group. Euconodonts were considered to be polyphyletic, stemming from the paraconodont genus *Prooneotodus* by various morphological changes, acquisition of white matter (*Prooneotodus* – *Teridontus*), posterior serration (*Prooneotodus* – *Proconodontus tenuiserratus*), granulation of the element surface (*Prooneotodus* – *Hirsutodontus*) and acquisition of a posterior keel (*Prooneotodus* – *Proconodontus posterocostatus*). If the phylogeny of *Proconodontus* proposed by Miller (1980) is correct (*P. tenuiserratus*, *P. posterocostatus*, *P. muelleri*, *P. serratus*), then the last of the suggestions made by An and Mei (1994) is unnecessary. From this, An and Mei (1994) proposed an evolutionary development of Cambrian conodonts very much in keeping with the ideas of Bengtson (1976), with three phases of evolution, phase 1 – protoconodont, phase 2 – paraconodont and phase 3 – euconodont.

As with the euconodonts, paraconodont genera can be grouped into families according to their apparatus composition and overall similarities in external morphology, although in the case of the paraconodonts, phylogenetic relationships between families, and often between genera within families, remain obscure largely due to the predominance of form taxonomy in the description of paraconodonts.

Family FURNISHINIDAE Müller and Nogami, 1971

Remarks. Initially erected by Müller and Nogami (1971) to include all coniform paraconodont genera, the Family Furnishinidae is modified here to contain only forms with broadly triangular basal cross-sections, two narrowly rounded to sharp antero-lateral margins and whose apparatuses possess a truly symmetrical element in addition to a suite of asymmetrical elements. Only two genera are included so far, *Furnishina* and *Prosagittodontus*, although further genera may be added in the future following further studies on different paraconodont faunas (e.g. *Dolabrodus* An, 1982). Genera originally placed in the Furnishinidae by Müller and Nogami (1971) that have been reassigned to other families include *Proacodus* (Proacodidae), *Prooneotodus* and *Problematoconites* (Prooneotodidae). *Hertzina* is now considered to be a protoconodont (Bengtson 1976) and *Proscandodus* is a junior synonym of *Furnishina.*

Genus FURNISHINA Müller, 1959

1959 *Furnishina* Müller, p. 452.
1971 *Proscandodus* Müller and Nogami, p. 18.

Type species. Furnishina furnishi Müller, 1959, p. 452, Gallatin Limestone, Port Clear Creek, Bighorn Mountains, Wyoming, USA.

Emended diagnosis. ?Quadrimembrate apparatuses of erect to recurved, coniform paraconodont elements bearing sharp or rounded antero-lateral margins bounding a well-developed anterior face. Posterior margin sharp or rounded, straight to strongly recurved. Postero-lateral flanks concave to convex, often unequally developed.

Description. Quadrimembrate apparatuses of symmetrical and asymmetrical, thin-walled, erect to recurved, coniform paraconodont elements. Posterior margin rounded to narrowly rounded or sharp, carinate in some forms, broadly to strongly curved. Flattened anterior face bounded by broadly to strongly curved, narrowly rounded, sharp or keeled antero-lateral margins. Postero-lateral flanks concave to convex with a secondary carina developed on one of the flanks in some elements. Outer surface of elements unornamented or faintly annulated. Basal cavity very deep, extending nearly to tip of element. Basal margins even to wavy, cross-section triangular to polygonal depending on the development of secondary carinae on the margins, faces and flanks of the elements. Basal opening variably flared, depending on species. Apical cross-section rounded to polygonal, again depending on the development of external ornament. Elements may be twisted or contorted laterally or antero-posteriorly, and in some cases only the tip of the element is deflected anteriorwards, away from its "natural" curvature.

Remarks. Müller (1959) originally described forms belonging to the genus *Furnishina* as single, non-symmetrical elements displaying "left" and "right" forms, with large, deep basal openings varying in shape from triangular to polygonal depending on the development of secondary carinae. He stated that the presence of a flattened anterior surface was in contrast to other conodonts within the Distacodidae, and noted similarities in overall shape and variability with the Lower Ordovician euconodont *Oneotodus variabilis* Lindström, 1954. Individual species were distinguished by Müller using the presence and number of secondary carinae, and the shape of the postero-lateral flanks, the basal cross-section and the basal opening as identifying characters.

Certain species, now referred to *Furnishina* by Müller and Hinz (1991), were originally assigned to the euconodont genus *Scandodus* Lindström, 1954, by Müller (1959). Elements of *Scandodus* described by Lindström (1954) were asymmetrical and possessed anterior and posterior keels, with the cusp of the elements being twisted laterally so that the base opened towards one side of those elements. A carina was often present on the face of the element towards which the basal cavity opened. Species assigned to *Scandodus* by Müller (1959), (*S. oelandicus*, S. *rara*, and *S. tortilis*) demonstrated this marked lateral twisting, although it has been shown by Müller and Hinz (1991) that the anterior and posterior keels, which were the characters used by Müller to include these elements in the genus *Scandodus*, are actually the antero-lateral margins in these particular elements. Following their assignment to the paraconodont genus *Proscandodus* by Müller and Nogami (1971) after histological studies of the elements, Müller and Hinz (1991) have reassigned *P. rara* and *P. tortilis* to *Furnishina* due to their correction of the original misinterpretation of the orientation of the elements. *Proscandodus oelandicus* had previously been reassigned to *Muellerodus* by Szaniawski (1971), and therefore *Proscandodus* is considered as a junior synonym of *Furnishina.*

Druce and Jones (1971) compared the genus *Furnishina* to both *Coelocerodontus* Ethington, 1959 and *Sagittodontus* Rhodes, 1953. Müller (1973) disputed the unification of *Furnishina* with *Coelocerodontus* because of histological differences between the two genera, although Landing (1983) and Müller and Hinz (1991) have questioned the placement of *Coelocerodontus* within the euconodonts, and have debated the paraconodont affinity of the genus, although Sweet (1988) assigned *Coelocerodontus* to the order Belodellida. *Sagittodontus* Rhodes, 1953 is now considered to be the M element in the euconodont prioniodontid *Icriodella* apparatus and does not bear a close relationship to *Furnishina*; the comparison of the two genera by Druce and Jones is therefore refuted.

Apart from the grouping of asymmetrical and symmetrical elements in bielemental apparatuses (Landing *et al.* 1980), or the distinction between asymmetrical, sub-symmetrical and symmetrical elements in an apparatus (An *et al.* 1983), only Hinz (1992) has attempted to provide a multielement apparatus reconstruction of the *Furnishina* apparatus. Hinz sub-divided the elements in an apparatus according to the outline of the basal opening, uniting elements of *F. furnishi*, *F. curvata* and *F. gossmannae* in the quinquemembrate apparatus *F. furnishi*, labelled according to the notation scheme of Armstrong (1990). A new scheme has been adopted for the description of *Furnishina* apparatuses to avoid confusion with schemes developed for euconodont apparatuses (see above), the elements are differentiated according to the curvature of the posterior margin, rather than the shape of the basal opening, in a similar way to the Type III apparatuses of Barnes *et al.* (1979) with erect (alpha), slightly recurved, symmetrical (beta), slightly recurved, asymmetrical (gamma) and strongly recurved (delta) element categories being erected. The reconstruction of *Furnishina furnishi* by Hinz (1992) is not supported because elements within the apparatus show differences in the cusp morphology that are considered to be great enough to allow division into two separate species, *F. furnishi* and *F. curvata* (see below).

Furnishina curvata Müller and Hinz, 1991

Plate 4, figures 1-4.

* 1991 *Furnishina curvata*, Müller and Hinz, p. 17, pl. 13, figs 15, 18, 20, 22-25; text-fig. 8I.

Holotype. Furnishina curvata, Müller and Hinz (1991), pl. 13, fig. 25, Upper Cambrian *Peltura scarabaeoides* Zone (Vc), Stenstorp-Dala, Västergötland, Sweden.

Material. 35 elements (17 alpha; 18 gamma)

Emended diagnosis. ?Quadrimembrate apparatus of small, delicate, erect or recurved, coniform paraconodont elements with sharp or narrowly rounded margins and a slender, spine-like cusp. Cross-section of the base triangular. Basal opening deep.

Description. ?Quadrimembrate apparatus of relatively small, erect to recurved, coniform paraconodont elements. Curved anterior face bounded by sharp antero-lateral margins. Posterior margin narrowly rounded or sharp from base to tip. Postero-lateral flanks flat to slightly concave. Curvature of the posterior margin marks the difference between the element types.

Alpha elements. Small, elongate, slender elements with an extended cusp and very narrowly tapering, sharp, antero-lateral margins. Posterior margin narrowly rounded, postero-lateral flanks flat. Both anterior face and posterior margin are very slightly curved, with the posterior margin extending for only half to three quarters of the element length. Basal opening triangular, but elongate. Basal opening deep. Transverse cross-section of the entire element is triangular.

Gamma elements. Small, slightly recurved, asymmetrical elements with a slender, spine-like cusp grading into a more widely flared basal region. Anterior face bounded by relatively broadly tapering, sharp antero-lateral margins, sharp posterior margin increasing in curvature from tip to base. Postero-lateral flanks concave, with one being slightly larger than the other due to a wider angle of taper between the antero-lateral and posterior margins. The tip of the element if often deflected towards the larger flank. Cross-section of the base and cusp triangular. Basal opening deep, extending to point of maximum curvature of the element.

Remarks. No symmetrical (beta) or strongly recurved (delta) elements have been observed during the course of the study, however they may be absent from the collections because of the relatively small number of elements that have been recovered. Müller and Hinz (1991, pl. 13, figs 18, 22) have illustrated more strongly recurved elements that may be included in the delta element category. In contrast with their specimens, those described here tend to possess sharp posterior margins that are not obviously rounded in their apical parts. Hinz (1992) included elements of *F. curvata* in her reconstruction of the *F. furnishi* apparatus. Elements of *F. curvata* from the studied material are markedly smaller and more fragile than those of *F. furnishi*, and for this reason they have not been united into one species. The holotype of *F. curvata* (Müller and Hinz 1991, pl. 13, fig. 25) is also smaller than the elements of *F. furnishi* and *F. gossmannae* which were united alongside *F. curvata* in the *F. furnishi* apparatus by Hinz (1992). Also in contrast to elements of *F. furnishi*, the cusp of *F. curvata* is drawn-out in a spine-like fashion, due to marked tapering of the element towards the tip, a feature that is not developed in *F. furnishi*.

Occurrence. O93-5, O93-6, VG93-17, Upper Cambrian Alum Shale, Öland and Västergötland, Sweden.

Furnishina furnishi Müller, 1959.

Plate 4, figures 5-11.

*p	1959	*Furnishina furnishi* Müller, p. 452, pl. 11, figs 5, 6, 9, 11-13, 17, ?18; pl. 12, figs 1, 6; text-fig. 6D, E (*non* pl. 11, figs 8, 14 [= *Furnishina kranzae*]).
?p	1966	*Furnishina furnishi* Müller; Nogami, p. 354, pl. 9, fig. 6 (*non* pl. 9, fig. 5 [= *Furnishina alata*]; pl. 9, fig. 7 [= *Furnishina kranzae*]).
?	1969	*Furnishina furnishi* Müller; Clark and Robison, p. 1045, text-fig. 1b.
?	1969	*Furnishina furnishi* Müller; Miller, p. 430.
	1971	*Sagittodontus furnishi* (Müller); Druce and Jones, p. 87, pl. 9, figs 1-4; text-fig. 28c, d.
	1971	*Furnishina furnishi* Müller; Müller, pl. 1, figs 9, 12, 14, 15.
	1973	*Furnishina furnishi* Müller; Müller, p. 39, pl. 1, figs 4, 5, 7, 10.
	1973	*Furnishina asymmetrica* Müller; Müller, p. 39, pl. 1, figs 6, 8, 9.
	1976	*Furnishina furnishi* Müller; Miller and Paden, p. 595, pl. 1, figs 8-12.
	1978	*Furnishina furnishi* Müller; Abaimova, p. 495, pl. 7, fig. 2.
	1979	*Furnishina furnishi* Müller; Bednarczyk, p. 427, pl. 1, figs 2, 3, 5-9, 12; pl. 3, figs 14, 20, 21.
?	1981	*Furnishina furnishi* Müller; Miller *et al.*, p. 188, text-fig. 4E, F.

1982 *Furnishina furnishi* Müller; An, p. 132, pl. 1, figs 14, 15; pl. 2, figs 3, 4, 6-9; pl. 3, fig. 13.

?p 1983 *Furnishina furnishi* Müller; An *et al.*, p. 99, pl. 2, figs 5, 7-11 (*non* pl. 2, figs 12, 15, 16 [= *Furnishina alata*]).

? 1983 *Furnishina furnishi* Müller; Landing, fig. 10M.

? 1985 *Furnishina furnishi* Müller; Wang, p. 226, pl. 3, fig. 17; pl. 5, fig. 6; pl. 9, fig. 1; pl. 10, fig. 11; pl. 12, figs 4, 5.

?p 1986 *Furnishina furnishi* Mueller; Chen and Gong, p. 145, pl. 17, figs 5, 16; pl. 18, figs 1, 19; pl. 52, figs 1, 7, 11; text-fig. 50, figs 3, 4 (*non* pl. 17, figs 4, 13 [= *Furnishina kranzae*]).

? 1986 *Furnishina furnishi* Müller; Chen, Zhang and Yu, p. 367, pl. 1, figs 11, 13, 17.

1986 *Furnishina furnishi* Müller; Jiang *et al.*, p. 242, pl. II-2, figs 12-14.

? 1987 *Furnishina furnishi* Müller; An, p. 106, pl. 1, fig. 23; pl. 3, figs 2, 5, 9, 11, 12.

1988 *Furnishina furnishi* Müller; Heredia and Bordonaro, p. 191, pl. 1, fig. 5.

? 1989 *Furnishina furnishi* Müller; Popov *et al.*, p. 143, pl. 17, figs 2-5; pl. 19, figs 8, 10, 11.

1991 *Furnishina furnishi* Müller; Müller and Hinz, p. 17, pl. 13, figs 1-7, 11, 12; text-fig. 8a.

1991 *Furnishina gossmannae*, Müller and Hinz, p. 20, pl. 13, figs 8-10, 13, 14, 16, 17, 21; text-fig. 8K.

1992 *Furnishina furnishi* Müller; Buggisch *et al.*, p. 170, pl. 1, figs 3-7.

1992 *Furnishina furnishi* Müller; Hinz, p. 251, pl. 1, fig. 7; text-fig. 6C.

1998 *Furnishina furnishi* Müller; Serpagli *et al.* p. 142, pl. 2.1.1, figs 8, 18.

Holotype. SUI 10295, Müller (1959), plate 11, figure 13, Gallatin Limestone, Port Clear Creek, Bighorn Mountains, Wyoming, USA.

Material. 157 elements from Sweden (79 alpha; 46 gamma; 1 beta; 3 delta) + 271 elements from Wyoming.

Emended diagnosis. Quadrimembrate apparatus of symmetrical and sub-symmetrical, thin-walled, erect to recurved, coniform paraconodont elements with sharp antero-lateral and posterior margins. Basal opening triangular in cross-section. Anterior face flattened, postero-lateral faces slightly concave to slightly convex, occasionally with a weak secondary carina on one postero-lateral face.

Description. Quadrimembrate apparatus of thin-walled, erect to recurved, coniform, elements. Anterior margin flattened to form a broad face, bounded laterally by sharp, carinate antero-lateral margins. Anterior face is usually straight to slightly curved from tip to base. Posterior margin sharp, more strongly curved than the anterior, with the degree of curvature distinguishing the different element types. Outer surfaces smooth.

Alpha elements. Slender, erect, elongate elements with relatively narrowly tapering antero-lateral margins. Anterior face straight, posterior margin only very slightly curved, often bent into a curve laterally. One posterior flank is strongly concave, the other is also concave, but to a lesser degree. The pointed tip of the element is laterally deflected towards the less concave side. Basal opening triangular, cross-section of element tip and base also triangular. Basal cavity very deep, extending almost to the tip of the element.

Beta elements. Symmetrical, slightly recurved elements with relatively narrowly tapering antero-lateral margins, resembling the aq elements, but lacking the development of a secondary carina on one of the postero-lateral flanks. Both flanks equally developed, slightly concave, forming a triangular cross-section of the cusp and base.

Gamma elements. Asymmetrical, slightly recurved elements with relatively narrowly tapering antero-lateral margins. Anterior face straight to slightly curved, posterior margin curved, with curvature increasing from tip to base. One posterior flank is markedly concave, the other often houses a short secondary carina extending for two-thirds of the element length. Between the posterior margin and the carina the flank is convex, over the longer distance between the carina and the antero-lateral margin the flank is flattened to slightly convex. The tip is often laterally deflected towards the carinate face. Basal cross-section triangular to weakly quadrate, depending on the presence and development of the secondary carina. Cusp cross-section triangular. Basal cavity deep, extending to just past the distal end of the secondary carina.

Delta elements. Asymmetrical, relatively short, recurved elements with broadly tapering antero-lateral margins and a flaring basal region due to the increasing curvature of the posterior margin basally. Towards the tip, the postero-lateral flanks are convex, with one being more convex than the other. The antero-lateral margin adjacent to the more convex flanks often longer that the opposing margin, emphasising the asymmetry of the elements. Cross-sections of the base and cusp are triangular, and the basal cavity is deep, extending almost to the tip of the element.

Remarks. The original description of *Furnishina furnishi* by Müller (1959) was broad, encompassing those forms of *Furnishina* with two sharp, carinate antero-lateral margins, a narrowly rounded to carinate posterior margin, and a triangular basal cross-section. In the same publication Müller described four further species of *Furnishina*, *F. asymmetrica*, *F. bicarinata*, *F. primitiva* and *F. quadrata*. Of these, *F. asymmetrica* is similar to *F. furnishi*, but distinguished from it because of its marked asymmetry and more prominent carinate margins. No strongly asymmetrical elements have been recovered during this study. *F. bicarinata* has convex postero-lateral flanks and a more inflated, almost ovate cross-section. *F. primitiva* has no sharp margins developed, and the entire outer surface is rounded but, similar to *F. furnishi*, the basal cross-section is triangular. The basal cross-section of *F. quadrata* is four-sided and clearly distinguished from *F. furnishi*.

Of the specimens of *F. furnishi* figured by Nogami (1966), one element (pl. 9, fig. 5) is referred to *F. alata* Szaniawski, 1971, because well-developed carinae are developed on the anterolateral margins, and the base is more widely flared laterally than is typical for elements of *F. furnishi*. The remaining two elements (pl. 9, figs 6, 7) are retained within *F. furnishi*. Miller (1969) stated that the specimens he recovered from the Notch Peak Limestone were basal cones that had become separated from the rest of the conodont element, but on the basis of their overall shape he assigned them to *F. furnishi*. No specimens were figured by Miller, however inspection of the collections of Prof. J F. Miller has confirmed that elements of *F. furnishi* are present. Müller (1971, 1973) stated that *F. furnishi* was the most common species of *Furnishina*, and maintained his original description of the species.

Druce and Jones (1971) included *F. furnishi* in the genus *Sagittodontus* Rhodes, 1953, because the elements possess sharp antero-lateral and posterior carinae, flattened faces and triangular cross-sections. However, *Sagittodontus* Rhodes 1953 is now known to belong in the apparatus of *Icriodella* Rhodes, 1953, an Ordovician – Silurian euconodont, and is unlikely to be closely related to the paraconodont genus *Furnishina*.

Elements of *F. asymmetrica* figured by Miller and Paden (1976) were described as having variable development of the posterior and antero-lateral carinae, typically being less pronounced that those found in the original type specimens. For this reason, Miller and Paden implied that the elements used in their study were transitional between *F. asymmetrica* and *F. furnishi*. Landing *et al.* (1980) also stated their belief that *F. furnishi* and *F. asymmetrica* were symmetrical (sub-symmetrical) and asymmetrical forms found within the same apparatus, although this idea has not been followed by other authors in subsequent work. An *et al.* (1983) divided the apparatus into three element types, symmetricus, sub-symmetricus and asymmetricus. Of these, the sub-symmetricus elements (pl. 2, figs 12, 15, 16) are tentatively reassigned to *Furnishina alata* Szaniawski, 1971, because of the presence of prominent antero-lateral carinae in the basal portion of the elements and the marked lateral extension of the basal opening. The symmetricus and the asymmetricus elements are cautiously retained in the synonymy of *F. furnishi*, although the quality of the plate makes definitive identification impossible. An *et al.* (1983) maintained the distinction between *F. furnishi* and *F. asymmetrica.*

Müller and Hinz (1991) reviewed the taxonomic classification of Cambrian conodonts from Sweden, including those species referred to *Furnishina.* Their descriptions have narrowed the scope of some of the species concepts previously found within *Furnishina*, by specifying exact characters that define each species. In the case of *F. furnishi*, the elements figured by Müller and Hinz (pl. 13, figs 1-7, 11, 12) all bear a sharp posterior margin, extending for most of the element length, antero-lateral costae extending from the base to very close to the tip of the element, a triangular basal cross-section with a basal opening that does not flare to any great degree and postero-lateral flanks that are slightly concave to slightly convex. Removed from *F. furnishi* were forms with particularly rounded posterior margins, and markedly recurved tips, which were referred instead to their new species *Furnishina kranzae* Müller and Hinz, 1991 (e.g. Müller (1959) pl. 11, figs 8, 14). Forms with a weakly-developed carina on one of the postero-lateral flanks, and a marginally quadrilateral basal cross-section, previously assigned to *Furnishina gossmannae* by Müller and Hinz (1991) are now placed in *Furnishina furnishi* (e.g. An 1987, pl. 3, fig. 2). Although not specified in the text, Hinz (1992) included elements previously assigned to *F. gossmannae* as the aq and r elements in her apparatus reconstruction of *F. furnishi* (Hinz 1992, text-fig. 6C) in addition to *F. curvata*, which was not figured however, or given a label according to her notation scheme.

Occurrence. WY96-17, WY96-18, Gallatin Formation, Bighorn Mountains, Wyoming, USA; O93-1, O93-2, O93-4, O93-5, O93-6, VG93-8, VG93-10, VG93-12, VG93-13, VG93-15, VG93-17; VG93-18, VG93-22, Upper Cambrian Alum Shale, Öland and Västergötland, Sweden.

Furnishina kranzae Müller and Hinz, 1991

Plate 4, figures 12-15.

p	1959	*Furnishina furnishi* Müller, p. 452, pl. 11, figs 8, 14 (*non* pl. 11, figs 5, 6, 9, 11-13, 17, ?18; pl. 12, figs 1, 6; text-fig. 6D, E [= *Furnishina furnishi*]).
p	1966	*Furnishina furnishi* Müller; Nogami, p. 354, pl. 9, fig. 7 (*non* pl. 9, fig. 5 [= *Furnishina alata*]; pl. 9, fig. 6 [= *Furnishina furnishi*]).
p	1986	*Furnishina furnishi* Mueller; Chen and Gong, p. 145, pl. 17, figs 4, 13 (*non* pl. 17, figs 5, 16; pl. 18, figs 1, 19; pl. 52, figs 1, 7, 11; text-fig. 50, figs 3, 4 [= *Furnishina furnishi*]).
*	1991	*Furnishina kranzae*, Müller and Hinz, p. 21, pl. 12, figs 1, 2, 6, 8, 12-14, 18; text-fig. 8B.
	1991	*Furnishina vasmerae*, Müller and Hinz, p.24, pl. 7, figs 1-4, 6-10, 12, 13, 15, 19, 21; text-fig. 8G.
	1992	*Furnishina kranzae* Müller and Hinz; Hinz, p. 251, text-fig. 8, fig. 3.
	1992	*Furnishina vasmerae* Müller and Hinz; Hinz, p. 254, pl. 1, fig. 2.
	1993	*Furnishina* cf. *kranzae* Müller and Hinz; Dong, p. 350, pl. 4, figs 1, 2, 5.
	1993	*Furnishina* cf. *vasmerae* Müller and Hinz; Dong, p. 351, pl. 4, figs 16, 17.

Holotype. *Furnishina kranzae*, Müller and Hinz (1991), pl. 12, figs 8, 13, Upper Cambrian *Olenus* Zone, Österplana, Sweden.

Material. 58 elements (34 alpha; 20 gamma; 4 delta).

Emended diagnosis. ?Quadrimembrate apparatus of erect to recurved, coniform paraconodont elements with rounded to slightly sharp posterior margins. Anterior margins rounded distally becoming sharp or keeled at the base. Basal cavity deep. Tips of elements consistently deflected towards the anterior.

Description. ?Quadrimembrate apparatus of erect to recurved, coniform, paraconodont elements. Anterior margin flattened, relatively straight to slightly curved, forming a broad face, bounded laterally at the base by sharp antero-lateral margins, which become rounded distally. Posterior margin sharp or narrowly rounded at the base, becoming rounded towards the tip, with the degree of curvature of this margin being the distinguishing feature between element types. The tip of the element is circular in cross-section and the tip is reversely curved towards the anterior of the element. Three element types have been distinguished on the basis of the degree of curvature of the cusp, symmetrical (beta) elements have not been recovered from the studied material.

Alpha elements. Asymmetrical, elongate, slender elements with very narrowly tapering antero-lateral margins. The most distal two-thirds of the long anterior face are rounded and gently curved, with the tip of the element being anteriorly deflected. At the termination of the basal opening on the posterior side, the anterior face bulges slightly, narrowing laterally towards the basal part of the bulge. Subsequently, the antero-lateral margins become sharp and taper outwards more widely, with the anterior face becoming flattened. On the shorter posterior side, the section of the element above the basal opening is rounded and curved towards the anterior, the basal opening is triangular and occupies the very antero-posteriorly compressed basal region of the element, which is usually more extended laterally than the distal parts of the element.

Gamma elements. Asymmetrical, slightly recurved elements with relatively broadly tapering antero-lateral margins. Anterior face flattened, slightly curved, bounded basally by sharp antero-lateral margins which become rounded towards the tip. Posterior margin rounded and slightly curved distally, becoming sharp and increasing in curvature towards the base. A weak secondary carina may be developed close to the posterior margin on one postero-lateral flank. Both postero-lateral flanks are convex along their entire length. Cross-section of the base triangular to slightly quadrate depending on the development of the secondary carina. Basal cavity moderately deep, extending to the point of maximum curvature.

Delta elements. Asymmetrical, strongly recurved elements with a widely flaring basal region. Anterior face flat, relatively short, bounded by narrowly tapering antero-lateral margins which are sharp at the base, becoming rounded distally. Posterior margin rounded, narrow at tip becoming increasingly wide towards the base. Postero-lateral flanks unequally developed. One bears a short indentation running close to and parallel with the antero-lateral margin, terminating at the tip of the basal cavity. In the region of the indentation, the flank is concave, becoming convex towards the posterior margin. The opposite flank bears a less marked depression and is also convex, becoming slightly concave close to the antero-lateral margin. Base flared, with basal cross-section broadly triangular to quadrate, depending on the width of the posterior margin at the base. Cusp is spine-like and deflected anteriorly, with a rounded cross-section.

Remarks. Elements previously assigned to *F. vasmerae* by Müller and Hinz (1991) have been included in the synonymy of *F. kranzae*, even though, in their original descriptions, the posterior margins of elements of *F. kranzae* are rounded and those of *F. vasmerae* are sharp or narrowly rounded. However, the deflection of the tips of the elements towards the anterior and the presence of slight keels in basal parts of the antero-lateral margins are very similar in both element types. In the studied material, elements that would have been assigned to the form taxon *F. vasmerae* are morphotypes that possess very widely flared bases and are strongly recurved (delta elements). Those that would previously have been assigned to *F. kranzae* are more elongate and less recurved (alpha and gamma elements) and so, when these morphotypes are united, they form an apparatuses similar to other species of *Furnishina*. No truly symmetrical elements have been recovered in the studied material, or observed in the published literature, and so the assignment of a quadrimembrate apparatus remains tentative until more material is investigated.

Occurrence. O93-6, VG93-7, VG93-16; VG93-18, Upper Cambrian Alum Shale, Öland and Västergötland, Sweden.

Furnishina primitiva Müller, 1959

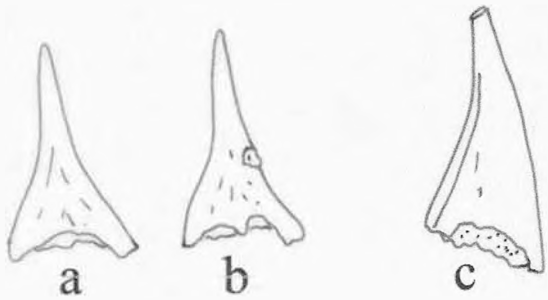
(Text-figure 5.6a, b, c)

*	1959	*Furnishina primitiva* Müller, p. 453, pl. 11, figs 1-4.
	1959	*Sagittodontus* aff. *dunderbergiae* Müller, p. 461, pl. 14, fig. 8.
	1971	*Furnishina primitiva* Müller; Müller, p. 8, pl. 1, fig. 11.
non	1978	*Proconodontus primitivus* (Müller); Fåhræus and Nowlan, p. 453, pl. 1, fig. 3 [? = *Prooneotodus gallatini*].
?	1982	*Furnishina primitiva* Müller; An, p. 133, pl. 3, figs 11, 12.
?	1983	*Furnishina* cf. *primitiva* Müller; An *et al.*, p. 101, pl. 2, fig. 6; text-fig. 9, fig. 23.
p	1986	*Furnishina primitiva* Müller; Chen and Gong, p. 146, pl. 17, figs 7, 11, 18; pl. 18, fig. 11; text-fig. 5.1, figs 1-3 (*non* pl. 20, fig. 8; text-fig 5.1, fig. 4 [? = *Prosagittodontus dunderbergiae*]).
?	1987	*Furnishina primitiva* Müller; An, p. 106, pl. 3, figs 3, 10.
	1991	*Furnishina primitiva* Müller; Müller and Hinz, p. 23, pl. 12, figs 3, 4, 7, 9, 10, 15-17, 19; text-fig. 8C, D.
	1991	*Prosagittodontus minimus* Müller and Hinz, p. 38, pl. 26, figs 10, 12-24; text-fig. 14a.
	1992	*Furnishina primitiva* Müller; Hinz, p. 252, pl. 1, fig. 3.
	1992	*Prosagittodontus minimus* Müller and Hinz; Hinz, p. 260, pl. 1, fig. 8.

Holotype. HUB ct 216, Müller (1959), p. 453, pl. 11, fig. 4, Upper Cambrian Zone 5d, Kuhbier, Prignitz.

Material. 21 elements (11 beta; 10 gamma)

Emended diagnosis. ?Quadrimembrate apparatus of erect to recurved, coniform paraconodont elements with rounded or sharp antero-lateral and posterior margins. Antero-lateral margins relatively widely tapering. Anterior face and postero-lateral flanks flat to concave.



Text-figure 5.6. Line drawings of elements of *Furnishina primitiva*, a, b) beta element, c) gamma element. X100.

Description. ?Quadrimembrate apparatus of erect to recurved, coniform paraconodont elements. Anterior margin flat or slightly concave in central parts, straight or gently curved, bounded laterally by rounded or narrowly rounded antero-lateral margins. Posterior margin rounded to broadly rounded, curved. Postero-lateral flanks concave. Cusp slender and spine-like. Outer surface smooth or faintly annulated.

Beta elements. Symmetrical elements with a concave or flat anterior face and very broadly tapering, narrowly rounded antero-lateral margins. These margins are curved, with the point of maximum curvature coinciding with the base of the spine-like cusp and the termination of the basal cavity. Posterior margin rounded and gently curved from base to tip. Postero-lateral flanks equally developed, concave. Basal cross-section triangular, antero-posteriorly compressed, with all margins concave. Cusp cross-section rounded.

Gamma elements. Asymmetrical elements with less widely tapering antero-lateral margins. Anterior face flattened, straight. Posterior margin narrowly rounded, curved, with curvature increasing to the base. One postero-lateral flank is concave and larger than the opposing, more strongly concave flank. The element tip is laterally deflected towards the more concave flank. Basal cross-section triangular, with concave posterior margins and a flattened anterior margin. The cross-section of the slender, spine-like cusp is rounded.

Remarks. The apparatus of *F. primitiva* is possibly quadrimembrate, in line with other species of the genus, however, alpha and delta elements have not been recognised in this study, although one element figured by Müller and Hinz (1991, pl. 12, fig. 4) does appear to be markedly recurved and is a likely candidate for a delta element. The recovery of further material may serve to solve this problem. Elements previously assigned to *Prosagittodontus minimus* have been included in the apparatus of *F. primitiva* because of similarities in the outer surface ornament, rounded margins, slender, spine-like cusp, broadly tapering antero-lateral margins in the base and co-occurrence in the studies material. Müller and Hinz (1991) found *F. primitiva* in Zones 3 and 5 of the Upper Cambrian Alum Shale, but *P. minimus* was not found until Zone 5. No detailed sample information was provided by Müller and Hinz, and therefore the possibility of the absence of the latter species from older samples due to relatively low element numbers cannot be excluded

Müller (1959) distinguished elements of *F. primitiva* from other species of *Furnishina* because of the broadly triangular basal cross-section of the elements, which have rounded rather than costate antero-lateral and posterior margins. A single element figured by Fåhræus and Nowlan (1978) was described as *Proconodontus primitivus* (Müller), with the elements of *F. primitiva* described by Müller (1959) included in their synonymy. The figured element, and the descriptions of similar elements in their collections do not confirm that they should be included in *F. primitiva,* and they are tentatively referred to *Prooneotodus gallatini* on the basis that the elements are markedly laterally compressed and have thin walls and elliptical cross-sections.

Müller and Hinz (1991) erected the new species *P. minimus* to encompass those forms of *Prosagittodontus* where the deep indentations of the basal margins and hence, a well-developed central lobe, are absent. In addition, the tip of the element is extended to form a spine-like cusp, with the flanks of the basal part of the element flaring widely and being more inflated than the flattened lateral flanks that are present on *P. dahlmani.* An element of *S.* aff. *dunderbergiae* figured by Müller (1959, pl. 14, fig. 8) was reassigned to *P. minimus* by Müller and Hinz (1991) because of its very weakly-developed central lobe, and relatively strong curvature of the tip of the element towards the posterior side. Elements previously assigned to *P. minimus* are removed to *F. primitiva* because of their similar overall morphology and occurrence.

Occurrence. O93-1, O93-2, O93-5, VG93-10, VG93-12, Upper Cambrian Alum Shale, Öland and Västergötland, Sweden.

Furnishina tortilis (Müller, 1959)

Plate 4, figures 16-21.

*	1959	*Scandodus tortilis* Müller, p. 264, pl. 12, figs 7, 8, 10.
	1971	*Scandodus tortilis* Müller; Müller, p. 11, pl. 2, fig. 1
?	1979	*Scandodus tortilis* Müller; Bednarczyk, p. 434, pl. 4, fig. 15.
	1981	*Proscandodus tortilis* (Müller); Miller *in* Robison, p. W114, text-fig. 64.5.
	1991	*Furnishina tortilis* (Müller); Müller and Hinz, p. 24, pl. 14, figs 2-19; text-fig. 8N, O.
	1992	*Furnishina tortilis* (Müller); Hinz, p. 254, pl. 1, fig. 11.

Holotype. SMF 10338, Müller (1959), pl. 12, fig. 8, *Elvinia* Zone, *Irvingella major* Subzone, Eureka District, Nevada, USA.

Material. 29 elements (25 alpha; 4 gamma).

Emended diagnosis. ?Quadrimembrate apparatus of strongly laterally contorted, coniform paraconodont elements with sharp to keeled antero-lateral margins and a sharp posterior margin.

Description. ?Quadrimembrate apparatus of erect to recurved, coniform paraconodont elements, characterised by the strong lateral torsion of the elements. Anterior face bounded by sharp, carinate antero-lateral margins, one of which becomes rounded distally. The tip of the element is laterally deflected towards the side with the shorter carinate margin. Face curved from base to tip, broadly rounded and convex. Posterior margin sharp, curved, with the degree of curvature distinguishing the different element types. Postero-lateral flanks concave and twisted, with the tip of the element deflected towards the more concave flank.

Alpha elements. Asymmetrical, erect, elongate, slender, coniform elements. Anterior face flattened and twisted to one side. Posterior margin sharp, but straight, so that the element is compressed antero-posteriorly. The antero-lateral margins are sharp and carinate. Basal cavity shallow, basal opening diamond-shaped, due to the extension of the anterior face below the termination of the posterior margin. Cross-sections of the base and the cusp of the element are triangular.

Gamma elements. Asymmetrical, slightly recurved, coniform elements. Anterior face flattened and laterally twisted, bounded by carinate antero-lateral margins. Posterior margin sharp, with curvature increasing to the base, causing the basal opening to flare posteriorly. Postero-basal margin arched. Posterior flanks convex close to the posterior margin, becoming concave towards the anterior margin. Element twisted, with the tip deflected towards the more strongly concave lateral flank. Basal opening deep, extending past the point of maximum curvature. Cross-section of the base broadly triangular, with convex postero-basal margins. Cross-section of cusp triangular.

Remarks. A quadrimembrate apparatus is only tentatively assigned to *F. tortilis* because no symmetrical (beta) or recurved (delta) elements have been recovered. However, elements of *F. tortilis* with widely flaring bases have been illustrated by Müller and Hinz (1991, pl. 14, figs 14, 16-19) and may constitute the delta elements of the apparatus.

Müller (1959) originally assigned this species to the euconodont genus *Scandodus* Lindström, 1954, due to the strongly twisted nature of the element, with the cusp and base not always aligned in the same plane, giving the appearance that the base opens towards one side of the element as opposed to towards the posterior. However, a strong similarity between some elements of *S. tortilis* and *F. furnishi* was noted by Müller (1959). The element of *S. tortilis* figured by Bednarczyk (1979, pl. 4, fig. 15) is only tentatively included in the synonymy, due to the element not appearing to show any great degree of torsion, although the quality of the illustration is relatively poor.

Müller and Nogami (1971) investigated the histology of various conodont elements, and included *S. tortilis* as the type species of the new genus *Proscandodus*. Müller and Hinz (1991) reassigned *P. tortilis* to *Furnishina* because of its tri-costate shape, and recognised that the sharp costate edges that were originally described as anterior and posterior margins by Müller (1959), are in fact antero-lateral margins, and that the base must therefore open in a posterior as opposed to lateral, direction. The same variety of element morphotypes noted and illustrated by Müller and Hinz (1991) has not been recovered during the course of this study, although their elements still fall into the three broad categories that are proposed.

Occurrence. VG93-7, Upper Cambrian Alum Shale, Västergötland, Sweden.

Genus PROSAGITTODONTUS Müller and Nogami, 1971

1971 *Prosagittodontus*, Müller and Nogami, p. 17.

Type species. *Sagittodontus dahlmani* Müller, 1959, p. 460, Upper Cambrian Zone 5d, Grönhogen, Öland, Sweden.

Emended diagnosis. Trimembrate apparatus of laterally symmetrical, sub-symmetrical, and markedly asymmetrical paraconodont elements bearing indentations of variable depth on the postero-basal margin. These characteristic indentations cause the elements to possess three basally directed projections (one median and two lateral).

Remarks. Paraconodont elements included in this genus are erect, with characteristic indentations of the basal margin on the posterior of the element. The indentations can be deep or shallow and are often unequally developed. The tips of the asymmetrical elements are laterally deflected towards the more deeply incised margin.

The type species of *Prosagittodontus* (*P. dahlmani*) was originally assigned to the Ordovician genus *Sagittodontus* Rhodes, 1953, by Müller (1959) on account of the triangular cross-section and the irregular nature of the posterior margin. However, as mentioned above, *Sagittodontus* is now considered to be the M element in the apparatus of the Ordovician prioniodontid *Icriodella*, and so a close relationship with the Cambrian genus *Prosagittodontus* may be ruled out. Müller and Nogami (1971) investigated the histology of *S. dahlmani* and found it to have a mode of growth similar to other elements assigned to the order Paraconodontida, and added the prefix 'Pro' to the generic name to note this difference in growth style and earlier stratigraphical appearance. The species *P. minimus* Müller and Hinz, 1991, is included in the apparatus of *Furnishina primitiva* because of the rounded lateral margins, and the lack of distinct indentations of the postero-basal margin.

Although only 10 elements of one species of the genus (*P. dahlmani*) have been recovered in this study, it is thought that a trimembrate apparatus can be inferred for that species, and hence the genus. Just as with the additional paraconodont apparatuses described, the apparatus of *Prosagittodontus* can be divided according to element curvature, though distinct variations in the bilateral symmetry of the elements are more immediately obvious. The genus is included in the Furnishinidae because the elements possess sharp margins and have a generally triangular cross-section.

Prosagittodontus dahlmani (Müller, 1959).

Plate 5, figures 7-9.

*	1959	*Sagittodontus dahlmani* Müller, p. 460, pl. 14, figs 5, 7, 10.
non	1971	*Sagittodontus dahlmani* Müller; Druce and Jones, p. 87, pl. 8, figs 6-9; text-fig. 28a, b [= *Prosagittodontus minimus*].
	1971	*Prosagittodontus dahlmani* (Müller); Müller and Nogami, p.17.
	1978	*Prosagittodontus dahlmani* (Müller); Abaimova, p. 501, pl. 8, figs 3, 5, 7.
?	1982	*Prosagittodontus dahlmani* (Müller); An, p. 147, pl. 5, fig. 6.
?	1985	*Prosagittodontus dahlmani* (Müller); Wang, . 237, pl. 3, fig. 16; pl. 5, figs 19-21; pl. 9, figs 4, 13.
	1986	*Prosagittodontus dahlmani* (Müller); Chen and Gong, p. 168, pl. 20, figs 1, 2, 4, 10, 15; text-fig. 65, figs 5, 6, 7.
?	1986	*Prosagittodontus dahlmani* (Müller); Chen, Zhang and Yu, p. 369, pl. 2, figs 14, 15.
	1987	*Prosagittodontus dahlmani* (Müller); An, p. 113, pl. 3, figs 23, 24.
	1991	*Prosagittodontus dahlmani* (Müller); Müller and Hinz, p. 37, pl. 25, figs 1-22; text-fig. 14B.
	1992	*Prosagittodontus dahlmani* (Müller); Hinz, p. 258, pl. 1, fig. 9.

Holotype. SMF 10354, Müller (1959), pl. 14, fig. 10, Upper Cambrian Zone 5d, Grönhögen, Öland, Sweden.

Material. 10 elements. 1 beta, 7 gamma, 2 delta.

Emended diagnosis. Trimembrate apparatus of symmetrical (beta), sub-symmetrical (gamma) and asymmetrical (delta) paraconodont elements. Indentations of the postero-basal margins are deep, lateral margins are keeled. Beta and gamma elements are markedly antero-posteriorly compressed but delta elements may be slightly inflated. A longitudinal carina is present in the centre of the median projection in all element types.

Description. Trimembrate apparatus of symmetrical, sub-symmetrical and asymmetrical trilobate elements. Anterior face is flat or slightly curved, antero-lateral margins keeled. The sharp posterior margin bears a longitudinal carina in the centre of the median projection, with deep indentations of the basal margin separating this central lobe from the two lateral ones. The lateral lobes are usually longer than the median. The anterior face bears no central lobe due to the presence of a single indentation of the basal margin. Three element types are distinguished on the basis of the depth of the indentations of the basal margin, lateral curvature, and antero-posterior inflation.

Beta elements. Bilaterally symmetrical, antero-posteriorly compressed elements in which both indentations of the basal margin are equally developed. Antero-lateral margins straight, meeting at an angle at the tip. No lateral curvature.

Gamma elements. Sub-symmetrical, antero-posteriorly compressed elements in which on of the indentations of the basal margin is slightly deeper than the other. The elements curve towards the side with the shallower indentation, so that the lateral margin closest to the deeper incision is convex, and the one closer to the shallower incision is concave. Left and right forms can be distinguished.

Delta elements. Strongly asymmetrical elements in which one basal indentation is markedly deeper than the other. In contrast to the gamma elements, delta elements curve laterally towards the side bearing the deepest indentation, so that the margin closest to the deepest incision is concave, and that closest to the shallower incision is convex. In comparison to the beta and gamma elements, delta elements show a greater degree of antero-posterior inflation, and the posterior margin is more strongly curved. Left and right forms present.

Remarks. Müller (1959) assigned this species to the genus *Sagittodontus* Rhodes, 1953 because of the triangular cross-section of the elements, the presence of three flat faces, the irregular basal margin and the very deep basal cavity. However, Müller and Nogami (1971) examined the histology of *P. dahlmani* and found it to have a growth style typical of a paraconodont. *P. dahlmani* was then used by Müller and Nogami as the type species of the new paraconodont genus *Prosagittodontus*. Druce and Jones (1971) considered the specimens that they referred to

P. dahlmani to be juveniles, and stated that *P. dahlmani* and *P. dunderbergiae* should be synonymised as adult and juvenile forms of the same species. Müller and Hinz (1991) noted that similarly sized elements of the two species have markedly different outlines, and co-occurrence in samples is relatively rare, and concluded that the ontogenetic relationship between *P. dahlmani* and *P. dunderbergiae*, suggested by Druce and Jones, is unlikely to exist. The elements figured by Druce and Jones are not included in the synonymy and are referred instead to *F. primitiva*. A single broken element figured by An (1982, pl. 5, fig. 6) is questioned in the synonymy, as its tip is rather extended apically similar to *F. primitiva*, although the lateral margins are sharp which is more typical of *P. dahlmani*. The specimens figured by Wang (1985) appear to be broken, and lack the distinctive indentations of the basal margin that diagnose *P. dahlmani*. In addition, the quality of the illustrations restricts conclusive identification of the specimens, and so it is only with caution that they are placed in the above synonymy. Müller and Hinz (1991) recognised two varieties of *P. dahlmani*, sub-symmetrical elements with well-defined lateral lobes, and asymmetrical elements which are laterally deflected so that the apex tends towards one of the flanks. However, examination of their illustrations (Müller and Hinz 1991, pl. 25) suggests that a further, symmetrical, element (pl. 25, figs 3, 5 8) could also have been added to this, whereby the posterior indentations of the basal margin are equally extended.

Occurrence. VG93-10, VG93-13, VG93-14, VG93-16, Upper Cambrian Alum Shale, Västergötland, Sweden.

Family PROACODIDAE nov.

Type genus. Proacodus Müller (1959), p. 458.

Diagnosis. Coniform paraconodont elements with a single, sharp or carinate lateral margin which is either unornamented or serrated.

Remarks. Coniform, paraconodont genera characterised by elements with a single sharp lateral margin, but an overall rounded nature are included in the new Family Proacodidae. *Proacodus* was originally assigned to the Furnishinidae by Müller and Nogami (1971). *Serratocambria* was first described by Müller and Hinz (1991), and has not been assigned to any suprageneric grouping outside of the Order Paraconodontida. The apparatuses of the genera assigned to the Proacodidae remain poorly understood, but are known to consist of at least one category of asymmetrical element that can be divided into sinistral and dextral morphotypes.

Genus PROACODUS Müller, 1959

1959 *Proacodus*, Müller, p. 458.
1991 *Trolmenia*, Müller and Hinz, p. 39.

Type species. Proacodus obliquus Müller, 1959, p 458, Upper Cambrian Zone 5d, Khubier in der Prignitz, Mark Brandenburg.

Description. Asymmetrical, proclined paraconodont elements. Posterior margin broadly rounded, straight or gently curved towards the posterior. Anterior margin also broadly rounded and gently curved. Tip pointed, occasionally laterally deflected, or uplifted towards the anterior. Lateral margins uneven, one extended away from the cusp of the element, sharp, opposite margin short, rounded, usually straight or slightly curved. In some forms, the extended margin bears a lamina which continues laterally from the limit of the basal cavity. In others, the basal cavity continues to the lateral margin of the element and may flare slightly. Length of the extended lateral margin is variable between species. Basal cavity deep, extending to point of maximum curvature of the element, single tip situated below the tip of the element. Margins of basal cavity run parallel to the margins of the element. Cusp cross-section rounded, cross-section of base tear-shaped to ovate. Outer surfaces of the elements unornamented or faintly annulated.

Remarks. Müller (1959) compared *Proacodus* to the genus *Acodus*, on the basis that elements belonging to *Acodus* are also symmetrical and possess a single carina, but have sharp anterior and posterior margins. However, in addition to *Acodus* being a euconodont, its lateral margin never becomes as markedly extended as that of *Proacodus* and any similarity in overall shape is likely to be due to evolutionary convergence. An (1982) included a species with a single drawn out lateral margin (*P. pulcherus*) in the genus *Muellerodus* Miller, however, the specimens bear a single lateral costa, but would need a second costa on the opposite lateral face in order to fit the diagnostic requirements of *Muellerodus*. Müller and Hinz (1991) noted this incorrect assignment, and removed *M. pulcherus* to *Proacodus*. *Trolmenia acies* Müller and Hinz 1991 is included in the genus *Proacodus* by the alteration of the orientation in which the elements are usually considered.

Proacodus acies is limited to Zone V of the Upper Cambrian Alum Shale (co-occurrence data from Müller and Hinz 1991), whereas the first appearances of *P. obliquus* and *P. pulcherus* are in Zones 1 and 2 respectively, with both species continuing through to the end of Zone 5. It is therefore unlikely that the three forms should be included in one apparatus.

Proacodus acies (Müller and Hinz 1991)

Plate 5, figures 1, 2.

* 1991 *Trolmenia acies* Müller and Hinz, p. 39, pl. 26, figs 1-9, 11; text-fig. 16A-C.
1992 *Trolmenia acies* Müller and Hinz; Hinz, p. 260, text-fig. 8, fig. 7.

Holotype. UB 1219, Müller and Hinz (1991), pl. 26, figs 4, 9, *Peltura scarabaeoides* Zone (Vc), Ödegården, Västergötland, Sweden.

Material. 14 elements.

Diagnosis. Proclined, coniform, strongly antero-posteriorly compressed paraconodont elements in which one lateral margin is keeled towards the base and slightly extended in relation to the other, which is rounded and not drawn out.

Description. Proclined, antero-posteriorly compressed, coniform elements. Anterior face broadly rounded and gently curved, posterior face also slightly curved and rounded. One lateral margin is curved and convex, slightly extended laterally bearing a sharp keel in basal parts. The opposite lateral margin is more strongly curved, concave and narrowly rounded, not keeled. Cusp cross-section rounded. Basal cross-section ovate, stretched laterally and drawn out into a sharp point on the more extended lateral margin. Basal cavity deep, extending to the point of maximum curvature. Outer surface smooth or faintly annulated.

Remarks. Müller and Hinz (1991) first described these laterally compressed, evenly curved paraconodonts, and compared them to both the euconodont genus *Eoconodontus* and the paraconodont genus *Prooneotodus*. A close relationship with *Eoconodontus* is disputed because *P. acies* (= *T. acies*) demonstrates paraconodont growth whereas *Eoconodontus* is a euconodont and in addition, *P. acies* does not appear to show an equivalent range of element morphologies to the known apparatus of *Eoconodontus*. Müller and Hinz excluded the possibility of a close relationship between *P. acies* and *Prooneotodus gallatini* because of the presence of a posterior keel in the former. *T. acies* is now included in the genus *Proacodus* by the alteration of the traditional orientation of the elements, with the posterior and anterior margins becoming lateral and the lateral faces becoming the anterior and posterior faces. The two other known species of *Proacodus*, *P. obliquus* and *P. pulcherus*, also possess a single, keeled lateral margin, with the opposing margin being rounded and not laterally extended. Slight curvature of the element tip towards the posterior is common to all three species of the genus.

Occurrence. O93-1, O93-2, VG93-10, VG93-12, Upper Cambrian Alum Shale, Öland and Västergötland, Sweden.

Proacodus obliquus Müller, 1959

Plate 5, figures 4, 5.

*p 1959 *Proacodus obliquus* Müller, p. 458, pl. 13, figs 1, 4 (*non* pl. 13, fig. 2 [= *P. pulcherus*]).

1971 *Proacodus obliquus* Müller; Müller, p. 11, pl. 2, fig. 2.

non 1979 *Proacodus obliquus* Müller; Bednarczyk, p. 433, pl. 1, figs 11, 14.

1981 *Proacodus obliquus* Müller; Miller *in* Robison, p. W112, text-fig. 64, fig. 4

1991 *Proacodus obliquus* Müller; Müller and Hinz, p. 34, pl. 22, figs 12-23; text-fig. 13C.

1992 *Proacodus obliquus* Müller; Hinz, p. 256, pl. 1, fig. 16.

Holotype. HUB ct 224, Müller (1959), pl. 13, fig. 4, Upper Cambrian Zone 5d, Kubier in der Prignitz.

Material. 1 element.

Diagnosis and description. See Müller (1959) p. 458-459.

Remarks. Müller (1959) erected this species to include all coniform elements with long, lateral extensions of the base, and commented that the length of the extension was an intraspecific variable. Anterior and posterior faces were rounded with a large, deep basal cavity. A carina was present along the extended lateral margin. Bednarczyk (1979) illustrated one element which he assigned to *P. obliquus* (pl. 1, figs 11, 14). The quality of the illustrations is relatively poor, but Bednarczyk (1979, p. 433) did note that this specimen differed from the type material by having a larger cusp, a flat right-lateral surface and a wider base with a more prominent costa. In the type material of Müller (1959) the lateral extensions are antero-posteriorly compressed, and it is therefore unlikely that the specimen illustrated by Bednarczyk should be referred to *P. obliquus*. The element figured by Bednarczyk (1979) bears a striking resemblance to an element of *Furnishina lingulata* figured by An *et al.* (1983, pl. 2, figs 17, 18), and it is likely that it should be included therein.

Müller and Hinz (1991) formalised the distinction between elements of *P. obliquus* with fully extended bases and *P. pulcherus* in which the bases terminate in a thin lamina and are not so markedly laterally extended. They also compared *P. obliquus* to *Serratocambria minuta* in relation to the similarity in the gross morphology of both species. Denticles are absent from the former, and no examples of a transitional form between the two species has been found.

Occurrence. O93-6, Upper Cambrian Alum Shale, Öland, Sweden.

Proacodus pulcherus (An, 1982)

Plate 5, figure 3.

p 1959 *Proacodus obliquus* Müller, p. 458, pl. 13, fig. 2 (*non* pl. 13, figs 1, 4 [= *P. obliquus*]).

* 1982 *Muellerodus pulcherus* An, p. 139, pl. 9, figs 13, 15; pl. 10, figs 12, 14.

1991 *Proacodus pulcherus* (An); Müller and Hinz, p. 34, pl. 22, figs 3-5, 7-11; text-fig. 13A, B.

1992 *Proacodus pulcherus* (An); Hinz, p. 256, pl. 1, fig. 14.

Holotype. PUG 8120, An (1982), pl. 9, fig. 13, Upper Cambrian Changshan Formation, Fuzhouwan, Fuxian, Liaoning, China.

Material. 9 elements.

Diagnosis. See diagnosis of *Muellerodus pulcherus* in An (1982), p. 139.

Description. Coniform, erect paraconodont elements. Anterior face convex, broadly rounded and curved. Posterior face concave, broadly rounded and curved. Tip of the element usually laterally deflected towards the opposite side to the extended lateral margin, and slightly recurved towards the posterior. One lateral margin is rounded and curved from tip to base, opposite margin is sharp and moderately laterally extended, and may continue as a sharp lamina in the parts of the element furthest from the cusp. Basal region below cusp is inflated, rounded and convex on both anterior and posterior margins. Below the lateral extension, the element becomes antero-posteriorly compressed, with the anterior face being convex and the posterior being concave. The basal cavity is deepest beneath the tip of the element and continues laterally to terminate just prior to the part of the lateral margin that extends as a sharp lamina. Basal cross-section tear-shaped, cusp cross-section ovate.

Remarks. P. pulcherus differs from *P. obliquus* in the length of the lateral extension of the base, and the degree to which the basal opening flares at the lateral margin of the extended base. In *P. pulcherus* the base is less markedly extended than in *P. obliquus*, and the basal opening terminates before the most lateral parts of the base, which extends as a thin lamina. An (1982) originally included *P. pulcherus* in the genus *Muellerodus* however, it was noted by Müller and Hinz (1991) that *Muellerodus* possesses a lateral costa on both sides of the element, as opposed to on a single side, and there the description of *P. pulcherus* by An (1982) falls outside of the diagnostic constraints of *Muellerodus*. A single element of *P. obliquus* figured by Müller (1959, pl. 13, fig. 2) is removed to *P. pulcherus* because the lateral extension of the base is far shorter than expected in *P. obliquus* and because the termination of the lateral extension is a sharp costa, not a rounded edge.

Occurrence. O93-1, O93-2, VG93-10, VG93-12, VG93-13, VG93-15, Upper Cambrian Alum Shale, Öland and Västergötland, Sweden.

Genus SERRATOCAMBRIA Müller and Hinz, 1991

1991 *Serratocambria*, Müller and Hinz, p. 38.

Type species. *Serratocambria minuta* Müller and Hinz, 1991, p. 38, Upper Cambrian Zone 5c (*Peltura scarabaeoides* Zone), Ödegården, Sweden.

Remarks. As noted by Müller and Hinz (1991) this genus bears a remarkable resemblance to *Proacodus* in overall form, with rounded anterior and posterior margins and an extended lateral margin to one side with a flattened to rounded margin on the other. The striking difference between the two genera is the presence of discrete denticles along the extended lateral margin of *S. minuta*, which increase in size away from the cusp. Denticles have not been observed in any *Proacodus* element yet described. The basal cavity is also far shallower in *Serratocambria* than that observed in *Proacodus*. The difference in depth of the basal cavity, and the presence of denticles along the lateral margin suggest that the generic separation between *Proacodus* and *Serratocambria* should remain. In addition the complex growth of *Serratocambria* elucidated by Müller and Hinz-Schallreuter (1998, text-figs 9, 10) in comparison to the relatively simple growth of *Proacodus* (Müller and Hinz-Schallreuter 1998, text-fig. 8, fig. 3) demonstrates that the two forms are unlikely to be found in the same apparatus.

Serratocambria minuta Müller and Hinz, 1991

Plate 5, figure 6.

* 1991 *Serratocambria minuta* Müller and Hinz, p. 38, pl. 27, figs 1-17; text-fig. 15A, B.

1992 *Serratocambria minuta* Müller and Hinz; Hinz, p. 260, pl. 3, fig. 2

Holotype. UB1307, Müller and Hinz (1991), pl. 27, figs 10, 11, *Peltura scarabaeoides* Zone (Vc), Ödegården, Västergotland, Sweden.

Material. 1 element.

Diagnosis and description. See Müller and Hinz (1991), p. 39.

Remarks. An and Mei (1994) have illustrated elements of a new species of *Serratocambria* (*S. dacryoidea*) in which the denticles on the posterior margin are narrow and peg-like, unlike the broad denticles in *S. minuta*. In addition, the denticles on the lateral margins of elements of *S. minuta* are deflected laterally in the direction of the extended margin, whereas the denticles in *S. dacryoidea* are more upright.

Occurrence. O93-6, Upper Cambrian Alum Shale, Öland, Sweden.

Family PROONEOTODIDAE nov.

