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COMPARATIVE MORPHOLOGY, HISTOLOGY AND GROWTH OF THE DENTAL PLATES OF THE DEVONIAN DIPNOAN *CHIRODIPTERUS*

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

[1] *Unit of Anatomy in relation to Dentistry, Division of Anatomy, United Medical and Dental Schools of Guy's and St Thomas's Hospitals, Guy's Hospital, London Bridge, London SE1 9RT, U.K.*
[2] *Department of Geology, Australian National University, P.O. Box 4, Canberra, A.C.T. 2601, Australia*

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The dental plates of the Devonian lungfish *Chirodipterus australis* Miles (Osteichthyes; Dipnoi) are shown to have achieved their characteristic morphology by a growth process different from that assumed for the plates of genera such as *Dipterus*. Each plate was thickened by the addition of layers of bone that also extended the plate labially, thus providing the base on which and into which dentine grew. Distinctive features of the dentition are: (*a*) labial increase of the dentine mass by the addition of blister-like denticles of simple enamel-covered dentine, which is initially ingrown by pleromic dentine and subsequently resorbed and replaced by petrodentine; (*b*) increase in the midline by a similar process that results in the addition of one (or possibly two) new ridges; (*c*) resorption of the posterior edge of the pterygoid plates and the posterior and posteromedial edges of the prearticular plates, with subsequent development over the resorbed surfaces of several generations of simple regenerative dentine; (*d*) resorption and redeposition of pleromic dentine and bone in a triangular region posteromedially on the pterygoid plates; (*e*) the formation of tuberosities that simulate teeth at a short distance in from the labial edge, by four processes: formation of an undulating plate margin, differential growth of petrodentine (hard compact dentine) within the pulp cavity, differential wear of the petrodentine and the adjacent bone plus pleromic dentine, and slightly greater growth of the petrodentine towards the occlusal surface relative to the adjacent bone and dentine; (*f*) expansion of the large flat surfaces of the plates by gradual replacement of the bone and dentine at the proximal ends of the furrows and also by the development of linkages of petrodentine across the furrows; (*g*) development of isolated tuberosities on the flat posterolateral parts of the plates.

The petrodentine of the ridges, tuberosities and plateaus of the plates is indistinguishable structurally and in its mode of growth from the petrodentine in extant species of dipnoans.

Plates similar to those of *C. australis* have been observed in *Stomiahykus*, *Archaeonectes*, *Conchodus*, *Palaedaphus* and *Sunwapta*, as well as several species usually referred to as *Dipterus*. *Sunwapta* may be congeneric with *C. australis*

We propose that the term 'dental plate' be used as a general term to cover the crushing plates of dipnoans; that the term 'tooth plate' be restricted to those types that grew by the addition of true teeth to the labial margins of the plates, to form radiate rows; and that the term 'dentine plate' be used for those that added dentine to their margins without the formation of teeth. The oldest known genera with tooth plates and dentine plates are *Speonesydrion* and *Dipnorhynchus* respectively.

1. Introduction

(*a*) *General review*

The concept of the dipnoan tooth plate was thought to be simple enough for more than a century. It was understood to be a mass of dentine with radiate ridges varying in number and carrying eminences of various shapes, attached to the pterygoids and prearticulars. The term was confidently applied to plates as different as those of *Dipterus* and *Neoceratodus*. Denison (1974) caused a reappraisal of the way the term was used by indicating that in his opinion *Dipnorhynchus* did not have tooth plates. The reason for his decision was not explicit, but presumably it was because the palate of that genus was observed to be covered with a continuous sheet of dentine, with no median suture between the pterygoids, and no radial tooth rows. Instead, a few large, irregular protuberances occur on the anterior part of the palate, and a crude rim is present around its labial margins. The prearticulars also are almost entirely covered with dentine that forms a continuous sheet across the lingual furrow, together with protuberances complementary to those on the palate. Clearly, discrete tooth plates of the *Dipterus* type were not developed in this genus.

Campbell & Barwick (1983) drew attention to one important aspect of the problem, namely that to exclude *Dipnorhynchus* from the tooth-plated genera, as Denison (1974) has done, was to obscure two important facts: that the dental surfaces of *Dipnorhynchus*, like those of recognized tooth-plated forms, were used for crushing and grew by marginal addition accompanied by basal growth of dentine. It was considered inconsistent that, except for *Dipnorhynchus*, all of the group that lacked tooth plates had buccal surfaces covered with denticles and various marginal structures that were all periodically shed or remodelled. Moreover, although the surfaces of the pterygoids and prearticulars of *Dipnorhynchus* are covered with dentine, they are completely devoid of the enamel-covered teeth that are a feature of such tooth-plated genera as *Dipterus*. Instead, a few irregular, crude tuberosities are present. The thick dental apparatus, the larger spaces for adductor muscles, and the associated shelly fauna, indicated that *Dipnorhynchus* was a shell feeder with a powerful crushing bite. Consequently it was allied with the genera with tooth plates, rather than the denticulate genera such as *Griphognathus* that fed by different means. This being acknowledged, the accepted definition of 'tooth plate' required modification, and the views expressed by White (1966) on this topic were open for reconsideration.

The discovery of *Speonesydrion* (Campbell & Barwick 1983, 1984) appeared to complicate the matter further; like *Dipnorhynchus* it had a continuous sheet of dentine on the palate and the dentine of the prearticular plates extended deep into the lingual groove, but in addition it had four or five radial tooth rows made up of enamel-capped subconical teeth similar to those in *Dipterus*. Hence this dental apparatus included some features of plates with a dentine plateau and some features of conventional tooth plates. More significantly, it was clear that during the early phases of growth, the dentition of *Speonesydrion* grew by the addition of more or less elongate denticles to its lateral margins (Campbell & Barwick 1983) and only later in its ontogeny were the large conical teeth added. Was it possible, therefore, that dentitions of the *Speonesydrion* type were produced phyletically from types that had low relief on the surface, by the gradual differentiation of discrete elevations of the denticle-forming margins of the plate, and by the addition of teeth? If so, the restriction of the term 'tooth plate' to forms in which each of the two pterygoidal plates and the two prearticular plates grew independently at all margins and bore radial tooth ridges, would clearly be arbitrary.

The significance of an adequate definition of a tooth plate has been further emphasized by the fact that several authors have regarded tooth plates as defining a monophyletic group (Miles 1977; Smith 1977). The effect of this on phylogeny has been to isolate *Dipnorhynchus* and *Speonesydrion* as primitive specialized forms (Miles 1977, figure 157). We note that *D. lehmanni* has been referred to *Speonesydrion* by Campbell & Barwick (1984). In an attempt to resolve this problem and to sharpen the tooth plate concept, we began to analyse the dentitions of Devonian genera afresh. It soon became apparent that even among genera normally considered to have tooth plates there was a variety of types that could not be encompassed within the current simple definition, and that confusion had arisen from a failure to take account of the contribution of different types of tissue, and different growth patterns, to the production of plates that had superficially similar adult forms. The first of these to be examined was the plate of *Chirodipterus australis* Miles, a member of the group generally accepted as bearing tooth plates. Bertmar (1968) and Miles (1977) both regarded this genus as a close relative of *Dipterus*. Our current investigations have shown that such a view cannot be sustained. The basis for these conclusions is a study of the growth patterns and histology of the tooth plates of *C. australis*, and comparison of these data with those of the primitive tooth plates of *Speonesydrion* and the more advanced *Dipterus* and *Sagenodus*. We note the considerable differences between the plates of *C. australis* and *C. wildungensis* Gross, the type species of *Chirodipterus*. For present purposes we see no need to explore the taxonomic significance of these differences.

(*b*) *Summary of growth in tooth plates*

Much has been written about the growth of dipnoan dental plates and it has been assumed that all organized tooth plates grow by the addition of teeth to their labial margins. This topic has been reviewed in a subsequent paper (Smith 1987). Whereas it is true that in all genera of extant dipnoans the tooth plates develop in ontogeny from rows of teeth aligned along the direction of the potential ridges (Kemp 1977; Smith 1985), the adult plates no longer grow by the addition of discrete teeth at the labial margins (Kemp 1977, figures 6 and 7; Bemis 1984, figures 5, 7 and 8). However, in many of the Palaeozoic forms, discrete new teeth can be seen at the labial ends of the rows in the adult plate, as well as the juvenile plates, the smallest of which consist of radiate rows of teeth diverging from a posteromedial primary group, just as in the larval stages of the extant forms (Smith 1985, figure 15). For example, enamel-covered teeth (Smith 1984, figures 49–51) are added to the labial margins of the tooth plates of *Dipterus valenciennesi* in line with each worn radiate tooth row, and this is true for most dipterid plates. The size of each tooth in the row increases in a labial direction as figured by Pander (1858, plate 5, figures 1–5 and plate 7, figures 6–9). This process of tooth addition also occurs in *Scaumenacia* (Denison 1974, figure 5), *Sagenodus* (Denison 1974, figure 7) and *Ceratodus parvus* (Denison 1974, figure 8; Peyer 1968, figure 63). Very small juvenile plates of *Dipterus* sp. consist of radiating rows of teeth that increase in size towards the labial margin (Smith 1987, figure 3). This also occurs in *Sagenodus* (Lund 1969, figure 8) and *Monongahela* (Lund 1969, figure 11; 1973, figures 3 and 4). The central region of each new tooth is the site of new growth of an extra hard, specialized type of dentine known as petrodentine (see §4(*a*)). This adds to the width of the columns of petrodentine making up the bulk of the tooth-plate ridges. Such growth has been demonstrated in *Sagenodus* (Smith 1979, figures 3, 4 and 9; Smith 1984, figures 45 & 47), in *Dipterus valenciennesi* (Smith 1984, figures 49–51), and in *Monongahela* (Smith 1984, figure 1); it has also been observed in *Ctenodus* (M.M.S.) and in *Uronemus* (Smith *et al.* 1987, figures 23 and 29).

It is important to recognize that in the dentition of the early Devonian genus *Speonesydrion*, large, conical, enamel-covered teeth were also added to the labial ends of short radiate tooth rows, with an increase in size of each successive tooth (Campbell & Barwick 1983, figure 10); the larger plates have four or five radiate rows of teeth. In addition, irregularly shaped, flattened, elongate denticles are present between the rows, the newest enamel-covered ones being at the labial margins (Campbell & Barwick 1983, figure 10; 1984, figure 30). It was observed by Campbell & Barwick (1983) that the smallest plates of *Speonesydrion* grew by addition of these elongate denticles to the margins, and only in larger plates were large conical teeth added. Smith (1987) has suggested that plates without radiate rows of teeth and margins provided only with denticles, evolved by a process of paedomorphosis. Campbell & Barwick (1985) recognized that the dental surfaces of *Dipnorhynchus* enlarged by marginal addition and basal growth of dentine, though they differ from those of tooth-plated genera such as *Dipterus* because enamel-covered teeth were entirely absent from dental surfaces. Other dental plates, in particular those of *Chirodipterus*, also lack enamel-covered, conical teeth. The plates of both *Chirodipterus* and *Dipnorhynchus* do have irregularly shaped, blister-liked denticles at the labial margins of the plates, similar to those of *Speonesydrion*. Because new tissue can be distinguished from old or worn tissue, and it is generally accepted that enamel-covered teeth at the labial ends of worn tooth rows in radiate tooth plates are evidence of growth, it is realized that the growth of dental plates in which teeth are absent requires a new explanation and that this could be possible by using the range of well-preserved material from the Gogo Formation, Western Australia.

The method of growth extrapolated from the data on a series of dentitions of *Chirodipterus* differs substantially from the accepted pattern for dipnoan dental plates in the following ways: growth at the anterolateral and lateral margins was initiated by sequential layers of blister-like denticles that contour the plate border, and not by conical teeth at restricted points along the margin; the elevated regions along the plate, in from the plate margin but at the labial ends of the radiate ridges, are tuberosities of petrodentine that were not derived from enamel-covered teeth as in tooth plates, but from growth of petrodentine initiated at a short distance in from the plate border.

2. Materials

(*a*) *Sources*

We have examined the complete collection of specimens of *Chirodipterus australis* Miles and *Chirodipterus paddyensis* Miles from the Gogo Formation, Canning Basin, Western Australia, now housed in the British Museum (Natural History) (BMNH). Specimen numbers have been listed by Miles (1977, p. 12). These are identified by the prefix P.

A collection of specimens from the Paddy's Springs locality of the Gogo Formation, housed in the Geology Department, Australian National University, Canberra, A.C.T., Australia, and another collection from the same locality housed in the Bureau of Mineral Resources, Canberra, A.C.T., Australia, has been studied in detail by a variety of techniques. Specimens from these two collections bear the prefixes ANU and CPC respectively.

For comparative purposes we have examined the type material of: *Stomiahykus thlaodus* Bernacsek and *Archaeonectes pertusus* von Meyer; collections of *Conchodus ostraeformis* McCoy; plaster casts of the type specimens of *Sunwapta grandiceps* Thomson and *Palaedaphus insignis* von Beneden & de Koninck. Finally, we have been able to make direct comparisons with the type and other material of the early Devonian *Dipnorhynchus sussmilchi* (Etheridge) and *Speonesydrion iani* Campbell & Barwick.

(b) Preparation

The Gogo specimens of *Chirodipterus* in the BMNH collection have all been prepared by the acetic acid technique, and previous histological studies (Smith 1977) using this material have depended on thin sections and broken surfaces that have lost detail as a result of this treatment. Further, small structures that were loosely attached to some of the dental surfaces, such as denticles in the early stages of formation, have probably been dislodged during preparation.

Thin sections of some ANU and CPC specimens still embedded in the limestone matrix were prepared by Campbell & Barwick (1983). This method ensures that all the fine detail is preserved. Further, the impregnation of even the finest of spaces within the hard tissues by chemically deposited carbonate makes examination in polarized light more effective, and permits the use of incident ultraviolet microscopy to reveal details that would otherwise remain obscure. This latter method is referred to in the appropriate section below.

We have also found it advantageous to cut the unetched specimens with a thin diamond-tipped blade, to prepare a thin section from one face of the cut, and then etch the other face in dilute HCl for examination by scanning electron microscopy (SEM). This comparison of adjacent surfaces by different methods has provided the opportunity to interpret otherwise obscure relationships.

Finally, some unetched fragments have been prepared by the ion-beam thinning method so that they could be examined by transmission electron microscopy (TEM). This has permitted the resolution of detail in the pattern of microcrystallites of hydroxyapatite forming the dentine.

3. Observations: macrostructure

(a) Terminology and form of the plates

It is necessary to define a number of new terms to describe adequately the gross morphology of these dental plates. Each plate consists of a smooth undivided posterior portion, termed the 'plateau', that breaks down anteriorly into a number of anteriorly and anterolaterally directed ridges. The only terms used by Miles (1977, p. 291) to designate gross plate form were 'a shelving mesial ridge' and 'diverging anterolateral ridges'.

The plateau of the pterygoid plate is gently concave and that of the prearticular more strongly convex. With the jaws in the closed position, each ridge interlocking with that of the opposite plate, the plateaus do not make contact. Therefore wear and tissue loss in this part could result from abrasion but not attrition; abrasion is wear that is consequent upon the type of food (i.e. wear due to tooth–food contact), and attrition is wear resulting from tooth–tooth contact, which in *C. australis* was possible only at the anterolateral and anterior margins of the plates (see §6(*c*)).

We have not distinguished between a 'mesial ridge' and those distal or lateral to it as did Miles (1977, p. 292) because we consider that plate growth occurs along the mesial as well as the lateral border. The first formed, or 'mesial', ridge is not the one adjacent to the midline suture in adults because of the late addition of a new ridge (§3(*c*)(i)). The region between adjacent ridges we have termed a furrow. The anterior portion of some furrows is deeply pitted; each pit occludes with a knob-like prominence on a ridge of the opposing plate to produce a pestle and mortar effect. A third new term is 'tuberosity', which we use for the discrete prominences at the anterior ends of established ridges, and the isolated posterolateral prominences in the position of a potential new ridge (figures 1 and 6). Miles (1977, p. 293) referred to these structures in *C. australis* as denticles, although he also described the same features in *C. wildungensis* as tubercles arranged in radiating rows. In thus defining 'tuberosity' we wish to draw attention to the morphological differences between denticles, tuberosities and teeth. The term 'denticle' is used for small enamel-covered structures, composed of simple dentine, and irregularly spaced on newly formed bone surfaces. In *Chirodipterus* those at the margins are blister-like and occur in close-formed clusters (§3(*d*)). They were not lost by resorption at their bases as were the sub-conical and isolated denticles on the palates and prearticulars of *Griphognathus*. Teeth, on the other hand, are larger enamel-covered structures, often formed of complex dentines, and are initiated at precise positions at the labial plate margins so as to produce radial ridges.

Throughout this account we have interpreted growth patterns from a size-graded series of adult plates in which details of the surface structure are well preserved (§3(*c*)). In addition, we have interpreted surfaces with distinctive resorption patterns (universal to all vertebrate hard tissue; see Smith (1977, figure 65) for an example in a fossil dipnoan of this period) as remodelling regions; and where relationships indicate that resorption has been followed in the same position by deposition of unworn, flat enamel-covered dentine, we have referred to such tissues as regenerate patches (§3(*e*) and §4(*d*)). Areas where only newly formed tissue is consistently observed, that is, areas where new tissue was continuously added to the plate, are termed 'constructional'.

The number of ridges and their lengths are not correlated with the size of the plate as can be seen in figure 1, which illustrates only the pterygoid plates. The same figure shows the variation in outline of the plates, but this feature does show a clear relation to size. The younger specimens are definitely pentagonal. In the late growth stages, however, the posterolateral angle becomes less prominent, largely as a result of resorption, but also because new ridges are added anterolaterally, expanding the plate in front of the angle in question.

The posterior edges of the plates reach almost to the parasphenoid on some specimens, but the sutures are never overgrown and no dentine ever occurs on the parasphenoid. On other specimens, for example ANU21639, ANU345639, and P56042 (figure 3) this edge of the plate is strongly resorbed and irregular in outline, and the margin of the plate is some distance from the pterygoid–parasphenoid suture. On ANU35639 resorption extends forwards along the median line to the mid-length of the plate. Again, there is no correlation between the size of the plate and the extent of the resorption. Therefore, throughout the life of the animal, resorption must have been a process that took place at intervals, the phasing of which may have been regulated with that of the basal bone growth.

(*b*) *Radial ridges, furrows and tuberosities*

Like the main body of the plate, the radial ridges are formed of hard, dark-coloured dentine, and the two elements (the ridges and the plateau) merge without any discontinuity. The ridges have a distinctive arrangement in specimens of all sizes. A strong one, almost invariably the second from the midline, has an arcuate form and runs backwards to make a hard, wear resistant, continuous shallow ridge bordering the plateau area of the plate (figures 2–9). This continuous ridge frequently stands proud of all the surrounding tissues and is presumed to be equivalent to the shelving mesial ridge of Miles (1977, p. 291). Medial to it on the anterior part

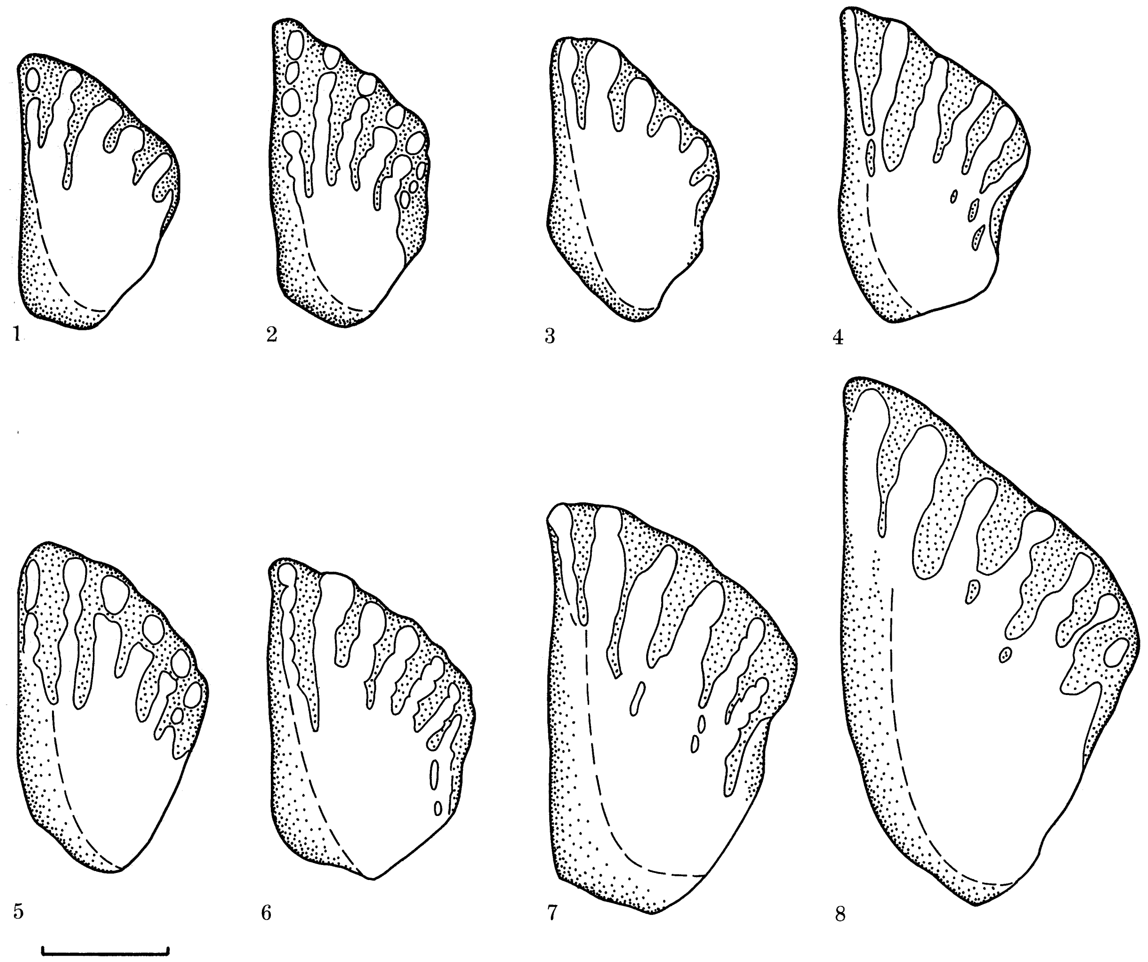


FIGURE 1. (Scale bar 1.0 cm.) Outlines of the right prearticular tooth plate arranged in an inferred growth series. Numbers 1–8 are from specimens ANU21638, ANU35637, P52561, P56042, ANU21639, P56038 and ANU35639. Increase in area between (1) and (2) occurs at the labial margin; the tuberose ridges may become continuous as in (3) and (4). By (5) a new medial ridge is beginning, until consolidated as one of the main ones as in (6). A second medial ridge may have been added in (7) and (8).

of the plate is a ridge of variable length. This joins, or almost joins, the strong arcuate ridge. From its position and its relation to the surrounding bone, which is impregnated with translucent dentine, it is clear from its structure that this medial ridge is not the first one to be formed, but is added after the juvenile stages as a consequence of growth of the plate towards the mid-line. So far as we can see, only one or rarely two ridges were added to each plate in this way, at least in the growth range that we have available. Tracking growth lines in sections of the plate provides support for this view, as illustrated in figure 70.

Ridges are also added at the posterolateral margin of the plate, and again this process conforms to the pattern being described as distinctive for *Chirodipterus*. Whereas a single tuberosity is formed at the anterior or anterolateral ends of the established ridges as the plate margin expands, at the most lateral margin (figures 6 and 8) irregular rows of tuberosities have been formed as the plate expanded laterally. Some of the smallest specimens, for example ANU35637 (figure 8), have these isolated tuberosities of hard dark dentine near the lateral margin of the plate, but interior to the actual margin; it is assumed that they initiate a complete new ridge. Somewhat larger specimens have a short row (ANU21639) or two or three rows (CPC56042) of such tuberosities still not joined by hard dark dentine to the main dentine mass. Finally, in the largest specimens, these have become confluent with one another and with the main mass.

On specimens with short ridges and without any divisions into tuberosities (figures 1 and 9), such as ANU21637 and ANU21638, new ridges have been added and now form contiguous growth zones with the rest of the plate. Two or three lateral ridges must have been added in this way during the growth of an individual, judging from the results of this growth observed on both the type of wear pattern of the ridges and the histology of the tissues (§4(*e*) and §4(*f*)). By extrapolation from the larger plates we conclude that a tooth plate 5 mm wide would have consisted of a small flat patch of hard dentine with three or four anteriorly directed ridges. We cannot infer the shape of smaller plates from the material currently available.

On some individuals, particularly those with ridges that are long relative to the remainder of the plate, the ridges have a markedly tuberose structure over most of their length. Some even show the tuberosities isolated from one another (ANU35637, P52563 and P52564, figures 8 and 10) though normally they are connected in a string-of-beads fashion. This gives an appearance similar to the worn tooth rows of some species of *Dipterus* or *Sagenodus*. However, the tuberosities are never enamel-capped, even near the plate margin, which is the position where new enamel-capped teeth are added to radiate tooth plates. Moreover, they never lie precisely at the plate margin; bone or dentine blisters or both (see below) always extend beyond them.

Other individuals show all variants from nodular to straight, smooth-edged ridges, occasionally on opposite sides of the same specimen (for example P50101, figure 9). The explanation of this is that the ridges are the sites of greatest differential growth of hard dark dentine (petrodentine as described in §4(*a*) on the histology) and bone in apposition. The deepest penetration of translucent dentine into the underlying bone occurs at the sites of the furrows (figure 53) (pleromic dentine as described in §4(*b*) on the histology). A ridge may increase its length by the uniform continuous growth of ridge dentine into the bone at its distal end, or it may grow episodically into the bone in patches. The former produces a continuous ridge, and the latter produces various degrees of tuberosity.

The furrows between the ridges are floored by bone partly filled in by translucent dentine. Because this dentine is much harder than the bone it infills, the bone is preferentially removed by wear and the surface appears irregularly pitted; and because the dentine is much darker or more translucent, the whole tissue appears speckled (figures 10 and 31). While the crests of the ridges became worn, resorption of the bone beneath the ridge was proceeding to produce an extensive pulp cavity. These resorption spaces were filled with further appositional growth of hard dark dentine, and other dentine penetrated into the small bone spaces both lateral and medial to the ridges. The pattern of invasion was not random. As is well shown by ANU35637 and ANU35639 (figures 3 and 8), it took place more rapidly between adjacent wear pits within a furrow, that is, in the areas of least tooth–tooth contact stress (intertuberose regions). In this way the tuberosities of adjacent ridges tended to become linked, leaving isolated lakes of translucent dentine and bone to become completely replaced after further wear and growth (figures 4 and 8). At the same time the proximal ends of the furrows were continually being remodelled, first by the bone spaces at the base of the ridge infilling with dentine, and then by the hard dark dentine (petrodentine) secondarily taking its place as the smooth part of the plate extended forwards (see §4 for the histology of these tissues).

After light etching of the worn surfaces, an SEM preparation of two of the most distal tuberosities from specimen P52564 revealed an extensive previous resorption surface at the junction between hard dark dentine and the bone-with-dentine (figures 12 and 13). This was a reversal surface where the process of tissue removal was stopped and changed to tissue deposition. This suggests an active remodelling of the junction between the petrodentine of the tuberosity and the intertuberose tissue of dentine and bone. As a result, petrodentine could grow occlusally relative to the bone-with-dentine, a form of transitional tissue at the margins, and thus increase the height of the tuberosities relative to the pits or furrows. Evidence of this remodelling is also demonstrated in the section on histology (§4(*e*)). Serial sections through the tooth plate *in situ* in fact do show extensive pulp cavities beneath the tuberosities (figure 70), as would be expected in a situation where a change of tissue is occurring.

The following summarizes our conception of ridge formation as outlined in this section:

(*a*) ridges mark sites of strong appositional growth of hard dark dentine (specialized compact dentine) within the underlying bone;

(*b*) such growth continued in a regular linear fashion at the anterior end of each ridge and spread more slowly into the mixed tissue of the furrows;

(*c*) at specific distances in from the plate margin this type of dentine growth took place either continuously or episodically, producing unbroken or tuberose ridges respectively;

(*d*) the most medial ridge and two or three of the most lateral ridges were added as the result of the formation of groups of tuberosities appearing at approximately the same time some distance in from the margin of the plate;

(*e*) the inter-ridge furrows were initially sites of growth of dentine into the bone spaces with little resorption of the bone, but with increasing age the form of dentine called dark dentine, a specialized compact type, grew into them from the borders of the ridges and the continuous posterior dentine sheet. With further wear this sheet then became more extensive.

Description of plate 1

Figure 2. (Scale bar 1.0 cm.) P56039. Palate showing: broad flat ridges without tuberosities; an incomplete medial ridge, late to develop; the irregular invasion of the furrows by worn-smooth petrodentine, and a continuous smooth surface of petrodentine in the arcuate shape of the medial region.

