AUSTRALIAN MUSEUM SCIENTIFIC PUBLICATIONS

The Devonian Dipnoan *Holodipterus:* Dental Form Variation and Remodelling Growth Mechanisms.

K.S.W. CAMPBELL[1] AND MOYA M. SMITH[2]

[1]Department of Geology, Australian National University,
G.P.O. Box 4, Canberra, ACT 2601, Australia
[2]Unit of Anatomy in relation to Dentistry, Division of Anatomy,
U.M.D.S., Guy's Hospital, London Bridge, SE1 9RT, England

ABSTRACT. The dentition of the Late Devonian *Holodipterus gogoensis* Miles (Osteichthyes: Dipnoi) is described from the original material and four new specimens. Variation between specimens is considerable because growth took place in cycles that involved extensive resorption of tissues of all types on the dental surface, followed by periods of reconstruction during which new distributions of hard tissues were established. The teeth have an enamel cover and a hard compact dentine core within which an unusual interstitial material is present. They were added alternately to the lateral margins of the pterygoids and the prearticulars. In this way new teeth were always added outside the occlusal surface. Enlarged marginal denticles around the edges of the bones provided a surface to protect against wear by opposing teeth during the growth of the new teeth on the opposing jaws. The surfaces of the pterygoids and the prearticulars were partly covered with superficial denticles that were shed individually, or episodically in large numbers during phases of total resorption at an advancing front. Isolated denticles were also shed and regrown independently of those around them. After the episodic resorption, newly formed denticles were gradually embedded in, and in some places overgrown by, a layer of simple superficial dentine. This was then invaded by hard pleromic dentine. The next resorption phase did not remove all this dentine, and callosities of hard, compact dentine remained to continue pleromic growth into the palate. The generic relationships inferred from this unique dental pattern are discussed. A consideration of the complex of features forming the feeding apparatus leads to the conclusion that *Holodipterus* shares more characters with members of the denticulate dipnoan lineage than the tooth-plated lineage. However, characters shared with the primitive tooth-plated genus *Speonesydrion* may be significant. Further information on the dental structure of some other genera, particularly *Fleurantia,* is required before more definite conclusions can be reached.

CAMPBELL, K.S.W. and MOYA M. SMITH, 1987. The Devonian dipnoan *Holodipterus:* dental form variation and remodelling growth mechanisms. Records of the Australian Museum 39(3): 131–167.

CONTENTS

Holodipterus has one of the most unusual of all known lungfish dentitions. It has large, enamel-covered, radially arranged teeth around the margins of the pterygoids and the prearticulars, and extensive areas of the surface of these bones are covered with denticles that were shed and regrown at irregular intervals (Miles, 1977; Smith, 1977; Campbell & Barwick, 1986). Thus it has the dental characteristics of the two groups of dipnoans - one, such as *Dipterus,* that crushed and triturated its food, and the other, such as *Griphognathus,* that depended largely on a shagreen of denticles lining the buccal cavity for the manipulation and any necessary reduction of food without crushing and triturating.

Several questions arise immediately. Are there really two discrete types of dentition that define separate evolving lineages, or does *Holodipterus* provide evidence of a true intermediate morphology? Is it possible, therefore, that tooth plates do not define a monophyletic group as has been proposed by many workers (Denison, 1974; Miles, 1977; Campbell & Barwick, 1983)? If *Holodipterus* is not a tooth-plated type, but a denticulated type that has secondarily produced a plate-like structure (Campbell & Barwick, 1987), what kind of evidence from development and histology would permit the recognition of simulated tooth plates?

As part of a review of Palaeozoic and Mesozoic dipnoan dentitions we have reinvestigated *Holodipterus gogoensis* from new and previously

described material. Representatives of this species are not common and specimens available for histological sections and for scanning electron micrography are at a premium. We are grateful to Dr Peter Forey, of the British Museum (Natural History), London, for making part of a palate available to us for these purposes, and Dr Gavin Young, of the Bureau of Mineral Resources, Canberra, for allowing us to etch and section specimens in his care.

MATERIALS AND METHODS

All the specimens examined are from the Gogo Formation of the Canning Basin, Western Australia. This is of Frasnian (Late Devonian) age. They have been prepared by etching from limestone nodules with acetic acid. Thin sections have been cut from some of this prepared material and some of it has been used for scanning electron micrograph (S.E.M.) work. The photomicrographs and the S.E.M.'s in Figures 10–18 are from vertical sections cut in a labio-lingual plane through the marginal tooth on the anterior row of the pterygoid (CPC25738). All S.E.M's in Figures 15–18 are from the block face immediately adjacent to the section (Fig. 10) polished and etched for 1 min. with normal H Cl.

A small fragment of the palate of CPC25738 was not etched, and this has been sectioned and scanned. We draw attention to the fact that by far the best histological detail is obtained from unetched material. This is because the etched material has to be impregnated with a mounting medium that may not completely fill the pore spaces, the walls of which may then collapse during sectioning. Of greater significance is the point that if the specimen is sectioned with the carbonate matrix in position, the birefringence of that mineral helps define the outlines of the biological tissues under crossed polars, and subtle details are revealed by examination in ultraviolet light.

We have examined all the specimens housed in the British Museum (Natural History) that were used by Miles (1977: 14) in his original description of the species. Details of specimen numbers and locations may be obtained from that publication. In this work, the B.M. (N.H.) specimens are indicated by the prefix 'P'. Four new specimens in the Commonwealth Palaeontological Collections, indicated by the prefix 'CPC', have also been used. They come from the holotype locality at Paddy's Springs.

GROSS MORPHOLOGY

The broad outlines of dental morphology have been provided by Miles (1977: 209–214, 294–296; Figs 4a,b, 40, 108–110). The most striking feature of his specimens is the range of variation they exhibit, and this has been increased by the addition of the four new specimens CPC25738–CPC25741 (Figs 1, 3,

19). The palates are highly arched, and occlusion takes place only around the labial margins. It is surprising, therefore, that a hard, dark-coloured, irregularly shaped, dentine mass always stands proud of the surrounding tissues on the median posterior part of the palate, and a similar but smaller median anterior mass is present on some specimens (Figs 1; 2; 4A; 5A,B). The posterior mass, hereinafter referred to as a callosity, is either simple, or extended anterolaterally to form ridge-like features that tend to align with the first or the second marginal tooth rows. These ridges are composed of continuous hard dentine, or two or three more or less discrete knob-like masses. The marginal teeth are always present, and either overhang the labial edges of the pterygoids or lie within their margins. The number of teeth in each row varies between specimens or even on opposite sides of the one specimen. Denticles cover large areas of the surface, or they are restricted to small patches, whereas the remainder of the surface is covered with a sheet of a relatively dense substance referred to by Miles (1977) as dentine.

Similar kinds of statements may be made about the mandibles (Figs 3A,B; 6A; 7A). The marginal teeth lie within or overhanging the labial edge of the prearticular, and the number of teeth in the tooth rows varies. The size and shape of the mass of dentine on the heel of the 'tooth plate' differs even on opposite sides of the one specimen, as also does the area covered by denticles. And finally, two specimens (P52565 and CPC25341) show the superficial sheet of dentine covering almost the entire buccal surface of the prearticulars (including the depths of the lingual furrow), the surface of the adsymphysial plate and the adjacent parts of the dentary, whereas P56045, which is almost exactly the same size, has exposed bone over the floor of the lingual furrow. The dentary on CPC25738 has a row of small teeth along the lateral crest (Figs 3A,B; 4D). Flanking this row on the outer side is a new layer of dentine on which new teeth are not developed.

These observations pose the fundamental question – is the variation the result of individual differences, or of a massive reorganisation of tissues undergone by all members of the species during growth? The answer to this question determines our understanding of the phyletic position of the genus.

The first point to make is that there seems to be no correlation between structural differences and specimen size. If this had been so, the matter would have been easily resolved. However, the absence of a correlation may mean that remodelling of the dental surface took place many times during the life history of a single animal, and that these processes extended well into the adult stage. Consequently, if the observed variation is to be interpreted as the result of death at various stages of the remodelling process, it is necessary to find evidence of resorption and redeposition of dental tissues at both the macroscopic and microscopic levels. For these purposes the

following structures were examined: marginal teeth, denticles, basal bone, surface sheets of dentine, and dentine callosities of the palate and prearticular.

Marginal Teeth

These are large conical bodies that are almost right-circular when free standing, but more commonly slightly compressed when closely juxtaposed to the previous member of their row. A maximum of four occur in any one row, and this is on the lingual row of the mandible P50197. Most rows have only two teeth, and the more posteriorly placed teeth are single. The most labial tooth in a row is invariably the largest and the most complete, those on the lingual side being progressively more worn. There is also a decrease in size of the component teeth from anterior to posterior along the pterygoid. The tooth rows are aligned so that the whole array of rows on a single pterygoid never covers an angle of more than about 70°.

The isolated and unworn teeth have an enamel external coating, and show evidence of being fluted around the base as a result of slight infolding of the basal dentine. Clearly they were formed in an epithelial invagination in the same manner as the teeth of *Dipterus* and *Sagenodus*. However, the conformation of the dental surfaces is such that if the highest tooth in the row is on the labial end, it must
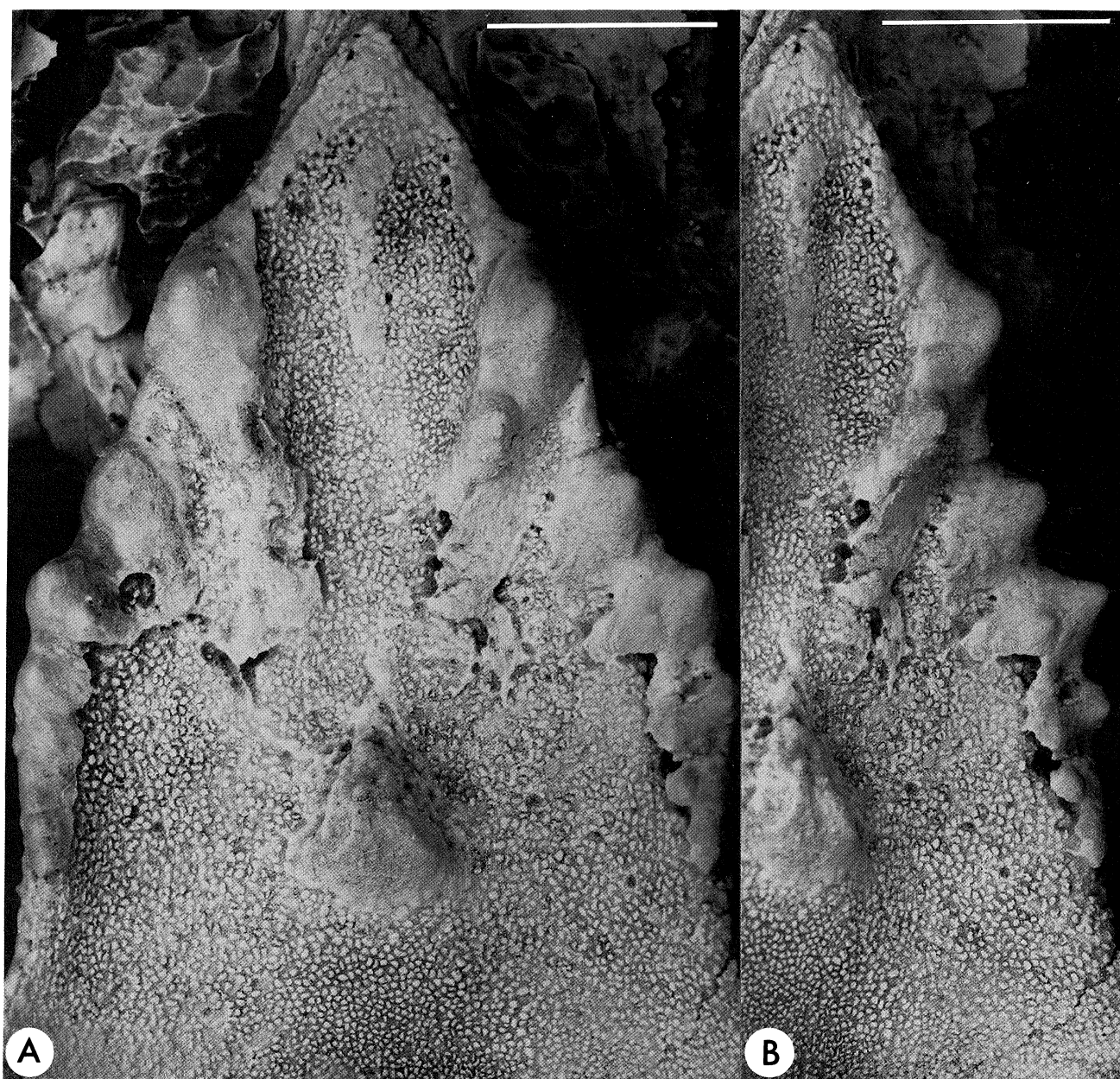

Fig. 1. (Scale bars = 10 mm). **A,B:** Ventral and ventromedial views of the palate of the smallest specimen available, CPC25740. Note the extent to which resorption of the superficial layer has taken place, and the way this has undercut the teeth, the resorbed surface being covered with new denticles.

have reached its fully formed shape and position by one of three modes. (a) The developing teeth in the two plates would be in opposing positions, but at a low level and out of the bite. They would move into the bite by appositional growth of dentine and bone at their bases. This seems to be the mode adopted by *Dipterus* and *Sagenodus*. (b) The developing teeth would be initially positioned as above but would come into the bite by means of wear on previously formed teeth in the same row. This effectively causes rotation of the occlusal plane relative to the base of the plate; dentine then would have to grow basally, into the bone, to maintain plate thickness. (c) The teeth of one plate would be formed outside the lateral margin of those in the opposing plate and at the same level as the previously formed tooth in the same row. By appositional growth of bone and dentine at their bases such newly formed, unopposed teeth would then have grown taller than previously formed ones.

Modes (a) and (b) receive no support from our observations, but mode (c) is substantiated by two unequivocal pieces of evidence. Two articulated individuals (P52568 and CPC25738) show the outer teeth on both mandibular rami lying outside the palatal marginal teeth (Figs 3D; 8); and, as noted above, one palate (Fig. 4A) and one mandible (Fig. 6) show the marginal teeth overhanging the edges of the bone on which they lie.

This mode of growth clearly implies that tissue was added along the labial margins of both pterygoids and prearticulars, and that little if any addition took place along the median line. Consequently, it is surprising to find that the tooth rows are so short and consist of so few elements. If growth were continuous radially, one would expect to find many worn teeth forming each row as is normal for dipnoan tooth plates. Moreover, the smallest known palate, CPC25740, has the same number of rows and the same number of teeth as the largest ones, though it is only about two thirds their size. The only conclusion that can be drawn from these data is that teeth on the palate were progressively lost from the lingual ends of the tooth rows as new ones are added to the labial margins. This, however, does not apply so uniformly to the tooth rows of the lower jaw in which resorption was not so extensive (see below).

These surprising conclusions are substantiated by an examination of the holotype (P52569) and CPC25740. On the holotype, a tooth of the third row on the left side is almost completely undercut, but has not been lost (Fig. 2A,B). The process of resorption was not completed before the next phase of tissue deposition began (see below). In addition CPC25740 shows extensive undercutting of the teeth of the third and subsequent rows on both sides of the palate (Fig. 1A,B).

When resorption was complete, even the thickest dentine forming the cores of the palatal teeth was removed. Because of the scarcity of material we are unable to demonstrate this by sections along the axis
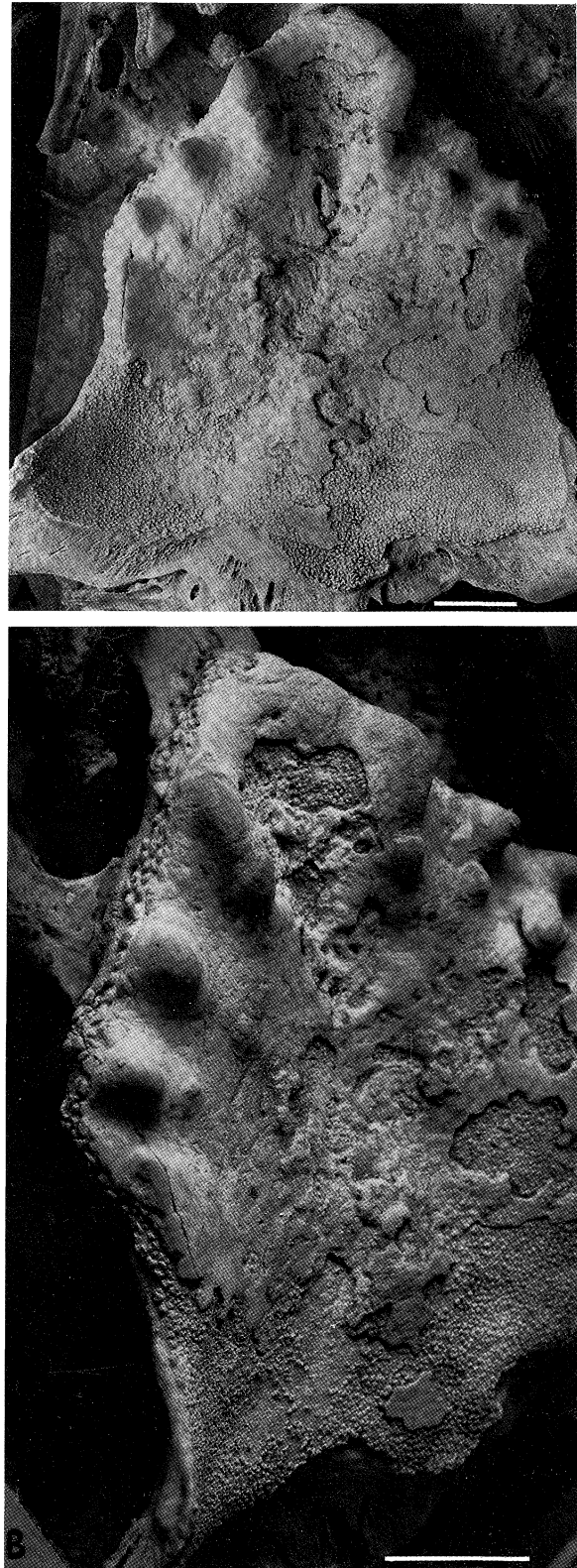
Fig. 2. (Scale bars = 10 mm). **A,B:** A larger specimen, P52569, of the palate in ventral and ventromedial views. Note in B, the numerous marginal denticles extending beyond the teeth, the superficial layer completely covering the bases of the teeth, and the denticles over large areas of the pterygoid. One of the teeth in the third row on the right side of the photograph in B has been under-cut, and a new superficial layer had been deposited when the animal died.

of a tooth ridge, though vertical transverse sections of the palate of CPC25739 show no sign of buried teeth in the position expected to be occupied by older teeth (Fig. 19C,E). In addition, P56045 shows a gap in the palatal surface where the second tooth of the third ridge has been shed, the floor of the gap now being occupied by newly formed denticles attached to new bone (Fig. 4A,C). Evidence of this type is as adequate as evidence from sections. Removal of all the tooth cores on the prearticulars was probably not so complete, and they may have contributed to further pleromic growth to produce a tooth plate-like structure (Figs 6A; 7A). However, it remains true that some of the radial ridges on the prearticulars are not developed from worn teeth because large specimens (P56045, CPC25341) have a ridge deep in the lingual furrow where no teeth ever existed (Fig. 6A).

The largest teeth are always at the anterior end of the lingual row. In the lower jaw, this largest tooth always lies immediately behind the posterolateral end of the dentary (Figs 3A; 4D). This means that new teeth were not added to the lingual row without considerable bone growth at the edge of the prearticular along its junction with the dentary, and marked lateral growth of the posteriorly directed parts of the dentary. As the suture between the prearticular and the dentary was kept open, there would have been no difficulty in producing prearticular growth of this kind. However, there is no median suture in the dentary, and hence lateral growth of that bone must have resulted from resorption along its junction with the prearticular and lateral deposition along the edge forming the margin of the labial furrow. This is well shown on Figure 4D. This complex mode of growth of the dentary apparently took place relatively slowly, because there is clear evidence that teeth were not added at the end of the lingual row at the same rate as at the ends of the more posterior rows. This evidence is best illustrated by reference to the palate (see Fig. 9). The smallest palate has an acute anterior terminus and a broadly convex lateral margin. Progressively larger palates have anterior angles increasing to almost a right angle, and their lateral margins are straight as far back as the end of the third or fourth tooth ridge at which point the width is abruptly constricted. Given that the most anterior tooth remains the largest, this change in palatal proportions can result only from the addition of marginal teeth progressively more frequently at the ends of the second, third and fourth rows.

Denticles

Denticles are found on two distinct areas: across the buccal surfaces of the pterygoids and prearticulars – superficial denticles; and along the steep labial margins of the teeth in both jaws – marginal denticles.

