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Structure and function of the tooth plates of the Devonian lungfish *Dipterus valenciennesi* from Caithness and the Orkney Islands

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Abstract – The teeth of the Middle Devonian Dipnoan *Dipterus valenciennesi* are described from new material from Caithness and the Orkney Islands, Scotland. The biostratigraphy of the Old Red Sandstone in these two areas is described on the basis of new information. The pallial dentine is made up of groups of hard clusters of material. The core dentine in the tooth plates is now understood in terms of the development of individual elements making up the structure of the dentine. The first deposited material is interstitial dentine, and the second is transparent dentine which is deposited from the pulp canals against the interstitial dentine. All the core dentine is perforate. Denteons continue to the tip of the tooth, and dentine tubules run from the pulp canals through the transparent dentine to the pallial dentine. The structure is not that of petrodentine. The difficulties of using living material for the understanding of dentine in remote structures in time are outlined. The relationships of organisms after the development of new palatal biting in gnathostomes is discussed.

INTRODUCTION

Dipterus valenciennesi Sedgwick and Murchison, 1829 from the Middle Old Red Sandstone of Scotland was studied by White (1965). References to previous work can be obtained from his paper. Later work by Schultze (1975) and Ahlberg and Trewin (1995) is available.

The solid-snouted, cosmine-coated specimens from the Thurso Flagstones, described by Agassiz in 1844 as *Polyphractus platycephalus*, was one of the reasons for Pander (1858) and Watson and Day (1916) to use the specific name *Dipterus platycephalus*. More recently Westoll (1949) described the skull roof patterns of specimens from Banniskirk (Caithness) and found them sufficiently aberrant to separate them into a new species, *Dipterus brachypygopterus*, and he revived Agassiz's specific name *platycephalus* for all other Scottish specimens of *Dipterus*. He advocated the abandonment of the name *Dipterus valenciennesi*. White (1965) concluded that the *brachypygopterus* pattern was a variation on other specimens that occurred at Banniskirk and elsewhere. The only other genus comparable with *Dipterus* is a new genus to be described by Newman and den Blaauwen from the Middle Old Red Sandstone of Caithness and Sutherland, formerly included in either *Pentlandia* or *Dipterus*. It has a different postcranial morphology and skull-roof pattern. Following White (1965) we consider *Dipterus valenciennesi* as a valid name.

STRATIGRAPHY

A stratigraphic table showing the distribution of the Middle Old Red Sandstone is attached (Figure 1).

D. valenciennesi is well known from Eifelian or Givetian cyclic sequences in the Orcadian Basin. The species is common in the fish-bearing laminites of Achanarras (Forster-Cooper 1937; Trewin 1986) and the equivalent laminites on Orkney, the Sandwick fishbed (Trewin 1976). These laminites were deposited in deep water in an extended lake in the Orcadian Basin. Small specimens lack cosmine on the scales and dermal plates, but specimens 20 cm or over in length, have cosmine on part of the scales on the ventral side and part of the dermal bones. Fully grown ones have a complete cosmine cover. *Dipterus* is also found in the calcitic nodules from the Moray Firth area where the sediments show fluvial domination in a southward extension of the Achanarras fishbed (Trewin and Thirlwall 2002).

Research in museum collections in the U.K. has shown that it is not possible to identify *D. valenciennesi* positively in sediments older than the Achanarras-Sandwick fishbed horizon.

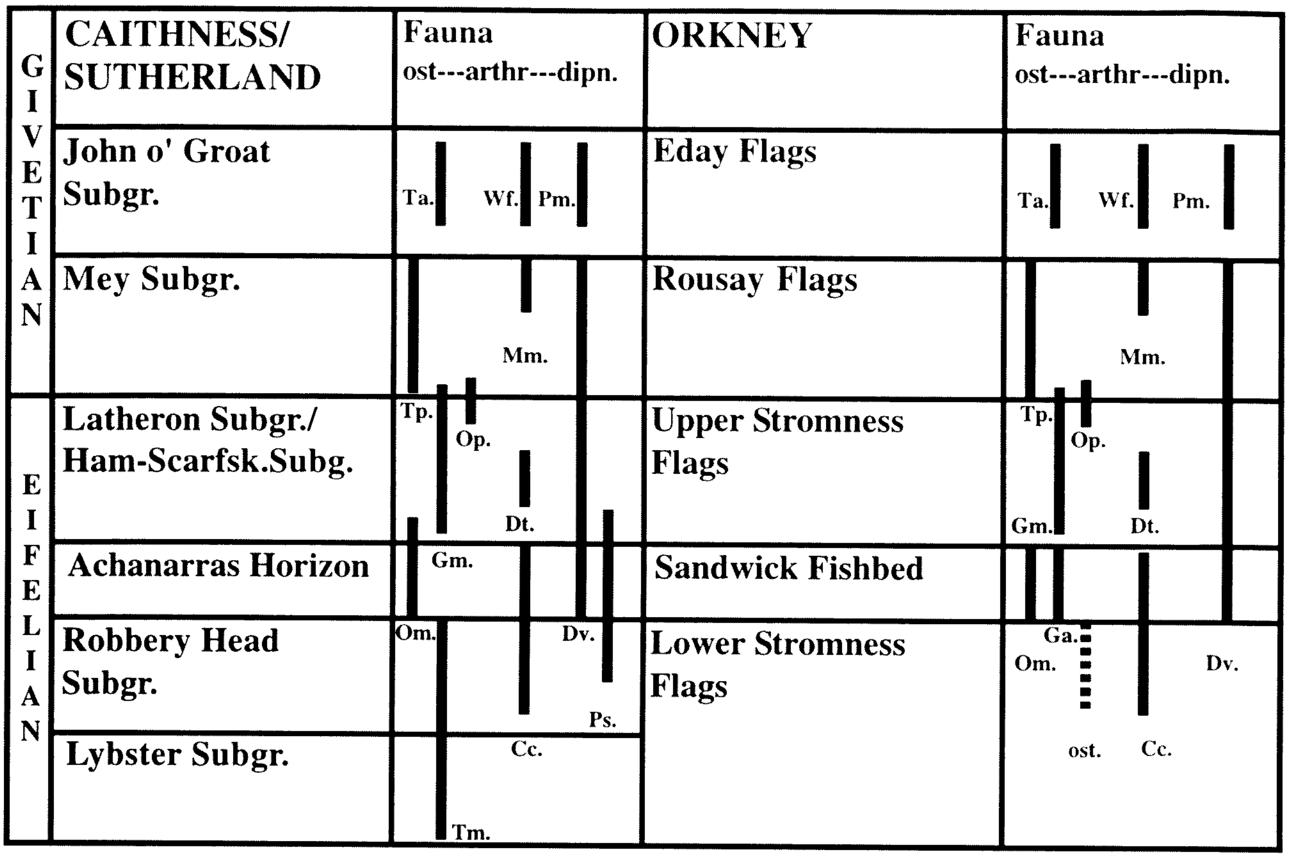

Figure 1 Biostratigraphic table of Caithness, Sutherland and Orkney indicating faunal elements which are of importance for correlation. Bars indicate the approximate range. Abbrev.: arthr. arthrodire; Cc. *Coccosteus cuspidatus*; dipn. dipnoan; Dt. *Dickosteus threiplandi*; Dv. *Dipterus valenciennesi*; Ga. *Gyroptychius agassizi*; Gm. *Gyroptychius milleri*; Mm. *Millerosteus minor*, Pm. *Pentlandia macroptera*; Ps. New Dipnoan Genus; Om. *Osteolepis macrolepidotus*; *Osteolepis panderi*; ost. osteolepid ; Ta. *Tristichopterus alatus*; Tm. *Thursius macrolepidotus*; Wf. *Watsonosteus*.

Specimens from the Lybster Subgroup which belong to the osteolepid *Thursius macrolepidotus* are often misidentified as *D. valenciennesi*. The specimens from the Robbery Head Subgroup include a new genus being described by Newman and den Blaauwen, and those from the John o' Groat Subgroup belong to *Pentlandia macroptera*.

The lacustrine sediments above the Achanarras-Sandwick fishbed show climatically controlled cycles resulting from long-term rise and fall of lake levels in an enclosed basin (Crampton and Carruthers 1914; Donovan *et al.* 1974; Donovan 1980; Trewin and Thirlwall 2002). These beds show playa-lake conditions, though in places the water may have been sufficiently deep to allow articulated fish skeletons to accumulate. The cyclicity of the sediments probably results from Milankovitch periodicities. Some of the sediments deposited in shallow water have polygonal mudcracks and shrinkage cracks. Many sediments show structures the shape of gypsum crystals or pseudomorphs showing gypsum crystal solution. These sedimentary structures are often preserved by sand infill, introduced by wind transport across the dried up lake floors (Astin and Rogers 1991; Rogers and Astin 1991). Sediments indicating very shallow lake deposits produce only disarticulated fish remains, sometimes locally concentrated in 'bonebeds'.

From extensive field work and mapping of fish remains a biostratigraphic pattern has been distilled. Naturally there are some difficulties in correlation of fresh water sequences in the Orcadian Basin, where drying of parts of the lake and the prevalence of desiccation features occur in contrast with widespread lake extension conditions in which laminites were deposited. Details of the issues will be discussed elsewhere by den Blaauwen *et al.*, but from the point of view of the dipnoans, *D. valenciennesi* has been identified from the base of the Achanarras Horizon to the top of the Mey Subgroup on the mainland, and the equivalent Sandwick fishbed to the top of the Rousay Flags in Orkney.

Specimens used in this study come from the units indicated in the Figure 1, above the Achanarras and Sandwick fishbeds. They are common in the Latheron Subgroup and the Mey Subgroup in Caithness and in the Upper Stromness Flags and the Rousay Flags of Orkney. Also specimens from Tynet Burn, one of the fishbeds from the nodule localities in the Moray Firth area, have been studied. Specimens of *D. valenciennesi* sampled in sediments indicating shallow lake conditions, are disarticulated and are mostly mature or even fully grown. Most specimens possess a well developed cosmine coating.

SPECIMENS EXAMINED

All the specimens examined have come from Caithness and the Orkneys. They have been taken from the collections of den Blaauwen, Michael Newman and Jack Saxon, and they have been placed in the National Museum of Scotland (NMS) collections. The new numbers are as follows:

G2004.10.1 From Clardon Haven, Caithness. Latheron Subgroup. Posterior end eroded *in situ*. Palatal tooth plates well developed.

G2004.10.2 From Clardon Haven, Caithness. Latheron Subgroup. Palate sectioned to show the 'cosmine' between the teeth.

G2004.10.3 From Clardon Haven, Caithness. Latheron Subgroup. Mandible with tooth plates.

G2004.10.4 From Thurso East, (the slates), Caithness. Latheron Subgroup. Mandible with left tooth plate lost.

G2004.10.5 From Thurso East, Caithness. Latheron Subgroup. Right palatal tooth plate. Sectioned horizontally, and vertically.

G2004.10.6 From Clardon Haven, Caithness. Latheron Subgroup. Pectoral girdle.

G2004. 10.7 From Thurso East, Caithness, Latheron Subgroup.

G2004.10.8 From Clardon Haven, Caithness, Latheron Subgroup.

G2004.10.9 From Buckquoy west of Aikerness, Mainland Orkney, Rousay Flags.

G2004.10.10 Same as 2004.10.9.

G2004.10.11 From Thurso East, Caithness, Latheron Subgroup.

G2004.10.12 to G2004.10.16 From Clardon Haven, Caithness, Latheron Subgroup.