Type genus. *Prooneotodus* Müller and Nogami (1971), p. 17.

Remarks. The new Family Prooneotodidae is erected to included coniform paraconodont genera characterised by elements that lack sharp margins and keels, but may have one or more costae developed on the lateral faces, and whose apparatuses are subdivided according to element curvature. Three genera are included in this family, *Muellerodus*, *Problematoconites* and *Prooneotodus*, of which the latter two genera were originally assigned to the Furnishinidae by Müller and Nogami (1971). *Muellerodus* was added to the Furnishinidae by Miller (*in* Robison 1981). The apparatus of *Problematoconites* remains poorly understood, but the similarity in external morphology with *Prooneotodus* suggests that the two genera are more closely related to each other than to any other paraconodont genera. In comparison to forms from the Furnishinidae, *Muellerodus* does not possess sharp antero-lateral margins, or a triangular cross-section, and so is unlikely to be closely related. Members of the Proacodidae possess a single, laterally extended keeled margin, which is lacking in *Muellerodus*, and there are no morphological similarities between *Muellerodus* and any form from the Westergaardodinidae. So, therefore, *Muellerodus* is assigned (albeit temporarily) to this family, even though the development of secondary carinae on the lateral margins of the elements remains an obvious difference between it and the other members of the Prooneotodidae.

Genus MUELLERODUS Miller, 1980

non 1965 *Muellerina* Bassiouni, p. 509-510. [= an ostracode].
1971 *Muellerina* Szaniawski, p. 407.
1980 *Muellerodus* Miller, p. 27.

Type species. *Distacodus*(?) *cambricus* Müller, 1959, p. 450, Upper Cambrian Zone 1, Gudhem, Västergotland, Sweden.

Description. Thin-walled, recurved paraconodont elements. Posterior margin broadly rounded, curved to strongly curved from base to tip. Tip may be slightly bent laterally and is usually recurved towards the anterior, forming a sigmoidally shaped cusp. Anterior margin rounded, gently and evenly curved from tip to base. Both lateral faces bear a costa, extending from near the tip to the base, becoming sharper and more pronounced towards the basal margin. Positions of the costae vary between species, and are situated centrally on the face in *M. cambricus*, posteriorly in *M. subsymmetricus* and anteriorly in *M. oelandicus*. Outer surface of the elements unornamented apart from the lateral costae. Basal cavity deep to very deep, always reaching the point of maximum curvature of the cusp. Basal cross-section rounded, ovate or with an uneven concavo-convex posterior margin, due to a depression of the lateral face between the costa and the posterior margin of the element. Cross-section of the cusp is round. Lateral twisting of the cusp and the development of depressed lateral faces causes asymmetry in the elements.

Remarks. The type species of *Muellerodus* was originally assigned, with some doubt, to the Ordovician euconodont genus *Distacodus* Hinde, 1879, by Müller (1959), even though the elements he described had rounded anterior and posterior margins as opposed to the sharp margins which are diagnostic for *Distacodus*. However, Szaniawski (1971) recognised that elements resembling *Distacodus*, but with rounded anterior and posterior margins should be included within a separate genus. He erected the genus *Muellerina* to include such elements, which also possessed deep basal cavities and slight anterior or lateral twisting of the cusp. *Scandodus oelandicus* was also removed to *Muellerina* by Szaniawski (1971), who noted that the cusp was not significantly twisted out of alignment with the base and that, therefore, the sharp edges should be regarded as lateral costae and not anterior and posterior margins as had been suggested by Müller (1959). Miller (1980) proposed *Muellerodus* as a replacement name for *Muellerina* Szaniawski, which was found to be a junior homonym of the ostracode genus *Muellerina* Bassiouni, 1965. *Muellerodus* is a paraconodont genus and is therefore not likely to be closely related to the Ordovician euconodont genus *Distacodus*, so instead it is referred to the new paraconodont Family Prooneotodidae. A cluster of elements of *M. subsymmetricus* has been figured by Müller and Hinz (1991, pl. 19, figs 13, 14), and on the basis of his cluster only appearing to contain elements assigned to that species, it is likely that the different species of *Muellerodus* cannot be united into one apparatus.

Muellerodus cambricus (Müller, 1959)

Plate 3, figure 17.

* 1959 *Distacodus*(?) *cambricus* Müller, p. 450, pl. 14, figs 1, 2.
1971 *Oneotodus cambricus* (Müller); Müller, p. 11, pl. 2, fig. 3.
1971 *Muellerina cambrica* (Müller); Szaniawski, p. 407-408.

1979 *Muellerina cambrica* (Müller); Bednarczyk, p. 429, pl. 2, fig. 8.

1981 *Muellerodus cambricus* (Müller); Miller *in* Robison, p. W114, text-fig. 64, fig. 3a.

p 1982 *Muellerodus pomeranensis* Szaniawski; An, p. 138, pl. 9, figs 6, 8 (*non* pl. 9, fig. 7; pl. 17, figs 1, 3 [= *M. pomeranensis*]).

1991 *Muellerodus cambricus* (Müller); Müller and Hinz, p. 29, pl. 18, figs 1-4, 6-13, 15, 17; text-fig. 10A, B.

1992 *Muellerodus cambricus* (Müller); Hinz, p. 255, pl. 1, fig. 12.

Holotype. SMF 10352, Müller (1959), pl. 14, fig. 1, Upper Cambrian Zone 1, Gudhem am Mösseberg, Västergotland, Sweden.

Material. 28 elements

Diagnosis and description. See Müller (1959) p. 450.

Remarks. Small, rounded elements with sigmoidally curved cusps and two sharp lateral margins are assigned to *M. cambricus*. Müller (1959) tentatively included *M. cambricus* in the genus *Distacodus* Hinde, 1879, but recognised that the elements did not fully correspond to the diagnosis of that genus, because the anterior margins of the elements were rounded as opposed to sharp. Müller (1971) removed *M. cambricus* to the genus *Oneotodus*, although no explanation for this reassignment was given. Szaniawski (1971) assigned *M. cambricus* as the type species of the new genus *Muellerina*, but he did not describe or illustrate any elements of *M. cambricus*. Miller (1980) substituted the name *Muellerodus* for *Muellerina*, which was already in use as a genus of ostracode (*Muellerina* Bassiouni, 1965). Intraspecific variations in the development and position of the lateral costae, the length of the cusp and the degree to which the element margins taper from the cusp were noted by Müller and Hinz (1991). They also suggested that *M. cambricus* is closely related to *M. pomeranensis* due to the presence, in their collections, of transitional elements between the two species (Müller and Hinz 1991, pl. 18, figs 9, 10 13; text-fig. 10A).

Occurrence. O93-1, O93-4, O93-6, VG93-7, VG93-12, VG93-13, VG93-16, Upper Cambrian Alum Shale, Öland and Västergötland, Sweden.

Muellerodus? *oelandicus* (Müller, 1959)

Plate 3, figure 18.

* 1959 *Scandodus oelandicus* Müller, p. 463, pl. 12, figs 14, 15; text-fig. 10.

? 1966 *Scandodus oelandicus* Müller; Nogami, p. 358, pl. 9, fig. 15.

? 1981 *Muellerina oelandica* (Müller); An, p. 218, pl. 1, fig. 7.

? 1983 *Muellerodus oelandicus* (Müller); An *et al*., p. 109, pl. 3, fig. 9.

? 1986 *Proscandodus oelandicus* (Müller); Chen and Gong, p. 171, pl. 34, figs 13, 17; text-fig. 67, figs 1, 2.

1991 *Muellerodus*? *oelandicus* (Müller); Müller and Hinz, p. 29, pl. 20, figs 1-13; text-fig. 10E, F.

1992 *Muellerodus*? *oelandicus* (Müller); Hinz, p. 255, pl. 1, fig. 4.

1993 *Muellerodus*? *oelandicus* (Müller); Dong, p. 360, pl. 3, figs 6, 11.

Holotype. SMF 10342, Müller (1959), pl. 12, fig. 15, Upper Cambrian, Zone 3, Grönhogen, Öland, Sweden.

Material. 6 elements.

Diagnosis and description. See Müller (1959), p. 463.

Remarks. Elements assigned to *M*? *oelandicus* tend to be larger and more robust than those assigned to *M. cambricus* and only possess one well-developed sharp lateral margin. The anterior margins of the elements are very broadly rounded, with the posterior margin taking the form of a concave face. The second lateral margin is narrowly rounded, not sharp and is less well-developed than the opposing margin.

In his original description, Müller (1959) assigned *M. oelandicus* to the genus *Scandodus* because he believed the sharp or narrowly rounded margins to lie in anterior and posterior, rather than lateral, positions. This gave the element a twisted appearance, with the base opening to one side as opposed to towards the posterior. An (1981) placed *S. oelandicus* in the new genus *Muellerina* Szaniawski, and An *et al.* (1983) altered the generic name of the species following Miller (1980) by using the replacement generic name *Muellerodus*. However, Müller and Hinz (1991), Hinz (1992) and Dong (1993) have placed a question mark against the generic assignation, because only one lateral margin of elements of *M*? *oelandicus* has a well developed keel, whereas all other representatives of the genus carry two keeled, lateral margins. This convention is followed because, although *M*? *oelandicus* appears to fall outside of the generic constraints particular to *Muellerodus*, the species shows a closer relationship to the other species contained within the genus than to any other paraconodont genus.

Occurrence. VG93-7, VG93-17, Upper Cambrian Alum Shale, Västergötland, Sweden.

Genus PROBLEMATOCONITES Müller, 1959

1959 *Problematoconites*, Müller, p. 471.

Type species. *Problematoconites perforata* Müller, 1959, p. 471, Upper Cambrian Zone 5d, Sellin auf Rügen, Germany.

Remarks. Rounded, erect to recurved, coniform paraconodont elements with characteristic circular to ovate perforations confined to their basal regions are assigned to the genus *Problematoconites*. In his original description, Müller (1959) did not include the new monospecific genus *Problematoconites* as a true conodont and stated that it was a problematic, cone-shaped, tooth-like fossil, similar in shape to a simple conodont. In 1962, Müller placed *Problematoconites* in the new Order Paraconodontida, as noted by Druce and Jones (1971) who compared elements of *P. perforata* to the basal cavity fillings (basal bodies) of true conodonts (euconodonts) from their collections. Müller and Nogami (1971) investigated the histology of *P. perforata* and proved the paraconodont nature of the species on the basis of its typical paraconodont-style mode of growth. Chen and Gong (1986) assigned an element of *Problematoconites* to the genus *Prooneotodus*, and regarded the holes in the basal region to be traces of endobionts as opposed to an original histological feature of the elements. The idea that the perforations are not primary histological structures has been raised by Müller and Nogami (1971, 1972b) and by Andres (1988), although these authors maintained the distinction between the genera *Problematoconites* and *Prooneotodus*.

Elements of *Problematoconites* are similar in overall shape to those of *Prooneotodus*, although the two genera can be distinguished according to the presence or absence of basal perforations on the outer surface. The absence of keeled or sharp margins marks the difference between *Problematoconites* and all other coniform paraconodonts.

Problematoconites perforatus Müller, 1959

Plate 3, figures 13-16.

* 1959 *Problematoconites perforata* [*sic*] Müller, p. 471, pl. 15, fig. 17.
1967 *Problematoconites perforata* [*sic*] Müller; Nogami, p. 212.
1971 *Problematoconites perforata* [*sic*] Müller; Druce and Jones, p. 85, pl. 8, figs 11a, b; text-fig. 27.
1971 *Problematoconites perforata* [*sic*] Müller; Müller, p. 10, pl. 2, figs 11, 13, 14.
1971 *Problematoconites perforatus* Müller; Müller and Nogami, p. 72, pl. 1, figs 1-4; text-fig. 1B.
1973 *Problematoconites perforatus* Müller; Müller, p. 42, pl. 4, figs 7, 8.
1981 *Problematoconites perforatus* Müller; An, p. 218, pl. 1, fig. 12.
1981 *Problematoconites perforata* [*sic*] Müller; Miller *in* Robison, p. W113, text-fig. 65.4.
? 1983 *Problematoconites perforata* [*sic*] Müller; An *et al.*, p. 123, pl. 3, fig. 6.
? 1985 *Problematoconites perforata* [*sic*] Müller; Wang, p. 231, pl. 2, fig. 22; pl. 3, fig. 26; pl. 8, fig. 12; pl. 12, fig. 14; pl. 14, fig. 17.
1986 "*Prooneotodus*" sp. Chen and Gong, p. 168, pl. 17, fig. 1; text-fig. 64, fig. 7.
? 1986 *Problematoconites perforata* [*sic*] Müller; Jiang *et al.*, p. 242, pl. 2, fig. 4.
1991 *Problematoconites perforatus* Müller; Müller and Hinz, p. 36, pl. 23, figs 1-10, 14, 15, 18-20, 22.
1992 *Problematoconites perforatus* Müller; Hinz, p. 258, pl. 1, fig. 5.

Holotype. HUB ct 237, Müller (1959), pl. 15, fig. 17, Upper Cambrian, Zone 5d, Sellin, Rügen.

Material. 6 elements.

Diagnosis and description. See Müller (1959), p. 471.

Remarks. Characteristic of this species, alongside the perforations in the basal parts of the element, is the oval to rounded cross-section and the relatively wide tapering of the anterior and posterior margins away from the tip of the element. Miller (*in* Robison 1981) stated that elements of *P. perforatus* are symmetrical however, elements commonly demonstrate asymmetry by being slightly flattened on one side, or by having their cusps twisted laterally relative to the base. Müller and Hinz (1991) included only recurved elements with large basal openings, widely-flaring bases and annulated outer surfaces, together with the characteristic perforations, in the species *P. perforatus*, and erected two new species of *Problematoconites* (*P. angustus* and *P.*

asymmetricus) to include other element morphotypes. They did not comment on the possibility of these morphotypes being part of a single apparatus. Elements recovered in this study are generally large, have rounded cross-sections, are erect or recurved and are often broken at the base, presumably due to weakness caused by the perforations. With a larger sample, it is likely that a multimembrate apparatus reconstruction could be made, probably based on element curvature and compression similar to other paraconodont species. An estimate of the apparatus composition can be attained using the specimens of *Problematoconites* figured by Müller and Hinz (1991, pl. 23, figs 1-26). Although Müller and Hinz (1991) derived three species of *Problematoconites* from their samples, it is likely that an apparatus similar to that of *Prooneotodus* can be predicted by uniting *P. asymmetricus* and *P. perforatus* in a single apparatus of alpha, gamma (*P. perforatus*) and delta (*P. asymmetricus*) elements. Typical examples of the three element types, taken from Müller and Hinz (1991) are pl. 23, fig. 9 (alpha), pl. 23, figs 1-3, 7, 18 (gamma) and pl. 23, figs 19, 21, 22, 26 (delta). Elements assigned to *P. angustus* have a characteristic hooked tip and may represent a separate species, although could equally be found as a specialised (alpha) element similar to that in the *Coelocerodontus* Ethington, 1959 apparatus.

Occurrence. O93-1, O93-2, O93-6, VG93-17, Upper Cambrian Alum Shale, Öland and Västergötland, Sweden.

Genus PROONEOTODUS Müller and Nogami, 1971

1971 *Prooneotodus*, Müller and Nogami, p. 17.

Type species. *Oneotodus gallatini* Müller, 1959, p. 457, Gallatin Formation, Port Clear Creek, Bighorn Mountains, Wyoming.

Emended diagnosis. Trimembrate apparatus of erect to recurved, coniform paraconodont elements. Elements laterally or slightly antero-posteriorly compressed, rounded, with no sharp margins or secondary carinae. Outer surface smooth or faintly annulated.

Description. Trimembrate apparatus of erect (alpha), slightly recurved (gamma) and strongly recurved (delta) paraconodont elements. Anterior and posterior margins rounded, keels and carinae absent. Outer surface of the elements smooth or faintly annulated, with annulations parallel to the basal margin of the element. Elements laterally compressed, rounded or very slightly antero-posteriorly compressed. Anterior and posterior margins narrowly or broadly tapering from the tip to the base. Basal and cusp cross-sections rounded to ovate, basal cavity deep, extending almost to the tips of the elements, always extending past the point of maximum curvature. Lateral twisting of the cusp of the elements occurs in some forms.

Remarks. Two of the species of *Prooneotodus* described herein were originally assigned to different genera, *P. gallatini* to *Oneotodus* by Müller (1959) and *P. rotundatus* to *Coelocerodontus* by Druce and Jones (1971). *Oneotodus* Lindström, 1954, of which the type species is *Distacodus simplex* Furnish, 1938, encompasses only euconodonts that are albid, coniform and have circular to sub-circular cross-sections of the cusp and base. *Coelocerodontus* Ethington, 1959, is characterised by the presence of keels. *C. primitivus* and *C.* cf. *C. burkei* (= *P. gallatini*) and *C. rotundatus* (= *P. rotundatus*) lack the necessary keels and extreme lateral compression needed to assign them to *Coelocerodontus*, but Druce and Jones (1971) believed that, although they had stretched the diagnosis of *Coelocerodontus* to include these forms that lack keels, the thin walls and deeply excavated basal cavity justified their inclusion in the genus.

Müller and Nogami (1971) erected the new genus *Prooneotodus* to include those elements with similar external morphology to *Oneotodus*, but with a paraconodont style of growth. Certain protoconodont species (*Phakelodus tenuis*, *Phakelodus elongatus*) were also included within *Prooneotodus* until the histological work of Szaniawski (1982) proved that their style of growth was different to that of the true paraconodonts. These forms are now placed in the protoconodont genus *Phakelodus* Miller, 1984.

A trimembrate apparatus is assigned to *Prooneotodus gallatini* and *P. rotundatus*. However, elements of *P.* aff. *rotundatus* do not show such a variety of form. Elements of the latter are rather rare in collections, so it may be that the small sample size has failed to encompass the less common strongly recurved forms.

Prooneotodus gallatini (Müller, 1959)

Plate 3, figures 7-12; Plate 11, figure B.

*p 1959 *Oneotodus gallatini* Müller, p. 457, pl. 13, figs 5, 6, 8-10 (*non* figs 7, 12, 18 [= *P. rotundatus*]).

non 1959 *Oneotodus* aff. *O. gallatini* Müller, p. 457, pl. 13, figs 16, 19, 21 [= *P. rotundatus*].

? 1969 ?*Oneotodus gallatini* Müller; Miller, p. 435.

1971 *Oneotodus gallatini* Müller; Druce and Jones, p. 81, pl. 9, fig. 9a-c.

1971 *Coelocerodontus* cf. *C. burkei* Druce and Jones, p. 61, pl. 9, fig. 7a-c.

1971 *Coelocerodontus primitivus* Druce and Jones, p. 62, pl. 9, figs 5a-6c, 8a-c; text-fig. 22b.

? 1971 *Prooneotodus* Müller and Nogami, p. 17.

? 1975 *Prooneotodus gallatini* (Müller); Lee, p. 82, pl. 1, figs 2, 12; text-fig. 2B, J.

? 1976 *Prooneotodus gallatini*? (Müller); Miller and Paden, p. 596, pl. 1, figs 16-19.

? 1978 *Proconodontus primitivus* (Müller); Fåhræus and Nowlan, p. 453, pl. 1, fig. 3.

? 1979 *Prooneotodus gallatini* (Müller); Bednarczyk, p. 433, pl. 3, figs 10, 15-16.

1980 *Prooneotodus gallatini* (Müller); Lee, pl. 1, fig. 4.

? 1980 *Prooneotodus* cf. *gallatini* (Müller); Szaniawski, p. 116, pl. 18, fig. 1.

1981 *Prooneotodus* sp., Miller *in* Clark, p. W113-114, text-fig. 64, figs 2a-c.

1981 *Prooneotodus gallatini* (Müller); Miller *et al.*, p. 190, text-fig. 4k-m.

1982 *Prooneotodus gallatini* (Müller); An, p. 144, pl. 11, figs 5, 6, 9-14; pl. 16, fig. 13.

1982 *Prooneotodus gallatini* (Müller); Fortey, Landing and Skevington, text-fig. 9h, o.

1983 *Prooneotodus gallatini* (Müller); An *et al.*, p. 128, pl. 5, fig. 7.

p 1985 *Prooneotodus gallatini* (Müller); Wang, p. 235, pl. 3, figs 23, 24; pl. 5, figs 4, 5; pl. 8, figs 11, 21; pl. 12, figs 22, 26; pl. 13, fig. 10 (*non* pl. 3, fig 25 [= *Proconodontus muelleri*]; pl. 14, fig. 5 [? = *P. rotundatus*]).

1986 "*Prooneotodus*" *gallatini* Mueller [*sic*]; Chen and Gong, p. 166, pl. 22, figs 13, 15-17; pl. 23, figs 2, 3, 7, 10, 16-19; pl. 24, fig. 12; text-fig. 64, figs 2, 3, 5.

? 1986 *Prooneotodus gallatini* (Müller); Chen, Zhang, and Yu, p. 369, pl. 2, figs 4-6.

1986 *Prooneotodus gallatini* (Müller); Jiang *et al.*, pl. 3, fig. 2.

1987 *Prooneotodus gallatini* (Müller); An, p. 112, pl. 3, figs 1, 2, 5, 6, 11, 15.

1987 *Prooneotodus gallatini* (Müller); Buggisch and Repetski, p. 159, pl. 8, fig. 2.

? 1987 *Prooneotodus* aff. *P. gallatini* (Müller); Buggisch and Repetski, p. 159, pl. 9, fig. 6.

1988 *Prooneotodus gallatini* Müller [*sic*]; Heredia and Bordonaro, p. 193, pl. 1, fig. 1; pl. 2, fig. 4.

? 1989 *Prooneotodus gallatini* (Müller); Popov *et al.*, p. 146, pl. 19, figs 7, 12.

1991 *Prooneotodus gallatini* (Müller); Müller and Hinz, p. 37, pl. 24, figs 1-28, ?29.

1992 *Prooneotodus gallatini* (Müller); Hinz, p. 258, pl. 1, fig. 10.

1994 *Prooneotodus gallatini* (Müller); An and Mei, pl. 2, fig. 11.

1994 *Prooneotodus gallatini* (Müller); Repetski *et al.*, p. 21, text-fig. 18, fig. AB.

1998 *Prooneotodus gallatini* (Müller); Müller and Hinz-Schallreuter, p. 101, fig. 8.1.

Holotype. SUI 10297, Müller (1959) pl. 13, fig. 5, Gallatin Limestone, Port Clear Creek, Bighorn Mountains, Wyoming, USA.

Material. 260 elements (USA), 179 elements (Sweden)

Emended diagnosis. Trimembrate apparatus of erect (alpha), slightly recurved (gamma) and strongly recurved (delta), thin-walled, coniform, paraconodont elements, with faintly annulated surfaces and laterally compressed, ovate cross-sections. Keels and carinae lacking.

Description. Trimembrate apparatus of coniform elements, lacking keeled or sharp margins together with secondary carinae. Anterior and posterior margins rounded, tapering narrowly or widely away from the tip. Lateral faces convex to concave with a variable amount of inflation. Element walls thin, outer surface annulated with annulations oriented parallel to the basal margin. Basal cavity deep, extending almost to the tip of the element. Elements are distinguished on the basis of their curvature into erect (alpha), slightly recurved (gamma) and strongly recurved (delta) elements.

Alpha elements. Erect elements, anterior margin broadly rounded, curved from base to tip. Posterior margin more narrowly rounded, with curvature increasing very slightly towards the base. Elements slightly antero-posteriorly compressed, lateral faces concave at the base, becoming convex and rounded towards the tip. One lateral face is always larger than the other, causing asymmetry. Cross-section rounded at tip, broadly triangular at base.

Gamma elements. Slightly recurved, laterally compressed, slender elements with narrow bases. Anterior and posterior margins rounded, curved, tapering narrowly at tip, becoming wider gradually towards the base. Inner lateral face convex to flattened, outer face convex and more distinctly inflated. Tip of the element deflected laterally towards the inner face. Cross-section of element rounded at the tip, ovate at the base.

Delta elements. Recurved, laterally compressed, squat elements, narrowly tapering at the tip, becoming very broad in basal regions. Anterior and posterior margins narrowly rounded, curved, with curvature increasing markedly towards the base. Inner face slightly convex, but often flattened or concave. Outer face convex. Cross-section rounded at tip, becoming ovate to the base. Tip of element deflected towards the inner margin.

Remarks. Müller (1959) figured a number of specimens which he assigned to *Oneotodus gallatini* or to a second closely related species, *O.* aff. *O. gallatini*. Of these specimens, those showing marked lateral compression have been included in the synonymy for *P. gallatini*, but those with rounded or inflated cusp and basal cross-sections have been placed within *Prooneotodus rotundatus*. From the figures in Müller's plate (pl. 13, figs 5, 6, 8-10, 16, 18, 19, 21), it is difficult to establish whether any of the specimens possess annulations on their outer surfaces. Müller and Nogami (1971) used *O. gallatini* as the type species of the new paraconodont genus *Prooneotodus*, but did not figure any specimens of *P. gallatini*, choosing *Problematoconites perforatus* Müller, 1959 and *Furnishina furnishi* Müller, 1959 to demonstrate the paraconodont style of element growth.

Druce and Jones (1971) included elements considered here to be united as *P. gallatini* in three different species, *O. gallatini*, *Coelocerodontus* cf. *C. burkei* and *Coelocerodontus primitivus*. Those elements assigned to *O. gallatini* remain unaltered in the present synonymy. Elements of *C.* cf. *C. burkei* appear to lack the keels necessary for their placement within the original description given by Druce and Jones of *C. burkei*, and all elements assigned to *C. primitivus* are now firmly recognised as elements of *P. gallatini*, with annulated faces, and laterally compressed cross-sections. An (1982) placed an element of *O. nakamurai* (figured by Nogami (1967) pl. 1, fig. 10, text-fig 3e) in his synonymy for *P. gallatini*, but this is refuted because the figured element has white matter developed in the cusp, a feature that does not exist in any known paraconodont and is considered to be unique to the euconodonts.

Wang (1985) implied that many specimens of *P. gallatini* have circular cross-sections, but also stated that the outline of the base is elliptical. Two specimens from Wang's synonymy are removed herein, one to be included in *P. rotundatus* on the basis of its smooth outer surface, and the relative thickness of the element walls, and the second placed tentatively in *P. muelleri* due to its more robust appearance, and that it has euconodont crown material developed, emphasised by the presence of keeled anterior and posterior margins.

Specimens from Sweden, figured by Müller and Hinz (1991) include two clusters of elements (pl. 24, figs 10, 26) and a bicuspid form (pl. 24, fig. 25). No similar material has been recovered from Wyoming or Sweden. However, the range of morphology demonstrated by the remaining specimens of Müller and Hinz is displayed by the specimens of *P. gallatini* used in the present study. In one of the two clusters (pl. 24, fig. 10) three elements are present, and do not seem to have a preferred orientation. Of these elements, one is erect and may represent an alpha element, a second is slightly recurved and may be a gamma element, but the base of the third element is obscured, and cannot be assigned to an element category. The second cluster contains only two elements, aligned with their cusps parallel in close lateral association. Both of these elements are gamma elements, implying that it is possible that more than one element of an element category could be present in an apparatus.

Hinz (1992) described a trimembrate apparatus for *P. gallatini*, including symmetrical elements with convex lateral margins (p elements), asymmetrical elements with one flattened or concave and one convex margin (q elements) and asymmetrical elements with an antero-posteriorly expanded base (r elements). Elements assigned to the p and q categories were divided according to their symmetry into asymmetrical (ap and aq) and symmetrical (sym p and sq) categories. In contrast to Hinz (1992) the apparatus outlined above is divided according to the element curvature and not the cross-section of the base, because the majority of specimens show a greater or lesser degree of asymmetry. However, it is noted that the more strongly recurved (delta) elements do tend to be more laterally compressed and may possess one convex and one concave lateral margin, similar to the r elements described by Hinz (1992).

P. gallatini is distinguished from *P. rotundatus* by the presence of faint annulations on the outer surfaces of the elements, and by the thinness of the walls. Lateral compression of the elements is more acutely marked in *P. gallatini* than in *P. rotundatus*.

Occurrence. WY96-17, WY96-18, Gallatin Formation, Bighorn Mountains, Wyoming. O93-1, O93-2, O93-4, O93-6, O93-7c, O93-7d, VG93-10, VG93-12, VG93-13, VG93-16, VG93-17, VG93-22, Upper Cambrian Alum Shale, Öland and Västergötland, Sweden.

Prooneotodus rotundatus (Druce and Jones, 1971)

Plate 3, figures 1-6; Plate 8, figures A, B; Plate 10, figure F; Plate 11, figure D;
Plate 14, figures A-F; Plate 15, figures A-C.

p 1959 *Oneotodus gallatini* Müller, p. 457, pl. 13, figs 7, 12, 18 (*non* pl. 13, figs 5, 6, 8-10 [= *P. gallatini*]).

1959 *Oneotodus* aff. *gallatini* Müller, p. 457, pl. 13, figs 16,19, 21.

* 1971 *Coelocerodontus rotundatus* Druce and Jones, p. 62, pl. 9, figs 10a-13b; text-figs 22c, 22d.

1971 *Coelocerodontus rotundatus* Druce and Jones; Jones, p. 45, pl. 1, fig. 1a-c.

? 1973 *Proconodontus* cf. *rotundatus* (Druce and Jones); Müller, p. 43, pl. 3, figs 1-3.

1975 *Prooneotodus rotundatus* (Druce and Jones); Lee, p. 83, pl. 1, figs 7, 11, 13; text-fig. 2F, I.

? 1976 *Prooneotodus rotundatus* (Druce and Jones); Miller and Paden, p. 596, pl. 1, figs 24, 25.

1981 *Prooneotodus rotundatus* (Druce and Jones); Miller *et al.*, p. 190, text-fig. 4n, o.

1982 *Prooneotodus rotundatus* (Druce and Jones); An, p. 144, pl. 4, fig. 12; pl. 11, figs 1-4, 7, 8.

1982 *Prooneotodus rotundatus* (Druce and Jones); Fortey, Landing and Skevington, text-fig. 9j, m.

1983 *Prooneotodus rotundatus* (Druce and Jones); An *et al.*, p. 129, pl. 5, fig. 6.

? 1983 *Prooneotodus*? *rotundatus*? (Druce and Jones); Landing, text-fig. 10d, e.

1985 *Prooneotodus rotundatus* (Druce and Jones); Wang, p. 236, pl. 3, figs 5, 6, 7; pl. 6, fig 13; pl. 7, figs 7, 8; pl. 8, fig. 6; pl. 9, fig. 2; pl. 12, fig. 6; pl. 13, figs 8, 32.

p 1985 *Prooneotodus gallatini* (Müller); Wang, p. 235, pl. 14, fig. 5 (*non* pl. 3, fig 25 [= *Proconodontus muelleri*], pl. 3, figs 23, 24; pl. 5, figs 4, 5; pl. 8, figs 11, 21; pl. 12, figs 22, 26; pl. 13, fig. 10 [= *P. gallatini*]).

1986 "*Prooneotodus*" *rotundatus* (Druce and Jones); Chen and Gong, p. 167, pl. 22, figs 1-6, 9-11, 18, 20; pl. 23, figs 1, 9, 12, 14, 20; pl. 26, fig. 9; text-fig. 64, fig. 1.

? 1986 *Prooneotodus rotundatus* (Druce and Jones); Chen, Zhang and Yu, p. 369, pl. 2, figs 11, 12.

1986 *Prooneotodus rotundatus* (Druce and Jones); Jiang *et al.*, pl. 3, fig. 3.

? 1987 *Prooneotodus rotundatus* (Druce and Jones); An, p. 112, pl. 1, figs 13, 17, 18.

1988 *Prooneotodus rotundatus* (Druce and Jones); Heredia and Bordonaro, p. 193, pl. 3, fig. 3.

1988 *Prooneotodus rotundatus* (Druce and Jones); Orndorff, p. A14, pl. 2, fig. 8.

1989 *Proconodontus rotundatus* (Druce and Jones); Popov *et al.*, p. 146, pl. 17, figs 1, 13.

? 1990 *Prooncotodus* [*sic*] sp. 2, Sarmiento, p. 146, pl. 1, fig. 1.

? 1994 *Proconodontus rotundatus* (Druce and Jones); An and Mei, pl. 1, fig. 27.

1994 *Prooneotodus rotundatus* (Druce and Jones); Repetski *et al*., p. 21, text-fig. 18, fig. AA.

Holotype. CPC8783, Druce and Jones (1971) pl. 9, fig. 12a, b, Chatsworth Limestone, Black Mountain, Queensland, Australia.

Material. 3276 elements from Wyoming.

Emended diagnosis. Trimembrate apparatus of erect (alpha), slightly recurved (gamma) and strongly recurved (delta), coniform paraconodont elements lacking keeled or sharp margins and secondary carinae. Outer surface of elements smooth, walls relatively thick.

Description. Apparatus consisting of three coniform element types, erect (alpha), slightly recurved (gamma) and strongly recurved (delta). Anterior and posterior margins rounded, narrowly or widely tapering from tip to base. Lateral faces convex to concave. Element walls thick, outer surface smooth. Basal cavity deep, extending almost to the tip of the element, or to the point of maximum curvature.

Alpha elements. Erect or slightly recurved elements with a minor degree of antero-posterior compression. Anterior margin rounded, gently curved from base to tip, posterior margin more narrowly rounded and strongly curved. Lateral margins unequally developed, one larger than the other, both concave at the base, becoming convex to the cusp. Cross-section triangular at the base, rounded at the tip. Basal cavity extending almost to the tip of the element.

Gamma elements. Elongate, slightly recurved elements with narrowly rounded and curved anterior and posterior margins. Curvature of element increases steadily from tip to base, margins narrowly tapering. Lateral faces convex, with the inner face being less convex or flattened. Element tip deflected towards the inner face. Element cross-section rounded at tip, ovate at base. Basal cavity extends to point of maximum curvature of the element.

Delta elements. Recurved, squat elements with narrowly rounded and strongly recurved anterior and posterior margins tapering widely away from the tip. Outer lateral face convex, inner face flattened to strongly concave. Element cross-section rounded at the tip but ovate at the base. Basal cavity extending as far as the point of maximum curvature of the element.

Remarks. In their original description of *Coelocerodontus rotundatus* (= *P. rotundatus*), Druce and Jones (1971) acknowledged that the species falls outside of the range of morphological variability of *Coelocerodontus*, extending the diagnosis to include forms where keeled margins are absent. Müller (1973) tentatively placed the specimens from his study in the genus *Proconodontus*, but the reduced degree of lateral compression, together with the lack of any evident crown material precludes this classification. Miller and Paden (1976) stated both of the above reasons for not including Müller's elements in *Proconodontus*, instead referring *C. rotundatus* to the new genus *Prooneotodus* Müller and Nogami, 1971. Wang (1985) figured an element of *P. rotundatus* as *P. gallatini* (pl. 14, fig. 5), but the element is rounded in cross-section, and the walls are too think for it to have been included in the latter species.

P. rotundatus is distinguished from *P. gallatini* by the lack of ornament on the outer surfaces of the element, the relative thickness of the walls, and by the overall lack of lateral compression. Without the aid of an SEM image or a thin section, some elements of *P. rotundatus* are difficult to tell apart from early specimens of *Proconodontus*, due to the elements showing very similar ranges of morphology between the two species. Miller (1976, 1980) suggested a close relationship between *P. rotundatus* (a paraconodont) and *Proconodontus tenuiserratus* (a euconodont), linked by a form that has as exceptionally thin crown-layer covering the element. Histological studies during the current investigation have not been able to prove this hypothesis. Elements from the apparatuses of *P. rotundatus* and *P. muelleri* show a similar range of morphologies, with both possessing three types of erect to recurved, laterally compressed elements, however, this may be a result of evolutionary convergence and not homology between the apparatuses.

Occurrence. WY96-17, WY96-18, Gallatin Formation, Bighorn Mountains, Wyoming.

Prooneotodus aff. *P. rotundatus* (Druce and Jones, 1971)

Material. 60 elements

Description. Proclined, coniform paraconodont elements. Basal part of posterior margin very short, straight, then bulging outwards slightly at a point approximately half-way along the length of the element before curving gently towards the tip of the element. Entire posterior margin broadly rounded. Bulge in posterior margin is a prominent feature continued at the same level around the entire circumference of the element. Rounded anterior margin curved, bulging outwards at half-way point, becoming straightened after this point, and extending further basally than the termination of the posterior margin. Element surfaces smooth and unornamented. Basal opening in extended apically on the posterior side of the element, with the lateral margins of the basal opening tapering slowly to meet one another just basal to the bulging central part of the element. Basal portion constitutes just under half of the element length. Basal and cusp cross-sections are circular, with no lateral compression. Basal cavity deep, extending almost to tip of element. Elements are symmetrical and show no lateral twisting.

Remarks. The upper parts of these elements resemble *P. rotundatus* in overall form and possess thick walls and a smooth outer surface, but no element of *P. rotundatus* is known to have a lower part that is extended basally below a central bulge, with a large, elongated basal opening. For this reason, these elements cannot be placed with certainty in *P. rotundatus*. The range of element morphologies is restricted in comparison to *P. rotundatus*, although this may be caused by the relatively low abundance of these elements in collections.

Occurrence. WY96-18, Gallatin Formation, Bighorn Mountains, Wyoming.

Family WESTERGAARDODINIDAE Müller, 1959

Remarks. Müller (1959) included two genera, *Westergaardodina* Müller, 1959, and an undescribed, asymmetrical genus in the family Westergaardodinidae, because the mode of growth and the position of the basal opening in these forms was different from the other Cambrian genera included in his study. Westergaardodinidae was included in the suborder Conodontiformes Branson and Mehl, 1944, of the order Conodontophorida Eichenberg, 1930, by Müller (1959). Müller (1962) again included the family Westergaardodinidae with the true conodonts, but did not refer to the undescribed, asymmetrical genus that he mentioned in his earlier publication. Although the new order Paraconodontida Müller, 1962 was created by Müller in the *Treatise* volume, he did not consider that the westergaardodinids might bear a closer relationship to the paraconodonts than the conodontophorids (euconodonts). Lindström (1964) did not regard the westergaardodinids as conodonts, but concluded that the idea that they were related to conodonts could not be dismissed, due to their laminated structure and the fact that, in some cases, they resembled the basal cones of euconodonts. Lindström (1970) chose not to use the already established order Paraconodontida, and opted to place the family Westergaardodinidae within the new order Westergaardodinida Lindström. In addition to *Westergaardodina*, the genera *Furnishina*, *Hertzina* and *Proacodus* were included in the family Westergaardodinidae, which together with the order Westergaardodinida, were still not considered to be part of the Conodontophorida Eichenberg, 1930.

Müller and Nogami (1971) conducted a histological investigation of a number of different conodontophorid elements and included the family Westergaardodinidae in the suborder Paraconodontidae Müller, 1962, due to the similarity in growth style between *Westergaardodina* and all other paraconodonts.

Miller (*in* Robison 1981) reviewed the classification of Cambrian conodonts and included the Westergaardodinidae in the superfamily Furnishinacea Miller of the Paraconodontida. Once again, *Chosonodina* was included alongside *Westergaardodina* as a member of the Westergaardodinidae. *Chosonodina* Müller, 1964, was also included in the Westergaardodinidae by Müller and Nogami (1971) due to its long, narrow basal opening that extends along the entire outer margin of the element, and the presence of a number of denticles or processes. However, *Chosonodina* has been demonstrated to be a Lower Ordovician euconodont due to the presence of white matter (Repetski pers. comm. in Miller 1984), and has been assigned to a new monogeneric family of an unknown order of euconodonts by Aldridge and Smith (1993).

Dzik (1991) followed Lindström (1970) by including the Westergaardodinidae in the order Westergaardodinida, but referred both to the class Conodonta Pander, 1856, implying that there is a relationship between the westergaardodinids and the remaining conodont (both para- and euconodont) groups. Only *Westergaardodina* was included in the Westergaardodinidae by Dzik (1991).

An (1982) described the new genus *Laiwugnathus*, elements of which are morphologically comparable to the central cusp of certain tricuspidate westergaardodinid species. An (1982) used *Westergaardodina muelleri* Nogami, 1966, as the most suitable example of this, and implied that an evolutionary link is present between the two genera, with *Westergaardodina* being more derived than *Laiwugnathus*. An (1982) also proposed an evolutionary intermediate between *Laiwugnathus* and a tricuspid westergaardodinid, the form *Parawestergaardodina obsoleta* (An, 1982, p. 140, pl. 8, fig. 12). The scope of the family Westergaardodinidae is expanded here to include the genera *Laiwugnathus*, *Parawestergaardodina* and *Westergaardodina* in accordance with the evolutionary relationships proposed by An (1982), although the two former genera have not been recovered during the course of this study.

Genus WESTERGAARDODINA Müller, 1959

1953 Problematicum I Westergård, p. 465.
1959 *Westergaardodina* Müller, p. 465.

Type species. Westergaardodina bicuspidata Müller (1959), p. 468, Upper Cambrian Zone 5b, Mark Brandenburg.

Description. Bicuspid or tricuspid, symmetrical to markedly asymmetrical paraconodont elements. Anterior face flat to gently curved, convex, but in rare cases undulating or concave. In many elements the anterior side is unornamented, but some bear a longitudinal furrow on the anterior margin of the median projections, or slight indentations or bulgings surrounding the single turning point in bicuspid forms or the two turning points in tricuspid forms. The posterior side of the elements usually carries more diagnostic features than the anterior. Median projections are of variable size, and may be ornamented with a longitudinal keel, which itself is of variable morphology between different species. Variations in length, width, roundness and elevation are common. Lateral projections may be erect, divergent or convergent, and of equal or unequal size and length. They may also be deflected laterally towards the left or right hand side. Inner margins of the lateral projections are usually sharp, whereas margins can be either sharp or inflated. Turning point(s) between projections vary in depth and width, from very deep to shallow and from wide to narrow and slit-like. They may also be situated in depressions of variable depth when viewed from the posterior side of the element. Basal margin can be broadly curved with a u-shaped outline, but in some cases an indentation of variable proportions is developed beneath the median projection of the element, making the basal outline w-shaped. Basal cavity openings may be developed continuously around the entire margin of the element, or may be present as lateral openings on the outer margins of the lateral projections, which may be discrete or connected by a furrow along the basal margin. In rare cases, a basal cavity opening is absent from the outer margin of the element, being developed only in the basal region of the median keel.

Remarks. Müller (1959) was the first author to fully describe species of *Westergaardodina*, although elements had been mentioned previously by Wiman (1893, 1903) and described and illustrated as Problematicum I by Westergård (1953). Westergård noted the presence of conodonts in the Tremadocian horizons from which westergaardodinids were recovered but did not propose any affinities for the problematic sclerites. Elements of *Westergaardodina* were originally described by Müller (1959) as symmetrical sclerites, who considered the tricuspid (w-shaped) elements to be primitive, and the bicuspid (u-shaped) elements to be derived. Phosphatic balls associated with the elements were thought to be part of the *Westergaardodina* apparatus by Müller (1959), but this has since been dismissed (Donoghue 1996).

Szaniawski (1971), using data from his own collections, and information from Nogami (1966) emended the diagnosis for *Westergaardodina*, including asymmetrical elements in the description of the genus, together with forms that possess only one lateral basal opening. Although Müller (1962) erected the new order Paraconodontida, *Westergaardodina* was not included as a paraconodont until the histological work of Müller and Nogami (1971), with Nogami (1966), Müller (1962, 1971) and Szaniawski (1971) referring the genus to the 'true' conodonts (euconodonts).

Müller and Hinz (1991) have provided the most up-to-date review of the genus *Westergaardodina*, but did not mention the evolutionary relationships proposed by An (1982). They stated that it was not possible to construct a phylogenetic tree for the westergaardodinids, and the present study cannot prove otherwise because of the relatively small number of specimens recovered.

Morphologically, the genus *Westergaardodina* encompasses a vast range of forms, which have been split into species, sometimes based on quite minor changes in shape of one or more characters. Although the amount of westergaardodinid material recovered in this study precludes a full taxonomic review, it is likely that a better understanding of the genus and its evolution will be possible in the future with further discoveries of *Westergaardodina* bearing horizons.

Westergaardodina bicuspidata Müller, 1959

Plate 6, figures 1, 2.

p	1953	Problematicum I Westergård, p. 465, pl. 5, figs 2, 3, 4 (*non* pl. 5, figs 6, 15 [= *W. bohlini*]).
*p	1959	*Westergaardodina bicuspidata* Müller, p. 468, pl. 15, figs 7, 9 (*non* pl. 15, figs 1, 10 [= *W. polymorpha*]; pl. 15, fig. 4 [= phosphatic ball]; pl. 15, fig. 14 [= *W. procera*]).
	1962	*Westergaardodina bicuspidata* Müller; Müller *in* Moore *et al.*, p. W246, text-fig. 152, fig. 2.
?	1971	*Westergaardodina bicuspidata* Müller; Druce and Jones, p. 100, pl. 7, figs 1-4; text-fig. 32.
non	1971	*Westergaardodina bicuspidata* Müller; Müller, p. 11, pl. 2, fig. 8 [= *W. polymorpha*]; pl. 2 fig. 9 [= *W. procera*].
	1971	*Westergaardodina bicuspidata* Müller; Müller and Nogami, p. 16, text-fig. 1D.
	1972	*Westergaardodina bicuspidata* Müller; Müller and Nogami, p. 14, text-fig. 10.
?	1973	*Westergaardodina bicuspidata* Müller; Müller, p. 47, pl. 2, fig. 3.
?	1978	*Westergaardodina bicuspidata* Müller; Landing, Taylor and Erdtmann, p. 76, text-fig. 2c.
	1979	*Westergaardodina bicuspidata* Müller; Bednarczyk, p. 435, pl. 2, figs 2, 13.
	1981	*Westergaardodina bicuspidata* Müller; An, p. 218, pl. 1, fig. 3.
	1981	*Westergaardodina bicuspidata* Müller; Miller *in* Robison, p. W114, text-fig. 66, fig. 1.
?	1982	*Westergaardodina bicuspidata* Müller; An, p. 151, pl. 7, figs 6-8.
?	1983	*Westergaardodina bicuspidata* Müller; An *et al.*, p. 162, pl. 1, fig. 9.
?	1985	*Westergaardodina bicuspidata* Müller; Wang, p. 243, pl. 3, fig. 29; pl. 9, fig. 3; pl. 12, figs 23-25.

p 1986 *Westergaardodina bicuspidata* Müller; Chen and Gong, p. 198, pl. 21, figs 1, 4, 6, 10, 14; text-fig. 84 (*non* pl. 21, figs 3, 14 [= *W. wimani*]; pl. 21, figs 5, 15 [= *W. ligula*]; pl. 21, fig. 2 [= *W. polymorpha*]).

1986 *Westergaardodina bicuspidata* Müller; Jiang *et al.*, p. 241, pl. II-1, fig. 17.

1987 *Westergaardodina bicuspidata* Müller; An, p. 115, pl. 3, figs 13, 18.

1988 *Westergaardodina bicuspidata* Müller; Heredia and Bordonaro, p. 195, pl. 3, fig. 6.

1991 *Westergaardodina bicuspidata* Müller; Müller and Hinz, p. 42, pl. 29, figs 13-19.

1992 *Westergaardodina bicuspidata* Müller; Hinz, p. 261, pl. 4, figs 4, 8.

? 1993 *Westergaardodina bicuspidata* Müller; Dong, p. 353, pl. 1, fig. 12.

Holotype. HUB ct 239, Müller (1959), pl. 15, fig. 7, Upper Cambrian Zone 5b, Mark Brandenberg.

Material. 11 elements

Diagnosis and description. See Müller (1959, p. 468).

Remarks. Elements of *Westergaardodina bicuspidata* are, as the name suggests, bicuspid and characterised by a distinctly semi-circular basal region, with parallel lateral projections and a poorly developed median projection which bears a longitudinal keel on its posterior margin. *Westergaardodina bicuspidata* is distinguished from *W. polymorpha* by the less marked divergence of the lateral projections towards the cusp, and by possessing lateral basal cavity openings that extend further basally. *Westergaardodina procera* possesses lateral projections that are more closely spaced than those of the other two species and which, in some cases, overlap. In addition, the fused basal region of *W. bicuspidata* is distinctly semicircular, whereas in the other two species it is extended, causing the lateral basal openings to be reduced in length.

In his original description, Müller (1959) stated that, with increasing knowledge, the species *W. bicuspidata* would be divided into more taxa. In agreement with Müller and Hinz (1991) two elements figured by Müller (1959, pl. 15, figs 1, 10) are reassigned to *W. polymorpha*, one element (pl. 15, fig. 14) to *W. procera* and another specimen (pl. 15, fig. 4) is a phosphatic ball not thought to be of conodont affinity.

Prior to Müller's (1959) formal description of *W. bicuspidata*, several examples of the species had been figured by Westergård (1953, pl. 5, figs 2-4), all of which compare closely to the holotype. Elements of *W. bicuspidata* illustrated by Druce and Jones (1971, pl. 7, figs 1-4) are only tentatively included in the above synonymy, because the quality of preservation of the specimens precludes accurate determination of diagnostic features such as the basal cavity openings, and the distal termination of the lateral projections. Elements referred to *W. bicuspidata* by Müller (1973), Landing *et al.* (1978), An *et al.* (1983) and Wang (1985) are all cautiously included in the synonymy, although the poor quality of the preservation prevents conclusive diagnosis. Neither of the two elements figured by Müller (1971) remain in the synonymy. The first (Müller 1971, pl. 2, fig. 8) is reassigned to *W. polymorpha* because of its elongate nature, with extended lateral basal cavity openings and the second (Müller 1971, pl. 2, fig. 9) is reassigned to *W. procera* because of the presence of a moderately sized median projection, and the relative closeness of the spacing of the lateral projections. A specimen figured by An (1982, pl. 7, fig. 7) can only be cautiously included because its median projection lacks a posterior keel and also the basal region of the element is longitudinally extended due to the rather distal opening of the lateral basal openings. Chen and Gong (1986) included several bicuspidate westergaardodinids under the title of *W. bicuspidata*, including *W. ligula* (Chen and Gong 1986, pl. 21, figs 5, 15), *W. polymorpha* (pl. 21, fig. 2) and *W. wimani* (pl. 21, figs 3, 11) by opting to use a wide ranging description of the species that included characters such as lateral projections of variable, and sometimes unequal, length, together with basal cavity openings in both the lateral and basal margins of the elements. Müller and Hinz (1991) redescribed *W. bicuspidata* erecting a more well-constrained range of characters which are diagnostic of the species, and also illustrated the very conservative variation in morphology of the elements.

Occurrence. O93-6, VG93-7, VG93-8, VG93-12, VG93-13, VG93-16, Upper Cambrian Alum Shale, Öland and Västergötland, Sweden.

Westergaardodina bohlini Müller, 1959

Plate 6, figures 3-6.

p	1953	Problematicum I Westergård, p. 465, pl. 5, figs 6, 15 (*non* pl. 5, figs 2, 3, 4 [= *W. bicuspidata*]).
*	1959	*Westergaardodina bohlini* Müller, p. 469, pl. 15, fig. 8.
	1979	*Westergaardodina bohlini* Müller; Bednarczyk, p. 435, pl. 2, fig. 1.
	1991	*Westergaardodina bohlini* Müller; Müller and Hinz, p. 43, pl. 29, figs 1-12.

Holotype. SMF 10366, Müller (1959), pl. 15, fig. 8, Upper Cambrian Zone 3, Grönhogen, Öland, Sweden.

Material. 7 elements.

Remarks. Müller and Hinz (1991) commented on this arrow-like feature on the tips of the lateral projections in some elements of *W. bohlini*, and noted that they have observed similar occurrences on the tips of the lateral projections of *W. bicuspidata.* The two species are similar on overall form, but the median projection is far more prominent in elements of *W. bohlini* and the outline of the basal margin is often quadrangular as opposed to semicircular in shape. Elements assigned to *W. bohlini* are bicuspidate, antero-posteriorly flattened, with a prominent keeled median projection and lateral projections which become narrow and diverge slightly towards the tip. The basal margin tends to be straight in the central region of the element, only beginning to curve close to the lateral margins. The element designated as the holotype by Müller (1959) bears arrow-like extensions on the tips of the lateral projections, with the lateral basal openings extending into this region. No similarly shaped elements have been observed in the studied material, but the elements conform to the remaining diagnostic features of the species.

Occurrence. O93-1, O93-6, VG93-7, VG93-8, VG93-16, Upper Cambrian Alum Shale, Öland and Västergötland, Sweden.

Westergaardodina concamerata Müller and Hinz, 1991

Plate 6, figures 10, 11.

*	1991	*Westergaardodina concamerata* Müller and Hinz, p. 44, pl. 34, figs 3, 5-12, 15, 16.
	1992	*Westergaardodina concamerata* Müller and Hinz; Hinz, p. 261, pl. 4, fig. 2.

Holotype. UB 1408, Müller and Hinz (1991), p. 44, pl. 34, figs 5, 11, 12, Upper Cambrian *Peltura scarabaeoides* Zone (Vc), Trolmen, Västergötland, Sweden.

Material. 4 elements.

Remarks. Elements assigned to this species are tricuspidate, with a distinctive arched basal margin and markedly antero-posteriorly compressed lateral projections. The median projection bears a posterior longitudinal keel. Turning points are deeply incised, with the lateral projections being only half as wide and half as long as the median projection. *Westergaardodina concamerata* has been compared to *W. curvata* by Müller and Hinz (1991), who noted that the major differences between the two species are that *W. curvata* possesses basal cavity openings and has a more angular basal margin outline. In comparison to *W. communis*, the median projection of *W. concamerata* is much wider in relation to the lateral projections, and the basal margin indentation is often wider. *Westergaardodina behrae* possesses slightly diverging lateral projections which narrow towards their cusps, unlike the lateral projections of *W. concamerata* which do not diverge so markedly, and which do not decrease in width towards their cusps.

Occurrence. VG93-12, Upper Cambrian Alum Shale, Västergötland, Sweden.

Westergaardodina excentrica Müller and Hinz, 1991
Plate 6, figures 8, 9.

* 1991 *Westergaardodina excentrica* Müller and Hinz, p. 45, pl. 33, figs 3, 5-16.

1992 *Westergaardodina excentrica* Müller and Hinz; Hinz, p. 261, pl. 3, fig. 4.

Holotype. UB1392, Müller and Hinz (1991), pl. 33, figs 3, 5, 8, *Agnostus pisiformis* Zone, Gum Quarry, Kinnekulle, Västergötland, Sweden.

Material. 7 elements.

Remarks. Elements of *W. excentrica* are markedly asymmetrical, with the small median projection being indistinct and out of alignment with the median keel. In all cases the median projection is deflected towards the smaller dextral lateral projection, in which the lateral margin is parallel to the base of the element. The sinistral projection is much larger and is also deflected towards the right hand side of the element. These elements conform to the original description of *W. excentrica* by Müller and Hinz (1991) who included all tiny, asymmetrical, tricuspidate sclerites, in which the median projection is small and indistinct, and both lateral projections are deflected towards the right hand side in the specific concept. *Westergaardodina excentrica* is closely comparable to *W. obliqua* Szaniawski, 1971, although the median cusp of *W. obliqua* is larger, the sideways deflection of the lateral projections is less pronounced, and the elements are strongly curved so that the anterior side is concave.

Occurrence. VG93-13, VG93-14, Upper Cambrian Alum Shale, Västergötland, Sweden.

Westergaardodina moessebergensis Müller 1959

Plate 6, figure 7.

p	1959	*Westergaardodina mössebergensis* [*sic*], Müller, p. 470, pl. 14, figs 11, 15 (*non* pl. 14, fig. 12 [= *Westergaardodina polymorpha*]).
	1966	*Westergaardodina mössebergensis* [*sic*] Müller; Nogami, p. 360, pl. 10, figs 1, 2.
	1971	*Westergaardodina moessebergensis* Müller; Müller, p. 10, pl. 2, fig. 5.
?	1973	*Westergaardodina moessebergensis* Müller; Müller, p. 48, pl. 2, fig. 6.
?p	1973	*Westergaardodina* cf. *moessebergensis* Müller; Müller, p. 48, pl. 2, figs 7 (*non* pl. 2, fig. 8 [= *Westergaardodina polymorpha*]).
?	1976	*Westergaardodina moessebergensis* Müller; Miller and Paden, p. 596, pl. 1, fig. 30.
?	1978	*Westergaardodina moessebergensis* Müller; Abaimova, p. 503, pl. 8, figs 8, 10, 11.
	1978	*Westergaardodina mossebergensis* [*sic*] Müller; Druce, p. 52, text-fig. 2a.
?	1979	*Westergaardodina moessebergensis* Müller; Bednarczyk, p. 436, pl. 2, fig. 9.
	1981	*Westergaardodina mössebergensis* [*sic*] Müller; Wang and Wang, p. 3, pl. 1, fig. 11.
?	1983	*Westergaardodina moessebergensis* Müller; An *et al.*, p. 165, pl. 1, fig. 7; text-fig. 9-4.
	1986	*Westergaardodina moessebergensis* Müller; Jiang *et al.*, p. 242, pl. II-1, fig. 19.
?	1987	*Westergaardodina* cf. *W. moessebergensis* Müller, Bagnoli *et al.*, p. 156, pl. 2, fig. 10.
?	1989	*Westergaardodina moessebergensis* Müller; Popov *et al.*, p. 148, pl. 17, fig. 19; pl. 20, figs 11-13.
	1991	*Westergaardodina moessebergensis* Müller; Müller and Hinz, p. 47, pl. 30, figs 1-8, 10.
?	1992	*Westergaardodina moessebergensis* Müller; Buggisch *et al.*, p. 176, pl. 2, figs 3, 4, 7.
	1992	*Westergaardodina moessebergensis* Müller; Hinz, p. 262, pl. 4, fig. 1.
	1994	*Westergaardodina distensa*, An and Mei, p. 33, pl. 4, figs 15, 16.
	1998	*Westergaardodina* cf. *moessebergensis* Müller; Hein and Nowlan, p. 180, pl. 3, figs 5, 7.

Holotype. SMF 10 359, Müller, p. 470, pl. 14, fig. 11, Upper Cambrian Zone 1, Kleva am Mösseberg, Västergötland, Sweden.

Material. 2 elements.

Remarks. Elements assigned to *W. moessebergensis* are bicuspidate, possess deep lateral and basal openings, and have a base that becomes narrower proximally. Lateral projections are parallel and become narrower towards the tip. Of the original material illustrated by Müller (1959), one element is removed from the synonymy (Müller 1959, pl. 14, fig. 12) because the anterior face of the element is markedly smaller than the posterior, unlike the holotype (pl. 14, fig. 11) and is reassigned to *W. polymorpha* on these grounds. Elements figured by Miller and Paden (1976), Bednarczyk (1979), An *et al.* (1983) and Popov *et al.* (1989) are poorly preserved and are only tentatively included in the synonymy. Abaimova (1978) described elements of *W. moessebergensis* which are markedly more elongate than is typical for the species and conversely, An and Mei (1994) illustrated elements, assigned by them to *W. distensa*, which resemble *W. moessebergensis* although they are relatively short and squat in comparison to the holotype.