Superficial denticles.   The denticles of this group vary greatly in shape from simple cones to complex multi-ridged forms with many separate points on the ridges (Smith, 1977: figs 58, 64). These are quite comparable in shape with those of *Griphognathus whitei* (Smith, 1977: figs 44–49; Campbell & Barwick, 1983: figs 18–19). Specimen P52569 is unusual in that on the posterolateral part of the palate many denticles are more or less equidimensional in outline at their bases, but rise to a single, sharp crescentic edge (Fig. 4B). A similar pattern occurs on the prearticular just in front of the glenoid fossa on P52569 (Fig. 5D). On all specimens old and new denticles occur on the same surfaces. This implies that replacement of denticles took place irregularly throughout the growing process, and was not restricted to separate phases. This process of replacements is of the same type as that observed in *G. whitei*. A denticle grew till it reached the wear surface and its enamel cap was gradually removed by wear. After a short period the denticle was shed, leaving an exposed concave resorption surface within which a new denticle appeared. These details have been reported and photographed previously (Smith, 1977: figs 58, 64, 65).

Such denticles grew only on new bone, details of which are given below. They appear a short distance behind a resorption edge as is well shown on the mandible of P52569 where new bone may be observed in a narrow strip in such a position. This resorption edge lies in a superficial layer of white dentine that incorporated a previous generation of denticles (Fig. 5D). From these observations it can be seen that denticles provided the first cover on all those parts of the buccal surface from which old tissues had been removed. New denticles also formed on the prearticulars in the median symphysis where new bone was added during growth. This is well shown on P50197 and CPC25738.

Marginal denticles.   These denticles are present on the labial sides of the teeth only if the specimen was not in the process of adding new teeth. Presumably once a new tooth was fully formed and the supporting bone had grown laterally beyond its outer margins, new denticles appeared in the region temporarily out of occlusion. Their crests were subsequently worn because they must have acted to protect this new bone from wear by the action of the newly formed teeth of the opposing jaw (Figs 2B; 7; 8).

Though these denticles show some irregular shapes, a high proportion of them are more regular in form, being approximately oval or triangular in plan. They also have several other distinctive features that provide clues to the mode of growth of the whole dental apparatus of the genus. Specimens P52565, P52569 and CPC25341 are of particular significance. The right side of P52569, a palate, has a large number of newly formed denticles around the margin (Fig. 2B). They are most abundant in the spaces between the ends of the teeth, which is what would be expected if they served the protective function mentioned

Fig. 3. (Scale bars = 10 mm). **A,B:** Dorsolateral and dorsal views of a mandible, CPC25738. **C:** Ventral view of the palate of the same specimen. The missing tooth from the anterior ridge is the one that has been sectioned and scanned. **D:** Dorsal view of the palate superimposed on the mandible in its natural position to show the occlusal relationships. Note the teeth on the right of the mandible more newly formed, biting outside those of the palate and not surrounded by marginal denticles.
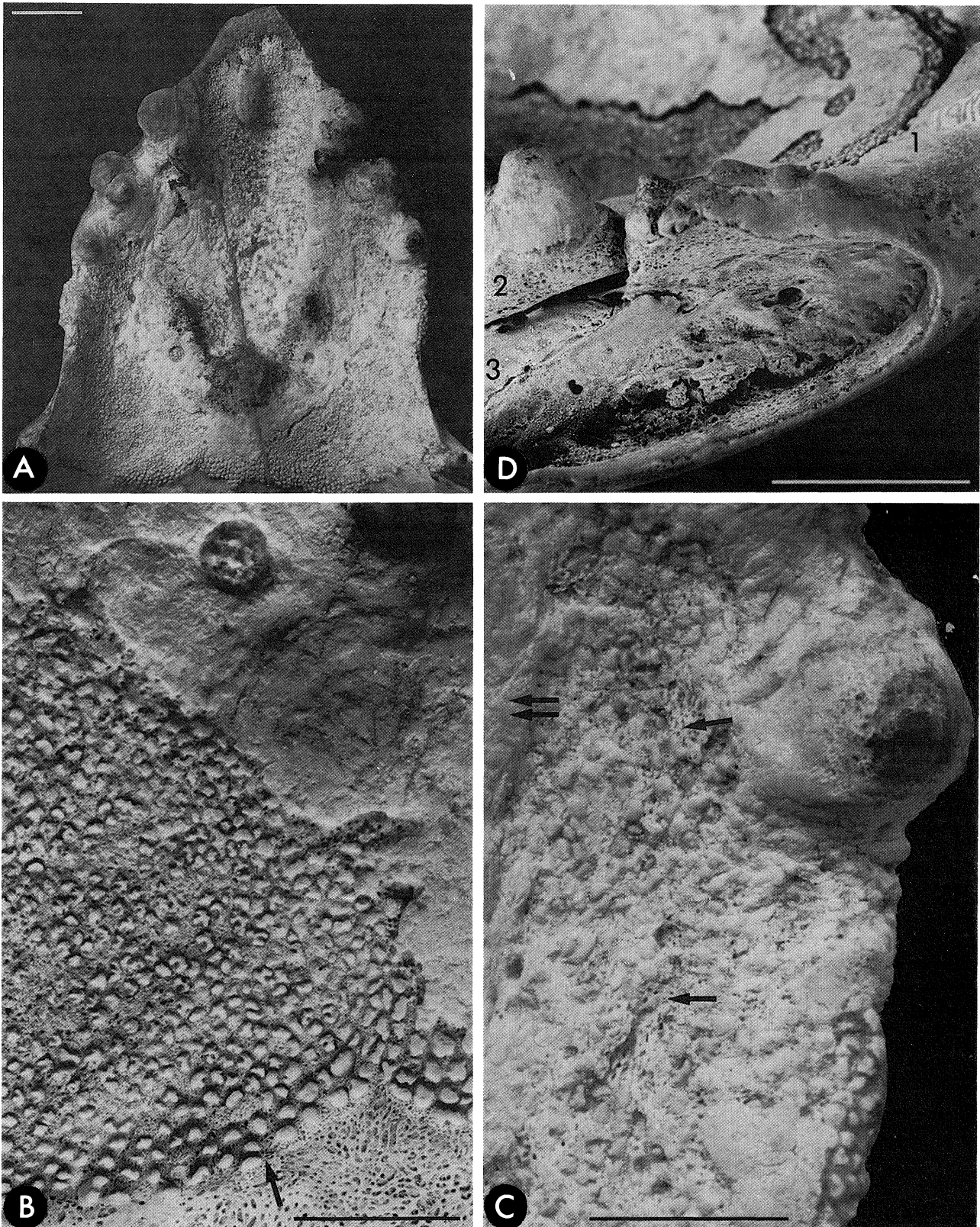
Fig. 4.   **A:** (Scale bar = 10 mm) Ventral view of a palate not whitened with NH 4 Cl. The dark colour of the hard compact dentine of the callus and the teeth shows up clearly. The superficial dentine was in an expanding phase. **B,C:** (Scale bars = 5 mm). **B:** Right posterior part of palate. Note the fine new bone (arrow) over the coarse old bone of the parasphenoid and the adjacent pterygoid; the circular patch of denticles that was being encroached upon by the superficial dentine layer; and the variety of shapes adopted by the denticles. **C:** The surface adjacent to the most lateral tooth on the left side of the palate. Note the central core of dark compact dentine, the less mineralised layer around it, and the superficial dentine layer. Medial and posterior to the tooth is a strip on which the basal bone is exposed in places (single arrow). On it there are numerous denticles between which new superficial dentine was growing. A complete sheet of this dentine has overgrown the denticles in one area (double arrow). **D:** (scale = 5 mm) Dorsolateral view of the labial pit and surrounding areas of the mandible, CPC25738. Note the lateral growth on the dentary, the relationships of the dentary (1), prearticular (2) and angular (3) bones around the cartilage bone forming the floor of the labial pit, and the longitudinally grooved base on the anterior prearticular tooth. A-C: P56045
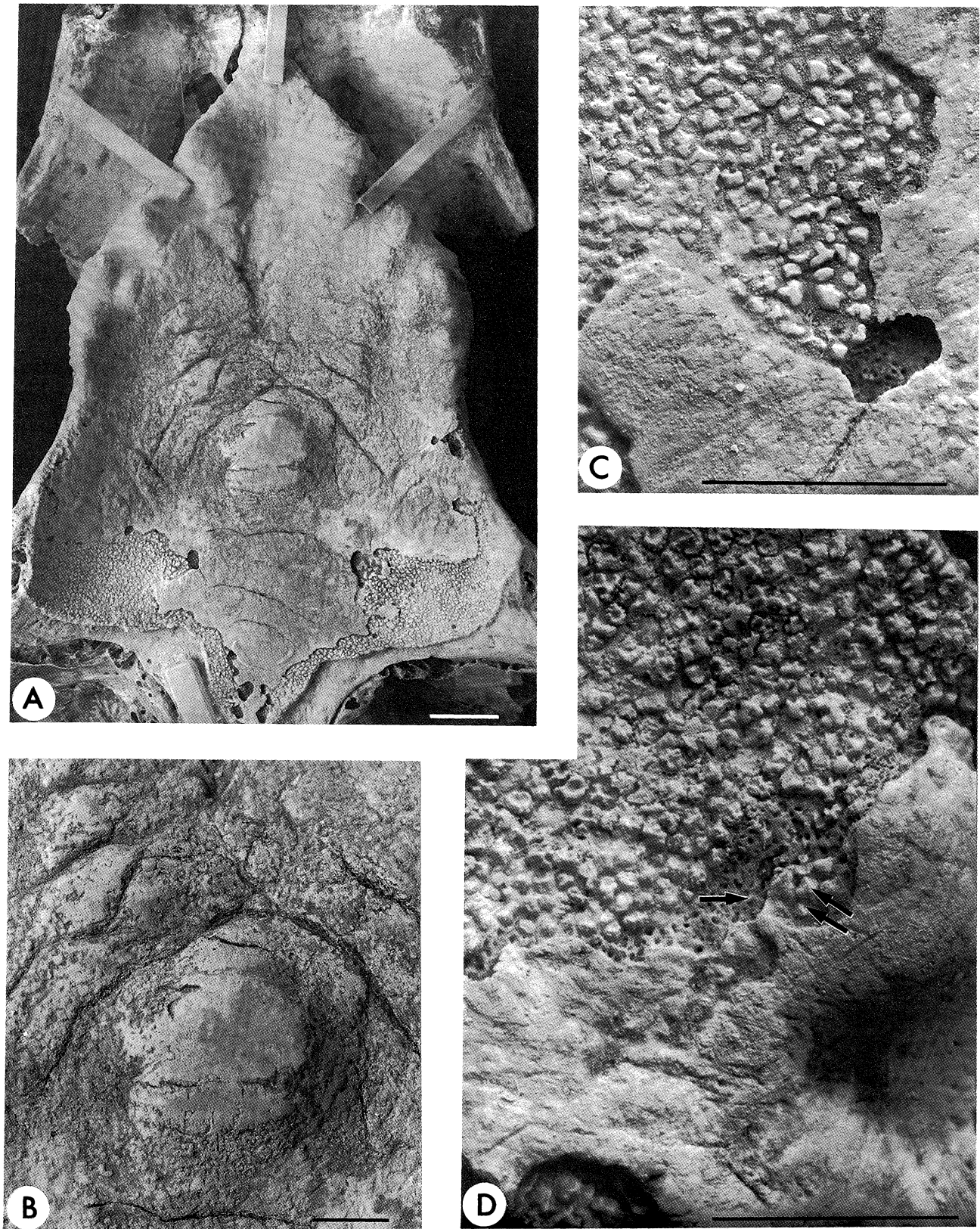
Fig. 5. (Scale bar of A = 10 mm; B–D, = 5 mm). **A:** Ventral view of a large palate, P50999; the individual died at the beginning of the resorption phase. Note the sub-concentric subdivisions of the old superficial layer producing pseudo-tooth ridges. In **B** these and the posterior median callosity show a polished surface. **C:** Right posterior part of palate of Figure A, slightly rotated clockwise, and showing denticles and a new deep resorption pit that has removed some denticles and part of the superficial layer. **D:** right posterior part of a mandible, P52569, showing a variety of denticle shapes, and a resorption edge behind which a strip of bone (arrow) is exposed, and in front of which the continuous sheet of old superficial dentine and a previously formed patch of denticles (double arrow) were in the process of being resorbed during a previous resorption phase.

above. Individual denticles are elongate in outline but those along the outer margins show radial struts around the bases of their labial faces where they can be seen attached to the basal bone. The occlusal and lingual edges of these denticles are all invested with the superficial layer of white dentine. Denticles still closer to the biting edge of the palate are completely surrounded by new bone and have become incorporated into the palate (Fig. 7C). The tops of the denticles are almost all worn, indicating that they became functional shortly after they appeared. There is no evidence of shedding, at least in the region of the major teeth.

The right side of specimen P52565, a mandible, shows a different stage in the development of these denticles (Fig. 7). Most of them are ovate in outline and are worn on top. Even those in the most labial position do not have exposed bases, but are partly encompassed by new trabecular bone (Fig. 7C). This bone has grown over the enamel coating of the denticles. Some of those in a more occlusal position are almost completely covered by new bone. Denticles at the labial margin in the furrows between the teeth are engulfed by the white superficial dentine. A similar pattern is shown on the right ramus of CPC25341.

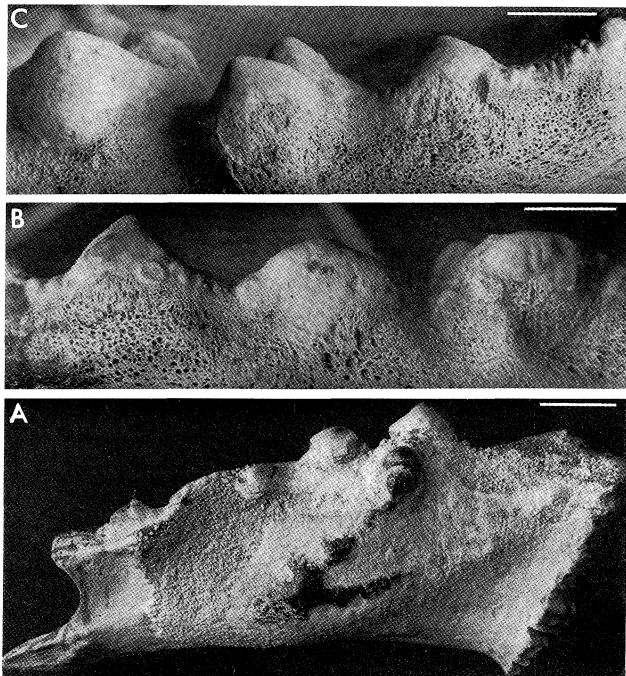We conclude from study of these specimens that

new denticles were added to the labial faces of the pterygoids and prearticulars after new teeth had been added and new bone had grown out to the level of the labial margins of these teeth. Denticles developed in the same way as the superficial denticles of the palatal surface, but as they reached full size new bone began to grow over them and they became completely incorporated within the pterygoid or the prearticulars. Though none of them was shed, they rapidly lost their identity once they were incorporated in the newly formed bone (Fig. 24A). New denticles were added while the bone grew slowly outwards until the phase was reached when new teeth were to be added. As is shown in Figure 7B,C, bone was then laid down relatively rapidly while denticle formation was in abeyance.

Basal Bone

The palate of this genus is unusually thin for a form that has so large a head. Its greatest thickness is lateral in position (Fig. 19C,E) where there is need to support the lateral teeth. No lateral palatal 'process' is present in that region but a long palatal ridge is developed in its place. In front of the parasphenoid the median part of the palate is thin.

Polished surfaces show that the palatal thickening took place by addition to its dorsal surface where increments are represented by sharply defined growth layers. Beneath these layers, particularly beneath the lateral palatal ridge, the bone has been resorbed and remodelled to allow the passage of vessels and nerves in the manner described and illustrated by Miles (1977: fig. 71). This bone is formed of large trabeculae that produce a very open texture. It is not represented medially. Beneath the teeth the bone has a more compact structure than that elsewhere on the palate. Towards the mid-line this tissue thins out except where a median callosity is present. The extensive resorption of bone that has taken place, as well as the resorption of the superficial dentine, is well illustrated in Figure 19D,F. The growth layers that form the dorsal part of the lateral palate were progressively resorbed towards the mid-line, and bone is exposed on the palatal surface except where the truncated ends of the bone trabeculae are covered with a new thin growth of superficial dentine or denticles.

Very finely trabeculated new spongiosa was formed on the old resorption surfaces prior to denticle formation (Fig. 4B). This is comparable with bone of attachment frequently formed with teeth or denticles.

Fig. 6. A: (Scale = 10 mm) Left prearticular, P56045, with median symphysis on right, without NH₄Cl coating. Note dark coloured compact hard dentine, especially the ridge in the lingual furrow where no teeth were developed, and absence of denticles in the floor of the lingual furrow. B,C: (Scales = 5 mm) Lateral views of the prearticular teeth of same specimen. Both show a stage where new teeth have been added completing a new phase of addition but without new marginal denticles.

Superficial Dentine Layer

This material covers a great deal of the surface at various stages of growth. It expands centrifugally. On several specimens (P56045, P52561) it is observed to have formed in advance of its continuous margins by

the development of narrow, isolated patches on the bone between denticles (Fig. 4C). These patches then coalesced and thickened, gradually burying denticles. Elsewhere, tissue of the same kind is found covering the enamel around the bases of the teeth on the lingual side. In addition, on several specimens it grew over the edge of the pterygoid, around the base of the marginal teeth, enveloping the denticles on the labial face of the bone. Its forming surface was not completely smooth; subsequent wear has abraded both this dentine and the associated denticles down to the level where the internal structure of the denticles can be clearly seen (Fig. 7B,C).

The tissue was temporary; some specimens show destructional and others show constructional edges. At resorption (destructional) edges the dentine sheet is often deeply undercut to expose a strip of fine-textured bone (Fig. 5D). At most locations a new generation of denticles lying well below the level of the functional surface borders the edge of this strip.

Only in the lingual furrow of P56045 is there a considerable area of exposed bone and only a few scattered denticles left by resorption of the overlying tissue sheet (Fig. 6A). This indicates a complete removal of the superficial dentine layer.

The superficial dentine developed as a covering layer on this fine-textured bone between the denticles. It consisted of thin spurs of dentine which gradually united with adjacent spurs, as can be well seen on P56045. These produced a more open texture than the underlying bone. With increasing age the spaces were gradually infilled by concentric layers of similar tissue until a continuous non-porous sheet was developed.

This dentine layer completely covered old denticles and encroached over the bases of the teeth and callosities. A fine example of this is the undercut tooth on the holotype palate, which has the gap beneath the tooth lined with smooth white dentine, indicating that before resorption was complete a new
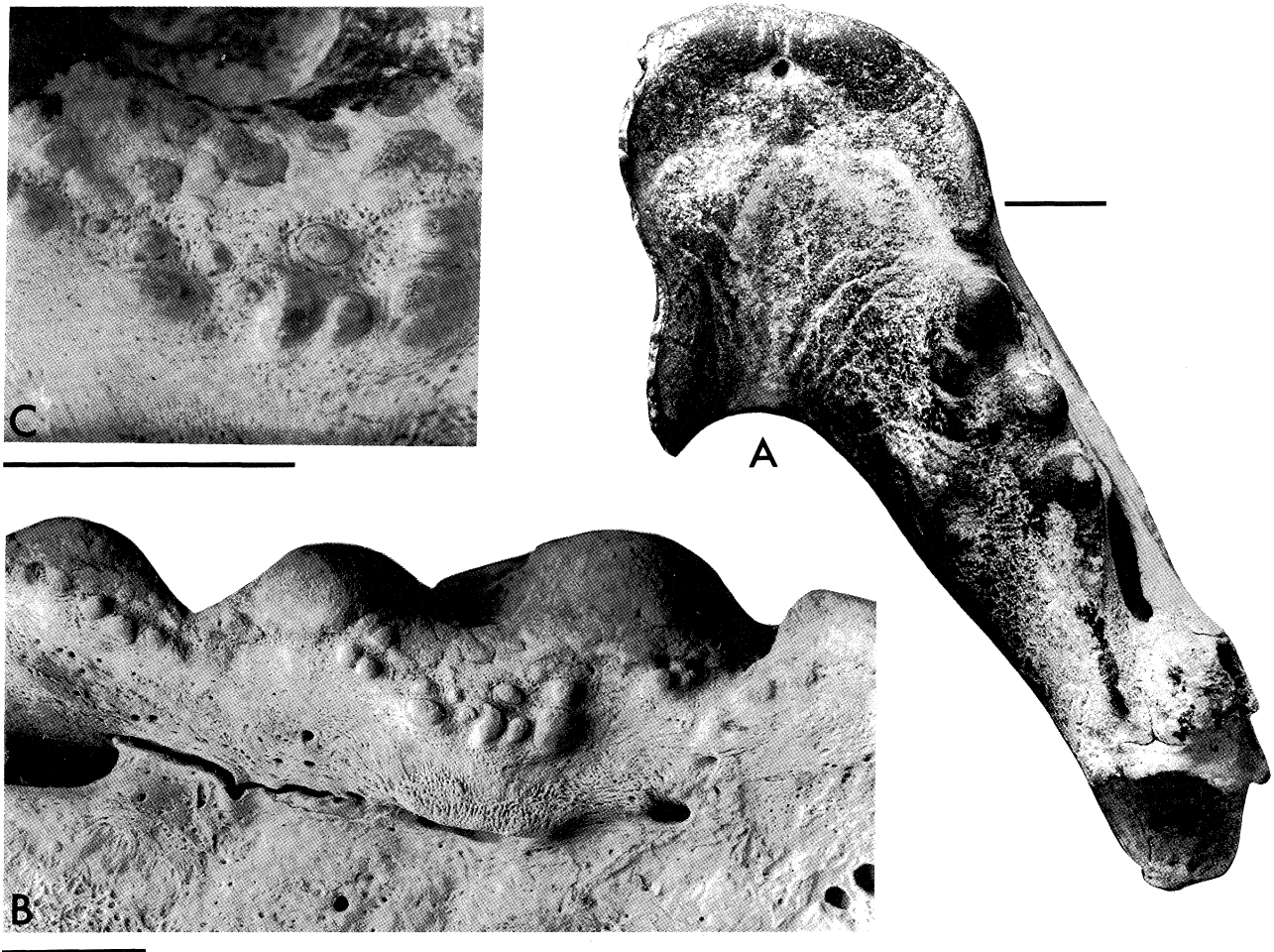
Fig. 7. **A:** (Scale = 10 mm) A larger mandible, P52565, at a stage of maximum development of the superficial dentine layer, with the sutures between the prearticulars, adsymphysial plate and dentary completely overgrown, and the simple dentine of the superficial layer almost completely invaded by dark pleromic dentine. Specimen without NH₄Cl coating. **B,C:** (Scales = 5 mm) Lateral views of same specimen showing marginal denticles fully grown, with worn tops, and partly overgrown by new bone. C, in particular, shows the ends of the dentine canals (dark coloured spots), the layer of enamel around the denticles (dark coloured rims) and the bone growing around the base of the denticles and in places almost covering them.

constructional phase began, and the superficial dentine braced the tooth sufficiently strongly for it to remain in position. The animal died during a subsequent resorption phase which had not advanced far enough to allow the tooth to fall free (Fig. 2A,B).

