THE MICROSTRUCTURE OF THE DENTITION AND DERMAL ORNAMENT OF THREE DIPNOANS FROM THE DEVONIAN OF WESTERN AUSTRALIA: A CONTRIBUTION TOWARDS DIPNOAN INTER-RELATIONS, AND MORPHOGENESIS, GROWTH AND ADAPTATION OF THE SKELETAL TISSUES

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Detailed descriptions of the microstructure, which includes both histology and ultrastructure, are given for each type of tissue in each of the three species of Australian dipnoan. Most of the tissues have not previously been recorded in this way even for other species within the same genera. The microstructure is interpreted from examination of ground sections in transmitted and polarized light, together with examination of functional, forming and fracture surfaces in the scanning electron microscope. No previous studies of dipnoan dental tissues have been published in which the histology is related to surface morphology as seen in the scanning electron microscope.

The histology, microstructure, growth and distribution of buccal denticles are described in *Griphognathus whitei* and *Holodipterus gogoensis*, and their morphogenesis and adaptation to function is discussed. It is concluded that the phyletic trend towards macromerism, as shown in chondricthyans and primitive teleostomes, is illustrated in the three species of dipnoan.

The continuous layer of dentine of the tooth ridges, lips and covering to the dermal snout is described and found to be similar in the three species and equivalent to the tissue described previously in other dipnoans, sometimes as a form of cosmine. A term not in current usage is suggested for this dentine, namely syndentine. Dentine terminology is reviewed and the relevance to dipnoan dental tissues is discussed with the conclusion that an older term should be reintroduced to eliminate the current anomalies in terminology.

Chirodipterus australis is the only species with typical tooth plates. The histology is compared with previous accounts of tooth plates in dipnoans and found to have some similarity with those of *Neoceratodus forsteri*. The microstructure is reported from examination of the worn functional surfaces and acid-etched functional surfaces with the scanning electron microscope, this information has not previously been reported for dipnoan tooth plates and is presented here as a basis for comparison with other species.

New features of cosmine structure are described from scanning electron micrographs of the surfaces and these are related to the probable mode of formation and the involvement of the epithelial cells. The structure is found to compare in some ways with the cosmine of osteolepids. The loss of cosmine and replacement by tubercles in *Griphognathus whitei* and *Holodipterus gogoensis* is explained as retention of an ontogenetic potential which is comparable with Ørvig's theory of cosmine regression in the porolepids. Superpositional growth in the dermal skull bones is described for the first time in dipnoans. It is postulated that the ancestors of dipnoans had superimposed denticles beneath a cosmine covering.

The information obtained from the microstructure is used to examine the hypothesis proposed by Miles (1977) in a paper on the phyletic relations within the dipnoans. This confirms that *Griphognathus whitei* has retained a primitive dentition with separate buccal denticles and tooth ridges; *Holodipterus gogoensis* has retained these features, denticles and lip ridges, together with an advanced feature of tooth cusps which are a divergent specialization phyletically preceding tooth plates; *Chirodipterus australis* has not retained buccal denticles but has lip ridges on the snout and anterior part of the lower jaw, and the specialized tooth plates.

Pleromic dentine is recorded in two of these species and discussed with other observed methods of adaptation to wear.

1. INTRODUCTION

The intention of this account is to provide details of the composition of the tissues which constitute the dentition and the ornamentation of dermal bones. The probable manner of formation and replacement are discussed whenever interpretation of the specimens makes this possible. Similarly the adaptation to wear of these tissues is discussed from the available evidence.

The morphology and general arrangement of cosmine, denticles, tubercles and tooth ridges on the dermal bones of the skull and jaws of this material have been described in a previous paper (Miles 1977). The histology is described from vertical sections through the bones which have been examined in normal and polarized light. The ultrastructure is described from scanning electron micrographs (s.e.m. s) of formed surfaces and fracture surfaces, and compared with s.e.m. s of recent mammalian and fish material. The composition and arrangement of the tissues in each of the species described is compared and used as a basis for phylogenetic considerations in support of the hypotheses outlined by Miles (1977).

2. MATERIAL

		specimen numbers
Griphognathus whitei	Miles	P52572, P52575, P52578 P50996, P52579, P52583 P50998, P56054.
Chirodipterus australis	Miles	P52562, P51000, P52561 P56058, P52560, P56042 P56038.
Holodipterus gogoensis	Miles	P52569, P50997.

3. METHODS

Pieces of bone were selected from a few less complete specimens and sectioned normal to the outer surface after embedment under vacuum in Araldite, before grinding and polishing. Sections were examined in normal and polarized light and drawn with a Zeiss Camera Lucida at magnifications up to × 500. Whole pieces of the fossil specimens were mounted and prepared for examination in the scanning electron microscope so that either natural surfaces could be examined or fresh fracture surfaces normal to the functional surface of the bone. In addition, surfaces were prepared by etching with 0.1 NHCl for 1 min. before examination of the specimens in the scanning electron microscope; observations of the surface morphology were made with a Zeiss stereo-microscope at maximum magnifications of × 100. The protective coating, polymethyl methacrylate was carefully removed from the fossil surfaces before both acid-etching and the application of a conducting coating of gold in a Polaron sputter coating unit. This was found to be essential as all the fossil specimens had been prepared by the acid technique (Toombs & Rixon 1959). Scanning electron micrographs were taken at magnifications from 50 to 5000 times on a Steroscan 600 in the Electron Microscope Unit at the British Museum (Natural History).

4. TERMINOLOGY

As generally accepted, the term enameloid is used to refer to the highly mineralized, shiny outer covering found on all tubercles, denticles, tooth ridges, tooth plates and covering layers on dermal bones. Enameloid is found in most groups of vertebrates which have evolved before the amphibians and is considered to be primitive to prismatic enamel, the tissue characteristic of reptilian and mammalian teeth.

The descriptions of the structure of dentine in both fossil and extant forms have evoked an unjustified variety of names for a variety of complex but surely simply related forms of dentine. Peyer (1968) refers to the structure of the dipnoan tooth plates in *Ceratodus* as trabecular dentine. Denison (1974) has also used the term trabecular dentine for the tissue which underlies the enameloid and orthodentine of the continuous tooth ridges in *Uranolophus* and the tooth plates of *Dipterus*, and *Lepidosiren*. He considers that trabecular dentine is primitive to a later specialization of tubular dentine in which the pulp canals are nearly parallel to each other and perpendicular to the tooth surface, as found in *Sagenodus*, and *Neoceratodus*. Yet another term, namely prism dentine, has been used for the type of dentine present in dermal bones of *Ganorhynchus splendens* Gross, described and illustrated by Gross (1956), in which columns or tubes of tubular dentine are arranged parallel to each other and packed closely together with little intervening tissue. Ørvig (1967) describes the tissue in lungfish tooth plates as tubular dentine which is comprised of denteons, each one of which surrounds a vascular canal, and between each denteon is what Ørvig terms interstitial pleromic hard tissue. Pleromic dentine is regarded as tissue which fills in soft tissue spaces within the spongiosa as a response to wear of the functional surface, and is secondary to the intial formation of dentine (Tarlo & Tarlo 1961). Used in this restricted sense it is probably not appropriate to use the term columnar pleromic hard tissue as proposed by Ørvig (1967). Presumably this term was suggested because the whole tissue is assumed to grow basally into the medullary spaces of the bone and in this slightly different sense is, infilling or pleromic. Ørvig (1976*a*, *b*) has subsequently modified this term to vascular pleromin for the hard tissue of dipnoan tooth plates.

Lison (1941) described the tooth plates of *Protopterus* and considered that the tissue was an osteodentine in the form of pseudo-haversian canals with an extra hard tissue filling in between these columns which he called petrodentine. Schmidt & Keil (1971) have adopted this terminology and equate petrodentine with durodentine. This is the tissue referred to by Ørvig as interstitial pleromic dentine. Denison (1974) also refers to the columns of hypermineralized dentine between the units of trabecular dentine as petrodentine. He rejects the term pseudo-haversian osteodentine for this tissue. Use of a more suitable term arising from a consideration of its probable development will be discussed in the present paper.

Within primitive crossopterygians, dipnoans and amphibians, a variety of dentine termed plicidentine is found, which has formed by repeated infoldings of the original layer of cells which produce the orthodentine. This tissue has a convoluted surface on the inner pulpal side and the convolutions radiate from the central pulp chamber to the outside of the tooth. The most complex form of plicidentine is formed within the labyrinthodonts. Peyer (1968) suggests that the term has a use which is restricted to a completely folded dentine which converges into a central pulp cavity. Tissue which forms by folding on the pulpal side of a tooth which has a continuous layer of orthodentine on the outside, should be termed trabecular dentine. The term 'trabecular dentine' has been used to cover a variety of dentines which differ from orthodentine in having a many-branched pulp chamber and thin struts of dentine separated by tissue spaces. In my view, the use of the term 'trabecular dentine' should be restricted to tissue similar to that of *Lamna cornubica* Risso in which there is an irregular arrangement of medullary spaces within the large pulp cavity from which odontoblast processes arise, also in an irregular way. This type of dentine is generally formed beneath an outer layer of orthodentine in which the odontoblast processes lie parallel to each other in an otherwise compact tissue. Columnar dentine would seem to be a better term for the composite tissues which form the tooth ridges and biting plates of the fossil dipnoan dental apparatus. It may even be more appropriate to return to the terminology proposed by Thomasset (1928), namely syndentine for which he gave *Ceratodus* as an example. He regarded this tissue as composed of units placed close together with small pulp canals and radiating canaliculi or tubules. A large pulp cavity is not present but the pulp canals open directly into the medullary spaces of the bone. This term is apposite for most of the tissue to be described in this paper. Until the evidence for an appropriate term has been presented, the tissue will either be described as compact dentine, composite denticles, or composite tubercles.

Based on the assumption that the primitive dipnoan dentition comprises evenly scattered buccal denticles and tooth ridges as found in *Griphognathus* (Miles 1977) these tissues will be described first to establish a basis for comparison with *Holodipterus* and *Chirodipterus*.

The tissues of each species of dipnoan will be described as far as possible in the same sequence starting with the snout and upper and lower lips, then buccal denticles, and tooth plates when present, and dermal ornament.

Other features of the primitive dentition which have not been established are the patterns of growth and replacement which enable the dentition to adapt to functional stress. A contribution to this aspect of dipnoan dentitions is attempted in the present investigation.

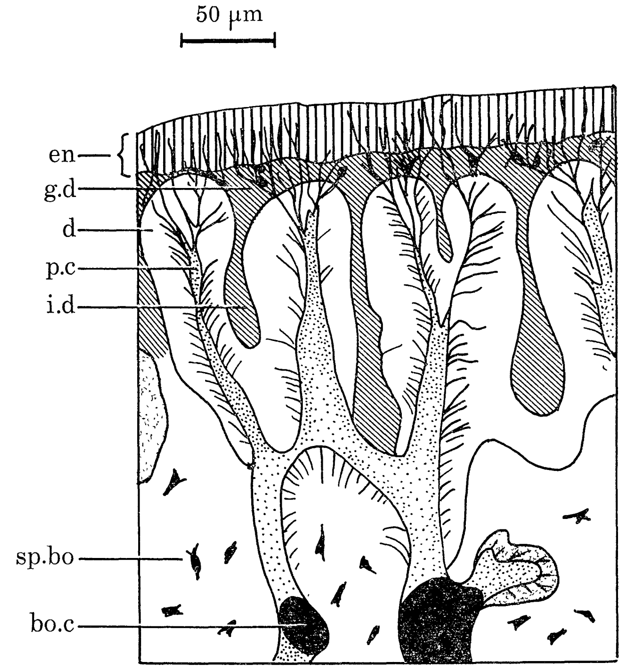
5. OBSERVATIONS

(*a*) *Griphognathus*

(i) *Snout*

The most conspicuous part of the upper jaw is the smooth continuous tissue which forms the dermal snout and biting ridge (figure 1.) Most of this region is covered by shiny enameloid, except in areas of presumed functional stress where the surface is fractionally lower and has a rough, non-shiny appearance (figures 19*a* and 19*b*, plate 1). This tissue is only interrupted by sparsely distributed sensory pores. At the posteroventral border of the dermal snout, the tissue changes into a region where large areas of spongy bone are uncovered. A few isolated groups of low rounded denticles covered with enameloid are fused to the surface of the bone (figure 20, plate 1). Some of the smaller denticles have a stellate appearance similar to the denticles which cover the bones in the buccal cavity. Alongside this region, the bone is more completely covered with dentine and enameloid which is perforated with numerous sensory pores and is only discontinuous where large shallow depressions have formed, many of which are resorption areas. These depressed regions, in sectioned material, are represented by scalloped borders typical of resorbing surfaces (figure 4). Resorbing surfaces are also found at the natural edges of the layer of continuous tissue, and these progress from the vascular canals at the base of the dentine onto the surface of the snout. At the dorsolateral borders of the dermal snout the continuous sheet of dentine also gives way to separate rounded denticles.

The major part of the dermal snout and tooth ridge is composed of a compact, thick layer of dentine arranged as parallel units which are perpendicular to the functional surface, all of which in unworn tissue is covered by a continuous layer of enameloid (figure 1, figures 21 *a* and 21 *b*, plate 1). Each unit (or odontode) has a central pulp canal with tubules radiating from the terminal part towards the enameloid layer; some of the tubules penetrate the enameloid layer. Along the length of the pulp canal, tubules radiate for a short distance into the dentine and are arranged perpendicular to the long axes of the units. The width of the pulp canals is around 30 μm but is never constant along their length. Basally the pulp canals open into the tissue spaces of the spongy bone; there is no distinct large pulp cavity. These canals both branch and taper before giving rise to the branching tubules which are aligned towards the surface layer. The primary dentine which surrounds the pulp canals is a dense homogeneous tissue and is clearly distinguished by its tubular structure and colour in transmitted light, from the intervening tissue which I will designate as interstitial dentine (figure 2, figures 21 *a* and 24 *a*, plate 1). In polarized light, the dentine surrouding the pulp canals is strongly birefringent and positive with respect to the surface. This indicates that the crystallites are regularly oriented and parallel to the pulp canal and that the original fibre direction was longitudinal rather than radial. The enameloid layer is relatively thick, 40 μm, and strongly



EXPLANATION OF ABBREVIATIONS USED IN FIGURES

bo.c	bone canal	p.c	pulp canal
d	dentine	p.d	pleromic dentine
en	enameloid	po.can	pore canal
g.d	globular dentine	pu.d	pulpal dentine
g.l	growth line	r.c	resorption cavity
h.d	hypermineralized dentine	s.d.c.	sub-dentinal cavity
hom.d	homogeneous dentine	sp.bo	spongy bone
i.d	interstitial dentine	w.s	worn surface
n.c	neck canals		

FIGURE 1. *Griphognathus whitei* Miles. The unworn upper lip of the dermal snout. From P52572. All the diagrams are from ground sections in the vertical plane unless otherwise stated.

birefringent with a mixed sign of birefringence, but more strongly negative to the surface (figure 21*b*, plate 1). This may be explained by crystallites arranged perpendicular to the surface (positive sign) but arranged in groups which give rise to rodlet birefringence (negative sign). Apart from the terminal portions of odontoblast tubules which penetrate the enameloid, the layer shows faint striations (crystals arranged as rodlets) perpendicular to the surface. All these features indicate a highly mineralized layer with crystallites arranged perpendicular to the surface as in many enameloids which have mineralized from an orginal mantle dentine in which the fibres are predominantly radial. In scanning electron micrographs, fractures through this layer show a highly organized semi-prismatic or rodlet structure which is quite distinct from the underlying dentine (figure 22, plate 1). Between the enameloid and the regular dentine units is a relatively thin layer, poorly mineralized with interglobular spaces, and containing the tapering terminal branches of the odontoblasts (figure 1 and figure 21, plate 1.) This layer can be compared with the granular or globular dentine in mammalian teeth and is probably equivalent to the von Korff layer of radial fibrillation or mantle dentine found in many vertebrate teeth.

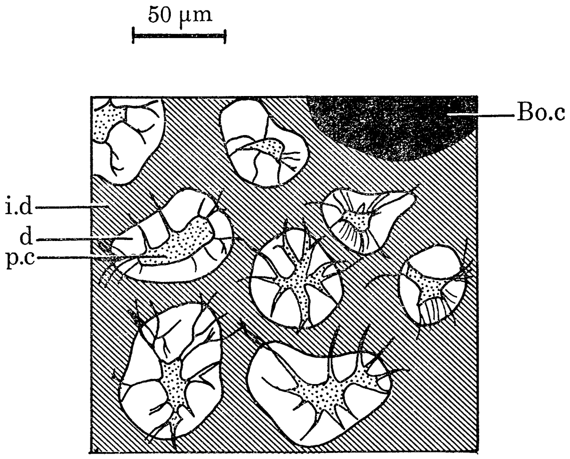


FIGURE 2. *Griphognathus whitei* Miles. Horizontal plan of the dentine. From P52572.

On worn surfaces, both the enameloid and globular mantle dentine are lost and the underlying dentine units have started to wear down giving rise to the characteristic ringed surface (figures 19*a* and 19*b*, plate 1). Only in a few instances are the pulp canals open to the surface. In most units the pulp canal has filled in with secondary dentine as a response by the odontoblasts to wear. The primary dentine has become more birefringent, and very translucent (figure 3, figures 24*a* and 24*b*, plate 1), presumably due to increased mineralization resulting in a hypermineralized dentine with occluded tubules. Comparing the depth of the worn layer with that of the adjacent unworn tissue (figures 21*a*, 24*a* and 25, plate 1), if we assume that the tissue when formed, was the same thickness, an increase in depth has been achieved by growth of the dentine into the medullary spaces of the spongy bone. This is another example of a mechanism of adaptation in response to wear in these tissues. Figure 23 illustrates the surface appearance of worn units of dentine with infilling secondary pulpal dentine which is surrounded by the primary circumpulpal, hypermineralized dentine.

Returning to the size of the dentine units and pulp canals, each unit is around 50–70 µm in diameter which agrees well with the 50–100 µm diameter of similar units of dentine in

Ganorhynchus splendens illustrated by Gross (1956, fig. 82) and *Rhinodipterus ulrichi* Ørvig (Gross 1956, fig. 6*c*). Gross has termed this 'prism dentine' in which the dentine units are apparently more closely packed together than the tissue in *Griphognathus*, but similar in having narrow pulp canals opening directly into the medullary spaces of the spongy bone. The size of the pulp canals, around 20 μm, would accommodate a small group of odontoblast cells and leave little room for any vascular tissue. Capillaries would be situated in the medullary spaces below with good access to the nearby pulp tissues.

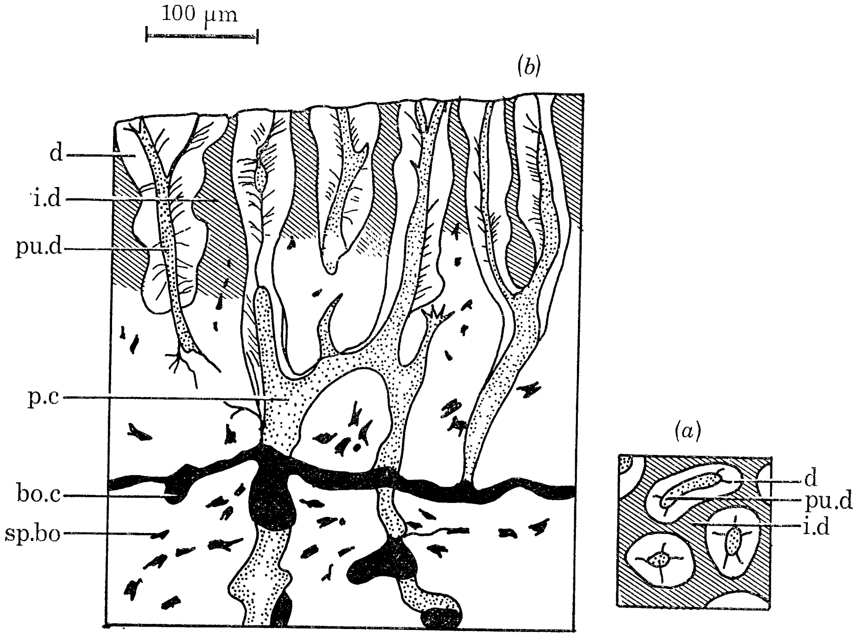


FIGURE 3. *Griphognathus whitei* Miles. Worn tissue of the upper lip, 3a in surface view. From P52572.

The separate tubercles on the dorsal surface of the snout where the continuous layer of dentine is perforated by many sensory pores are composed of dentine with a less regular arrangement of pulp canals than in the dermal snout (figure 4 and figure 20, plate 1). The surface is covered with a similar thick layer of enameloid which extends down the sides of the denticles as a thinner layer tapering towards the base. The enameloid of the cosmine layer in *Chirodipterus* and *Megalichthyes* does not extend down into the pores which regularly divide the dentine layer of the cosmine. The dentine of these composite tubercles is formed from multiple anastomosing pulp canals from which the tubules radiate irregularly and branch many times. Some of the terminal portions of these tubules extend into the enameloid layer (figure 4).

(ii) *Tooth ridges of the dentary and prearticular*

The tissues of the tooth ridge on the lower jaw are arranged in an identical way to those of the dermal snout, a compact system of dentine units in which the pulp canals are perpendicular to the enameloid covered surface and parallel to each other; the pulp canals open directly into the spaces within the spongy bone (figure 26, plate 2). On worn surfaces the enameloid is lost and hypermineralized dentine forms in regions which relate to the position of the pulp canals. Translucent dentine forms around the pulp canals and secondary reparative dentine fills in the canal itself. This results in the typical ringed appearance of worn surfaces of compact dentine (figure 3*a* and figure 27, plate 2) in which translucent dentine surrounds a small central opaque region, these together comprise a unit or odontode. These units of dentine are relatively closely spaced and all embedded in opaque, interstitial dentine. Occasionally tubules from adjacent pulp canals penetrate the interstitial dentine and anastomose with each other (figure 2). This is the typical appearance of a functional surface of compact dentine with histological features of that described for the snout. The entire medial surface of the lower lip, illustrated in figure 27, plate 2, is of this type, whereas the contiguous surface on the lateral side is still covered with enameloid. The biting edge of the dentary (figure 27, plate 2), was examined in the scanning electron microscope after pre-treatment with concentrated acid which gives a differential etch pattern, the more highly mineralized regions remain proud of those which are less mineralized (figures 28–31, plate 2). The ringed worn surface seen in figure 27 is accentuated (figure 28, plate 2), the circumpulpal primary dentine can be clearly distinguished from the interstitial matrix, and then from the secondary dentine filling in the pulp cavity. Tubules extend from the pulp cavity through both primary and secondary dentine. These features can be identified on untreated worn surfaces (figure 23, plate 1) but with greater difficulty. Another consistent feature of these preparations is the poorly mineralized junctions between the component tissues, i.e. between the interstitial and circumpulpal dentine, and between the latter and the secondary pulpal dentine. Different degrees of mineralization of the dentine units are apparent, depending on the level of wear; discussion of this will be left to a subsequent paper.

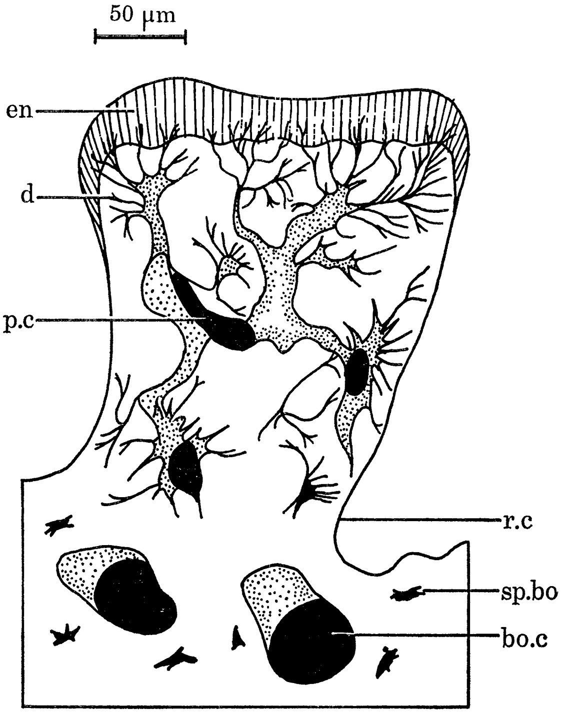


FIGURE 4. *Griphognathus whitei* Miles. Tubercle on the dorsal surface of the snout. From P52572.

On both medial and lateral surfaces of the tooth ridge, the compact dentine layer is replaced by a dense covering of separate denticles with little free space between. Some indication of a linear relation is apparent with alternate rows of denticles linking with lateral extensions to the tooth ridge. Many stages of development are evident in these fields of denticles: from the newly formed in which the surface is covered with shiny enameloid, and shallow crests radiate from the centre of the denticle; to positions where only the bone at the base of the denticle remains. In many of the denticles the composite structure of units of dentine is seen (figure 27, plate 2). In an acid etched specimen, the dentine units are clearly seen on a worn, flat topped denticle (figure 32, plate 3) and are comparable with those seen on the worn surface of the tooth ridge (figure 29, plate 2). The base of one of these denticles is illustrated in figure 33, plate 3. The bone and part of the denticle have undergone resorption, as evidenced by the raised borders of the Howship's lacunae, and in this region the dentine units are seen in longitudinal view.

(iii) *Denticles of the dentary and prearticular*

The histology of the denticles on the medial surface of the dentary and prearticular is the same as that of the denticles on the basibranchial tooth plates. This is illustrated in figures 5, 6, and 34, 35, plate 3. The shape of the denticles in the sections will depend upon the orientation of the plane of section relative to each denticle, discussion of variation in shape is more appropriate after consideration of the SEM appearance of all the fields of denticles. It is pertinent to describe here some findings which relate to attrition, growth and eruption of a series of buccal denticles in a section through the prearticular (figure 26, plate 2). Each denticle is composed of relatively short multiple pulp canals from which branching tubules radiate in many directions.

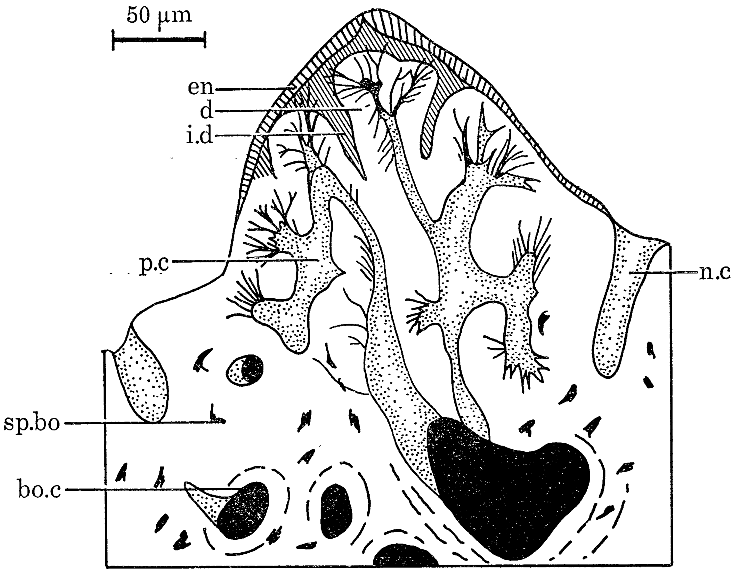


Figure 5. *Griphognathus whitei* Miles. Denticle on the basibranchial. From P50998.

Each pulp canal is similar to the dentine units in the tooth ridge and snout with a slightly less regular arrangement. The newer denticles are more pointed and covered with a layer of enameloid which continues down the sides of the denticle (figure 5). Of the series of 15 denticles examined in sequence from the biting ridge inwards, numbers 5, 10 and 12 were relatively new. All were forming in a region where bone resorption had occurred and the apex of the new denticle was on a level with the basal tissue of the adjacent worn denticles. Assuming that these denticles were formed from typical eruptive dentine and would achieve a functional position later in time, one must conclude that appositional growth of dentine and selective resorption and deposition of bone at the base of the denticle is the mechanism by which increase in height of the denticle is attained. In *Latimeria chalumnae*, an extant actinistian in which separate buccal denticles are retained, new teeth form in resorption pits in the bone and erupt by deposition of new bone between the dentine and the bone of the jaw (Grady 1970; Smith, in manuscript). In older worn denticles, the enameloid is lost and hypermineralized dentine forms at the surface in relation to the pulp canals, while resorption areas are commonly found at the base of the older denticles. Differences in the arrangement of the component units of dentine will determine to a large extent the surface morphology of the denticles.

The distribution of denticles on the medial surface of the prearticular varies with the position in the buccal cavity. A typical pattern of organization is illustrated in figure 36, plate 3 of a region towards the anterior end of the prearticular. These are composite denticles with sharp crests joined by ridges; some ridges are also serrated (figure 37, plate 3). The proportion of denticles with worn surfaces is very small. One can assume that either these denticles are non-functional compared with the flat grinding surfaces of the tooth ridges and the denticles on the ascending process of the prearticular, or that they have a relatively high replacement rate arising possibly from a prehensile function.

The assumption has been made that each serration on the ridge marks the apex of one odontode (dentine unit). The concept that each pulp canal and associated dentine represents a primitive ontogenetic unit must be subjected to careful scrutiny (see discussion p. 68).

On the medial surface of the ascending process of the prearticular, the denticles form a dense covering to the bone. The majority of the denticles have worn, flat tops which again reveal the characteristic ringed shape of the dentine units. The translucent zones to these units are illustrated in figure 38, plate 4. A direct comparison can be made with figures 38, 39 and 41, plate 4 in which the same denticles (figure 38, plate 4) are seen in the scanning electron microscope. The translucent zones are seen to correspond to the raised areas in figure 39, plate 4 and the opaque central zone to a pit of irregularly mineralized dentine, the secondary reparative dentine which fills in the pulp canals. The interstitial dentine is less resistant to wear than the circumpulpal dentine as, like secondary dentine, it is less well mineralized. Sometimes the pulp canal is open to the surface and in these examples where occlusion of the pulp canal is not complete, the branching tubules can be seen in the walls of the canal. The larger worn denticles show a regular arrangement of the dentine units (figure 40, plate 4). Most of the worn denticles have large resorption areas at the sides in which new denticles are frequently seen (figure 41, plate 4). These newly formed denticles are covered with shiny enameloid over the entire surface which is shaped by ridges radiating from the central point (figure 41, plate 4). A regular arrangement of openings to the vascular canals surround the base of these newly formed denticles. Resorption surfaces are often adjacent to the vascular canals around the older denticles (figure 42, plate 4) and have the identifying feature of a mosaic of irregular pits whose raised borders mark the sides of Howship's lacunae left as the osteoclast resorbs the bone from the central region. The thin enameloid covering to the denticles frequently fractures off, leaving the unworn dentine exposed. These surfaces have the remarkable feature of a regularly pitted surface (figure 43, plate 4), which I interpret to be the poorly mineralized mantle dentine in which 'organic' spaces or pits remain. The enameloid covering this layer is more highly mineralized, and its rodlet structure, also derived from radial fibrillation, is characteristic of many enameloids.

(iv) *Denticles of the basibranchial tooth plates*

The denticles on the basibranchial tooth plates are similar to the buccal denticles but dome shaped rather than stellate; they also do not completely cover the bone surface (figure 44, plate 5). Enlarged denticles with worn flat surfaces are found at both anterior and posterior margins of the bone (figure 45, plate 5). All of these reveal the worn units of dentine as previously described. Many of the denticles in the central region are unworn and have a complete covering of shiny enameloid. As described for the dentary and prearticular, these newly formed denticles are surrounded at their base by a ring of openings (neck canals) which lead into the vascular canals of the supporting bone (figures 5, 6, and figure 44, plate 5). These are obscured around the base of the older denticles by the further growth of bone. Several of the new denticles have an incomplete covering of enameloid around their base (figure 46, plate 5). It is possible to regard this area as a forming enameloid surface and to extrapolate some information on the mode of formation of enameloid in these denticles.

The preliminary information shows that the pattern of mineralization is fibrillar and calcospheretic (figure 47, plate 5) with a second phase infilling the remaining spaces to give a smooth homogeneous tissue. Detailed consideration of the structure and formation of enameloid should depend upon examination of further material and comparison with similar tissue from extant forms (Smith, in manuscript). The completed enameloid surface has fine longitudinal striations and odontoblast tubules frequently open onto the lateral surfaces of the denticle. Resorbing surfaces are often at the base of denticles and these also reveal the tubular extensions of the odontoblasts in the outer layer.

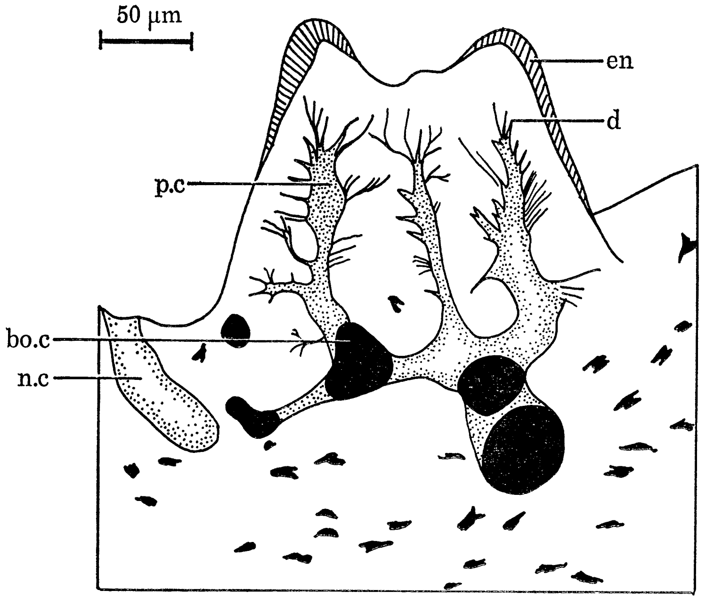


FIGURE 6. *Griphognathus whitei* Miles. Denticle on the prearticular. From P50998.

The histology of the denticles is illustrated in figures 5, 6, and figures 34, 35, plate 3. The multiple pulp canals open into the vascular spaces of the spongy bone, some are situated beneath the apices of the crests on the denticle which are also the thickest regions of enameloid. Around these pulp canals the translucent dentine forms in a comparable way to that described for the compact dentine of the snout (figure 5 and figure 35, plate 3). It seems reasonable to regard each denticle as a composite of dentine units (odontodes), each unit with a pulp canal, circumpulpal dentine and enameloid covered tip or crest (figure 6). These tips are seen in scanning electron micrographs as crenulated ridges, or even as in some dermal tubercles as separate points (figure 48, plate 5). In worn denticles the enameloid is lost from the surface, but retained down the sides (figure 34, plate 3). The exposed dentine has become hypermineralized at the surface, seen in figure 34, plate 3, as increased birefringence. The circumpulpal dentine has the same sign of birefringence as that in the compact dentine (p. 34). The surface appearance of these worn tops has been previously described, a ring of translucent dentine surrounds each occluded pulp canal. At the base of worn denticles, scalloped resorption surfaces are frequently observed (figure 34, plate 3) which correspond with the occurrence of resorbing surfaces identified in the scanning electron microscope.

(v) *Tubercles of the outer dermal bones*

The bones of the skull roof, cheek and the gular and submandibular plates that are covered by perforated sheets of enameloid, have a similar structure to that described for the tubercles of the snout. Large areas of resorption can be identified in the scanning electron micrographs and in sections these are evident as shallow, uneven depressions in the bone surface. Resorption areas interrupt the smooth surface of the bone and in some specimens new tubercles have developed.

Bones which have a fine ornament of tubercles reveal a structure which has not been observed in any regions of the dentition, namely superpositional growth of tubercles (figures 7 and 8).

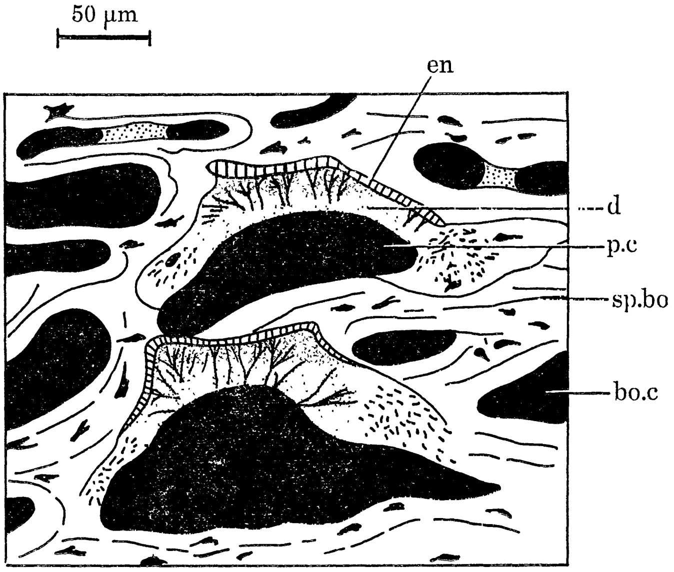


Figure 7. *Griphognathus whitei* Miles. Buried tubercles in a dermal skull bone. From P52583.

As many as 4–5 generations of unworn tubercles contribute to the thickness of the superficial layers of the bone. The most superficial tubercles project a little above the surface of the bone and are identical in shape and structure to the buried tubercles (figure 8). Irregular short branching tubules penetrate the dentine from the large pulp cavity which opens directly into the spaces of the spongy bone. Enameloid is thickest over the tip and extends down the sides of the dentine until the basal bone is reached. The resemblance of these tubercles to those on the scales of *Latimeria chalumnae* is notable (Smith, Hobdell & Miller 1972, fig. 2*d*). This mechanism of growth in which resorption does not play a significant part is found in the body scales of *Uranolophus* (Denison 1968) and also in the scales of a primitive holoptychiid *Porolepis* (Gross 1965, Miles 1977). In these genera, superposition of successive superficial layers of free odontodes on bone is a method of increasing the thickness of the bone.

The dermal ornament of separate tubercles is illustrated in figure 49, plate 5 taken from the margins of the jaw. Some of these composite tubercles are similar to buccal denticles. An example where the apex of one dentine unit is proud of the surface at one end of a ridge on the tubercle is seen in figure 48, plate 5. Many of these tubercles are larger than those typical of the dermal covering to the skull. The larger openings into the spongy bone can be contrasted with the smaller openings on the bone surface between denticles of the prearticular. Also the basal bone is more obtrusive, masking any openings to the vascular canals which frequently surround the denticles.

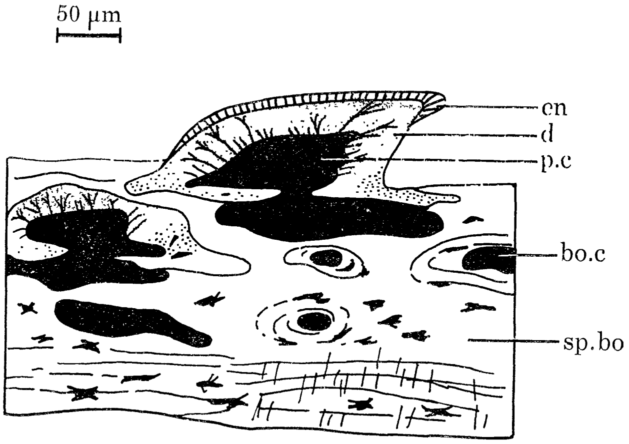


Figure 8. *Griphognathus whitei* Miles. Surface tubercles on a dermal skull bone. From P52583.

All the dermal bones are composed of the classical three layers; beneath the denticulate layer is the spongy bone, then basally the lamellated isopedine (figure 8). The trabeculae of the spongy bone are generally of the coarse-fibred woven type, with many large irregular osteocytes. Frequently the vascular spaces have become surrounded by concentric lamellae of fine-fibred bone with a more regular arrangement of osteocytes, and these regions can be considered as secondary osteons. Each one has formed by apposition of bone on a previously resorbed surface, the irregular reversal line marks the junction between coarse-fibred bone and the fine-fibred lamellar bone. Some of the dermal bones show a third type of bone, namely bundle bone, probably at the sites of muscle attachment. Periosteal lamellar bone forms from consecutive lamellae, parallel to the surface, then perpendicular to this, many parallel fibre bundles pass for some distance into the bone. The sign of birefringence supports the fact that the original fibres were perpendicular to the free surface of the bone.

(*b*) *Holodipterus*

The three types of dentine tissue present in *Griphognathus* have also been identified in the tissues of *Holodipterus,* namely compact dentine, composite denticles and composite tubercles. In addition, there are two further tissues, one, a homogeneous compact dentine which forms a tooth cusp on the prearticular; two, a pleromic dentine found on worn surfaces between tooth cusps, on palatal bones and on the dentary adjacent to the tooth ridge.

(i) *Snout*

On the surface of the snout there is a patchy distribution of enameloid with irregular worn areas where the surface is non-shiny and fractionally lower. Enameloid is mostly retained around the pores to the sensory pits where the surface is sloping down towards the opening of the pit. In a few of the worn regions, units of dentine are evident where the circumpulpal dentine is translucent and less worn down than the surrounding interstitial material which is opaque and fills in the area between the dentine units. These observations are consistent with the tissue being compact dentine, similar to that described for *Griphognathus*, with a similar tissue response to wear, that is secondary formation of dentine in the pulp canals and hypermineralized primary circumpulpal dentine. The histology is the same as the biting ridge of the lower lip.

In a worn surface on the snout, tubules within which the odontoblast processes would lie, arise from the occluded pulp canal and pass through the circumpulpal dentine. Some of these may interconnect with the pulp canal of the adjacent dentine unit. In one specimen (P52569) a small area of the snout was not covered by compact dentine (figure 50, plate 5), and the exposed bone surface retained separate denticles of the characteristic shape seen in most buccal denticles. Two of the denticles adjacent to the compact dentine (figure 51, plate 5) appeared to have 'bone' partly filling in one of the concavities in their surface between two side ridges. The interpretation, from these observations, of formation and growth of the tissue is not obvious. Either the denticles become overlaid by a layer of compact dentine, or the bone continues to surround them and later infills with a pleromic dentine (see p. 45).

(ii) *Lip ridges and pleromic dentine of the dentary*

The continuous tissue which forms a tooth ridge or cover to the dentary bone is illustrated in an unworn condition in figure 9 and figure 52, plate 6. The pulp canals of the dentine layer are regularly spaced and open directly into the vascular spaces of the spongy bone. The dentine

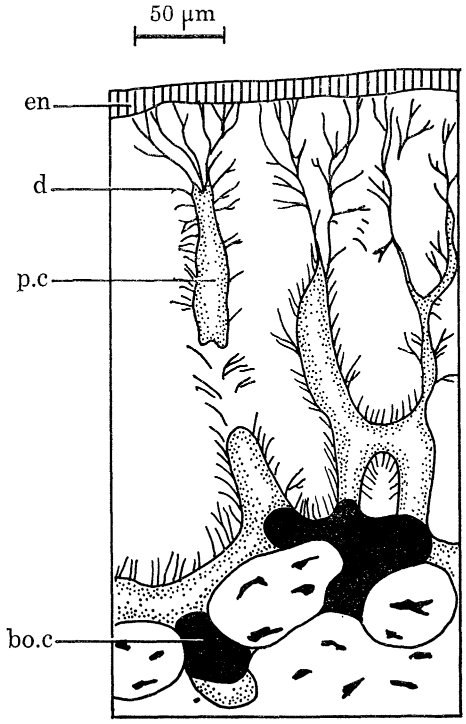


FIGURE 9. *Holodipterus gogoensis* Miles. Unworn lower lip. From P52569.

tubules radiate from these canals in an irregular way; many from the terminal portion of the pulp canal run towards the enameloid and penetrate this layer. This tissue which resembles the compact dentine of *Griphognathus* in many features, is not at this stage of development subdivided into circumpulpal translucent dentine and interstitial dentine; the dentine is only weakly birefringent in contrast to that of *Griphognathus* and *Chirodipterus*. The enameloid layer is also less birefringent than that of *Griphognathus*, exhibits radial bands in polarized light (figure 52, plate 6) and has a mixed negative and positive sign of birefringence (intrinsic negative birefringence of normal crystallites and the form birefringence of rodlet spaces – Schmidt & Keil 1971, p. 88). The enameloid layer is lost from worn surfaces (figure 10) and in these situations greater birefringence of the superficial dentine is detected, presumably due to increased oriented mineralization (figure 53, plate 6).

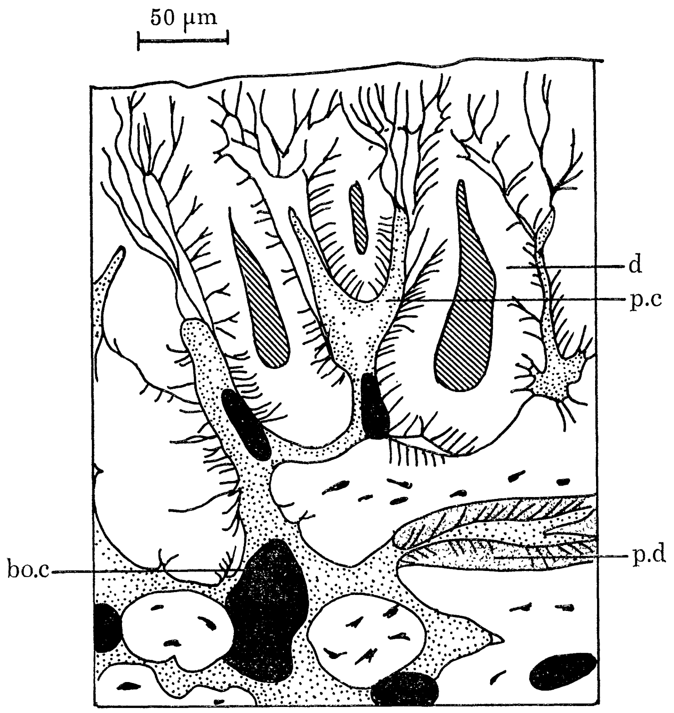


FIGURE 10. *Holodipterus gogoensis* Miles. Worn tissue of the lower lip. From P52569.

Gorizdro-Kulczycka (1953, figs 2 and 3, pl. 1) has described and illustrated what appears to be identical tissue on the splenial bone of *Holodipterus sanctacrucensis*, a compact dentine formed from repeated units of dentine united by what is termed both interstitial dentine and cement.

Dentine grows into the spaces within the spongy bone below as a response to wear, and this tissue is pleromic dentine. Very flat worn surfaces of this type, translucent dentine infilling spongy bone, have been observed on the postero-ventral surface of the snout, adjacent to a resorption area, and what is interpreted as a replacement layer of compact dentine; also on the dermopalatine; on the medial surface of the dentary adjacent to the compact dentine of the tooth ridge (figure 11, figures 54 and 55, plate 6), and on the medial surface of the prearticular adjacent to a tooth cusp (figure 14).

Neither enameloid nor dentine units are present over a large area on the medio-dorsal surface of the lower lip, the remaining flat, worn surface is a functional adaptation to wear formed from pleromic dentine within the vascular spaces of the spongy bone and may correspond to the sinuous osteodentine (osteodentine méandriforme) described by Thomasset (1930). The typical appearance of the tissue in a section normal to the surface is illustrated in figures 11, 14, figures 54 and 55, plate 6. Small, irregularly positioned pulp canals arise from the vascular canals in the spongy bone, the dentine is arranged around these short pulp canals and contains many short tubules arising from the pulp surface. Dentine also lines the longer canals within the spongy bone and again short tubules radiate from these surfaces. Pleromic dentine begins to form at the base of the worn compact dentine of the lower lip (figure 10); in this example the pulp canal of the pleromic dentine is horizontal relative to the vertical units of dentine. Some of the spaces within the pleromic tissue may have been previously eroded by osteoclastic activity (r.c. figures 11 and 14). The tissue between the infilling dentine is typical bone with osteocytes enclosed in lacunae. Some of the bone is arranged as lamellae concentric with the vascular canals; this is a result of appositional growth of bone. The entire tissue thus becomes relatively compact bone with small vascular spaces. It should be noted that the tissue described here does not fit the histological description of pleromic dentine in the heterostracian dermal armour as first described by Tarlo & Tarlo (1961). However, as it is a tissue of secondary formation in response to wear which infills existing spongy bone, it is considered to be a good example of physiological pleromic dentine where the mechanism of growth is easily visualized in cellular terms.

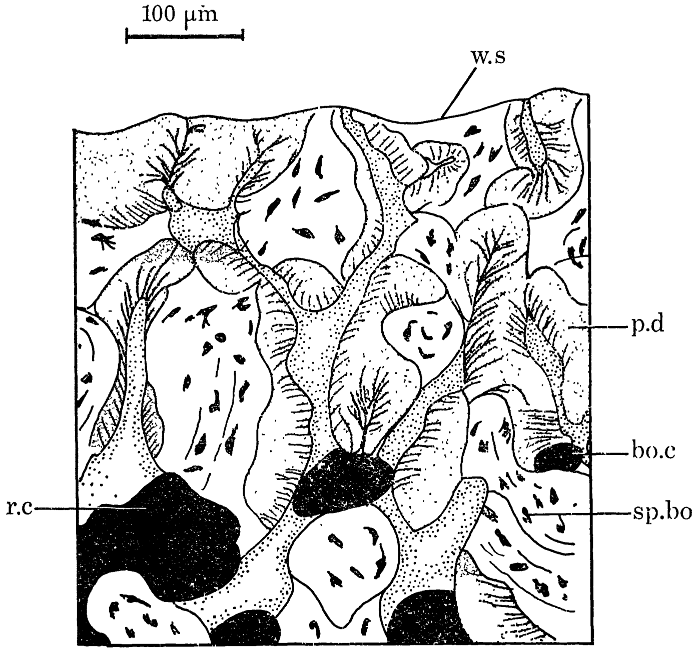


Figure 11. *Holodipterus gogoensis* Miles. Pleromic dentine on worn surface of the lower lip. From P52569.

Similar pleromic tissue from the prearticular is illustrated in figure 14, taken from a vertical section adjacent to the cusp of a prearticular tooth. The regular structure of the bone is interrupted by areas of pleromic dentine which infill the relatively large vascular spaces, possibly enlarged by resorption before new dentine formation. A similar tissue is illustrated in the dentary of *Holodipterus sanctacrucensis* (Gorizdro-Kulczycka 1953, fig. 1). Denison (1974, p. 40) has also described a similar repair tissue in *Dipterus valenciennesi* which he regards as a pleromic dentine in the strict sense, which fills the cavities in the spongy bone between rows of denticles.

At the antero-ventral border of the lower lip, the continuous dentine layer is interrupted by the regular arrangement of sensory pits which open at the enameloid surface through wide canals. This region is illustrated in figure 12 and figure 56, plate 6, from a vertical section through the composite tubercles and sensory pits. Enameloid covers the surface and also extends as a tapering layer down the sides of the tubercles. The pulp canals are arranged in a similar way to those of the compact dentine, neck canals open at the base of the tubercles from the spongy bone layer (figure 12). The histology is very similar to that described for the tubercles of *Griphognathus*.

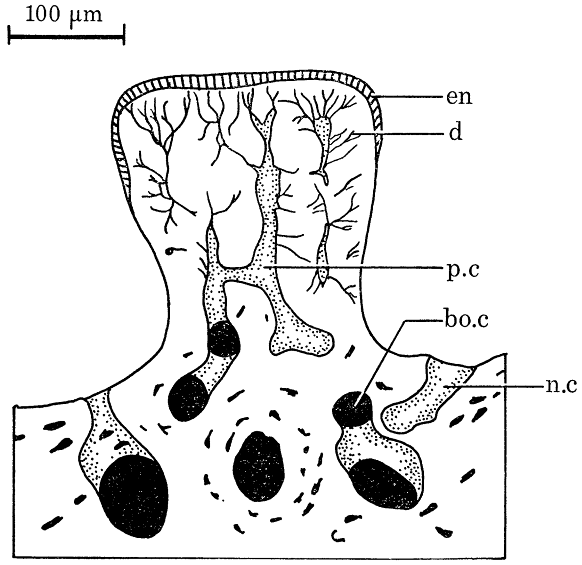


FIGURE 12. *Holodipterus gogoensis* Miles. Tubercle on the ventral border of the lower lip. From P52569.

(iii) *Tooth cusp and denticles of the prearticular*

The dorsal margin of the prearticular bears a row of blunt teeth (Miles 1977). A vertical section through one of these teeth is illustrated in figure 57. The tissue is unlike any seen in *Griphognathus* but very similar to the tooth plates of *Chirodipterus australis*. Enameloid is not present on the worn surface; most of the tissue is formed from an amorphous acellular mass, superimposed on the supporting spongy bone. It is most readily described as a homogeneous, compact dentine in which tubular processes from the pulp canals are very short. The pulp canals are almost completely occluded except in the basal region where they are confluent with the vascular spaces of the spongy bone. The dentine is not strongly birefringent in polarized light, shows little organization into oriented elements, has a granular texture and is probably not highly mineralized relative to other tooth plates.

The denticles which cover the medial surface of the prearticular are illustrated in figure 13. They are composite denticles with several vertical pulp canals, and numerous branching tubules which radiate towards the upper surface and the lateral surfaces of the denticle. Enameloid extends down the sides of the denticles and may become partly buried with the growth of adjacent bone. These denticles are very similar in their basic structure to those which cover the buccal cavity of *Griphognathus*. Similar denticles are found on the other bones of the palate, and in small localized areas of the snout where resorption has occurred, and the covering of compact dentine is not complete. The surface appearance of these denticles is illustrated in the scanning electron micrographs of the prearticular (figure 58, plate 7). Unworn denticles have many lateral ridges radiating from a longer central ridge (figure 58, plate 7). This is similar to the structure of many placoid denticles of elasmobranchs (Reif 1973). In some denticles the ridges feature small crenulations at regular intervals (figure 58, plate 7), similar to those described in *Griphognathus* and likewise thought to mark the tops of the dentine units when unworn. Worn denticle tops show the characteristic ringed surface of the dentine units which comprise the structure of these denticles. In many denticles the enameloid layer has been fractured and lost from the surface leaving an unworn dentine surface and a relatively thick fractured edge to the enameloid.