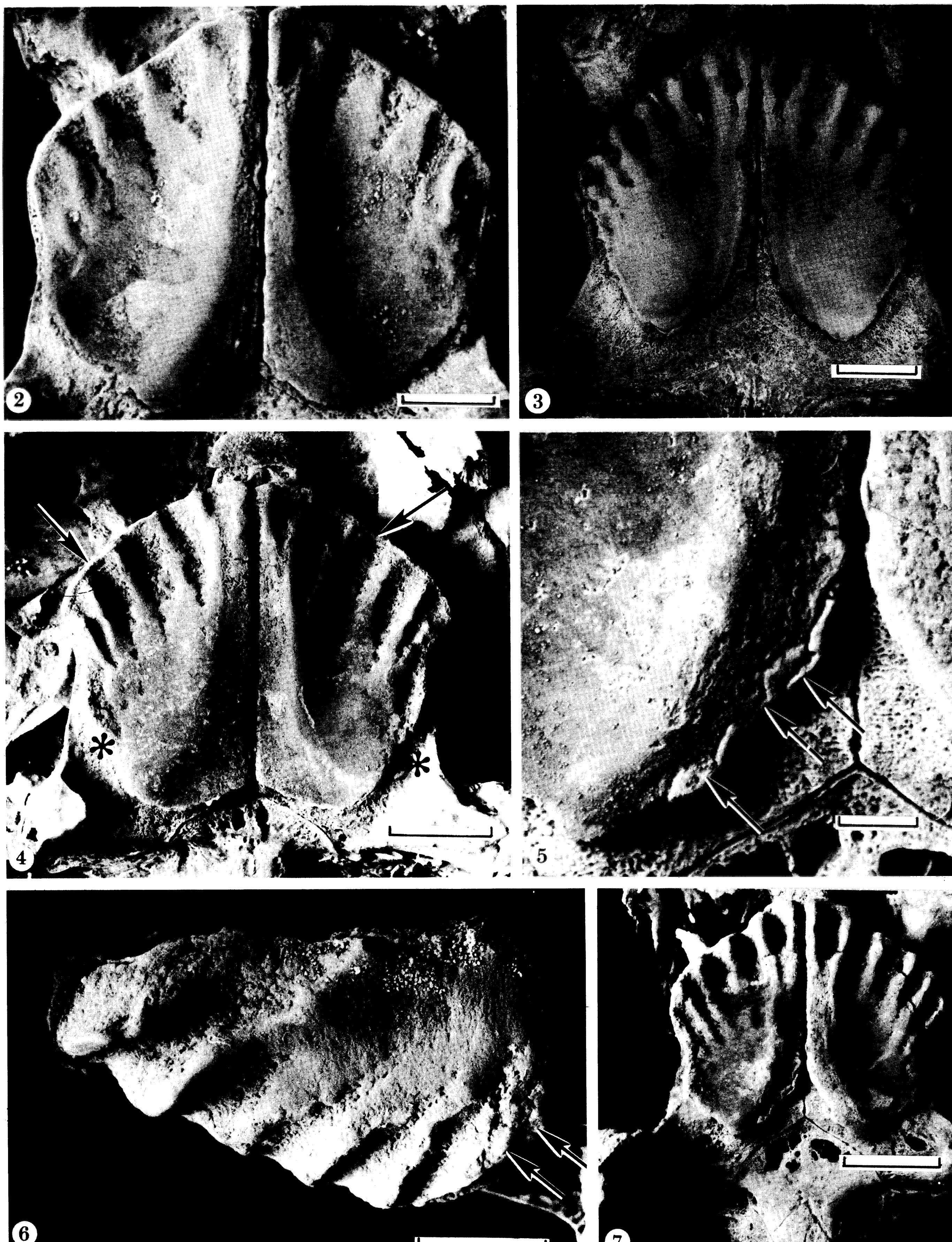
Figure 3. (Scale bar 1.0 cm.) ANU35639. Palate of a large specimen showing maximum resorption around the posteromedial and posterolateral edges of the entire posterior half of the plates. Resorption is less complete medially on the right plate. Regenerative tissue is present in two small patches on the right plate.

Figure 4. (Scale bar 1.0 cm.) P56038. Palate with worn, slightly tuberose ridges. Note the band of bone-plus-pleromic-dentine around the anterolateral margins of the plates (arrows) and the similar patch formed posterolaterally (asterisks), relative to the more complete posteromedial tissue.

Figure 5. (Scale bar 0.2 cm.) P56042. Posteromedial part of the palate of a small individual (as in figure 7) in the process of regrowth after a period of extensive resorption. Note the roughness of the worn surface relative to the adjacent smooth petrodentine and the irregular blisters of regenerative dentine (arrows; see also figure 7).

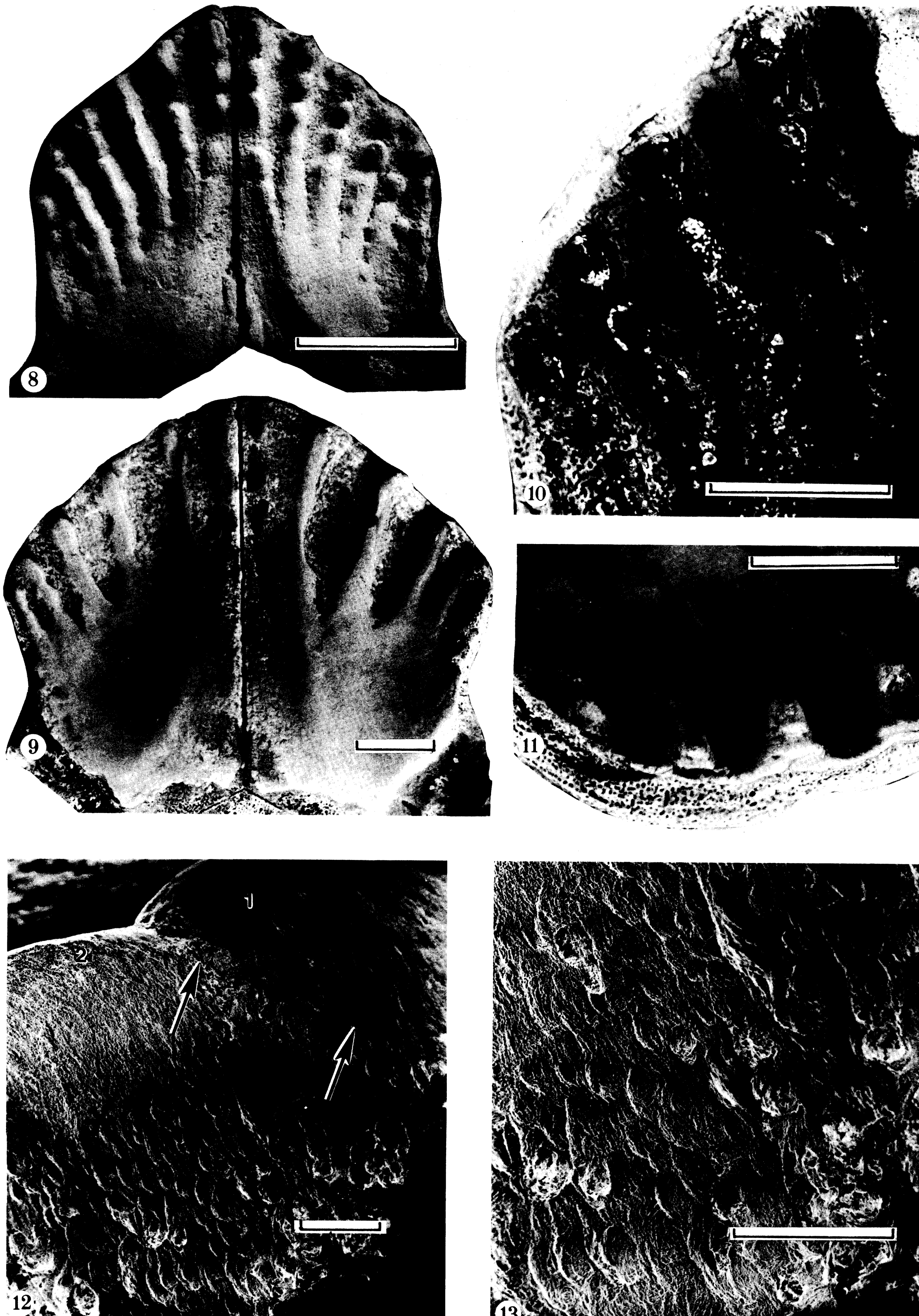
Figure 6. (Scale bar 0.5 cm.) P56042. Left prearticular plate of specimen in figure 5, oriented with anterior end to the left. This also shows is a phase of growth by the formation of two rows of semi-isolated, rounded tuberosities on the posterolateral part of the plate (arrows).

Figure 7. (Scale bar 1.0 cm.) P56042. The whole palate of the specimen figured in (5) above. Note the effect of a marked growth disturbance producing a disruption in the ridges, and more obvious tuberosities at the end of the fifth ridges in the latest growth phase.



FIGURES 2–7. For description see opposite.

(*Facing p.* 338)



FIGURES 8–13. For description see opposite.

Description of plate 2

Figure 8. (Scale bar 0.5 cm.) ANU35637. The palate of a small individual of *Chirodipterus australis* with long tuberose ridges, and transverse bridges of petrodentine in the central region. These isolate small patches of bone-plus-pleromic-dentine at the proximal ends of the furrows. Note also the shape of the bands of bone-plus-dentine forming the posteromedial parts of the plate and the isolated tuberosities making partly formed ridges on the posterolateral part of each plate.

Figure 9. (Scale bar 0.5 cm.) P50101. A moderately large palate with very narrow ridges and indistinct tuberosities. The furrows are much wider and the shape is distinctive. Note also that even at this size the medial ridge is still almost isolated from the arcuate ridge bordering the main petrodentine plateau.

Figures 10 and 11. (Scale bars 0.5 cm.) P52564. Ventral and anterolateral views of the anterior part of a right and left pterygoid respectively. Figure 10 has not been whitened with NH_4Cl, and hence shows the contrast between the petrodentine of the ridges and tuberosities and the bone-plus-pleromic-dentine of the furrows. Figure 11 is whitened and shows the layering in the basal bone and above the marginal blisters on the surface of the bone at the base of the established ridges, but still a short distance lateral to the centre of the tuberosities.

Figure 12. (Scale bar 300 μm.) P52564. Scanning electron micrograph of two fragments of the tooth plate margin, just two tuberosities (1 and 2) of the prearticular plate prised out from between the second and third ridges of the palate in the previous figures (10 and 11). The surface of the specimen has been etched with HCl, up to the line (arrowed: the rest protected by varnish) to reveal details of the tissue, petrodentine at the top of the tuberosity, and the extensively resorbed basal tissue (from the asterisks downwards, and magnified in figure 13).

Figure 13. (Scale bar 300 μm.) Enlargement of the basal part of the tuberosity in figure 12, showing the typical scalloping of previous episodes of resorption by osteoclasts at the junction between growing petrodentine and the bone-plus-pleromic-dentine.

FIGURES 14–20. For description see opposite.

Description of plate 3

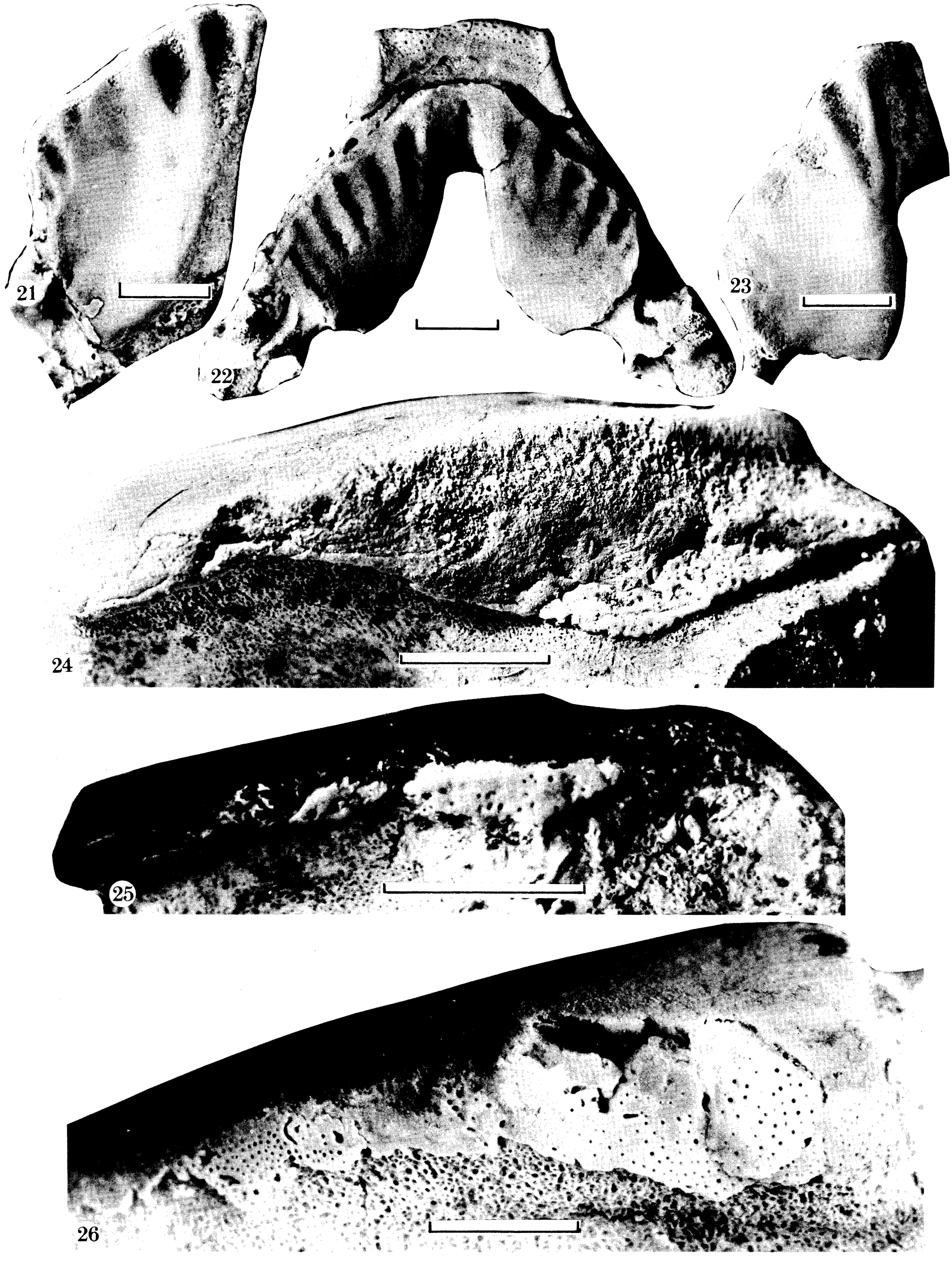
Figure 14. (Scale bar 0.5 cm.) P56034. Right side of mandible of *Chirodipterus paddyensis* Miles, showing the strongly undulose margins of the prearticular plate and the numerous small dentine blisters aligned with this undulose margin (see also figure 32*a*).

Figure 15. (Scale bar 0.5 cm.) P56034 enlarged showing the blisters at the ends of the second and third ridges. They have become progressively worn as they merge with the worn surface of the ridge ends.

Figures 16 and 17. (Scale bar 0.5 cm.) P56034 in dorsal and posteromedial views. Note particularly the double row of tuberosities forming the medial ridge, the large number of irregularly shaped denticles around the medial and posterior edges of the plate, and the incomplete dentine sheet extending from the medial ridge down into the furrow. The dark patches in this sheet are the result of staining during fossilization.

Figures 18 and 19. (Scale bars 0.5 cm.) NM22600. Ventral and ventrolateral views of the palate of the holotype of *Stomiahykus thlaodus* Bernacsek. Note the marginal blisters, the incomplete ridges at the medial side of the plate, the exposed pulp cavity (arrow) where a ridge has been broken away, the enlarged tuberosities at the anterior end of the medial rows, and the non-tuberose surface forming the posterolateral part of the left plate.

Figure 20. (Scale bar 0.5 cm.) NM22600. Enlargement of the anterior end of the parasphenoid and adjacent pterygoids. Note the irregular denticles forming a strip across the posterior end of the pterygoids and the median part of the parasphenoid. The granulose surface on the parasphenoid and adjacent pterygoids results from the ends of hard pleromic dentine patches standing slightly proud of the surrounding tissues.



Figures 21–26. For description see opposite.

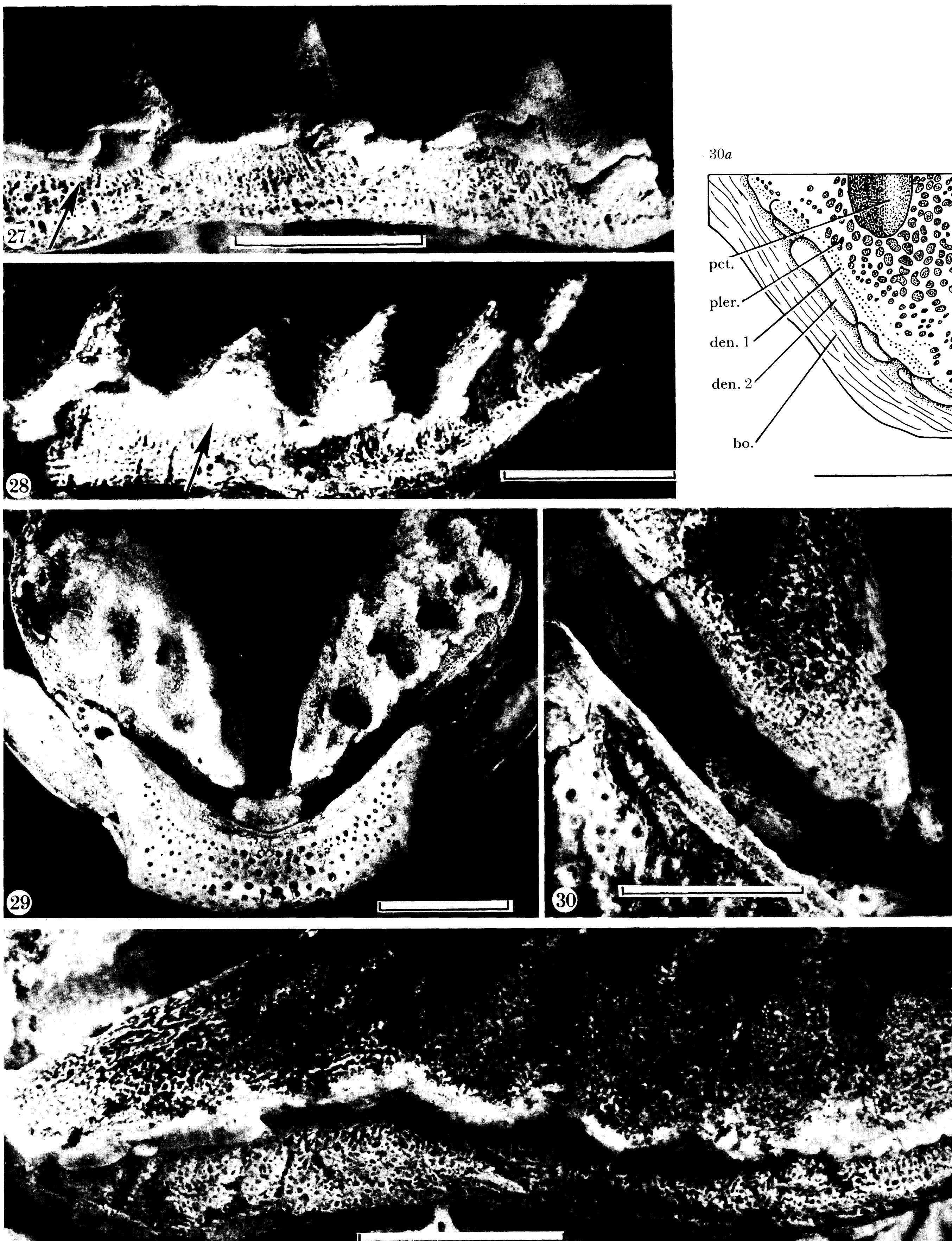
Description of plate 4

Figure 21. (Scale bar 0.5 cm.) P52561. Right pterygoid tooth plate of a small specimen of *Chirodipterus australis* showing where the central flat portion extends to the extremity of some of the ridges.

Figure 22. (Scale bar 1 cm.) P52584. Dorsal view of the mandible of *Chirodipterus australis* showing dentine growing across the anterior end of the lingual groove, the posterior corner having been removed by resorption.

Figure 23. (Scale bar 0.5 cm.) P52561. Left prearticular plate. Note the growth laminae in the bone and dentine around the labial margin with the petrodentine of the ridges forming within it.

Figures 24–26. (Scale bars 0.5 cm.) CPC25727, P52561 and P52585. The lingual sides of the prearticular plates of three mandibles showing patches of regenerative dentine. Figures 24 and 25 have the anterior to the right and figure 26 to the left. Figure 26 shows as many as nine episodes of growth. The dentine has grown on bone and in old petrodentine. Figure 25 (unwhitened) shows the black petrodentine, the black and white, pleromic dentine in bone and the white enamel-covered regenerative dentine. Figure 26 shows the deep resorption bays cut into the petrodentine, filled with punctate regenerative dentine, and the finely trabeculated new bone.



FIGURES 27–31. For description see opposite.

Similar comments may be made about the radial ridges and tuberosities of *Chirodipterus paddyensis* Miles, which also comes from the Gogo Formation. Tooth plate material is rare, but the right prearticular is well preserved on P56034. Distinctive features are the presence of an ancillary row of tuberosities lateral to the main row forming the medial ridge (figures 16 and 17), the existence of three main ridges and an incipient fourth, and the reduction of the posterolateral corner of the plate compared with that of *C. australis*. Wear pits are well developed, particularly in the labial ends of the more posterior furrows (figure 16). The gross form of the plate, and the elongate shapes of the tuberosities on the three main ridges, set this species apart from *C. australis*, but the plate type and structure and the mode of formation of the tuberosities leave no doubt that the two species are closely related.

(*c*) *Medial and posterior growth of the plates*

Throughout this account we have interpreted growth from a size-graded series of adult plates and from observations of the position of new (constructional) tissue relative to worn tissue and to resorption areas undergoing remodelling.

As indicated previously, the larger plates show that they have also expanded medially and posteriorly relative to the smaller ones. This can be seen to have taken place by the addition of tissue of the same type as that between the anterior ends of the ridges. As the new bone was added along the posterior part of the median suture it was rapidly invaded first by dentine and subsequently replaced by the hard, dark, specialized compact dentine. We need to consider this process in the anteromedial, posteromedial and posterolateral regions separately, because the processes involved in each are distinctive.

(i) *Pterygoidal plate*

The medial ridges occur only on the anterior half of the plates and are usually narrower and higher because they are less worn than the adjacent ridges, which they usually join in a distinctive fashion. On some specimens (figures 4 and 7), and as clearly shown in the composite drawing (figure 1), these ridges are close to the medial suture, but in others (for example ANU35636) they are separated from it by a narrow strip of bone intergrown by dentine. These features suggest that certainly one ridge, and possibly two, are added to the plate after it is half grown, and that these ridges are the product of growth in both anterior and medial

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Description of plate 5

Figures 27 and 28. (Scale bars 0.5 cm.) P57000 and P56042. Lateral margins of a pterygoid and a prearticular plate of *Chirodipterus australis* showing two variations in the conformation of marginal blisters. Note the stack of blisters (arrow) adjacent to one ridge-end. These are most easily compared with the drawing (figure 32*b*).

Figure 29. (Scale bar 0.5 cm.) ANU21634. Anterodorsal view of a mandible with the adsymphysial plate in position, showing the undulating row of blisters and extension of the anteromedial part by anteriorly placed blisters.

Figures 30, 30*a* and 31. (Scale bars 0.5 cm.) P52584. The anterior end of a right prearticular, and dorsolateral view of a left prearticular of the same specimen. Surface unwhitened. Note particularly the three degrees of wear of blisters, first the newest unworn (den.2), second worn (den.1) to expose the very narrow lumen of the terminal ends of the pulp canals, and third where denticle tissue is transformed by dark pleromic dentine growing within the trabecular dentine. The drawing (figure 30*a*) shows the position of these tissues in figure 30; note that the dark pleromic dentine is less extensive, towards the anterior extremity of the plate. Note that the highest elevations of the ridges are entirely black petrodentine, and the slopes leading up to them have progressively more black, pleromic dentine within the bone.

directions. The ridges are extended at their anterior ends, and all tissues expand medially with further growth. In some individuals, the rate of addition at the median suture is too fast for ridge growth to keep pace, and so a strip of bone-plus-dentine is developed along this edge.

The pattern along the posterior part of the median suture is quite different from this. Medial expansion takes place by the addition of regenerative patches of new bone and dentine, followed by dentine as an infill to the vascular spaces in the bone and the dentine, to form a strip of tissue that is an elongate triangle in outline (figure 9). Hard dark dentine grows across from the body of the plate into this tissue, expanding the area of the plateau, as the primary regenerative tissue is remodelled. Concurrently, episodic resorption took place from the posterior end of the median suture and moved forwards to the mid-length of the plate, until most of the worn dentine-impregnated bone was removed. Regrowth then began, the new area of dentine being laid down at a slight angle to the midline (figure 5). The adaptive or functional significance of this is not understood.

The posterolateral margins of the plates do not show evidence of new construction (areal growth) because bone strengthened with dentine is not observed within these edges. They are entirely formed of dark hard compact dentine, the margins of which show strong evidence of resorption but not rebuilding. Occasionally temporary patches of thin perforate dentine occur infilling embayments in this region, deep to the tritural surface. These are discussed below as regenerative patches.

(ii) *Prearticular plate*

The prearticular plates sometimes show that areal growth has occurred anteromedially so that the two plates meet in the midline (figure 22). This growth is produced by new bone with dentine infill of the same type as that on the palate. However, many specimens show the plates entirely separate. Within this medially growing anterior part, a partly developed ridge occurs on some specimens, for example P52584, although on that specimen it is present on the left side only.

Because a space has to be left for the basihyal–basibranchial system between the plates, and this has to be increased in size during growth, the whole length of the medial margins of the plates shows strong evidence of resorption that cuts deeply into the dark compact dentine. Deep embayments are frequently covered with regenerative dentine of several generations (figures 24, 25 and 26). The different degrees of wear can be seen in the same way as discussed below (§3(*d*)) for the generations of marginal blisters.

The posterolateral margins of the plate also show extensive resorption, and temporary repair as described for the pterygoid plate.

(*d*) *Marginal blisters*

On both pterygoid and prearticular plates there is a series of blister-like denticles of dentine covered with enamel (figure 32) along what are regarded as constructional margins. These denticles are either isolated or form overlapping series, and occur on the anterior, lateral and medial edges. As many as four generations of blisters can be observed on P52561, a small left prearticular plate; on P57000, a right prearticular plate; and on P50101, a pterygoid plate (figures 27, 28 and 31).