Behind the developing front, thin, steeply inclined columns of brownish pleromic dentine formed within the white layer. These columns of dentine have resulted from the pleromic infill of spaces that were not completely occupied during the formation of the white dentine sheet, or spaces that were resorbed subsequently. This process of pleromic infill must have preceeded apace, and a stage was reached when almost all the white dentine was replaced. At that stage, only small patches of bone appeared on the buccal surface surrounded by the mass of dark-coloured dentine. A fine example showing the complete sequence from unaltered bone to solid dentine is to be found on the posterior part of the right ramus of the mandible P52565. This is an example of the provision of a framework essential for pleromic dentine to develop as a consolidating tissue. If the only dentine in this region was that of the primary denticles, then it is most likely that pleromic growth of dentine developed from them. This type of extention of dentine has been illustrated previously (Smith, 1977: figs 14, 62, 63). Entire worn surfaces of pleromic dentine and bone feature strongly in the dentition of *Holodipterus* (Smith, 1977: fig. 60).

At the stage of complete dentine cover, the surfaces of the pterygoids and the prearticulars are irregularly pitted and coarsely rugose. The pitting results from wear of the softer white dentine patches, and the linear depressions marking the rugosities result from wear of elongate, irregular strips of white dentine. These are thought to have marked the margins of previous resorption phases prior to the addition of new superficial dentine layers. On specimen P50999 these strips cut obliquely across the median part of the palate, producing a pattern of irregular and graded subdivisions of the callosities which mimic a row of old tooth bases, though the resulting ridges are set at an angle to the three tooth-bearing ridges (Fig. 5A).

At its most extensive phase of development, the pleromic dentine on the mandible covers most of the prearticulars, the whole adsymphysial plate and the dorsal surface of the dentary (Fig. 7A). Over this entire region, the surface has the same irregularly pitted pattern, and shows a number of rugae that extend from deep in the lingual furrow across to the medial aspect of the tooth rows.

This dentine provided a hard-wearing surface which took on a high polish in some regions. It has every appearance of permanence, but it, too, was subject to extensive resorption and replacement. However, resorption was rarely if ever complete, as is apparent on the specimen illustrated in Figure 1. This individual shows extensive resorption, but the palatal callosity shows at least three stepped edges marking

successive resorption phases. This observation leads to a discussion, in the following section, of the remaining features of the dentition – the dentine masses on the median region of the palate and the heels of the prearticulars.

Dentine Callosities

Dense masses of dark-coloured dentine, with irregular surfaces and outlines, occur on the median part of the palate and on the heel of each prearticular. They do not have enamel on their surfaces.

The larger palatal callosity is posteromedial and is present on all five specimens available to us. It is approximately equidimensional in some specimens, but has linear anterolateral extensions on others. Its margins are never sharply demarcated as formed surfaces, but show extensive resorbed embayments. Some specimens (P56045, CPC25739 and CPC25740) have a second callosity on the anteromedial part of the palate, but such a feature is lacking on others. It is approximately oval in outline but its margins also usually show signs of resorption. Presumably resorption was complete on some individuals.

The posteromedial callosities also show extensions of various lengths directed towards, but usually not precisely in line with, the first and second marginal teeth, giving the impression that long, radial tooth rows are present. If this were true, the radial ridges would represent extensively worn replacement growth of dentine beneath each tooth; however, the difference in tissue arrangement between this region and the most lingual tooth in each row makes this interpretation improbable. Also, in extensively resorbed individuals (Figs 1A,B; 2A,B), these ridges are shorter and denticles cover the surface of the palate between them and the adjacent teeth, so that they can be seen to be relicts of the formerly continuous dentine sheet, and not worn down enamel-covered teeth.

The problem of the growth of the callosities may be resolved as follows. Those specimens in which the surface layer of dentine has been most completely replaced by pleromic ingrowth have dense dark dentine all around the callosities. Those with a minimum of superficial and pleromic dentine on the palate overall have callosities surrounded first by a narrow, incomplete zone of partly replaced bone, and then a sheet of denticles. Presumably during the phase of maximum resorption, part of the pleromic dentine sheet adjacent to the callosity was not removed. During the next expansive phase the dentine in this zone was able to grow pleromically into the underlying bone. It would then have been even more difficult to remove during the next resorption phase, being either too thick to resorb and/or being raised above the resorptive tissue. Because resorption does not leave regular margins, the outlines of the callosities would be irregular, and

different between specimens or even on the two sides of the one specimen. Specimen P50999 illustrates this sequence very well (Fig. 5A,B). Successive resorption edges are clearly defined around both anterior and posterior edges of the posterior median callosity. In this way, starting from a small patch of unresorbed pleromic dentine around a number of denticles, each callosity increased in area and thickness.

Another factor to be considered is that the cells responsible for resorption would have been least effective in areas of maximum wear stress, and the dentine would have remained unresorbed in these areas. The median callosities which worked against food manipulated by the basihyal/basibranchial tooth plates, and the sub-radial ridges that directed food inwards from the marginal teeth, would have been areas of wear stress. This matter is discussed in more detail in the subsequent section on occlusion and wear.

Growth of Pterygoids

As is normal for members of the denticulate group, denticles cover the main part of the parasphenoid as well as the pterygoids, and the sutures between these bones are completely obscured. However, palates that can be viewed dorsally show the outlines of the parasphenoid very clearly; the posteromedian callosity lies across its anterior junction with the pterygoids. Because this callosity is present in all specimens available to us, including even the smallest ones, and because it never shows resorption in the mid-line, the pterygoids and parasphenoid have been able to grow areally only by addition to their free lateral and posterior margins (see Fig. 3C,D). This
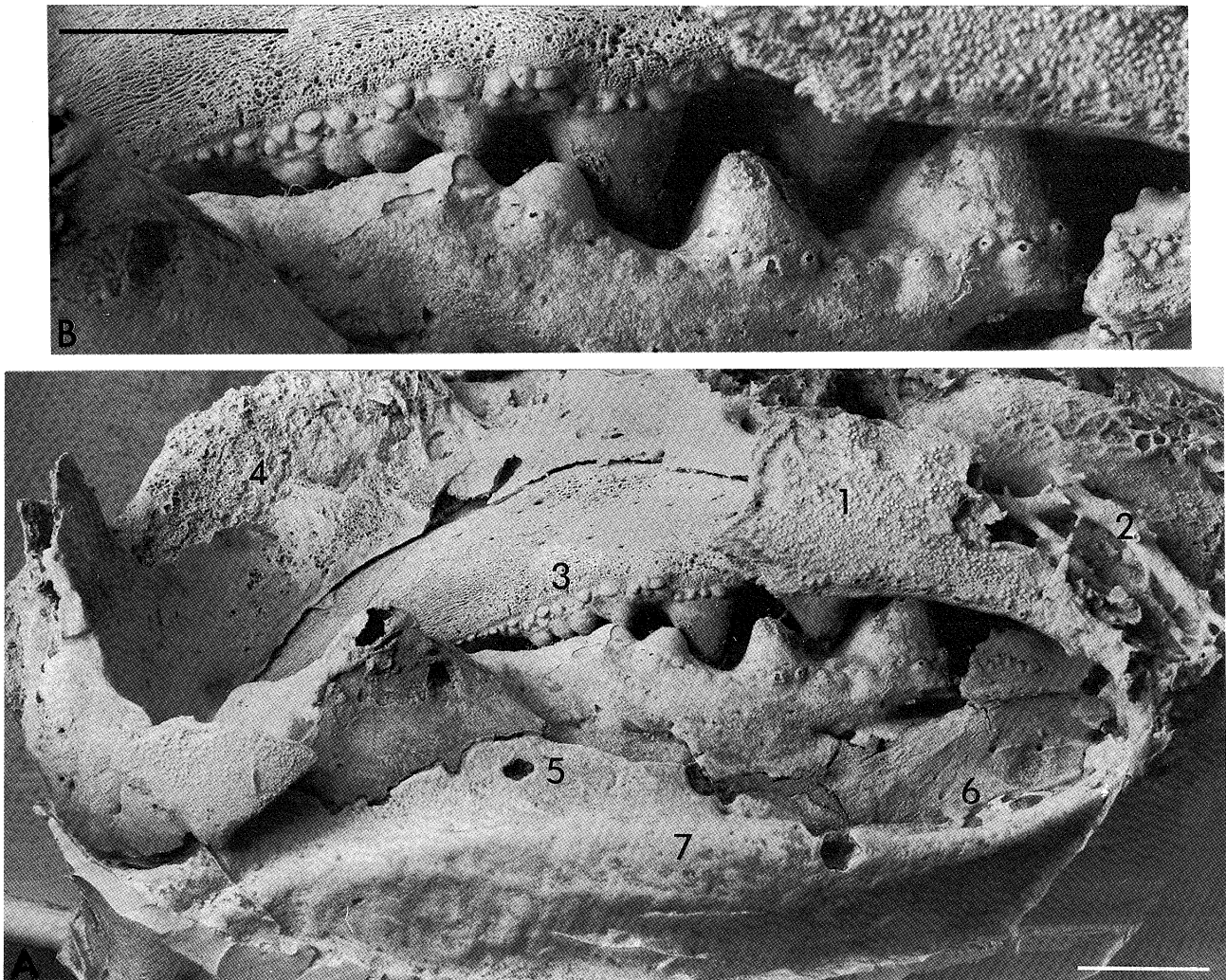
Fig. 8.   (Scale = 5 mm) Lateral view of an eroded skull and mandible, P52568. The mandible had been largely lost by solution prior to collection, and the vacated bone space has been filled with PVC prior to laboratory etching. The marginal denticles on the prearticular have bubbles where the PVC did not completely fill the mould. **1,** cheek bones forming a deep arch; **2,** tubuli of the snout; **3,** pterygoid; **4,** side of braincase; **5,** upper edge of surangular; **6,** deep labial pit; **7,** upper edge of originally cosmine-covered part of external dermal bones.

point is well demonstrated also by the transverse palatal sections illustrated in Figure 19. We cannot demonstrate this for other denticulate genera but nevertheless it probably was the situation in all of them. However, we note that *Dipnorhynchus* and *Speonesydrion*, with their dentine-covered palates and posteromedian callosities, could not have added to their pterygoids in the mid-line, (see Campbell & Barwick, 1985). We believe that this was a character shared by all primitive dipnoans. It was soon lost in the lineage that developed crushing plates – e.g. *Dipterus, Scaumenacia* and *Chirodipterus* – in which the median suture opened and became a site of growth.

OCCLUSION, WEAR AND REMODELLING

Specimens P52568 (Fig. 8) and CPC25738 (Fig. 3D) show the occlusal relationships very clearly. As indicated previously, on P52568 the marginal teeth of the lower jaw lie outside the line of those of the upper jaw. Consequently, the second tooth on each row in the lower jaw occludes with the outer row in the upper jaw. The surface of the mandible drops away steeply on the lingual side of the second teeth and the palate is highly arched inside the second tooth in each row. Consequently, occlusion is restricted to the marginal rim of the palate.

These observations explain the presence of a
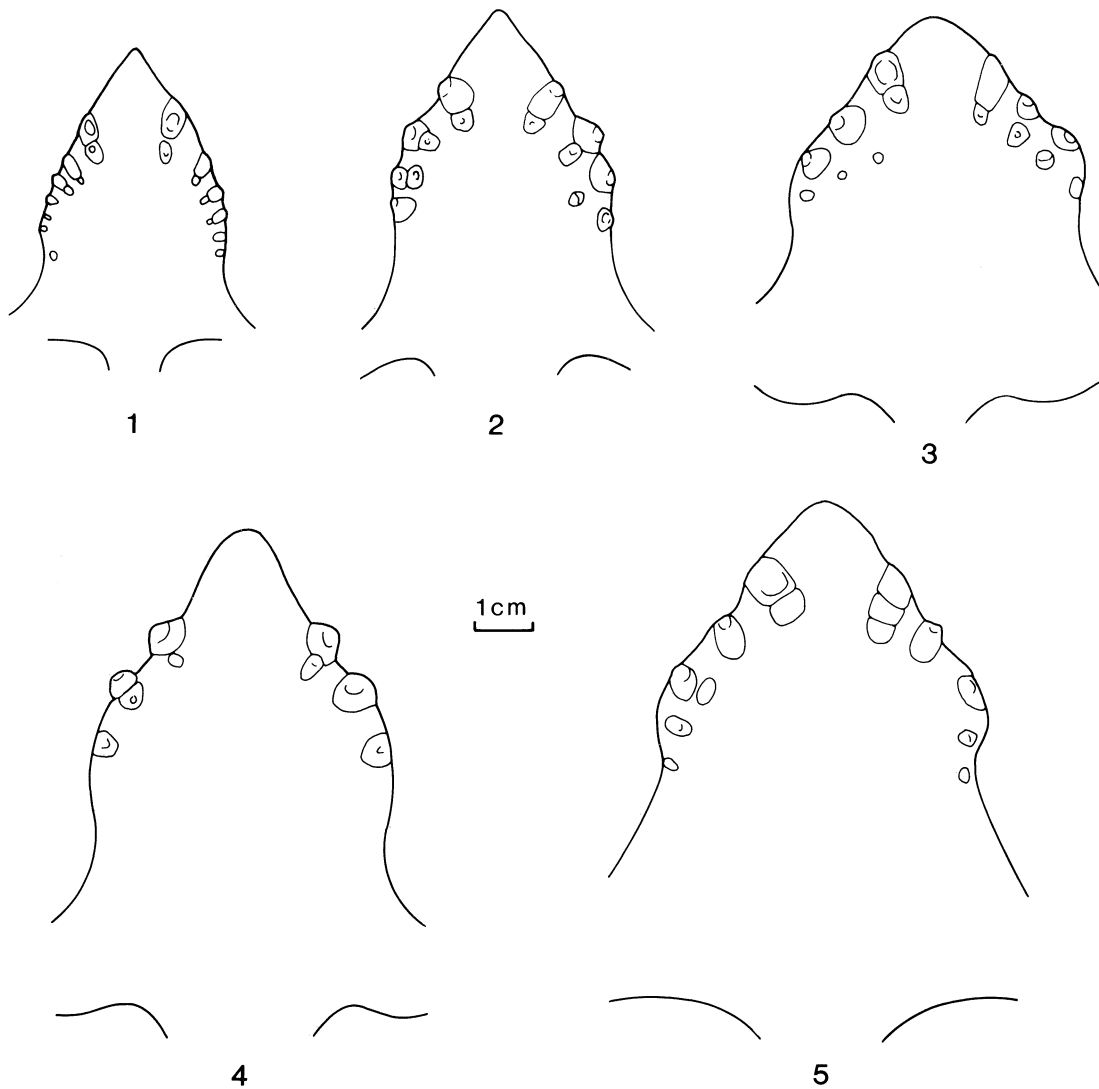
Fig. 9. Palate outlines of five specimens drawn at natural size showing the variation of palatal outline with the addition of new teeth at the ends of the rows. The large lateral lobes are produced by the addition of teeth at the ends of rows 2, 3 or 4 without corresponding additions to row 1. The anterior angle of the palate is clearly controlled by the addition of new teeth to row 1 and the rate of forward growth of the anterior ends of the pterygoids. 1 = CPC25740; 2 = CPC25738; 3 = P52569; 4 = P56045; 5 = P50999.

maximum of two teeth in the second and third rows on the palate. For occlusion to occur while the arch of the palate was maintained, the second tooth in each row of the lower jaw had to occlude while the outside (labial) one was being added; the inside (medial) one was out of occlusion and therefore it was shed. Those specimens that have only one tooth in the row died in a transition stage when an inner tooth had been lost just after the outer one had become functional.

Wear on the posteromedian callosity of the palate is always obvious, so much so that it often has a polished appearance. Specimen P50999, which has extensive dentine on the palate, also shows a great deal of polish on the areas adjacent to the callosity (Fig. 5A,B). Specimen P56045, which has most of the superficial dentine resorbed, has the crests of the adjacent denticles, particularly those behind the callosity, worn down to approximately the same level. These phenomena are to be explained as the result of abrasion by food moved by the basihyal/hypobranchial tooth plates against this part of the palate.

A model for control of resorption and regrowth, based on electrophysical theories of balanced bone growth and resorption, could be considered as applicable to the changing morphology of *Holodipterus.* This proposes that cyclic growth is a result of negative feedback in the oral system (Bassett, 1971). The theory relies on the observed phenomena of bone loss on the endosteal surface together with bone deposition on the corresponding periosteal surface, with the result that the bone in that region changes position or shape. Experiments have elucidated several phenomena that can explain this selective differential activity on opposing bone surfaces. One is that application of a cantilever force to a bone will cause a potential difference to occur at the two bone surfaces, a negative one at the concave surface and a positive one at the convex surface. The second is that, in response to extrinsic negative charge, osteoblasts become active and put down bone at an increased rate; in response to positive charge, osteoclasts remove bone at that surface in excess of any later deposition. The explanation of how the charge is generated is generally accepted as a piezzo electric effect in the crystals of the bone tissue; this effect results from the bending of either the hydroxyapatite or the collagen protein crystals. It must be assumed that this can also happen in the bone tissue of *Holodipterus, in vivo,* thus producing different phenotypes as a result of epigenetic control through tensional forces.

CYCLIC DEVELOPMENT

It will be obvious from the above account that the buccal dentition in *H. gogoensis* grew by a series of cycles involving massive resorption and redeposition of tissues. We have no knowledge of how many cycles were involved in a single life history. Judging from the size and spacing of the teeth, and assuming that growth has involved the loss of a tooth in each successive cycle, the number is unlikely to be less than six or more than ten.

Arbitrarily taking the onset of a cycle to begin with the initiation of bone growth to support a new generation of marginal teeth on the mandible, we recognise the following phases.

(i)   New bone was laid down along the mandibular symphysis while remodelling of bone elsewhere took place by resorption and deposition, and lobes of bone began to form on the prearticular margins at the sites where new teeth were to form.

(ii)   New teeth were formed at each of the above sites on both prearticulars at approximately the same time; concurrently, denticles continued to grow and to be replaced over most of the exposed bone of the buccal surface, and the dentine in the callosities grew into the underlying and surrounding bone.

(iii)   On completion of tooth growth, the superficial layer of dentine began to grow outwards to envelop both denticles and tooth bases; denticles continued to be shed and to be replaced in an irregular fashion in advance of the dentine sheet; new marginal denticles appeared on the outer vertical faces of the prearticulars below the level of the teeth.

(iv)   Pleromic dentine gradually replaced much of the superficial bone layer as wear on the teeth and callosities proceeded.

(v)   Resorption began at the margins of the superficial layer but also in patches within the boundaries of the layer; occasionally the base of a tooth was resorbed and it dropped off; behind the advancing resorption fronts new fine-textured bone grew over the stripped surface, and on this bone new denticles began to develop, reach maturity and then shed.