GROSS FEATURES OF THE DENTAL SYSTEM

The Palatal Tooth Plates

New rows of teeth are introduced between the anterior sets of rows as spaces become available (Figures 2, 8A). Some specimens show symmetrical insertions of the two plates of the one specimen, but others do not. The specimen figured by White (1965, plate 1, figure 1) shows small teeth inserted between the first and second rows, and in places these teeth are more closely spaced. Specimen G2004.10.8 (Figure 2A) is remarkable in that it has a new irregular row of teeth anteromedially inserted, and part of the original median row resorbed. The same specimen shows gaps for the occlusion with the mandibular teeth. Irregularity of rows is shown by G2004.10.5 which leaves spaces for the insertion of new rows on the mediolateral parts of the teeth. Obviously the new rows were formed wherever a space exists because of irregular growth in old rows, and we conclude that genetic control on the precise position of new teeth was limited. New rows occupy only a small part of the length of the head.

The parasphenoid is well defined, is up to three times the length of the tooth plates, and has a well-defined buccohyphophysial foramen. The nasal capsules occupy about two thirds of the length of the plates. Most of the posterior buccal cavity is therefore not roofed by the dental plates. This point is emphasized by the mandible in which the dental plates are relatively small in relation to the whole structure.

Structure of the Mandible

The best specimens we have are of individuals which are a little above half grown, and show features which we consider significant. The tooth plates are 0.33–0.40 the length of the jaw (Figures 3 A,B), and the distance between the two tooth plates is large in comparison with the Early Devonian genera *Dipnorhynchus* and *Speonesydrion* (Campbell and Barwick 1984). The ratio of the median length to the total length of the mandible, is only about one third. Note also that the mandibular dental plates have a short median length in comparison with the posterior length. This is different from the shape of the palatal dental plates, suggesting that the contact between the mandibular and palatal plates was not one-to-one. This interpretation is supported by the fact that the inner face of the mandibular plate is turned ventrally, and could not have met the palatal plate on full closure of the jaw. This is standard for the assembled Late Devonian species (Barwick and Campbell 1996; Campbell and Barwick 1998).

A second point is that the anterior gap between the two mandibular plates is very large, and the unencumbered space for the tongue pad would be not only wide but also long and deep. The point of origin of the tooth rows have been resorbed, and on G2004.10.3 restorative dentine has been added to the anteromedian side of the tooth plate. The tooth plates of *Dipterus platycephalus* from a Scottish specimen in the Manchester Museum, and figured by Watson and Gill (1923, figure 34), also shows the reduced tooth plates similar to those described above. The cavities for the cartilage forming the articulation with the quadrate are deep and slightly doubled (Figure 3C), thus limiting the lateral movement of the mandible.

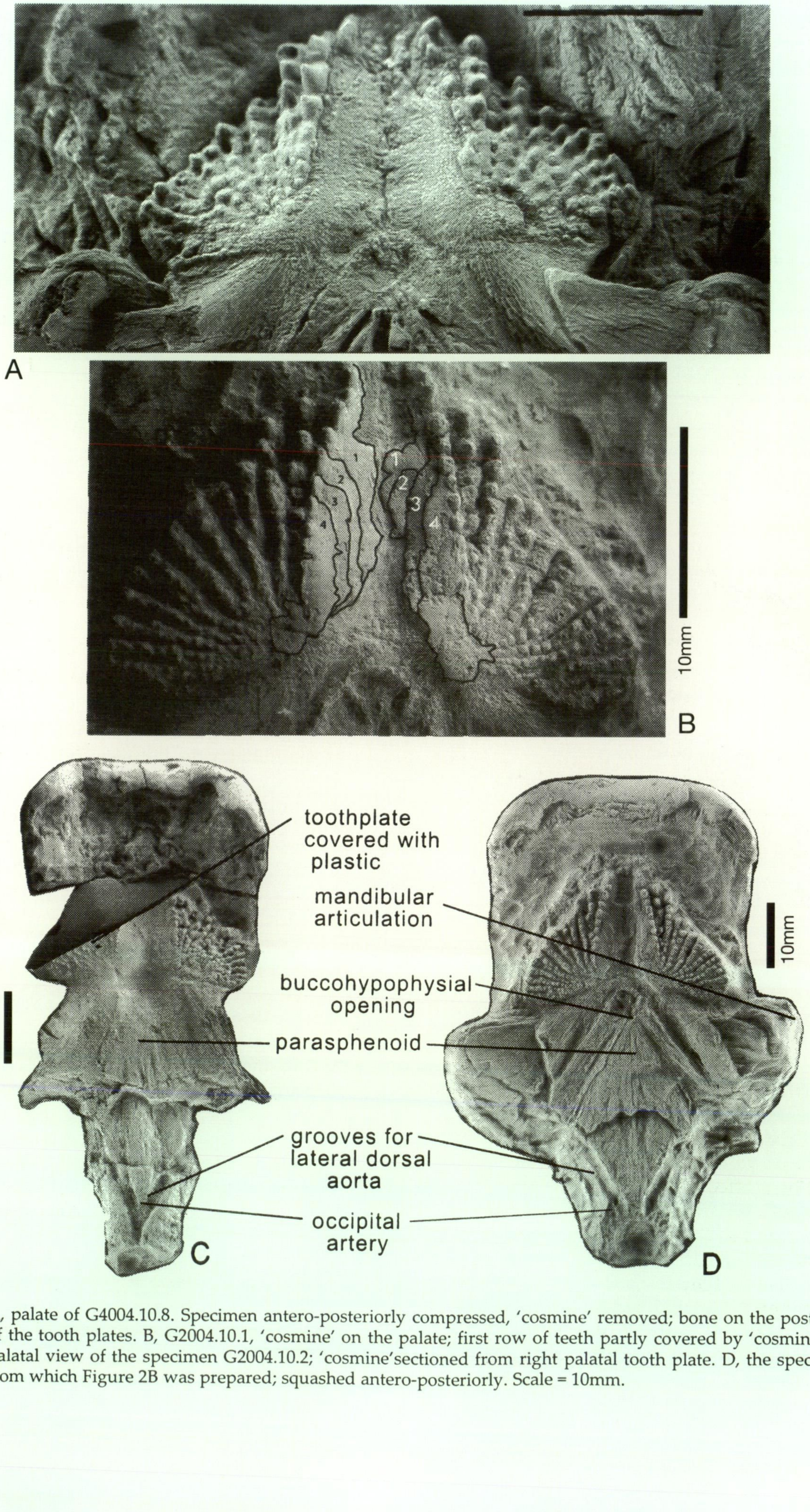

Figure 2 A, palate of G4004.10.8. Specimen antero-posteriorly compressed, 'cosmine' removed; bone on the posterior of the tooth plates. B, G2004.10.1, 'cosmine' on the palate; first row of teeth partly covered by 'cosmine'. C, palatal view of the specimen G2004.10.2; 'cosmine'sectioned from right palatal tooth plate. D, the specimen from which Figure 2B was prepared; squashed antero-posteriorly. Scale = 10mm.

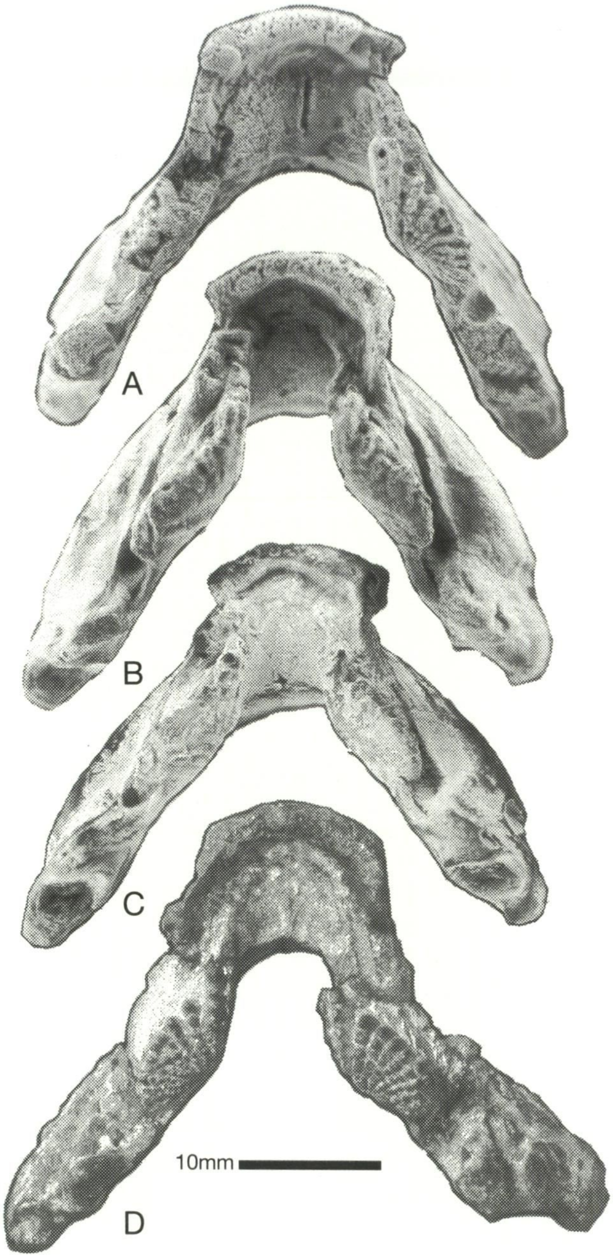

Figure 3 A–C, two small mandibles G2004.10.3 and G2004.10.4; A and B are dorsal views showing tooth-plates. C is a more posterior view of B showing the articulation cavities and the position of the adductor fossae. D, G2004.10.7 showing both tooth plates.

'Cosmine' on the Medial Parts of the Palatal Tooth

White (1965, plate 2) and Denison (1974, figure 4) figured a thin layer of tissue occupying the space between the two palatal tooth plates. It was termed 'cosmine' by both the above authors, because this layer has a shiny surface, it often contains a large number of pores, and superficially it has a resemblance to cosmine. But pores are not always present, and where pores are present, no pore canals can be found beneath them. This point and the reality of Westoll lines will be considered later in this paper. The presence of enamel on the surface of this tissue is the most important point to be considered here.

Significance of These Gross Features

The functional significance of these features is largely related to air breathing. We consider these points under the following headings: extant air breathers; palatal plates and parasphenoid; tongue pad space; and brachial laminae

Extant air breathers

Extant dipnoans fall into two groups – *Lepidosiren* and *Protopterus* which are obligate air breathers, and *Neoceratodus* which is a facultative air breather. These two groups have been discussed by Thomson (1969), who has also compared them with the Middle Devonian *Dipterus*.

In *Lepidosiren* and *Protopterus* (Bishop and Foxon 1968) the tongue fits between the pterygoid tooth plates and makes a closing valve when air is depressed into the lungs. This is done by the anterior rotation of both the ceratohyal and the pectoral girdles. The air is stored in the parabranchial cavity partly roofed by the elongate parasphenoid, the teeth are small with respect to the size of the head and they are separated to leave a space for the tongue to close off the buccal cavity when air is forced into the lungs. Associated with this procedure is the increase in space between the mandibular tooth plates which allows the tongue pad to expand forwards. The ventral surface of the head is also able to expand the buccal cavity to permit more space for the retention of air. *Neoceratodus* has a different arrangement based on an opercular pump, and Thomson (1969, figure 5) shows the movement of the opercular fold during a breathing phase. In addition *Neoceratodus* has a massive ceratohyal which takes part in breathing movements.

Palatal Plates and Parasphenoid

The palatal plates in *Dipterus* are situated well anterior in the mouth, and they are well separated from each other. In comparison with such Early Devonian genera as *Dipnorhynchus* or the Late Devonian *Chirodipterus* the plates are very short. The parasphenoid has a long posterior projection, and extends back over a long distance behind the pterygoids. Both these features make for long orobranchial and parabranchial cavities.