Occurrence. VG93-14, VG93-16, Upper Cambrian Alum Shale, Västergötland, Sweden.

Westergaardodina polymorpha Müller and Hinz, 1991

?p	1959	*Westergaardodina bicuspidata* Müller, p. 468, pl. 15, figs 1, 10 (*non* pl. 15, figs 7, 9 [= *W. bicuspidata*]; pl. 15, fig. 4 [= phosphatic ball]; pl. 15, fig. 14 [= *W. procera*]).
p	1959	*Westergaardodina mössebergensis* [*sic*] Müller, p. 470, pl. 14, fig. 12 (*non* pl. 14, figs 11, 15 [= *W. moessebergensis*]).
p	1971	*Westergaardodina bicuspidata* Müller; Müller, p. 11, pl. 2, fig. 8 (*non* pl. 2, fig. 9 [= *W. procera*]).
	1971	*Westergaardodina* cf. *moessebergensis* Müller; Müller, p. 11, pl. 2, fig. 6.
p	1973	*Westergaardodina* cf. *moessebergensis* Müller; Müller, p. 11, pl. 2, fig. 8 (*non* pl. 2, fig. 7 [= *Westergaardodina moessebergensis*]).
p	1986	*Westergaardodina bicuspidata* Müller; Chen and Gong, p. 198, pl. 21, fig. 2 (*non* pl. 21, figs 1, 4, 6, 10, 14 [= *W. bicuspidata*]; pl. 21 figs 3, 14 [= *W. wimani*]; pl. 21, figs 5, 15 [= *W. ligula*]).
*	1991	*Westergaardodina polymorpha* Müller and Hinz, p. 48, pl. 31, figs 1-21.
	1992	*Westergaardodina polymorpha* Müller and Hinz; Hinz, p. 262, pl. 4, figs 3, 7.

Holotype. UB 1367, Müller and Hinz (1991), p. 48, pl. 31, fig. 13, Upper Cambrian *Peltura Minor* Zone (Vb), Möckelby-Degerhamn, Öland, Sweden.

Material. 7 elements.

Remarks. *Westergaardodina polymorpha* can be distinguished from *W. bicuspidata* because of its more elongate general outline, and because the basal cavity openings are apparent along the entire length of the outer margins of the lateral processes. In addition, the anterior side is the larger side in *W. bicuspidata*, whereas it is the smaller side in *W. polymorpha*. In comparison to *W. procera*, *W. polymorpha* has a much reduced or absent median projection, larger basal cavity openings and divergent, as opposed to convergent, lateral projections. *Westergaardodina ligula* has a flatter profile than *W. polymorpha* and also have much reduced basal cavity openings.

Müller (1959, 1971) illustrated specimens of *W. polymorpha* as *W. moessebergensis* and *W.* cf. *moessebergensis*. Both of these figures (Müller 1959 pl. 14, fig. 12; Müller 1971, pl. 2, fig. 6) show the anterior (smaller) side of the specimens which, in *W. moessebergensis* should be the larger part of the element, and it is for this reason that these elements are included in the above synonymy. Some elements assigned to *W. bicuspidata* by Müller (1959, pl. 15, figs 1, 10) are tentatively referred to *W. polymorpha* because of their elongate outline and because their lateral projections diverge towards the cusp. It is not possible to infer the relative size of the anterior side from the illustrations given by Müller (1959). Müller (1971, pl. 2, fig. 8) also figured an element of *W. polymorpha* as *W. bicuspidata* and this is reassigned for the same reasons as outlined above. Müller and Hinz (1991) erected the new species *W. polymorpha* and illustrated the highly variable morphology of this taxon between juvenile and adult growth stages. Specimens used in the present study are not closely comparable to the designated holotype of the species, but are similar to other elements figured under the title of *W. polymorpha* by Müller and Hinz (1991).

Occurrence. VG93-8, VG93-13, Upper Cambrian Alum Shale, Västergötland, Sweden.

Westergaardodina procera Müller and Hinz, 1991

Plate 6, figures 12, 13.

p	1959	*Westergaardodina bicuspidata* Müller, p. 468, pl. 15, fig. 14, (*non* pl. 15, figs 1, 10 [= *W. polymorpha*]; pl.15, fig. 4 [= phosphatic ball]; pl. 15 figs 7, 9, [= *W. bicuspidata*]).
p	1971	*Westergaardodina bicuspidata* Müller; Müller, p. 11, pl. 2, fig. 9 (*non* pl. 2, fig. 8 [= *W. bicuspidata*]).
*	1991	*Westergaardodina procera* Müller and Hinz, p. 49, pl. 32, figs 1-18.
	1992	*Westergaardodina procera* Müller and Hinz; Hinz, p. 262, pl. 4, fig. 5.

Holotype. UB 1376, Müller and Hinz (1991), pl. 32, figs 1, 2 6, *Peltura scarabaeoides* Zone (Vc), Grönhogen, Öland, Sweden.

Material. 4 elements.

Remarks. Elements assigned to *W. procera* are elongate and bicuspidate, with a prominent median projection. The median and lateral projections are widely spaced at the base but converge towards the tip, overlapping distally in some cases. *Westergaardodina procera* differs from *W. bicuspidata* by possessing a more prominent median projection, and by being more longitudinally elongate. Commonly, the lateral projections are either parallel or slightly convergent, so that they overlap distally, whereas in *W. bicuspidata* these projections are either parallel or slightly divergent towards the cusp. Müller (1959) included elements of *W. procera* in his original description of *W. bicuspidata*, but it is noted that Müller did state that, with increasing knowledge, the species would be divided into more conservative taxa. Müller and Hinz (1991) erected *W. procera*, and compared the species to *W. polymorpha*, noting that the major difference between the two species is the direction to which the cusps of the lateral projections trend.

Occurrence. O93-1, O93-2, O93-5, Upper Cambrian Alum Shale, Öland, Sweden.

Westergaardodina quadrata (An, 1982)

*	1982	*Westergaardodina moessebergensis quadrata* An, p. 153, pl. 6, figs 5-8, 10.
?p	1983	*Westergaardodina moessebergensis* Müller; An *et al.*, p. 164, pl. 1, fig. 6 (*non* pl. 1, fig. 5 [= *W. moessebergensis*]).
?	1987	*Westergaardodina bicuspidata* Müller; An, p. 115, pl. 3, figs 13, 18.
	1991	*Westergaardodina quadrata* (An); Müller and Hinz, p. 50, pl. 30, figs 9, 11-21.
	1992	*Westergaardodina quadrata* (An); Hinz, p. 264, pl. 3, fig. 5, pl. 4, fig. 9.

1993 *Westergaardodina quadrata* (An); Dong, p. 359, pl. 2, figs 6, 7, 9, 10, 12.

Holotype. An (1982), pl. 6, fig. 6, Upper Cambrian, *Blackwelderia paronai* Zone, Gushan Formation, Kouzhen, Laiwu County, Shandong Province, China.

Material. 1 element.

Remarks. An (1982) first described *Westergaardodina quadrata* as a subspecies of *W. moessebergensis*, due to the overall similarity in shape between the two types of element. However, as noted by Müller and Hinz (1991), differences between the two species are apparent. In *W. quadrata* the right lateral projection is always smaller than the left; the opposite to the situation observed in *W. moessebergensis*. In addition, the turning point of *W. quadrata* is much deeper than that of *W. moessebergensis*, and in adult forms of both *W. moessebergensis* and *W. matsushitai*, to which *W. quadrata* has also been compared, the anterior and posterior sides are fused and do not separate during ontogeny. *Westergaardodina matsushitai* also possesses a smaller left, as opposed to right, lateral projection. The basal margin of *W. moessebergensis* has a tendency to be curved, and is not as broadly quadrate as that of *W. quadrata.* An *et al.* (1983, pl. 1, figs 5, 6) figured two specimens which were assigned to *W. moessebergensis* however, one specimen (pl. 5, fig. 6) is reassigned to *W. quadrata* due to the quadrate nature of the basal margin, and because the right lateral projection is smaller than the left. An (1987, pl. 3, figs 13, 18) illustrated two elements which were referred to *W. bicuspidata*, but are now reassigned to *W. quadrata* because they lack a median projection, are relatively elongated in comparison to *W. bicuspidata* and possess right lateral projections which are smaller than the left. However, it is postulated that they are likely to be juvenile forms.

CHAPTER 6

EUCONODONT SYSTEMATIC PALAEONTOLOGY

6.1 Introduction

Before embarking on the description of the euconodont elements used in this study it is necessary to summarise the current situation concerning the nomenclature applied to the various types of euconodont apparatuses that are known. Elements from the *Proconodontus-Cordylodus* lineage were placed in a separate group (Cavidonta) to the true euconodonts (Conodonta) by Sweet (1988), but this is not supported because both apparatus composition and histology (Chapter 10) demonstrate that the euconodonts form a single monophyletic clade, with a common ancestor of paraconodont affinity (Chapter 9).

6.2 Notation schemes

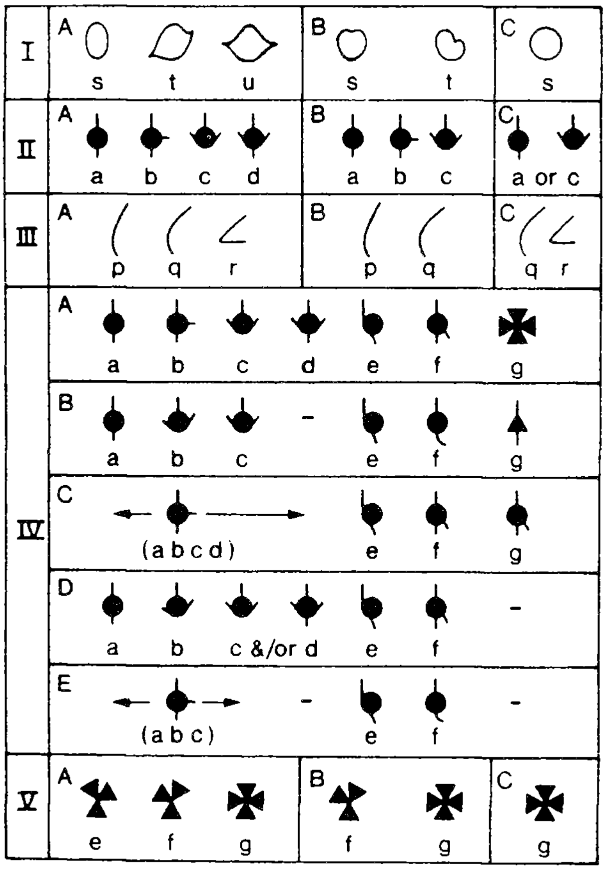
As soon as it was realised that the majority of euconodonts possessed multielement apparatuses, a need arose for a simplified system of apparatus nomenclature, as the use of long, generically-derived adjectival descriptors for the different elements in an apparatus persisted. Jeppsson (1971) and Klapper and Philip (1971) created early notation schemes for ramiform-pectiniform apparatuses (Text-figure 6.1), applying abbreviated versions of the previous, form-taxonomic names to each element type in an apparatus. Although adopted by some authors (Dzik and Drygant 1986; Dzik 1991), these schemes are not widely used at the present day.

The most commonly used multielement apparatus notation scheme currently employed is that of Sweet and Schönlaub (1975, modified by Sweet (*in* Clark 1981)), based on the prioniodinid *Oulodus* Branson and Mehl, 1933. In a similar way to Jeppsson (1971), Sweet and Schönlaub (1975) described an apparatus of elements defined by form-taxonomic names (prioniodiniform, oulodontiform (or lonchodinform), neoprioniodiniform, trichonodelliform, zygognathiform and cordylodontiform (or ligonodiniform). Elements were then classified according to their morphology and their position within the apparatus, with three element morphotypes and six locational positions in each apparatus. Element morphotypes were named P, M and S (abbreviations for pectinate (blade-shaped), makelliform (pick-shaped) and symmetry-transition series elements respectively), and further divided into the six positions (Pa, Pb, M, Sa, Sb, Sc) found in the apparatus. The pectinate elements were placed in Pa and Pb positions, and the array of symmetry-transition elements was divided into Sa, Sb and Sc positions. The Sa position is occupied by a bilaterally symmetrical, unpaired element with well-developed lateral processes. The Sb positions are paired and filled by asymmetrical elements with distinct lateral processes, and the Sc positions are also paired and occupied by slightly asymmetrical elements that lack lateral processes. The term Sd was later introduced for a quadriramate S element found in some apparatuses (Sweet *in* Robison 1981, 1988). No division of the M element category was made by Sweet and Schönlaub (1975). Although originally defined for use in the description of prioniodinid conodont apparatuses (but probably *derived* from ozarkodinid apparatuses (Purnell 1993)), some subsequent authors (e.g. Nicoll 1990, 1992, 1994, 1995; Nicoll *et al.* 1999a, b; Löfgren 1997a, 1997b, 1998, 1999a, 1999b; Löfgren *et al.* 1999) have applied the Sweet and Schönlaub scheme to coniform apparatuses. Löfgren (1999a) stated that, although homologies between element positions in coniform and non-coniform apparatuses had yet to be proved, the similarities in apparatus structure between the two groups are significant enough to be able to apply the Sweet and Schönlaub (1975; Sweet *in* Robison 1981) scheme. Nicoll (1990, 1992, 1994, 1995) however, has applied the Sweet and Schönlaub scheme to coniform element morphotypes, rather than element positions within an apparatus, although this was not stated explicitly. The phylogenetic relationships between early coniform and later ramiform-pectiniform apparatuses remain to be fully elucidated and it should be emphasised, therefore, that the use of the notation scheme outlined by Sweet and Schönlaub (1975; Sweet in Robison 1981) to describe apparatuses in which the arrangement of the elements is unknown, is merely to facilitate a morphological comparison of element types within those apparatuses, and not to demonstrate homology between element positions.

Jeppsson (1971)	Klapper and Philip (1971)	Sweet and Schönlaub (1975)	Sweet (*in* Clark 1981)	Dzik (1991)
tr	A_3	Sa	Sa	tr
hi	A_2	Sb	Sb	ke
hi	A_1	Sc	Sc	hi
pl			Sd	lo/pl
oz	O	Pa	Pb	oz
sp	P	Pb	Pa	sp
ne	N	M	M	ne

Text-figure 6.1. Table to illustrate the various notation schemes initially introduced to compare different euconodont apparatuses.

Barnes *et al.* (1979) introduced an apparatus notation scheme that encompassed both ramiform-pectiniform and coniform apparatuses. Five apparatus types were distinguished and then further subdivided into seventeen sub-types according to the combination of elements found within each apparatus (Text-figure 6.2). Coniform elements were placed mainly, but not wholly, in Type I or Type III apparatuses, depending on whether overall symmetry and compression (Type I), or degree of curvature of the cusp (Type III), was the principal character used to define the elements in the apparatus. Elements assigned to Type I apparatuses were labelled as either s, t, or u elements, s elements being symmetrical and laterally compressed, t elements being asymmetrical and u elements being symmetrical and antero-posteriorly compressed. Type III apparatuses possessed p, q and r elements, with p elements being erect, q elements being moderately to markedly curved and r elements being strongly reclined. Ramiform-pectiniform elements were labelled a, b, c, d, e, f or g according to the symmetry, presence or absence and position of processes and general overall morphology of the elements. These were then placed in Type II, Type IV or Type V apparatuses.



Text-figure 6.2. Diagram to show the five types and seventeen sub-types of apparatuses described by Barnes *et al.* (1979). (From Barnes *et al.* 1979).

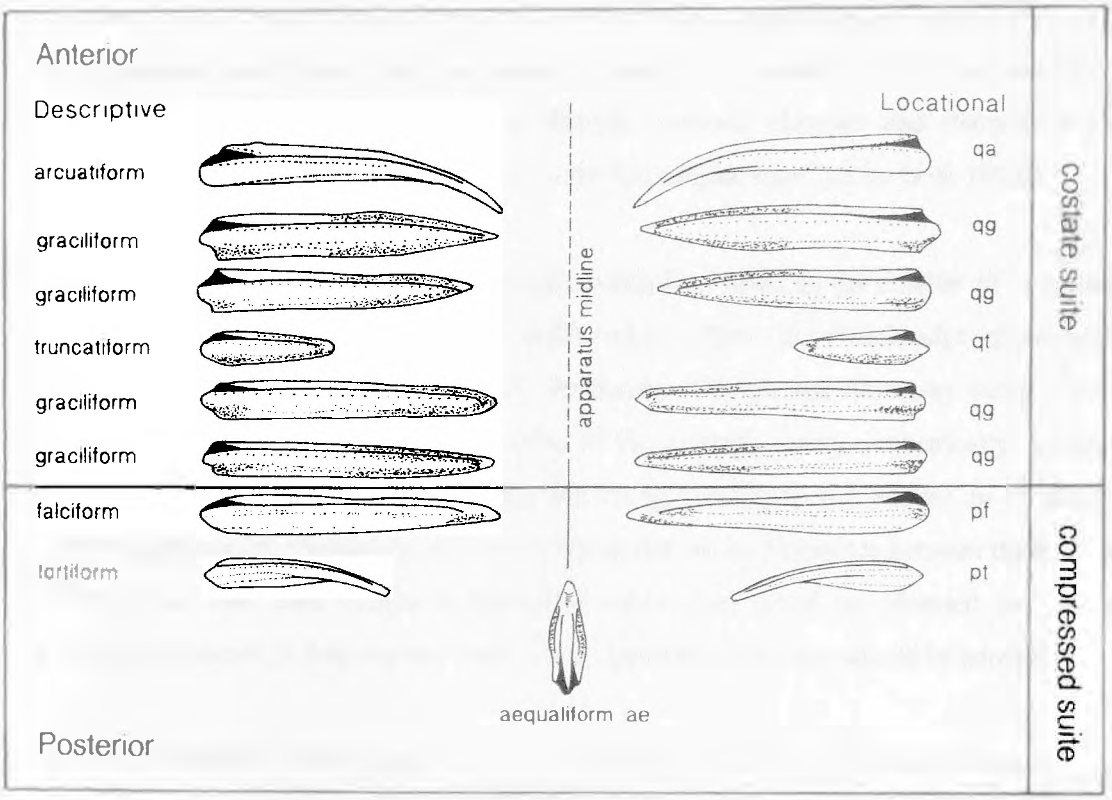
Using the different element categories, the majority of coniform apparatuses could be described using the Barnes *et al.* (1979) scheme. Ji and Barnes (1990, 1994a, b) subsequently modified the scheme of Barnes *et al.* (1979) using evidence derived from Early Ordovician, mostly coniform, elements. Only five element-types were recognised in the new notation scheme, labelled a, b, c, e or f, with these being divided into two transition series. Elements found in the first transition series are symmetrical, rounded to sub-rounded and reclined (a-elements), symmetrical, slightly compressed on one lateral side, reclined to recurved (b-elements) or symmetrical, posteriorly compressed, erect to sub-erect with an expanded base (c-elements). Those in the second transition series are asymmetrical, laterally or orally compressed (e-elements) or symmetrical, laterally compressed and sub-erect (f-elements). Coniform apparatuses are easily distinguished using the Ji and Barnes (1990, 1994a, b) scheme, however the more subtle differences between the elements in an apparatus are overlooked due to the encompassing nature of the element categories described by these authors.

Ramiform-pectiniform apparatuses were described by Armstrong (1990) using the Sweet and Schönlaub (1975) scheme, but this notation was rejected as a valid tool for the description of coniform apparatuses in which element positions and apparatus architecture and function are unknown, or at least poorly understood. Instead, Armstrong (1990) chose to modify the notation scheme of Barnes *et al.* (1979) using their Type III apparatus nomenclature to describe various Upper Ordovician and Lower Silurian coniform apparatuses, in order to directly compare apparatus composition between these forms. Armstrong (1990, p. 40) redefined the p elements of Barnes *et al.* (1979) as "erect elements with a long base and a short, proclined cusp", with q elements being more strongly recurved and laterally compressed than the p elements. Several discrete element types were recognised in each category, symmetrical (sym. p), asymmetrical (ap) and twisted (tp) elements in the p category and symmetrical (sq) and asymmetrical (aq) elements in the q category. The strongly recurved r elements were not subdivided further.

Using evidence from fused clusters and a bedding plane assemblage of elements, Sansom *et al.* (1994) were able to modify the scheme proposed by Armstrong (1990) for the genus *Panderodus* Ethington, 1959, the only coniform taxon adequately represented by natural assemblages. Sufficient data were available to introduce parallel systems of morphological and locational/architectural nomenclature for the apparatus of *Panderodus*, which still remains the most fully understood apparatus of coniform, euconodont elements.

Three locational domains were recognised in the *Panderodus* apparatus by Sansom *et al.* (Text-figure 6.3), an anterior costate suite (q elements), a posterior compressed suite (p elements) and the aequaliform (ae) domain lying on the midline, probably towards the posterior of the apparatus. Six morphological element categories were described (based mainly on descriptions of

Panderodus elements by Sweet (1979)), with arcuatiform, graciliform and truncatiform elements occupying the anterior domain (qa, qg and qt elements respectively), falciform and tortiform (pf and pt) elements occupying the posterior domain and the aequaliform (ae) element lying on the midline (Text-figure 6.3). The three-dimensional architecture of the *Panderodus* apparatus has been discussed by Smith *et al.* (1987) and by Sansom *et al.* (1994), who concluded that the apparatus consists of two bilaterally opposed linear, possibly arched, element arrays, with a single symmetrical element apart from these on the midline of the apparatus. Armstrong (1997) has since applied the Sansom *et al.* (1994) notation scheme to a number of Ordovician coniform apparatuses.



Text-figure 6.3. The apparatus composition and architecture of *Panderodus* as described by Sansom *et al.* (1994) following the earlier notation scheme of Armstrong (1990). (From Sansom *et al.* 1994).

6.3 *Apparatus architecture and homology*

Using evidence from fused clusters and bedding plane assemblages of elements, attempts can be made to reconstruct the three-dimensional architecture of conodont apparatuses. The majority of bedding plane assemblages comprise ramiform-pectiniform apparatuses and, therefore, it is these apparatuses that have been studied in the most detail. Purnell and Donoghue (1998) provided a full review of the historical development and current opinion of the architecture of ozarkodinid apparatuses and have described the 3D apparatus arrangement using photographic techniques outlined by Briggs and Williams (1981), and used by Aldridge *et al.* (1987), to reconstruct collapsed apparatuses found on bedding planes. Assemblages of prioniodontids and prioniodinids are fewer in number than ozarkodinids (Purnell and Donoghue 1998), however they appear to comply to a plan similar to the ozarkodinid apparatus (e.g. the prioniodinid *Kladognathus* described by Purnell (1993); the prioniodinid *Gondolella* described by von Bitter and Merril (1998) and the prioniodontid *Promissum pulchrum* described by Aldridge *et al.* (1995)). Descriptions of the architecture of coniform apparatuses, based on bedding plane assemblage data, are restricted to *Panderodus* (Smith *et al.* 1987; Sansom *et al.* 1994), although Dzik (1991) has attempted to reconstruct the architecture of other coniform apparatuses using evidence from fused clusters (e.g. *Besselodus* from the cluster illustrated by Aldridge (1982)) and also from tentative morphological homologies between discrete coniform elements and elements in the apparatus of *Ozarkodina* (e.g. *Drepanodus* from the homologies described by Dzik 1990)).

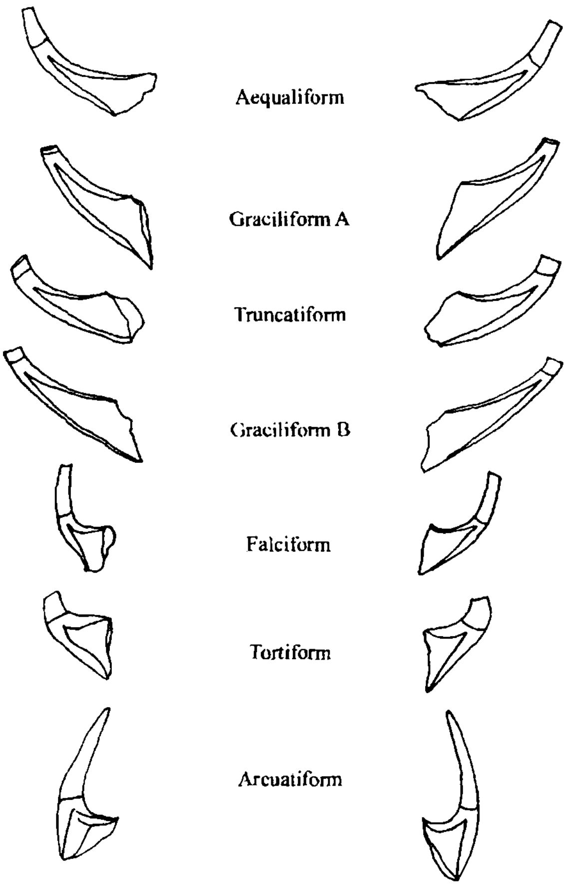
Sansom *et al.* (1994) emphasised that, although similarities (such as the number of locational domains) exist between the architecture of ramiform-pectiniform and *Panderodus* apparatuses, important differences can also be recognised. Particular attention was drawn by Smith (1990) and by Sansom *et al.* (1994) to the orientation of the elements, being diametrically opposed, perpendicular to the midline in *Panderodus*, but being parallel to the midline in ramiform-pectiniform apparatuses. Sansom *et al.* (1994) stated that no intermediates between these styles are known, and that until further architectural information could be obtained for Lower Ordovician apparatuses, a conservative approach to apparatus homology should be adopted.

Purnell and Donoghue (1998) argued that, with such a limited amount of evidence (three clusters and a bedding plane assemblage), the model of apparatus architecture developed by Sansom *et al.* (1994) for *Panderodus* may be modified if further evidence comes to light, and indeed may prove to be more closely comparable to the ozarkodinid architecture advocated by them, than envisaged by Sansom *et al.* (1994). Purnell and Donoghue acknowledged that their hypothesis, based on the apparatus collapse pattern demonstrated by the Waukesha assemblage (Smith *et al.* 1987, p. 98, fig. 6.7) is speculative, but were optimistic that homologies between coniform and ramiform-pectiniform architectures will be demonstrated in the future.

Without being able to recognise homologies between apparatuses, it is impossible to erect a stable suprageneric classification scheme for euconodonts, and indeed the question of polyphyly of the euconodont clade remains unresolved. For this reason it is necessary to establish a notation scheme that is applicable to Cambrian euconodonts from the *Proconodontus* lineage, and to attempt to recognise similarities between these and other late Cambrian and early Ordovician euconodont apparatuses.

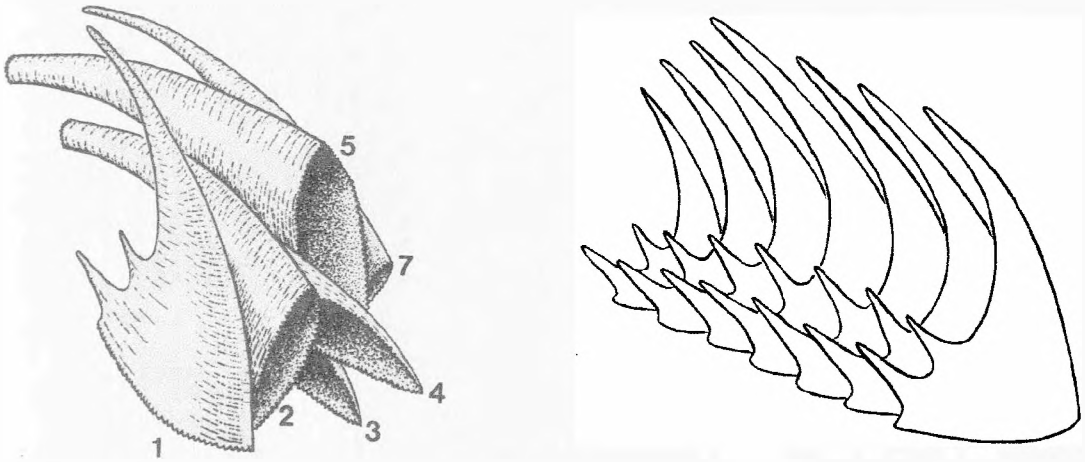
6.4 *Comparison of* Proconodontus *lineage and other coniform euconodont apparatuses*

The brief historical review outlined above demonstrates the various methods by which apparatus reconstructions have been developed, and some of the problems associated with the nomenclatural schemes employed to describe them. What follows is a comparison of the apparatus composition of the various genera from the *Proconodontus* lineage, with other coniform apparatuses that have been reconstructed in recent years.



Text-figure 6.4. Reconstruction of the apparatus composition of *Eoconodontus notchpeakensis* (Miller). Elements were traced using a camera-lucida, illustrations on the left-hand column are of the inner lateral face of the element, those on the right-hand column are of the outer lateral face of the same element.

Apparatus reconstructions of genera from the *Proconodontus* lineage (*Proconodontus*, *Eoconodontus*, *Cambrooistodus*, *Cordylodus*) remain hypothetical due to the rarity of fused cluster data and the absence of evidence from bedding plane assemblages. In this study, the apparatus of *Proconodontus muelleri* is reconstructed as being trimembrate, possessing aequaliform, graciliform and arcuatiform elements, and *Eoconodontus notchpeakensis* is reconstructed with a septimembrate apparatus of aequaliform, graciliform, truncatiform, arcuatiform, falciform and tortiform elements (Text-figure 6.4). An apparatus reconstruction has not been formalised for *Cambrooistodus*, but it is likely that it is similar to that of *Eoconodontus*. The lack of specimens of *Cordylodus* in the studied material means that the apparatus reconstructions proposed by other authors (Repetski 1980; Andres 1981, 1988; Nicoll 1990, 1992) must be used for reference.



Text-figure 6.5. A cluster of *Cordylodus* elements, and the interpretation of that cluster by Andres (1981). (From Andres 1981).

Two clusters of *Cordylodus* elements have been previously reported (Andres 1981, 1988; Repetski 1980). The cluster described by Andres (1981, 1988; Text-figure 6.5) comprises seven elements which, according to Andres, are not strongly morphologically differentiated apart from in size, and probably represent a juvenile stage in ontogeny. However, the three elements in the cluster of *C. lindstromi* described by Repetski (1980) do show morphological differences with variation in cusp curvature between the straight, the curved and the strongly curved elements. Additionally, Repetski (1980; pers. comm. October 1999) noted the presence of remnants of at least two additional elements in opposed position, represented only by the distal ends of the denticles, and hence both Andres (1981) and Repetski (1980) have reconstructed the apparatus as having two opposing arrays of elements (Andres 1981, p. 27, text-fig 20) similar to the protoconodont *Phakelodus* Miller for which the apparatus reconstruction is well known from many fused clusters and bedding plane assemblages (Miller and Rushton 1973; Müller and Andres 1976; Landing 1977, 1983; Landing *et al.* 1980; Andres 1981, 1988; Fortey *et al.* 1982; Bergström and Orchard 1985; Buggisch and Repetski 1987; Heredia and Bordonaro 1988; Müller and Hinz 1991; Hinz 1992; Dong 1993). Smith, Repetski and Donoghue are in the process of conducting further work and re-describing this specimen (Donoghue pers. comm., August 2000; Smith pers. comm., October 2000).

Apart from these clusters of *Cordylodus*, clusters of *Eoconodontus* elements have been reported from siliceous deposits from the Upper Cambrian *E. notchpeakensis* Zone of the Burubaital Suite of south-central Kazakhstan (Tolmacheva at the Palaeontological Association meeting in Cardiff, 1997), and also from the Vinini Formation of north-central Nevada (Repetski 1980). However, the cluster of *E. notchpeakensis* reported by Repetski is now thought to be of a species of *Utahconus*, not *Eoconodontus*, (Repetski pers. comm. October, 1999). Details were difficult to discern in the material presented by Tolmacheva, and in her photographs of these elements viewed by myself at the Palaeontological Association meeting at Cardiff in December 1997, and until these data are fully reported by Tolmacheva, it remains inappropriate to add further comment.

Apparatuses of *Cordylodus*, reconstructed from discrete element collections, have been illustrated by Nicoll (1990, 1992) who used the Sweet and Schönlaub scheme of M, P and S elements to describe in detail a septimembrate apparatus for three species of the genus (*C. proavus*, *C. lindstromi* and *C. angulatus*). Problems associated with the taxonomy and phylogeny of *Cordylodus* determined by Nicoll are outside of the scope of this thesis (in the 'acknowledgements' section of Nicoll's (1990) publication, it was stated that the reviewers did not necessarily agree with the interpreted reconstruction), however, the elements included in the apparatus reconstruction of *Cordylodus proavus* show close morphological similarities with the elements included in the apparatus composition outlined for *Eoconodontus notchpeakensis* Inspection of material provided by Prof. J. F. Miller (Southwest Missouri State University) has shown that the elements described by Nicoll are present in collections for both *C. proavus* and *C. lindstromi*. Nicoll's inclusion of *C. intermedius* in the apparatus of *C. angulatus* is questionable. The apparatus reconstructions provided for *Cordylodus* by Nicoll (1990, 1992) include a symmetrical Sa element, asymmetrical S, Sc and Sd elements, laterally twisted, asymmetrical Pa and Pb elements and a compressed M element. Use of this notation is contrary to the original purpose intended by Sweet and Schönlaub (1975), as a locational, not morphological scheme, however its use as a tool for comparing morphologically similar elements from different apparatuses is inevitable, now that its use is commonplace in coniform apparatus terminology (Nicoll 1990, 1992, 1994, 1995; Nicoll *et al.* 1999a; Löfgren 1997a, 1997b, 1998, 1999a, 1999b; Löfgren *et al.* 1999).

Since the original description of the monoelemental apparatus of *Iapetognathus* by Landing (*in* Fortey *et al.* 1982), it has been thought that the genus evolved from *Cordylodus* by the loss of the 'compressed' element morphotype (at the time it was believed that *Cordylodus* possessed a bimembrate apparatus of 'rounded and 'compressed' elements), and by the change in the orientation of the process from posterior in *Cordylodus* to lateral in *Iapetognathus* (Landing 1982; Sweet 1988). In the latest publication concerning the latter genus, Nicoll *et al.* (1999a, p. 48) acknowledged that it is difficult to ascertain the true orientation of the elements, due to the curved nature of the cusp and process and indeed, without prior knowledge of the apparatus architecture, it remains impossible to assign terms pertaining to the true biological orientation to any part of the elements within an apparatus. For this reason, in this study and in that of Nicoll *et al.* (1999a) conventional terms have been applied to the various parts of the element (e.g. anterior, posterior and lateral margins in regards to the cusp compression and curvature, together with the characteristics of the basal cavity). Nicoll *et al.* (1999a) have reconstructed septimembrate apparatuses for species of *Iapetognathus* Landing, 1982 and its ancestor, the new genus *Iapetonudus* Nicoll, Miller, Nowlan, Repetski and Ethington, although certain elements are yet to be described for some species of the two genera. Again the M, P, S notation scheme of Sweet and Schönlaub (1975) has been utilised although the apparatus of *Iapetognathus* (and probably *Iapetonudus*) lacks Sa and M elements (Nicoll *et al.* 1999a), both of which possess distinctive morphologies in other coniform apparatuses, the Sa being symmetrical and the M element being geniculate or at least strongly recurved. Two element types were placed in a new category of X elements (Xa and Xb), because they do not conform to the shape categories proposed by Nicoll (1977). This new X category was not meant to be a permanent addition to the notation scheme, but was intended to make comparison between the elements in the apparatuses easier (Nicoll *et al.* 1999a, p. 43). The absence of the Sa (aequaliform) and M (arcuatiform) elements, and the presence of two new element types (Xa, Xb) marks a clear difference between the apparatuses of *Iapetognathus* and *Iapetonudus* and their supposed close relatives within the *Proconodontus* lineage, which possess both aequaliform (Sa) and arcuatiform (M) elements and lack elements from the X category (according to the interpretation of the apparatus presented herein). From the overall shape of the cusp of *Iapetognathus* specimens, which are generally rounded and not strongly antero-posteriorly or laterally compressed, and also from the presence of microstriae on the outer surface of the elements of the new species *Iapetognathus landingi* Nicoll, Miller, Nowlan, Repetski and Ethington, together with the lack of an M element in the apparatus, it is tentatively suggested that *Iapetognathus* might share a closer relationship with forms from the *Teridontus* lineage, and not the *Proconodontus* lineage, although this hypothesis remains to be rigorously tested.

6.5 Comparison with forms not usually included within the Proconodontus *lineage*

Since multielement taxonomy became the favoured mechanism for describing the conodonts from discrete element collections, many coniform apparatuses have been reconstructed. However, given the nature of this project, it is inappropriate to attempt to comment on all of them, and so some of the genera most relevant to the early evolution of euconodonts have been selected, together with those that are considered to be the most fully understood. A summary of these reconstructions is given in Text-figure 6.6.

Genus	Authors	Element types								
Eoconodontus	This study	ae	qg	qg	qg	pf	pt	qa		
Cordylodus	Nicoll (1990)	Sa	Sb	Sc	Sd	Pa	Pb	M		
Cordylodus	Ji and Barnes (1994)	c	a	b	a	?a	?a	e		
Iapetognathus	Nicoll *et al.* (1999)		Sb	Sc	Sd	Pa	Pb		Xa	Xb
Drepanodus	Löfgren (1997a)	Sa	Sb	Sc	Sd	Pa	Pb	M		
Drepanodus	Ji and Barnes (1990)	c	a	a	a	e	E			
?Drepanodus	Dzik (1991)	tr	he/ke/pl/lo			sp	oz	ne		
Protopanderodus	McCracken (1989)	c	a/b					e		
Protopanderodus	Armstrong (1997)	ae	qg	qt	qg	pf	pt	qa		
Paroistodus	Löfgren (1997a)	Sa	Sb	Sc	Sd	Pa	Pb	M		
Paltodus	Löfgren (1997b)	Sa	Sb	Sc	Sd	Pa	Pb	M		
Teridontus	Nicoll (1990)	Sa	Sb	Sc	Sd	Pa	Pb			
Semiacontiodus	Ji and Barnes (1994)	c	a	b	a	?a	?a	e		
Semiacontiodus	Löfgren (1999b)	Sa	Sb	Sc	Sd	Pa	Pb			
Cornuodus	Armstrong (1997)	ae	qg	qt	qg	pf	pt	qa		
Cornuodus	Löfgren (1999a)	Sa	Sb	Sc	Sd	Pa	Pb			
Variabiliconus	Löfgren *et al.* (1999)	Sa	Sb	Sc	Sd	Pa	Pb			
Decoriconus	Löfgren (1998)	Sa	Sb	Sc	Sd	Pa	Pb			
Panderodus	Sansom *et al.* (1994)	ae	qg	qt	qg	pf	pt	qa		

Text-figure 6.6. Apparatus reconstructions of various coniform apparatuses by various different authors. The terms used in the description of the *Eoconodontus* are abbreviated to the locational terms first applied to the *Panderodus* apparatus by Sansom *et al.* (1994). In this case, these terms refer only to the morphological comparison of the elements, because as yet the apparatus architecture of *Eoconodontus* is unknown.

In some cases, more than one apparatus reconstruction has been developed for a particular genus by one or more authors, and these have been included to demonstrate the relationships between the various notation schemes that are in use. It must be noted that these comparisons between apparatuses are my interpretations, based on morphological similarities between element types observed in the illustrations provided by those authors. The generalised set of morphological characteristics that have been recognised for each element type are summarised in Text-figure 6.7.

Element type		Characteristics
Sa	tr, c, ae	Symmetrical elements
Sb	he/ke/pl/lo, qg, a, a/b	Elements similar in form to the symmetrical element, but being asymmetrical due to the flattening of a lateral face or due to lateral twisting of the cusp. These forms usually possess a relatively long base.
Sc	he/ke/pl/lo, qt, a, b, a/b	Asymmetrical elements with a relatively short base and often being more strongly recurved than the remaining S elements.
Sd	he/ke/pl/lo, qg, a, a/b	Asymmetrical elements with a long base, often appearing quite delicate in relation to the remaining S elements.
Pa	sp, pf, e, ?a	Asymmetrical elements with a flaring base and a laterally twisted cusp. The flared basal opening often opens to one side of the element. In elements that are not flared basally, the twisting of the cusp is diagnostic. The base is short in comparison to the S elements.
Pb	oz, pt, e, ?a	Asymmetrical, laterally compressed elements in which the base is elongated antero-posteriorly and the antero-basal corner is widely rounded. The base is short in comparison to the S elements.
M	ne, e, qa	Asymmetrical, markedly laterally compressed, strongly recurved or geniculate, often laterally twisted elements.
X		Elements so far only recognised in the genus *Iapetognathus*, often possessing a posterior and a lateral denticulate process.

Text-figure 6.7. A summary of the general morphological characteristics of each element type recognised in a number of different coniform apparatuses.

If the X elements are disregarded, due to their presence in only one genus of uncertain affinity, it can be noted that of the remaining seven morphological element categories, some apparatuses comprise all seven morphotypes, whereas others possess only six element morphotypes, usually lacking an M (strongly recurved or geniculate) morphotype. However, occasionally there is some discrepancy between the number of element types included in the apparatus reconstructions for a single genus by different authors (e.g. the reconstruction of the apparatus of *Cornuodus* by

Löfgren 1999a is seximembrate, whereas that by Armstrong 1997 is septimembrate), which emphasises the difficulties faced in reconstructing coniform apparatuses from discrete element collections, especially because of the subtle morphological differences between the element types.

Nicoll (1990, 1994) has commented that apparatuses of coniform elements seem to fall in to two categories, those with six and those with seven elements. According to Nicoll, septimembrate apparatuses are composed of S, P and M elements, with seximembrate apparatuses lacking the M element morphotype. Nicoll's hypothesis concurred with the views of Ji and Barnes (1990, 1994) who erected two 'complexes' of euconodonts named after the oldest representative of each group of forms, namely the '*Teridontus*' and the '*Proconodontus*' complexes. This followed Miller (1980, 1984) who divided the late Cambrian euconodonts into the *Teridontus* and *Proconodontus* lineages, but expanded the number of genera investigated. The apparatus reconstructions outlined in Text-figure 6.7 largely follow the designation of genera to each complex described by Ji and Barnes (1990, p. 346, fig. 9), with *Teridontus* complex forms being seximembrate and *Proconodontus* complex forms being septimembrate (the reconstruction of *Cornuodus* by Armstrong (1997) does not fit this rule).

The evolutionary relationships that were suggested by Sweet (1988), and followed in part by Aldridge and Smith (1993), are not supported by these apparatus reconstructions, especially in the case of forms assigned to the Acanthodontidae (*Drepanodus*) and to the Drepanoistodontidae (*Paltodus*, *Paroistodus*) which, according to Sweet (1988) are more closely related to the protopanderodontid genera *Teridontus*, *Utahconus* and *Monocostodus* (the Oneotodontidae of Aldridge and Smith 1993) than the Proconodontidae and Cordylodontidae.

Using these apparatus reconstructions, it is suggested that genera with septimembrate apparatuses such as *Drepanodus*, *Paltodus*, *Paroistodus* and probably *Protopanderodus* and *Panderodus* may be more closely related to the *Proconodontus* lineage than has been previously suggested (Sweet 1988). These apparatus reconstructions also support the hypotheses of Miller (1980, 1984), that at least two groups of euconodonts evolved (perhaps separately) during the late Cambrian, and that these had different apparatus compositions. Alternatively, it could be argued that, during these early stages in euconodont evolution, the elemental composition of the different apparatuses was an unstable characteristic and that element morphotypes were frequently lost and gained during the euconodont phylogeny. Both of these ideas rely on the apparatus reconstructions, outlined above, being the correct interpretation, or at least the best estimate of the true biological apparatus composition of each of the genera investigated.

Unfortunately, for the majority of these apparatuses, fused clusters or bedding plane assemblages of elements have not been recovered, and so conclusive evidence of apparatus composition in not available. However, some fused clusters of coniform euconodont genera have been described, and it is possible to us these as a potential template for these hypothetical apparatus reconstructions.

6.6 *Fused cluster evidence*

Several authors have described and/or illustrated fused clusters of coniform euconodont elements (Barnes 1967; Pollock 1969; Nowlan 1979; Repetski 1980; Andres 1981, 1988; Aldridge 1982; An *et al.* 1983; Mikulic *et al.* 1985a, 1985b; Dzik and Drygant 1986; Smith *et al.* 1987; McCracken 1989; Smith 1991; Müller and Hinz 1991; Sansom *et al.* 1994). Some of these are more complete than others, for example the Podolia cluster of thirteen *Panderodus unicostatus* elements described by Dzik and Drygant (1986) and by Sansom *et al.* (1994), and the cluster of seven elements of *Besselodus arcticus* described by Aldridge (1982). The apparatus composition and architecture of *Panderodus* has been fully described by Sansom *et al.* (1994), who compared their model to other coniform apparatuses (Sansom *et al.* p. 794, text-fig. 8) including *Belodina*, *Besselodus* and *Coelocerodontus*, for which fused cluster evidence is available. In one of the two fused clusters of *Belodina* elements described by Nowlan (1979), a grandiform element is fused to a geniculate eobelodiniform element, and in the other cluster a compressiform element is fused to a grandiform element, similar to the cluster of four *Belodina* elements (two compressiform, two grandiform) illustrated by Barnes (1967). Similarly, in the cluster of seven *Besselodus* elements described by Aldridge (broken during handling into two sub-clusters, Aldridge 1982, p. 428), a geniculate (oistodontiform) element is present at one end of the assemblage, and is grouped with distacodontiform elements of similar size, showing no variation in curvature (Aldridge 1982, p. 428). Sansom *et al.* (1994) compared the apparatus of *Coelocerodontus* described by Andres (1988, fig. 17) to that of *Panderodus*, *Belodina* and *Besselodus*, and concluded that the anterior, unicostate element was homologous to he arcuatiform (qa) element of *Panderodus* and to the geniculate element of both *Besselodus* and *Belodina.*

In comparison with the apparatus outlined for *Eoconodontus*, it is possible that the strongly recurved, compressed element (homologous to the geniculate element of *Cambrooistodus*) may be homologous to the geniculate (arcuatiform) element in these other apparatuses. Conversely, the observed similarity may be due to evolutionary convergence, and not strict biological homology. In addition, the apparatuses compared by Sansom *et al.* (1994) that are represented by fused clusters also possess a suite of graciliform and truncatiform (distacodontiform) elements, which may be likened to the asymmetrical, rounded element morphotypes found in the *Eoconodontus* apparatus. Sansom *et al.* (1994) suggested that elements filling the proposed p positions are absent in the *Besselodus* apparatus, but are present in the other forms, and on this basis assigned *Besselodus* (and *Dapsilodus*) to the Protopanderodontida, and *Belodina*, *Coelocerodontus* and *Panderodus* to the Panderodontida. In the *Eoconodontus* apparatus, two rare elements are compared to the falciform and tortiform elements of *Panderodus* because of their gross morphology, one being laterally twisted and the other being strongly laterally compressed and often quite small in relation to the other elements in the sample. In all apparatuses, including *Eoconodontus*, there is a symmetrical element morphotype that is assumed to lie on the midline of the apparatus. Although present in the Waukesha bedding plane assemblage of *Panderodus* (Sansom *et al.* 1994, text-fig. 3), the symmetrical element has not been found in any of the fused clusters reported to date.

These fused clusters (including those of *Cordylodus* sp. outlined above), in conjunction with the evidence described from the bedding plane assemblage of *Panderodus* (Sansom *et al.* 1994) suggest that all these apparatuses were composed of two opposing arrays of elements, with the element tips perpendicular to the midline of the animal. The similarities with the proposed *Eoconodontus* apparatus imply that the elements in forms from the *Proconodontus* lineage were arranged in a comparable manner.

6.7 The notation scheme that can be applied to Proconodontus *lineage apparatuses*

Until further evidence is obtained, the apparatus reconstruction of *Panderodus* developed by Sansom *et al.* (1994) is the best model for a coniform euconodont apparatus. However, there is still no consensus of opinion as to whether to apply the terms introduced by Sansom *et al.* to all coniform euconodont apparatuses, or whether to use a version of the M, P, S scheme of Sweet and Schönlaub (1975) modified to be applied to morphological, as opposed to locational, homology. These are the two most commonly applied schemes at the present day and there appears to be a division into two schools of thought, one headed by Nicoll and Löfgren who advocate the use of the Sweet and Schönlaub scheme, and the other being headed by Armstrong and Sansom who favour the Sansom *et al.* scheme. Löfgren (1997a, p. 915) implied that the M, P, S notation scheme is difficult to apply to more advanced coniform genera, such as *Panderodus*, and that therefore the Sansom *et al.* scheme is more applicable to these genera than to the more 'primitive' Lower Ordovician euconodonts that are the focus of her studies so far.

However, Armstrong (1997, p. 771) considered the Sansom *et al.* scheme to be widely applicable to all coniform apparatuses and, following his earlier work (Armstrong 1997), emphasised that the Sweet and Schönlaub (1975) scheme should be used to compare locations within an apparatus, and not element morphotypes.

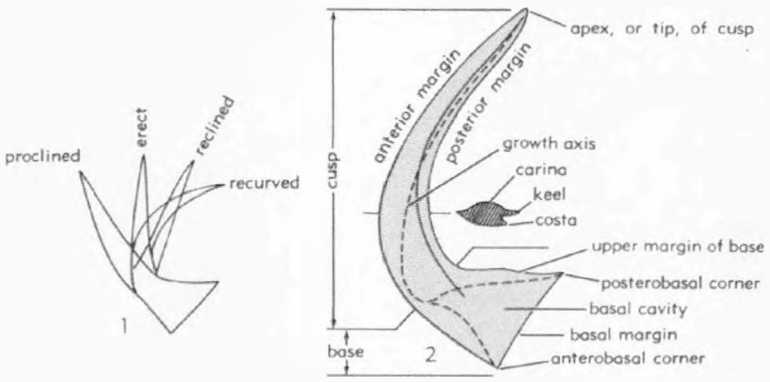
At the present day, the majority of euconodont apparatuses must be reconstructed using discrete element collections, and a certain amount of shoe-horning of elements into the morphological categories that are recognised in more well-known apparatuses is evident. Until this is resolved, there is a great danger that apparatus homologies will be an artefact of the preconceptions of the particular author(s) that are producing the most up-to-date reconstructions. This may account for the slightly different reconstructions proposed for the same genus by separate authors, as mentioned earlier. It is still far too easy to fall into the trap of applying a locational scheme to an apparatus, based on morphological similarity between elements that may, or may not, occupy those positions. This has occurred in the case of the use of the Sweet and Schönlaub (1975) scheme by Nicoll (1990, 1992, 1994, 1995) to describe coniform apparatuses, and is in danger of occurring in the case of the Sansom *et al.* scheme if the distinction between morphological comparison and locational homology is not clearly stated.

In this study, the apparatus reconstruction for *Eoconodontus* has been compared with the apparatus reconstructions of various genera by various authors. It is notable that, based on morphological similarities between elements, the apparatus of *Eoconodontus* compares very closely with the reconstructions of *Drepanodus*, *Paltodus* and *Paroistodus* by Löfgren (1997a, 1997b) and also the reconstruction proposed for *Cordylodus* by Nicoll (1990,1992). In addition, the apparatus is composed of similar element categories to those included in *Panderodus* by Sansom *et al.* (1994). To this end, during the course of this study, terms from both notation schemes have been applied to *Eoconodontus* at one time or another, but the use of the Armstrong (1990) scheme as modified by Sansom *et al.* (1994) is preferred because of its sound basis using fused cluster evidence in association with large discrete element collections. In addition, this scheme allows the user to distinguish coniform apparatuses from those containing ramiform-pectiniform elements and emphasises the possible non-homology of the elements as stated by Sansom *et al.* (1994) who noted that the anatomical orientation of the elements was not comparable in coniform and ramiform-pectiniform apparatuses.

6.8 A note on anatomical orientation and notation

Purnell *et al.* (2000) have introduced a new system of terminology that can be applied to elements in euconodont apparatuses that are known from bedding plane assemblages, or are closely related to these well-known forms (mostly ozarkodinids, prioniodinids and prioniodontids). The new terminology replaces the traditional terms that were used to define the arbitrary orientation of an element, so that the elements are now described according to their position and alignment within a known apparatus architecture. Replacement terms include 'rostral' and 'caudal' (instead of anterior and posterior), 'dorsal' and 'ventral' (no change = upper and lower), 'sinistral' and 'dextral' (no change = left and right) and 'adaxial' and 'abaxial' (towards or away from the rostrocaudal (longitudinal) axis). The locational terminology of P, M and S positions (Sweet and Schönlaub 1975) remain in use, as the majority of euconodont apparatuses can be divided into these three locational domains. Elements in the S-array are numbered away from the element on the midline, so that the element in the central position is S_0, the first element to the right of this is S_1^d, the first on the left is S_1^s and so on. P elements are numbered from caudal (P_1) to rostral (P_{1+x}) and the M element remains undivided. This new terminology (Purnell *et al.* 2000) seems relevant for most well-known ramiform-pectiniform apparatuses, although a certain amount of scepticism must be retained, since it is possible that a P_2 element in one apparatus could prove to be homologous to the P_3 element in a second apparatus (or *vice versa*, or indeed any combination of homology or non-homology between various elements), and this is likely to lead to a certain amount of confusion. In addition, it seems possible that the different processes in the more complex elements may also prove difficult to homologise, for instance if the rostral process of one P_2 element was found to be homologous to the sinistral process of a P_2 element from a different apparatus, thus adding an extra degree of complexity to the already problematic concept of 'homology' (i.e. homologous structures being given different names).

More importantly, the new terminology introduced by Purnell *et al.* (2000) is not suitable for use with coniform euconodonts, since only *Panderodus* has a well-constrained architectural model, and this may prove not to be universally applicable to all coniform apparatuses. In cases where true anatomical orientation is unknown (or uncertain), Purnell *et al.* suggested that terms pertaining to the orientation of an element should be placed in inverted commas, and illustrated this point by re-writing the description of the P element of *Eucharodus apion* given by Smith (1991). In the re-description, Purnell *et al.* replaced the term *basal* with the term *aboral*, and placed inverted commas around each mention of the terms *anterior*, *posterior* and *inwards*, making a total of 14 changes, of which two (basal - aboral) were strictly new terms. As expressed by M. P. Smith (pers. comm., August 2000) these minor changes seem a little unnecessary, especially in a species of euconodont for which an apparatus is, as yet, unknown. Similarly, in the descriptions of the new apparatus compositions that follow (*Proconodontus muelleri*, *Eoconodontus notchpeakensis*), no strict changes would be made to the terminology that has been used, since the apparatus architecture of these forms is unknown. There would, however, be an overabundance of inverted commas in the text. Purnell *et al.* (2000) acknowledged that their new scheme cannot yet be applied to coniform euconodont apparatuses, and since their scheme is not applicable in the following descriptions, all the terms used refer to the conventional element orientation as illustrated in Text figure 6.8.



Text-figure 6.8. Diagram to show the terms used to describe the elements, in the traditional sense of element orientation. (From Sweet *in* Robison 1981, after Lindström 1954).

6.9 EUCONODONT SYSTEMATIC PALAEONTOLOGY

Phylum CHORDATA Bateson, 1886
Subphylum VERTEBRATA Linnaeus, 1758
Class CONODONTA Eichenberg, 1930; *sensu* Clark, 1981
Subclass EUCONODONTA Nov.

Order PROCONODONTIDA Sweet, 1988

Remarks. Miller (*in* Clark 1981) erected the superfamily Proconodontacea as part of the order Conodontophorida Eichenberg, 1930. Included therein were the Clavohamulidae Lindström 1970, the Cordylodontidae Lindström, 1970 and the Oneotodontidae Miller, 1981. The monogeneric Proconodontidae (including only *Proconodontus* Miller, 1969) was omitted from this grouping by Miller, and placed in the superfamily Distacodontacea Bassler, 1925, alongside other families, including the Teridontidae Miller, 1981. It is not possible to reconcile this suprageneric classification scheme with the earlier work of Miller (1980) in which clear evolutionary relationships were proposed between *Proconodontus*, *Eoconodontus*, *Cambrooistodus* and *Cordylodus*, of which the latter three species were included in the Proconodontacea by Miller (1981), and the former with *Teridontus* as part of a separate taxonomic grouping. However, it is noted that the publication of the Treatise volume was delayed and that much of the information contained in it was written significantly earlier than 1981. Publications that appeared in the literature during the late 1970s were often produced subsequently to the work contained in the Treatise, and hence the evolving ideas of some authors (for example those of Miller 1980, 1981) do not appear in the correct chronological order. Fåhræus (1984) has listed additional reasons why the Treatise classification scheme of Clark (*in* Robison 1981) is unacceptable according to the International Code of Zoological Nomenclature. He noted (Fåhræus 1984, p. 294) that Proconodontacea Miller is a junior homonym of the Proconodontidae Lindström, and that the grouping was also erected without a type genus.

Sweet (1988) divided the euconodonts into two groups, the Cavidonti and the Conodonti. The former included thin-walled, mainly coniform species possessing uni- to quinquemembrate apparatuses, lacking elements in the P positions, which Sweet placed into either the Proconodontida or the Belodellida. All other euconodonts were grouped within the Conodonti by Sweet. Aldridge and Smith (1993) did not follow this division, and it is not used herein, because two distinct lineages of euconodonts are recognised from the Cambrian, the *Proconodontus* lineage and the *Teridontus* lineage, with the latter forming the stem group of all euconodont taxa, except for those species found in the *Proconodontus* lineage, which is thought to be a short-lived (?possibly unrelated) branch of the euconodonts (Sweet 1988). However, apparatus reconstructions of *Proconodontus muelleri* and *Eoconodontus notchpeakensis* have demonstrated that the *Proconodontus* lineage may be more closely related to the Ordovician genera *Drepanodus*, *Paltodus* and *Paroistodus* than previously recognised. Cavidonti and Conodonti *sensu* Sweet (1988) are therefore not considered as valid taxonomic groupings, since the Belodellida are now thought not to be closely related to the Proconodontida (Aldridge and Smith 1993) and the group is thus polyphyletic.

Dzik (1991) did not maintain the Proconodontida, opting instead to place the Proconodontidae, Cordylodontidae, Fryxellodontidae, and an uncertain family grouping (including *Loxodus* Furnish, 1938, *Cristodus* Repetski, 1982, *Coleodus* Branson and Mehl, 1933, *Leptochirognathus*, Branson and Mehl and *Thrincodus* Bauer, 1987), within the superfamily Cordylodontacea Lindström, 1970. In turn, the Cordylodontacea were included as part of the Panderodontida Sweet, 1988, but this idea is not upheld in this study, because of the supposed distant relationship between the Proconodontida and the Panderodontida.