(vi)   This process proceeded in all the regions taken out of the functional biting surface by upward growth of teeth and callosities, until all the dentine except that in one or two marginal teeth in each row, and that in the callosities and their immediate environs, had been removed. The cycle was then completed.

A similar cycle would have operated on the palate, but because teeth were added alternately in the upper and lower jaws there must have been a 180° phase difference. As tooth growth was completed and the superficial dentine layer began to expand in the mandible, resorption would have been nearing completion, and new bone growth for the initiation of new teeth on the pterygoids would have been about to begin.

This may seem to be an improbable scenario, but it is susceptible to testing because, as we have shown, specimens P52568 and CPC25738, have the opposing jaws in position. In P52568 the mandible had reached the stage where the marginal teeth had been added and new denticles had begun to appear on the outer face of the prearticulars, though the

addition of bone and denticles of the development stage had not been completed (Fig. 8). It was probably in the late stage (iii) of the above sequence when it died. The denticles on the lateral face of the pterygoid, on the other hand, are somewhat worn and in several places their bases were being overgrown by new bone. In the vicinity of the tooth bases they had been partly engulfed by superficial white dentine. In one place there is a small outgrowth of new bone capped by a new enamel-coated denticle. The pterygoids must have been just entering a new phase of lateral growth prior to the initiation of a new series of marginal teeth. The surface of the palate has a continuous sheet of denticles across the part posterior to the median callosity. In front of that the superficial sheet of white dentine was extensive, extending around the bases of the remaining teeth. A couple of small circular patches and a rather larger anteromedian patch of denticles occupy areas from which the dentine sheet had been recently resorbed. The posterior edge of the main sheet also shows resorption. In this respect too, the palate shows the initiation of a new growth phase. Both lateral and ventral palatal surfaces suggest that it had begun stage (v). The specimen therefore clearly corroborates the hypothesis.

Specimen CPC25738 (Fig. 3D) has the palate and mandible precisely articulated, and the most lateral teeth on the prearticulars lie outside the line of the most lateral teeth on the pterygoids. The prearticular teeth had obviously just been added because they overhang the underlying bone and are almost unworn. No marginal denticles are present. The marginal teeth on the pterygoids are supported by their underlying bone, and show a few marginal denticles some of which are worn. A new row of pterygoidal teeth was about to be added when the animal died.

HISTOLOGY

In view of the many unusual morphological features of the dentition, including the extensive changes produced episodically by massive phases of resorption, it has become essential to reconsider previous interpretations of the histology of the tissues and, where possible, their histogenesis and growth. In particular we regard information on the marginal teeth, the superficial dentine layer, the callosities, and the relative position of the denticles, as crucial to a decision on the relationships of *Holodipterus*. Apart from those at the margins of radiate 'tooth plates' (for example in *Speonesydrion)* isolated large teeth have been described only in *Fleurantia* and *Holodipterus,* both of which were considered to be members of the denticulate group by Denison (1974), Miles (1977) and Campbell & Barwick (1983). *Uronemus* has recently been placed in the group with tooth plates (Smith, Smithson & Campbell, 1986).

The histology of the teeth has always been problematical since originally the only available vertical section of a tooth was affected by preparation artefacts (Fig. 10D; Smith, 1977), and it comes from the posterior end of a prearticular plate where teeth are rather poorly developed. However, three new vertical sections through a marginal tooth of the anterior ridge on a pterygoid have now been prepared from specimen CPC25738. In addition, the adjacent block-face has been prepared for S.E.M. by polishing and etching with 1 normal HCl for 1 minute. As a result, completely new information is available, including the relative hardness of the tissues, and this, together with re-examination of the original section (P52569), has enabled us to modify our previous understanding.

The histology of five structures will be described: the teeth, dentine callosities, superficial dentine layers, and both marginal and superficial denticles.

Marginal Teeth

The original section and the new ones are illustrated in Figures 10–18. They show a worn tooth tip and, in the new sections, a distinctive basal margin on the labial side of the tooth. This is formed of pallial dentine covered with enamel (Figs 10–11). In all sections, larger spaces between the dentine and the bone are present in the centre of the tooth, and this is presumed to be a region where continued growth of the central dentine could occur (Fig. 10A–D). The tissue at the centre of the tooth tip is very compact and relatively homogeneous, the pulp canals being much narrower than those at the base (Figs 10A–C; 15A). This tissue beneath the worn tip shows little distinction between regions of interstitial and circumpulpal dentine. More basally the two tissues can be readily distinguished, particularly at the margins (Figs 11A, 12A) and where the tissue joins the bone. These three regions, and the arrangement of the pulp canals are shown in Figure 13. All of the compact dentine (but not the interstitial or pallial dentine) has a cross-hatched appearance in polarised light (Fig. 10B) similar to that of petrodentine (Smith, 1984: fig. 28); in particular it is similar to the petrodentine of *Chirodipterus* (Smith & Campbell, 1987: fig. 35). However, there appear to be differences between the two genera in several details. In *Holodipterus* only short channels for cell processes (Fig. 12B) can be seen at the formative surfaces which are continuous over fairly wide areas within the extensive system of pulp canals. Many extremely delicate tubules can be seen throughout this region of developing dentine prior to the formation of any circumpulpal dentine (Fig. 12B). A region with fine branching tubules, most of which are wider immediately adjacent to the pulp canal, is illustrated in Figure 14. The interpretation of this region in Figure 13B shows the wide tubules in the circumpulpal dentine branching into finer ones in the main dentine mass. It is not unusual in extant forms
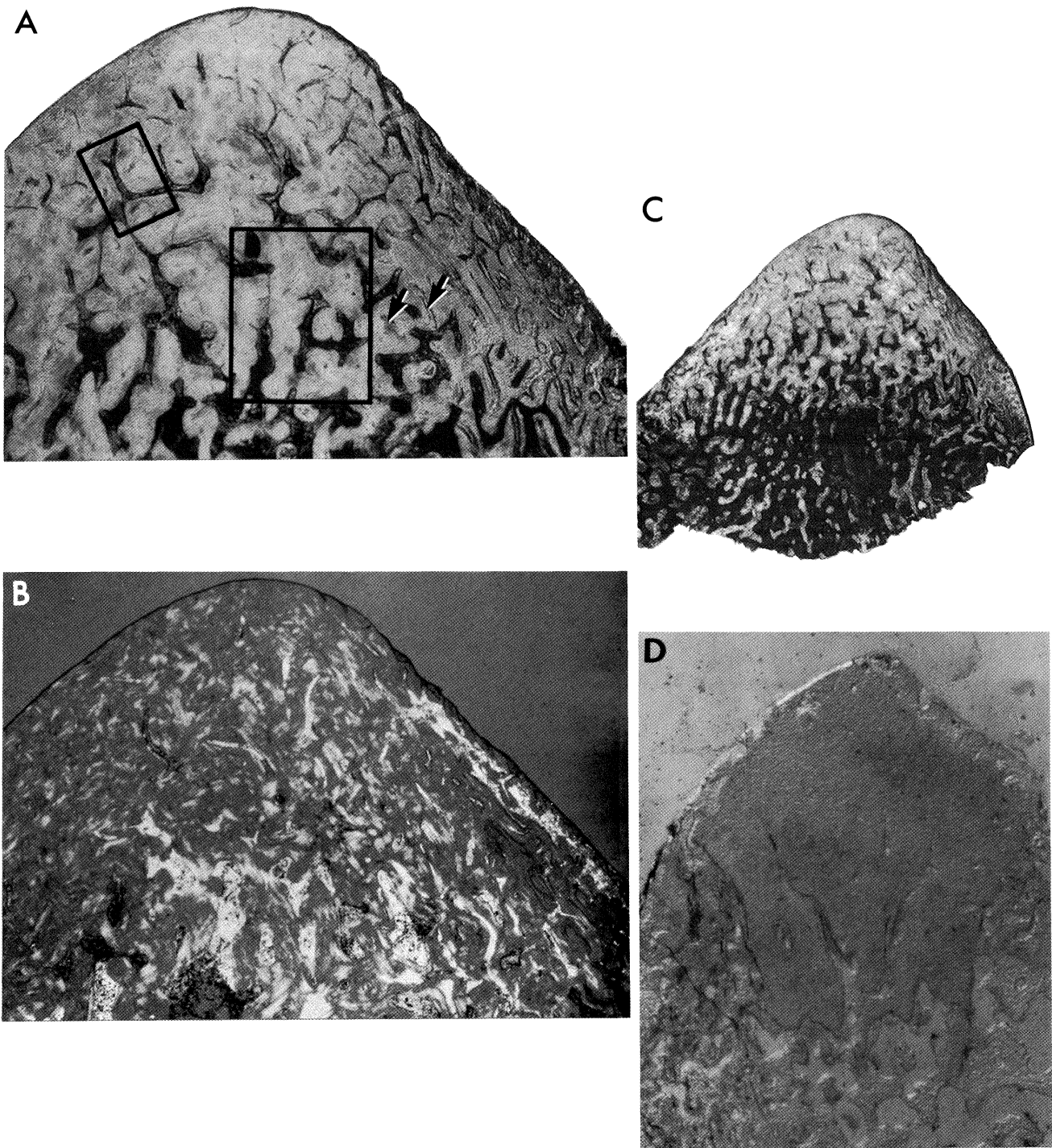
Fig. 10.   A,B: (x 40) The worn tooth tip is compact dentine above trabecular dentine at the base. Enamel covers a thin layer of pallial dentine on the right at the basal labial margin. The dentine at the tip is relatively translucent (A) and contains very narrow, branching pulp canals. These lead into wider canals in the basal dentine which join with the medullary spaces of the bone. Within the basal dentine, in contrast with that of the tip, small patches of interstitial dentine remain (arrows). In polarized light (B) the canals filled with calcite are strongly birefringent, the dentine shows regions of weaker birefringence, with bands of opposite sign in a woven pattern. **C:** (x 16) The whole tooth section; two other sections were cut either side of this and the remaining block face prepared for the S.E.M. **D:** (P52569, as in Smith, 1977: fig. 57) (x 40) shows the poor preservation of tissues in this specimen relative to the new sections, but emphasises the region of compact dentine at the centre.

[The photomicrographs and the S.E.M.'s in Figs 10–18 are from vertical sections cut in a labio-lingual plane through the marginal tooth on the anterior row of the pterygoid (CPC 25738).]

to find some delicate tubules within the petrodentine, but usually these are not extensive and they run only a short distance into the petrodentine. The distinctive features of the tooth of *Holodipterus* are the very irregular arrangement of pulp canals (Fig. 10A) forming a network through the tooth, and numerous fine branching tubules extending from them. The compact dentine seems to have formed initially by adding layers onto the smooth lamellar tissues forming trabeculae (which are assumed to have been dentine), and subsequently directly on to itself. These trabeculae were at first rather porous as they were readily impregnated with dark-stained calcite during diagenesis (Figs 10A; 11A,B). In the tooth tip it is difficult to distinguish these trabeculae. Continuous growth lines are not seen across the tooth as in the tooth plates of *Chirodipterus* (Smith & Campbell, 1987: figs 65, 66).

A parallel surface immediately adjacent to the one from which the histological section was cut, and which shows all the same tissue regions, has been prepared as a polished-etched surface and examined in the S.E.M. (Figs 15–18). The tissue complex of the tooth tip (Figs 15; 16A,B) is very compact hard dentine, the bulk of which has an apparently random arrangement of woven, crystal-fibre bundles with very small spaces of narrow diameter between them (Fig. 15D). These may be the fine tubules seen in thin section in Figure 14. The pulp canals in this region are lined with two distinct layers. The first is formed of tissue similar to that making up the main dentine mass of this region; the second is a more homogeneous and relatively narrower lining to the pulp canal itself (Fig. 15B,C). This double layering is also seen in the optically examined thin sections in which a translucent layer of circumpulpal dentine lines the canal (Fig. 12A), and a thin layer of tissue that is possibly diagenetically altered, lies adjacent to this.

In the tooth tip, the zones of dentine surrounding adjacent pulp canals are juxtaposed leaving isolated irregular interstitial regions (Fig. 13). These regions
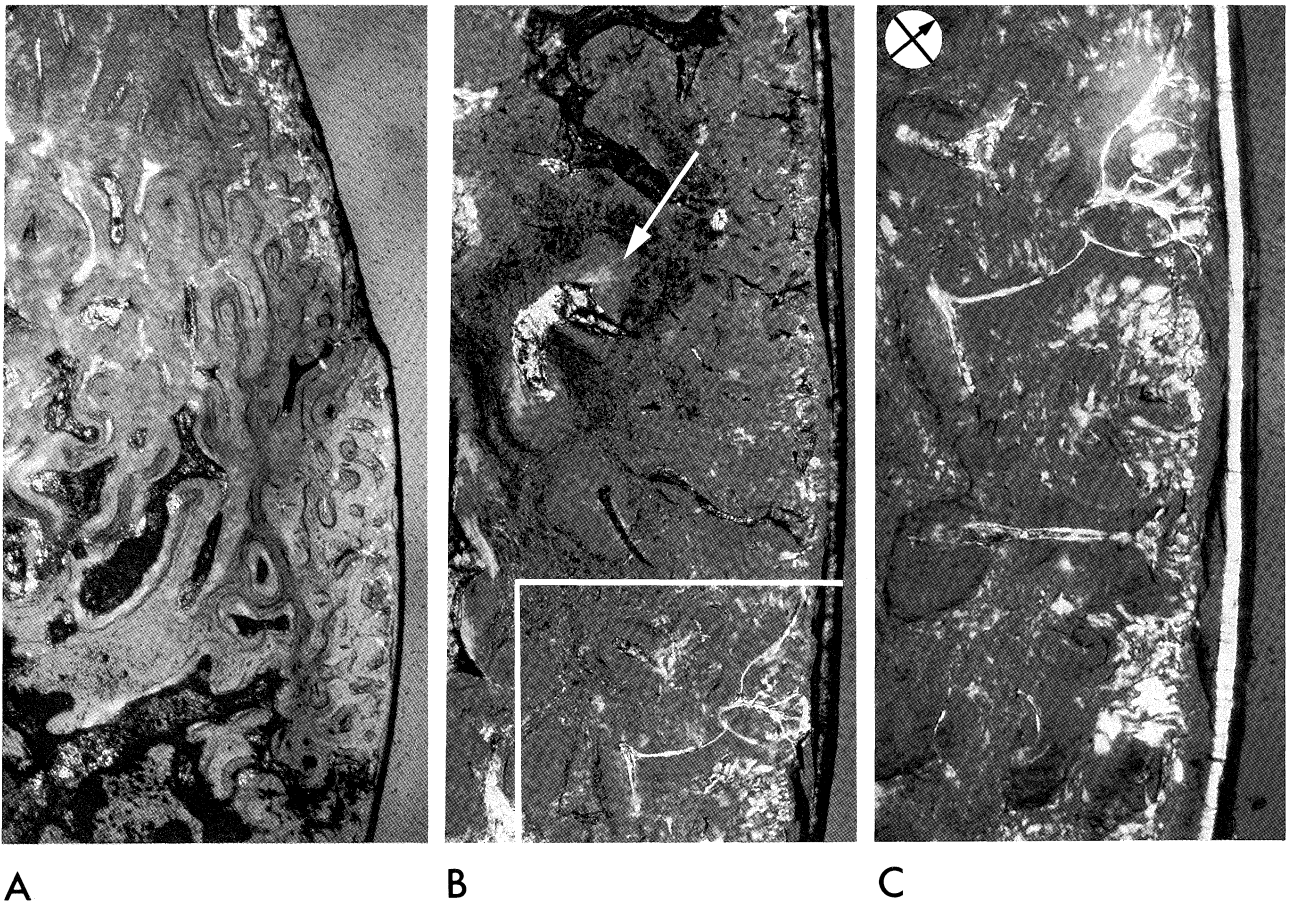

A   **B**   **C**

Fig. 11.   Basal lateral margin of the tooth in Fig. 10C to show the structure of pallial dentine, the basal dentine and the enamel layer. **A:** (x 64) Extensive pulp spaces between the bone and immature basal dentine lead into narrower canals within the compact dentine, mostly lined with dark calcite. Regions of circumpulpal dentine are distinct from the interstitial regions; the latter show a diffuse black stain (arrow, Fig. 10B). **B:** (x 160), **C:** (x 250) A magnified and extended area of the box in B. The pallial dentine contains fine terminal branches of the narrow pulp canals, radial to the tooth surface and ending below the enamel dentine junction. Strong birefringence of the enamel layer in C shown between crossed polars (direction of polarizer and analyser as shown).

are defined in S.E.M.'s by changes in the direction of the crystal fibre bundles (Fig. 16A,B). In contrast, the regions towards the tooth base (Figs 16C,D; 17) have the junctions between adjacent dentine zones marked by progressively wider spaces that are occupied by the smooth homogeneous tissue mentioned above, in which no crystals have been observed (Fig. 17C,D). The wide open canal spaces are clearly seen in this region (Figs 16C,D; 17A–C), and they are interpreted as forming-surfaces of this type of compact, hard dentine with many very small open spaces between the crystal groups. The pulp canals are not, at this stage, lined with further dentine, and the youngest region of this compact dentine is very open, the canals being permeated in many regions by calcite crystals (Fig. 17C). The junction between the forming compact dentine and the dentine trabeculae shows little continuity of structure across the boundary (Fig. 17D). This would be consistent with a different tissue

type forming from this boundary onto an initial framework of less mineralised trabeculae of dentine. These features (viz. the hard dentine deposited on to soft trabeculae) make the type of dentine in the *Holodipterus* tooth different in its mode of growth and arrangement from petrodentine. However, in its hardness and microstructure it is very similar to petrodentine. At the margins of the tooth (Figs 15A; 18A,B) the extensive development of this hard dentine has left limited areas of pallial dentine beneath the enamel layer. Here, also, regions of smooth homogeneous tissue (dentine trabeculae) remain within the harder dentine (Fig. 18B).

In summary, the interpretation of this extensive hard compact dentine is problematic. The best that can be said at present is that it is clearly a form of hypermineralised dentine, but its mode of growth is different from the hypermineralised dentine found in any dental plates. In some respects it is like an
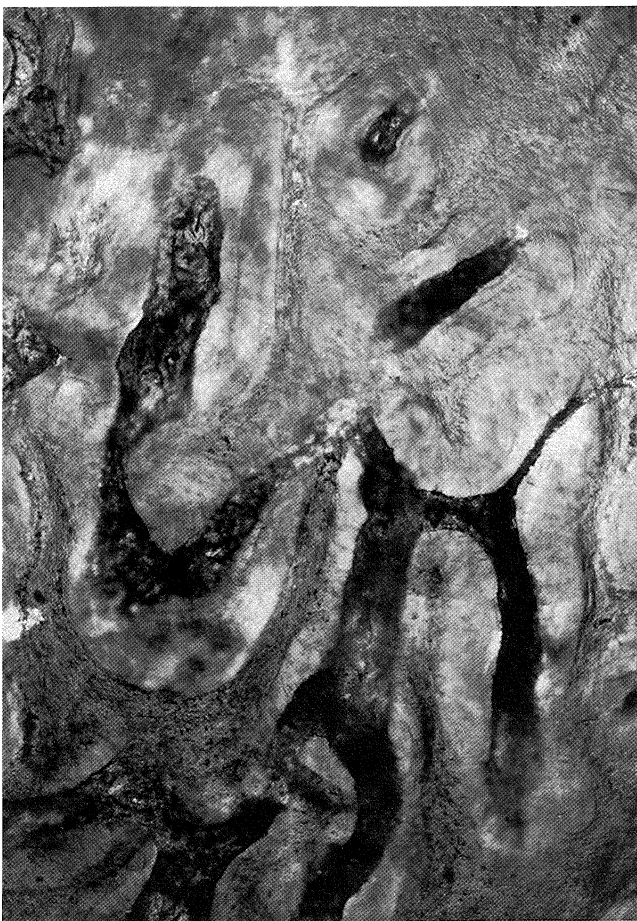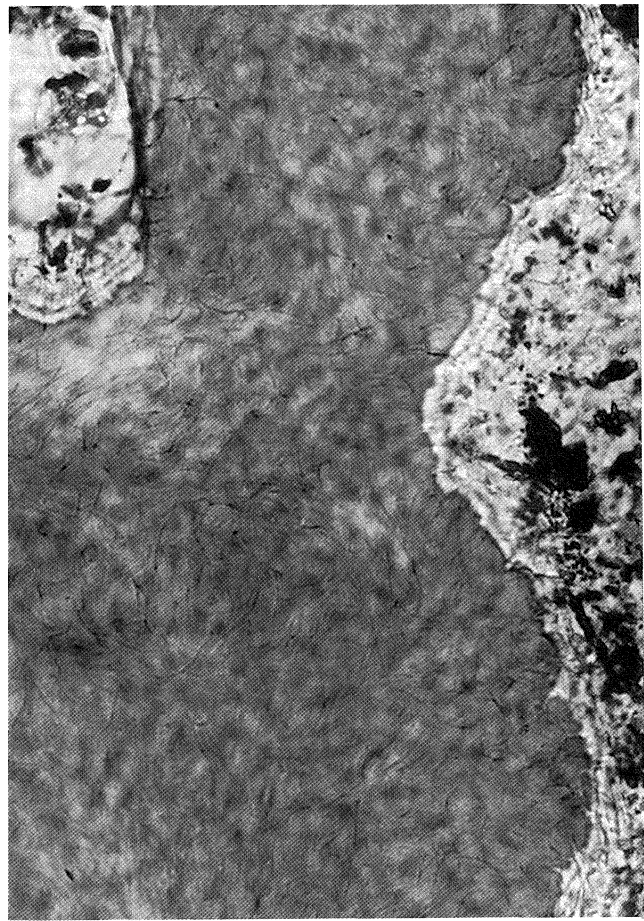
A   **B**

Fig. 12.   A: (x 180) Dentine at the base of the tooth. A clear difference can be seen between interstitial and circumpulpal regions of dentine. The wide pulp canals in the formative zone at the bottom of the illustration have relatively narrow regions of circumpulpal dentine and the interstitial dentine has a diffuse black stain. **B:** (x 450) One region from the centre of the tooth where there are forming surfaces of dentine in which short wide tubules lead into extremely fine tubules branching and coursing throughout the dentine. No zone of circumpulpal dentine exists and the pulp canal is relatively wide.

intermediate between pleromic dentine and petrodentine, the two being used together to make the composite hard tissue. This difference may be related to the fact that in *Holodipterus* the teeth have only limited periods of growth before thay are shed, whereas in normal tooth plates growth is continuous throughout life.

