THE FORMATION OF MUSCLE SCARS IN ARTICULATE BRACHIOPODS

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[Plates 1–11]

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Distinct impressions (muscle scars) commonly mark the sites of attachment of muscle bases on the interiors of both brachial and pedicle valves of articulate brachiopods. Such impressions are formed as a result of modifications in the fine structure and secretory behaviour of outer epithelial cells (responsible for shell secretion) to which the muscles become attached. Muscles are not attached directly to outer epithelium but are separated from it by a very thin layer of connective tissue. In outer epithelial cells underlying muscle bases the two most apparent changes in cell morphology, compared with epithelial cells unaffected by muscle attachment, are a reduction in optimum cell dimensions and the development of a fibrillar supporting framework (tonofibrils) which extends between the inner and outer plasma membranes. As each muscle base enlarges during ontogeny, outer epithelial cells in the path of the advancing muscle base are progressively overlapped. Below the arcuate anterior margin of the muscle base cell division takes place in the outer epithelium.

Changes in secretory behaviour are equally drastic. Around the arcuate anterior margins of scars the standard secondary shell mosaic is replaced by a much more irregular deposit (myotest). Evidence of a zone of vigorous cell division within the associated outer epithelium can be seen in the way that smooth spatulate terminal faces, once they become incorporated within the periphery of scars, split up into two or three minor lobate branches. In addition cell division is accompanied by an increase in organic exudation and a corresponding decrease in mineral secretion. Whereas normal shell secretion involves the exudation of a single organic membrane across an arcuate zone in the anterior part of each secreting plasmalemma and calcite secretion across the remaining surface area, epithelial cells underlying muscle bases exude two thin triple unit membranes which ensheath each individual myotest fibre. The calcite secretory zone is restricted to a narrow central zone on each secreting plasmalemma and the second organic membrane is exuded over the posterior sector and continues posteriorly to join up with the anterior membrane in the cell behind. In some scars, adjacent fibres may amalgamate to produce a localized laminar fabric. In at least one rhynchonellid genus, *Notosaria nigricans*, mineral secretion under muscle bases may periodically cease with the development of a relatively thick organic layer.

Within a species the morphology of exposed parts of fibres in any one muscle scar tends to be fairly consistent and generally each muscle base imparts to the underlying shell a characteristic fabric which can be readily distinguished from that of neighbouring scars. In an initial survey of a number of unrelated genera ultrastructural modifications within homologous muscle scars were found to exhibit a fair degree of similarity. The fact that homologous muscles perform basically the same function would account for this structural similarity.

In general it is evident that disruptions and modifications of the standard secretory régime associated with the emplacement of muscle bases arise in response to a need for stronger adhesion between the shell and outer epithelium. Such additional adhesion as is required is facilitated by the widespread exudation of organic membranes to which each outer epithelial cell can remain firmly attached by strong hemidesmosomal connections. The dense framework of tonofibrils extending between the inner and outer plasma membranes serves to brace the cells internally against external stresses applied during muscle contraction.

The recognition of myotest fabrics in fossil genera which are closely comparable with the myotest fabrics of living articulates would seem to indicate that similar localized disruptions in secretory behaviour occurred also in the geological past.

Introduction

Structural modifications in shell fabric below the areas of muscle attachment in brachiopods can usually be seen, on a macroscopic scale, as a number of impressions or 'muscle scars' on the shell interior. Although periodically subject to modification in several unrelated stocks, the general arrangement of muscle scars, first established in Cambrian articulate brachiopods, has persisted until the present day. *Notosaria nigricans* (Sowerby) which lives in coastal waters around New Zealand, possesses a muscle system which is fairly typical of articulate brachiopods and it is appropriate that this species should be selected for study since, as well as being readily accessible, it is one of about a dozen living genera assigned to the most ancient articulate order still extant, the Rhynchonellida. To appreciate the significance of ultrastructural modifications in the skeletal morphology of living brachiopods, it is necessary that some attention should first be given to the tissues with which they are so intimately related. Indeed this is especially relevant in any attempt to rationalize fabric changes accompanying the definition of muscle scars, although a comprehensive investigation of the form and function of the various muscular and associated epithelial tissues is beyond the scope of this paper. Accordingly, in the account which follows, the morphology of outer epithelial cells attached to muscle scars receives priority and this is followed by descriptions and assessment of the variation of the skeletal fabrics of the various muscle scars of *Notosaria*. In this way a model for shell secretion within muscle scars is established then used to interpret the skeletal fabrics of other present-day articulate brachiopods. Finally the development of muscle scars in fossil stocks is examined.

MATERIALS AND METHODS

Both surfaces and sections of calcareous shells were examined by scanning electron microscope. Sections of brachiopod mantle and muscle tissue were examined under both light and transmission electron microscopes.

To prepare parts of the mantle and musculature of *Notosaria nigricans* (Sowerby) for examination under the transmission electron microscope, the following schedule was carried out. Specimens were fixed in 4 % glutaraldehyde made up in 3 % sodium chloride, then decalcified in 10 % EDTA. After washing in sucrose, each specimen was treated for 1 h with 2 % osmic acid: all solutions were buffered to pH 7.2 with phosphate buffer. Following embedding in Epon Araldite epoxy resin, sections were cut with a Porter–Blum microtome and stained with aqueous uranyl acetate and aqueous lead citrate.

For the examination of shell surfaces, soft tissue was removed where necessary by immersing specimens in sodium hypochlorite for 30 min then washing well in water. Sections of Recent and fossil shells were obtained by embedding material in Epon Araldite resin then cutting and grinding, first on a diamond grinder and then on fine grade (C600) silicon carbide paper. A relatively scratch-free finish was obtained by using a paste of Aloxite optical smoothing powder along with the silicon carbide paper. Surfaces prepared in this manner were finally polished on a cloth-covered disk which was impregnated with stannic oxide or slow cutting polishing alumina. Before mounting, embedded specimens were cut to a convenient area and thickness and ultrasonically cleaned in a mild detergent solution then in acetone. Fragments of shell surfaces requiring investigation were cleaned in the same way. Once dry, specimens were mounted on aluminium stubs and coated with a thin deposit (about 30–50 nm thick) of gold-palladium alloy.

MUSCLE SCAR FORMATION IN *NOTOSARIA*

(*a*) *The distribution of muscle scars*

In the pedicle valve of *Notosaria* (figure 1*a*) the muscle scars tend to be grouped together to form one large muscle field. The two diductor muscle scars are prominent and lie symmetrically on either side of a slight median ridge. Posteriorly, they diverge to enclose the small heart-shaped adductor muscle scars. Both the diductor and adductor scars are themselves bordered posterolaterally by a pair of ventral adjustor muscle scars which, when taken collectively with the other two pairs, constitute the main ventral muscle field. In addition, two small scars lie behind the main muscle field and define the bases of attachment of a pair of small accessory diductor muscles which join the main diductor muscles at the cardinal process in the brachial valve. In early accounts of brachiopod anatomy (see, for example, Thomson 1927, p. 30), a median 'pedicle muscle scar' (paired in the Rhynchonellida but not in the Terebratulida) is sometimes mentioned. This is not a true muscle scar, but the attachment area for a dense bundle of fibrous connective tissue which anchors the base of the pedicle to the interior of the ventral valve (Williams & Rowell 1965, p. H15).

In the brachial valve (figure 1*b*), the muscle scars are more scattered. There are two pairs of adductor muscle scars which lie symmetrically on either side of a slight median ridge. The anterior pair are larger and more closely spaced together than the posterior pair. The diductor muscles are inserted on the cardinal process which, in *Notosaria*, consists of a plate-like ridge bearing a transversely elongate furrow. On the inner faces of the inner socket ridges, two small scars define the area of attachment of the dorsal adjustor muscles.

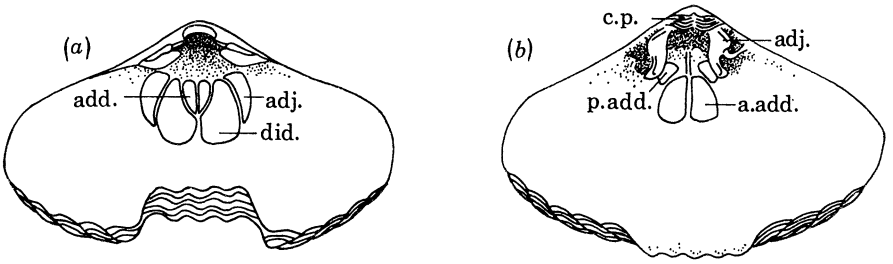

FIGURE 1. Views of the distribution of muscle attachment areas on the interiors of the pedicle valve (*a*) and the brachial valve (*b*) of *Notosaria*. c.p., cardinal process; adj., adjustor; did., diductor; add., adductor; p.add., posterior adductor; a.add., anterior adductor.

(*b*) *Morphology of outer epithelial cells underlying muscle bases in* Notosaria

It is common practice to refer to the elastic tissue controlling the opening and closing of brachiopod valves as 'muscle'. In fact only the ventral diductor and dorsal adductor muscle bases are composed of discrete bundles of muscle fibres whereas the opposing ends are tendonous. However there does not appear to be any significant difference in the way in which adherent epithelium is affected by the emplacement of muscle bases whether it be tendon or muscle fibre. In the discussion which follows the term 'muscle base' is used loosely to include both contractile muscle tissue and tendon.

In all living brachiopods, valve interiors, including muscle scars, are lined with outer epithelium which is responsible for shell secretion. The standard process of shell secretion in articulate brachiopods is now well understood and is known to involve the deposition of commonly two (Williams 1968) and sometimes three (MacKinnon & Williams 1974) mineral layers on top of a thin organic periostracum. Secretion of the relatively thin primary calcareous layer is confined to a narrow strip of epithelium around the valve margins. Fibrous secondary shell material is secreted over the remainder of both valve interiors and gives rise to all exoskeletal outgrowths such as brachial supports, septa and cardinalia. In some brachiopods, notably a number of living and fossil Terebratulida, a tertiary layer of prismatic calcite may succeed the secondary fibrous layer over the greater part of the shell interior. Muscle scars may form in areas of either secondary or tertiary shell deposition.

Outside muscle scars, deposition of secondary layer fibres is relatively uniform. Each outer epithelial cell secretes one fibre, plus a protein sheet (Williams 1968, p. 4). Exudation of the protein sheet is confined to an arcuate zone in the anterior part of each cell membrane whilst calcite is secreted across the remainder. At the site of protein exudation, the outer plasma membrane and protein sheet are attached to one another by desmosomes and sporadic tonofibrils appear within the cytoplasm but over the calcite secretory zone, desmosomes are absent.

In *Notosaria*, the muscle bases are separated from outer epithelium by a thin layer of connective tissue, on average about 500 nm wide, which consists principally of collagen fibres with their long axes aligned parallel to the shell surface (figure 2; figure 3, plate 1). Long microvillous extensions of individual muscle fibres, possessing terminal cell membranes packed with hemidesmosomes, permeate the connective tissue thereby affording an increased area of attachment for the basal part of each muscle fibre. Following the contour of this adhesive membrane but separated from it by a light zone about 40 nm wide is a fairly continuous,

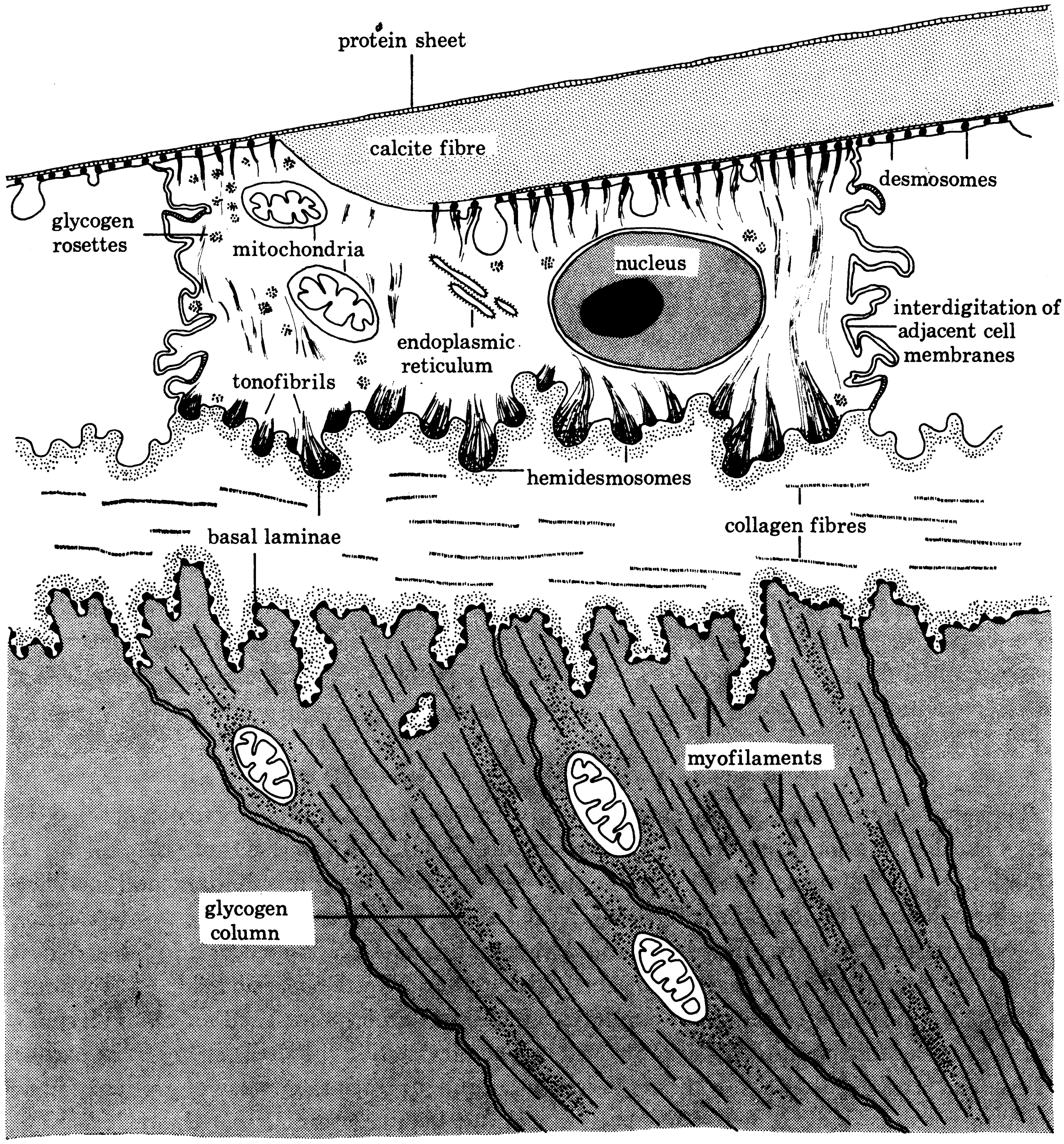

FIGURE 2. Stylized longitudinal section through an outer epithelial cell associated with a muscle base showing the nature and distribution of the mineral and organic secretory products.

moderately electron-dense band 50–70 nm thick. This layer, the basal lamina, occurs in association with many epithelia and is probably a mucopolysaccharide (Fawcett 1966, p. 353). At the opposing margins of the connective tissue layer a similar extraneous coating is found lining each inner plasma membrane of the outer epithelium. The most striking structural modification occurring within the outer epithelial cells underlying the muscle bases in *Notosaria* is the development of a dense framework of tonofibrils which extends between the inner and outer cell membranes. Against each inner cell membrane the tonofibrils terminate in large hemidesmosomes which afford a strong adhesive contact between the outer epithelium and collagenous connective tissue. Across each outer plasma membrane shell deposition takes place. As in unmodified epithelium outside muscle scars, a protein sheet is still spun off from the anterior part of each plasma membrane, but instead of wholly calcite being deposited by the posterior part, in that area there is a gradual build up of another organic membrane. This sheet can be traced across the posterior boundary of the cell to join up with the sheet spun off by the anterior part of the cell in the row immediately behind. Secretion of calcite is therefore confined to a narrow transverse zone which is located on each plasmalemma immediately behind the spin-off point of the anterior protein sheet.

The actual chemical processes of shell deposition in brachiopods are not, as yet, clearly understood. However, a considerable amount is known of the depositional processes in Mollusca which also possess a mineralized skeleton. Between their shell and mantle, there is a narrow 'extrapallial' zone filled with fluid from which the various organic and inorganic constituents (i.e. Ca^{2+} and HCO_3^- ions and organic components of any membranes) are precipitated out, and deposition of the shell is maintained by replenishment of the necessary constituents from within the outer epithelial cells. In view of such findings, it appears highly likely that a similar fluid-filled extrapallial zone occurs between the mantle and shell of living articulate brachiopods. Recently Williams (1970, pp. 15–16; Figs 7–9) has recognized a narrow zone, presumably fluid-filled, between the outer epithelium and laminar shell of the inarticulate brachiopod *Crania anomala* Müller. Likewise, in *Notosaria*, a narrow space (10–20 nm thick) exists between the outer plasma membrane and the thin, continuous organic sheet which it secretes (figures 3 and 4, plate 1). In decalcified sections, it is not possible to verify the presence of extrapallial fluid in this space or external to that part of the plasma membrane involved in the secretion of calcite, but it is likely to occur in life.

(*c*) *Migration of muscle bases and development of myotest*

The microscopic shell structure characteristic of muscle scars is commonly so distinct that it is best regarded as a localized development of an additional shell layer. Krans (1965, p. 95), in examining the shell structure of Devonian spiriferides, appreciated this fundamental modification in shell secretion and termed the layer the *myotest*. In radial section, the myotest can be traced running backwards towards the umbo where it becomes overlapped by normal secondary layer fibres secreted in that part of the shell lying posterior to the muscle field. As Westbroek (1967, p. 28) has pointed out, the boundaries of myotests are isotopic shell unit boundaries.

When its organic constituents are removed by chemical action the shell readily splits parallel to the long axes of the fibres so that it becomes possible to trace the course of groups of fibres for some considerable distance. If the shell is split just behind a muscle scar that is located on a valve floor the trails of those fibres along the plane of parting become exposed. Significantly, parts of the myotest are exposed at a lower level within the shell, and the trails of those secondary layer fibres with smooth terminal faces, which on the unsplit shell succeeded myotest, are seen to run back into freshly exposed myotest. Clearly the cells responsible for secreting those fibres posterior to the muscle scar were, at an earlier stage of growth, involved in secreting myotest. At an even lower level the irregular, gnarled trails of the myotest merge once more with smooth trails that must have been secreted by cells which at that moment in time were situated in front of the muscle field. The muscle base responsible for creating the myotest must therefore migrate anteriorly at a faster rate than the underlying epithelium and as outer epithelial cells are left behind in the wake of the advancing muscle base, they revert once more to their normal depositional rôles. The initial effects of muscle encroachment upon the normal secretory régime are to be found around the anterior margins of muscle scars.

(*d*) *Ventral diductor muscle scars*

In an arcuate zone, about 1.5 mm in front of the muscle field, the normally smooth terminal faces of fibres (up to 40 μm long and 25 μm wide) begin to show the development of fine, irregular pits which are usually less than 500 nm in diameter (figure 5, plate 2). The pits tend to be concentrated more in the posterior half of the terminal face and are commonly aligned parallel to the rhombohedral angles of each fibre. Traced backwards towards the muscle field, their distribution may become so dense that adjacent ones coalesce and give rise to irregular troughs and ridges which may measure 1–2 μm in width (figures 6 and 7, plate 2). Around the anterior margin of the muscle field, a slight but prominent ridge occurs which involves about 10 consecutive rows of fibres. The outlines of the terminal faces just anterior to its crest lose their characteristic spatulate shape and become jagged. Behind the crest of the ridge, long trails of fibres, 50–100 μm in length, are exposed. Further behind, preceding trails become progressively more irregular in outline until they become broken up into a number of small isolated fragments. With this break up, trails at a lower level in the shell succession are exposed. Since the net result is to produce a lowering of the level of the valve floor, it is evident that the exposed trails of fibres on the flanks of the ridge have undergone resorption. However, the process does not continue indefinitely, for at a lower level, the surfaces of exposed trails are relatively smooth. These fibres do not possess recognizable terminal faces and are taken to represent the 'base level' to which the process of resorption was active.

Behind this zone of resorption there is a drastic change in the secondary shell fabric (figure 8, plate 2). Instead of being arranged in alternate rows with fibres of one horizontal row being overlapped by the two contiguous halves of fibres in the row immediately behind as in the standard secondary shell mosaic pattern, the fibres tend to be stacked in longitudinal rows with one behind the other (figure 9, plate 2). At irregular intervals the pattern may be disrupted due to several rows overlapping in more orthodox fashion, but there is no consistency to this occurrence. Occasionally the lateral edges of two or three adjacent fibres may become welded together, but the outline of each individual fibre is still discernible. The extent to which the secretory processes of the outer epithelial cells underlying the diductor muscle bases become modified is best reflected in the shapes of the growing (terminal) faces of the fibres which they secrete. On each exposed fibre, the terminal face is confined to a narrow strip at its anterior edge. Its surface is irregularly studded with rough pits up to 1 μm in diameter which extend right to the leading edge of each fibre (figure 10, plate 2). As a result, the anterior edge which is already jagged becomes even more irregularly serrated. Because the fibres are arranged in longitudinally overlapping rows, the rhombohedral angle defining the boundary of each terminal face is highly skewed so that its V-shaped apex is usually situated close to one or other antero-lateral edge. The shape of each terminal face is therefore controlled, to a certain extent, by the spacial relations of the outer epithelial cells secreting adjacent fibres in the immediate vicinity. As Williams (1968, p. 12) has shown, the outlines of mature outer epithelial cells of articulate brachiopods are rhombohedral, thereby reflecting the degree to which each plasma membrane becomes increasingly adapted to the accretion of a calcite rhomb. The fact that the fibres within the myotest are generally stacked one behind the other and not arranged in alternating rows relative to the shell edge, as is the case in the rest of the shell, indicates that the cells responsible for secreting the myotest must be subject to external stresses which tend to distort the outlines of the growing face of each fibre. On the exposed trails behind each terminal face, small pits usually no more than 500 nm in diameter are inserted along a series of wavy grooves 1–2 μm apart. The V-shaped apices of intersecting furrows are directed posteriorly and aligned parallel to the posterior edge of each terminal face. The regularity of insertion of pits has been interpreted as evidence of pauses in the advance of outer epithelium (Williams 1968, p. 22).

By comparing the shapes of terminal faces with the pattern of furrows on exposed trails, it is possible to define intercellular boundaries with a fair degree of accuracy. Only a narrow zone close to the anterior boundary of each epithelial plasmalemma is involved in the deposition of calcite. As seen in decalcified section of outer epithelium, the remainder of the plasmalemma exudes a thin organic sheet to which the cell is rigidly attached by large desmosomes (figure 2). Thus external to each row of cells, thin wedges of calcite are contained between consecutive organic sheets and, as mineral deposition continues, the desmosomes attached to the organic sheets which represent microvillous extensions of the cell membrane containing groups of tonofibrils become encased in calcite. In this way, coarse pits are developed on the surface of the terminal faces of fibres.

Close to the posterior margins of the muscle field there is an acceleration in calcite deposition, for the terminal faces display differentially thickened, transverse ridges of calcite which are separated by anteriorly convex furrows or rows of obliquely inserted pits (figure 11, plate 2). Initially the ridges are narrow, about 1–2 μm in width, but close to the posterior margin they amalgamate and give rise to smooth, raised pads of calcite which begin to take on the aspect of orthodox terminal faces (figure 12, plate 2; figure 13, plate 3). In addition, a more characteristic stacking of fibres is restored, but only temporarily, since it again becomes disrupted posteriorly as the fibres are incorporated in parts of the adductor and adjustor muscle fields.

(*e*) *Ventral adductor muscle scars*

The adductor muscle scars in the pedicle valve are small and lie close together on either side of the slight median ridge. They are bordered anteriorly by the posterior end of the diductor muscle scars and postero-laterally by the rear lobes of the ventral adjustor scars (figure 1*a*), so

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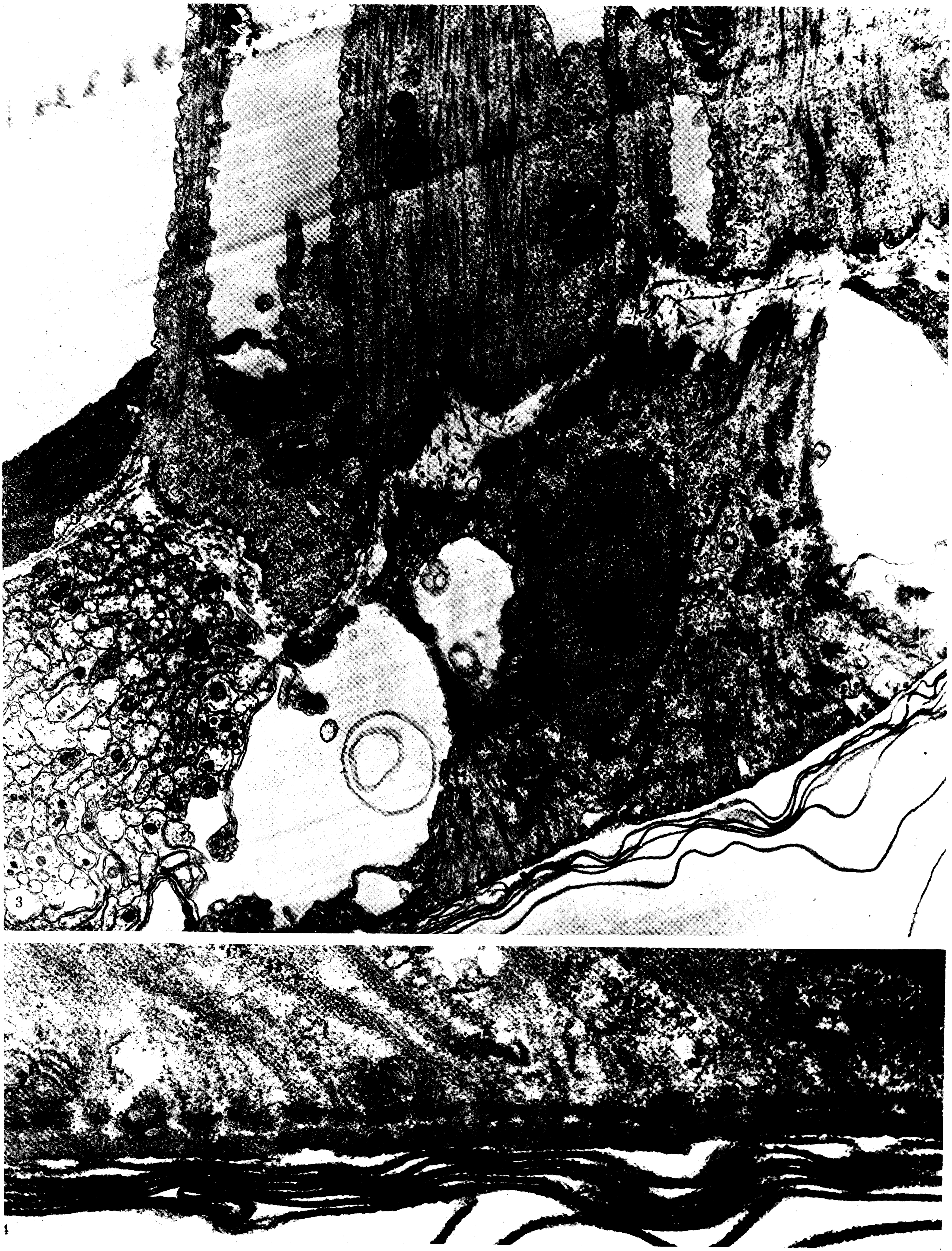
DESCRIPTION OF PLATE 1

Transmission electron micrographs of *Notosaria nigricans* (Sowerby).

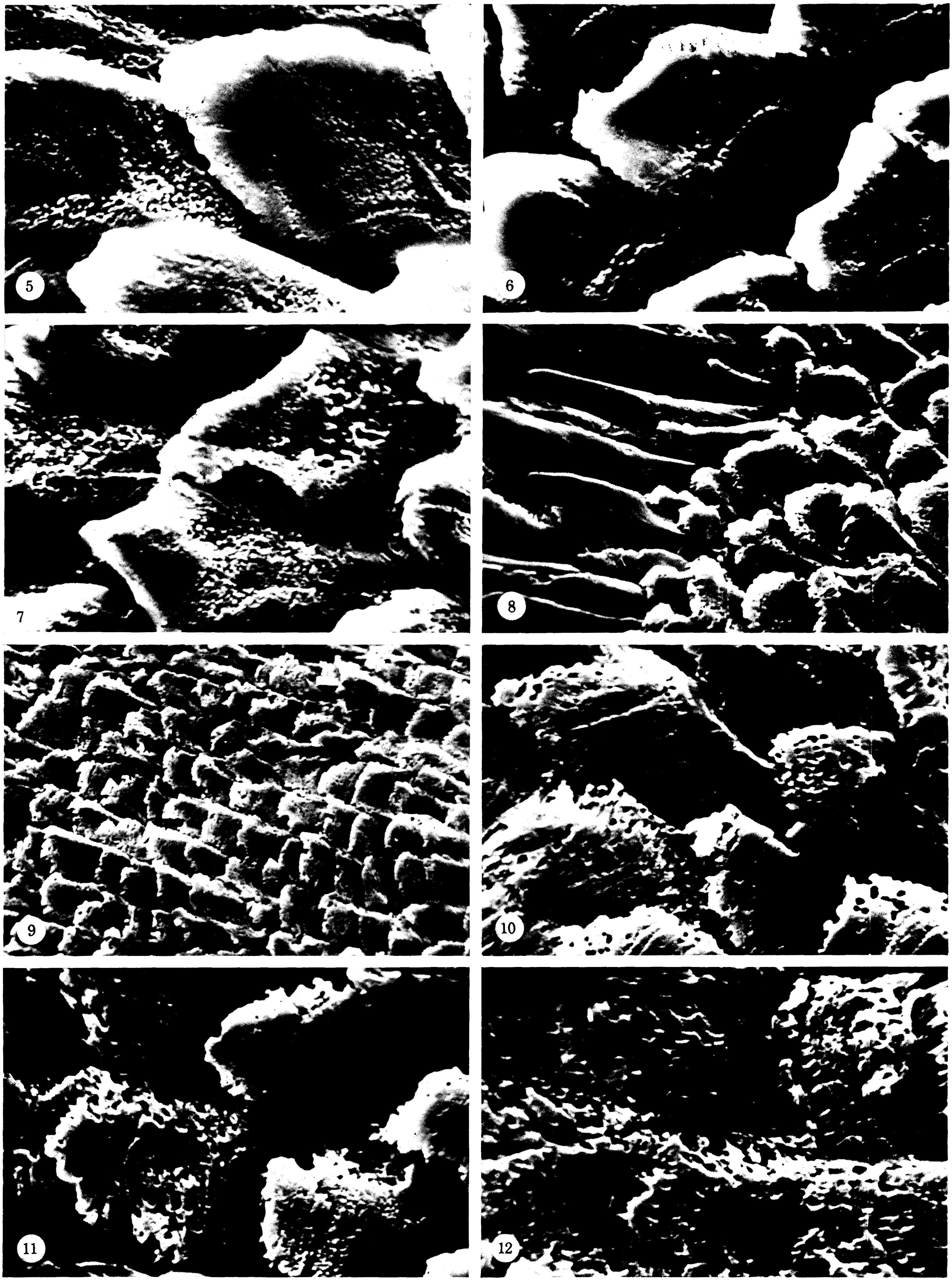
FIGURE 3. Section through decalcified shell, outer epithelium and part of the anterior adductor muscle base (magn. × 20625).

FIGURE 4. Section through part of an outer epithelial cell underlying a diductor muscle base showing the development of a thick organic layer which is attached to the secreting plasmalemma by closely spaced desmosomes (magn. × 82500).



FIGURES 3–4. For description see opposite.

(*Facing p.* 8)



FIGURES 5–12. For description see opposite.

that there is no real opportunity to evaluate the observed changes in skeletal fabric in terms of structural modifications of the standard secondary shell mosaic. However, the junctions between the adductor and diductor muscle fields are quite distinct with the adductor scars, if anything, being slightly more deeply impressed on the floor of the valve, so that a direct comparison of the surface topographies in both these areas can be made.

The exposed parts of the fibres, which are normally long and narrow, bear no recognizable terminal faces. In general they are only about half as wide as those in the diductor muscle field (6–8 μm in width) and their stacking is so disorganized that exposed trails may be greatly extended posteriorly (up to 50 μm in length) as a result of incomplete overlap by the fibres immediately behind (figure 14, plate 3). The overall profile of each fibre depends very much on the nature of the overlap of succeeding fibres. If a fibre is overlapped in normal fashion by the two contiguous halves of a pair of fibres in the row behind, then that fibre will possess a medial ridge or keel (Williams 1968, p. 8) along its length. However, if it is overlapped by the greater part of one of these fibres, the keel will be displaced either to one side or the other. Fibres with asymmetrical profiles are exceedingly common within the adductor muscle scars.

Nearly all fibres are traversed by anteriorly arcuate troughs and ridges with an average periodicity of 1.2 μm (figure 15, plate 3) which suggests that, within the myotest, deposition of calcite is not continuous but, judging from the uniform periodicity, occurs at regular intervals. In some cases, the furrows separating consecutive arcuate ridges of calcite may be so deeply incised that fibres are broken up into several isolated fragments. As well as exhibiting a depositional banding, the fibres are intermittently studded with fine pits up to 500 nm in diameter but in no part of the adductor muscle field do they occur so densely distributed as in the neighbouring diductor muscle field.

Since the fibres of the adductor muscle scars bear no recognizable terminal faces, it is evident that they are ensheathed by a proteinous membrane for the greater part of their length. The nature of the depositional banding is such that at any moment in time it would appear that accretion of calcite is only taking place at the extreme anterior edge of each fibre.

Behind its posterior margin, the adductor myotest is succeeded by orthodoxly stacked fibres

Description of plate 2

Scanning electron micrographs of the shell of *Notosaria nigricans* (Sowerby).

Figure 5. Detail of profile and microtopography of the secondary shell mosaic situated 1.5 mm in front of a ventral diductor muscle scar (magn. × 2400).

Figure 6. Detail of profile and microtopography of the secondary shell mosaic situated 0.75 mm in front of a ventral diductor muscle scar (magn. × 2400).

Figure 7. Detail of profile and microtopography of the secondary shell mosaic situated at the anterior margin of a ventral diductor muscle scar (magn. × 2400).

Figure 8. View of the anterior margin of a ventral diductor muscle scar showing the overlap of myotest fibres upon the long exposed trails of fibres situated within the zone of resorption (magn. × 1200).

Figure 9. General view of a ventral diductor myotest showing the unorthodox shape and stacking of fibres (magn. × 500).

Figure 10. More detailed view of ventral diductor myotest fibres showing the jagged outlines of terminal faces, rough pits and transverse furrows (magn. × 2400).

Figure 11. Terminal faces of fibres close to the posterior margin of a ventral diductor muscle scar showing the distribution of pits and transverse furrows (magn. × 2400).

Figure 12. Terminal faces of fibres slightly closer than those of figure 11 to the posterior margin of the same ventral diductor muscle scar showing calcite ridges, pits and transverse furrows (magn. × 2400).

exhibiting a good secondary shell mosaic pattern. However, it is noticeable that the first few rows of fibres are significantly smaller than those further away from the myotest, but within 5 or 10 rows of the actual junction their terminal faces attain normal dimensions (figure 16, plate 3).

(*f*) *Ventral adjustor muscle scars*

In front of the anterior margin of each adjustor muscle scar, the terminal faces of fibres show signs of modification similar to that affecting the standard secondary shell mosaic in front of the diductor muscle scars. Traced posteriorly from some distance in front of the muscle scar, the outlines of terminal faces become jagged while their normally smooth surfaces become increasingly furrowed by irregular pits and grooves which are usually aligned parallel to the rhombohedral angles defining the posterior margins of each terminal face. Around the anterior margin of the muscle scar, the surface level of the shell drops gently backwards to expose long trails of fibres which show signs of having undergone resorption. Posterior to this zone, one or two earlier formed ridges of similar appearance may be present. It is not clear whether the presence of more than one ridge is the result of an accidental removal of myotest from the anterior part of the muscle scar, or merely a temporary retardation in its secretion. However, just posterior to the marginal ridges the terminal part of each fibre branches into several smaller irregular lobes which overlap the larger trails at the base of the ridge immediately in front.

The exposed parts of fibres constituting the ventral adjustor myotest exhibit considerably more variation in shape and stacking then either the adjacent diductor or adductor myotests. In some areas, the secretory régime of the overlying outer epithelial cells may be so drastically altered that the surface of the myotest becomes a clutter of small, thin, irregularly lobate pads of calcite, welded together here and there by sinuous ragged trails which overlap one another in a completely disorganized fashion (figure 17, plate 3). In other parts of the myotest, individual fibrous outlines are discernible, and, like those occurring in the other two ventral myotests, the exposed trails are traversed by wavy rows of grooves and pits, indicative of periodic deposition (figure 18, plate 3).

Around the posterior margins of the muscle scar, the transition from myotest to standard secondary shell mosaic is abrupt. Immediately behind the myotest the exposed parts of fibres are noticeably small (similar in size to fibres in the region behind the ventral adductor myotest), but within a few rows they attain standard dimensions.

(*g*) *Dorsal adductor muscle scars*

The fact that the dorsal ends of the adductor muscles are composed of two different types of muscle, 'striated' and 'smooth' (Rudwick 1961, p. 1021), prompted an investigation as to whether the known differences in the type of muscle responsible for producing each impression would give rise to any ultrastructural variations in the skeletal fabric of the scars themselves.

Close to the leading edge of each dorsal adductor muscle scar of *Notosaria*, the terminal faces of fibres become smaller and degenerate into irregularly lobate pads (figure 19, plate 3). As happens in front of the ventral muscle scars, the surfaces of those terminal faces and exposed trails are increasingly broken by rough pits and grooves aligned parallel to the terminal faces of adjacent fibres in the row immediately behind. Within the muscle scar, small fibres with lobate or anteriorly truncated terminal faces overlap the curved anterior boundary. On average, they are about one-third the size of those outside the muscle scar, but although lateral edges of adjacent fibres may become welded together, the outlines of individual fibres are usually retained as longitudinal ridges or grooves on exposed faces (figure 20, plate 3). However, in certain parts of the muscle scar, the pattern of shell deposition may be so drastically altered that no trace of intercellular boundaries remain. Small, irregularly lobate accretions of calcite may form as encrustations on parts of the earlier formed, though noticeably more uniform myotest (figure 22, plate 4). This type of shell fabric has been found to be most prevalent in the anterior part of the anterior adductor myotest. In contrast, over the greater part of the posterior adductor scar, no myotest comparable with that in any of the other scars has been found. Its surface is usually composed of one or more anteriorly arcuate zones of fibres which are readily picked out on account of their distinctive growth patterns (figure 21). Each zone is divisible into two parts; an anterior part made up of large, fairly smooth, spatulate terminal faces each up to 40 μm wide and a posterior part consisting of long ragged exposed trails of fibres. Since this fabric is a particular example of a more fundamental feature of the calcareous shell succession within the muscle fields of *Notosaria*, it will be considered separately after the skeletal fabrics of the remaining muscle attachment areas in the brachial valve of *Notosaria* are described.

(*h*) *Dorsal adjustor muscle scars*

The pair of small dorsal pedicle adjustor muscles are attached to the brachial valve of *Notosaria* along the crest of each inner socket ridge. Williams has already described the ultrastructure of its crus (1968, p. 16) which is composed of secondary shell with the fibres on the posterior surface closely packed and overlapping regularly towards the distal end. Where the base of the crus merges with the inner socket ridge, the regular mosaic is replaced by dorsal adjustor myotest. The fibres of the myotest consist of fairly smooth, narrow, sinuous lobes of calcite with only faint traces of transverse banding indicative of periodic deposition (figure 23, plate 4). Although the fibres are not normally wider than 10 μm, they frequently exceed 40 μm in length. Around the anterior margin of the myotest, the regular mosaic gives way to an anteriorly arcuate zone composed of fibres exhibiting long, exposed trails, similar, though on a much smaller scale, to that found around the anterior borders of the more prominent scars. At the posterior end of the muscle scar, the myotest is succeeded once more by the regular mosaic (figure 24, plate 4). The junction is abrupt, but although the exposed parts of fibres in the first few rows posterior to the myotest are somewhat irregular in outline and unevenly stacked, the more orthodox arrangement of alternately overlapping rows is quickly restored.

(*i*) *The cardinal process*

In *Notosaria*, the cardinal process consists of a raised, plate-like ridge bearing a transversely elongate furrow (figure 25, plate 4). The complete area of attachment for the dorsal ends of the diductor muscles is contained within this broad furrow. The floor of the furrow is not smooth but is itself broken up into a series of minor grooves and ridges which follow the contour of the major depression. Like all other skeletal outgrowths of *Notosaria*, the complete structure is built up of secondary shell material, but the exposed parts of fibres occurring within the area of muscle attachment possess small, irregular outlines which are rarely more than 5 μm wide (figure 26, plate 4). Growth of the cardinal process is maintained by the addition of secondary shell material to the front of the elevated ridge defining the anterior extremity of the muscle attachment area. In longitudinal section (figure 30), each minor ridge is seen to mark a period of growth in the formation of the cardinal process. From the groove between each ridge, a more prominent row of fibres curves gently backwards within the shell. The fibres constituting each row define areas of synchronous growth which, during consecutive stages of shell deposition, formed the exposed surface of the gently curved ridge at the anterior extremity of the cardinal process. As the cardinal process grows, it envelops other parts of the cardinalia. Peripheral expansion antero-laterally of that part of the mantle responsible for secreting the cardinal process leads to its encroachment on the earlier formed parts of the dental sockets. As growth proceeds, the apical regions of the sockets are overlapped and subsequently infilled. In longitudinal cross sections through the cardinal process, a distinct surface of unconformity can be recognized between the now obsolete parts of the dental sockets together with its adjacent inner and outer socket ridges, and the overlying, more recently deposited shell fabric of the cardinal process.

(*j*) *Growth and development of the muscle scars*

Within each muscle scar, the small fibres with lobate or anteriorly truncated terminal faces making up the myotest contrast sharply with the smooth, rounded terminal faces of the standard secondary shell mosaic found elsewhere. In most cases, the myotest fibres are at least three times as small as those outside the muscle scars (figures 27, 28 and 29, plate 4). The substantial reduction in size of fibres inside the boundaries of muscle scars is significant since it is indicative of a similar reduction in size of the secretory zones of the outer plasma membranes in the overlying outer epithelial cells. However, since the overall fibre density within the muscle field is greatly increased, the generation of additional outer epithelial cells must take place around the periphery of the muscle base. At the posterior margin of each muscle field the transition from a modified to standard mosaic pattern is abrupt (figure 31, plate 5). At this location, the outer epithelial cells revert to the normal secretory régime, but the fibres in an arcuate zone behind the muscle scar are still distinctly smaller than those elsewhere on the shell surface. Traced posteriorly, their size quickly increases so that these fibres soon become indistinguishable in appearance from the rest of the secondary shell mosaic. Evidently, the optimum size range of

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DESCRIPTION OF PLATE 3

Scanning electron micrographs of the shell of *Notosaria nigricans* (Sowerby).

FIGURE 13. Relatively smooth raised pads of calcite comprising the terminal faces of secondary layer fibres situated at the posterior margin of the ventral diductor muscle scar (magn. × 2400).

FIGURE 14. Long exposed trails of fibres comprising the ventral adductor myotest (magn. × 2500).

FIGURE 15. Strong development of transverse troughs and ridges on the exposed parts of fibres comprising the ventral adductor myotest (magn. × 2500).

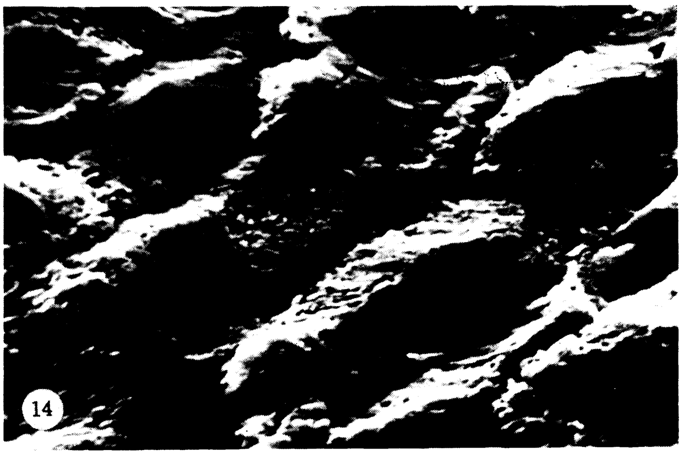
FIGURE 16. Posterior margin of a ventral adductor myotest showing the initial regrowth of the standard secondary shell mosaic (magn. × 1200).