Space for the Tongue Pad

The gap left for the tongue between the prearticulars is large and deep in comparison with that of Early Devonian genera *Dipnorhynchus* and *Speonesydrion*. The gap between the palatal tooth plates is covered with 'cosmine', and this shows that the large tongue pad had ample room to lie between these plates when the mouth is closed. The enamel surface on the 'cosmine' shows that the epidermis was in contact with this surface. This is the ideal arrangement for the stop valve when the air was being forced into the lungs from the orobranchial and parabranchial cavities.

Pectoral Girdle of D. valenciennesi

We have access to several specimens of *D. valenciennesi* which are better preserved than any specimens previously described. The four specimens are now labeled G2004.10.6, G2004.10.13, G2004.10.14 and G2004.10.15. We will describe this material in a separate paper. The pattern of the branchial laminae and the scapulocoracoid are very similar to those on *Chirodipterus australis* (Campbell and Barwick, 1987) a marine form from the Late Devonian Gogo Formation, Western Australia. The branchial laminae would have operated in the same way in the two species.

Summary

Dipterus has a large opercular plate as well as small suboperculars, the movement of which would have produced a large expansion and contraction of the parabranchial chamber as detailed by Thomson (1969). We note that *Neoceratodus* uses a opercular parabranchial pump when breathing air, and uses the very large ceratohyals to push the air from the orobranchial and parabranchial chambers into the lung. On the other hand, the branchial laminae are so large and the ceratohyal so short, that *Dipterus* could not have used the methods of breathing adopted by *Lepidosiren* and *Protopterus*. We have concluded that *Dipterus* was a facultative air breather, though the structures could not have been as efficient as those of *Neoceratodus*.

We note that Schultze and Chorn (1997) consider that lungs were a feature of primitive osteichthyans, quoting the fact that lungs are present in primitive actinopterygians (e.g., *Polypterus*), actinistians, lungfish, and tetrapods. Campbell and Barwick (1999: 137–138) have commented on their arguments, and these will not be repeated here. Incidentally they offer no mechanism supporting their views. *Neoceratodus* is also gill breathing, and spends most of its life submerged. Comparison with *Dipterus valenciennesi* suggests that this Devonian form also had the capacity to use gill respiration as well as aerial respiration.

Our arguments are based on morphology of *Dipterus* and the extant dipnoans, and not on cladistics or the range of air breathing in some extant animals. Contrary to the argument of Schultze and Chorn (1997), we still maintain the *marine* Devonian dipnoans lacked the morphological features which would indicate that they were air breathers.

DESCRIBED HISTOLOGY OF THE TOOTH PLATES

The histological structure of *D. valenciennesi* was not described from Scottish material until recently, because like all the bones at the fossiliferous localities, the teeth were deeply stained by organic carbon. White (1966, plate 1, figure 2) published a figure of a section of a tooth plate in which the end tooth was sectioned medially and showed a translucent core. The figured adjacent teeth apparently showed a bony core, presumably because they were from marginal sections of the teeth. Denison (1974: 39) commented on these structures, but his work has not been confirmed.

Smith (1984) described teeth from the specimens described by White (BMNH P44691), and later another specimen, BMNH P53537, from Caithness (Smith 1989). These papers give no details of the pallial dentine, and their structure of the tooth core is obscure. Comments will be made on this work later in this paper.

Kemp (2001) in her paper on petrodentine does not describe the histological structure of *D. valenciennesi*, and most ancient forms dealt with are of Carboniferous age. Because of this lack of direct analysis of *Dipterus valenciennesi* tooth plates, the discovery of well-preserved specimens now gives us an opportunity to place these plates in the primitive position which their stratigraphic position accords them.

INTERPRETATION OF DENTINE IN NEW MATERIAL

There is nothing more contentious than the terminology of dentine in dipnoan teeth. For present purposes Smith (1984, 1985, Table 1) has provided the basis on which subsequent work has developed. Further work on this topic can be found in Lison (1941), Barwick *et al.* (1997), Campbell and Smith (1987), Lund *et al.* (1992), Kemp (2001) and Reisz *et al.* (2004).

Vertical Sections of Teeth

The considerable advantage we have is the availability of growth stages of the teeth. Growth of the layers in the dentine can be outlined by a number of specimens. In the first instance we describe a number of teeth from a single section.

Sections through sediment with placoderm plates

Some specimens have structures sufficiently well preserved to show histological detail throughout the teeth. Section G2004.10.9 shows the best vertical

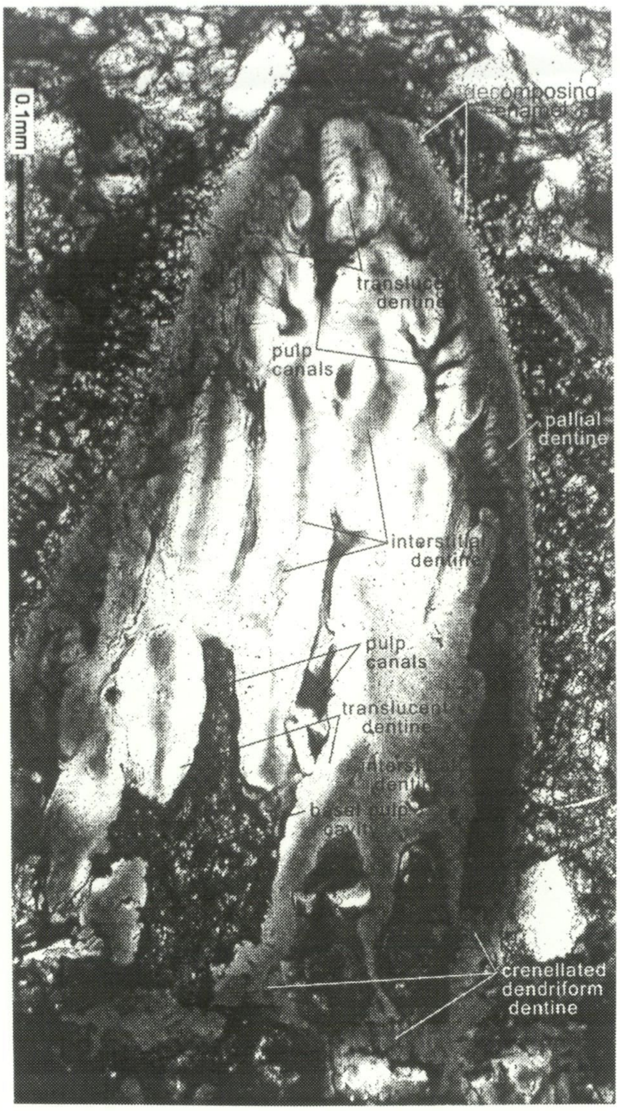

Figure 4 G2004.10.9. Vertical section in single polarized light; specimen was incompletely grown; enamel is largely destroyed; interstitial dentine grey in colour; translucent dentine around pulp canals.

tooth sections we have seen (Figures 4–6; 14E). The largest tooth in the section has a large basal pulp cavity, and the smaller teeth are in process of formation. These show the development of the histological structures.

The largest tooth has lost its apex, but on the same section two other small teeth, one at the lateral edge of the plate (referred to as the **lateral tooth** below) and the other being cut tangentially to the axis of the tooth (referred to as the **tangential tooth** below, Figures 6; 14E). The enamel is present around the margin of the lateral tooth, but it is partly destroyed by decomposition on all sides of the larger tooth. The core dentine consists of two different types of structure, **clear translucent** columns, and **interstitial dentine** columns (Figure 14E).

As Figure 4 shows, the **pallial dentine** is thickest towards the apex but fades away somewhat towards the base. The edges contain some branched tubules which arise directly from the pulp canals, and these are either simple or branched. At higher magnifications, the tubules subdivide extensively towards their outer edges (Figure 5A) making a meshwork-like pattern. In the lower half of the tooth the pallial dentine shows very fine tubules, but at the base of the tooth, the pallial dentine turns inwards (Figure 5B) and has crenellated dendriform pattern. This is best known as **pedestal dentine**. Pallial dentine is well shown on the lateral tooth and the tangential tooth (Figure 6). It forms a dark layer which is also penetrated by tubules. In places the boundary between the pallial dentine and the core dentine is sharp, but in other areas the boundary is gradational.

On G2004.10.9, **interstitial dentine** is clearly exposed (Figures 4, 6). Dark columns of interstitial dentine extend into the basal pulp cavity where their outlines are clear. In the basal pulp cavity at high magnification the interstitial dentine shows an open-work structure, which is seen on all three teeth (Figures 5B; 6B; 14E). The implication is that the growing edge of the material in the basal pulp cavity is made of crenellated dendriform material, which has the same appearance as the pedestal dentine, and laterally this material joins the pallial dentine (Figure 5B). In the central part of Figure 4, and the distal parts of Figures 6A,C, the interstitial dentine becomes vaguely outlined, not because the section is marginal to the dentine layer but the dentine is partly transformed into translucent dentine.

The marginal tooth is very informative with respect to the formation of the interstitial dentine. As shown on Figure 6A, in the core of the tooth the interstitial dentine becomes rough in its outline towards the basal pulp cavity. On the left ventrolateral margin the interstitial dentine grades into the pallial dentine and ventrally into the pedestal dentine as shown on Figure 6B. The tangential tooth (Figure 6C) also shows the interstitial dentine extending to the basal pulp cavity.

The **translucent columns** are the most striking part of the core, and show up in plain light as a clear translucent structure. Near the crest of the large tooth the structure is clear (Figure 5A) and the translucent layer carries many tubules which are derived from the pulp canals, and in places these run through the layer into the pallial dentine. This is in an early stage of the tooth formation. In the central part of the tooth, the fine structure of the translucent layers is not clear, but it does contain small openings and vague lines. The mode of formation of this tissue is clearly demonstrated by this section (Figures 4; 5B; 14E). It was deposited against the interstitial dentine by cells in the pulp canals. The base of the large tooth shows a layer of

