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BASAL TISSUE STRUCTURE IN THE EARLIEST EUCONODONTS: TESTING HYPOTHESES OF DEVELOPMENTAL PLASTICITY IN EUCONODONT PHYLOGENY

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Typescript received 21 March 2003; accepted in revised form 17 February 2004

Abstract: The hypothesis that conodonts are vertebrates rests solely on evidence of soft tissue anatomy. This has been corroborated by microstructural, topological and developmental evidence of homology between conodont and vertebrate hard tissues. However, these conclusions have been reached on the basis of evidence from highly derived euconodont taxa and the degree to which they are representative of plesiomorphic euconodonts remains an open question. Furthermore, the range of variation in tissue types comprising the euconodont basal body has been used to establish a hypothesis of developmental plasticity early in the phylogeny of the clade, and a model of diminishing potentiality in the evolution of development systems. The microstructural fabrics of

the basal tissues of the earliest euconodonts (presumed to be the most plesiomorphic) are examined to test these two hypotheses. It is found that the range of microstructural variation observed hitherto was already apparent among plesiomorphic euconodonts. Thus, established histological data are representative of the most plesiomorphic euconodonts. However, although there is evidence of a range in microstructural fabrics, these are compatible with the dentine tissue system alone, and the degree of variation is compatible with that seen in clades of comparable diversity.

Key words: Vertebrate, Conodonts, histology, skeleton, dentine, developmental evolution.

THE comparative histology of conodont hard tissues is extremely controversial, though needlessly so. The chordate, craniate and vertebrate affinity of conodonts has been established solely on the basis of evidence of soft tissue anatomy provided by ten specimens from the Lower Carboniferous of Scotland (Aldridge *et al.* 1993) and a single specimen from the Late Ordovician of South Africa (Gabbott *et al.* 1995). These data suggest that although the anatomy of conodonts is common to that of a generalized chordate/craniate, it includes a suite of more exclusive characters that diagnose less inclusive clades (Donoghue *et al.* 1998, 2000). Comparative histology can only be undertaken within a phylogenetic context and in light of evidence from soft tissue anatomy it is possible to interpret conodont hard tissues within a chordate context, at the very least (Donoghue 1998). Among all known living and fossil chordates, conodont hard tissue complexes only bear comparison with the dental complexes of the teeth and scales of living and fossil vertebrates, and they do so on microstructural, developmental and topological criteria (Sansom *et al.* 1992, 1994; Sansom 1996; Donoghue 1998; Donoghue and Chauffe 1999).

The histology of conodont hard tissues is understood well only for the euconodonts, and then mainly among the most derived clades. These data indicate that conodont skeletal elements are bicomponent complexes, composed of an upper crown and lower 'basal body'. The crown is coarsely crystalline and has been compared to enamel (Dzik 1986; Andres 1988; Sansom 1996; Smith *et al.* 1996; Donoghue 1998, 2001). Crown tissue can include an enigmatic tissue known as white matter, compared to cellular dermal bone by Sansom *et al.* (1992), but which is apomorphic to conodonts (Donoghue and Chauffe 1999). The structure of the basal body varies considerably, including a range of microstructures from tubular, to atubular lamellar, and spheritic (Andres 1988; Sansom *et al.* 1994; Donoghue 1998), and it has also been suggested to be composed of two structural divisions, the basal cone and cone-filling (Gross 1957). This division is only apparent in some taxa, and it appears that the so-called 'basal cone-filling' is absent from the vast majority. All basal tissue microstructures are similar to dentine, and the tubular fabrics particularly so (Andres 1988; Sansom *et al.* 1994; Donoghue 1998). Growth lines

within both crown and basal tissue demonstrate centrifugal growth, and the one-to-one relationship between incremental layers in the crown and base, which meet all along a single plane, indicate appositional growth (where the cone-filling is present, its pattern of growth is centripetal). This topological and developmental relationship is directly comparable to the relationship between dentine and enamel in living and fossil vertebrates (Donoghue 1998). To clarify, when dentine is secreted in concert with enamel, successive layers of the two are added in a one-to-one relationship, meeting at the enamel-dentine junction, and apposition continues until the final external morphology is established; a centrifugal pattern of growth. Later infilling of the pulp cavity by dentine is centripetal. Where dentine develops together with enameloid, or where it constitutes a scale or tooth wholly, the final morphology of the tooth is established before mineral deposition, and dentine layers are added centripetally, infilling the preformed mould. The growth of conodont elements is compatible only with the enamel-dentine system, to which all previous comparisons have been made (e.g. Sansom 1996; Smith *et al.* 1996; Donoghue 1998). Note, however, that the practised distinction between centrifugal and centripetal growth patterns is entirely subjective and contingent upon the degree of curvature of the basal lamina represented by the crown-basal body junction in conodonts, or the enamel-dentine junction, or outer morphology of a tooth or scale. Strictly, the pattern of growth is always centrifugal as layers are added on top of one another away from this epithelial junction.

The microstructural, topological and inferred developmental similarities between conodont and vertebrate hard tissues are observations and they would stand regardless even if it were demonstrated that they are convergent. Nevertheless, the proposed homologies are disputed (Kemp and Nicoll 1995*a, b*, 1996; Schultze 1996; Kemp 2002*a, b*). Indeed, it is possible that conodont hard tissues represent an evolutionary experiment in skeletonization that is entirely independent of other vertebrates but, given that conodonts are resolved as the sister-group to skeletonizing vertebrates on soft tissue evidence alone (Donoghue *et al.* 2000), this scenario is not altogether plausible, let alone parsimonious, particularly given the corroborative similarities based on so many independent criteria.

