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Tooth histology patterns in early tetrapods and the presence of 'dark dentine'

Anne Warren and Susan Turner

ABSTRACT: The presence of a petaloid pattern (previously known as 'dark dentine') in cross sections of teeth of the embolomere *Pholiderpeton attheyi* has been used as a synapomorphy of the embolomeres or of the embolomeres plus the stem tetrapod, *Crassigyrinus scoticus*. Among the taxa studied, dentine that appears dark results from closely packed dentine tubules and can be found in any part of a tooth section in which such crowding occurs. The petaloid pattern is restricted to tooth sections of a particular diameter, and is obliterated in larger sections of teeth that show complex folding. Petaloid dentine has been found in all tetrapod teeth with plicidentine that were sectioned in this study, whether from stem tetrapods, the Embolomeri, Temnospondyli, or Stereospondyli, and has been recognised in some sarcopterygian fish, an extant actinopterygian fish, ichthyosaurs, and *Varanus*. The presence of petaloid dentine is neither a synapomorphy of the tetrapod node nor of any node within tetrapods.

KEY WORDS: dark dentine, Embolomeri, petaloid dentine, Rhizodontida, stem tetrapods, Stereospondyli, Temnospondyli, tooth histology.

The pattern known as 'dark dentine' in sections of early tetrapod teeth with folded dentine (plicidentine) was first recognised in 1876 by Thomas Atthey when describing teeth of the Carboniferous embolomere, *Pholiderpeton attheyi* (Clack 1987; ='*Anthracosaurus russelli*' in error in Atthey 1876 p162, pl. 11; Fig. 1a). Atthey described the appearance of the *Pholiderpeton attheyi* tooth sections as stellate (=petaloid in the present paper) with a number of fusiform bodies of light coloured dentine radiating from the pulp cavity to the circumference and embedded in dentine of a dark colour. The first reference to 'dark dentine' was to the interstices between the fusiform bodies, but Panchen (1977, 1985) noted that the colour arrangement could be reversed. Tooth sections that show 'dark dentine' may resemble either a light coloured daisy on a dark background when seen in transmitted light (e.g. Fig. 1a) or a dark coloured daisy on a light background when seen in reflected light (e.g. Fig. 3a).

The petaloid pattern is known in the early tetrapod literature as 'dark dentine' (e.g. Panchen 1985). The presence of 'dark dentine' has been used as a synapomorphy of *Crassigyrinus scoticus* and embolomeres (Panchen 1985; Panchen & Smithson 1988), and of *Ichthyostega stensioei* and most other tetrapods (Coates 1996), although Smithson (1980) implied that the phenomenon might be size-related, having been described in only the larger anthracosauroids (most embolomeres) with the condition unknown in smaller forms. The purpose of this paper is to review the pattern of tooth folding in early tetrapods, and to determine the distribution of petaloid dentine among them. The Ducabrook locality from the Lower Carboniferous of Queensland, Australia (Thulborn *et al*. 1996), yields histologically intact specimens of both the stem tetrapod *Ossinodus pueri* (Warren & Turner 2004) and the rhizodontid *Strepsodus* sp. (Johanson *et al*. 2000) with which to test the hypothesis of the phylogenetic usefulness of tooth dentine characters, in particular the phenomenon of petaloid dentine among early tetrapods.

1. Methods and materials

1.1. Terminology

Schultze (1969, 1970) termed the folded teeth of some sarcopterygians and tetrapods 'polyplocodont', and of tetrapods (other than 'Ichthyostegalia' and 'Loxommatoidea') labyrinthodont. In this paper the more general term plicidentine (Owen 1841; Tomes 1878; Schultze 1969) is used for all folded dentine (see section 3.1). The pattern of fusiform bodies of dentine first described by Atthey (1976) is termed 'petaloid' and the separate fusiform bodies delineated by the natural curve of the dentine tubules are termed 'petals'. An area of a plicate tooth in which the dentine tubules are crowded through folding may appear darker than the surrounding area in which tubules are less densely packed. The term 'dark dentine' has been used for this area of crowded tubules, but this is not related to the patches of darkened dentine known as dead tracts in mammalian teeth (see section 3.1).

The tooth folds are described following the terminology of Warren & Davey (1992) whereby folds arising from the tooth margin may be unbent, may have simple primary bending, the primary bends may themselves be bent resulting in secondary bending, and branches may arise from the bends. The globular zone (=mantle dentine) is the area of dentine immediately beneath the enamel and extending into the tooth folds (see section 3.2). Terminology associated with the description of tooth sections is presented in Figure 1b, and most taxa in which petaloid dentine is recognised in the present paper are shown in Figure 1c.

1.2. Identification of isolated teeth

Whilst teeth of both tetrapods and rhizodontids from the Ducabrook Formation deposits are present on otherwise identifiable cranial or mandibular bones, in most cases individual isolated teeth have been sectioned in this study. The following features were used to allocate individual plicate teeth from the

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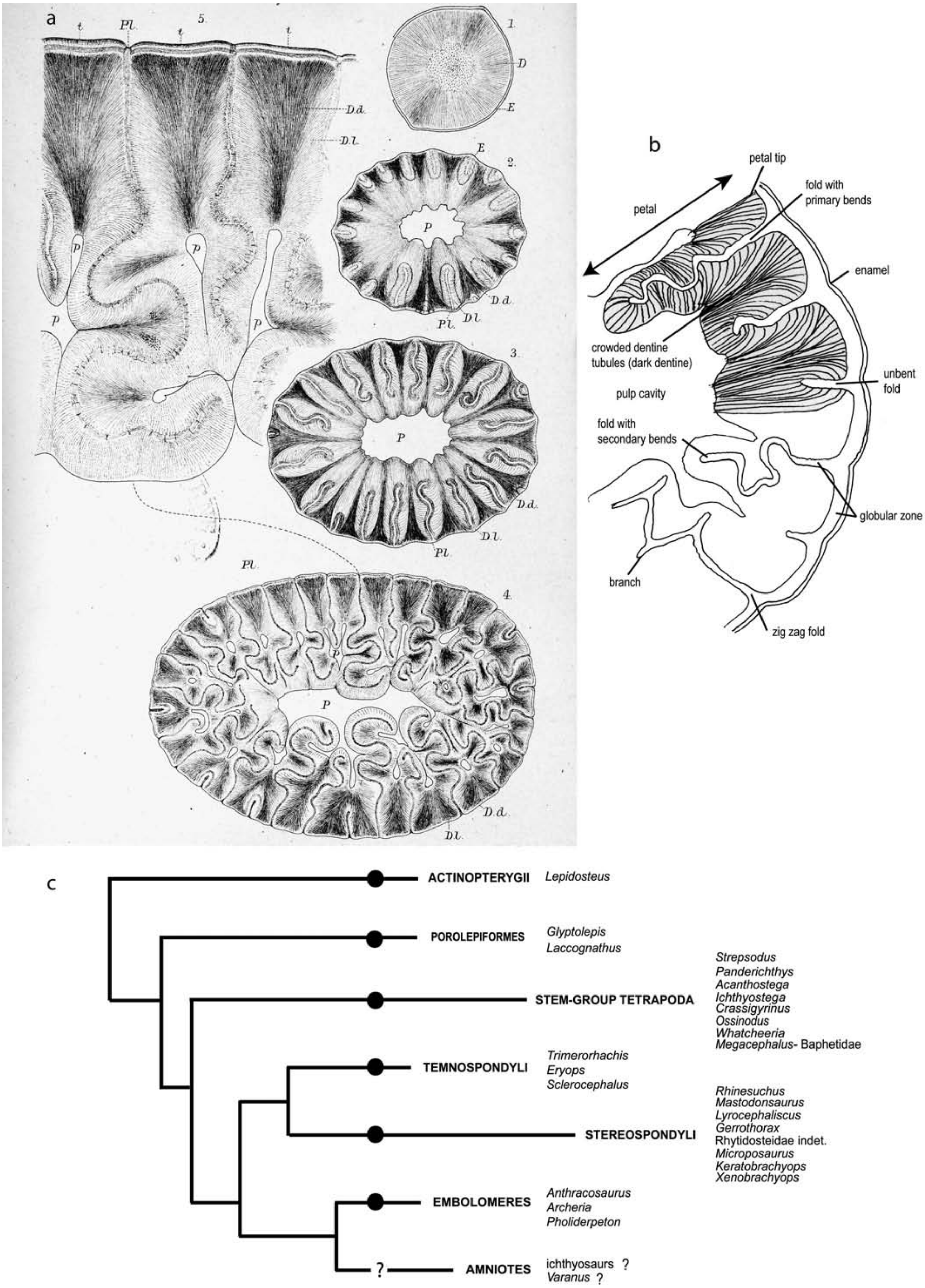

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Ducabrook Formation to Tetrapoda or Rhizodontida. Externally, rhizodontid teeth are usually slimmer and more recurved, folding is looser so that the tooth surface is rounded in outline between folds, and the bone of attachment enters between the folds. Internally, branching of dentine occurs, especially in basal sections, and patches of dark dentine are absent or restricted. Tetrapod teeth are more conical externally and the bone of attachment does not enter between the folds so that the folds are tighter; whilst internally, branching of dentine is rare, and petaloid dentine is always present in tooth sections with a diameter greater than approximately 2–3 mm. Both tetrapod and rhizodontid teeth have raised longitudinal striae on the outside of the enamel; however, in teeth of approximately equal size, the rhizodontid striae are smaller and more closely spaced.

1.3. Level of tooth sections

Because early tetrapod teeth are usually protothecodont (set in shallow sockets) and marginal teeth are pleurodont (attached to the jaw primarily by their labial surface), the part of the tooth contacting the bone of the jaw is greater on the labial than the lingual surface, so that a section that includes part of the bone of attachment (i.e. a basal section) could be taken from anywhere on the lower one third of a tooth. A truly basal section (one that is taken where the tooth begins on the lingual side of the jaw) is largely composed of bone. In the present paper, sections are referred to as 'basal' if they incorporate bone of attachment, 'mid' if such bone is absent and they are still folded, and 'tip' if folding is minimal or absent. Teeth or 'tusks' that are not part of the marginal series are acrodont so that basal sections are more complete.

1.4. Materials sectioned

Rhizodontida. *Strepsodus* sp. Early Carboniferous Ducabrook Formation, Queensland. QMF 37497, mid and near base; QMF 37502, tooth row near base, basal section of one tooth; QMF 37508, near tip.

Stem Tetrapoda *Ossinodus pueri*. Early Carboniferous Ducabrook Formation, Queensland. QMF 37498, mid tooth section; QMF 37499, tip, mid and basal sections; QMF 37500, tip, mid and basal sections; QMF 34600, ground mid section of maxillary tusk attached to partial maxilla; QMF 37506, basal section; QMF 37504, near basal section of shed tooth.

Embolomeri. *Archeria crassidisca*. QMF 37496, Permian Nocona (Admiral) Formation, Texas, marginal tooth row.

Temnospondyli. *Eryops megacephalus*. MCZ 1140 A, Permian Petrolia (Belle Plains) Formation, Baylor County, Texas. Ground surface of marginal dentary tooth attached to partial mandibular ramus, section of parasymphyseal tooth; QMF 37505, Admiral Formation, Archer County, Texas, basal section of tusk, vomerine teeth.

Trimerorhachis insignis. MCZ 8357, Permian Petrolia (Belle Plains) Formation, Baylor County, Texas, mid section of two teeth.

Stereospondyli. *Gerrothorax* sp. MCZ FN12/89G, Late Triassic Fleming Fjord Formation, Jameson Land, East Greenland, near basal section of three teeth.

Mastodonsaurus giganteus. QMF 37503, Late Triassic, Germany (no locality data), vomerine teeth near base, tusk at base.