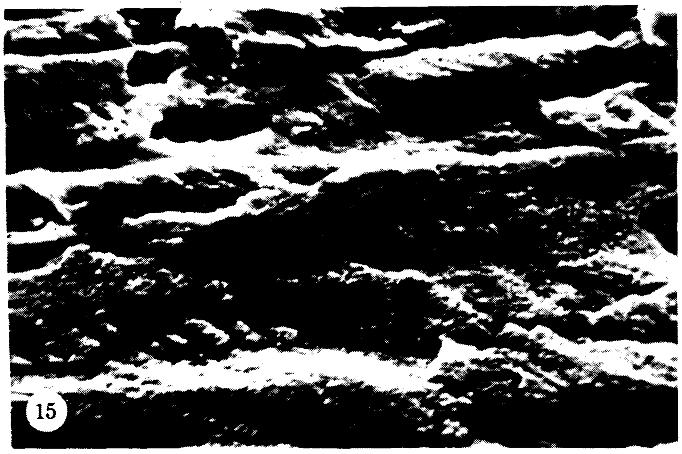
FIGURE 17. Part of the surface of a ventral adjustor muscle scar showing a highly irregular myotest fabric (magn. × 1200).

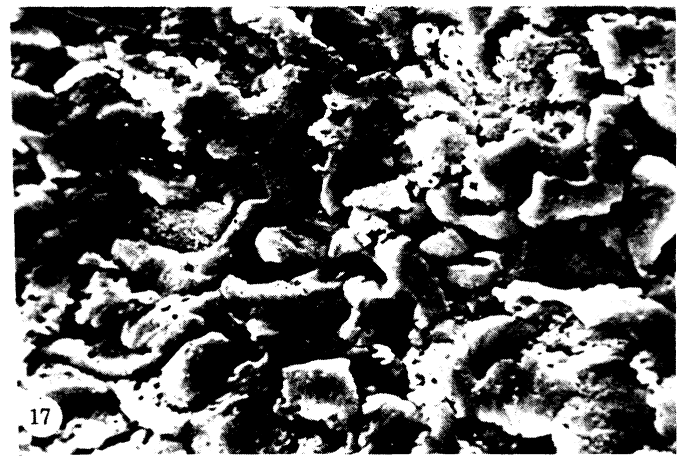
FIGURE 18. Ventral adjustor myotest showing exposed parts of fibres which are traversed by series of wavy grooves and sporadically pitted (magn. × 1220).

FIGURE 19. Terminal faces of fibres located around the anterior margin of a dorsal adductor muscle scar showing the initial breakdown of the standard secondary shell mosaic (magn. × 670).

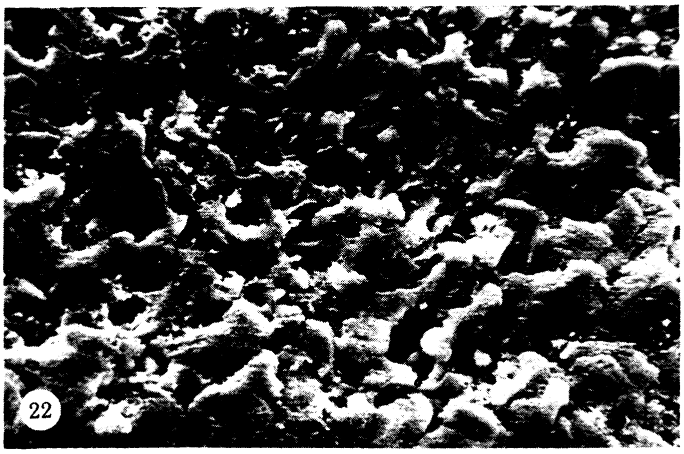
FIGURE 20. View within part of a dorsal adductor muscle scar showing the irregular outlines of fibres with fused lateral margins (magn. × 650).







FIGURES 13–20. For description see opposite.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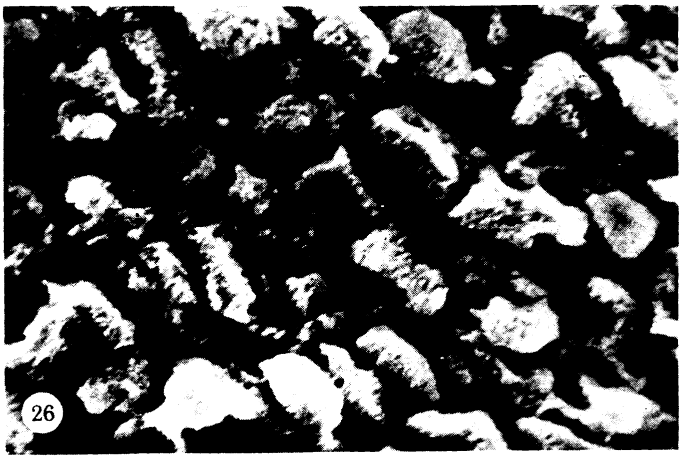
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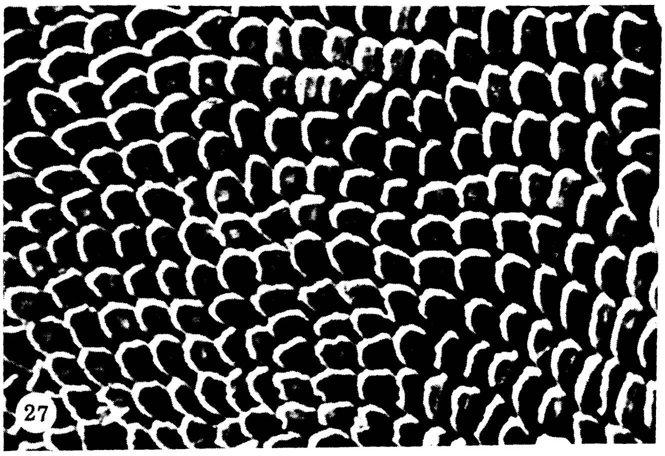
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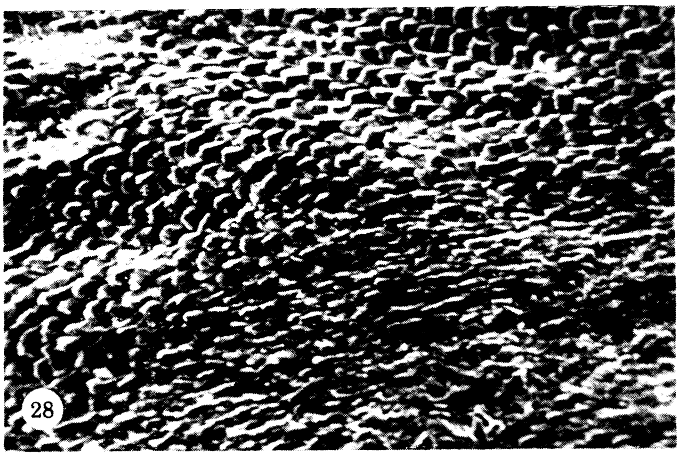
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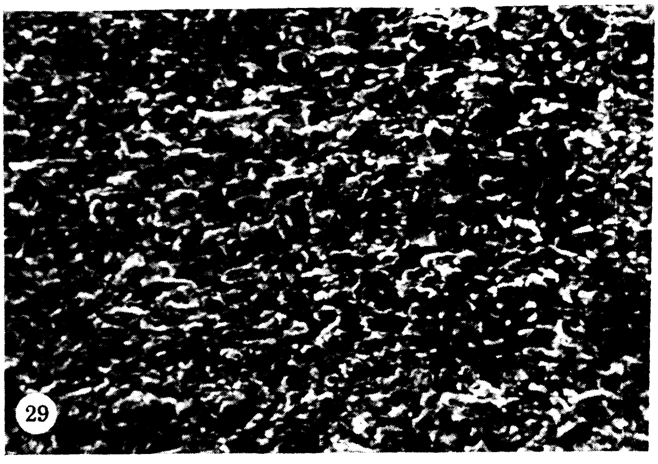
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FIGURES 22–29. For description see opposite.

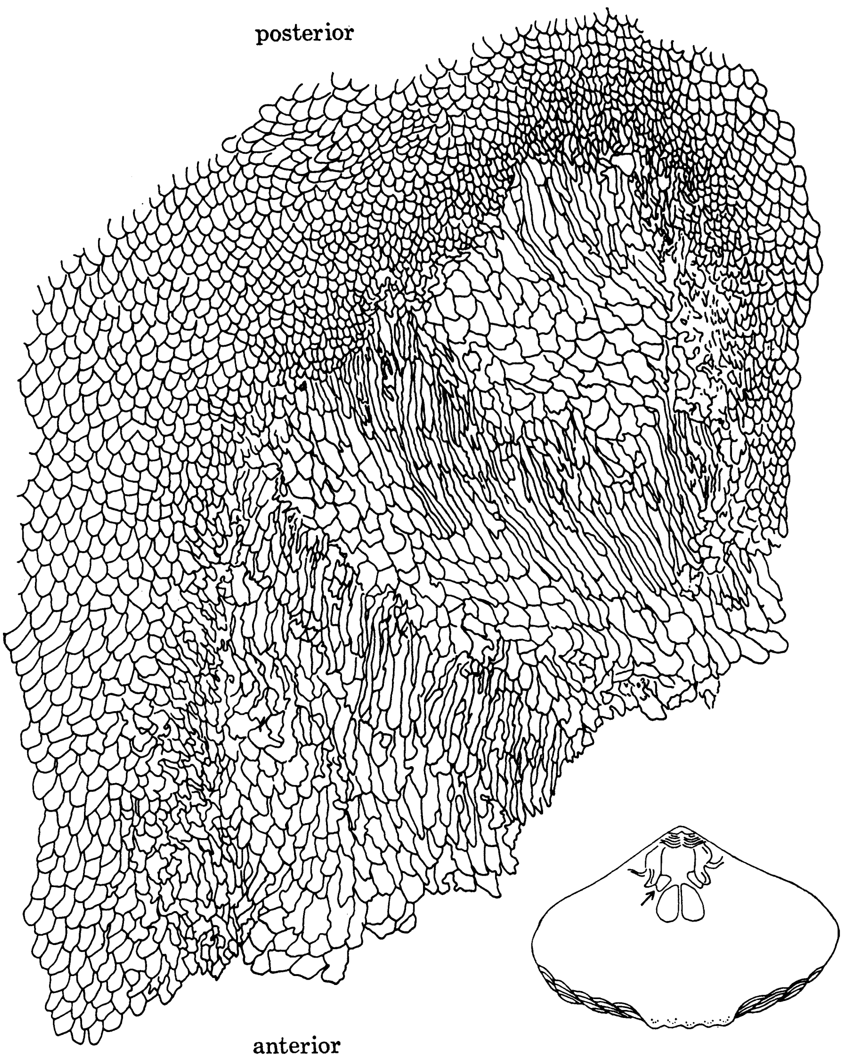

Figure 21. Skeletal fabric of a posterior adductor scar in the brachial valve of *Notosaria* (arrowed) showing several anteriorly arcuate zones of large spatulate terminal faces alternating with zones of long exposed trails which are overlapped by very small fibres crowded around the posterior margin of the scar.

Description of plate 4

Scanning electron micrographs of the shell of *Notosaria nigricans* (Sowerby).

Figure 22. Part of a dorsal adductor myotest showing the development of an additional deposit of irregular calcite accretions (magn. × 650).

Figure 23. Fibres comprising the dorsal adjustor myotest showing the relatively smooth, lobate nature of exposed parts (magn. × 1300).

Figure 24. Overlap of dorsal adjustor myotest by orthodox secondary layer fibres (magn. × 260).

Figure 25. Slot-like cardinal process showing several transverse grooves and ridges which mark successive growth stages (magn. × 120).

Figure 26. Exposed parts of fibres comprising the cardinal process (magn. × 2500).

Figures 27, 28 and 29. Views of the standard secondary shell mosaic, junction of a ventral diductor myotest (top left) and ventral adductor myotest (bottom right), and ventral adjustor myotest respectively photographed at the same magnification (all magn. × 250) to illustrate the size differential that exists between fibres secreted within and outside muscle scars.

the secretory areas of the outer epithelial cells underlying muscle bases is considerably less than that in the remainder of the outer epithelium attached to the floor of the valve.

When it is appreciated that muscle bases located in the valve floors migrate anteriorly at a more rapid rate than the underlying epithelium it is not surprising to find that fibres around the posterior boundaries of muscle scars are much smaller than those in other undisturbed parts of the shell.

The isotopic boundary between myotest and earlier formed secondary layer is also a surface of weakness in the shell. When a muscle is removed from the shell, myotest may break away with the soft tissue to expose a completely different surface. This surface consists of a number of arcuate ridges placed one behind the other which are similar in size and roughly parallel to the one occurring around the anterior edge of the muscle field. The anterior part of each ridge exhibits a fairly regular mosaic while long exposed trails of fibres are exposed on the posterior side (figure 32, plate 5). Judging from the regularity in spacing of the ridges and their similarity of structure it would appear that the muscle bases do not migrate at a uniform rate. Since the skeletal fabric is least affected within the comparatively narrow arcuate zones made up of regular mosaic, it is likely that such zones register momentary pauses in the advance of the overlying muscle base. Further evidence of a non-uniform rate of migration of muscle bases is forthcoming from an examination of that part of the secondary shell succession located just posterior to a muscle scar. It has already been demonstrated that the cells responsible for secreting those fibres posterior to the muscle scar are likely to have been involved in secreting myotest at an earlier stage of growth. At certain levels, trails of fibres exposed by splitting the shell behind the myotest are cut across and reveal several breaks in the succession. Along the plane of each break, a mosaic of secondary fibres similar to that seen on the inside surface of the valve is preserved (figure 36; figure 33, plate 5). In radial section, the myotest can be traced running backwards towards the umbo where it is overlapped by normal secondary layer fibres secreted in that part of the shell lying posterior to the muscle field. In such sections, the planes registering interruptions in secondary shell growth dip posteriorly inwards from the isotopic boundary between myotest and that part of the secondary shell succession deposited behind the myotest (figure 37). Close to the myotest a clear break in deposition occurs; more posteriorly, the trails of fibres intersected by each plane are not truncated but sharply flexed (figure 34, plate 5). Although such planes terminate at the inner isotopic boundary of the myotest, their structure closely resembles that of the regression planes described by Brunton (1969, p. 193) for a number of Recent Rhynchonellida and Terebratulida. Regression planes are formed when the outer mantle lobe withdraws from the valve margins, causing a break in both the primary and secondary shell succession. With retraction of the mantle, parts of the earlier formed secondary shell mosaic are exposed while fibres located posterior to, but in line with the regression plane become distorted by the deposition of calcite in a posterior direction. After each mantle regression there is a subsequent transgression, but primary shell is deposited over the greater part of the exposed area before the regrowth of secondary shell, so that the old internal surface of the valve is preserved as a false mosaic. Similar internal mosaics without the intervening wedge of primary shell material occur on the internal surfaces of the inclined planes interrupting the secondary shell succession behind the muscle scars. At the posterior end of each plane, where calcite deposition remained continuous, all flexures are directed posteriorly or postero-laterally. It is evident, therefore, that the outer epithelial cells situated directly behind the myotest became detached periodically from the shell surface, accompanied by a slight backward shift.

The occurrence of breaks in deposition behind a muscle scar serve to indicate how growth of the shell and migration of the muscle bases are so intimately related. As long as shell growth continues by the proliferation of new calcite-depositing cells around the valve margins, migration of the advancing muscle base continues smoothly (figure 37*a*). In this way a delicate balance is maintained between the rates of growth of the shell and musculature. If a regression of the mantle occurs, the balance is upset and anterior migration of the muscle base comes to a halt. However, although the cells underlying the muscle base are temporarily restricted in their growth, the outer epithelial cells posterior to the muscle base still continue to follow their former course. As a result, there is a pile-up of cells at the posterior margins of the muscle scars with the formation of an epithelial 'blister' (figure 37*b*). As soon as conditions are favourable enough for growth to recommence at the valve margins, the muscle bases start to migrate once more across the outer epithelium. In this way, an additional buried surface, or 'false' mosaic, is preserved within that part of the shell succession where the epithelium becomes detached behind the muscle base as well as around the shell edge (figure 37*c*).

In a number of specimens of *Notosaria* examined, it was found that the shell fabric characteristic of a muscle attachment area is not present. Instead, the surface of a scar is built up of a series of anteriorly arcuate ridges (figure 35, plate 5; also figure 21) identical to that found in other specimens where myotest was intentionally removed along with the adherent muscle tissue. Around the posterior margins of such muscle scars, the exposed parts of successive ridges are overstepped by orthodoxly stacked fibres exhibiting typically small, but well developed terminal faces. Since the mosaic of the secondary shell deposit laid down behind the posterior margin of the muscle scar may overstep either the large, spatulate terminal faces on the anterior part of a ridge or the elongate trails making up the posterior limb (or both at the same time), there must occur a clear depositional break between the two parts of the succession. As previously mentioned, the shell fabric within areas of muscle attachment, where no myotest is present, is identical to that found in specimens where the myotest has been stripped away. Therefore it is likely that in the former case the deposition of myotest has been completely inhibited. In decalcified sections of young *Notosaria* prepared for histological examination, an organic sheet up to 60 nm thick was found sandwiched between the outer epithelium and underlying muscle scar (figure 4, plate 1). This sheet is in continuity with the thin, triple-layered membranes ensheathing the calcite fibres of the underlying part of the shell as well as being firmly attached to the outer epithelium. Such sheets are probably deposited instead of myotest; although once the epithelial cells lie posterior to the migrating muscle base they revert to their more normal depositional rôles by secreting on the intervening organic layer the first-formed calcite seeds of a standard secondary shell mosaic. It is not clear why myotest should be present in some specimens of *Notosaria* and absent in others. However it is noticeable that younger specimens tend not to have a proper myotest developed.

Muscle scar formation in other recent brachiopods

The development of a dense meshwork of tonofibrils within outer epithelial cells underlying muscle bases has been recognized in a variety of living brachiopods. Cuboidal epithelium packed with tonofibrils is well developed in *Terebratulina caputserpentis* (Linné) (Williams & Rowell 1965, p. H110) and is confirmed by the author in *Waltonia inconspicua* (Sowerby), *Neothyris lenticularis* (Deshayes) and *Pumilis antiquatus* Atkins. Indeed since epithelium of a

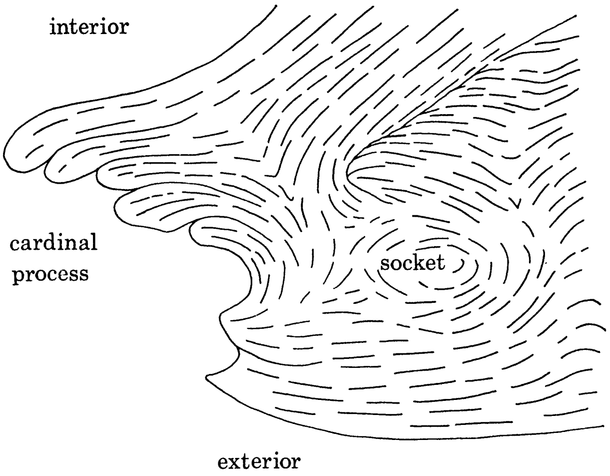

Figure 30. Stylized longitudinal section through the cardinal process of *Notosaria* showing the general overlap to earlier formed parts of the shell succession.

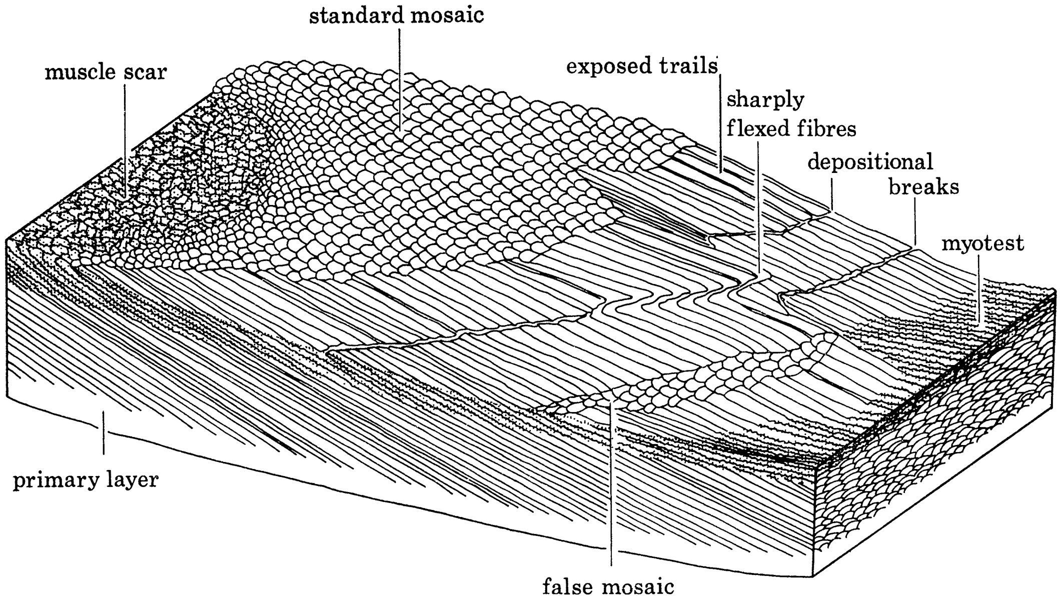

Figure 36. Stylized block diagram of part of a brachial valve of *Notosaria* that has been split posterior to a muscle scar, showing flexures and depositional breaks within the secondary layer.

Description of plate 5

Scanning electron micrographs of the shell of *Notosaria nigricans* (Sowerby).

Figure 31. Posterior margin of an anterior adductor muscle scar showing the abrupt change from myotest to small but well formed secondary layer fibres (magn. × 500).

Figure 32. View within a ventral adjustor scar showing where myotest has been partially stripped off to expose a submerged ridge, composed of large spatulate terminal faces, which is flanked posteriorly by long exposed trails (magn. × 260).

Figure 33. Detailed view of a break in the secondary shell succession exposed by splitting the shell behind a muscle scar (magn. × 1400).

Figure 34. View of part of a pedicle valve which has been split behind a ventral muscle scar to expose long trails of fibres which are sharply flexed (magn. × 280).

Figure 35. Montage of anterior and posterior adductor muscle scars (brachial valve) showing the development of several anteriorly arcuate ridges composed of large spatulate terminal faces which are separated from one another by zones of long, narrow exposed trails (magn. × 64).


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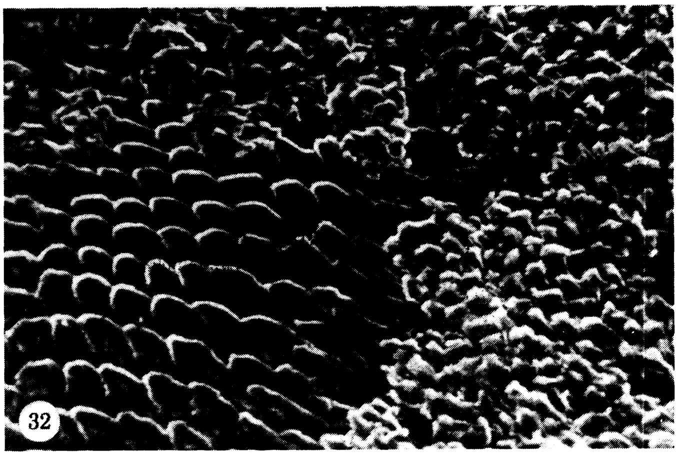
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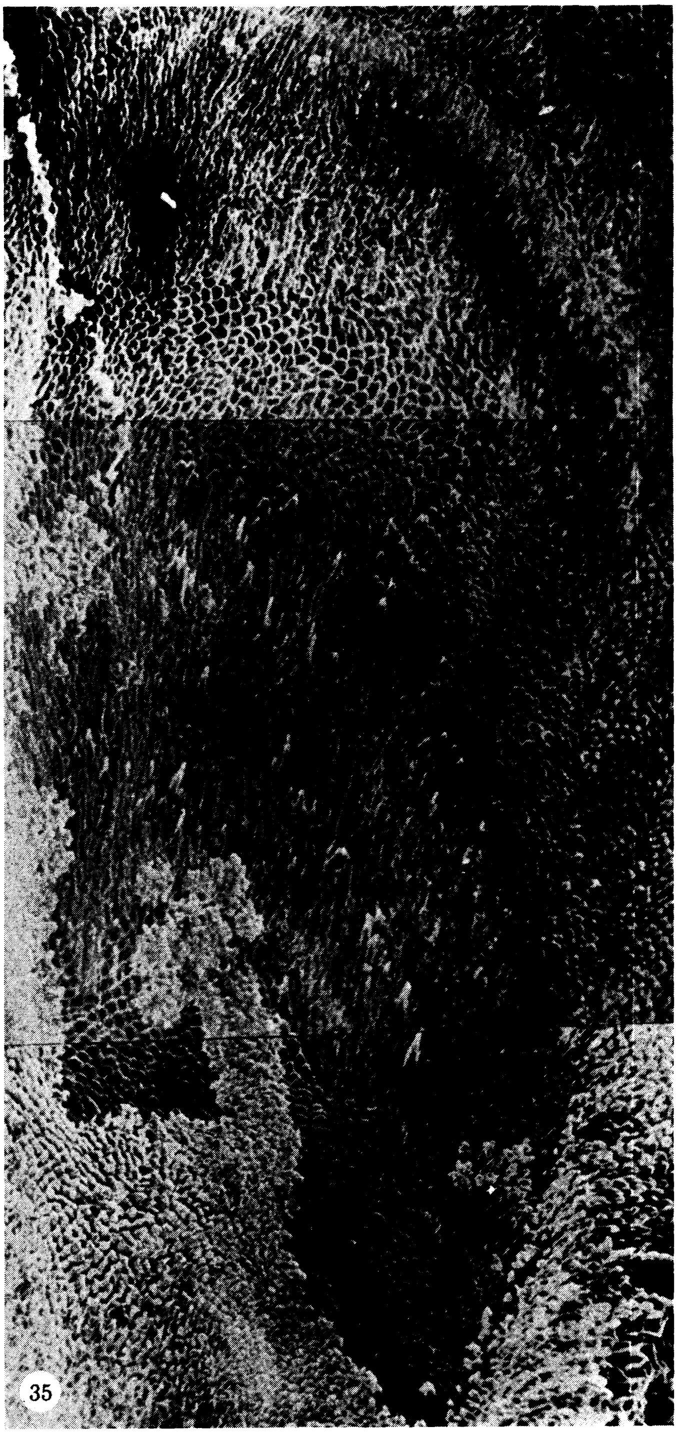
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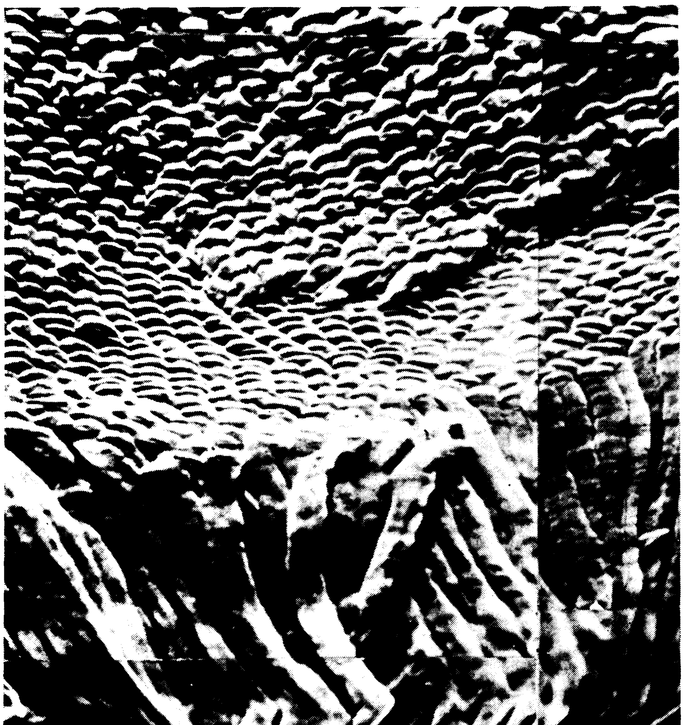
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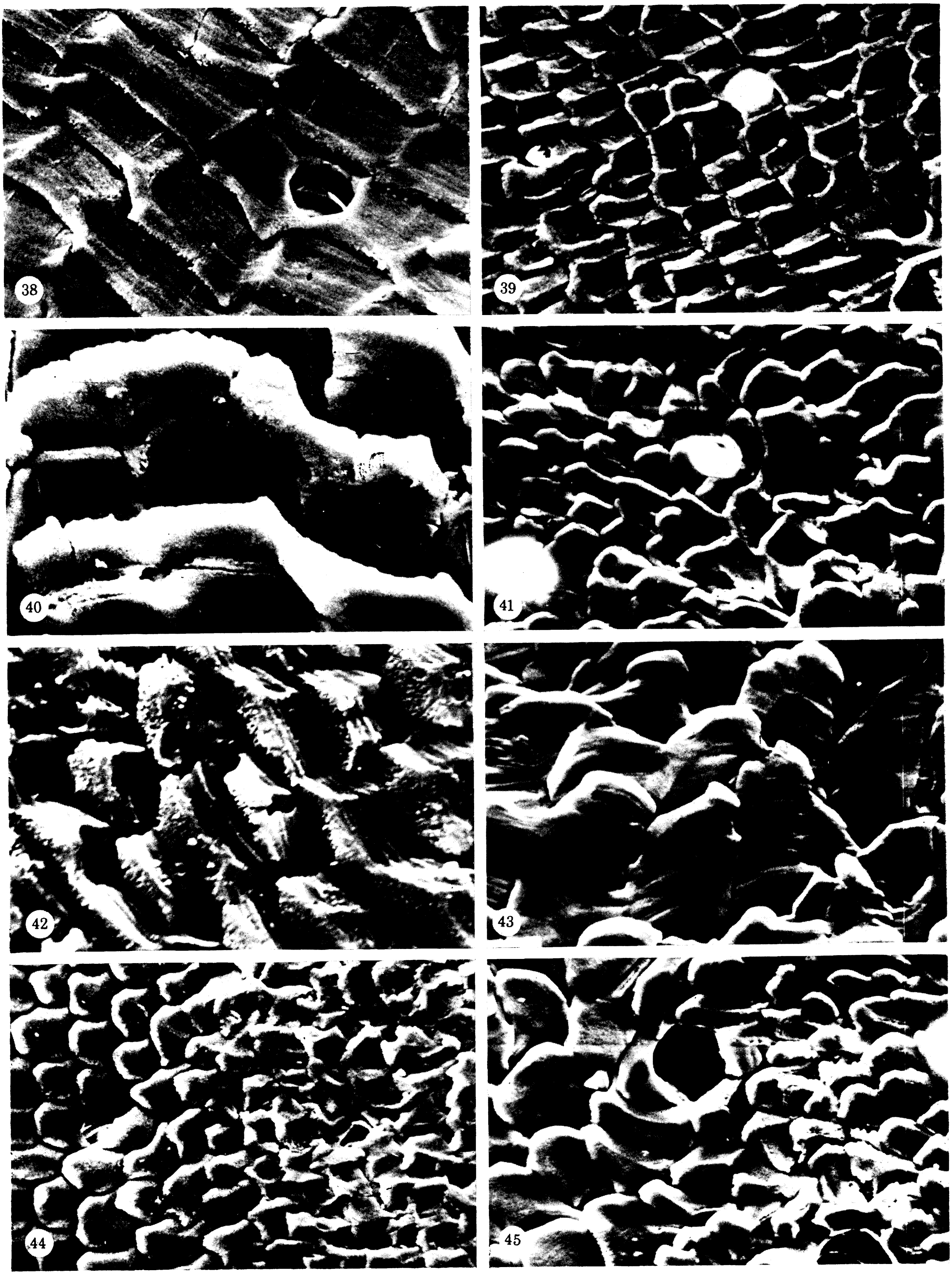
FIGURES 31–35. For description see opposite.



Figures 38–45. For description see opposite.

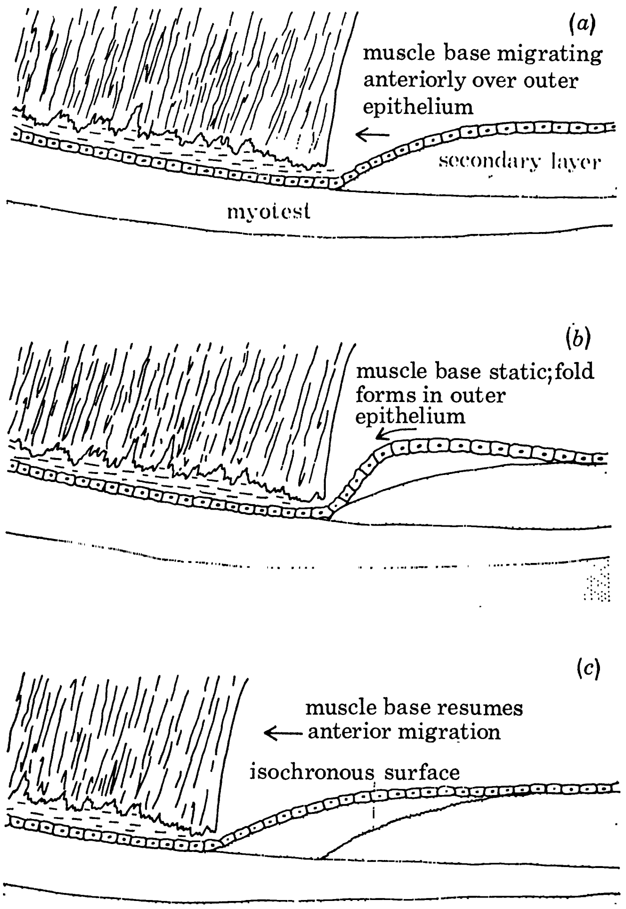


FIGURE 37. Stylized longitudinal sections through a muscle base, outer epithelium, and shell of *Notosaria* showing the development of a depositional break posterior to a muscle scar.

DESCRIPTION OF PLATE 6

Scanning electron micrographs of various Recent brachiopods.

FIGURE 38. Exposed parts of fibres comprising the dorsal adductor myotest of *Macandrevia cranium* (Müller) (magn. × 2600).

FIGURE 39. Exposed parts of fibres comprising the dorsal adductor myotest of *Terebratalia transversa* (Sowerby) (magn. × 650).

FIGURE 40. More detailed view of part of a dorsal adductor myotest of *Terebratalia transversa* (Sowerby) showing welding together of adjacent parts of fibres (magn. × 2700).

FIGURE 41. Exposed parts of fibres comprising the dorsal adductor myotest of *Waltonia inconspicua* (Sowerby) (magn. × 600).

FIGURE 42. Exposed parts of fibres comprising an anterior adductor scar of *Hemithiris psittacea* (Gmelin) (magn. × 2300).

FIGURE 43. Exposed parts of fibres comprising the dorsal adductor myotest of *Terebratulina retusa* (Linné) (magn. × 1400).

FIGURE 44. Anterior margin of a dorsal adductor scar of *Terebratalia transversa* (Sowerby) showing the breakdown of the standard secondary shell mosaic. A number of bilobed terminal faces are recognizable (magn. × 700).

FIGURE 45. Anterior margin of a dorsal adductor scar of *Waltonia inconspicua* (Sowerby) showing the breakdown of the standard secondary shell mosaic. Several of the terminal faces are bilobed (magn. × 600).

similar nature has been described in such diverse forms as *Crania anomala* (Müller) (Williams & Wright 1970, p. 28) and *Thecidellina barretti* (Davidson) (Williams 1973, p. 455) there seems little doubt that epithelia packed with tonofibrils are associated with the muscle attachment areas of most, if not all, brachiopods.

Muscle scar formation within the dominantly primary shell succession of Recent and fossil thecideidines has already been described by Williams (1973) as have the effects of muscle emplacement on the tertiary shell succession of certain living and fossil Terebratulidae (MacKinnon & Williams 1974). It remains therefore to assess the variation of ultrastructural modifications in the standard secondary shell succession affecting other Recent articulate brachiopods. Species included in this present survey were *Terebratalia transversa* (Sowerby), *Waltonia inconspicua* (Sowerby), *Macandrevia cranium* (Müller), *Terebratulina retusa* (Linné) and *Hemithiris psittacea* (Gmelin). Within each species, modifications in the secondary shell mosaic pattern varied from one muscle field to another, but the shell structure of corresponding muscle fields in unrelated genera was often found to be similar. This is not altogether surprising since the corresponding muscles in each specimen are bound to perform similar functions.

(*a*) *Dorsal adductor muscle scars*

Although the general shape and clarity of the dorsal adductor impressions varies from one genus to another, the nature of the ultrastructural modifications affecting the skeletal fabric are remarkably uniform. In *Macandrevia*, the exposed parts of fibres comprising the dorsal adductor myotest are rectangular in outline and are, on average, about 12 μm wide by 7 μm in length (figure 38, plate 6). Over the greater part of the muscle field, the lateral edges of most adjacent fibres are fused together so that the succession becomes, in reality, a series of overlapping calcareous laminae which are separated from one another by thin triple-layered protein membranes. In *Terebratalia*, the lateral edges of most adjacent dorsal adductor myotest fibres are also welded together, but their leading edges are not so evenly truncated as those of *Macandrevia*, so that the outlines of exposed parts of fibres are more often trapezoidal or even scalenohedral (figure 39, plate 6). Furthermore, as the stacking of fibres is not quite as regular as in *Macandrevia*, the lateral edge of one fibre (being displaced out of line with its lateral neighbours) may become welded to a part of one of the fibres belonging to a 'lamina' in the row immediately behind (figure 40, plate 6). In *Waltonia*, the fusion of adjacent parts of fibres is fairly common, but as the fibres are much more irregularly stacked a laminar shell fabric is not developed to any great extent (figure 41, plate 6). In addition the leading edges of most fibres are not sharply truncated as in *Macandrevia* and *Terebratalia*, but usually lobate. In *Hemithiris*, the anterior adductor scar possesses a shell fabric (figure 42, plate 6) similar to that found in *Terebratalia*, but the posterior myotest is built up of small, irregularly sutured fibres, normally longer than wide, which possess ragged edges (see figure 47, plate 7). It is interesting to record that although differences exist between the skeletal fabric of the anterior and posterior adductor scars of *Notosaria* and *Hemithiris*, no such variation has been recognized within the corresponding areas of muscle attachment in the Terebratulida examined. The dorsal adductor myotest of *Terebratulina* is composed of narrow sinuous fibres with relatively smooth outlines (figure 43, plate 6). Although adjacent fibres may be joined together along part of their lateral margins, for the most part, the surface of the myotest is built up of irregularly stacked fibres displaying a fine depositional banding. In fact, the exposed parts of fibres belonging to every myotest examined exhibit some form of depositional banding. Since these transverse striations extend in most cases to within 2 μm of the leading edge of each fibre, it must be concluded that the growing (terminal) face of the fibre on to which calcite is being actively deposited, must occupy only a narrow zone, less than 2 μm wide, at the anterior edge of the fibre while an organic sheet is deposited across the remainder to provide a convenient seeding sheet for the overlapping fibre in the row behind.

As in *Notosaria*, the skeletal fabric around the anterior margins of the muscle scars shows the first stages of modification in the standard secondary shell mosaic. For example, in *Terebratalia* and *Waltonia*, fibres with smooth rounded terminal faces at the anterior margin of the adductor scar are succeeded by smaller, more densely packed fibres whose exposed parts adopt the shape and stacking typical of that described above. As well as reflecting a major physiological change in the outer epithelium, the anterior margin of the scar also marks out a line of sudden cell division, for fibres seen undergoing transition from the one shell fabric to the other are frequently bilobed (figures 44 and 45, plate 6). Around the posterior margins of the dorsal adductor scars, the transition from myotest to standard mosaic is abrupt in *Hemithiris*, as in *Notosaria*, but more gradual in the Terebratulida examined. In *Hemithiris*, the exposed parts of fibres comprising the first few rows behind the myotest are small (about 7 μm wide) and irregular in outline, but further behind the terminal faces once more become smooth and rounded (figure 46, plate 7). The fibres located in front of the posterior margin of the dorsal adductor myotest of *Macandrevia* are neatly stacked behind one another in successive rows with fused lateral edges. Traced further posteriorly across the border of the muscle scar, adjacent fibres cease to be joined together and the leading edges of exposed parts instead of being truncated, revert to exhibiting smooth rounded profiles (figure 47, plate 7).

(*b*) *The cardinal process*

In *Terebratalia*, *Waltonia* and *Terebratulina*, the cardinal process is inserted upon a raised, transverse platform situated at the centre of the dorsal umbonal region. Although ultrastructurally alike, the general topography of the surface of each process is quite distinct. In *Terebratalia*, the surface comprises a series of evenly spaced, sinuous, longitudinal grooves and ridges (figures 48 and 49, plate 7). The ridges, each about 50 μm wide, emerge from the posterior shell edge and terminate anteriorly as prominent buttresses which rise steeply from the valve floor (figure 50, plate 7). Groups of fibres also swell into posteriorly inclined buttresses of similar size along the anterior edge of the cardinal process of *Terebratulina*, but the buttresses do not extend back towards the posterior shell edge as unbroken ridges (figure 51, plate 7). In contrast to the relatively regular skeletal framework displayed in *Terebratalia*, the greater part of the surface of *Terebratulina* consists of a large number of small, irregular, fibrous mounds, on average 30–40 μm wide (figure 52, plate 7). In *Waltonia* also, the shell surface is moulded into a number of small mounds, but the front edge of the cardinal process is continuous and not fashioned into separate buttresses (figure 53, plate 7; figure 54, plate 8). The ridges in *Terebratalia* and the fibrous mounds in *Terebratulina* and *Waltonia* possess a fine structure which is remarkably alike. Every ridge and mound is built up of clusters of long, narrow, fibrous stalks usually no more than 3–4 μm wide. The growth pattern of such protuberances is obscure, for the elongate exposed trails are plastered together in such a way that they do not overlap one another in any sort of orderly fashion. Indeed, the exposed parts of fibres bear no recognizable terminal faces, but many fibres exhibit minor lobes and offshoots which tends to suggest that the generation of most additional outer epithelial cells involved in secreting the intricate skeletal outgrowths is brought about by subdivision within the pre-existing epithelium.

No raised cardinal platforms exist in either *Macandrevia* or *Hemithiris*. In *Macandrevia*, the dorsal ends of the diductor muscles are attached to a small, triangular hollow situated at the umbo of the brachial valve. At low magnifications, the surface of the hollow appears roughened and is traversed by fine, impersistent growth lines which run parallel to the gently convex anterior edge of the attachment area (figure 55, plate 8). When viewed under higher magnification, the surface is found to consist of an anastomosing network of very narrow calcite ridges which combine overall to form a rough honeycomb pattern (figure 55, plate 8). The dimensions of each 'cell' (about 4–5 µm wide) of the honeycomb are such that it is reasonable to suppose there is a one-to-one correspondence between the honeycomb 'cells' and the outer epithelial cells. However the shell structure of this particular muscle impression is so unlike that of the normal secondary shell succession or even of other muscle attachment areas that its growth is not readily explained in terms of modification of any standard secretory régime. Around the anterior margins of the scar, the terminal faces of the standard secondary shell mosaic lose their characteristic spatulate shape and degenerate into irregularly lobate pads of calcite with exposed trails which are deeply dissected by fine pits and grooves. Traced posteriorly within the attachment area, the terminal faces become smaller and more irregular in outline and adjacent parts of fibres become welded together so that a branching network of irregular calcite ridges is formed. Further inside the muscle field, the irregular arrangement of branching ridges becomes more uniform and takes on the aspect of the more typical 'honeycomb' skeletal fabric.