Nevertheless, existing works on the comparative histology of conodont hard tissues are compromised by reliance upon data from extremely derived taxa. For instance, Sansom *et al.* (1992, 1994) and Smith *et al.* (1996) are based largely upon panderodontid, prioniodinid and ozarkodinid taxa, as well as the systematically enigmatic *Cordylodus* and *Neocoleodus*, while Donoghue (1998) is based mainly upon prioniodontids, prioniodinids, ozarkodinids, plus some of the other taxa already

mentioned. More plesiomorphic taxa have been analysed and, in particular, Andres (1988) has compared surface features of the basal bodies of *Proconodontus* and *Cordylodus* to dentine. However, most histological studies of early euconodonts have made little or no attempt at a comparison with other groups (Müller and Nogami 1971; Bengtson 1976, 1983; Szaniawski 1987; Szaniawski and Bengtson 1993, 1998; Müller and Hinz-Schallreuter 1998). Thus, the degree to which the more completely understood taxa are representative of their more plesiomorphic relatives remains an open question.

The plesiomorphic condition of conodont basal tissue is of particular significance given its proposed homology to dentine (Andres 1988; Sansom *et al.* 1994; Donoghue 1998; Smith and Sansom 2000). The identification of globular calcified cartilage constituting the basal tissue in one of the most plesiomorphic taxa analysed fully hitherto (*Cordylodus*; Sansom *et al.* 1992) was taken by Forey and Janvier (1993) to cast significant doubt over the hypothesis of a vertebrate affinity for conodonts. This is because tubular dentine is a readily recognized tissue that is both exclusive and plesiomorphic to vertebrates (although all collagen-based skeletal connective tissues are absent from lampreys, which are also vertebrates, by definition). Andres (1988) had earlier compared features of *Proconodontus* and *Cordylodus* to dentine and so, together with the subsequent description of tubular dentine in *Chirognathus* and *Neocoleodus* (Sansom *et al.* 1994), there is indeed evidence of this key vertebrate apomorphy in conodonts. But the presence of dentine, topologically in place of globular calcified cartilage, suggested a degree of developmental plasticity in the tissues constituting conodont elements (Sansom *et al.* 1994), a phenomenon also apparent in other early vertebrates (Moss 1964; Halstead 1987; Smith *et al.* 1996; Smith and Sansom 2000). This has been reinforced by subsequent evidence of microstructural variation in the atubular (dentine) basal tissues of most other conodonts (Donoghue 1998). In this study we provide new evidence and review existing evidence on the structure of the basal tissues in representatives of the earliest and, presumably, most plesiomorphic euconodonts with the aim of addressing whether (1) dentine or cartilage constitutes the basal body plesiomorphically, (2) the atubular or tubular dentines are plesiomorphic for the clade and (3) the model of developmental plasticity in early euconodont phylogeny stands up to scrutiny.

MATERIAL AND METHODS

Conodont histology has conventionally been studied using thin section and etched ground section techniques (Donoghue 1998). The small size of early euconodonts precludes these as routine techniques, but the small size

and thin-walled nature of these taxa does allow for the ready application of the oil immersion technique for whole mount specimens (Donoghue 1997). This has the advantage of being non-destructive, and also provides a means of identifying specimens most suitable to conventional, destructive techniques. Clove oil was used as the immersion medium and specimens were examined using a Zeiss Axiophot fitted with differential interference contrast (Nomarski) optics. Photomicrographs were obtained using a Nikon Coolpix 990 fitted via a c-mount and interchange lens to the microscope. Figured specimens are deposited at the Geological Museum of Peking University, Beijing, PR China (GMPKU), Lapworth Museum of Geology, Department of Earth Sciences, School of Geography, Earth and Environmental Sciences, University of Birmingham, UK (BU), and US National Museum of Natural History, Washington, DC, USA (USNM).

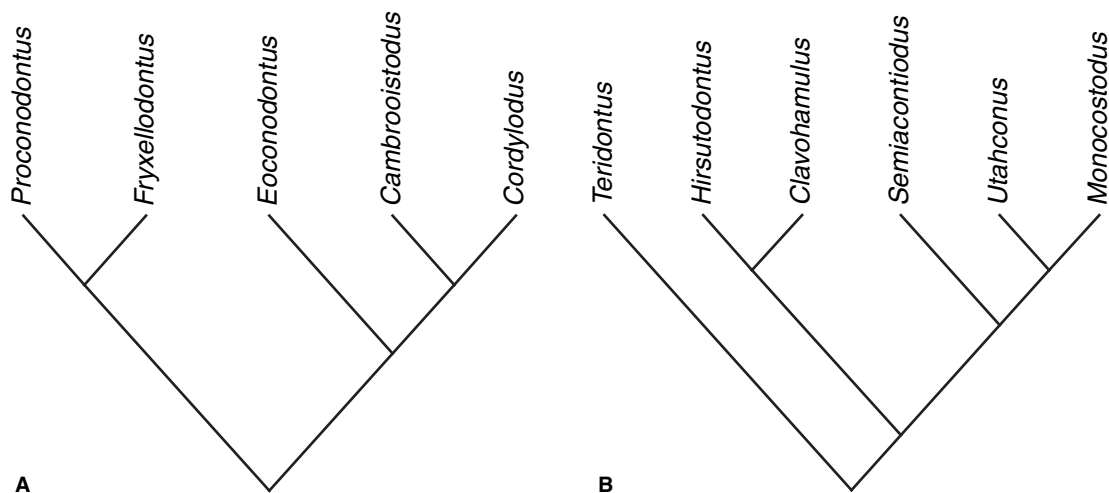
THE INTERRELATIONSHIPS OF EARLY EUCONODONTS

