THE SECRETION AND STRUCTURAL EVOLUTION OF THE SHELL OF THECIDEIDINE BRACHIOPODS

By A. WILLIAMS, F.R.S.
Department of Geology, The Queen's University, Belfast

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CONTENTS

Secretion of the exoskeleton of *Thecidellina barretti* proceeds in the same way as in other living brachiopods, but the structure of the mantle edge is different. Mucin cells occupy the core of the outer mantle lobe, and periostracal secretion begins within a slot separating lobate cells charged with secretion droplets from long vesicular cells. The former exude an impersistent mucopolysaccharide film and may be regarded as an integral part of the generative zone; the latter secrete most of the periostracum and, thereafter, the carbonate succession as they become part of the outer epithelial layer of the mantle. The periostracum consists of an outer coat initially differentiated into a triple-unit structure and a polysaccharide layer. It is rarely more than 200 nm thick except at the hinge-line where it forms a narrow fold secreted by columnar cells as a cover to the interareas of both valves. Papillose outgrowths of the mantle (caeca), rich in secretion droplets, arise at the mantle edges at regular intervals and persist throughout life. The distal cells are highly microvillous at first, and as they withdraw from the periostracum they secrete numerous proteinous sheaths (the brush) containing mucopolysaccharides, which become encased within the carbonate succession. As the mineral layer thickens, the caeca retreat with the mantle and periodically secrete proteinous partitions within vacated distal parts of the canals (puncta).

The carbonate skeleton mainly consists of acicular and granular calcite forming a primary layer with an internal surface ornamented by tubercles, rhombic bodies, and regularly arranged pits accommodating epithelial cells underlying muscle tissue. The teeth and socket ridges, however, are composed of fibres sheathed in anastomosing proteinous sheets and stacked in alternating rows as in fibrous secondary layers found in most other articulate brachiopods. Superficial traces of fibres also occur as patches and on tubercles in both valves. A similar distribution of secondary fibres is found in *T. australis*; but fibres are limited to spinose outgrowths in the pedicle valve of *T. hedleyi*, while incipient fibres develop only on the surfaces of mature teeth in *Lacazella mediterranea*.

Study of the shell fabric of nine fossil genera shows that a continuous fibrous secondary layer occurs in all of the earliest thecideidines. During subsequent evolution the layer became neotenously reduced in the

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three post-Jurassic Subfamilies of the Suborder; and, although the loss was accelerated in the Lacazellinae, the main change to a sporadic secretion of secondary shell took place during late Jurassic or early Cretaceous times in all three groups.

A review of the principal morphological features of thecideidines, on balance, corroborates the evidence of the ultrastructure of the shell that the Suborder was caenogenetically derived from spiriferide rather than strophomenide brachiopods.

Introduction

The distinctiveness of the thecideidine brachiopods has been recognized since 1822 when Defrance (in Férussac, 1821–2) proposed the generic name *Thecidea* for a Cretaceous species which had hitherto been known as *Terebratulites papillata* Schlotheim. By 1826, Risso had identified the living species *Thecidea* (now *Lacazella*) *mediterranea*; and by the late 1870s not only had the geological range of the Suborder been greatly extended by the discovery of Lower Jurassic species like *Thecideum duplicatum* Moore, 1854, but the anatomy and development of *Lacazella mediterranea* had been described by Lacaze-Duthiers (1861) and Kowalevsky (1874). Differences between cemented thecideidines and pedicle-bearing brachiopods, with their respective simply folded and elaborately coiled lophophores, were obvious. They prompted Gray (1848) to segregate the thecideidines from all other articulate brachiopods and assign them to a separate Order, the Cryptobrachia. But thecideidine ancestry did not become an important issue in comprehending brachiopod evolution until 1891 when Beecher proposed classifying the phylum on the development of the shell in relation to the pedicle, and pronounced the Thecideidae to be living relicts of the Protremata. In his interpretation of the development of *Lacazella mediterranea* as described by Kowalevsky, Beecher paid particular attention to the early appearance of a plate on the dorsal surface of the pedicle rudiment. He claimed that this 'deltidium' (now known as a pseudodeltidium) was initially a discrete third valve which later became ankylosed to the ventral (i.e. pedicle) valve (see figure 64, plate 48). He also asserted that the pseudodeltidium is structurally distinguishable because it is not permeated by puncta accommodating papillose outgrowths (caeca) of the underlying secretory epithelium as is the rest of the shell. In this way Beecher advanced compelling reasons for regarding the thecideidines as fundamentally different from other living articulate brachiopods but closely related to the Strophomenida, an essentially Palaeozoic group of 'protrematous' brachiopods. Members of this Order which includes cemented species that lacked a pedicle were also alleged by Beecher to have punctate valves and an impunctate pseudodeltidium.

The fallacies in Beecher's main assumptions are now fairly well known. They include the probability that Kowalevsky's illustration of the rudimentary pseudodeltidium does not depict a discrete plate but the lateral view of an exoskeletal ring continuous with the pedicle valve (Arber 1942), and the demonstration that the structure of the pseudodeltidium has always been identical with that of the pedicle valve even in *Lacazella* (Williams 1955, 1956). The pseudodeltidium, therefore, need no longer be regarded as a unique feature signifying close relationship between species characterized by its presence. Yet, the derivation of thecideidines from a strophomenide stock still remains an attractive thesis for most palaeontologists who now accept the loss of pedicle and a cementing habit as more diagnostic of affinity than the development of a pseudodeltidium. Pajaud (1970, p. 60), in an exhaustive study of every aspect of thecideidine morphology, concluded that the group arose from the productidines. Grant (1972, p. 243), inspired by exquisitely preserved material from Idhra, was even more precise and linked them

with the strophalosiaceans. Rudwick (1968, p. 357), on the other hand, was equally convinced that they had evolved out of the davidsoniaceans. Thus the choice of antecedent has been widely contended, but all three authors have unequivocally rejected a non-strophomenide ancestry and in so doing reflect popular opinion.

Any attempt to identify the progenitors of the thecideidines has to take two important aspects of their morphogeny into account. The first is the likelihood that the group arose neotenously (Elliott 1953, p. 698) or paedomorphically (Williams and Rowell in Williams *et al.* 1965, p. 197). If this were so, many of the morphological comparisons drawn between thecideidines and prospective ancestral groups may have no phyletic significance. The second is the fact that most students of the Suborder have paid little or no attention to thecideidine skeletal fabric, although the shell is known to be punctate (Williams 1955) and to be composed of a granular banded primary layer (Williams 1968, p. 50) with a variably developed fibrous secondary layer (Baker 1970, p. 80) in contrast to the pseudopunctate laminar shell of the strophomenides. Grant (1972, p. 244) revealed a motive for this neglect when he said 'Shell structure seems to have been ignored...perhaps correctly inasmuch as all other criteria point to a strophomenide ancestry for the Thecideacea'. There is some extenuation for this mistaken attitude. Sections or replicating peels of the thecideidine shell are notoriously difficult to decipher optically, while the fabric has so greatly changed since early Jurassic times that even electron microscope studies, if restricted to only a few species, give a misleading picture of subordinal shell structure. Moreover, no histological account of the epithelium lining the shell of living thecideidines has ever been published so that the nature of the mantle edge and caeca is unknown. None the less, it is now a fact that, although shell structure has evolved in the course of brachiopod history (Williams 1971), basic textures are at least as stable as any macroscopic feature, and differences between them are actually more sharply defined.

The prospect for repairing these gaps in our knowledge and promoting more serious consideration of shell structure in tracing thecideidine evolution did not arise until 1969 when the late Professor T. F. Goreau of the Department of Physiology in the University of the West Indies sent me a sample of *Thecidellina barretti* (Davidson) appropriately fixed in buffered solution for electron microscope studies of soft tissues. While this material was being examined, papers published by Baker (1970) and by Pajaud (1970) confirmed a suspicion that a comprehensive review of fossil thecideidines was also necessary. For this purpose the collections of the British Museum (Nat. Hist.) were placed at my disposal, and although they do not contain every known taxon, they include a sufficient number of genera to ensure that the main lines of descent recognized by Backhaus (1959) and Pajaud were adequately represented in this study.

The investigation has followed the procedure adopted in the study of other brachiopod groups. Having completed a survey by transmission and scanning electron microscopy of the soft and hard parts of living and fossil *Thecidellina* and of the shell structure of Recent *Lacazella*, progressively older extinct species were then examined, preferably attached to, or associated with, skeletons of non-thecideidine brachiopods or even other phyla with previously determined textures. By using such controls it has been possible to identify those differences in the shell fabric of fossil thecideidines that were original and not the result of *post-mortem* alteration by diagenetic processes affecting the enclosing sediments. In many specimens some recrystallization had occurred; but even when this process had been accompanied by replacement including silification, enough of the original fabric usually survives to determine shell successions.

The procedure has also determined the layout of the paper which has, at least, the advantage

of progressing in prescribed Huttonian fashion from known relationships between shell and mantle to those that have to be inferred from the study of shell alone.

Materials and methods

The only living specimens obtainable for this study were several mature individuals of *Thecidellina barretti* (Davidson) collected by Professor T. F. Goreau at depths of about 60 m from the fore-reef slope of Discovery Bay, Jamaica. The specimens were growing in less well-illuminated crevices on the undersides of fronds of the coral *Agarica* which were air-lifted to the sea surface and transferred to the laboratory where the brachiopods were carefully freed from the substrate and kept in running sea water overnight. To facilitate fixation they were then transferred to a mixture of 1 part 7.5 % $MgCl_2$ (isotonic) and 5 parts sea water for about 2 h. This treatment had no adverse effects on specimens which continued to react normally up to the moment of transfer to a fixative consisting of 6 % gluteraldehyde in 0.2 M cacodylate buffer adjusted to pH 7.35 and made isotonic with 0.51 M sucrose. Fixation was for 24 h in the cold, after which the specimens were changed to 0.1 M phosphate buffer at pH 7.38 made up in 0.2 M sucrose.

On receipt of these specimens, some were prepared for electron microscope study of soft parts by being decalcified in 10 % EDTA, washed in sucrose, treated for 1 h with 2 % osmic acid, dehydrated and embedded in an epoxy resin. Sections cut from blocks trimmed to specification were stained with aqueous uranyl acetate and aqueous lead citrate. Other specimens were used for histochemical tests after transfer to 10 % neutral formalin followed by decalcification in Gooding & Stewart's fluid and the embedding of organic residues in 56 °C paraffin wax. Prepared sections were subjected to Mazia protein stain, perodic acid–Schiff reaction (PAS), alcian blue, Mayer's haemalum and eosin.

The remaining specimens as well as dried shells of two other living species (*Thecidellina australis* (Tate) from a submarine cave at a depth of 40 m on the seaward side of Rigli Island, Eniwetok Atoll; and *Lacazella mediterranea* (Risso) from unknown depths in the Mediterranean especially off Bone, Algeria), were freed of soft parts by immersion in sodium hypochlorite for some hours. Natural and fracture skeletal surfaces of fossil as well as living species were freed of any loosely adherent particles by brief sonication in a weak detergent and then in acetone. Differentially etched surfaces were also prepared by mounting shells in Araldite resin, cutting sections in a preferred plane, polishing the cut surfaces with tin oxide or alumina and immersing in 2 % EDTA for between 20 and 30 min, depending on the geological age and texture of the shell. All surfaces were coated with gold/palladium for examination under a Stereoscan scanning electron microscope (purchased by NERC grant GR/3/443).

Skeletal secretion in *Thecidellina*

(*a*) *The mantle edge and periostracum*

At first sight the mantle edge of *Thecidellina barretti*, which may extend up to 50 μm anteriorly of the mantle groove, is more like that of bivalves (Kennedy, Taylor & Hall 1969, p. 500) than of other living brachiopods (Williams 1956, p. 244). This superficial resemblance results from the deep insertion of the first-formed part of the periostracum between secretory epithelial cells (periostracal slot) forming the edge of the mantle which is, thereby, divided into two units

simulating the outer and middle folds of the bivalve mantle. There is no doubt, however, that together they represent the undivided outer mantle lobe of the living rhynchonellide *Notosaria* because they also are immediately separable from the inner mantle lobe of ciliated epithelium. The mantle groove is admittedly less conspicuous in *Thecidellina*, but this condition reflects the absence of setae which accentuate the depth of the groove in *Notosaria*. In fact, lack of setae and the intercellular origin of the periostracum clarify relationships between the different types of

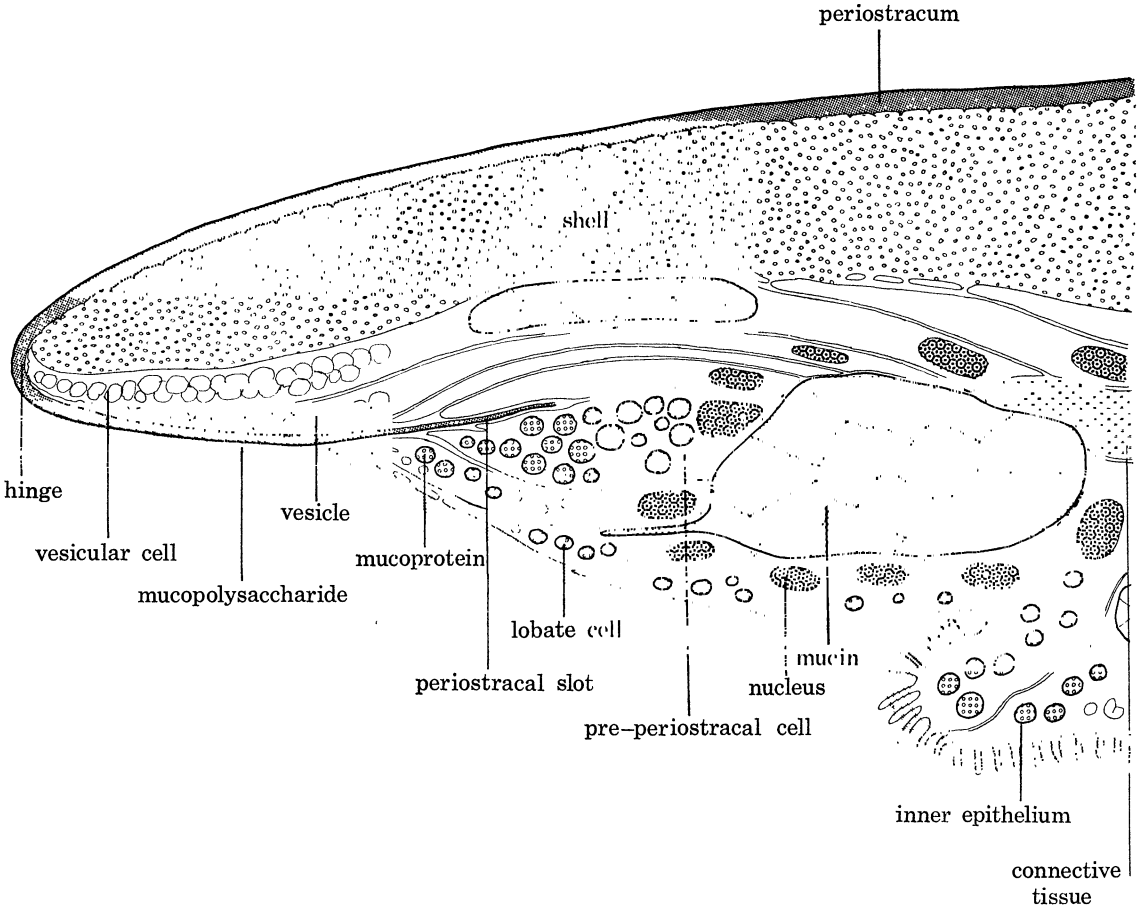


FIGURE 1. Diagrammatic longitudinal section of the edge of a valve of *Thecidellina* showing the relationship between the shell and mantle (× 4000).

cells constituting the mantle lobes and lead to some reconsideration of current views on the migration and secretory activities of epithelial cells at the mantle edge of the brachiopod shell.

In radial section, the posterior part of the outer mantle lobe of *Thecidellina* is seen to be dominated by a large cell, up to 16 μm across, filled with closely packed, medium electron dense, membrane-bound secretion droplets (figure 1; figure 2, plate 40). The cell lies immediately anterior to the terminal zone of the connective tissue layer and the closure of the mantle groove where cells with regularly occurring cilia in an even fringe of microvilli about 1 μm long represent the beginnings of the inner epithelium. The secretion droplets were only weakly PAS positive but stained strongly in Alcian blue. These reactions are consistent with their identification, inferred from their ultrastructural appearance here and elsewhere in the mantle, as mucin inclusions.

Well-developed mucin cells are nearly always present in random sections of the mantle edge (compare figures 2 and 3, plate 40) and must therefore, form an integral part of a compact circumferential generative zone giving rise to microvillous inner epithelium posteriorly and outer epithelium anteriorly. This differentiation accords with that found in *Notosaria* but there are differences in detail. The mucin cell is flanked anteriorly by about eight cells. The first three or four adjacent to the inner epithelium, are characterized by many vesicles and membrane-bound, electron dense secretion droplets in various stages of disintegration. These cells tend to overlap one another anteriorly in tongue-like lobes and culminate in a narrow lobate cell extending forward of the mucin cell for up to 10 μm. This preperiostracal cell is remarkably constant in its position and appearance. It forms the internal boundary of the periostracal slot and is invariably rich in the same granular electron dense inclusions, about 450 nm in diameter, found in the more posteriorly situated lobate cells. This secretion is strongly PAS positive, a reaction that persisted in saliva-treated sections, which, like the ultrastructure of the inclusions, indicates a polysaccharide, probably a mucoprotein complex.

The lobate cells sustain, by continuous secretion from intercellular spaces and external plasmalemmas, a medium electron dense, granular and filamentar coat of mucopolysaccharide. The coat is rarely more than 120 nm thick and extends anteriorly from the closure of the mantle groove. Exudation along intercellular pathways and the periostracal slot from the mucin and the pre-periostracal cells respectively, contributes to the maintenance of the coat, but it does not persist for more than 8 to 10 μm anterior of the slot as an outer cover to the periostracum.

The periostracum first appears in the intercellular space representing the slot as a triple-unit structure about 8 nm thick composed of two electron dense bounding surfaces separated by an electron light zone (figure 4, plate 40). This zone persists during further deposition of the periostracum and is seen in section as a thin but readily detectable line separating two distinctive inner and outer layers. The former is always the thicker varying from 50 nm where it emerges from the slot some 4 μm anterior of the first traces of the periostracum to 100 nm or more at the mantle edge. The layer is a granular, medium electron dense secretion with a strong PAS positive reaction persisting in partly digested sections, and has been identified as a polysaccharide. It is secreted by two or three flat, highly vesicular cells which may extend forward for up to 25 μm to occupy the hinge of the periostracal fold (figure 5, plate 41) where their convoluted anterior edges normally appear in sections as a series of isolated irregular processes.

The outer periostracal layer (figure 5, plate 41) is more electron dense than the inner and there are indications that it is differentiated into a triple unit structure between 9 and 15 nm thick when it emerges from the slot. Here it is externally coated with a fuzzy filamentar layer about 25 nm thick, and it is probable that the pre-periostracal cell contributes material to both the layer and its filamentar coat. Beyond the slot, the external layer ceases to increase in thickness, although further polymerization may occur because it usually assumes an extremely electron dense aspect and also tends to lose its filamentar coat.

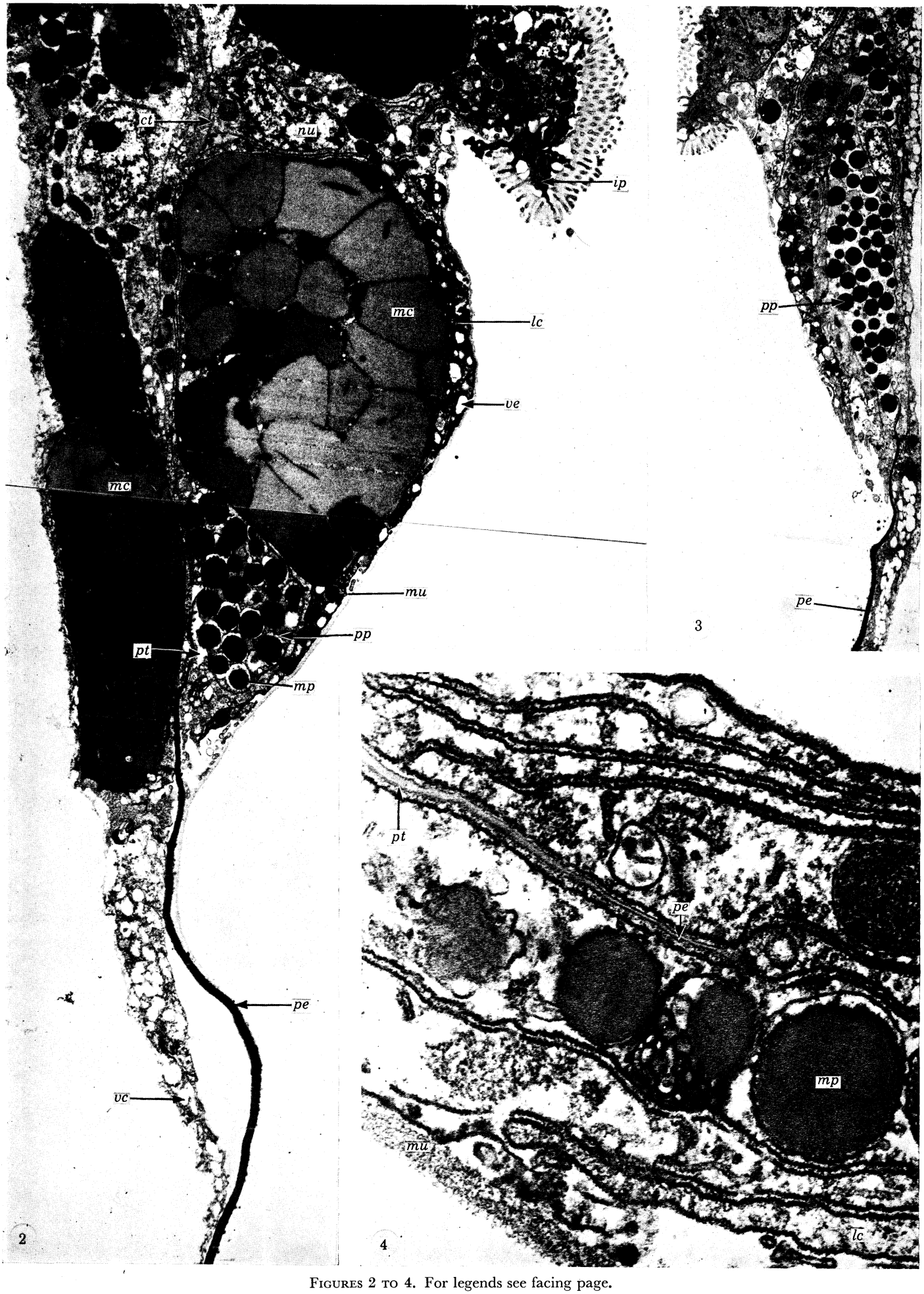
Description of plate 40

Transmission electron micrographs of the mantle edge of *Thecidellina barretti* (Davidson), Discovery Bay, Jamaica

Figure 2. Longitudinal section showing the outer mantle lobe with a mucin cell in relation to the periostracum and the inner epithelium (× 5500).

Figure 3. Longitudinal section of the outer mantle lobe without a mucin cell (× 4100).

Figure 4. Detail of a longitudinal section of the outer mantle lobe showing the origin of the periostracum (× 82500).



FIGURES 2 TO 4. For legends see facing page.

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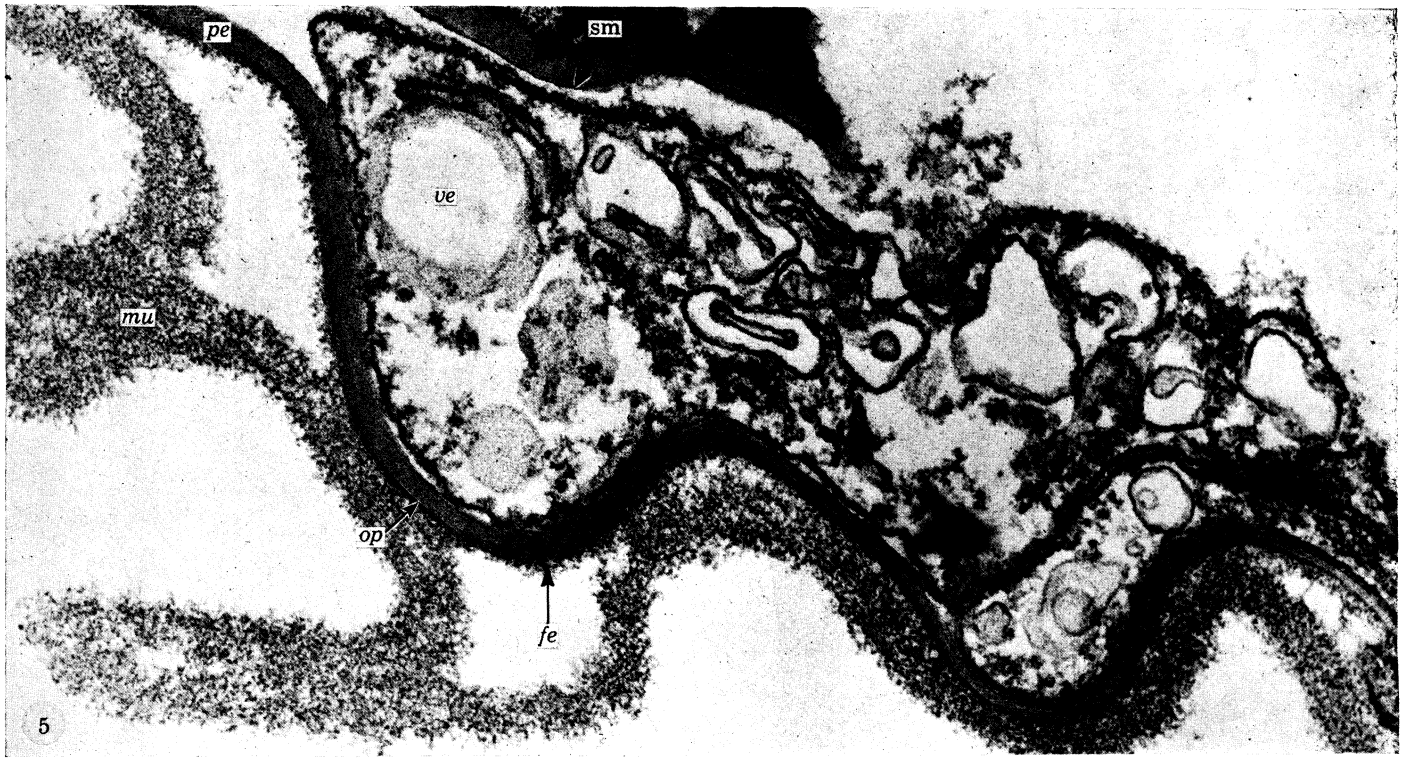

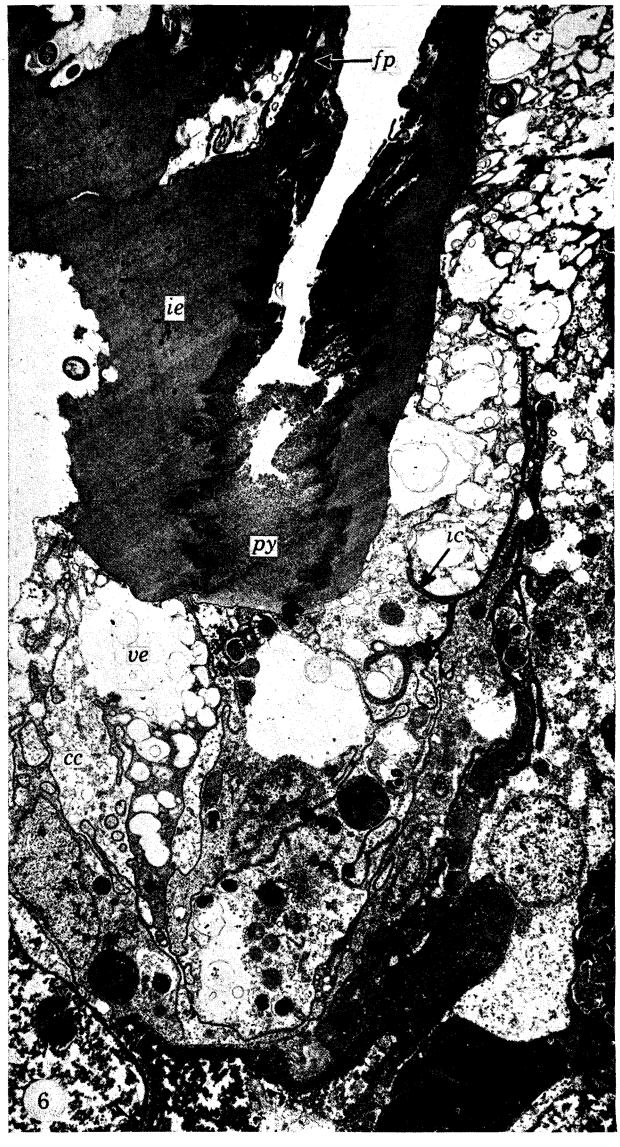

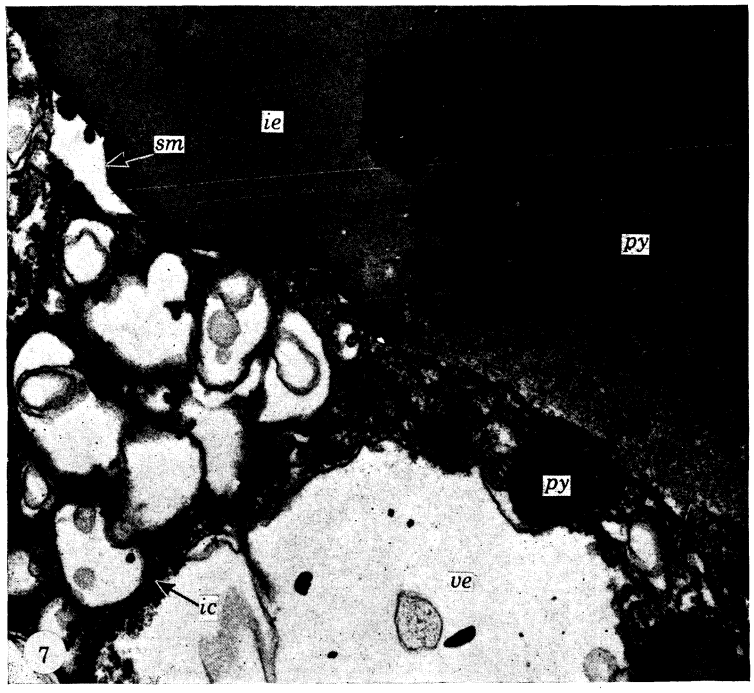

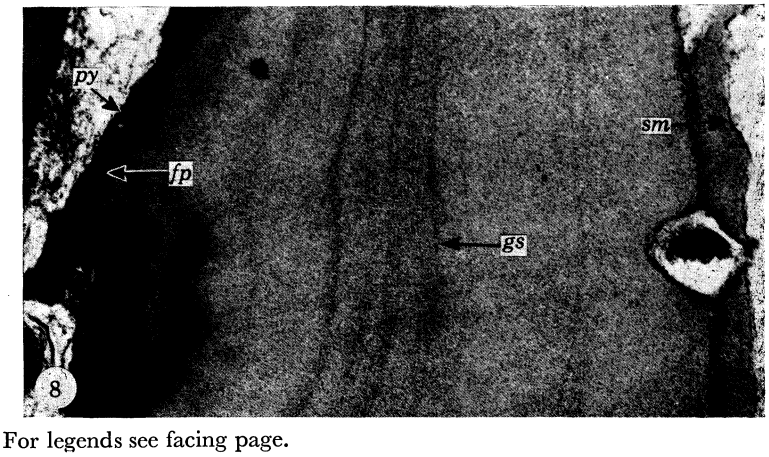

FIGURES 5 TO 8. For legends see facing page.

The hinge of the periostracal fold constituting the mantle edge in decalcified sections marks a change from organic to carbonate secretion. At the hinge the inner periostracal surface is usually sealed off by an electron dense membrane supporting irregular trails of polysaccharides up to 100 nm long, between which the first calcite crystallites of the primary carbonate layer are seeded on the sealing membrane. Correlation of soft tissue sections with those of the mineral shell shows that the long flat vesicular cells are responsible for the secretion of both periostracum and primary carbonate layer. Moreover, as will be shown later, arrays of proteinous tubules (the brush) appear at regular intervals at the hinge and permanently connect the periostracum with caecal extensions of the mantle (figure 49, plate 46) which become encased in a thickening calcareous shell away from the mantle edge. Consequently each vesicular cell must secrete a strip of periostracum *ab initio* and accompany that strip as it migrates from its place of origin within the periostracal slot. When, however, the secretory plasmalemma of a vesicular cell reaches the hinge and begins to rotate to face externally, a change occurs in the secretory régime of the cell and carbonate deposition begins. Meanwhile, new cells proliferating from the generative zone are constantly being incorporated in the postperiostracal complex thereby providing a continuous sheet of periostracum and an appropriate supply of outer epithelium.

These processes of cell proliferation and of shell variation and growth controlled by changes in the secretory régime of migrating epithelium, are identical with the 'conveyor belt system' described for other living brachiopods (Williams 1968) except in one respect. In *Thecidellina*, the lobate cells adjacent to the inner epithelium as well as the preperiostracal cell lie internal to the first-formed periostracum. They cannot, therefore, take part in cell migration; and, because they secrete the outer polysaccharide coat and may even contribute to the external layer of the periostracum, these constituents cannot be regarded as an integral part of the full succession deposited by a cell as it migrates away from the generative zone. In view of such relationships, the lobate cells, like the mucin cell, are interpreted as specialized secretory units constantly associated with the generative zone. Whether some of the preperiostracal cells become involved in the conveyor belt process of migration remains to be seen. It is, however, noteworthy that the lobate and mucin cells are always distinguishable from other constituents of the outer mantle lobe. The connective tissue separating the inner and outer epithelia of the mantle terminates along the posterior margin of the mucin cells, while the vesicular and first-formed inner epithelial cells have many youthful features including large nuclei, few mitochondria and simply disposed plasmalemmas loosely connected by septate desmosomes to delineate relatively large intercellular spaces.

Further consideration of the cell arrangement and sequence of secretion at the mantle edge of *Notosaria* suggests that the distinction just drawn in *Thecidellina* between migratory and static secretory cells may also be typical of other living brachiopods. In the outer mantle lobe of

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Description of plate 41

Transmission electron micrographs of *Thecidellina barretti*

Figure 5. Detail of a longitudinal section of the outer mantle lobe showing the relationship between vesicular cells and the periostracal fold (× 68700).

Figure 6. Dorso-ventral section of the periostracal fold and columnar cells at the hinge-line (× 5500).

Figure 7. Detail of the junction between the medial part of the periostracal fold and the columnar cells at the hinge-line (× 41200).

Figure 8. Section of the periostracal cover of the pseudodeltidium (× 68700).

Notosaria, the first cell to secrete the periostracal outer bounding membrane, which may be correlated with the outer layer of the *Thecidellina* periostracum is also preceded by three or four cells exuding an impersistent external polysaccharide coat. If these latter and the lobate cells of *Thecidellina* are homologized and interpreted as part of the generative zone, the only difference between the two mantle edges is the relatively unimportant development of an intercellular periostracal slot in *Thecidellina*.

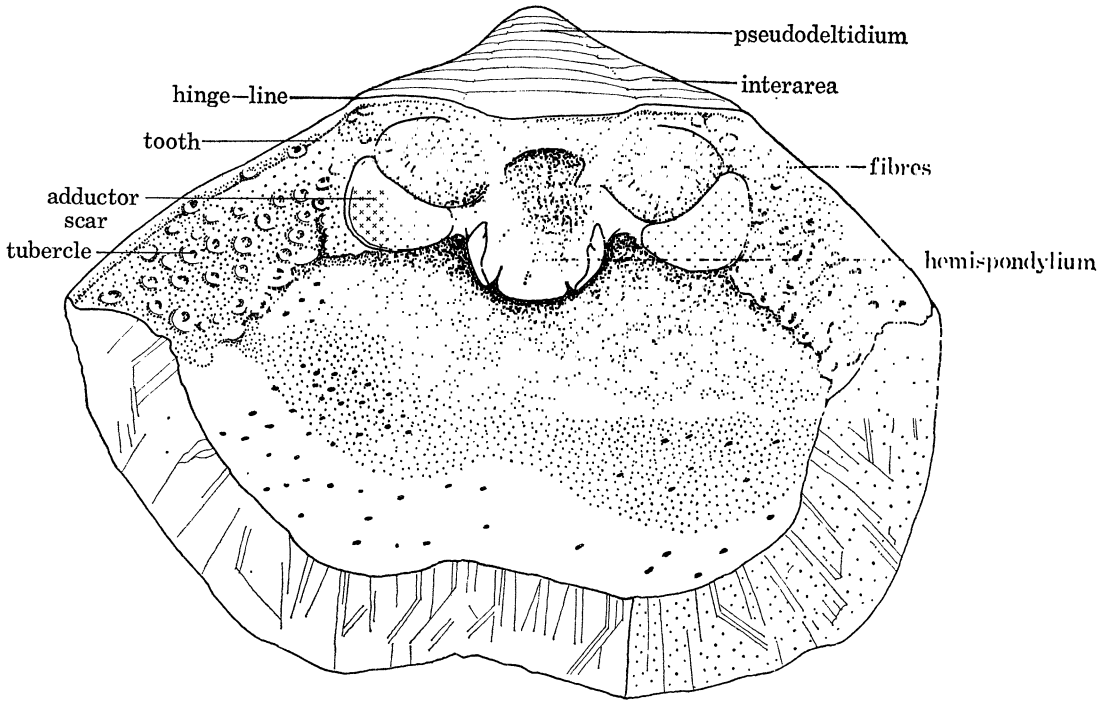

FIGURE 9. Antero-dorsal view of the interior of the pedicle valve of *Thecidellina* showing the main morphological features (× 30).

(*b*) *The mantle at the hinge-line*

In all articulate brachiopods, the only part of the mantle found at the hinge-line (or cardinal margin) is the outer epithelial layer. Changes in the relationship between the dorsal and ventral mantles leading to the absence of inner epithelium from the posterior region of the shell are

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DESCRIPTION OF PLATE 42

Transmission and scanning electron micrographs of *Thecidellina barretti*

FIGURE 12. Section of the mantle underlying the subperipheral rim of the brachial valve (× 5500).

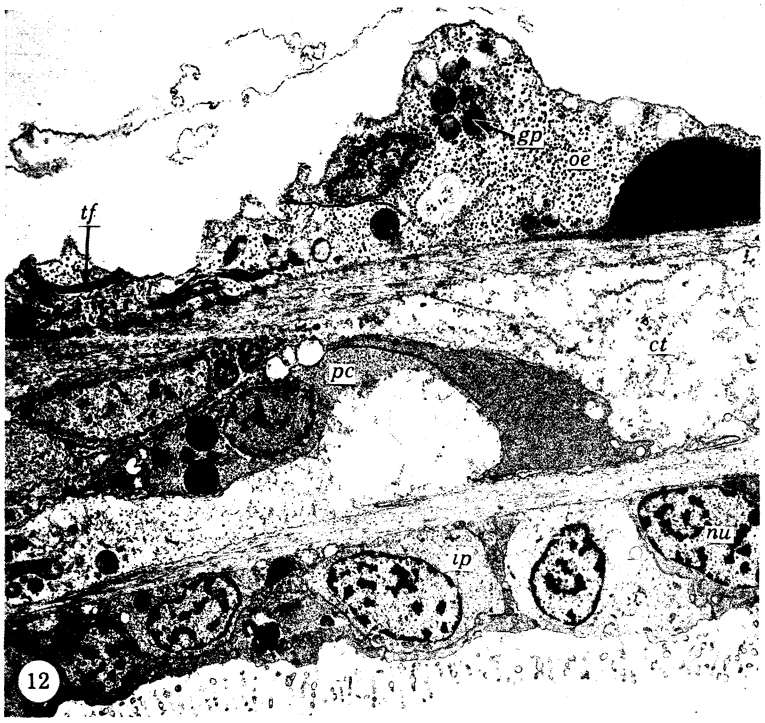
FIGURE 13. Section of the mantle at the peribrachial ridge showing the concentrations of tonofibrils in the outer epithelium (× 11000).

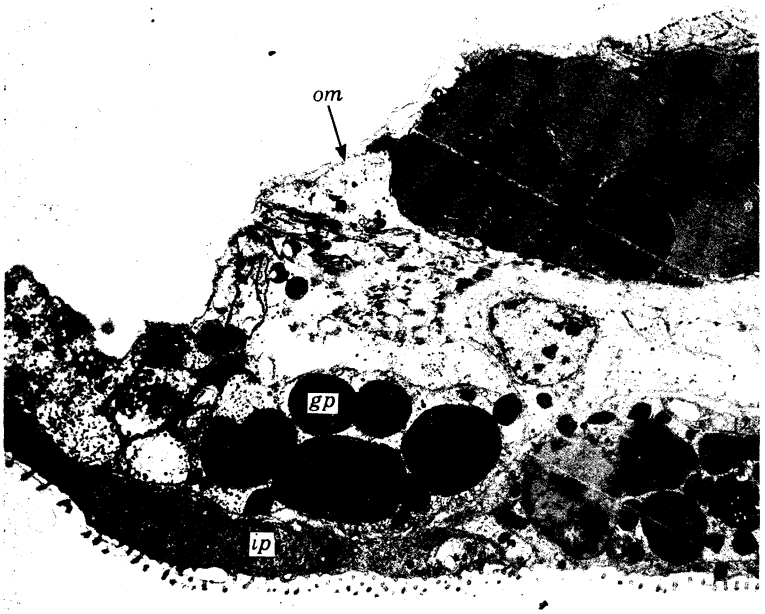
FIGURE 14. Section of the mantle showing variation in thickness complementary to the topography of a tubercle to the right (× 5500).

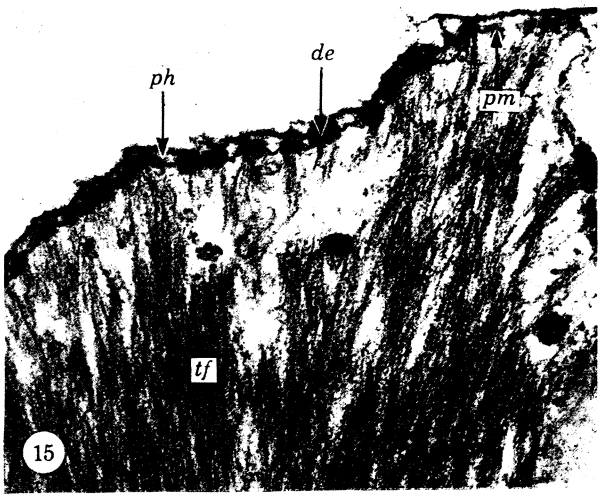
FIGURE 15. Detail of a section of an outer epithelial cell with tonofibrils showing the desmosome attachments between the plasmalemma and an extracellular proteinous sheet (× 68700).

