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Growth and patterning in the conodont skeleton

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Recent advances in our understanding of conodont palaeobiology and functional morphology have rendered established hypotheses of element growth untenable. In order to address this problem, hard tissue histology is reviewed paying particular attention to the relationships during growth of the component hard tissues comprising conodont elements, and ignoring *a priori* assumptions of the homologies of these tissues. Conodont element growth is considered further in terms of the pattern of formation, of which four distinct types are described, all possibly derived from a primitive condition after heterochronic changes in the timing of various developmental stages. It is hoped that this may provide further means of unravelling conodont phylogeny. The manner in which the tissues grew is considered homologous with other vertebrate hard tissues, and the elements appear to have grown in a way similar to the growing scales and growing dentition of other vertebrates.

Keywords: conodont; agnathan; histology; odontode; enamel; dentine

1. INTRODUCTION

Conodont affinity has been the subject of debate ever since the microscopic tooth-like elements were first discovered (Pander 1856; for a review, see Aldridge 1987). The topic remains controversial even after 140 years of research and the discovery of soft tissue remains of conodonts. More recent discussion has narrowed the debate to the acraniate–craniate level within the chordates, based primarily on characters of soft tissue anatomy (Aldridge *et al.* 1993; Aldridge & Purnell 1996; Aldridge & Donoghue 1997).

In the years preceding the discovery of preserved soft tissues, the affinity of the tooth-like phosphatic microfossils remained enigmatic. Palaeobiologists had attempted to resolve this conundrum using comparative anatomy of the architecture of the feeding apparatus (e.g. Schmidt 1934, 1950; Schmidt & Müller 1964), element morphology and histology. Although there are some notable exceptions, histological studies failed to take full advantage of comparative histology. Without any degree of constraint over affinity this proved an unprofitable line of research, resulting in a series of esoteric accounts of hard tissue ultrastructure.

In retrospect, it would never have been possible to reach an unequivocal conclusion regarding conodont affinity just by analysing element morphology and internal structure. A parallel can be seen in the debate over the affinity of *Hadimopanella* Gedik, which is represented in the fossil record almost exclusively by microscopic phosphatic sclerites. The sclerites are two-component hard tissue complexes composed of a microcrystalline base containing tubules, overlain by a hypermineralized glassy cap (Bengtson 1977). The structure and morphology of the sclerites, therefore, made *Hadimopanella* and related taxa convincing micromeric agnathans (Dzik 1986; Märss 1988; van den Boogaard 1988). However, the discovery of exceptionally preserved specimens composed of secondarily phosphatized soft tissues and articulated sclerites revealed *Hadimopanella* to be a palaeoscolecid, a poorly known group of Early Palaeozoic worms (Hinz *et al.* 1990; Müller & Hinz-Schallreuter 1993).

Now that we have a much clearer perception of conodont affinity, a new era in conodont comparative histology has begun. Dzik (1986), Sansom *et al.* (1992) and, to a lesser extent, numerous others (e.g. Andres 1988; Burnett & Hall 1992), have reviewed element histology in the context of our new phylogenetic understanding. The drawback of these studies is their reliance on direct comparison between specific structures within tissues, without considering other factors such as the interplay between the component hard tissues during growth. Because they failed to consider relative growth, these authors were unable to reconcile their interpretations with existing models of growth in conodont elements, or knowledge of tissue interaction in modern organisms. These studies have also been criticized because of their failure to consider the full spectrum of chordate hard tissues (Kemp & Nicoll 1995*a*).

One subject that has been ignored entirely is patterning. At present, we have only a broad understanding of how a few conodont elements grew, and then only at the simplest level. The growth of more complex elements can only be resolved by identifying recurrent patterns of growth in the internal structure of the hard tissues. Furthermore, there are a number of recurrent morphological patterns expressed by conodont elements through their fossil record. Do these reflect common ancestry or convergence? The pattern of formation is potentially a useful tool in discriminating homology from analogy. Knowledge of pattern formation would also be useful in comparing the growth of conodont elements with other vertebrate hard tissue complexes, and would enable investigation of the

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complexity shown during this early craniate experiment with skeletal mineralization.

The present study addresses the interpretation of the hard tissues after consideration of growth and patterning, and is organized into two sections. The first addresses pattern and is concerned primarily with the description of conodont hard tissues and their patterns of intergrowth. A new model of conodont hard tissue growth is presented, based on these patterns, and patterns of whole element growth are described. The second section considers process and evaluates competing hypotheses of hard tissue homology in the light of results from the first section, and a new interpretation of hard tissue histology is outlined. Patterns of whole element growth are evaluated in the light of these results, and compared with those shown by the hard tissues of taxa outside the Conodonta.

2. A HISTORICAL REVIEW OF STUDIES OF CONODONT HARD TISSUE HISTOLOGY

Conodont histology is currently in a state of disarray. Largely, this has arisen because the most recent studies have failed to address previous observations and interpretations. It is therefore pertinent to review our accumulated knowledge of conodont histology in an attempt to resolve differences in the current debate which persist for mainly historical reasons.

In the first paper on conodonts, Pander (1856) noted the lamellar nature of crown tissue and the presence of cells or cavities within the albid white matter. However, he incorrectly interpreted the direction of growth in the crown as inward, and it was more than 80 years before this was corrected by the work of Furnish (1938) and Hass (1941).

Although intervening years were occupied by various contentions over the affinities of conodonts, 30 years elapsed before Zittel & Rohon (1886) reviewed conodont histology and affinities. They were the first to attempt to homologize conodont hard tissues with those of another group. They considered lampreys and annelids as possible descendants, and compared the ultrastructure of the toothlets of these two groups with the histology of conodont hard tissues, concluding that conodonts were annelids.

Stauffer & Plummer (1932) provided an excellent review of the conodont controversy to that time. They compared their own observations on element microstructure with ivory (dentine), and also tentatively considered conodont element growth, concluding that the denticles, which were composed of white matter, were inserted into elements after the hyaline crown tissue had been fully formed.

Branson & Mehl (1933) were the first to use histology as a taxonomic character in conodonts, recognizing a group of 'fibrous' conodonts, the Neurodontiformes, which they later erected to the rank of suborder, distinct from all other conodonts (Branson & Mehl 1944).

Furnish (1938) briefly considered the growth of conodont elements, clarifying the mode of outer apposition of successive crown tissue layers, and was probably also the first to recognize internal discontinuities in the crown as evidence of *in vivo* damage and repair. This observation is normally attributed to Hass (1941), who recognized the relevance of internal discontinuities as evidence of external and not internal growth. Hass also noted the occurrence of hollow spaces or tubules within white matter and the presence of interlamellar spaces in lamellar crown tissue. Beckmann (1949) later exhumed Pander's contention of vertebrate affinity, interpreting all component hard tissues as dentine. He was the first to develop a model for conodont element growth, and this remains the only synthesis of complex element morphogenesis (figure 1*a*). Beckmann identified cavities within lamellar crown tissue that he believed to have been interconnected, and to have supplied nutrients from the pulp (basal cavity) to interconnected tubules within white matter. He believed that the nutrients were finally transported to the outer surface of the element, which was covered by a temporary mesh-like secreting tissue. The renowned vertebrate histologist Ørvig considered Beckmann's model 'untenable' as, in his opinion, 'the substance of which the cusps are built up is clearly different from all hard tissues met with in vertebrates' (Ørvig 1951, p. 381). However, Ørvig's criticisms were only aimed at the final proposed homology of the hard tissues with dentine and did not consider the growth model itself. The presence of the cavities within lamellar crown tissue has subsequently been verified by light microscopy (Müller & Nogami 1971, 1972) and electron microscopy (Barnes *et al.* (1973*a*), who similarly suggested that their function was to transport nutrients); that they are interconnected has yet to be demonstrated. Interconnections between the white matter cavities that could facilitate transport of fluids from the basal cavity to the external surface of the crown are not present, and Pietzner *et al*. (1968) failed to find any evidence of interconnection whatsoever. Therefore, Beckmann's (1949) model is untenable not because the component tissues of conodont elements fail to resemble dentine, but because there is no ultrastructural evidence to support it.

Gross (1954, 1957, 1960) published a series of studies on conodont microstructure, in which he compared conodont hard tissues with those of vertebrates, particularly heterostracan dermal armour. Gross believed that growth increments within the crown did not coincide with the ridges apparent in the basal cavity or on the recessive basal margin (figure 1*b*,*c*, part *i*) which align with the incremental layers in the basal tissue. He conceded that the ridges were parallel with the incremental layers of the crown, but he concluded that incremental layers in the crown and basal body were not secreted synchronously. Gross invoked an elaborate, *ad hoc* hypothesis whereby special cells partly resorbed each incremental layer of crown tissue shortly after their secretion and prior to secretion of the subsequent layer of basal tissue. In this way, concentric ridges were formed over the base of the crown, parallel to the incremental layers, but not coinciding with them (figure 1*c*, part *i*). Hence the incremental layers abut with these ridges, but are not confluent with incremental layers within the crown. However, Gross believed that the earliest phase of growth was restricted to the crown, although his contention was probably based on oblique thin sections, or sections which failed to coincide with the growth centre of the elements. Furthermore, he did not perceive the basal body as a homogeneous structure, and proposed instead that it was composed of a 'Basistrichter' and 'Trichterfüllung' (basal cone and cone

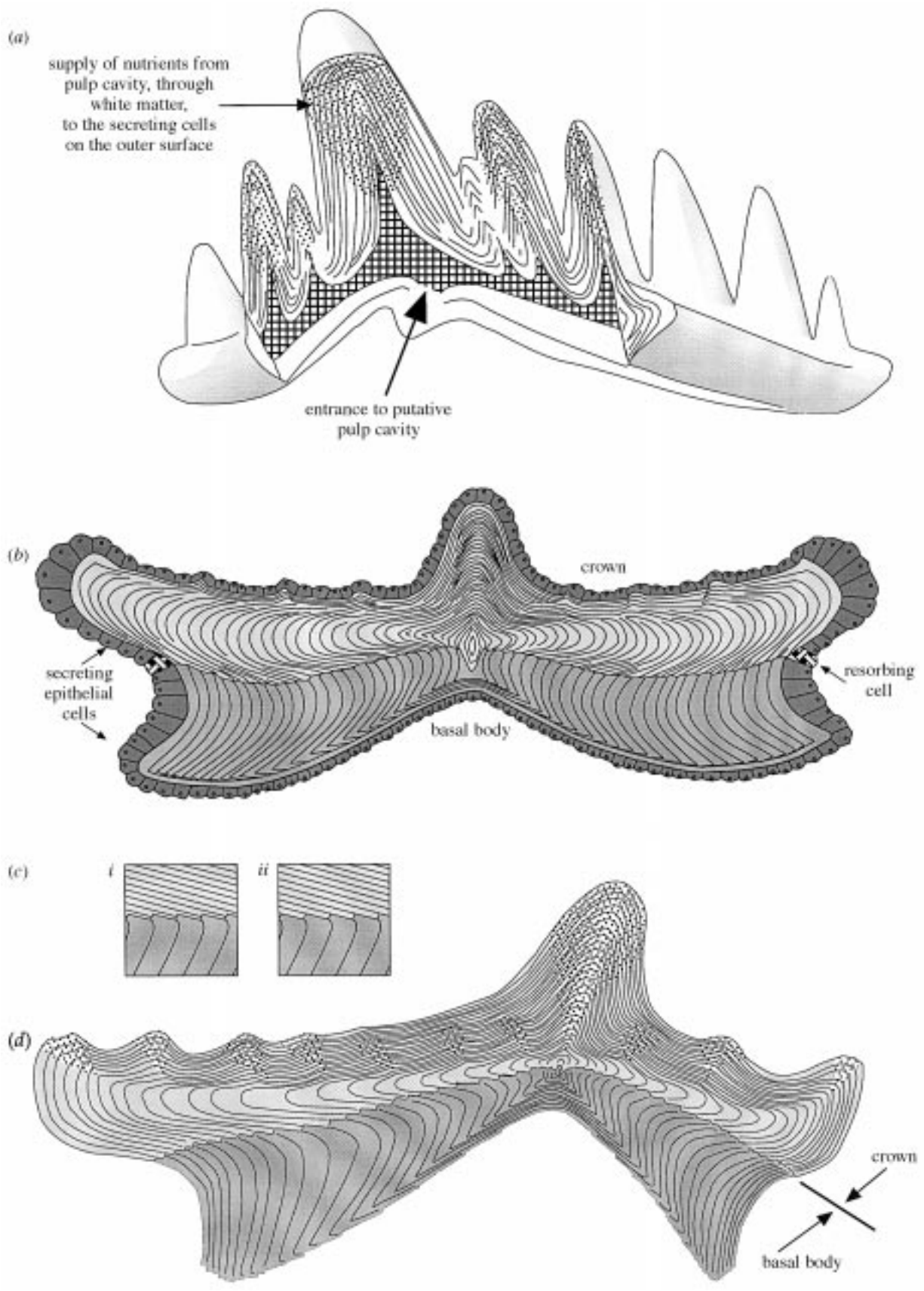


Figure 1. Previous growth hypotheses of Beckmann (1949), Gross (1957, 1960) and Müller & Nogami (1971, 1972). (*a*) Beckmann's was the only model to account for growth in multidenticulate elements. (*b*) Gross believed that growth increments within the crown had not been been secreted synchronously with those of the basal body. (*c*) Comparison of (*i*) Gross's and (*ii*) Müller & Nogami's hypotheses of growth. (*d*) Müller & Nogami finally resolved the synchronous growth relationship between the crown and basal body.

filling). Gross rejected the idea that conodont hard tissues were homologous with dentine and enamel as he erroneously believed that the conodont mode of centrifugal growth was incompatible with such an interpretation. He instead concluded that the elements were composed of exoskeletal bone. Gross's model of conodont element growth was subsequently negated by Müller & Nogami (1971) who clearly demonstrated the confluent passage of growth increments between crown and basal body (figure 1*c*, part *ii*, and *d*).

Quinet (1962*a*) provided a detailed account of the histology of *Ancyrodella* Ulrich & Bassler and *Polygnathus* Hinde Pa elements, confirming much of Hass's work and concluding that conodont elements could not have been teeth, or have performed a tooth function, because of their outer-appositional mode of growth. He also suggested that the ultrastructure of the elements compared well with exoskeletal bone, which is also covered by soft tissue in life. In a later publication, Quinet (1962*b*) described the histology of *Belodus* Ethington with which he compared the feeding elements of the polychaete *Nereis*, concluding that *Belodus* was a polychaete, and that the Conodonta represented a polyphyletic group.

One of the most unconventional interpretations of conodont affinity was proposed by Fahlbusch (1964) who partly justified his hypothesis on histological grounds. Fahlbusch compared the histology of conodont elements to fossil algal material, reinterpreting Gross's model of growth for conodonts to fit his predilections. Fahlbusch's model was poorly received and severely criticized (Beckmann *et al.* 1965).

Lindström (1955) made preliminary observations on the histology of Lower Ordovician conodont elements, describing basal bodies with lamellar and globular internal structures. Later, Lindström (1964) reviewed all aspects of earlier research and produced an excellent outline of conodont ultrastructure. His conviction that 'One may assume *a priori* that the inner structure must have a great systematic significance, greater perhaps than that of the surface morphology' (Lindström 1964, p.22), was to spark new interest in the histology of conodont elements that was sustained for the following two decades. Amongst many other observations and contentions, he believed that white matter had been formed by a process of resorption of crown tissue resulting in a series of hollows and inclusions within an otherwise lamellar structure (following Gross 1954). He resolved Gross's (1957, 1960) bizarre two-part division of the basal body into a single structure with partly discontinuous growth increments, and cast doubt on the basal resorption hypothesis by demonstrating the clear relationship between lamellar crown increments and the ridges on the aboral surface of elements. Lindström also disagreed with Gross's suggestion that the conodont crown was homologous with exoskeletal bone, but followed Gross's erroneous reasoning in discounting enamel and dentine as component tissues of the conodont skeleton.

Schwab (1965) described lamellar structure in the crowns of neurodontiformes, thereby reinstating them as conodonts. Schwab also distinguished the two structural forms of basal body: a 'cartilage-like' lamellar structure and a 'bone-like' spherular structure, later reinterpreted as atubular dentine (Sansom 1996) and globular calcified cartilage (Sansom *et al.* 1992), respectively. In a later paper, Schwab (1969) described the histology of *Panderodus denticulatus* Schwab as three-layered, including an inner lining surrounding the basal cavity, and inner and outer lamellar layers, the last containing what he believed to be dentine tubules. His distinction of separate layers is tenuous, and the 'dentine tubules' he described from the outer lamellar layer more probably represent alignment of the long (c) axes of the component crystallites.

Müller & Nogami (1971, 1972) produced the last reviews that were primarily based on light microscope study. These were probably the most influential of all works on conodont histology, describing a wide range of conodont taxa and producing a taxonomic grouping based solely on the internal structures of elements. Although often attributed to Gross, Müller & Nogami were also responsible for resolving the pattern of synchronous growth between the crown and basal body (figure 1*c*, part *ii*, and *d*). They also elaborated on Staesche's (1964) histological work by distinguishing a number of different types of white matter, which they proposed would be useful in taxonomy.

Three years earlier than Müller & Nogami (1971), the first of a series of studies which heralded a new era in ultrastructural research had been undertaken by Pietzner *et al.* (1968). This work included geochemical, transmission electron microscope (TEM) and scanning electron microscope (SEM) analyses of conodont elements, through which these authors refined knowledge of chemical composition and of the varying organic content of different tissues. They also described the discrete porous nature of white matter, and the structure of the other hard tissues. Structural differences between the crown and the basal body, including different crystal sizes and organic matter content, were also noted. Pierce & Langenheim (1969) were the only other authors to attempt a TEM study, in this case using Pa elements of *Palmatolepis* Ulrich & Bassler and *Polygnathus*, but their work failed to reveal any new information.

An SEM study of fractured surfaces led Lindström & Ziegler (1971) to conclude that white matter was secondarily derived from lamellar crown tissue by a process of recrystallization during the animal's life. In a later paper (Lindström & Ziegler 1972), they documented variation in crystal structure throughout the various tissues and suggested that the crown and basal body were not secreted synchronously, although each corresponding increment of the two tissues had been secreted in step. They suggested that the basal tissue increment was secreted first, and was subsequently matched by an increment of crown tissue. However, they presented no evidence in support of this model. They went on to review advances of conodont histology published since Lindström's (1964) monograph, paying particular attention to alternative interpretations of the growth of protuberances on the surfaces of Pa elements of *Pseudopolygnathus* Branson & Mehl (Ziegler & Lindström 1975).

During the early 1970s, Barnes and his co-workers published a series of studies on conodont histology with the aim of constructing a suprageneric classification scheme based on ultrastructure (Barnes *et al.* 1970, 1973*a*,*b*, 1975). This work revealed a number of characters that appear unique to specific groups, thereby at least partly fulfilling their objective. Most notably, a new internal microtexture was described from neurodontiform

hyaline elements—elongate crystallites containing microspheres 0.5 μm in diameter. Later, Wright (1989, 1990) interpreted these structures as microspherules expelled by Golgi apparatuses during mineralization. The Barnes team advocated a secondary origin for white matter from lamellar crown tissue, supporting the earlier contention of Lindström (Lindström 1964; Lindström & Ziegler 1971; Lindström *et al.* 1972).