The phylogenetic relationships of early euconodonts are extremely poorly understood. This occurs primarily because the distinction between the different grades (though not necessarily clades; it is possible that they are not close relatives) of conodontiform fossil taxa, euconodonts, paraconodonts and protoconodonts, is entirely histologically based and, given the paucity of microstructural studies, it is not clear which taxa should be considered within a phylogeny of euconodonts. The elements of early euconodonts are morphologically very simple and, thus, there has been little attempt to reconstruct relationships other than through empirical morphological

analysis in hand with biostratigraphic range data (e.g. Miller 1980; Szaniawski and Bengtson 1998). This is problematic because genuinely new taxa continue to be discovered (e.g. *Cambropustula*, the oldest euconodont currently known; Müller and Hinz-Schallreuter 1998) and, until recently, the majority of research effort has been devoted to describing taxa from north-west Europe, North America and China, providing a relatively biased geographical sampling of the available rock record.

These issues notwithstanding, existing hypotheses suggest that the earliest record of euconodonts is represented by two distinct lineages whose first representatives are *Proconodontus* and *Teridontus*, respectively (Miller 1980, 1984; An and Mei 1994; Text-fig. 1; *Cambropustula* has yet to be incorporated into a specific hypothesis of euconodont phylogeny). It has never been suggested that the latest common ancestor of the two lineages was of euconodont grade and Miller (1980, 1984), among others (Sweet 1988; Szaniawski and Bengtson 1993), has explicitly argued that euconodonts are polyphyletic, although their precise relationships are unknown.

However, the data supporting distinction between the two lineages amounts largely to the relative size of the basal cavity, such that taxa with deeply excavated, thin-walled crowns are united in the *Proconodontus* lineage, and taxa with shallow basal cavities and relatively thick-walled crowns are united in the *Teridontus* lineage. This is a labile developmental character that relates only to the degree to which the successive lamellae of basal tissue recede during appositional growth (cf. Lindström and Ziegler 1971), and it is set against a greater number of synapomorphies uniting the two lineages and successively less inclusive subsets of these taxa. These include the presence of white matter, many details concerning the morphological differentiation of element



TEXT-FIG. 1. Hypotheses of relationships within the two putatively distinct lineages of euconodont grade taxa converted to trees from published phylogenies, based on Miller (1980, 1984) and An and Mei (1994), and the present study. A, the *Proconodontus* lineage; note that in the published phylogenies *Proconodontus* and *Eoconodontus* are resolved as ancestral to the respective sister included. B, the *Teridontus* lineage; note that in the published phylogenies *Teridontus* is resolved as ancestral to all sister taxa.

morphology from the simplest of 'simple cones' represented by *Proconodontus* and *Teridontus* and, in correlation, the differentiation of the apparatus into a number of distinct element morphotypes (though not necessarily a change in the number of elements comprising the apparatus). Furthermore, the taxa included in these schemes are highly selective and there are a number of other taxa that fit somewhere in the milieu, including *Cambropustula*, *Coelocerodontus*, *Dasytodus* and *Granatodontus*. The last of these has hitherto been considered a paraconodont (Chen and Gong, 1986), but our histological analysis demonstrates its euconodont grade of organization (Pl. 1, figs 6–9). It is likely that a number of other taxa currently considered to be of paraconodont grade, but which have yet to be investigated histologically, will be similarly reassigned. Thus, with at least one-third of the (known) earliest euconodonts yet to be included into phylogenetic schemes, and the number of potential synapomorphies uniting all of these taxa greatly outweighing the only potential synapomorphy distinguishing two polyphyletic lineages, it is both more plausible and parsimonious to conclude that euconodonts are monophyletic.

Thus, in the absence of a defensible scheme of phylogenetic relationships it will not be possible to resolve in detail the phylogenetic polarity of any variable in the basal tissues of the earliest euconodonts. Rather, we shall examine the degree to which variation is manifest and how this compares to the range of basal tissues encountered among more derived euconodonts.

BASAL TISSUE STRUCTURE AMONG THE EARLIEST EUCONODONTS

New data

Cambrooistodus. All specimens examined exhibit an atubular lamellar fabric (Pl. 1, figs 1–2) in which successive layers of basal tissue are deeply invaginated and extend around all exposed margins of preceding incremental

layers in an appositional growth relationship with the overlying crown tissue (Pl. 1, fig. 2), resulting in lamellae that are W-shaped in cross-sectional profile, reflecting a three-dimensional arrangement of stacked inverted cone-shaped layers with upturned rims.

Dasytodus. The basal body is a single structural unit that exhibits two microstructures (Pl. 1, figs 3–5). The dominant microstructure is lamellar and atubular, with successive lamellae arranged as relatively deeply invaginated layers that are \wedge -shaped in cross-sectional profile. The lamellar fabric typifies early growth of the basal body and, moving away from the crown-basal body junction, the lamellar microstructure degrades into concentrically layered calcospheres (Pl. 1, fig. 5), reflecting late-stage growth of multiple independent nucleation sites, rather than apposition. This may reflect the relatively confined nature of the centripetally in-filled basal cone.