Xenobrachyops allos. QMF 10119, Early Triassic, Arcadia Formation, Queensland, mandibular teeth, mid sections.

Keratobrachyops australis. QMF 14477, Early Triassic, Arcadia Formation, Queensland, marginal tooth row.

Rhytidosteidae indet. QMF 14476, Early Triassic, Arcadia Formation, Queensland, marginal tooth row.

Buettneria sp. QMF 37597, Late Triassic, Dockum Group, Howard County, Texas, marginal tooth mid section.

1.5. Tooth sections borrowed

Rhizodontida. *Rhizodus hibberti*. NMS G 1974.2.3., probably Lower Carboniferous, Burdiehouse Limestone, Scotland. Sectioned by A. R. I. Cruickshank.

Stem Tetrapoda. *Megalocephalus pachycephalus* ('*Loxomma allmani*'). NEWHM:2003.H2828, NEWHM:2003.H2829 (=4/47/44 T. Atthey 1876), Carboniferous (Westphalian B), Low Main Seam, Newsham, Northumberland, England. Sectioned by T. Atthey.

***Pholiderpeton attheyi* ('*Anthracosaurus russelli*').** NEWHM: 2003.H2830, NEWHM:2003.H2831, NEWHM:2003.H2832, NEWHM:2003.H2833, NEWHM:2003.H2834, NEWHM: 2003.H2835, Carboniferous (Westphalian B), Low Main Seam, Newsham, Northumberland, England. Sectioned by T. Atthey.

1.6. Techniques

All specimens sectioned at La Trobe University were embedded in epoxy resin before sectioning by standard geological techniques. The thickness of each section was decreased by grinding on a diamond wheel or a glass plate until the histological structure became clear. In some instances it was difficult to grind the section thin enough to transmit light without losing the dentine tubules. Teeth still *in situ* were photographed under water using reflected light. Whole tooth sections were photographed with a Mamiya RB67 camera with a Leitz 25 mm photar macro lens and transmitted light. Detail was photographed using a Nikon Coolpix 950 digital camera and a Leitz Laborlux 12 petrographic microscope.

2. Descriptions of tooth histology

2.1. Rhizodontida

***Strepsodus* sp.** Teeth of *Strepsodus* sp. from the Ducabrook Formation, Queensland (Johanson *et al.* 2000), varied from 5 mm to 1·5 mm in diameter. A near tip section (QMF 37508, 2 mm, Fig. 2a) had a large pulp cavity, a narrow peripheral band of unfolded dentine of uneven width, and an

Figure 1 (a) *Pholiderpeton attheyi* (=*Anthracosaurus russelli* of Atthey 1876, syn. *Eogyrinus attheyi*), Carboniferous, Low Main Seam, Newsham, Northumberland, England. Successive sections of a single maxillary tooth. (1) near the apex; (2) mid section showing folds without bends (=NEWHM:2003.H2833 Fig. 8(b)); (3) mid section showing folds with primary bends; (4) basal section showing folds with primary and a few secondary bends; (5) a portion of (4). Petaloid dentine is clearly seen in (2) and (3), whereas in (4) only the tips of the petals are visible. In (4) and (5) dark dentine can be seen in places where the dentine tubules are crowded together by bends of the folds, and some islands of separated pulp cavity are present. Reproduced from Atthey (1876), with permission. Atthey's abbreviations for this figure were: (D) dentine; (D.d) dark dentine; (D.l) light dentine; (E) thin enamel; (P) pulp cavity; (Pl) foldings of peripheral bands into apices of fusiform light dentine (=globularzone); (t) toothlets. (b) diagram of composite mid tooth section to illustrate terminology used in the present paper. (c) cladogram to illustrate the position of taxa described or discussed in the present paper. Black circles indicate clades in which petaloid dentine has been found.

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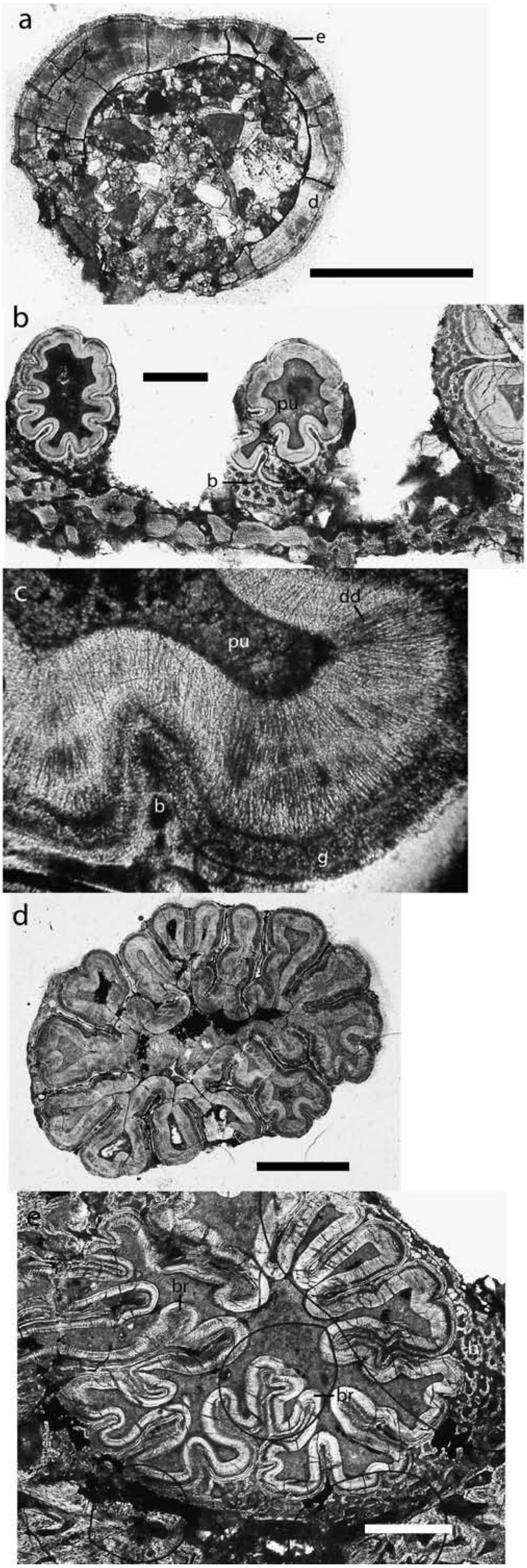

outer enamel rim. The dentine in most, like QMF 37502 (largest tooth 3·5 mm, 11 folds; Fig. 2b) and QMF 37497 (4 mm, 20 folds; Fig. 2c–d), was loosely folded without bending or branching, although the dentine seen in larger sections, QMF 37502 (4·5 mm, approximately 22 folds; Fig. 2e), taken from below the jaw line, and QMF 37497 (5 mm), showed some minor bending and branches that were pronounced and occasionally longer than the folds. In all teeth the dentine layer was of a similar thickness throughout the tooth, whether on the margin of a tooth or part of a fold, and in almost all cases the folds of dentine were of a similar length to the complementary incursions of the pulp cavity between the folds. Additionally the teeth were loosely folded with wide globular zones. Patches of closely packed dentine tubules forming dark dentine were rare (see section 3.2). They were visible in QMF 37497 (Fig. 2c) although the dark dentine patches were not as pronounced as shown by Schultze in *S. sauroides* (1969, pl. 12, fig. 3). As the tooth diameter increased, the number of folds increased as in all plicate teeth (see section 2.3).

All other Rhizodontida in which tooth sections have been described, namely *Archichthys sulcidens* (Barkas 1876/7, fig. 92), *Rhizodus hibberti* (Barkas 1875/76, fig. 78; Schultze 1969, pl 11, Cruickshank 1968, fig. 9a), and *Strepsodus sauroides* (Schultze 1969; pl 12, figs 3–5) had teeth that were similar in section. All were folded loosely, resulting in relatively fewer folds than in teeth of similar cross section in, for example, *Ossinodus pueri* (see section 2.3). Larger teeth were increasingly complex at the base. Dark (=petaloid) dentine was reported in *Strepsodus sauroides* (Vorobyeva & Schultze 1991) and was figured by Schultze (1969 pl. 12, fig. 3). Schultze also figured crowded dentine tubules that approached the petaloid pattern in *Rhizodus* sp. (=*Megalichthys intermedius* pl. 10, fig. 3). It was not visible in the *Rhizodus hibberti* teeth described by Cruickshank (1968).

2.2. Other sarcopterygians

The pattern of folding in various sarcopterygians was detailed by Schultze (1969), with small areas of petaloid dentine evident in several taxa (see section 3.1). In the porolepiform *Laccognathus*, a petaloid dentine pattern was apparent in a mid tooth section (Schultze 1969, pl. 23, fig. 1), while a more basal section (Schultze 1969, pl. 2, fig. 2) showed a complex arrangement of dark dentine patches similar to that seen in large teeth of the stereospondyl *Mastodonsaurus* sp. (see section 2.5).

2.3. Stem tetrapods

Ossinodus. The presence of a petaloid pattern was noticeable on all cleanly broken teeth of *Ossinodus pueri*, where the petals appeared dark with light interstices (QMF 34600, Fig. 3a) in reflected light, but light with dark interstices in transmitted light. The petals formed a circular arrangement radiating from the pulp cavity to the circumference. The number of folds of primary dentine were counted across a range of tooth sizes; these counts were necessarily estimates as some folds that were in their initial stages were not counted. Tooth sections of small diameter had fewer folds, whether from towards the tip of a larger tooth (QMF 37504, 3 mm, 15 folds) or nearer the base of a smaller tooth (QMF 37430, 3 mm, 20 folds). The three 8 mm sections measured had folds varying in number from 25 (QMF 37504) through 35 (QMF 34281) to 41 (QMF 34600,

Figure 2 *Strepsodus* sp. Early Carboniferous, Ducabrook Formation, Queensland: (a) QMF 37508 tooth near tip; (b) QMF 37502 tooth row near base; (c)–(d) QMF 37497 tooth at base (c) enlarged; (e) QMF 37502 tooth base. Note bone of attachment extending between the folds and loose folding of the dentine. Scale bars = 1 mm.