Aldridge and Smith (1993) included three families in the Proconodontida: the Cordylodontidae Lindström, 1970, the Proconodontidae Lindström, 1970, and the Fryxellodontidae Miller, 1981. Sweet (1988) however, also placed the Pygodontidae Bergström, 1981, with the Proconodontida based on evidence presented by Dzik (1983) and Bergström (1983), who implied that the earliest forms of the *Pygodus* lineage (*Polonodus*) are closely related to the Fryxellodontidae due to the lack of a well-defined cusp, and the broadly conical shape of the elements. Aldridge and Smith (1993) placed *Pygodus* Lamont and Lindström, 1957, and *Polonodus* Dzik, 1976, into the Balognathidae Hass, 1959, as part of the Prioniodontida Dzik, 1976, and did not consider the Prioniodontida to be closely related to the Proconodontida. This study follows Aldridge and Smith (1993) by including only the Cordylodontidae, Proconodontidae and Fryxellodontidae in the Proconodontida.

Family PROCONODONTIDAE Lindström, 1970

Remarks. Lindström (1970) erected the family Proconodontidae to encompass all thin-walled, deeply excavated, mainly coniform conodonts, with the exception of some forms that also have posterior, but not lateral processes. Included within the Proconodontidae were two further subfamilies, the Proconodontinae and the Cordylodontinae. The former was said to include only coniform elements, that lack a posterior process, and that may or may not possess denticles on the posterior margin. The Cordylodontinae included all forms that possess a posterior process carrying well-defined denticles. Miller (*in* Clark 1981) placed the monogeneric Proconodontidae in the Distacodontacea Bassler, 1925, including only *Proconodontus* in this grouping based on the lack of white matter in the cusp and the deeply excavated basal cavity. *Eoconodontus*, *Cambrooistodus* and *Cordylodus* were placed within the Cordylodontidae Lindström, 1970, as part of the Proconodontacea. The generally accepted hypothesis, first suggested by Miller (1980) and supported by this study due to the similarity of the apparatus composition of these forms, is that the aforementioned genera are closely related to *Proconodontus*, and therefore the Treatise classification of Miller (1981) cannot be supported.

Sweet (1988) modified Lindström's (1970) classification so that *Proconodontus* and *Eoconodontus* were retained in the Proconodontidae, with *Cambrooistodus*, *Cordylodus* and *Iapetognathus* being assigned to the Cordylodontidae, the division being based on the development of a posterior (or lateral) process in the latter three genera. Dzik (1991) placed the Proconodontidae in the superfamily Cordylodontacea Lindström, 1970, including only *Proconodontus* in his family-level grouping. *Eoconodontus* was grouped by Dzik (1991) alongside *Cambrooistodus*, *Cordylodus*, *Iapetognathus* and, tentatively, *Paracordylodus*, within the Cordylodontidae, on the basis that the elements were either denticulate, or geniculate in the earliest forms.

A further re-arrangement of the genera within the two families by Aldridge and Smith (1993) removed *Eoconodontus* from the Proconodontidae, placing it as the earliest member of the Cordylodontidae. The classification scheme of Aldridge and Smith (1993) is followed in preference to that of Dzik (1991) because the development of white matter in the cusp is a more consistent character of the Cordylodontidae than the presence of either denticles or a geniculate element, as suggested by Dzik (1991).

Genus PROCONODONTUS Miller, 1969

1969 *Proconodontus*, Miller, p. 437.

1978 *Proconodontus* Miller; Fåhræus and Nowlan, p. 452.

1980 *Proconodontus* Miller; Miller, p.28.

1981 *Proconodontus* Miller; Miller (*in* Clark), p. W146.

1983 *Proconodontus* Miller; Landing, p. 1179.

1986 *Proconodontus* Miller; Chen and Gong, p. 159.

1991 *Proconodontus* Miller; Müller and Hinz, p. 55.

1998 *Proconodontus* Miller; Szaniawski and Bengtson, p. 17.

Type species. *Proconodontus mülleri mülleri* [*sic*] Miller, 1969, p. 437, Notch Peak Limestone, House Range, Utah.

Diagnosis. Trimembrate apparatus of entirely hyaline, proclined, laterally compressed, coniform elements. Fully or partially developed, serrated or non-serrated keels present on one or both of the anterior or posterior margins. Element surfaces smooth or faintly annulated. Basal cavity deep, extending almost to tip of element.

Description. Entirely hyaline, laterally compressed, proclined coniform elements. Serrated or non-serrated keels wholly or partially developed on the broadly curving anterior and posterior margins. Faces usually unornamented, but with occasional faint, oblique annulations on both the inner and outer faces of some elements. Symmetrical and asymmetrical forms present. Asymmetry marked by the flattening of, and occasional lateral twisting towards, the inner face. Basal cavity very deep, extending almost to the tip of the elements, which in some cases may show regeneration and slight recurvature. Basal and element cross-sections rounded to ovate, but always showing a degree of lateral compression.

Remarks. Miller (1969) erected the genus to include all coniform elements in which there is a degree of lateral compression, a very deeply excavated basal cavity, and keeled posterior and/or anterior margins. He distinguished symmetrical and asymmetrical forms by the lateral twisting of the cusp towards the inner face. Included within this description were *P. notchpeakensis* and *P. carinatus* (= rounded and compressed elements of *E. notchpeakensis* respectively), both of which are forms with white matter developed in the cusp. These were later removed from *Proconodontus* by Miller (1980) who restricted the genus to include only hyaline forms.

Symmetrical and asymmetrical elements are present in some species, *contra* the views of Miller (1969) who proposed a unimembrate apparatus for all *Proconodontus* species comprising *either* symmetrical or asymmetrical elements. Miller (1980) acknowledged the presence of symmetrical and asymmetrical elements within the same apparatus, but still maintained that each apparatus was unimembrate, with a single element type in a symmetry transition series. A trimembrate apparatus for *P. muelleri*, the type species of *Proconodontus*, is discussed, but there are as yet insufficient data to determine whether the other species assigned to *Proconodontus* have similar apparatus compositions. Additional material from the collections of J. F. Miller has been examined, and it is apparent that the elements of *P. tenuiserratus* and *P. posterocostatus* studied so far are symmetrical, with the ornamentation on the posterior margin located centrally, no lateral twisting of the element and no differential development of the element faces (i.e. a unimembrate apparatus). However, Szaniawski and Bengtson (1998) noted the presence of two element morphotypes (rounded and compressed) in *P. serratus*, *P. tenuiserratus*, *P. tenuiserratus bicostatus*, *P. tenuiserratus* cf. *bicostatus* and *P. transitans*, and three element morphotypes (rounded, compressed and nearly geniculate) in *P. muelleri*.

At this early stage in the evolution of euconodonts, a fundamental difference in apparatus composition constitutes a character difference of generic rank. However, the lack of definitive evidence in the collections used in this study precludes a formal generic division, at this stage, of the species currently assigned to *Proconodontus*. It is noted that the apparatus of *P. muelleri* may or may not be more complex than the more primitive species (*P. tenuiserratus*, *P. posterocostatus*), and that the clarification of the generic concept relies on the discovery or description of an improved data-set.

Included in the genus *Proconodontus* are some of the most primitive euconodonts which, during the Late Cambrian, appear to show a gradual but distinct evolution from those elements with tiny serrations on the upper part of the posterior margin, through those with a keel developed distally and then completely on the posterior margin, to those forms where the keel on the posterior margin is both well-developed and serrated in proximal parts of the element (Miller 1980). A biostratigraphical zonation scheme was developed by Miller (1975, 1978, 1980) using this distinction between species to subdivide the Late Cambrian of North America.

Proconodontus muelleri Miller, 1969

Plate 1, figures 1-7; Plate 9, figures A-C; Plate 10, figure A.

1959 *Scandodus* n. sp. a, Müller, p. 464, pl. 12, fig. 11.

*v 1969 *Proconodontus mülleri müllerí* [*sic*], Miller, p. 437, pl. 66, figs 30-40; text-fig. 5H.

p 1971 *Coelocerodontus burkei*, Druce and Jones, p. 61, pl. 11, figs 9-12; text-fig. 22a (*non* pl. 11, figs 5, 6; text-fig. 22e [= *P. tenuiserratus*]; pl. 11, figs 7, 8 [= *P. posterocostatus*]).

1971 *Proconodontus mulleri mulleri* [*sic*] Miller; Ethington and Clark, p. 71, pl. 1, fig. 25.

1971 *Proconodontus muelleri muelleri* Miller; Miller and Melby, p. 123, pl. 2, fig. 18.

?p 1973 *Proconodontus muelleri* Miller; Müller, p. 42, pl. 3, figs 4-7, 10 (*non* pl. 3, fig. 8 [= *E. notchpeakensis*]).

1976 *Proconodontus muelleri* Miller; Miller and Paden, p. 595, pl. 1, figs 4, 5.

non 1978 *Proconodontus muelleri muelleri* Miller; Fåhræus and Nowlan, p. 453, pl. 1, figs 1, 2 [? = *Coelocerodontus* sp.].

1978 *Proconodontus* cf. *P. muelleri muelleri* Miller; Tipnis, Chatterton and Ludvigsen, pl. 1, fig. 13.

1978 *Proconodontus notchpeakensis* Miller; Tipnis, Chatterton and Ludvigsen, pl. 1, fig. 14.

1978 *Proconodontus muelleri muelleri* Miller; Tipnis, Chatterton and Ludvigsen, pl. 1, fig. 17.

1980 *Proconodontus muelleri* Miller; Miller, p. 29, text-fig. 4C; pl. 1, fig. 7.

1981 *Proconodontus muelleri* Miller; Zhang, p. 5, text-figs 1-7.

1982 *Proconodontus muelleri* Miller; An, p. 141, pl. 12, figs 8-9, 11-13; pl. 16, figs 10, 12.

1982 *Proconodontus magezhuangensis* An, p. 141, pl. 13, figs 13, 14.

1982 *Proconodontus muelleri muelleri* Miller; Fortey, Landing and Skevington, text-fig. 6s; text-fig. 9k.

1982 *Proconodontus notchpeakensis* Miller; Fortey, Landing and Skevington, text-fig. 9i.

p 1983 *Proconodontus muelleri* Miller; An *et al.*, p. 126, pl. 5, figs 15, 16, 21-23 (*non* pl. 5, fig. 24 [= *P. serratus*]).

p 1983 *Proconodontus cambricus* (Miller); An *et al.*, p. 124, pl. 5, figs 8, 9 (*non* pl. 5, figs 13, 14 [= *C. cambricus*]).

1983 *Proconodontus muelleri* Miller; Landing, p. 1180, text-fig. 11g, h.

? 1984 *Proconodontus* aff. *muelleri* Miller; Burrett and Findlay, p. 724, text-fig. 3e.

1984 *Proconodontus muelleri* Miller; Wang and Luo, p. 276, pl. 1, figs 19, 24.

1985 *Proconodontus muelleri muelleri* Miller; Nowlan, p. 114, text-fig. 5.1.

1985 *Proconodontus muelleri* Miller; Wang, p. 231, pl. 2, figs 16-21; pl. 4, figs 17-19; pl. 7, figs 10, 27; pl. 8, figs 17, 18; pl. 9, figs 16-18; pl. 12, fig. 7; pl. 13, figs 1, 6, 25.

? 1985 *Prooneotodus gallatini* (Müller); Wang, p. 235, pl. 3, fig. 25.

1986 *Proconodontus muelleri* Miller; Chen and Gong, p. 159, pl. 19, fig. 6; pl. 32, figs 1, 3, 10, 12-14, 17; pl. 33, figs 3-5, 11; text-fig. 60.

? 1986 *Proconodontus muelleri* Miller; Chen, Zhang and Yu, p. 368, pl. 2, figs 7-10.

1986 *Proconodontus muelleri* Miller; Jiang *et al.*, pl. 3, figs 9-11.

1987 *Proconodontus muelleri* Miller; An, p. 109, pl. 2, figs 4, 17.

1987 *Proconodontus* aff. *Muelleri* [*sic*] Miller; An, p. 110, pl. 2, figs 19-21.

1987 *Proconodontus posterocostatus* Miller; An, p. 111, pl. 1, fig. 28; pl. 2, fig. 18.

? 1987 *Proconodontus muelleri* Miller; Dong, p. 169, pl. 1, figs 3-5.

1988 *Proconodontus muelleri* Miller; Andres, p. 125, fig. 20; p. 126, figs 21,22; p. 127, fig. 23; p. 128, fig. 25; p. 151; pl. 10, figs 1-8; pl. 11, figs 1-8; pl. 12, figs 1-4.

? 1989 *Proconodontus rotundatus* (Druce and Jones); Popov *et al.*, p. 146, pl. 17, figs 1, 13.

? 1989 *Proconodontus primitivus* (Müller); Popov *et al.*, p. 146, pl. 19, figs 1, 2.

1990 *Proconodontus muelleri* Miller; An and Zhang, p. 159, pl. 2, figs 4-6.

1990 *Proconodontus muelleri* Miller; Bryant and Smith, fig. 12b.

1991 *Proconodontus muelleri* Miller; Müller and Hinz, p. 56, text-fig. 22b; pl. 42, figs 1-16.

? 1991 *Proconodontus muelleri* Miller; Taylor *et al.*, text-figs 6.14, 6.15, 6.25.

1992 *Proconodontus muelleri* Miller; Hinz, p. 267, pl. 8, fig. 6.

1993 *Proconodontus muelleri* Miller; Landing, text-fig. 4.5.

1993 *Eoconodontus notchpeakensis* (Miller); Landing, text-fig. 4.6.

p 1993 *Proconodontus* sp. Szaniawski and Bengtson, p. 641, text-fig. 2, figs 13-16; text-fig. 3, figs 11-12 (*non* text-fig. 1, figs 1, 2, 8-11; text-fig. 2, figs 7-10; text-fig. 3, fig. 10 [= *P. posterocostatus*]; text-fig. 1, figs 3-7, 12; text-fig. 2, figs 1-6, 11, 12; text-fig. 3, figs 5-9 [= *Proconodontus* sp.]).

? 1995 *Proconodontus muelleri* Miller; Harris *et al.*, pl. 1, fig. Z.

1995 *Proconodontus muelleri* Miller; Repetski *et al.*, pl. 1, fig. Z.

non 1996 *Proconodontus muelleri* Miller; Taylor *et al.*, text-fig. 6Q [= *P. posterocostatus*].

? 1998 *Proconodontus muelleri* Miller; Dubinina, p. 568, pl. 1, fig. 35.

? 1998 *Proconodontus mulleri* [*sic*] Miller; Hein and Nowlan, p. 180, pl. 3, fig. 9.

1998 *Proconodontus muelleri* Miller; Szaniawski and Bengtson, p. 17, pl. 2, figs 4-17; text-fig. 4g-k.

Holotype. UW 1352, Miller (1969) plate 66, figs 37-39, Notch Peak Limestone, House Range, Utah, USA.

Material. 162 elements. 24 Aequaliform, 115 Graciliform, 23 Arcuatiform.

Emended Diagnosis. Trimembrate apparatus of *Proconodontus* elements comprising symmetrical, asymmetrical and compressed morphotypes, with a fully developed, non-serrated keel present on both the posterior and the anterior margin of the element.

Description. Trimembrate apparatus of hyaline, laterally compressed, proclined, coniform elements. Posterior and anterior margins keeled, broadly curved, with fully developed crown material extending throughout the whole length of the element. A regenerated tip is occasionally apparent. Inner and outer faces usually unornamented, but in stratigraphically younger, more robust specimens, faint oblique annulations may be present on the faces. Basal cavity extending almost to the tip of the element, with the anterior and posterior margins of the basal cavity running close to and parallel with the margins of the element.

Aequaliform element. Symmetrical elements, faces equally developed, convex, basal and element cross-sections ovate, pinched anteriorly and posteriorly.

Graciliform elements. Asymmetrical elements, outer face convex, inner face flattened over entire element length. Distal parts of the element laterally twisted towards the inner face to a greater or lesser extent. Basal and element cross-sections asymmetrical, ovate, pinched anteriorly and posteriorly, flattened on the inner margin.

Arcuatiform elements. Markedly laterally compressed elements, outer face convex, inner face flattened posteriorly, becoming convex towards the anterior margin. Keel on posterior margin pronounced. Element usually bent slightly towards the inner face. Basal and element cross-sections asymmetrical, compressed posteriorly, expanded anteriorly, inflated towards the anterior of the inner margin.

Remarks. Initially erected as a subspecies by Miller (1969), *Proconodontus muelleri* is now recognised as a species in its own right. *Proconodontus muelleri serratus*, the second subspecies of *P. muelleri*, is also considered to be a separate species by most authors. *P. muelleri* is distinguished from other *Proconodontus* species by having fully developed, non-serrated, crown material forming sharp edges or keels on both the posterior and anterior margins of the elements.

Elements of *P. muelleri* were originally assigned to *Scandodus* n. sp. a by Müller (1959), but these were placed in the newly erected genus *Proconodontus* by Miller (1969). Some of the elements figured as part of the apparatus of *Coelocerodontus burkei* by Druce and Jones (1971) are also included in the synonymy due to the presence of fully developed anterior and posterior keels.

Müller (1973) was the first author to elevate *P. muelleri* and *P. serratus* to full species level rank, although the specimens figured by him are in part only tentatively assigned herein to *P. muelleri* (Müller 1973, pl. 3, figs 4-7, 10). Miller (1980) voiced his concern that the elements described by Müller (1973) were associated with an anomalously young fauna (Assemblage Zone 4 of Müller (1973) corresponding to Fauna A of Ethington and Clark (1971)). This study is in agreement with this opinion, and it is observed that, in North America, elements of *P. muelleri* occur in stratigraphically different horizons to elements from the various species of *Cordylodus*. Specimens figured by Fåhræus and Nowlan (1978) possess hooked tips, a feature that is more characteristic of *Coelocerodontus* than *Proconodontus*, and are accordingly removed from the present synonymy. The practice of using a subspecies level division continued until the mid-1980s (Nowlan 1985).

An *et al.* (1983) proposed a trimembrate apparatus for *P. muelleri*, comprising 'symmetricus', 'asymmetricus' and 'oistodontiform' elements. The 'oistodontiform' element (An *et al.* 1983, pl. 5, figs 22, 23) is not truly geniculate, possessing only a sharply curved posterior margin which is comparable to the 'compressed' element morphotype of the trimembrate apparatus outlined above. 'Asymmetricus' elements (An *et al.* 1983, pl. 5, figs 15, 16) show a close similarity in morphology to that of the compressed element morphotype, and the 'symmetricus' element (An *et al.* 1983, pl. 5, fig. 21) also seems to merit placement within the compressed category. Elements referred to *Proconodontus cambricus* by An *et al.* (1983, pl. 5, figs 8, 9) strongly resemble the asymmetrical, rounded elements of *P. muelleri*, and so the trimembrate apparatus reconstruction suggested by An *et al.* does not comply with the proposed trimembrate *P. muelleri* apparatus.

Range. Base *P. muelleri* Zone - Top *C. minutus* Subzone.

Occurrence. WY96-17, WY96-18, Gallatin Formation, Bighorn Mountains, Wyoming, USA.

Proconodontus posterocostatus Miller, 1980

Text-figure 6.9a

p	1971	*Coelocerodontus burkei*, Druce and Jones, p. 61, pl. 11, figs 7, 8 (*non* pl. 11, figs 5, 6; text-fig. 22e [= *P. tenuiserratus*]; pl. 11, figs 9-12; text-fig. 22a [= *P. muelleri*]).
*v	1980	*Proconodontus posterocostatus*, Miller, p. 30, text-fig. 4b; pl. 1, figs 4-6.
	1982	*Proconodontus posterocostatus* Miller; An, p. 142, pl. 12, figs 3, 4, 6, 7, 10.
?	1984	*Proconodontus posterocostatus* Miller; Burrett and Findlay, p. 724, fig. 3a-c.
	1985	*Proconodontus posterocostatus* Miller; Nowlan, p. 114, text-figs 5.2-5.5.
non	1987	*Proconodontus posterocostatus* Miller; An, p. 111, pl. 1, fig. 28; pl. 2, fig. 18, [= *P. muelleri*].
p	1993	*Proconodontus* sp.; Szaniawski and Bengtson, p. 641, text-fig. 1, figs 1, 2, 8-11; text-fig. 2, figs 7-10; text-fig. 3, fig. 10 (*non* text-fig. 1, figs 3-7, 12; text-fig. 2, figs 1-6, 11, 12; text-fig. 3, figs 5-9 [= *Proconodontus* sp.]; text-fig. 2, figs 13-16; text-fig. 3, figs 11, 12 [= *P. muelleri*]).
	1996	*Proconodontus muelleri* Miller; Taylor *et al.*, text-fig. 6q.
?	1998	*Proconodontus posterocostatus* Miller; Hein and Nowlan, p. 180, pl. 3, fig. 10.
	1998	*Proconodontus* cf. *tenuiserratus bicostatus*, Szaniawski and Bengtson, p. 19, pl. 4, figs 7, 8.
p	1998	*Proconodontus transitans*, Szaniawski and Bengtson, p. 19, pl. 3, figs 3-12; pl. 4, figs 1-6 (*non* pl. 3, figs 1, 2 [= *Proconodontus ?transitans*]).

Holotype. USNM 303275, Miller (1980), plate 1, fig. 4, text-fig. 4b, Wilberns Formation, Llano Uplift, Texas, USA.

Material. 1 element.

Description. Entirely hyaline, very slightly laterally compressed, erect, coniform element. Anterior margin rounded, very broadly curved from base to tip. Posterior margin also gently curved, rounded in basal regions, but sharp in the upper third of the element, where a distinct keel is formed on the central part of the posterior margin. Basal cavity very deep, extending almost to the tip of the element. Transverse cross-section of the element tear-shaped at the tip due to the development of the posterior keel, but ovate at the base where the keel is absent. Element symmetrical, with both lateral faces equally developed. There is no lateral twisting of the element, and no ornamentation on the outer surface of the element.

Remarks. Similar in morphology to *Proconodontus tenuiserratus*, *P. posterocostatus* was first figured as part of the apparatus of *Coelocerodontus burkei* by Druce and Jones (1971). This species incorporated rounded to elliptical coniform elements with "knife-edges" (keels) developed on the posterior margin. Elements figured therein, that have well-developed keels present only on the upper part of the posterior margin, are included within this present species concept. Those with small projections on the posterior margin are included in *Proconodontus tenuiserratus* and those with an extended posterior keel are referred to *Proconodontus muelleri*.

Miller (1980) erected the new species *P. posterocostatus* to include forms with an incomplete posterior keel, and suggested that they evolved from *P. tenuiserratus* by the expansion of the small, serrated keel found on the posterior margin of that species, in disagreement with Druce and Jones (1971) who believed that the serrated posterior margin of *P. tenuiserratus* was a product of the reduction of the posterior keel of *P. posterocostatus* or *P. muelleri* into a series of very small, discrete denticles or bumps.

Szaniawski and Bengtson (1998) included elements of *P. posterocostatus* in their new species *Proconodontus transitans*, and also in their new sub-species *Proconodontus* cf. *tenuiserratus bicostatus*. The similarity of some of their *P. transitans* specimens to those of *P. posterocostatus* was noted by them, but they did not state why they were included in the new species, and not referred to the already established one. Elements that they assigned to *P.* cf. *tenuiserratus bicostatus* have only very poorly developed posterior keels but, as with other specimens of *Proconodontus*, there is likely to be some intraspecific variability in the degree of development of certain characters. The description of *P. posterocostatus* in this study includes all *Proconodontus* elements where an incomplete and non-serrated posterior keel is present. To start subdividing this further on the basis of the degree of development of this feature would cause an amount of unnecessary confusion. The validity of *P. transitans* as a species is not questioned, as it is useful to include within this species those euconodont elements that have a very thin crown, but which lack either a marginally serrated or a keeled posterior margin.

The element recovered from Wyoming is associated with an anomalously young fauna, since it has not previously been found in association with *Cambrooistodus minutus* (Miller) however, it complies with the species description of Miller (1980) and cannot be included elsewhere.

Range. Base *P. posterocostatus* Zone - Top *P. muelleri* Zone.

Occurrence. WY96-18, Gallatin Formation, Bighorn Mountains, Wyoming. (Additional material from Threadgill Creek, Texas, from the collections of J. F. Miller, samples TC-1245, TC-1265, TC-1268).

Proconodontus serratus Miller, 1969

Text-figure 6.9b

*v	1969	*Proconodontus mülleri* [*sic*] *serratus*, Miller, p. 438, pl. 66, figs 41-44.
	1973	*Proconodontus serratus* Miller; Müller, pl. 4, figs 1, 2.
	1980	*Proconodontus serratus* Miller; Landing, Ludvigsen and von Bitter, p. 33, figs 8I-L.
	1980	*Proconodontus serratus* Miller; Miller, p. 31, fig. 4d; pl. 1, fig. 13.
non	1982	*Proconodontus muelleri serratus* Miller; Fortey, Landing and Skevington, p. 124, text-fig. 9L [= *P. tenuiserratus*].
p	1983	*Proconodontus muelleri* Miller; An *et al.*, p. 126, pl. 5, fig. 24a, b (*non* pl. 5, figs 15, 16, 21-23 [= *P. muelleri*]).
non	1983	*Proconodontus serratus* Miller; Landing, p. 1180, text-fig. 11i [= *P. tenuiserratus*].
	1985	*Proconodontus serratus* Miller; Wang, p. 233, pl. 6, fig. 26.
	1986	*Proconodontus serratus* Miller; Chen and Gong, p. 162, pl. 33, figs 1, 6, 10; text-fig. 62.
	1991	*Proconodontus serratus* Miller; Müller and Hinz, p. 56, fig. 22a; pl. 42, figs 17-21; pl. 43, figs 1-3, 6, 7.
p	1991	*Proconodontus serratus* Miller; Taylor *et al.*, p. 860, text-fig. 6.16 (*non* text-figs 6.13, 6.17 [= *P. tenuiserratus*]).
	1992	*Proconodontus serratus* Miller; Hinz, p. 267, pl. 8, fig. 5.
	1993	*Proconodontus serratus* Miller; Szaniawski and Bengtson, p. 641, text-fig. 2, figs 17-19; text-fig. 4, figs 11, 15.
	1993	*Proconodontus* aff. *P. serratus* Miller; Szaniawski and Bengtson, p. 647, text-fig. 3, figs 8, 9, 10.
	1998	*Proconodontus serratus* Miller; Dubinina, p. 568, pl. 1, fig. 34.
	1998	*Proconodontus serratus* Miller; Szaniawski and Bengtson, p. 18, pl. 1, figs 1-3, 7; pl. 4, figs 9-10, 13, 17-19.

Holotype. UW 1358, Miller (1969) plate 66, figs 43, 44, Notch Peak Limestone, House Range, Utah, USA.

Material. 2 elements.

Description. Entirely hyaline, laterally compressed, erect coniform elements. Anterior margin gently curved, with a smooth, narrow keel present from base to tip. Posterior margin also keeled, and slightly more strongly curved than the anterior margin. The keel is serrated in the basal half of the posterior margin, with the serrations being relatively large and confluent as opposed to small and discrete. Basal cavity deep, extending almost to the tips of the elements. Elements asymmetrical with one lateral face being more flattened than the other, which is slightly inflated. Transverse cross-section of the element ovate and both the base and the tip, being slightly pinched towards the anterior and posterior. Faint oblique annulations are present on the outer surfaces of the elements.

Remarks. Initially erected as a subspecies to describe those specimens of *Proconodontus muelleri* possessing serrated posterior margins by Miller (1969), Müller (1973) was the first to elevate the elements to species level. During the early stages in the evolution of Cambrian euconodonts, the presence or absence of a serrated posterior margin on one or more of the elements in the apparatus is generally considered to be a valid character for defining two separate species so, in agreement with Müller (1973) and Miller (1980), *P. serratus* is maintained as a valid species concept. However, similar to the problems faced when assessing the *Cambrooistodus* apparatus, it may be that elements with a serrated posterior margin (*P. serratus*) are present in an apparatus alongside elements lacking this character (*P. muelleri*). After the appearance of *P. serratus* in the Late Cambrian, all *Proconodontus* forms could be assigned to *P. serratus*, on the basis that all *Proconodontus* species would have possessed this character, but it is just as likely that only some of the fauna developed a serrated posterior margin and that not all of the *Proconodontus* elements from a particular sample can therefore be assigned to *P. serratus*. In the above description and synonymy, only those elements in the *P. serratus* apparatus with a serrated posterior margin are recognised. The stratigraphical range of *P. serratus* is such that it does not occur outside of the range of *P. muelleri* and, therefore, the full suite of elements likely to occur in the apparatus of *P. serratus* is difficult to constrain.

In comparison to the serrations found on the posterior margin of *P. tenuiserratus*, those found in *P. serratus* are larger and are confined to the basal regions of the element. No other species of *Proconodontus* possess this character and so the species remains distinct from all other coniform elements lacking white matter that are found in the Cambrian. Serrations are sometimes found on the posterior margin and on the upper edge of the base of *Cambrooistodus* elements, but these elements have white matter in the cusp and are easily distinguished from *P. serratus*.

Range. Mid *E. notchpeakensis* Subzone - Top *C. minutus* Subzone.

Occurrence. WY96-18, Gallatin Formation, Bighorn Mountains, Wyoming.

Proconodontus tenuiserratus Miller, 1980

Text-figure 6.9c

p	1971	*Coelocerodontus burkei*, Druce and Jones, p. 61, pl. 11, figs 5, 6; text-fig. 22e (*non* pl. 11, figs 7, 8 [= *P. posterocostatus*]; pl. 11, figs 9-12; text-fig. 22a [= *P. muelleri*]).
*v	1980	*Proconodontus tenuiserratus*, Miller, p. 31, text-fig. 4a; pl. 1, figs 1-3.
	1982	*Proconodontus tenuiserratus* Miller; An, p. 143, pl. 12, figs 1, 2, 5.
	1982	*Proconodontus muelleri serratus* Miller; Fortey, Landing and Skevington, text-fig. 9L.
	1983	*Proconodontus serratus* Miller; Landing, p. 1180, text-fig. 11i.
?	1985	?*Proconodontus posterocostatus* Miller; Nowlan, text-fig. 5.6.
?	1985	*Proconodontus tenuiserratus* Miller; Wang, p. 233, pl. 8, fig. 7; pl. 12, fig. 8.
	1986	*Proconodontus tenuiserratus* Miller; Jiang *et al.*, pl. 3, fig. 8.
?	1987	*Proconodontus* cf. *tenuiserratus* Miller; Dong, p. 169, pl. 1, fig. 6.
	1987	*Proconodontus tenuiserratus* Miller; Heredia, p. 147, text-fig. 2
	1988	*Proconodontus tenuiserratus* Miller; Heredia and Bordonaro, p. 192, pl. 2, fig. 3.
p	1991	*Proconodontus serratus* Miller; Taylor *et al.*, text-figs 6.13, 6.17 (*non* text-fig. 6.16 [= *P. serratus*]).
	1993	*Proconodontus* aff. *P. tenuiserratus* Miller; Szaniawski and Bengtson, p. 647, text-fig. 4, figs 6, 14.
?	1998	*Proconodontus tenuiserratus* Miller; Dubinina, p. 568, pl. 1, fig. 33.
	1998	*Proconodontus tenuiserratus bicostatus* Szaniawski and Bengtson, p. 18, pl. 4, figs 11-12, 14-16.

Holotype. USNM 303277 Miller 1980, plate 1, figure 2, text-figure 4a, Wilberns Formation, Threadgill Creek, Texas, USA.

Material. 1 element.

Description. Entirely hyaline, very slightly laterally compressed, erect, coniform element. Anterior margin rounded, very broadly curved from base to tip. Posterior margin also rounded and gently curved, with a series of tiny, discrete serrations situated centrally on the posterior margin in the upper half of the element. Basal cavity very deep, extending almost to the tip of the element. Transverse cross-section of both the tip and the base of the element ovate. Element symmetrical, displaying no lateral twisting, curvature or external ornament.

Remarks. Druce and Jones (1971) first figured elements of *Proconodontus tenuiserratus* as part of the new species *Coelocerodontus burkei.* Included in this description were hollow, coniform elements with extremely poorly developed crown material, often with "knife-edges" (keels) developed as thin flanges on the posterior margin. Druce and Jones attributed the tiny projections on the posterior margin of some elements to the breaking down of the knife-edge to form denticles. Conversely, Miller (1980) erected the species as the most primitive in the *Proconodontus* lineage, differentiating it from its descendant *Proconodontus posterocostatus* by the lack of a well developed keel (i.e. implying that the projections on the posterior margin were the primitive, rather than the derived, character).

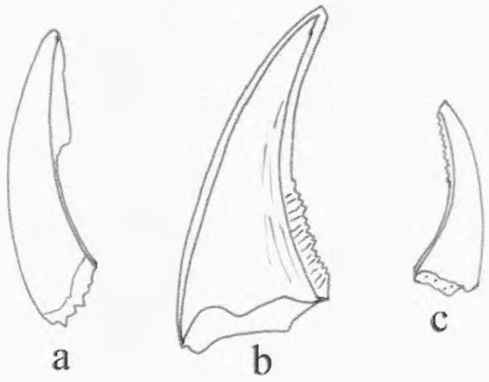
Two species of *Proconodontus*, *P. tenuiserratus* and *P. serratus* are diagnosed by the presence of serrations on the posterior margin, however the differences between the two species are marked by the location, distribution and size of the serrations (*P. tenuiserratus* has small, often well-spaced projections situated on the upper half of the posterior margin, *P. serratus* has large, well-developed, often confluent serrations on the basal portion of the posterior margin). Landing (1983) figured an element of *P. tenuiserratus* in which the projections on the posterior margin are relatively pronounced and, therefore, described the element as *P. serratus.* In the specimen figured by Landing (Landing 1983, text-fig. 11i), no posterior keel is developed, and the serrations occur towards the tip of the element, implying that it must be synonymised with the stratigraphically older form, *P. tenuiserratus.*

Szaniawski and Bengtson (1998) subdivided *P. tenuiserratus* into two sub-species, *P. tenuiserratus bicostatus* and *P.* cf. *tenuiserratus bicostatus.* Of these, the latter is synonymised with *P. posterocostatus* because no discrete serrations are present on the posterior margin of the element, and the former with *P. tenuiserratus* because the element does bear discrete serrations on the upper part of the posterior margin. The diagnosis of the new sub-species (*P. tenuiserratus bicostatus* Szaniawski and Bengtson, 1998) includes forms in which a keel was developed on the anterior margin of the element, extending from tip to base. The degree to which this feature is developed is probably an intraspecific variable within *P. tenuiserratus* and the erection of a new sub-species is refuted on these grounds.

The element recovered from the Gallatin Limestone is associated with an anomalously young fauna, but remains within the species concept of *P. tenuiserratus* and cannot, therefore, be excluded.

Range. Base *P. tenuiserratus* Zone - Mid *P. posterocostatus* Zone.

Occurrence. WY96-18, Gallatin Formation, Bighorn Mountains, Wyoming. (Additional material from Threadgill Creek, Texas, from the collections of J. F. Miller, samples TC-1154, TC-1160, TC-1170, TC-1180, TC-1193, TC-1198, TC-1200).



Text-figure 6.9. Line drawings to illustrate elements of *Proconodontus posterocostatus* (a), *Proconodontus serratus* (b) and *Proconodontus tenuiserratus* (c). x100.

Family CORDYLODONTIDAE Sweet, 1988

Remarks. Initially erected as a subfamily (Cordylodontinae) by Lindström (1970), the Cordylodontidae originally included all forms of the Proconodontida with a deep basal cavity and a well developed posterior process carrying denticles. Miller (*in* Clark, 1981) assigned elements with relatively deep basal cavities, cusps composed of white matter, and bimembrate apparatuses comprising 'rounded' and 'compressed' elements, to the Cordylodontidae, including *Eoconodontus*, *Cambrooistodus* and *Cordylodus* in this taxonomic grouping, even though the former two species lack denticles. Sweet (1988) then returned *Eoconodontus* to the Proconodontidae because of its lack of a well-developed posterior process. *Iapetognathus* Landing, 1982, was also included in the Cordylodontidae by Sweet, who shared the opinion of Landing (1982) that the genus is closely related to *Cordylodus*, even though the denticulate process is laterally, rather than posteriorly, situated and specimens often possess surface microstriae more typical of the *Teridontus* lineage. Dzik (1991) relocated *Eoconodontus* from the Proconodontidae to the Cordylodontidae because his description of the Cordylodontidae included species in which one or all of the elements was geniculate or possessed a posterior process. However, no truly geniculate elements are present in *Eoconodontus* and so, although Dzik's classification is seemingly followed, the presence of white matter in the cusp is the character that unites *Eoconodontus* with *Cambrooistodus*, *Cordylodus* and *Iapetognathus*, and distinguishes it from *Proconodontus*, as implied by Aldridge and Smith (1993).

Nicoll (1990) described the apparatus of several *Cordylodus* species (*C. proavus*, *C. caseyi*, *C. lindstromi*, *C. angulatus*), concluding that the apparatuses of these *Cordylodus* species are septimembrate. Nicoll described the elements found in the apparatus according to the notation scheme of Sweet and Schönlaub (1975), with S, M and P element-types. All seven element types appear to be directly comparable to element types found within the septimembrate apparatus of *E. notchpeakensis*, described below (see also separate discussion about the apparatus development of forms from the *Proconodontus* lineage). The similarity of the apparatus of *E. notchpeakensis* to that of the various species of *Cordylodus* supports the hypothesis that *Cordylodus* is the evolutionary descendant of *Eoconodontus* as proposed by Miler (1980). Both *Cambrooistodus* and *Iapetognathus* have apparatuses that are poorly known and little understood, even though it is probable that the apparatus of *Cambrooistodus* is very similar in composition to that of *Eoconodontus* with the geniculate (*Cambrooistodus*) element potentially replacing the arcuatiform (M, compressed, *Eoconodontus*) element in the apparatus. The *Iapetognathus* apparatus has recently been elucidated by Nicoll *et al.* (1999a, b).

Genus CAMBROOISTODUS Miller, 1980

1980 *Cambrooistodus*, Miller, p. 9.

1981 *Cambrooistodus* Miller; Miller (*in* Clark), p. W116.

Type species. *Oistodus cambricus* Miller, 1969, p. 431, Notch Peak Limestone, House Range, Utah, USA.

Diagnosis. Geniculate, laterally compressed, coniform elements with white matter developed in the tip of the cusp, forming a sharp, planar junction with the mostly hyaline material of the base. White matter also weakly developed in the keeled anterior and posterior margins of the elements. Lateral twisting of the cusp of the elements towards the inner face is common. Depth of basal cavity variable between species, from moderately-deep to deep.

Description. Poorly known, and probably incomplete, apparatus diagnosed by a single, laterally compressed, partly albid, geniculate element. Upper edge of base short, straight or slightly convex, meeting posterior margin at a variable, although usually acute, angle. Posterior margin straight, sharp or keeled and serrated in some forms. Anterior margin sharp or keeled, broadly curved to base. Antero-basal corner angular or rounded. Inner face flattened apically, becoming inflated towards the base, with a slight carina developed in the lower part of the element, located centrally. Outer face broadly convex throughout. Diagnostic elements may be slightly laterally twisted towards the inner face. Sinistral and dextral forms present. White matter fully developed in the cusp, forming sharp planar junction with the hyaline material of the base, and partially developed in the keeled anterior and posterior margins of the base. Cross-section of base asymmetrical, ovate, pinched anteriorly and posteriorly, inflated along the inner margin. Cusp cross-section ovate, sub-symmetrical with the inner margin flattened in comparison to the broadly convex outer margin. Basal cavity moderately shallow to deep, extending to base of white matter. Posterior margin of basal cavity follows basal and posterior margins of the element in proximal regions, but tapers away from the margin apically, forming a basal cavity tip towards the centre of the element. Anterior margin of the basal cavity runs close to and parallel with the anterior margin of the element.

Remarks. Miller (1969) originally assigned the two species of *Cambrooistodus* (*C. cambricus* and *C. minutus*) to the genus *Oistodus* Pander, 1856, because of the geniculate nature of the elements. However, in the taxonomic revision of this work, Miller (1980) noted that elements assigned to *Oistodus* are entirely hyaline, and erected the new genus *Cambrooistodus* to incorporate those older geniculate elements that possess white matter. Miller (1969) had implied that *O. cambricus* and *O. minutus* (= *C. cambricus* and *C. minutus*) had monoelemental apparatuses, comprising only right and left forms of the geniculate element, but reviewed this idea in a later publication (Miller 1980), describing a bimembrate apparatus for the two species of *Cambrooistodus*. Included in this apparatus were a geniculate element and a 'rounded' element, which was thought by Miller to be indistinguishable from the rounded elements of *E. notchpeakensis*.

Landing (1983) reduced *Cambrooistodus* to the rank of subgenus, being a subgroup of *Eoconodontus*, with the two subgenera *E.* (*Eoconodontus*) and *E.* (*Cambrooistodus*) distinguished by the presence of an asymmetrical scandodiform element in the former and an oistodiform element in the latter. A suite of 'symmetrical drepanodiform' elements was said to be common to three species of the two subgenera, but in *E.* (*Eoconodontus*) *alisonae* Landing, 1983, elements have well-developed longitudinal costae on their outer surfaces, and are unlike the elements of *E. notchpeakensis*, *C. cambricus* and *C. minutus* which have smooth outer surfaces.

The apparatuses of both *C. cambricus* and *C. minutus* remain poorly understood, although it is likely that they are each part of a multielement apparatus that closely resembles that of *E. notchpeakensis*. The geniculate elements characteristic of *Cambrooistodus* would replace the arcuatiform (compressed, M) element morphotype in the *Eoconodontus* apparatus.

Cambrooistodus cambricus (Miller, 1969)

Plate 1, figure 9; Plate 8, figure D; Plate 10, figure C; Plate 11, figure A.

*v	1969	*Oistodus cambricus*, Miller, p. 431, pl. 66, figs 8-12; text-fig. 5a.
p	1969	*Proconodontus carinatus*, Miller, p. 437, pl. 66, figs 13, 14 (*non* pl. 66, figs 15-20; text-fig. 5I [= *E. notchpeakensis*]).
?	1978	*Oistodus* cf. *O. cambricus* Miller; Tipnis, Chatterton and Ludvigsen, pl. 1, fig. 19.
	1980	*Cambrooistodus cambricus* (Miller); Miller, p. 9, text-figs 3a, 4e; pl. 1, fig. 9.
p	1982	*Cambrooistodus cambricus* (Miller); An, p. 128, pl. 15, figs 2-7; pl. 16, fig. 9 (*non* pl. 15, figs 1, 8, 9, 12, 13 [= *C. minutus*]).
p	1983	*Proconodontus cambricus* (Miller); An *et al.*, p. 124, pl. 5, figs 13, 14 (*non* pl. 5, figs 8, 9 [= *P. muelleri*]).

p 1985 *Cambrooistodus cambricus* (Miller); Wang, p. 213, pl. 2, figs 4-6; pl. 13, figs 15-17, 28 (*non* pl. 2, fig. 7; pl. 6, figs 1, 25 [= *E. notchpeakensis*], pl. 3, fig 3 [? = *T. nakamurai*]).

1986 *Cambrooistodus cambricus* (Miller); Chen and Gong, p. 20, pl. 31, figs 1, 3-5, 7, 11-14; pl. 32, fig. 5; text-fig. 33.

? 1986 *Cambrooistodus cambricus* (Miller); Chen, Zhang and Yu, p. 365, pl. 1, figs 1, 2.

? 1987 *Cambrooistodus cambricus* (Miller); Dong, p. 153, pl. 1, figs 16, 21.

1991 *Cambrooistodus cambricus* (Miller); Taylor *et al.*, p. 860, text-fig. 6.19.

1996 *Cambrooistodus cambricus* (Miller); Taylor *et al.*, p. 156, text-fig. 6v.

1998 *Cambrooistodus cambricus* (Miller); Hein and Nowlan, p. 180, pl. 3, fig. 15.

Holotype. UW 1328, Miller (1969), plate 66, figs 8, 9, Notch Peak Limestone, House Range, Utah, USA.

Material. 672 elements.

Emended diagnosis. Cambrooistodus elements with a straight upper edge of base meeting posterior margin with sharp acute angle. Basal cavity deep, white matter present in cusp, forming sharp junction with hyaline base just above basal cavity tip. Antero-basal corner angular.

Description. Laterally compressed, geniculate elements. Upper edge of base short, sharp, straight, forming an angular junction with the posterior margin of the element. This angle is always less than 90°, but rarely less than 45°. Posterior margin sharp or keeled, straight, with occasionally robust serrations present in both the lower part of the posterior margin and on the upper edge of the base. Anterior margin broadly curved and sharp, although a keel may be developed particularly towards the base. Antero-basal corner angular. Inner face convex, but more inflated in basal region than in cusp. Outer face broadly convex in all regions. Cusp may be laterally twisted towards inner face. White matter well-developed in the cusp above basal cavity tip, and occasionally weakly developed in parts of keeled anterior or posterior margins. Basal cross-section asymmetrical, but ovate, with an inflated inner margin. May be pinched anteriorly and posteriorly towards keeled margins. Cusp cross-section ovate and sub-symmetrical, pinching towards anterior and posterior. Basal cavity depth usually moderately deep, extending to base of fully developed white matter. Posterior margin of basal cavity mimics posterior margin of element in the basal region, but tapers towards the centre of the element in the cusp. Anterior margin of basal cavity is broadly curved to antero-basal corner, with the tip of the basal cavity found towards the centre of the element.

Remarks. Miller (1969) originally described *Oistodus cambricus* as a mono-elemental apparatus consisting of laterally compressed, geniculate elements with deeply excavated basal cavities and white matter present predominantly in the cusp. Miller (1980) proposed an alternative, bimembrate apparatus for *C. cambricus*, and also erected the genus due to the completely hyaline nature of all other *Oistodus* species. Only the compressed (geniculate) element of *C. cambricus* was figured by Miller (1969; 1980). The description of the second element in the bimembrate apparatus is generalised, and is included under the generic, as opposed to the specific, description. Overall, the discussion of this element appears to be a description of a generalised 'rounded' element of *E. notchpeakensis* element, and indeed later in the text Miller stated that the rounded elements of *E. notchpeakensis*, *C. cambricus* and *C. minutus* are indistinguishable from one another. A discussion of the problems that this hypothesis creates is included under the remarks for *E. notchpeakensis*.

Landing (1983) followed Miller (1980) by assigning a bimembrate apparatus of drepanodiform and geniculate elements to *C. cambricus*, but tried to solve the problem of the vicarious 'rounded' elements by introducing a new subgeneric classification, whereby *Cambrooistodus* became a subgenus of *Eoconodontus*. The presence of a truly geniculate element in an apparatus is believed to represent a valid character on which to base the distinction between the two different genera, and Landing's (1983) classification is not followed. An *et al.* (1983) introduced a trimembrate apparatus for *C. cambricus* comprising symmetricus, asymmetricus, and oistodontiform elements. In accordance with Chen and Gong (1986), the symmetricus element is reassigned to *P. muelleri*, but in disagreement with their views, the asymmetricus element is also tentatively placed in *P. muelleri* as opposed to *E. notchpeakensis*. This opinion is based on the overall morphology of the figured element (An *et al.* 1983, pl. 5, fig. 9), particularly the recurved tip of the element, which is a feature more characteristic of *P. muelleri* than *E. notchpeakensis*. Oistodontiform elements figured by An *et al.* remain synonymised with *C. cambricus*. Wang (1985) returned to the original ideas of Miller (1969), and discussed *C. cambricus* in terms of a monoelemental apparatus of geniculate elements, but figured compressed elements of *E. notchpeakensis*, together with the truly geniculate *C. cambricus* elements. Chen and Gong (1986) continued with the bimembrate theme, but imply in their description that both of the elements in the apparatus are geniculate with well-developed posterior processes, one element being compressed and the other rounded. They also drew attention to the laterally twisted compressed element but no further comment was made concerning the rounded morphotype. No rounded, geniculate elements of *Cambrooistodus* have been found in the present study.

Cambrooistodus cambricus is distinguished from the arcuatiform (compressed) element of *E. notchpeakensis* by the geniculation of the upper edge of the base and the posterior margin, and by the increased depth of the basal cavity. A shallower basal cavity, shorter, more curved upper edge of the base, and rounded antero-basal corner are the characters that mark the difference between *C. minutus* and *C. cambricus*. In addition, elements of the latter are often more robust than those of the former.

Range. Mid-*E. notchpeakensis* Subzone - Top *C. minutus* Subzone

Occurrence. WY96-17, WY96-18, Gallatin Formation, Bighorn Mountains, Wyoming.

Cambrooistodus minutus (Miller, 1969)

Plate 1, figures 10, 11; Plate 9, figures E-G.

*p	1969	*Oistodus minutus*, Miller, p. 433, pl. 66, figs 1-4; text-fig. 5b (*non* pl. 66, figs 5-7 [= *E. notchpeakensis*]).
	1980	*Cambrooistodus minutus* (Miller); Miller, p. 11, text-fig. 4f; pl. 1, fig. 8.
non	1982	*Cambrooistodus minutus* (Miller); An, p. 129, pl. 11, figs 15, 16; pl. 15, fig. 10 [= *E. notchpeakensis*].
p	1982	*Cambrooistodus cambricus* (Miller); An, p. 128, pl. 15, figs 1, 8, 9, 12, 13 (*non* pl. 15, figs 2-7; pl. 16, fig. 9 [= *C. cambricus*]).
	1985	*Cambrooistodus minutus* (Miller); Nowlan, p. 107, text-figs 5.10, 5.11.
	1986	*Cambrooistodus minutus* (Miller); Chen and Gong, p. 122, pl. 32, fig. 16.
	1987	*Cambrooistodus minutus* (Miller); Dong, p. 153, pl. 1, figs 11, 13.
	1991	*Cambrooistodus minutus* (Miller); Taylor *et al.*, p. 860, text-figs 6.20-6.23.
	1996	*Cambrooistodus minutus* (Miller); Taylor *et al.*, p. 156, text-fig. 6w.
?	1998	*Cambrooistodus minutus* (Miller); Dubinina, p. 568, pl. 1, fig. 17.
	1998	*Cambrooistodus minutus* (Miller); Hein and Nowlan, p. 180, pl. 3, fig. 16.

Holotype. UW 1331, Miller (1969), plate 66, figs 2-4, Notch Peak Limestone, House Range, Utah, USA.

Material. 68 elements.

Emended diagnosis. Cambrooistodus elements with a short, slightly curved upper edge of base meeting posterior margin with sharp acute angle. Basal cavity shallow, white matter present in cusp, forming sharp junction with hyaline base just above basal cavity tip. Antero-basal corner rounded.

Description. Laterally compressed, geniculate elements. Upper edge of base short, sharp, straight to very slightly convexly curved, meeting posterior margin at an acute angle. Posterior margin sharp to keeled, straight to broadly curved. Anterior margin broadly curved, sharp to slightly keeled, extending to rounded antero-basal corner. Inner face convex, but inflated towards the base of the element. Outer face broadly convex in all regions. Cusp may be laterally twisted towards inner face in some elements. White matter fully developed in cusp above basal cavity tip, and occasionally poorly developed in posterior and anterior keeled margins. Basal cross-section asymmetrical, but ovate with more inflated inner margin. There may be slight narrowing towards the anterior and posterior of the basal cross-section. Cusp cross-section laterally compressed and ovate, pinched towards anterior and posterior. Basal cavity shallow, extending only just further than the point of geniculation of the element. Posterior margin of basal cavity curved forming tip towards centre of the element. Anterior margin of basal cavity also broadly curved to the antero-basal corner of the element.

Remarks. The systematic development of *C. minutus* is very similar to that of *C. cambricus*. Miller (1969) assigned *O. minutus* (= *C. minutus*) a unimembrate apparatus of geniculate elements, differing from *O. cambricus*(= *C. cambricus*) in the relative shallowness of the basal cavity, and by the presence of regeneration at the tip of the cusp. The latter character is not considered to be a valid diagnostic feature as, in many cases, cusp tips have been removed by breakage. In the later revision of his original work, Miller (1980) reassigned *O. minutus* to the new genus *Cambrooistodus* on the basis of the presence of white matter in the cusp, and described a bimembrate apparatus for both *C. cambricus* and *C. minutus*, including the rounded element of *E. notchpeakensis* with the respective geniculate element of each species. Landing (1983) concurred with this hypothesis, but relegated *Cambrooistodus* to the taxonomic rank of subgenus, in order to solve the biological problem of the vicarious rounded elements being attributed to two distinct genera.. Chen and Gong (1986) also erected a bimembrate apparatus for *C. minutus*, composed of a rounded and a compressed geniculate element. Only three specimens of *C. minutus* were included in their study, and only one geniculate element is figured (Chen and Gong 1986, pl. 32, fig. 16).

Cambrooistodus minutus differs from *C. cambricus* by having a shallower basal cavity, a shorter upper edge of the base and a rounded antero-basal corner. It is distinguished from the compressed element of *E. notchpeakensis* by the presence of a sharp angle between the upper edge of the base and the posterior margin.

Range. Base *C. minutus* Subzone - Top *C. minutus* Subzone.

Occurrence. WY96-17, Gallatin Formation, Bighorn Mountains, Wyoming.

Genus EOCONODONTUS Miller, 1980

1980 *Eoconodontus*, Miller, p. 21.
1981 *Eoconodontus* Miller; Miller (*in* Clark), p. W116.
1983 *Eoconodontus* Miller; Landing, p. 1175.
1986 *Eoconodontus* Miller; Chen and Gong, p. 140.

Type species. *Proconodontus notchpeakensis* Miller, 1969, p. 438, Notch Peak Limestone, House Range, Utah.

Emended diagnosis. Septimembrate apparatus of proclined to recurved, laterally compressed, coniform elements with a moderately deep to deep basal cavities. Anterior and posterior margins slightly keeled or rounded. White matter present in the tip of the element forming a sharp planar junction with the hyaline basal material. Elements ornamented or unornamented.

Remarks. Miller (1980) erected the genus *Eoconodontus* to include two forms previously assigned to *Proconodontus* (*P. notchpeakensis* and *P. carinatus*) and, based on co-occurrence data and white matter distribution, united them in the bimembrate apparatus *E. notchpeakensis*. *P. notchpeakensis* and *P. carinatus* were excluded from *Proconodontus* because the genus was restricted by Miller (1980) to include only hyaline forms. Fortey *et al.* (1982) and Landing (1983) divided *Eoconodontus* into two subgenera, *E.* (*Eoconodontus*) and *E.* (*Cambrooistodus*), based on their views that the species *E. notchpeakensis*, *C. cambricus* and *C. minutus* share a common group of vicarious rounded elements in their apparatuses. He also introduced the new species, *E. alisonae*, which has well-developed lateral costae, but is otherwise similar to *E. notchpeakensis*. *E. alisonae* has not been recovered from any samples used during the course of this investigation, and so although the apparatus is likely to be similar to that of *E. notchpeakensis*, the reconstruction remains to be studied in more depth. The apparatuses of these species (*E.* (*E*) *alisonae*, *E.* (*E*) *notchpeakensis*, *E.* (*C*) *cambricus* and *E.* (*C*) *minutus*) were described by Landing (1983) as being bimembrate, comprising drepanodiform (rounded), and either scandodiform (compressed) or oistodiform (geniculate) elements. Of the elements included in the rounded (drepanodiform) category of Landing (1983), only one element morphotype is now known to be symmetrical (aequaliform), with the remaining four morphotypes being asymmetrical (graciliform/truncatiform). Landing's (1983) view of the apparatus reconstructions of *Eoconodontus* and *Cambrooistodus* was similar to that of Miller (1980), who also stated that the rounded elements of *C. cambricus* and *C. minutus* are indistinguishable from both *E. notchpeakensis* and from one another.

In the present study, the generic positions of *Eoconodontus* and *Cambrooistodus* are retained on the basis of the presence of a truly geniculate element in the latter and a scandodiform element in the former. In view of the relatively limited number of characters available for the division of Cambrian euconodont taxa, the presence or absence of a geniculate element is considered to be a key character for defining genera. The septimembrate apparatus of *E. notchpeakensis* described here has been derived from the study of faunas in which *Cambrooistodus* elements are both present and absent but, due to the confinement of the stratigraphical ranges of *C. cambricus* and *C. minutus* to within the known range of *E. notchpeakensis*, the apparatus of *Cambrooistodus* remains poorly understood. It is for the reasons outlined below that the rounded (drepanodiform, aequaliform, graciliform, truncatiform) elements remain synonymised as part of the apparatus of *E. notchpeakensis* and that, although it is likely that the apparatus of *Cambrooistodus* is multimembrate and incorporates similar elements to that of *E. notchpeakensis*, the description and synonymy of both *C. cambricus* and *C. minutus* is based on the geniculate element morphotype of each species originally outlined by Miller (1980).

Elements of *Eoconodontus* differ from those of *Teridontus* Miller, 1980, because of their marked lateral compression, their strongly ovate, as opposed to sub-circular, basal cross-section and the absence of fine longitudinal striae which are present on the external surfaces of *Teridontus* elements. In addition, Nicoll (1994) has described a seximembrate apparatus for *Teridontus nakamurai* (Nogami, 1967), which lacks an element in the arcuatiform (M) position and is, therefore, easily distinguished from the septimembrate apparatus that is assigned to *Eoconodontus*. Although the septimembrate apparatus of *Cordylodus*, described by Nicoll (1990), is similar to that of *Eoconodontus*, elements of the latter are clearly different to primitive elements of *Cordylodus* because they lack denticles on the posterior margin. *Proconodontus* is distinguished from *Eoconodontus* because of the hyaline nature of the elements, and also because the apparatus may be less differentiated than that of *Eoconodontus*, comprising only three element categories. Ordovician forms such as *Drepanodus*, *Paltodus* and *Paroistodus* are known to possess septimembrate apparatuses that are very similar indeed to *Eoconodontus* and *Cordylodus* (Löfgren 1997a, 1997b, 1998), but have much shallower basal cavities and may not be closely related, with the similarities in apparatus composition being due to evolutionary convergence as opposed to a direct relationship.

Eoconodontus notchpeakensis (Miller, 1980)

Plate 2, figures 1-26; Plate 8, figure C; Plate 9, figure D; Plate 10, figure B

p	1967	*Oneotodus nakamurai*, Nogami, p. 216, pl. 1, figs 10, 11, ?12 (*non* pl. 1, figs 9a, 9b, 13 [= *T. nakamurai*]).
*v	1969	*Proconodontus notchpeakensis*, Miller, p. 438, pl. 66, figs 21-29; text-fig. 5G.
p	1969	*Proconodontus carinatus*, Miller, p. 437, pl. 66, figs 15-20; text-fig. 5I (*non* pl. 66, figs 13, 14 [= *C. cambricus*]).
p	1971	*Oneotodus nakamurai* Nogami; Druce and Jones, p. 82, pl. 10, figs 1, 2, 4, 5, 6; text-fig. 26j (*non* pl. 10, figs 3, 7, 8; text-fig. 26i [= *T. nakamurai*]).
	1971	*Proconodontus notchpeakensis* Miller; Miller and Melby, p. 123, pl. 2, figs 19-20.
	1973	*Proconodontus notchpeakensis* Miller; Müller, p. 43, pl. 4, fig. 6.
	1973	*Proconodontus muelleri* Miller; Müller, p. 42, pl. 3, fig. 8.
	1978	*Proconodontus notchpeakensis* Miller; Tipnis, Chatterton and Ludvigsen, pl. 1, fig. 14.
	1980	"*Proconodontus*" *carinatus* Miller; Landing, Ludvigsen and von Bitter, text-fig. 8D-H.
	1980	*Eoconodontus notchpeakensis* (Miller); Miller, p. 22, text-fig. 3D, E; pl. 1, figs 10-12.
	1981	*Proconodontus notchpeakensis* Miller; An, p. 220, pl. 2, fig 7.
?	1981	*Proconodontus carinatus* Miller; An, p. 220, pl. 2, fig. 10.
	1982	*Proconodontus notchpeakensis* Miller; An, p. 142, pl. 8, fig. 2; pl. 13, figs 1-11.
non	1982	*Proconodontus notchpeakensis* Miller; Fortey, Landing and Skevington, text-fig. 9I [= *P. muelleri*].