Bengtson (1976, 1983) described and compared the histology of proto-, para- and euconodonts, proposing that they represented an evolutionary series. Szaniawski (1982, 1983, 1987) compared the most primitive group, protoconodonts, with the histology of modern chaetognath spines, concluding that protoconodonts were indeed the spines of fossil chaetognaths. Hence, if the proto-, para- and euconodont evolutionary series were correct, this would indicate that the affinity of true conodonts lay with the chaetognaths. By 1993, protoconodonts were considered a distinct group of animals, although the evolutionary relationship between para- and euconodonts was reaffirmed (Szaniawski & Bengtson 1993).

The advances made in conodont hard tissue histology during the late 1960s and the 1970s led to the possibility of using histology to distinguish conodonts from the sclerites of other organisms. Clark *et al.* (1981) even went so far as to include the histological complexity of conodont elements as a character in his diagnosis of the Conodonta. Chauff & Price (1980) used histological characters to justify the conodont affinity of their new Devonian genus *Mitrellataxis*, which they briefly compared microstructurally with fish scales from the same deposits. Wang (in Wang & Klapper 1987; Wang 1989) similarly used internal structure as a means of justifying the affinity of *Fungulodus* Gagiev. The presence of white matter, apparent in thin sections, was taken as unequivocal support for a conodont affinity, offering a contrast with the histology of thelodont dermal denticles. However, this interpretation remains equivocal (Wang & Turner 1985; Wang 1993). Adding further confusion, Wang (in Wang & Klapper 1987) disputed the conodont affinity of *Mitrellataxis* (Chauff & Price 1980) on histological grounds, concluding a vertebrate affinity. Histology was also used by Klapper & Bergström (1984) to assess the affinity of *Archeognathus* Cullison. They described *Archeognathus* as bearing a 'fibrous' crown and a lamellar basal body entirely lacking tubules or cell spaces. Klapper & Bergström thus concluded that dentine and bone were not present and that the fossils represented the remains of a conodont, and not a vertebrate.

In contrast, Barskov *et al.* (1982) described spongy and lamellar forms of basal body in *Neocoleodus* Branson & Mehl and *Coleodus* Branson & Mehl, compared spherical structures in the spongy form with osteocyte lacunae, and homologized the tissue with bone, concluding a vertebrate affinity for conodonts.

Von Bitter & Merrill (1983) described the histology of *Ellisonia* Müller using naturally fractured specimens. The fibrous nature of the crown tissue led them to suggest that ellisoniids were neurodonts, a group of conodonts conventionally deemed restricted to the Ordovician. Their observations suggested that the neurodonts were present at least as late as the Late Carboniferous (Pennsylvanian).

Before 1983, conodont histologists were evidently in a state of confusion; some authors recognized vertebrate hard tissues amongst conodont elements and used this as evidence of vertebrate affinity for conodonts. Conversely, other authors recognized a distinct histology which they used to discriminate conodonts from vertebrate microremains. This all changed with the discovery of conodont soft tissues (Briggs *et al.* 1983; Aldridge *et al.* 1986; Aldridge & Briggs 1986); conodont histologists finally had a context in which to evaluate the histology of the feeding elements (Dzik 1986). Dzik was the first to take advantage of this, and began by homologizing conodont basal tissue with dentine, and comparing conodont crown tissue with enamel. Similarly, when Andres (1988) described the histology of a number of Cambrian and early Ordovician conodonts representative of para- and euconodonts, he homologized basal tissue with dentine and crown tissue with enamel. Again, following Dzik, Andres concluded that paraconodonts were the ancestors of both euconodonts and vertebrates. Later, Burnett & Hall (1992) compared lamellar crown tissue with protoprismatic enamel.

Krejsa *et al.* (1990*a*,*b*) introduced a neontological perspective to conodont palaeobiology, comparing and homologizing the tissues of conodont elements with those of myxinoid keratinous toothlets (figure 2). They suggested that the basal body was a developing replacement tooth for the overlying functional crown, enabling the conodonts periodically to shed and replace their 'teeth'. They also interpreted spaces within white matter as homologous with the goblet-shaped pokal cells that underlie the keratinous toothlet covering in hagfish, apparently confirming the myxinoid affinities of conodonts. However, Krejsa *et al.*'s model ignores conodont histological features which render it untenable, such as the confluence of growth between the crown and basal body indicating that the two structures grew synchronously, not as separate generations. Furthermore, the histogenesis of hagfish toothlets is poorly understood; attempts to draw homology between them and conodont elements should be reserved until the histogenesis of hagfish toothlets has been properly documented.

In a series of papers, Sansom and his colleagues reviewed element histology in the light of the chordate affinity of conodonts (Sansom *et al.* 1992, 1994; Sansom 1996). Many of the observations of their 1992 paper had been made earlier by other authors (Barnes *et al.* 1975; Dzik 1986; Jeppsson 1980; Smith *et al.* 1987; Smith 1990), but Sansom *et al.* (1994) were the first to describe unequivocal dentine from conodonts, most notably in *Neocoleodus*. Sansom (1996) also described protoprismatic enamel from the Ordovician–Devonian conodont lineage *Pseudooneotodus* Drygant and placed the model of conodont element growth established by Müller & Nogami (1971, 1972; figure 1*c*, part *ii*, and *d*) into a biological and developmental perspective. M. M. Smith *et al.* (1996) extended the number of conodont taxa covered, and reviewed the relevance of the affinity and relative antiquity of conodonts to understanding the early evolution of the vertebrate skeleton.

The interpretations of conodont hard tissues by Sansom *et al.* (1992, 1994) remain controversial even though many accept conodonts as vertebrates (= craniates). Forey & Janvier (1993) aimed their criticisms primarily at the proposed homology between lamellar crown tissue and

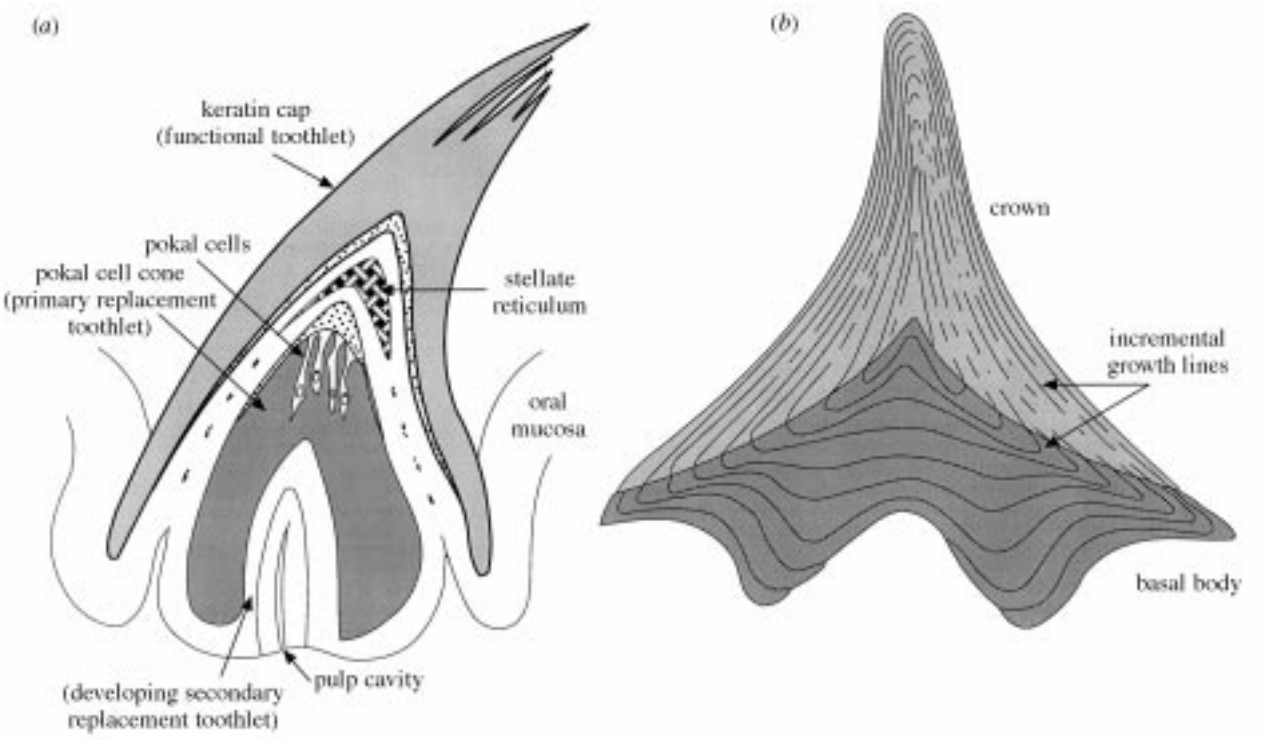


Figure 2. (*a*) Lingual tooth of *Myxine* Linnaeus in longitudinal section, after Dawson (1963) and Kresja (1990*a*,*b*). (*b*) Pa element of *Ozarkodina* in transverse section, after Müller & Nogami (1971). The functional keratin cap and replacement toothlet (pokal cell cone) of the myxinoid grow as distinct structures, whereas the crown and basal body (putative replacement crown of Kresja (1990*a*,*b*)) grew in intimate association.

enamel. The extreme variation in the orientation of crystallites in lamellar crown tissue, ranging from parallel to a highly angular relationship with the surface (particularly evident in taxa figured in Sansom *et al*. (1992); figure 3*i*), was thought to be incompatible with enamel, neither orientation corresponding precisely. The description of prismatic structure in the lamellar crown of *Pseudooneotodus* (Sansom 1996) has demonstrated that the lamellar crown can mirror the structure of some enamels. However, Sansom and his colleagues have still failed to reconcile the wide variation in conodont crown structure with the range of known enamels. Further, although Sansom (1996) has been able to reconcile his interpretations of hard tissue histology with both Müller & Nogami's (1971) model of conodont growth, and modern developmental systems, he has achieved this reconciliation without *a priori* considering how the tissues grew. Janvier (1995, 1996*a*,*b*) has further criticized the suggested homology of white matter with cellular dermal bone, suggesting a mesodentine affinity to be more likely. Schultze (1996) also disagreed with Sansom and his colleagues over their interpretations of conodont hard tissue histology. Most of these criticisms have been made earlier, but other points of contention result from Schultze's assumption that the work of Gross (1954, 1957, 1960) is correct, and he concludes 'the placement of conodonts in the animal kingdom will be solved as soon as a recent relative can been found' (Schultze 1996, p. 283).

Histological study of conodont elements has not been restricted to the mineralized hard tissues. Fåhraeus & Fåhraeus-Van Ree (1987) undertook a histochemical study (using haemalum and eosin) of preserved soft tissue remnants from the organic components of the mineralized tissues, finding them to be histochemically reactive after 415 Myr! Much of the tissue is very similar to modern collagen and also appears to preserve cell spaces; however, many of the structures remain enigmatic, and Fåhraeus & Fåhraeus-Van Ree (1987, p. 109) preferred to wait 'until stained tissue sections of early Palaeozoic vertebrate tissue (e.g. ostracoderms) have been produced', before firm conclusions were reached. However, although this work had already been undertaken over 20 years earlier (Tarlo & Tarlo 1961; Halstead Tarlo & Mercer 1966), the fidelity of preservation is too poor to be useful in comparison.

Kemp & Nicoll (1995*a*,*b*, 1996) also attempted to identify organic molecules within the mineralized matrix by staining them *in situ*, applying histochemical tests for collagen (picrosirius red), DNA (DAPI), keratin (Gram's stain), cartilage (Alcian blue) and protein (toluidine blue). These tests used a series of positive and negative controls (Kemp & Nicoll 1993, 1995*a*,*b*, 1996). Lamellar crown stained positive for collagen, so Kemp & Nicoll rejected the hypothesis that lamellar crown tissue is homologous with enamel, which is a purely epidermal product and contains no collagen. White matter and basal tissue failed to stain for collagen, but bone, cartilage and dentine are derived from ectomesenchymal and epidermal interaction, and contain collagen in life. Kemp & Nicoll (1995*a*) concluded that conodont hard tissues are not comparable with those of vertebrates. Attempts to repeat the results, even with modern vertebrate material and unequivocal fossil vertebrates, have failed (M. M. Smith, personal communication). Kemp & Nicoll have also failed to demonstrate the effectiveness of this test on uncontested fossil vertebrate material. Towe (1980) has shown that,

although tissues like collagen may be preserved physically with high fidelity, biochemical preservation is negligible. Furthermore, the instability of collagen is such that it can only be expected to survive biochemically intact for a few million years (Bada 1991). Therefore, although Fåhraeus & Fåhraeus-Van Ree (1987, 1993) may well have been correct in interpreting their isolated organic residues as containing collagen, it is unlikely that Kemp & Nicoll's results are meaningful.

Many questions regarding conodont hard tissue histology remain unanswered: the primary or secondary nature of white matter has yet to be conclusively determined; no clear model has been published to show how conodont elements grew, other than at the very simplest of levels (Müller & Nogami 1971, 1972); and we need to address the problem of how more complex elements were grown.

3. MATERIAL AND METHODS

(a) *Material*

The present study was based primarily on material from the reference collection of the Micropalaeontology Unit, Leicester University Geology Department. Of the figured material, specimens with numbers prefixed by BU are reposited at the Lapworth Museum, University of Birmingham; those with a ROM prefix are reposited at the Royal Ontario Museum, Toronto, and those with a C prefix are reposited at the Geological Survey of South Africa, Pretoria.

(b) *Methods*

Conodont element ultrastructure has been examined using a variety of methods including thin sectioning, the examination of naturally and artificially fractured specimens, and the use of scanning electron, incident light, transmitted light and laser confocal microscopy.

Thin sections were made by embedding elements in cold-curing polyester resin, set in nitrile Beam capsules, the elements oriented according to the required section. The polyester cylinders were then ground to the appropriate level and polished on a rotating felt lap with 0.05 μm alumina powder. The polished surface was bonded to a frosted glass slide using cold-curing epoxy resin (Buelers' Epothin). The opposing side of the polyester cylinder was removed using a diamond-tipped annular saw and the excess resin ground away using 600 and 1000 grade carborundum powder until the desired level within the conodont element was reached. The exposed surface was polished as before, either by hand, or by using an automated attachment to the rotating felt lap.

Thin sections were studied using transmitted light and laser-confocal microscopy. For SEM, the thin sections were etched using 0.5% orthophosphoric acid for varying periods, always less than 10 min. The sections were either permanently coated with gold, or temporarily coated with carbon (following Repetski & Brown 1982) or silver (following Mills 1988).

Of the naturally and artificially fractured specimens studied, natural fractures were found to be less revealing due to diagenetic alteration of element ultrastructure. Artificial fractures were produced using an entomological needle mounted in a pin vice; inverted conodonts elements were fractured by applying pressure to the pin, which was seated in the basal cavity of the element. Immersion of the specimen in a small droplet of water was found to prevent loss during this procedure. Specimens were subsequently etched using 0.5% orthophosphoric acid for 6–8 min and coated for SEM study.

There has been some discussion in the literature relating to the relevant merits of the microstructural study via thin section versus fractured surfaces (Lindström & Ziegler 1971; Barnes *et al.* 1973; Müller 1981). Both methods have the potential to produce 'artefacts' that do not truly reflect microstructure. However, care in the interpretation of thin sections can obviate this problem. The use of fractured surfaces in studying microstructure is more contentious (see, for example, discussion in Barnes *et al.* (1973*b*)), although by employing etching techniques it is possible to discern artefacts from true microstructure. In addition, despite the mistrust of the etch-fracture technique by some conodont histologists, this methodology is commonly used in vertebrate palaeohistology (e.g. Smith 1989). The technique is also supported in theoretical consideration of the behaviour of brittle solids during failure (e.g. Dally & Riley 1991).

The simplest and most rapid method of studying microstructure is by immersion of elements in oil of a refractive index close to that of apatite (1.68). It is also important for the oil to have a relatively high viscosity, thus preventing flow away from the specimen. In this way, tens of elements can be studied at once using traditional light and laser confocal microscopy. For laser confocal microscopy the specimen was first bonded to the slide using a small amount of gum tragacanth. In contrast with other techniques, this method is non-destructive and the oil can readily be removed by washing the specimens in ethanol.

Light micrographs were taken using a Leitz Aristoplan fitted with differential interference contrast. Scanning electron micrographs were taken on a Hitachi S-520.

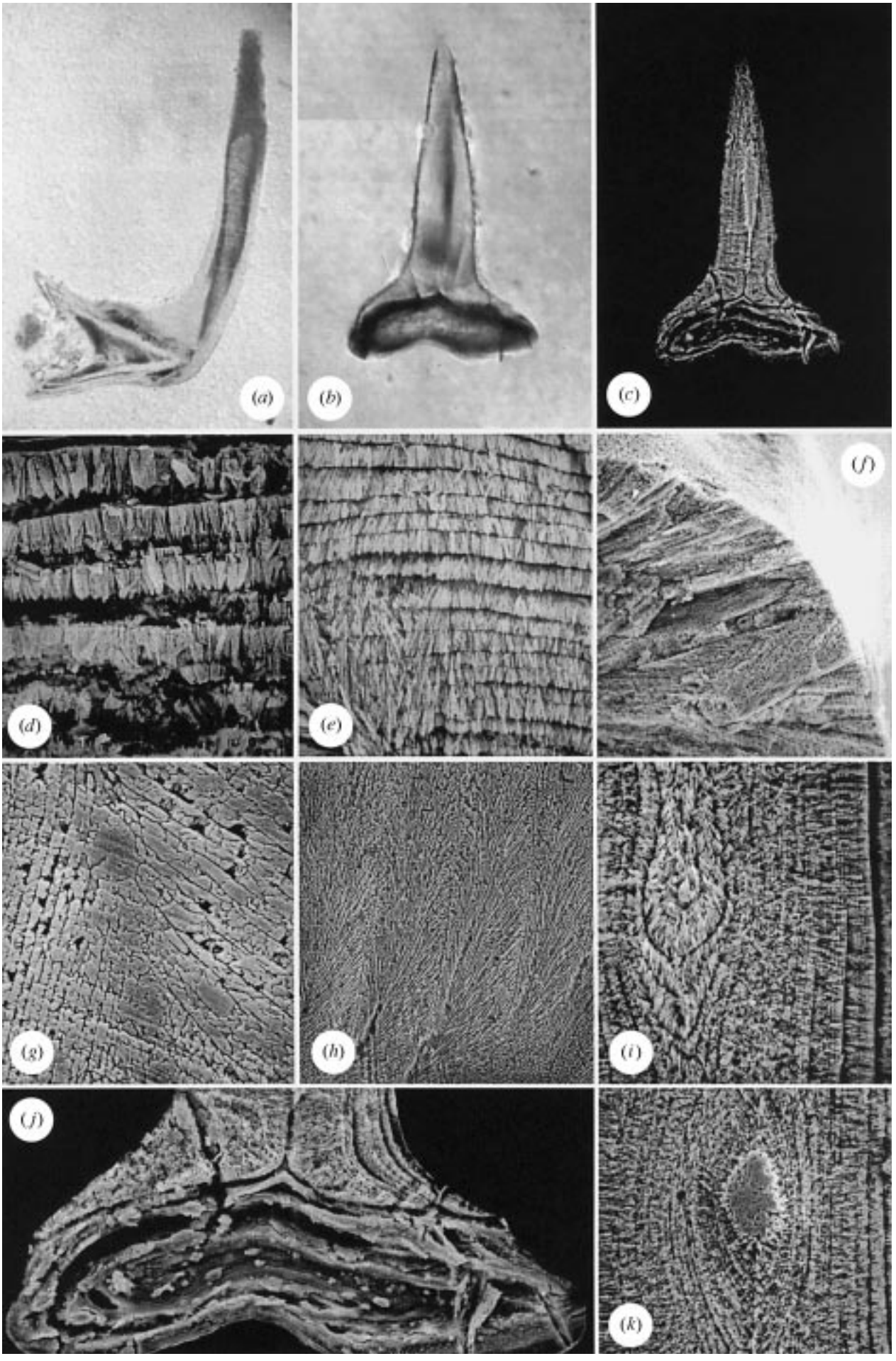
4. PATTERN: THE CONODONT ELEMENT

Characteristically, conodont elements are constructed from two basic units: the crown and underlying basal body (figure 3*a–c*). The crown is composed either entirely of hyaline lamellar crown tissue (figure 4*e–j*), or of a combination of lamellar crown and white matter (figure 3*a–c*). The basal body is a single component structure composed from a hard tissue herein termed basal tissue.