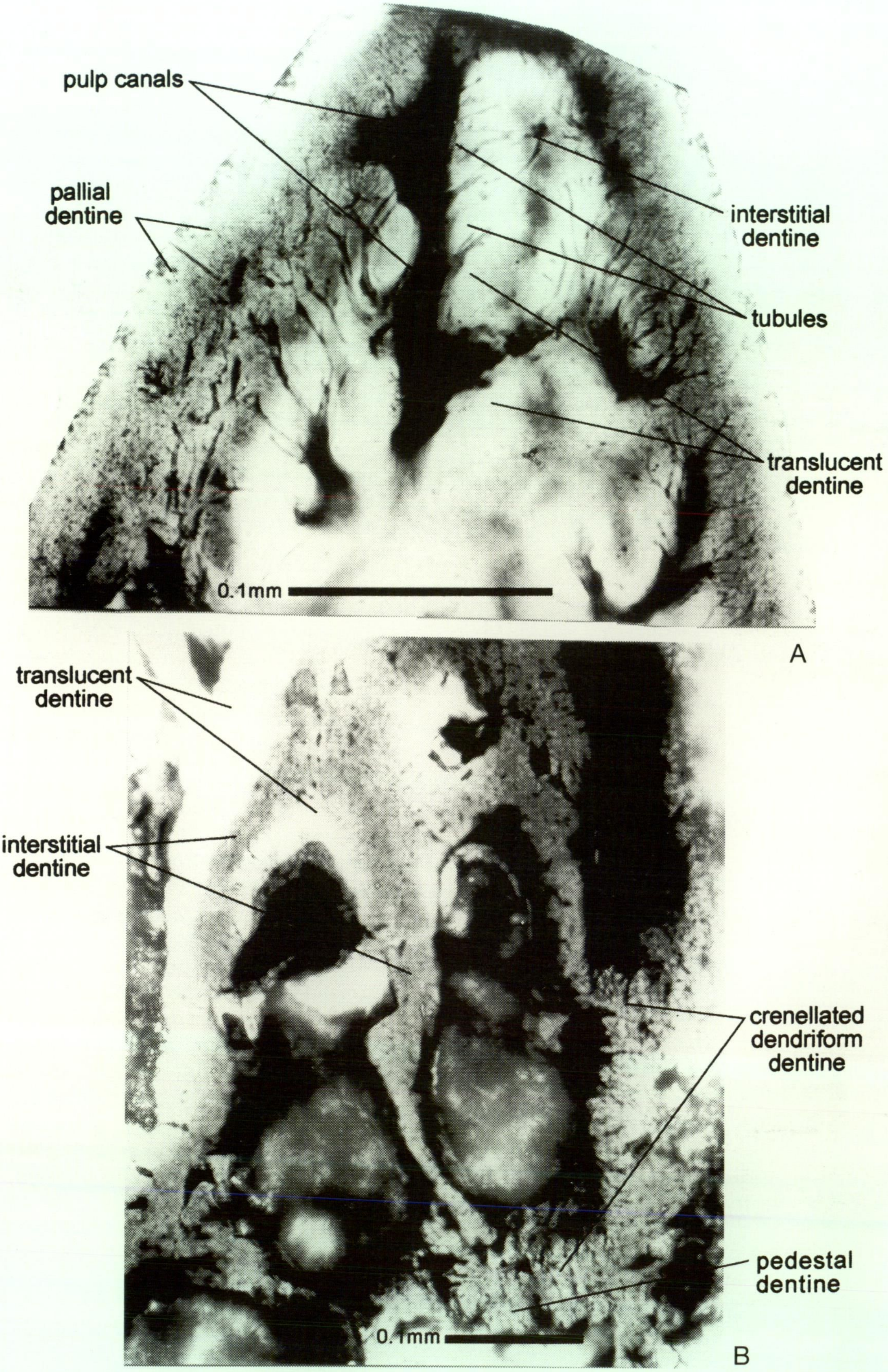

Figure 5 A, apex of Figure 4; tubules penetrating the translucent dentine and connecting with the pallial dentine; translucent dentine has replaced most of the interstitial dentine. B, enlargement of the bottom right of Figure 4; interstitial dentine around the pulp canals and translucent dentine deposited from the pulp canals on the interstitial dentine; crenellated edge of the pallial dentine joined by a column of vertical interstitial dentine, and basally joining the pedestal dentine.

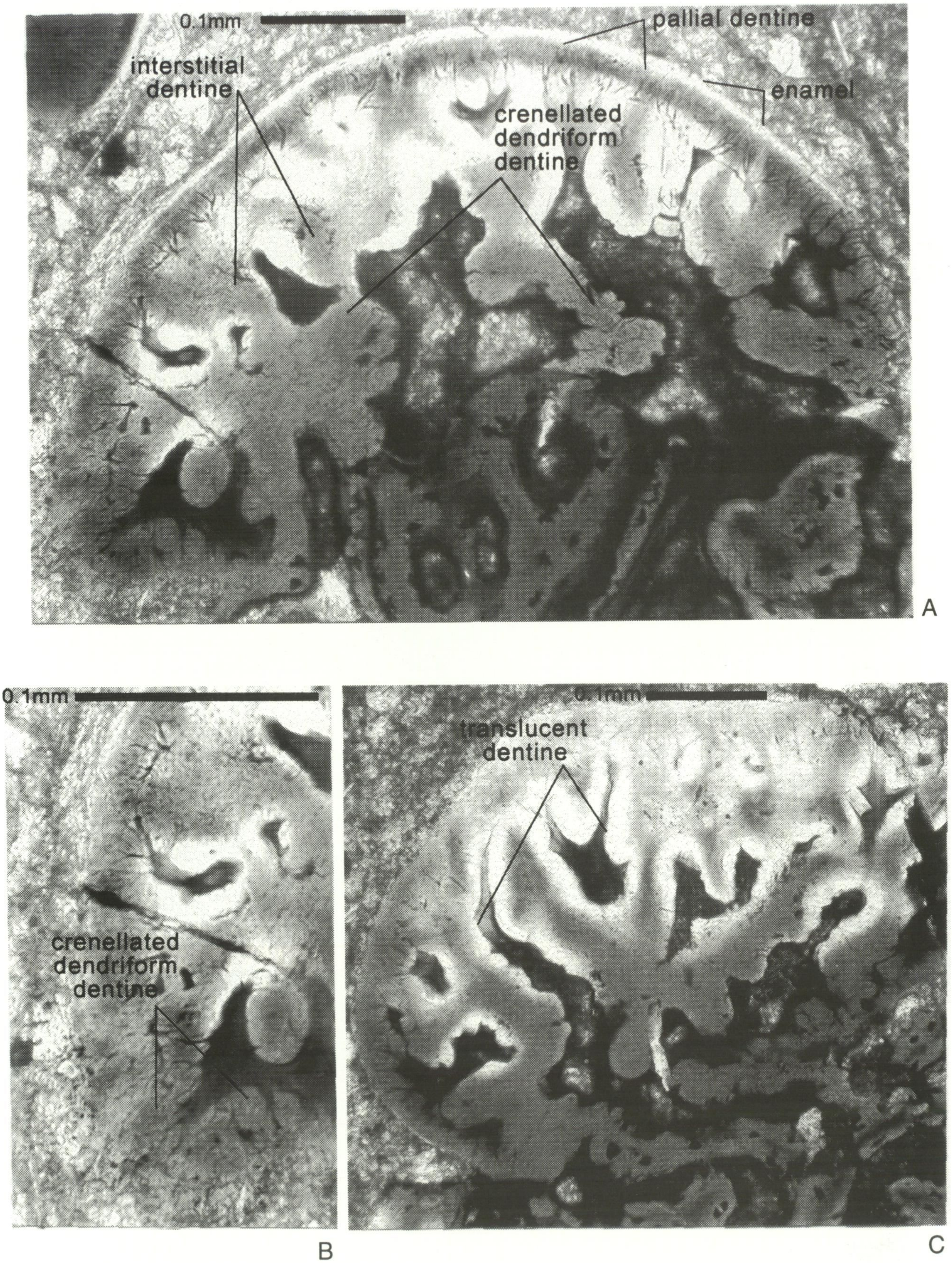

Figure 6 G2004.10.9 as on Figure 14E. A, the lateral tooth rotated; interstitial dentine runs from pulp to pallial dentine; pallial dentine with tubules; translucent dentine around pulp canals. B, bottom left of Figure 6A with pallial dentine joining with the pedestal dentine. C, the tangential tooth, Figure 14E; contact between interstitial and translucent dentine intergrading; translucent dentine often bulbous.

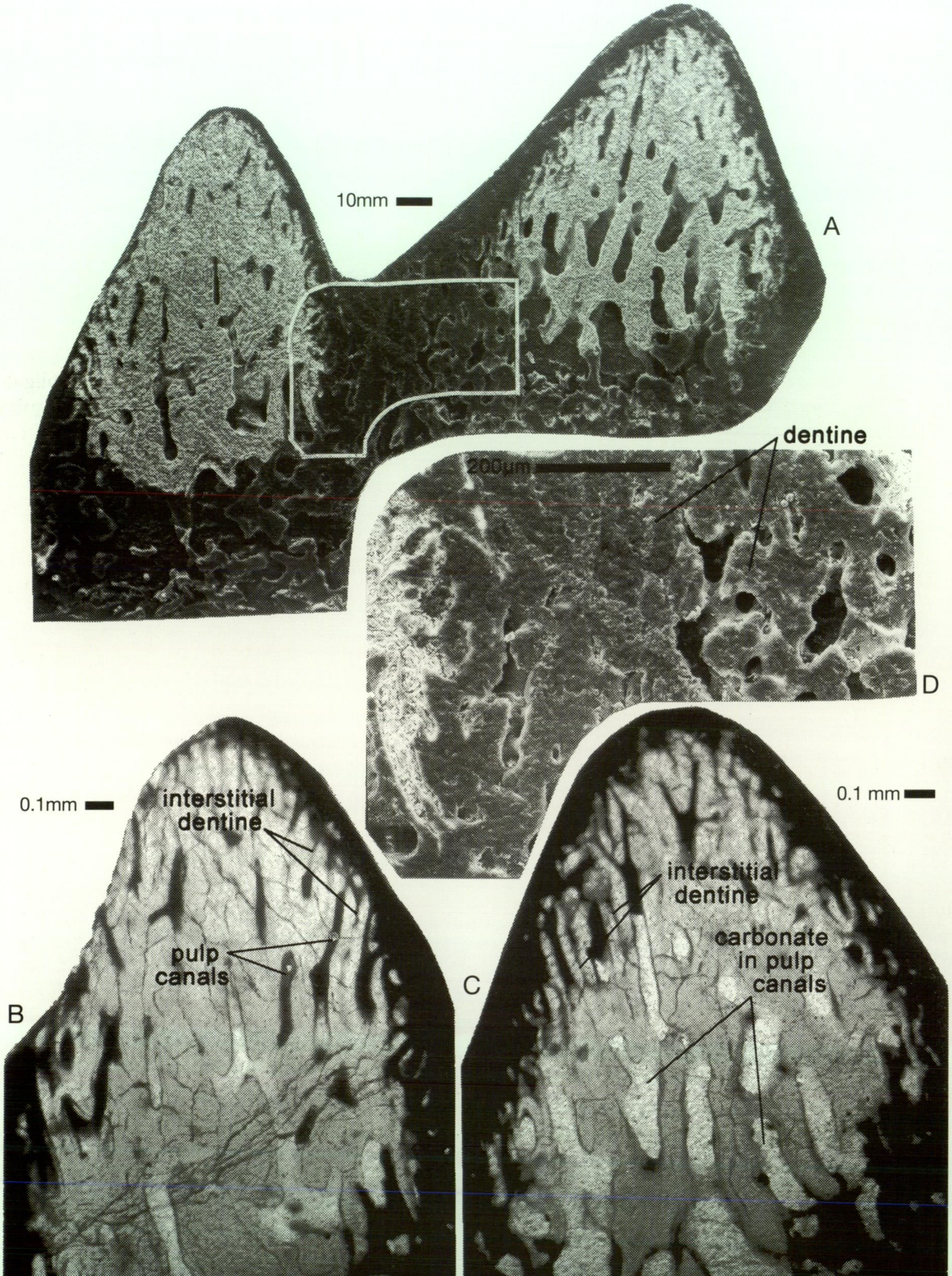

Figure 7 A, G2004.10.5C, slightly etched in acetic acid; core of each tooth extends into the basal bone. B and C, optical sections cut from the opposite face of Figure 7A; base of pulp canals with $CaCO_3$; interstitial dentine near margins but replaced medially by translucent dentine. D, enlargement of the area outlined in A; pallial dentine on left joined with pedestal dentine of right tooth.

translucent material deposited on both sides of the interstitial dentine, which grew down into the basal pulp cavity.

The tangential tooth shows new translucent layers deposited on pulp canals on the left side and open pulp canals with new translucent material on the right. The inner face of the translucent layers form slightly bulbous surfaces against the pulp canals (Figure 6C). The bone below the tooth is clearly distinguishable from the other layers because of the osteocyte spaces. Under high magnification, the pedestal dentine is not solid, but consists of a dendriform mass of material with numerous openings (Figure 6C), and this passes towards the tooth tip as interstitial dentine. The tangential tooth also shows the formation of the translucent layers. It is clearly laid down on the interstitial layers, has a bulbous surface in the pulp canals, and fades away into the basal pulp canal.

