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THE RELATIONSHIPS OF *URONEMUS*: A CARBONIFEROUS DIPNOAN WITH HIGHLY MODIFIED TOOTH PLATES

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Previous accounts of the dentition of the Carboniferous dipnoan *Uronemus* have stressed the significance of the scattered small denticles. These, together with the marginal teeth and ridges, have been interpreted as primitive characters of the dipnoan dentition shared with three other genera: the Devonian *Uranolophus* and *Griphognathus* and the Carboniferous to Permian *Conchopoma*. Genera with tooth plates have been considered to be a monophyletic group in which tooth plates are a derived character; *Uronemus* has been excluded from this group in all previous investigations dealing with the significance of the dentition for determining relationships among dipnoans.

The macromorphology of the dentition of *Uronemus* has been re-examined and correlated with the histology of all the dental tissues. Optical study of thin sections and scanning electron microscope study of the adjacent cut surfaces has shown that the hard, wear-resistant dentine of the teeth and ridges is petrodentine. The arrangement, growth, wear and histology of the dental tissues have been compared with those of denticulated and tooth-plated genera. The arrangement of new teeth relative to the tooth ridge, the pattern of wear along the ridge, and the type of dentine and its growth indicate that the dentition of *Uronemus* is best interpreted as a tooth plate with one long lingual tooth ridge and reduced lateral tooth rows. Therefore the marginal tooth ridges are not considered to be homologous with those of denticulate dipnoans such as *Uranolophus*. The presence of petrodentine, a tissue type only found in forms with tooth plates, is consistent with the view that the dentition is derived by modification of a radiate tooth plate. The denticles covering restricted regions of the palate and lower jaw are considered to have been a secondary acquisition.

The suggestion that *Conchopoma* is a close relative of *Uronemus* is not accepted, and possible new relationships have been proposed. New data on *Scaumenacia* and *Phaneropleuron*, two other genera previously compared with *Uronemus*, are presented. *Rhinodipterus*, a form with elongate lingual ridges, is also discussed. *Phaneropleuron* is shown to have radiate tooth plates and not a marginal row of conical teeth as previously described. It is proposed that the tooth plate of *Uronemus* is derived from a dipterid type of plate. A discussion of some of the other factors involved in determining the relationships of the genus is given.

From an examination of the use of the tongue for respiration and feeding by the extant *Lepidosiren paradoxa*, it is concluded that many features of dipnoan evolution in the tooth-plated lineage result from the adoption of air breathing after an early evolutionary phase of gill respiration, and that *Uronemus* was adapted for air breathing. The 'denticulated' lineage, which included genera such as *Uranolophus* and *Griphognathus*, shows none of the skeletal features associated with the presence of a tongue, and presumably did not become air breathing.

1. Introduction

their description of the Scottish Carboniferous dipnoan *Uronemus splendens* Traquair (1873) and Watson & Gill (1923, p. 204) noted that the pterygoid dentition comprised a row of marginal teeth and a large number of small denticles covering a narrow area within the margin. They observed that these denticles were arranged in rows that did not agree in orientation with the tooth rows on the pterygoids of *Dipterus* and *Sagenodus*. They did not regard the marginal teeth as part of a tooth plate, but they did consider the possibility that the denticles may have been in some way related to the development of such a plate. Basing his views largely on this account of *Uronemus*, Denison (1974) elected to exclude this genus from his group of dipnoans with tooth plates.

In the most comprehensive discussion of the evolution of the dipnoan dentition yet published, Miles (1977, pp. 296–299) accepted Denison's (1974) hypothesis that tooth plates were a derived character and proposed that the primitive condition for dipnoans was a scattering of buccal denticles, together with marginal tooth ridges, the latter having the disposition and occlusal relations seen in *Griphognathus*. He considered *Uranolophus* and *Griphognathus* to have the most primitive dentition of known dipnoans, and *Uronemus* and *Conchopoma* to be the next most primitive. Miles (1977) also considered that the series of large, compressed conical teeth in *Uronemus* was a development of the tooth ridge. This judgement was based on his argument that the shagreen of buccal denticles is the primitive condition for all gnathostomes, and that the tooth ridges are primitive because their presence in these four genera would otherwise require parallel or convergent evolution to have occurred on four separate occasions. He found the most parsimonious hypothesis to be the one in which the tooth ridge of *Uronemus* is a primitive character. These tooth ridges were not considered to be related to tooth plates, but rather to have evolved during the earliest stages of dipnoan history, at the same time as the marginal bones of the presumed ancestor were being lost. As he went on to point out, such a view caused difficulty because these genera are advanced in many other features of their palates. For example, *Uronemus* has a large parasphenoid that lacks denticles, and *Conchopoma* has an enormous denticulated parasphenoid together with highly reduced pterygoids. In addition, the skull roof of *Uronemus* is advanced in the loss of bones K and A, the increase in the size of X, the reduction of Y, and possibly in the loss of Z. *Conchopoma* has also lost K and has the Y series reduced, but it is distinctive in that it has lost bones C and J, while retaining the primitive bone A and the lateral line commissure passing through it. Despite these considerable difficulties, Miles (1977, figure 157) illustrated *Uronemus* and *Conchopoma* as early-derived forms in his cladogram, because he regarded that solution as the least objectionable of all possible explanations. For him, the teeth and ridges in *Uronemus* were just modifications of a marginal ridge, the most primitive example of which is that of *Uranolophus*.

The proposal of Campbell & Barwick (1983) that there was a fundamental division of dipnoan dentitions into those with a shagreen of denticles that were shed during growth, and those with dentine-covered surfaces of various kinds that were added to during growth, led to the assignment of *Uronemus* and *Conchopoma* to the denticle-shedding group (Campbell & Barwick 1983, 1987). No discussion was given of the more detailed relationships of these genera in the light of this interpretation. However, in their 1987 paper, these authors noted that in addition to shedding denticles and marginal ridges of various kinds, the denticulate group is also characterized *inter alia* by basibranchial–basihyal tooth plates, the absence of petrodentine, narrow glenoid fossae, large cheeks and distinctively shaped cleithra. *Conchopoma* is known to have shed its denticles in an irregular pattern, and it had large basibranchial–basihyal tooth plates as well as appropriately formed cleithra. Its other relevant features are unknown because the specimens are always crushed. *Uronemus*, on the other hand, is known only from crushed material that has produced no basibranchial–basihyal tooth plates. In effect, then, *Uronemus* was placed with the denticulate group because its buccal cavity was covered with robust denticles that showed evidence of continual replacement and had a primitive dentine structure. The marginal ridges on both the pterygoids and the prearticulars, which were formed of isolated enamel-covered teeth joined by enamel-sheeted dentine at their bases, were considered to be modifications of a ridge of *Uranolophus* type.

This investigation has involved examination of both existing and newly prepared specimens of *Uronemus*. Also, sections were prepared of selected regions of the dentition for optical examination, combined with scanning electron microscopy (SEM) of the equivalent regions. In particular, we have looked for evidence of the newest growth in the teeth and ridges, the pattern of wear, the arrangement of the new teeth relative to the worn regions of the tooth ridge, and the disposition of the enamel layer around the tooth bases and the ridge. These data on the macromorphology and histology of all the dental tissues have been compared with those of the denticulated and tooth-plated genera. They have also enabled us to comment on growth and wear of the dental tissues. The combined SEM and histology of the hard, wear-resistant dentine of the ridges have allowed a direct comparison with similar information obtained from the equivalent tissue, petrodentine, in tooth-plated genera. These observations have led us to reject the previous concepts of the dentition of *Uronemus* and to suggest a new interpretation: that the marginal ridges in this genus are one component of a highly modified form of tooth plate. This, together with the absence of abrasion on the denticles and our failure to find evidence for the presence of basihyal–basibranchial tooth plates, has led us to the conclusion that the whole dental system is modified for a special mode of feeding. This, in turn, has led us to consider the arrangement of the tooth plates, with the large median space, as part of an adaptation to accommodate the 'tongue' and associated tissues that close the buccal cavity at one phase of the air-breathing cycle.

In a search for new relationships based on these findings we have presented new data on three other genera: *Scaumenacia*, *Phaneropleuron* and *Rhinodipterus*.

2. MATERIAL

Uronemus splendens

RSM GY 1926.57.10/11	Holotype. Incomplete fish showing most of the head. Part and counterpart as natural mould. Burghlee Ironstone, Loanhead, U.K.
RSM GY 1886.87.21	Right ramus of mandible. Burghlee Ironstone, Loanhead, U.K.
RSM GY 1886.89.3A	Palatal fragment. Burghlee Ironstone, Loanhead, U.K.
RSM GY 1891.7.26	Palatal fragment. Burghlee Ironstone, Loanhead, U.K.
NUZ 78.1.42	Crushed skull and mandible. Dora Bone Bed, Dora opencast site, near Cowdenbeath, U.K.
BMNH P11470	Prearticular fragment, Burghlee Ironstone, Loanhead.
BMNH P11458	Right pterygoid fragment, three sections. Carboniferous Limestone, Loanhead, U.K.

Uronemus sp.

RSM GY 1976.19.3	Right pterygoid. Dora Bone Bed. Dora opencast site, near Cowdenbeath, U.K.
BMNH P11460	Mandible, Burghlee Ironstone, Loanhead, U.K.
BMNH P604709, P6786	*Scaumenacia curta*, pterygoid tooth plates. Escuminac Bay, Province of Quebec, Canada.
SMNH 2610	*Scaumenacia curta*, section of a tooth plate. Escuminac Bay, Province of Quebec, Canada.
BMNH P49774	*Rhinodipterus ulrichi*, pterygoid tooth plate, Bergisch-gladbach, F.R.G.
SMNH 1568	*Rhinodipterus ulrichi*, section of tooth plate, Bergisch-gladbach, F.R.G.
BMNH P24839, P26117	*Phaneropleuron andersoni*, Old Red Sandstone, Dura Den, Fifeshire, U.K.

Abbreviations used: BMNH, British Museum (Natural History), U.K.; NUZ, Department of Zoology, University of Newcastle upon Tyne, U.K.; RSM, Royal Museum of Scotland, U.K.; SMNH, Swedish Museum of Natural History, Sweden.

There appear to be two species of dipnoan with an ornament and dentition of the *Uronemus* type at Loanhead and Cowdenbeath. One form exhibits paired E bones and separate bones 3 and 4 (Watson & Gill 1923, figure 31) whereas the other has single bones in the E and 3+4 positions (Watson & Gill 1923, figure 30). Watson and Gill (1923) referred both forms to *Uronemus splendens*. In addition, among the specimens we have studied, there are two distinct patterns of the dentition. One pattern, of those observed in this paper, comprises the characteristic elongate lingual ridge and three to four lateral rows of small teeth that extend a small distance anteriorly (figures 14 and 15, plate 2) whereas the second and more common pattern has the lingual ridge flanked by 6–8 lateral rows of large teeth that extend forward more than half way along the tooth row (figure 12, plate 2 and figure 17). This second pattern is present on specimens with single bones in the E and 3+4 positions. In this account these specimens are referred to as *Uronemus splendens*, and they form the basis of the reconstructions in figures 19 and 20. Two specimens (RSM GY 1976.19.3 and BMNH P11460) showing 3–4 lateral rows are referred to as *Uronemus* sp. A third Scottish species, *U. lobatus*, has been collected from the Burdiehouse Limestone (Traquair 1873). Little of the cranial morphology of this species is known and it has not been referred to during the course of this study. A complete redescription and systematic revision of *Uronemus* is in preparation by T.R.S.

3. OBSERVATIONS: *URONEMUS*

(*a*) *Morphology*

(i) *Marginal tooth plates*

Several specimens show that instead of being single or double, the marginal ridges in each jaw consist of up to eight short posterior rows of teeth and an elongate lingual row that extends well forwards on the pterygoid (figures 5, 6, and 7, plate 1 and figure 12). All the teeth, even those on the posterior ridges, are considerably larger than any denticles in the same vicinity. They are all conical and well formed, and each is covered with a thick layer of enamel. The elongate lingual row is oriented posterolaterally (figures 1 and 5, plate 1) in a similar manner to the tooth ridge of *Uranolophus*. In all other dipnoans the tooth ridge and lingual tooth rows are oriented either anteroposteriorly or anterolaterally.

Most of the available material is crushed and the variation in the teeth and their ridges cannot be described in detail. The following summarizes all the observations made to date.

The posterior end of the tooth row complex terminates abruptly where four to six tooth rows are confluent (figure 6, figures 12 and 16, plate 2 and figure 17). The surface of the lingual row in this region is often so worn that it is impossible to be precise about the number and the spacing of the teeth in all specimens. Two of the better, presumed younger, specimens are illustrated in figures 14 and 15, which show the outlines of most of the teeth. It is clear, however, that the teeth of the more lateral rows were added at their lateral ends, grew directly on the basal bone (figure 13, plate 2) and were placed at a low position on the bone relative to the worn tissue of the lingual ridge. The newly added teeth show little sign of wear. The axes of the tooth cones are steeply oriented relative to the occlusal plane. No growth series is available to enable us to determine the way in which tooth rows were added, but examination

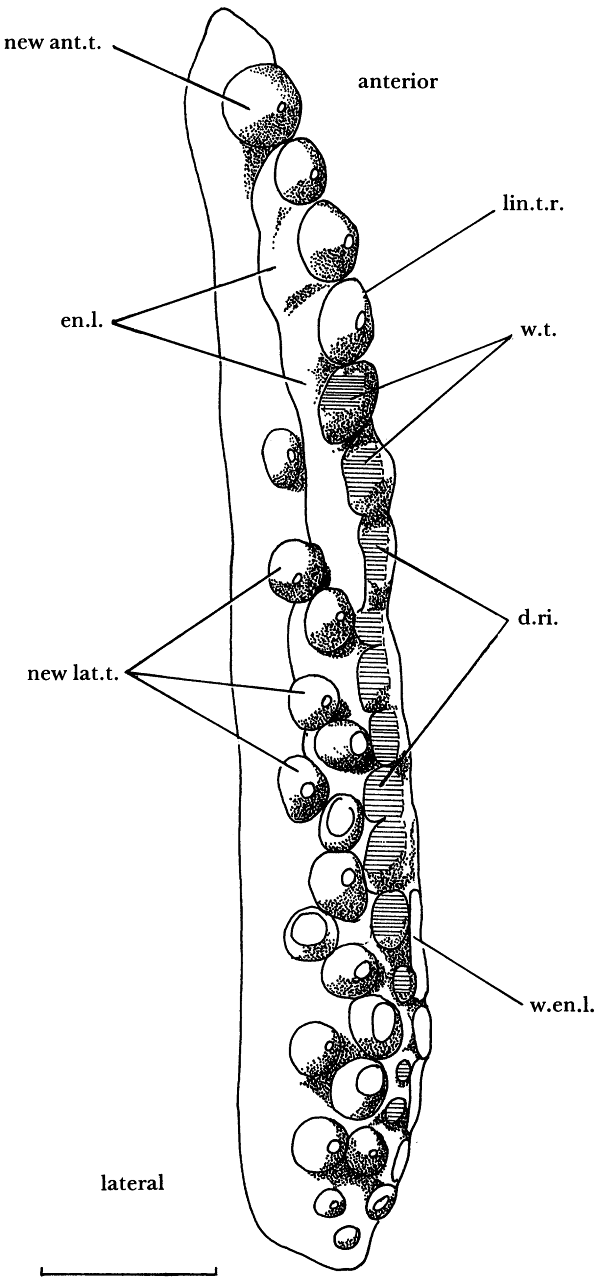


Figure 17. RSM GY 1886.89.3A. Right pterygoid tooth plate to show the wear facets on the lateral side of the lingual tooth row (hatched) and the arrangement of many short rows of teeth on the lateral side (as in figure 12). Scale bar 0.5 cm.

of the disposition of the rows and the wear on the older teeth shows that although some new rows were added at the posterolateral corners of the plate during later phases of growth, new rows were also developed between the lingual row and the previously formed rows. Interposed tooth rows occur in *Dipterus valenciennesi*, so this feature is also present in structures generally accepted as radiate tooth plates.

Over most of the lingual row, the teeth are not isolated and separated by bone, but form part of a continuous ridge of dentine (figure 7, figures 8 and 9, plate 2 and figure 17). It is possible in well-prepared specimens to see the outline of the bases of the teeth where they contribute to the ridge tissue (figures 10 and 12, plate 2). Each lingual ridge examined, however, terminates anteriorly with almost totally unworn teeth and an abrupt end to the bone (figures 8, 9, 13 and 17). At first, these terminations were thought to be broken ends, but the regularity of the bone surface and the fact that the anteriorly encroaching lateral sheet of enamel had a smooth finished edge suggest that they are natural. The holotype also shows that the tooth ridges terminate as suggested above (figures 1, 3 and 4, plate 1). Along both lingual and lateral flanks of this ridge there is a continuous sheet of enamel that shows highly irregular growth increments (figure 13). These appear as small patches with a conchoidal pattern, indicating that the additions took place by small lapping growths of the epithelium, the newest growth of enamel forming in a resorption bay in the bone (figure 13). Towards the anterior ends of the ridges this enamel layer becomes progressively narrower until it disappears around the bases of the most anterior teeth. As would be expected, the enamel terminates where the dentine ridge tissue gives way completely to isolated teeth. New teeth forming this ridge were added at its anterior end by growth directly on the bone (figures 13, 14 and 17).

The enamel on the surface of each tooth shows growth rings, indicating that it erupted through the dental epithelium in the normal way for a tooth. In addition to covering each tooth, a separate enamel layer gradually covered the entire marginal surface of the tooth plate at some stage of its growth, investing both tooth base and bone. From the histology it is apparent that a thin layer of dentine was added beneath this enamel and these together appear to have contributed to the worn margins of the ridge (figures 10 and 17).

In particular, the posterior end of the plate is, as expected, completely confined within an enamel layer (figure 16). The total pattern of tooth and ridge distribution indicates that the tooth plate grew by the rapid increase of the length of the lingual row and the relative suppression of growth of all the other rows.

All the above comments apply to the tooth plates in both jaws, but the pterygoid and prearticular plates have some quite distinctive features on their lingual tooth rows. The teeth at the anterior end of the pterygoid row are almost right-circular cones (figures 8, 13 and 15), and their bases are sometimes slightly fluted. More posteriorly placed teeth are similarly conical where they can be observed, but many are too worn for us to be sure of their original shape.

The dorsal surface of the pterygoid exhibits a narrow marginal ridge of bone which, together with the encroaching enamel layer, acts as a buttress for the new teeth at the anterior end of the lingual ridge (figure 4). In addition, a very extensive thick ridge of bone extends the full length of the tooth plate on the dorsal surface of the pterygoid. This replaces the lateral palatal process of such genera as *Speonesydrion* and *Dipterus*. Occasionally a few denticles adjacent to the tooth ridges had become heavily worn as a result of occlusion with opposing ridges (figure 10).

The teeth of the prearticular lingual ridge have a laterally compressed conical form, their anterior and posterior edges forming quite sharp crests. Occasionally these crests bear two to four points, producing a serrated edge (figure 11, plate 2). The specimen of *Uronemus* illustrated by Woodward (1891, Plate IV, figure 5) exhibits three points on each tooth. The teeth are not always arranged so that their axial planes are coplanar. Sometimes they are placed *en enchelon*, their anterior ends directed slightly inwards.

The distribution of wear on the teeth, the absence of any resorption of the enamel along the margins, and the progressive enclosure of newly added teeth in the layer of communal embracing enamel, all indicate that these teeth and their associated ridge-forming bases were not shed at any stage of ontogeny. They have the characteristic properties of tooth plates.

Wear on the tooth plates is quite distinctive. Teeth on the anterior third of the lingual ridge of each jaw are unworn (figures 3, 7, 8 and 9). The median third shows strong vertical wear facets, those on the pterygoid being on the lateral face and those of the prearticular on the lingual face (figures 8 and 9). The wear facets are shallowest and most sharply defined towards the anterior end of this median third of the row. Because the teeth in opposing jaws alternate in position, the facets at first emphasize the divisions between the teeth, and then as wear proceeds the divisions are obliterated. The posterior third shows so much wear that the teeth are not recognizable as separate entities and only the dentine ridge remains (figures 12 and 17). This shows a ribbed pattern of wear, somewhat similar to the ridges on the tooth plates of some lepidosirenids. Of the teeth on the lateral ridges, those nearest the lingual ridge are most severely worn, and some are almost worn down completely to the tooth base. By far the most important observation is that of wear pits on specimen RSM GY 1886.87.21 (figures 14 and 18), a prearticular in which these pits, formed by the opposing teeth of the pterygoid, fit between the short radial rows of the posterior parts of the plate. This is illustrated in figure 18, where a

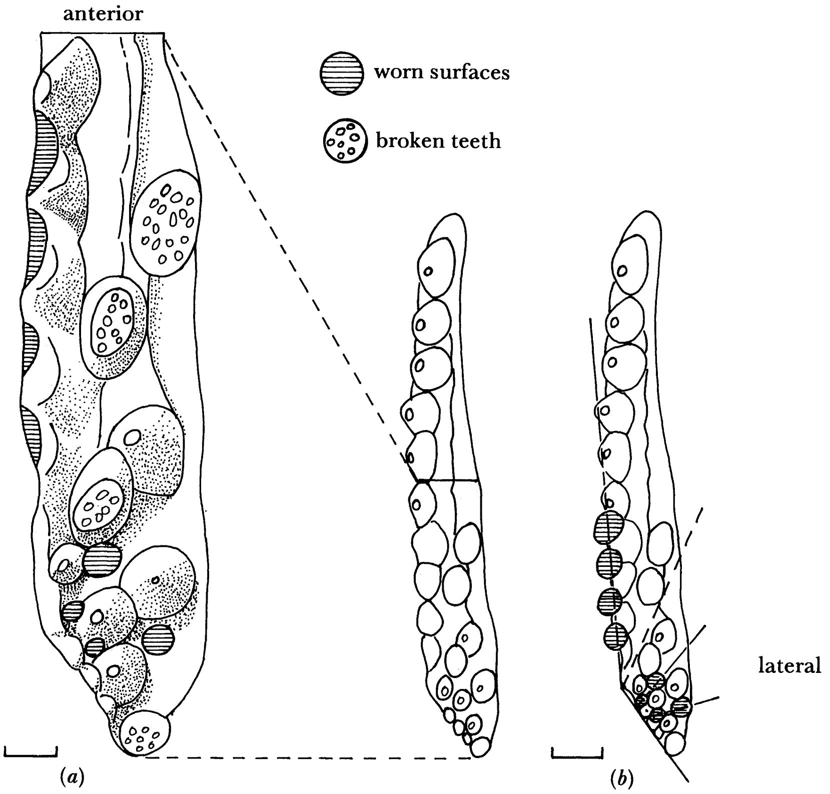


FIGURE 18. RSM GY 1886.87.21. Right prearticular tooth plate illustrated in figures 9 and 14 to show the entire number of teeth in the composite plate. (*a*) The posterior portion enlarged to show the position of wear facets (hatched) on the lingual side of the main tooth row and wear pits interposed between the short lateral rows of teeth (hatched). (*b*) An outline of the whole plate reconstructed with the probable position of four of the tooth rows of the upper plate indicated by lines superimposed along the positions of the wear facets (dashed line for presumed tooth row but no wear facets recorded). Scale bars 0.1 and 0.25 cm.

reconstruction is shown. In the holotype, which has opposing jaws in approximation (figure 3), the newest teeth to develop at the lateral margins alternate and would interlock at full occlusion. This type of occlusion is analogous with a cusp-to-fossa occlusion in mammalian teeth with many cusps.

(ii) *Dermopalatines and other small isolated plates*

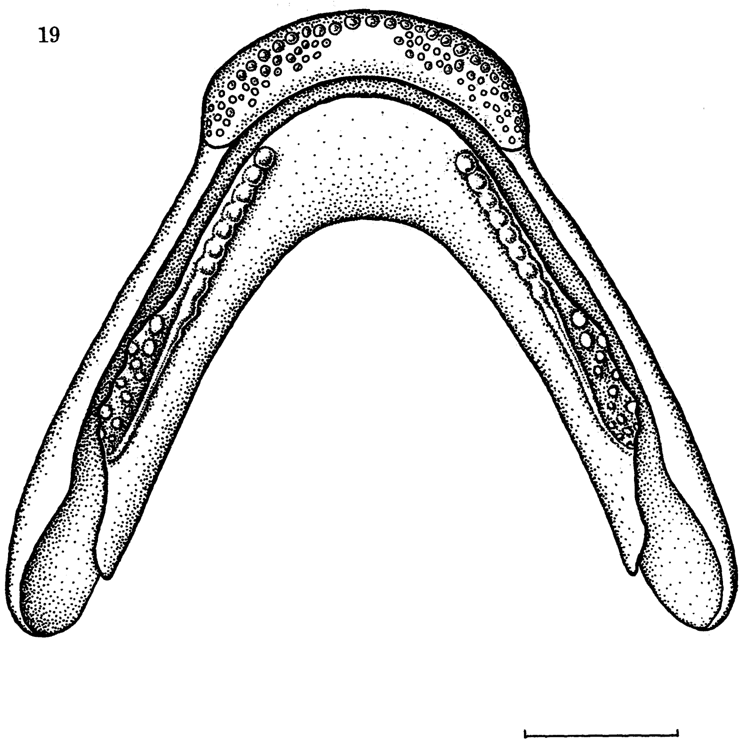
On the holotype (figures 1 and 2, plate 1) and on NUZ 78.1.42 there are isolated plates carrying teeth of the same size and shape as those at the anterior ends of the lingual ridges. These were interpreted by Watson & Gill (1923, figure 30A) and by Westoll (1949) as isolated prevomers and vomers respectively. They consist of four teeth mounted on a robust basal bone (figure 2). The holotype shows a well-defined embayment in the anterior tip of the pterygoid that received this bone (figure 4), and the tooth row was thus continuous with the lingual row of the pterygoid. The largest of the teeth is posterior, and they become progressively slightly smaller anteriorly. These plates, which are the dermopalatines, would not have met in the midline. They are separated by a V-shaped notch at the anterior extremity between the pterygoids. This notch must have been occupied by another small plate, the anterior median plate of Campbell & Barwick (1984) or the fused vomers of Miles (1977). We consider that an isolated plate to the right of the dentary is the plate in question (figure 2). Its surface is covered by a number of denticles. This plate needs further study.

