THE FUNCTION, HISTOLOGY AND CLASSIFICATION OF SELECTED PRIONIODONTID CONODONTS

THESIS SUBMITTED FOR THE DEGREE OF DOCTOR OF PHILOSOPHY AT THE UNIVERSITY OF LEICESTER

BY

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By Stephanie Barrett

ABSTRACT

The prioniodontids were the first conodonts to develop a functionally differentiated apparatus. The apparatuses of selected prioniodontid taxa are reconstructed by direct comparisons between elements from disjunct collections and those preserved in natural assemblages of *Promissum pulchrum*. These comparisons and evidence of internal morphology have enabled the recognition of homolgous elements.

Examination of prioniodontid hard tissues has provided a clearer understanding of conodont hard tissues. Polished sections have provided evidence of intergradation between white matter and hyaline tissues confirming their synchronous deposition. Also surface ornamentation is shown to be directly related to internal structure.

Apparatus reconstructions and studies of internal and external wear patterns also reveal new evidence for element function. Elements occluded in a way broadly comparable to those of the ozarkodinid elements (Donoghue and Purnell, 1999a), though interlocking occlusion only occurs in association with a well formed blade. Where a blade is not developed, elements simply worked against each other, wearing down the oral surfaces

Phragmodus inflexus represents the second prioniodontid apparatus preserved as a natural assemblage and its architecture, presented here, differs markedly from that of *Promissum*. This has important implications for prioniodontid apparatus architecture, as the elements of *Phragmodus* are comparable to those typical of many prioniodontids not included within the balognathids. This may suggest that apparatuses of most prioniodontids had an ozarkodinid-like apparatus and that *Promissum* possesses a more derived plan.

This new evidence is important for understanding phylogenetic relationships between prioniodontids. Realistic cladistic studies should be based on clearly understood homologous characters and it is hoped that in the future, cladistic analyses will draw from detailed data, such as those presented here.

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INTRODUCTION

Between the years of 1833 and 1844, Christian Heinrich Pander discovered numerous microscopic tooth-like fossils in the washed residues of Lower Ordovician and Silurian rocks collected from Estonia. Pander named these fossil remains *Conodonten* and speculated that they were the remains of an otherwise unknown group of Palaeozoic fish (Pander, 1856). The group is almost exclusively represented by its microscopic feeding elements that normally became disarticulated and scattered on the ocean floors following the death and decay of the animal which bore them. These preserved elements form a record of the feeding adaptations of this ancient craniate, from its earliest primitive coniform apparatuses through to the functionally differentiated apparatuses, able to grasp, slice and crush food.

Subsequent studies have shown that conodonts were a successful, prolific and diverse group of primarily soft bodied organisms that possessed a phosphatic feeding apparatus; they colonised the oceans from the Late Cambrian to the latest Triassic (see Briggs *et al.* 1983; Aldridge *et al.* 1993). Although the subject of much debate, general consensus to date places the conodonts amongst the earliest vertebrates or craniates (e. g. Sansom *et al.* 1992; Aldridge *et al.*, 1993; Purnell *et al.*, 1995; Janvier, 1996). This is based on detailed evidence that has been revealed following the study of the relatively rare finds of conodont carcasses, preserved on bedding surfaces in association with the elements of the skeletal feeding apparatus (for reviews see Aldridge 1987; Aldridge and Purnell, 1996; Purnell and Donoghue, 1998).

Classification and apparatus structure.

Donoghue *et al.* (2000) have undertaken the most recent cladistic analyses of conodonts to assess the phylogenetic position of conodonts. Apparatus templates and hard tissue histology were reviewed to justify the inclusion of conodonts in such a detailed analysis and to explain the coding of the characters. The analysis included seventeen chordates and considered one hundred and three different morphological, physiological and biochemical characters which were coded for presence/absence and multistate.

The characters included preserved remains of myotomes, a notochord, a differentiated tail with fin radials, eye capsules, possible otic capsules and extrinsic eye muscles. Indirect evidence was also proposed, including characters such as a differentiated brain and a cartilaginous head skeleton. For example the presence of a cartilaginous head skeleton was based on the observation that other fossilised agnathans that possessed cranial cartilages only preserved faint traces of the cranial structures, demonstrating that the preservation of such tissues is subject to much preservational bias (Donoghue *et al.*, 1998). The authors also drew from histological work that analysed the structural tissues of the feeding elements of conodonts (Aldridge *et al.*).

1993; Samson *et al.* 1992, 1994; Donoghue, 1998). Important information of soft tissue ultrastructures was provided by the exceptionally preserved conodont animals found in the Soom Shale of South Africa (Gabbott *et al.*, 1995).

Donoghue *et al.* (2000) experimented with several combinations of the coding including taxon deleting and the use of constraint trees and produced results that consistently placed conodonts within the vertebrates. In all cases but one the results consistently showed that conodonts were more derived than lampreys or hagfish. Therefore, based on the possession of a calcified dermal skeleton, and not the nature of the mineralised hard tissues, conodonts were positioned as basal members of the Gnathostomata showing that the inclusion of conodonts within the Vertebrata remains unrefuted (Donoghue *et al.* 2000).

Early classification systems, limited by the lack of architectural and soft part information, made any true understanding of conodont phylogeny impossible. Although the first conodont bedding plane assemblages were discovered by Schmidt (1934) and Scott (1934, 1942), it was still a gradual process for conodont workers to accept that conodont feeding apparatuses probably comprised several different element morphotypes. Barnes et al. (1979) stated that many conodont workers remained unconvinced of the reality of the assemblages until the description of the Pennsylvanian assemblages described by Rhodes nearly thirty years later (1952). Early conodont research, however, following careful studies of different morphotypes, showed that some elements (previously identified as individual form taxa) represented element pairs (Bryant, 1921; Lane, 1968). It was not until several years later, however, that it was fully accepted that together, several morphotypes comprised the apparatus of one species (e. g. Bergström and Sweet, 1966; Lindström, 1970; Sweet and Bergström, 1972). This realisation forced a movement away from form taxonomy, which had been in use for more than a hundred years. The need for multielement taxonomy was suggested by the constant association of groups of elements that commonly shared the same stratigraphic and geographic ranges, where the occurrence of one morphotype normally meant that representatives of the rest of the group were also invariably present (Sweet and Bergström, 1972). The original single element taxonomy, erected before the conodont skeletal apparatus was more clearly understood, has now been completely replaced with a multielement taxonomy (see Sweet 1988 for overview), even for coniform apparatuses, where the architecture is still, in the main, enigmatic. This taxonomy has now become standard and it is possible to address the phylogenetic relationships between the different conodont taxa from within this multielement context.

With the erection of multielement taxonomy, there became a need for an additional anatomical notation, to differentiate between the different element types of each apparatus and to recognise homologous elements. Earliest attempts included the letter code introduced by Jeppsson (1971), based on a group of closely related Silurian species. Klapper and Murphy (1971) also proposed a notation where the general types of elements in the apparatus were distinguished by individual letter codes. Barnes *et al.* (1979) criticised the notation scheme of Jeppsson (1971) because the letters were derived from the original form taxa but felt that the scheme of Klapper and Murphy (1971) encompassed a broader range of species and was not so closely reliant on the original form genera. Sweet and Schönlaub (1975) departed totally from any reference to the form

genera introducing letters that referred only to the general morphology of individual elements in an attempt to categorise elements that occupied homologous positions. Barnes *et al.* (1979, p. 127) felt that the earlier notational schemes were too "cumbersome and space-consuming" and that the great diversity of forms made it difficult to devise a scheme that could encompass all conodont genera. They came up with five major apparatus types (Types I-V) with seventeen subtypes (e.g. IA-IC) and assigned a new notation code to the element types that comprised them. This was too sophisticated for the type of data conodont workers were considering at the time.

Sweet (1981) reviewed and criticised all of these schemes because they were based on element morphology and failed to distinguish between different element positions. He proposed yet another scheme, based on that of Sweet and Schönlaub (1975), where the emphasis lay with the major element positions in a common type of apparatus and was independent of general element morphology. Sweet named the elements at the posterior of the apparatus Pa and Pb elements, and the array of elements anterior to these the Sa-d elements, with a pair of M elements anterior to these. Sweet (1981) went further to suggest that when properly applied his new notational scheme would not automatically imply that elements were homologous and should be used solely as a "vehicle for analogy". Previously Sweet and Bergström (1972) emphasised the need for caution when trying to understand the relationships between different conodont taxa based on comparative anatomy. For example, they (Sweet and Bergström, 1972, p. 38) suspected that "despite strong skeletal similarities, the Prioniodontacea is an unnatural group within which direct genetic connections never existed".

The scheme of Sweet and Schönlaub (1975; Sweet 1981) was premature, as at that time knowledge of conodont apparatus architecture was almost non-existent (Purnell *et al.*, 2000); therefore it was impossible to utilise the new scheme in the way Sweet intended. This was because there was no independent way of assigning elements to different positions, without relying on the general morphology that characterised elements that occupied particular positions.

The confused history of application of these notational schemes has made it almost impossible to determine clearly homologous elements or even homologous positions - essential information if natural phylogenetic groups are to be identified. Purnell *et al.* (2000) have recognised this and have introduced a revised notational scheme, which is based purely on location, and devised in the light of the current state of conodont research. This anatomical notation is based solely on the topological relationships between elements, with reference to the principle axes of the body. The ozarkodinid apparatus is used as a standard, because it is the apparatus type most clearly understood due to the relatively numerous natural assemblages and large disarticulated collections (see Purnell and Donoghue, 1998). The notation was derived from Sweet's original designation of letters but used numbered subscripts to differentiate between different positions. Sweet's Pa and Pb positions became P₁ and P₂; the Sa-d element array; S₀-S₄ and the M elements retained the same name. This scheme is totally independent from any morphological connotations indicated by tradition or misinterpretation and provides a fresh template with which to classify conodont apparatuses. The authors proposed that the scheme could be applied to all taxa that are known from natural assemblages and to those taxa known only from

collections of disarticulated elements when they can be homologised with elements from natural assemblages. These characters include similar process disposition or morphologies, basal body morphologies and modes of denticulation. If clear homologies cannot be recognised between elements from disarticulated collections and those from natural assemblages, then Sweet's original notation can be applied. This would serve to distinguish between elements with clear homologues (that would be identified using the Purnell *et al.* 2000, scheme) from those whose homologies are unknown or uncertain (that would be identified using the scheme proposed by Sweet, 1981).

The Conodonta is currently divided into seven different orders (Sweet, 1988; Aldridge and Smith, 1993) of which three are characterised by having elements of complex morphology within their apparatuses. The three orders are the prioniodontida, the ozarkodinida and the prioniodinida. Because it is commonly accepted that the Ozarkodinids and the Prioniodinids are derived from Prioniodontid stock, Donoghue *et al.* (2000, p. 4, fig. 2) recently proposed a reinterpretation of Sweet's (1988) proposed relationships by subsuming the Ozarkodinida and the Prioniodontida.

According to Sweet (1988, p. 89) the basic skeletal components of ozarkodinid apparatuses comprise an array of S elements, a pair of M elements and P positions filled by carminate or angulate pectiniform elements or their platformed equivalents. The prioniodinids are also classified according to the morphology of their P elements, with an array of S elements and a pair of M elements; the P positions in this case are occupied by distinctive extensiform digyrate elements (Sweet, 1988, p. 78). The prioniodontids comprise the most problematic taxa. Sweet (1988, p. 59-60) states that P element positions of the Prioniodontida are occupied by pastinate coniform or pectiniform elements, or by "elements that are formally carminate or angulate but can be shown (or reasonably inferred) to have arisen through ontogenetic or phylogenetic modification of pastinate elements". Dzik (1991) advocated the classification of Sweet (1988), but remodified the classification of the taxa characterised by simple cones and interpreted the interrelationships between the ozarkodinid, prioniodinid and prioniodontid families. This resulted in four main orders, of which two, the prioniodontids and the ozarkodinids, were characterised by having an apparatus of complex feeding elements.

Most bedding plane assemblages known belong to the ozarkodinids and have provided the basis on which most other conodont apparatuses have been reconstructed (Aldridge, 1987). Purnell and Donoghue (1997) have provided a succinct report addressing the architecture and functional morphology of the skeletal apparatus of the ozarkodinids. Analysis of all the natural assemblages of *Idiognathodus* from the Pennsylvanian of Illinois allowed the authors to construct a precise scale model of the feeding apparatus. The positions of the elements were ascertained using a combination of physical modelling and photographic techniques; an approach pioneered by Briggs and Williams (1981) and subsequently used by Aldridge *et al.* (1987, 1995). The apparatus comprised "an axial Sa element, flanked by two groups of four close-set elongate Sb and Sc elements which were inclined obliquely inwards and forwards; above these elements lay a pair of arched and inward pointing M elements. Behind the S-M array lay transversely orientated and bilaterally opposed Pb and Pa elements" (Purnell and Donoghue, 1997. p. 1545). Using the new scheme proposed by Purnell *et al.*

(2000), the element notation is changed to: an axial S_0 element, flanked by two groups of four close-set elongate S_1 to S_4 elements which were inclined obliquely inwards and forwards; above these elements lay a pair of arched and inward pointing M elements. Behind the S-M array lay transversely orientated and bilaterally opposed P_2 and P_1 elements.

The ozarkodinid apparatus plan is also shared by the prioniodinids, as shown by Purnell and von Bitter (1996), with two pairs of P elements at the caudal end of the apparatus, behind an array of S elements and a pair of M elements.

As with the apparatus studies, most studies of element function have concentrated on the ozarkodinid apparatus, due to the abundance of material and the clear understanding of the apparatus (Purnell and von Bitter, 1992; Purnell, 1995). It has been possible to study discrete elements for recurring evidence of wear on the element surfaces and damage to the internal structures, from which methods of function can be inferred (Donoghue and Purnell, 1999a and b). It has also been possible to 'lift' elements from natural assemblages thereby being certain that real life element pairs are being studied (Donoghue and Purnell, 1999a). These studies have shown that the ozarkodinid P elements "crushed food by rotational closure, which brought the oral surfaces into complex interpenetrative occlusion" (Donoghue and Purnell, 1999a, p. 58).

Until recently the ozarkodinid plan was the only template known; however, in 1986 the first prioniodontid natural assemblage was discovered in South Africa (Theron *et al.*, 1990). The assemblages are preserved because clay minerals have replaced the mineralised hard parts of the feeding apparatus; in many cases, the eye capsules and some of the musculature has also been replaced and preserved with exquisite resolution (Gabbott *et al.*, 1995; Gabbott, 1998). Many other natural assemblages have been found at this location since the first find, numbering over 500 (Aldridge, 2000, pers com); however, they all belong to the same prioniodontid species: *Promissum pulchrum* Kovács-Endrödy a prioniodontid belonging to the balognathid family. Reconstructing the apparatus of *Promissum* has raised a number of important issues (Aldridge *et al.*, 1995). The apparatus comprises a pair of M elements at the rostral end, an array of nine S_{0-4} elements and above these four pairs of opposing P elements P_1 - P_4 The architecture of this South African condont has been closely analysed and modelled, and although it is possible to recognise characters that are homologous to the ozarkodinid architecture, a number of major differences are also obvious:

• The apparatus is larger than any other conodont apparatus discovered to date; whether in discrete collections or in natural assemblages.

• The apparatus possesses four pairs of P elements in comparison to the two pairs of the ozarkodinids: in *Promissum* these are positioned above the S element array instead of behind the S elements.

• The S elements appear to exhibit two main positions architecturally, possibly implying two functional positions.

It is apparent that the apparatus plan of *Promissum*, one of the only prioniodontids represented by natural assemblages, was not the same as that of the ozarkodinids.

There is now a second prioniodontid apparatus known, provided by the recently discovered, well preserved natural assemblages of *Phragmodus*, an Upper Ordovician prioniodontid (Repetski, 1997). The multielement composition of this apparatus has been uncontroversial since the 1960's, when element associations and similarities in morphology, microstructure and histology provided evidence for apparatus reconstruction (e. g. Sweet and Bergström, 1966). The architecture of *Phragmodus* can now be shown to be clearly similar to that of the ozarkodinids, confirming the historical reconstructions.

It the light of this new prioniodontid natural assemblage, it is even more uncertain which prioniodontid taxa share the ozarkodinid apparatus architecture and which possess an apparatus like *Promissum*. It is possible that *Promissum* was a very derived conodont, and that the rest of the taxa within the prioniodontids were more conservative, following the ozarkodinid skeletal plan (Purnell *et al.*, 2000). Aldridge *et al.*, (1995, p. 288) commented on this and stated that "rigorous re-examination of well preserved collections of prioniodontids is now required to test the applicability of the *Promissum* blueprint".

Development of functional studies. Prioniodontid elements have not featured in many functional studies to date. Jeppsson (1979) included drawings of elements of Amorphognathus ordovicicus to demonstrate the striking similarities between conodont elements and teeth. Jeppsson (1979a) made detailed observations of the asymmetry displayed by sp and oz elements (P_1 and P_2) including examples of *Icriodella* platform elements. He reconstructed possible occlusal models for pairs of P_1 elements based on morphological optimality. Simple line drawings were used, but the dimensions of the platform troughs were hypothetical, as he relied on two dimensional drawings copied from Lindström (1964).

Nicoll (1995) provided a functional interpretation for conodonts, using some prioniodontid examples to argue his case. Nicoll believed that S and M conodont elements were analogous to the buccal tentacles of amphioxus. The Pa and Pb elements were thought to be analogues of the wheel organ or the velar tentacles. He postulated that all of the elements were covered with soft tissue with the S and M elements performing a food gathering, not grasping, function and the function of the Pa and Pb elements was thought to be variable according to the type of prey. Nicoll's conclusions are based on a hypothesis of analogy, with the P elements preventing entry of large particles of food into the back of the buccal cavity and the pharynx, in a way directly analogous to the buccal cirri of *Branchiostoma*. This is in direct contradiction to the functional interpretation of P elements proposed by Purnell and von Bitter (1992), who proposed that the carminate Pa elements. Nicoll discounted this hypothesis because his reconstructed pair of Pa elements, selected from disarticulated specimens of the prioniodontid *Oepikodus*, could not have occluded directly against each other in such a way. The fact that the P elements of *Oepikodus* possess a different morphology from those

of Vogelgnathus, suggests that they had a different function, not that the elements of Vogelgnathus did not function against each other to cut food particles. The hypothesis of function proposed by Purnell and von Bitter (1992) is, however, also based on morphological optimality and, in that way, is comparable to the work of Nicoll (1995) even though the conclusions contrast.

The relatively new knowledge of the prioniodontid apparatus provided by the natural assemblages of Promissum raises a number of interesting functional implications (Aldridge et al., 1995). Prior to the discovery of Promissum evidence of apparatus location came from the ozarkodinid natural assemblages found in Scotland (Briggs et al., 1983; Aldridge et al., 1993). Traces of soft body parts indicated that the apparatus of ozarkodinids lay ventral and posterior to the eyes, presumably within an oral cavity. Similar evidence found in the natural assemblages of Promissum have shown (Aldridge and Theron, 1993; Gabbott et al., 1995) that the position of the prioniodontid apparatus was comparable. Because the P elements of Promissum lay above and not caudal to the S elements, the apparatus could not have worked in exactly the same way as the ozarkodinids (Aldridge et al., 1995). The arrangement of elements within the ozarkodinid apparatus probably demonstrates some form of functional differentiation, which is also mirrored by the grouping of elements with broadly comparable morphologies. It is possible that the P element architecture imposes few operative constraints, whereas the more compact arrangement of elements within the apparatus of Promissum calls for a more complicated mode of function. However, the elements of Promissum still show a grouping of different morphologies with the S and M elements being ramiform, elongate and denticulated and the P elements being more robust with shorter processes. It is likely that this represents a division of functions (Aldridge et al. 1995) analogous to those of the ozarkodinids.

The most recent papers addressing ozarkodinid element function (Purnell, 1995; Purnell and Donoghue, 1997; Donoghue and Purnell, 1999a and b) have identified several important investigative techniques that shed light on the function of all conodont elements. These techniques include evidence of internal discontinuities, surface damage and microwear and have not relied on assumptions or morphological optimality or preconceived functional hypotheses. These techniques have been rigorously applied to elements of ozarkodinids, but, the analysis of prioniodontid elements remains open to investigation.

THESIS OBJECTIVES.

The original objective of my thesis was to investigate the relationships between feeding adaptations and evolutionary patterns throughout the Ordovician diversification of the prioniodontid conodonts. The prioniodontids are an important group as they were among the first conodonts to develop morphologically complex and functionally differentiated apparatuses, long before the more derived ozarkodinids. Studies of apparatus architecture, element histology and function, were intended to investigate the evolutionary relationships within the group. The resulting thesis, has concentrated on apparatus structure, element histology and element function of a few selected prioniodontids.

Conventional terminology based on a modification of that first presented by Sweet (1981, 1988) has been retained for the elements within the apparatus reconstruction chapters (Chapters 1.1, 2.1, 3.1, 4.1) to emphasise the difference between elements from natural assemblages and those being reconstructed from disjunct collections.

Conventionally identification of processes relies on locating where the process joins the cusp (Clark, 1981), i. e. where a process erupts off of the 'anterior' face of the cusp, it is termed 'anterior' etc. Within elements of *Baltoniodus* the 'posterior' process is always easy to identify, as it is aligned with the concave margin of the cusp, but the 'lateral' and 'anterior' processes often appear to both erupted from the anterior face of the cusp. Sectioning at the apex of the basal body reveals the true identity of each process, as the 'lateral' process has a clear junction with the main axis that is formed by the 'anterior' and 'posterior' processes during the early juvenile stages of growth. Where the identification of processes of elements belonging to other taxa is problematic, the internal structure is consulted to differentiate between the main axis of the element, and the identification of the attached 'lateral' process. This sometimes means that the original point of eruption of the 'lateral' and 'anterior' processes is not expressed externally; however, the terminology is retained. This is to ensure that homologous processes are identified and compared especially where the diverse morphologies of some elements may obscure the true homologous processes.

Elements from natural assemblages are referred to using the new topological terminology proposed by Purnell *et al.* (2000). Subsequent chapters incorporate the new terminology (Purnell *et al.*, 2000), inferred by these apparatus reconstructions. Element notation therefore refers to the biological location of processes and the conventional 'posterior' and 'anterior' are replaced by dorsal and ventral respectively and the 'lateral' term is replaced by caudal. Element locational terms replace the conventional ones, where homologies with elements from natural assemblages can be ascertained and new topological terms applied.

This study is based primarily on material from the reference collection of the micropalaeontology unit, University of Leicester Geology Department.

HISTORICAL REVIEW OF STUDIES OF THE INTERNAL STRUCTURE OF PRIONIODONTID CONODONTS PRIOR TO 1998.

The first illustrations of the internal structure of prioniodontid conodont elements were presented in Pander's famous publication of 1856, where the basal cavities of elements of *Oistodus* Pander and *Prioniodus* Pander were discussed and described. Pander also discussed the internal tissue of conodont elements, recognising lamellar crown tissue and identifying opaque and translucent tissues within this. The presence of opaque tissues was considered to be such an important taxonomic character that Pander used it to distinguish between two main groups of conodonts: those with 'obliquely layered teeth' and those with 'lamellar teeth' (as translated from the German by Hass, 1941).

Since 1856 palaeontologists have gradually built up a clearer picture of the structure of conodont elements. Their work has not concentrated on any one group, but taxa presently accommodated within the prioniodontids have appeared sporadically in many of the major papers.

Branson and Mehl (1933a) also used histology as a taxonomic character to distinguish between different types of conodont found in the Harding Sandstone Formation (Upper Ordovician). A distinct group of conodonts was identified as the 'fibrous conodonts' (Branson and Mehl, 1933a, p. 22). Elements of fibrous conodonts were generally robust and when fractured, tended to produce a 'lengthways' break, aligned with the long axis of the element, resulting in a fibrous appearance. The remaining conodonts possessed a lamellar structure and many had areas of opaque tissue within the denticles and cusps. A subgroup within the lamellar conodonts was the hyaline conodonts, whose elements shared the general morphology of the lamellar conodonts, but possessed no opaque areas. Many of the species that Branson and Mehl (1933a) classified as fibrous conodonts described: "Dichognathus prima" Branson and Mehl, (part of the Phragmodus apparatus, see Clark in Robison, 1981) and "Trichognathus prima" (part of the Plectodina apparatus, according to Clark in Robison, 1981). Branson and Mehl (1933a) classified elements of *Phragmodus* and *Plectodina* amongst the conodonts in which the 'fibrous structure' was not present.

Hass (1941, pl. 13, fig. 6) used a prioniodontiform element of *Prioniodus* to show how some areas within conodont elements were opaque and some translucent. The opaque areas in the cusp and the denticles showed the same characteristic tissue type as Pander's (1856) 'obliquely layered teeth' and the opaque tissues of the lamellar conodonts described by Branson and Mehl (1933). Hass (1941, p. 78) described tubules and cellular structures within the opaque areas and observed that the tissue had a "cellular or cancellate structure", stating that "a denticle often had several areas of cancellation along its length, between each of which a distinct laminated cone-in-cone structure is visible". This suggested to Hass that the characteristic laminar structure of the conodont element was still present during the formation of the opaque areas.

Beckmann (1949) presented a study of the ultrastructure of weathered conodont elements and used rough line drawings to show his interpretations of the conodont elements which included the prioniodontid *lcriodus* Branson and Mehl 1938. Beckmann followed Pander (1856) in his conclusion that conodont elements grew by inner apposition (Müller *in* Robison, 1981). He homologised conodont elements directly with teeth and identified 'pulp cavities' and 'dentine tubules' amongst the element structures. The line drawing of *lcriodus* clearly shows a single apex to the basal cavity, although the poor quality of the material on which the drawing is based renders it unreliable (Beckmann 1949, taf. 2, fig. 3).

Lindström (1964) produced a comprehensive book reviewing previous work and assessing the issues current at that time in conodont research. *Oistodus* elements were mentioned (although not figured) as an example of differential growth rates within one element and possible mechanisms for the different rates were discussed. These included the intercalation of additional lamellae at the "fastest growing points", thickening of individual lamellae, or spaces being left between successive lamellae. A drawing of a section through the distal end of the anterior process of an *lcriodus* element clearly shows spaces between lamellae (Lindström, 1964 p. 16, fig. 3D). Lindström named the tissues forming the white and opaque areas of elements (previously identified by Pander 1856, Branson and Mehl 1933a and Hass 1941) as 'white matter' although he did not discuss prioniodontids specifically. White matter was described in detail and it was noted that the tissue contained numerous 'cellules' that were frequently branched and crowded, though Lindström doubted the presence of tubules. He concluded that the white matter tissue was probably formed by the resorption of lamellar tissue. The structure and tissue of white matter had received limited attention up till 1964 and Lindström felt that his own ideas and those of previous authors still warranted further testing.

Schwab (1965) examined sections of "Zygognathus" Branson et al. ("Zygognathus" is now reconstructed as an element of *Plectodina* Stauffer 1935 [see Clark *in* Robison 1981]) and found that the basal tissues appeared to be "bone like" with areas of cell-like structures and folded distorted remnants of lamellae. The sections did not reveal a large amount of detail, although they did support the author's suggestion that the elements were composed of two major units; an 'outer laminated layer', and a 'non laminated inner lining' (Schwab, 1965, p. 592)

Barnes et al. (1970) produced a detailed study of the inner structures of fibrous and lamellar conodonts, paying particular attention to structures that could be used to characterise the individual groups. The authors studied elements of *Drepanodus homocurvatus* Lindström and *Belodina compressa* (Branson and Mehl) to represent the lamellar conodonts and "*Polycaulodus bidentatus*" Branson and Mehl and "*Ptiloconus gracilis*" (Branson and Mehl) to represent the fibrous conodonts. "*P. gracilis*" was classified within the Multioistodontidae Bergström, as a part of the apparatus of *Erismodus* Branson and Mehl by Clark *in* Robison (1981); *Erismodus* is, however, currently classified as a prioniodinid (Sweet, 1988). Barnes *et al.* (1970) described the microscopic textures that characterised the fibrous conodonts, noting that the crystallites were elongate, poorly fused and of varied dimensions. They also noted that in the sections studied (Barnes *et al.*, 1970, p. 19, Plate VIII, Fig. 5a) the crystallites were orientated with their long (c) axes parallel with the growth axis

of the denticle or cusp. This was in contrast to the flaky, loose, porous structure of the crystallites within elements of lamellar conodonts for which no generalised orientation could be ascertained (Barnes *et al.*, 1970, p. 20, Plate IX, figs 1-3). These crystallite orientations contrasted with the observations of Hass (1941) and Lindström (1964) who both described crystallites with their long (c) axes perpendicular to interlamellar spaces. Pietzner *et al.* (1968) broadened these observations by noting that the crystallites within the conodont elements that the authors studied were oblique to interlamellar spaces; however Pietzner *et al.* (1968) noted that this might be the result of disruption due to preparation techniques. Barnes *et al.* (1970, p. 16) demonstrated that sections through the apices of denticles and cusps of elements of "*P. gracilis*" provided some lamellar resolution, but showed the crystallites more clearly towards the "outer part of the denticle or cusp than the inner core".

Barnes et al. (1970, p. 2) concluded that to classify different conodonts an "important approach would be to find important differences of internal structure and growth patterns". They managed to distinguish between three forms of conodont: fibrous conodonts, hyaline lamellar conodonts and lamellar conodonts. Though preliminary, the work of Barnes et al. (1970) went some way to show how this could be done, taking advantage of the relatively new advances of scanning electron microscopes and more sophisticated sectioning and polishing techniques.

Müller and Nogami (1971) sectioned elements of *Plectodina*. The authors identified a number of different kinds of white matter within the conodont elements; these are elaborated below. A section of a coniform element of *lcriodus* was also included and revealed a clear kink at the apex of the cusp. Müller and Nogami (1971) suggested that this was due to breakage and repair of the cusp tip during life. This section does not exhibit very good resolution, especially around the apex of the cusp, so it is not clear how the laminations are behaving around the break, which limits assessment of the nature of the apparent repair. Müller and Nogami (1971) concluded their study by providing a detailed review of conodont internal microstructures and textures and concluded that there was no taxonomically significant character to separate the fibrous conodonts of Branson and Mehl (1933a) from the lamellar conodonts.

Müller and Nogami (1972) readdressed the histology of conodont elements, considering all of the major conodont groups. The authors claimed that almost all conodonts contained white matter and identified three main types of structure found within white matter tissue:

- Interlamellar spaces were observed along the main growth axis as funnel shaped cavities. The authors noted that these funnel shaped cavities were often infilled by white matter.
- Peglike bubble structures in the centre of denticles were identified as suppressed denticles and not 'germ denticles' as they had been termed in early conodont terminology. Müller and Nogami (1972) noted that there appeared to be an intergradation between the lamellar tissue and the white matter within the peglike structures. Elliptical bubbles were apparent in growth laminations around the outer limit of the white

matter and towards the centre the abundance of bubbles increased so much that the lamellar boundaries disappeared.

• A third kind of white matter structure was identified as layers of bubbles cutting across growth laminations. The bands formed perpendicular swathes across the growth lamellae and also formed a variety of cone and M-shaped structures within the lamellar tissue [it seems likely that these are regions of the elements that exhibit a change in the crystallite orientation within the hyaline laminations and do not represent true white matter, with cellular and cancellate textures (see Donoghue, 1998)].

Müller and Nogami (1972, p. 26-27, fig. 9) also looked carefully at well preserved growth lamellae within conodont elements and described what they identified as 'resorption surfaces'. They thought that these surfaces represented resorption of phosphate material; in one specimen as many as three different resorption horizons were identified which accounted for as many as thirty-five laminations being resorbed. The resorption surfaces were always followed by regeneration with abnormally wide laminations, which contrasted with the very thin laminations immediately before the resorption surface.

Müller and Nogami (1972, p. 27) concluded that conodonts served as an "organ for temporary deposition of a phosphate substance, which might later be utilised to form another conodont element in the same animal or possibly be available to the animal in time of other needs."

Lindström et al. (1972) produced the only paper dedicated solely to the microstructure of prioniodontid conodont elements, although only external features of the elements were discussed. The authors included elements of Gothodus (now interpreted as an M element of Baltoniodus Bergström), Prioniodus n. sp. aff., Prioniodus evae Lindström, and three different species of Baltoniodus. The occurrence and nature of ropy surface microstructures on different kinds of element were observed and measured; in particular, an element of Gothodus had some exceptionally well preserved ropy ornament. The authors also described the occurrence of reticulate patterning on the flanks of the elements and described how the ropes anastomosed to form this reticulate ornamentation. It was noted that crystallites of each element were orientated with their crystal faces, the long (c) axes, parallel to the long axis of the element. This orientation of crystallites became confused around the basal margin of some elements and where denticles had become fused together (the latter change was attributed to independent growth axes within the two different denticles). Apical 'dental pits' were figured on the "trailing edge of the first proximal denticle" (Lindström et al. 1972, p. 33), of the 'prioniodontiform' element of Baltoniodus n. sp. A. These were identified as muscle attachment pits and the structure was interpreted as the first evolutionary stage of later platform ornamentation. Because of this the authors suggested that the P elements of Baltoniodus n. sp. A were homologous with the P elements of Icriodus Branson and Mehl, which has similar structures on its P element platforms.

Barnes et al. (1973) readdressed the internal structures of some Ordovician conodont elements to assess the main structural differences between the 'fibrous' forms (Branson and Mehl 1933a), hyaline forms and

cancellate forms (Hass 1941). The authors adopted the term 'neurodont' to replace 'fibrous', following Branson and Mehl (1933a). Prioniodontids were included within the hyaline and cancellate groups but not within the neurodonts. *Erismodus* and *Ptiloconus* (both part of the *Erismodus* apparatus) were chosen to represent the neurodonts. *Oistodus* represented the hyaline conodonts, and *Ambalodus* Branson and Mehl (now considered an element in the apparatus of *Amorphognathus*, see Clark *in* Robison, 1981), "*Dichognathus* Branson and Mehl" (now considered part of the apparatus of *Phragmodus*, see Clark *in* Robison, 1981) and "*Trichonodella* Branson, Mehl and Branson" (considered part of the apparatus of *Plectodina* Stauffer, Clark *in* Robison, 1981) were included with the cancellate forms.

Barnes et al. (1973) found the crystallites of neurodonts to be poorly fused together and needle-like. Growth canals and a structure called a septum were identified axially in specimens of Erismodus but were less well defined in the section of "Ptiloconus". Hyaline conodont elements were found to be constructed of fused laminae, composed of partly fused crystallites; the structure of this crown tissue is therefore much more compact than and distinct from the internal texture of neurodont elements. Barnes et al. (1973) found no evidence of septa in the hyaline conodonts that they sectioned although growth canals were identified. The cancellate conodonts sectioned showed an expansive growth canal system. This structure was observed axially in the lower half of the denticles and was also seen as a horizontal structure beneath the denticles within the process. The growth canal system and details of the micro-ornament of white matter were the features concentrated on by the authors and considered the most important characters to distinguish the cancellate conodonts from the neurodonts and the hyaline conodonts. "Ambalodus" sections revealed minute spheres which rarely appeared to be loosely occupying holes (Barnes et al., 1973, fig. 8-13). The boundary between the white matter and the lamellar tissue was not considered to be sharp and the authors identified what they called 'incipient white matter' zones surrounding the white matter areas (Barnes et al., 1973, p. 15, figs. 7-12.7-13). The presence of incipient white matter was used to support the theory that white matter represented secondarily altered lamellar tissue. The structures identified as growth canals are in fact two different things. The cavities seen underneath processes are the upper region of the basal body which is broader and more conspicuous if sectioned lower down in the element. The 'growth canals' identified at the bases of the denticles are aligned growth cavities which develop between individual laminae during the initial development of the denticle. "Zygognathus" is figured as an example showing these (Barnes et al., 1973, fig 7-11). Because of the growth cavities between each successive lamella along this axis, they are more likely to break down when the sections are etched forming an elongate canal-like structure.

Sections of *lcriodus* showed the arrangement of the lamellae, pits on the surfaces of the denticles and biapical basal bodies (Lindström 1964, p. 16, fig. 3D). Nicoll (1991) figured elements of *Cordylodus* Pander 1956 with basal apices apparent in the cusp and within the base of the 'posterior process' denticle most proximal to the cusp. The elements are sufficiently thin to allow light to pass through them and the apices are clearly visible. This character was used by Nicoll to differentiate between species of *Cordylodus*. The biapical basal body shown by Lindström might also be an important characteristic for homologising elements with common growth strategies and hence recognising different taxonomic groups. It is, however, difficult to

resolve exactly which region of the *lcriodus* element has been sectioned. Also Lindström's figures contrast with those of Beckmann (1949) whose section of an element of *lcriodus* showed only one basal cavity.

RECENT PROGRESS IN STUDIES OF CONODONT ULTRASTRUCTURE.

Sansom *et al.* (1992) examined the histology of elements of conodonts from the Harding Sandstone Formation, Colorado (Ordovician) and compared them to vertebrate remains found in the same collection. White matter was found in all of the elements examined and the presence of lacunate spaces and interconnected tubules led the authors to homologise it with Recent and fossil cellular bone. The lamellar tissue found in the elements examined was categorised into two main tissue types; lamellae composed of crystallites orientated with their long (c) axes perpendicular to the lamellae surfaces, which was homologised with enamel and lamellae composed of crystallites orientated with their long (c) axes perpendicular to the lamellae surfaces, which was homologised at the lamellae surfaces, which was considered to be enigmatic, but probably related to enamel. The scalloped lamellae found within the basal body of all elements was considered to be so comparable to structures within calcified cartilage that Sansom *et al.* (1992) considered it likely that basal tissues represented a closely related tissue type. At this stage Sansom *et al.* (1992) did not find any tissues that were homologous to dentine.

In 1994 Sansom *et al.* published a short paper that described the basal body of *Chirognathus* Branson and Mehl, a conodont that possessed no white matter. On examining the basal body the authors found scalloped lamellae and tubule structures that they identified as structures characteristic of dentine. Elements of *Neocoleodus* Branson and Mehl were also examined and were found to contain only branching tubules. Both of these tissues were identified as dentine and the diversity between the two types was explained as experimentation during the early stages of vertebrate biomineralisation. Lamellar crown and basal body tissues found in elements of *Pseudooneotodus* Drygant, a Devonian conodont found in the Pernäs Limestone, Sweden were also homologised with enamel and dentine respectively (Sansom, 1996). The lamellar tissue seen in figure 3a (Sansom, 1996, p. 52) appears to be indistinguishable from the enamel of human teeth.

Although the work of Sansom *et al.* (1992; 1994) and Sansom (1996) did not consider elements belonging to prioniodontid conodonts, the interpretation of the crown and basal tissues have important implications for future work considering the histology of prioniodontid conodont elements.

It is useful to review the work of Donoghue (1998), as he has provided one of the most comprehensive review and study of conodont element histology. Although Donoghue did not concentrated on any one order of conodonts, prioniodontids are included within the study, and it is apparent the prioniodontids share several histological homologies with representatives of other conodont orders.

Donoghue (1998) studied the internal structure elements of selected conodonts including prioniodinids, prioniodontids and ozarkodinids and was able to describe two basic units: the crown and the underlying basal body. He described the basal body as being composed of a hard crystalline tissue, called basal tissue, and the

crown as composed either purely of hyaline lamellar tissue or of hyaline lamellar tissue with inclusions of white matter.

Donoghue observed that lamellae are composed of coarse crystallites, normally a few microns long bounded at either end by punctuated growth lines. The crystallites in Donoghue's prepared specimens are often orientated with their long axis perpendicular to the outer surface, although this orientation was variable in elements with complex morphologies.

Donoghue (1998) considered white matter to be more finely grained than lamellar crown tissue, lower in organic content and generally lacking in lamellar increments. White matter occurs exclusively in denticle cores and cusps and has sharply defined margins. Donoghue noted that this tissue is riddled with microcavities, including tubular and irregular cell-shaped cavities that he interpreted as possible sites of mineral secreting cells. The cell-shaped cavities are rarer than the tubules and normally occur at the oral end of interconnected tubules. Donoghue thought that the boundaries of white matter and lamellar tissue are imperceptible in transmitted light but distinct when etched sections are studied. Donoghue (1998, p. 642, fig. 4e-g) sectioned elements of *Cordylodus* to illustrate that not all albid areas of conodonts represent white matter and that many of the regions identified as white matter by Müller and Nogami (1971) and Müller (1981, *in* Clark) are, in fact, different forms of lamellar tissue.

Donoghue's work showed that basal tissue is finely crystalline, with each successive layer of tissue completely encapsulating the previous older layer. Donoghue noted that basal tissue is the most variable tissue of all, sometimes showing extreme variability between different taxa. There may even be variability within taxa; for example, *Cordylodus* has basal tissue structures varying from spheroids to lamellae. Donoghue stated that, basal bodies of conodonts are most commonly atubular; this is especially true of the ozarkodinids, which have concentric growth increments equivalent to the growth lamellae of the crown. He noted that basal tissue lamellae are rarely perfectly concentric and are often disrupted or disturbed by microcalcospheres. Donoghue postulated that the intergradations of different forms of basal tissue structure within one taxon indicated that all the structures are common to one tissue type and that it is possible that the form taken by the tissue is dependent on the amount of time taken to grow it.

Donoghue's (1998) observations of damage to lamellae and subsequent repair by overlying lamellae confirmed previous interpretations (Müller and Nogami, 1971; Purnell, 1995; Donoghue and Purnell, 1999a, 1999b) that conodonts grew by outer apposition. Donoghue (1998, p. 640, fig. 3j) has shown that the crystallites are perpendicular to the lamellar surface immediately adjacent to the basal body/lamellar crown junction indicating that the two components must have grown in opposing directions, away from the junction (cf. Sansom, 1996). Donoghue (1998, p. 646, fig. 7g, i, k-m) figured elements of ozarkodinids with planar margins between white matter and lamellar tissue, and elements with stepped margins between the two tissues (1998, p. 644, fig. 5i, j, k); in both cases the lamellar increments pass from hyaline tissue to albid tissue without any obvious boundary. This pattern suggests that these two different tissue types grew

synchronously. Donoghue noted that the length of tubules within the white matter greatly exceeds the thickness of individual hyaline lamellae and indicated that the growth of white matter was more continuous than that of the encapsulating lamellar crown. He postulated that the white matter grew by outer apposition like the lamellar increments. Donoghue (1998) also suggested that the position of the cell-shaped cavities indicated that the secreting cells migrated orally ahead of the mineralised front, resulting in just the cell processes (tubules) remaining preserved within the matrix of the white matter. Donoghue (1998, p. 645) noted that "the polarisation of the shorter, perpendicular tubules and attached cavities indicated that they grew away from their junction with the lamellar crown tissue". This indicated to Donoghue that there was a strong contrast between the growth directions of white matter tissue and lamellar tissue and he concluded that the secretion of white matter and lamellar tissue were independently controlled.

Internal sections through conodont elements have shown that much of the element surface is worn down and lost during function (Müller, 1981, p. W35, fig. 28). Bearing this in mind, it is curious that there does not appear to be a surface ornament that coincides with the white matter cores, that differs from surface ornament occurring elsewhere on the element as a result of having lost the outermost layers of lamellar crown.

Donoghue (1998) divided the modes of ramiform morphogenesis into four different types. Type I ramiforms are composed of numerous, effectively isolated denticles. The main evidence was drawn from the bedding plane assemblages of *Promissum pulchrum* Kovács-Endrödy, a balognathid prioniodontid, that have been preserved within the Soom Shale, South Africa, as clay minerals (Gabbott, 1998). Ramiform elements of this conodont appear to consist of denticles which are only united by a single underlying structure which is neither lamellar crown nor basal body (Donoghue, 1998, p. 646, fig. 71-d). Even though some of the processes of these ramiform elements appear to support tri-denticulate units (where each unit appears to have a large denticle, with two or more smaller denticles either side), a basal cavity has been identified for each denticle this indicated to Donoghue (1998) that each denticle grew independently from the rest. The denticles most proximal to the cusp have become incorporated and fused to the main element. Nicoll (1982) similarly interpreted coniform elements in fused clusters of *Icriodus* as component denticles of multidenticulate S elements. Van den Boogaard (1990) and Miller and Aldridge (1993) arrived at similar conclusions for elements of *Coryssognathus*.

Type II ramiform morphogenesis is primarily based on the ramiform elements of *Carniodus*, which have compound units of denticles (rather than individual denticles as in type I). Each unit has its own single basal body, for three or four denticles. Denticle growth and addition within the compound units is typical of type III growth (see below). Like type I morphogenesis, the denticle units then become fused to the main cusp and element as successive layers of lamellae slowly envelop the new units. According to Donoghue, type II growth is typical of *Amorphognathus*, *Prioniodus* and *Microzarkodina*.

Donoghue's (1998) type III ramiform morphogenesis produces an element where each denticle is composed of white matter surrounded by a small amount of lamellar tissue; this type is characteristic of the ozarkodinids

and the prioniodinids. In this form of element genesis the processes are developed by adding denticles to the distal end of the existing process, instead of incorporating independent units as is the case for types I and II. Donoghue (1998) observed that the first stage of growth could be seen in a small disturbance in the lamellae at the distal end of the process. The lamellae gradually contort, becoming separated by small cavities stacked one above the other, to start forming the morphology of a new denticle. The denticles are normally slightly inclined away from the cusp. Once denticle growth has been initiated by a few layers of lamellae, a white matter core gradually develops as the denticle increases in size. Elements of *Plectodina* were included by Donoghue (1998) within this category; *Plectodina* is considered by Sweet (1988) to be a prioniodontid and the ancestor of the ozarkodinids.

Type IV ramiform morphogenesis is similar to type III, but has a more complicated morphogenetic pattern. Donoghue (1998) observed that the first disturbance of lamellae is generally palm-shaped, with each digit relating to an individual denticle. The initial palm shaped evagination is developed horizontally with respect to the main axis of the process, and gradually becomes more erect with maturity. Donoghue (1998) ascertained that early distal growth occurred synchronously with late proximal growth. *Phragmodus*, a common middle Ordovician prioniodontid, characteristic of the North American fauna, was included by Donoghue (1998) as a representative of this group.

Donoghue (1998) suggested that the development of blade-like P elements and the blade portion of platformbearing elements is very similar to type III ramiform generation. The element adds new denticles to the distal ends of the processes by marginal evagination of the lamellar tissue. Initially, the element is wholly lamellar crown tissue; however, as the element grows white matter forms in the denticles and the cusp. During later stages of maturity the white matter deposition is halted and the white matter cores are enveloped by successive layers of lamellar tissue, whilst the ventral portions of the element continue to grow without white matter inclusions.

Donoghue (1998) divided platform morphogenesis into Type A and Type B and described the first category as a modification of the blade morphogenesis. The platform is restricted to the dorsal portion of the element, and the crown incorporates a series of cavities that can be compared to those developed in ramiform and blade genesis. However these cavities differ in that they are not wholly encapsulated within the crown and can be traced down to the basal body, where they open through a restricted opening. Donoghue stated that the ridges or denticles on platform surfaces are similar to ramiform denticles in that they are each formed as a discrete prism, centred above a stack of aligned growth cavities. Whether the growth prisms merged or remained individual is directly related to the overlying morphology of the platform ridges or denticles. Donoghue (1998, p. 652, fig. 11e) noted that if the platform had a high relief, such as in *Icriodella*, then the growth prisms remain discrete, and if the platform has a low relief, such as in gnathodids (p. 652, Fig. 11h) then the prisms could be seen to merge. In almost all platform elements that bear transverse ridges the ridges occur in pairs on either side of the long axis of the element. Donoghue (1998, p. 654, fig. 13a-c) produced a section of *Cavusgnathus* that revealed the juvenile growth of the element, reflecting an original blade-like

morphology. Donoghue was able to show that this single growth axis bifurcated and developed two distinct growth axes oblique to each other. Donoghue (1998) stated that the ontogenetic bifurcation of denticles appeared to be the main method of platform genesis for type A platform-bearing taxa. According to Donoghue, platforms of this type appear to be completely lacking in white matter.

Type B platforms differ from type A platforms in that they develop by lateral expansion of the incremental layers of lamellar tissue at the base of the denticles. Lateral expansion is achieved by leaving patches of poorly mineralised tissue and large cavities; consequently the growth increments are prominent and vary in thickness. White matter is only present in the free blade and carina of type B platforms.

The component crystallites and their arrangement with respect to lamellae and growth direction led Donoghue (1998) to conclude that lamellar crown tissue can be homologised with enamel. He pointed out that the lamellar nature of crown tissue, with its small crystallites aligned with a preferred orientation in respect to the growing surface, shows close similarities to the ultra-structure of enamel (Schmidt and Müller, 1964). This is a conclusion also reached by several other authors (e.g. Dzik, 1986; Burnett and Hall, 1992; Sansom *et al.*, 1992). A homology with enameloid is discounted because it is more usual for enameloid to be composed of large crystallites that show no preferred orientation and are not arranged within incremental lines.

The basal body is the tissue that has received the broadest range of interpretations (Barskov *et al.*, 1982; Dzik, 1986; Sansom *et al.*, 1992; 1994; Sansom, 1996) ranging from bone, globular calcified cartilage to different types of dentine. Donoghue (1998) pointed out that, although not all the structures that characterise the basal tissues of conodont elements are seen in dentine, many of the characters chosen to support opposing theories are. Because dentine has such a wide range of different structures, Donoghue (1998) suggested that it was possible that basal body tissue represented some form of dentine and this is substantiated by his studies of the relative growth between the component tissues. He pointed out, however, that it is difficult to reconcile the interpretation of basal body tissue as dentine with the reduced mineralisation and gradual loss of the conodont basal body during the Middle and Upper Palaeozoic, as the signal for enamel secretion is the presence of a mineralised surface i.e. dentine. This means that the taxa that are characterised by having just a thin layer of mineralised basal tissue beneath the crown (a phenomenon common in many Devonian taxa, Smith *et al.*, 1987) are not difficult to incorporate into the interpretation, but those that show complete loss of a mineralised basal tissue are more difficult to explain.

Smith and Hall (1993) suggested that the loss of the basal body could perhaps be explained by a change in the timing of histogenetic processes. They homologised conodont elements with odontodes, the basic unit of the vertebrate dermal skeleton, that were perceived as flexible enough to allow any of their component tissues (enamel, dentine and bone) to have evolved before the others, or be present independently of the others, by uncoupling or independently regulating odontoblast (dentine related secretory cells) and ameloblast (enamel related secretory cells) differentiation (Smith and Hall, 1993). Donoghue (1998) pointed out that, if this is

the case, then almost any combination of enamel and dentine types could occur permitting the variety of forms found in conodont elements.

Donoghue (1998) discounted the hypothesis that white matter is a form of cellular bone (Sansom *et al.*, 1992, 1994; Sansom, 1996; Smith *et al.*, 1996) because the arrangement of the internal structures of white matter are irreconcilable with such an interpretation. A homology with enameloid was also discounted on the basis that the coarse elongate fibre-like crystallites characteristic of enameloid cannot be compared to the microcrystalline nature of white matter, despite the common occurrence of cell spaces. Instead Donoghue (1998) discussed the parallels with mesodentine (the most primitive type of dentine known). However, mesodentine is characterised by pulp canals and laminar structures, both of which, according to Donoghue (1998), are absent from white matter tissues. Donoghue concluded that it is most likely, based on the growth and structure, that white matter is a dentine related tissue, possibly comparable to mesodentine. However, he also pointed out that there is a regular relationship between the position of the growth cavities within the lamellar crown and the point of initiation of white matter secretion. Donoghue stated that it is possible that the growth cavities are a source of odontoblastic cells that could have combined with the ameloblasts of the forming enamel to secrete a form of enameloid.

Donoghue (1998) considered that the individual units of type I elements represent the most basic form of the conodont skeleton and that they are homologous with the units that make up the type II elements. He further stated that juvenile elements of types III and IV are homologous to types I and II and that mature elements of types III and IV represent composite elements of several such units. He also considered that the individual denticles of type III units are homologous with the differentiated units of type IV elements. This means that all mature conodont elements represent composite units. Donoghue pointed out that this shows that the theory of Smith *et al.* (1996), which argued for a homology between conodont elements and odontodes, is over-simplified. On the basis of Donoghue's (1998) work it can be seen that conodont elements are composed of many odontodes, forming an odontocomplex. The different combinations of tissue types reflect heterochronic shifts in the timing of development stages. Donoghue concluded that each conodont element is homologous, or analogous to a tooth family, though it probably provided a closer comparison with dermal scales and oral odontodes rather than true teeth.

In 1998 Donoghue and Chauffe investigated the affinities of three Late Devonian, phosphatic microfossils: *Conchodontus, Mitrellataxis* and *Fungulodus*. The histology of the fossils was studied in conjunction with the micro-ornamentation to ascertain whether it was possible to identify characters that were unique to conodonts, that could be used to distinguish them from other lower vertebrates. Because the taxa being studied were of Late Devonian age, basal body tissues were only poorly represented; however, there were several different forms of tissue present within the crown of each specimen examined. Common to all three was a coarse crystalline, hyaline fabric, contained within incremental lines. The crystallites were orientated with their c axes either perpendicular or subperpendicular to the outer surface. Donoghue and Chauffe (1998) noted that specimens of *Fungulodus* possessed a central, slightly opaque region above the hyaline base that was characterised by a dense crystalline structure that appeared to truncate the incremental lines from the base of the specimen. The denser regions have a broken fabric that appears to be roughly formed into irregular elongate wedges (approximately 3µm wide) that widen slightly towards the upper surface of the specimen. There is no distinct boundary between the two crown tissue types and the entire fabric of the tissue shares the same patterns of Nomarski interference implying that the two tissue types shared an overall continuity of crystallite orientation. Donoghue and Chauffe (1998) thought that the upper tissue type had been subjected to diagenetic recrystallisation that had caused the apatite crystals to reform completely, masking the primary fabric. A coarse surface ornamentation on the upper surfaces of the specimen coincided with the fine grained fabric beneath and was absent from the flanks of the structure, where the fine grained fabric did not occur.

It was observed that specimens of *Mitrellataxis coronella* also possess a central opaque area, although the whole unit shared the same crystallographic continuity when using Nomarski optics. The central core is finely crystalline and arranged into elongate sinuous, platy columns that taper towards their bases and are approximately 1µm wide. Donoghue and Chauffe (1998) observed that this columnal tissue often underlay a projection in the centre of the upper surface.

The specimens of *Mitrellataxis dombrowskii* figured by Donoghue and Chauffe (1998, p. 289, fig. 3 C, D, E) also possess a central massive, slightly opaque tissue, although the opacity appears to vary with different specimens (compare Donoghue and Chauffe, 1998, p. 289, figs 3A and 3B). In this instance some regions of the fabric are dominated by clearly formed parallel columns that extend from the base of the tissue and the surface. Where these columns form there are no growth increments visible. The columns are formed of a dense tissue that has several small cavities which are approximately 1µm across; however, in the same specimen, a region adjacent to the columnar fabric lacks a longitudinal fabric and is characterised by numerous small cavities (approximately 1µm across). Both tissue types grade into the lower crystalline fabric, without any distinct boundary. Donoghue and Chauffe (1998, p. 289, fig. 3I) were confident that the internal longitudinal columns were aligned with the margins of the external polygonal microstructures.

Specimens of *Mitrellataxis chevronella* possess a central tissue which is closely comparable to that of *Fungulodus*. Donoghue and Chauffe (1998) proposed an interrelationship between this internal dense tissue and the external ridges that are the common form of external microstructure characteristic of *Mitrellataxis chevronella*.

In all three cases it was stated (Donoghue and Chauffe, 1998) that the internal structures coincided precisely with the external surface ornament, confirming the hypothesis that the polygonal imprints represented imprints of secretory cells (von Bitter and Norby, 1994). However, Donoghue and Chauffe (1998) thought that surface ornament provided a very poor tool for distinguishing conodonts from other vertebrate hard

tissues, because it was indistinguishable from surface ornament found on scales, teeth and plates of other vertebrates.

Donoghue and Chauffe (1998) concluded that the coarse crystalline fabric of all three taxa examined could be successfully compared to enamel tissues found in lower vertebrates; however the fine grained tissues were unlike any other tissue found in a lower vertebrate. They did not believe that all the fine grained tissue types represented white matter, believing that true white matter should be opaque in transmitted light, finely crystalline, cancellous and resistant to etchants (following interpretations presented by Sansom et al., 1992; Donoghue, 1998). Donoghue and Chauffe (1998) placed the greatest emphasis on the opaque nature of white matter, and used this to distinguish what they interpreted as true white matter. Because of this it was thought that species of *Mitrellataxis* were the only taxa to possess *true* white matter as they possessed a tissue that appeared to be opaque in transmitted light and massive and cancellous in etched sections. Fungulodus and Conchodontus were not thought to possess true white matter because they did not have tissues that appeared opaque in transmitted light although the dense crystalline tissues shared the same structural fabric. The primary difference, therefore, was the absence of cavities within the microcrystalline tissues of Fungulodus and Conchodontus, allowing the tissues to appear hyaline. However, figures shown by Donoghue and Chauffe, (1998, p. 285, fig. 1H, p.287, fig. 2O), show that the etched sections of Fungulodus and Mitrellataxis share a very similar fabric to each other. Also, as commented on by the authors (Donoghue and Chauffe, 1998, p. 289, fig. 3D), columnar structures and cancellous structures both intergrade with each other in the same specimen of Mitrellataxis dombrowskii. As a result, it was concluded that the two tissue types are in all probability effectively the same and, because such a tissue could not be homologised with any other vertebrate hard tissue, it was a good diagnostic character for distinguishing conodonts from other lower vertebrates.

The white matter in these taxa was not interpreted as a form of dentine, as previously suggested (Wang and Klapper, 1986; Donoghue, 1998) because the dense microcrystalline tissue lacked tubules, possessed growth increments and graded into the coarse crystalline tissue below. Donoghue and Chauffe (1998, p.288) stated that "although it [white matter] was not histologically comparable it was probably homologous in a developmental sense to hard tissues of vertebrates". Donoghue and Chauffe (1998) thought that an interpretation of the homology of white matter with the hard tissues of other vertebrates was beyond the scope of the paper being presented.

Simonetta *et al.* (1999) supported the homologisation of conodont lamellar crown with vertebrate enamel and suggested that it was probably most comparable to ganoine, a form of primitive fish enamel. Polygonal ornamentation was thought to be directly comparable to the imprints of secretory cells because they were so easily compared to the cell imprints found on the inner ganoine epithelium of primitive fishes and also to mammalian ameloblasts (Dzik, 1986, 2000). On the basis of this Simonetta *et al.* (1999) proposed that conodont secretory cells were secreted directly onto the element surface as a thin layer and became subsequently mineralised in a way comparable to enameloid secretion in fish. Simonetta *et al.* (1999)

identified what they interpreted as a direct and negative correlation between the size of cell and the thickness of apatite secreted. They believed that the smaller the cell imprint, the more apatite deposition and conversely the larger the cell imprint the less apatite deposition; they related this to an interpretation that each cell had a similar secretion abilities that a cell covering a large surface area could only deposit a thin layer of apatite while a cell covering a small surface area, could deposit a relatively large amount of apatite. Simonetta *et al.* (1999, p. 105) stated that this seemed "sufficient to explain the complexities of conodont element surface morphology".