These generations are recognized by the extent to which they are fused with the tissue of the plate, their overlapping relationships, and the varying degrees of wear, clearly identified by the

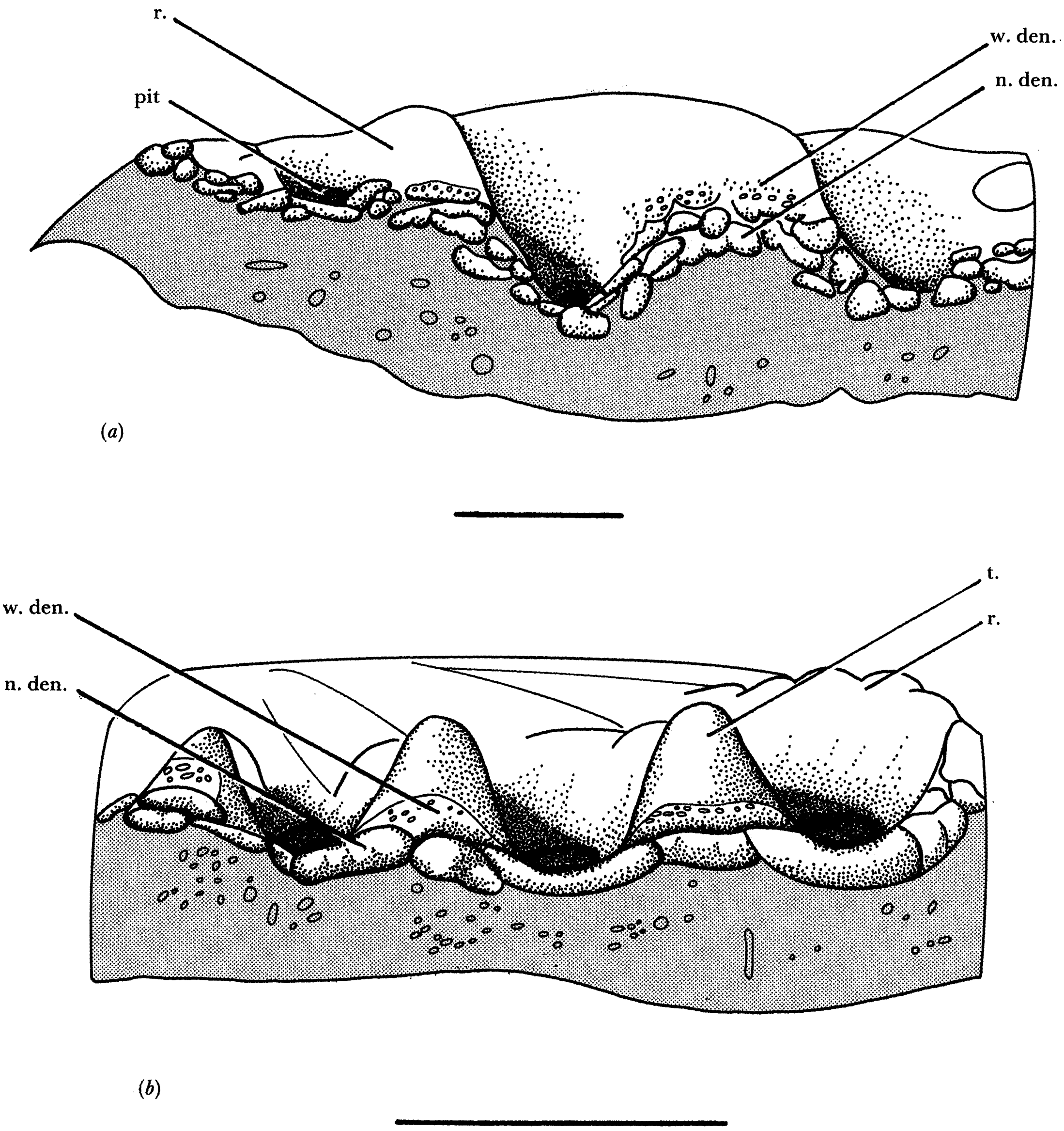


FIGURE 32. (Scale bar 0.5 cm.) Drawings of the labial margin of the tooth plates in *Chirodipterus paddyensis* (*a*) and *Chirodipterus australis* (*b*) to illustrate the addition of marginal denticles on the vertical labial bone surface and their progressive wear as they merge with the distal ends of the ridges (specimens P56034 from figure 14, and P52564).

size of the exposed dentine structures. With increasing wear, denticle surfaces change from smooth unworn enamel, through a stage with fine punctations which are the terminal dentine tubules, to the less fine exposed pulp canals of the dentine surrounded by rings of translucent dentine (figures 30 and 31). These features have been previously illustrated in the denticles and worn surfaces of *Griphognathus whitei* (Smith 1977, figures 3, 4 and 5) and discussion of them is developed in the following account of a time-and-wear-graded series of denticles in *Chirodipterus australis*.

New denticles vary in size and shape: the smallest ones are almost equidimensional, the largest are five or six times longer than they are high (figures 29–31). The elongate ones that occur in an age sequence have the oldest members inside and fused with the dentine-and-bone of the plate, and their surfaces are worn to expose the ends of the pulp canals which are still smaller than those of the adjacent dentine of the plate; progressively younger ones cascade away from the functional surface and are less worn, the youngest ones retaining a complete enamel cover. Such blisters build out the edge of the plate in advance of the ridges and result in marginal layering which is well seen on P52561 and P52584 (figure 23).

Blisters form across the dentine–bone junction and thus prepare the way for the advance of dentine replacement in a later phase of development. Although they are clearly adding to the plate margin and are associated with actively expanding regions of the plates, they do not directly transform into the ridges or the tuberosities in the same manner as a new tooth at the margin of a *Dipterus* plate is converted into a worn tooth or toothed ridge. However, because they mould themselves to the established undulose plate edge and they determine the position of the subsequent growth of dentine by acting as a primary scaffold, they reinforce the pattern of ridges. Development of the ridge tissue is by growth of hard dark dentine into the secondary scaffold of bone-plus-dentine. In this regard it is interesting to observe that the length and discreteness of the ridges and tuberosities were at least in part determined by the disposition of these blisters. This was achieved in the following way: at the end of a ridge, either a stacked series of larger blisters or a strongly undulating continuous row of blisters, one of which is enlarged and therefore higher, was produced; an intertuberose position was formed by a less undulating row of smaller blisters; in addition to the pattern outlined in this statement, which refers to the vertical lateral margins of the plate, blisters sometimes extended horizontally at the ends of ridges, and into these extensions the compact hard dentine grew more rapidly to initiate new tuberosities (figures 27 and 31).

Similar blisters were also present along the medial and posteromedial edges of the pterygoid plates just in front of the parasphenoid. In the latter region they were present only during growth phases. For example, P56042 had previously undergone considerable resorption, and when it died it was beginning the process of regrowth (figures 5 and 7).

In summary, the blisters in *C. australis* serve to initiate the growth of dentine on bone in a superficial position at expanding plate margins, whether this is at a continuously growing edge (for example anteriorly and anterolaterally in both tooth plates) or at regrowing resorption edges (the posteromedial edges of the pterygoid plates).

In *C. paddyensis* the marginal blisters along the labial edge of the plate are small and form a highly undulose edge (figures 32*a*, 14 and 15). They encroach high up on the end of the lingual ridges and it is probable that their positions have influenced the peculiar double row of tuberosities that this ridge shows (figures 14, 16 and 17). There is a greater depth to the blister area than in *C. australis*. It is considered that the different distribution of marginal denticles reflects genetic differences between the species, and accounts for the difference in the form of the plate.

(*e*) *Regenerative patches*

As indicated above, the lingual edges of the mandibular plates and the posterolateral edge of the pterygoid plates of *C. australis* are sites where extensive periodic resorption occurred without evidence of significant regrowth – certainly no permanent regrowth. Resorption removed compact dentine as well as bone impregnated with dentine. If the animal died before the resorption phase was complete (ANU21639) a ragged sharp edge was left as the evidence of ongoing resorptive activity. However, after completion of that phase temporary repair took place and unworn enamel-covered patches were left on the surface. This is best preserved on P52585, a larger mandible (figure 26). First, the resorbed surface was covered by a thin layer of finely trabeculated new bone. Secondly, this was covered by a thin layer of enamel-coated dentine, the surface of which shows numerous perforations. The new tissue occurs in irregular patches without any sign of pattern, suggesting that it was formed in a number of episodes with the tissue of successive stages lapping around the margins of its predecessors. The edges of the resorbed surfaces may still be exposed in places, giving the impression of an imperfect repair. On CPC25737 as many as nine episodes of deposition are recorded (figures 24–26). These vary from small patches about the size of denticles, to elongate strips 5 mm long. In general they become progressively younger towards the deeper parts of the lingual furrow.

It must be emphasized that though this tissue is to some extent rebuilding the plate margin its main function appears to be the provision of a temporary surface, or a regeneration phase between periods of resorption. In this sense it effects temporary repairs to a non-growing edge while an expansive phase is proceeding along the anterior and anterolateral plate margins.

This tissue bears a superficial similarity to the so-called cosmine on the medial parts of the pterygoid tooth plates of some specimens of *Dipterus valenciennesi* (White 1965; Denison 1974). This is largely the result of its perforate enamel cover. However, in *D. valenciennesi* the 'cosmine' is not reparative, lapping as it does across the first tooth row and around the bases of the teeth where no resorption has taken place.

Posteriorly the plate of *C. paddyensis* is extensively resorbed, but there are no reparative patches like those of *C. australis*. Rather, there is a mat of interconnected 'denticles' composed of enamel-covered simple dentine (figures 16 and 17). These extend around the posteromedial angle of the plate and form a layer flooring the whole lingual furrow (figure 17). In places they appear to have coalesced. In general appearance these 'denticles' are similar to the so-called vermiform denticles of *Speonesydrion*.

4. Observations: histology

The tissues of the plates are considered under the following six headings: (1) specialized compact dentine forming the main part of the plate; (2) the pleromic dentine and bone between the ridges and along the medial border of the pterygoid plates; (3) the marginal blisters; (4) the regenerative patches as temporary repair tissue; (5) the furrows and intertuberose regions; (6) growth lines.

It is necessary to use specialized terms to make adequate descriptions and comparisons between the different tissues, and these will be briefly defined.

'*Petrodentine*' (Smith 1977, pp. 65; 1979, pp. 19, 32 and 36; 1984, pp. 368–376 and 396–405) is extremely highly mineralized relative to dentine and bone, the level of mineralization being comparable to that of enameloid; crystallites are large and packed closely together in regular arrangements, with very little organic matrix. It is formed by a sheet of closely integrated and highly specialized cells situated within the pulp cavity between dentine and bone. It is compact, with few canals or cell process spaces, and is extremely hard and translucent. The entire tissue is regarded as a specialized type of dentine, and as a derived character of dipnoans with dental plates.

'*Pleromic dentine*' (Smith 1977, pp. 32, 45, 47, 51 and 68 and figures 11 and 17; 1979, pp. 17 and 37) is a secondary dentine formed by invasive growth of dentine into soft-tissue spaces of trabecular bone or trabecular dentine. This dentine grows as a lining on the existing bone–dentine surfaces, making the vascular spaces smaller and leaving behind a tissue with few short cell processes. It is often very hard and translucent. It takes the form of pockets of dentine within the primary trabecular framework. For these pockets the new term 'pocules' is used. Pleromic dentine forms on existing (resting) surfaces within the bone or dentine, or on resorption (reversal) surfaces where new spaces have been created within the bone or dentine or both during remodelling of tissue.

'*Circumpulpal dentine*' (Smith 1977, pp. 49 and 52 and figures 72 and 77; 1979, p. 21 and figure 11) is dentine formed in the region immediately surrounding narrow pulp canals. It forms within denticles and other dentine structures once the primary framework of dentine has been put down. It may be slightly harder and more translucent than the dentine on which it is deposited.

'*Interstitial dentine*' (Smith 1977, pp. 34 and 52 and figure 1) is the framework of dentine first put down as trabeculae within a soft tissue space and remaining between the vascular systems of pulp canals lined with circumpulpal dentine.

(*a*) *Specialized compact dentine: petrodentine*

The major part of the tooth plate, i.e., all the continuous flat surface, the radial ridges and the tuberosities, appears as shiny, black, translucent tissue on the surface (figures 2–4). All this tissue is of the type referred to previously as petrodentine. It shows the properties of petrodentine found in other dipnoan tooth plates (Smith 1984). As demonstrated in this investigation (figures 33–34) it has a characteristic formative front, bordering the extensive pulp cavity, clearly different from that of pleromic dentine. The growth of this tissue is extensive beneath the tritural surface and each successive increment is marked by a slightly longer growth line at each successive level, to accommodate the increasing size of the tooth plate (figures 65 and 70; Smith 1977, figure 16). In most of the regions of new additions to the plate area, there is an extensive pulp chamber between the dentine and the bone. It is necessary for this to be formed by resorption of the bone and associated pleromic dentine in the new tissue at the margins before petrodentine can increase its extent. New observations on a complete series of coronal sections of a *Chirodipterus* palate and lower jaw *in situ* have made it possible to comment on this transformation (figures 65, 66 and 70).

Although in all of these accounts petrodentine is described as being composed of crystal-fibre-bundles (CFB) or crystal domains, the former assumes that the parallel alignment of the crystals in alternating bundles or domains is based on the original fibre matrix. Current work on extant forms will resolve the developmental origin of this tissue arrangement.

The extent of the space between forming petrodentine and trabecular bone is seen in figures 33 and 34, where the active growth surface of petrodentine has a fringe of lightly calcified crystal-fibre-bundles in process of formation, penetrated by large cell process spaces, as deduced by analogy with such tissues in extant species (Smith 1984, figures 8 and 14). This formative surface has regular pulp canals arranged normal to the surface; the fringe characteristic of forming petrodentine is clearly seen against the calcite infill of the soft tissue space. In contrast with this, the soft tissue space at the junction between the central mass of petrodentine and the marginal tissue is less extensive, and struts of bone join with the dentine.

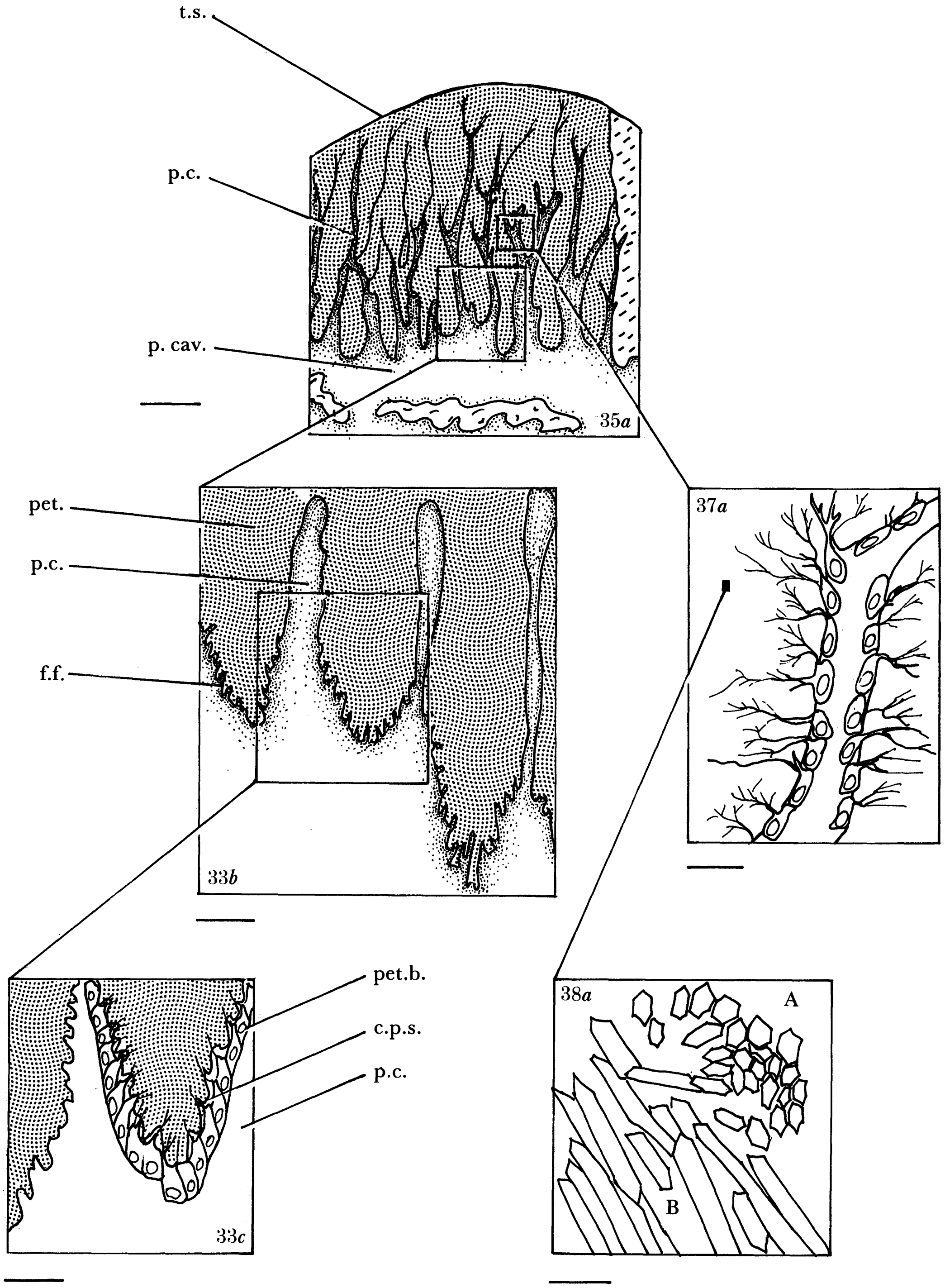
Here the pleromic dentine has separately invaded the vascular, soft tissue to line the spaces in the bones; the forming surfaces contrast with those of the adjacent trabeculae of petrodentine (figure 42), which in this region are at a very early stage of their development.

The ultrastructure of petrodentine has been figured previously (Smith 1977, figure 71; 1984, figures 52–56) but it is notable that the domains of crystals are in the form of a basket-weave with numerous fine perforations that are not always present in petrodentine. In a favourably preserved region of the sections where an organic stain has filled all the cell process spaces, it can be seen that many very delicate tubules extend through from the pulp canals into the petrodentine (figures 36 and 37). The inclusion of fine processes from the cells within the petrodentine is, therefore, one explanation of the perforations in the scanning electron micrographs. (Extremely thin cell processes have been observed in transmission electron micrographs of *Protopterus* in work in progress by M.M.S.). A growth line is also clearly defined in the scanning electron micrographs and at high magnification this is resolved as a region of an interwoven mesh of fine crystallites (figure 68) as demonstrated also in *Ceratodus runcinatus* (Smith *et al.* 1984, figure 5). After the last growth line a narrow fringe of petrodentine had formed. This fringe tissue etches more deeply than the earlier formed petrodentine, indicating the partial mineralization of the forming front as is common in all petrodentines.

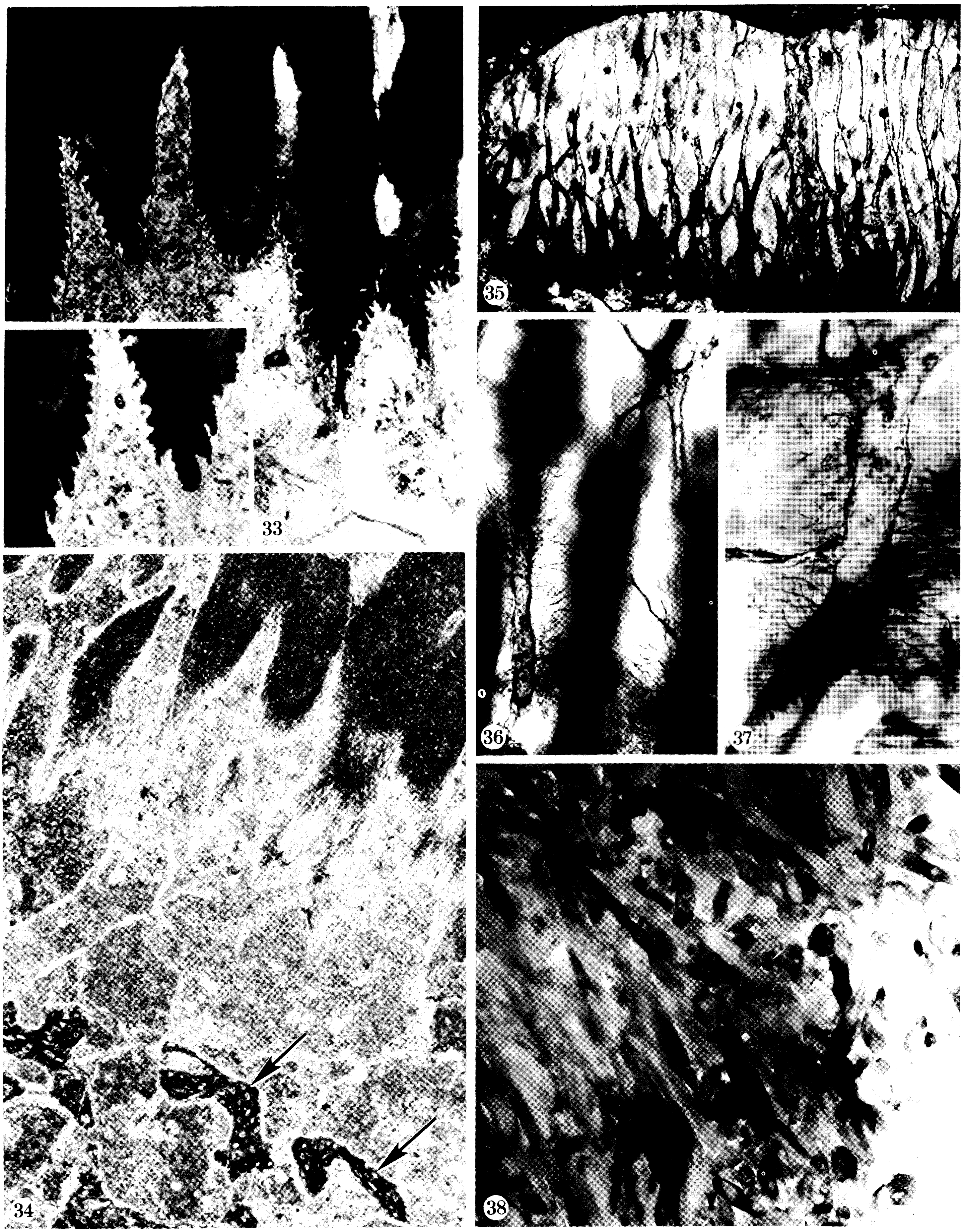
Ion-beam thinned ultrathin sections of the same specimen of *C. australis* permitted us to examine the central tissue of the tooth plate by TEM. The crystals are close-packed and all parallel in restricted arrays forming regions or domains (figure 38). The crystals within a domain lie with their *c*-axes parallel to one another, but within adjacent domains the crystals lie approximately at right angles. Selected-area diffraction-pattern analyses confirm that a high degree of orientation is present, and that the mineral is an apatite. On the *c*-axes, crystals are infinitely long and in the transverse plane they are flattened hexagons. The dimensions of these crystals are well outside the range of dentines found in all types of teeth. They are more comparable to those of enamel and enameloid (Smith 1986). These observations show conclusively that much of the dentine in these regions of the plates is entirely comparable to petrodentine as described in extant forms.

(*b*) *Pleromic dentine*

This dentine type has been defined previously and observed in the tissues of many dipnoans (Smith 1977, p. 47 and figure 14). It is so named because it fills spaces in the bone or dentine or both (figures 39–42). From the way in which it develops, the tissue complex of bone-plus-dentine could be regarded as endosteal dentine (a new term proposed in this paper for dentine deposited on an inner bone surface); by analogy with endochondral bone it also served as a temporary structure before replacement by petrodentine, in the same way as primary spongiosa in endochondral bone does before lamellar bone formation. Initially, pleromic dentine grew within the bone basal to all the superficial dentine structures of a tooth plate, e.g. denticle-blisters or regenerative patches, but it soon became extensive within the marginal bone of the posterolateral and posteromedial regions of the plate, and at the anterior extremities of its furrows. Pocules (see the introduction to §4) of this dentine grew on to existing surfaces (figure 39) which may be one of four types: resting bone or resorbing bone, resting dentine or resorbing dentine. Pleromic dentine can be recognized by its greater translucency, by its relationships, and by its formative surfaces. The junction between pleromic dentine and previously formed tissue may sometimes be seen as a reversal line (figures 40 and 44). These



Figures 33*b*, *c*, 35*a*, 37*a* and 38*a*. These are all drawn from the same fields as the photomicrographs in plate 6, interpreted from the equivalent extant tissue, to show the pulp canals and spaces for cell processes. The numbers are the same as the corresponding photomicrographs, and the boxed areas show the equivalent region at a higher magnification. In 33*c* the petroblasts are shown relative to the fringed formative front, and in 37*a* the odontoblasts are shown as mature cells lining the pulp canal surface, where they may form a lining of circumpulpal dentine. In 38*a* some of the crystal profiles are shown in the two adjacent domains: A, hexagonal shape, *c*-axes at right angles to the section; B, *c*-axes parallel. Figure 33 (*c*), scale bar 100 µm; figure 33 (*c*), scale bar 50 µm; figure 35 (*a*), scale bar 500 µm; figure 37 (*a*), scale bar 25 µm; figure 38 (*a*), scale bar 0.2 µm.



FIGURES 33–38. For description see facing plate 7.

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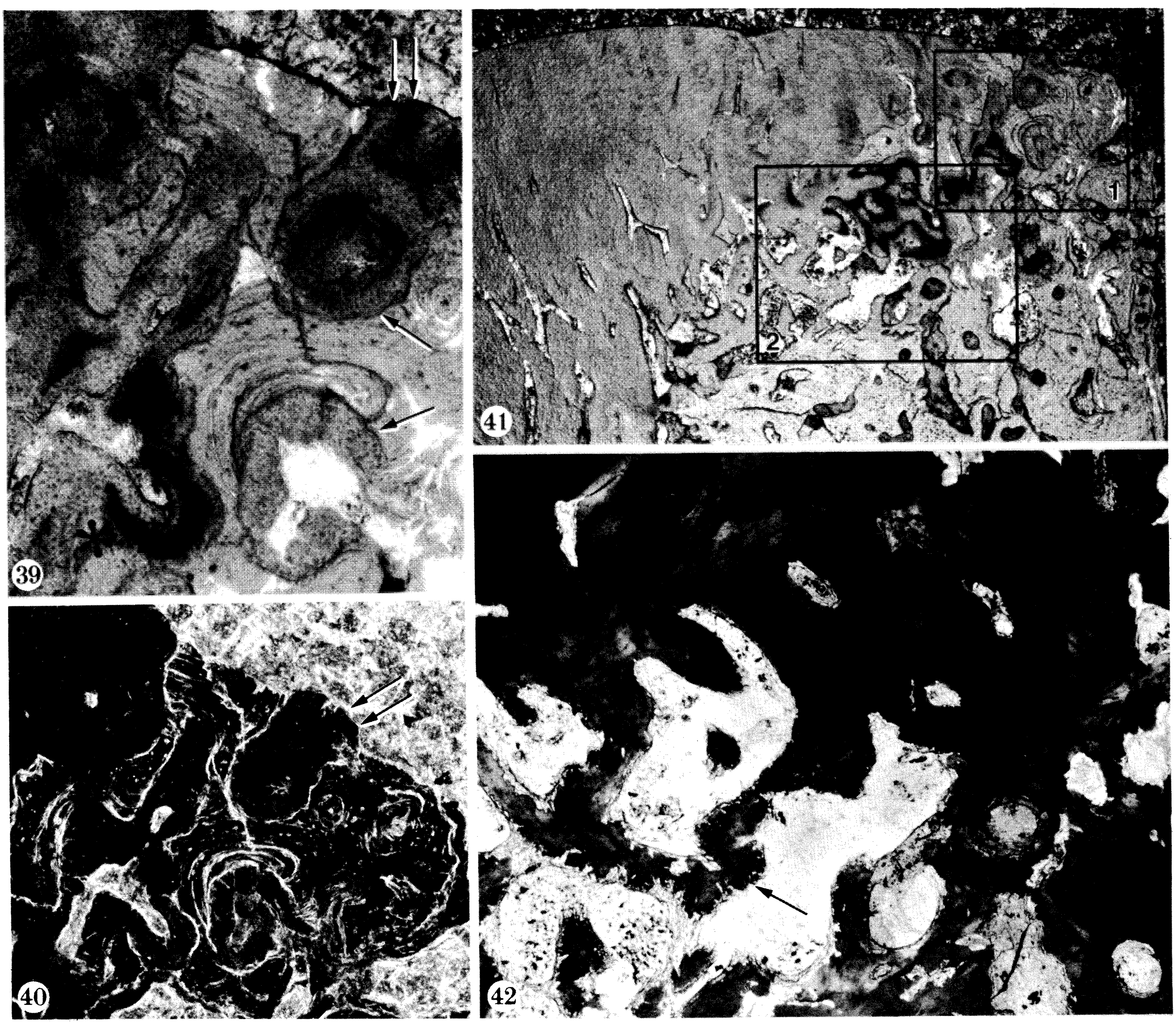


FIGURES 39 AND 40. (Magn. × 120 and × 75 respectively.) Both these figures are from box 1 in figure 41. They illustrate in ordinary light and phase contrast the distribution of pleromic dentine within partly resorbed bone; the junction between resorbed bone and pleromic dentine is a reversal line (single arrows). Part of the pleromic dentine has been infiltrated by black staining material (asterisk) and this is interpreted as the last-formed, least hard dentine (as in figure 42). Layer lines and lacunae are seen in the bone in both figures. The harder pleromic dentine is proud of the bone at the worn surface (double arrow on figures 39 and 40).

FIGURE 41. (Magn. × 30.) Lingual margin of the lower tooth plate. Extensive thickness of petrodentine on the left. The two boxes, 1 and 2, (figures 39, 40 and 42) show regions of pleromic dentine and developing pleromic dentine and petrodentine.

FIGURE 42. (Magn. × 100.) Region of developing pleromic dentine (black stained tissue) growing onto bone surfaces from reversal lines. Bottom left trabeculae of petrodentine at the beginning of development (arrow) fill the space between the bottom of the petrodentine and the bone. It has a typical fringed edge as in figure 33.

Description of plate 6

All the photomicrographs are from five sections, cut in the coronal plane, of the specimen *in situ* in the nodule, CPC22592.

When examined between crossed polars the difference between biological mineral and fossil mineral can be demonstrated. The biological mineral is black when the majority of crystals are oriented either parallel to or normal to the polarizer; it is only birefringent where some of the crystals are at 45° to the polars. The mineral deposited during fossilization is strongly birefringent. This contrast between the two allows interpretation of the forming biological surfaces; the drawings facing plate 6 aid interpretation.