In *Hemithiris*, the cardinal process is not conspicuous. It consists of a small triangular area at the umbo and is divided by a cleft in the hinge plate which extends to the apex. The surface of the cardinal process is rough and traversed by wavy grooves and ridges which follow the contours of its anterior margin (figure 57, plate 8). The ridges and grooves are similar to those described for *Notosaria* and are considered to mark successive stages of growth in the advance of the anterior border of the attachment area. As with *Macandrevia*, the mode of deposition of the shell within this muscle field is difficult to decipher. The surface is composed of irregular accretions of calcite which bear no resemblance to the standard secondary shell mosaic (figure 58, plate 8).

DESCRIPTION OF PLATE 7

Scanning electron micrographs of various Recent brachiopods.

FIGURE 46. Posterior margin of a posterior adductor muscle scar of *Hemithiris psittacea* (Gmelin) (brachial valve) showing the abrupt regrowth of standard secondary shell mosaic (magn. × 700).

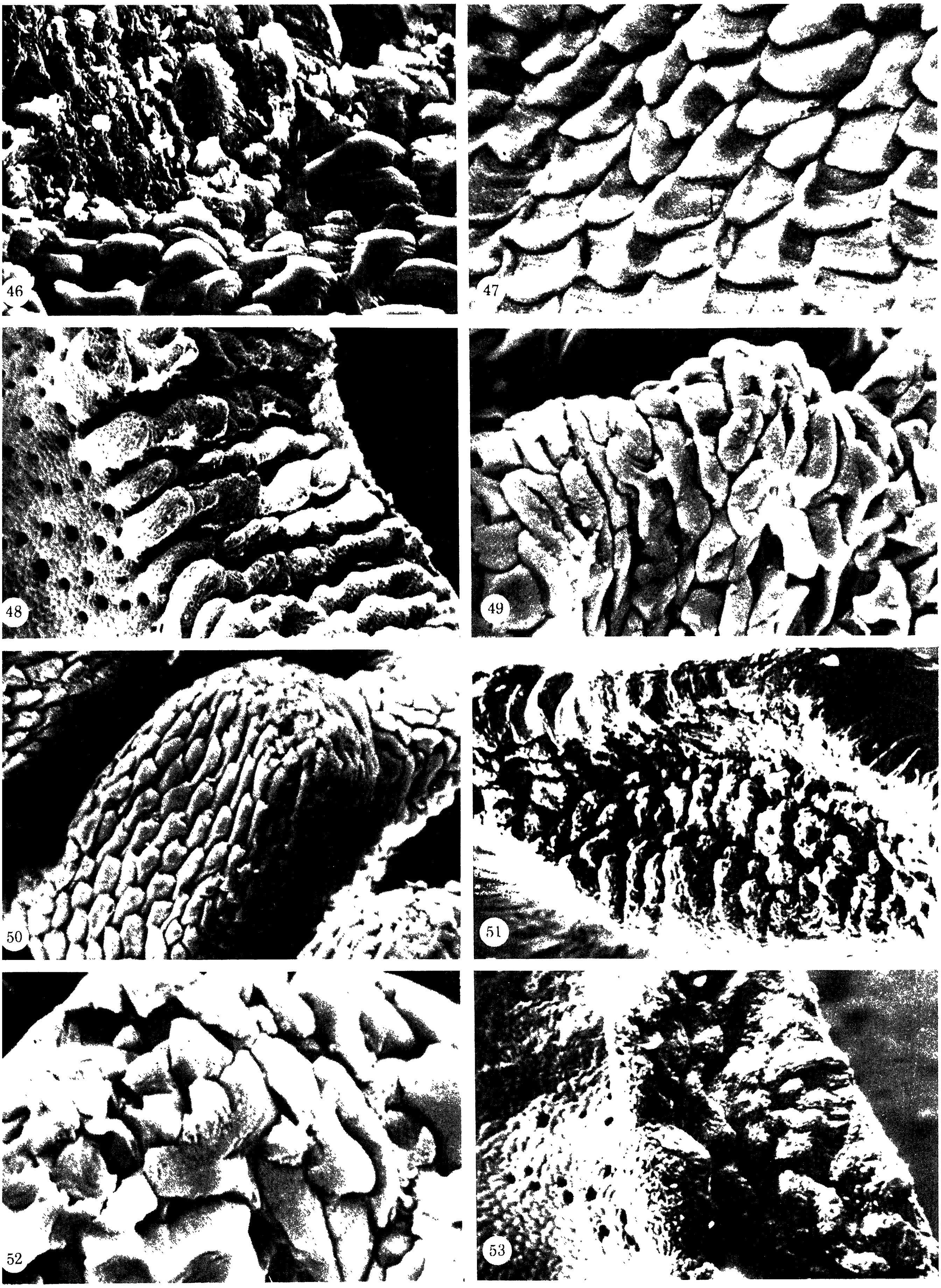
FIGURE 47. Posterior margin of a dorsal adductor muscle scar of *Macandrevia cranium* (Müller) showing the regrowth of the standard secondary shell mosaic (magn. × 1300).

FIGURES 48 AND 49. General and detailed views respectively of the cardinal process of *Terebratalia transversa* (Sowerby) showing the alignment of ridges and the unorthodox shape and stacking of fibres (magns × 135 and × 1350 respectively).

FIGURE 50. Secondary layer fibres comprising the anterior extremity of a longitudinal ridge within the cardinal process of *Terebratalia transversa* (Sowerby) which terminates anteriorly as a steep buttress (magn. × 670).

FIGURES 51 AND 52. General and detailed views respectively of the cardinal process of *Terebratulina retusa*(Linné) showing the irregular surface topography and the unorthodox shape and stacking of fibres (magns × 145 and × 2600 respectively).

FIGURE 53. General topography of part of the cardinal process of *Waltonia inconspicua* (Sowerby) (magn. × 130).



Figures 46–53. For description see opposite.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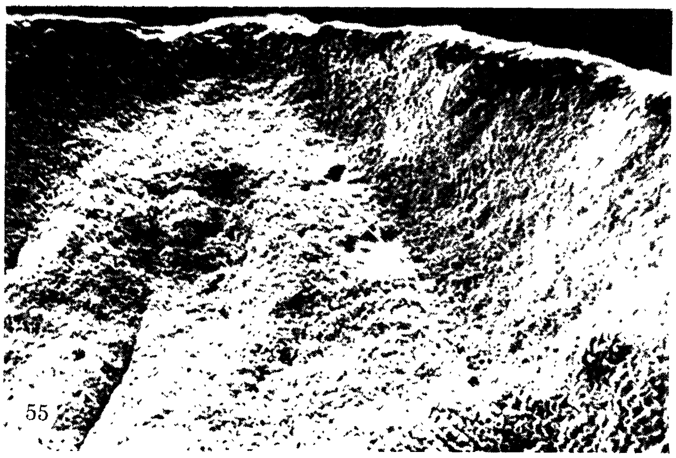
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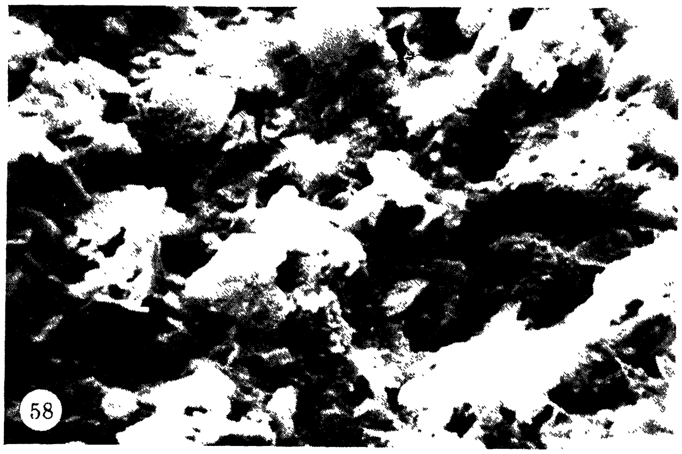
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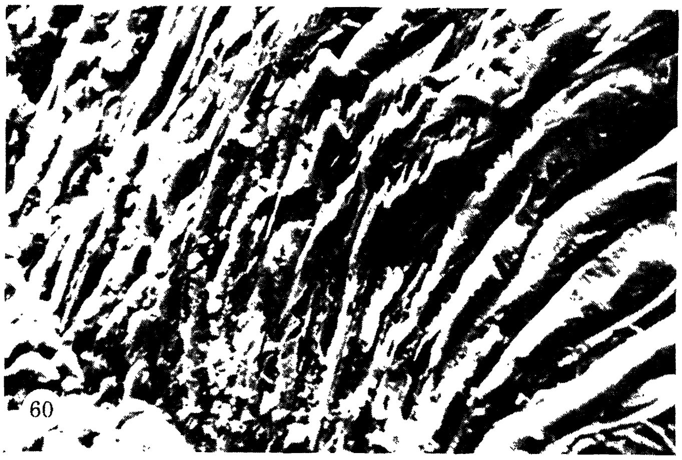
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FIGURES 54–61. For description see opposite.

(*c*) *Dorsal adjustor scars*

In most articulate Brachiopoda, including *Macandrevia*, *Terebratalia*, *Terebratulina* and *Hemithiris*, the dorsal pedicle muscles are attached to the shell along the length of each inner socket ridge. In other genera such as *Waltonia*, the dorsal adjustor scars are impressed on an elevated process occupying the space between the two inner socket ridges. From the junctions of the socket ridges and crural bases two simple hinge plates descend gently towards the floor of the valve and meet one another in an obtuse angle on the top of a raised median septum. Despite this variation in the location of the dorsal adjustor scars, modifications in the secondary shell fabric conform to a general pattern. Like *Notosaria*, fibres comprising the dorsal adjustor myotests of the other general examined are relatively narrow but long and sinuous. In *Terebratalia*, irregularly lobate exposed parts of fibres are not normally more than 10 μm wide or 50 μm in length (figure 59, plate 8). However, in *Hemithiris*, the adjustor myotest is built up of fibres displaying terminal stalks 100 μm or more in length but usually less than 7 μm wide (figure 60, plate 8). Elongate, sinuous fibres which frequently bifurcate are also typical of the dorsal adjustor myotests of *Terebratulina* (figure 61, plate 8) and *Waltonia* (figure 62, plate 9).

(*d*) *The ventral muscle scars*

Unlike the muscle scars of the brachial valves, those of the pedicle valves belonging to the genera examined do not display such variety of modification in skeletal fabric. This may in part be due to the fact that the areas of muscle attachment in the pedicle valve are closely grouped together to form one large impression on the valve floor while those of the brachial valve are considerably more widespread. The nature of the breakdown of the standard secondary shell mosaic around the anterior margins of the ventral muscle field is similar in all genera examined and varies little from that observed in most dorsal scars. The transition is well seen at the anterior edge of the ventral diductor muscle scar of *Waltonia* where the regular mosaic pattern, built up of smooth, spatulate terminal faces on average 25 μm wide, is suddenly succeeded by small, irregularly lobate, closely stacked fibres which are, on average, only 7 μm wide (figure 63, plate 9). If a shell is split behind the muscle scar, so that earlier formed parts of the shell succession are exposed, the sudden transition from smooth, regularly stacked trails to smaller, more numerous, gnarled trails is equally striking (figure 64, plate 9). This sudden increase in fibre density by a factor of more than three is significant and reflects a similar

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DESCRIPTION OF PLATE 8

Scanning electron micrographs of various Recent brachiopods.

FIGURE 54. Detailed view of the surface fabric of the cardinal process of *Waltonia inconspicua* (Sowerby) (magn. × 1280).

FIGURES 55 AND 56. General and detailed views respectively of the cardinal process of *Macandrevia cranium* (Müller) showing the nature of the surface topography (magns × 120 and × 2400 respectively).

FIGURES 57 AND 58. General and detailed views respectively of the cardinal process of *Hemithiris psittacea* (Gmelin) showing the nature of the surface topography (magns × 130 and × 2600 respectively).

FIGURE 59. Skeletal fabric of a dorsal adjustor scar in *Terebratalia transversa* (Sowerby) (magn. × 1500).

FIGURE 60. Part of a dorsal adjustor scar in *Hemithiris psittacea* (Gmelin) showing long exposed parts of fibres (magn. × 650).

FIGURE 61. Part of a dorsal adjustor scar in *Terebratulina retusa* (Linné) showing long exposed trails which periodically bifurcate (magn. × 750).

numerical increase in the corresponding outer epithelial cells. Since the first few rows are seen to arise as offshoots from the orthodoxly stacked fibres just incorporated within the muscle scar, it is evident that vigorous cell division is taking place within the outer epithelium around the periphery of the muscle base. An examination of the morphology of exposed parts comprising the ventral diductor muscle scars of the genera examined reveals that, in general, the fibres are normally elongate and narrow (usually not more than 15 µm long by 7 µm wide) (figures 65, 66 and 67, plate 9), but parts of the myotest of *Terebratulina* display abnormally large trails up to 120 µm long by 25 µm wide (figure 68, plate 9). This type of shell fabric, peculiar to *Terebratulina*, is similar to that found within the myotest of some specimens of *Notosaria* where deposition of a thin organic sheet inhibited the formation of a more typical muscle scar shell fabric. Although no such layer was found in any specimens of *Terebratulina* (all organic material having been chemically removed), it is considered that patches of a similar deposit may have covered those areas where the larger fibres are found.

In *Waltonia*, the ventral adjustor myotest fibres are indistinguishable from those of the diductor myotest (figure 69, plate 9) but in the other genera inspected, the exposed parts of fibres, though of similar dimensions, show a greater tendency to occur with lateral edges fused together (figures 70 and 71, plate 10). The welding together of adjacent margins of contemporary fibres reflects a change in the secretory behaviour of the overlying cells. The existence of a prominent transverse depositional banding over the greater part of each exposed trail and the relegation of the terminal face to a narrow strip at the anterior extremity of each fibre serve to indicate the extent to which the zone of calcite secretion is localized on the plasmalemma of each corresponding outer epithelial cell. When the zones of two or more adjacent cells become contiguous, lateral fusion of the fibres takes place and their bounding organic membranes unite.

In most articulate brachiopods, the ventral adductor scars occupy a small heart-shaped depression situated symmetrically on either side of the median line and enclosed by the posterior parts of the ventral diductor and adjustor scars. Unlike the dorsal adductor scars where the exposed parts of adjacent fibres tend to unite with one another to form a laminar shell, the fibres

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DESCRIPTION OF PLATE 9

Scanning electron micrographs of various Recent brachiopods.

FIGURE 62. Part of a dorsal adjustor muscle scar in *Waltonia inconspicua* (Sowerby) showing narrow, elongate, sinuous exposed parts of fibres (magn. × 700).

FIGURE 63. Anterior margin of a ventral diductor muscle scar of *Waltonia inconspicua* (Sowerby) showing the breakdown of the standard secondary shell mosaic (magn. × 700).

FIGURE 64. Part of a fracture surface on a fragment of *Waltonia inconspicua* (Sowerby) showing the transition from smooth, orthodoxly stacked secondary layer fibre outlines into smaller, more numerous, gnarled trails of myotest fibres (magn. × 650).

FIGURE 65. Part of the ventral diductor myotest of *Terebratalia transversa* (Sowerby) showing the fairly regular outlines of exposed parts (magn. × 680).

FIGURE 66. Part of the ventral diductor myotest of *Macandrevia cranium* (Müller) showing fairly regular outlines of exposed parts (magn. × 650).

FIGURE 67. Part of the ventral diductor myotest of *Hemithiris psittacea* (Gmelin) showing very irregular outlines of exposed parts (magn. × 630).

FIGURE 68. Part of the ventral diductor myotest of *Terebratulina retusa* (Linné) showing long sinuous exposed trails (magn. × 260).

FIGURE 69. Exposed parts of fibres comprising part of a ventral adjustor myotest of *Waltonia inconspicua* (Sowerby) (magn. × 650).


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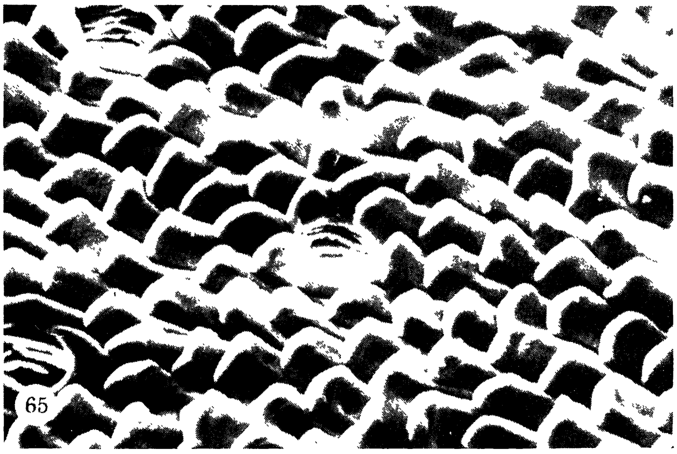
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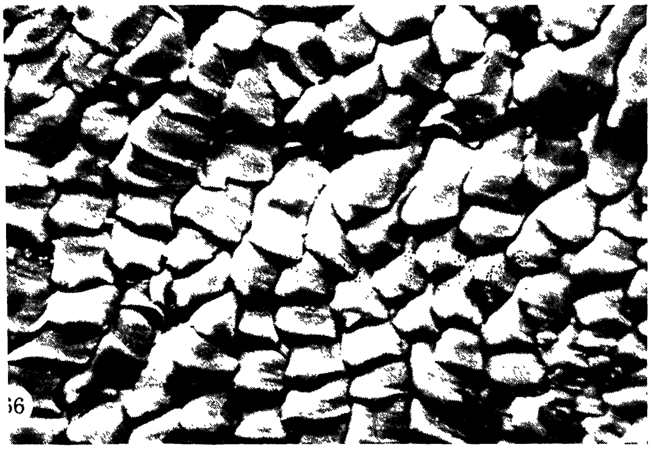
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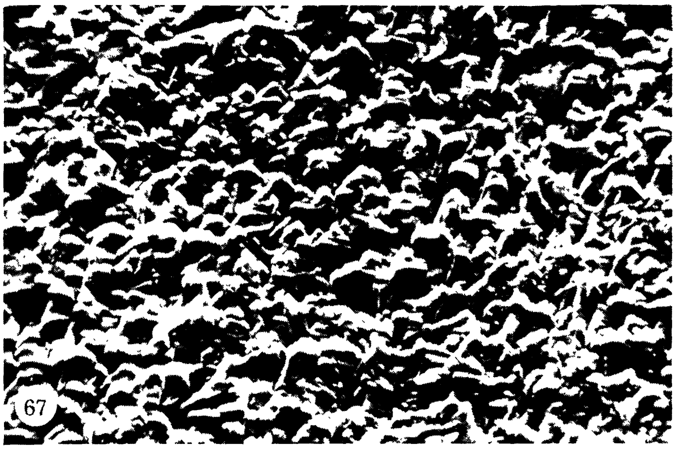
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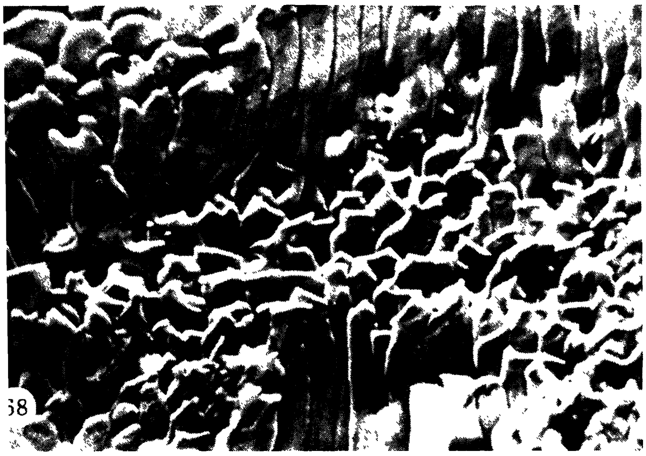
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FIGURES 62–69. For description see opposite.

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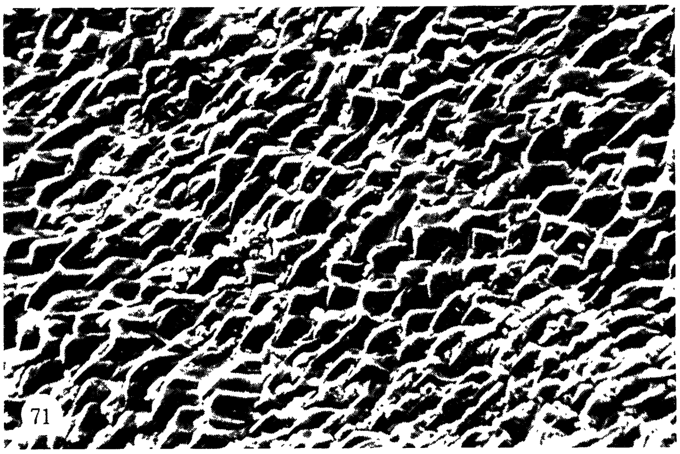

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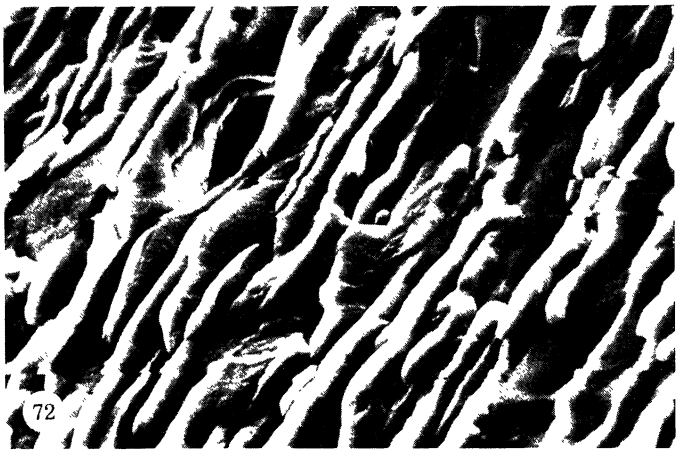

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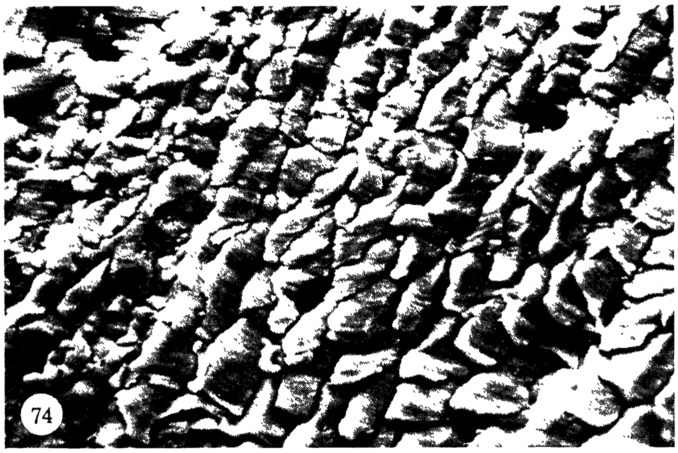

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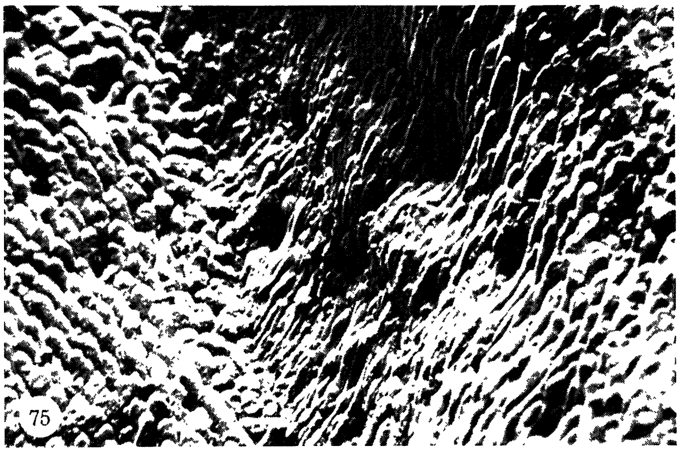

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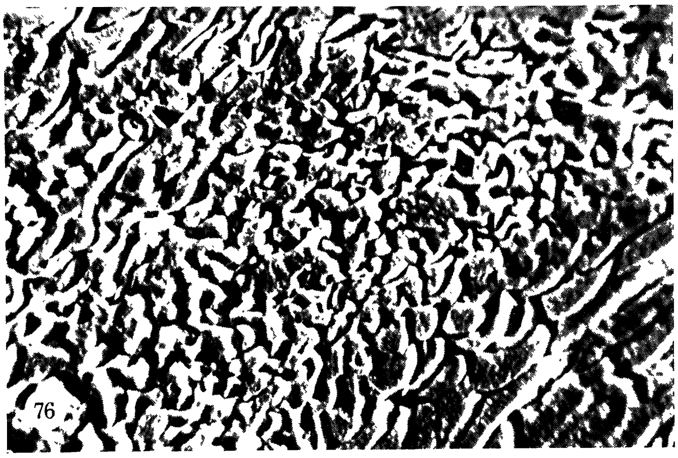

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FIGURES 70–77. For description see opposite.

comprising the ventral adductor myotests seldom occur joined together and are generally very narrow and elongate. For example, within the ventral adductor muscle scars of *Terebratalia*, *Waltonia* and *Macandrevia* the myotests are composed of fibres 30–40 μm in length but on average 6 μm in width (figures 72, 73 and 74, plate 10).

Around the posterior margins of the ventral scars, the regrowth of the standard mosaic fabric is characterized by the development of a zone of very small fibres similar to that occurring at the posterior margins of all the dorsal adductor scars. Williams (1968, pp. 16, 21) referred to these zones as 'secondary generative zones', but current research indicates that the small fibres located around the posterior boundaries of muscle scars are secreted by the same outer epithelial cells which, at an earlier stage of growth, secreted myotest. Extra outer epithelial cells do occur, but they are generated around the anterior margins of the muscle fields. Consequently, since the optimum size range of epithelial cells incorporated within a muscle base is significantly less than that outside, the first few rows of fibres secreted behind a muscle scar can be expected to have the dimensions of those fibres deposited immediately behind the primary generative zone at the mantle and shell edge.

MUSCLE SCARS OF FOSSIL BRACHIOPODS

A basic skeletal succession consisting of a thin outer primary layer and relatively thick fibrous secondary layer is characteristic of fossil brachiopods belonging to the Orders Rhynchonellida, Terebratulida, Spiriferida, Pentamerida and Orthida (excluding Triplesiacea) (Williams 1968). A tertiary prismatic layer is present in some Rhynchonellida, Terebratulida, Pentamerida and Spiriferida but has not yet been recognized in any Orthida. Because of the striking similarity of skeletal fabrics in extinct stocks to that of living Terebratulida and Rhynchonellida it has been inferred logically that the nature and secretory processes of the outer epithelium of most articulate brachiopods has changed little in the past five to six hundred million years. Apart from the neotenous reduction of the fibrous secondary layer in modern thecideidines, the only

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DESCRIPTION OF PLATE 10

Scanning electron micrographs of Recent brachiopods.

FIGURE 70. Exposed parts of the fibres comprising part of a ventral adjustor myotest of *Terebratalia transversa* (Sowerby) showing frequent fusion of lateral margins (magn. × 1300).

FIGURE 71. Exposed parts of fibres comprising part of a ventral adjustor myotest of *Hemithiris psittacea* (Gmelin) (magn. × 630).

FIGURE 72. Exposed parts of fibres comprising part of a ventral adductor myotest of *Terebratalia transversa* (Sowerby) (magn. × 1400).

FIGURE 73. Exposed parts of fibres comprising part of a ventral adductor myotest of *Waltonia inconspicua* (Sowerby) (magn. × 640).

FIGURE 74. Exposed parts of fibres comprising part of a ventral adductor myotest of *Macandrevia cranium* (Müller) (magn. × 650).

Scanning electron micrographs of *Spiriferina walcotti* (Sowerby), Lower Jurassic,
Radstock, Somerset, England.

FIGURE 75. Posteriorly inclined slope of the arcuate ridge developed around the anterior margins of a ventral muscle scar showing the breakdown in standard secondary shell mosaic (magn. × 240).

FIGURE 76. Section through the ventral median septum showing ventral adductor myotest fibres (magn. × 850).

FIGURE 77. Part of the topography of the striate cardinal process (magn. × 690).

major disparity in secretory behaviour is that shown by the Paleozoic Strophomenida (excluding Plectambonitacea) in which the secondary layer consists of a series of flat-lying blades which usually amalgamate laterally to form a succession of plates or laminae. No living brachiopod secretes a laminar shell of precisely this sort, therefore the relationship between shell and outer epithelium at the ultrastructural level in strophomenides is uncertain (Brunton 1972, p. 17).

Study of fossil material often requires additional preparation for, although adherent tissue is long since lost, micritic crusts and other sedimentary infillings often tend to obscure the skeletal fabrics on the shell surfaces. Occasionally ultrasonic cleaning will expose the original surface fabric, but where this technique proves unsatisfactory precisely oriented sections have to be prepared. Although sectioning fails to reveal the true shape and stacking of myotest fibres as seen on the internal shell surface, it does have the added advantage of enabling this particular shell fabric to be traced deep within the enclosing shell layers. It is also necessary to recognize the effects of diagenesis. Silicification is easily recognized as the original shell fabric is obliterated, but more subtle changes are liable to be overlooked especially within muscle scars where fibrous patterns are so often irregular. Myotest fabrics were therefore examined only in those fossils which showed well developed standard secondary shell mosaic patterns on internal surfaces and the orthodox stacking of secondary layer fibres in sections.

The myotest shell fabrics of a number of spiriferide genera ranging from Ordovician to Jurassic in age have already been described and illustrated in considerable detail (MacKinnon 1974). In well preserved specimens of the Jurassic *Spiriferina walcotti* (Sowerby), for example, the breakdown in standard secondary shell mosaic around the anterior borders of the ventral muscle scars (figure 75, plate 10) is reminiscent of that in Recent *Notosaria*, although the fabric within the scars is less drastically altered. Cross sections through the high blade-like median septum in the pedicle valve on which the ventral adductor muscle bases are impressed (figure 76, plate 10) reveal a zone of small gnarled, irregularly stacked myotest fibres which contrast with larger adjacent orthodoxly stacked fibres. In the brachial valve, the comb-like cardinal process of *Spiriferina* closely resembles in fine structure that of the terebratellacean *Terebratalia transversa* (Sowerby) in that it comprises a series of radially disposed, corrugated ridges, between 50 μm and 100 μm wide made up of tightly interlocking secondary layer fibres (figure 77, plate 10). In some genera, such as *Atrypa*, muscle scars are developed within the tertiary layer and produce a surface fabric (figure 78, plate 11) that is almost identical to that of the living terebratulid

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DESCRIPTION OF PLATE 11

Scanning electron micrographs of various fossil brachiopods.

FIGURE 78. Adductor myotest fabric in the pedicle valve of *Atrypa* sp. from the Devonian (Hamilton Group), New York (magn. × 1400).

FIGURES 79 AND 80. Anterior and posterior margins respectively of a dorsal adductor myotest of *Diplospirella wissmani* (Münster), Triassic (St Cassian Beds), Carbonin, Trentino, Italy (both magn. × 280).

FIGURES 81 AND 82. Standard secondary shell mosaic and dorsal adductor myotest respectively of *Resserella* sp. Silurian (Mulde Marl), Gotland (both magn. × 780).

FIGURE 83. Section of a junction between well stacked secondary layer fibres and ventral diductor myotest in *Rhynchotrema capax* Conrad, Ordovician (Richmond Group), Ohio (magn. × 780).

FIGURE 84. Section through part of a ventral diductor myotest developed within the tertiary layer of *Rensselaerina haragana* Cloud, Devonian (Haragan Formation), White Mound, Nebo, Oklahoma (magn. × 780).

FIGURE 85. Part of a dorsal adjustor muscle scar showing outlines of fibres in *Magadina* aff. *clifdenensis* Finlay, Miocene, South Canterbury, New Zealand (magn. × 920).


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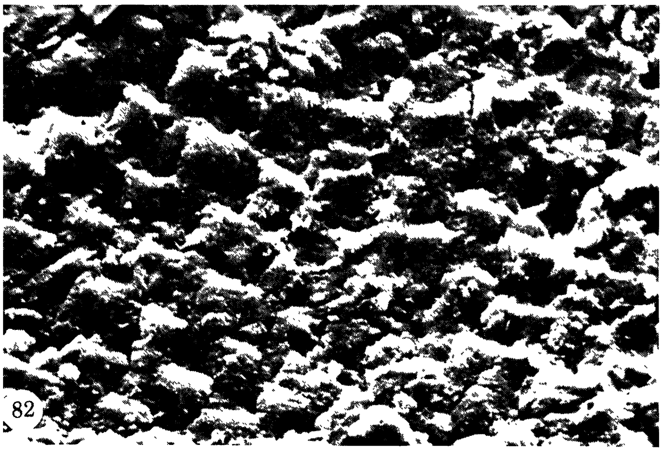
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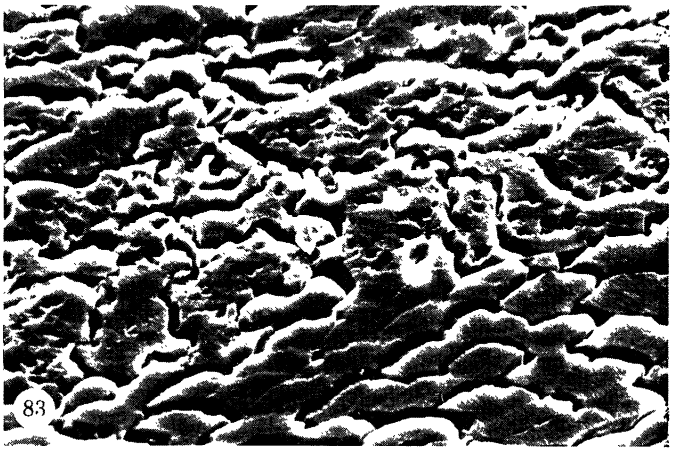
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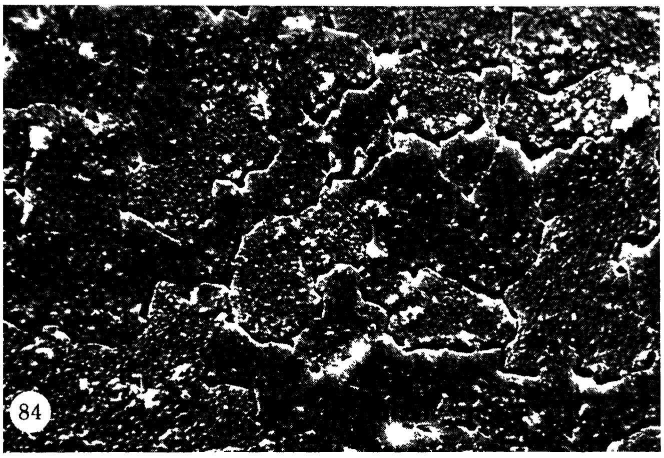
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FIGURES 78–85. For description see opposite.

Gryphus vitreus (Born) described by MacKinnon & Williams (1974). A rather different sort of fabric is that developed within the muscle scars of the Triassic athyridacean *Diplospirella wissmani* (Münster) where orthodoxly stacked secondary layer fibres located around the anterior margins of the scars are succeeded by fibres with long irregular, exposed trails (figure 79, plate 11). The exposed trails themselves are little narrower than the fibres of the standard mosaic which they succeed (about 60 μm in width), but the posterior margins of the scars are delineated by an overlapping zone of very small fibres with terminal faces averaging less than 10 μm in width (figure 80, plate 11). This type of muscle scar fabric with the associated cluster of small fibres around the posterior margin is very similar to that recognized in young *Notosaria* where a relatively thick organic layer intervenes between outer epithelium and shell.

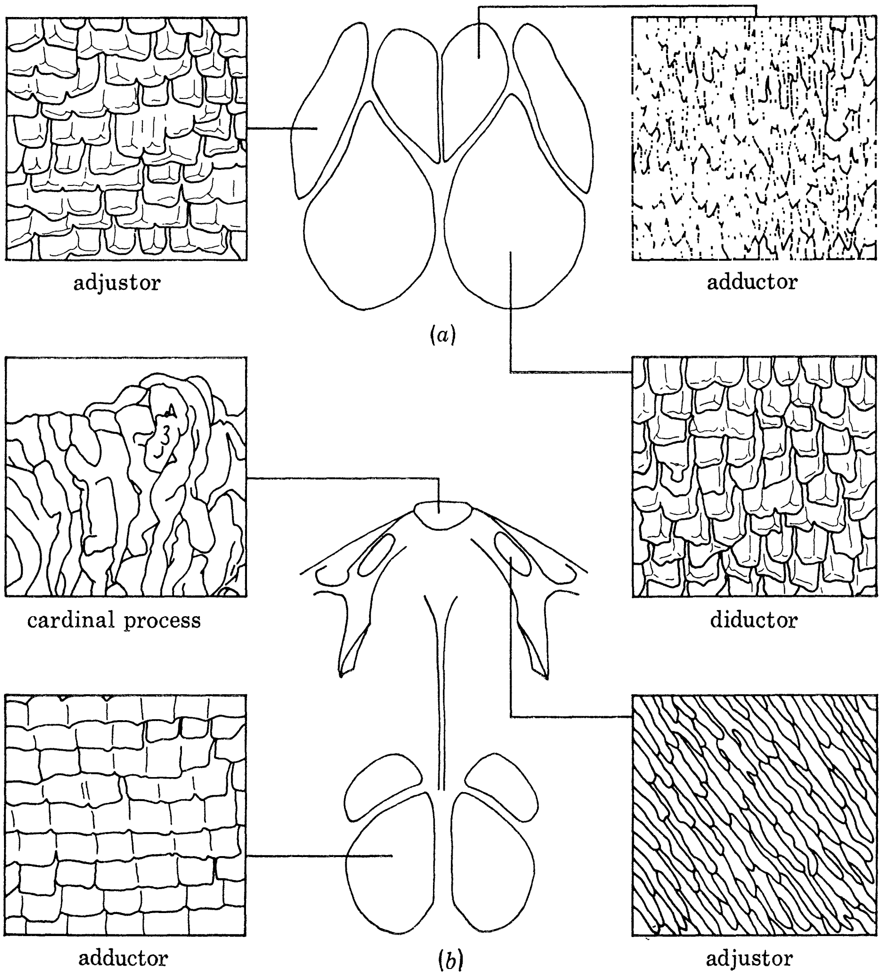

FIGURE 86. Schematic diagram of the skeletal fabrics within the main muscle attachment areas of the pedicle valve (*a*) and brachial valve (*b*) of a Recent articulate brachiopod.

Myotest shell fabrics have also been examined in fossil Orthida, Rhynchonellida and Terebratulida. In several orthids including *Resserella* sp. from the Silurian of Gotland, well preserved secondary shell mosaic gives way within dorsal adductor muscle scars to an irregular array of small, sinuous fibres with wavy outlines (figures 81 and 82, plate 11). At the posterior margins of the scars the junction from myotest to standard mosaic pattern is abrupt. In sections of the rhynchonellid *Rhynchotrema capax* Conrad from the Ordovician Richmond Group of Ohio, U.S.A., irregular gnarled myotest fibres contrast markedly with those of the regularly stacked secondary layer (figure 83, plate 11) indicating an abrupt modification of the standard secretory régime within both dorsal adductor and ventral diductor muscle scars. At the sites of dorsal and ventral muscle attachment in the early Devonian centronellid *Rensselaerina haragana* Cloud, valves are floored with a thick tertiary prismatic layer whose irregular fabric (figure 84, plate 11) is comparable with that found in lower Palaeozoic atrypidines such as *Catazyga*, *Dayia* and *Coelospira*. The irregular outlines of interlocking 'prisms' are almost certainly part of the original shell fabric since secondary layer fibres adjacent to the tertiary layer are beautifully preserved and stacked in orthodox fashion. Although the tertiary layer fabric in *Rensselaerina* is less regular than that found in living *Gryphus* and *Liothyrella*, it is unlikely that the outer epithelium in both living and extinct stocks was much different. In terebratulids that exhibit myotest fabrics derived from the secondary layer, such as *Magadina* aff. *clifdenensis* Finlay from the Miocene of South Canterbury, New Zealand, modifications of the standard mosaic pattern are virtually identical to that found in Recent genera (figure 85, plate 11).

Conclusions

In Recent Brachiopoda modifications of the standard mosaic due to the encroachment of muscle bases fall into three broad categories governed by fibre shape (figure 86). The exposed parts of fibres comprising the dorsal adductor, ventral diductor and ventral adjustor myotests are roughly equidimensional or only slightly longer than wide. Those of the ventral adductor and dorsal adjustor myotests are, on the other hand, long and sinuous but narrow in width. The fibres incorporated within the cardinal processes do not conform to just one or other category, but may be long and sinuous (e.g. *Waltonia*) short and stubby (e.g. *Notosaria*) or completely unlike any other shell fabric yet come across (e.g. *Macandrevia*).

The first category, typified by the dorsal adductor, ventral diductor and ventral adjustor myotests, can be further subdivided on the basis of the frequency with which laterally adjacent fibres are welded together. In dorsal adductor scars, the frequency is exceedingly high (over 95 % in *Macandrevia*). However, in the ventral diductor scars, the converse is the case (about 5 % in *Terebratalia*). The ventral adjustor scars show no consistency and the percentage of laterally united fibres may be high (about 80 % in *Notosaria*) or low (about 1 % in *Waltonia*).

Modifications of the standard secondary shell mosaic, within the areas of muscle attachment in Recent brachiopods, can be directly correlated with the secretory behaviour of the outer epithelial cells responsible for depositing those parts of the shell succession. The changes in morphology of exposed parts of fibres incorporated within a muscle scar are so delicate that, in many cases, each muscle base imparts to the underlying shell a characteristic fabric which can be readily distinguished from that of neighbouring scars in the same specimen. In spite of the diversity of genera included in this survey, modifications in secondary and tertiary layer fabrics within muscle scars of most fossil brachiopods are sufficiently comparable with those observed in living articulates to support the conclusion that the processes of myotest formation have remained essentially unchanged since at least the Ordovician.

I am especially indebted to Dr A. Williams, F.R.S., of Glasgow University whose inspiration and guidance has greatly contributed to the completion of this work.