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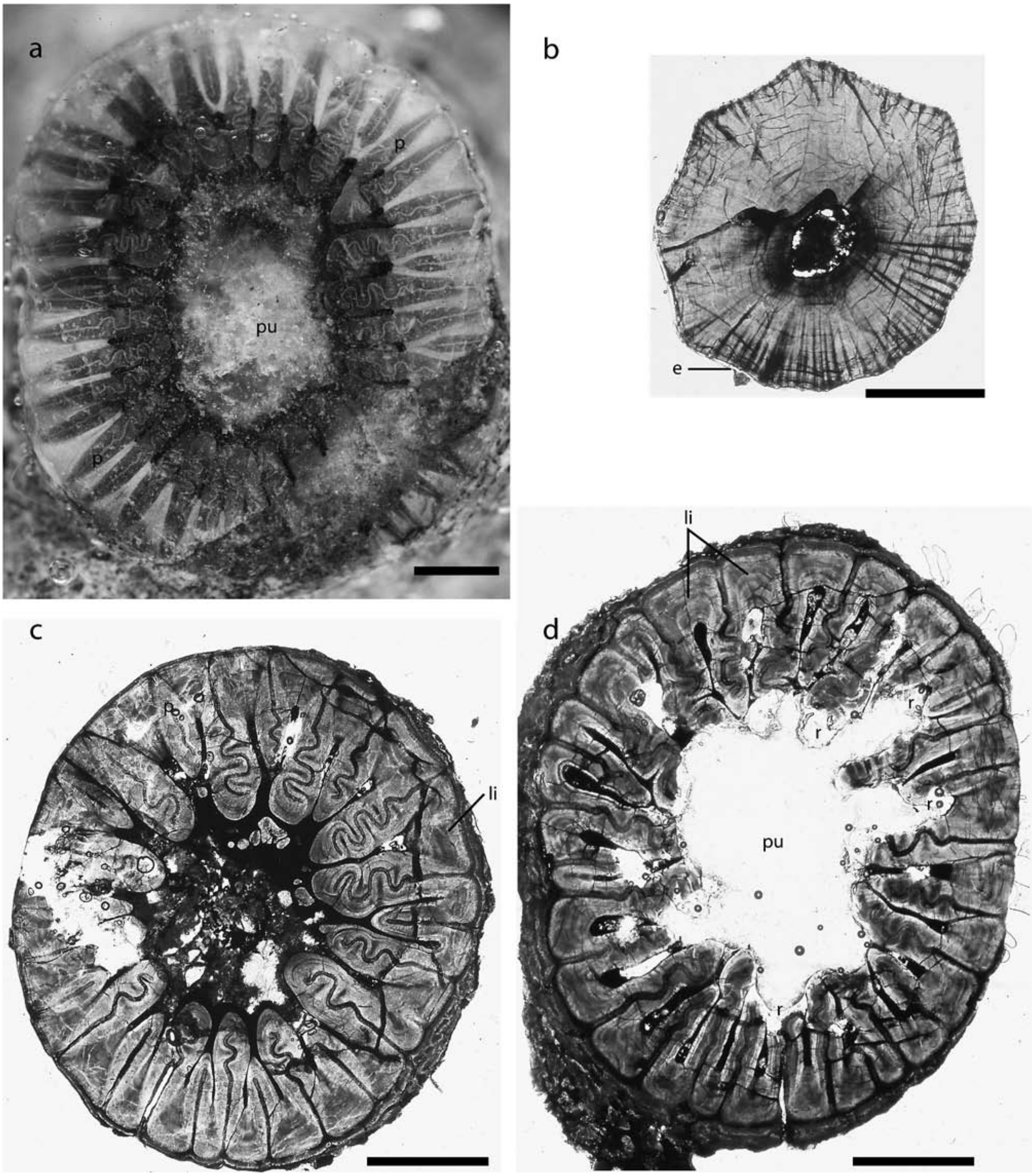

Figure 3 *Ossinodus pueri* Early Carboniferous, Ducabrook Formation, Queensland: (a) QMF 34600 maxillary tusk in reflected light to show dark petaloid pattern; (b)–(d) QMF 37500 tooth sectioned at tip, mid and base, all in transmitted light by which the petaloid pattern in (c) appears light. Note stellate outer margin of the tooth tip and external enamel layer in (b); in (c) inner margins of the petals are defined by the pulp cavity extending between them; in (d) some resorption of dentine has taken place. Scale bars = 1 mm.

Fig. 3a). The most complex tooth (QMF 37506, Fig. 4d) was fragmented but was estimated to have a diameter of 9 mm with 46 folds. It was clear that, in *Ossinodus*, the number of folds increased with the size of the tooth section, either within a single tooth or between teeth of different sizes. The dentine began to fold at about 3 mm diameter, with a few scattered folds. These increased to about 20 folds soon after folding began, with this number increasing slowly to about 30 folds at 8 mm diameter, followed by a rapid increase where the tooth flared out near the base with, for example, a 9 mm tooth having 46 folds.

Two teeth, QMF 37500 (Fig. 3b–d) and QMF 37499 (Fig. 4a–c), were sectioned at three levels. Towards the tip, QMF 37500 (3 mm) was stellate in outline, with no folds present. A narrow rim of enamel was visible in places on this section but not on those from lower in the tooth. At 5 mm diameter 23 folds with primary bending were present (Fig. 3c), and a petaloid pattern of dentine was evident, although not marked. In this section, the pulp cavity extended between the petals towards the periphery, so that each petal was delineated at the pulp side as well as at the periphery, forming an obovate element. This clear demarcation of the inner part of the petal

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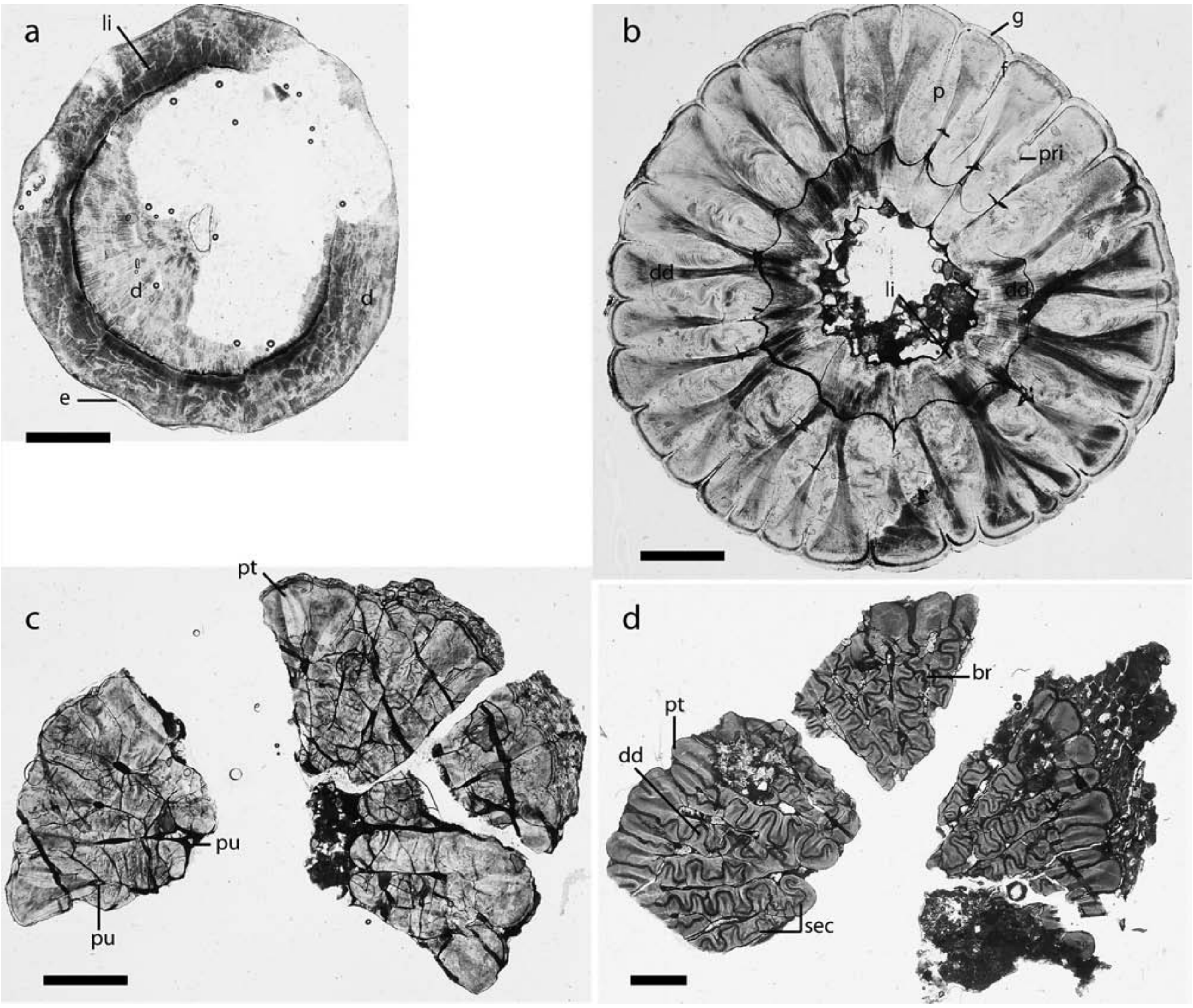

Figure 4 *Ossinodus pueri*: (a)–(c) QMF 37499 tooth sectioned at tip mid and base; (d) QMF 37506 tooth sectioned at base. In (b) note growth line not yet obliterated by the incursions of the pulp cavity between the petals; in (c) portions of pulp cavity occasionally enclosed by dentine; in (d) secondary bends, a single branch, and petaloid pattern restricted to the periphery of the tooth. Scale bars = 1 mm.

was not always present, occurring only in mid sections of teeth. The lowest section of QMF 37500 (6 mm) (Fig. 3d) incorporated some of the bone of attachment. This section had 29 folds, some of which showed signs of resorption from the pulp cavity. More extensive evidence of resorption was present in QMF 37504 (7·5 mm, Fig. 5a). Evidence of resorption is likely to be present in most teeth found isolated from bone, the implication being that they were teeth shed by the animal. Similar resorption of older teeth has been reported in the temnospondyl *Benthosuchus* (Bystrow 1938, fig. 14–15).

The most apical section of QMF 37499 (5 mm, Fig. 4a) had a stellate margin on one side with enamel clearly visible on the external tooth surface and unfolded dentine. At 6 mm diameter this tooth had 32 folds (Fig. 4b), a clear petaloid pattern, and the pulp cavity slightly indented beside each petal. At approximately 10 mm diameter the tooth was too fragmented to count the folds; nevertheless the pattern was of interest as in some areas the bending had isolated parts of the pulp cavity in this plane (Fig. 4c), and individual petals were obovate as in the lower section of QMF 37500.

The tooth section exhibiting the most convoluted dentine (QMF 37506, 9 mm) showed some secondary bending and a single branch (Fig. 4d). In such complex tooth sections, only the outer ends of the petals were evident, with the inner segments tending to be obscured by folding. Furthermore, although the arrangement of dentine tubules that caused the pronounced petals at the tooth periphery was present internally on primary and secondary bends, a petaloid structure was obscured because it occurred on both sides of the folds (Fig. 4d).

In a 6 mm section (QMF 37498, Fig. 5b) folding had just begun. Each fold was marked by a petal tip of varying size. It was clear that the petals were the result of the tubules of dentine being less densely packed beside the globular zone of the folds, while the areas of darkened dentine were enhanced by crowding of tubules as the folds made incursions towards the pulp cavity. Higher magnification of the 5 mm section of QMF 37499 (Figs 4b, 6) showed that sometimes the dentine tubules originating from the folds were cut off by tubules arising from the periphery of the tooth, as in *Megalocephalus* (Embleton & Atthey 1874) and *Crassigyrinus* (Panchen 1985, fig.15).