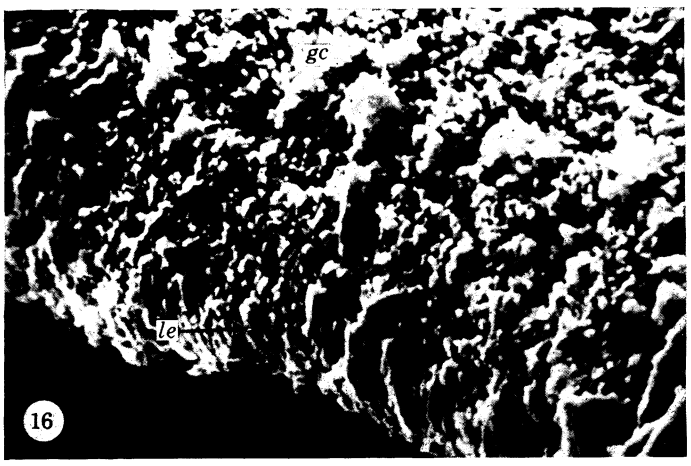
FIGURE 16. Edge of a brachial valve showing the mixture of calcitic crystallites, granules and lenses making up the primary layer (× 6200).

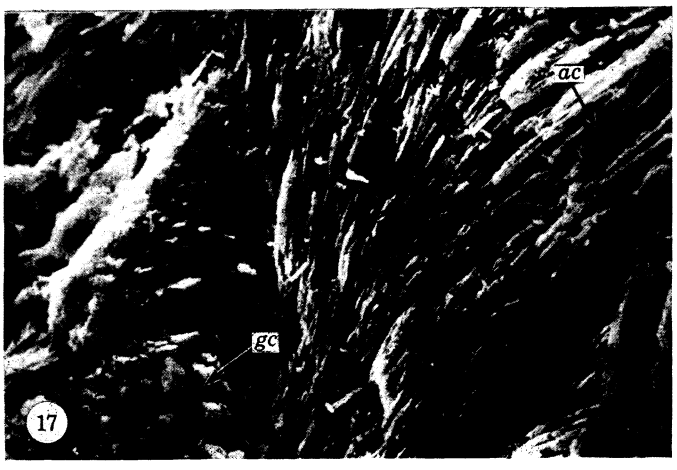
FIGURE 17. Fractured edge of a brachial valve showing acicular crystallites and granules of calcite in a tubercle of the primary layer (× 1400).











FIGURES 12 TO 17. For legends see facing page.

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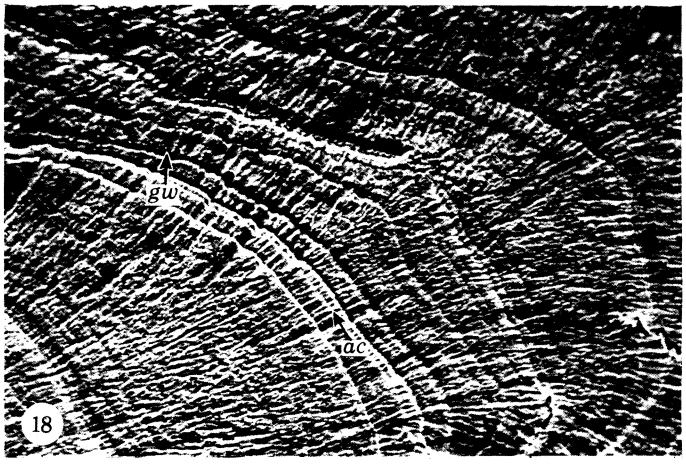

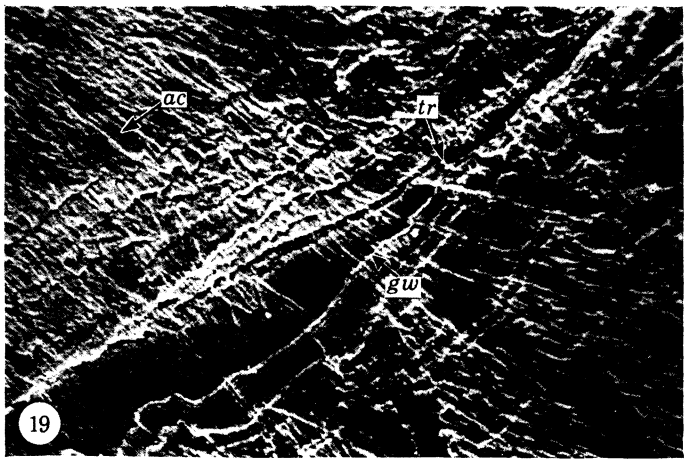

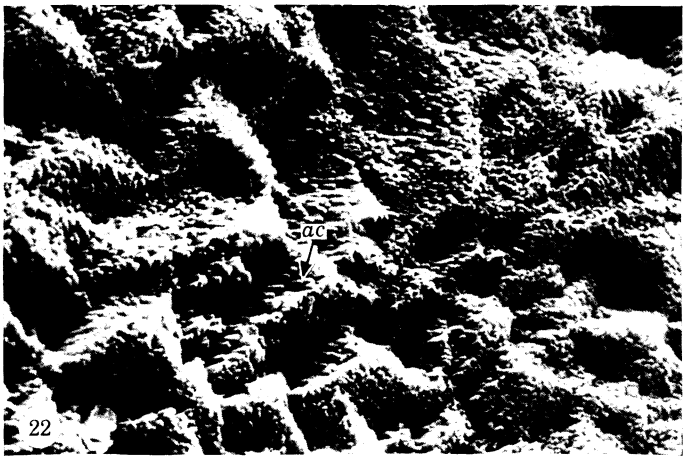

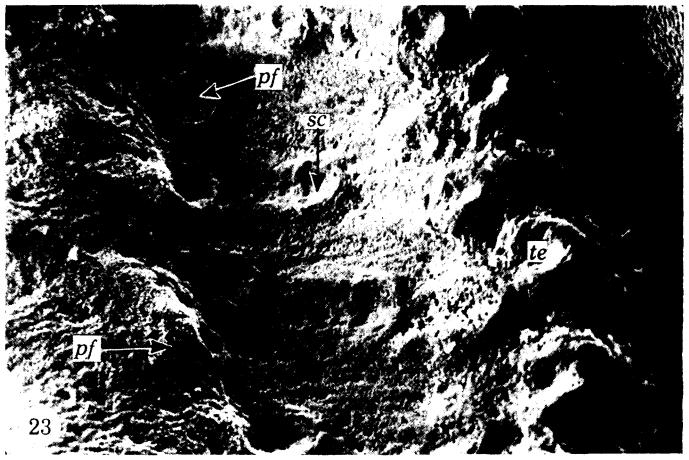

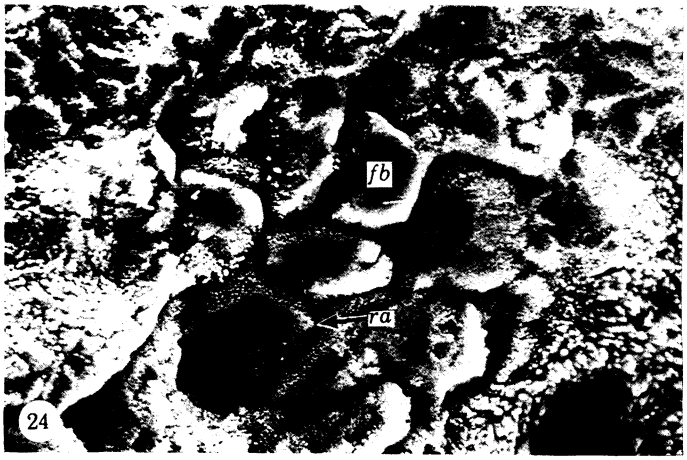

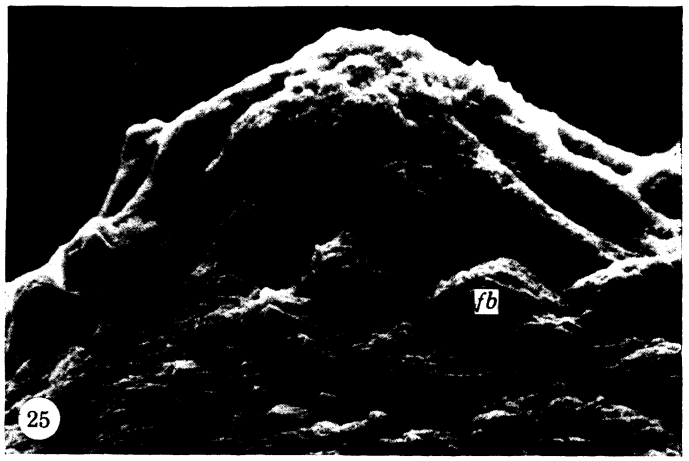

FIGURES 18 TO 25. For legends see facing page.

known for *Terebratulina* (Williams 1956, p. 255) and also occur in *Thecidellina*. Both mantle edges remain discrete around the gape of the shell as far as the cardinal extremities. Here at the lateral ends of the hinge-line, the mantle edges join and simultaneously divide in another plane to accommodate the coelomic cavity. First, the inner mantle lobes of inner epithelium fuse into one layer which falls away to become the anterior body wall. Then the outer lobes of both edges come together to form a complex of cells. These constitute a generative zone proliferating two strips of outer epithelium which secrete the carbonate ventral and dorsal interareas and their periostracal covers.

The posterior outer epithelial generative zone is well developed in *Thecidellina* but differs fundamentally from that of other Recent articulate brachiopods through lack of a pedicle (figure 9). In living rhynchonellides and terebratulides, the outer epithelium underlying the cardinal margin is continuous medially with another generative zone giving rise centripetally to cells which secrete the polysaccharide cover of the pedicle. This junction between outer and pedicle epithelia is effectively the border of the pedicle where it emerges from the shell; and, although it may describe topologically complex figures in mature shells, it is essentially a suboval boundary coincident, in early growth stages, with the open delthyrium and notothyrium of the pedicle and brachial valves respectively. In *Thecidellina*, no pedicle develops from the so-called 'caudal' rudiment of the embryo. Instead, the periostracum of the pedicle valve is directly attached to the substrate (figure 20, plate 43) presumably by a film of mucopolysaccharide exuded by the outer lobe of the ventral mantle as in *Crania* (Williams & Wright 1970, p. 19). With no pedicle developed to occupy the delthyrium and the apex of the notothyrium, both openings become respectively covered by the pseudodeltidium and filled by the back of the cardinal process (figure 10; figure 64, plate 48). Growth of both these features complement each other as do the ventral and dorsal interareas so that the posterior outer epithelial generative zone extends continuously along the hinge-line from one cardinal extremity to another.

In dorso-ventral sections the generative zone typically consists of an inner row of 6 to 8 columnar cells grouped around a fold of periostracum about 15 μm deep, and an outer row of larger cells (figure 11; figure 6, plate 41). The columnar cells contain numerous vesicles and membrane-bound secretion droplets of an electron dense granular polysaccharide in various stages of disintegration; glycoproteins are also present but much less common. The droplets and vesicles are normally up to 400 nm in size but large vesicles in the vicinity of the periostracal base attain diameters of 3 μm. Composite mucin droplets additionally form in the outer row of cells

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Description of plate 43

Scanning electron micrographs of *Thecidellina barretti*

Figure 18. Etched section of a brachial valve showing acicular crystallites in epitaxial continuity through growth surfaces (× 1400).

Figure 19. Etched section of a brachial valve showing a transgression within the carbonate succession (× 1300).

Figure 20. Etched section of a pedicle valve showing the zone of attachment to a substrate (× 1500).

Figure 21. Internal surface of a brachial valve showing a rhombic mosaic (× 2500).

Figure 22. Internal surface of a brachial valve showing acicular crystallites in rhombic arrays (× 3000).

Figure 23. Internal edge of a pedicle valve showing location of fibrous patches (× 150).

Figure 24. Patch of secondary fibres on the internal surface of a pedicle valve (× 1500).

Figure 25. Tubercle in a brachial valve with a superficial layer of secondary fibres (× 1500).

which are also vesicular but much more loosely aggregated than the columnar epithelium. These larger cells are continuous with those of the outer epithelium underlying the carbonate shell, which differ only in their cuboidal outline and tighter intercellular connexions. Since the large cells occur laterally as well as anteriorly of the columnar epithelium, the latter are

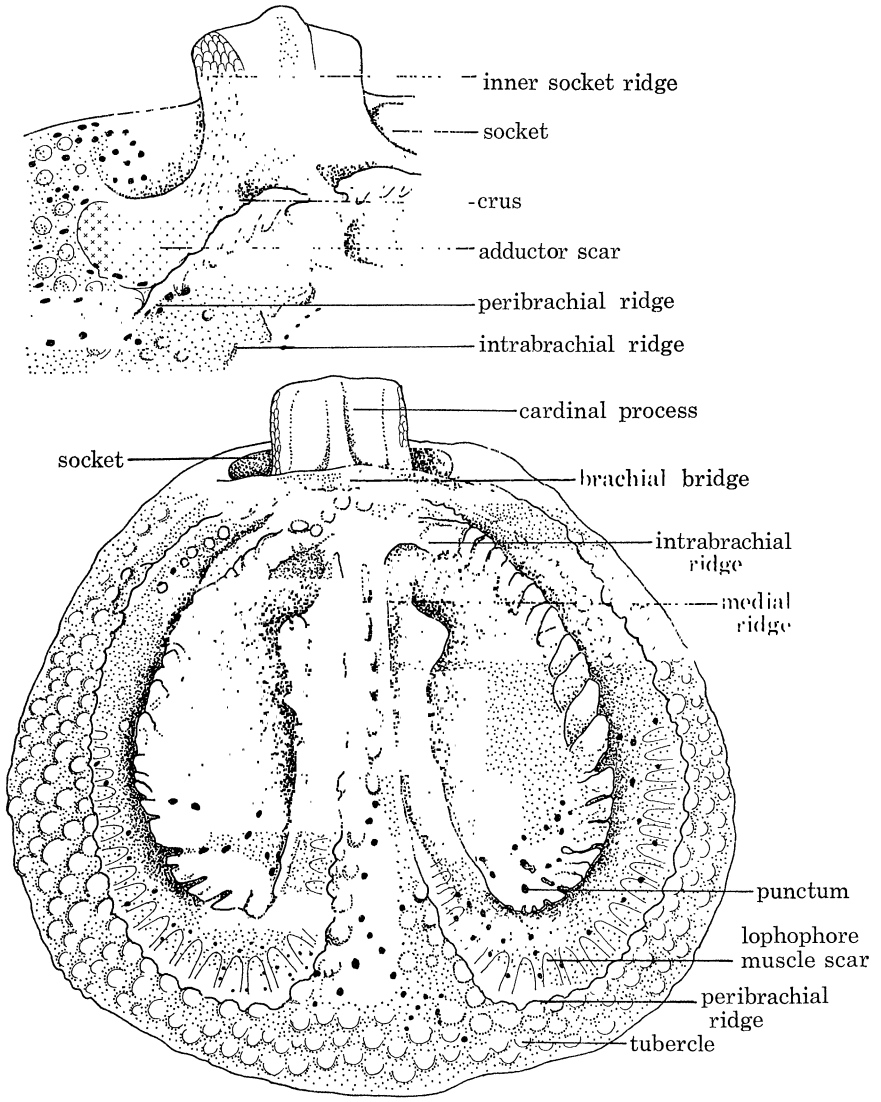


FIGURE 10. Ventral and ventro-lateral views of the interior of the brachial valve of *Thecidellina* showing the main morphological features (×40, × 80).

DESCRIPTION OF PLATE 44

Scanning and transmission electron micrographs of *Thecidellina barretti*

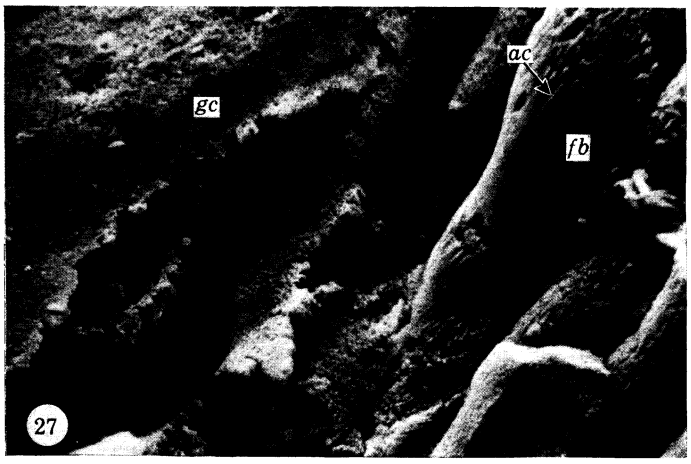
FIGURE 27. Junction between granular calcite layers and fibres along the posterior face of a tooth (× 2400).

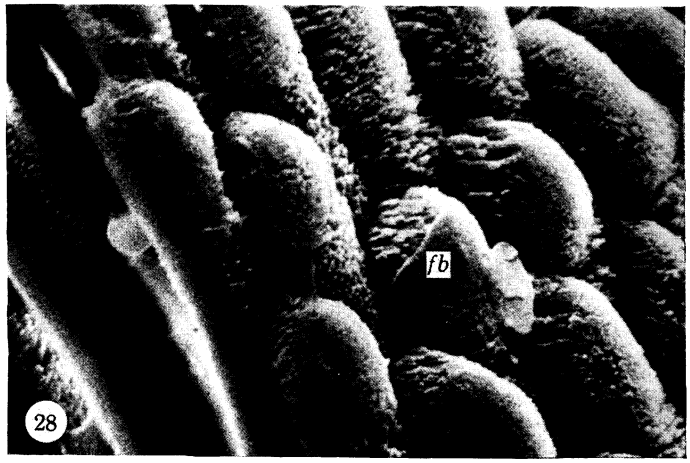
FIGURES 28, 29. Arrangement of fibres in a tooth and detail of their crystallite structure (× 2400, × 6500).

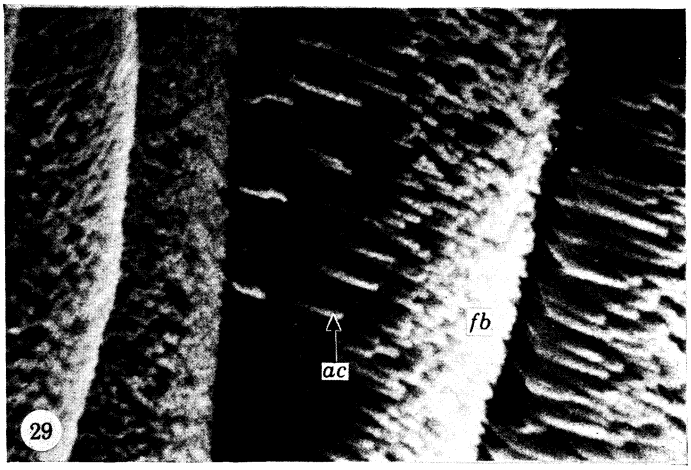
FIGURE 30. Dorsal surface of a mature tooth showing the superficial layer of granular calcite (× 2400).

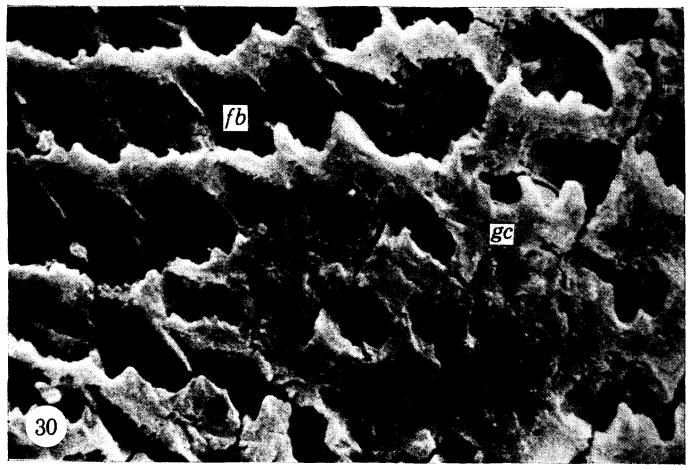
FIGURES 31, 32. Etched sections of the tip and middle part respectively of the inner socket ridge of a brachial valve (× 2900, × 1400).

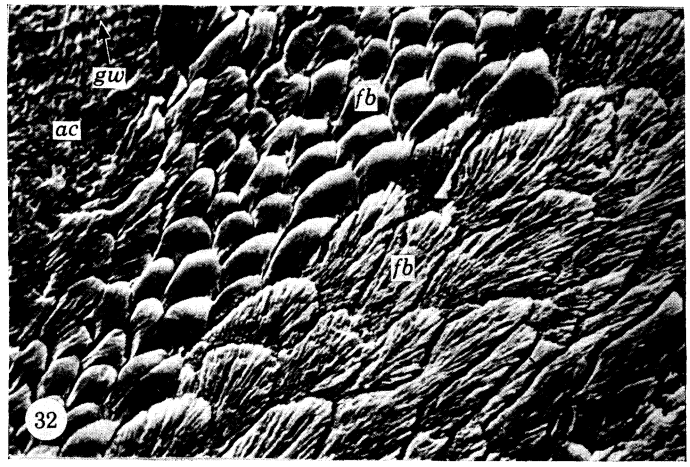
FIGURE 33. Section of outer epithelium associated with the postero-lateral adductor muscles (× 8200).











FIGURES 27 TO 33. For legends see facing page.

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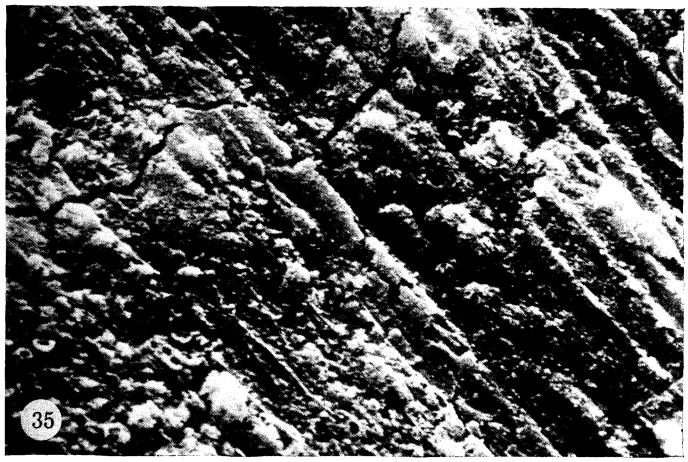

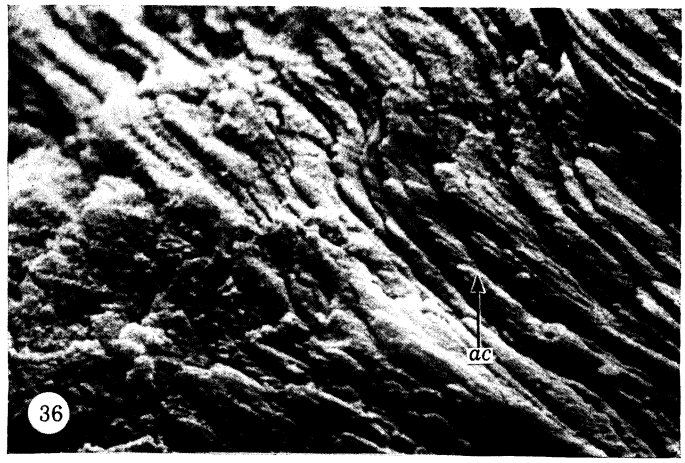

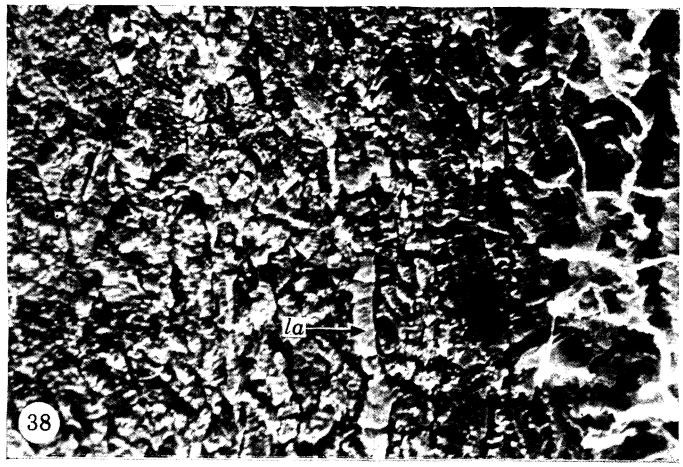

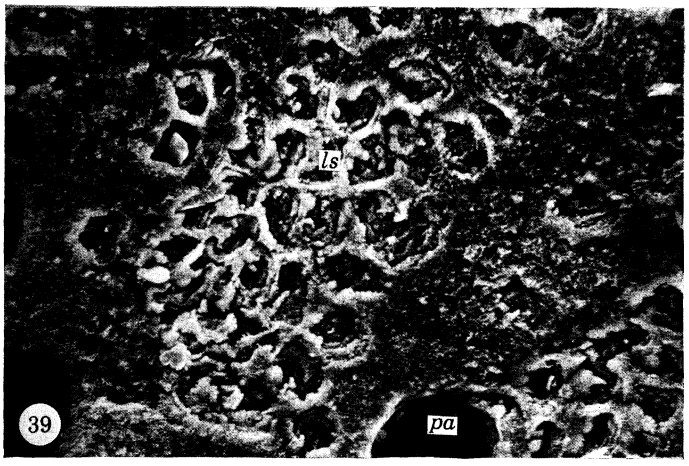

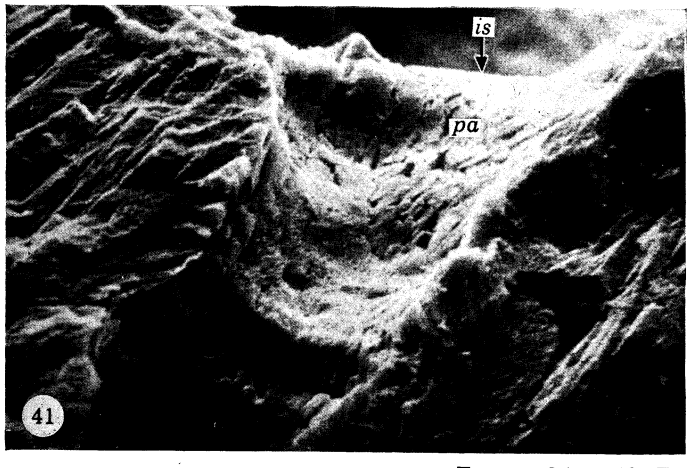

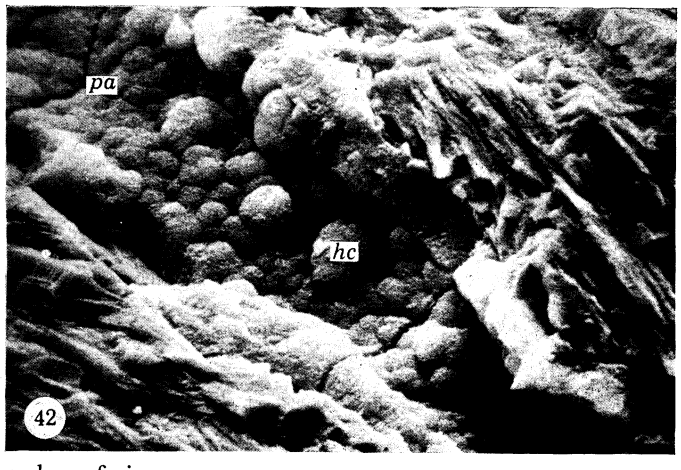

FIGURES 35 TO 42. For legends see facing page.

regarded as the core of the generative zone, and the order of deposition of the different layers composing the interareas is attributed to changes in the secretory régime of newly formed cells as they migrate ventrally and dorsally from the core.

Secretion of the periostracum begins in the antero-medial zone of the periostracal fold along the hinge line. Here exudation of an electron-dense granular material is sustained not only by the posterior plasmalemmas of two or three medially situated columnar cells but also by supplies moving along intercellular pathways from the entire complex of cells (figure 7, plate 41). Consequently intercellular spaces are strongly defined in section as electron dense bands normally about 25 nm thick. The exudation is probably a polysaccharide with properties similar to those of the impersistent film secreted by the outer mantle lobe because, within 2 μm of its deposition as a continuous mass, it parts irregularly into two layers to form external coats of the ventral and dorsal interareas. These coats, which may initially be about 1.5 μm thick, do not persist as a uniform cover outside the fold. They tend to fret away in clumps or irregular sheets especially from the undersides of the flap-like extensions of the persistent layer of the mature periostracum.

The main succession of the periostracum is immediately distinguishable as a persistent inner electron light layer with a very finely granular texture (figure 6, plate 41). Even within the fold it is secreted as two discrete layers quite distinct from the medial mass of the external coat although it, too, is PAS positive and probably a closely related polysaccharide. In sections of mature specimens, the interface between the two layers within the folds is highly serrated and normally emphasized by an electron dense membrane a few nanometres thick. The serrations represent flaps (figure 8, plate 41) overlapping one another towards the dividing plane of the fold and are usually a few micrometres long although some, up to 15 μm in length, occur. Flaps are rare in the thinner immature part of the periostracum found near the umbones, and it is assumed that their later development results from periodic changes in the number of cells engaged in secreting the two different polysaccharides of the external and internal periostracal layers within a deepening fold when forward growth of the interareas was decreasing relative to their thickening. Trails of electron dense particles extending obliquely across the main layer of the periostracum more or less parallel with the flaps are evidently sections of depositional surfaces and may, therefore, be treated as growth lines (figure 8, plate 41). They show that the main succession of the periostracum is deposited as a series of acutely disposed overlapping wedges becoming progressively younger towards the fold. Secretion of periostracum terminates at the edge of the fold with the exudation of a sealing membrane a few nanometres thick. As at the

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Description of plate 45

Scanning electron micrographs of *Thecidellina barretti*

Figure 35. Ventral surface of a cardinal process showing grooves and ridges of diductor scars (× 2800).

Figure 36. Internal surface of the lateral wall of a hemispondylium showing overlapping plates composed of acicular crystallites (× 3000).

Figure 37. Surface detail of the postero-lateral adductor scar in a brachial valve (× 2400).

Figure 38. Etched section of a hemispondylial floor showing the succession of calcitic laminae and lenses (× 2800).

Figures 39, 40. General view and detail of the muscle scars resulting from the attachment of the lophophore to a brachial valve (× 700, × 2800).

Figures 41, 42. Two views of the interiors of puncta seen in fracture surfaces of a pedicle valve (× 1300, × 1200).

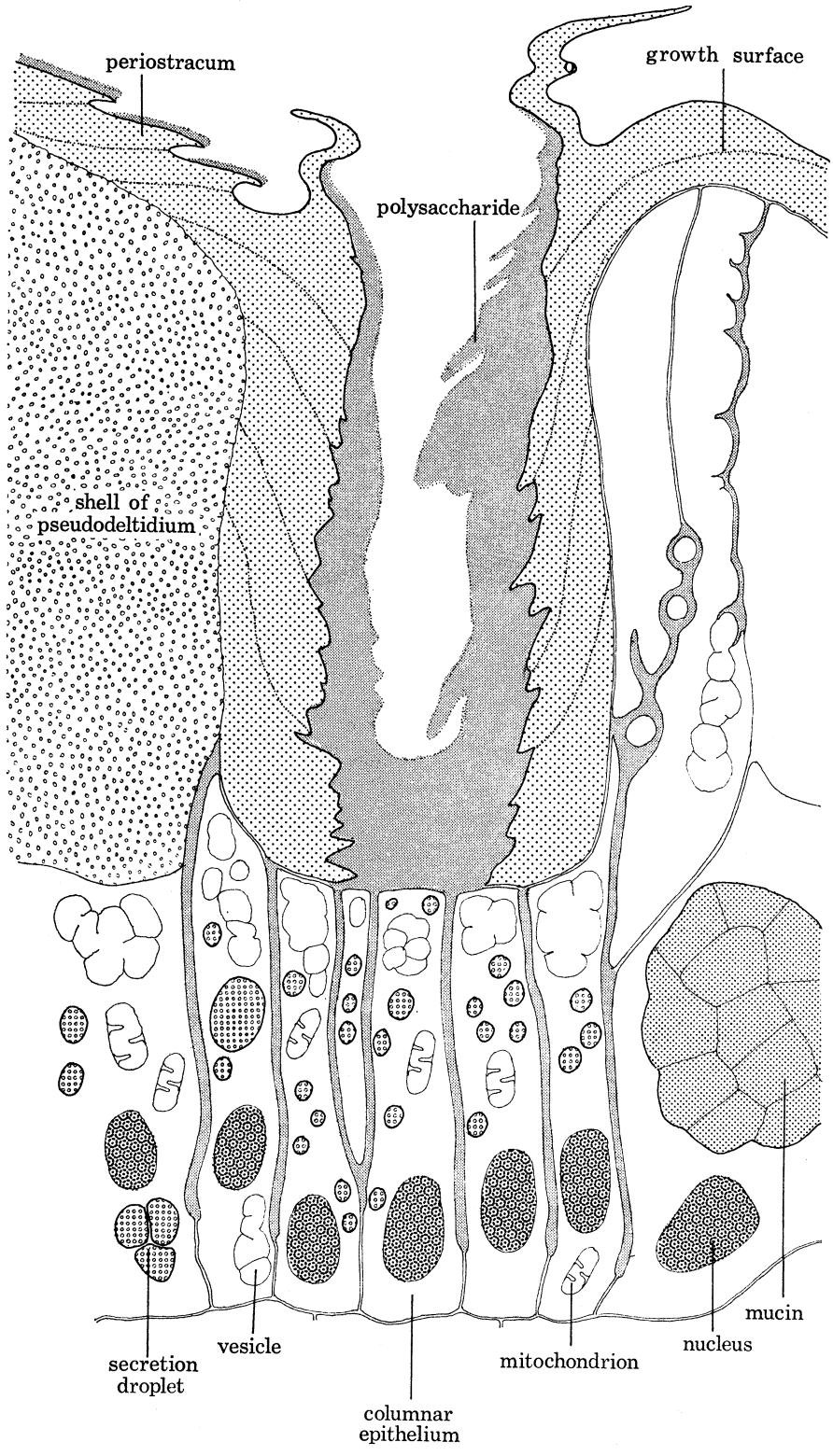


FIGURE 11. Diagrammatic longitudinal section of the hinge-line of *Thecidellina* showing the relationship between the periostracum and secreting epithelium (× 5000).

mantle edge, this membrane acts as a seeding sheet for calcite crystallites representing the beginnings of the carbonate layer of the interareas.

(*c*) *Outer epithelium and the carbonate shell*

The first carbonate crystallites deposited at the mantle edge and the hinge-line accrete with one another and earlier formed shell to become part of the rigid carbonate frame underlying the periostracum. At the mantle edge, new vesicular cells arriving at the hinge of the periostracal fold continue this process so that the shell enlarges radially. Relative to this expanding edge, each vesicular cell which continues to secrete or resorb more or less within the same area of the internal shell surface throughout life, comes to occupy an increasingly posterior position in the growing mantle. As it does so, each cell undergoes a number of changes, the most obvious of which is its conversion from extensible columnar to flat cuboidal epithelium about 15 μm across (figures 12 and 14, plate 42). The cells remain vesicular but, although mucin droplets are present here and there, the dominant inclusions are electron dense, lacking membranes and intimately associated with glycogen rosettes which, in conjunction with a PAS positive reaction persisting even in saliva-treated sections, suggest a glycoprotein composition. The glycoproteins tend to occur in large composite inclusions up to 15 μm long and 8 μm thick distending some cells four- or fivefold compared with adjacent ones which may be represented by little more than a folded plasmalemma stretched across the underlying connective tissue. These differences are accentuated by the development of mantle canals delineated by flat peritoneal cells within a predominantly collagenous connective tissue (figure 12, plate 42). The canals may be up to 3 μm in dorso-ventral diameter and are concentrated beneath the thicker cells so that the connective tissue separating the thinner parts of the outer epithelium from inner epithelium may be no more than 60 nm thick. Such variation in mantle thickness causes the secretory plasmalemmas of the outer epithelium to form regular undulations up to 40 μm across. These are complementary to tubercles developed on the internal surface of the shell with the thin parts of the mantle forming caps to tubercles (figure 14, plate 42). A noteworthy feature of the secretory surface of the outer epithelium is the presence of a moderately electron dense discontinuous layer about as thick as the underlying plasmalemma from which it is separated by a space about 100 nm across. As will be shown, no organic sheets are secreted with the main part of the carbonate shell and this discontinuous layer possibly represents a persistent organic mesh marking the external limit of a liquid film saturated with Ca^{2+} and HCO_3^- ions which sustain the secretion of the calcitic skeleton.

The basic mineral constituents of the primary layer are calcitic crystallites between 250 and 400 nm thick and up to 15 μm long with rhombic or scalenohedral terminal faces (figure 17, plate 42). Those seeded on the sealing membrane of the periostracum tend to form obliquely disposed overlapping rows with an average external spacing of 2 μm in the specimens examined (compare figure 65, plate 48). The junctions between rows, the so-called growth lines, could correspond to concentrations of the proteinous trails seen on the inner surface of the periostracum and thereby represent periodic adjustments in the change from organic to mineral secretion. As the shell thickens, crystallites are secreted normal to the internal surface and frequently amalgamate, even at the shell edge, into impersistent lenticular blades up to 5 μm across or smaller granules (figure 16, plate 42). The preponderant acicular crystallite fabric, however, is well seen in fracture or polished sections of the shell. Even growth lines, which impart a banded appearance to sections of the shell, cross cystallites without disturbing their vertical extension

(figure 18, plate 43). This, however, may reflect only expitaxial continuity from one layer to the next because growth lines can represent surfaces of interrupted accretion or resorption. The surface over which the interbrachial ridges expand laterally, for example, is seen in section as a growth line transgressing truncated tubercles which may have been more than 20 μm high before they were resorbed (compare figure 19, plate 43).

Intramarginally, the microtopography of the internal surface being secreted by unspecialized outer epithelium is dominated by two kinds of features (figure 26). The more prevalent are

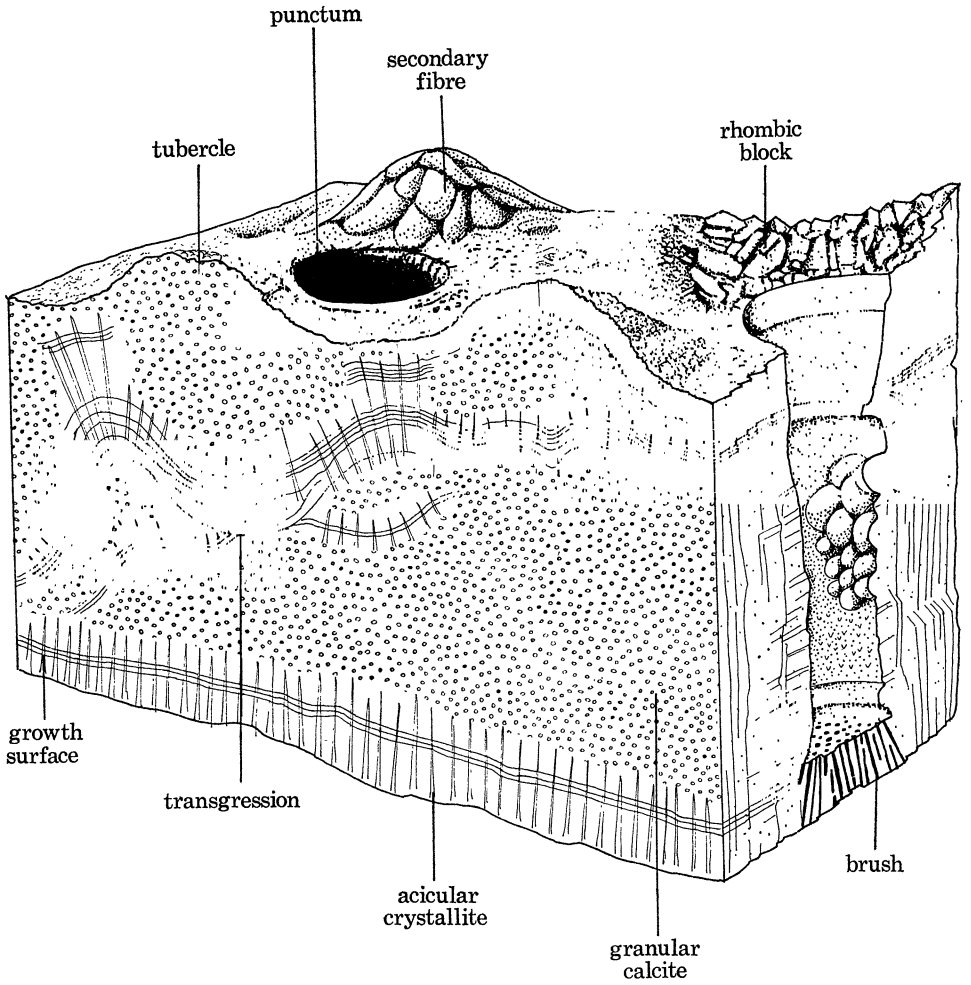


FIGURE 26. Diagrammatic view of a piece of *Thecidellina* shell showing some of the microtopographic features and a typical distribution of shell fabric (× 800).

DESCRIPTION OF PLATE 46

Scanning and transmission electron micrographs of *Thecidellina barretti*

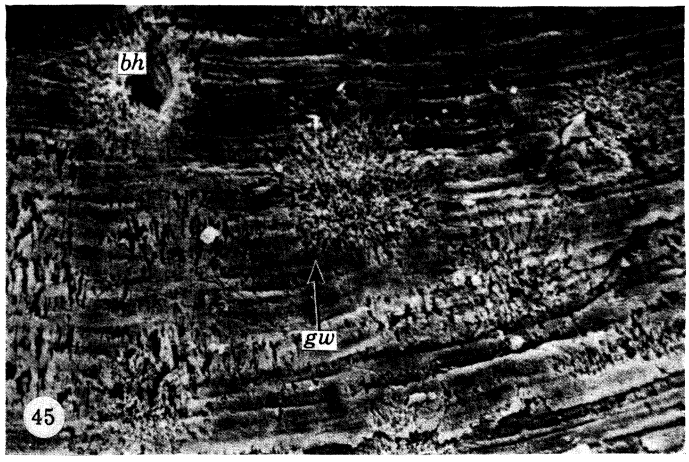
FIGURES 45, 46. External surface of a brachial valve showing the distribution and detail of brushes overlying puncta (× 600, × 2400).

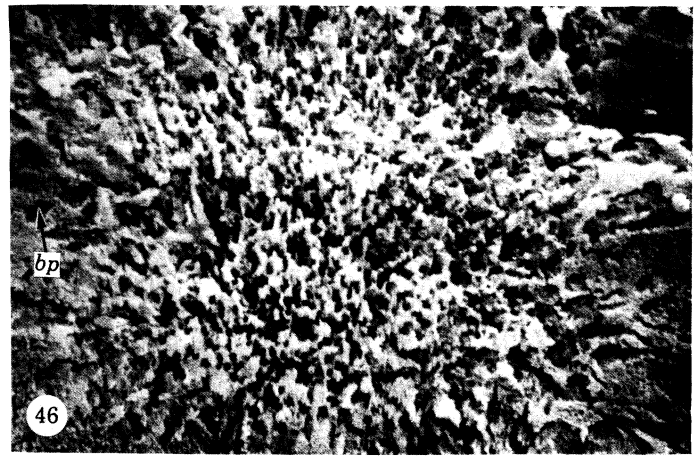
FIGURE 47. Detail of the junction between the periostracum and tubules of a brush (× 82500).