(a) *The component tissues*

(i) *Lamellar crown tissue*

This is the most coarsely crystalline of all conodont hard tissues and usually comprises the major component of conodont elements. The length of individual crystallites is extremely variable, ranging from less than 1 μm to in excess of 30 μm, but they are usually no more than a few microns long. The crystallites are bounded at either end by the punctuating growth lines which define the lamellae that are so characteristic of the tissue (e.g. figure 3*d*,*e*). The orientation of the crystallites relative to the growth increments, and thus the surface at the time of growth, is inconsistent (e.g. figure 3*i*) and has in the past been attributed to 'the direction in which the main ontogenetic growth occurred at the place in the lamella where the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crystal is located' (Hass & Lindberg 1946, p. 501). In many simple coniform elements the crystallites are arranged with their long (c) axes parallel or sub-parallel to the long axis of the element, such that the entire crown is composed of a single homogeneous prism of crystallites in a fan-like arrangement. In 'complex' conodont elements, the prismatic structure of the element is broken up into a number of individual prisms, each comprising a denticle (figure 3*h*). Because the crown of a multidenticulate element is structurally more differentiated than the crown of a coniform element, the main ontogenetic vector of growth is not so extreme. As a result, the more extreme variations of crystallite arrangement, such as sub-parallel to the growth lines, are less prevalent than in coniform elements. 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 oriented perpendicular to the outer surface (e.g. the variation in figure 3*i*,*k*). Crystallites adjacent to the basal cavity are inclined upwards and outwards relative to the junction of the crown with the basal body (figure 3*j*).

(ii) *White matter*

White matter is a term derived from the appearance of this tissue in reflected light. White matter contrasts sharply with lamellar crown tissue because of its more finely crystalline composition (figure 4*a–d*), its markedly greater resistance to standard dental acid etchants (e.g. Stauffer & Plummer 1932; figure 4*b*), its lower organic content (Pietzner *et al.* 1968) and the lack of punctuating growth increments. White matter occurs exclusively in denticles as cores (figure 5*i*) and has sharply defined lateral margins. The cores appear dark in transmitted light (figures 3*a* and 5*i*,*j*) because of the cavities enclosed within the fine-grained groundmass (figure 4*a*,*c*,*d*). These cavities vary considerably in their size, shape and orientation. Most common are tubular cavities (figure 4*d*), which occur in two size distributions both of which are predominantly oriented with their long axes parallel to the long axis of the denticle: longer tubules, typically 20–30 μm in length, and shorter tubules (figure 4*c*), usually only a few microns in length. The calibre of the tubules is usually in the order of 0.25 to 1 μm, but they sometimes expand into a large (3–7 μm diameter), sometimes irregular, cell-shaped cavity, from which other tubules may splay (figures 4*c* and 5*l*). These larger cavities are rare but ubiquitous, and usually occur at the oral end of connected tubules (figure 5*l*). It is likely that the tubules and cavities represent the sites of mineral-secreting cells.

Although white matter and lamellar crown tissue are extremely distinctive tissues, the junction between the two is imperceptible in transmitted light (figure 5*j*,*k*). This is the main reason why conodont histologists in the 1970s generally interpreted white matter as secondarily derived from lamellar crown tissue. However, when these tissues are studied in etched sections, their mutual boundary is extremely sharp (compare figures 3*b* and *c*).

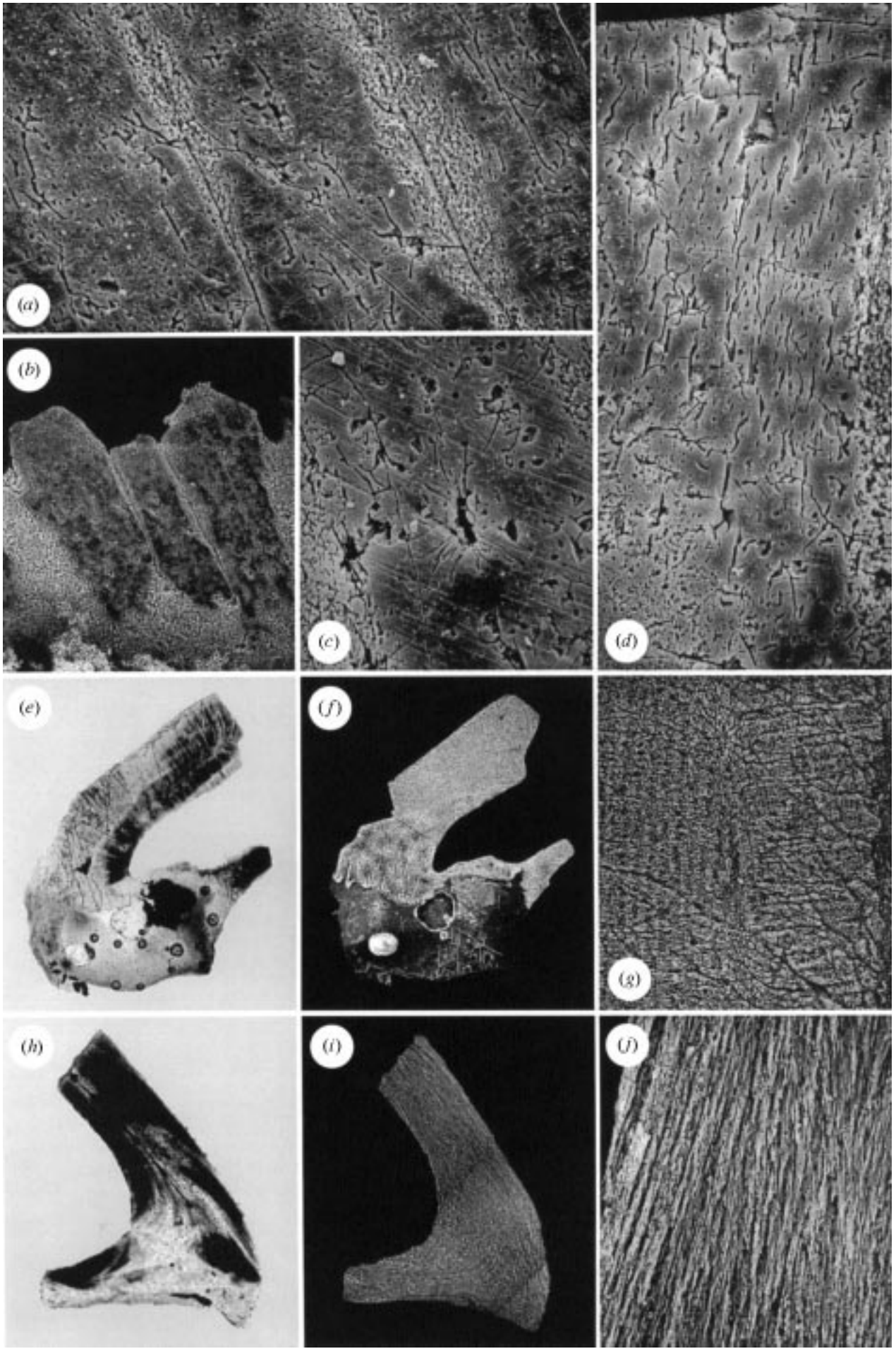
The transitional zone apparent to Barnes *et al.* (1973*a*) between the two tissues does not appear to be lamellar, coarsely crystalline or cancellate in transmitted light, so it is difficult to resolve whether it is lamellar crown, white matter or a third, previously unrecognized tissue. However, in properly etched sections, no transitional tissue is evident, and the boundary between white matter and lamellar crown is extremely sharp. The apparent transitional zone is in fact white matter that lacks cavities.

The problem of distinguishing white matter from lamellar crown is further complicated because not all the tissues that appear albid in reflected light are true white matter; when they are examined in fracture or thin-section they can be seen to be forms of lamellar crown tissue (figure 4*e–j*). In most cases, the albid area occupies a site where crystallites in successive increments of lamellar crown are not aligned. An albid effect can also result from hypocalcification (figure 13*f*), and may additionally occur at sites of radiating prismatic structure. Such 'pseudo white matter' includes Müller's (1981) white matter categories 3*a–d* and can usually be distinguished by transmitted light examination under immersion oil. True white matter is cancellated in appearance and can only be identified unequivocally by thin sectioning and examination of etched surfaces with a SEM.

(iii) *Basal tissue*

Basal tissue comprises the entire basal body and is often clearly punctuated by growth striae (figure 3*a*). The tissue is so finely crystalline that individual crystallites cannot be discerned under light microscopy. In complete specimens, successive increments extend over the lower surface of the basal body, thereby encapsulating all previous increments (figure 3*j*). However, basal tissue is the most variable of all conodont hard tissues, both between taxa and within a

Figure 3. (*a*) Longitudinal section through an Sc element of *Coryssognathus dubius* composed of a basal body (to left) and crown (to right); the crown includes an opaque core of white matter. Specimen BU 2616, frame width 547 μm. (*b*) Light micrograph, and (*c*, *j*) scanning electron micrographs of a transverse section through a Pa element of *Ozarkodina confluens*. Note the relationship between the white matter in (*b*) and (*c*), and the variation in crystallite orientation at the crown–basal body junction in (*j*). Specimen BU 2617, (*b*, *c*) frame widths 458 μm, (*j*) frame width 158 μm. (*d*) Perpendicular arrangement of crystallites in a Pa element of *Ozarkodina confluens*. Specimen BU 2618, frame width 27 μm. (*e*) Pre-prismatic arrangement of crystallites in a Pa element of *Scaliognathus anchoralis* Branson & Mehl. Specimen BU 2613, frame width 55 μm. (*f*) Protoprismatic arrangement of crystallites in a Pa element of *Idiognathodus* sp. Specimen ROM 53261, frame width 114 μm. (*g*) Transverse section through the cusp of a Pa element of *Ozarkodina confluens*. Note the oblique orientation of crystallites relative to the bounding incremental growth lines. Specimen BU 2615, frame width 22.5 μm. (*h*) Arrangement of crystallites into distinct prisms which form the denticles in the free blade of a Pa element of *Mestognathus beckmanni* Bischoff. Specimen BU 2620, frame width 284 μm. (*i*, *k*) Variation in crystallite arrangement in a horizontal section through a Pa element of *Ozarkodina confluens*. (*i*) Changing from perpendicular at the margin of the element, and oblique at the core of the element. Specimen BU 2621, frame width 76 μm. (*k*) Subvertical arrangement of crystallites adjacent to the core of white matter. Specimen BU 2621, frame width 118 μm.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single taxon. For instance, the structure of the *Cordylodus* Pander basal body is known to vary from coarse spheroids (Müller & Nogami 1971; Sansom *et al*. 1992; figure 5*a–c*) to laminated (Kemp & Nicoll 1995*a*); *Pseudooneotodus* exhibits both spheroidal structure (figure 5*d*,*e*) and lamellar form with microspherules (Sansom 1996). Some specimens of *Chirognathus* Branson & Mehl possesses a basal body with lamellar structure and perpendicular fine calibre tubules (Sansom *et al*. 1994; Müller & Nogami 1971, 1972), but other specimens apparently have a clearly atubular laminated structure (Kemp & Nicoll 1995*a*). Müller & Nogami figured a single specimen of *Neocoleodus* with a lamellar basal body, whereas Sansom *et al*. (1994) have recorded a non-lamellar basal body that includes branching tubules. Some basal tissue is neither laminated, spheroidal nor tubular.

The fine calibre tubules described from the basal body of *Chirognathus* and *Neocoleodus* have only rarely been recorded in conodont elements, whereas coarser tubules have been recorded in many more taxa, including all those claimed to possess dentine tubules prior to the work of Sansom *et al*. (1994) (e.g. Andres 1988; Dzik 1986). The coarser tubules are typically 50 μm diameter (too coarse to be dentine processes) and meander throughout the basal body.

Most basal bodies are atubular, particularly those of the order Ozarkodinida (*sensu* Sweet 1988), and they usually occur within concentric growth increments equivalent to growth striae in the crown (figure 5*f*,*g*). The basal tissue lamellae are rarely perfectly concentric and are discontinuous or disrupted, usually because of incorporated microcalcospheres that often occupy much of the area just below the crown–basal body junction, and frequently occupy the core of the structure (figures 3*j* and 5*e*,*f*). Intergradation between all forms can occur within a single taxon, and sometimes within a single specimen (figures 3*j* and 5*c*), indicating that all the structures are features of a common tissue possibly affected by the timescale of growth. The presence of the microspherules in a homogeneous, unstructured matrix therefore indicates rapid growth, and the well-organized lamellar and tubular structures represent slower, ordered growth.

Reduced mineralization of the basal body is a consistent feature of Early to Late Palaeozoic conodont elements, and many lineages have no record of a basal body. Pathological features of crown morphology in elements of some taxa (e.g. *Polygnathus xylus xylus* Stauffer in Nicoll (1985), text-fig.1H, V) indicate the presence of an inflexible structure, and so a basal body was certainly present *in vivo*; the reason for lack of preservation of the structure is unknown, although the most likely reason is that it was not completely mineralized.

By the Carboniferous, very few taxa have any record of the presence of a mineralized basal body. This is evident in the Carboniferous conodonts with soft tissue preservation (Aldridge *et al*. 1993), and the exceptionally preserved 'bedding plane assemblages' that represent the undisturbed but collapsed remains of the feeding apparatus (Purnell & Donoghue 1997, 1998). Not one of the many hundreds of articulated skeletal remains of ozarkodinids possesses even the remnants of a basal body. Interestingly, although gondolellid elements (order Prioniodinida) have been recovered with intact basal bodies from sediments of the Carboniferous and later (e.g. Müller & Nogami 1971, pl. 15, fig. 4), the many bedding plane assemblages of *Neogondolella* Bender & Stoppel and *Gondolella* Stauffer & Plummer (Rieber 1980; Orchard & Reiber 1996; Merrill & von Bitter 1977) possess no basal tissue. This is also true of all recorded fused clusters. However, this bias may be taphonomic as collections from the Devonian of Western Australia contain polygnathid clusters with no basal tissue, whereas isolated elements from the same sample have fully preserved basal bodies (Nicoll 1985, personal observation).

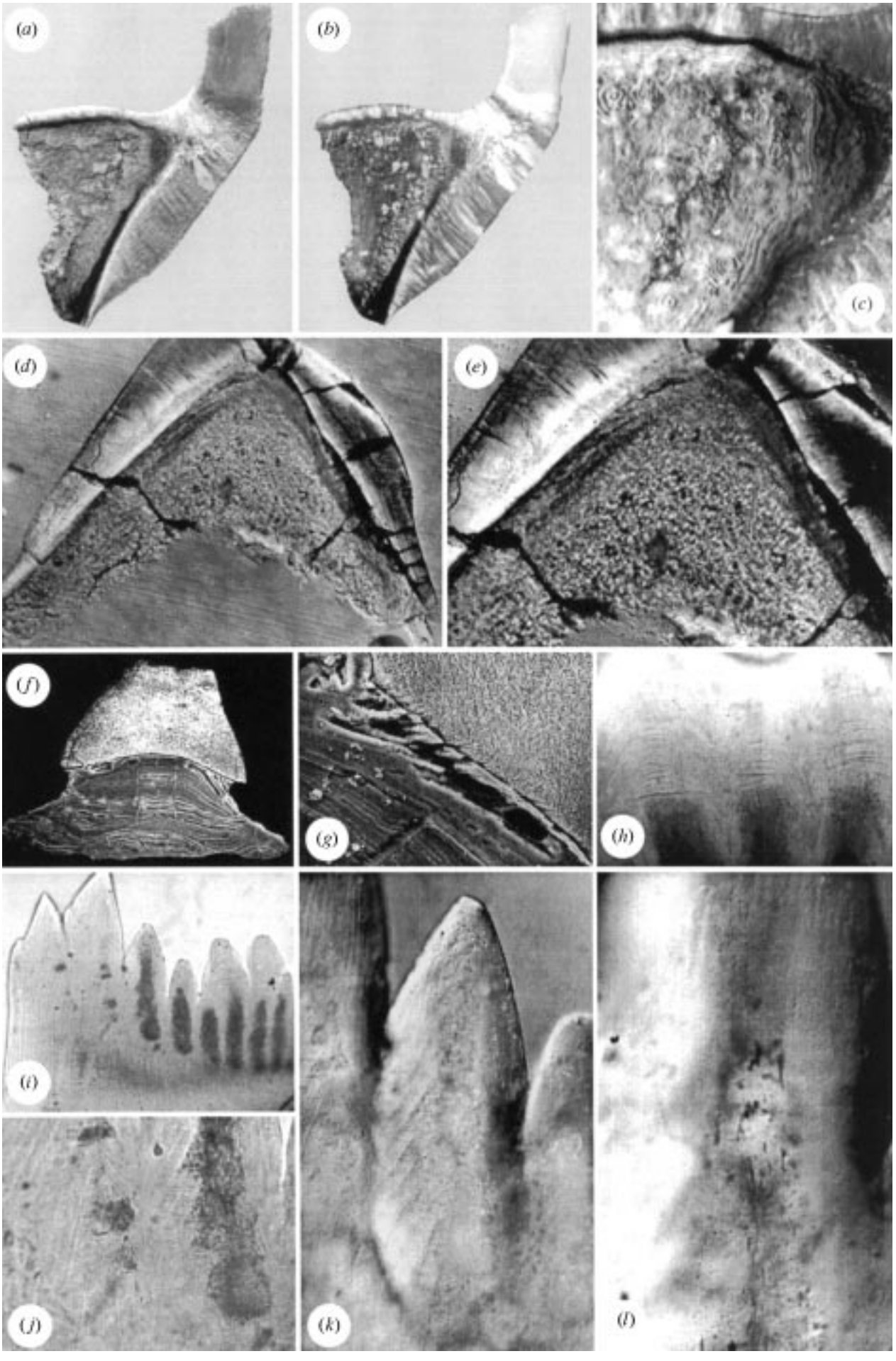
(b) *Interrelationships of the tissues during growth*

The crown is known to have grown by outer apposition because many elements display evidence of episodes of damage and subsequent repair (Furnish 1938; Hass 1941; figure 5*h*). The confluent passage of incremental growth striae between the crown and basal body indicates that the two structures were grown synchronously (*contra* Gross 1957, 1960; Krejsa *et al*. 1990*a*,*b*) and, by inference, that the basal body also grew by outer apposition. The innermost core of each element therefore represents the earliest growth stage, and the outermost layer the latest.