Most sections of *Ossinodus pueri* teeth examined that were taken from near the tips of teeth had at least one circular dentine growth line (incremental line). In lower sections, where folding had commenced, one or more circular growth lines were present towards the pulp cavity (e.g. QMF 37499, 6 mm, Fig. 4b). Because larger sections of teeth included growth from

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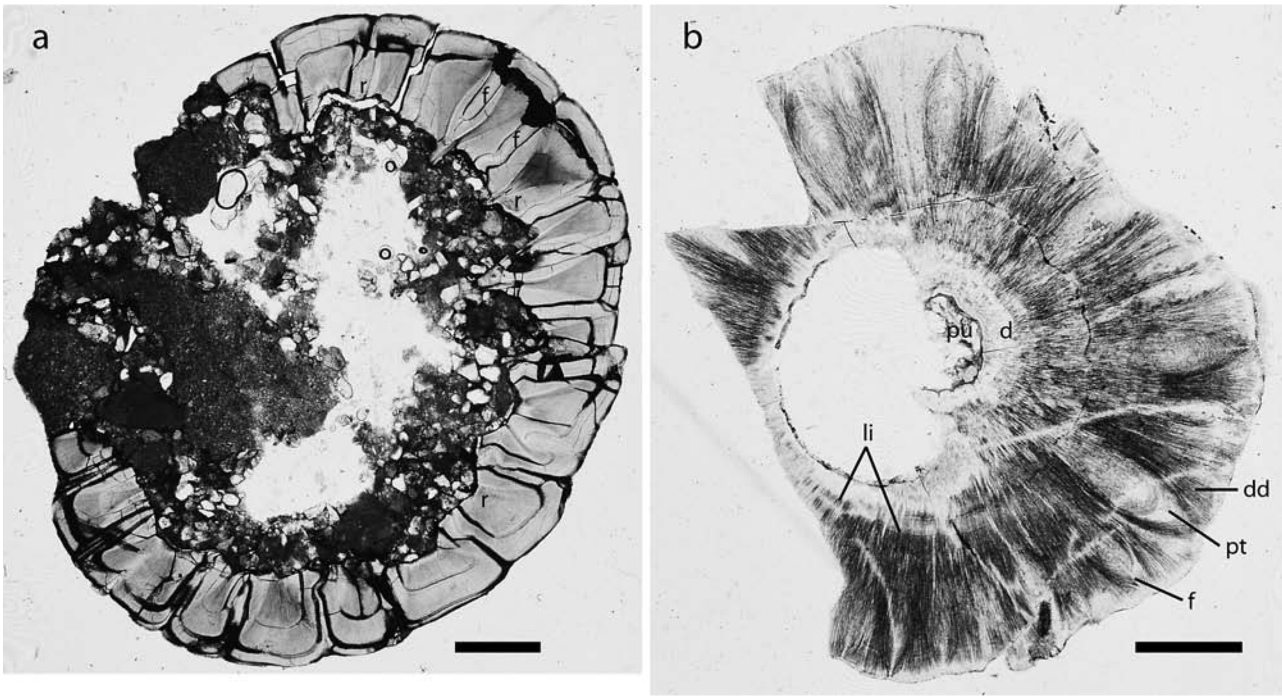

Figure 5 *Ossinodus pueri*: (a) QMF 37504 near base of a tooth being resorbed from the pulp cavity; (b) QMF 37498 near tip of tooth showing the beginning of folds accompanied by petaloid pattern and inner growth lines. Scale bars = 1 mm.

the pulp cavity between the folds, these inner circular lines were not present (Fig. 3c). In these teeth growth lines sometimes could be seen running parallel to the periphery between the folds, and turning towards the centre of the tooth beside the folds, so that they were U-shaped (QMF 37500; Fig. 3c,d). In the largest tooth (QMF 37506) there were up to 9 lines.

Baphetidae: *Megalocephalus.* Several of the *Megalocephalus pachycephalus* (= *Loxomma allmanni*) teeth sectioned by Atthey were restudied and two were photographed (NEWHM:2003.H2828, 5 mm, 38 folds; NEWHM:2003. H2829) (Fig. 7), but these were basal sections only. Dentine that formed a petaloid pattern at the periphery of the tooth was clearly visible in these sections, although the petal tips were split by slight incursions from the bone (Fig. 7c). Dark dentine was also present internally associated with primary bends and branches arising from them (Fig. 7c). These teeth were distinctive in that each primary bend was extended by a branch so that individual folds assumed a zigzag appearance. Secondary bends were absent. In both sections, isolated areas of the pulp cavity were present. Characteristic of *Megalocephalus* teeth is the large number of growth lines near the periphery. These were drawn by Dinning (Embleton & Atthey 1874, pl. 7, fig. 6), but they were less pronounced in photographs of *Megalocephalus* teeth (Fig. 7c) than in the drawings. Schultze (1969, pl. 2, fig. 3; pl. 14, fig. 1) illustrated a vomerine tusk of *Megalocephalus*. This tooth was similar to those described above in that the folds had many primary bends, all with branches, and petaloid dentine was present, especially associated with folds near the periphery.

Overall the tooth sections of *Megalocephalus* resembled those of *Eryops* (see section 2.5) of a similar size, with similarity especially evident in lower sections where the high degree of branching present on the simple bends of the dentine folds forms a zigzag. A tooth section of *Megalocephalus* taken from between the level at which folds began (Embleton & Atthey 1874, pl. 7, fig. 4) and the level where branching was well established (Embleton & Atthey 1874, pl. 7, fig. 5; Fig. 7) should appear typically petaloid.

Crassigyrinus. A posterior palatine tusk of *Crassigyrinus scoticus* sectioned by Panchen (1985) had a similar structure to tusks of *Pholiderpeton* (see 2.4), although the folds were less tortuous. Panchen figured enlarged tooth portions only (Panchen 1985, figs 14, 15), and these showed a strongly petaloid structure in which long dark dentine tubules arising from the tooth periphery cut off tubules arising from the folds. Bending of the folds was slight in the portion of the tooth illustrated.

Whatcheeria. Petaloid dentine was present in *Whatcheeria deltae* (Lombard & Bolt 1995). Specimen PR 1747 showed a petaloid pattern on a single, broken right maxillary tooth of 4 mm diameter. No teeth were sectioned.

2.4. Embolomeri

Pholiderpeton. Several sections of *Pholiderpeton attheyi* teeth, sectioned by Thomas Atthey as *Anthracosaurus*, were examined. They ranged from near tip to basal sections. All except near tip sections were petaloid, but none are as markedly so as those drawn by Dinning (Atthey 1876, pl. 11; Fig. 1). This is because the contrast between the light petals and the dark interstices is slight in most instances. The least folded section, presumably near to a tooth tip (NEWHM:2003.H2832, 6 mm, Figs 8a, 9) had three folds grouped together and marked by petal tips, and three clear growth rings. Elsewhere on this tooth, dark dentine tubules radiated straight from the margin of the tooth to the pulp cavity. One section (NEWHM: 2003.H2833, 3 mm, Atthey 1876 pl.11, fig. 2; Fig. 8b) had 17 short folds without bends, and showed extremely dark interstices between light petals. Dark areas of dentine in this particular section may be an artifact of preservation or sectioning. Section NEWHM:2003.H2834 (6 mm, Fig. 8c) had an estimated 21 simple unbent folds and a pulp cavity that had not yet extended towards the periphery, so that several growth lines were recognised. Section NEWHM:2003.H2831 (5 mm, Fig. 8d) had an estimated 22 folds with primary bends and a pulp cavity that has begun to penetrate between the folds

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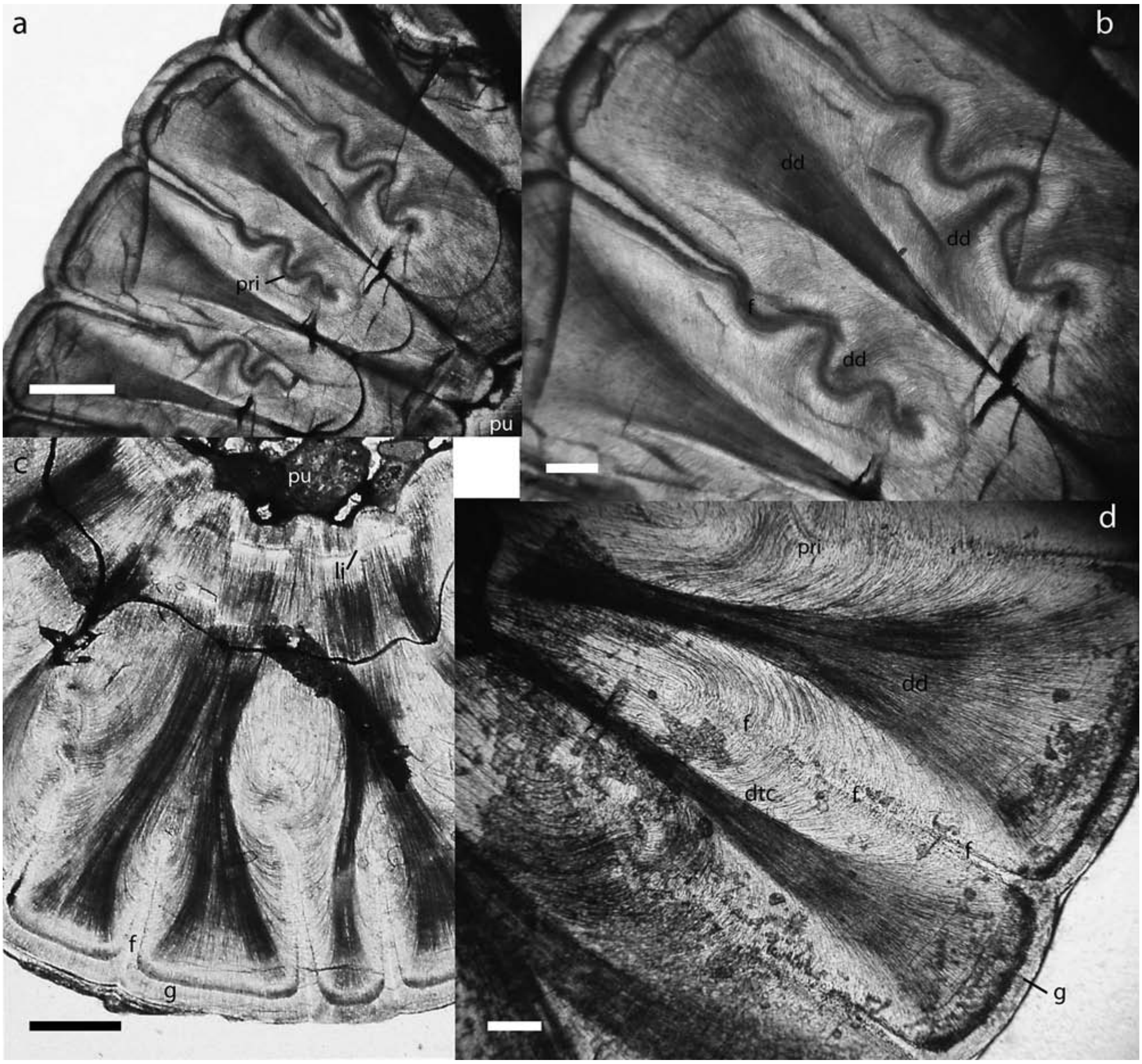

Figure 6 *Ossinodus pueri*: (a)–(d) enlarged parts of QMF 37499 showing detail of petaloid dentine and primary bends. Note that in some instances the dentine tubules from the folds are cut by those from the periphery, and in some this does not occur. (a), (b), (d) photographed using a microscope; (c) photographed macroscopically. Scale bars = 0·5 mm.

resulting in an overall pattern that was more markedly petaloid. NEWHM:2003.H2830 (6 mm, Fig. 8e) had approximately 24 folds with strong primary bending and several branches, and a pulp cavity penetration that approached the periphery of the tooth. The largest section examined, NEWHM:2003.H2835 (Fig. 8f), a basal section including a large proportion of bone, was more complex. A petaloid pattern was confined to the periphery of the tooth, there was secondary bending of the folds such that parts of the pulp cavity were isolated, and some branches were present. In this section patches of dark dentine were present associated with secondary bends.

The mid sections of *Pholiderpeton attheyi* teeth were comparable in pattern to most other petaloid teeth of a similar diameter, such as those of *Ossinodus pueri* (see section 2.3), mid sections of *Eryops* sp. (see section 2.5), and small *Mastodonsaurus* sp. teeth (Fig. 12e), whilst the larger sections of *P. attheyi* (Fig. 8f; Schultze 1969 pl. 14, fig. 2) were hard to distinguish from mid sections of *Mastodonsaurus* sp. (Fig. 12f), given that teeth of a similar diameter were compared.

Anthracosaurus. A palate of *Anthracosaurus russelli* (BGS 28317) had several broken teeth showing a petaloid pattern of dark petals in a pale background. Left maxillary teeth of this specimen were folded as follows: 9 mm diameter, 45 folds; 4 mm, 35 folds; 9 mm, 44 folds.