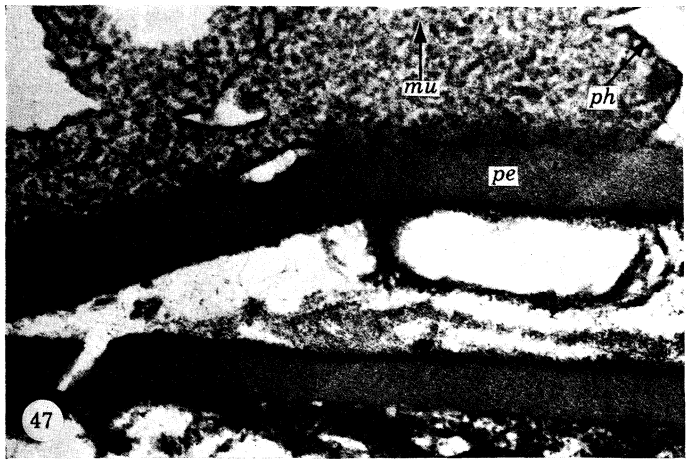
FIGURE 48. Detail of the junction between the secretory cells of a caecum and tubules of a brush (× 41500).

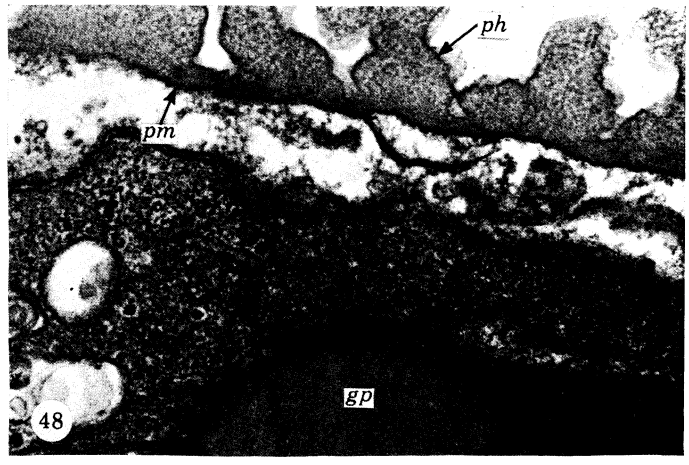
FIGURE 49. General view of a young caecum showing its relationship to the periostracum and mantle (× 3100).

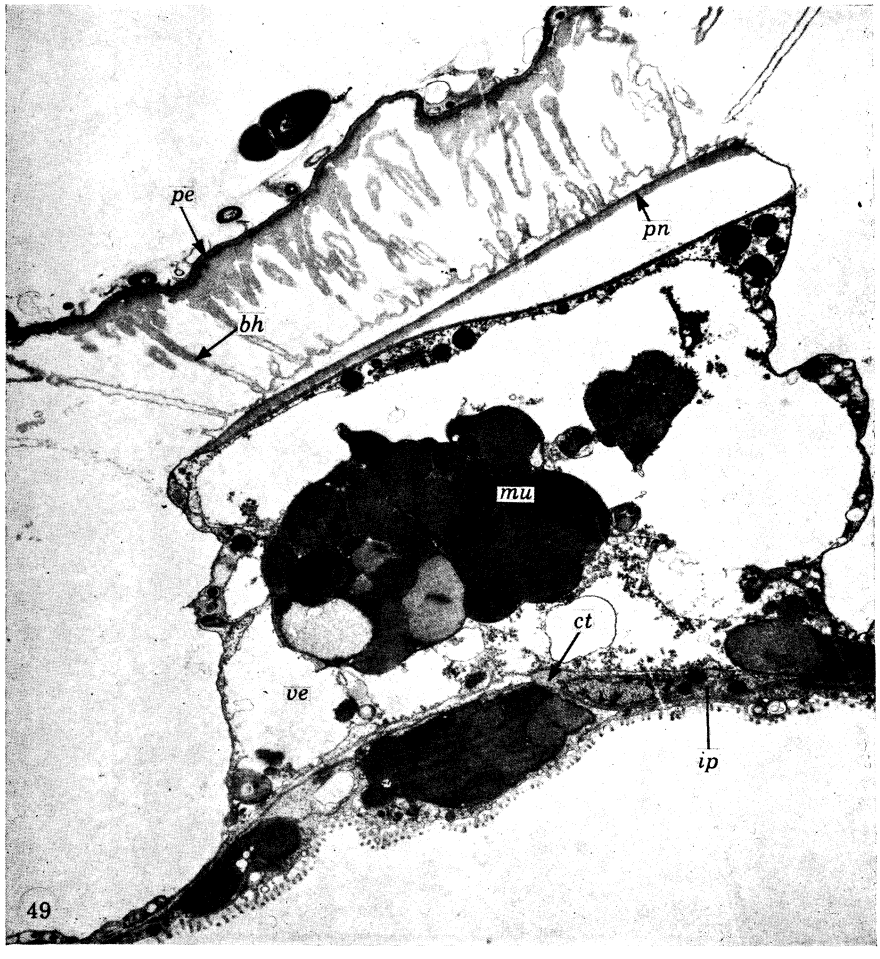
FIGURE 50. Part of a mature caecum showing the relationship of secretory cells to proteinous partitions (× 5500).











FIGURES 45 TO 50. For legends see facing page.

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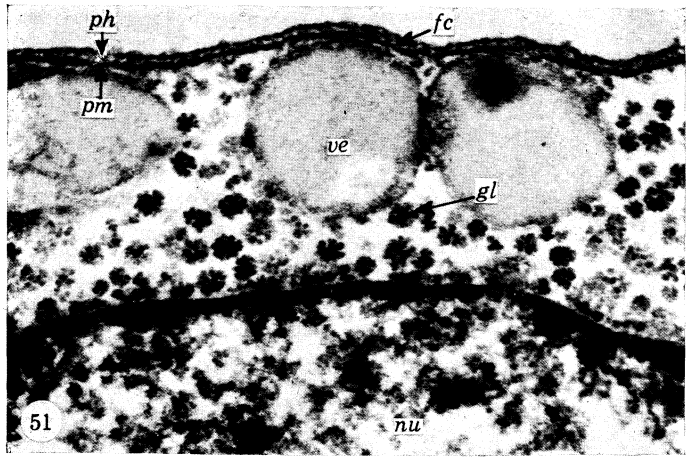
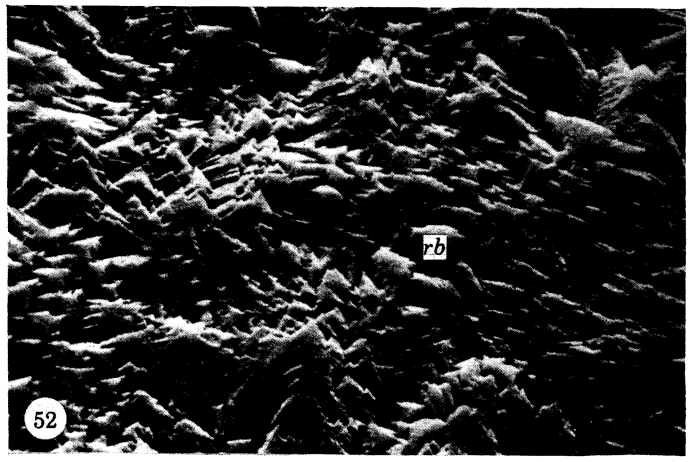
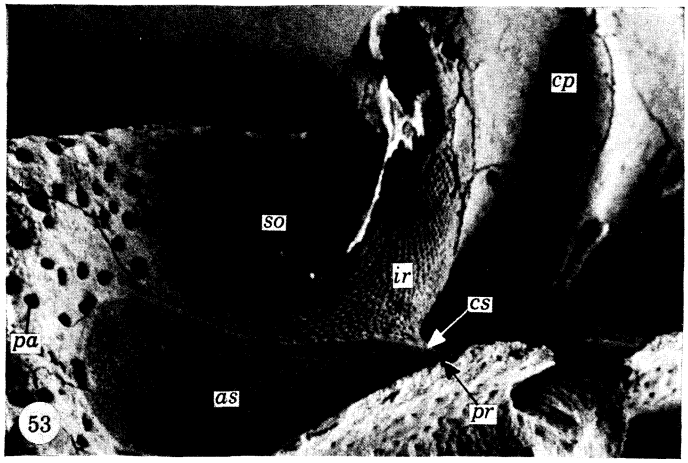
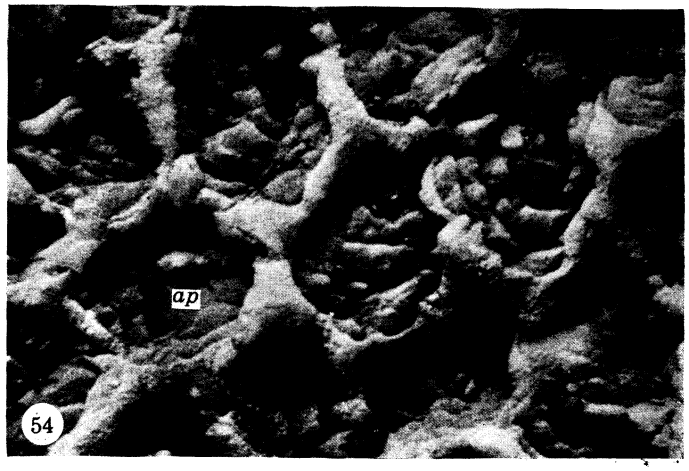
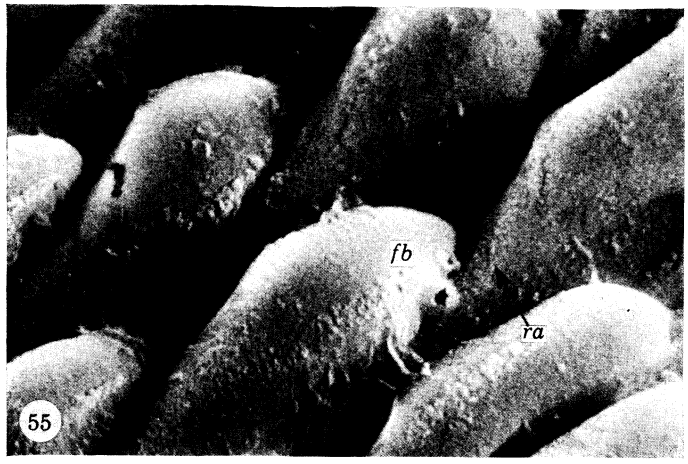
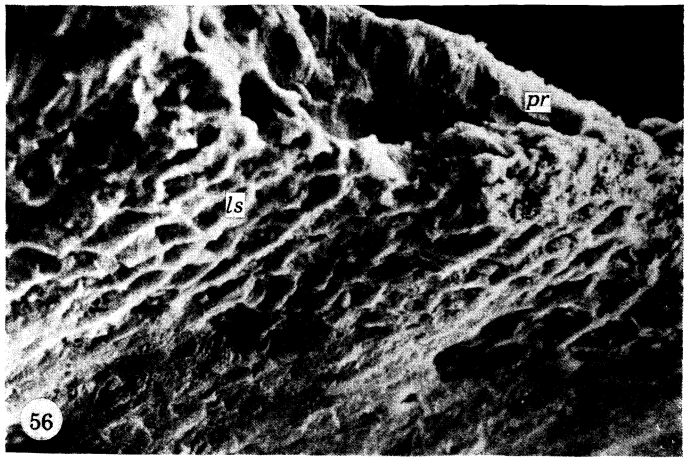


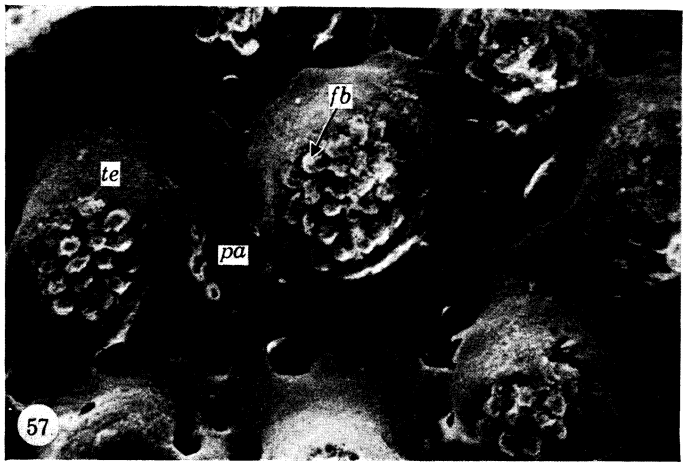


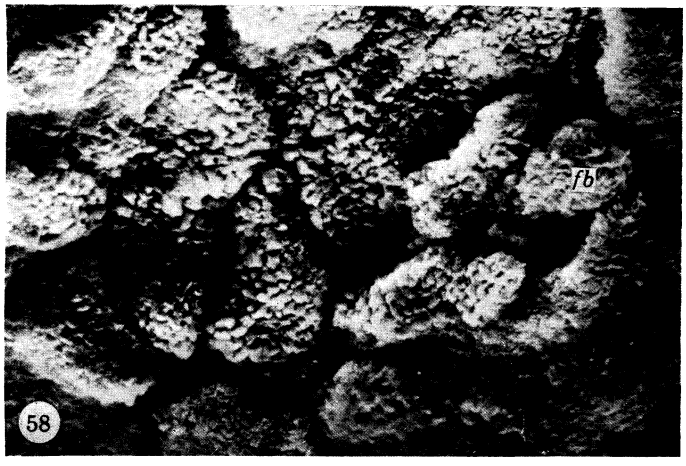












FIGURES 51 TO 58. For legends see facing page.

subconical tubercles varying in diameter from 20 to 100 μm and attaining heights of up to 30 μm (figure 23, plate 43). They occur almost everywhere in both valves except on muscle bases, cardinalia and articulatory devices, but are especially common in the subperipheral rims. Here they are usually composed of acicular crystallites disposed normal to the surfaces of deposition so that they tend to splay outwards radially (figure 17, plate 42). However, granular calcite is also commonly secreted and may form the tip of a tubercle although it has never been found aggregated into a continuous medial rod.

The other distinctive microtopographic features found in both valves consist of rhombs, up to 10 μm across, which form a spectacular pattern of closely packed blocks (figure 21, plate 43). These are prevalent in the medial and posterior parts of the shell and are a manifestation of the later phases of primary shell deposition. In both valves, a transitional zone of undulating ridges or tubercles composed of smaller rhombohedra usually intervene between the peripheral crystallite-granular and inner blocky rhombic surfaces. Yet acicular crystallites, disposed parallel with the cleavage planes, are evident on all faces of even the most perfect rhombohedra and still constitute the fundamental unit in the secretion of primary shell (figure 22, plate 43).

The occurrence of organic-carbonate deposits representing secondary shell, is very restricted in *Thecidellina barretti* compared with many fossil thecideidines. Superficial traces occur on the floor of the pedicle valve as a series of oval patches or depressions about 35 μm across arranged in arcs along the peribrachial ridge (figure 23, plate 43). Each patch consists of about 10 fibres up to 12 μm across (figure 24, plate 43), frequently with rhombohedral angles defining terminal faces and composed of acicular crystallites about 150 nm thick. Decalcified sections show that the fibres are separated from one another by incipiently developed proteinous sheets in the manner of secondary fibres of living rhynchonellides. The reason for this particular distribution of secondary shell is not known with certainty. However, peripheral to the depressions in the outermost arc there occur narrow depressed lobate areas of finely granular relatively smooth calcite (figure 23, plate 43). Each lobate strip undoubtedly underlies terminal branches of the coelomic canal system pervading the mantle, and since more than one strip may converge on depressions, the latter may underlie nodes in the mantle canals.

Similar patches or depressions composed of secondary shell are unknown in the brachial valve; but some tubercles, developed postero-medially in adult specimens, show the characteristic segregation of carbonate into 10 or 12 fibres (figure 25, plate 43). Again, the crystallite-granular fabric of the deposit is evident.

Description of plate 47

Figure 51. Transmission electron micrograph of *Thecidellina barretti* showing the relationship between the proteinous lining of a punctum and caecum (× 68700).

Scanning electron micrographs of *T. australis* (Tate) *sensu lato*, Eniwetok Atoll

Figure 52. Internal surface of a pedicle valve showing rhombs and blades of calcite (× 1500).

Figure 53. Ventro-lateral view of the cardinalia and posterior part of the lophophore support in a brachial valve (× 75).

Figure 54. Surface view of the adductor scar in a hemispondylium (× 3000).

Figure 55. Surface detail of an inner socket ridge showing fibres (× 3100).

Figure 56. Undersurface of the posterior part of a peribrachial ridge showing muscle scar pits for attachment of the lophophore (× 750).

Figures 57, 58. Internal surface of a brachial valve showing the distribution of tubercles and the texture of secondary fibres (× 300, × 1600).

In contrast to their superficial and sporadic occurrence on the valve floors, secondary fibres are well developed in the articulatory devices of the shell, i.e. the teeth of the pedicle valve and the inner and outer socket ridges of the brachial valve (figure 34).

The teeth which project dorsal of the hinge-line for almost 250 μm have cores of fibres arranged more or less parallel to the long axes of the teeth (figures 27 and 28, plate 44). The

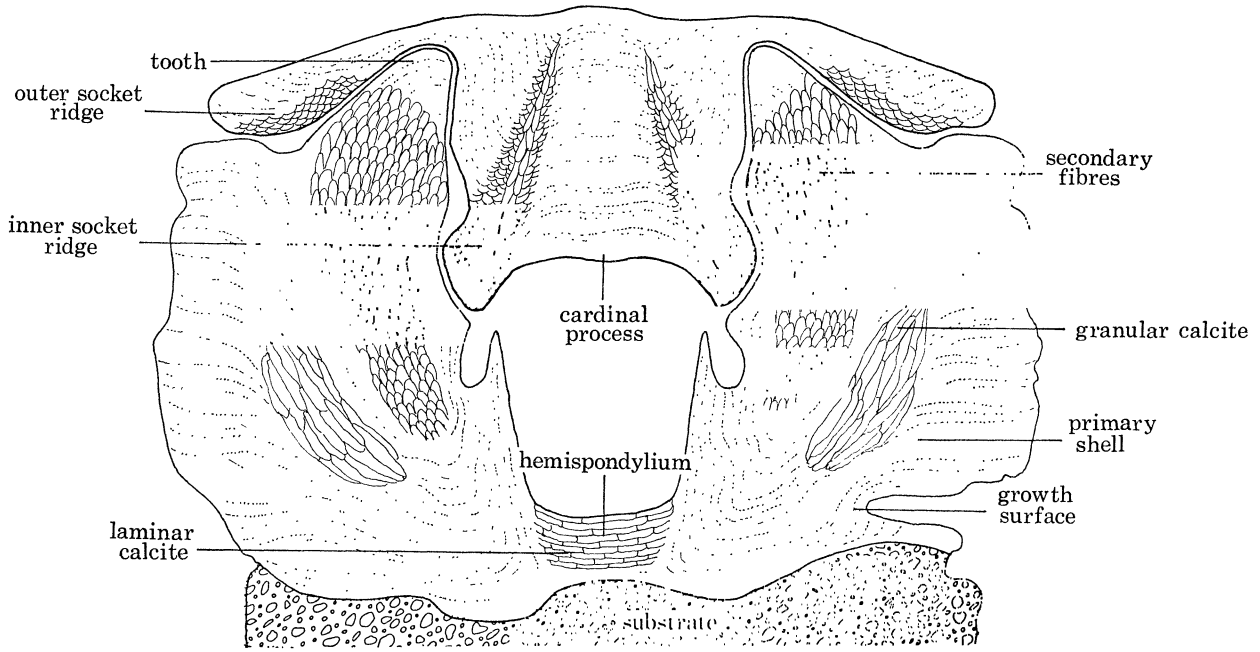


FIGURE 34. Diagrammatic section of the posterior region of conjoined valves of *Thecidellina* showing the distribution of the main shell textures (× 100).

fibres are between 5 and 10 μm thick and are arranged in alternating rows so that they are seen in fracture surfaces or sections to be stacked in mosaics, characteristic of the fibrous secondary shell in other articulatory brachiopods, with convex surfaces facing the secretory epithelium. The fibres themselves are composed of acicular crystallites (figure 29, plate 44) alined normal to, or parallel with, their long axes, and are separated from one another by proteinous sheets

DESCRIPTION OF PLATE 48

Scanning electron micrographs of '*Thecidellina*' *hedleyi* Thomson, Oligocene (Everett's Quarry Limestone), Oamaru, New Zealand

FIGURE 59. Etched section showing the typical texture of the shell (× 2900).

FIGURE 60. Surface view of the junction between the base of the inner socket ridge and the postero-lateral adductor scar (× 750).

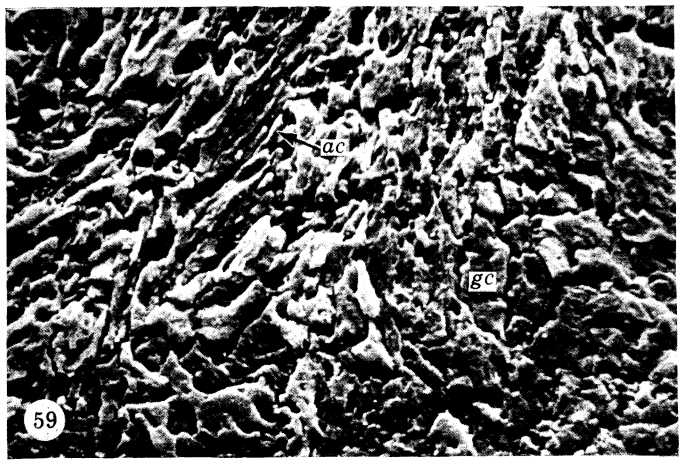
FIGURES 61, 62. Dorsal view and detail of spines attached to the floor of a pedicle valve (× 750, × 1500).

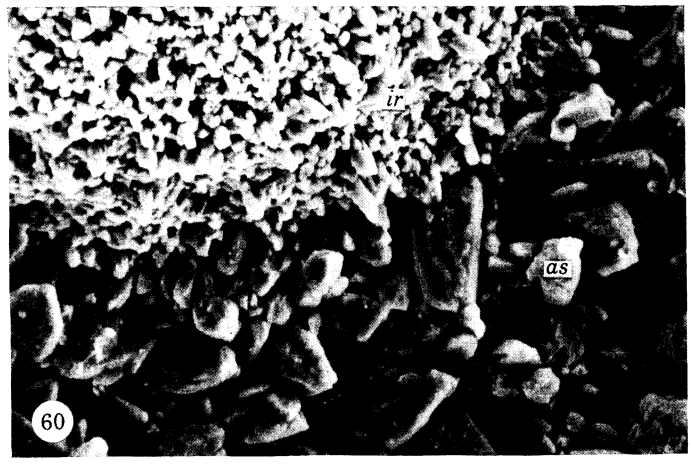
Scanning electron micrographs of *Lacazella mediterranea* (Risso), the Mediterranean

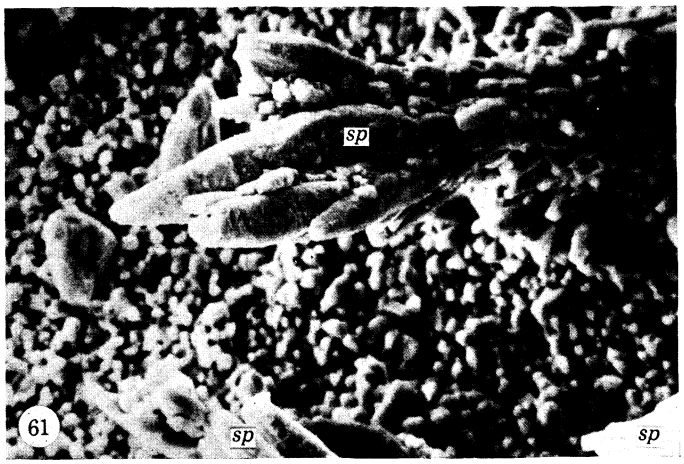
FIGURE 63. External surface of a dorsal protegulum (× 1400).

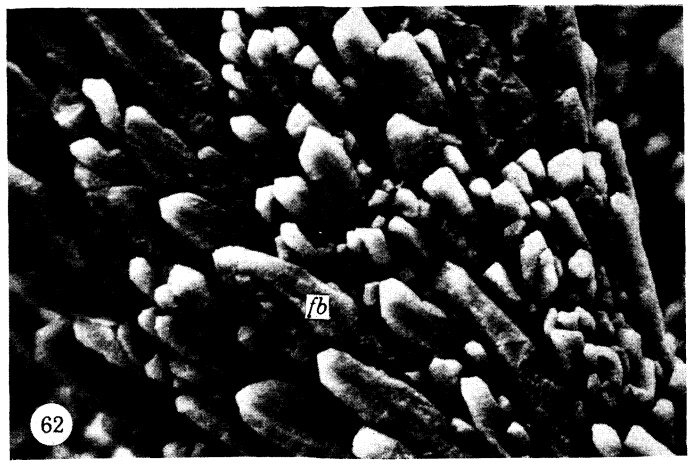
FIGURE 64. Posterior view of a complete shell to show the hinge-line between the two valves and the punctate nature of the pseudodeltidium (× 150).

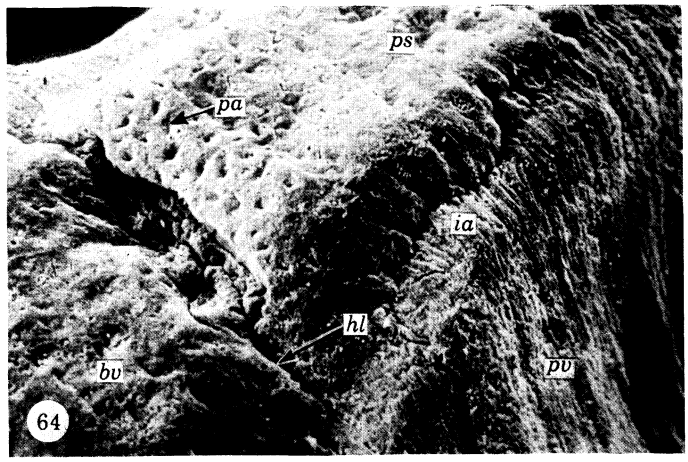
FIGURES 65, 66. The brush seen externally and as perforations and canals in the fracture surface of the canopy of a punctum (× 1400, × 3000).

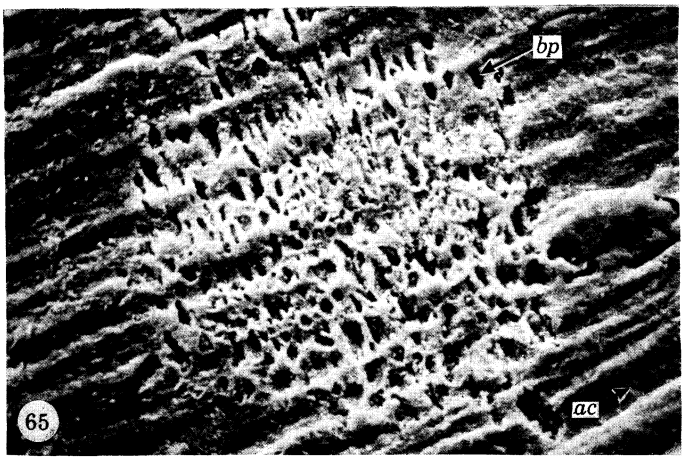


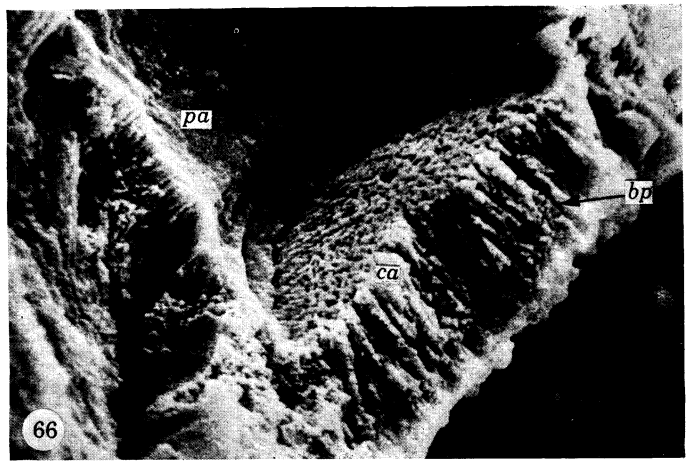












FIGURES 59 TO 66. For legends see facing page.

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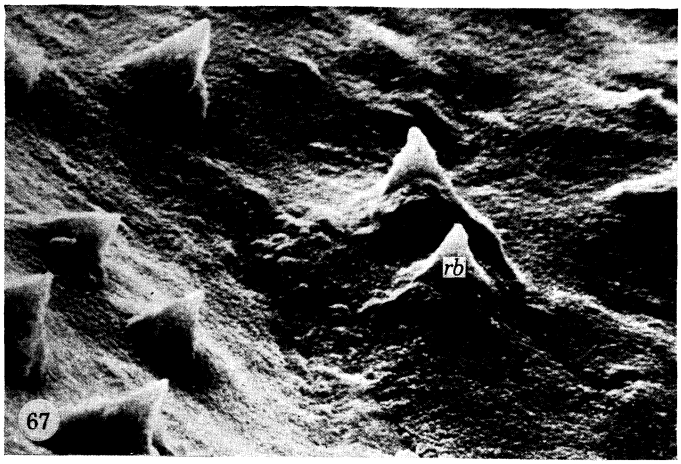

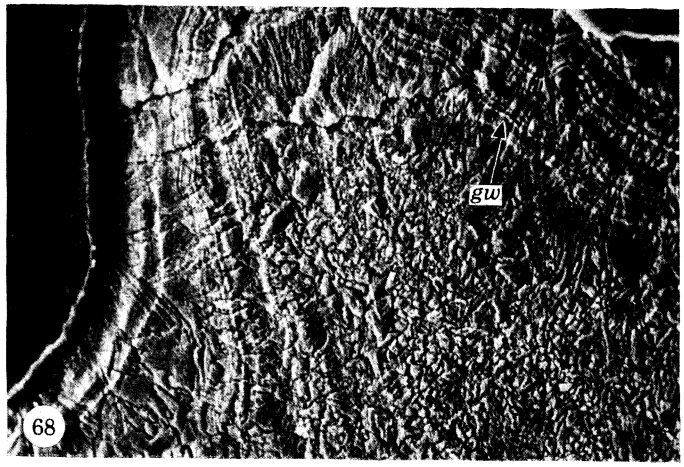

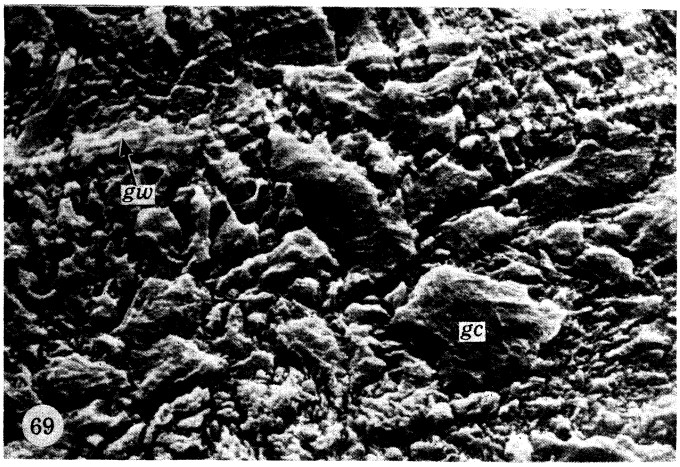

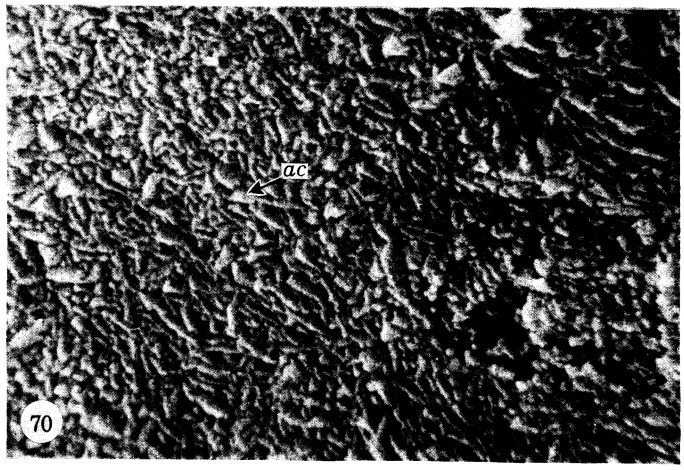

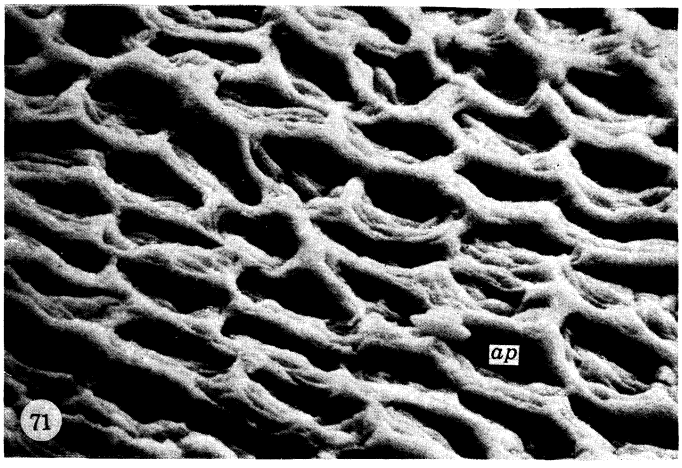

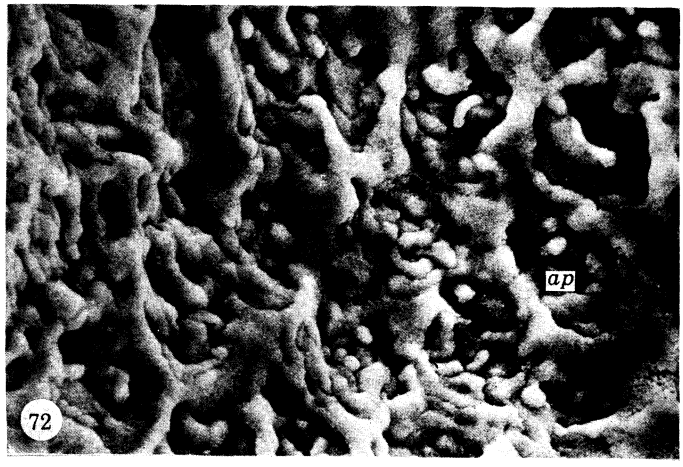

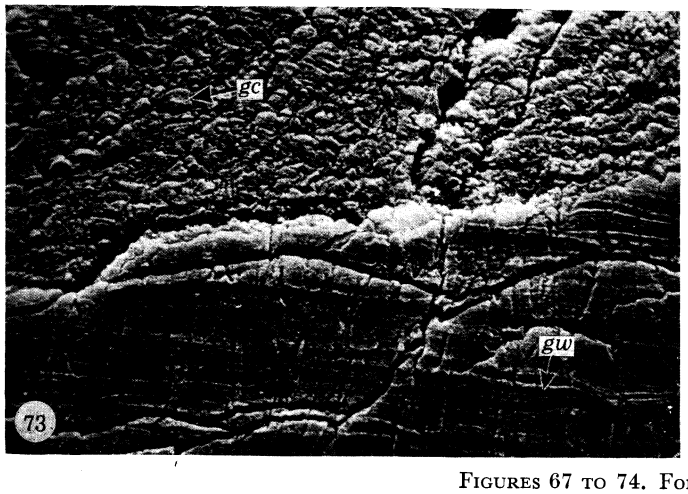

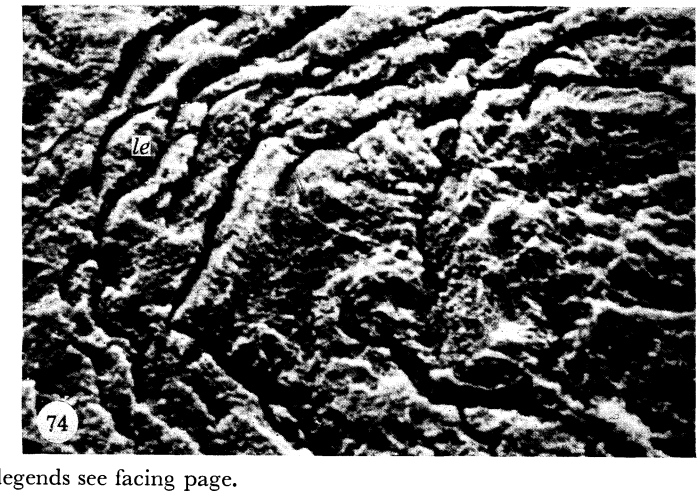

FIGURES 67 TO 74. For legends see facing page.

about 4 nm thick. These sheets may become seeding sheets for crystallites independent of aggregates making up the fibres so that they appear as relatively thick walls in differentially etched sections (figure 31, plate 44). Indeed in mature specimens, the terminal faces of fibres at the tip of the tooth may be partly or completely covered by a finely granular calcite which is continuous with the carbonate coating the proteinous sheets and is well seen in surface view (figure 30, plate 44) and section. Such deposits presumably accumulate in late adult stages of growth when the teeth and their complementary sockets are fully developed and undergo little further modification. Finely granular layers of calcite also envelop the base of a tooth and encroach on the more ventral parts of the tooth itself especially along the posterior and anterior surfaces (figure 27, plate 44). Although these deposits are necessarily secreted later than the secondary fibres they cover, they may still be regarded as part of the primary layer accumulating simultaneously with localized cylindroid projections of secondary shell.

In the brachial valve, orthodoxly arranged secondary fibres define the outer socket ridges but are more spectacularly developed in the inner socket ridges which also act as the lateral boundaries of the cardinal process. Abraded surfaces of these ridges reveal fibres beneath a thin deposit of finely granular calcite, but the structural relationships with the rest of the cardinalia is best seen in section (figure 34, figures 31 and 32, plate 44). In cuts just below the hinge-line, the inner socket ridges appear as a pair of acute triangles with their bases resting on the inner flanks of the teeth (crural fossettes). These triangular zones are sharply distinguishable from the banded acicular crystallites composing the cardinal process and the hinge of the socket. Moreover, the fibres of the ridges are themselves differentiated into three zones. At the apex of the triangle representing the first-formed part of the inner socket ridge, the fibres are somewhat irregular and attain widths of 30 μm. These large fibres persist as a narrow medial wedge with never more than three or four fibres in a row. This wedge is flanked by regularly arranged smaller fibres about 4 μm wide with up to nine and sixteen per row in the narrower medial and wider lateral zones respectively.

(*d*) *Muscle scars*

The shell fabric of *Thecidellina* is variably modified by the emplacement of muscle bases. Three types of deposits result, dependent on whether they are associated with the diductor or adductor muscles or with tonofibrils responsible for the attachment of the lophophore base to the brachial ridges. In all three, outer epithelial cells intervening between the shell and muscle base or lophophore connective tissue have similar characteristics (figure 33, plate 44). The cells tend to be cuboidal rarely exceeding 12 μm across or 6 μm in height. They are traversed by bundles of tonofibrils with internal desmosomes crossing the intercellular spaces or basal lamina

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Description of plate 49

Scanning electron micrographs of *Lacazella mediterranea*

Figure 67. Internal surface of a brachial valve showing discrete rhombohedra (× 2800).

Figures 68, 69. Etched section showing the general texture and details of a tubercle (× 780, × 3100).

Figure 70. Ventral surface of a cardinal process showing convoluted topography associated with diductor muscle bases (× 2900).

Figures 71, 72. Details of the postero-lateral and hemispondylial adductor muscle scars (× 1300, × 1300).

Figure 73. Etched section showing junction in the lateral wall of a hemispondylium between the lining of granular calcite underlying diductor muscle scars and the outer layer of banded calcite (× 1500).

Figure 74. Etched section of the tip of the medial ridge in a hemispondylium showing lenses of calcite (× 3000).

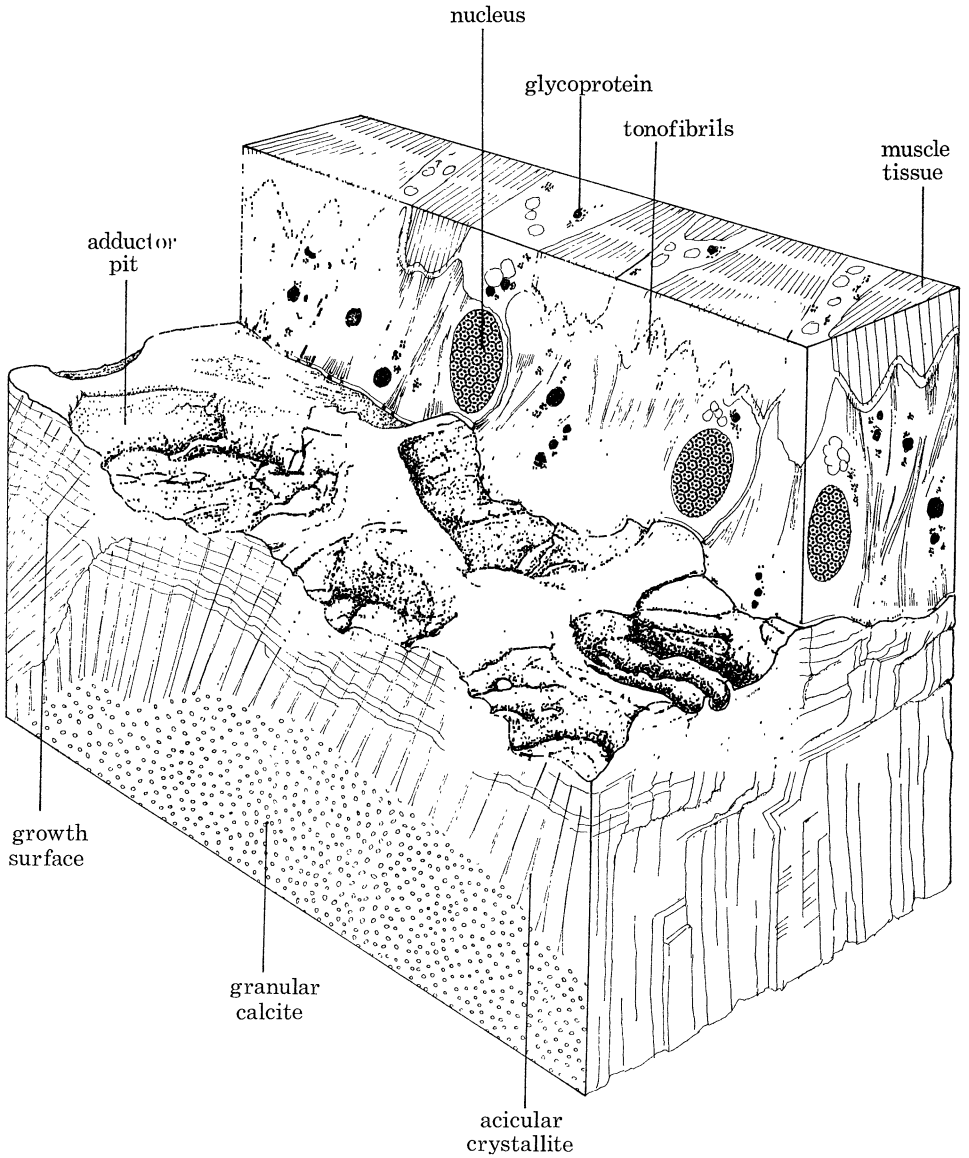


FIGURE 43. Diagrammatic reconstruction of a pitted muscle scar in relation to the outer epithelium underlying the adductor muscle base (×3000).