1982 *Eoconodontus notchpeakensis* (Miller); Taylor and Landing, text-fig. 5o.

1983 *Proconodontus notchpeakensis* Miller; An *et al.*, p. 127, pl. 5, figs 10-12, 19, 20.

1983 *Eoconodontus* (*Eoconodontus*) *notchpeakensis* (Miller); Landing, p. 1177, text-fig. 11p, q.

1983 *Proconodontus integratus* Zhang and Zhang; An *et al.*, p. 124, pl. 5, figs 17, 18.

1984 *Proconodontus notchpeakensis* Miller; Wang and Luo, p. 276, pl. 1, figs 3, 9.

1985 *Eoconodontus notchpeakensis* (Miller); Wang, p. 223, pl. 3, figs 8-10; pl. 4, figs 10, 11; pl. 7, figs 1-3; pl. 13, figs 4, 13, 14; pl. 14, fig. 18.

? 1986 *Eoconodontus notchpeakensis* (Miller); Chen and Gong, p. 140, pl. 19, fig. 13; pl. 31, figs 2, 6, 8; pl. 32, figs 2, 4, 6-7, 9, 11; pl. 33, figs 2, 8; text-fig. 48.

? 1986 *Eoconodontus notchpeakensis* (Miller); Chen, Zhang and Yu, p. 366, pl. 1, figs 9, 10.

1986 *Proconodontus notchpeakensis* Miller; Jiang *et al.*, pl. 3, figs 12-14.

1986 *Proconodontus intergratus* [*sic*] Zhang and Zhang; Jiang *et al.*, pl. 3, fig. 7.

1987 *Proconodontus notchpeakensis* Miller; An, p. 110, pl. 1, figs 21, 22, 25.

1987 *Eoconodontus notchpeakensis* (Miller); Buggisch and Repetski, p. 155, pl. 6, figs 8, 9; pl. 9, figs ?3, ?9, 12.

1987 *Eoconodontus notchpeakensis* (Miller); Dong, p. 163, pl. 1, figs 1, 2; pl. 3, figs 20, 21.

1987 *Eoconodontus notchpeakensis* (Miller); Viira, Sergeyeva and Popov, p. 148, pl. 1, figs 9-11.

? 1989 *Econodontus* [*sic*] *notchpeakensis* (Miller); Popov *et al.*, p. 145, pl. 17, fig. 14; pl. 18, figs 7-9.

1990 *Proconodontus notchpeakensis* Miller; An and Zhang, p. 159, pl. 2, figs 1-3.

1990 *Eoconodontus notchpeakensis* (Miller); Bryant and Smith, p. 804, text-fig. 12a.

? 1993 *Eoconodontus* (*E.*) *notchpeakensis* (Miller); Landing, text-figs 4.4, 4.6, 4.9.

1994 *Eoconodontus notchpeakensis* (Miller); Lehnert, p. 250, pl. 1, figs 1, 2.

1995 *Eoconodontus notchpeakensis* (Miller); Harris *et al.*, p. 24, pl. 1, figs X, Y.

1995 *Eoconodontus notchpeakensis* (Miller); Repetski *et al.*, p. 201, pl. 1, figs X, Y.

1996 *Eoconodontus notchpeakensis* (Miller); Taylor *et al.*, p. 156, text-fig. 6Y.

1998 *Eoconodontus notchpeakensis* (Miller); Dubinina, p. 568, pl. 1, figs 18-21, 23, 24.

1998 *Eoconodontus notchpeakensis* (Miller); Hein and Nowlan, p. 180, pl. 3, figs 17-19.

Holotype. UW 1360 (rounded element) Miller (1969), plate 66, figs 27, 28, Notch Peak Limestone, House Range, Utah, USA.

Material. 9203 elements in total: 237 Aequaliform, 598 Graciliform A, 6855 Truncatiform, 494Graciliform B, 203 Falciform, 237 Tortiform, 579 Arcuatiform.

Emended diagnosis. Septimembrate apparatus of proclined to recurved, laterally compressed, coniform *Eoconodontus* elements, with smooth external surfaces lacking well developed longitudinal costae.

Description. Septimembrate apparatus of proclined to recurved, laterally compressed coniform elements with white matter confined to region above the tip of the basal cavity within the cusp, and forming a sharp planar junction with the hyaline base, immediately above the basal cavity tip. Anterior and posterior margins sharp. Basal cavity depth variable but always extending to point of maximum curvature of the cusp.

Aequaliform element. Symmetrical, laterally compressed, proclined coniform element. Posterior margin broadly curved, sharp, with or without a slight posteriorwards extension at the white matter junction making the cusp of the element very slightly wider where white matter is present. Anterior margin sharp, broadly curved to antero-basal corner. Length ratio of cusp:base is approximately 1:2. Faces unornamented, symmetrically convex from anterior to posterior margin. Basal cross-section ovate, symmetrical with slight pinching at anterior and posterior. Cusp cross-section ovate, symmetrical. Basal cavity deep. Posterior margin of basal cavity found close to posterior margin at base, gradually becoming more distal to this margin towards the tip, with basal cavity tip found towards the anterior of the element. Anterior margin of basal cavity broadly curved following curvature of the anterior margin of the element.

Graciliform element A. Long-based, markedly proclined elements. Posterior margin sharp, very broadly curved. Anterior margin very broadly curved, sharp. Length ratio of cusp:base approximately 1:6. Inner face flattened, bearing a longitudinal depression immediately posterior to the anterior margin; depression variably developed. Outer face convex. Basal cross-section compressed, asymmetrically ovate, with flattened inner margin and convex outer margin. Anterior part may be slightly pinched due to longitudinal depression. Basal cavity deep. Posterior margin of basal cavity runs close to the posterior part of the element from the base to approximately two thirds of the element length where it tapers towards the centre of the element, forming a tip close to the anterior of the element. Anterior margin of basal cavity runs parallel with and close to the anterior margin of the element.

Truncatiform element. Asymmetrical, sub-erect to strongly recurved elements. Posterior margin broadly to strongly curved, sharp. Anterior margin sharp, moderately to broadly curved to antero-basal corner. Length ratio of cusp:base ranging from 2:1 to 1:2. Inner face flattened, with slight groove or depression running just posterior to, and parallel with, the anterior margin. Element occasionally slightly laterally bent towards inner face. Outer face convex, unornamented. Basal cross-section laterally compressed, ovate, flattened on inner side, marginally inflated on outer side, pinched towards anterior. Cusp cross-section asymmetrical flattened inwards, convex outwards. Basal cavity deep. Posterior margin of the basal cavity found close to the posterior margin of the element at the base, but becoming more distal towards the cusp. Tip found towards anterior of element, with anterior margin of basal cavity following curvature of the anterior margin of the element.

Graciliform element B. Short-based, markedly proclined elements. Posterior margin sharp, very broadly curved. Anterior margin very broadly curved, sharp. Length ratio of cusp:base approximately 1:4. Inner face flattened, bearing a longitudinal depression immediately posterior to the anterior margin; depression variably developed. Outer face convex. Basal cross-section compressed, asymmetrically ovate, with flattened inner margin and convex outer margin. Anterior part may be slightly pinched due to longitudinal depression. Basal cavity deep. Posterior margin of basal cavity runs close to the posterior part of the element from the base to approximately two thirds of the element length where it tapers towards the centre of the element, forming a tip close to the anterior of the element. Anterior margin of basal cavity runs parallel to and close to the anterior margin of the element.

Falciform element. Erect to strongly reclined element with a widely flaring base. Posterior margin markedly curved above base, becoming less curved and straightening towards the element tip. Margin broad at base, but sharpening apically. Anterior margin broadly curved, sharp distally and broadening towards the base. Length ratio of cusp:base approximately 2:1. Inner and outer faces unornamented, with very slight lateral twisting of the cusp towards the inner face. Base of element widely flared, broadly ovate to sub-circular in cross-section. Cusp-cross-section compressed, ovate. Basal cavity moderately deep. Posterior margin of basal cavity strongly curved forming tip towards centre of element. Anterior margin of basal cavity broadly curved running sub-parallel to the anterior margin of the element.

Tortiform element. Strongly reclined and markedly laterally compressed elements. Posterior margin strongly curved at based, then straightening distally. Margin sharp for entire element length. Anterior margin sharp, broadly curved with slightly increased curvature towards the based. Antero-basal corner rounded. Length ratio of cusp:base approximately 1:1. Inner and outer faces unornamented with very slight lateral twisting of the cusp towards the inner face. Base of element flared antero-posteriorly, compressed laterally, ovate in cross section with the postero-basal margin corner slightly recessed into the posterior margin of the element. Basal cross-section ovate, compressed. Cusp cross-section flattened and pinched towards the anterior and posterior. Basal cavity shallow. Posterior margin of basal cavity straight forming a tip towards the centre of the element. Anterior margin of the basal cavity broadly curved, running sub-parallel to the anterior margin of the element.

Arcuatiform element. Strongly reclined, laterally compressed elements. Posterior margin sharp, strongly curved towards base, straightening towards cusp. Anterior margin sharp, broadly curved. Length ratio of cusp:base between 2:1 and 4:1. Broad carina present on inner face extending from white matter junction to base, carina positioned central to the element face distally, following curvature of the element to be positioned more posteriorly at the element base. Element laterally twisted towards inner face. Outer face convex, broadly curved and unornamented. Basal cross-section asymmetrical with inner margin constrained by carina shape, and outer margin broadly convex. Basal opening may be slightly narrowed towards anterior and posterior. Cusp cross-section laterally compressed and ovate. Basal cavity shallow. Posterior margin of basal cavity runs from postero-basal corner close to the posterior of the element until the onset of straightening, continuing in the same direction to a tip in the centre of the element. Anterior margin of the basal cavity broadly curved from tip to antero-basal corner.

Remarks. Nogami (1967) included elements of *Eoconodontus notchpeakensis* in his original description of *Oneotodus nakamurai* (= *Teridontus nakamurai*). Outline drawings of the basal cross-sections (Nogami 1967, p. 216, figs 3D, E) showed the marked lateral compression of some of the elements encompassed by the description, but subsequent work (Miller 1980; Nicoll 1994) has shown that the basal and cusp cross-sections of all *Teridontus* elements are rounded, and that elements with a high degree of lateral compression should not be included. Druce and Jones (1971) also figured and described elements of *O. nakamurai* (= *T. nakamurai*) with laterally compressed cross-sections, and these are here included in *E. notchpeakensis*. An element with a flared base is amongst those figured (Druce and Jones 1971, pl. 10, figs 4a-c), and is the only known occurrence of a figured flared-based element in the literature.

Miller (1969) established two laterally compressed, non-geniculate coniform species in which white matter was present in the cusp, namely *Proconodontus notchpeakensis* and *Proconodontus carinatus*. A later revision of this work by Miller (1980) involved the erection of the new genus, *Eoconodontus*, to encapsulate those elements with white matter development that could no longer be included with the (by definition) entirely hyaline forms of *Proconodontus*, and also formulated a bimembrate apparatus for *E. notchpeakensis* consisting of "rounded" (*P. notchpeakensis*) and "compressed" (*P. carinatus*) elements.

Nicoll (1990) assigned a septimembrate apparatus to *E. notchpeakensis*, and stated that a geniculate *Cambrooistodus* element should occur within the apparatus model (Nicoll 1990, p. 530). However, Nicoll did not figure the apparatus, and no detailed description of the elements was given. As suggested above, this species concept is unlikely to be valid because the known stratigraphical range of *E. notchpeakensis* falls outside of the known ranges of both *C. cambricus* and *C. minutus*. The septimembrate apparatus assigned to *E. notchpeakensis* in this study agrees well with the apparatus of various *Cordylodus* species described by Nicoll (1990), strengthening the hypothesis that *Eoconodontus* and *Cordylodus* are closely related.

It is noted from inspection of younger material, (collections of Prof. J. F. Miller), that the anterior and posterior margins of *E. notchpeakensis* elements become gradually more rounded through time, from keeled forms early in the phylogeny, to more rounded forms in stratigraphically younger faunas. The very earliest elements may have only very slight development of white matter, usually in a narrow band, just above the tip of the basal cavity, with hyaline material found apical to this.

Range. Base *E. notchpeakensis* Subzone - *C. angulatus* Zone.

Occurrence. WY96-17, WY96-18, Gallatin Formation, Bighorn Mountains, Wyoming.

Order PANDERODONTIDA Sweet, 1988

Remarks. Sansom *et al.* (1994) proposed an amendment to the order Panderodontida, to include all coniform euconodonts whose apparatuses could be three locational domains (anterior qa-qg, posterior pf-pt, symmetrical ae). Sweet (1988) and Aldridge and Smith (1993) had placed *Coelocerodontus* in the order Belodellida, and did not agree that a close relationship between *Panderodus* and *Coelocerodontus* could be demonstrated. Sansom *et al.* (1994) drew attention to the apparatus model of Andres (1988) which shows clear similarities with the apparatus proposed by Sansom *et al.* for *Panderodus* and, on this basis, *Coelocerodontus* is considered to belong in the Panderodontida.

Family BELODELLIDAE Khodalevich and Tschernich, 1973

Remarks. Sweet (1988) assigned *Coelocerodontus* to the Belodellidae along with *Stolodus*, *Belodella*, *Walliserodus* and *Dvorakia* because of the common attributes of a quadri- to quinquemembrate apparatus of slender coniform elements with deeply excavated basal cavities, smooth surfaces and the presence of a number of longitudinal keels and costae. The family Belodellidae was originally included in the order Belodellida by Sweet (1988) and Aldridge and Smith (1993), but is now thought to belong in the Panderodontida because of the nature of the apparatus composition and architecture proposed by (Sansom *et al.* 1994).

Genus COELOCERODONTUS Ethington, 1959

1959 *Coelocerodontus*, Ethington, p. 273.
1974 *Coelocerodontus* Ethington; van Wamel, p. 55.
1983 *Coelocerodontus* Ethington; Landing, p. 1171.
1986 *Stenodontus*, Chen and Gong, p.186.
1987 *Diaphonodus*, Bagnoli, Barnes and Stevens, p. 155.
1991 *Coelocerodontus* Ethington; Müller and Hinz, p. 53.
1992 *Coelocerodontus* Ethington; Hinz, p. 265.

Type species. *Coelocerodontus trigonius* Ethington, 1959, p. 273, Stewartville Member, Locality 9, Ordovician Galena Formation, Kendallville, Iowa, USA.

Remarks. Ethington (1959) erected the genus *Coelocerodontus* to include horn-shaped, coniform elements with deep basal cavities, thin walls and sharp margins. Different species were distinguished according to the shape of the element cross-section. Landing (1983) emended the diagnosis of *Coelocerodontus* to form a multielement genus comprising elements from three species (*C. trigonius*, *C. tetragonius* and *C. digonius*) in one apparatus. He commented that the genus may be of proto- or paraconodont affinity, because of the lack of white matter and the exceptionally deep basal cavity. *C. bicostatus* was only tentatively assigned to *Coelocerodontus* by Landing (1983) because he only recognised a monoelemental apparatus for the species. Bagnoli, Barnes and Stevens (1987) also noted the lack of white matter and the presence of transverse growth lines on the surface of the elements, which is a feature typical of paraconodonts. Elements of *Coelocerodontus* were included in the 'euconodont' section of Müller and Hinz's (1991) monograph on Cambrian conodonts from Sweden, although they stated that no change to the suprageneric taxonomy should be made until a comprehensive review of the histology of *Coelocerodontus* had been carried out. They remained sceptical that the transverse annulations on the surface were true representations of growth lines. Due to the lack of abundant suitable material, this problem remains unsolved.

Coelocerodontus bicostatus van Wamel, 1974

Plate 1, figure 8.

*	1974	*Coelocerodontus bicostatus*, van Wamel, p. 55, pl. 1, fig. 1a, b.
	1974	*Coelocerodontus latus*, van Wamel, p. 56, pl. 1, fig. 2a, b.
?	1978	*Proconodontus muelleri muelleri* Miller; Fåhræus and Nowlan, p. 453, pl. 1, figs 1, 2.
?	1978	*Coelocerodontus*? sp., Löfgren, p. 49, pl. 1, fig. 40.
?p	1983	*Coelocerodontus cambricus* (Nogami); Landing, p. 1172, text-fig. 10A, B (*non* fig. 10C [? = *Proconodontus muelleri*]).
?	1983	*Coelocerodontus*? *bicostatus* van Wamel; Landing, p. 1172, figs 7P, 11V.
?	1986	*Stenodontus compressus*, Chen and Gong, p. 186, pl. 24, figs 11, 16; pl. 25, figs 2-5, 7-13, 16; text-fig. 76.
?	1986	*Stenodontus jilinensis*, Chen and Gong, p. 187, pl. 18, figs 2, 4-7, 9, 17-18; pl. 19, figs 3, 7; pl. 24, figs 1, 9, 18; pl. 34, figs 9, 14, 15, 19; text-fig. 77.
	1987	*Coelocerodontus bicostatus* van Wamel; An, p. 104, pl. 1, fig. 11.
	1987	*Diaphonodus latus* (van Wamel); Bagnoli, Barnes and Stevens, p. 155, pl. 2, figs 11-13.

1988 *Coelocerodontus* Ethington; Andres, p. 121, pl. 9, figs 3-8; text-figs 17, 18, 19.

1988 *Ceolocerodontus cambricus* (Nogami); Heredia and Bordonaro, p. 190, pl. 1, figs 2, 3.

1988 *Rotundoconus mendozanus* Heredia and Bordonaro, p. 194, pl. 3, fig. 5; pl. 4, fig. 3.

1988 Gen *et.* sp. indet. A, Heredia and Bordonaro, p. 195, pl. 3, fig. 7; pl. 4, fig. 4.

1991 *Coelocerodontus bicostatus* van Wamel; Müller and Hinz, p. 53, pl. 41, figs 1-21; text-fig. 20A-D.

1992 *Coelocerodontus bicostatus* van Wamel; Hinz, p. 265, text-fig. 8, figs 1, 4.

Holotype. T191-13, van Wamel (1974), pl. 1, fig. 1, lowermost part of member $D_{\text{ä-d2}}$ at Köpingsklint, Öland, Sweden.

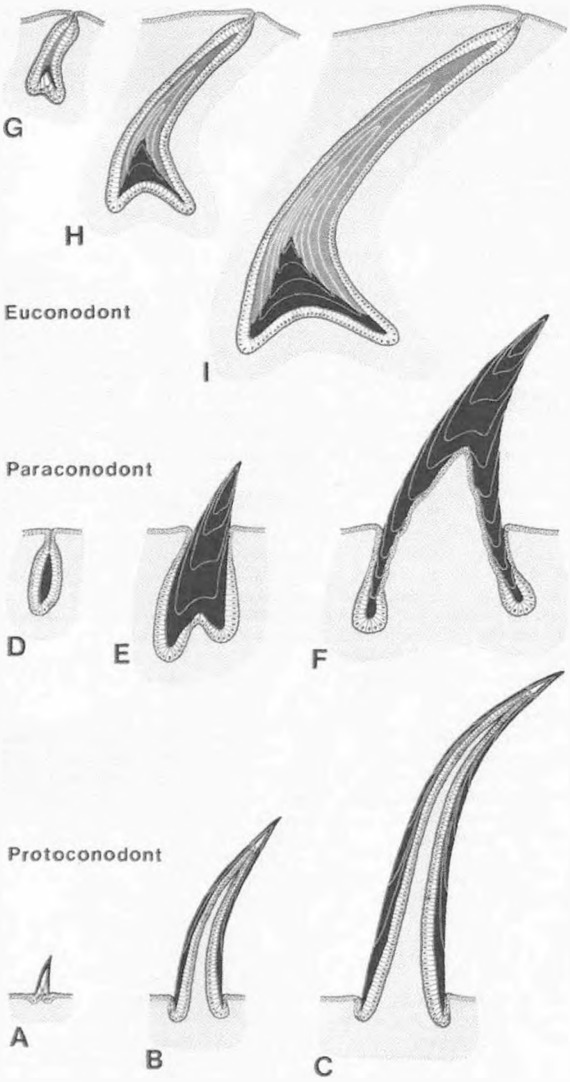
Material. 3 elements.

Remarks. Elements of two species initially erected by van Wamel (1974), *Coelocerodontus bicostatus* and *C. latus* are considered to be part of the apparatus of the multielement species *C. bicostatus*. Andres (1988) illustrated a fused cluster of *C. bicostatus* elements, and assigned a quinquemembrate apparatus to the species. Elements are markedly compressed, with sharp anterior and posterior margins, a deep basal cavity and a single sharp costa developed on one or both of the lateral faces. According to Andres (1988), each half-apparatus consists of a small, short, asymmetrical element with a triangular cross-section on one end, followed by a single, broad element with a characteristically hooked tip. Next is a transition series of more than five elements with two lateral costae, the largest element of which is situated in the centre of the array. Subsequent to the transition series of elements becoming more asymmetrical towards the margin is another small, asymmetrical element with a triangular cross-section. Müller and Hinz (1991) and Hinz (1992) recognised only two element types in the *C. bicostatus* apparatus. Alpha morphotypes are homologous to the transition series elements of Andres (1988), with sharp anterior and posterior margins and a variously developed costa on each lateral face. Beta elements possess hooked tips. No short, asymmetrical forms with triangular cross-sections were remarked upon by Müller and Hinz (1991). Too few elements have been found during the course of the present study to contribute more to the understanding of the apparatus or histology of this species.

Occurrence. VG93-10, VG93-12, Upper Cambrian Alum Shale, Västergötland, Sweden.

CHAPTER 7

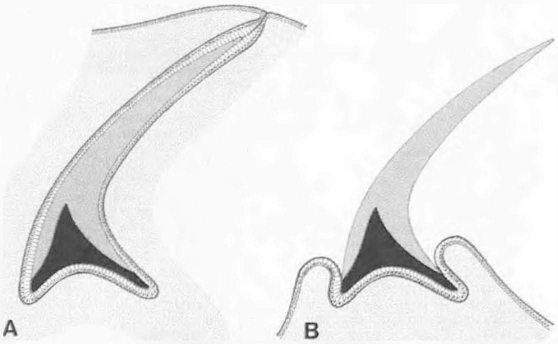
PREVIOUS STUDIES OF CONODONT HISTOLOGY



Text-figure 7.1. Bengtson's growth hypothesis. The diagram shows the relation of the secreting epithelium to the element during growth, and illustrates the direction in which growth takes place. (From Bengtson 1976).

7.1 Introduction

Historical reviews of studies of euconodont hard tissue histology have been compiled by Sansom (1992) and Donoghue (1998) and so, to avoid repetition, this introduction to conodont element histology will concentrate mainly on the more recent advances, and the studies that are particularly pertinent to the investigation of Cambrian proto-, para- and euconodonts. The most appropriate starting point for this summary is the publication by Bengtson (1976) who established an hypothesis of conodont phylogeny, whereby euconodonts evolved via paraconodonts from protoconodonts during the Late Cambrian (Text-figure 7.1). Bengtson (1976) noted that protoconodonts grew centripetally by accretion of tissue on the inner margin, whereas euconodonts grew by the centrifugal deposition of new material. Paraconodonts formed an intermediate stage in Bengtson's model, with addition of new mineralised tissue on both the inner and outer margins of the base (Müller (1962) and Müller and Nogami (1971) had previously recognised the paraconodont style of growth). It was hypothesised by Bengtson (1976) that the change in growth style from proto- to para- to euconodont grade was accompanied by the gradual retraction of the elements into secretory (epithelial) pockets during phylogeny, protoconodonts being completely exposed during ontogeny, paraconodonts being partially retracted and euconodonts being entirely covered by the secreting tissue, at least during times of growth (Text-figure 7.2). Following earlier suggestions by Lindström (1964, p. 32) and Müller and Nogami (1971, p. 53), Bengtson (1976) proposed that paraconodont elements were homologous with the basal bodies of euconodonts, due to their style of growth and apically open growth lamellae. Subsequent investigations have, however, cast doubt on the validity of Bengtson's model, because of conflicting ideas concerning the affinities of protoconodonts and euconodonts.

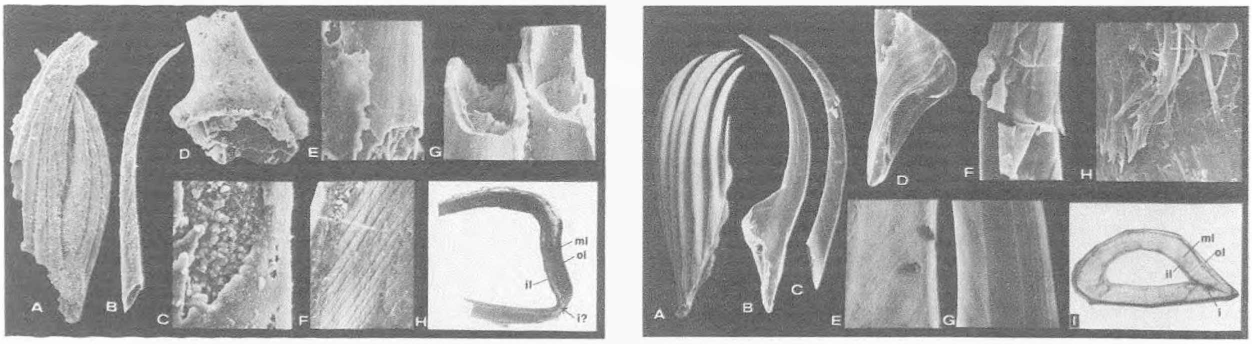


Text-figure 7.2. Diagram to show the putative position of a euconodont element relative to the secreting epithelium. A, fully enclosed during growth and B, enclosed at the base only during function. (from Bengtson 1976).

7.2 *Protoconodonts – histology and affinity*

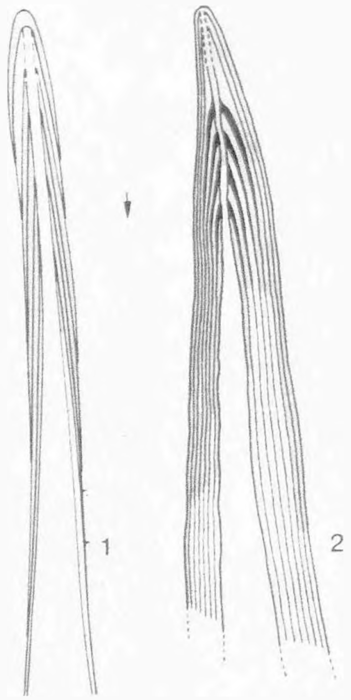
Prior to histological studies, Müller and Andres (1976) compared protoconodont elements to the grasping spines of Recent chaetognaths, because of the apparatus composition and architecture of *Prooneotodus tenuis* (= *Phakelodus tenuis*). Müller and Andres stated that this similarity may be due to evolutionary convergence rather than a close phylogenetic relationship, and predicted that studies of the fine-structure of the elements of protoconodonts and the chaetognath *Sagitta* could determine homology between these elements in the future.

Szaniawski (1982, 1983, 1987) studied the histology of protoconodont elements and found them to have a three-layered internal structure comprising a thin, organic inner layer, a thicker, laminated middle layer and a thin, structureless outer layer (Szaniawski 1982; Text-figure 7.3). Szaniawski also investigated the histology of *Sagitta*, finding the chaetognath grasping spines to have a three-layered structure directly comparable to that of the protoconodont elements. One contrasting feature of the histology is the presence of siliceous tips on the grasping spines of Recent chaetognaths (Bone *et al.* 1983) which were not observed by Szaniawski (1982, 1983, 1987) in protoconodont elements. From these investigations, Szaniawski concluded that protoconodonts and chaetognaths shared a close relationship, a view that has been accepted by many authors (Andres 1981, 1988; Repetski and Szaniawski 1981; Bengtson 1983; Sweet 1985; Aldridge *et al.* 1993; Donoghue *et al.* 2000; Dzik 2000).



Text-figure 7.3a. Illustration to show the similarities in apparatus architecture and element histology between the Cambrian protoconodont *Phakelodus tenuis* (left hand diagram) and the Recent chaetognath *Sagitta* (right hand diagram). (From Szaniawski 1982).

Investigations of the histology of a number of protoconodont genera have been conducted by Müller and Hinz-Schallreuter (1996, 1998), who have found that two different growth styles are present (Text-figure 7.3). Elements of *Phakelodus* and *Protohertzina* are said to grow by the addition of oblique lamellae which make the basal region of the element very fragile, since they are composed of only one growth increment, whereas elements of *Gumella* (= *Gapparodus*) and *Hertzina* add growth increments at the tip which continue parallel to the margins, to the base of the element. Müller and Hinz-Schallreuter did not comment on whether this difference in growth style is of importance in order to divide the informal group 'protoconodonts' (*sensu* Bengtson 1976) into more stable taxonomic categories. Evidence to support this has not been forthcoming during the course of this study (Chapter 8), and so the informal classification of Bengtson (1976) is retained.



Text-figure 7.3b. Diagram illustrating the two styles of protoconodont growth recognised by Müller and Hinz-Schallreuter (1998). 1, represents *Phakelodus* or *Protohertzina* type growth and 2, represents *Gapparodus* or *Hertzina* style growth. (from Müller and Hinz-Schallreuter 1998).

In terms of soft-tissues, conclusive evidence for the affinity of the protoconodonts is lacking. Taxa interpreted as fossil chaetognaths have included *Amwiskia sagittiformis* Walcott from the Middle Cambrian Burgess Shale, *Paucijaculum samamithion* Schram, from the Middle Pennsylvanian Mazon Creek fauna of Illinois, and *Titerina rokycanensis* Kraft and Mergl, from the Arenigian Klabava Formation of the Prague Basin. There is also undescribed material from the Burgess Shale that may represent chaetognaths. Tarlo (1960) maintained the original placement of *Oesia* by Walcott (1911) in the annelids but this idea was not supported by Andres (1988) who cited *Oesia* as a chaetognath. In addition, *Amwiskia sagittiformis* and *Paucijaculum* have been reassessed as nemertines by Conway Morris (1977) and Richardson (1982) respectively. *Titerina rokycanensis* described by Kraft and Mergl (1989) remains the most plausible candidate for a fossil chaetognath, with a bilateral array of grasping elements, a gut, possible ovaries and a ray-supported, laterally orientated caudal fin being preserved. Kraft *et al.* (1999), in their description of *Titerina*, interpreted the poorly preserved grasping elements as possible protoconodont elements in the head region, and have stated explicitly that, because euconodonts are early vertebrates and protoconodonts are chaetognaths, this should 'lead to a part of the protoconodonts, at least, being removed from the 'conodont-taxonomic-basket' and re-sited among the chaetognaths.' (Kraft *et al.* p. 452).

Some authors have, even in the light of evidence supporting the vertebrate nature of the euconodonts (see below) and the chaetognath affinity of protoconodonts, maintained that proto-, para- and euconodonts are part of one monophyletic group. Azmi (1996) gave evidence of the soft-tissue basal support of protoconodonts to infer a relationship with chaetognaths, but compared the longitudinal orientation of the crystallites in the crown of *Panderodus* (following Sansom *et al.* 1992) to those in the middle layer of protoconodonts to imply vertebrate affinity. Since Azmi (1996) chose to support Bengtson's (1976) hypothesis, he concluded that the relationship of proto-, para- and euconodonts with either chaetognaths or vertebrates remained unresolved, but that it was more likely that they formed a monophyletic group and that their affinities were probably with the vertebrates. Kasatkina and Buryi (1996a, b, 1997) have used the soft-part anatomy of the Carboniferous Granton conodonts to favour a chaetognath affinity of all conodonts, erecting a new superphylum the Chaetodonta which includes the new phylum Euconodontophylea (euconodonts) and the phylum Chaetognatha Leuckart, 1854, into which the proto- and paraconodonts were placed. The interpretation of the soft-tissue anatomy of conodonts presented by Kasatkina and Buryi (1996a, b, 1997) is not in agreement with other current hypotheses of vertebrate affinity (see Aldridge *et al.* 1993 and Donoghue *et al.* 2000), and will not be discussed further.

Dzik (2000) recognised that the most parsimonious view of the nature of protoconodonts is that they are chaetognaths, based on comparable element morphology and histology, but stated that confirmation of this relationship could only come from new discoveries of the soft-parts of protoconodonts. Following the hypothesis of Bengtson (1976), Dzik (2000) noted that if the proto-, para- and euconodonts form a single group, then the anatomies of three phyla are present, chaetognaths (protoconodonts, *Odontogriphus* (paraconodonts, see below) and chordates (euconodonts), but that these could be linked if a common ancestor bearing an oral grasping apparatus was found. The presence of a protective horny cap overlying the euconodonts elements, proposed by Dzik (2000) was thought by him to demonstrate a close relationship between the euconodonts and the Recent myxinoids, therefore providing evidence that chaetognath spines, which are not homologous to hagfish toothlets, could not be homologous to the horny caps of euconodont elements. The existence of horny caps covering euconodont elements has yet to be unequivocally demonstrated, since their remains have not been found in the fossil record (Dzik 2000).

Other studies have investigated the phylogenetic placement of the chaetognaths with regards to modern phyla using cladistics within a scenario-like character framework (Christoffersen and Araújo-de-Almeida 1994), or molecular phylogenies (Telford and Holland 1993; Wada and Satoh 1994), with various outcomes. Christoffersen and Araújo-de-Almeida (1994) found that chaetognaths were the sister group of vertebrates, by suggesting that certain characters that are present in vertebrates had been secondarily lost during the evolutionary development of chaetognaths. These characters included reduction of the heart and vascular system due to small size of the animals, loss of the gill slits, loss of a dorsal nerve chord, loss of the endostyle in association with the loss of the gill slits, loss of the notochord, loss of the myotomes and the loss of the metameric nerves. In addition, Christoffersen and Araújo-de-Almeida (1994) suggested that the grasping spines and the vestibule of chaetognaths are homologous to the pharyngeal bars and the pharynx of vertebrates respectively. Molecular studies do not support the placement of the chaetognaths as the sister group of vertebrates, or even the positioning of the chaetognaths within the deuterostomes, siting them instead within the protostomes (Telford and Holland 1993; Wada and Satoh 1994; Conway Morris 1994; Nielsen 1995; Nielsen *et al.* 1996).

Since the exact phylogenetic position of the chaetognaths remains unresolved, at least two scenarios are possible concerning Bengtson's (1976) evolutionary hypothesis of conodont phylogeny:-

1. Chaetognaths are the sister group of vertebrates (Christoffersen and Araújo-de-Almeida 1994) and therefore a protoconodont (chaetognath) – paraconodont – euconodont (vertebrate) transition is theoretically possible,

2. Chaetognaths (protoconodonts) are protostomes, vertebrates (euconodonts) are deuterostomes (Telford and Holland 1993; Wada and Satoh 1994), and the proto-, para- euconodont transition model is untenable because of the large phylogenetic separation of the two end members.

As noted by Dzik (2000), the placement of the chaetognaths in the deuterostomes as the sister group of vertebrates by Christoffersen and Araújo-de-Almeida (1994) is largely based on secondary absence of characters, without supporting evidence, and so the protostome position of the chaetognaths is preferred. As a result of this, protoconodonts are unlikely to share a close relationship with the euconodonts, as is also demonstrated by differences in the histology of the two groups and, therefore, the first stage of Bengtson's growth hypothesis cannot be supported.

7.3 Euconodonts – histology and affinity

7.3.1 Introduction

Prior to the discovery of the soft-part remains of conodonts in the early 1980s (Briggs *et al.* 1983), the question of conodont affinity was a subject of much speculation (see Miller 1981 for a review). Following the discovery of further soft-part remains, and subsequent description and elucidation of the anatomy and structure of these soft-tissues (Mikulic *et al.* 1985a, 1985b; Aldridge *et al.* 1986, 1993; Smith *et al.* 1987; Aldridge and Theron 1993; Gabbott *et al.* 1995), renewed attempts were made to interpret and understand the hard tissue histology of the euconodonts. To begin with, comparisons between the hard tissues of euconodonts and the hard tissues of other groups were based on morphological similarity alone (Dzik 1986; Andres 1988), but later investigations have concentrated on the growth, development and relationships of the constituent tissues, providing a more precise model on which to base interpretations of the hard issue histology (Sansom *et al.* 1992, 1994; Sansom 1996; M. M. Smith *et al.* 1996; Donoghue 1998). With the exception of some authors (e.g. Kasatkina and Buryi 1996a, 1996b, 1997), the consensus of opinion is that the euconodonts are chordates, based on both soft tissue anatomy and hard tissue histology, but their systematic position within this group is still contested (see Aldridge *et al.* 1993; Schultze 1996; Pridmore *et al.* 1997; Donoghue *et al.* 2000 for some of the alternative viewpoints). As noted by Donoghue *et al.* (2000, p. 201) there are two schools of thought concerning the interpretation of euconodont hard tissues, those who consider them to be homologous to vertebrate hard tissues, and those who oppose this idea. The following sections will review the various arguments that have been proposed for and against the vertebrate nature of euconodont hard tissues.

7.3.2 Euconodonts as vertebrates

Since the euconodont elements used in this investigation have not been found in association with soft tissues, it is necessary to make two assumptions before attempting to interpret the histology of the mineralised hard tissues. The first of these is that the members of the order Proconodontida, that have formed the main focus of this study, are related to the rest of the euconodont clade. Sweet (1988, p. 133) referred to members of the Proconodontida as 'mostly short-lived, experimental stocks...which appeared briefly during the initial radiation...but were apparently not ancestral to anything else', but other authors have contested this view (Ji and Barnes 1990, 1994a, b) and have proposed that the Proconodontida are closely related to stratigraphically younger forms (see Chapter 6 – Euconodont systematics). Following the comparison of apparatus composition of species from the Proconodontida with more derived euconodonts, the views of Ji and Barnes are accepted, and the Proconodontida is found to comprise the earliest members of the euconodont clade. Secondly, it must be assumed that the soft tissue anatomy of the known Ordovician, Silurian and Carboniferous euconodonts can be extrapolated to include older forms, and that similar anatomical characters were found in Cambrian euconodonts.

Having made these assumptions, it is necessary to summarise recent interpretations of euconodont histology in order to compare these with the findings of the present study of Cambrian euconodonts.

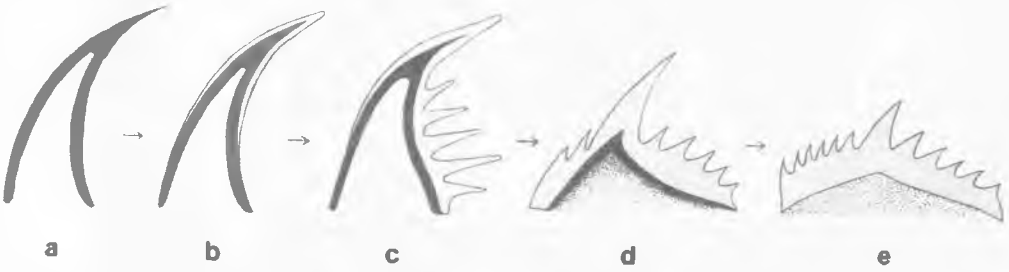
Dzik (1986) noted the histological similarity between euconodont and chordate hard parts, concluding that euconodont crown tissue is homologous to vertebrate enamel and the basal body tissue is homologous to dentine. Dzik based these interpretations on evidence that demonstrated that the crystallites in the euconodont crown differed only in their larger size and ordered orientation from those in the enamel cap of *Astraspis* Walcott, (the capping tissue of *Astraspis* is now considered to be enameloid (M. M. Smith and Hall 1990; M. M. Smith *et al.* 1996; Sansom *et al.* 1997)), and that the numerous tubuli in the basal filling (= basal body) did not differ in diameter, mode of branching or distribution from those tubuli found in thelodont scales. However, because Dzik only found well-developed basal bodies in the larger, presumably adult specimens, he suggested that mineralisation of the mesodermally derived basal filling occurred subsequently to that of the ectodermally derived crown. This is in contrast to the view of Smith and Hall (1990) who described the series of epithelial-mesenchymal interactions which lead to the differentiation of preodontoblasts, preameloblasts, odontoblasts and ameloblasts, which in turn deposit the dentine and enamel of vertebrate teeth. Smith and Hall (1990, p. 339) stated that 'These differentiated cells can then interact to initiate the deposition of predentine and dentine followed by enamel.', demonstrating that dentinous basal bodies could not have formed secondarily to the enamel crown, as suggested by Dzik, because the presence of mineralised dentine is a prerequisite for the deposition of enamel. Diekwisch *et al.* (1995) have demonstrated that some initially formed enamel crystals are not spatially associated with mineralised dentine, a line of evidence which may support Dzik's (1986) opinion that the basal body is mineralised secondarily to the crown in euconodonts. However, even in the study of Diekwisch *et al.*, a mineralised dentine later and an enamel-dentine junction (EDJ) were present prior to the formation of enamel crystals, as predicted by Smith and Hall (1990).

Rather than there being a paraconodont ancestor of euconodonts, Dzik (1986) suggested that *Fomitchella infundibuliformis* Missarzhevsky, with its similar microstructure to the enamel camp of *Astraspis*, may be the sclerite from which the 'true' conodonts stemmed. To bridge the morphological and stratigraphical distance between *Fomitchella* and *Astraspis*, Dzik used various phosphatic microfossils including *Hadimopanella* Gedik, *Utahphospha* Müller and Miller and *Milaculum* Müller, forms which are now considered to be members of the Palaeoscolecida (Hinz *et al.* 1990; Müller and Hinz-Schallreuter 1993). Histological investigations of *Milaculum* during the course of this study (Plate 18, Figs A, B) do not support a vertebrate affinity or therefore, a close relationship with the euconodonts, and the interpretations by Hinz *et al.* (1990) and Müller and Hinz-Schallreuter (1993) of *Milaculum* as a palaeoscolecid are supported. Bengtson (1983) had previously described the histology of *Fomitchella*, finding it to have fine incremental lines, open to the inner surface, implying that growth occurred in an outward direction, similar to the crown of euconodonts. Bengtson found no basal body and no large crystallites in the 'crown', and concluded that, because of stratigraphical separation and histological differences, *Fomitchella* is not related to either para- or euconodonts.

Following on from this study, Dzik (1993) re-iterated his earlier views that euconodonts are chordates, citing the two tissue types (crown + basal body) and their distinct origin as supporting evidence. Even more recently, Dzik (2000) has interpreted conodonts (= euconodonts) as the most primitive chordates bearing a well-developed mineralised dermal skeleton, an opinion not entirely concordant with the views of other workers (e. g. Sansom *et al.* 1992, 1994; Sansom 1996; M. M. Smith *et al.* 1996; Donoghue 1998) who believe euconodonts to be agnathan vertebrates, or even stem-group gnathostomes (Donoghue *et al.* 2000), (see later for a discussion of these publications). Also in contrast to the commonly accepted view that euconodont elements functioned externally as food gathering or processing organs, as demonstrated by their apparatus architecture and functional morphology (Purnell and Donoghue 1997, 1998) together with microwear on their surfaces (Purnell 1995), Dzik (2000) proposed that euconodont elements were covered by an hypothetical 'horny cap' during ontogeny, an idea previously expressed by Schmidt and Müller (1964) and Priddle (1974). As evidence for the presence of a 'horny cap' Dzik cited the occurrence of secretory cell imprints across the entire occlusal surface of some euconodont platform elements (see also Hass 1941; Pierce and Langenheim 1970; Müller and Nogami 1971; Lindström *et al.* 1972; Burnett 1988; Conway Morris and Harper 1988; von Bitter and Norby 1994; Zhuralev 1994), which he used to state that a uniform cover of ameloblast cells must have been present, thus refuting Bengtson's (1976) hypothesis predicting the sporadic retraction of elements into epithelial pockets. Dzik attributed the presence of microwear patterns (Purnell 1995) to post-mortem taphonomic processes. In the past the reticulate pattern on the surface of conodont elements has been used to infer the presence of secretory cells (Hass 1941; von Bitter and Norby 1994; Zhuralev 1994) or even to assess the genome size of conodonts (Conway Morris and Harper 1988), but none of these studies have taken the presence of cell imprints to imply that a secondary covering was found overlying the epithelium of euconodont elements. In the light of evidence that euconodonts functioned externally (see above) and the lack of evidence to support the presence of the keratinous caps proposed by Dzik (2000), the views of previous authors (Purnell 1995; Purnell and Donoghue 1997, 1998) are adopted, euconodonts functioned externally and there is currently no evidence for a keratinous cap.

Andres (1981, 1988) studied the apparatus composition and architecture of proto-, para- and euconodonts, together with their histology, in order to test Bengtson's (1976) hypothesis of conodont phylogeny. Andres (1981) investigated the ontogenetic and phylogenetic development of the euconodont genus *Cordylodus*, and suggested that early growth stages of *Cordylodus* elements lacked denticles and would have possessed only a thin covering of crown material over the upper parts of the element, with denticles appearing in succession on the posterior margin and crown material becoming thicker and more ubiquitous during ontogeny (Andres 1981, text-figs 14-18). Andres compared the basal bodies of euconodonts to complete paraconodont elements citing evidence of holes in the basal regions of *Cordylodus* and *Problematoconites* as features that could be used to demonstrate a relationship between forms. In addition, Andres (1981) followed Gross' (1957) tripartite division of the entire euconodont element into the 'eigentlichen conodont' (conodont proper = crown), 'basistrichter' (basal cone) and 'trichterfüllung' (cone filling), to propose that the most primitive euconodonts consisted of only a basal cone (=

paraconodont) and a thin layer of crown material, with more advanced euconodonts developing a cone filling at the expense of the basal cone, until the most advanced euconodonts possessed only a basal filling (= basal body), overlain by a thick layer of crown material (Andres 1981; Text-figure 7.4). Early euconodonts investigated during the course of this study have been shown to possess well-developed basal bodies, and the structural development hypothesis suggested by Andres (1981) is rejected.



Text-figure 7.4. Diagram illustrating the growth model described by Andres (1981). Dark shaded areas are the basal cone, light grey shaded areas are the crown material and the speckled areas represent the basal filling. (from Andres 1981).

The views outlined above were expressed by Andres (1981) prior to the discovery of conodont-bearing animals from the Carboniferous Granton Shrimp Bed in Scotland (Briggs *et al.* 1983; Aldridge *et al.* 1986, 1987), and Andres (1988) focused on the two groups to which the conodont animals were most commonly compared at that time, the chordates and the chaetognaths. Andres (1988, p. 142) discounted a close relationship between euconodonts and chaetognaths on the grounds that the soft-tissue evidence described by Briggs *et al.* (1983) and Aldridge *et al.* (1986, 1987) showed the Scottish euconodont animals to be metameric, whereas Recent chaetognaths are unsegmented, and that a closer affinity to the chordates was likely. Following this conclusion, Andres went on to compare the histology of para- and euconodonts to that of the dermal skeleton of various heterostracans and cephalaspids. Andres (1988) likened the basal opening of para- and euconodonts to the pulp cavity of heterostracan tubercles, and noted that the distinctly two-layered nature of the euconodonts (crown + basal body) was similar to the differentiation of ectodermal enamel and mesodermal dentine in teeth and placoid- and ganoid scales. Wrinkling of growth lamellae in the basal region of primitive euconodonts and the paraconodont *Problematoconites* were compared with similar structures in the dentine layer of *Ganosteus* figured by Halstead-Tarlo (1964, pl. 10, fig. 1) and spherical bodies in the basal body were considered to be similar to those found in *Eriptychius*, *Alaspis* and human teeth. Larger pores, surrounded by smaller scars in the basal cavities of *Problematoconites* and primitive euconodonts were thought by Andres to be the result of vascular canals or connective tissues with branching terminal networks, similar to those observed in heterostracans and the placoid scales of sharks. Although he considered these structural features as indicators of a relationship of both para- and euconodonts with chordates, Andres stressed that chemical similarity (elucidated earlier by Rhodes and Wingard (1957) and Pietzner *et al.* (1968)) could not be used to support this view, since organisms with phosphatic hard-parts were common in the Palaeozoic, particularly during the Cambrian.

Considering that Andres had contested a close relationship between protoconodonts (chaetognaths) and para- and euconodonts, he concluded (Andres 1988, p. 144) that a phylogeny (following Bengtson's (1976) hypothesis) from the Middle Cambrian *Oesia* Walcott, 1911, from the Burgess Shale (considered by both Walcott (1911) and Tarlo (1960) to be an annelid) to the Silurian *Panderodus* animal from Waukesha and finally the Carboniferous euconodont animals of Scotland was possible. For this phylogeny to have occurred, Andres noted that it would have had to be accompanied by a lengthways stretching of the apparatus, a differentiation of the elements within the apparatus to perform different functions, the development of V-shaped segments and a change in the direction of flattening of the animal from dorso-ventral in *Oesia* and *Panderodus* to lateral in the Scottish animals (*Clydagnathus*). Using similarities in histology, but differences in function, Andres (1988, text-fig. 39) stated that euconodonts were indeed chordates and that euconodonts and 'fish' both stemmed from a paraconodont group (or possibly separate groups) during the Late Cambrian, with the appearance of 'fish' (*Anatolepis*) slightly pre-dating that of the euconodonts. Very recently however, it has been demonstrated that, cladistically speaking, euconodonts are 'fish', and that *Anatolepis* could not have preceded euconodonts (Donoghue *et al.* 2000).

Smith and Hall (1990) included conodonts in their study of vertebrate skeletogenic and odontogenetic tissues, because of the soft-part anatomy described by Briggs *et al.* (1983) and Aldridge *et al.* (1986), but stated explicitly that conodonts 'are certainly not...primitive examples of oral odontodes', (Smith and Hall 1990, p. 289) and that 'they [conodonts] simulate teeth but are not homologues of teeth' (*ibid.* p. 288).

Two important terms were used by Smith and Hall in the above statements, the first of which is *odontode* and the second is *teeth*. Ørvig (1967) used the term odontode to refer to tooth-like structures in the dermal skeleton, but this definition was refined by Reif (1982) as part of his

Odontode Regulation Theory. The following definition of an odontode is quoted from Reif (1982, p. 290):-

> 'An odontode is an isolated superficial structure of the dermal skeleton which consists of a dentinous tissue (mesodentine, semidentine or metadentine). A hypermineralised cap of enamel or enameloid is either present or can be lacking. Vascular supply takes place through basal canals and/or neck canals. The base of the odontode consists of (acellular or cellular) bone, which functions as an attachment tissue. Anchoring of the odontode occurs either by anchoring fibres which originate in the bony base, or the odontode can be ankylosed to an underlying bone. Formation of an odontode takes place in a single, undivided dental papilla of mesenchyme which is bounded at its outer surface by an epithelial dental organ.'

Reif (1982) recognised two types of odontodes, isolated *dermal denticles* and *teeth*. Teeth are distinguished from dermal denticles by their mode of formation, whereby teeth form in a deep epidermal invagination called the dental lamina, but the dermal denticles form superficially at the junction between the mesenchyme and the overlying epithelium, with no deep invagination. A single dermal element or tooth is usually the product of a single odontode, although 'odontocomplexes' (*sensu* Ørvig 1977) are known to exist, whereby early-formed odontodes are incorporated into, or overgrown by, successive generations. Some non-coniform euconodonts are considered to be the product of odontocomplexes by Donoghue (1998, see below).

Blieck (1992) disputed the vertebrate affinity of the euconodonts, expressing concern that the typically two-layered (crown + basal body) structure of euconodonts could not be homologous to the four-layered structure of heterostracan hard parts (enamel/enameloid cap + dentine + spongy aspidin + lamellar aspidin). However, if euconodont elements and individual heterostracan hard parts are considered to be odontodes, it is theoretically possible according to Smith and Hall (1990, 1993) and M.M. Smith (1995) to alter the products of odontodes by heterochronic shifts in the cell differentiation or for a cell type not to have acquired competence in the odontode system. If this is the case, it is possible that in euconodonts, the ability of the odontode system to produce basal tissues (bone or aspidin) was lacking, which is why euconodont elements possess only a two-layered structure. Blieck (1992) considered the primitive condition of vertebrate hard tissues to be cellular, and although some lineages (including the heterostracans) had secondarily derived acellular tissues, the acellular nature of the euconodont tissues could not, according to Blieck, prove the vertebrate affinity of the group. The claim by Dzik (1986) that the euconodont basal tissue was dentine was dismissed by Blieck, who stated that the dentine tubules illustrated by Dzik (1986, text-fig. 1c) were unlike those observed in early vertebrates (e.g. thelodonts).

New techniques used to make thin-sections and the use of Nomarski interference contrast microscopy enabled Sansom *et al.* (1992) to demonstrate for the first time that the euconodont lamellar crown tissue was homologous to vertebrate enamel, and that the basal body of the euconodont genus *Cordylodus* was composed of globular calcified cartilage. Sansom *et al.* also suggested that euconodont white matter was homologous to vertebrate cellular bone, a view that has since been retracted (Sansom pers. comm. 1996).

Forey and Janvier (1993) questioned the interpretations of euconodont histology advocated by Sansom *et al.* (1992), stating that the crystallites in the lamellar crown did not correspond precisely to those in vertebrate enamel, and that the variable orientation of these crystallites between species was also not a typical feature of enamel. M. M. Smith (1995, p. 139) however, stated that there are 'major changes in the crystallite arrangement among taxa' and so the first objection by Forey and Janvier can be refuted. The second concern of Forey and Janvier (1993) was that euconodont elements lacked dentine, a tissue which had been considered as the most primitive hard tissue by Smith and Hall (1990). Smith and Hall (1993) changed their earlier views of euconodont affinity and, based on additional soft part evidence presented by Aldridge *et al.* (1993) together with the description of hard part histology in terms of vertebrate tissues by Sansom *et al.* (1992), agreed that euconodonts should be included in the vertebrate clade.

Dentine was discovered in euconodonts by Sansom *et al.* (1994), therefore addressing the second of the doubts voiced by Forey and Janvier (1993). Two types of dentine were observed in the basal bodies of euconodonts from the Ordovician Harding Sandstone of Colorado by Sansom *et al.* (1994). The first was tubular dentine in *Chirognathus*, with scalloped growth increments, occasional spherulitic structures and tubules with a diameter of approximately 1 µm running perpendicular to the growth surface, and the second was mesodentine in *Neocoleodus*, with similarly sized (1 µm) branching tubules, approximately perpendicular to the growth surface, but without scalloped growth lamellae or spherulitic structures.

A dentinous (atubular dentine) basal body was found to occur beneath the enamel crown in *Pseudooneotodus* by Sansom (1996). In *Pseudooneotodus*, crystallites of the lamellar crown are arranged almost perpendicular to the growth surface, but fan out slightly into swallow tail, a pattern that was compared by Sansom (1996) with the enamel in the teeth of the Triassic amphibian *Mastodontosaurus*. A sharp junction separates the crown from the basal body, which is characterised by scalloped growth increments and spherulitic structures and which, when viewed in cross-polarised light exhibits a striped extinction pattern caused by pervasive structures which Sansom (1996) attributed to either attachment fibres or closed tubules. Appositional growth of the crown and basal body tissues away from their mutual junction (enamel-dentine junction, EDJ), indicated by the angular relationship of the growth increments with the junction, was also described and illustrated by Sansom (1996, text-fig. 4), comparing the growth of the euconodont tissues to the growth of vertebrate mineralised tissues for the first time.

M. M. Smith *et al.* (1996) summarised the available histological data for euconodonts, finding that five different tissue associations were present within euconodonts, enamel overlying mesodentine (*Neocoleodus*), enamel overlying tubular dentine (*Chirognathus*), enamel overlying atubular dentine (*Pseudooneotodus*), enamel + white matter overlying atubular dentine (*Oulodus*) and enamel + white matter overlying globular calcified cartilage (*Panderodus*). These were compared to the variability of tissue types among known vertebrates (Vertebrate Indet. A of Denison (= *Skiichthys halsteadi* M. M. Smith and Sansom, 1997) *Astraspis* and *Eriptychius*) from the Harding Sandstone. Growth of the crown and basal body away from a common junction was noted by M. M. Smith *et al.* (1996) as a feature indicative of presumed epithelial-mesenchymal apposition, which occurs during the growth of enamel and dentine in dermal denticles and teeth.

In addition to euconodonts, Sansom and his colleagues have continued to elucidate the histology of a variety of Palaeozoic microvertebrates in a series of publications (Sansom *et al.* 1995, 1996, 1997, 2000; M. M. Smith *et al.* 1995, 1996; M. M. Smith and Sansom 1997, 2000; M. P. Smith and Sansom 1995; M. P. Smith *et al.* 1996), with the most recent (Smith and Sansom 2000) concentrating on the origin, evolution, diversity, development and function of dentine.

M. M. Smith and Sansom (2000) have reviewed the terminology applied to the different types of dentine from a historical perspective, largely following Ørvig (1951, 1967). This has demonstrated that a revised terminology will be of use in the future, to move away from the now defunct early theories of the evolution of dentine types and the proposed relationship of dentine with bone. It has been noted by M. M. Smith and Sansom (2000, p. 70) that fossil dentines can be recognised using a number of features including differences in the level of mineralisation, processes and patterns of growth (incremental lines, mineralisation patterns), inclusion of cell bodies (lacunae) or cell processes (tubules), hypermineralisation of tubule spaces (peritubular dentine) and other features such as the presence of vascular canals and spaces. Since euconodonts became extinct at the end of the Triassic, these features are invaluable for the identification of dentine in conodont elements. Functional aspects of dentine were also investigated by Smith and Sansom, who described how dentine could have a sensory function, could be used as a support (pertinent to conodonts) or as a reparative tissue in worn-out denticles or teeth. The findings of the study were that dentine predates bone in the fossil record, tubular dentine was present in the first fish (*Anatolepis* Bockelie and Fortey, histology described by M. P. Smith *et al.* 1996) and, because of the phenotypic plasticity of dentine, it is difficult to place the different types of dentine in an evolutionary scheme, especially in terms of characters used in a cladistic analysis. Smith and Sansom pointed out that a revision of the terminology applied to dentine is necessary, and that the phylogeny of dentine types will result from a cladistic analysis of early vertebrates which incorporates both histological and anatomical data.