It is possible to determine the growth relationship between the lamellar crown tissue and the junction with the underlying basal body. At the base of the crown, crystallite orientation indicates growth up and away from the junction with the basal body (figure 3*j*). Unfortunately, the crystallites that compose the basal tissue are too small to determine orientation, and the growth direction can only be resolved by inference. However, the nature of the growth relationship between the crown and the underlying basal body indicates a mirroring of the pattern of growth apparent in the crown.

The two basic units that compose a typical conodont element therefore grew in opposing directions relative to the crown–basal body junction (figure 1*c*, part *i*, and *d*;

Figure 4. (*a*,*b*) Longitudinal section through an Sc element of *Ozarkodina confluens*. The white matter cores are bound by a thin sheath of lamellar crown tissue (arrowed) which expands orally. Specimen BU 2622, (*a*) frame width 121 μm, (*b*) frame width 233 μm. (*c*) Cell-shaped space incorporated within the fine-grained groundmass of white matter from a Pa element of *Ozarkodina confluens*. Specimen BU 2615, frame width 26.7 μm. (*d*) White matter core of an Sc element of *Ozarkodina confluens*. The tissue is dominated by vertically orientated tubules, many of which branch in the plane of the section. Specimen BU 2619, frame width 50 μm. (*e–g*) Longitudinal section through an element of *Cordylodus angulatus*. Note the relationship between the opaque areas in (*e*) and the scanning electron micrograph in (*f*), which indicates a complete absence of true white matter. The opaque areas probably result from optical effects produced by the prism bounadries in (*g*). Specimen BU 2623, (*e*, *f*) frame widths 1541 μm, (*g*) frame width 200 μm. (*h–j*) Longitudinal section through an element of *Ligonodina* sp. Bassler. As in (*e–g*), despite the presence of opaque areas in (*h*), (*i*) reveals an absence of true white matter resulting from interfering crystallite arrangement in (*j*). Specimen BU 2624, (*h*, *i*) frame widths 805 μm, (*j*) frame width 90 μm.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cf. Sansom (1996), although his methodology followed *a priori* interpretations of the component tissues). This pattern alone is evident in many coniform conodont elements that lack white matter, but elements with an albid component are far more complex structurally and their growth is much less well understood. Given their antiquity and importance in our understanding of the early evolution of vertebrates and their skeletons, this is an important area of investigation.

Although the flanks of white matter cores are usually planar (figure 4*a*,*b*), more rarely they are stepped (figure 5*i*–*k*), each step coinciding and confluent with incremental layers in the surrounding crown tissue, thereby providing an insight into the relationship between these two tissues during growth. This arrangement appears to indicate that the two tissues grew synchronously and at the same rate. Examples where increments of the lamellar crown pass conformably into white matter have been figured many times (e.g. Barnes *et al.* 1973*a*, fig. 6.6; Sansom *et al.* 1992, fig. 3e), but in figure 5*i*–*k* the white matter is bounded by the growth increments. The length of the long tubules within the white matter core greatly exceeds the thickness of individual increments of the adjacent crown tissue (figures 4*a* and 5*l*). This indicates that growth of white matter was more continuous than the punctuated growth of lamellar crown, and that the control over the secretion of the two tissues was distinct. Because of the outer appositional mode of growth of the surrounding tissue, it is likely that white matter also grew in this way. The polarized nature of the cell-shaped cavities within white matter therefore suggests that the secreting cells retreated orally, usually ahead of the mineralizing front, and hence only the cell processes (the tubules) were commonly incorporated into the mineralized matrix. Furthermore, the polarization of the shorter, perpendicular tubules and attached cavities indicates that they grew away from their junction with the lamellar crown tissue. This contrasts strongly with the direction of growth of the lamellar crown tissue, which from the orientation of the crystallites was usually perpendicular (figure 5*j*,*k*) or sub-perpendicular (figure 3*g*) to the flanks of the white matter cores and long axes of the denticles.

White matter was therefore secreted as a continuous core of mineralized tissue, partly controlled at the margins by the secretion of lamellar crown. White matter, therefore, forms a series of upwardly tapering collars around, and merging with, the core (figure 6). Although secretion of the two tissues was independently controlled, the lack of a plane of weakness, such as at the junction of the crown and basal body (figure 5*g*), suggests that mineralization of the two tissues was simultaneous rather than staggered.

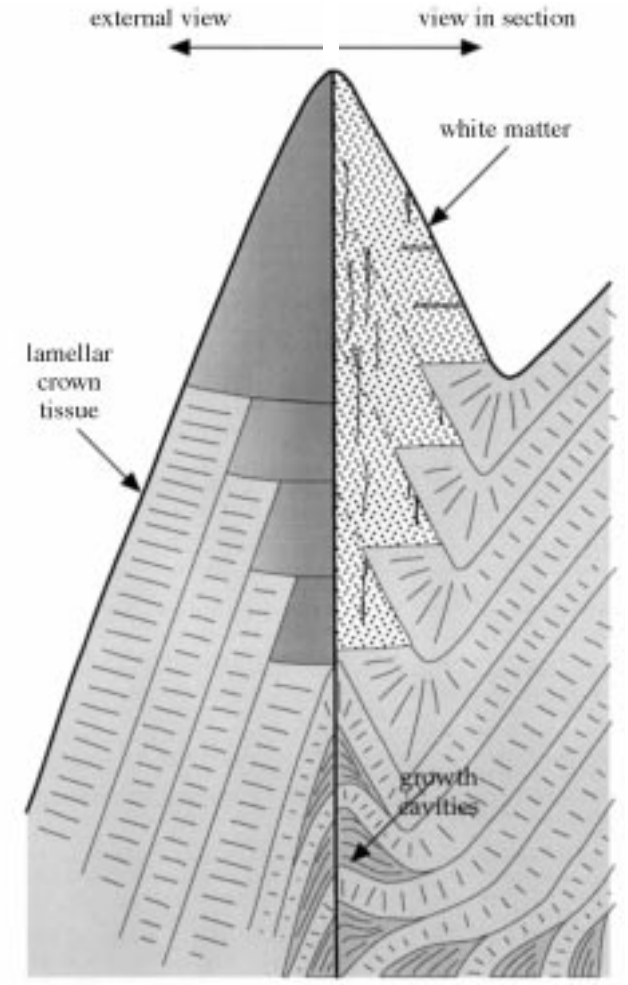
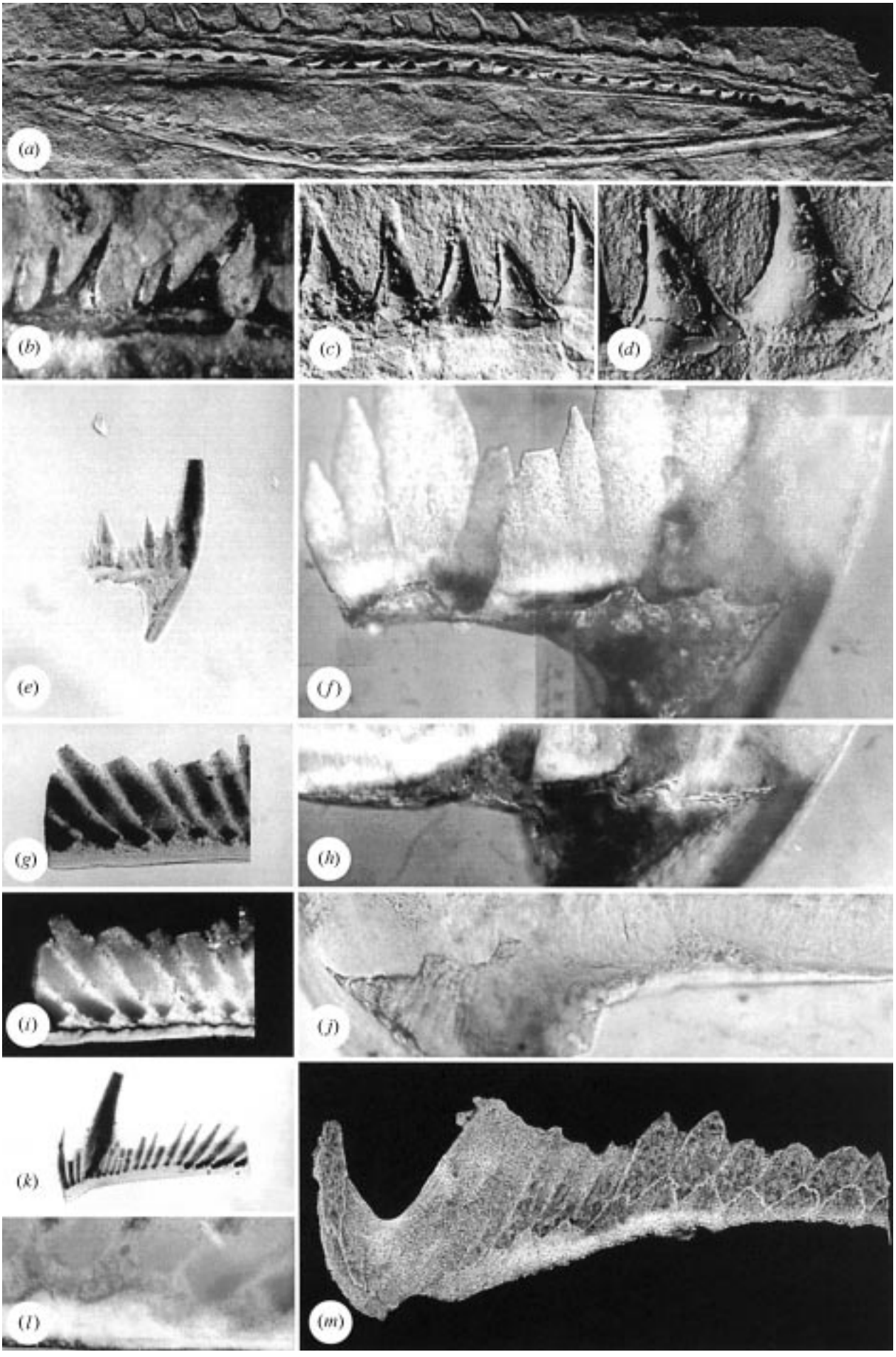


Figure 6. Diagrammatic representation of relative growth of white matter and surrounding lamellar crown tissue.

5. PATTERN: GROWING THE CONODONT SKELETON

Although I have outlined the morphogenetic pattern of intergrowth between the two structural units and three component tissues comprising most conodont elements, this goes little further than explaining the morphogenesis of the conventional perception of a simple coniform

Figure 5. (*a*–*c*) Longitudinal section through an Sc element of *Cordylodus angulatus*. The basal body is dominated by spherulitic structure, each spherule indicated by an extinction cross in cross-polarized light (*b*). Specimen BU 2614, (*a*, *b*) frame widths 644 μm, (*c*) frame width 204 μm. (*d*, *e*) Transverse section through an element of *Pseudooneotodus* sp. in plane-polarized light (*d*) and cross-polarized light (*e*). The basal tissue of this specimen also exhibits a spherulitic structure. Specimen BU 2625, (*d*) frame width 531 μm, (*e*) frame width 337 μm. (*f*, *g*) Longitudinal section through a Pa element of *Ozarkodina confluens* with a basal body exhibiting lamellar structure. Note the confluence of growth increments between the basal tissue and lamellar crown tissue in (*g*). Specimen BU 2626, (*f*) frame width 380 μm, (*g*) frame width 72 μm. (*h*) Pa element of *Ozarkodina gulletensis* Aldridge photomicrographed under oil. This element exhibits a conspicuous internal discontinuity with evidence of subsequent repair. Specimen lost, frame width 225 μm. (*i*–*l*) Pa element of *Ozarkodina confluens* photomicrographed under oil. (*i*) Ventral portion of the element viewed in plane polarized light, the denticle in the centre of the frame exhibits a staggered ventral margin where the increments of white matter and lamellar crown tissue are clearly confluent. Specimen BU 2627, frame width 453 μm. (*j*, *k*) Denticle in (*i*) at higher magnification. Specimen BU 2627, frame widths 88 μm. (*l*) Tubules and cell-shaped cavities within the white matter. Specimen BU 2627, frame width 35 μm.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element, or a single denticle in a complex element. Most conodont elements are far more complex and their morphogenesis can only be explained by studying recurrent patterns of growth. This study has revealed a restricted number of morphogenetic patterns expressed by complex elements; these are described primarily with reference to conodonts of the order Ozarkodinida, but some evidence from members of the orders Prioniodinida, Prioniodontida and Proconodontida is included.

Different groups of conodonts have followed different morphogenetic pathways in the construction of their feeding elements and, as a result, there is a great diversity of element morphology. However, a number of element morphologies have been converged upon by different morphogenetic paths; these can only be discriminated by considering pattern formation in reconstructing conodont phylogeny.

(a) *Ramiform element morphogenesis*

(i) *Type I*

This first group includes taxa bearing elements composed of numerous isolated denticles. The best source of evidence is *Promissum pulchrum* Kovács-Endrödy, a balognathid with a 19-element apparatus from the late Ordovician Soom Shale of South Africa, which is found almost exclusively in bedding plane assemblages (Theron *et al*. 1990; Aldridge *et al*. 1995; figure 7*a–d*). The ramiform elements of *Promissum pulchrum* consist of denticles that are united by a single underlying structure that appears to be neither part of the crown nor the basal body (figure 7*a*). The denticles themselves are variable; those on the (conventional) posterior processes are structurally differentiated into tri-denticulate units (figure 7*a*,*b*); denticles on other processes are structurally distinct (figure 7*a*,*c*,*d*; Theron *et al*. 1990). In both cases, each denticle possesses a distinct crown and basal body (figure 7*b*,*d*), indicating that they grew independently of adjacent denticles (figure 8*a*). In ontogenetically older specimens, the cusp and adjacent denticles exhibit a tendency to fuse at the margins of their crowns and their basal bodies. Each denticle therefore appears to be homologous with the conventional view of a simple coniform element, although it represents only part of a complex element. It is likely that each denticle would have been regarded as a single element if found only in a discrete element collection. Thus, Nicoll (1982) appears to have been correct in interpreting fused clusters of hundreds of simple cones in association with P elements of *Icriodus* Branson & Mehl as component denticles comprising multidenticulate elements. Van den Boogaard (1990) and Miller & Aldridge (1993) reached a similar conclusion in their interpretations of the ramiform elements of *Coryssognathus* Link & Druce.

(ii) *Type II*

Carniodus Walliser is a Silurian conodont genus of unclear affinity (family 6, order unknown of Aldridge & Smith (1993)). Like the ramiform elements of type I, *Carniodus* grew many of its denticles as morphogenetically distinct units (figure 8*b*), but unlike type I, the denticles on *Carniodus* ramiform processes are compound structures (figure 7*e*). Each of the denticle units is defined by a rostral and/or caudal border with adjacent units, conspicuous only in transmitted light (figure 7*f*,*h*,*j*). Each of the units has its own basal cavity, and is composed from a distinct crown and basal body (figure 7*f*,*h*,*j*), indicating that each of the units grew independently. Unlike type I elements, the crowns of type II elements were entirely fused prior to growth of the subsequent unit. New units began to grow separately from the rest of the element, usually some distance caudally (figure 8*b*). The unit began to grow equally in rostral and caudal directions until eventually it reached the caudal edge of the preceding unit. Later increments would then envelop both the new unit and the entire pre-existing element, leaving the join between successive units imperceptible on the surface of the crown or basal body.

Carniodus possesses a very characteristic, repetitive denticulation that relates directly to the underlying morphogenetic units (figure 7*e*,*f*). The basal cavity does not appear to be directly linked with any specific denticle within the repeated unit, although the conspicuously large denticle may be considered the cusp of each unit. The basal cavities instead relate to the growth of each morphogenetic unit as a whole. Each of the denticles in a *Carniodus* element cannot, therefore, be considered equivalent to the denticles of elements conforming to type I growth, which are instead homologous with each unit of type II growth. Denticle formation and addition within these units follows a pattern typical of type III elements (figure 8*b*; see below). This same pattern of growth is also found in the ramiform elements of taxa including *Amorphognathus* Branson & Mehl and *Prioniodus* Pander. Alternatively, in early representatives of *Cordylodus* (e.g. *C. angulatus* Pander), the crown of each unit remains undifferentiated, each denticle composed of a distinct crown and basal body (e.g. Nicoll 1991).

Microzarkodina Lindström also exhibits the type II morphogenetic pattern in all but its M elements. In this genus, the successive units consist simply of a large proximal and small distal denticle. The smaller denticle is subsequently encapsulated during growth of the next morphogenetic unit, resulting in an external pattern of denticulation more akin to *Ozarkodina* Branson & Mehl and type III growth.

Figure 7. (*a–d*) Details of elements of *Promissum pulchrum*. (*a*) Sc element with a posterior process composed from individual multidenticulate units (*b*), and lateral processes composed from individual denticles (*c*, *d*). (*a*, *b*) Specimen C424, frame widths 21 234 μm and 2037 μm, respectively; (*c*, *d*) specimen C679, frame widths 836 μm and 495 μm, respectively. (*e*, *f*, *h*, *j*) Sc elements of *Carniodus* sp. Note the optical distinction between the multidenticulate units comprising these elements; each unit includes a distinct basal cavity. (*e*, *f*) Specimen BU 2628, frame widths 1375 μm and 438 μm, respectively; (*h*) specimen BU 2629, frame width 288 μm; (*j*) specimen BU 2630, frame width 294 μm. (*g*, *i*, *k–m*) Sc elements of *Ozarkodina confluens*. (*g*, *i*) Plane-polarized light and cross-polarized light, respectively. Specimen BU 2631, frame widths 562 μm. (*k*, *l*) Growth cavities along the ventral margin of the element. Specimen BU 2632, (*k*) frame width 1406 μm, (*l*) frame width 225 μm. (*m*) Scanning electron micrograph of an etched ground section exhibiting distinct white matter cores within the lamellar crown tissue. Specimen BU 2633, frame width 1098 μm.

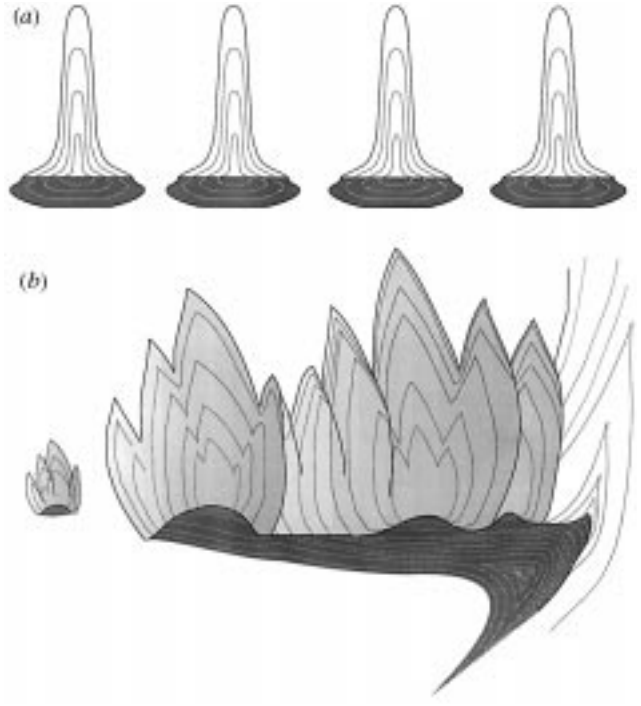


Figure 8. (*a*) Growth type I typified by *Promissum pulchrum* ramiform elements where individual denticles grew synchronously. (*b*) Growth type II typified by *Carniodus* ramiform elements where the repetitive sets of denticles gradually became incorporated into the rest of the element as it continued to grow.