DESCRIPTION OF PLATE 50

Scanning electron micrographs of *Lacazella mediterranea*

FIGURE 76. Detail of the muscle scar resulting from the attachment of the lophophore to the peribrachial ridge of a brachial valve (× 2800).

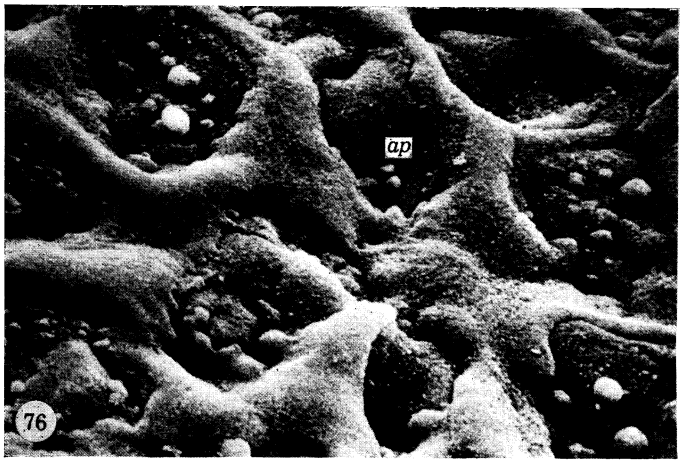
FIGURE 77. Etched section showing the junction between the core and external coat of a tooth (× 3000).

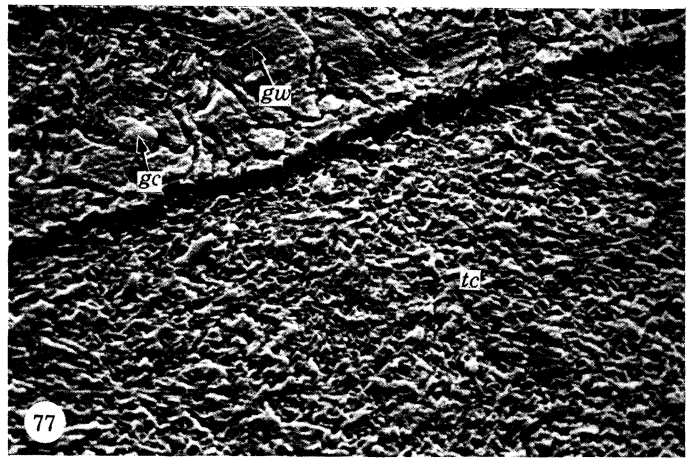
FIGURES 78, 79. Dorsal view of a tooth and detail of superficial secondary fibres respectively (× 250, × 1300).

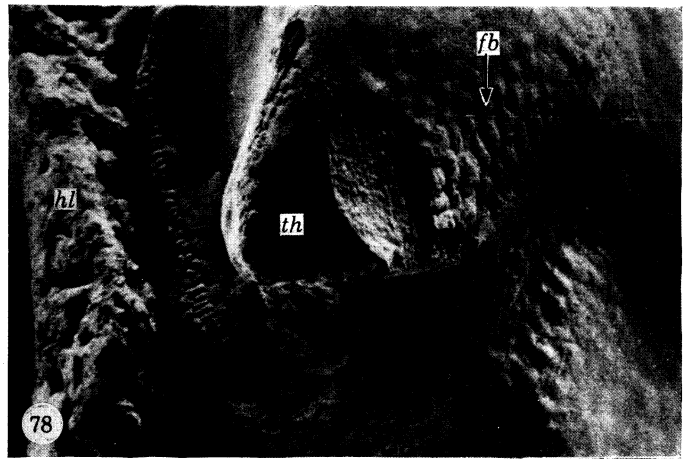
Scanning electron micrographs of etched sections of fossil thecideidines

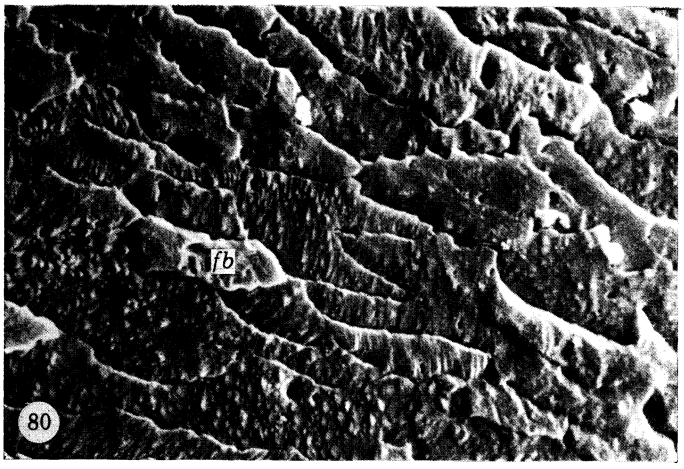
FIGURES 80, 81. Inner part of the secondary layer and the junction between the primary and secondary layers of a brachial valve of *Davidsonella sinuata* (Eudes-Deslongchamps), Upper Lias, May-sur-Orne, Calvados, France (× 2800, × 2800).

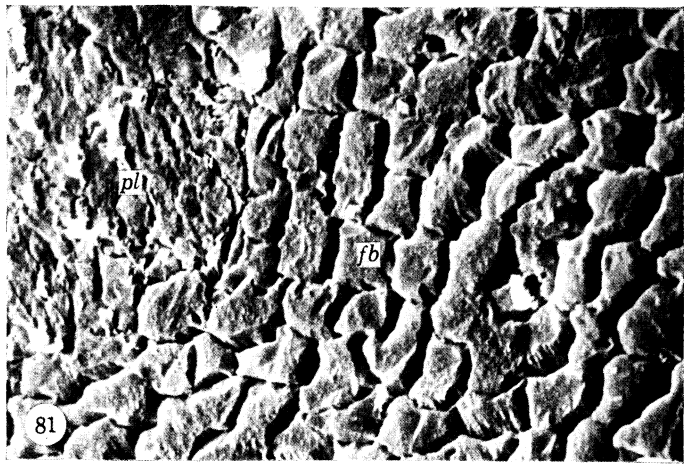
FIGURES 82, 83. Primary and secondary layers penetrated by a punctum in the floor of a pedicle valve, and the succession in the pseudodeltidium of *Moorellina* cf. *granulosa* (Moore), Upper Jurassic (Corallian), Shellingford Cross-Road Quarry, Stanford in the Vale, England (× 1500; × 2900).

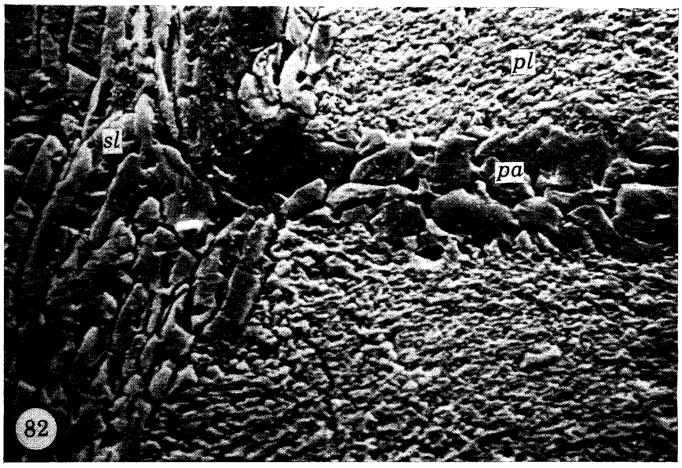


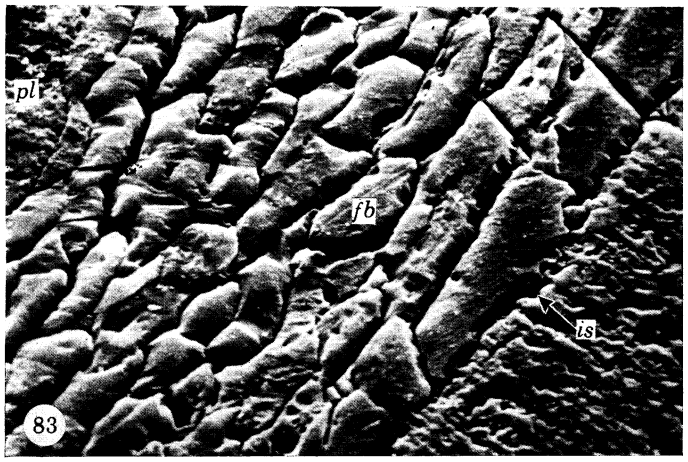












FIGURES 76 TO 83. For legends see facing page.

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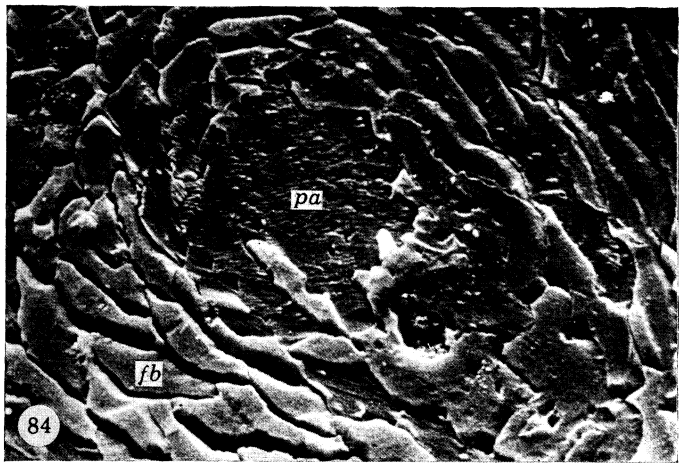
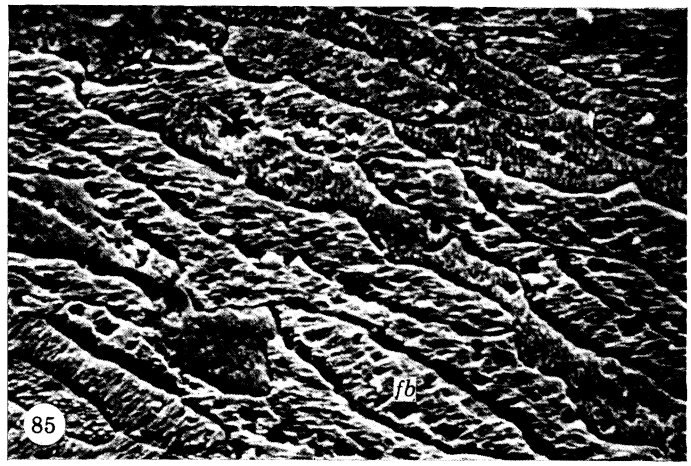
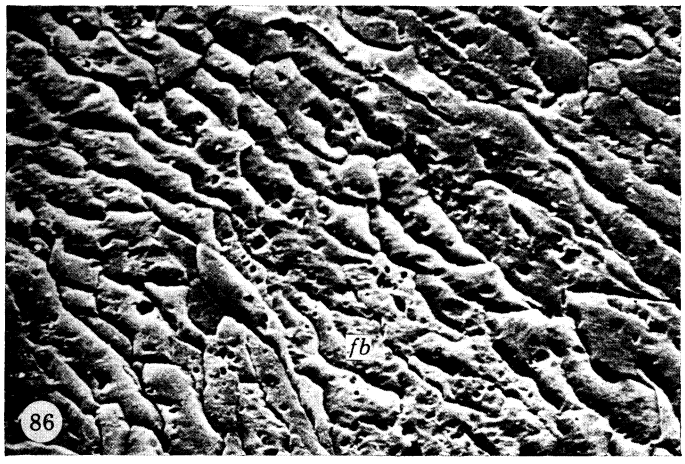
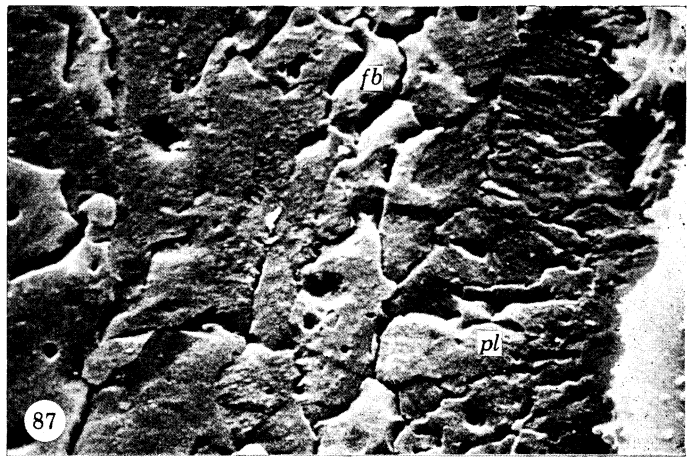
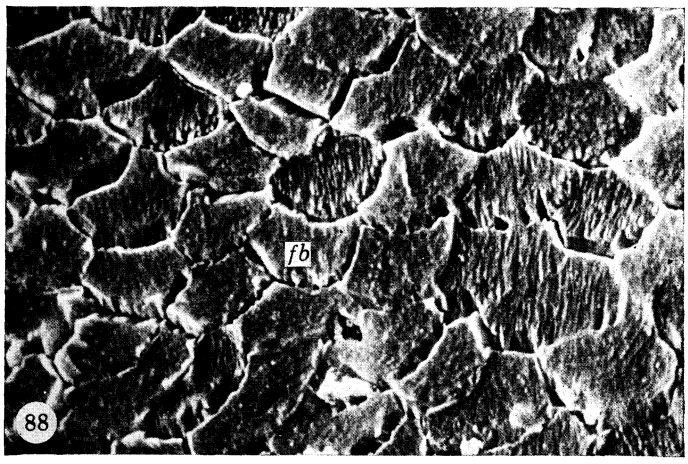
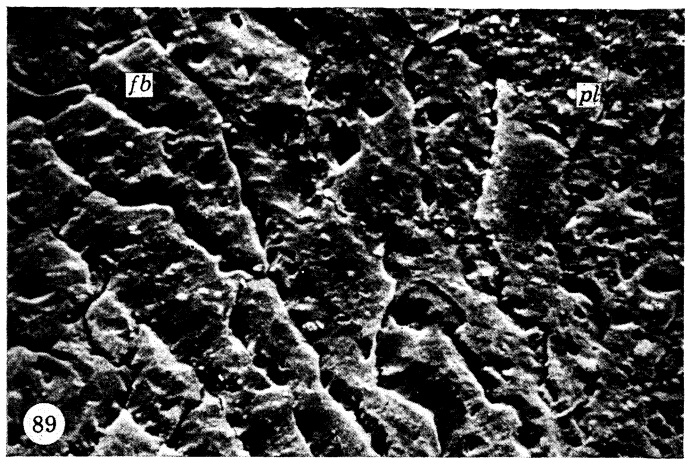


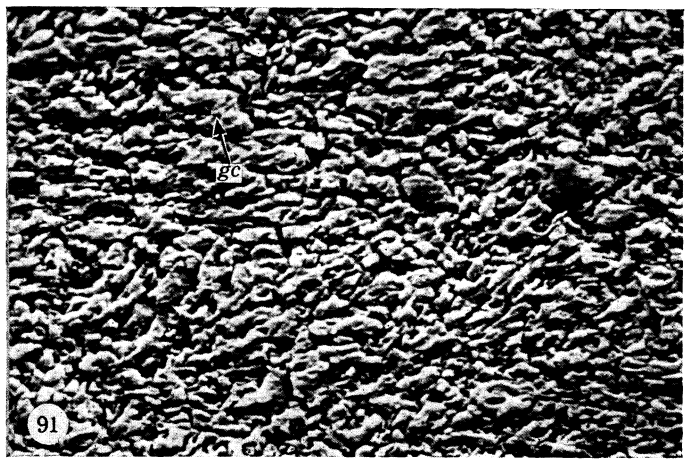












FIGURES 84 TO 91. For legends see facing page.

between epithelium and muscle base or epithelium and connective tissue respectively, and external desmosomes connecting an outer proteinous membrane, 4 nm thick, with the secretory plasmalemma of the epithelium (compare figure 15, plate 42). This membrane is part of a complex of sheets secreted by the cells as an integral part of skeletal deposition. But only within the adductor scars and hemispondylial floor do the sheets interconnect with one another to appear as anastomosing lines in section.

The least conspicuous changes in the typical fabric of the carbonate skeleton are those consequential to the emplacement of the diductor muscle bases on the ventral face of the cardinal process and on the sides and the inner surfaces of the floor and lateral walls respectively of the hemispondylium. In the first two zones the calcite is finely granular and forms longitudinal groove and ridges between 300 and 400 nm in wavelength (figure 35, plate 45). On the inner sides of the hemispondylial walls, however, overlapping plates about 350 nm thick are the prevalent deposit (figure 36, plate 45). They are composed of flat-lying acicular crystallites and are superficial deposits encroaching across highly inclined crystallites making up the walls and well seen along the anterior edges of the hemispondylium.

The postero-lateral adductor scars are oval patches about 200 μm in maximum diameter with a strikingly different pattern (figure 43). They consist essentially of a series of pits about 6 to 10 μm across and up to 3 μm deep (figure 37, plate 45). They are defined by ridges between 2 and 3 μm thick and are floored by bars of similar size all composed of crystallites, up to 200 nm thick, disposed more or less normal to the secretory surface. In relation to adductor muscle bases these dimensions are consistent with each pit accommodating the tonofibril zone of an outer epithelial cell with the bounding ridges corresponding to the wide peripheral and intercellular parts of adjacent cells. The interconnected protein sheets seen in decalcified sections presumably act as sheaths for the discrete bars and ridges defining the hollows.

The small submedial adductor scars at the base of the cardinal process and on the hemispondylial floor have a similar microtopography, although on a subdued scale in the specimens examined, because the pits are represented by shallow depressions and the bounding ridges are correspondingly poorly defined. They are, moreover, superimposed on layered successions which, in section of the hemispondylium, are seen to consist of laminae and lenses of calcite up to 1.5 μm thick (figure 38, plate 45). Such a pattern is probably an early stage in the differentiation of the adductor scars when the associated outer epithelium is not so greatly specialized as that underlying the more powerful postero-lateral adductors, either in the density of tonofibrils or in the selective secretion and resorption of the carbonate shell.

Description of plate 51

Scanning electron micrographs of etched sections of fosssil thecideidines

Figure 84. Fibrous secondary layer with punctum of a pedicle valve of *Moorellina* (*Elliottina*) *deslongchampsi* (Davidson), Middle Lias, May-sur-Orne, Calvados, France (× 1500).

Figure 85. Fibrous secondary layer of a brachial valve of *Eudesella mayensis* (Eudes-Deslongchamps), Upper Lias, May-sur-Orne, Calvados, France (× 2600).

Figures 86, 87. Fibrous secondary layer and junction between primary and secondary layers of a brachial valve of *Rioultina ornata* (Moore), Upper Jurassic (Oxfordian), Ayton, Scarborough, England (× 1500, × 3000).

Figures 88, 89. Fibrous secondary layer and junction between primary and secondary layers of a pedicle valve of *Thecidella rustica* (Moore), Upper Lias, May-sur-Orne, Calvados, France (× 2800, × 2800).

Figures 90, 91. Ultrastructure of the lateral wall and core of the tooth of a pedicle valve of *Eolacazella affinis* (Bosquet), Upper Cretaceous (Maestrichtian), Bemelen, Netherlands (× 3000, × 3000).

The muscle scars resulting from the attachment of the lophophore to the brachial valve are like adductor impressions in some respects (figures 39 and 40, plate 45). They occur as petaloid patches about 100 μm long and 35 μm wide impressed on the inner slopes of the peribrachial ridges at intervals of about 35 μm. The epithelial cells responsible for the scars underlie sectors of the lophophore bearing filaments (figures 13 and 15, plate 42). Correlation of skeleton and epithelium suggests that those parts of the cells with densely distributed tonofibrils fit into suboval pits about 6 to 7 μm across which distinguish the scars. The pits are probably produced by resorption as well as secretion of bounding walls over 1 μm wide by the peripheral zones of adjacent cells because three or four layers are exposed along the sides and floor of a pit. Each layer is about 500 μm thick and is separated from its neighbour by a proteinous sheet. It is composed of vertically stacked acicular crystallites identical with those characteristic of the areas between the scars and the intrabrachial ridges and their spines, although granules up to 4 μm are also found in the ridges.

(*e*) *Structure and growth of the caecum*

The carbonate shell of *Thecidellina* is permeated by puncta (figure 26) similar to those found in living Terebratulida (Owen & Williams 1969), although caecal outgrowths of the mantle accommodated by both types of canals differ in important respects (figure 44).

Puncta are unbranched canals about 25 μm in diameter arranged more or less alternately and concentrically at intervals of about 45 μm. A smooth finely granular or roughened acicular crystalline layer usually lines the bounding wall of a punctum but ledges develop here and there as well as hemispherical accretions up to 10 μm in diameter (figures 41 and 42, plate 45). Puncta penetrate the entire mineral layer except for an external canopy about 7 μm thick underlying the periostracum (compare figure 66, plate 48). The canopy itself is perforated by about 900 fine canals (the brush) averaging 280 nm in diameter and radiating slightly from the distal end of a punctum (figures 45 and 46, plate 46).

Both the punctum and individual perforations forming the brush are lined by an electron dense monolayer, presumably proteinous in composition, between 30 and 50 nm thick. Within a brush, electron dense particles, about 150 nm in diameter, in a lighter matrix which may be a mucopolysaccharide normally form a thick coat adhering to the proteinous lining of the canals (figures 47 and 48, plate 46). The periostracum overlying the canopy is usually about 250 nm thick and, as a medium electron dense granular layer broken only by sporadically distributed tension cracks bearing no relationship to the brush, is no different in composition or morphology from those parts covering interpunctate patches of the carbonate shell surface (figure 47, plate 46). The junction between the periostracum and the organic contents of the brush is normally indicated by a membrane or a sharply defined interface although a textural gradation from one to another is also found. The proteinous lining of a punctum is separated from the plasmalemmas of any cells that may be present by a gap of about 100 nm bridged by fibrillar connexions (figure 51, plate 47). Cells found within puncta invariably display features indicating that they act as storage centres for various protein and carbohydrate complexes and rare lipids (figures 49 and 50, plate 46). Electron light, membrane-bound secretion droplets, identified as mucopolysaccharides, frequently occur as large aggregates up to 20 μm in size, as do electron dense granular glycoprotein bodies which lack membranes, but are associated with stellate clusters of glycogen. Large vesicles and intercellular spaces may also occur. However, in contrast to the terebratulide caecum with its core of storage cells located near the brush and usually

separated from the mantle proper by large intercellular spaces, the core cells in *Thecidellina* normally remain connected with mantle epithelium irrespective of the thickness of the enclosing shell. In newly formed caeca up to 20 μm long, core cells extend from the inner surface of the

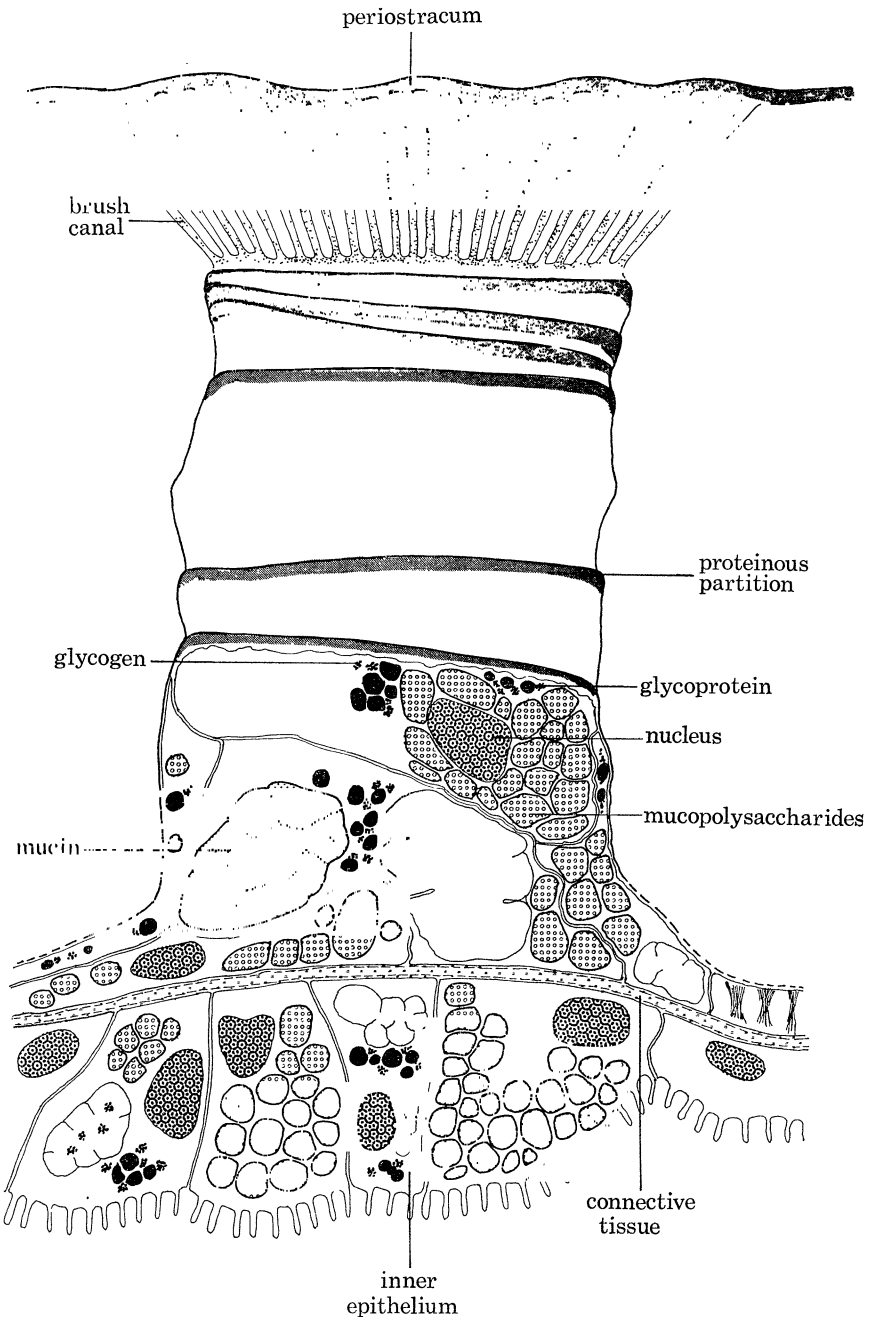


FIGURE 44. Diagrammatic sagittal section of a caecum of *Thecidellina* showing its main features (× 5000).

canopy to the layer of connective tissue in the mantle. In mature caeca the core cells are separated from the canopy by organic partitions, between 300 and 500 nm thick, which vary in number according to the length of caeca (figure 50, plate 46). The partitions with their finely granular texture grading internally from a relatively dark to light electron density, compare

closely with periostracum and are, also, probably composed of mucopolysaccharide. Two or three partitions are usually secreted within a few microns of the canopy but inwardly they become more widely spaced so that up to eight sealed segments of punctum, each up to 6 μm long, may separate the core cells from the canopy region.

Although attempts to prepare decalcified sections showing a brush being formed at the mantle edge were unsuccessful, its origin as well as the subsequent growth of a caecum are easily visualized. The plasmalemmas of vesicular cells responsible for secreting the inner layer of the periostracum bear widely spaced irregular microvilli which tend to disappear when carbonate deposition begins. Periodically, however, the microvilli of small groups of cells, which are more densely and regularly distributed, must remain in contact with the inner surface of the periostracum subsequent to the rotation of the cells around the hinge of the periostracal fold. Calcite crystallites secreted between the microvilli then coalesce to form the canopy and in so doing delineate canal-like casts of the microvilli which constitute the brush. With continuing secretion of the canopy the microvilli are gradually withdrawn, exuding as they retreat the proteinous linings and the coarsely granular material that form tubules within the brush. This process of growth is the same as that deduced for the brush of Terebratulida (Owen & Williams 1969, p. 196). But in species belonging to that Order, the core cells remain in the distal part of a punctum and retain their microvilli which occupy the space immediately below the canopy. In *Thecidellina*, on the other hand, the microvilli disappear so that by the time the first partition is secreted, the plasmalemmas are more or less featureless and the partition correspondingly simple. Thereafter as the shell thickens, the core cells periodically shift inwardly with the retreating mantle and the newly vacated segment of the punctum is sealed off by secretion of a partition. There is no evidence to suggest that any significant quantities of carbonate are secreted in these partitioned segments after migration of the core cells and it is assumed that, once formed, they remain empty.

(*f*) *Shell structure of other* Thecidellina

The shell structure of two other species of *Thecidellina* has been studied to determine whether any fundamental changes in texture occur at infrageneric level. The results are interesting in that the skeletal fabrics of living *T. australis* (Tate) *sensu lato* from Eniwetok Atoll and *T. barretti* are essentially alike, although both are so different from that of the Oligocene *T. hedleyi*

Description of plate 52

Scanning electron micrographs of etched sections of fossil thecideidines

Figures 92, 93. Ultrastructure of an inner socket ridge and tooth showing secondary fibres in *Bifolium farringdonensis* (Davidson) Lower Cretaceous (Aptian), Farringdon, England (× 2800, × 1400).

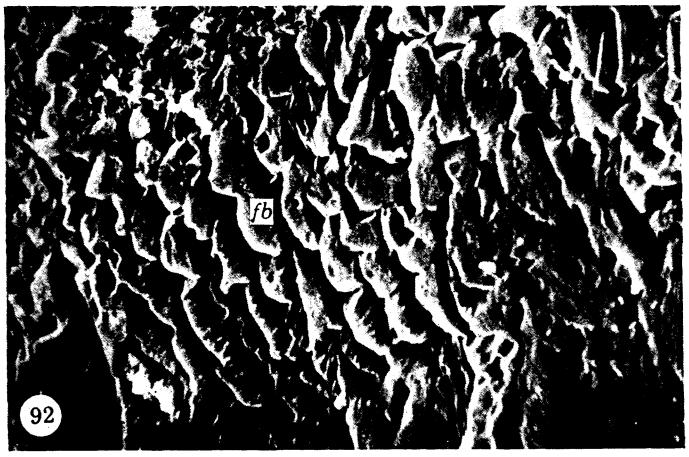
Figures 94, 95. Ultrastructure of the tooth and lateral wall of the hemispondylium showing the distribution of secondary fibres in a pedicle valve of *Thecidiopsis essenensis* (Roemer), Upper Cretaceous (Cenomanian), Essen, Germany (× 3000, × 2900).

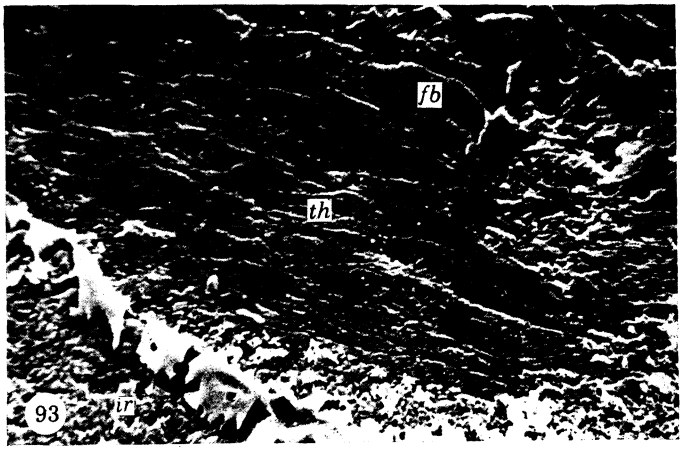
Figure 96. Ultrastructure of the primary layer in a brachial valve of *T. essenensis* (× 1500).

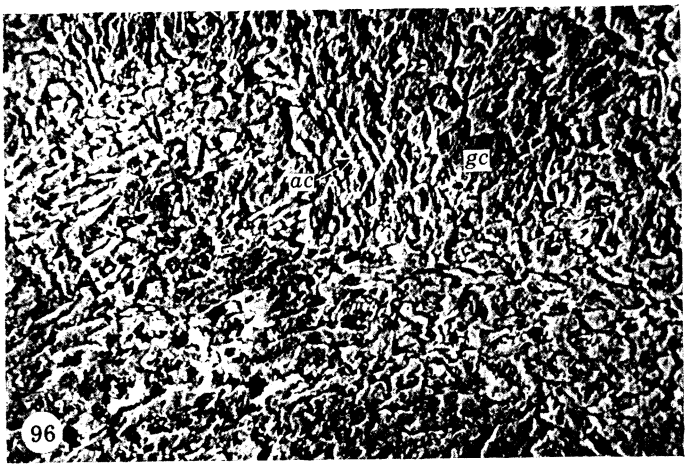
Figures 97, 98. Ultrastructure of the tooth and the lateral wall of a pedicle valve of *Thecidea papillata* (Schlotheim), Upper Cretaceous (Maestrichtian), Maestricht, Netherlands (× 3000, × 2900).

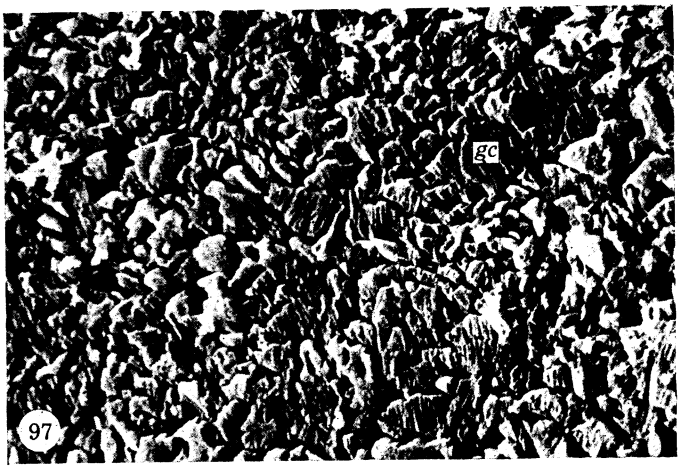
Scanning electron micrograph of *Schellwienella* cf. *aspis* (Smythe), Lower Carboniferous (Lower Limestone Group), Lennoxtown, Scotland

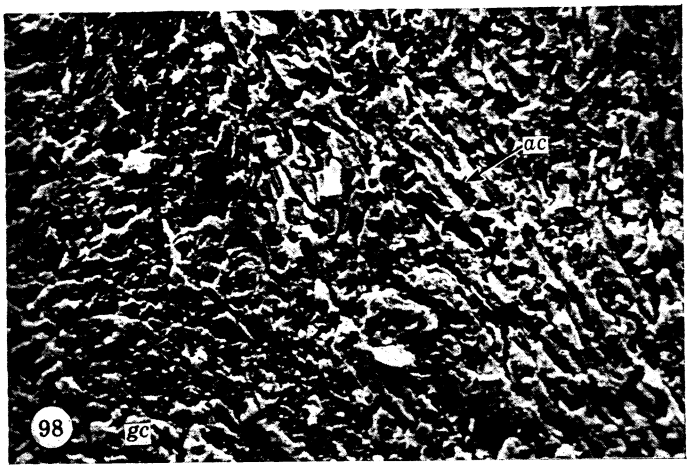
Figure 99. Internal surface of a pedicle valve showing the overlapping arrangement of laminae (× 2800).

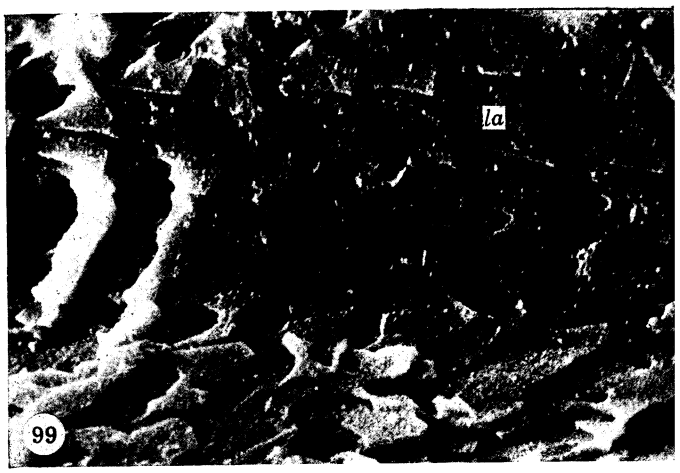






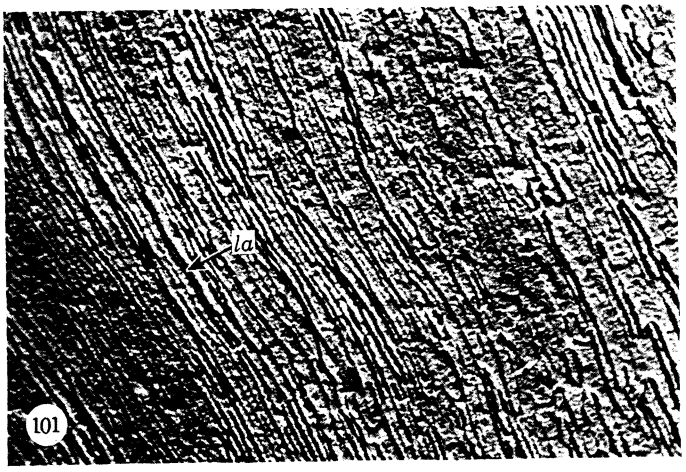


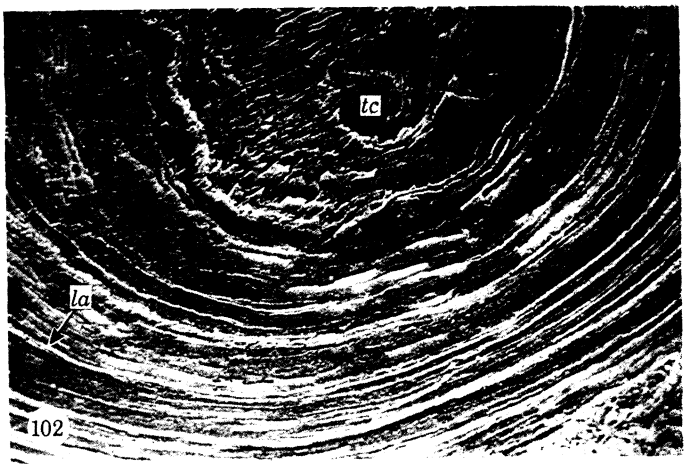


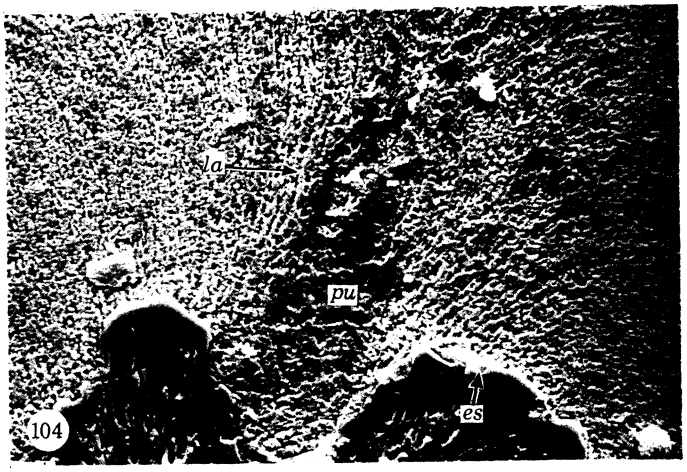


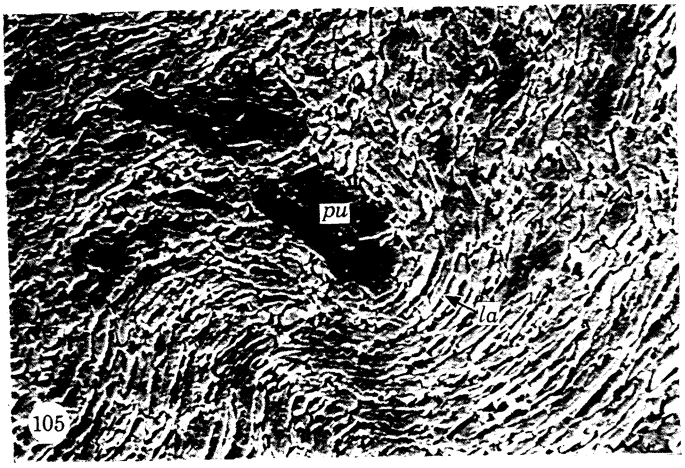
FIGURES 92 TO 99. For legends see facing page.

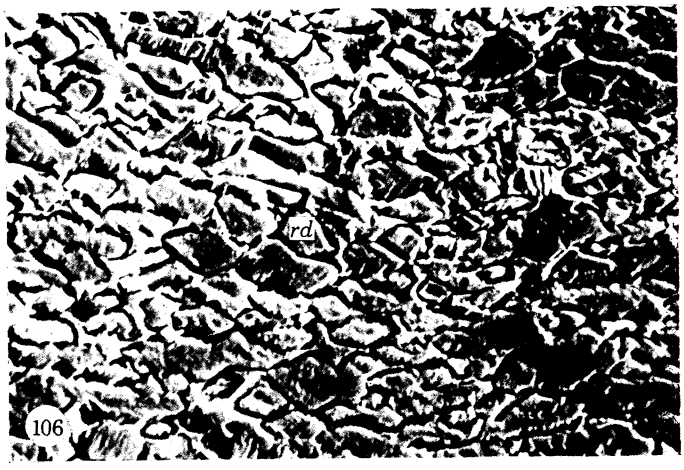
(*Facing p.* 460)

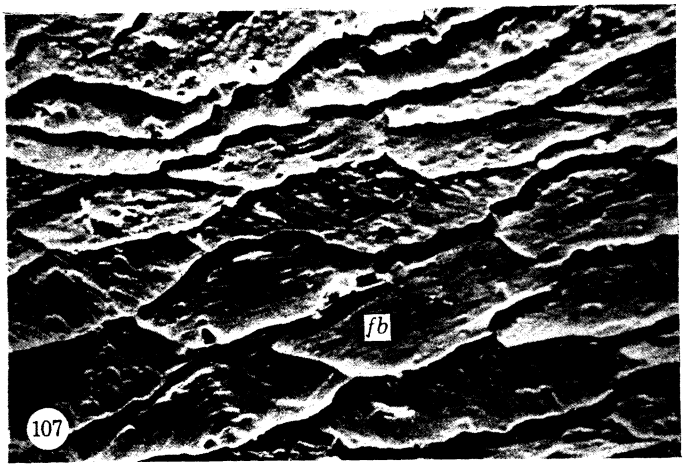


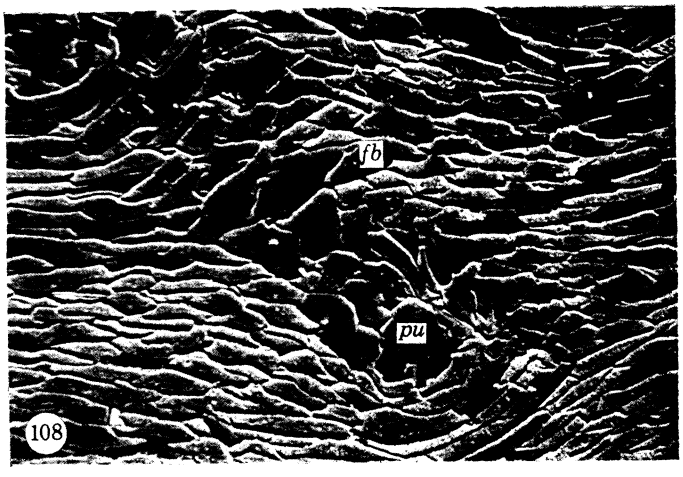












FIGURES 101 TO 108. For legends see facing page.