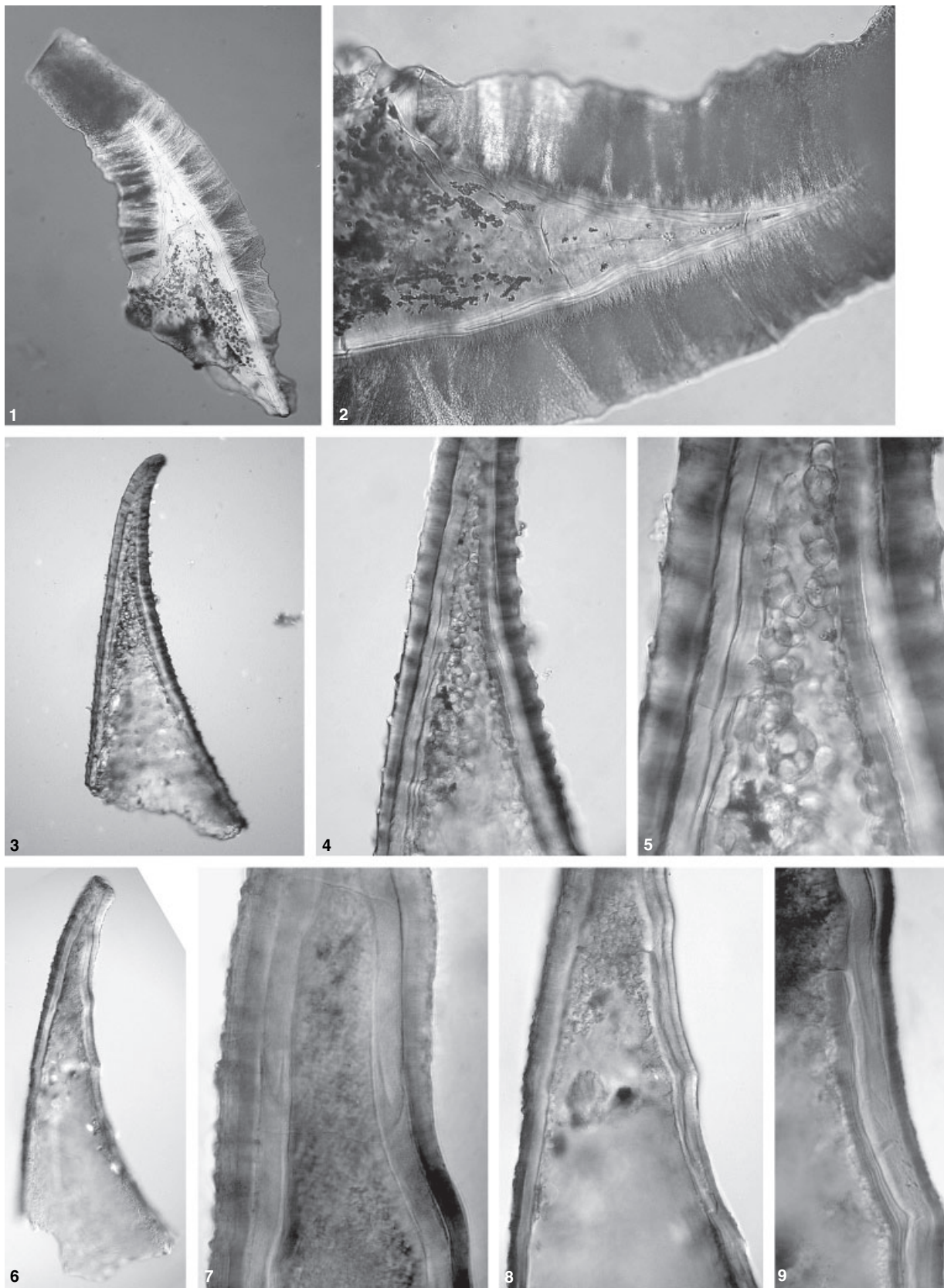
Granatodontus. The basal body can be interpreted as composed of two main structural units distinguished on the basis of fabric (Pl. 1, figs 6–9). The component immediately adjacent to the crown, the basal cone, is atubular, lamellar, with successive lamellae appearing as extremely deeply invaginated layers that have a greatly exaggerated W-shaped outline in cross-sectional profile (Pl. 1, fig. 7). Thus, the rim of the successive inverted cone-shaped sheets represents by far the thickest part of the layer, producing an extremely thin-walled structure with a very large surface area. The growth lines that demarcate successive lamellae indicate episodic growth (Pl. 1, fig. 7), comparable with growth patterns observed in more derived euconodonts (Zhang *et al.* 1997; Donoghue and Purnell 1999; Armstrong and Smith 2001). The second basal tissue fabric is represented by late-stage centripetal infilling of the inner 'basal cone' or cone-filling within the basal body (Pl. 1, figs 8–9). This tissue is demonstrably lamellar, but degrades into concentrically layered calcospheres which represent multiple point nucleation sites.

EXPLANATION OF PLATE 1

Figs 1–2. *Cambrooistodus* sp.; Gros Ventre Formation, Late Cambrian, Bighorn Mountains, Wyoming, USA; BU 4420. 1, overshoot; $\times 134$. 2, detail of the basal tissue fabric revealing incremental growth lines in an appositional growth relationship with the overlying crown tissue; $\times 352$.

Figs 3–5. *Dasytodus* sp.; GMPKU2110; Upper Cambrian Fengshan Formation, Lashushan section, Jinzhou District, Dalian City, Liaoning Province, north-east China; note the outer lamellar structure of the basal tissue which intergrades with the core of calcospheres; 3, $\times 113$; 4, $\times 299$; 5, $\times 759$.

Figs 6–9. *Granatodontus* sp. Chen and Gong (1986); Late Cambrian; Whipple Cave Formation equivalent, lower part of the Pogonip Group, near Steptoe, White Pine County, Nevada, USA; USNM 521006. 6, lamellar fabric intergrades with a core of calcospheres; $\times 140$. 7, note that the episodic growth increments are confined to the outer margin of the basal tissue; $\times 744$. 8–9, the core is composed of layered sheets that cut across earlier growth increments, indicating late-stage infilling of the core, eventually intergrading with calcospheres. 8, $\times 223$; 9, $\times 433$.