One of the most recent papers to review conodont histology has been published by Donoghue *et al.* (2000). The review was incorporated within a conodont affinity discussion, where the characters used to code conodonts were evaluated and explained. Lamellar crown was described as a crystalline tissue, bounded between growth increments, with the arrangement of the crystallites varying throughout the element. Distinct boundaries were only apparent between lamellar crown and white matter when polished sections were etched and the less resistant lamellar crown became etched away. The authors reported that the white matter and lamellar crown grew synchronously and because of this were products of a common developmental process, supporting the earlier theory of Donoghue and Chauffe (1998). Donoghue *et al.* (2000) thought that lamellar crown was most comparable to enamel or enameloid. The authors (Donoghue *et al.*, 2000, p. 12) considered that the variety of crystallite orientation (used by Forey and Janvier [1993] to argue against an enamel homology) did not refute such a comparison because it "coincided precisely with requirements of function, relating to biomechanical forces imposed on elements during feeding".

White matter was reported to be more finely crystalline than lamellar crown crystallites and distinguished by graded boundaries and its opacity in transmitted light; the opacity was caused by numerous cavities incorporated within the fabric. Following on from the work of Donoghue and Chauffe (1998), Donoghue *et al.* (2000) suggested that the developmental relationship between white matter and lamellar crown negated the possibility of a homology with dentine or enameloid. It was considered more likely that white matter was comparable to enamel because it was probable that it was deposited by a slightly modified set of the population of cells which would normally have secreted enamel.

Basal body was reported to be the most variable of tissue types, normally possessing incremental lines but with a variety of other structures, including globules and tubules. Donoghue *et al.* (2000) followed the interpretation of Sansom *et al.* (1992) for the interpretation of cartilage for the basal body of *Cordylodus angulatus* because they could demonstrate that the calcospheres were not incorporated into the lamellae and appeared to have grown independently, a character not shared by dentine. However the majority of basal bodies were thought to be purely lamellar and atubular, resembling lamelin, a form of dentine found in a Silurian chondrichthyan (Donoghue, 1998).

CHAPTER 1.0 INTRODUCTION

THE ARCHITECTURE, HISTOLOGY AND FUNCTION OF THE FEEDING APPARATUS OF BALTONIODUS VARIABILIS (BERGSTRÖM 1962)

Introduction

Baltoniodus conodonts range from Lower to Middle Ordovician and are recognised from Europe, North America, South America and Australia (Bergström, 1981). A full apparatus has been recognised; including two forms of P element and array of S elements and a pair of M elements (Bergström, 1966, 1971). Both Pa and Pb elements of *Baltoniodus* are pastinate.

In 1956 Pander described some pastinate elements for which he erected a new genus, *Prioniodus* Pander 1856, and assigned the elements to *Prioniodus elegans* Pander 1856. Öpik (1936) and Lindström (1955) found similar elements and provided a more complete description. Lindström's (1955, p. 589) amended diagnosis of *Prioniodus* stated that the genus was characterised by "compound conodonts with a suberect cusp, from the base of which diverge three denticulate edges or processes, one posteriorly, one anteriorly, and one laterally".

Bergström (1961) described *Prioniodus variabilis* Bergström 1961, a new species of *Prioniodus* that occurred in the Ludibundus limestone of Sweden, of Middle Ordovician age.

Diagnosis of *Prioniodus variabilis* according to Bergström (1961). "Stout, suberect cusp and subequally long orally multidentulate posterior and lateral processes and a generally shorter anterior process. The lateral process is directed anteriorly and the anterior process deflexed and recurved. The angle between the anterior and posterior processes amounts to 60-80°, and the one between the anterior and lateral processes there is often a ledge running near the aboral margin" (Bergström, 1961, p. 51).

Remarks. The species was named *P. variabilis* because of the large amount of variation observed in the pastinate element that characterised the new taxon. Bergström (1961) remarked on this variability and suggested that with more material it would be possible to split *P. variabilis* into several species.

Bergström (1968) presented the first attempt to group different form taxa together to reconstruct natural multielement apparatuses for species of *Prioniodus*. In particular, Bergström suggested that there was strong evidence that suggested that there were at least five different element types in the apparatus of *Prioniodus* elegans (one type of P element, one M and three types of S elements).

Bergström built on this work in his 1971 paper and suggested that younger Ordovician Prioniodus species, including P. navis Lindström 1955, P. prevariabilis Fåhræus 1966, P. variabilis Bergström 1961, P. gerdae Bergström 1971, and P. alobatus Bergström 1971 had similar apparatuses to that which he proposed for P. elegans. However, the younger apparatuses all differed from Prioniodus elegans by having a "prioniodontiform element which is differentiated into two morphological types" (Bergström 1971 p. 145), therefore forming an apparatus with at least six different element types. At this stage Bergström was reluctant to attach generic significance to this difference, believing that these younger conodonts with differentiated prioniodiform elements were derived from the same stock as Prioniodus elegans.

Lindström (1971) did not follow Bergström and identified a new genus, *Baltoniodus*, to accommodate all of the conodonts previously classified as species of *Prioniodus* that had two types of morphologically distinct prioniodontiform elements. Lindström identified some morphological differences between the prioniodontiform elements of the two groups stating that species of *Baltoniodus* had differentiated prioniodontiform elements with deeper basal cavities than those of *Prioniodus* and an inner lateral flare on the posterior process.

The Catalogue of Conodonts (Ziegler 1975, Vol. II, p. 11) diagnosis given for Baltoniodus follows Lindström (1971, p. 55): "Baltoniodids in which the prioniodiform elements are denticulate and, in the case of the amorphognathiform element, provided with an inner lateral flare. There are no platform ledges in most species. The set of accessory non-prioniodiform elements is complete [including: gothodiform (bipennate), tetraprioniodiform (quadriramate), trichonodelliform (tertiopedate) and oistodontiform (geniculate) element.] The oistodiform element may carry denticles anteriorly." It is stated in the remarks that it is essential that there are two kinds of prioniodiform elements and that this is what distinguishes the genus from *Prioniodus*.

In the *Treatise*, Clark (in Robison, 1981) classifies *Baltoniodus* within the family Prioniodontida Bassler 1925, along with *Prioniodus*. The family is recognised as containing species with pastinate P elements, geniculate M elements and a full set of S elements, all with denticulate processes, distinct cusp and basal cavity extending along the entire length of the processes.

Work undertaken by Fåhræus and Nowlan (1978) has suggested that *Prioniodus elegans* cannot be differentiated from younger taxa such as *P variabilis* because it only had one morphotype of prioniodontiform element. For instance, Fåhræus and Nowlan (1978) concluded that prioniodontiform elements of *Prioniodus elegans* incorporated two different morphologies and that these two represent two P element positions. This conclusion was corroborated by Stouge and Bagnoli (1988), who discussed the evolution of *Prioniodus* and identified a trend within the genus of P element differentiation comparable to that of *Baltoniodus*, but were unable to throw any light on the ancestry of *Baltoniodus*. The authors (Stouge and Bagnoli, 1988, p. 132) stated that "*Baltoniodus* has an apparatus which is identical with that of *Prioniodus*", suggesting that it is morphological details of the elements which differentiate between the two genera. Stouge and Bagnoli (1990) maintained, however, that *Baltoniodus* was not synonymous with *Prioniodus* (Bergström, 1971), nor was it a
subgenus of *Prioniodus* (Löfgren, 1978). It was stated that *Prioniodus* had its own evolutionary history and became extinct in the early Arenig before the first appearance of *Baltoniodus*. Stouge and Bagnoli (1999) thought that both genera were members of the Prioniodontidae.

Dzik (1994) followed Lindström in the recognition of *Baltoniodus* and stated that the relationship between *Prioniodus* and *Baltoniodus* still required clarification. He suggested "the *Baltoniodus* lineage appeared in the Baltic region as an effect of migration from an unknown area after the transition from early *Prioniodus* to *Baltoniodus* had taken place. This is suggested by the complex migration pattern in the early evolution of *Prioniodus* as shown by Stouge and Bagnoli (1988)". (Dzik, 1994, p. 80).

Discussion. It is considered here that there is a taxonomically significant (as well as stratigraphic [Stouge and Bagnoli, 1988]) difference between *Prioniodus* and *Baltoniodus*. Lindström did not erect the genus *Baltoniodus* solely on differentiated P element morphologies. He also considered the development of an inner lateral flare, a deeper and wider basal cavity for the Pa element and a fully differentiated array of S and M elements (gothodiform (bipennate), tetraprioniodiform (quadriramate), trichonodelliform (tertiopedate) and oistodontiform (geniculate) elements) to be phylogenetically significant characters. These differences are upheld in this work, and more characters are considered.

The arrangement of costae about the cusp of the prioniodiform elements of *Prioniodus* and *Baltoniodus* is different. Both have anterior and posterior costae but on *Prioniodus elegans* the lateral costa is clearly positioned on the lateral face of the cusp, whereas in *B variabilis* the lateral costa derives from the anterior face of the cusp. This is a consistent difference. There are also differences in denticle size and morphology; in species of *Prioniodus*, the denticles of the pastinate elements are relatively taller, in comparison to the cusp size, than those of *Baltoniodus* (compare Stouge and Bagnoli, 1988, p. 164-167, plates 11-12, that figure: *P. adami* Stouge and Bagnoli, 1988, *P. oepiki* (McTavish, 1973), *P. gilberti* Stouge and Bagnoli, 1988 to Stouge and Bagnoli, 1990, p. 30-33, plates 1-2, that figure: *B. clavatus* Stouge and Bagnoli, 1990, *B.* n.sp. A, Stouge and Bagnoli, 1990 and *B. norrlandicus* Löfgren, 1985). The development of an inner lateral flare, a deeper basal cavity, the denticle morphology and the costa arrangement on the pastinate elements are the characters which should be included in the diagnoses to distinguish between *Baltoniodus* and *Prioniodus*.

The shape of the basal cavity and the arrangement of costae about the cusp of conodont elements directly reflect the method of element growth. This is considered a taxonomically important character. The P elements belonging to species of *Prioniodus* (such as *P. evae* Lindström 1971, *P. oepikodus* Lindström 1955) are far more comparable to each other than to P elements of species of *Baltoniodus*. The relationship proposed by Sweet (1988) and Stouge and Bagnoli, 1988, 1999) that *Prioniodus* and *Baltoniodus* represent lineages that evolved independently of each other from a common ancestor is confirmed by these morphological differences.

As a consequence the taxonomic division between *Prioniodus* and *Baltoniodus* is upheld, but not on the original basis of identical prioniodiform elements in *Prioniodus*. Close morphological similarity between species assigned to *Prioniodus* and differences from those assigned to *Baltoniodus* suggests that species of *Prioniodus* are more closely related to each other, rather than to species of *Baltoniodus*.

CHAPTER 1.1

THE APPARATUS ARCHITECTURE OF BALTONIODUS VARIABILIS

Introduction.

Baltoniodus Lindström 1971 has been identified as the ancestral stock of the balognathid clade (Sweet 1988). The balognathids were the longest surviving family of the prioniodontids and represent some of the most characteristic, widespread and abundant conodonts that occurred in many Ordovician faunas (e.g. Löfgren, 1978; Dzik, 1994; Bagnoli and Stouge, 1997). Several of the genera are represented by large well preserved collections of disarticulated specimens. However, prioniodontid natural assemblages are rare and the apparatus plan is only known categorically for *Promissum pulchrum* Kovács-Endrödy (Aldridge *et al.*, 1995). *Promissum* is currently assigned to the family Balognathidae of the Order Prioniodontida (Theron *et al.*, 1990).

Prior to 1995 most prioniodontid apparatus reconstructions were only taken as far as describing the number of different element morphologies in each apparatus and comparing them to the ozarkodinid template, which is clearly understood due to the relatively prolific collections of natural assemblages (for reviews see Aldridge *et al.* 1987; Purnell and Donoghue 1997). The apparatus of *Promissum* has a different composition from that of ozarkodinids, therefore, for the first time, the reconstruction provided by Aldridge *et al.* (1995) provided a new template with prioniodontid elements in their true biological positions.

In the light of the new evidence from the natural assemblages of *Promissum pulchrum* the apparatuses of balognathids and their close relatives can be reassessed.

Baltoniodus variabilis Bergström (1961) is here chosen as a case study and the interpretation of its feeding apparatus is re-evaluated.

Materials and Methods.

Upper Ordovician natural assemblages of *Promissum* collected from the Soom Shale in South Africa (Theron *et al.*, 1990), were made available to me by R. J. Aldridge, from the collections currently at the University of Leicester. The elements of *Baltoniodus* are from the Middle Ordovician, Suhkrumagi section, exposed south east of Tallinn (for details of locality see Kaljo and Nestor, 1990), Estonia, collected by R. J. Aldridge.

Several of the *Promissum* assemblages have a mouldic preservation, which made it possible to make silicon rubber casts of individual elements. The casts provide previously unrevealed information of element morphology that allow detailed comparisons between the elements of *Promissum* and *Baltoniodus* and help to identify homologous characters.

The ozarkodinid template.

Representatives of the Order Ozarkodinida dominated conodont faunas throughout most of the Palaeozoic and this abundance is also reflected in the number of natural assemblages that have been found. This has resulted in almost all conodont apparatus reconstructions being based on ozarkodinid natural assemblages (see Purnell and Donoghue, 1997 for review). Aldridge *et al.* (1987) followed a technique originally developed by Briggs and Williams (1981) incorporating careful modelling and photography to reconstruct the apparatus architecture of ozarkodinids. The architectural model was further refined by Purnell and Donoghue (1997, 1998) who analysed all known ozarkodinid natural assemblages, ranging from the Silurian to the Upper Carboniferous (Purnell and Donoghue, 1998 and Fig. 1A) and reviewed previous reconstructions. They confirmed the earlier hypothesis that ozarkodinids consistently possessed a fifteen element apparatus comprising a pair each of bilaterally opposed P elements; an anterior, axial Sa element, two groups of four close-set, inward and forward inclined Sb₁, Sb₂, Sc₁ and Sc₂ elements; and above and outside each S group, an inward and forward pointing M element (Purnell and Donoghue, 1998). The element terminology was adapted from that proposed by Sweet (1981, 1988).

A different model of architecture was proposed by Dzik (1991). The model was based mainly on a natural assemblage of *Pandorinellina remscheidensis* (Ziegler) described by Mashkova (1972). Dzik envisaged the S elements with their long axes oriented dorso-ventrally with their cusps in opposition across the sagittal plane, arranged in a V-shaped structure that gaped in a rostral direction. Aldridge *et al.* (1995) and Purnell and Donoghue (1997) criticised this model because it placed elements in positions that were not observed in natural assemblages.

The Promissum template.

Promissum pulchrum is currently assigned to the Family Balognathidae of the order Prioniodontida. Aldridge et al. (1995) recognised several similarities between the apparatus of *Promissum* and that of the ozarkodinids and used similar techniques to Aldridge et al. (1987) to reconstruct the nineteen element apparatus (Figure 2A). The apparatus of *Promissum* has been reconstructed with four pairs of bilaterally opposed P elements (Pa, Pb, Pc and Pd) in comparison to the two pairs of opposed P elements of the ozarkodinids; the homologies between the P element positions in the two taxa are not certain (Purnell et al. 2000). The S and M elements of *Promissum* are, however, clearly homologous to the S and M elements within the ozarkodinid apparatus. The axial ramiform element was designated Sa and the array of flanking elements were designated Sb₁, Sd, Sb₂ and Sc. Terminology was adapted from that proposed by Sweet (1981, 1988).

Sweet (1981) had intended his element notation to provide a system that could be used to recognise elements that could be broadly assigned to the P, S or M elements categories, but established the notation prior to

detailed knowledge of architecture. It was therefore impossible to utilise Sweet's notation independently from element morphology. He stated that the scheme initially proposed by Sweet and Schönlaub (1975) and advocated in the Treatise (Sweet, 1981, p. W20) was not intended to identify elements that occupied homologous positions, but to "be a vehicle for expressing analogy". As the knowledge of conodont apparatus architecture improved, the application of Sweet's locational scheme has become increasingly subject to inconsistencies and misinterpretations. For instance, the Sd position (seen in Figure 2A), was originally intended to refer to a quadriramate element that may have occupied an axial position. However, in the light of architectural information derived from natural assemblages Aldridge et al. (1995) recognised that the quadriramate element occupied a position between the two Sb element positions. Purnell and Donoghue (1998) have provided some of the most recent work on ozarkodinid apparatus recontructions. Because the ozarkodinids did not possess a quadriramate element it was easier to apply Sweet's terminology, recognising an axial Sa element, and two groups of four close-set Sb₁, Sb₂, Sc₁ and Sc₂ elements. Although Aldridge et al. (1995) recognised that the nine S elements of Promissum were homologous with the S elements of ozarkodinids they did not follow the labelling of the ozarkodinid S elements seen in Figure 1A. This was to avoid applying the term Sb_2 to a quadriramate element that was widely recognised as an Sd in the contemporary literature.

The apparatus of *Promissum* is now represented by more than five hundred natural assemblages (Aldridge, 1999, pers. comm.) and the architecture is well understood. However, it is still not known to what extent this apparatus is typical of the prioniodontids. The apparatus is possibly typical of the balognathids (Purnell *et al.*, 2000) but the assemblages described by Nowlan (1993) and Stewart (1995), though probably faecal, suggest that other prioniodontid taxa had fewer elements (Purnell *et al.*, 2000). In addition, the natural assemblages of *Phragmodus*, described by Repetski (1997) and Chapter 5.0, the only other prioniodontid natural assemblages known, do not appear to possess more than two pairs of P elements.

It is now essential to test whether the skeletal plan of *Promissum* represents a standard for the prioniodontids, or is typical of the balognathids alone. This can be done by direct morphological comparisons between elements of taxa from natural assemblages and elements from disarticulated collections.

New terminology.

Purnell et al. (2000) have presented a new notation for conodont apparatuses derived from the topology of ozarkodinid apparatuses (Figure 2B). The new terms can be applied to "taxa which are known from natural assemblages or where a topological homology can be inferred from secondary morphological criteria" (Purnell et al., 2000, p. 120). These new terms express firm topological homologies. The authors propose that the well understood ozarkodinid apparatuses can be used as a standard against which other conodont apparatuses can be compared. The advantage of the new notation is that it provides a system that can run parallel with

the scheme proposed by Sweet (in Robison, 1981; 1988). The scheme proposed by Sweet (in Robison, 1981; 1988) can be applied to conodont taxa from disarticulated collections, where homologies are unknown.

With the new terminology, the elements are labelled from the caudal end of the apparatus with two pairs of P elements, P_1 and P_2 . The ramiform array, S_0 - S_4 , is labelled laterally from the axial S_0 element to the flanks of the apparatus. Purnell *et al.* (2000) have also applied this new notation to the apparatus of *Promissum* (Figure 2B).

To apply the new terminology, the homologies between new apparatuses and the ozarkodinid apparatus have to be clearly understood. Identifying which elements of the *Promissum* apparatus are homologous with which elements within the ozarkodinids is potentially problematic as discussed below. Within the apparatus of *Promissum* the two caudal pairs of P elements appear to be morphologically identical (see Figure 2, 3Ai), whereas the two remaining pairs are morphologically differentiated. It is possible that the most caudal element pairs are "serial homologues, arising by duplications of the P₁ element of an hypothetical ancestor" (Purnell, *et al.*, 2000, 118). If this is correct then the element designations proposed by Purnell *et al.* (2000) imply misleading homologies with the ozarkodinid apparatus that could lead to comparisons with elements from other taxa that are not homologous. The implications of this are considered below.

Homologies between the Promissum apparatus and the ozarkodinid apparatus.

When the homologies of P elements within the *Promissum* apparatus were considered the dorso-ventral orientation of the two caudal pairs of P elements suggested to the authors that the two elements were homologous with the dorso-ventrally orientated P_1 and P_2 elements of the ozarkodinids (Theron *et al.*, 1990; Aldridge *et al.* 1995). These were the only P element homologies identified and it was thought that, because of this orientation and position within the apparatus, the other P elements of *Promissum* had no homologues within the ozarkodinid apparatus. However, if the P_1 and P_2 elements of *Promissum* represent serial homologues then the two positions should be termed P_{1a} and P_{1b} and the element position rostral to these would then be homologous with the P_2 position in the ozarkodinid apparatus. This interpretation is, however, premature and awaits additional information from other natural assemblages

For clarity, the use of Sweet's original terminology (1981; 1988) is retained for elements of *Baltoniodus* and the new terminology proposed by Purnell *et al.* (2000) is used for elements of *Promissum*. This is to allow distinction between elements from the known apparatus of *Promissum* and those of the apparatus being reconstructed, belonging to *Baltoniodus*.

Previous reconstructions of prioniodontid apparatuses from disarticulated collections.

Aldridge et al. (1995, p. 287) observed that "morphologically the elements of *Promissum* compare well with those of other taxa from the same family, the Balognathidae, and it is probable that these close relatives were architecturally similar". It is not a new idea that earlier prioniodontid taxa had topological templates that differed from the ozarkodinids. For example, an additional pair of M elements was interpreted for *Gamachignathus* by McCracken et al. (1980), based on the recognition of an element morphology that was thought to characterise M element positions (reflecting the problems of a morphologically based notational scheme). It is of course also possible that there were two different M element morphologies, that perhaps represent a form of dimorphism. Aldridge et al. (1995) suggested that this additional pair of 'M' elements could in fact be an additional pair of P elements, in the light of the evidence of the new *Promissum* template. This would seem the most likely hypothesis as it is now known that M and S element morphologies are comparable between different taxa and the positions. There are also several Silurian taxa that have been reconstructed with three P elements; for example, Männik and Aldridge (1989) recognised three different morphologies of P elements; of P elements, Männik and Aldridge.

Armstrong (1997) suggested that in addition to Pa elements the apparatus of *Eoplacognathus* contained additional P elements and ramiform elements that were normally associated with *Baltoniodus variabilis*. This was based on a distinctive ledge common to all of these elements, which Armstrong identified as a feature that united them within the same apparatus. Similarly elements of *Carniodus* were included within the apparatus of *Pterospathodus* because the "co-occurrence, similarities in evolutionary patterns and in ecology... indicate that both sets of elements belonged to the same apparatus" (Männik, 1998, p. 1001). Armstrong's reconstruction is not followed here as elements of *Eoplacognathus* do not always co-occur with elements of *Baltoniodus*. Also clear homologies can be observed that relate Pa elements of *Eoplacognathus* to Pa elements of *Baltoniodus* (see Chapters 1.2 and 2.2) inferring that they would have both occupied the same architectural position, therefore negating the apparatus reconstruction proposed by Armstrong (1997) (see Chapter 2.1, Figures 3B, E in comparison to Figures 3C, F respectively).

The elements of Baltoniodus.

Baltoniodus possessed two types of pastinate P elements, Pa and Pb (Figures 4A-D; 5A-D); an M element and four types of S element: bipennate, quadriramate, tertiopedate, and alate. The elements are well preserved, with good detail of denticles and gross surface ornamentation. The different elements are constantly associated with each other geographically and stratigraphically, and the morphologies are distinct, so the apparatus of Baltoniodus has been reconstructed following the ozarkodinid plan by several conodont workers (e.g. Sweet 1988; Dzik 1994).

Comparing elements of Baltoniodus with elements in the apparatus of Promissum.

P1 and **P2** elements of *Promissum*. The P1 element of *Promissum* and the Pa element of *Baltoniodus* share several characters (Figure 3Ai and 3iii). When comparing silicone rubber casts of the *Promissum* element to SEM photographs of the Pa element of *Baltoniodus* it is clear that the main axis of each element includes the process that develops from the concave margin of the cusp (dorsal in *Promissum*). When viewed orally this process usually makes a straight line with the 'lateral' process (caudal in the case of *Promissum*) and is normally of a similar or slightly shorter length. The shortest process of each element is the 'anterior' process (ventral in the case of *Promissum*), which, when viewed orally, curves away from where it meets the cusp face, making an angle of approximately 90-100' with the 'posterior' process (dorsal in *Promissum*). *Baltoniodus* lacks a 'postero-lateral' process, but has an expanded lobe on its platform in an equivalent position; however, the similarities outlined above are considered strong enough to suggest that the Pa element of *Baltoniodus* is homologous with the P1 element of *Promissum*. Both the P1 and P2 elements of *Promissum* share the same morphology and it is followed here that they represent a serial homologue. If this is the case, then it is possible that the Pa element of *Baltoniodus* similarly occupied two positions within its apparatus.

 P_3 elements of *Promissum*. The 'posterior' process of *Promissum* elements in the P_3 position appears to be absent. Only the conventional 'anterior' and 'lateral' processes remain (ventral and caudal in this instance) (Figures 3B iv-vi; 6A-C) which, when viewed laterally, form an angle of approximately 150- 170° between each other. The costae giving rise to the 'anterior' and 'lateral' processes (ventral and caudal) are clearly preserved on the convex faces of the cusp, the concave margin is orientated dorsally but has not developed a 'posterior' costa or process.

The Pb element of *Baltoniodus* has processes that share the same angular disposition about the cusp; (Figures 3B i-iii). The Pb element of *Baltoniodus* possesses 'anterior' and 'lateral' processes that compare well to the long ventral and caudal processes of the P_3 element of *Promissum*. These shared morphological characters imply that the Pb element of *Baltoniodus* is homologous with the P_3 element of *Promissum*.

S and M elements. The S and M elements of *Baltoniodus* have clear homologues in the apparatus of *Promissum*. For example, the alate Sa element of *Baltoniodus* compares morphologically to the element occupying the S_0 position in the *Promissum* apparatus. Similar morphological comparisons can be made with the rest of the S elements of *Baltoniodus*, showing that the entire S element array of elements seen in the apparatus of *Promissum* was also present in the apparatus of *Baltoniodus*. None of the elements of *Baltoniodus* have such long processes as those seen in the *Promissum* elements. The M element morphology is not so clearly comparable; however, it is suggested here that the M element of *Baltoniodus* occupied the same position as the M element of *Promissum*.

Discussion.

 P_4 elements of *Promissum*. Morphological comparisons have shown that the P_1 , P_2 and P_3 elements of *Promissum* can be compared to elements of *Baltoniodus* and homologies can be recognised. However, the P_4 element of the *Promissum* apparatus is more problematic and appears to have a very different morphology. The principal difference evident between the P_3 and P_4 elements is a variance in angle between the two processes; otherwise, they share a similar morphology. It is possible that the two processes of the P_4 are homologous to the conventional 'anterior' and 'lateral' processes in a way comparable to the P_3 element. Figures 7A-F shows how the disposition of the 'lateral' process of the Pb elements of *Baltoniodus* varies. When the element is viewed orally the 'lateral' process can form a straight line with the 'posterior' process (180°), or can vary as much as 90° from this position and make an angle of approximately 90° with the 'posterior' process resulting in the 'anterior' and 'lateral' processes forming a straight line (see Figure 7A). Thus it is possible that an element with similar morphology to the Pb element of *Baltoniodus* occupied the P_4 position in the *Promissum* apparatus. This would mean that specimens currently considered to be Pb element of *Baltoniodus* could have occupied more than one position within the apparatus.

P element ratios. Within my collections, to date, twelve samples (approximately 1kg) of Suhk 96/2 (for location details see Kaljo and Nestor, 1990) have been processed. 151 elements of *Baltoniodus variabilis* have been picked of which 52 specimens are Pa elements, and 99 are Pb elements. 185 elements of *Eoplacognathus reclinatus* have been processed of which 64 are Pa elements and 121 are Pb elements. Collections of Dzik (1994) from the Mójcza limestone and also those from Jämtland studied by Löfgren (1978) also show a recurring pattern of proportional representation where the Pb elements are over-represented. There is a consistent over-representation of the Pb elements (often twice as many) throughout all three of these large collections. The collections are from different localities and all possess elements of wide ranging morphologies and sizes. Therefore, it is possible that such recurrent patterns represent a biological signal which reflects apparatus composition during the life of the conodont.

However, it is possible that the proportional representation has resulted from minor sorting, and that all of the elements have been transported a short distance, sorting the more symmetrical Pb elements from the more elongate Pa elements. McGoff (1991) and Broadhead and Driese (1994) have produced studies that investigate the susceptibility of different conodont elements to different environmental regimes and demonstrate the sorting tendencies of disarticulated collections. Also, the more compact morphology of the Pb elements in comparison to the elongate morphology of the Pa elements might lead to a preferential preservation of Pb elements during Intuitively it might be predicted that post burial pre-cementation breakage processes would effect the elongate processes of the Pa elements above the more compact Pb elements. On the other hand, laboratory recovery techniques might be expected to favour the recovery of the distinctive Pa elements.

Despite all of these potential reasons for bias of element representation, it is possible that classic 'postmortem' sorting/preservation and preparation techniques are not necessarily required to account for the ratios of P elements discussed above. The apparatus architecture of *Baltoniodus* is not known precisely, and prior to this investigation has not been reconstructed using the apparatus of *Promissum* as a template. Therefore, although it is likely that the ratios have been somewhat altered, is it certain that the true biological signal has been completely masked by this process, just because the ratios appear to be counter intuitive? Until a natural assemblage of the apparatus of *Baltoniodus* is discovered, this question will remain unanswered.

If the element proportions represent a true biological signal the evidence from disarticulated collections of *Baltoniodus* favours a duplication of the Pb element and not the Pa element. This perhaps lends support to the theory that the P_4 position was filled by an element with a similar morphology to the Pb element of *Baltoniodus*. If this is the case, the Pb element of *Baltoniodus* occupied two quite different positions within the apparatus (rather than the adjacent positions of the P_1 and P_2 elements of *Promissum* which are thought to be possible serial homologues, Purnell *et al.*, 2000). This means that serial homology cannot account for the apparent duplication of this element morphology within one apparatus. A more convincing explanation may be inferred from the fact that all of the P elements of *Baltoniodus* have the same basic plan, with a similar disposition of processes about the cusp. This is possibly a plesiomorphic character of the family and would suggest that the pastinate form is the basic plan to which all the P elements of simple prioniodontids were restricted. Therefore, it would be expected that a third P element morphology (P_1 , P_3 and P_4) would not vary greatly in morphology from the rest of the P elements in the apparatus of a prioniodontid that had not produced very specialised P elements.

Conclusions.

The elements of *Baltoniodus* have clear homologues with the elements within the apparatus of *Promissum* and hence display a closer relationship to the balognathid conodonts, rather than the ozarkodinids. Therefore, it is considered more appropriate to use the *Promissum* template to try and reconstruct the apparatus of *Baltoniodus*.

The present reconstruction of *Baltoniodus* is confined by homologues that are clearly recognised. It is not possible to discuss the number of elements within the apparatus or to pursue the hypotheses discussed above without further natural assemblage data for other balognathids. It is proposed that the Pa element of *Baltoniodus* occupied the most caudal position in the apparatus and the Pb element occupied the P₃ position (Figure 8). Because the S elements compare so precisely with the S elements of *Promissum* they probably occupied equivalent positions in the apparatus of *Baltoniodus*. It is thought that the M elements also occupied a comparable position and were located towards the rostral end of the apparatus.



Figure 1. Apparatus template for ozarkodinids. 1A. Terminology as used by Purnell and Donoghue (1997,1998). 1B. New terminology of Purnell *et al.* (2000).





Figure 2. Published apparatus templates for the *Promissum* apparatus. A. Terminology for the apparatus of *Promissum pulchrum* following Aldridge *et al.* (1995). B. New terminology for the apparatus of *Promissum pulchrum* following Purnell *et al.* (2000).



Figure 3A. i. Specimen C976A *Promissum* P1 element. ii. Specimen 247 *Lenodus pseudoplanus* Pa element. iii. Specimen 117 *Baltoniodus variabilis* Pa element. All elements orientated with concave face of cusp directed towards the bottom of the page.



Figure 3B. *Baltoniodus variabilis* Pb element and *Promissum* P3 element comparisons. i. Specimen 245 sinistral Pb *Baltoniodus variabilis*. ii-iii. Specimen 246 dextral Pb *Baltoniodus variabilis*. iv-v. Specimen C506B P3 *Promissum*. vi. Specimen C488 P3 *Promissum*. i, iv. viewed with the concave margin of the cusp directed towards the left of the image. ii,v. viewed with cusp directed towards the bottom right of both images. iii, vi. cusp directed towards to left of both images.



Figure 4. A-D P elements of *Baltoniodus variabilis*, all elements orientated with dorsal process directed towards top of page, in vivo postion. A. Pa (P1) element, oral view specimen 235. B. Pb (P3) element, oral view specimen 236. C. Pa (P1) element, lateral view specimen 245. D. Pb (P3) element, lateral view specimen 236.





Figure 5. Elements of *Baltoniodus variabilis*, with biological terms (after Purnell *et al.*, 2000) and traditional terms (after Sweet, 1981, 1988) labeled (traditional terms in brackets). A. Dextral Pa (P1) element, lateral view. B. Dextral Pb (P3) element, lateral view. C. Dextral Pa (P1) element, oral view. D. Dextral Pb (P3) element, oral view.



Figure 6. Latex moulds of P3 element of *Promissum* showing costate cusp. A. Specimen 937A. Whole element lateral view. B-D. Specimen 838A. B. Oblique oral view down cusp showing concave face of cusp and lack of dorsal process. C. Oblique dorsal view showing ventral process costa. D. Oblique dorsal view showing caudal process costa.



Figure 7. Pb (P3) elements of *Baltoniodus variabilis* showing the variance seen in process disposition, all elements seen in oral view. A, specimen 237; C, specimen 242; E, specimen 239. Sinistral specimens. B, specimen 238; D, specimen 243; F, specimen 244. Dextral specimens. All specimens orientated with dorsal process towards the top of page.



Figure 8. Reconstruction of the caudal part of the apparatus of *Baltonidodus variabilis.* View from rostral.

CHAPTER 1.2

THE HISTOLOGY AND INTERNAL STRUCTURE OF P₁ AND P₃ ELEMENTS OF BALTONIODUS VARIABILIS.

Introduction.

The P_1 element has a long dorsal and caudal process that are almost aligned when viewed both orally and laterally. The ventral process is generally small and sometimes adenticulate, and is deflected towards the dorsal of the element. The P_3 element is similar to the P_1 , but the processes are more evenly distributed about the cusp and the dorsal and the caudal processes are not as long as in the case of the P_1 . When viewed laterally, the caudal process is directed in an aboral direction, making an angle of approximately 100° with the dorsal process. For biological terms refer to Chapter 1.1, figs 5A-D. Both elements have distinctive surface microstructures; ropy ornamentation on the flanks of the cusp and smooth on the costae and along the processes beneath the denticles (see Chapter 1.3 for full discussion).

Materials and methods.

The material is from the Suhkrumagi section on the outskirts of Tallinn, Estonia (for details of locality see Kaljo and Nestor, 1990), and was collected by Viive Viira and Richard Aldridge. The sample is of middle Ordovician age containing conodonts of the *Eoplacognathus reclinatus* zone. Elements were embedded in resin and ground down, polished and etched following methods outlined by Donoghue (1998). Specimens were then examined with the SEM. Limited data were supplied by immersing the elements in oil and viewing through transmitted light.

The sections are taken in three main orientations. In horizontal sections the section plane is horizontal with the aboral margin of the element. Longitudinal sections are parallel with the long axis of the denticles and cusp, and parallel with the long axis of the process. Transverse sections are parallel with the long axis of the denticles, but perpendicular to the long axis of the process. Figure 1F illustrates the orientation of longitudinal and horizontal sections and full diagrams illustrate the section orientations in Chapter 2.2, fig. 1.

Internal structures

Crystallites.

 P_1 elements. It has not been possible to identify individual discrete crystallites in the horizontal sections of P_1 elements. There is, however, a clear fabric within the hyaline crown tissue. In horizontal sections

taken just below the apex of the cusp the structure of the element is clear (Figures 1A-D). Centrally, just beneath the cusp, is the basal body with its long axis aligned with the ventral and dorsal processes. The basal body is completely surrounded by hyaline crown tissue that appears to be composed of crystallites orientated with their long (c) axes parallel with the long axis of the cusp and parallel or oblique to the boundary of the basal body (Figures 1C, D). Longitudinal sections reveal that the crystallites are orientated with their long (c) axes parallel with the long axis of the denticles and oblique or parallel with the boundaries of the basal body (Figures 1E, 2A, C).

P₃ elements. In horizontal sections P_3 elements differ from the P_1 elements because the ventral process makes a smaller angle with the caudal process. This results in the ventral process being aligned with the dorsal process, rather than curving away from the main axis of the element (as in the case of the P_1 elements) (compare Figures 1A to 3A). The crystallites of P_3 elements are arranged with their c axes parallel or slightly oblique with the long axis of the cusp. The crystallite orientation through a zone of approximately 12 μ m around the basal body is unclear, as the tissue appears to be very dense and finely crystalline (see Figure 3D). In longitudinal sections the crystallites are clearly orientated with their long axes parallel or oblique to the long axis of the cusp, sometimes arranged in longitudinal bundles (Figures 4A-D)

Lamellae and growth structures.

 P_1 elements. Within P_1 elements, horizontal sections show that the majority of the hyaline tissue has no clear growth increments and that its texture is dominated by narrow, longitudinal gaps radiating from the margins of the basal body; these extend to the boundary of the element (Figures 1A-D). A faint fabric within the radial structures indicates that there is a very fine lamellar structure developed parallel to the boundaries of the basal body (Figures 1C-D). The radial structure dominates much of the crown tissue at this stage of element growth and is only interrupted where the ventral, dorsal and caudal processes develop denticles (Figures 1B-C). The crystallites are closely packed with no clear orientation or fabric within the centre of each developing process and growth increments are only visible in the last 2 μ m of the crown tissue at the outer boundary of the caudal and ventral processes (Figures 1C, D respectively). The dimensions of the crystallites are too small to measure.

Longitudinal sections of P_1 elements reveal that the crystallites overlap each other, with their c-axes arranged parallel with the long axes of the denticles and cusp (Figures 2A, C, D). The crystallites are slightly oblique to the plane of the section, consequently, only the lower region of each crystallite is visible with the upper region hidden within the section. The resolution of crystallite morphology is lost for approximately 12 μ m around the margins of the basal body, and it is impossible to distinguish between individual crystallites (Figure 2A, B). There is no lamellar structure apparent within the crown tissue in longitudinal sections.

Figures 2C and D show the crystallites adjacent to the apex of the basal body of a P_1 element in a longitudinal section. The crystallites are arranged in longitudinal bundles that are approximately $3\mu m$ wide. This type of crystallite arrangement contrasts with the crystallites seen in Figure 2A where there is clearly no structure.

Section 234 (Figures 5A, B) shows the base of the white matter core of a dorsal process denticle of a P_1 element. Beneath the white matter core, within the crystalline tissue, a concentric structure is visible. The structure is formed by crystallites that are arranged radially, with their oral crystal tips converging in a central cavity that has a diameter of approximately 5 μ m.

In transmitted light, P_1 elements reveal an internal longitudinal fabric within the hyaline tissues that are adjacent to the white matter core of the cusp (Figure 5E). This pattern of internal structure is also seen in the P_3 elements.

 P_3 elements. Horizontal sections of P_3 elements show a radial fabric of narrow, longitudinal gaps radiating from the central basal body that is comparable to that in the P_1 elements. Figure 3A shows how the concentric growth increments about the basal cavity appear disrupted where the caudal process has developed.

Section 218 (Figures 4A-D) shows a longitudinal section through a P_3 element. There are two main structures of crystalline tissue visible in the cusp of the element. It is possible that preservational processes are responsible for the type of crystallite resolution, but there are clearly two types of crystallite fabric present (Figures 4B, C). The faces of the cusp are composed of crystallites orientated in continuous longitudinal bundles that have their long axes parallel with the long axis of the cusp (Figure 4C) whereas the costae of the developing processes are composed of crystallites that have a preferred orientation, but no structure (Figure 4B). Between the bundles of crystallites distinct gaps are generated and truncated between the longitudinal structures. The 'ropes' are approximately 4 μ m wide and vary in length, although 40-50 μ m is common.

Figure 4E shows a P_3 element sectioned horizontally across the base of the element, revealing the tips of the dorsal and caudal processes. The prismatic cores of the distal denticles are clearly visible and the crystallites within are orientated oblique to the plane of the section. The oral tips of the crystallites meet at the central apex of the denticle (Figure 4F).

White matter.

 P_1 elements. In horizontal sections taken just below the apex of the basal body, the white matter cores that occupy the denticles have slightly graded margins (Figure 5A, B) at the hyaline crown tissue boundary. In transmitted light it is clear that the level of white matter secretion within each denticle is aligned with the

rest of the denticles in the process (Figures 5E, 7A-B). Secretion of white matter begins at approximately 10-20µm from the basal body/lamellar crown boundary. The white matter tissue occupies the core of each denticle, with a thin margin of lamellar crown. The aboral base of each white matter core forms a horizontal line, with respect to the aboral edge of the element. The surface of the white matter appears to be structureless (Figure 1A, C).

Longitudinal sections of P_1 elements reveal more structural detail. Denticles of the dorsal process of specimen 234 (Figure 1E) are dominated by white matter tissue. The lower margin of the white matter cores has an uneven boundary that is relatively diffuse (Figure 5A, B). The lateral margins are controlled by the width of the denticle and the upper margins are not revealed in the specimens examined. In photographs taken in transmitted light, however, the white matter cores occupy the entire denticle tip, with only a very narrow hyaline margin (Figure 5E, 7A-D).

The white matter in has three main types of structure. Most common are circular cavities with a diameter of less than 1 μ m (Figure 5A, C) that are arranged randomly. The largest structures are tubules that are normally branched once or twice and randomly distributed (Figures 5B, D). The tubules have a calibre of less than 1 μ m and vary greatly in length, between 2 μ m and 16 μ m. Occasionally the tubules radiate around a larger irregularly shaped cavity, approximately 4 μ m across. At high magnification, it is possible to identify growth increments within the white matter that are approximately 0.4 μ m wide (Figures 5C).

P₃ elements. The morphology and position of the white matter cores found within the denticles of the P₃ elements is comparable to that of the P₁ elements (Figure 5F, 7A-C). Transmitted light images show that there is a concentration of dense white matter tissue towards the aboral base of each white matter core. The white matter within the cusp of the P₃ element is also characterised by sub-circular cavities and tubules. The sub-circular cavities are approximately 0.5m to 2.0 μ m across (Figure 6B, E). The tubules have a calibre of less than 1 μ m, a random distribution and are usually branched once or twice (Figure 6C, E). The lower margin is ragged, but sharp, comparable to the lower boundary of white matter in the P₁ element (Figure 6B).

The white matter in specimen 218 has some interesting structures (Figure 6F). The lower region (described above) of the white matter core is dominated by a characteristic fine crystalline matrix, cut by tubules and cavities. This tissue type gradually grades upwards, towards the apex of the denticle, into a second tissue type that has a coarser crystalline matrix (although it is still impossible to identify individual crystallites) (Figure 6D). This coarse crystallite matrix has regular tubules, some are continuous from the lower tissue type, orientated parallel to each other and parallel with the long axis of the cusp (Figure 6D, F). The calibre of the tubules is approximately $2\mu m$ and the length approximately $6\mu m$ (Figure 6F). It is possible that where some of the tubules are aligned they form a continuous structure (Figure 6F). It is much rarer to see tubules branching in this upper region of the white matter core, and there are no instances of tubules radiating about cavities. Cavities are still present in this second tissue type, but they are commonly longitudinal and aligned with the long axis of the cusp. It has not been possible to identify lamellar structures within the white

matter of the P_3 elements examined, it is thought this is probably due to the quality of preservation. Only one specimen has produced such resolution and detail. However, both P_1 and P_3 elements seen in transmitted light all reveal a similar distribution of tissue types, with a more opaque dense tissue towards the base of each core, and the upper regions dominated by a more translucent tissue (Figure 7A-D).

Basal Bodies.

The basal body of both the P_1 and P_3 elements is a dense homogenous, atubular tissue with a distinct boundary separating it from the crown tissue of the element (Figures 8, 9). In the sections examined the boundary is a gap (normally between 1-3µm across) between the two tissues (Figures 8C, 9A, C-E). Distinct lamellae are clear in horizontal, lateral and transverse sections (Figures 8B, D, 9B, D-E). Transverse sections through processes show that the lamellae are roughly concentric although some of the growth increments are difficult to distinguish and possibly discontinuous (Figure 9A, B). The basal body growth increments are distinguished from the crown lamellae by their complex convoluted structure and discontinuous outline.

Interpretation.

Hyaline tissue. Both the P_1 and P_3 elements of *Baltoniodus* appear to be composed of crystallites that all share a common orientation; parallel or oblique to the long axis of the denticles and the cusp. Within a radius of approximately 12 μ m around the border of the basal body the density of crystallite structure is increased and it is possible that this is due to a reduction in the size of the crystallites (Figures 2A, 3D), although this is not always observed. It is possible that the appearance of the crystallite fabric adjacent to the basal body is different because the orientation of the crystallites is slightly different from the crystallites in the outer margins of the element.

Donoghue (1998) described complex conodont elements as a number of individual prisms, each comprising a denticle. Growth prisms comprise and dominate the internal ultra-structure of individual denticles with crystallites radiating from the lamellar crown/basal body boundary, orientated parallel or oblique with the long axes of the denticles. Although contained within individual increments, the crystallites have a common orientation that is arranged within a three dimensional fan-like, cone in cone structure that is continuous throughout the denticle (Figure 7E). Figures 1A and figure 3A represent horizontal sections through a single growth prism outlining the main vector of growth of the cusp. The regions that disrupt the influence of the single growth prism result from the formation of additional growth prisms where new denticles have developed (Figure 1C, D; 3B). The radial cracks are probably some kind of contraction resulting from loss of organic material or possibly due to etching.

Figure 2D and Figure 4C show longitudinal sections through P_1 and P_3 elements respectively. Of particular interest is the contrasting texture within the hyaline tissues. Figures 4A-C show the contrast particularly well. The surface ornamentation of these elements reveals a similar division of different textures. Cusp faces are dominated by a ropy ornamentation where individual ropes have comparable dimensions to the ropy textures revealed internally (Chapter 1.3, fig. 2C). Externally the cusp faces are divided by strongly defined, high ridged costae, which have smooth, featureless surfaces (Chapter 1.3). It seems that the distribution of surface ornamentation mirrors the distribution of internal crystallite structure (this is discussed fully, in conjunction with a detailed description of the outer surface structures of *Baltoniodus* in Chapter 1.3). This occurrence of different ultrastructures within the same tissue reflects a precise and sophisticated secretory process, the complexities and controls of which are not understood to date.

The secretion of vertebrate enamel has been closely examined and the sequence of its development well understood in mammalian enamel (Boyde, 1976; Berkovitz et al., 1992). Prior to amelogenesis, the division and organisation of cells into secreting ameloblasts is required. The cell increases in length and the internal structure is rearranged in preparation for the secretory process: the nucleus and mitochondria move away from the mineralising interface and the cytoplasm accumulates a supply of rough endoplasmic reticulum and ribosomes. The onset of amelogenesis is marked by an aggregation of vesicles at the secretory pole of the cell, these vesicles fuse with the cell wall and become extracellular, initialising the formation of the matrix for the mineralisation (Osborn and Ten Cate, 1976). The cells retreat orally and aprismatic enamel is deposited immediately adjacent to the dentine surface (Yaeger, 1976). The cells form an extension into the matrix, called a Tomes' process and after the initial aprismatic layer of enamel, the formation of enamel crystals is controlled by the surfaces of each process, resulting in an elongated rod, or prism (Boyde, 1976). When growth is complete, the rods extend from the dentine/enamel junction to the outer surface, the crystallites orientated perpendicular to both the enamel/dentine junction and the outer surface; parallel with the direction of maximum growth. The secreted material is initially formed from both organic and inorganic material, (approximately 30% mineralised) forming a soft, semi-mineralised matrix as the cells retreat orally (Osborn and Ten Cate, 1976). Each rod varies from 3-5µm in width and is aligned perpendicular to the enamel dentine junction. The enamel is fully matured into a hard matrix (95% mineralised) during the final stage of amelogenesis, with the replacement of the Tomes' process with a ruffled surface which facilitates the resorption of proteins and water (Osborn and Ten Cate, 1976). The replacement of the Tomes' process with a straight ruffled edge results in the final layers of enamel lacking internal structures.

The major difference between the enamel and hyaline crown of conodonts, is the apparent continuity of enamel secretion in comparison to the incremental secretion of hyaline conodont tissues. Daily increments are apparent within enamel but they are represented by faint pinching of the rods. Overriding the cross striations is a second pattern of striations known as Retzius striae, which are visible in section as increments marked by brown lines. It is thought that the Retzius lines mark a 4-16 day cycle, and in some cases appear to be represented by (Boyde, 1976, p. 343, fig. 11) narrow gaps. The mechanism that causes this cyclicity is

unknown, however, it is possible that the striae reflect a fluctuating rate of new matrix release that controls the amount of mineral secretion (Boyde, 1976).

If the hyaline tissues of *Baltoniodus* elements were deposited in a comparable way, then the general orientation of crystallites suggests that the secretory organ retreated in an oral direction, parallel with the longitudinal ropes that compose the hyaline tissue. It is possible that the elongate 'spindles' of crystallites found within the P elements of *Baltoniodus* represent individual growth rods and are comparable to those deposited in vertebrate enamel (see below). The presence of this type of structure adds weight to the interpretation of hyaline tissues as a developmental homologue of enamel.

The arrangement of crystallites and the presence of growth increments compares closely to the ultrastructure of enamel (as seen by the similarity in structure between enamel found in the tooth of *Mastodontosaurus* (figured by Smith, 1992, fig. 6c) and conodont ultrastructure. Donoghue and Chauffe (1999) and Donoghue (1998) made similar observations about the ultrastructure of hyaline conodont tissues, and it is followed here that hyaline, lamellar tissue is closely comparable, and developmentally homologous to vertebrate enamel (Donoghue and Chauffe, 1999; Donoghue, 1998; Donoghue *et al.*, 2000; for counter arguments see Donoghue, 1998).

White matter. The dimensions of the white matter structures compare well to those described by Donoghue (1998) (and figured by Zhang *et al.* 1997, p. 71, plate 4, fig. 3) who interpreted the cavities as cell spaces and the tubules as cell processes. Generally the cell processes appear to be random in their distribution, although there is some general alignment with the long axis of the denticle because of the lack of tubules visible in horizontal sections of white matter cores. The apices of white matter cores in horizontal sections possess relatively few structures and are dominated by subcircular cavities. It is possible that these cavities represent transverse sections of tubules.

Donoghue (1998, p. 658) discussed growth cavities within the lamellar crown, beneath white matter cores, and suggested that the cavities might "represent a source of odontoblastic cells that combined with ameloblasts of the forming enamel to produce an enameloid". It is unsure whether the cavity observed in the element of *Baltoniodus* (Figure 5B) compares to the growth cavity figured by Donoghue (1998, p., 656, Fig., 14 e, g). It has not been possible to identify any evidence to suggest that the structure seen in Figure 5B has in any way affected or controlled the deposition of the white matter; further sectioning is required to verify or refute this hypothesis. Contra to this interpretation, the occurrence of common structures in both white matter and hyaline crown tissues suggest that it is possible that the process of secretory processes that formed these two tissues might have been related.

There is a distinct distribution and different nature of the two different tissue types apparent in Figures 6A-F. The lower tissue type in the base of the white matter core is typical of white matter tissue and closely comparable to the white matter figured by Donoghue (1998, p., 642, fig 4b) from a P_1 element of *Ozarkodina*

confluens. The upper region of the white matter core possesses structures characteristic of white matter set in a coarse crystalline matrix, of the type that is perhaps more characteristic of hyaline tissue. This second tissue type is also seen in sections prepared from elements of *Parapachycladina peculiaris* Zhang figured by Zhang *et al.* (1997, pl. 4, fig. 3). The tubules are continuous between the two tissue types. Only one specimen has revealed such clear resolution, but its close comparison to the tissue type figured by Zhang *et al.* (1997) suggests that a more extensive survey will reveal more cases, thereby broadening the number of tissue types that represent white matter. Also, the transmitted light images of white matter consistently show a concentration of a more opaque tissue within the white matter cores which grades into a more translucent tissue above (Figures 5E, F; 7A-D). This probably confirms the presence of a more opaque ultrastructure towards the base of white matter cores.

The regular presence of thin $(0.4\mu m)$ lamellae within the white matter tissue is in contrast to observations made by other conodont workers (e. g. Barnes *et al* 1973; Donoghue, 1998, p. 641). However, increments are clearly visible within the white matter tissues of *Baltoniodus* (Figure 5C). In the case of *Baltoniodus* the white matter possesses structures common to the crown tissue (course crystallites and a fibrous structure), and the crown tissue possesses structures common to white matter (tubules of the white matter also seem to be present in a hyaline-like tissue).

A histological study of three Devonian conodont taxa also included a detailed description of the component tissue types (Donoghue and Chauffe, 1999). The sections did not all reveal as much resolution as seen in the sections presented for this study, but the basic structural integrity compares. Interestingly, elongate columns (5-10µm wide) of white matter were described in one species, that extended from the aboral regions of the denticle, to the outer surface. These elongate columns corresponded to the surface polygonal ornamentation and suggested to Donoghue and Chauffe (1999, p. 290) that "each of the paraprisms [columns] were secreted by an individual cell, a condition met with in the developing enamel of at least some mammals". The elongate structures found within the elements of *Baltoniodus* can also be compared to structures found within mammalian enamel. The dimensions and position of the rods found within mammalian enamel (Boyde, 1976, p. 344, figs 13, 24; Yaeger, 1976, p. 54, fig. 3-11) compare well with the elongate crystalline structures of *Baltoniodus*; this suggests that each rope may have been secreted by an individual cell during the development of the tissue.

The presence of structures typical of white matter tissue and hyaline tissues within the same tissue type complicates Donoghue's (1998) proposal that the secretion of the crown and white matter tissues were independently controlled. It is more likely, as stated by Donoghue *et al.* (2000), that they were deposited synchronously from the same cell population.

Basal body tissue.

The basal bodies of *Baltoniodus* are composed of distinct lamellae that are contorted and convoluted (Figures 8B, 9B), and show none of the variation that has been found in other taxa (Müller and Nogami, 1971; Sansom *et al.*, 1992; Kemp and Nicoll, 1995; Sansom, 1996). The tissues described here compare well with those described and interpreted by Donoghue (1998) for the *Ozarkodina* taxa. The tissue within the basal bodies of *Baltoniodus* elements compare particularly well with the ultrastructure seen towards the centre of the basal body of *Ozarkodina confluens* figured by Donoghue (1998, p. 640, fig., 3j) where similar irregular, convoluted increments can be seen. Donoghue stated that he had observed a disruption of the lamellar tissue at the flanks of the basal bodies of ozarkodinid elements; however, it has not been possible to achieve sufficient resolution or find elements well enough preserved to search for comparable features in elements of *Baltoniodus*. This is probably because the basal body tissue from the crown tissue. The tissues of *Baltoniodus* are atubular and lamellae and are amongst the basal body tissues that Donoghue (1998) and Donoghue *et al.* (2000) have interpreted as forms of dentine.

The growth of Baltoniodus variabilis P elements.

Sweet, in the *Treatise*, (1981) states that a primary process is a process that is continuous from the cusp at the proximal end of the process and that its basal cavity is continuous with the basal pit of the cusp. The P_1 and P_3 elements of *Baltoniodus variabilis* are pastinate prioniodontid P elements, with three primary processes. The internal structure shows that, in both cases, during the early stages of ontogeny there was a clear junction between the lateral process and the main axis of the element.

This shows that the nature of a primary process is not as simple as its definition implies. The sections of *Baltoniodus variabilis* P elements have revealed that the processes erupting from the cusp did not develop simultaneously and that during very early stages of ontogeny *Baltoniodus variabilis* P elements were angulate or carminate in shape (approximately 100-150µm in length) and not pastinate. This sequence of process development provides previously unknown information about the heterochronic pattern of growth, that is not revealed externally.

Knowledge of the sequence of process development and the timing of eruption of processes could provide additional information to help recognise homologous elements and elucidate evolutionary relationships.







Figure 2. Longitudinal sections through P1 element of *Baltoniodus variabilis*. A-C Specimen 234. Longitudinal section through dextral element. A. Close-up of dorsal process denticle. B. Close-up of lamellar crown/basal body boundary beneath dorsal process. C. Close up of apex of basal body beneath cusp and adjacent crown tissue. D. Specimen 213, longitudinal section, detail showing ropy texture adjacent to basal body of crystallites within cusp, seen towards the left of the image.



Figure 3. Sections of P3 elements of *Baltoniodus variabilis* orientated with dorsal process towards bottom of page and ventral process towards the top. A-C Specimen 206, approximately 50um from apex of basal cavity, horizontal section of sinistral element. A. Whole image, dorsal process directed towards base of image. B. Close up of crystallites adjacent to basal cavity. C. Close up of crystallites seen in D, laminations can be seen in detail running from top right to bottom left of image, the crystallites are being viewed with their c axes perpendicular to the plane of section. D. Specimen 206, 100um from apex of basal cavity.



Figure 4. Sections through P3 element of *Baltoniodus variabilis*. A-C. Specimen 218 longitudinal section of dextral element, the ventral process has been biscected by the section and is central of the image, the dorsal process is directed towards the right and the caudal process towards the left. A. Whole image. B. Close up of crystallites of ventral process costa. C. Close up of ropy crystallite structure of the dorsal face of the cusp. D. Figure showing the approximate location of figures B and C. E-F. Specimen 220, horizontal section of sinistral P3 element. E. Whole image, dorsal process towards bottom of page, ventral to the right and caudal to the left. F. Close up of dorsal process denticle.



Figure 5. White matter in P1 elements of *Baltoniodus variabilis*. A-D Specimen 234 (also seen in figure 1E), longitudinal section denticles of sinistral element. A. Dorsal process denticle. B. Close up of possible growth cavity beneath white matter core seen in A. C. Close up of laminations in white matter of A. D. Close up of cavity seen in A, at base of white matter, surrounded by radiating, branched tubules. E-F Elements of *Baltoniodus* in transmitted light. E. Specimen 262. Dextral P1 element. F. Specimen 13. Dextral P3 element. Scale bars 200um.