Other vertical sections

Two **fully developed teeth** on G2004.10.5 are joined together (Figure 7A). The translucent columns extending to the basal pulp cavity lying on the pterygoid bone. The pallial and pedestal dentine occupy a large part of the space between the adjacent teeth (Figure 7A,D). The enlarged illustration of this space shows the base of the left tooth and the broad base of the right tooth with the pallial, plus pedestal dentine also, preserved. The perforate nature of the translucent dentine as seen in single polarised light, and this is apparent over the whole length of the tooth. Only translucent dentine is visible in most of this section, as the interstitial dentine has been converted to translucent dentine. This change can be seen in both Figures 7B and C. The interstitial dentine is more obvious marginally, and this is what the illustrations on Figure 8 also show. The pallial dentine and the interstitial dentine merge at their junction on the sides of the tooth, and above the basal pulp cavity the two tissues also join. SEM examination shows that this material is composed of clumps of material which are roughly joined together.

This specimen also shows how new material is added to the margins of the tooth during growth. Figure 7B,C, shows the central part of the tooth formed from pulp canals that extend vertically from the basal pulp canal. Laterally some of these pulp canals branch and open to the margins of the tooth. In addition, as the width of the basal pulp cavity expands laterally during growth, new vertical pulp canals are developed and these also produce canals that open to the pallial dentine on the lower surface of the tooth.

On the lateral margins of Figures 7B,C, interstitial dentine is visible. These open to the pallial dentine marginally, but deeper into the tooth they disappear and are transformed into the translucent dentine. Interpretation of these structures is best understood from the transverse sections of the teeth.

Transverse Sections of Teeth

Sections through G2004.10.5

A palatal plate, showing a number of teeth, has been cut transversely (Figure 8A), and this is one of the most illuminating sections we have seen. In the second row from the left, the second tooth from the front has the greatest number of pulp cavities, and we regard this as the most fully developed tooth in the section (Figure 8B). It shows the large central pulp cavities and new marginally added pulp cavities introduced to increase the diameter of the tooth. The second tooth in the third row from the left has fewer pulp canals and we use this as a tooth which has been cut closer towards its tip (Figure 10A,B).

Each tooth section shows that the margins have the most recently added dentine as shown on the vertical sections described above. Internally to this tissue is the dentine added earlier on in the tooth growth. By examining the sections from the margins to the central part of the core, the sequence of changes that took place can be observed.

The core dentine meets the pallial dentine in a clear edge. Some of the arcs of the crystalline material open outwards to the pallial dentine and are partly filled with pallial dentine (Figure 9C). Others are closed, and the spaces between the arcs are filled with a shiny substance which must be interstitial dentine (Figures 8E,F). This should be compared with Figures 7B,D. We also note that the columns of crystalline material are asymetrical in that the pulp canals are displaced towards the lateral margins. And finally towards the pallial dentine, the crystalline arcs were open (Figures 8C–F).

What is the nature of these crystalline rings? Under crossed polars transverse sections through the teeth in the central part of the tooth, show that they have a band of dark coloured material around the pulp canals (translucent dentine) and lateral to that is a ring of the light coloured appearance (interstitial dentine). Towards the margin of the tooth, the central ring (translucent dentine) decreases in size and its lateral face is the most reduced; finally only an arc-shaped, incomplete crystalline ring remains. Surrounding these rings, both complete and incomplete, is dark coloured material which we infer from the vertical sections is interstitial dentine. The structure is illustrated in Figures 9A–C; 10C; 13E.

Tracing these dark layers towards the centre of the tooth, they join with shiny layers which separate the crystalline layers, and even further internally

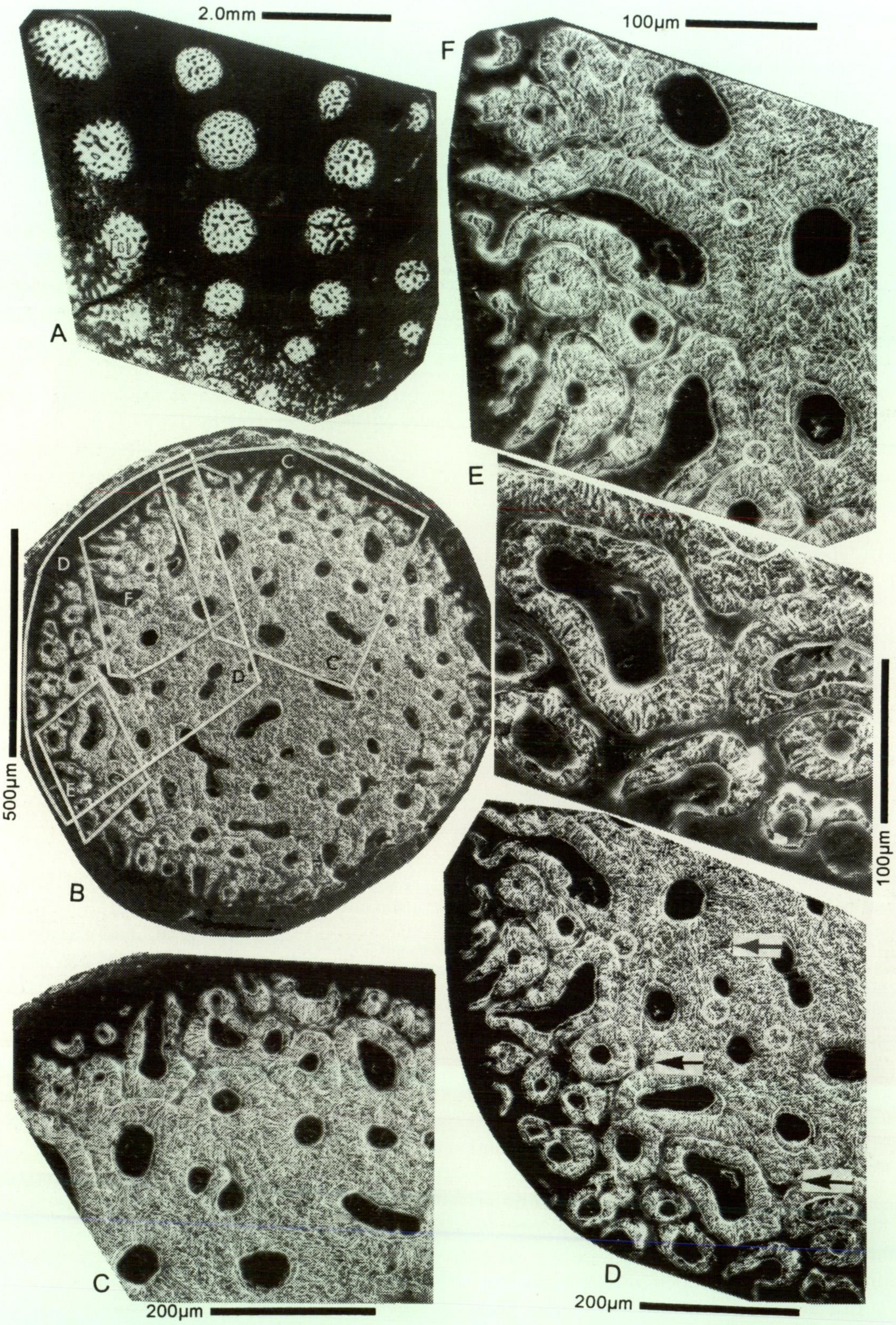

Figure 8 G2004.10.5D. A, SEM of polished surface of a palatal tooth plate; right row with branching. B, clockwise rotation of tooth second from the front in second row in A: large pulp canals central, smaller canals marginally; small marginal units surrounded by dark interstitial dentine; outlines of Figures C–F marked in white lines. C and D, several crystalline layers open to the pallial dentine; outer crystalline layers separated by dark material (interstitial dentine); dark layers become thinner medially, gradually replaced by transformation of the interstitial dentine to modified translucent dentine; circles mark the junction between crystals around adjacent pulp canals; arrows mark the transition of the interstitial dentine incomplete; E and F, dark layers between the crystalline material with a shiny surface; white circles mark junction between adjacent crystalline areas.

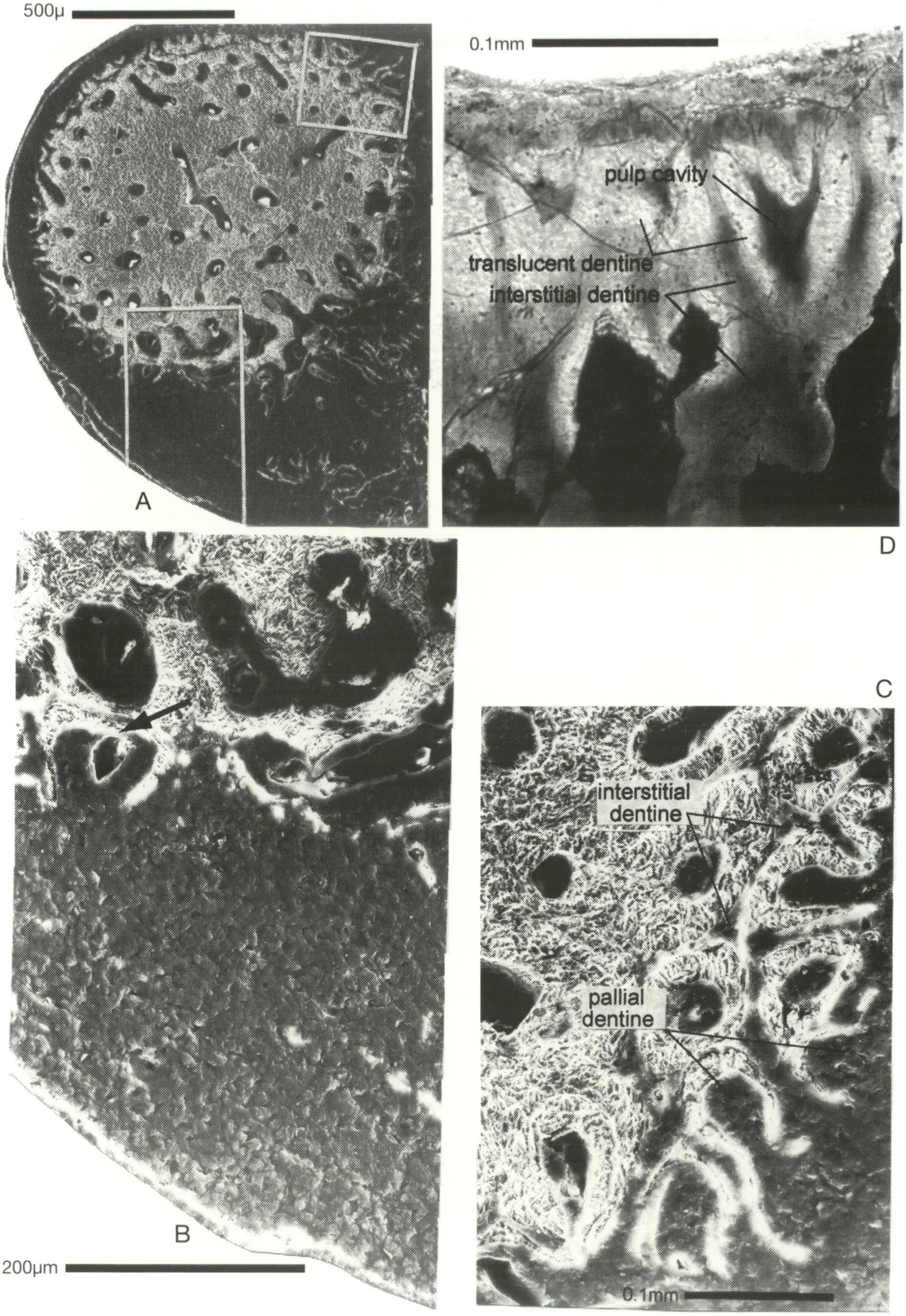

Figure 9 A, rotated oblique cross section of the anterior tooth in top left row in Figure 8A. B, enlargement of the lower area marked on Figure 9A; black arrow marks a pulp canal opening into the space in the open translucent dentine. C, enlargement and rotated area marked on the top right of Figure 9A. Crystalline material passing into pallial dentine; pallial dentine and interstitial dentine occupying spaces in translucent material. D, part of the flat dentine occupying the marginal edge of the tooth plate in G2004.10.10.