Perhaps the most comprehensive review of conodont element hard-tissues and growth has been compiled by Donoghue (1998) who summarised all previous studies of euconodont histology and formulated a precise model for the growth and development of euconodont elements. Donoghue made the point that, on the basis of soft-tissue remains, euconodonts were at least chordates, and so examined the possible range of phosphatic hard-tissues associated with fossil and Recent members of that group. After dismissing amorphous mineralisation of dahllite in tunicates, and the statoliths and statoconia of myxinoids because of chemical instability, Donoghue (1998, p. 653) concluded that the only possible homologues of the lamellar crown were enamel or enameloid, and that because of the preferred orientation of the crystallites in euconodont crown material, enameloid could be discounted. Due to the divergent growth of the mineralised tissues away from the crown-basal body junction Donoghue stated that the basal body was only likely to be composed of dentine, cartilage or bone. After rejecting bone (as had been suggested by Barskov *et al.* 1982), on the basis that the structures typical of bone (osteocyte lacunae, vascular canals) were not apparent in the basal bodies so far investigated, Donoghue also questioned the presence of cartilage because of an earlier statement by Smith and Hall (1990) that cranial exoskeletal cartilage is usually associated with bone, a tissue not known in conodont elements. Dentine was therefore thought by Donoghue to be present in most, if not all, euconodont basal bodies, although problems with the lack of basal bodies in Middle and Upper Palaeozoic euconodont genera were cited (Donoghue 1998, p. 657-658). A more precise definition of white matter was proposed by Donoghue (1998, see also Donoghue and Chauffe 1998), such that 'true' white matter is more finely crystalline than the lamellar crown tissue, has a greater resistance to acid etching, possesses a lower organic content, has a lack of growth increments, has sharply defined lateral margins, is opaque in thin-section and possesses tubular or spherical cavities. Donoghue (1998) disputed the presence of 'true' white matter in *Cordylodus*, an opinion that is particularly pertinent to this study (see later), because no distinct white matter occurs in etched specimens, even though opaque areas can be observed in thin-sections viewed in transmitted light. The presence of opaque areas was attributed to optical effects caused by prism boundaries in the lamellar crown (Donoghue 1998, p. 643).

Concerning the growth of euconodont elements, Donoghue (1998) found four different growth patterns in complex ramiform elements and two varieties of platform growth. Since only primitive coniform euconodonts have been used, together with various species of the denticulate genus *Cordylodus*, during the course of this study, the majority of these will not be discussed, although it is noted that *Cordylodus angulatus* is presumed to have grown according to Type II development, where later denticles grew separately to the main unit, consisting of their own crown and basal body, before incorporation of the main unit during ontogeny. However, Donoghue (1998, p. 647) described *Cordylodus angulatus* as an early representative of the genus, a view that is inconsistent with published interpretations of the phylogeny of *Cordylodus* (e. g. Miller 1980, Bagnoli, Barnes and Stevens 1986, Nicoll 1990; see Huselbee 1998 for a review), where *C. angulatus* is found to be the most derived species of the genus. In addition, the apparatus composition of *Cordylodus* remains a contentious issue, with various conflicting hypotheses being forwarded by a number of authors (Nicoll 1990; Bagnoli, Barnes and Stevens 1986; Ji and Barnes 1990, 1994a, b; amongst others), with some of these including elements with bi-apical basal bodies in apparatuses alongside elements with only a single basal body tip (Landing 1980; Bagnoli, Barnes and Stevens 1987). Others prefer to unite elements with bi-apical basal bodies together into apparatuses (e.g. *C. lindstromi*, Nicoll 1990), without additional (uni-apical) elements. To date it appears unlikely that each individual denticle on the posterior margin of *Cordylodus* elements is the result of a subsequent odontode generation, as is inferred by the type II growth mechanism described by Donoghue (1998), although this idea is worthy of further investigation.

Donoghue *et al.* (2000) have summarised all the anatomical and histological data that are available for euconodonts, and used this to perform a cladistic analysis to establish a phylogenetic position for the euconodonts within the chordates. Results of this cladistic analysis placed euconodonts as the most primitive members of the stem-Gnathostomata, crownward of both the hagfish and lampreys. Tests were performed during the course of their analysis, because of doubts voiced by other authors concerning the coding of certain characters. Those characters that have been contested in the past include the nature of the hard tissues (enamel and dentine) and also the presence of extrinsic eye musculature.

To test whether these characters are important in the phylogenetic positioning of the euconodonts, Donoghue *et al.* (2000) performed analyses whereby these characters were set to question marks and also to zeros in the coding. With all euconodont histological characters set to '?', the results remained identical, with the presence of a mineralised dermal skeleton placing euconodonts as more derived that hagfishes or lampreys. When the presence of extrinsic eye musculature was also set to '?' the same results were produced again. In the test where the codings of the histological characters together with the coding for the presence of extrinsic eye musculature were set to 'zero', there was still no change in the outcome of the analysis, and only when the presence of a mineralised dermal skeleton was set to '0' did the euconodonts change position in the phylogeny, becoming more primitive than both hagfish and lampreys. The results of these tests have demonstrated that the placement of euconodonts as stem-Gnathostomata is not dependent on the interpretation of the hard tissues as enamel and dentine, or on the presence of extrinsic eye musculature.

Donoghue *et al.* (2000) then placed their phylogenetic classification into a stratigraphical framework, which predicts the presence of hagfish and lampreys in the Cambrian, some 200 million years prior to their first appearances in the fossil record (Bardack and Zangerl 1968; Bardack 1991). An inmplication of this is that the euconodonts (in the phylogenetic scheme of Donoghue *et al.* (2000)) were the first group of vertebrates to acquire a mineralised dermal skeleton.

7.3.3 Opponents of the 'euconodonts are vertebrates' hypothesis

Not all authors agree with the hypothesis that euconodonts are vertebrates. Some argue that euconodonts should be included within the chordates, but contest the idea that euconodonts should lie within the vertebrate clade (Kemp and Nicoll 1995a, 1995b, 1996; Schultze 1996; Müller and Hinz-Schallreuter 1998). Others maintain that all three conodont groups (proto-, para-, euconodonts) are closely related to the chaetognaths (Kasatkina and Buryi 1996a, 1996b, 1997), with some placing the euconodonts in their own phylum (Sweet 1988). Some have suggested that euconodont elements are homologous to the toothlets of the myxinoids (Krejsa *et al.* 1990a, 1990b), and others chose not to express a preference (Szaniawski and Bengtson 1993).

Using various techniques Szaniawski (1987) investigated the histology of proto-, para- and euconodont elements and found that, subsequent to etching, a cone of more resistant material was left lining the basal cavity of some elements. Szaniawski chose to refer back to the tripartite division of the element structure described by Gross (1957), consisting of the crown, the basal cone and the cone filling, stating that the basal cone, built of fine lamellae parallel to the cone surface, was more organic-rich than the more heavily-mineralised basal filling. In the text Szaniawski did not emphasise the presence of spherulitic structures within the otherwise parallel lamellae in the base of *Cordylodus* sp. (Szaniawski 1987, pl. 2.3, figs 1a, b, c), suggesting that the origin of these spherical structures was still uncertain. In addition Szaniawski, in contrast to other authors (Müller and Nogami 1971; Lindström and Ziegler 1971) was not convinced that the growth lamellae of the crown and basal body were concordant, having found non-continuous lamellae. From his demineralised sections, Szaniawski found that underneath the thin coating of the crown in *Eoconodontus* was a network of fibrils, but could not determine whether these were relics of primary organic structures, or were of secondary origin. The features with which Szaniawski (1987) chose to demonstrate a relationship between proto-, para- and euconodonts were considered by other authors (e.g. Andres 1988) to be controversial, and included chemical composition, lamellar structure, growth direction, distribution of organic matter and the presence of an organic coating, all of which could quite easily be attributed to convergent evolution between disparate groups. Szaniawski went on to conclude that it was possible for euconodonts and chaetognaths to share a relationship, and for all three groups of conodonts (*sensu* Bengtson 1976), together with chaetognaths, to share a common ancestor.

In 1993, Szaniawski and Bengtson attempted to demonstrate how the transition between paraconodonts and euconodonts may have taken place (Szaniawski and Bengtson 1993, text-fig. 7). Their starting point was a paraconodont that possessed a two-layered element, formed from continuous lamellae that were thicker at the apex and on the outer margin, becoming thinner on the inner surface. Subsequently, a mineralised apical portion developed on each lamella, becoming more prominent and extending basally in later growth stages. This model is in opposition to the view of Dzik (1986) that the basal body of euconodonts was acquired secondarily to the crown, as opposed to being the primitive condition. Szaniawski (1987) and Szaniawski and Bengtson (1993) stated that the junction between the crown and the basal body in primitive euconodonts is not as sharply defined as that in more advanced forms, due to the gradual increase in the phosphatic content of each subsequent growth lamella, and hence the occurrence of an inter-fingering of organic basal material and heavily-mineralised crown tissue at the crown-basal body junction (Text-figure 7.5). This has not been recognised in similar material used during this study and, if it does occur, could be explained by alternative growth strategies. One implication of this hypothesis explaining the paraconodont-euconodont transition and the ontogenetic development of primitive euconodont elements is that it appears to be a single epithelium that secretes two differently-structured materials, possibly simultaneously, similar to the recent theory that white matter and lamellar crown tissue are developmentally homologous and are deposited by cells that were originally from the same population.

Text-figure 7.5. Diagrammatic representation of the growth of (1) paraconodonts, (2) primitive euconodonts and (3) derived euconodonts according to Szaniawski and Bengtson (1993). Note the layers of crown and basal material are continuous in figures 2 and 3. (from Szanaiwski and Bengtson 1993).

Fåhræus and Fåhræus-van Ree (1987, 1993) used histochemical studies, staining decalcified euconodont elements with haemalum and eosin, to attempt to identify the nature of the soft-tissue matrix freed from the elements. Kemp and Nicoll (1995a, 1995b, 1996) followed this idea but used other histochemical staining agents to test for the presence of collagen, proteoglycans, and protein molecules in decalcified conodont elements. The results of their experiments are given in Kemp and Nicoll (1996, tables 1 and 2) and, in general, they did not confirm a vertebrate affinity, with Kemp and Nicoll choosing to place the euconodonts in a systematic position more closely allied with the cephalochordates. For example, their results for the genus *Cordylodus* show that the hyaline material of the crown contains cartilage (positive reaction with alcian blue) and collagen (positive reaction with sirius red), but no keratin (negative reaction to Gram's Stain) or protein (negative reaction to toluidine blue). The albid tissue (white matter) stains only with alcian blue, and the basal body showed positive responses for all reactions (i.e. would contain cartilage, collagen, keratin, and unspecified proteins), although the positive reaction for keratin was later dismissed as possible contamination or a reaction to the glueing agent (gum tragacanth) (Kemp and Nicoll 1996, p. 295). The interpreted presence of collagen in the hyaline crown material led Kemp and Nicoll to dismiss its relation to vertebrate enamel, in which collagen is not normally found. A problem with the use of histochemical analysis in such ancient material is that it is unlikely that, although structural preservation is known to occur, biochemical activity of tissues cannot survive for such long stretches of time (Bada 1991), and in addition, M. M. Smith (pers. comm. *in* Donoghue 1998 and Donoghue pers. comm. 2000) has failed to reproduce the results of Kemp and Nicoll (1995a, b, 1996) using known fossil vertebrate remains. Kemp and Nicoll (1995a) also claimed to have discovered histochemically active DNA in euconodont element, but it is unlikely for this to have remained active for such extensive periods of time.

In response to discussions concerning the soft-tissue morphology of the Carboniferous conodont animals (Briggs *et al.* 1983; Aldridge *et al.* 1986; 1987) and the subsequent suggestion that their affinities may be with the primitive chordates, craniates or vertebrates, Krejsa and Slavkin (1987) and Krejsa *et al.* (1988, 1990a, 1990b) formulated an hypothesis that suggested that conodont elements were possibly homologous with myxinoid teeth. Evidence used to support this hypothesis was based on similar body dimensions in juvenile hagfish and the Granton conodont animals, together with comparable ratios of tooth length to body length during ontogeny (Krejsa *et al.* 1990b, text-fig. 2), in addition to element histology. Krejsa *et al.* (1990b) proposed that the spaces found in the white matter of conodont elements corresponded in size to keratin microspaces, and that during life these holes may have housed cellular pigments, lipids, organelles and tubules that are characteristic of the pokal cells more commonly associated with hagfish tooth development. They also suggested that conodont basal bodies could represent a replacement tooth, as is found in myxinoid teeth if conodonts were indeed lost and replaced (Carls 1977). Problems concerning the biomineralised nature of conodont elements in contrast to the keratinous ('horny') teeth of hagfish were discussed, using the evidence that hagfish do produce enamel protein-like epitopes (Slavkin *et al.* 1983) and that although the ancient ancestors of the myxinoids may not have been able to mineralise dentine, they could mineralise enamel, an ability that was subsequently lost.

M. M. Smith *et al.* (1996) outlined a number of objections to the suggestion by Krejsa *et al.* that hagfish toothlets and conodont elements are homologous structures. The first of these objections stated that conodont elements are the result of biomineralisation in an apatitic system, whereas hagfish toothlets are keratinous, and that there is no evidence to show that a switch between these two systems is possible. Following this, M. M. Smith *et al.* (1996) argued that there is also no evidence that demonstrates that the basal body of euconodonts could be a replacement crown because the basal body and the crown of conodonts grow appositionally away from one junction as a single unit, the crown and the basal body are not formed from identical tissues, no cone-in-cone elements have been found in discrete element collections of conodonts (as would be expected if replacement elements were present), and because the shape of the upper surface of the basal body is not always similar to the upper surface of the crown. For these reasons the hypothesis of homology between hagfish toothlets and conodont elements suggested by Krejsa *et al.* was refuted by M .M. Smith *et al.* (1996). Subsequent work on the ontogenetic growth of conodont elements (Donoghue 1998) has also demonstrated that this hypothesis of a close relationship between hagfish teeth and conodont elements is untenable.

Janvier (1995) renounced his belief that euconodonts were not vertebrates, but remained sceptical concerning the interpretation of their hard-tissues as enamel, dentine, cartilage or bone, preferring to maintain that the histology of euconodonts is unique to the group, possibly being derived from more conventional vertebrate skeletal tissues (Janvier 1995, 1996a, 1996b).

Six reasons were given by Schultze (1996) as to why the lamellar crown of euconodonts cannot be homologous with vertebrate enamel, including the relatively high ratio of crown to basal body material (an unknown situation in enamel), orientation of the crystallites, high organic content (collagen), timing of tissue formation, the interpretation of white matter in the crown as bone by Sansom *et al.* (1992) and the interpretation of globular calcified cartilage in the basal tissue (Schultze stated that enamel is not found in contact with globular calcified cartilage). Schultze acknowledged that globular calcified cartilage may be present in the basal bodies of some euconodonts, but justified this acceptance by using the histochemical arguments of Kemp and Nicoll (1995) (Schultze 1996, p. 282), a line of evidence not commonly accepted by other authors. He dismissed evidence for dentine by claiming that the dentine tubules described in euconodont basal bodies by previous authors were not like accepted vertebrate dentine structures because they did not branch, and they passed too far into the tissue. In conclusion Schultze (1996) categorically stated that conodonts are not homologous to teeth (following Smith and Hall 1990) and accepted the attainment of euconodont grade following the hypothesis of Bengtson (1976) and Szaniawski and Bengtson (1993), with paraconodont elements becoming the basal bodies of euconodonts, and noted that any similarities (morphological or histological) between euconodonts and vertebrates were superficial.

Using mainly soft tissue evidence, but also the presumed absence of a cartilaginous skeleton, Pridmore *et al.* (1997) claimed that euconodonts could not lie within the vertebrates (lampreys + gnathostomes) or even the craniates (hagfishes +vertebrates), placing them instead as the sister group of the craniates, crownward of the cephalochordates. Pridmore *et al.* (1997) supported the views of Kemp and Nicoll (1995a, 1995b, 1996) and those of Schultze (1996) concerning the nature of the euconodont hard tissues, and used the presence of bodies of calcium phosphate in the ears of hagfishes and lampreys to suggest that the ability to secrete a mineralised skeleton was acquired prior to the radiation of the craniates. The presence of radials in the euconodont caudal fin was accepted, but the apparent absence of radial muscles was used as evidence against the inclusion of euconodonts in the vertebrates (but this can be argued against, to quote Donoghue *et al.* (1998, p. 212) 'absence of evidence should not be taken as evidence of absence'). Pridmore *et al.* (1997) also discussed the interpretation of the paired lobate structures in the head region of euconodonts as eyes, suggesting instead that they may be otic capsules. In addition, they made reference to the lack of head cartilages in conodonts (that are present in extant craniates), to the lack of dermal scales or denticles in conodonts and to the V-shaped myomeres which are found in cephalochordates, but not craniates (which have W-shaped myomeres according to Pridmore *et al.*). However, Pridmore *et al.* (1997) added that the V-shaped myomeres may be incompletely preserved, but went on to infer that, because the dorsal portions of the myomeres were seemingly complete in some specimens, the structure of the myomeres was likely to be M-shaped rather than W-shaped, with the points of the V-shaped parts facing anteriorly.

Müller and Hinz-Schallreuter (1998) investigated the histology of some Late Cambrian proto-, para- and euconodonts but found no evidence to support a vertebrate-euconodont relationship, and supported the chordate assignment of the group by Kemp and Nicoll (1995).

7.4 Paraconodonts – histology and affinity

7.4.1 Introduction

If protoconodonts are considered to be chaetognaths and euconodonts are considered to be vertebrates, it appears that the complete transition between proto-, para- and euconodonts predicted by Bengtson (1976) is unlikely. However, it is possible that one aspect of the hypothesis may still be tenable, with paraconodonts being closely related to either the proto- or the euconodonts. Histological information is vital in order to discover whether either of these scenarios is possible, and on current evidence it appears likely that a link between the para- and the euconodonts is the more probable of the two ideas. It is necessary to summarise the previous work on paraconodont histology before going on to present evidence from the current study that supports a close relationship between a subset of the paraconodonts, and the euconodonts.

7.4.2 *Previous studies of paraconodont histology and affinity*

Müller (1962) erected the order Paraconodontida to distinguish conodont elements that grew by basal accretion of material at the lower rim, from the elements included in the order Conodontophorida which grew by the addition of material on their outer surfaces. Subsequently, Müller and Nogami (1971) included the Paraconodontida as a suborder of the Conodontophorida and refined the diagnosis of the paraconodonts, citing six key histological differences that separated the Paraconodontida from the suborder Conodontiformes. The six histological differences were:

1. The amount of organic matter in the hard parts is higher in paraconodonts than in later conodonts (euconodonts), and there is often a well-preserved, relatively thick organic layer covering the outer surface of paraconodont elements, which is not present in later conodonts.

2. Growth lamellae observed in paraconodont elements are closed in the early growth stages, becoming open on the upper and lower surfaces of the element in the later stages of ontogeny.

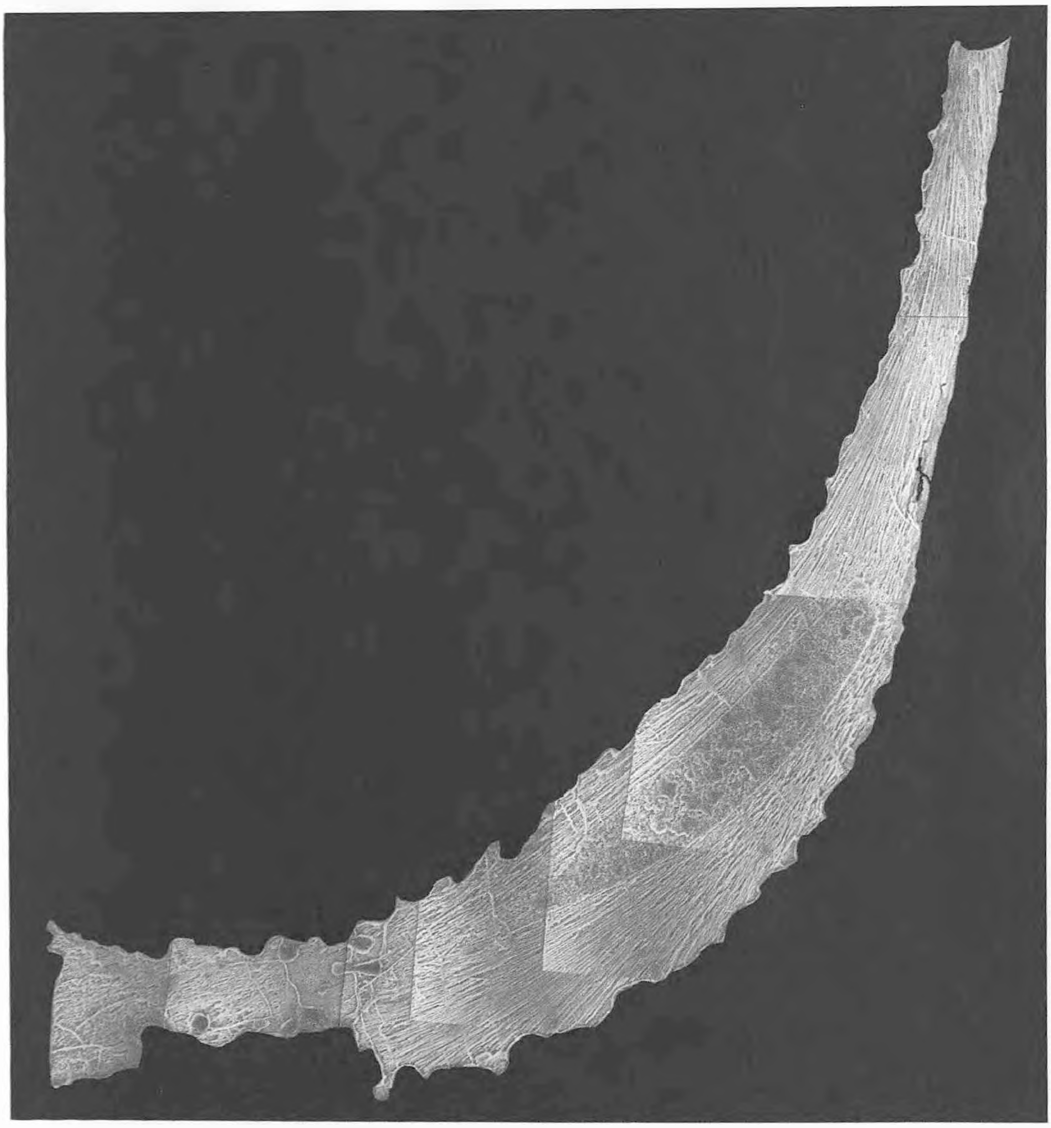
3. There is no differentiation of the paraconodont elements into a crown and a basal body.

4. There is no differentiation of 'bubble-structures' or white matter in paraconodont elements.

5. The main growth direction is towards the base in paraconodonts, but towards the tip in euconodonts.

6. In comparison to euconodonts of the same size, only a relatively small number of growth lamellae are observed in paraconodont elements.

In addition (as mentioned in Chapter 5), Müller and Nogami (1971) altered the generic names of those conodonts included in the Paraconodontida by placing the prefix 'Pro' in front of the original generic name, and also included genera not previously assigned to the Paraconodontida by Müller (1962) under the new definition. Other genera (*Pygodus*, *Rhombocorniculum*) that were initially included in the Paraconodontida by Müller (1962) were removed from the suborder. Histological studies of *Rhombocorniculum* (Landing *et al.* 1980; this study, Text-fig. 7.6) have demonstrated that *Rhombocorniculum* elements are constructed in an entirely different manner to any member of the Paraconodontida and that, therefore, *Rhombocorniculum* cannot be included within the group. *Pygodus* is now considered as a euconodont (Müller and Nogami 1971; Clark 1981). Following an earlier statement by Lindström (1964, p. 32) that some Cambrian conodonts 'would make rather plausible basal cones', Müller and Nogami (1971, p. 53) tentatively proposed an hypothesis which stated that paraconodont elements were homologous to the basal bodies of euconodonts.



Text-figure 7.6. Photo-montage of a thin-section through an element of *Rhombocorniculum* from Comley, Shropshire. Note that the individual crystallites are elongated and that they crop-out on the external surface of the element. Scale X400.

The suggestion that paraconodont elements and euconodont basal bodies are homologous has been made a number of times since the initial statement by Lindström (1964). In a personal communication to Miller (1969), Ethington concluded that the holotype of *O. gallatini* (= *P. gallatini*) was a basal cone, which led Miller (1969) to suggest that the species concept of *P.*

gallatini was problematic. Szaniawski (1980) came to a similar conclusion regarding elements of *P*. aff. *gallatini*, stating that they may represent the basal cone of another conodont.

Bengtson (1976) used the observations of Müller and Nogami (1971) as an integral part of his evolutionary growth hypothesis. In accordance with other authors he stated that paraconodont elements are homologous to euconodont basal bodies, and based his views on several lines of evidence including the apically open growth lamellae, the small size of the crystallites and the higher organic content of both structures. It was noted by Bengtson (1976) that, for the earliest paraconodont growth lamellae to be entirely closed, they would have had to have been completely embedded in the secreting epithelium, only erupting when they had reached a certain size. This posed a problem for the growth hypothesis, since the junction between the crown and the basal body of euconodonts can be traced into the growth centre of the element, and so even the most juvenile elements in the earliest growth stages would have possessed differentiated crown and basal body material. However, Bengtson (1976), Andres (1988) and Szaniawski and Bengtson (1993) challenged earlier views that the initial growth stages of paraconodont elements are completely enclosed and demonstrated that the growth lamellae of paraconodont elements are all open to the surface, with the closed lamellae being attributed to the positioning of the thin section through the element.

Miller (1976, 1980) was the first author to propose a relationship between named paraconodont and euconodont genera, and stated that *Prooneotodus rotundatus* was the paraconodont ancestor of an as yet unnamed euconodont genus, which was in turn the predecessor of the *Proconodontus* lineage. As suggested previously by Müller and Nogami (1971) and Bengtson (1976) the intermediate form was thought by Miller to have a basal body homologous to the paraconodont element, with a thin covering of crown material possibly arising from the mineralisation of the organic layer that is thought to cover the outer surface of paraconodont elements.

A further interpretation of the phylogenetic development from paraconodonts to euconodonts was presented by Andres (1981) who followed Gross' (1957) division of euconodont elements into three structural components, conodont proper (=crown), basal cone and cone filling. In this model, paraconodont elements were homologous to the basal cone, which was reduced during euconodont phylogeny due to the increased dominance of the cone filling.

Andres (1988) described the histology of the paraconodonts *Furnishina*, *Prooneotodus gallatini* and *Problematoconites*, and noted various similarities and differences between these forms.

Although all the forms were shown by Andres to grow in a similar manner with growth lamellae open on both the upper and lower surfaces of the element (typical paraconodont growth), elements of *Furnishina* and some elements of *P. gallatini* possessed a basal opening with a smooth inner surface, lacking any small-scale structural features. On the other hand, some elements of *P. gallatini* and *Problematoconites* were found to possess pores, canals and channels on their inner surfaces, with the canals and channels running parallel to the long-axis of the elements. Two sets of pores were observed by Andres, some of the larger pores being surrounded by smaller, scar-like depressions, which were thought to be attachment sites for fibres (Andres 1988, pl. 8, fig. 7). In the canals, Andres (1988, pl. 7, fig. 8) observed what he thought to be the diagenetically phosphatised remains of organic material. Some elements of both *P. gallatini* and *Problematoconites* were thought to have a two-layered wall structure (excluding the outermost organic covering), with the features described above present on the innermost of these two layers, and the outermost layer demonstrating a typical paraconodont element structure (Text-figure 7.7).

Text-figure 7.7. Diagrams to show the similarities between paraconodont element histology (A = *Problematoconites*) and primitive euconodont histology (B = *Proconodontus*) proposed by Andres (1988). Note the pits in the basal tissue, together with the longitudinal canals and the two-layered growth. (from Andres 1988).

As noted above, Andres (1988) compared the histology of para- and euconodont elements with that of the heterostracans dermal scales and suggested that certain homologies existed between the two structures. Andres believed that the inner hollow space (pulp cavity) of heterostracan dermal scales was homologous to the basal opening of conodonts, that the dentine tubules of heterostracans were of a similar size to the canals and channels observed in the basal cavities of para- and euconodont elements and that both para- and euconodonts had a two-layered structure, similar to the heterostracan dermal elements. In addition, the pores found in the basal region of paraconodonts were thought by Andres (1988) to be the remains of vascular canals, with the smaller, scar-like pores representing the termination sites of fine branches of these canals. The bony base of the heterostracan dermal skeleton was compared to the bone-like structures that Andres observed in the basal openings of etched specimens of *P. gallatini* and *Problematoconites*, and because of this feature, Andres proposed that the paraconodonts were more closely related to the chordates than were the euconodonts. Andres also stated that the euconodonts and the fishes were separate lineages that had both evolved from a paraconodont ancestor, however this is disputed since euconodonts are fish and because other early vertebrates such as *Anatolepis* (see M. P. Smith *et al.* 1996 for a discussion) are unlikely to have evolved from paraconodonts.

Dzik (1986) discounted the hypothesis that paraconodonts were homologous to the basal bodies of euconodonts because he believed that the basal body of euconodonts was mineralised secondarily to the crown, and that the basal body could not, therefore, be the most primitive euconodont structure. In fact, since the euconodont crown and basal body are considered to be homologous to enamel and dentine respectively (Sansom *et al.* 1992, 1994; Donoghue 1998), and because dentine is known to mineralise prior to enamel (M. M. Smith and Hall 1990; M. M. Smith 1995) it is likely that the basal body will appear to be the most primitive unit because the development of the crown is dependent on the presence of an underlying tissue that has the potential to become mineralised (see above). However, both the crown and the basal body of euconodonts form as part of the same developmental system and, therefore, neither can be regarded as primitive or derived relative to the other. Dzik (1986) also stated that, although paraconodonts grew internally and externally at the base, there was no separation into a crown and basal body, and that even though paraconodonts (or westergaardodinids according to Dzik's terminology) resemble euconodonts in external morphology, the difference in histogeny precludes the possibility that there is a transition between the two groups.

The histology of proto-, para- and euconodont elements was investigated by Szaniawski (1987) who concluded that the evolutionary transition between the three forms, proposed by Bengtson (1976), was tenable. Paraconodont elements were shown by Szaniawski (1987) to grow by addition of material at the base of the element, with the growth lamellae wrapping around the base and cropping out on both the internal and external surfaces, as had been demonstrated by other authors (see above). The initial lamellae were thought to be enclosed, with the basal opening being produced by the gradual invagination of subsequent growth lamellae. Transmission electron microscopy studies by Szaniawski showed that paraconodont elements are dominantly organic, with various amounts of phosphate, concentrated more in some growth layers relative to others. This differential concentration of organic and phosphatic matter allowed Szaniawski to recognise individual growth lamellae under the TEM. Szaniawski's investigations of non-demineralised and demineralised sections through paraconodont elements demonstrated that the organic portion of the elements was concentrated in the fine, almost equidimensional crystallites in each growth lamellae (Szaniawski 1987, pl. 2.1, fig. 9). In agreement with previous authors, Szaniawski stated that paraconodont elements are homologous to the basal bodies of euconodonts, and suggested that the outer organic layer of paraconodonts may correspond to the crown of euconodonts. However, because Szaniawski (1982, 1983) had demonstrated that protoconodonts are likely to share a close relationship with chaetognaths, and he supported the evolutionary growth hypothesis of Bengtson (1976), Szaniawski concluded that all three groups of conodonts were related to the chaetognaths.

Following Andres (1988), Szaniawski and Bengtson (1993) suggested that paraconodonts, particularly *P. gallatini* and *Problematoconites*, had developed a two-layered structure and had attained a euconodont grade by acquiring the ability to increase the amount of mineralised phosphate in the outermost layer, producing a euconodont crown. Thin growth lamellae, found to be continuous around the basal opening of the element, comprised the inner layer, which was thicker in relation to the outer layer at the base, but which became thinner towards the tip. Similar structures (pores, canals, channels) to those observed by Andres (1988) were noted by Szaniawski and Bengtson (1993) in the innermost of the two layers. The outer layer retained the typical paraconodont growth appearance, with apically open lamellae on the outer surface of the elements. Both the inner and the outer layers were formed as parts of one individual growth phase, i. e. each growth lamellae comprised an inner layer and an outer layer component. Such two-layered elements were thought by Szaniawski and Bengtson to be transitional forms between paraconodonts and euconodonts, and they stated that euconodonts with an absent, or poorly-developed crown could easily be confused with morphologically similar paraconodont elements, since the crown component did not usually form until the element was quite large. However, this does not concur with the current opinion that growth of the crown and basal body of euconodonts is appositional (see Sansom 1996; Smith *et al.* 1996; Donoghue 1998), with each growth increment of the basal body corresponding to a growth increment in the crown. Both the crown and the basal body are therefore deposited as part of one developmental system during a cascade of cell differentiations and tissue interactions (Smith and Hall 1990). If this is accepted then, even in the earliest growth stages of euconodont elements, there is a division into crown and basal body components. Szaniawski and Bengtson (1993) have shown that it is possible for paraconodont elements to be homologues of the euconodont basal body, but their model for the transition from crownless paraconodonts to crowned euconodonts is not sustainable, given the current hypothesis of euconodont element growth and development.

Müller and Hinz-Schallreuter (1998) have provided the most recent documentation of the histology of some Cambrian paraconodonts, and have described a number of hypotheses concerning the growth and development of some of the morphologically more complex forms. As with other authors, Müller and Hinz-Schallreuter (1998) recognised a typical growth style for the paraconodonts they studied, with apically open lamellae and a basal opening produced by invagination of the lamellae in subsequent growth phases, but they confirmed that the presence of closed lamellae in the earliest-formed part of the element could be attributed to features of obliquely-cut thin sections that did not slice through the exact centre of the element. An outer organic layer was not always recognised by Müller and Hinz-Schallreuter, although they predicted that it could be inferred by the presence of a smooth external surface on the paraconodont elements. Differences in the density, frequency and symmetry of the growth increments were thought by Müller and Hinz-Schallreuter to be the main factors controlling the morphology of the different species, and they noted that in the case of *Serratocambria*, additional lamellae were inserted in the main direction of growth of the element.

For *Problematoconites* and *P. gallatini*, Müller and Hinz-Schallreuter (1998) discussed the observations of Andres (1988) finding support for the presence of an outer organic coating, apically open growth lamellae and channels and canals running both longitudinally and perpendicular to the long-axis of the elements. They described an inner 'warty' layer lining the basal cavity, and this is presumed to be analogous to the inner layer described by Andres (1988). Müller and Hinz-Schallreuter were, however, uncertain as to whether all elements of *Problematoconites* were transitional forms between para- and euconodonts, with preservation dictating the presence or absence of the inner layer, or whether on some individuals possessed the inner layers, whilst others did not.

Proacodus obliquus is characterised by the presence of an extended lateral process, which Müller and Hinz-Schallreuter (1998) have demonstrated to be the result of allometric growth, with the growth lamellae becoming thicker and more widely-spaced as they curve towards the upper margin of the process. Elements of *Serratocambria* also possess an extended lateral process but, unlike *Proacodus*, the process bears denticles. Müller and Hinz-Schallreuter have shown that extra lamellae are inserted in the main growth direction, in addition to the thickening and wider spacing of the initial growth lamellae. Growth lamellae appear to be traceable across from one denticle to the previous one, and Müller and Hinz-Schallreuter gave two reasons why this could occur. The first was that resorption of mineralised tissue could have occurred to form discrete denticles from an originally smooth surface, and the second was that there could have been a zone of non-secretory cells between each of the denticles. However, the specimen illustrated by Müller and Hinz-Schallreuter (1998, text-fig. 10, fig. 2) is a naturally fractured specimen viewed in transmitted light, and appears to show the element in three-dimensions, as opposed to as a planar slice through the element, so that the growth lines do not represent the internal structure of the element, but show instead how the apically open growth lines curve around the surface of the element. This gives the appearance that entirely distinct growth lamellae are continued in other denticles, whereas in reality they only extend to the element surface.

Müller and Hinz-Schallreuter also studied the histology and development of *Westergaardodina*, and described an unusual mode of growth for the elements. In comparison to coniform elements, tricuspid and bicuspid elements of *Westergaardodina* are more difficult to visualise three dimensionally in terms of their growth. As with coniform elements, westergaardodinid elements grow by the addition of lamellae from the tip towards the base, but Müller and Hinz-Schallreuter (1998) have suggested that their more complex morphology is a direct result of their growth. The hypothesis suggested by Müller and Hinz-Schallreuter is that, in tricuspid elements of *Westergaardodina*, the initial growth lamellae were formed as a wavy structure which, in response to pressure from distal and lateral directions, formed a W-shaped surface before being torn apart by continued pressure. According to Müller and Hinz-Schallreuter, the cause of the pressure was a restricted amount of space in which the element could be secreted. Subsequent lamellae were secreted and torn apart by the continued pressure, although some of the later-formed lamellae were not physically broken. The two turning points in tricuspid elements were presumed to be the result of two pressure points, whereas a single pressure source produced bicuspid elements. As supporting evidence for this model, Müller and Hinz-Schallreuter noted that, the growth lamellae were more densely spaced at the turning points, and that the pressure was accommodated by the formation of bulges perpendicular to the major stress direction. The lack of 'wavy' juvenile specimens in the collections of Müller and Hinz-Schallreuter was attributed to a preservational bias, where the early ontogenetic stages of the element were only weakly mineralised and were, therefore, either not preserved or were dissolved during the extraction process. No specimens of *Westergaardodina* suitable for a detailed histological analysis have been recovered during the course of the present study, but the growth and development of westergaardodinid elements should certainly be the focus of a future investigation, perhaps to find evidence that supports the tearing apart of growth lamellae during ontogeny. A TEM study to look into the distribution of organic material in successive growth increments, as performed by Szaniawski (1987) may be able to provide this information.

7.5 Other problematic phosphatic microfossils from the Late Cambrian and Early Ordovician

Additional phosphatic material from the Late Cambrian and Early Ordovician has also been briefly investigated. *Phosphannulus* Müller, Nogami and Lenz, 1974 often occurs alongside proto- para- and euconodont elements in acid-etched residues, and was compared to conodonts by Müller *et al.* (1974) because both conodonts and *Phosphannulus* grow by outer apposition. A close relationship between the forms was, however, dismissed by Müller *et al.* because conodont elements possess basal bodies and white matter and are therefore more highly differentiated than *Phosphannulus*. This idea is supported based on the histological evidence found during this study (Plate 18, Figs C-F). A second phosphatic sclerite that has been studied in minor detail is *Palaeobotryllus* (Plate 17, Figs A-G), a form that was originally described as a fossil ascidian tunicate by Müller (1977) due to the similar morphology of the hard-parts of *Palaeobotryllus* and the soft-parts of the Recent *Botryllus*. Members of the Recent Tunicata (Urochordata) do not mineralise well-structured phosphatic hard-parts, although some do secrete spicules composed of amorphous calcium phosphate in the form of dahllite (Lambert *et al.* 1990) and so it is unlikely that *Palaeobotryllus* is a tunicate, unless the ability to secrete a well-developed phosphatic skeleton has been lost by the Recent members of the group.

CHAPTER 8

HISTOLOGY OF PROTOCONODONTS

8.1 Material

In comparison to that of euconodonts and paraconodonts, protoconodont material from the Late Cambrian of the USA was unsuitable for histological investigation because of its very small size, and pale to translucent coloration. However, material from the Swedish Alum Shale was much larger and was often stained brown or black by organic matter, and was much more amenable to the thin sectioning techniques employed. Following on from the studies of Bengtson (1976, 1983), Szaniawski (1982, 1983, 1987), Andres (1981, 1988) and Müller and Hinz-Schallreuter (1998), little more can be added to the current state of knowledge from the results of the present study. Elements of *Phakelodus tenuis*, *Phakelodus elongatus* and *Gapparodus cuneatus* were thin sectioned, but the most convincing examples of protoconodont histological features were observed on the slightly etched surface of an element of *G. cuneatus* in which the outer layer had been partially destroyed either taphonomically, or during processing.

8.2 Results

In agreement with all the previous studies, the protoconodont elements investigated are constructed from three layers, a thin external coating, a thicker, fibrous middle layer, and a thin, resistant inner layer (Plate 16, Fig, A, B, C, G). This has been demonstrated by the inspection of thin sectioned and whole fractured elements in which the constituent layers have been revealed. Elements of *G. cuneatus* (Plate 16, Figs A, B, C) that have been damaged at the tip show the removal of the outer and middle layers in this region, with the inner layer that lines the basal opening remaining as a prominent spine. Elements with two tips to the basal cavity were observed by Müller and Hinz (1991, pl. 4, figs 1-7, 10, 15), with a main cavity developed in a similar manner to the specimens in Plate 16, with the addition of a smaller canal in the posterior part of the element. The fibrous nature of the middle layer, noted by Müller and Hinz (1991) has also been observed in the current study (Plate 16, Figs D, F). Removal of the thin external covering has exposed fine fibres running oblique to the length of the main part of the element, sloping towards the posterior margin but, posterior to the lateral groove the fibres are parallel or slightly oblique to the length of the element, sloping anteriorly. The fibres are parallel to one another, and are less than 1 μm in diameter, but are commonly elongate and possible more than

50 μm long, although the true length of the fibres is obscured by the material of the outer layer (Plate 16, Fig. D).

The transverse cross-section of an element of *Phakelodus elongatus*, illustrated in Plate 16, Figure E, demonstrates the poor resolution of the histological features that are observed under the SEM. In transmitted light, the element of *Phakelodus tenuis* (Plate 16, Fig. G) shows the presence of a thin inner layer (prominent spine) and a thicker middle layer, although the outer layer is not apparent.

8.3 Discussion

Fibrous structures, as observed in *G. cuneatus* (Plate 16, Figs D, F) have also been described in the protoconodont *P. tenuis* and the Recent chaetognath *Sagitta maxima* by Szaniawski (1982). Bone *et al.* (1983) illustrated a grasping spine of Sagitta that also possessed a fibrous tip. Measurements taken from the illustrations of Szaniawski (1982, text-figs 1F, 2E) show that the growth increments observed in *P tenuis* are substantially larger (width 8 μm) than those seen in *Sagitta* (width 2.5 μm), however, the grasping spines of the Recent genus are considerably smaller than the ancient examples that were illustrated. Fibrous structures in *G. cuneatus* and in *Sagitta* are of similar dimensions, both being in the range of 0.75-1 μm in width, but of unknown length.

The similarities between the histology and apparatus composition and architecture of ancient protoconodonts and Recent chaetognaths, as elucidated by Szaniawski (1982, 1983), is evidence that supports a close relationship between these stratigraphically separated groups. *Titerina* from the Ordovician, described by Kraft and Mergl (1989) and Kraft *et al.* (1999) shortens this stratigraphical disparity and strengthens the hypothesis that protoconodont elements and chaetognath grasping spines are homologous structures. The limited results from the current study are in agreement with those of other authors and, therefore, support the previous conclusions.

An interesting point has, however, been raised by Müller and Hinz-Schallreuter (1998) in their study of Late Cambrian proto-, para- and euconodonts, showing that there are two distinct styles of protoconodont growth. Some elements (e.g. *Phakelodus*) grew by addition of lamellae only in the basal region of the inner surface of the element, whilst others (e.g. *Gumella* = *Gapparodus* in the current study) added lamellae in the tip which were then continuous for the length of the element. This difference in growth style needs further detailed investigation, since it may be of taxonomic importance. Unfortunately, evidence of this was not forthcoming during the course of the current investigation.

CHAPTER 9

HISTOLOGY OF PARACONODONTS

9.1 *Material*

Miller (1976) proposed that the paraconodont *Prooneotodus rotundatus* was likely to be related to forms from the euconodont *Proconodontus* lineage, and suggested that an intermediate genus, possessing only a thinly-developed crown, would link the two (Miller 1980). Morphological similarities between elements of the paraconodont *Prooneotodus* and the euconodont *Proconodontus*, together with the proposed agreement between the apparatus compositions of the two genera, support Miller's hypothesis, but until now histological investigations have failed to demonstrate a close affinity.

Much of the paraconodont material used in this study has been unsuitable for histological investigation, often being very small, delicate and easily damaged or destroyed during the thin sectioning process. Additionally, polished thin sections of paraconodont specimens have not consistently shown any structural or histological features when viewed in transmitted light, or when etched and observed with an SEM. Elements of *Prooneotodus* from Texas, kindly donated by J F. Miller are, however, more robust than much of the material from Wyoming and Sweden, and have provided some very interesting and important results.

9.2 *Terminology*

Since this study has found that elements of *Prooneotodus* are formed from a two-component system of hard tissues, it is necessary to introduce new terminology with which to describe these. Previously the two components have been described as 'outer' and 'inner' layers, but the material in the basal cavity of the element is not found as a layer, and should not be referred to as such. The terms 'crown' and 'basal body' are used in connection with euconodont element histology, and their use should be avoided in relation to paraconodonts, since confusion will arise from the possible application of the same term to non-homologous structures. For this reason the terms 'outer lamellar layer' and 'inner core' are applied to the two distinct hard tissue components of paraconodont elements.

9.3 Outer lamellar layer

As is characteristic of paraconodont elements, the outer lamellar layer of *Prooneotodus* is composed of a relatively small number of growth increments in comparison to euconodonts of a similar size (16 growth lamellae are visible on the posterior margin of the element illustrated in Plate 15, Fig. C). The growth increments are open apically on the outer surface of the element (Plate 14, Figs A, B), bending around basally so that the lamellae run back towards the tip on the inner part of the outer lamellar layer (Plate 14, Fig. F; Plate 15, Figs A, C). A result of the small number of growth increments is that they are thicker than those observed in euconodont crowns or basal bodies, being 8 μm in width on the outer, apically open, limb of the lamellae, extending to up to a width of 48 μm at the point where the lamellae curves back towards the tip on the inner side of the outer lamellar layer. On the inner limb, the lamellae are less well-defined, but appear to return to their original thickness of approximately 8 μm. Close to the posterior corner of the base, features caused by a combination of the oblique nature of the thin section through the element, and the presence of 'ghost structures', are visible, with growth lamellae appearing to split, curve around on themselves and open towards the inside of the element (Plate 14, Figs C, D; Plate 15, Fig. C; Text-figure 9.1). Ghost structures occur because the scanning electron microscope focuses slightly below the surface on each specimen. A zone of lighter coloration is observable around the margin of the element (Plate 14, Fig. A; Plate 15, Figs A, C; Text-figure 9.1), and it is in this region that the SEM is producing an image of the part of the element that is not exposed at the surface, but is present beneath a thin layer of the embedding resin. The image taken from the SEM is therefore slightly three-dimensional and this, together with the obliqueness of the section, causes these anomalous features.

The nature of the fine crystallites forming the outer lamellar layer has not been resolved, primarily because of the high organic content of the paraconodont elements, which reduces the effect of the etching agent. From the extinction pattern of the outer lamellar layer (Plate 11, Figs B, D), it appears that the long axes of the potential crystallites are aligned parallel to the growth increments, but this feature has not been observed under the SEM.

9.4 Inner core

Between the crown and the basal body of euconodonts lies a very sharp, distinct junction caused by the appositional growth of tissues away from this contact. The junction between the outer lamellar layer and the inner core of *Prooneotodus* is not as distinct when viewed under the SEM, but this can be easily explained. The crown of euconodont elements has a much lower organic content than the basal body, and therefore etches is a different manner, highlighting the structural differences between the two tissues, but in paraconodonts the difference in the organic content between the two tissues appears to be negligible and so both tend not to etch very successfully. For this reason the junction between the outer lamellar layer and the inner core is not emphasised as a result of the etching process. When observed in transmitted light, however, the junction between the outer lamellar layer and the inner core is more distinct (Plate 8, Fig. A; Plate 11, Figs B, D; Plate 14, Fig. A; Plate 15, Fig. B; Text-fig. 9.1).

The tissue forming the inner core of *Prooneotodus* is globular in appearance (Plate 8, Fig. B; Plate 10, Fig. F; Plate 14, Figs C, E, F; Plate 15, Fig. C), although the individual spherules are not as clearly visible as in the basal bodies of euconodonts (e.g. *Eoconodontus*, Plate 8, Fig. C, or *Cordylodus*, Plate 8, Fig. H). Dark spots, such as those seen in Plate 14, Fig. C, represent the cores of mineralised units that have been replaced by a secondary mineral, such as the replacement by iron oxide which is apparent in some specimens of *Cordylodus* from the same material (Plate 11, Fig. E). Growth increments in the basal tissue, although generally poorly defined, are apparent and are typically in the range of 0.5-1 μm in width, which is comparable to the growth increments observed in the basal bodies of euconodonts used during the course of this study (except *C. angulatus*, see above).

A particularly interesting feature is, however, the extinction pattern observed in the inner core tissue of *Prooneotodus* (Plate 11, Figs B, D). Across the entire area of the inner core a banded effect is seen, with alternate dark and light stripes running parallel to the long axis of the element. All the bands have slightly wavy margins so that they bulge and thin along their entire length. The optical continuity of the extinction pattern throughout the entire base suggests that only one tissue type is present in this zone. When the extinction pattern of the inner core of *Prooneotodus* (Plate 11, Fig. D) is compared to that in the basal bodies of the euconodonts *Cambrooistodus* (Plate 11, Fig. A), *Pseudooneotodus* (Plate 11, Fig. C) and *Cordylodus intermedius* (Plate 11, Fig. E), no discernible differences are observed. All of the extinction bands are of similar size, they all run parallel to the lengths of the elements, and in each of the specimens, the margins of the stripes are slightly wavy, producing a bulging and thinning effect. From this it can be deduced that these extinction patterns are probably caused by the same phenomenon.

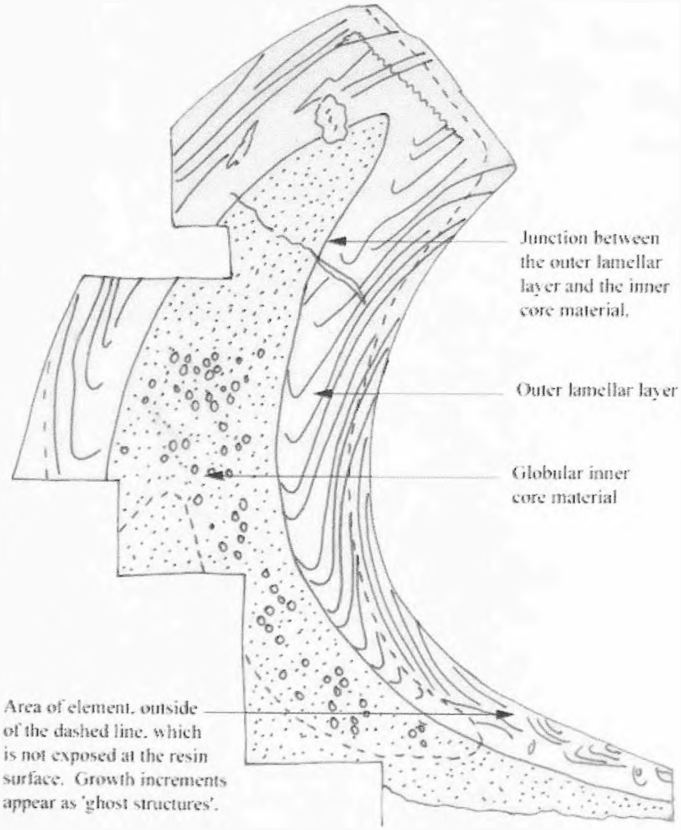
9.5 *Interpretation and discussion*

Results from the current investigation show that, histologically, the tissue forming the inner core of the paraconodont *Prooneotodus* has more in common with the basal body tissue in primitive euconodonts than has been demonstrated previously. Both tissues are globular, or at least partially globular, and both share a very distinctive extinction pattern when viewed in cross-polarised transmitted light. Sansom (1996) attributed the characteristic extinction pattern of the basal tissue of *Pseudooneotodus* to the presence of either closed tubules or attachment fibres. Since no tubules were observed in the specimens studied by Sansom, the basal tissue of euconodonts with this extinction pattern, in association with spherulitic structures composed of fine growth lamellae, has therefore been interpreted as atubular dentine (Sansom 1996). The presence of spherulitic structures in the inner core tissue of *Prooneotodus* has not been convincingly demonstrated because they have not been observed in polished, etched specimens when viewed under the SEM. However, spherules can be inferred by the 'frog-spawn'-like appearance of the basal tissue in transmitted light in addition to the faint appearance of some growth increments.

From these observations, the conclusions that can be drawn are that both the tissue in the inner core of *Prooneotodus*, and the tissue forming the basal body of some primitive euconodonts are globular and have attachment fibres running through them. Although morphological similarity does not demonstrate unequivocal homology, it is more parsimonious to suggest that two structures that share a number of characteristics are related, than to suggest that they are unrelated. It is, therefore, probable that *Prooneotodus* and primitive euconodonts share a close relationship.

This conclusion has been arrived at previously by a number of authors (Lindström 1964; Müller and Nogami 1971; Bengtson 1976; Szaniawski 1987; Szaniawski and Bengtson 1993; Müller and Hinz-Schallreuter 1998), but there is a major discrepancy between the results of this study and the hypotheses of the previous authors. In Bengtson's (1976) hypothesis explaining the phylogenetic development from paraconodonts to euconodonts, paraconodont elements were homologised with the basal bodies of euconodonts because of the apically open growth lamellae that are observed in the outer lamellar layer of paraconodonts and also in the basal body of euconodonts. The results of the current investigation show, however, that it is not the outer lamellar layer, but the material found in the inner core of the paraconodont elements, that shares more common features with the basal bodies of euconodonts. If, perhaps, the characteristic extinction pattern was continuous throughout the inner core and the outer lamellar layer, then the initial hypothesis of Bengtson (1976) could be supported, but this is not the case. Apparently the inner core tissue of paraconodonts (if it is truly homologous to the basal tissue of euconodonts) was overlain not by enamel as it is in euconodonts, but by another, more organic-rich, phosphatic hard tissue, that was subsequently replaced by enamel in the more derived forms.

If euconodonts are considered to be vertebrates, then the outer lamellar layer of the closely related paraconodonts should be potentially composed of one of the known suite of vertebrate hard tissues. However, no vertebrate hard tissue that possesses comparable growth relationships with the underlying tissues has been observed in any group of extinct or extant vertebrates. It is, therefore, probable that the outer lamellar layer of paraconodont elements is composed of a unique hard tissue, that was confined to the paraconodonts, and that was replaced by the enamel crown in the euconodonts.



Text-figure 9.1. Line drawing (original traced from Plate 15, Figure C) showing the relationships between the outer lamellar layer and the inner core material. Ghost structures have also been labelled. X150.

CHAPTER 10

HISTOLOGY OF LATE CAMBRIAN EUCONODONTS

10.1 Material

Elements of six Late Cambrian euconodont genera are included in this study of the histology of early euconodonts. These were selected because they include some of the most primitive euconodont genera from each of the two euconodont lineages that were proposed by Miller (1980). *Proconodontus*, *Eoconodontus*, *Cambrooistodus* and *Cordylodus* are the four members of one of these lineages, that were placed in a separate category of euconodonts (cavidonts) by Sweet (1988), whilst *Teridontus* and *Clavohamulus* are thought to be part of the stem group of the so-called 'true' euconodonts. An implication of this separation is that the euconodonts may be a polyphyletic group, a problem which a study of the histology of the most primitive elements may be able to resolve.

10.2 Features of the crown

10.2.1 Lamellar tissue

Features of the lamellar part of the crown are similar in each of the Late Cambrian euconodont genera investigated. Crystallites forming the crown are always less than 1 μm in diameter, and commonly less than 10 μm in length. They are arranged with their long-axes sub-perpendicular to the junction between the crown and the base, and are sometimes grouped into bundles, with the needle-like crystallites fanning-out towards the outer surface of the element. A fanning-out arrangement of the crystallites can be observed in SEM section (Plate 9, Figs D, F), and can also be inferred by the swallow-tail extinction patterns seen in the crown when viewed in transmitted light (Plate 8, figs C, D, E, G; Plate 11, Figs A, E). A swallow-tail extinction pattern is most obvious in specimens of *Eoconodontus*, *Cambrooistodus* and *Cordylodus*, but is not so readily observed in elements of *Proconodontus*, *Teridontus* or *Clavohamulus*.

The crystallites forming the crown are continuous across the growth increments which run parallel to one another, approximately perpendicular to the long-axes of the crystallites. The growth lamellae are spaced at intervals of less than 1 μm, and meet the junction between the crown and the base at an oblique angle (Plate 8, Fig. G; Plate 9, Fig. D; Plate 12, Fig. B; Plate

13, Figs B, E). In *Proconodontus*, *Eoconodontus* and *Cambrooistodus* this angle is very small, less than 5° (Plate 9, Fig. D), but in *Cordylodus*, *Teridontus* and *Clavohamulus* (Plate 8, Fig. G; Plate 12, Fig. B; Plate 13, Figs B, E) the angle between the growth increments of the lamellar crown and the underlying junction with the basal body is usually steeper (<15°). However, the growth increments in the latter three genera are slightly asymptotic towards the crown-base junction, becoming steeper as they move away from this region (Plate 13, Fig. E). No insertion of additional lamellae have been observed in parts of the elements with greater amounts of crown material (e. g. keeled margins), and it is therefore probable that the extension of the crown in these areas was achieved by slight thickening of the individual growth increments.

10.2.2 'White Matter'

Donoghue (1998) and Donoghue and Chauffe (1998) have demonstrated that not all tissues that have previously been described as white matter can be referred to as true white matter, since some lack the spaces that cause the material to appear opaque in transmitted light. Some of the taxa used in this study fall into this category. *Proconodontus* lacks white matter in the cusp, and is therefore distinguished from *Eoconodontus* which possesses well-developed white matter in the very tip of the cusp and, in stratigraphically younger specimens, also more weakly-developed white matter in the anterior margin. In the tip of the cusp of *Eoconodontus*, the tissue is very finely crystalline, possesses approximately spherical spaces of up to 2 μm in diameter, together with smaller, elongate spaces of 2 μm in length and less than 0.5 μm in diameter, and is clearly more resistant to etching agents than the remainder of the lamellar crown material (Plate 9, Figs D, E, F, G). There is some evidence of a preferred orientation of the elongated spaces in the white matter, with the long axes of the spaces aligned parallel to the long axis of the element, but no branching canaliculi have been observed radiating from the spherical spaces. A clearly defined planar junction appears to separate the area of well-developed white matter from the lamellar tissue (Plate 9, Figs D, F), although on closer inspection this junction is less distinct, with a marginal zone of more coarsely crystalline material that lacks spaces. No growth increments are present in the white matter, and this material is directly comparable to the true white matter as described by Donoghue (1998, p. 641).

In contrast, no true white matter was observed in polished thin sections of *Cordylodus proavus* viewed under the SEM although, in transmitted light, parts of the cusp, anterior margin and denticles appeared opaque (Plate 8, Fig. E; Plate 12, Fig. A). Elements of *C. lindstromi* possess what appears to be true white matter in the cusp and denticles (Plate 12, Figs d, F), but this is weakly-developed in places, where crystalline lamellar crown tissue with incremental lines is present. Donoghue (1998, fig. 4e, f, g) illustrated an element of *Cordylodus angulatus* in which no white matter is developed anywhere in the crown. Similarly, in *Teridontus*, the entire tip of the cusp appears opaque in transmitted light (Plate 13, Fig. C), but when viewed under the SEM (Plate 13, Figs D, F) only a small core of material resembling white matter is observed. The crown of *Clavohamulus*, on the other hand, is dominated by white matter, which appears opaque in transmitted light (Plate 13, Fig. A), due to the presence of spherical and elongate spaces that are characteristic of true white matter, as can be clearly seen when the specimen is observed under the SEM (Plate 13, Fig. B).