Several other small plates, each with three to five small conical teeth or denticles attached to a bony base and arranged in one or two rows, lie loose on the holotype (figures 1 and 2). Some of these were doubtfully identified by Watson & Gill (1923) as premaxillae and maxillae. In addition, several isolated teeth with little or no bone of attachment are present around the anterior part of the specimen. They could be teeth that have been shed, or the residue of a larger number of small teeth (figures 1 and 2). In the absence of any bony surface to which these plates would have been attached, we conclude that they lay loose in the skin over the ventral surface of the nasal capsules as did the tooth plates of *Holodipterus gogoensis* (Miles 1977, figure 72). In such a position they would have been opposed by the denticulated surface of the 'dentary'. The nature of the denticles or teeth on these plates is also in need of further study. They are no larger than the denticles on the 'dentary'. The 'dentary' is preserved on the holotype where it is broken into two equal pieces through the midline (figure 1). Its dorsal surface bears numerous teeth arranged in irregular curved rows set obliquely to the anterior edge of the bone. We are not certain if the teeth or denticles on the dentary or on these plates were shed and replaced during growth, but we consider it probable that they are entirely comparable to the denticles of the pterygoids. A reconstruction of the dentition on both the lower jaw and the upper jaw is shown in figures 19 and 20.

(*b*) *Histology of the tooth plates and denticles*

(i) *General comments*

The histology has been studied by thin sections and scanning electron micrographs of teeth on the lingual ridge from a fragment of the pterygoid (BMNH P11458). The central question is: does the tooth ridge exhibit histological features in common with those known for tooth-plated types? Therefore, it becomes important to decide if the same tissues, particularly petrodentine, found in all those forms with dental plates (both dentine plates and tooth plates, 19



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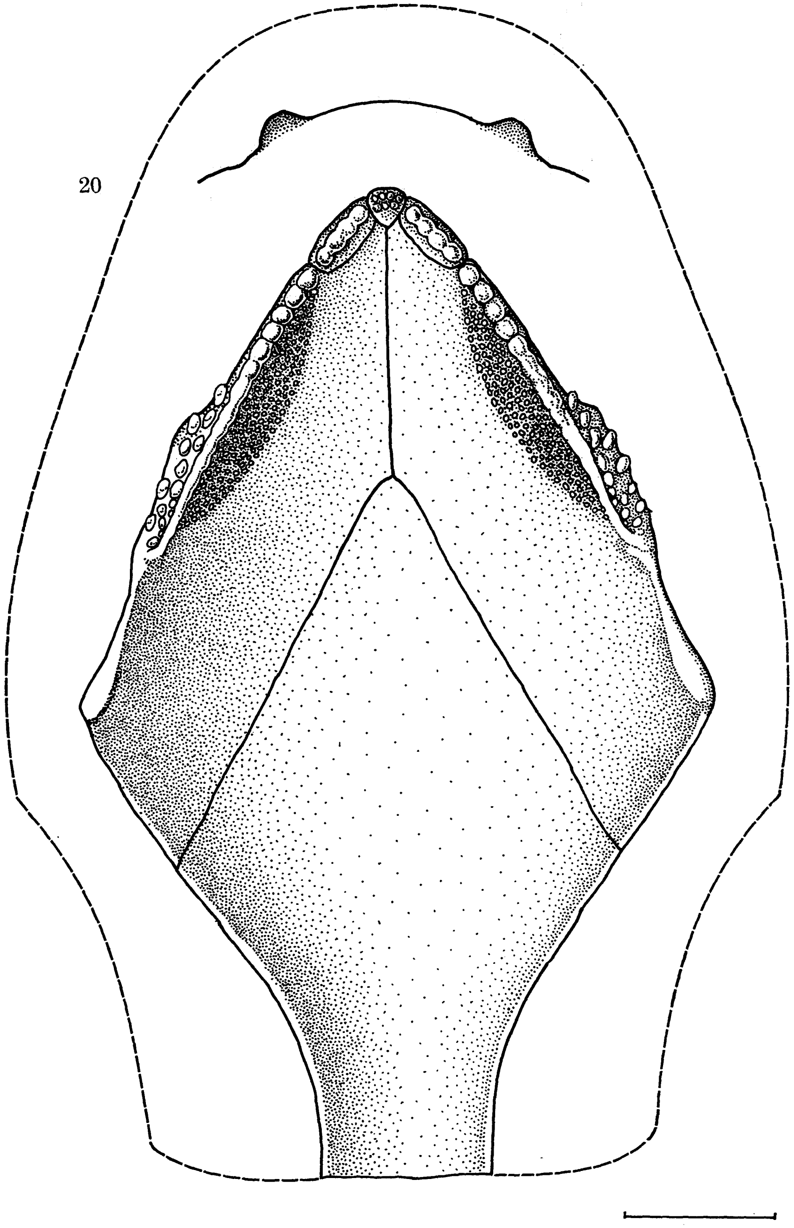


FIGURE 19. Composite reconstruction of lower jaw based on BMNH P11460, NUZ 78.1.42 and RSM GY 1926.57.10/11. Scale bar 0.8 cm.

FIGURE 20. Composite reconstruction of palate based on NUZ 78.1.42, RSM GY 1926. 57.11 and RSM GY 1976.19.3. Scale bar 0.8 cm.

Smith (1984); Smith & Campbell (1987)) are present in *Uronemus*. The histology of the tooth ridge is therefore described first. Denticles are described in a later section, as part of the replacement component of the dentition. Particular attention will be given to the presence or absence of a pulp cavity, the presence or absence of tubules, the development and distribution of translucent dentine (hypermineralized) and the evidence for resorption and remodelling of the dental tissues.

The thin sections were selected so that two of them passed vertically through teeth on the ridge at two distinct stages of their development, and the third horizontally through the segment of tooth ridge posterior to the teeth (figure 21). The surface adjacent to the third section was prepared for SEM by polishing and etching (Smith 1977, 1979*b*) to allow examination of the regions comparable to those of the sections (figure 21 and figure 35, plate 5). The first tooth is unworn, the enamel layer intact, and only the outer layer of dentine is present, the central part being occupied by an extensive pulp cavity in which only a small proportion of the specialized compact dentine has begun to form (S_1; figure 21 and figure 22, plate 3). By contrast, in the section through the more posterior tooth the enamel is worn and the pulp cavity is filled in with extensive areas of specialized compact dentine (S_2; figure 21 and figure 23, plate 3), that is, it has petrodentine as the interstitial dentine and linings of circumpulpal dentine around the residual narrow pulp canals. The tooth itself is clearly seen to be attached by new bone to the old basal bone, each separated by a junction identified as a reversal line (figure 43, plate 6).

(ii) *Specialized compact dentine of the tooth*

The development of this region of the tooth is clearly seen by comparing all sections. One of the characteristics of the tissue in dipnoan tooth plates is that the hypermineralized dentine, petrodentine, is formed within a central pulp cavity only after a shell of dentine has formed as a template for the cone, which will become the tooth by solid infill of the entire pulp. This is true for *Sagenodus* (Smith 1979*a*) and for most specimens where the histology of new teeth has been observed (Smith 1984).

The outer part of the tooth, the pallial dentine, is notable for the clusters of extensive branching tubules, organized as groups radiating towards the enamel from the alveoli of the pulp canals (figures 22 and 24, plate 3). This is the only region of the dentine with such an array of tubules. Below this layer of pallial dentine the dentine becomes trabecular and is without tubules initially. It is important to note that the formative surface of these trabeculae of dentine exhibits a calcospheretic mineralizing front as is typical of all dentines but is atypical of bone (figure 25, plate 3). This also contrasts with petrodentine, the crystallites of which form in long, parallel, linear arrays and not radial clusters contributing to a calcospheretic pattern of mineralization. The trabeculae had at first left large intervening spaces which became the pulp canals, each becoming constricted by a further deposit of more regular circumpulpal dentine, formed as concentric layers with radial striations (figure 25 and figure 32, plate 4). This radial striation is possibly the result of the collagen fibre bundles running through each layer up to the junction with the trabecular dentine. Only a few irregular tubules run through this circumpulpal dentine, and they terminate within the junctional tissue. The dentine of these interstitial regions remained poorly calcified as judged by interglobular spaces (regions where calcospherites remain separate, with poorly mineralized matrix between) and a few stranded cell spaces.

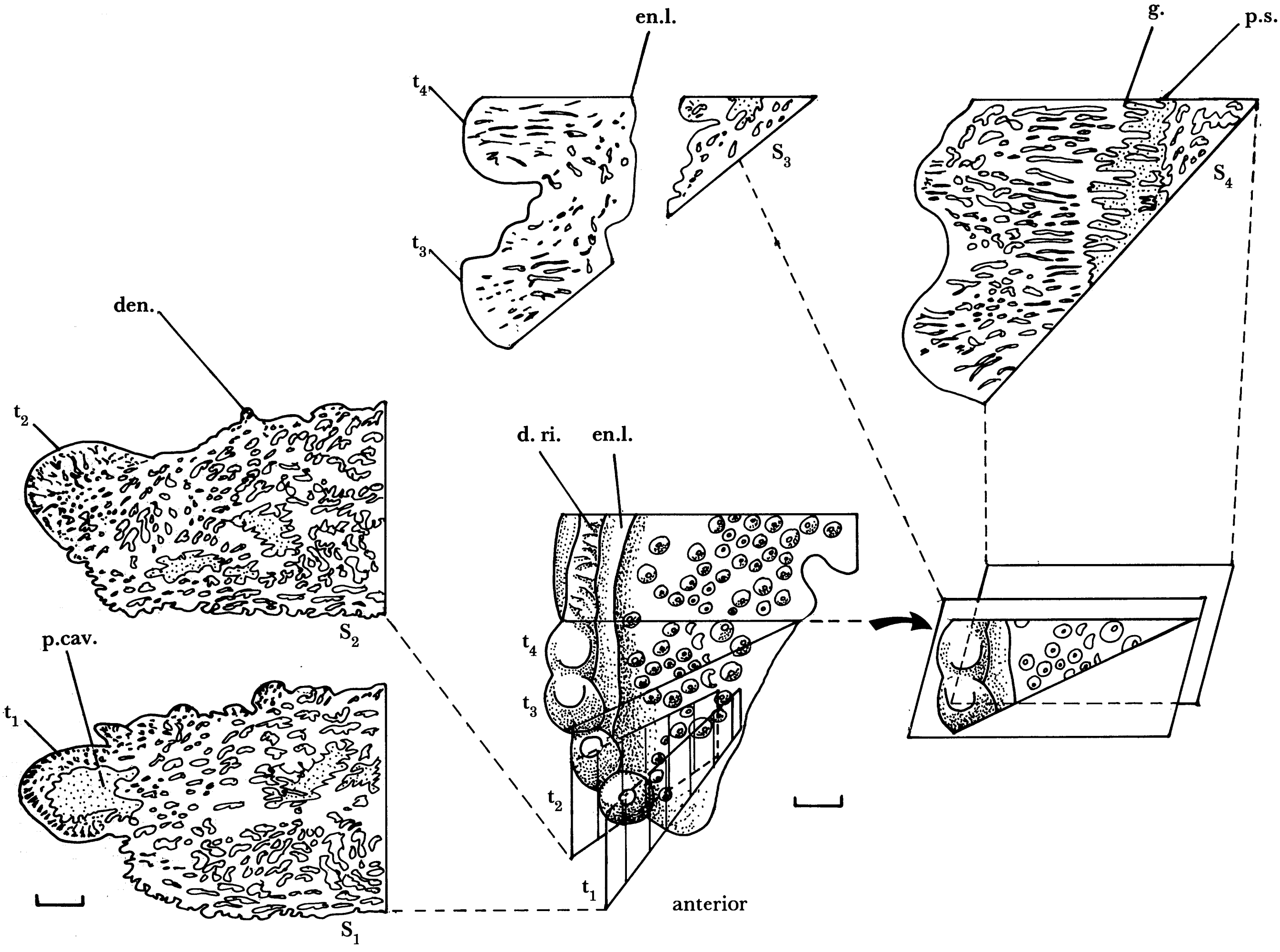


FIGURE 21. BMNH P11458. A portion of the left pterygoid tooth plate to show the positions of cuts made before the preparation of three sections S_1, S_2 and S_3. S_1 and S_2 pass through the two adjacent new teeth (t_1 and t_2) at the anterior end of the main tooth row and the scattered denticles (den.), S_1 is of a very new tooth with a large pulp cavity (p.cav.). Photomicrographs of these sections are shown in figures 22 and 23. Section S_3 (photomicrographs in plate 4) was cut from the remaining piece immediately behind the cut for S_2. The plane was approximately horizontal and at right angles to S_1 and S_2. This section included two worn teeth (t_3 and t_4) joined to the dentine ridge (d.ri.) by the communal enamel layer (en.l.). It also cut through a small piece of the denticulated plate. The remaining block face S_4 was deep to the section S_3 and included a pulp space (p.s.) and a growth zone (g.) of the dentine contributing to the ridge tissue. This surface prepared for SEM is illustrated in plate 5. All the photomicrographs in plates 3 and 4 are from this specimen, as are the scanning electron micrographs in plate 5. Scale bars 0.1 cm and 0.2 cm.

Deep to this outer layer of trabecular dentine a patch of different dentine formed, more translucent, without tubules and with a fringed forming surface rather than a calcospheretic one (figures 24 and 25). We interpret this as petrodentine in the process of formation; its structure can be compared with that in a more mature region of the older, more worn tooth (figure 26, plate 3, and figure 32).

The central region (primary pulp cavity) of the older tooth has been completely filled with a compact type of dentine, part of which is petrodentine, in which the many pulp canals have been narrowed by the deposition of circumpulpal dentine (figures 23 and 26, plate 3, and figure

29, plate 4). A small space (pulp cavity) remained between this compact tissue and the basal bone in which forming surfaces of petrodentine are observed. These have a distinctive appearance and do not, in the first stage of development, have circumpulpal dentine deposited on them. It can be seen that the central tissue of these mature teeth is filled with translucent, atubular dentine (the fully formed petrodentine), with relatively narrow regions of circumpulpal dentine (figures 26, 27 and 28, plate 3, and figure 32). A few, longer, narrow tubules run through restricted regions of petrodentine, and we assume these to be due to trapped petroblast processes (figure 32). A feature very similar to this is found within the teeth on the ridges of *Ctenodus*. We note that there are marked similarities between the tissues of *Uronemus* and those of *Sagenodus* and *Ctenodus*. The latter have been examined in newly prepared sections (M.M.S.).

The block prepared for SEM with an etched face parallel to the horizontal section but at a deeper level shows, at the base of the worn teeth, tissue that is continuous with the much more highly organized tissue of the ridge (figures 35 and 38, plate 5). The ultrastructure of the central tissue in both these regions (see §3 (*b*) (ii)) is comparable with that previously described as petrodentine (Smith 1984). Within this central compact dentine the interstitial regions forming the centre of the trabeculae have been shown, by this method, to be more highly mineralized than in any other region (figure 39, plate 5). It consists of larger and more organized crystals. Where this region of petrodentine adjoins the bone there is an extensive continuous space, or pulp cavity, and here the tissue of the ends of the dentine trabeculae has the appearance of newly deposited petrodentine (figure 36, plate 5). This forming surface of petrodentine is deep to the worn surface of the ridge.

(iii) *Ridge tissue*

It is notable that the tissue of the ridge is the same as that of the mature teeth and is continuous with it; that is, it has the same tissues with the same arrangement as the specialized compact dentine. The pulp canals remain relatively narrow; in fact, towards the worn surface they become occluded with the continued development of circumpulpal dentine and finally intrapulpal dentine within the lumen of the canal. Many tooth plates have their tissues arranged in this way. This distribution of petrodentine and circumpulpal dentine, in which the former provides the interstitial framework on which the latter is deposited, accounts for the wear pattern observed on the worn parts of the teeth and ridge, the petrodentine forming the ribs raised above the softer circumpulpal dentine (figures 10 and 12).

(iv) *Pleromic dentine*

At the bases of the mature teeth the dentine has continued to develop, and where little resorption of the bone occurred, the dentine lined the bone spaces as pleromic dentine thus forming the tissue complex known as osteodentine. In regions at the basal margins of the teeth, patches within the bone have been resorbed, and the resulting space infilled with pleromic dentine (figures 33 and 34, plate 4, and figures 37 and 40, plate 5). This appears to be a widespread remodelling mechanism in most dipnoan dental tissues.

SEM of the equivalent region between two teeth shows the important features of pleromic dentine (figures 37 and 40). The junction between the old tissue and the new dentine is marked by a scalloped border (or reversal cement line), and within the dentine several consecutive growth lines are aligned parallel to the inner surface of the pulp canal. SEM confirms that the

DESCRIPTION OF PLATE 1

FIGURES 1–4. These are all of the holotype RSM GY 1926.57.10/11 (Watson & Gill 1923, figure 30A), photographed from a latex peel.

FIGURE 1. (Scale bar 1 cm.) This shows the relative proportions of the bones bearing the teeth and denticles in dorsal view with anterior at the top. The best preserved tooth rows are on the left, a dorsal view of the prearticular. This is shown more clearly in figure 3, a lateral view with anterior to the left.

FIGURE 2. (Scale bar 0.5 cm.) This field from the anterior end of the specimen in figure 1 illustrates the irregular rows of denticles on the right part of the dentary (double arrow). Several isolated bones bearing a few denticles represent the separate plates that covered the ventral surfaces of the nasal capsules (single arrows). Four large teeth are present on a displaced dermopalatine (asterisk).

FIGURE 3. (Scale bar 0.5 cm.) View of left prearticular in figure 1 from the lateral aspect, with the posterior accessory tooth rows showing the newest teeth to form (single arrows). On the main lingual row an enamel layer (double arrow) encompasses all but the last two teeth to be added at the anterior end. Also shown are two teeth of the lateral rows (asterisk) of the pterygoid in their approximate occlusal relationship with the prearticular teeth.

FIGURE 4. (Scale bar 0.5 cm.) Anterior part of the right pterygoid from figure 1 in dorsal view showing a bone ridge associated with the tooth bases and an articular facet (arrow) at the anterior extremity to accommodate a dermopalatine.

FIGURE 5. (Scale bar 1 cm.) NUZ 78.1.42. Ventral view of the palate with anterior at the top, showing the relations of the two pterygoid tooth plates, each with one long ridge merging anteriorly with progressively less worn teeth, and with short rows of teeth situated laterally to the worn ridge. Lingual to each tooth ridge is a scattering of denticles. Figures 6 and 7 show parts of the right and left tooth plates. The posterior parts of both right and left rami of the lower jaw are preserved outside pterygoids (asterisk) shows left ceratohyal.

FIGURE 6. (Scale bar 0.5 cm.) NUZ 78.1.42. Posterior end of right pterygoid tooth plate showing the worn part of the lingual tooth ridge and lateral to that 3–4 short rows of teeth compressed towards the lingual tooth row. The newest unworn tooth of one of the short rows can be seen deep to the worn ridge (arrow).

FIGURE 7. (Scale bar 0.5 cm.) NUZ 78.1.42. Anterior is to the left in this ventral view of the left pterygoid tooth plate, although broken in many places it shows the large size of the teeth added at the anterior end to the lingual tooth row. These have become progressively worn into a continuous ridge at the posterior end. New teeth are seen at the lateral margins of the short rows (single arrows).

DESCRIPTION OF PLATE 2

FIGURE 8. (Scale bar 1 cm.) RSM GY 1976.19.3. Lateral view of right pterygoid tooth plate with anterior to the left (same specimen as in figures 13 and 15) shows the worn flat ridge at the posterior end grading into worn laterally facing facets of old tooth bases (arrow) giving rise to a serrated edge in the central part. Anterior to this are four separate teeth. The fourth tooth plus the worn teeth and ridge are all encompassed in an enamel layer (see figure 13, of this region; also figure 17, of another pterygoid).

FIGURE 9. (Scale bar 0.5 cm.) RSM GY 1886.87.21. Lingual view of right prearticular tooth plate with anterior to the left (same specimen as in figure 14) to contrast the lingual position of wear facets with the pterygoid tooth plate above (figure 8). These wear facets (arrow) in the central part of the lingual row accentuate the serrations initiated by the positions of the separate teeth. In this specimen only the last, most anterior tooth is not enclosed by the enamel layer surrounding the tooth bases.

FIGURE 10. (Scale bar 0.5 cm.) BMNH P11460. Dorsal view with anterior to the left of a right prearticular of a small specimen, which shows the worn surface texture of the pitted and ribbed ridge tissue derived from the tooth bases. This appearance fits well with the description of the arrangement of petrodentine from the SEM in plate 6. Also a few new teeth are situated laterally (single arrows). The communal enamel layer formed around all the tooth bases contributes a shelf to the lingual margin of the tooth plate (double arrows). (Adjacent to this are a few enlarged denticles.)

FIGURE 11. (Field width 0.5 cm.) BMNH P11470. Lingual view of prearticular fragment showing three laterally compressed teeth with two small cusps either side of the main cusp (see Woodward 1891, Plate IV, figure 5).

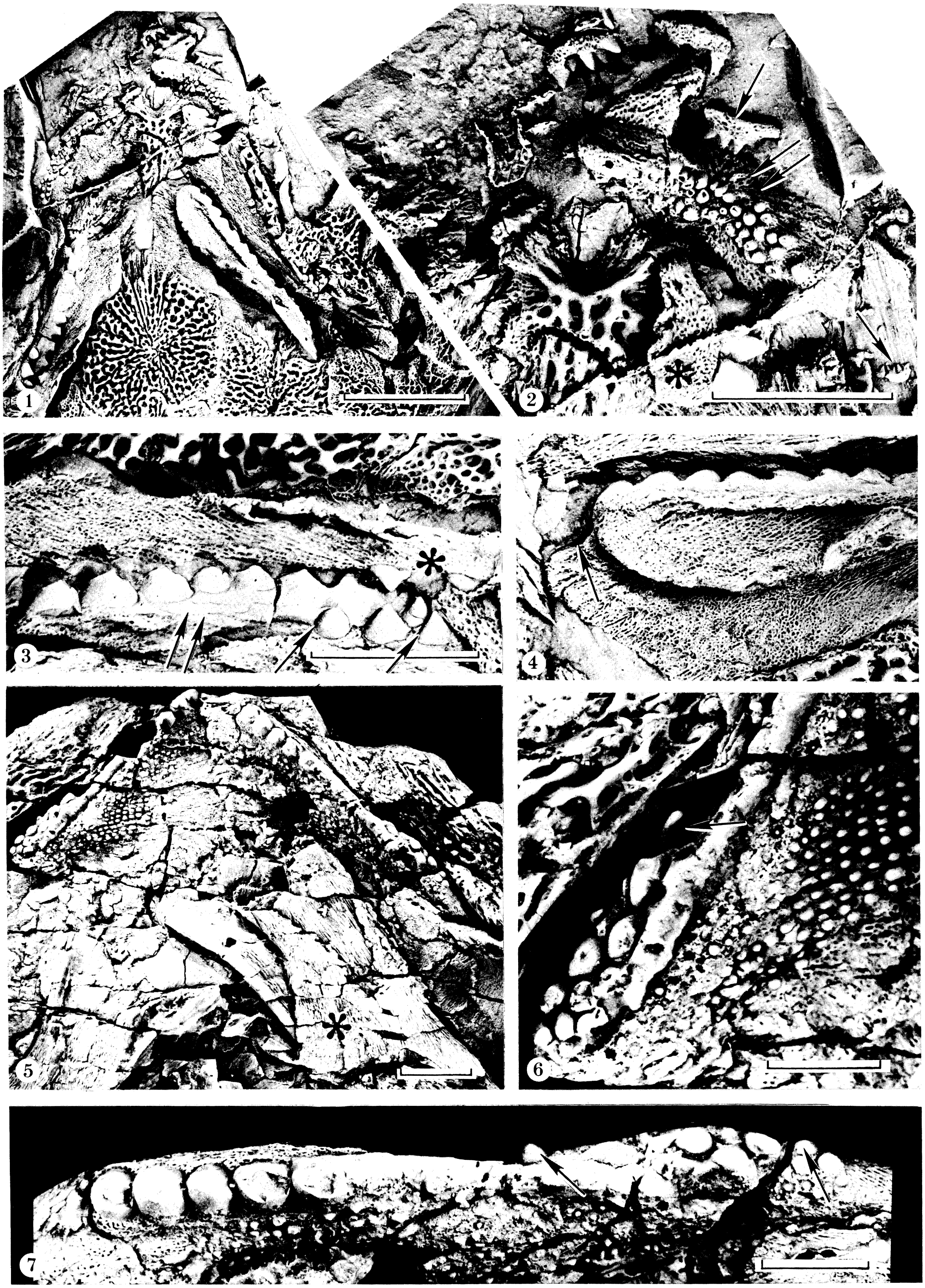
FIGURE 12. (Scale bar 0.5 cm.) RSM GY 1886.89.3A. Ventral view of posterior part of right pterygoid, anterior to the left, shows the worn ribbed and pitted tissue of the ridge; part of this is formed from worn tooth bases of the oldest teeth, and lateral to this are the short rows of two or three teeth, the most lateral being very new (arrow). A drawing of the whole of this tooth plate is in figure 17.

FIGURE 13. (Scale bar 0.5 cm.) RSM GY 1976.19.3. Detail of the long tooth row in figure 8 to show the conchoidal, lapping pattern of enamel layer deposition, the newest of which (arrow) is onto a resorption pit in the bone surface. The most anterior three teeth, on the left, are situated directly on the basal bone of the pterygoid and are not yet engulfed by the enamel layer.

FIGURE 14. (Field width 0.5 cm.) RSM GY 1886.87.21. Dorsal view of the same prearticular as in figure 9, and the drawing (figure 18). Presumed to be from a young individual, the worn part of the posterior end of the ridge is not very extensive but prominently shown are two wear pits produced from the opposing tooth plate (hatched in figure 18). The crack in the specimen has caused the loss of one tooth from the short rows at the lateral margin.