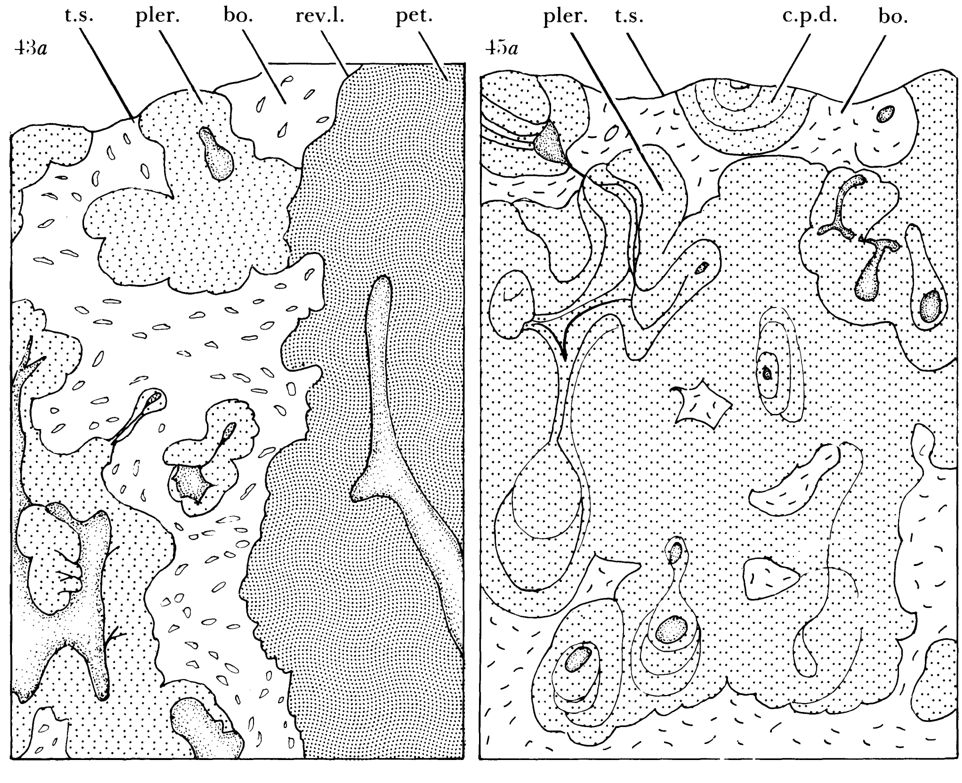
FIGURE 33. (Magn. × 100; 33*a* (inset) magn. × 200, crossed polars.) Forming edge of petrodentine adjacent to the pulp cavity, typical fringed edge is emphasized by the calcite infills of the original soft tissue space. The line marking the outline of the pulp canals is assumed to be a junction between the first fossil infill of the cell spaces and a subsequent one. This surface was lined by the cells forming the petrodentine, each small indentation influenced by a cell process and each large invagination is part of a pulp canal. Figure 33*b,c* shows the probable relationship of cells to petrodentine.

FIGURE 34. (Magn. × 100.) Similar region to figure 33 in which the gap (pulp cavity) between the petrodentine and bone is extensive. Taken in phase contrast, which enhances the difference between petrodentine and the geological mineral, and demonstrates the fringed edge of a forming surface of petrodentine. The pulp cavity is full of calcite and the bone trabeculae show the osteocyte lacunae (arrows).

FIGURE 35. (Magn. × 20, crossed polars.) In this orientation of the polarizer the biological mineral is birefringent and the soft tissue spaces are black. It shows the alignment and changing diameter of the pulp canals throughout the petrodentine, in a section through a tuberosity at the labial margin. Each one opens into the extensive pulp cavity, also shown in the drawing (figure 35*a*, see figure 70 (2)).

FIGURE 36 AND 37. (Magn. × 100 and × 400 respectively.) Region from the tissue of the tuberosity in which tubules run from the pulp canal into the petrodentine, each branching into numerous finer ones. This is also shown in the drawing (figure 37*a*).

FIGURE 38. (Magn. × 50000.) Transmission electron micrograph from a mature region of petrodentine taken from the same series of sections and prepared by ion-beam thinning. The *c*-axes of the crystals are extremely long and their shape is hexagonal at right angles to this. They are close packed and all parallel in one domain, then at right angles to this in the adjacent one. Their size, orientation and packing is similar to enamel and enameloid. This is also shown in figure 38*a*.



FIGURES 43*a* AND 45*a*. These are drawn from the same fields as the photomicrographs in plate 8, to show the distribution of the three tissues, bone, pleromic dentine and petrodentine. The major reversal line in figure 43*a* separates the block of petrodentine from the bone-plus-pleromic-dentine. It is equivalent to the resorption surfaces seen in figures 12 and 13. In figure 45*a* the successive bands of circumpulpal dentine show growth concentric with the pulp canals of the pleromic dentine. Figure 43*a*, scale bar 62.5 μm; figure 45*a*, scale bar 62.5 μm.

DESCRIPTION OF PLATE 8

FIGURE 43. (Magn. × 160.) On the right is petrodentine and on the left the mixed tissue bone-plus-pleromic-dentine. The junction between the two is marked by a reversal line (arrows) where episodes of resorption have removed some of the bone and some of the pleromic dentine before petrodentine grew against these tissues. The worn surface of the plate is at the top left. Figure 43*a* is a drawing of this field.

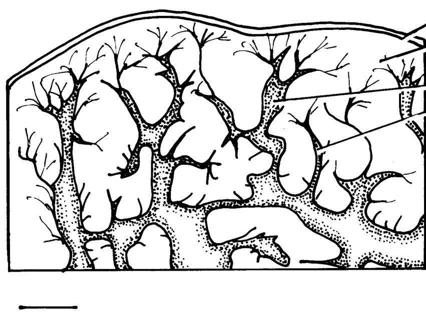
FIGURE 44. (Magn. × 160.) A field below that in figure 43 showing a remaining patch of bone with trabeculae of petrodentine forming beneath it (asterisk), identified by their fringed forming surfaces.

FIGURE 45. (Magn. × 160.) This photomicrograph is produced by a new method of examination in ultraviolet light to show the tissue distribution in a region in which bone (white) is mixed with pleromic dentine (grey to black); the worn surface to the dentine plate is at the top. The polished surface of the section (with biological mineral and mineral due to fossilization all preserved) was illuminated with ultraviolet light; regions with most calcite fluoresce strongly and are shown as white zones. Regions that are the least permeated with calcite do not fluoresce and are black, such as those nearer to the tritural surface; these are the oldest pleromic dentine. Regions of high porosity, seen as white lines concentric with the canals, are interpreted as resting growth lines. Compare this figure with a region of petrodentine photographed in the same way (figure 69).

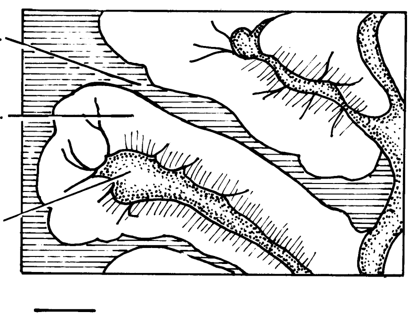
FIGURE 46. (Magn. × 160.) For comparison with figure 43, a region of compact bone at the base of the tooth plate in which there is no dentine infilling any of the spaces. Instead some of the vascular canals are infilled with concentric layers of bone (arrows), and here the difference between this and pleromic dentine is apparent.

FIGURES 43–46. For description see opposite.

51a



52a



Description of plate 9

FIGURE 47. (Magn. × 63.) (Phase contrast.) Lower tooth plate, medial margin, shows a resorption bay (arrows) in a region of mixed tissue, bone-plus-pleromic-dentine as in figures 39 and 40. The tritural surface is emphasized with a line.

FIGURE 48. (Magn. × 25.) Left lateral margin, through the tuberose region of both tooth plates, one tuberosity of petrodentine fitting into worn mixed tissue, bone-plus-pleromic-dentine, of the opposite plate.

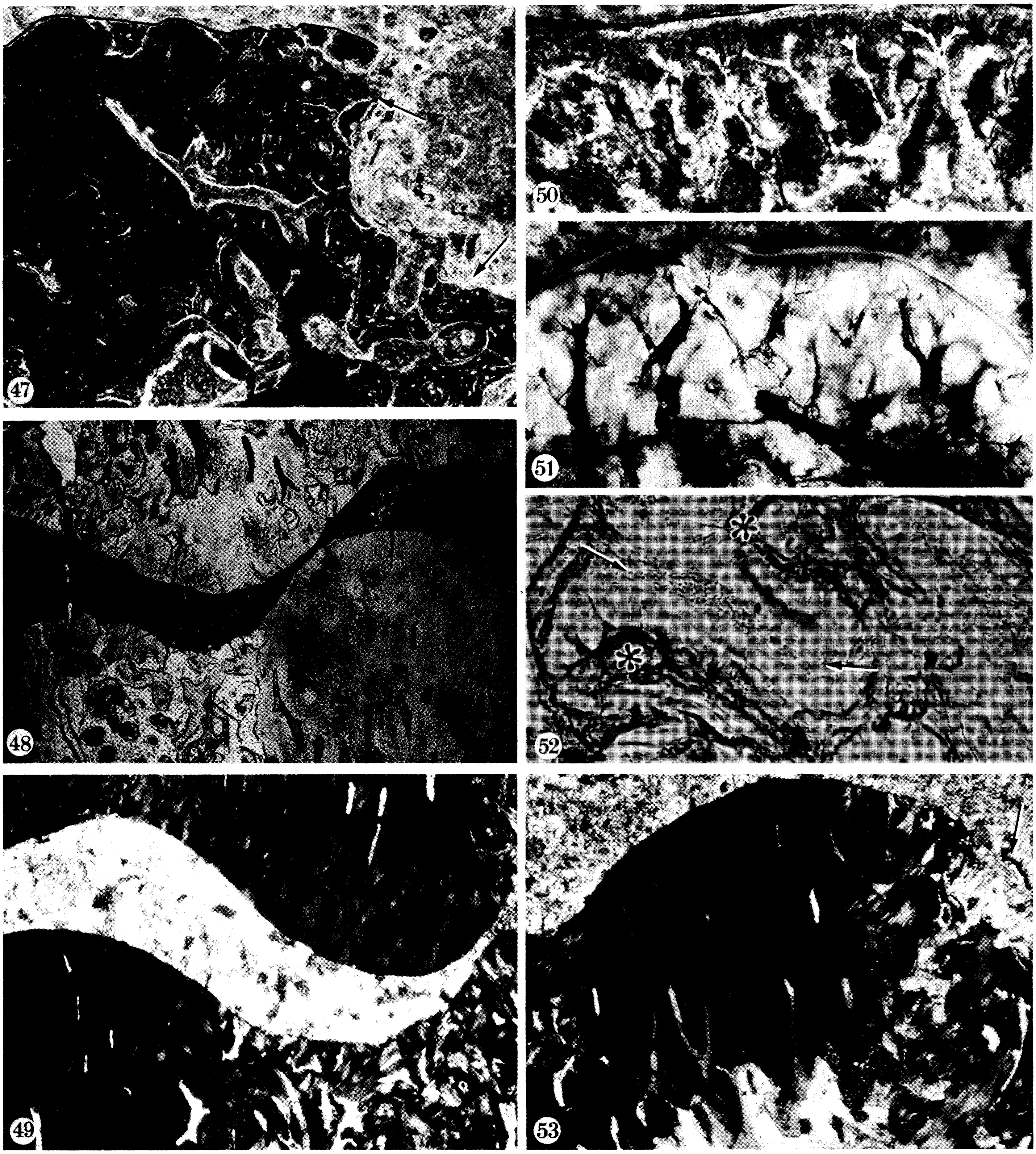
FIGURE 49. (Magn. × 25.) Right lateral margin, also through both tooth plates, as in figure 48 through two tuberosities. The structural difference between the mixed tissue and the petrodentine of the tuberosities can be easily demonstrated in polarized light (see also figure 53).

FIGURE 50. (Magn. × 160.) Lingual margin of the lower tooth plate to show the regenerative dentine, taken in partial polarized light. An enamel layer, at the top, covers a thin region of pallial dentine with fine odontoblast tubules as branches from the pulp canals, the latter filled with calcite.

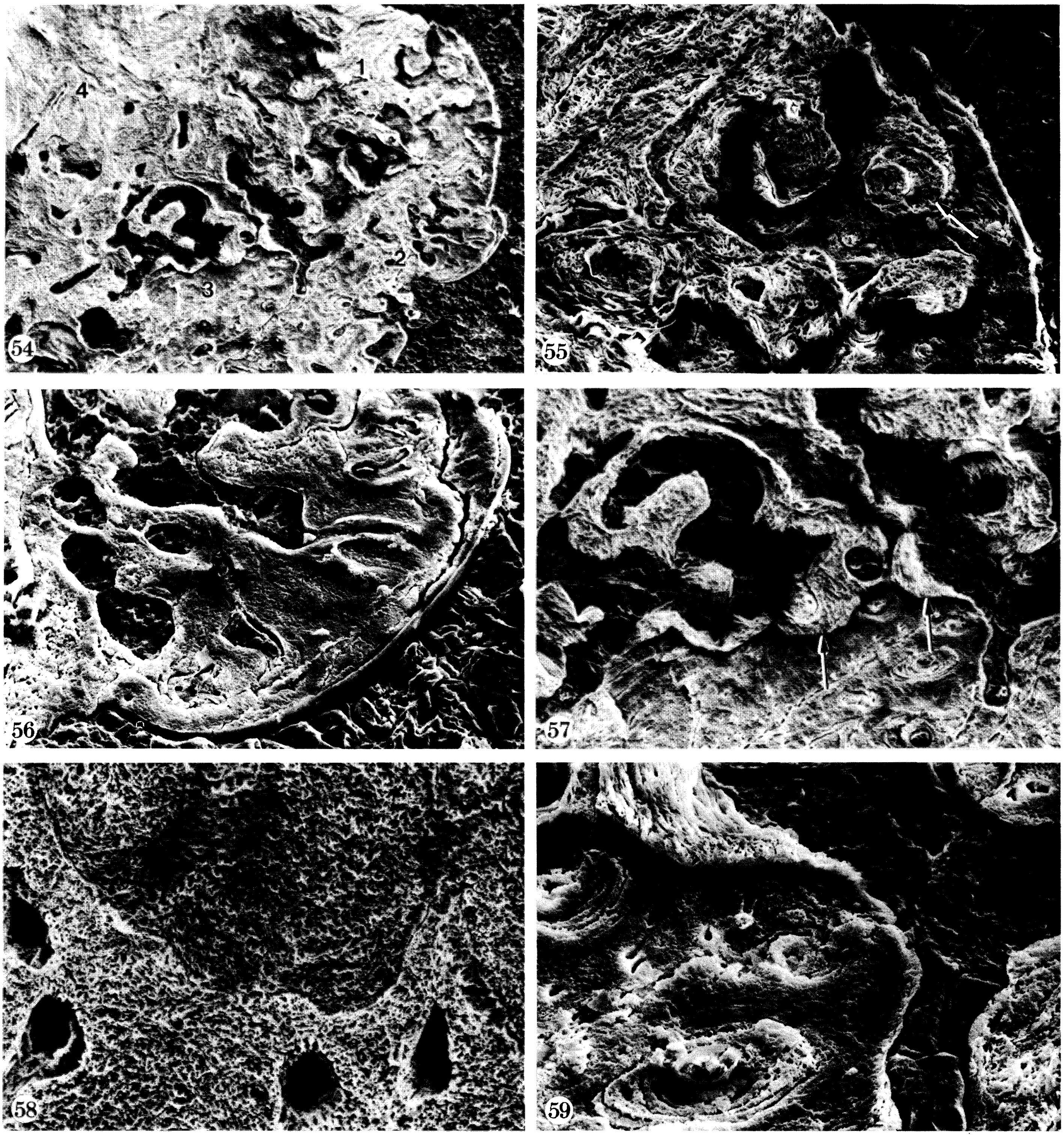
FIGURE 51. (Magn. × 120.) Similar to figure 50; a patch of regenerative dentine with rounded, enamel-covered margins. The simple structure of the dentine is seen with many branched pulp canals and sprays of fine branching odontoblast tubules within the pallial dentine. Figure 51 *a* is a drawing of figure 51 to show the simple arrangement of the dentine, pulp canals and tubules. Scale bar 88.3 μm.

FIGURE 52. (Magn. × 480.) A field from a young denticle to contrast with the regenerative dentine. In the denticle, well developed regions of circumpulpal dentine can be seen around each pulp canal (asterisks). This tissue has radial striations in addition to short, irregular tubules. Between each region of circumpulpal dentine is a region of less organized, atubular interstital dentine (arrows). Figure 52*a* is a drawing of figure 52 to show the circumpulpal dentine with radial striations and the trabeculae of interstitial dentine. Scale bar 20.8 μm.

FIGURE 53. (Magn. × 30.) (Polarized light.) Lateral margin, region of new tuberosity to show part of an extensive pulp cavity (filled with calcite, white) beneath petrodentine (black). The marginal tissue has extensive soft tissue spaces, is made of bone and pleromic dentine and is undergoing extensive remodelling to allow upward growth of the petrodentine. A new denticle has begun to grow (arrow) at the extreme margin and this is illustrated in figure 62.



FIGURES 47–53. For description see opposite.



FIGURES 54–59. For description see opposite.

differences allow pleromic dentine and petrodentine to be clearly distinguished from each other by their mode of formation and their disposition within the tissues of the dental plate.

Pleromic hard tissue in bone (endosteal dentine) is different from Ørvig's (1967, pp. 104–105) vascular pleromin and compact pleromin, which are types of petrodentine (see Smith (1984) for a review of this topic). Ascertaining the relative degree of hardness of this pleromic dentine is a problem, but its appearance in several different observational modes shows beyond doubt that it is hypermineralized relative to dentine and bone. It is translucent, projects above the adjacent dentine-and-bone on worn surfaces (figure 40), and etches less deeply with dilute mineral acids as shown by the scanning electron micrograph appearance (figures 54–59). These all consolidate the view that it is formed of swatches of crystal-fibre-bundles. This suggests a different type of dentine from that found in circumpulpal positions in the primary dentine.

The appearance of this tissue under incident ultraviolet light has been found to be relevant to an interpretation of the structure (figure 69). This is a completely new method of examining polished sections to determine bone histology. Calcite impregnating the tissue through the microspaces causes a pale blue fluorescence of the softer, more permeable, tissues, and this contrasts with the brown of the translucent, hard dentines; both pleromic dentine and petrodentine are brown to yellow. The forming surface of the pleromic dentine, however, is never invaginated by the wide channels that are typical of a forming surface of petrodentine (figure 42). This feature shows up particularly well in ultraviolet light. It is impossible to determine the relative degrees of hardness of the two quantitatively, but from their translucency, and their resistance to wear and etching, they are both hypermineralized relative to dentine. Frequently, a diffuse black carbonaceous stain occurs in what is inferred to be new pleromic dentine which is more permeable than when it is older (figure 42). This is not seen in petrodentine because it becomes hard very soon after its formation (Smith 1984, figure 8).

Description of plate 10

Figure 54. All these scanning electron micrographs are prepared from a polished surface of a section etched with 1 M HCl for 1 min. The surface was consecutive with the sections used for histology illustrated in figures 65 and 66 and the region is the medial edge of the left lower tooth plate adjacent to the section ((3) in figure 70). This low magnification scanning electron micrograph shows the area where petrodentine adjoins the pleromic dentine and bone, and where a new blister denticle has been added to the surface. The numbers 1–4 indicate positions of the higher magnification scanning electron micrographs (field width 2.8 mm).

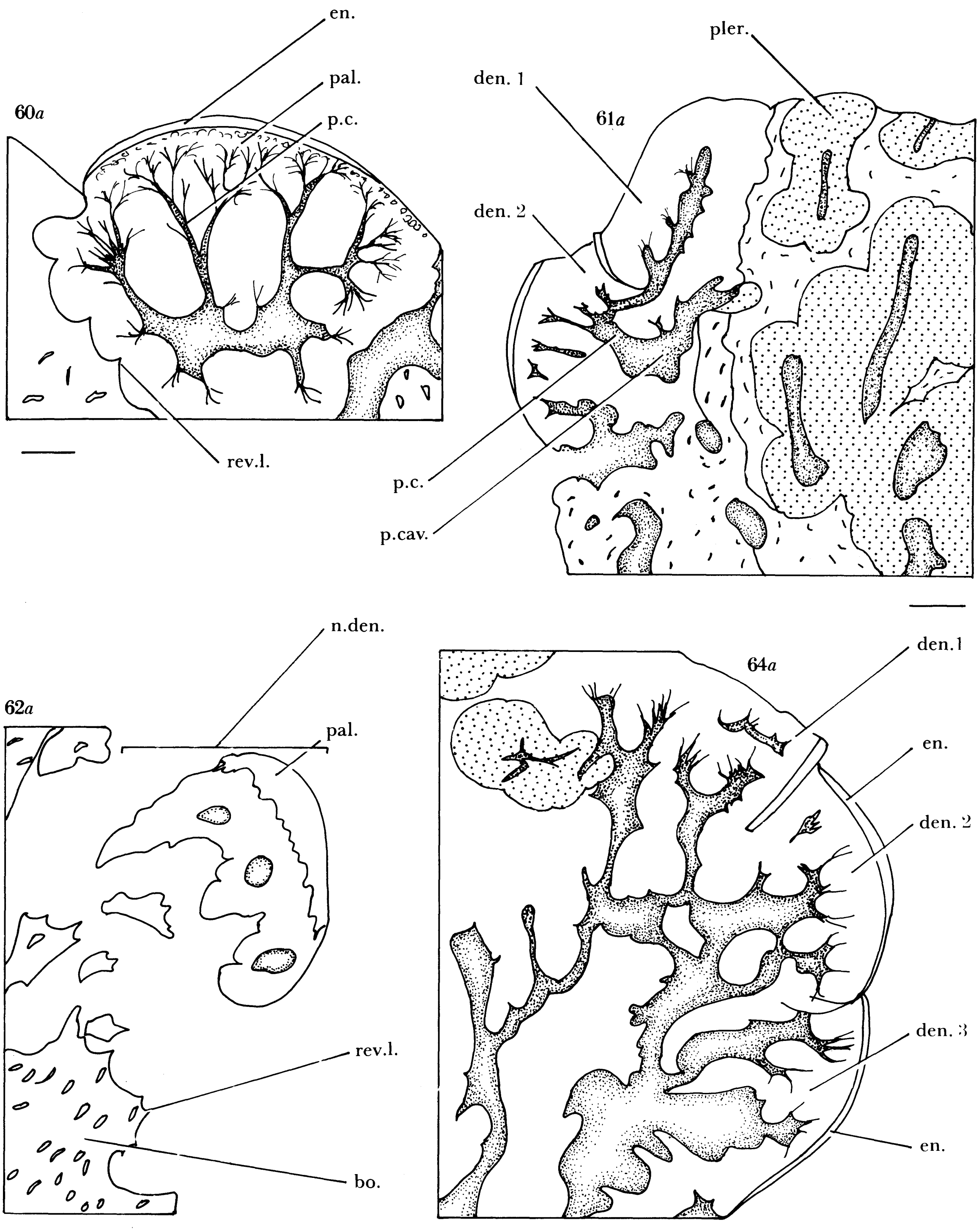
Figure 55. (Field width 600 μm, from 1 in figure 54.) The harder pleromic dentine has etched less deeply than the surrounding bone. Concentric lines where several layers have grown in sequence are present in the patches of pleromic dentine (arrow).

Figure 56. (Field width 450 μm, from 2 in figure 54.) New enamel-covered denticle in which the dentine is homogeneous, formed of small crystallites, and low mineral density relative to the pleromic dentine and petrodentine. Pulp canals link with spaces in the bone.

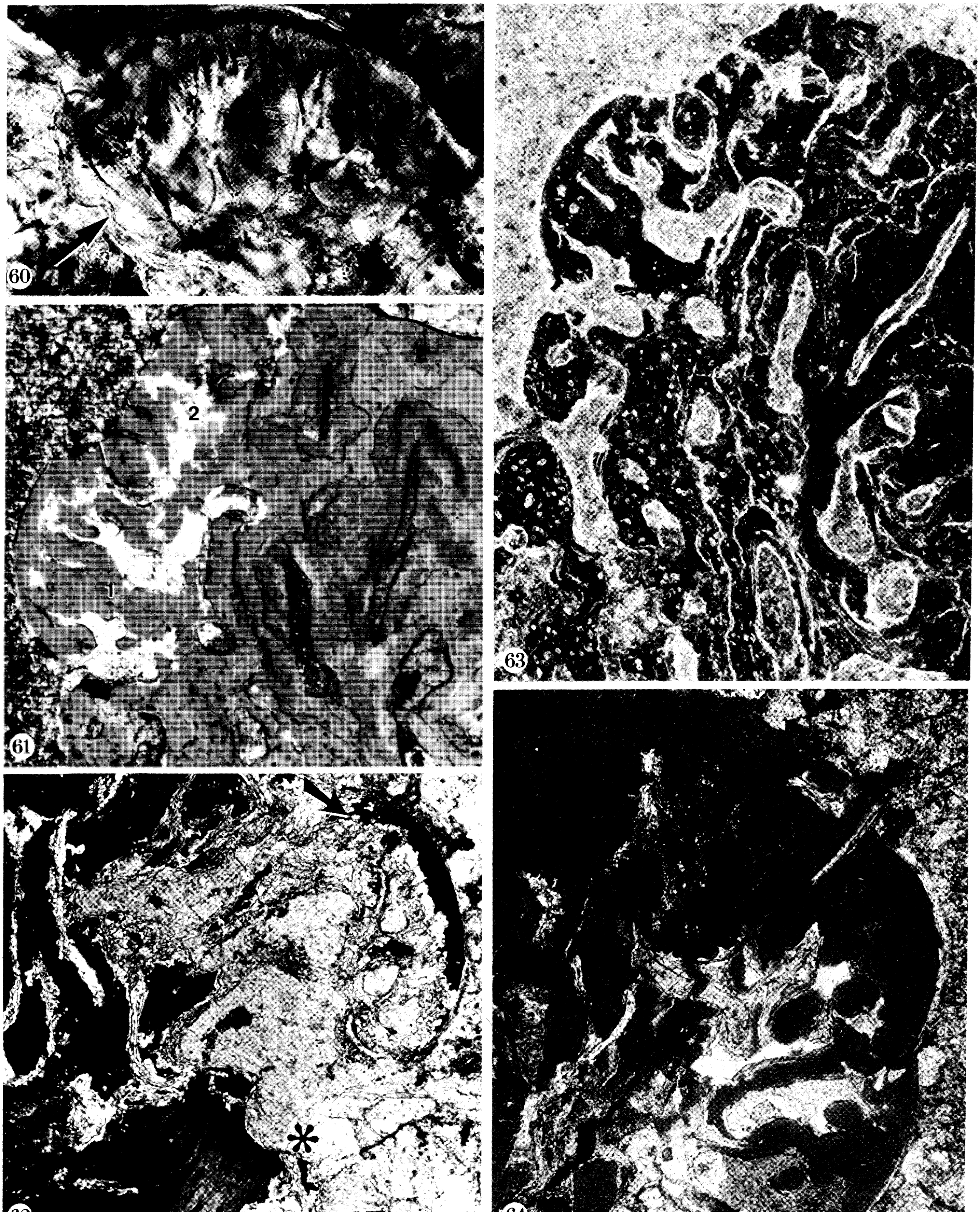
Figure 57. (Field width 900 μm, 3 in figure 54). This figure shows how the pleromic dentine has grown onto resorbed bone surfaces, one cutting across an osteon (arrows, higher magnification shown in figure 59). One piece of bone is isolated within growing regions of pleromic dentine. Soft tissue spaces are filled with rock matrix, but *in vivo* these would have been forming surfaces.

Figure 58. (Field width 450 μm, from a region similar to 4 in figure 54, also shown in figure 67.) Compared with the denticle in figure 56 at the same magnification it shows the different texture of petrodentine from dentine, and two regions of the tissue separated by a growth line.