Figure 6. Longitudinal section of sinistral P3 element of *Baltoniodus variabilis* showing white matter in cusp. A-F. Specimen 218. A. Cusp with two types of white matter. B. Close-up of boundary lower boundary of white matter. C. Close-up of tubules in lower tissue type. D. Close up boundary between two types of white matter. E. Close-up lower white matter tissue. F. Close-up of upper white matter tissue.



Figure 7A-D. Internal structures of white matter in denticle cores of P elements of *Baltoniodus variabilis*. A-C, P3 element, specimen 386. A. Lateral view, scale bar 200um. B. Close-up of dorsal process, showing denticles with white matter cores. Most dense areas show up in white at the base of the denticles, scale bar 100um. C. Close-up of cusp seen in A, most dense area towards base of the white matter core, corresponding with dense tissue seen in section, cusp width 80um. D. P1 element, specimen 387, base of white matter core seen in of cusp. Dense tissue seen in black, tubules visible towards centre of cusp, continuous between the dense base and denticle tip, cusp width 100um. E. Diagram to show the proposed radiating cone in cone arrangement of crystallites within lamellae of denticles and cusp.



Figure 8. Longitudinal sections of the basal body of P1 elements of *Baltoniodus variabilis*. A. Specimen 164, sinistral element, dorsal process towards left of image and ventral process sectioned in centre, caudal process towards the right. B. Close up of laminations in basal body of ventral process, seen at the apex of the cusp A. C. Specimen 234. Sinistral element, orientated as for A. D. Close up of laminations of basal body beneath dorsal process seen in C.



Figure 9. Basal bodies of P elements of *Baltoniodus variabilis*. A. Specimen 213. Transverse section through ventral process of sinistral P1 element. B. Close-up of A, showing convoluted laminations in centre of basal tissue. C-E. Specimen 220 horizontal section through sinistral P3 element. C. Whole section with dorsal process directed towards bottom of page, venral towards the right and caudal towards the top. D. Close-up of distal denticle of dorsal process. E. Close-up of basal tissue and laminations about the junction of the caudal process (directed towards top of page).
CHAPTER 1.3

THE PRIMARY SURFACE MICROSTRUCTURES OF P ELEMENTS BELONGING TO BALTONIODUS VARIABILIS

Introduction.

Throughout the range of *Baltoniodus*, the basic morphology of the elements within the apparatus change little (Figure 1) and it is subtle changes in element morphology that merit the division of species. The primary surface microstructure of *Baltoniodus* elements is simple and it is shown here that there is a strong link between the internal structure of the element and its external surface microstructures.

Pierce and Langenheim (1970) examined the surface patterns found on selected Mississippian conodonts and identified smooth surfaces, reticulate networks and parallel columns. Importantly it was noted that there was a taxonomic division reflected in the occurrence of different ornamentation forms. Pierce and Langenheim (1970, p. 3228) followed Hass (1941) by suggesting that the polygonal network, that represented the reticulate ornamentation, was best explained as "duplicating surface features of the tissue that covered the conodont". The parallel columns were described as bundles of spindle like fibres aligned with their long axes parallel with the long axes of the denticles and cusp. These columns were likened to the microstructures found on the teeth of Mississippian fish.

Lindström and Ziegler (1971) presented a detailed paper that took advantage of the advances in SEM technology and described the internal and external structures of Panderodontacean conodonts. The ultrastructure of the individual tissue types was described and the characteristic furrows and basal wrinkles were examined. Lindström, McTavish and Ziegler (1972) extended this study to include the Prioniodontidae a year later. They observed that longitudinal striae (comparable to the spindle like bundles described by Pierce and Langenheim [1970]) dominated the surface microstructure of the prioniodontid conodonts examined and provided detailed descriptions of its distribution. The longitudinal striae were observed to be aligned with the long axis of the element, and were actually convex ridges on the element surface, approximately 1µm wide at the tip of the cusp and 2.5µm towards the base. The authors thought that the "vertical striation on denticles is related to the orientation of prism surfaces of crystallites" (Lindström, McTavish and Ziegler, 1972, p. 33).

Amongst the basic different kinds of surface microstructures Lindström and Ziegler (1981, p. W42) identified "primary micro-ornamentation striae" as the most common type to be found on conodont element surfaces. The authors proposed that there was a strong relationship between the morphology of the coarse striations and the orientation of the crystallites within the tissue. Internal structural observations revealed apatite crystals "arranged with their prism surfaces (c axis) parallel to the direction of growth" (Lindström and Ziegler, 1981, p W45, 46). Therefore the crystallites in the flanks of the cusp and denticles were oriented with their c-axis parallel to the ropy ornamentation commonly found on denticle surfaces, parallel to the long axis of the

denticle and parallel or oblique to the outer surface. Lindström and Ziegler (1981) suggested that this crystallite orientation may have influenced the surface ornamentation. There were originally six different kinds of surface microstructures described, including smooth surfaces, coarse and fine striations, longitudinal furrows, basal wrinkles, microdenticles and dental pits (Lindström and Ziegler, 1981). This study was based on the panderodontid conodonts.

Burnett and Hall (1992) also thought that the form of surface microstructure was related to crystallite orientation in the tissue beneath. They observed that crystallite orientation showed that the crystals grew with their c-axis "parallel to the maximum growth axis" (Burnett and Hall, 1992, p. 275). The authors noted that the crystallites within the platform areas of elements had their c axes perpendicular to the outer surface, and the crystallites within the denticles and cusp, beneath the striated microstructures, had c axes that were oblique or parallel to the outer surface. This orientation of crystallites was thought to point to "conodont secretion by a laterally continuous (epithelial?) tissue" (Burnett and Hall, 1992, p. 275) and suggested that the striations on denticles and the cusp possibly reflected apatite deposited by columns of secretory cells.

Donoghue (1998) described crystallites within simple coniform elements as being arranged with their long (c) axes parallel or subparallel to the long axis of the element. He also noted (1998, p. 641) that "in more complex elements the prismatic structure of the element is broken up into a number of individual prisms, each comprising a denticle" (discussed fully in Chapter 1.2) Donoghue (1998) states that where the element is not developing new morphological features and successive growth increments are simply increasing the size, the crystallites within the lamellae are normally oriented perpendicular to the outer surface. He thought that the presence of the prismatic structure within denticles and the elaborate and varied surface ornament present in some taxa suggested that the method of enamel secretion was extremely sophisticated.

Donoghue and Chauffe (1999) published a meticulous study of three enigmatic Devonian microfossils that were alternatively interpreted as conodont elements or fish scales. The histology of the fossils was found to be directly comparable to conodont elements and contained tissue types that were unique to conodonts, thereby confirming their affinities. The fossils were characterised by ropy surface ornamentation (comparable to the striated surface ornamentation described above) and polygonal ornamentation. Donoghue and Chauffe (1999) were able to show that the micro-ornament of the conodont elements examined were indistinguishable from that of other vertebrates.

Dzik (2000) based their understanding of morphogenesis of conodont elements on the distribution of surface ornamentation. The polygonal imprints were thought to represent ameloblast imprints, and the longitudinal ornamentation, the imprints of ameloblasts that had experienced extension and become translated orally, during the secretory process.

Enamel has three characteristic internal structures: rods (prisms), cross striations and striae of Retzius (discussed fully in Chapter 1.2). The rods are formed of bundles of enamel crystallites aligned with their long c-axes parallel with the long axis of each rod. Externally the rods normally have no expression, as the final stages of maturation form a structureless margin. If the outer layers of the tooth are etched away, it is possible to expose subcircular structures that represent cross section of the rods. The subcircular structures represent the presence of Tomes' processes, forming a pit in the oral surface of each rod during secretion (see Chapter 1.2). The structures normally form a key hole shape in human enamel, but the range of surface polygons varies greatly throughout the different mammalian groups (Boyde, 1976, p. 342, fig. 8). Within human enamel, the rods are never expressed externally in a longitudinal section with respect to the oral surface of the tooth due to the final stages of maturation, when the Tomes' processes are lost and the final layer of enamel is aprismatic. When the enamel is artificially fractured, the rods are arranged longitudinally, perpendicular to the outer surface (Boyde, 1976, 351, fig. 24).

Materials and Methods.

The elements of *Baltoniodus* examined in this study were collected from the Suhkrumagi section, located within a road cut in the SE part of Tallinn (for details of locality see Kaljo and Nestor, 1990). The limestone was dissolved with a buffered, 10% solution of acetic acid and the elements separated from the residue with bromoform heavy liquid before picking.

The elements are well preserved, with good detail of denticles and gross surface ornamentation. This study has concentrated on the P elements of the apparatus. Both P elements are pastinate, but the P_1 element differs from the P_3 element by having a proportionally smaller dorsal process and a slightly different disposition of processes about the cusp (see Figure 1).

Elements were examined using the scanning electron microscope to search for well preserved specimens and distinguish the different types of surface microstructures.

Surface microstructures of P elements of Baltoniodus.

 P_1 and P_3 elements of *Baltoniodus* possess two basic types of surface microstructures: coarse ropy ornamentation (Figure 2C) and smooth surfaces (Figure 3E). The coarse ropy ornamentation is equivalent to the longitudinal striations described by Lindström, McTavish and Ziegler (1972), Lindström and Ziegler (1981) and Burnett and Hall (1992). The term 'ropy ornamentation' is preferred to striation as this clearly refers to rounded, longitudinal ridges and better describes the morphology, rather than striations which could refer to a flat surface which has striations or scratches within it (cf. Purnell, 1995).

The coarse ropy ornamentation occurs on the flanks of the cusp, diverging from the cusp tip, with the ropes gradually becoming reduced in width towards the base of the cusp (Figure 2A, B). Where the ropes converge at the tip of the cusp they are typically 3-5 μ m across (Figure 2A). Approximately half way down the cusp the ropes have similar, or slightly larger dimensions before narrowing towards the base of the cusp (figure 2B. Each rope is tightly packed against the adjacent rope and where each end narrows, the spaces generated between adjacent narrowed ropes are filled by the narrow ends of new ropes (Figure 2C, 3C). Occasionally the ropes bifurcate aborally, where one wide tip towards the apex of the cusp will become two towards the base. The bifurcation junctions are not always smooth and are sometimes confused and slightly overlapped (see Figure 2C) The ropes narrow rapidly towards the base, ranging from 6μ m to less than 1μ m in only one third of the cusp height. At the base of the cusp each individual rope narrows slowly to a point, and is replaced by a narrower one. This results in very narrow ropes around the lower boundary of the cusp (figure 2B, D).

The lateral extent of the ropy ornamentation on the cusp is constrained between the distinct costae of the three processes (Figure 2C). The costae form borders for the ropy ornamentation and are themselves smooth and featureless (Figure 2C). Where denticles of the ventral and dorsal processes have developed, the ropy ornamentation expands laterally from the base of the cusp and continues developing parallel with the long axis of the cusp but only at the base of the denticles (Figure 2D). This leaves the surfaces of the denticles smooth without any surface microstructures (Figure 3F). The denticles of processes, and the process flanks, distant from the cusp are smooth and have no ornamentation. The large lobe which develops off the dorsal process is also smooth with no ornamentation (Figure 3E).

Interpretation.

The elements of *Baltoniodus* show a simple type of surface ornament and the specimens examined appear to lack any reticulate ornament as observed on some other conodonts (e. g. Lindström and Ziegler, 1981). It is likely that the simple surface microstructures are controlled by an equally simple internal crystalline structure. Sections have shown that the elements of *Baltoniodus* appear to have an internal crystallite fabric that is similar to that described by Branson and Mehl (1933a) as fibrous and constructed of long needle like crystals orientated parallel to the growth axis. Branson and Mehl (1933a) proposed that the fibrous conodonts differed from other conodont elements by having no lamellae, although this was later discounted by Barnes *et al.* (1973) who described lamellae that were composed of elongate needle like crystals.

The sections of elements of *Baltoniodus* have revealed that the flanks of the cusps are composed of elongate, spindle like bundles of needle-like crystallites that do not have a lamellar structure when sectioned (see chapter 1.2, Figures 2D, 4C). It is thought that the pattern of secretion is constructed of new hyaline tissue with lamellae that are not clearly distinguishable because of the large ropy structures. The pattern of deposition in this case is in elongate ropy structures and it is these which are reflected at the element surface.

It is possible that the ropy ornamentation found on the flanks of elements corresponds to the rods that are found within the enamel of human teeth, their composition and dimensions are comparable. The orientation of the crystallites within seems to support this suggestion, as they, like those within human enamel tissues are perpendicular to the basal body/lamellar crown junction (thought to be homologous to the enamel/dentine junction in enamel, see Chapter 1.2).

One of the main differences between the ultra-structure of enamel and the hyaline tissues of an element of *Baltoniodus* is the orientation of crystallites with respect to the outer surface. In human teeth, the crystallites are oblique to the outer surface, within *Baltoniodus* they appear to be almost parallel. This would seem to suggest that the ameloblasts would have had to retreat orally, in a direction parallel with the long axis of the cusp. This presents extreme difficulties envisaging how and where the cells could accumulate with respect to the element surface; however, the close similarity of the structures is convincing.

There are no polygons at the denticle surfaces, to support the theory of Dzik (2000), nor are there any elongated polygons at the flanks of the cusp and denticles.

Smooth areas of the elements have shorter narrow crystallites which are very closely arranged and do not display such a fibrous nature. For example, the costate area of the cusp is clearly visible in section because the crystallites have a more homogenous close structure in comparison with the fibrous ropy bundles of the cusp face that are next to this tissue.

Conclusion.

The elements of *Baltoniodus* are not directly comparable to the fibrous conodont elements described by Branson and Mehl (1933a) because of their ropy ultra structure which is visible externally as well as internally. However, such a dominance of ropy ornamentation could possibly account for the early misinterpretation of lamellar structure of fibrous conodonts. The external micro-structure is subtly different to forms of micro structure found on P elements of *Eoplacognathus* which also possesses a ropy ornament (see Chapter 2.2).

The lack of clear laminations and the presence of continuous ropy ornament might suggest that elements of *Baltoniodus* underwent longer periods of continuous growth, than has been suggested for other conodonts (Donoghue, 1998), if the ropes represent hyaline crown deposited by a single secretory cell.

This internal structure has not been described before but forms similar to the external structure are common to many of the Prioniodontidae. It is possible that studies of the surface microstructures and their variation across different taxa will help to provide diagnostic characters that will be useful as taxonomic characters.





Figure 1. Elements of *Baltoniodus variabilis*. A Dextral P1 element, lateral view. B. Dextral P3 element, lateral view. C. Dextral P1 element, oral view. D. Dextral P3 element, oral view.

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Figure 2. P1 element of *Baltoniodus variabilis*, Specimen 236. A. Cusp tip showing worn ropy ornament. B. Base of cusp between caudal and dorsal processes. C. Close up of B, showing detail of ropy ornament. D. Ropy ornament at base of caudal process. E-F. Close up of ropy ornament on cusp, showing primary ropy ornament in E, and worn flattened ornament in F, closer to the apex of the cusp.



Figure 3. Specimen 236, Dextral P1 element of *Baltoniodus variabilis*. A. Base of cusp between caudal and dorsal processes. B. Base of cusp on inside of element next to ventral process. C. Ropy ornament on cusp showing grading of rope sizes. D. Base of cusp showing grading into micro ropes. E. Lobe of platform showing lack of ornament. F. Denticles showing lack of ornament.

CHAPTER 1.4

FUNCTION OF PELEMENTS OF BALTONIODUS VARIABILIS

Introduction.

Baltoniodus, classified amongst the Balognathidae, represents a successful lineage that appeared in the Early Ordovician and ranged, through a succession of species, to the end of that period (Sweet, 1988). The general morphology of the P elements within the apparatus of *Baltoniodus* is common to most of the balognathids. Therefore, an understanding of the function of these elements may provide a useful model against which the function of other balognathids can be tested. The apparatus of *Baltoniodus* is composed of two pairs of opposing P elements, P_1 and P_3 (Figures 1A-D), and an array of S and M elements (see Chapter 1.1 for discussion). A study of internal structures (Chapter 1.2) and a detailed analysis of element surfaces (Chapter 1.3) are combined with a clear understanding of apparatus architecture to propose a hypothesis of function.

Promissum is the only prioniodontid that is clearly represented by natural assemblages (Aldridge *et al.*, 1995). Consequently the architecture of *Promissum* is the only prioniodontid apparatus known with a high degree of confidence. This potentially provides an invaluable template for reconstructing other prioniodontid taxa. Crucial information can be incorporated into functional models, with regard to the location of different elements and their orientation with relation to the opposing element. Aldridge *et al.* (1995) reconstructed the apparatus of *Promissum* and provided terminology for the apparatus and elements (Figure 1E and Chapter 1.1) based on the original terminology proposed by Sweet (1981; 1988). Purnell *et al.* (2000) introduced a new terminology that can be used exclusively to infer homologies (Figure 1F and Chapter 1.1). The new terminology has been designed to operate alongside the system introduced by Sweet (1981, 1988). The new system can be applied to elements that can be recognised as homologous to the well known elements of the original terminology. The new terminology and biological orientations are incorporated into this work, and the homologies recognised by Purnell *et al.* (2000) for the apparatus of *Promissum* are followed.

The apparatus of *Promissum* is composed of four pairs of opposing P elements at the caudal end of the apparatus termed: P_1 , P_2 , P_3 and P_4 . P_1 , P_2 and P_3 elements of *Promissum* have their conventional 'posterior' directed dorsally (see Chapter 1.1) and the 'anterior' process directed in a rostral direction. The 'posterior' process is designated the dorsal process, because the process junction is directed dorsally. The 'lateral' process is designated caudal, as it develops off of the caudal face of the cusp before becoming directed ventrally. Finally, the 'anterior' process is initially directed ventrally before curving round to a rostral position, and is therefore, termed a ventral process. The element of *Baltoniodus*, commonly known as Pa, is homologous to the element that occupies the P_1 and P_2 position in the *Promissum* apparatus; it is, therefore, termed P_1 here (see Chapter 1.1). The Pb element of *Baltoniodus* is homologous with the element that

occupies the P_3 position in the *Promissum* apparatus and is consequently called a P_3 element (Chapter 1.1, 1.2).

Previous research into conodont element occlusion.

Early functional studies have been restricted to indirect methods that were poorly constrained due to the paucity of evidence. Viira (1972) described the asymmetry of selected Middle Ordovician platform conodont elements, concentrating on *Ambalodus*, *Eoplacognathus* and *Polyplacognathus* (the *Polyplacognathus* elements are now reconstructed as part of the apparatus of *Eoplacognathus* (Bergström, 1971; Chapter 2.1). Important morphological comparisons were made, though not associated with function at that time.

Jeppsson (1971) made detailed observations of the asymmetry displayed by sp and oz elements (P_1 and P_2). Jeppsson reconstructed possible occlusal models for pairs of P_1 elements based on simple line drawings, but the dimensional drawings copied from work published by Lindström (1964). Jeppsson was, however, still able to suggest that platform elements of ozarkodinids, that had developed asymmetrical blade morphologies, might have "passed by each other and in that way navigated the remaining parts of the elements together" (1971, p. 119). This was an important observation which was not thoroughly verified until Purnell and Donoghue (1997, 1998) and Donoghue and Purnell (1999a) considered pairs of elements dissected from natural assemblages and compared them with discrete elements to test a similar hypothesis. Jeppsson's occlusal models were based on basic morphological constraints, which alone were not reliable criteria; Purnell and Donoghue's (1997) models were also based on morphological constraints but further verified by rigorous tests including direct evidence from natural assemblages, patterns of surface wear and damage and internal discontinuities.

Nicoll (1987, 1995) expanded the work of Jeppsson, but where these authors were unable to find elements whose morphology allowed them to occlude, the hypothesis of occlusion was rejected. The authors identified no constraints for the paired reconstructions proposed i. e. element orientations within the apparatus derived from bedding plane assemblages, but had an *a priori* hypothesis of function which precluded other modes of function. Nicoll (1995) envisaged that condont elements functioned as opposing tissue covered supports. Direct element on element occlusion was refuted because of a lack of apparent surface damage. It was proposed that the morphology of some condont elements would have prevented close occlusion; therefore the authors concluded that condont elements could not have functioned like teeth. These tests were not sufficient to prove the tissue-cover hypothesis nor to refute a tooth like function. Purnell and Donoghue (1998) noted that the authors might have been unable to find elements that could obviously occlude together because the elements were from different individuals. Also, the type of function being envisaged may have been too constrained and some of the elements (particularly elements of *Oepikodus* Nicoll, 1995, p 257, Text fig. 10) could well have functioned like teeth, but not necessarily in close opposition. Evidence of surface

damage is rare because it is dependent on the preservation and identification of microscopic damage on the denticle surfaces that can be attributed to *in vivo* functional damage and distinguished from post-mortem damage.

Weddige (1990) produced the first detailed paper that described conodont elements that exhibited what he interpreted as pathological conditions resulting from function. Weddige focused on examples of elements that had experienced damage due to food processing or occlusion and been subsequently repaired or 'adapted' for subsequent function. The identification of 'adapted' morphologies was flawed due to the author's assumption that the morphology of elements and development of denticles and processes directly reflected the functional mechanism of the conodont elements. Weddige described basic element damage and repair that was clearly due to function, but failed to identify this as damage due to regular use, he preferred to identify these elements as abnormal. For example, the condition he termed 'fusio', where the element figured has clearly worn and broken denticles that have been overglazed as the new crown tissue has regenerated the oral surfaces of the denticles (Weddige, 1990, p. 588-89, pl. 4, 3b, 7b). If this element had been examined internally and its position within the apparatus considered, it is likely that this would prove to be an example of unequivocal functional damage, providing direct evidence of how the element was used during the life of the conodont.

Purnell (1999) summarised the difficulties of undertaking functional analyses on disarticulated conodont elements. He pointed out that conodont element functional analyses have long been hindered by a poor knowledge of what conodonts are or even of how their skeletal apparatus was constructed. He therefore concentrated on identifying microscopic features of wear (microwear) on element surfaces as the "closest possible approximation of functional data in fossils" (Purnell, 1999, p. 140). These surface textures have been directly compared to surface textures found on mammalian teeth. Basic textures have been identified: "distinctive polishing, and scratched or pitted surfaces caused by *in vivo* action of abrasive food and by the compressive and shearing forces that act on enamel during feeding" (Purnell, 1999, p. 142). However, recognising direct microwear on conodont elements is complicated by the potential confusion of possible post-mortem damage. This problem can be avoided by only analysing conodont elements that are have well preserved primary surface ornamentation and only have damaged surfaces in specific areas i. e. on one side of the denticles of a process. If these areas of damage are repeated on several specimens, then functional damage can be inferred and incorporated into a functional model.

Some of the most recent papers addressing ozarkodinid element function (Purnell, 1995; Purnell and Donoghue, 1997; Donoghue and Purnell 1999a and b) have shown that it is possible to test different hypotheses of function by considering evidence of internal discontinuities, surface damage and microwear. Using this approach, functional models for conodonts only represented by disarticulated elements can be proposed and tested.

Materials and Methods.

The elements of *Baltoniodus* examined in this study were collected from the Suhkrumagi section, located within a road cut in the SE part of Tallinn (for details of locality see Kaljo and Nestor, 1990). The apparatus of *Baltoniodus* is composed of two morphologically differentiated pastinate P elements, one pair of geniculate M elements and a single alate S element and four pairs of S elements: two bipennate pairs, one quadriramate pair and one tertiopedate pair. This study has concentrated on the P elements of the apparatus. The P elements are pastinate. P₁ elements differ from the P₃ elements by having a proportionally smaller ventral process and a slightly different disposition of processes about the cusp (see Figures 1A-D).

 P_1 elements have a large cusp about which three denticulated processes are disposed. The dorsal process is generally the longest, or of subequal length to the caudal process and is straight, forming an angle of 90° with the cusp in oral view, the denticles that are often fused together towards the base (Figures 1A, C). The caudal process forms a junction with the caudal face of the cusp, and plunges in a ventral direction making an angle of approximately 160° with the aboral margin of the dorsal process when viewed laterally (Figures 1A, C). The long axes of the denticles are parallel with that of the cusp (Figures 1A, C). The ventral process is short, developing from a costa that originally developed from the ventral face of the cusp, but directed rostrally forming an angle of 90/100° with the dorsal process when viewed orally (Figures 1A, C). The denticles are small and fused.

 P_3 elements are also pastinate and share many of the general characteristics of the P_1 elements. In this case, however, generally the caudal process is longest. The angle between the aboral margins of the dorsal and caudal processes, when viewed from the lateral/rostral direction is approximately 90-100° (Figure 1D). In the case of the P_3 element the ventral process is longer, with larger denticles developed, than the corresponding process of the P_1 element (Figure 1D). Both the P_1 and P_3 elements of *Baltoniodus* vary in the disposition of processes about the cusp. The caudal process shows the most plasticity, whereas the ventral process maintains a relatively consistent angle of approximately 90-100° with the dorsal process, when viewed orally (Figure 1B).

More than 20 P_1 and P_3 elements were examined using a scanning electron microscope and a transmitting light microscope to search for evidence of wear and repair due to function. Scaled plasticine replicas were used to test possible functional hypotheses and to test the possible movement of element when orientated in their correct positions within the apparatus. It is hypothesised that the elements were used to either collect and direct food towards the oral cavity of the conodont, or to process and break up food, as in the case of some ozarkodinids (Purnell and Donoghue, 1997).

Methodology and a hypothesis of function.

Plasticine replicas. Using scaled replicas of the elements of *Baltoniodus* to test for possible methods of element occlusion shows that the large cusp and the disposition of processes about this cusp preclude direct process on process contact in both elements. If a precise occlusion was achieved and parts of the elements occluded against each other with denticle tips or the cusp coming into contact, then discrete facets, or damage to the denticle tips would be expected.

The *Promissum* template. P_1 and P_2 elements of *Promissum* are located at the posterior of the apparatus opposing each other across the mid axis of the apparatus. They are positioned with the long axis of each element aligned opposite the long axis of the opposing element, with the concave face of the cusp directed dorsally. The ventral process curves away from the main axis of the element in a rostral direction. If the elements of *Baltoniodus* are placed in this position, it can be hypothesised that their cusps would come into contact first, and possibly the denticles immediately adjacent to the cusp as the elements met across the mid axis of the apparatus (Figures 2A, B).

The P_3 elements of *Promissum* are opposed across the sagittal plane, both elements orientated with the concave face of the cusp directed dorsally. Because there is such a wide angle between the ventral and caudal processes they appear to form a straight line that is parallel with the long axis of the apparatus, opposing across the mid axis of the apparatus with the denticles inclined slightly dorsally. With the P_3 element of *Baltoniodus* positioned within the apparatus with this orientation, the cusps would have prevented any close occlusion of the processes. In this position, if the elements were in contact with food materials, then the denticles of the ventral and caudal process that were adjacent to the cusp, are likely to have been worn down during food manoeuvring or processing (Figure 2B).

Hypothesis of function.

Both the plasticine replicas and the element orientation within the apparatus suggest that the function of *Baltoniodus* P elements was simple. Both types of P element possessed a prominent, large projecting cusp and were positioned directly opposite the opposing element, thereby severely constraining the complexity of any occlusion. It is likely that the cusps of the P_1 and P_3 elements would have been the first part of each element to encounter food as the elements moved together across the mid axis of the apparatus, whether processing or manoeuvring items. This model of function would result in the cusp and the adjacent denticles being prone to damage, the surfaces of these regions of the elements would be expected to exhibit evidence of wear.

Testing the hypothesis.

Surface evidence. P_1 elements. Figures 3D-E and 4C show denticles that are immediately adjacent to the concave face of the cusp on the dorsal process of a dextral P_1 element. Six denticles are clearly truncated and broken and appear to be more damaged and sheared on the rostral side of the element. The opposite side, orientated towards the caudal end of the apparatus, appears to show less direct damage though all the denticles are rounded and truncated. The broken surfaces of these denticles appear smooth and do not display any jagged edges or clean breaks that would be expected if damaged during processing or handling. The denticles towards the end of the process are not rounded and truncated (contrast Figures 4C with 4D) and appear large and discrete in comparison. Denticles at this end of the process often show small grooves parallel to the long axis of the denticles. This shows that the process has grown rapidly and has overglazed and incorporated two denticles into one (Chapter 1.3, fig. 3F).

The ventral process is continuous with a costa on the ventral face of the cusp, and develops small denticles on its lower half Figure 3B. Denticles on both the ventral and the caudal processes show no clear evidence of wear. The costa of the ventral process is sometimes extremely smooth and almost flat on the upper half of the cusp Figure 4F. This is possibly evidence of polishing and smoothing as food particles wore away prominent surface features. It is unlikely to be element on element contact, as this would be expected to cause more damage and discrete facets either on the processes or denticle tips.

The cusp tip exhibits the most convincing evidence of wear (Figures 4B, E and F). In specimen 236 in figure 4B the tip has not been broken and it is clear that a wear facet has been polished out of the ventral face of the cusp tip. The characteristic ropy texture has also been lost around this region, providing evidence of continued polishing of the tip of the cusp during food processing or manoeuvring (Figures 4B, F).

Surface evidence on P_3 elements also reveals evidence of wear. Denticles adjacent to the cusp on the dorsal, ventral and caudal processes exhibit evidence of truncation and damage Figure 5A-F. All the denticles of the dorsal process appear to be approximately the same width, (when viewed laterally), but are much shorter, rounded and sometimes all truncated to a level ridge close to the cusp (Figures 5A-B). Denticles of the caudal process are often broken, damaged and overglazed (Figures 5C-D). The ventral process of the P_3 element is often represented by a ridge running from the ventral face of the cusp, and it is difficult to observe if this area of the element has been worn (Figures 5E, F) or is displaying its original surface morphology. P_3 elements also exhibit loss of the ropy texture at the tip of the cusp.

Internal structures. Examination of P elements of *Baltoniodus* in transmitted light reveals a simple internal structure (Figures 6A, B). The denticles and cusps of both the P_1 and P_3 elements are occupied by white matter. All of the denticles and cusps have this internal structure and are normally more than two thirds occupied by the albid tissue which has a straight lower boundary (Figure 6B). The external surface

structures are characteristic of hyaline tissue, suggesting that there is a thin layer of hyaline crown around the white matter core, this is also confirmed by a thin margin of hyaline tissue apparent in transmitted light. During stages of regeneration the hyaline layer must be subsumed between the old and newly generated white matter before the phase is completed with a new thin hyaline crown. It has not been possible to detect earlier thin layers of hyaline crown incorporated within the white matter cores. This may suggest that the layer is too thin to be observed, or that it is lost during the generation of new tissue. Alternatively the development of each white matter core may represent just one growth stage.

This is potentially an important pattern of growth which could be used to distinguish *Baltoniodus* from other conodonts, but would require an extensive survey of internal structures belonging to different taxa. For example within this study, the internal structure of P elements belonging to *Eoplacognathus* display a different pattern, where cores of white matter in mature specimens are commonly clearly truncated and subsequently regenerated with hyaline crown and not more white matter (Figure 6C; for full discussion see Chapters 2.2, 2.4).

Function of white matter. Hyaline crown tissue has been compared to enamel because it shares a similar internal structure and composition and is thought to be developmentally homologous (Donoghue *et al.*, 2000). These shared characteristics imply that hyaline crown is likely to have similar resistance to wear and similar brittle properties. Enamel typically fractures along the prism/rod boundaries, as these provide longitudinal lines of weakness that are perpendicular to the surface (Rensberger, 1995). Hyaline tissue does not possess continuous longitudinal lines of weakness perpendicular to the surface and instead is constructed of individual lamellae that are normally horizontal to the surface. The boundaries between these lamellae are likely to provide planes of weakness that would be exploited under stress in a way comparable to the prism boundaries within enamel (Rensberger, 1995). The introduction of a homogeneous, dense tissue that did not possess such prominent structural weaknesses would reduce the number of directions in which cracks could propagate. This would protect the integrity of the tissue and help to prevent the flaking and cracking of denticle tips that might have occurred if the denticle was purely hyaline.

Function of Baltoniodus elements.

 P_1 elements of *Baltoniodus* show several instances of damage, which are almost certainly caused by *in vivo* abrasion of the element surface. The distribution of damage on the dorsal process suggests that it was the denticles closest to the cusp that experienced the most damage and wear. This is suggested because the distal denticles are overglazed, but have not lost the sharp outline and height that has clearly been worn away from the more proximal denticles, although it is possible that this is because the element only added new growth to the distal parts of the element. Denticles with chipped oral surfaces appear to be concentrated along the rostral facing side of the element. This is further supported by the wearing of the cusp tip, which is also concentrated on the rostral side. However, this is not certain, as wear is not always clear on P_1 elements of

Baltoniodus. The absence of any obvious wear on the ventral and caudal processes suggests that these processes were not damaged during the function of the element. The plasticine models and figure 2A show that it is possible for the dorsal process and cusp to process or manoeuvre food particles without the ventral or caudal processes becoming involved.

 P_3 elements. The dorsal process of the P_3 elements often has truncated or worn denticles adjacent to the cusp (Figure 5). Figure 5A shows a particularly good example that is interpreted as denticles that have been broken or worn down, and then regenerated with an overglazing of new tissue, resulting in a smooth rounded surface. Alternatively the denticles have become worn down and not regenerated by any new layers of lamellae. The denticles of the ventral and caudal processes also show this type of wear on proximal denticles, whilst the distal denticles are generally discrete and large in comparison. This suggests that the P_3 element used all three processes to help to process food, or manoeuvre food towards the posterior of the apparatus.

Relationship between types of wear and possible food substances.

The P elements of *Baltoniodus* display no evidence of pitted textures or fine parallel striations on the element surfaces that are characteristic of crushing or shearing respectively (Purnell 1995). The main types of damage are denticle breakage and surface polishing. Polished surfaces are thought to represent either the absence of food or the presence of non-abrasive food particles (Purnell 1995). The polished facets and well preserved ropy ornament found on the P elements would suggest that *Baltoniodus* ate or manipulated relatively soft food particles that did not scratch or wear down the element surface significantly.

The breakage of dorsal and caudal process denticles appears to contradict this, unless the damage is caused by element on element occlusion. However the plasticine replicas show that direct element occlusion is unlikely, so it seems likely that if the breakages are true evidence of wear, then the damage and truncation of denticles is due to encounters with hard food particles. The lack of extensive pitted textures or fine parallel striations on the element surfaces can be explained by the internal crystalline structure of the elements. Sections of both P_1 and P_3 elements have shown that the ropy ornament of the cusps is not just a surface feature but an integral part of the internal crystalline structure. This would mean that even if the elements lost hyaline tissue from their surfaces, the damage would result in exposing more ropy ornamentation and would not immediately produce smooth wear facets, or scratched surfaces except when substantially worn down.

Implication of internal structure and responses to stress during function.

If the crown tissue of conodont elements is closely related to enamel, it is useful to look at different types of enamel structures that are thought to have evolved in response to stress invoked by function. Although enamel is the most resistant dental tissue to wear, its strength is restricted by its brittleness (Rensberger, 1995; Chapters 1.2, 1.3). Subtle ultrastructural modifications have resulted in a number of responses to this weakness.

Within human teeth, the process of amelogenesis is understood with some clarity. The enamel is secreted by a palisade of orally retreating ameloblasts that each deposits a continuous rod or prism of enamel from the enamel dentine junction to the outer surface of the tooth (Rensberger, 1995; Boyde, 1976). Therefore, the enamel, when forming simple morphologies, will be composed of an array of radiating elongate prisms that are perpendicular to the growing surface. With this simple internal structure, human teeth would be extremely susceptible to fracture, as pressures applied to the tooth cusp would result in cracks exploiting the longitudinal fabric of the tissue. In thin sections the enamel, at cusp tips, possesses a 'gnarly' fabric caused by the prisms developing at different angles to each other. This results in small regions of enamel constructed of prisms with a common orientation being bounded by groups of prisms that have a different orientation (Boyde, 1976). The boundaries between the different sets of prisms are known as decussation planes (Koenigswald *et al.*, 1987; Berkovitz *et al.*, 1992; Rensberger, 1995).

The resulting wavy fabric seen at the cusps of human teeth cause the light to pass through sections at different angles, resulting in the appearance of dark and light bands, which are called Hunter-Schreger bands (HSB) (Boyde, 1976; Berkovitz et *al.*, 1992). The gnarled enamel would protect the surface of the tooth by diverting and preventing large cracks propagating and following the boundaries of rod boundaries.

Koenigswald et al. (1987) studied the changes of enamel found in early Cenozoic herbivores and carnivores. It was found that HSB first appeared in the teeth of the arctocyonid condylarths in the early Palaeocene. The authors sectioned enamel found in the molars of Arctocyon primaevus, A. matthesi, Arctocyonides weigeltis and the middle Palaeocene phenacodontid condylarth Tetraclaenodon. Within these sections, the enamel possessed HSB. This contrasted with sections of early Palaeocene mammals from the lower part of the Nacimiento Formation of the San Juan Basin. From this collection Koenigswald et al. (1987) sectioned teeth of Conacodon, an early periyptychid that possessed enamel constructed of elongate parallel prisms that were parallel to the enamel/dentine junction and possessed no HSB. They also sectioned molars belonging to these forms exhibited poorly formed HSB, and disruption to the enamel prisms only occurred towards the centre of each tooth Koenigswald et al. (1987).

Koenigswald *et al.* (1987, p. 151) correlated this distinction in enamel ultrastructure with the "emerging radiation of mammals of increasing size after the disappearance of dinosaur-dominated Cretaceous faunas". The authors observed that among the Cenozoic etherians, HSB were generally absent in the smaller insectivores and present in the carnivores and herbivores. The authors concluded (Koenigswald *et al.*, 1987, p. 152) that the "polyphyletic appearance of the HSB during the early Cenozoic, dominance in large forms and appearance in small forms with specialised mechanisms that increase dental stress, imply that enamel

strength thresholds were critical in the transitions to Cenozoic herbivores and carnivores". The introduction of decussation planes strengthened the enamel by reducing its susceptibility to crack along prism boundaries.

The crown tissue of conodonts, although thought to be comparable to enamel (Donoghue and Chauffe, 1998; Donoghue, 1998; Donoghue *et al.*, 2000), has an important structural difference due to its mode of growth. Conodont crown tissue is grown by outer apposition and is secreted as a number of *punctuated* growth increments, the resulting growth structure possesses lines of weakness along the lamella boundaries, rather than along aligned crystallites that have resulted from a *continuous* secretion, as in the case of mammalian enamel. The position and orientation of lamellae varies greatly throughout the conodont element (see Chapter 1.2), and is responsible for the formation of the complex morphologies of some. However, this large range of variation has been used by some to suggest that conodont crown is not homologous with enamel (Forey and Janvier, 1993). Donoghue *et al.* (2000, p. 12) argue that this variety "coincides precisely with the requirements of element function and relates to the different biomechanical forces that are imposed on the element during feeding (e. g. Donoghue and Purnell, 1999a).

It is likely that the occurrence of white matter also coincides with stresses induced by feeding (Donoghue, 1998). White matter secretion within denticle and cusp cores coincides with areas of the element that are normally involved with food processing (see Donoghue and Purnell, 1999b; Chapter 1.4). Denticles and cusps, where white matter is not secreted, are composed of lamellae that are parallel with the long axis of the denticles and are composed of crystallites that are also orientated parallel, or slightly oblique (see Chapter 1.2). If the cusp or denticles were subjected to tensile stresses normal to the long axes of the crystallites and the lamellae boundaries, cracks could potentially propagate and extend down the length of the denticle, comparable to the way that mammalian enamel behaves under tensile stresses (Rensberger, 1995). The dense unstructured fabric of white matter (see Chapter 1.2) would have the same effect as the decussation planes found in mammals, by preventing the spread of fractures and cracks along planes of weakness.

The introduction of decussation planes in mammals appears to have coincided with a size increase in tooth size (Rensberger, 1995, p. 153, fig. 9.1d). There is no such recognisable increase in conodont element sizes. It is possible that white matter was an experimental evolutionary response to dental stresses that was unique to conodonts. It is possible that the strength of the derived tissue was the limiting factor behind the evolutionary diversification of conodonts.

Proposed motion of elements during function.

Any proposed motion of elements is reliant on an assumption of function. Potential hypotheses of function can be deduced from the distribution and type of wear recurrent on the element surfaces. Food can be hard, soft, brittle, ductile or fibrous, properties that all require different methods of mechanical handling.

If the elements were simply involved with manoeuvring food substances around and never came into contact, then, dependent on the food substances, the only evidence of function would result from damage occurring during contact and manipulation of the food. There are no clearly preserved scratch marks or gouges found on the surfaces of the elements examined. If the food substances were softer than the element tissue, then this type of function would leave no record on the element surface. If the food substances were hard, but the elements were on either side of the apparatus and never came close to each other, it is likely that this function would only result in wear at the cusp tips. Figure 4B shows what is clearly a wear facet. It is likely that this was caused by repeated wear against a substance which was as hard, or harder than the surface tissue. It is possible that the position of the facet also reflects a high degree of precision, if the element constantly repeated the motion that resulted in the wearing of such a small region. It is suggested that the wear facet has resulted from abrasion against the opposing element, and reflects malocclusion.

If the elements did process the food, and contribute to breaking up material, the position of the elements within the apparatus, according to the *Promissum* model, suggests that the cusp would have encountered material in the oral cavity first. If the cusp impaled the food, then denticles adjacent to the cusp would also be damaged to some extent. If the food substances were hard, then a high degree of damage would be expected including shearing of denticle tips, breakages, scratches and gouges. If the food was softer than the element surface, then a gradual wearing down and polishing of denticle surfaces would be expected, with the cusp exhibiting the most obvious damage.

The P_1 elements of *Baltoniodus* were opposed across the mid axis of the apparatus. The morphology of these elements prevents them from occluding together and working processes against processes in a way analogous to the ozarkodinids (Purnell and Donoghue, 1998). The distribution damage is centred about the cusp and possibly the immediately adjacent denticles of the caudal process, whilst the caudal process denticles appear to remain undamaged. This would mean that each element could have rocked across the sagittal plane, with the cusp encountering the food first and either plunging into the food particles far enough to engage the proximal denticles, particularly those of the dorsal process. Alternatively the element may have manipulated very soft food substances around in the oral cavity. The morphology of the element would have prevented the caudal process from coming into contact with the food particles if this type of motion was employed (Figure 2A).

The P_3 element is proposed to have a similar type of motion during function. In this case, however, the different morphology allowed the caudal process to be aligned with the ventral process along the rostro-caudal axis. A rocking motion across the mid axis of the apparatus would result in the cusp impaling the food particles, or manipulating food substances, the flaring caudal and ventral processes could also be employed in a similar way. This type of motion would put severe pressure on the large denticles of the caudal process and could be the cause of the breakage and truncation observed in figure 5E.

Conclusions.

The reconstruction of the function of P elements of *Baltoniodus* relies strongly on the homologies observed with the *Promissum* apparatus, as reconstructed by Aldridge *et al.* (1995). However, independent of this, the evidence of wear found on the surfaces of the elements of *Baltoniodus* supports the model of function suggested by the constraints imposed by the plasticine replicas. The type of function proposed for both the P_1 and P_3 elements of *Baltoniodus* is very simple in comparison with the function proposed for the P elements of some ozarkodinids (see Donoghue and Purnell, 1999a; 1999b) but similar in the proposed motion of elements during the processing of food.



Figure 1. A-D P elements of *Baltoniodus variabilis*, all elements orientated with dorsal process directed towards top of page, in vivo postion. A. P1 element, oral view specimen 235. B. P3 element, oral view specimen 236. C. P1 element, lateral view specimen 245. D. P3 element, lateral view specimen 236. E-F Templates for the *Promissum* apparatus. E. Terminology for the apparatus of *Promissum pulchrum* following Aldridge *et al.* (1995). F. Element notation as applied by Purnell *et al.* (2000).



Figure 2. Proposed motion of *Baltoniodus variabilis* P elements during function. A. P1 elements. B. P3 elements.





Figure 3. Evidence of wear on P1 elements of *Baltoniodus variabilis*. A-E Specimen 236, dextral element. A. Diagram to show processes detailed in B-E. B. View of ventral process seen from dorsal angle. C. Caudal process proximal to cusp. D. View of dorsal process from dorsal angle, rostral side of process. E. View of dorsal process from dorsal angle, caudal side of process.



Figure 4. Evidence of wear on P1 elements of *Baltoniodus variabilis*. A. Diagram to show location of C-D, specimen 250. B. View of cusp tip, showing clear wear facet on ventral face, specimen 236. C. View of dorsal process from dorsal angle, rostral side of process. D. Caudal side of process shown in C. E. Broken cusp that shows evidence of repair, dorsal face, specimen 250. F. Oral view of cusp showing ventral face, to the left of the image, specimen 236.



Figure 5. Evidence of wear and breakage due to function on P3 elements of *Baltoniodus variabilis.* A-B Specimen 237. Dorsal process seen from lateral views . C. Specimen 240. Caudal process seen from lateral view. D. Close up of C, showing fused denticles. E. Specimen 239. Ventral process (on right of image) ventral view. F. Specimen 235. ventral process (on right of image) dorsal view.



Figure 6. Elements of Baltoniodus variabilis in transmitted light. A. Specimen 13. Dextral P3 element, ventral process in centre of element and caudal process directed towards bottom of image. B. Specimen 262. Dextral P1 element, ventral process in centre of element and caudal process towards the left . C. Specimen 15. P1 (Platform) element of Eoplacognathus showing truncated white matter in dorsal ('posterior')

process.

CHAPTER 2.0

INTRODUCTION

THE ARCHITECTURE, HISTOLOGY AND FUNCTION OF THE FEEDING APPARATUS OF EOPLACOGNATHUS RECLINATUS (FÅHRÆUS) 1966

Eoplacognathus was first described by Hamar (1966). Hamar erected the genus for conodonts with Y-shaped platform elements only and designated *Ambalodus lindstroemi* Hamar as the type species. Bergström (1971) emended this diagnosis when he observed that a "star-like" platform element (previously classified within the genus *Polyplacognathus* Stauffer 1935) was constantly associated with the Y shaped platform elements and that both types of element shared morphological similarities. He redescribed *Eoplacognathus* as a conodont with both ambalodiform and polyplacognathiform elements but no additional element types. *Eoplacognathus* stelliplanate elements (previously identified as *Polyplacognathus* elements), are distinguished by the absence of additional nodes and denticles alongside the conventional 'posterior' processes, and unpaired markedly dissimilar sinistral and dextral ambalodiform elements (Bergström 1971).

The lineage of *Eoplacognathus* extends from the Llanvirn through to the base of the Caradoc (*Eoplacognathus suecicus* to *Amorphognathus superbus* zones) rapidly evolving through several different species which are well documented. The lineage appears to have evolved in the Baltoscandic province where at least seven species are recognised, ranging from the Llanvirn to the Llandeilian (Bergström 1983). It appears that there was a second centre of early diversification in the Hubei Province in The People's Republic of China (Sheng, 1980; An, 1981), though the data are still unclear (Zhang, 1998). However, *Eoplacognathus* species have a wide distribution across provinces with some species exhibiting a cosmopolitan distribution whilst others remained more localised (see Bergström, 1983 for a summary).

There is no indication that any S or M elements are associated with the platform elements of *Eoplacognathus*. Armstrong (1997, 2000) suggested that *Eoplacognathus* had more than two pairs of P elements, by recognising Pc and Pd elements. Armstrong did not recognise any S or M elements. Dzik (1994) suggests that although ramiform elements have not been identified in most of the species of the genus, "sparse data strongly suggest a presence of small elements similar to the S elements of *Lenodus*" (Dzik 1994, p. 96). This is also the case for *Cahabagnathus*, a conodont classified in the same family as *Eoplacognathus* and believed to be descended from the same line (Sweet 1988). My work has shown that although *Eoplacognathus* only has two different morphological types of element, its apparatus does not necessarily have only two different element positions and here a different apparatus plan is proposed. This new apparatus plan is based on direct morphological comparisons with the elements in bedding plane assemblages of *Promissum pulchrum* (Aldridge *et al.* 1995).

The material used in this study is from the Suhkrumagi section on the outskirts of Tallinn, Estonia (Kaljo and Nestor, 1990), and was collected by Viive Viira and Richard Aldridge. The material is exceptionally well preserved, which facilitated the study of microwear and surface structures of the elements. The sample is of middle Ordovician age, containing conodonts of the *Eoplacognathus reclinatus* Biozone.

CHAPTER 2.1

APPARATUS ARCHITECTURE OF EOPLACOGNATHUS RECLINATUS

Introduction.

When the first ozarkodinid bedding plane assemblages were found (Scott, 1934; Schmidt, 1934) the elements present supported the concept that conodont apparatuses in general possessed two pairs of P elements and an array of ramiform elements. Nearly all of the subsequent finds of bedding plane assemblages revealed the same composition (for review see Purnell and Donoghue, 1997, 1998).

This pattern of two pairs of morphologically differentiated P elements, an array of S elements and a pair of M elements is characteristic of the ozarkodinids, one of the three conodont orders with complex elements within their apparatuses. Rare finds of bedding plane assemblages of prioniodinids (e. g. Purnell 1993) suggest that they share a plan similar to the ozarkodinids. The prioniodontids, long unrepresented by complete natural assemblages, were also thought to follow this apparatus plan until finds of the first prioniodontid natural assemblage, *Promissum pulchrum* Kovács-Endrödy, were interpreted (Theron *et al.*, 1990; Aldridge and Theron, 1993; Aldridge *et al.*, 1995) and revealed a different pattern. When reconstructing taxa known only from disarticulated collections it is necessary to refer architectural information that is derived from natural assemblages. The apparatus compositions of the ozarkodinids and *Promissum* provide two different templates that can be consulted.

Bergström (1971) was the first conodont worker to recognise that there were two basic types of P element associated with the apparatus of *Eoplacognathus*. He described a 'star-like' platform element (polyplacognathiform) and a Y-shaped platform element (ambalodiform) each represented by sinistral and dextral examples (Figure 1). *Eoplacognathus* was classified as a member of the Polyplacognathidae (Bergström, 1981, p. W129); a new family erected for conodonts that possessed an apparatus that was "apparently reduced to a bimembrate type by loss of S and M elements". 'Bimembrate' is a term introduced by Sweet (1981), for apparatuses considered to have only two morphologically distinct element types. Sweet (1988) followed the *Treatise*, with his classification of *Eoplacognathus* as a polyplacognathid.

Materials and Methods.

Over 400 natural assemblages of *Promissum* were made available to me by R. J. Aldridge, from the collections currently at the University of Leicester. A small number of the *Promissum* assemblages have a mouldic preservation, which made it possible to make silicon rubber casts of individual elements. The casts provided information of element morphology that allowed detailed comparisons between the elements of *Promissum*, *Eoplacognathus* and selected prioniodontid taxa to identify homologous characters between

elements. Of the selected prioniodontids included in this study, *Eoplacognathus* and *Baltoniodus* elements are from the Middle Ordovician Suhkrumagi section exposed south east of Tallinn, Estonia (for details of locality see Kaljo and Nestor, 1990). Elements of *Lenodus* are from a Lower Ordovician Nappa section of Kunda Regional Stage on the River Purtse, north east of Estonia and were donated by Viive Viira.

New terminology.

Following the new terminology introduced by Purnell *et al.* (2000), the elements within the templates are labelled from the caudal end of the apparatus with the pairs of P elements, P_1 , P_2 . The ramiform array, $S_0 - S_4$, labelled laterally from the axial S_0 element to the flanks of the apparatus (Figure 2). The new terminology is based on natural assemblages of ozarkodinids, however, Purnell *et al.* (2000) have also applied this new notation to the apparatus of *Promissum* (Figure 2B). Where element positions within an apparatus are unknown, the original terminology, proposed by Sweet (1981; 1988) has been retained (for full discussion see Chapter 1.1).

The ozarkodinid template.

Representatives of the Order Ozarkodinida dominated conodont faunas throughout most of the Palaeozoic and this abundance is reflected in the number of natural assemblages that have been found. This has resulted in almost all conodont apparatus reconstructions being based on the ozarkodinid template (see Purnell and Donoghue, 1997 for review, and Chapter 1.1). Extensive studies have shown that the ozarkodinids possessed a fifteen element apparatus comprising: a pair each of bilaterally opposed P_1 and P_2 elements; an anterior, axial S_0 element, two groups of four close-set, inward and forward inclined S_1 - S_4 elements; and above and outside each S group, an inward and forward pointing M element (Purnell *et al.*, 2000) (Figure 2A).

The Promissum template.

Promissum has a more complex, nineteen element apparatus composed of four pairs of bilaterally opposed P elements (P_1 - P_4) (in comparison to the two pairs of opposed P elements of the ozarkodinids), axial S_0 element, two groups of four S_1 - S_4 elements and a pair of M elements (for discussion see Chapter 1.1, Aldridge *et al.*, 1995, Purnell *et al.*, 2000); (Figure 2B).

Elements of Eoplacognathus.

Within the Estonian fauna and throughout the literature, elements of *Eoplacognathus* are represented by a pair of pastiniplanate elements with dissimilar morphologies and a pair of stelliplanate elements (Figures 1A, B; 3B, E); by convention these pairs are referred to as Pb and Pa elements, respectively. No ramiform elements have been identified. Within my collections, those of Dzik (1994) from the Mojcza limestone and the collections from Jämtland studied by Löfgren (1978) a recurring pattern of proportional representation for each element type of *Eoplacognathus* occurs. There is a consistent over-representation of the pastiniplanate Pb elements (often twice as many) throughout all three of these large collections.

Ratios of elements.

The two common hypotheses offered to account for element ratios in collections are postmortem sorting (McGoff, 1991) and the possibility that the number of elements within a conodont apparatus was not constant, either due to shedding (Carls, 1977) or due to differences between different taxa. However, there are a number of other possible selective processes that, when combined, could potentially disrupt the original biological signal (see Chapter 1.1 for full discussion).

Before burial, decomposition of carcasses and scavenging, would expose the elements to possible breakage and redistribution. It is likely that the more robust P elements might survive these processes, but the more fragile elongate ramiform elements would be more subject to breakage and winnowing, resulting in broken fragments and a concentration of the more robust P elements. McGoff (1991) and Broadhead and Driese (1994) have investigated these processes in the lab and shown that the ramiforms are preferentially sorted before the P elements. Although many samples have been found which appear to have an over-represented proportion of P elements, the corresponding collection, enriched in ramiform elements, has yet to be found. This is perhaps to be expected, as if the ramiforms are sorted by current action, once winnowed from the deposition site, they would become diluted over a much larger area. During burial, the ramiforms are also likely to be damaged and broken if subjected to compaction, due to their relatively delicate, elongate morphology. This process is extremely difficult to quantify and is dependant on different sediment types and the timing of lithology cementation and diagenesis. And finally sampling and processing bias is likely to have a large effect on collections. For example, many of the lithologies processed are limestone, and are therefore characteristic of a specific environment, hence the ratios of elements will reflect the dynamics of that specific environment. Lithologies that are more difficult to process, may have very different ratios of elements, perhaps yielding collections that are richer in the more delicate conodont elements. Actual picking of the samples is also likely to reflect a bias towards the more complete elements, and even if selected, it is not always easy to identify broken fragments, resulting in an apparent enrichment of robust, unbroken elements.

It is, therefore, likely that the proportions of *Eoplacognathus* elements reflect some of these selective processes; however, it is possible that such recurrent patterns could represent the remnants of a true biological signal and reflect apparatus composition during the life of the conodont.

Previous reconstructions of the apparatus of Eoplacognathus.

Armstrong (1997, 2000) suggested that in addition to platform elements the apparatus of *Eoplacognathus* contained additional P elements that resembled elements traditionally included in *Baltoniodus variabilis* Lindström (see Chapter 1.2 and 1.1 for full discussion). This hypothesis is not followed here because of the homologies that can be demonstrated between elements of *Eoplacognathus* and *Baltoniodus* (Chapters 1.1)) (see Figure 3B, E in comparison to 3C, F respectively). On the strength of these homologies, a full apparatus has been reconstructed for *Baltoniodus* (see Chapter 1.1). It is more reliable to study homologous characters between individual elements of *Eoplacognathus* and those of *Promissum* to identify which elements occupied which position within the apparatus.

The relationship demonstrated by the comparable internal structures of the P elements of *Eoplacognathus* and *Baltoniodus* (Chapters 1.2, 2.2) could suggest that the apparatuses might also be comparable. It is, therefore, possible that ramiform elements of *Eoplacognathus* have not been identified because they are indistinguishable from those of *Baltoniodus*. To verify this hypothesis, it is necessary to find a collection that possesses sufficient numbers of *Eoplacognathus* elements in the absence of *Baltoniodus*, to demonstrate if the ramiform elements are truly absent. Such a collection has yet to be found.

Dzik (1994, p. 96) suggested that "although ramiform elements have not been identified in most of the species of the genus [*Eoplacognathus*] sparse data strongly suggest a presence of small elements similar to the S elements of *Lenodus*." It was not possible to identify the third morphology of P element identified by Armstrong or any of these small elements recognised by Dzik within the material studied for this work. Because the Suhkrumagi collections include a great variety of different sized elements it is considered unlikely that small S elements would be missed, and more likely that the apparatus of *Eoplacognathus* lacked ramiform elements.

Comparing the elements of *Eoplacognathus* and other related prioniodontids to the elements of *Promissum*.

The P_1/P_2 of *Promissum*. The morphology of the elements in the P_1/P_2 positions can be compared directly to the Pa element of *Lenodus* (Figures 4B i-ii). The long dorsal (posterior) process of both *Promissum* and *Lenodus* are elongate and aligned with the caudal (lateral) process. In the case of the P_2 element of *Promissum*, seen in Figure 4Bi, the process attached to the ventral face of the cusp, immediately

curves away from the main axis of the element. This pattern is duplicated by the 'anterior' process of the element of *Lenodus* (Figure 4Bii). The close similarity of the elements provides sufficient evidence to support the hypothesis that the Pa element of *Lenodus* is homologous with the elements that occupy the P_1/P_2 positions of *Promissum*. Both *Lenodus* (Figures 3A, D) and *Eoplacognathus* (Figures 3B, E) possess Pa and Pb elements that share convincing morphologically similarities and therefore, it is likely that these elements are also homologous. Thus the Pa element of *Eoplacognathus* is a probable homologue of the elements that characterise the P_1/P_2 positions of *Promissum*.

Elements in the P_3 position. Elements in the P_3 position have two processes (rostral and caudal) arising from the cusp, with an angle of approximately 150- 170° between them when viewed orally, the dorsal process is not formed (Figures 4A iv-vi; 5A-D) (see Chapter 1.1 for full description).

The morphology of the Pb elements of *Eoplacognathus* are not readily homologised with the elements within the P_1/P_2 , P_3 or P_4 positions within the apparatus of *Promissum*. In fact no collections of disarticulated prioniodontid apparatuses have revealed elements which can be compared directly to the interpreted morphology of the elements occupying the P_3 or P_4 positions (for descriptions see Aldridge *et al.*, 1995).