DONG *et al.*, Cambrian euconodonts

Hirsutodontus. The basal body is composed dominantly of an atubular, lamellar fabric that corresponds to the early and main phase(s) of growth (Pl. 2, figs 1–2). Later lamellae within the basal tissue are convoluted, and convolutions between successive lamellae are aligned (Pl. 2, fig. 2). The convolutions may correspond to fine or infilled tubules in a perpendicular orientation.

Proconodontus. The basal tissues are lamellated and arranged about a deeply invaginating pulp cavity (Pl. 2, figs 3–6). Two distinct tissue fabrics are apparent: atubular and tubular. The atubular tissue (Pl. 2, figs 3–4) is clearly lamellated, although the lamellae are scalloped, and the undulations correspond from lamella to lamella. The latest layers of basal tissue are sometimes disrupted by concentrically layered calcospheres that can occupy much of the cavity. This gives the impression of a two-layered structure, compatible with the distinction of a basal cone and cone-filling, as per Gross (1957), but Szaniawski and Bengtson (1993) resolved the layers in the cone-filling to be continuous with layers in the basal cone, in the distal part of the element. Where the tubular fabric is apparent (Pl. 2, figs 5–6; observed in a number of specimens of *P. tenuiserratus*, but only this taxon), the tubules are orientated perpendicular to the base of the crown tissue (surface of the basal cavity) and are co-ordinate with undulations in the background fabric of the lamellated tissue. The tubules maintain a consistent diameter throughout their length and do not appear to branch, although in all specimens exhibiting this fabric, the distal end of the tubules, which open into the division of the basal body sometimes referred to as the 'basal cone', are not preserved. These findings correspond well with those of Müller and Hinz-Schallreuter (1998), who observed fine-calibre tubules, orientated perpendicular to the crown, in the basal body of *Proconodontus muelleri*. Andres (1988) observed a suite of intermittent fine-calibre (*c.* 1 μm), longitudinally aligned canals penetrating the surface of the basal body, as well as a fabric of much coarser (7–8 μm) canals aligned perpendicular to the wall of the element, restricted to a distal portion of the basal body not overlain

by crown tissue. These were not observed in any of our materials, but their presence in other collections has been verified by Szaniawski and Bengtson (1993).

Teridontus. The basal body is composed of two optically distinct units (Text-fig. 2). An outer basal cone, which lies immediately adjacent to the crown, is composed of an atubular lamellar fabric, although it often contains large spaces and appears to have been less well mineralized than the cone-filling. The cone-filling is quite distinct, with a fibrous fabric which, under cross-polarized light, reveals variation in the arrangement of the crystallites that constitute it (Text-fig. 2C). The growth lines, which demarcate successive lamellae within the basal body, are only apparent within the basal cone, becoming imperceptible at the border between the two optically distinct units. Their arrangement corresponds to the W-shaped lamellae comprising the basal body of *Cambroistodus*.

Existing data on other Cambrian euconodont taxa

Cambropustula. Müller and Hinz-Schallreuter (1998) described a lamellated, apparently atubular structure to the basal body, but provided no histological evidence for this.