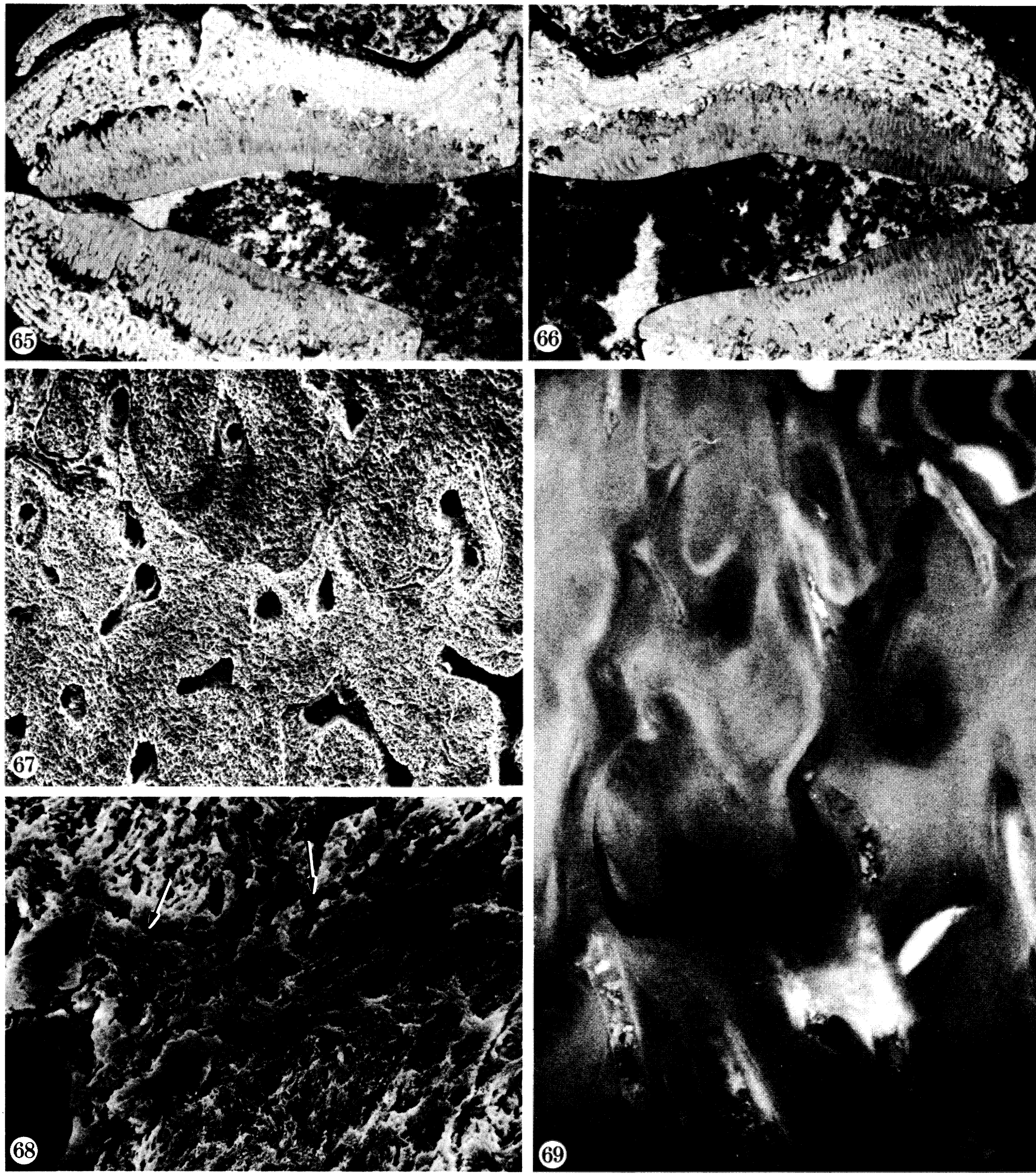
Figure 59. (Field width 270 μm, higher magnification of figure 57.) The lower etch level of the compact bone, with osteones and lacunar spaces, contrasts with a growing region of pleromic dentine with a high level of mineralization.



FIGURES 60*a*, 61*a*, 62*a* AND 64*a*. The same fields as the corresponding photomicrographs to show the relationship of new tissue in the form of denticles, added to resorption or resting surfaces at the margins of the tooth plates. The marginal tissue is always bone-plus-pleromic-dentine. Figure 60*a*, scale bar 50 μm; figure 61*a*, scale bar 100 μm; figure 62*a* and 64*a*, scale bar 62.5 μm.



FIGURES 60–64. For description see page 349.



Figures 65–69. For description see opposite.

(*c*) *Marginal blisters*

As described in the previous section, blisters develop mainly at the anterolateral margins where they form on the bone surface, providing constructional tissue added to the growth margin of the basal bone; this includes dentine, pulp canals and associated bone of attachment. The tissue of the blisters is the same as that found in the denticles of all dipnoans (Smith 1977, figures 5, 6, 34 and 35); that is, a thin outer region of pallial dentine formed before the development of dentine trabeculae that provided interstitial regions on which circumpulpal dentine grew (figures 60–64). This also results in a pulp region that is divided into pulp canals; it never exists as one central pulp cavity. A descriptive term for this type of development of dentine, analogous with the development of intramembranous bone, would be intrapulpal dentine – a first-formed framework of dentine that could subsequently be infilled or remodelled.

At the base of the blisters, pleromic dentine grew into the basal bone. Successive blisters lap

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Description of plate 11

Figure 60. (Magn. × 200.) Medial margin, showing new denticle added on to a previous resorption surface clearly seen as a reversal line (arrow) cutting across previous structures in the dentine and bone.

Figure 61. (Magn. × 100.) Lateral margin, showing a very new denticle (1) with pulp spaces infilled with calcite, formed inferior to worn denticle (2), both at the vertical margin of the tooth plate. These have formed on top of bone into which pleromic dentine has grown. The worn surface to the tooth plate is top right and is made of the mixed tissue (bone and pleromic dentine). The same area is shown in figure 63.

Figure 62. (Magn. × 160.) Polarized light, lateral margin of lower tooth plate field from the region in figure 53 (arrow), shows just the shell of pallial dentine (arrow) of a developing denticle. The bone surface below (asterisk) has been resorbed and any tissue between was so poorly mineralized or partly formed that it has been permeated by calcite. This is referred to as an incipient denticle, (i.e. unattached).

Figure 63. (Magn. × 100.) Phase contrast, lateral margin, same region as in figure 61, new denticle attached to the vertical bone surface of tooth plate margin in a region of mixed tissue; bone with lacunae, and pocules of pleromic dentine lining the canals. The two observation modes (transmitted light as in figure 61, and phase contrast) allow these tissues to be compared.

Figure 64. (Magn. × 160.) Partial polarized light, lateral margin, worn surface to the tooth plate is top left. This figure shows a stack of three denticles, successive ones lapped against the enamel of the previous one. The top denticle is worn, the two new ones are covered by enamel, the youngest one is at bottom right.

Description of plate 12

Figures 65 and 66. (Magn. × 12.) Both upper and lower tooth plates appear in the same section *in situ* as in occlusion. The drawings in figure 70 are taken from four similar sections. The extent of the pulp cavities can be seen (infilled with black) together with the faint growth lines within each block of petrodentine forming the flat surface of the plates and the ridges or tuberosities at the margins.

Figure 67. (Field width 900 μm.) Scanning electron micrograph of a region of petrodentine in which one major growth line can be seen (see also figure 58). The characteristic shape of this line with scallops and indentations is influenced by the positions of the pulp canals. A similar appearance is shown in figure 69, which is a completely different way of visualizing the growth zones.

Figure 68. (Field width 100 μm.) A higher magnification of a part of a growth band beneath a line (arrows), similar to that in figure 67. It shows a change in this band to smaller crystallites, but tubule spaces are also present as in the rest of the petrodentine.

Figure 69. (Magn. × 160.) Polished surface of petrodentine examined with incident ultraviolet light (as in figure 45). The calcite filling the pulp canals fluoresces (white) and only the zones in the petrodentine which are slightly permeable will show up lighter. The dark regions are less permeable and this effect enhances the growth lines which are reflections of different levels of mineralization. This figure can be compared with figure 45 of a region of pleromic dentine viewed in the same way; they emphasize the different ways in which the tissues were formed and their different structure.

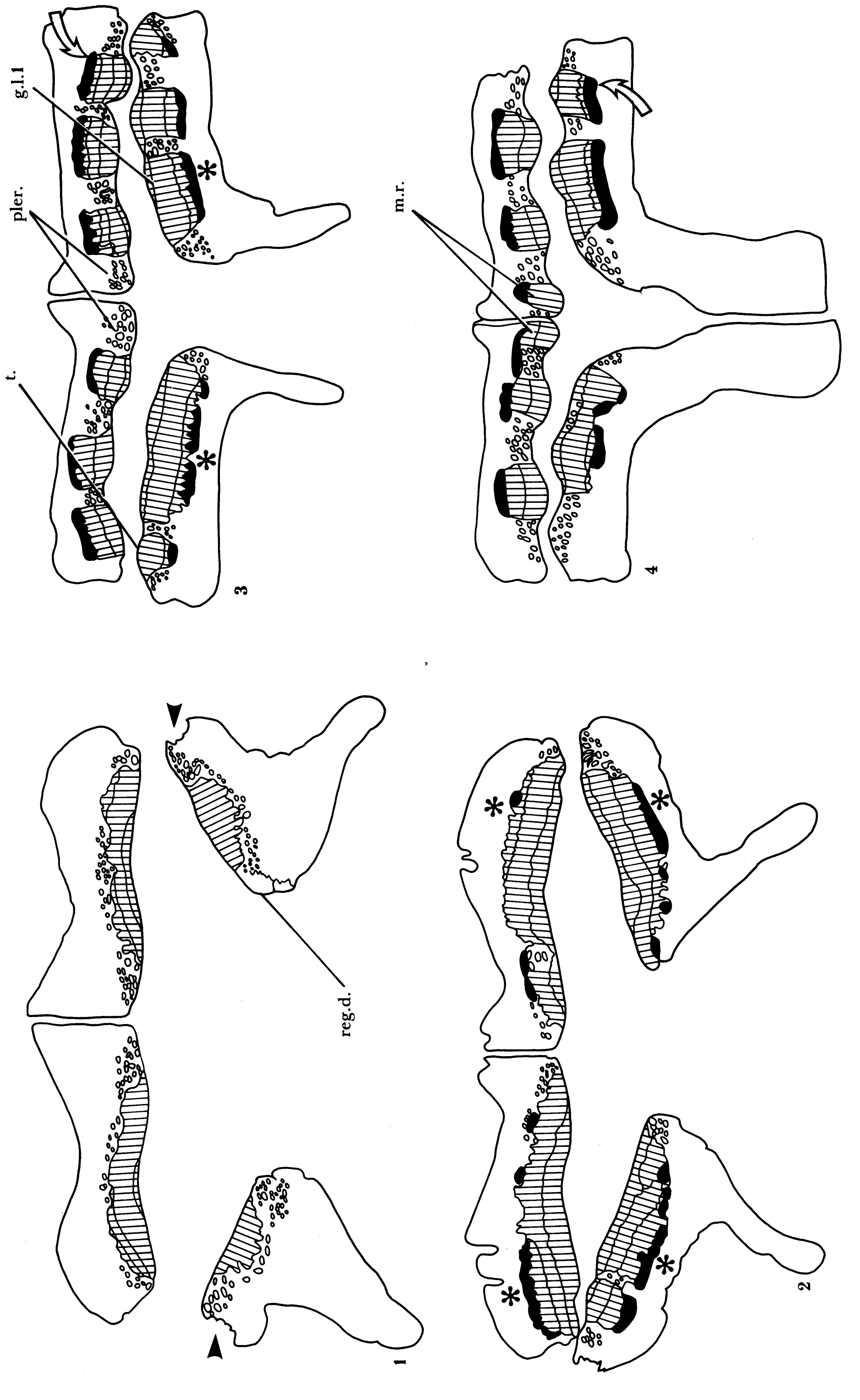

FIGURE 70. For description see opposite.

against each other with the enamel surface of one generation partly covered by the next (figure 64). Each generation shows the sequence of dentine formation outlined above. Because the sections are prepared from specimens still in the rock matrix, the denticles in the earliest stages of development, which are normally lost in acid-prepared specimens, are retained. In these the dentine is only lightly attached to the bone surface. One such incipient denticle (figure 62) shows a layer of pallial dentine with only an exceedingly thin layer of enamel and a few short irregular tubules in the pallial dentine. The formative surface is heavily impregnated with calcite and is therefore presumed to have a low level of biological mineralization. In the regions of lapped denticles, the transition from young to old tissue is also seen. Within the pallial dentine short, spriggy tubules radiate from the blunt-ended pulp canals. The dentine trabeculae which were at first free of the bone, later became continuous with it. Once this had happened, the trabeculae became lined with circumpulpal dentine. In a similar way pleromic dentine grew onto the bone trabeculae at the base of the blisters. This gives the typical appearance of an endosteal dentine with pocules of dentine lining every available bone surface as described in §4(*b*).

(*d*) *Regenerative patches*

Deep embayment caused by resorption of the tissue at the medial and posteromedial plate margins left an exposed surface of pleromic dentine and bone (figure 47). This surface was then partly covered by patches of regenerative tissue with a similar structure to the blisters but flat-topped and with a very thin layer of simple dentine above the bone of attachment (figure 50); the latter forms the junction tissue between the old bone and the dentine. This dentine is

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FIGURE 70. (Scale bar 1.0 cm.) These sections have been taken in sequence across a whole head with the tooth plates *in situ*, in normal occlusal relations; (1) is the most posterior, through the plateau; (4) is the most anterior, through the ridges. Each diagram shows one, two or three growth lines, the last-formed growth line is the deepest one in the plate. The sections are almost certainly oblique coronal, the left of the diagram being more posterior than the right. The following points may be made:

(*a*) the medial ridge is shown in (4) in a position occupied by bone-plus-pleromic-dentine in (3), but the growth line across the petrodentine in (4) shows that it had been developing in phase with the rest of the plate but as an isolated region within the bone-plus-dentine;

(*b*) the addition of bone-plus-pleromic-dentine around the labial margins of the plates in all sections shows the mode of growth very well. Note especially that in all instances the growth of basal bone has proceeded in advance of the margins of the tooth plates, and that the petrodentine forming a tuberosity in one plate (arrows; prearticular plate in (4), pterygoid plate in (3)) was added so as to occlude with a pit of bone-plus-pleromic-dentine in the opposing plate;

(*c*) the petrodentine of the flat posterior part of each plate grows more extensively on the labial half of the plate (especially well seen on (2)) because a pulp cavity has been created in the underlying bone allowing a thicker band of petrodentine to be formed. Medial to this, the previous layer has not been added to because the petrodentine was in direct contact with the bone of the pterygoid. The petrodentine is thickest where the pulp cavity is largest at the expense of the bone (asterisks);

(*d*) some estimate of the amount of wear that has taken place can be obtained from the shape of the growth lines on the pterygoid plates in (2). These retain no flexuosity, as they should if any tissue remained from the time when this region was effectively at the plate margin;

(*e*) the resorption areas on the labial margins of the prearticular plates (arrowheads), and the regenerative patches on the lingual margin are well shown on (1);

(*f*) the labial tuberosities (t.) on the prearticular plates in (3) have apparently been added after the oldest growth line (g.l.l.) on the remainder of the plate was formed;

(*g*) relatively large pulp cavities are found beneath the ridges and tuberosities in the anterior section, and smaller ones in the more posterior sections. For example, in (1) no estensive pulp cavities exist, and pleromic dentine forms here at the junction between bone and petrodentine.

Key: vertical hatching, petrodentine; black, pulp cavity; small circles, pleromic dentine.

termed 'simple' because the pulp canals branch freely, and from their ends tubules spray out irregularly into a very thin region of pallial dentine (figure 51). There is a reversal line where the new regenerative dentine abuts the old surface. Again, pleromic dentine grew within all this tissue, and this resulted in the appearance of raised rings of hard dentine on its worn surface before replacement by the encroaching petrodentine took place, a process described in a previous section.

(*e*) *Furrows and intertuberose regions*

These are composed of a tissue of mixed origin described in the section on pleromic dentine (§4(*b*)) as endosteal dentine, or in Baume's (1980) evaluation of dentine terminologies, as a genuine osteodentine. The latter term has been used for a variety of dentine types that do not always include trabeculae of bone. This mixed tissue was gradually resorbed and new, more extensive growth of petrodentine occupied the resorption spaces (figure 53). The distribution of these two tissues is clearly seen in low-power photomicrographs (figures 48, 49 and 53) and is illustrated in the drawings of the sections in an anterior–posterior sequence (figure 70). The growth lines within the petrodentine do not continue into these regions of endosteal dentine. As already discussed in the section on the macrostructure (§3(*b*)), the scanning electron micrographs confirmed that there is a major junction of change, or remodelling, between the endosteal dentine of the inter-tuberose and inter-ridge regions on the one hand and the petrodentine of the tuberosities on the other. This has been demonstrated as a scalloped reversal surface; it is further confirmed by a similar observation in the sections of a reversal line interrupting the dentine and bone structure at the junction between the mixed tissue and the petrodentine (figure 43). The position of this mixed tissue (endosteal dentine) is clearly seen in figures 48, 49 and 53, in which the concave worn surface of the furrow is moulded to the shape of the opposing tuberosity. The different birefringent patterns of the petrodentine and endosteal dentine are demonstrated here with crossed polars in the normal position. As shown by the scanning electron micrographs (figures 12 and 13) and the polarized light photomicrograph (figure 53), it is possible that the petrodentine could grow differentially relative to the tissue at its margins because of the extensive remodelling.

(*f*) *Growth lines*

These occur as a regular pattern within the petrodentine; in thin sections they transmit less light, thus producing thin brown lines. On etched surfaces the lines are slightly deeper than the petrodentine (figures 67 and 68) and are seen to be narrow bands of smaller, thinner crystallites. In ultraviolet light the growth lines exhibit intrinsic fluorescence and follow the outline of a previous resting growth band, with invaginations around the borders of the pulp canals where growth slowed preferentially (figures 67 and 69). All these features suggest synchronous activity by the cell population forming petrodentine, producing a narrow zone of low calcification. This zone is more permeable, allowing changes during fossilization such as impregnation with calcite which fluoresces under ultraviolet light.

The course followed by the individual growth lines is shown in the composite drawing of the series of sections through the tooth plates *in situ* (figure 70). The interpretation of these lines is complex because their positions result from the interplay of a variety of depositional rates and moving sites of wear. The main points are brought out in the text accompanying the figures.

5. Other genera with chirodipterid plates

Five genera – *Stomiahykus*, *Sunwapta*, *Conchodus*, *Palaedaphus* and *Archaeonectes* – have plates similar to those of *Chirodipterus*. *Stomiahykus* is known from a single incomplete skull with well-preserved pterygoid plates (Bernacsek 1977). It is Eifelian in age, and comes from marine limestones in the Yukon Territory, Canada. *Sunwapta* is represented by a single, incomplete mandible from Upper Devonian marine rocks in Alberta, Canada (Thomson 1967). *Conchodus* is known from several isolated plates found in the Old Red Sandstone (Upper Devonian) of Morayshire, Scotland, U.K. *Palaedaphus* is represented by part of a mandible, and pterygoid plates, and comes from the Upper Devonian of Belgium. *Archaeonectes* is from the Upper Devonian of Germany. We have new information on *Stomiahykus* and *Archaeonectes*, the type specimens of which we have examined. Details are presented below.

(*a*) *Stomiahykus*

The gross form of the pterygoid plates is similar to that of *Chirodipterus* (figures 18–20): their outlines are ostreiform rather than subtriangular, the lateral margins being subparallel with the mid-line; the arcuate plate ridges are anteriorly or anterolaterally directed; a shelf of mixed tissue (bone-plus-dentine) lies posterolateral to the main ridged dentine mass; and the posterior third of the plate is flat as a result of wear and infill of furrows by hard dark dentine. The anterior ends of the plates together form an acute angle, whereas in *Chirodipterus* the anterolateral plate margins meet at more than a right angle. In this, *Stomiahykus* is similar to *Dipnorhynchus*.

The tuberosities, which are subconical in form when unworn, are arranged in regular rows and increase in size towards the labial margins. Tuberosities are also arranged in concentric rows that reflect successive growth bands. A medial ridge is added after the development of three or more anterolateral ridges. Its tuberosities become lower anteriorly and merge progressively into the mixed bone-plus-dentine. The most anterior tuberosity of the medial row is higher and longer than any other on the plate (figure 18). The significance of this observation is discussed in a subsequent part of the text.

Tuberosities on the posterolateral shelf are represented by isolated dense patches of hard dark dentine formed well in from the plate margin. Elsewhere, tuberosities were added at the ends of the ridges, but still inside the plate margins. No tuberosity shows evidence of an enamel cap.

The anterior and lateral plate margins are formed of a series of crescent-shaped dentine blisters, their thickest part being aligned with the midpoint of the ends of the tuberose ridges. Two or three rows of stacked blisters are present (figure 19). The outermost member is composed of enamel-covered dentine, but the inner ones have the enamel removed by wear to expose the circumpulpal dentine around the ends of the pulp canals.

Unlike *Chirodipterus*, *Stomiahykus* has dentine in the midline covering the pterygoid–pterygoid and pterygoid–parasphenoid sutures. We consider that a parasphenoid is present in *Stomiahykus*. Its posterior stalk can be outlined beneath the occipital region, but its anterior end is obscured. It must have been under the posterior end of the continuous dentine sheet. This dentine (figure 20) is generally thin and made of circumpulpal and presumably interstitial dentine, with the former standing slightly proud as it does in the teeth of *Speonesydrion* and the ridges of *Griphognathus* (Smith 1977, figures 28–31). Between the posterior parts of the dentine plates this dentine forms a continuous sheet that seemingly laps onto the sides of the plates. At its posterior end two or three generations of dentine, separated by resorption lines, are present. They show slightly different levels of wear. Behind these, and also extending laterally behind the partly resorbed pterygoid plates, numerous irregularly shaped enamel-covered denticles represent the formative stages of a new generation of dentine (figure 20). Along the medial edge of the plates, forward of their midlength, there is a low elongate median ridge composed of the same type of dentine as that of the continuous sheet (figure 18). Little evidence of a median suture has been observed (cf. Bernacsek 1977, figure 5). Anterior and lateral to this median ridge the plates are formed of mixed bone-and-dentine of the same type as that forming the furrows between the ridges elsewhere.

As indicated above, the anterior end of the palate is acute. In the anterior angle each plate has its highest and most elongate tuberosity, which stands well above the element immediately posterior to it. Although these latter elements are broken on the left plate, those on the right are well enough preserved for this statement to be justified. Two generations of blisters, and a layer of mixed bone-and-dentine, form the marginal tissue anterior to the larger tuberosities. The shape of the area and the anomalous arrangement of the tuberosities suggest that dermopalatines may be fused to the pterygoids. No sutures can be observed to support this view, but the holotype of *Dipnorhynchus sussmilchi* has the sutures completely obscured by fusion, and so their absence in *Stomiahykus* is not conclusive evidence against the existence of fused dermopalatines. However, we consider the discrepancy in the sizes of the most anterior tuberosity and the ones immediately behind it to be highly significant. We consider that the more posterior tuberosities have been inhibited in their growth, because we assume that the development of tuberosities of the kind typified by chirodipterid plates required initiation of growth from the marginal blisters, and the tuberosities of the medial ridge were separated from such blisters by the independently growing dermopalatines. On balance we consider dermopalatines are fused in, but confirmation of this conclusion will require the discovery of other specimens.

Deep elongate wear pits are present between the tuberosities near the lateral margins of the plates. These are particularly well developed between the medial and the next ridge, and also in the midline. This latter pit is bordered in front by the massive tuberosities of the dermopalatines. It may have been produced by wear on a median anterior plate by an elongate tuberosity on an adsymphysial plate in the lower jaw. We note that a median anterior plate is present in *Dipnorhynchus sussmilchi* and *D. kurikae*, though it sometimes falls free of the surrounding bones. A similar situation occurs in *Archaeonectes*. We are unable to confirm or deny the presence of such a plate in *Stomiahykus*.

(*b*) *Archaeonectes*

This is another poorly known genus from the German Upper Devonian (von Meyer 1859; Bernacsek 1977). The type specimen of *A. pertusis* von Meyer is housed in the British Museum (Natural History) where we have been able to examine it. Only the anterior part of the palate is known. It is completely covered with dentine that is raised to form a small number of elongate eminences. No thin sections are available, but one cut surface shows that these eminences are formed of dark-coloured hard pleromic dentine (possibly petrodentine), extending as short projections into the underlying bone. Although the surface features are reminiscent of *Dipnorhynchus*, the type of dentine forming them is advanced relative to the dentine of that genus. Other similarities include the fusion of the dermopalatines to the pterygoids and an anterior opening that presumably held an anterior median bone in life. Bernacsek (1977, p. 192) has already drawn attention to the relation between *Archaeonectes* and *Stomiahykus*, suggesting that the large anterior 'tusks' and the deep depression between them are comparable. In our view *Archaeonectes* shows two characters that are derived relative to those of *Dipnorhynchus*, namely a more differentiated palate and the presence of petrodentine-like tissue.

6. Discussion

(*a*) *The concept of dentine plates*

In evaluating the dentition of *Chirodipterus* we have compared it with three other Palaeozoic dipnoan dentitions: organized tooth plates, such as those of *Dipterus valenciennesi* (Miles 1977, p. 297); poorly organized tooth plates such as those of *Speonesydrion iani* (Campbell & Barwick 1983, 1984); and finally tuberose dentine sheets that are not generally accepted as being true tooth plates, such as those of *Dipnorhynchus sussmilchi* (Denison 1974, p. 35). As a result of these comparisons it has become evident that more than one type of dental plate exists, and for the purposes of discussion and for phylogenetic evaluation we have decided to use one general term, namely 'dental plates', and two special terms, namely 'tooth plates' and 'dentine plates'. The bases of these distinctions will become apparent from the following comparative discussion.

C. australis has dental plates that simulate normal tooth plates in their gross shape and in the presence of tuberosities arranged in radial rows. However, lateral growth did not take place by the additon of enamel-covered teeth at the plate margins. Instead, new lateral growth is evidenced by the distinctive arrays of blister-denticles contouring the bone or dentine margin at the labial extremity of each tooth plate. Only within this primary framework of denticles could the petrodentine of the tuberosities and ridges subsequently develop. That is, the tuberosities could only arise by differential growth of petrodentine in apposition to the bone surfaces after extensive pleromic-dentine infilling of the bone. Tuberosities were not preformed in a soft-tissue morphogenetic unit as were the teeth added to the labial margins of the tooth plates of *Sagenodus* (Smith 1979) and *Uronemus* (Smith *et al.* 1987). This accounts for their organization a short distance in from the edge of the plates, and the variation in form and extent of the tuberosities within the species.

We believe that this mechanism is sufficiently distinctive to allow two types of dental plate to be distinguished. The first type, which we designate as a 'dentine plate', was shaped only by the continuous but differential growth of hypermineralized dentine (petrodentine in more derived forms) beneath the tritural surface. The second type, which we designate as a 'tooth plate', was shaped by the addition of teeth at the labial extremities of the ridges, and, in later forms, petrodentine initiated from within the teeth. This concept has been further discussed in relation to dipnorhynchids by Campbell & Barwick (1985) and by Smith (1987) for all types of dental plate.

Another difference is that growth of the pterygoid plates of *Chirodipterus* took place along the medial as well as the labial margin, and a new ridge was added on the medial side of the plate. No plate that grew by the addition of marginal teeth, as in radiate tooth plates in the sense in which that term is normally used, added tooth rows in that position.

Periodically the pterygoid plates of *Chirodipterus* were resorbed and regrown along their posteromedial edges. The tissue in that region, which forms a distinct part of the functional surface of the plate, is bone that has been partly replaced by pocules of pleromic dentine. Regrowth from this resorption surface initially took the form of non-contoured regenerative patches. No dentine was deposited on the parasphenoid. The prearticular plates, on the other hand, show little evidence of progressive regrowth but were progressively resorbed along their medial and posterior margins, although during intervals of stasis punctate regenerative patches covered the resorbed edges. These are all distinctive features of chirodipterid dentine plates.

(*b*) *Plate morphogenesis*

The development of tuberosities, their distribution and their shape depend on three primary factors: (i) the initiation and growth of petrodentine at specific sites that are arranged in radial rows; (ii) differential growth rates of petrodentine and adjacent tissues balanced with rates of wear; and (iii) the subsequent formation of an extensive basal pulp cavity extending laterally from these sites so that the cavities beneath adjacent ridges become confluent. In addition, further modification of shape occurs by the differential wear of bone-plus-pleromic-dentine and petrodentine. Each of these points will now be discussed.

(i) The initiation of petrodentine growth sites is not uniform on all specimens of the one species. As indicated above, growth may be more or less continuous, so producing continuously growing smooth-topped ridges, or it may be discontinuous, producing a linear series of irregular protuberances. The fact that the growth sites produce radial ridges on a clearly defined pattern in the two jaws indicates that this process is the phenotypic expression of a genotype produced by the interaction of extrinsic factors resulting from the type of jaw action and ability of the tissues to differentiate petrodentine separately from marginal denticles. Alternatively, the phenotypic expression could result from the type of food taken by each organism: those taking hard shelly prey develop short continuous ridges with large, flat, grinding plates, and those taking softer (crustacean) prey develop longer tuberose ridges with shorter grinding plates. The system may be more adaptable than one based on the addition of teeth at predetermined sites.

This does not address the problem of the origin of the petroblasts that formed the tuberosities, assuming these are specialized cells related to the production of a derived tissue type in dental plates. We think they developed from the cells that formed the previous tuberosity in the same row, rather than from the cells that formed the dentine in the marginal blisters along the plate margin. A population of stem cells, or cells committed to differentiate into petroblasts, would already be in existence beneath the previously formed tuberosity and would be stimulated to proliferate and differentiate as the pulp cavity was extended distally by resorption. There is no evidence of pulp cavities being formed independently beneath blister tissue, which would be necessary if a stock of precursor cells for petroblasts were to form independently in that region.

(ii) Part of the explanation of the development of tuberosities must be the accelerated rate at which the petrodentine in the specified sites grew against the underlying bone. This was made possible by accelerated resorption of pulp cavity space beneath the forming tuberosity, allowing a greater rate of growth of the forming tissue by petroblasts (as in the forming root of continuously growing mammalian teeth). It was also made possible by the continuous remodelling of the contact zone between the petrodentine and the tissue of the furrows flanking the ridges. This would allow upward movement of the petrodentine relative to the surrounding tissue. These phenomena are best seen by the growth lines in the sections in the region of the most recently added tuberosities (figure 70) and the scanning electron micrographs (figures 12 and 13) of the remodelling surface of the most lateral tuberosities.