Archeria. Three small marginal teeth of *Archeria crassidisca* (QMF 37496) were sectioned initially in order to test whether embolomeres from North America had similar dental patterns to those from Scotland and Northumberland. In basal section (3–4 mm, Fig. 10a) the teeth were more complex than some teeth of other taxa of a similar diameter, with approximately 30 folds. Most of the folds had simple primary bends but some showed secondary bends and occasional branches, and some sections of the pulp cavity had been isolated. While the dentine tubules were arranged such that a petaloid appearance should have been present, this was rarely seen, although patches of dark dentine tubules were sometimes present both at the periphery and on the internal folds. One of the few distinctly petaloid areas is shown in Figure 10b. The poor preservation of these teeth might account for the rarity of a petaloid profile.

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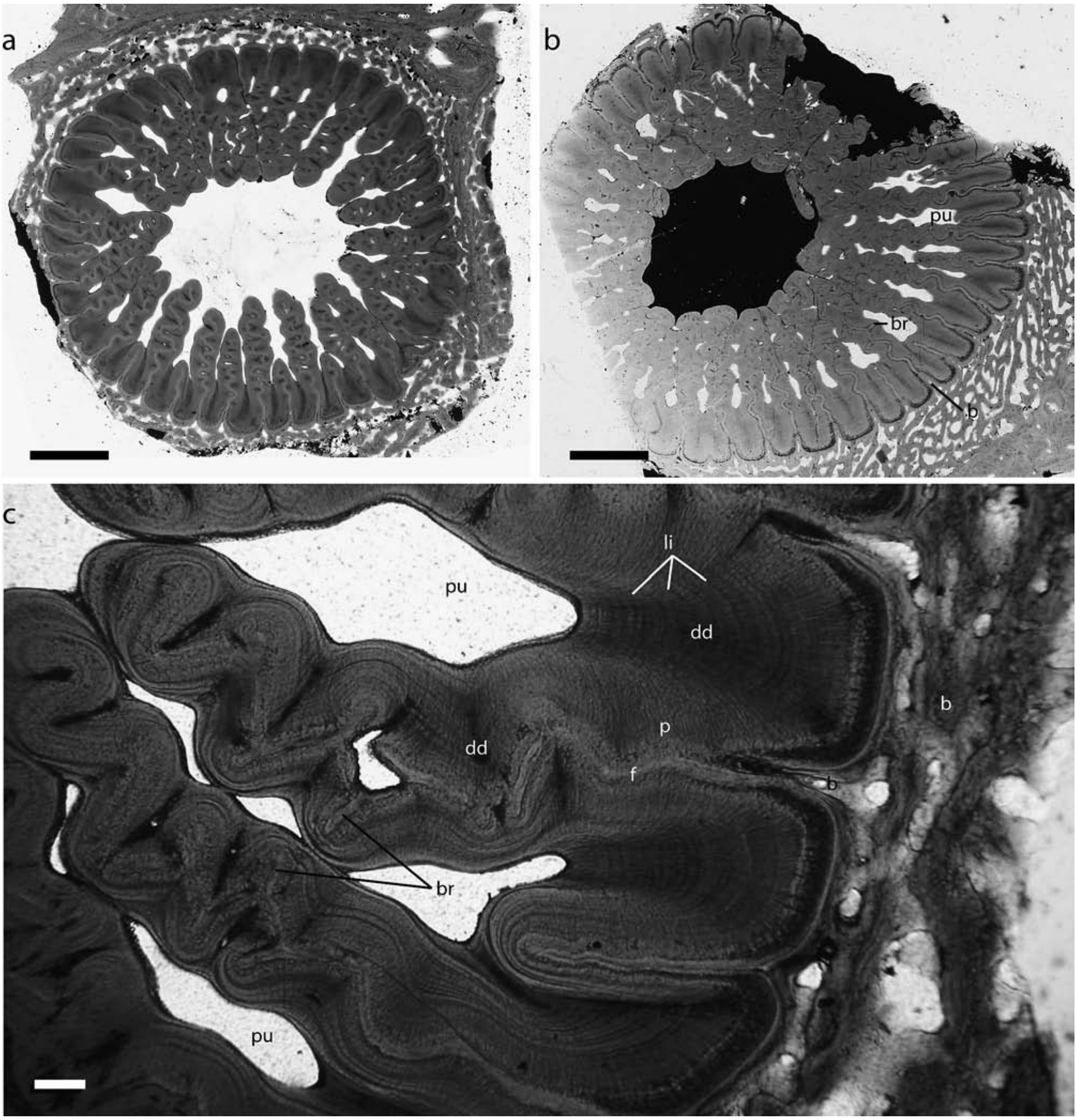

Figure 7 *Megalocephalus pachycephalus* Carboniferous, Low Main Seam, Newsham, Northumberland, England, basal tooth sections: (a) NEWHM:2003.H2828; (b) NEWHM:2003.H2829; (c) enlarged area of (b) to show dark dentine interstices, branched primary bending, and growth lines. Note the primary bends always bear branches and the petaloid dentine is restricted to the periphery. Scale bars = 1 mm (a, b); 0·1 mm (c).

2.5. Temnospondyli

Eryopidae. ***Eryops.*** Sections through the teeth of *Eryops megacephalus* showed a variable expression of the pattern of dark dentine. In MCZ 1140, the anterior end of a left mandibular ramus, ground surfaces of two teeth had a marked petaloid pattern (Fig. 11a) so that they were not distinguishable macroscopically from teeth of *Ossinodus* (Fig. 3a), or *Anthracosaurus russelli* (see section 2.4). In reflected light (Fig. 11a) the petals were dark, with pale interstices, while in transmitted light (Fig. 11b,c) the parasymphyseal tooth sectioned (6·5 mm, 30 folds) had petals that were light with dark interstices. Few branches were present in this section, but the tight primary bends of the folds, marked by densely packed dark dentine tubules, were the precursors to branches. A tusk of *Eryops* (QMF 37505, 8 mm) showed a regular zigzag pattern of branches from each primary bend (Fig. 11d) so that it resembled *Megalocephalus* (see section 2.3, Fig. 7). In this larger *Eryops* tooth petaloid dentine was less obvious but petal tips were present peripherally.

Trimerorhachidae. ***Trimerorhachis.*** Mid sections of teeth of *Trimerorhachis insignis* (MCZ 8357, 6 mm, 4 mm, 2 mm) all showed petaloid dentine (Fig. 12a). The tightly folded primary bends of the folds with narrow bands of dark dentine were similar to those of eryopoids and baphetids, suggesting incipient branching, although no branches were present, perhaps because these teeth were too small.

Plagiosauridae. ***Gerrothorax.*** Marginal teeth of *Gerrothorax* sp. sectioned (MCZ FN 12/89G, 4 mm, 31 folds, Fig. 12b) were similar to those figured by Warren & Davey (1992, fig. 13, = *Plagiosuchus*) in that the pulp cavity was large, the folds short, and there was no primary bending of the folds. A petaloid pattern was clearly visible in reflected light, where

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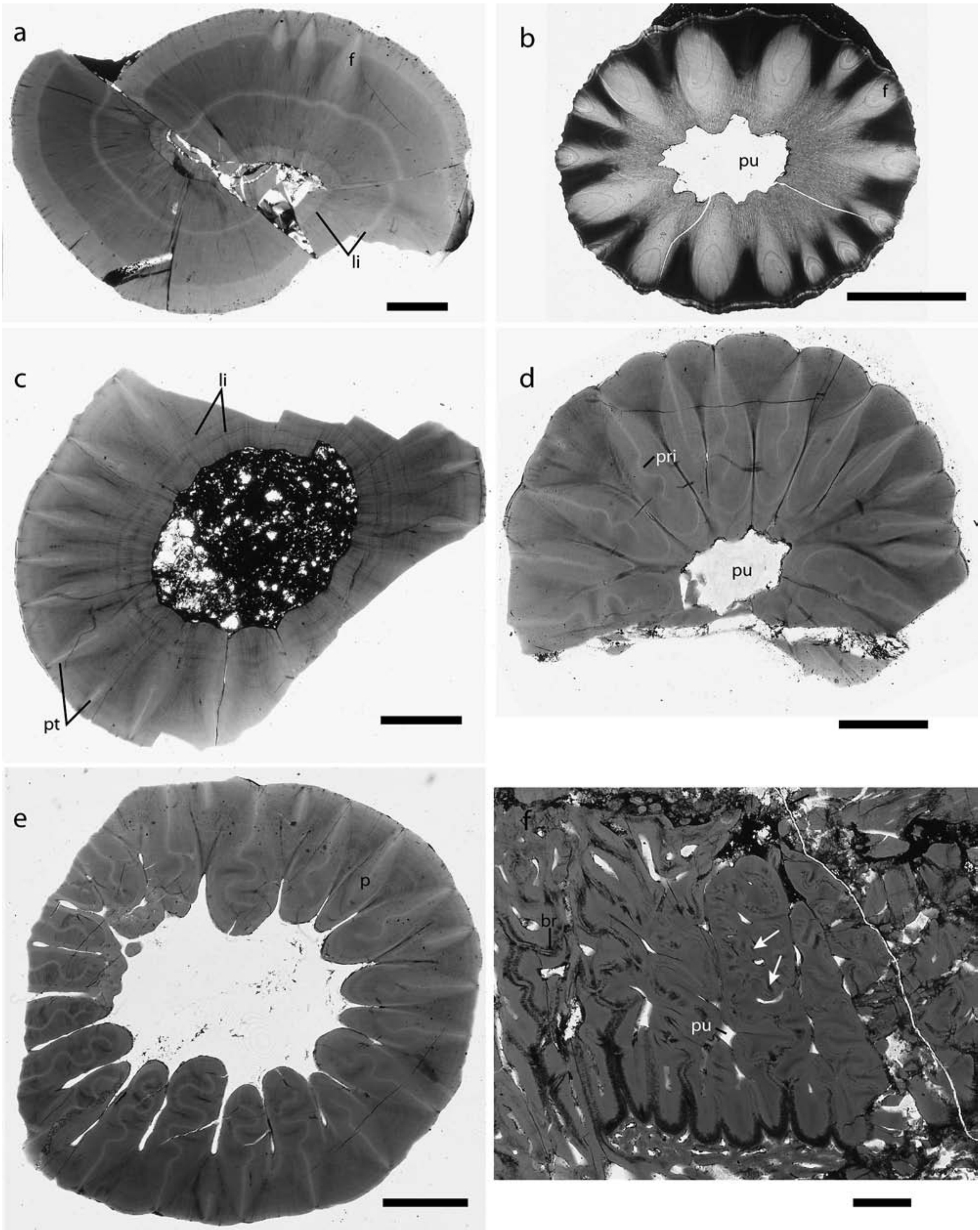

Figure 8 *Pholiderpeton attheyi* Carboniferous, Low Main Seam, Newsham, Northumberland, England: (a) NEWHM:2003.H2832 showing the early stages of three folds and a number of growth rings; (b) NEWHM:2003.H2833 showing early stages of folding; (c) NEWHM:2003.H2834; (d) NEWHM:2003.H2831 showing petaloid pattern in which the pulp cavity has just begun to penetrate between the petals; (e) NEWHM:2003.H2830 showing further penetration of the pulp cavity and a marked petaloid pattern; (f) NEWHM:2003.H2835 basal section of complex tooth showing patches of dark dentine internally (arrowed), a single branch, and isolated parts of the pulp cavity. Scale bars = 1 mm.

the petals appear darkly translucent and the interstices light, but the petals were less striking in thin section (Fig. 12b). A greater magnification (Fig. 12c,d) clearly showed the dentine tubules outlining petals, although in Fig 12a a thick globular zone in the fold made the petals less marked. Sections of *Gerrothorax* sp. made by Warren & Davey (1992, fig. 13) could have been ground too thin as the characteristic petals rarely showed and few dentine tubules remained.