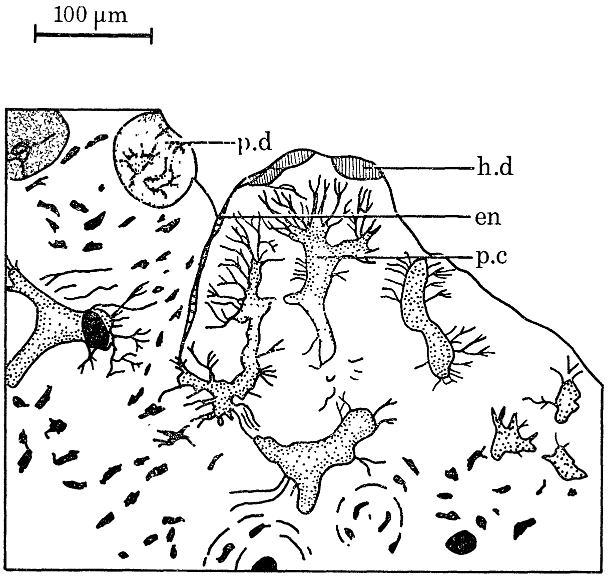


FIGURE 13. *Holodipterus gogoensis* Miles. Worn tissue of the prearticular, pleromic dentine and a denticle. From P52569.

In recently formed denticles, the basal part of the concavities between denticle ridges often has a poorly mineralized surface. This type of surface reflects a calcospheretic pattern of mineralization in which the growing focii of calcification have not fused into a continuous layer of calcified tissue (figure 59, plate 7). This structure probably represents a surface which will later become a poorly mineralized boundary between these units of dentine and new infilling pleromic dentine. This type of surface is often contiguous with a more basally situated resorbing surface which may be a prelude to pleromic dentine formation.

(iv) *Pleromic dentine and denticles of the dermopalatine*

In many specimens the dermopalatine is covered by a plateau of pleromic dentine which represents a functional worn surface (figure 60, plate 7) and has the histological structure of the tissue previously described for the dentary (p. 45). Only at the margins of this tissue can separate denticles be identified. A similar surface is illustrated in the scanning electron micrographs (figures 62 and 63, plate 7) where also at the margins of the pleromic dentine separate denticles are found. In some specimens the entire surface is covered with separate denticles, with the exception of one fused row (figure 61, plate 7). Bone surfaces on which pleromic dentine has not formed bear denticles which represent various stages of growth from newly formed to worn bases, and denticle sites which are now represented by resorption pits (figure 65, plate 7). Unworn denticles are of the characteristic shape, crests joined by ridges with lateral ridges joining the central one (figure 64, plate 7). A typical resorption surface is illustrated in figure 65, plate 7, the sites of active resorption are marked by the raised edges of Howship's lacunae, these areas indicate that resorption is progressing both between the vascular canals and around their borders. The base of a worn denticle marks the limit of resorption of this surface.

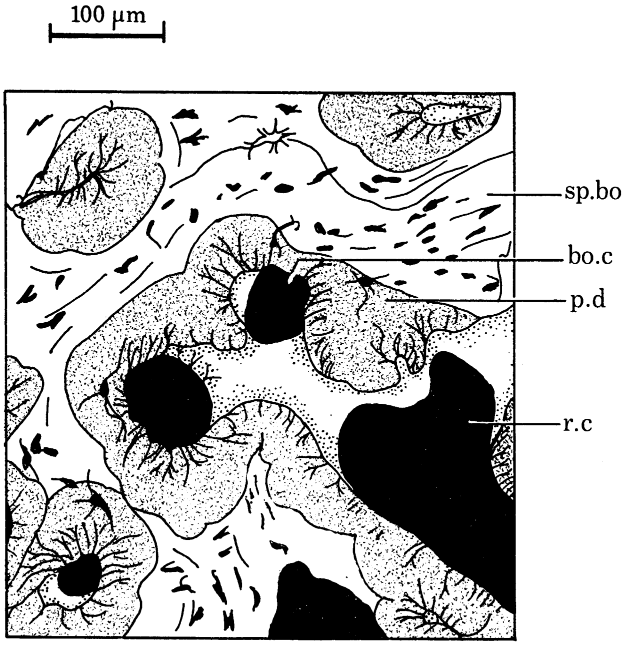


FIGURE 14. *Holodipterus gogoensis* Miles. Pleromic dentine on the prearticular. From P52569.

Figure 62, plate 7 is a scanning electron micrograph of a typical worn surface of pleromic dentine where smooth, resistant dentine lines the thin canals and the tubules emerge perpendicular to the length of the canal. This compares well with the pleromic tissue illustrated in figures 11 and 14. At the edges of this tissue are resorption areas, and separate composite denticles (figures 64 and 65, plate 7). In this region (figure 63, plate 7) one of the concave surfaces of the denticle is filled in by a unit of pleromic dentine (extrinsic odontode), and the components of the denticle (intrinsic odontodes) are themselves partly worn down. This formation together with that from the snout and prearticular suggests that the pleromic tissue forms as a result of a secondary formation of dentine units between the first formed denticles probably in relation to the vascular canals. This conforms with the concept of pleromic dentine as originally suggested by Tarlo & Tarlo (1961) for dentine infilling spongy aspidin between the tubercles.

(v) *Tubercles of the sub-opercular and other dermal bones*

The covering on the sub-opercular bone ranges from a continuous layer of enameloid, interrupted by a regular arrangement of pores (figure 66, plate 8), to rounded tubercles with a complete covering of enameloid. The enameloid is a relatively thick layer which extends down the sides of the tubercules, and the dentine arises from multiple, branched pulp canals as previously described (figure 67, plate 8). The organization of this tissue is not the same as cosmine.

In general the dermal bones have a generous covering of low tubercles which are slightly sculptured. The basal shape is round, oval or kidney shaped, and low ridges radiate from a central longitudinal ridge, similar to the buccal denticles previously described. In a section, submerged denticles form several layers of dentine and bone beneath the superficial layer. This superpositional growth of denticles is similar to that described for *Griphognathus* (p. 41), and it accounts for one eighth of the bone thickness ($\frac{3}{8}$ spongy bone, $\frac{4}{8}$ isopedine). The vascular spaces within the spongy bone are frequently lined with concentric lamellae which mark the layers of appositional bone growth within the secondary osteon as described for *Griphognathus* (p. 42). As a result of this bone growth the outer layers of the bone become more compact with smaller vascular canals. In the dermal bones of the oral cavity, pleromic dentine also contributes to hard tissue growth in the formation of a compact bone tissue.

(*c*) *Chirodipterus*

The only tissue common to *Griphognathus*, *Holodipterus* and *Chirodipterus* is the compact dentine which forms the tooth ridges of the snout and lower lip. The homogeneous compact dentine which is absent from *Griphognathus*, but present to a limited extent in *Holodipterus* is more extensive and more organized in the tooth plates of *Chirodipterus*. The third tissue, cosmine, is only present in *Chirodipterus*. Separate buccal denticles are rarely found and dermal tubercles are not present in *Chirodipterus*. Pleromic dentine forms at the edges of the tooth plates, also on the buccal surfaces of the vomer and dermopalatine.

(i) *Snout*

The ridges of the upper lip on the ventral surface of the dermal snout are medially and laterally placed and the tissue is a compact dentine similar to that described for *Griphognathus*. This tissue is continuous with that covering the anterior surface of the snout (pre-oral area) and is perforated by a regular arrangement of sensory pores. The dorsal surface of the snout is covered with cosmine with the characteristic pore canals. The junction between anterior and dorsal surfaces, the rim of the dermal capsule (Miles 1977) marks the position of a change from compact dentine to cosmine. This slightly raised ridge bears a surface with the ringed appearance of worn units of dentine as previously described for *Griphognathus* and *Holodipterus*. Between this tissue and the cosmine covered surface are many small resorption areas.

(ii) *Lip ridges of the dentary*

The continuous layer of tissue on the antero-lateral part of the dentary forms the hard lower lip and is a compact dentine very similar to that in the snout and lower lip of *Griphognathus*. Thin pulp canals are regularly spaced within the dentine, generally perpendicular to the functional surface and with basal openings into the small vascular spaces of the spongy bone (figure 15, figures 68 and 69*a* and *b*, plate 8). The enameloid layer is frequently worn away leaving the exposed dentine surface with the characteristic ringed appearance as described for *Griphognathus* and *Holodipterus* (pp. 36, 43.) The dentine units are closely packed with little intervening tissue except granular interstitial dentine. The circumpulpal dentine is translucent, and strongly birefringent, positive to the surface, indicating a high degree of oriented mineral crystals (figure 69*b*, plate 8). Sensory pores may interrupt the dentine layer, and these open into the vascular spaces of the spongy bone (figure 68, plate 8).

The vomer, dermopalatine and autopalatine are covered by a similar layer of dentine with worn surfaces showing an irregular distribution of dentine units.

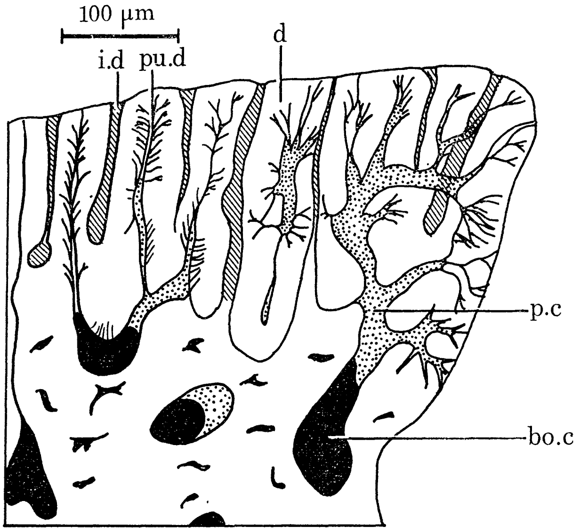


FIGURE 15. *Chirodipterus australis* Miles. Worn tissue of the lower lip. From P5100.

(iii) *Tooth plates of the prearticular and pleromic dentine*

The form and arrangement of the tooth plates on the entopterygoid and prearticular have been adequately described by Miles (1977). Their histology is illustrated from vertical sections in figure 16 and figure 70, plate 8 and their surface morphology in scanning electron micrographs (figures 71 to 77, plates 8 and 9).

The component tissue is best described as a homogeneous, compact dentine lacking in tubules and pulp canals in the upper part nearest to the functional surface. There are three to four zones of growth each marked by a line parallel to the most basal growing surface (g.l. figure 16). The basal dentine surface lines a large sub-dentinal cavity with a resorbing bone surface on the opposite border. Short pulp canals open from this cavity and tubules radiate from these canals a short distance into the dentine (figure 16 and figure 70, plate 8). The dentine is not strongly birefringent and no concentric or radially arranged zones have been observed in polarized light. Ørvig (1976*a*) regards the whole tissue in dipnoan tooth plates as vascular pleromin and the units of dentine as denteons each with concentric lamellae around the vascular canals. While agreeing that the terms osteodentine and trabecular dentine are inappropriate, I cannot accept that vascular pleromin is a justifiable alternative. The hypothesis that the canals contained blood capillaries must be regarded as doubtful but, of more importance, the interstitial tissue should not be regarded, as Ørvig claims, as pleromic in the strict sense of dentine infilling bone tissue spaces, but more probably a primary dentine which may or may not become hypermineralized. Ørvig (1976*a* and *b*) has elaborated on the formation of pleromin by stating that it is characterized by collagen reduction and hypermineralization, a process also referred to by Schmidt & Keil (1971) and called metaplastic. The circumpulpal dentine is translucent and from all physiological criteria the most likely to be highly mineralized in the same way as the

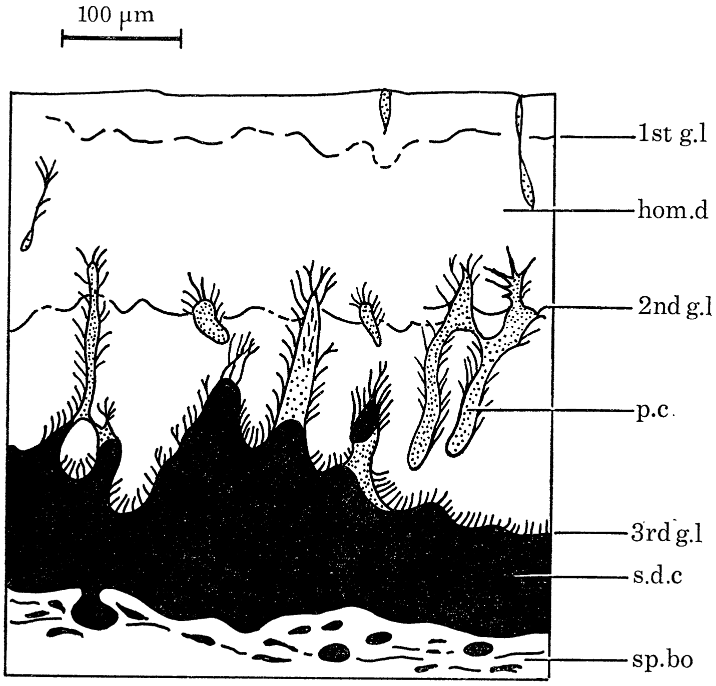


FIGURE 16. *Chirodipterus australis* Miles. Tooth plate parallel to the long axis. From P52561.

circumpulpal dentine of the tooth ridges in all three species. However, there are distinct differences from the compact dentine of the tooth ridges both in the histology and the appearance in the scanning electron micrographs. The dentine of the tooth plates is more homogeneous and relatively more of the matrix is hypermineralized, both in the interstitial and the circumpulpal dentine. The dentine of the tooth plates is constantly renewed by basal growth where the supporting bone is apparently resorbed in advance. At the sides of the tooth plate, dentine invades the spongy bone and infills the vascular cavities with hard translucent dentine to provide a more resistant tissue, a genuine example of pleromic dentine (figure 17). The tissue is exactly comparable with the pleromic dentine described for *Holodipterus* and is also present on other functional bone surfaces as on the vomer and the dermopalatine. When unworn these bone surfaces are covered by a continuous layer of compact dentine.

The functional surface of the tooth plate examined in the scanning electron microscope after brief etching with acid, reveals less difference between the circumpulpal dentine and the interstitial dentine than was apparent on the functional surfaces of the tooth ridges in *Griphognathus* (figures 71, plate 8 and 74, plate 9). In most regions, open pulp canals are found, each canal bordered by a very smooth dense tissue equivalent to the translucent circumpulpal dentine (figure 72, plate 9). The surrounding interstitial tissue is, however, equally highly mineralized judging from the level of the surface after acid-etching. Surrounding the circumpulpal dentine are one or two concentric regions which may represent successive layers of pulpal dentine which fill in the pulp canal as it becomes progressively occluded, as shown in figure 74, plate 9 where a large central pulp canal is not apparent. In many regions, smooth dense tissue is found in the interstitial regions (figures 71, plate 8 and 74, plate 9) which is probably equivalent to the petrodentine (Lison 1941), pleromic dentine (Ørvig 1951, 1967, 1976*a*), and metaplastic dentine (Schmidt & Keil 1971) described in other dipnoan tooth plates. Comparison with tissues in tooth plates of other species of dipnoan will only be possible after further detailed examination. Many of the tubules which radiate from the pulp canals would have contained cell processes as extensions from the pulpally situated odontoblasts. Other spaces within the dentine may have contained collagen fibre bundles as part of the unmineralized organic matrix (figures 71–75, plates 8, 9).

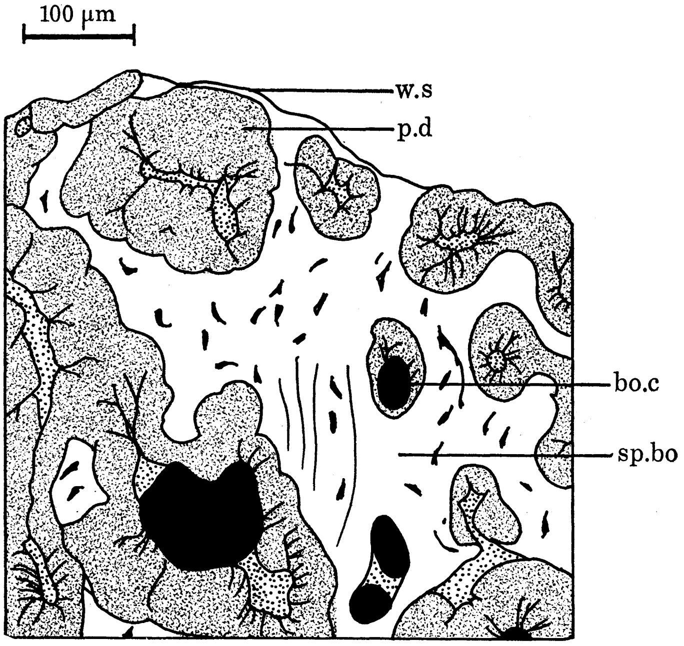


FIGURE 17. *Chirodipterus australis* Miles. Pleromic dentine medial to the tooth plate. From P52561.

In some regions where the functional surface has been worn further down, the pulp canals branch and the internal surface of the pulp canal is exposed where it passes in a horizontal direction relative to the surface (figure 73, plate 9). Here the smooth surface of the circumpulpal dentine is perforated by openings to the tubules which contain the cell processes from the odontoblasts (figure 75, plate 9). In longitudinal view these tubules are walled by a dense compact layer of mineralized tissue, possibly equivalent to mammalian peritubular dentine. Whether or not the canals contained blood capillaries, as blind capillary sprouts, seems to be problematical and unlikely to be clarified from examination of fossil material. The diameter of the open canals of the order of 20–30 μm would make it possible for either a group of 2–3 odontoblasts to occupy the space or a thin capillary sprout and one odontoblast alongside the capillary. It does not seem possible without measurements of extant forms to choose between the two alternatives. The difficulty of terminology is avoided if the structures are regarded as pulp canals essentially containing the odontoblasts which produce and sustain the dentine in a vital tissue.

Towards the edges of the tooth plate the tissue changes to one which much more resembles the compact dentine of the tooth ridges, figure 76, plate 9, and eventually merges into the bone where an intermediate zone resembles the pleromic dentine previously described and illustrated in figure 17. Closer examination of the surface shows the highly mineralized circumpulpal dentine, proud of the surrounding interstitial tissue, features which were demonstrated in the tooth ridges (figure 77, plate 9).

(iv) *Cosmine on the dermal bones*

As described by Miles (1977) all the typical features of dipnoan cosmoid plates are exhibited by those of *Chirodipterus*. The histology is illustrated in figure 18 and is typical of cosmine in general in so far as the dentine layer is broken up into 'tubercles' or units of cosmine by the regular arrangement of pores which open from the horizontal canal system. Unlike the tubercles of *Griphognathus* and *Holodipterus* the enameloid layer does not extend down the sides of the 'tubercle'. The dentine is confined to the superficial layer of cosmine (figure 18), which in the region illustrated, does not show superposition of successive generations. The pulp canals are short with many branches, and the majority of tubules run towards the enameloid surface although several run towards the sides of the dentine and may anastomose around the wall of the ascending pore canal with the adjacent dentine tubules. Many of the tubules penetrate the enameloid layer which is approximately 25 μm thick and exhibits rodlet birefringence with a mixed positive and negative sign as described for *Griphognathus* (p. 35).

The dentine layer of the cosmine in the dermal bones is about two thirds the thickness of the dentine in the tissue covering the lip. Also it is not differentiated into circumpulpal and interstitial dentine, and does not grow basally into the spaces of the spongy bone in the way that pleromic dentine forms. This accords with the different requirements of the two tissues, cosmine not being subjected to the same degree of wear as the tooth ridges on the dermal bones. The mode of replacement and growth of this cosmine is presumably the same as all cosmine in the Devonian dipnoans, by periodic resorption and regrowth of cosmine. The growth of cosmine in the squamation of Devonian dipnoans has been comprehensively described by Ørvig (1969) in an excellent account of consecutive areal growth on these scales. Ørvig allows for the possibility that in the cosmine cover of dermal bones there may be in addition to areal growth, local resorption and new formation of cosmine. Miles (1977) has noted the absence of extensive resorption on the dermal skull bones of both *Chirodipterus australis* and *Chirodipterus paddyensis*, and commented that the typical features of dipnoan plates include raised areas and generations of layers. The observations on the histology of these bones have not been sufficiently extensive to establish how frequently superpositional growth occurs, although some of the fracture surfaces through the cosmine bones appear to show superposition of one layer of cosmine over the preceeding one (figure 78, plate 9). This is most likely an overlap of one generation by the next.

In the scanning electron micrographs of cosmine covered bones the even distribution of pore canals is readily observed (figures 79 and 84, plates, 9 10). This pattern of small pore canal openings is only interrupted by the much larger openings to the sensory canals which extend through the cosmine and into the tissue spaces within the spongy bone (figure 79). In the figured specimen, the cosmine does not completely cover the entire bone and in these exposed areas of spongy bone the surface is one on which bone is in the process of forming. The edge of the cosmine can be regarded as a forming or resting edge and may be of use in extrapolating some information on how cosmine is formed during histogenesis of the tissue (figures 80 and 81, plate 10). Three features are of interest in this region; one is that no pore canals are found in this peripheral ring of cosmine, the nearest pore canals to the edge being almost exactly the same distance from the edge as the average inter-pore distance, suggesting a strong influence of the cell-groups contained within the pore canals over the formation and arrangement of the cosmine. Thomson (1975) in an account of the biology of cosmine based on a osteolepid, *Ectosteorhachis nitidus*, concluded that the architecture of the dentine in the cosmine layer was a reflection of the arrangement of the neuromast organs. The neuromast sensory cells were probably situated at the base of the flask-shaped pore canals with the kinocilia projecting into the mucous containing space immediately below the opening to the pore canal (Thomson 1975, figure 20).

The second feature on the forming cosmine surface to be noted is the hexagonal pattern of the enameloid layer. This is only barely detected at magnifications of 200 times (figure 80, plate 10) but is clearly seen at 500 times and 2000 times as in figures 81 and 82, plate 10). The order of size of these hexagonal units is 5–10 μm and within the region of 15–20 of these span the distance between the pore canals (figure 82, plate 10). One obvious explanation of this pattern is that it in some way reflects the size and arrangement of the epithelial cells overlying the enameloid. The enameloid layer in vertical histological sections is strongly birefringent with a rodlet arrangement of the crystallites. The epithelial cells undoubtedly influence the formation of mineral salts within this layer and the boundaries between the cells may be equivalent to the borders of the hexagons. Many regions of the cosmine surface reflect this hexagonal pattern particularly on the surfaces sloping towards the pore canals where it is unworn.

The third feature on the forming edge of the cosmine is the slightly serrated surface at the lower border of this edge (figure 81, plate 10) from which the hexagonal pattern is missing. This suggests an unfinished region without a complete enameloid cover in which the primordial cones of dentine are proud of the surface and represented as separate points, similar to those described in the buccal denticles and dermal tubercles of *Griphognathus*.

In sections of cosmine, the natural border to cosmine often presents a rounded or pointed edge with enameloid extending over the dentine border. These cosmine margins were considered by Gross (1956) to be 'finished' margins in the sense that no further growth of cosmine could take place once the surface had been completed by enameloid. These margins were distinguished from 'unfinished' margins which are clearly resorption surfaces. Thomson (1975) has critically discussed this evidence and agrees with the conclusion that any existing cosmine surface is incapable of growth. In view of the present observations with the scanning electron microscope the suggestion that part of the cosmine margin has not completely formed must be tested by further examination of cosmine surfaces. The ways in which these observations relate to previous accounts of the growth of cosmine are expanded in the discussion.

Some of the cosmine surfaces were lightly etched with acid which revealed the underlying structure of the cosmine, rather as a series of horizontal sections would do in the optical microscope (figures 83 and 85, plate 10). As could be predicted from the sections (figure 18) the small pore canals now appear as wider canals as the flask-shaped part of the pore canal is reached (figure 83, plate 10). By comparing figures 84 and 85, plate 10 taken at the same magnification it can be seen that the distances between the centres of the pore canals are equivalent. Between these large pore canals are several smaller irregular openings to the pulp canals (figures 83 and 85, plate 10). These can be compared with the pulp canals in the sectioned material (figure 18) where several branches to the pulp canal extend throughout one cosmine unit between adjacent pore canals. In regions where the cosmine has been etched further away (figure 85, plate 10), the pore canals connect with each other as can also be observed in the sections. Thomson (1975) has also used etched cosmine surfaces to interpret the structure in *Ectosteorhachis* and described the pattern of interconnection between the pore-canal system and the pulp-canal system. In his material the fossil matrix casts of these canals were left proud after the biological mineral was removed, unlike the present material in which the fossil matrix had been removed first. Both the pulp canals and the pore canals interconnect within the vascular spaces of the spongy bone. Initially the pore canals open into the horizontal canals of the mesh canal system (figure 86, plate 10). Gross (1956, fig. 72A) has illustrated the arrangement of canals in the dermal bones of *Dipterus*. In *Chirodipterus* there is a similar arrangement, the pore-canal system is enmeshed within the cosmine layer and superficial to the basal canals which link with the descending pulp canals. The latter are more numerous than the pore canals and are dispersed between them as part of the dentine system.

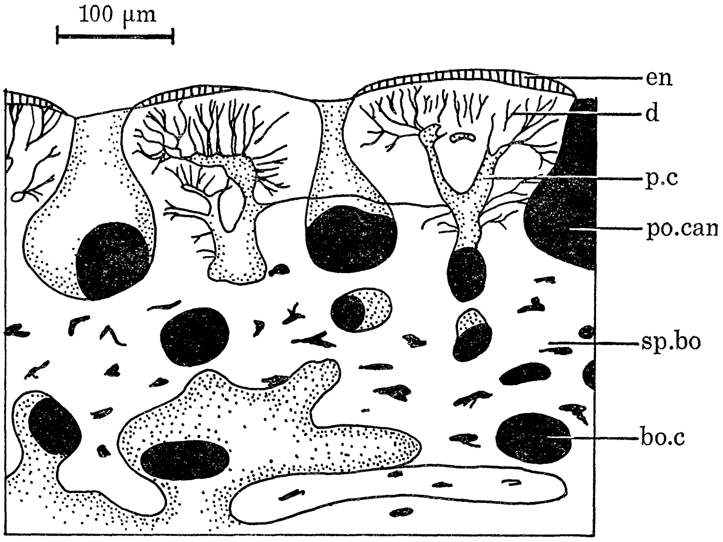


FIGURE 18. *Chirodipterus australis* Miles. Cosmine on a dermal skull bone. From P52562.

The structure of the dermal bone beneath the cosmine layer is the same as described for *Griphognathus*. There is an extensive layer of spongy bone between the outer dentine cover and the basal isopedine (figure 78, plate 9). Within the upper layers of the spongy bone, secondary osteons have formed infilling the vascular canals with regular lamellae of bone. Seen at relatively low magnifications in the scanning electron microscope, these secondary osteons consist of smooth homogenous material lining the vascular spaces of the spongy bone (figure 87, plate 10). The horizontal mesh canals immediately beneath the cosmine layer and the basal canals are not generally infilled with lamellar bone in the same way (figure 86, plate 10). Thomson (1975) made the interesting observation on the cosmine of *Ectosteorhachis* that primary osteonal bone is always present immediately underneath the dentine except when cosmine is absent. He interpreted this as a bone of attachment which is resorbed together with the cosmine, and reforms under the influence of the cells producing the cosmine layer. In most systems where dentine units are fused to the underlying bone, the area of bone immediately between the dentine and the spongy bone can be regarded functionally and developmentally as a bone of attachment, particularly where it is resorbed with the dentine and reforms to link the new dentine unit with the existing bone. The cosmine of *Chirodipterus* conforms to this general pattern and is similar to the cosmine of osteolepids in this respect as well as in its general structure.

6. Discussion

(a) *The primitive dipnoan dentition: a contribution to the relations from the microstructure of the tissues*

Miles (1977) has cogently discussed the evidence for establishing the primitive dipnoan dentition and concludes that it comprises evenly scattered buccal denticles, a feature in agreement with Denison (1974), and in addition tooth ridges, while tooth plates or blunt teeth are absent. All these primitive features are retained in *Uranolophus* (Denison 1968) and *Griphognathus* (Miles 1977).

Analysis of the microstructure of the tissues in *Griphognathus whitei*, *Holodipterus gogoensis*, and *Chirodipterus australis* lends support to this hypothesis and more importantly does not refute it. Consideration of the microstructure of the buccal tissues also provides further evidence towards the probable interrelations of these genera. Miles (1977) has concluded that the three genera of Australian dipnoans are divergently specialized in their dentitions. He has further concluded that tooth plate bearing dipnoans comprise a monophyletic group. Discussion of the microstructure of the dental tissues is presented here to examine these hypotheses.

It is considered valid to use the microstructure of dental tissues to establish the interrelations of closely related genera. This assumes a common genetic pool, in a theoretical ancestor, which controls tissue genesis and response to wear, and accounts for adaptive radiation. It may not be valid to compare the tooth structure of genera within different major groups or classes, as Radinsky (1961) has also stated, and conclude that a similarity of dental structure indicates a common phylogeny. This is because it may be more economical to assume the ontogeny and phylogeny of the tissues are different, resulting in a similar functional structure because the functional requirements which have selected the structure are similar. It is not, therefore, thought to be correct to say as Jarvik (1964, 1967) does, that dipnoan tooth plates are comparable

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Description of plate 1

Griphognathus whitei Miles

Figure 19. (*a*) Photomicrograph of upper lip with worn areas and sensory pores, from P52572 (× 25). (*b*) Photomicrograph of the ringed surface on a worn area shown in figure 19*a*; see also figure 3*a*, from P52572 (× 50).

Figure 20. S.e.m. of denticles on the ventral surface of the dermal snout. P52572 (field width 960 μm).

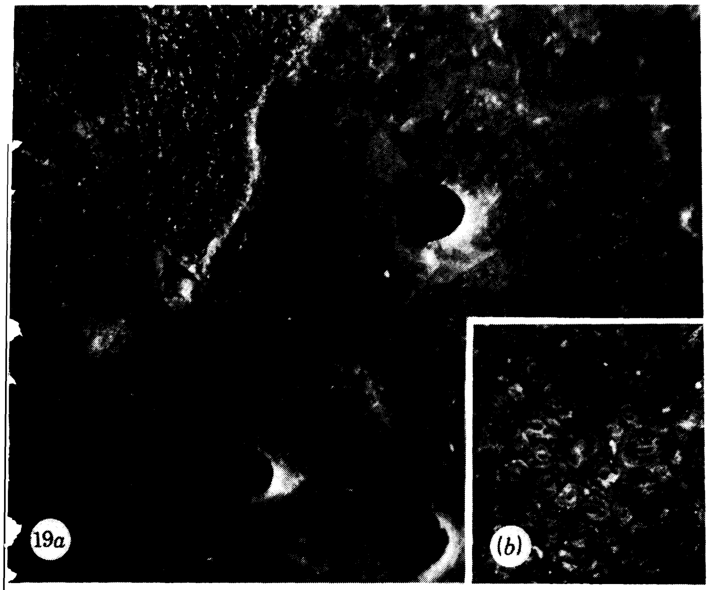
Figure 21 (*a*) Photomicrograph of a vertical section through the unworn surface of the upper lip. The dermal snout in ordinary transmited light; see also figure 1, from P52572 (× 140). (*b*) Photomicrograph of the same region as figure 21*a* in polarized light. The birefringence of the enameloid is contrasted with the underlying globular dentine, and the less strongly birefringent circumpulpal dentine from P52572 (× 140).

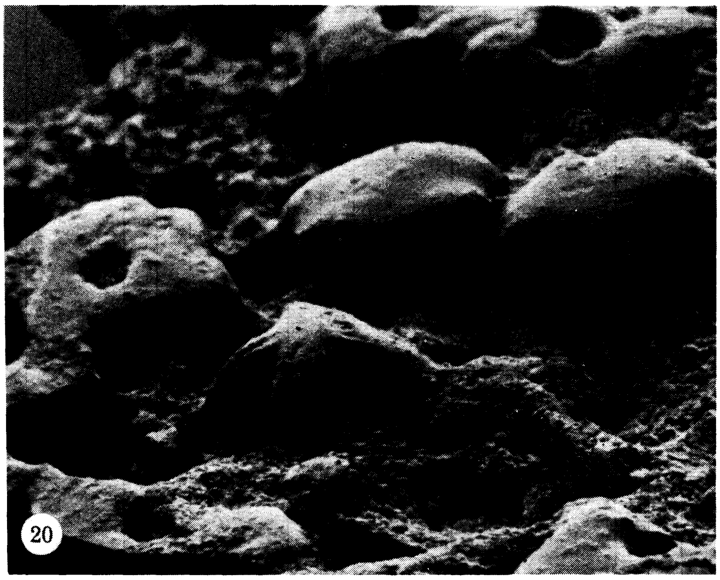
Figure 22. S.e.m. of a fracture surface through the dermal snout which shows the rodlet structure of the enameloid layer. P50998 (field width 50 μm).

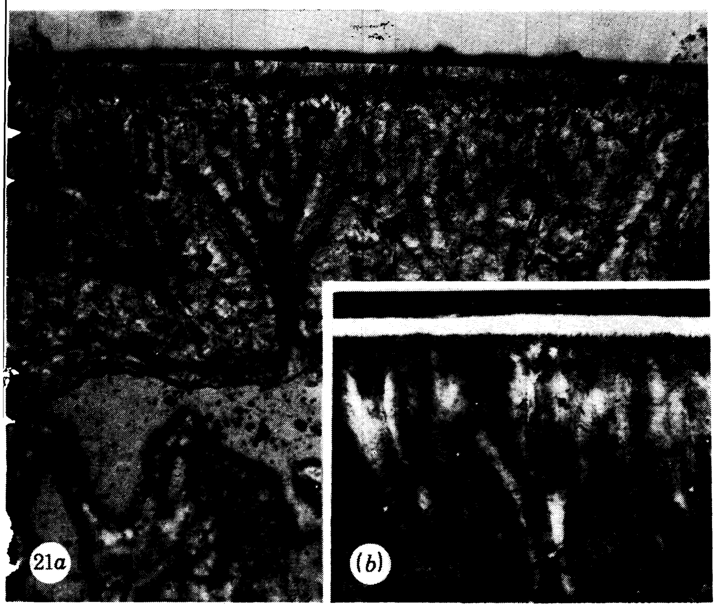
Figure 23. S.e.m. of a worn surface of the snout, similar to the ringed surface in figure 19*b*. The circumpulpal dentine is raised above the interstitial dentine and the pulp canals have infilled with secondary pulpal dentine. Holotype P50996 (field width 90 μm).

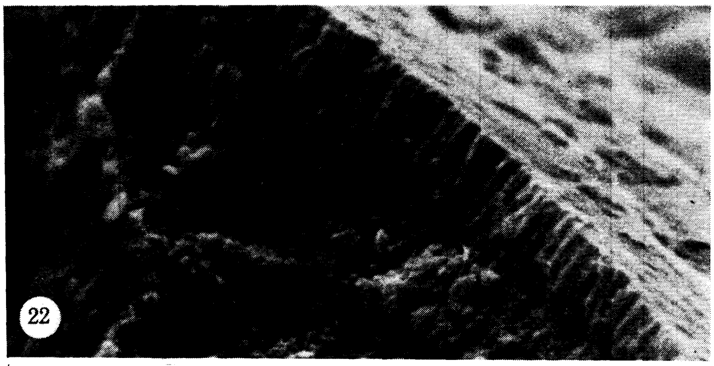
Figure 24. (*a*) Photomicrograph of a vertical section through the worn surface of the upper lip of the dermal snout in ordinary transmitted light; see also figure 3, from P52572 (× 140). (*b*) Photomicrograph of the same region as figure 24*a* in polarized light. Compared with figure 21*b* the enameloid and globular dentine is lost and the circumpulpal dentine is strongly birefringent as is the secondary pulpal dentine. From P52572 (× 140).

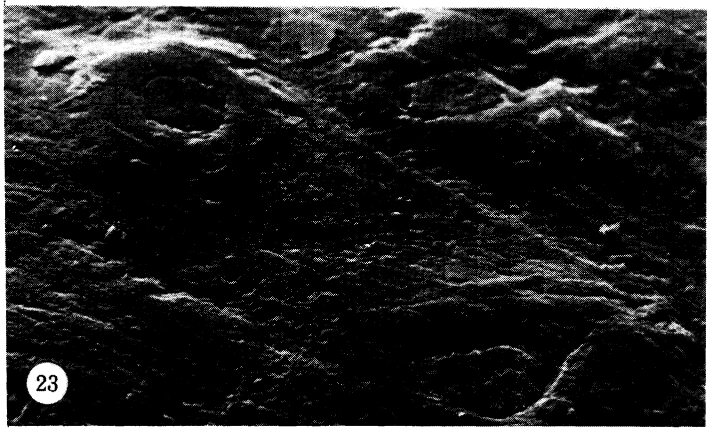
Figure 25. Photomicrograph of a vertical section through the upper lip of the dermal snout which shows the regions of figures 21 and 24 above the extensive spongy bone. From P52572 (× 35).

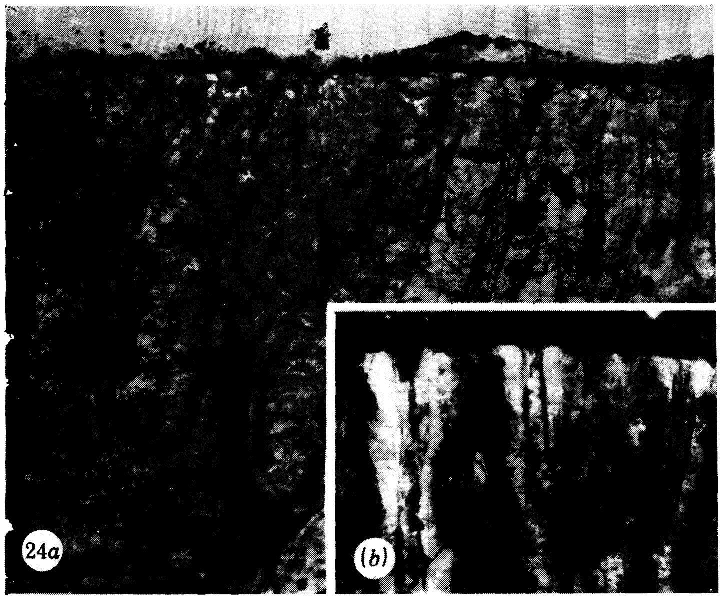


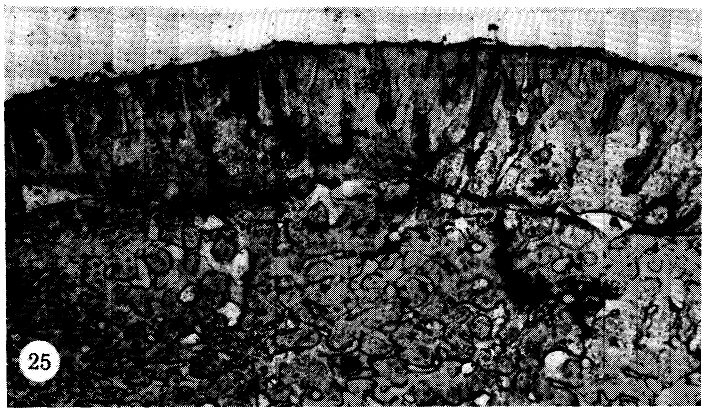












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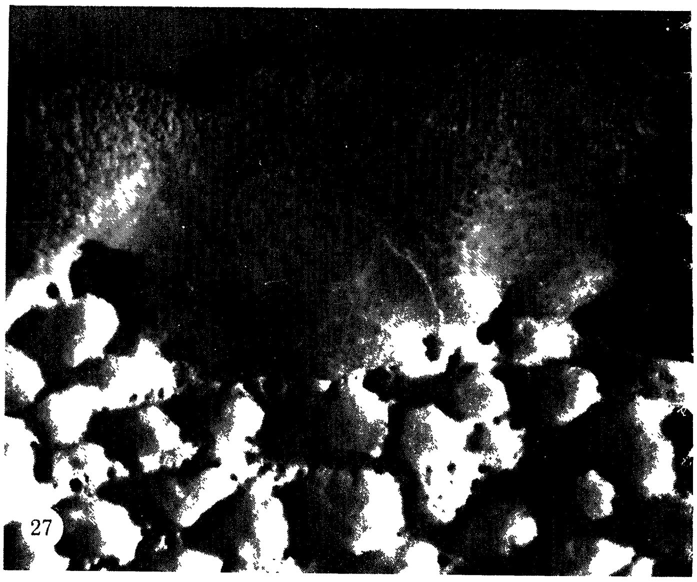
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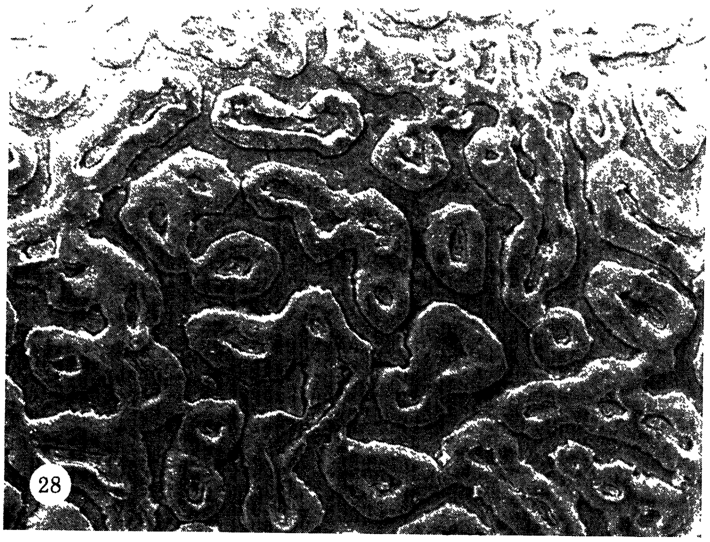
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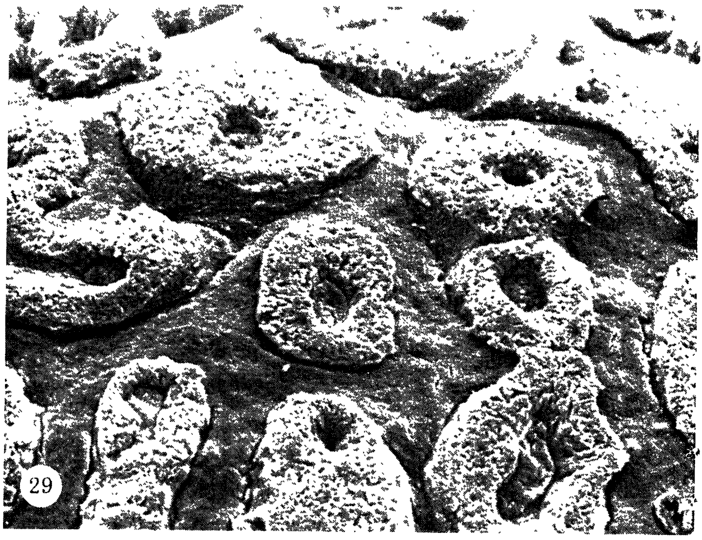
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Griphognathus whitei Miles

FIGURE 26. Photomicrograph of a vertical section through the tooth ridge and denticles of the dentary. These tissues are shown in surface view in figure 27. From P52578 (× 35).

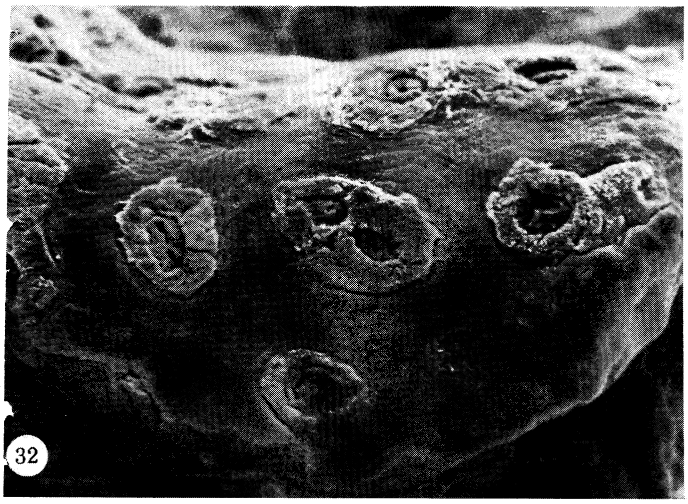
FIGURE 27. Photomicrograph of the tooth ridge and denticles on the medial surface in which the ringed worn surface of the ridge and some of the denticles are shown – as in figure 19*b* of the snout. P52572 (× 18).

FIGURE 28. S.e.m. of the surface of the tooth ridge shown in figure 27 after treatment with 0.1 N HCl for 1 min. The rings of circumpulpal dentine are proud of the interstitial and pulpal dentine. P52572 (field width 460 μm).

FIGURE 29. S.e.m. of one region adjacent to figure 28 in which the tubules in the circumpulpal dentine are seen to arise from the pulpal canal. P52572 (field width 186 μm).

FIGURE 30. S.e.m. of a region in figure 28 in which the circumpulpal dentine is more highly mineralized than that in figure 29. P52572 (field width 93 μm).

FIGURE 31. S.e.m. of one of the pair of dentine units shown in figure 30. P52572 (field width 46 μm).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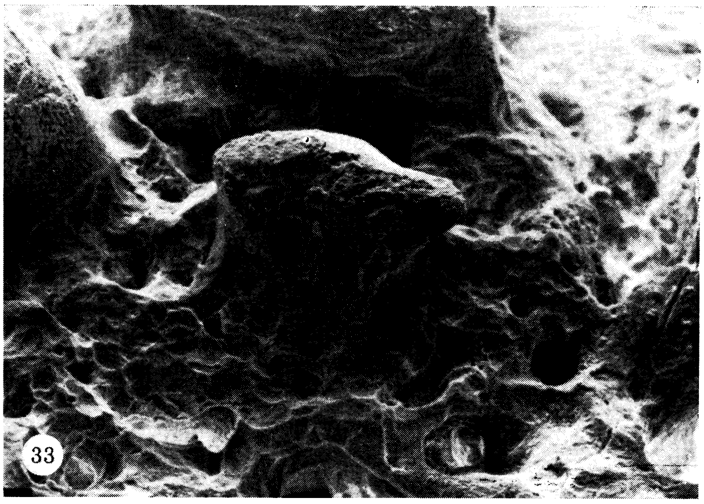
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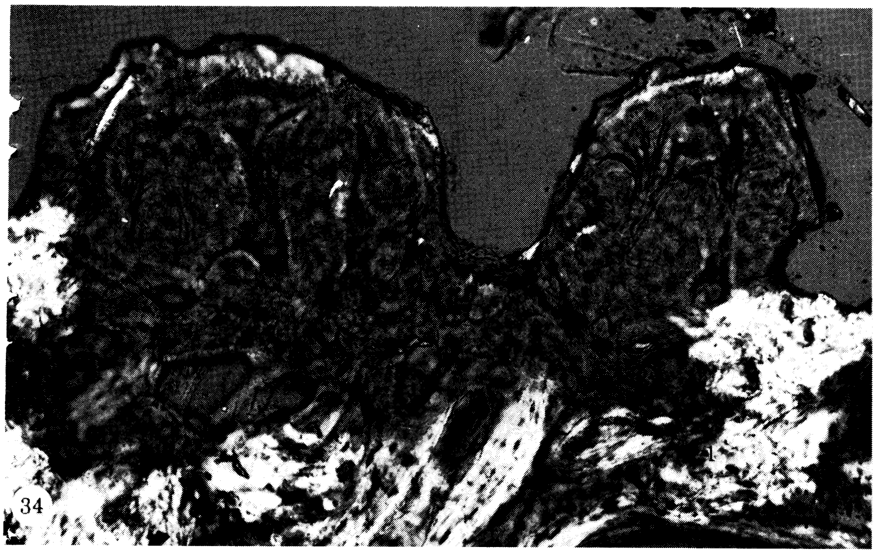
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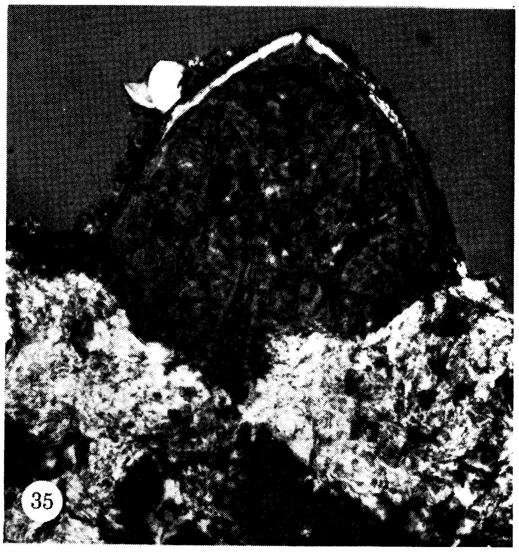
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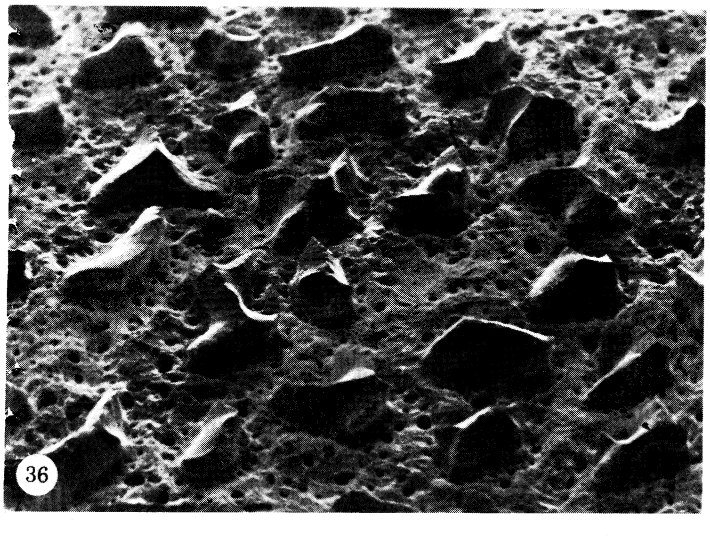
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Griphognathus whitei Miles

Figure 32. S.e.m. of the surface of a denticle medial to the tooth ridge of the dentary, after treatment with 0.1 N HCl for 1 min. The dentine units are similar to those in figure 29. P52572 (field width 186 μm).

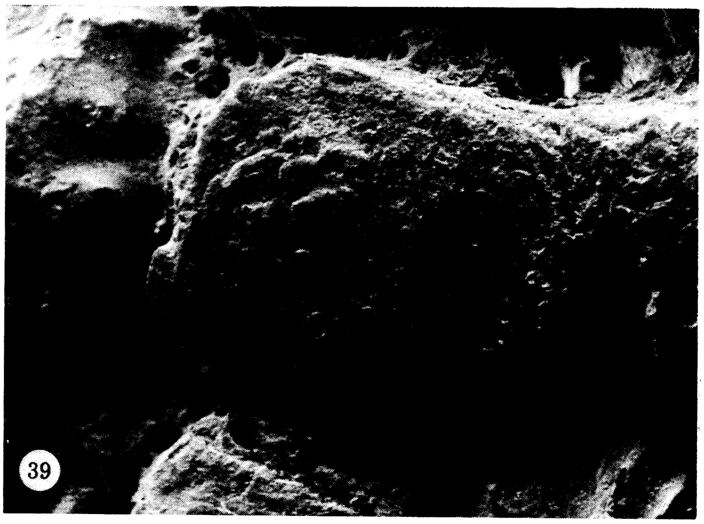
Figure 33. S.e.m. of the side of a denticle adjacent to figure 32 in which the dentine units are seen in longitudinal view where resorption has removed part of the denticle base and surrounding bone, as evidenced by the scalloped surface. P52572 (field width 460 μm).

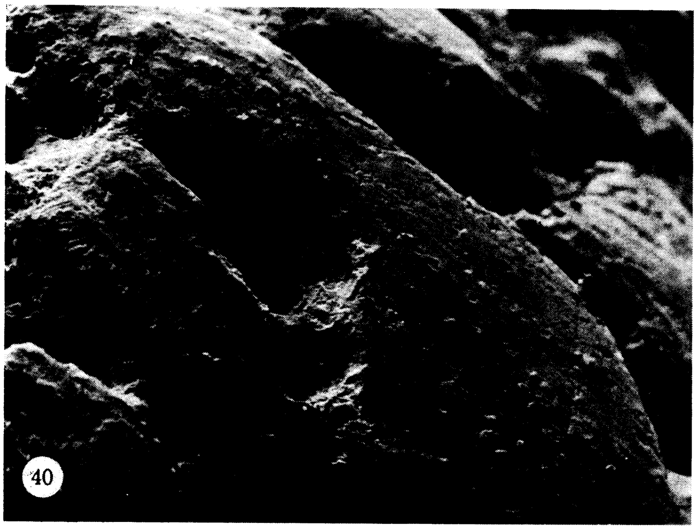
Figure 34. Photomicrograph of a vertical section through the denticles on the basibranchial seen in partial polarized light. Enameloid is lost from the worn surface but retained at the sides, and the superficial dentine is slightly birefringent. At the base of one denticle is a resorption surface. See figures 5 and 6. From P50998 (× 140).

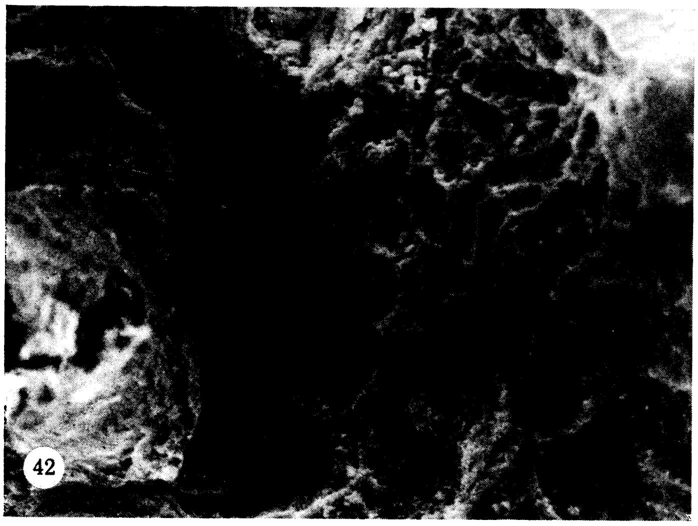
Figure 35. Photomicrograph of a vertical section through an unworn denticle on the basibranchial tooth plate with enameloid intact above the multiple pulp canals, also in partial polarized light. See figures 5 and 6. From P50998 (× 140).