10.3 Basal body

Between the crown and the basal body, in all the elements studied, lies a sharp junction characterised by a zone, less than 1 μm wide, in which no material is apparent in polished, etched specimens viewed under the SEM. The basal tissue adjacent to this junction is often amorphous, with no discernible growth increments or crystallites, and this extends for approximately 5 μm into the basal tissue. In *Proconodontus*, *Eoconodontus*, *Cambrooistodus* and *Cordylodus* the basal tissue then becomes lamellar rather than amorphous and towards the centre of the element changes its appearance gradually, becoming more irregular and wavy at first before incorporating spherulitic structures further from the crown-base junction. The basal bodies of *Clavohamulus* and *Teridontus* that were thin-sectioned did not etch well (Plate 13, Figs B, D), but a sharp junction between the material of the crown and that of the base is clearly visible, and lamellar structures can just be made out in the basal tissue. In transmitted light (Plate 13, Fig. C), the presence of iron oxide staining in the material has obscured the details of the base.

Close to the outer margin of the basal body in elements of *Proconodontus*, *Eoconodontus* and *Cambrooistodus*, growth increments in the basal tissue are sub-parallel to the junction with the crown, but curve away from this orientation becoming more steeply inclined away from the junction towards the centre of the element (Plate 8, Figs C, D; Plate 9, Figs A, D, F; Plate 10, Figs A, B, C). Rare spherules are clearly visible (Plate 9, Figs B, C), but it is likely that more would be observed had the etching process been more successful (see Plate 8, Fig. C). The spherules attain a maximum size of 10 μm in diameter, with growth increments in the spherules, and in the basal material as a whole, being approximately 0.5 μm in width. Often, the spherulitic structures are incorporated into the wavy, lamellar tissue of the base, with ontogenetically later growth increments wrapping around the earlier formed spherules.

Material in the base of *Cordylodus proavus* is arranged in a similar manner to that in *Proconodontus*, *Eoconodontus* and *Cambrooistodus*, with lamellar material close to the junction between the crown and the basal body, following a narrow zone of amorphous tissue (Plate 12, Fig. C). Towards the centre of the element the growth increments curve away from the crown-base junction so that the lamellae in central parts of the element are sub-perpendicular to that junction. Again, the lamellae are at first laminar, becoming wavy with incorporated spherules appearing and increasing in size towards the centre of the element (Plate 10, Figs D, E; Plate 12, Figs C, E). Individual growth increments in the spherules and the lamellar tissue are slightly larger than those in *Proconodontus*, *Eoconodontus* and *Cambrooistodus*, being up to 1.5 µm in width. The size of the spherules is also slightly increased, with the larger spherules in the centre of the basal body being as much as 25 µm in diameter (Plate 10, Fig. E).

The histology of the basal tissue in *Cordylodus angulatus* has been previously described by Sansom *et al.* (1992), but since this species is pertinent to the current study, a brief reiteration of the structures in the base is necessary. As with the elements already discussed, the basal tissue in *C. angulatus* is lamellar close to the crown-base junction, becoming increasingly spherulitic towards the centre of the element (Plate 8, Fig. G). However, in contrast to the aforementioned elements, in the centre of the specimen individual discrete spherules that are not incorporated into the surrounding material by subsequent growth lamellae (Plate 8, Figs G, H; Plate 10, Fig. G). Additionally, the growth increments forming the lamellar and the spherulitic material are thicker than have been observed in *Proconodontus*, *Eoconodontus*, *Cambrooistodus* and even *Cordylodus proavus*, a more primitive member of the genus, being up to 5 µm in width. This is an order of magnitude larger than the equivalent structures in the other investigated specimens, however, the spherules are not significantly more sizeable, with the largest spherule in the centre of the element having a diameter of 30 µm.

When the basal tissue of *C. angulatus* is observed in cross-polarised transmitted light, each of the individual spherules is characterised by an extinction cross, suggesting that in the spherules, the crystallites are arranged in a radial pattern, however, a similar situation is not observed in any of the other elements studied. Instead of spherules with extinction crosses, the entire basal tissue shows a characteristic extinction pattern, whereby thin bands of material go into extinction in alternation, producing a striped effect (Plate 11, Figs A, E). Each of these bands is approximately 2 µm in width and runs parallel to the long axis of the element. The extinction pattern is characteristic of the entire body of tissue in the base, implying that even though there are differently structured zones of material, each of these is composed of the same tissue type. A similar extinction pattern has been observed in the basal region of other euconodonts, namely *Pseudooneotodus* (Plate 11, Fig. C) and also *Oulodus* (M. M. Smith *et al.* 1996), with important consequences for the interpretation of this material. In addition, exactly the same extinction pattern has been recognised in the basal region of the paraconodont *Prooneotodus* (Plate 11, Figs B, D), which has implications for evidence supporting a paraconodont-euconodont relationship.

10.4 Discussion and interpretation of the hard tissue histology

10.4.1 Lamellar crown tissue

As with many of the more derived euconodonts, the lamellar crown tissue of Late Cambrian euconodonts is crystalline, with the elongate crystallites arranged perpendicular to the growth increments, which in turn diverge from the distinct crown-basal body junction at a shallow angle. Crystallites are sometimes arranged into radiating bundles, which produce a swallow-tail extinction effect when the crown is viewed in transmitted light. In terms of morphology, the crystallite size and arrangement does not differ from other euconodonts, and the interpretation of this material as enamel as suggested by other authors (*inter alia* Dzik 1986; Sansom *et al.* 1992, 1994; Donoghue 1998) is supported. However, morphology alone does not support homology, and it is only when the relationship of the lamellar crown with the underlying basal body is considered can this interpretation be validated.

10.4.2 White matter

The recent study by Donoghue (1998) has shown that not all white matter can be classified as white matter *sensu stricto*. Donoghue outlined a definition of 'true' white matter, which included several key characters that differentiate it from the lamellar crown tissue, stating that white matter is more finely crystalline, markedly more resistant to etching agents, has a lower organic content and lacks punctuating growth increments in comparison to the remainder of the crown material. In addition, the white matter contains cavities of variable size, shape and orientation, which are thought to be sites that were originally occupied by mineral-secreting cells (Donoghue 1998, p. 641).

An interesting paradox occurs in the case of the specimens used in the current study. Whilst some elements, for example *Eoconodontus* (Plate 9, Figs D, E, G), appear to possess well-developed, true white matter in their cusps, others do not (*C. proavus*, Plate 12, Fig. A), and some possess areas of white matter that are interspersed with areas of lamellar crown material (*C. lindstromi*, Plate 12, Fig. D). There are various possible causes of these observations,

1. True white matter is developed in some elements, but not in others and, even in the different species belonging to a single genus (e.g. *Cordylodus*), white matter can be present or absent and this feature is not of taxonomic use.

2. True white matter is present in all of the elements studied, but has been partially or completely destroyed by the etching process in some specimens, but retained in others.

3. True white matter is not present in any of the specimens studied and the tissue that resembles white matter in the elements is a product of incomplete etching, or some other process that was used to free the specimens from the rock samples.

4. True white matter arose independently in different taxa. Its presence or absence is of taxonomic importance.

Not enough is known about the factors that caused euconodonts to develop white matter, although Donoghue (1998) has demonstrated that the same population of cells secreted both white matter and lamellar crown tissue at the same time and at the same rate, and that white matter and the lamellar crown tissue share a developmental origin. It has been suggested that white matter was developed by euconodonts in order to strengthen the cusp (Barnes, Sass and Monroe 1973), and may therefore have had a selective advantage, and indeed the presence of white matter in an otherwise brittle enamel crown would certainly have improved the durability of the elements (Donoghue 1998). It is interesting to note that the most primitive elements of *Eoconodontus notchpeakensis* have only a very thin band of white matter present just above the tip of the basal cavity, a zone that was particularly at risk from breakage if regeneration patterns in elements of both *Eoconodontus* and *Proconodontus* are considered (Miller 1969, plate 66). Through time the development of white matter in the cusp becomes more substantial, eventually filling the entire tip of the cusp in the stratigraphically younger specimens, and this would support the hypothesis that the possession of white matter was advantageous. As a response to the fourth of the arguments outlined above, it would seem that white matter is of taxonomic use, since its presence distinguishes elements of *Eoconodontus* from those of *Proconodontus*.

In terms of arguments two and three, it must be noted that, although the specimens used in the current study are derived from different samples, they have undergone the same extraction process, the same thin-sectioning process and have been etched with the same etching agent (0.5% orthophosphoric acid) for the same length of time (7½ minutes). However, it is possible that areas of weakly-developed white matter would have been less resistant to the etching agent, and may have been removed in a shorter time period than the more resistant areas. This may be the cause of features observed in *C. lindstromi* (Plate 12, Figs D, F).

The presence of elements with areas of weakly-developed white matter interspersed with zones of lamellar crown material suggests that a second category of white matter is necessary. If true white matter is developed as a defined body, then poorly defined zones of white matter could be defined by a second term, for example the 'pseudo white matter' of Donoghue (1998). In this case, *Eoconodontus* from this study, together with *Cambrooistodus*, *Cordylodus* and *Teridontus* all possess 'pseudo white matter' which, when weakly-developed, can be destroyed during the etching process. *Proconodontus* lacks white matter, but *Clavohamulus* appears to possess well-developed, true white matter possessing all the characters needed to classify it as such. So, in response to the first of the consequences outlined above, it can be stated that three conditions exist in euconodonts, elements with a lamellar crown and no white matter, elements with a lamellar crown and true white matter, and elements with a lamellar crown and pseudo-white matter. The presence or absence of white matter, and the type of white matter present are therefore of taxonomic importance.

Pseudo-white matter can be defined as a poorly defined zone of finely crystalline material, that is in places more resistant to etching agents than the lamellar crown, and that may possess spherical and elongate voids. Areas of lamellar crown material may be closely associated with the pseudo white matter. In transmitted light, pseudo white matter appears opaque, but it may not be a distinct feature in polished, etched specimens when viewed under the SEM.

10.4.3 Basal body

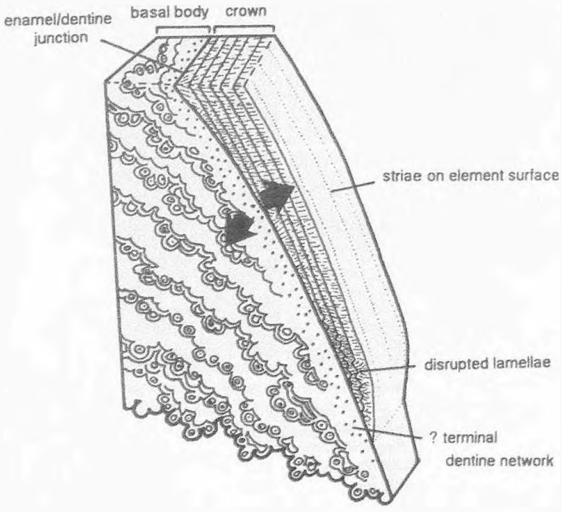
Elements of *Proconodontus*, *Eoconodontus*, *Cambrooistodus* and some elements of *Cordylodus* (*C. proavus*, *C. lindstromi*, *C. intermedius*) possess basal bodies with similar morphological and optical properties. Lamellar, wavy lamellar and spherulitic tissues are present in the base, but the single extinction pattern apparent in the basal body in cross-polarised transmitted light demonstrates that the three features are different structural arrangements of the same tissue. Growth increments in this tissue are very small in *Proconodontus*, *Eoconodontus* and

Cambrooistodus, being only 0.5 µm in width, but are slightly wider, up to 1.5 µm, in *C. proavus*.

Cordylodus angulatus, however, has a differently structured basal body, being lamellar at the margins, but becoming rapidly spherulitic, with discrete spherules occurring in the centre of the element. Each spherule has its own extinction cross, and these can be observed throughout the basal body. Growth increments in the basal tissue are significantly larger, up to 5 µm in width, although the size of the spherules is not markedly different to those in the more primitive species of the genus.

Sansom *et al.* (1992) interpreted the material that constitutes the basal body of *C. angulatus* as globular calcified cartilage, comparing it to the same tissue found in *Eriptychius*, a known vertebrate from the Harding Sandstone of Colorado. However, it appears that the tissue found in the basal bodies of the other elements investigated does not share the same characters, and in fact, has more features in common with the tissue found in the basal body of *Pseudooneotodus*, which has been interpreted as atubular dentine by Sansom (1996).

The extinction pattern observed in the basal region of *Pseudooneotodus* (Plate 11, Fig. C) is directly comparable to that observed in the basal bodies of *Proconodontus*, *Eoconodontus*, *Cambrooistodus* and some of the more primitive species of *Cordylodus*. The striped nature of the extinction pattern was attributed by Sansom (1996) to the presence of a pervasive structure running through the basal body, and suggested that this may be either attachment fibres or closed tubules. Sansom (1996) demonstrated that some of the material constituting the basal body was globular, with growth increments being in the region of 0.5 µm in width, a value which is consistent with those observed in the globular basal bodies of the above genera and species, but which is an order of magnitude smaller than the growth increments observed in *C. angulatus*. Growth lamellae in the base of *Pseudooneotodus* curve away from the crown-base junction, and the growth increments of the crown also meet that junction at an angle. Appositional growth away from a common junction is characteristic of the growth and development of enamel and dentine away from the EDJ (enamel dentine junction) (Text-figure 10.1). Tubular structures have not been observed in the basal bodies of any of the elements investigated, and based on strong morphological similarities with the basal tissue of *Pseudooneotodus*, it is concluded that the material in the basal bodies of *Proconodontus*, *Eoconodontus*, *Cambrooistodus*, *Cordylodus proavus*, *C. lindstromi*, *C. intermedius* and possibly *Teridontus* and *Clavohamulus* is homologous to that of *Pseudooneotodus* and can be referred to as atubular dentine.



Text-figure 10.1. Diagram to show appositional growth of the lamellar crown tissue (enamel) and the basal body tissue (atubular dentine) in *Pseudooneotodus* and other, more primitive euconodonts such as *Proconodontus*, *Eoconodontus* and *Cambrooistodus*. (from Sansom 1996).

This conclusion poses a considerable systematic problem. Based on considerable evidence, the most primitive euconodont genera appear to possess an enamel crown overlying a basal body of atubular dentine, but more derived species of the same proposed lineage (Miller 1980) and even the same genus (*Cordylodus*) possess a basal body of globular calcified cartilage below an enamel crown. One of a number of hypotheses could possibly solve this paradox,

1. The interpretation of one the mineralised tissue types found in the basal bodies of the investigated species as different from the other is incorrect. The tissue in the basal body of *C. angulatus* is a variant of that in the other elements, or *vice versa*.

2. Following on from this, the difference in the size of the growth increments is due to the amount of space available for growth. Larger increments will occur in larger elements, and both tissue types are the same.

3. The interpretation of the mineralised tissues is correct, and is of taxonomic relevance. *C. angulatus* is not as closely related to the more primitive forms of the genus as previously thought.

4. Conversely, the interpretation of the mineralised tissue types in correct, and is not of taxonomic relevance. *Cordylodus angulatus* developed the ability to mineralised cartilage rather than dentine in the basal body, possibly by a heterochronic shift in the timing of the differentiation of the cells in the odontode.

It is possible to suggest arguments for and against each of these hypotheses. Firstly, on the available evidence, the tissue types are not the same. The size of the growth increments is a magnitude larger in *C. angulatus* than in the other examples of the genus and members of the same lineage, and in cross-polarised transmitted light the two basal body tissues demonstrate different extinction patterns. The two tissue types are therefore unlikely to be the same, since they show clear morphological and optical differences. In terms of the amount of space available for growth, the elements used are of comparable size (Plate 8, Figs E, G), and the spherules are not significantly larger in *C. angulatus* than they are in *C. proavus*, so the hypothesis that size matters cannot be supported.

Although the systematic classification of the numerous species of *Cordylodus* remains unstable (for reviews see Bagnoli, Barnes and Stevens 1987; Nicoll 1990, 1991, 1992; Huselbee 1998), there is little doubt that the generic assignment of the species used in this study is valid. Morphological differences between the different species are often very slight, and although this *could* be due to evolutionary convergence, it is unlikely that the transition between *C. proavus*, *C. intermedius* and *C. angulatus*, recognised by the gradually increasing concave shape of the anterior margin of the basal body from straight (*C. proavus*) to anteriorly recurved at the tip (*C. angulatus*) could have arisen through convergence.

If the generic assignment of *C. angulatus* is valid, and the interpretation of the mineralised tissues is correct, then the fourth hypothesis must be accepted. Different species of a single euconodont genus appear to have had the ability to mineralise different tissue types in their basal bodies. As noted by M. M. Smith *et al.* (1996) and Donoghue (1998) euconodont elements are homologous to odontodes, structures which have the potential to mineralise enamel, dentine, bone (Reif 1982), and also cartilage (Smith and Hall 1990). Heterochronic changes in the timing of cell differentiation that lead to the secretion of these four tissues are possible (Smith and Hall 1990), with the most well documented of these being the mineralisation of enameloid by the earlier differentiation of the ameloblasts relative to the odontoblasts during development (M. M. Smith 1995). It is theoretically possible therefore, that during the early evolution of euconodonts (and consequently the early evolution of the vertebrate mineralised dermal skeleton) that such shifts in the timing of cell differentiation could result in a number of tissue combinations, such as enamel directly overlying globular calcified cartilage, that are not commonly observed in the Recent.

Returning to the question of the polyphyly of the euconodont clade, the results of the histological study described here suggest that there are no significant differences between the forms assigned to the *Proconodontus* lineage and those assigned to the *Teridontus* lineage. Conclusions that can be drawn from this are that either the vertebrate mineralised dermal skeleton arose more than once to produce two separate clades currently grouped as the euconodonts, or that the two groups proposed by Miller (1980) are closely related and share a common ancestor. New results concerning the histology of certain paraconodonts have important implications for the resolution of this problem, as were discussed in the previous chapter.

CHAPTER 11

CONCLUSIONS

11.1 Late Cambrian environments in Laurentia and Baltoscandia

Flat-pebble conglomerates of the Snowy Range Formation in the Bighorn Mountains, Wyoming were deposited below the fair-weather wave-base, but above the storm wave-base in an intrashelf basin setting. Limestone units with occasional hard-ground communities formed in well-ventilated conditions and were often disrupted by storm activity which redeposited the coarse limestone clasts within a silty matrix. In contrast, the Alum Shale Formation of Baltoscandia was deposited in a relatively constant environment, on a broad stable shelf that was prone to long periods of stagnation (shale deposition) with occasional ventilation of the seafloor and subsequent limestone deposition. Water depths of 200 m or less have been predicted for the Alum Shale, whereas the Snowy Range Formation was deposited in water less than 40 m deep. Proto-, para- and euconodont faunas reflect these environmental differences, with proto and paraconodonts dominating the deeper, more constant conditions of the Alum Shale, and euconodonts being dramatically more diverse and abundant in the Snowy Range Formation.

11.2 Protoconodonts

11.2.1 Apparatuses. Protoconodont apparatuses are unimembrate. Species such as *Phakelodus elongatus* and *Phakelodus tenuis* which possess elements of similar morphology (distinguished, in this case, by the presence of a sharp posterior margin in the former species) are not united in multimembrate apparatuses because fused clusters of elements are, without exception, monotypic. For this reason, other protoconodont species (e.g. *Gapparodus bisulcatus*, *Gapparodus cuneatus*) for which fused clusters of elements are unknown, are assigned unimembrate apparatuses and, despite similarity in external form, and not united as one species.

11.2.2 Histology. Protoconodont elements have a three-layered structure comprising thin inner and outer layers and a thicker, fibrous, middle layer. Different styles of growth have been recognised by Müller and Hinz-Schallreuter (1998), but these have not been recognised during the course of the present investigation. Since the term 'protoconodont' is regarded as an informal systematic name for a group of phosphatic, coniform elements with a three-layered internal structure, this difference in histology noted by Müller and Hinz-Schallreuter may represent a feature of taxonomic importance, and should receive further attention in the future.

11.2.3 Affinity. In the absence of any contradictory evidence, the relationship between protoconodonts and Recent chaetognaths elucidated by Szaniawski (1982) cannot be disputed. The soft-part remains found by Aldridge and Repetski (Aldridge, pers. comm. 2000) may hold further evidence to either support or reject this hypothesis.

11.3 Paraconodonts

11.3.1 Apparatuses. Although previously described as form taxa (except by Hinz 1992), some paraconodonts are now thought to possess multielement apparatuses, comprising a number of element types that can be recognised in the different species of each genus. Whether these elements are homologous between genera is uncertain, since the characters by which the different element types are recognised are morphological, and may represent evolutionary convergence and not true homology. Text-figure 11.1 summarises the paraconodont apparatuses that have been reconstructed, following the assumption that elements of similar overall morphology can be homologised.

Species / Element type	Alpha	Beta	Gamma	Delta
Furnishina curvata	✓	?	✓	?
Furnishina furnishi	✓	✓	✓	✓
Furnishina kranzae	✓	?	✓	✓
Furnishina primitiva	?	✓	✓	?
Furnishina tortilis	✓	?	✓	✓
Prosagittodontus dahlmani	?	✓	✓	✓
Prooneotodus gallatini	✓	?	✓	✓
Prooneotodus rotundatus	✓	?	✓	✓

Text-figure 11.1. Summary table showing the elemental composition of the various paraconodont apparatuses that have been reconstructed during the course of this study.

Other paraconodont genera (*Proacodus*, *Muellerodus*, *Westergaardodina*) have been assigned unimembrate apparatuses in the absence of abundant material and co-occurrence data, however, it is likely that multielement apparatuses may be recognised for the various species of these genera in the future.

Multielement taxonomy in paraconodont systematics is particularly important in the light of histological discoveries made during this investigation. If some paraconodont species (*Prooneotodus gallatini*, *Prooneotodus rotundatus*) are indeed closely related to the most primitive euconodonts, then it stands to reason that similarities between the apparatuses of paraconodonts and euconodonts will be found. To this end, it is proposed that the alpha and gamma elements of *P. gallatini* and *P. rotundatus* correspond to the graciliform elements of the euconodont genus *Proconodontus* (particularly *Proconodontus muelleri*), and that the delta elements of *Prooneotodus* correspond to the arcuatiform (compressed) element of *Proconodontus* (Text-figure. 11.2).

Genus	Element			
Proconodontus	Aequaliform	Graciliform		Arcuatiform
Prooneotodus	?	Alpha	Gamma	Delta

Text-figure 11.2. Table to illustrate the possible comparison between the apparatuses of the euconodont *Proconodontus* and the paraconodont *Prooneotodus*.

An attempt has been made to erect a suprageneric classification for paraconodonts, including two new families (Proacodidae and Prooneotodidae) alongside the already established Furnishinidae Müller and Nogami, 1971 and Westergaardodinidae Müller, 1959. This classification system may come under scrutiny in the future, as paraconodont apparatuses and relationships become more fully understood.

11.3.2 Histology. For the first time a clear, unequivocal comparison has been made between the hard tissues of paraconodonts and euconodonts. However, these similarities are so far restricted to only a single paraconodont genus, *Prooneotodus*. New terms have been applied to the two component hard tissues of *Prooneotodus*, the 'outer lamellar layer' and the 'inner core', of which only the outer lamellar layer corresponds to the current perception of paraconodont elements. The inner core material had not been comprehensively described prior to this study.

The outer lamellar layer demonstrates typical paraconodont growth, as first fully described by Müller and Nogami (1971) with growth increments cropping-out on the external surface of the element. On the inner side of the outer lamellar layer, the growth increments curve around and continue in the direction of the cusp. A junction between the outer lamellar layer and the inner core material is recognisable, but is not as distinct as the junction between the crown and the basal body of euconodonts, since the difference in the organic content of the two tissues is not as great in paraconodonts as it is in euconodonts.

In the centre of the element, the inner core tissue is globular. The centres of some of the spherules have been replaced by secondary mineral and now appear as dark spots in the inner core material. In cross polarised light the inner core tissue demonstrates an extinction pattern directly comparable to that previously described in the euconodont genus *Pseudooneotodus* by Sansom (1996), and also in elements of *Proconodontus*, *Eoconodontus*, *Cambrooistodus* and *Cordylodus* investigated during this study. Sansom (1996) interpreted the globular material with the characteristic extinction pattern in the basal body of *Pseudooneotodus* as atubular dentine.

The similarities between the inner core tissue of *Prooneotodus* and various euconodonts do not prove definitive homology, but they do add support to the hypothesis proposed by Bengtson (1976), that a close relationship exists between para- and euconodonts. The outer lamellar tissue is, however, problematic and may represent a tissue that is unique to the paraconodonts.

11.3.3 Affinity. If the proposed relationship between paraconodonts and euconodonts is accepted, then the history of the mineralised dermal skeleton of vertebrates can be extended into the Middle Cambrian. To date, histological results for other paraconodont genera have not demonstrated features comparable to either *Prooneotodus* or euconodonts, but this should not necessarily lead to the conclusion that these similarities do not exist or will not be discovered in the future. For this reason, the Paraconodontida have been included in the new subclass Paraconodonta as part of the Class Conodonta as part of a revised classification in which the subclass Euconodonta has also been established.

11.4 Euconodonts

11.4.1 Apparatuses. Primitive euconodont genera including *Proconodontus*, *Eoconodontus*, and possibly *Cambrooistodus* are now known to possess complex, differentiated multielement apparatuses which can be compared to the apparatuses of more derived euconodonts. The apparatus model developed by Armstrong (1990) and Sansom *et al.* (1994) for *Panderodus* has been applied to the apparatus of *Eoconodontus notchpeakensis* with excellent correlation. Seven element types have been described (aequaliform, graciliform A, truncatiform, graciliform B, falciform, tortiform, arcuatiform) and, although bedding plane assemblage and fused cluster evidence is lacking, it is assumed that these elements would have been found in the three locational domains suggested by Sansom *et al.* (1994) for *Panderodus* (Text-figure 11.3).

Elements of *Proconodontus muelleri* have been divided into three categories, aequaliform, graciliform and arcuatiform, however, *P. muelleri* was less abundant than *Eoconodontus* in the studied material, and so the possibility of finding further element types cannot be ruled out.

Genus	Elements						
Eoconodontus	Aequaliform	Graciliform A	Truncatiform	Graciliform B	Falciform	Tortiform	Arcuatiform
Panderodus (Descriptive)	Aequaliform	Graciliform	Truncatiform	Graciliform	Falciform	Tortiform	Arcuatiform
Panderodus (Locational)	ae	qg	qg	qg	pf	pt	qa

Text-Figure 11.3. Table summarising the apparatus composition of *Eoconodontus* and *Panderodus* and the possible locational homology between the element types.

11.4.2 Histology. In addition to the similarity in apparatus composition between Late Cambrian and more derived euconodonts, the histology of the more primitive euconodonts is also directly comparable to that of the younger, more well-documented, forms. The lamellar crown tissue comprises fine crystallites arranged sub-perpendicular to the growth increments, often in a 'fanning-out' arrangement that gives a swallow-tail extinction pattern when the element is viewed in transmitted light. Growth increments meet the crown – basal body junction at a shallow angle. These features confirm that the crown of primitive euconodonts is homologous to that of more derived euconodonts, and that the tissue can therefore be interpreted as vertebrate enamel.

The basal material of primitive euconodonts is lamellar close to the crown-base junction, following a thin (20 μm) zone of amorphous tissue. Towards the centre of the element the basal tissue becomes globular, with growth increments of less than 1.5 μm in width. Tissues of the crown and basal body grow appositionally away from their common junction. However, a derived species of *Cordylodus* (*C. angulatus*) possesses basal material in which the spherules are discrete and not formed within the bounds of growth lamellae, unlike the basal tissues in the more primitive euconodonts. This tissue has been interpreted as globular calcified cartilage by Sansom *et al.* (1992). More primitive species of *Cordylodus* (*C. proavus*, *C. lindstromi*, *C. intermedius*) have basal bodies that are histologically more comparable to those of *Proconodontus*, *Eoconodontus* and *Cambrooistodus* than *C. angulatus*. Additionally, each discrete spherule in the base of *C. angulatus* bears its own extinction cross, whereas the extinction pattern in the basal tissue of the other species of *Cordylodus* and the more primitive euconodonts is typically striated with alternating dark and light bands parallel to the longitudinal axis of the element more characteristic of the dentine of *Pseudooneotodus* than the globular calcified cartilage of *C. angulatus*. If the systematic position of *C. angulatus* and the interpretations of the tissues are accepted then it is likely that, even at the generic level, euconodonts were experimenting with different hard tissue combinations as part of the odontode system.

White matter remains problematic, and some of the forms investigated in this study are found not to possess 'true' white matter, but a less well-developed tissue that is easily removed by etching, but sometimes takes on the appearance of true white matter. This tissue has been termed 'pseudo white matter'.

11.4.3 Affinity. As shown by previous studies using evidence from both soft-part anatomy and hard-tissue histology (e.g. Sansom *et al.* 1992; Aldridge *et al.* 1993), euconodonts are vertebrates. Primitive euconodonts from the Late Cambrian are no different and remain as part of the vertebrate clade. Since no marked differences in the histology of elements from the *Proconodontus* and *Teridontus* lineages (*sensu* Miller 1980, 1984) have been discovered, and the proposed apparatuses of these primitive groups differ only by the absence of an arcuatiform element in *Teridontus*, it seems likely that the euconodonts can now be considered as a monophyletic clade, with both the *Proconodontus* and *Teridontus* lineages sharing a common, probably paraconodont, ancestor.

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APPENDICES

1. LOCALITY INFORMATION
2. ALUM SHALE SAMPLE DATA
3. BIGHORN MOUNTAINS SAMPLE DATA

Sample	**Grid Reference**	**Quarry/Location**
O93-1	GR363380	Grönhogen
O93-2	GR363380	Grönhogen
O93-4	GR376471	Degerhamn
O93-5	GR376471	Degerhamn
O93-6	GR376471	Degerhamn
O93-7c	GR376471	Degerhamn
O93-7d	GR376471	Degerhamn
VG93-7	8D Skara NV	Trolmen
VG93-8	8D Skara NV	Trolmen
VG93-10	8D Skara NV	Trolmen
VG93-12	8D Skara NV	Trolmen
VG93-13	8D Skara NV 561930	Backeborg
VG93-14	8D Skara NV 561930	Backeborg
VG93-15	8D Skara NV 566924	Gum
VG93-16	8D Skara NV 566924	Gum
VG93-17	8D Skara NV 566924	Gum
VG93-18	8D Skara NV 619961	Haggården
VG93-22	GR 8D Skara SO 801618	Stenstorp-Dala
ENKC	Sample donated by Prof. Euan Clarkson, 1996	
WY96-17	US Highway 16 Crazy Woman Creek	Bighorn Mountains
WY96-18	US Highway 16 Crazy Woman Creek	Bighorn Mountains

Species/Sample	O93-1	O93-2	O93-4	O93-5	O93-6	O93-7c	O93-7d	VG93-7	VG93-8	VG93-10	VG93-12	VG93-13	VG93-14	VG93-15	VG93-16	VG93-17	VG93-18	VG93-22	ENKC	Total
Furnishina curvata				3	27											3				33
Furnishina furnishi	6	11	16	5	75				2	1	4	2		1		8	16	10		157
Furnishina kranzae					1			42							8		7			58
Furnishina primitiva	4	1		2						13	2									22
Furnishina sp. (juveniles)			24		39	1				4		13	4	5	4		14			108
Furnishina tortilis								29												29
Muellerodus cambricus	1		1		6			12			2	3			3					28
Muellerodus? oelandicus								5								1				6
Proacodus acies	4	1								8	1									14
Proacodus obliquus					1															1
Proacodus pulcherus	1	1								3	1	1		1	1					9
Problematoconites perforatus	2	1			1											2				6
Prooneotodus gallatini	11	20	5		8	1	1			76	42	3			1	1		10		179
Prosagittodontus dahlmani										3		4	2		1					10
Serratocambria minuta					1															1
Westergaardodina bicuspidata					1			1	1		1	4			3					11
Westergaardodina bohlini	1				1			1	3						1					7
Westergaardodina concamerata											4									4
Westergaardodina excentrica												5	2							7
Westergaardodina moessebergensis													1		1					2
Westergaardodina polymorpha		1							4			2								7
Westergaardodina procera	1	2		1																4
Westergaardodina quadrata?											1									1
Gapparodus bisulcatus																			12	12
Gapparodus cuneatus												68	31	28	49					176
Hertzina elongata	633	33	38	15	35	2	2		10	19			3		1	21	2			814
Phakelodus elongatus	32	22	44	25	45		4	1	4	10		119	39	18	58	28	2			451
Phakelodus tenuis	519	183	221	34	171	5	4	12	53	151		26	27	15	15	126	37			1599
Coelocerodontus bicostatus										1	2									3
Cordylodus primitivus					1															1
Proconodontus muelleri					2					2			1							5
Total elements	1215	276	349	85	415	9	11	103	77	291	60	250	110	68	146	190	78	20	12	3765
Phakelodus elongatus clusters											4				6	1				
Phakelodus tenuis clusters											7				6	7				
Phakelodus spp. Clusters			2	1								5	4							
Phosphannulus												2								

Species/Sample	WY96-17	WY96-18	Total
Proconodontus muelleri Total	111	51	162
Aequaliform	17	7	24
Graciliform	84	31	115
Arcuatiform	10	13	23
Proconodontus posterocostatus		1	1
Proconodontus serratus		2	2
Proconodontus tenuiserratus		1	1
Cambrooistodus cambricus	388	284	672
Cambrooistodus minutus	68		68
Eoconodontus notchpeakensis Total	5119	4084	9203
Aequaliform	140	97	237
Graciliform A	326	272	598
Truncatiform	3879	2976	6855
Graciliform B	312	182	494
Falciform	105	98	203
Tortiform	162	75	237
Arcuatiform	195	384	579
Furnishina furnishi	238	33	271
Prooneotodus gallatini	92	168	260
Prooneotodus rotundatus	1606	1670	3276
Prooneotodus aff. *rotundatus*		60	60
Prosagittodontus dahlmani		2	2
Westergaardodina spp.	1	12	13
Phakelodus elongatus	156	83	239
Unidentified	195	2000	2195
Total	7974	8451	16425

PLATES

EXPLANATION OF PLATE 1

Figures 1-7. *Proconodontus muelleri* Miller.

Fig. 1.	BU2879, WY96-18, aequaliform element, lateral view; x130.
Figs 2, 3.	BU2880, WY96-18, graciliform element (dextral); 2, inner lateral view; 3, outer lateral view; x110.
Figs 4, 5.	BU2881, WY96-18, arcuatiform element (dextral); 4, inner lateral view; 5, outer lateral view; x130.
Figs 6, 7.	BU2882, WY96-18, unique element with a squat, fat morphology; 6, inner lateral view; 7, outer lateral view; x90.

Figure 8. *Coelocerodontus bicostatus* (van Wamel)

Fig. 8.	BU2883, VG93-12, lateral view of characteristic 'hooked' element. Lateral costae are not visible in this specimen; x420.

Figure 9. *Cambrooistodus cambricus* (Miller)

Fig. 9.	BU2884, WY96-17, lateral view of dextral element. Note the strongly keeled posterior margin and deep basal cavity; x100.

Figures 10-11. *Cambrooistodus minutus* (Miller)

Figs 10, 11.	BU2885, WY96-17, lateral views of sinistral element. Basal region is more extended at the antero-basal corner than is usual for members of this species, but the specimen is figured because of its particularly well-developed cusp; x120.


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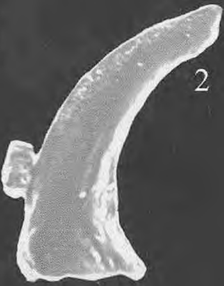
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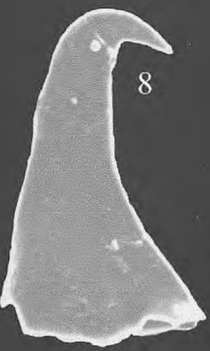
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EXPLANATION OF PLATE 2

Figures 1-26. *Eoconodontus notchpeakensis* (Miller)

Figs 1, 2. BU2886, WY96-18, lateral views of a symmetrical, aequaliform element; x100.

Figs 3, 4. BU2887, WY96-18, graciliform element A (dextral); 3, outer lateral view; 4, inner lateral view; x100.

Figs 5, 6. BU2888, WY96-18, graciliform element A (sinistral); 5, inner lateral view; 6, outer lateral view; x100.

Figs 7, 8. BU2889, WY96-18, truncatiform element (dextral); 7, outer lateral view; 8, inner lateral view; x90.

Figs 9, 10. BU2890, WY96-18, truncatiform element (sinistral); 9, inner lateral view; 10, outer lateral view; x90.

Figs 11, 12. BU2891, WY96-18, graciliform element B (dextral); 11, outer lateral view; 12, inner lateral view; x95.

Figs 13, 14. BU2892, WY96-18, graciliform element B (sinistral); 13, inner lateral view; 14, outer lateral view; x95.

Figs 15, 16. BU2893, WY96-18, falciform element (dextral); 15, outer lateral view; 16, inner lateral view; x 80.

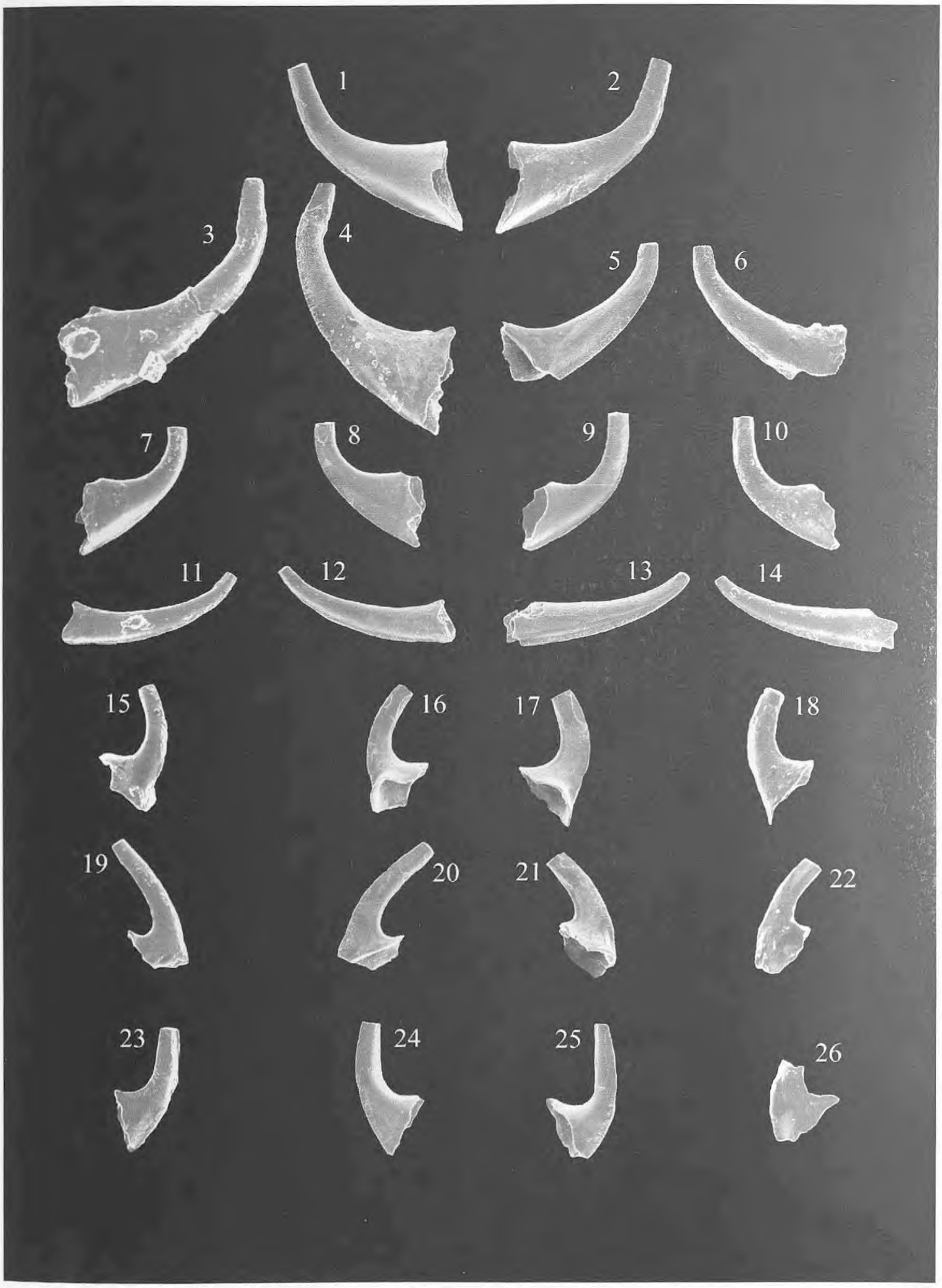
Figs 17, 18. BU2894, WY96-18, falciform element (sinistral); 17, inner lateral view; 18, outer lateral view; x 90.

Figs 19, 20. BU2895, WY96-18, tortiform element (dextral); 19, outer lateral view; 20, inner lateral view; x100.

Figs 21, 22. BU2896, WY96-18, tortiform element (sinistral); 21, inner lateral view; 22, outer lateral view; x90.

Figs 23, 24. BU2897, WY96-18, arcuatiform element (dextral); 23, outer lateral view; 24, inner lateral view; x90.

Figs 25, 26. BU2898, WY96-18, arcuatiform element (sinistral); 25, inner lateral view; 26, outer lateral view; x90.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EXPLANATION OF PLATE 3

Figures 1-6. *Prooneotodus rotundatus* (Druce and Jones)

Fig. 1.	BU2899, WY96-18, alpha element, posterior view; x120.
Fig. 2.	BU2900, WY96-18, alpha element, anterior view; x150.
Figs 3, 4.	BU2901, WY96-18, gamma element (sinistral); 3, outer lateral view; 4, inner lateral view; x130.
Figs 5, 6.	BU2902, WY96-18, delta element (sinistral); 5, outer lateral view; 6, inner lateral view; note the particularly thick walls on this specimen and also that the basal region is not as flared as it is in other delta elements of the species; x 130.

Figures 7-12. *Prooneotodus gallatini* (Müller)

Fig. 7.	BU2903, WY96-18, alpha element, posterior view; x190.
Fig. 8.	BU2904, WY96-18, alpha element, lateral view; note the annulations on the outer surface of the element; x130.
Figs 9, 10.	BU2905, WY96-18, gamma element (dextral); 9, inner lateral view; 10, outer lateral view; x190.
Figs 11, 12.	BU2906, WY96-18, delta element (dextral); 11, inner lateral view; 12, outer lateral view; x190.

Figures 13-16. *Problematoconites perforatus* Müller

Figs 13, 14.	BU2907, VG93-17, dextral element; 13, inner lateral view; 14, outer lateral view; x120.
Figs 15, 16.	BU2908, O93-1, dextral element; 15, inner lateral view; 16, outer lateral view; note the relatively large size of this element; x40.

Figure 17. *Muellerodus cambricus* (Müller)

Fig. 17.	BU2909, VG93-7; x250.

Figure 18. *Muellerodus ?oelandicus* (Müller)

Fig. 18.	BU2910, VG93-17; x240.


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EXPLANATION OF PLATE 4

Figures 1-4. *Furnishina curvata* Müller and Hinz

Figs 1, 2. BU2911, O93-6, alpha element; 1, anterior view; 2, posterior view; note the poor development of the basal opening; x290.

Figs 3, 4. BU2912, O93-6, gamma element; 3, posterior view; 4, lateral view; note the extended, spine-like cusp; x200.

Figures 5-11. *Furnishina furnishi* Müller

Figs 5, 11. BU2913, O93-6, symmetrical, beta element; 5 posterior view; 11, lateral view; x120.

Figs 6, 7. BU2914, O93-6, alpha element; 6 and 7 antero-lateral views; x95.

Figs 8, 9. BU2915, O93-6, gamma element; 8, posterior view; 9, lateral view; x90.

Fig. 10. BU2916, O93-6, delta element; note the widely flaring base; x95.

Figures 12-15. *Furnishina kranzae* Müller and Hinz

Figs 12, 13. BU2917, VG93-7, alpha element; 12, anterior view; 13, posterior view; note the poor development of the basal opening, and the similarity to the alpha elements of *Furnishina curvata*. However, elements of *F. kranzae* are considerably larger than those of *F. curvata*; x100.

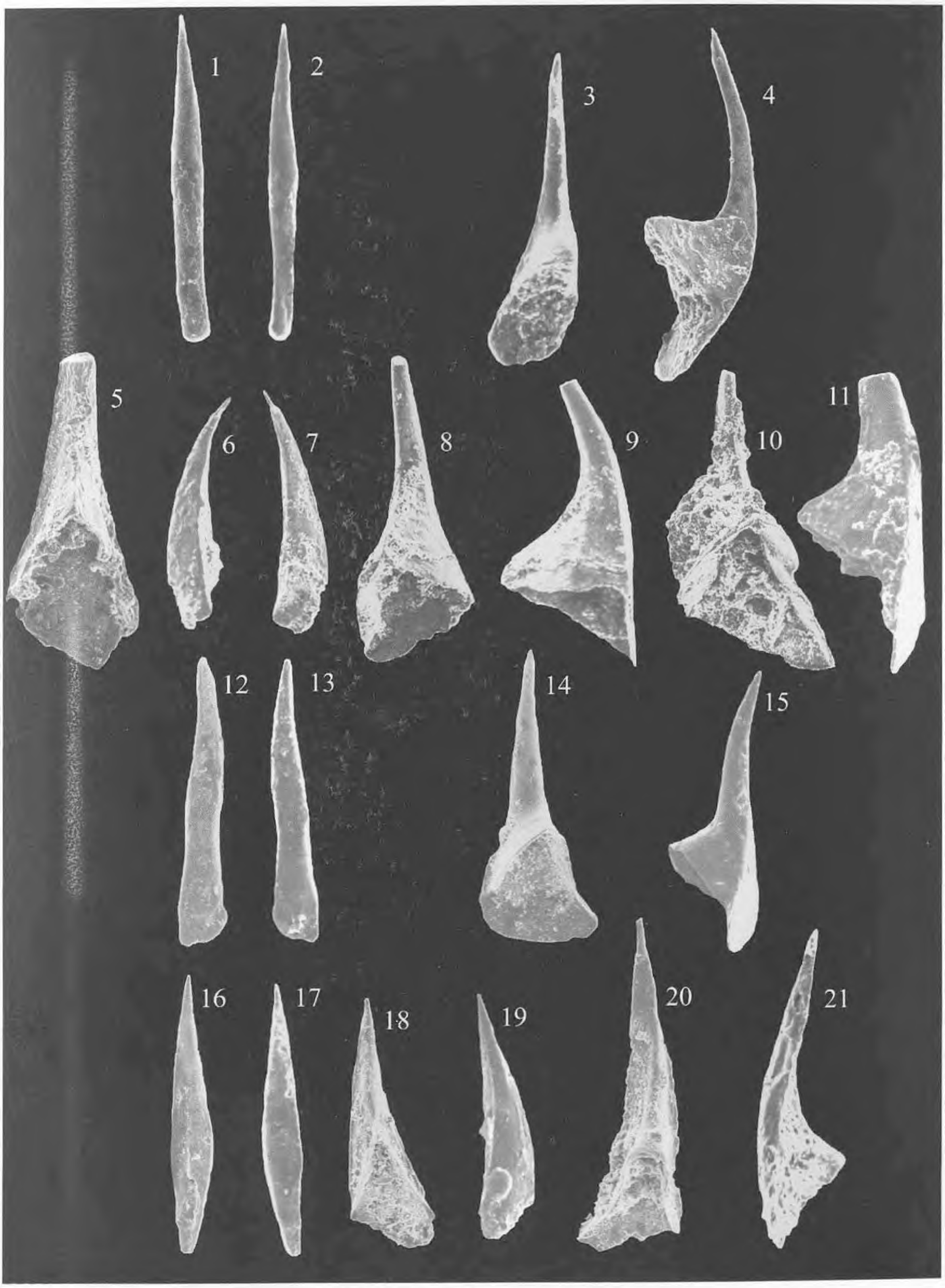
Figs 14, 15. BU2918, VG93-7, gamma element; 14, posterior view; 15, lateral view. The tip of the cusp is characteristically directed slightly towards the anterior; x100.

Figures 16-21. *Furnishina tortilis* (Müller)

Figs 16, 17. BU2919, VG93-7, alpha element; 13, posterior view; 14, anterior view. As with the alpha elements of the other *Furnishina* species, the basal opening is poorly-developed; x100.

Figs 18, 19. BU2920, VG93-7, gamma element; 18, posterior view; 19, antero-lateral view; x90.

Figs 20, 21. BU2921, VG93-7, gamma element; 20, posterior view; 21, inner lateral view; x90.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EXPLANATION OF PLATE 5

Figures 1-2. *Proacodus acies* (Müller and Hinz)

Figs 1, 2. BU2922, VG93-10, dextral element; 1, posterior view; 2, anterior view. The sharp lateral margin is clearly visible in this specimen; x190.

Figure 3. *Proacodus pulcherus* (An)

Fig. 3. BU2923, VG93-7, sinistral element, posterior view; x190.

Figures 4-5. *Proacodus obliquus* (Müller)

Figs 4, 5. BU2924, O93-6, dextral element; 4, posterior view; 5, anterior view; x250.

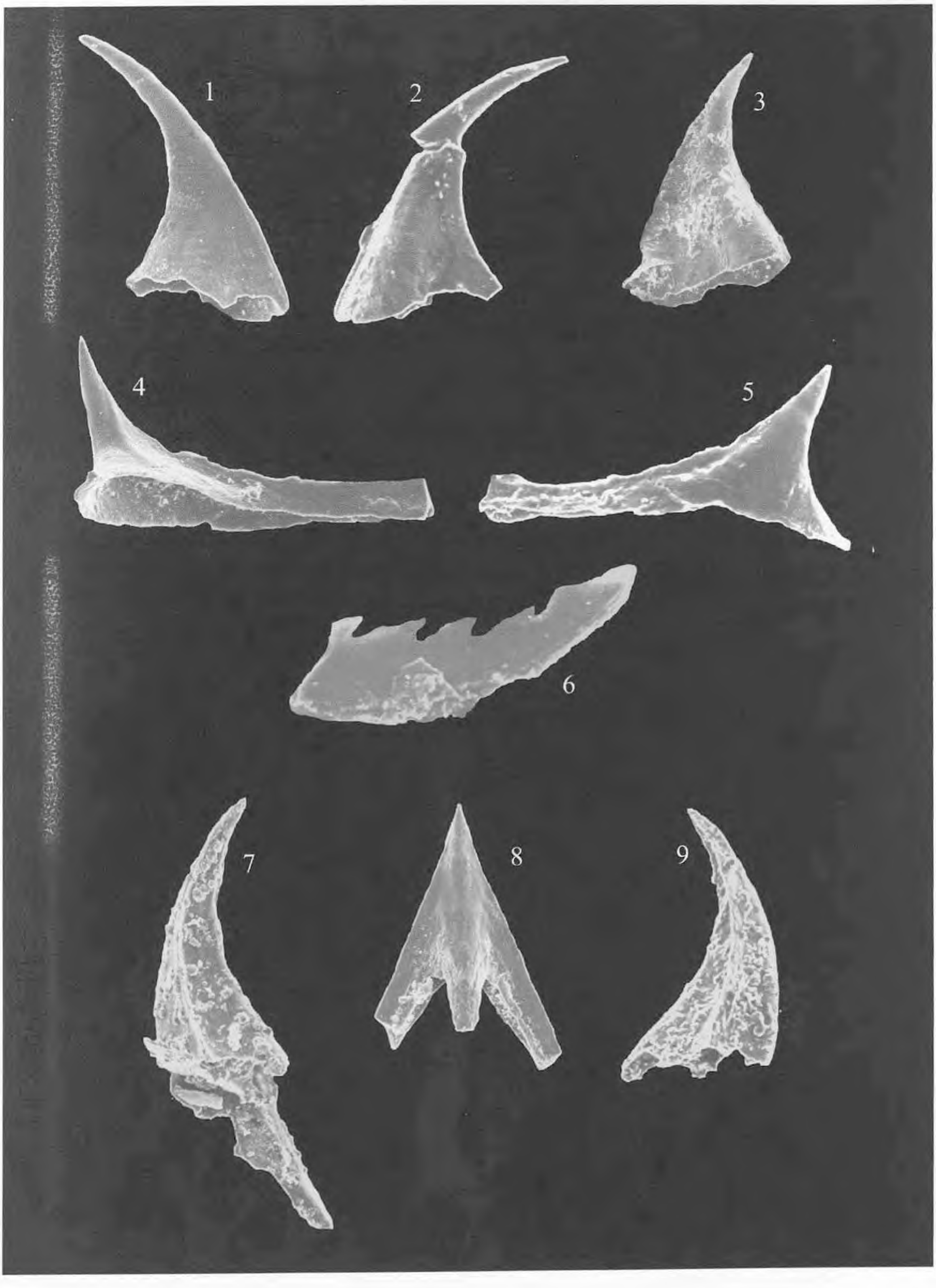
Figure 6. *Serratocambria minuta* (Müller and Hinz)

Fig. 6. BU2925, O93-6, poorly preserved, broken element; x360.

Figures 7-9. *Prosagittodontus dahlmani* (Müller)

Figs 7, 9. BU2926, VG93-13, poorly-preserved delta element, lateral views; x170.

Fig. 8. BU2927, VG93-10, arrow-head shaped, symmetrical beta element; x180.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EXPLANATION OF PLATE 6

Figures 1-2. *Westergaardodina bicuspidata* Müller

Figs 1, 2. BU2928, VG93-13; 1, posterior view; 2, anterior view of the same element, broken during handling; x190.

Figures 3-6. *Westergaardodina bohlini* Müller

Figs 3, 4. BU2929, O93-1; 3, posterior view; 4, anterior view; x190.

Figs 5, 6. BU2930, VG93-8; 5, posterior view; 6, anterior view; x190.

Figure 7. *Westergaardodina moessebergensis* Müller

Fig. 7. BU2931, VG93-14; anterior view.

Figures 8-9. *Westergaardodina excentrica* Müller and Hinz

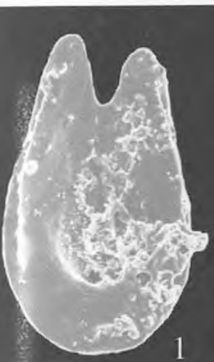
Figs 8, 9. BU2932, VG93-14; 8, posterior view; 9, anterior view. Note how the elements has an arched anterior face, and how the median projection is deflected dextrally; x250.

Figures 10-11. *Westergaardodina concamerata* Müller and Hinz

Figs 10, 11. BU2933, VG93-12; 10, posterior view; 11, anterior view; x250.

Figures 12-13. *Westergaardodina procera* Müller and Hinz

Figs 12, 13. BU2934, O93-2; 12, posterior view; 13, anterior view; x 250.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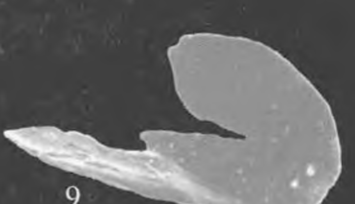
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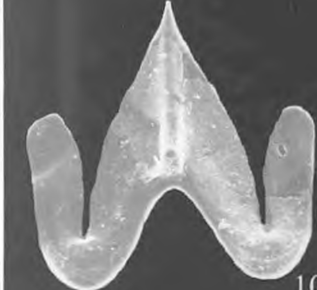
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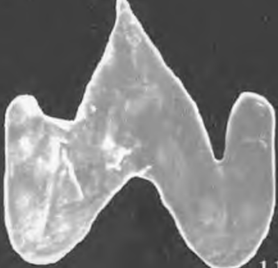
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EXPLANATION OF PLATE 7

Figures 1-2. *Phakelodus tenuis* (Müller)

Figs 1, 2. BU2935, O93-2, lateral views, x50.

Figures 3-4. *Phakelodus elongatus* (Zhang)

Figs 3, 4. BU2936, O93-1, lateral views, x100.

Figures 5-6. *Hertzina elongata* Müller

Figs 5, 6. BU2937, O93-1, lateral views, x60.

Figure 7. Fused cluster of *Phakelodus tenuis* elements.

Fig. 7. BU2938, VG93-14, cluster of at least 8 elements, some broken, in the typical 'non-functional' arrangement. Note that the larger elements are in the centre of the assemblage; x380.

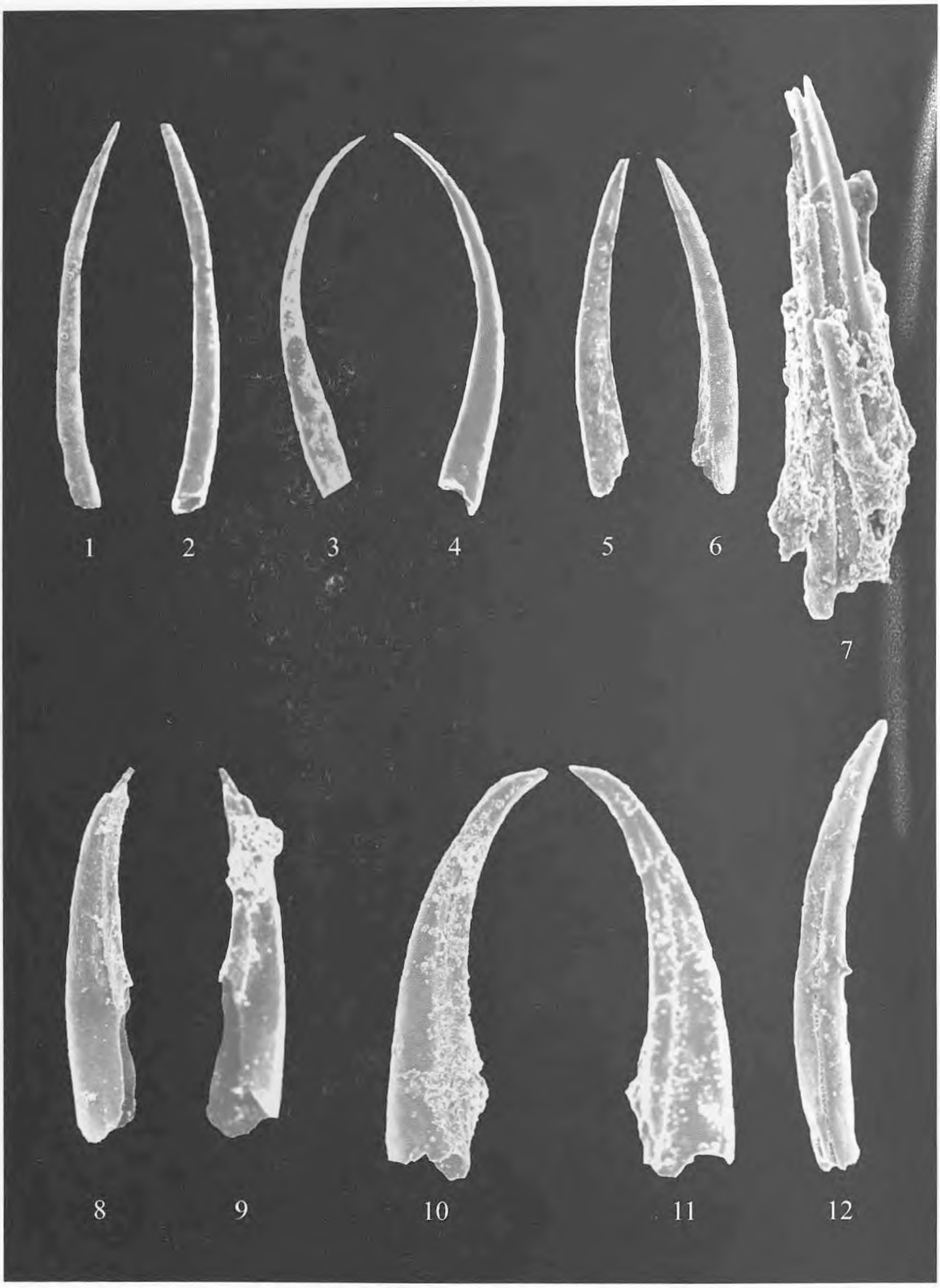
Figures 8-11. *Gapparodus cuneatus* (Müller and Hinz)

Figs 8, 9. BU2939, VG93-14, lateral views; x95.