Figure 9 *Pholiderpeton attheyi* Carboniferous, Low Main Seam, Newsham, Northumberland, England, enlarged areas of teeth: (a) NEWHM:2003.H2830 (Fig. 8e) showing a petal with primary bends separated by centrifugal extensions of the pulp cavity; (b) NEWHM:2003.H2831 (Fig. 8d) showing detail of dentine tubules and simple unbent folds; (c) NEWHM:2003.H2832 (Fig. 8a) to show the orientation of the dentine tubules around an unbent fold, and the dark tubules of dentine passing from the periphery towards the pulp cavity through pale growth zones. Scale bars=0·1 mm.

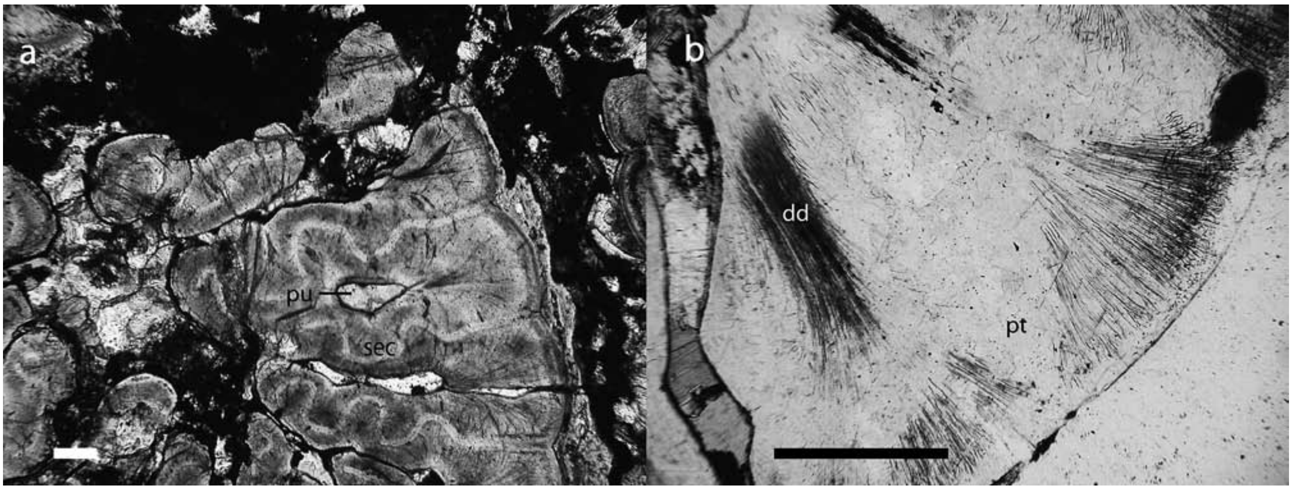

Figure 10 *Archeria crassidisca* Permian, Admiral Formation, Texas, QMF 37496: (a)–(b) enlarged areas of tooth. Note that the petaloid pattern is present but not marked and patches of dark dentine are present associated with primary bends. Scale bars=0·1 mm.

Mastodonsauridae. ***Mastodonsaurus.*** Petaloid dentine was clearly seen in small vomerine teeth of *Mastodonsaurus giganteus* QMF 37503 (2 mm, 23 folds, Fig. 12e). One tooth (not figured) had dark dentine tubules radiating towards a tiny pulp cavity, and a single fold. A second was simply folded and a third more complex. In all of these teeth petaloid dentine was associated with folds. A larger, marginal tooth (9 mm, approximately 41 folds, Fig. 12f) showed an early stage of the extremely complex folding characteristic of *Mastodonsaurus* teeth, whilst a tusk (24 mm) was so convoluted that it was

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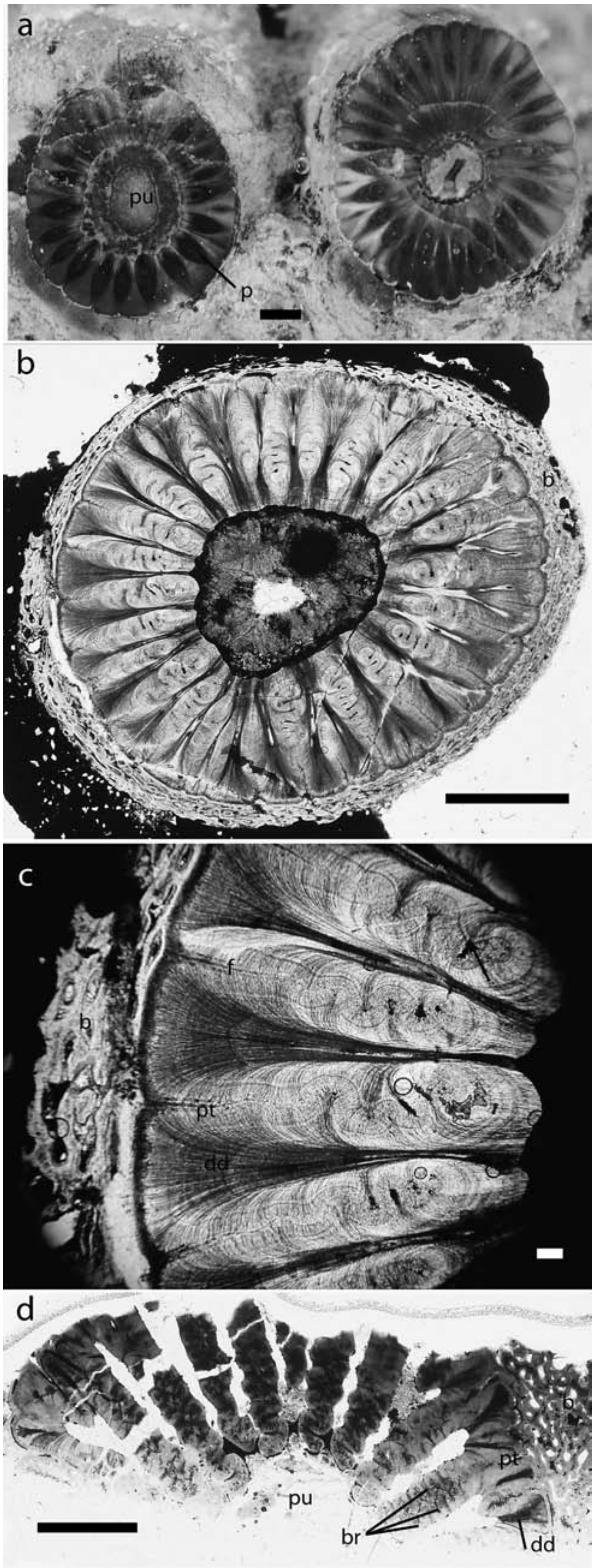


Figure 11 (a)–(c) *Eryops megacephalus* Permian, Belle Plains Formation, Texas, MCZ 1140: (a) polished sections of two marginal dentary teeth showing a dark petaloid pattern in reflected light; (b) basal section of paraphyseal tooth from the same specimen to show light petaloid pattern in transmitted light. Note the tight primary bends that have not yet branched; (c) enlarged portion of (b) to show detail of bends, and the first branch beginning to appear on a primary bend (arrowed). (d) *Eryops* sp., Admiral Formation, Archer County, Texas, QMF 37505: basal section of a large tooth to show tight primary bends each with a branch arising from it, forming a zigzag pattern. Scale bars = 1 mm (a, b, d); 0·1 mm (c).

difficult to find the origin of most folds (Fig. 12g). Secondary bending was present in all *Mastodonsaurus* teeth greater than 2 mm in diameter, with bends frequently isolating small parts of the pulp cavity. Despite this degree of complexity only a single branch was found in the largest *Mastodonsaurus* tooth section. Whilst all *Mastodonsaurus* teeth showed a petaloid pattern, in the larger teeth this was confined to a narrow peripheral zone of petal tips. Dark dentine was conspicuous, associated with internal primary and secondary bends in the section of a maxillary tooth (Fig. 12f).

Brachyopidae. ***Xenobrachyops.*** Sections of *Xenobrachyops allos* teeth were too thin to show a marked petaloid profile but the distal parts of petals outlined by dark dentine tubules were present in a marginal tooth (QMF 11018, 3·5 mm, est. 40 folds, Fig. 12h). Another tooth, (4 mm, circa 37 folds, Fig. 12i), showed two keels on the tooth outline and was also notable for the many incremental lines present.

Chigutisauridae. ***Keratobrachyops.*** Although most sections of *Keratobrachyops australis* were too thin to show dentine tubules, a small portion of a basal section of one tooth (QMF 14477, 3 mm) showed a petaloid pattern of dentine (Fig. 13a).

Metoposauridae. ***Buettneria.*** Sections of teeth of *Buettneria* sp. (e.g. QMF 37597, Fig. 13b) were folded loosely so that, near the periphery of the tooth, each fold was separated from the next by a small enclosed part of the pulp cavity. This meant that the dentine tubules contacted the pulp cavity after only a short distance so that petaloid dentine did not form. Folds were complex with secondary bending and occasional branches. No petaloid dentine was found near the periphery of the tooth but patches of dark dentine were present at the periphery and in some of the secondary bends. A smaller tooth section should show petaloid dentine.

Rhytidosteidae indet. Several teeth from a marginal tooth row (QMF 14476) were loosely folded with few bends and clearly show dark dentine, with some teeth approaching the petaloid morphology (Fig. 13c).

Trematosauridae: ***Microposaurus.*** Petaloid dentine was present in marginal teeth and tusks of *Microposaurus casei* (R. J. Damiani, pers comm. 2003), while *Lyrocephaliscus* cf. *johanssoni* showed petaloid dentine in teeth sectioned by Schultze (1969, pl. 14, figs 3–4).

Stereospondyli indet. A petaloid pattern of dentine was present in a stereospondyl from the Permian of Namibia (Warren *et al*. 2001, fig. 6).

2.6. Amniota

Varanus. Some sections of *Varanus indicus* teeth (Schultze 1969, pl. 15, figs 3–4) appeared to show the beginning of folds with a petaloid dentine structure that is remarkably similar to that in a near tip section of *Pholiderpeton* (Fig. 8c).

Ichthyosauridae. Ichthyosaur teeth have a plicate pattern that is clearly different histologically (Schultze 1969, pl. 16). Nevertheless, they show a petaloid pattern of dentine tubules towards the periphery of the tooth.

3. Discussion

3.1. Historical overview

Owen (1841, fig. 1) was the first to describe and figure labyrinthine teeth, in the stereospondyl *Mastodonsaurus* sp., which he renamed *Labyrinthodon* sp. for the intricate tooth section. He described both primary and secondary bending (undulations) in the folds of *Mastodonsaurus* teeth, noting that the degree of folding increased with the diameter of the tooth, that the substance in the core of the bends was cement, and that enamel was present on the outside of the upper part of the tooth only. Owen's interpretation of these teeth was accurate except that cement is now known to be present only in mammals and occasionally reptiles. Subsequently, Wyman (1844) and Burmeister (1849) figured tooth sections of the stereospondyl *Trematosaurus brauni*, Barkas (1873) figured tooth sections from several Northumberland tetrapods, and Embleton & Atthey (1874) described teeth of the baphetid *Megalocephalus pachycephalus* ('*Loxomma allmanni*' in error). Atthey (1876) first drew attention to petaloid dentine, in the embolomere *Pholiderpeton attheyi*. Although tooth sections from the eryopoids *Sclerocephalus* (Credner 1893, fig. 25) and *Eryops megacephalus* (Stickler 1899), and additional illustrations of the stereospondyl *Mastodonsaurus giganteus* (Fraas 1889, Pl 17; figs 5–8), were published subsequent to Atthey's (1876) initial description of petaloid dentine, these temnospondyl teeth were not recognised as also showing a petaloid pattern. Additionally, Atthey (1877) did not recognise the pattern in *Megalocephalus pachycephalus*. The pattern was redescribed in the holotype of *Pholiderpeton attheyi* by Panchen (1981), nearly 100 years later, as "giving the appearance of a nearly black daisy-like flower with a white centre on an orange background". Thus, the phenomenon has long been associated with the embolomeres and was thought confined to tetrapods.