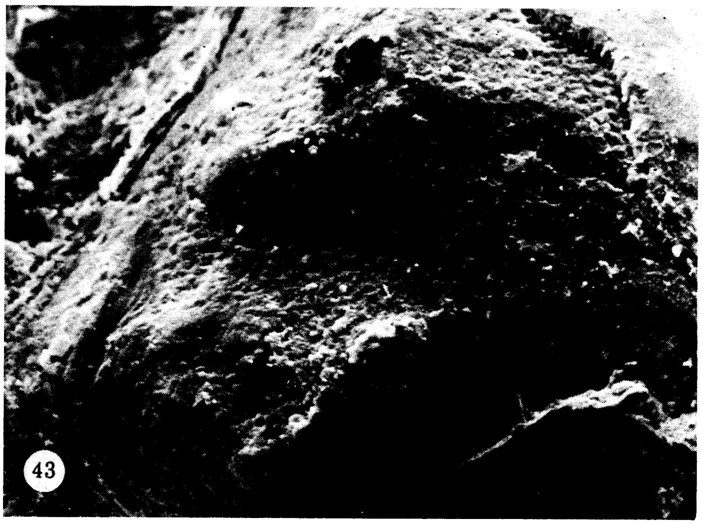
Figure 36. S.e.m. of the denticles on the surface of the prearticular. (Number unknown; field width 1840 μm).

Figure 37. S.e.m. of one of the newly formed denticles from the region in figure 36. Separate points are seen along the crests of the ridges which are described as the tips to the component dentine units. P52579 (field width 460 μm).









Griphognathus whitei Miles

Figure 38. Photomicrograph of the denticles on the surface of the ascending process of the prearticular. Worn tops show the ringed pattern as shown in figures 19 and 27. The unworn, new denticle has a shiny enameloid surface. P52579 (×45).

Figure 39. S.e.m. of the worn denticles seen at the top of figure 38. The translucent rings of circumpulpal dentine are raised above the level of the interstitial dentine and the secondary pulpal dentine. P52579 (field width 930 μm).

Figure 40. S.e.m. of an adjacent worn denticle which shows a regular arrangement of the dentine units. P52579 (field width 930 μm).

Figure 41. S.e.m. of the new denticle in figure 38 which is forming in a resorption cavity at the base of the worn denticle. P52579 (field width 930 μm).

Figure 42. S.e.m. of a resorption surface at the base of a worn denticle which is alongside a vascular canal. P52575 (field width 92 μm).

Figure 43. S.e.m. of the surface of a denticle on the prearticular in which the enameloid layer has fractured leaving a regularly pitted surface to the dentine. P52575 (field width 186 μm).

(implied homologous) with holocephalan teeth because they have tubular dentine (Jarvik 1964), or columnar pleromic hard tissue (Jarvik 1967). Indeed the choice of terminology for the tissue should ideally take account of its mode of development, both ontogenetic and phylogenetic, as well as its definitive structure. I intend to return to the question of the terminology later in the discussion (§6*c*).

The variety of dental tissues found in the jaws and palate of *Griphognathus whitei* demonstrate that in this genus the dental apparatus had not become highly specialized but had retained a flexible developmental system with the potential to form a range of dental structures. Denison (1974) suggested that the variety of dental structures present in the early dipnoans probably represents experimentation rather than stabilization into a non-flexible developmental system. Denison (1974), like Thomson & Campbell (1971), considers that tooth plates are specialized adaptations to a particular manner of feeding. Ridged tooth plates are absent from *Griphognathus whitei* and no comparable tissue has been observed in any of the specimens which have been examined. However, in *Holodipterus gogoensis*, tissues which are very similar in their basic histology to all the types present in *Griphognathus* have been recorded in the present investigation, and in addition a further tissue type, in the form of blunt, knob-like teeth, which is comparable although not identical with the tissue which comprises the tooth plates of *Chirodipterus australis*. These structures would seem from their histology to be an early or abortive example of the radiating rows of ridges found on the tooth plates of many dipnoans (Miles 1977). Denison (1974) suggested that the four radiating rows of teeth in *Fleurantia* illustrate an ancestral condition, but the histology of these teeth is not known. Miles (1977) concludes that the rows of teeth on the palate of *Fleurantia* and *Holodipterus* have a functionally determined orientation and not a phyletic relation, because of the other characters used in his argument, although a similar histological structure would argue in favour of a common phyletic origin. The rounded tuberosities of *Dipnorhynchus sussmilchi* are regarded as a specialized feature (Thomson & Campbell 1971), the histology of these teeth has not been recorded. The palatal dentition of *Dipnorhynchus lehmanni* (Lehmann & Westoll 1952; Jarvik 1954) also comprises one or two rows of blunt teeth but the histology is not featured because of poor preservation. Miles (1977) has suggested that these may all represent 'specialized' features which are sidelines to the more advanced tooth plates, and my own observations on the histology of *Holodipterus* are in agreement with this view.

Separate buccal denticles of similar structure are present in both *Griphognathus* and *Holodipterus* but not in *Chirodipterus*. Similar denticles have been described in *Griphognathus minutidens* (Gross 1956), and *Ganorhynchus splendens* (Gross 1965). Denison (1968) describes similar buccal denticles in *Uranolophus wyomingensis* as comprising simple orthodentine. The genera in which separate buccal denticles are present have been listed by Denison (1974). The histology of the majority of them has not been adequately described to make comparisons with the present observations.

The tissue which forms the tooth ridges of the upper and lower lips has been identified as similar compact dentine in all three genera of the Australian dipnoans, although of differing distribution and extent. Tooth ridges have been accepted by Miles (1977) as a primitive dipnoan feature, although specialized within the dipnoans as a group. Ørvig (1976*a*) has examined material of *Griphognathus whitei* from the Gogo collection and concluded that 'it has no equivalents in the odontodes of any crossopterygian or actinopterygian, but may be regarded as an elasmobranch character'. If the conclusion from this statement is that tooth ridges of *Griphognathus* are homologous with the teeth of some elasmobranchs as judged by their histological structure, then it cannot be accepted as a valid statement. As stated previously, tooth structure and histology may be adaptive and common to all durophagous types, a result of convergent evolution rather than a common phylogeny (Radinsky 1961). The supporting evidence for Ørvig's statement is that the tissue is to be regarded not as an osteodentine or pleromin (as found in dipnoan tooth plates), but as a 'coronal pleromic hard tissue' of the same type as in the teeth of most bradyodonts and certain selachians (Ørvig 1969, 1976*a*). Ørvig (1976*a*) considers that the tissue is otherwise unique to *Griphognathus* and *Uranolophus* and is, therefore, to be regarded as a specialized feature which has evolved independently of dipnoan tooth plates. While accepting that the tissue of the tooth ridges has evolved independently of the tooth plates, the reasons are not because it is a specialized feature unique to *Griphognathus*, but because it is a feature primitive to dipnoans which evolved before and independently of tooth plates which are a later specialization. I consider that the tissue arrangement in the tooth ridges is more widely distributed than *Griphognathus* and *Uranolophus*, and I also find that I cannot agree with Ørvig's interpretation of the histological structure. It seems more appropriate to evaluate Ørvig's terminology later in the discussion when terminology of the tissues as a whole can be considered, as distinct from considerations of their phylogenetic significance. It should be sufficient to state here that I have identified a tissue, referred to as compact dentine, in *Griphognathus whitei*, *Holodipterus gogensis* and *Chirodipterus australis* and Gorizdro-Kulczycka (1953, fig. 2) has also figured an identical tissue in the splenial tooth ridge of *Holodipterus sanctacrucensis*. Gross (1965) has featured what appears to be an identical tissue to the compact dentine on the upper and lower lips of *Ganorhynchus splendens* Gross. Gross similarly has not found any of the previous terms convenient but has referred to it as a 'dentine field'. Gorizdro-Kulczycka (1950) and Denison (1968) have suggested that *Ganorhynchus* and *Holodipterus* are related, although Denison (1968) admitted that they were inadequately known. The microstructure of the tissues which form the upper and lower lips is one feature common to these two groups. Denison (1968) has described the tissue of the tooth ridges in *Uranolophus wyomingensis* which he has termed trabecular dentine, and concluded that it has the characteristic structure of dipnoan teeth. From his description and his illustrations of sections through the splenial, dentary and pterygoid tooth ridges (figs 23A, E and F) I have concluded that the tissue of the tooth ridges and upper and lower lips in *Uranolophus* is identical with the compact dentine of the same regions in *Griphognathus*. A similar arrangement within the dentine layer of the skull roof bones has been described by Gross (1965) in *Rhinodipterus ulrichi* Ørvig, only in this tissue the dentine layer is more organized into close-packed parallel units which Gross has termed prism dentine. The structure of the tooth ridge in *Chirodipterus australis* is closest to this type of tissue, which in all probablity represents a more specialized stage of the similar tissue in *Griphognathus* and *Holodipterus*. Denison (1968) made the point that he could find no evidence in *Uranolophus* of the prismatic structure of the dentine as described by Gross (1965) in *Dipterus*, *Rhinodipterus* and *Ganorhynchus*. The tissue of the lower lips in *Dipterus valenciennesi* described by Watson & Gill (1923) as cosmoid bone with a shiny punctate surface is probably of the same structure as I have described for the compact dentine of the tooth ridges. Westoll (1949) and Lehmann & Westoll (1952) also regarded the tissue of the lips of *Dipterus valenciennesi* as an abnormal development of cosmine and inferred that this hard tissue was only found in specimens with well developed cosmine. This is no longer a tenable view as in *Griphognathus* and *Holodipterus* the tissues of the upper and lower lips are extensive and yet there is no cosmine on the dermal bones of the skull. The histology of the dental tissues in *Dipnorhynchus sussmilchi*

Etheridge is only sketchily reported by Thomson & Campbell (1971) who state simply that an enamel layer covers the snout, dentary and palate. This would predictably be a layer of compact dentine as described for these Upper Devonian dipnoans. The information which is available on the microstructure does not contradict the hypothesis (Miles 1977) that tooth ridges on the snout and lower jaw are a primitive feature of dipnoans and unique for the group.

Of the three Australian species of dipnoan, only *Chirodipterus* has tooth plates. The microstructure corresponds well with previous descriptions of dipnoan tooth plates (Densison 1974; Peyer 1968). The tissue is quite distinct from the dentine which forms the denticles and tooth ridges in the other species, and from the tooth ridge in *Chirodipterus*. A distinguishing feature is the relatively large sub-dentinal pulp cavity, which is in accord with the proposed method of growth; that is, extensive bone resorption in advance of basal growth of the dentine. Replacement of this tissue is by continuous basal growth rather than shedding and replacement of the tooth plate as a whole. Incremental growth lines in the tooth plates of *Chirodipterus australis* are aligned parallel to the lower surface of the dentine, and are continuous across the extent of the dentine. Miles (1977) has taken the wide-open pulp chamber and continuous growth pattern as diagnostic of advanced dipnoan tooth plates, and as a specialization not encountered in the primitive dipnoan dentition. One can assume that resorption of the tooth plates is not necessary as wear on the dentine, resorption of the basal bone, and basal deposition of dentine are all in synchrony. Denison (1974) in his account of the evolution of tooth plates postulated a change from shedding of individual teeth to a condition where teeth were retained, firmly attached (I presume around their margins), with continuous basal growth of dentine to keep pace with wear at their functional surface.

The tissue which comprises the major part of the tooth plates in *Chirodipterus australis* is clearly specialized and adapted to resist wear and to function as a flat grinding or crushing surface. I have referred to it as a homogeneous compact dentine. Denison (1974) and Peyer (1968) refer to similar tissue in dipnoan tooth plates as trabecular dentine; Thomasset (1930) called the tissue in *Ceratodus* 'syndentine', Ørvig (1967) termed it 'columnar pleromic hard tissue' which he later (Ørvig 1976*a*) modified to 'vacular pleromin', and Lison (1941) described the tissue in *Protopterus* as 'osteodentine with infilling petrodentine'. It is beyond the scope of this paper to review tooth plate structure, as ideally this should take account of the formation in extant forms. The investigations discussed here are preliminary but do allow one to state that the tissue is a continuous layer of dentine which started as dentine built around pulp canals and became progressively more mineralized as the pulp canals and tubules became occluded with deposition of pulpal dentine. This homogeneous, highly mineralized compact dentine can only continue to grow at the basal surface. The tooth plate is firmly attached at the margins to the supporting spongy bone by an ingrowth of dentine into the vascular spaces, which I regard as pleromic dentine; this may be equivalent to the earlier terminology, osteodentine; or to Thomasset's (1930) 'dentine méandriforme' which he considered to be a general phenomenon. The usage of terminology is fully discussed in §6*c*. The main conclusion from the microstructure of tooth plates in *Chirodipterus* is that they conform to the general pattern of dipnoan tooth plates in providing a hypermineralized, resistant, compact dentine of continuous growth. The structure of tooth plates in *Chirodipterus* may represent an early specialization on the way to the more advanced structures in later dipnoans. Only detailed comparisons with the tooth plates of related dipnoans will provide some understanding of the probable derivations among tooth plate bearing forms. Denison (1974) has reviewed the relations between many of the dipnoan tooth plates where the histology is known, and cited *Dipterus* and *Scaumenacia* as primitive types and *Sagenodus* as advanced. The tooth plates of *Chirodipterus australis* most closely resemble those of *Neoceratodus forsteri* Krefft (Denison 1974, fig. 9). It is relatively more difficult to relate the microstructure of *Chirodipterus* tooth plates to that of *Lepidosiren* and *Protopterus* and to the description of tooth plate development in *Protopterus* by Lison (1941). Semon (1899) has shown that in the early stages of development the tooth plates of *Neoceratodus* are represented by rows of small individual teeth, and as discussed in § 6 *d* it is envisaged that those of *Chirodipterus* develop by consolidation of many primary dentine units. If the hypothesis of Miles (1977) is accepted, that the tooth plate bearing dipnoans comprise a monophyletic group, then the diversity of microstructure found in the tooth plates must have arisen from divergent specialization from a primitive type; it is not possible to characterize the primitive type of tooth plate with the currently available information.

(*b*) *The dermal ornament: its relation to the phylogeny and growth of cosmine*

Of the three species of Australian Devonian dipnoans examined histologically, only *Chirodipterus australis* has an outer covering on the dermal bones which is typical of cosmine. The microstructure corresponds with that of *Dipterus* described by Gross (1956, fig. 69), in which the pore-canal system is contained within the dentine layer. Schultze (1969) concluded that only dipnoans and rhipidistian crossopterygians possess a pore-canal system in the dentine layer and that both are closely related. Ørvig (1969) also concluded that cosmine is restricted to dipnoans and primitive choanates and Miles (1977) accepted these findings together with those of Schultze (1969) and commented that true cosmine is a unique specialization uniting dipnoans and choanates. Miles (1975, 1977) has, therefore, concluded that cosmine is a primitive feature of dipnoans. If we accept this hypothesis as being the most economical explanation of the occurrence of cosmine, then the cosmine cover has been lost or reduced in *Griphognathus* and *Holodipterus*. The

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Description of plate 5

Griphognathus whitei Miles

Figure 44. S.e.m. of the denticles on the basibranchial tooth plate which are a different shape to those on the prearticular. A ring of neck canals surround many of the unworn denticles. Holotype P50996 (field width 1860 μm).

Figure 45. S.e.m. of the worn surfaces of enlarged denticles at the anterior margin of the basibranchial. Regularly spaced worn dentine units are seen with raised areas of circumpulpal dentine. Holotype. P50996 (field width 930 μm).

Figure 46. S.e.m. of a new denticle on the basibranchial in which the enameloid covering is incomplete around the base. This is seen at higher magnifications in figure 47. Holotype. P50996 (field width 460 μm).

Figure 47. S.e.m. of the base of the denticle in figure 46 with a fibrillar and calcospheretic pattern in which the underlying region has filled in with homogeneous material. Holotype. P50996 (field width 5 μm).

Figure 48. S.e.m. of a dermal tubercle at the margin of the upper jaw in which the separate points of the dentine units can be seen on the surface. P50998 (field width 450 μm).

Figure 49. S.e.m. of the dermal tubercles on the bone surface of the jaw margins. P50998 (field width 1860 μm).

Holodipterus gogoensis Miles

Figure 50. S.e.m. of the upper lip with a gap in the compact dentine layer where separate denticles have developed. Holotype. P52569 (field width 1780 μm).

Figure 51. S.e.m. of a denticle in figure 50 with hard tissue infilling a large part of the concave surface of the denticle. Holotype. P52569 (field width 450 μm).


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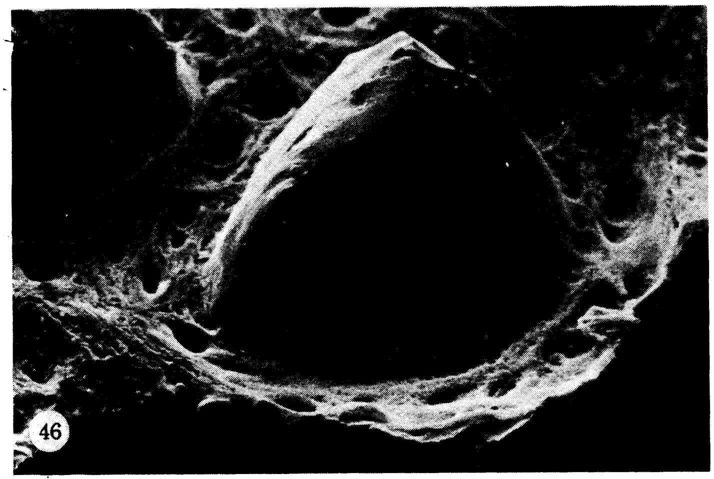
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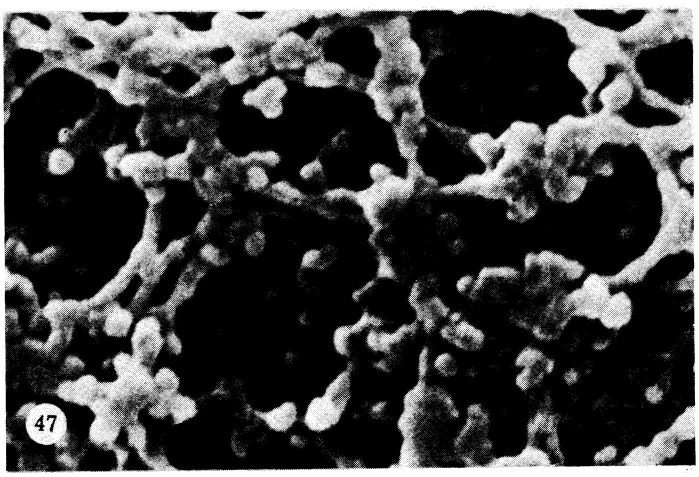
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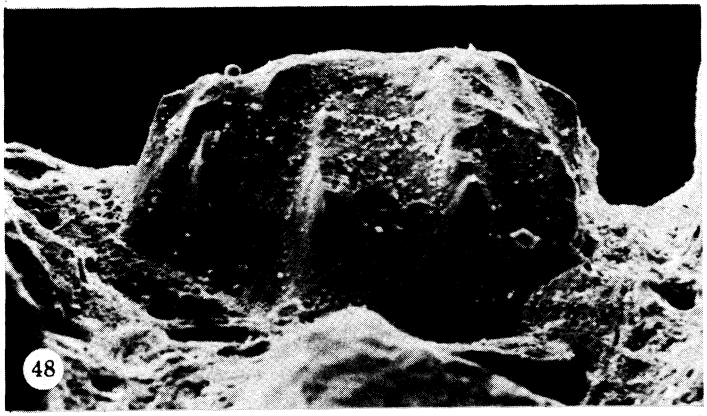
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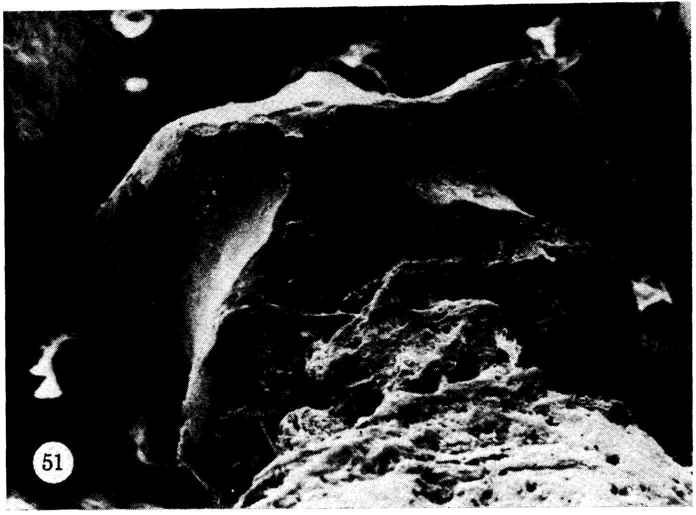
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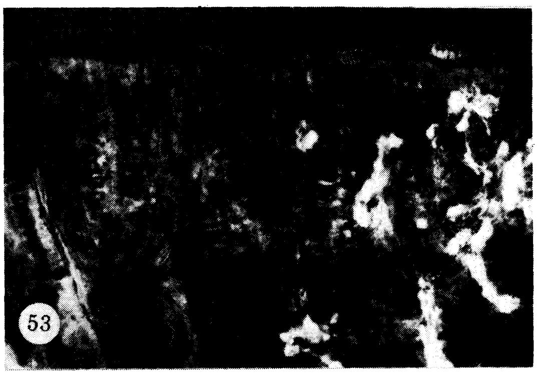

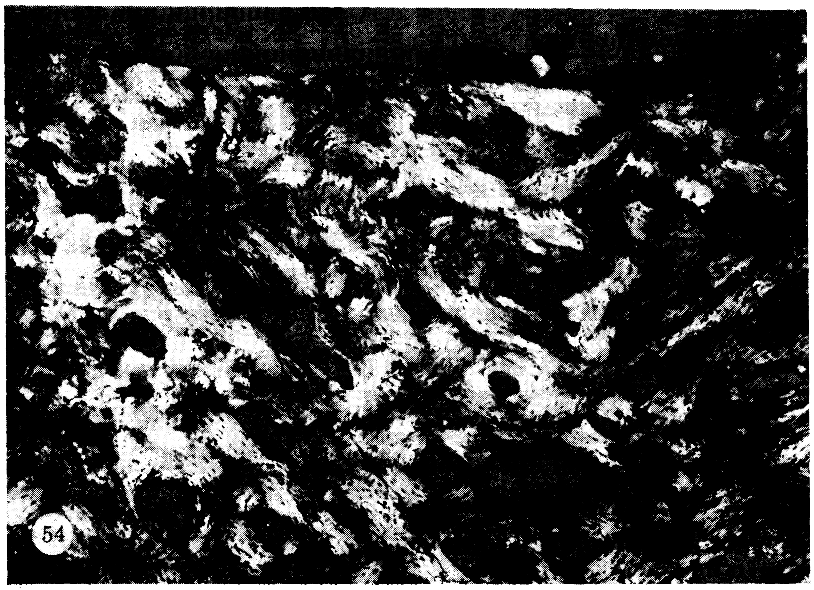

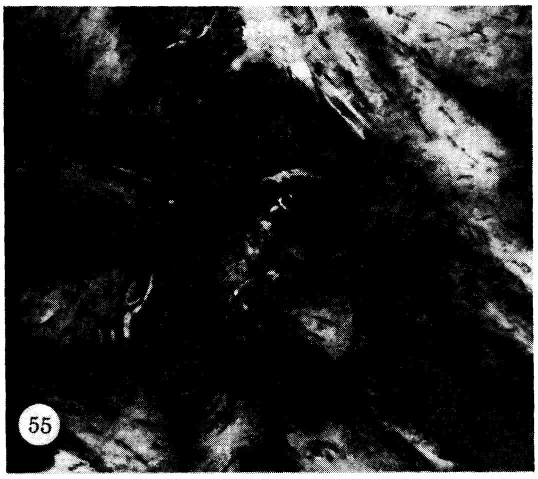

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DESCRIPTION OF PLATE 6

Holodipterus gogoensis Miles

FIGURE 52. Photomicrograph of a vertical section through the unworn surface of the lower lip of the dentary viewed in partial polarized light. The radial birefringence of the enameloid is seen and the dentine is only weakly birefringent, see also figure 9. Holotype. P52569 (× 140).

FIGURE 53. Photomicrograph of a vertical section through the worn surface of the lower lip viewed in polarized light. No enameloid is present and some of the dentine is birefringent, see also figure 10. Holotype. P52569 (× 220).

FIGURE 54. Photomicrograph of a vertical section through the dentary, medial to the lower lip. Near the worn surface the spongy bone is infilled with pleromic dentine. Holotype. P52569 (× 56).

FIGURE 55. Photomicrograph of a region of pleromic dentine from figure 54. See also figure 11. Holotype. P52569 (× 140).

FIGURE 56. Photomicrograph of a vertical section through the antero-ventral border of the lower lip where sensory pits open between tubercles of dentine. See also figure 12. Holotype. P52569 (× 140).

FIGURE 57. Photomicrograph of a vertical section through a blunt tooth on the dorsal margin of the prearticular viewed in ordinary light. Short pulp canals open from the vascular spaces of the spongy bone and very few tubules are found. Holotype. P52569. (× 35).

DESCRIPTION OF PLATE 7

Holodipterus gogoensis Miles

FIGURE 58. S.e.m. of a newly formed denticle on the prearticular with separate points on the crests of the ridges. Holotype. P52569 (field width 460 μm).

FIGURE 59. S.e.m. of a poorly mineralized calcospheretic surface. Holotype. P52569 (field width 46 μm).

FIGURE 60. The worn surface of the dermopalatine with marginal denticles and pleromic dentine. P50997 (× 5).

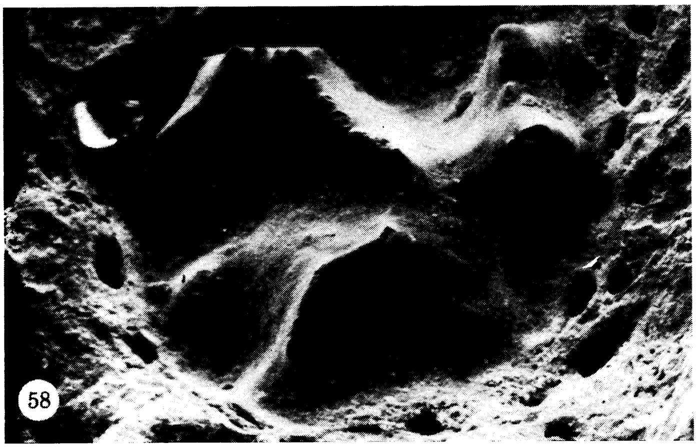
FIGURE 61. Denticulate surface of the dermopalatine. P52568. (× 5).

FIGURE 62. S.e.m. of the dermopalatine with a worn surface of pleromic dentine. P50997 (field width 460 μm).

FIGURE 63. S.e.m. of a denticle adjacent to figure 62 which shows pleromic dentine infilling a concave surface of the denticle. P50997 (field width 460 μm).

FIGURE 64. S.e.m. of an unworn denticle on the dermopalatine within a previous resorption area. P50997 (field width 930 μm).

FIGURE 65. S.e.m. of an extensive resorption surface on the dermopalatine. P50997 (field width 460 μm).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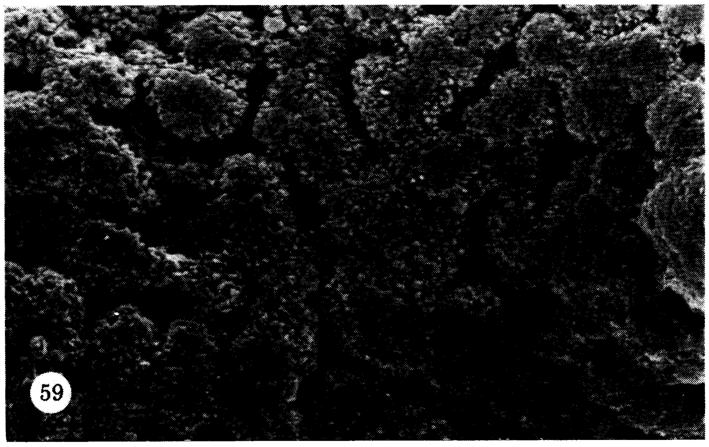
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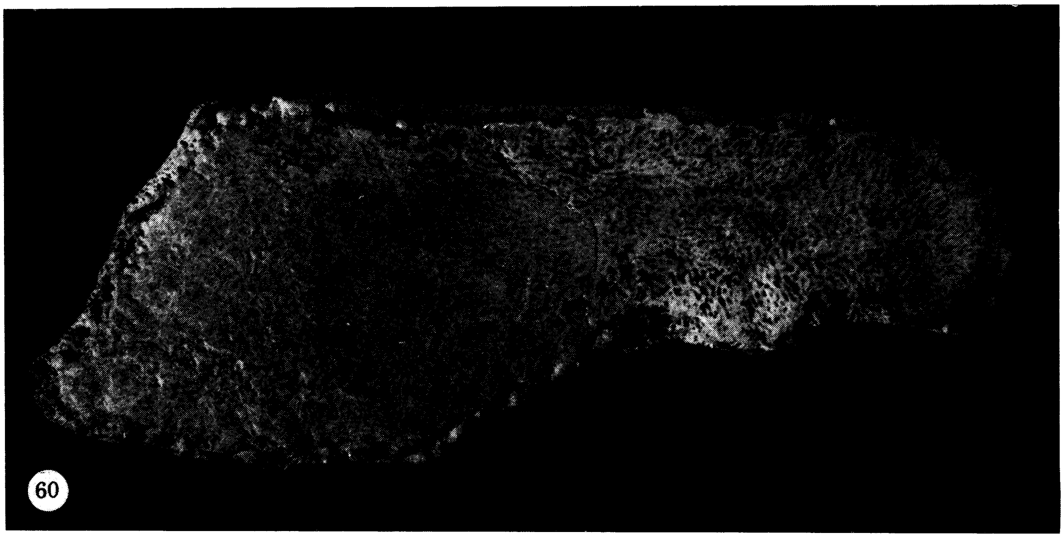
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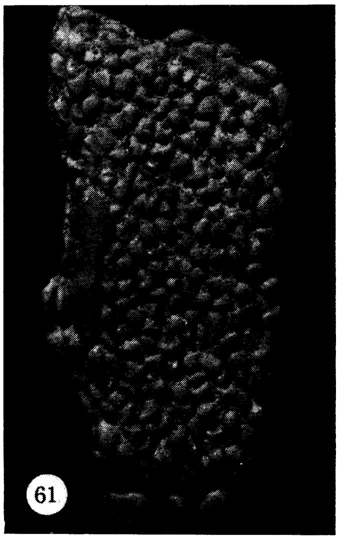
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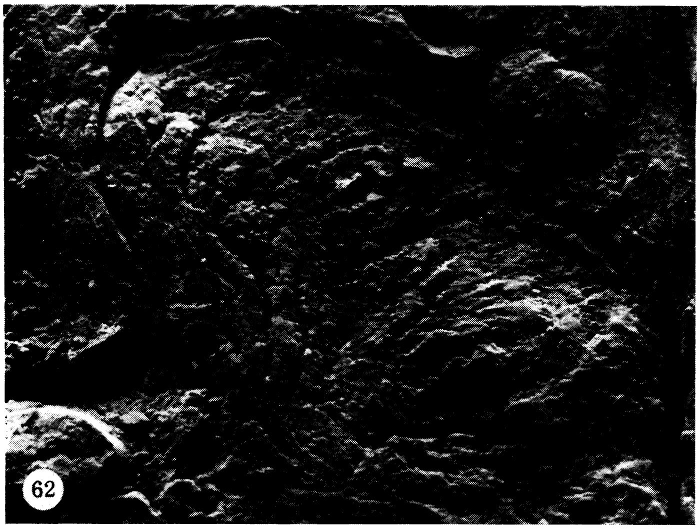
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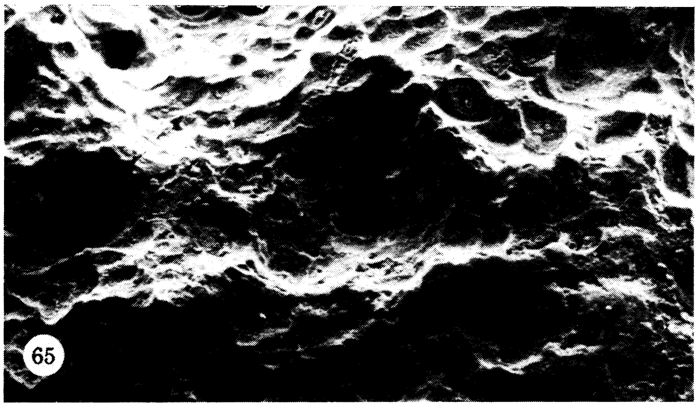
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For description see previous page.

covering of separate dentine tubercles is therefore a derived character which is achieved either by retention of an earlier developmental stage in which cosmine had not developed, or the potential to form cosmine, present in the ancestors, has been lost in at least one line of evolution and in its place a new feature has developed. According to Miles's 1977 phylogeny cosmine has been lost in several lines of evolution. Goodrich (1908) used a similar argument to explain the separate denticles (tubercles) on the scales of coelacanths; namely that they represented a degenerate cosmoid scale with denticles secondarily attached to the surface. We have previously discussed our findings on the structure of the scales in *Latimeria chalumnae* (Smith, Hobdell & Miller 1972) when the conclusion was reached that the tubercles were secondarily developed. The current view proposed by Miles (1977) is that actinistians never had cosmine. Accepting this phylogeny it is better to regard the tubercles on the scales of coelacanths as derived from a primitive condition in which separate tubercles formed, probably with superpositional growth. It is of some interest that the structure of the tubercles in the dermal ornament of *Griphognathus*, also a derived character, strongly resembles that of the tubercles in *Latimeria*.

The cosmine cover may have become functionally obsolete as it almost certainly involved periods of simultaneous growth alternating with periods of resorption and periods of quiescence, which Westoll (1936) concluded were probably seasonal in occurrence. Thomson (1975) in a review of the earlier work on cosmine, considered that one of Gross's major contributions arising from his detailed histological investigations (Gross 1956) was to establish that any existing cosmine surface was incapable of growth. The consequence of accepting this fact is that any growth in areas of cosmine must be preceded by complete resorption of the original cosmine before regrowth of a larger portion of cosmine. Therefore the protection offered by the cosmine sheet is totally lost for certain periods of time. In *Griphognathus* and *Holodipterus* the continuous layer of cosmine has been replaced by separate tubercles of dentine with many generations of tubercles beneath the most superficial ones. Both areal growth and superpositional growth could occur simultaneously in these forms in different parts of the dermal covering without loss of protection. The mucous canals and sensory neuromast cells which are thought to be contained within the pore-canal system of cosmine (Thomson 1975) are either present in the soft tissue surrounding the tubercles or contained within the tissue spaces of the spongy bone surrounding the tubercles. It has been noted that the openings into the tissue spaces of the spongy bone are relatively large on the bone surface which surrounds the tubercles in *Griphognathus*. These biological activities of areal and appositional growth which could occur without prior resorption of the superficial layer, could have been of greater benefit to the species than the possession of cosmine.

The papers of Jarvik (1950), Ørvig (1969) and Thomson (1975) give reviews of the earlier work on cosmine by Westoll (1936), Bystrow (1942) and Gross (1933, 1956 and 1965) and also reassess the evidence for the method of growth from subsequent observations. The present investigation has not been directed towards the surface morphology and distribution of cosmine, therefore, it is not appropriate to comment on the significance of cosmine blisters and Westoll-lines. Thomson (1975) has discussed these phenomena as they relate to osteolepid rhipidistians and Ørvig (1969) has described the growth of cosmine in dipnoan scales, although he also points out that the growth of cosmine on the skull and jaw covering may be quite different from that on the scales.

The question of superpositional growth in the cosmine cover of dipnoan skull bones has not been adequately answered. Denison (1968) described many generations of buried denticles in the scales of *Uranolophus* but commented that this did not usually occur in the skull bones. He further concluded that growth of the cranial and lower jaw dermal plates in *Uranolophus* is distinctly different from that of its scales. It is, therefore, not appropriate to compare information on cosmine growth in scales with cosmine growth in the dermal skull covering, as they may have been subjected to different functional requirements resulting in a different pattern of evolutionary change. Denison (1968) described the histological features of various skull bones in *Uranolophus* and included the operculars and gulars as well as the plates of the cranial roof. He found very few examples of buried tubercles beneath the cosmine and he concluded that resorption of the cosmine was a regular process and probably as extensive as in *Dipterus*. Regrowth included formation of either tubercles or cosmine; a point to which I shall return. Earlier in the discussion I advanced the concept that loss of cosmine in *Griphognathus* and *Holodipterus* could be due to retention of an ontogenetic character, but for this to be established we need to know the pattern of cosmine growth. Does it include an earlier stage with the formation of tubercles preceding the growth of cosmine? Ørvig (1969) pointed out that in scales of *Porolepis*, one or more generations of tubercles (odontodes) formed ontogenetically prior to superposition of a layer of cosmine. In the context of this concept it is interesting that in a series of three operculars from *Uranolophus*, Denison (1968) described the surface of the smallest (implied youngest) as tuberculate with one buried denticle also partly resorbed, the larger two had a cosmine cover and no buried denticles. It is possible that the younger tissues have the potential only to form denticles; later ones can form either denticles or cosmine; and the oldest ones cosmine only. If resorption is supressed then superposition of successive denticle generations can occur. Superpositional growth of this kind occurs in other crossopterygians for example *Porolepis* and in actinopterygians, and in the scales of *Uranolophus* (Denison 1968) where beneath the cosmine cover are several generations of denticles. I have observed several generations of denticles in the dermal bones of the skull in *Griphognathus* and *Holodipterus* neither of which possess cosmine, but not in the dermal bones of *Chirodipterus* which are covered by an extensive layer of cosmine. These are the first reported examples of superpositional growth in the skull bones of dipnoans, although Denison (1968) was first to note this pattern of growth in the scales of a dipnoan, *Uranolophus*. The conclusions from this information could be that the primitive condition found in the ancestors of dipnoans and in primitive choanates, was a layer of cosmine over several generations of buried tubercles as in the scales of *Porolepis*. This structure became modified in two ways, either by loss of tubercles and growth of cosmine only, or by retention of separate tubercles and loss of cosmine. Both of these derived conditions are found within the dipnoans. Ørvig (1969) stated that the ability to form generations of tubercles (odontodes) was still present in the early holoptychiids as they evolved from the porolepid stock, although not overlain by cosmine. *Uranolophus* may be an example in which separate tubercles are retained in the younger stages and cosmine develops in the older specimens, a condition closer to the ancestral condition. Denison (1968) regarded *Uranolophus* as a very primitive dipnoan. The conclusions presented in this discussion of cosmine phylogeny in the dipnoans are in agreement with Ørvig's basic assumptions. These were based mainly on the holoptychiids and stated that during regression of the dermal skeleton, which involved the loss of cosmine, the ability to form generations of tubercles (odontodes) was not lost. My interpretation of Ørvig's statements is that the ornamentation of separate tubercles does not represent a disintegration product of cosmine but rather retention of an earlier ontogenetic condition, which is also a phylogenetic condition of actinistians. This does not refute the concept stated previously that the condition of separate tubercles on the dermal bones of *Griphognathus* and *Holodipterus* may be due to the development of a neotenous character.

(*c*) *Terminology of dentine: its application to the dipnoan dentition and dermal ornament*

Ørvig has written prolificly on the terminology of hard tissues in chondrichthyan and osteichthyan vertebrates. His accounts of 1951 and 1967 review the classification of the mesodermal hard tissues. Bradford (1967) in an account of the microanatomy of dentine has reviewed the classification and distribution of non-mammalian dentines, which he has placed in two broad categories; first mantle dentine (after Weidenreich 1925) in which he has included all the terms which relate to a modified, highly mineralized outer layer and which are now generally referred to as enameloid; secondly, circumpulpal dentine for which he has used Weidenreich's (1925) subdivisions of osteodentine and orthodentine. Within the category of circumpulpal dentine, Bradford (1967, table 1) has compared the terminology of Tomes (1898), Thomasset (1928) and Ørvig (1951) and concluded that there is broad general agreement in so far as they all have a group of tissues classified as osteodentines which exclude orthodentine, vasodentine and plicidentine. There is general acceptance of the definition of the last three terms as mentioned in the introduction, and none of them is applicable to dipnoan tissues although Gross (1956) has described the separate tubercles as orthodentine, and Denison (1974) has adopted this term. Confusion has arisen over the use of the term osteodentine, a point to which I shall return, and Bradford (1967) has not clarified this aspect of the terminology. Bradford (1967) has used the trabecular dentine in a teleost as an example of osteodentine, as well as the dentinal-osteonal tissue of *Rhinobatis*. This seems to me to be exactly the point at which confusion arises. Ørvig (1951) also grouped together trabecular dentine, vasodentine and osteonal dentine under the heading osteodentine, largely because he regarded the hard tissue between the circumferentially arranged dentine systems as bony trabecules, a finding with which Herold (1971) has disagreed. Ørvig (1951) reinforced this choice of terminology by the concept that the external pallial dentine and internal osteodentine could be regarded as equivalent to compact periosteal bone and primary osteonal bone (Ørvig 1951, fig. 1D), a concept which I find to have little significance for an understanding of the structure, histogenesis and phylogeny of dental tissues. Bradford (1967) also has apparently overlooked what I regard as a major distinction in Thomasset's (1930) classification and that is the grouping of all bone-like dentines as those without a central pulp chamber. It follows from this statement that all the other dentines, are grouped as having a central pulp chamber and Thomasset (1930) describes two varieties, vasodentine and orthodentine although it may be argued that there are more, but this is not a concern of the present discussion. Thomasset's classification of dentines without a central pulp chamber will be a central part of this discussion.

I should like to return first to Ørvig's (1951) discussion of the terminology and agree with his comment that 'the classification of dentine has been a mattter of considerable terminological confusion'. This, in Ørvig's opinion, is due to a failure to take account of the phylogenetic transformations as well as structural and ontogenetic characters. Ørvig (1967) has attempted to do this with a revision of his 1951 classification where he has specified the characters for the tissues which form in the mesoderm immediately underlying the epidermis (the corium) as two major types; dentine-like, of two kinds mesodentine and semidentine, which are regarded as transitional forms in the phylogenetic change from bone to dentine; dentine-proper, which is subdivided into orthodentine, pallial dentine, and osteodentine. All these dentines are formed by mineralization with an organic matrix which is retained more or less intact. The next category is formed by hypermineralization with a concomittant reduction in organic matrix, and within this group is placed the columnar pleromic tissue of dipnoan tooth plates. Despite this comprehensive reclassification of the dentinal tissues, I do not find it a logical scheme to adopt for dipnoan dental tissues. I do not feel inclined to accept that dentine is a highly specialized end-product derived by transition from bone as claimed by Ørvig (1967), because both are probably equally ancient tissues. Consequently I have considered that some of the dentine in the Devonian dipnoans may be primitive especially if one considers that it does not contain a central pulp cavity. For these reasons I also believe that it is not of great value to classify dentine according to whether it does or does not resemble bone, which has resulted in more confusion than clarification. In fact Ørvig (1969) has found it necessary to resort to what he regards as a non-appropriate term for the tissue in dipnoan tooth plates, namely composite pleromic tubular dentine. I find this terminology as confusing as the preceding ones, although Ørvig (1976*a* and *b*) in recent publications has altered this terminology to vascular pleromin (see §6*e*).

Denison (1963) and Halstead (1969) both report that dentine tubercles are present in the earliest vertebrates at the same time as aspidin and that this occurred before cellular bone developed. This is not consistent with the hypothesis that dentine is derived from cellular bone by a process of cell retraction. It is suggested by Ørvig (1967) that at least in the osteostracians dentine and bone cannot always be easily distinguished one from the other. This could mean that both are derived from the same primitive tissue. Schaeffer (1977) has also concluded that Ørvig's hypothesis, that acellular dentine is derived from cellular bone, cannot readily be examined as both tissues are very ancient and it is not, therefore, possible to judge which is the more primitive. Since his original statements on the choice of terminology (Ørvig 1951), Ørvig (1976*a*) has reaffirmed that he regards the term trabecular dentine, introduced by Röse (1898), as inappropriate and disagrees with its reinstatement by Peyer (1968) and Denison (1968, 1974). His reasons being mainly that the tissue does not remain trabecular but fills in with secondary denteons and hence becomes compact. I accept this view of Ørvig's for many of the tissues and also do not find the term trabecular dentine as used by Denison (1968, 1974) an appropriate term for dipnoan dentine. I have previously stated (§4) where the term 'trabecular dentine' may be appropriate, which is in agreement with Peyer (1968, pp. 61–64) who in a review of the earlier authors' usage of osteodentine and trabecular dentine decided to avoid the term osteodentine completely and use only trabecular dentine *sensu* Röse (1898). Peyer (1968, pp. 94–100) also in a discussion of the usage of these terms for actinopterygians proposed the term 'osteal dentine' for the tissue which Röse had originally called osteodentine, that is a tissue with dentinal tubules and cells enclosed within the hard tissue (Peyer 1968, p. 336). I should like to emphasize a statement made by Peyer (1968) that the lack of uniformity in the use of terms results primarily from choosing different criteria for their identification. It is, therefore, important to stress the criteria which seem to be the most significant. Choosing the significant criteria is the most difficult part in arriving at a suitable definition.

I propose to adopt for dipnoan tissues some of the terminology suggested by Thomasset (1930) which falls under his major division of dentine without a central pulp cavity and open at the base; this precludes use of the terms orthodentine and vasodentine. Syndentine seems to embrace the criteria of which most are present in dipnoan dentine. Thomasset has defined this as a tissue formed from a group of systems which are joined together; each one has a pulp canal with radiating canaliculi (tubules) and the pulp canals may be branching or parallel to each other. He considered that each of these systems was equivalent to a simple denticle and gave the tooth plates of *Ceratodus* as an example of syndentine (Thomasset 1930, fig. 20). The tissue of the tooth ridges and lip ridges in *Griphognathus*, *Holodipterus* and *Chirodipterus* could, from the present description, be classified as syndentine, and the tissue of the tooth plates as syndentine which has become highly mineralized. One could incorporate the term 'petrodentine' as suggested by Lison (1941) for the extra-hard tissue infilling between what he termed pseudo-haversian canals, now regarded as pulp canals, in the tooth plates of *Protopterus* and derive the term petrous syndentine. This eliminates the difficulties of terminology inherent in, for example, coronal pleromic osteodentine (Ørvig 1976*a*). Lison (1941) was critical of Thomasset's classification on the basis of the presence or absence of a pulp cavity as he concluded that this made the tooth plates of *Protopterus* unclassifiable, for the reason that they have both pulp canals and a pulp cavity. It would, however, seem more reasonable to regard this as a sub-dentinal cavity allowing space for growth between the basal dentine and the bone, rather than a true pulp cavity. Gorizdro-Kulczycka (1950, p. 97, fig. 2) refers to the tissue in the tooth plates of *Conchodus elkneri* as syndentine and also (1953, p. 43, figs 3, 4) the tissue of the lip ridges in *Holodipterus sanctacrucensis*.

The tissues which remain to be fitted into this classification are those of what I have called composite denticles and composite tubercles. These tissues could be regarded as syndentine also, perhaps of a simple kind in which the multiple, branched pulp canals are not as regularly arranged into a continuous layer. The tubercles of the dermal skeleton where I have illustrated superpositional growth conform in many ways to the preceding category of Thomasset's, namely pseudodentine, in which he also considered that the single central canal, which was closed at the base, had the role of a pulp cavity and, therefore, the tissue only resembled true dentine surrounding an open pulp cavity.

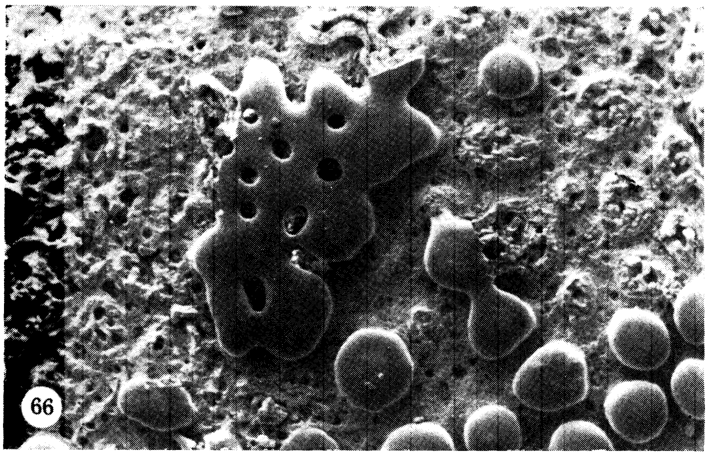
The conclusion that I have reached, to regard the denticles and the tooth ridges as composite structures, comes from a conviction that each one is formed by several distinct groups of odontoblasts, each forming dentine beneath a continuous layer of enameloid and retreating as a group of cells within their own pulp canal towards the base of the denticle. The resulting structure is a multiple-branched pulp canal with tubular extensions which penetrate the dentine and terminate within the enameloid layer. Discussion of the morphogenesis of this tissue is given in § 6*d*.

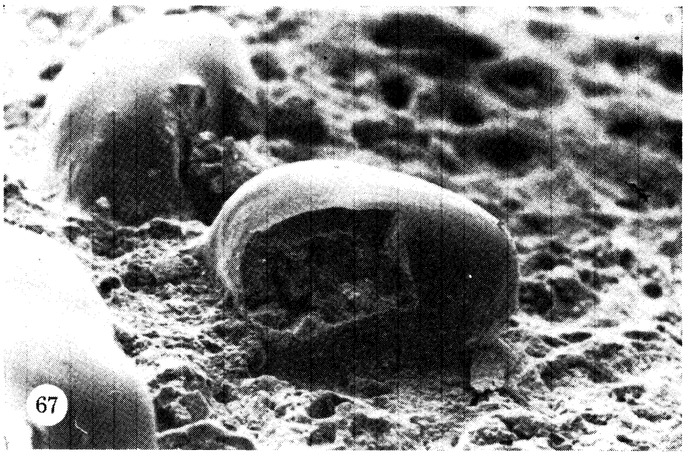
(*d*) *Buccal denticles*: *macromerism*, *morphogenesis and growth*

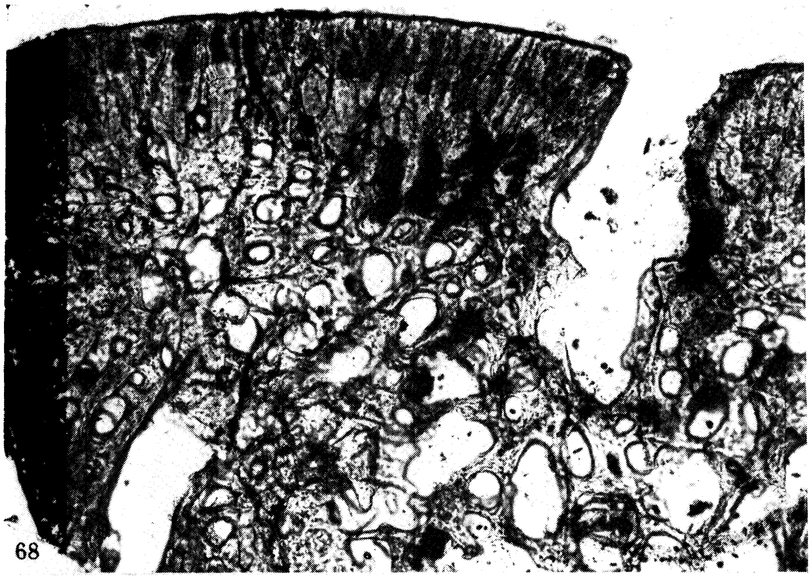
As previously stated (§ 6*a*) the separate buccal denticles are one feature of the primitive dipnoan dentition. Extensive areas of small separate denticles within the buccopharyngeal cavity are considered to be primitive for the gnathstomates as a whole (Nelson 1970). Enlarged or consolidated denticles may occur in areas which are functionally more important; Nelson gives *Chlamydoselachus anguineus* as an example where this has occurred in some of the pharyngeal teeth. Nelson also considers that parallel evolutionary trends result in similar concentrations of denticles in primitive teleostomes such as *Eusthenopteron*. He concludes that phyletic trends associated with the arrangement of buccal denticles seem to progress towards the consolidation and differentiation in localized areas. The trend is from a primary micromeric stage to a macromeric stage. These concepts can be tested by application to the dipnoan dentition. In *Griphognathus whitei* the primary micromeric stage is present in many regions, on the prearticular, dentary, basibranchial tooth plates, dermopalatine, entopterygoid and others. The macromeric stages are found in regions of wear, subjected to functional stress, such as the ascending process of the prearticular and the margins of the basibranchial tooth plate. In these regions, the denticles are longer and broader with worn surfaces which reveal the component units of the denticle. The microstructure of these denticles supports the concept that they have formed by consolidation of dentine units from the micromeric stage. This concept has also influenced the choice of terminology for the dentine (§6*c*) as syndentine defined by Thomasset (1930). In *Holodipterus gogoensis* many more regions of the dentition have become macromeric and fewer regions have retained separate buccal denticles. One region of the buccal cavity where adaptation to a feeding function is not a factor selecting morphology, is the area of the nasal pit and here separate buccal denticles are retained. In *Chirodipterus australis*, a dipnoan with more specialized features than *Griphognathus* and *Holodipterus* (§6*a*), no separate buccal denticles are retained and the macromeric stage is well established. I conclude that the trend towards macromerism is a phyletic trend within the dipnoans, as also found in the chondricthyans and primitive teleostomes; this is based on the assumption that *Griphognathus* has retained a primitive dentition and *Chirodipterus* a more specialized dentition (§6*a*). Either these areas of the dentition have an important function and therefore have become macromeric, as suggested by Nelson (1970), or they are functionally unimportant and have, therefore, not retained the more functional micromeric form. The latter hypothesis is not supported by the facts on abrasion and adaptation to wear as found in the dipnoan dentition. The macromeric areas are areas of abrasion and infilling with 'repair' tissue, or pleromic dentine (§6*e*). I, therefore, conclude that the phyletic trend towards consolidation of denticles, as proposed by Nelson (1970) for the chondrichthyans and primitive teleostomes is enhanced in areas of functional stress in the dipnoans as an adaptation to a durophagous diet. The alternative hypothesis that macromeric areas revert to micromeric as a phyletic trend within the dipnoans would seem to be upheld by the dermal covering (§6*b*), where cosmine as a continuous layer of dentine regresses to separate tubercles, perhaps because the region of the dermal covering acquires a different function from that for which cosmine was evolved; due to a greater need of flexibility.