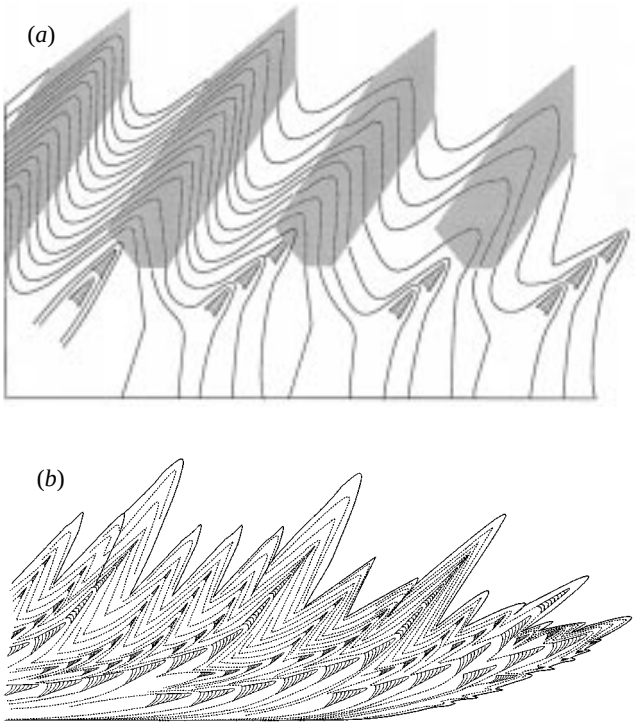


Figure 9. (*a*) Type III growth typified by *Ozarkodina* ramiform elements where new denticles were added periodically during marginal secretion of lamellar crown tissue. Denticle genesis was first instigated by evagination of normal lamellar growth and incorporation of a 'growth cavity'. (*b*) Type IV growth typified by gnathodid ramiform elements where denticles were added continually during marginal accretion of crown tissue. The repetitive denticulation results from differentiation of the denticles.

(iii) *Type III*

The ramiform elements of *Ozarkodina confluens* (Branson & Mehl) bear an undifferentiated denticulation pattern, with each denticle almost entirely composed of white matter and surrounded marginally and aborally by a small amount of lamellar crown tissue (figure 9*a*). Growth increments are clearly apparent within the crown tissue but are only rarely traceable through the blocks of white matter (figures 7*g*,*i*,*k*,*l*,*m* and 10*a*,*b*). Unlike the growth patterns outlined above in types I and II, the type III growth pattern produces a compound structure that extends processes by marginal accretion of individual denticles (figure 9*a*). The first stage of growth of an individual denticle is marked by an evagination of an incremental layer of crown tissue at the distal extremity of the process. The evagination encloses a hollow cone-shaped, distally tapering cavity with step-shaped margins representing the abutment of surrounding microlamellae, and crowned by an all-enveloping final layer (figures 7*l* and 10*a*,*b*). This is succeeded by a series of thick growth increments encapsulating similar cone-shaped cavities. The successive cone-shaped cavities or 'growth cavities' are stacked one upon another, but aligned in an arcuate, distally convex pattern (figures 9*a* and 10*a*,*b*). The growth of an individual denticle finishes with a final phase of white matter secretion. The first point of denticle formation, enclosing the first cavity, is close to the first point of white matter secretion because growth is concentrated in an oral, and not distal, direction (as in type IV; figure 10*a*,*b*). No specimens have yet been discovered where the growth cavities contain any mineralized tissue. This category also includes elements of '*Plectodina*', the putative ancestor of all ozarkodinids (Sweet 1988).

Type III growth also occurs in many of the taxa once placed within the now defunct order Neurodontiformes. Although the elements appear to have grown by marginal accretion, such taxa remain histologically distinguishable from other euconodonts, and the separate classification of a subset of the defunct order may well be biologically valid. In addition to the more obvious Ordovician forms, many Middle and Late Palaeozoic forms retain this unique histology, particularly taxa that are assigned to the order Prioniodinida (*sensu* Sweet 1988): e.g. *Idioprioniodus* Gunnell, *Cryptotaxis* Klapper & Philip, *Ellisonia* (cf. von Bitter & Merrill 1983). The structure of the crown differs from most conodonts in its 'fibrous' nature; growth increments are present but very faint (figure 4*h–j*). The tissue is dominated by elongate fibre-like crystals (figure 4*j*) which can reach 20–30 μm in length, and their arrangement is more complex than that seen in any other group of conodonts. Early growth, and growth along the axes of individual denticles, exhibits a divergent arrangement of crystal fibres; subsequent growth records a reversal in arrangement of the fibres so that they converge distally (note the subtle change in crystal fibre orientation to the left of figure 4*j*). It is this arrangement of crystallites that produces Müller & Nogami's (1971; Müller 1981) 'M'-shaped type 3D white matter. Clearly it is not true white matter.

(iv) *Type IV*

This group includes gnathodids, *Cavusgnathus* Harris & Hollingsworth, *Vogelgnathus* Norby & Rexroad, *Lochriea* Scott, polygnathids, some palmatolepids and at least some cyrtoniodontids (e.g. *Phragmodus* Branson & Mehl). Most of these families and genera are derived from *Ozarkodina* (Sweet 1988) but display a more complicated morphogenetic pattern of growth (figure 9*b*). The ramiform elements are generally much more elongate than those of their ancestor and possess a differentiated pattern of denticulation, similar to that of *Carniodus* but apparently achieved via a different pattern of formation. The elements are composed predominantly of lamellar crown tissue, and white matter generally becomes sparser from Middle to Late Palaeozoic. The denticles of palmatolepids and polygnathids are almost entirely composed of white matter extending deep into the elements, whereas the denticles of gnathodids usually only include white matter in the portion of the denticle emerging from the main body of an element, and even then only during late ontogeny (figure 10*c*).

Transmitted light clearly reveals the complex growth history of type IV elements (figure 10*c–j*). Cone-shaped growth structures of the type seen in *Ozarkodina* are present, but in this case occurring in sets relating directly to the overlying denticulation (figure 10*c*,*j*). The first evagination is palm-shaped (figure 11*a*,*b*), each digit relating to, and ultimately resulting in, a single and specific denticle (figures 10*j* and 11*g*). The denticles within each unit are distinct optical units, traceable as discrete prisms through ontogeny (figure 10*f*,*i*). During the ontogeny of each denticle set, the angle of inclination of each denticle increases progressively from nearly parallel with the long axis of the element to the erect position more typical of 'mature' denticulation (figure 10*j*). This is expressed in surface morphology by a transition from suberect to erect denticulation proximally (figure 10*c*,*e*). Elements conforming to type IV growth were constantly undergoing morphological change by addition of new denticles. This condition is different from type III growth where elements underwent enlargement between episodes of denticle addition. The long axis of a process in a type IV element was the main axis of growth from which the developing denticle sets diverged. The progressive development of the individual denticles within each unit can be traced by the presence of the cone-shaped cavities (figure 10*j*). After the axis of growth of the large denticle diverged from the main axis of growth of the process, the growth axes of the smaller denticles diverged in turn from the growth axis of the larger denticle (figure 10*e*,*f*,*g*,*i*,*j*). The growth axes then translated their orientation into a progressively higher angle relative to the process. As in *Ozarkodina*, the proximal margins of the growth structures are aligned in a convex-distal arrangement. The last cone-shaped cavity occurs exactly at the point at which white matter secretion first occurred (figures 10*g*,*j* and 14*e*,*g*). The large denticle represents the distal extremity of each unit.

Early growth distally occurs synchronously with late growth proximally. Because of the pattern of growth exhibited by type IV taxa, each unit of denticulation is considered equivalent to each unit in taxa with type II growth, and to an individual denticle in taxa with types I and III growth.

(b) *Morphogenesis of elements in P positions*

Elements filling P positions within the apparatuses of complex conodonts can be broadly divided into blade-like and platform-bearing morphologies and, more rarely, ramiform morphologies (prioniodinids, see earlier). Most, if not all platform-bearing P elements are essentially modified type III ramiforms and therefore exhibit similar growth patterns. However, some attempts at platform construction are merely elaborations of type III pattern of element formation. Instead of arranging denticles linearly, P elements of this type are composed of three-dimensionally arranged denticles; in *Promissum*, for example, these remain structurally distinct, but in *Coryssognathus* they are gradually fused together during ontogeny (cf. van den Boogaard 1990). Despite the more variable morphology exhibited by elements filling Pa positions, the morphogenetic patterns are much more conservative than those exhibited by elements in S and M positions.

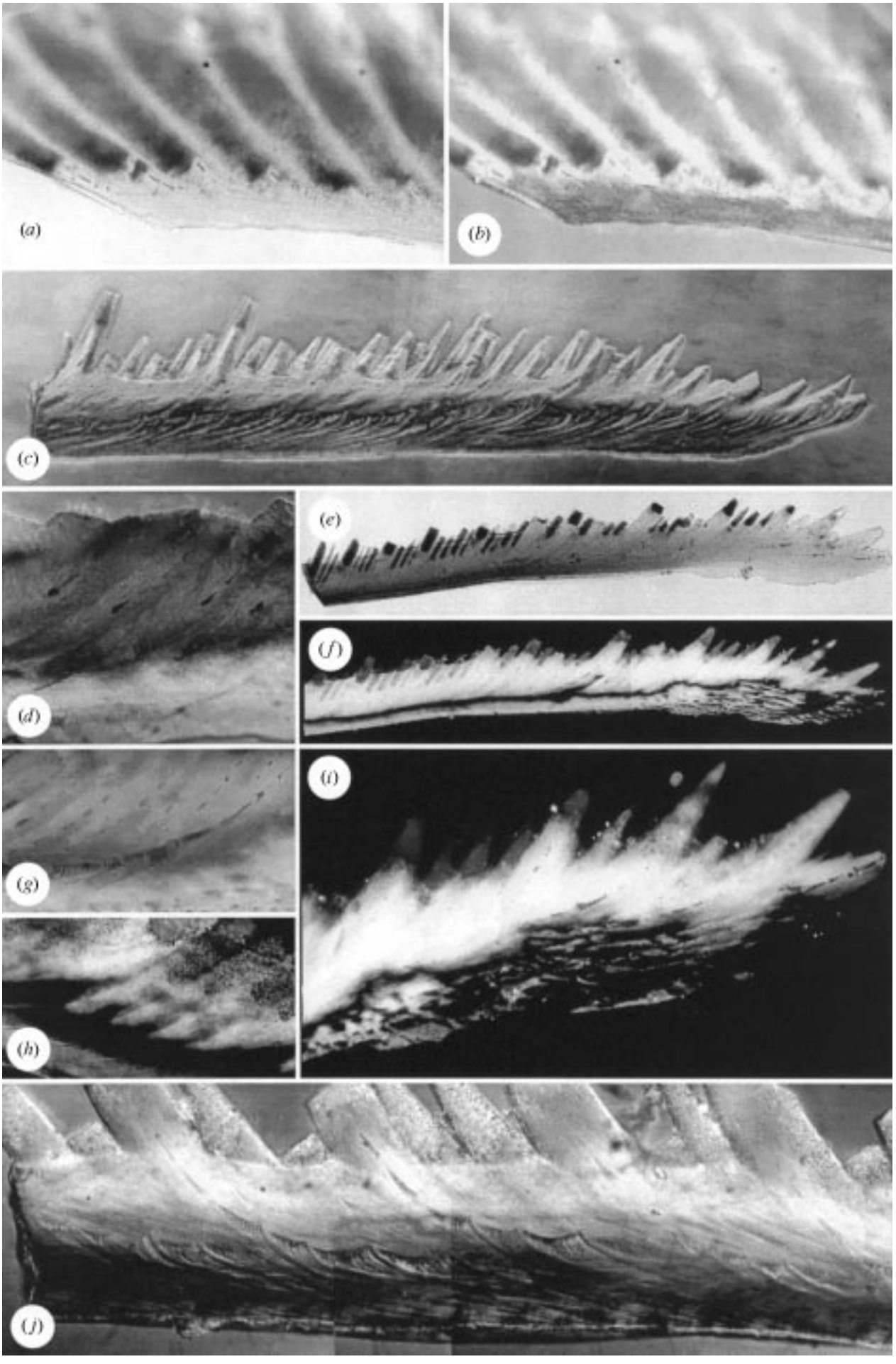
(i) *Blade morphogenesis*

The morphogenesis of blade-like elements and the blade portion of platform-bearing elements is very similar to type III ramiform growth and is typified by the P elements of *Ozarkodina*. Initial growth of the crown involved only lamellar crown tissue and very soon afterwards white matter secretion began. Denticles formed as distinct optical units as in ramiform elements. Maximum growth was in dorsal and ventral directions and new denticles are added marginally by localized evagination of a layer of lamellar crown tissue. White matter forms the core of all denticles in juvenile elements, but later growth, which modifies the shape of an element, is generally restricted to the ventral portion of the element and is devoid of white matter. During late-stage growth, white matter deposition is halted and the cores are enveloped by layers of lamellar crown tissue. The tips of denticles forming dorsal or mid-oral surfaces are generally devoid of crown tissue, although this condition may be due to attrition resulting from function rather than reflecting a pattern of growth.

The blade portions of platform elements were constructed by a pattern of growth identical to that of wholly blade-shaped elements (figure 9*a*). All the following patterns are derived from this.

(ii) *Type A platforms*

This first category of platform morphogenesis represents a modification of the standard blade pattern (figure 12*a*). In taxa such as *Idiognathodus* Gunnell (*sensu* Baesemann 1973; Grayson *et al.* 1991), *Gnathodus* Pander and *Icriodella* Rhodes the platform is restricted to the dorsal portion of the element, and the internal construction of its crown incorporates a series of cavities within the lamellae, along the main growth axis of the element (figure 11*d–i*). The cavities mimic the arrangement of cone-shaped cavities present in ramiform and blade-shaped elements, where the proximal margins of the cavities are aligned in ascending fashion, with the structure ultimately produced (denticle or ridge; figure 11*e*,*h*). However, these cavities are not wholly encapsulated by the crown; they extend down to the base of the crown where they open into the basal cavity through a restricted opening which can often be observed in SEM (figure 11*e*,*g*). The upper margins of the cavities are aligned in an undulating arrangement,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directly reflecting the overlying ridge morphology (figure 11*e*,*h*).

In almost all platform elements that bear transverse ridges, the ridges occur in pairs on either side of a central trough which directly overlies the axial cavities, and varies in its development from a large dividing depression to a narrow slit. The ridges have a structure similar to denticles, being formed as discrete and homogeneous prisms that are centred about the apices of each set of 'growth cavities' (figure 11*h*,*i*). The symmetry or asymmetry of each prism is a direct reflection of the shape of the overlying structure; whether or not the prisms merge at their margins is dependent on whether the ridges are of low relief (e.g., gnathodids; figure 11*h*), or whether the ridges are more peg-like (e.g. *Icriodella;* figure 11*e*).

Paired platform ridges occur in a number of different taxa, particularly among Middle and Upper Carboniferous ozarkodinids. The significance of this is borne out by examination of the juvenile component of the internal growth record. For instance, the early growth stage of a *Cavusgnathus* platform reveals an original blade-like morphology (figure 13*a*–*c*; and see Purnell (1992) for the ontogeny of *Taphrognathus* Branson & Mehl, a closely related taxon). Prismatic structure and maximum growth coincide with the axis of the blade (figure 13*b*; in transverse view). However, after relatively few increments, the axis of primary growth bifurcates into two distinct growth axes, oblique to the original axis (figure 13*c*). The crystallites in subsequent layers of crown tissue are organized in two prisms, disposed about the new primary growth axes, and with an intervening area which is aprismatic, where all crystallites are organized approximately parallel to each other, perpendicular to the outer surface. Ontogenetic bifurcation of denticles appears to be the main method of platform formation within type A platform-bearing taxa, and may have implications for deducing their evolutionary origin.

Additional nodes may be incorporated into the platform. Like the ridges, their internal structure is optically distinct from the surrounding crown tissue. Cross-crystallographic arrangement of the prisms of crystallites within the platform results in an albid appearance in reflected light. True white matter is usually absent from the platform but may occur in the blade (if one is present).

(iii) *Type B platforms*

This category includes such taxa as gondollelids, palmatolepids, polygnathids, and *Siphonodella* Branson & Mehl (figure 12*b*). They differ from type A in that their platforms are formed by lateral expansion of the incremental layers of lamellar crown tissue (figure 13*e*,*g*). The axes of growth are dorsoventral in most of these elements (and a third lateral process in some taxa, e.g. palmatolepids), and contain growth cavities strongly resembling those along the growth axis of type A platforms (figure 13*d*). These cavities are generally larger than their type A counterparts and are overlain by fewer layers of crown tissue.

Away from the main axes of growth, successive increments include patches of poor mineralization and often enclose large cavities, particularly in areas of maximum growth on the outer margins of elements (figure 13*e*,*f*). As a result, prominent growth increments vary in thickness from a few microns to 30 or 40 microns. The outer surfaces of each of the increments in the areas of maximum growth parallel surface morphology.

The internal structure of surface morphological structures such as ridges and nodes also differ from those of type A elements that bear prismatic structure. Surface morphological features are produced by site-specific increases in the thickness of layers of the enamel relative to adjacent regions of the enamel within these individual layers (figure 13*e*).

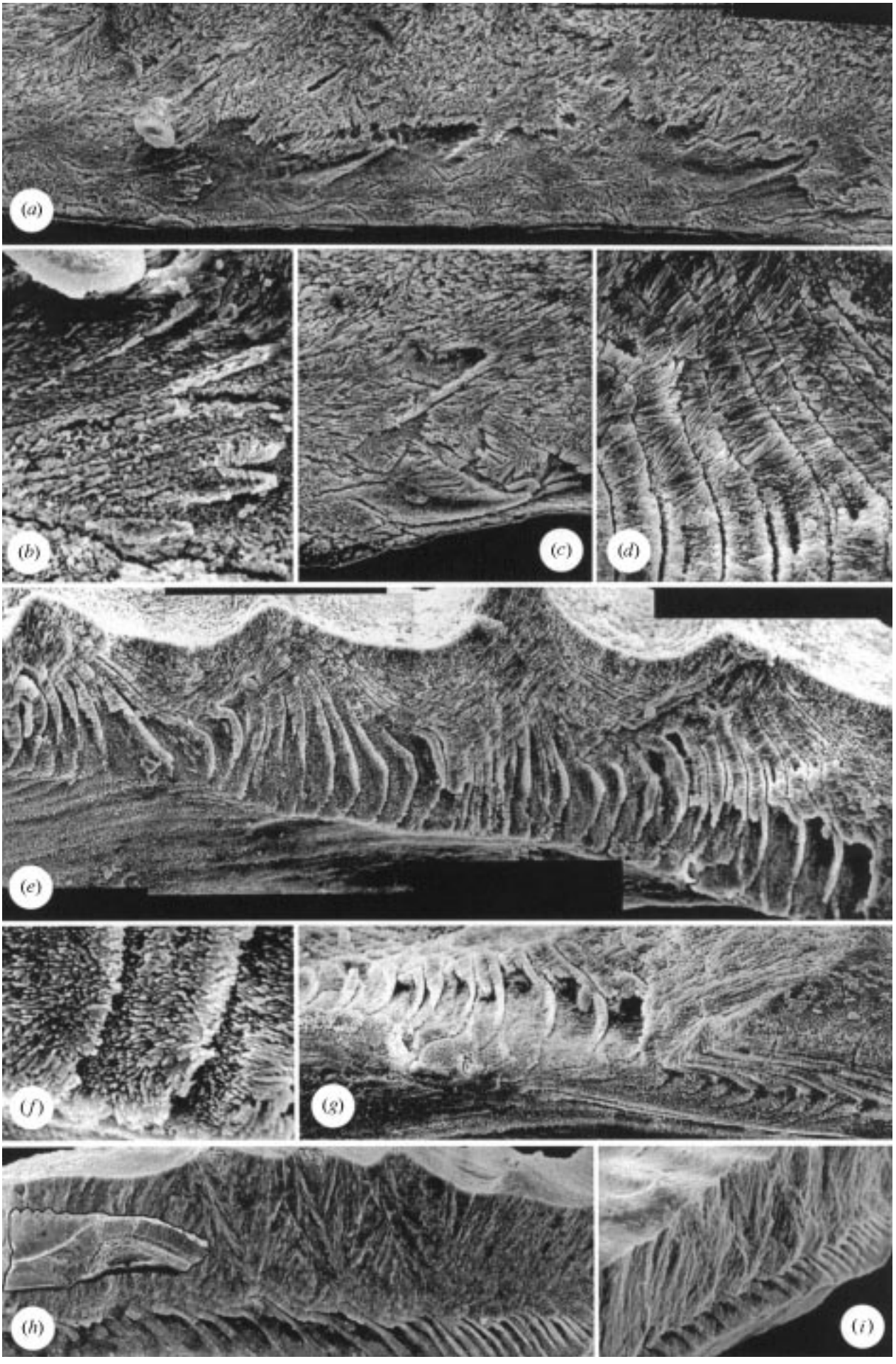
Like type A platforms, type B platforms also lack true white matter within the platform although they exhibit areas of albid appearance in reflected light. White matter is present in the free blade and carina.