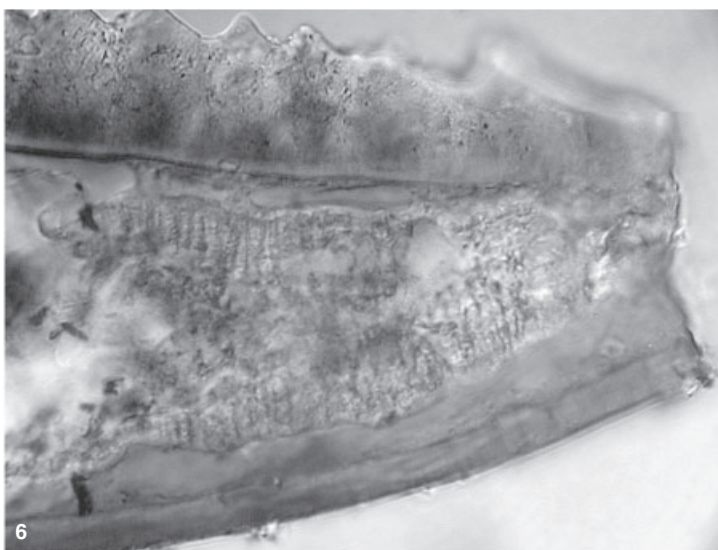
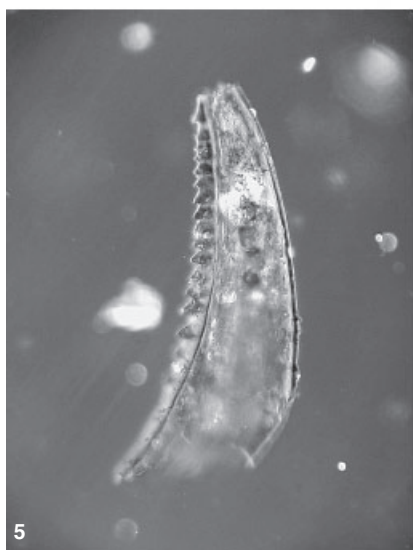
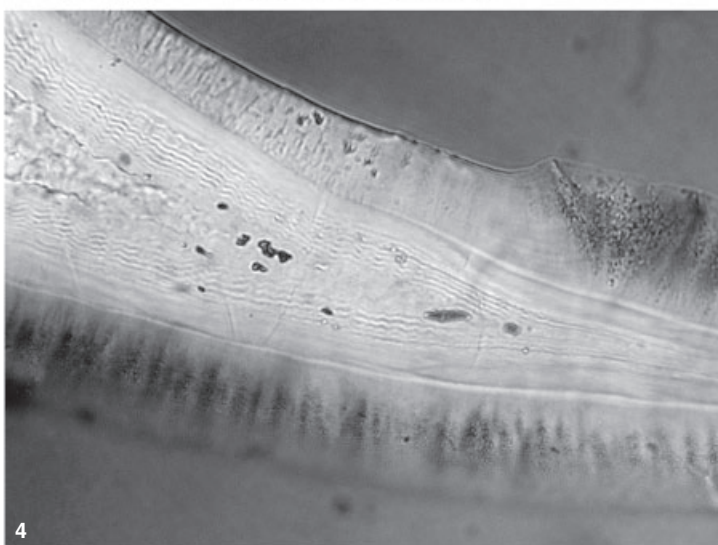
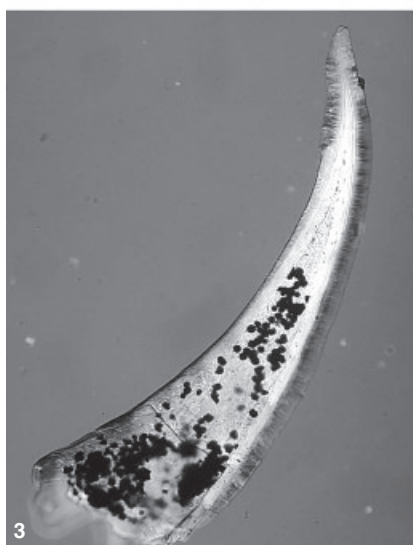
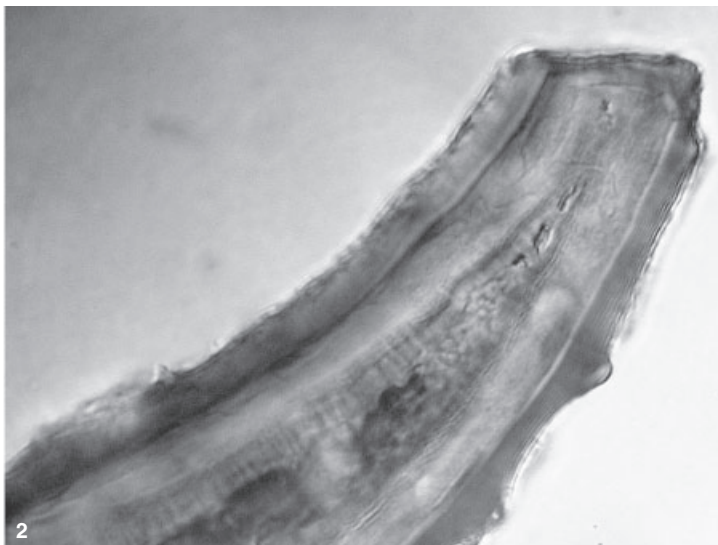
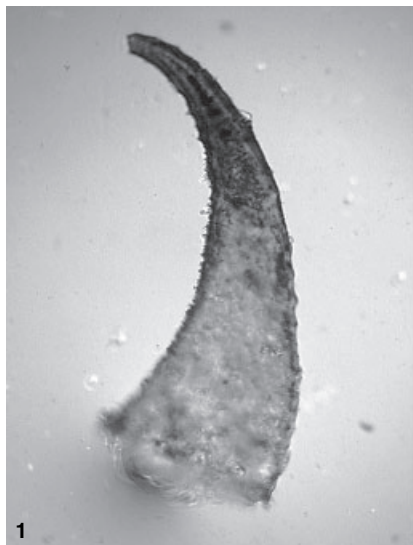
Cordylodus. The structure of the basal tissue in *Cordylodus* has been described in a number of publications (Müller and Nogami 1971; Szaniawski 1987; Andres 1988; Sansom *et al.* 1992; Szaniawski and Bengtson 1993; Donoghue 1998) and, in many instances, it has been revealed to be composed of a thin zone of centrifugally added lamellae immediately adjacent to the crown, succeeded by a complete infilling with concentrically layered calcospheres that frequently encapsulate one another, and can be encapsulated by continuous layers corresponding to episodic growth. In addition, Andres (1988) described the presence of coarse- and fine-calibre pores/canals penetrating the base and margins of the basal body that extend beyond the limit of the crown, much as in *Proconodontus*.

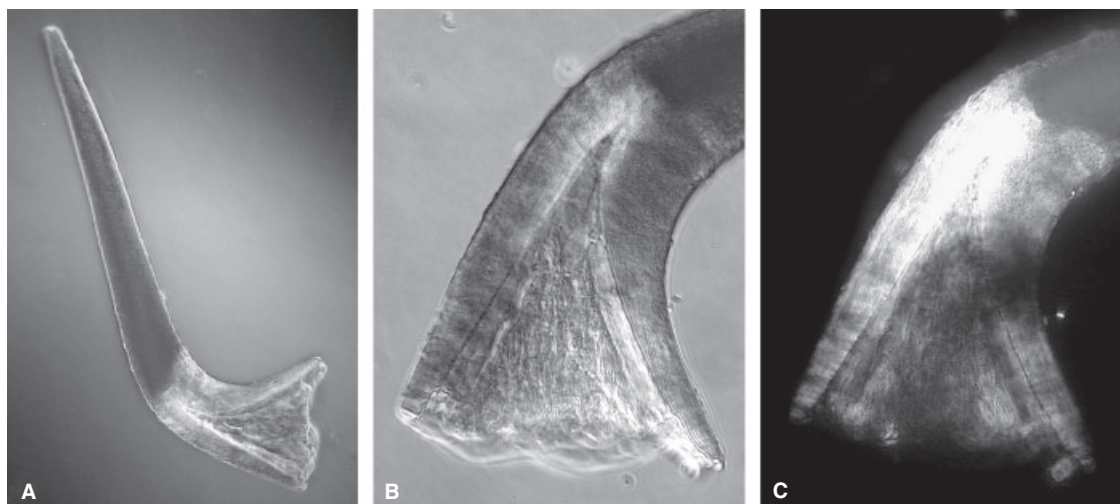
EXPLANATION OF PLATE 2

Figs 1–2. *Hirsutodontus* sp.; Upper Cambrian Fengshan Formation, Lashushan section, Jinzhou District, Dalian City, Liaoning Province, north-east China, GMPKU2111. 1, overshoot; $\times 103$. 2, lamellar growth increments within the basal tissue showing evidence of a scalloped outline and possible tubules towards the core; $\times 836$.