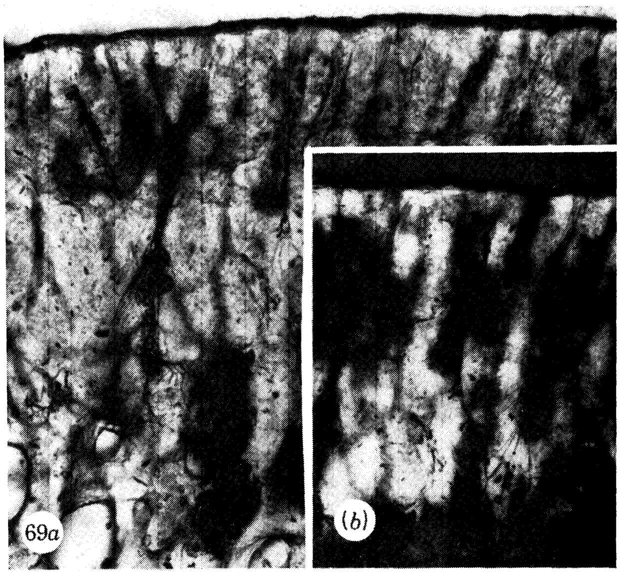
This concept of consolidation of separate denticles leads into consideration of the arrangement and structure of the primary micromeric stage, or the primary ontogenetic denticle from which all other morphological types are derived. It should be possible to explain the dental elements in the same way as Reif (1974) explained the ontogeny of the exoskeleton in elasmobranchs; that is a system which can allow for the transition from one tooth type to another. Reif explained this as a system of isolated elements each capable of morphological variation both within the same stage and in homologous areas at different stages. It is possible to postulate for dipnoans, a primary dentine unit which is capable of morphological change, also a field of influence (retained within the ectoderm or ectomesenchyme) which has the potential to increase or decrease the spacing of these units and the timing of their development. With extinct forms it is not possible to test the hypothesis with direct observation; it is only possible to extrapolate probable ontogenetic development from developmental stages within one individual. This theoretical primitive dentine unit may not be realized in any adult phenotype, only present in the ontogenetic genotype.

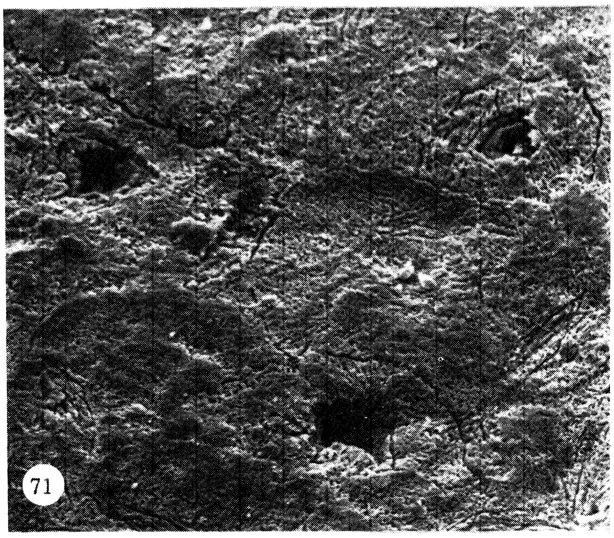
The buccal denticles vary in their morphology from region to region in *Griphognathus whitei*. No distinct pattern to this variation could be detected and no obvious primary denticle shape, although it is possible to distinguish young denticles from old ones and, therefore, arrange them in a developmental or growth sequence. Some explanation of the morphological variation can be attempted from these observations, based on the assumption that a system of primary dentine units (odontodes) develop at some stage in the ontogeny of the animal. The second assumption is that skeletal assimilation can only occur with continuing growth. Continuing growth does occur in dipnoans and can operate in several different dimensions to produce the range of











Holodipterus gogoensis Miles

FIGURE 66. S.e.m. of the dermal covering on the sub-opercular with separate tubercles. P50997 (field width 188 μm).

FIGURE 67. S.e.m. of a separate tubercle in figure 66 with a fractured surface showing the underlying pulp canals. P50997 (field width 460 μm).

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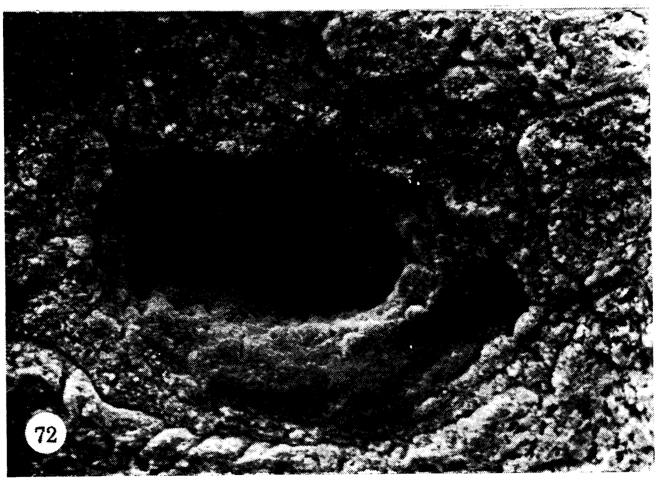
FIGURE 68. Photomicrograph of a vertical section through the lower lip of the dentary in ordinary transmitted light. See also figure 15. P51000 (× 56).

FIGURE 69. (*a*) Photomicrograph of the lower lip in figure 68 which shows the worn surface of compact dentine. P51000 (× 140). (*b*) Photomicrograph of the same region as figure 69*a* viewed in polarized light which shows the strong birefringence of the circumpulpal dentine. P51000 (× 140).

FIGURE 70. Photomicrograph of a vertical section through the tooth plate, with the attachment of the dentine to the basal bone at the margins. See also figure 16. P52561 (× 35).

FIGURE 71. S e.m. of the functional surface of the tooth plate after treatment with 0.1 N HCl for 1 minute. Three pulp canals open at the surface with partial infilling of pulpal dentine, and hypermineralized interstitial dentine. P52561 (field width 184 μm).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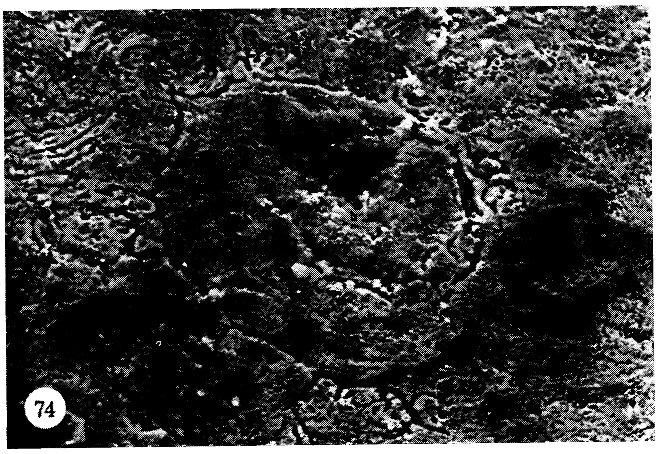
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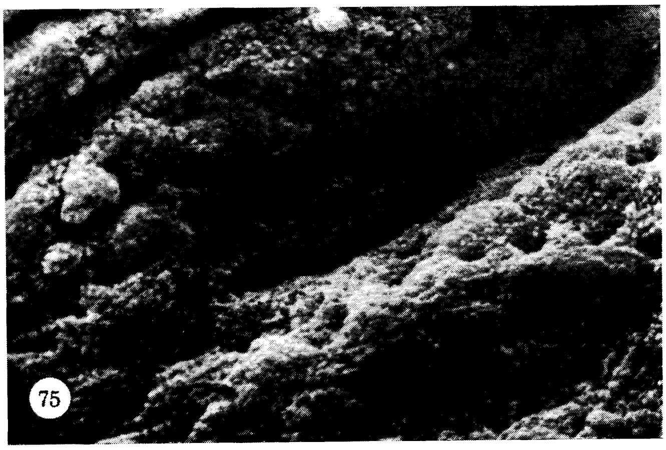
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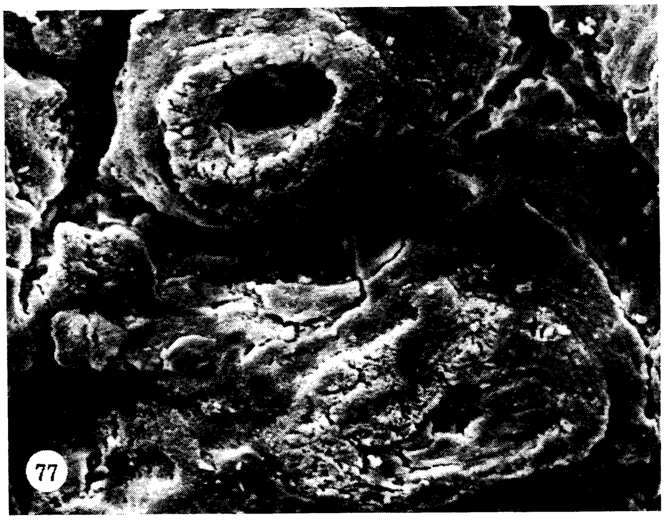
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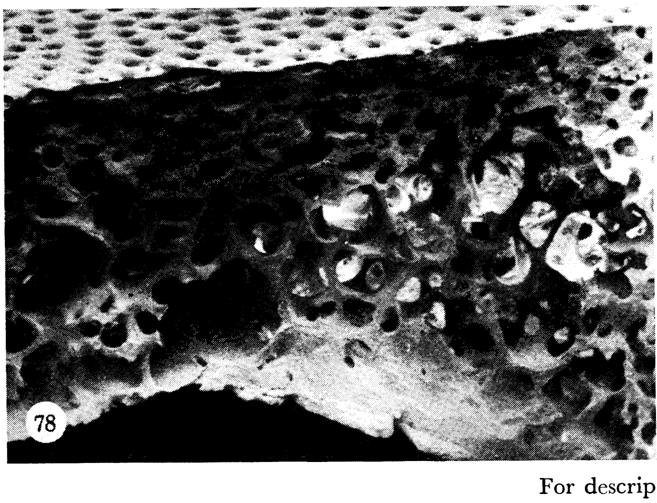
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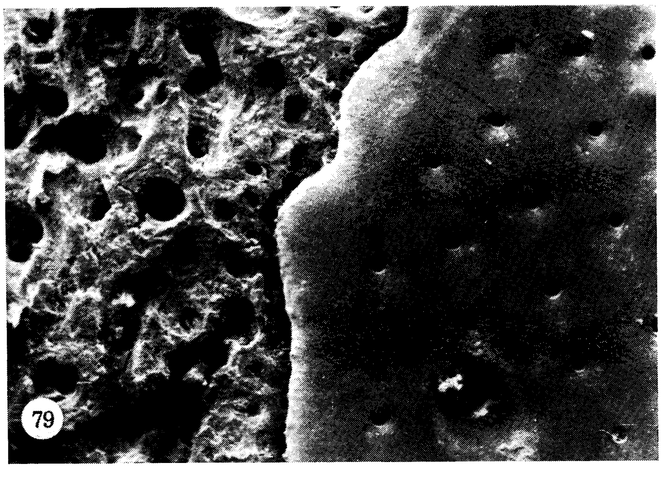
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For description see opposite.

DESCRIPTION OF PLATE 9

Chirodipterus australis Miles

FIGURE 72. S.e.m. of an open pulp canal with smooth, homogeneous circumpulpal dentine. P52561 (field width 46 μm).

FIGURE 73. S.e.m. of the wall of a horizontal part joining two pulp canals. P52561. (field width 46 μm).

FIGURE 74. S.e.m. of an occluded pulp canal with concentric layers and hypermineralized interstitial dentine. P52561 (field width 94 μm).

FIGURE 75. S.e.m. of the pulp canal wall in figure 73 with openings for the odontoblast processes. P52561 (field width 18.4 μm).

FIGURE 76. S.e.m. of the marginal tissue of the tooth plate which is like the compact dentine of the tooth ridges and pleromic dentine. P52561 (field width 920 μm).

FIGURE 77. S.e.m. of a region in figure 76 which shows the tubular circumpulpal dentine and infilling pulpal dentine. P52561 (field width 94 μm).

FIGURE 78. S.e.m. of the fracture edge through a cosmine covered skull bone with superficial cosmine over extensive spongy bone and basal compact lamellar bone. P52562 (field width 1840 μm).

FIGURE 79. S.e.m. of the surface of a natural border of cosmine over spongy bone with one sensory canal and numerous pore canals. P52560 (field width 920 μm).

DESCRIPTION OF PLATE 10

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FIGURE 80. S.e.m. of a natural cosmine border in lateral view. P52560 (field width 460 μm).

FIGURE 81. S.e.m. of the cosmine border with hexagonal pattern and projections of the surface. P52560 (field width 46 μm).

FIGURE 82. S.e.m. of the cosmine surface with hexagonal pattern. P52560 (field width 20 μm).

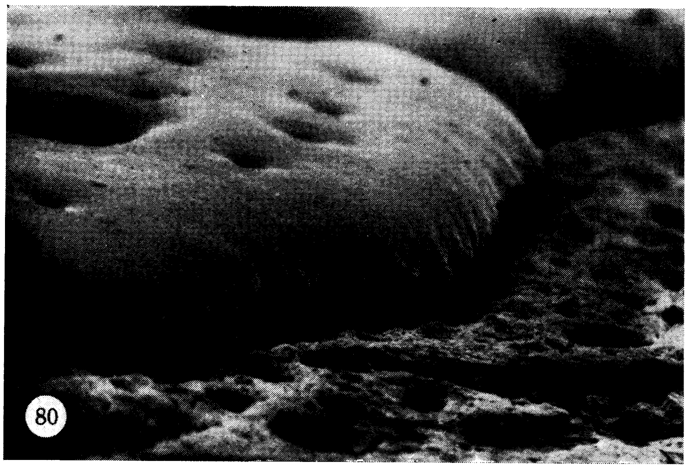
FIGURE 83. S.e.m. of acid-etched cosmine with large pore canals and small pulp canals. P52562 (field width 460 μm).

FIGURE 84. S.e.m. of cosmine surface with sensory canals and pore canals to compare with figure 85. P52560 (field width 920 μm).

FIGURE 85. S.e.m. of cosmine surface after acid-etching, larger pore canals and small pulp canals in between, see figure 84. P52562 (field width 920 μm).

FIGURE 86. S.e.m. of fracture through cosmine with surface pore canals and horizontal mesh canal, see also figure 18. P52562. (field width 186 μm).

FIGURE 87. S.e.m. of fracture surface through bone beneath the tooth plate, with secondary osteonal bone infilling the vascular spaces. P52561 (field width 460 μm).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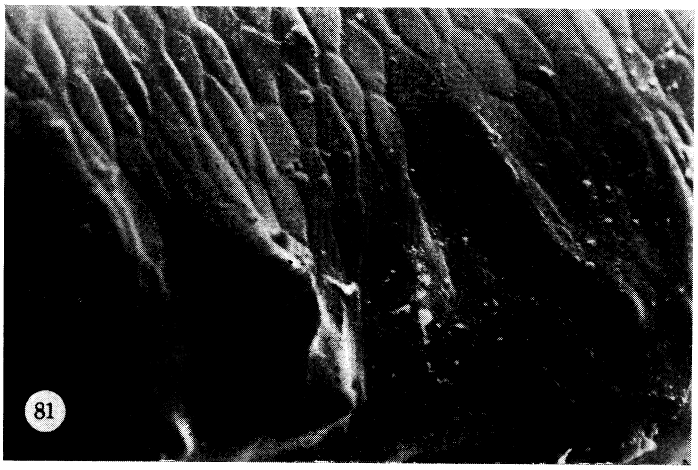
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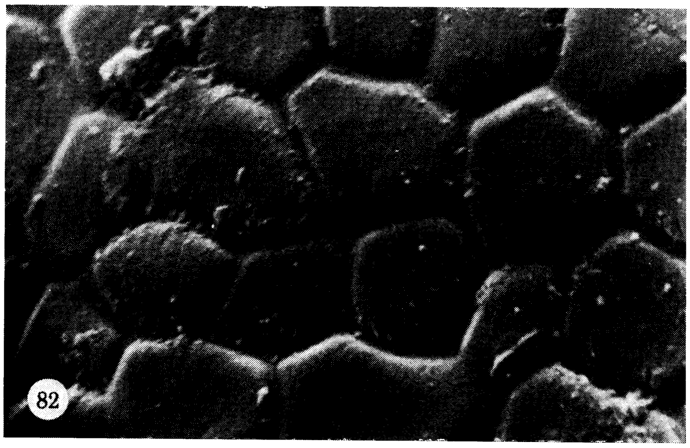
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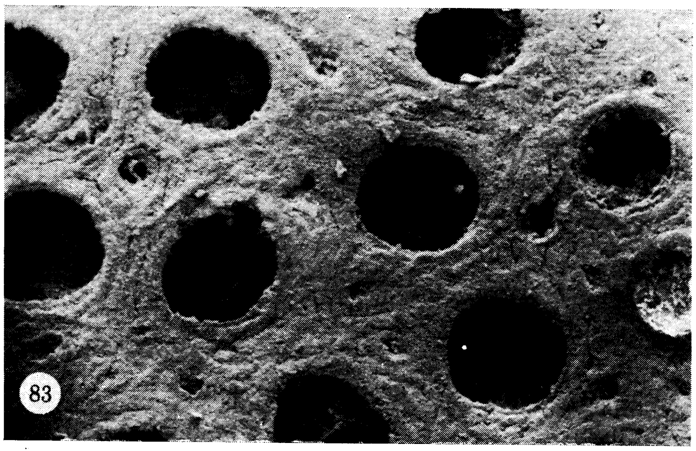
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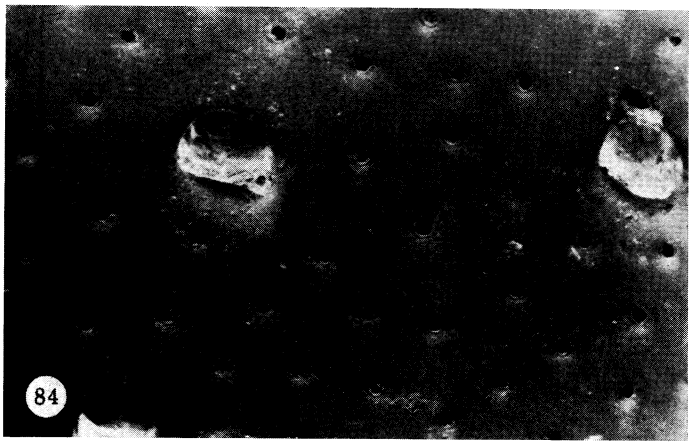
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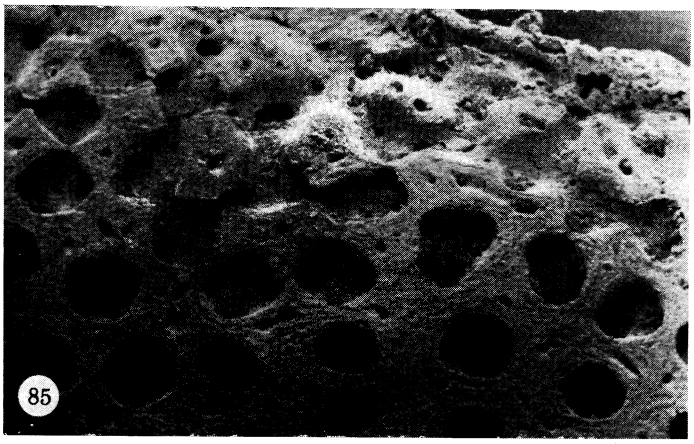
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For description see previous page.

observed morphologies in the buccal denticles. Vertical or eruptive growth is altered when ankylosis occurs and may be changed to a remodelling growth. This is achieved by hard tissue resorption, of which many examples have been given above, together with regrowth of tissue in the created space as a form of pleromic dentine. If resorption completely removes the denticle and part of the basal bone then regrowth of a second generation denticle will occur within the old site, this has been noted in the buccal denticles of *Griphognathus* and *Holodipterus*. If no resorption occurs then superpositional growth takes the place of replacement growth, examples of this are in the dermal covering to the skull bones of *Griphognathus* and *Holodipterus* (§6*b*). Horizontal growth increases the area covered by denticles and can be either zonal if the dentine units are induced in a sequence of growth waves or a continuous layer of dentine units if induction is simultaneous. Replacement denticles in the buccal dentition of *Griphognathus* are apparently randomly placed but the dentine units of the tooth ridges of all three species are probably replaced simultaneously, all the groups of cells being competent to produce dentine at the same time, this results in the continuous layer of syndentine (§6*c*). A second type of replacement growth may occur in which a second wave of induction and growth produces denticles between the existing denticles to infill the superficial soft tissue spaces, this has been regarded as a form of pleromic dentine in the psammosteids (Ørvig 1967), where the dentine also invades deeper into the aspidin. Examples of this growth have been noted in *Griphognathus* and *Holodipterus*.

Halstead (1969) describes this phenomenon as a strengthening of the dermal armour in psammosteids and considers that some examples figured by Bystrow (1955) demonstrate transitional stages between the formation of second generation tubercles and pleromic dentine. He further concluded that the production of second generation dentine tubercles evolved initially as a healing mechanism in response to abrasion or irritation. This could apply to the infilling denticles observed in regions of the buccal dentition in *Griphognathus* where abrasion and resorption are noted features.

In general, dentine in vertebrates, once formed, has the ability to continue growth by apposition of new layers on the old; in a tooth with an enclosed central pulp cavity this encroaches on the area of the pulp tissue and also may add to the length of the root. The dentine of dipnoans may grow in a basal direction into the soft tissue spaces of the supporting bone where new dentine grows by apposition on bone and has been described as pleromic dentine beneath the tooth ridges, tooth plates and buccal denticles of *Griphognathus*, *Holodipterus* and *Chirodipterus*.

The structure of the buccal denticles in *Griphognathus whitei* is derived from the simultaneous growth of many units of dentine; each pulp canal probably represents a group of odontoblasts which have been induced to form dentine at only fractionally different times. The denticle shapes are similar to those figured by Gross (1965) for *Ganorhynchus splendens* and also similar to some of the body denticles in the elasmobranch *Heterodontus portjacksoni* figured by Reif (1973, 1974). Typical shapes of primary buccal denticles in *Griphognathus whitei* are illustrated in figure 37, and in *Holodipterus gogoensis* in figures 58 and 64, while the range of shapes is seen in figure 36. In regions where the denticles are larger and more bulbous, the primary denticle shape has been replaced by one in which the dentine units have become consolidated by simultaneous growth. In *Pycnaspis*, the primary outer layer of the dermal covering is one of small pointed tubercles which are later overgrown by large bulbous tubercles (Denison 1963). The youngest primary denticles are unworn and have a characteristic surface of long ridges with many separate points along each ridge and also along the side ridges which join up to the main ridge. These all give the impression of representing the tips of the component dentine units which are incompletely covered by enameloid. Like the tissues of the tooth ridge these composite denticles are made of syndentine. The conclusion that the units of syndentine are equivalent to primary odontodes or primary ontogenetic denticles is supported by factors other than the surface topography. The alignment of the collagen fibres in the matrix is longitudinal, relative to the pulp canal, as in many denticles with a larger pulp cavity. The pulp canals are relatively narrow, perpendicular to the surface and open basally into the larger vascular spaces within the bone. The thickest point of enameloid is situated immediately above the axis of the pulp canal. The pulp response to produce secondary dentine is found in all pulp canals of the composite tissue. Also a ring of vascular canals surrounds the base of the denticles, sometimes referred to as neck canals. No attempt has been made to fit this information into the lepidomorial theory proposed by Stensiö and Ørvig (Stensiö 1961) as the method by which complex placoid scales were derived from simple ones, although the primary dentine units are analogous with the simplest elements, or lepidomoria of the scales.

In regions where the primary denticles are replaced by worn pleromic tissue forming a continuous plateau, separate denticles are still found marginally. From these regions the probable manner of conversion can be predicted, from primary denticles with ridges and separate points to worn flat denticles with worn tissue in between. The concavities on the outer walls of the denticle become filled in with new units of dentine which may form around the individual neck canals at the base of the denticle. This occurs at the same time as the dentine around the pulp canals of the denticles becomes worn and itself fills in with secondary pupal dentine, as shown in figure 63. Once the denticle becomes worn down to the basal tissue and the pleromic dentine also becomes worn it is impossible to distinguish one from the other. The covering to the dermal bone has changed from denticulate to a flat abraded surface as illustrated in figures 60 and 61 of one of the dermopalatines from two specimens of *Holodipterus*.

In the first part of this discussion it was concluded that the phyletic trend towards macromerism can be demonstrated within the dipnoans and that it occurs in functionally important areas. In the second part I have discussed how changes from the primary denticles to larger, consolidated denticles could occur during the growth of individual specimens in response to wear or functional stress. The variety of ways in which growth of dentine can occur in *Holodipterus* in particular constitute a very flexible system able to respond to localized patterns of wear. This is discussed further in the next section (6*e*).

(*e*) *Adaptive structures: pleromic and secondary dentine*

Throughout the previous sections of the discussion, reference has been made to pleromic dentine and secondary pupal dentine. The intention of this part of the discussion is to bring together some of this information in the context of adaptations of the dentition to wear. Halstead (1969) in a review of calcified tissues in the earliest vertebrates concludes that 'there is no doubt that originally pleromic dentine arose as a direct response to wear', although isolated instances are cited where pleromic dentine has formed alongside tissue with no evidence of surface abrasion. Contrary to this view, Ørvig (1976*b*) in a review of pleromin (pleromic hard tissue, Ørvig 1967) in the psammosteid heterostracans, concludes that pleromin does not form in response to abrasion but is initiated in a superficial position before any abrasion on the external surface. Ørvig has stated that pleromin is a hypermineralized tissue of continuous growth which he suggests spreads inwards at a faster rate than the abrasion on the external surface, and is a product of fusion of successive odontode generations. Ørvig concludes that pleromin is not a secondary dentine, in the sense that it does not fulfill a reparative function but a prophylactic function.

Halstead (1964) has described the arrangement and probable mode of formation of pleromic dentine in the Middle and Upper Devonian psammosteids. In this group of early vertebrates, the pleromic dentine contains very long tubules which wind through the original soft tissue spaces of the aspidin and originate from the bone spaces between the tubercles. Halstead equated this tissue with that described by Gross (1930, 1935) as massive spongiosa. Ørvig (1967, 1976*b*) has illustrated pleromic dentine in the psammosteid dermal armour with some of his diagrams based on Kiaer (1915) and Gross (1930), and has described the various types of pleromic dentine which can occur in elasmobranchs, dipnoans, holocephalans and ptyctodontids. Ørvig (1967) comments that 'pleromic tissues are, in general, characterised by their hardness, transparency, and homogeneity' and adds that 'in other respects they vary to a considerable extent'. The pleromic dentine which invades the spaces within the spongy bone of the dipnoans has the properties of translucency and hardness but the dentine tubules do not extend continuously through the infilled bone spaces, but are relatively short tubules which radiate from the central vascular canal around which the pleromic dentine has formed. Pleromic dentine of this kind has been identified in the buccal tissues of *Holodipterus* and *Chirodipterus* but not in *Griphognathus*, this apparent absence may be due to a failure to examine the appropriate regions of the dentition of *Griphognathus*. The pleromic tissue is always found in regions of excessive abrasion and at the margins of the tooth cusps and tooth plates either as the result of occlusal friction or as the response to a requirement for stronger union of the tooth plate to the marginal and basal spongy bone. Similar pleromic tissue has been described in *Holodipterus* (Gorizdro-Kulczycka 1953) and *Dipterus* (Denison 1974).

The tissue which forms within the pulp canals in the dentine of the tooth ridges and some of the buccal denticles, and in the tooth plates, I have described as pulpal secondary dentine. This develops after surfaces have begun to be abraded and is assumed to develop by secretion from the odontoblasts within the pulp canal and not from newly initiated mesenchymal cells. It is analogous with secondary dentine which develops in many mammalian teeth in response to steady attrition at the surface of the dentine. This secondary dentine in dipnoans is less highly mineralized than the primary circumpulpal dentine and less resistant to wear as demonstrated in many of the surfaces examined at the relatively high magnifications which are possible in the scanning electron microscope. I have not found any previous references to secondary pupal dentine in dipnoans. However, Halstead (1964) has drawn attention to the distinction between pleromic dentine in the psammosteids (which is a form of secondary dentine) and secondary dentine formed immediately beneath the primary dentine which is deposited within the pulp cavity by the first generation odontoblasts, also in response to wear. He has claimed that in a few instances, secondary dentine was formed immediately below the original dentine of the tubercle but this develops after pleromic dentine has begun to form.

A third kind of infilling tissue which strengthens the bony skeleton is produced by the appositional growth of bone lamellae to produce both primary and secondary osteons in spongy bone. These have been noted in all three species of Australian dipnoans. Ørvig (1951, 1967) has referred to the existence of osteons in all craniate vertebrates and Schultze (1970) has described resorption and secondary osteons in the centra of *Griphognathus sculpta* Schultze.

The enameloid on the surfaces of the tooth ridges and buccal denticles is relatively thick and very highly mineralized. Undoubtedly its highly organized structure is formed by cooperative activity between the odontoblasts and dental epithelial cells and once it is worn, cannot be replaced. Dentine from which the enameloid is lost, responds to abrasion by becoming hypermineralized; this is observed as resistant, translucent dentine in which many of the tubules have become occluded. This adaptive feature has been observed on most functional surfaces of the tooth ridges and denticles as translucent rings around the secondary pulpal dentine; in scanning electron micrographs these are seen to be raised areas of dentine around the pulpal tissue, separated by less resistant interstitial dentine. None of these features has been previously reported for dipnoan or other non-mammalian dentine.

Resorption is an integral part of the tissues growth pattern and adaptation to wear. Denticles are certainly periodically resorbed, not simultaneously but each at different times. Resorption removes the surrounding bone and progresses until a pit is formed and the denticle is shed or totally resorbed or abraded. New denticles can be found developing in these depressions in the spongy bone adjacent to older worn functional denticles. The enameloid tips of these denticles are on a level with the base of adjacent denticles which suggests that some eruptive growth must take place to bring the denticle into the functional level. Resorption of the syndentine of the tooth ridges progresses from the vascular canals at the base of the natural borders to the dentine. In very limited regions, the tooth ridge is replaced by separate buccal denticles. This interchangeability of a continuous dentine layer with separate denticles may be a reversion to an earlier ontogenetic stage, as discussed for the dermal covering (§6*b*). What is certain is that resorption of bone progresses basally beneath the tooth plates of *Chirodipterus australis* and that this allows for basal growth of the dentine to keep up with wear on the functional surface. The tooth plates are not periodically shed and replaced by new ones.

I am indebted to R. Miles for his guidance throughout the project and for his encouragement and helpful criticism in reading the text, and to Kim Dennis for her constant assistance particularly with the scanning electron microscopy and section preparation. I should also like to thank Jenny Middleton for translating my rough sketches into publication diagrams, J. Mercer for photographic assistance, all the staff of the Electron Microscopy Unit at the British Museum (Natural History) for their continuing help, and Maggie Gregson for typing the manuscript. I should also like to acknowledge useful discussions I have had with Beverly Halstead, B. Gardiner, P. Forey and R. Hamilton.

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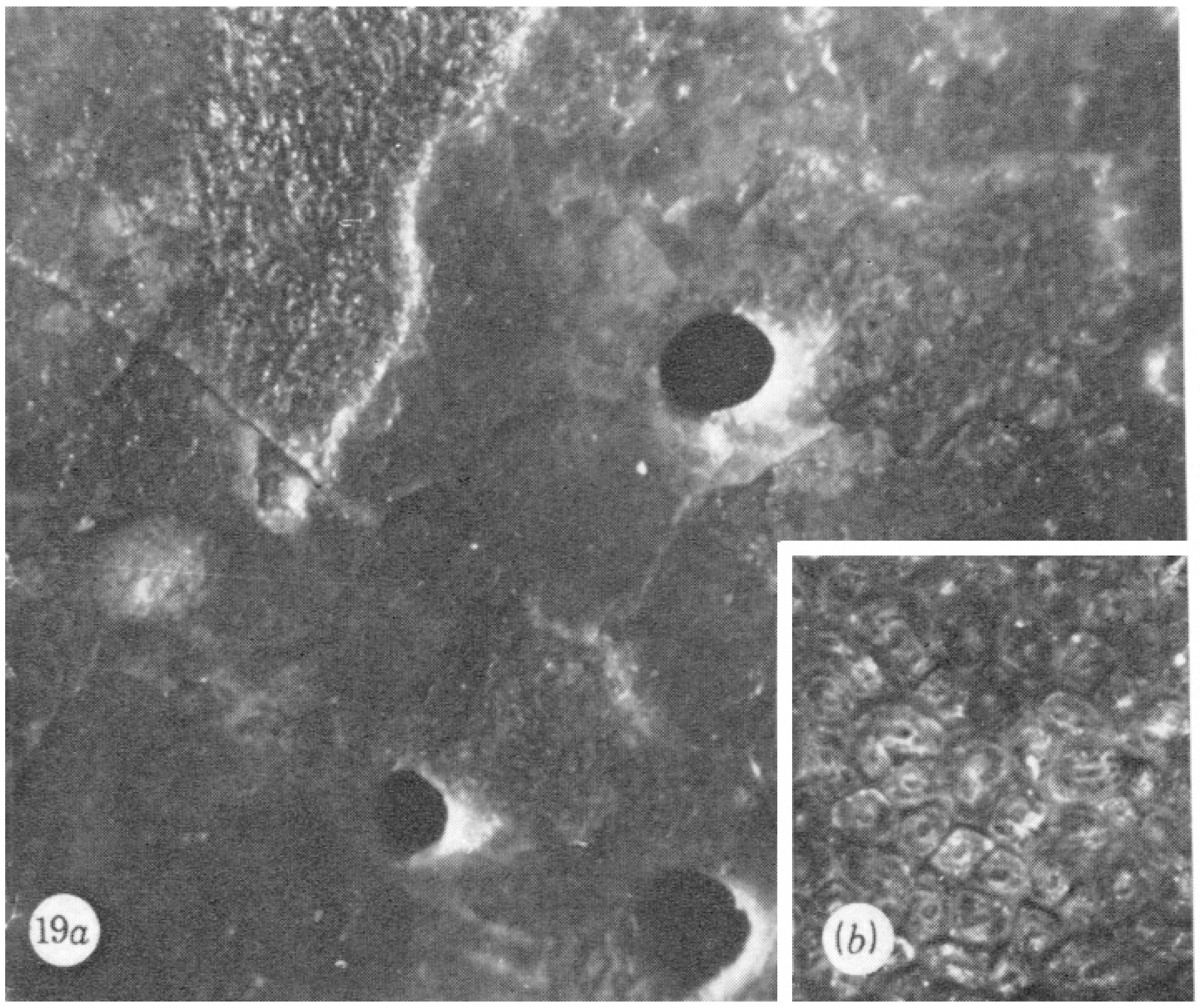

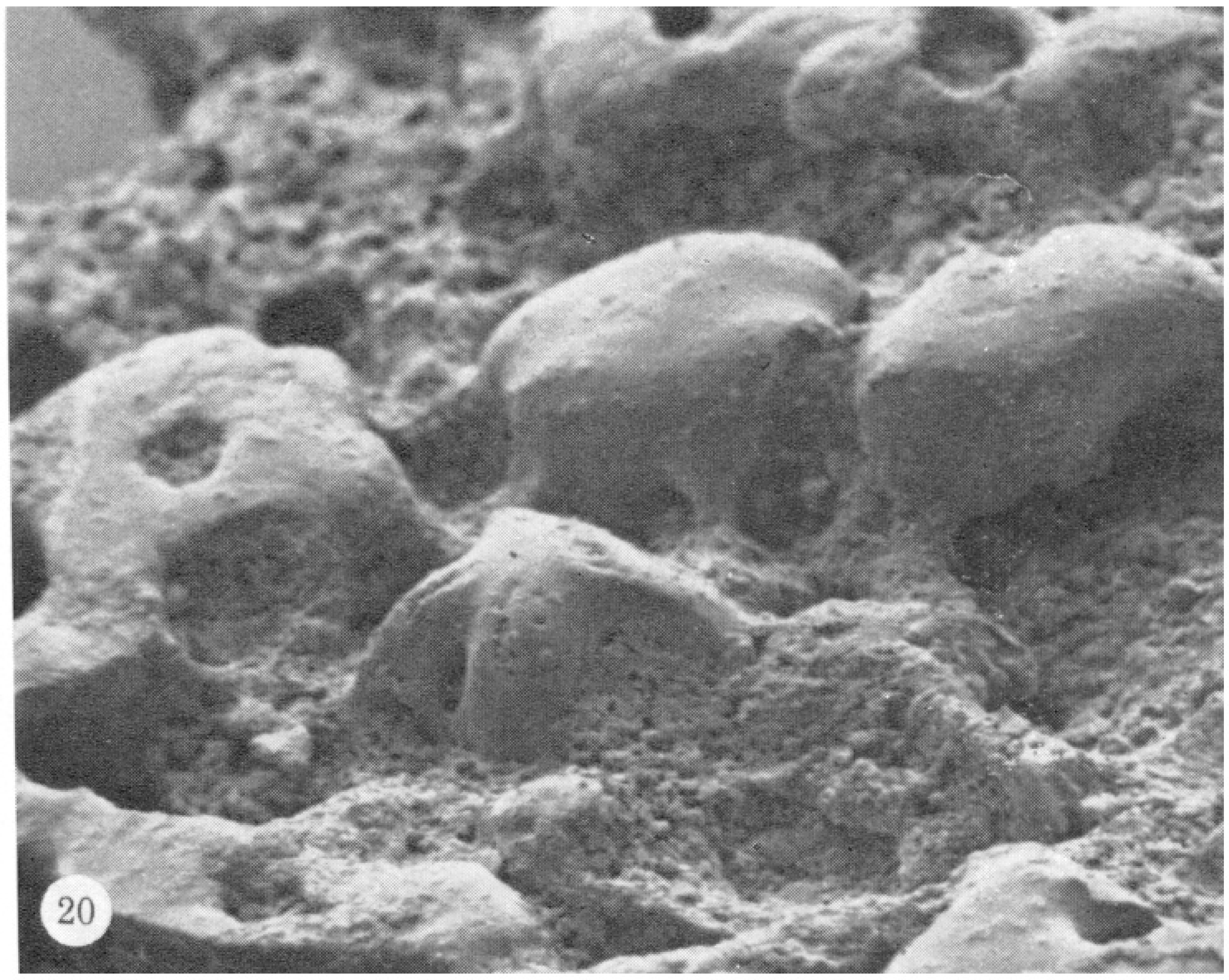

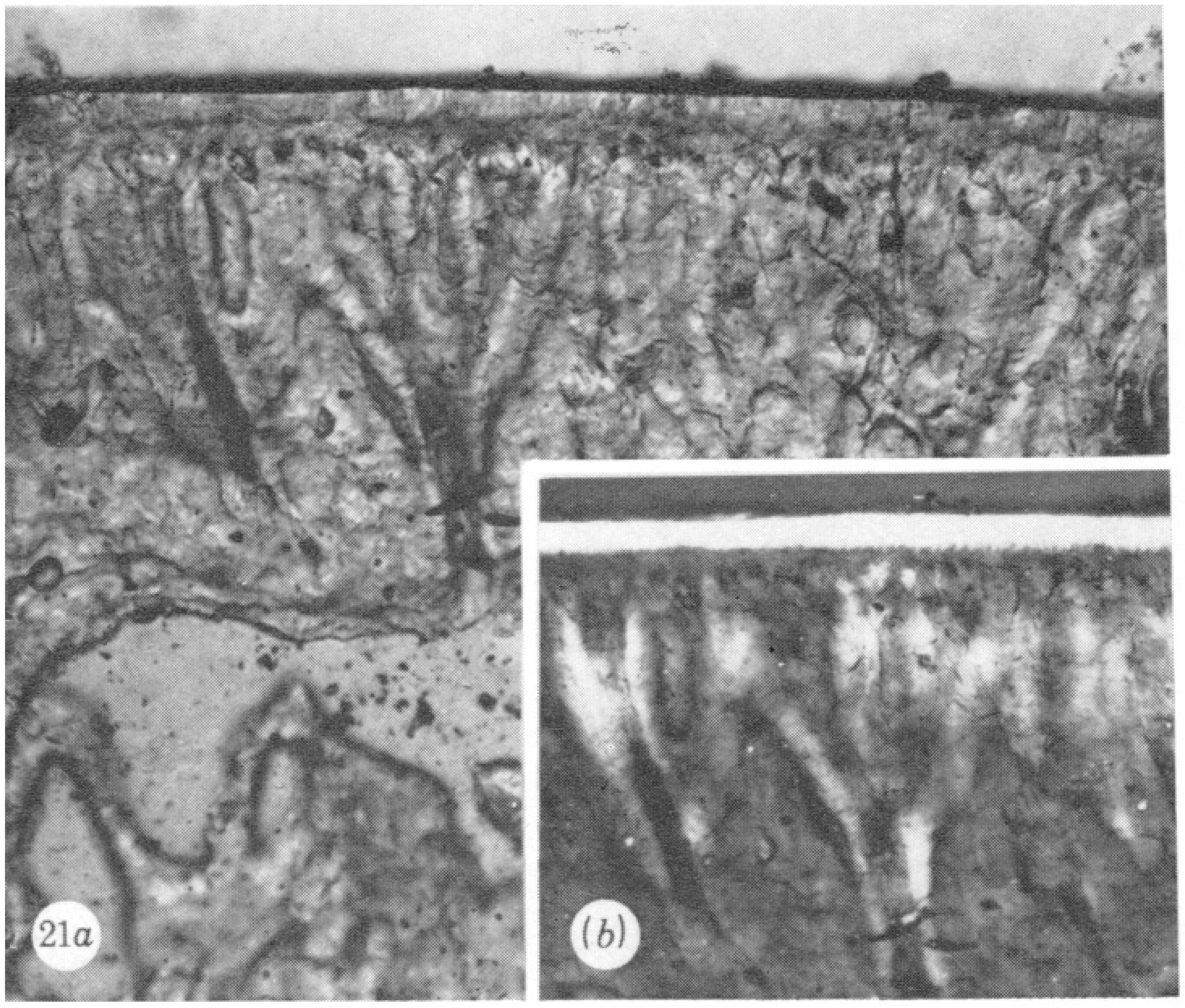

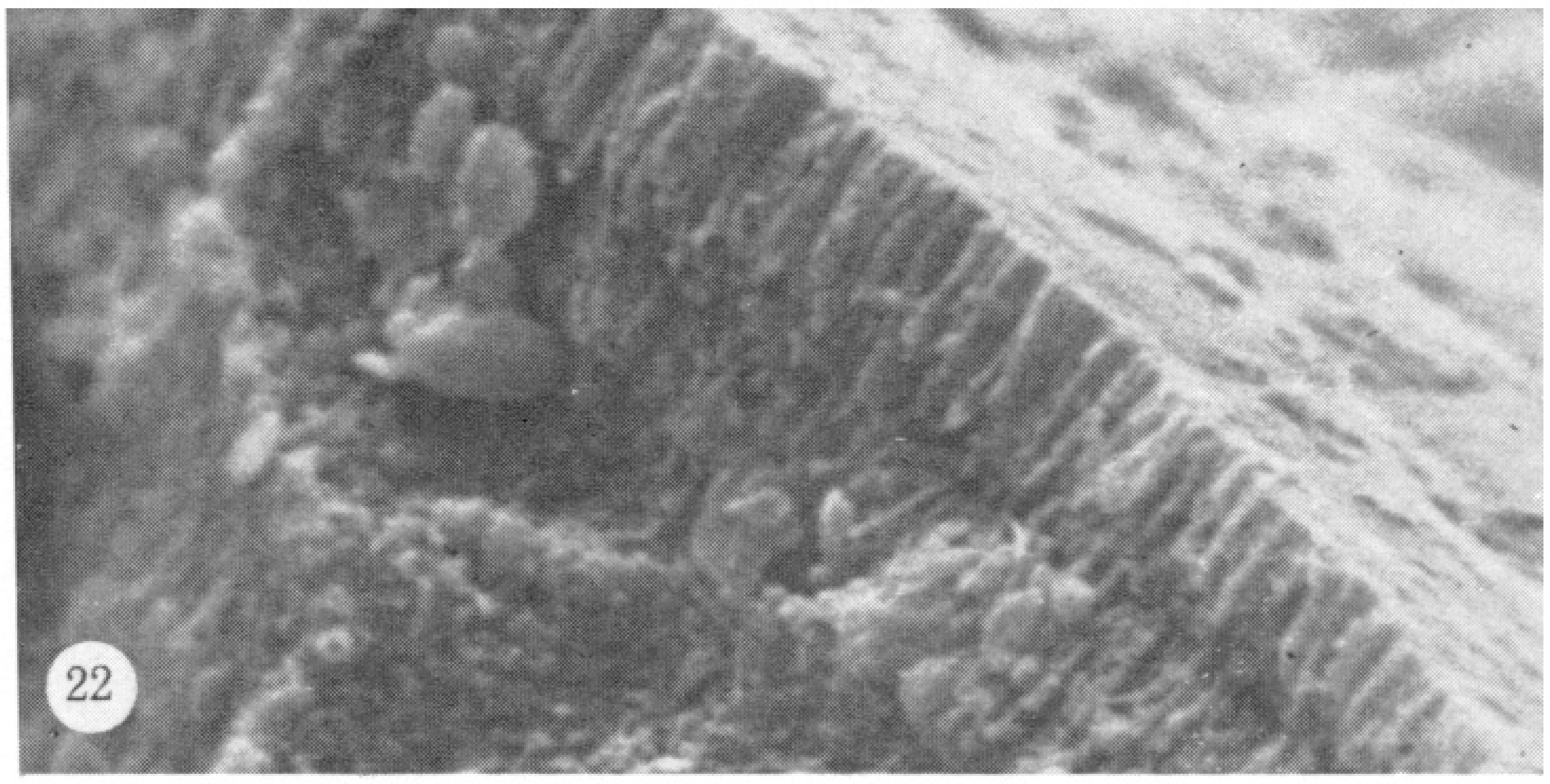

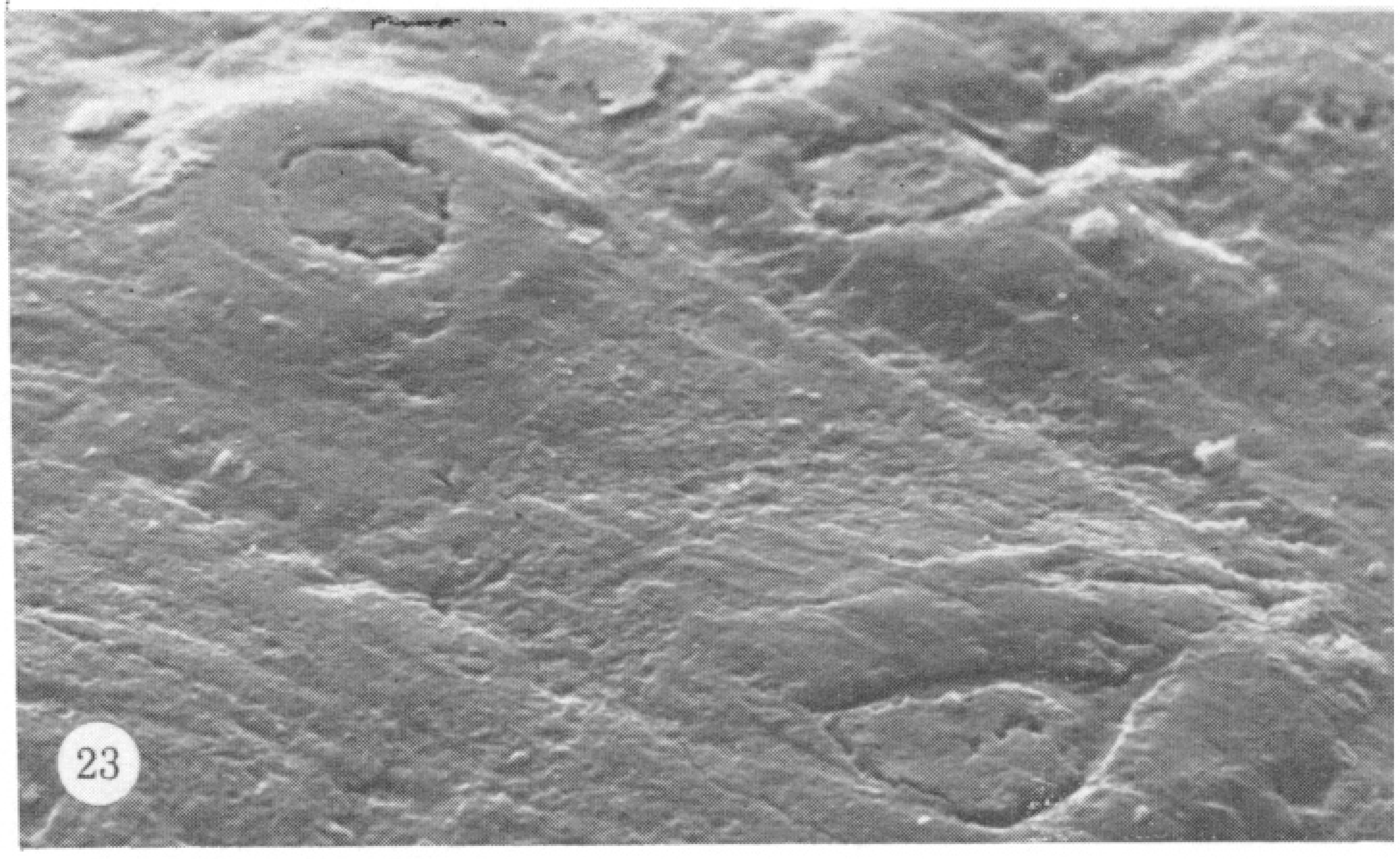

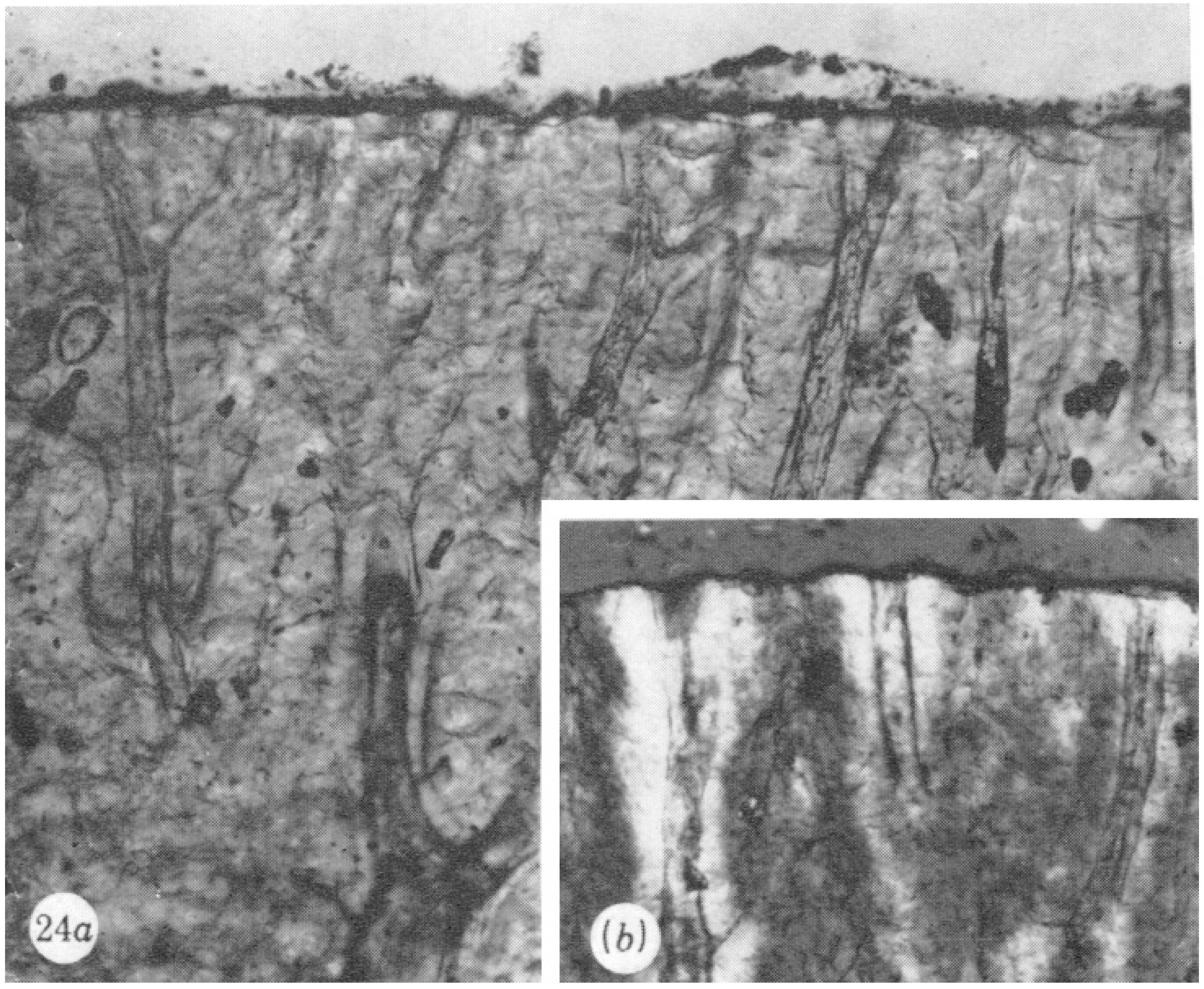

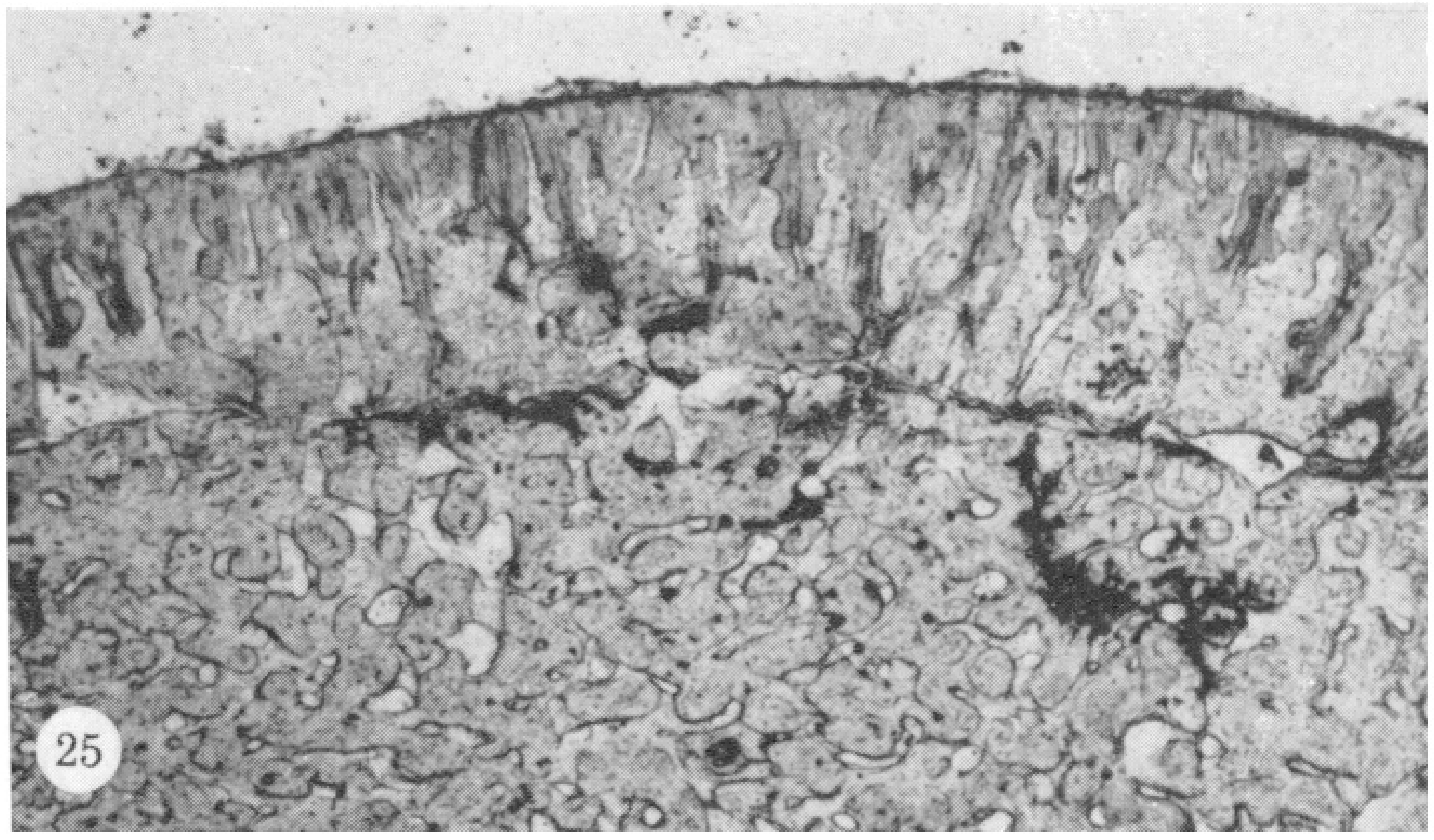

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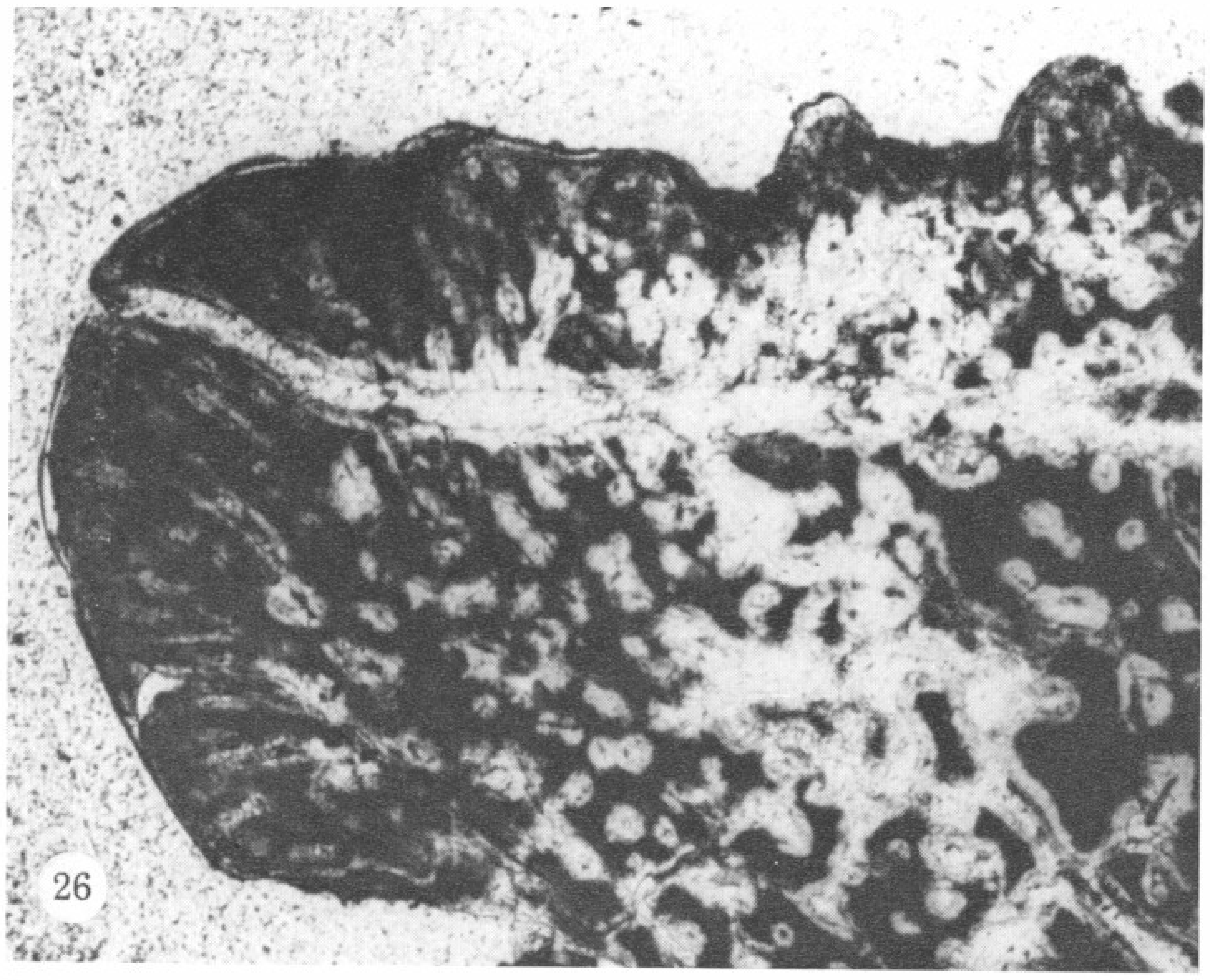