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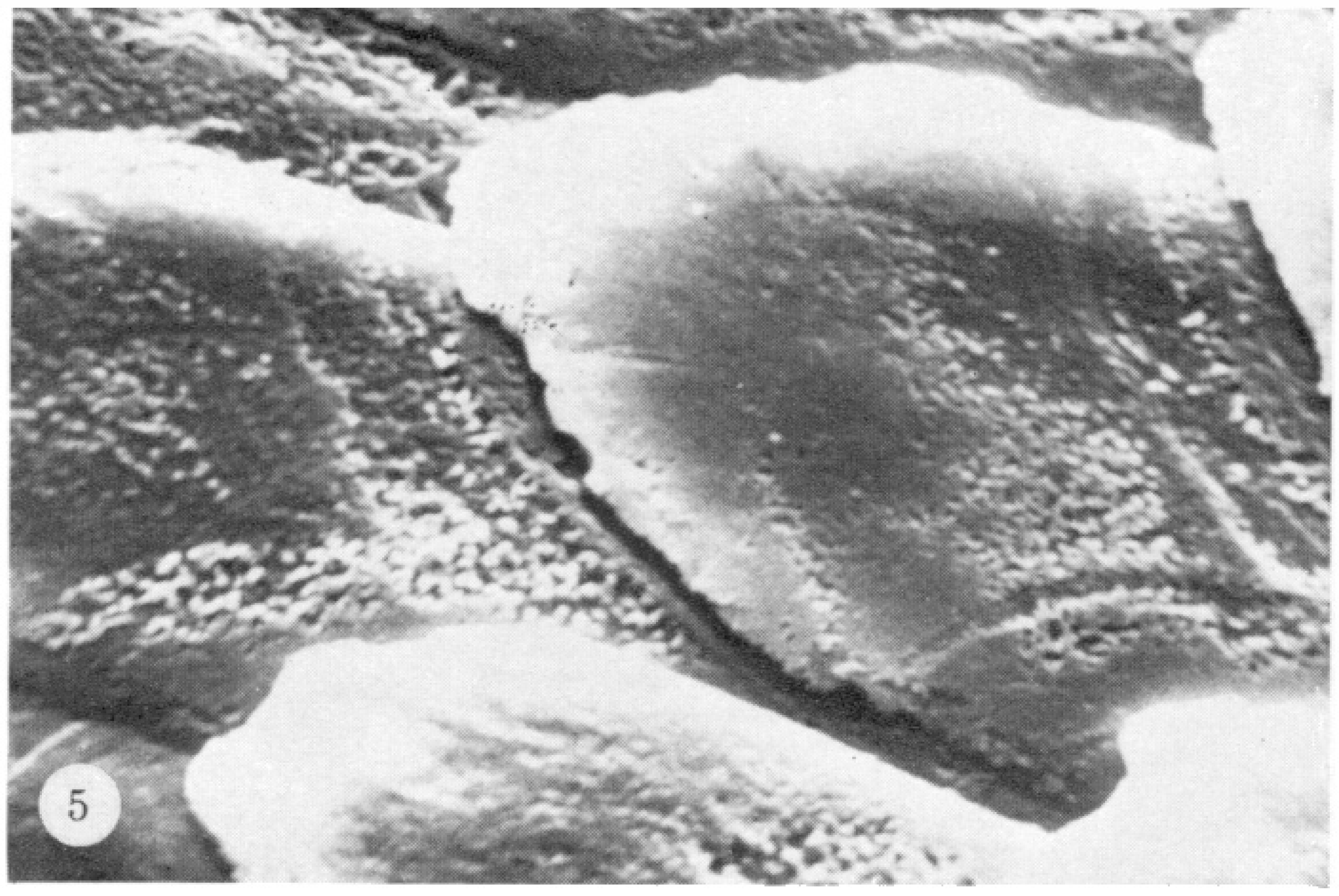
FIGURES 3–4. For description see opposite.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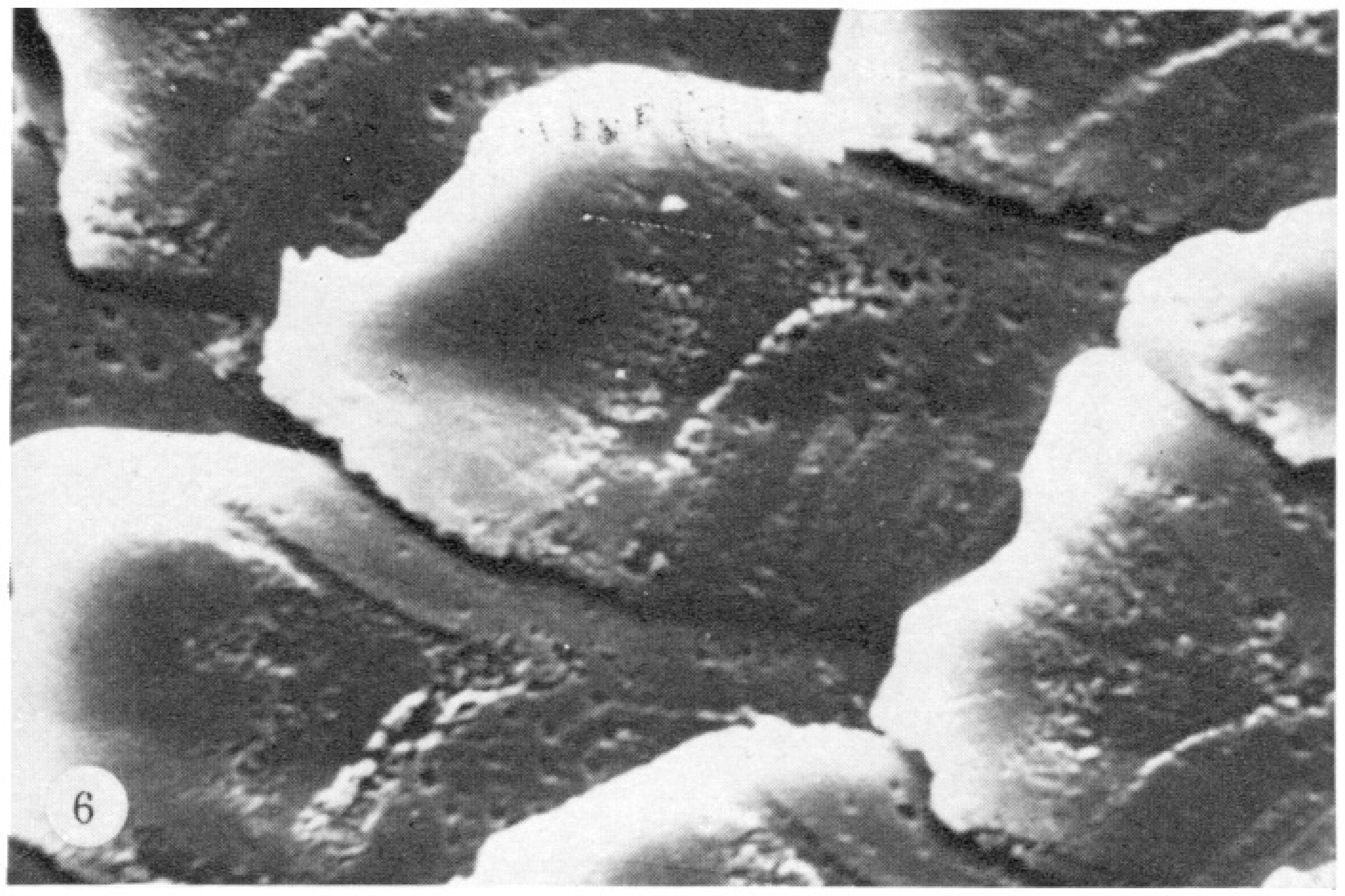
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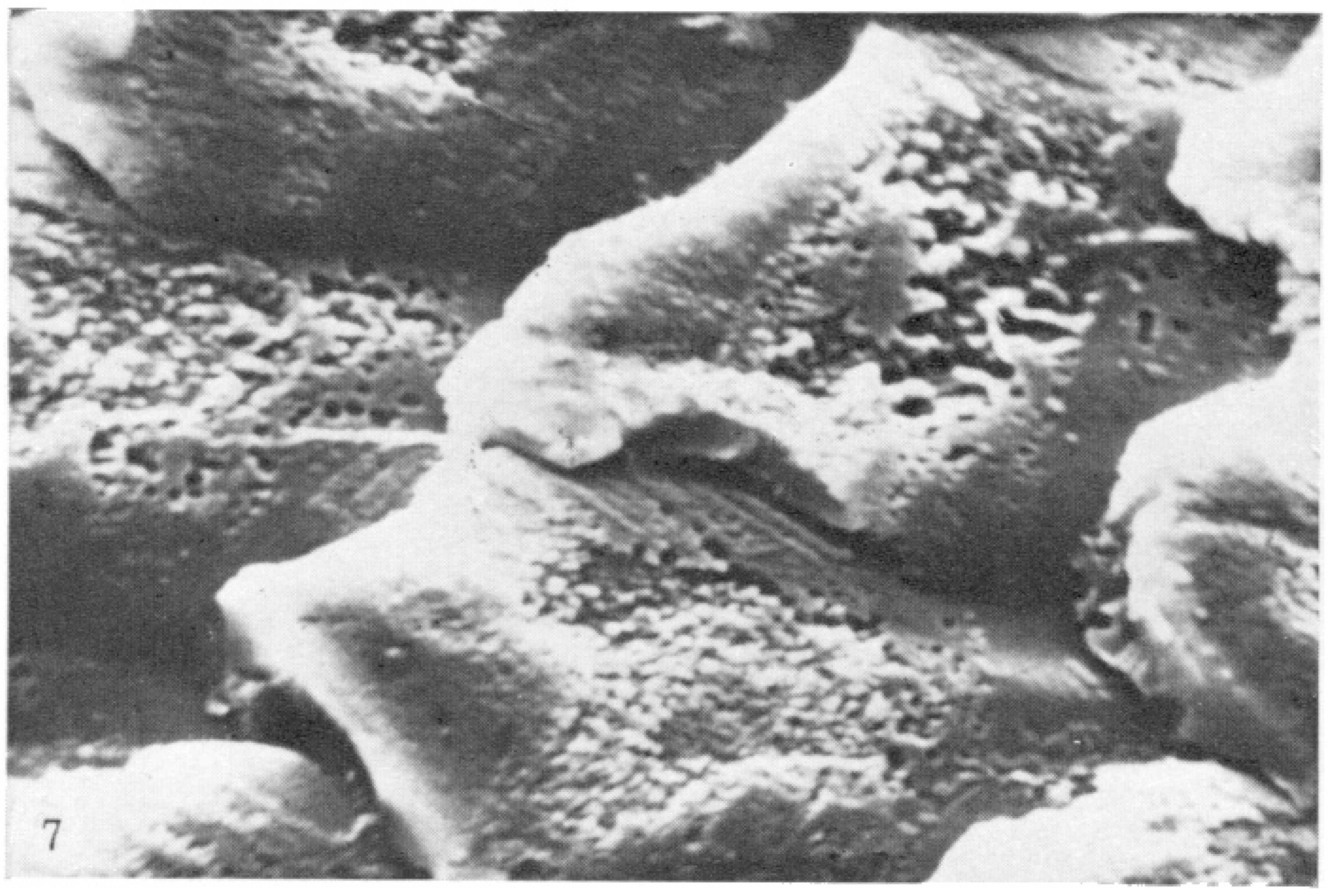
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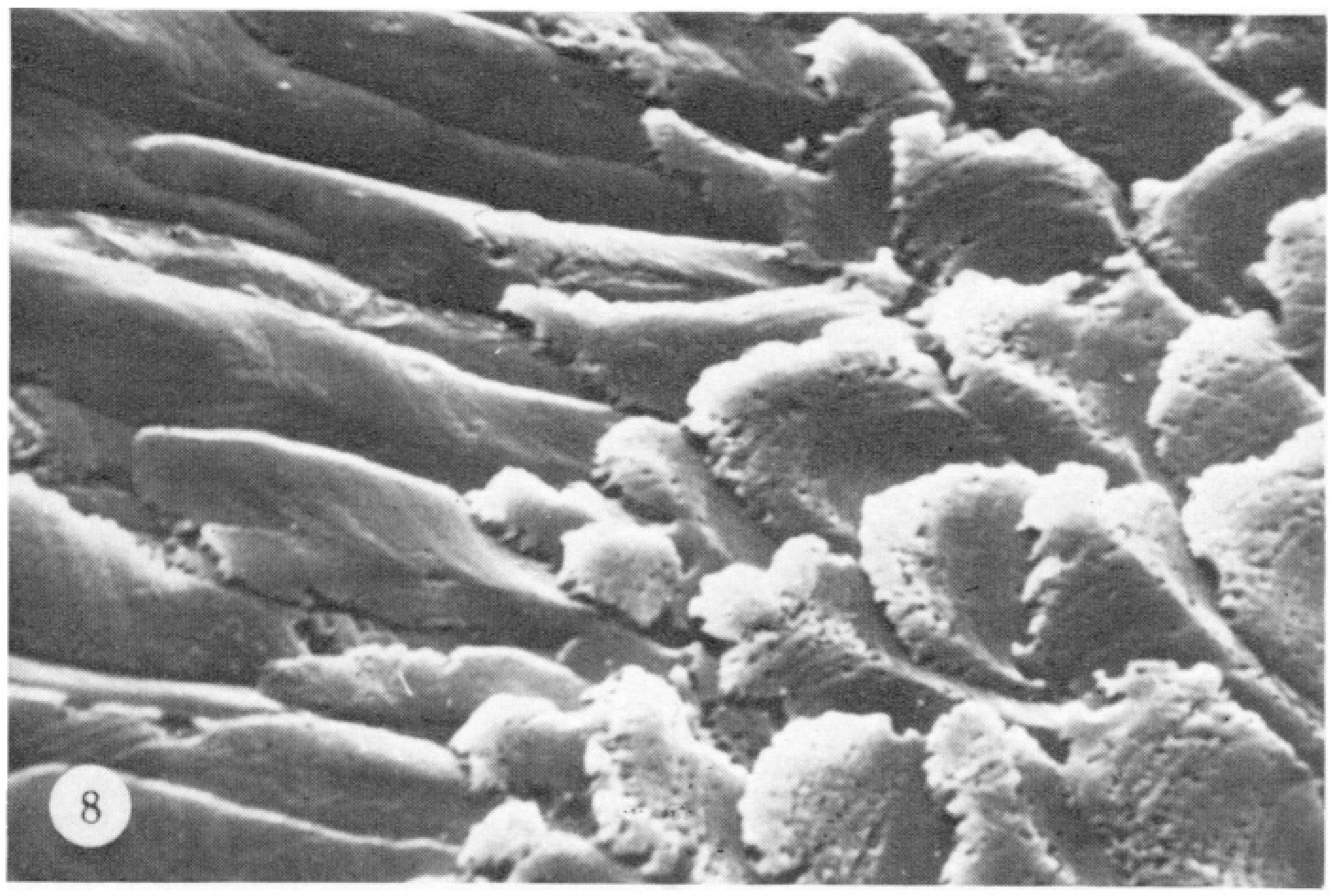
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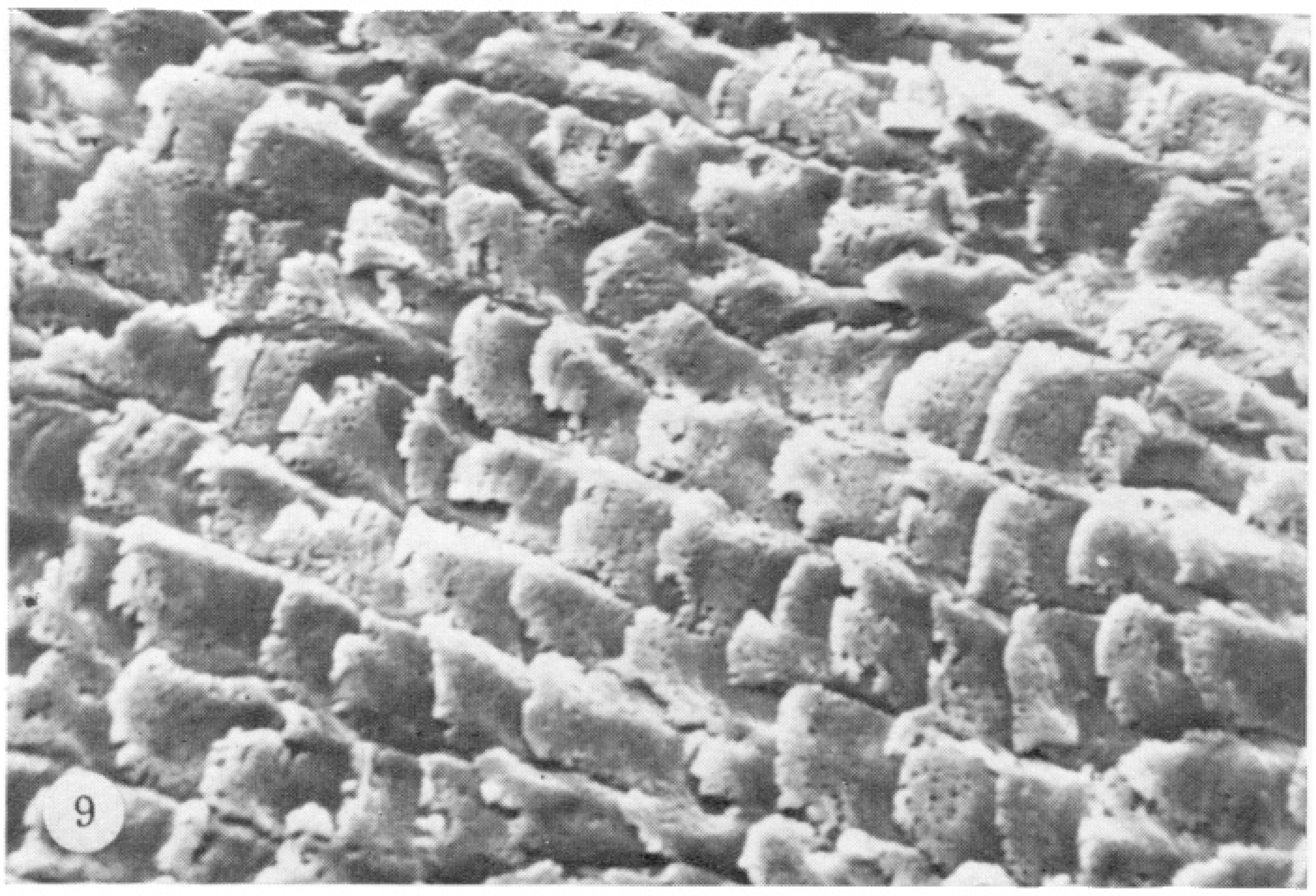
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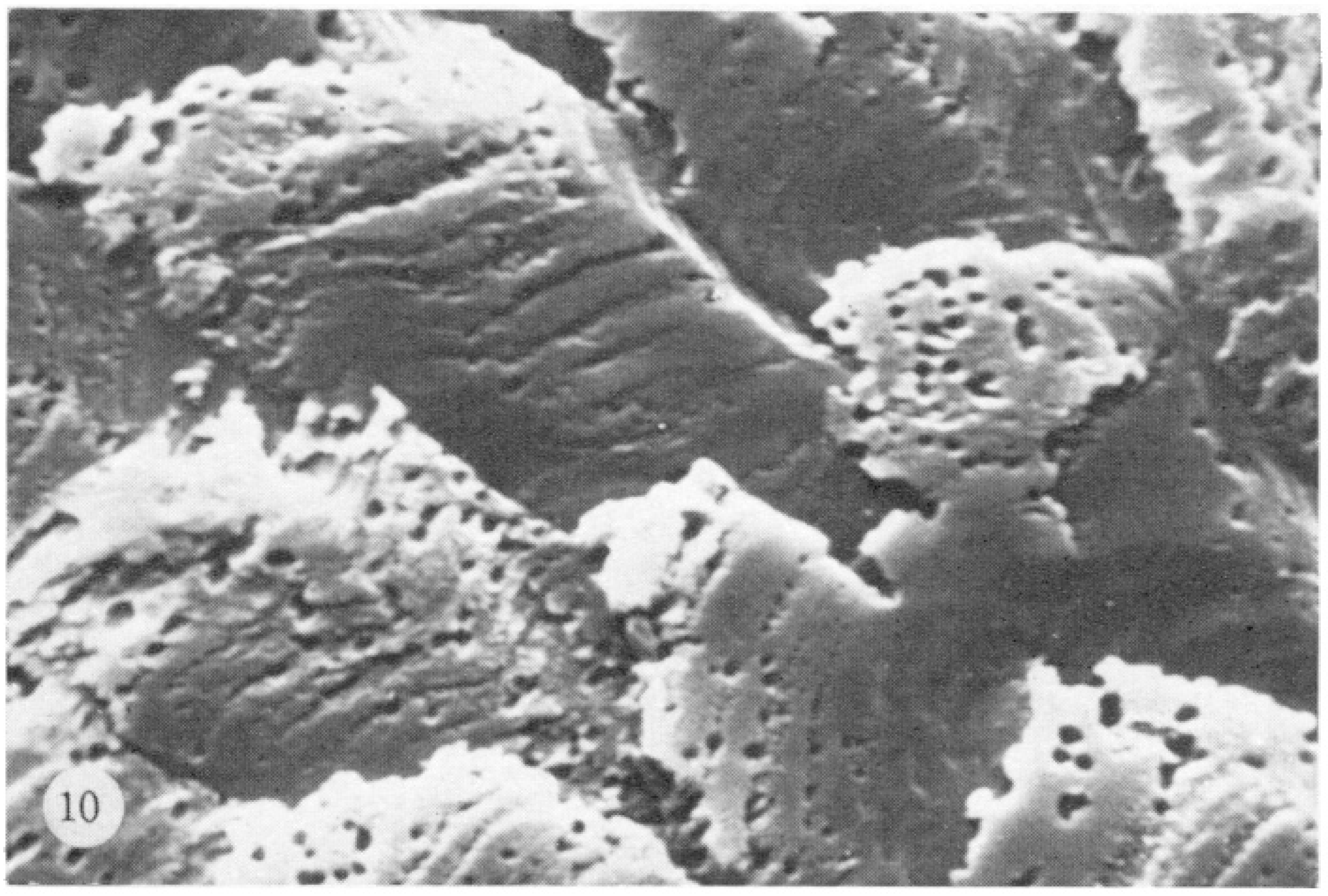
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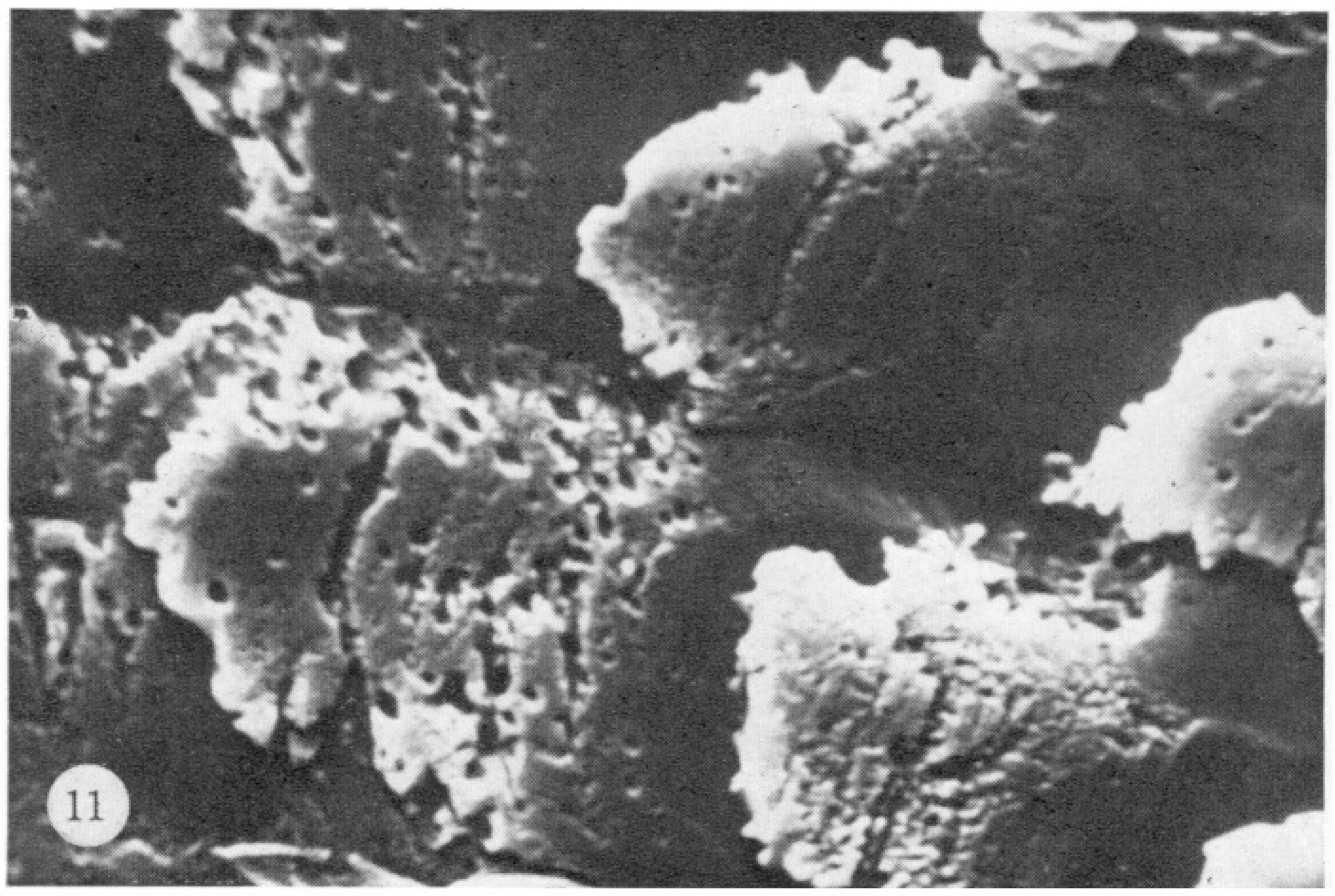
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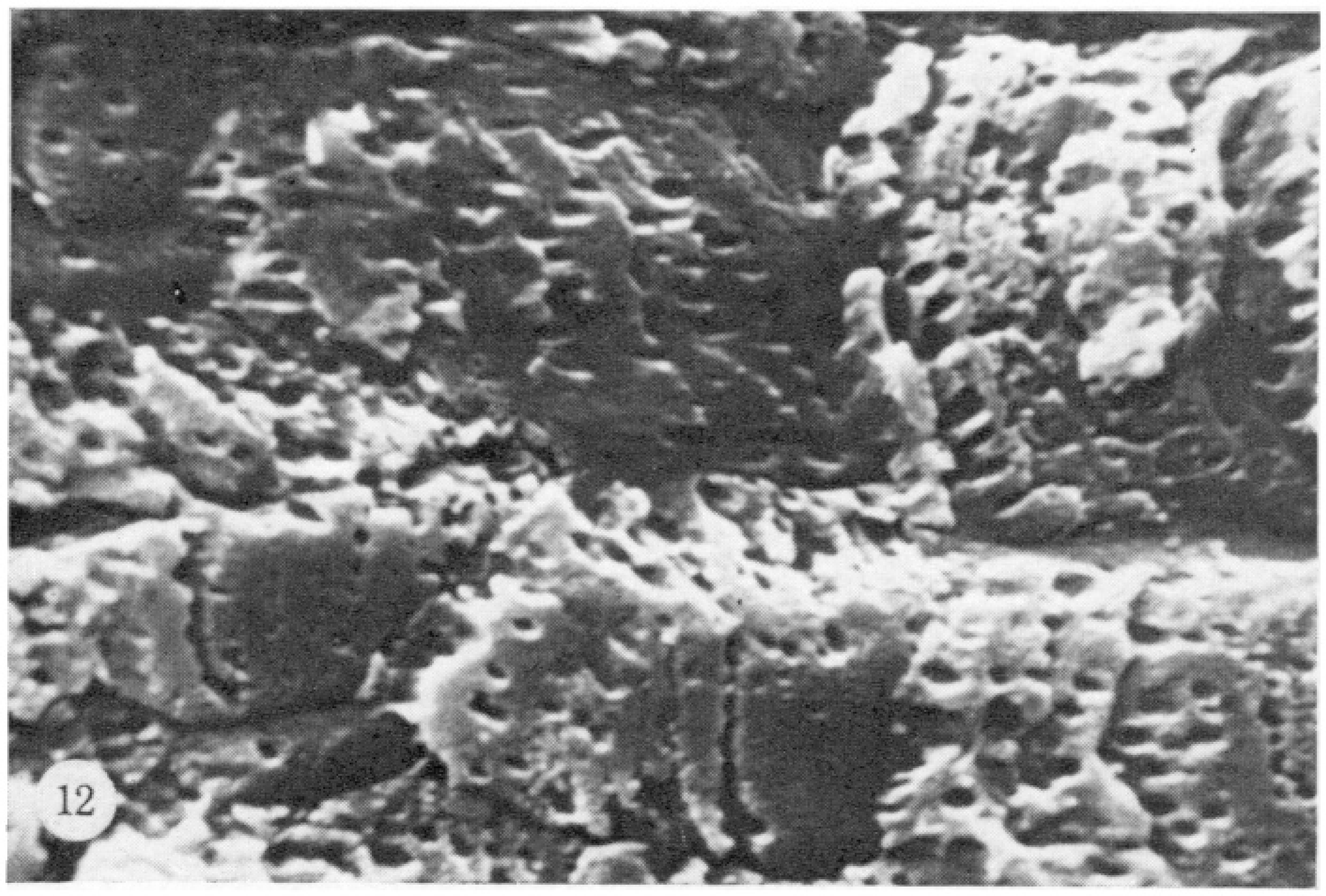
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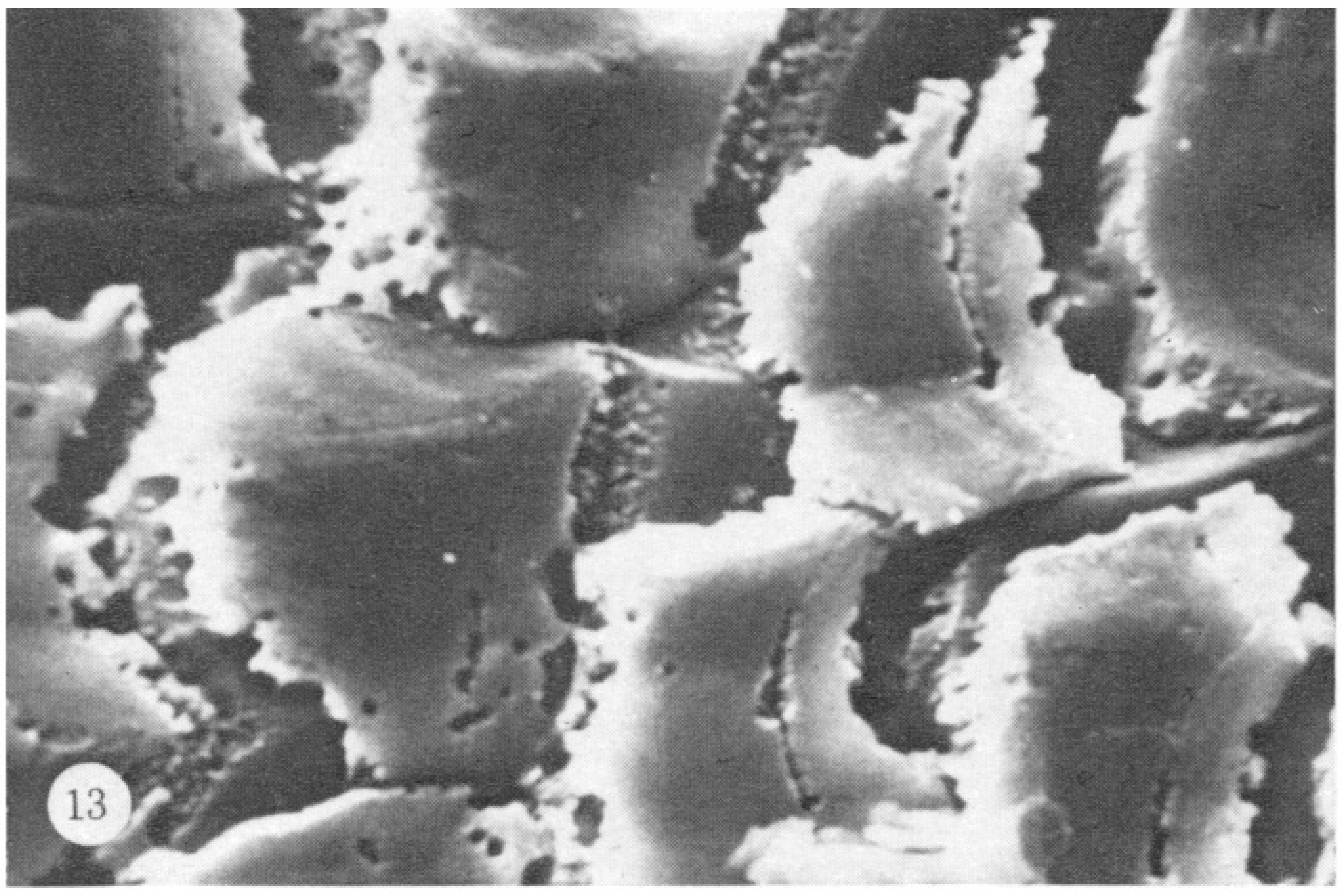
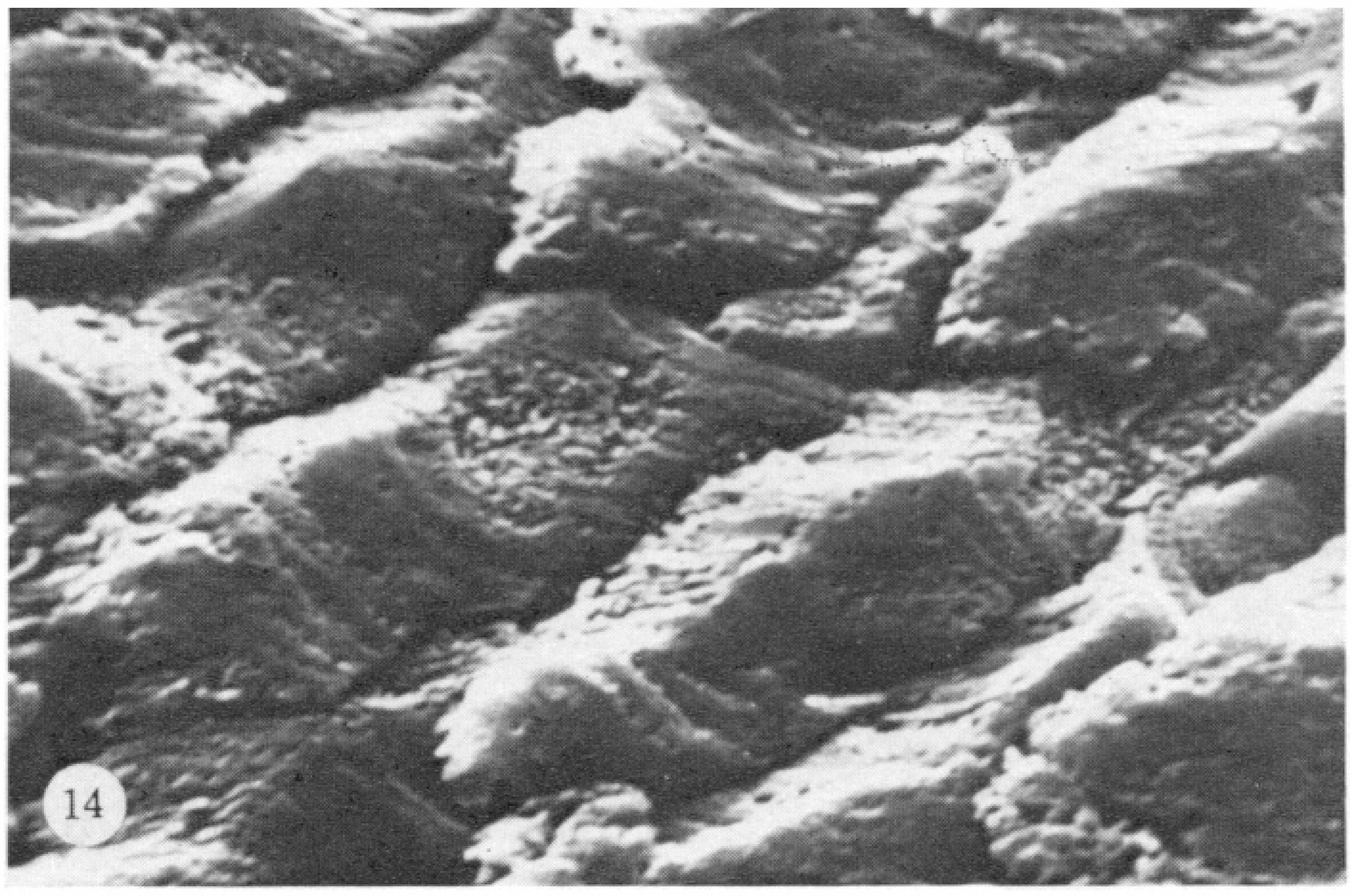
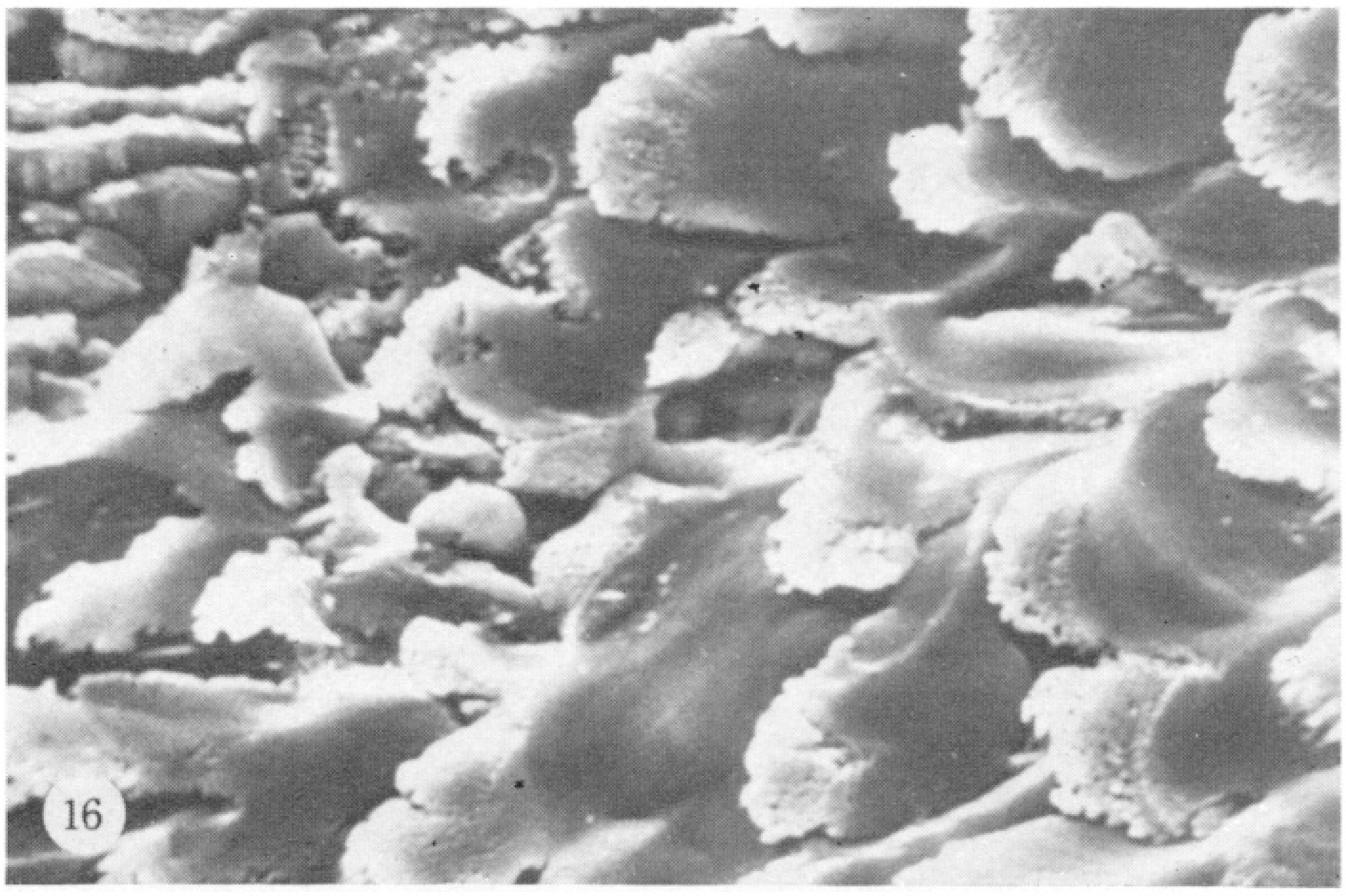
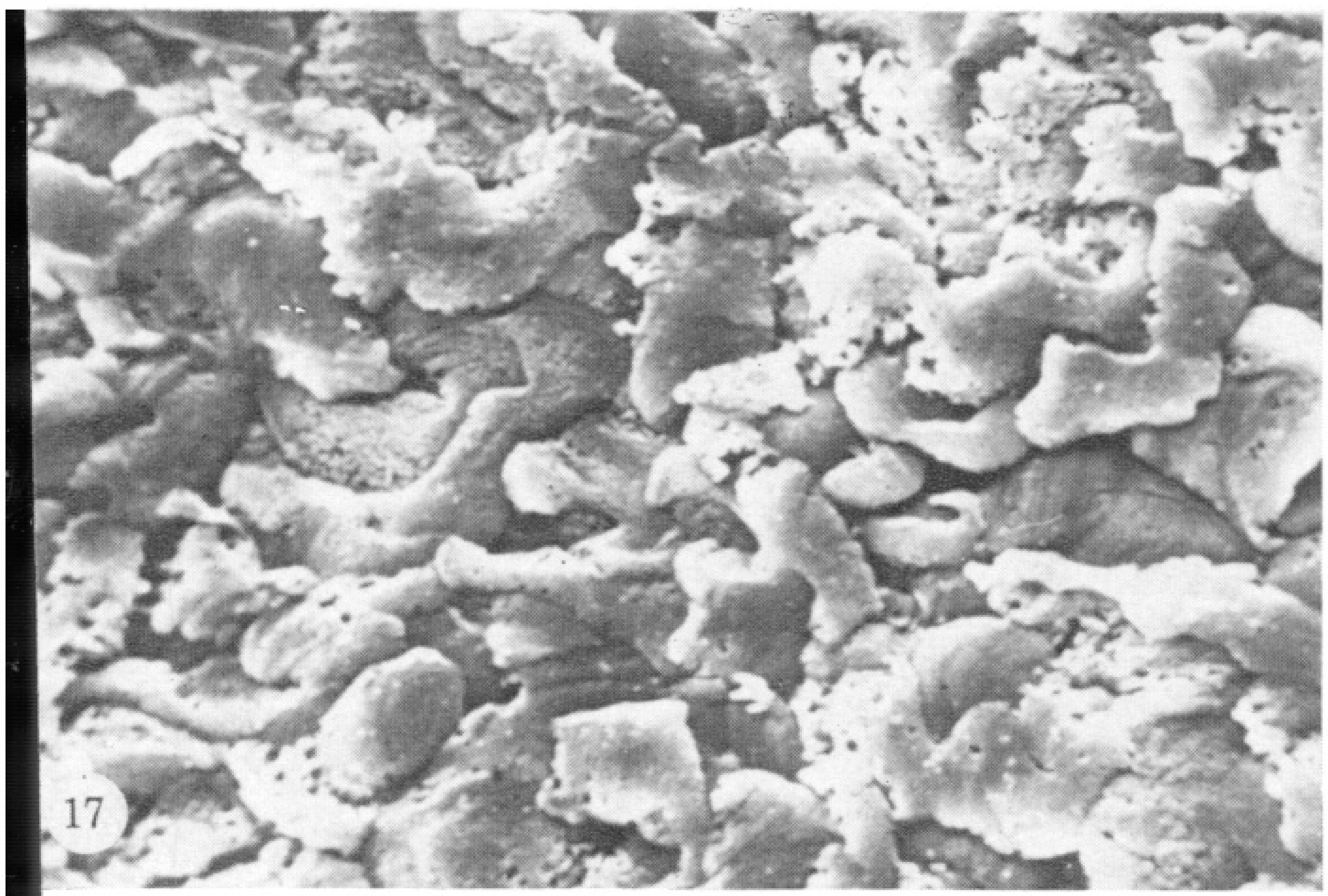
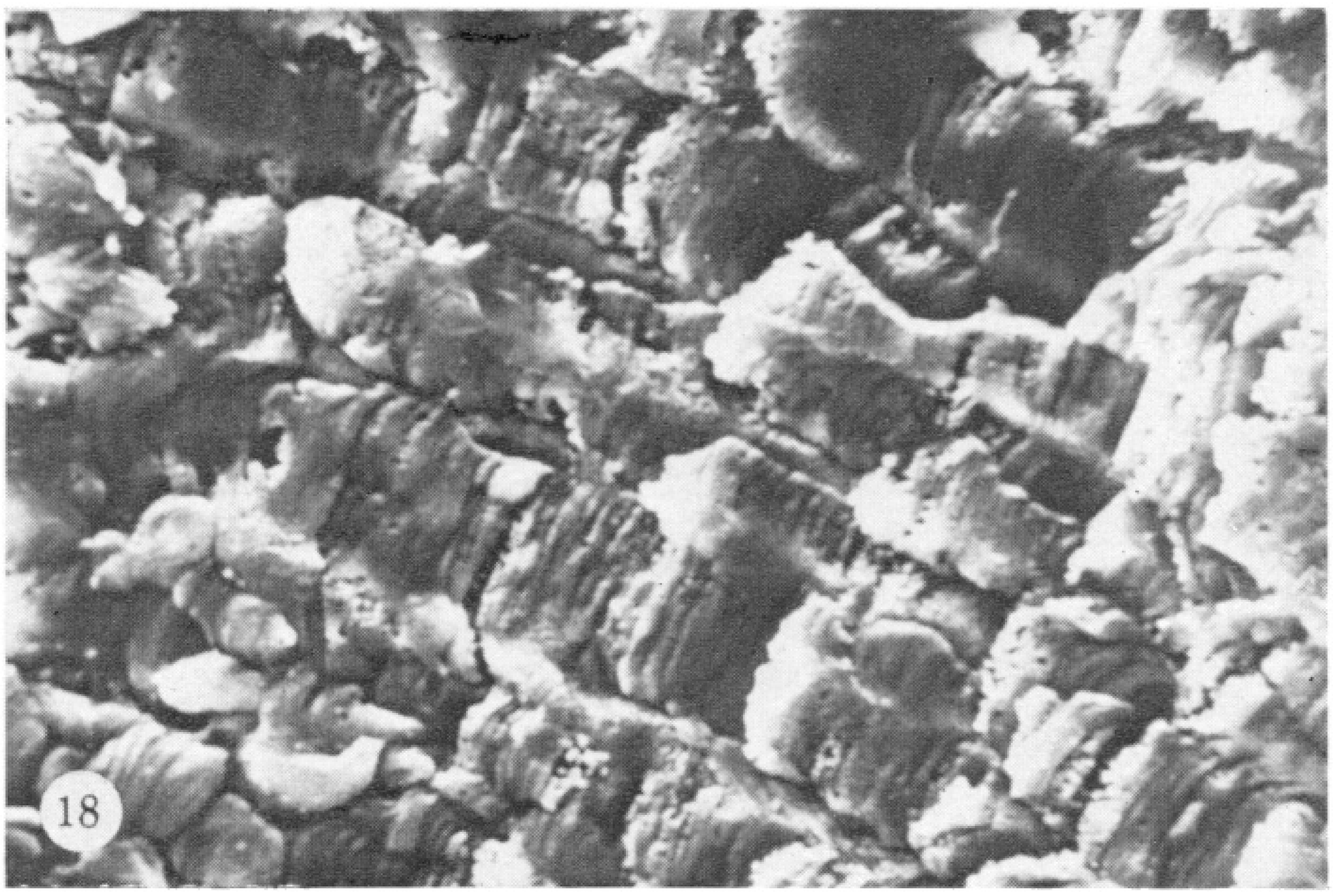
FIGURES 5–12. For description see opposite.