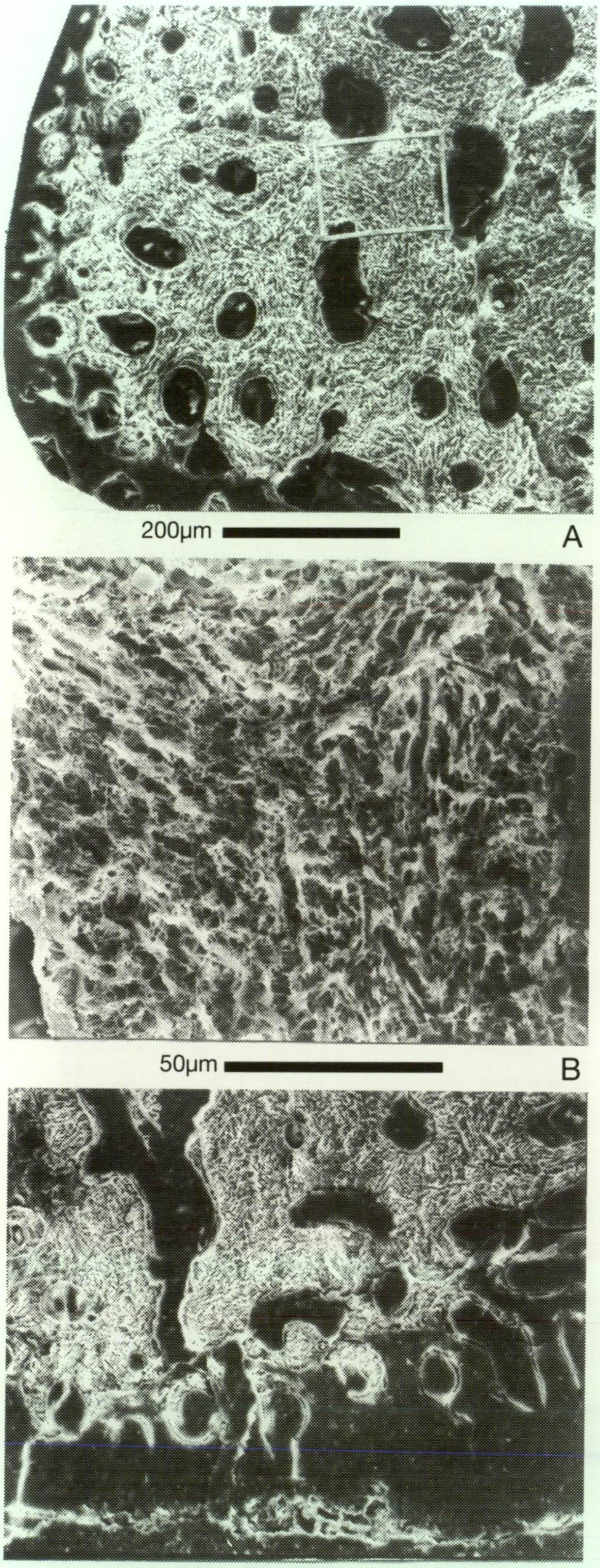

Figure 10 A, tooth second from the end in the third row of Figure 8A. B, enlargement of the area marked in A, with fine divisions in dentine. C, left side of the third tooth in the third row from left in Figure 8A; double edged crystalline layers, beginning to form around the new pulp canals.

these shiny layers become narrower and finally disappear. This is well shown on Figures 8D–F. In Figure 8F the junction between the three crystalline layers around the pulp canals is clear, and are occupied by very narrow bands of shiny material.

From these data we infer that the interstitial dentine is transformed to have a crystalline structure. To do this, histogenetic fluids must pass through the translucent dentine, and produce crystalline dentine from layers which have no internal structure when it is first deposited. The core of the tooth is therefore a composite structure, and shows different features at different levels of growth. This is what we saw in the vertical sections. The whole core structure of the tooth is a dynamically evolving tissue, composite in structure, and containing abundant pores. It does not have most of the features used for defining petrodentine.

These sections also show features of importance with regard to the pallial dentine. In several places the pallial dentine appears as a mass of clusters within which no detail can be seen. The best illustration comes from the margin of the first tooth on the left side, where the pallial dentine is obliquely cut (Figure 9A–C). Clusters of small patches of tissue make up the pallial dentine. Small gaps separate each patch and in places these are joined together to make a narrow canal. Compare this section with the vertical section on Figure 7D.

Isolated teeth from G2004.10.5

Slightly oblique sections show the internal structures admirably (Figures 13A,D,E). The presence of newly added marginal pulp canals in these sections together with the small number of total pulp canals, indicate that the teeth were either juveniles or cut half way along their adult length. The core material is crammed with perforations.

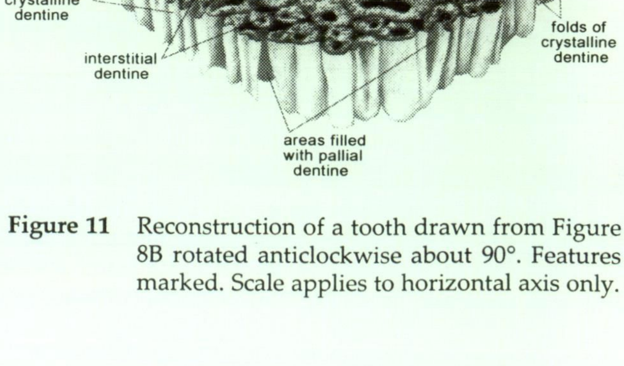

Figure 11 Reconstruction of a tooth drawn from Figure 8B rotated anticlockwise about 90°. Features marked. Scale applies to horizontal axis only.

Presumably the interstitial dentine was converted to translucent material, because the perforations were connected by microscopic canals along which histogenic substances were transmitted. Under crossed polars there is a band of dark-coloured material, and around that is a band of lighter coloured interstitial material. The size of the translucent material is not as large as one would expect from the other figured specimens.

The cross sections examined optically all have very similar structure. This is very important because it is necessary to interpret the section given by Smith (1984, figure 51).

Figures 13B,C,F from G2004.10.12 show a larger tooth which has been cut from near its base. The central part of Figure 13B shows the pattern where around each pulp canal is light coloured material (translucent dentine). Marginal to that the dark brown material (interstitial dentine) shows up well near the margins of the white material, but becomes more obvious marginally where the white material becomes narrower. The central part of the tooth is the oldest section and newer elements were added to the margins. Figures 13C and 13D show up well the different arrangement of the crystals in the translucent and interstitial dentines. In these figures the pallial dentine is very narrow, and gives a better impression of the fully grown tooth.

Compare Figures 13B,C, F with those of 13A,D,E, which is a smaller specimen that has lost its outer edges.

CRYSTALLINE ARRANGEMENT OF THE DENTINE

In this section we examine the crystallographic features of the tissue described above (see Figures 13–14). The dark coloured zone around the pulp canals in the central part of the core as shown up under crossed polars, could be the interpreted in two ways. It may consist of fluorapatite crystals with the Z-axis approximately vertical; or alternately a random array of fluorapatite crystals, appreciably smaller than the thickness of the section, so that their net interference colour is close to zero. SEM images of the structure show an array of crystals and perforations which suggest that the second interpretation is correct.

Under crossed polars, there is another ring of light coloured material around this central ring. This seems to be made of crystals more or less parallel with the surface of the section, and fibrous bundles have weak rough ends on the light bands. This band represents the interstitial dentine. Examination under crossed polars and a gypsum plate, but with two quarter wave plates set at right angles forming a Benford Plate (Craig 1961), has been used, because this plate eliminates the quadrate effect produced by the extinction position. The results of this are best shown on Figures 13E,F and 14D where the circularity of the interstitial dentine is more obvious than on the sections under crossed polars with a gypsum plate. In the corners between the separate pulp canal units there is often a small gap between the circular interstitial dentine. This would have been expected from the cross sections on Figure 8D where the arrows show gaps where the interstitial dentine has not been transformed. In the areas where the interstitial dentine has been altered, these small patches show up with a slightly different pattern.

In the marginal areas of the tooth each pulp canal has its own discrete, sometimes incomplete ring, which have been described above, and which is not in contact with the adjacent rings. The rings are separated by a dark coloured layer which is connected with the interstitial layer deeper in the tooth. Under crossed polars, with the gypsum plate and with the Benford plate inserted, the interference colours on the edge of these rings shows that the tissue represents the translucent dentine. This observation should be compared with the diagram of Smith (1984, figure 51).

COMPARISON WITH THE INTERPRETATION GIVEN BY SMITH (1984)

Smith (1984, figure 51) commented that her cross section of a tooth showed "birefringent bands of opposite sign in tissue between the dentine adjacent to the pulp canals". The central core of the tooth shows the dark array of crystallites formed from the translucent columns around the pulp canals. Note that this dark band of crystallites becomes narrower in the pulp canals closer to the tooth margin, and then opens out into the marginal pallial dentine. This is as we have described above for our material. The light bands in the figure are the interstitial dentine which has been transformed in the central part of the tooth, but marginally it has the appearance of isolated interstitial dentine. As we have shown from our specimens (Figures 8D–F; 13A,D,E) this marginal tissue is crystalline and is surrounded by dark layers which we interpret as interstitial dentine. Figure 51 of Smith's paper matches our interpretation exactly.

The statement by Smith (1984, figure 51) on the figure is not very meaningful, and the comment on page 394 that the presence of petrodentine is indicated by "bands of birefringence of opposite signs produce a woven appearance in polarized light (figure 50)" requires clarification. The inner layer around the pulp canals is translucent dentine and the outer layer is interstitial dentine which has an independent origin from the translucent dentine. The composite nature of the core dentine, made up of interstitial and translucent dentine, make it difficult to interpret her statements.

The other two of her figures of *D. valenciennesi* (figures 49–50) are also difficult to interpret. The plane polarized illustration (figure 49) has many pores and the core shows little differentiation into columns. Smith's figure 50, photographed under crossed polars, has patterns difficult to interpret compared with our Figure 4. Despite this, there is no doubt that it is the same tissue.

COMMENTS ON PETRODENTINE

The reader should examine the definition of petrodentine, a term first used by Lison (1941). In his original paper Lison makes the following points – petrodentine is light in colour; looks roughly homogeneous except near the pulp cavity where it contains cellular prolongations that are petroblasts; does not take up biological stains; much less birefringent than osteodentine in polarized light; calcified bands similar to the collagen bands; and contains little organic matter. Subsequent work by authors working on *Protopterus* and *Lepidosiren* which were used by Lison (Smith 1985; Kemp 2001) shows that petrodentine continues to grow from the from the core dentine in the earliest formed teeth; and petrodentine contains no denteons. Smith (1984) listed in a Table the criteria for the recognition of petrodentine, and this has been a valuable guide.