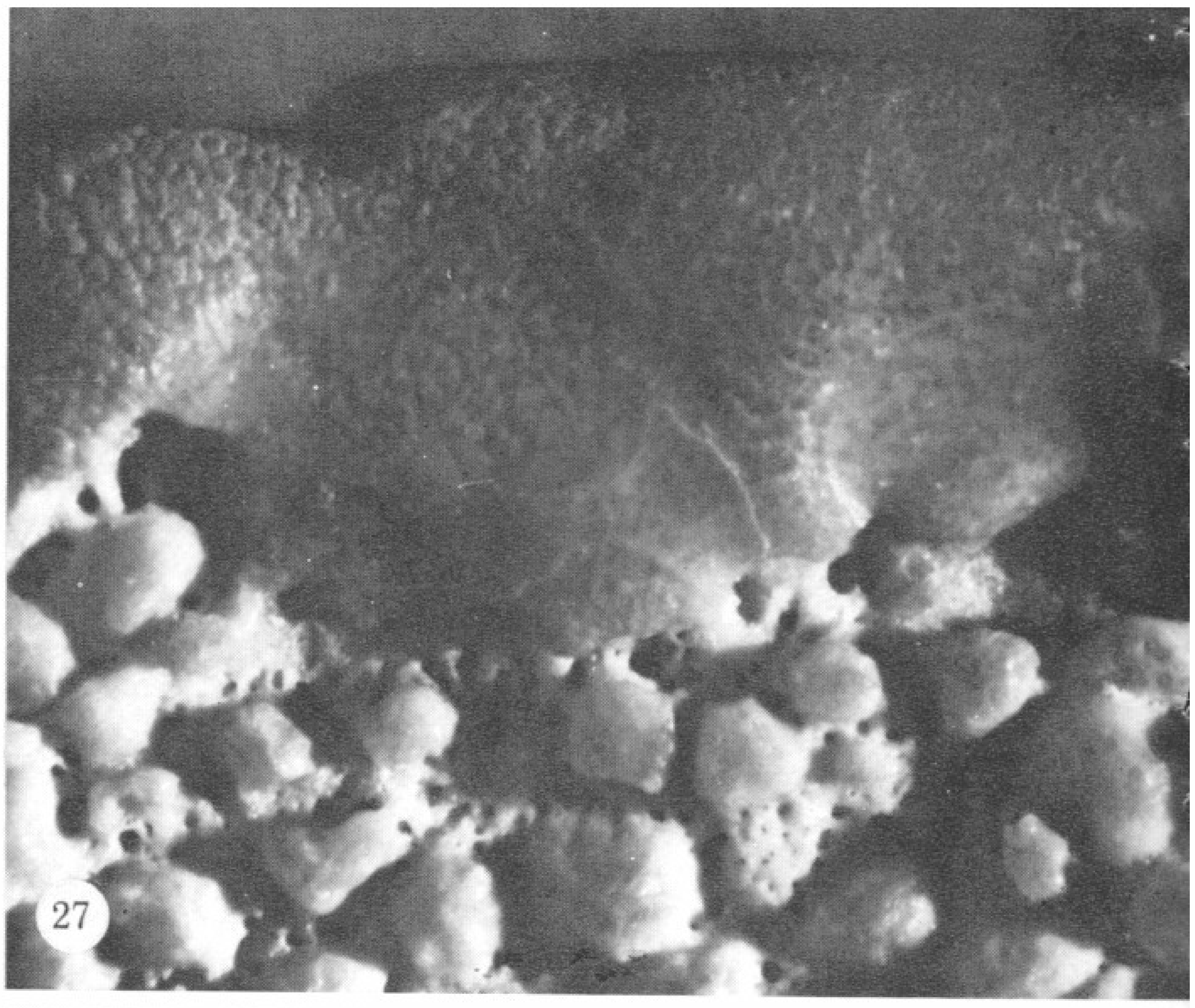

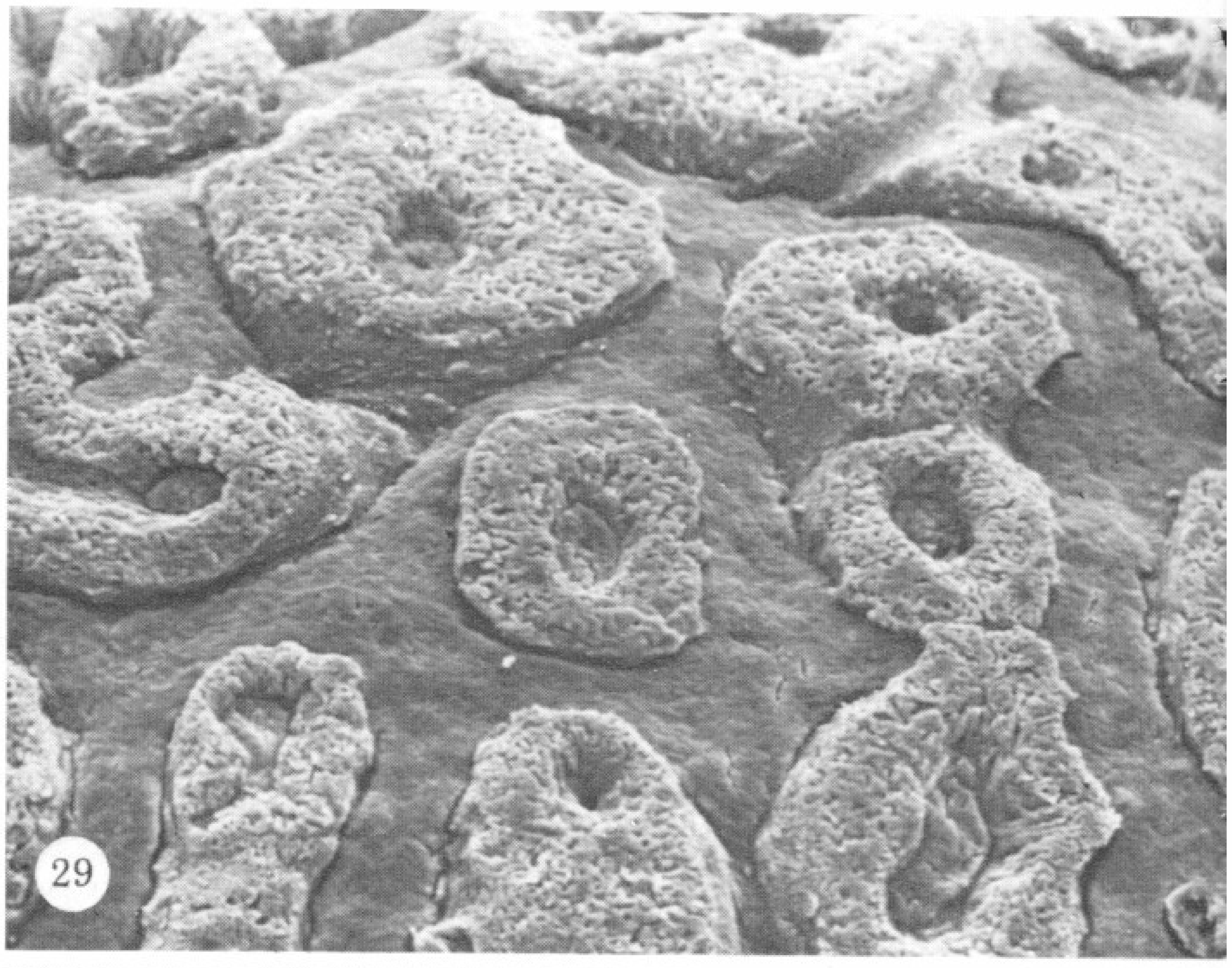

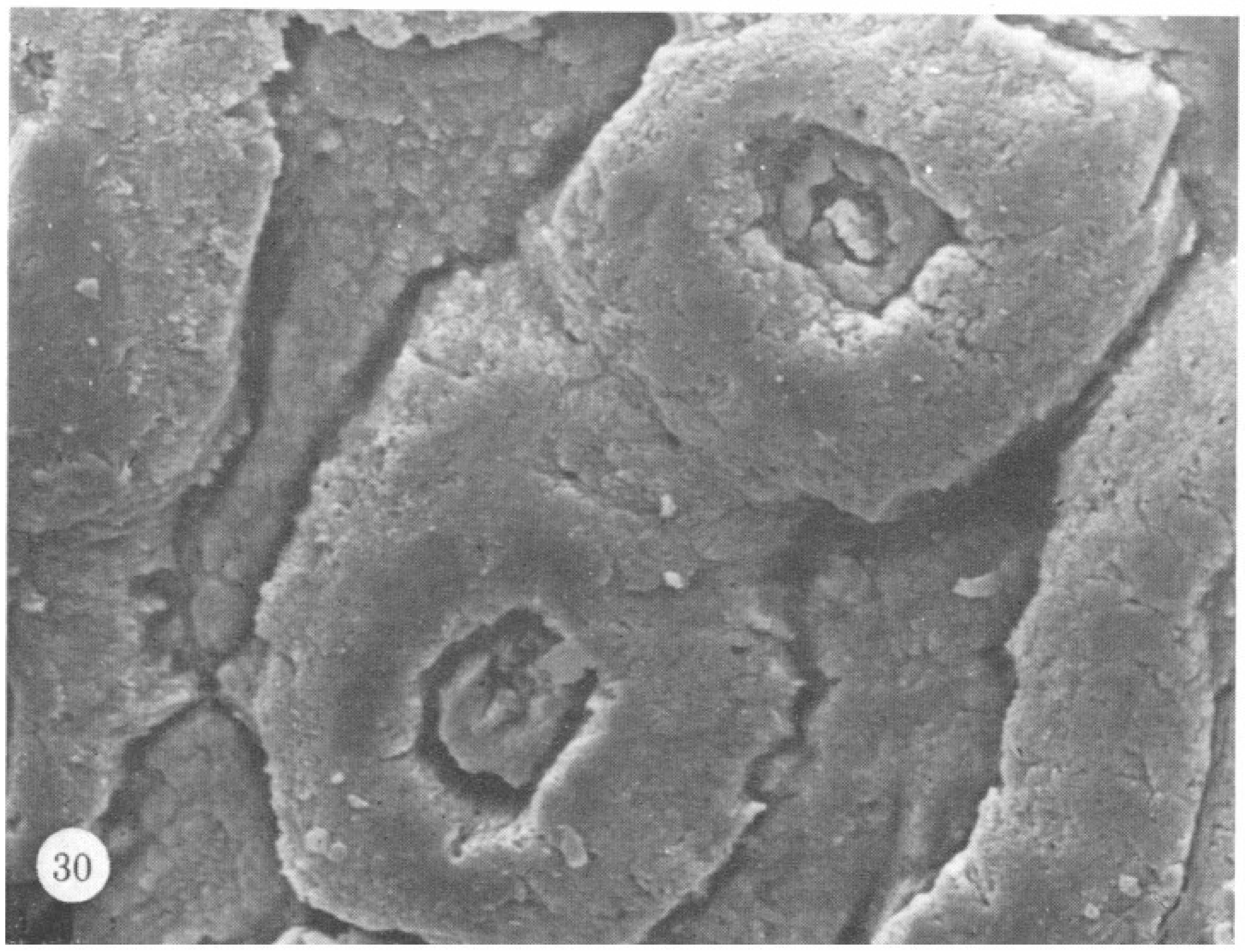

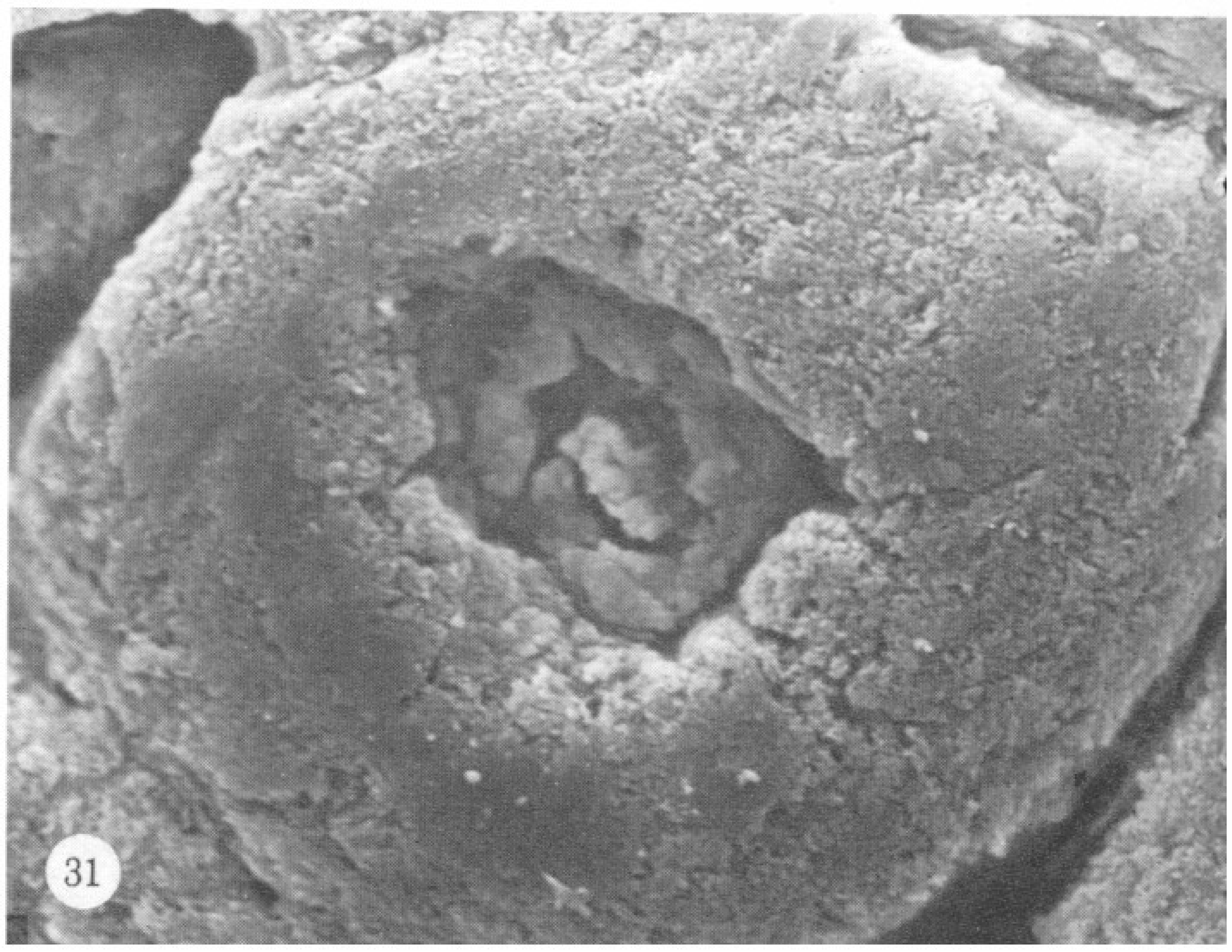

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Figure 26. Photomicrograph of a vertical section through the tooth ridge and denticles of the dentary. These tissues are shown in surface view in figure 27. From P52578 (× 35).

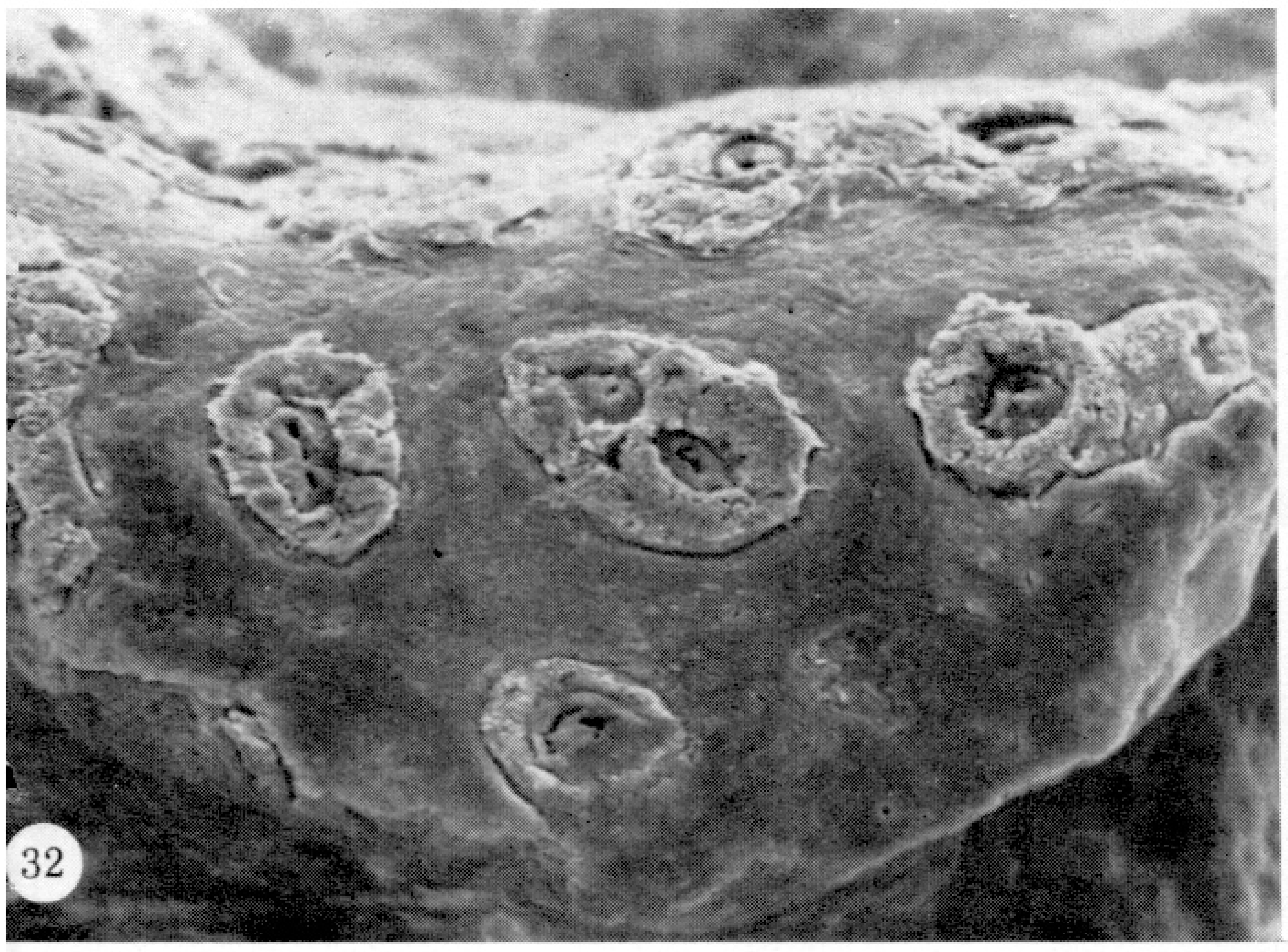
Figure 27. Photomicrograph of the tooth ridge and denticles on the medial surface in which the ringed worn surface of the ridge and some of the denticles are shown – as in figure 19*b* of the snout. P52572 (× 18).

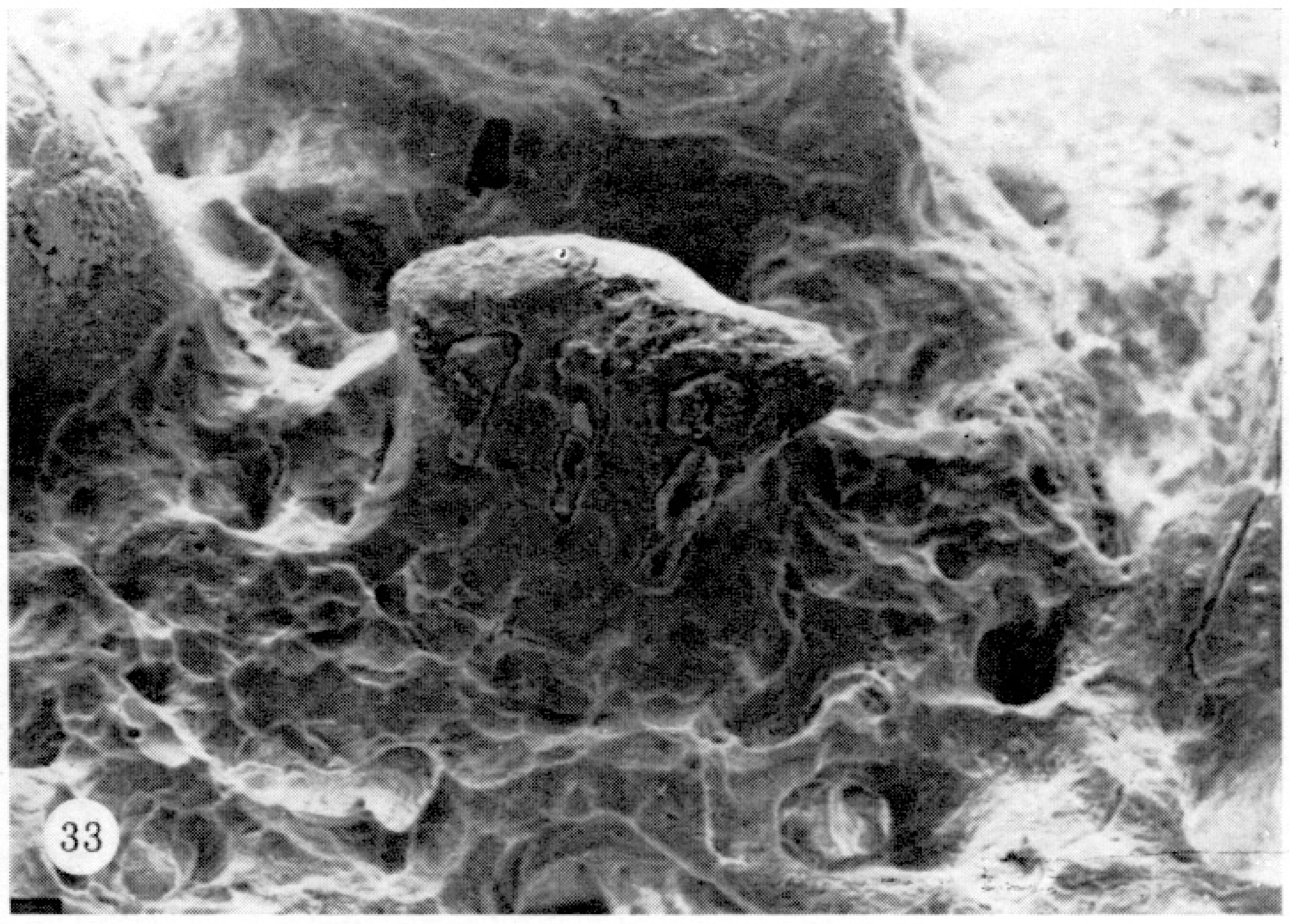
Figure 28. S.e.m. of the surface of the tooth ridge shown in figure 27 after treatment with 0.1 N HCl for 1 min. The rings of circumpulpal dentine are proud of the interstitial and pulpal dentine. P52572 (field width 460 μm).

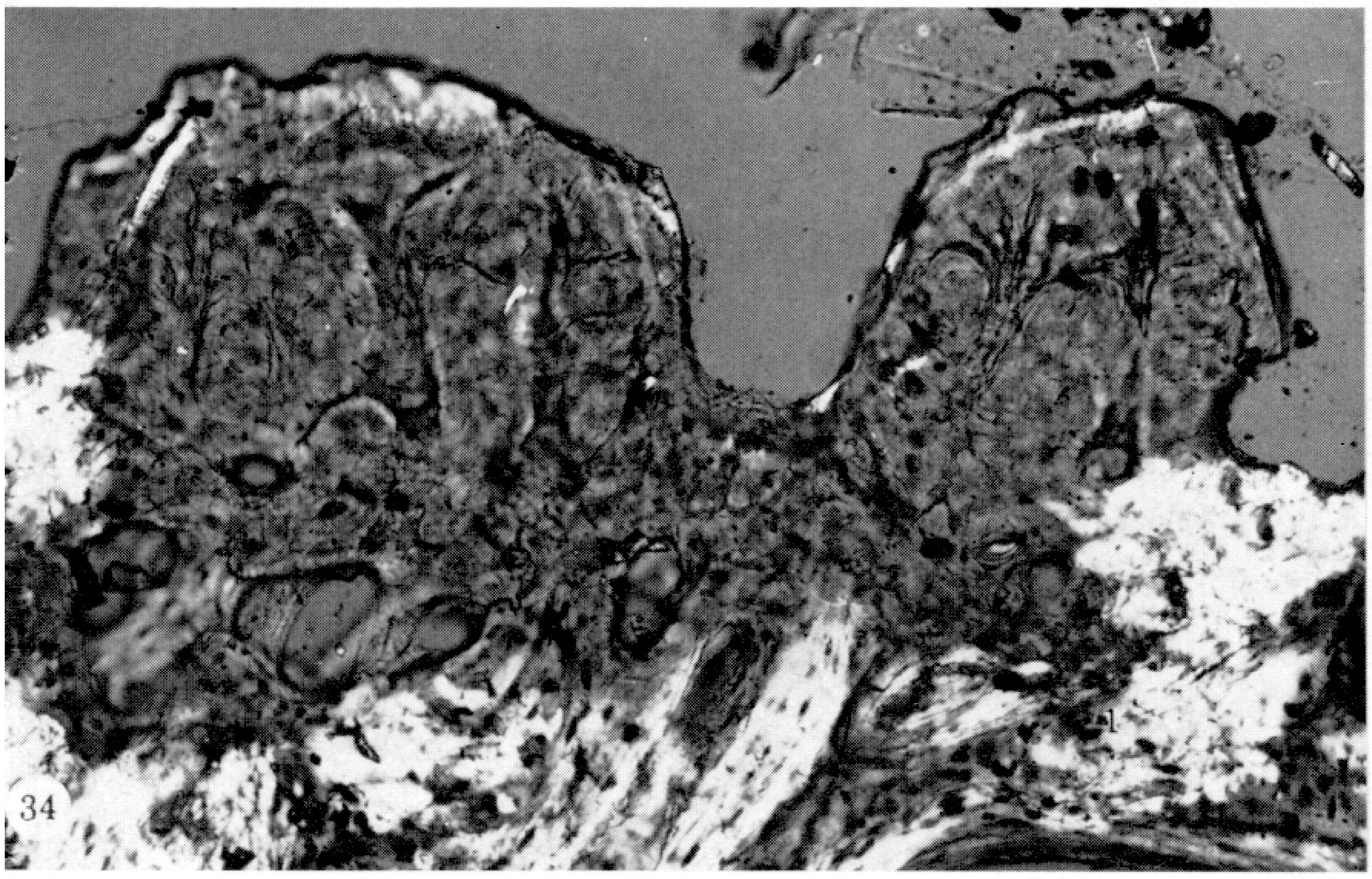
Figure 29. S.e.m. of one region adjacent to figure 28 in which the tubules in the circumpulpal dentine are seen to arise from the pulpal canal. P52572 (field width 186 μm).

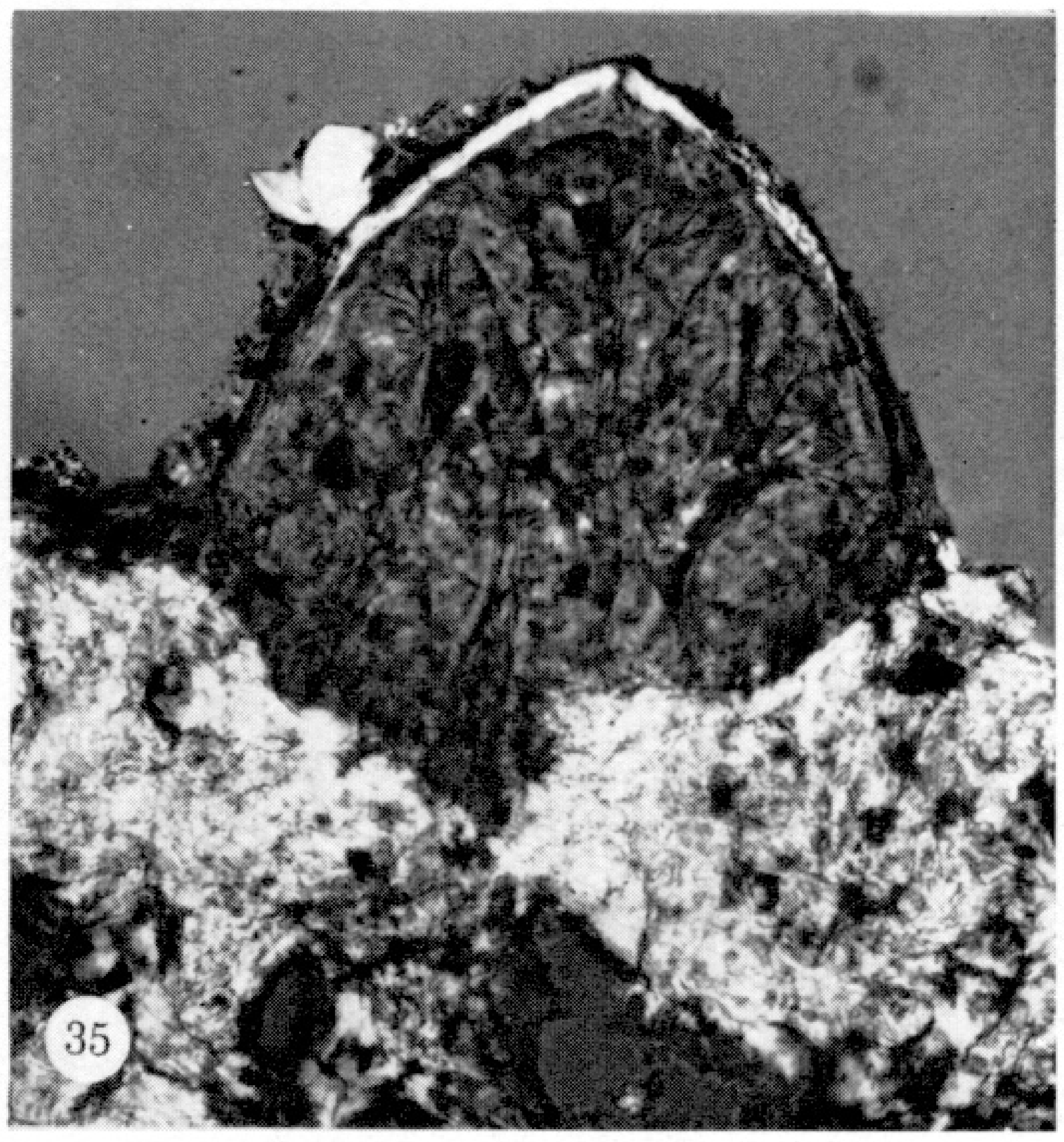
Figure 30. S.e.m. of a region in figure 28 in which the circumpulpal dentine is more highly mineralized than that in figure 29. P52572 (field width 93 μm).

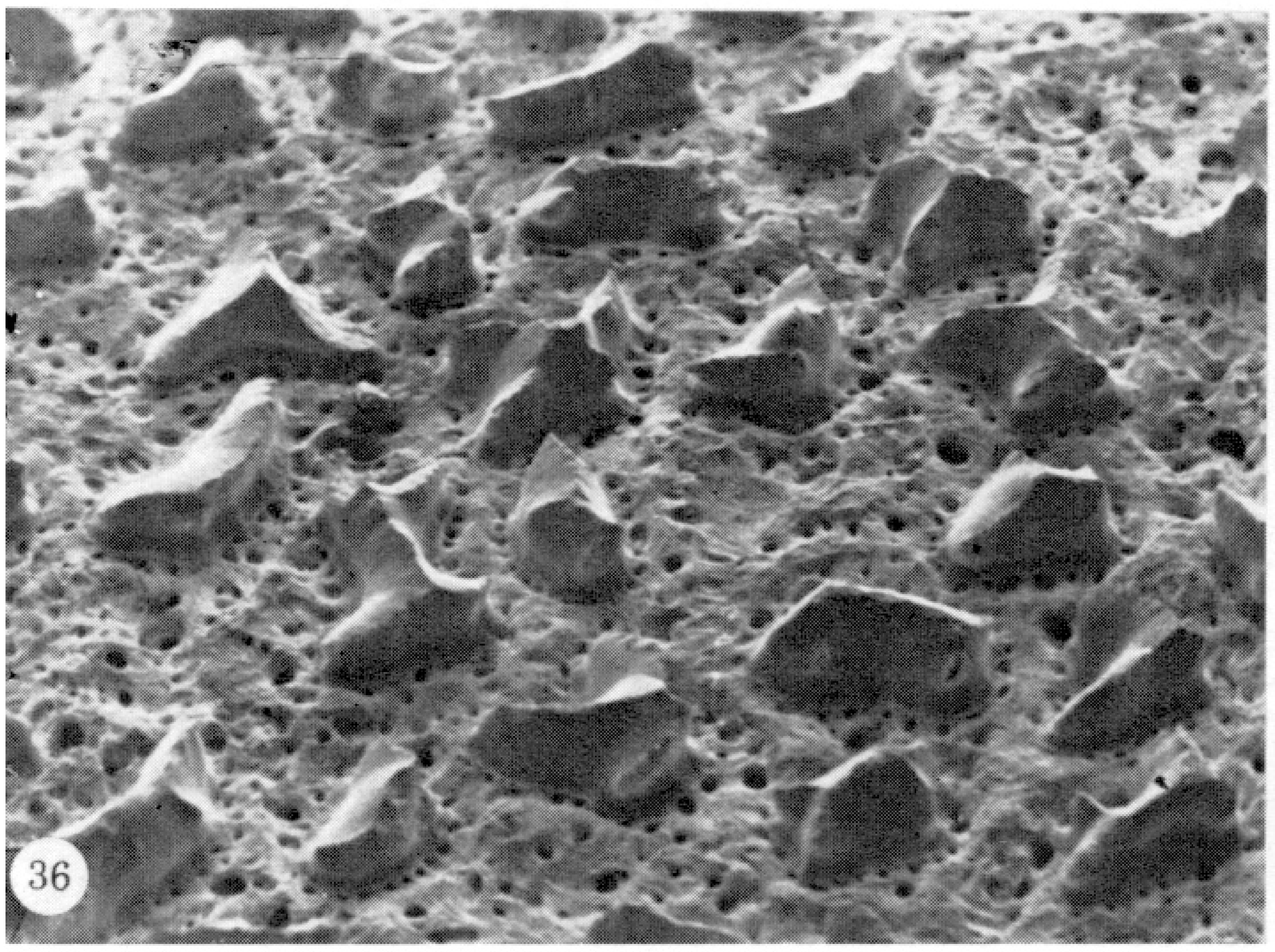
Figure 31. S.e.m. of one of the pair of dentine units shown in figure 30. P52572 (field width 46 μm).











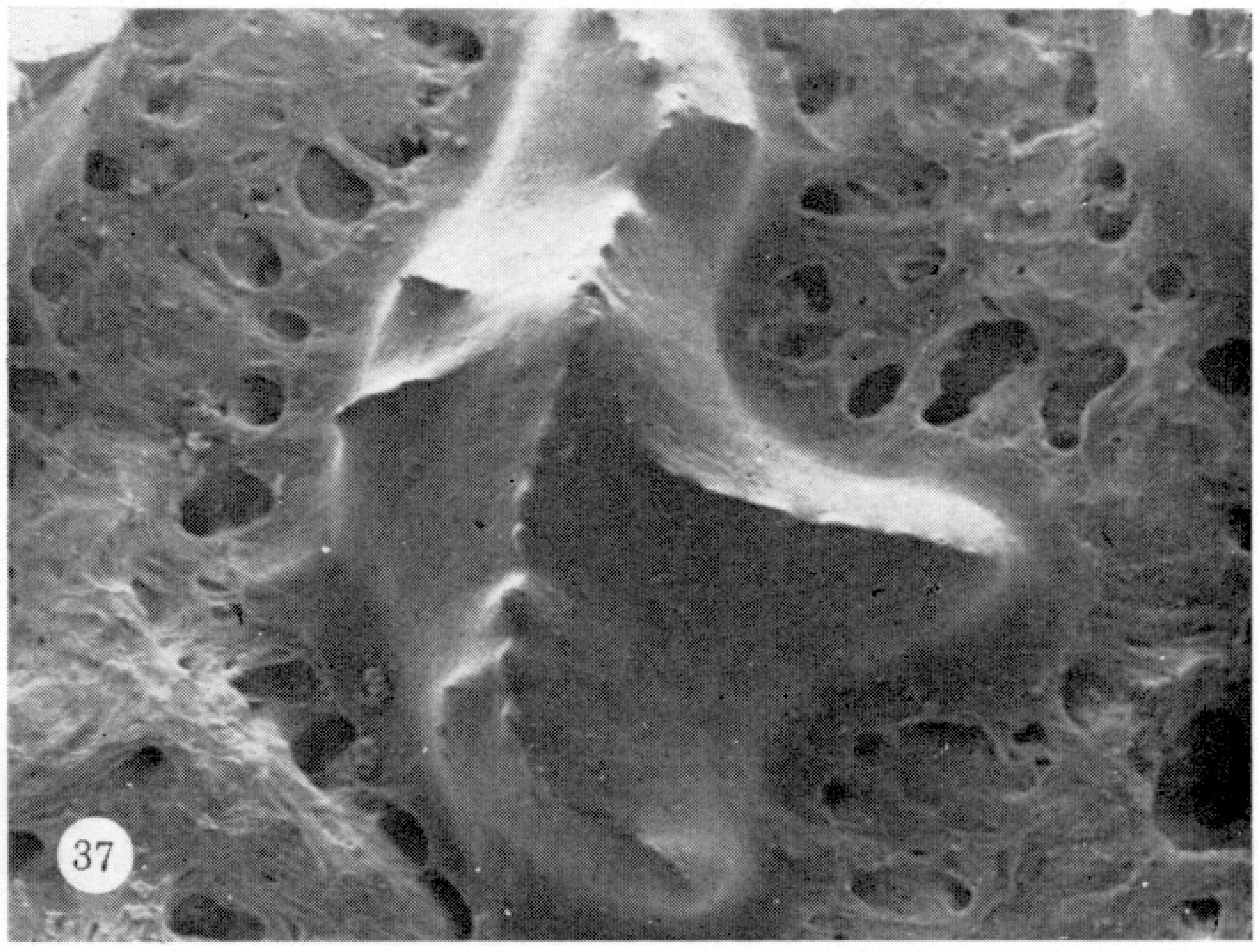


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Figure 32. S.e.m. of the surface of a denticle medial to the tooth ridge of the dentary, after treatment with 0.1 N HCl for 1 min. The dentine units are similar to those in figure 29. P52572 (field width 186 μm).

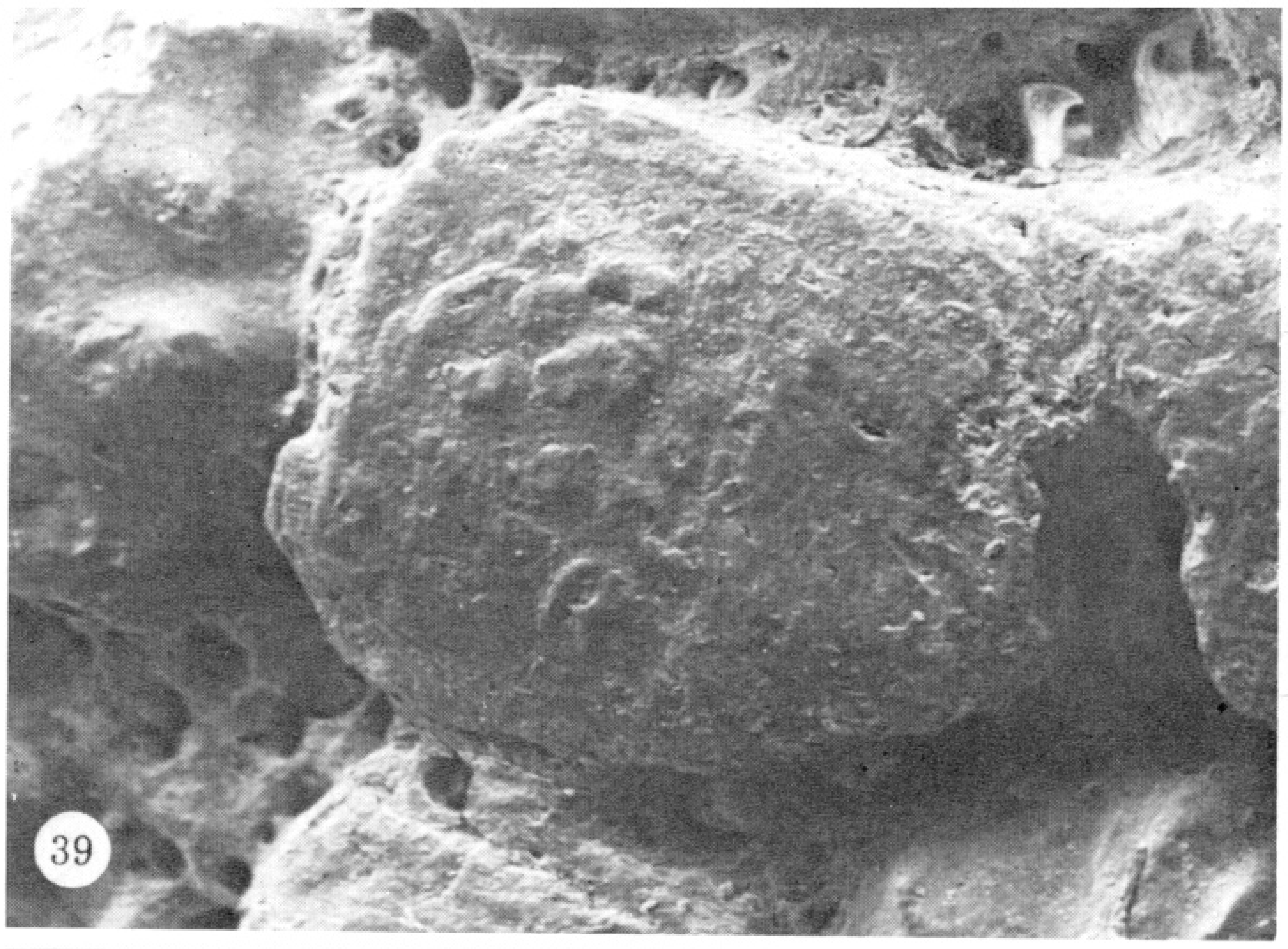
Figure 33. S.e.m. of the side of a denticle adjacent to figure 32 in which the dentine units are seen in longitudinal view where resorption has removed part of the denticle base and surrounding bone, as evidenced by the scalloped surface. P52572 (field width 460 μm).

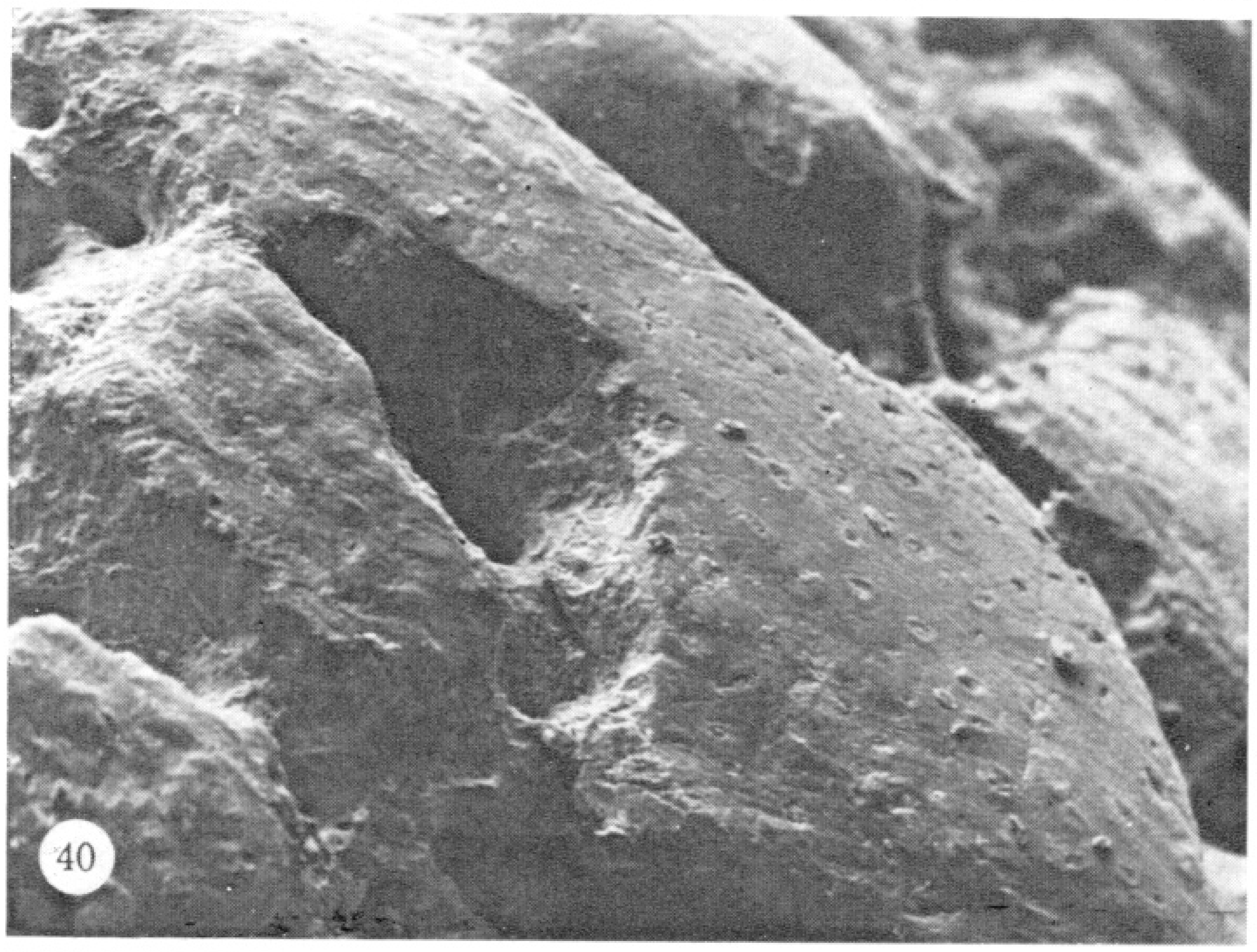
Figure 34. Photomicrograph of a vertical section through the denticles on the basibranchial seen in partial polarized light. Enameloid is lost from the worn surface but retained at the sides, and the superficial dentine is slightly birefringent. At the base of one denticle is a resorption surface. See figures 5 and 6. From P50998 (× 140).