One region at the base of the tooth on the lingual side, suggests that the tissue between adjacent teeth on the radiate ridges forms from growth of the compact hard dentine onto the bone surfaces (Fig. 20). This is a continuation of the hard dentine of the tooth and is similar to the tissues of the callosities, described in the next section.

Dentine Callosities

Vertical sections through the posteromedial callosities, which appear superficially to be made of shiny black dentine, show a translucent, compact tissue closely intermingled with the bone (Fig. 21A–D). The extent of this tissue relative to the

parasphenoid bone is clearly seen in Figure 19A & B. The pulp canals are narrow and surrounded by circumpulpal dentine through which short irregular tubules run from the pulp canals. The dentine between the pulp canals is translucent, homogeneous, and exhibits a pattern of birefringence in which alternating crystal bundles have opposite signs; these are features of petrodentine and pleromic dentine as found at the margins of the tooth plate in *Chirodipterus* (Smith & Campbell, 1987).

In restricted regions, a free surface between the bone and the dentine can be observed, and from this surface the dentine grew. Immediately above this there are strong growth lines within the dentine, following the contours of the forming surface below (Fig. 21D). This is a feature of intermittent dentine growth following creation of a resorption space within the bone, similar to that shown by petrodentine growth in *Chirodipterus*. Similarly, outgrowths of dentine occur as pocules (i.e. small cup-shaped bodies) occupying spaces in the adjacent bone. This has been previously illustrated by Smith
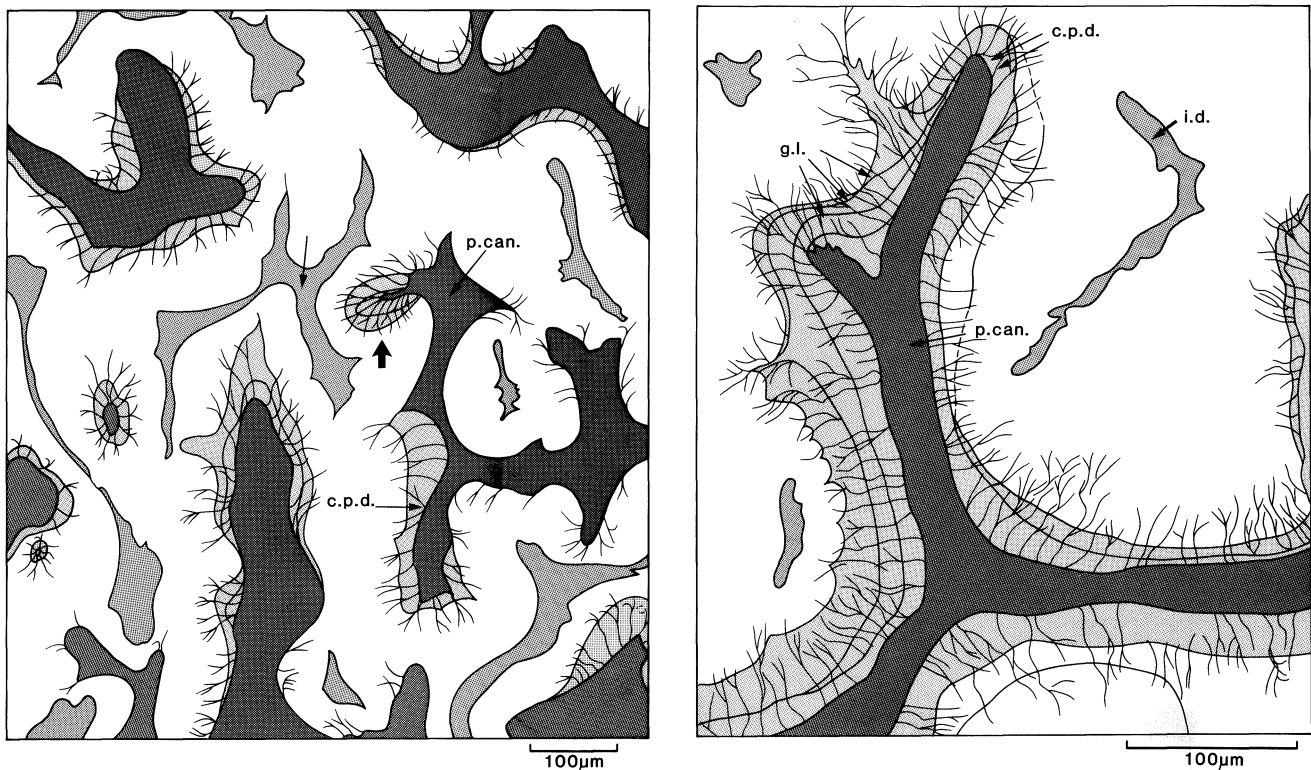

Fig. 13. (Scale bars = 100μ). A: Drawing of the central dentine beneath the tooth tip and towards the basal tissue, to show the arrangement of the different regions of dentine and separate growth zones around the pulp canals (p. can.). Smaller branches of the pulp canals are surrounded by several concentric layers of circumpulpal dentine (c.p.d., arrow) through which run irregular tubules. The mass of tissue between the pulp canals is hard compact dentine, but centrally amongst this are several islands of interstitial dentine (i.d.). The larger pulp canals towards the bottom are only partly lined by circumpulpal dentine. B: Drawing of the end of one pulp canal immediately beneath the tip of the tooth. This shows the same three regions of dentine as in Fig. 10A, but thick layers of circumpulpal dentine (c.p.d.) have narrowed the lumen of the canal and several growth lines (g.l.) can be seen. Numerous tubules run through these layers of dentine formed by addition to the surface of the compact hard dentine; the latter is generally without tubules, except the fine terminations of the wide tubules in the circumpulpal dentine, as shown in 14A and B.

(1977: fig. 14), where it was referred to as pleromic dentine.

Occasionally a bone surface can be seen covered only with vestiges of this hard dentine (Fig. 21A–C), most of which has been completely worn away. Nowhere is there any covering of enamel, but some surfaces are completely covered by denticles (Fig. 21A), or by the superficial dentine (Figs 21D; 22C). The most remarkable feature is that these denticles and the superficial dentine lie on a resorption surface where a reversal line marks the extent of resorptive activity in a phase where even this hard translucent dentine was removed from the surface downwards. After these phases of resorption the subsequent repair tissue is a single layer of denticles (Fig. 22A, B), or superimposed layers of denticles (Fig. 23B, D), or a very simple dentine layer (Fig. 22C). These may grow over old bone or partially resorbed pleromic dentine. Also, in some places a layer of finely trabeculate new bone formed over the resorption surface in conjunction with the formation of the denticles.

Superficial Dentine Layer

This is the white material observed on many surfaces and found surrounding the denticles, covering the bone surface and also enveloping the bases of the marginal teeth. It is exceedingly thin in many areas on both the pterygoids and prearticulars (Fig. 22C). Its histology is that of a very poorly developed, primitive type of dentine. This kind of tissue can occur anywhere in a subepithelial position, but is normally formed beneath an enamel layer.

In specimens preserved at the end of a depositional phase, considerable wear has occurred and the white tissue surrounding the tooth has been worn away to expose pleromic dentine that formed within this tissue as it was worn down.

Superficial Denticles

These are considerably smaller than the marginal denticles and have a simple structure as in
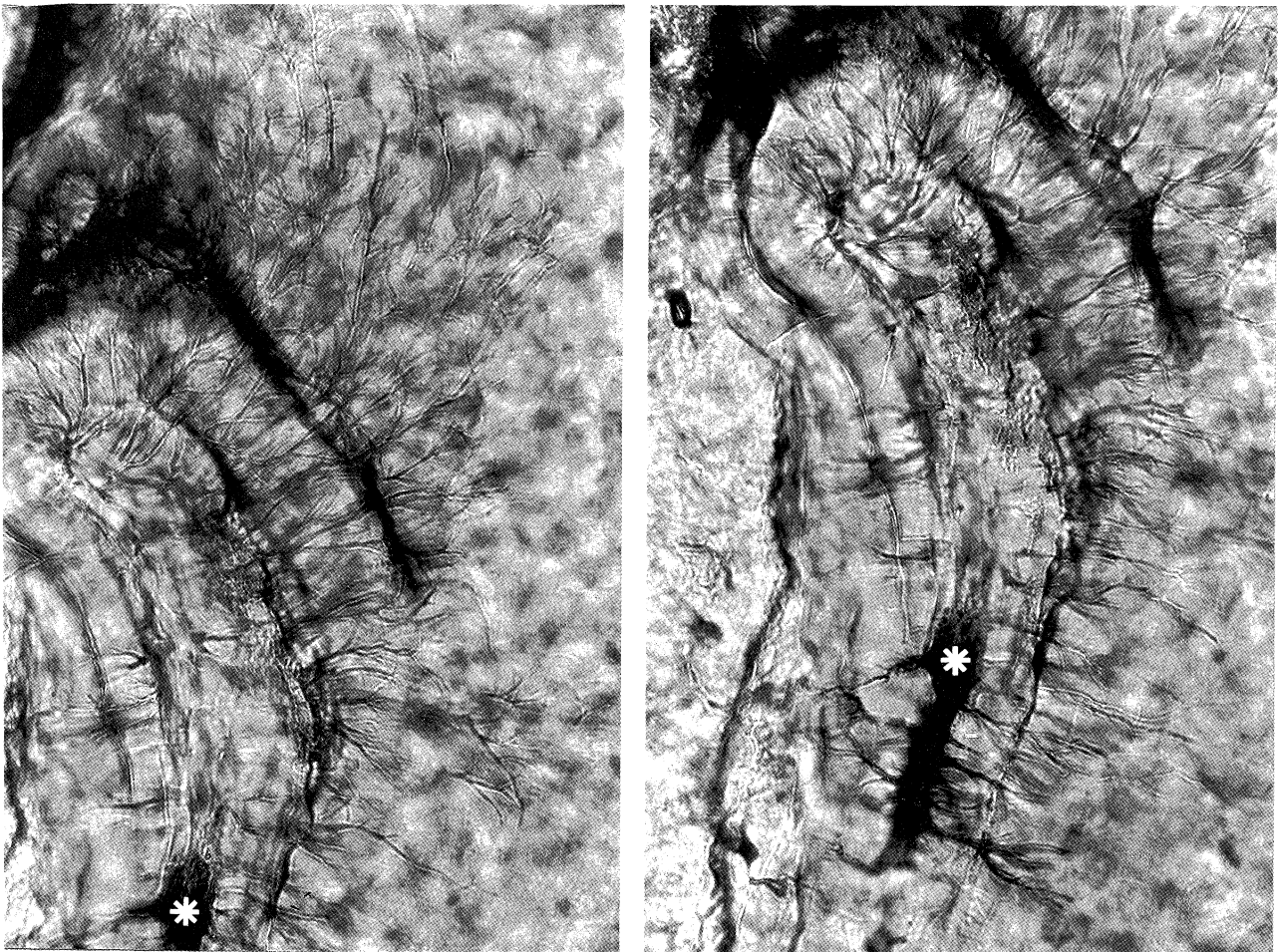

Fig. 14. (x 720) Two levels of a through-focus series, approx. 2μ apart, to show the same region of circumpulpal dentine around a narrow pulp canal (asterisk). The wide tubule spaces open into the pulp canal and lead into progressively finer and more branched tubules within the dentine. The lines parallel to the pulp canal surface, crossing the tubules at right angles, are assumed to be junctions between successive growth layers, i.e. growth lines. The asterisk is in the same position on the two photographs.
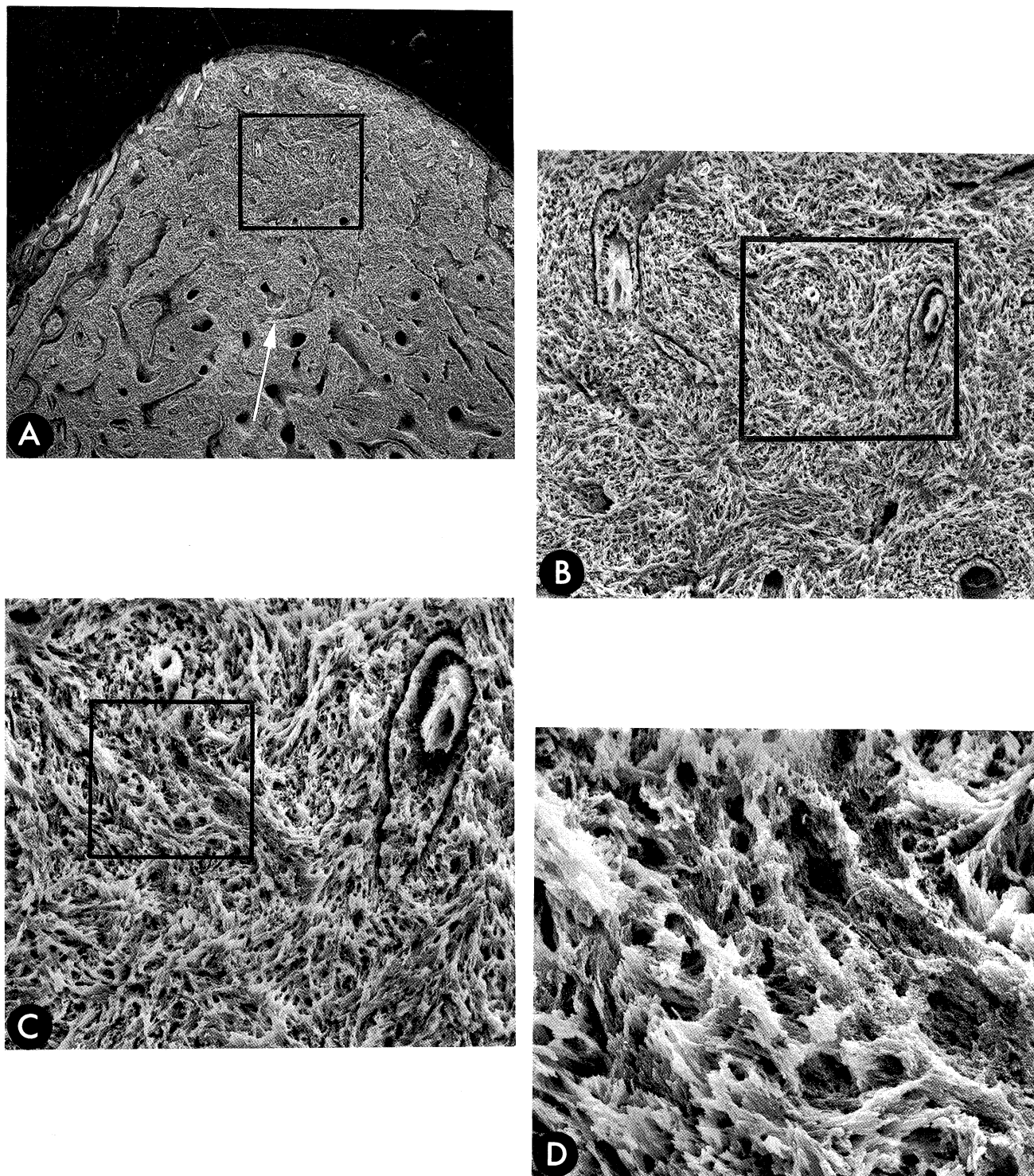
Fig. 15. **A:** field width = 2.7 mm. Field of the mature tissue, compact dentine at the tooth tip. Immediately beneath the worn surface the canals are infilled with biological apatite; towards the base the canal spaces are shown by the removal of the infilling sediment. (Rectangles show fields of B–C; arrow, field of Fig. 16A). Field widths: **B** = 0.6 mm, **C** = 0.27 mm, **D** = 90μ (0.09 mm). Fields from the region of the asterisk in A at increasing magnification show at least one layer of dentine concentric with each pulp canal. Groups of parallel crystals lie in several different planes within the compact hard dentine and are permeated by many small canals. Figs 15–18: CPC25738: see Fig. 10.
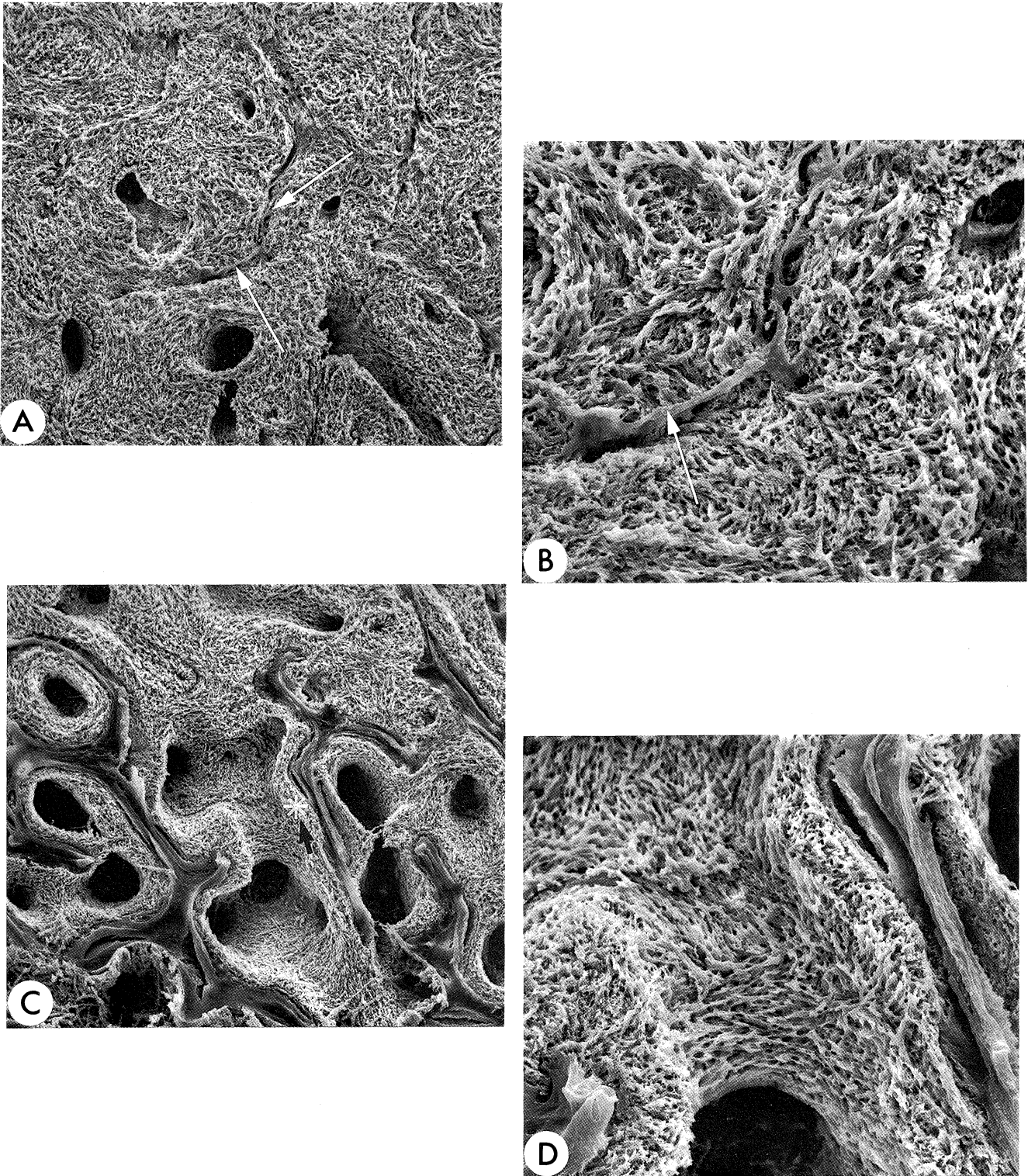
Fig. 16. Field widths: **A** = 0.9 mm, **B** = 0.27 mm. Zones of compact hard dentine are separated by narrow strands of smoother and more homogeneous interstitial tissue (arrows). The region is central to the tooth, immediately below the tip (arrow Fig. 15A). **C,** field width = 0.9 mm and **D,** field width = 0.27 mm. A region lateral and basal to that of A & B, both at comparable magnifications, with longer wider zones of interstitial tissue and wide, open canals with forming surfaces of compact hard dentine, but no infilling, concentric zones. (Field D, from asterisk in C.)
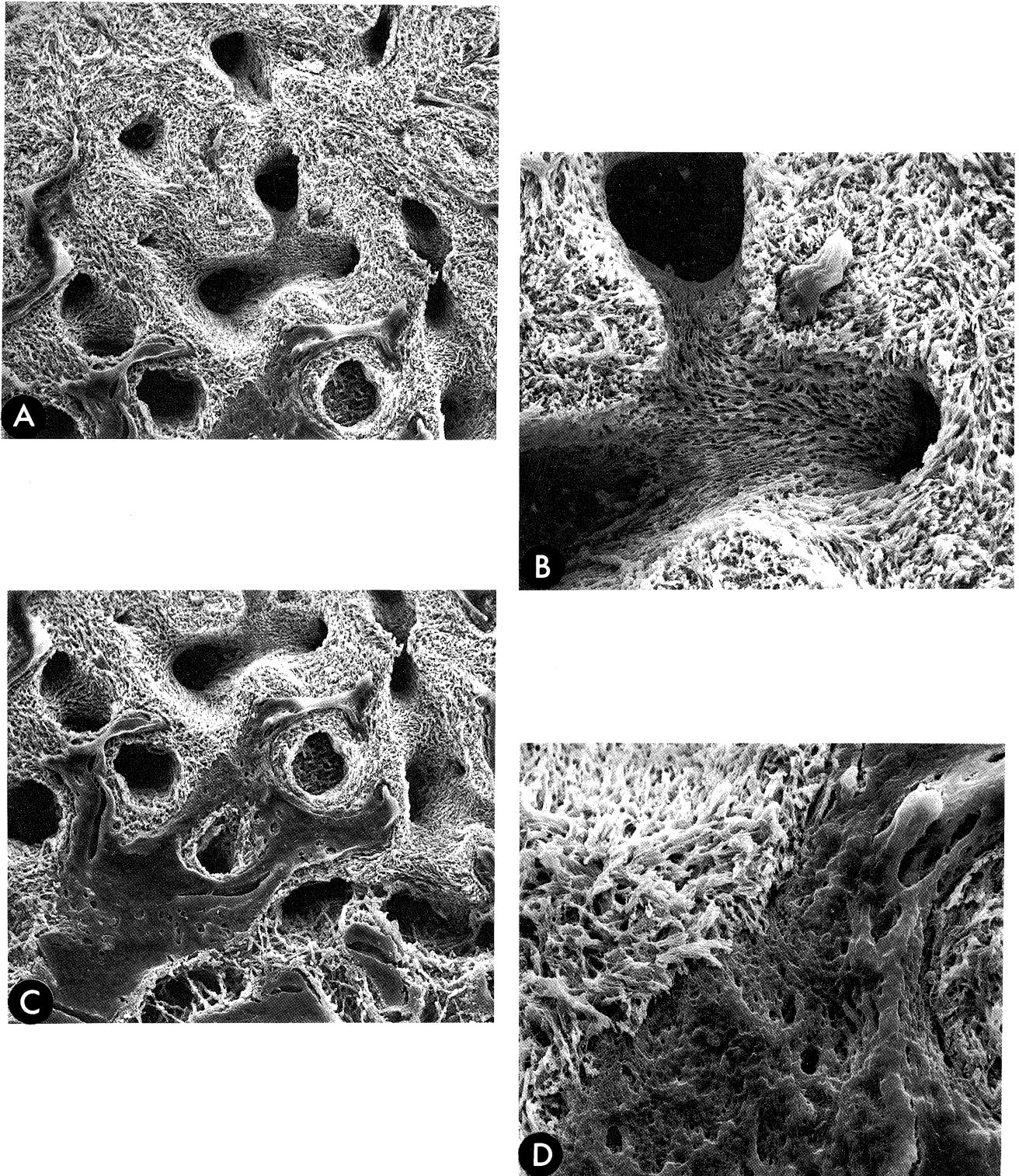
Fig. 17.   Field widths: **A** = 0.9 mm, **B** = 0.27 mm. Region of basal central dentine with extremely thin interstitial regions and narrow zones of compact hard dentine around wide canals which show forming surfaces of this dentine in B. **C** field width = 0.9 mm, **D** = 0.18 mm. More basal than region A & B with very wide interstitial zones of smooth, homogeneous tissue and thin layers of compact hard dentine. The wide canal spaces are occupied by the remnants of etched calcite crystals. The junction between the compact hard dentine and the interstitial dentine is irregular, as is well shown in D.