In the light of our current observations, we note the following characteristics of the core dentine in *Dipterus valenciennesi.*

(a) It was deposited at several levels in the tooth core, and was not deposited only in the early growth stages of the tooth. (b) Translucent dentine was first deposited from the pulp canals, in some instances well away from the basal pulp cavity. (c) Pulp canals are present even to the apical core of the tooth. (d) Tubules appear in the translucent dentine near the apex of the tooth, and extend into the pallial dentine. (e) Thin sections under crossed polars show that the growing translucent material was deposited in layers around the pulp canals. (f) Interstitial dentine occurs between the translucent dentine, and was first formed in the basal pulp cavity and also in the margins of newly formed additions to the tooth as it increases its width. (g) As the tooth grew, the interstitial dentine gradually converted to what appears to be translucent dentine. Additions to the tooth margin during growth also shows similar modifications to the interstitial dentine. (h) Both translucent and modified interstitial dentine contain large numbers of canals throughout their structure.

The next question arises – is there any evidence that the translucent material was deposited from a special layer of cells known as petroblasts? Alternatively could it have been deposited from some other kinds of cells spread more widely through the pulp canals? Naturally one cannot observe petroblasts in fossils and so one has to observe features which indicate the presence of special cells from the position and distribution of certain hard tissues.

Firstly, the cells depositing the translucent dentine must have been very widely distributed and they were active during much of the life of the tooth. Secondly, the translucent material was not deposited to make a hard surface on which the wear of the teeth could be curtailed. It is even deposited in the core of the basal pulp cavity well away from the wear surface. Thirdly, the translucent material in the most exposed core of the tooth contains large numbers of tubules which would not have strengthened the tooth against wear. These points indicate that the cells used to deposit the translucent material were not petroblasts. The layering of the translucent material and its distribution show that the cells forming the material must have formed on the surface of the pulp canals throughout history of the tooth.

HISTOLOGY OF 'COSMINE' ON THE MEDIAN PALATE

Depositional Sequence of the 'Cosmine'

As we have indicated above, the distribution and histology of the materials forming the 'cosmine' is a matter of concern. The presence of an enamel (see below) layer on the surface indicates that an epithelial layer must have been present. As the tooth plates grew anteriorly and medially, the new sequences of 'cosmine' were added. Each 'cosmine' unit has a down-turned edge, or an edge against which the new layer of dentine was formed. This means that the sequence was not the result of resorption and redeposition, but rather a sequence of successive depositional layers. The same conclusion was reached by Denison (1974: 41).

The pattern of deposition figured by Denison (1974) is different from what we observe in our specimens, and from specimens figured by White (1965, plate 2, figures 2–4). The surface of specimen G2004.10.1 shows the central parts of the palate (Figure 2B). The right palatal plate has five layers of shiny smooth substance laid down in sequence. The oldest layer, labeled 4, lies up against the first formed teeth in the median tooth row. On the left plate the sequence is not so clear, but the pattern is the same. Some of the increments show fine perforations, but the others do not. Some show perforations along the line of increments, and some of these are up to 0.5mm in diameter. In addition the innermost layer covers up the posterior part of this tooth row, and on the left plate it extends posterior to the tooth plate. Presumably this means that soft tissue covered the posterior part of the

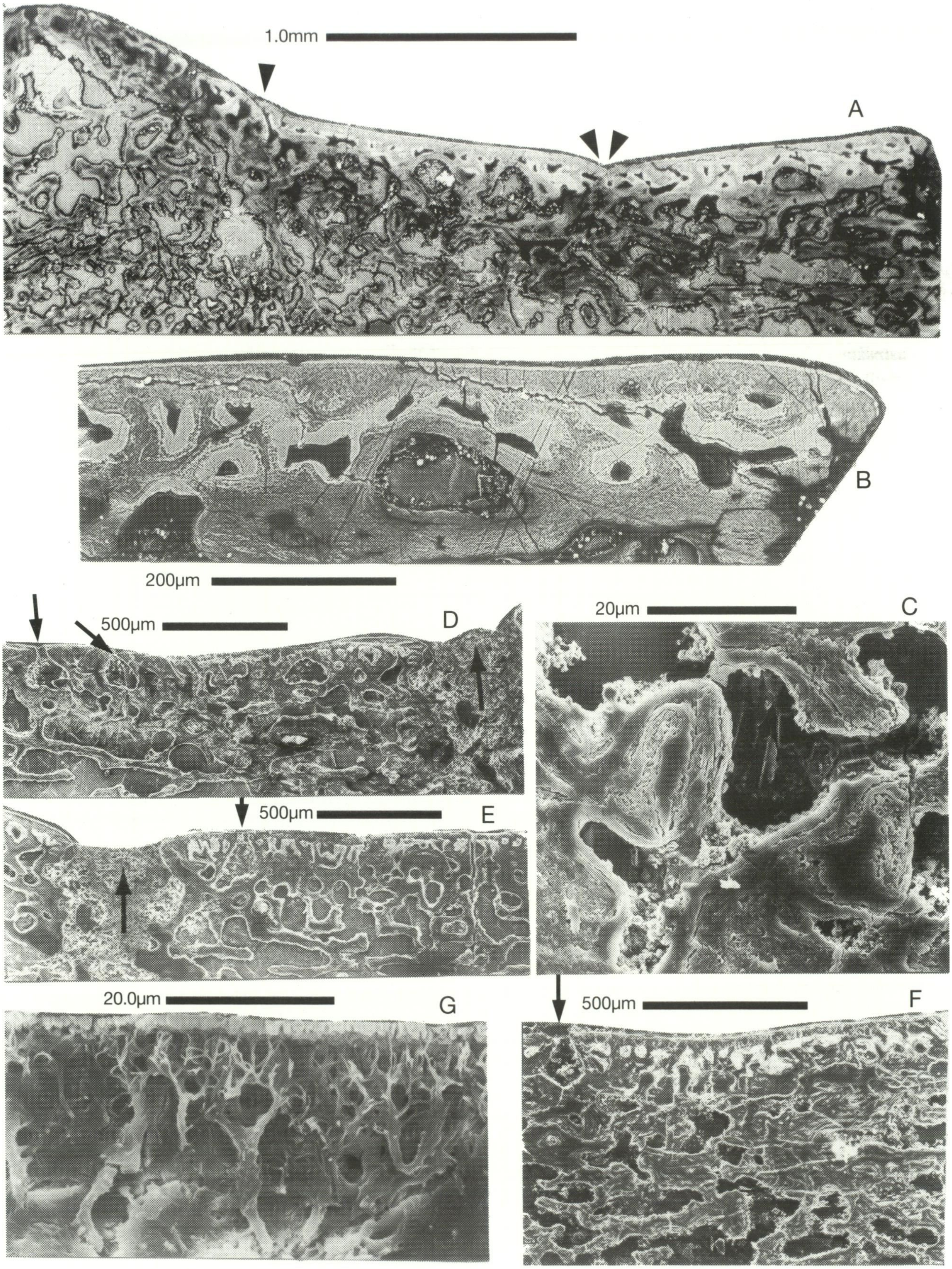

Figure 12 SEM cross sections of the cosmine on the palate. A–C, G2004.10.12; tooth on the left; single arrow marks overlap of completed unit; double arrow another unit completed on left side. B, right side of Figure 12A; white layer around pulp canals; bone at base. C, laminar character of the bone. D and E, G2004.10.2, large arrows indicate the mid-line; small arrows are pores in surface. F, G2004.10.2, cross section of cosmine, bone with osteocytes deeper. G, enlargement of the surface fine pores in the enamel; dentine tubules clear.

plate in the later periods of growth, and this would have been possible because this part of the palatal plate was not in contact with the mandibular plates in the later stage of growth. From the study of this specimen and the illustrations given by White (1965), we conclude that the distribution of the layers and the arrangement of the pores is highly variable, not only between the specimens but also on the two sides of the one specimen.

This still leaves unsolved the significance of the pores in the 'cosmine'. It is unlikely that they contained sensory tissue, but they must have allowed contacts between the soft tissue over the surface, and soft tissue in the canals. Enamel was deposited from an epithelium and this would have been served by nutrients carried through the pores from the canals. This would also account for the lack of symmetry in the distribution of the pores, and also for the concentration of pores along the junction between successive layers in some specimens, where the growing edge would have needed a supply of nutrients. But there are further tests that can be carried out before we reach a conclusion about the use of the term 'cosmine'.

Internal Structure of the 'Cosmine'

One test of the 'cosmine' hypothesis would be the presence of pore-canals beneath the pores in the surface. We note that the specimen figured by White (1965, plate 2 figure 1) does have a surface with many pores, and pores are found in places on some of our specimens. The shiny surface of the 'cosmine' is formed of radially arranged crystals as is normal for enamel. The enamel layer is perforated by abundant pores in Figure 12G. The pores open into the underlying layer with triangular pores (Figure 12D,E), but they have no indication of any internal structure. No section we have examined shows any sign of pore-canal systems, and in this respect it shows no similarity to most dermal cosmine. The large pores penetrate beneath the dentine pores into the underlying bone, but they have no lined connections to the surrounding tissues. The pores are just the means by which the nutrients were transferred to the epithelium which covered the palatal surface of the 'cosmine' during development.

Under the layer of tissue containing the dentine tubules is a layer with pulp canals surrounded by a light coloured material (Figure 12A,B), and around these are layers of banded material. The banded material therefore extends deeply into the light layer (Figure 12B). Beneath that is a layer with complex folding but without cytoplasmic spaces (Figure 12C). This layer of tissue lies directly on bone (Figure 12A).

Most of the above description is derived from G2004.10.12, but similar features can be seen on G2004.10.2.

COMPARISON WITH OTHER PRIMITIVE DIPNOANS

The structure of the dentine in the cores of the teeth of the tooth plates of *Dipterus valenciennesi* has structures different from other Early and Middle Devonian tooth plates whose details now have to be investigated. The following types of plates have been described – *Dipnorhynchus* and *Speonesydrion* from the Emsian of New South Wales (Campbell and Barwick 1984, 2000); *Tarachomylax* from the Early Devonian of Severnaya Zemlya (Barwick *et al.* 1997); *Ichnomylax* from the Taimir Peninsula (Reisz *et al.* 2004); and *Westollrhynchus*, from the Hunsrück Mountains in Germany (Schultze 2001). We do not include the Canadian Early Devonian genus *Melanognathus* here, despite Schultze's (2001) comments. It is a denticulated form with marginal teeth. *Westollrhynchus* is based on a single specimen from which no histology has been obtained. One can only consider this genus as having dubious validity.

Tarachomylax is the only genus which has plates comparable with those of *Dipterus*. Histologically, the translucent layers are separated from one another by layers of material described as interstitial dentine. No internal structure of the interstitial dentine was observed. These layers extend into the basal pulp cavity (Barwick *et al.* 1997, figure 9: 1–4; figure 10: 1–2; figure 13). Deposition of the translucent material took place from cells in the pulp canals. As shown by Barwick *et al.* (1997, figure 11:2), the translucent dentine is porous as is the translucent material in *Dipterus*. Because of the unusual features of this dentine, the authors could not refer to it as petrodentine, and we used the term 'compact dentine'. This view was queried by two of the reviewers of the paper who complained that there was no need for a new term. Barwick *et al.* persisted with the new name, but they did not suggest that it should have a formal status. They did indicate that this dentine did not have the characters of normal petrodentine.