Figs 3–4. *Proconodontus* sp.; Gros Ventre Formation, Late Cambrian, Bighorn Mountains, Wyoming, USA; BU 4421. 3, overshoot; $\times 139$. 4, lamellar growth increments within the basal tissue which show an appositional growth relationship with the crown, and a crenulated-scalloped outline basally and towards the core; $\times 842$.

Figs 5–6. *Proconodontus tenuiserratus* (Miller, 1980); Basal *Proconodontus* Zone, Upper Cambrian Shenjiawan Formation, Wa'ergang Section, Wa'ergang village, Taoyuan county, north-west Hunan, South China, GMPKU2112. 5, overshoot; $\times 145$. 6, tubules penetrating the fabric of the basal tissue, perpendicularly to growth increments in this tissue, and to the basal margin of the crown; $\times 1020$.





TEXT-FIG. 2. *Teridontus nakamurai* (Nogami, 1967); Wilberns Formation, Late Cambrian, Threadhill Creek, central Texas; BU 4419. A, overshoot; $\times 58$. B–C, basal body with an outer homogenous fabric and an inner fibrous core in plane and cross polarized light, respectively; $\times 385$.

Eoconodontus. Szaniawski (1987) provided data on the structure of the basal body in this taxon based upon etched sections. These revealed a lamellar fabric to the tissue, with possible evidence of a distinction between the nature of the tissue fabric at the crown/basal body margin, as compared with the basal tissue in the core of the basal body.

No data are available on the basal tissues of *Clavohamulus*, *Fryxellodontus*, *Semiacontiodus*, *Monocostodus* and *Utahconus*, in part because some taxa have yet to be analysed histologically, but mainly because most of these taxa do not, generally, preserve basal tissue (e.g. *Clavohamulus*).

DISCUSSION

The one obvious pattern apparent from the structure of the basal tissues among the earliest euconodonts is that they reflect the full spectrum met with among the more derived taxa examined hitherto. Thus, at least with regard to basal tissues, concerns regarding the degree to which current knowledge is representative of euconodonts, as a whole or plesiomorphically, are dispelled. Furthermore, the aim of resolving the plesiomorphic nature of euconodont basal tissue is confounded: there is apparently no single plesiomorphic basal tissue type. What is the significance of this variation for understanding tissue homologies, and the degree to which our existing knowledge of conodont histology is representative of euconodonts as a whole?

Basal tissue homology: dentine vs. cartilage

Within the context of chordate affinity, there have been two proposed tissue homologies for conodont basal

tissues: globular calcified cartilage (Sansom *et al.* 1992) and dentine (Andres 1988; Sansom *et al.* 1994). These homologies are not necessarily mutually exclusive; instead some taxa have been considered to possess a basal body composed of cartilage, in others, dentine. Both hypotheses were proposed on microstructural grounds alone, although Donoghue (1998) found topological and developmental support for homology with dentine alone. This argument follows the observation that the key microstructural characteristics used in the identification of globular calcified cartilage (spheres with concentric growth layering) are also met with in dentine, while the characteristic used in the identification of dentine (perpendicularly orientated tubules) is diagnostic only of dentine. Furthermore, in all examples of euconodonts where the basal tissue is composed of calcospheres, this fabric intergrades proximally with a lamellar fabric. This is not incompatible with the structure of globular calcified cartilage, but its appositional growth relationship with the overlying crown tissue, a putative enamel homologue (although see Donoghue 2001), is. Thus, given that the characteristics of globular calcified cartilage are also met with in dentine, and that the basal tissues of euconodonts exhibiting these characteristics also exhibit other features incompatible with cartilage, but compatible with dentine, all euconodont basal tissues are more appropriately homologized with dentine, without caveat. Thus, the main justification for the hypothesis of developmental plasticity among early euconodonts can be rejected.

This has important implications for the homologies of euconodont and vertebrate hard tissues insofar as it confirms that the observed similarities established on the basis of derived taxa are common also to the very earliest euconodonts. More specifically, the observation of tubular

dentine in *Proconodontus*, the earliest euconodont for which histological data on basal tissue are available, resolves that the tubular dentines observed in *Chirognathus*, *Neocoleodus* (Sansom *et al.* 1994) and *Oulodus* (Smith and Sansom 2000) are not a convergent peculiarity of these taxa, but reflect a symplesiomorphy of the euconodont clade, a condition that is secondarily absent among most derived euconodonts.

The architecture of the fine-calibre tubules in *Proconodontus*, straight, parallel-sided, unbranched and of relatively coarse calibre, is common to the condition in *Chirognathus* and *Oulodus*, and differs significantly from the condition in *Neocoleodus*, in which the tubules ramify repeatedly. The idealized architecture of dentine tubules, as understood from living vertebrates, and humans in particular, is one where the tubules taper only very slightly, and have very fine ramifications along their length, though concentrated at the distal extremity of the odontoblast process, in proximity to the enamel-dentine junction (orthodentine). Stem-gnathostomes, however, exhibit a wide range of dentine tubule architectures (e.g. see Smith and Sansom 2000) that include conditions more comparable to those found in euconodonts. In particular, the ramifying condition met with in *Neocoleodus* is directly comparable to mesodentine in the dermoskeleton of osteostracans and some thelodonts, whilst the unramified dentine condition is most closely comparable to the so-called orthodentine of *Astraspis*, although it differs significantly in terms of scale.