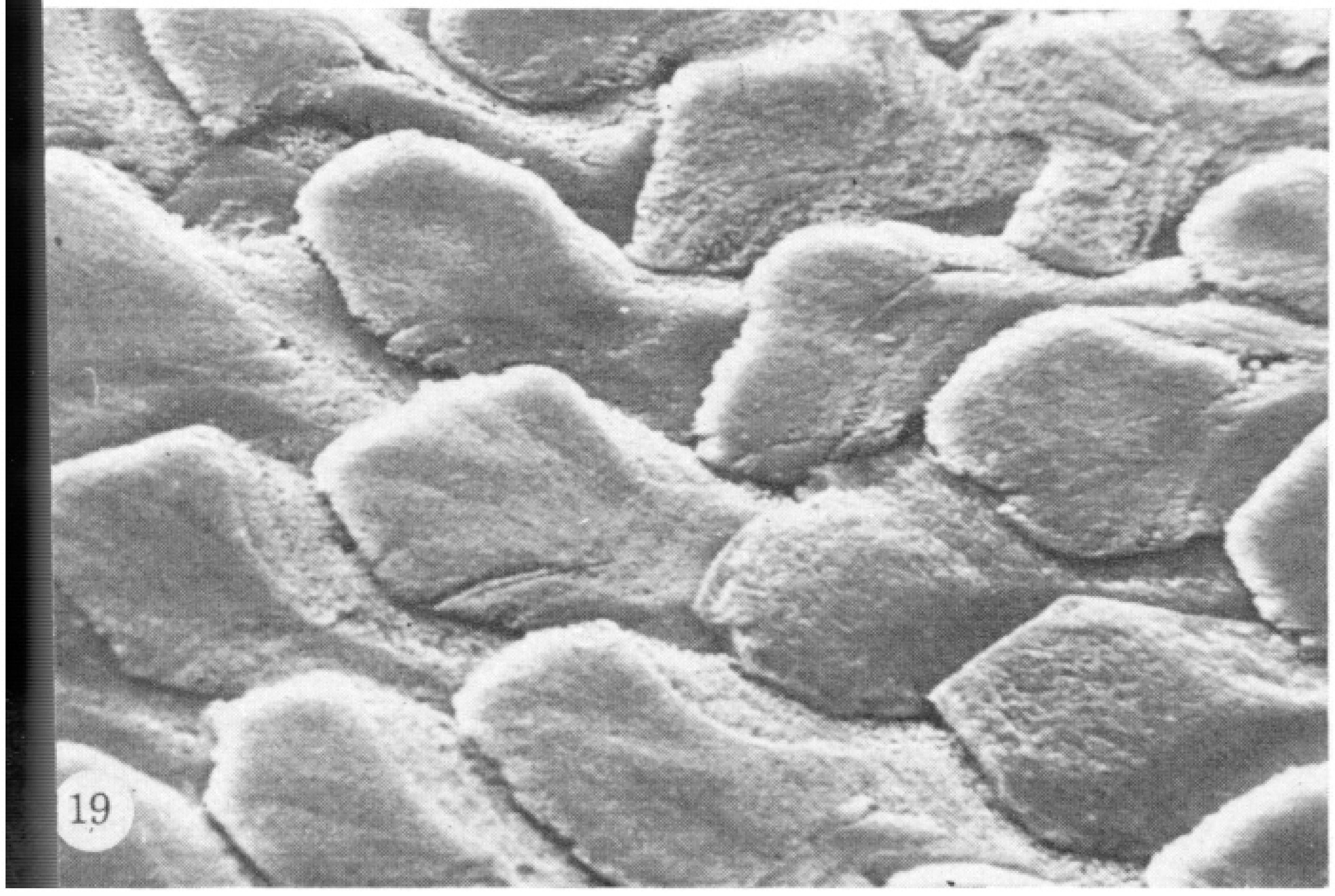


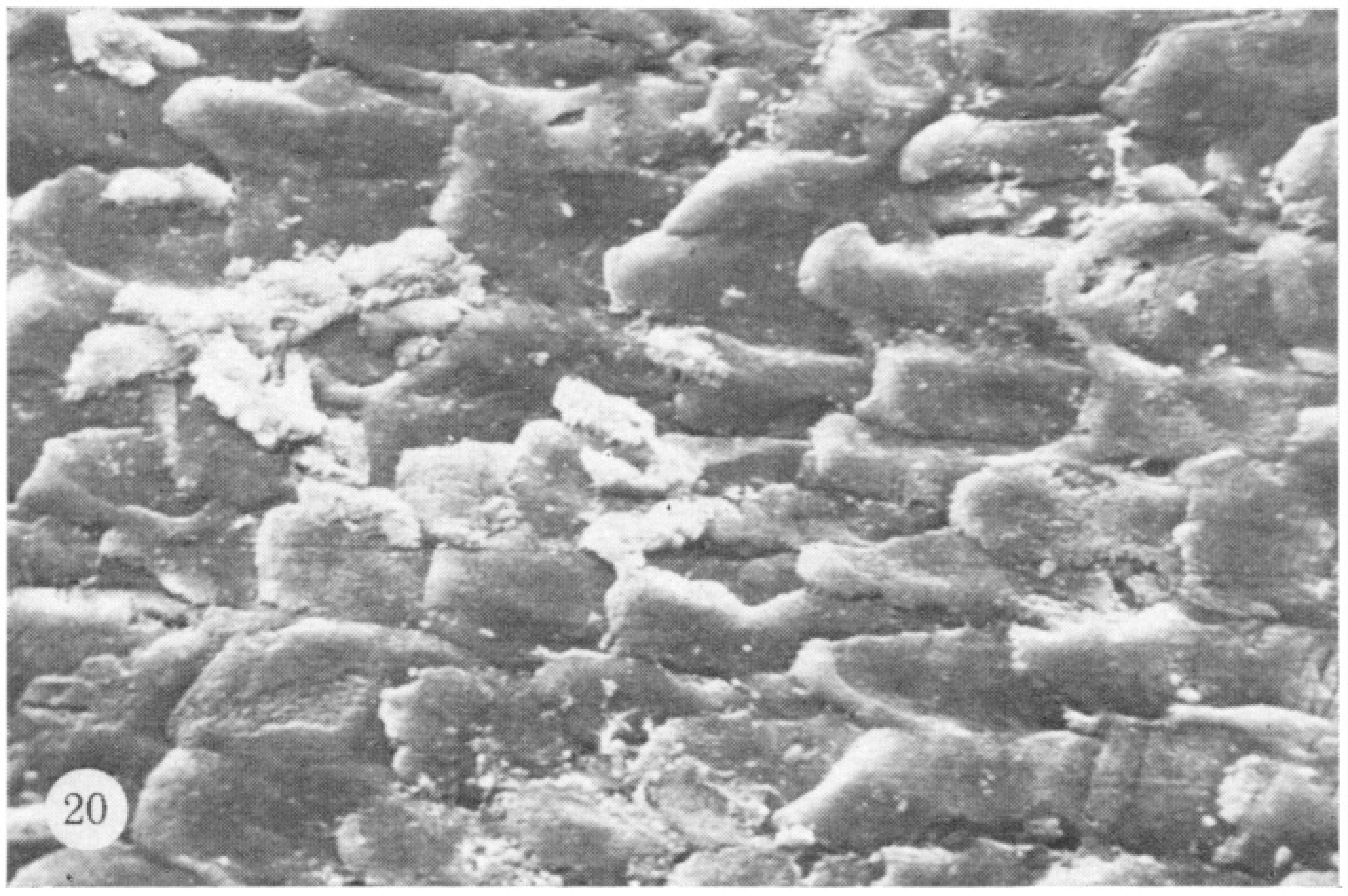




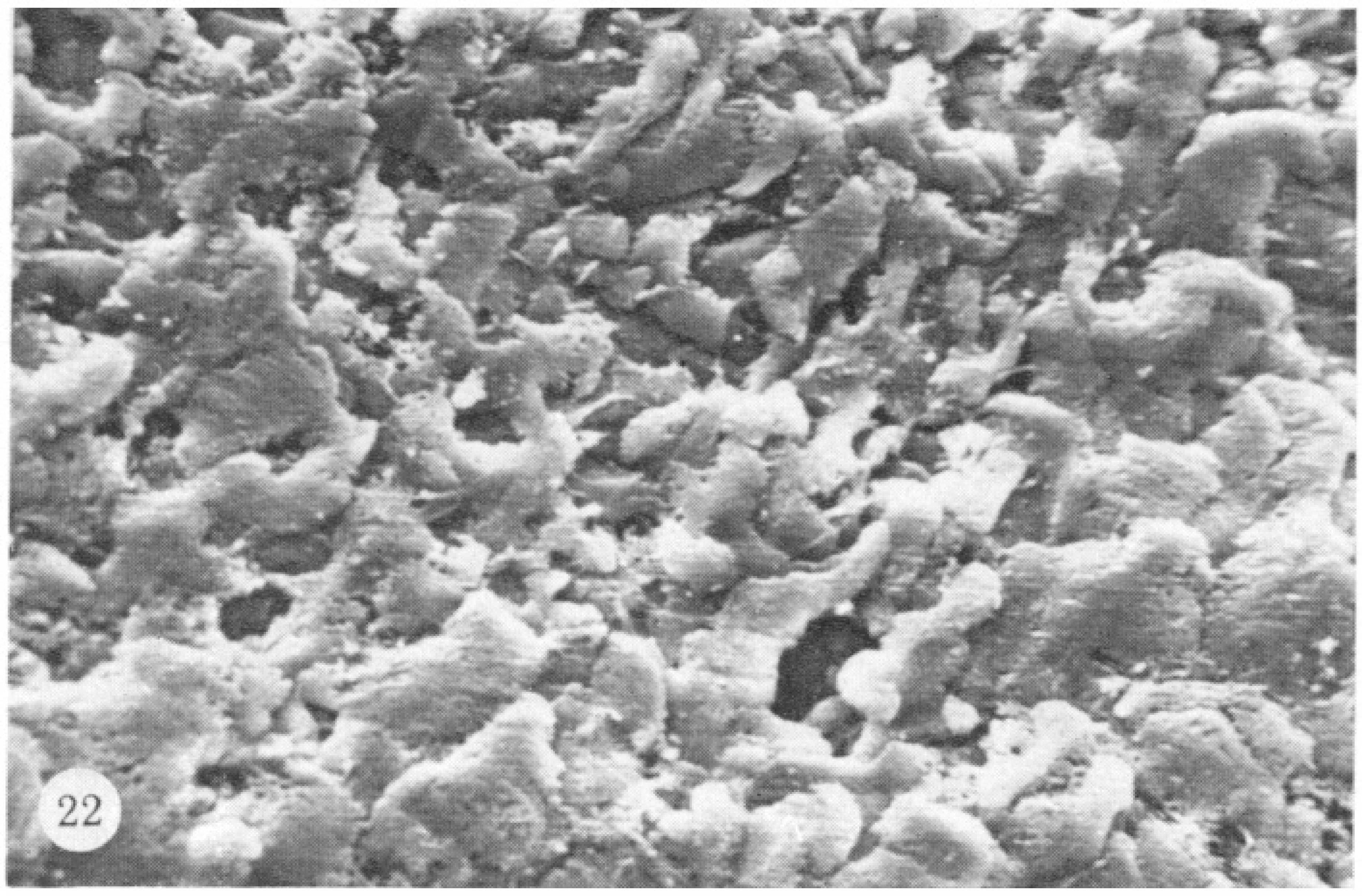








FIGURES 13–20. For description see opposite.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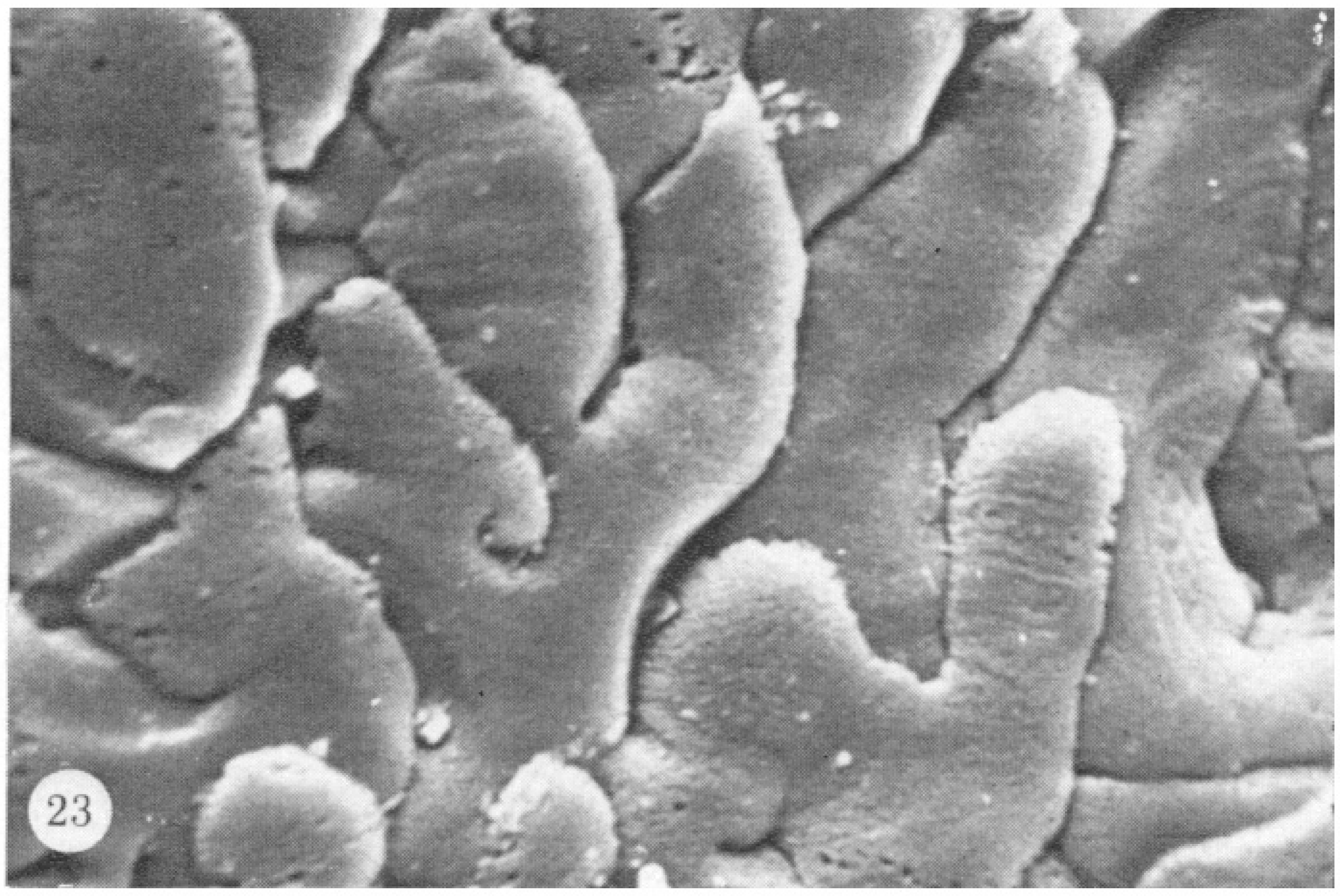
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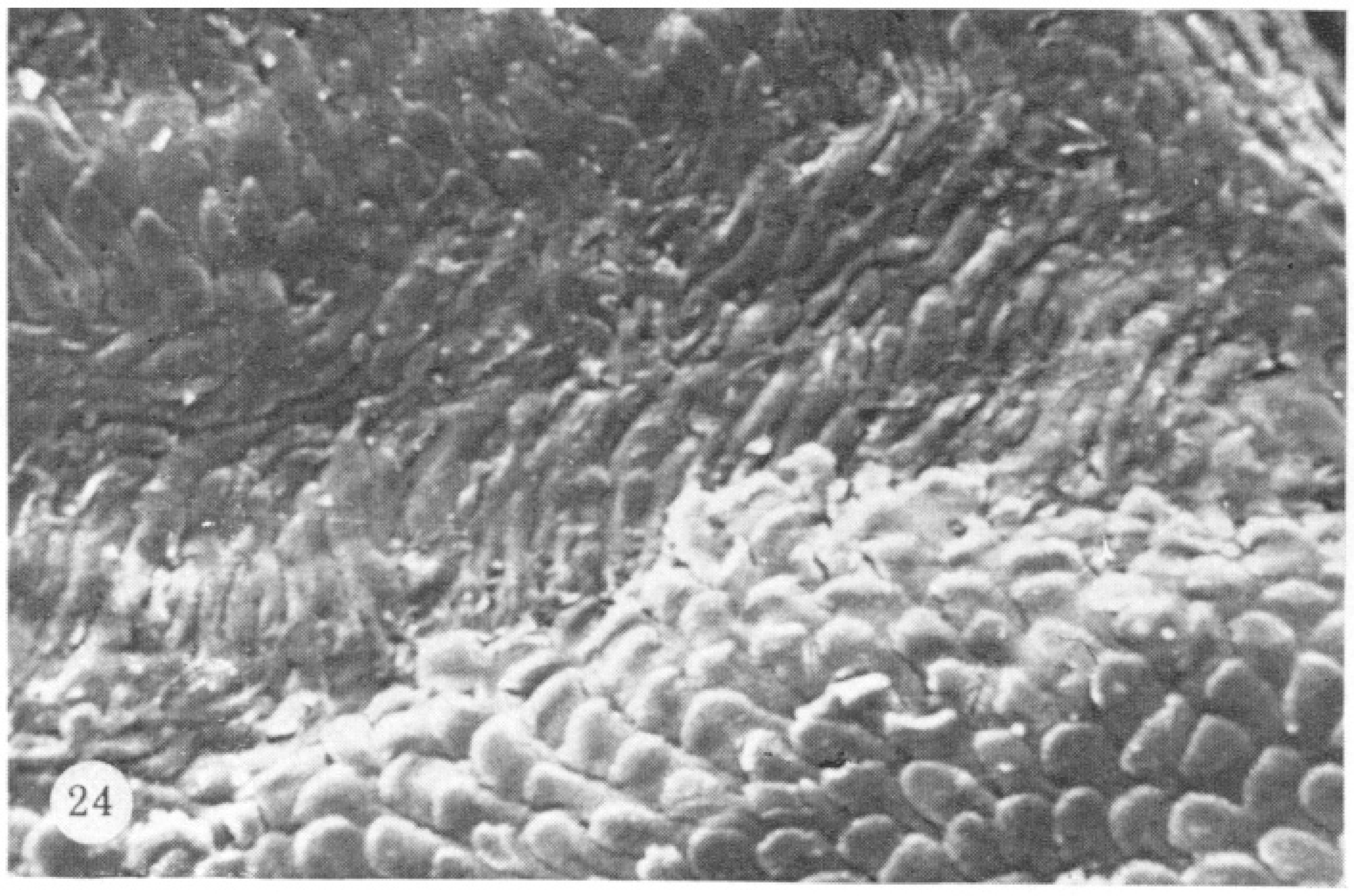
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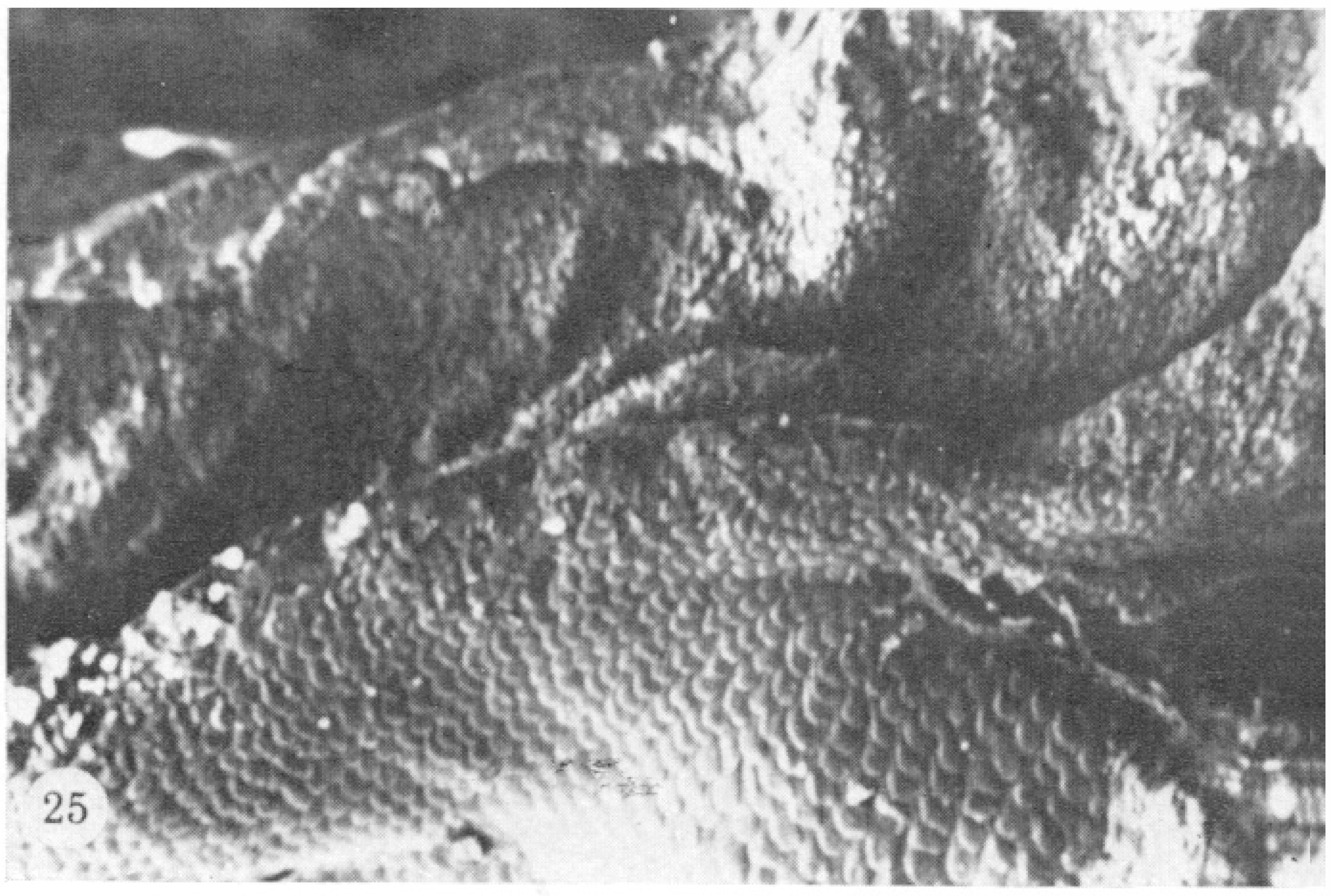
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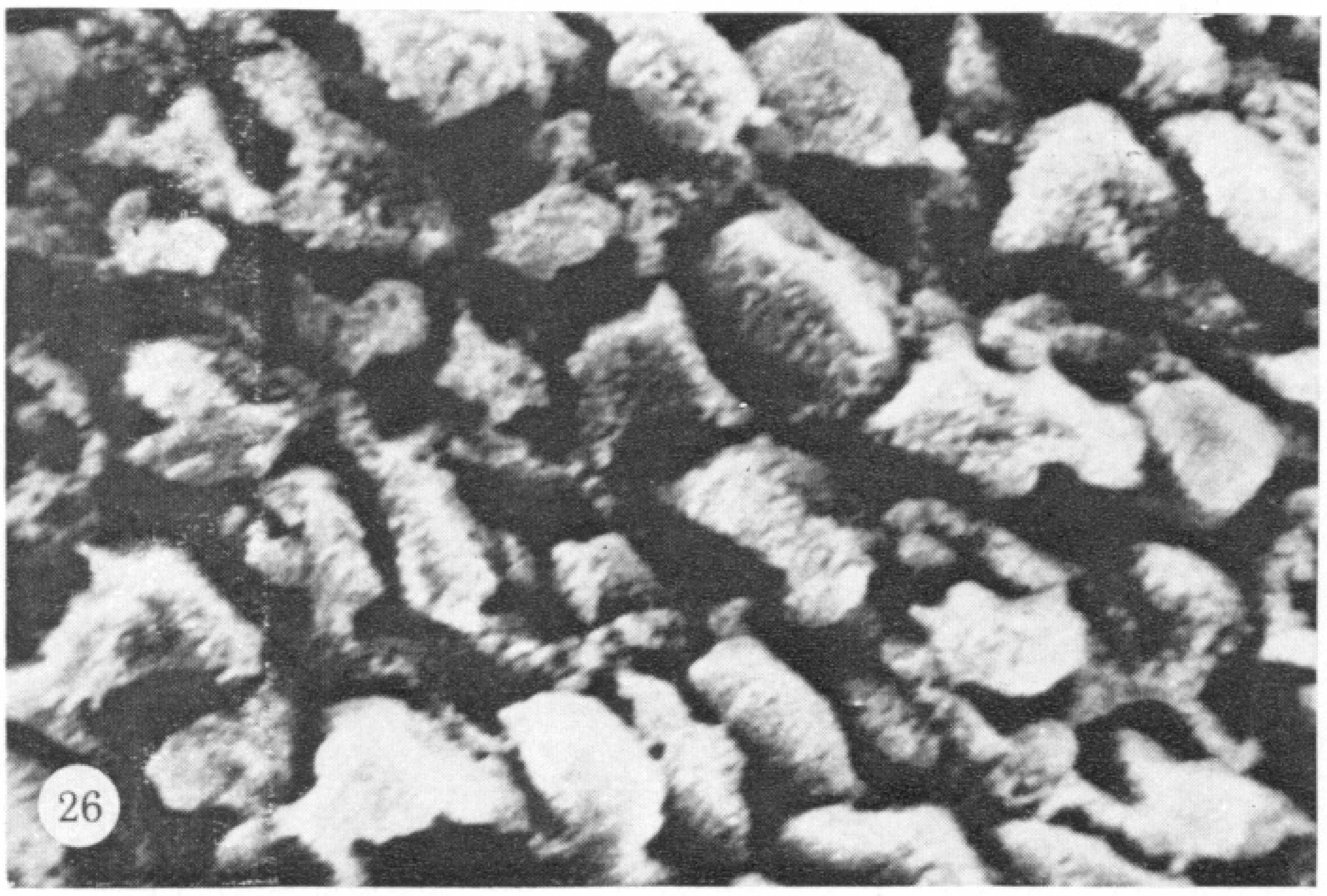
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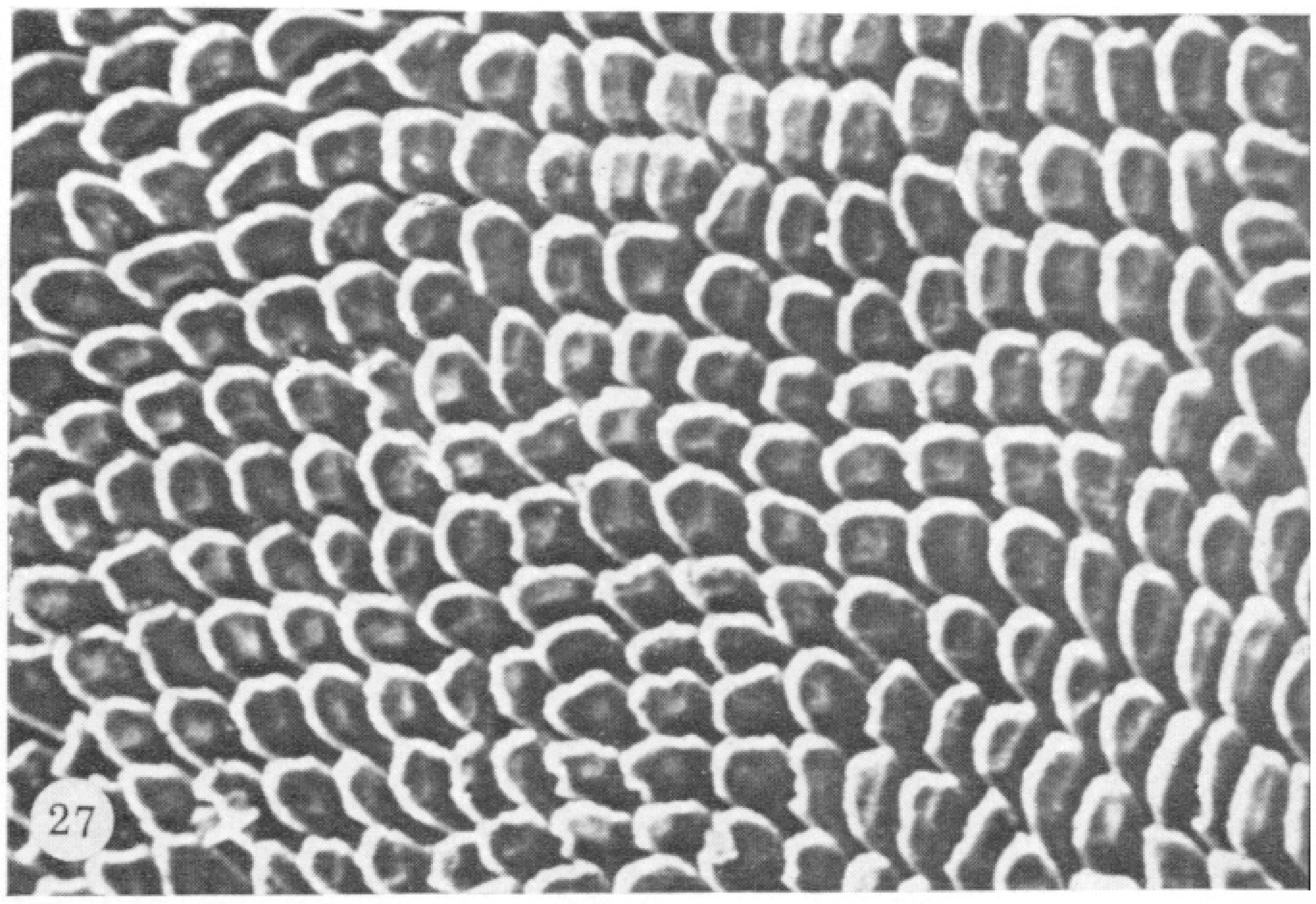
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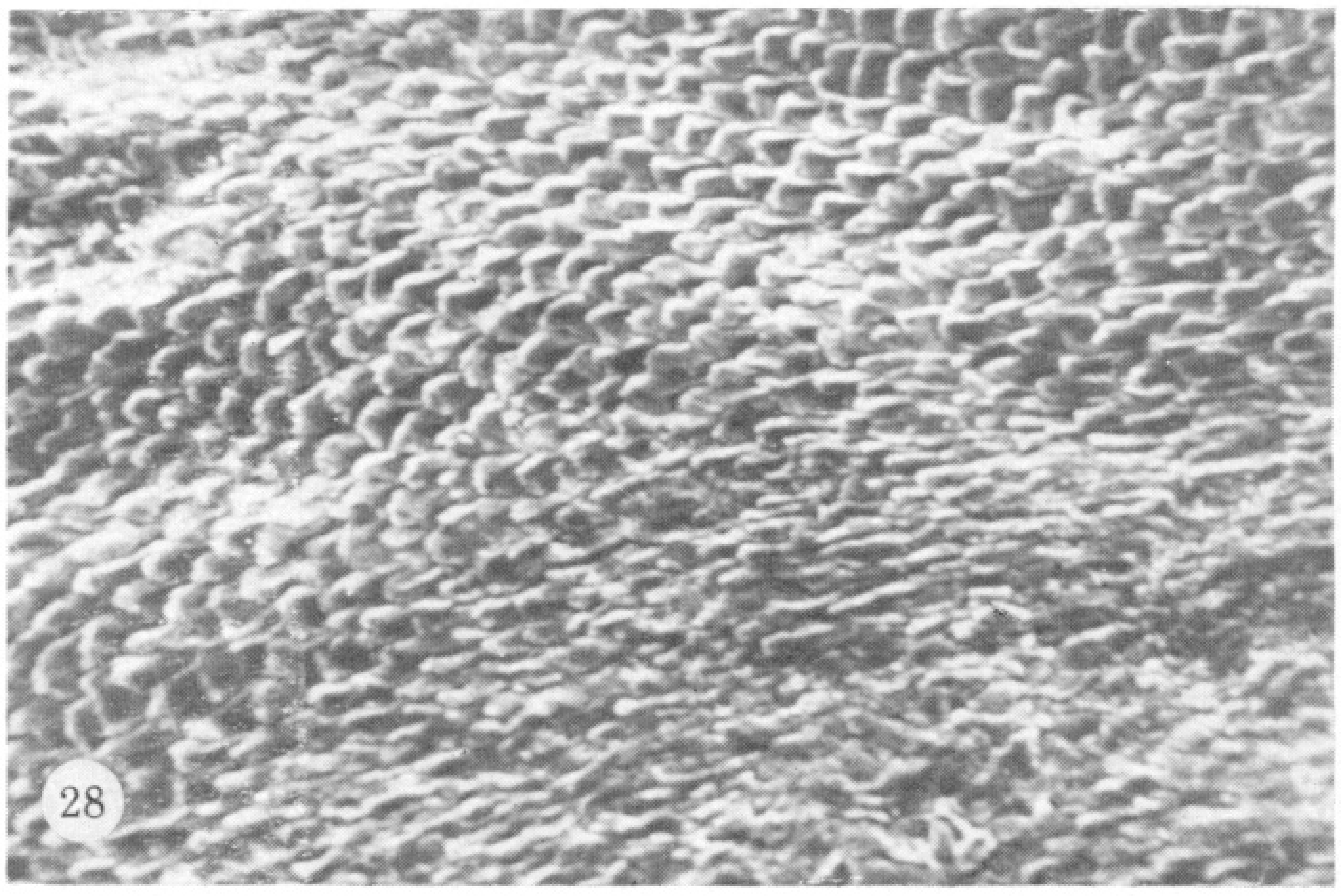
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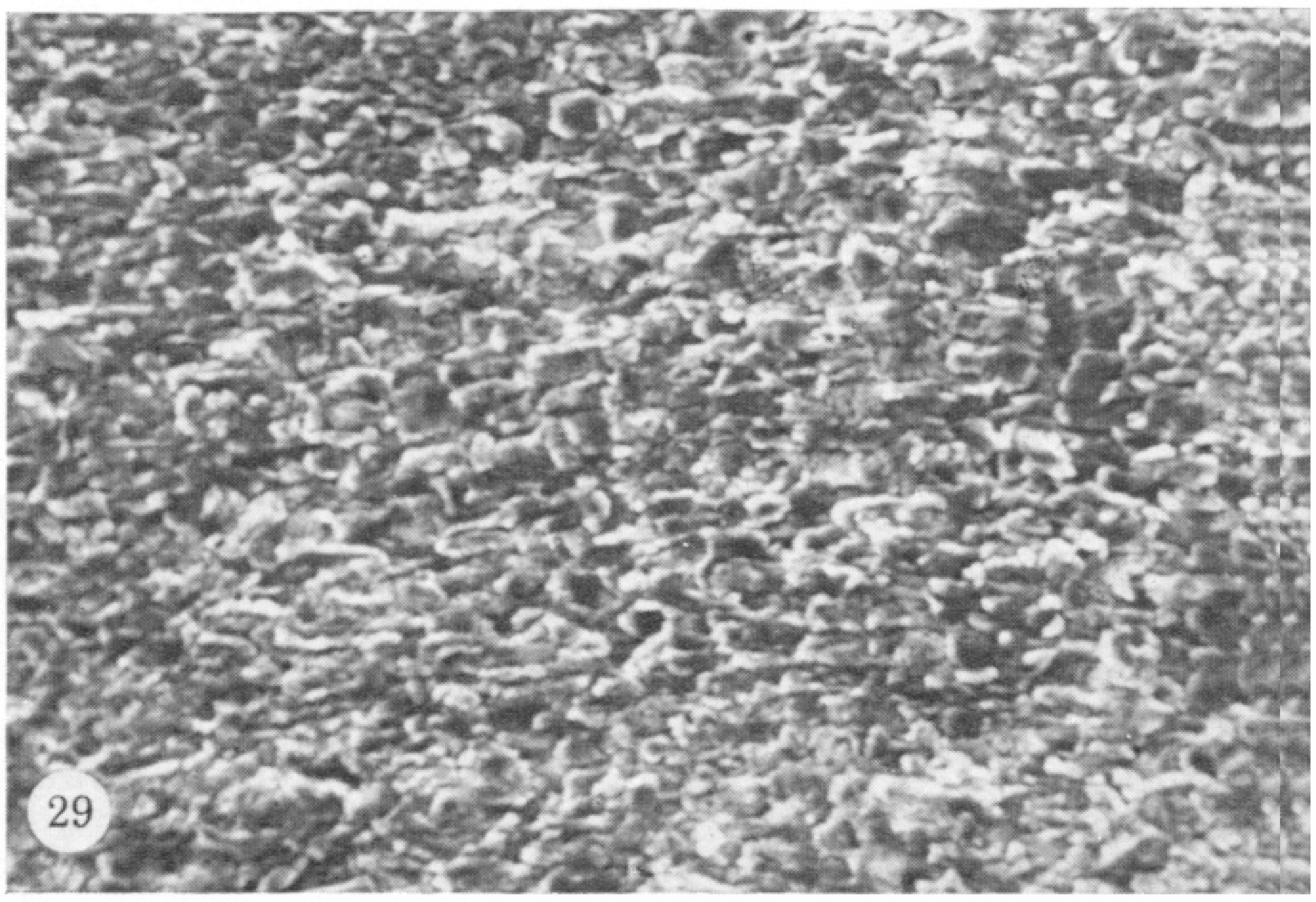
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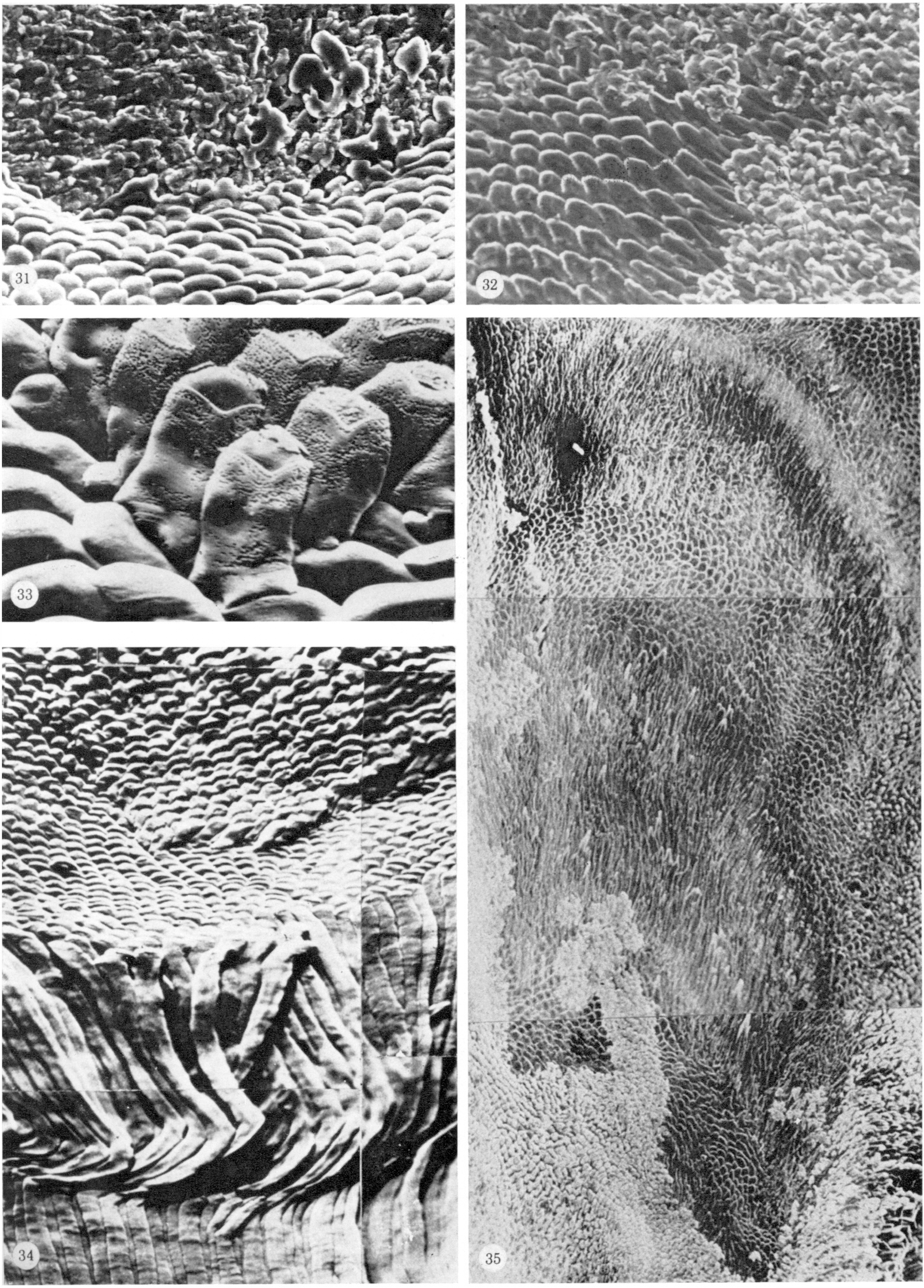
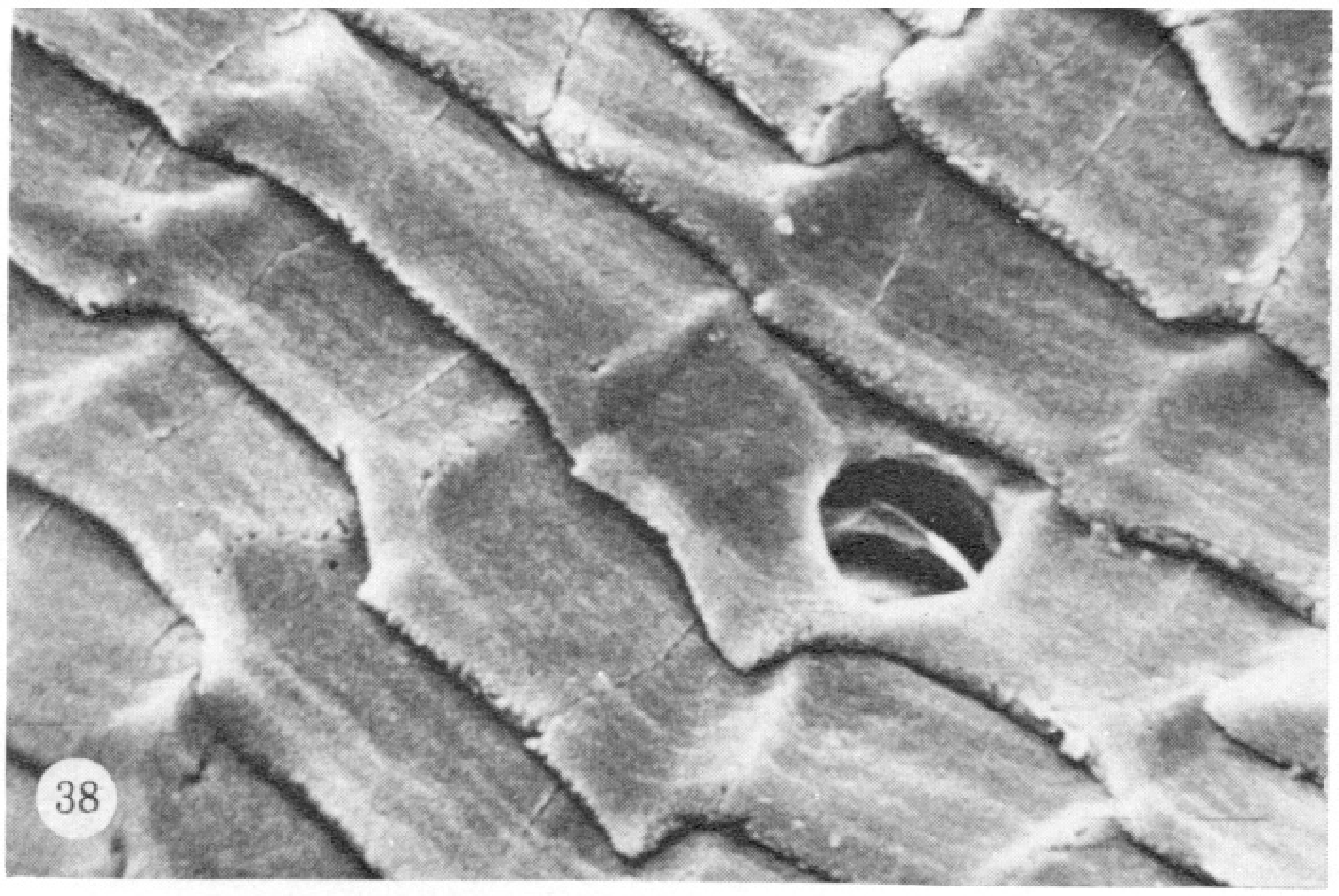
Figures 22–29. For description see opposite.