Griphognathus, as was shown by Smith (1977: figs 34, 35). Beneath a thick layer of enamel there are many short, branched pulp canals from which tubules radiate into the pallial dentine; frequently the denticles have many accessory crests, each with a pulp canal (Fig. 22A). Superpositional growth of denticles occurred in many regions (Fig. 23B,D) but the denticle layer always formed on top of a resorbed surface of bone or dentine, demarcated by a reversal line and an interruption of the structure of the bone trabeculae (Fig. 23C). Many of these denticles became worn and served as a protective cover to the relatively delicate trabecular bone forming most of the palate (Fig. 22B). They may also have initiated pleromic growth of dentine on this surface. However, quite a few were removed through resorption of small patches, and therefore had a temporary role in formation of the dental surface.

Marginal Denticles

Marginal denticles are substantial structures relative to the denticles covering the palate and lingual surfaces. They formed tightly packed groups on the vertical margins of the pterygoids and prearticulars (Fig. 24A). It is notable that their histology is different from the scattered buccal denticles in that, beneath a very thin layer of pallial dentine, trabeculae of dentine form a robust framework for the circumpulpal dentine, leaving a system of interconnecting pulp canals linking up with the bone spaces (Fig. 24B,C). The cells that produced the dentine have left many irregular tubules with finer branches within the circumpulpal and trabecular dentine; these all link with the pulp canals.

The marginal denticles are of a type that could be regarded as semi-permanent structures that may have provided centres from which pleromic dentine could grow into the bone and later become associated with the worn tissues at the base of the teeth. Judging from the position in which they had formed, it is quite possible that they could have developed from the epithelium of an invaginated epithelial cuff at the margins of the prearticular and pterygoid dental plates. Though it is not possible to refute this or substantiate it by observations on these specimens, the position of the newest denticles at a distance deep to the lateral surface makes a subsurface position for their development more probable than a superficial one. In this, as in many other respects, they are unlike the marginal blisters in *Chirodipterus* (Smith & Campbell, 1986), though these too remain intact until worn or ingrown by pleromic dentine. Sections through a worn region of these marginal denticles show, in fact, that pleromic dentine had formed within the bone and contributed to the worn surfaces of the troughs between the teeth.

DISCUSSION

Review of Dental Form

Previous evaluations of the position of *Holodipterus* in a scheme of relationships have placed this genus within the group that lacks tooth plates (Denison, 1974; Miles, 1977; Campbell & Barwick,
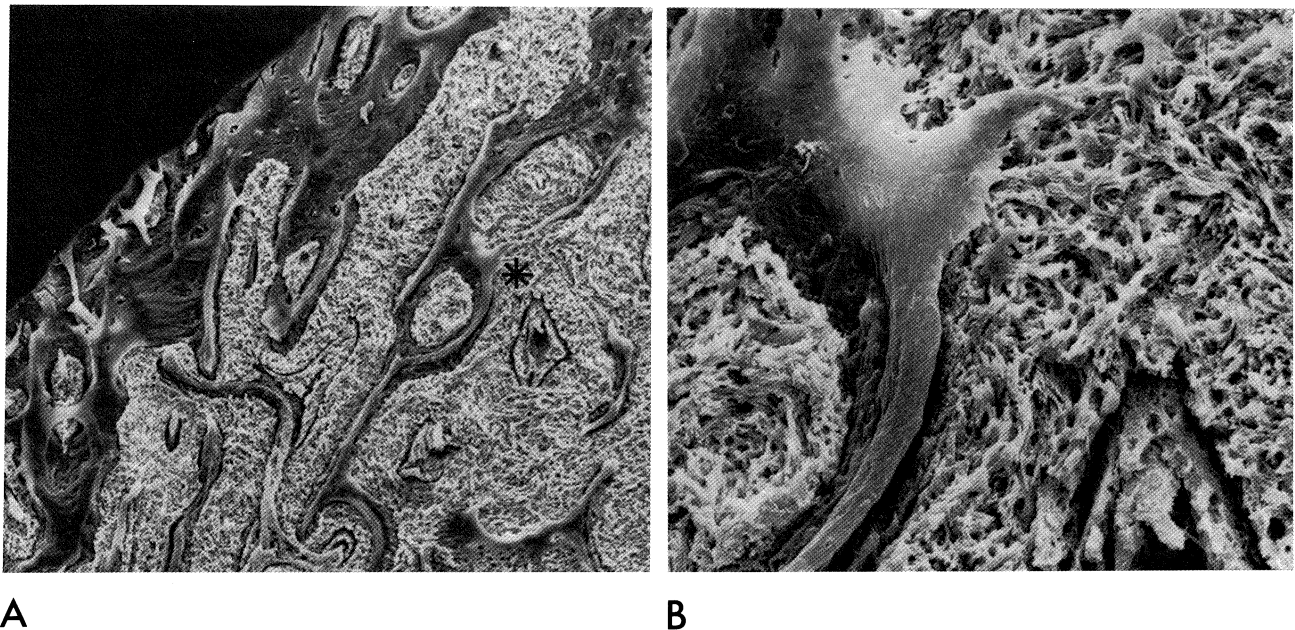

A   **B**

Fig. 18. Field widths: **A** = 0.9 mm, **B** = 0.18 mm. Regions at the lateral basal margin of the tooth to show extensive regions of smooth, homogeneous tissue of the pallial dentine continuous in places with the interstitial material (B, from the region asterisked in A).
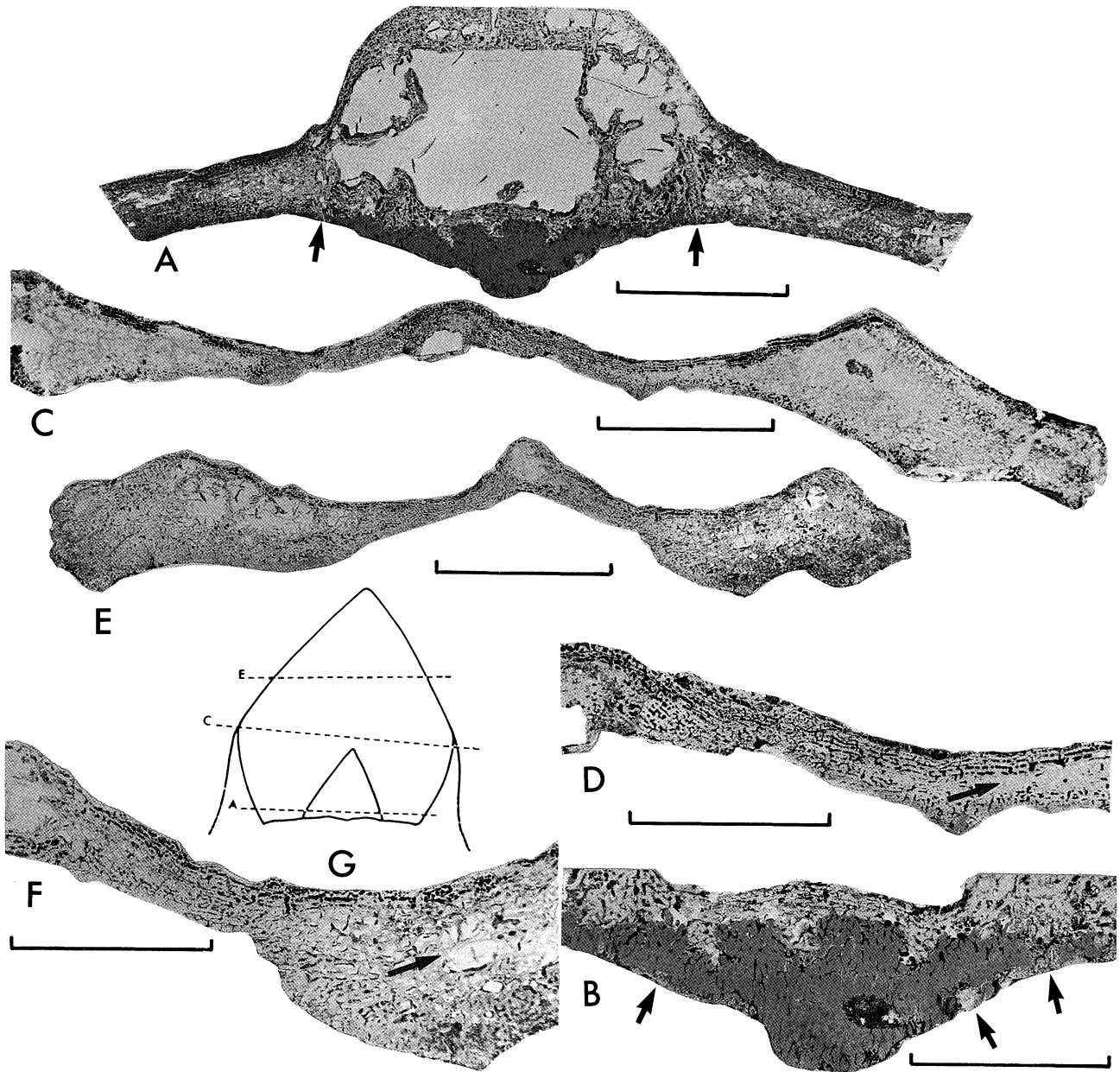
Fig. 19. (A, C, E, scale bars = 10 mm; B, D, F, scale bars = 5 mm). **A–F:** Cross sections of a palate, CPC25739, at positions shown in G. A, shows a section through the high, lightly ossified parasphenoid (boundaries marked by arrows), and the dark hard compact dentine of the posterior median callosity. C and E show the thin central part of the palate produced by extensive resorption on the buccal surface. Compression of such specimens would produce cracking along the junction between the medial thin region and the lateral thick regions, thus simulating a long narrow parasphenoid (e.g. in *Uranolophus* Denison, 1968). The large medial space in C is the result of loss during preparation of the section. B, D and F show enlargements of parts of A, C and E. B shows detail of the median callosity. (Note especially the disruption of the bone lamellae by the dentine, and the superficial dentine layer that has overgrown the callosity at the points marked by arrows.) F and D show the new continuous bone layers on the dorsal surface, the disrupted resorbed layers on the ventral surface, and the large open vascular spaces in the thicker lateral parts of the pterygoids (arrowed).

1983). However, Miles (1977) and Campbell & Barwick (1983) acknowledged that large teeth (cusps and tusks) have a rudimentary radial arrangement on both the palate and prearticulars, and that in *H. gogoensis* they interlock around the lateral margins. Further, Campbell & Barwick (1983) suggested that *Holodipterus* showed the short-headed titurating mode of feeding, and approached the gross morphology of a primitive tooth-plated genus. They suggested that it had developed this simulated tooth plate from the denticle-shedding form. A similarity with the tooth plates of *Fleurantia* was noted, a point that should be reconsidered in the light of the information on histology presented here.

Fleurantia has a subradial array of teeth disposed similarly to those of tooth-plated genera, though they are generally smaller. On the other hand, the genus has a very thin, arched palate that is covered with small denticles as far back as the posterior end of the tooth array. Denticles occur between the tooth rows. Teeth at the proximal ends of the rows have been shed and, within the spaces thus created, many new denticles have grown. This was particularly well described by Graham-Smith & Westoll (1937: 249–

Fig. 20. Bright field micrograph of a region of older worn dentine at the lingual surface of the tooth base, in which translucent compact hard dentine has completely joined onto the bone. This contrasts with the region at the opposite margin, the labial side (Fig. 11A).

252). As a result of this process, the radial tooth array moved anterolaterally on the pterygoid and was replaced on the lingual side by shedding denticles. This is quite comparable to the situation in *Holodipterus.*

Though not explicitly stated by any author, the reasons for considering *Fleurantia* to be a member of the non-tooth-plated group are: the small size of the teeth; the tooth shedding so that a 'plate' in the sense of a *Dipterus* plate was not developed; the long-snouted form of the skull with the large lateral embayments suggesting relationship to *Griphognathus* and *Soederberghia;* the thin pterygoidal bone that suggests a light bite unlike that of the usual tooth-plated types; and the ability of typical denticulated types such as *Griphognathus* to produce enamel-covered, tooth-like structures in a marginal row, though not in any predetermined radial pattern. Considerations such as these seem to have led Miles (1977: 299) to conclude that "the rows of teeth on the palate in *Fleurantia* and *Holodipterus* have a functionally determined orientation, and they tell us nothing about the phyletic relations of these forms". Such a conclusion, of course, does not mean that he considered these genera to be tooth-plated, but rather that within the non-tooth-plated group their relationships could not be determined on the basis of tooth patterns.

An alternative approach would be to consider the presence of radiate tooth rows in *Holodipterus* to be indicative of a relationship with primitive tooth-plated genera such as *Speonesydrion,* a genus that was described subsequent to Miles's account. Primitive pterygoidal tooth plates met in the midline, forming a continuous dentine sheet that covered the anterior end of the parasphenoid as well as the pterygoids, and added to their lateral margins by the incorporation of small irregular denticles. Primitive prearticular tooth plates had large callosities on the heel and denticles in the lingual furrow. *Holodipterus* dentition shares some of these characteristics, and those that it lacks could be derived by a number of changes, some relatively minor, but others requiring qualitative innovation. These include the production of mechanisms for: growth of more regular marginal denticles; resorption of old teeth from the palate and prearticulars, and replacement with shedding denticles; deposition of the superficial dentine layer that engulfed denticles and tooth bases; growth of palatal callosities; and systematic reduction of palatal thickness.

One way of examining these possibilities is to analyse the histology of the dental tissues and the morphology of the structures related to food reduction. This is done in the following section.

Relationships of *Holodipterus*

The gross structure of the whole dental apparatus, the morphogenetic sequence involved in its
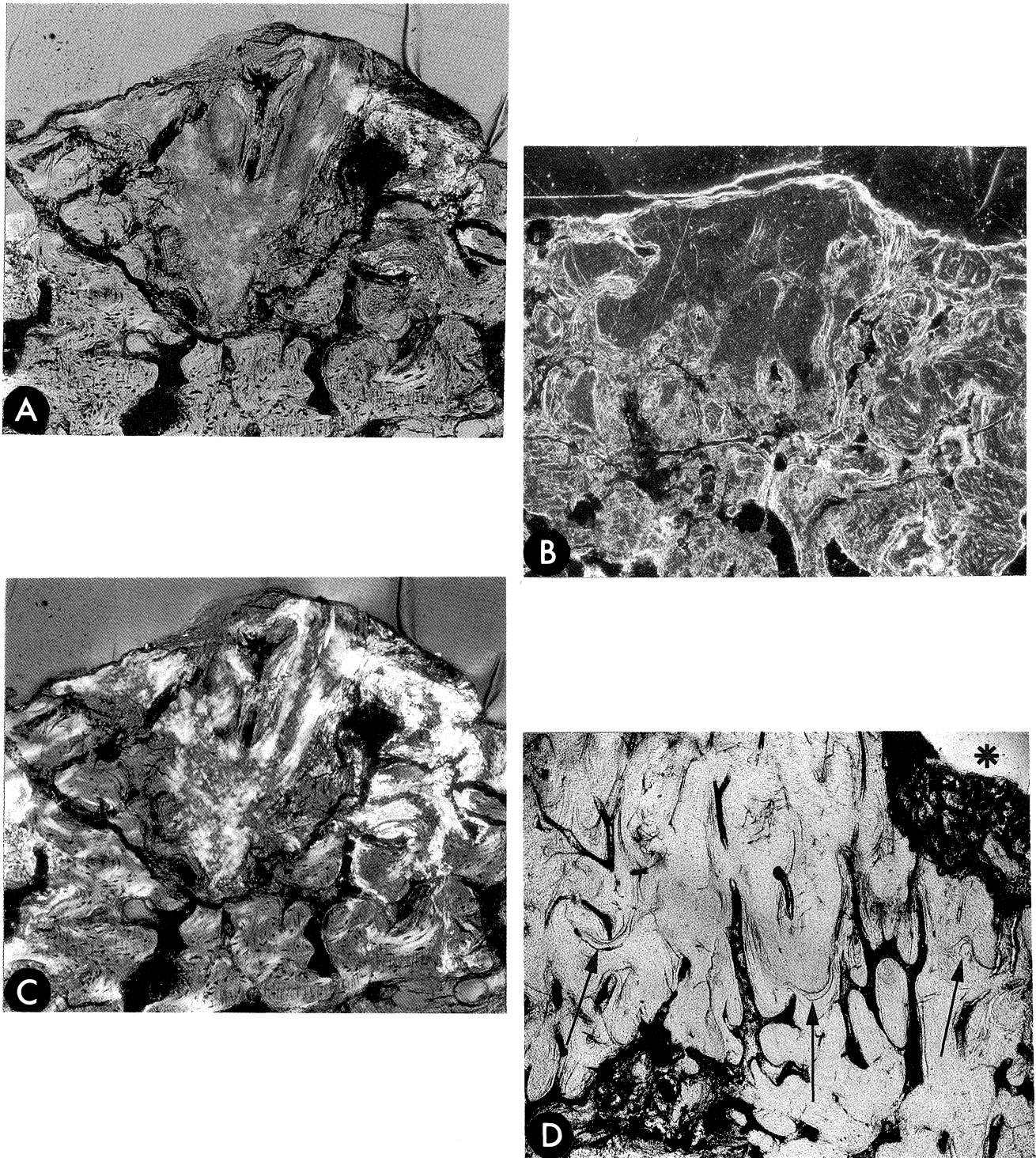
Fig. 21. **A–C:** (x 70) Vertical section through one of the paramedial callosities with a worn smooth surface and no covering denticles. The dentine of the callosity is translucent in ordinary light (A), and exhibits coarse, woven birefringent bands in polarized light (C). B shows a similar section through part of the callosity taken in phase contrast which emphasises the translucency of the hard compact dentine. **D:** (x 35) A region of the callosity in which pulp canals run vertically through the central part from larger spaces within the bone. In several zones (arrows) there are growth lines conforming with the shape of the forming surface. The surface of the callosity to the right shows evidence of a resorptive phase prior to growth of superficial dentine onto this surface (asterisk). CPC 25739

formation, and the histology of some of the tissues, are all unique. In the absence of any modern form to use as model, or even any post-Devonian form that could be used to provide a perspective on the evolution of this dental type, we are restricted to an analysis of characters held in common by *Holodipterus* and more primitive dipnoans in attempting to propose relationships of the genus. It is necessary to compare *Holodipterus* with both dental-plated genera and denticulated genera as the two major types. Within dental-plated genera we have discussed the existence of two types – those with dentine plates and those with tooth plates (Smith & Campbell, 1987). In the following section we discuss whether the dentition of *Holodipterus* should be considered to be a distinct type, or a modification of one of the previously defined types.