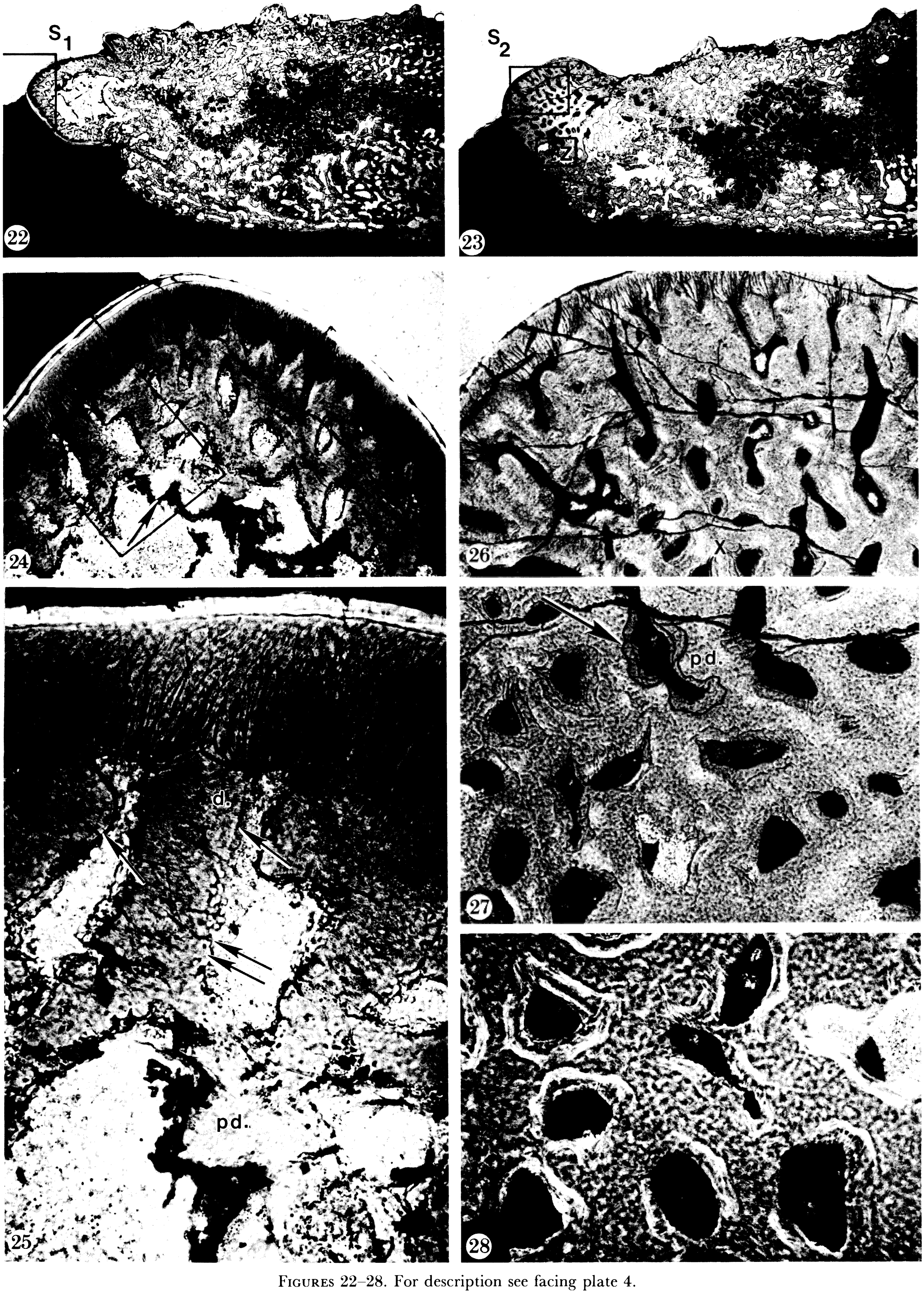
FIGURE 15. (Scale bar 1 cm.) RSM GY 1976.19.3. Ventral view of the same pterygoid as in figure 8 shows the elongation of the lingual tooth row and increasing tooth size towards the anterior end. The very short lateral tooth rows converge on the posterior end of the tooth plate.

FIGURE 16. (Scale bar 0.5 cm.) RSM GY 1891.7.26. Fragment of posterior end of pterygoid tooth plate of an old individual, an enamel layer (single arrow) encloses both parts of the worn tooth ridges and two new teeth (double arrow) appear on the lateral side. Lingual to the tooth plate are many separate denticles, some of which are relatively new.



Figures 1–7. For description see opposite.

FIGURE 8–16. For description see page 312.



FIGURES 22–28. For description see facing plate 4.

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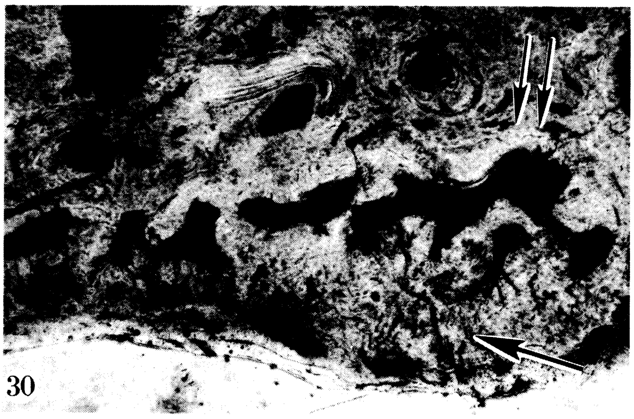

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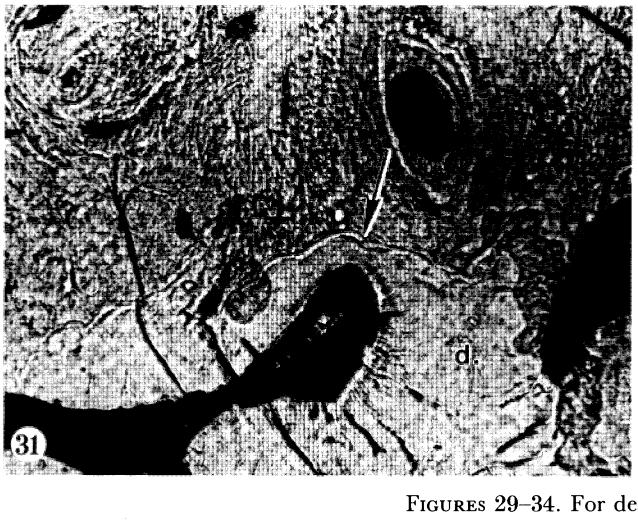

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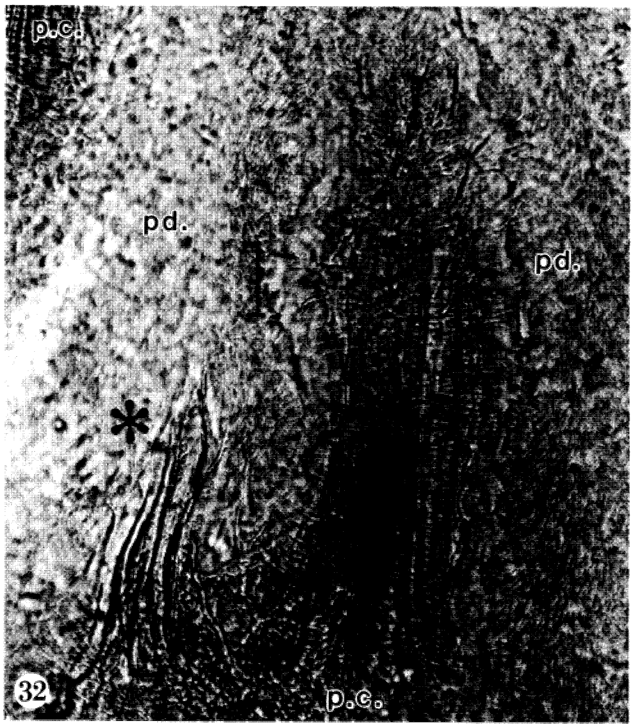

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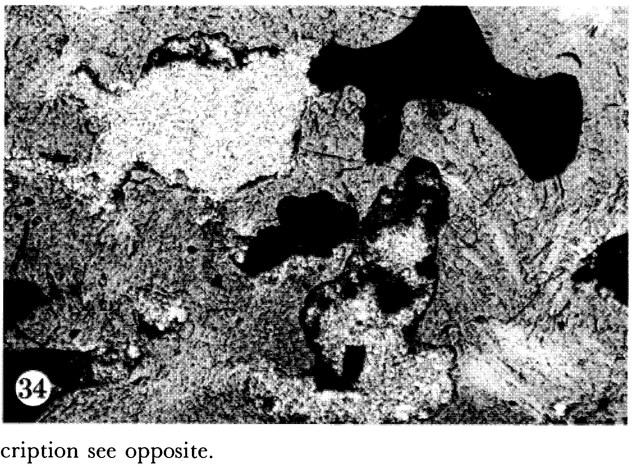

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FIGURES 29–34. For description see opposite.

DESCRIPTION OF PLATE 3

FIGURES 22 and 23. (Magn. × 10.) BMNH P11458 Photomicrographs from the two sections S_1 and S_2 as shown in figure 21, cut vertically through the anterior end of the tooth ridge and the palatal denticles. The tissue within the newest tooth on the ridge (S_1 in figure 22) compared with an older tooth (S_2 in figure 23) shows that the central pulp cavity in the young tooth has become infilled with compact dentine. (Boxes indicate the positions of the fields in figures 24 and 26, Z is shown in figure 34.)

FIGURE 24. (Magn. × 75.) Detail of young tooth (box in figure 22) showing enamel layer, pallial dentine with clusters of branching tubules, terminating just below the enamel layer; internal to the pallial dentine is trabecular dentine, and centrally a small patch (arrow) of strongly birefringent, translucent dentine. This represents the initial production and early formative front of petrodentine within the outer shell of dentine of the tooth. (Box shows the region of figure 25.)

FIGURE 25. (Magn. × 190.) Detail (box in figure 24) in which incremental lines in the enamel can be seen plus radial striations due to crystallite arrangement. Fine terminal branches of the dentine tubules end at the enamel dentine juction. The trabecular dentine (d.) beneath the pallial dentine shows a finished surface (single arrows) close to the small pulp canals assumed to house the cell bodies with processes leading into the pallial dentine, and a forming calcospheretic front (double arrow) adjacent to the wider pulp chamber spaces. The petrodentine (pd.) developing below this has a ragged fringed edge, observed in most regions where petrodentine is forming.

FIGURE 26. (Magn. × 75.) Detail (box in figure 23) at the same magnification as figure 24, showing very narrow pulp canals (filled with black manganese dioxide and some white calcite), a worn enamel layer and compact dentine entirely filling the central part of the tooth.

FIGURE 27. (Magn. × 120.) Detail (from region X fig. 26) of the most central region showing two zones within the dentine, circumpulpal with irregular tubules, and translucent, birefringent petrodentine (pd.) occupying the interstitial regions. A black line has been drawn to mark the boundary of one zone of circumpulpal dentine (arrow).

FIGURE 28. (Magn. × 190.) Part of the left-hand side of the field in figure 27 taken in phase contrast to emphasize the difference between the two zones of dentine; circumpulpal dentine shows concentric growth lines, radial lines and radial tubules. Its formation is not complete around some of the larger canals.

DESCRIPTION OF PLATE 4

FIGURE 29. (Magn. × 25.) Detail of the tooth base (t_4 section S_3, figure 21); the lateral margin is at the top and the enamel layer of the lingual margin at the bottom. As illustrated in figure 8 the lateral margin is a wear surface and here the dentine is extensively worn. The compact dentine (d.) of the tooth base has bulp canals that run almost parallel to the section plane. The dentine is closely apposed to the bone (bo.) of the tooth ridge. The lingual surface opposite to the worn lateral surface of the tooth is covered by the enamel layer seen to enclose all the tooth bases in the gross specimens. Figures 30 and 33 are fields X and Y to show details of the way in which tissues are added to both these surfaces.

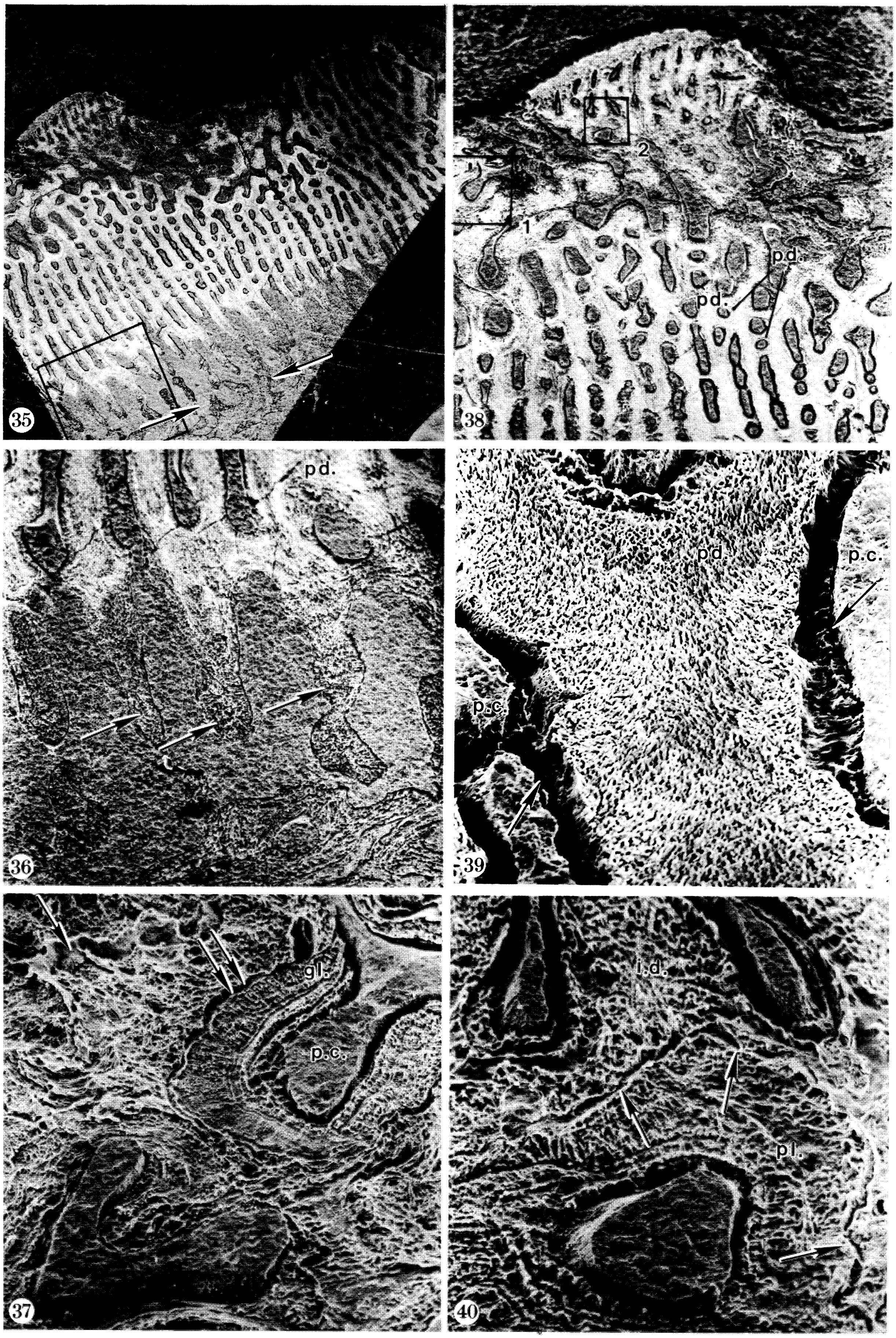
FIGURE 30. (Magn. × 120.) Detail (from box X, figure 29) of the superficial dentine layer with only sparse irregular tubules, formed beneath the thin covering of enamel (arrow); these two tissues together form the communal enamel covered layer. Addition of this layer is only possible if built onto a resorption surface of the bone; evidence of this process can be seen as a reversal line (double arrow) between the bone and the simple dentine.

FIGURE 31. (Magn. × 190.) Detail to show the scalloped border of a typical reversal line (arrow) and the dentine (d.) within which there are tubules leading from the pulp canal surfaces (some of these are filled *post mortem* with a black mineral deposit as in the pulp canals).

FIGURE 32. (Magn. × 250.) Detail of compact dentine from the central region in figure 29 showing parts of three pulp canals (p.c.) From the pulp canals tubules run irregularly through the circumpulpal dentine and end in extremely fine branches within the adjacent petrodentine (pd.). In one region (asterisk) the tubules are shown along their entire length with many short, twig-like branches. The circumpulpal dentine displays a regular arrangement of radial lines in addition to the tubules. The maximum width of the circumpulpal dentine lies between the vertical bars.

FIGURE 33. (Magn. × 100.) Detail from Y, figure 29, the lateral margin to show the region between the two teeth (shown in S_3 figure 21). Originally this surface was enamel covered, now it is worn and shows pleromic dentine which has grown into the bone, from which it is separated by a reversal line (arrow).

FIGURE 34. (Magn. × 120.) Detail from Z, figure 23, the lateral side at the base of the tooth, showing in addition to pulp canal spaces (black) two or three new spaces created by resorption (*post mortem*, filled with birefringent calcite), before any infilling with new dentinal tissue.



FIGURES 35–40. For description see opposite.

Description of plate 5

These are all scanning electron micrographs of the surface (S_4, figure 21); they show the relatively more organized basal tissue of the tooth row. It is a region deep to the worn surface of the tooth bases (t_3 and t_4 in figure 21). Etching with 1 N HCl has allowed the highly mineralized petrodentine to be seen in contrast to the softer pallial dentine of the tooth and the bone. Within the original soft tissue space there is infilling mineral, not affected by etching and relatively homogenous.

Figure 35. (Magn. × 25.) The lateral surface of the tooth row is at the top and the sectioned surface goes through a major junction between forming petrodentine and bone (arrows; marked as g. in S_4, figure 21). This is in effect an extending pulp chamber to allow further growth of the petrodentine, the latter is seen at higher magnification in figure 39. (Boxed area is figure 36.)

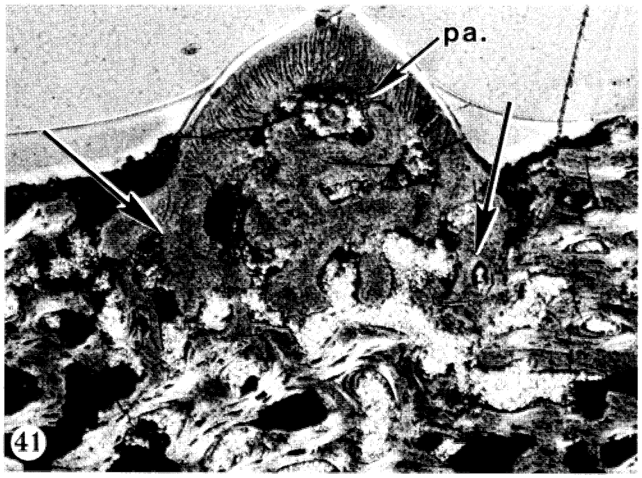
Figure 36. (Magn. × 100.) This forming front of petrodentine (boxed area in figure 35) shows primary trabeculae (arrows) of different texture from the more mineralized petrodentine (pd.) constituting the older regions. The deeper etch level is a reflection of its lower mineralization.

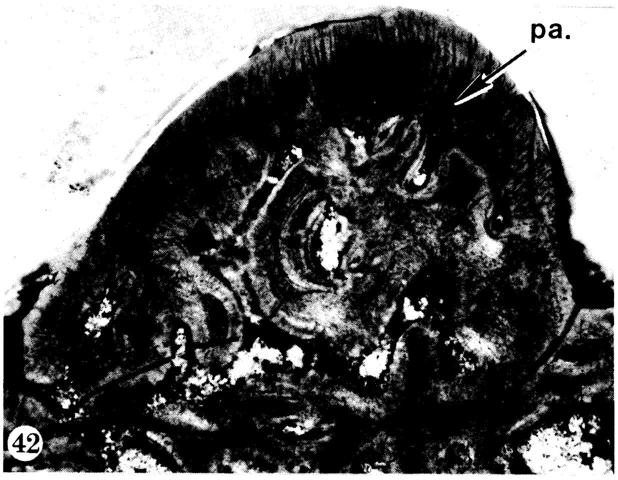
Figure 37. (Magn. × 250.) This region (from box 1, figure 38) shows the lateral surface between adjacent teeth onto which the surface layer of enamel has formed from a resorption surface (single arrow). Pleromic dentine has also formed by growth into the resorption space (double arrow). Within this dentine there are several concentric growth lines (g.l.) parallel to the pulp canal surface (p.c.) and radial striations normal to the pulp canal surface, all of which complement the information from the histology in plates 3 and 4. The infilling mineral within the pulp canals remains proud of the biological mineral.

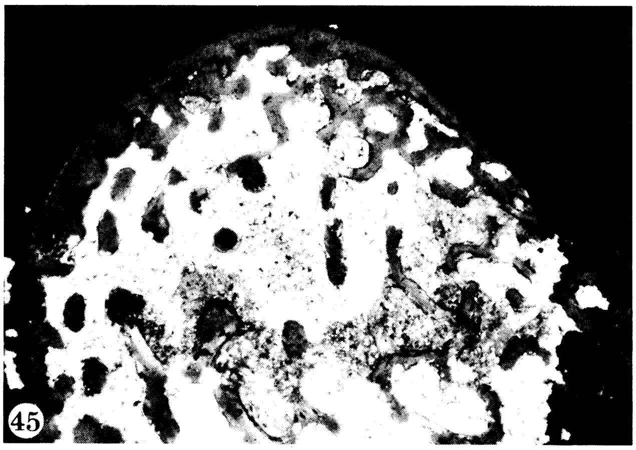
Figure 38. (Magn. × 50.) Tooth base with petrodentine adjacent to petrodentine of the tooth ridge (pd.) (from the tooth base on the left of figure 35). The positions of the fields for figures 37 (box 1) and 40 (box 2) are indicated; these show regions of pleromic dentine infilling the tissues at the lateral margin between the teeth.

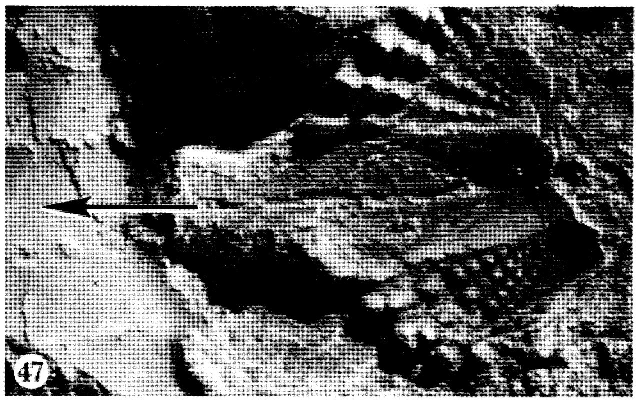
Figure 39. (Magn. × 500.) A field from the central region of the ridge tissue in figures 35 and 38, showing one zone of petrodentine between two pulp canals; this shows organized crystallite groups. The shallow etch depth of the petrodentine (pd.) contrasts with the more deeply etched circumpulpal dentine (arrows); this forms only a thin layer around the margins of the pulp canals (p.c.).

Figure 40. (Magn. × 500.) The same magnification as figure 39, to compare with the structure of petrodentine, shows lack of organization of crystallites in pleromic dentine (pl.) which is infilling a resorption space (arrows) in older interstitial dentine (id.) (box 2, figure 38).









FIGURES 41–48. For description see opposite.

tissue between the two teeth is pleromic dentine. In the equivalent position to this, on the whole specimens, a superficial layer of enamel must have grown around between the teeth after each one was initiated. This enamel, together with a layer of simple dentine, lies over the bone between the tooth bases, and, therefore, it is assumed that the pleromic dentine developed from this as part of an infilling mechanism to add to the dental tissues at the base of the teeth. This type of dentine growth is not found beneath the denticles on the lingual surfaces.

(v) *Enamel*

A very thick layer of enamel formed on the outside of each tooth of the ridges. This exhibits incremental lines (figure 25), the direction of which shows addition from the outside as sequential layers. The enamel also has a rodlet birefringence commonly found in early enamel types, such as that found in the marginal teeth of sarcopterygians.

Independently of the enamel cover on each tooth, a second enamel-covered layer developed around the bases of the individual teeth and in particular along the lingual margin. From the macroscopic views this can be seen to develop only after surface resorption of the bone (figure 13)

DESCRIPTION OF PLATE 6

FIGURE 41. (Magn. × 75.) Enamel covered denticle on the pterygoid, from the palatal surface of S_2, figure 23, which has formed within a depression in the bone. The structure of the bone, identified by enclosed lacunae, ends abruptly at a previous resorption surface. Dentine trabeculae (arrows) join the pallial dentine (pa.) to this bone surface.

FIGURE 42. (Magn. × 120.) The structure of the denticle (from S_1) figure 22, is shown here to contrast with that of the teeth. The interstitial regions of dentine are small relative to the circumpulpal dentine, are poorly organized, and lightly mineralized. No translucent dentine like petrodentine can be demonstrated. The pallial dentine contains arrays of almost parallel tubules similar to that in the teeth.

FIGURE 43. (Magn. × 190.) Tissue at the base of a tooth (palatal surface of the tooth in S_1, figure 22), the old bone tissue ends abruptly at a reversal line (arrow) and joining onto this new dentine (d.) and new bone (bo.) of the tooth base, comparable to bone of attachment in all osteichthyan teeth. The junction between old bone and new attachment bone is emphasized with a black line.

FIGURE 44. *Scaumenacia curta* Whiteaves (BMNH P604709, magn. × 4). Pterygoid tooth plates to show the relative positions of the tooth rows. Anterior towards the top and the median line in the position of the arrow. The first row is slightly more elongate and all rows converge towards the midline, the teeth increasing in size and with the largest newest teeth at the lateral margin. The right tooth plate is incomplete and the left one is eroded at the posteromedial margin. The pattern is dipterid-like.

FIGURE 45. *Scaumenacia curta* (SMNH 2610, magn. × 75). Vertical section through a young tooth to compare with the teeth of *Uronemus*. The pallial dentine, at the outer margin of the tooth, is thin and poorly organized with only short sprigs of very few tubules. Only very few trabeculae of dentine had developed within the central pulp cavity, now filled with calcite (white). The enamel layer is missing, presumed to have been lost or only partly formed at this stage of development.

FIGURE 46. *Scaumenacia curta* (SMNH 2610, magn. × 75). Taken in partial polarized light. Older tooth than in figure 45. Within the outer shell of pallial dentine there are central trabeculae of a type of dentine which is translucent, more strongly birefringent and which resembles petrodentine in the arrangement of the birefringent crystal bundles. In this tooth a thick enamel layer has developed and shows evidence from incremental lines of apposition from the outside.

FIGURE 47. *Rhinodipterus ulrichi* Gross (BMNH P49774, magn. × 3). Anterior is to the left and the median line in the position of the arrow. Pterygoid tooth plates to show the relative positions of the tooth rows and the newest, largest lateral tooth to each tooth row. Also shown is the region of smooth dentine extending both from the lingual row to the median suture, and also anteriorly (in the direction of the arrow) beyond the last tooth of the ridge.

FIGURE 48. *Rhinodipterus ulrichi* (SMNH 1568, magn. × 120). Section through part of the tooth plate showing worn, translucent petrodentine (pd.) with small pulp cavities between it and the bone and a fringed forming surface (arrow).

and in thin sections this new layer of tissue is demarcated from the bone by a reversal line (figure 31, plate 4). It is clear that beneath the superficial enamel there is a layer of simple dentine (figures 29 and 30, plate 4) which again adds to the structure of the teeth and the ridge by pleromic growth of dentine. Together these tissues form the communal enamel-covered layer that grew by apposition onto the tooth–bone surfaces. This feature is part of the growth pattern of the tooth plates of extant dipnoans (Smith 1979*b*).