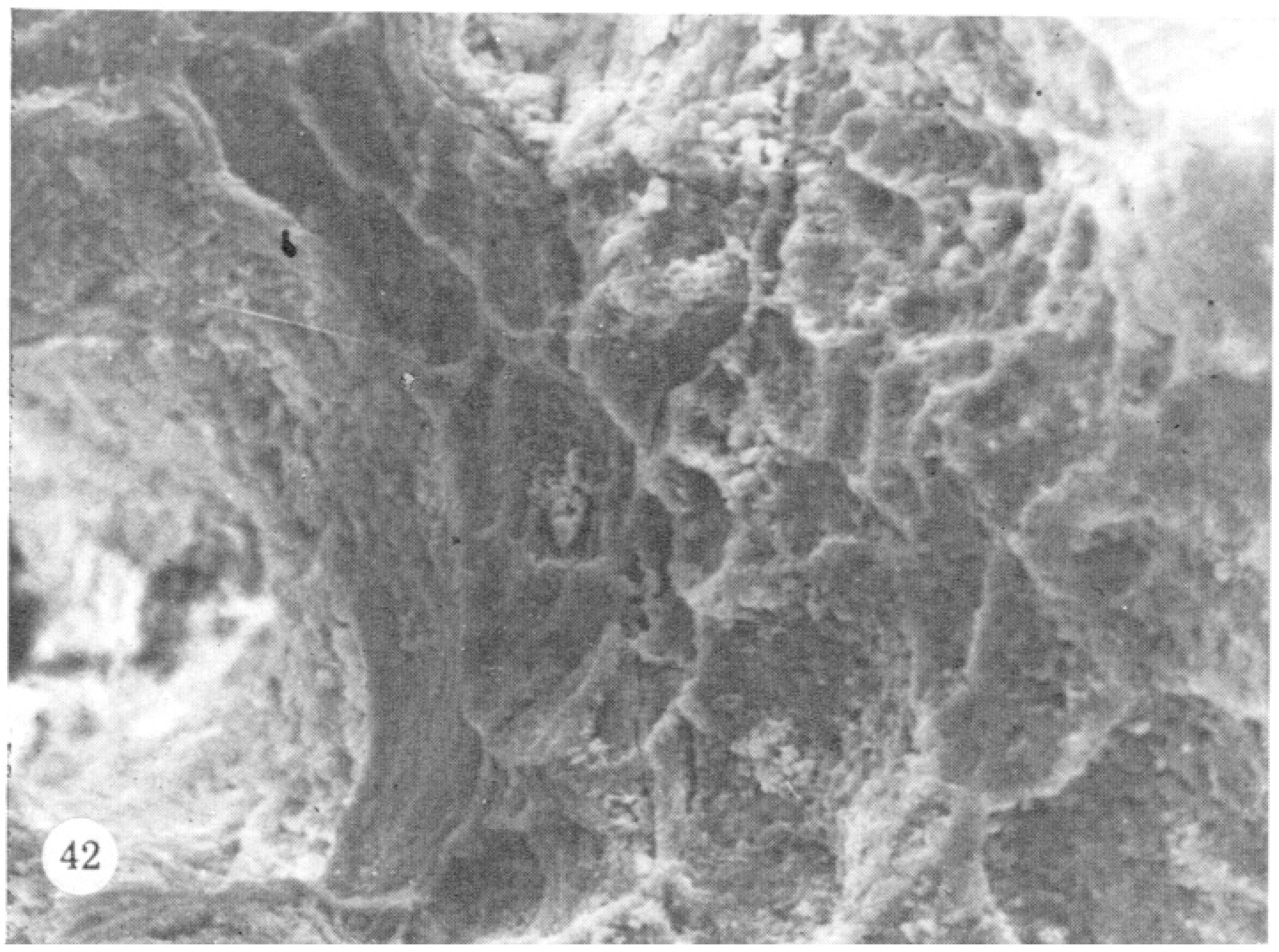
Figure 35. Photomicrograph of a vertical section through an unworn denticle on the basibranchial tooth plate with enameloid intact above the multiple pulp canals, also in partial polarized light. See figures 5 and 6. From P50998 (× 140).

Figure 36. S.e.m. of the denticles on the surface of the prearticular. (Number unknown; field width 1840 μm).

Figure 37. S.e.m. of one of the newly formed denticles from the region in figure 36. Separate points are seen along the crests of the ridges which are described as the tips to the component dentine units. P52579 (field width 460 μm).







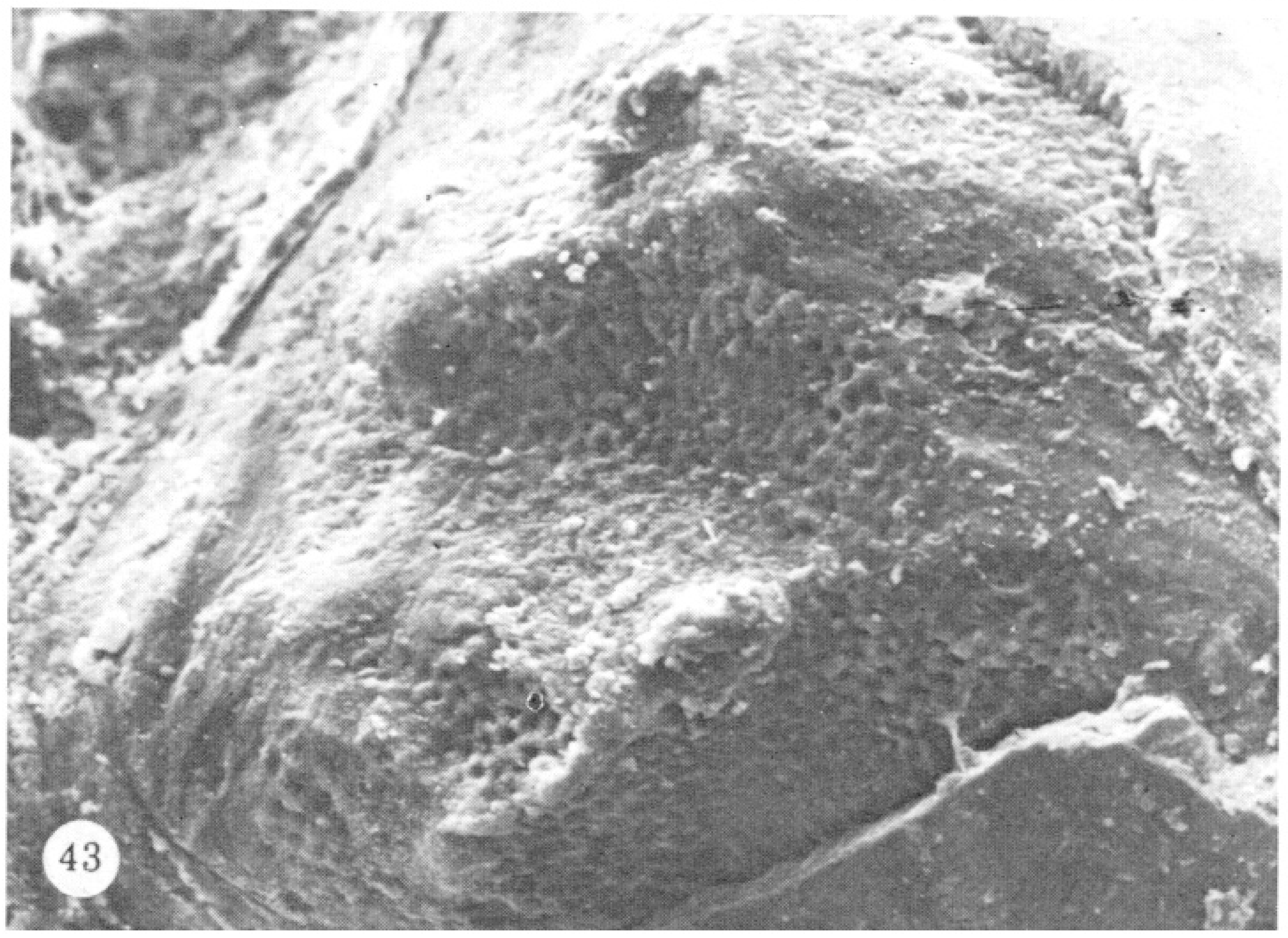


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FIGURE 38. Photomicrograph of the denticles on the surface of the ascending process of the prearticular. Worn tops show the ringed pattern as shown in figures 19 and 27. The unworn, new denticle has a shiny enameloid surface. P52579 (× 45).

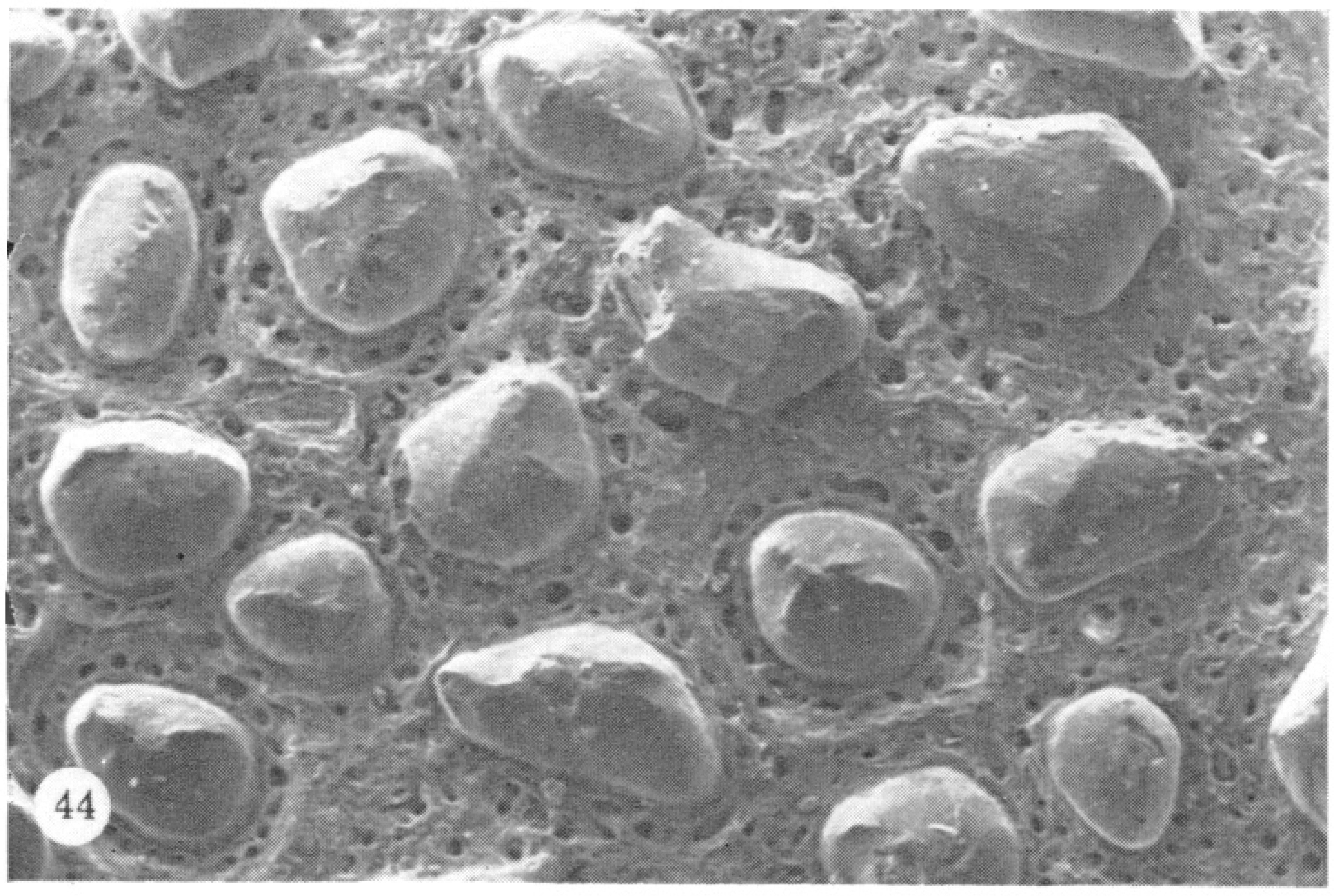
FIGURE 39. S.e.m. of the worn denticles seen at the top of figure 38. The translucent rings of circumpulpal dentine are raised above the level of the interstitial dentine and the secondary pulpal dentine. P52579 (field width 930 μm).

FIGURE 40. S.e.m. of an adjacent worn denticle which shows a regular arrangement of the dentine units. P52579 (field width 930 μm).

FIGURE 41. S.e.m. of the new denticle in figure 38 which is forming in a resorption cavity at the base of the worn denticle. P52579 (field width 930 μm).

FIGURE 42. S.e.m. of a resorption surface at the base of a worn denticle which is alongside a vascular canal. P52575 (field width 92 μm).