The most conspicuous difference between surface morphology of type A and B platforms is the absence and presence of a carina, respectively. The platform in type A platforms often lack a carina because the denticles that comprised the dorsal blade in juvenile (and ancestral?) forms were split ontogenetically to form the paired ridges common to this element type. Type B elements retain a prominent carina throughout ontogeny because the denticles perform no role in formation of the platform. However, some forms appear to combine both morphogenetic patterns, e.g. *Gnathodus bilineatus* (Roundy). Some species of *Cavusgnathus*, a typical type A platform, also exhibit evidence of a combination of the two growth types where a small carina at the dorsal-most tip of the Pa element is developed in specimens representing late ontogeny. All work so far suggests that beside minor elaborations, such as platform development, pattern formation is the same in all elements in a given apparatus.

6. PROCESS: INTERPRETATION OF THE HARD TISSUES

Considering the widely diverging views of conodont affinity expressed over the past 140 years, there have been

Figure 10. (*a*, *b*) *Ozarkodina confluens* Sc element viewed (*a*) in plane-polarized light, and (*b*) in differential interference contrast. Note the conspicuous growth cavities along the ventral margin of the element. Specimen BU 2634, frame widths 562 μm. (*c*) S element of *Idiognathodus* photomicrographed under oil and in differential interference contrast. Note the conspicuous growth cavities within the main body of the element, each set of growth cavities relate to the overlying sets of alternating denticulation. Specimen ROM 53262, frame width 1894 μm. (*d*–*i*) S element of *Mestognathus beckmanni*. (*e*, *f*) Photomicrographed in plane-polarized light and cross-polarized light respectively. Note the extinction pattern exhibited by the prisms which represent the gradual development of denticles. Specimen BU 2635, (*e*) frame width 1894 μm, (*f*) frame width 1660 μm. (*i*) Detail of the caudal portion of the element in cross-polarized light. Specimen BU 2635, frame width 625 μm. (*d*, *g*, *h*) Detail of denticle structure. Specimen BU 2635, (*d*) frame width 225 μm, (*g*) frame width 225 μm, (*h*) frame width 225 μm. (*j*) S element of *Idiognathodus* photomicrographed in plane-polarized light and differential interference contrast. Note the relationship between the sets of growth cavities and overlying alternating denticulation. Specimen ROM 53263, frame width 425 μm.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surprisingly few competing hypotheses to explain element histology. Most authors have contended that the hard tissues represent forms homologous to those of vertebrates and, except for a few off-beat interpretations (Zittel & Rohon 1886; Quinet 1962*b*; Fahlbusch 1964; Bischoff 1973), all other considerations of conodont hard tissue histology are refutations of the vertebrate hypothesis (Kemp & Nicoll 1995*a*,*b*, 1996; Schultze 1996).

Conodonts are now widely regarded as craniates probably most closely related to the extant agnathans (Aldridge *et al*. 1993; Forey & Janvier 1994; Gabbott *et al*. 1995; Janvier 1995, 1996*a*,*b*), although some authors believe that conodonts represent a more primitive condition akin to amphioxus (Kemp & Nicoll 1995*a*,*b*, 1996; Nicoll 1995; Pridmore *et al*. 1997). However, there is currently consensus over the chordate affinity of conodonts and it is in this context that the following interpretation of conodont hard tissues has been considered.

(a) *Lamellar crown tissue*

Among protochordates only the ascidiacean and soberacean tunicates are able to secrete biomineralized tissues (Lambert *et al*. 1990). Amongst these two groups, phosphatic biomineralization is largely restricted to amorphous deposits and in some cases dahllite. However, even this one record of mineralized phosphate may be questionable because of the inherent instability of amorphous calcium phosphate (e.g. Lowenstam & Weiner 1985). In either case, lamellar crown tissue is clearly not composed from dahllite (Pietzner *et al*. 1968).

Although myxinoids are capable of secreting non-skeletal calcium phosphate in the form of statoliths and statoconia (Carlström 1963), this system is also unlikely to be responsible for conodont hard tissues. Agnathan statoliths are composed from an amorphous (polyhydroxyl) calcium phosphate, which is highly unstable and dissolves in a solution of pH 8 or less (R. W. Gauldie, personal communication). Lamprey biomineralization is similarly restricted to the formation of statoliths, although under the right conditions (*in vivo* or *in vitro*) lampreys are capable of skeletal biomineralization, in particular, calcification of cartilage (Langille 1987; Langille & Hall 1993; Bardack & Zangerl 1971).

Considering the range of chordate hard tissues, the only possible homologues of lamellar crown tissue are enameloid and enamel. Both enamel and enameloid are hypermineralized, but enameloid crystallites are generally much larger than those of enamel, the crystalline structure of which is punctuated by incremental growth lines. Enamel crystallites are aligned in a preferred orientation, which is usually perpendicular to the growing surface, although this alignment can vary considerably. Enameloid crystallites, which more usually resemble long fibres, are not always aligned preferentially and can range from a completely random arrangement (e.g. tangled fibre enameloid; Preuschoft *et al*. 1974, pl. 8, fig. d) to highly ordered woven and interwoven sheets (e.g. parallel fibre enameloid; Preuschoft *et al*. 1974, pl. 8, fig. e). Lamellar crown tissue most closely resembles enamel, and I interpret them as homologous. This conclusion has been reached by several authors in the past (e.g. Dzik

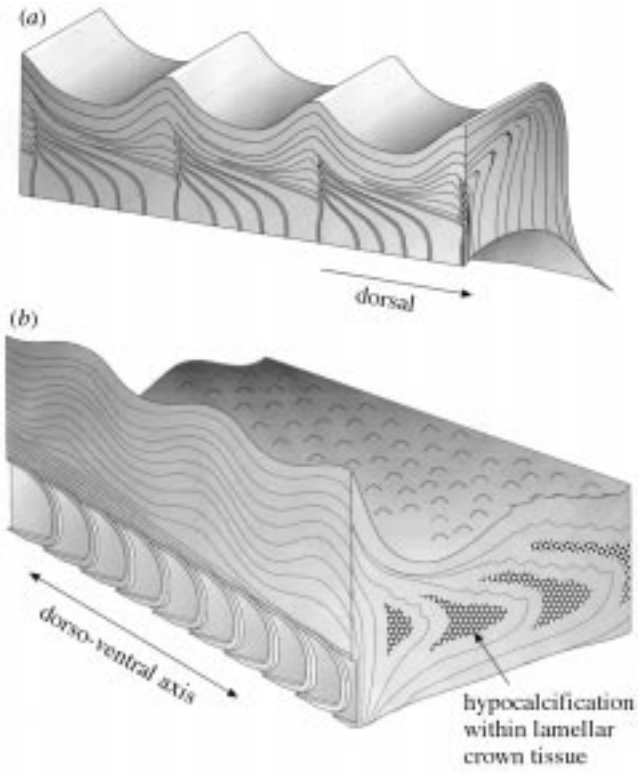
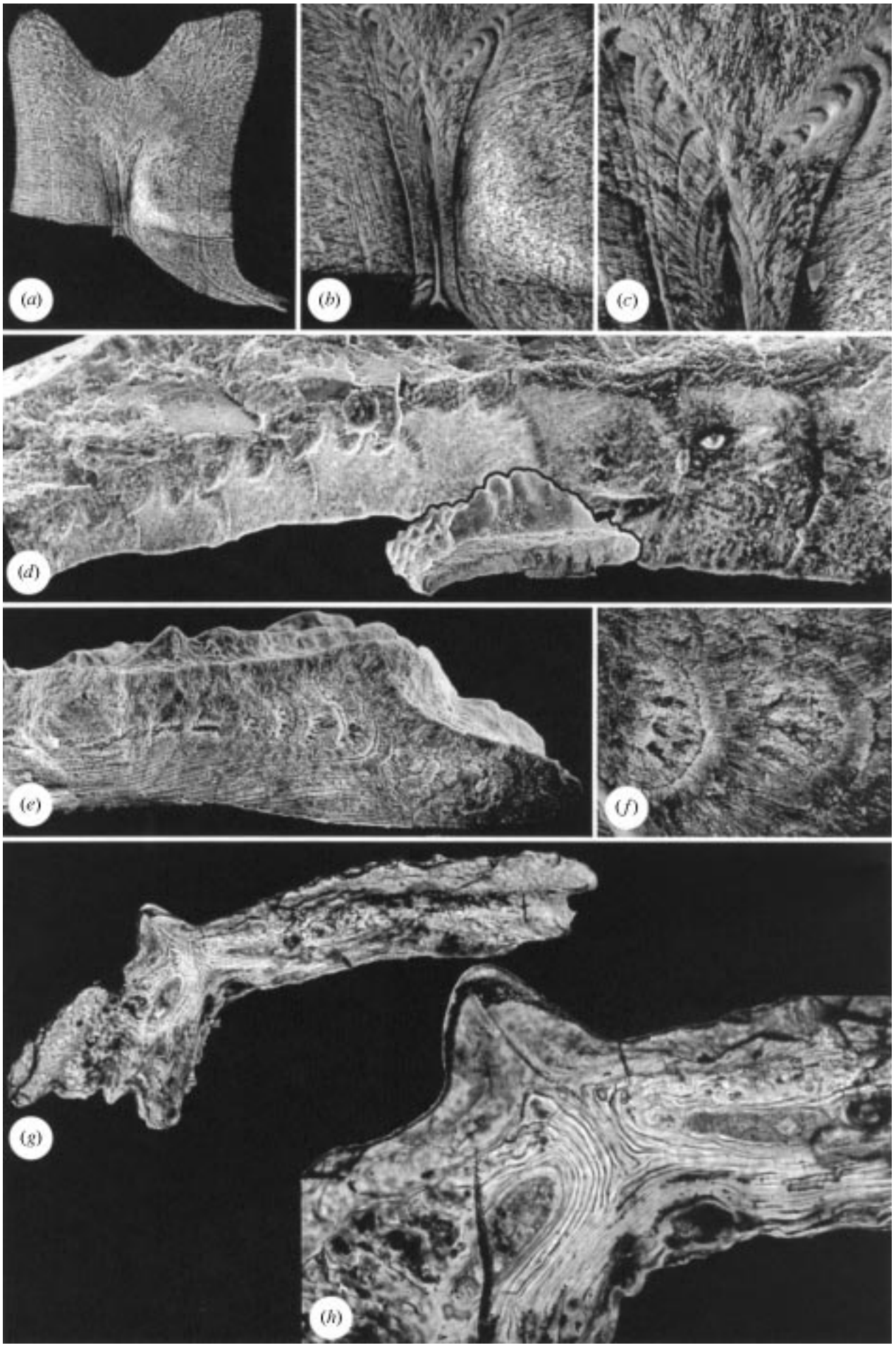


Figure 12. (*a*) Growth type A typified by the platforms of gnathodid Pa elements. The junction between the crown and the (unpreserved) basal body is irregular, the basal body invading the crown between successive increments of lamellar crown tissue. The paired ridges are often derived from differentiation of individual denticles in juvenile stages. (*b*) Growth type B typified by the platforms of *Palmatolepis* Pa elements. The crown–basal body junction is similarly irregular, but the crown is formed by exaggerated lateral growth, often resulting in hypocalcification within the enamel.

Figure 11. (*a–c*) Etched ground-section of an S element of *Mestognathus beckmanni*. The growth cavities along the axis of the element can clearly be seen, and individual denticles can be traced throughout growth as distinct prisms from inception. Specimen BU 2636, frame width of (*a*) 410 μm. (*b*) Palm-shaped growth cavity representing one of the first growth stages of a forming set of denticles, each digit representing a distinct prism and denticle. Specimen BU 2636, frame width 32.5 μm. (*c*) Growth cavity representing the inception of a new set of denticles at the caudoventral margin of the element. Specimen BU 2636, frame width 93 μm. (*d–g*) Etched, artificially fractured specimen of a Pa element of *Icriodella inconstans* Aldridge. (*e*) Growth cavities in sets along the dorsoventral axis of the element; each set relates to the overlying denticulation. Specimen BU 2637, frame width 388 μm. (*d*) Crystallite arrangement adjacent to the growth cavities. Specimen BU 2637, frame width 47 μm. (*f*) Perpendicularly oriented crystallites forming the walls of the growth cavities. Specimen BU 2637, frame width 27 μm. (*g*) Oblique view of the basal margin showing that the growth cavities are open to the basal body (not preserved). Specimen BU 2637, frame width 185 μm. (*h*, *i*) Etched, artificially fractured section of the platform component of a Pa element of *Idiognathodus* sp. (inset) exhibiting sets of growth cavities relating to the overlying denticulation and intervening preprismatic structure. (*h*) Specimen ROM 53264, frame width 267 μm, width of inset 736 μm. (*i*) Specimen ROM 53264, frame width 153 μm.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1986; Burnett & Hall 1992; Sansom *et al.* 1992), but heavily criticized (e.g. Blieck 1992; Kemp & Nicoll 1993, 1995*a*,*b*, 1996; Schultze 1996; Forey & Janvier 1993; Janvier 1995, 1996*a*,*b*).

Although Forey & Janvier (1993) felt that the apparent 'extreme variation' of crystallite orientation in conodont lamellar crown tissue was irreconcilable with enamel, it is not without parallel in known enamels (e.g. Smith 1989), although the sub-parallel arrangement of crystallites is unusual. The dearth of comparable microstructures in other vertebrates probably results from the lack of enamel-bearing structures of comparably intricate morphology. Although other vertebrates may produce dental and other structures that are as intricate, such elements invariably lack enamel and are instead largely composed of various types of enameloid.

The presence of prismatic structure and elaborate surface ornament in some conodont taxa indicates that the enamel organ responsible for secretion of the tissue was relatively sophisticated, capable of controlling mineral secretion and mineral alignment in any one site, and of producing textures comparable with the surface ornamentation of the tooth enamel of gnathostomous fish (cf. Smith 1989, text-fig. 5, *Laccognathus biporcatus* Gross).

(b) ***Basal body***

Interpretations of basal tissue have varied more than those of any other tissues of conodont elements. They range from bone (Barskov *et al.* 1982), to globular calcified cartilage (Sansom *et al.* 1992), and various dentines (Dzik 1986; Sansom *et al.* 1994; Sansom 1996), to 'a mineralised extracellular matrix, organised like connective tissue or the inner core of embryonic or chordate notochord' (Kemp & Nicoll 1995*a*, p. 238).

The last interpretation warrants separate discussion because it is so conspicuously different from the other competing hypotheses. Kemp & Nicoll (1993, 1995*a*,*b*, 1996) have followed earlier work (Fåhraeus & Fåhraeus-Van Ree 1987, 1993) concerned with organic remnants retrieved after acid dissolution of conodont elements. The organic matrices retrieved from the basal tissue of *Prioniodus amadeus* Cooper and *Cordylodus* sp. form the basis of this interpretation and are shown in fig. 3a–e of Kemp & Nicoll (1996) and pl. 1, figs 4, 7, 8, pl. 2, figs 9–12 of Kemp & Nicoll (1995*a*). It is remarkable that organic remnants or replacements of original soft tissues could be preserved, but the least remarkable factor is the low fidelity of preservation. Indeed the preservation is such that the organic remnant cannot be compared with any specific modern tissue with any confidence because of the lack of distinguishing characters. The organic remnant does, however, compare well with connective tissue, which led to Kemp & Nicoll's interpretation of conodont basal tissue as their hypothetical 'extracellular mineralised matrix' tissue; they proffer no homologous tissue from any animal extant or extinct.