(vi) *Denticles*

The denticles are simple in form and are generally conical. In places they can be observed in the process of regeneration, lying well below the level of the surrounding denticles. New denticles and resorption pits are distributed randomly over the surface. These features are best exhibited on NUZ 78.1.42, and RSM GY 1891.7.26 (figure 16).

On each pterygoid the denticles are arranged within an arc whose chord lies between the posterior end of the plate and the second tooth from the front of the lingual row (figure 8). Within this arc the denticles show no regular size distribution; they are arrayed in rather regular rows that fan out forwards and inwards from its posterior angle. There are no denticles on the pterygoids towards the midline, and none on the parasphenoid; nor are there any on the labial face of the pterygoid lateral to the lingual tooth row.

Denticles are not widely distributed on the inner face of the prearticular. The holotype, for example, shows only two in this position. The largest number is on BMNH P11460 (figure 10) where they are restricted to an irregular patch immediately below the tooth row. It is important to notice that the disposition of the marginal teeth implies that the pterygoids formed a high arch, and that the denticles therefore lay on a steeply inclined surface along the medial edge of the lingual tooth ridge with their axes directed vertically.

Though there is clear evidence that denticles were normally shed, occasionally a denticle adjacent to the lingual tooth ridge was enveloped by the enamel of the ridge and it became incorporated in the ridge tissue (figures 9 and 16).

The dentary is shown only on the holotype (figures 1 and 2). Its dorsal surface is covered with a band of denticles in three or four irregular rows. The most anterior row, particularly towards the midline, has slightly larger denticles. All denticles are attached directly to the bone as are the denticles on the pterygoids. There is no evidence that they were joined at their bases by either dentine or enamel. The posterior wall of the dentary forming the anterior wall of the anterior furrow, is exposed on both sides of the specimen. It is free of denticles. A small patch of about eight denticles occurs on a bone on the left side. These could be on a broken fragment from the anterior end of the prearticular.

Thin sections of the denticles show that they are covered by an unusually thick layer of enamel that has the standard growth lines of that tissue (figures 41 and 42, plate 6). The larger denticles have a more organized arrangement of pulp canals, but all have an outer layer of pallial dentine in which groups of tubules spray out from the terminations of the pulp canals as in the teeth. In young denticles the development follows the same pattern: trabeculae of dentine form within the pulp and these are later narrowed by circumpulpal dentine. This type of development we are calling intrapulpal dentine in the discussion of denticle histology in *Chirodipterus* (Smith & Campbell 1987). All denticles develop from an old resorption surface which, in thin sections, is indicated by a reversal line (figures 41 and 42).

4. COMMENTS ON THE TOOTH PLATES OF OTHER GENERA

The genera whose dentitions have been compared with those of *Uronemus* are *Fleurantia* (Graham-Smith & Westoll 1937, pp. 260–261), and *Scaumenacia* and *Phaneropleuron* (Westoll 1949). In addition, the remarkably elongate tooth plates of *Rhinodipterus ulrichi* Gross (Jarvik 1967) and the laterally compressed teeth on the lingual rows of *R. secans* Gross (Gross 1956) have suggested that comparative work could be of value. Of these forms we have new data on *Scaumenacia curta* Whiteaves, *Phaneropleuron andersoni* Huxley and *Rhinodipterus ulrichi*.

(*a*) *Scaumenacia curta Whiteaves*

This genus has pterygoid plates that are not marginal in the sense of *Uronemus*, but are more comparable in position to those of *Dipterus valenciennesi*. Moreover, the specimens available to us show no evidence of denticles medial to the tooth plates, but rather simple sheets of dentine. Specimens BMNH P6786 and BMNH P604709 show the gross structure of the plates well, the latter specimen being from an unusually large individual (figure 44, plate 6). There are up to nine tooth ridges with many teeth that increase in size laterally. The lingual row is slightly elongated relative to more posterior rows. Around the plate there is no bounding layer of enamel like that found in more advanced genera such as *Sagendous* and *Ctenodus*.

The teeth of the more lingual rows tend to be slightly compressed laterally, but those of the more lateral rows are more equidimensional. The teeth share a common bone of attachment but are closely juxtaposed. They must have been added individually as in *Dipterus*. When unworn, the valleys between the ridges are floored by enamel (BMNH P6786), but most sites show occlusal wear pits. The heels of the tooth plates are rounded as is normal for such species as *D. valenciennesi*, the specimen figured being incomplete in this area. The tooth rows converge and decrease in number towards the heel.

The internal structure of the teeth is interpreted from the worn surfaces of the above specimens, the section figured by Denison (1974, figure 5) and the sections made available to M.M.S. by Professor T. Ørvig. In their earliest phases of growth, the newest (lateral) teeth have an open central pulp cavity within a shell of dentine (figure 45, plate 6). This cavity subsequently fills with trabecular dentine and then a central core of hard translucent petrodentine (figure 46, plate 6). The nature of this tissue is clear from the sections, and it has been corroborated by Professor Ørvig using SEM of the same material (personal communication). When the tooth is fully formed the pulp chamber has been almost completely obliterated, and in this respect it is similar to the situation in *Dipterus*. The pallial dentine is different from that of *Uronemus* in that dentine tubules are scarce or absent, whereas in *Uronemus* the tubules are characteristically arborescent arrays of long sub-parallel tubules.

A further feature of the histology that is now interpreted as primitive for tooth-plated and dentine-plated forms, is the presence of pleromic dentine that has grown into the bone around the bases of the teeth.

In summary, the tooth plates of *S. curta* are not placed marginally in the same sense as those of *Uronemus*, they show no bounding layer of enamel, the teeth do not join at their bases to form a marginal dentine tooth ridge with distinctive histology, and there are no denticle patches on the lingual side of the tooth plates. In all these features, as well as the extent of petrodentine development and the structure of the pallial dentine, *Scaumenacia* is closer to *Dipterus valenciennesi* than to *Uronemus splendens*. We see no distinctive feature shared by *Scaumenacia* and *Uronemus* to support any useful comparison.

(*b*) *Phaneropleuron andersoni Huxley*

The dentition of *Phaneropleuron andersoni* Huxley from the Upper Devonian (Old Red Sandstone) has been described only briefly in the early publications (Huxley 1861; Traquair 1873; Woodward 1891), and all refer to a single series of sharp, well-separated conical teeth forming ridges. Examination of this material (BMNH P24839 and BMNH P26117) after further preparation has allowed a more direct comparison with the dentitions described here. This genus has opposing tooth plates, each one consisting of converging rows of conjoined teeth. In each row the teeth form a series of the same shape becoming progressively smaller posterolingually. The most anterior row has laterally compressed teeth, and one face of the tooth is flattened by wear. These are all characteristics of interlocking tooth plates and it is clear that *Phaneropleuron* is a member of the tooth-plated group. We are not able to add any other data on tooth-plate morphology or histology that would be helpful for the present discussion, and hence have no reason to comment further on Westoll's (1949) suggestion of a relationship with *Uronemus*.

(*c*) *Rhinodipterus ulrichi Gross*

Jarvik (1967) has figured the mandibular plates of *Rhinodipterus ulrichi* and we have examined that specimen and the palatal tooth plates of specimens of the same species (figure 47, plate 6). The plates are well separated from the midline, and a sheet of dentine extends forwards medially between the nasal capsules. The lateral margins of this sheet seem to have borne a row of teeth, but these are not aligned with the lingual row of teeth on the tooth plate proper. Clearly they did not occlude with the lingual tooth row of the mandibular plates, and they must have been opposed by some structures, as yet unknown, forming a modified mandibular adsymphysial plate.

The teeth were added individually to the margins of the tooth plates, and there is no sign of a continuous bounding enamel layer. The tooth ridges converge posteromedially. Posterolateral to the last formed ridge there is evidence of posterior growth of a flat sheet of dentine. This is unlike the arrangement in *Uronemus*.

Our understanding of the histology of this species has been derived from thin sections of a small part of a tooth plate made available to M. M. S. by Professor T. Ørvig. A relatively thin layer of translucent, atubular dentine covered the bone surface at the base of the tooth ridge without a significant space between the dentine and the bone. Only the margins of the ridge and the margins of the separate teeth had a thin enamel cover; the surface was worn and bare of enamel. Beneath parts of the ridge small resorption spaces had been created and, in these, an extension of the translucent dentine had begun to grow (figure 48, plate 6). These new surfaces were frayed as described for the forming front of petrodentine. The pulp canals are very irregular, only a few irregular tubules extend from them into the petrodentine. Because the section plane did not go through separate teeth it is not possible to comment on the initiation of the ridge tissue.

We conclude, therefore, that the tooth plates of this genus are comparable to those of *Dipterus valenciennesi* in that the teeth are formed as isolated enamel-capped entities, have a petrodentine core, have irregular pulp canals and fine dentine tubules, and the plate has no bounding enamel layer. The similarities with the plates of *Uronemus* are considered to be superficial.

5. Discussion

(*a*) *Food reduction*

As was pointed out by Watson & Gill (1923) and Westoll (1949), the teeth of the lingual row on the lower jaw pass outside those of the pterygoid, producing a sectorial effect. The efficiency of this action is enhanced by the sharp-edged, laterally compressed, conical form of the mandibular teeth. Although this is the most obvious functional feature of the dentition, we should also note that the absence of wear on the most anterior teeth in the lingual row, the extensive wear on the more posterior teeth in the row, and the general abrasion of the inner teeth of the lateral rows, also imply important functions. Presumably the anterior teeth were used for grasping, those near its midlength for slicing and those at the posterior end for pulverizing the sliced fragments. The pattern of teeth and wear pits suggests a type of action comparable to that of the cusp-to-fossa pattern in mammalian teeth.

As previously indicated, the palatal denticles took little part in food reduction and were probably used only to prevent the food from moving away from the teeth towards the midline. The relatively small number of denticles on the lower jaw suggests the presence of thick soft tissues, such as a 'tongue' and its associated connective tissues, over and lateral to the basihyal–basibranchial system. Their function would have been to hold the food against the palatal denticles to prevent movement towards the midline. The fact that the basibranchial system performed some significant function either in feeding or in respiration, is demonstrated by the relatively enormous ceratohyals preserved on NUZ 78.1.42. Although they are incomplete at each end, enough of them remain to demonstrate that they extended well forwards beneath the buccal cavity, and provided large areas for muscle attachment.

(*b*) *Tooth plates*

At first sight, the tooth plates of *Uronemus* seem bizarre, but they are comparable in some respects to those of *Oervigia* (Lehman 1959) in which the mandibular tooth plates had retreated from the midline and the lingual tooth row had become relatively elongate, the teeth forming that row being strongly compressed. This genus is from the Upper Devonian. At that time few genera had lost their ossified snouts and dentaries, and it is significant that *Oervigia* apparently was among those in which this had occurred. The mandible is too poorly known for comment on the 'dentary' to be of value.

Another late Devonian genus, *Rhinodipterus*, also developed elongated tooth plates in which the lingual row of teeth became unusually long (Gross 1956; Jarvik 1967). However, examination of specimens of *R. ulrichi* in the BMNH and another supplied by Dr H.-P. Schultze shows that the teeth of the lingual row on the palate were not sectorial and, unlike *Uronemus*, the wear is on the lingual side of the row. As we have indicated elsewhere (see §4(*c*)), the elongation of the pterygoid tooth plate in *R. ulrichi* is produced by an anterior extension of the dentine-covered tissue between the lingual tooth ridges and not by the ridges themselves. Tooth-plate elongation must have been produced by more than one means.

Formally, however, it may be possible to derive the mandibular plates of *Uronemus* from an *Oervigia*-like plate by further suppression of the lateral tooth rows, concomitant increase in the length of the lingual row, the introduction of new tooth rows between the lingual row and the next one, and an increase in the amount of petrodentine in the teeth. The suppression of the size of the lateral tooth rows could be achieved by a delay in the initiation of the rows and by longer periods between each new tooth in the row being initiated. Interpolated teeth do occur in other genera, i.e. *Dipterus valenciennesi*, *Gnathorhiza bothrotreta* (Berman 1979, figure 6), and this feature could be exaggerated in *Uronemus*. The development of enamel around the margins of the plates in *Oervigia* has not been described. Primitive forms such as *Speonesydrion* have no bounding layer. Instead, a number of enamel-coated denticles form the plate edge and are bound onto the marginal teeth of each row. *Uronemus* had advanced well beyond this stage and an enamel layer encompassed the separate teeth after they had been added at the anterior and lateral margins. This enamel, together with a layer of simple dentine, overlapped the enamel-covered base of the teeth. This is an advance on the pattern in *Dipterus valenciennesi* in which the teeth were added separately but were never encompassed in a layer of enamel around the plate margin. However, it is not as advanced as that of some late Devonian species commonly assigned to *Dipterus* (Denison 1974), or the early Carboniferous *Sagenodus* (Smith 1979*a*), in which new teeth were added within a bounding enamel layer, and the whole unit grew as an entity.

The new observation on the dentition of several recently prepared specimens, which led to the suggestion that *Uronemus* should be considered as a form with tooth plates, was that new teeth could be seen at the lateral margins deep to the worn surface of the tooth ridge. These teeth aligned with rows of progressively more worn teeth that are fused with the main tooth ridge. This pattern of replacement and wear fits best with known patterns of growth in genera with radiate tooth plates.

The histological findings described above have reinforced this interpretation. The wear-resistant tissue of the ridges is true petrodentine (Smith, 1984), indistinguishable from that found in normal tooth plates. It is present in the newly formed teeth added at the anterior extremity of the lingual ridge of the tooth plate, and is not just a late development in the mature part of the plate. These histological features by themselves would not be sufficient to place the genus within the tooth-plated group, because it could be argued that *Uronemus* had marginal tooth ridges in which petrodentine had been secondarily evolved. However, the observation that an additional layer of thin enamel and simple dentine was added to the surface of the bone around the tooth bases, and that this developed only after some resorption of the underlying tissue (Smith 1979*b*), provides another character in common with tooth-plated forms. It is apparent that the formative front of this communal enamel layer migrates away from the worn ridge surface laterally and along the length of the ridges to encompass the newest teeth at the lateral and anterior margins.

The wear facets on the lingual ridges show that shearing and interdigitation occurred, the lower jaw biting outside the upper. A similar shearing bite may have been present in the tooth-plated genus *Oervigia*. It is not possible to draw clear inferences about relationships from this observation alone, because shearing may have been a feature of the bite in the denticulate genus *Griphognathus*. The most convincing argument is based on two facts; (*a*) the shearing bite in *Uronemus* was achieved by a 'pinking-shear' mechanism quite unlike that of *Griphognathus* or any other denticulate genus; (*b*) the wear pits arranged in rows between the radial teeth are found only in genera with radiate tooth plates organized to interlock at full occlusion. An interpretation of how this occurred is given in figure 18. The newest teeth in the lateral rows can be observed in the holotype (figure 3), and these also add alternately, further reinforcing the above interpretation. The interdigitation of opposing plates is a feature of all forms with radiate tooth plates, from the earliest known member of the group, *Speonesydrion*, to the extant genera.

An alternative view, and one that seems to have been in the minds of previous workers (Denison 1974; Miles 1977; Campbell & Barwick 1987), is that the tooth plates of *Uronemus* are modified marginal ridges of the type found in primitive genera such as *Uranolophus* and perhaps *Griphognathus*. These genera have a continuous or semicontinuous ridge of enamel-flanked dentine that is not formed by the wear of a row of continuously growing teeth. Resorption and regrowth plays a major part in this ridge formation. Basal pulp cavities never develop within these ridges and petrodentine is never present, even at the end of a depositional phase of growth. Hence they have none of the characteristics that would be expected in primitive members of the group to which *Uronemus* was alleged to belong.

We have concluded that previous evaluations of the dentition of *Uronemus* are incorrect, and that our observations lead to the conclusion that it has many characters found only in tooth-plated genera. These conclusions are the main basis for the discussion on relationships considered in §5 (*f*).

The significance of the presence of denticles, not normally a feature of tooth-plated genera, is discussed in the following section, 5 (*c*).

(*c*) *Denticles*

Palatal denticles are a feature of *Uronemus* not known in any other form with tooth plates. Carboniferous genera with advanced tooth plates, such as *Sagenodus* and *Ctenodus*, have no dentine between the pterygoid plates. They are bounded by a more or less continuous layer of enamel. In more primitive forms, such as *Dipterus valenciennesi* and *Rhinodipterus ulrichi*, in which the tooth ridges are separated from the midline, the plates are in contact but a sheet of unridged dentine forms the medial part of the palate. This sheet does not extend onto the parasphenoid, the sutures of which are clearly exposed. We believe that the palate of *Uronemus* must have evolved from a palate of this type by lateral movement of the tooth plates and the reacquisition of denticles on the bone medial to them. Such a process of secondary acquisition would account for the absence of denticles on the parasphenoid and the pterygoids towards the midline, a feature that Miles (1977) explained as a retreat from a previously fully denticulated condition. We would regard it as a failure of attached denticles to develop in that region of the palate because the mode of feeding did not promote their development over the entire palate. The spacing and the unworn nature of the denticles on the palate of *Uronemus* suggest a different functional role from those of the denticulate group. The latter were abraded by basibranchial tooth plates. No median callosity has been observed in *Uronemus*, whereas one is present in some members of the denticulate group. Unlike *Holodipterus*, proposed as a member of the denticulate group that has simulated tooth plates (Campbell & Barwick 1983, 1987), the denticulate palate in *Uronemus* was not used for food reduction by the action of basibranchial tooth plates. The denticulation of *Uronemus* is therefore considered to be a secondary phenomenon, and does not indicate a relationship with denticulated genera such as *Uranolophus* and *Griphognathus*.

A re-examination of *Conchopoma* is now urgently required. Although it is known to have basihyal tooth plates, its denticles are large and simple, and it is difficult to establish the precise nature of the palatal margins. Clearly the denticles of the parasphenoid were shed, as is well shown by the specimen of *C. gadiforme* housed in the Royal Museum of Scotland (RSM GY 1894.77.19) and the specimen of *C. edesi* in the Field Museum, Chicago (PF 5904). To date, no evidence of marginal ridges has been forthcoming. Further work should be directed towards the examination of the pterygoid margins and towards the determination of the fixed or shedding nature of any marginal ridge tissues, should they be found.

(*d*) *Small, isolated tooth plates*

As indicated above, several of these small structures were present around the anterior end of the palate, but were not firmly attached to any of the major bones. Small, isolated lateral nasal tooth plates are known from *Griphognathus*, *Holodipterus* and *Conchopoma*, all of which belong to the denticulate lineage. Campbell & Barwick (1984) have argued that in *Griphognathus* they are neomorphic, having developed in the skin over the ventral and lateral surfaces of the nasal capsules to accommodate the peculiar bite developed by members of that genus. The number and position of the tooth plates in the other two genera are not definitely known. However, *Holodipterus* is known to have a broad, depressed snout in which the nasal capsules would have been in a vulnerable position, and hence a similar argument could be developed to account for the lateral nasal tooth plates in that genus.

In *Uronemus* the rostral region was unossified, but the 'dentary' was a solid denticulated structure that must have passed around the anterior end of the palate to fit up under the nasal capsules at full occlusion. The dermopalatines, being loosely attached to the pterygoids, would not have provided any rigidity in this region to compensate for the flexibility of the unossified snout. In any case, they probably did not occlude with the inner edge of the dentary, but passed inside it. Hence, in this genus also, denticulation must have developed in the skin over the ventral side of the nasal capsules to provide a surface to occlude with the 'dentary'. We do not consider that the presence of these plates gives any indication of a relationship to the denticulated lineage.

(*e*) *Respiration and the form of the buccal cavity*

Food reduction is only one of the functions that shapes the buccal cavity and the structures that line it. The other major function is respiration. As has been pointed out by Thomson (1969) and Campbell & Barwick (1987), the early dipnoans probably respired exclusively with their gills. The shape of the buccal cavity therefore would be moulded mainly by the need to produce a buccal pump to force water over the gills, and to produce suction for ingestion. These functions do not require a large buccal cavity, and the gill chamber does not have to be disposed in any special way around the posterior end of the buccal cavity. The main requirements are the ability to increase the volume of the buccal cavity by opening the mouth, and dropping the hyoid and pectoral girdle systems, and the capacity to seal the opercular chamber (see Lauder 1980). Closure of the mouth is correlated with the opening of the opercular chamber so that water can be forced out of the buccal cavity over the gills at the same time as ingested food is being bitten. Such processes can be accomplished with a small buccal cavity occupied by an extensive dental apparatus, and large operculars covering a large gill chamber behind and below it. This is the standard arrangement in Devonian dipnoans in which this region is preserved, and it is clearly the primitive condition. In addition to the extensive dental apparatus, the important osteological features associated with this type of organization are the steeply inclined front wall of the gill chamber (generally referred to as the steeply inclined quadrate), the short parasphenoid which roofs the posterior end of the buccal cavity, and the large operculars.

Lung respiration requires a large number of modifications to these systems. Observations of *Lepidosiren paradoxa* during respiration permits these modifications to be outlined clearly (Bishop & Foxon 1968). The basic breathing operation involves swimming to the surface, opening the mouth to emit air expelled from the lungs, then gulping new air into the buccal cavity, which expands as the hyoid arch and pectoral girdle drop and the opercular slits close, and finally closing the mouth and raising the hyoids and pectorals to force the trapped air down into the lungs. The functional requirements are a large buccal cavity whose volume can be increased dramatically by movement of the hyoid and pectoral systems, effective seals at the anterior end of the mouth and around the posterior and ventral edges of the gill chamber, and a reduction of the size of the gill chamber.

Lepidosiren has met these requirements by the following morphological changes:

(i) the tooth plates are situated anteriorly and occupy only a small part of the buccal cavity;

(ii) the jaw articulation has moved forwards with the consequence that the quadrate is very obliquely inclined;

(iii) a deep cavity is present between the tooth plates posteriorly and this is roofed by soft tissue. The connective tissue pad of the 'tongue' fits into this cavity and forms an effective seal preventing the expulsion of gulped air when the buccal cavity contracts;

(iv) the size of the posterior end of the buccal cavity is expanded and this is accompanied by the development of a long broad stem on the parasphenoid;

(v) the hyoid arch, and particularly the ceratohyal, is large and highly mobile; when it drops it distends the ventral surface of the buccal cavity;

(vi) the pectoral girdle extends forwards beneath the reduced gill chamber and it drops in sequence with the hyoid to distend the posterior part of the buccal cavity;

(vii) the opercular slit is greatly reduced, as also is the size of the opercular cover.

These considerations have implications for the interpretation of *Uronemus* in particular, but also for dipnoan evolution in general. *Uronemus* is found in non-marine, coal-measure sediments. Although the gill arches have not been preserved to provide a check on the pattern of gill respiration, the environment in which members of the genus lived would be consistent with an air-breathing habit. The following morphological features are relevant to this interpretation: the jaw articulation is well forwards; the tooth plates occupy only a small part of the buccal cavity; the median part of the palate has no attached denticles and presumably was covered by soft tissue against which a 'tongue pad' could form a seal; there is a deep medial space in the lower jaw into which a 'tongue' and associated connective tissues and muscle would fit; no basihyoid–basibranchial tooth plates that would interfere with the sealing function of a 'tongue' were present; the parasphenoidal stalk is long and broad, extending well behind the posterior end of the roofing bones; the pterygoids are expanded widely behind the tooth plates and form a broad, high arch with the parasphenoid, thus defining a very large posterior buccal cavity; the ceratohyals are large.

The above positively identified features of *Uronemus* are shared with most non-marine late Palaeozoic dipnoans (see Westoll 1949). Even those genera that retained extensive tooth plates, e.g. *Sagenodus*, have a deep space between the posterior end of the plates into which a 'tongue' would fit to make a seal. Features such as the long parasphenoid, reduced operculars and gulars, lightly ossified pectoral girdles, and obliquely inclined quadrates, have been well known for a long period of time. They are probably all associated with the adoption of air breathing, and this in turn was associated with a change from a marine to a freshwater environment.

We wish to draw attention to several important concomitants of the above conclusions. Genera such as *Uranolophus* and *Griphognathus* have smoothly arched denticulate palates with the denticulation extending back onto the parasphenoid, and denticulate basihyal–basibranchial tooth plates. If a 'tongue' was present, and we consider that to be improbable, it would not have been able to form a seal sufficiently far forwards in the buccal cavity to produce a significant reservoir of air that could be forced into the lungs. This is consistent with the view that these genera were dependent on gill respiration. Their ceratohyals were large because they were involved with the use of basihyal–basibranchial plates for feeding; those of *Uronemus* were large because they were involved with lung respiration. It could be anticipated that the muscle attachment surfaces on the two groups would be different. This cannot be checked at present because this detail of *Uronemus* remains unknown.

A further consequence relates to the cheek structure in the non-tooth-plated or denticulate group that includes *Uranolophus* and *Griphognathus*. As pointed out by Campbell & Barwick (1987) a large fleshy cheek is a feature of that group. It has been interpreted as a device for collecting partly processed food and returning it to the buccal cavity. No such cheeks are known in living species and they were clearly not present on genera such as *Chirodipterus*, *Dipterus* and *Scaumenacia*, for which complete cheek-bone series are known. This difference between the two stocks now becomes understandable. The extant genera suck in food and then spit it out in a cloud of mucus in a series of discrete protrusions. These appear to be controlled by the action of the 'tongue' pushing the food out between bites. It is then sucked in again and the process repeated. Bemis & Lauder (1986) have published morphological and electromyographical data on feeding mechanisms of *Lepidosiren*. In that paper they describe the hydraulic transport system, with water movement mediated by the hyoid apparatus and suggest that it is analogous to the functions of the tetrapod tongue. As they conclude, the hyoid apparatus is a fundamental part of the mechanism of food transport. It is, therefore, appropriate to comment that the control of food transport is not under the direction of a muscular tongue as in tetrapods but is under the control of the muscles associated with elevation and lowering of the hyoid apparatus. If the denticulated genera had no 'tongues', such a protrusion would have been impossible unless the same function was performed by a forward push of the whole basibranchial system. In any case there would be no point in such an action because in such genera as *Griphognathus* there was no biting surface to pulverize the food between protrusions. The cheek pouch system is a more efficient alternative for denticulate feeders because of the marginal ridges.

(*f*) *Relationships of Uronemus*

With the recognition that *Uronemus* is a member of the large group of lungfishes characterized by the presence of pterygoid and prearticular tooth plates, and not of the group with a dentition of variously formed marginal ridges and a shagreen of denticles that are episodically shed during growth, its relationships must be reconsidered.