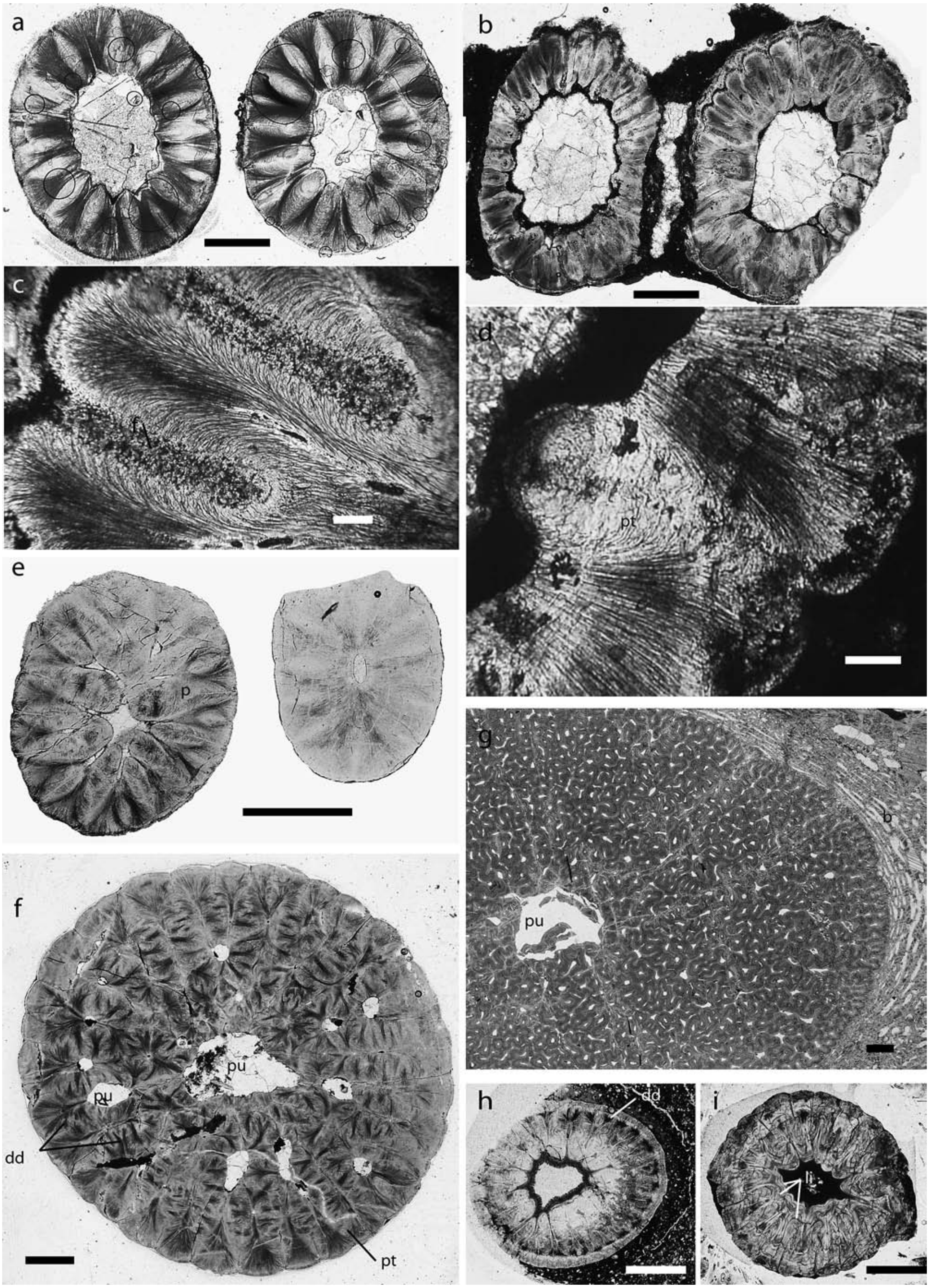
Other types of patterns found in the histology of the teeth of early tetrapods, and their closest relatives among the sarcopterygians, were emphasised by Bystrow (1938, 1939) and especially by Schultze (1969, 1970). Schultze (1969) used the term plicidentine, originally coined by Owen (1841), and made formal by Tomes (1878) for "a tissue with true dentinal tubules, which is derived from the calcification of a pulp, the odontoblast-carrying surface of which has been rendered complicated by foldings of its surface". The seminal work by Schultze divided teeth in which the dentine is folded (plicidentine) into three main types: dendrodont, found in Porolepiformes; eusthenodont, found in some osteolepidids; and polyplocodont, found in some sarcopterygians and early tetrapods. In polyplocodont teeth the bone of attachment extended between the folds, the pulp cavity was free of osteodentine, and the dentine was folded simply and irregularly with first or second degree branching. Schultze (1970) observed that the polyplocodont teeth found in *Crassigyrinus scoticus*, embolomeres and most temnospondyls were differentiated from the polyplocodont teeth of sarcopterygians in that the bone of attachment did not penetrate between the folds, and the branches of the folds, characteristic of some sarcopterygian teeth, were lost. These derived polyplocodont teeth were termed labyrinthodont (Schultze 1969, 1970). *Panderichthys* sp., *Ichthyostega* sp. and the baphetid, *Megalocephalus allmanni*, were seen as intermediates by Schultze (1969) with branching especially evident and bone penetrating further between the folds at the base of the tooth than in, for example, *Pholiderpeton attheyi*. Schultze (1970) suggested that the intensity of folding sometimes increased with the loss of branching following these forms. Teeth of early temnospondyls such as *Trimerorhachis* sp. and the Edopidae were described as simple labyrinthodont (Schultze 1969). Both Schultze and Bystrow (1938) noted that occasional branching occurred among more derived labyrinthodont teeth.

A detailed study of teeth in the stereospondyl *Benthosuchus sushkini* by Bystrow (1938) showed that the degree of folding increased with the size of the tooth, as was originally documented by Owen (1841). Bystrow also pointed out that, unless basal tooth sections were used, counting the number of folds was of little benefit as the number decreased with distance away from the base. In a later paper, Bystrow & Efremov (1940) sectioned large and small teeth from old and young specimens of *Benthosuchus sushkini* showing again that, regardless of age within that taxon, the degree of folding increased with the size of the tooth. In fact, it is evident that in *B. sushkini*, a section towards the tip of a large tusk would look similar to a basal section of a small tooth, if the diameter of the sections were similar.

A study by Warren & Davey (1992) of folded teeth among temnospondyls reiterated the conclusion that, within a taxon, tooth size influenced the degree of folding (Owen 1841; Bystrow 1938). They also showed that some higher taxa of stereospondyls consistently had teeth that, in basal section of teeth of similar size, were less complex than those of the other taxa. In Rhytidosteidae and Plagiosauridae the teeth were folded but the folds were unbent, except occasionally in large tusks, whereas even small marginal teeth in Mastodonsauridae (*sensu* Damiani 2001) and Metoposauridae were complex. They found that there was an absolute size at which folding began, with teeth and denticles less than 1 mm in diameter consistently unfolded in most taxa. This conclusion was supported by teeth from the early tetrapod *Doragnathus woodi* that were only convoluted below the margin of the gums, where they measured 1·5 mm (Smithson 1980), and was reiterated by Panchen & Smithson (1988). The distribution of plicate teeth in which the folds usually developed short side branches was extended to include *Eryops* sp. (Warren & Davey 1992). Neither Bystrow (1938) nor Warren & Davey (1992) recognised petaloid dentine in the stereospondyls they sectioned.

Although Schultze concentrated on tooth patterning, he figured petaloid dentine in *Ichthyostega* sp. (1969 pl. 13, figs. 2a–b), the baphetid *Megalocephalus* sp. (pl. 2, fig. 3), the stereospondyl *Lyrocephaliscus* cf. *johanssoni* (pl. 14, fig. 4a–b), and also in non-tetrapods, for example, the panderichthydid *Panderichthys* sp. (pl. 7, fig. 3), the porolepiforms *Glyptolepis paucidens* (pl. 2, fig. 4) and *Laccognathus* sp. (pl. 2, fig. 2; pl. 23, fig. 1), and the rhizodontids *Strepsodus sauroides* (pl. 12, fig. 3) and *Megalichthys intermedius* (pl. 10, fig. 3). Vorobyeva & Schultze (1991) were the first to recognise dark (=petaloid) dentine in a fish, the rhizodontid *Strepsodus sauroides*. Strangely, one early paper (Wyman 1844) compared the teeth of the living *Lepidosteus* with 'labyrinthodonts'. Wyman sectioned teeth at different levels and his drawings of upper tooth levels closely resembled petaloid teeth (Wyman 1844, figs 1, 2), while the lower section (Wyman 1844, fig. 4) resembled sections of *Megalocephalus* sp. peripherally, but were unmistakably from a fish as the pulp cavity was filled with osteodentine.

The above survey of the literature, whilst far from comprehensive, shows that petaloid dentine has traditionally been associated with tetrapods only, especially amongst the large anthracosaurs now termed embolomeres. Petaloid dentine was clearly present, but previously unrecognised, in figures of many other plicate teeth of fish and tetrapods. Teeth sectioned in this study and observations of actual material have demonstrated the presence of petaloid dentine in several stem tetrapods and a range of stereospondyls, as well as in embolomeres. Earlier predictions (Owen 1941; Bystrow 1938; Warren & Davey 1992), that the degree of folding increases with the size of the tooth, have been confirmed both within a tooth and between teeth, for the stem tetrapod *Ossinodus pueri*, the embolomere *Pholiderpeton attheyi*, and the rhizodontid *Strepsodus* sp., although some slight variation in the number of folds in teeth of the same diameter may be present both within and between taxa.



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3.2. The nature of petaloid dentine

Dentine is composed of a matrix of intertubular dentine traversed by dentine tubules. During dentine formation, odontoblasts grow centripetally from the inner surface of the tooth periphery so that the youngest part of the cell is adjacent to the pulp cavity (Osborn 1981). Trailing behind each odontoblast is a protoplasmic process surrounded by a dentine tubule. Mature dentine tubules may be hollow following the retraction and death of the protoplasmic process. In mammalian dentine, hollow tubules collectively form patches of dark dentine known as dead tracts. In mammalian dead tracts hollow tubules scatter the light in reflected light (appearing light), and diffract it in transmitted light (appearing dark) (Provenza 1988).

In thin sections of early tetrapod teeth, in transmitted light, tubules sometimes form an irregular patch of dark coloured dentine, but this appears to be the result of tight packing of the dentine tubules, rather than a collection of dead tracts as seen in mammalian teeth. Such patches of dark coloured dentine tubules were apparent in all plicate teeth studied, whether from fish or tetrapods, ranging from the Devonian to the Recent.

The phenomenon, known among early tetrapod workers as 'dark dentine', that results in a petaloid appearance in tooth sections, is quite different from the patches of dark dentine described above, although both appear to be the result of crowded dentine tubules. In petaloid tooth sections the petals appear light in transmitted light but dark in reflected light, the opposite to mammalian dead tracts. Although the colour difference between petals and interstices in petaloid dentine must be a result of the different light conducting properties of the two areas, it is unlikely to be the result of either petals or interstices being formed from dead tracts as the arrangement is too regular. The present study has shown that the petals of petaloid dentine are always dark in reflected light and light in transmitted light. This was first noticed by Panchen (1985) in *Crassigyrinus scoticus*, *Anthracosaurus russelli* and *Pholiderpeton attheyi*, but the distinction can now be extended to all taxa in which we could examine both whole and sectioned material: *Ossinodus pueri*, *Eryops megacephalus*, *Trimerorhachis insignis*, and *Gerrothorax* sp.