FIGURE 43. S.e.m. of the surface of a denticle on the prearticular in which the enameloid layer has fractured leaving a regularly pitted surface to the dentine. P52575 (field width 186 μm).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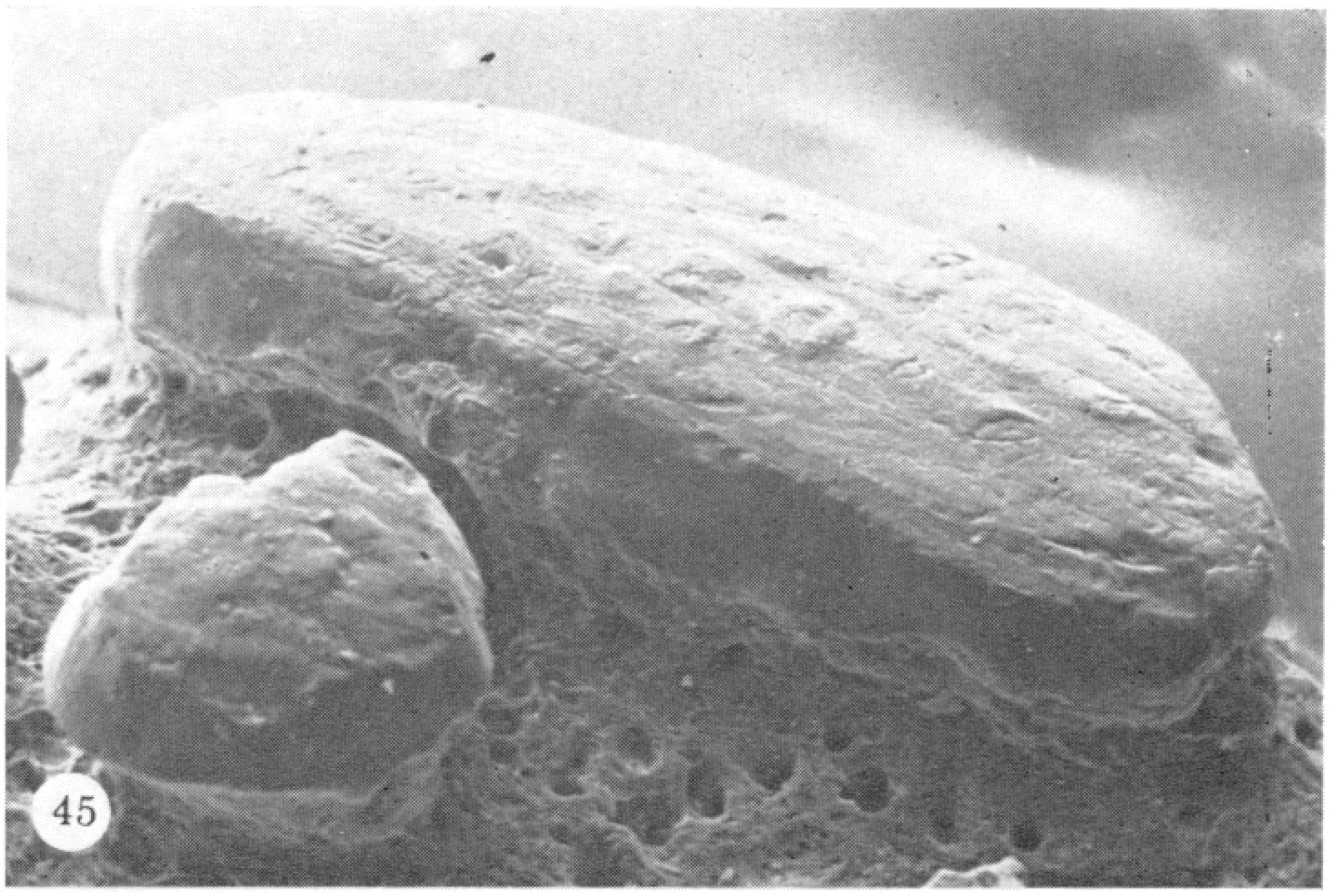
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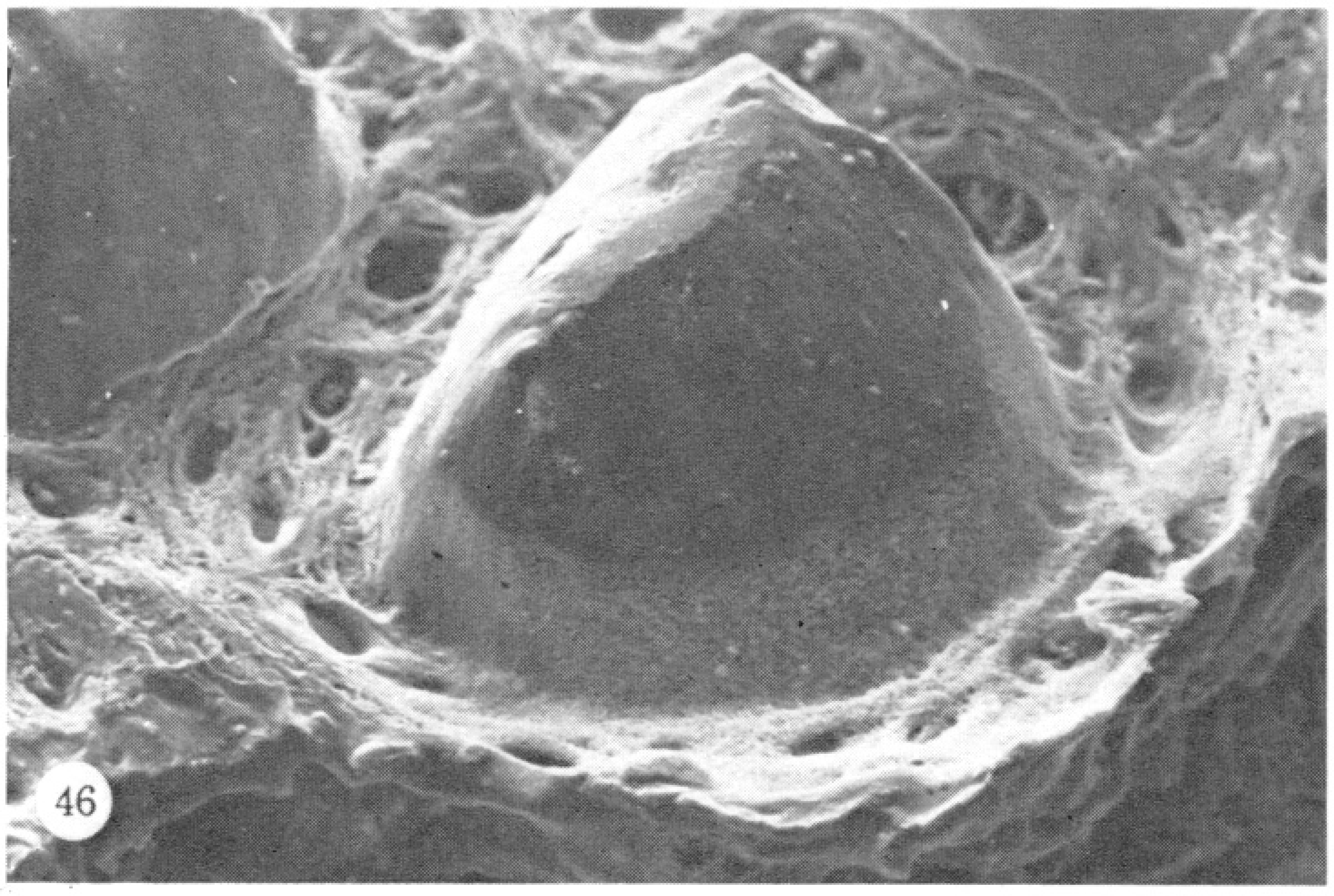
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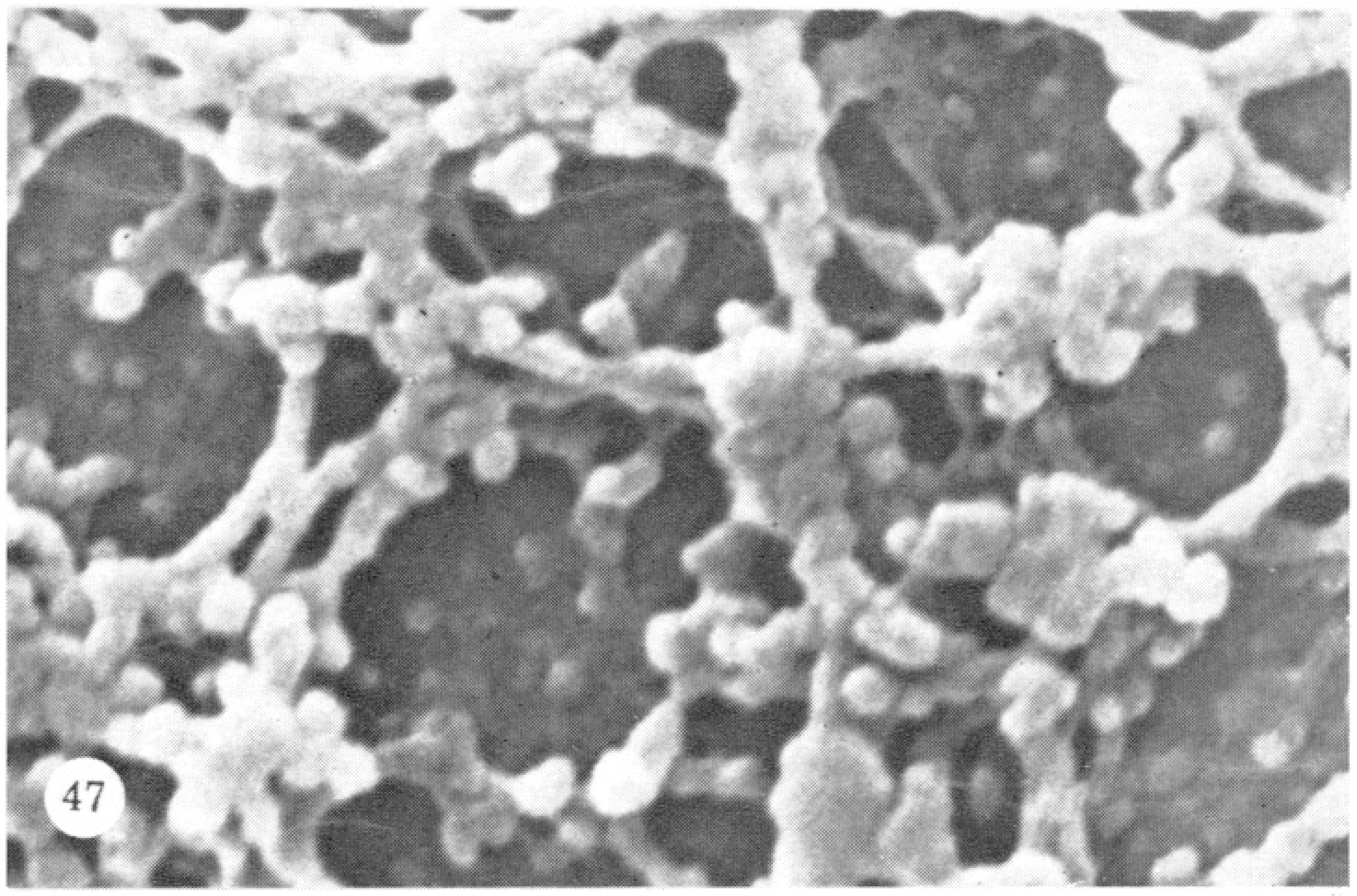
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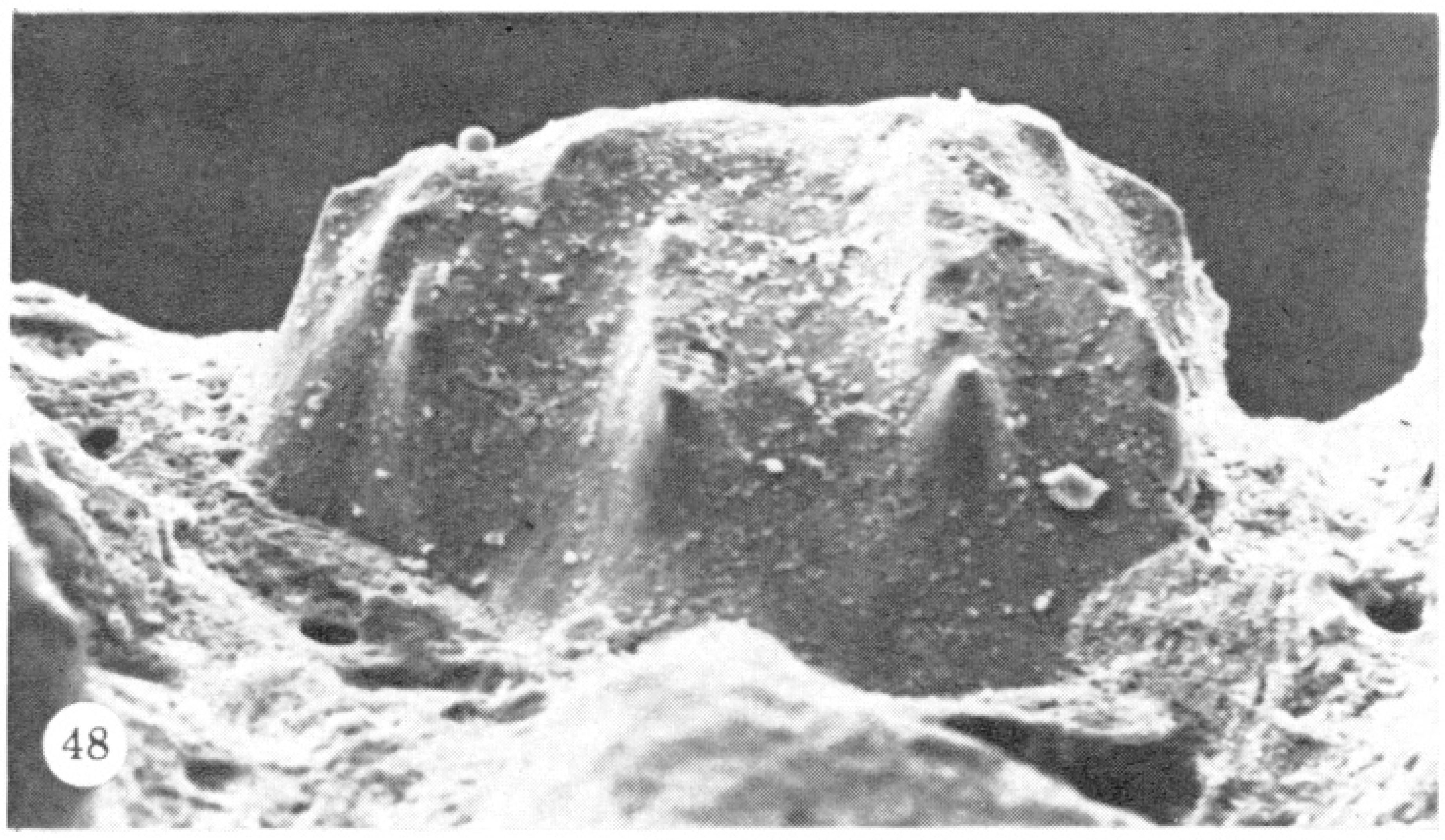
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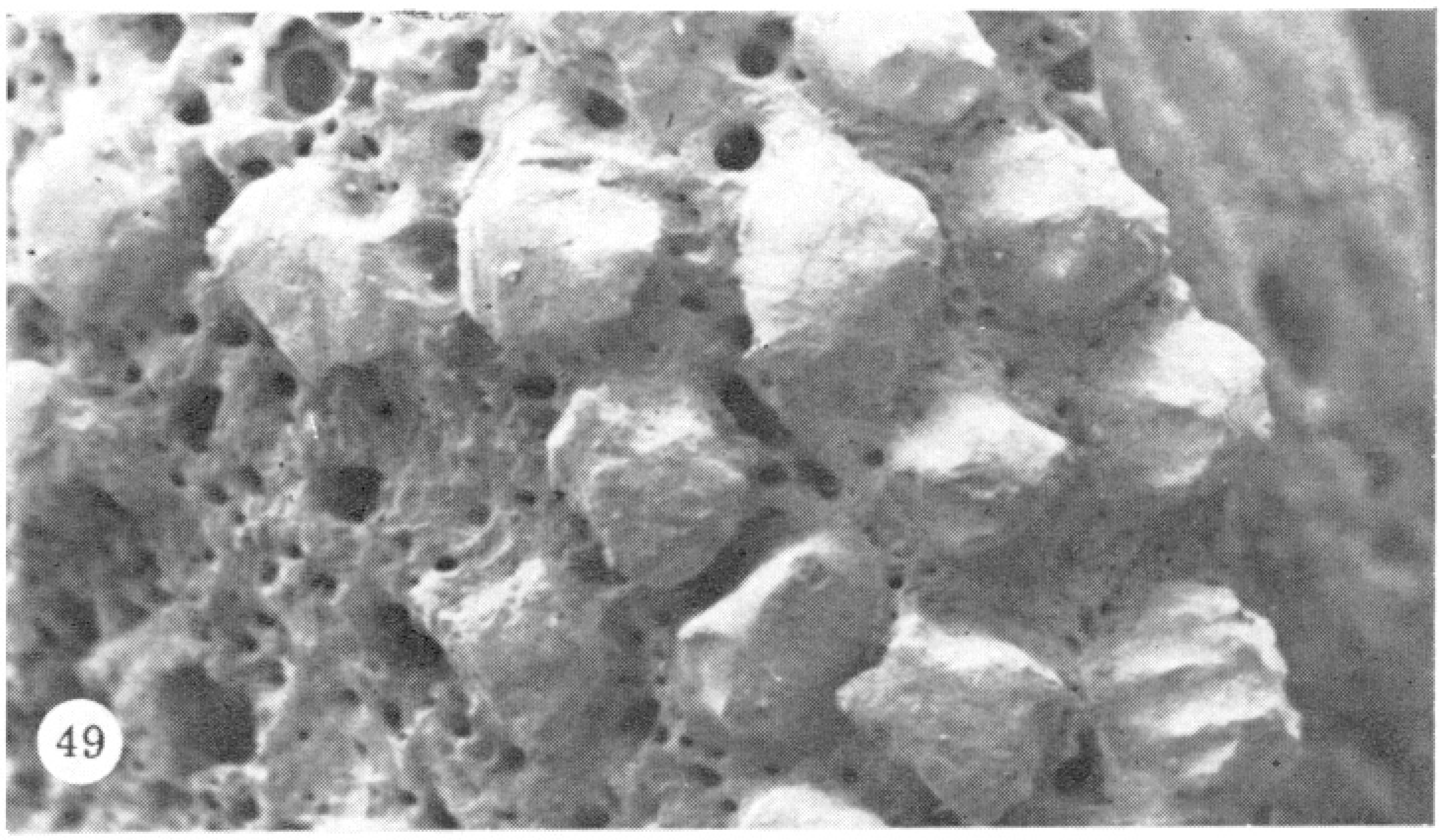
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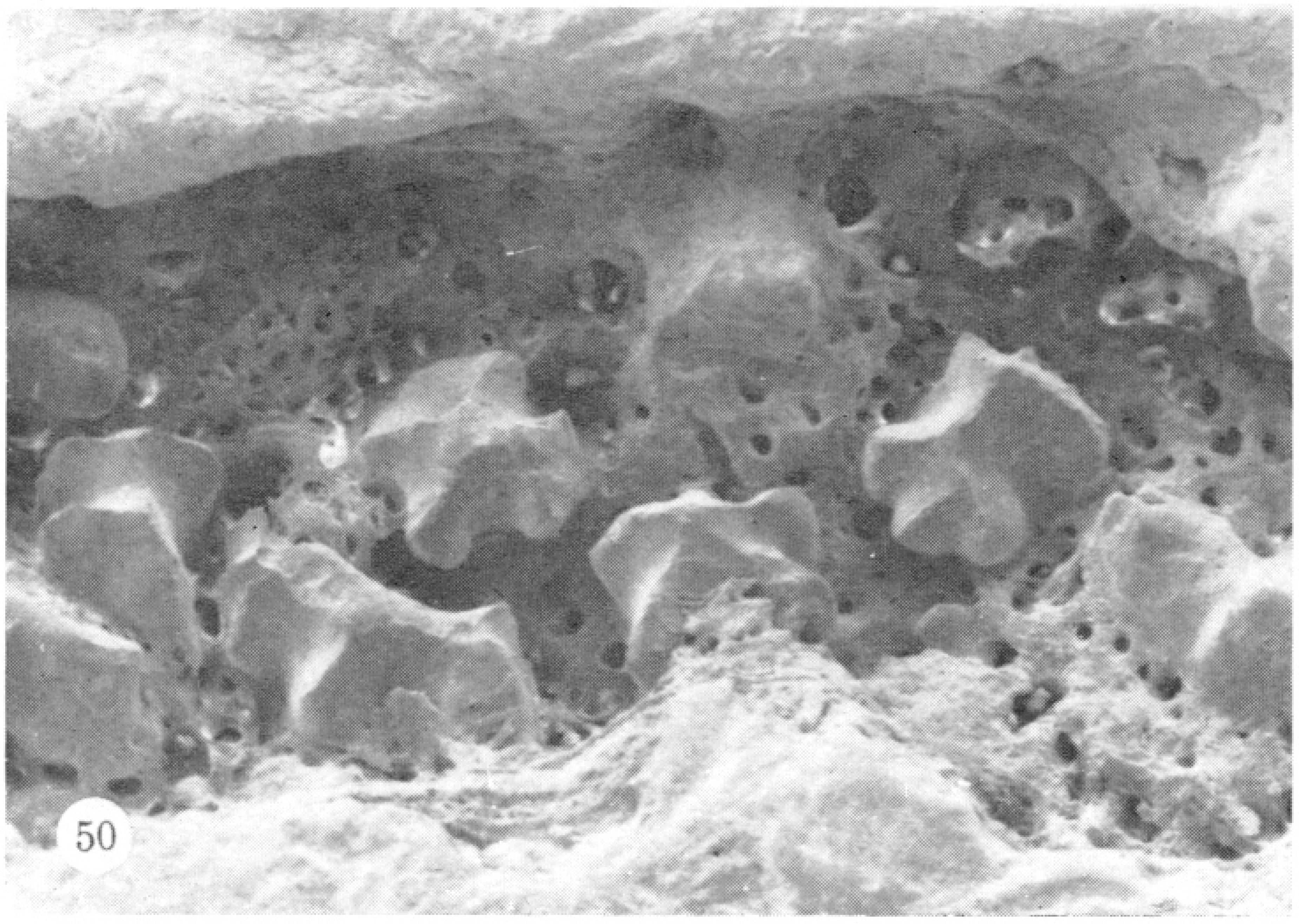
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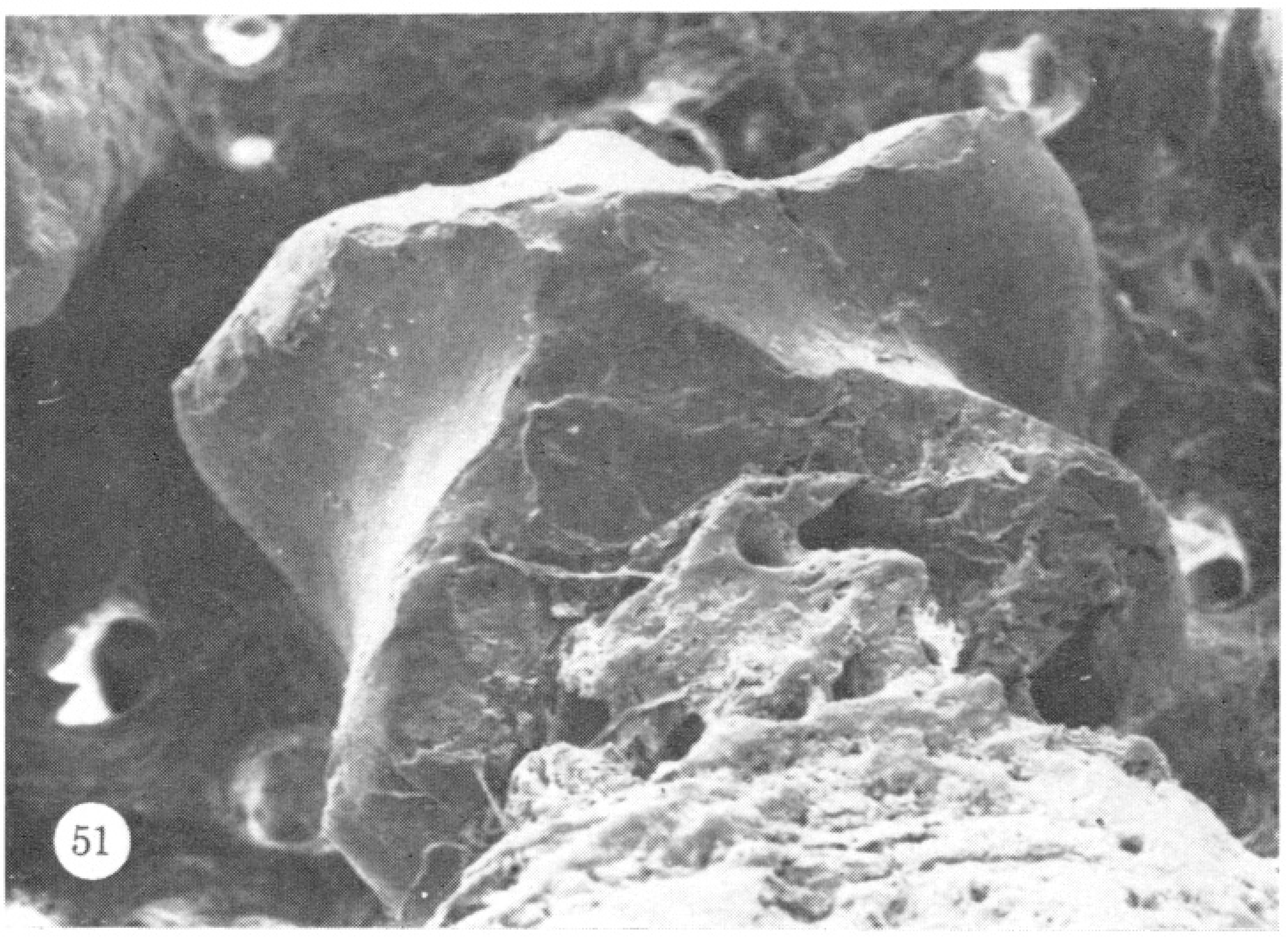
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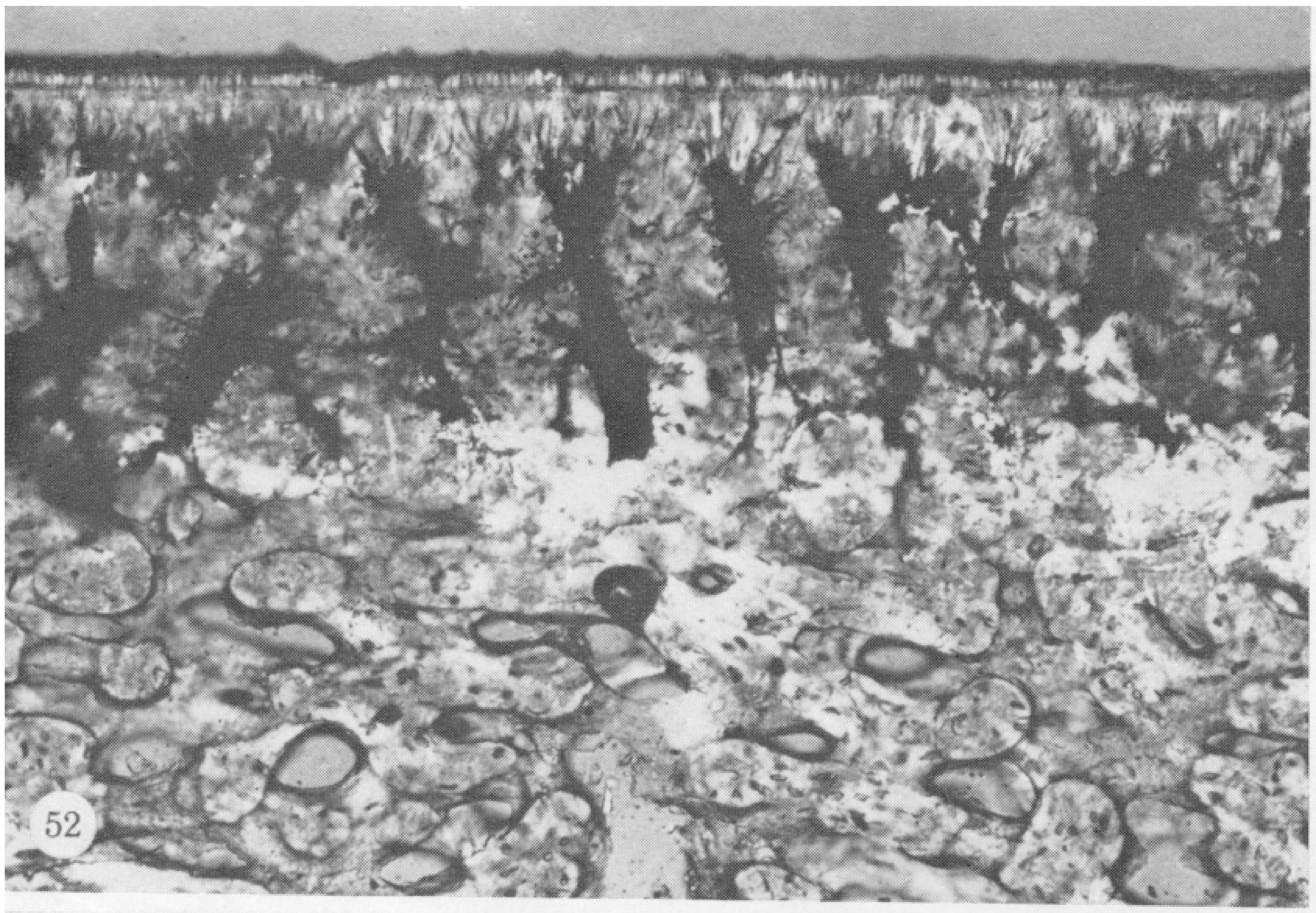
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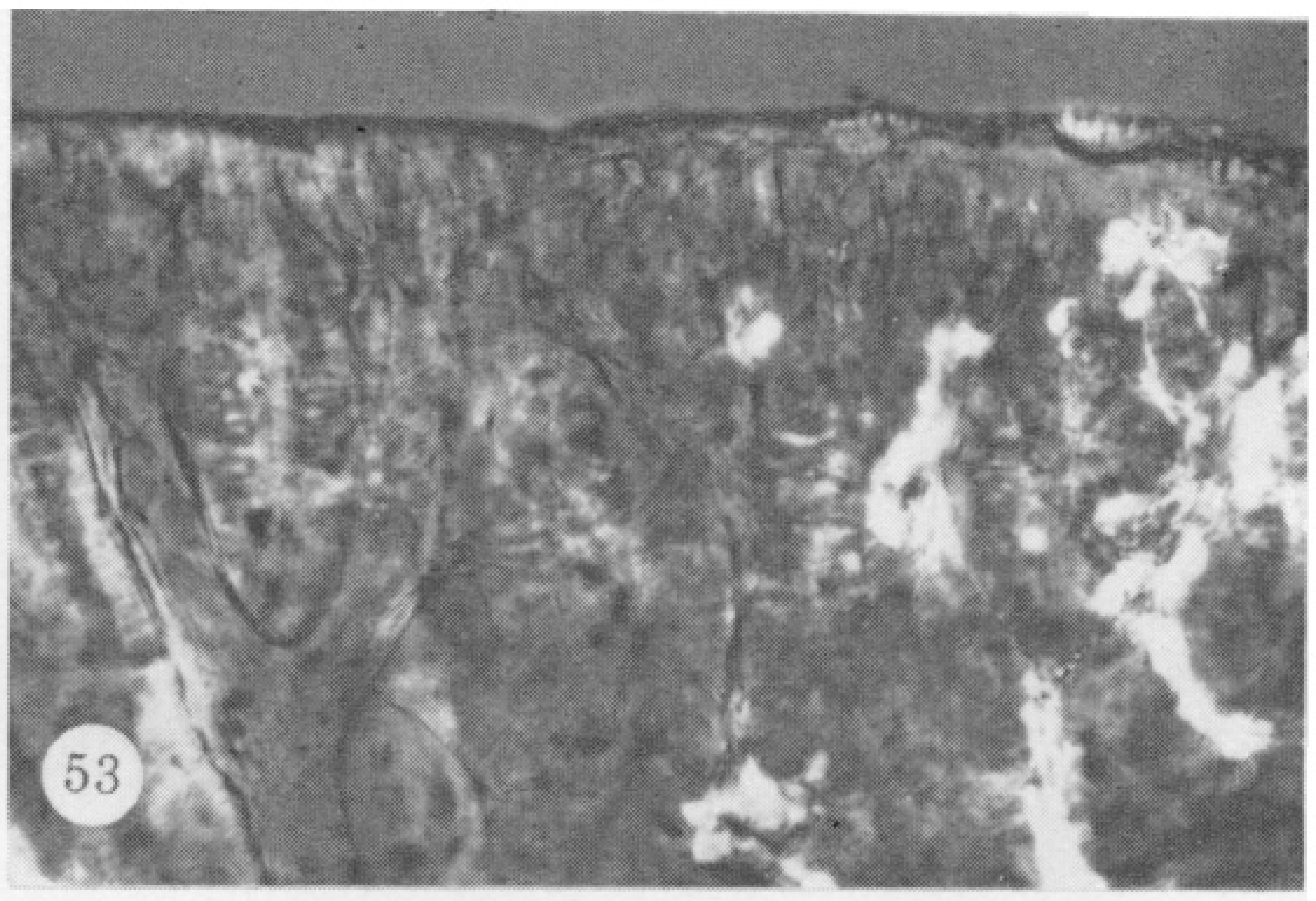
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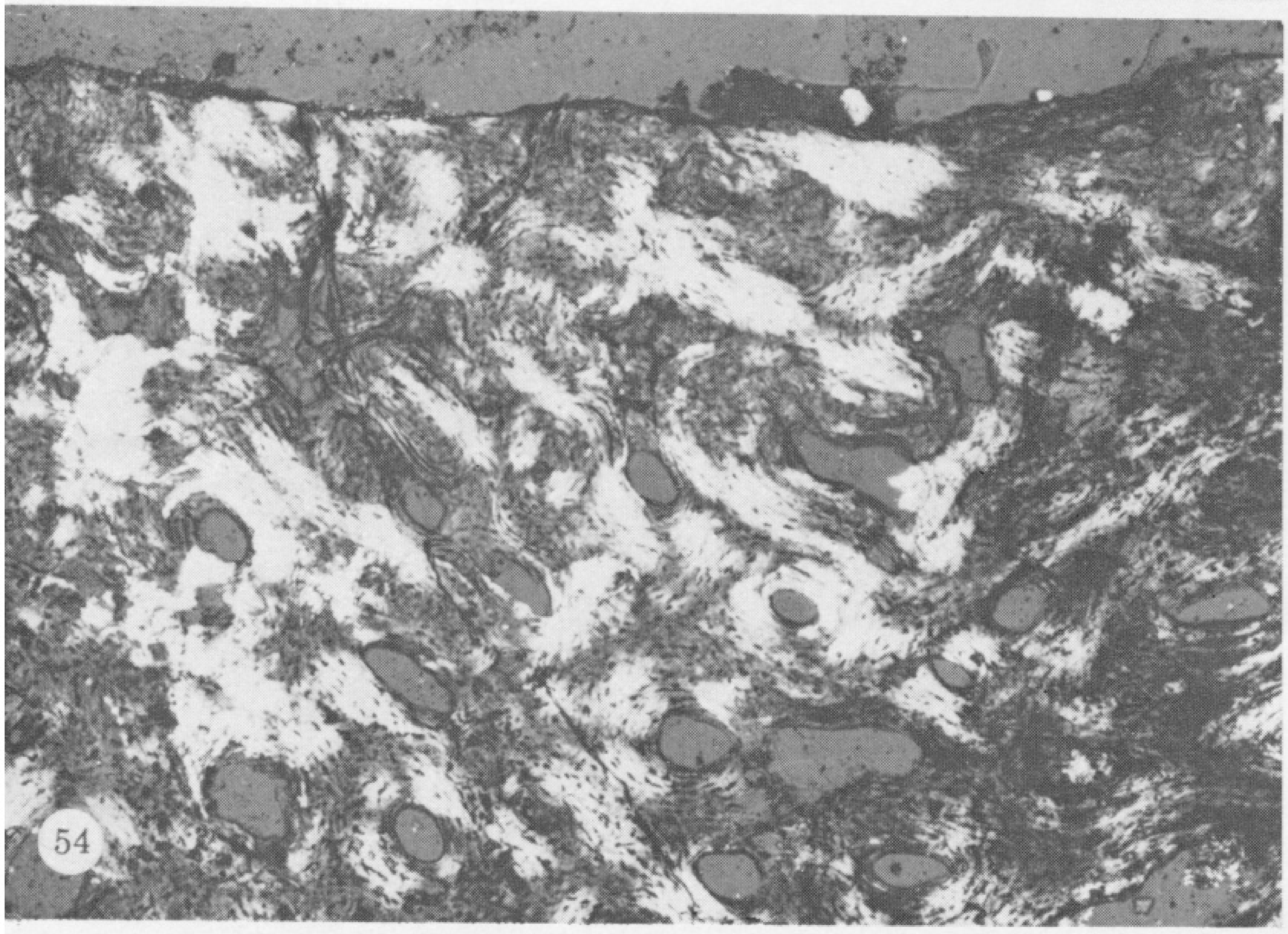
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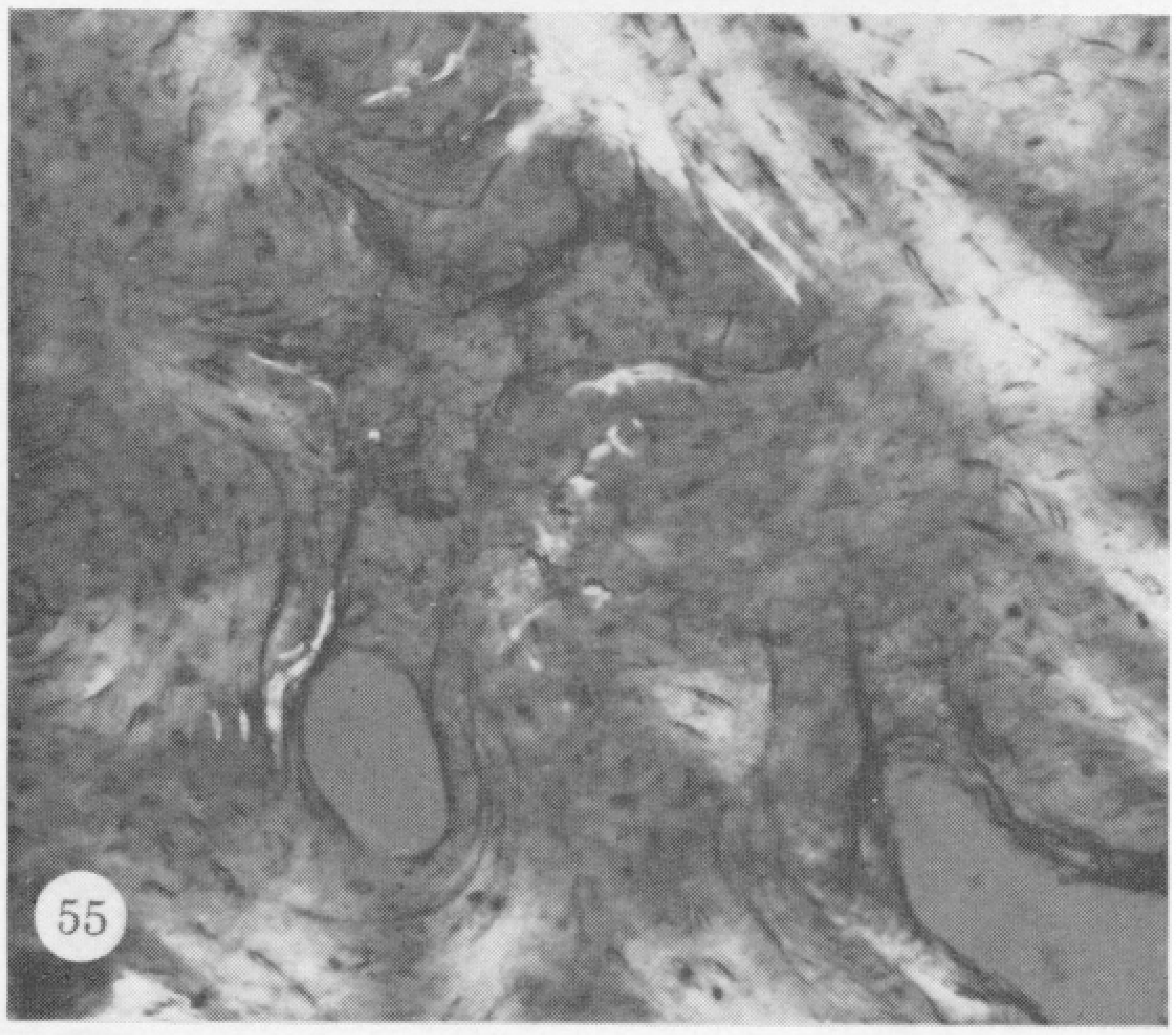
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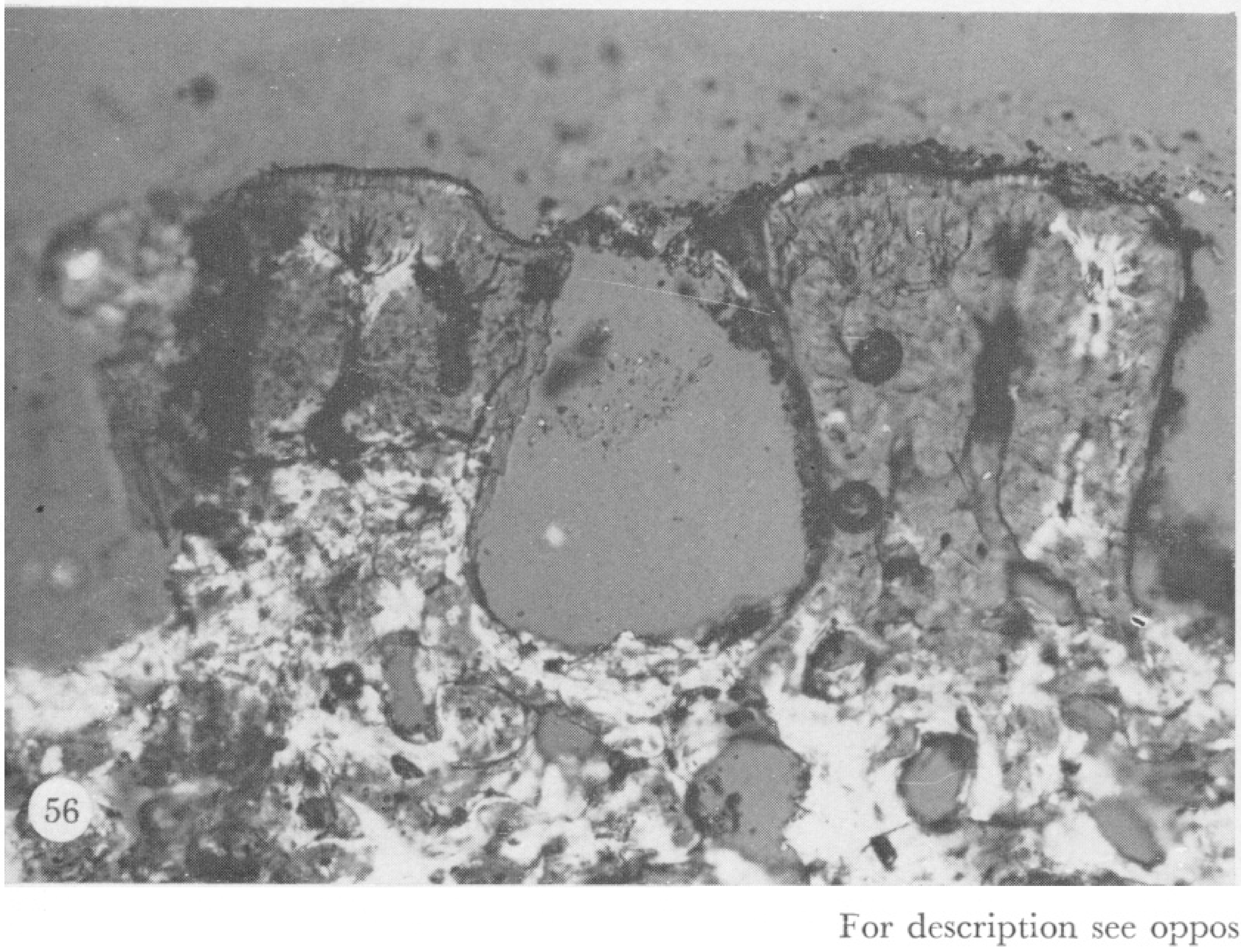
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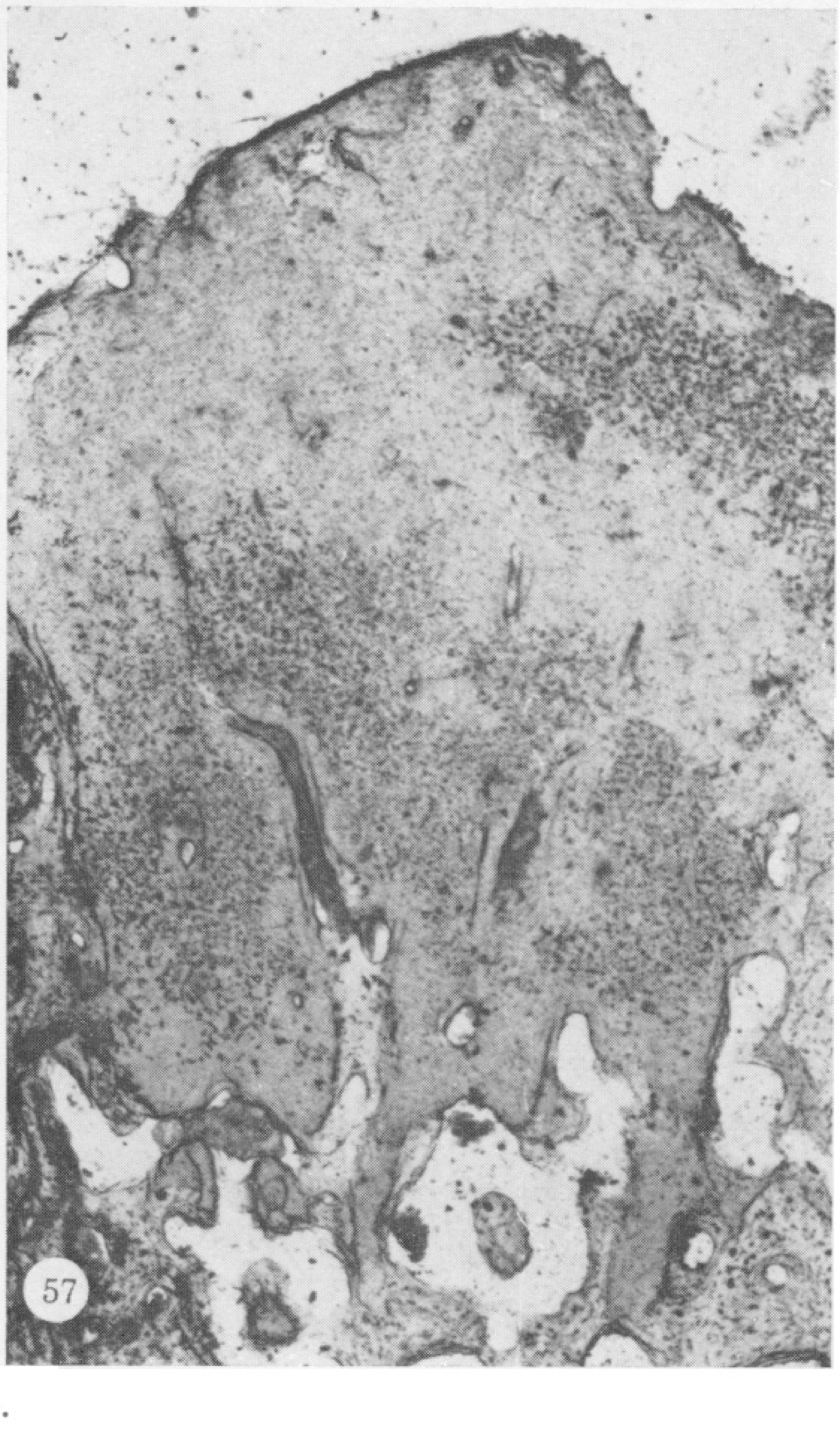
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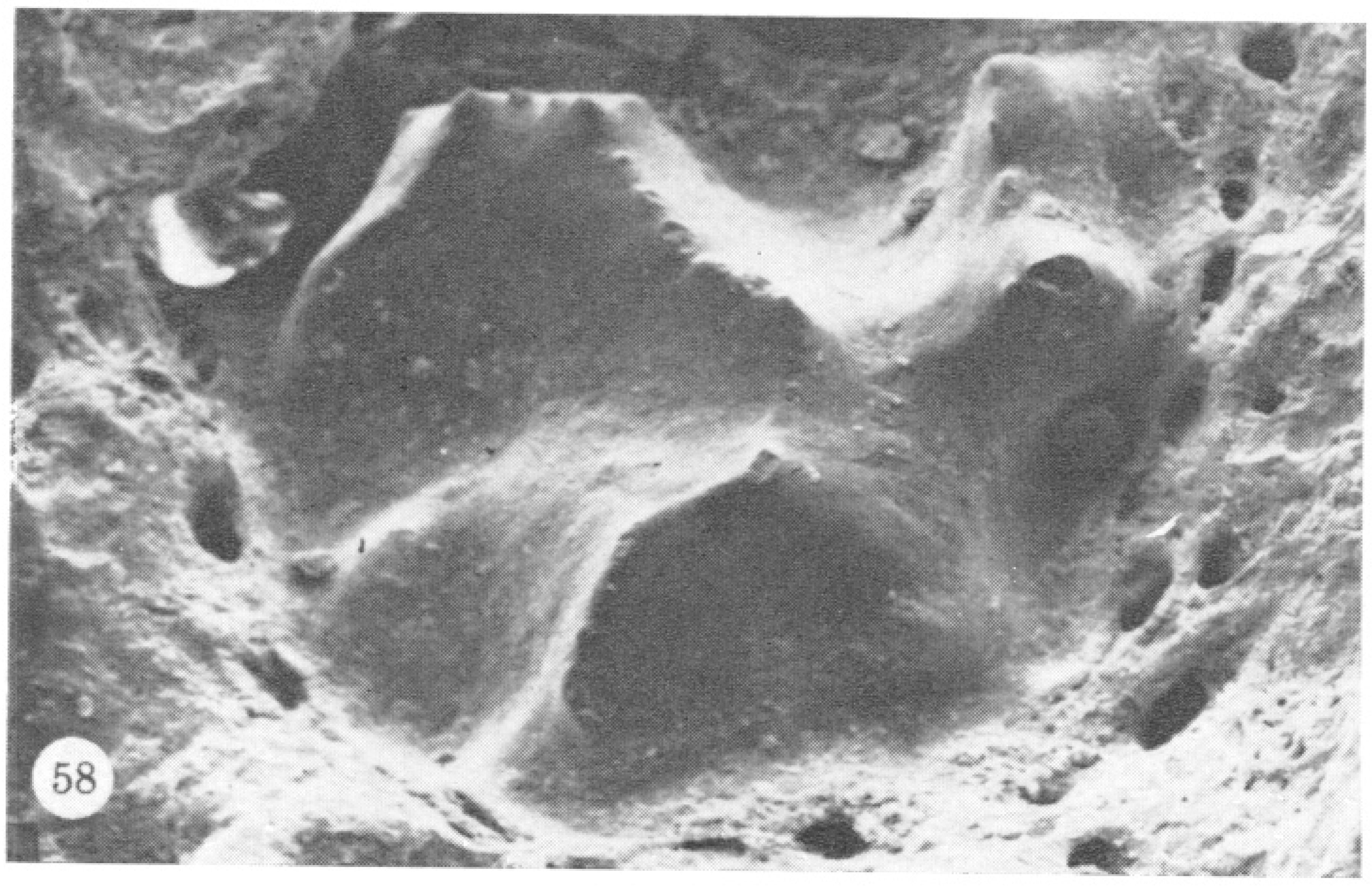
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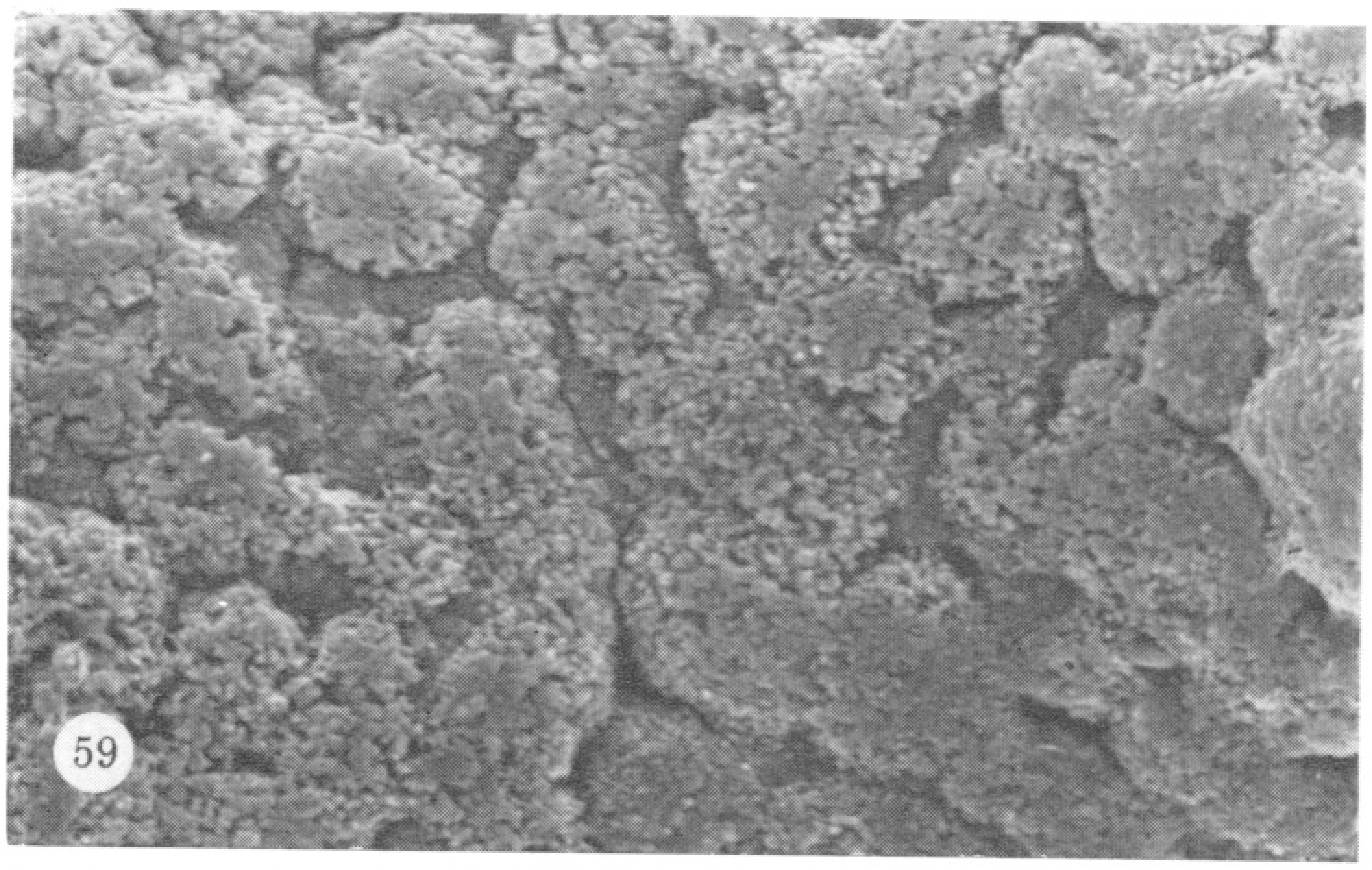
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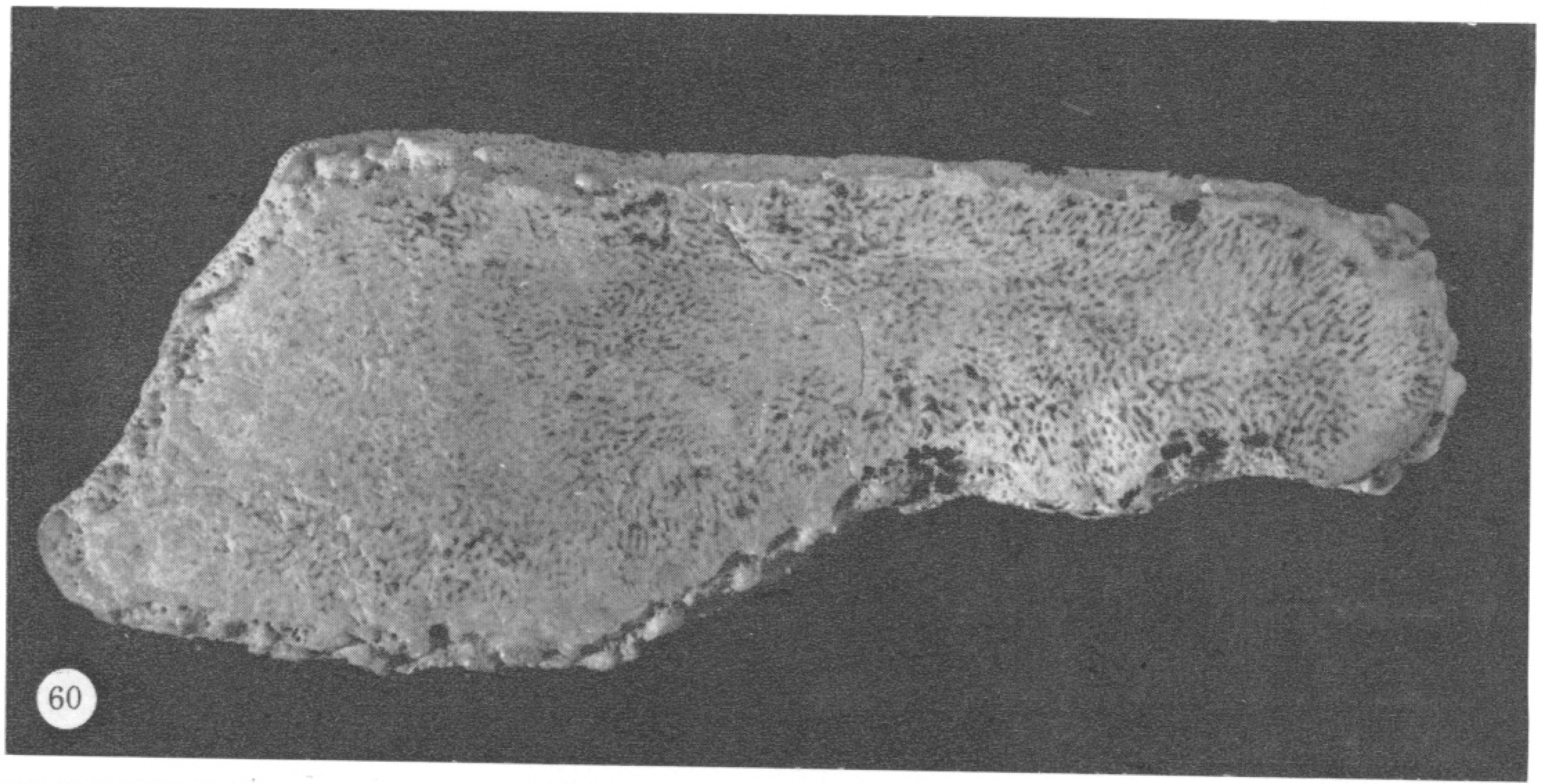
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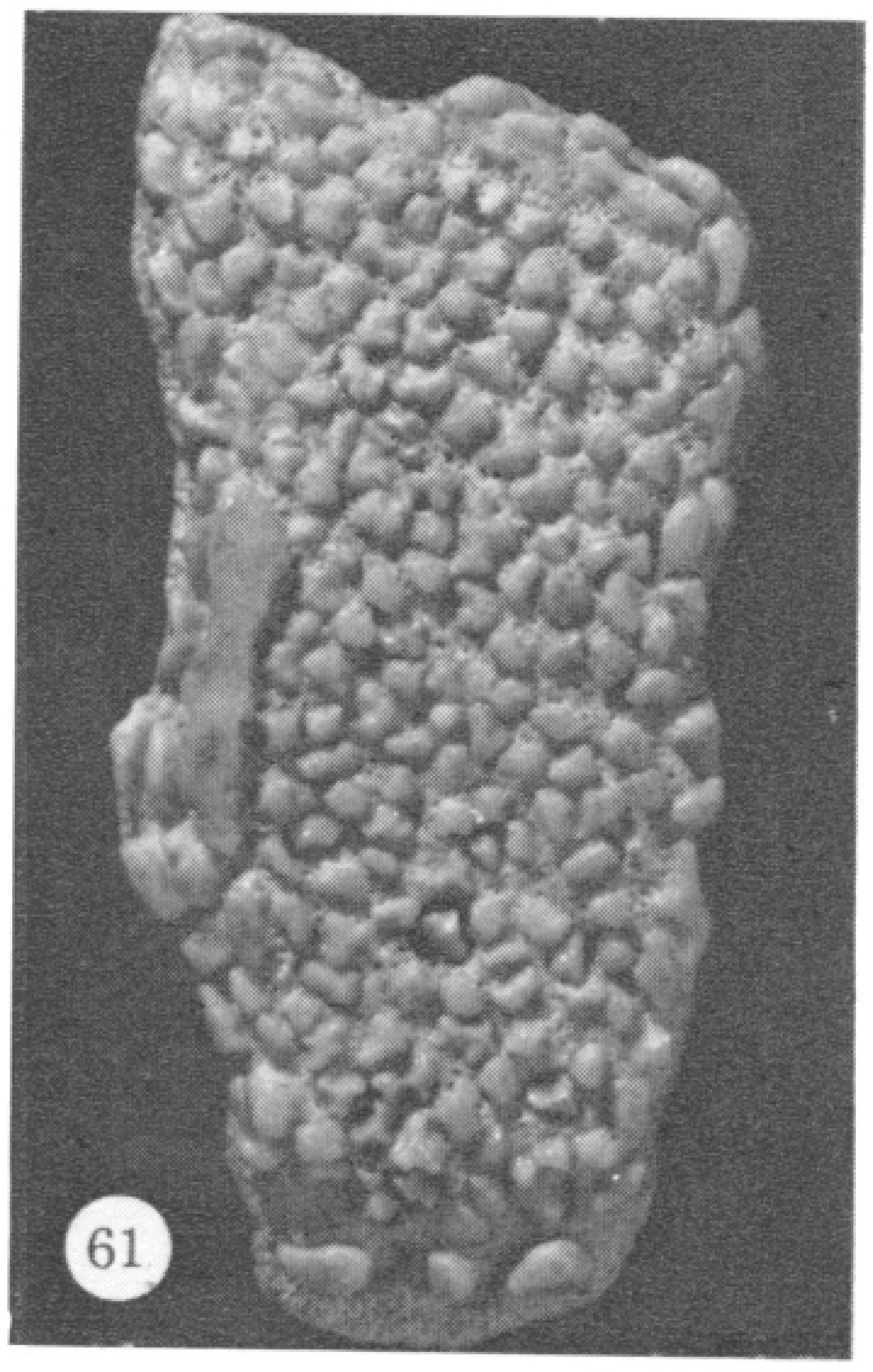
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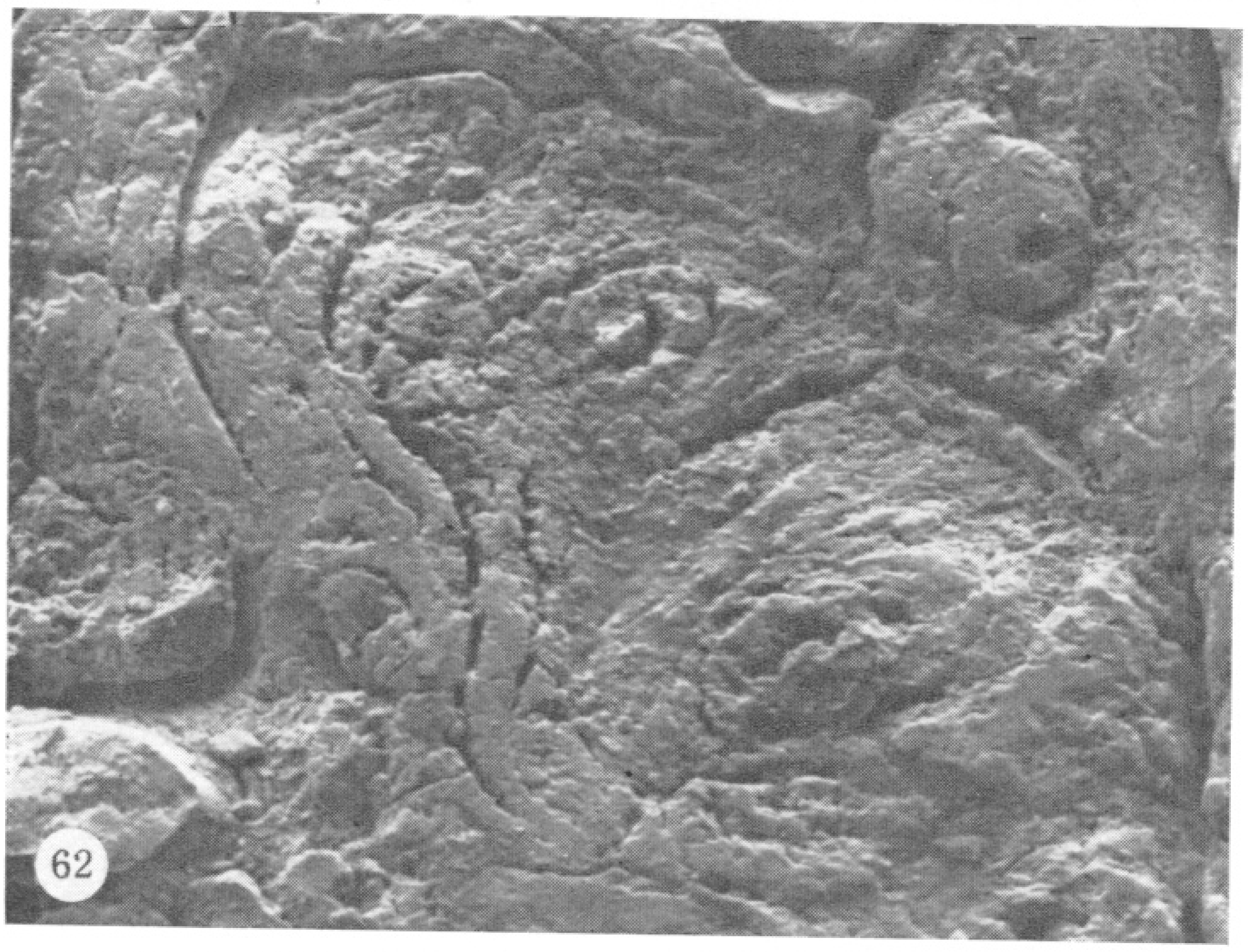
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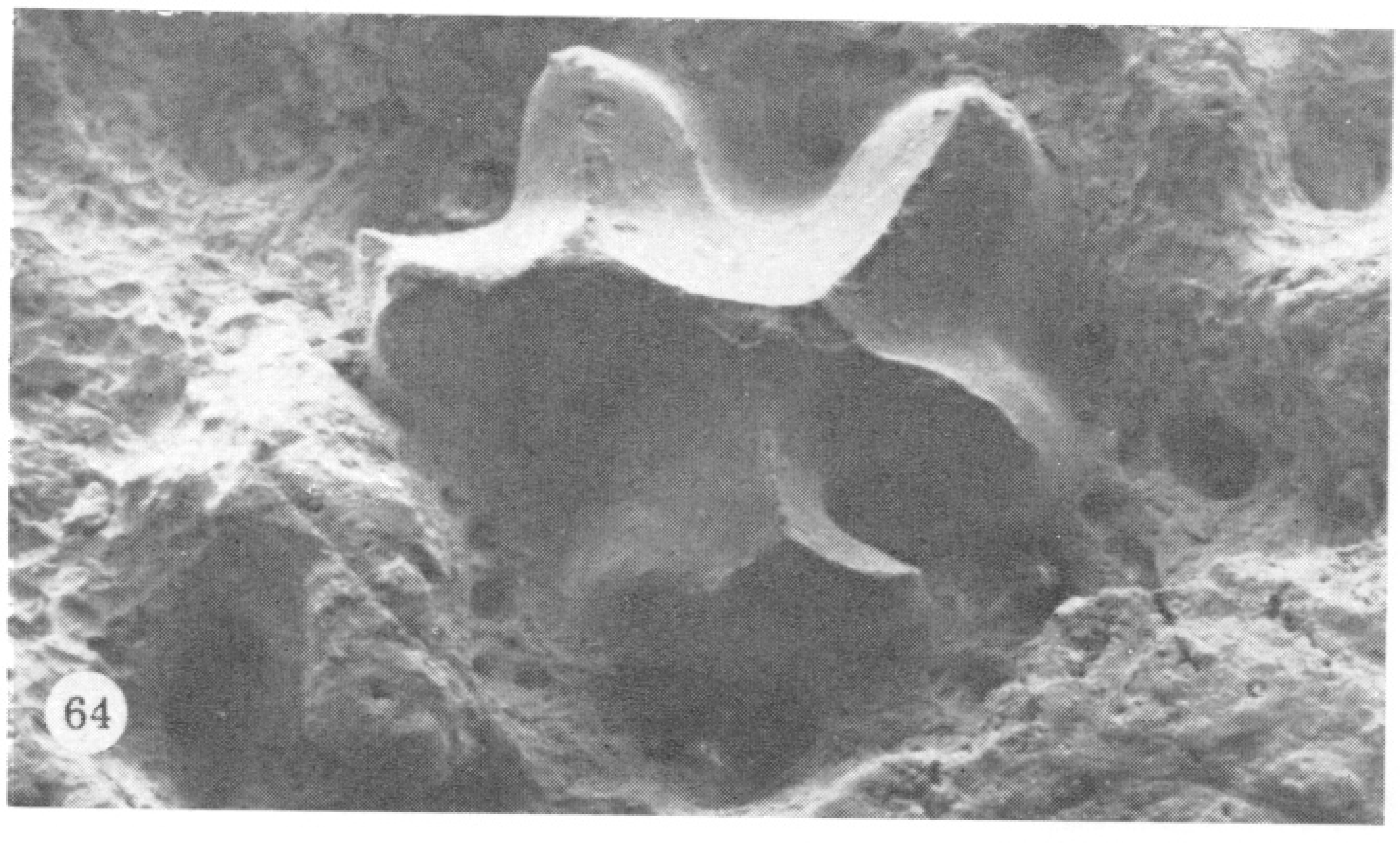
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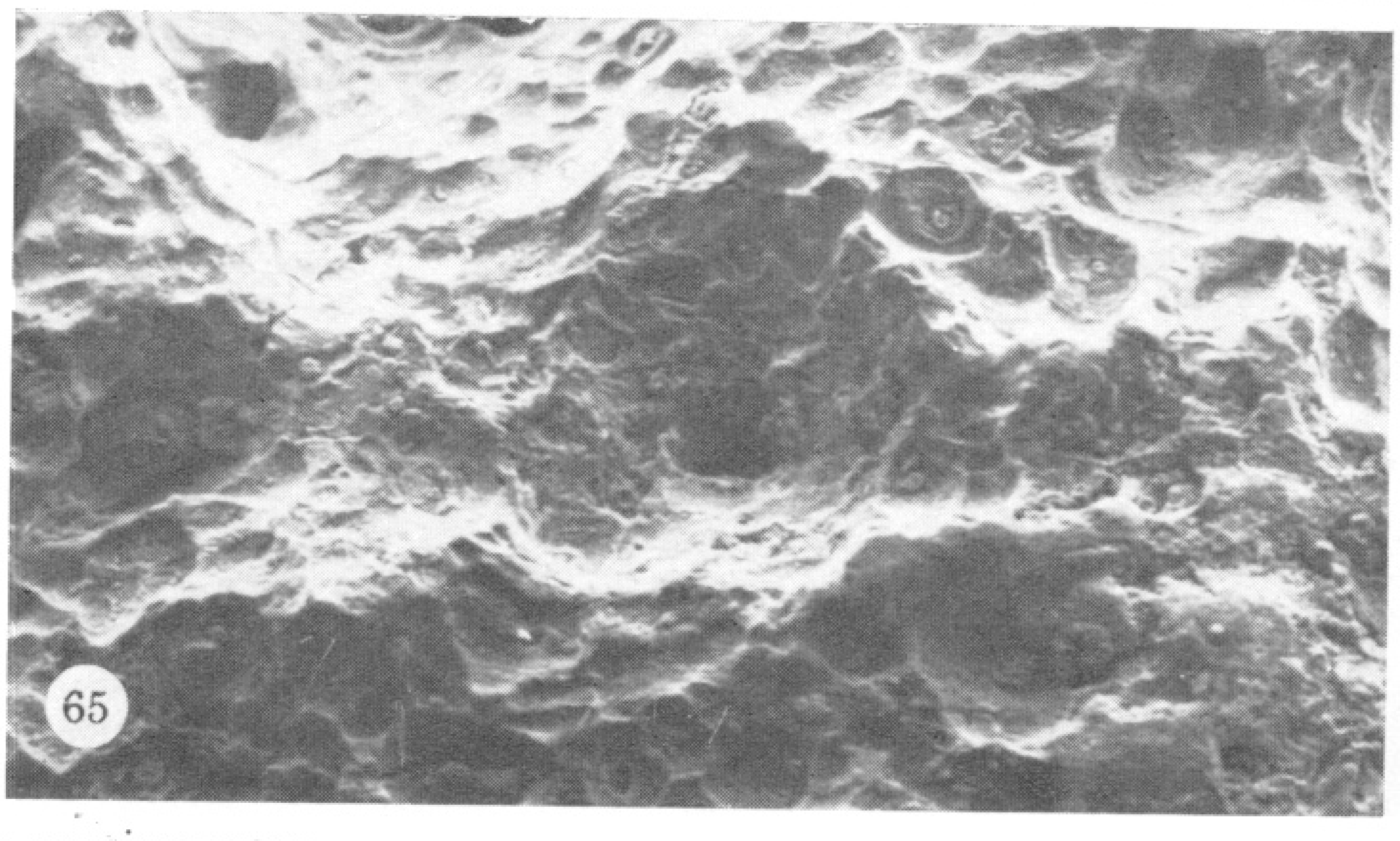
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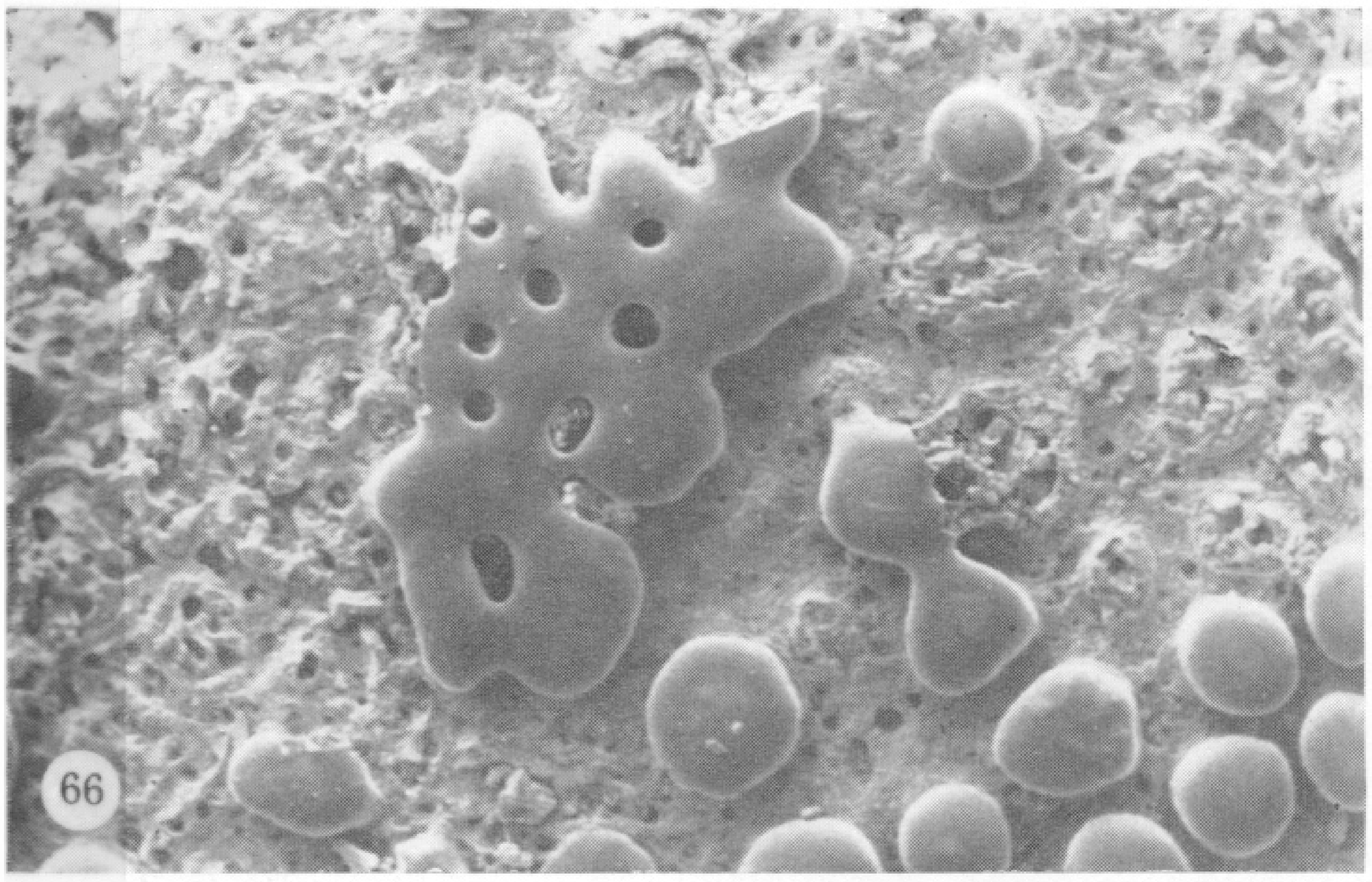
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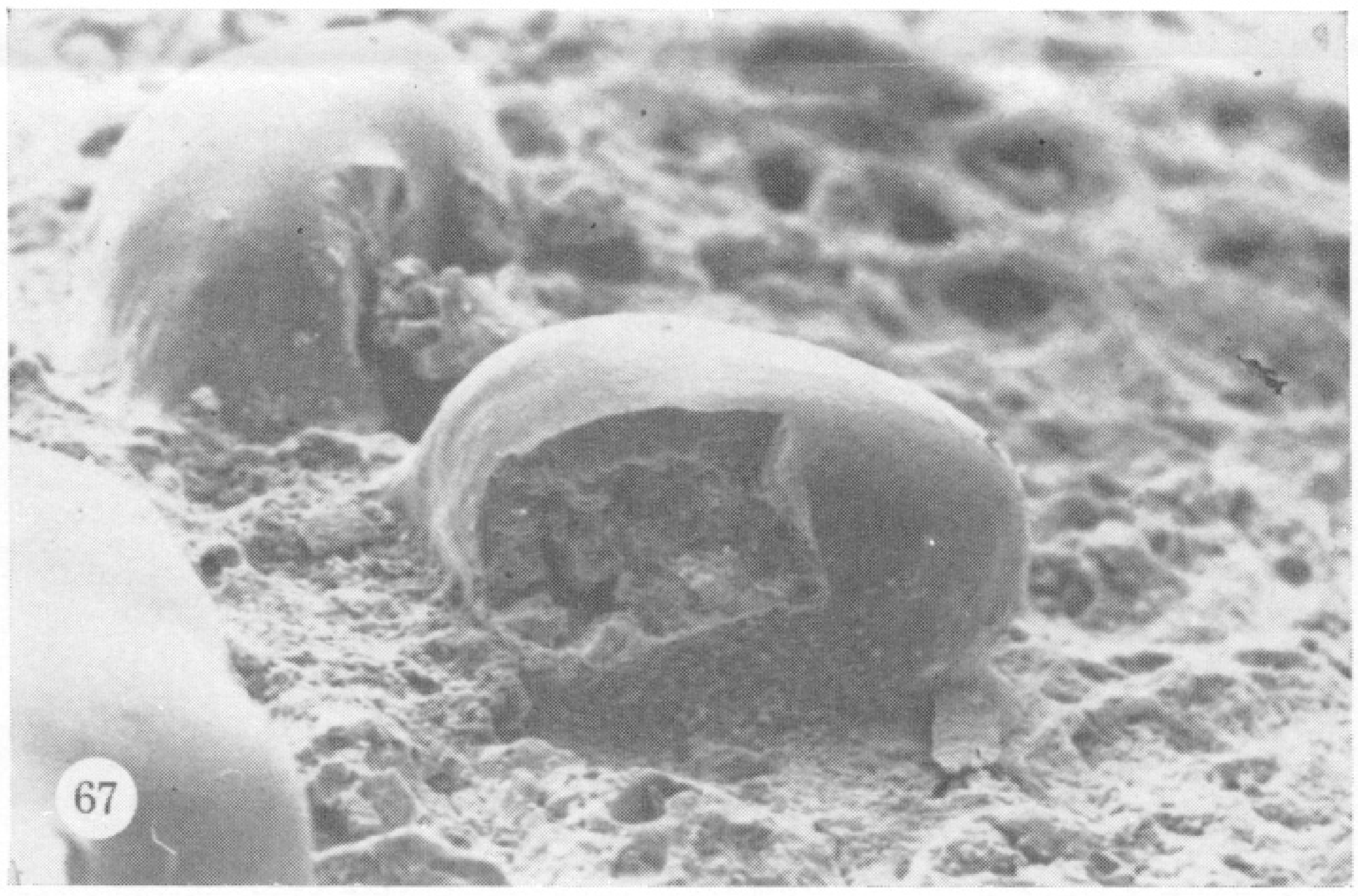
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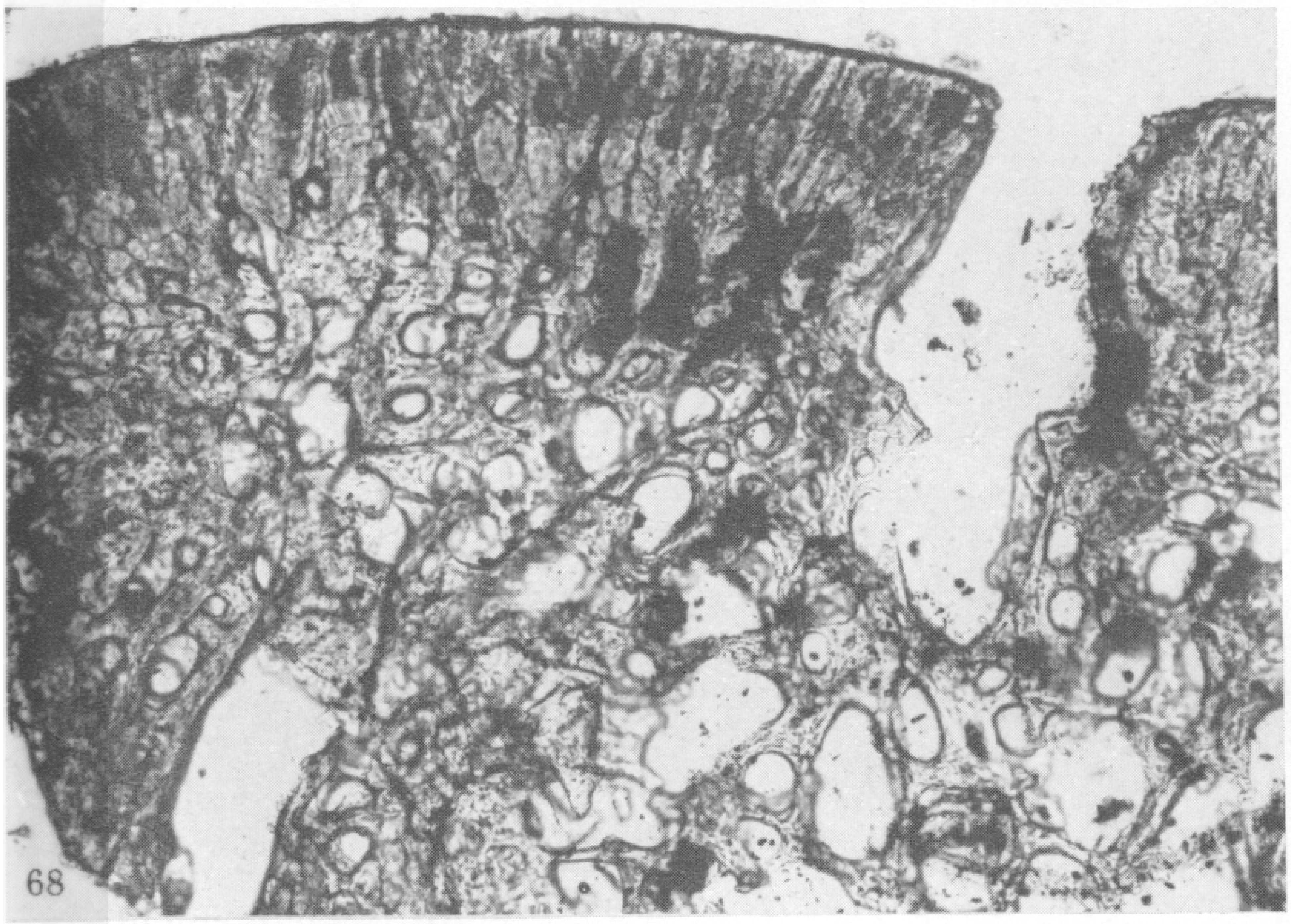
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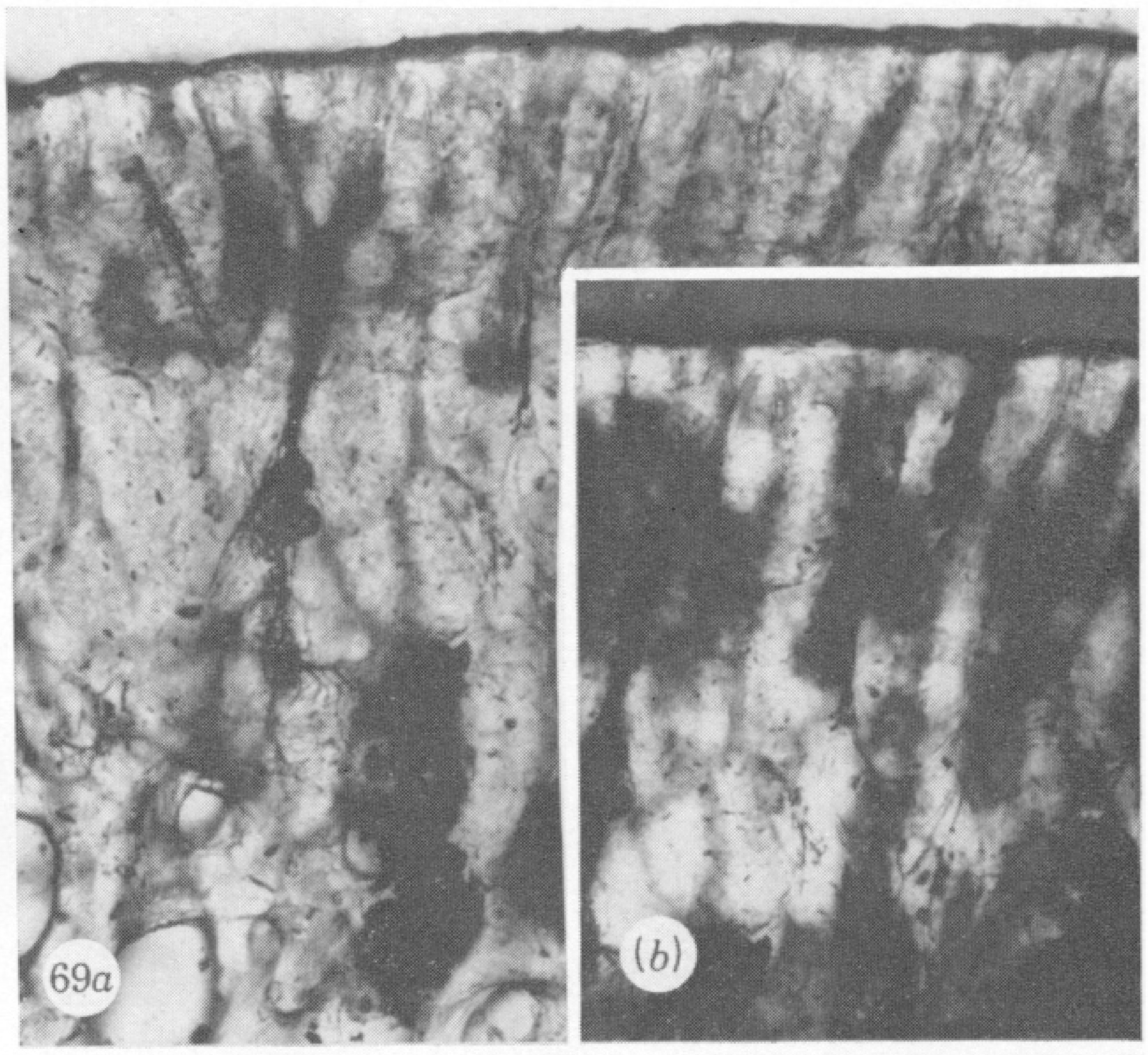

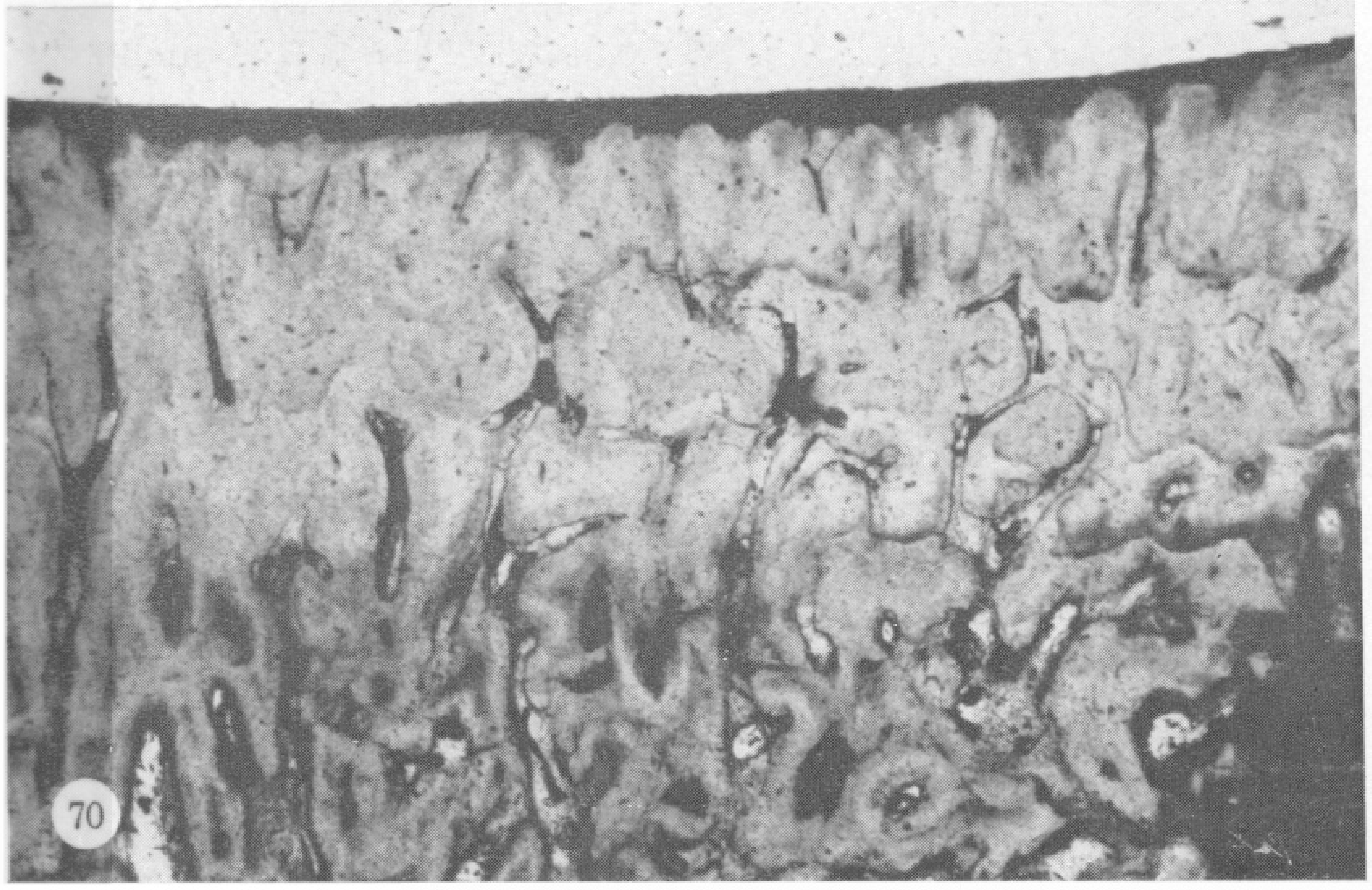
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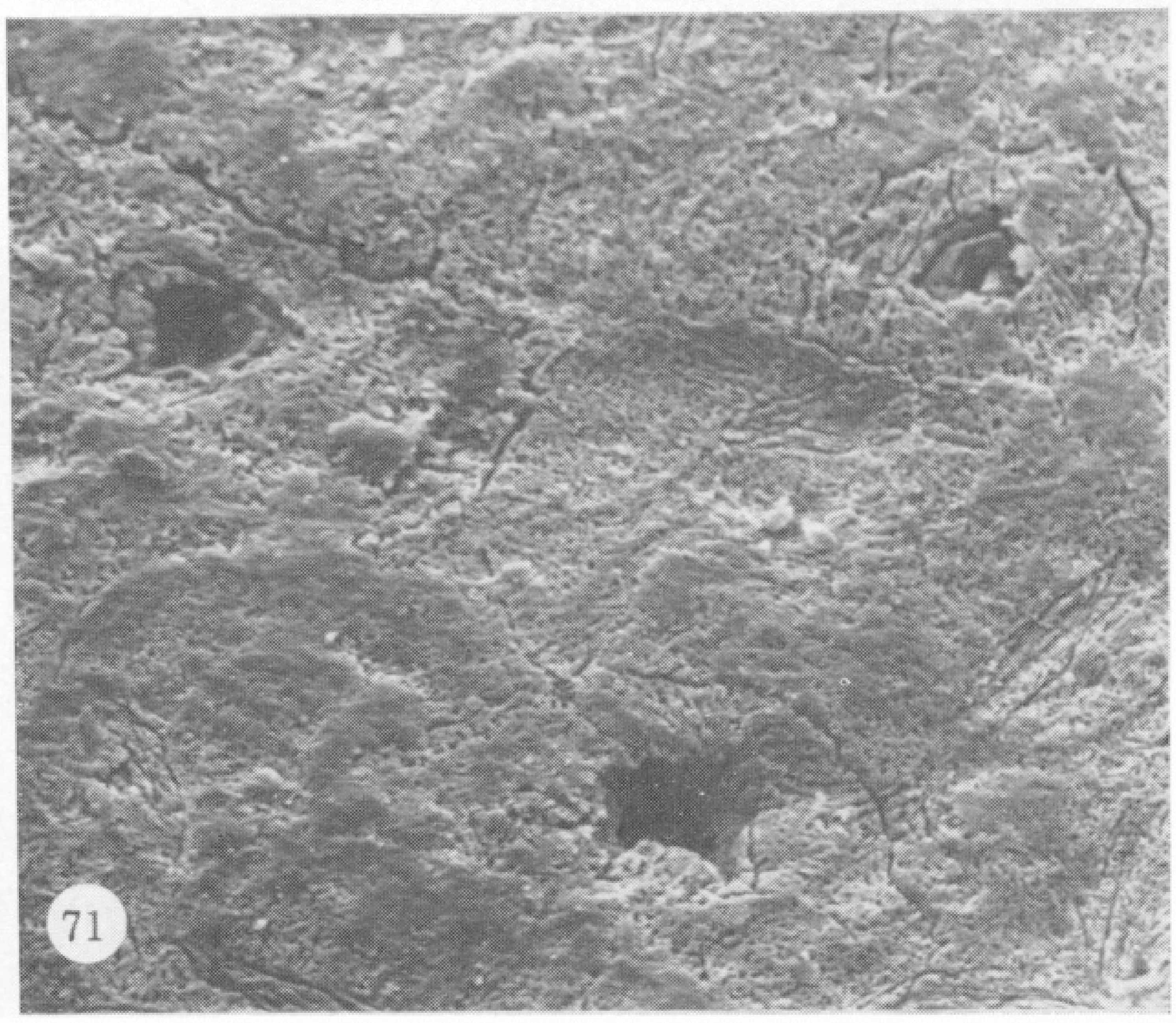
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Holodipterus gogoensis Miles

FIGURE 66. S.e.m. of the dermal covering on the sub-opercular with separate tubercles. P50997 (field width 188 μm).