The morphology of the Pb element of *Baltoniodus* is closely comparable to the elements of *Promissum* that occupy the P_3 position and possibly the P_4 positions (see Chapter 1.1). This close morphological resemblance supports the hypothesis that the Pb elements of *Baltoniodus* are (figure 4A i-iii) homologous with the P_3 elements of *Promissum* (Figure 4A iv-vi). The morphology of the Pb element of *Eoplacognathus* is most closely comparable to the P_3 (Pb) of *Baltoniodus* than the P_1 (Pa) element and it is therefore it is likely that they are homologous (Figure 3E, F). It is possible to extrapolate this inferred homology between the Pb element of *Baltoniodus* and the P_3 element of *Promissum* to suggest that the Pb element of *Eoplacognathus* is also homologous with the P_3 element of *Promissum*, even though not directly comparable morphologically.

The morphological comparisons described above have shown that the P_1 , P_2 and P_3 elements of *Promissum* can be compared to prioniodontid elements and homologies can be recognised. However, the P_4 element of the *Promissum* apparatus is more problematic. In nearly all of the specimens, the P_4 element is either obscured by the surrounding elements, or very poorly preserved. The basic morphology appears be angulate, with an angle of approximately 45-50° between two processes. The principal difference evident between the P_3 and P_4 elements is a variance in angle between the two processes; otherwise, they share a similar morphology. It is possible that the two processes of the P_4 are homologous to the conventional 'anterior' and 'lateral' processes in a way comparable to the P_3 element. The morphology of the Pb elements of *Baltoniodus* varies in the disposition of the 'lateral' (caudal) process. When the element is viewed orally the lateral process can form a straight line with the 'posterior' (dorsal) process (180°). However, the process position can vary as much as 90° from this position and make an angle of approximately 90° with the 'posterior' process resulting in a straight line being made across the 'anterior' (ventral) and 'lateral' (caudal)

process axis (see Chapter 1.1, fig. 7). This shows that it is possible that the Pb element of *Eoplacognathus* could be a homologue of the element that occupied the P_4 position in the apparatus of *Promissum*.

Possible reconstructions of the Eoplacognathus apparatus.

The template. Eoplacognathus is represented in my disarticulated collections by two morphotypes of P element, so it is possible that the apparatus only had two morphologically differentiated P element positions $(P_1 \text{ and } P_2)$ and in this respect was similar to the P element architecture of ozarkodinids. This seems unlikely because the morphology of the elements within the ozarkodinid template are not as closely comparable to the elements of *Eoplacognathus* as to those of *Promissum*. Elements of *Eoplacognathus* possess a number of balognathid characteristics, such as the rostral deflection of the ventral processes and large wide cusps, characters also shared by *Promissum*. This suggests *Eoplacognathus* is closely related to *Promissum*. Therefore, the *Promissum* template is considered more appropriate and has been examined more closely.

Discussion.

There are proportionally less stelliplanate Pa elements of *Eoplacognathus* represented in the disarticulated collections. If this can be taken as a true signal of original apparatus composition then because the stelliplanate Pa element of *Eoplacognathus* is thought to be a homologue of the P₁ or P₂ elements of *Promissum* it is suggested that the P₁ position was not duplicated in the apparatus of older balognathids. The pastiniplanate Pb elements are, however, over represented suggesting that it is possible that the Pb element occupied more than one position within the apparatus. The Pb element of *Eoplacognathus* is recognised as a homologue of the element in the P₃ position of *Promissum*, but it has not been possible to identify an element that is unequivocally homologous with the P₄ element of *Promissum*. There are two main hypotheses that could provide positions for the duplicated Pb elements.

The pattern of over-represented Pb elements may mean that the Pb element was serially reproduced, as has been hypothesised for the P_1 element of *Promissum*. If this is the case then the apparatus of *Eoplacognathus*, based on morphological comparisons, could have had a P_1 position filled with a stelliplanate platform element (that might also have been duplicated in a P_2 position), and a serially reproduced P_3 position, occupied by the pastiniplanate Pb elements. This would leave the P_4 position unfilled. However, this would rely on the independent duplication of the P_3 position, for which there is no evidence.

There is a third apparatus architecture suggested by direct morphological comparisons between the overrepresented Pb elements from disarticulated collections and the element located in the P_4 position of the *Promissum* apparatus. If the morphology of the P_3 and P_4 elements of *Promissum* are comparable, as discussed above, then the element occupying the P_4 position can also be compared to Pb elements of prioniodontids from disarticulated collections. If the element in the P_4 position of *Promissum* is considered homologous with the Pb elements of *Baltoniodus*, and hence *Eoplacognathus*, then it is possible that the over-represented Pb elements occupied both P_3 and P_4 positions. The Pb elements of *Eoplacognathus* vary greatly intraspecifically, by a variance of angles between processes about the cusp; this supports the hypothesis that similar elements with a Pb like morphology could have occupied both P_3 and P_4 positions. This would suggest that a Pa element occupied the P_1 position (and possibly the P_2), and the P_3 and P_4 positions were both occupied by Pb elements that had a similar morphology to each other (Figure 6).

Both of these hypotheses are only supported by the proposed morphological similarities of elements and the possible signal of over-representation of the Pb element within disarticulated collections. However, the proportional representation of elements within disarticulated collections is notoriously unreliable (see above for discussion), and in reality, the actual numbers of elements within balognathid apparatuses, other than *Promissum*, are still unknown.

Reconstruction of the apparatus of Eoplacognathus.

The compelling morphological comparisons between the elements of *Eoplacognathus* and those of *Promissum* support the hypothesis that the balognathids possessed an apparatus that was more similar to that of *Promissum* than the ozarkodinids (Aldridge *et al.* 1995, Purnell *et al.*, 2000). The reconstruction followed here, constrained by the evidence currently available, proposes that the apparatus of *Eoplacognathus* shared the same basic apparatus plan as *Promissum*, but that several of the element positions were unfilled. The apparatus of *Eoplacognathus* was composed of a stelliplanate Pa element in the P₁ position, that was possibly duplicated, at the caudal end of the apparatus. Rostral to this the P₃ position was occupied by the pastiniplanate Pb element. However, it is still unknown whether the P₄ position was occupied. A better understanding of the P₄ morphology of *Promissum* will help to determine if there is a homologous element in disarticulated collections of other prioniodontid taxa. There is currently no evidence for the presence of any S or M elements within the apparatus of *Eoplacognathus* was first proposed by Bergström and Sweet (1966). It is possible that the S elements have not been identified because they are indistinguishable from S elements belonging to other taxa. Testing of this hypothesis awaits the discovery of a monospecific collection of elements of *Eoplacognathus*.



Figure 1A. Stelliplanate elements of *Eoplacognathus reclinatus*. A. Sinistral stelliplanate element. B. Dextral stelliplanate element.



Figure 1B. Pastiniplanate elements of *Eoplacognathus*. A. Sinistral pastiniplanate element. B. Dextral pastiniplanate element.


Figure 2. Published apparatus templates for the apparatus of the ozarkodinids and that of the *Promissum* apparatus. A. New notation of Purnell *et al.* (2000) for the apparatus template of the ozarkodinids. B. Application of new terminology to the apparatus template of *Promissum* following Purnell *et al.* (2000).

SPECIAL NOTE

This item is tightly bound and while every effort has been made to reproduce the centres force would result in damage.



Figure 3. Comparison of different prioniodontid P elements, orientated to illustrate relationships between homologous processes, 'posterior' dorsal process orientated towards the base of the images. A. *Lenodus pseudoplanus* P1(Pa) element, specimen 300. B. *Eoplacognathus reclinatus* P1(Pa) element, specimen 102. C. *Baltoniodus variabilis* P1(Pa) element, specimen 192. D. *Lenodus pseudoplanus* P3(Pb) element, specimen 302. E. *Eoplacognathus reclinatus* P3(Pb) element, specimen 103). F. *Baltoniodus variabilis* P3(Pb) element, specimen 193.



Figure 4A. *Baltoniodus variabilis* 'Pb' element and *Promissum* P3 element comparisons. i. Specimen 245 sinistral Pb *Baltoniodus variabilis*. ii-iii. Specimen 246 dextral Pb *Baltoniodus variabilis*. iv-v. Specimen C506B P3 *Promissum*. vi. Specimen C488 P3 *Promissum*. i, iv. viewed with the concave margin of the cusp directed towards the left of the image. ii,v. viewed with cusp directed towards the bottom right of both images. iii, vi. cusp directed towards to left of both images.



Figure 4B. i. Specimen C976A *Promissum* P1 element. ii. Specimen 247 *Lenodus pseudoplanus* Pa element. Both elements orientated with concave face of cusp directed towards the bottom of the page.



Figure 5. Latex moulds of P3 element of *Promissum* showing costate cusp. A. Specimen 937A. Whole element lateral view. B-D. Specimen 838A. B. Oblique oral view down cusp showing concave face of cusp and lack of dorsal process. C. Oblique dorsal view showing ventral process costa. D. Oblique dorsal view showing caudal process costa.



Figure 6. Reconstruction of the caudal part of the apparatus of *Eoplacognathus reclinatus*, viewed towards the caudal end of the apparatus.

CHAPTER 2.2 THE HISTOLOGY AND INTERNAL STRUCTURE OF P₁ ELEMENTS BELONGING TO EOPLACOGNATHUS RECLINATUS

Materials and Methods.

The material used in this study is from the Suhkrumagi section on the outskirts of Tallinn, Estonia (for details of locality see Kaljo and Nestor, 1990), and was collected by Viive Viira and Richard Aldridge. The material is exceptionally well preserved, which facilitated the study of microwear and surface structures of the elements (Chapters 2.3, 2.4). The sample is of Middle Ordovician age containing conodonts of the *Eoplacognathus reclinatus* zone. Several sinistral and dextral platform elements were sectioned (Figure 1A, B). The specimens are not thermally altered, and although the elements were relatively robust, some internal structures were visible when viewed in oil using a transmitted light microscope, following a technique used by Donoghue (1998). The specimens were ground and polished and etched following a technique detailed by Donoghue (1998), and then examined using a scanning electron microscope.

Sections are taken in three main orientations (Figures 1C-E). Longitudinal sections are orientated parallel with the long axis of the element and the long axes of the denticles. Transverse sections are also parallel with the long axes of the denticles, but perpendicular to the long axis of the element. Horizontal sections bisect the element in a plane that is perpendicular to the long axes of the denticles, but parallel with the long axis of the element (i. e. parallel with the aboral margin of the element). In several cases it has been necessary to provide diagrammatic location figures due to the complexity of the platform elements.

Internal Structures.

Crystallites. Throughout the element, crystallite sizes range from $0.19 - 4.5\mu m$ in length and average about $0.5\mu m$ in width. Individual crystallites are elongate and are often broad at one end, and pointed at the other. This morphology helps to identify the individual lamellae within the conodont element (Figures 2C, 3D). Where crystallites are aligned with their c axis perpendicular to the lamellar surface it can be seen that the individual crystallites widen in the direction of the outer surface (Figures 3D, 4D). In Figure 3D the outer surface of the element is towards the bottom of the image and forms the aboral edge of the platform.

Structure of lamellae. A large proportion of stelliplanate elements is composed of lamellar tissue. This tissue is distinguished from the basal body and the white matter by its crystalline nature and generally characterised by its lamellar structure. Within the platform regions of the element individual lamellae are distinguished from each other by the aligned ends of the crystallites which compose them (Figures 3D, 4D and 5D).

Where the crystallites are oblique or parallel to lamellar surfaces it is more difficult or impossible to see individual lamellae, as there are no aligned wedge-shaped crystallite tips (Figures 3C, 5A). In this case the tissue appears as a jumble of crystal tips regardless of section orientation. Laminations are only apparent in transmitted light, as seen in Figures 6D, F, H and Figure 7C. The denticles are composed of incremental laminations, with crystallites that are oblique or parallel to the axial plane of the process and the long axis of the denticle. Distinct lamellae can be seen in some specimens, when sectioned horizontally sections, due to a defined gap between the layers of crystallites (Figure 8C).

Where the crystallites are orientated with their c-axes perpendicular to the lamellar surface the maximum thickness of a lamella is normally reflects the maximum length of crystallites within. Consequently, the widest lamella measured was 4.5μ m and the narrowest was 0.19μ m corresponding to the maximum and minimum crystallite dimensions. Less commonly a lamella is made up of the crystallites that are not aligned in the same orientation and occur in differently orientated 'groups' of crystallites each with a slightly displaced orientation with respect to the adjacent group. In the best example thin parallel laminations (approximately 1.5μ m) adjacent to the basal body are succeeded by thick laminations (up to 4.5μ m) composed of bundles of crystallites (Specimen 133, Fig. 2C). A second type of disrupted crystallite orientation occurs within the lamellae of the ventral process of a sinistral stelliplanate element (Specimen 133 Figure 2D). In this case the crystallites appear to be orientated with their long axes oblique to the lamellar surface, but are not organised into groups. It has not been possible to reveal sufficiently large regions of lamellar crown to recognise distribution patterns of crystalline microstructure or any sign of periodicity or grouping of increments (see Zhang *et al.*, 1987).

Within the denticles, where crystallites are orientated with their c-axes parallel or oblique to lamellar surfaces, it is not normally possible to determine the thickness of incremental lines because there is no clear distinction between individual lamellae. Figure 8C shows a rare example where interlamellar gaps make it possible to ascertain lamellae thickness. In this case the lamellae have an apparent thickness of approximately $0.6-1.0\mu m$.

Elements viewed in transmitted light are generally too thick to allow clear lamellar resolution, normally only revealing the distribution of tissue types within the crown rather than micro-structural details. However, it is possible to identify the general orientation of lamellae and the internal crystallites within the caudal process denticles, as, in this case, the comparative narrowness of this process allows greater resolution of the internal structures. The lamellae that form the denticles are continuous with the platform lamellae and can be seen along the aboral base, extending the length of the process. The lower regions of the denticles have crystallites that have the aboral tip of their c axes deflected towards the more mature regions of the element. In the upper regions of the denticles the crystallites are orientated within a radiating cone in cone structure, with their c axes oblique or parallel with the long axis of the denticles centrally, and oblique to perpendicular within the flanks of the denticles (Figures 6H, 7C).

Most of the crown tissue of stelliplanate elements is composed of lamellae which are parallel to the axial plane of the process and composed of crystallites oriented with their long axes oblique or parallel to lamellar surfaces. This generally makes incremental lines difficult to observe as longitudinal sections reveal either the surfaces of lamellae, composed of elongate aligned crystallites (seen in Figures 3B, C, 5A-B), or the edges/sides of lamellae, that are composed of crystallite tips. Sections taken perpendicular to the lamellae (i.e. horizontal sections) reveal lamellar edges composed of crystallite tips that rarely provide resolution between individual lamellae (Figure 8C). Some longitudinal axial sections show excellent resolution of white matter cores but fail to reveal individual incremental lines within the lamellar crown of the denticles, although these may be evident within the platform where the lamellae and crystallites have a different orientation to those within the denticles (Figure 3B, D-E).

White matter. The caudal process denticles tend to be more elongate than those of the dorsal process (Figures 9A-H). Denticles of the caudal process commonly develop a narrow 'lozenge' area of white matter that tapers aborally to form a rounded point below the base of the denticle and within the aboral regions of the process. The tapered point is deflected towards the more mature region of the element, reflecting the orientation of the adjacent crystallites. The distribution of white matter within the caudal process denticles is not constant and in larger specimens appears to vary greatly.

The denticles of the dorsal process are smaller and squatter than those of the caudal process with a concomitant development of white matter and a slightly pointed aboral boundary (Figures 9 A-H). Within most specimens, unlike in the caudal process, the white matter of the dorsal process rarely develops below the confines of the denticle.

The white matter tissue contrasts with the lamellar tissue by being extremely fine grained (Figures 3E, 5A-B, and 10A-D). It is impossible to detect individual crystallites, although there is some evidence of incremental lines (Figs. 3E; 10A, C, D). The individual lamellae seen in Figure 3E are approximately 2-3 μ m thick and separated by very small gaps between each sheet. The tissue has many small cavities that are mainly rounded (approximately 0.5-1 μ m in diameter), some within the lamellae and others at the junctions between them. White matter in Specimen 212, Figures 5A, B possesses randomly orientated tubules. The outer margins of the white matter cores in Figures 10C, D; 5B show that the small cavities are more concentrated in this region and appear to be roughly aligned in a linear fashion parallel with the margins of the cores. The interiors of the cores are characterised by larger cavities and tubule structures cutting across the white matter tissue in random directions. The large cavities are typically 1-3 μ m in diameter sometimes with short tubules radiating from them. Longer tubules cut randomly across the white matter cores often extending to more than 20 μ m in length and just a few microns in calibre (Figure 10B).

Figures 5A-B and 10C show that the oral boundary of the lamellar tissue/white matter junction is gradational (i.e. the margin directed away from the basal body towards the denticle tip). Tubules radiate into the lamellar

crown from the oral margin of the white matter core where it becomes more porous and fragmented (Figure 10C). This pattern of crown tissue secretion is also seen in elements of *Baltoniodus* (Chapter 1.2). The lateral margins of the white matter cores are often sharp. In transmitted light the margins of the white matter cores reflect the same sharp lateral boundaries and diffuse oral margin whilst the aboral margin appears to have a distinct boundary that narrows to a rounded, tapered point (Figure 9D). White matter cores within the denticles of the caudal processes appear to be more sharply defined than those of the dorsal process.

Process morphology and basal body.

There is a clear junction between the basal body and the lamellar tissue. The basal body normally appears to shrink back from the margins of the cavity and is made of a homogenous, dense tissue (Figures 2C, 11B). In mature specimens the ventral and dorsal processes have deep basal cavities and the broad platforms of these areas are mirrored aborally by broad flaring edges of the basal cavity (Figures 2B, 8B, 12A).

When viewed orally, the caudal process continues in a straight line with the dorsal process where the ventral process curves away making an angle of approximately 90° with the dorsal process (Figures 1A, B; 8B). With maturity, the crown tissue of the caudal process extends beyond the tip of the basal body (Figure 2B) which is not as wide or deep as the basal body of the dorsal process. The distal tip of the caudal process has no visible basal body and the crown laminations close around beneath the process tip (Figures 12D-F). The distal tip of the basal cavity of the ventral process develops a bifurcation as the curvature changes (Figures 2B, 12A, C) resulting in a ventral-lateral process. Although not as large as the caudal process, the ventral-lateral process is identical in structure and morphology (Figures 2B, 12A, C-D).

The basal body continues to widen beneath the ventral and dorsal processes with maturity, but remains narrow beneath the caudal and ventral-lateral processes (Figures 2B, 12A).

Interpretation of internal tissues.

Hyaline tissue. Nearly all of the sections that have revealed clear lamellae are those taken along a longitudinal or transverse plane through regions of the element composed of tissue where the c-axes of crystallites are perpendicular to lamellar surfaces (Figures 3D, 4D). This arrangement of crystallites occurs predominantly in the platform areas of the element (Figure 3D), within the central cores of denticles (Figure 8C) and where incremental layers have expanded laterally with respect to the long axis of the denticles (Figure 4A-D). Donoghue (1998, p. 640 fig 3 e) figured crystallites with their c-axes perpendicular to the surface of each lamella in a Pa (P₁) element of *Scaliognathus anchoralis* Branson and Mehl. The platform lamellae of *Eoplacognathus* (section 132, Figure 3D) display similar lamellar thickness, crystallite orientation and dimensions.

Unusually the incremental lines and crystallite orientation within the caudal process are clearly visible in Specimen 141 (Figure 8C); where the crystallites are oriented with their long axes parallel or slightly oblique to the long axis of the denticle. A similar arrangement of lamellae and crystallites was observed by Barnes *et al.* (1970, pg. 18, fig. 5a) who named the gaps between the lamellae, 'interlamellar spaces'. Donoghue (1998, p. 640, fig 3, i) also figured a Pa (P₁) element of *Ozarkodina confluens* where the crystallites within the lamellae, immediately adjacent to the denticle cores, are orientated oblique to the long axis of the denticle. Donoghue's (1998) figure shows that only the first few lamellae have this crystallite orientation, the succeeding lamellae becoming too thin to discern crystallite orientations. It is possible that the outer lamella of *Eoplacognathus* processes might also be thin; this may account for the general difficulty in detecting individual lamellae within horizontal sections of *Eoplacognathus* elements.

Donoghue (1998, p. 640-1, Fig. 3h) described the crystallite orientation within a longitudinal axial section of the blade of *Mestognathus beckmanni* Bischoff, recognising a number of individual prisms of crystallites arranged in a three-dimensional fan like cone in cone structure. Each individual growth prism forms an individual denticle, with the c-axes of the crystallites within orientated parallel or oblique to the long axis of the denticle and the lateral extent of each three dimensional, cone in cone fan confined within straight parallel margins (Chapter 1.2, Figure 7E). The crystallites of *Eoplacognathus* are similarly oriented with their c axes parallel or oblique to the long axes of the denticle within laterally defined, distinct growth prisms. Specimen 212 (Figure 5B), a longitudinal axial section, shows vertical structures, parallel with the long axes of the denticles, that may represent the internal lateral boundaries of each denticle; and appear to be directly comparable to the margins of the growth prisms described by Donoghue (1998). Figure 3C shows a close up of the crystallite orientation within the cusp of specimen 132; the crystallites exhibit a radial fabric, which again appears to represent the arrangement of crystallites within a growth prism. Figure 7C also shows a radial crystalline fabric, visible in transmitted light.

The structure and composition of the hyaline tissues found in elements of *Eoplacognathus* compare closely to those described and discussed by Donoghue (1998) and are also comparable to Devonian and Triassic conodonts sectioned by Zhang *et al.* (1997) and Donoghue and Chauffe (1999) respectively. The incremental lines and the crystallite arrangement within led these authors to compare this tissue type directly with enamel. Although not organised into obvious rods (for full description of enamel formation see Chapter 1.2), the hyaline tissues within the platform elements of *Eoplacognathus* are also interpreted as a tissue type that is closely comparable to enamel.

Enamel is deposited as individual rods composed of elongate bundles of crystallites that are orientated with their long axes perpendicular to the enamel/dentine junction. The rods radiate around the central dentine core when viewed in lateral section. Individual rods are each deposited by an ameloblast cell, that retreats orally from the enamel/dentine junction, an enamel rod is formed as it retreats. Donoghue (1998) proposed that an individual tooth was comparable to a single growth prism found within conodont element. This would infer

that conodont elements are grown by a number of individual populations of cells, each responsible for the formation of an individual denticle and resulting in the complicated morphologies that characterise many conodont elements.

It has been suggested by Hass and Lindberg (1946) that crystallite orientation within conodont elements is parallel to the direction in which the main growth occurred. Crystallite growth within the ultrastructure of human and other mammalian enamels (Boyde, 1976; Berkovitz *et al.*, 1992; Rensberger, 1995) is orientated this way, lending support to this suggestion. On the basis of these observations the crystallite orientation within elements of *Eoplacognathus* imply that the main ontogenetic growth was in a direction roughly parallel to the long axes of the denticles and cusp and perpendicular to the lamellar crown/basal body junction.

White matter. The white matter cores of the caudal process denticles commonly exhibit a characteristic lozenge shape of opaque tissue with the aboral 'tail' deflected towards the mature regions of the process (Figures 9B, D, E, G-H). It is possible that this morphology reflects and is confined within the cone in cone structure of the growth prisms described above. The lateral margins of the white matter cores are distinct in section (Figures 5B, 10C) and probably reflect the lateral margins of the growth prisms. This suggests that the deposition of the white matter cores is controlled by the same growth mechanism that controls the form of the growth prisms.

The white matter cores of the dorsal process denticles do not appear to have a deflection in the lower regions of the tissue (Figures 6C, E, G, 9A-H). The denticles at the distal tip of the process are generally fully occupied by white matter cores and it is rare to see even the most distal denticles lacking white matter cores.

Horizontal sections of stelliplanate elements reveal the apex of the basal body beneath the dorsal process before any of the other processes (Figures 11D, F). This shows that the basal body is in its most oral position within the dorsal process, with the basal body/lamellar crown boundary close to the base of the denticles, as seen in Figures 6E, 11D, F. The basal body of the caudal process occupies a narrow, shallow cavity that develops in a position slightly behind the propagating tip of the developing process (Figures 11D, F). These differences in basal body/lamellar crown boundaries correspond to the differing forms of growth prisms and white matter cores. It is possible, therefore, that the form of the growth prisms and therefore the morphology of the white matter core bases maybe dependent on the position and proximity of the basal body/lamellar crown boundary beneath the developing denticles.

The morphology of the cone in cone structure of each growth prism is reflected in the general morphology of white matter cores, delineated by crystallites at the hyaline margins (Figures 6H, 7C, 8C). Figure 6H shows that the growth prisms were initially directed away from the distal tip of the basal body, in a direction oblique with the long axis of the process. The crown tissue continued growth by apposition to the initial evaginations of incremental lines that formed the new denticles, and the direction of growth gradually

changing until parallel with the long axes of the rest of the denticles and the cusp. Secretion of white matter starts just above the basal body, but is contained within the growth prism of the denticle (Figures 9D). Similarly, in both mature and juvenile stelliplanate elements only the upper half of the cusp possesses white matter tissue; sectioning has shown that this is where the basal body/lamellar crown boundary is highest with respect to the oral surface of the element (Figures 6A-B, 9B, F, G).

Juvenile stelliplanate elements possess white matter within the denticles of the dorsal processes (Figures 6A-B). This appears to confirm that the white matter of the dorsal process denticles is developed as soon as the process began developing. Contrary to this, Jeppsson (1979) noted that white matter was absent from the cores of denticles during the early stages of element growth. Eoplacognathus either differs from this, or it is possible that smaller, more juvenile specimens equivalent to those studied by Jeppsson (1979) have been lost. Elements that possess no white matter in their most distal caudal denticles show that white matter of the caudal process denticles only occurred after several hyaline increments had been laid down (Figures 9A, E, F, G, H). It is possible that the distribution of white matter is related to the position of the basal body/lamellar crown boundary. Within the dorsal process the junction is close to the base of the new distal denticles and the white matter is secreted almost instantaneously, within caudal process denticles, where the junction is distant, the initiation of white matter secretion is not instantaneous. This may relate developmentally to the initial stages of enamel secretion, where the first layers of enamel crystallites, adjacent to the enamel/dentine boundary, are aprismatic and unstructured (Berkovitz et al., 1992). It is only after the modification of the secretory pole of each ameloblast, that the development of individual rods is instigated. This may compare to some kind of modification that occurs to the cell populations, responsible for the formation of hyaline crown in conodont elements, that results in a switch to the formation of white matter.

Figures 6C-D show the dorsal and caudal processes of a stelliplanate element, where the white matter within the denticles has been truncated by wear from the element surface (see Chapter 2.4). This type of internal truncation is also seen within the Pa (P₁) element of *Ozarkodina confluens* (Branson and Mehl) (Sansom *et al.*, 1992, p. 1210, fig. 3A). This suggests that the platform elements of *Eoplacognathus* were functionally active between phases of regeneration and infers that the white matter was only secreted once in each denticle, and not during subsequent growth phases.

Donoghue (1998, p. 645) found that the crystallite orientation within the lamellae about the white matter cores of ozarkodinid elements was "perpendicular or sub-perpendicular to the flanks of the white matter cores and long axes of the denticles". Specimens of *Eoplacognathus* show a different type of internal structure, with crystallites orientated oblique or parallel to the denticle flanks and therefore also oblique or parallel to the flanks of the white matter cores. Donoghue (1998) identified polarised cell shaped cavities within the white matter that he thought indicated that the secreting cells retreated orally. He suggested that "this contrasts strongly with the direction of growth of the lamellar crown tissue, which from the orientation of the crystallites was usually perpendicular or subperpendicular to the flanks of the core" (1998, p. 645). It has

not been possibly to identify such clear polarisation amongst the cavities of white matter cores in *Eoplacognathus* elements. However, if the secreting cells of the white matter cores retreated orally in accordance with Donoghue's (1998) model then, in this case, there is no contrast between the growth direction of white matter and lamellar crown found in stelliplanate elements of *Eoplacognathus*.

The presence of lamellae in white matter tissues and the intergrading of white matter into hyaline tissue imply that the crown tissues of platform elements of *Eoplacognathus* grew synchronously. Donoghue and Chauffe (1999) and Donoghue *et al.* (2000) have proposed that white matter was secreted in concert with the hyaline crown tissues, by the same cell population to form a new type of tissue that is unique to conodonts, but developmentally homologous to enamel. The interpretation of the ultrastructures in elements of *Eoplacognathus* conforms with this hypothesis.

Basal body tissues. It has not been possible to reveal any internal structures of the basal body tissues. Amongst vertebrates, it is common for enamel tissues to overlay dentine (Ten Cate, 1987; Donoghue, 1998), so by inference, if the basal body of *Eoplacognathus* is overlain by an enamel like tissue, it is possible that it represents a form of dentine. Dentine is an extremely varied tissue (Donoghue, 1998), therefore, although restricted by the limited success of the sectioning, it is tentatively suggested that the basal tissue of *Eoplacognathus* could fall within the category dentine.

Growth of the element.

Figures 5A and 5C show a longitudinal section through a stelliplanate element and detail of the base of the caudal process. The basal lamellae represent new increments expanding beyond the distal tip of the process to initiate new growth. Unfortunately only the lower regions of the lamellae are clearly resolved in Figures 5A, C; however, transmitted light images (Figure 7A-C) reveal that the lamellae in this location are continuous with the lamellae that built the denticles. The cavities seen in Figure 5C may represent the successive growth increments extending the length of the process and initiating new growth prisms. This structure is also seen in the construction of the aboral surface of the element where laminations are closed about the distal tip of each process (Figures 12 D, F). Donoghue (1998, p. 652, fig. 11e) figured sections of *lcriodella*, that possess a structure that have been categorised as a Type A platform, a modification of Type III growth, *sensu* Donoghue (1998). The arrangement of lamellae within the platforms of *Eoplacognathus* compare closely to the structures seen in *lcriodella* (Figures 5C, 7C) and may suggest that this blade shaped process should also be categorised as a Type A platform (Donoghue, 1998).

The lamellae of the ventral-lateral process figure 4D are clearly visible because the crystallites within are all orientated with their c-axes perpendicular to the lamellar surfaces. The orientation of the crystallites seen within the ventral-lateral process in Figure 4 implies that the main growth axis of the prism reflects a lateral expansion, increasing the width of the base of the process, as well as the height of the process. This is also

indicated by the gross morphology of the outline of the process seen in the section, where the platform is laterally expanded. In effect this is a transverse section through a growth prism that reflects a lateral expansion. In contrast the denticles of the dorsal and caudal processes (Figures 3C, 7C) are composed of crystallites that are orientated parallel with the long axis of the denticles and therefore represent orally expanding growth prisms.

Polished sections show that the earliest basal cavity of the element only extended beneath the cusp and posterior process. Because conodont elements are known to grow by outer apposition (Furnish, 1938; Hass, 1941; Donoghue, 1998), away from the lamellar crown/basal body boundary, this shows that this was the first region of the element to develop (Figures 11D-F). In section it is clear that the cavity is largest directly beneath the cusp, where it is lozenge shaped, with sharp points at both the dorsal and ventral ends of the cavity (Figure 11D, F). This configuration of processes and the development of basal body show that the element was angulate or carminate in the early stages of ontogeny with a cusp and dorsal and ventral process, approximately 100µm in length.

Functional implications of crystallite microstructure.

Figures 2C and 2D show lamellae that are composed of crystallites that have a regular fabric, but are not all uniformly aligned. This effect might be caused by the angular orientation of the section relative to the lamellae; however, the crystallites have a distinct prismatic fabric and it is possible that there is an ontogenetic or functional reason for this crystallite arrangement.

Rensberger (1995) under took a detailed study of mammalian enamel and its responses to stress. He was able to show that when enamel was composed of aligned elongate structures (rods), the tissue was liable to fail in a direction that was parallel to the longitudinal tissues. Mammalian enamels have developed a number of tissues with subtly different ultrastructures that are able to prevent fractures that exploit planes of weakness (Koenigswald *et al.*, 1987; Ten Cate, 1987; Rensberger, 1995). Early Palaeocene mammals developed a complicated structure, where groups of individual rods were bounded by adjacent groups that had grown in a different orientation, the planes between each group were called decussation planes. This type of structure prevents cracks propagating through more than one decussation plane (see Chapter 1.4 for full discussion). Human enamel also has this specialised ultra structure at the tips of tooth cusps (Ten Cate, 1987). In section, the individual rods have a gnarly appearance, because each group of rods is adjacent to another that has a different orientation (Berkovitz *et al.*, 1992).

The prismatic crystallite structure seen in Figure 2D compares well to the crystallites figured by Donoghue (1998, pp. 652-3, Fig. 11d) that occur within the platform region of *lcriodella inconstans* Aldridge. SEM studies of *lcriodella* have shown that damage found on the platform nodes can be attributed to functional damage during the life of the conodont (Chapter 4.4). Functional studies have revealed that the caudal and

dorsal process denticles of *Eoplacognathus* functioned by shearing down or against the opposing caudal and dorsal process during function (Chapter 2.4). This type of function could have resulted in large stresses around the edge of denticles, and at the junction of processes. Prismatic crystallite structures occur in elements of *Eoplacognathus* (Figures 2C, D) and *Icriodella*, within regions that are thought to be functionally active. The structure of the hyaline tissue in these regions may represent the evolution of a specialised tissue structure within conodont elements, that performed a function comparable to the decussation planes and gnarly enamel that are found in higher vertebrates.

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Figure 1. A-B *Eoplacognathus reclinatus*, stelliplanate elements with labeled processes, oral view. A. Sinistral stelliplanate. B. Dextral stelliplanate. C-E Orientation and notation of sections.



Figure 2. Specimen 133. Horizontal section through *Eoplacognathus reclinatus* sinistral stelliplanate element. A. Diagram showing position of figures. B. Whole section, showing outline of basal body and surrounding lamellar crown. C. Crystallites adjacent to basal body of caudal process. Image shows basal body to left of image and possible prismatic crystallite arrangement at edge of element, seen towards the right of the image. D. Prismatic crystallite arrangement adjacent to basal body next to ventral process (basal body, top left of image).



Figure 3. Specimen 132. Longitudinal axial section through *Eoplacognathus reclinatus* stelliplanate element. A. Diagram showing position of figures. B. Whole image, showing distribution of lamellar tissue. C. Tip of cusp showing preferred longitudinal arrangement of crystallites. D. Detail of crystallites along dorsal process edge, showing crystallites with their long (c) axes perpendicular to element surface. E. Edge of most distal denticle of dorsal process showing thin laminations in white matter and small cavities aligned with incremental lines.







Figure 4. Specimen 140. *Eoplacognathus reclinatus* transverse section through ventral and ventral-lateral processes of dextral stelliplanate element. A. Position of transverse section. B. Diagram to orientate transverse section. C. Whole image of section showing position of basal body and lamellar crown. D. Crystallites within lamellar of ventral process, showing perpendicular orientation of long (c) axes with respect to incremental lines. The outer surface of the element is towards the right hand side of the image, and the crystallites are perpendicular to the lamellae surfaces.



Figure 5. *Eoplacognathus reclinatus*, stelliplanate element, specimen 212. A. Longitudinal section through sinistral stelliplanate. x400. B. Close up of dorsal process denticles and white matter. x 1.3K. C. Close up of caudal process base. The lamellae form cavities that appear to be open to the basal body. x 1.3K. D. Close up of edge of dorsal process platform. Lamellae can be seen curving around the aboral edge. x 1.3K.



Figure 6. Platform elements of *Eoplacognathus reclinatus* seen in transmitted light. A. Specimen 360, juvenile sinistral stelliplanate element x700. B. Specimen 361, juvenile dextral element x700. C. Specimen 362, sinistral element, mature dorsal process showing truncated white matter x 400. D. Specimen 362, mature caudal process showing clear truncations of white matter due to wear x 600. E. Specimen 364 Dorsal process with basal body visible beneath x500. F. Specimen 364, dextral element. Caudal process denticles showing growth increments at denticle tips (Faint in large central denticle) x1000. G. Specimen 365, sinistral element. Dorsal process showing truncated white matter cores and clear regenerated hyaline crown forming new ridge x400. H. Specimen 364. Caudal process with growth increments (faint, centre of page) at base of denticles x1000.



Figure 7. TLM images of *Eoplacognathus* stelliplanate elements . A. Specimen 268, sinistral element. Caudal process showing incremental lines within denticles x500. B. Specimen 269, sinistral element. Caudal process showing incremental lines at base of process x500. C. Specimen 270, sinistral element. Caudal process showing incremental lines and radiation of growth prism within the denticle x600. D. Specimen 270. Base of caudal process showing structure of incremental lines at base of process x550.



Figure 8. *Eoplacognathus reclinatus*, specimen 141, horizontal section through sinistral platform element. A. Diagram of element and locations of B and C. B. Whole image showing outline of basal body. C. Close up of denticle cores of caudal process, proximal to junction with dorsal and ventral processes.



Figure 9. TLM Images of platform elements of *Eoplacognathus*. A. Specimen 260. Dextral stelliplanate. B. Specimen 261. Sinistral stelliplanate. C. Specimen 262. Dextral stelliplanate. D. Specimen 263. Sinistral stelliplanate. E. Specimen 264. Sinistral stelliplanate. F. Specimen 364. Dextral stelliplanate. G. Specimen 266. Sinistral stelliplanate. H. Specimen 365. Sinistral stelliplanate. A, C, F show caudal process towards the left of the image. B, D, E, G-H show caudal process towards the right of the image. All images approximately x150.



Figure 10. Eoplacognathus reclinatus, longitudinal section of sinistral stelliplanate element, specimen 212 (also seen in Figure 5). Specimen orientated as for Figure 5, with apex of denticles towards top of page. A. White matter in denticle of caudal process. x 1.3K. B. White matter in denticle of dorsal process. x 1.3K. C. A x 3K. D. C x 6K.











Figure 11. *Eoplacognathus reclinatus* basal bodies of stelliplanate elements. A. Diagram showing position of Figure B. B Specimen 002. Sinistral stelliplanate element showing dorso-lateral process and corresponding basal body expansion. C. D Diagram showing position of Figure D. Specimen 001. Apex of basal body at cusp and dorsal process. E. Diagram showing position of Figure F. F. Specimen 209. Apex of basal body showing continuous basal body within dorsal and ventral processes at early juvenile stage of element growth.



Figure 12. Basal bodies and cavities of platform elements of *Eoplacognathus reclinatus*. A. Specimen 100. Whole sinistral stelliplanate element, basal cavity. B. Detail of A, showing dorsal and dorso-lateral processes. C. Detail of A, ventral-lateral process. D. Detail of A, caudal process. E. Specimen 227, detail of ventral process basal body at distal tip. F. Detail of A, distal tip of caudal process showing lamella crown around edges of basal cavity.

CHAPTER 2.3 THE PRIMARY SURFACE MICROSTRUCTURES OF P₁ ELEMENTS BELONGING TO EOPLACOGNATHUS RECLINATUS

Introduction.

The most common type of primary microstructure is a longitudinal rope-like pattern, commonly found on the cusps and denticles, a second type is polygonal ornamentation, where the longitudinal ornamentation sometimes becomes sinuous and sometimes anastomoses to form a polygonal ornamentation. Both these types of surface microstructure are present on the elements of *Eoplacognathus*. Many authors have described polygonal ornamentation, and selected cases are discussed below. The material used in this study is from the Suhkrumagi section on the outskirts of Tallinn, Estonia (for details of locality see Kaljo and Nestor, 1990), and was collected by Viive Viira and Richard Aldridge.

Lindström, McTavish and Ziegler (1972) described a form of reticulate ornamentation found on the elements of *Gothodus* n. sp. A (Lindström, McTavish and Ziegler, 1972, Table 3, figures 4-6). Reticulate ornamentation was also found on elements of *Prioniodus* sp. aff. *evae* (Lindström, McTavish and Ziegler, 1972, Table 2, figures 1,4) formed by a series of anastomosing fine ridges. The authors considered the two forms of reticulate ornamentation to be different because the form found on the *Gothodus* element appeared poorly defined in several areas, whereas the ridges of the reticulation found on the *Prioniodus* element clearly reunited to form coarse striae resulting in a continuous ornamentation. It is likely that these two forms of reticulate ornamentation are in fact comparable, but that the element of *Gothodus* has a discontinuous ornamentation because the element surface had been worn during function in life.

Coarse ropy ornament on the denticles and reticulate polygonal ornament found on the platforms of pectiniform elements were described by Lindström and Ziegler in the *Treatise* (1981). Interestingly these authors also noted that there was a tendency for longitudinal facets in certain elements to meet at angles of about 120°, corresponding to the hexagonal geometry of apatite crystals. This observation was not extended to other surface microstructures and the crystallite orientation within the platform regions of pectiniform elements was not commented on.

Conway Morris and Harper (1988) investigated the possibility of a correlation between genome size and the size of polygonal surface microstructures on pectiniform elements. The assumption behind this hypothesis, first proposed by Pierce and Langenheim (1970), is that the polygons correspond to cell "imprints of [the] secretory epithelium" (Conway Morris and Harper, 1988, p 1230). The dimensions of 8580 surface polygons were obtained from a variety of published and unpublished sources using elements covering almost the entire stratigraphic range of the conodont group. Conway Morris and Harper (1988) observed that there was a consistent lower limit on polygon size (about 4μ m) that appeared to persist throughout the history of

conodonts, although from the Permian onwards the dimensions rarely fell below 6µm. Ordovician, Silurian and early Devonian conodonts showed consistently low values for polygon dimensions. From the Devonian onwards a large increase in polygon dimensions was observed with some conodont elements having polygons measuring more than 18µm across. Conway Morris and Harper (1988) conceded that the data were too scanty to draw reliable conclusions from these general trends and concluded that variations in polygonal surface structures and hence genome size (according to the authors) lacked an obvious adaptive explanation.

Burnett (1988) accepted the hypothesis that polygonal surface ornamentation represented the imprints of secretory epithelial tissue and presented a study of polygonal ornament in the platform element of the conodont *Siphonodella*. He suggested that the external microstructures of polygons represented the portion of the element that was permanently covered in soft epithelium tissue. Within the specimen he sectioned (Burnett, 1988, figs. 1B, 1C p. 412), the juvenile surface lamellae were apparently ornamented with polygonal structures, whereas the succeeding mature surface layers were smooth and lacking in any ornamentation. Burnett (1988) suggested that the polygons were preserved on the internal layers of elements because organic layers of tissue laid down at the termination of each secreting phase, now represented by interlamellar spaces, protected their surfaces during secretion of the succeeding lamellae. The preservation of these delicate polygons on juvenile denticles indicated that they could not have experienced any wear, and had not erupted from the soft tissue Burnett (1988). Burnett (1988) concluded that it was only in later life that the element erupted and functioned to process food.

Burnett (1988) examined several specimens of *Siphonodella* and observed that the polygonal structures normally occurred on flat upper (oral) surfaces and were absent from the upstanding processes, which sometimes had longitudinal striations. Burnett (1988, p. 414) thought that this recorded "the different relationships with, or the nature of, secretory epithelium for oral/horizontal and oral/vertical deposition. It is possible that the striae represent a linear pattern within the secretory tissue, but not necessarily elongate arrangements of cells".

Burnett (1988) thought that because the elements may show ornamented and unornamented areas, the polygonal structures must have had some kind of function. He proposed that the polygonal structures, as well as representing the imprint of epithelial cells, might also have represented regions where muscle tissue was attached to the conodont element itself. In Burnett's view the muscle attachment could have anchored tentacle-like structures similar to those in Lindström's (1973, 1974) hypothetical model of the conodont animal or the epithelial covering of elements proposed by Bengston (1976).

Burnett and Hall (1992) discussed the significance of ultrastructural features in etched conodont elements. In this paper a smooth organic layer was recognised and purported to cover the outer surface of most conodonts. Burnett and Hall (1992) artificially etched elements and caused this outer layer to flake off and reveal the arrangement of apatite crystallites that formed the outermost lamella layer. Crystallite orientation showed that the crystals grew with their c-axis "parallel to the maximum growth axis" (Burnett and Hall, 1992, p.

275). Therefore, the crystallites within the platform regions beneath the polygonal surface microstructures were perpendicular to the outer surface, and the crystallites within the denticles and cusp beneath the striated microstructures were oblique or parallel to the outer surface (Figure 1).

Von Bitter and Norby (1994b) noted that polygonal structures only occurred on the nodes of the denticles of the platform elements of *Lochriea commutata* (Branson and Mehl). This location of surface structure is unusual and it was noted by the authors that it seemed to correlate with the development of white matter i.e. where the white matter was well developed the polygonal structure was also well developed. The authors (von Bitter and Norby, 1994b, p. 197) suggested that this relationship might be due to a "direct, but poorly understood, physiological relationship between the internal osteocyte cells (of the white matter, Sansom *et al.*, 1992) and the outer epithelial cells of conodonts".

Donoghue and Chauffe (1999) were able to demonstrate that the internal structures of some Devonian conodonts corresponded with the distribution and position of surface microstructure, and followed von Bitter and Norby (1994) with the conclusion that the polygonal ornament represented imprints of epithelial cells.

Dzik et al. (2000) discussed the surface ornamentation of conodont elements within the context of understanding the early evolution of the mineralised skeleton of vertebrates. Interpretation was based on the pattern of surface ornamentation which was used to account for the process of secretion and the control of The authors were satisfied that the crown tissue of conodont elements was element morphology. homologous with vertebrate enamel and interpreted the polygonal imprints found on some element surfaces to be the imprints of the secretory ameloblasts and homologous with mammalian ameloblasts. Dzik et al. (2000, p. 104) noted that the cells found on element surfaces were not uniform in size or shape and that "there was a negative correlation between size of contact area of ameloblasts with the conodont element crown tissue surface and intensity of secretion". Dzik et al. (2000, 104-105) based their theory on the assumption "that each of the cells had a similar ability to produce and secrete calcium phosphate". The authors thought that the polygons were smallest at denticle tips and on the surfaces of platform areas, therefore, facilitating intense mineralisation. The elongated cell imprints found at the bases of denticles had a larger surface areas, indicating the cells reduced ability to secrete over a relatively larger area, thereby resulting in reduced build up of crown tissue on the denticle flanks. Dzik et al. (2000) thought that the elongation of cells was "as a result of mechanical extensional stress created by the denticle tip being elevated during growth [because of the intense secretion at its tip]".

Dzik *et al.* (2000, p. 105) concluded that this uniform ability to secrete crown tissue was sufficient to explain the complexities of conodont element surface morphology, and that "morphogenesis was executed by a controlled supply of mineralised tissue at specific sites".

Description of the surface microstructure of Eoplacognathus elements.

Well preserved specimens are relatively common in collections from Estonia and have been examined for primary surface microstructures. Specimens range from 200 to 600µm in length (from the tip of the dorsal process to the tip of the caudal process). The location of different surface microstructures is not affected by the size of the element. Pristine stelliplanate elements are entirely covered with surface microstructures of which there are two basic kinds; a polygonal ornamentation and an elongate, ropy, ornamentation.

Polygonal ornamentation. The polygonal patterning is composed of numerous interlocking polygons, spread over the platform regions of the element and extending to the lower flanks of some denticles. Each polygon has a subcircular morphology with approximately 6 sides, where it is possible to count; well defined hexagonal polygons occur rarely. This boundary is a raised region of the surface topography, approximately 1-2 μ m high and normally less than 2 μ m wide (see Figure 2B). The diameter of the polygons varies between 6 and 10 μ m, although some have been observed with maximum dimensions in excess of 21 μ m (Specimen 225 Figures 2C, D). Where the 'horizontal' regions of the platform begin to pass into an inclined area, at the base of the denticles, the morphology of the reticulate ornamentation changes (Specimen 203, Figure 2F; Specimens 150, 226 Figures 3A-C; Figure 4). The polygons become elongated, though not narrowed, with their long axes parallel to the long axis of the denticle. In many cases (Specimens 015, 226, Figures 3A-D) the polygonal ornamentation persists for almost two-thirds of the denticle, but in most cases after one or two 'elongated' polygonal forms the ornamentation changes to a ropy structure (Figure 2F).

Ropy ornamentation. The ropy ornamentation is composed of anastomosing elongate ridges, which are orientated parallel to the long axis of the denticle. The ridges are formed by raised topography of the lamellar surface and are approximately $1-2\mu$ m wide. In the specimens observed it was difficult to discern the tips of each 'rope', as they fade in and out amongst each other by gradually becoming reduced in width and height (Figure 3A-B). The 'ropes' converge at the denticle tip (Figure 3E), though this is normally the area most poorly preserved and often has a granular or smooth surface (Figure 3C). The smooth tips of the denticles may be exhibiting evidence of wear (Chapter 2.4), and that there were originally surface microstructures over the entirety of the denticle, as it is often the case that the side opposite to that which is smooth still preserve primary surface textures (Figure 3C). The anastomosing ornamentation is essentially elongated polygons, with their long axes parallel with the long axes of the denticle at the bases of the denticles that are transformed into closely arranged anastomosing ropes in the upper regions of the denticles (Figure 3A-B, F). The ropes are not as tightly packed as those found on the surfaces of *Baltoniodus* (Chapter 1.3) and the surfaces are ornamented by them rather than composed of them.

Interpretation of surface microstructures of Eoplacognathus elements.

Internal structure and its relationship to external surface microstructure. Within the platform elements of *Eoplacognathus* there is a direct correlation between the angle of slope of the outermost crown and the type of surface ornamentation developed. Areas called 'vertical' in this study have a ropy surface microstructure, and areas that are 'horizontal' have a polygonal surface microstructure, with an entire gradation between polygonal and ropy surface textures on the intermediate slopes (Figure 4A, B). This corresponds to the denticles and the platform areas respectively and concords with the studies outlined above.

Sectioning has shown that there is a strong link between crystallite orientation within lamellae and the type of surface texture, (as suggested by Lindström and Ziegler [*in* Robison, 1981]; Burnett, 1988). Figures 4, 5A-D show that internal crystallites orientated with their c-axes parallel to the outer surface correspond to a ropy surface ornamentation, and those with their c-axes perpendicular to the outer surface correspond to a polygonal ornamentation. Polygonal ornamentation on the lower regions of the denticles does not appear to follow this pattern and suggests that the crystallites are oriented with their c-axis perpendicular to the outer surface, in an area which is not horizontal. It has been postulated by Donoghue (1998, p. 641) that " in areas of complex elements that are simply being enlarged by successive increments of lamellar crown tissue, without developing new morphological features, the crystallites are usually oriented perpendicular to the outer surface." This might explain the occurrence of polygonal ornamentation on the lower flanks to the denticles.

Within enamel, the crystallites are orientated with their long axes parallel with the main vector of growth (Ten Cate, 1989, Chapter 1.3 for full discussion). Therefore, where the width as well as the height of denticles is increasing, the crystallites within will reflect the path of the retreating secretory organ and hence the direction of maximum growth. Figure 4D (Chapter 2.2) shows a section through a caudal and ventro-lateral processes of an *Eoplacognathus* stelliplanate element and it is clear that the crystallites within the ventro-lateral process crystallites are oriented with their c axes perpendicular to the outer surface of the denticle. With crystallites orientated perpendicular to the outer surface, it is likely that the lower flanks of this denticle have a polygonal ornamentation comparable to that seen in Figures 2C and 3A-C.

The process of enamel formation is discussed in detail in Chapter 1.3. During amelogenesis, the cells retreat orally and secrete enamel into a protein based matrix, once the secreting end of the cell has formed an extension, called a Tomes' process. As each cell retreats it leaves a rod, or prism, which is orientated perpendicular to the enamel dentine junction. During this stage of mineralisation, the morphology of the Tomes' process results in the formation of a pit at the oral head of the rod. Crystallites formed in the centre of each rod are orientated with their c-axes perpendicular to the growing surface, the c-axes of crystals that have formed the margins are orientated oblique and are influenced by the "shearing and sliding translation... slewed round in a direction more nearly parallel with the direction of progress of the ameloblasts" (Boyde, 1976, p. 341). In enamel, the pits formed at the mineralising front (as a form of polygonal ornamentation)

are only visible if the secreting organ is removed during the process of enamel formation (Boyde, 1976). This is because during the final stages of mineralisation the Tomes' processes are replaced with a flat ruffled edge, which is required for the final stages of enamel maturation (Boyde, 1976). Due to the loss of the Tomes' processes, the final margin of enamel and its surface retains no internal structure.

The polygonal ornament found on the surfaces of *Eoplacognathus* elements may be formed in a similar way and therefore, developmentally homologous to the polygonal patterning found at the mineralising front of enamel. In enamel the internal borders of the polygons define the edges of the Tomes' processes and reflect the course of an individual secretory cell, as an individual rod was formed and the cell retreated. Several forms of polygonal patterning have been described for enamel and are related to the amount and direction of ameloblast translation during the formation of enamel. The patterning found on the elements of *Eoplacognathus* compare most closely to Pattern 1 (Boyde, 1976) which reflects a type of enamel that is formed when ameloblasts retreat in a direction that is roughly perpendicular to the growing surface.

The polygonal structures represent horizontal surfaces that are perpendicular to the direction of growth. The structures that have formed the ropy ornamentation are parallel to the direction of growth and are formed by structures that are comparable to the boundaries of the polygons found on platform surfaces. This suggests that it is possible that they also define where the edges of the tomes' processes would have been and reflect the course of an individual secretory cell. If this hypothesis is correct, it infers that the secretory cells must have retreated in a direction that was parallel with the growing surface, a pattern of secretion that is not seen in enamel.

This interpretation differs from the conclusions discussed in Chapter 1.3, where the surface ornamentation of elements belonging to *Baltoniodus* were studied. Surfaces of elements belonging to *Baltoniodus* possess elongate spindle like structures that may be developmentally homologous to the elongate rods found in prismatic enamel. The two types of surface microstructures differ in that the surfaces of *Baltoniodus* are composed of elongate ropy structures, and the surfaces of elements of *Eoplacognathus* are ornamented by elongate ropy structures.

Enamel has been shown to show a variety of reactions to demineralising agents. It is possible that this reflects the different physical and chemical properties (Berkovitz *et al.*, 1992. p. 117, fig. 217a-c) of the rod boundaries and rod cores. This may mean that the two different forms of microstructures apparent on the surfaces of elements of *Baltoniodus* and *Eoplacognathus* are a product of preservation.

There is no reticulate ornamentation on the tips of the denticles of *Eoplacognathus* platform elements comparable to that on the nodes of *Lochriea* reported by von Bitter and Norby (1994b). This is probably because there are no comparably broad 'horizontal' regions at the apices of the denticles, and that crystallites within are not arranged with their long axes perpendicular to the outer surface.

Functional implications of surface microstructures of Eoplacognathus elements.

The reticulate ornamentation may represent areas of the element that were permanently covered with soft tissue, resulting in the preservation of delicate imprints of the secreting epithelium, as proposed by Burnett (1988) and Donoghue (1998). If this suggestion is correct, then the fact that some denticles have half of their lower regions covered by reticulate ornamentation suggests that the soft tissue could have covered large parts of the platform element. My functional studies (Chapter 2.4) have shown that the dorsal process denticles of stelliplanate *Eoplacognathus* elements occluded against each other and the caudal process denticles probably sheared past or against each other. With this method of processing it might have been possible for the platform regions of the element, and to some extent the bases of the denticles, to have remained covered in soft tissue without impairing the function of the element.

It is difficult to explain the reticulate ornamentation found by von Bitter and Norby (1994b) on the nodes of *Lochriea* by a permanent epithelium covering in this area only. If this were the case, it would imply that the platform element of *Lochriea* did not occlude and process food between its platform denticles, or that the denticles did not come into contact with each other or processed food substances that were incapable of wearing away the polygonal and ropy ornamentation.

Donoghue (1998) did not agree with Bengston's (1976) model of element growth, where it was proposed that elements could be withdrawn into an epithelial pocket. Instead, he proposed that the elements could have "periodically sunk within the dermis, or else the dermis must have grown over the surface of the element, to facilitate growth and repair." (Donoghue, 1998, p. 660). If the dermis grew over the surface of the element, it would be worn away once the element became functional active again, only wearing off the functional surfaces as seen in figure 3C-D. Although possible it is considered unlikely that the distribution of different surface microstructures represent the different modes of secretion required to produce an element of such complex morphology and the controls for its removal after a period of growth are not yet fully understood.



Figure 1. Cross section of a platform element showing hypothetical epithelial secreting cells and detail of the corresponding crystallite orientation beneath microsurface structures. Redrawn from Burnett and Hall (1992, p. 3, Fig. 1). A. Crystallite orientation in platform regions also figured in Figure 5D. B. Crystallite orientation within the denticle lamellae also figured in Figure 5A, B, C.






Figure 3. Surface ornamentation on platform elements of *Eoplacognathus reclinatus*. Specimen 150. A. Caudal process denticles, showing polygonal ornament anastomosing into ropy ornament on denticle flanks. B. Close up of A, showing junction between two types of surface microstructures. C-F Specimen 226. C. Polygons on surface of caudal process denticles. D. Opposite side of same process showing smooth areas probably caused by function of element. E. Tip of dorsal process denticle, showing ropy ornament converging at tip of denticle. F. Ropy ornamentation on denticles of dorsal process.





Figure 5. A. Longitudinal axial section through stelliplanate element of *Eoplacognathus reclinatus*, showing location of section close-ups, Specimen 132. B. Longitudinal axial section through dorsal process denticle showing crystallites oriented with c axis parallel with long axes of denticles. C. Horizontal section through caudal process of stelliplanate element, showing crystallites oriented with c axis parallel with long axes of denticles, specimen 141. D. Longitudinal axial section through platform laminations showing crystallites with c axes perpendicular to outer surface.

CHAPTER 2.4

THE FUNCTION OF P1 ELEMENTS OF EOPLACOGNATHUS RECLINATUS

Introduction.

Conodonts were early representatives of the vertebrates (see Aldridge and Purnell, 1996 for a review). This interpretation has great significance, as conodonts represent one of the earliest and longest lived, and most diverse clades of jawless fish (Donoghue and Purnell, 1999a). They could potentially provide information crucial to the understanding of the early evolution and function of vertebrate hard tissues.

It is thought that the acquisition and processing of food was central to the evolution of aquatic vertebrates (Pough *et al.*, 1996), therefore an understanding of conodont element function is important in understanding conodont evolution.

Studies of morphology, patterns of surface damage, wear, and internal details have shown that conodont elements functioned as teeth (Purnell, 1995; Donoghue and Purnell, 1999a and 1999b). This information is based largely on evidence derived from ozarkodinid conodonts. Ozarkodinids were one of the three conodont orders, the prioniodinids, prioniodontids and ozarkodinids, that developed an apparatus with morphologically complex elements. Ozarkodinids were the most derived and successful conodonts and represent the only conodont order for which clear functional models are understood. Some prioniodinids and prioniodontids also developed molarised P elements within their apparatuses; however, it is not known how appropriate the ozarkodinid functional model is as a general plan for understanding conodont element function for other conodont orders.