FIGURES 31–35. For description see opposite.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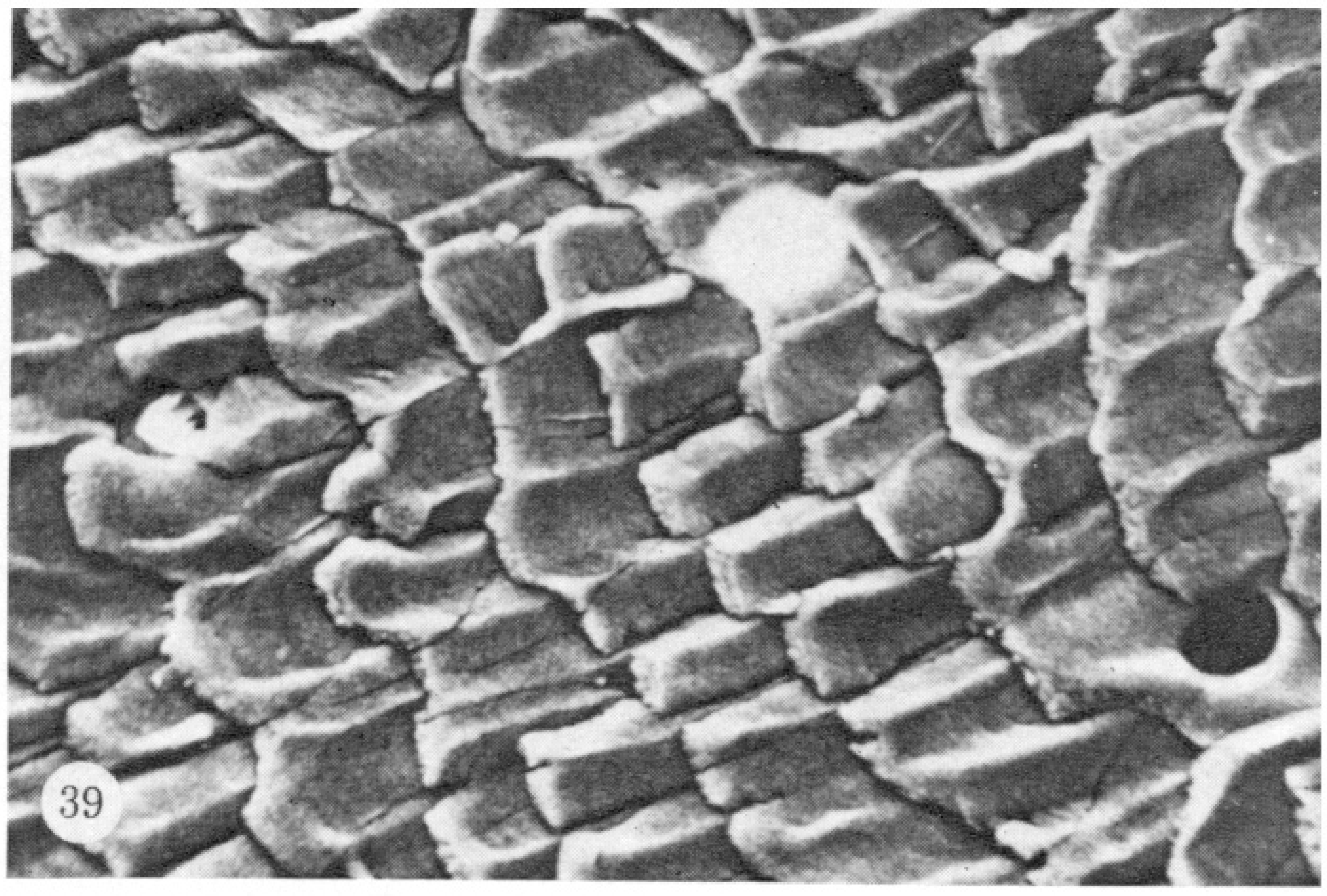
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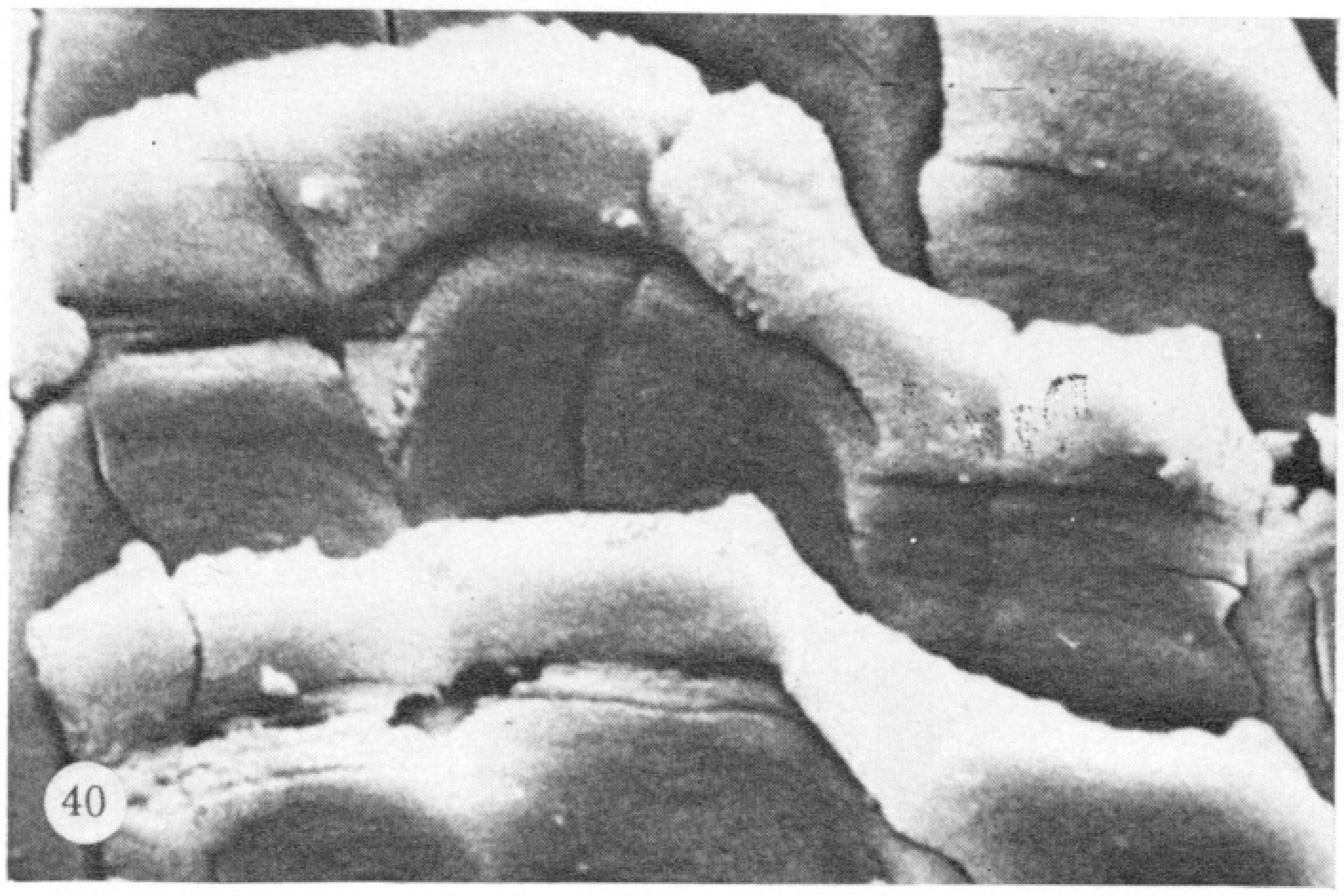
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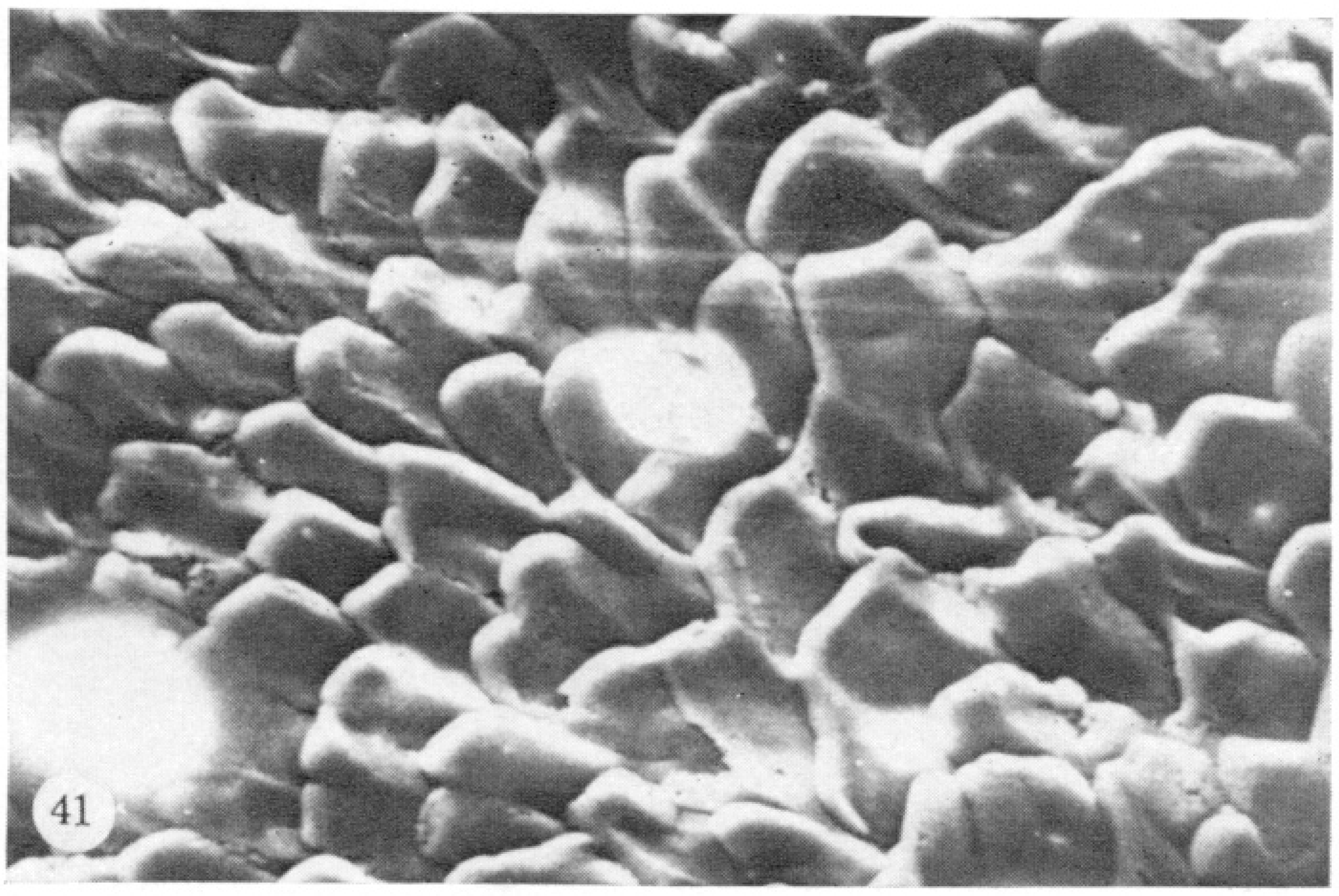
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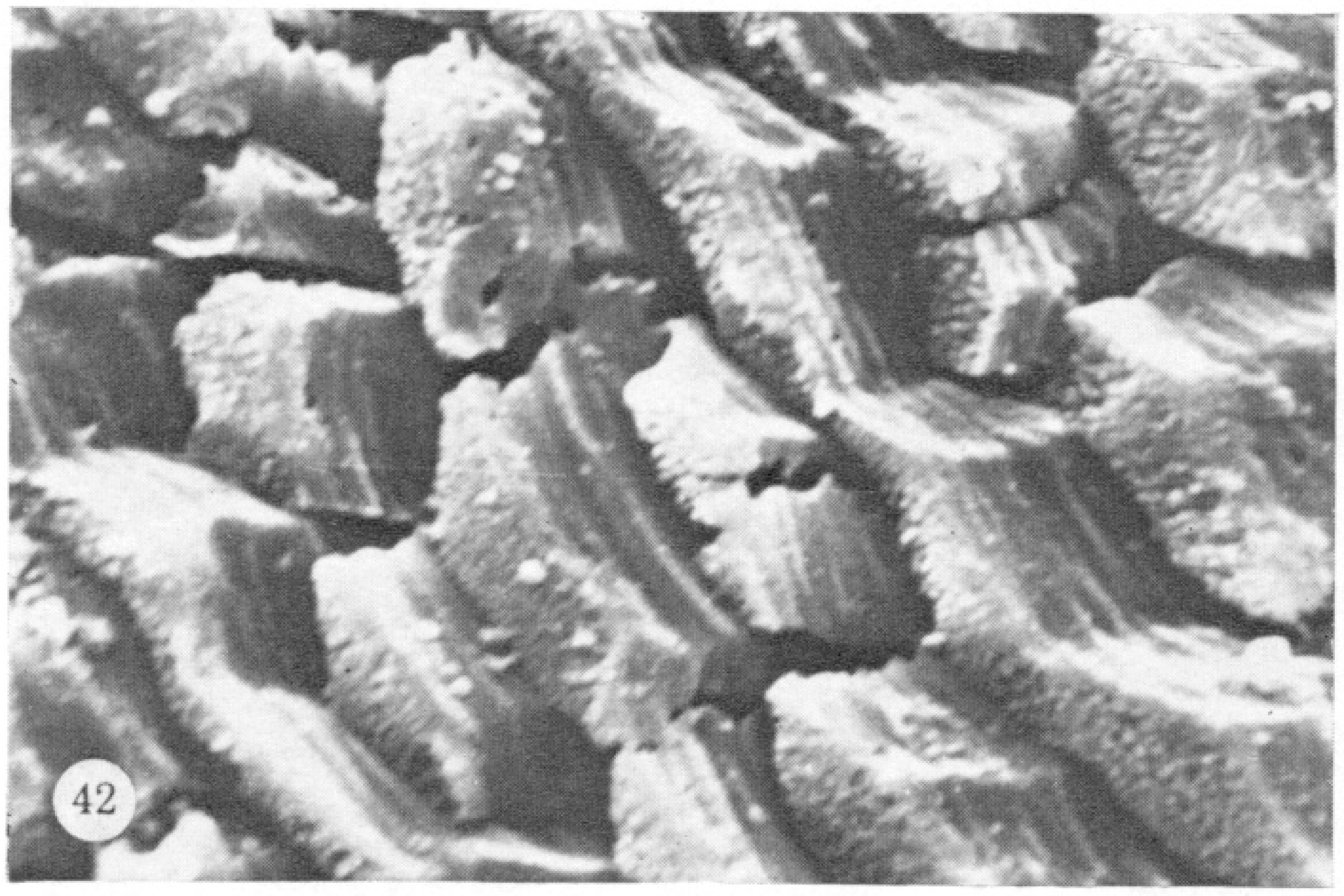
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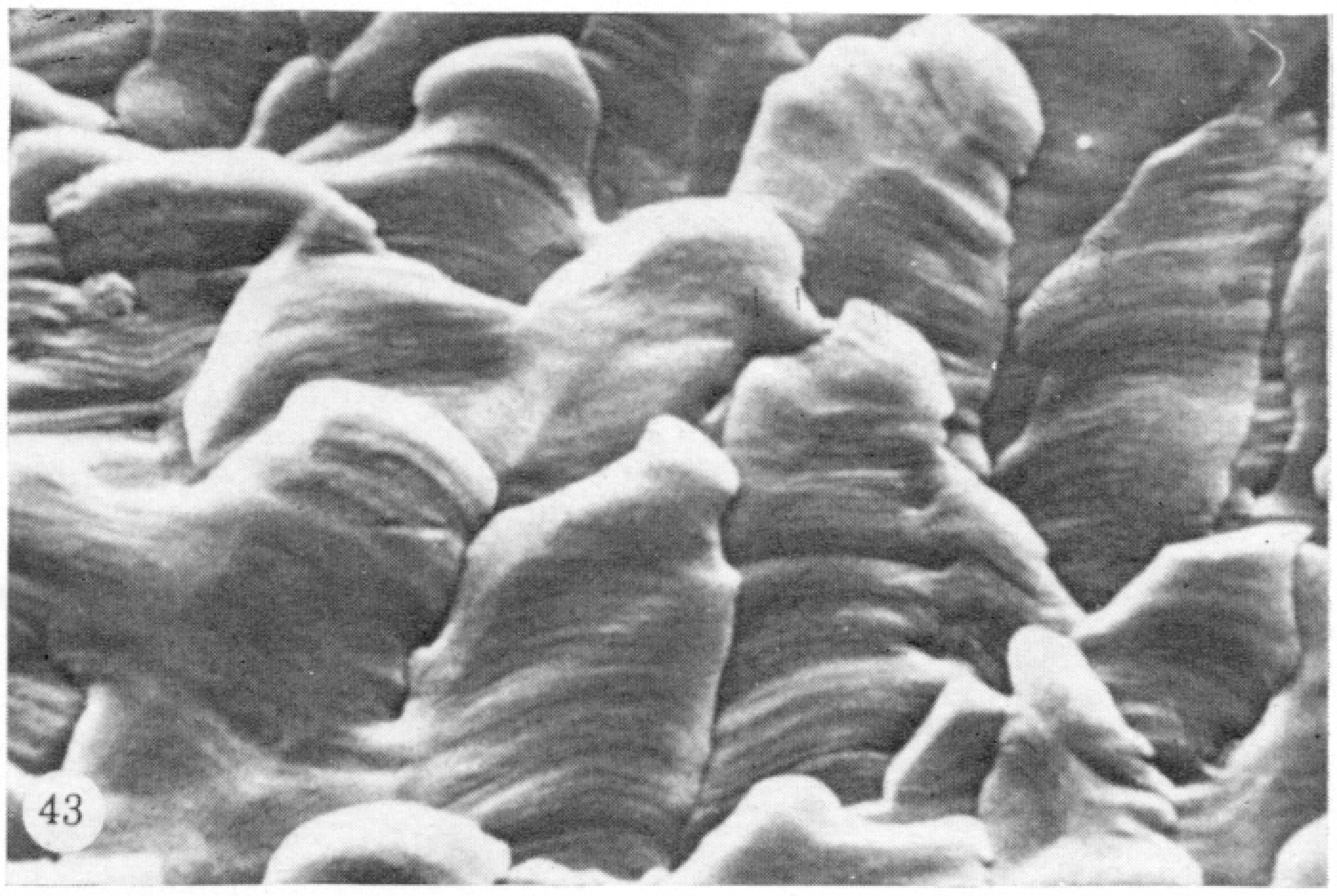
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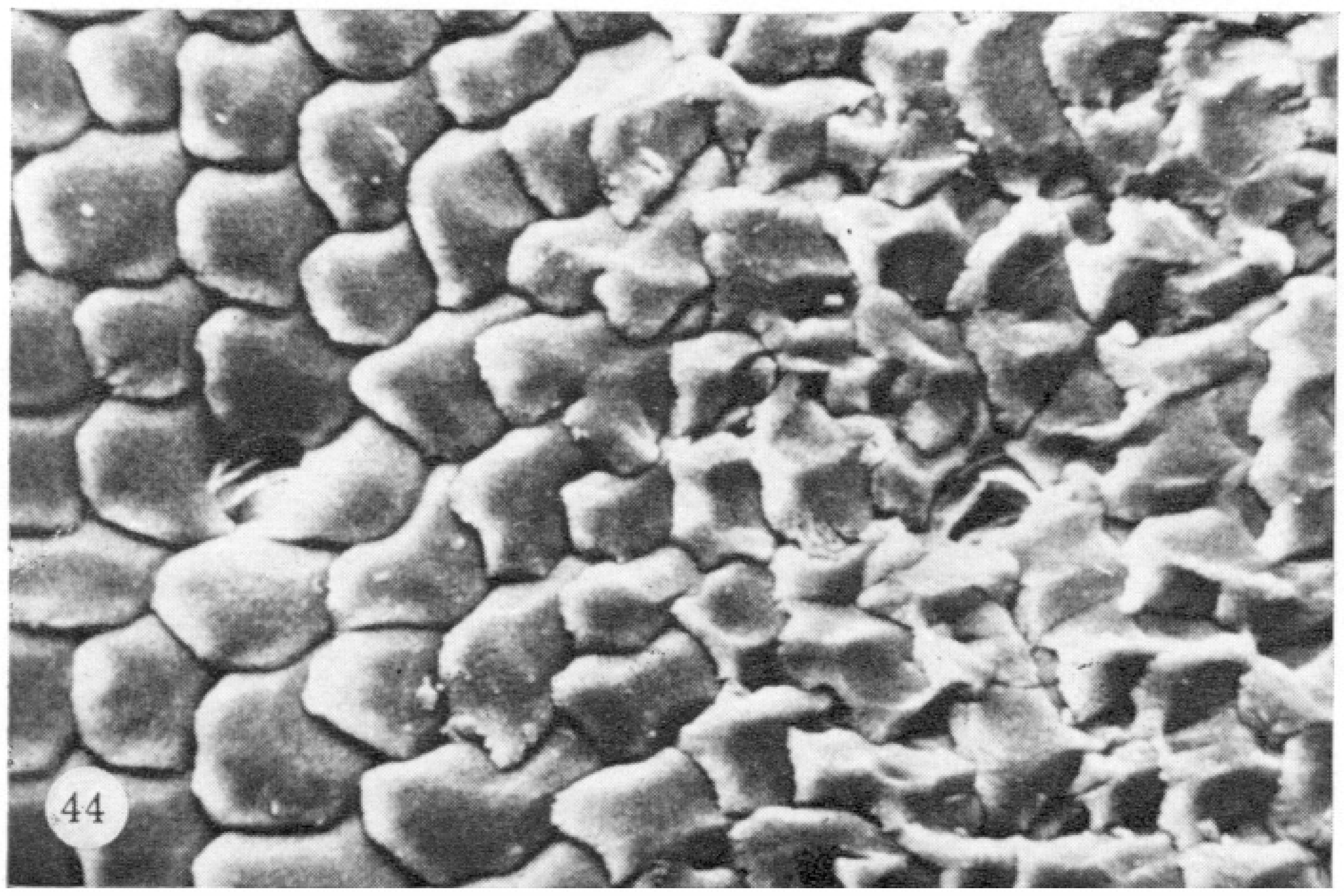
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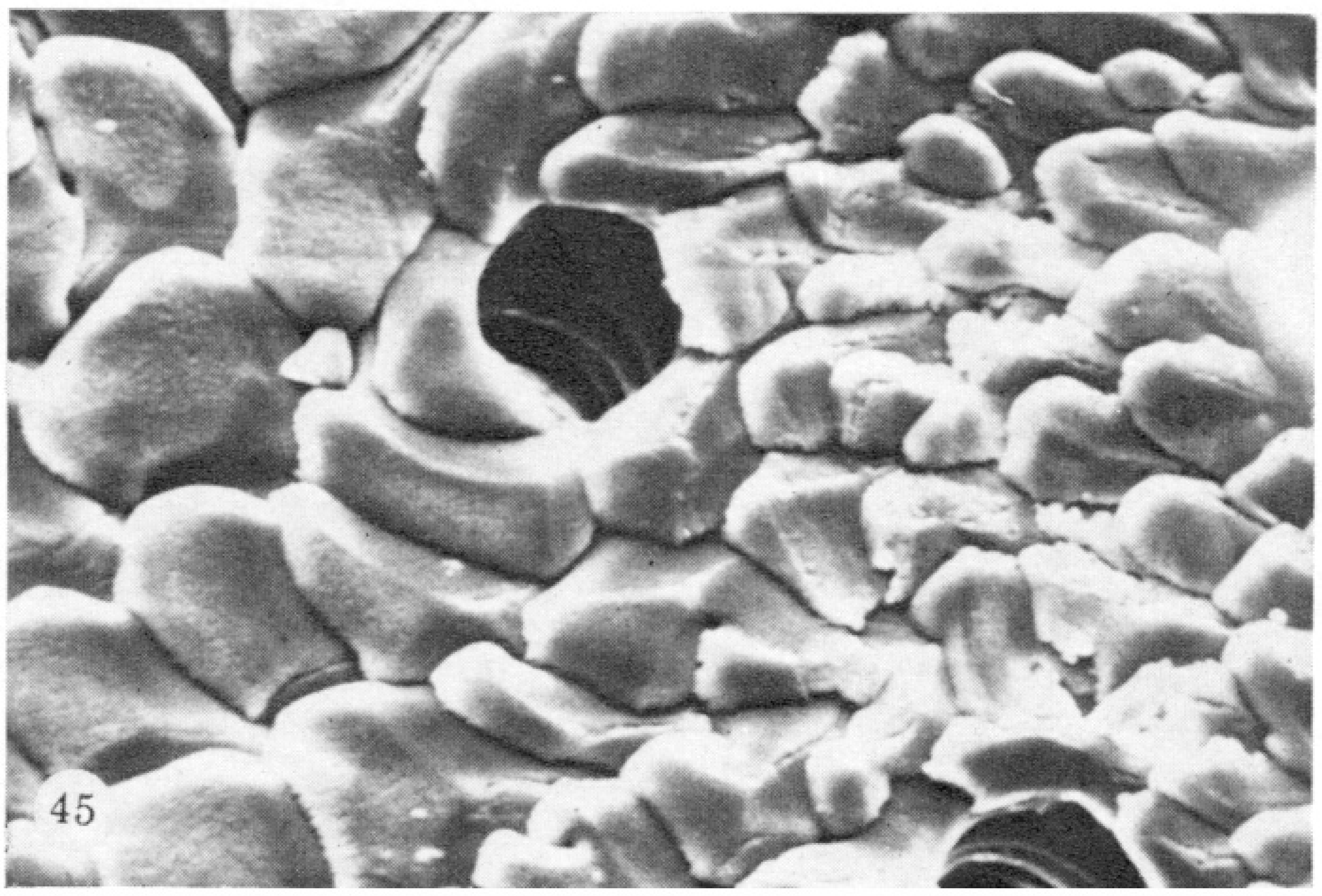
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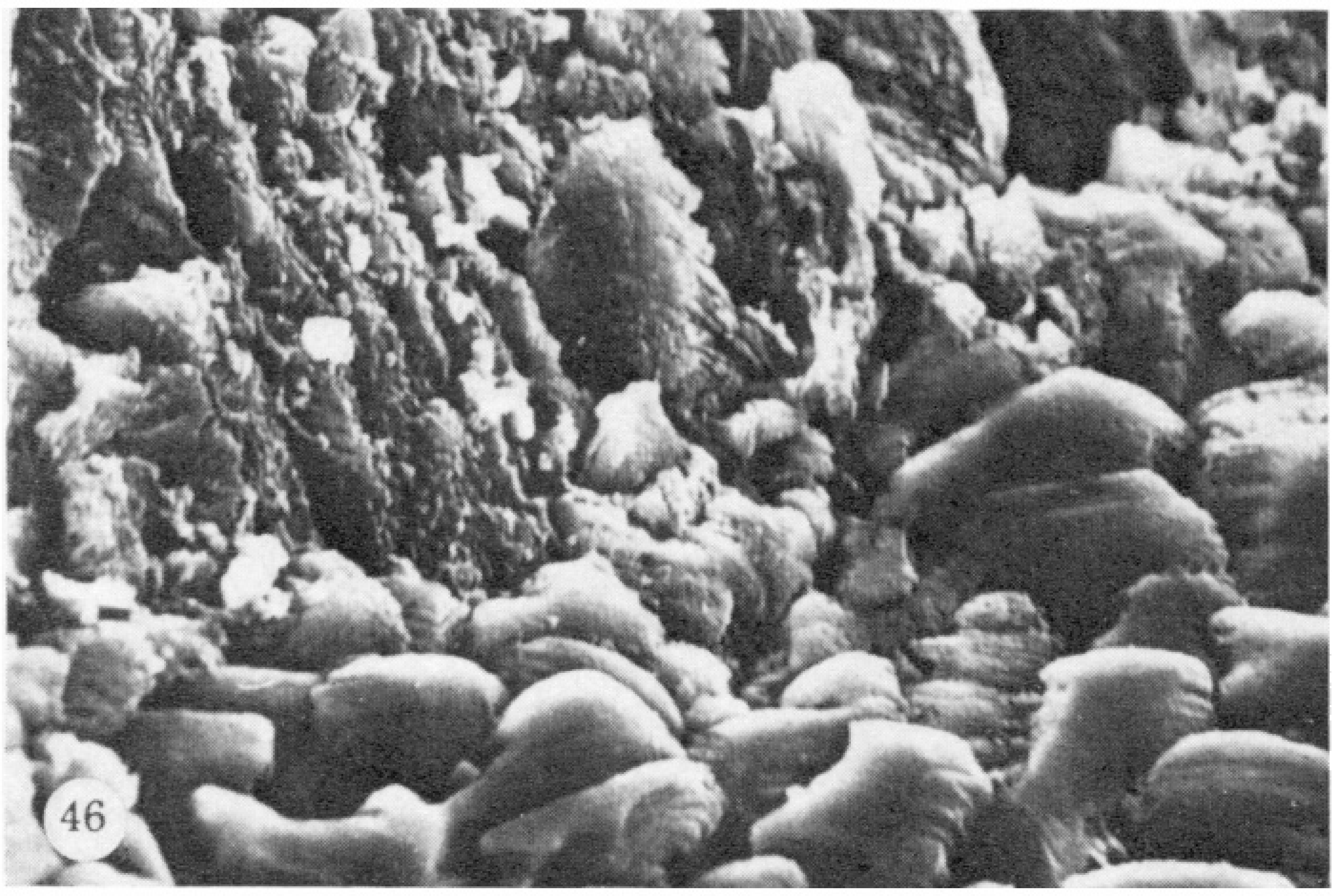
FIGURES 38–45. For description see opposite.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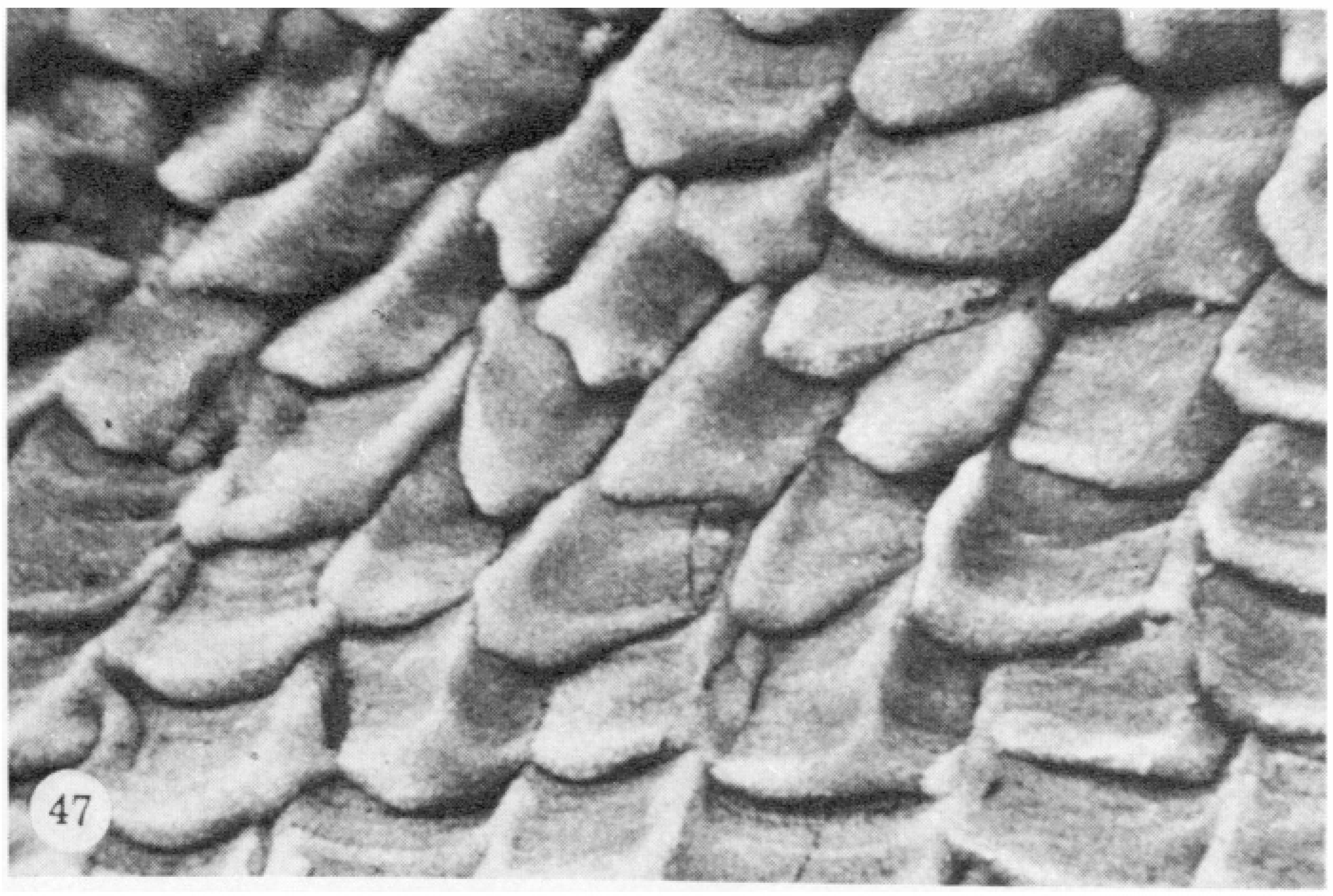
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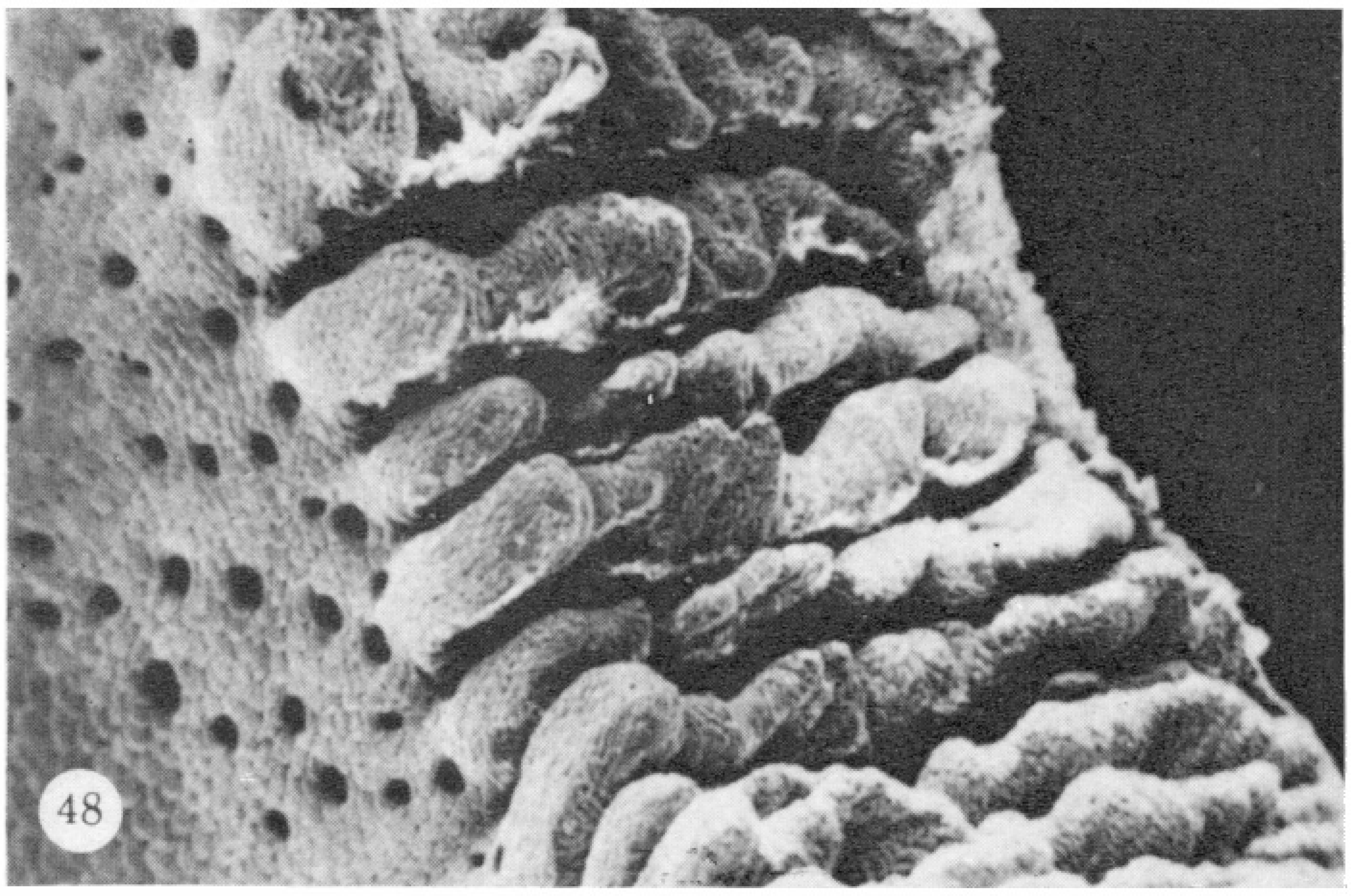
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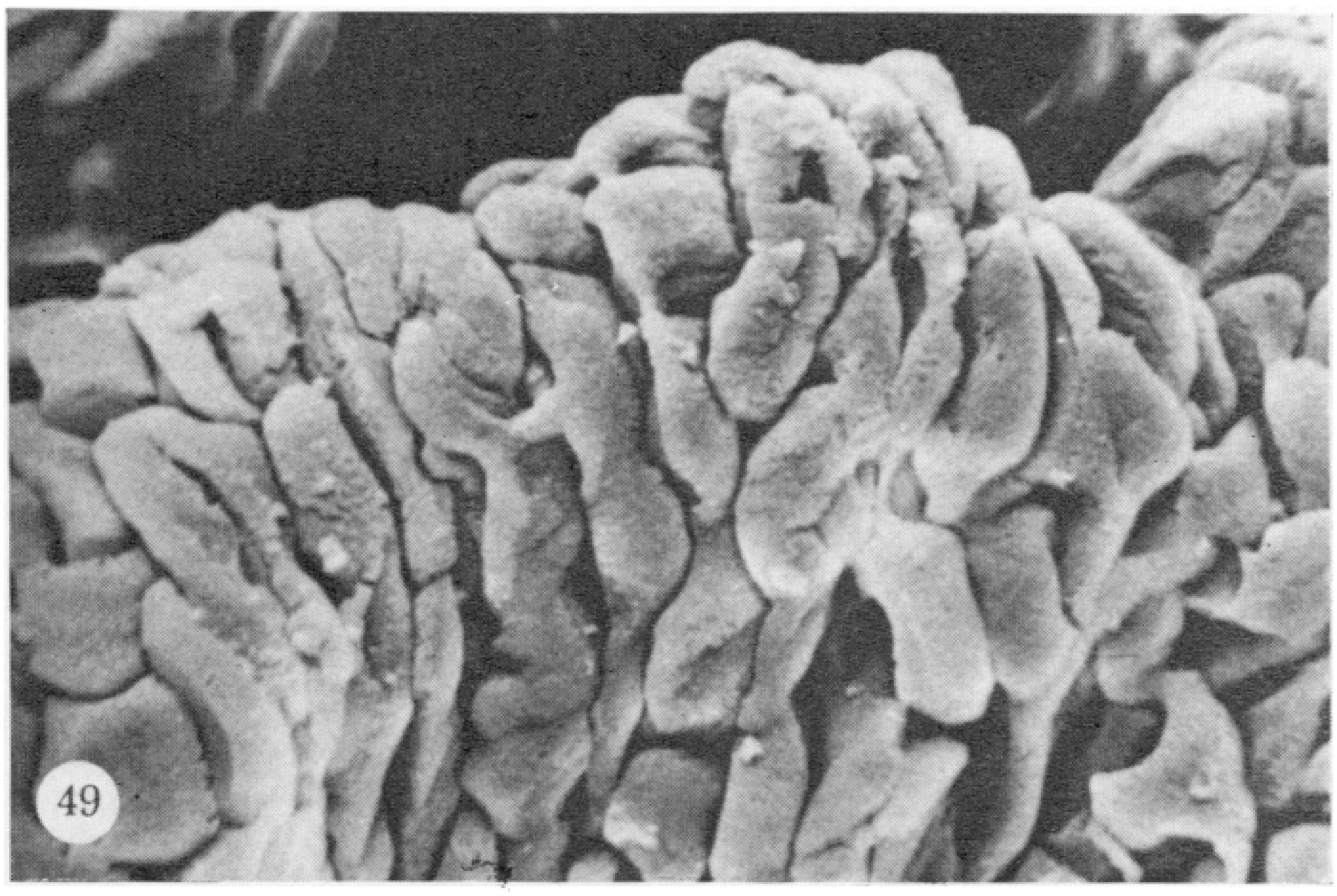
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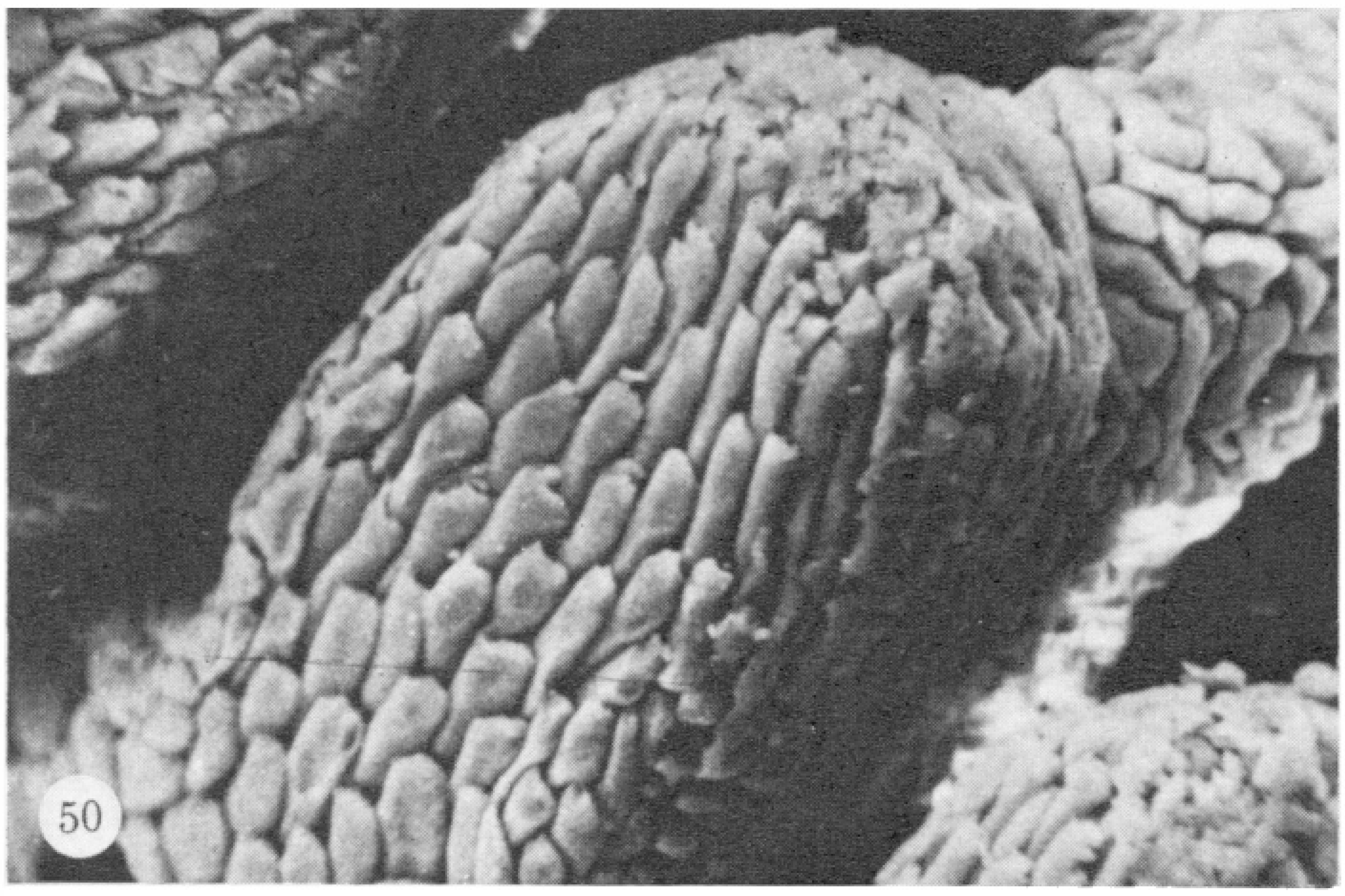
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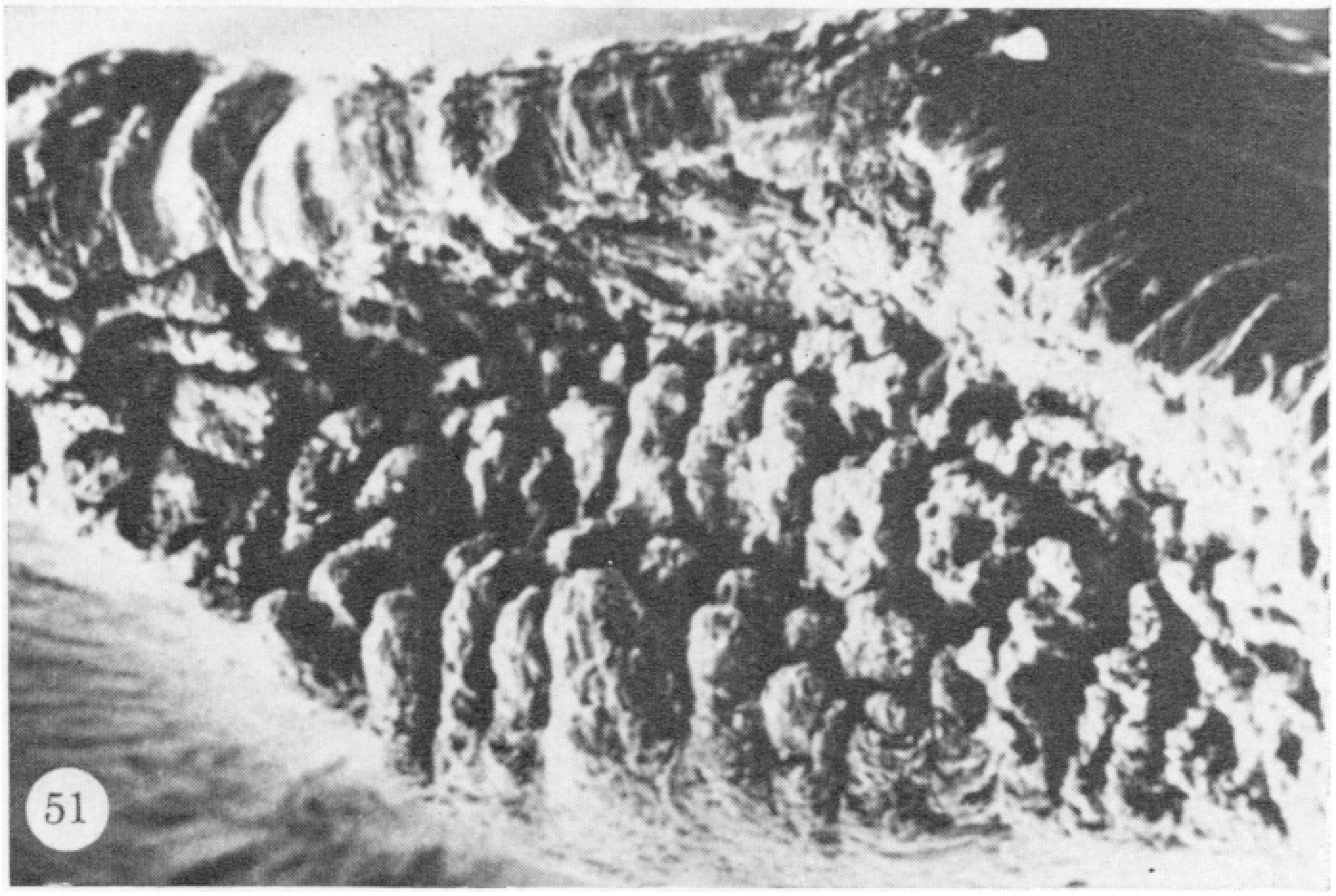
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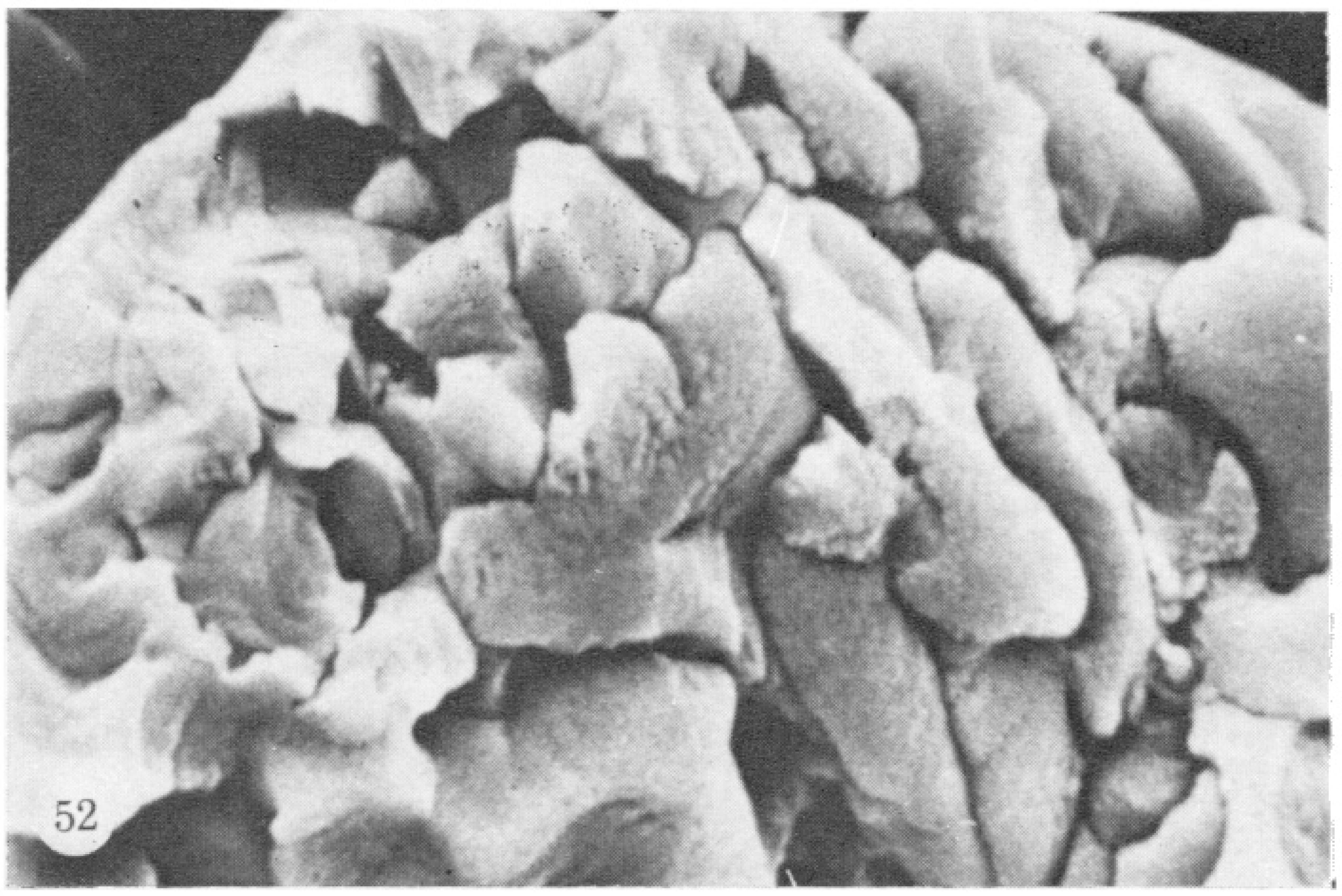
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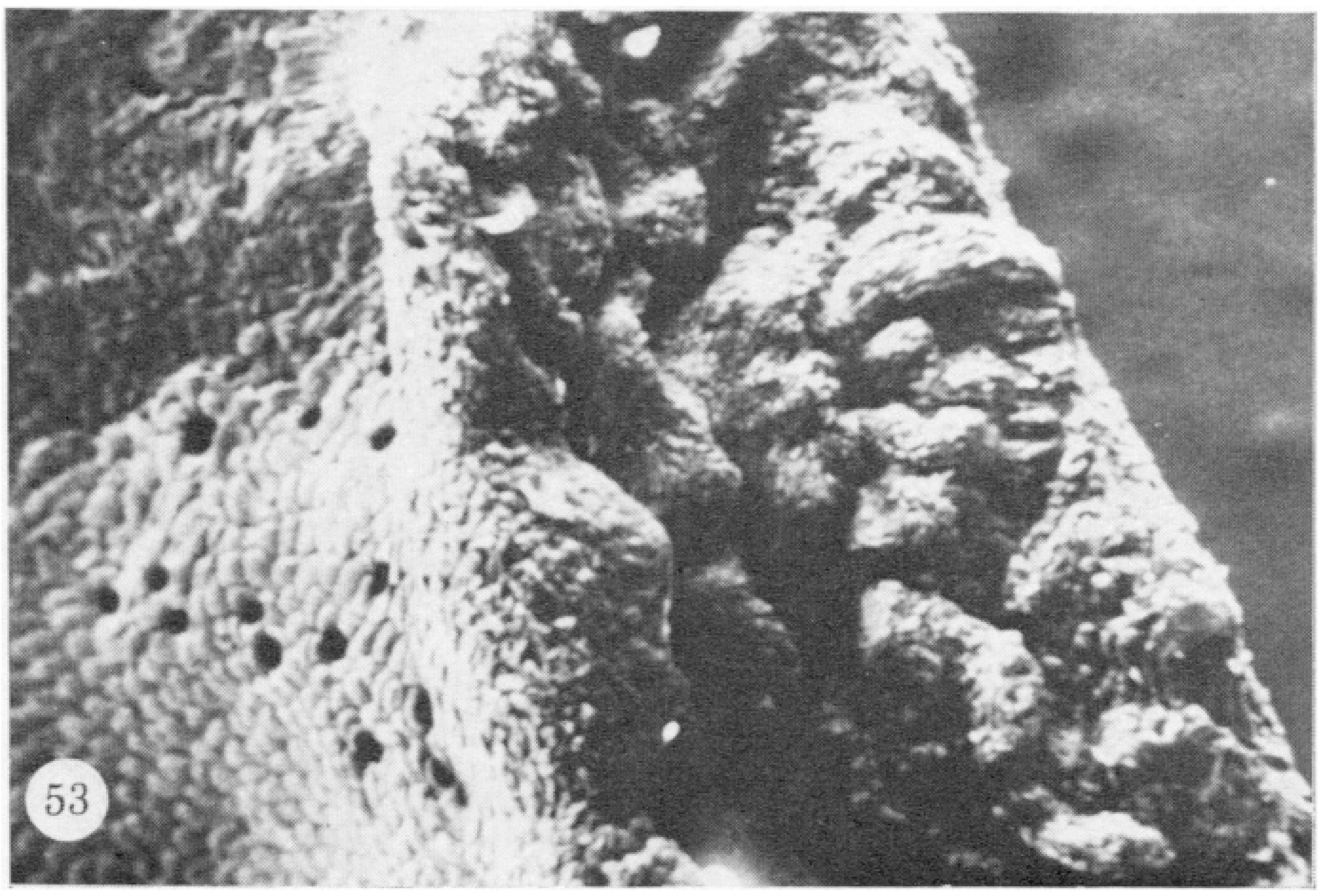
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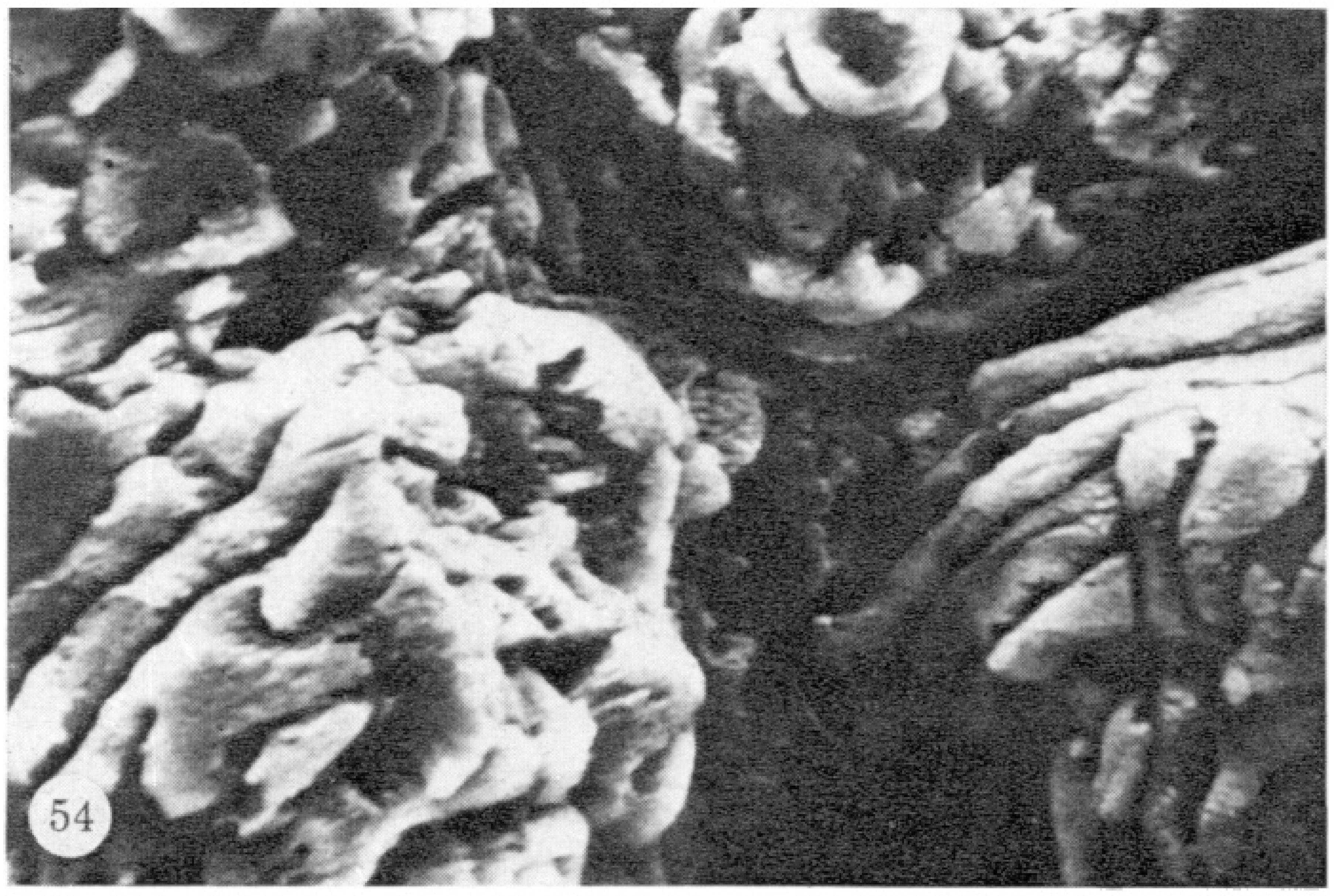
FIGURES 46–53. For description see opposite.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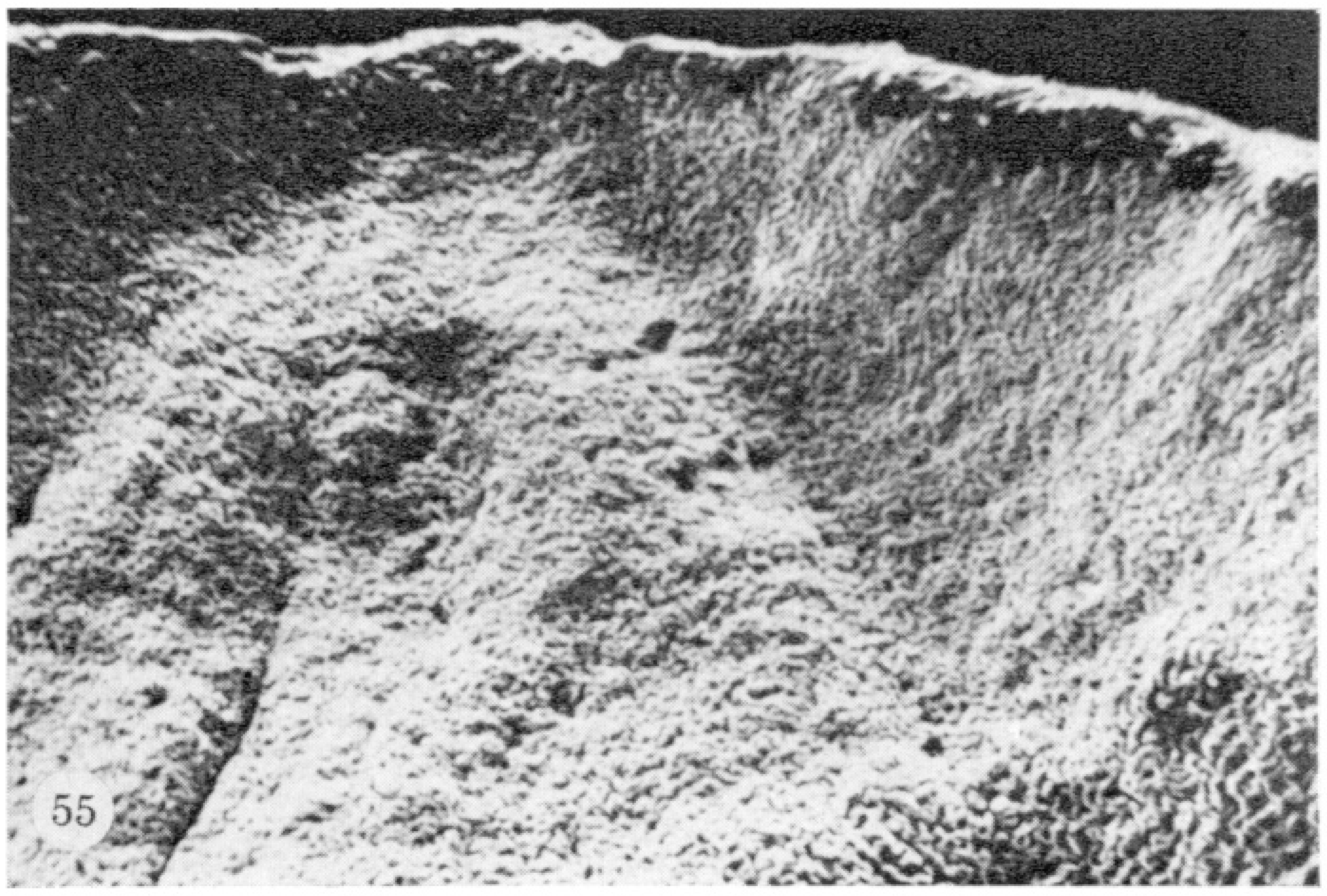
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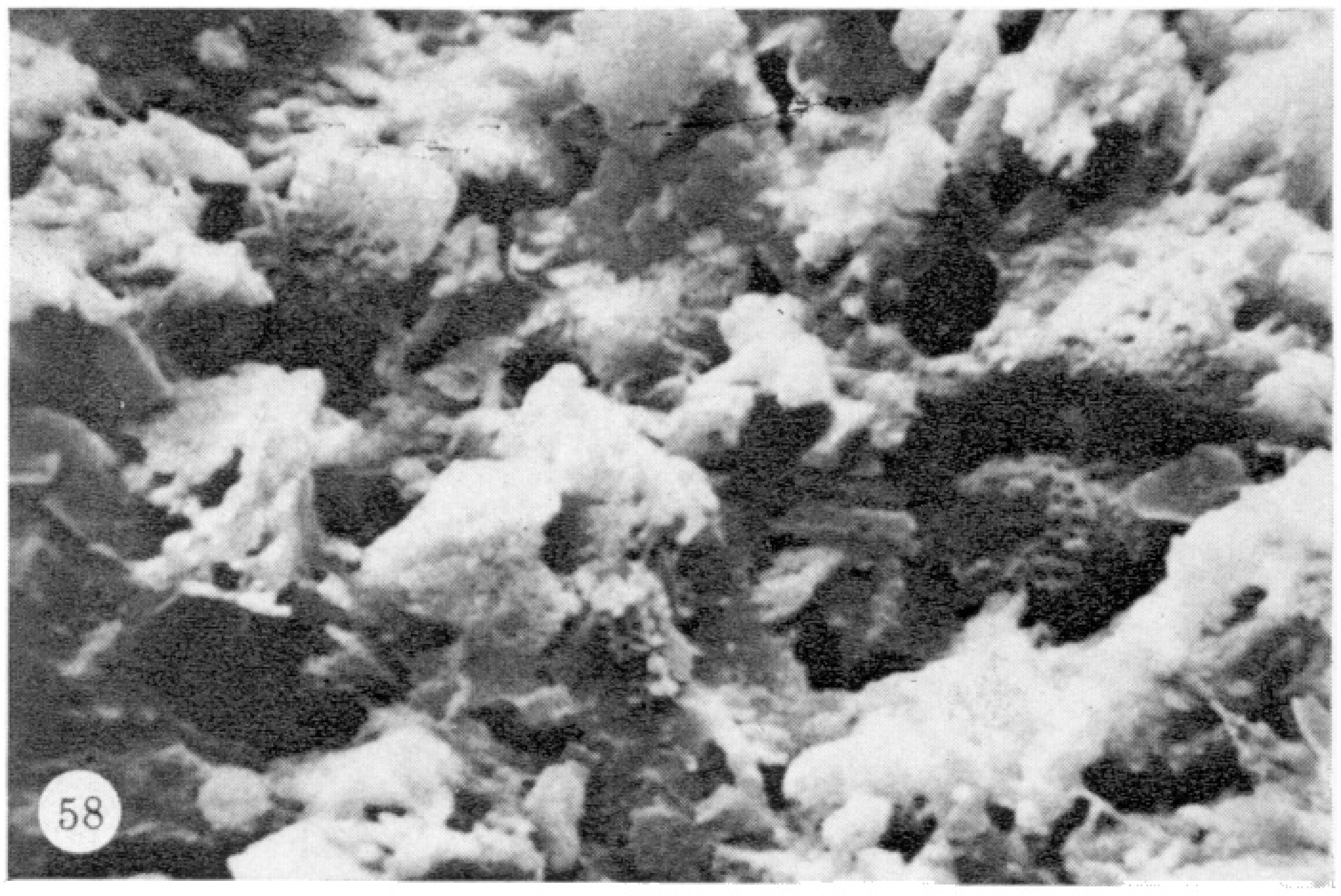
56