This brings us to a position where we have to discuss why there are so many types of dental structures appearing in the Early Devonian (Campbell and Barwick 1990). Palatal biting first appeared in the Early Devonian, and this is a major change from marginal biting. In *Dipnorhynchus* the margins are added to by small enamel-covered excresences and the plate thickens by deposition of dentine at the bone dentine boundary. In *Speonesydrion* the conical teeth are added marginally to the tooth plate, and thickening takes place by the deposition of new dentine at various points at the bone-dentine boundary. *Uranolophus* has marginal enamel covered ridges around the plate margins and small denticles covering the main mass of the plates (Campbell and Barwick 1988).

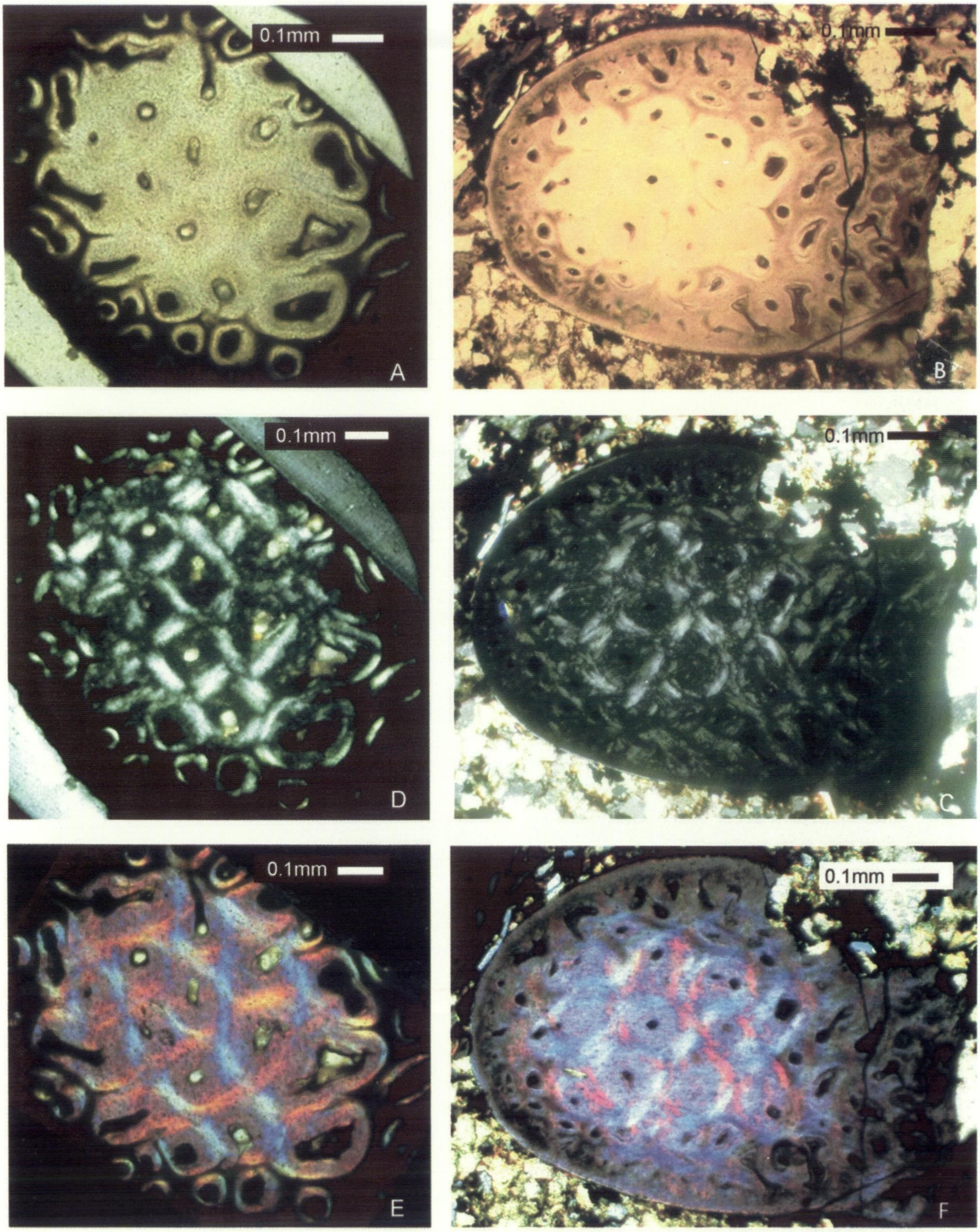

Figure 13 G2004.10.5B. A, in single polarized light; D, under crossed polars; and E with a gypsum plate and a Benford Plate. A, core dentine is finely perforate. D, pulp canals surrounded by dark layers of translucent dentine; bands around the translucent dentine are modified interstitial dentine, grey in colour and forming quadrate bands. E, zones around the pulp canals wider, and the interstitial dentine narrower than in D; circular arrangement of the interstitial dentine bands clearer; from middle of tooth to base, translucent dentine becomes narrower; in E rings of coloured bands formed of altered transitional dentine surrounded by dark interstitial dentine. B,C,F, G2004.10.12. Three similar photos of a single tooth; significance of the different colours explained in the text; F, emphasizes the small new dentines on the lower side, and the larger more open pulp canals at the top where new translucent dentine was being added.

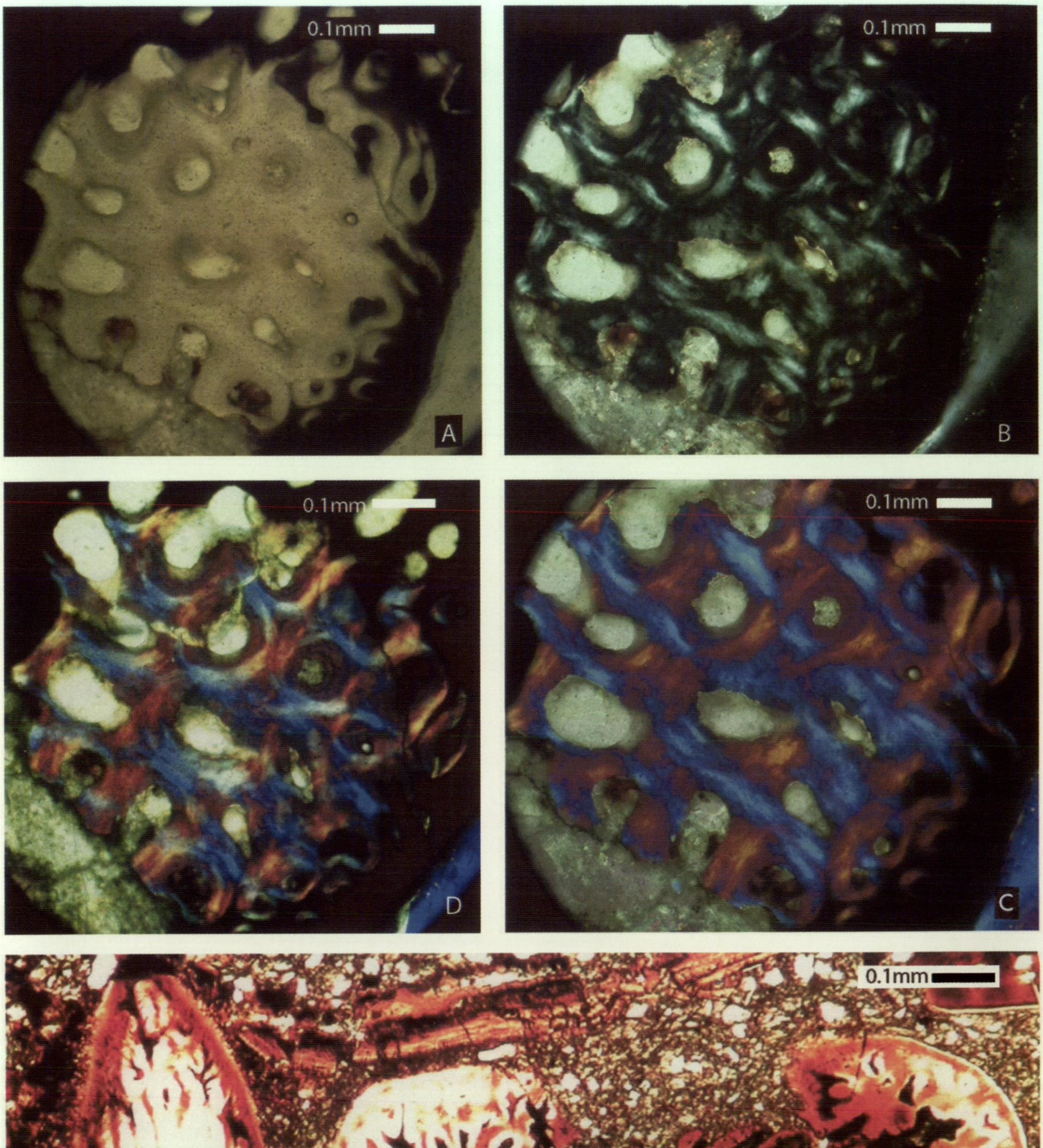

Figure 14 G2004.10.5A. Single tooth. A, in single polarized light; B, under crossed polars; C, under gypsum plate; D, gypsum plate and a Benford Plate. D, slightly rotated, and interstitial dentine shows a more circular pattern. E, G2004.10.9. Three teeth on a single slide; also illustrated on Figures 4–6.

And *Tarachomylax* has teeth as described above. That is, there are four types of plate formation introduced in the Early Devonian. Only teeth of the *Tarachomylax* type are successful in the later history of the Dipnoi. It has been shown that teeth are added marginally in later dipnoans and have a 360 Myr history (Krupina 1995, Reisz and Smith (2001) and Smith and Krupina (2001).

All of these types are discrete; they cannot be transformed from one type to the other. This then raises the question of the origin of new structures at a time when a major new development takes place in evolution – in this case palatal rather than marginal biting. This matter has been discussed in works by Raff (1996), Shubin and Marshall (2000) and Minelli (2003). It is becoming apparent that the introduction of new major features in the phenotype is probably the result of production by gene regulation. As Shubin and Marshall (2000, p. 331) report... 'major evolutionary changes may not be due to changes in the number or structure of genes *per se*, but may be due to changes in their regulation (Carroll, 1995, 2000). Indeed the changes in the spatial pattern and timing of the gene activity play an important role in generating variation at both small and large phylogenetic scales.' This article was reviewed by Russell (2001). The new designs have a genetic basis, and there is no way these designs can be changed from one type to another.

If gene regulation is the controlling factor in producing new designs in organisms with palatal biting, as the above quotation indicates, similar regulation factors may have operated on each of the basic designs later in their history. Consequently each of the tooth patterns found in the Early Devonian could have developed new structures, and these would be the basis for outlining changes in the Middle and Upper Devonian. So the use of cladistic methods to recognize relationships in these later forms will involve comparison between genera which have already separated into groups which have separated by gene regulation. Hence comparison of so-called synapomorphies will involve comparisons which are convergences carried over from the primitive forms which gave rise to the original dispersion. For this reason the cladistic analysis of the kind given by Schultze (2001), which uses the statistical methods to develop character-state optimization, will be valueless. Attention must be paid to such a possibility in outlining the evolutionary pattern in late Palaeozoic dipnoans A more complete discussion is given in work on *Speonesydrion* (Campbell and Barwick in press).

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Reviews, observations and results of research into all branches of natural science and human studies will be considered for publication. However, emphasis is placed on studies pertaining to Western Australia. Longer papers will be considered for publication as a Supplement to the *Records of the Western Australian Museum*. Short communications should not normally exceed three typed pages and this category of paper is intended to accommodate observations, results or new records of *significance*, that otherwise might not get into the literature, or for which there is a particular urgency for publication. All material must be original and not have been published elsewhere.

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