The patchy record of tubular dentines among euconodonts, and the variation in tubule architecture between taxa, is very curious and suggests that the growth of euconodont dentines (basal tissue) operated close to developmental (or other) constraints.

Reconciling variation in basal tissue microstructure

As mentioned above, all of the microstructural fabrics exhibited by the basal tissues of euconodonts can be reconciled with known variation in dentine. The tubular-lamellar fabric is the typical condition met with in dentine, while the lamellar-calcospheritic fabric has been observed in the dermoskeleton of the earliest (putative) chondrichthyans ('lamellin': Karatajuté-Talimaa *et al.* 1990; Sansom *et al.* 2000). Lamellin ranges from conditions in which calcospheres are common to those in which they are rare, the entirely lamellar (atubular) condition met with in some euconodonts reaches the extreme, where calcospheres are not manifest. Although it is possible to find such comparisons, it may be significant that no single group parallels the range of microstructural diversity met with in the putative dentines of euconodonts. Thus, although we have dispelled the notion of

variation in fundamental tissue types comprising the basal body of euconodont elements through the preclusion of homology to calcified cartilage in some taxa, it is possible that the range of dentine microfabrics may, nevertheless, provide justification for the view that euconodonts experimented with tissue types early in their phylogeny (at least at a very low level), as did other groups of jawless vertebrates (Moss 1964; Halstead 1987; Sansom *et al.* 1994; Smith *et al.* 1996; Smith and Sansom 2000).

However, a number of observations argue against such an interpretation: the known variants of euconodont basal tissues are convergent on dentines met with in other skeletonizing early vertebrates (e.g. see Smith and Sansom 2000 for a survey); within euconodonts, such variation is manifest with only slight taxonomic variation, such as between and within species of *Proconodontus* (Pl. 2, figs 3–6); microstructural fabrics are lost and reappear time and again throughout euconodont phylogeny; such microstructural fabrics have also been lost and reappear time and again throughout vertebrate phylogeny. Thus, rather than reflecting developmental plasticity, and the character of an evolving developmental system, in which we would expect histological variation between clades but to be phylogenetically conserved within these clades, it is more likely that the variation in euconodont basal tissue reflects dynamic influences on the development of the tissue. For instance, calcospheritic dentine is commonly associated with poor mineralization (Halstead 1974; Shellis 1983), rapid growth or disease (Appleton 1994; these are not necessarily mutually exclusive) of otherwise tubular fabrics. Furthermore, it is generally thought that calcospheres may be the main mode of dentine intertubular matrix mineralization (Smith and Sansom 2000) and, thus, it would be expected to be the only mineralization process in the absence of dentine tubules and peritubular calcification. The small scale of the euconodont pulp cavity as well as the episodic growth pattern (Donoghue 1998; Donoghue and Purnell 1999) of euconodont elements are also potential contributing factors to the prevalence of atubular dentines.

Thus, although tubular dentines have been recorded only rarely among those taxa analysed histologically thus far (which remain few), it appears plesiomorphically among euconodonts and to have been a latent character throughout the phylogeny of the clade, providing a basis for the reappearance of tubular dentines in more derived taxa given the necessary developmental conditions.

Finally, it could be argued that the degree of histological variation met with in euconodonts has been overplayed, at least to an extent. Such variation should be considered within the context that euconodonts are an extremely numerically diverse clade (cf. Sweet 1988) and in comparison to histological diversity among other vertebrate clades it may be more appropriate to entertain

larger groups, such as Chondrichthyes, that are increasingly revealed to exhibit a range of histological diversity that vastly exceeds that met with in euconodonts (e.g. Sansom *et al.* 2000).

CONCLUDING REMARKS

The basal tissues of the earliest euconodonts exhibit a range of microstructural fabrics that encompasses that seen hitherto in more derived taxa. Although, in the absence of a defensible scheme of phylogenetic relationships it is not possible to provide a complete understanding of phylogenetic polarity in the histological evolution of euconodonts, it is possible, nevertheless, to conclude that the tubular-lamellar microstructural fabric is one of the plesiomorphic conditions. Thus, it appears unlikely that the most diagnostic fabric supporting homology between basal tissue and dentine is a convergent peculiarity exclusive to more derived taxa. The challenge remains to resolve the phylogenetic relationships of the putative ancestors of the euconodonts, the paraconodonts, thus providing a comparative framework for the interpretation of their histological condition.

Acknowledgements. We thank Guichun Wu, Wei Guo and Caifa Zhu for field and lab work, for collecting samples and recovering the conodont specimens from Liaoning, north-east China; Ivan Sansom and Paul Smith (both Birmingham University) very kindly provided access to specimens from the Gros Ventre Formation, Wyoming; Ronald Austin (Swansea) provided samples from Threadhill Creek, central Texas, USA. This research was funded by NERC Research Fellowship GT5/99/ES/2 (to PCJD) and funding from the NSFC (Grants 40372001 and 40072007 to X-PD), RFDP (Grant 2000000127 to X-PD), Laboratory of Paleobiology and Stratigraphy, Nanjing Institute of Geology and Palaeontology, Academia Sinica (Grant 021306 to X-PD), and The Royal Society for two study visits by Dong to Donoghue (2000, 2002).

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