Thomson from New Zealand as to raise doubts about the taxonomic identity of the last-named species.

As in *T. barretti*, the punctate shell of *T. australis* consists predominantly of primary acicular crystallites disposed normal to the surface of secretion except for the external layer where they also lie obliquely as growth bands. The microtopography of the internal surface is similar in being coarsely tubercular but the blocky rhombic texture of *T. barretti* is subordinate to one in which smaller rhombs, no more than 5 μm in size, are interspersed with blades delineated by concordant cleavage planes and rhombic and dihexagonal terminal angles (figure 52, plate 47). The muscle scars in adult specimens are so well differentiated that the floor of the hemispondylium as well as the postero-lateral adductor fields bear regularly arranged pits about 7 μm across defined by ridges 2 μm thick (figure 54, plate 47). Evidently they, too, accommodate central tonofibril zones of outer epithelial cells underlying muscle bases. With equal clarity the petaloid clusters of suboval pits accommodating muscle attachment zones of the lophophore, which occur on the inner slopes of the peribrachial ridges, are well developed even on the inner (anterior) side (figure 56, plate 47) of the brachial bridge (transversarium of Pajaud 1970, p. 41).

A more important difference resides in the degree of development of the secondary shell. The outer socket ridges and especially the teeth and the inner socket ridges flanking the cardinal process (figure 53, plate 47), consist of orthodoxly stacked fibres about 6 μm wide. Some of the fibres have well-defined terminal faces with a semicircular outer boundary and an inner boundary subtending a rhombohedral angle as in other fibrous-shelled articulate brachiopods (figure 55, plate 47); but the general arrangement is identical with that found in *T. barretti*. In contrast, secondary fibres found in the rest of the shell of *T. australis* are not restricted to a few ventral tubercles but form caps on all mature tubercles studding the interiors of both valves (figures 57 and 58, plate 47). Such tubercles can vary from 40 to 80 μm in diameter and bear up to 25 fibres, not more than 25 μm long, arranged in whorls and surrounded by finely granular calcite. They show that the potential development of a fibrous secondary shell in *Thecidellina* is greater than its distribution in *T. barretti* indicates.

All shells examined of the fossil species *T. hedleyi* had undergone some recrystallization but not enough to obliterate the original fabric. This consisted of a primary layer composed mainly of acicular crystallites about 700 nm thick (figure 59, plate 48). Interlocking granules of calcite up to 12 μm in size also occur especially in the teeth, the core of the cardinalia and the areas of muscle attachment, like the adductor scars impressed on the floor of the hemispondylium and postero-laterally, where they are terminated by scalenohedral, pinacoidal or rhombohedral faces at the scar surface (figure 60, plate 48). The absence of secondary shell from the articulatory

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Description of plate 53

Scanning electron micrographs of etched sections of various fossil species

Figures 101, 102. Laminar succession and ultrastructure of the tooth core in a pedicle valve of *Derbya* cf. *cymbula* Hall and Clarke, Lower Permian, Putnam, Texas (× 3000, × 725).

Figures 103, 104. Laminar succession in the posterior flap of a pedicle valve, and outwardly directed pseudopunctum at the external surface of a brachial valve of *Oldhamina decipiens* (De Koninck), Permian, Salt Range, Pakistan (× 3000).

Figures 105, 106. Outwardly directed pseudopunctum in a brachial valve, and rods and laminae in the core of a septum in a pedicle valve of *Leptodus* cf. *richthofeni* Kayser, Permian (Sosio Beds), Sicily (× 1200, × 2800).

Figures 107, 108. Details of fibres and a pseudopunctum in the secondary layer of a pedicle valve of *Bactrynium emmrichii* (Gümbel), Rhaetic, Kaisersteffel, Austria (× 2900, × 1100).

pieces cannot be attributed to size differences because, although adult *T. hedleyi* are not usually more than about 2.5 mm long, secondary fibres are well developed in the teeth and inner socket ridges of smaller, immature specimens of *T. barretti*. Moreover, the hemispondylium of *T. hedleyi* is supported by a medial septum arising from the valve floor and extending forward for over one-half the length of the pedicle valve. The septum itself is composed of acicular crystallites and blades of calcite disposed more or less parallel with the long axis of the septum. Anteriorly, however, it is flanked by about 15 spines, up to 15 μm long, standing erect above the floor of the valve (figure 61, plate 48). Each spine is composed of fibres of calcite about 8 μm thick secreted in open spirals about the long axis of the spine (figure 62, plate 48). In disposition and size, the fibres are like those making up the secondary shell of other thecideidines, and their presence emphasizes the anomalous ultrastructure of the teeth and sockets of *hedleyi* as a species of *Thecidellina*. Indeed this difference and the presence of a medial septum in the pedicle valve suggests that *hedleyi* and possibly *T. japonica* (Hayasaka) (see Pajaud 1970, p. 247) evolved independently of *T. barretti* and *T. australis* and constitute a new genus.

Shell structure of *Lacazella*

The other thecideidine genus surviving to the present day is typified by *Lacazella mediterranea*. Attempts to obtain living specimens for study of the soft parts were unsuccessful, but it is unlikely that differences, other than in the morphology and structure of the shell, exist. *Lacazella* is distinguishable from *Thecidellina* mainly in the development and configuration of the lophophore supports which, according to Pajaud (1970, p. 82), are so disparate as to warrant the assignment of the two genera to different subfamilies. Comparison of shell structures shows fewer differences in texture, although those that do occur may well indicate independent evolution of the two stocks through as long an era of geological time as is suggested by morphologic and stratigraphic considerations.

The carbonate skeleton of *Lacazella* is almost exclusively composed of primary shell, mainly consisting of acicular crystallites or granules of calcite less than 1 μm in diameter. The dorsal protegulum is better known than in *Thecidellina*. It is about 300 μm in diameter and is finely granular in texture with regularly spaced hollows up to 3.5 μm in size (figure 63, plate 48) in contrast to the rest of the shell surface with obliquely disposed acicular crystallites culminating in concentric bands about 2 μm wide medially (figure 65, plate 48). The shell, including the pseudodeltidium (figure 64, plate 48), is permeated by puncta with internal openings about 25 μm in diameter and terminating in a complex of about 350 canals which accommodate the brush. The canals average 550 nm in diameter and penetrate a canopy about 7 μm thick (figure 66, plate 48) to form external perforated subcircular patches up to 40 μm across (figure 65, plate 48).

The interior of both valves is ornamented by tubercles up to 110 μm in diameter, but patches of closely packed rhombic blocks have not been seen. Instead, the tubercles and the rest of the surface are studded with discrete rhombohedra or scalenohedra up to 7 μm high and 9 μm wide distributed in a matrix of acicular crystallites between 150 and 500 nm thick (figure 67, plate 49). This contrast in texture is equally conspicuous in section which shows that the acicular crystallites may be up to 10 μm long and that growth banding at intervals of about 250 μm is common (figures 68 and 69, plate 49).

The muscle scars of adult *Lacazella* are well developed. Even the diductor bases are underlain

by differentiated shell consisting of randomly orientated ridges of crystallites giving a convoluted appearance to the ventral face of the cardinal process (figure 70, plate 49), and of groups of acicular crystallites forming calcitic granules up to 12 μm in size on the inner surfaces of the lateral walls of the hemispondylium. All adductor muscle bases, on the other hand, are underlain by scars with regularly arranged pits between 7 and 12 μm in diameter (figure 71, plate 49).

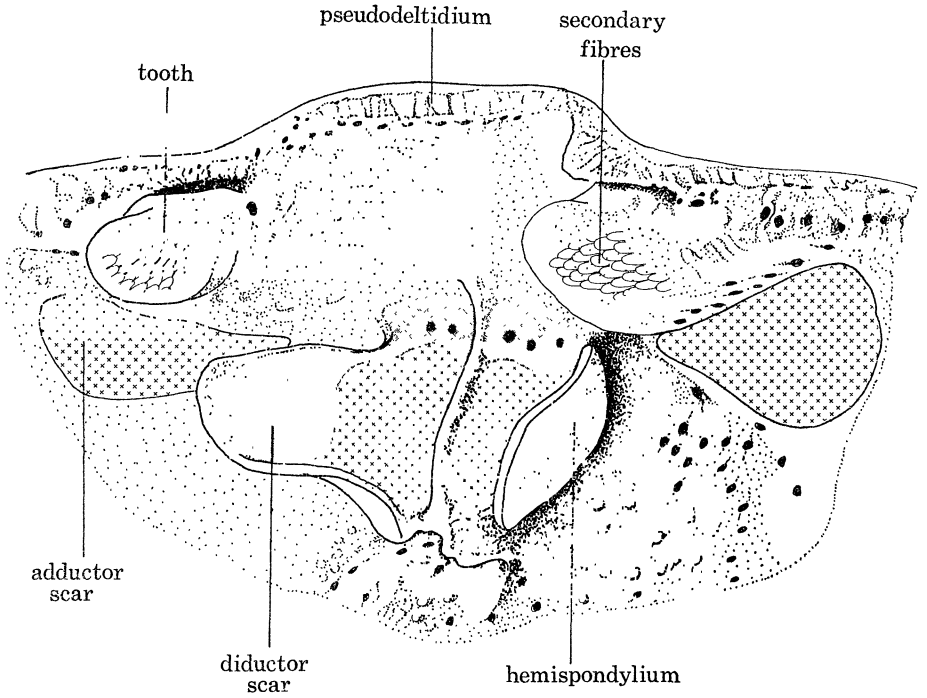

FIGURE 75. Antero-dorsal view of the interior of the umbonal region of *Lacazella* showing the main morphological features (× 100).

Those accommodating the medial set of adductors are as well defined as the postero-lateral scars, being impressed on the floor of the hemispondylium on either side of the medial ridge (figure 75; figure 72, plate 49) and just anterior to each inner socket ridge. Sections show the floor and medial ridge of the hemispondylium to be composed of incompletely segregated lenses of banded or granular calcite (figure 74, plate 49). It is probable that the joint system defining the lenses, traces the location of discontinuous protein sheets secreted simultaneously with the calcite. The lenses do not occur in the granular succession underlying the diductor scars of the hemispondylium (figure 73, plate 49).

The inner slopes of the peribrachial ridge are also strongly pitted in patches like those of *Thecidellina* (figure 76, plate 50). It is therefore likely that the pits resulted from differential secretion and resorption by epithelial cells similarly equipped with centrally placed bundles of tonofibrils attaching the base of the lophophore to the brachial valve.

Although there are differences between *Lacazella* and *Thecidellina* in the general fabric of the primary layer, they are essentially related to size variation in the crystallite components of the shell. Such a change in emphasis is even more spectacularly shown by the distribution of secondary shell. In *Lacazella* both teeth and inner socket ridges are strongly developed, yet neither are composed of secondary fibres as in *Thecidellina*. In section, the core of a fully grown tooth consists of coarse crystallites up to 4 μm in diameter while the outer layer is composed of banded acicular

crystallites which are exposed on the surface as fine granules about 200 nm in size (figure 77, plate 50). The dorsal surface of the tooth also bears up to 50 low, rounded or suboval mounds about 7 μm across (figure 78, plate 50). These may occur in a cluster or strung out in two or three rows. They have been interpreted as incipient fibres and are the only traces of a superficial secondary layer found anywhere in the *Lacazella* shell (figure 79, plate 50).

Shell structure of fossil Thecideidina

Excluding the strophalosiacean *Cooperina* for reasons given by Cooper & Grant (1969, p. 17), the Thecideidina, as understood by Pajaud (1970, pp. 82–83), embraces twenty-two genera distributed among five Subfamilies. The suprageneric taxa in the Suborder have always been based on the nature of the lophophore supports (Elliott in Williams *et al.* 1965; Backhaus 1959). In the Pajaud classification, for example, the Subfamilies are distinguished on whether the ascending (i.e. medial) part of the peribrachial ridge is depressed or elevated, simple or lobate, and the intrabrachial shell surface undifferentiated or elaborated into ridges (figure 10). Yet convenient as this scheme may be, it is not entirely satisfactory. Any grouping of the Subfamilies into larger taxa dependent on the relief of the medial ridge is artificial as Pajaud himself admitted (1970, p. 85) when he informally assembled the Davidsonellinae and Lacazellinae, and the Moorellinae, Thecideinae and Thecidellininae into the *Lacazella* and *Thecidellina* groups respectively. Also some genera like *Agerinella* and *Konstantia* are poorly known while representatives of others were unobtainable. None the less nine of the twenty recognized fossil genera have been studied and, since they are well distributed in time and have been drawn from all five Subfamilies recognized by Pajaud, their skeletal fabrics are probably a reliable guide to the main evolutionary trends affecting thecideidine shell structure.

Despite some reservation about thecideidine taxonomy, it has proved most convenient to describe the carbonate successions of the species studied in the context of the current classification beginning with the oldest Subfamilies the Jurassic Davidsonellinae and Moorellinae. An account is also given of the few extinct Lacazellinae examined and of the Cretaceous Thecideinae, but all available representatives of the Thecidellininae have been described and need no further comment.

The davidsonellinid *Davidsonella sinuata* is characterized by having a fully developed secondary as well as primary layer in both valves (figures 80 and 81, plate 50). The primary layer is about 30 μm thick and consists of elongate crystallites up to 3 μm thick disposed normal to the junction with the secondary shell. They may represent recrystallized groups of acicular crystallites. The secondary layer is composed of orthodoxly stacked fibres with keels and interlocking lateral areas becoming well defined in sections of mature fibres away from the primary–secondary junction.

Except for *Konstantia*, all genera assigned to the Moorellinae have been investigated and again show the full development of secondary as well as primary carbonate layers in both valves. The primary layer, consisting of prismatic or elongate granules up to 3 μm thick lying normal to the surface of secretion, varies from 35 to 50 μm in thickness in *Moorellina* (*Moorellina*) *bouchardi* (Davidson), *M.* (*Elliottina*) *deslongchampsi* (Davidson) (figure 84, plate 51) and *Eudesella mayensis* (Eudes-Deslongchamps) (figure 85, plate 51). In the diminutive *Roultina ornata* Moore, however, the primary layer is only 7 μm thick, although it is similarly textured (figures 86 and 87, plate 51). In all four species, the secondary shell consists of normally fashioned fibres up to 5 μm thick

arranged in mosaics of alternating rows so characteristic of other fibrous articulate brachiopods, while puncta and shell succession are particularly well displayed (figures 82 and 83, plate 50) in *M.* (*Elliottina*) cf. *granulosa* (Moore), the species described by Baker (1970) in his pioneer study of thecideidine fossil ultrastructure.

The Lacazellinae, as conceived by Pajaud (1970, p. 101), is the longest lived thecideidine group. Nine genera have been assigned to the Subfamily but only *Thecidella rustica* (Davidson) and *Eolacazella affinis* (Bosquet), in addition to living *Lacazella*, have been studied. However, since the Liassic *T. rustica* is the oldest known species and the Maestrichtian *E. affinis* is a stock which appeared during the climax of lacazellinid evolution, differences in the carbonate succession of the three taxa probably reflect the main phylogenetic changes in shell structure for the entire Subfamily. The differences are certainly striking. In *Thecidella*, the carbonate succession is differentiated into a granular primary layer about 25 μm thick and a fully developed secondary layer composed of regularly arranged fibres up to 5 μm thick (figures 88 and 89, plate 51). In contrast, no secondary shell was identified in sections of an adult pedicle valve of *Eolacazella* (figures 90 and 91, plate 51). The valve had been affected by recrystallization, but patches of acicular crystallites each about 300 nm thick survived as did the coarsely granular core of the teeth indicating the similarity of the primary layer to that of other thecideidines. Pajaud considers *Eolacazella* to have been a deviation from the main course of lacazellinid evolution on the evidence of its brachial apparatus. The absence of a secondary layer in the genus appears to confirm this interpretation. Vestiges of the layer are, after all, found on the teeth of living *Lacazella* so that one would expect to find more widely distributed traces of fibres in any stratigraphic intermediaries descended from *Thecidella* which were also ancestral to *Lacazella*. In this respect, studies of *Danella* and *Praelacazella* should prove informative.

The Thecideinae consists of six genera, and although only species of *Bifolium*, *Thecidea* and *Thecidiopsis* have been examined, they show an interesting variation in the development of a double carbonate layer. In *Thecidiopsis* which ranges throughout the Cretaceous, the principal layer is a primary shell of acicular crystallites lying normal to the valve surface and granular calcite up to 7 μm in size (figure 96, plate 52). However, in the Cenomanian *T. essenensis* (Roemer) at least, a secondary layer of orthodoxly stacked fibres about 3.5 μm thick forms the teeth and the base and outer walls of the hemispondylium which is lined by a granular myotest (figures 94 and 95, plate 52). Traces of secondary fibres have also been found in the inner socket ridges and teeth of the Aptian *Bifolium faringdonense* (Davidson), although they have been positively identified in only one of three specimens (figures 92 and 93, plate 52) and the dominant primary fabric is granular. In contrast, the valves of the Maestrichtian *Thecidea papillata* (Schlotheim) are composed exclusively of primary acicular crystallites and granules (figures 97 and 98, plate 52). The latter may be as much as 20 μm in maximum length within the core of teeth, but their irregularly intersertal boundaries confirm their primary origin.

Conclusions

The two main problems posed by any study of the Thecideidina concern the evolutionary history and ancestry of the Suborder. Thecideidine evolution has been the subject of much research especially by Elliott (1953; in Williams *et al.* 1965), Backhaus (1959) and Pajaud (1970) who reached different conclusions on the nature and taxonomic content of the main channels of descent. The affinities of the Suborder are even more controversial and have been the source of

comment by many students of the phylum (Pajaud 1970, p. 49). Contrary to preliminary expectation (Williams 1968, p. 50), knowledge of the skeletal ultrastructure has greatly helped in resolving these problems. A survey of representative living and fossil species has shown that the apparently contradictory conclusions of Williams (1968) and Baker (1970) are not only reconcilable but also consistent with previously expressed ideas on thecideidine history and ancestry based on different considerations (Williams and Rowell in Williams *et al.* p. H189).

(*a*) *Shell structure in relation to thecideidine evolution*

Although the unique combination of characters distinguishing the Thecideidina from all other Brachiopoda tends to obscure the ancestry of the group, full differentiation of even the earliest species unequivocally assignable to the Suborder, like the Rhaetic *Davidsonella rhaetica* (Zugmeyer) and *Moorellina* (*Moorellina*) *prima* Elliott, makes its phylogeny comprehensible. A number of features found in a more or less unmodified state in all thecideidine species, represent the immutable fraction of the morphological facies of the Suborder. They include: the planoconvex to ventri-biconvex profile of the shell and the strophic hinge-line with hypercline dorsal and apsacline ventral interareas; the loss of the pedicle and the growth of an entire pseudodeltidium with the consequential attachment of the pedicle valve to the substrate by cementation in nearly all species; the articulatory device of teeth, normally unsupported and developed independently of the hemispondylium, and sockets defined by inner socket ridges fused medially into an erect cardinal process; and the postero-laterally situated adductors. In contrast, both shell structure and lophophore supports underwent profound evolutionary changes, although the cumulative effects resulted in different phylogenetic trends.

The influence of both ontogenetic and phylogenetic factors in promoting morphological changes in thecideidine lophophore supports has long been acknowledged, although their relative importance is controversial. A significant aspect of the disposition of the lophophore is that it has always been attached to the floor of the brachial valve. The persistence of this arrangement throughout thecideidine history is confirmed by the presence of a variably shaped peribrachial ridge in adult valves. The outer filament-bearing part of the lophophore has always been accommodated by the peribrachial ridge except posteromedially where the segment immediately behind the mouth is carried by apophyses (crura) forming the brachial bridge. This intimate relationship between lophophore and valve floor has restricted any increase in lophophore length to deformation of the juvenile circular trocholophe by folding in the commissural plane. Hence, since the trocholophe includes a pair of discrete generative tips situated anteromedially, it is not surprising to find that the first stages in lophophore enlargement invariably entailed the backward growth of these generative tips on either side of a medial ridge (the ascending apparatus of Backhaus). Further significant expansion of the resultant bilobed structure (schizolophe) could only come about by a folding of the lophophore and a concomitant lobation of the peribrachial ridge and/or medial ridge by differential growth and resorption. The lobate lophophore is normally referred to as a ptycholophe, but Pajaud (1970, p. 33), following Backhaus, prefers to use that term for a folded lophophore with lobes coincident with undulations of the peribrachial ridge. A folded lophophore with lobes supported by crenulations exclusively or mainly developed from the medial ridge has been distinguished as a thecidiolophe. Both these lobate conditions may be regarded as equipotential adult elaborations of an immature schizolophe and may, therefore, have recurred many times in thecideidine history. The only other noteworthy change occurring during evolution of the lophophore-supporting apparatus

was the tendency to develop intricate intrabrachial ridges interdigitating with the ptycholophous and thecidiolophous lobes.

In their interpretation of the evolution of the thecideidine lophophore supports, Elliott and Backhaus reached contrary conclusions. Elliott (1953, p. 698) regarded the evidence then available to him as indicating a palingenetic progression within the Suborder towards a ptycholophous condition. He drew attention to the occurrence of a bilobed peribrachial ridge, indicative of a schizolophe, in the adult shells of all early thecideidines and in the immature shells of later ptycholophous species. Similarly equipped adults like those of *Bifolium* and *Thecidellina*, also appear in later phases of thecideidine evolution and, although these genera are distinguishable from early ones by the elaboration of intrabrachial ridges, they prompted Elliott to emphasize the heterochronous nature of the palingenetic trends.

In rejecting Elliott's interpretation of the evolution of the thecideidine lophophore supports, Backhaus drew attention to consistent differences between species equipped with broad or narrow medial ridges. The distinction has been further explored and refined by Pajaud (1970, p. 82) to segregate all thecideidines into two groups. The Lacazellinae and Davidsonellinae, with broad depressed medial ridges becoming lobate and associated with well-developed intrabrachial ridges in later species, constitute the *Lacazella* group. The *Thecidellina* group, on the other hand, is composed of the Thecidellinae, Thecidinae and Moorellinae characterized by a relatively narrow medial ridge which more rarely became lobate. Both groups include early Jurassic species so that *Lacazella* is regarded by Backhaus and Pajaud as having been descended from a prototypic thecideidine akin to *Thecidella* and *Davidsonella* and *Thecidellina* from an ancestor like *Moorellina*. In the opinion of Backhaus (1959, p. 77), changes in the lophophore supports in both groups were neotenously induced. Species of the Jurassic *Thecidella*, for example, display an elaboration of a bilobed support for a schizolophe into a septate structure accommodating a thecidiolophe. This pattern was faithfully repeated during the Tertiary history of *Lacazella* after its neotenous derivation via a schizolophous *Praelacazella* from a *Thecidella* (s.l.) stock.

Pajaud, in a comprehensive survey of all known thecideidine species and a much more detailed study of available ontogenetic records, concluded that the evolution of lophophore supports was more complex than previously recognized. Thus during the Jurassic, the pre-eminent thecideidine possessed a bilobed lophophore support and developed a regular intrabrachial ridge. The Cretaceous, on the other hand, was a Period when ptycholophous and thecidiolophous thecideidines proliferated; while during the Cenozoic Era there was a return to the simple schizolophe and thecidiolophe, typified by *Thecidellina* and *Lacazella* respectively, although the supports were generally more complex than those found in Jurassic species especially in the elaboration of the intrabrachial ridges. The information recorded by Pajaud led him to believe (1970, p. 81) that both palingenetic and neotenous processes were operative during thecideidine evolution. The juvenile lophophore supports, that grew into the complex lobate structures found in adults of the Cretaceous *Praelacazella* and *Thecidiopsis*, are morphologically identical with the adult supports of Jurassic *Thecidella* and *Rioultina* respectively. These relationships are irrefutable examples of palingenesis. In contrast, adult supports of *Lacazella* and *Thecidellina* are indistinguishable from transient immature ones developed during the ontogeny of *Danella* and *Backhausina* respectively, and confirm the neotenous derivation of the former genera from the latter.

The principal interpretations of the evolution of the lophophore and its skeletal support have

been reviewed in some detail because it is crucial to know which taxonomic arrangement best expresses thecideidine phylogeny based on gross shell morphology. There seems little doubt that Pajaud's careful evaluation of morphological variation among all known thecideidines

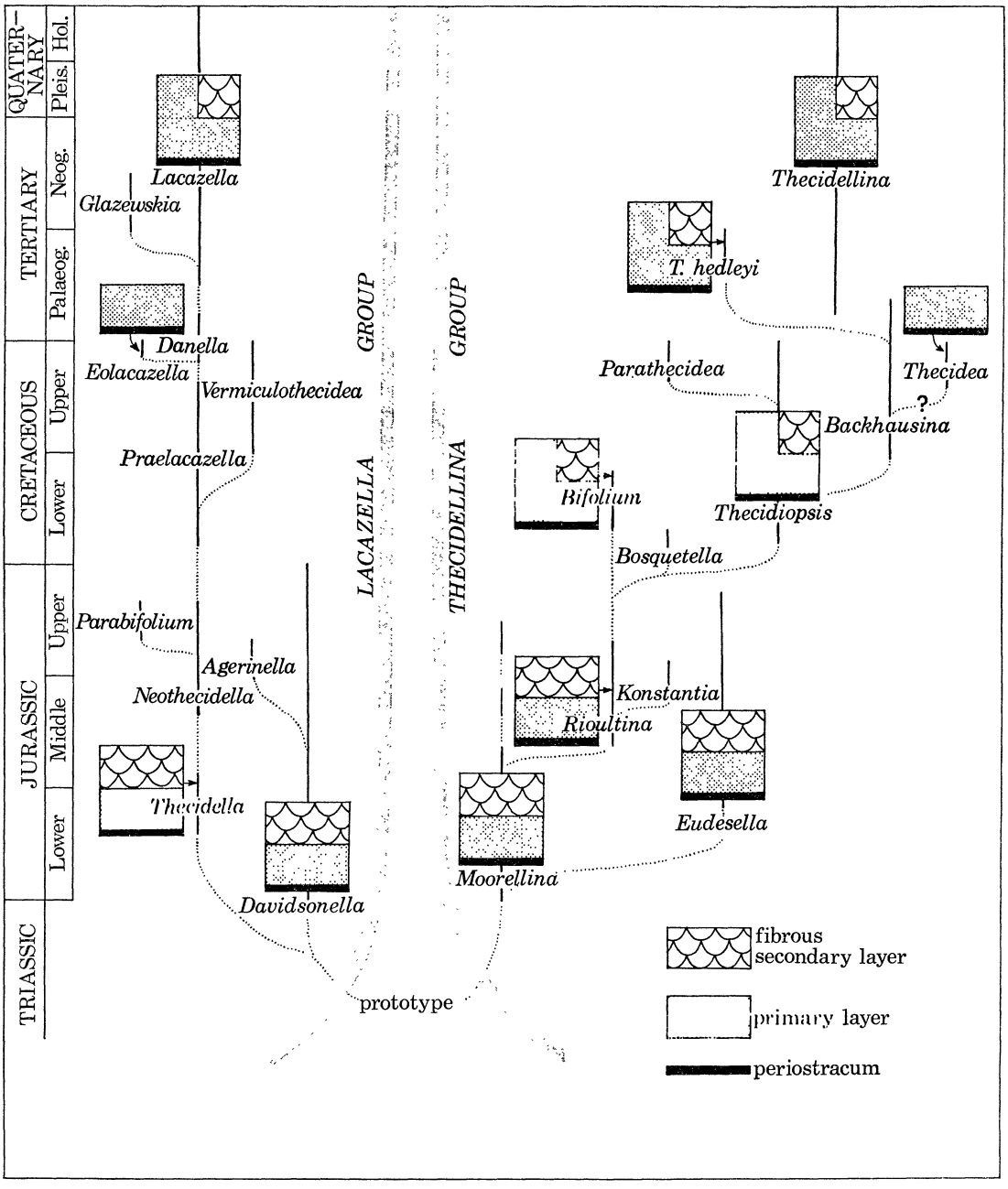

FIGURE 100. Phylogenetic chart showing the variation in the shell structure of certain thecideidine genera.

affords the most reliable phylogenetic reconstruction. His scheme has been used as a model against which changes in the ultrastructure of the shell may be considered. The results are striking and are illustrated in figure 100. Ignoring the invariably punctate condition of the shell, it is significant that the valves of the oldest genera of both groups, i.e. *Thecidella*, *Davidsonella*, *Moorellina*, *Rioultina* and *Eudesella*, were lined with a continuous layer of secondary

fibres. In all descendants examined ultrastructurally, however, this secondary layer became neotenously reduced irrespective of any increase in species size or shell thickness. In the less well documented *Lacazella* group only a few secondary fibres vestigially survive on the teeth of adult *Lacazella*. Indeed, in the one specimen of *Eolacazella* available for study, no trace of fibres was found which may reflect accelerated neoteny in a sideline off the main plexus of descent, although it is also possible that superficial fibrous growths, like those in living *Lacazella*, may have escaped notice.

Knowledge of the skeletal ultrastructure of Lower Cretaceous species provides a more complete picture of the neotenous trend in shell secretion within the *Thecidellina* group. In contrast to all Jurassic members of the group, with their fully developed, double-layered carbonate successions, secondary fibres are restricted to the teeth and inner socket ridges of *Bifolium* and additionally to the hemispondylium of *Thecidiopsis*. Orthodoxly stacked fibres also survive in small vestigial patches on the valve floors and especially as the cores of the teeth and the inner and outer socket ridges of *Thecidellina*. These fibres, unlike those occurring superficially on the teeth of *Lacazella*, are deeply embedded in adult shell successions and, therefore, indicate a less advanced stage in the shedding of the secondary shell than in the *Lacazella* group. There are, admittedly, two species currently included in the *Thecidellina* group, in which teeth and associated features are composed exclusively of primary shell. It is interesting to note, however, that one of them, *Thecidea papillata*, has only been tentatively placed by Pajaud (1970, p. 223) in this group because there are equally good reasons for deriving it from *Danella* along with the contemporaneous *Eolacazella*, to which it bears a strong skeletal similarity. With regard to *Thecidellina hedleyi* it appears that, although the teeth and cardinalia are composed of primary shell, spines made of secondary fibres sporadically developed as out-growths from the floor of the pedicle valve. The general morphology of the species certainly suggests its inclusion in the Thecidellinae and, provisionally at least, one must conclude that acceleration in the neotenous shedding of the secondary layer gave rise to this particular stock.

Comparison of the rate of neotenous changes affecting the skeletal ultrastructure of both groups is currently handicapped by lack of data especially among the Lacazellinae. It is, however, significant that the principal change from deposition of a fully developed secondary layer to the secretion of vestigial patches of fibres especially in the medial region of the shell, must have occurred within the *Thecidellina* group during late Jurassic or early Cretaceous times. It is possible that an equally drastic reduction in secondary shell secretion took place in the *Lacazella* group at about the same time. If this proves to be so, evolution of the ultrastructure of the thecideidine skeleton is a remarkable example of synchronous as well as parallel neoteny.

(*b*) *Origin of the Thecideidina*

The sudden appearance of indisputable thecideidines in the Rhaetic is not entirely due to our relative lack of knowledge of Permo-Triassic faunas because there are unmistakable signs of their neotenous and caenogenetic derivation from some contemporaneous articulate brachiopod not very long before the beginning of the Jurassic Period. The caenogenetic changes contributing to the emergence of the thecideidines were sufficiently profound to mask immediate ancestry while the neotenous effects were deceptive enough to lead to erroneous assumptions. In this respect, the identification of *Cooperina* by Termier, Termier & Pajaud (1966) as a prototypic thecideidine linking the Suborder with the Productidina is a good example. These authors concentrated their attention on the bilobed disposition of the ridges in the brachial valve, which probably supported

a schizolophe. In so doing they ignored a host of other characters listed by Cooper & Grant (1969, p. 18), like the absence of teeth and the presence of spines, which patently identified *Cooperina* as a strophalosiacean. The fact that *Cooperina* was probably equipped with a schizolophous feeding organ signifies only that the genus, like many thecideidines, fell within the size range of species normally served by a simple schizolophe, and not that it is any more closely related to the thecideidines than, say, the inarticulate *Pelagodiscus* which is also a small schizolophus form. Even after the publication of Cooper & Grant's review of the systematic position of *Cooperina*, Pajaud (1970, p. 80) persisted in regarding the genus as a thecideidine. He maintained that the shape of the cardinal process, brachial ridge and muscle bases, the pseudopunctate shell structure and the undifferentiated pseudodeltidium were not only diagnostic of productidines, but also characteristic of some thecideidines. The comparisons quoted by him in support of this argument are, however, either incorrect like his identification of the shell structure of *Davidsonella* as typically pseudopunctate, or contrived as in his use of the alleged undifferentiated pseudodeltidium of living *Thecidellina australis blochmanni* to establish Permian ancestry. The only feature of the *Cooperina* shell conceded by Pajaud to be uniquely productidine is its spinose condition, although he maintained that this was the kind of relict character one would expect to find in an ancestral stock. He made no mention of the well-developed teeth and sockets among thecideidines and their absence in *Cooperina*; presumably these were regarded by him as a caenogenetic acquisition. In all, his case for retaining *Cooperina* and its allies within the Thecideidina is unconvincing and his conclusion that thecideidines were descended from the strophalosiaceans and should, therefore, be assigned to the Productidina, remains open to challenge.

Pajaud is not alone in believing that the ancestors of the Thecideidina were productidines. In fact Grant, in contradiction to his earlier joint statement with Cooper, has recently (1972, pp. 243–245), come out strongly in support of a strophalosiacean, even possibly a cooperinid, progenitor for the Suborder. Among the features favouring his conclusion, Grant has listed the cementing habit of the pedicle valve, the plano– to concavo–convex profile of the shell, the strophalosiacean teeth and pseudodeltidium, the pseudopunctate shell structure indicated by the tubercles occurring peripherally in the thecideidine shell, and the folded peribrachial ridge supporting a ptycholophe which is comparable in shape, but *not* in its relationship to the brachial valve, with the brachidium of the strophalosiacean *Falafer*. He dismisses shell structure in general and punctation in particular as being unimportant in deciding thecideidine affinities and further declares, without clarification, that thecideidine puncta 'differ in some respects from those of Terebratulacea' (Grant, p. 244).

Even if other palaeontologists familiar with the problem are unenthusiastic about a productidine ancestor for the Thecideidina, the great majority are, at least, in favour of their derivation from some allied strophomenide stock. This was Elliott's opinion in 1953 (p. 696) and again in 1965 (in Williams *et al.* 1965, p. H 857), while Rudwick (1968, p. 359) and Baker (1970, pp. 96–97) more specifically identified the Davidsoniacea as the source of the thecideidine prototype. Rudwick argued in respect of thecideidine ancestry that the cemented pedicle valve with its pseudodeltidium and lobed food grooves (i.e. peribrachial ridge) are strophomenide characteristics, while the strophic hinge line and lack of spines are more strictly diagnostic of the davidsoniaceans. Even Baker, having demonstrated the presence of a fibrous secondary layer in *Moorellina*, concluded that the fibres differed in details of shape from those of the spiriferide or terebratulide brachiopods, that the tubercles were comparable with strophomenide pseudopuncta, and that the

species was closest to the spiralia-bearing *Thecospira* which had been retained by Rudwick (1968, p. 350) within the Davidsoniacea. In effect, since 1893 when Schuchert first suggested that the Thecideidina were descended from the Strophomenida, the only recorded dissent has been that of Williams and Rowell (in Williams *et al.* 1965, p. H188) and Williams (1968, p. 54), who in consideration of general morphology as well as shell structure identified the Spiriferida (especially the Suessiacea) or the Terebratulida as possible ancestors of this problematic group. Two other articulate brachiopod Orders, the Rhynchonellida and the Orthida, are represented in the Permian rocks and are, therefore, chronologically eligible to be ancestral to the thecideidines. But neither has ever been seriously regarded as morphologically qualified for this role and there is no new information favouring reconsideration of them at this juncture.

Before examining the evidence afforded by comparison of shell structure which, not withstanding the advice of Grant, does play a crucial part in reducing the range of possible ancestry, it is worthwhile commenting on the pedigree of other basic elements of thecideidine morphology.

The thecideidine profile is typically unequally biconvex and not concavo–convex as indicated by Grant (1972, p. 244), although the relationship between the valves is usually obscured by the effects of the attachment of the pedicle valve and reduction of the brachial valve. Of all known species only adult shells of *Davidsonella sinuata* are concavo–convex like those of strophalosiaceans. The typical thecideidine profile, however, is not only like that of many terebratulides and spiriferides but also reminiscent of the biconvex strophomenides, the davidsoniaceans, so that this feature does not single out one Order more than any other as having closer affinities with the thecideidines. The strophic hinge line and well-developed interareas found in thecideidines are equally unhelpful. They may be pre-eminently characteristic of the strophomenides, except for non-strophalosiacean productidines which lack interareas, but they are also characteristic of many spiriferides and a minority of terebratulides.

Apart from noting the lack of articulatory devices in non-strophalosiacean productidines, the nature of the teeth and cardinalia has usually been over-looked in discussions on thecideidine affinities. The neglect is all the more unfortunate because, only a small number of easily identifiable yet definitively diagnostic variants of these features have appeared during brachiopod evolution. Jaanusson (1971, pp. 34–35), for example, has demonstrated that there are basically only two types of teeth: the deltidiodont tooth, a simple projection expanding dorsally by incremental secretion of secondary shell over its distal surface; and the cyrtomatodont tooth, a knob or hook-shaped structure 'with a posteromedially protruding process', which can only grow by differential resorption of the protruding process and deposition on the anterolateral surface. The two types are remarkably consistent in their distribution. Deltidiodont teeth are limited to the Orthida, Strophomenida and Pentamerida, while the few species with cyrtomatodont teeth, currently assigned to those Orders, include stocks like *Tropidoleptus* which, as a loop-bearing orthide, is of disputable affinities. On the other hand, the knob-like teeth of all Thecideidina, like those found in the Rhynchonellida, Spiriferida and Terebratulida are cyrtomatodont and, contrary to Grant (1972, p. 244), bear no likeness in morphology or inferred growth to those of the strophalosiaceans or any other strophomenides.

The structure of the thecideidine cardinalia is as decisive as that of the teeth in precluding a strophomenide ancestry. The cardinalia of the Orthida and Strophomenida (Williams and Rowell in Williams *et al.* 1965, p. H96) pre-eminently consist of a notothyrial platform flanked by low socket ridges and bearing a cardinal process. Elaboration of this basic pattern led to the appearance in Permian strophomenides of a bilobed (or derived trilobed) cardinal process

secreted independently of socket ridges. The latter were atrophied or reduced to vestigial traces in productidines and oldhaminidines, or they evolved into recurved or divergent plates reaching to the floor of the valve in the davidsoniaceans and chonetidines. As study of the shell structure has shown, thecideidine cardinalia are differently constituted. The sockets are defined by a pair of large inner socket ridges which converge posteriorly so that the erect cardinal process with a hint of trilobation in its shape really consists of the posterior parts of a pair of socket ridges connected by an undifferentiated wedge of shell. This apparatus is not only unlike that of any strophomenide, but is also structurally comparable with the cardinalia of many spiriferides and terebratulides like those of the retziidines and dielasmataceans respectively.

No clue to ancestry can, at present, be gleaned from a study of thecideidine musculature and its mode of attachment. The muscle scars of the medial set of adductors and diductors are normally distributed, and the hemispondylium accommodating the ventral bases is strictly homologous with variously named structures found in species belonging to every Order of articulate brachiopods. The uniqueness of the postero-lateral adductors suggests that they were the result of a genetic deviation and therefore unknown in the thecideidine progenitors.

Identification of thecideidine ancestry by means of the configuration and disposition of the apparatus supporting the lophophore has led to many inconsistencies in the arguments of those advocating this recourse. Rudwick (1968, p. 357) contended that the presence of a folded peribrachial ridge must indicate connexion with the strophomenides because a lophophore support attached to the floor of the brachial valve was typical of that Order. Yet in the same paper (p. 351) he argued for the removal of the spiralia-bearing koninckinaceans from the Spiriferida, and their assignment to the Strophomenida because they resemble *Cadomella*, an early Jurassic stock widely accepted as a relict strophomenide chonetidine until the discovery by Cowen & Rudwick (1966) that it possessed calcareous spiralia. At that time another spiralia-bearing genus, the Triassic *Thecospira* was classified, with the approbation of Rudwick (1968, p. 350), as a strophomenide (Williams 1953). Consequently, in defence of his own revision of the systematic position of the koninckinaceans (embracing *Cadomella*), Rudwick was obliged to assert that such complex lophophore supports as spiralia evolved twice among contemporaneous strophomenides independently of the spiriferides; whereas relatively simple convoluted ridges arising from the floor of the valve were unique to, and therefore diagnostic of, the strophomenides. At this juncture one need only emphasize that the allegedly newly evolved spiralia did not arise by a simple calcification of, say, the connective tissue of the lophophore by scleroblastic secretion. They were sheathed in outer epithelium and were identical in origin, growth and fibrous ultrastructure with those of all spiriferide species.

Grant (1972, p. 245) argued in a similar vein to Rudwick and even maintained that discovery of a blade-like ptycholophous support in *Falafer*, although fundamentally different in its growth and relationship to the brachial valve from the lobate peribrachial ridges of *Vermiculothecidea* which he cited for comparison, greatly favours thecideidine derivation from the strophalosiaceans.

The arguments used by Rudwick and Grant in their claim that the nature of the thecideidine lophophore support points to a strophomenide ancestry are selective and generalized. The emergence of the megathyrids with loops supporting schizolophes or ptycholophes attached to the floor of the brachial valve, either directly as in *Phragmothyris* or by ridges as in *Megathiris*, is a convergence among indisputable terebratulides towards a thecideidine lophophore support. Even more significant is the appearance during the Holocene of the minute terebratulide, *Gwynia*, with a trocholophe supported only by vestiges of a loop continuous with the valve floor,

which illustrates how fundamentally neoteny can change the basic morphology of a stock. In fact there are a host of small orthide species, like the skenidiids and kayserellids, which are likely to have been equipped with a schizolophe supported by a medial septum, so that lophophore supports arising directly from the floor of the brachial valve are by no means exclusive to the strophomenides.