Unique features of dentition of *Holodipterus*.

SUPERFICIAL DENTINE LAYER. The extensive superficial dentine layer is not comparable with the thin layer of dentine on the palatal surface of

Dipnorhynchus (or presumably *Speonesydrion* which is poorly known in this respect) either in its histology or its development. That is: it has a simple structure with few tubules; was formed as an infill between denticles; grew over the surface of partly resorbed older dentine as well as bone; and was itself subject to episodic resorption.

REMODELLING MODE. The episodic remodelling involved all dental tissues – the superficial dentine layer, denticles, callosities and teeth – essentially every structure situated within an advancing resorption 'front'. This distinctive remodelling was accomplished by a specific sequence of events – first the growth of a thin layer of new trabecular bone immediately behind the resorption edge, the development of denticles within this bone, the growth of superficial dentine, and finally the replacement of the superficial layer by pleromic ingrowth.

POSITION OF NEW BONE ON DENTINE. The growth of new bone and associated denticles is remarkable because it formed, in part, over the partially resorbed
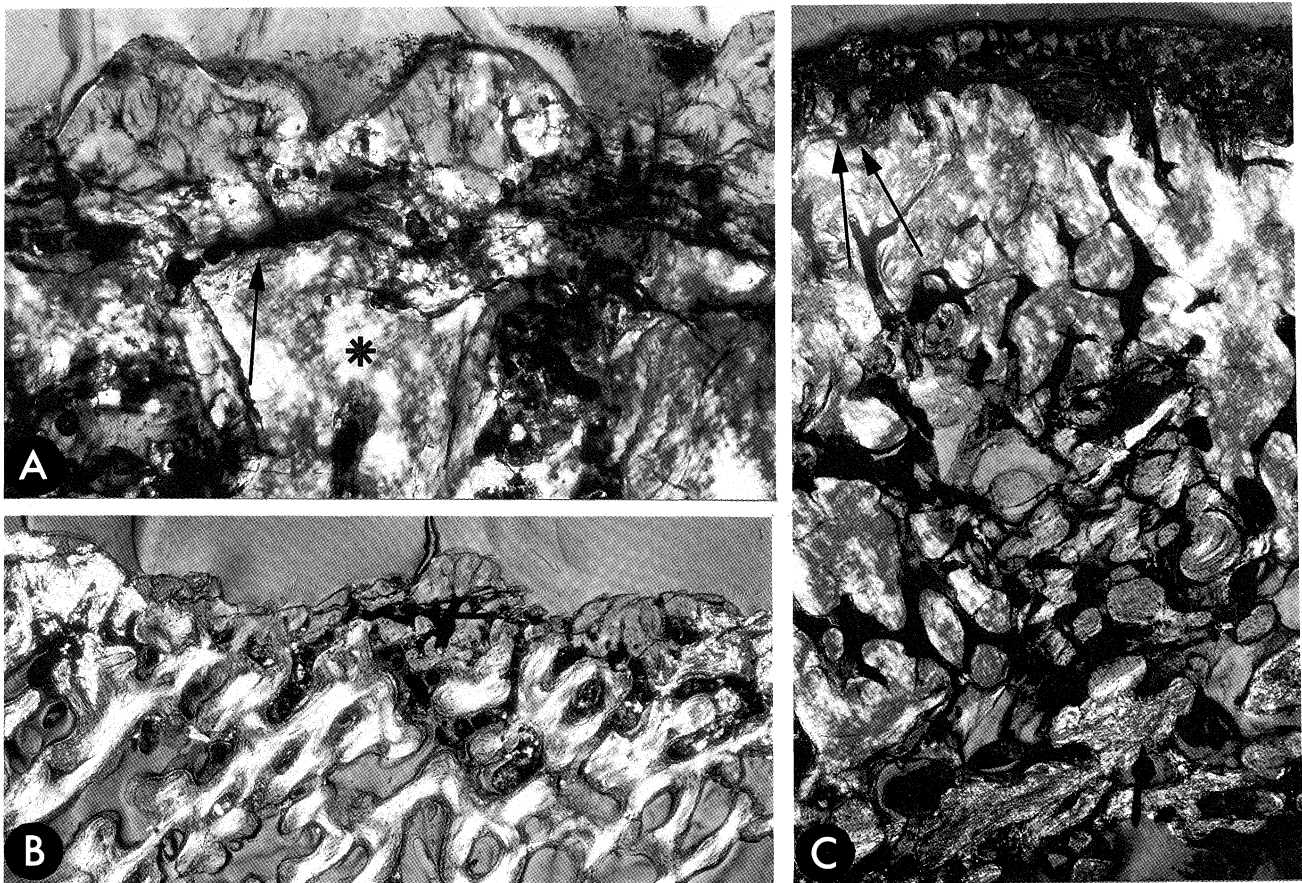

Fig. 22. A: (x 85) Two newly formed denticles on top of a resorption surface (arrow) formed on the compact hard dentine (asterisk). **B:** (x 35) A layer of denticles forming a thin covering to the trabecular bone, shown in partially cross polarised light. **C:** (x 40) (Field from the right of Fig. 21D.) A layer of the poorly mineralized superficial dentine overlying a resorption surface (double arrow) of hard compact dentine. The latter tissue has distinctive birefringence in cross-polarized light. CPC 25739

hypermineralised dentine that makes up the callosities.

MARGINAL DENTICLES. The development on the vertical lateral faces of the pterygoids and the prearticulars of large denticles that became overgrown and incorporated in the new bone, only to become resorbed during subsequent remodelling, is apparently unique. These accessory denticles provided an initial holding surface against which the most lateral teeth in the opposite jaw could be opposed during the subsequent growth phase. *Speonesydrion* had denticles at the margins of the prearticulars, and *Dipnorhynchus* had denticles around its pterygoids, but none of these denticles were submerged by bone during lateral growth. In *Speonesydrion* some of them came into contact with the tissues of the opposing plate, but in *Dipnorhynchus* none of them did. For present purposes it is sufficient to note that they may be regarded as only superficially similar to the lateral denticles of *Holodipterus*. Alternatively they may be regarded as primitive features that do not indicate a close relationship between the genera that carry them.

MODE OF TOOTH ADDITION. The teeth were added in sites adjacent to the short tooth rows along the lateral margins of the pterygoids and the prearticulars in alternate phases. Moreover, teeth were not added at the ends of all rows at each growth phase. Smaller teeth were added more frequently to successively more posterior rows. These features are unknown in any other dipnoan, but because uncrushed complete heads are very rare, it is impossible to say that they do not occur. However, it is possible to conclude from
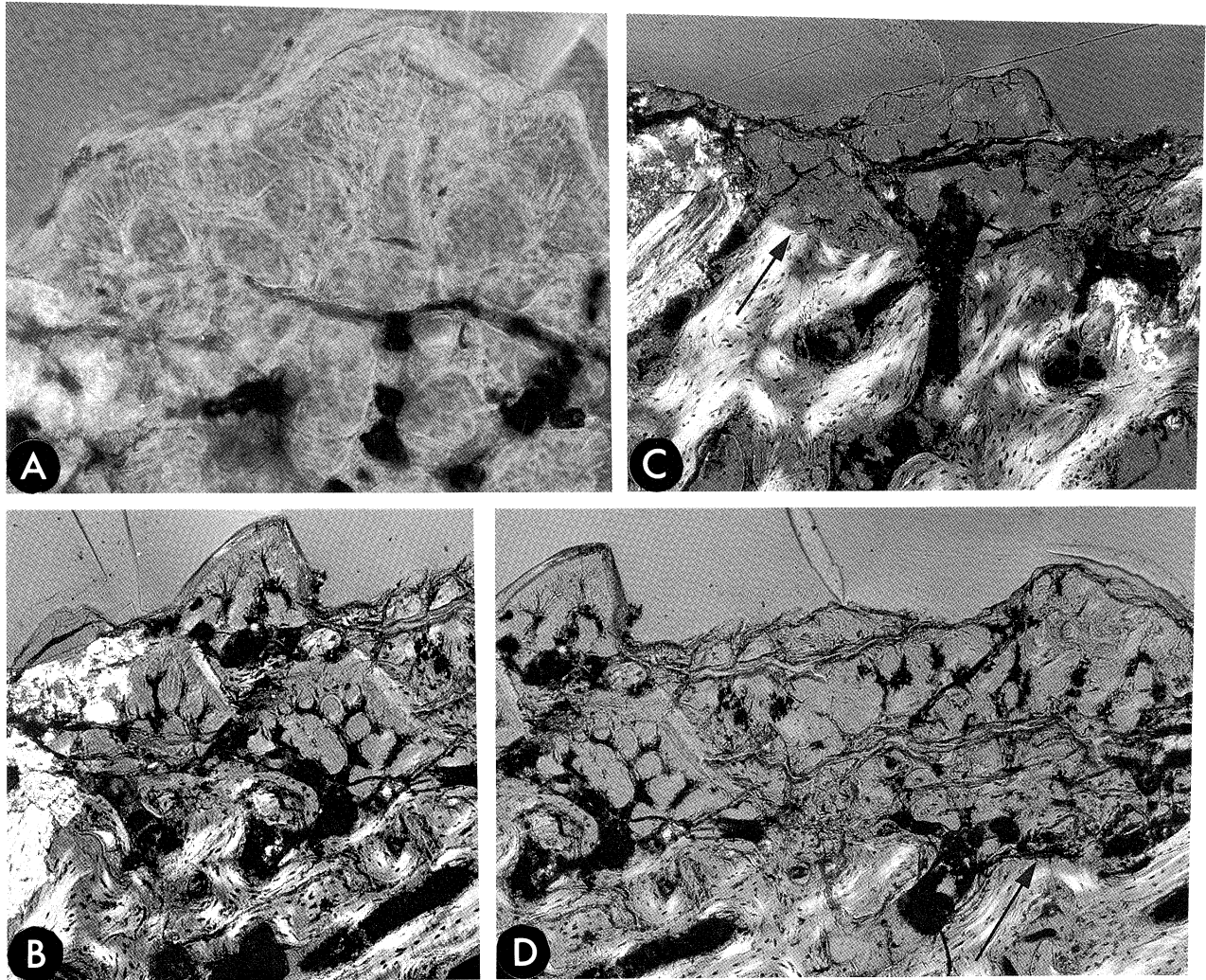

Fig. 23.   A: (x 220) A superficial denticle, with a simple structure of many small pulp canals with arborescent terminal branches, beneath an enamel layer. **B–D:** (x 85) Section through the layer of superficial denticles with denticles superimposed, and all growing from a resorptive surface of the bone (arrows), most clearly seen as distinct tissues by their different birefringences in cross-polarized light (C). The pulp canals of the denticles are seen to be continuous with the medullary spaces of the bone. CPC 25739

the mode of growth of isolated tooth plates in such genera as *Sagenodus, Ctenodus* and *Gnathorhiza*, that they increased laterally in the same manner as the plates in *Neoceratodus*, and that this mode was not similar to that of *Holodipterus*. *Dipterus* and *Speonesydrion* are ambiguous in this respect. The only possible way to show a similarity to these genera would be via the discovery of some individuals with teeth overhanging the margins and others with bone extending well beyond the most lateral teeth, but bearing denticles along the lateral surfaces. So far as we are aware such specimens have not been observed. As we have shown elsewhere (Smith & Campbell, 1987), chirodipterids did not add true teeth, and so they provide no comparison. We conclude that among all the dipnoan genera known at present, *Holodipterus* is unique in this respect.

Features of *Holodipterus* dentition shared with tooth-plated genera. PRESENCE OF TRUE TEETH. *Holodipterus* has enamel-covered teeth that were added at the labial plate margins. In form and position these teeth are entirely comparable with those of normal tooth-plated genera such as *Speonesydrion, Dipterus* and *Ctenodus*, though in histological detail they show distinctive features.

Using the analogy of tooth plate growth in extant genera, Reif (1982) concluded that each tooth was formed in a dental lamina and that each tooth ridge is homologous with a tooth family in other vertebrates.

The concept has been amplified in a study of the larval teeth of *Protopterus aethiopicus* (Smith, 1985). According to this model, new teeth are added to each family at the labial end. Although she did not use the tooth family concept in this sense, Kemp's work (1977) on larval *Neoceratodus* shows that the same mechanisms of plate growth are used by that genus. The presence of true teeth in *Holodipterus* could be used to imply the presence of a dental lamina. This could then be considered to be an argument in favour of relating *Holodipterus* to tooth-plated genera. For example, *Holodipterus* and *Speonesydrion* could be regarded as sharing the character of true teeth added in a regular pattern at the labial margin (see below for further discussion).
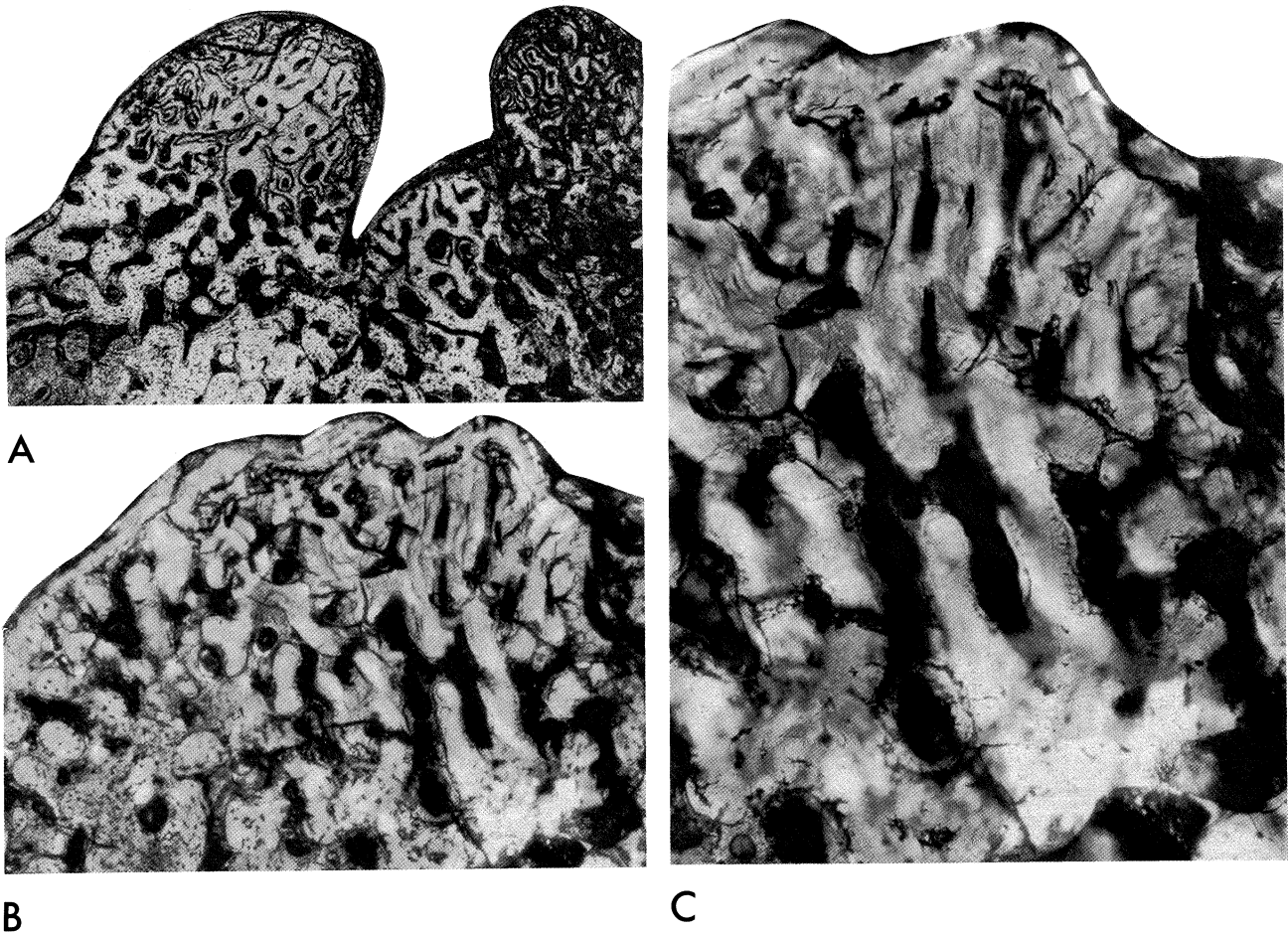

Fig. 24. A: (x 35) Two of the larger marginal denticles overlapping the base of a third showing a relatively compact structure to the dentine and a thin enamel layer (dorsal direction to left). **B** (x 85), **C** (x 160): one of this type of denticle to show the forming trabecular dentine at the base and poorly differentiated regions of circumpulpal dentine. CPC 25739

The force of the argument lies in the sharp distinction it makes between 'tooth' structures formed in dental laminae at predetermined positions, and 'tooth-like' structures formed superficially in any possible position without restriction to tooth primordial tissue as in a dental lamina. It would be necessary to assume that such dental laminae arose only once in the Dipnoi, and that genera with true teeth form a monophyletic group. It should also be noted that some forms with dental plates do not have true teeth, for example *Chirodipterus* (Smith & Campbell, 1987).

HYPERMINERALISED DENTINE OF TEETH AND CALLOSITIES. The teeth and callosities of *Holodipterus* are formed of translucent, compact, hard dentine that shows the cross-hatched structure under crossed polars, and the pattern of crystal-fibre-bundles in S.E.M., typical of petrodentine. However, it shows some differences from typical petrodentine, particularly in its mode of growth. The petrodentine of extant dipnoans has a characteristic structure in the region where it is formed along the edge of the pulp cavity, and this is not the structure observed in *Holodipterus*. In addition, in extant forms the regions of petrodentine between the pulp canals are not separated by homogeneous tissue that increases in thickness towards the pulp cavity, which is the arrangement in *Holodipterus*. The interpretation of the growth and significance of this tissue is problematical.

As we have concluded in the section on histology, the hypermineralised dentine in the teeth of *Holodipterus* is similar to petrodentine but not identical to it. Insofar as true petrodentine has been found only in dipnoans with dental plates, the above evidence may be used to support the view that *Holodipterus* is related to that group. If so, the different compact hard dentine, and the presence of the distinctive homogeneous tissue found in interstitial positions, suggest that it is not a normal member of the group. If, however, *Holodipterus* is related to *Speonesydrion* because they both are regarded as having true teeth, these histological differences can be explained as the result of independent development.