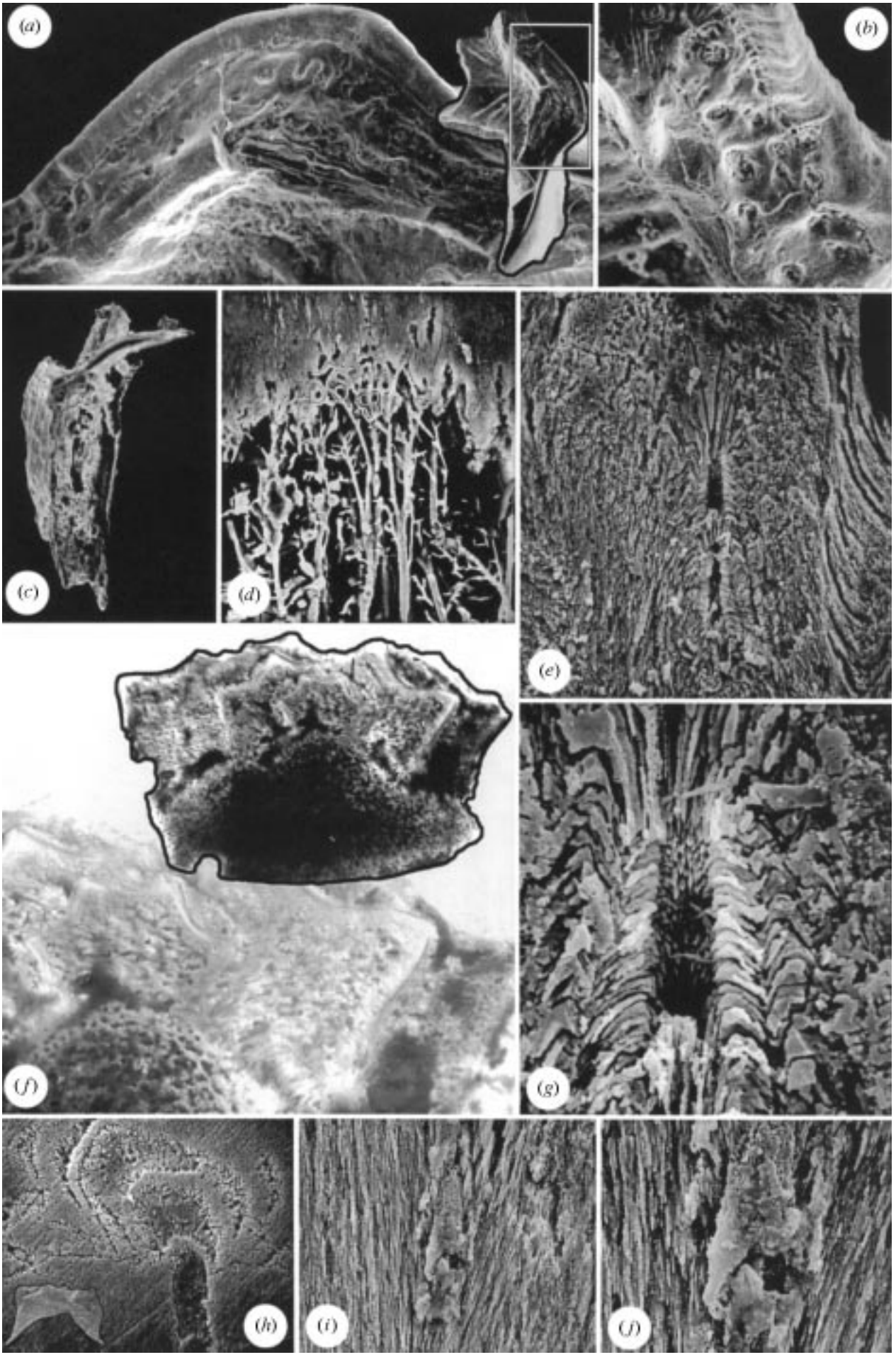
The divergent growth relationship between the basal tissue and the enamel supports interpretations of basal tissue as bone, mineralized cartilage or dentine. All three tissues are involved in odontogenesis in extant and extinct vertebrates, are neural crest derived, and can often occur together with enamel/enameloid as a result of epithelial–ectomesenchymal interaction. Enamel overlying dentine is a pattern characteristic of the vertebrate dermal skeleton and, contrary to Kemp & Nicoll (1995*a*) and Schultze (1996), enamel overlying bone is not unparalleled among the vertebrates (Smith 1979; Sire 1994). Although hypothetically possible, no examples have been reported where enamel can be observed directly overlying cartilage.

Sansom *et al.* (1994) contended that during the Ordovician acme of vertebrate evolution (Halstead 1987) the conodonts, like all the other armoured agnathan groups, were experimenting with different tissue combinations. However, the other vertebrate groups were expressing this experimental episode in the production of variably structured dermal armour. Based on new histological evidence presented here and elsewhere, the scenario presented by Sansom *et al.* (1994) would be extrapolated to suggest that conodonts were directly substituting different tissues in a homologous site of an otherwise entirely unchanged mineralized skeleton, sometimes within individual species. Clearly, this is highly unlikely.

The case for the interpretation of conodont basal tissue as bone, as made by Barskov *et al.* (1982), was based on the presence of concentric hollow spheres and tubules within a lamellar matrix, respectively suggested to be osteocyte lacunae and vascular canals. However, the putative cell lacunae bear little resemblance to structures in bone; the spheres are infilled, bear no processes and are better interpreted as components of dentine. Evidence for the presence of vascular tubules is also very poor, although structures similar to these have been described in other conodont taxa (e.g. *Problematoconites* Müller in Andres (1988), and *Semiacontiodus* Miller in Dzik (1986)).

The case for the interpretation of basal tissue as mineralized globular cartilage is considerably stronger. Smith *et al.* (1987), Smith (1990) and Sansom *et al.* (1992) have all compared the basal tissue of *C. angulatus* (figure 5*a*–*c*) to the globular calcified cartilage found in the Harding Sandstone vertebrate *Eriptychius* Walcott (Denison 1967). However, Smith & Hall (1990) have postulated that cranial exoskeletal cartilage is always associated with bone, which, as we shall see below, was

Figure 13. (*a*–*c*) Etched transverse section through a Pa element of *Cavusgnathus alta* Harris & Hollingsworth in progressively higher magnification. Note the change from blade to paired-ridge morphology during ontogeny. Specimen BU 2638, (*a*) frame width 436 μm, (*b*) frame width 150 μm, (*c*) frame width 76 μm. (*d*) Etched, artifically fractured section through a Pa element of *Palmatolepis* sp. (inset). Specimen BU 2639, frame with 472 μm, inset width 967 μm. (*e*, *f*) Etched, artifically fractured section through a Pa element of *Palmatolepis* sp. (*e*) Relationship between structure and morphology. Specimen BU 2640, frame width 285 μm. (*f*) Hypocalcification within lamellar crown tissue. Specimen BU 2640, frame width 42 μm. (*g*, *h*) Transverse section through a Pa element of *Palmatolepis* sp. photomicrographed in plane-polarized light with differential interference contrast. (*g*) Entire element. Specimen BU 2641, width 1523 μm. (*h*) Detail of the basal body exhibiting large internal cavities which indicate that the basal tissue was secreted both from the inside and outside. Specimen BU 2641, frame width 562 μm.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evidently lacking in conodonts. Furthermore, as Sansom *et al.* (1992, p. 1310) admitted, 'it is possible that other mineralisation processes could produce spherulitic structures such as these'.

The strongest case is for an interpretation of conodont basal tissue as dentine. Dentine exhibits a great variation in structure, including forms that do or do not include cells, i.e. mesodentine, semidentine and orthodentine (for reviews, see Ørvig 1967*a*; Smith & Hall 1990). Variations also occur within these categories due to factors such as environmental and physiological stress (e.g. Appleton 1994). Although the claims of dentine in conodont elements by Dzik (1986) and Andres (1988) are equivocal, the identification of mesodentine in *Neocoleodus* (Sansom *et al.* 1994) is unequivocal. The assertion by Kemp & Nicoll (1995*a*) that the structure of the *Chirognathus* basal tissue is a preservational artefact is unfounded, unless the histological integrity of the whole Harding Sandstone vertebrate fauna is called into question.

Thus, at least some basal bodies are demonstrably composed of dentine, and other structures, which apparently support alternative interpretations, are also sometimes displayed by dentine. The spheroidal structure compares favourably in morphology and scale with dentine calcospherites which commonly occur within dentine (figure 14*d*) and result from poor mineralization (Halstead 1974), rapid growth or other factors such as disease (Appleton 1994). Atubular dentine has been described from the basal body of *Pseudooneotodus* (Sansom 1996), but other material of *Pseudooneotodus* (figure 5*d*,*e*) reveals a spherulitic structure directly comparable with the basal body of *Cordylodus*, also described by Sansom *et al*. (1992) but interpreted as globular calcified cartilage. Most basal bodies are lamellar and lack evidence of tubules, but even these fit within the range of known dentines, specifically (atubular) lamellar dentine (e.g. Karatajute-Talimaa *et al.* 1990; Karatajute-Talimaa & Novitskaya 1992). In most dentines these structures can occur together, so that lamellar dentine contains calcospheres, as do most tubular dentines. This is also observed in conodont basal tissues. Interpretation of all conodont basal tissue as dentine is therefore supported by the structural variation and integradation seen in a range of conodont taxa. However, the possibility remains that different tissue combinations were present in the early evolution of the Euconodonta, particularly if this clade is considered polyphyletic (e.g. Miller 1984), although further histological analysis of Early Ordovician conodonts is required.

The pattern of growth displayed by the basal tissue is extremely variable. The basal body of *Pseudooneotodus* is dominantly lamellar but is spheritic at the crown junction, the site of the terminal dentine network (Sansom 1996). The basal body of *Ozarkodina* is usually lamellar, except for the flanks of the structure below the contact with the crown, which may result from either disruption of the mineralizing dentine by vascular supply from the pulp, or represent the site of attachment fibres. Similarly, the coarse structures previously interpreted as dentine tubules (Dzik 1986; Andres 1988) can be homologized with pulp canals.

The basal body of *Palmatolepis* also has a variable structure, although this may result from processes of preservation. In optimally preserved specimens, the flanks of the squat plate-like structure incorporate coarse calibre canal-like structures which are infilled from the outside inwards (figure 13*g*,*h*). Thin-sectioned elements reveal a hollow internal structure which indicates that as the element grew rapidly laterally, the successive growth increments of basal tissue incorporated large spaces into the structure (mirroring hypocalcification in the crown). The specimens examined exhibit evidence of gradual enlargement without morphological modification, punctuated by periodic lateral expansion of the structure, again, by incorporation of a large space. The spaces did not remain hollow, but were gradually infilled by successive lamellae, the secreting tissue probably maintained via the canals in the flanks of the basal body (figure 14*a*–*c*). The rapid growth has resulted in the incorporation of pulp tissue within the mineralized structure. The lateral walls of the basal body occupied by vascular canals are poorly or weakly mineralized; this may explain the less completely mineralized state of most *Palmatolepis* basal bodies, where only the portion above the vascular region is present. In these specimens the growth increments do not exhibit closure around the lower surface of the basal body. Either the lower half fell away *post mortem* or it was never mineralized. Most often the basal body is not preserved at all.

The temporal trend towards unmineralized basal bodies is potentially a serious weakness in the interpretation of basal tissue as dentine, as this homology relies partly on evidence from relative growth between the component tissues of elements. Within the vertebrate dermal skeleton the signal for enamel secretion is believed to be the presence of a mineralized surface, typically mineralized dentine (Smith 1992). Reduced mineralization in conodont basal bodies poses no developmental problem as long as dentine adjacent to the enamel–dentine junction

Figure 14. (*a*, *b*) Detail of Pa element of *Palmatolepis* sp. (inset) exhibiting the position of infilled pulp canals. (*a*) Caudal margin. Specimen BU 2642, frame width 1650 μm, length of element in inset 2723 μm. (*b*) Rostroventral margin of element. Note the section of a concentrically infilled tubule at upper left. Specimen BU 2642, frame width 492 μm. (*c*) Ventral view of a Pa element of *Palmatolepis* sp. with a hollow basal body which opens to the venter. Specimen BU 2643, frame width 488 μm. (*d*) Ground section through a crushing tooth of *Lissodus minimus* (Agassiz), a Rhaetian elasmobranch. The scanning electron micrograph details mantle dentine with remnants of the associated dentine tubules. Specimen BU 2644, frame width 153 μm. (*e*, *g*) Etched ground section through an S element of *Polygnathus* sp. exhibiting the recurrent relationship between growth cavities, the bounding crystallites and white matter. (*e*) White matter secretion appears to have been initiated immediately after a growth cavity. Specimen BU 2645, frame width 93 μm. (*g*) Typical arrangement of crystallites adjacent to growth cavity. Specimen BU 2645, frame width 23 μm. (*f*) Thin section through the dermal scale of *Gomphoncus* sp. Pander, an acanthodian (inset). Specimen BU 2646, frame width 357 μm, inset width 586 μm. (*h*) Ground section through a Pa element of *Idiognathodus* sp. (inset) exhibiting growth cavities infilled by a tissue similar to white matter. Specimen ROM 53265, frame width 37 μm, inset width 578 μm. (*i*, *j*) Thin section through an S element of *Idioprioniodus* exhibiting growth cavities infilled by a tissue similar to calcospheric dentine. Specimen ROM 53266, (*i*) frame width 55 μm, (*j*) frame width 23 μm.

was mineralized. This could explain why many Devonian conodont taxa retain a thin remnant of basal tissue which would otherwise have performed no useful purpose (e.g. see Smith *et al*. 1987).

Enameloid displays a different relationship with dentine to that between enamel and dentine. In enameloid, the epidermal cells (ameloblasts) begin secretion before mineralization of the dentine instead of after. As a result, the extracellular matrices of the two tissues intermix and the resulting tissue mineralizes from the outer surface inwards, the opposite of how enamel grows. The difference between enameloid and enamel, therefore, has been proposed to be the result of a heterochronic shift in the timing of secretion by the ameloblasts from post- to pre-mineralization of dentine (Smith 1992, 1995). In conodonts, all histological data point toward interpretation of crown tissue as enamel, but the lack of a basal body could not be explained away even if the crown were enameloid because the growth increments of the crown are still sharply truncated by the basal cavity.

To explain the then apparent absence of dentine in conodont elements (only the basal body of *C. angulatus* had by then been described), Smith & Hall (1993) suggested a shift in timing of ameloblast differentiation to an even earlier phase, prior to odontoblast differentiation. In such a scenario, epithelial–ectomesenchymal interaction would have taken place to produce ameloblast and chondroblast precursors, ultimately resulting in the secretion of enamel and mineralized cartilage. Sansom *et al*.'s (1992) interpretation of the *C. angulatus* basal body has just been discussed and so this scenario may no longer be necessary or appropriate. However, could such a heterochronic shift in timing be invoked to explain the absence of dentine in Middle and Upper Palaeozoic conodonts? The mechanism is not unparalleled (Smith 1992, 1995; M. M. Smith, personal communication) and it is certainly plausible, but it would indicate that the signal for enamel secretion is not the presence of a mineralized surface. M. M. Smith *et al*. (1996) have attempted to homologize conodont elements with odontodes—basic units of the vertebrate dermal skeleton—which are viewed as 'single, modifiable morphogenetic system[s]' (Schaeffer 1977). Odontodes are theoretically (and often in practice) 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 and ameloblast differentiation (Smith & Hall 1993). If conodont elements are homologous to odontodes, the lack of preserved mineralized dentine in many conodont elements could quite easily be explained.

(c) *White matter*

White matter is perhaps the most problematic of all conodont hard tissues. The most recent interpretation of white matter contends that the tissue is cellular dermal bone (Sansom *et al*. 1992, reiterated in 1994; Sansom 1996; M. M. Smith *et al*. 1996). The polarized arrangement of the putative cell processes and cell spaces within white matter, however, argue against an interpretation of white matter as dermal bone.

Although the arrangement of cell spaces and processes within white matter adjacent to lamellar crown is like a dentine, the inclusion of cell-shaped spaces within the groundmass appears atypical. Most modern dentines are highly organized in structure and include only spaces left by cell processes. Cells themselves are not included within the matrix because they retreat ahead of the mineralizing front. However, the fossil record of dentine reveals an evolutionary series of dentine types from a poorly organized cell-including primitive condition, through increasingly more-organized arrangements of cells and cell processes, to a rigidly organized acellular advanced condition (Ørvig 1967*a*). White matter resembles the disorganized structure of mesodentine (e.g. figure 14*f*), the most primitive in this evolutionary lineage. However, the match is not exact because white matter lacks associated pulp canals which often occur in mesodentine. The organization of white matter indicates, however, that the tissue grew orally, so the lack of associated pulp structures may not be so surprising. The implication is that white matter was dead once the sustaining vascularization had been removed to facilitate element function.

The tissue lacks punctuating growth striae which (except for the most primitive types) commonly occur in most dentines. The tissue also reacts differently from the dentine of basal bodies when etched with acid. One possible alternative interpretation is that white matter is a form of enameloid, which commonly includes spaces left by the processes of odontoblasts, close to the dentine–enameloid junction. However, the microcrystalline groundmass of white matter is inconsistent with this hypothesis, as most forms of enameloid are composed of elongate fibre-like crystals.

At present, the most likely interpretation, on the basis of growth pattern and structure, is that white matter is a dentine-related tissue comparable with mesodentine, but exclusive to conodonts. Similarity to primitive enameloids may be shown in the future, e.g. tubercles of the heterostracomorph fish *Astraspis* Walcott possess a 'glassy cap', although the lack of large crystal fibre bundles suggests that this tissue is not homologous with the enameloids of higher vertebrates (Smith *et al*. 1995), and is more similar to white matter. The interpretation of white matter as enameloid appears flawed because white matter is usually completely enveloped by enamel, and is never in contact with the dentine basal tissue. However, there is a direct relationship between the occurrence of growth cavities in the enamel crown and the initiation of white matter secretion (figure 14*e*). The few examples in which such cavities are infilled reveal a mineralized tissue resembling white matter (in *Idiognathodus*, figure 14*g*) or calcospheritic dentine (in *Idioprioniodus*, figure 14*i*,*j*). Furthermore, the step-sided margins of the cavities, resulting from the abutment of surrounding enamel increments, could represent appositional growth of enamel and dentine (figure 14*g*). These cavities could, therefore, represent a source of odontoblastic cells that combined with ameloblasts of the forming enamel to produce an enameloid (bitypic enamel of Smith (1989)). Such a scenario may be analogous to the formation of acrodin blisters on the dermal denticles of some fossil actinopterygians (e.g. Ørvig 1978*a*,*b*,*c*).

Refutation of the presence of cellular dermal bone in conodont elements negates the conclusions of Smith & Hall (1990) and M. M. Smith *et al*. (1996) with regard to

the primacy of cellular over acellular bone, and both tissues retain their previously established (coeval) antiquity (Smith 1991).

White matter is not ubiquitous amongst conodonts and is absent from many taxa. The tissue was not essential to the formation of denticles as elements of almost all taxa contain denticles without white matter. The presence of white matter was, however, certainly beneficial in terms of structural integrity. Conodont element crowns are composed almost entirely from enamel, which is the hardest wearing of all vertebrate biominerals but is extremely brittle. Simple enamels that lack the strengthening effect of prismatic structure are particularly weak. The incorporation of a second tissue, such as white matter, which has different rheological properties, helps to strengthen the element and aids in the decussation of propagating cracks. Through the Upper Palaeozoic, many conodont lineages, particularly ozarkodinids, record a pattern of reduced white matter in P elements in favour of increased complexity in enamel microstructure.

White matter appears to be unique to conodonts, but because it is not present in the earliest of conodont elements it cannot be considered an autapomorphy of the group.

(d) *Discussion*

Examination of patterns of growth recorded by conodont hard tissues has facilitated testing of recent hypotheses of homology with tissues of other organisms. Patterns of growth displayed by individual tissues and by combinations of tissues are consistent with homologies with specific vertebrate dermal hard tissues. This supports the main conclusions of Sansom and colleagues (Sansom *et al.* 1992, 1994; Sansom 1996) although some reinterpretation of their results is necessary. The complexity in patterns of growth previously unrecognized in multidenticulate elements highlights the difficulty in identifying homology between the conodont skeleton and other vertebrate hard tissue systems. This study implies, however, that conodonts must have mineralized their skeleton through the evolution of a suite of hard tissues indistinguishable from those of vertebrates. To even the most ardent opponents of parsimony analysis, an entirely independent origin must appear unlikely. Nevertheless, whatever the outcome of the debate over affinities, the patterns of growth of conodont hard tissues and of element morphogenesis remain valid.

7. PROCESS: UNDERSTANDING CONODONT ELEMENT GROWTH

(a) *Homology within the growing skeleton*

The full interpretation of conodont hard tissues now available allows reassessment of the morphogenetic patterns described earlier, taking into consideration patterns of growth of comparable tissues in extant and well-documented extinct vertebrates. The descriptions of the morphogenetic growth patterns included some attempt to draw homology between the different categories. It is clear that individual denticles of type I elements represent the basic unit of the conodont skeleton. It is also apparent that these undifferentiated units are homologous with the individual multidenticulate units, which collectively comprise type II elements. Furthermore, these units are homologous with multidenticulate elements of more derived taxa such as the ozarkodinids, representative of types III and IV. This last stage of homology is, however, misleading as both type III and IV elements exhibit evidence of repair. These repair events are reinterpreted as episodes of post-functional growth indicating that these elements, like type II elements underwent post-eruptive growth, by envelopment by subsequent odontodes. Whereas juvenile multidenticulate elements of type III and IV taxa are homologous to individual units of type I taxa, gerontic specimens are composed of several such units. Elements of type III and IV are homologous at coeval stages in ontogeny, but the differentiated denticle units of type IV are homologous to individual denticles of type III elements.