Following the discussion of tooth plates in §5(*b*) and denticles in §5(*c*), we conclude that *Uronemus* is not closely related to the Devonian genera *Uranolophus* and *Griphognathus*, nor to the Carboniferous *Conchopoma* as proposed by Miles (1977, p. 298). Miles (1977) and Campbell & Barwick (1987) also considered that the denticulated palate indicated a relationship with rhynchodipterids and fleurantiids, although their arguments for doing so were differently based. Graham-Smith & Westoll (1937) had earlier drawn attention to a possible relationship between *Uronemus* and *Fleurantia* because of the shape of the parasphenoids, the form of the radial rows of 'teeth' and the presence of denticles. We consider, in the present discussion, that the 'teeth' of *Fleurantia* are radially arranged, enlarged denticles that are shed in the manner of normal denticles. Consequently *Fleurantia* should be regarded as a specialized member of the denticulate group, and is not closely related to *Uronemus*.

With acceptance of the conclusion that the dentition of *Uronemus* is derived by modification of a form with tooth plates it is necessary to consider its relationships with genera in which tooth plates are recognized. In the most recent discussion of the phylogeny of tooth-plated dipnoans, Miles (1977) considered *Dipterus valenciennesi* to be the most primitive lungfish with radiate tooth plates. In the light of recent information on tooth plates and the description of a new genus with tooth plates (Campbell & Barwick 1983), this statement now needs to be modified to consider *Speonesydrion iani* Campbell & Barwick to be more primitive than *Dipterus*. The tooth plates of *Dipterus* contain petrodentine (Smith 1984), and each tooth has a small pulp chamber between the growing fronts of petrodentine and the bone. This tissue develops in each new tooth added to the lateral margin of the tooth plate, as described also in *Sagenodus inaequalis* (Smith 1979*a*). Both these characters, petrodentine and separate pulp chambers, are considered to be early-derived characters within tooth-plated genera. In the Lower Devonian species *Speonesydrion iani*, the form of the tooth plates is similar to that of *Dipterus*, with teeth arranged in radial rows and new teeth added laterally; however, petrodentine is absent and pulp chambers are not conspicuous. Petrodentine is present in all other dipnoan tooth plates (Smith 1984) and has now been shown to be present in each new tooth added to the lateral margins of the modified tooth plate in *Uronemus*. It is also a major part of the worn tooth ridge in *Uronemus*, just as it is an integrated tissue in the worn regions of all tooth-plated forms. Further, a small pulp chamber exists between the petrodentine and the bone. *Speonesydrion* must now be regarded as the most primitive known dipnoan with radiate tooth plates, and *Dipterus* the most primitive known form with petrodentine. Petrodentine is not known in any denticulate genus. A discussion of the presence or absence of petrodentine in *Holodipterus*, a genus assigned by previous workers to the denticulate group, is given in Campbell & Smith (1987), together with an analysis of the morphology and growth of its dentition. In that paper *Holodipterus* is shown to have had a radiate dentition that simulated tooth plates, and teeth that consisted of compact hard tissue with similarities to petrodentine, but with differences that may be significant.

In addition to petrodentine, *Uronemus* has a layer of enamel enveloping parts of the plates, and well-separated pterygoid plates, all of which indicate a more evolved condition than that found in *Dipterus valenciennesi*. On the other hand, it does not have the totally enveloping marginal enamel layer, the more regularly arranged pulp canals in the dentine, or the extensive continuous pulp chambers characteristic of *Sagenodus* and *Ctenodus*, and in these respects, at least, it is more primitive. On the other hand, *Uronemus* shares with these genera such derived characters as (i) the loss of bone A, (ii) the presence of the occipital commissure in bone B, and (iii) possibly the integration of bone Z into the skull roof. We are dubious about the last point because no specimen with this part of the skull well preserved is known to us. However, characters (i) and (ii) are not necessarily indicative of immediate relationship because they have appeared in independent evolutionary lines. For example, they occur in *Jarvikia* which is a member of the denticulate group related to *Fleurantia*. *Fleurantia* itself shows evidence of an approach to this condition in that Graham-Smith & Westoll (1937) found some individuals with the commissural canal in bone B, others with canals in bones A and B, and still others with a canal apparently restricted to bone A. Consequently, we do not consider that characters

(i) and (ii) contradict the evidence from tooth plates that *Uronemus* evolved independently of *Ctenodus* and *Sagenodus*, although it would be possible for all three genera to be derived from a form in which bone A had been lost and the commissural canal had become incorporated in bone B.

The significance of these points is that they demonstrate *Uronemus* to be more derived than *Rhinodipterus*, *Scaumenacia*, *Phaneropleuron* and probably *Oervigia*. These four genera, with *Chirodipterus*, occupy a position on the cladogram of Miles (1977, figure 157) between *Dipterus valenciennesi* and *Ctenodus/Sagenodus*, but Miles (1977) was unable to characterize the nodes by which they are positioned on the cladogram. We are able to improve on this part of the cladogram with only one firm statement: that *Uronemus* is placed above *Rhinodipterus*, *Oervigia*, *Phaneropleuron* and *Scaumenacia*. A similar conclusion is reached from an analysis of the Y–X–K region of the skull roof. *Uronemus* is derived in having few bones covering this region. *Chirodipterus* is not discussed by us in this context because, after a detailed analysis of the dentition, it is not considered to have comparable radiate tooth plates. Instead, it has distinctively constructed dentine plates (Smith & Campbell 1987). In that paper the concept of these two types of dentition evolving along divergent lines is discussed.

In addition to these genera, Miles (1977) has considered the gnathorhizids to be derived earlier than *Ctenodus* and *Sagenodus* but later than *Rhinodipterus* and the phaneropleurids, and consequently we feel obliged to make reference to the gnathorhizids. Miles (1977) united *Ctenodus* with its more derived relatives like *Sagenodus* on the basis of the form of the parasphenoid. *Uronemus* and the Permian genus *Gnathorhiza* do not share this character, and they were therefore considered to be less derived than *Ctenodus/Sagenodus*. However, *Gnathorhiza* has several remarkable specializations of the skull roof, such as the large medial bone in front of the paired C bones, the large lateral line bone above and in front of the orbit with the concomitant loss of bones 3 and 2, and the modification of the relative positions of bones I and Y. We see no feature of the skull roof that would enable us to relate this genus directly with *Uronemus* or any of the genera previously discussed. It is more derived than any of them. The tooth plates of the gnathorhizids, assuming that Miles (1977) is correct in placing *Gnathorhiza* and *Monongahela* together in the same family, are also uniquely specialized. The gross form of their plates has been described by Berman (1979) and by Lund (1973) respectively. Both genera have much reduced, well-separated, pterygoidal plates, and deep embayments on the lateral margins separating a few strong tooth-bearing ridges. The histology of the plates of *Gnathorhiza* is poorly known (Dension 1974, figure 15), but *Monongahela* has been described and figured by Denison (1974, figures 12 and 13). Its plates have a large basal pulp cavity, high columns of petrodentine forming the core of each tooth, and a distinctive array of dentine tubules. Neither the gross structure nor the histology suggests a close relationship between the gnathorhizids and any other Palaeozoic dipnoans. Moreover, the above data do not enable us to be more constructive with regard to relationships of the gnathorhizids than Miles (1977) was in his cladogram. From this discussion it is apparent that we are unable to place *Uronemus* in a definite position on the cladogram proposed by Miles (1977), but we can propose that *Uronemus* is more derived than all genera below the phaneropleurids, and is probably most closely related to the *Ctenodus/Sagenodus* assemblage. We anticipate that the complete redescription of *Uronemus* will provide the additional data necessary for a more complete statement on its relationships.

6. CONCLUSIONS

(1) *Uronemus*, previously considered to have a primitive dentition of marginal ridges around a denticulate palate and to belong to the denticulate lineage of dipnoans (Campbell & Barwick 1983, 1987), is shown to have laterally compressed tooth plates and a restricted distribution of palatal denticles. Therefore it is considered to be a derived member of the tooth-plated lineage.

(2) The palatal tooth plates of primitive Dipnoi met in the midline (*Speonesydrion*), but in more evolved forms they became widely separated. *Uronemus* has a highly derived condition in which the palatal tooth plates are so widely separated that they are restricted to the margins of the pterygoids. This condition is associated with the development of a shearing bite.

(3) The presence in *Uronemus* of denticles that were shed in an irregular fashion throughout growth is considered to be the result of the re-covering of part of the pterygoids as the tooth plates became progressively more lateral in position. The absence of denticles from the palatal midline and the mandibular lingual furrow indicates the presence of soft tissue in these regions. A large anteriorly placed 'tongue' and associated connective tissues were probably present, judging from the arrangement in extant genera. There is no evidence of basihyal–basibranchial tooth plates. It is argued that the 'tongue' would have met the soft tissues of the palate to seal the large buccal chamber while air was being forced into the lungs by raising the hyoid and pectoral systems.

(4) The presence of shedding denticles cannot be taken as indicating a primitive dentition *per se*. They must have developed in the skin of the buccal cavity of locations where they were effective in serving a variety of functions. The presence of shedding denticles is considered to be a secondary acquisition and not a character linking *Uronemus* with those genera with a primitive dentition.

(5) The dentitions of the denticulate lineage are characterized by the repeated complete or partial resorption of marginal ridges and tusks, as well as by the presence of a cover of shedding denticles on the pterygoids, parasphenoids, prearticulars, and basihyal–basibranchial 'tooth plates'. As we have demonstrated, none of these characters is found in *Uronemus* and therefore a relationship with denticulate genera is not accepted.

(6) A number of denticle-bearing bones and isolated denticles preserved around the anterior end of the palate are taken to represent a covering in the skin over the ventral surface of the nasal capsules. These occlude with the denticulate dentary. Their size and number, together with the unossified nature of the snout, indicate that they developed in response to the special requirements of the bite. They do not indicate a relationship with such genera as *Griphognathus* and *Holodipterus*.

(7) Many of the well-known features of the evolution of tooth-plated dipnoans, such as the inclination of the quadrate, extension of the parasphenoid, restriction of the tooth plates to the anterior part of the buccal cavity and reduction of the pectoral girdle, are interpreted as resulting from the adoption of air breathing after an initial period of evolution during which they were entirely dependent on gill respiration.

(8) The sectorial occlusal relations of the tooth plates of *Uronemus*, with the lingual ridge of the prearticular biting outside the lingual ridge of the pterygoid, are very distinctive and may be unique among dipnoans, though further work on *Oervigia* is needed to check this statement. Although in *Griphognathus* the marginal mandibular ridge bites outside the palatal margin, the

arrangement of the bite is dissimilar to that of *Uronemus* in all other respects. Moveover, the marginal ridges in *Griphognathus* are not formed of true teeth, but of irregular bodies of dentine that are remodelled during the life of the animal.

(9) Derived features of the skull roof of *Uronemus* are the absence of bone A, the presence of the canal in bone B, and the single bones in the K–Y_1 and the L–M spaces. The assignment of the genus to the tooth-plated group with secondary palatal denticles simplifies the problems of skull roof evolution that result from placing it with rhynchodipterids on a cladogram, as was done by Miles (1977).

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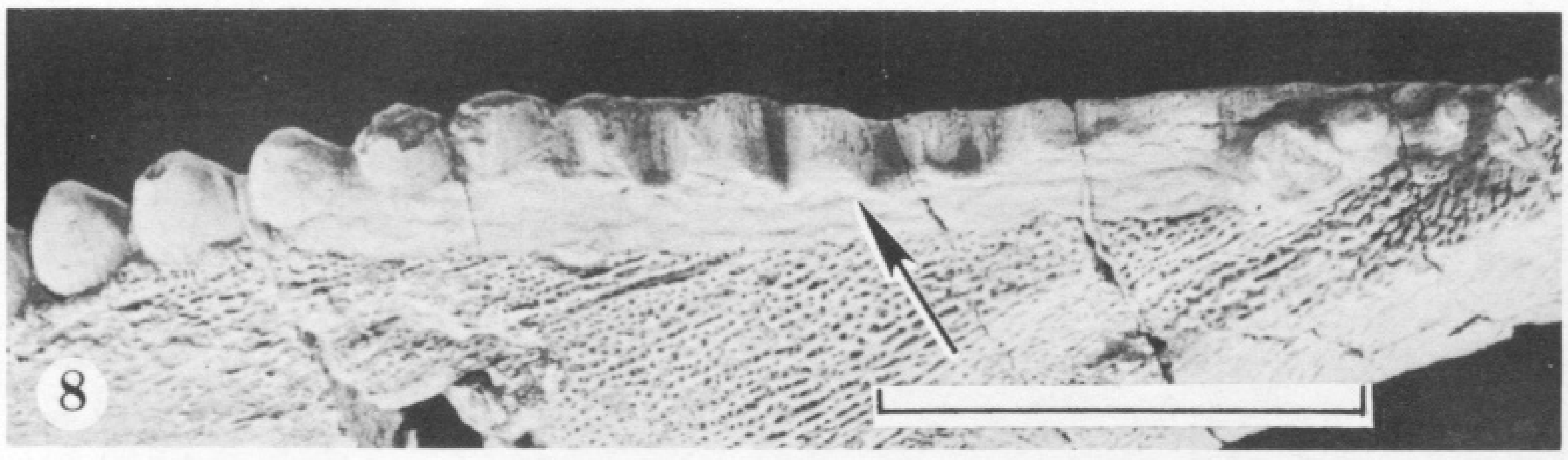
ABBREVIATIONS USED ON THE FIGURES

bo.	bone	pa.	pallial dentine
d.	dentine	p.cav.	pulp cavity
den.	denticles	p.c.	pulp canal
d.ri.	dentine ridge	p.d.	petrodentine
en.l.	enamel layer	pl.	pleromic dentine
g.	growth zone	p.s.	pulp space
g.l.	growth lines	t.	tooth
i.d.	interstitial dentine	t_1, t_2	first, second, etc. tooth in lingual row
lin.t.r.	lingual tooth ridge	w.en.l.	worn enamel layer
new ant.t.	new anterior tooth	w.t.	worn tooth
new lat.t.	new lateral tooth	S_1, S_2, S_3	sequence of three sections