The prioniodontids, a diverse and possibly polyphyletic group (Sweet and Bergström, 1972) were the first conodonts to develop a functionally differentiated feeding apparatus with complex elements (Sweet, 1988). *Eoplacognathus* was one of the first prioniodontids to develop morphologically complex platform elements. Previous reconstructions interpret the apparatus of *Eoplacognathus* as a pair of platform Pa elements and a robust pair of Pb elements, with no associated ramiform elements (e. g. Bergström, 1971; Chapter 1.1). Here I analyse the function of the derived prioniodontid platform element and assess this in the light of the ozarkodinid functional model.

Materials and methods.

This analysis is based on elements of *Eoplacognathus reclinatus* from the Suhkrumagi section located 4 km south east of Tallinn, Estonia (for details of locality see Kaljo and Nestor, 1990). Physical models have been used to understand the spatial constraints of different occlusal models. *Eoplacognathus* P_1 elements show some intraspecific variation, but the significant structural differences are constant. Complete, well preserved,

sinistral and dextral stelliplanate elements were chosen from the collections to represent typical specimens of *Eoplacognathus* P_1 elements. Precise scaled plasticine models were made of both sinistral and dextral elements, using scanning electron microscope photographs taken from different angles to ensure accuracy. Latex moulds were then made and plaster of paris models cast.

The occlusion of *Eoplacognathus* elements was investigated by placing the sinistral and dextral models together to ascertain how the elements could have occluded and to recognise the morphological constraints. Orientation terms and process identifications are seen in Figure 1 and oral and lateral views of the elements provided in Figures 2A-D.

The surfaces of the elements were occasionally exceptionally well preserved, and these specimens have been concentrated on for this functional study. However, generally the surfaces of the elements were slightly recrystallised which precluded microwear studies and only allowed the recognition of larger primary surface structures.

Orientation of elements.

The P_1 elements of *Eoplacognathus* can be homologised with the P_1 and perhaps the P_2 elements of *Promissum*; hence, their orientation within the apparatus can be incorporated into the functional model (Chapter 2.4). *Promissum* P_1 and P_2 elements occluded across the central axis of the feeding apparatus with the conventional 'posterior' process oriented in a dorsal direction (Aldridge *et al.*, 1995). This places the *Eoplacognathus* platform element with its long axis oriented dorso-ventrally, with the conventional 'posterior' process oriented dorsally, and the conventional 'ventral' and 'ventro-lateral' processes oriented rostrally.

Tests of functional hypothesis.

The physical models allow development of a functional hypothesis based on morphological constraints. The functional hypothesis can be tested by analysing well preserved elements in the scanning electron microscope for presence and absence of surface damage to the denticles and processes in regions where wear would be predicted by the hypothesis. This analysis can be further evaluated by studies of internal structures which provide evidence of internal discontinuities resulting from recurrent patterns of surface damage due to function (Donoghue and Purnell, 1999b).

A functional hypothesis constrained by element morphology.

Eoplacognathus stelliplanate elements have a maximum of six processes in mature specimens (Figure 2A-D). Both the dextral and the sinistral elements share the same gross morphology, with dorsal and caudal processes forming a straight line; this is the main axis of the element. The caudal process denticles are always tall in comparison to the dorsal process denticles. In oral view the ventral process can be seen to curve away from the main axis forming an angle of approximately 50° with the dorsal process. At the point where the ventral process begins to curve, adjacent to the main axis of the element, a ventro-lateral process is attached, forming an angle of approximately 90° with the ventral process. Dorso-lateral processes are attached to the inner or outer edge of the dorsal process, though they are normally only expressed in mature specimens. In more juvenile specimens dorso-lateral processes are represented by an extended lobe of the dorsal process platform. Though both sinistral and dextral elements share this basic morphology, they do not form precise mirror images of each other (Viira, 1972).

The ventral process denticles of sinistral elements, where the process forms a junction with the cusp, are large (Figure 2C). The ventral process of the dextral element has small, low, rounded denticles or often just a narrow costa adjacent to the main axis (Figure 2D); the denticles of the process are low and rounded or there is a low adenticulate region next to the main axis of the element. There is much variation at this process junction but in general the denticles of the ventral process of the sinistral element are always larger, more discrete and join the cusp at a much higher level than those of the dextral element.

The main axes of the sinistral and dextral elements display a sinuous complementary symmetry, with the sinuosity most strongly expressed in the denticles at the end of the dorsal processes (Figure 2A-B). The denticles of the dorsal process are often deflected towards the inner edge of the process in both elements.

These morphological observations restrict possible functional hypotheses; consequently, there are two possible modes of occlusion. Hypothesis 1 predicts that the all the process denticles worked against each other, crushing food between their tips without close element occlusion. A second hypothesis proposes the caudal process denticles sheared past each other allowing the dorsal process denticles to occlude against each other. Because of morphological restrictions hypothesis 2 predicts that the main axes of each element occluded down the opposite side of the opposing element's main axis, allowing a much closer occlusion (Figure 3A-B). The denticles of the dorsal process could have occluded directly against the opposing denticle tips or have sheared past each other as proposed for the caudal process denticles.

Basic morphological features support the second hypothesis. The outside edge of the dorsal and caudal processes of the sinistral element could have occluded against the inside edge of the dorsal and caudal processes of the dextral element. Occlusion would have been impossible down the opposite side of each element due to the high topography of the ventral process of the sinistral element.

Testing the hypotheses.

To test which hypothesis is most appropriate it is necessary to study the distribution of patterns of surface damage and wear and to search for corresponding structures internally. If the elements occluded down either side of the main axis of each element then surface damage to the sides of the denticles would be expected. However, if the denticles occluded against each other then well preserved denticle tips will show evidence of wear, as their topography is worn down. It is predicted that if the denticles worked directly against the opposing denticles, internal structural damage will be particularly apparent, as the cores of the white matter would be worn down. It is possible that damaged denticles can be identified by extensive overglazing where subsequent regeneration has resulted in layers of lamellae growing over the damaged areas; however, it is necessary to find concurrent surface or internal damage to verify this type of growth as evidence of damage.

Surface evidence. Most examples examined have not preserved unequivocal evidence of wear, generally exhibiting poor preservation, overglazing or denticle deformation which could be the result of functional damage.

It has not been possible to identify actual wear facets or microwear (Donoghue and Purnell, 1999a and b), but several denticles have lost their primary ornamentation. Figures 4 A, C, E and F show the inside edge of dorsal process denticles of dextral elements. The loss of primary microstructures and worn denticle surfaces are possible evidence of denticle damage due to function. The denticle morphologies reflect this wear and are deflected away from the area of function (Figure 4 F). It is uncertain whether this is an effect of wear or the original morphology of the denticles. Similar wear has also been observed on the tips of the denticles of the sinistral element, although in this case the areas worn are on the 'outer' side of the element. It is difficult to verify this evidence of wear because unequivocal examples are rare and areas on the opposite side of the denticles only rarely preserve clear primary ropy ornamentation and appear recrystallised, or poorly preserved (Figures 4 B, D).

It has only been possible to identify one dextral specimen where the denticles of the caudal process exhibit unequivocal evidence of wear. Figures 5A-B show that both the inner and outer edges of the lateral (caudal) process denticles have been polished and have lost part of their primary surface textures. The outside edge (Figure 5B) appears to have lost most of its primary ornamentation with only smooth surfaces up to the tips of the denticles. There is also clear damage on the denticles of the inner side of the 'lateral' (caudal) process (Figure 5A).

Two specimens have been found where the dextral element has revealed unequivocal wear on the outside edge of the first few denticles of the ventral process (Figures 5 C-F). It is clear that the element has only lost its primary textures on one side of this process (Figure 5E) and that the primary texture is still preserved on the opposite side of the process (Figure 5F). Corresponding wear on sinistral elements has not been found. It is

possible that this wear was not predicted by the hypothesis because the sinistral and dextral elements chosen to model were not from the same individual in life. Therefore dimensions of the occlusal surfaces would not replicate exactly how these two elements would have occluded against their natural partners.

The caudal process denticles are large (relative to the dorsal process denticles) often fused together and heavily overglazed although the denticle tips generally remain discrete. The dorsal process denticles generally remain more discrete and retain their morphology.

Internal structures. Generally the white matter within large, discrete denticles of the caudal process occupies regions within both the denticles and the process, forming an elongate lozenge shape (Figures 6B, D, E). There is however significant variation of white matter distribution (Figures 6A-H). In more mature specimens the white matter lozenges are of irregular height and sometimes it is clear that their upper margins are truncated (Figures 6D-E, 7C, E, G, 8A-B). In some specimens white matter is completely absent from some denticles even though the element appears to have reached maturity (indicated by its size, and the obvious overglazing of denticles) (Figures 6A, F, 7H).

Purnell (1995) and Purnell and Donoghue (1998) Donoghue and Purnell (1999a and 1999b) have demonstrated that repeated functional use of denticles against food substances or the denticles of the opposing element results in denticle surfaces being damaged and worn down. It is predicted here that the internal record of this function will be clear oral truncations of white matter tissue, followed by regeneration. This form of function and then regrowth is particularly well represented within processes of *Eoplacognathus* as it appears that following denticle damage, repair is in the form of hyaline crown tissue and not through the regeneration of white matter tissue (Chapter 1.2). This results in clearly truncated white matter cores followed by hyaline crown tissue that records the functional history of the element (Figure 7C, D).

The internal tissues of the dorsal process denticles often have a morphology that differs from the cores in the caudal process (Figure 6A-G). The white matter of the caudal process denticles forms elongate lozenge shaped cores that extend into the process beneath the denticles. Occasionally the oral margins of the white matter cores appear to be truncated and do not extend into the tips of the denticles; this is in accordance with the last stages of crown tissue growth only generating hyaline tissues (Figure 6B, D, E, H). The dorsal process denticles possess white matter cores that are smaller than those of the caudal process denticles, with slightly pointed lower margins that do not extend below the confines of the denticle, and generally have rounded oral margins.

Specimen 376, seen in Figure 8C, possesses white matter cores that appear banded, rather than solid. Only one specimen was found with this distinctive internal white matter formation. The light bands represent hyaline bands between the opaque white matter bands. It is possible that the hyaline bands represent the outer layer of hyaline crown that was deposited during the final stages of mineralisation. It is difficult to understand why this phenomenon is not always apparent within white matter cores as externally. The hyaline

layers may be present in all white matter cores, but not always clearly visible and obscured by new layers of white matter. Specimen 376 might, in this case, represent an element that had unusually long phases of outer hyaline tissue production.

Function of white matter.

The homogenous structure of white matter does not provide aligned planes of weakness as purely hyaline tissues do. It is possible that it prevents tissue failure in a way that is comparable to decussation planes that are found in enamel (Koensberg *et al.*, 1987). Decussation planes prevent the propagation of cracks by reducing the number of directions in which they can propagate (see Chapter 1.4 for full discussion). Studies of *Eoplacognathus* elements appear to support this theory. Figures 7C, D and G show examples of the dorsal process of a dextral stelliplanate element. These figures show dorsal processes that have very little white matter. The denticles have been worn down orally and only regenerated with an overglazing of hyaline crown tissue that has formed a straight ridge instead of retaining the morphology of the denticles. Müller (1981, p. W38) also noted that within elements that showed forms of internal truncation "the white matter terminates abruptly and the regenerated portion contains little white matter and is somewhat more translucent".

Normally the white matter of the denticles of the caudal process occupies much of the denticle and extends beneath into the process. Specimens 260, 263, 362 (Figures 6A, D and 7D respectively) have caudal processes that show unusual overglazed morphologies and lack well formed white matter in their denticles. It is possible that excessive damage results from reduced white matter within denticles and this might be responsible for the entire loss of some denticles. Figure 8C shows actual denticle loss that was possibly caused by the absence of or dissipated white matter.

Sectioning has shown that the basal body/lamellar crown boundary within the dorsal process is very close to the base of the denticles and is in its most oral position within the cusp. The basal body of the caudal process contrasts with this and is only developed within the lower part of the process, within a narrow shallow cavity. It is possible that the distribution of white matter is related to the morphology of the underlying basal body/lamellar crown boundary and that this in some way controls where and when the white matter cores are secreted. This would account for the seemingly larger white matter cores that occupy the process and denticles of the caudal process, and the smaller white matter cores of the dorsal process, which never extend into the process or the lower region of the cusp (Chapter 2.2).

Relationship between possible food types and wear.

The elements of *Eoplacognathus* examined, where well preserved, have denticle surfaces that have lost their primary ornamentation and are polished smooth. This type of wear is not consistent with the pitted surfaces caused by compression and crushing of food particles, nor does it display the fine parallel striations that are thought to indicate a shearing motion (Purnell 1995). These denticles were probably worn down by repeated mashing of soft food substances between the two elements but not by direct denticle occlusion, where food substances are crushed between two element surfaces. Polishing indicates element on element function in the absence of food or presence of non abrasive food (Purnell 1995).

Occlusion.

Homologies with the apparatus of *Promissum* can be used to orientate the elements of *Eoplacognathus*, positioning them occluding across the mid axis of the apparatus, with the main axis of the element orientated dorso/ventrally. This is comparable to the position and orientation of ozarkodinid P_1 elements, which are known to occlude across the mid axis of the apparatus with the left element behind the right (Purnell, 1995; Purnell and Donoghue, 1997; Donoghue and Purnell, 1999a, b). The complex morphology of the *Eoplacognathus* P_1 elements restricts possible occlusion between sinistral and dextral stelliplanate elements and suggests that it was the main axes of the elements that occluded, in a way broadly comparable to that of the ozarkodinids. Evidence of wear supports hypothesis 2, but it is difficult to propose a precise method of occlusion from the data.

The models used show that it is impossible for the distal portions of the ventral processes to come into contact if the elements occluded along their main axes. However, it is possible that the most proximal regions of the ventral process of the sinistral element could have damaged the ventral process of the dextral element during full occlusion. This could account for the damage observed on the ventral process of the dextral element figured and discussed above (Figures 5C-D).

Although sporadic, occurrences of wear suggest that the elements occluded by working the dorsal processes against each other, gradually damaging and wearing the denticle tips. This could also account for the damaged denticles of the ventral process that may have occurred during full occlusion, with the outside edge of the sinistral dorsal process acting against the inside edge of the dextral dorsal process (Figure 9). The lack of regular wear on the surfaces of the caudal process denticles suggests that this process might not have occluded against the opposing element, and that the two processes moved beside each other, making it possible for the dorsal processes to come into contact with each other. It is possible that the elements did not always occlude closely thereby explaining the sporadic, sometimes poor, evidence of wear.

The denticles of caudal processes exhibit a great variety of morphologies (as discussed above), both internally and externally (Figure 6), inferring that they were damaged and broken more frequently than those of the

dorsal process. Donoghue and Purnell (1999a, p. 69, Figure 7A-C) provided a diagram illustrating the proposed power stroke of *ldiognathodus* P_1 elements. They proposed that the elements pivoted about a central axis, with the ventral blades (equivalent to the caudal processes of *Eoplacognathus*) partially occluded at the start of the powerstroke, moving completely apart as the elements pivoted and the platforms come into occlusion. The ventral blades came back together from this greatest distance as the elements reset themselves for another powerstroke. It is likely that the caudal process of *Eoplacognathus* did not have such precisely controlled occlusion and that there was often malocclusion and damage. Malocclusion is reflected by the internal truncation of individual white matter cores, damage to denticles that do not possess white matter cores and counterintuitive wear, as this early conodont lacked the control for more precise methods of occlusion.

Purnell and Donoghue (1997, 1998) Donoghue and Purnell (1999a, 1999b) proposed that blade-like processes of ozarkodinid platform elements moved past the each other, allowing the element to pivot and occlude closely about a central axis. This facilitating precise occlusion of the platform region of the element in the absence of jaws (Purnell and Donoghue, 1997, 1998; Donoghue and Purnell 1999a, 1999b). Although the function of elements of *Eoplacognathus* is not as clearly understood and the evidence of wear not so explicit as that from the ozarkodinid platform elements, the limited information suggests that occlusion could have been achieved in a similar way, but without such precision.

Functioning in this way, rocking in the plane defined by the dorso-ventral and medial-lateral axes, across the rostro-caudal axis of the apparatus, would make it impossible for the distal regions of the ventral processes ever to occlude against each other. It is possible that these processes acted to hold larger food particles in the oral cavity of the conodont in the absence of any ramiform elements (Chapter 2.1), although it is not possible to test this with the data available.

Using the *Promissum* template, it is apparent that the *Eoplacognathus* elements were orientated with ventral and ventro-lateral processes rostrally directed. This means that the hypotheses of element occlusion outlined above dictates that the elements occluded with the conventional right element behind the left element. When considered functionally, it seems likely that these two processes would have been orientated towards the rostral end of the apparatus and perhaps had a sweeping/grasping/retaining action. This element arrangement is the opposite of that of the ozarkodinid apparatus, where the P_1 elements occluded left behind right (Purnell, 1995; Purnell and Donoghue 1997, 1998; Donoghue and Purnell 1999a, 1999b). This fundamental difference could have significant implications for phylogenetic relationships between the prioniodontids and the ozarkodinids.

Conclusions.

A more resolved model for *Eoplacognathus* stelliplanate occlusion is reliant on finding better preserved specimens with clear surface textures, so that the precise method of occlusion and processing can be ascertained. The parallels with the ozarkodinid model go as far as the position within the apparatus and the proposed motion of the elements. The method of occlusion is also broadly comparable. If the denticles of the dorsal process only occluded at the denticle tips rather than shearing down the sides of each other, then the method of occlusion of *Eoplacognathus* stelliplanate elements has strong parallels with at least some ozarkodinids.



Figure 1. Oral view of *Eoplacognathus reclinatus* sinistral and dextral stelliplanate elements illustrating the conventional inner and outer sides of element.



Figure 2. Sinistral and dextral stelliplanate *Eoplacognathus reclinatus* elements. A-B orientated with dorsal process towards bottom of page. A. Specimen 003, sinistral element, oral view. B. Specimen 120, dextral element, oral view. C. Specimen 016, sinistral element, lateral view. D. Specimen 030, dextral element, lateral view.



Figure 3. Hypotheses of occlusion for platform elements of *Eoplacognathus reclinatus*. A. Dorsal and caudal processes occluding with denticle tips together. B. Dorsal process denticles occluding with denticle tips and caudal process denticles shearing past each other at full occlusion.



Figure 4. Dorsal process wear of *Eoplacognathus reclinatus* stelliplanate elements. A-D Specimen 234, dextral element. A. Inside of dorsal process, showing worn surfaces of denticles, especially cusp seen towards top left of image. B. Outside of dorsal process showing distribution of surface microstructures, cusp still preserving much of surface microstructure, seen towards top right of image. C. Distal tip of dorsal process, showing functional damage. D. Outside surface of same region, showing same degree of disruption, and overglazing. E-F Specimen 181, dextral element. E. View down dorsal process (seen towards left of image). F. Same view, showing close up of dorsal denticles.



Figure 5. Platform elements of *Eoplacognathus reclinatus* showing caudal and ventral process wear. A-B, specimen 226 dextral element. A. Inside edge showing loss of surface microstructures. B. Outer edge of process showing showing preservation of surface microstructures. C-D Specimen 014, dextral element. D. View of ventral and ventro-lateral processes (left and right respectively). D. Close up of ventral process showing smooth flattened surfaces of denticles. E-F. Specimen 015, dextral element. E. View showing wear and facets (arrows) on ventral process, immediately next to junction with dorsal process. F. Opposite side of process, showing preservation of surface microstructures.



Figure 6. TLM Images of platform elements of *Eoplacognathus reclinatus* (all specimens are broken with only dorsal and caudal processes remaining). A, C, F, with caudal process to left of page. B, D, E, G-H with caudal process towards right of page. A. Specimen 260. Dextral stelliplanate. B. Specimen 261. Sinistral stelliplanate. C. Specimen 262. Dextral stelliplanate. D. Specimen 263. Sinistral stelliplanate. E. Specimen 264. Sinistral stelliplanate. F. Specimen 364. Dextral stelliplanate. G. Specimen 266. Sinistral stelliplanate. H. Specimen 365. Sinistral stelliplanate. All images approximately x150.



Figure 7. Platform elements of *Eoplacognathus reclinatus* seen in transmitted light. A. Specimen 360, juvenile sinistral stelliplanate element x700. B. Specimen 361, juvenile dextral element x700. C. Specimen 362, sinistral element, mature dorsal process showing truncated white matter x 400. D. Specimen 362, mature caudal process showing clear truncations of white matter due to wear x 600. E. Specimen 364 Dorsal process with basal body visible beneath x500. F. Specimen 364, dextral element. Caudal process denticles showing growth increments at denticle tips (Faint in large central denticle) x1000. G. Specimen 365, sinistral element. Dorsal process showing truncated white matter cores and clear regenerated hyaline crown forming new ridge x400. H. Specimen 364. Caudal process with growth increments (faint, centre of page) at base of denticles x1000.



Figure 8. Internal structures of stelliplanate elements of *Eoplacognathus reclinatus* in transmitted light. A. Dextral stelliplanate element, showing white matter cores, specimen 268 x200. B. Close up of caudal process seen in A x400. C. Caudal process showing white matter within incremental lines of lamellar crown, specimen 376.



Figure 9. *Eoplacognathus reclinatus* stelliplanate elements occluding. A. View from dorsal, showing dextral element in lower position and sinistral in upper, with denticles of caudal and dorsal processes of sinistral element occluding with outside edge against inside edge of dextral element. B. Rostral view showing sinistral element to the left and rostral process denticles occluding fully alongside the rostral process denticles of the dextral element and the dorsal processes of both elements with tips in possible occlusal position. Sinistral element has outside surface of denticles operating against the dextral elements inside edge.

CHAPTER 3.0

INTRODUCTION

THE ARCHITECTURE, HISTOLOGY AND FUNCTION OF THE FEEDING APPARATUS OF *PTEROSPATHODUS*

Elements of pterospathodontids first appeared in the fossil record during the middle Llandovery and the family went into extinction during the lowermost Wenlock (Sweet, 1988; Männik and Aldridge, 1989). However, although short lived, a number of distinct lineages evolved which colonised European, Asian and North American provinces (Clark, 1981). Little is known about the ancestors of this family although it has been suggested that the family has ancestors within the species of *Pranognathus* Männik and Aldridge an early Llandovery genus (Sweet, 1988; Männik and Aldridge, 1989).

Pterospathodus was first described from a Silurian sequence in the Carnic Alps of Austria (Walliser 1964). Walliser (1964) tentatively placed the form species *Pterospathodus amorphognathoides* Walliser and *Ozarkodina gaertneri* Walliser together to form bimembrate 'Apparatus C'. At this stage the generic name of *Pterospathodus* was only applied to the large platform element of the apparatus and Walliser was unsure which other elements from the sequence came from the same apparatus. Schönlaub (1971) was the first author to apply the formal generic name, *Pterospathodus*, to the bimembrate 'Apparatus C' proposed by Walliser (1964).

Barrick and Klapper (1976) from their study of the conodonts from the Clarita Formation, Oklahoma, expanded this interpretation by proposing a quadriramate apparatus including two types of P element, a ramiform 'S element' and a dolabrate M element. Mabillard and Aldridge (1983) identified a fifth element, represented by a small denticulated ramiform element, associated with the apparatus. However, the S element recognised by Barrick and Klapper (1976) is not truly ramiform and is more similar to the element thought to occupy the Pb position. Because of this Männik and Aldridge (1989) reinterpreted this element as a third type of P element. Hence, *Pterospathodus* at that stage was understood to have an apparatus containing five types of element in all, including three types of P element; one pastiniscaphate or carminiplanate and two angulate. The S element is a conservative small ramiform element with a reduced posterior process. The M element is dolabrate and has a large cusp.

Jeppsson (1979) proposed that elements considered to belong to *Carniodus* were in fact part of the *Pterospathodus* apparatus. Männik and Aldridge (1989) argued against this because they believed that the stratigraphic ranges of the two taxa were not compatible. New information presented by Männik (1992, 1998) provided data that countered this criticism and supported Jeppsson (1979). Männik (1998) proposed that each taxon of *Pterospathodus* was associated with a distinct set of *Carniodus* type elements and that the two sets display parallel evolutionary patterns. He concluded that *Carniodus* did not exist as a separate apparatus but represented additional elements of the *Pterospathodus* apparatus.

Pterospathodus has been classified as a prioniodontid (Clark, 1981) and also an ozarkodinid (Sweet, 1988). Pterospathodus is classified as a prioniodontid in the *Treatise* (Clark, 1981) because the Pa and Pb elements both occur in pastinate forms; however, it was also noted in the diagnosis that the Pa element could also occur as a carminiscaphate form. Dzik (1976) and Aldridge and Smith (1993) followed the *Treatise* classifying *Pterospathodus* as a prioniodontid. Sweet (1988) classified *Pterospathodus* as an ozarkodinid because he believed that the pterospathodontid P elements are most comparable to the P elements of *Ancyrodelloides*, a conodont he classified amongst the Spathognathodontidae, which he identified as the root stock of the ozarkodinids.

CHAPTER 3.1

THE APPARATUS ARCHITECTURE OF PTEROSPATHODUS.

Introduction.

Although the elements of *Pterospathodus* have been widely recognised for more than thirty years, knowledge of the apparatus has remained limited (for review see Jeppsson, 1987). The evolution and relationships between different species of *Pterospathodus* were evaluated by Männik and Aldridge (1989), who reconstructed the apparatus with five different elements: Pa, Pb, Pc, M and Sa/b (Figure 1A). The authors recognised important sequential changes seen in populations of *Pterospathodus* and documented the morphological differences between sinistral and dextral Pa elements. This resulted in the conclusion that pennate forms (with single unbranched or branched 'postero-lateral' processes) and nonpennate forms (with no 'postero-lateral' processes), previously regarded as separate species were conspecific and assigned to *Pterospathodus* formed part of the apparatus of *Pterospathodus* because data at that time did not support consistent co-occurrence of the two taxa.

Männik (1998) returned to Jeppsson's (1979b) theory after extensive work on faunas from Estonia and Gotland, Sweden. He provided data sets that showed that *Pterospathodus* and *Carniodus* did, in fact, share exactly the same stratigraphical range, and reconstructed an apparatus for *Pterospathodus*, incorporating elements of *Carniodus*, that comprised 14 different types of element (Figure 1B). This reconstruction is assessed here using detailed internal and external analysis of elements to test whether the elements belong to the same apparatus. The evidence is also used to investigate the most likely architecture of the apparatus of *Pterospathodus*.

Reconstructing the apparatus of conodonts known only from collections of disarticulated elements that are phylogenetically distant from conodonts known from natural assemblages.

When the component elements of a taxon are not easily identified, the reconstruction of the apparatus is problematic. Apparatus reconstructions have been addressed by several different authors, for example see Sweet and Bergström (1966) and Jeppsson (1971). Sweet and Bergström (1972, p. 30) outlined the multielement approach and summarised the previous five years of research which had embraced this new concept. They recognised that "Individual components of these [conodont] groups, previously described as form-species, are related to others in size, mode of denticulation, shape and conformation of basal cavity, distribution of white matter and surface micromorphology." Jeppsson (1971, p. 101-104) advocated the "logical and numerical approach" to multielement taxonomy, where a combination of factors such as

stratigraphical and geographical co-occurrence coincided with similar element frequencies and morphological appearances to unite elements from a single species.

Co-occurrence of form taxa stratigraphically and geographically is the best indication that elements with different morphologies might be from the same species. However several taxa may co-exist because they share the same types of environment, so co-occurrence on its own is not sufficient. For example *Baltoniodus navis* coexists with *Trapezognathus quadrangulum* throughout the *Baltoniodus navis*, *Paroistodus originalis* and *Microzarkodina parva* zones of the Baltoscandic Region (Stouge and Bagnoli, 1990), but the two are not thought to represent parts of a single species. The best evidence for apparatuses is represented by occurrence in monospecific faunas.

An important character that may be used to recognise relationships between elements is the morphology and form of the basal body within the element. For example, Donoghue (1998, p. 647 fig. 7e, f, h) recognised that elements referred to *Carniodus* had a distinct method of growth. Transmitted light images clearly showed junctions between units of denticles and individual basal bodies, indicating that each unit grew separately, with its own basal body, before becoming incorporated into the main unit of the element. It is now possible to identify the discrete units, even when dislocated from the main element, based on the basal body morphology. This is a distinct mechanism of growth that unites elements referred to *Carniodus*, though may be specific to ramiform-like elements.

It is useful to recognise a suite of characters that unite a group of elements and allow them to be assigned to a particular species. For example, similar white matter distribution, similar hyaline crystalline structures or similar denticulation. Although all of the elements might not share all of the characters, it is likely that a combination will provide sufficient evidence to verify their inclusion within an apparatus. If the designation is based on only one character it is possible that incorrect apparatus reconstructions will result. For example, Armstrong (1997) proposed that *Eoplacognathus* might have possessed Pb, Pc and Pd elements in addition to the Pa element in his reconstruction; the specimens he proposed to include would normally be identified as elements of *Baltoniodus*. The basis for this proposal was the presence of a distinctive ledge along the processes of all of the elements. However, his specimens are fragmentary and difficult to identify, so it is not possible to confirm these observations with evidence of consistent co-occurrence, or to undertake any extensive examination of element ultrastructure or growth patterns.

To reconstruct the architecture of an apparatus in the absence of direct evidence from natural assemblages it is important to identify the most appropriate template. Currently there are two main templates known: the ozarkodinid template (Purnell and Donoghue, 1998) and the *Promissum* template (Aldridge *et al.* 1995) representing the ozarkodinids and the prioniodontids respectively. The ozarkodinid template is well understood thanks to the relatively common natural assemblages that have been found (for review see Purnell and Donoghue, 1998), with two pairs of P elements that were caudal to an array of S elements and a pair of M elements (Figure 2B). A only well known prioniodontid template is known from the natural assemblages

of *Promissum* (Figure 2A). The apparatus of *Promissum*, now represented by more than four hundred natural assemblages (Aldridge, pers. comm. 1999) is the most architecturally complex apparatus known to date. *Promissum* possessed four pairs of P elements that were positioned above an array of S and a pair of M elements (Aldridge *et al.* 1995). This architecture of *Promissum* is also well known, and the morphology of the component elements has been closely analysed (see Chapter 1.1 for discussion).

The best criterion for identifying the most appropriate template relies on identifying homologues between disarticulated elements and those from either the ozarkodinid or the *Promissum* template, i. e. a hypothesis of relationship. If the elements are morphologically distant from the elements in either template, then it is necessary to determine the phylogenetic relationships of the taxa represented by the disarticulated elements to determine the most likely alliance. It will often be the case that there is no unequivocal solution without additional information from new discoveries of natural assemblages.

Although it is often possible to recognise component elements of an apparatus and to propose apparatus positions for them, it is difficult to ascertain the total number of elements within the apparatus and to establish whether an element of particular morphology occupied more than one position. If the Promissum plan appears to be the more appropriate for the reconstruction, then there may have been more than two pairs of P elements present in the apparatus. Ratios of elements from disarticulated collections can suggest what might be true biological signals. For example, it would be expected that the S elements of an apparatus would be more strongly represented, numerically, than the P elements, as there are nine S elements present in both the Promissum and the ozarkodinid apparatuses in comparison to the four or eight pairs of P elements. Some authors have suggested that it is possible to reconstruct apparatuses using simply the numerical proportions of different element morphologies (Kohut, 1969), but it is impossible to know how much post-mortem sorting has occurred. Jeppsson (1971, p. 104) believed that the most reliable results would be retrieved from large collections that only contained elements that were well preserved and shared a similar size range. It is suggested here that this is the most problematic type of collection, as it is impossible to know if the similar size range is a result of post-mortem disturbance and sorting rather than reflecting the lack of it. The most reliable type of collection would comprise well preserved elements of all sizes, that show no preferential sorting. However, even where apparatuses are well known from natural assemblages, numerical proportions from disjunct collections very commonly show an imbalance in element ratios which does not reflect invivo numbers (McGoff, 1991). On this basis, it is probably impossible to be sure of the correct apparatus architecture without additional data from a natural assemblage (see Chapter 2.1 for further discussion).

The classification and apparatus of Pterospathodus.

The lack of unanimity with regards to the classification of *Pterospathodus* (see Chapters 3.0, 3.4) presents difficulties when trying to reconstruct the apparatus of the genus. The ozarkodinid apparatus architecture is well known, but differs significantly from that of the prioniodontid, *Promissum pulchrum*. The reinterpretation of the Pa element of *Pterospathodus* (Chapter 3.2), however, has made it possible to include *Pterospathodus* within the prioniodontids because it possesses a pastinate P element and this lends support to a prioniodontid phylogeny. The suggestion that *Pterospathodus* possessed an apparatus that was comparable to that of *Pranognathus* (proposed by Männik and Aldridge 1989) is also compatible with this classification. This means that the apparatus of *Promissum* is the most appropriate template to use, because it is likely that they share homologous pastinate elements.

Materials and Methods.

The elements of *Pterospathodus* and those referred to *Carniodus* are from extensive collections processed by R. J. Aldridge from Estonia. The conodonts are of Upper Llandovery age from the Adavere Stage (upper part), Velise-Kõgekalda - low cliff of the river Päärdu west-south-west of a bridge across the river in Velise village, central Estonia (for details see Männik, 1998). Most of the elements are slightly recrystallised, but it is possible to identify basic surface microstructures. Importantly, a large range of element sizes has been preserved, including several specimens not more than 50-100µm long.

The elements have been carefully examined and the distribution and character of surface microstructures has been assessed, using the SEM. Internal characters, such as the position of the basal body, have been examined using a TLM. All of these characters have been analysed to see if it is possible to identify a common suite of secondary characters that unite the elements referred to *Pterospathodus* and *Carniodus* within a single apparatus of one taxon, as suggested by Männik (1998).

Elements of *Pterospathodus* are described using terminology that is modified from that of Sweet (1981, 1988) and elements from known apparatuses and templates are described using the revised terminology proposed by Purnell *et al.* (2000). This is to clarify where elements from disarticulated collections for which homologies are unsure, are being compared to elements from natural assemblages.

The apparatus of Pterospathodus.

Männik (1998) has identified 14 different components to the apparatus using a modification of the terminology proposed by Sweet (1981, 1988) (Figure 1B). Studies of basal body morphology, ontogeny and surface microstructures have been used here to assess Männik's reconstruction and to re-assess the apparatus

architecture of *Pterospathodus*. The elements identified by Männik (1998) are briefly described, with additional details of basal body morphology and surface microstructures provided from studies of *Pterospathodus celloni*.

Elements of Pterospathodus.

Pa element. The Pa element of *Pterospathodus* was described by Männik (1998) as carminate, pastinate or stellate (rare examples) (Figure 3). The species *Pterospathodus celloni* considered for this study, possessed a pastinate platform element with a pennate 'posterolateral' process and an expanded lobe approximately midway along the element on the other side (Chapter 3.2, 3.4). Sectioning has shown that this expanded lobe is an unexpressed process which may represent an 'anterior' process that does not become any larger with maturity (Chapter 3.2, 3.4). The element has a clearly preserved pattern of ropy surface microstructures (Chapter 3.3) on the denticle flanks, (Figure 3B). The basal body of the Pa element is low and narrow beneath the 'lateral' process and deep with individual cavity tips beneath the 'posterior' process denticles (Figure 3C-E).

Pb₁ element. The Pb₁ element was described by Männik (1998) as angulate with a distinct cusp (Figure 4). The element also has a morphology that suggests that it is technically pastinate. Figure 4A shows the side of the cusp and it is clear that there is a lobe and costa developed on the cusp. This may represents an process that is not fully expressed. Aboral outlines figured by Männik (1998) suggest that this expansion is part of the main 'posterior'/'anterior' (dorsal/caudal) axis of the element and that the continuation of the 'posterior' process represents a process that has developed off this axis. The 'posterior' process denticles are short and squat and the process is usually shorter than the 'anterior' process, decreasing rapidly in size with distance from the cusp. The 'lateral' process denticles are larger than those of the 'posterior' process and are more evenly sized. Denticles adjacent to the cusp are sometimes fused to the sides of the cusp and become incorporated, as a single unit (Figure 4C). The surface ornamentation is limited to ropy patterns on the cusp and denticles, that gradually becomes reduced to such microscopic proportions that the lower flanks of the denticles appear to be smooth (Figure 4D). The basal body is deep beneath both the 'lateral' and 'posterior' processes (Figure 4E). The outline of the basal body is straight and rapidly tapers to a narrow tip beneath each process with distance from the cusp; the cusp and 'posterior' process denticles have individual basal cavity tips.

Pb₂ element. The Pb_2 element was originally described as *Carniodus carinthiacus* (Walliser). The species described here possesses an angulate Pb_2 element (Figure 5). In lateral view the lower margin of the element forms a smooth arc, and the cusp and denticles radiate over this. Occasional specimens have a smooth costa on one side of the cusp (Figure 5B), that leads to a small expansion at the base of the element; however, in most specimens, both sides of the cusp are smooth. The denticles are evenly sized and it is common to see the size of the denticles rivalling the size of the cusp. The denticles have a ropy surface microstructure that

fades towards the base (Figure 5C). The basal body is simple, tapering either side of a single basal peak beneath the cusp (Figure 5E).

Pc element. The Pc element is pastinate, with a wide erect cusp and short denticulated 'anterior' and 'lateral' processes. The 'posterior' process is generally longer with squat denticles (Figure 6). The surface ornamentation is in the form of narrow ropy microstructures, which diminish in size towards the base of the element (Figure 6D). The basal body beneath the crown shows that as well as the cusp, the denticles of the 'posterior' and 'lateral' process each have individual basal cavity tips (Figure 6E). This is unusual for an element that occupies a P element, as normally basal cavity tips are limited to the cusp and the 'posterior' process denticles. This is a feature more commonly seen in the basal bodies of ramiform elements.

 M_1 element. The M_1 element is makellate with an adenticulate 'outer lateral' process that is directed straight down. The 'inner lateral' process is short with small denticles (Figure 7). The cusp is strongly curved as seen in Figures 7A-B. The element possesses ropy surface microstructures that are strongest on the cusp and become reduced in size towards the base of the element (Figure 7D). The basal body forms a clear basal pit beneath the cusp and forms individual basal pits beneath the denticles of the processes (Figure 7E) SEM photographs were largely unsuccessful with because of the three dimensional nature of the element. M_2 elements have not been identified in the collections kept at The University of Leicester, it is possible they have not been seperated from juvenile forms of the M_1 element.

Sa element. Männik (1998) identified an element that has a symmetrical disposition of processes (Figure 8A). The 'lateral' process denticles are elongate, evenly sized and discrete, and those of the 'posterior' process are slightly smaller. Männik suggested that the element is amongst those originally described as *Roundya latialata* by Walliser (1964). Within the collections examined the cusp of the Sa sometimes has traces of ropy surface ornamentation, although it has not been possible to find specimens that show a good quality of preservation (Figure 8C). The basal body extends beneath all processes and there are high pointed basal body pits beneath the cusp and the denticles of the 'lateral' and 'posterior' processes (Figure 8D-E).

Sb₁₋₂ elements. The tertiopedate Sb elements identified by Männik (1998) have a comparable morphology to that of the Sa element, but differ in the asymmetric disposition of processes about the cusp (Figure 8B). Both elements were originally assigned by Walliser (1964) to *Roundya latialata*. However, Männik was able to distinguish two different morphologies amongst them (Walliser, 1964, pl. 31, fig. 13; pl. 6, fig. 15 and pl. 31, figs 11-12 respectively) and reclassified them as the Sb₁ and Sb₂ elements of *Pterospathodus* The surface microstructures and basal body morphology are also comparable, with basal pits beneath all of the denticles and the cusp.

 Sc_{1-2} elements. Männik (1998) identified three different types of bipennate Sc element; some of which he stated are species specific. Sc_1 and Sc_2 both occur within the apparatus of *P. amorphognathoides*. Sc_1 elements are bipennate and possess a relatively short denticulated 'anterior' process, with irregular denticulation along the 'posterior' process (Figure 9A). Männik stated that the Sc_2 element is dolobrate with an 'anterior' process that is poorly developed. The 'posterior' process is short and has denticles that rapidly decrease in size with distance from the cusp (Figure 9A-B). The Sc_1 morphotype was originally assigned to *Carniodus carnus* (Walliser, 1964). The Sc_2 element was assigned to *N. subcarnus* (Walliser, 1964). These elements have a ropy surface microstructure that is strongest on the cusp. The basal body forms a pit beneath the cusp, and there are pits beneath the larger denticles along the 'posterior' process of all of these element types (Figure 9E).

Carnuliform elements. Carnuliform elements are angulate to carminate and are highly variable in form. They comprise a cusp with approximately three to five small denticles either side on what Männik (1998) called 'anterior' and 'posterior' processes (Figure 10D). The surface microstructures are ropy (Figure 10C), and the basal cavities are simple with a single basal pit beneath the cusp (Figure 10E). Elements identified by Männik (1998) as modified forms have developed a third process, essentially forming a pastinate element.

Curved elements. These elements are similar to the carnuliform elements but the processes are not disposed symmetrically and are strongly curved forming a distinctive aboral outline in lateral view (Figure 10A-B).

Reconstruction of the apparatus of Pterospathodus.

The basic morphology of the basal bodies and comparable surface microstructures may support the suggestion that elements of *Carniodus* were part of the same apparatus as *Pterospathodus*. These characters in concert with the co-occurrence of the elements in the same faunas presents a strong argument for their inclusion within a single apparatus (Männik, 1998). However, it is difficult to understand how 14 different elements could have fitted into a single conodont apparatus.

Each of the ramiform elements examined possessed characteristic individual basal peaks beneath each of the denticles. Donoghue (1998) documented the growth of *Carniodus* S elements and the way the elements are constructed may account for the large number of components associated in the apparatus of *Pterospathodus*. Donoghue (1998, p. 647) described this mode of growth as a *Type II* ramiform morphogenesis. He described how individual basal body pits beneath denticles indicated that the element was made up of several discrete components. The components became incorporated into a single unit once lamella from the main unit extended sufficiently to envelop them and join them to the distal end of the process. It can be seen that the carnuliform elements described by Männik (1998) strongly resemble the discrete units figured by Donoghue (1998, p. 646, fig. 7e, f, h). The carnuliform elements described by Männik (1998) strongly resemble the discrete units figured by Donoghue (1998, p. 646, fig. 7e, f, h). The carnuliform elements described by Männik (1998). The second incorporated into a single element unit at the time of death of the animal. The Sc₂ and Sc₃ elements can also be explained on the basis of this growth hypothesis. It is likely

that the Sc_3 elements represent Sc_2 elements that had not been extended by adding carnuliform elements to the distal tip of its 'posterior' process.

The individual units represented by the carnuliform elements may never have become completely joined to the main element, in a manner analogous to Donoghue's (1998, p. 647) *Type I*, ramiform element morphogenesis. This growth hypothesis was based on evidence from the natural assemblages of *Promissum*, where the long 'posterior' processes of the S elements are formed by rows of denticles, united by a single underlying structure that appears to be different from the crown and the basal body tissue. It is also probable that the numerous small elements (carnuliform and curved) that Männik (1998) associated with the apparatus of *Pterospathodus* represent units of this type of ramiform element genesis.

If the ramiform element genesis of *Pterospathodus* was comparable to that of *Promissum*, then it is difficult to be sure of the precise number of different types of S elements that are represented by the small ramiform and single unit elements identified by Männik (1998). However, the morphology and process configuration of the S and the M elements appear to compare closely to those of *Promissum*. On this basis it is proposed that the S element array of *Pterospathodus* was homologous to those of *Promissum*, and that a total of 9 S elements occurred in the apparatus.

The element which Mannik designated Pc is also characterised by having individual sharp peaks beneath the denticles as well as the cusp. This suggests that the element may not have occupied a P position, because of the difference between it and the other elements that have been designated as characteristic of P elements. The basal body is characteristic of ramiform element basal bodies which may infer that the Pc occupied a S position in the apparatus. The element morphology is also broadly comparable to elements that are characteristic of M position occupants, but without evidence from natural assemblages, it is difficult to designate its position.

Using the Promissum template to recognise homologues.

Comparing the elements within the apparatus of *Promissum* to those of *Pterospathodus* provides several possible homologues. The Pa of *Pterospathodus* is a large robust pastinate element, with a long denticulate 'posterior' process, and an equally long, aligned 'lateral' process (see Chapter 3.2). These characters are in common with the elements that occupy the P_1 and P_2 positions of *Promissum*. This may mean that the Pa element of *Pterospathodus* is homologous to both the P_1 and P_2 of *Promissum*, as in the case of the Pa of *Eoplacognathus* (see Chapter 2.1). These elements share a characteristic morphology and process configuration and it is probable that they are all homologous.

The Pb_1 of *Pterospathodus* may also possess a characteristic morphology. The aboral margin (in lateral view) seen in Figure 4A shows an aboral projection that may represent an unexpressed process. If this is

evidence that the ancestors of *Pterospathodus* possessed a Pb_1 element that was originally pastinate, then the Pb_1 element may be comparable to the P_3 (Pb) element that characterises the apparatuses of the balognathids (see Chapters 1.1, 2.1).

It can be shown that the Pb element of *Baltoniodus* is homologous with the P_3 element of *Promissum* because it has the same broad angle between its 'lateral' and 'anterior' processes. It is possible that the P_3 element of *Promissum* was also a pastinate element, but in this case the dorsal ('posterior') process was unexpressed, resulting in an element that appears to be bipennate when submerged in the substrate. The Pb₁ element of *Pterospathodus*, may therefore, by extrapolation be homologous with the P_3 element of *Promissum*.

This apparatus reconstruction is problematic, however, as there are two additional P elements of *Pterospathodus* and only one position left if the apparatus of *Pterospathodus* shared the same architecture as *Promissum*.

The Pc element of *Pterospathodus* has a slightly different process configuration about the cusp that provides a possible clue to its position within the apparatus. It is possible that the element in the P_4 position of *Promissum*, was a pastinate element, comparable with the P_3 but with a reduced angle between the caudal ('posterior') and ventral ('anterior') processes (see Chapter 1.1). The Pc element of *Pterospathodus* does not have a reduced 'posterior' process, but is a pastinate element. This type of element may have occupied a P_4 position, or as discussed above or maybe an M or S position.

Promissum does not have a P element that possesses morphological characters that indicate a homology with the Pb_2 element of *Pterospathodus*. The Pb_2 of *Pterospathodus* resembles a Pb type morphology, as can be seen in Figure 5B where there is a costa developed in the place of an 'anterior' process. However, if the Pb_2 occupied the P_3 position, this would displace the Pb_1 .

The external morphology of the Pb_2 is similar to that of the Pb_1 and it might be argued that it represents a juvenile form of it. However, internal studies (Figures 4E, 5E) show that the basal bodies of the two elements are not comparable and that they could not represent the same element at different ontogenetic stages.

Another solution might be that the Pb_1 element of *P*. amorphognathoides might have occupied a P_2 position. This would mean that the Pc of *Pterospathodus* could have occupied the P_3 position, and the Pb_2 could have occupied the P_4 position.

Alternatively the duplication of an element apparently characteristic of the P₃ position could indicate that the elements might represent two dimorphic apparatuses. Possible dimorphic division may also be indicated by

the Pa element morphology, where elements with single unbranched 'posterolateral' processes coexist with elements with no 'posterolateral' processes (Männik and Aldridge, 1989).

Conclusions.

The denticulation, surface microstructures and basal body morphologies are common to all of the elements considered within the apparatus composed by Männik (1998), and the proposed apparatus composition can be upheld. The Pa, Pb₁, Pc and the S and M elements have possible homologues in the *Promissum* template although many of the homologies are reduced to speculation due to the phylogenetic distance between *Pterospathodus* and *Promissum*. The Pa is may be homologous with the element that occupied the P₁ and possibly the P₂ positions in the apparatus of *Promissum* and the Pb₁ may have occupied the P₃ position. No other homologues can be confidently proposed for the P element positions. The large numbers of ramiform-like elements discussed are likely to have positions within the ramiform array of *Promissum*, but it is not possible to clearly identify those positions.

Because the apparatus of *Pterospathodus* possesses the unfamiliar Pb_2 element, it is difficult to produce an apparatus reconstruction based on the *Promissum* template. The Pb_2 element may have occupied a new element position that has not been seen in the natural assemblages discovered to date. The morphology and simple basal body suggest that it may be analogous to the individual units that built the 'posterior' processes of the S elements. It is possible that one of these individual units began to grow independently from a main element unit somehow becoming isolated and forming a new element position. Alternatively the element may represent a non-attached process of the occupant of one of the other P element positions.

It is otherwise impossible to suggest an apparatus for *Pterospathodus*, based on that of the *Promissum* template, without discarding the Pb_2 element. However, it has been possible to find several shared characters between the other disarticulated *Pterospathodus* elements and those of *Promissum*. These represent homologues that suggest that there is a strong link between the apparatus architecture of *Pterospathodus* and that of *Promissum*

This study has shown that there are still some apparatus plans that do not conform with the known templates. These apparatuses will not be fully understood until further natural assemblages have been discovered, that provide more evidence of element growth and apparatus architecture.



Figure 1A. The quinquimembrate apparatuses of *Pterospthodus celloni* and *P. amorphognathoides* proposed by Männik and Aldridge (1989). All specimens x40. A-F *P. celloni* (Walliser) A-B lateral and upper views of Pa element. C. Lateral view of Pb element. D. Lateral view of Pc element. E. Lateral view of M element. F. Posterior view of Sa/Sb element. G-L *P. amorphognathoides* Walliser G, H. Lateral and upper views of Pa element. I. Lateral view of Pb element. J. Lateral view of Pc element. K. Lateral view of M element. L. Posterior view of Sa/Sb element. Illustrations from Männik and Aldridge (1989, p. 894, fig. 1)



Figure 1B. Apparatus of *Pterospathodus* according to Mannik (1998). Redrawn from illustrations composed by Mannik (1998, p. 1003, fig. 2) detailing the different types of elements recognised and their suggested positions within the apparatus following the terminology of Sweet (1981, 1988). ccf - carnuliform element; cf,a-b - carnuliform morphs a and b; cf,s - carnuliform short morph; mcf - modified carnuliform; mcf,s - modified carnuliform short morph; cur,a-c - curved elements morph a-c.





Figure 2. Apparatus templates of prioniodontids and ozarkodinids. A. New terminology proposed for the apparatus of *Promissum pulchrum* following Purnell *et al.* (2000). B. New terminology for the ozarkodinid plan following Purnell *et al.* (2000).


Figure 3. Pa elements of *Pterospathodus celloni*. A-B Specimen 321, Dextral element. A. Inner lateral view of element. Supressed 'anterior' process clearly visible. B. Surface microstructures on cusp. C. Sinistral element viewed in TL showing outline of basal body x200. Specimen 311. D. Close-up of basal body beneath 'posterior' process, showing basal cavity tips. Specimen 310 x400. E. Close up of 'lateral' process, showing straight outline. Specimen 310 x400.



Figure 4. Pb1 Elements of *Pterospathodus celloni*. A-B Specimen 294. A. Inner 'lateral' view of sinistral element. B. Outer 'lateral' view. C. Close-up of unexpressed 'anterior' process of sinistral element and well developed surface microstructure. Specimen 209. D. Close-up of surface microstructure. Specimen 289. E. TL image of internal morphology of basal body. Note the basal cavity tips beneath 'posterior' process denticles and smooth outline beneath 'lateral' process denticles. Specimen 280 x150.



Figure 5. Pb2 elements of *Pterospathodus celloni*. A-C Specimen 290. A. Lateral view. B. Oblique lateral view showing costa and small protrusion from base of element. C. Surface microstructures on cusp. D. Lateral view. Specimen 291. E. TL of Pb2 element, image showing internal morphology of basal body with single peak under cusp. Specimen 278 x200.



Figure 6. Pc element of *Pterospathodus celloni*. A-C Specimen 292. A. Inner 'lateral' view. B. Outer 'lateral' view. C. View down 'posterior' process. D. Closeup of surface ornamentation of cusp. Specimen 293. E. TL image of internal morphology basal body, showing basal cavity tips beneath denticles of the 'posterior' process, and the 'lateral' process. Specimen 320 x500.



Figure 7. M elements of *Pterospathodus celloni*. A-D Specimen 324. A. Oblique lateral view. B. Opposite oblique lateral view. C. Surface microstructures at tip of cusp. D. Surface microstructures on cusp face. E. TL image showing single basal cavity tip beneath cusp. Specimen 312 x400.



Figure 8. Sa and Sb element of *Pterospathodus celloni* (see text for original identification of elements). A. Lateral view of Sa element. Specimen 296. B. Lateral view of Sb element. Specimen 297. C. Closeup of surface microstructure of cusp of Sb element. Specimen 297. D-E Specimen 303 x400. D. Oblique lateral TL image of Sa element showing the morphology of the basal body, and basal cavity tips within cusp and 'lateral' process denticles. E. TL image through the 'posterior' process showing distinct cavities beneath cusp and denticles.



Figure 9. Sc elements of *Pterospathodus celloni* (see text for original identification of elements). A Sc₂ element, lateral view. Specimen 324. B. Sc₂ element, lateral view. Specimen 323. C. Close up of surface microstructures found on cusp of specimen 323. D. Distal tip of 'posterior' process of specimen 323. E. TL image of internal morphology of basal body showing basal body tips beneath cusp and the large denticles of the 'posterior' process. Specimen 327 x400.



Figure 10 Carnuliform and curved elements of *Pterospathodus celloni* (see text for original identification of elements). A-C Curved element. Specimen 287. A. Lateral view. B. 'Lateral' process view. C. Surface microstructures of cusp. D. Carnuliform element, lateral view. Specimen 285.E. TL image of carnuliform element showing morphology of basal body, and single tip beneath cusp. Specimen 329 x200.

CHAPTER 3.2

THE HISTOLOGY AND INTERNAL STRUCTURE OF THE PLATFORM ELEMENT BELONGING TO *PTEROSPATHODUS*.

Introduction.

Pterospathodus amorphognathoides Walliser, 1964 possesses an elongate, denticulated pastiniscaphate platform element, where the cusp is often indistinguishable (Figure 1). Either side of the main carina, a wide platform is developed. On the outside of the element a bifurcating dorso-lateral process is attached at approximately midway. There is often a triangular or rounded lobe on the opposite side of the element in a more ventral position. The dorsal process possesses short squat denticles and the platform is normally the broadest with the distal tip of the process often curved towards the inside of the element. Continuous with this process is the caudal process (according to the internal structure, see below for discussion), which often possesses taller, slimmer denticles. The platform elements of *Pterospathodus celloni* (Walliser, 1964) differ by being more strongly laterally compressed and lacking a platform. The elements often lack a dorso-lateral process.

Materials and methods.

Specimens are of *Pterospathodus amorphognathoides* from the Malvern Hills, Cowleigh Park, Herefordshire, 10582, slide I. The specimens were collected from the top of the Telychian Wych Formation (SO/760468) Birches Farm Lane (see Aldridge, 1972). Specimens of *Pterospathodus celloni* (Walliser 1964) were also examined and represent the oldest member of the *P. amorphognathoides* lineage according to Männik (1998). Elements of *Pterospathodus celloni* are from Estonia, the Velise Section, Adevere stage, RC126, Velise-Kõgekalda - a low cliff of the river Päärdu west-south-west of a bridge across the river in Velise village, central Estonia (for details see Männik, 1998). For sections each element was embedded in resin and polished and ground down according to the techniques reported by Donoghue (1998). The sections were taken horizontally and longitudinally (see Chapter 2.2, figs 1C-E). Each prepared section was viewed using a scanning electron microscope. Where possible, elements were immersed in oil and examined in transmitted light. Terminology used has followed that of Purnell *et al.* (2000) and the true biological terms are used instead of the conventional terminology (Sweet, 1988).

Internal structures.

Crystallites. The crystallites of *Pterospathodus* P_1 elements have an elongate irregular shape. It is difficult to ascertain if there is any regularity in morphology, as the crystallites are very densely packed. The long (c) axes of crystallites throughout the element, range in length between approximately 0.25-6µm and they are approximately 1µm wide. Figure 2A (specimen 163) shows crystallites within the outer flanks of a caudal process that has been sectioned horizontally. The crystallites have their long (c) axes orientated perpendicular to the lamellar surfaces and have the form of squat deformed rectangles. The ends of the crystallites are clearly aligned and this is what defines each of the lamellae. Figure 2B shows an oblique longitudinal section through the centre of the dorsal process of a dextral element. The crystallites that compose this process are orientated with their long (c) axes parallel with the long axis of the denticle, and do not provide any lamellar resolution. These crystallites are slightly recrystallised, and it is difficult to be sure of their morphology; however, the fabric of the tissue is clear.

Lamellae. The greater part of the platform element of *Pterospathodus* is composed of hyaline crown, characterised by its crystalline fabric and lamellar nature. Laminations are only clear where sections cut laminations composed of crystallites that have their long (c) axes perpendicular to lamella surfaces with the crystallite tips perpendicular to the edges of each lamella surface. Where crystallites have their long (c) axes parallel with or oblique to the lamella surfaces it is not always possible to distinguish between individual lamellae. This is because the edges of the lamellae are not clearly defined by aligned crystallite tips.

Horizontal sections through the element reveal the distribution of lamellae and the orientation of the crystallites within. Figure 2C shows a horizontal section through the edge of the caudal process platform, the surface of the platform, and the flanks of the bases of the denticles adjacent to the platform. The edge of the platform is at the bottom of the photograph, and is composed of laminations that are orientated perpendicular to the plane of the section. The crystallites within are orientated with their long (c) axes perpendicular to the lamellar surfaces. The surface of the platform is composed of lamellae that are horizontal or oblique to the plane of section, following the outline of the platform. The surfaces of the platform lamellae expose the polished ends of the crystallites that are orientated with their long (c) axes perpendicular to the now horizontal lamellar surface (Figure 2C). The outer flanks of the denticles are composed of lamellae that are perpendicular to the plane of the section and composed of crystallites with their long axes perpendicular to the lamellar surface.

Figure 2D shows the distal tip of a process that has been built by successive layers of lamellae extending beyond the previous distal tip, each lamella forming an evagination. Where there is a larger evagination, successive increments follow the morphology propagating the development of a new denticle; this is seen in Figure 2D. The first few lamellae of denticle cores are composed of crystallites that are orientated perpendicular or oblique to lamella surfaces (Figure 2E). The crystallites of successive lamellae gradually

become more oblique in orientation with distance from the denticle core. Denticle pits are also revealed in longitudinal sections (Figure 2B) although it has not been possible to achieve much resolution. Horizontal sections show a varying degree of resolution of the lamellae and crystallites, depending on the where the section cuts through the element. Sections taken close to the bases of the denticles reveal denticle core lamellae that are composed of crystallites with their long (c) axes perpendicular to the surface of the lamella (Figure 2C, D). Sections taken towards the centre of the upper regions of the dorsal process, above the denticle pits reveal laminations around the margins of the process and no resolution towards the centre (Figure 3D).