Figs 10, 11. BU2940, VG93-13, lateral views; x150.

Figure 12. *Gapparodus bisulcatus* (Müller)

Fig.12. BU2941, ENKC, lateral view; x190.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EXPLANATION OF PLATE 8

Figures A, B. *Prooneotodus rotundatus* (Druce and Jones)

Fig. A. BU2942, TCU+4.5, Lange Ranch, Texas, whole element view of a longitudinal thin section taken with Nomarski differential interference optics (Nomarski DIC). Material in the inner core (central region) is globular, the outer lamellar layer demonstrates typical paraconodont growth with externally open growth increments; x80.

Fig. B. BU2942, close up view of globular basal material seen in Nomarski DIC. Growth increments in the outer lamellar layer are visible in the bottom right-hand corner of the illustration; x175.

Figure C. *Eoconodontus notchpeakensis* (Miller)

Fig. C. BU2943, WY96-17, view of the basal region of an etched longitudinal section through a graciliform element seen in Nomarski DIC. The swallow-tail extinction pattern in the crown material shows the fanning-out arrangement of the crystallites. Basal body material in the centre of the element is globular, but towards the crown-basal body junction the material is lamellar; x140.

Figure D. *Cambrooistodus cambricus* (Miller)

Fig. D. BU2944, WY96-18, view of the basal region of an etched longitudinal section through a characteristic '*Cambrooistodus*' (arcuatiform) element seen in Nomarski DIC with a gypsum plate. Similar to *E. notchpeakensis* the crown material shows a swallow-tail extinction pattern reflecting the orientation of the enamel crystallites, whilst the basal body material is lamellar at the crown-base margin, becoming globular towards the centre; x190.

Figures E, F. *Cordylodus proavus* Müller

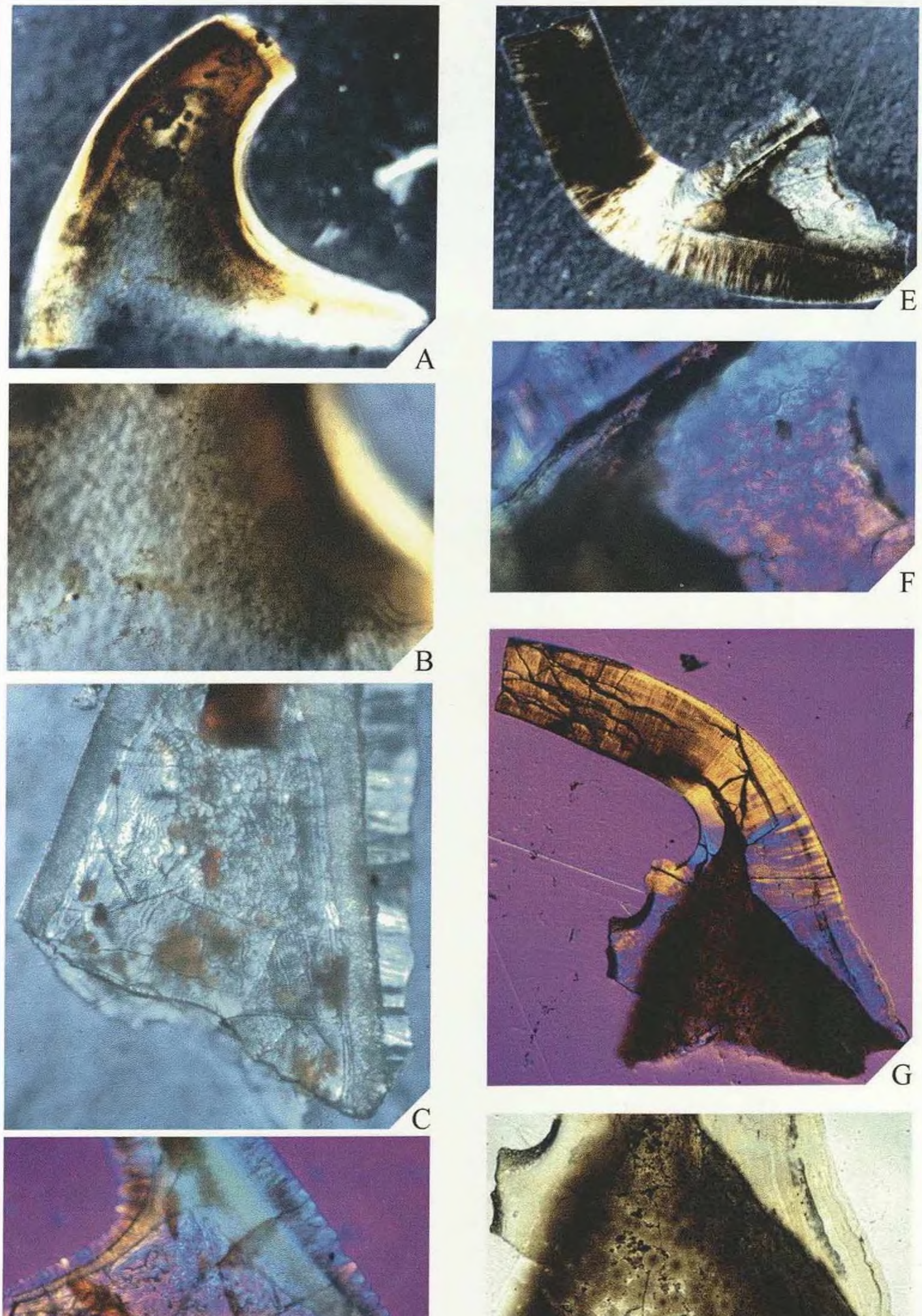
Fig. E. BU2945, TC1413, Threadgill Creek, Texas, whole element view of a longitudinal section through a symmetrical element seen in Nomarski DIC. Crown material shows poorly developed swallow-tail extinction. Tip of cusp opaque due to the presence of pseudo white matter. Basal material globular in the centre of the basal body, lamellar close to the junction with the crown, x60.

Fig. F. BU2945, TC1413, Close up view of basal material showing well-developed globular structure seen in Nomarski HDIC with a gypsum plate; x230.

Figures G, H. *Cordylodus angulatus* Pander

Fig. G. BU2156, Tremadoc of Maardu, Estonia, whole element view of a longitudinal section seen in Nomarski DIC with a gypsum plate. Swallow-tail extinction pattern present in crown material. Pseudo white matter poorly-developed in the cusp, hence the translucent nature of the distal part. Tissue globular in the majority of the basal body, with some lamellar material close to the crown-base junction. Individual spherules are discrete and not enclosed by surrounding growth lamellae; x65.

Fig. H. BU2156, close up of basal region of the same element seen in plain polarised light. The concentric growth lamellae that form the discrete spherules are clearly visible and the growth increments of the crown are seen to meet the crown-base junction at an oblique angle; x90.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EXPLANATION OF PLATE 9

Figures A-C. *Proconodontus muelleri* Müller

Fig. A. BU2946, WY96-18, whole element view of a longitudinal thin section through a graciliform element observed under an SEM. Individual crystallites of the crown are clearly visible. The junction between the crown and the base is sharp. Material in the base is lamellar towards this junction, with occasional development of spherules; x95.

Fig. B. BU2946, close up of anterior margin of the element showing the crystallites and growth increments of the crown material in greater detail, together with the sharp crown-base junction and the lamellar nature of the basal body, including a single spherule. Growth increments in the basal material are approximately 0.5 μm in width; x800.

Fig. C. BU2946, close up view of spherule; x2400.

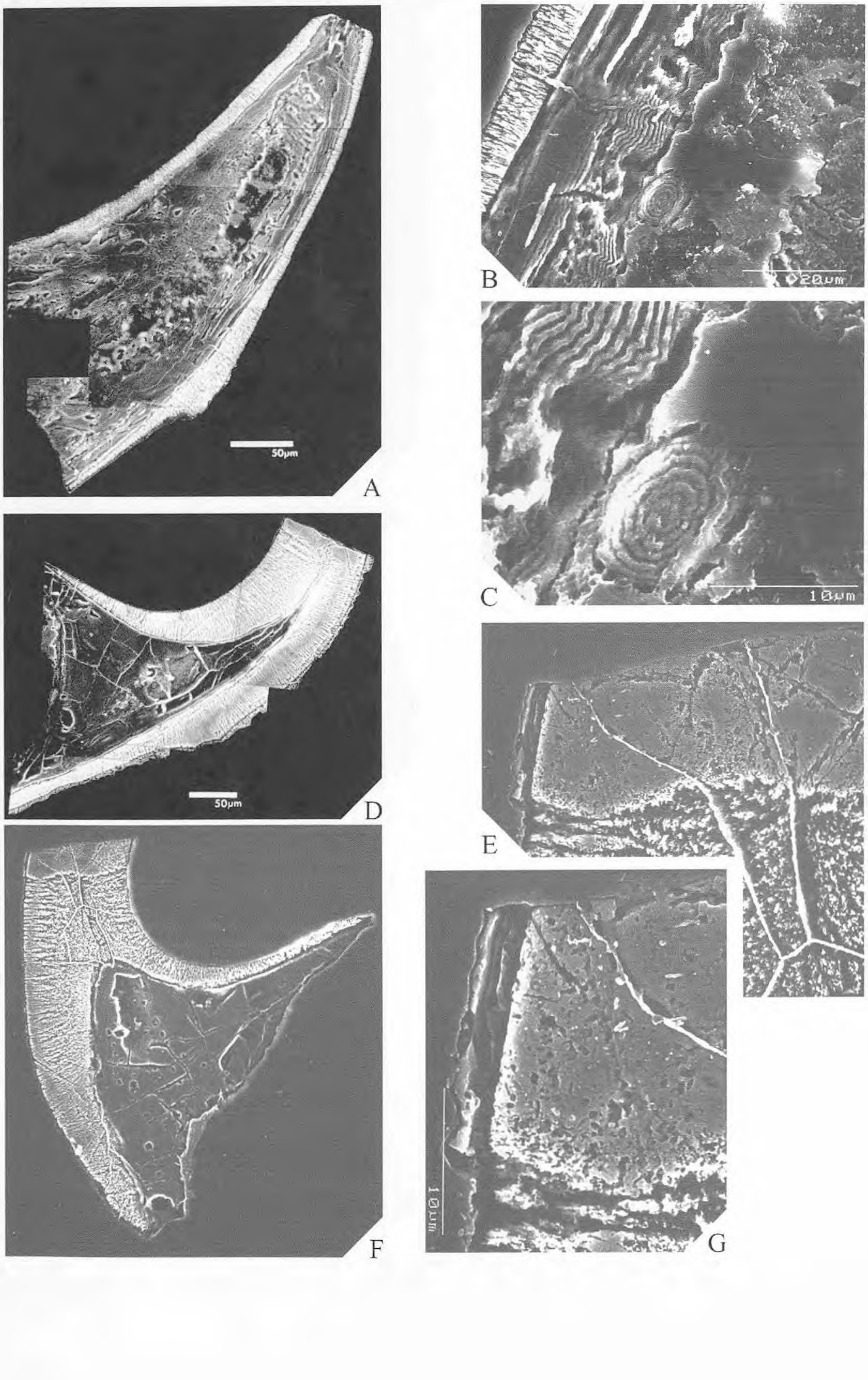
Figure D. *Eoconodontus notchpeakensis* (Miller)

Fig. D. BU2947, WY96-17, whole element (SEM) view of a longitudinal section through a graciliform element with well-developed lamellar crown material and a basal body demonstrating growth increments and occasional spherules. Pseudo white matter is developed in a narrow zone in the cusp of the element; x60.

Figures E-G. *Cambrooistodus minutus* (Miller)

Fig. F. BU2948, WY96-18, whole element (SEM) view of a longitudinal thin section through a characteristic '*Cambrooistodus*' (arcuatiform) element. Basal body material is relatively poorly-preserved, but pseudo white matter is well-developed in the cusp of the element; x100.

Figs E, G. BU2948, close up views of the narrow zone of pseudo white matter in the cusp. Large spherical and smaller elongate spaces are present giving this tissue a very similar appearance to true white matter; E, x440; G, x920.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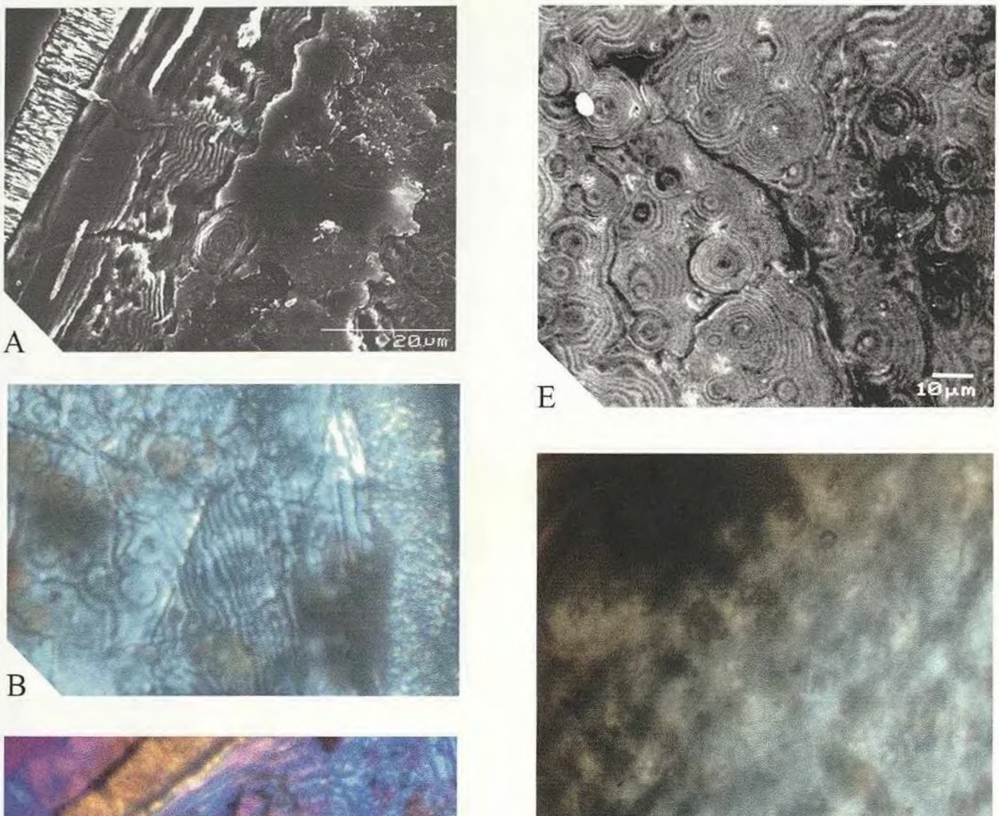
EXPLANATION OF PLATE 10

Figures A-G.	Details of the structures in the basal tissue of various para- and euconodonts.
Fig. A.	BU2946, *Proconodontus muelleri*, close up view under the SEM of an etched longitudinal thin section showing the sharp junction between the crown and the basal material. The basal material is lamellar with occasional spherules. Growth increments of the basal tissue are approximately 0.5 µm in width; x850.
Fig. B.	BU2943, *Eoconodontus notchpeakensis*, view of the basal material seen in Nomarski DIC optics. As with *P. muelleri* the basal tissue is lamellar with occasional spherules. Growth increments are approximately 0.5 µm in width; x370.
Fig. C.	BU2944, *Cambrooistodus cambricus*, view of the basal material seen in Nomarski DIC with a gypsum plate. Basal material is lamellar towards the margin of the basal material, becoming globular towards the centre. Growth increments approximately 0.5 µm in width; x750.
Figs D, E.	BU2945, *Cordylodus proavus*, figure D is viewed with a gypsum plate and Nomarski DIC. Spherulitic material is clearly visible. Figure E is an SEM view of the same thin section following etching. Lamellae are often found enclosing individual spherules. Growth increments of the basal tissue are approximately 1 µm in width; D, x630; E, x500.
Fig. F.	BU2942, *Prooneotodus rotundatus*, basal (inner core) material viewed with Nomarski HDIC. The basal tissue appears globular, however individual spherules and growth increments are not clearly visible throughout the basal material. Probable growth lamellae (bottom centre of illustration) are approximately 0.5 µm in width; x730.
Fig. G.	BU2156, *Cordylodus angulatus*, thin section through basal material seen in plain polarised light. Discrete spherules clearly visible. Growth increments are markedly thicker than those in *P. muelleri*, *E. notchpeakensis*, *C. cambricus*, *C. proavus* and *P. rotundatus* being up to 5 µm in width; x260.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EXPLANATION OF PLATE 11

Figures A-E. Elements viewed in cross-polarised light.

Fig. A. BU2944, *Cambrooistodus cambricus*, Crown material with a swallow-tail extinction pattern is visible, separated from the basal material by a sharp junction. The structureless part of the illustration is a result of the etching process. The extinction pattern of the basal material has distinctive dark and light coloured striations which run parallel to one another and to the long axis of the element. The pattern is pervasive throughout the base; x220.

Fig. B. BU2949, *Prooneotodus gallatini*, WY96-18, paraconodont incremental growth lines are clearly visible in the outer lamellar layer, however the inner core tissue demonstrates an extinction pattern which is directly comparable to that of the basal tissue in *C. cambricus*. Alternating dark and light coloured striations are aligned parallel to the long axis of the element; x170.

Fig. C. BU2277, *Pseudooneotodus tricornis* Drygant, Clarita Formation, Wenlock, Silurian, Arbuckle Mountains, Oklahoma (figure 3c in Sansom 1996). Specimen demonstrating the characteristic striated extinction pattern in the basal tissue. This tissue was interpreted as atubular dentine by Sansom (1996) with the striated pattern attributed to either attachment fibres or closed tubules; x200.

Fig. D. BU2942, *Prooneotodus rotundatus*, view of basal region of element demonstrating the same extinction pattern as elements of *Cambrooistodus*, *Prooneotodus gallatini*, *Pseudooneotodus* and *Cordylodus intermedius* (Fig E). The extinction pattern is continuous throughout the inner core tissue; x120.

Fig. E. BU2950, *Cordylodus intermedius* Furnish, Threadgill Creek, Texas, view of whole element with swallow-tail extinction visible in the crown material. The striated extinction pattern in the base is directly comparable to that in the other elements figured; x70.

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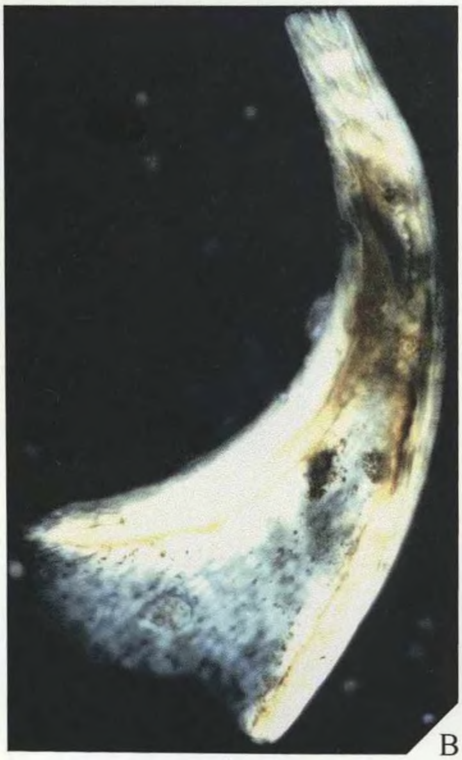

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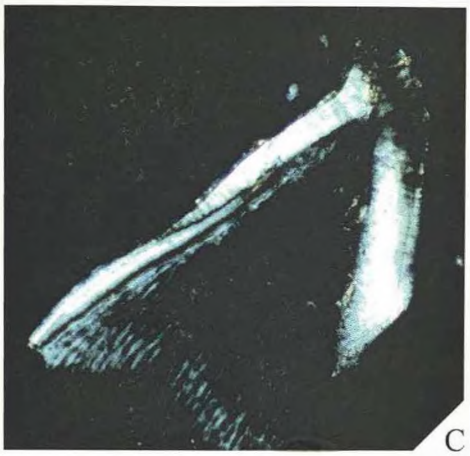

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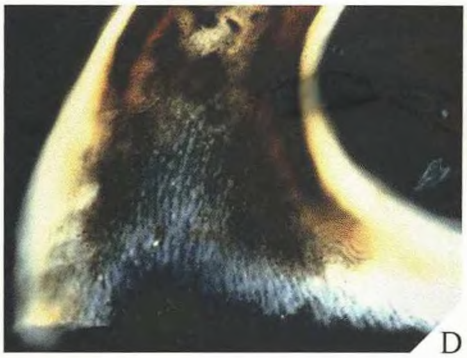

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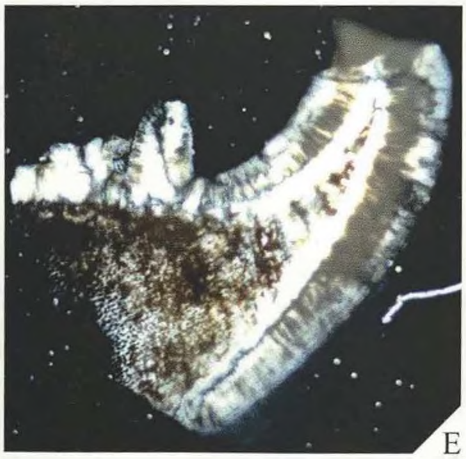

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EXPLANATION OF PLATE 12

Figures A, B, C, E. *Cordylodus proavus* Müller

Fig. A. BU2945, whole element view under the SEM. Note the lack of well-developed white matter; x80.

Fig. B. BU2945, SEM view of anterior margin of element showing the oblique relationship between the growth increments of the crown material and the sharp junction between the crown and the basal body (basal body is visible in the top right-hand corner of the illustration). Growth increments of the crown meet the crown-base junction at a shallow angle, steepening as the distance from the junction increases. This partially demonstrates the appositional mode of growth of the crown and basal body; x280.

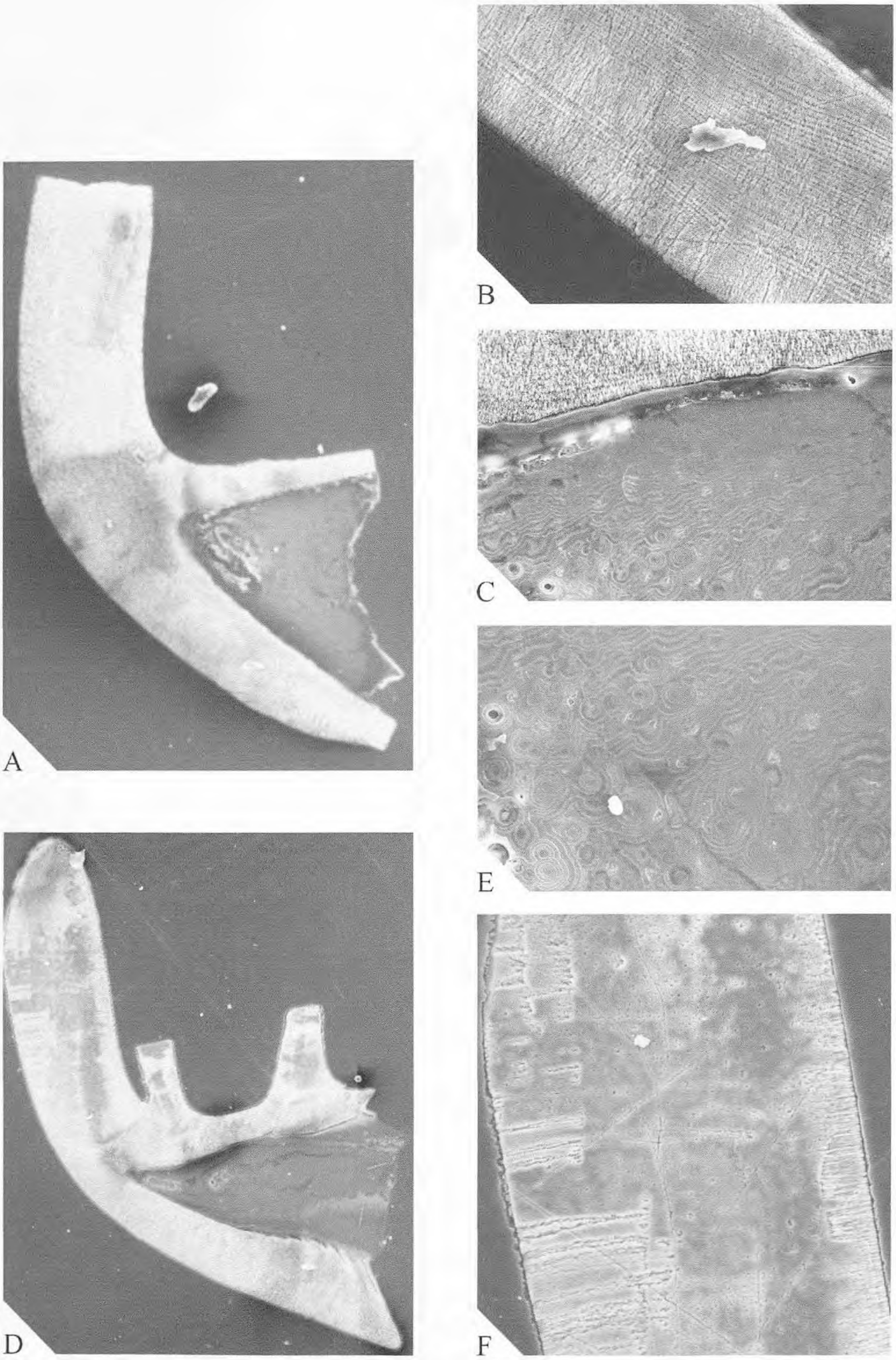
Fig, C. BU2945, view of posterior margin showing oblique relationship between the growth lamellae of the crown and the crown-base junction and also the amorphous nature of the basal material immediately adjacent to that margin. The junction between the crown and the basal body is sharp, and the basal material adjacent to the junction is structureless, becoming lamellar about 20 µm further in and then globular towards the centre of the element; x250.

Fig. E. BU2945, view of globular material in the centre of the basal body; x420.

Figures D, F. *Cordylodus lindstromi* Druce and Jones

Fig. D. BU2951, TCU92, Lange Ranch, Texas, whole element view under the SEM showing the sharp junction between the crown and the basal body, and the variable development of pseudo white matter in the crown. The second denticle on the posterior margin was lost during the thin sectioning process; x75.

Fig. F. BU2951, close up view of cusp showing development of pseudo white matter. Areas of more well-developed 'white matter' resemble 'true' white matter with spherical and elongate spaces, but lamellar crown material is also apparent along the anterior and posterior margins, in zones parallel to the long axes of the crystallites of the crown; x260.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EXPLANATION OF PLATE 13

Figures A, B. *Clavohamulus elongatus* Miller

Fig. A. BU2952, TCU+30, Lange Ranch, Texas, view of whole element taken with Nomarski DIC and a gypsum plate. Cusp of element is completely opaque, demonstrating the presence of well-developed true white matter Growth increments are clearly visible in the crown material adjacent to the base. Basal body material is also opaque, and no structures are visible; x 210.

Fig. B. BU2952, same element seen under the SEM. Well-developed white matter is clearly defined, containing both spherical spaces alongside elongate voids. A weakly-developed polygonal pattern is also developed within the white matter, but the origin of this structure is unknown. Growth increments of the crown are also clearly seen, composed of crystallites arranged with their long-axes perpendicular to the growth increments; x280.

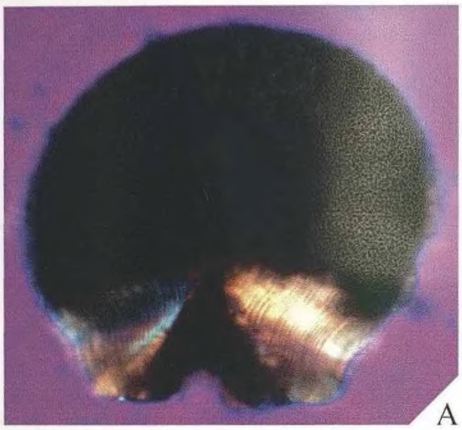
Figures C-F. *Teridontus nakamurai* Miller

Fig. C. BU2953, TCU+30, Lange Ranch, Texas, whole element view taken with Nomarski DIC. Pseudo white matter is developed in the tip of the cusp, and is found in a zone separated from the rest of the crown material by a planar junction roughly perpendicular to the anterior and posterior margins of the element. Growth increments in the crown material are clearly visible, and meet the junction between the crown and the basal body at a shallow angle. The basal body material is stained by a secondary mineral (possible iron oxide), and structural details have been obscured by the opacity of the tissue; x170.

Fig. D. BU2953, whole element view taken under the SEM. Pseudo white matter appears only as a core in the centre of the cusp, but is not developed close to the anterior or posterior margins as would have been expected from Plate 13C. Crystallites of the crown material are arranged with their long-axes perpendicular to the growth increments, which meet the crown-basal body junction at a shallow angle. The basal body tissue is poorly-structured, but some lamellar material is present close to the anterior and posterior margins of the basal cavity; x170.

Fig. E. BU2953, close up SEM view of anterior margin, showing the shallow angle at which the growth lamellae of the crown meet the crown-basal body junction, and how these lamellae become steeper away from this margin; x560.

Fig. F. BU2953, close up SEM view of the tip of the element showing the development of pseudo white matter in the core of the cusp, and not towards the margins; x 360.



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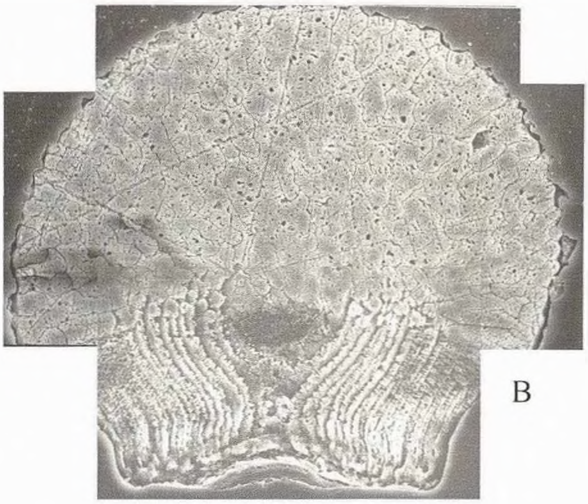

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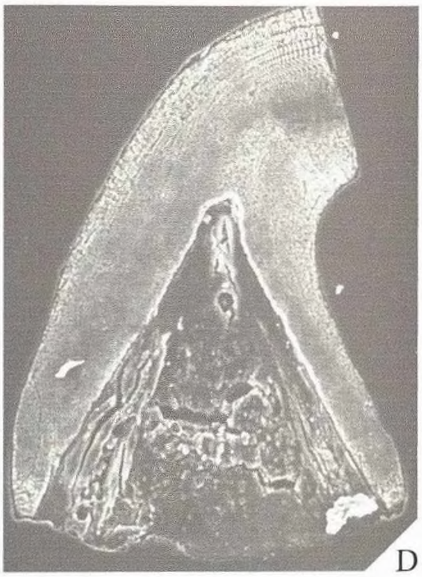

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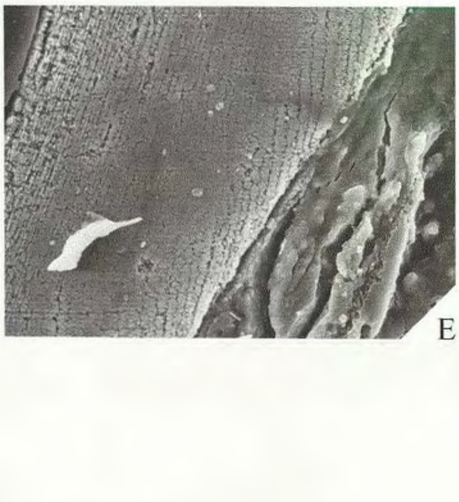

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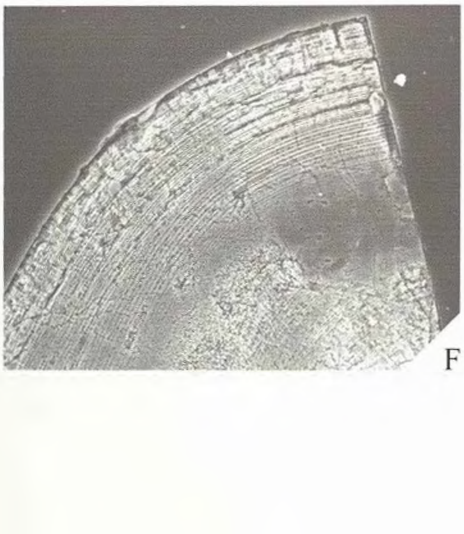

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EXPLANATION OF PLATE 14

Figures A-F. *Prooneotodus rotundatus* (Druce and Jones)

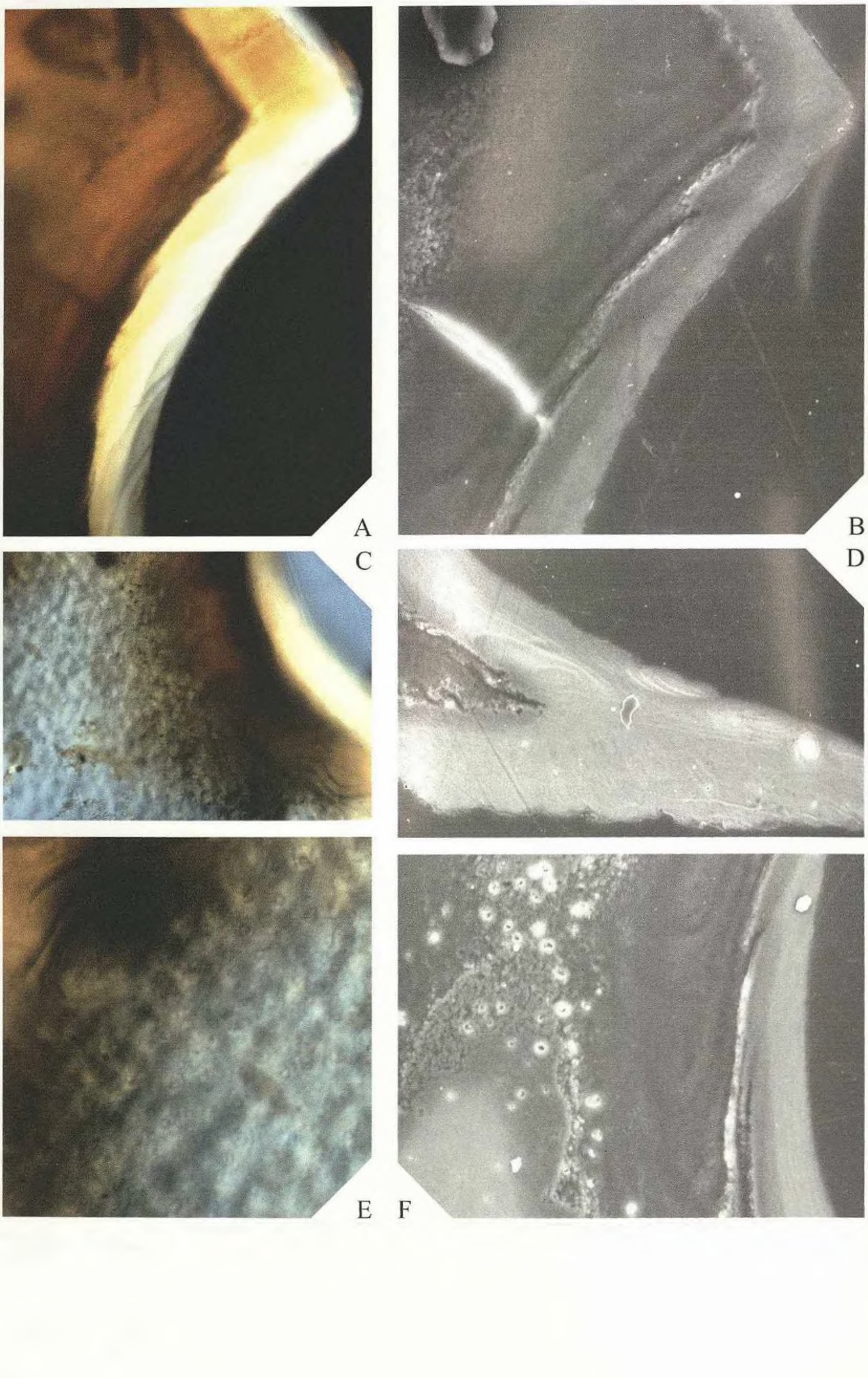
Figs A, B. BU2942, close up views of the posterior margin close to the tip of the element in cross-polarised light (A) and under the SEM (B). Typical, externally outcropping, paraconodont growth lamellae are present, and can be seen curving back around towards the tip in figure B. The lighter coloured zone at the edge of the element in figure B shows where the SEM is taking an image from beneath the surface of the embedding resin, where the element is not exposed at the surface; A, B, x480.

Fig. C. BU2942, view of globular inner core material and growth increments of the outer lamellar layer on the posterior margin taken with Nomarski DIC. Growth increments appear to be curving round the edge of the element and, similar to the situation outlined above, this is due to the thickness of the specimen, making the image appear three-dimensional; x200

Fig. D. BU2942, view of postero-basal corner of the element under the SEM. All of the light coloured part of the element is beneath the surface of the resin and, because of the thickness of the section, the resultant image is three-dimensional. The darker grey part of the image (centre left) comprising a small part of the outer lamellar layer and some of the inner core material is exposed at the resin surface; x375.

Fig. E. BU2942, close up view of the globular material in the inner core of the element taken with Nomarski HDIC; x 570.

Fig. F. BU2942, SEM view of the posterior margin with the typical curving around paraconodont growth lamellae (right hand side of illustration) and the material in the inner core of the specimen. Individual spherules are not seen, but the small, spherical spaces which are seen to be charging slightly in this image are likely to be where the secondarily mineralised core of the spherules has been removed during etching; x360.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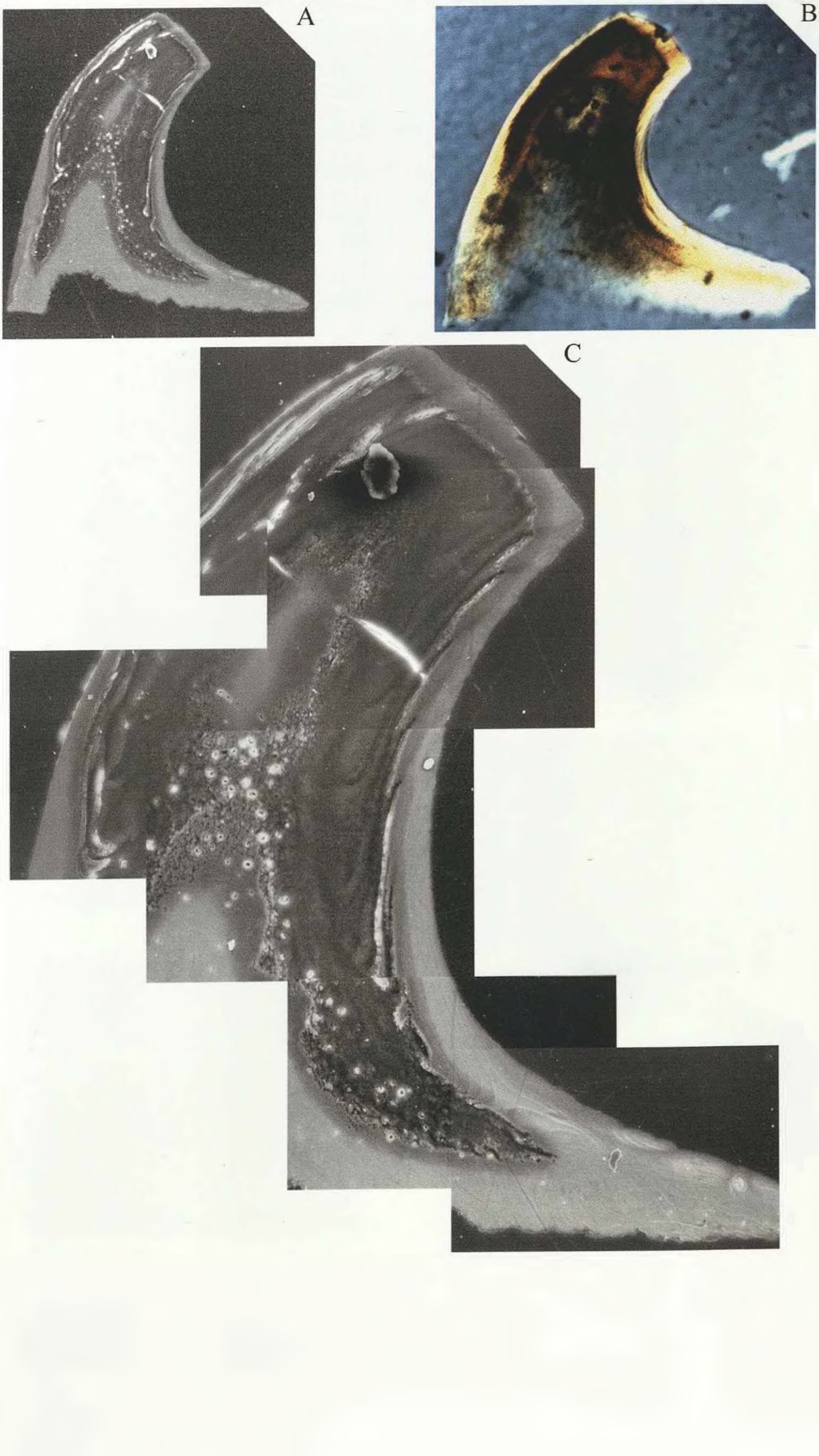
EXPLANATION OF PLATE 15

Figures A-C. *Prooneotodus rotundatus* (Druce and Jones)

Figs A, B. BU2942, whole element view of specimen viewed under the SEM (A) and with Nomarski DIC on a light microscope (B); A, B, x80.

Fig. C. BU2942, composite photograph taken under the SEM to show the typical paraconodont growth lines exhibited by this specimen. Growth increments crop out on both the anterior and posterior margins of this section, and can be seen curving round towards the tip of the element on the inner margin of the outer lamellar layer. The junction between the outer lamellar layer and the inner core is not as distinct as it is between the crown and the basal body in euconodonts, but this can be attributed to a similarity in organic composition between the two tissues in paraconodonts and the corresponding difference in euconodonts. Material in the inner core has not etched particularly well, but the centres of the spherules have been removed, and show up as spherical spaces which are prone to charging under the SEM; x250.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EXPLANATION OF PLATE 16

Figures A-D, F. *Gapparodus cuneatus* (Müller and Hinz)

Fig. A. BU2954, VG93-17, Alum Shale, Västergötland, Sweden, whole element view under the light microscope with Nomarski DIC; x70.

Fig. B. BU2954, close up view of the broken tip of the element showing the three-layered structure typical of protoconodonts. The inner tip is composed of the thin inner layer, whilst the outer layer is visible where the tip of the element has broken. The thicker middle is situated in the gap between the inner and outer layer; x100.

Fig. C. BU2939, close up view of a broken element tip under the SEM. The inner and middle layers are clearly visible, but it appears that the outer layer is missing; x 350.

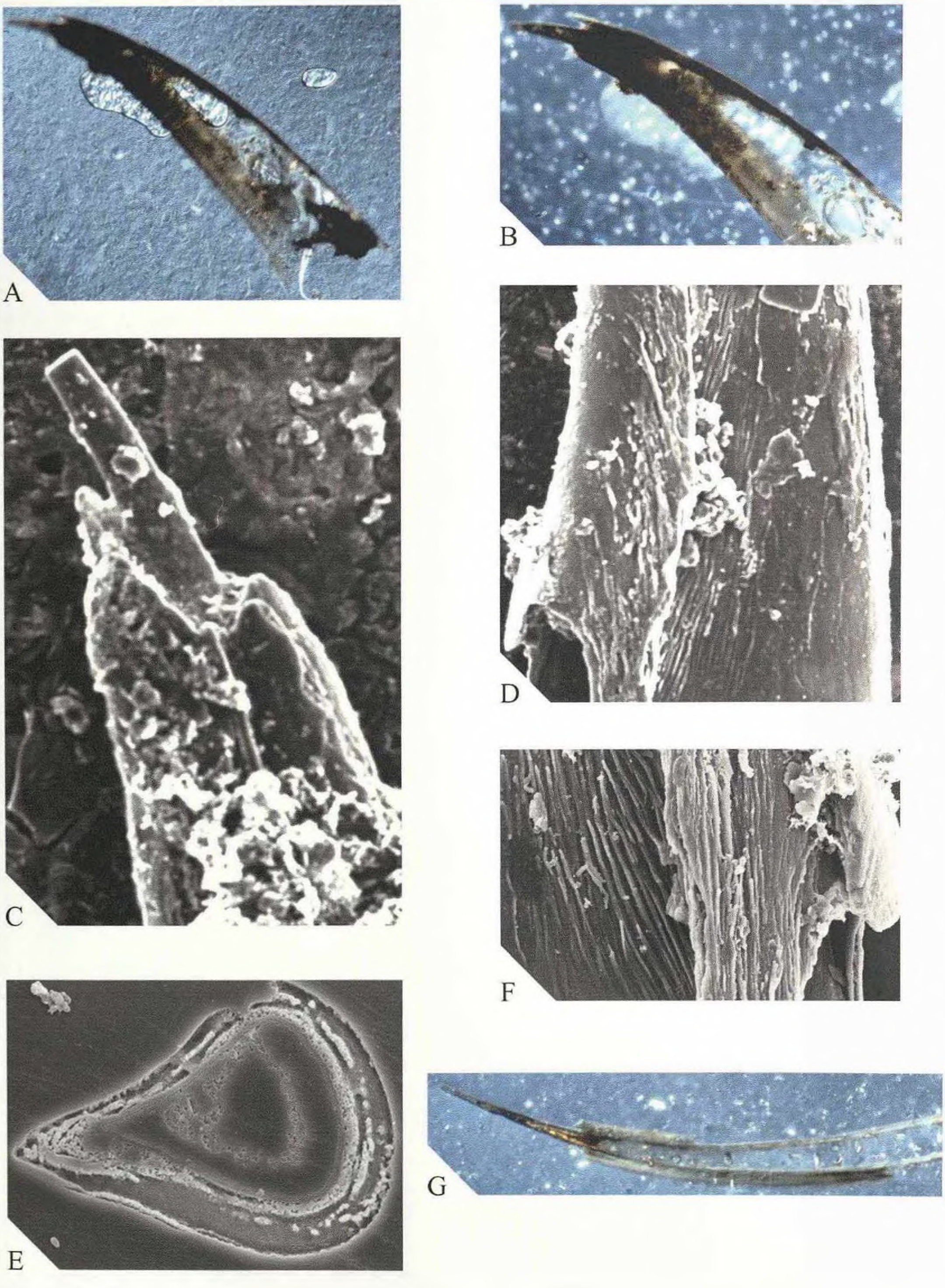
Figs D, F. BU2939, close up (SEM) views of the posterior margin of the element, close to the longitudinal lateral furrow, where the outer layer has been removed to exposed the fibrous nature of the middle layer; D, x500; F, x920.

Figure E. *Phakelodus elongatus* (Zhang *in* An *et al.*)

Fig. E. BU2955, VG93-16, Alum Shale, Västergötland, Sweden, SEM view of transverse cross-section through the element, showing the tear-shaped outline ad the layered nature of the specimen; x430.

Figure G. *Phakelodus tenuis* (Müller)

Fig. G. BU2956, VG93-16, Alum Shale, Västergötland, Sweden, view under the light microscope with Nomarski DIC of an element with a broken tip, showing the three-layered nature of the specimen; x120.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EXPLANATION OF PLATE 17

Figures A-D. *Palaeobotryllus taylori* Bengston

Fig. A. BU2957, LC-RT-36, Lawson Cove, Australia, SEM view of large, broken specimen comprising 16 individual segments, arranged around two centres; x50.

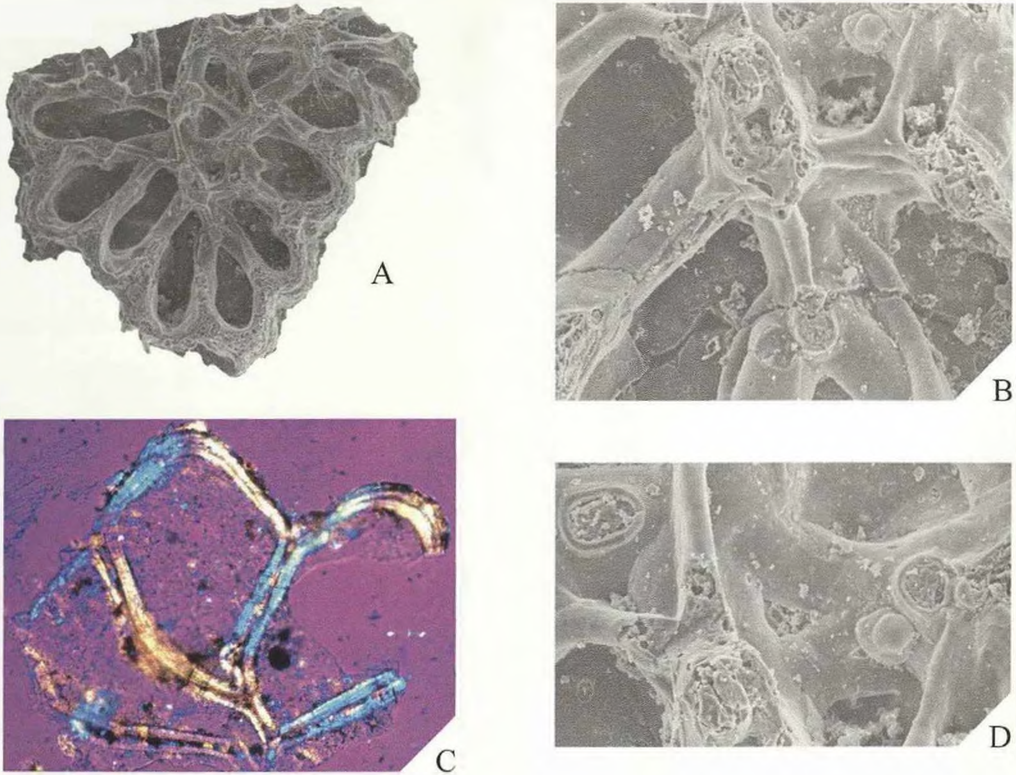
Figs B, D. BU2957, close up views of structures on the surface of the sclerite, presumably added by the organism during growth to add strength and support to the hard-parts; B, x250; C, x500.

Fig. C. BU 2958, LC-RT-36, Lawson Cove, Australia, view of a transverse thin section of a sclerite seen in Nomarski DIC with a gypsum plate added. The extinction pattern suggests that the crystallites forming the structure are arranged with their long-axes perpendicular to the growth increments of the sclerite; x110.

Figures E-G. Gen. et sp. nov. A, Lehnert *et al.* 1999.

Fig. E. BU2959, GB90-002, Black Mountain, Queensland, Australia, SEM view of an etched, transverse thin section through the sclerite. Growth lamellae are continuous around each of the individual segments, and do not overlap onto adjacent parts of the sclerite. The large sub-circular dark coloured areas within the segments are air bubbles trapped in the resin; x120.

Figs F, G. BU2959, close up views of the growth centre (F) and the margin (G) of the sclerite to show that the concentric growth increments do not wrap around or pass into those of other segments; F, G, x370.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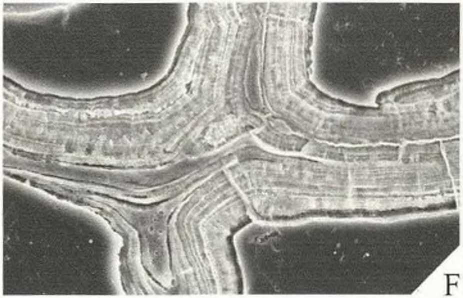
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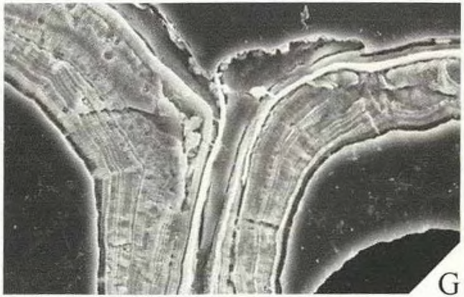
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EXPLANATION OF PLATE 18

Figures A, B. *Milaculum* sp.

Fig. A. BU2960, Wah Wah Formation, Ibex Area, Utah, view of a longitudinal section through a sclerite, seen in transmitted light with Nomarski DIC. Dark and light zones oriented perpendicular to the upper and lower surfaces of the element are apparent, but growth increments and other structures are absent; x150.

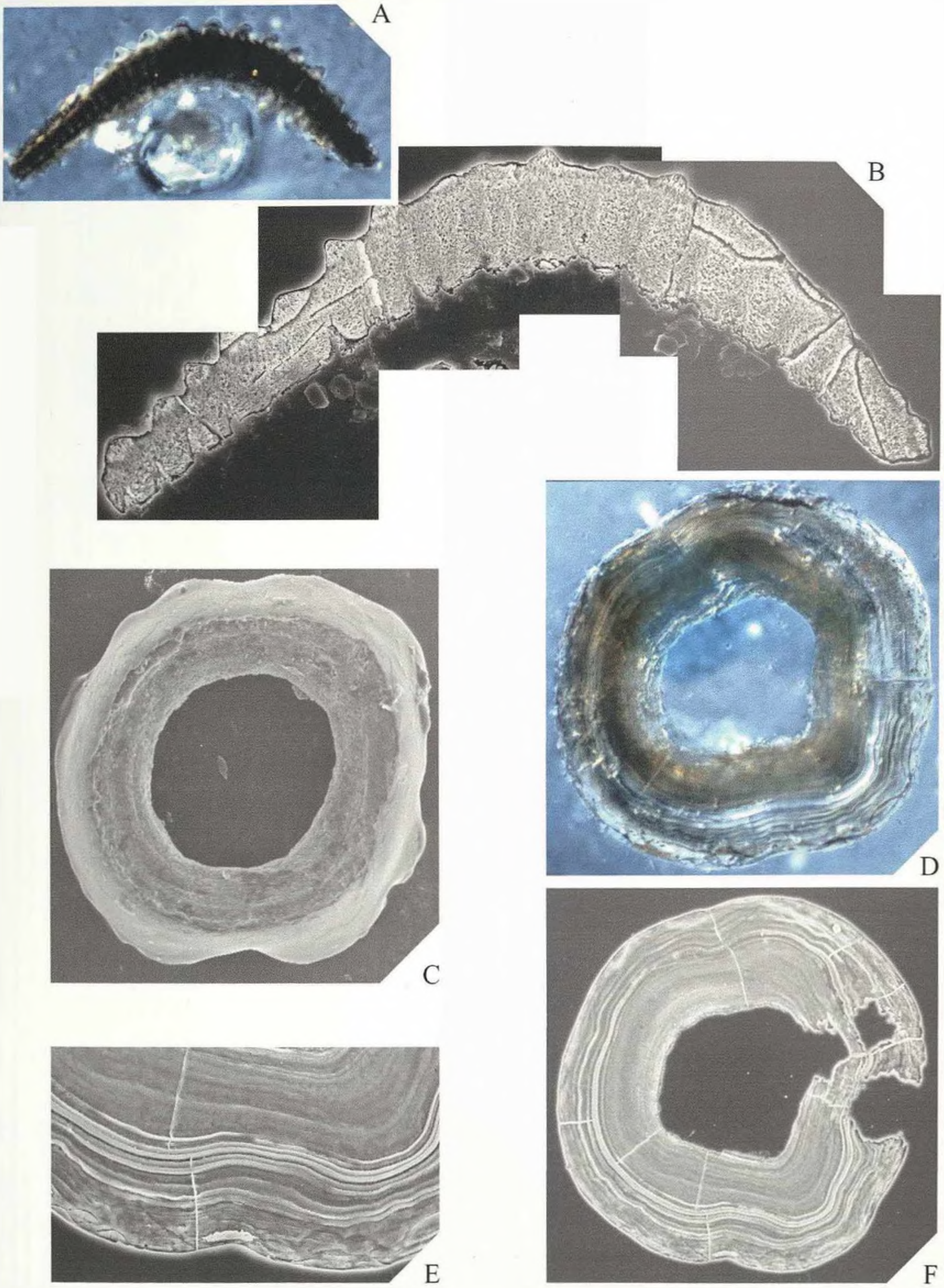
Fig. B. BU2960, composite photograph taken under the SEM, showing zones of coarser and finer crystallites perpendicular to the upper and lower surfaces of the sclerite. These correspond to the light and dark areas visible in transmitted light. No growth increments or other structures are visible; x 330.

Figures C-F. *Phosphannulus universalis* Müller, Nogami and Lenz

Fig. C. BU2961, TC 1155, Threadgill Creek, Texas, SEM image of whole element; x150.

Figs D. F. BU2962, TC 1155, Threadgill Creek, Texas, whole element viewed under the light microscope with Nomarski DIC (D) and under the SEM (F). Concentric growth lamellae clearly visible; D, F, x120.

Fig. E. BU2962, close up view of basal (relative to Figs D ad F) margin of sclerite showing concentric growth lamellae. Individual crystallites have not been resolved; x260.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EXPLANATION OF PLATE 19

Figure A. Bighorn Mountain locality on US Highway 16 where samples WY96-17 and WY96-18 were collected. Steeply dipping beds of the Snowy Range Formation are seen on the roadside cutting to the right of the photograph. Paul Smith for scale.

Figure B. Flat-pebble conglomerate lithology of the Snowy Range Formation in the Bighorn Mountain locality.

A

B