(iii) Beneath the dentine sheets forming the plateau of the plate, pulp cavities were not extensive. However, beneath each ridge, pulp cavities were developed. During growth these cavities were expanded around their edges by resorption of the adjacent bone. Petrodentine can grow only around a pulp cavity within which petroblasts can differentiate. The above mode of cavity expansion therefore ensures that thick petrodentine will form beneath the proximal ends of the furrows and ridges. In young plates the cavities beneath adjacent ridges have become confluent in restricted regions to produce a series of tunnels. Petrodentine has formed at the sites of these tunnels in young adults. As a result of the extensive wear across the surface (see below) the relatively soft mixed tissue (of bone-with-dentine) that was not resorbed during pulp cavity formation and hence had not been replaced by petrodentine, was removed by abrasion and the area of petrodentine exposed on the plate surface was expanded. Thus the area occupied by the sheet of dentine forming the plateau increased. Its surface is smooth partly because any tuberosities involved in its formation have been removed by wear and partly because the intervening spaces are composed of petrodentine that wears at the same rate as the ridge petrodentine (as discussed in §6(*c*)).

(*c*) *Modification of shape by wear*

The opposing plates occlude only around their margins. However, while wear produced by tooth-on-tooth activity could occur only in this narrow occlusion zone, the plates are designed so that food would have passed in a posteromedial direction along the furrows. If such food contained mineralized tissue, extensive wear of the plates would take place by abrasion. Also, as is commonly seen, pits would develop in the furrows by a type of 'pestle and mortar' action.

Both attrition and abrasion would have operated to form the tooth-plate patterns of *C. australis*. A petrodentine tuberosity that occluded with a furrow floored by bone-plus-pleromic-dentine would soon wear a pit of complementary shape in the furrow, and at the same time develop smooth wear surfaces on the tuberosities adjacent to the pit, thus producing closely interlocking tuberosities and pits. In this way the tuberosities would be shaped into cones and emphasized relative to the surrounding tissues. The effects of abrasion would be less precise in that hard food particles of no special shape would produce generalized wear surfaces. This, together with the gradual wear of the tops of the tuberosities and their movement out of the zone of tooth-on-tooth action as a result of the marginal growth of the plate, results in fewer well-defined tuberosities towards the plateau of the plate. This argument depends a great deal on the nature of the food of *C. australis*.

Fortunately we know a great deal about the associated invertebrate fauna. It included a number of hard-shelled and relatively soft-shelled organisms such as brachiopods, molluscs and phyllocarid crustaceans. In addition a large, lightly mineralized organism of unknown affinities is common. Presumably, soft invertebrates also occurred. *Chirodipterus* had powerful adductor mandibulae muscles oriented to apply considerable power in the bite. Also, the supporting bone of the pterygoids and the prearticulars is thick and well buttressed against the neurocranium and roofing bones, and the meckelian and dermal bones respectively. Therefore the structure of the teeth, supporting bones and muscles are all consistent with a durophagous habit, and an appropriate shelly food source is known to have been available.

Hence not only is it possible to affirm the role of wear in the formation of the various ridge elements of the plate, it is also possible to postulate that a large amount of tissue was removed from the plate surface, thus enabling the continuous sheet of petrodentine forming the plateau to progress further out into the furrows towards the labial margins.

(*d*) *Comparison with other dipnoans*

None of the characters of the dental complex associated with denticle-shedding types is found in species of *Chirodipterus*. Denticles of the type found in *Griphognathus* do not occur anywhere in the buccal cavity; and despite the large number of carefully etched heads of specimens of *C. australis* that had mandibles associated, there is no evidence of denticulated basibranchial (basihyal) plates. Moreover, the pterygoid and prearticular plates are added to extensively so that a large tritural surface remains with only relatively minor areas of resorption. These are retained growing plates in the same way as those of *Dipterus* or *Sagenodus* or even *Neoceratodus*. The minor resorption that took place along the medial and posteromedial edges of the prearticular plates was to allow space for other developing structures in the lingual region; it was not to permit the redeposition of a new structure of the same type, which is the role of resorption in *Uranolophus* and *Griphognathus*. Therefore comparison must be made with the continuous growth, dentine-additive type of dentition such as that found in dipnorhynchids and dipterids.

(i) *Dipnorhynchus and Speonesydrion*

Compared with such early Devonian genera as *Dipnorhynchus* and *Speonesydrion*, *C. australis* is advanced in the extent of its pulp cavities, growth in the palatal mid-line, the absence of dentine on the parasphenoid and the presence of petrodentine. However, the plates of *C. australis* did not develop from teeth and they added to their margins by small irregular blisters or denticles. In these respects they are comparable to the young plates of *Speonesydrion*. It would be possible to produce a *Chirodipterus* plate from a juvenile *Speonesydrion* plate by the suppression of labial marginal tooth development, initiation of basal pulp cavities to permit the growth of petrodentine, palatal midline growth and the loss of dentine on the parasphenoid. None of these innovations would be in conflict with what is known of evolution in early dipnoans. We regard *Speonesydrion* as having the most primitive tooth plates known (Campbell & Barwick 1985) and if the above interpretation were sustained, dentine plates would be interpreted as paedomorphic tooth plates (see Smith 1987). On the other hand, enamel-covered teeth are derived structures relative to undifferentiated dentine sheets, which are features of the dentition of most primitive dipnoans. This suggests that simple dentine plates would be expected to be the primitive dental plates of dipnoans, which was the view adopted by Campbell & Barwick (1985, 1987). Dentine plates of the *Chirodipterus* type would have developed as a result of pulp cavity formation and differential growth of petrodentine beneath a previously undifferentiated dentine sheet, with concomitant introduction of growth in the mid-line and opening of the parasphenoid sutures. This difference of interpretation has not been resolved.

We also draw attention to similarities between the *Dipnorhynchus* dentition and that of *Chirodipterus*. This developed by the marginal addition of denticles and by the development of eminences that are based on thick compact bone and are covered with dentine. These eminences must also have grown at some distance from the margins of the plate. In other words, the pterygoids and prearticulars remodel the shapes of their buccal surfaces from within during growth, and thicken the dentine over the resulting eminences by inward growth. This involves differential inward growth at a distance from the plate margins after an initial period of growth when the plates were almost featureless. As in *Chirodipterus* this results in a continuous sheet of dentine over the plates, although of course the margins are relatively straight rather than undulose. It may be tempting to consider *Chirodipterus* as representing a further stage of development from a dipnorhynchid form, but that would ignore the point that the eminences on the plates of *Dipnorhynchus* were formed mainly of bone whereas those of *Chirodipterus* were the results of fluting at the labial margins of the plates, and subsequent differential growth of petrodentine. The plates of these two genera probably represent independent evolutionary developments of a primitive dentine plate, the one adapted for the crude crushing of heavy shells, and the other for crushing lighter shells or soft tissues or both.

(ii) *Stomiahykus thlaodus Bernacsek*

After examination of the type specimen of this species (details given above) we consider that the gross form of the plates, the nature of the tuberosities, the absence of true teeth, the production of marginal growth by blisters and the addition of a new ridge medially after the plate has been established, demonstrate conclusively that *Stomiahykus* is allied with *Chirodipterus*. The thin layer of dentine in the posteromedial region of the palate completely obscures the sutures in this region, whereas *Chirodipterus* has open sutures and no dentine sheet. It is clear from the fact that a new plate ridge is introduced medially in *Stomiahykus* that growth in the midline was possible at some stages of the ontogeny. The growth layering and resorption lines in the posteromedial dentine sheet show that this growth was accomplished after at least partial resorption of the superficial dentine layers. This is not remarkably different from the situation in *C. australis* in which extensive resorption of the bone-plus-pleromic-dentine in the posteromedial regions of the palate took place episodically. In this respect, therefore, *Stomiahykus* is a morphological intermediate between genera such as *Speonesydrion* and *Dipnorhynchus*, which have a continuous layer of dentine covering all the sutures and hence preventing bone growth in this region, and *Chirodipterus* in which the sutures were open at all stages. We consider this condition in *Speonesydrion* and *Dipnorhynchus* to be primitive for all Dipnoi with dental plates. Another primitive dipnoan feature is the presence of attached dermopalatines that meet in the midline and, as we have shown, a good case can be made for their presence in *Stomiahykus*. Finally, we note that this is a marine genus of Eifelian age, i.e. it is appropriately placed to be a phyletic as well as a morphological intermediate between a primitive early Devonian dipnoan and *Chirodipterus*. Further discussion of this matter, involving the structure of the posterior face of the neurocranium, will be offered elsewhere. For the present we note that the presence of the large foramen in the position of a 'spiracular recess', the single attachment of the hyomandibular to the lateral otic bone, the isolated position of the attachment point of the ceratohyal, and the arrangement of the otic series of bones, all indicate that *Stomiahykus* retains many of the primitive neurocranial features displayed by *Dipnorhynchus* and probably *Speonesydrion*.

(iii) *Archaeonectes pertusus von Meyer*

As we have indicated above, this species retains a number of primitive palatal features, but it is advanced in others. We consider that it is close to *Stomiahykus*, and is an early member of the group containing *Chirodipterus*.

(iv) *Sunwapta grandiceps Thomson*

The incomplete mandible, which is the sole representative of this species, has a similar conformation to that of *Chirodipterus*. Its dentary, anterior furrow and dentine plates raised above the level of the 'dentary' in anterior view are all very similar to *C. australis*. In addition, the continuous dentine sheet (plateau) of the posterior region of the plates, the tuberose ridges showing medial as well as lateral addition, the marginal blisters and the posterolateral shelf with its distinctive new tuberosities are all so similar to the corresponding features of *C. australis* that we see no reason for separating the two species generically. Miles (1977, p. 293) had also noted that the tooth plates of *C. australis* were similar to those of *Sunwapta grandiceps*.

(v) *Conchodus ostreiformis McCoy*

Conchodus is known only from 'tooth plates' that are commonly broken. Examination of a specimen of *C. ostreiformis* from the Boghole Beds (Upper Old Red Sandstone) of Whitemire, Scotland (RSM 1900.60.22), shows the characteristic medial ridge of *Chirodipterus* type. The tuberosities are regularly conical and have the form of true teeth, but we see no evidence of an enamel cover. Further study of more complete material is required, but meanwhile we consider that the genus should be regarded as a member of the group with dentine plates.

(vi) *Palaedaphus insignis von Beneden & de Koninck*

From the late Devonian of Belgium comes the largest of all known dipnoans, represented by pterygoid plates and the anterior part of a mandible. We have examined casts of these specimens in the British Museum (Natural History). The mandible has the characteristic chirodipterid form, with an arcuate 'dentary' separated from the 'prearticulars' by a narrow continuous anterior furrow. All the 'tooth plates' are radiate and the ridges are composed of poorly formed 'teeth'. These were not introduced at the plate margin and are probably the same as the tuberosities described here in *Chirodipterus*. A strip of tissue lies between the most labial 'teeth' (tuberosities) and the plate edges. We suspect that the genus has chirodipterid plates, but study of the original specimens is necessary to confirm this.

(vii) *Dipterus spp.*

We draw attention to the illustrations of *Dipterus glaber* by Pander (1858, plate 7, figures 10A–D). Clearly, he had observed the features we record in *Chirodipterus*: the tuberose nature of the ridges and, at the margins of the ridges, the stacked rows of marginal blisters.

Denison (1974, figure 6) illustrated a thin section of a plate assigned to '*Dipterus*' *mordax* Eastman. This illustration has been published with the occlusal surface downwards, the reverse of the normal arrangement. We suggest that this specimen will prove to be chirodipterid in its histology and mode of growth.

The specimens figured as *Dipterus digitatus* Eastman (Eastman 1908) from the late Devonian in Iowa are of chirodipterid type as is indicated by the overall shape of the plates and the presence of a separate medial ridge.

Sneddon (1969, p. 29, figure 9) illustrated a specimen *Dipterus* sp. cf. *D. digitatus* Eastman from the late Devonian of Western Australia. This individual has the characteristic growth pattern and tuberosity distribution of a chirodipterid.

Another example of dipterid tooth plates described from the Eifelian of Eastern Albourz, Iran, by Blieck *et al.* (1980, figures 18 and 19), is almost certainly of chirodipterid type, as judged from the shape of the plate, number and disposition of the ridges and the position of the tuberosities on the ridges being inset from the margin. What is particularly relevant to the present discussion is that Blieck *et al.* (1980) comment that although these plates are similar to those of *C. australis*, they are more elongate and are strikingly similar to the tooth plates of *Stomiahykus thlaodus*. However, the tooth plates from Iran are not as long as those of *Stomiahykus* and the proportion of tuberose ridges to flat tooth plates is only 1:5, whereas it is 3:5 in *Stomiahykus*. In some of the *C. australis* tooth plates (ANU21638) the proportion is, in fact, also 1:5. Blieck *et al.* (1980) have commented on the variability in shape and size and suggested the difference may be due to wear and a change of diet from young to old fish. We have noted in this paper that the morphology of chirodipterid plates is very dependent on wear and differential growth.

7. Conclusions

Re-evaluation of the concept of tooth plates in Palaeozoic dipnoans has been possible because the detailed morphology of chirodipterid plates is so well preserved in the Gogo fauna from Western Australia. Also, interpretation of growth has been possible from an extensive series of specimens, all from Gogo.

Information on the surface features, histology and ultrastructure of tissues deep to the growth and wear surfaces, has been integrated with palaeoecological information from the Gogo Formation to provide an interpretation of the growth and wear patterns of the dental plates. With the realization that different patterns of growth may operate to produce chirodipterid plates on the one hand and dipterid plates on the other, it has become necessary to define the terms relating to dental plates more precisely. The term 'dentine plate' is used for plates with the characteristics of chirodipterids, and 'tooth plate' for those with the characteristics of dipterids, the general term 'dental plate' being reserved for these plus other possible types. The addition of marginal blisters to the growth margins, as layers of successively formed denticles with some variation in size along each layer, is known only in chirodipterids. This contrasts with the radiate tooth plates in which teeth are added at predetermined positions at the labial end of each tooth row, in sequence with the last previously formed tooth.

The recognition of a 'distinctive dentine plate' suggested that, as well as *Chirodipterus*, other dipnoans may have been incorrectly assigned to groups with 'radiate tooth plates' because their dentitions have been inadequately understood. The plates of several named genera, and several species loosely assigned to *Dipterus*, have been examined with this in mind. We have concluded that *Sunwapta* and *Stomiahykus* certainly have 'dentine plates', and *Conchodus* and *Palaedaphus* probably have them. In addition various 'tooth plates' ascribed to *Dipterus* by authors over a large number of years are also shown to be true 'dentine plates'. We consider that these determinations will play an important role in reconstructing phylogenetic relationships among primitive dipnoans.

Specimens of *C. australis* have been provided for study by Dr Peter Forey and Dr Colin Patterson of the British Museum (Natural History) London, U.K., and Dr Gavin Young of the Bureau of Mineral Resources, Canberra, Australia. Dr Mahala Andrews, Royal Scottish Museum, Edinburgh, U.K., gave us access to specimens of *Conchodus* and Professor Richard Fox, University of Alberta, Canada, sent a cast of *Sunwapta*. Professor David Dineley and Dr Liz Leoffler, Bristol University, U.K., gave us access to the type of *Stomiahykus*. Dr John Long, Australian National University (ANU), Canberra, allowed us to use casts of the Iranian dipterids described by Blieck *et al.* (1980), and drew several other tooth plates to our attention. Sections for optical examination and SEM have been prepared by Mr H. Zapasnik and Mr R. Popovic, ANU. We are indebted to Dr Tony Eggleton and Mr C. Foudoulis of the Geology Department, ANU, for collaborative work on the TEM of ion-beam-thinned tissue. Photographic prints were made, from negatives by M.M.S., in the Photographic Units of the Anatomy School of Guy's Hospital, London, U.K., and the Science Faculty, ANU. Scanning electron micrographs were prepared in the SEM units at the same two institutions. Mrs L. Wittig, ANU, prepared figures 1, 32 and 70 in their final form.

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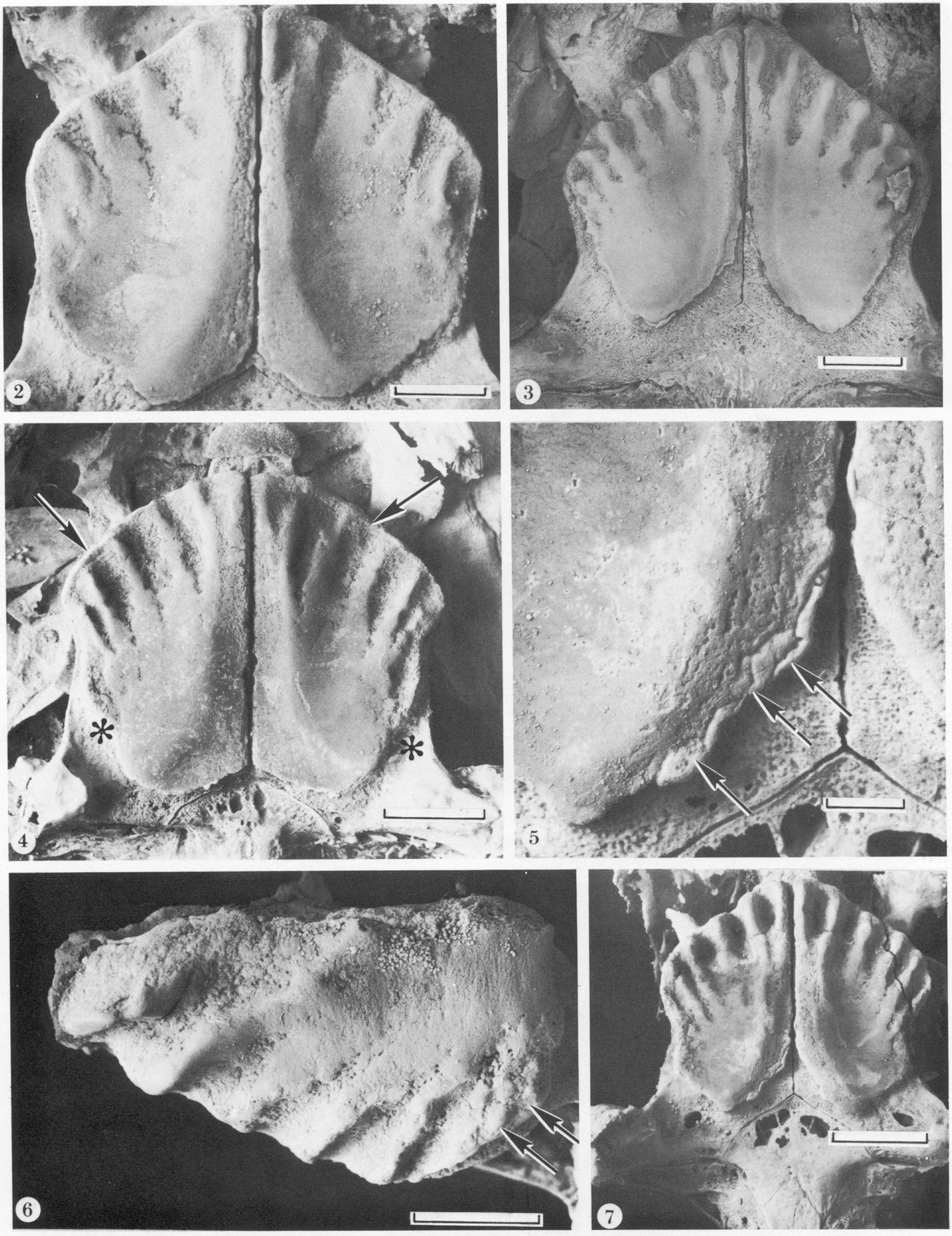
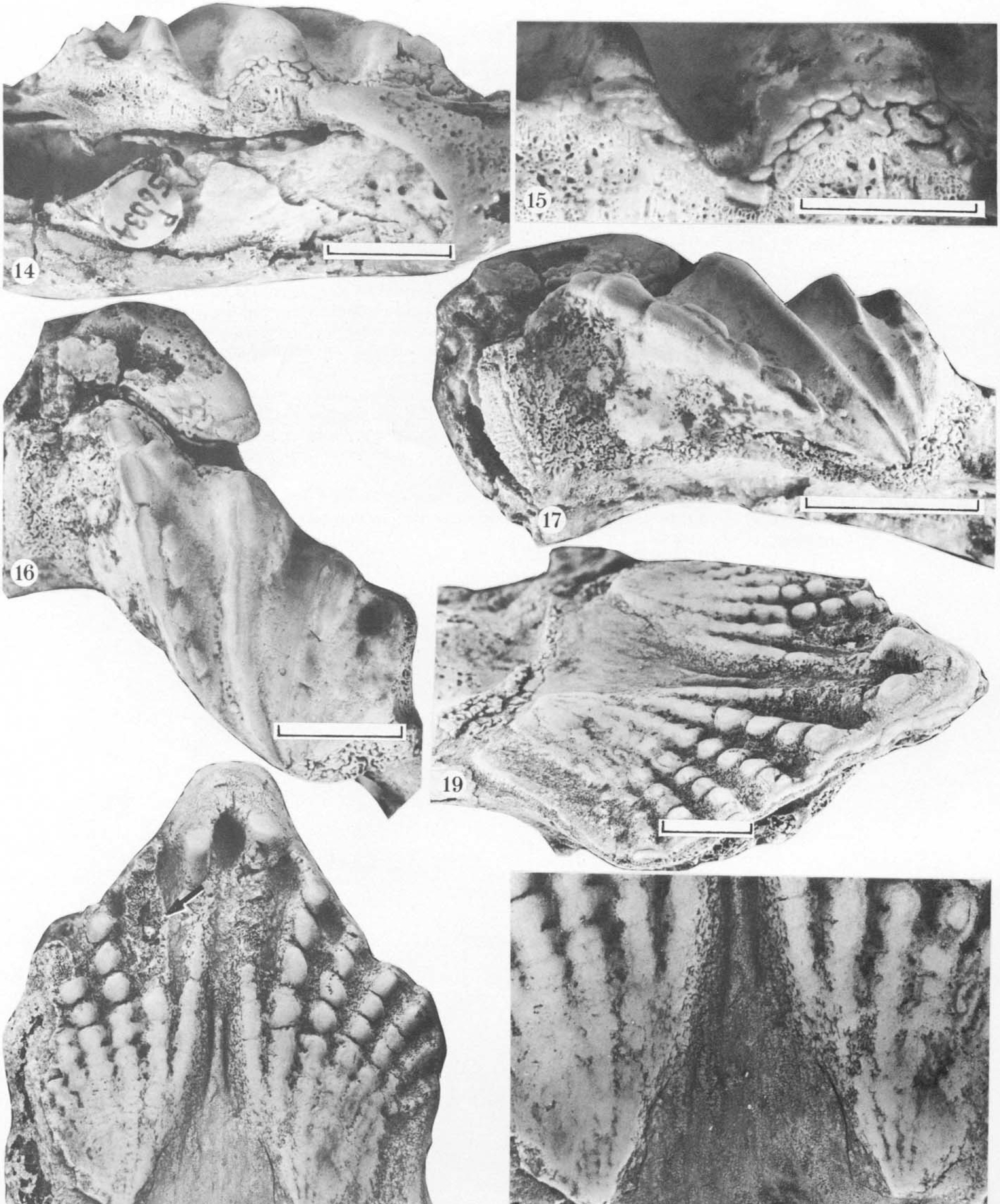
Abbreviations used on the figures

bo.	bone	pet. b.	petroblasts
c.p.s.	cell process spaces	p.c.	pulp canals
c.p.d.	circumpulpal dentine	p.cav.	pulp cavity
den.1,2	denticle in sequence, 1,2, etc.	pit	wear from opposing tuberosity
en.	enamel	pler.	pleromic dentine
fs.	forming surface	r.	ridge
ff.	forming front	reg. d.	regenerative dentine
g.l.1	growth line 1, 2 etc.	res.	resorption surface
i.d.	interstitial dentine	rev. l.	reversal line
m.r.	medial ridge	t.	tuberosity
n. den.	new denticle	t.s.	tritural surface
pal.	pallial dentine	w.den.	worn denticle
pet.	petrodentine		

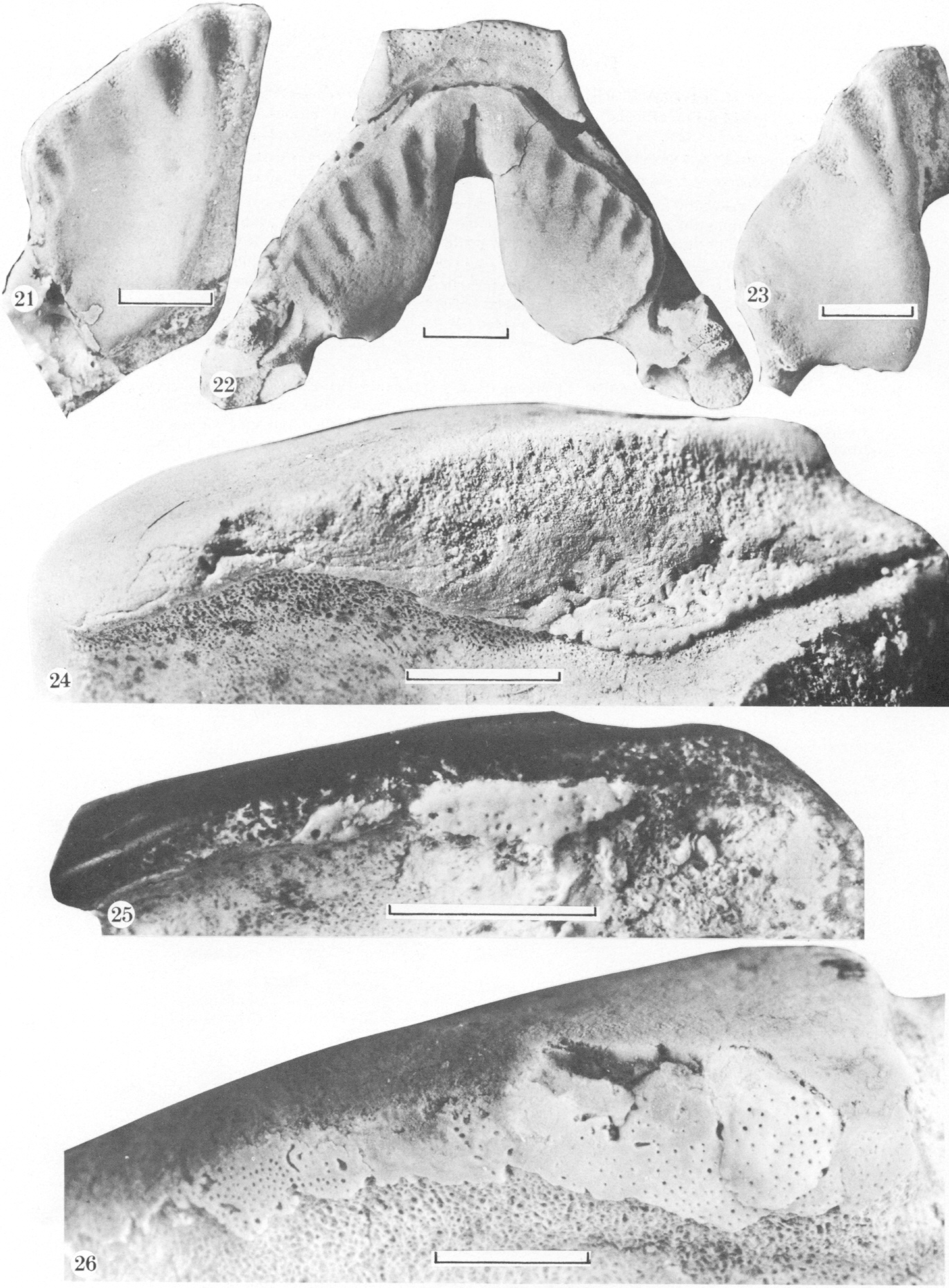


FIGURES 2–7. For description see opposite.