57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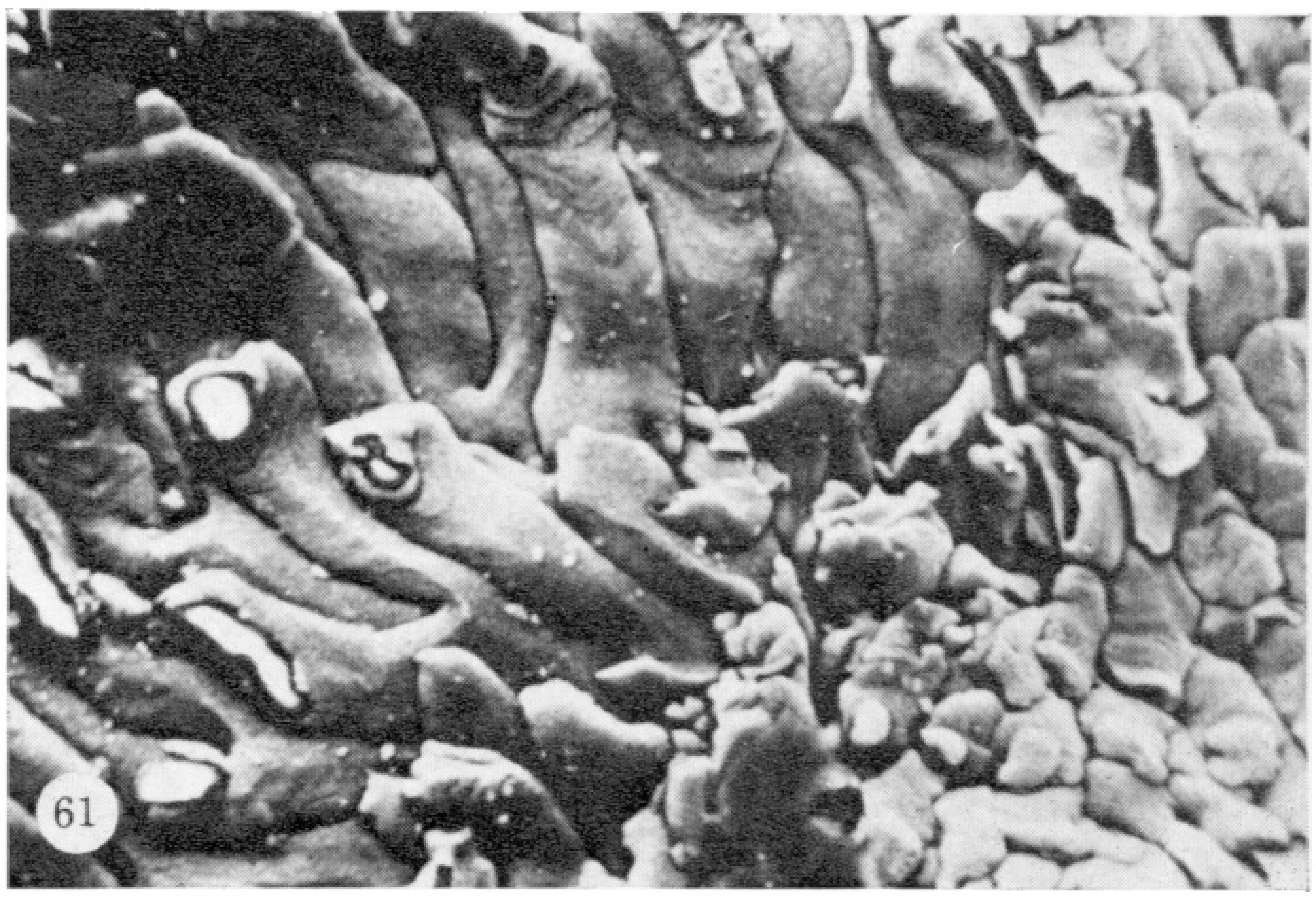
59


60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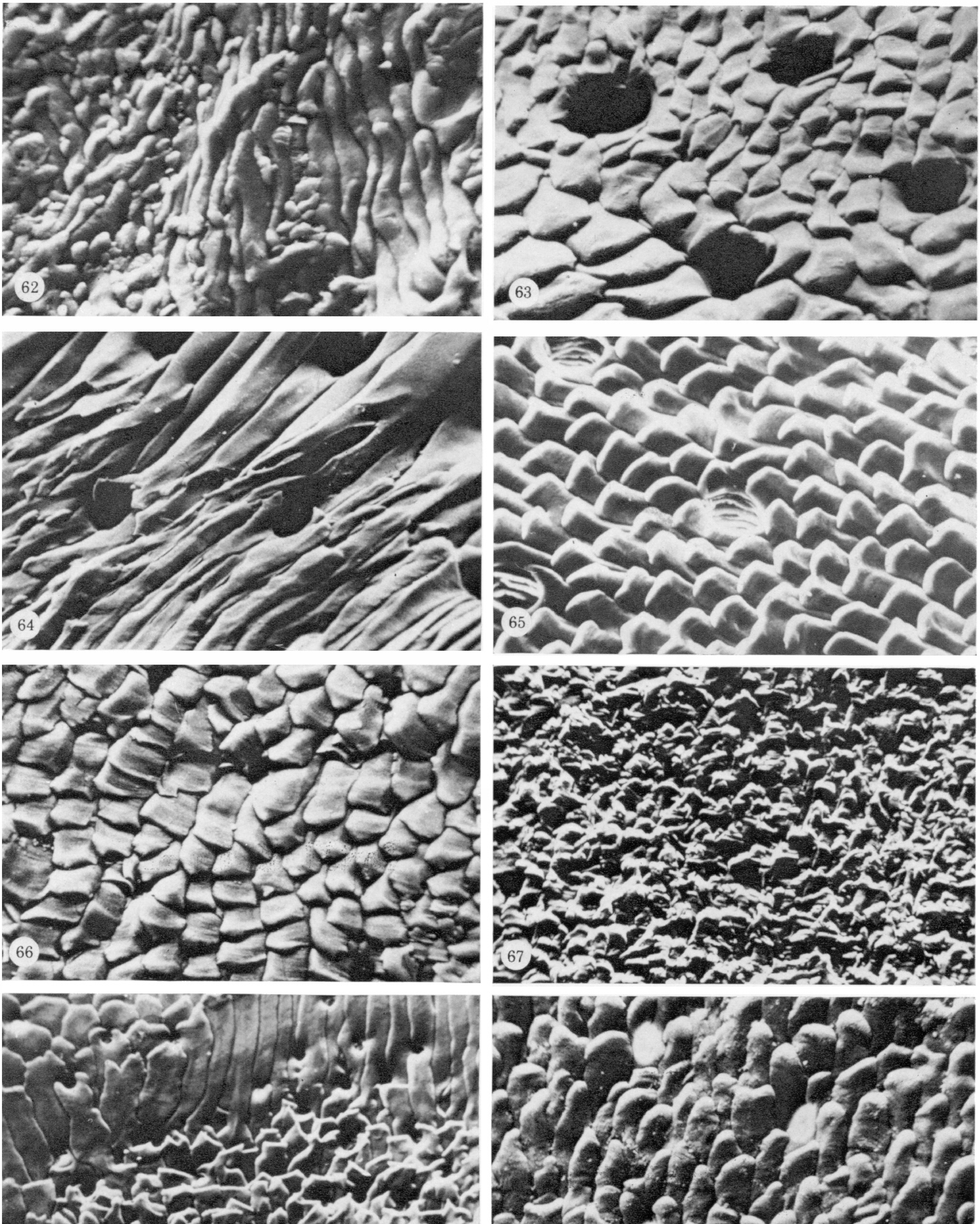
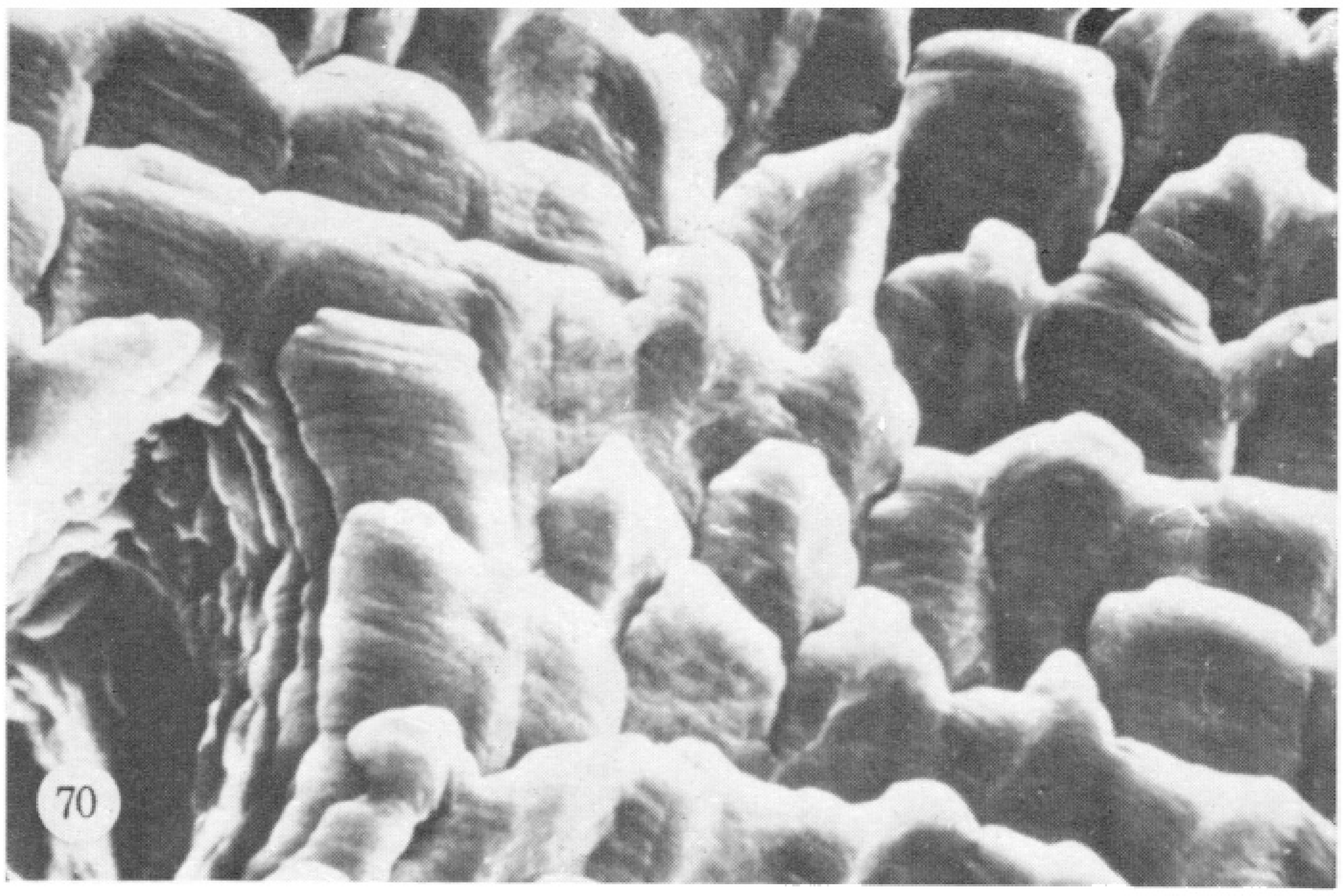
FIGURES 54–61. For description see opposite.