More important than any of these comparisons, however, is the implication of the structure of the brachial bridge. This postero-medial support of the mouth segment of the lophophore is made up to two apophyses, which grow anteriorly from the base of the inner socket ridges and remain discrete or unite medially. In origin and attitude they are homologous with the crura of the spiriferides and terebratulides (compare the cardinalia and crura of *Hustedia* and *Terebratulina* respectively), and fundamentally different from any structure inferred to have given support to the postero-medial segment of the strophomenide lophophore. Indeed projections which undoubtedly functioned like crura were almost invariably absent in strophomenides. A pair of lateral septa (anderidia) seen in some well-preserved chonetidines probably supported the postero-medial part of the lophophore (Brunton 1968, p. 60). But they grew out of the anterior part of the notothyrial platform close to the medial septum and well forward of the cardinalia, and are evidently not homologous with the thecideidine brachial bridge.

Cementation of the shell to a substrate and development of an entire cover to the delthyrium are really consequential to loss of the pedicle. Baker (1970, p. 90) has identified a sheath-like structure in the ventral umbo of *Moorellina*, which may have enclosed a rudimentary pedicle. Adult specimens, however, were invariably cemented to a substrate and, in view of what is known about the development and habit of living thecideidines, it appears that a pedicle could never have provided more than a transitory means of attachment which probably has always been effected by a mucopolysaccharide film binding the periostracum to the substrate. This kind of attachment also occurs in the living inarticulate *Crania* and, presumably, all cemented fossil craniaceans. Among articulate brachiopods, umbonal attachment to the substrate by cementation is characteristic of the strophomenides. Following the phylogenetic loss of a functional pedicle, this mode of attachment evolved independently in the davidsoniaceans, strophomenaceans and strophalosiaceans. Evidence of a rudimentary pedicle protected by a carbonate sheath is, however, found in most early strophomenides even when that organ atrophied during adult stages of growth and the foramen became plugged by secondary shell (Williams and Rowell in Williams *et al.* 1965, p. H88). The pedicle, when present emerged, through a supra-apical foramen and not the delthyrium which was invariably covered by an entire pseudodeltidium. A few undoubted spiriferides, notably the Triassic *Bittnerula* and *Thecocyrtella*, have also been described as cemented forms. But Cowen & Rudwick (1967) have demonstrated the presence of a subapical foramen in *Bittnerula* and, having accepted Dagys's interpretation of the *Thecocyrtella* cicatrix of cementation as a fracture surface in an otherwise normal umbo, they concluded (*op. cit.* p. 158) that cementation attachment has never evolved in any articulate brachiopod group other than the strophomenides.

In this way, attachment by cementation, supplemented by the presence of a supra-apical foramen and an entire pseudodeltidium, has become the prime symbol of strophomenide ancestry. Of these features, the supra-apical position of the foramen with its implication of an asymmetrical cleavage of the mantle rudiment (Williams 1956, p. 258) may well be the most important key to strophomenide affinities. After all, there are only two prerequisites for attachment by cementation. The first is the loss of a functional pedicle which has taken place many

times in brachiopod evolution. The second is the exudation of a bonding glue which could never have greatly differed in composition from the impersistent film of mucopolysaccharide secreted external to the periostracum at the mantle edge of every brachiopod species so far examined. Cowen & Rudwick (1966, pp. 403–404) have claimed that the pedicle foramina of the koninckinaceans, *Cadomella*, *Koninckella* and *Amphiclina* are supra-apical. But very well preserved specimens described by Brunton & Mackinnon (1972) show the openings to be apical like those in many other spiralia-bearing species; and these authors have convincingly argued for the reassignment of the koninckinaceans to the Spiriferida.

The ultrastructure of the thecideidines is as unambiguous as any morphological feature could be in indicating the ancestry of the Suborder. Irrespective of neotenous modifications in younger species, the essential carbonate succession consists of a primary layer of fine crystallites or granules and a secondary layer of fibres sheathed in anastomosing proteinous sheets and tightly stacked in alternate rows with concave surfaces facing externally. The layers are penetrated by puncta with distal canopies bearing fine perforations. Tubercles are particularly conspicuous along the internal margins of the valves and subject to resorption during shell growth. In living species they are composed of acicular crystallites and granules which are not texturally distinct from constituents of the surrounding primary shell. According to Baker (1970, p. 87) the tubercles of *Moorellina* have persistent cylindroid cores structurally similar to the primary shell with which they are continuous. However, they also underwent resorption and burial by fibrous secondary shell.

This succession is identical with that of terebratulides or punctate spiriferides down to such fine details as the brush penetrating the distal canopy of the punctum (Owen & Williams 1969; Mackinnon 1971*b*). Moreover, the tubercles are like those found in the living terebratulide *Megerlia* (Mackinnon 1971*a*), which also undergo resorption but are not necessarily continuous with the primary layer as in *Moorellina*.

In contrast, the ultrastructure of the typical late Palaeozoic strophomenide shell is strikingly different. In all species the dominant secondary fabric consists of successions of thin blades (laminae) usually between 200 and 300 nm thick. On exceptionally well-preserved internal surfaces like that of a young, Carboniferous *Schellwienella* (figure 99, plate 52), the laminae, each about 3.5 μm wide, are seen to form alternating overlapping rows. The laminar successions of the chonetidines (Brunton 1972), productidines (Williams 1968) and davidsoniaceans (figures 101 and 102, plate 53) are remarkably regular, while a thin recrystallized primary layer is not always preserved (Williams 1971, p. 54). In the oldhaminides *Oldhamina* (figures 103 and 104, plate 53) and *Leptodus* (figures 105 and 106, plate 53) the laminae vary in thickness from 150 nm to 1 μm and those in the core of the ventral septa may be intermingled with rods with variable cross-sections. However, with the exception of the plectambonitaceans and Thecospiridae, no strophomenide shell has yet been found consisting of orthodoxly stacked fibres in place of laminae. The plectambonitaceans which became extinct during the Devonian, were ancestral to all strophomenides except the davidsoniaceans (Williams 1970) and the fibres were, in any event, neotenously lost in all descendants by the Ordovician period. The secondary layer of *Thecospira* consists of fibres differing only in size and details of shape from those so characteristic of other articulate brachiopods. *Thecospira* is punctate and tuberculate, although the latter are impersistent because they were subjected to resorption (Mackinnon 1971*a*) as in the thecideidines, koninckinaceans and *Megerlia*. The impersistence, through resorption, of tubercles ornamenting the interiors of the thecideidines, koninckinaceans and thecospirids, is noteworthy.

The typical strophomenide is also tuberculate (pseudopunctate); but the pseudopuncta, which usually have cylindroid granular cores distinguishable from the surrounding shell, persisted throughout life and are, accordingly, evenly distributed over the shell interior.

The systematic positions of *Thecospira* should now be considered. The nature of its carbonate succession, the presence of spiralia composed of orthodoxly arranged secondary fibres as in all spiriferide species, the cyrtomatodont teeth, the cardinalia dominated by inner socket ridges supporting crura, all suggest that the writer (1953, p. 13) and Cowen & Rudwick (1966, p. 406) were mistaken in assigning *Thecospira* to the Strophomenida and that this taxon should now be returned to its original place among the Spiriferida, along with the koninckinaceans as advocated by Brunton & Mackinnon.

This revision in the systematic affiliations of *Thecospira* and the koninckinaceans clears the way for considering the relative merits of the strophomenides (as now amended), spiriferides and terebratulides as ancestors to the thecideidines. The prototypic thecideidine must have been a ventribiconvex species cemented to the substrate by the ventral umbo and equipped with strong interareas and an entire pseudodeltidium, cyrtomatodont teeth, well-developed inner socket ridges fused into a cardinal process and supporting crura, a bilobed peribrachial ridge, a hemispondylium and a punctate, impersistently tuberculate shell with a crystallite-granular primary layer and a fibrous secondary layer. Of these features, the teeth, cardinalia, crura and shell structure are unequivocally spiriferide or terebratulide in affinities and only attachment by cementation and the peribrachial ridge are more strophomenide according to frequency of occurrence. Profound changes, of course, can be introduced by the degree of neoteny and deviation that gave rise to the thecideidines. But, in view of the irreversibility of evolution, it is unlikely that the laminar strophomenide shell should suddenly have reverted to the fibrous condition of some remote Cambrian ancestor. It is also more likely for an evolving descendant from a spiriferide (or terebratulide) to lose a functional pedicle and spiralia (or loop) than for a derived strophomenide to develop a complex system of articulation and posterior lophophore support structurally identical with that found in contemporaneous spiriferides and terebratulides.

Rejection of a strophomenide ancestry for the thecideidines applies with equal pertinence to another problematic Triassic genus, *Bactrynium*, which has been classified by the writer (in Williams *et al.* 1965, p. H521) as an oldhaminidine and by Grant (1972, p. 246) as a strophomenide close to the strophalosiaceans. Rudwick (1968, p. 356), however, associated the genus with the thecideidines and the discovery that its shell succession includes a normally developed fibrous secondary layer with impersistent tubercles (figures 107 and 108, plate 53) as well as other more general morphological considerations support his conclusions.

Finally in choosing between spiriferides and terebratulides as the more likely group from which the thecideidines were descended, one has to rely on less fundamental aspects of their shell morphology and anatomy. On the morphological side there is evidence that at least one spiralia-bearing genus, *Thecospira* became cemented by attachment following the loss of its pedicle; no similarly anchored terebratulide has yet been found. Anatomically, too, there are some differences. In particular the structure of the mantle edge with its periostracal slot and the secretion of proteinous partitions sealing off the distal parts of puncta, are not found in living terebratulides. On balance, therefore, it is suggested that the thecideidines were derived from punctate spiriferides.

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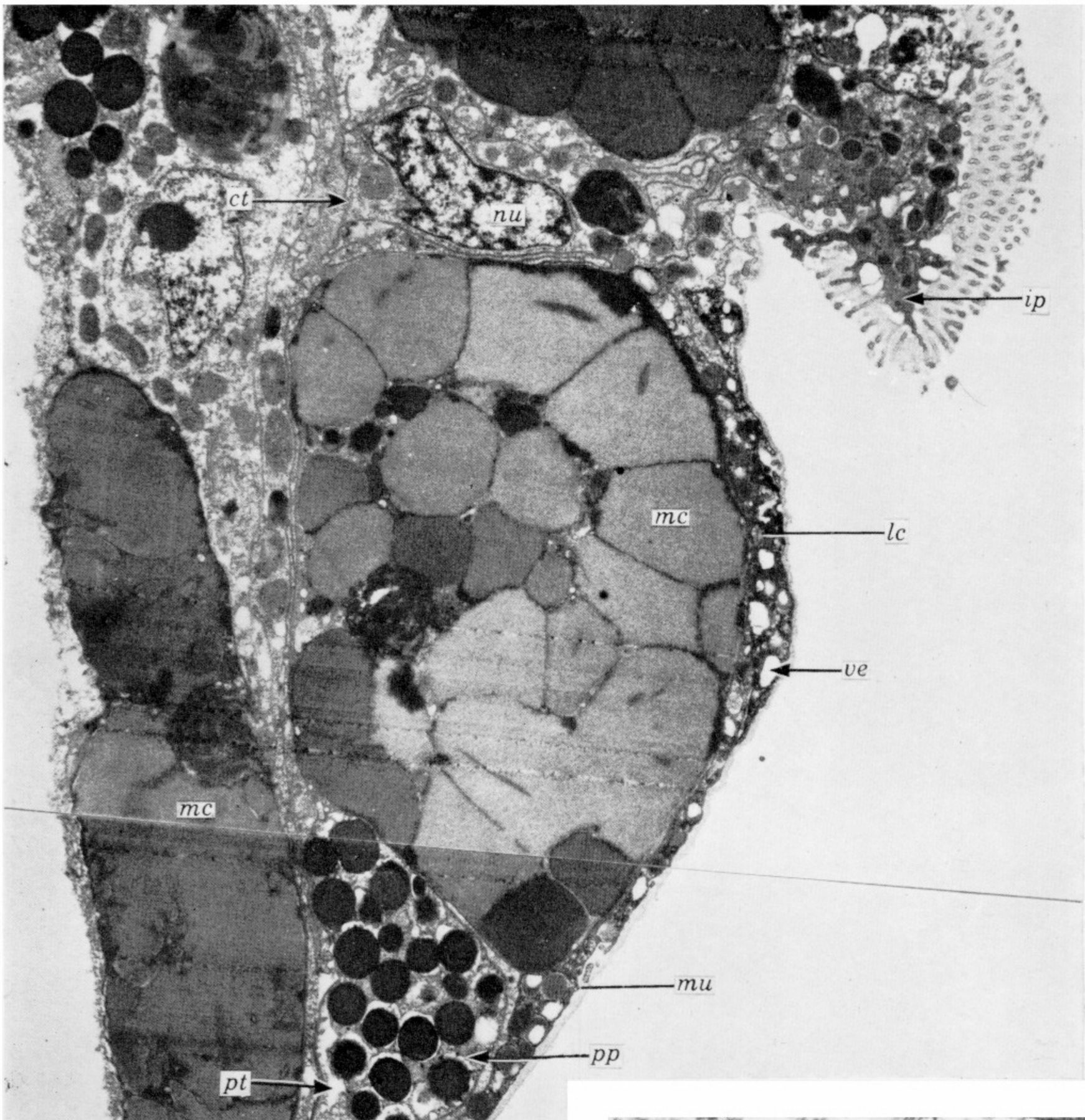
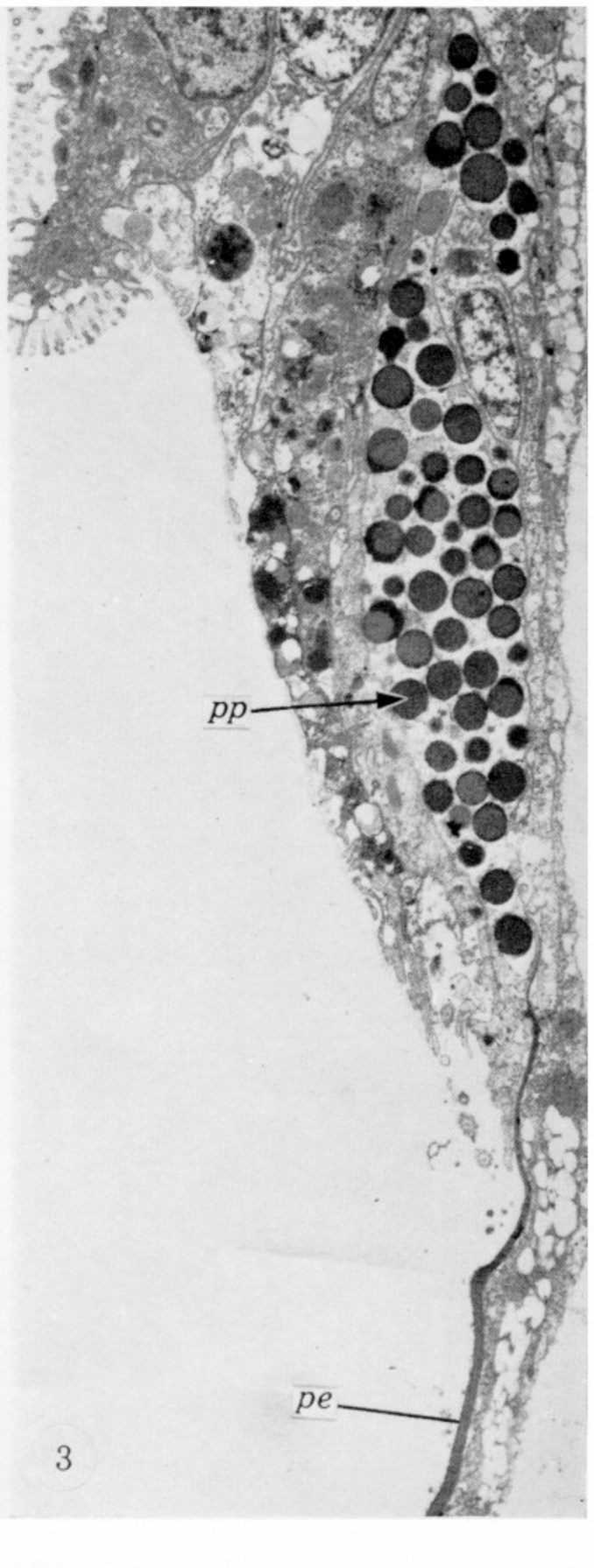
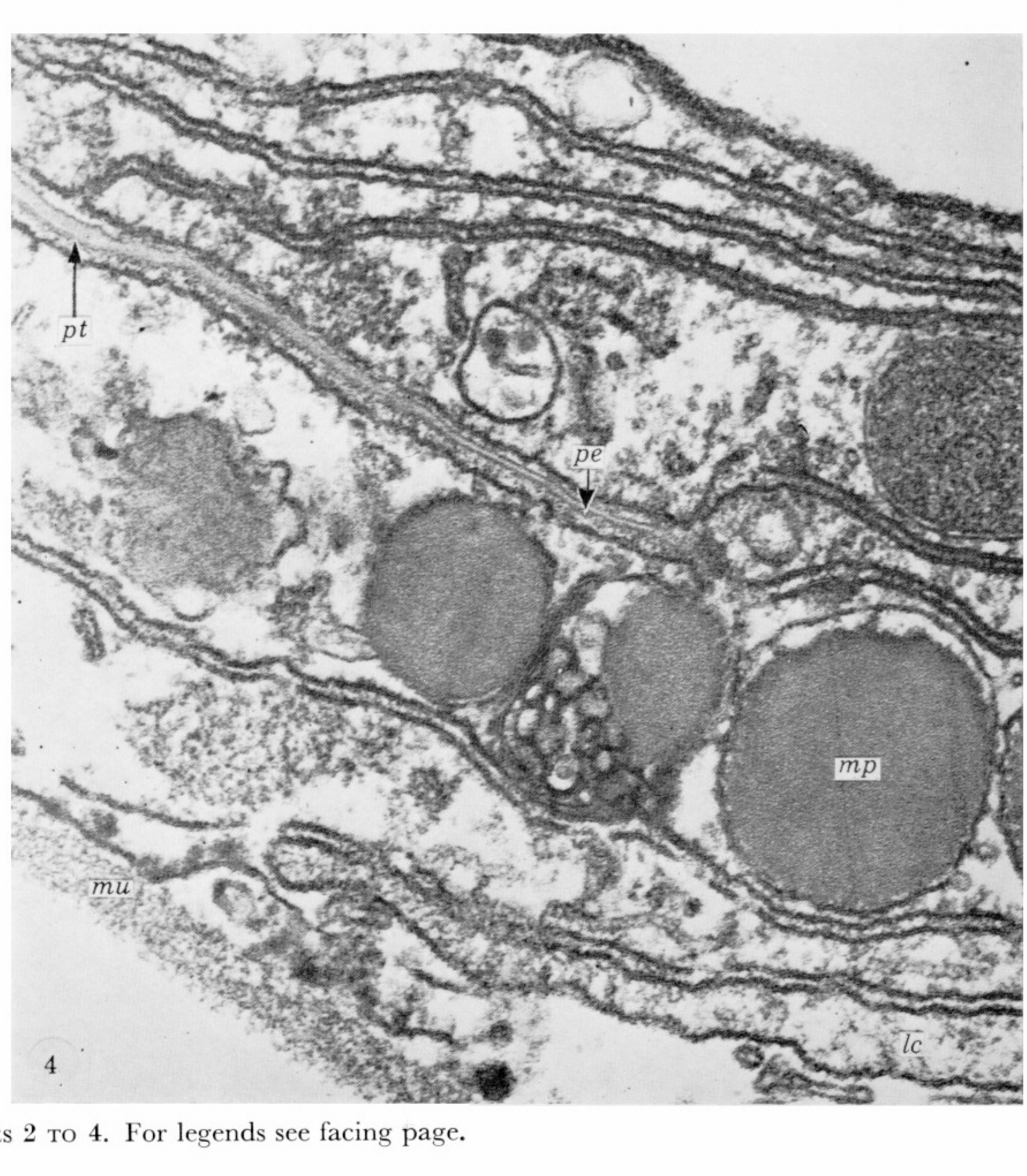
List of abbreviations

ac	acicular crystallite
ap	adductor pit
as	adductor scar
bh	brush
bp	perforations of brush
bv	brachial valve
ca	canopy
cc	columnar cell
cp	cardinal process
cs	crus
ct	connective tissue
de	desmosome
es	external surface
fb	fibre
fc	fibrillar connexions
fe	filaments
fp	flap
gc	granular calcite
gl	glycogen
gp	glycoprotein
gs	growth surface
gw	growth line
hc	hemispherical accretion
hl	hinge-line
ia	interarea
ic	intercellular polysaccharides
ie	inner layer of periostracum
ip	inner epithelium
ir	inner socket ridge
is	internal surface of valve
la	laminar calcite
lc	lobate cell
le	lens of calcite
ls	lophophore muscle scar
mc	mucin
mh	resorption pit
mi	microvillus
mp	mucoprotein
mt	muscle tissue
mu	mucopolysaccharide
nu	nucleus
oe	outer epithelium
om	organic mesh
op	outer periostracal layer
pa	punctum
pc	peritoneal cell
pe	periostracum
pf	patches of secondary fibres
ph	protein sheet (or lining)
pl	primary layer
pm	plasmalemma
pn	proteinous partition
pp	pre-periostracal cell
pr	peribrachial ridge
ps	pseudodeltidium
pt	periostracal slot
pu	pseudopunctum
pv	pedicle valve
py	polysaccharide
ra	rhombohedral angle
rb	rhombic block (or rhombohedra)
rd	calcite rod
sc	finely granular lobate areas
sl	secondary layer
sm	sealing membrane
so	socket
sp	spine
su	substrate
tc	tooth core
te	tubercle
tf	tonofibrils
th	tooth
tr	transgression
vc	vesicular cell
ve	vesicle







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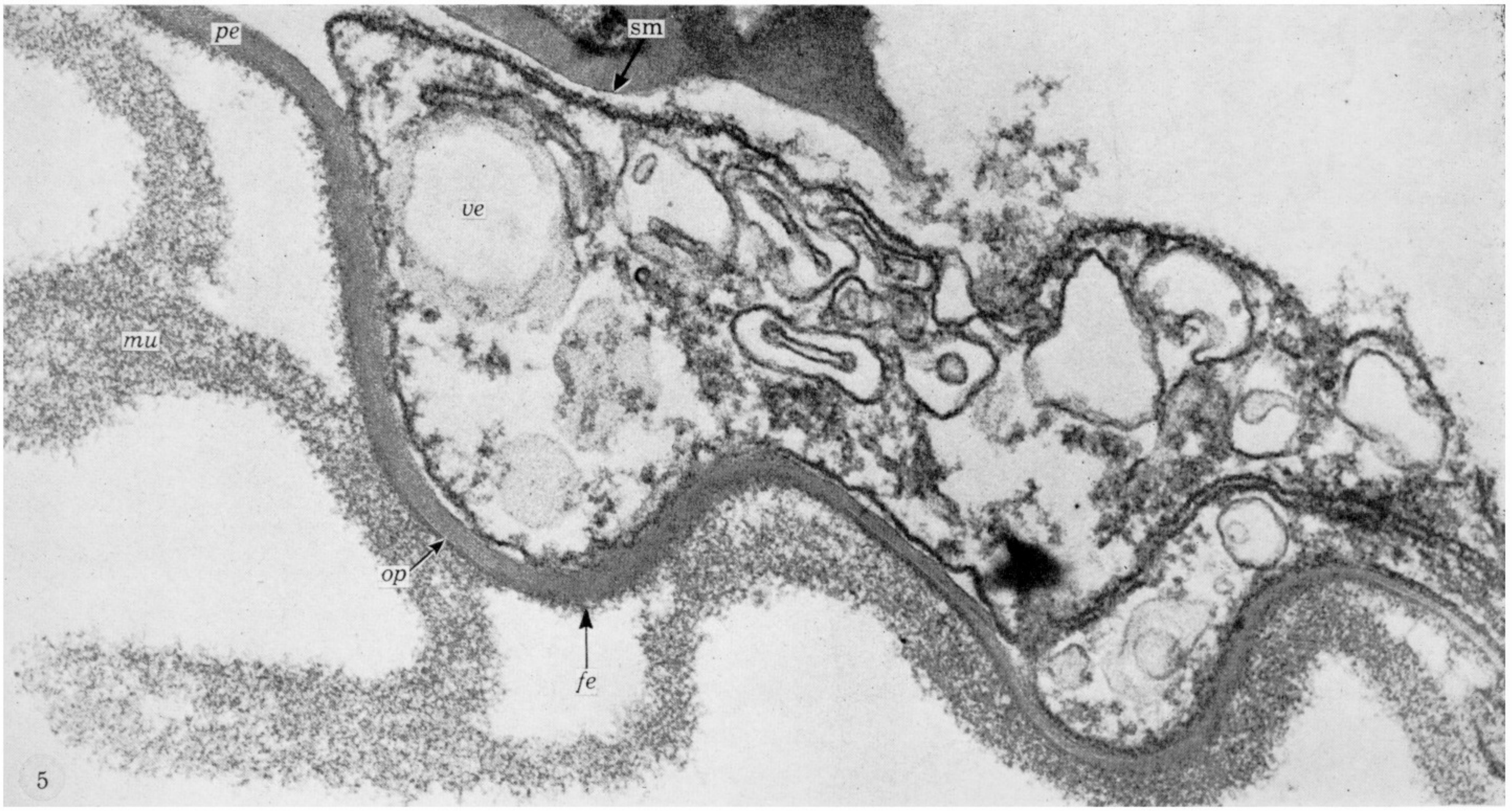

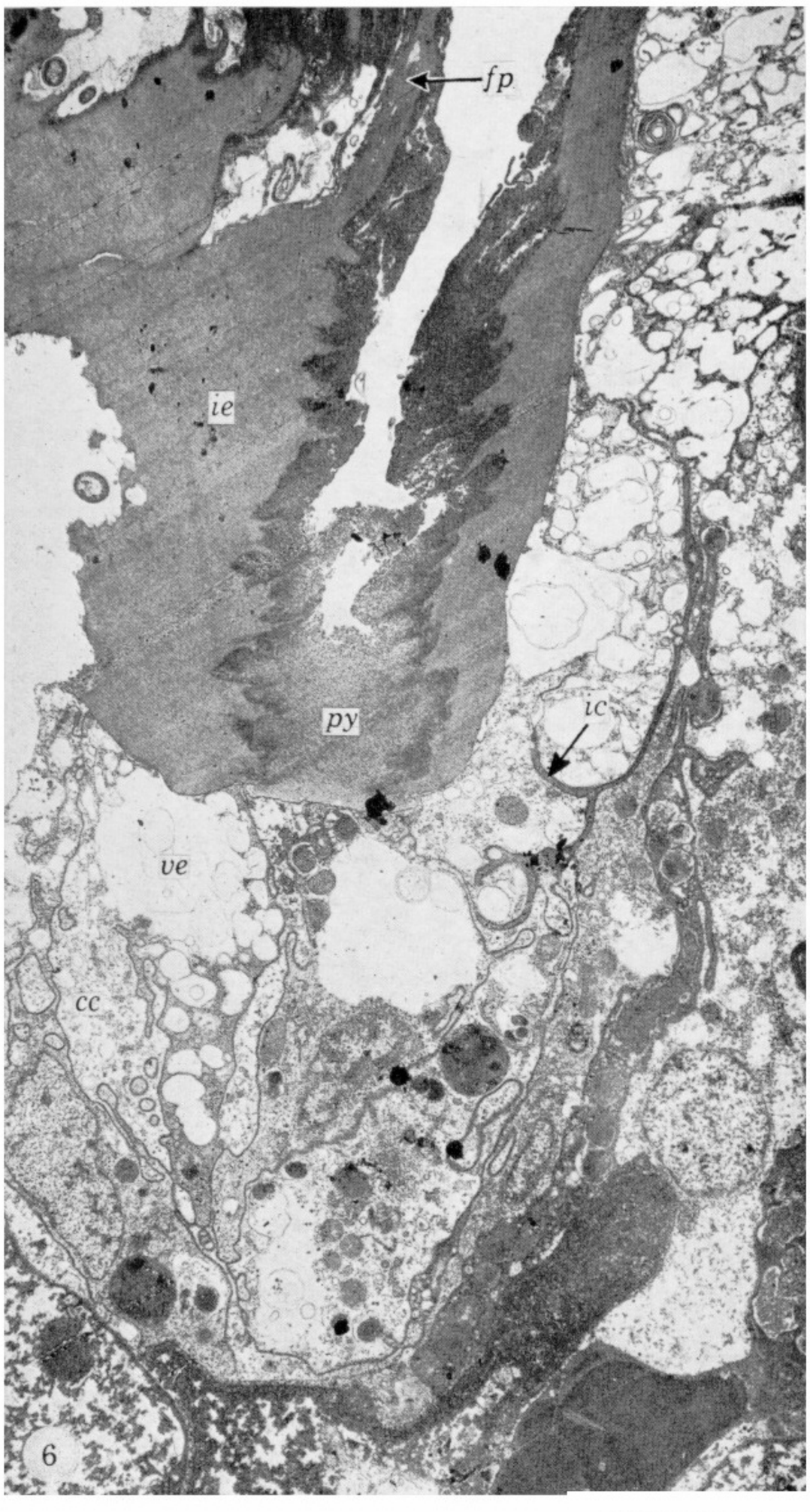

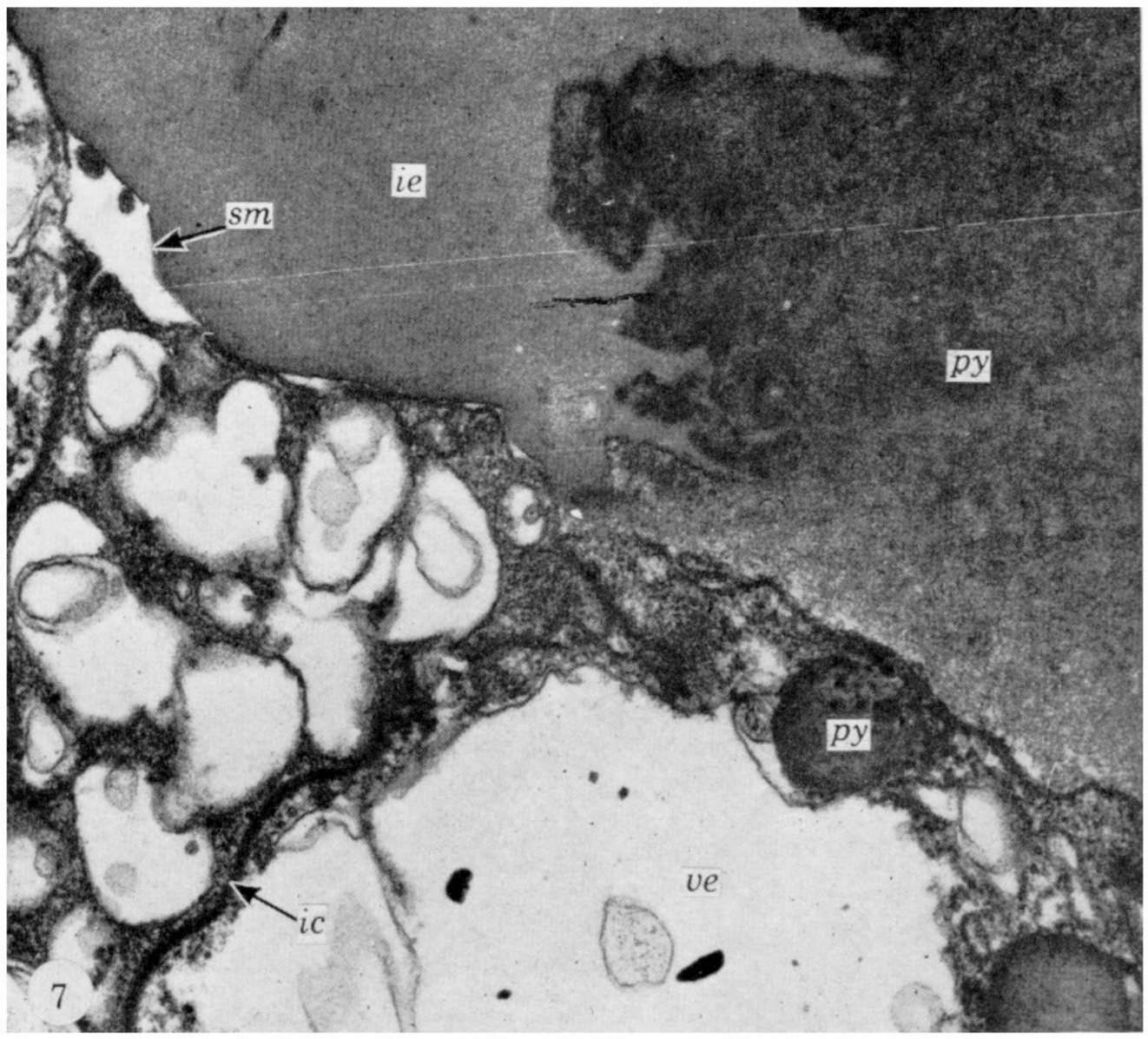

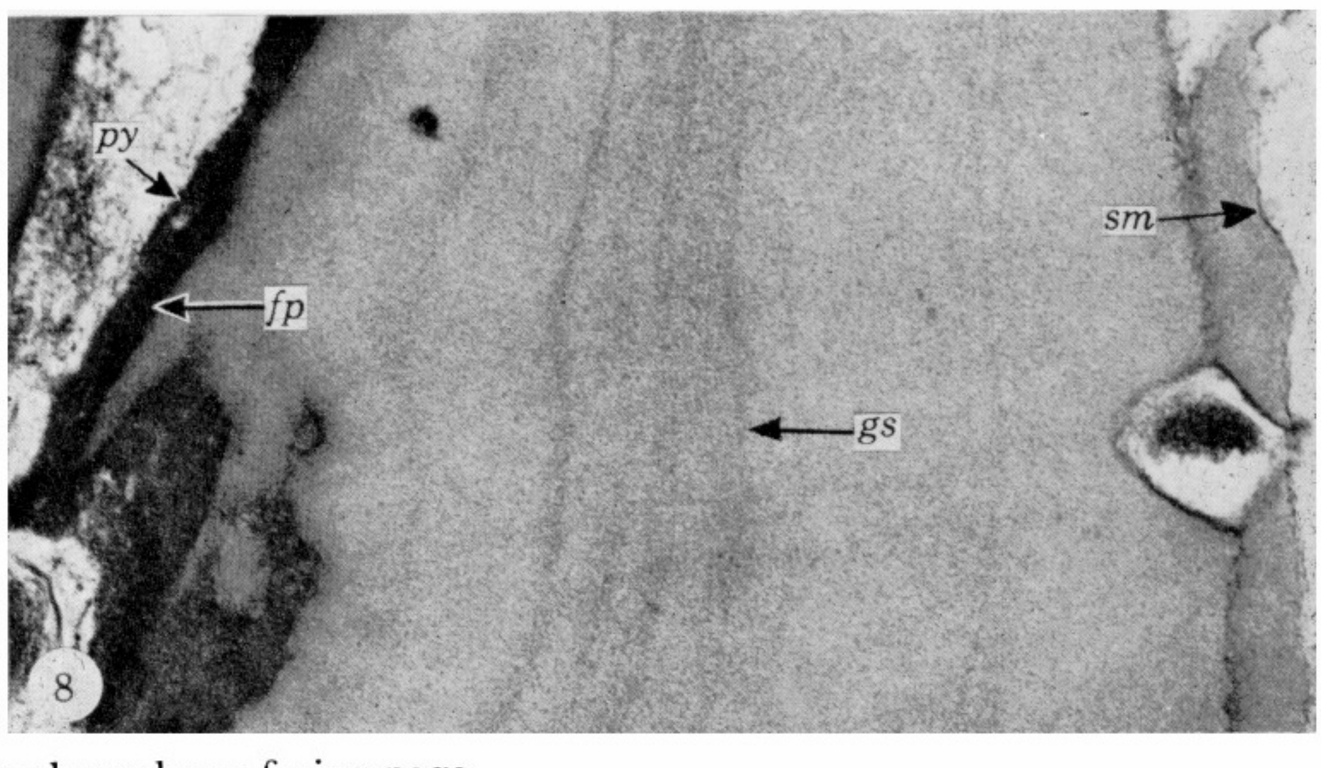

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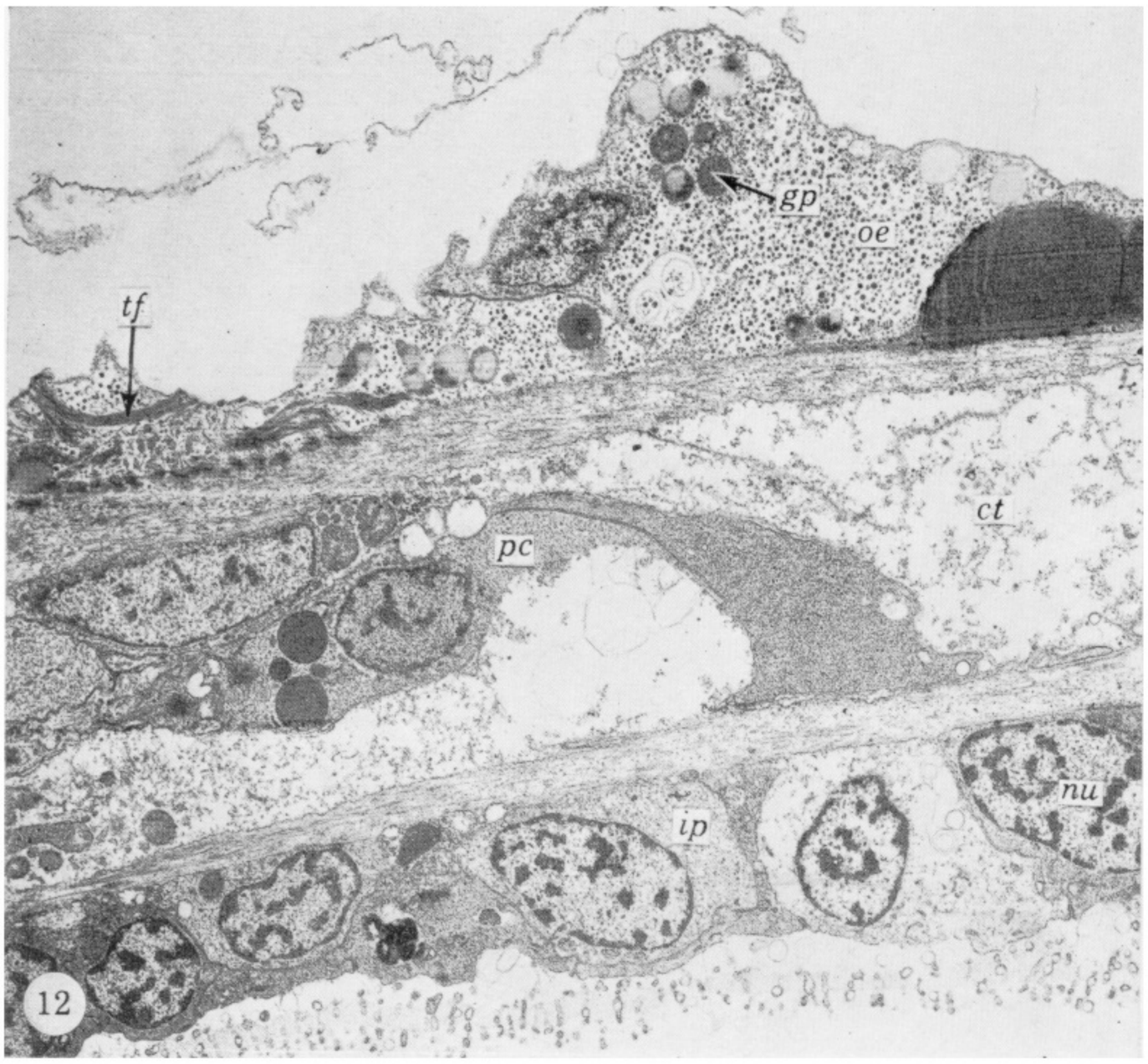