CALLOSITIES ON PREARTICULARS. The heel of the prearticular produced a prominent callosity very similar in appearance to that of *Speonesydrion* and *Dipnorhynchus*. In these latter genera the callosities are not well understood, but they must result from pleromic growth of hard tissue associated with wear of the surrounding regions. The prearticular callosity in *Holodipterus* grew in the same way as the callosities on the palate – that is, it resulted from downward and lateral growth of the hypermineralised dentine from a residual body of that tissue that had been considerably altered by resorption during successive phases of development. This is different from the mode of growth of the heel in the other two genera, in which no such surface resorption phases were involved.

We draw attention to the fact that in none of these genera do the heels of the prearticulars come into contact with the pterygoid plates; a large gap remains even at full occlusion. Such a relationship provides space to crush larger items of food prior to moving them towards the labial plate margins for further reduction. It would not be surprising if large callosities developed independently in several groups to serve this function.

RETAINED DENTICLES OVERLYING CALLOSITIES. Denticles that are normally shed are sometimes incorporated into the retained dentine forming the callosities in *Holodipterus*. In *Speonesydrion*, denticles are incorporated at the advancing dentine margins as a normal means of tooth-plate growth; and in *Uronemus*, a genus bearing modified dental plates, the developing elongate tooth ridges occasionally trap one or more of the shedding denticles so that they are incorporated into the retained ridge. It may be thought that the involvement of such denticles in permanent dentine formation provides grounds for relating these genera. However, once again the processes involved were quite different. In *Uronemus* the dental epithelium advanced over some adjacent denticles before they could be shed, which was their normal fate before an advancing depositional front. Their entrapment was abnormal and the ridge would have developed even if entrapment had not occurred. In *Holodipterus* the denticles were covered with superficial dentine, then subsequently they became involved with pleromic growth and were not resorbed. Only then did they contribute to the growth of the callosities which would not have been initiated, and could not have expanded, without their contribution.

Features of *Holodipterus* dentition shared with denticulate genera. SHEDDING DENTICLES. *Holodipterus* has shedding denticles of the *Uranolophus* and *Griphognathus* type on the pterygoids and prearticulars. We need to make a clear distinction between the denticles of the type found in the lingual furrow of *Speonesydrion* and those of the above genera. As has been well shown by Smith (1977), the denticles of *Griphognathus* were shed and regrown at irregular intervals on an irregular pattern during the life of an animal. If they were incorporated into the marginal ridges they were subsequently lost when these tissues were resorbed during remodelling. The denticles of *Speonesydrion* were not lost in this manner, but continued to grow until they were incorporated into the advancing dentine front that formed a tooth plate. The same is true of the denticles in the lingual furrow and on the posterior part of the pterygoids and the parasphenoid of *Dipnorhynchus*. The denticles of *Holodipterus* are simple, like those of *Griphognathus*, and most of them were shed, although during certain phases of growth those that had not been shed were overgrown by bone, simple

dentine, or more denticles, and thus were temporarily retained on the dental surface until the next phase of resorption took place. The exceptions to this are the callosities on the palate and the prearticulars, but these do not form parts of tooth plates.

As indicated above, at least one tooth-plated genus, *Uronemus*, has on the pterygoids denticles that were shed, although they have a more complex histology than those of *Griphognathus*. Further, many other groups of gnathostome fishes have denticles that are shed. The argument is regularly advanced that such a condition is primitive (Nelson, 1969) and therefore is not of significance in determining relationship. This is a superficial judgement. In the first place, *Uronemus* is an advanced genus in which the tooth plates have retreated to a lateral position, exposing the surface of the pterygoids in the buccal cavity. Much of this surface was then adapted for the appropriate positioning of the 'tongue-pad' during buccal pump action, as an essential part of the air-breathing process. The remainder of the surface became covered with shedding denticles which functioned as an essential part of the distinctive shearing bite of the genus (Smith, Smithson & Campbell, 1987). In other words, the denticles of *Uronemus* are secondarily developed for a specific function. This conclusion does not deny the proposition that the capacity to develop such denticles is a primitive feature of the epithelium. What it asserts is that this capacity was retained but not necessarily expressed in advanced forms. It was expressed when the need arose. This points up once again the fallacy of categorising a structure as primitive or advanced without a consideration of the developmental and evolutionary processes involved in its formation. Such a fallacy results from failure to take into account the variety of morphological, histological and functional data available, while concentrating on apparent similarities of physical entities, in this case, denticles. It ignores the complexity and richness of the biological system by treating the products of such processes as though they were inorganic entities whose relationships are to be determined by the application of principles appropriate to inorganic processes. Further, it is no response to this criticism to suggest that all that is required is a refinement of the character analysed – that is, denticles with a certain disposition on the pterygoids rather than denticles in general. In the first place one has to perform a preliminary developmental, functional and stratigraphic analysis to appreciate that a feature is significant. In the second place it could always be claimed that the denticles indicated that the organism was primitive in this respect, unless it was appreciated that the main issue is the capacity of the epithelium to produce denticles at points of functional necessity, and not the presence of the denticles themselves. The issues of the argument are the identification of the character to be analysed, the relation of that character to

surrounding observed and inferred soft tissues, and the history of the character through geological time. None of these issues are even approached by a method that excludes a thorough biological analysis prior to an attempt to infer taxonomic significance.

REMODELLING OF MARGINAL STRUCTURES. A feature of the marginal structures of *Uranolophus* and *Griphognathus* is the extent to which they are resorbed and remodelled during growth. Juveniles of *G. whitei* have a number of short, anteriorly directed ridges on the anterior part of the palate (Campbell & Barwick, 1983: figs 16–17) but these were subsequently lost and replaced by a variety of temporary ridges and tuberosities. The marginal ridges, which occur on both the pterygoids and the prearticulars, are very varied in form, and do not produce a regular persistent pattern. *Uranolophus* has more or less continuous marginal ridges on the pterygoids and prearticulars, and these were apparently totally resorbed and regrown at certain stages of development (Denison, 1974). In both these genera, this marginal remodelling permitted the lateral expansion of the denticulated surfaces of both pterygoids and prearticulars. This is also a feature of *Holodipterus*.

PRESENCE OF BASIHYAL/BASIBRANCHIAL DENTAL PLATES. *Holodipterus gogoensis* probably had basihyal/basibranchial dental plates. Though dental plates are rarely preserved, this should not be taken as evidence that they are not always present. Specimens of the species are not common, and they are almost always disarticulated. The dental plates would have fallen free and, even if found, would not be recognised as belonging to the species. In addition, the palates themselves show evidence of the presence of dental plates on the basihyal/basibranchial system because the posterior medial palatal callosities are usually worn smooth and some show a polish.

A most important feature in this regard is the disposition of the tooth rows in the mandible. Devonian genera of the dental-plated type *(Dipterus, Chirodipterus, Scaumenacia, Speonesydrion)* have the lingual tooth rows on the prearticulars well medial of the limits of the posterior ends of the dentary. The lingual space is obviously limited. However, *Holodipterus gogoensis* has the lingual rows on the mandible aligned with the ends of the dentary, thus leaving a large lingual space. This is similar to the arrangement in *Griphognathus whitei* in which the marginal ridges of the prearticulars and the ends of the dentary are confluent. The lingual space was occupied by the basihyal/basibranchial system. Thus the pattern in *H. gogoensis* is consistent with, though it does not prove, the presence of such a system.

Taken together, the presence of isolated pieces of denticulate tooth plate, the median callosities that sometimes have a polished surface, and the disposition of the tooth rows, strongly suggest the presence of a basihyal/basibranchial system such as is

found in the typical denticulate genus *Griphognathus*.

MEDIAN CALLOSITIES. Many denticulated species do not have median callosities, but they are known on one specimen of *Uranolophus wyomingensis* where they presumably served the same function as in *Holodipterus*. Callosities in denticulate species result from the pleromic growth of dentine and the failure to resorb tissue that is normally shed. It is worth noting that some of the palatal tusks of *Griphognathus whitei*, though not situated medially (see Campbell & Barwick, 1986: fig. 4B) are formed by precisely the same process. They are not present in some specimens of that species because resorption has completely removed them.

PALATAL SHAPE. A feature of the dentition of members of the denticulated lineage is the high arch of the palate and the extension of the denticulation over the whole surface of the pterygoids and the anterior part of the parasphenoid. This is known in *Uranolophus*, *Griphognathus*, *Soederberghia*, *Jarvikia* and *Conchopoma*. Such a distribution is related to the presence and position of the basihyal/basibranchial tooth plates. *Holodipterus gogoensis* is a normal member of the lineage in this respect; *Fleurantia*, usually put with this group, may be an exception, and further work on the genus is necessary.

CHARACTERISTIC CHEEK POUCH. The extant genera *Protopterus*, *Lepidosiren* and *Neoceratodus*, all of which have tooth plates, break down their food in a distinctive way. After sucking a piece of food into the mouth, it is pushed out again in short movements by the action of the tongue-pad. After each forward projection the food is bitten by the anteriorly placed tooth plates. The partly pulverised food is held together by a mass of stringy mucous. After complete expulsion, the food and mucous are sucked back into the mouth. The process is repeated several times.

This mechanism could be effective only if a tongue-pad (or perhaps a modified part of the basihyal apparatus) was placed far enough forwards to eject the food, and the tooth plates were able to bite it as it was ejected. It is unlikely that such denticulated genera as *Griphognathus* had a tongue pad that could perform such a function because the basihyal/basibranchial apparatus itself would preclude such an arrangement, and they certainly had no anteriorly placed dental plates. Presumably they had adopted some alternative means of recycling food through the buccal cavity or they ate food that did not require chewing. The presence of the basihyal/basibranchial dental plates suggests that the latter proposal is not correct. In addition to this, the dentition of such forms consisted of lateral marginal ridges and denticles of various kinds indicating that food would have been passed laterally rather than forwards. This is consistent with the view of Campbell & Barwick (1983) that genera such as *Griphognathus* and *Soederberghia* had large muscular cheek pouches into which the food was passed. The cheeks of contemporaneous tooth-plated genera such as *Dipterus* and *Chirodipterus* were covered with dermal bones that left no space for such pouches.

Although the roofing and cheek bones of *Holodipterus* are poorly known, one specimen in the British Museum (Natural History), P524568, is sufficiently well preserved to show the characteristic profile of the cheek bones (Fig. 8). This is of the *Griphognathus* type rather than the *Dipterus* type, and is therefore consistent with the interpretation of *Holodipterus* as a genus without an anteriorly placed tongue-pad, and with a feeding mechanism typical of the denticulated lineage.

CONCLUSIONS

Many of the aspects of the dental tissues of *Holodipterus gogoensis*, and the processes that produced them, are unlike those of any other dipnoan that has been studied in detail. The most unusual features are the superficial layer of simple dentine, the resorption of all types of dental tissues including those forming the teeth, the growth of new bone and dentine over the remaining unresorbed hypermineralised dentine forming the callosities, the mode of pleromic infill of the superficial layer, the pleromic mode of growth of the callosities, the cyclical addition of teeth in a distinctive sequence, and the structure of the dentine forming the main mass of the teeth. Differences between specimens are considerable, and result, at least in part, from the death of individials at different stages of the resorption/remodelling cycle. Comparative work on species of this genus obviously has to be based on a growth sequence.

We have attempted to examine the features of the dentition that would allow us to relate *Holodipterus* to tooth-plated genera such as *Speonesydrion* and *Dipterus*, or to denticulate genera such as *Uranolophus* and *Griphognathus*. The outcome of the discussion has not proved conclusive. On the one hand the presence of the marginal denticles, and radiate rows of true teeth composed of a hypermineralised tissue with some of the properties of petrodentine, may be taken to weigh heavily in favour of the former relationship. On the other hand, this proposal is weakened by: the failure to develop true tooth plates because all teeth, except those near the margin, are removed by resorption of their bases; the lightly ossified palate that is repeatedly thinned by resorption of its buccal surface; the distinctive hypermineralised dentine; the smooth lamellate dentine trabeculae in the teeth; and similarities with the tooth pattern of the denticulate genus *Fleurantia*. The suggestion that *Holodipterus* is more allied to the denticulate genera is supported by evidence of the presence of a basihyal/basibranchial dental system, the cheek structure that goes with such a system, the type and distribution of the denticles, the repeated

remodelling of the buccal tissues including the bony surface of the palate, and the fact that *Fleurantia* resorbs its teeth and replaces them with denticles.

The conclusion reached depends on one's philosophy of establishing relationships. M.M.S. accepts that the presence of true teeth implies the development of dental laminae, a primitive character linking all those dipnoans 'with teeth' and not likely to have been lost and secondarily acquired in some dipnoans (for further discussion see Smith, 1987). Hence, a relationship with primitive tooth-plated forms such as *Speonesydrion* is indicated. The many distinctive features of the dentition of *Holodipterus* imply that it evolved divergently from the more advanced Devonian tooth-plated genera such as *Dipterus* and *Scaumenacia*. K.S.W.C. prefers the view that the feeding system should be treated as a functional developmental entity, and considers that relationships with the denticulated genera are indicated; teeth would have evolved more than once in the Dipnoi. It is obvious that the structure of *Fleurantia*, a generally acknowledged member of the denticulate group, is important for the above argument, and work on the precise details of its dental development and histology is now required. In addition, other characters of the two genera, particularly the basihyal/basibranchial systems, need further study.

References

Bassett, C.A.L., 1971. Biophysical principles affecting bone structure. **In** "The Biochemistry and Physiology of Bone". (G.H. Borm ed.) Vol. 3: 1–76. Academic Press, London.

Baume, L.J., 1980. The biology of pulp and dentine. A historic, terminologic, taxonomic, histologic, biochemical and clinical survey. Monographs in Oral Science, 8. S. Karger, Basel.

Campbell, K.S.W. & R.E. Barwick, 1983. Early evolution of dipnoan dentitions and a new genus *Speonesydrion*. Memoirs of the Association of Australasian Palaeontologists 1: 17–49.

——— 1987. Paleozoic lungfishes – a review. Journal of Morphology Supplement 1: 93–131.

Denison, R.H., 1974. The structure and evolution of teeth in lungfishes. Fieldiana: Geology 33: 31–58.

Graham-Smith, W. & T.S. Westoll, 1937. On a new long-headed dipnoan fish from the Upper Devonian of Scaumenac Bay, P.Q., Canada. Transactions of the Royal Society of Edinburgh 59: 241–256.

Kemp, A., 1977. The pattern of tooth plate formation in the Australian lungfish, *Neoceratodus forsteri* Krefft. Zoological Journal of the Linnean Society of London 60: 223–258.

Miles, R.S., 1977. Dipnoan (lungfish) skulls and the relationships of the group: a study based on new species from the Devonian of Australia. Zoological Journal of the Linnean Society of London 61: 1–328.

Nelson, G., 1969. Gill arches and the phylogeny of fishes, with notes on the classification of vertebrates. Bulletin of the American Museum of Natural History 141: 475–552.

Reif, W.E., 1982. Evolution of dermal skeleton and dentition in vertebrates: the odontode regulation theory. Evolutionary Biology 15: 287–368.

Smith, M.M., 1977. The microstructure of the dentition and dermal ornament of three dipnoans from the Devonian of Western Australia: a contribution towards dipnoan interrelations, and morphogenesis, growth and adaptation of the skeletal tissues. Philosophical Transactions of the Royal Society of London (B) 281: 29–72.

——— 1979. Structure and histogenesis of tooth plates in *Sagenodus inaequalis* Owen considered in relation to the phylogeny of post-Devonian dipnoans. Proceedings of the Royal Society of London (B) 204: 15–39.

——— 1984. Petrodentine in extant and fossil dipnoan dentitions: microstructure, histogenesis and growth. Proceedings of the Linnean Society of New South Wales 107: 367–407.

——— 1985. The pattern of histogenesis and growth of tooth plates in larval stages of extant lungfish. Journal of Anatomy 140: 627–643.

——— 1987. The dentition of Palaeozoic lungfish, implications for the phylogeny of dipnoans. VIIth International Symposium Dental Morphology, Paris (in press).

Smith, M.M. & K.S.W. Campbell, 1987. Comparative morphology, histology and growth of the dental plates of the Devonian dipnoan *Chirodipterus*. Philosophical Transactions of the Royal Society of London (B) (in press).

Smith, M.M., T.R. Smithson & K.S.W. Campbell, 1987. The relationships of *Uronemus* – a Carboniferous dipnoan with highly modified tooth plates. Philosophical Transactions of the Royal Society of London (B) (in press).

APPENDIX

Dentine terminology is still in a state of flux, despite several recent attempts to clarify some specific points (Smith, 1979, 1984, 1985). To some extent the variety of terms reflects the diversity of dental tissues found, in particular, in the dentitions of Palaeozoic lungfish. The tissues of *Holodipterus* show specific features for which it is necessary to give our definitions in this paper. Reference should also be made to the three articles listed above. Note that we use the terms 'primary', 'secondary' and 'tertiary' to refer to the sequence in which the various types of dentine are formed during the growth of a tooth. The terms pallial, interstitial, circumpulpal and intrapulpal are topogenic terms (Baume, 1980: 49) indicating the site of initial formation.

Microstructure

Pallial dentine. Lightly mineralised primary dentine (i.e. the first-formed dentine in a tooth) with randomly oriented small crystals and containing the distal ends of the dentine tubules extending from the underlying more complex dentine; forms a thin layer immediately beneath the enamel cover of a tooth or a denticle; deposited from undifferentiated odontoblasts in the primary pulp cavity (derived from the mesenchymal dental papilla of the tooth germ).

Interstitial dentine. Secondary dentine occupying the space in the core of a tooth with a divided pulp cavity or a callosity between the deposits of circumpulpal dentine; sometimes continuous with the pallial dentine; usually without dentine tubules; variable levels of mineralization; may be formed from either mesenchymal cells or differentiated odontoblasts in the pulp cavity. Equivalent to the initial dentine trabeculae of intrapulpal dentine, later invested with circumpulpal dentine (denteones).

Petrodentine. A special type of intrapulpal dentine between pallial and circumpulpal dentine; hypermineralised relative to any other dentine or bone; hard and translucent; formed of crystal-fibre-bundles consisting of parallel, large hydroxyapatite crystallites; diameter and arrangement of the crystal-fibre-bundles varies amongst the genera; in extant genera arranged so that adjacent bundles (domains of crystals) alternate through 90° to each other; dentine tubules scarce, restricted to the borders with the circumpulpal dentine; formed from a special cell population (petroblasts), initially from the dental papilla, subsequently from those in the pulp cavity at the base of a tooth.

Circumpulpal dentine. Tertiary dentine with normal levels of mineralisation, composed of small crystals; traversed by numerous branching tubules;

arranged as sequential layers concentric with the pulp canals in teeth where the pulp cavity is divided by infilling with dentine, or in the dentine of callosities around the vascular canals; formed from odontoblasts within the pulp canals.

Superficial dentine. Formed as a layer beneath the epithelium without division into odontodes (units of dentine, see Smith, 1979); lightly mineralised dentine with randomly oriented small crystals; traversed by short irregular pulp spaces from which extend numerous dentine tubules; pulp spaces connect directly with the medullary spaces in the underlying bone; found in sheets filling in the space between denticles on the palate and prearticulars in *Holodipterus;* similar in structure to the pallial dentine of the associated denticles.

Pleromic dentine. Dentine filling an existing medullary space in bone (or other dentine) or a space produced by resorption; always invasive in form; commonly with numerous dentine tubules restricted in their extent; frequently translucent and may be composed of crystal-fibre-bundles; typically formed as poculae (small pockets of dentine, see Smith, 1977: fig. 14) in areas of wear stress, such as callosities, or beneath and within old dentine, and denticles on pterygoids and prearticulars.

Trabecular dentine. An arrangement of dental tissue in which struts of dentine divide a pulp cavity into many large, soft-tissue compartments which may subsequently be reduced in size by further growth of dentine by apposition onto the primary trabeculae.

Compact dentine. An arrangement of dentine types leaving proportionally very small, soft tissue spaces, as pulp canals, within a dense dentine mass (frequently called osteodentine) filling in the primary pulp cavity.

Macrostructure

Denticles. Small enamel-covered dentine eminences of various shapes formed superficially on demand at any place on the palate and lower jaw at any time, wherever prior resorption makes a space that can be occupied by mesenchyme beneath an epithelium; allows a complete denticulated cover to be maintained at all times (Reif, 1982). Alternatively, similar eminences formed at the lateral margins of the pterygoids or prearticulars on top of new bone (see Smith, 1987).

Teeth. Enamel-covered cones of specialized dentine formed in specific loci at the lateral margins of the palate and lower jaw, aligned with existing older, worn teeth and initiated at predetermined times; allows alternation of sequential teeth in opposing jaws and alternation of opposing tooth rows.

Callosities. Hypermineralized, translucent dentine forming a hard, wear-resistant region raised above the denticulated surface; promoted by growth of pleromic dentine into the subjacent tissues, presumed to grow continuously and to wear less rapidly than the adjacent dental tissues; never enamel covered.

Heel. A raised area of hypermineralized dentine at the posteromedial corner of the pre-articular 'tooth plate'; similar mode of growth to callosities on the palate.