FIGURE 67. S.e.m. of a separate tubercle in figure 66 with a fractured surface showing the underlying pulp canals. P50997 (field width 460 μm).

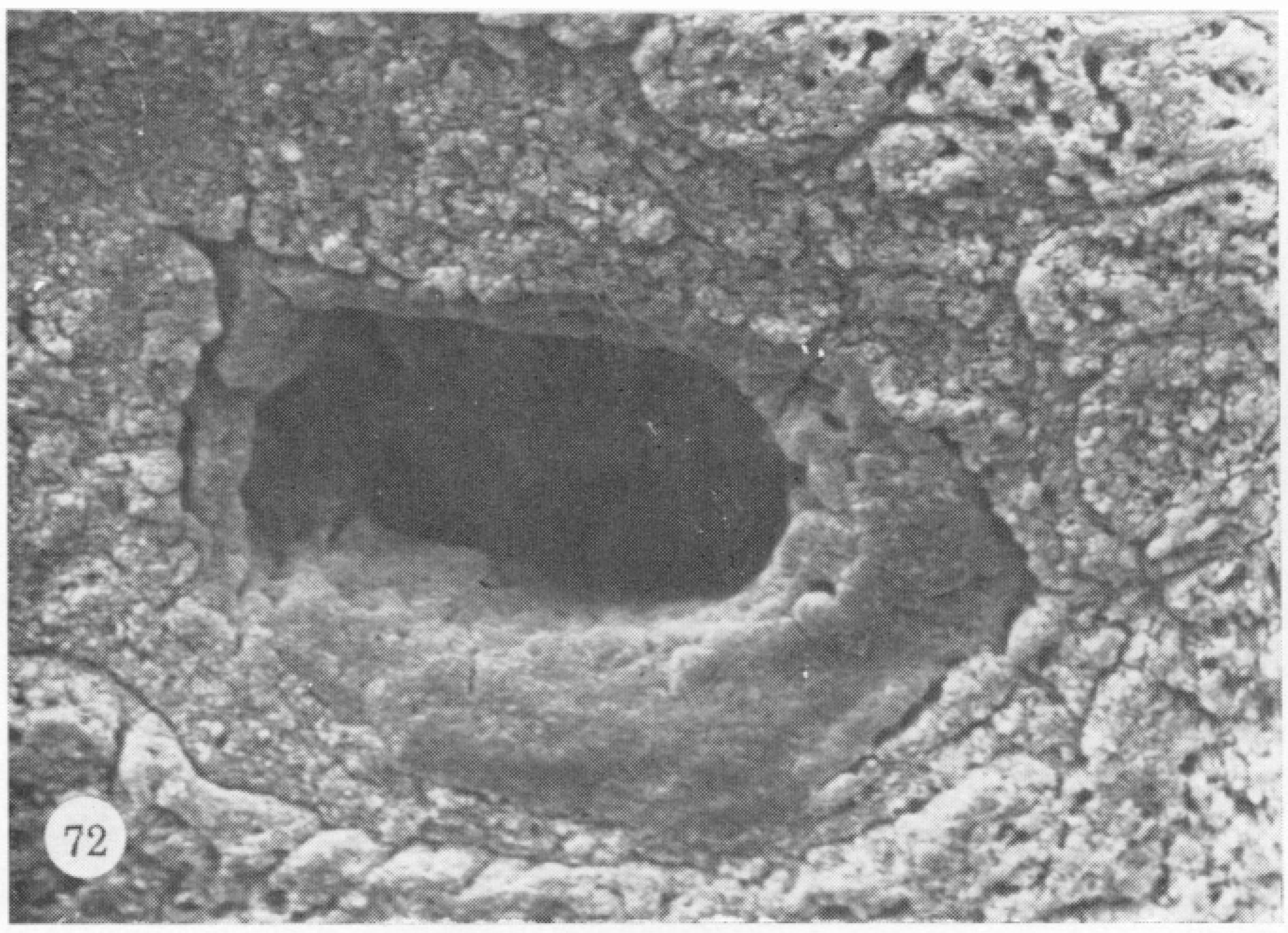
Chirodipterus australis Miles

FIGURE 68. Photomicrograph of a vertical section through the lower lip of the dentary in ordinary transmitted light. See also figure 15. P51000 (× 56).

FIGURE 69. (*a*) Photomicrograph of the lower lip in figure 68 which shows the worn surface of compact dentine. P51000 (× 140). (*b*) Photomicrograph of the same region as figure 69*a* viewed in polarized light which shows the strong birefringence of the circumpulpal dentine. P51000 (× 140).

FIGURE 70. Photomicrograph of a vertical section through the tooth plate, with the attachment of the dentine to the basal bone at the margins. See also figure 16. P52561 (× 35).

FIGURE 71. S e.m. of the functional surface of the tooth plate after treatment with 0.1 N HCl for 1 minute. Three pulp canals open at the surface with partial infilling of pulpal dentine, and hypermineralized interstitial dentine. P52561 (field width 184 μm).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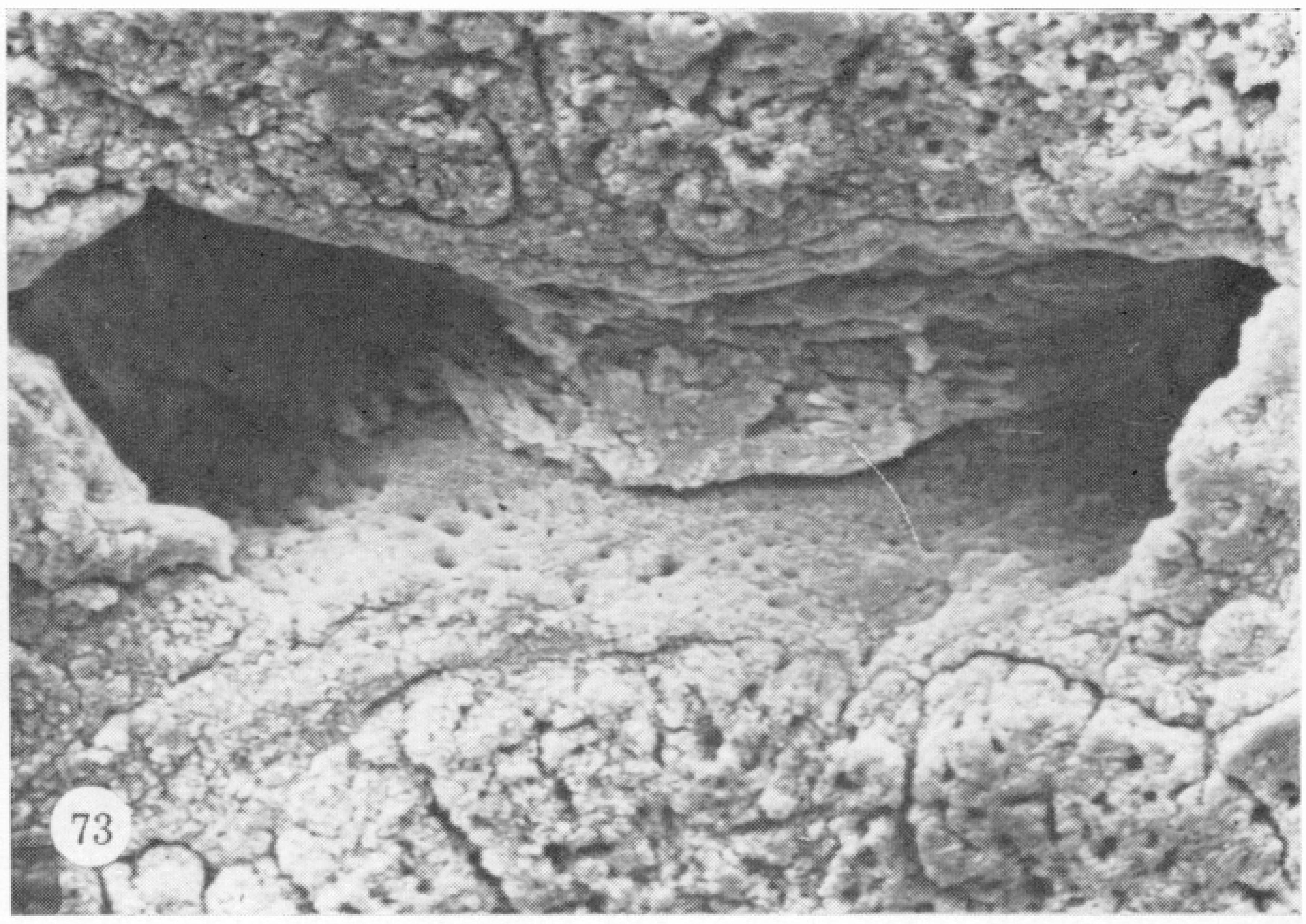
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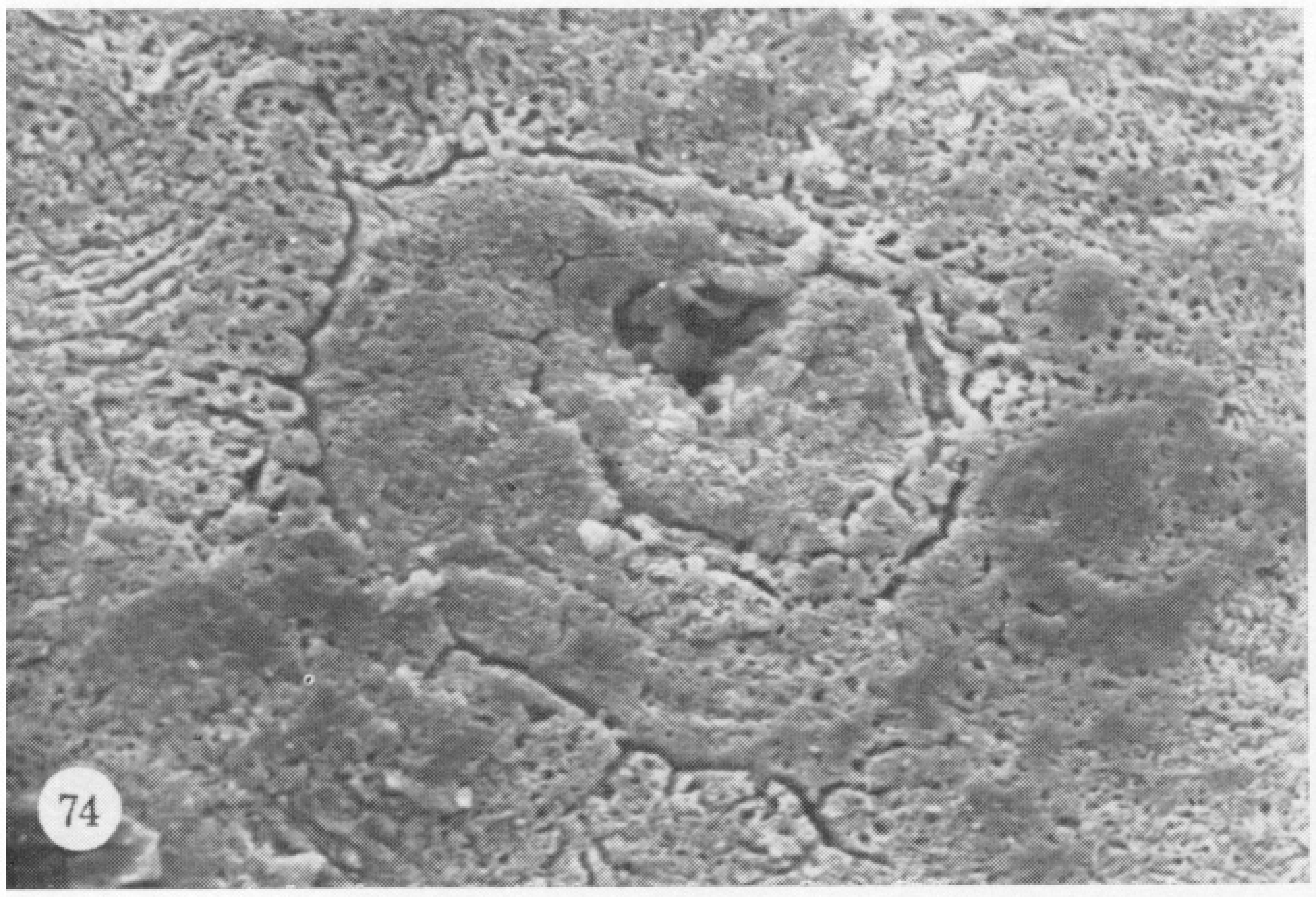
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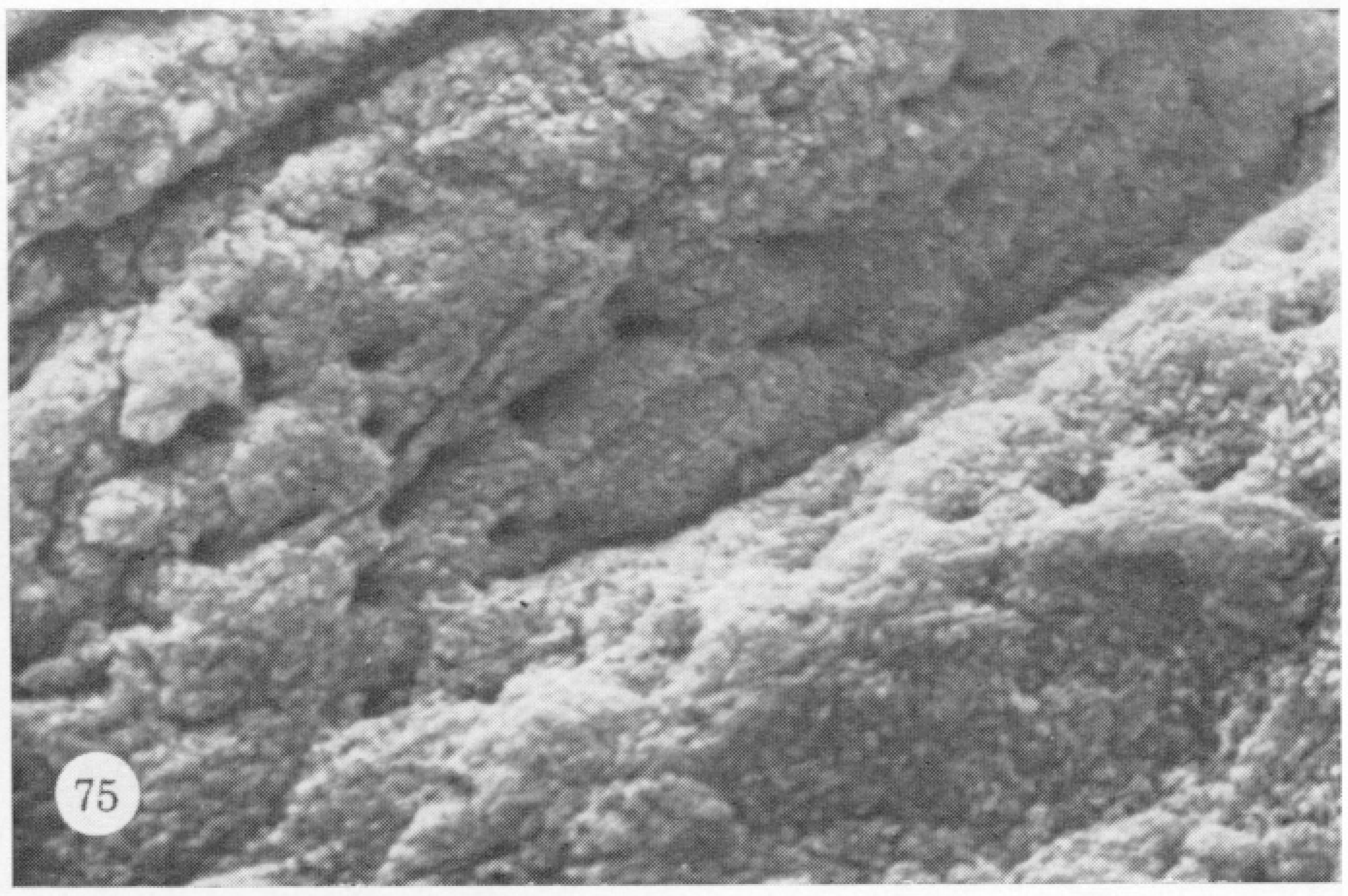
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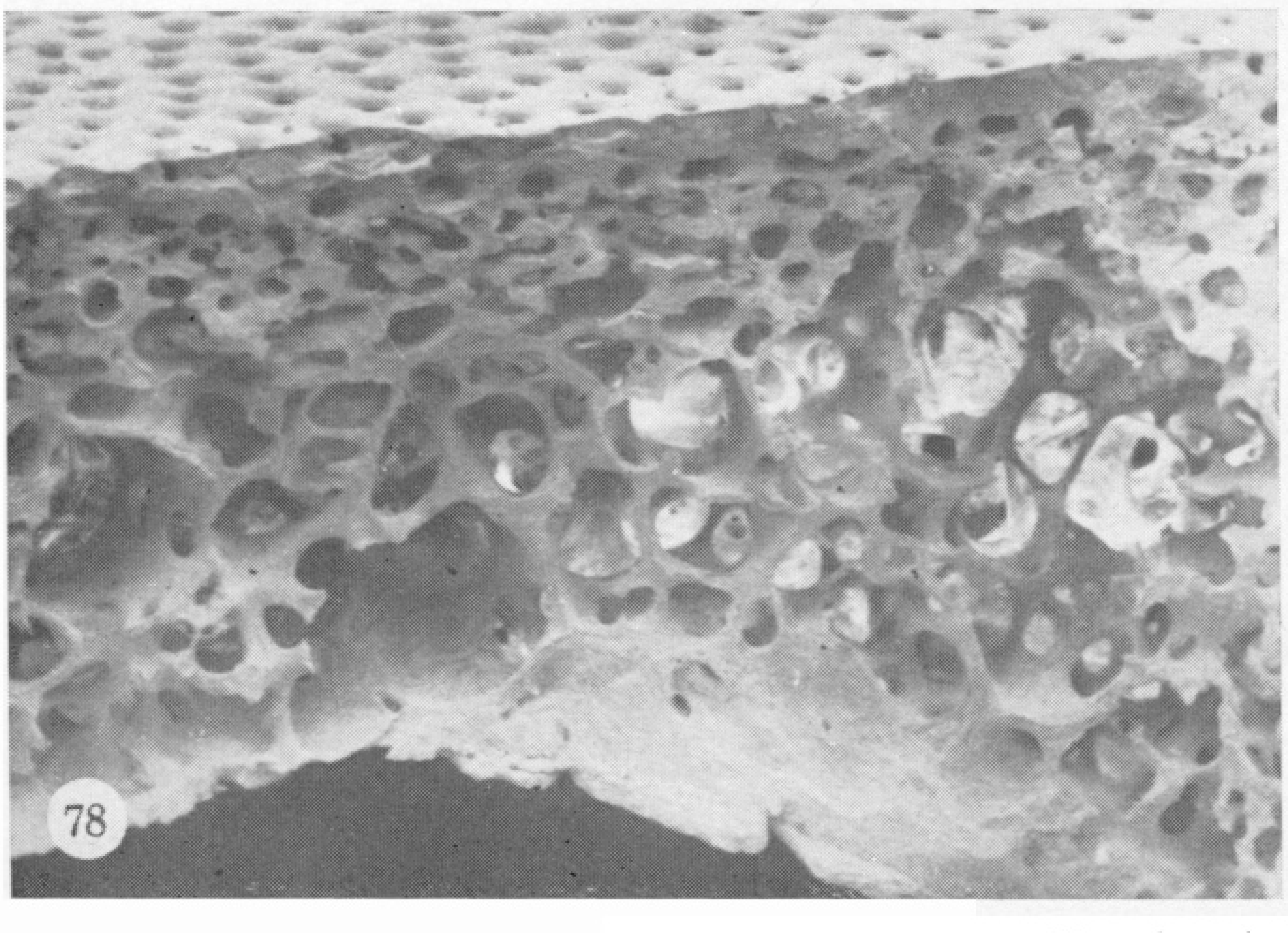
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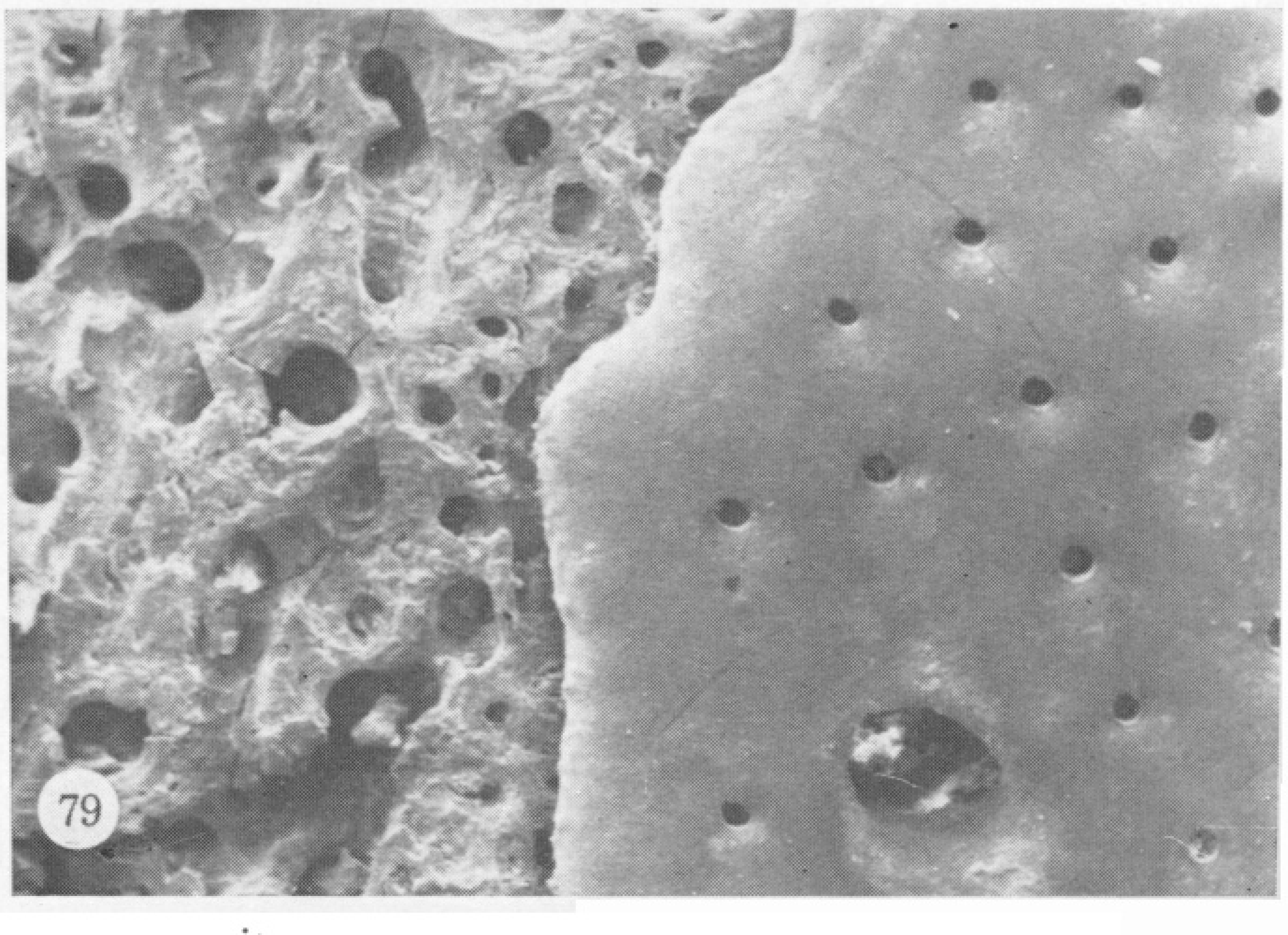
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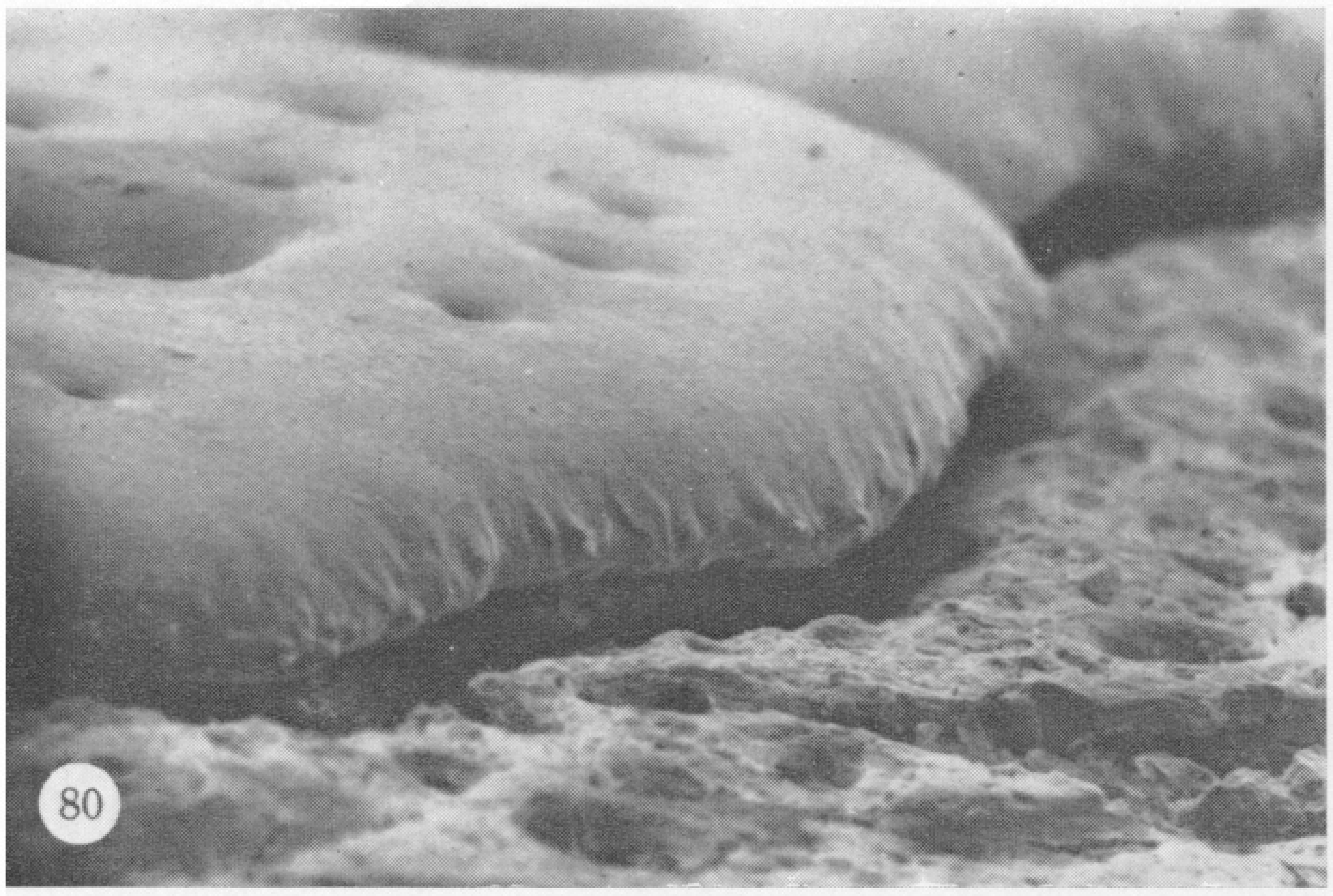
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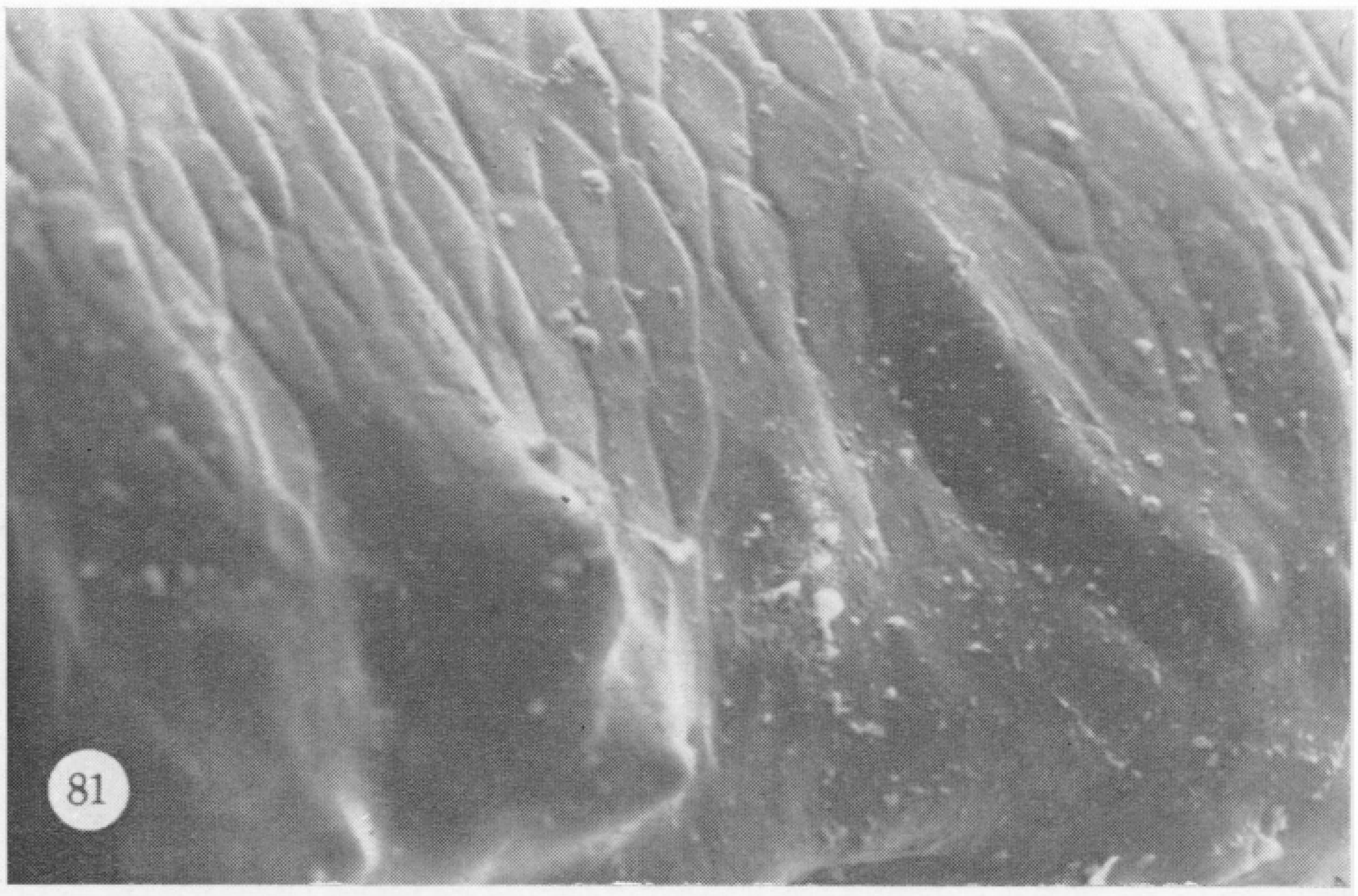
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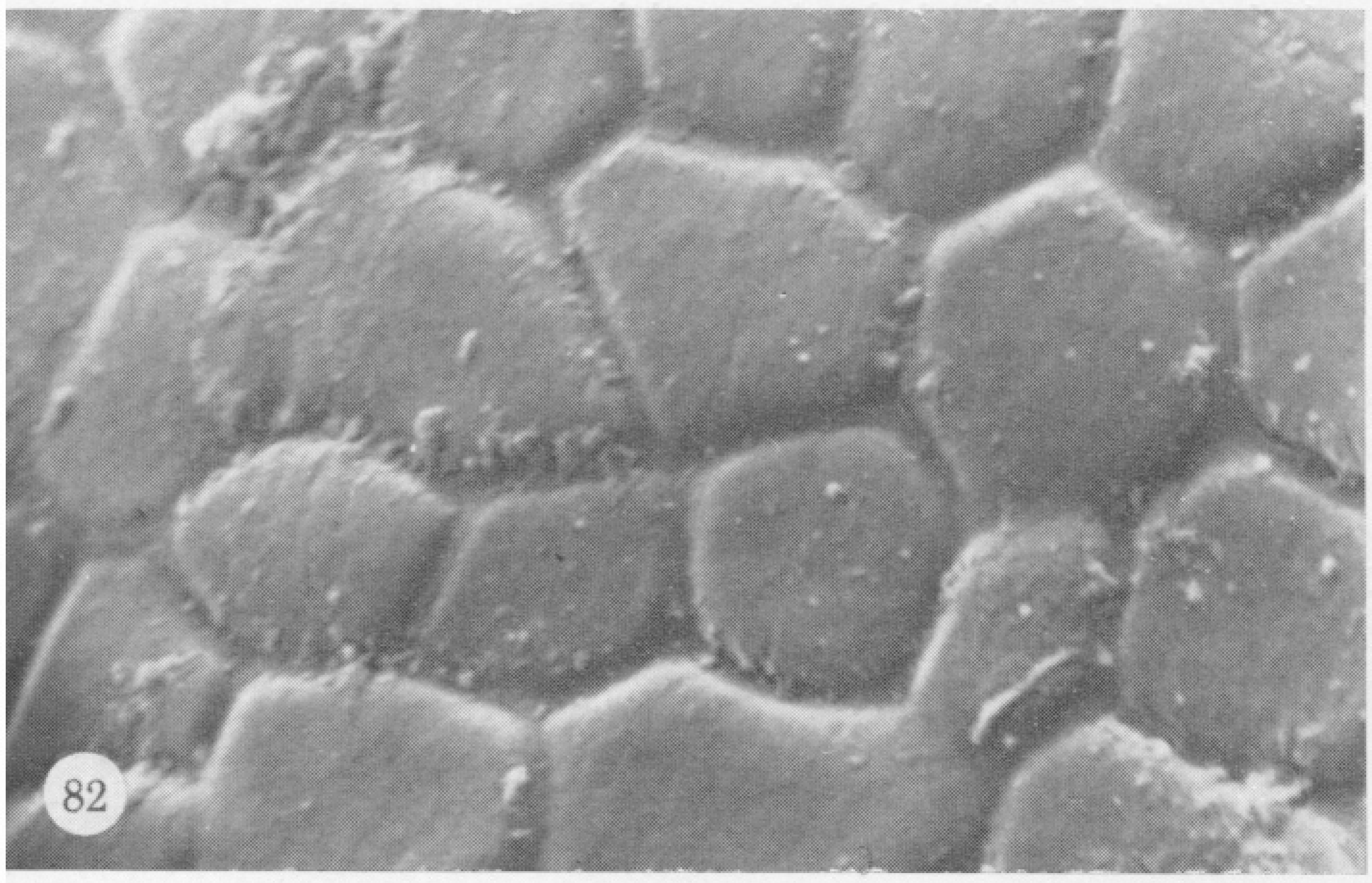
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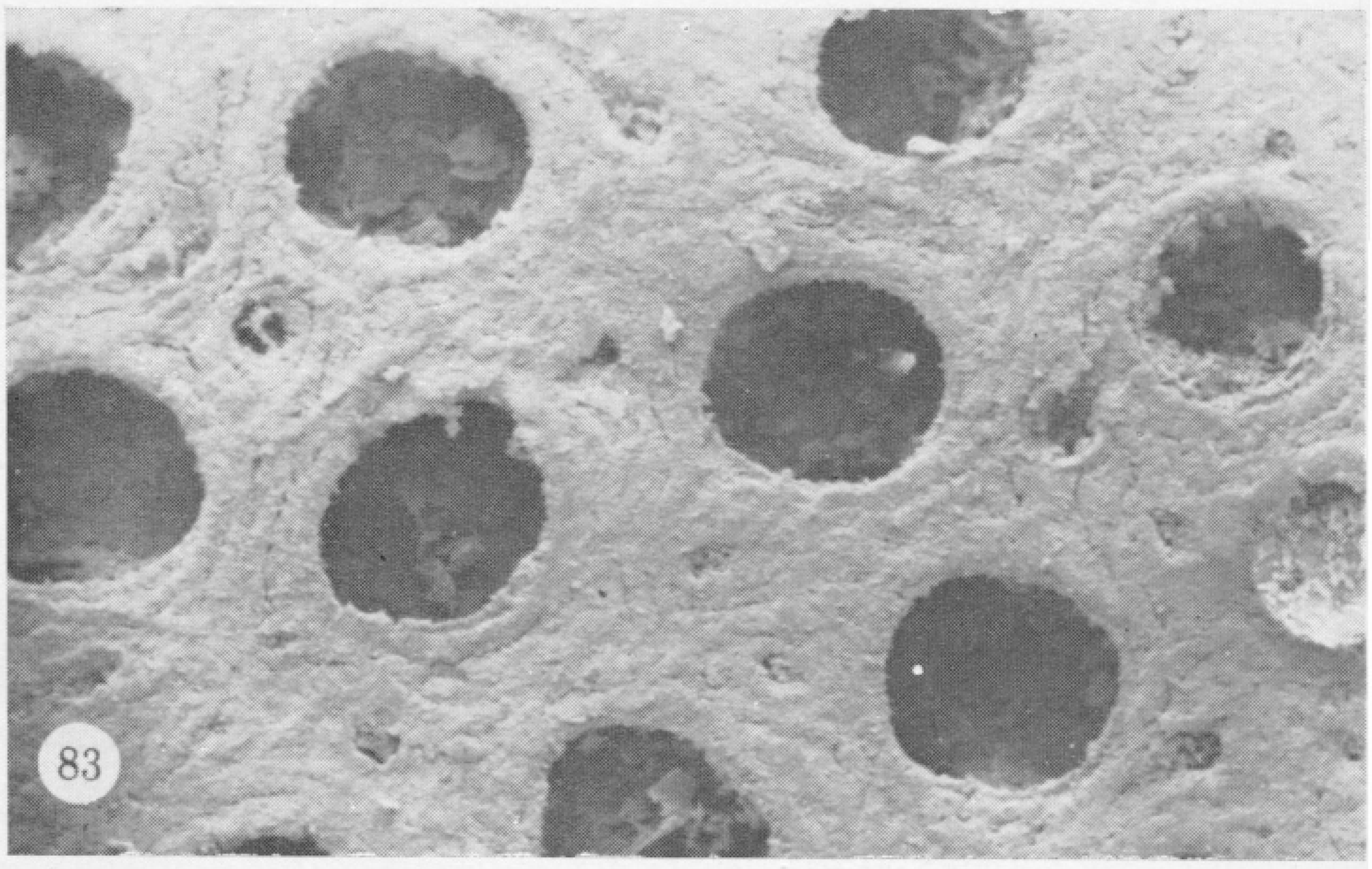
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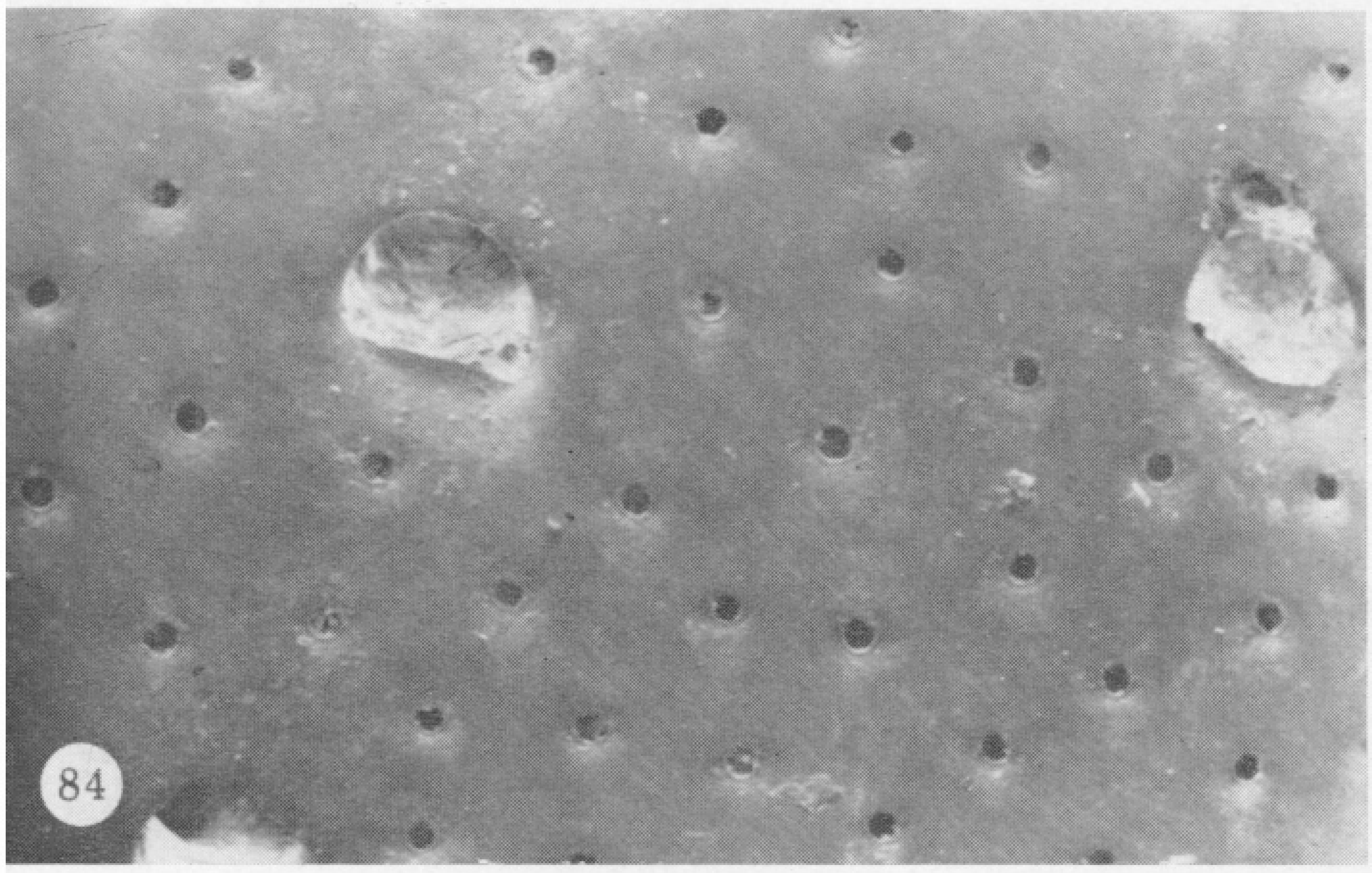
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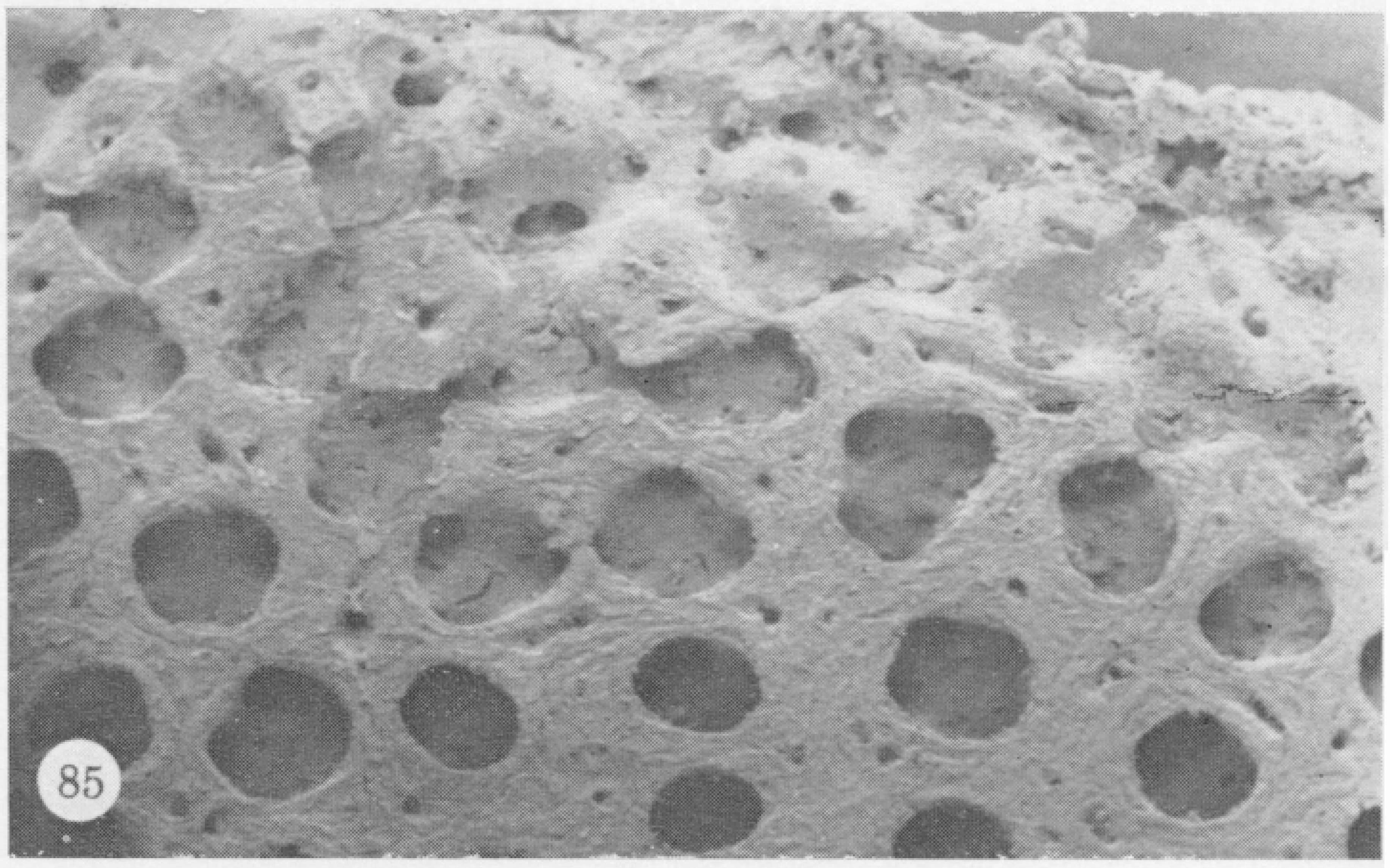
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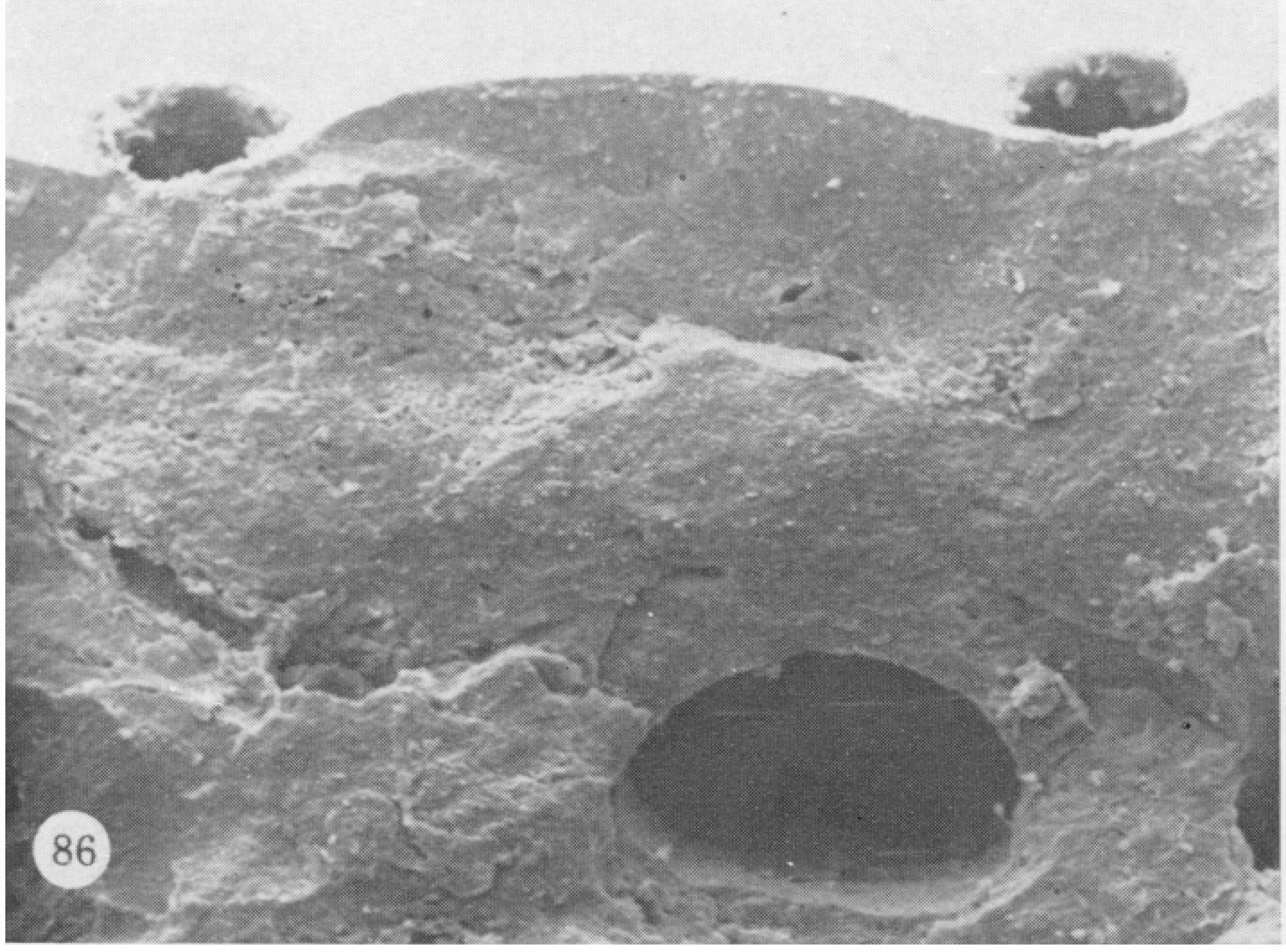
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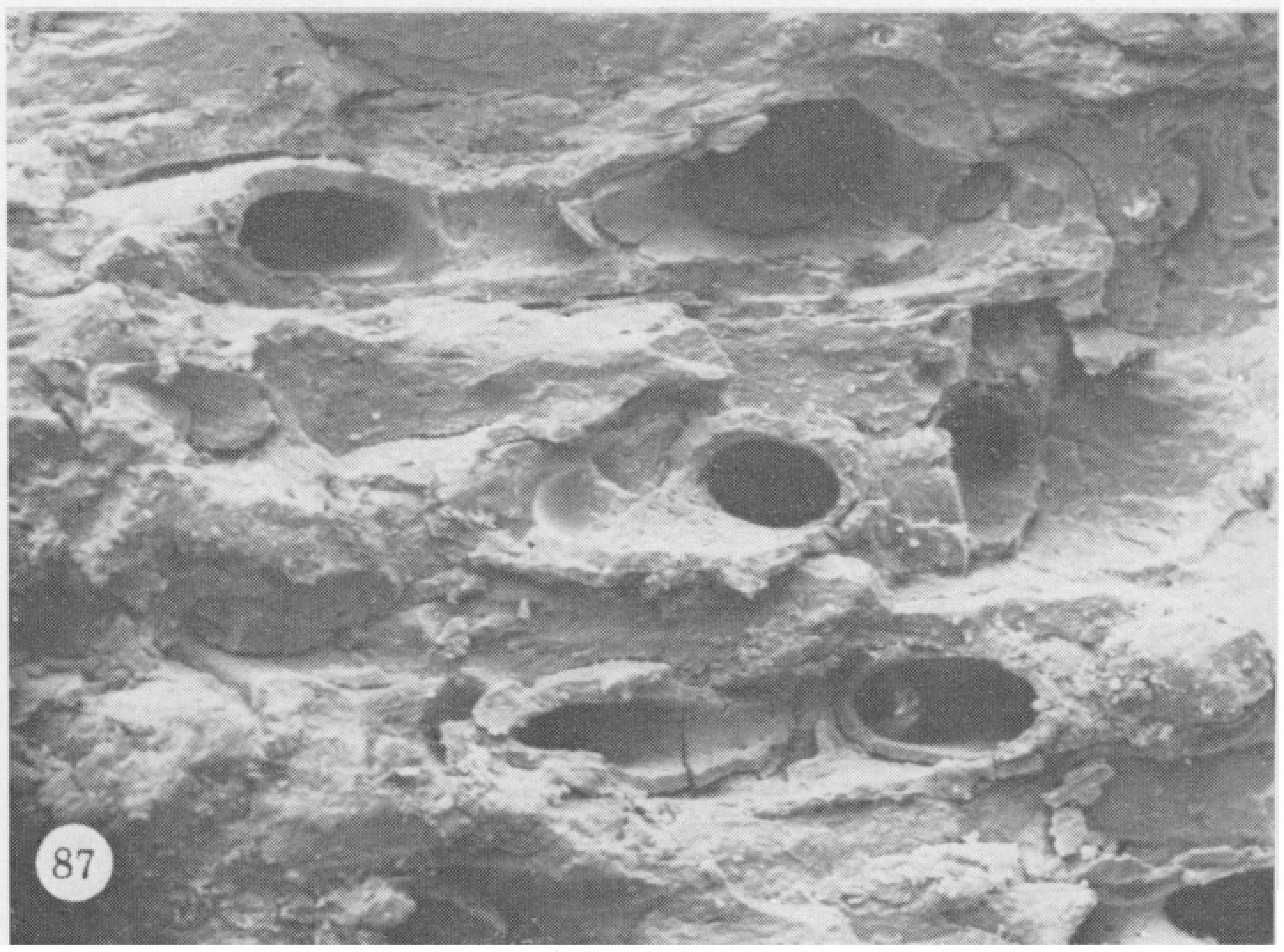
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