FIGURES 62–69. For description see opposite.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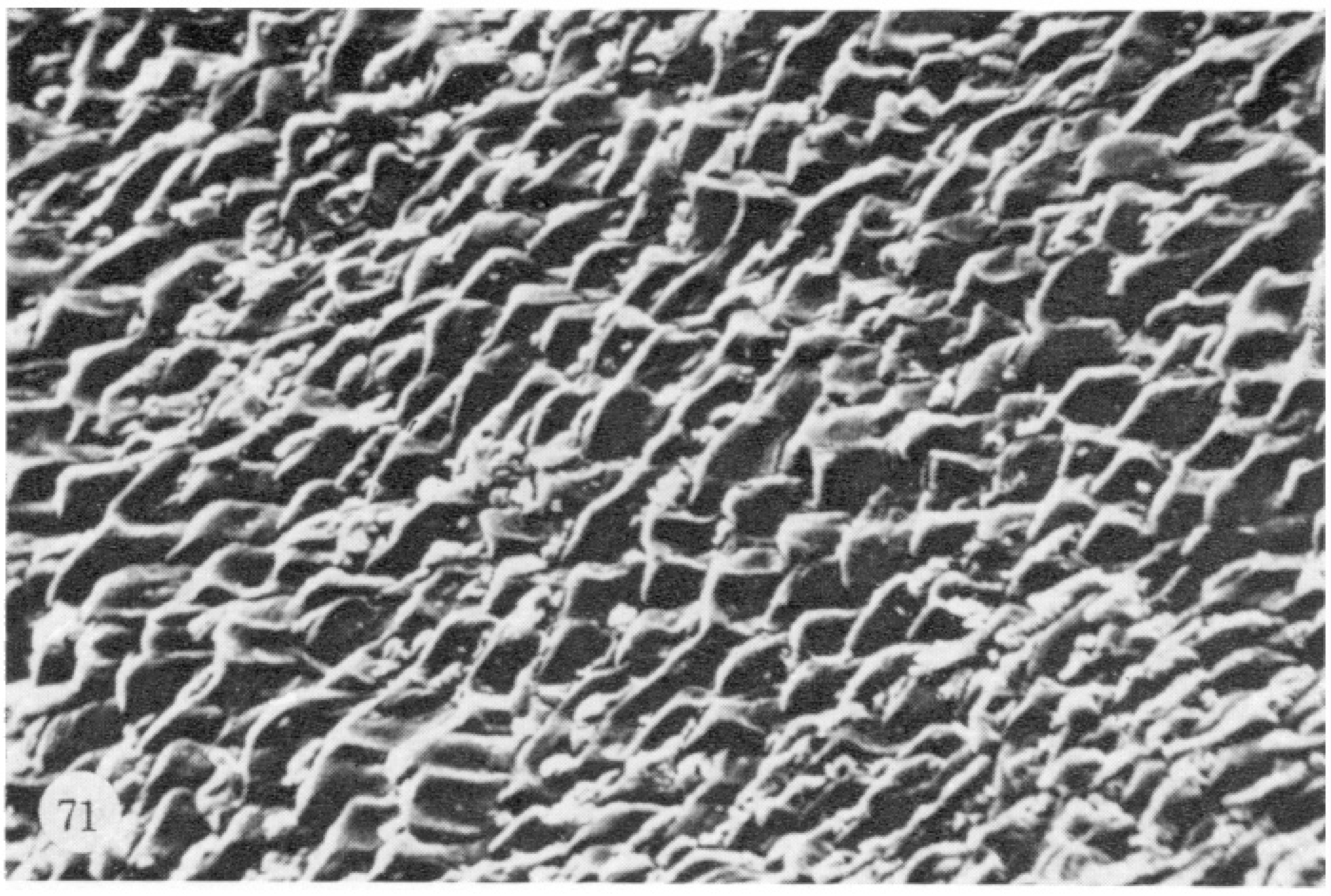
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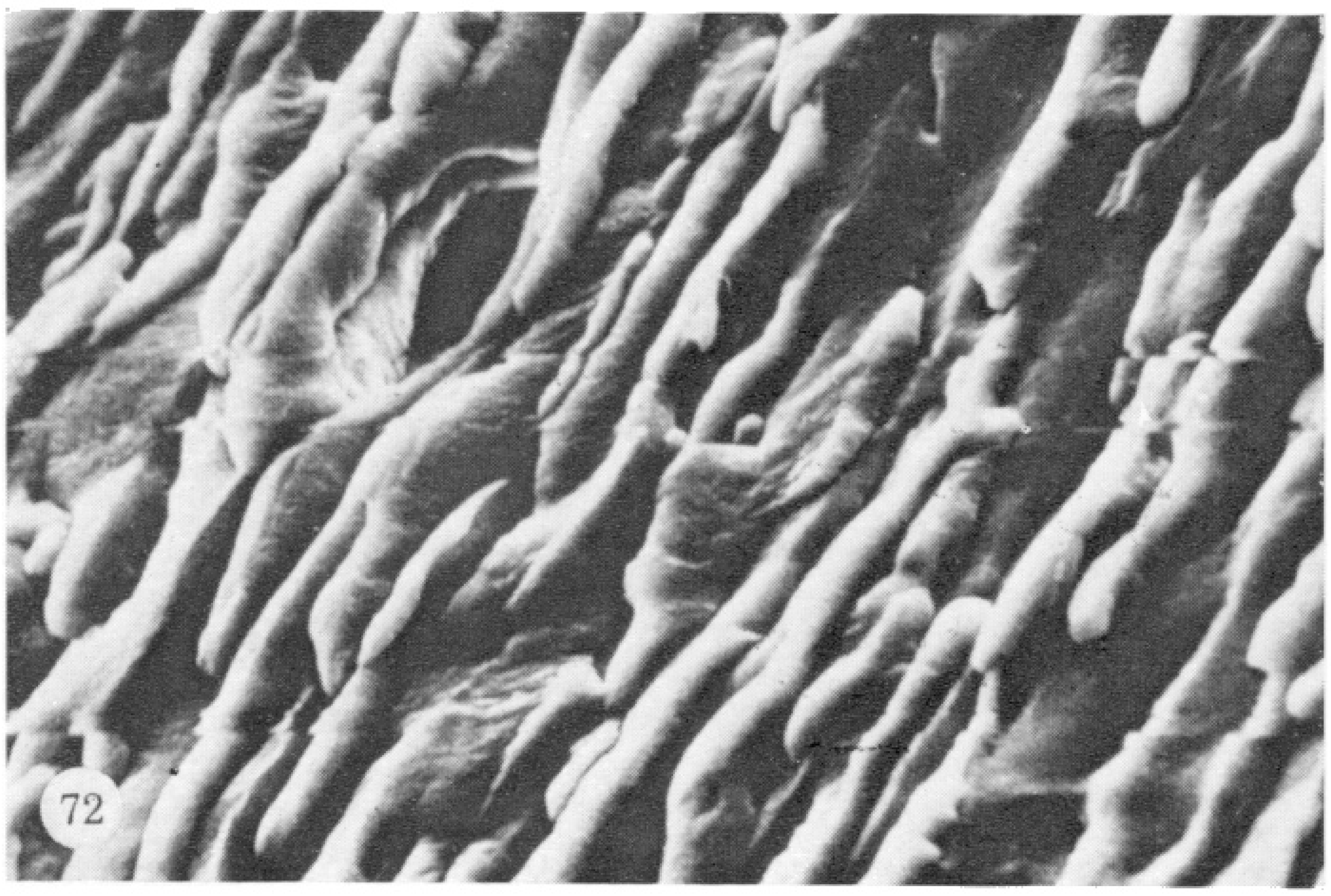
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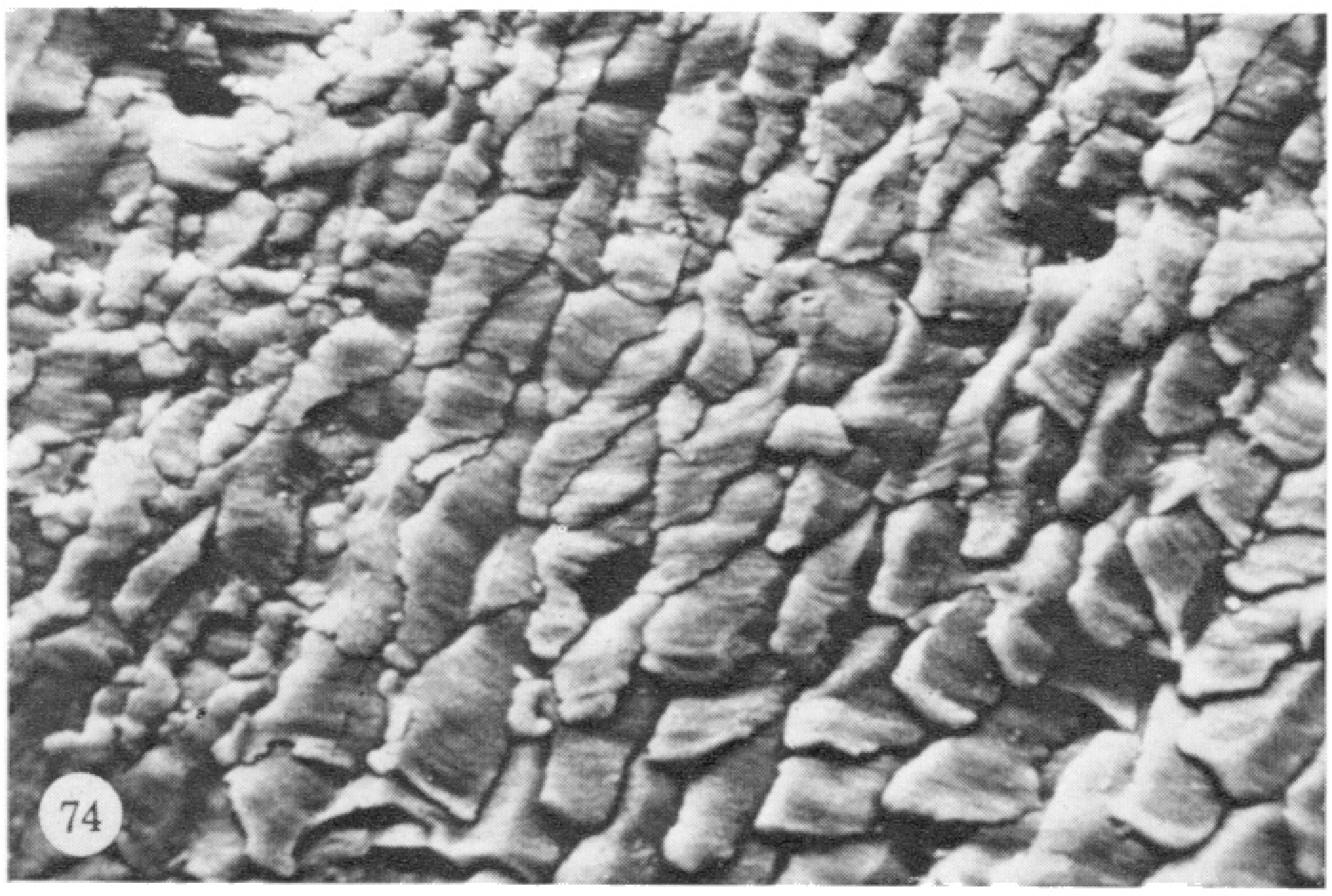
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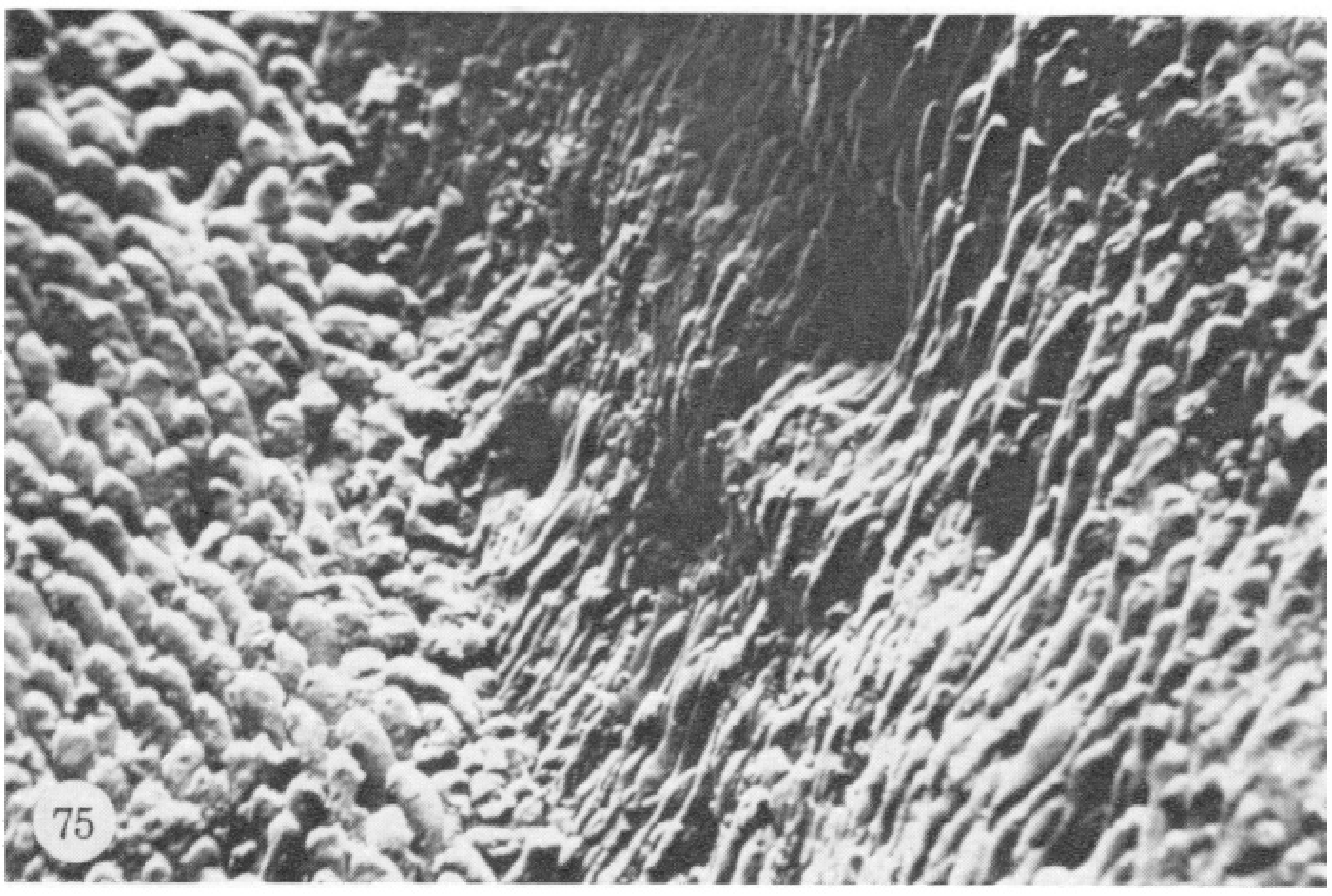
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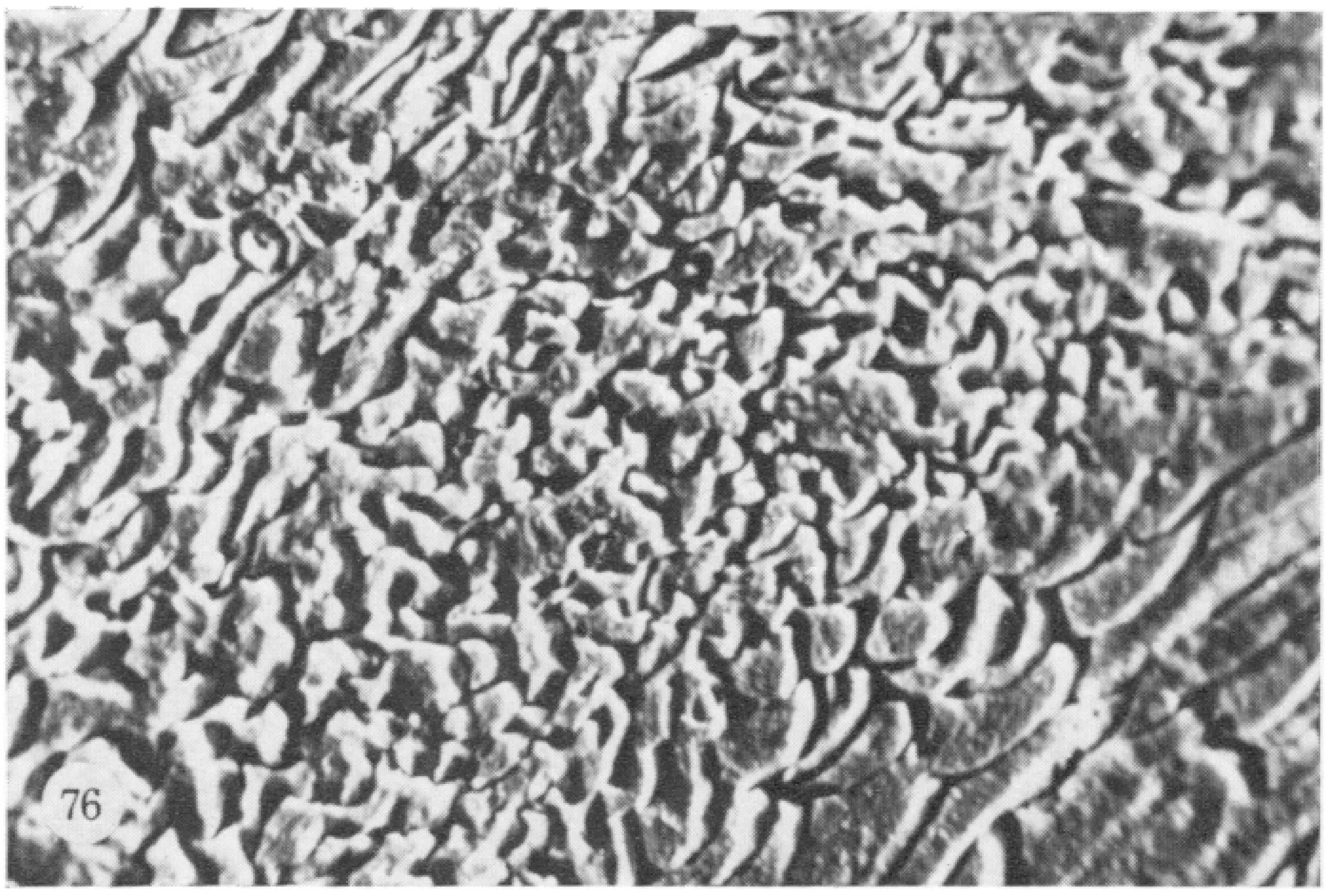
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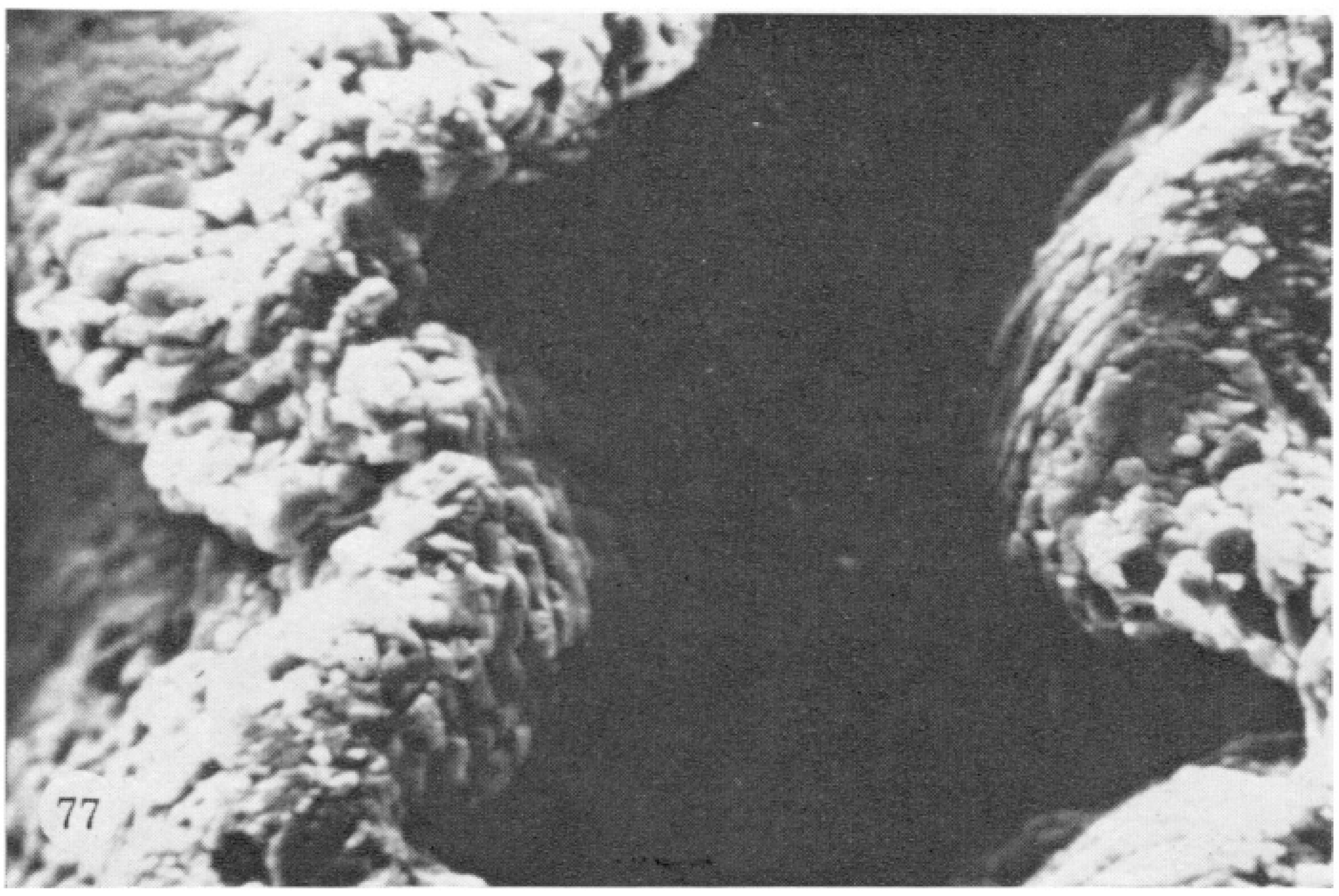
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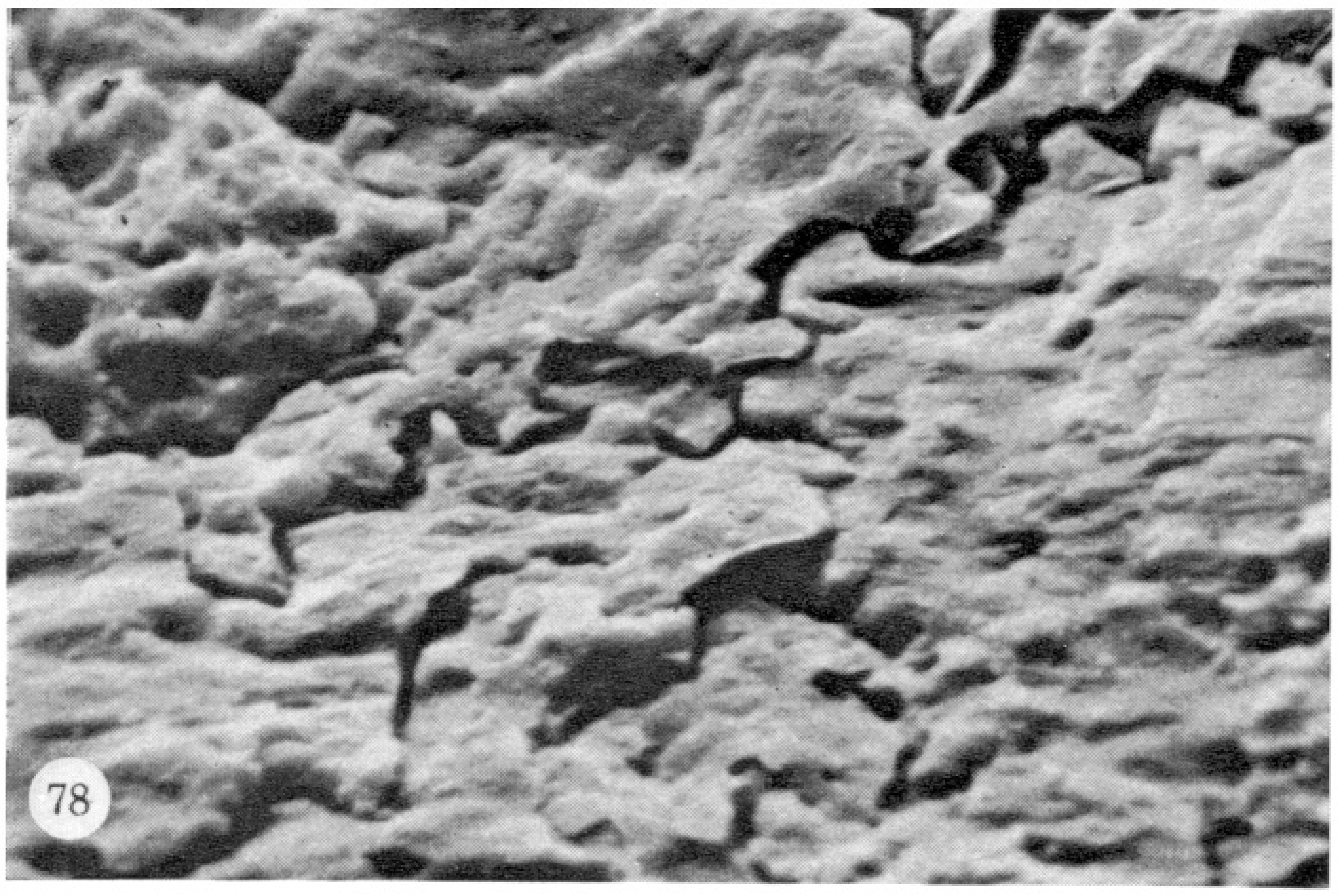
FIGURES 70–77. For description see opposite.



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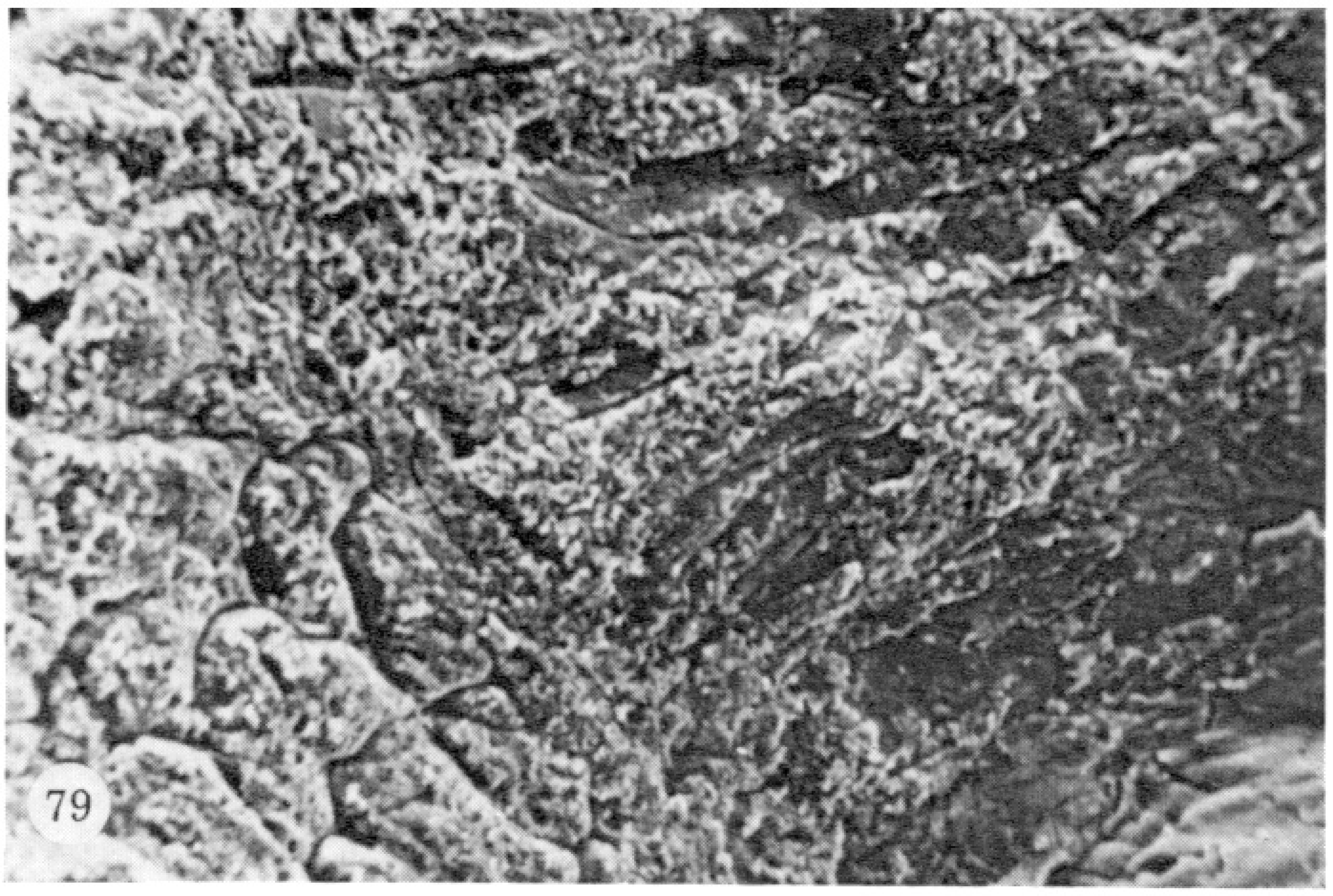

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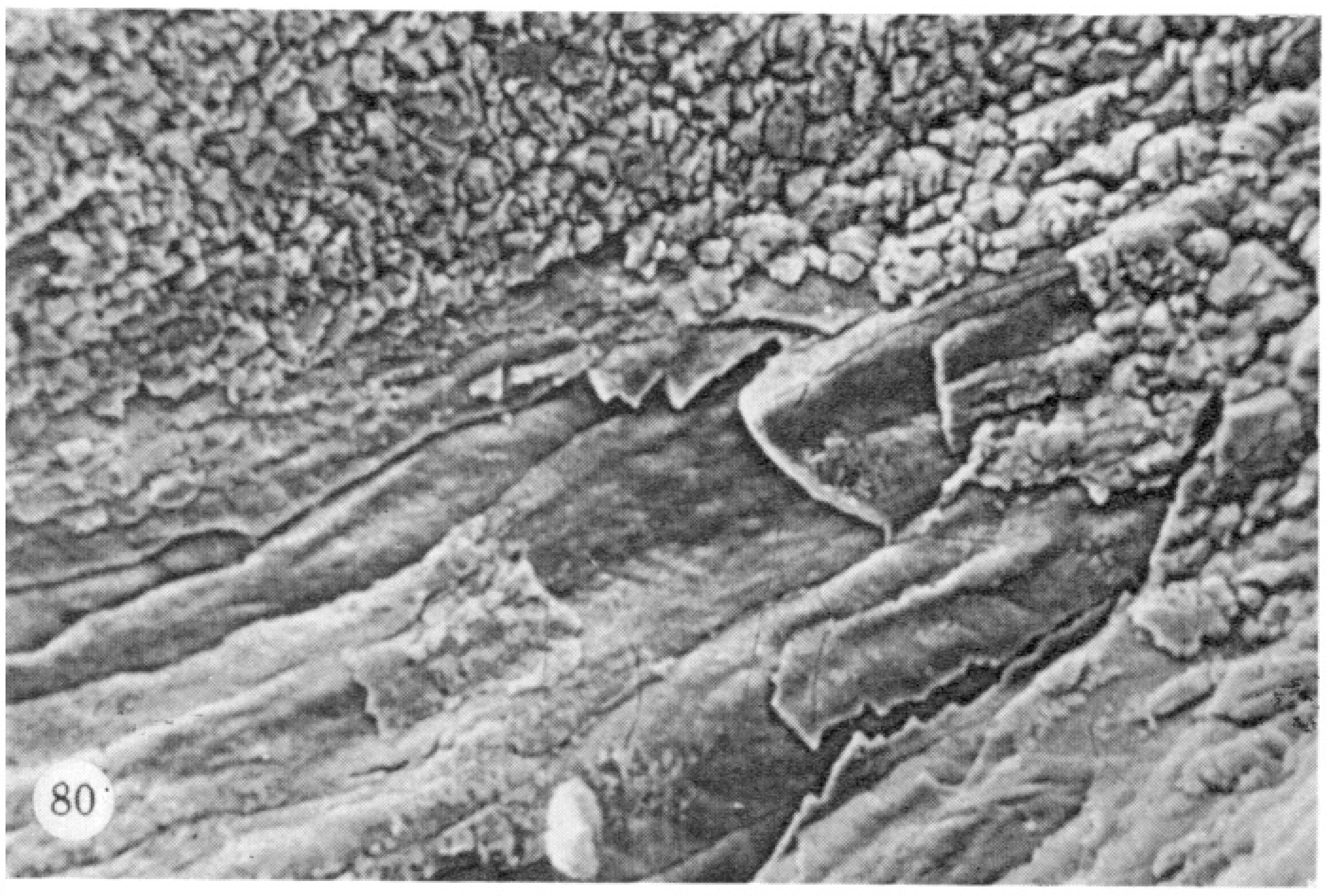

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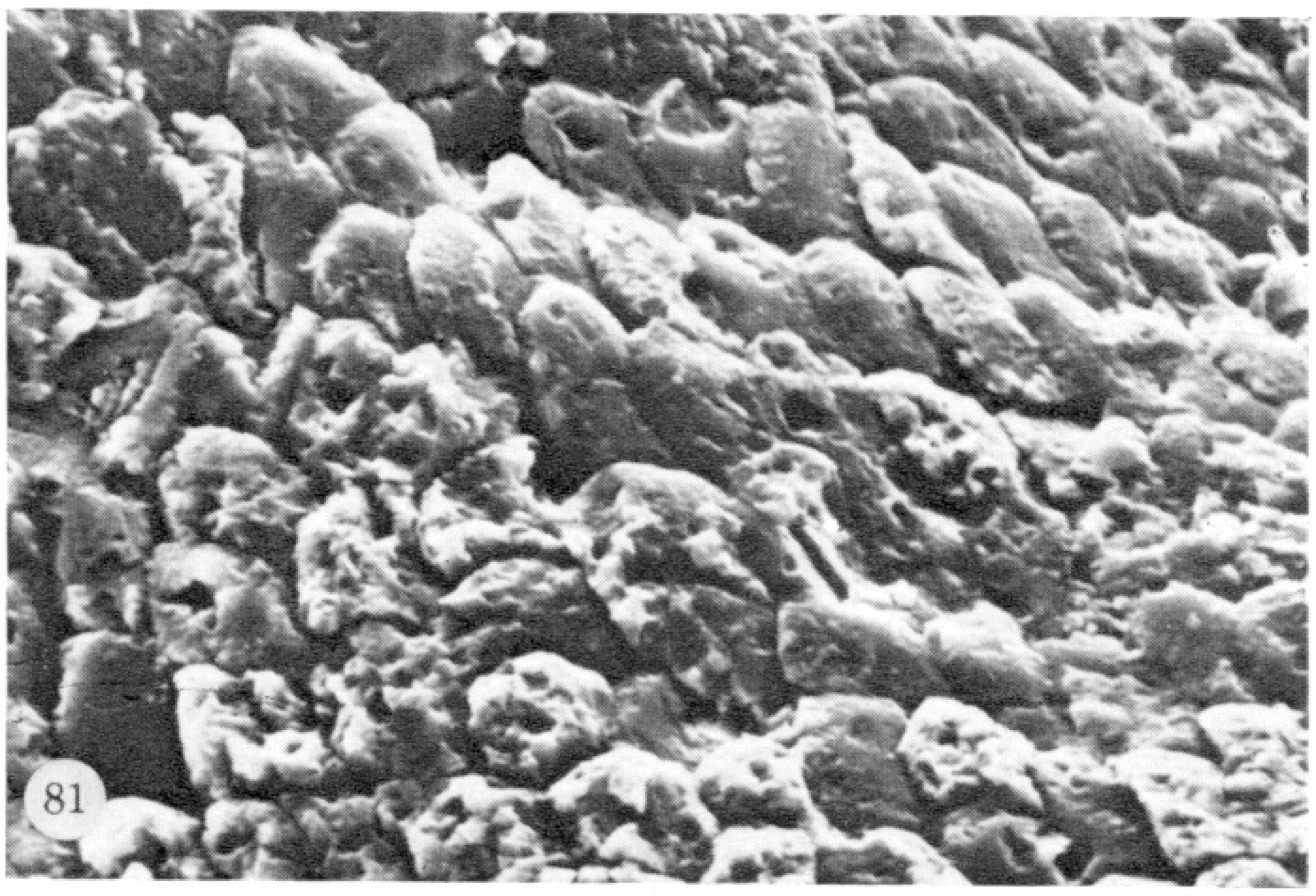

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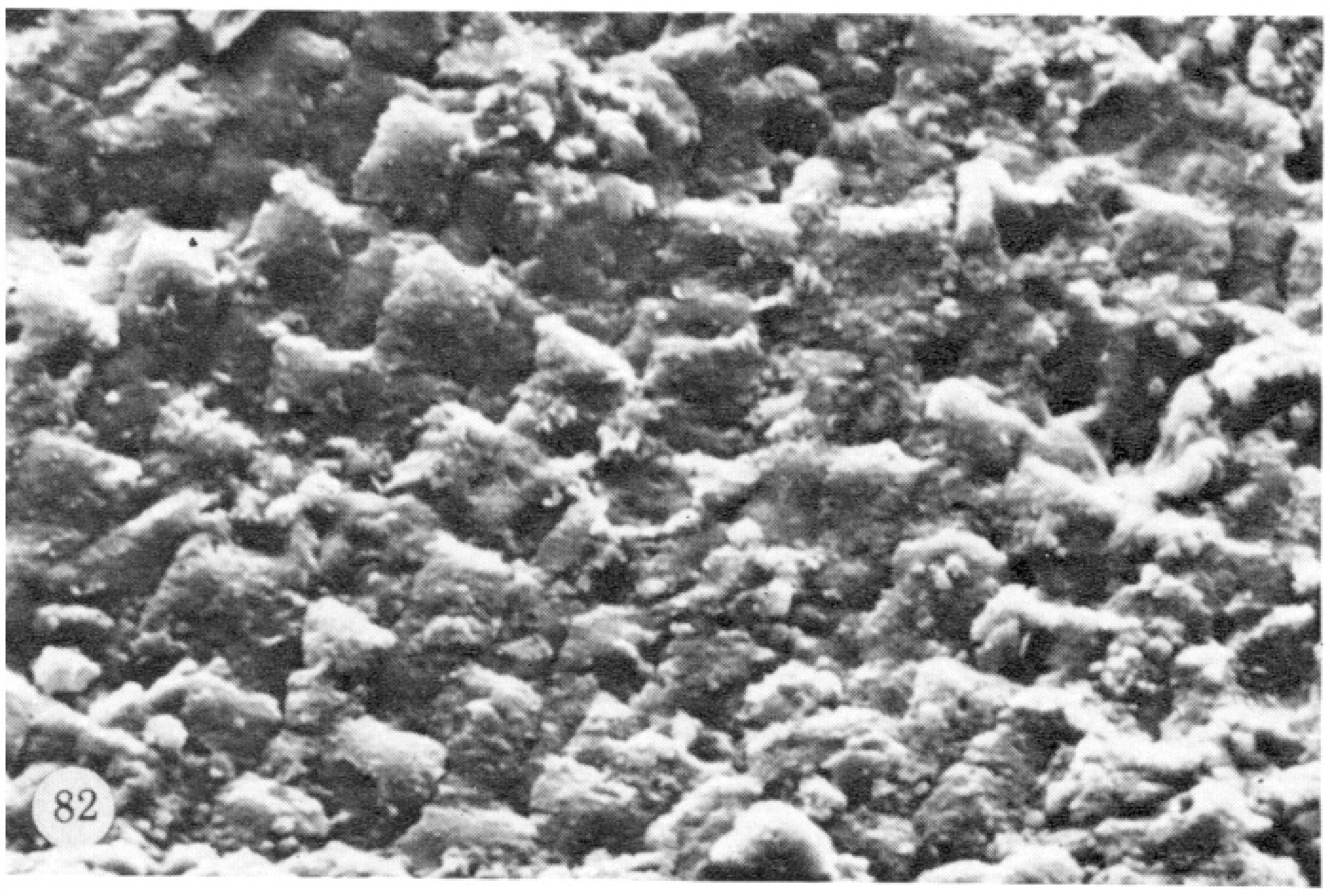

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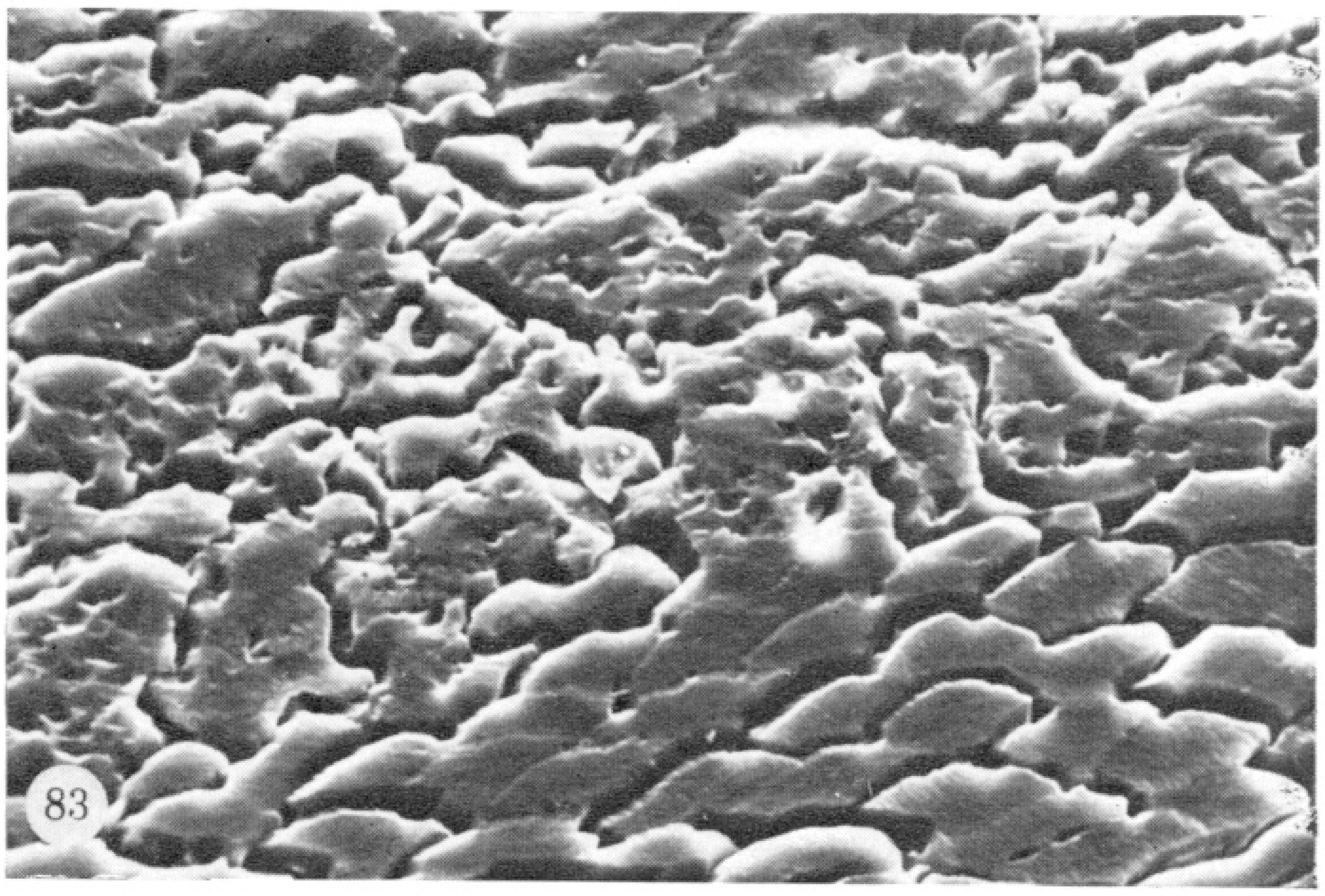

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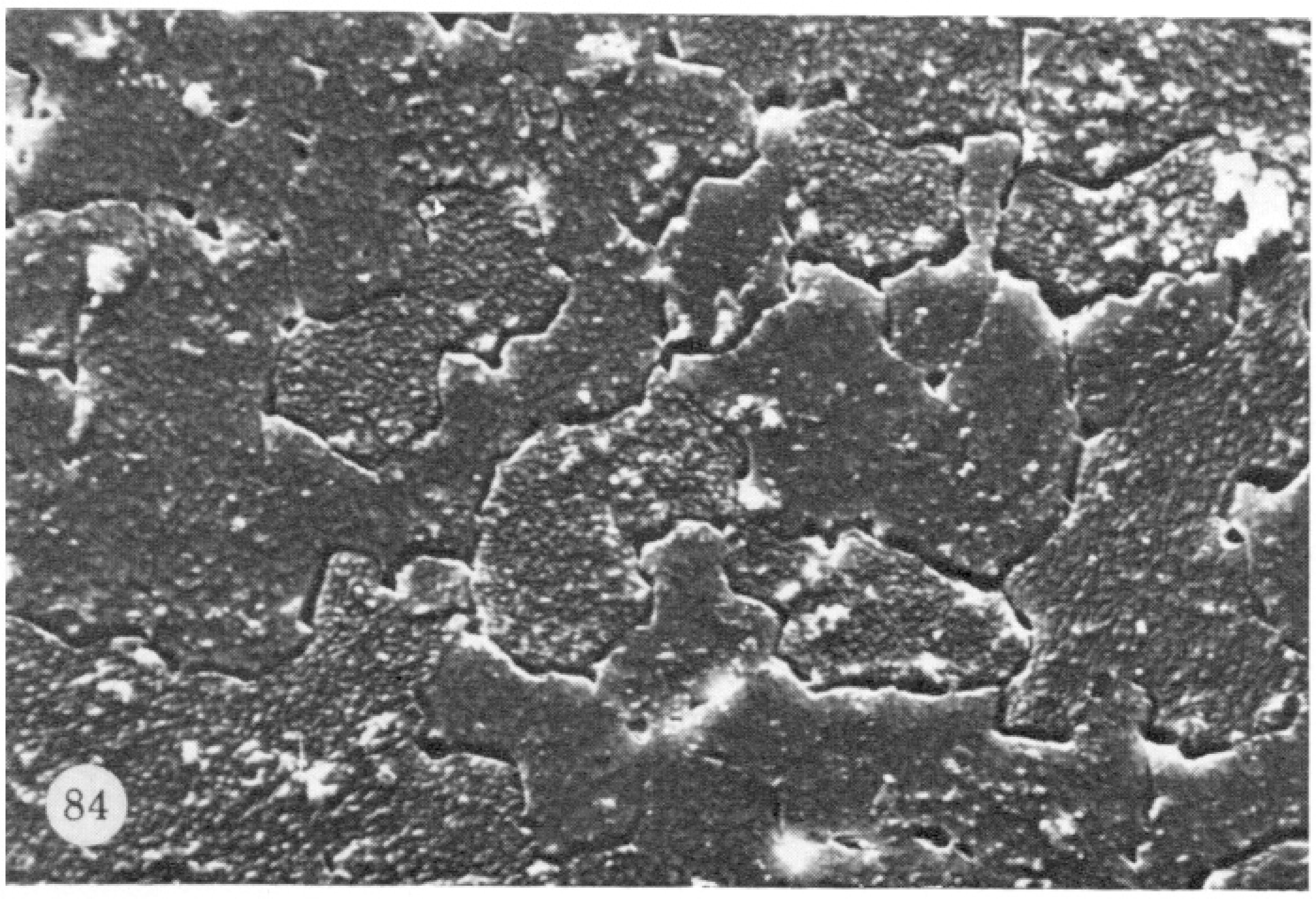

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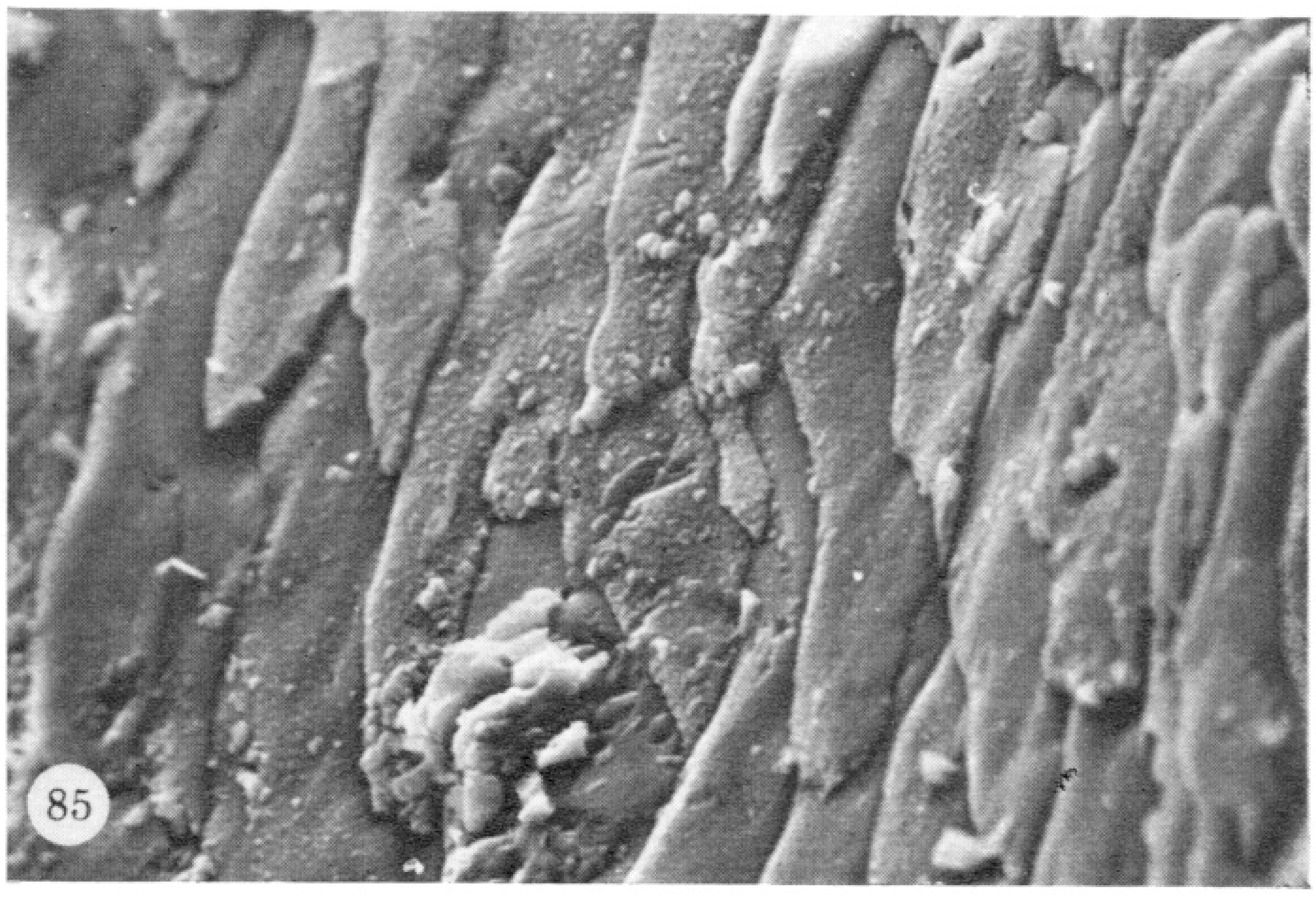

85

FIGURES 78–85. For description see opposite.