FIGURES 1–7. For description see opposite.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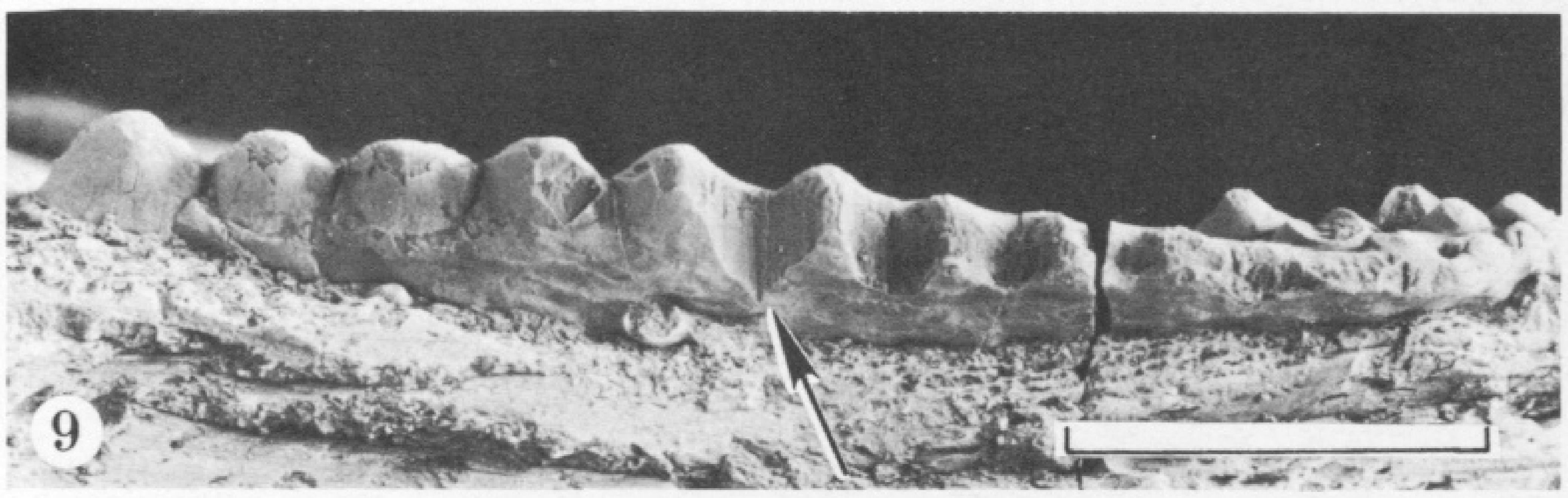
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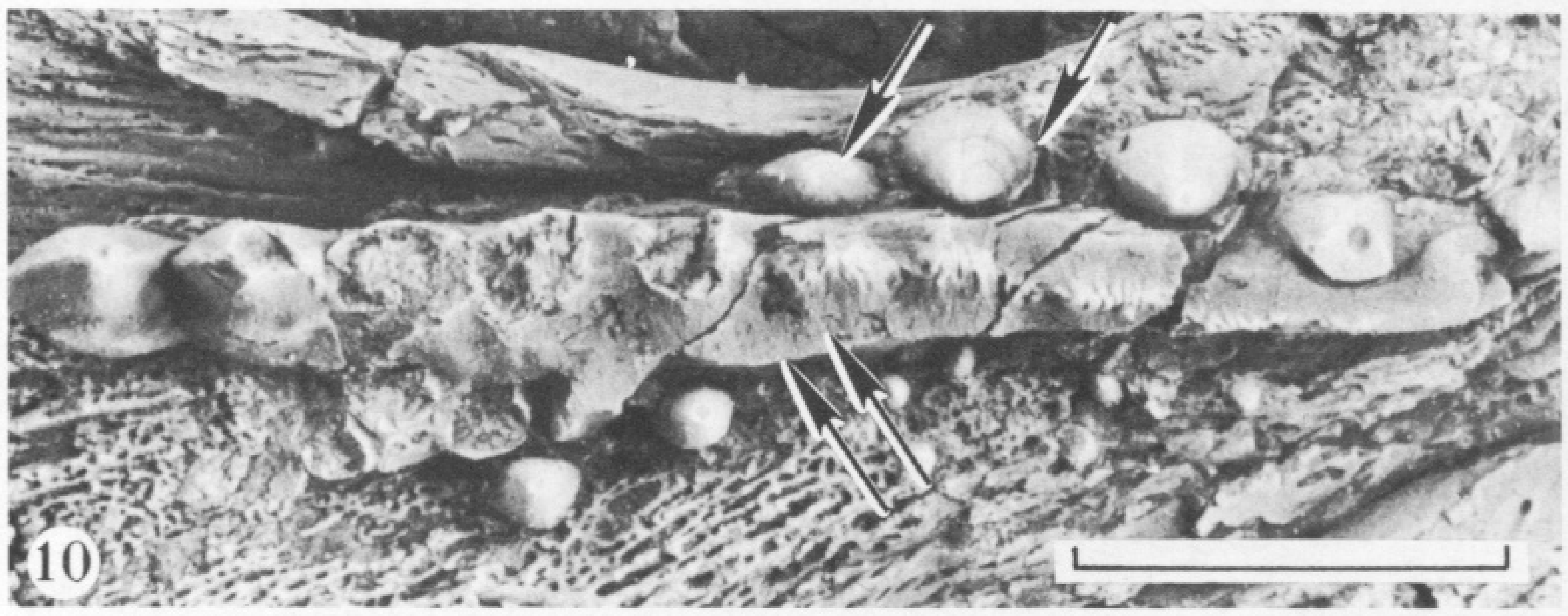
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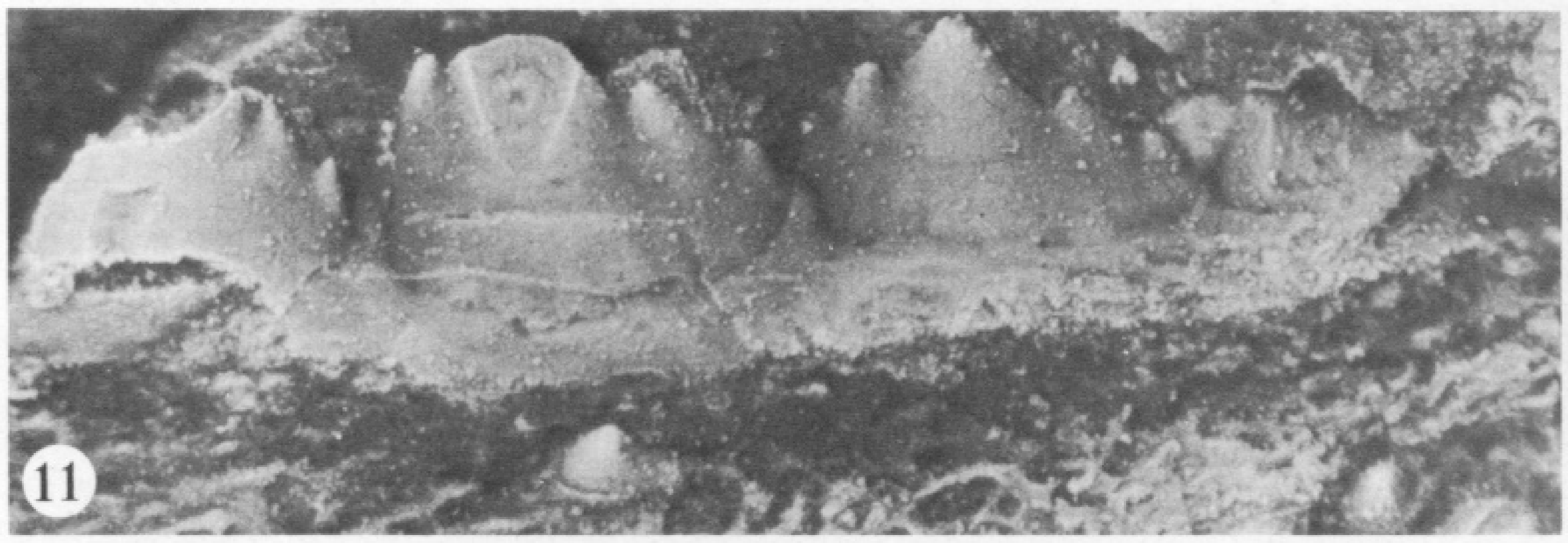
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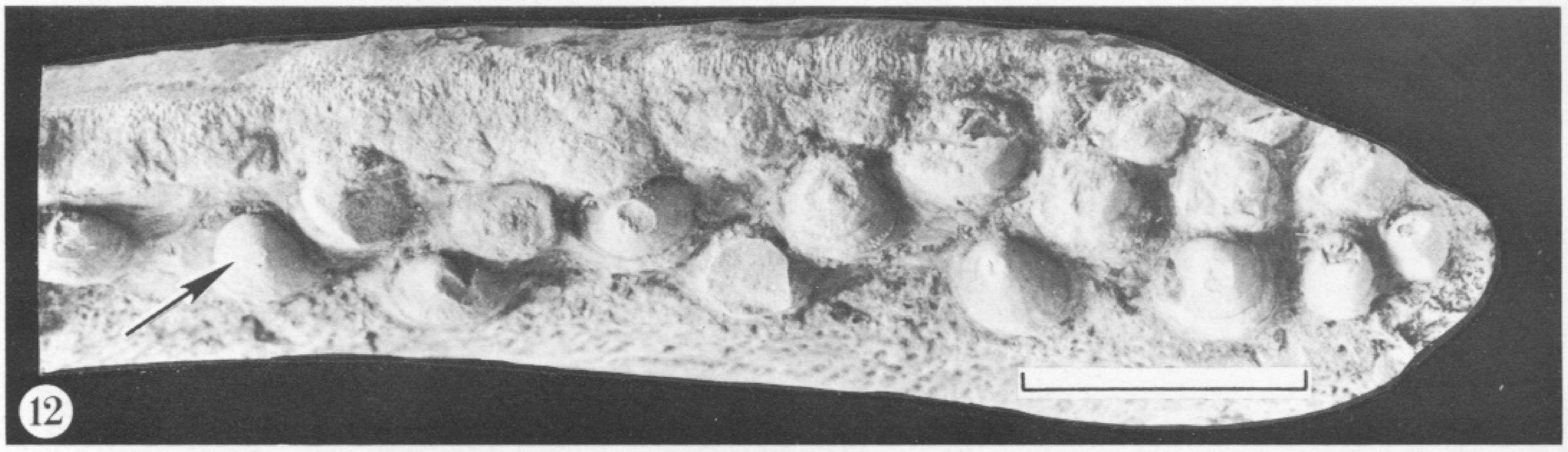
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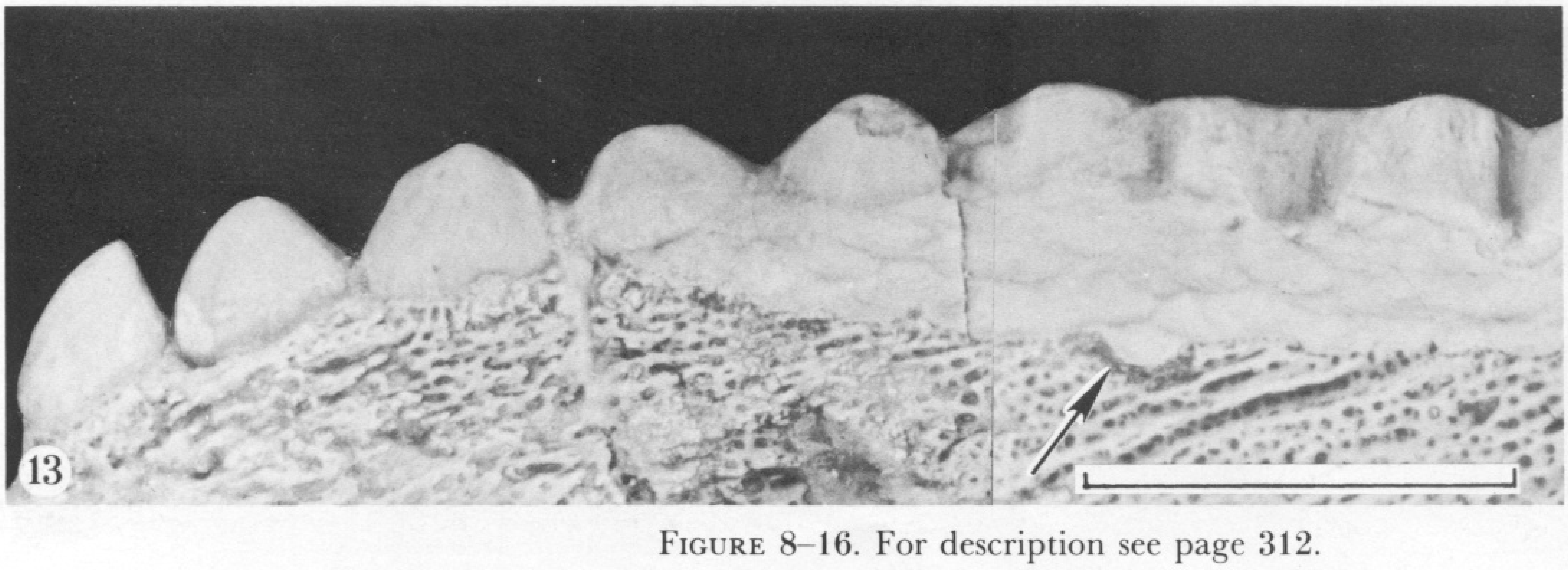
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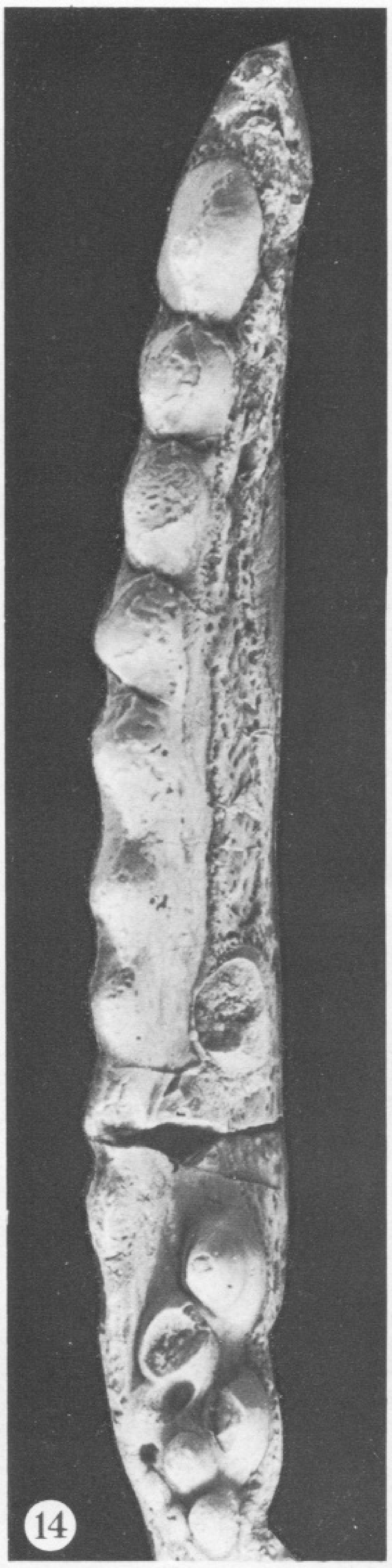
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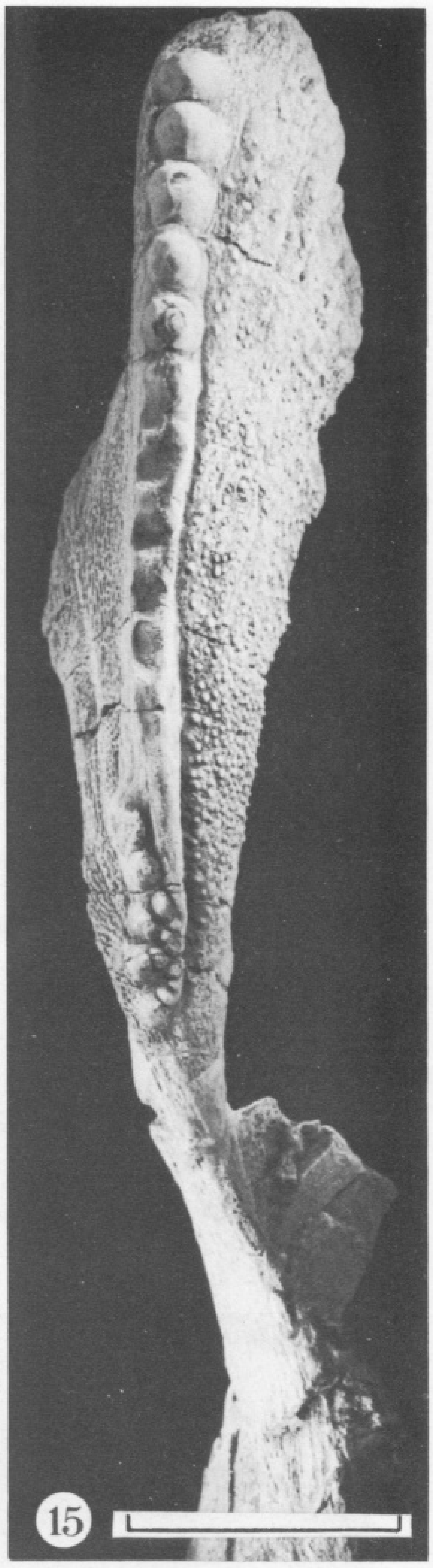
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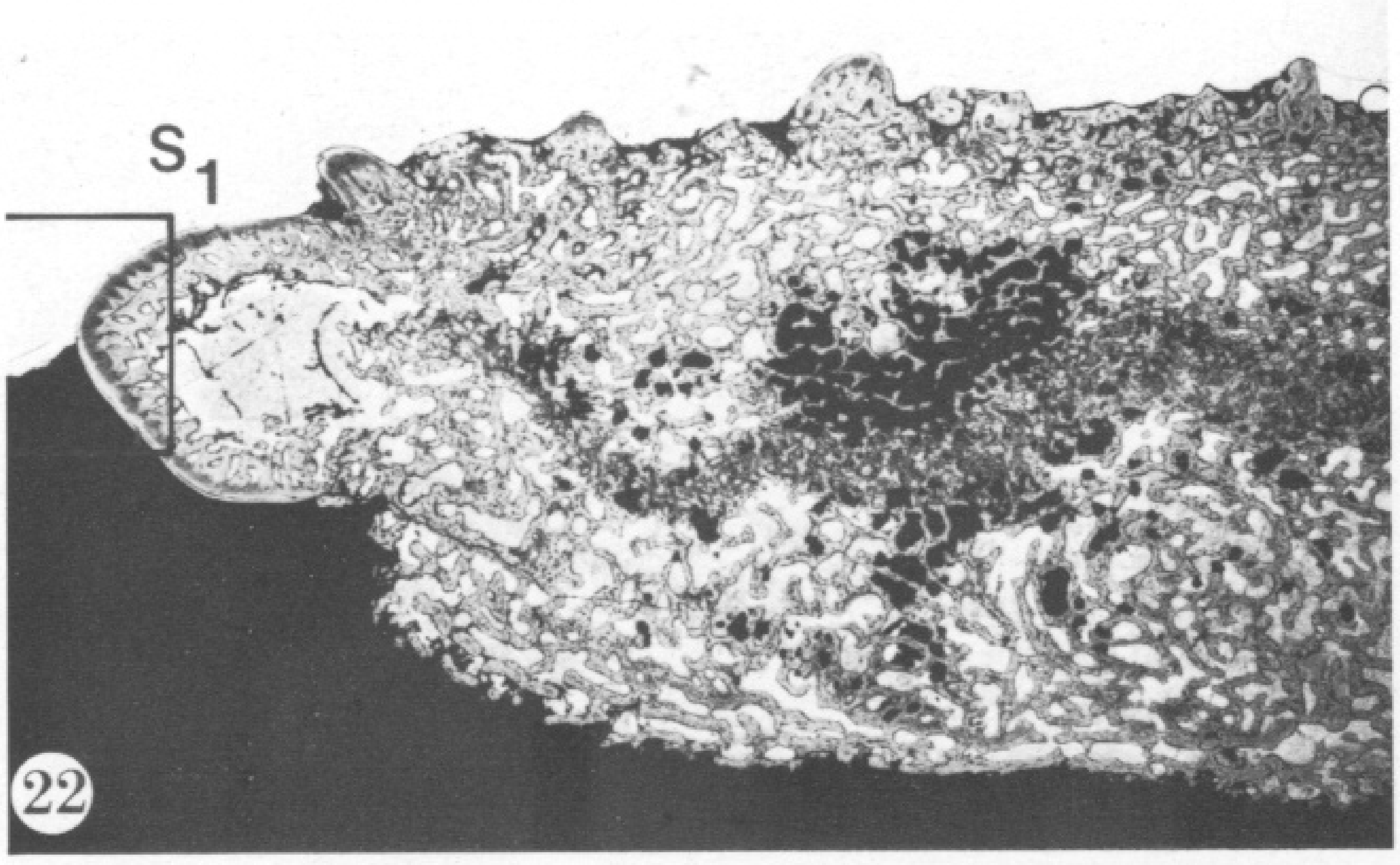
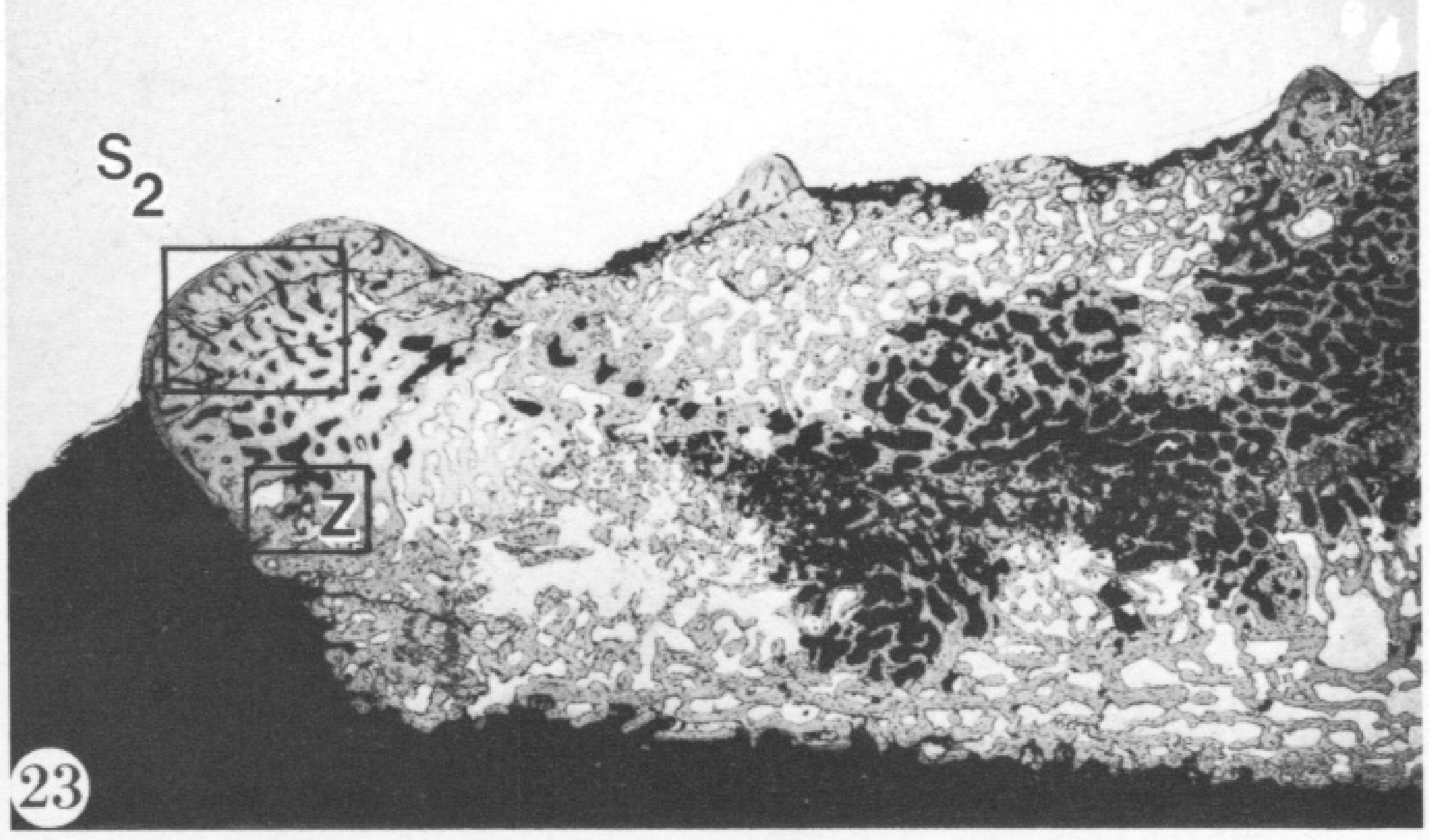
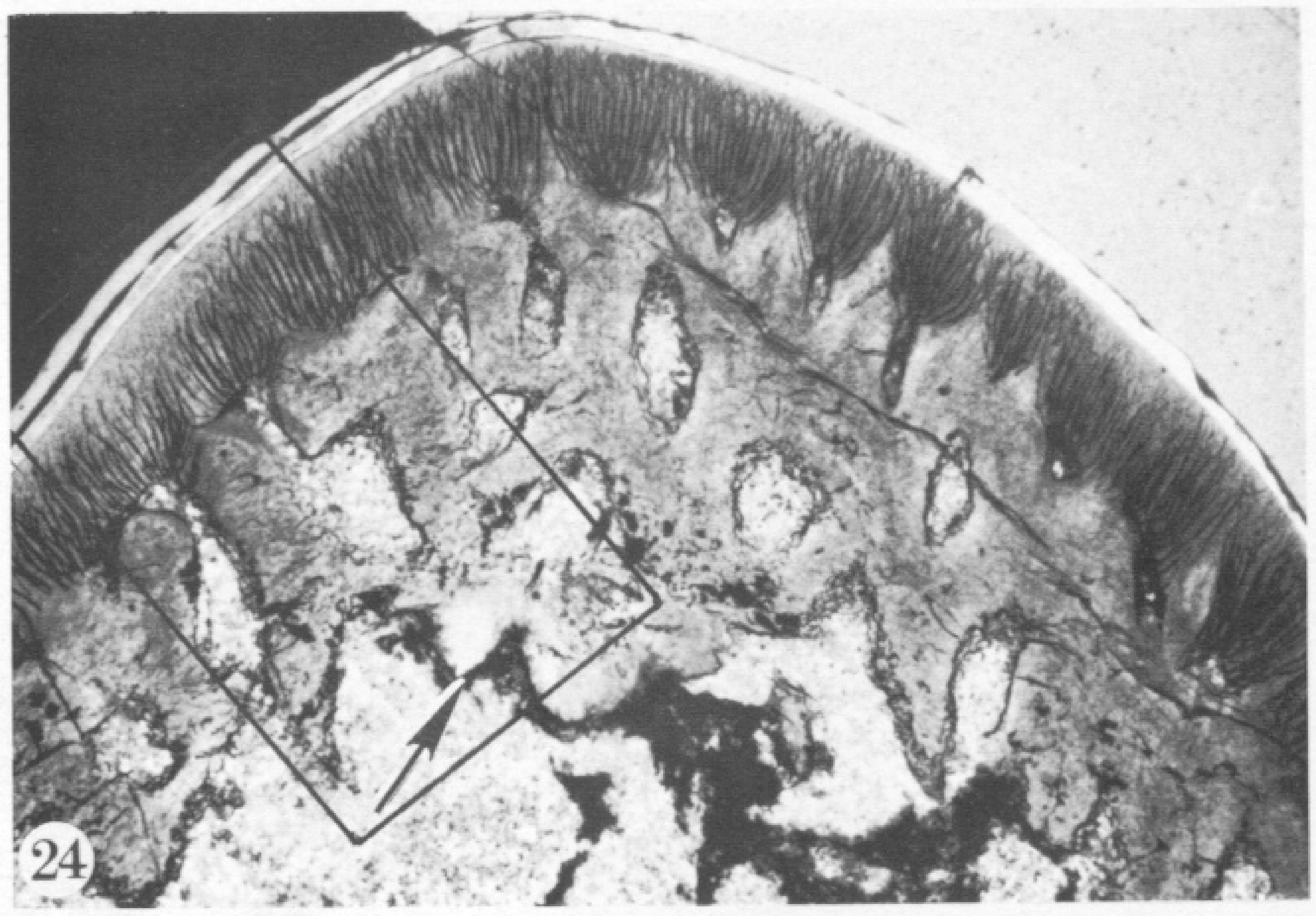
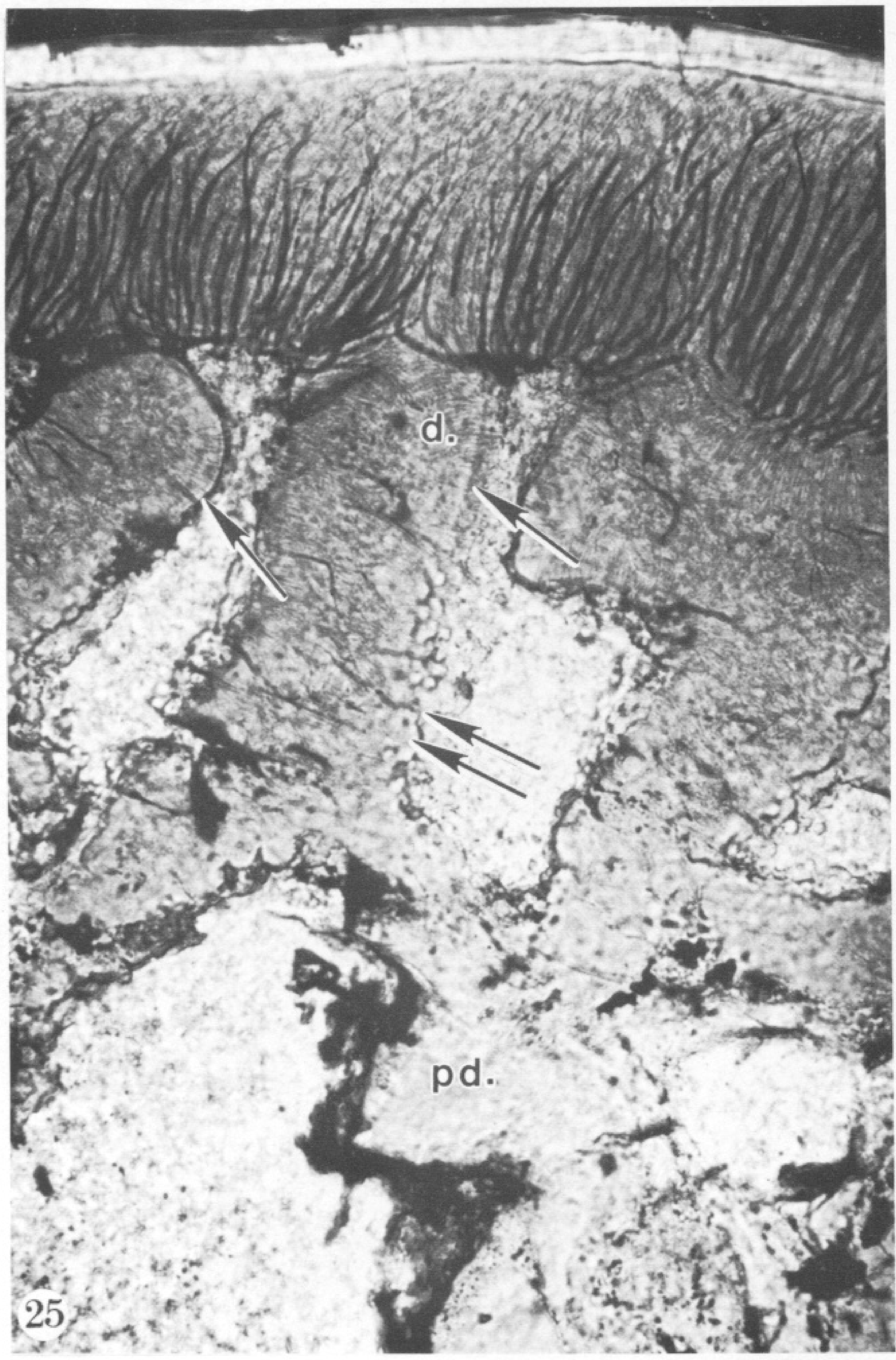
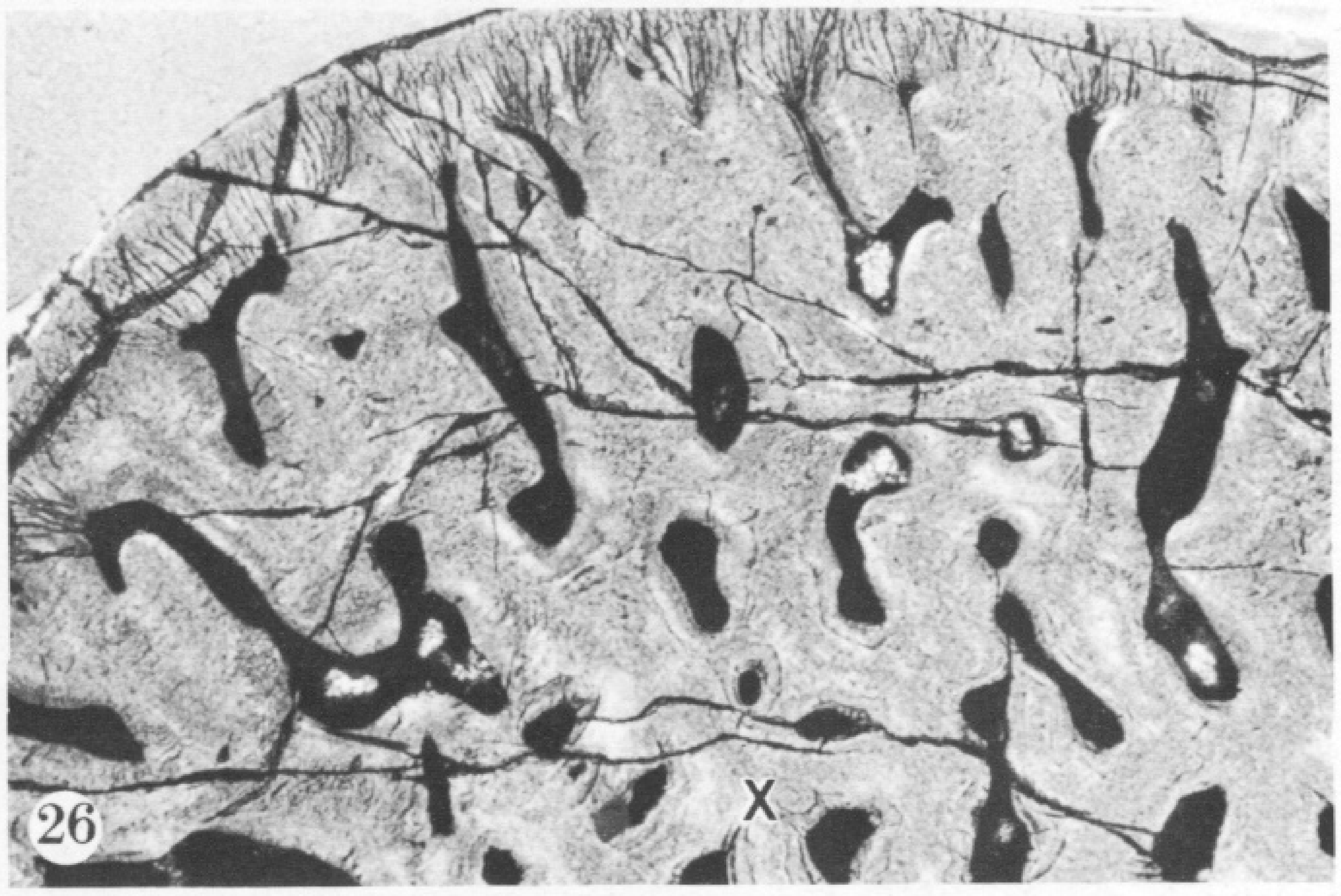
FIGURE 8–16. For description see page 312.