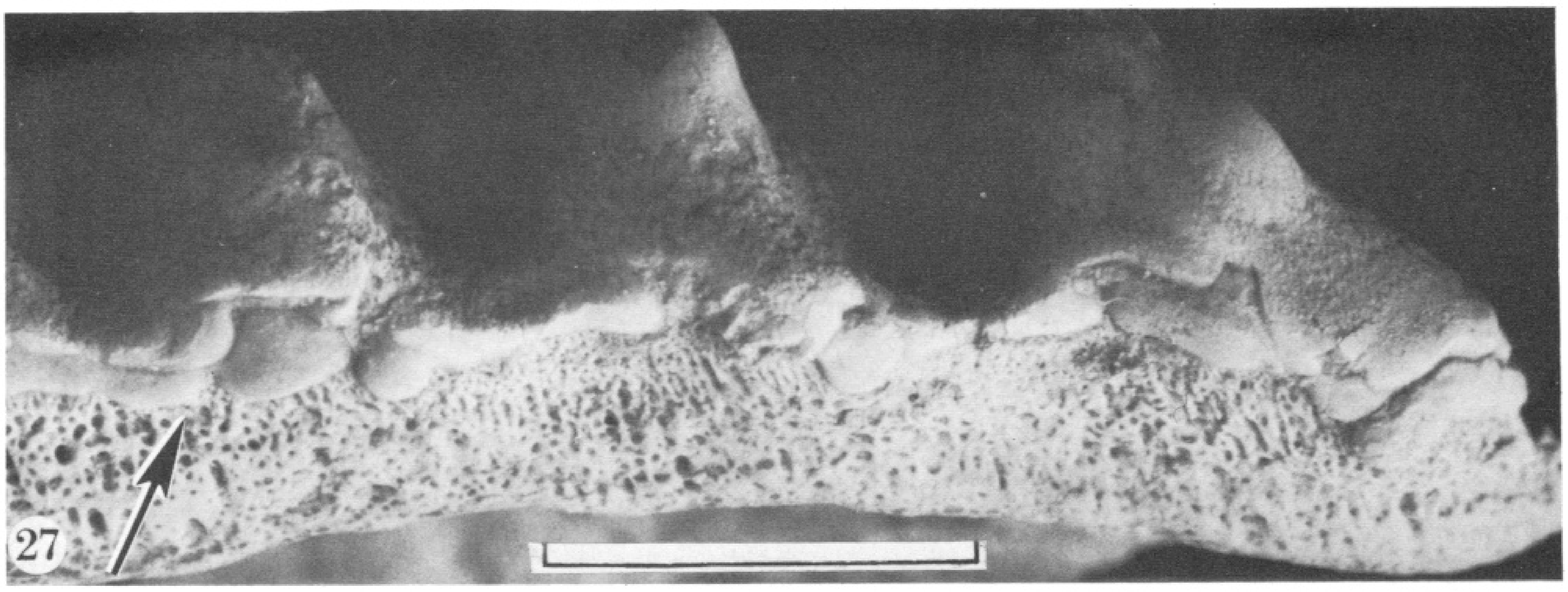
FIGURES 8–13. For description see opposite.

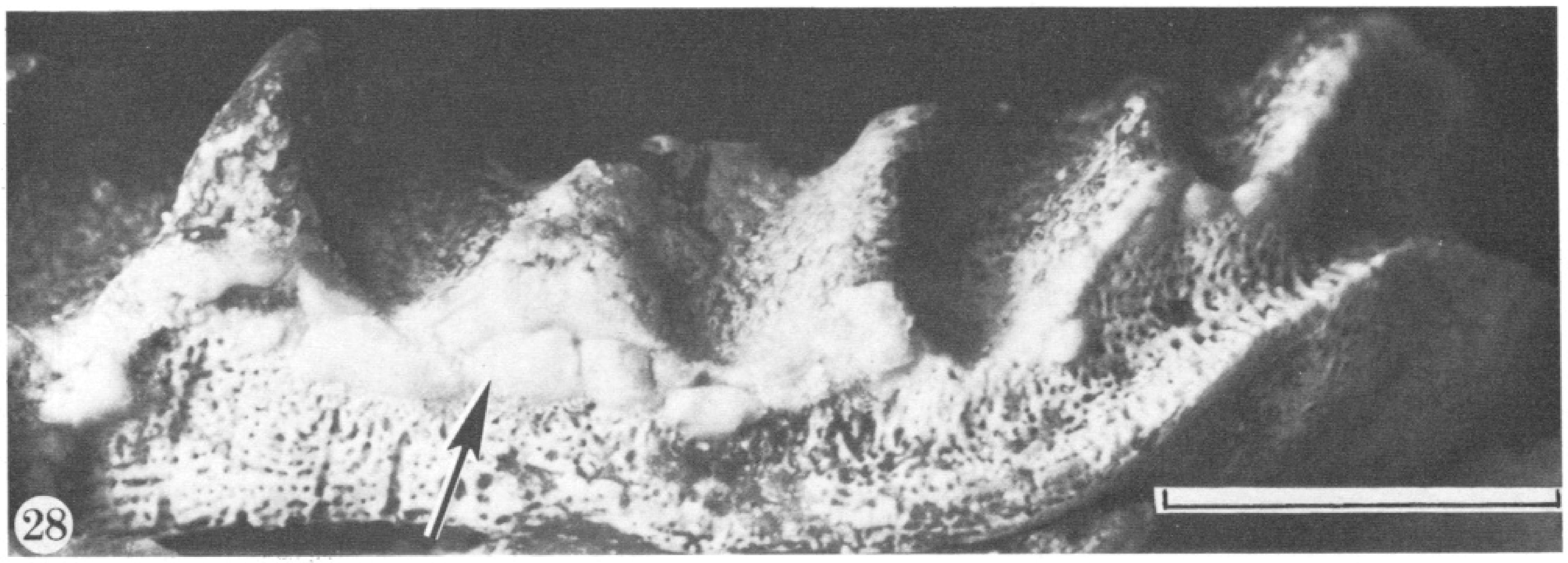


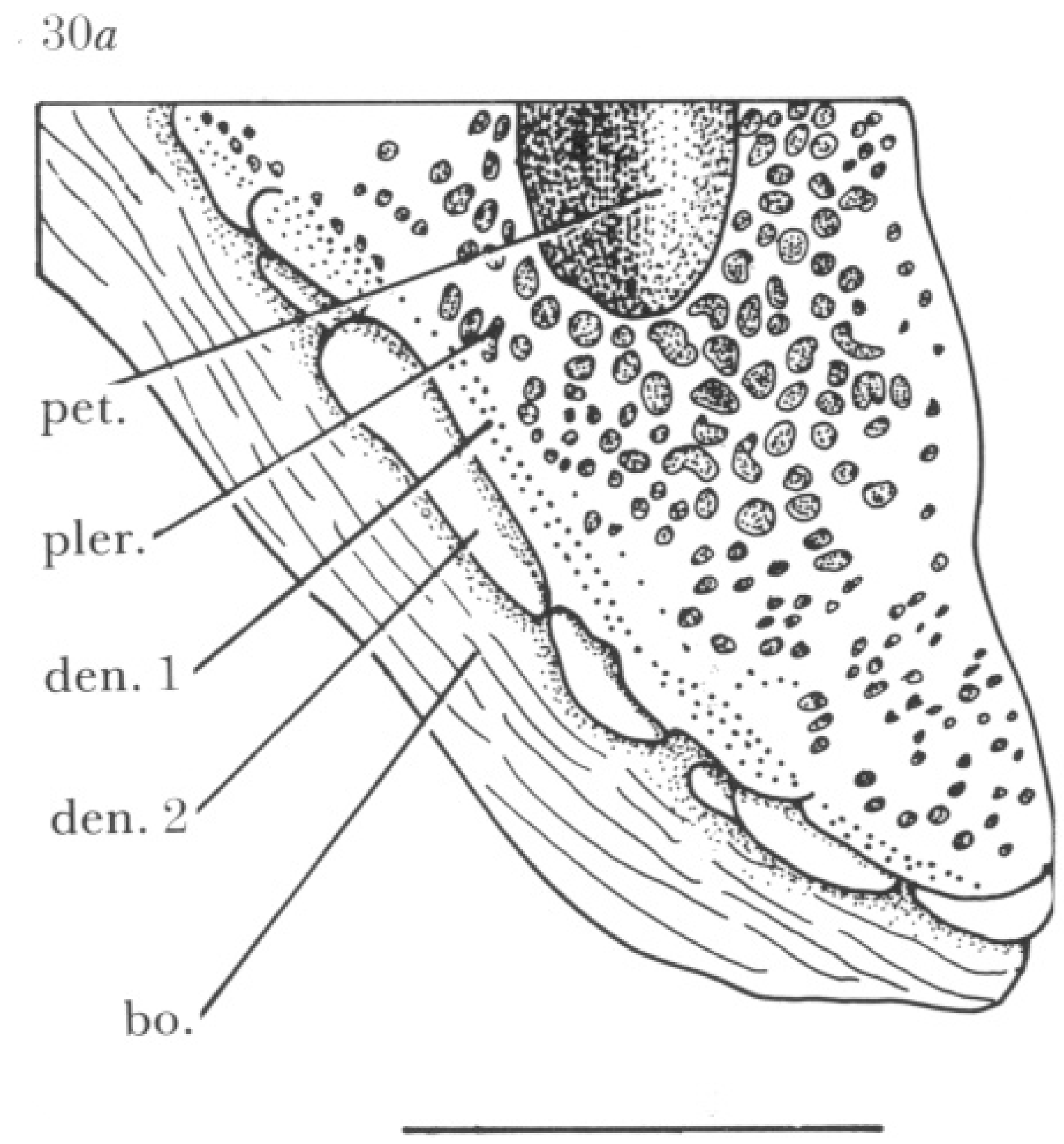
FIGURES 14–20. For description see opposite.

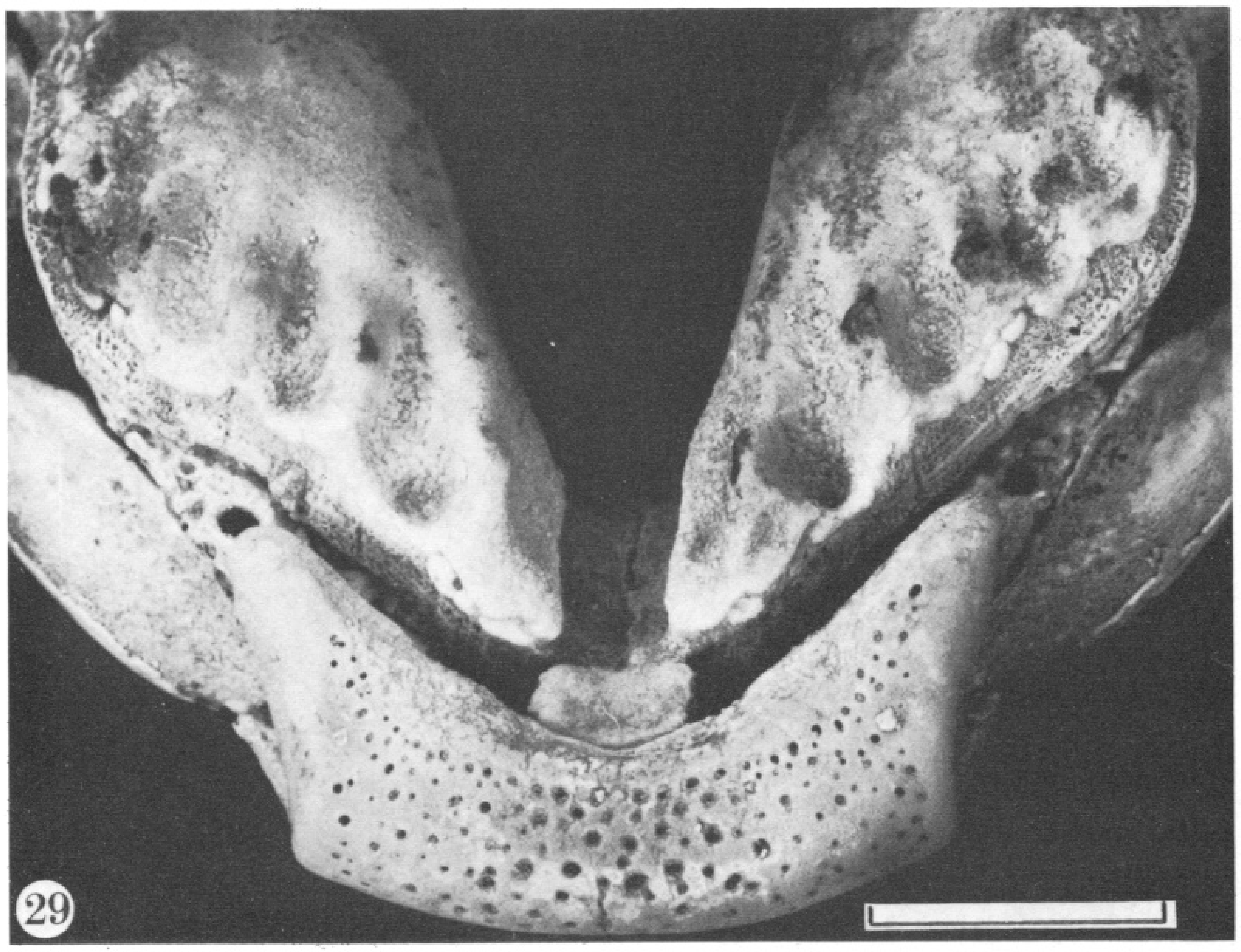


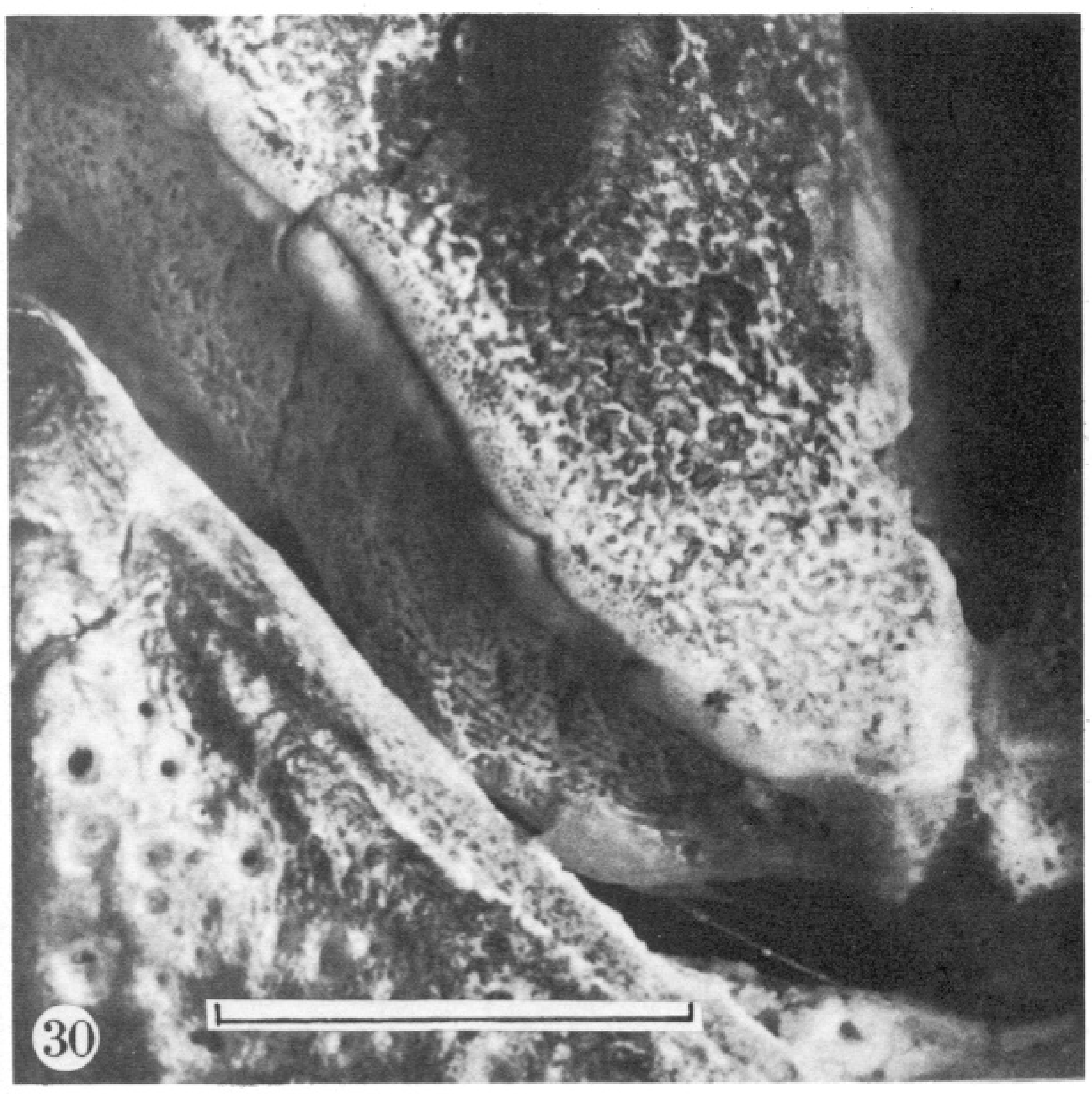
Figures 21–26. For description see opposite.