The petaloid dentine pattern is the result of differential densities in the packing of dentine tubules. Because the folds of dentine are continuous with the globular zone beneath the enamel at the tooth margin (=granular-looking layer of Embleton & Atthey (1874); globular zone of Bystrow (1938)), tubule growth begins at the globular zone of the folds as well as at the periphery (Fig. 1b). Tubules grow until they reach the central pulp cavity. When the folds begin to develop, either towards the tip of a tooth, or in a small tooth, dentine tubules are already in place, arranged in lines radiating from the periphery of the tooth towards the pulp cavity. As folds develop in the periphery, tubules originating along the folds grow initially at right angles to the fold surface, and then curve towards the pulp cavity at the tooth centre. These additional tubules from the folds meet others originating from the periphery, causing the new tubules to turn towards the centre

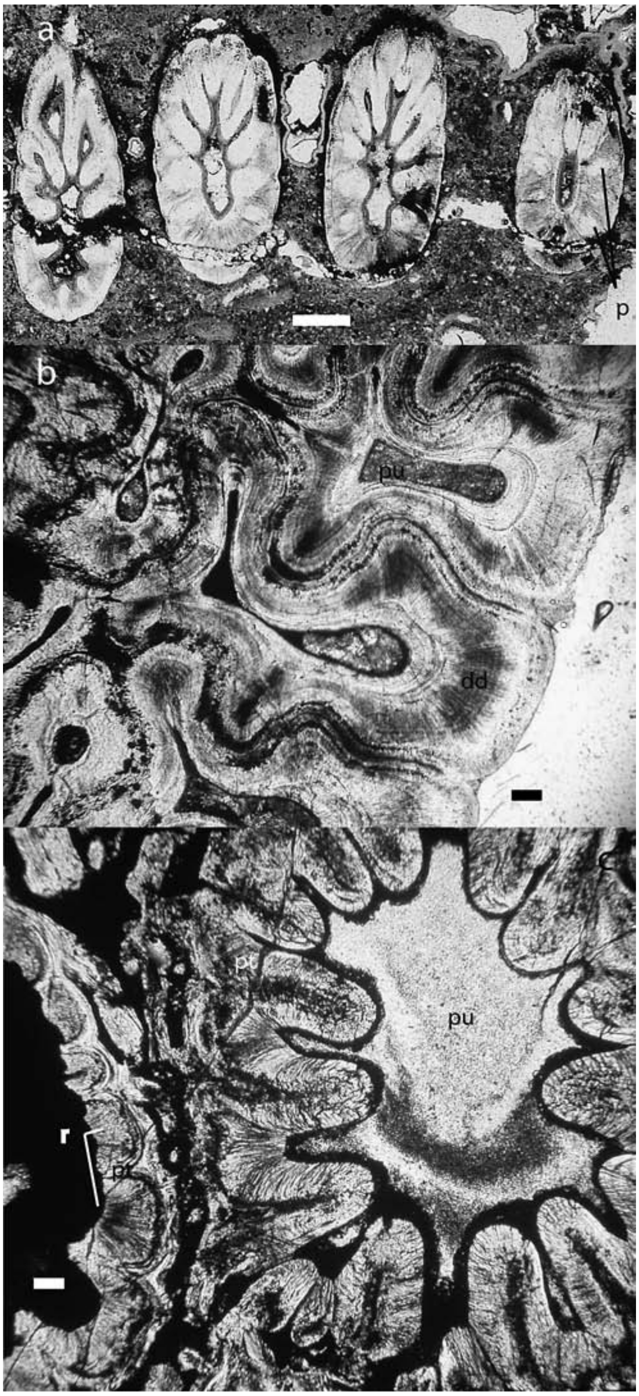

Figure 13 (a) *Keratobrachyops australis*, Early Triassic, Arcadia Formation, Queensland, QMF 14477: marginal tooth row, patch of petaloid dentine arrowed; (b) *Buettneria* sp., Late Triassic, Dockum Group, Howard County, Texas, QMF 37597: part of marginal tooth showing the presence of dark dentine but absence of petaloid dentine, many isolated parts of the pulp cavity, and secondary bending; (c) Rhytidosteidae, Early Triassic, Arcadia Formation, Queensland, QMF 14476 marginal teeth showing patches of dark dentine and faint petaloid pattern. Scale bars = 1 mm.

Figure 12 (a) *Trimerorhachis* sp. Permian, Belle Plains Formation, Texas, MCZ 8357: mid section of two teeth showing petaloid pattern. (b)–(d) *Gerrothorax* sp. Late Triassic, Fleming Fjord Fmn, Jameson Land, East Greenland, MCZ FN#12/89G: (b) tooth row with slight petaloid pattern and large pulp cavity; (c)–(d) enlarged portions of (b) showing petaloid dentine. In (c) the tooth is loosely folded so that the tips of the petals are less obvious. (e)–(g) *Mastodonsaurus* sp. Late Triassic, Germany, QMF 37503: (e) vomerine teeth showing petaloid pattern in a near tip (right) and mid section (left); (f) marginal tooth showing petaloid pattern beginning to be disrupted by secondary bending and frequent internal patches of dark dentine; (g) part of a basal section of a tusk showing obliteration of petaloid pattern. (h)–(i) *Xenobrachyops allos*, Early Triassic, Arcadia Formation, Queensland, QMF 10119: (h) tooth from mandible with marginal petaloid pattern; (i) mid section of tusk showing a large number of incremental rings around the pulp cavity. Scale bars = 1 mm.

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of the tooth. At this point the tubules originating from the folds either terminate, as in, for example, *Crassigyrinus* (Panchen 1985, fig. 15) and in some *Ossinodus* folds (Fig. 6d), or run parallel to the tubules originating from the outer margin of the tooth. Hence, the further the dentine tubules are from the periphery the closer they are crowded together. This crowding delineates the outer margins of the petals of dentine, and causes the dark colour (in transmitted light) of the interstices between the petals. The same effect is present at bends in folds deeper in the tooth. In these cases the dark dentine is expressed as half petals, when primary bends are present, or as a more complex, irregular pattern where secondary bends are involved. The fact that, at the periphery of the petals, the dentine tubules originating from the folds are more widely spaced than the crowded tubules originating from the tooth margin, undoubtedly accounts for the colour differential between petals and interstices.

The petaloid pattern of plicidentine has been found in all tetrapod taxa examined except *Buettneria* sp., and is present in some sarcopterygian fish. It occurs only in tooth sections of a particular diameter. In taxa with large, complex teeth, such as *Mastodonsaurus giganteus*, *Megalocephalus pachycephalus* and *Eryops megacephalus*, the true petaloid pattern is found only in mid tooth sections of large teeth, or in more basal sections of small teeth, such as those of the inner palate, for example the vomerine teeth of *M. giganteus* (Fig. 12e). In tooth sections of large diameter in these taxa the tips of petals can often be seen at the tooth periphery, but internally the pattern is disrupted by secondary bends in the tooth (Fig. 12f). We predict that petaloid dentine is present in the teeth of all early tetrapods with plicidentine, in tooth sections of between about 2 and 8 mm diameter in which the folding has not yet become complex. The petaloid pattern is absent in all sections of adult or immature teeth below this diameter. As teeth grow, they initially fold at the base only. Folding, and the petaloid pattern, will become more extensive with increasing tooth diameter, with a true petaloid pattern expressed at about 8 mm diameter. If the tooth base grows beyond this diameter the petaloid pattern will begin to be obliterated by secondary folding of the dentine, however more distal tooth sections will have a true petaloid section while towards the tooth tip the section will be unfolded.

If a tooth is loosely folded, as in rhizodontid fish and the *Buettneria* sp. section (Fig. 13b), the dentine tubules go directly to the inner border of the dentine at the pulp cavity without being constricted by the folds, and petaloid dentine is rare. Occasionally, a tighter fold is marked by a patch of dark dentine, as in *Strepsodus* sp. from the Ducabrook Formation, and even a petaloid appearance in part of a tooth, as in *Strepsodus sauroides* (Schultze 1969, pl.12, fig.3).

4. Summary

We recommend that the term 'petaloid dentine' be used when the distribution of crowded dentine tubules results in a daisy-like pattern in a tooth section, and 'dark dentine' be applied to any area of a plicate tooth section where dentine tubules are crowded, and hence the region appears dark.

A petaloid appearance in a sectioned tooth results from a combination of regular tight folding of the dentine, the failure of the pulp cavity to extend far towards the periphery of the tooth between the folds, and a greater depth of dentine at the periphery of the tooth than in the folds. Complete petals of dentine occur only when the folds of the teeth are unbent or have primary bends. When secondary bends are present, the pattern is confined to the tips of the petals. Thus, the petaloid pattern may be partly obscured in a basal tooth section but present in a mid section of the same tooth, and absent near the unfolded tooth tip. Teeth, whether they are from the stem tetrapod *Ossinodus pueri*, the embolomere *Pholiderpeton attheyi*, or the stereospondyl *Mastodonsaurus* sp., are indistinguishable in both basal sections and mid sections, providing the sections being compared are of approximately the same diameter. Tooth sections in which a side branch arises from the apex of each primary bend (the zigzag pattern) are characteristic of large teeth of the only member of the Baphetidae (*Megalocephalus* sp.) in which teeth have been sectioned, and of *Ichthyostega stensioei* and *Panderichthys* sp. as first noted by Schultze (1969). We extend this zigzag pattern to the Eryopidae (*Sclerocephalus* sp. and *Eryops* sp.), where it is present in sections in which primary bending is well established. Mid sections of *Eryops* sp. and *Sclerocephalus* sp., where the teeth are folded but few primary bends have developed, appear petaloid as in other early tetrapods. Although occasional branches were found in most taxa studied, frequent branching is otherwise restricted to some sarcopterygian fish. In all teeth and all taxa the degree of folding and the degree of bending of the folds increased with the basal diameter, and hence the age, of the tooth. A similar increase in folding and bending is found within individual teeth as the tooth diameter increases from tip to base.

The petaloid pattern of dentine can be found in all taxa of tetrapods with plicidentine, as well as in some sarcopterygian fish, and *Lepidosteus*, and hence does not appear to carry any phylogenetic significance (Fig. 1c). Detailed examination of the teeth of a wide range of plicate taxa might reveal slight constant variation in, for example, the tightness of the primary bends of the dentine folds. A variant of the petaloid pattern in which tight bending results in a zig-zag pattern is found in *Panderichthys* sp., *Ichthyostega* sp., the baphetid *Megacephalus pachycephalus* and two eryopoids, a distribution that does not suggest it carries a phylogenetic signal.

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6. Abbreviations used in figures

b—bone
br—branch
d—dentine
dd—area of dark dentine
dt—dentine tubules
dtc—area where dentine tubules from a fold are cut off by tubules from the periphery
e—enamel
f—fold (globular zone)
g—peripheral globular zone
li—growth (incremental) line
mar—petal margin
MCZ—Museum of Comparative Zoology, Harvard University
MCZ FN—Museum of Comparative Zoology, Harvard University, Field Number
NEWHM—Hancock Museum, Newcastle on Tyne
NMS G—Royal Scottish Museum, Edinburgh
p—petal
pri—primary bend
pt—petal tip
pu—pulp cavity
QMF—Queensland Museum Fossil
r—resorption area
sec—secondary bend.

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