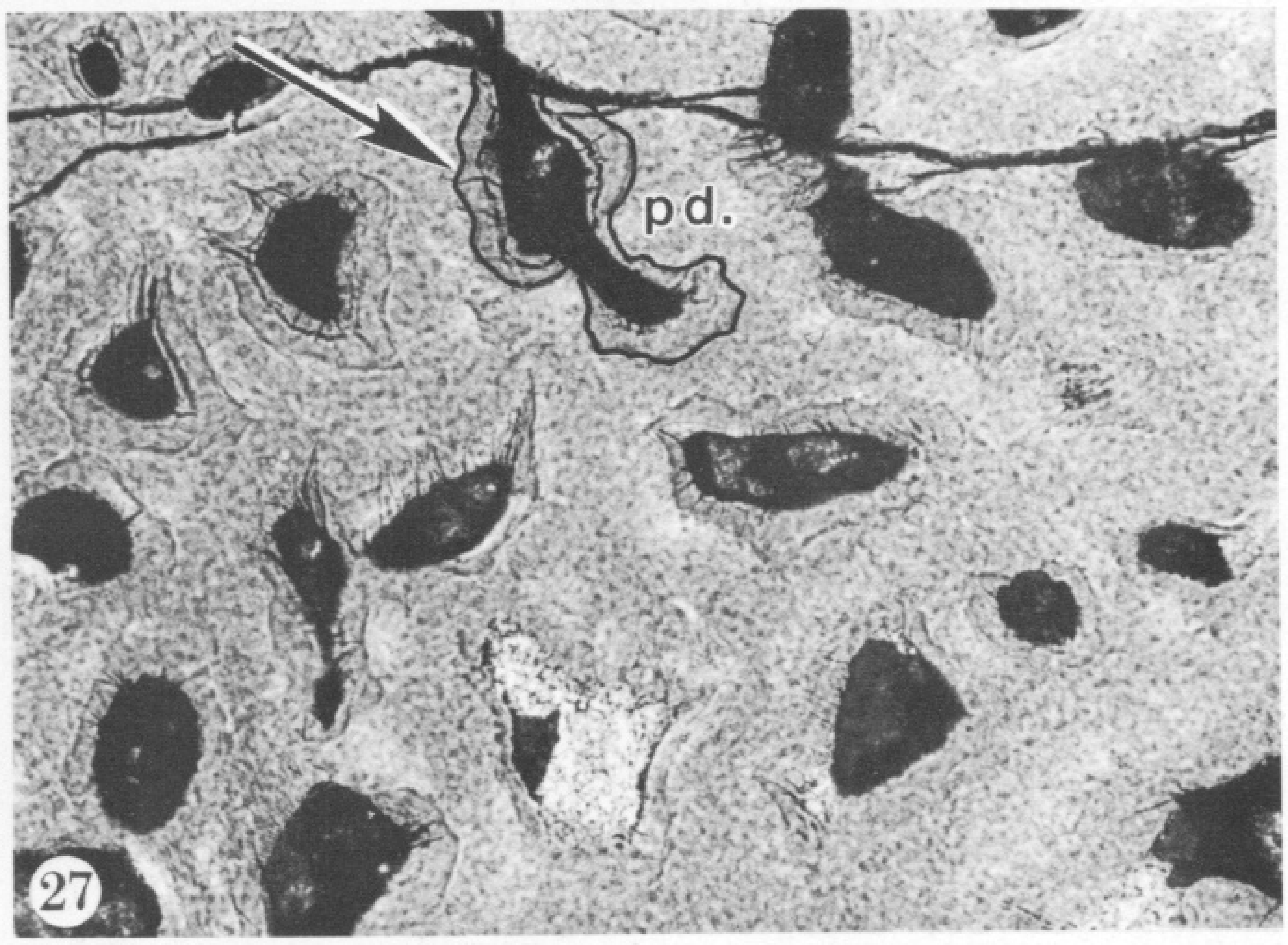


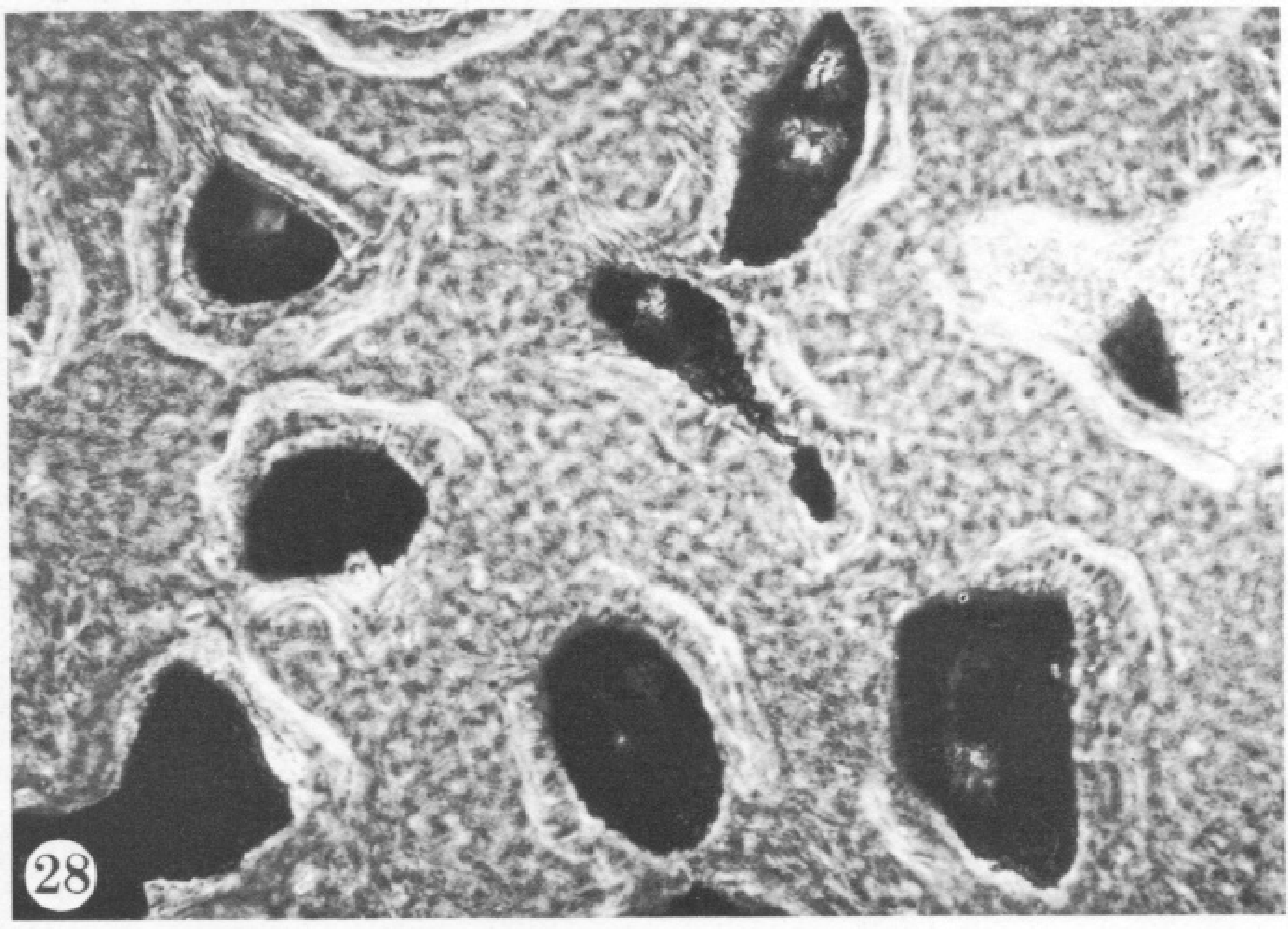




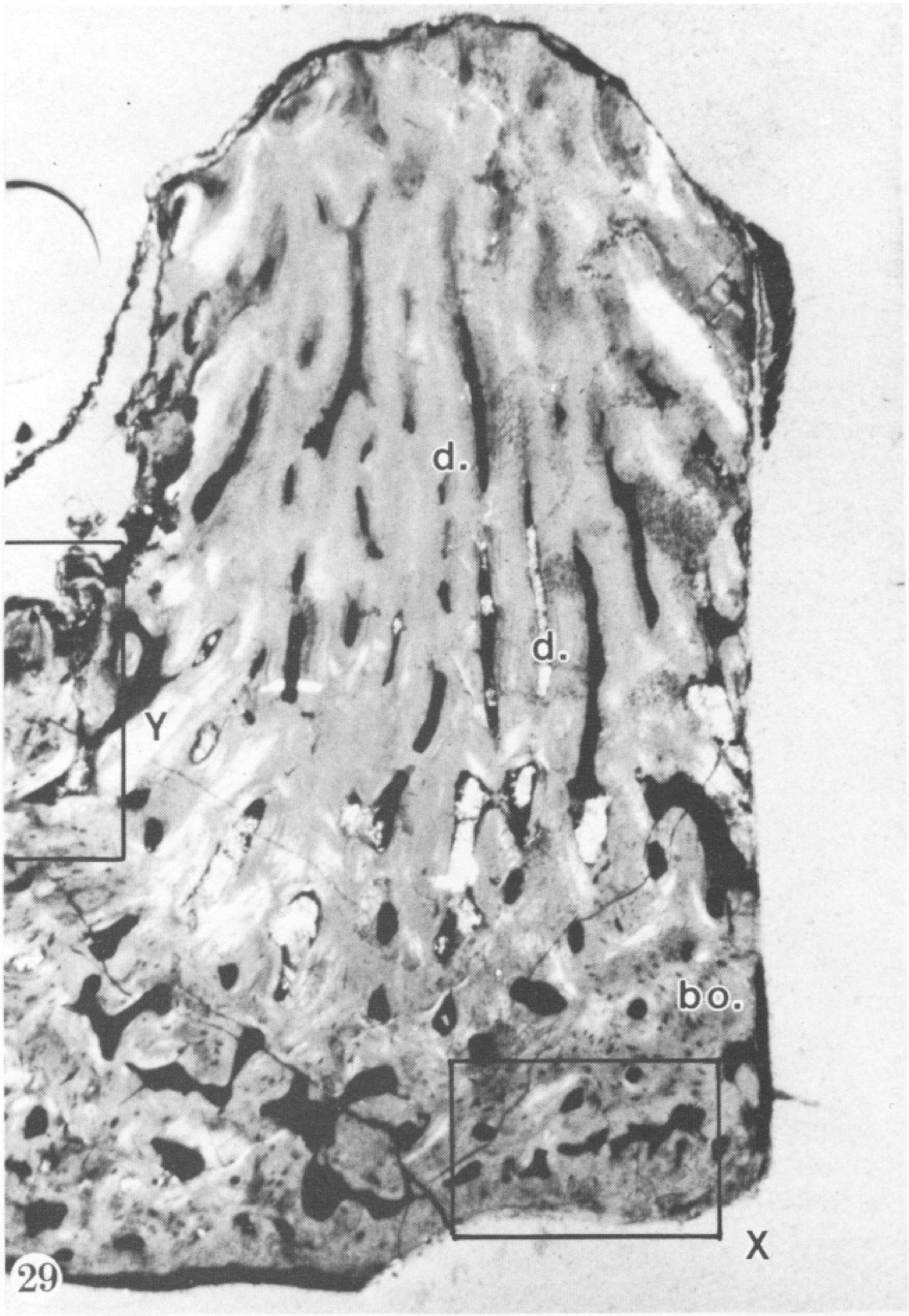


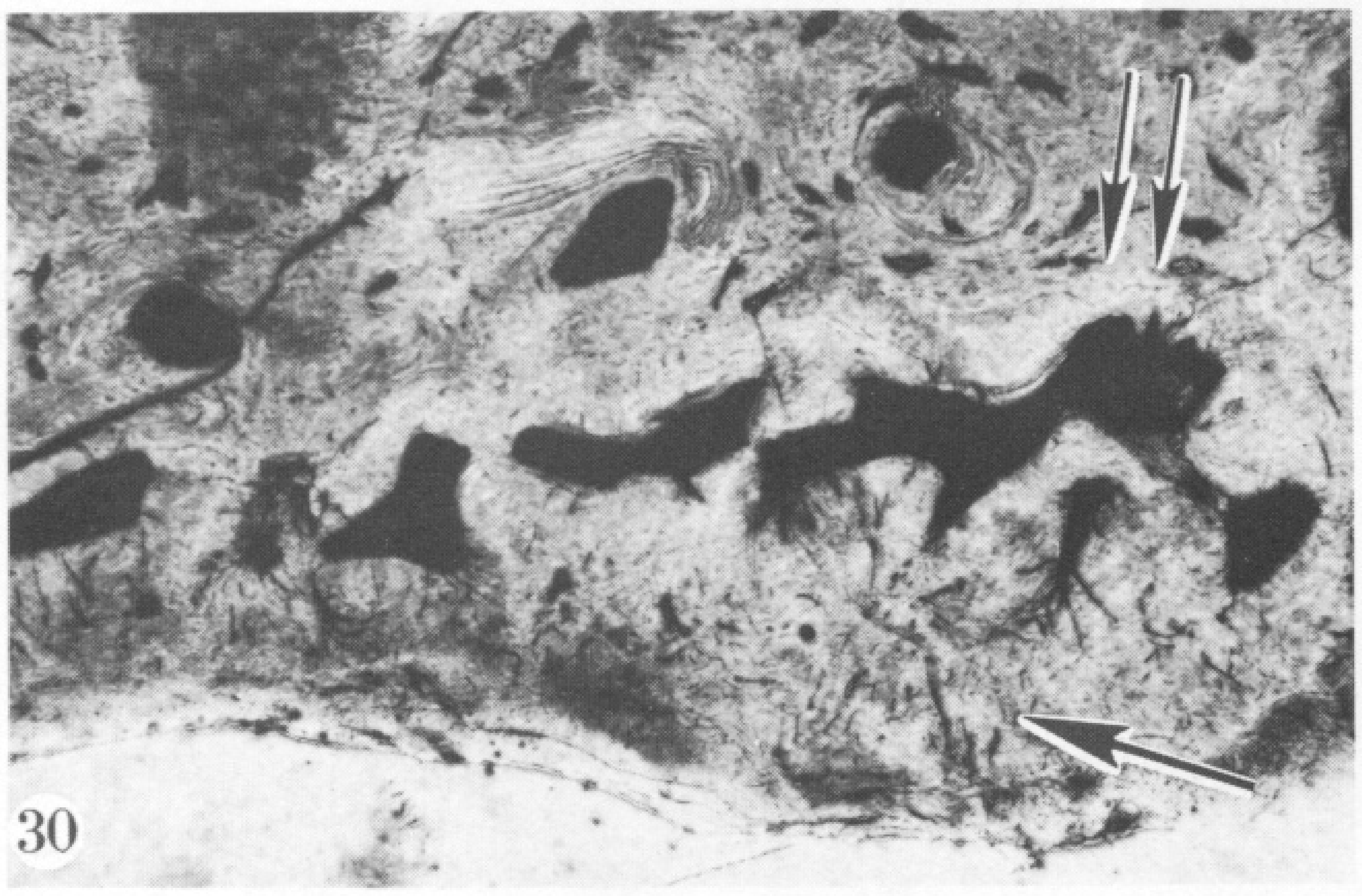


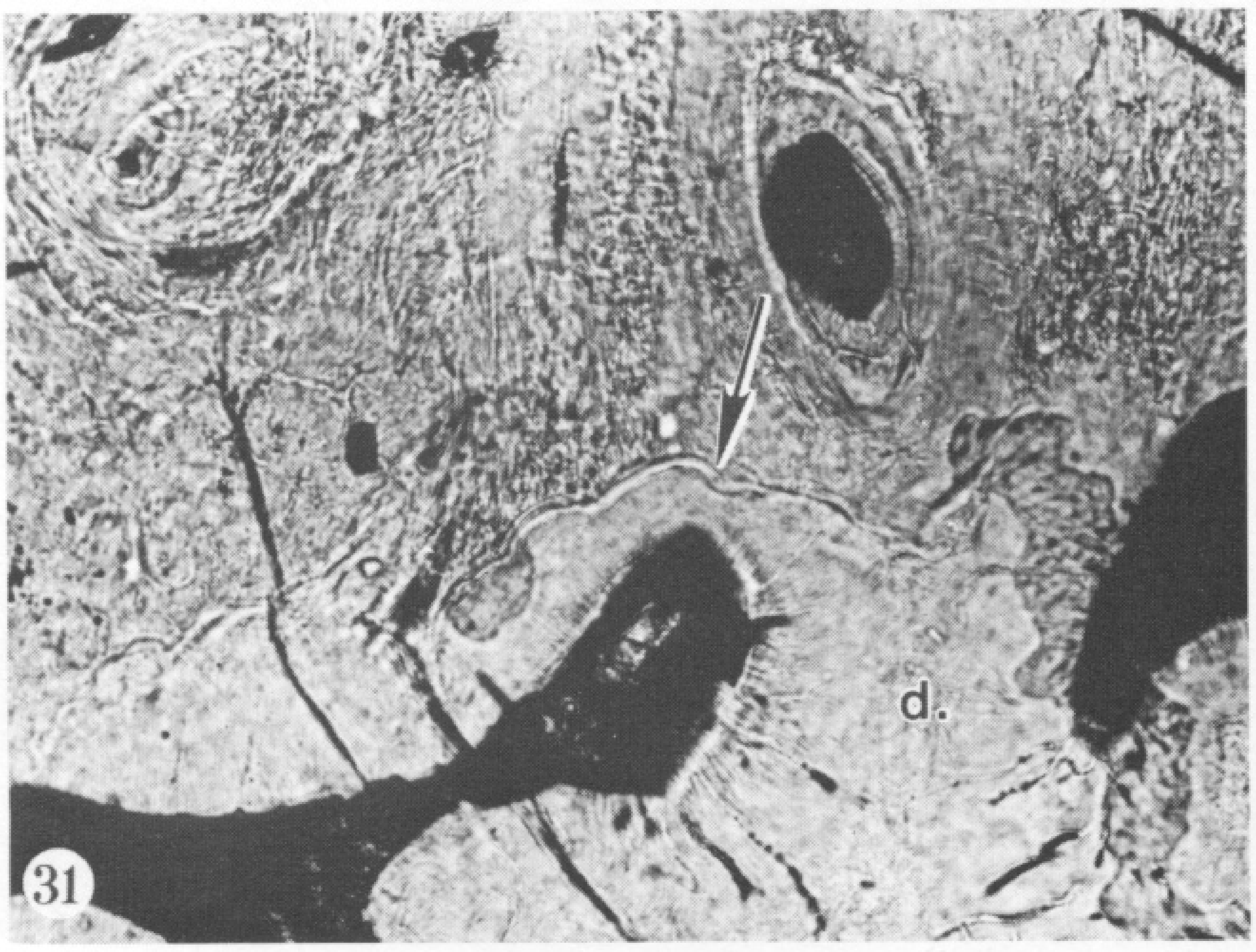


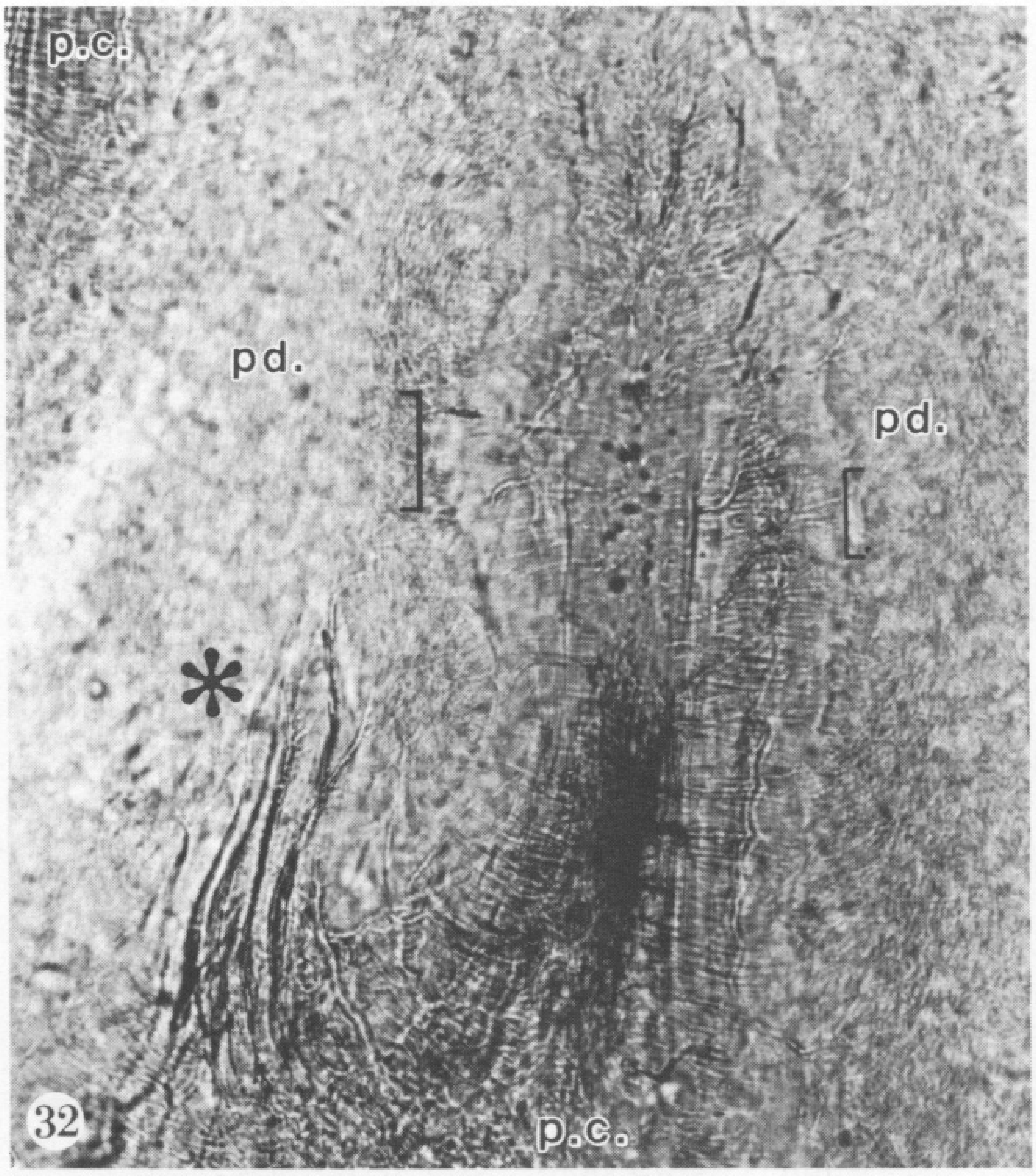


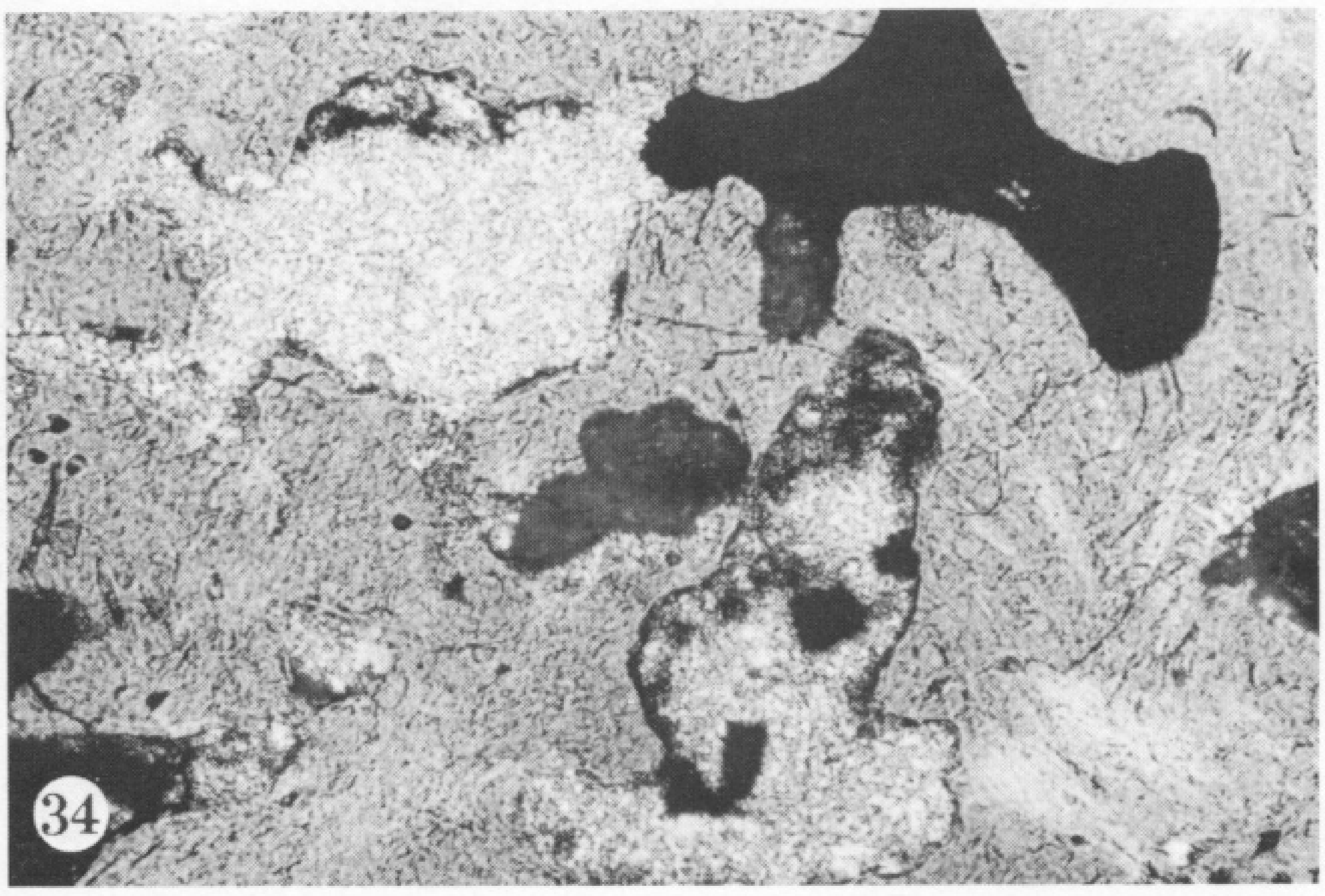
FIGURES 22–28. For description see facing plate 4.