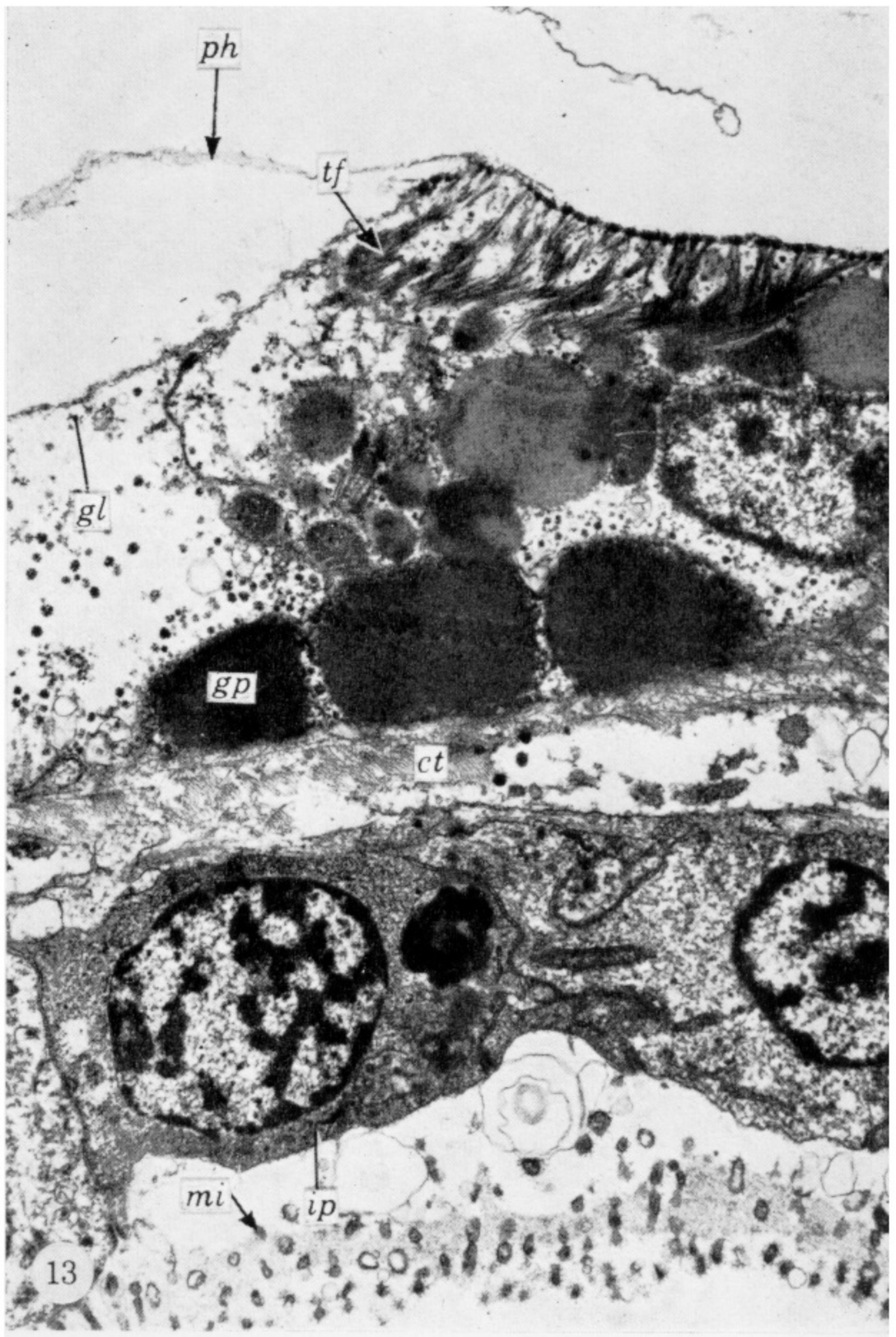

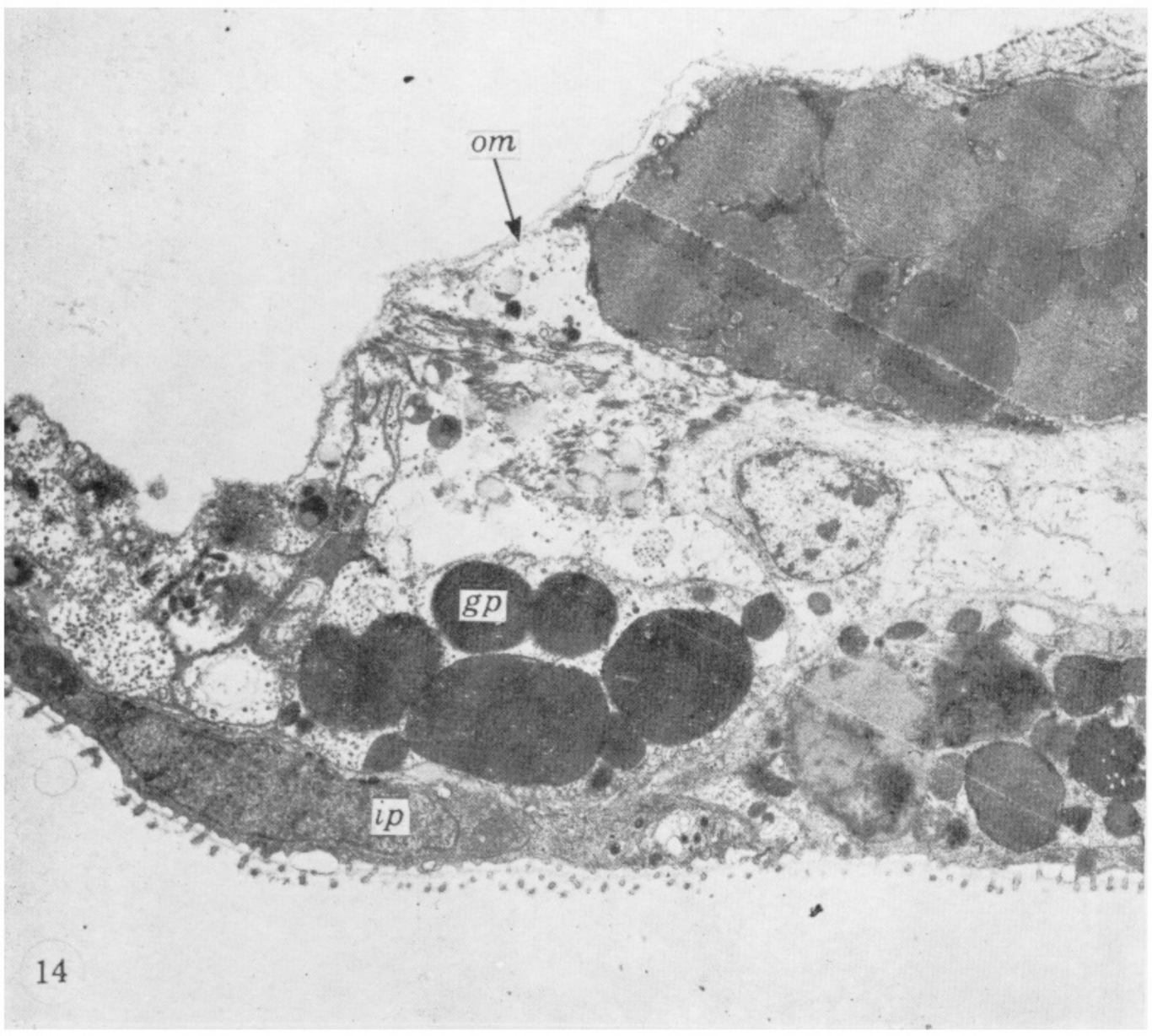

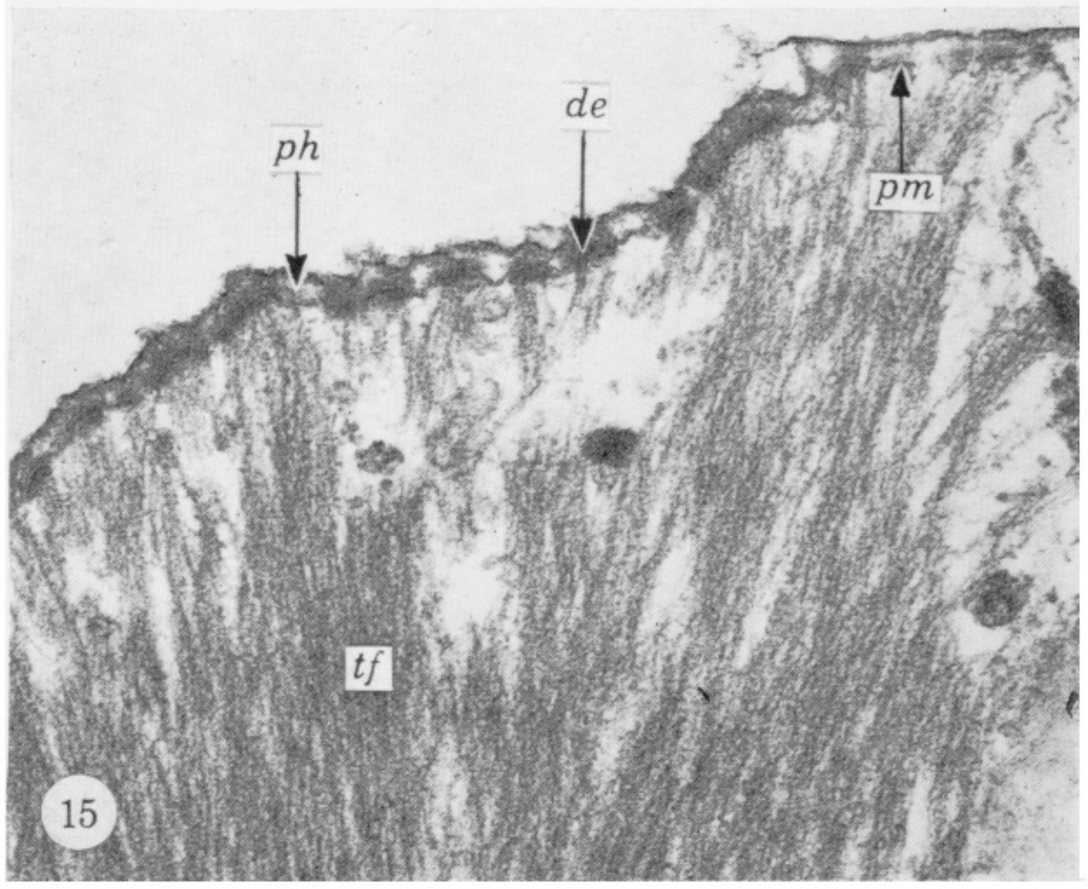

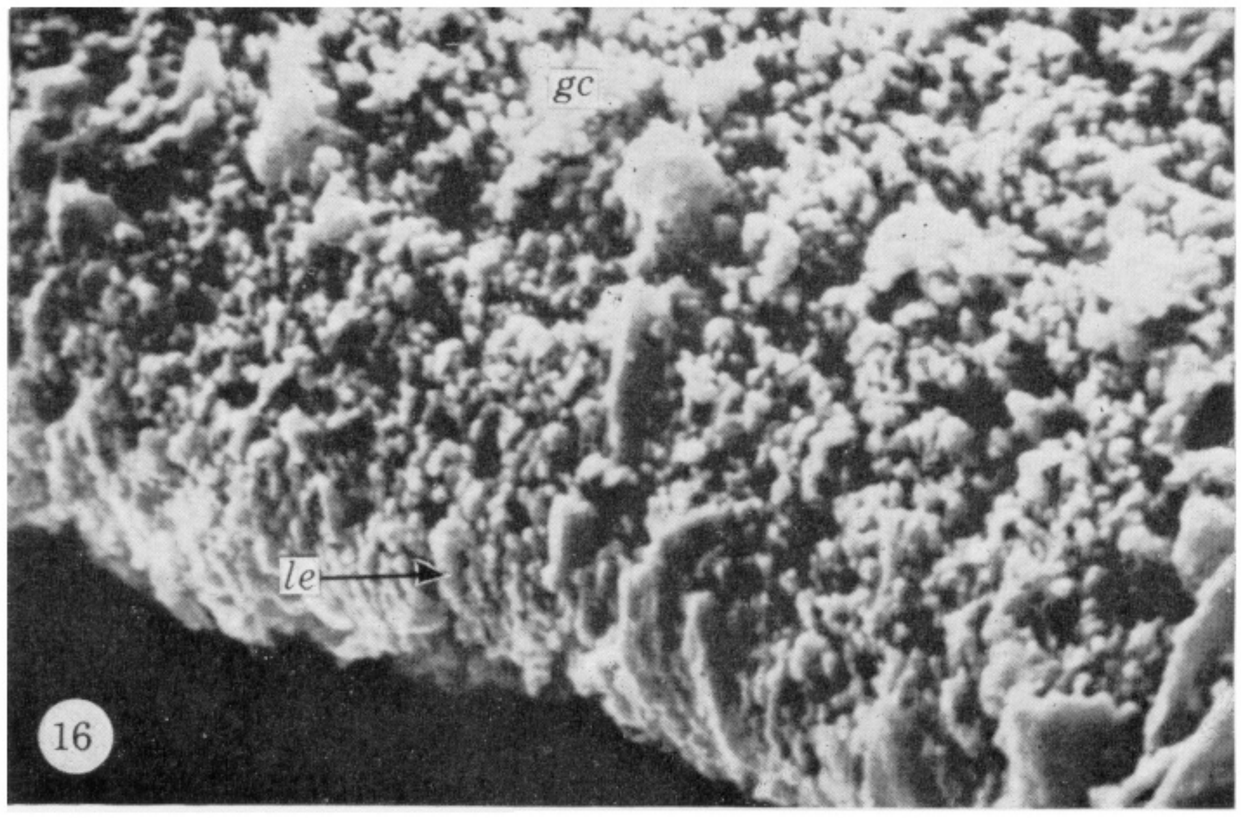

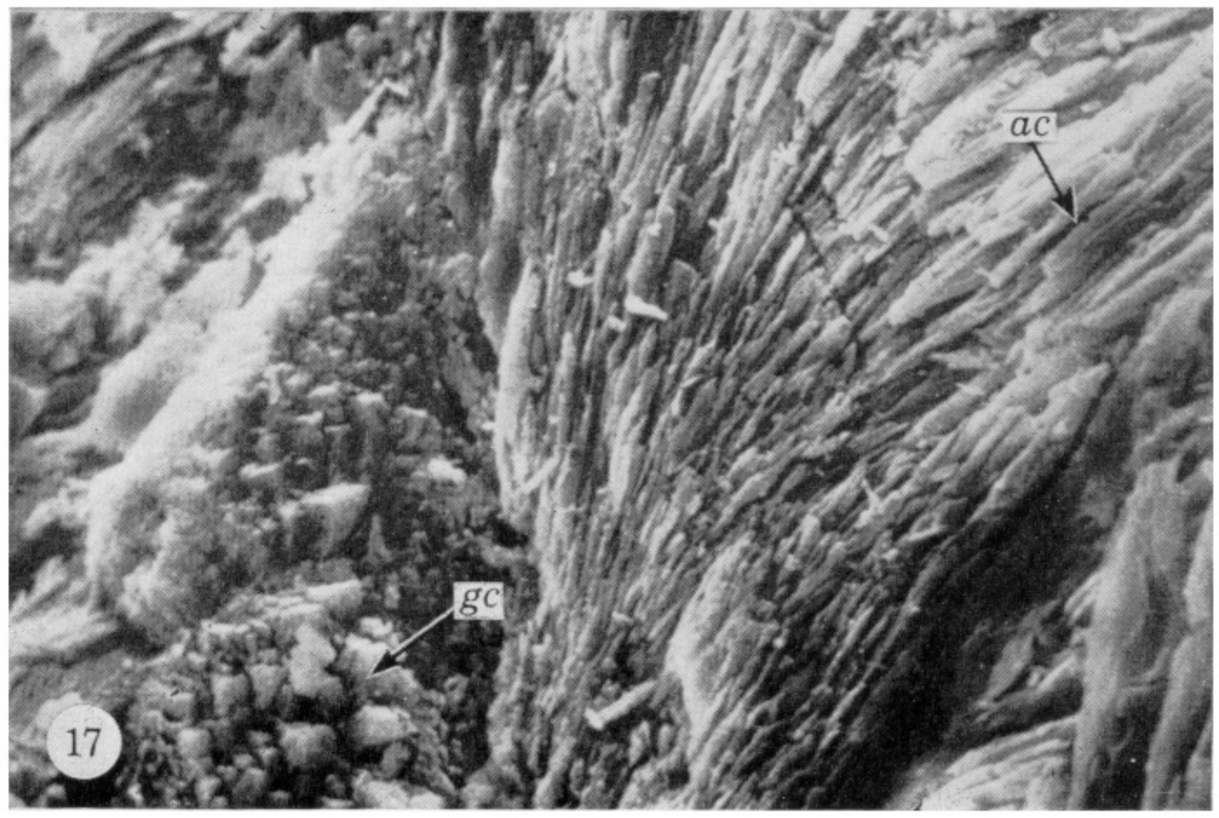

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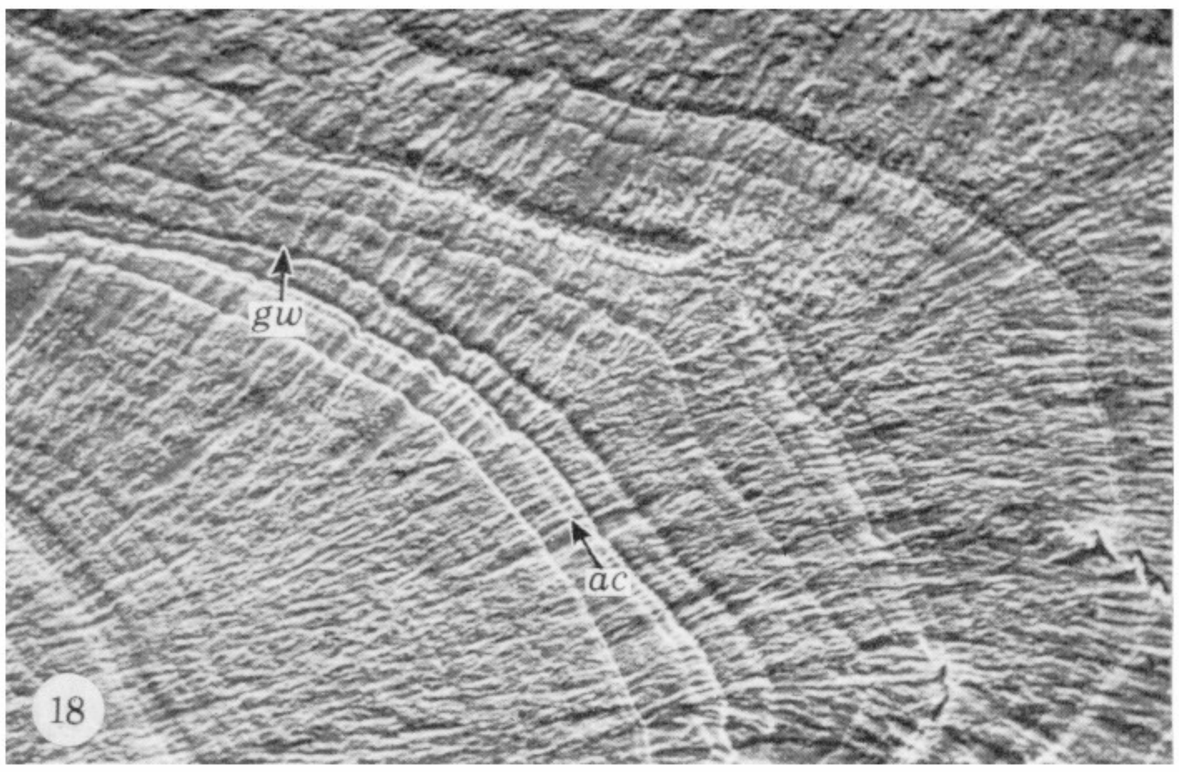

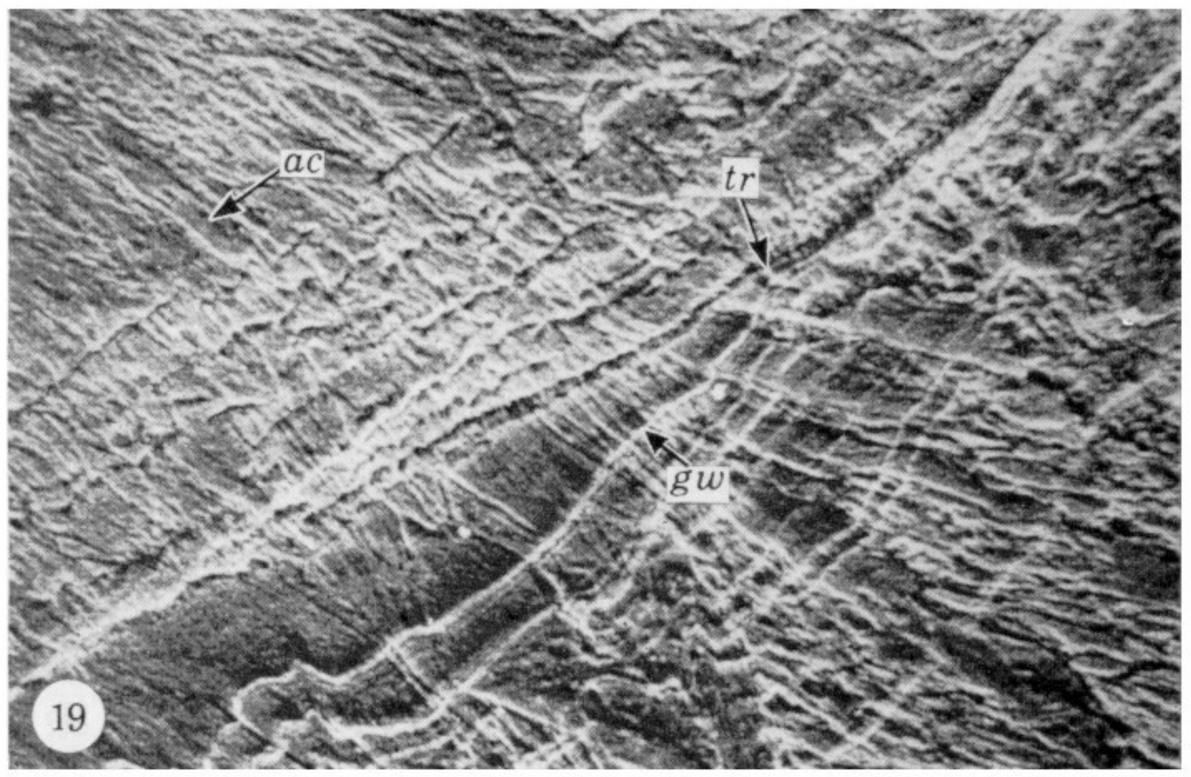

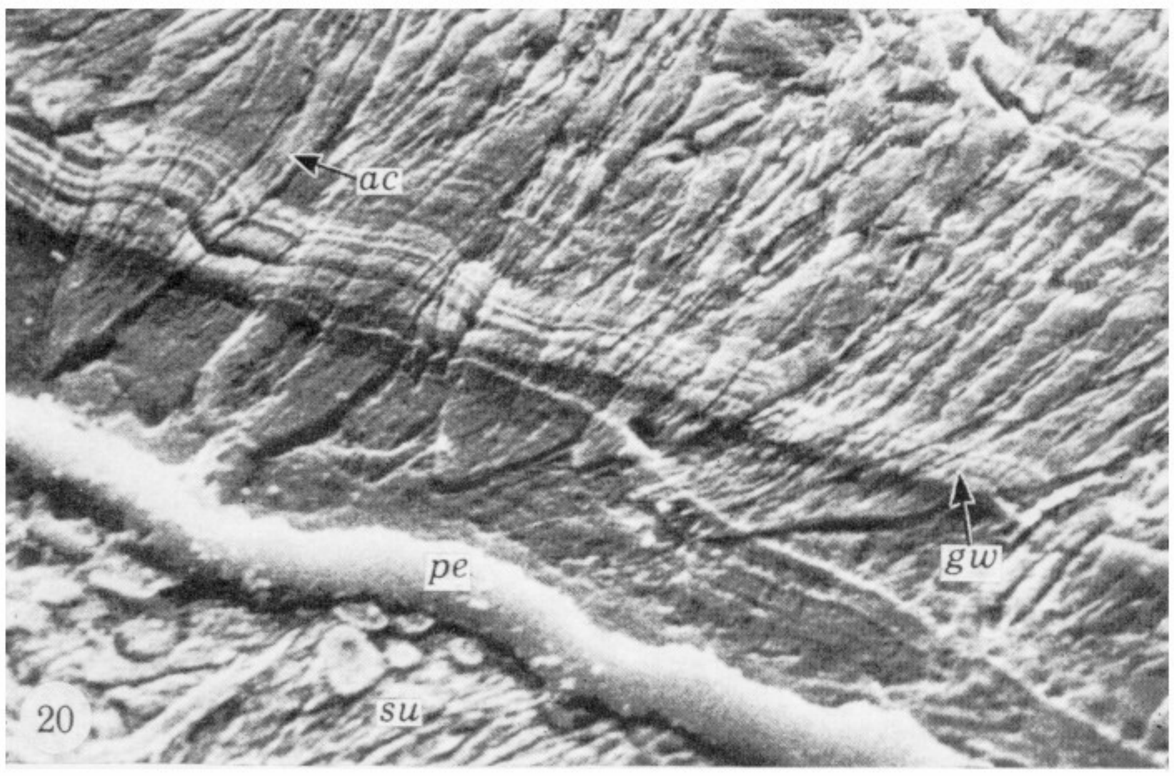

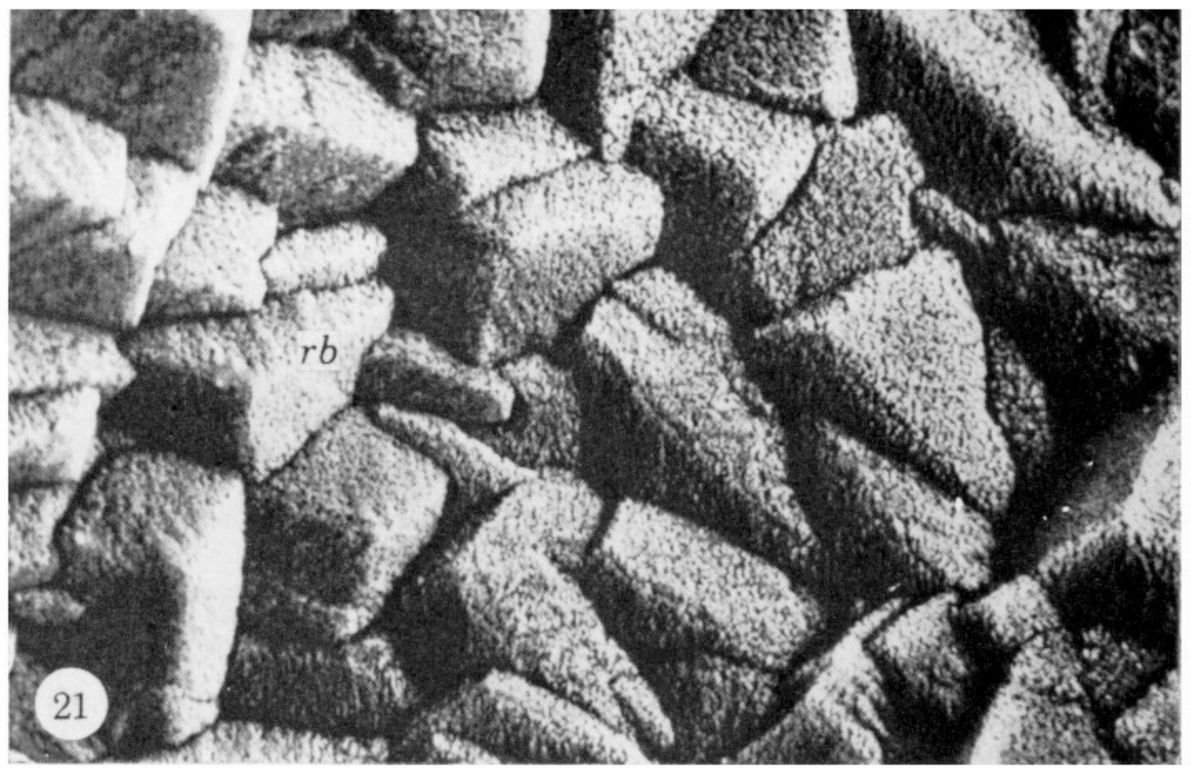

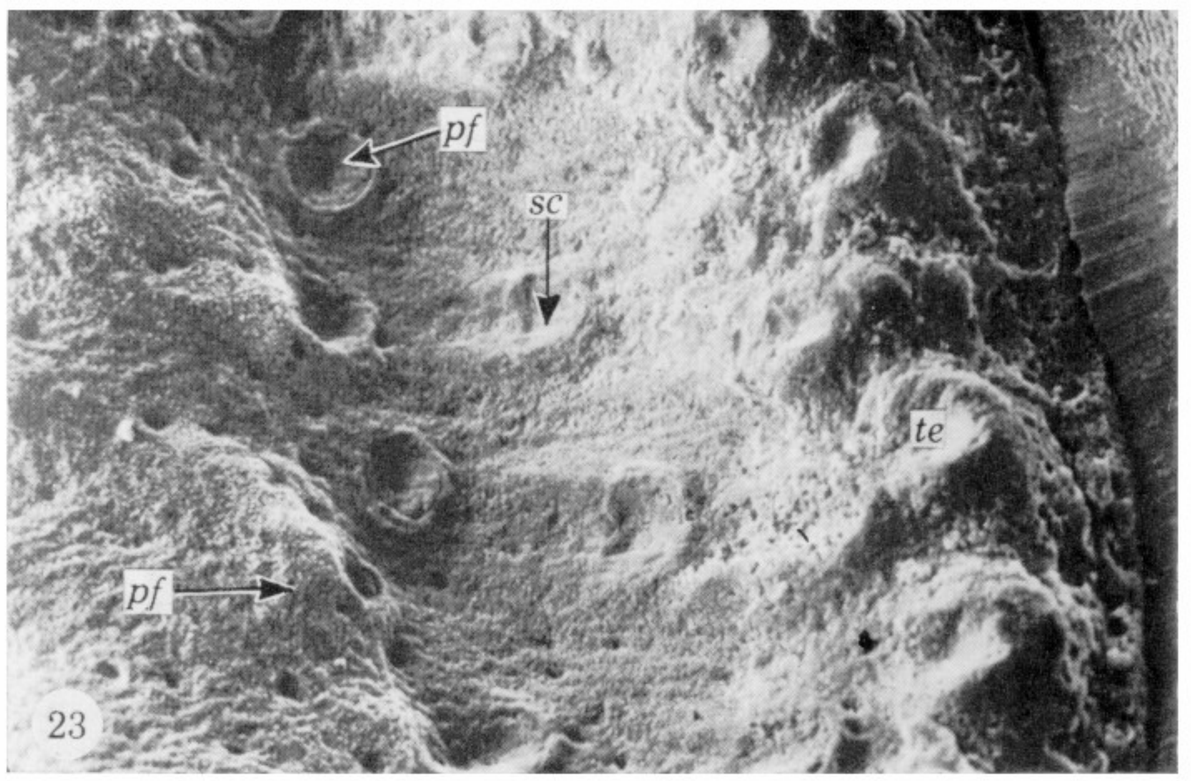

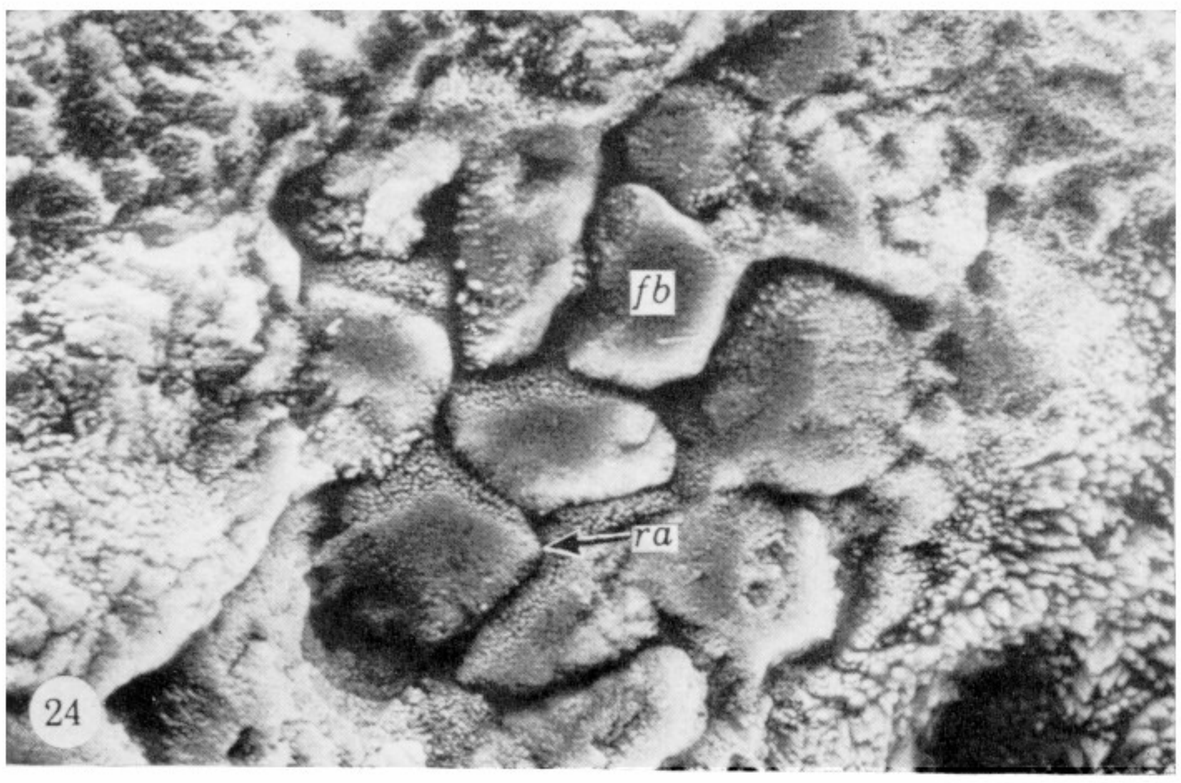

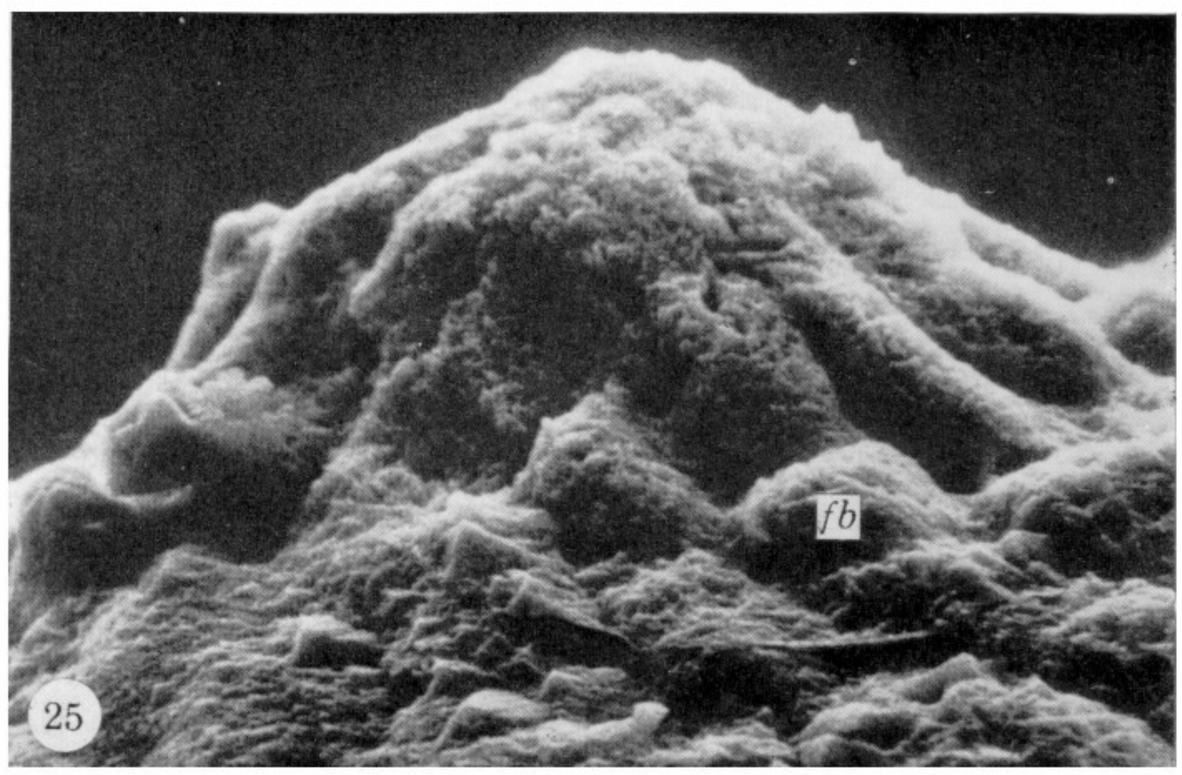

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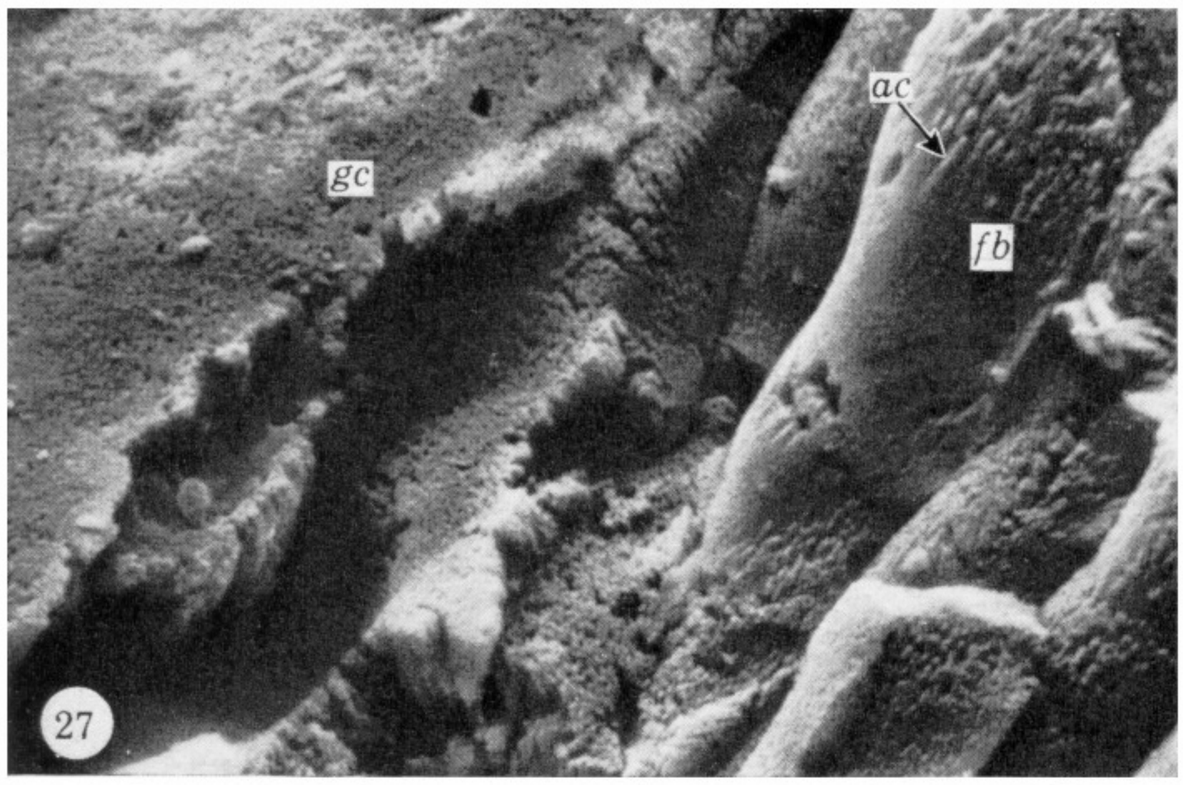