Horizontal sections reveal that the dorso-lateral process is composed of extremely thin laminations, approximately $0.5\mu m$ (Figure 2F). It is difficult to be sure of the crystallite orientation, although the microscopic dimensions suggest that it is crystallite tips that are being viewed in horizontal sections and that the c-axes of the crystallites are orientated with their c-axes parallel or oblique to the lamella surfaces.

Lamellae appear to be extremely thin in some regions of the element. Figure 3A shows an oblique horizontal section through a dorsal process denticle. The lamellae that surround the white matter cores are extremely narrow (approximately 0.5µm). This is also seen in Figure 3E, where the section is also slightly oblique. The lamellae at the bottom of the image are sectioned diagonally making them appear wider than they really are whereas those at the top of the image are sectioned closer to perpendicular across the edges of the lamellae. Crystallite orientation is difficult to discern, the lamellae seen in the upper region of Figure 3E are possibly composed of crystallites that have their c-axes oblique to the lamellae margins and therefore parallel to the long axis of the denticle.

White matter. White matter of platform elements is confined to the cores of denticles. Denticles of the dorsal process all have a core of white matter, whereas the most distal denticles of the caudal process are sometimes hyaline. White matter cores are revealed well in horizontal and longitudinal sections and are also clearly seen in transmitted light (Figures 4A, C, F; 5A-D). Each denticle is filled with the albid tissue, which forms an elongate rectangular core that has straight parallel sides when mature (Figure 5A). The oral and lateral boundaries are defined by the morphology of the denticle. The aboral boundaries of white matter cores in the dorsal process are level. This contrasts with aboral boundaries of white matter cores in the caudal process which are diffuse with deflected tails directed towards the more mature regions of the element (Figures 4F, 5A, C).

There are three principal types of structure that characterise the microcrystalline fabric of white matter; fine traces of lamellae, subcircular cavities and elongate tubules.

Several of the sections reveal faint traces of lamellar fabric within the white matter areas (Figure 4B, C). Individual lamellae range between approximately 0.5 and $1\mu m$ in width and are defined by faint grooves in the

fine crystalline mass of the white matter, that may have been accentuated by acid etchants during the preparation of the sections.

Small subcircular cavities are common and appear evenly distributed in longitudinal sections of white matter cores (Figure 4C); in horizontal sections they are concentrated towards the periphery of each core (Figure 4A). The cavities have a diameter of approximately 1µm.

Longitudinal sections reveal tubules that are generally orientated with their long axes parallel with the long axes of the denticles (Figure 4E). Oblique horizontal sections through the middle of white matter cores reveal a fabric dominated by randomly distributed tubules that have no preferred orientation (Figure 4D), whereas Figure 4A shows white matter cores in horizontal section and reveals a concentration of larger subcircular cavities towards the centre of the denticle.

Figure 4C shows the outer edge of a white matter core that has been sectioned longitudinally. The internal structures are small cavities that are often aligned along the faint boundaries of the lamellae. Figure 4E shows the centre of a white matter core that has also been sectioned longitudinally; possess several small cavities but are dominated by elongate tubules.

Basal bodies. The basal bodies of the P_1 elements of *Pterospathodus* have a simple elongate morphology. The cavity is deep and narrow beneath the dorsal process shallow and narrow beneath the caudal process and shallow beneath the bifurcating dorso-lateral process (Figure 6A). In horizontal sections, the basal body beneath the dorsal process can be revealed at a juvenile stage, when sectioned just beneath the apex of the basal tip (Figure 6B, D). Later stages of development can be seen in sections that remove more tissue and reveal a surface approximately 10-20 μ m below the apex of the basal body tip (Figure 6C, E). Horizontal sections reveal that before growth continued in a straight line with the dorsal process, a stunted expansion occurred to one side, resulting in a small lip or bulge on the edge of the platform (Figure 6A). Once this expansion had been developed, growth continued along what was to become the main axis of the element.

The tissue of the basal body is composed of a homogenous dense tissue. It is not possible to identify individual crystallites. In horizontal section, it has been difficult to reveal any structural resolution, but in longitudinal section, laminations are apparent. The laminations are parallel with the aboral margin of the element with the lamellar crown/basal body boundary. Individual increments are discontinuous and convoluted (Figure 6F).

It was not possible to view specimens of *Pterospathodus amorphognathoides* in transmitted light, due to the wide platform that commonly occurs along the carina of the platform element. Specimens of *Pterospathodus celloni* (Walliser 1964) were examined. The basal body of the caudal process is often lost, but in specimen 390 (Figure 5C), it is present. The basal body is shallow beneath the caudal process and basal body tissues are absent from the distal tip of the process. There are clearly no basal pits beneath the denticles (Figure 5C)

and it is possible that some of the basal tissue laminations terminate at the basal body/lamellar crown boundary. Aboral images of *Pterospathodus amorphognathoides* (Figure 6A) show that the laminations are closed beneath this region of the process and it is possible that the distal tip was formed of purely lamellar crown tissues.

The basal body occupies almost half of the dorsal process. The convoluted laminations of the basal body are visible beneath the process and there are basal pits beneath the denticles (Figure 5B). In specimen 288 (Figure 5D), the basal body laminations are clearly parallel with the junction of the lamellar crown/basal body boundary. This indicates that the laminations grew continuously with the crown tissues and do not represent the generation of independent units.

Interpretation.

Hyaline tissues. The internal hyaline tissues of *Pterospathodus* possess lamellae that are composed of elongate apatite crystallites. This structure is closely comparable to the ultrastructure of enamel (for full discussion see Chapters 1.2, 1.3). The hyaline tissues of elements of *Pterospathodus* are also comparable to the hyaline tissues belonging to both Triassic and Devonian conodonts (Zhang *et al.*, 1986; Donoghue and Chauffe, 1999) which were found to share a close structural similarity to the ultrastructure of enamel. Therefore, the hyaline tissue of *Pterospathodus* may have been deposited in the wake of an orally retreating palisade of secretory cells, in a way that is developmentally homologous to enamel.

The hyaline tissue that built the platform elements of *Pterospathodus* is constructed of crystallites that are dominantly orientated with their long axes oblique or parallel to the longitudinal plane of the element. The lamellae that are composed of these crystallites were laid down in several different orientations as they constructed the platform and the denticles of the element, but the crystallites within maintained this general orientation. Each denticle represents the formation of a growth prism (see Chapter 1.2 for full discussion). The orientation of the growth prisms and the crystallites within suggest that the palisade of secretory cells retreated in a roughly uniform direction that was aligned with the longitudinal plane of the element (for full discussion see Chapter 1.2).

More detail of this is revealed in sections cut through the upper regions of the dorsal process denticles (for example Figure 3D, specimen 171). The central core of the process is composed of crystallites that are closely packed and either perpendicular or slightly oblique to the plane of section. It is probable that this type of crystallite orientation provides no lamellar resolution because the surfaces of the lamellae are parallel with the crystallites contained. The flanks of the process reveal lamellae because the crystallites have an oblique orientation with respect to the surfaces of the lamellae. Figure 7A shows the proposed orientation of crystallites within an individual growth prism of a denticle. It is possible that the radiating fabric that is

formed by rods, in human teeth also represents a form of growth prism comparable to those as hypothesised for the individual denticles belonging to elements of *Pterospathodus*.

Donoghue (1998) proposed that individual growth prisms within single denticles comprise crystallites that have their long (c) axes parallel or subparallel to the long axis of the denticle. In the case of *Pterospathodus* it has been possible to provide greater resolution and to trace the precise influence of the growth prism on the orientation of the crystallites within the surrounding lamellae. Figures 3A, and 4A show the sharp discontinuities that demarcate the lateral margins of the denticles. These represent the confines of each individual growth prism and may indicate the presence of individual populations of secretory cells that were responsible for the formation of each growth prism. Figure 3E shows the cores of two denticles that may represent two distinct growth prisms. With distance from the centre of the core, the crystallites within the lamellae gradually become more oblique to the lamellar surfaces. The junction between the two growth prisms is composed of irregular crystallites (Figure 3F). This might reflect the individual populations of cells (associated with each growth prism) having conflicting effects on the orientation of periphery crystallites.

Donoghue (1998, p. 640, fig. 3i) figured a horizontal section through the blade of a Pa (P₁) element of *Ozarkodina confluens*. The horizontal section reveals the core of a denticle that has a crystallite arrangement that is comparable to the denticle core of *Pterospathodus* shown in Figure 2C and represents a horizontal section through a growth prism. The dimensions of the lamellae and crystallites of *Ozarkodina confluens* appear to be slightly greater than those of *Pterospathodus* although it is difficult to be accurate when measuring oblique structures. Donoghue's (1998, p. 641) stated that "in areas of complex elements that were simply being enlarged by successive increments of lamellar crown tissue, without development of new morphological features (e.g. growth around the main body of blade-like or platform elements), the crystallites are usually orientated perpendicular to the outer surface". Successive laminations that have enlarged the platform and the lower half of denticles are composed of crystallites that are orientated with their long (c) axes perpendicular to the lamellar surface (Figure 2C), this is appears to be in accordance with Donoghue (1998).

White matter. The boundaries of the white matter cores found in elements of *Pterospathodus* are generally diffuse; however, the boundaries that demarcate each denticle are sharp (Figure 4A). The boundaries of the white matter cores in the caudal process denticles are diffuse and the white matter tissues and structures intergrade with the hyaline crown (Figure 4E, D). The intergradation of white matter tissues and lamellar crown is also seen in elements of Late Devonian conodonts (Donoghue and Chauffe, 1999) and suggests that the mechanism for depositing the two tissues was related. This has led Donoghue and Chauffe (1999) to suggest that white matter represents a tissue that is developmentally homologous to enamel and was probably secreted by the same cell population (Donoghue *et al.*, 2000).

If this interpretation is correct, then it is likely that the pattern of deposition of white matter is closely related to the pattern of hyaline crown deposition. It is possible that the aboral boundaries of the white matter cores reflect the attitude, and are defined by, the c-axes of crystallites within each growth prism. This would imply that crystallites within the dorsal process reflect a lateral vector of growth and are orientated parallel with it, defining a white matter core with a wide angled base. The caudal denticles are more elongate, laterally compressed, composed of crystallites that are orientated parallel or oblique to the lamellar surfaces, this internal structure represents the influence of growth prisms that had a predominantly oral expansion forming taller, laterally compressed denticles. The attitude of these aboral crystallites would define a more acute aboral angle, and the deflected tails of the white matter cores seen in the denticles of the caudal process may be reflecting this pattern of growth.

Figure 4F shows the relative positions of the white matter cores and their proximity to the aboral margin of the element. Figure 5B and 5C show the positions of the basal bodies beneath the dorsal process and caudal process respectively. The secretion of white matter appears to occur approximately 10µm above the basal body/lamellar crown boundary, in both processes, but the basal body of the dorsal process is in a more oral position than that of the caudal process. It is not known what the signal for white matter secretion is, but it is possible that the signal is related to the position of the basal body/lamellar crown boundary, beneath the developing crown. In enamel, the formation of prismatic enamel is dependent on the formation of Tomes'' processes at the secretory pole of the ameloblasts. Consequently, the first enamel to be deposited is aprismatic, prior to this modification (Boyde, 1976). It is possible that some form of modification is required before white matter can be formed, thereby resulting in the formation of hyaline crown prior to the onset of white matter secretion. This pattern of white matter secretion is closely comparable to that of the platform elements of *Eoplacognathus* (Chapter 2.2).

Structures within white matter cores have a recurring pattern of distribution. The small subcircular cavities are found throughout each core, but are more common towards the periphery. It is possible that these represent the cavities of secreting cells that were trapped within the fine grained matrix of the white matter and did not retreat orally. The tubules are more common towards the centre of the tissue and might represent the processes of cells that retreated orally (Donoghue 1998). It is possible that the tubules in Figure 4D represent a greater concentration of mineral-secreting cells at the apex of the denticle. The tips of the white matter oblique to the section at this level. These cavities might represent tubules that are perpendicular to the section.

The unbranched tubules seen in Figure 4E have a similar type of morphology to those presented by Donoghue (1998, p. 656, fig. 14e). His figure shows the initiation of white matter secretion immediately above the growth cavity of a denticle of an S element of *Polygnathus*. Although Specimen 165 (Figure 4E) does not show a growth cavity, the orientation of the adjacent crystallites suggests that the apex of each lamination is positioned directly beneath the core of white matter and a growth cavity would be revealed if the section was polished further.

Basal body. The basal body of the *Pterospathodus* platform element is composed of a homogenous finegrained tissue. The tissue is so fine grained that it is impossible to discern individual crystallites. Resolution of the basal body tissues of elements of *Pterospathodus* has been difficult to achieve. Longitudinal sections have been more successful and reveal lamellae that are perpendicular to this plane of section. It is possible that the basal body of *Pterospathodus* fits within the range of atubular dentines, an interpretation that Donoghue (1998) and Donoghue *et al.* (2000) proposed for conodont basal bodies that are atubular and lamellar.

Growth of the element.

The dorsal process possesses a basal cavity that is at its highest position in the element, therefore representing the earliest stages of ontogeny. The sections described above reveal that the 'posterior' (dorsal) process is initially continued with a lateral expansion (Figure 6A-F). Although this expansion is clearly orientated away from the main axis of the element, prior to the development of the blade of the element, during the earliest stages of ontogeny, in the absence of a third process, this process would have represented a 'anterior' (ventral) process. This sequence of growth shows that the rectilinear continuation of the 'posterior' (dorsal) process is, therefore, technically a 'lateral' (caudal) process, and the expanded lip of the platform represents a poorly formed ventral process. This means that the platform element of *Pterospathodus* is a true pastinate element.

The basal body extends beneath the dorsal and caudal processes, but is most substantial beneath the dorsal process. In transmitted light it is clear that the denticles of the dorsal process have individual basal pits (Figure 5D). It is possible that this is evidence that the element extended its dorsal process by enveloping discrete denticle units that had begun growth separated from the main element (Donoghue, 1998). Both the main element and the distinct unit would have continued growth until it was possible for later increments to encompass both of the units thereby joining the two and leaving no surface evidence of their previous separation. There are no perceptible optical discontinuities within the hyaline crown tissue to confirm that each denticle represents an incorporated unit, but the distinct basal bodies lend support to the theory. This type of growth is comparable to the type II ramiform element morphogenesis, which is also recognised in elements that have been referred to *Carniodus* (Donoghue, 1998). However, examination of the basal body immediately below the denticles of the dorsal process reveal basal body laminations that are parallel with the lamellar crown/basal body junction (Figure 5A, D). If the basal pits beneath the denticles represented the formation of individual units, the laminations immediately beneath it would not be expected to show evidence of continuous growth between the units. It would seem that despite the presence of basal pits beneath the denticles, the pattern of growth is more comparable to Donoghue's (1998) type III ramiform genesis.

The morphogenesis of the caudal process is in the form of incremental lamellae extending beyond the tip of the process, forming an evagination, and eventually forming a denticle pit. Each denticle pit and resulting

denticle represent the formation of a new growth prism that controls the secretion of new hyaline crown in that region. The growth axis of the new prism often remains inclined away from the more mature regions of the element and the morphology of the white matter cores reflects this. The narrow, shallow basal body beneath this process is characteristic of growth of this kind, where the process extends crown tissue beyond the distal tip of the basal body and the generation of basal body follows later (Figure 5C). Donoghue (1998, p. 649) proposed that new denticles of this type were "added marginally by localised evagination of a layer of crown tissue". The growth of the caudal process of *Pterospathodus* adheres to Donoghue's (1998) criteria for type III ramiform genesis and follows his hypothesis of blade morphogenesis.



Figure 1. Line drawings of elements of *Pterospathodus amorphognathoides* showing biological terminology according to the apparatus reconstruction presented in Chapter 3.1. A. Oral view of element. B. Aboral view of element showing morphology of basal body. C. Lateral view of element.



Figure 2. Crystallite arrangements within the Platform element of *Pterospathodus amorphognathoides* specimen 163. A. Crystallites with long (c) axes perpendicular to lamellar surface, specimen 163. B. Longitudinal section through dextral element, showing lack of resolution of interlamellar spaces where crystallites are orientated with long (c) axes parallel to lamellar surfaces, specimen 216. C. Horizontal section through platform and base of denticles of dorsal process, specimen 163. D. Horizontal section through distal tip of caudal process showing oblique crystallite orientation within individual evaginations, specimen 171. E. Horizontal section through caudal process showing individual denticle pits and oblique crystallites, specimen 163. F. Horizontal section through dorso-lateral process and the thin laminations that are not part of the the basal body of the main element when first initiated, specimen 160.



Figure 3. Crystallites within horizontal sections of platforms of *Pterospathodus amorphognathoides.* A-C, E-F specimen 163. A. Junction between denticles of dorsal process. B. Point of eruption where dorso-lateral process joins to main axis of element. C. Section through edge of platform, showing where the lamellae curve around the edge of platform but the crystallites remain perpendicular to lamellar surfaces, edge of platform at bottom of image. D. Section showing middle of denticles of dorsal process showing a close crystallite fabric and lack of lamellae resolution, indicating that the section is closer to apex of denticle, specimen 171. E,F. Junction between seperate growth prisms of dorsal process showing distorted crystallite orientations at junction (F) and adjacent aprismatic crystallites that appear uninfluenced by individual growth prisms.



Figure 4. White matter in platform element of *Pterospathodus amorphognathoides*. A. Horizontal section of white matter core with laminations and small cavities aligned, in denticle of caudal process of sinistral element, specimen 172. B. Enlarged image of F, showing distribution of structures within white matter core. C. Longitudinal section of sinistral element, edge of white matter core of denticle in caudal process showing laminations and distribution of cavities, specimen 216. D. Oblique/horizontal section showing distruibution of structures in white matter of the dorsal process, specimen 163. E. Oblique/longitudinal section of white matter core in caudal process denticle, specimen 165. F. TLM image (X200), showing areas of denticles occupied by white matter and blunt bases of white matter cores, specimen 271.



Figure 5. Transmitted light images of platform elements belonging to *Pterospathodus celloni*. A-C. Specimen 390. A. Image orientated with the caudal process directed towards the left of the image. Basal body is visible beneath the dorsal process, and beneath the proximal region of the caudal process, x200. B. Close-up of dorsal process and basal body beneath. Shallow peaks are visible beneath the denticles, x400. C. Close-up of caudal process, there is no evidence of peaks beneath the denticles, x400. D. Specimen 288. Basal body beneath dorsal process, basal body laminations are visible and continuous beneath the denticles the caudal process is directed towards the right, x400.



Figure 6. The Basal body of platform elements of *Pterospathodus amorphognathoides*. A. Aboral view showing lip of supressed process, specimen 272 (X 500). B. Horizontal section of dextral element with only apex of basal body revealed, specimen 176. C. Horizontal section of sinistral element, with the basal body of dorsal process exposed and the narrow apex of the caudal process just visible, specimen 161. D. Close-up of apex of cavity in B. E. Close-up of cavity seen in C. F. Longitudinal section of basal body laminations just below dorsal process, specimen 210.



Diagram 7 Platform element of *Pterosphathodus amorphognathoides*. A. The distribution of lamellae and the influence of the growth prism on crystallite orientation within denticles. B. Orientations of processes and basal body within.

CHAPTER 3.3

THE PRIMARY SURFACE MICROSTRUCTURES OF THE PLATFORM ELEMENT OF PTEROSPATHODUS.

Introduction.

The majority of the elements within the apparatus of *Pterospathodus* changed little throughout the evolution of the genus; it was the platform element that was least conservative. The variation of the platform element is most notably marked by the appearance, disappearance and occasional bifurcation of the dorso-lateral process. This provides the character that distinguishes between different species. Three types of surface ornamentation occur on element surfaces and are discussed and interpreted below. The type species *Pterospathodus amorphognathoides* is chosen here as a representative for study.

Materials and methods.

Specimens for this study have been selected from the disarticulated collection from the Malvern Hills, Herefordshire, Cowleigh Park 1, 10582, collected by Professor Aldridge and kept at Leicester University. The specimens were collected from the top of the Telychian Wych Formation (SO/760468) Birches Farm Lane (see Aldridge, 1972). The elements are well preserved and several specimens have clear surface microstructures. Some of the finer details of the surface microstructures have been slightly recrystallised; however, it has been possible to recognise the distribution and nature of different structures. Detailed descriptions have been produced that have resulted from extensive SEM work and interpreted with the use of polished sections that have revealed detail of the underlying crystallite orientations.

Description of surface microstructures.

Polygonal surface microstructure. Polygonal ornamentation found on platform elements of *Pterospathodus* is formed by a number of interlocking polygons. Each polygon is bounded by a positive ridge and has a diameter of approximately 2-6 μ m (Figure 1A, B). The ridges are approximately 0.5 μ m wide and 0.75 μ m high. Where clearly formed and preserved, each polygon is essentially hexagonal.

There is a distinct distribution pattern of polygonal surface structures, where the polygons are restricted to the platform region of the element (Figure 1B), and the tips of damaged or worn denticles (Figures 1A, C, 2D). The denticles on which polygons occur, are flattened or damaged and the polygons have a diameter that normally ranges between 2-4 μ m (Figure 2D). Where the denticle tips show irregular surfaces the polygons tend to have a greater range of sizes and to be more distorted (Figure 1C, 1E), although this is possible the

effect of crystallites growing on the element surface during diagenesis. Polygons become elongate at the edges of the polygonal region and the parallel edge of each marginal polygon forms a transition to the ropy surface microstructure of the denticle.

Polygons on the platform regions of the elements have a regular structure and have a diameter that ranges between 3-6µm, which is slightly larger than those of the denticle tips, (Figure 1B). Where the platform is broad the polygons are restricted to the outer half and cover the outer edge of the platform before fading and disappearing just under the platform on the aboral surface of the denticle. Between the platform and the base of the denticles the polygons are replaced by a smooth surface that appears to have a faint longitudinal fabric that is aligned with the long axis of the element (Figure 1B). Occasionally it is possible to observe polygons that have become elongated at the transition between the two surface microstructures, with their long axes parallel with the long axes of the denticles (Figure 1F).

Ropy ornamentation. Ropy ornamentation is restricted to the denticles. Longitudinal straight ropes extend up the height of the denticle, converging together where they meet at the denticle tip (Figure 2A, B). Each rope is approximately 2-3µm wide and often extends up the entire length of the denticle (Figure 2B). Where ropy surface microstructures are continuous with the polygonal structures it is clear that the secretion of both forms of microstructure is related, as the polygons are transformed into ropes, not replaced. Several of the specimens examined have lost the ropy surface microstructures at the tip of the denticles and there are many examples where the denticle has lost most of the ropy ornament (Figure 2C-D).

Interpretation.

Various interpretations of polygonal surface microstructures have been proposed and the general consensus is that they represent the imprints of the cells belonging to the secretory organ as discussed in Chapter 1.3. Conway Morris and Harper (1988) believed that polygonal imprints on P elements corresponded to individual cell imprints. This theory was followed by Burnett (1988) who proposed that areas of the element with polygonal surface microstructures represented regions that were permanently buried beneath soft epithelium tissue and proposed that they might have represented muscle attachment surfaces. Donoghue (1996, p. 61), in contrast, suggested that "conodont elements must have periodically sunk within the dermis, or else the dermis must have grown over the surface of the element to facilitate growth and repair".

It is followed here that the polygonal surface microstructures represent epithelial cell imprints, formed during the formation of new crown tissue when the element was temporarily submerged beneath the dermis. It is possible that the outer platform areas that possess polygonal patterning might have remained covered by tissue once the element became functionally active, but it would have been impossible for the denticle tips to be permanently covered in tissue. This is because the elements functioned across the mid-axis of the apparatus, either occluding directly against each other or crushing food between the element surfaces (Chapter 3.4). The denticle tips would be the first regions to experience abrasion and wear during function and therefore it would have been impossible to preserve a covering of soft tissue.

The ropy surface microstructures are comparable to those described by Lindström and Ziegler (1971) Lindström, McTavish and Ziegler (1972), Lindström and Ziegler (1981) and Burnett and Hall (1992). Ropy surface microstructures are continuous with the polygonal surface microstructures, so it is likely that they are developmentally comparable. The boundaries of the polygons represent the outline of the secretory cell, and a lack of continuity in crystallite orientation in this region due to the controls imposed by the secretory process (see Chapter 1.3 for full discussion). It is possible that the longitudinal fabric represents the shearing of secretory cells as they retreated orally, leaving behind this characteristic surface ornamentation, as discussed in Chapter 1.3. In juvenile specimens the ropes cover the entire denticulated surface with polygonal ornamentation only developed where the denticle surfaces have been flattened due to function. Loss of the ropy surface microstructures from the denticle tips is due to wear on the element surface during the processing of food (see Chapter 3.4). Some specimens were found that had remnants of ropes faintly preserved, it is likely that these elements had only just erupted from a phase of growth and had not been functionally active for a long period of time prior to death.

Discussion.

Deposition of polygonal surface structures appears to be directly related to flat, level surfaces of the element. However, with this criterion it would be expected that the surface of platforms would be covered with polygons. However, contra to this, polygonal ornamentation only occurs on mature specimens along the edge of the platform. Horizontal sections of *Pterospathodus* have shown that there is a pattern of crystallite orientation that correlates with this distribution of surface microstructures. Figure 3 shows a horizontal section of a *Pterospathodus* platform element that has exceptionally good resolution of the crystallite fabric.

The marginal areas of the section are constructed of lamellae perpendicular to the plane of section, with the margins of the lamellae clearly defined by the crystallite tips; the crystallites are orientated with their c-axes perpendicular to the lamella surface. The region adjacent to the denticles is composed of lamellae that are oblique to the plane of section with crystallites within slightly inclined towards the core of the denticle. This is apparent at the junction between the lamellae. Between these two regions, the lamellae are almost horizontal to the plane of the section, and contain crystallites that are perpendicular to the lamellae surfaces. Although a gradation of the laminations adjacent to the denticle cores is apparent. The c-axes of the crystallites in this area have an oblique orientation.

The section shows two distinct crystallite fabrics that correspond to the polygonal and ropy surface microstructures described. The perpendicular lamellae at the edge of the element correspond to the curved edge of the platform where polygons cover the edge and parts of the aboral surface. The middle horizontal

laminations correspond to the smooth surface microstructure and the oblique laminations at the base of the denticles correspond to the base of the denticle where the ropy surface microstructures occur. Specimen 184 possesses this distribution of surface microstructures along its caudal process figured in 1D, where the platform is not very wide. This pattern of crystallite orientation is in accord with the interpretation of Donoghue (1998), where he suggested that when elements were simply enlarging structures that were already formed (e. g. platforms); the crystallites within are orientated with their c-axes perpendicular to the lamellar surface. If compared developmentally to enamel, it is, however, more likely that the crystallites reflect the path of the retreating secretory cells and are orientated in a direction that reflects the direction of maximum growth. This would mean that the secretory palisade of cells would have almost completely surrounded the oral surface of the element and retreated in a wide range of directions. Juvenile specimens that are dominated by ropy ornamentation may represent a less diverse array of directions in which the secretory cells could retreat.

There is a clear correlation between the underlying crystallite orientation and the surface expression of new lamellae. The detailed distribution of crystallites within the platform elements of *Pterospathodus* reflects an extremely sophisticated secreting epithelium.



Figure 1 Polygonal surface microstructures on the platform element of *Pterospathodus amorphognathoides*. A,B,D specimen 184, C specimen 253. A. Oral view of polygons on edge of platform of dorsal process. B. Oral view of dorsal process showing distribution of polygons on platform. C. Distorted polygons over broken denticle tip of caudal process. D. Lateral view of caudal process showing distribution of polygons around platform edge. E-F Specimen 202. E. Oblique oral view of dorsal process denticle, polygons developed over regrown denticle tip, smooth area on tip probably due to polishing due to wear (Chapter 3.4). F. Polygons at distal tip of caudal process, gradual grading into ropy ornamentation obvious at base of denticles.



Figure 2 Ropy surface microstructures on the *Pterospathodus amorphognathoides* platform elements. A, B, D Specimen 184. A. Caudal process denticle showing ropy microstructure. B. Close-up of ropes seen in A. C. Specimen 253. Polished dorsal process denticle, showing worn ropes. D. Ropes transforming into polygonal micro structures at tip of broken denticle of dorsal process.



Figure 3. Horizontal section through the platform and adjacent denticles of *Pterospathodus amorphognathoides*. Lamellae are perpendicular to the plane of section at the edge of the platform (towards the bottom of the image) becoming horizontal towards the centre of the platform and approaching perpendicular up the flanks of the denticles. Specimen 163.

CHAPTER 3.4

THE FUNCTION OF THE PLATFORM ELEMENT OF PTEROSPATHODUS

Introduction.

The Pterospathodontidae (Cooper, 1977) first appeared in the fossil record during the mid Llandovery and colonised European, Asian and North American provinces before becoming extinct during the Wenlock (Männik, 1998).

According to Männik and Aldridge (1989) the apparatus is composed of three types of P element, a ramiform S element and a dolabrate M element (Figure 1A). Männik (1998) adapted this reconstruction when he proposed that the elements of *Carniodus*, a taxon which co-occurred with *Pterospathodus*, did not represent a distinct genus but were part of the apparatus of *Pterospathodus*. The apparatus of *Pterospathodus* is discussed in detail in Chapter 3.1. In this paper the platform element of *Pterospathodus amorphognathoides* Walliser, is analysed functionally.

Materials and Methods.

The elements examined for this study are from the Malvern Hills, Herefordshire, Cowleigh Park I (10582). The specimens were collected from the top of the Telychian Wych Formation (SO/760468) Birches Farm Lane (see Aldridge, 1972). Many of the specimens have a slightly sugared surface; however, some were found with excellently preserved surface microstructures and detailed element morphologies.

The internal structure of the platform element of *Pterospathodus* is re-evaluated and a revised interpretation of process configuration presented. This new understanding of the process configuration of the platform element has been used to homologise the elements of *Pterospathodus* with those of other well known prioniodontids. These relationships can be extrapolated to recognise homologues within the only well known prioniodontid bedding plane assemblage of *Promissum*. The apparatus of *Promissum* has been used as a template to predict the positions and orientations of the elements of *Pterospathodus* in life.

Scaled plasticine replicas have been made and used to investigate the possible models of function and to predict where damage would and would not occur during function.

The hypothesis of function developed from study of the plasticine replicas and constrained by the architecture of the *Promissum* template has been tested by detailed examination of the *Pterospathodus* element surface microstructures.

Terminology and locational notation follow that introduced by Purnell *et al.* (2000) where homologies are known and the terminology of Sweet (1981; 1988) is reverted to where homologies are unknown or uncertain.

The platform element of Pterospathodus.

The external morphology of the platform element of *Pterospathodus amorphognathoides* appears to be carminate (Figures 1A, i, iii). A bifurcating secondary dorso-lateral process occurs, with a low junction, approximately half-way along the element. A small lateral expansion of the platform occurs on the opposite side of the element, approximately three fifths along from the dorsal end of the element. The denticles of the dorsal process are squat but have a rounded base, each undamaged denticle has a sharp point (Figure 2A, C). In mature specimens the denticles remain squat, but are rounded and short (Figure 2F). The denticles that extend in line with the squat denticles of the dorsal process are narrower, taller and pointed (compare Figure 2E to Figure 2F) and in mature specimens they become more rounded and sometimes inclined away from the dorsal process (Figure 3C, D). When viewed laterally the denticles on the dorsal process have shorter bases than those of the rest of the element, and in mature specimens the denticles become so fused and rounded they appear as a rounded low ridge (Figure 2B). Horizontal sections of this element reveal that the expanded lobe on the inner side of the element represents an unexpressed 'anterior' process (Chapters 3.1, 3.2) that formed the original dorso/ventral ('posterior/anterior') axis, therefore, the process that is now aligned with the 'posterior' process is technically a 'lateral' (caudal) process.

Implications of the reinterpretation of the platform element of Pterospathodus.

Pterospathodus has been designated a member of the superfamily Prioniodontacea Bassler, 1925 by Clark (1981) and as a member of the Order Prioniodontida Dzik, 1976 by Aldridge and Smith (1993) in the Fossil Record 2, but as an ozarkodinid by Sweet (1988) and Fåhræus (1984). Both Sweet and Fåhræus classified Pterospathodus as an ozarkodinid because they both believed that its ancestor originated within the ozarkodinid lineage and that Pterospathodus was not related to any of the taxa classified as prioniodontids. Männik and Aldridge (1989) classified Pterospathodus as a prioniodontid because they established clear homologies between the elements of Pterospathodus and Pranognathus and thought that the two taxa shared a similar type of apparatus. It is thought that Pranognathus was related to other prioniodontids such as Icriodella? sanderi (Mabillard and Aldridge, 1983) and possibly Gamachignathus (McCracken et al., 1980). Therefore, by extrapolating these observations, Männik and Aldridge (1989) proposed that the apparatus of Pterospathodus was more closely comparable to a prioniodontid apparatus than to an ozarkodinid one.

One of the major differences between the prioniodontid and ozarkodinid conodonts is the morphology of the P elements possessed by the two taxa. Prioniodontids commonly possess pastinate P elements whereas

ozarkodinid P elements are almost exclusively angulate or carminate. The platform element of *Pterospathodus* is clearly not pastinate in the technical sense. The validity of the prioniodontid diagnosis is questionable if it can to be modified to include taxa that do not possess all of the diagnostic characters.

The new understanding of the process configuration of platform elements (Chapter 3.1) of *Pterospathodus* supports Clark (*in the Treatise*, 1981), Männik and Aldridge (1989) and Aldridge and Smith (1993) in their classification of *Pterospathodus* as a prioniodontid. However, *Pterospathodus* is classified here as a prioniodontid primarily because it complies with the diagnosis of prioniodontids and not because other elements of the apparatus can be compared to elements from other prioniodontids. Such a morphology is comparable to elements within the apparatus of *Promissum* and not comparable to P elements within the apparatus of ozarkodinids.

Models of function.

Using the *Promissum* template. The apparatus of *Promissum* is composed of four opposed pairs of P elements, arranged with the conventional 'posterior' and 'anterior' processes orientated dorsally and ventrally, respectively; an array of S elements, and a pair of M elements (Figure 1B, C). The detailed knowledge of this apparatus provides a template with which to reconstruct prioniodontid apparatuses from disarticulated collections of elements. The apparatus of *Pterospathodus* has been reconstructed in Chapter 3.1, and the platform element interpreted as homologous to the elements in the P₁ and P₂ positions of the *Promissum* apparatus. This places the platform element of *Pterospathodus* with its dorsal process directed dorsally, which would result in its caudal process being directed ventrally and the unexpressed ventral process directed rostrally. The dorso-lateral process is positioned on the opposite side of the element to the unexpressed process, consequently, it would be directed towards the caudal end of the apparatus. The elements in the P₁(P₂) positions of *Promissum* would have formed opposed pair(s), and it is thought that they occluded across the mid-axis of the apparatus.

Plasticine replicas. The use of plasticine replicas indicates that the elements of *Pterospathodus* could have occluded in three different ways. The denticles of each opposing element could have occluded directly against each other and manipulated or processed food particles between the denticle tips. The elements could also have functioned by occluding down either side of each main axis or they could have combined both modes of function, forming an integrated shearing and crushing device.

If the elements functioned by working the denticle tips against each other then the row of denticles of mature specimens would be expected to exhibit rounded shortened or chipped denticles, damaged orally. If the denticles sheared past each other, damage down the sides of the denticles would be expected, confirming that the occlusion did not stop once the denticle tips were level with each other. A combination of both types of wear would be expected if an integrated functional technique was employed.

Testing the possible models of function.

Surface damage and wear of *Pterospathodus* elements. In juvenile specimens the blade (caudal process) of platform elements of *Pterospathodus* is made up of sharp, triangular denticles that all have similar outlines when viewed laterally (Figure 2A). In larger specimens, the dorsal and caudal process denticles are more obviously differentiated, and it is obvious, when viewed down the long axis of the element, that the dorsal process denticles are almost circular at the base whereas those of the caudal process are laterally compressed (Figure 2E, F).

Extensive ropy microstructures are only present on juvenile specimens, where they can be seen to dominate the surfaces of denticles. In more mature specimens the ropes are clearly absent, leaving a rounded denticle and a smooth surface (Figure 2D).

Mature specimens are characterised by a variety of morphologies. It is common to see the dorsal process with denticles that have preserved their discrete, rounded bases but have developed short sharp tips, that are sometimes pinched just below the tip, with a slight neck (Figure 2C, F). The denticulated area of the element that is aligned with the bifurcating dorso-lateral process and the unexpressed ventral process is sometimes reduced to a levelled off featureless ridge (Figure 2D). This ridge is often overgrown with a reticulate surface ornamentation. Both the dorsal and caudal process denticles of mature specimens have a rounded morphology and are sometimes broken and chipped.

Specimen 184 (Figure 3A, B) shows clear surface damage on the caudal process denticles. The damage occurs on the same side of the element as the bifurcating lateral process (Figure 3B). The denticles are chipped and deformed on this side in comparison with the opposite side, which has the primary surface ornament preserved up to the tip of each denticle (Figure 3A).

Specimen 202 displays a similar kind of damage, but this time, on the opposite side of the element to the bifurcating process (Figure 3D). Clear facets are apparent on the denticles and some of the denticle tips are flattened orally. The deformed areas have ropy and polygonal surface ornamentation developed over the facets (Figure 3C-E).

In more of the larger specimens, the bifurcating dorso-lateral process also exhibits extensive surface damage. Figure 3F shows a dorso-lateral process that has wear and damage comparable to that of the main axis of the element; in both cases denticles appear to have been flattened and subsequently overgrown by a reticulate ornamentation. The height of the dorso-lateral process and the main axis of the element are at approximately the same level in this specimen, in contrast to more juvenile specimens (compare Figures 2A and 2B). In juvenile specimens, the junction of the dorso-lateral process is at the base of the main axis of the element.

Interpretation.

The flattened central portion of specimen 202 is directly comparable to damage figured on platform (P_1) elements of Pennsylvanian *ldiognathodus* figured by Donoghue and Purnell (1999b, p. 252, fig. 1). However, much of the damage seen on the elements of *ldiognathodus* represents layers of lamellae shearing off the side of the blade. The reoccurrence of similar damage on the denticles of *Pterospathodus* implies that the specimens examined were subject to brittle failure of hyaline tissue. This possibly represents evidence of malocclusion. The most central portion of specimen 202 (Figure 2D) is flattened with worn rounded denticle surfaces that are typical of crushing and compression (Crompton and Hiiemae, 1970; Purnell, 1995). The distribution of this characteristic type of wear on *Pterospathodus* is found in an equivalent position to that found in *ldiognathodus*. This has important implications for the possible motion of the element during function (see below). Damage is not in the form of clear facets, or striations, and this may reflect that the element did not function by shearing elements past each other (Crompton and Hiiemae, 1970). The internal structure of the elements may help to prevent breakage and loss of denticles. White matter cores provide a dense, unstructured internal structure for the denticles and would help to prevent the propagation of cracks or flaking of denticle surfaces due to the lack of distinct planes of weakness that are present in hyaline lamellar crown tissue (see Chapters 1.4, 4.4 for full discussion).

The denticles bordering the flattened denticles preserve polygonal ornamentation. Polygonal ornamentation is restricted to the bases of the denticles, the platform and in mature specimens, to flattened areas of denticles. Detailed internal analyses of other prioniodontids (Chapter 2.2) have shown that polygonal surface microstructures only occur where the crystallites within are secreted with their long (c) axes perpendicular to the growing surface. It is possible that the polygonal ornamentation found on the dorsal process denticles (Figure 2D) and the caudal process denticles (Figure 3D) represents the element's response to the worn and damaged areas. New lamellae have overgrown the damaged areas as horizontal layers overgrowing the edges of the older truncated lamellae, which are orientated parallel with the long axis of the denticle. Where the new layers are sufficiently horizontal, a strong reticulate pattern has formed. Figure 2D shows where the reticulate pattern is becoming worn away as the element became functionally active after repair. It may be that the pinched denticle tips seen in figure 2F represent an element that has just undergone regeneration of its surface, over denticles that had previously lost their pointed tips during function. Unfortunately, the elements are too robust and thick to allow successful resolution in transmitted light.

Donoghue and Purnell (1999b, p. 253, fig. 2) also figured Pa (P_1) elements of *Ozarkodina confluens* that exhibit wear on the blade part of the element. This type of wear appears to be directly comparable with the
damage found on the caudal process of *Pterospathodus*. The polished denticles are typical of processes that performed a shearing function (Purnell, 1995).

The distribution of wear on the caudal and dorsal process denticles indicates that when the *Pterospathodus* Pa (P_1) elements were in the apparatus they would have occluded with the dextral element slightly behind the sinistral element. The denticles of the dorsal process functioned against each other, whilst the caudal process of each element sheared against the opposing caudal process. The worn surface of the dorso-lateral process of specimen 202 shows that the elements could not have occluded at their denticle tips, and must have sheared past to allow the opposing elements to occlude close enough to flatten the dorso-lateral denticles.

According to Donoghue and Purnell (1999a) the worn central portion of the *Idiognathodus* Pa (P_1) element is due to the pivoting motion and close contact of the elements during function. The distribution of wear that has been found on the elements in this study shows that elements of *Pterospathodus* may have functioned in a comparable way (Figure 4). However, ozarkodinids occluded with the left element behind the right element (Purnell, 1995; Purnell and Donoghue, 1997; Donoghue and Purnell, 1999a); the reconstruction presented here implies that the Pa (P_1) elements of *Pterospathodus* occluded with the right element behind the left.

Conclusions.

The plasticine replicas show that only three occlusal models are possible. The distribution and type of surface damage found on elements of *Pterospathodus* further limit the possibilities. The different types of surface damage are characteristic of both shearing and crushing suggesting that there must have been some way to ensure relatively precise occlusion thereby only effecting certain regions.

Männik and Aldridge (1989) believed that the ancestry of *Pterospathodus* would remain cryptic until an Ordovician species with homologous P elements was found. The new understanding of the ultrastructure of the platform element provides sufficient evidence to place *Pterospathodus* within the prioniodontids, without the identification of this unknown ancestor, because of the possession of a pastinate P element.





Figure 1A. Elements in the apparatus of *Pterospathodus amorphognathoides* according to Männik and Aldridge (1989). i. Lateral view of Pa (P1) element. iii. Oral view of Pa (P1) element. ii. Pb (P3) element. iv. Pc (P4?) element. v. M element. vi. S element.

Figure 1B-C The apparatus template of *Promissum pulchrum*. C. Terminology for the apparatus following Aldridge *et al.* (1995). D. New terminology proposed for the apparatus following Purnell *et al.* (2000).



Figure 2. Platform element of *Pterospathodus amorphognathoides* showing evidence of wear. A. Juvenile dextral element, lateral view; specimen 183. B. Mature specimen, lateral view; specimen 202. C. View of dorsal process of sinistral element, from dorso-lateral process angle; specimen 252. D. View of dorsal process, view from caudal process; specimen 202. E. View along caudal process; specimen 202. F. View along dorsal process; specimen 202.



Figure 3. Platform elements of *Pterospathodus amorphognathoides*. A. Ropy texture preserved to tips of denticles; specimen 184 sinistral element, on caudal process; B. Opposite side of process shown in A, showing wear and damage; C-F dextral element, specimen 202. C. Rounded, undamaged denticles of caudal process; D. Opposite side of same process figured in C, showing wear facets; E. Polygonal surface micro-structures on caudal process denticle; F. Dorso-lateral process, showing worn denticles.



Figure 4. Motion of platform elements of *Pterospathodus amorphognathoides*. Position and movement of elements with respect to each other when positioned within the apparatus. Elements initially guided by denticles of caudal process, before dorsal process denticles come into contact. Elements positioned as if in apparatus in most caudal position and viewed from the rostral, therefore the dorso-lateral processes are directed towards the caudal of the apparatus.

CHAPTER 4.0

INTRODUCTION

THE ARCHITECTURE, HISTOLOGY AND FUNCTION OF THE FEEDING APPARATUS OF *ICRIODELLA* RHODES, 1953

Introduction.

The icriodellids were originally classified by Lindström (1970), Sweet and Bergström (1972), Cooper (1977), Klapper and Bergström (Robison, 1981) and Dzik (1991) within the Icriodontidae Müller and Müller, 1957. At the time of the *Treatise* (Robison, 1981, p. W125) these conodonts were thought to range from the Middle Ordovician to Lower Silurian (this incorporated the range of the icriodellids) and from the Middle Silurian to the Upper Devonian.

Lindström (1970), Dzik (1976), Cooper (1977) and Klapper & Bergström (*in* Robison, 1981) have designated *lcriodella* as a member of the Icriodontidae Müller and Müller 1957. However with greater knowledge and appreciation of apparatus architecture Fåhræus (1984) suggested that *Icriodella* was not related to the Icriodontidae and proposed that it should be classified as a new un-named subfamily of the Balognathidae along with Balognathinae (containing *Amorphognathus* Branson and Mehl, 1933) and Polyplacognathinae (containing *Polyplacognathus* Stauffer, 1935, and *Eoplacognathus* Hamar, 1966). However, there is no evidence to suggest that *Icriodella* was sufficiently closely related to any of these genera to merit its inclusion within the Balognathidae (Aldridge, pers. com., 2000) stated that.

The icriodontid apparatus was thought to be trimembrate, possessing scaphate, pastinate, pastiniscaphate or stelliscaphate Pa elements, and Pb and S elements that were simple cones, or modification of simple cones. Ordovician icriodontids were thought to be quinquimembrate. The Pa element of *Icriodella* was thought to possess a long 'anterior' process that bore a double row of denticles, a short cusp and adenticulate lateral process and a blade-like 'posterior' process. The Pb element was more or less pyramidal, the M elements bipennate or dolobrate. The S elements were recognised in two different forms; tertiopedate, one with three denticulated processes and one with an adenticulate 'anterior' process.

Fåhræus (1984) pointed out that the S elements of *Pedavis* (the type genus of the icriodontids) were ribbed cones and that those of *Icriodella* were denticulated ramiform elements. He thought that is was impossible to have derived the S elements of *Pedavis* from the *Icriodella* S elements and on this basis thought that *Icriodella* was in fact phylogenetically distinct from the rest of the genera that the *Treatise* included within the Icriodontidae. Fåhræus (1984) preferred to accommodate *Icriodella* within a subfamily of the Balognathidae.

Sweet (1988) regrouped four genera from the Icriodontid within a new family; Icriodellidae. Sweet included Icriodella, Pedavis Klapper and Philip, 1971, Sannemannia Al-Rawi, 1977, and Steptotaxis Uyeno and

Klapper, 1980 within his new family because he thought that they all shared sufficient apparatus similarities to merit the erection of a new family, distinct from the Icriodontids. Aldridge and Smith (1993) could find no evidence that suggested any close relationship between *Icriodella* and the other members of the Icriodellidae and suggested that *Pedavis*, *Sannemannia* and *Steptotaxis* were more closely related to the Icriodontidae and removed them from the Icriodellidae.

CHAPTER 4.1

THE APPARATUS ARCHITECTURE OF ICRIODELLIDS.

Introduction.

Icriodellids range from the Middle Ordovician to the top of the Lower Silurian (Aldridge and Smith, 1993). They were first recognised for their distinctive Pa elements that are characterised by two main processes: a blade and a platform with transverse pairs of stubby, rounded denticles, slightly offset from each other (Rhodes, 1953) (Figure 1).

The classification of Klapper & Bergström (1981) differs from that of Fåhræus (1984) because characters of P elements were used to unify different taxa within the Icriodontids. In contrast, Fåhræus (1984) placed no emphasis on the P element morphologies and considered the characters of the ramiform elements of *Icriodella* to be of more importance, and on this basis, they were not included within the Icriodontidae.

The Icriodellidae are an important group of conodonts, as they are classified within the Prioniodontida Dzik, 1976 (Sweet, 1988), and form one of the few taxa, along with the Distomodontidae Klapper (1981) and the Rhipidognathidae Lindström 1970 belonging to this order, that contain lineages that survived into the Lower Silurian (Figure 2A).

The morphology of P elements of *Icriodella* differ markedly from those of other better known prioniodontids, for example *Baltoniodus* (see Chapter 1). Hence, it is necessary to ascertain the structure and ontogeny of the elements of *Icriodella*, so that relationships between *Icriodella* and the better known prioniodontid taxa can be identified. This will enable assessment of whether the ozarkodinid or the *Promissum pulchrum* apparatus template represents the more appropriate type of plan for the apparatus of *Icriodella* (Figure 2B, C).

Materials.

Specimens of *Icriodella* have been examined from collections that span the Ordovician/Silurian boundary. Specimens of *Icriodella deflecta* were from Gullet Quarry in the Malvern Hills (SO/761318) from the Telychian Wych Formation (10560 L28 II) (for further details see Aldridge, 1972); Specimens of *Icriodella discreta*, were from Roligheten (R2) Norway, near Oslo (NM 8490 3465), 264° from Vik town (for more details see Mohamed, 1983).

Elements of Icriodella discreta Pollock, Rexroad and Nicoll 1970.

Pa element. The Pa element is pastiniscaphate with a blade and platform of subequal length (Figure 3A). The elongate platform is constructed of two rows of paired or off set stubby denticles, the element is slightly bowed. The blade is straight, with denticles decreasing in height distally. Juvenile specimens possess a proportionately higher blade and cusp. There is sometimes an offset between the platform and the blade. Rarely a low axial ridge develops on the platform and low transverse ridges interconnect denticles. An outer lateral expansion is triangular in outline with a low axial costa from the tip of the expansion to the tip of the cusp (Figure 3D). A small inner lateral expansion occurs posterior of mid-element length in the form of a rounded unornamented lobe (Figure 3B). The basal cavity is wide and deep, especially beneath the cusp though is closed at the process tips of mature specimens.

When seen in transmitted light, the junction of the basal body and crown tissue of Pa elements belonging to *I. discreta* is normally straight beneath the blade and the platform. In some cases it has been possible to unequivocally identify the main basal pit beneath the cusp of the element (Figure 3C). In horizontal sections, the basal body has a pastinate structure (Figure 4A; Chapter 4.2). It is revealed that the 'posterior' process is represented by the blade of the element. This is also supported by the inclination of the denticles, which are inclined towards the distal tip of the blade. A 'lateral' process is represented by the platform of the element, where as the 'anterior' process is commonly unrepresented by any external morphology. It is aligned with what Aldridge (1972) described as a poorly formed outer lateral process. For full description see Chapter 4.2

Pb element. Pastinate with a short, stout cusp that has wide faces and encloses a deep cavity (Figure 5C, D). All the processes arise from costae about the cusp and have poorly developed denticulation. All processes are directed aborally. The denticles are flat, basally fused and sometimes reduced to a smooth ridge, discrete denticulation most commonly occurs on the lateral process. Longitudinal striae occur on the cusp between the costae and on proximal areas. White matter fills the cusp and the denticles, above a basal cavity that is deepest beneath the cusp, and extends beneath the processes as a deep groove.

When seen in transmitted light the junction of the basal body and crown tissue of Pb elements, is normally straight beneath both the 'posterior' process and the 'lateral' process (Figure 5D). In rare cases it has been possible to observe rounded basal pits beneath distal denticles of both the processes.

M element. Makellate in form, with short outer lateral process normally bearing one to three flattened triangular denticles (Figure 6A, B). The anterior process is adenticulate and short. Surface microstructures are restricted to ropy ornamentation on the cusp. White matter fills the cusp and denticles, and the element has a deep basal cavity.

In transmitted light the basal body can be seen projecting discrete basal pits beneath denticles of the 'lateral' process (Figure 7A).

S elements. The S elements are similar in morphology differing in the disposition of processes about the cusp (Figure 6C-F). Cusp is stout in all specimens and triangular in cross-section for the alate and tertiopedate specimens. Lateral processes bear one to three erect denticles sometimes flattened and partially fused. The posterior processes have two or three erect discrete denticles. The basal cavities develop beneath the cusp and extend as grooves beneath the processes. The cusp and the denticles have longitudinal ropy ornament and are occupied by white matter. Discrete, clearly defined individual basal pits are clear beneath denticles of the 'lateral' and 'posterior' processes (Figure 7B-D).

Historical review of the apparatus reconstruction of Icriodella.

Bergström and Sweet (1966) provided the first multielement reconstruction of Icriodella. They recognised that there were several distinctive elements, consistently associated with Icriodella platform elements, that were at that time assigned to other taxa. Bergström and Sweet's (1966, p. 338) diagnosis stated that the apparatus of Icriodella included elements previously classified as Sagittodontus and Rhynchognathodus and identified five form-species in a quinquimembrate apparatus that comprised Pa, Pb, M, Sa/Sb and Sc elements. The apparatus proposed by Klapper and Bergström (Robison, 1981, fig. 74. 1a-j, p. 125-6) was based on this reconstruction. They used plates that showed the aboral view of the Pa element (fig 1c, p. W126) with a wide flaring basal cavity that illustrates the early ontogenetic pastinate structure (discussed in Chapter 4.2). Cooper (1975, p. 1003) emended this diagnosis, when he provided the first reconstruction of a Silurian Icriodella, stating that the apparatus of Icriodella discreta Pollock et al. was built on the prioniodontid plan and included four different element types including icriodellid, sagittodontiform and rhynchognathodontiform elements. The M element identified by Cooper was in fact homologous with the Pb element designated for Icriodella superba and his Pb element homologous with the corresponding M position. McCracken and Barnes (1981) further refined this apparatus plan by recognising three different S element morphologies, Sa, Sb and Sc.

Because the Pa element of *Icriodella* is commonly over-represented in disjunct collections, it is possible that it occupied P_1 and P_2 positions within an apparatus template that was comparable to that of *Promissum pulchrum* (Aldridge *et al.* 1995; Aldridge, pers. com., 2000). Aldridge proposed that this would mean that the element that was identified as the Pb was actually a P_3 element. This hypothesis is problematic, as it relies heavily on the ratios of elements from a disjunct collection, which are notoriously unreliable (see Chapter 1.1 for full discussion).

Apparatus templates.

Evidence derived from sectioning of the basal body of *Icriodella* has revealed that the morphology of the Pa element of *Icriodella* is a pastinate element (see Chapter 4.2). This type of morphology suggests that the Pa element of *Icriodella* can be homologised with the P elements of other well known prioniodontids (for example *Baltoniodus*).

It is important to closely analyse the morphology of elements from disjunct collections to allow detailed element comparisons with specimens from natural assemblages. This provides a means to choose a template type that is likely to be the most appropriate and to recognise specific homologues within it. Where direct comparisons are not possible it is necessary to base the template choice on a hypothesis of relationship, and extrapolate from such a hypothesis. The two basic types of template known are that of the balognathid prioniodontid; *Promissum pulchrum* (Aldridge *et al.* 1995) and the simpler ozarkodinid template that appears to be common to all ozarkodinids and some prioniodontids (Purnell and Donoghue, 1997, 1998; Chapter 5) (Figures 2B, C). Given the pastinate structure of both the Pa and Pb elements and the full compliment of S and M elements associated with the apparatus of *lcriodella*, it is most appropriate to use the prioniodontid template represented by natural assemblages of *Promissum* (Aldridge *et al.*, 1995).

Elements of Icriodella compared with those of Promissum.

The Pa element of Icriodella. The internal morphology Pa elements of Icriodella is comparable to the P_1 element within the apparatus of Baltoniodus (Chapter 1.2, Figure 4), with the long axis comprising of the dorsal and ventral processes ('posterior' and 'lateral'). Although the P_1 of Baltoniodus does not have the same morphologically complex platform, the basal body reflects a comparable pastinate structure when observed in transmitted light. The P_1 element of Eoplacognathus also shares the pastinate structure and the smooth outline of the basal body beneath the processes. Because the Pa of Icriodella compares to the P_1 of both Baltoniodus and Eoplacognathus it is likely that it also occupied a P_1 position.

The Pb element of Icriodella. Within the apparatus of Promissum, the two caudal pairs of P elements, the P_1 and P_2 , appear to be morphologically identical (and may be serial homologues, see Chapter 1.1), whilst the P_3 and P_4 elements are morphologically differentiated. If the Pa element of Icriodella is homologous to the elements that occupied the P_1 and P_2 and positions of Promissum, there are two remaining P element positions are left unfilled: P_3 and P_4 . If the apparatus of Icriodella was closely homologous to the apparatus of Promissum then the Pb element of Icriodella must have been positioned in one of these locations. The processes of the Pb elements of the Silurian icriodellids bear fused denticles with relatively thick layers of lamellar crown. It is hypothesised that the prioniodontiform element of Baltoniodus is homologous to the element that occupies the P_3 position within the apparatus of Promissum (Chapter 1.1). The prioniodontiform (P₃) of Baltoniodus has several characters in common with the Pb of Icriodella

including the disposition of processes about the cusp and the form of basal body beneath the processes (compare Figures 5A, B and 5C, D). The basal body of P_3 elements of *Baltoniodus* is straight beneath both the dorsal ('posterior') and the caudal ('lateral') processes, directly comparable to the Pb element of *Icriodella*. It is considered here that the Pb element of *Icriodella* is homologous with the P_3 element of *Baltoniodus* and therefore may be homologous with the element that occupies the P_3 position within the apparatus of *Promissum*.

The S and M elements of *Icriodella*. Aldridge and Mohamed (1982, Pl. 1, figs 11-15) figured two types of elements that they thought possibly represented two morphotypes of an M element. However, suggested that both morphotypes did not consistently co-occur with the other elements of the apparatus and that it is likely that one was an element belonging to a distomodontid species. It is possible that the M elements are directly homologous to the M elements of *Promissum*.

The S elements of *Icriodella* can be matched with homologues within the S element array of *Promissum*, with the Sa occupying the S_0 position, the Sb occupying the S_1 and S_3 positions, and the Sc occupying the S_4 position. However, the elements associated with the apparatus of *Icriodella* provide no direct homologue for the quadriramate element that occupies the S_2 position in *Promissum*. It is therefore, possible that the quadriramate elements of *Promissum* are only present in balognathid type apparatuses.

Problems with the Promissum template.

There are several problems when trying to reconstruct the apparatus architecture of *lcriodella* using the *Promissum* template. Most important is the apparent lack of elements of *lcriodella* that could have filled the P_4 position.

The architecture and composition of the *Promissum* apparatus is well known (Aldridge *et al.*, 1995), however, it is possible that the apparatus is only typical of the balognathids (Purnell *et al.*, 2000). It is therefore unclear how widely typical the apparatus of *Promissum* is of the prioniodontids and it is possible that most prioniodontid taxa possessed apparatuses that were comparable to the simpler architecture of the ozarkodinids.