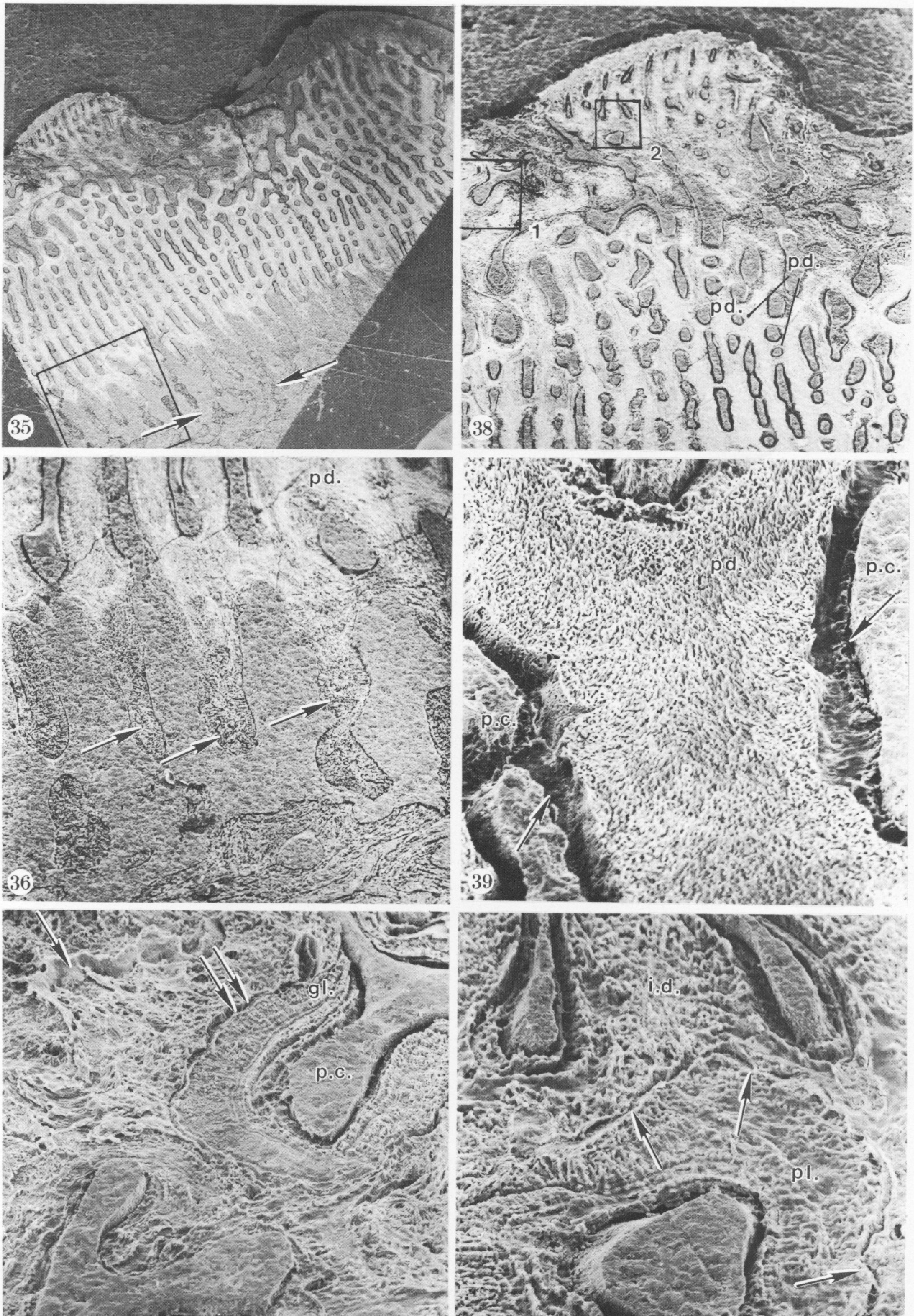




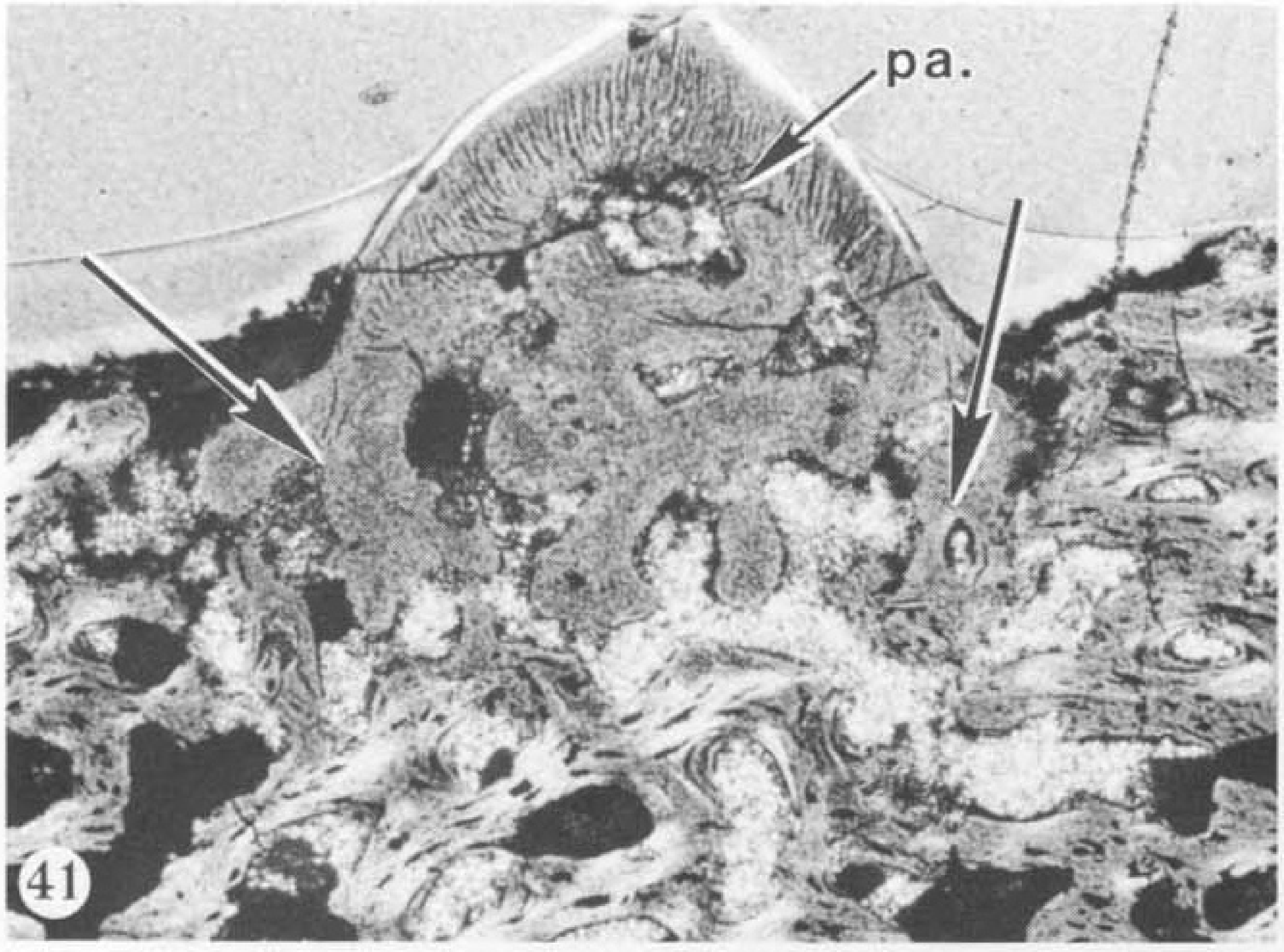


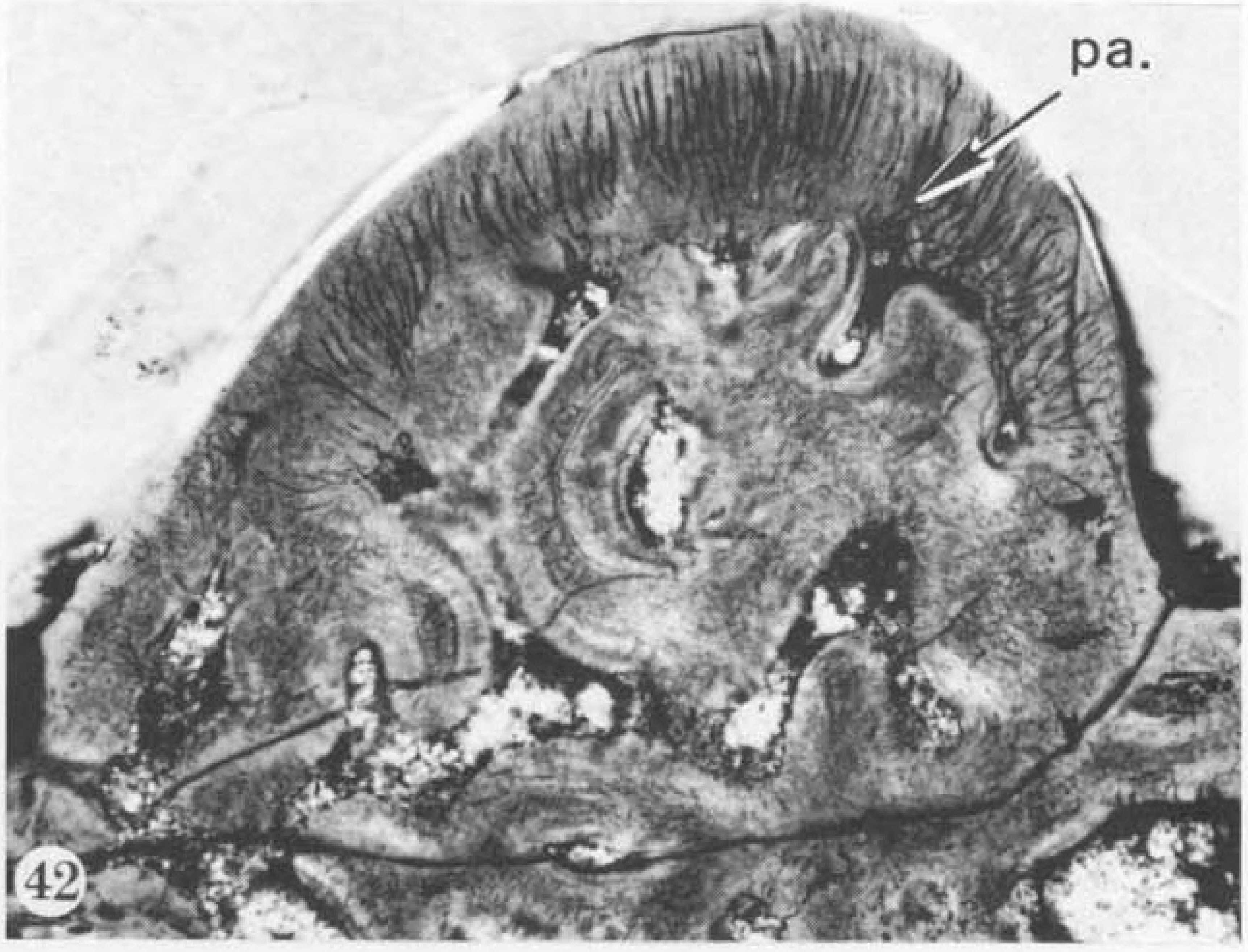


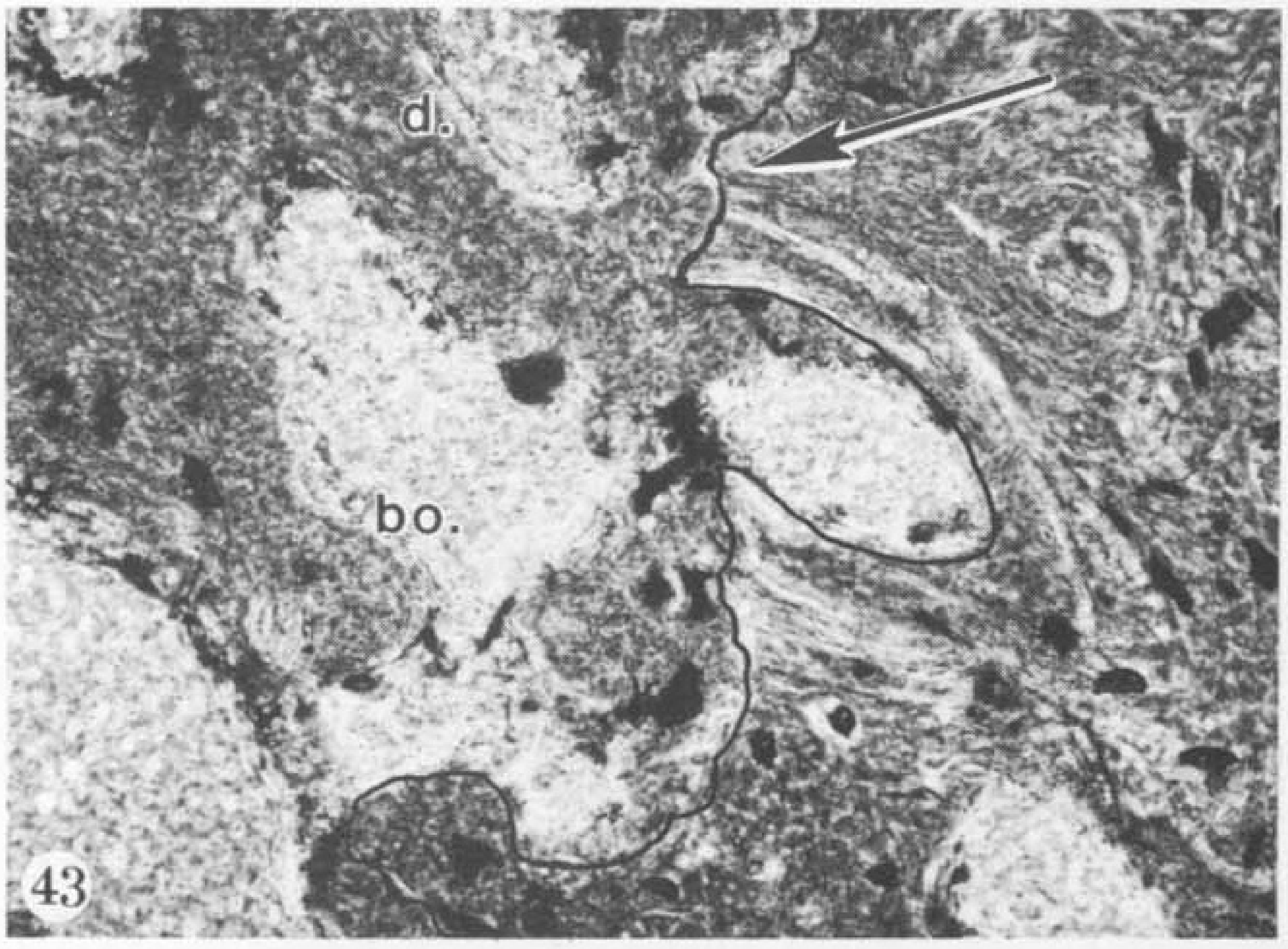
FIGURES 29–34. For description see opposite.

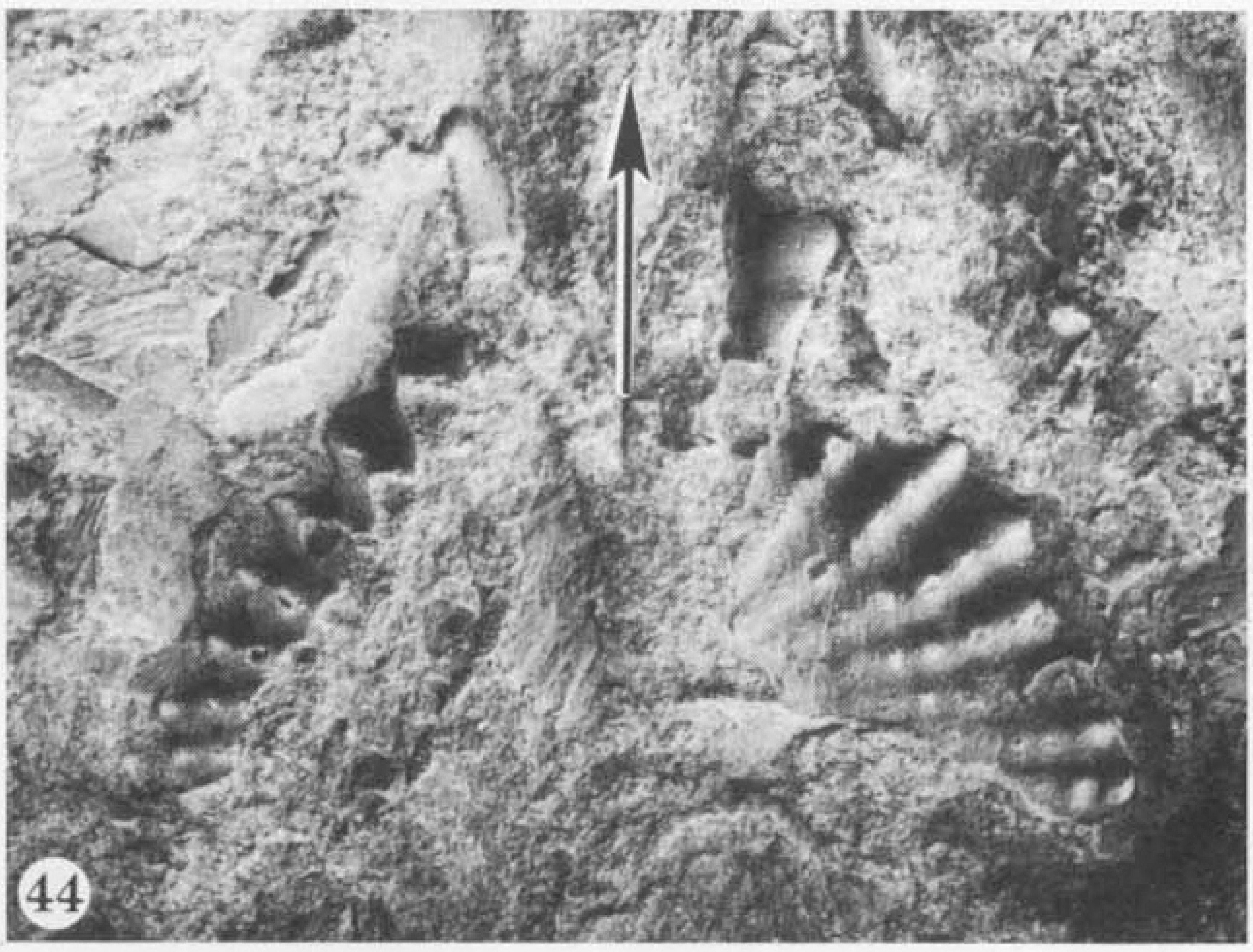


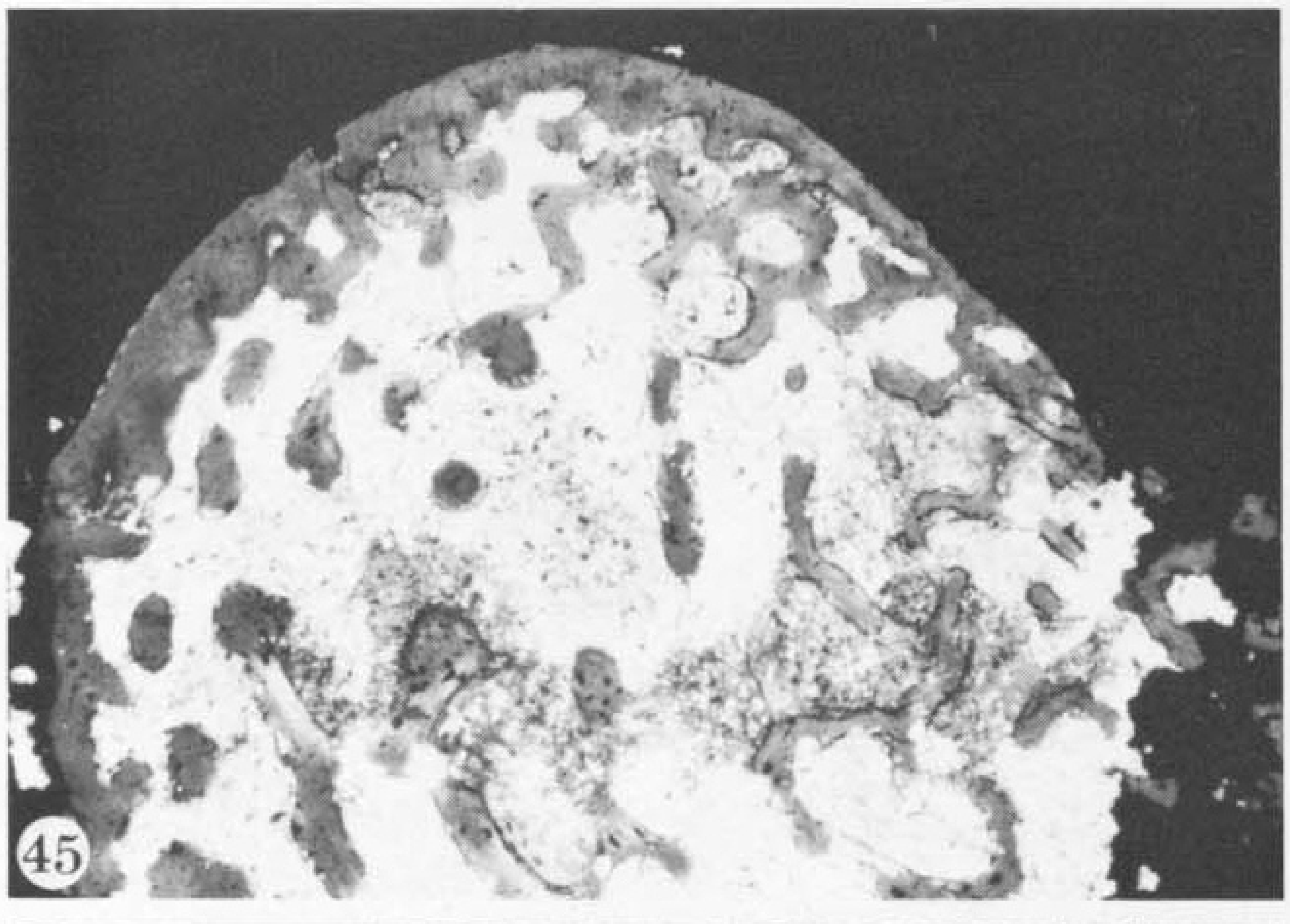
FIGURES 35–40. For description see opposite.

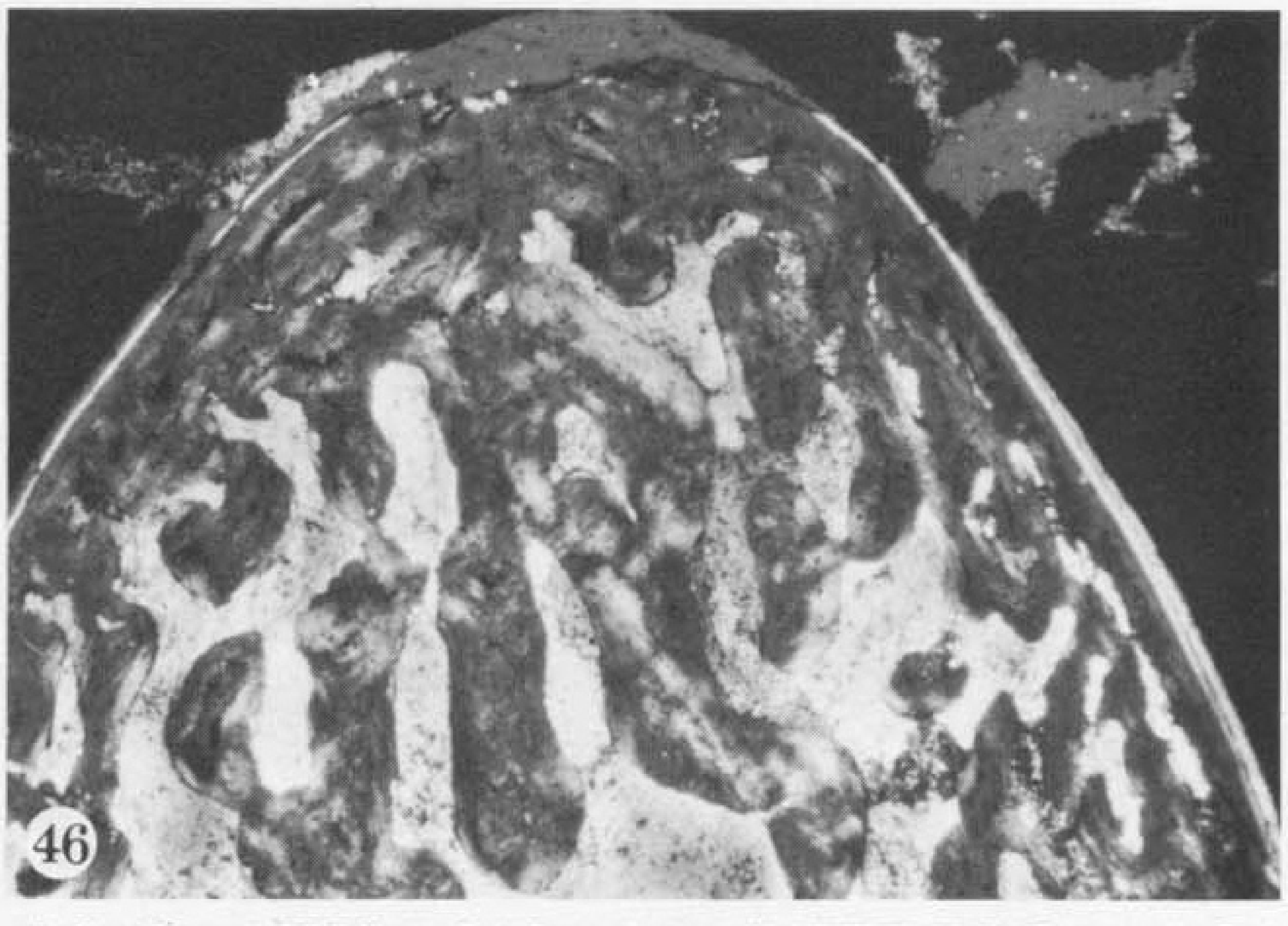


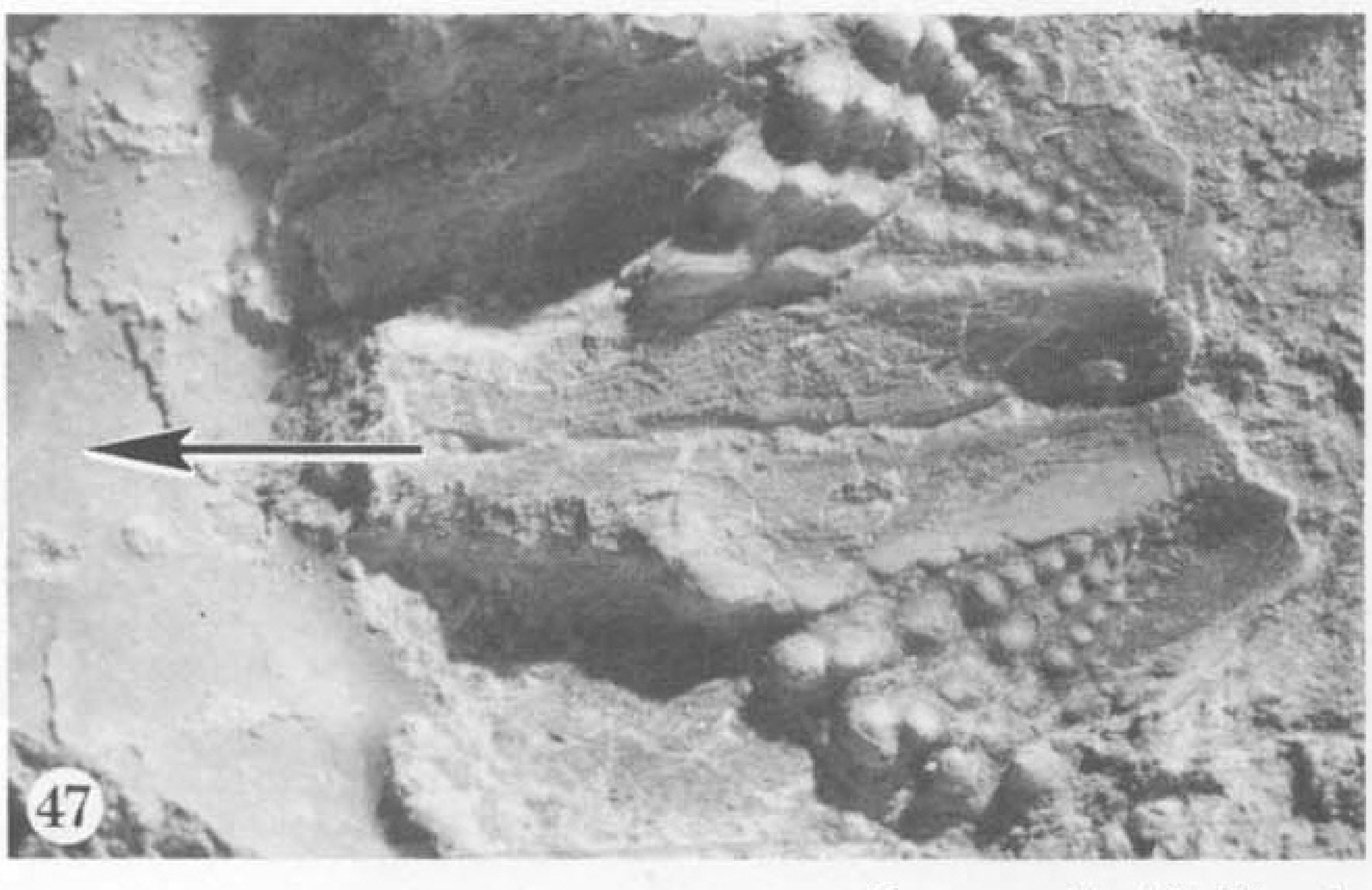












FIGURES 41–48. For description see opposite.