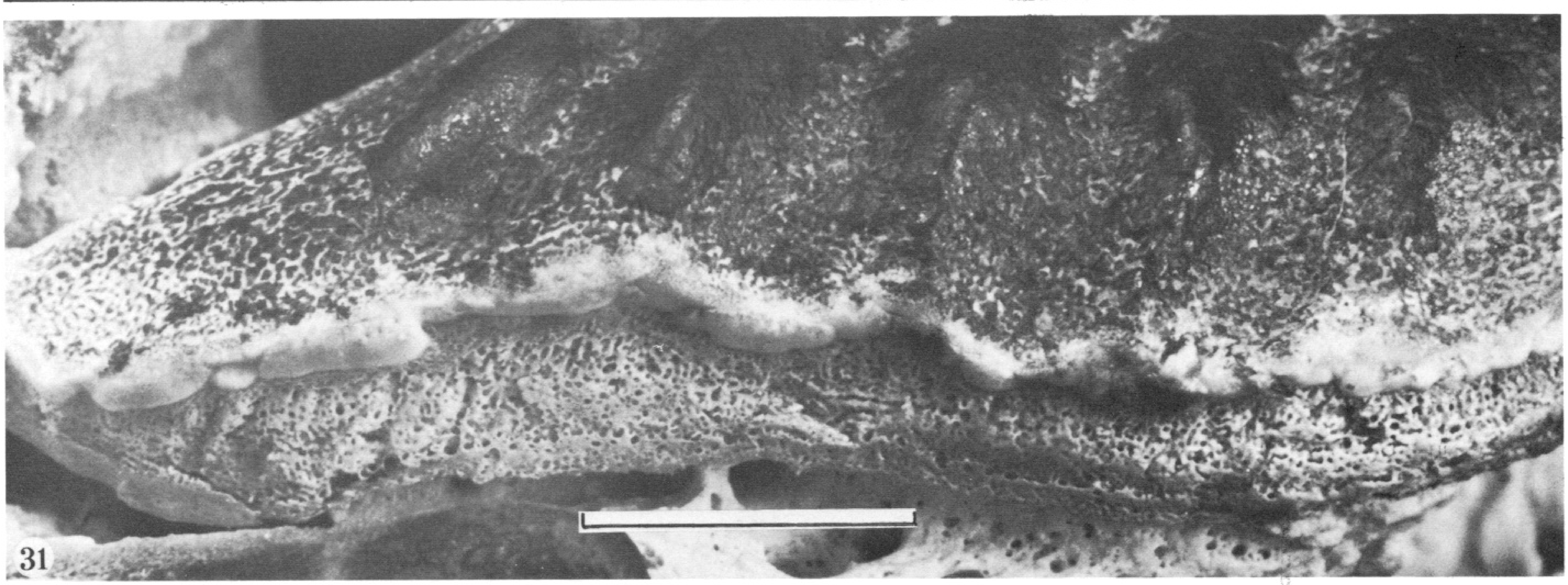




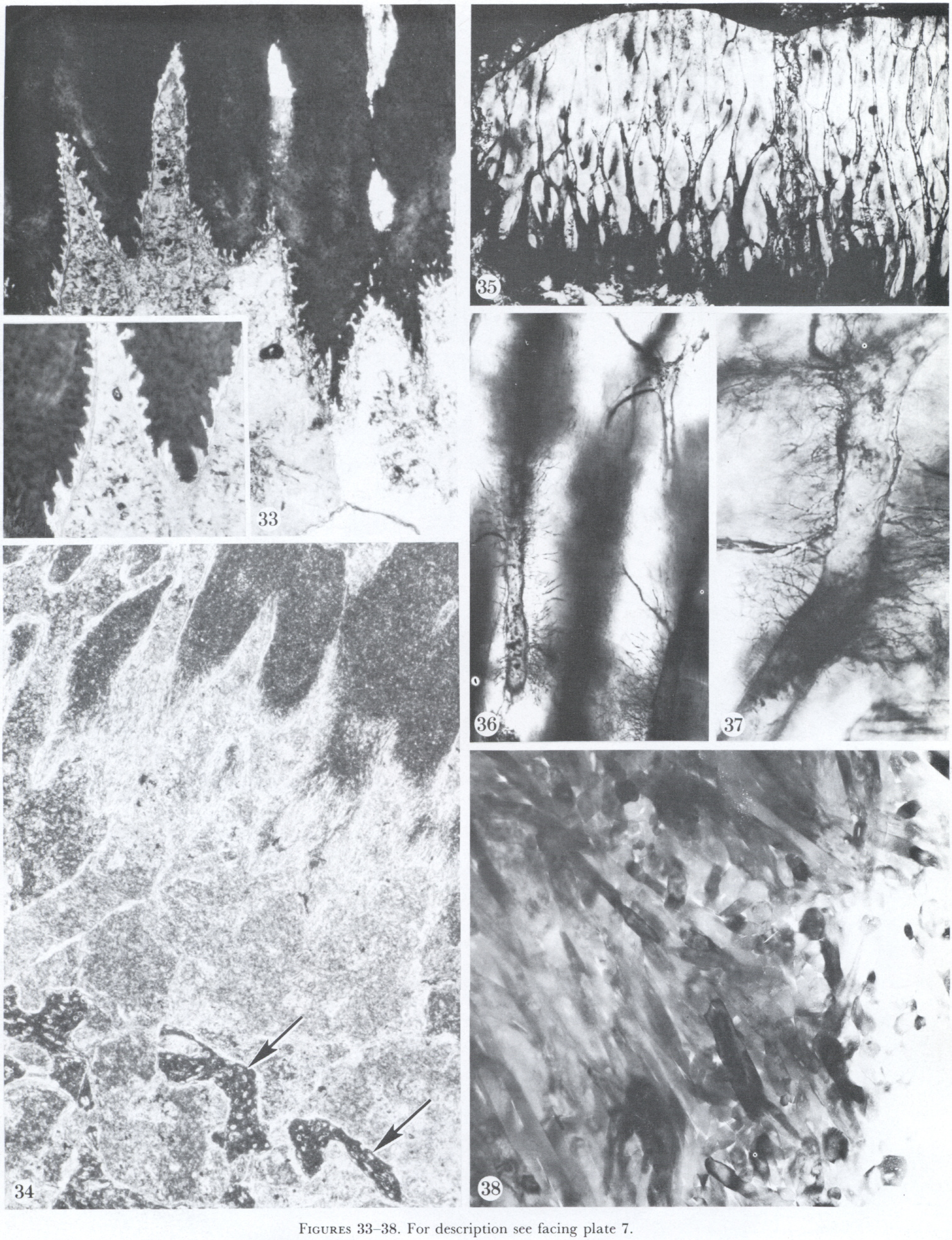




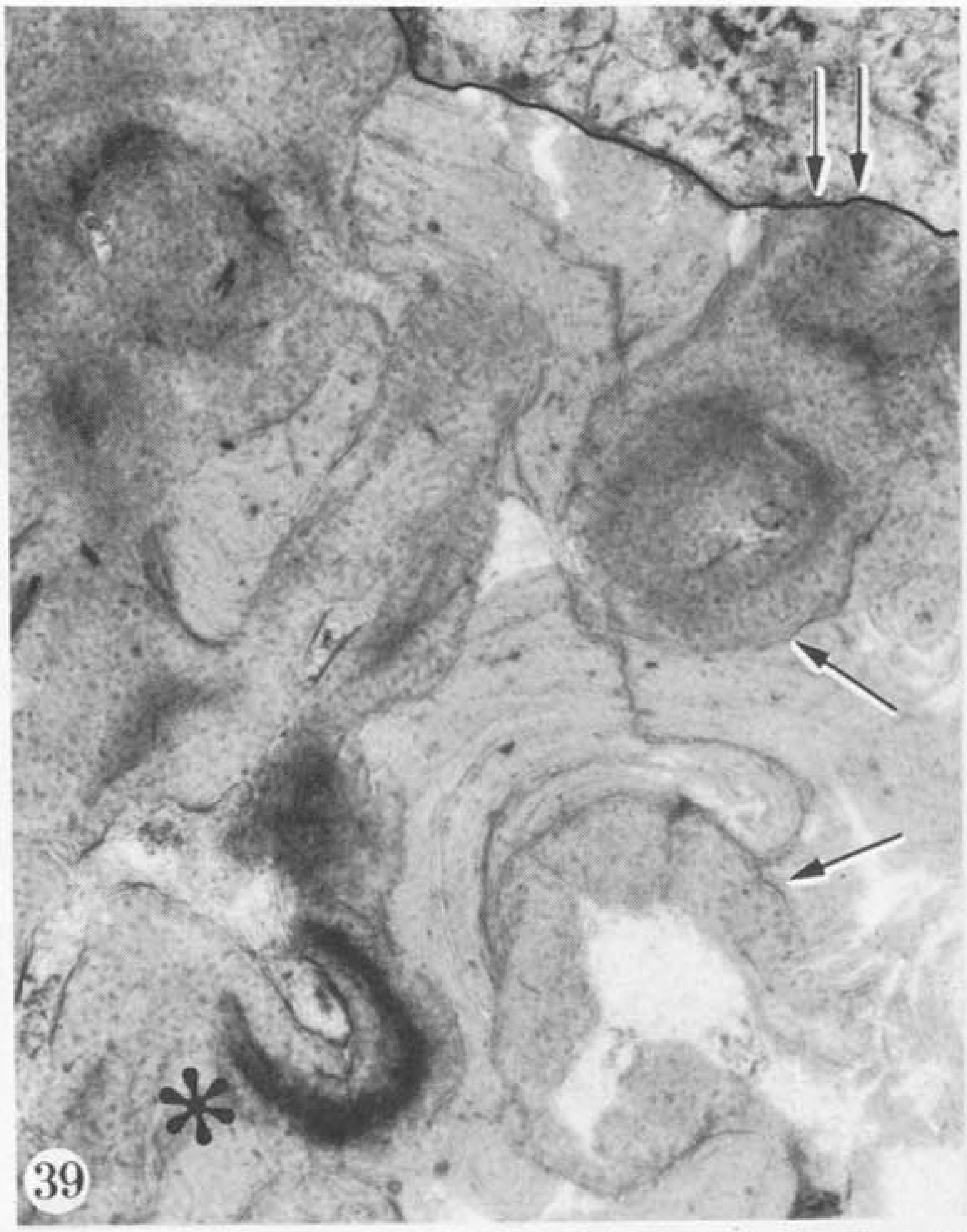


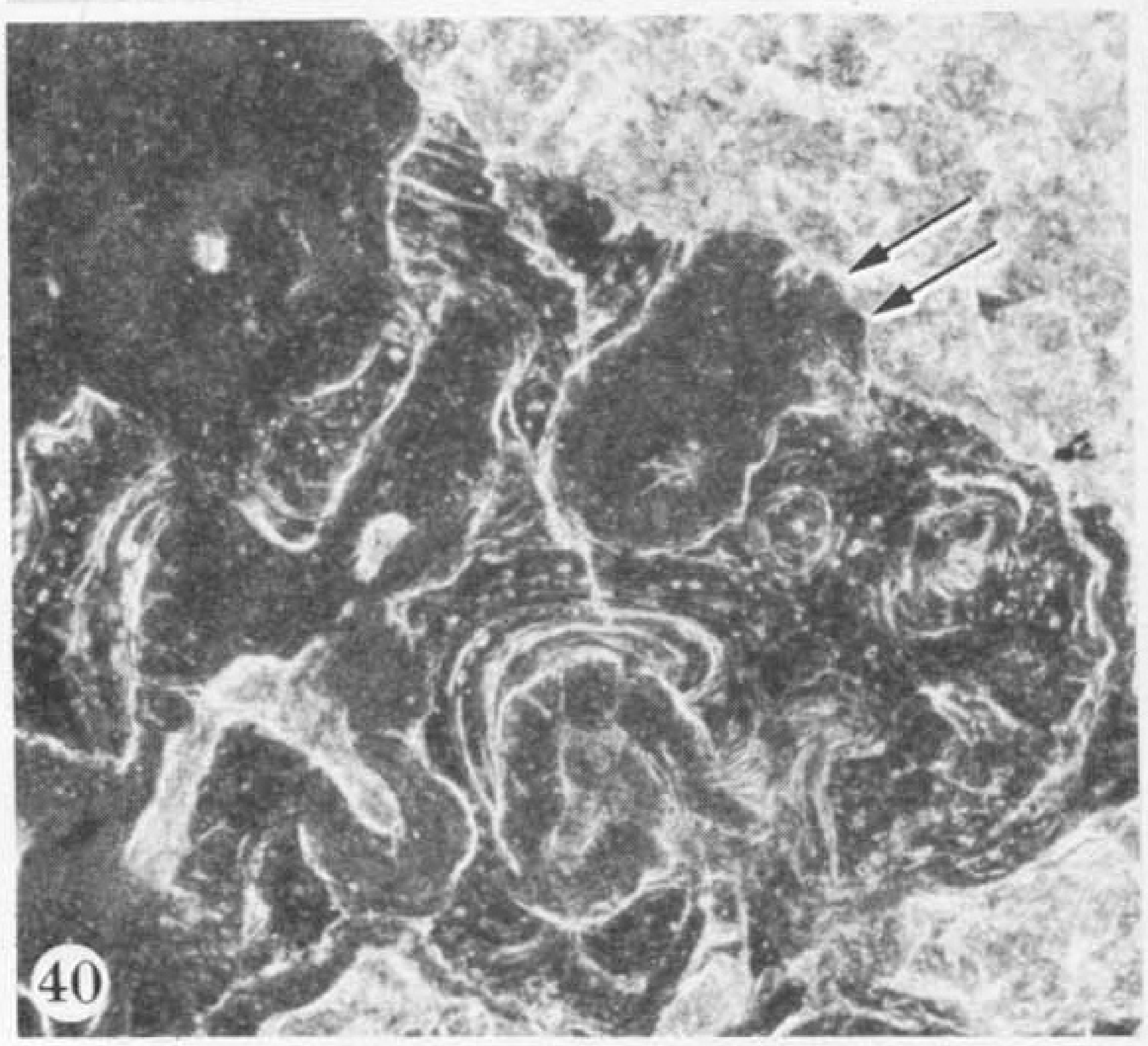


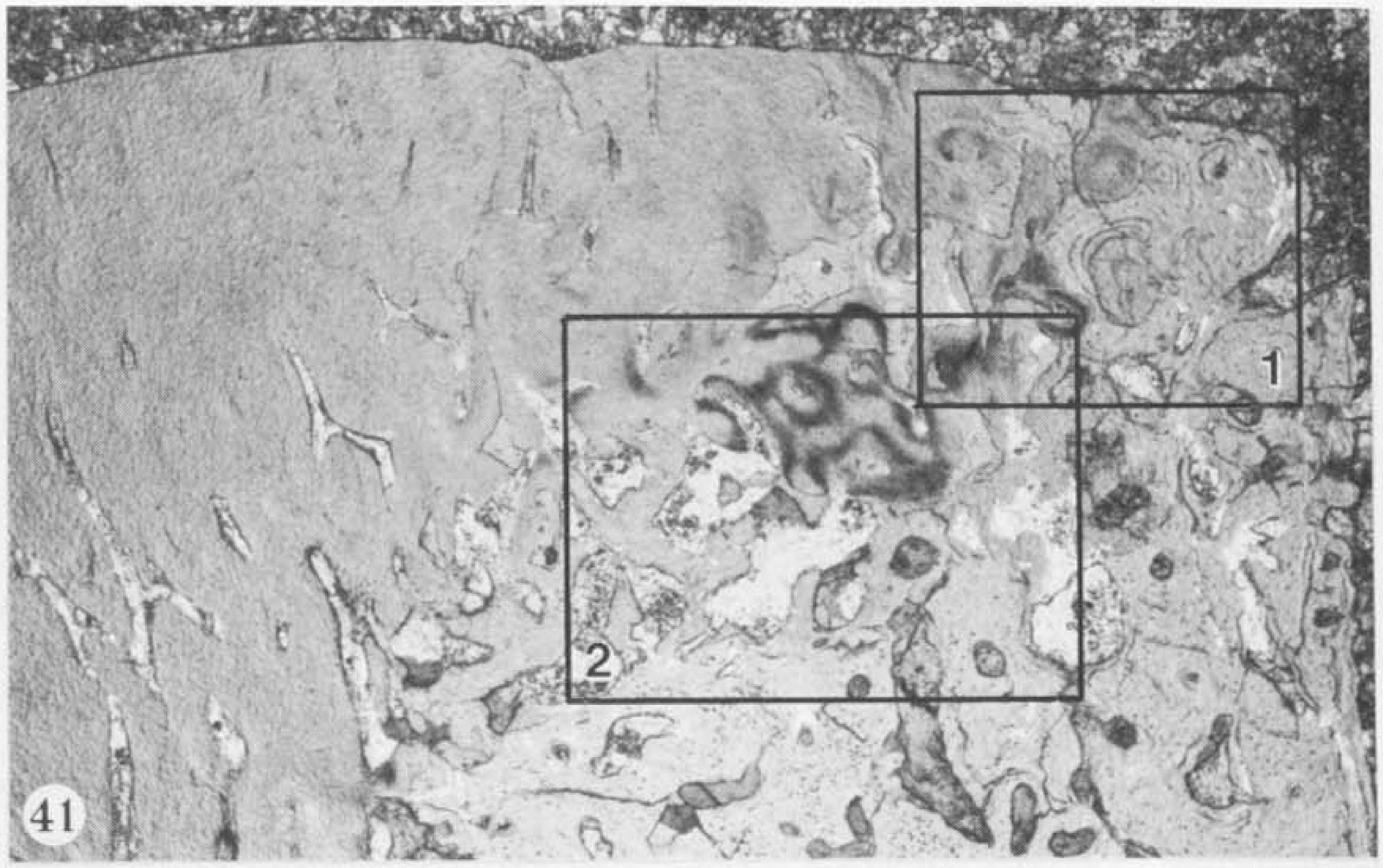
FIGURES 27–31. For description see opposite.

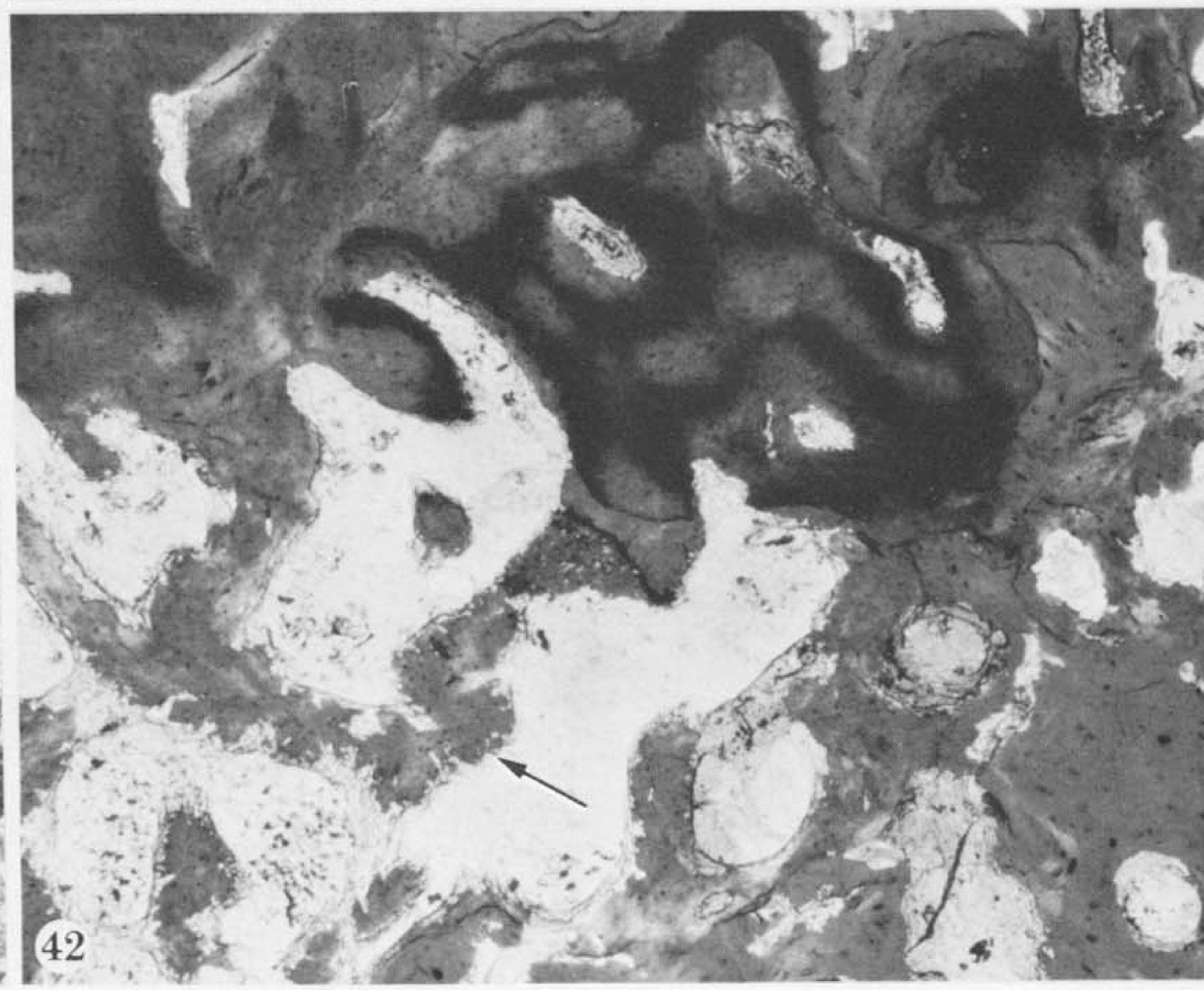


Figures 33–38. For description see facing plate 7.





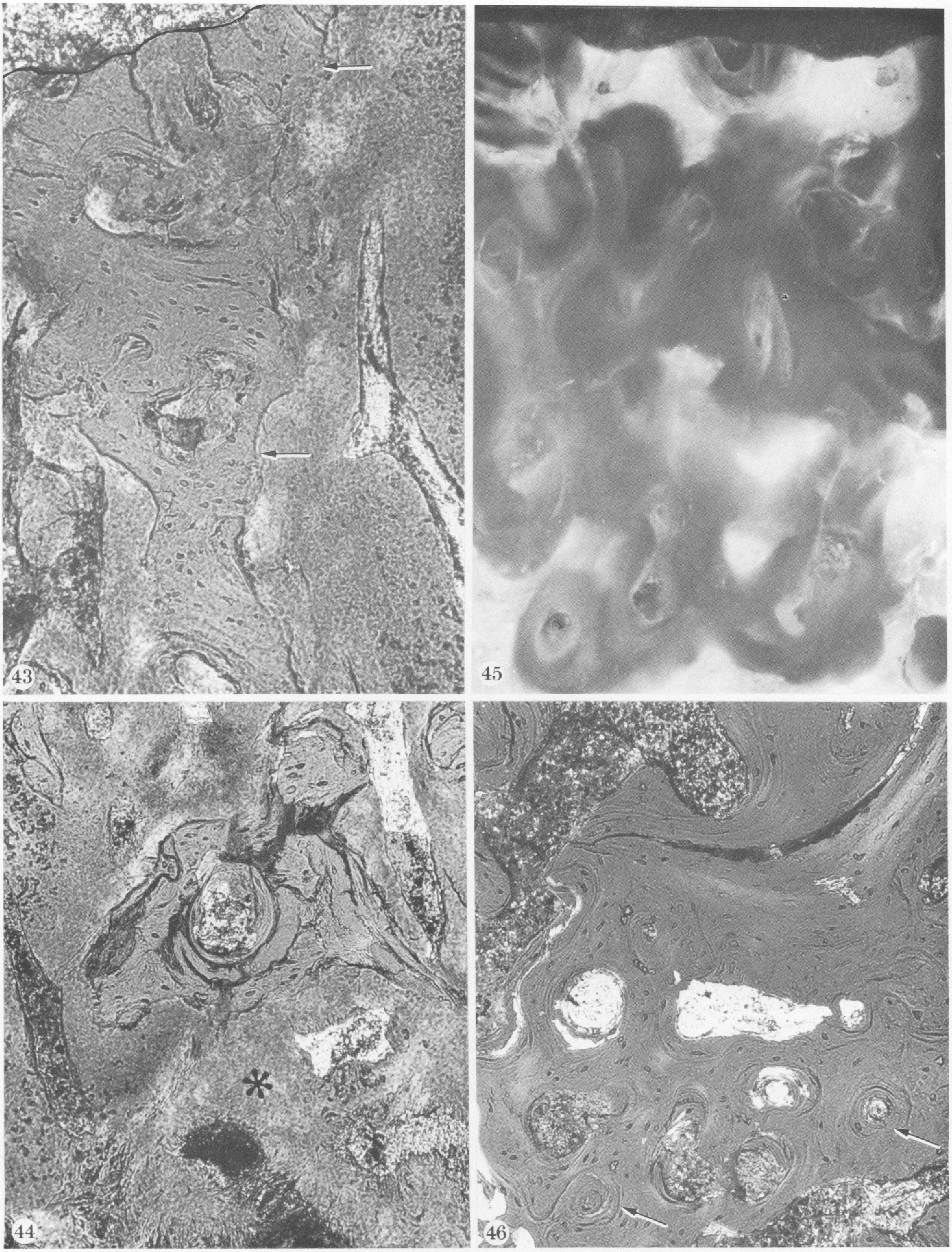




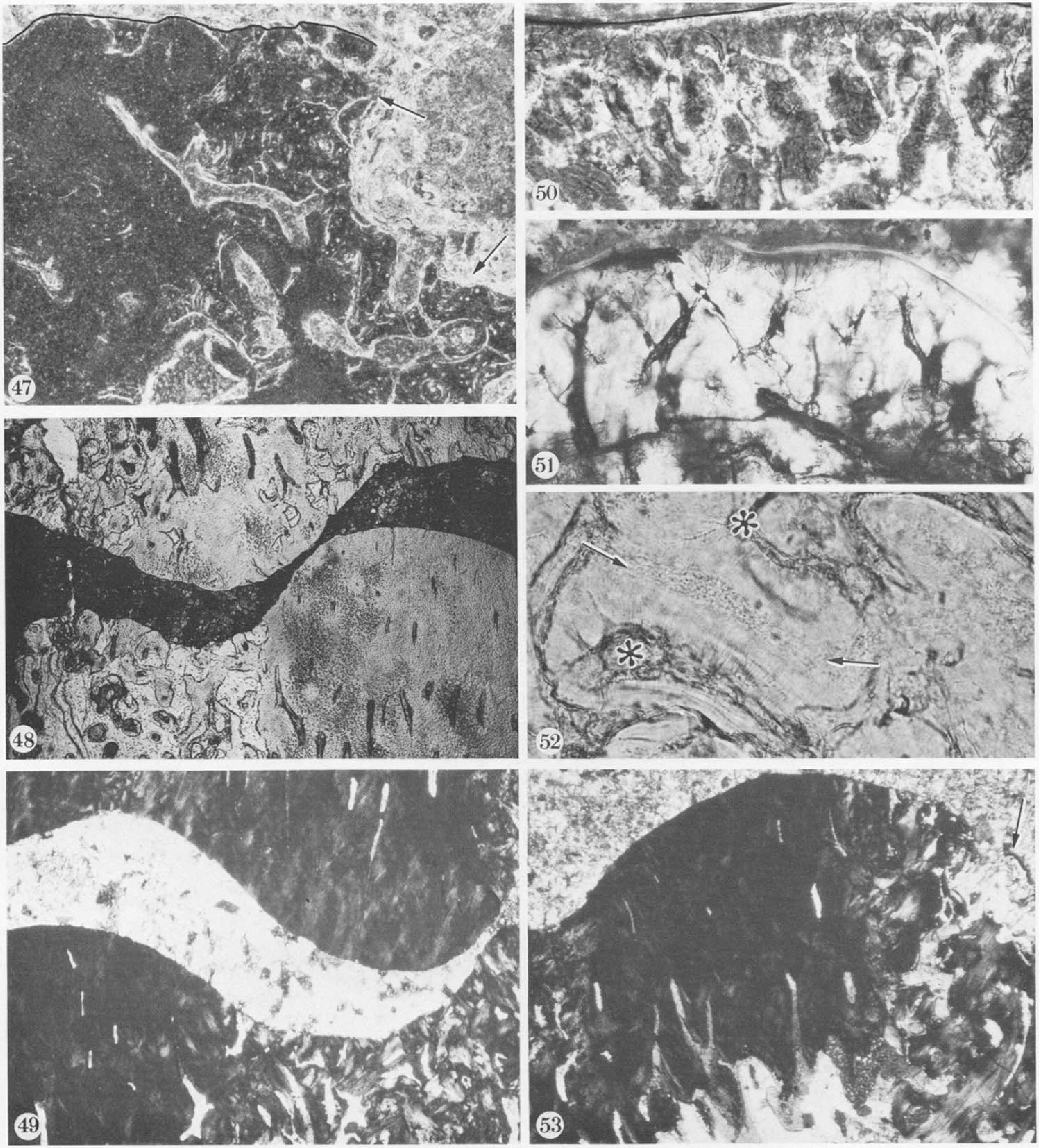
FIGURES 39 AND 40. (Magn. × 120 and × 75 respectively.) Both these figures are from box 1 in figure 41. They illustrate in ordinary light and phase contrast the distribution of pleromic dentine within partly resorbed bone; the junction between resorbed bone and pleromic dentine is a reversal line (single arrows). Part of the pleromic dentine has been infiltrated by black staining material (asterisk) and this is interpreted as the last-formed, least hard dentine (as in figure 42). Layer lines and lacunae are seen in the bone in both figures. The harder pleromic dentine is proud of the bone at the worn surface (double arrow on figures 39 and 40).

FIGURE 41. (Magn. × 30.) Lingual margin of the lower tooth plate. Extensive thickness of petrodentine on the left. The two boxes, 1 and 2, (figures 39, 40 and 42) show regions of pleromic dentine and developing pleromic dentine and petrodentine.

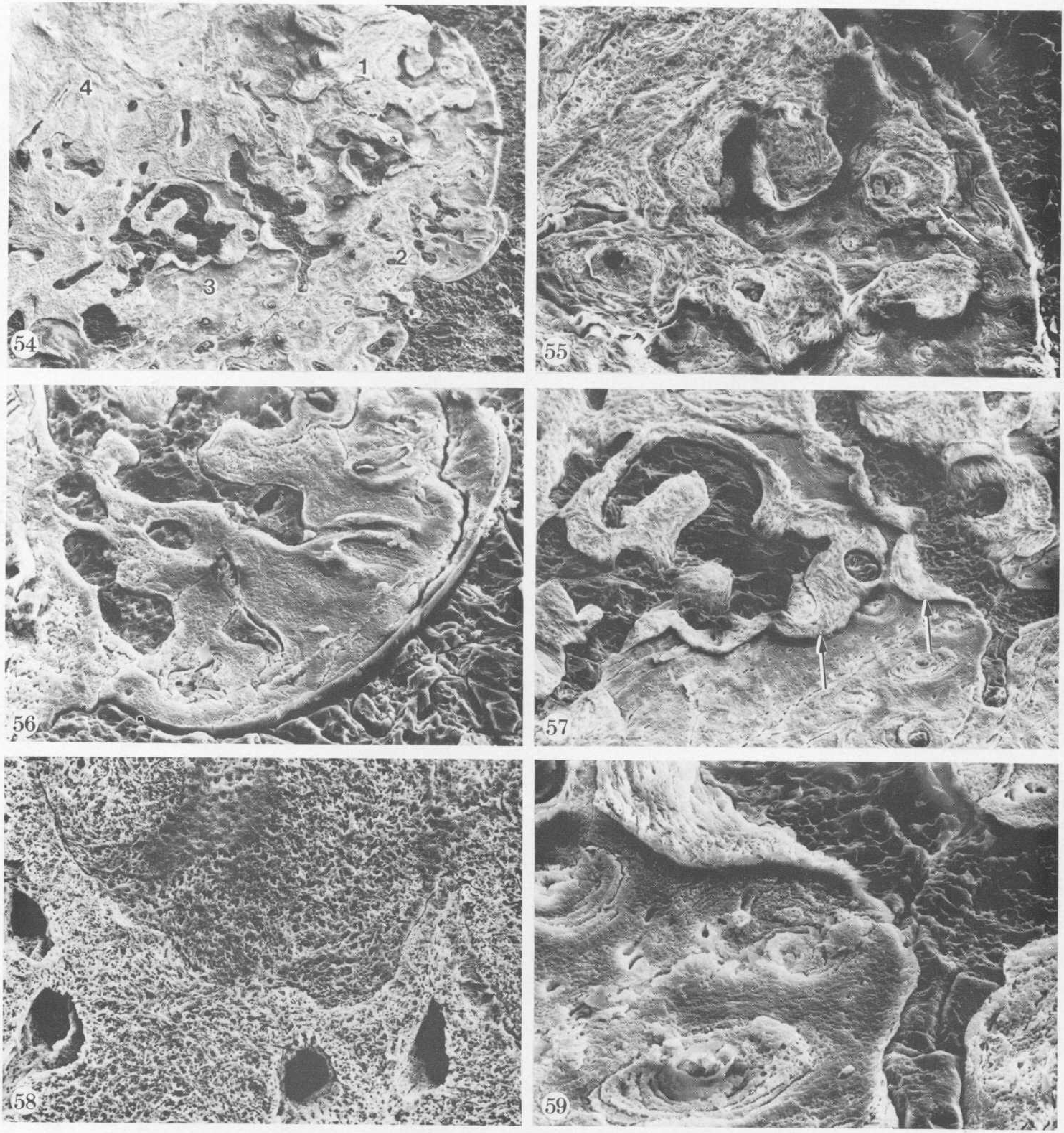
FIGURE 42. (Magn. × 100.) Region of developing pleromic dentine (black stained tissue) growing onto bone surfaces from reversal lines. Bottom left trabeculae of petrodentine at the beginning of development (arrow) fill the space between the bottom of the petrodentine and the bone. It has a typical fringed edge as in figure 33.



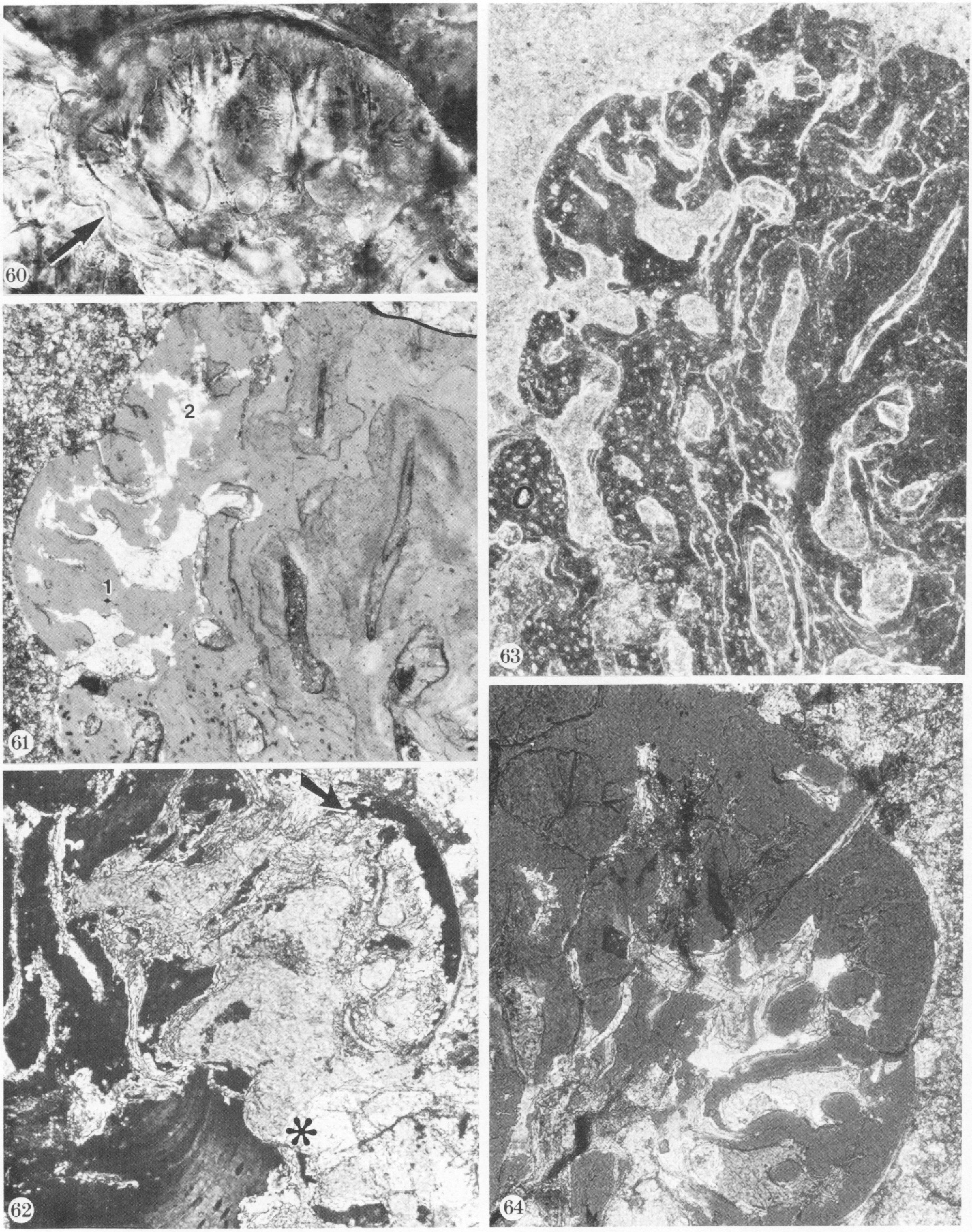
FIGURES 43–46. For description see opposite.



FIGURES 47–53. For description see opposite.



FIGURES 54–59. For description see opposite.



FIGURES 60–64. For description see page 349.

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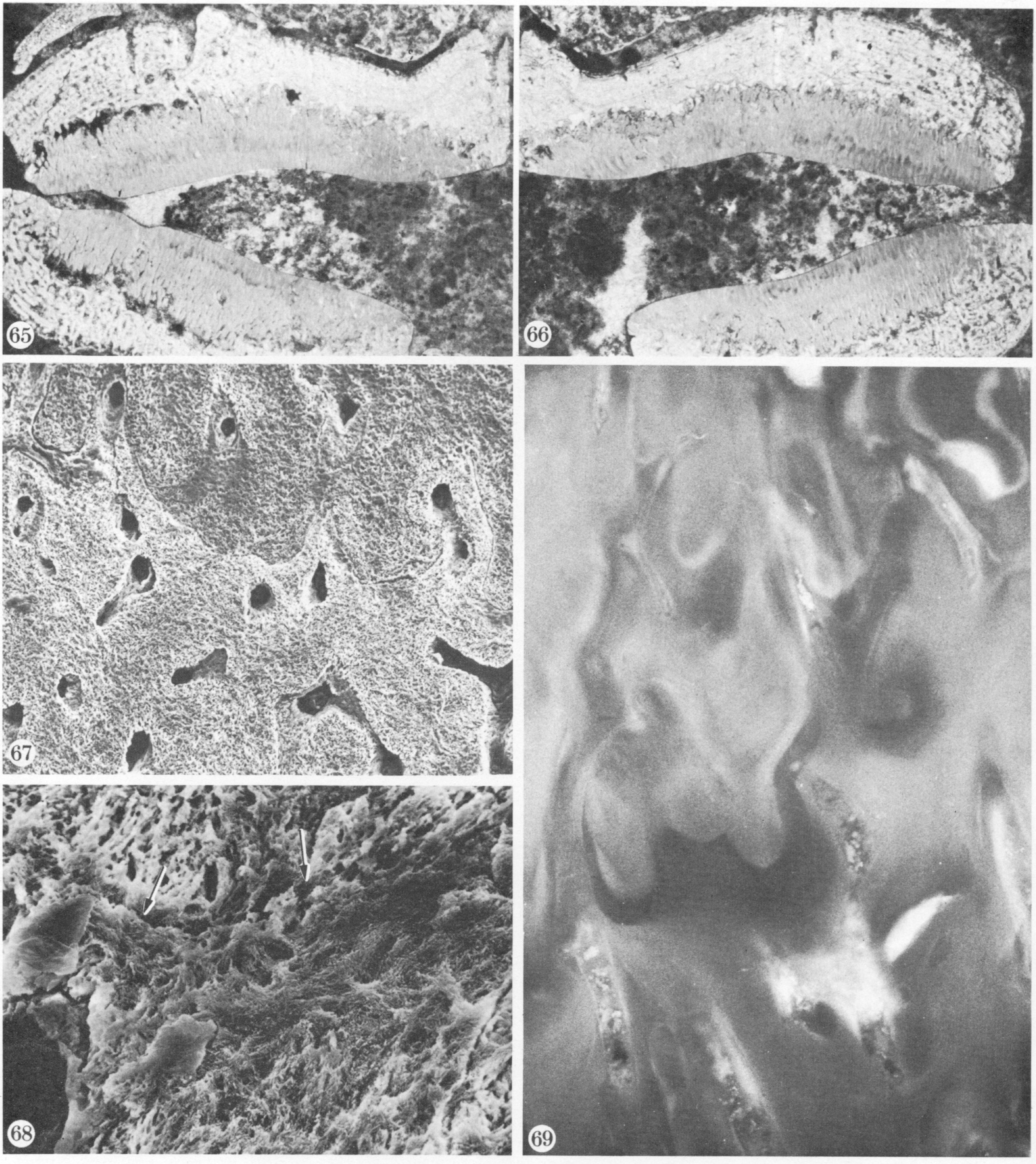

FIGURES 65–69. For description see opposite.