It is proposed in Chapter 1.1 that the P_3 and the P_4 elements of *Promissum* share a similar type of morphology. This suggests that apparatus of *Icriodella* may have possessed a complicated P element architecture and that the Pb element assigned to *Icriodella* occupied both the P_3 and the P_4 positions. This is also proposed as a possibility for other prioniodontid taxa (Chapters 2.1). It would only be possible to prove this, however, if a bedding plane assemblage of *Icriodella* was discovered; the idea is, therefore, currently speculative.

As discussed above it is difficult to be sure of the morphology of the element occupying the P₄ position within the Promissum apparatus. One possible insight is provided by the reconstruction of the apparatus of Pterospathodus (Chapter 3.1). Pterospathodus possesses three distinct P element morphotypes that have been incorporated into an apparatus plan based on the architecture of Promissum. The morphology and internal structures of the elements of Pterospathodus, designated P1 and P3, are comparable and probably homologous, to the Pa and Pb elements of Icriodella respectively. It is suggested that the third P element morphotype of Pterospathodus might represent an element that occupied a P_4 position. This is because of the acute angle between the ventral and caudal processes which are thought to be comparable to the two processes possessed by the P₄ element of *Promissum*. The basal body of this element in *Pterospathodus* has a distinct characteristic: small discrete basal cavity tips are present beneath denticles of the ventral and caudal processes (Figure 5E), similar to the basal body morphologies of S and M elements rather than P elements. It is possible that the element that normally occupied the P₄ position is in fact a ramiform type of element and that it did not commonly possess P element characteristics, such as a stout cusp and smooth basal body junctions at the basal body/lamellar crown boundary. This may account for the large number of prioniodontid taxa, known only from disjunct collections, that only appear to possess two P element morphotypes. No elements with these characters have been found associated with the apparatuses of *Icriodella*; this is either evidence showing that this position was unfilled, filled by an element that is indistinguishable from the Pb element, or that the P₄ element of Icriodella strongly resembled the ramiform elements, and has not as yet been distinguished.

Discussion.

A further complication in considering the apparatus of *Icriodella* is that it shows an apparent reduction of nonplatform elements among the younger taxa Silurian taxa, for example *I. inconstans* Aldridge. It is possible that the Silurian apparatuses of *Icriodella* possessed an apparatus architecture that lacked S and M elements, however, non-platform elements have been found in association with the platform elements of late Ordovician icriodellids. Such a sudden loss subsequently would require an unusually rapid evolutionary reduction, which Aldridge (pers. comm., 2000) considers unlikely.

It is possible that the proportional representation of element types is the result of hydrodynamic sorting (McGoff, 1991) or post-mortem processes (see Chapters 1.1 and 2.1 for discussion of disarticulated collections), especially as *Icriodella* is common in high-energy environments (Aldridge, 1976).

A third possibility (also considered for *Eoplacognathus* Chapter 2.1) is that the non-platform elements of *Icriodella* resemble those of another taxon so strongly that they are regularly mis-identified, leaving *Icriodella* with an apparent platform-only complex. The S and M elements of *I. deflecta* resemble their counterparts in the apparatus of *Distomodus kentuckyensis* Branson and Branson and it is possible that specimens of the two genera have sometimes been mis-assigned. Another consideration is that it may be unlikely that the general

morphology of the Pa element would retain its basic blade/platform structure, if the mechanism of the apparatus function changed so radically to allow loss of all the other elements. A discovery of collections rich in Pa elements of *Icriodella* without Pa elements of *Distomodus* could provide a solution.

It is difficult to be certain of the apparatus architecture of *Icriodella*. If the pastinate morphology of the P elements is considered the most convincing basis for the determination of architecture, then a reduced version of the *Promissum* template is suggested, lacking a quadriramate element (although the position may have been occupied by a simpler S element) and lacking a P_4 element.

In facing this problem, Klapper and Bergström (1981) and Fåhræus (1984) proposed different solutions. Klapper and Bergström considered that P elements were more reliable evolutionary indicators than ramiform elements and emphasised them in their classification, whereas Fåhræus chose ramiform element characters to demonstrate that taxa were not closely related erecting his classification. Testing of these different approaches requires the discovery of relevant bedding plane assemblages or the application of a thorough cladistic analysis in which all the characters are considered without *a priori* weighting.

Conclusion.

The evidence suggests that the apparatus of *Icriodella* possessed two types of P element, a pastinate element with a platform in the most caudal position (P_1/P_2) (possibly duplicated rostrally) and a pastinate element rostral to it (P₃), with both elements positioned with the concave 'posterior' face of the cusp directed dorsally. This would mean that the platform of *Icriodella* Pa elements would have been directed ventrally, in contrast to the platform elements of the ozarkodinids, which had their platforms directed dorsally. The S element array would have been positioned either beneath the P elements or in front of them rostrally, with their cusps directed dorsally and the paired M elements would have been rostral to these with their cusps inclined inwards.

An unfilled P_4 position in conjunction with only two pairs of P elements and a reduced number of S element morphotypes would mean that *Icriodella* possessed an apparatus that was not as complex as that of *Promissum*. This may mean that the apparatus of *Promissum* represents a derived apparatus plan typical only of the Balognathids and maybe other closely related genera. This suggests that the apparatus of the ozarkodinids may represent the most pleisiomorphic template and more derived apparatus plans are variants from this original plan.



Figure 1. Elements of *Icriodella discreta* x 100. R2 Roligheten. i. Oral view of Pa(P1) element, Specimen 277. ii. Lateral view of Pa(P1) element, Specimen 277. iii. Lateral view of Pb(P3) element, Specimen 278. iv. Lateral view of M element, Specimen 279. v-vi. Sa/b(S0/S1) element, Specimens 280 and 281 respectively.



Figure 2A Proposed phylogeny of *Icriodella* according to Sweet (1988, p. 65, fig. 5.17) showing the icrodellids surviving throughout the Silurian. B-C. Apparatus templates of prioniodontids and ozarkodinids. B. New terminology proposed for the apparatus of *Promissum pulchrum* following Purnell *et al.* (2000). C. New terminology for the ozarkodinid plan following Purnell *et al.* (2000).



Figure 3. Platform element of *Icriodella discreta* all specimens from Roligheten R2, A-B, D specimen 358. A. Oral view. B. View along 'lateral'(caudal) process with 'postero-lateral'(dorso-lateral) lobe in view. C. TL image of specimen 342, showing straight margin of basal body beneath 'posterior'(dorsal process) x 200. D. View of 'anterior' (ventral process) attached to cusp in the form of a costa, platform to the right and blade to the left. Biological terms (following Purnell *et al.*, 2000) included in brackets.



Figure 4. Outline of basal body of dextral platform element of *Icriodella discreta*. A. Outline of section showing orientation and position of basal body exposed when polished to just below the apex of the basal pit beneath the cusp. Specimen 301, Roligheten R2. B. Basal body of sinistral P1 element of *Baltoniodus*. Outline of section showing orientation and position of basal body when polished to the same level. Specimen 205. In both cases the 'anterior'/ventral process is weakly formed. Both elements show a similar type of symmetry, with the 'lateral'/caudal process projected at an angle of approximately 40 degrees from the 'anterior'/ventral process. Biological terms, following Purnell *et al.* (2000) are included in brackets in the diagrams.



Figure 5. Comparison of the Pb(P3) element of *Icriodella discreta* with the Pb(P3) elements of other prioniodontid taxa (all specimens of *Icriodella discreta* from Roligheten R2). A. Pb(P3) element of *Baltoniodus variabilis*, specimen 238. B. TL image of Pb(P3) element of *Baltoniodus variabilis*, specimen 18. x150. C. Pb(P3) element of *Icriodella discreta*, specimen 351. D. TL image of Pb(P3) element of *Icriodella discreta*, specimen 344. x200. E. Pc(P4?) element of *Pterospathodus amorphognathoides*, TL image of internal morphology basal body, showing basal pits beneath denticles of the 'posterior'/dorsal process, and the 'lateral'/caudal process. Specimen 320.



Figure 6. S and M elements of *Icriodella discreta*, all specimens from Roligheten R2. A-B. M element specimen 353. A. Lateral view. B. Concave margin of cusp. C-E Sa(So) element specimen 352. C. Lateral view. D. Concave margin of cusp. E. Detail of cusp showing costae and ropy surface microstructures. F. Sb(S1/2) element specimen 354. Lateral view.



Figure 7. Transmitted light images of S and M elements of *Icriodella discreta*, showing basal pits beneath denticles, proposed biological position (following Purnell *et al.*, 2000) supplied in brackets after conventional desigations, all specimens from Roligheten R2. A. M element, specimen 339. B. Sa/b(S0/1) element, specimen 348. C. Sa/b(S0/1) element, specimen 349. D. Sc(S3/4) element, specimen 346. All specimens x300.

CHAPTER 4.2

THE HISTOLOGY AND INTERNAL STRUCTURE OF THE PLATFORM ELEMENT OF *ICRIODELLA*.

Introduction.

The P_1 element of *Icriodella* has a platform and blade structure (Figure 1A-B). The narrow blade is constructed of denticles that are inclined away from the platform region of the element and the denticles that make up the platform are paired across the central groove of the structure, with a distinctive rounded morphology. The basal cavity is deep and narrow. In most specimens the surface microstructures are simple, limited to smooth unornamented surfaces on the platform nodes and fine ropy ornament on the cusp and areas immediately adjacent (Chapter 4.3). It is only in mature specimens that have experienced wear, that polygonal surface microstructures cover the tops of flattened platform nodes (see Chapter 4.4).

The internal microstructures of P_1 elements of *Icriodella* reveal much about element growth and help to refine the growth types introduced by Donoghue (1998). Sectioning has highlighted the internal record of the juvenile stages of ontogeny, revealing the basic structure of the element and the timing of process development.

Materials and methods.

Specimens of *Icriodella* have been examined from several collections that span the Ordovician/Silurian boundary; the specimens examined were collected by Professor R. J. Aldridge and are kept at the University of Leicester, Department of Geology. Specimens of *Icriodella deflecta* were from Gullet Quarry in the Malvern Hills (SO/761318) from the Telychian Wych Formation (10560 L28 II) (for further details see Aldridge, 1972); Specimens of *Icriodella discreta*, were from Roligheten (R2) Norway, near Oslo (NM 8490 3465), 264° from Vik town (for more details see Mohamed, 1983). *Icriodella deflecta* provided information regarding internal crystallite arrangement and the distribution of white matter when sectioned. The collections examined were chosen because they have been exposed to little thermal alteration and it was hoped that the internal structures would be preserved. The surface preservation, however, is poor and subject to recrystallisation.

Studies of the morphology of the basal body have been facilitated by artificially fracturing parts of the element, and etching the broken surfaces with 0.5% orthophosphoric acid solution and examining the specimens in the SEM.

Sectioning techniques followed methods refined by Donoghue (1998). Most of the specimens proved to be so recrystallised that internal information was obliterated, and it was not possible to produce a large number of successful sections. However, though limited, the results reveal some details of the crystallite structures and internal distribution of tissues types (for section orientations, consult Chapter 2.2, Figures 1C-E).

The internal structures.

Crystallites. The crystallites range between 2μ m and 5μ m along the c-axes (Figure 2A). Each crystallite is elongate and straight, broadening slightly towards the growing surface of the element (Figure 2A, C). Horizontal sections, perpendicular to the c-axes of crystallites, show irregular margins; the crystallites are approximately 2-4 μ m in diameter (Figure 2B). Crystallites are longest towards the apex of the individual growth axes of the denticles and shorter around the flanks of each axis (Figure 2C). Within the blade, the crystallites are orientated roughly parallel to the long axes of the denticles (Figure 2D); within the platform; however, the crystallite pattern is very sinuous (Figure 2E). Longitudinal sections through the distal portion of the platform reveal that the crystallites are orientated subparallel to the base of the element before becoming gradually more upright and then parallel to the long axes of more mature platform denticles (Figure 2C, E). This crystallite orientation is also seen in horizontal sections, where concentric rings of lamellae can be seen, composed of crystallites that are orientated perpendicular to the plane of section (Figure 2F). Within longitudinal sections, the outer tissue at the aboral base of the platform is composed of crystallites that have their long (c) axes orientated perpendicular or oblique to the section (Figure 3E, F).

Lamellae. Horizontal and longitudinal sections have revealed laminations in both the platform and blade regions of the element (Figure 2C, D). The lamination widths vary between 2-5 μ m thick. The boundaries of the lamellae are formed by the aligned ends of the crystallites and there is a narrow gap between each lamination (Figure 2A).

Longitudinal sections through the blade reveal lamellae that have formed the individual denticles (Figure 3A). The lamellae at the base of the denticle in Figure 3A are composed of crystallites that are all perpendicular to the long axis of the denticle. There is a slight flaring of crystallites at the edges of the base of the prismatic structure.

Longitudinal sections through the platform reveal a more complicated arrangement of lamellae (Figure 2E). The lamellae within the flanks of the denticles are composed of crystallites that have their long (c) axes orientated parallel/oblique to the lamellar surface and those towards the centre contain crystallites with their long (c) axes perpendicular to the lamellar surface (Figure 3B). The first few denticles of the platform, adjacent to the cusp, originate as an evagination that is above the basal body (Figure 3B). The initial increments of subsequent platform denticles are constructed of lamellae that are formed near the base of the most recently formed denticle (Figure 2E, 3C). Successive denticles are initially orientated with their long

axes parallel to the basal body/lamellar crown boundary (Figure 3C), before becoming more perpendicular, in relation to the basal body/lamellar crown boundary, with the addition of successive growth increments. This form of growth becomes magnified with distance from the cusp, until the initiating evaginations of each denticle form from the flanks of the lamellae of more mature denticles and are no longer open to the basal cavity. The crystallites within these lamellae have varied orientations. Towards the base of the platform, the crystallites are parallel to the basal body/lamellar crown boundary, and as the lamellae curve round to form the upright denticle, the crystallites become reorientated to become roughly parallel to the long axis of the denticle (Figure 3C).

Horizontal sections of platform denticles show that the crystallites are perpendicular or oblique to this orientation, and gradually flare outwards in the marginal lamellae, with the oral tip of each crystallite being slightly inclined towards the outer surface (Figure 3D). Several of the concentric lamellae seen in horizontal sections are separated by abnormally wide gaps (Figure 3D). It is difficult to determine if there is any regularity about the occurrence of these wide gaps.

White matter. White matter only occurs within the blades of the elements and appears to be poorly formed (Figure 2D, 3A) in specimens where structural resolution was achieved. There is no evidence of white matter that has formed within the platform denticles. White matter was first formed at the base of each denticle as a small inverted point, the core became wider as the denticle increases in dimension; the boundaries of the cores are diffuse (Figure 4B, C).

White matter occurs as a dense tissue, concentrated towards the central cores of the denticles (Figure 3A). The base of each white matter core is above a clearly defined evagination formed by a lamella (Figure 2D, 3A). The sides of the areas of white matter are parallel with the orientation of the long (c) axes of the bordering crystallites (Figure 4A). The boundaries of the white matter areas grade into the surrounding lamellar crown and only become sharp towards the base of the denticle (Figure 4A, C). In Specimen 329 (Figure 2D) the distribution of white matter is alternated with more hyaline tissues; dense at the base and then alternating dense and hyaline towards the apex of the denticle. There are approximately three dense areas of white matter visible in Figure 2D.

There are two kinds of structure present within the white matter tissue, cavities and tubules. Most common are subcircular cavities, which occur in two size distributions. The whole tissue is perforated by common, evenly spaced subcircular cavities approximately 0.25-0.75µm in diameter (Figure 4C). Less common are larger subcircular cavities that range between 1.0-4.0µm in diameter (Figure 4D). Tubules are rare in the sections prepared, and difficult to identify, as the adjacent lamellar crown tissue has similar longitudinal gaps between individual crystallites (Figure 4C). Examples seen in Figure 4D show tubules that have a calibre of approximately 0.5µm and length of approximately 4.0µm. The crystallites adjacent to the white matter have irregular boundaries and are sometimes perforated by small subcircular cavities (Figure 4E). None of the specimens revealed any trace of laminations, however it is possible that they would become apparent with more sectioning success. It is likely that the specimens have been subject to etching during processing, which has obscured some of the primary ultra structure.

Basal body. The basal body occupies a deep cavity along two thirds of the platform, and approximately two-thirds of the blade (Figure 1C). The distal regions of both these processes extend beyond the tip of the basal body and are clearly composed of lamellae that are closed around the base (Figure 1C). Horizontal sections have revealed a basal body that has three clear projections (Figure 5A, B). It is possible to see the main basal pit within the cusp in some specimens when viewed in transmitted light (there is too much depth of field to allow successful photography). In the figure (Figure 5A) it is clear that the blade (the dorsal process) is represented by a basal body projection, as is the platform (the caudal process). The third projection is expressed by a basal cavity peak in section and orally as a costa and sometimes a projection, half way along the element (Figures 1A-C; 5A). In transmitted light there is a straight junction between the basal body and the lamellar crown of the blade and it has not been possible to identify any individual basal cavity tips beneath the denticles within the specimens studied (Figure 5D).

Artificially fractured platforms reveal that the basal body has simple flaring morphology with a single apex that is between the two divided rows of denticles (Figure 5C).

Interpretation.

Hyaline tissues. The long (c) axes of the crystallites within the denticles of platform elements of *lcriodella* are all broadly parallel to the long axes of the denticles and the surfaces of the element. The only place where this general orientation is complicated is within the distal regions of the platforms where the crystallite orientations are varied.

Figure 3E shows the outside flanks of a platform. The crystallites can be seen within the core of the denticle to be slightly oblique, but generally parallel to the long axis of the denticle. Towards the base of the denticles the orientation of the crystallites changes by almost 90° and the crystallites have their long (c) axes orientated perpendicular to the section (Figure 3F). This is because externally the base of the platform is undercut (Figure 5C), and to expand the width of the platform node, the crystallite orientation mirrors this morphology.

The arrangement of lamellae and crystallites indicates that the growth of the hyaline tissue is controlled by growth prisms (as discussed in detail in Chapters 1.2, 2.2). The crystallites within the denticles of the blade and the platform can be seen to be vertical within the central core and slightly flared towards the margins (Figure 2D, 3B). Each crystallite within the marginal lamellae has its base slightly inclined towards the core of the denticle and its oral tip inclined towards the outer surface. This produces a crystallite fabric that forms a fan of crystallites, each fan forming a growth prism directly comparable to the growth prisms identified by

Donoghue (1998) and figured in Chapter 1.2, fig. 7E. Donoghue (1998, p. 641) stated that "the more extreme variations of crystallite arrangement, such as sub parallel to growth lines, are less prevalent [in multidenticulate elements] than in coniform elements". However, in the case of *Icriodella* the growth prisms within the platform appear to have a strong influence on crystallite orientation, causing gentle flaring and preventing the crystallites from being truly perpendicular to lamellar surfaces except at the apices of the prisms (Figure 3A, B).

Sections that reveal lamellae are rare, as in most sections lamellae and crystallites are oblique to the plane of section. To reveal distinct incremental lines, sections have to cut denticles directly through the centre of the growth axis and core of the denticle, thereby revealing lamellae that are perpendicular to the plane of section. Within the platform, the largest crystallites are concentrated towards the centre of each growth prism, within regions of the lamellae that are directed orally (Figures 3A, B). This suggests that the centre of the growth prism grew the fastest and in the case of *lcriodella* increased the height of the denticles more rapidly than the width of the denticle flanks, forming an orally expanding growth axis. Growth prisms within the platform show a greater amount of elaboration, each with a contorted curved axis. Areas between prisms within the platform appear to be aprismatic and lacking in structure (Figure 2C).

The orientation of the long (c) axes of the crystallites within the denticles of the blade are very straight, and parallel, only subtly fanning away from each other at the base. This shows that the growth prisms of the blade are straight and narrow and represent a significant oral expansion, and not lateral. The white matter within the denticles of the blade reflects this structure with straight lateral boundaries controlled by the morphology of the growth prisms (Figures 2D).

All of the growth prisms have their bases deflected back towards the more mature regions of the element (Figures 2C, E, 3A). The deflection of the lower parts of the prisms is more pronounced within the distal parts of the platform and the blade, where laminations are closed around their distal tips and white matter is rarely formed (Figure 2E). This suggests that there is a relationship between the position of the basal body, the propagation of new crown tissue and the deposition of white matter that controls how and where new populations of secretory cells can develop to initiate a new growth prism/denticle during phases of growth.

The incremental lines and elongate apatite crystallites indicate that the hyaline tissues described above share close similarities with enamel tissues found in vertebrates (see chapters 1.2, 1.3 for full discussion). Hyaline tissue of *Icriodella* is also closely comparable to the hyaline conodont tissue described by Zhang *et al.*, (1997), Donoghue (1998) and Donoghue and Chauffe (1998). All of these tissues have been compared to vertebrate enamel.

White matter. Denticles that develop white matter are restricted to the blade of the element. It is possible that this restriction of white matter secretion is controlled by the ultrastructure of the growth prisms within. The growth prisms of the blade are simple straight structures and the white matter forms directly above the

basal body, forming white matter cores that are orientated roughly perpendicular to the basal body/lamellar crown boundary.

The crystallites within the growth prisms of the blade are closely packed and evenly spaced. This is also the case in P elements of *Eoplacognathus* and *Baltoniodus* (see chapters 1.2, 2.2). The growth prisms within the platform are generally contorted and the majority of prisms are not above the initial lamellae evaginations at the base; the lamellae within the denticles are wide and the crystallites well spaced. It is possible that the mechanism for depositing the contorted prisms of the platform is not suitable for the deposition of white matter or prevent the formation of white matter secreting cells.

The white matter of *lcriodella* elements is poorly formed and commonly has a longitudinal fabric distributed throughout the tissue. Where the white matter tissue is very dispersed it appears to be intermittent, incorporating elongate crystallites that have an irregular boundary and are sometimes perforated by subcircular cavities. This suggests that the white matter in the blade of *lcriodella* is constructed from densely packed, large plate like crystallites that are not comparable to the white matter structures found in elements of *Baltoniodus* (Chapter 1.2), *Eoplacognathus* (Chapter 2.2) and *Pterospathodus* (Chapter 3.2). This may suggest that it is more compatible with tissues described by Donoghue (1998) which he claimed did not represent true white matter. However, the intergradation of the two tissue types indicates that they were both deposited by the same secretory process.

It is possible that the distribution of white matter does in some way reflect some sort of intermittent secretory stages paralleling the periodic growth patterns discussed below (Zhang *et al.*, 1997). The intergrading of white matter structures with the adjacent hyaline crystallites indicates that white matter was secreted in concert with the lamellar crown tissue (a hypothesis discussed in Chapter 1.2). Donoghue *et al.* (2000) concluded that the white matter, although probably secreted by the same cells as the hyaline crown which has been compared to enamel (see above), represented a tissue unique to conodonts; the structures found within the tissues of *Icriodella* appear to support this hypothesis.

Basal body. Sectioning of the basal body tissues of icriodellid specimens has provided no ultrastructural or compositional resolution. The signal for enamel secretion is known to be reliant on the presence of a mineralised surface, typically dentine (Smith, 1992), therefore, the presence of a dentine tissue is tentatively inferred due to the structure and composition of the overlying tissue that has been interpreted as enamel. Verification of this suggestion awaits the preparation of more successful sections.

Growth discontinuities within hyaline tissues.

A horizontal section through the platform of *Icriodella* (Specimen 301, Figure 3D) shows clear resolution of the lamellae. The lamellae appear to be grouped into four sets. There are approximately three or four individual growth increments within the central sets and then a final group, forming the most recent

increments, that number in excess of forty increments. It is difficult to be accurate with this estimation as the lamellae are narrow and numerous.

Few discussions have addressed the presence of distinct horizons within the lamellae of conodont elements. Hass (1941) interpreted growth discontinuities as evidence of accidental damage followed by the regeneration of new crown tissue. Rhodes (1954) proposed that discontinuities within the lamellar crown represented abnormal deformation during growth. Müller and Nogami (1971) identified horizons within conodont elements that they identified as evidence of resorption. Müller and Nagomi (1971) identified up to four resorption surfaces that alternated with regeneration and suggested that the events served a specific purpose during the life of the conodont.

Donoghue and Purnell (1999b) discounted accidental damage (Hass, 1941) as the cause for growth discontinuities, because of the recurrent distribution of the discontinuities. They also discounted abnormal deformation, because of the undistorted regeneration of the crown tissue, which suggested that the mineral-secreting organ was completely undamaged. The possibility of resorption was refuted because of the absence of irregular pitted surfaces that characterise resorption surfaces in vertebrate teeth. Donoghue and Purnell (1999b) pointed out that the distribution of the horizons was unlikely to represent resorption events as these would be expected to affect the whole surface of the element, not discrete areas.

Zhang et al. (1997) pointed out that the zones of postulated resorption seen in the specimens examined by Müller (1981, p. W34-W36, figs. 27-30) did not coincide with periods of regeneration. This meant that it was possible that lamellae were truncated when the element was not regenerating new crown tissue and that regeneration occurred during a separate phase. It was also noted that the specimens had different numbers of lamellae between each postulated horizon, within different regions of the element. More significant than this is that all specimens figured show a constant reduction of lamellae across the oral surfaces of elements, in comparison with the number of lamellae down the flanks of elements, as pointed out by Müller and Nogami themselves (1971). Work by Purnell (1995) and Donoghue and Purnell (1999b) has identified regions of elements that are subject to damage and wear that coincide with these postulated resorption surfaces. This suggests that most of the 'resorption' surfaces are, in fact, evidence of wear, highlighting where the element has had to regenerate and repair lost crown tissue.

Donoghue and Purnell (1999b) provided their discussion of growth discontinuities to support their argument that the observed discontinuities represented prolonged periods of everyday wear during the function of the element. These horizons not only represent truncation of crown tissues, but also mark the beginning of phases of regeneration and repair.

Zhang *et al.* (1997) thought that the features that appeared in the Müller and Nogami (1971) specimens were not comparable to the structures that they described in elements of *Parapachycladina peculiaris* Zhang (Zhang *et al.*, 1997, p. 69). In *P. peculiaris* the aboral surfaces display a "central pit surrounded by a scar-like

recessive area, where the edge of each lamella did not extend as far basally as its predecessor". In this area the lamellae are separated from each other by an interlamellar space, groups into sets of lamellae are further divided into sets separated by markedly larger interlamellar spaces.

Zhang *et al.* (1997) proposed that because there was convincing evidence that linked conodonts with primitive vertebrates, it was appropriate to consider the skeletal structures of other vertebrate groups in a search for comparable episodic growth patterns. They concluded, however, that the periodic growth of fish skeletons that express the seasonal spawning cycle, and cyclic deposition observed in vertebrate enamel, scales, dentine and cementum of various vertebrate groups were impossible to identify as comparable to the conodont structures, because conodonts are so distantly related.

It is probable that conodont elements were permanent and not shed (Donoghue, 1998), (contra Carls, 1977), so the internal structure of conodont elements provides a record of growth and function throughout the life of the conodont. Zhang *et al.* (1997), therefore, concluded that the lamellar pattern represented either episodic growth over days, weeks, or months throughout the conodont's life, similar to the process envisaged in Bengtson's (1976) growth theory. Bengtson (1976) proposed that the termination of each individual lamella represented the interruption of element growth as the element was everted from the phosphatic secreting epithelial pocket. Zhang *et al.* (1997) proposed that instead of the individual lamellae representing repeated evertion of the element, individual lamellae represented daily increments during much longer phases of growth.

It is possible that the broader divisions either reflect the termination of these longer phases of growth, or broader environmental effects such as phosphate solubility in water as suggested by Müller and Nogami (1971). Not all regions of the element will have the phases of growth highlighted by function causing the lamellae to be truncated. Where the element was not damaged the next phase of growth would directly overlie previous undamaged lamellae, with only a small gap, and no truncated surfaces.

The specimens described by Zhang *et al.* (1997) appear to show directly comparable lamellar distribution to that observed within denticles of *Icriodella* platforms. The specimen studied here (Figure 3D, specimen 301) shows four major groups of lamellae, with the first three evenly sized and the last being much larger. The divisions between the groups are not highlighted by lamellar truncations as in the Müller and Nogami (1971) specimens, but by large interlamellar spaces as in the specimens considered by Zhang *et al.* (1997). It is possible that the growth discontinuities are apparent in sections of *Icriodella* because the platform region of the element does not develop white matter, therefore leaving the original structure preserved. It is more common in prioniodontids for all of the denticles of the platform elements to develop white matter. Interestingly there appear to be three main concentrations of dense white matter tissue seen in specimen 329 (Figure 2D). There is possibly some kind of relationship between the pattern of white matter secretion and the postulated growth discontinuities apparent in the platform of the element, reflecting some kind of periodicity

Growth of the element.

Externally the basal body of *Icriodella* has a similar structure to the basal bodies of P elements of *Baltoniodus*, where the ventral process is often only represented by an adenticulate costa (see chapter 1.1); however, in the case of *Icriodella* there is often no external expression. The dorsal process is represented by the blade of the element and the caudal process is represented by the platform. Horizontal sections of the platform element of *Icriodella* reveal a distinctive basal body morphology. The structure of the basal body clearly shows that the element was pastinate and that only two processes are strongly expressed. Comparing this morphology to other prioniodontid basal bodies indicates that the unexpressed process may represent a ventral process. The internal structure of platform elements of *Icriodella* reveals an important similarity to early prioniodontid taxa (Chapters 1.2, 2.2, 3.2). Although the P elements of different prioniodontids display a variety of the different morphologies it appears that they retain the same basic pastinate internal structure during the earliest stages of ontogeny.

Donoghue (1998, p. 654, Fig. 13a-c) figured a sectioned etched platform of *Cavusgnathus* that also possesses a platform with paired platform ridges. The sectioned element revealed that the platform of *Cavusgnathus* originally possessed a blade like morphology with a single growth prism. After fewer than ten lamellae, the growth axis bifurcated and formed two individual growth prisms. Donoghue (1998) thought that the ontogenetic bifurcation of denticles appeared to be the main means of generating platforms of taxa that possessed type A platforms. Figure 5C of *Icriodella*, shows a single apex to the basal body. The basal body occupies more than half the height of the element. It is possible that elements of *Icriodella* generated platforms with a bifurcating growth axis, but juvenile specimens show that the nodes of the platforms are slightly offset. This suggests that the platforms have a blade like structure, with each denticle growing from an evagination of lamellae formed next to the previous denticle, but that each denticle is strongly offset, resulting in a broad platform.

Donoghue (1998) described three main types of morphogenetic processes that produced P elements and suggested that most P elements were essentially modified type III ramiforms. Type III ramiforms were produced by marginal accretion of individual denticles, forming a compound structure with an undifferentiated denticulation pattern. This is clearly seen in Figure 3C.

Donoghue (1998, p. 652, figs 11d-g) also figured an artificially fractured and etched platform element of *lcriodella inconstans* Aldridge, this study has revealed comparable structures that are seen in Figure 3B. The specimen figured by Donoghue (1998) differs from Figure 3B because the upper regions of the growth prisms are absent. It is likely that these truncations are the result of element function and loss of the upper surface of the platform denticles (Chapter 4.4).

Figure 3C shows a more distal region of the platform that does not have evaginations that are open to the basal cavity, indicating that the growth mechanism is more complex than that categorised by Donoghue (1998) and shows that the mechanism of growth varied along the length of the platform. The crystallite arrangement is also subtly different. It is not known if this is a taxonomic difference, or a contrast produced by preservation or positioning of the section.



Figure 1. Platform element of *Icriodella discreta*. A-B specimen 327 Gullet L28, x 200. Oral view. B. Lateral view showing unexpressed 'anterior' (ventral) process. C. Aboral view showing outline of basal cavity. Specimen 393 Roligheten R2, x400.



Figure 2. Crystallites within platform elements of *Icriodella*. A. Crystallites within longitudinal section of blade. Specimen 329 *I. deflecta* Gullett L28 II. B. Crystallites within horizontal section of core of denticle within platform showing crystallites that have been sectioned perpendicular to their long (c) axes. Specimen 301 *I. discreta* Roligheten R2. C. Crystallites within longitudinal section of platform showing the distribution of crystallite sizes, the longest crystallites occurring towards the centre of each growth axis. Specimen 149 *I. discreta* Roligheten R2. D. Crystallites within longitudinal section of blade and white matter core of denticle showing general fabric of the crystallites. Specimen 329 *I. deflecta* Gullett L28 II. E. Crystallites within longitudinal section of platform showing sinuous axes of growth prisms. Specimen 149 *I. discreta* Roligheten R2. F. Horizontal section through platform, crystallites are orientated perpendicular to the plane of section. Specimen 301 *I. discreta* Roligheten R2.



Figure 3. Lamellar structures and crystallite arrangement within platform elements of *lcriodella*. A. Lamellae and flaring crystallites at base of denticle within longitudinal section of blade. Specimen 329 *I. deflecta* Gullett L28 II. B-C. Arrangement of lamellae within longitudinal section of platform showing contorted growth prisms and varied crystallite sizes. Specimen 149, C x700 *I. discreta* Roligheten R2. D. Horizontal section showing gradual grading of crystallite orientation becoming more inclined towards the outer surface with distance from denticle core, also shows grouping of lamellae. Specimen 301 *I. discreta* Roligheten R2. E-F. Specimen 329 *I. deflecta* Gullett L28 II. Longitudinal section showing crystallite orientations within the outer flanks of a platform denticle. F. Close-up of base of denticle.



Figure 4. White matter and internal structures of platform element, longitudinal section through blade. *Icriodella deflecta*, Specimen 329 A, C-F Gullett L28 II. A. Flanks of white matter aligned with orientation of adjacent crystallites. B. White matter viewed with transmitted light. *Icriodella discreta*, Specimen 337 Roligheten R2, x200um. C. Profuse small subcircular cavities within the oral regions of the white matter tissue, note graded boundary between white matter and crown tissue. D. Larger cavities and possible tubules in most concentrated in aboral region of white matter tissue. E. Crystallites immediately adjacent to white matter core, scale bar 230um.





Figure 5. Basal body of platform element of *Icriodella discreta*. A. Outline of section figured in B. showing orientation and position of basal body exposed. B. Specimen 301, R2 Roligheten. Basal body, sectioned horizontally just below apex of basal pit within cusp. C. Specimen 335, R2 Roligheten. Artificially broken and etched platform showing single apex of basal body. D. TL image of blade showing prismatic arrangement of crystallites within denticles and straight boundary at junction of basal body and crown tissue. x300um. Specimen 336, R2 Roligheten.
CHAPTER 4.3

THE PRIMARY SURFACE MICROSTRUCTURES OF PLATFORM ELEMENT OF ICRIODELLA

Introduction.

In Chapter 4.2, it was noted that the crystallites within platform elements of *Icriodella* are arranged with their c-axes orientated parallel to the maximum growth axis. Crystallites of expanded platform edges are thus orientated with their c axes perpendicular to the surface and those within the cusps and denticles are orientated with their c-axes parallel or oblique to the outer surface. If a strong relationship between the surface microstructures and the internal crystallite structures can be shown it is also possible that the ornamentation of the element surface can be used to identify the internal structures without sectioning and polishing elements. Additionally, it is important to understand the precise distribution and nature of the primary ornamentation of different elements if functional analyses are to be successful, as it is necessary to be able to differentiate between primary ornamentation and secondary surface microwear.

Materials and methods.

Specimens of *Icriodella* have been examined from several collections that span the Ordovician/Silurian boundary; the specimens examined were collected by Professor R. J. Aldridge and are kept at the University of Leicester, Department of Geology. Specimens of *Icriodella discreta*, were from Roligheten (R2) Norway, near Oslo (NM 8490 3465), 264° from Vik town (for more details see Mohamed, 1983). All the elements show some degree of thermal maturation and as a consequence are not translucent. This does not appear to have strongly affected the preservation of surface microstructures, which have been examined by mounting the elements on stubs, coating in silver and using a scanning electron microscope.

Description.

Three basic surface textures occur on the surface of the platform element of *lcriodella*: ropy, polygonal and smooth. Ropy surface microstructures are restricted to the cusp, (Figures 1A-E) although it is common to see specimens that appear to have no ornamentation on the cusp at all. In such cases there appears to be a smooth surface, with a faint longitudinal fabric aligned with the long axis of the cusp. Where well formed it is clear that the dimensions of the ropes are reduced with distance from the cusp tip (Figures 1A-E). The width of the ropes at the tip of the cusp is approximately 1-2 μ m and they are approximately 20 μ m long (although it is difficult to be sure of this dimension because the ropes are generally very faint) (Figure 1B). At the base of the cusp, the ropes are densely packed and have diminished dimensions of not more than 1 μ m

across (Figure 1E). The ropes do not extend onto the denticles of the platform or the blade and have not been observed preserved at the denticle tips (Figure 1D, E).

Polygonal surface microstructures are restricted to the larger (length in excess of 500 μ m) elements where the platforms possess denticles that have broad flattened tips (Figures 2A, B). The occurrence of this ornamentation is rare and has only been observed on a few specimens. The flattened surface of each denticle is evenly covered by polygons when rounded, or unevenly covered if the denticle is misshapen. Specimen 900 (Figure 2F) shows a denticle that has a concave facet which is bounded by a ridge, covered with polygonal ornamentation; the polygons are approximately 2 to 3μ m across. Specimen 327 (Figure 2A) shows a rounded denticle which is covered with undisrupted polygonal ornamentation, which fades around the edges. The polygons are approximately 5μ m across. The polygons are clearly hexagonal with edges of adjacent polygons meeting at angles of approximately 120°. The denticles at the distal tip of the platform commonly have less surface area covered by polygonal ornamentation (compare Figure 2C, D).

The third type of surface texture lacks any sort of structure and is simply smooth. All of the platform, apart from the flattened upper surfaces of some denticles, bears no ornamentation and possesses a smooth surface (Figure 2D). This type of surface texture also dominates the blade of the element (Figure 1D), except for the cusp and immediate proximal areas. There is a faint longitudinal texture that is aligned with the long axes of the denticles. Crystallites beneath these smooth surfaces are orientated parallel with the surface of the element as seen in Chapter 4.2; Figures 2D and 3E, F.

Interpretation.

The distribution of ropy ornament appears to be comparable with that evident on the P_1 element of *Eoplacognathus* (Chapter 2.3) and it is likely that the interpretation discussed in Chapter 2.3 may account for the formation of this ornamentation. The ropy ornament of *Eoplacognathus* is concurrent with the internal crystallites being orientated with their c axes parallel with the long axis of the cusp. There is evidence that the crystallites within the cusp of *Icriodella* are also orientated this way (see Chapter 4.2). However, the ropes of *Icriodella* also show some similarity to the ornamentation of elements of *Baltoniodus* but are not as broad or closely packed (Chapter 1.3) and not so pronounced, or continuous. The diminishing dimensions of ropes ornamenting the cusp possibly indicate a reduction in crystallite sizes or maybe a reduction of secretory cell size, although testing this interpretation awaits greater resolution in thin section and knowledge of internal tissue structure.

It is likely that the polygonal ornamentation represents the imprints of epithelial cells as suggested by Pierce and Langenheim (1970), Conway Morris and Harper (1988) and Burnett (1988). The outlines of the polygons are directly compared to the surface microstructures found in enamel, as discussed and interpreted in Chapter 2.3. Elements of *Icriodella* functioned by occlusion of the platform nodes, which would have eroded any soft

tissue that remained over the element surface following a growth stage (Chapter 4.4). Therefore, polygonal ornamentation over platform nodes indicates that this area could not have been permanently covered in soft tissue. It is more likely that the imprints represent periodic covering during growth phases, which is then worn away during functional phases. Donoghue (1998) presented a modification of Bengtson's (1976) growth theory where elements periodically sunk beneath the soft tissue, or the dermis gradually grew over elements to facilitate extended phases of growth and repair, during which the element was functionally inactive. It is possible that elements of *Icriodella* regenerated new hard tissues in this way, gradually wearing off surface microstructures once the element became functionally active.

The polygons found on platform elements of *Icriodella* are also closely comparable to polygons found on P elements of other prioniodontid taxa, particularly the denticles of *Pterospathodus*. In *Pterospathodus* it is only the flattened and rounded denticles that develop polygonal ornamentation (Chapter 3.3), which is directly comparable to the polygonal ornamentation of *Icriodella* platform elements.

Burnett and Hall (1992) stated that crystallites beneath polygonal ornamentation are orientated with their c axes perpendicular to oral surfaces and parallel with the main growth axis as I have observed in elements of *Eoplacognathus* (Chapter 2.3) and *Pterospathodus* (Chapter 3.3). The denticles of *Icriodella* elements, closest to the cusp, normally have larger regions covered by polygonal surface microstructures, this suggests that regions closest to the cusp were more subject to wear during functional phases than the more distal regions (see Chapter 4.4). Denticles that were levelled until the outer surface was perpendicular to the long axis of the denticle and perpendicular to the growth axis (Chapter 4.4) would be regenerated with lamellae layered perpendicular to the main growth axis across the damaged surface. The crystallites of undamaged platform denticles of *Icriodella* are normally orientated parallel or oblique to the long axes of the denticles. The regeneration of damaged denticles would result in lamellae composed of crystallites that are still be orientated parallel with the main axis of growth, but perpendicular to the outer surface, resulting in the formation of polygonal surface microstructures.

It has not been possible to prepare sections of *Icriodella* that have polished the surface immediately beneath the polygonal structures of the platform denticles; however, it is suggested that these flattened areas are a result of function and subsequent repair (see Chapter 4.4) the crystallites within would be orientated perpendicular to the lamellar surface.

Platform elements of *Icriodella* clearly illustrate that there is no relationship between the deposition of white matter and the formation of polygonal surface microstructures, as suggested by Von Bitter and Norby (1994b). White matter only occurs within the blade of the element (Chapter 4.2) and this is the region that lacks polygonal ornamentation in contrast to the platform, which contains no white matter (Chapter 4.2) and has clearly formed surface polygons.

It is difficult to ascertain whether that the smooth denticle surfaces represent worn areas that have lost original primary ornamentation or lack of levels of preservation that preserve any original ornamentation. There is, however, no evidence to suggest that the surfaces are recrystallised and this may suggest that the smoothness is primary. Beneath these surfaces, the crystallites are orientated with their c axes parallel to the main growth axis (parallel with the long axis of the denticle, Chapter 4.2), and it is difficult to explain why the surface expression differs from the flanks of the cusp. It is possibly the result of a difference in crystallite sizes, with the crystallites beneath the smooth surfaces being smaller than those within the cusp, or of a subtle difference in crystallite orientation. The outer layer of enamel possesses no internal or external structure, due to the loss of tomes' processes during the resorption of proteins and waters from the newly deposited enamel tissues in the final stages of enamel maturation (Boyde, 1976) (see Chapter 1.2). It is an interesting coincidence that the elements examined from this collection frequently have a smooth outer layer; however, it has not been possible to reveal the structure of tissues immediately beneath these layers to ascertain any internal structures.

Burnett and Hall (1992) suggested that an organic layer represented the final phase of each mineralisation stage and would also be represented internally between each growth increment. This has not been observed in sections of *Icriodella*, and is not reconcilable with developmental homologue suggested between hyaline tissues and enamel. Clarification of these speculations will require sections with good resolution of crystallite morphology and structure within the growth prism and a more detailed knowledge of the secretory organ of conodont elements.



Figure 1. Ropy surface microstructures and surface detail on platform elements of *lcriodella discreta*, Roligheten R2. A-E specimen 327. A. Cusp of sinistral element showing concentration of ropy ornament. B. Tip of cusp seen in A, showing coarsest ropes, and possible outer organic layer. C, E. Diminishing dimensions of ropy ornament on cusp seen at mid height (C) and at the base (E). D. Denticles of blade, lacking ropy ornament. F. Possible layering evident in lobe expansion of blade of sinistral element, specimen 358.



Figure 2. Surface microstructures on platform element of *Icriodella discreta*. Roligheten R2. A-B Specimen 327. A. Polygonal ornamentation on denticles proximal to cusp. B. Close-up of A. B-F Specimen 900. B. Distribution of polygonal microstructures on platform area close to cusp. C. Distribution of polygonal structures on distal portion of platform. E. Denticles proximal to cusp showing apparent wear facets. F. Close-up of distribution of polygonal ornament on denticle exhibiting possible wear.

CHAPTER 4.4

THE FUNCTION OF THE PLATFORM ELEMENT OF ICRIODELLA

Introduction.

Functional analyses rely on an understanding of conodont apparatus architecture and the orientation of elements within. This provides the basis of a model that, in conjunction with morphological studies, can be used to predict where microwear would be most likely to occur on opposing elements. In the case of the ozarkodinids, numerous bedding plane assemblages have provided extensive knowledge of element orientations and their physical juxtaposition (Purnell and Donoghue, 1998). Assemblages have shown that the P_1 elements are positioned with the concave margin of the cusp directed dorsally, paired across the mid axis of the apparatus and that they occluded with the left element behind the right at the caudal end of the oral cavity (Purnell, 1995). It has also been possible to dissect pairs of elements from a single apparatus, thereby studying specimens that provide indisputable evidence of the nature of occlusion (Donoghue and Purnell, 1999a, 1999b).

Prioniodontids are poorly represented by bedding plane assemblages. There are only two genera known to be preserved with their apparatuses intact: *Promissum* (Aldridge *et al.* 1995) and *Phragmodus* (Repetski *et al.*, 1997). The morphology of P elements of prioniodontids is diverse, incorporating a very wide range of different forms. If genera are only represented by disarticulated collections and are morphologically and phylogenetically distant from both *Promissum* and *Phragmodus*, precise architectural predictions become increasingly difficult. The P₁ element of the prioniodontids, like that of the ozarkodinids, is paired across the mid axis of the apparatus and positioned with the concave margin of the cusp directed dorsally. In the absence of contradictory information from other prioniodontid assemblages this provides a basic orientation for all P₁ elements in opposition. Further functional analysis of prioniodontid elements is reliant upon indirect examination of morphology and patterns caused by surface damage and microwear.

Icriodella provides an interesting test case, as the morphology of the P_1 element displays several strong parallels with that of the P_1 elements of ozarkodinids (for example *Idiognathus*). In both cases the elements possess a molarised process, that has become a wide platform, and a narrow, blade like process. Although the morphologies are strikingly similar it appears that the modification of the different types of processes is not homologous. In the case of the ozarkodinids, the dorsal process has formed the platform of the element and the ventral process is a blade. This is not the case in the icriodellid element, where the dorsal process has formed the blade and the caudal process the platform; the ventral process is very poorly expressed as an expansion from the side of the main axis of the element (see Chapter 4.2).

The function of the P_1 element of *Icriodella* is investigated here in the light of this evidence and compared to the ozarkodinid model of function to ascertain if the convergence of morphology is linked with a convergence of function.

Materials and methods.

Specimens of *Icriodella* have been examined from several collections that span the Ordovician/Silurian boundary; the specimens examined were collected by Professor R. J. Aldridge and are kept at the University of Leicester, Department of Geology. Specimens of *Icriodella deflecta* were from Gullet Quarry in the Malvern Hills (SO/761318) from the Telychian Wych Formation (10560 L28 II) (for further details see Aldridge, 1972); Specimens of *Icriodella discreta*, were from Roligheten (R2) Norway, near Oslo (NM 8490 3465), 264° from Vik town (for more details see Mohamed, 1983). The surfaces of the elements are slightly recrystallised, and display surface microstructures but no clear evidence of microscopic scratching or pitting. This has prevented detailed microwear analyses, but facilitated surface damage studies. Element surfaces have been examined using a scanning electron microscope (SEM).

Model of function.

The P_1 element of the ozarkodinids with platform elements occluded by rocking about a central pivot point, located close to the junction between the blade and the platform, shearing the blade surfaces past each other and bringing the platform surfaces into occlusion (Purnell, 1995; Donoghue and Purnell, 1999a). If this type of occlusion also occurred in the icriodellids evidence of functional wear and damage would be expected on the central portion of the element effecting both the platform and the blade. It is possible that the occlusal sides of the blade might also exhibit damage or shearing if the elements occluded closely or mal-occluded occasionally. This type of damage has been clearly documented in the ozarkodinids (Purnell, 1995; Donoghue and Purnell 1999a, 1999b).

Evidence of function on the blade of the P_1 element of *Icriodella*.

The blade elements of *Icriodella* occasionally display clear evidence of wear. Figure 1A and B show the outer and inner surfaces of the blade of a sinistral element. The outer surface displays a smooth surface, with a faint longitudinal fabric, that represents a primary surface ornament (see Chapter 4.3). The inner surface of the blade has a surface texture that clearly contrasts with this. Damage is in the form of clear wear facets where large areas have been flaked off from the crest of the blade. This type of wear is also seen in Figure 1D but in this case the dextral element has also lost large flakes of surface tissue on the outer side of the element but retained an undamaged surface on the inner side of the element. The cusp of the blade is also often

damaged, although the patterning is not so distinct, Figures 3C and D show the irregular worn surfaces of two cusps. Figures 1E and F show the type of preservation that is more common amongst the specimens examined, where well preserved smooth surfaces have a faint longitudinal fabric on both sides of the element (see Chapter 4.3). Less than ten elements were found that exhibited these patterns of wear, the surfaces of most elements examined were recrystallised and all primary ornamentation or surface damage was lost.

Evidence of function on the platform of the P_1 element of *Icriodella*.

Figures 2A and B show the platform of a large dextral element. In lateral view (Figure 2A) the denticles appear to have a deformed morphology and when viewed along the platform, appear to be flattened orally. In contrast, denticles of juvenile specimens have a high topography and are rounded. Views of the denticles proximal to the cusp (Figures 2C, E, F) show possible wear facets that are concave and smooth. These possible facets are bounded by polygonal surface microstructures. There appears to be a greater concentration of possible wear facets and polygonal surface microstructures on regions of the platform proximal to the cusp, when compared to distal regions (Figure 2D).

Interpretation.

The wear found on the blade of the P_1 element of *Icriodella* is distinctive and the pattern of distribution is repeated in different specimens. This provides clear evidence that the elements were damaged during the life of the conodont and not during postmortem processes.

In mammalian teeth the formation of cusps and blades have been shown to reduce the total area of tooth on tooth contact, resulting in the concentration of stresses at the sites of contact (Rensberger, 1995). This results in increased fracturing and damaging at these points (Rensberger, 1995). Mammalian enamel has responded to this with subtly different forms of enamel that are able to resist the propagation of large cracks. These forms of enamel comprise of groups of enamel rods or prisms that all possess subtly different orientations, thus reducing the length and number of directions that cracks can propagate in (Koenigswald *et al.*, 1987). The planes that divide the differently orientated rods are known as decussation planes. Koenigswald *et al.* (1987) documented the first occurrence of decussation planes and connected this appearance with the radiation and diversification of early Cenozoic herbivores.

The occurrence of white matter in conodonts may represent a selective response of crown tissues that were able to resist damage to denticles and cusps (discussed fully in Chapters 1.4, 2.4). Without white matter, the lamellar structure of hyaline crown could potentially provide lines of weakness that might be exploited if exposed to stresses. The lamellae within the flanks of denticles of icriodellids are orientated parallel with the long axes of the denticles, and white matter does not extend to the outer regions of the denticles. The facets

that have been flaked off the denticle tips seen in Figures 1B and 1D might reflect the loss of outer lamellae in the absence of white matter, due to stresses imposed at denticle tips.

The sinistral element is damaged along the outer edge of the blade and the dextral element along the inner edge showing that it is these surfaces that were under stress during the function of the element. This pattern of surface damage implies that the outer edge of the dextral element occluded against the inner edge of the sinistral element (Figure 4). If opposed the blades could either occlude closely against each other with a shearing action or food may have been crushed or manipulated between both blades, resulting in the damaged surfaces. Because damage is not always apparent, the elements may not always have occluded directly against each other, or against food, but instead passed each other cleanly, not meeting at the denticle tips. This implies that the damage would have been caused when the elements maloccluded.

The morphology of the denticles and the surface microstructures found on the platform provide potentially good evidence of damage due to function. The facets seen in Figures 2C and F form clear indentations bounded by polygonal surface microstructures. It is possible that the smooth interiors of the facets represent the most recent wear that has removed the evidence of the latest phase of growth, which is now only preserved around the margins of the denticle surface. In the absence of microwear it is difficult to be certain if this is evidence of wear, or if it represents primary morphology and distribution of surface microstructures. The presence of polygonal surface microstructures is possibly indicative itself of damage due to wear or damage due to function. Generally platforms of Icriodella are preserved with a smooth element surface, bearing only a faint longitudinal fabric, which is aligned with the long axes of the denticles. When denticles are damaged, it is predicted that replacement crown tissue would be deposited as new layers that would be laid down horizontally across the old truncated lamellae. The crystallites within would still grow with their c axes parallel to the growth axis therefore in the new laminations, this would result in them being orientated perpendicular to the lamella surface. It is postulated that such a crystallite orientation would result in a polygonal ornamentation during secretion as discussed in Chapter 4.3. Figure 3E shows a platform denticle that has developed polygonal surface microstructures. Platform elements of Idiognathus also possess polygonal surface microstructures it is possible that this represents a similar process of functional wear and repair in the form of horizontal lamellae expressed externally with polygonal surface microstructures (Donoghue and Purnell, 1999a, p. 62, fig. 3C, D; p. 68, fig. 6).

The damage to the cusps illustrated in Figures 3C and D indicate that occasionally this prominent part of the element was also involved functionally. The small, but deep area that has been gouged from specimen 011 (Figure 3D) may indicate that the damage has resulted from a regular short movement. It is likely that the abrasion was caused by some kind of permanent obstacle encountered during the processing of food, such as part of the opposing element. Alternatively this may suggest damage due to an occlusal malfunction and the facet may represent brittle failure. Verification would require the preservation of microwear within the facet, which unfortunately, is not available.

Possible food substances.

Purnell (1995) described three basic types of microwear found on mammal teeth and correlated them with wear found on conodont elements. Frosting or smooth polishing are indicative of parts of the element that were not in contact with food substances, or that the conodont ate food that was not as abrasive as the surface of the element. Pitted surface microwear indicates that food was crushed between two element surfaces and parallel scratching and chipping of elements is be diagnostic of shearing between two element surfaces.

The common form of preservation of icriodellid P_1 elements, where the surfaces of elements are smooth and not indented or broken, indicates a lack of hard food substances, resulting in the gradual polishing and wearing down of element surfaces without any obvious damage. The rare cases of wear are in the form of chips and flaked surfaces along the edge of the blades, directly comparable to wear on the blade of *Ozarkodina confluens* figured by Donoghue and Purnell (1999b, p. 253, fig. 2A, B). Each individual facet represents one encounter with a hard surface during occlusion. It is possible that this means that the conodont occasionally encountered hard food substances. It is also possible that the damage represents malocclusion between the denticle tips due to poor control of element movement.

Possible motion of elements.

The absence of a region of low topography towards the centre of the element of *Icriodella* does not preclude a pivoting motion of the element pairs, analogous to the motion proposed for the platformed ozarkodinid elements (Donoghue and Purnell 1999a). The high topography of the cusp in conjunction with the damage seen in Figure 2C means that the elements would have had to function with the blades occluding down either side of each other to allow the platforms of the opposing elements to come into contact with each other (Figure 4). The damaged platforms in concert with the damaged cusp tips may represent the effects of complete occlusion of the element. The height and position of the blade would have controlled the occlusal motion, positioning the platforms against each other and also allowing a certain degree of movement before the elements came completely apart. The damage found on some blades suggests that not all elements occluded cleanly and some damage was caused if the elements moved too far apart and then returned to an occlusal position; it is possible that the occasional cusp damage represents over occlusion. It is hypothesised that the elements of *Icriodella* occluded in a way analogous to that of the ozarkodinid platformed elements, pivoting across the mid axis of the element, with the blade controlling precise occlusion of the platform as it crushed food substances.

Conclusion.

Comparing the platform element of *Icriodella* to platformed elements amongst the ozarkodinids has shown that the elements probably functioned in a similar way, pivoting about the mid-axis of the element. The major difference between the occlusion of the icriodellids and that of the ozarkodinids, is the position of the elements with respect to each other across the mid axis of the apparatus. Evidence from the natural assemblages of *Promissum* (Aldridge *et al.*, 1995) and *Phragmodus* (Repetski, 1997; Chapter 5) indicates that the concave margin of the cusp of prioniodontid P_1 elements was certainly directed in a dorsal direction. This is directly comparable to P_1 elements of *Icriodella* occluded with the right element behind the left. This is in contrast to the ozarkodinid P_1 elements, which are though to have occluded with the left element behind the right (Donoghue and Purnell, 1999a).



Figure 1. Evidence of wear on the blade of platform element of *Icriodella discreta* Roligeten R2. A-B Specimen 327 sinistral element. A. Outside edge of blade, showing smooth surface and preservation of primary ropy microstructures on cusp. B. Inside edge of blade showing clear chips and shears on denticle edges, three priniciple chips on three denticles from top of image. C-D Specimen 002 dextral element C. Inside edge of blade showing smooth surface. D. Outside edge of blade showing chips and shears, especially on cusp. E-F Specimen 331 sinistral element. Inside edge (E) and outside edge (F) showing absence of wear.



Figure 2. Evidence of wear on platform element of *Icriodella discreta* Roligeten R2. A-B Specimen 011. A. Lateral view of platform showing possible wear facets and the morphology of denticles. B. View along platform towards cusp, showing flattened tops of denticles. C-F Specimen 900. C. View of denticles proximal to cusp and possible wear facets bounded by polygonal microstructures. D. Denticles at distal tip of platform. E. Lateral view showing denticles with possible wear facets. F. Close-up of E, showing facet in denticle and polygonal microstructures.



Figure 3. Evidence of function on elements of *lcriodella discreta* Roligeten R2. A. Sinistral element. Dorsal ('Posterior') process directed to bottom of page and 'lateral' process directed to top, ventral ('anterior') process represented by expansion to right of element, specimen 010. B. Dextral element. Orientation same as for A, but ventral ('anterior') process expanded towards left of image. C. Damaged cusp of dextral element, specimen 022. D. Damaged cusp tip of dextral element, specimen 011. E. Rounded denticle of platform showing even distribution of polygonal surface microstructures, specimen 327. It is apparent that the conventional identification of sinistral and dextral elements differs from an identification derived from an examination of the internal structure of the elements. The traditional identification has been retained at this time.



Figure 4. Platform elements of *Icriodella discreta* Roligeten R2 juxtaposed into a possible occlusal position. Dextral element is located in the lower position, specimen 001. The sinistral element is located in the upper position, specimen 011. The view would be from a ventral position if the elements were within an apparatus and the ventral process can be seen originating from the ventral face of the cusp. If the blades occluded fully the platforms would be aligned the denticle nodes would come into opposition. In this position it is demonstrated that the distal deflection of the blades is complimentary. The platforms are approximately 100um across.