The basic structural component of the conodont skeleton can now be seen as a denticle consisting of an enamel lamellar crown cap and a dentine base. Incremental lines within both the enamel crown and dentine basal body meet at the enamel–dentine junction (basal cavity surface), indicating that the two tissues grew in opposing directions, beginning at the enamel–dentine junction with a layer of dentine, followed by a layer of enamel. This pattern is widely recognized amongst vertebrate dermal units and is known as appositional growth. In the vertebrate dermal skeleton, the incremental lines within the two tissues usually share an angular relationship. This is dependent on the shape of the enamel–dentine junction, which is rarely as evaginated in conodont elements. In conodonts, an acute angular relationship is restricted to coniform elements with deep pulp (basal) cavities.

Discrete dermal units within the vertebrate skeleton consisting of enamel and dentine are known as odontodes (Ørvig 1967*a*) and are the basic building blocks of the dermal skeleton. Odontodes usually include a third component, bone, which acts as a tissue of attachment. However, bone is not ubiquitous within odontodes and is absent from the scales of thelodonts, a group of extinct jawless fish, and the scales and teeth of most chondrichthyans. On this basis, M. M. Smith *et al.* (1996) have argued for a homology between conodont elements and odontodes, but in the light of morphogenetic patterns described here, their contention is clearly an oversimplification. Type I elements are composed of up to tens of individual odontodes, but they remained structurally as well as histogenically distinct from each other, united only by an underlying supporting structure. Although the individual odontodes of type II elements were histogenically distinct, their lack of structural identity makes the resulting element an odontocomplex (*sensu* Ørvig 1977; Reif 1982). Odontocomplexes vary in their mode of formation such that successive odontodes may be added to one side, from above or circumferentially. Type III and IV elements are also odontocomplexes and exhibit circumferential addition of successive odontodes. The establishment of the new dental papilla for each odontode, at the boundary between the pre-existing crown and basal body, makes distinguishing the successive odontodes difficult, although pathological specimens confirm this

pattern, e.g. Müller & Nogami (1971, pl. 11, fig. 1) and Müller (1981, fig. 30), where the succeeding odontode has added to one side of the growth centre in a Pa element of *Siphonodella*.

(b) *Discussion*

If the growth patterns described here are to be considered in terms of current hypotheses of conodont phylogeny their arrangement from primitive to advanced would be II–(I)–III–IV; the simplest form, type I, is an evolutionary offshoot, apparently restricted to forms such as *Promissum*, *Coryssognathus* and *Icriodus*. The differences between the four categories are most easily rationalized as resulting from heterochronic changes in the timing of various developmental stages. Type II is found in *C. angulatus*, one of the earliest taxa bearing multidenticulate elements. It has been interpreted as either an evolutionary dead-end (Sweet 1988), or as the stem group of all conodonts (Dzik 1991). *C. angulatus* elements exhibit a pattern of morphogenesis typical of type II, suggesting that either the slightly later forms exhibiting the same pattern are convergent (after Sweet 1988), or else *C. angulatus* is ancestral to all subsequent multidenticulate element-bearing taxa (or possibly they have a common ancestor and *C. angulatus* is divergent). This pattern was elaborated upon in later forms and perhaps within *Cordylodus* itself, where the growth units differentiated morphologically producing multidenticulate units, as in *Carniodus*. Type I appears to be secondarily simple, derived from type II stock and representing a condition where preceding units continued growth after subsequent units were added. This change may have been facilitated by an extension of the early ontogenetic stage of odontode growth in a type II ancestor. Type III probably represents a change in the timing of development in a type II ancestor such that the adult stage is delayed and the primary unit allowed to extend its growth. As there are no spatial restrictions on growth, the element may continue extending along its growth axes. At first it appears as though both III and IV have abandoned the ancestral condition of adding odontodes after primary growth. However, the pattern of periodic repair and enlargement exhibited by these taxa is evidently a vestige of the ancestral growth strategy. The subsequent growth stages are adapted from marginal accretion to completely surround the existing structure, homologous with the growth of acanthodian scales (see below).

The timing of white matter secretion is potentially another important character when comparing the different growth categories, particularly as it consistently represents the latest stage of growth in individual denticles. Whereas denticles in type III elements are dominated by white matter, denticles of type IV elements contain less. Through the Devonian and Carboniferous white matter is further reduced, until by the Carboniferous, many taxa bore elements where only in late stage growth and only the portion of denticles emergent from the main body of the element, contain white matter. As a result, type IV elements resemble the juvenile stage of denticle growth in type III elements, suggesting a heterochronic shift in the timing of secretion of the different tissues.

The complexity of denticle genesis, described here, clearly contradicts Szaniawski & Bengtson's (1993) hypothesis on the origin and genesis of denticulation in euconodonts. Their model proposed that denticles originated in early euconodonts by the accretion of layers of lamellar crown tissue onto a worn, jagged region of primitive coniform elements. If early euconodonts do indeed exhibit this pattern of growth, it is more likely that the denticles formed by repair, having replaced pre-existing, but worn denticles. The pattern of denticle genesis proposed by Szaniawski & Bengtson (1993) is certainly not present in any of the ozarkodinids, prioniodinids, prioniodontids, panderodontids, belodellids or proconodontids observed by this author.

8. COMPARISON OF THE MORPHOGENESIS OF CONODONT ELEMENTS AND OTHER VERTEBRATE HARD TISSUES

The pattern of periodic regrowth in conodont elements, which facilitates repair and enlargement, is unusual in the vertebrate dental record, particularly as the elements are dominated by enamel. In most systems that include enamel, the enamel organ is destroyed during the process of eruption and even in those where the enamel organ survives eruption, enamel secretion is spatially restricted (e.g. rodent teeth), and it cannot facilitate repair to the functional surface. There are very few dental systems that facilitate repair, mainly because most craniates have adopted a strategy of shedding and replacement. However, 'growing' scales are much more common than 'growing teeth' in the vertebrate record and include a facility for post-eruptive repair (if the scale does indeed erupt): for example, some acanthodian (e.g. figure 14*f*) and actinopterygian scales. After some period of time, an erupted scale sinks within the dermis and is enlarged by the growth of another odontode around, above, or to one side of the pre-existing structure. As a result, scales are enlarged and can thus be repaired by successive layers of ganoine (a homologue of enamel; Sire *et al*. 1987; Sire 1994) over the outer surface, occurring in step with successive layers of dentine around the lower surface. Such scales must have spent much time enclosed within soft tissue, in contrast with conodont elements, which, although not teeth in the strictest sense, functioned as such. Conodont elements must periodically have sunk within the dermis, or else the dermis must have grown over the surface of the element, to facilitate growth and repair. As many elements, particularly types I and II, exhibit marginal growth independent of the remainder of the structure, it is possible that at least some elements were partly enclosed within soft tissue throughout life.

The pattern of denticulation in type II and IV is paralleled in a great number of gnathostome dentitions, particularly amongst teleosts. In most cases each denticle is a structurally distinct odontode (tooth), which is situated in a jaw and individually shed and replaced. Conodont elements were not situated within a jaw apparatus and were permanent, not shed and replaced (M. M. Smith *et al*. 1996). Some acanthodian dentitions were also permanent and bear a remarkable similarity to conodonts in 'tooth' arrangement and pattern of growth. Ischnacanthid acanthodians bore dentigerous jaw bones in which the teeth were incorporated and remained undifferentiable from the jaw proper (figure 15*a*); it is largely for this

reason that these groups were believed to have possessed permanent dentition. Like type II and IV conodont elements, the jaw bone grew by marginal accretion and dental units comprising alternating dentition were added sequentially (figure 15*b*(*i*)–*b*(*iv*)). The sequential units are not divisible into distinct teeth and are considered multidenticulate teeth (Ørvig 1973). The dentigerous jaw bones grew rostrally in contrast to the caudal direction of marginal accretion in type I–IV conodont ramiform elements. Acanthodian tooth spirals also exhibit the same pattern of marginal accretion, although the dentigerous units are unidenticulate and grew by accretion on the caudal margin of the spiral. The tooth spirals differ from those of elasmobranchs because the successive teeth are fused together in a single structural unit (figure 15*c*), and so, as each tooth was replaced by its successor, it was not immediately shed but retained and shed with the whole spiral when the last tooth was no longer functional (Ørvig 1973). Although growth of acanthodian dentigerous jaw bones has been poorly documented, there appears to be no evidence of repair to existing dentition during the addition of new dental units, a significant difference from conodont elements. In addition, acanthodian jaws are entirely composed of dentine and bone in the upper and lower portions respectively; they completely lack enamel and there is no evidence for enameloid, again, differing considerably from the condition of conodont elements.

The pattern of growth displayed by the toothplates of modern lungfish represents another possible analogue to the pattern of formation of some conodont elements. The lungfish toothplate is a permanent tooth that grows by accretion of odontodes onto the growing margin (labial in this case). The new odontodes are aligned with ridges of the toothplate, which represent fusion of previously formed odontodes; each ridge is thereby interpreted as homologous with a tooth family (Kemp 1977). Lungfish toothplates are also capable of some degree of repair, but this is achieved by hypermineralizing the dentine, infilling the spaces left by the cell processes that were responsible for the secretion of the original tissue (Smith 1979). The pattern of odontode addition is directly comparable with the addition of denticles in type II conodont ramiform elements and the bifurcation of toothplate toothfamilies comparable with the addition of secondary and tertiary processes in conodont elements such as ramiform elements.

Young *et al.* (1996) challenged the primacy of the odontode as the plesiomorphic patterning component of the vertebrate dermal skeleton. Their new model of the primitive dermal skeleton is based upon fragments of putative dermal armour from the Late Cambrian of Australia, slightly younger than the first records of *Anatolepis* Bockelie & Fortey, another putative vertebrate (Bockelie & Fortey 1976; Repetski 1978; Smith & Sansom 1995; M. P. Smith *et al*. 1996), and the first true conodonts. These broken plates are composed of a tripartite tissue complex including a laminated basal layer, calcospheritic middle layer and continuous hypermineralized capping layer. The middle layer is composed of a series of polygonal fields, radially arranged about vertical canals that traverse the capping layer and open onto the surface through tubercles. The capping tissue is considered homologous to enamel, and although Young *et al.* (1996) refrain

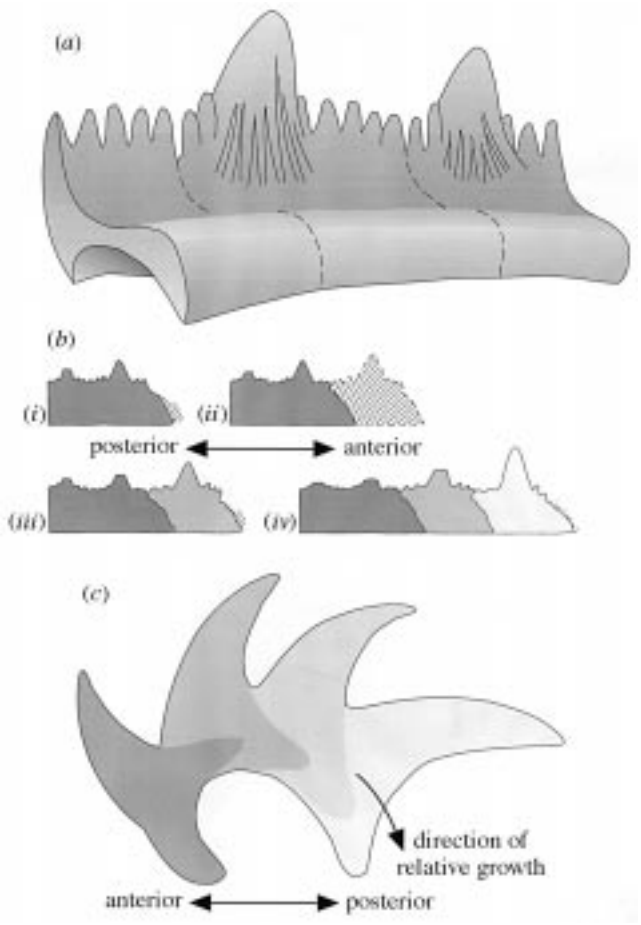

Figure 15. (*a*) Part of a dentigerous jaw bone in *Xylancanthus grandis* Ørvig, after Ørvig (1967*b*, 1973) with omission of the supporting jaw cartilage. Dashed lines delineate units of growth. (*b*(*i*)–*b*(*iv*)) Illustration of growth of acanthodian dentigerous jaw bone by marginal accretion at the anterior end of the jaw. Illustration also includes successive wearing-down of the teeth, after Ørvig (1973). (*c*) Illustration of growth of acanthodian tooth whorl, based on *Nostolepis* Pander. Shading delineates units of growth that were added to the posterior of the whorl, after Ørvig (1973).

from attempting to draw homology between the middle and basal layers and the tissues of other vertebrates, they consider dentine absent. The lack of dentine or bone of attachment in this material is taken as evidence that they are not primitive for the dermal skeleton of vertebrates, and thus an unreliable indicator of vertebrate affinity. In the light of this, one wonders on what basis the new Cambrian material from Australia is ascribed to the vertebrates? The identification is based largely on comparative morphology of surface ornament, and the tripartite tissue combination from which the sclerites are composed. Comparative morphology has, in the past, been recognized as an unreliable indicator of affinity (e.g. Schallreuter 1983, 1992). Furthermore, the tripartite tissue combination is typical of vertebrate dermal armour because odontodes are three-layered, and yet Young *et al.* (1996) conclude that odontodes are not plesiomorphic in the vertebrate exoskeleton. Yet on this basis, Young *et al.* go on to reinterpret the hard tissue histology of *Anatolepis* and conodonts, concluding that the two groups 'represent divergent specialisation's with the early diversification of

vertebrate hard tissues' (p. 812) and that conodont hard tissues are unique. Even if the new Cambrian material were vertebrate, there is no evidence, stratigraphic or otherwise, that it is any less derived than *Anatolepis* or the hard tissues of conodonts. It could as easily have been derived from *Anatolepis*. The evidence from *Anatolepis* and from conodonts suggests that odontodes are plesiomorphic patterning units of the vertebrate dermal skeleton.

9. DISCUSSION

The apparent complexity inherent within the structure of conodont elements is remarkable. Conodonts were capable of producing elements of diverse shape and structure, from unidenticulate coniform elements to multidenticulate ramiform elements, through the addition of any number of odontodes. However, the basic architectural plan of the feeding apparatus remained conservative throughout the conodont record. The architecture of the feeding apparatus of ozarkodinids is known to have remained stable in element number and position throughout much of its record (Silurian–Carboniferous from a record extending latest Ordovician to Permian; Purnell & Donoghue 1998). Given the variety of morphogenetic patterns exhibited by different conodont taxa, architectural stability is even more remarkable.

Prioniodinids also bore a standard 15-element apparatus (Purnell & von Bitter 1996), and although *Promissum* possessed a 19-element apparatus, other evidence suggests that this apparatus is representative of balognathids alone and not the prioniodontid order as a whole (Stewart 1995). Current available evidence indicates, however, that this plan is not plesiomorphic for the Euconodonta as taxa representative of ancestral stocks, such as *Panderodus* Ethington, may have had up to 17 elements (Sansom *et al*. 1994).

There must have been a controlling factor in the growth of the conodont apparatus which prevented deviation from the standard 15-element PMS division through much of the conodont record. The elements as unitary structures are not directly comparable with teeth or dermal teeth, but with aggregations of them, so it is convenient to consider each element position to be analogous to a gnathostome tooth family, where growth is restricted to within the 'tooth position'. Growth between such positions in conodont elements, as in tooth families, may have been prevented by a 'zone of inhibition'. However, unlike most tooth families, functional teeth were not replaced in successive generations, but added to by new teeth, as in the dentigerous jaw tooth families of ischnacanthid acanthodians.

The difference between teeth and other odontodes is the locus of formation; teeth are formed only within a dental lamina, which probably did not evolve until after the mandibular arch (Reif 1982). However, if conodont elements are homologous to vertebrate teeth (e.g. Gaengler & Metzler 1992), they must have formed within a dental lamina. Such a dental lamina would have had to be permanent, but instead of facilitating growth of replacement teeth, it would have been responsible for periodic growth and repair of damaged elements. If such a scenario is realistic, it is likely that the dental lamina was discontinuous and the proposed 15-element plan of the conodont feeding apparatus, autapomorphic to all complex conodonts, was a result of segregated dental laminae of the same number.

10. THE REST OF THE CONODONT SKELETON

The feeding elements are the only part of the conodont skeleton to have been consistently mineralized, but is there any other evidence of skeletal biomineralization? Phosphatic spheres found associated with conodont elements have been attributed to the conodont animal and have been coined 'conodont pearls' (Glenister *et al*. 1976, 1978). Glenister *et al*. further proposed that the structures represented the animal's response to irritation, whether by detritus or parasitic invasion. The animal alleviated the irritation by secretion, around the stimulus, of the mineral normally used to grow the feeding elements. The pearls have since been demonstrated as belonging to an extinct group of bryozoans (Donoghue 1996).

The only other mineralized structure associated with conodonts is a small phosphatic object found adjacent to the feeding apparatus in one of the Scottish conodont animals. This sphaeroid strongly resembles lamprey statoliths which are also phosphatic, and appears in a position within the head consistent with the otic capsules (Aldridge & Donoghue 1997), organic remnants of which may also be preserved in another of the Scottish specimens (Briggs *et al*. 1983; Aldridge *et al*. 1993). However, otoliths, statoliths and statoconia are non-skeletal (Maisey 1987).

The conodont animal must also have possessed some form of internal skeleton, if for no other reason than to have provided support and articulation for manipulation of the feeding apparatus (Purnell & Donoghue 1997) and also support to the gills. Despite preservation of soft tissues (Briggs *et al*. 1983; Aldridge *et al*. 1986, 1993; Aldridge & Theron 1993), sometimes in exquisite detail (Gabbott *et al*. 1995), there is still no record of such an internal skeleton, mineralized or otherwise. It is likely that the animal possessed a cartilaginous endoskeleton much like that of the extant agnathans, hagfish and lampreys. Fossil representatives of these groups also lack preserved evidence of their cartilaginous endoskeleton (Bardack & Zangerl 1968, 1971; Bardack & Richardson 1977; Bardack 1991).

11. CONCLUSIONS

Description of growth patterns in conodont elements has provided a means of testing competing hypotheses of hard tissue histology which were originally based simply on isolated morphological characters. The results of the study have vindicated the suggestion that there is homology between conodont and vertebrate hard tissues. Conodont elements are more complex structures than previously recognized. They are not homologous with 'odontodes' (*contra* M. M. Smith *et al*. 1996), but each element appears to comprise one or a number of odontodes, analogous (or homologous) to a tooth family. The different patterns of formation are believed to reflect heterochronic shifts in the timing of developmental stages. The growth patterns in conodont elements were evolved entirely independently from similar patterns in more advanced vertebrates. Conodont elements offer closer

comparison with dermal scales and oral odontodes than with true teeth.

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