CHAPTER 5

THE APPARATUS ARCHITECTURE OF PHRAGMODUS INFLEXUS STAUFFER 1935.

Introduction.

A general understanding of the composition of the apparatus of *Phragmodus* has evolved since the mid 1960's. Bergström and Sweet (1966) were amongst the first to identify the principle components of the apparatus; the S, M and P elements and subtle differences in the S element morphologies were subsequently appreciated as larger collections became available and were assessed in the light of multielement taxonomy. Most apparatus reconstructions are based on evidence derived from ozarkodinid natural assemblages, the only group for which there are a large number of different taxa represented (for review see Purnell and Donoghue, 1997, 1998). The components of *Phragmodus* appear to reflect the architecture of the ozarkodinid apparatuses, however, *Phragmodus* is currently classified as a prioniodontid (Sweet, 1988; Aldridge and Smith, 1993). *Promissum* represents the only well preserved prioniodontid natural assemblage and is currently classified within the balognathids. The architecture differs from that of the ozarkodinids in its more complex P element architecture and the positioning of the different components within the apparatus. It has already been suggested that it is possible that the apparatus of *Promissum* is not typical of all prioniodontids (Purnell *et al.*, 2000). The *Phragmodus* natural assemblages provide unequivocal proof that the apparatus plan of *Promissum* is not typical of all prioniodontids.

Historical reconstructions of Phragmodus.

Bergström and Sweet (1966) based their reconstructions of *Phragmodus* on the proportional representation of the different components. On the basis of this it was suggested that *Phragmodus inflexus* might have had up to eighteen elements present in a single apparatus; six dichognathus-like elements and 12 phragmodus-like forms for which they described three different forms. Sweet and Bergström (1972) proposed that there were strong similarities between the components of the apparatus of *Phragmodus* and those of other prioniodontids, for example, *Prioniodus elegans* and on the basis of this classified the phragmodonts within the Prioniodontacea. In this case it was proposed that the apparatus *Phragmodus inflexus* was composed of two pairs of P elements, an M element pair and an S element array of sinuous phragmodontiform elements.

Barnes et al (1979) re-addressed the notation applied to multielement taxonomy and included elements of *Phragmodus undatus* within their study. The apparatus was reconstructed as an apparatus type IVC characterised by a lack of differentiation within the S element array, two pairs of P elements and a pair of M elements. The S elements were each identified as a-d based on the arrangement of costa about the cusp. Elements designated a types possessed an anterior and posterior costa, b types were similar to a types, but also sometimes possessed a weakly developed lateral costa, the c type was a sub-symmetrical element with a

posterior, and two antero-lateral costae which possessed basal extensions. The d element type was symmetrical with anterior, posterior and two lateral costae.

Subsequent work has agreed with these early reconstructions of *Phragmodus* apparatuses, for example Clark (1981) Sweet (1988) and Dzik (1994).

Notation.

Until recently the most generally accepted form of notation was that proposed by Sweet (1981, 1988). This type of notation segregated the basic element positions. Three principal positions were identified and Sweet (1981, 1988), described the type of element that normally characterised that position. Because at that stage the scheme was mainly supported by ozarkodinid natural assemblages, the reconstruction of other taxa relied solely on morphological comparison with the element types characterised by Sweet. However, Sweet had stated that at the stage that he erected the locational scheme, it was meant to be a vehicle for expressing analogy and not homology. In the light of the current evidence, where more natural assemblages are now known, Purnell *et al.* (2000) proposed a new scheme that provided a notation that identified elements that are clearly homologous with each other, for which a position within the apparatus is certain. This allows the identification of homologous elements in natural assemblages and those elements that can be clearly homologised with them. It is intended that the scheme proposed by Sweet (1981, 1988) should be retained and used for elements where homologies are uncertain. The new notation proposed by Purnell *et al.* 2000 is used in this study to indicate that the element positions are certain and that clear homologues can be drawn with other natural assemblages (Figure 1).

The material.

Conodont natural assemblages have been recovered from the black shale that infill the Ames impact crater, Major County, Oklahoma (Repetski, 1997). The material was concentrated in D. & J. no. 1-20 James and Nicor no. 19-4 Chestnut wells that have been dated as the middle of the Middle Ordovician. The preservation of the elements is exceptionally good in some cases, where traces of the basal body are apparent and details of element structures and morphology are clear. The natural assemblages exhibit little postmortem disturbance, indicated by the orientation of the elements and the type of collapse patterns that can be compared to those known from ozarkodinid assemblages (Purnell and Donoghue, 1997, 1998). The host rock is a fissile fine grained black shale that is rich in organic content. The conodont assemblages are extremely small (for example, between 1 and 2mm across the broadest dimensions) and the elements preserved as thin, almost transparent calcium phosphate. It has been possible to ascertain the position of each element, with respect to the other elements using a combination of SEM studies and stereo-pairs. Elements from the assemblage were compared to disarticulated elements from Estonia, Khotla section (horizon F1 top) of Middle Ordovician age, which are stored at the University of Leicester. These may represent *P. flexuosus*, though identification was hampered by the limited numbers of specimens and poor preservation of costae edges.

Description of elements.

Specimen 395 (Figure 2) provides an example of all the component elements and allows a detailed study of the individual element morphologies. Elements are described from the most central S element (S_0) to the most external S element (S_4) and from the most caudal P element (P_1) to the most rostral (P_2), following the notation provided by Purnell *et al.* (2000).

The central S element (S_0) is an arched element, with large discrete denticles on the caudal process that are slightly inclined in a caudal direction. As well as being clearly preserved in specimen 395 (Figure 2), it has also been preserved as an individual element in specimen 394 (Figure 6G). There is a short length of process with no denticulation, just caudal of the cusp. The cusp is approximately half the width of the broadest denticles of the caudal process and is approximately half to two thirds of the height. The rostral edge of the element appears to be drawn out into a costa that is positioned on the lateral face of the cusp. This costa continues the curvature of the element and delineates the outline of the basal body. A lot of the curvature of the element is formed by the base of the cusp and continues through the rostral half of the element.

The S_1 element is closely associated with and is probably comparable morphologically to the S_2 element. There are few good examples of S_1 or S_2 elements preserved. In Figures 2 and 3 it can be seen that the caudal process is arched in a way comparable to the S_0 element. The denticles are discrete and large distal from the cusp, but are small immediately caudal of the cusp leaving no gap in between the caudal face of the cusp and the beginning of the denticulation. The cusp is approximately half the width of the denticles and is half the height. The rostral edge of the cusp is either rounded or costate and directed in a ventral direction. The dextral S_2 element of specimen Le Po/a (Figure 4) possesses a costa running along the lower edge of the outside face of the element, this is especially clear in Figure 4B. The same region of the S_2 element is poorly preserved in Figure 2. The costa continues beneath the cusp reflecting some of the curvature of the element, although this curvature is less pronounced than that of the S_0 element. The element's curvature is expressed by the caudal process and is most pronounced in the areas immediately adjacent to the cusp as is the case for the S_0 element.

The caudal process of the S_3 and S_4 elements are the least arched of the entire array and are composed of discrete denticles that are smallest adjacent to the cusp. In Figure 2 the caudal processes of the sinistral S_3 and S_4 elements are not clearly preserved, however the dextral caudal processes are and exhibit a notable straight lower margin. The cusps are the largest of all the S elements in this specimen and clearly show convex outer margins. Both S_3 and S_4 elements have a ventral costa and the dextral S_3 element possesses a weakly formed lateral costa on the outside face of the cusp, that is not expressed in the S_4 element.

Three of the P elements and possibly a fragment of a fourth element are preserved in specimen 395 (Figure 2). Most caudal (the P_1 element pair) are two elements that possess robust cusps and straight dorsal processes. The denticles on the dorsal processes carry discrete denticles that are approximately half the size of the cusp, with about the same width. The ventral edge of the cusp appears to be costate, there is possibly some denticulation along the leading ventral edge. The apparent absence of a third process might suggest that it developed at an angle from the plane of the dorsal and ventral processes. This would result in it being embedded in the substrate of the specimen; as in this instance the elements are both preserved with either their rostral or caudal faces exposed (depending on the life orientation, that is in this case slightly disrupted, because of the oblique lateral collapse of the specimen).

The third P element, rostral to the P_1 element pair, possesses a number of characters that differentiate it. The dorsal process possesses discrete triangular denticles that appear to be of a comparable size to the cusp. Although poorly preserved, a second process is also preserved and the lower margin of both the dorsal and this second process form a broad obtuse angle, approximately 150°.

The M elements are preserved in close juxtaposition with a cusp and a dorsal process. The cusp is broad and almost twice as wide as the dorsal process is deep. The denticles of the process are small, triangular and discrete. There is an angle of approximately 90° between the dorsal face of the cusp and the dorsal process. The lateral face of the cusp is convex and the ventral face costate.

The components of the S element architecture.

All of the S elements within the apparatus, do initially appear to share the same dolobrate morphology. There are, however, subtle differences that are expressed by the absence or presence and arrangement of costae. The most lateral pair of S elements, the S_4 are bipennate, with a caudal process and a rostral costate edge. The S_3 elements have a similar morphology, but also possess a lateral costa on the outside face of the cusp. The S_2 element is only clearly preserved in one instance (Figure 4). There is clearly a costa that runs down the centre of the lateral, outer face of the cusp (Figure 4B). It is not known whether there is a costa on the inner face, however, if the reconstruction seen in Figure 3 is correct, then the inner face of the S_2 element is either lacking a lateral costa or the costa is positioned along the most anterior edge of the lateral face. This type of morphology compares very closely to the quadriramate S element (Figure 6E, F) of *Phragmodus* that is identifiable from discrete element collections.

The S_1 elements are not so clearly preserved, but it seems apparent that they either have no costa along their lateral faces, or a costa that is positioned very rostrally. The S_0 element is the most clearly understood element and possesses caudal and lateral costa arranged in a symmetrical manner. It is possible that the S_1

and S_2 element morphology is closely comparable to this and the lateral costa are sometimes so rostral that they are difficult to identify.

The P element architecture.

Knowledge of the morphology of P elements of *Phragmodus* is well known and it is usual for both Pa and Pb elements to have a small ventral process and a caudal process that is of comparable size to the dorsal process (Figure 6A, C). Comparing images of Pb elements from discrete collections it seems likely that the view preserved in Figure 6B represents the dorsal and ventral processes. This means that both of the P_1 elements are preserved with their rostral face up. If the P_2 element seen in Figure 6D shares the type of morphology displayed by the Pa elements from the discrete collection (Figure 6C) then the process that is directed ventrally probably represents the caudal process and not a ventral process. The region where the ventral process would have been apparent (if the elements are positioned with their rostral faces exposed), is not preserved in this case.

The collapse pattern.

The apparatus has been collapsed as the conodont was lying on its side resulting in an oblique lateral collapse. It is clearly oblique because the sinistral and dextral S element arrays have become displaced with the dextral array becoming more caudal and the sinistral array reflecting the same displacement, but in a rostral direction. Both the M and the P elements have not expressed such a great sense of movement. The M elements are closely juxtaposed, with the dextral element orientated close to life position (extrapolated from ozarkodinid and prioniodontid templates, Purnell and Donoghue, 1998, 1999. Aldridge *et al.*, 1995). The sinistral element has twisted round and its position is probably disturbed, it shows the same sense of displacement as the sinistral array of S elements. The P elements do not reflect the same displacement. The P_1 pair show the opposite sense of displacement displayed by the S elements might have been caused by the distance between the arrays during life. If each array was positioned on either side of the apparatus with a relatively wide space between, then an oblique lateral collapse would be expected to be expressed with more displacement. The movement of the P elements during collapse might have limited because in life these elements are closely juxtaposed therefore only likely to flip over, so that their broadest dimensions were perpendicular to the collapse pressures.

Discussion.

The architecture of *Phragmodus* is closely comparable to the apparatus plan of the ozarkodinids. The S element array, with a symmetrical alate element positioned centrally and two pairs of tertiopedate S elements flanking, followed by two pairs of dolobrate elements is directly comparable. The M elements are also in a position that is comparable to that of the ozarkodinids.

The P element architecture is also comparable with two pairs of robust elements paired at the caudal end of the apparatus, behind the S and M elements, with the largest element positioned most caudally. The dorsal ventral orientation of the elements in the *Phragmodus* apparatus is also comparable.

It is also possible to observe some characters that can be compared to the *Promissum* apparatus. The S elements of *Promissum* are more complex than the simple elements of *Phragmodus* but do display a similar decrease in complexity with distance from the S_0 element. *Promissum*, however, possesses a quadriramate element in the S_2 position. A quadriramate element has not been described for *Phragmodus*, but this is probably because general practice has dictated that a costate anterior edge found on elements from disarticulated collections has not been noted. If there are costate anterior, posterior and lateral faces, then the element is technically quadriramate. It has not been possible to unequivocally identify such an element in the natural assemblages, however, the S_2 element seen in figure 6F compares very closely to the lateral view of the element figured in figure 6E that does possess anterior, posterior and lateral costa and may therefore have occupied the S_2 position.

The P element architecture of *Phragmodus* is fundamentally different from that of *Promissum*. *Promissum* possesses four pairs of opposing P elements, of which the two most robust pairs are positioned most caudally. The most obvious difference between the apparatus of *Phragmodus* and that of *Promissum* is the number of P elements. If the P_1 and P_2 elements of *Promissum* are serially reproduced, as suggested by their identical morphologies (see Chapter 1.4), then P element architecture of *Phragmodus* can be compared. Figure 2 clearly shows that the most caudal P elements of *Phragmodus* are the largest and most robust components, this is also the case in *Promissum*. This, however, is the only comparison possible as there is no further similarity between the P_2 element of *Phragmodus* and the P_3 of *Promissum*. There is also no suggestion of a fourth pair of P elements present in the apparatus of *Phragmodus* that could be compared to the P_4 element of *Promissum*.

Conclusions.

The P elements within the apparatus of *Phragmodus* are clearly pastinate. This places *Phragmodus* unequivocally within the prioniodontids. However, the natural assemblages of *Phragmodus* show that the apparatus plan was that of the ozarkodinids. This shows that at least some of the conodonts currently

classified within the prioniodontids shared an apparatus plan that was identical to the ozarkodinids and that the apparatus plan of *Promissum*, the only other prioniodontid represented by a well preserved natural assemblages (Aldridge *et al.* 1995), is probably only typical of the balognathids. This suggests that it is likely that the ozarkodinid apparatus plan represents a template that is plesiomorphic to the conodonts as suggested by Purnell *et al.* (2000).



Figure 1. A. New terminology for the apparatus of *Promissum pulchrum* following Purnell *et al.* (2000). B. New terminology for the apparatus of ozarkodinid conodonts following Purnell *et al.* (2000).



Figure 2. Specimen 395. Counter part of natural assemblage of *Phragmodus inflexus*. Oblique lateral collapse.



Figure 3. Reconstruction of natural assemblage of *Phragmodus inflexus* specimen 395. The dark grey coded elements show the dextral S elements that have been slightly transposed to the caudal end of the apparatus and the light grey coding, the sinistral elements that have been moved towards the rostral end of the apparatus. The P elements show less displacement and are still more or less aligned probably all showing the rostral view of each element with the rostral process seen. The difference in displacement might be due to the fact that the P elements were in life close to each other, where as the S elements occupied either side of the apparatus, and therefore display an apparently amplified movement.



Figure 4. A. Specimen LePo/a *Phragmodus inflexus*. Array of dextral S elements showing S4 element as the outer most component and also showing detail of S3 element directly beneath the two outer elements. A. Whole image. B. Close-up of the arrangement of cusps.



Figure 5. Reconstruction of Le Po/a *Phragmodus inflexus*. The two outer S4 and S3 elements are recognised because they are positioned on the outside of the array. Directly beneath lies a costate element that clearly illustrates the tertiopedate morphology of the S2 element. Other elements of the assemblage are identified with less confidence.



Figure 6. Elements of *Phragmodus inflexus* from natural assemblages, compared to elements of *Phragmodus inflexus* from the discrete cellection (see text). A. Specimen 30. Sinistral Pb element. The denticles are poorly preserved on the dorsal process, but the angular relationship of the processes still allows comparison. B. Enlargement of Specimen 395 showing sinistral P1 element frame width 250um. C. Specimen 40. Dextral Pa element. D. Enlargement of specimen 395 showing dextral P2 element frame width 200um. E. Specimen 6. Asymmetrical dextral quadriramate element. F. Enlargement of S2 from specimen Le Po/a. G. Isolated S element specimen 394. Possibly S0, frame width 500um.

CHAPTER 6

THE CLASSIFICATION OF THE PRIONIODONTIDA Dzik 1976.

Introduction.

Prior to 1970, the classification systems erected for the Conodontida merely represented a utilitarian method of ordering and grouping individual form taxa. This approach arranged conodont elements together in groups according to their individual forms, with no consideration of the structure of the conodont skeleton, and in the absence of knowledge of the true nature of the conodont animal. Even when the first natural assemblages were discovered (for example see Schmidt (1934) and Scott (1934, 1942)) form taxonomy was not abandoned. It is possible that this reflected a reluctance to abandon a system that allowed relatively easy communication between conodont workers, at a time when anatomical information was practically non existent for the greater majority of taxa known. Müller (1956) discussed the multielement concept, introducing the problem of individual conodont species possessing several different names, as a result of form taxonomy. He suggested that a dual nomenclature was necessary, where the individual components retained their names and were known as partial genera, instead of form genera, thereby differentiating between whole apparatuses and their components. Sweet and Bergström (1972) pointed out that at such an early stage it would have been premature to propose a refined classification system because of the paucity of data available. Conodont classification has now been completely overturned and is based on the multielement approach and where possible (and also where not possible), apparatus reconstructions have now been proposed for most conodont taxa. This paper explores and reviews conodont classification, discussing the criteria used to establish individual taxa. It is suggested that a more detailed approach could be employed to refine conodont classification, based on detailed apparatus reconstructions and the internal structures of the apparatus components.

Historical review of Prioniodontid multielement classification.

Lindström (1970) was the first to present a classification system based on a multielement concept. Lindström based his classification on his own interpretations (Lindström, 1964, 1970), geological occurrence, element morphology and element ultrastructure; he also incorporated the results of the most recent work that addressed the multielement reconstructions of several well known taxa (for example that of Bergström and Sweet, 1966). On the basis of these criteria Lindström recognised two orders: Westergaardodinida and Conodontophorida. The proper conodonts (the Conodontophorida) were divided into eight superfamilies: Distacodontacea, Panderodontacea, Chirognathacea, Prioniodontacea, Prioniodinacea, Bryantodontacea, Gondolellacea and Polygnathacea. The Prioniodontacea (Bassler 1925) were recognised as conodonts that possessed an apparatus containing oistodiform elements, an array of ramiform elements and platform-like elements that were prioniodiform or ozarkodiniform. Families classified within the superfamily Prioniodontacea included:

Periodontidae Prioniodontidae Balognathidae Icriodontidae

Lindström noted that some of the members of the Balognathidae (such as *Eoplacognathus* Hamar 1966 and *Polyplacognathus* Stauffer 1935) were represented only by platform apparatuses. This first suprageneric classification provided an essential starting point that has been refined and modified many times.

Sweet and Bergström (1972) followed on from, and attempted to refine, Lindström's classification system in their consideration of Ordovician prioniodontacean conodonts. Sweet and Bergström (1972) attempted to delineate and understand the range of morphological variation present within multielement species. Along with morphological considerations, the groupings were based on apparatus structure, stratigraphic ranges and geographic distribution. The authors admitted to several gaps in their taxonomy due to the limited data, for instance, at that time the knowledge of coniform apparatuses and the apparatuses that were then characterised as having hyaline components was only basic.

Sweet and Bergström (1972) noted that the hyaline conodonts were probably closely related to non-hyaline conodonts, as they shared similarities in apparatus structure, and predicted that in the future they would be classified together. They postulated that the fibrous structure of hyaline conodonts might simply be an expression of shallow water, or hyper-saline environmental adaptations. On the basis of this, Sweet and Bergström's (1972) analysis was restricted to non-hyaline forms, ramiform apparatuses and ramiform/platform apparatuses, and grouped all of these taxa within the Prioniodontacea.

In the main they followed Lindström's (1970) classification, but took the classification further by providing a diagram to illustrate possible phylogenetic pathways (Figure 1). The genera included conodonts that were thought to possess a prioniodiform apparatus (i. e. two pairs of platform elements, a pair of M elements and an array of S elements) and also platform only genera. They included the following families:

Periodontidae Balognathidae Prioniodontidae Cyrtoniodontidae

The composition of the families was somewhat different from Lindström's original groupings; for instance, *Icriodus* was classified within the Prioniodontidae and the rest of the Icriodontidae were not considered for the

study. The familial classification was based on the proposed apparatus structures, and this in turn was based on the number of morphologically distinct components assigned to each apparatus. Unfortunately a clear analysis of the composition of the component genera of each family is hampered by a confusing discussion of proposed relationships, though Sweet and Bergström (1972) suggested that the root lineages for all major conodont stocks could be found within the Prioniodontacea. Sweet and Bergström (1972) concluded with a note of warning. They thought it possible that the Prioniodontacea might not represent a true natural group and that it simply reflected a group of conodonts that all shared the same apparatus plan. Sweet and Bergström (1972, p. 38) feared that "the prioniodontid plan may turn out to be merely a map of the way in which all but a few conodont skeletons were organised and we may be deceiving ourselves at this point by conferring genetic respectability on a group of diverse origins just because their skeletal apparatuses achieved the same (or similar) stage of development in the Ordovician".

Dzik (1976) proposed a classification of conodonts based almost solely on apparatus structure. He assumed that all the component elements were present at all evolutionary stages and that they were subjected to gradual morphological changes that eventually merited species, and subsequently, generic status. He divided the Conodontophorida into three main suborders characterised by their apparatus types: Group I, Westergaardodinina Lindström, which he included within the Conodontophorida (and thereby did not follow Lindström (1970) who had formed a distinct order for this taxon; Dzik did, however, add that the apparatus structure of the westergaardodinid conodonts was unknown); Group II, Prioniodontina Dzik, with prioniodiform elements with three distinct forms (with branches at obtuse angle – amorphognathiform, with branches at acute angle – ambalodiform, and flattened elements – keislognathiform), three morphologies of ramiform element and an oistodiform element; Group III, Ozarkodina Dzik, with ozarkodiniform elements), three types of ramiform element and one neoprioniodiform element that Dzik thought was probably homologous to the oistodiform element of group II. Dzik (1976, figs. 5, 6) presented several carefully constructed diagrams that illustrated his interpretation of the phylogeny and homologous elements of several important taxa including *Prioniodus* and *Amorphognathus*.

Barnes *et al.* (1979) criticised the then current conodont notation and stated that whilst the majority of multielement taxa had been diagnosed and were probably well understood, the notation system was not adequate to handle such complex apparatuses. The authors endeavoured to produce a new type of notation that identified and distinguished between the different types of apparatuses that they recognised. In the light of this appraisal of apparatus types, Barnes *et al.* (1979) re-evaluated the classification of Ordovician conodonts on the basis of apparatus architecture, stratigraphical occurrence and province. The authors (Barnes *et al.*, 1979, p. 145) thought that "if these apparatus types provide valid divisions with certain homologous relationships having been recognised, it is possible that they represent major natural divisions of unknown rank". All of the taxa were classified as genera, and no further classification into families or orders was provided (Figure 2).

In 1981 Clark *et al.* presented a comprehensive re-evaluation of conodont classification in the *Treatise*. The authors stressed that the classification had to be regarded as provisional, especially at suprageneric level, and pointed out that they had to leave out forty-eight genera out due to lack of data. A diagram demonstrating the phylogenetic relationships between different taxa was not provided. The authors recognised two orders based on structural and chemical differences: Paraconodontida and Conodontophorida; they also proposed 11 superfamilies based on similar apparatus architectures and 47 families, which were accordingly divided into 180 genera, distinguished by distinctive apparatuses and element morphologies.

Within this classification system the Prioniodontacea contained many new families:

Balognathidae Cyrtoniodontidae Icriodontidae Oepikodontidae Paracordylodontidae Periodontidae Phragmodontidae Phragmodontidae Pioniodontidae Pygodontidae Rhipidognathidae Pterospathodontidae

This entire re-evaluation of conodont classification was extremely ambitious at the time and was not universally accepted, nor did it go without criticism. Fåhræus (1984) was one of the most vocal and accused the *Treatise* authors of failing to follow convention with regard to the International Code of Zoological Nomenclature. His greatest criticism (Fåhræus, 1984, p. 293) was that the classification lacked "a precise philosophical and methodological foundation". The main concern of Fåhræus was to present a classification system that reflected the phylogenetic relationships between different taxa. Fåhræus re-evaluated the classification of many of the genera included within the Prioniodontacea regrouping them into three superfamilies (Prioniodontacea, Hibbardellacea and one new; Icriodontacea) and used subfamilies to try and emphasise the diversity that was apparent during the Ordovician (Figure 3):

Superfamily - Prioniodontacea Family - Prioniodontidae Subfamily - Prioniodontinae Subfamily - Oepikodontinae Subfamily - Pygodontinae

Family - Balognathidae

Subfamily – Balognathinae Subfamily – Polyplacognathinae Subfamily – Icriodellinae

Family – Paracordylodontidae Subfamily – Paracordylodontinae Subfamily – Periodontinae Superfamily – Hibbardellacea

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Family - Hibbardellidae

Family - Cyrtoniodontidae

Superfamily – Icriodontidacea Family – Icriodontidae Family - Distomodontidae

Within Fåhræus' (1984, p. 303) classification 'superfamily rank' distinguished monophyletic groups each derived from an ancestor having a conodont apparatus with a markedly distinct symmetry relation. 'Family rank' designated all those conodonts that shared the same apparatus plan or had apparatuses that were directly derived from those basic plans. 'Subfamily rank' included genera that shared identical conodont apparatuses.

Fåhræus (1984) left out the Rhipidognathidae because he believed that there were several important architectural differences that prevented its inclusion within the Prioniodontacea. Also the Pterospathodontids were excluded as Fåhræus believed that they originated within the Polygnathacea (the ozarkodinid sensu Sweet, 1988) and not the Prioniodontacea. However, Cooper (1977) also claimed that *Pterospathodus* was closely related to *Llandoverygnathus*, which he thought to be closely related to *lcriodella*. Fåhræus (1984) kept the icriodellids within the Prioniodontacea, thereby presenting a circular argument.

Fåhræus (1984) noted that the Hibbardellacea (the prioniodinids sensu Sweet, 1988) were characterised by apparatuses that contain P, M and S elements that are of similar size and are often laterally compressed. Families of the Prioniodontacea commonly possessed S and M elements that were substantially smaller than the P elements, which were often robust and sometimes developed platforms. On the basis of this, Fåhræus (1984) recognised what he interpreted as a dichotomy amongst the Prioniodontacea and the Hibbardellacea (sensu Clark *et al.*, 1981) and believed that it was controlled by diphyletic origins of the two groups and by biogeographic provincialism.

Sweet (1988) did not follow the classification of Fåhræus (1984) and produced a scheme based on that of the *Treatise* (Robison, 1981). Sweet (1988) attempted to characterise the main conodont groups and the features that indicated their phylogenetic relationships to each other. He regarded his classification as a revised version of the basic classification framework provided in the *Treatise*, with modifications based on discoveries

made after the *Treatise* manuscript was completed. Many of the changes were dictated by personal prejudice, a fact that Sweet freely admitted.

Sweet considered that the conodont group, represented by the Conodontophorida in the *Treatise* (Robison, 1981), required phylum status and subdivided it into two classes: Conodonti and Cavidonti. The Cavidonti included conodonts that possessed thin walled smooth, primarily coniform elements. Sweet (1988) thought that the two classes represented two different major stocks and could find no evidence that suggested that Conodonti were descended from the Cavidonti. The Cavidonti were further divided into five orders: Protopanderodontida, Panderodontida, Prioniodontida, Prioniodinida and Ozarkodinida.

The Prioniodontida in Sweet's sense included conodonts that were believed to have had sexi- or septimembrate apparatuses that included pastinate or their platformed analogues in one or both P element positions, an array of S elements and pair of M elements. Sweet (1988) regarded this group as comparable to the superfamily Prioniodontacea of the *Treatise* but included the Oistodontidae (previously classified in the *Treatise* as a separate superfamily) and excluded the Pygodontidae and the Pterospathodontidae (Figure 4). The families that he thought should be included in the Prioniodontida were:

Oistodontidae Prioniodontidae Balognathidae Icriodellidae Distomodontidae Icriodontidae Polyplacognathidae Multioistodontidae Plectodinidae Cyrtoniodontidae Rhipidognathidae

Dzik (1991) reassessed the classification of conodonts basing his work on that of Sweet (1988). He believed that during the Ordovician there was a great diversity of apparatus plans and this provided the basis for the classification proposed; families were distinguished according the basic type and form of elements within these apparatuses. Dzik (1991) noted that during the Late Palaeozoic the basic conodont plan became more conservative and stated that "a strict application of the same criteria for the Ordovician and later conodonts would thus result in an unnecessary exaggeration of the otherwise well established fact that this was the period of the most intense diversification of the group." Dzik claimed that his main modifications to Sweet's (1988) classification concerned the only the coniform apparatuses, following the development of architectural

data and evolutionary studies that had been undertaken since Sweet's (1988) work. Dzik's reclassification of the Prioniodontids included the reintroduction of the rank 'superfamily' (Figure 5):

Superfamily - Prioniodontacea

Family - Prioniodontidae Family - Balognathidae Family - Ansellidae Family - Pygodontidae Superfamily - Icriodontidacea Family - Pterospathodontidae Family Icriodontidae

The classification proposed by Dzik (1991) incorporated many revisions of Sweet's (1988) classification. In particular, the Prioniodontida were represented by only two superfamilies and six families, in contrast to the twelve families recognised by Sweet (1988). The Pterospathodontidae were returned to the Prioniodontida, into which the Distomodontidae (of Sweet, 1988) were subsumed. Several other families recognised by Sweet (1988), were also reclassified within the six recognised by Dzik (1991): the Icriodellidae within the Icriodontidae, the Cyrtoniodontidae into the Prioniodontidae and the Polyplacognathidae into the Balognathidae. This reflects Dzik's (1991) re-interpretation of the weighting of different morphological characters in comparison to Sweet's (1988) and his concern that a more rigorous classification would place too great an emphasis on the diversification of the period. For instance, Sweet (1988, p. 71) classified the Polyplacognathidae as a separate family because of the apparent reduction of non-platform elements within the apparatus; because the morphology of their P elements could be compared to those of the balognathids, Sweet (1988) suggested that this family was derived from the balognathidae as members of the Balognathidae, presumably because he believed the possession of large platform-bearing elements to be a stronger classifying character than a contrasting apparatus plan.

Aldridge and Smith were asked to review conodont classification in 1993. Their resulting classification divided the conodonts into seven different orders, four of which were characterised by possessing coniform apparatuses and three characterised by functionally differentiated apparatuses. The Prioniodontida contained fourteen different families:

Balognathidae Cyrtoniodontidae Distomodontidae Icriodellidae Icriodontidae Multioistodontidae
Oistodontidae Paracordylodontidae Periodontidae Plectodinidae Polyplacognathidae Prioniodontidae Pterospathodontidae Rhipidognathidae

Although the work basically followed that of Sweet (1988), some modifications were included. The inclusion of the Pterospathodontidae followed Dzik (1991) and the work of Männik and Aldridge (1989), which supported the inclusion of *Pterospathodus* within the prioniodontids. Aldridge and Smith (1993) also challenged the inclusion of *Pedavis*, *Sannemannia* and *Streptotaxis* within the icriodellids and preferred to refer them to the icriodontids.

Stouge and Bagnoli (1999) have presented the most recent paper to consider the classification of prioniodontid condonts. They suggested that one of the main reasons that the suprageneric classification of prioniodontids has remained controversial was because of the number of different apparatus plans present within the group. The new classification proposed by Stouge and Bagnoli (1999) was based on the identification of genera that possessed distinct apparatus plans and persisted as unbroken lineages. Once apparatus plans were identified the authors then studied the taxa to decide how they related to each other. Stouge and Bagnoli (1999) focused on the prioniodontid order, as recognised by Sweet (1988) and the superfamilies Prioniodontoidea Bassler and Balognathoidea Hass. They introduced a new order, Polyplacognathida, composed of Polyplacognathidae Bergström and the new family Cahabagnathidae.

Stouge and Bagnoli (1999) recognised a basic prioniodontid plan that was characterised by two or four pairs of pectiniform P elements with three processes, nine S elements and a pair of M elements. The authors suggested that *Tripodus* and *Oistodus* possessed an apparatus that was fundamentally different from the prioniodontid apparatus outlined above. On the basis of this, they suggested that the Oistodontidae genera were not closely related to the Prioniodontida, as suggested by Sweet (1988), and that it is more appropriate to designate the genus *Oistodus* as a member of the Ozarkodinida (see Dzik, 1991).

A new order, Polyplacognathida Stouge and Bagnoli was created to include conodonts characterised by possessing bimembrate apparatus plans, therefore excluding these taxa from the Prioniodontida where they were previously classified by Sweet (1988) and Aldridge and Smith (1993). Stouge and Bagnoli (1999) thought that this was an appropriate classification, because they believed that the taxa within the Polyplacognathida possessed their own distinct evolutionary history. The families and orders considered by Stouge and Bagnoli (1999) are listed below (Figure 6):

Order Prioniodontida

Superfamily – Prioniodontoidea Family Prioniodontidae Family Phragmodontidae Family Oepikodontidae Superfamily – Balognathoidea Family Balognathidae Family Pygodontidae

Order Polyplacognathida

Family Polyplacognathidae Family Cahabagnathidae

Discussion.

It is apparent that many of the pieces of work reviewed above regarded apparatus structure as one of the most important criteria for classifying conodonts. Other factors considered included geological occurrence, stratigraphical occurrence and element morphology and ultrastructure. Dzik (1976, 1991) and Stouge and Bagnoli (1999) obviously regarded apparatus structure as of paramount importance and used it almost solely as a basis for their classification schemes. At this stage, it is almost impossible to classify prioniodontids according to their apparatus structures, as there is so little information. Only two types of natural assemblage have been found that have revealed clear architectural data (Aldridge *et al.*, 1995; Repetski, 1997, Chapter 5) and it is not known to what extent these reflect the Prioniodontida as a whole.

Most authors have regarded their classification criteria as flexible and designated taxa according to the character they considered to carry the greatest weight. For instance, Lindström (1970) originally included taxa that possessed only platform elements as prioniodontids, but the now commonly accepted diagnosis for the Prioniodontacea describes conodonts that possessed P, M and S elements. Sweet and Bergström (1972), Sweet (1988) and Robison (1981) have had to 'bend the rules' to include platform only conodonts (such as *Eoplacognathus*) within the prioniodontids. Fåhræus (1984) attempted to distance himself from this practice by rigidly following strict guidelines; in particular apparatus structure. As a result, when he re-evaluated the Prioniodontacea, many of the taxa became reclassified amongst the Hibbardellacea. This reclassification was not generally accepted (Sweet, 1988; Aldridge and Smith, 1993) because the elements of the taxa that are now accepted to belong within the Hibbardellacea (see Sweet, 1988) are morphologically characteristic and therefore probably phylogenetically distant from those elements belonging to many of the prioniodontid taxa.

The work of Sweet (1988) has successfully replaced the original form taxonomy and provided a starting point from which condont taxonomy can be communicated and further refined. The general outline of Sweet's

classification (1988) is still followed here because there is still only limited data with which to compile a new classification to infer a more meaningful phylogeny. However, following the work of Männik and Aldridge (1989), Dzik (1991) and Aldridge and Smith (1993), compounded by data presented in Chapter 3.1, *Pterospathodus* is reclassified as a prioniodontid.

Some of the families identified, for instance the balognathids, probably represent distinct, biological groups that are united by stratigraphic and geographic ranges, element morphologies and element ultrastructure. However, some of the families require more data to clarify whether they represent a biological group or a group of conodonts that have been assembled together because some of their elements are morphologically similar, for instance the classification of *Icriodella* and *Icriodus* in the *Treatise* (Robison, 1981). Groupings such as these have occurred during the many attempts of conodont classification because of a lack of data. Commonly, this lack of data is replaced by personal bias, and by loose application of diagnostic criteria.

Classification Criteria.

The classification of conodonts requires a "concise philosophical and methodological foundation" (Fåhræus, 1984). Because the data are derived solely from the palaeontological record, some relationships will never be known, due to the disjunct nature of conodont collections. It is only possible to provide a framework that can be used to ascertain, with as little personal bias as possible, the most likely phylogenetic position for each conodont taxon.

Obviously, the primary criteria to be considered when assessing the phylogenetic relationships between different taxa are the stratigraphic and geographic occurrences of the taxon. For example, species of *Periodon* and *Phragmodus* share the same type of apparatus, and similar component elements, but biogeographic studies show that it is impossible for them to be closely related, as demonstrated by Barnes *et al.* (1979) (Figure 2).

Recent work (Repetski, 1998; Purnell and Donoghue, 1998, Chapter 5) indicates that the apparatus plan for many of the prioniodontid conodonts was probably more conservative than has been suggested previously. It is possible that close examination of elements belonging to other prioniodontid taxa will further support this claim. The elements of conodonts belonging to the Polyplacognathidae appear to possess an apparatus plan that differentiates them from those with a more conventional 'prioniodontiform apparatus', as described by Sweet (1988); even so the only unequivocal evidence for clearly differentiated plan is seen in the natural assemblages of *Promissum* (Aldridge *et al.*, 1995). It is apparent that the bauplan of a conodont apparatus is a distinctive characteristic and can certainly be used to identify different families within the prioniodontids.

If a basic prioniodiform apparatus plan proves to be standard for many conodont taxa, then element morphology and ultrastructure will be of paramount importance if elements are to be successfully homologised to evaluate possible phylogenies. There are at least two orders of classification rank that can be identified following studies of element morphologies and ultrastructures.

For example, if the component P elements of two apparatuses that are thought to share the same basic bauplan (e. g. *Baltoniodus* and *Icriodella*), are pastinate and carminate respectively (Chapters 1.1, 4.1), then it is probable that these two morphologies represent a wide phylogenetic gap and are not characteristic of the same family.

Within the same family, the morphology of elements can also differentiate between species. For example P_1 elements of *Baltoniodus variabilis* are pastinate, with narrow ledges along the processes. Elements of *Baltoniodus gerdae* have developed a large platform along the sides of the processes and are clearly not the same species as *Baltoniodus variabilis*, but the basic morphology of the elements is still comparable and because both taxa share the same apparatus plan, so they have been included within the same family.

The criteria listed by Lindström (1970) are still important, but the level of use of application of each individual criterion, has resulted in the multitude of different classification systems. Previous classification systems have provided a means of categorising conodonts, but are not reliable as true phylogenetic impressions of the relationships between different taxa. Without a full cladistic study, incorporating all of the classification criteria discussed above, it is impossible to present an unbiased report of conodont phylogeny. However, many taxa are so poorly known that it is impossible to provide enough information to enable a full analysis. Work presented here provides the kind of detailed information that is required before a full cladistic study can be applied.

The classification of selected prioniodontids.

The classification of Sweet (1988) has been most widely accepted. Work presented here has considered four prioniodontid taxa: *Baltoniodus, Eoplacognathus, Icriodella* and *Pterospathodus*. Comments are made about their positions within the classification of Sweet (1988) and more detail and resolution has been provided using detailed studies of element morphology and ultrastructure. *Baltoniodus* represents a stock of prioniodontids that originated in the Early Ordovician and persisted through to the beginning of the Late Ordovician (Sweet, 1988). Several taxa are thought to have evolved from *Baltoniodus* (Sweet, 1988, Stouge and Bagnoli, 1999), so a clear understanding of its apparatus should provide a useful insight into the possible apparatus plans of taxa thought to be closely related. *Eoplacognathus* is currently classified as a polyplacognathid because of its reduced apparatus plan. A consideration of the apparatus plan is presented (Chapter 2.1) and it appears likely that *Eoplacognathus* did have a reduced apparatus, but that it is possible that there were not just two types of element within the apparatus. The P elements of *Icriodella* and *Pterospathodus* have been closely examined and a clearer understanding of ontogeny and morphology has been

presented (Chapters 3.2, 4.2). This helps position these taxa within what is currently understood to be the Prioniodontida.

Baltoniodus. By comparing the disarticulated elements associated with *Baltoniodus* with the apparatus of *Promissum* (Chapter 1.1) it is clear that the S elements can be directly homologised and therefore their positions known with some confidence. It has also been possible to identify the most likely positions for the P elements of *Baltoniodus* within the apparatus. These studies have shown that the apparatus of *Baltoniodus* possessed nine S elements, a pair of M elements and at least two pairs of P elements, thus agreeing with the reconstructions of Bergström (1966) and later authors (for example Dzik, 1994). There is, however, a close homology between the elements of *Baltoniodus* and *Promissum*, and one would not expect to find a radically different P element architecture; never the less, *Promissum* had four pairs of P elements and *Baltoniodus* may only have had two. It is possible that *Baltoniodus* had three pairs of P elements (Chapter 1.1), homologous to the P₁ to P₄ elements of *Promissum*, if the P₁ and P₂ positions that are serially duplicated in *Promissum* are only represented by one position in *Baltoniodus*. If this hypothesis were corroborated then an apparatus containing three pairs of P elements would represent a clearly distinct apparatus structure that characterised the balognathids and their close relatives.

Eoplacognathus. P elements of *Eoplacognathus* grew in a way comparable to *Baltoniodus* and they are probably homologous to the P elements found in the apparatus of *Promissum* (Chapter 2.1). That such close homologies can be demonstrated indicates that all three of these taxa shared a common ancestor. Despite such close homologies the apparatus of *Eoplacognathus* (Chapter 2.1) is clearly different from that of *Baltoniodus* and *Promissum*. It is clear that although *Eoplacognathus*, *Baltoniodus* and *Promissum* possessed homologous P elements, they did not have comparable apparatus plans. Following the procedure proposed by Sweet (1988) *Eoplacognathus* should be classified within a separate family.

Icriodella. Close examination of the P_1 element of *Icriodella* has revealed the true pastinate nature of the element, thereby confirming the classification of *Icriodella* amongst the prioniodontids (Chapter 3.2). Importantly this also provides important information with regard to the identification and coding of processes for cladistic analysis. In the past P_1 elements of *Icriodella* were thought to possess a 'posterior' and 'anterior' process (e. g. Aldridge, 1972, Sweet, 1988). My studies presented here (Chapter 3.2) have shown that these processes should really be called 'posterior' and 'lateral' (dorsal and caudal respectively) thereby allowing accurate comparisons between different taxa.

Pterospathodus. Pterospathodus has been classified by Sweet (1988, p. 99) within the ozarkodinids because he envisaged that the P_1 elements developed their lateral expansions by the modification of a carminate ozarkodinid type of element. However, studies presented here (Chapter 4.2) have shown that it is not the obvious lateral expansions that provide *Pterospathodus* P_1 elements with their pastinate nature. What makes these elements truly pastinate is the small bulge on the opposite side of the 'lateral' process that is a subdued 'anterior' process, only expressed internally (Chapter 4.2). This substantiates Aldridge and Smith's

(1993) reclassification of *Pterospathodus* within the prioniodontids. Aldridge and Smith (1993) classified *Pterospathodus* within the prioniodontids because there were strong comparisons to be made between *Pterospathodus* and other prioniodontids taxa such as *Pranognathus*. Now the internal structure of *Pterospathodus* P_1 elements is understood it is no longer necessary to 'bend' the rules to include the pterospathodontids within the prioniodontids. This information also allows accurate identification of processes, facilitating cladistic studies.

Conclusions.

If the prioniodontids represent a natural group it should be possible to identify a unifying character. The taxa presented in this study can all be shown to possess pastinate P elements, and it is possible that this character, first clearly described by Lindström (1970), is still suitable.

Stouge and Bagnoli (1999) placed much emphasis on apparatus structure as a classifying character and distinguished between different orders on the strength of different plans. Work here has shown that it is possible that the apparatuses of *Promissum, Baltoniodus* and *Eoplacognathus* all possessed different apparatus templates; yet detailed work on the ontogeny and morphology of their P elements has shown that they all share several characters that indicate a close homologies. It is, therefore, likely that species of *Eoplacognathus* do not belong in a separate order from the Prioniodontida, as has been suggested by Stouge and Bagnoli (1999). In reality, it is possible that all these taxa should be classified together within a larger family that is united by its element characteristics, and separated by the different apparatus plans that are becoming increasingly evident with more detailed studies (see Chapters 1.1, 2.1, 3.1, 4.1).

Work presented here and by other authors (Sweet, 1988, Aldridge and Smith, 1993, Stouge and Bagnoli, 1999) has shown that several different apparatus plans are present within prioniodontid taxa; therefore, the prioniodontiform apparatus template (Sweet and Bergström, 1972) does not provide a suitable diagnostic character for the order. It is thought here that the possession of a pastinate element is a suitable synapomorphy and it is likely that this still provides a suitable basis for diagnosis of the Prioniodontids. What is uncertain is what degree of morphological diversion from this basic element plan merits further classification, a problem first addressed more than thirty years ago (Sweet and Bergström, 1972).

Sweet and Bergström (1972) suggested that it is possible that the root stocks for all major conodonts could be found within the taxa classified within the Prioniodontacea. If this is true then it would be expected that there must be some type of uniting character that characterises this common ancestry. All four of the taxa studied here possess an internal pastinate structure although not all of them express this externally. Detailed analyses of Silurian conodont taxa, including those currently classified within the ozarkodinids might also reveal similar internal evidence of the legacy of a common ancestry.



Figure 1. Phylogenetic diagram of Ordovician Prioniodontacea according to Sweet and Bergström (1972).



Figure 2. The stratigraphic ranges of different apparatus types and possible evolutionary relationships of the main Ordovician conodont multielement taxa, according to Barnes *et al.* (1979).



Figure 3. Phylogenetic proximity of genera referred to the super families Priniodontacea, Hibbardellacea and lcriodontacea and outline of generic composition of their families, according to Fåhræus (1984).



Figure 4. Ordovician and earliest Silurian families and genera of the Prioniodontida, according to Sweet (1988).



Figure 5. Phylogenetic relationships and stratigraphical distribution of higher taxa discussed by Dzik (1991).



Figure 6. Evolution of genera in the Prioniodontida Dzik 1976 and the new order Polyplaconathida of Stouge and Bagnoli (1999), from Stouge and Bagnoli (1999).

CONCLUSIONS AND IMPLICATIONS FOR FUTURE WORK.

Much of the most recent conodont research has concentrated on ozarkodinid taxa because the large number of natural assemblages available and amount of data available. Prioniodontids have not received such close attention due to the dearth of natural assemblages and the lack of understanding of the complex forms of P elements that are common to the group. The discovery of the natural assemblages of *Promissum* (Aldridge *et al.*, 1995) provided a new template for conodonts that possessed pastinate elements, but did not lead to many changes to prioniodontid apparatus reconstructions. This is due to the unusual morphology of some of the P elements within the apparatus of *Promissum* that appear to have no homologues within prioniodontid taxa known only from disjunct collections.

Apparatuses. The apparatus of ozarkodinid conodonts is known to a high degree of detail due to the large number taxa represented by natural assemblages (see Purnell and Donoghue, 1997 for review). Reconstructing prioniodontid apparatuses is a more ambiguous process, as there are only two taxa preserved as natural assemblages. This means that apparatus reconstructions have to rely on hypotheses of relationships and the identification of elements that are homologous to those represented in the natural assemblages. I have attempted to reconstruct prioniodontid apparatuses, basing my apparatus reconstructions on a reinterpretation of the P elements of the apparatus of *Promissum*. The additional information, revealed by silicon rubber moulds, has provided previously unknown information about the disposition of processes about the cusps of P1, P2 and P3 elements. A clear understanding of the elements of Promissum has facilitated apparatus reconstructions of prioniodontids known only from disjunct collections, which previously had no known homologues occurring in natural assemblages. The new understanding of element morphology within the apparatus of Promissum allows direct morphological comparisons with disarticulated elements, and convincing homologies can be recognised. However, with phylogenetic distance it becomes increasingly difficult to homologise elements of younger more derived taxa with those of Promissum, for instance Pterospathodus (Chapter 3). The internal structure of these elements provides the only evidence which can be used to understand the development of the element and recognise their possible homologues in elements from Promissum.

The apparatus architecture of *Promissum* differs from that of the ozarkodinids because there are two additional pairs of P elements. Due to their identical morphologies it is possible that one of the most caudal pairs of P elements represents a serial homologue. This may indicate that the apparatus plan was not common to other prioniodontids and that there were not two pairs of identical elements in the caudal position of other prioniodontids. The P₄ element remains problematic and its morphology is still unclear. It may have a ramiform type morphology, or may have a morphology that is more closely related to the element that occupies the P₃ position. Detailed information derived from the Pc element of *Pterospathodus*, a possible homologue of the P₄ element, has shown that it differs from the other P elements and may have more allegiance with the ramiform array. This lends support to the suggestion that the P₄ position was occupied

by an element that possessed a ramiform type morphology and may explain its apparent absence from disjunct collections.

Because of the apparent absence of an element in the P_4 position, and the possibility of a reduced number of P elements, resulting apparatus reconstructions have indicated that the apparatus of *Promissum* may represent an extremely derived apparatus plan and that the homologies between the apparatus of *Promissum* and the ozarkodinids will need readdressing. It may be that both the P_1 and P_2 positions in *Promissum* are homologous to the P_1 position that occurs in the apparatus of the ozarkodinids and should be termed P_{1a} and P_{1b} . This would imply that the P_3 position is homologous with the P_2 of the ozarkodinids. This is a solution that I would favour as it is likely that the process aligned with the dorsal process in ozarkodinid elements. A closer understanding of the ozarkodinid elements and their phylogeny may help to confirm or refute this hypothesis. It is considered premature to use this revised apparatus interpretation in this project, as additional evidence is still required to homologise the P elements of the ozarkodinids to the P elements of *Promissum*.

It appears that the more pleisiomorphic plan is represented by *Phragmodus* and the ozarkodinids, a plan that appears to have remained stable for more than two hundred million years (Donoghue, 1996).

Histology. The histology of ozarkodinid conodonts has been examined in great detail (Donoghue, 1998) where the interrelationship of the different tissues was examined and a model of growth proposed. My analysis of prioniodontid histology has attempted to examine the internal tissues and patterns of growth of four prioniodontid taxa that span from the lower Ordovician, through to the middle Silurian. The sections have shown that all four taxa possess comparable hyaline tissues and that these are also closely comparable to those of the ozarkodinids. White matter varies the most, but much of this variation may be down to the success of sectioning resolution. Despite this, it has been possible to clarify the internal structure of white matter cores within denticles, and further analysis of the distribution of component structures may lead to a greater understanding of the growth and development of the tissue.

Close examinations of ultrastructure has revealed subtle differences, for instance the internal structure of *Baltoniodus* P elements is organised into clearly distinguished spindles, this type of internal structure was not found in the other taxa examined. Also, elements of *Icriodella* possess a form of white matter that differs in its distribution and ultra structure when compared to the other taxa in this study. The correct identification homologous characters, such as element formation and histological structures is essential if the classification of prioniodontids is to be refined.

A large number of sections through different regions of the elements have provided a greater understanding of the growth of individual odontodes. The inter-relationships between the component tissues of the elements examined add weight to the interpretation of crown tissues as a developmental homologue of enamel.

Internal crystallite patterning has been compared directly to the ultrastructure of enamel and the process of enamel formation linked with the pattern of surface ornamentation found on conodont elements. A strong relationship is suggested that links the position of the retreating secretory organ, and the external patterning that results. The mineralising front of enamel, formed by a palisade of cells, leaves a characteristic pattern, dependant on the direction in which it retreats (Boyde, 1976; Berkovitz *et al.*, 1992). During enamel formation, circular structures are formed if the enamel organ retreated in a direction that was perpendicular to the enamel surface.

It is possible that the polygonal patterning found on conodont surfaces also replicate the structure of a mineralising front. The morphology of the polygons suggests that the secretory organ may have retreated in a direction perpendicular to the element surface, in a way directly analogous to the formation of enamel. The gradation of the more elongate stretched polygons, or ropy ornamentation from that of the polygonal ornamentation implies that it also replicates the presence of an enamel front and may result from an enamel front that retreated in an extremely oblique direction.

This was also suggested by Dzik (1999, 2000), where he proposed that orientation of the cell controlled the amount of mineralised tissue deposited and accounted for the element morphology. The rate of hyaline secretion and development of element morphology is considered more complicated than this. It is likely each odontode was secreted by an individual population of cells and that these responded to processes, not clearly understood, that controlled the direction and rate of retreat. Therefore, the morphology of each odontode was reliant on the position and rate of retreat of the population of secretory cells, not the size of the secretory pole of the cell, or its angle of contact.

Internal structure of elements and the application of terminology. The revised terminology (Purnell *et al.*, 2000) provides a means to identify biological orientations and apply terminology to the processes of prioniodontid elements. Conventionally processes have been identified by their positions on the cusp, i. e. a process that develops off of the anterior face of the cusp represents a 'anterior' process. My internal studies have shown that the P_1 elements of all four taxa develop a 'posterior' (dorsal) process with a 'anterior' (ventral) process, which is often recurved away from the main axis of the 'posterior' process. After this a 'lateral' process joins the 'posterior/anterior' (dorsal ventral) axis, often continuing in a straight line with the 'posterior' process.

Technically the 'lateral' process should be termed 'lateral' because it forms a junction with the lateral face of the cusp. This is normally clearly apparent in juvenile specimens, where the processes form distinct junctions with the cusp. With maturity, however, the origin of these processes often becomes obscured as they increase in size and a process that was originally 'lateral' often ends up occupying a position that is 'anterior' to the cusp. Also, in cases where the 'anterior' process is unexpressed externally, the element is composed of a 'posterior' and 'lateral' (dorsal and caudal) process that both form the main axis of the element.

This type of growth is common throughout the prioniodontids and it is probably the main type of growth that forms elongate platform elements (for example *Gamachignathus*, McCracken *et al.* (1980) and *Lenodus*, Stouge and Bagnoli (1990).

In some cases the discrepancy between the internal structure of elements and the external expression has resulted in the misidentification of processes i. e. platform elements of *lcriodella* (Chapter 4.1). However, internally the record of the juvenile morphology is still maintained and the 'lateral' process is easily identified, as it develops off the pre-existing 'anterior/posterior' axis.

This mode of growth may also account for the morphology of P elements belonging to the ozarkodinids, where the 'anterior' (ventral) process is no longer unexpressed externally. In the future it may be appropriate to provide a different terminology for the processes, so that the terms have no orientation implications. This would avoid having to call the process that is directed ventrally, a caudal process, because of the internal arrangement of processes.

Function. The function of P elements belonging to prioniodonts has been addressed and compared to the function of the ozarkodinid P elements. Each taxon has been dealt with independently, and the type of function analysed incorporating apparatus reconstructions and element modelling. Hypotheses of function were methodically tested by analysing patterns of surface damage and wear. The hypotheses were further tested by studying the distribution of internal tissues. The apparatus reconstructions placed the P elements opposite each other with the long axis of the element orientated dorso-ventrally and occluded across the mid axis of the apparatus. It is not certain how closely elements of *Baltoniodus* or *Pterospathodus* occluded and it is possible that there was not always direct element on element contact. Elements of *Eoplacognathus* and *Icriodella* almost certainly occluded closely with the right element behind the left, this is shown by the pattern of wear that was apparent on the element surfaces.

Within enamel tissues, the formation of decussation planes are thought to have allowed the diversification of early ungulates and increased the durability of enamel to the greater stress levels required for the change of diet (Rensberger, 1995). Decussation planes protect enamel by preventing cracks from propagating down continuous planes of weakness. The distribution of white matter within conodont elements may indicate that the development of such a tissue represents a selective response to the imposition of increased stress that might have resulted from the occlusion. This would have allowed increased experimentation and diversification of P element morphologies. This is perhaps clearly demonstrated by the unequivocal damage where layers of hyaline tissue have been broken off the apical tips of the blades of *lcriodella*, within a region of the element where stress regimes are predicted to be high, but white matter is poorly formed.

Element juxtaposition within the apparatus. The P_1 element of *Icriodella* is morphologically comparable to the platform elements of ozarkodinids. However, internal studies (Chapter 4.1, 4.4) have shown that the processes are not homologous. Sectioning the elements of *Icriodella* has revealed that it is the

caudal process that has formed the platform whereas it is the dorsal process that has formed the platform in the ozarkodinids. Functional studies and natural assemblages have shown that the P_1 and P_2 elements of ozarkodinids occluded with their left element behind the right (Purnell, 1995; Donoghue and Purnell, 1999a). This contrasts to my studies of both *Eoplacognathus* (Chapter 2.4) and *Icriodella* (Chapter 4.4) which have concluded that P_1 elements occluded with the right element behind the left.

All four of the taxa studied possess P elements that have a comparable internal structure which suggests that they may have derived from a common ancestor. However, it is not known whether this element plan represents be a very broad homologous character that is shared by all conodonts characterised by complex differentiated feeding apparatuses.

Prioniodontids may represent a single clade, that has retained a plesiomorphic P element form and sectioning of ozarkodinid conodonts may reveal a relic of internal pastinate morphology, supporting the proposed evolution of the ozarkodinids from the prioniodontids (Sweet, 1988). Confirmation of these hypotheses await a detailed cladistic analysis based on homologous element structures and apparatus reconstructions.

The research described in this thesis has opened up several lines of further work. Detailed histological studies of other prioniodontid taxa will provide a broader understanding of the types of hard tissues present and their variation across different taxa. Closer analysis of the distribution of white matter tissues within conodont elements and its distribution appears to differ subtly between different taxa, as is inferred by the data presented here. Also broadening the study of the distribution and precise form of surface ornamentation found on prioniodontid elements may provide a set of characters that distinguish between different lineages, an idea proposed by Lindström and Ziegler (1971). Examination of the basal bodies of the four taxa studied has revealed a simple laminated atubular dentine like tissue and further research is now required to analyse which groups are characterised by this tissue type.

This project has concentrated on the P elements of prioniodontid apparatuses, however, it is possible that S elements may possess histological characters that unite different forms of related taxa, such as the distinctive growth of elements of *Carniodus*. Also, little research has considered the function of the S elements, save for postulating that they acted as a grasping or rasping array (Aldridge *et al.* 1995; Purnell and Donoghue, 1997). A detailed study of ramiform element surfaces for possible surface wear or damage may help to elucidate the role played by the ramiform array.

The reconstruction of prioniodontid apparatuses is by no means resolved, and it is not known which, if any prioniodontids are characterised by the apparatus of *Promissum*. The discovery of the natural assemblages of *Phragmodus* confirms that not all prioniodontids had a complex architecture comparable to *Promissum*. Resolution of this paradox will require the discovery of more prioniodontid apparatuses.

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