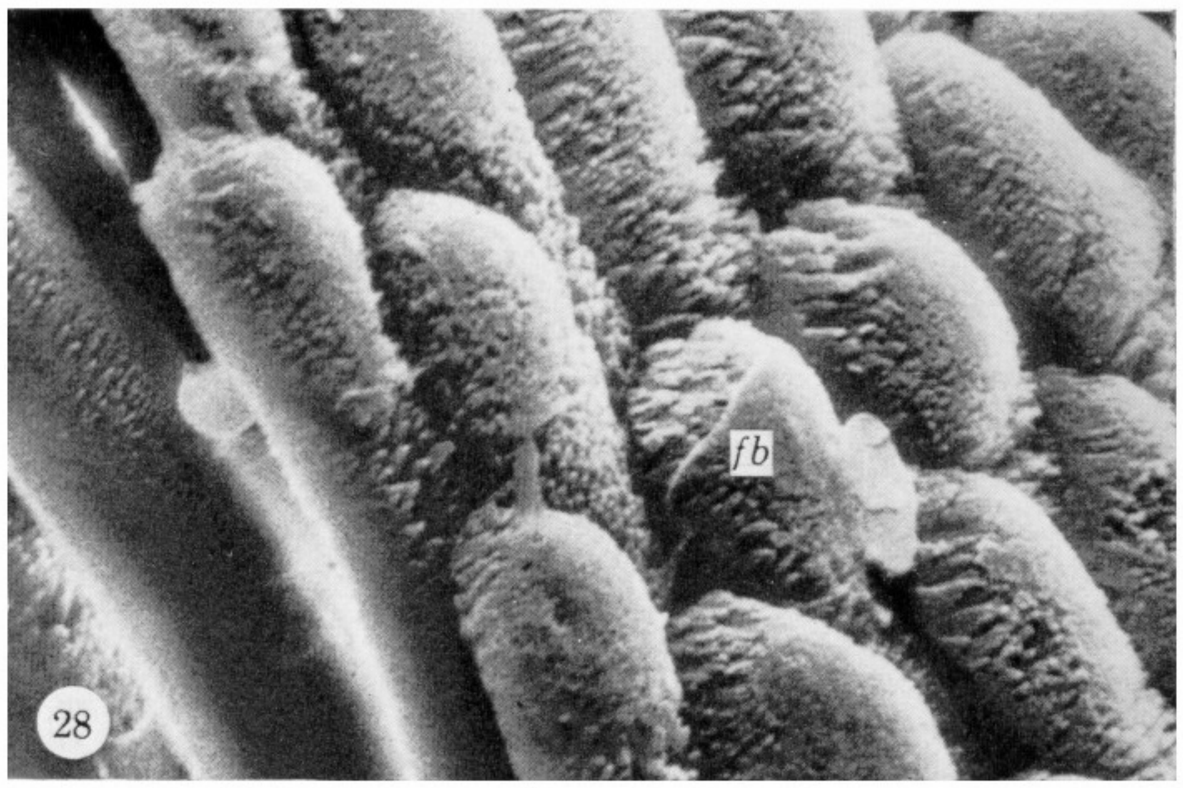

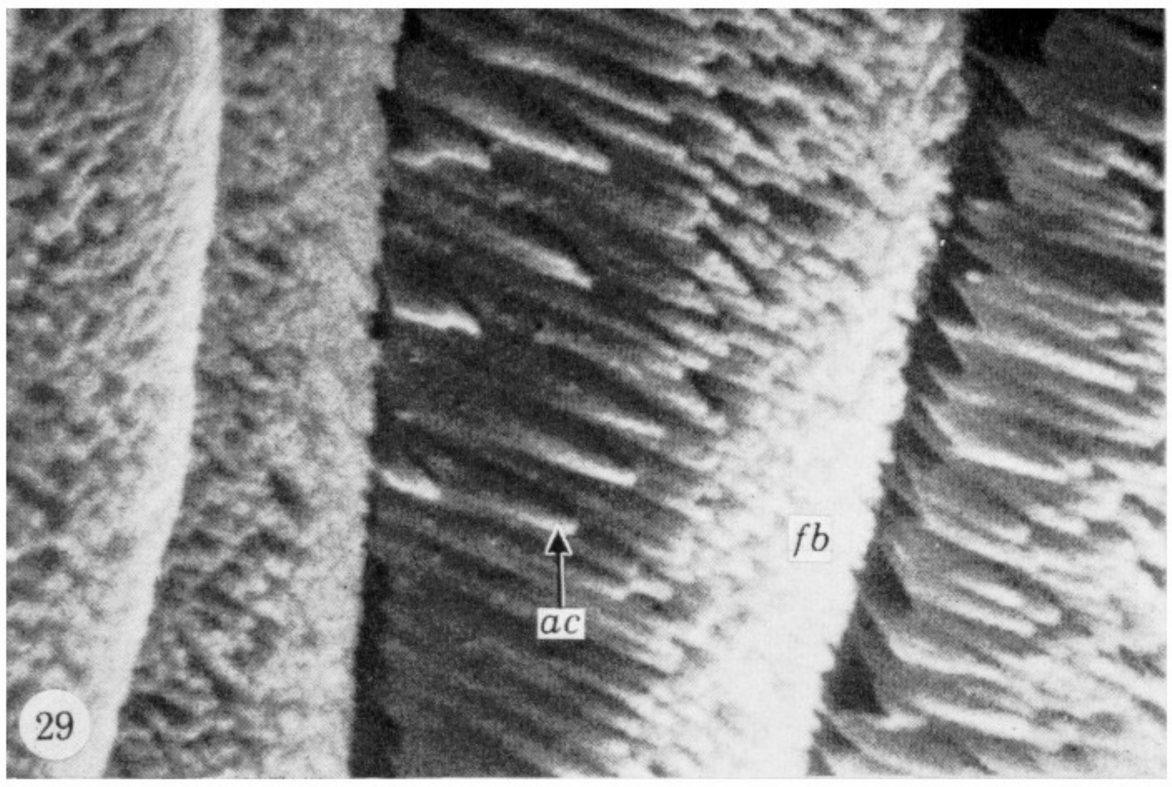

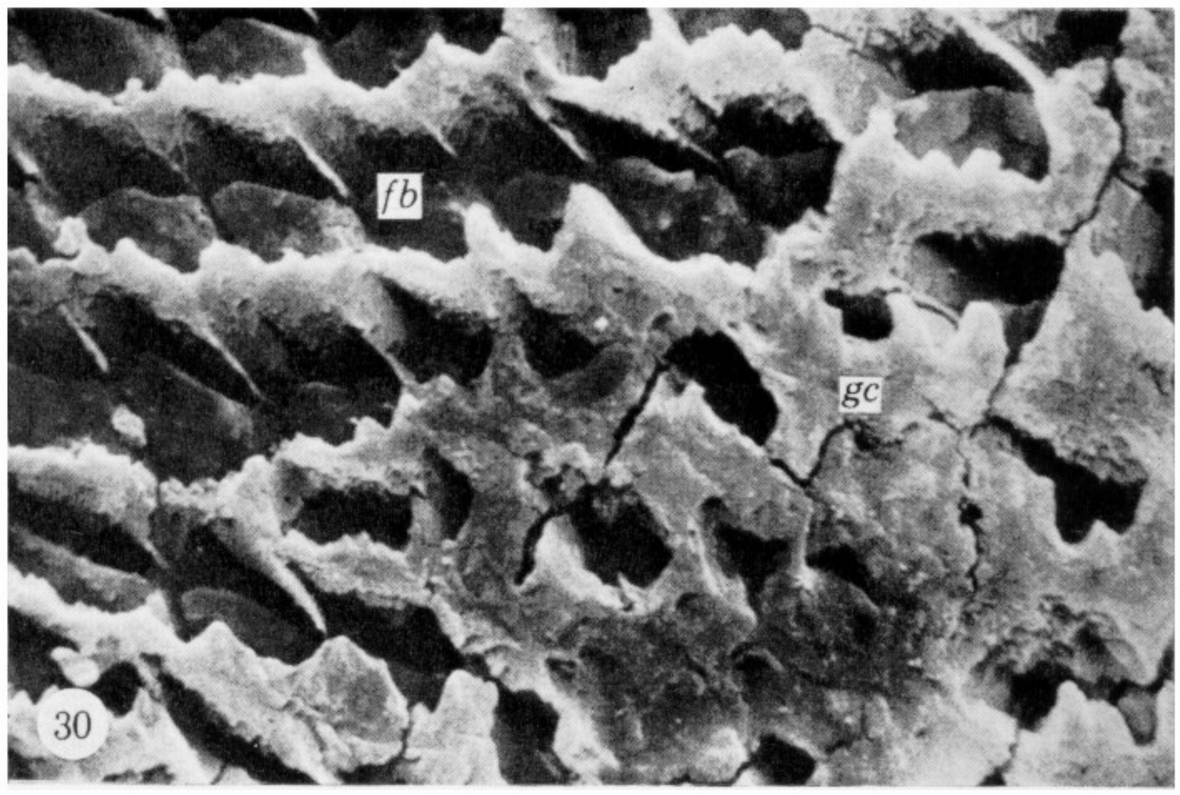

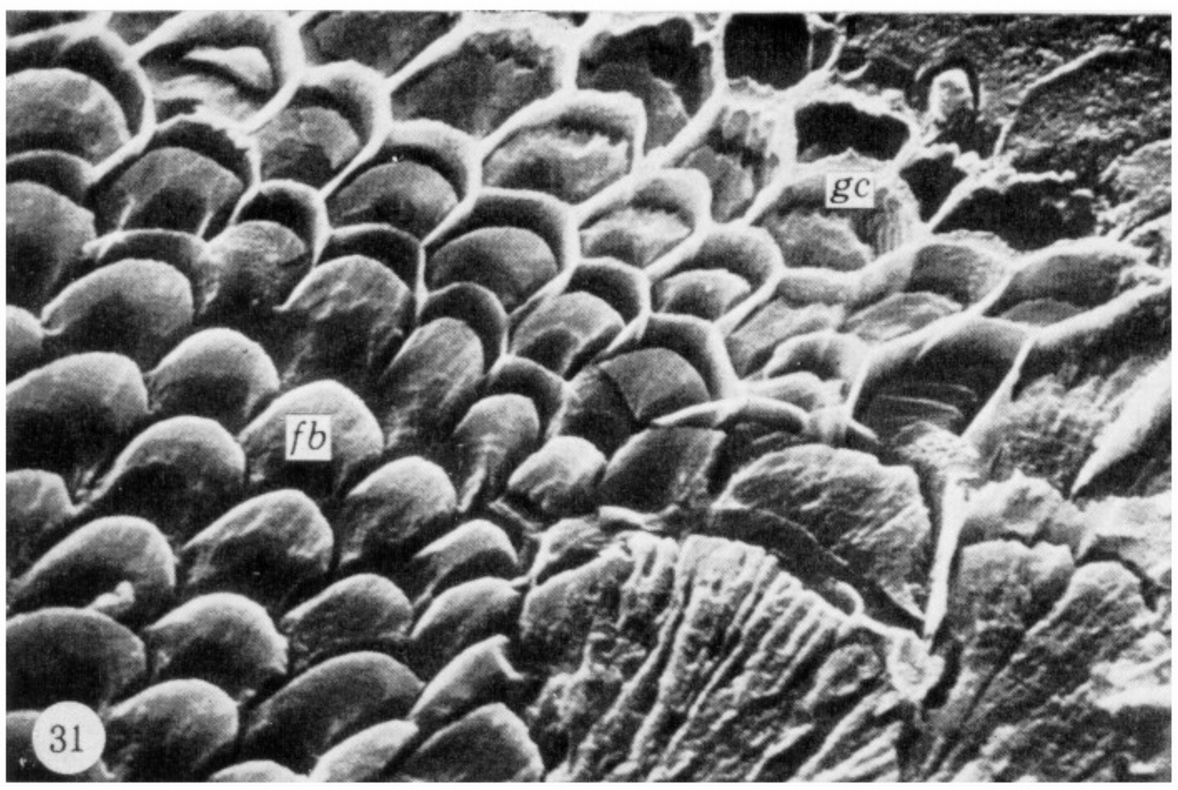

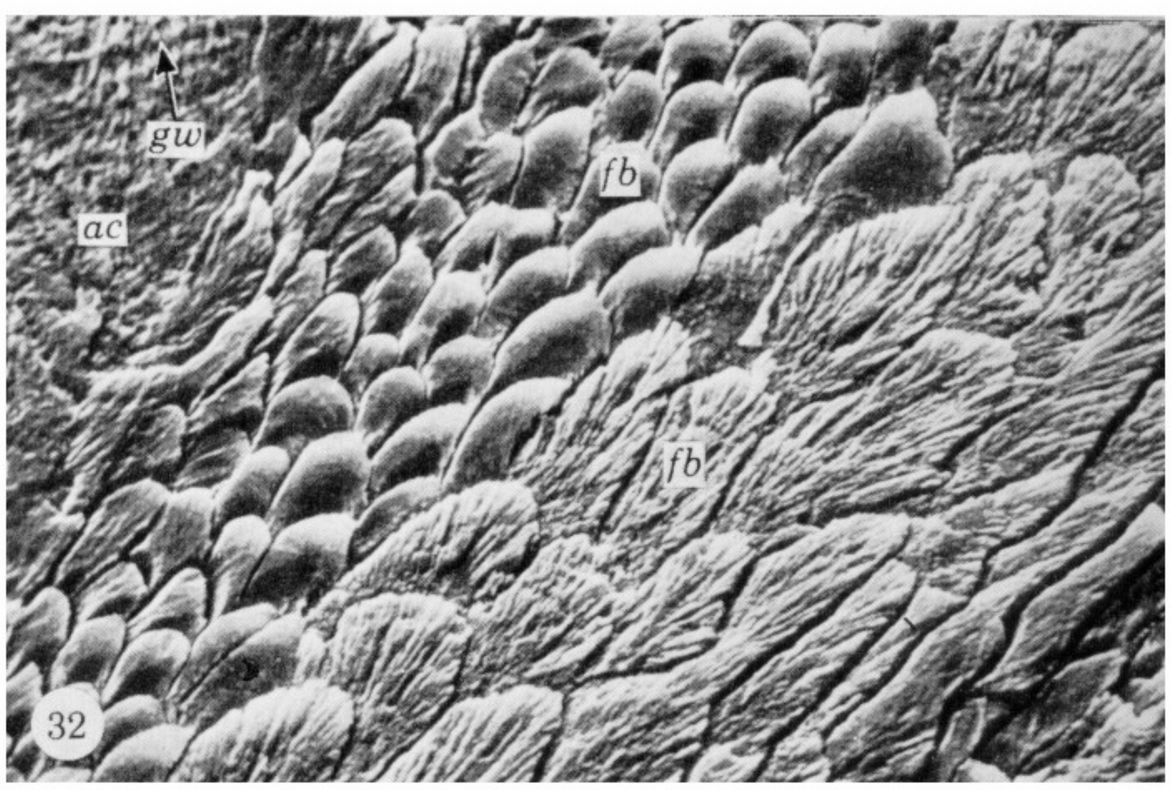

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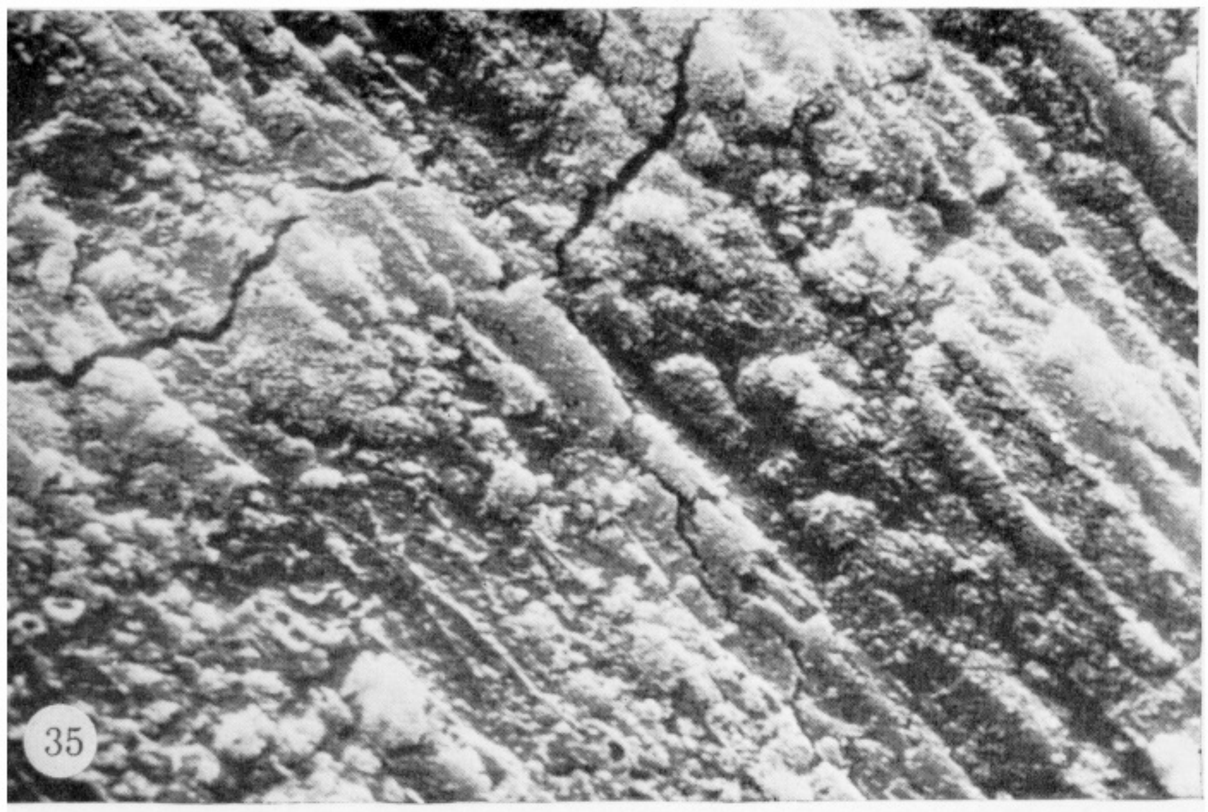

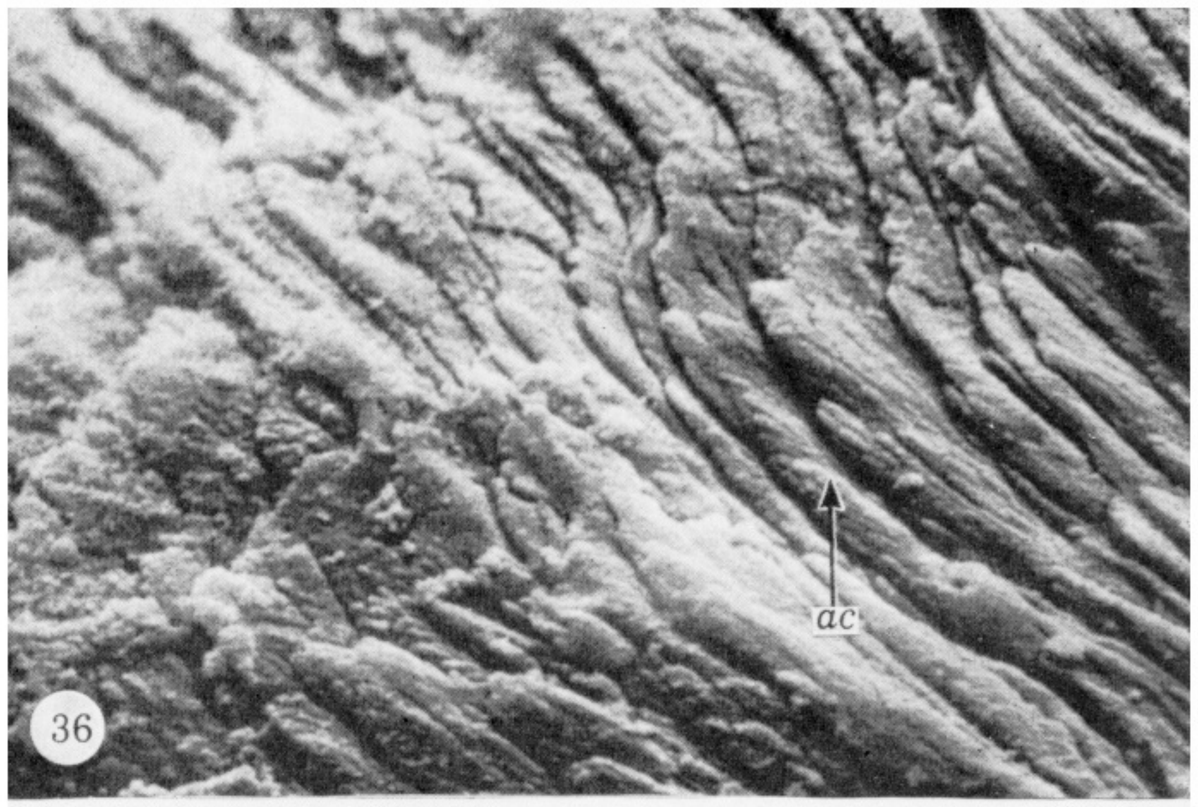

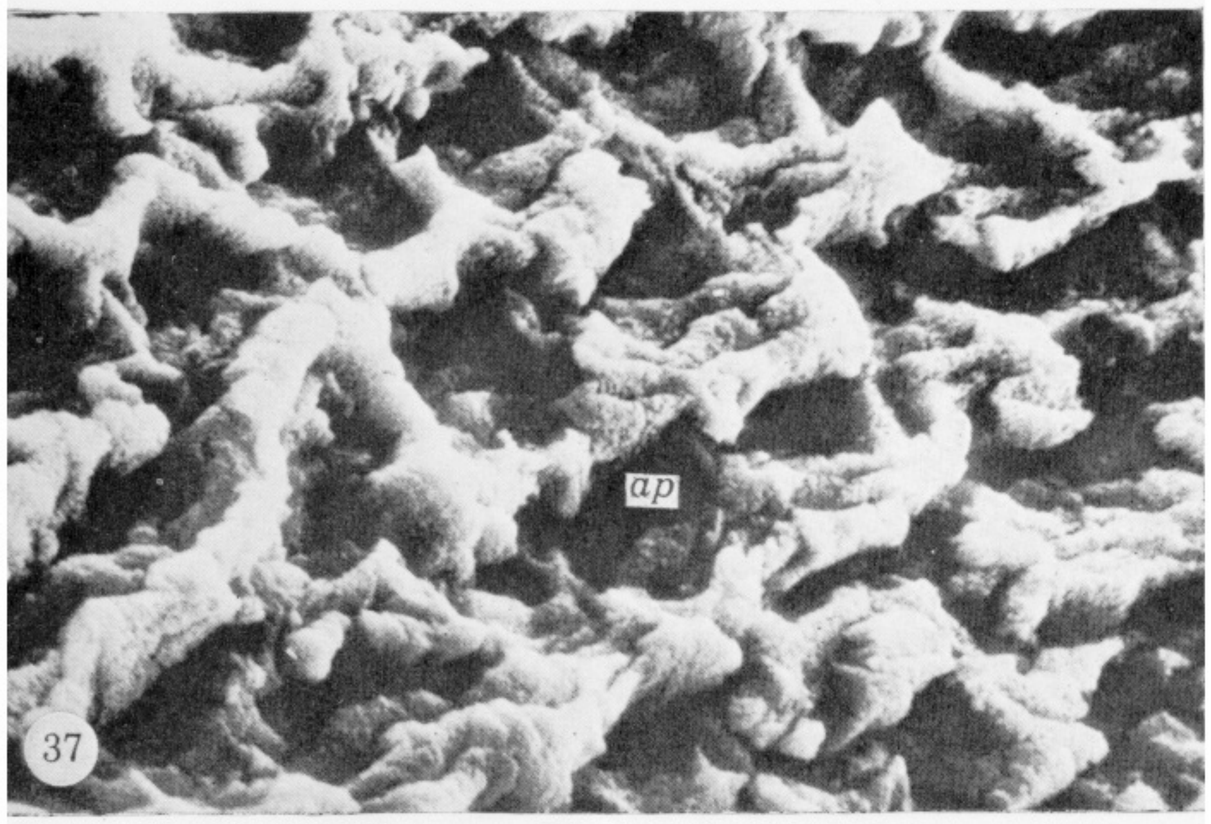

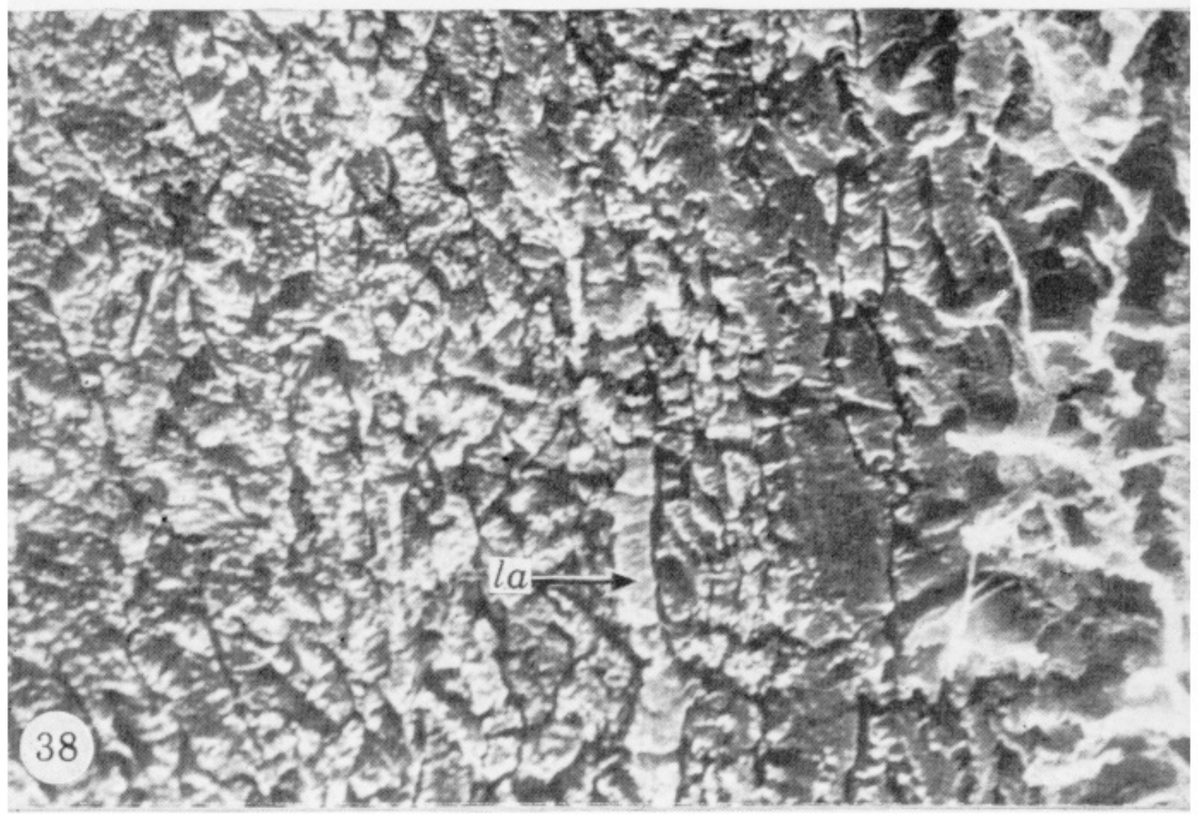

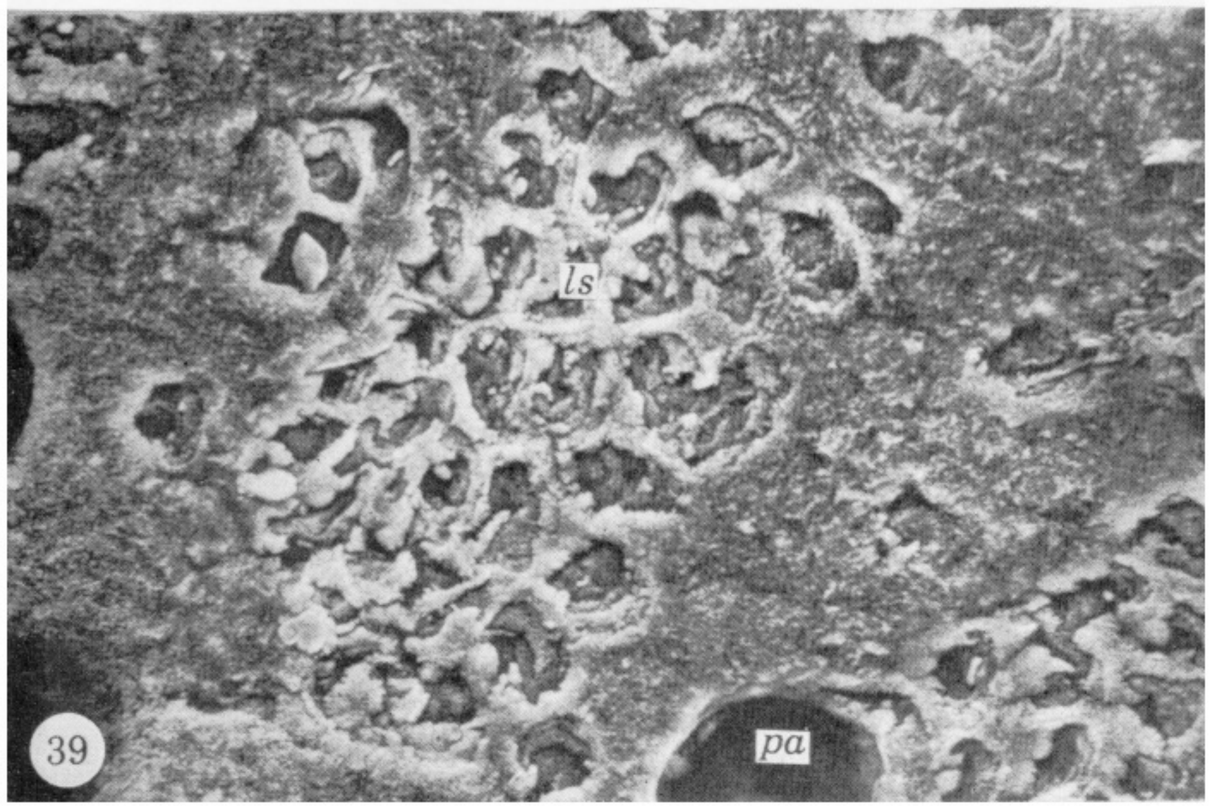

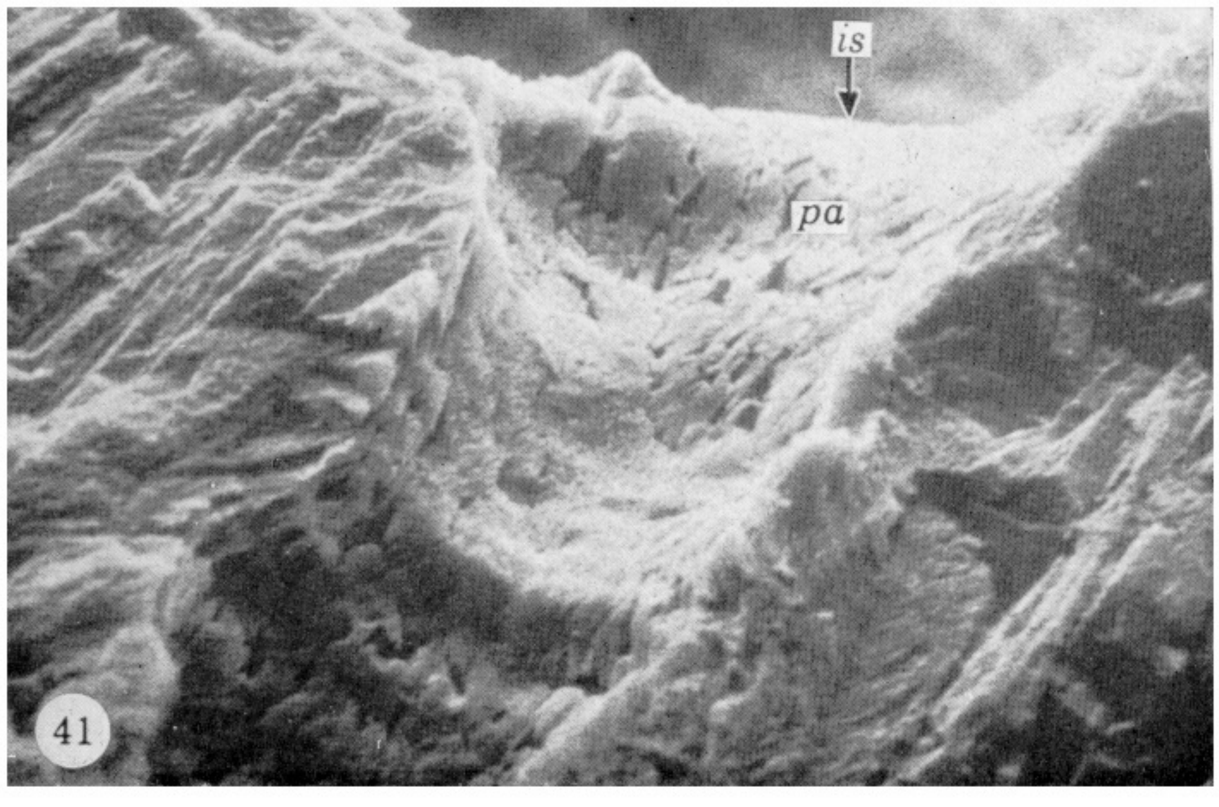

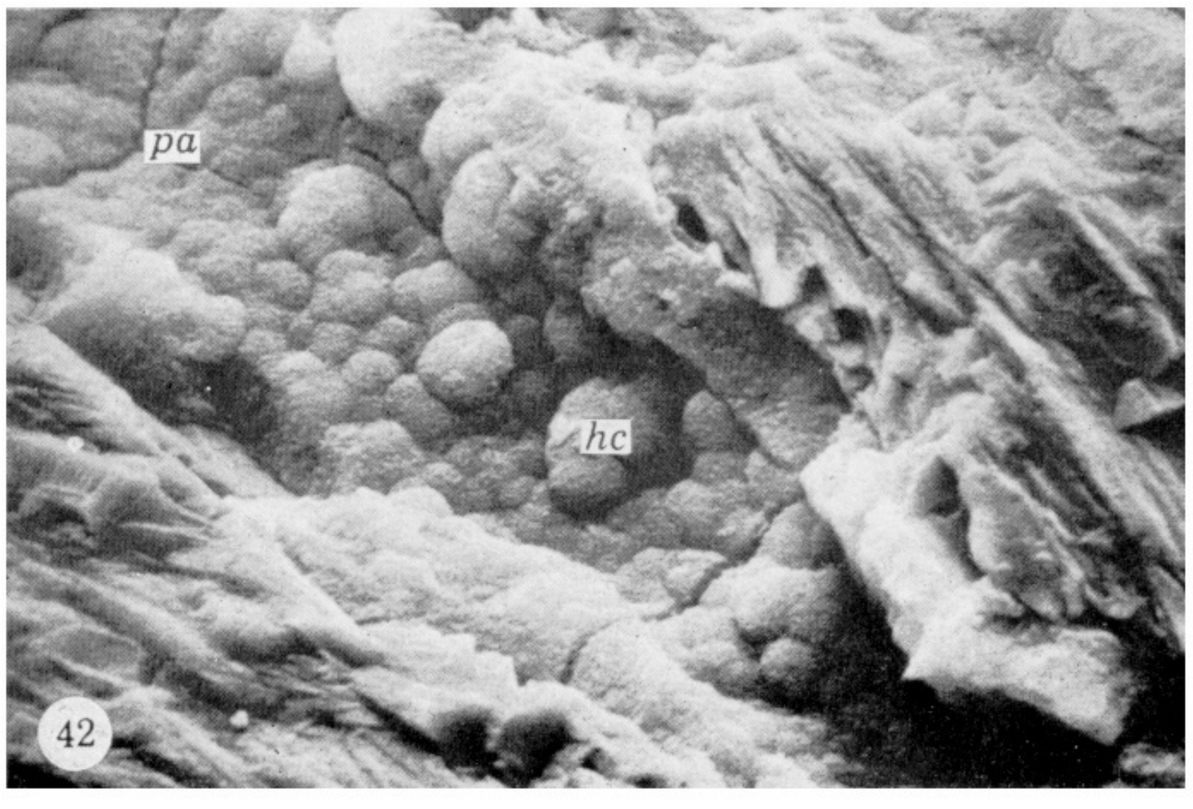

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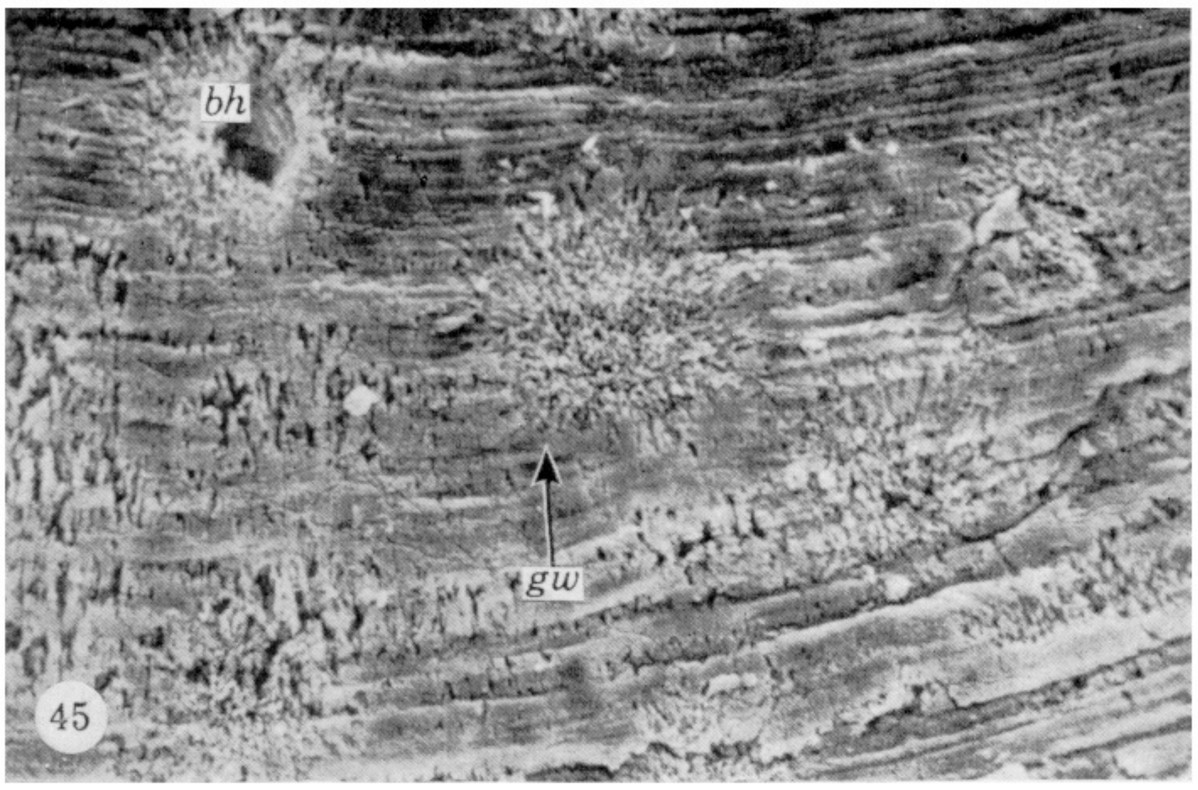

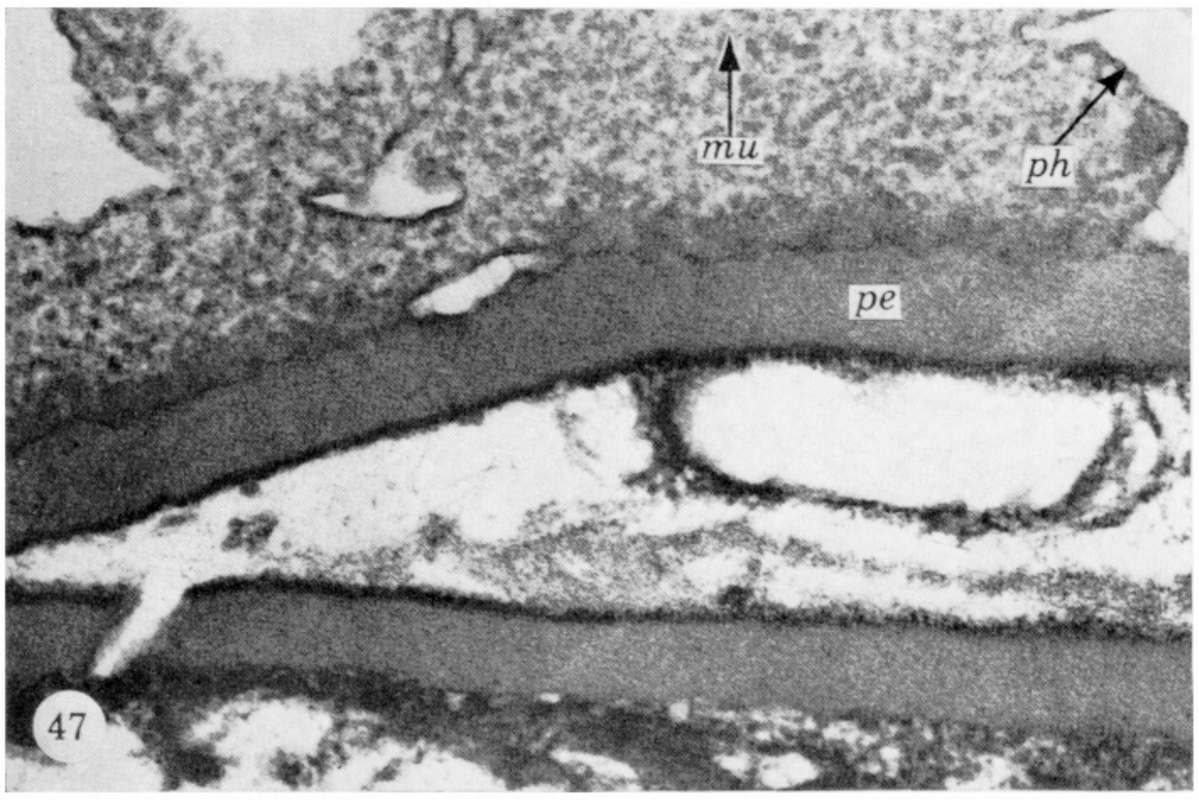

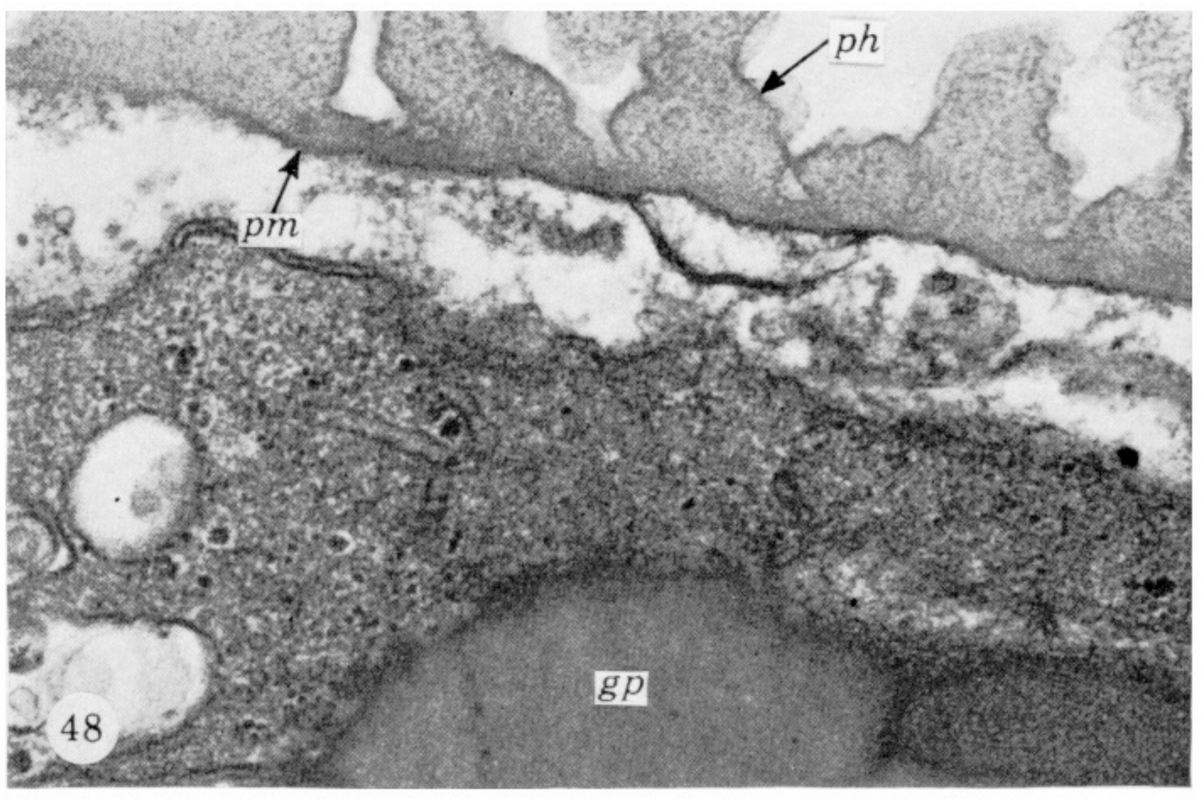

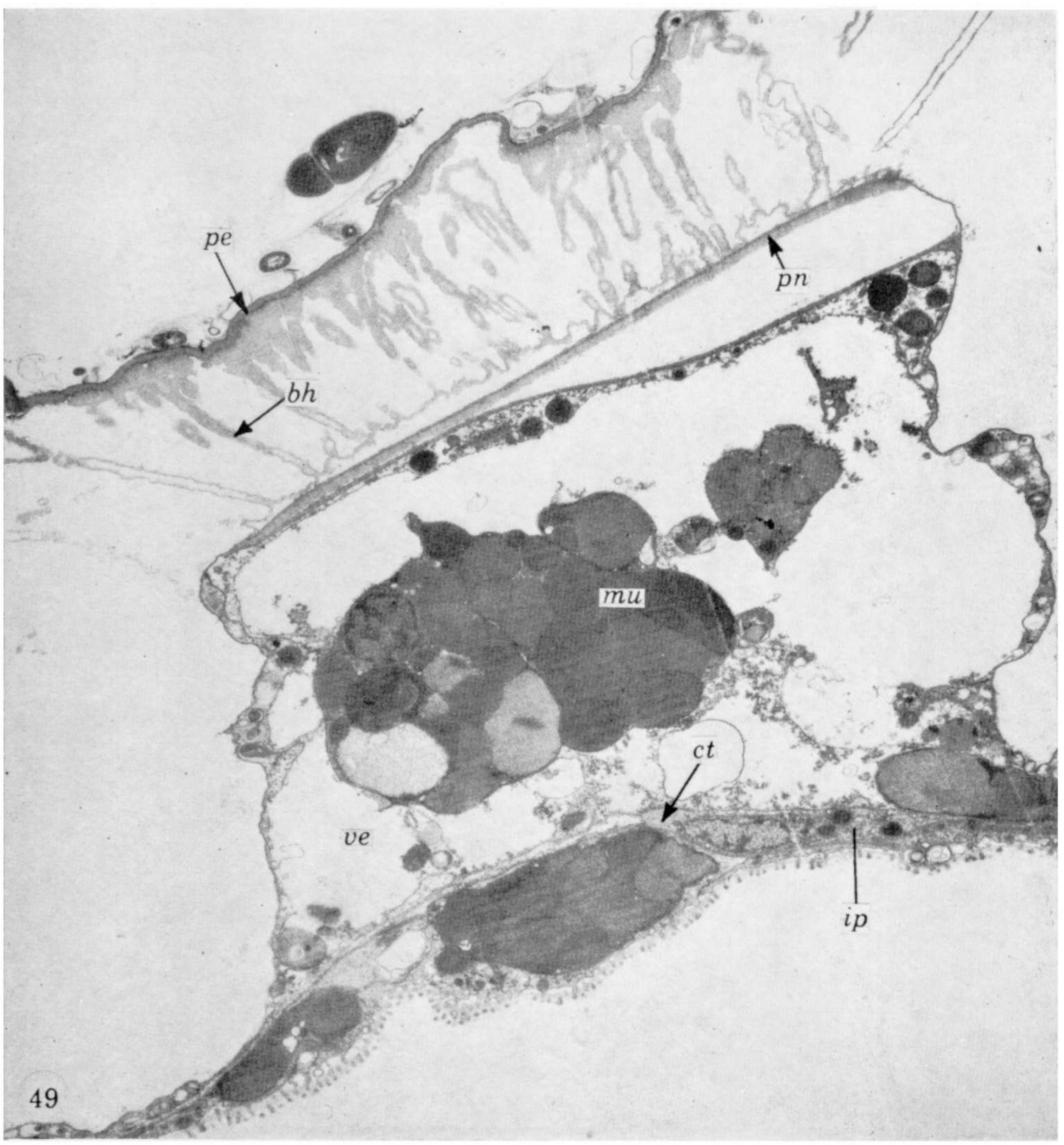

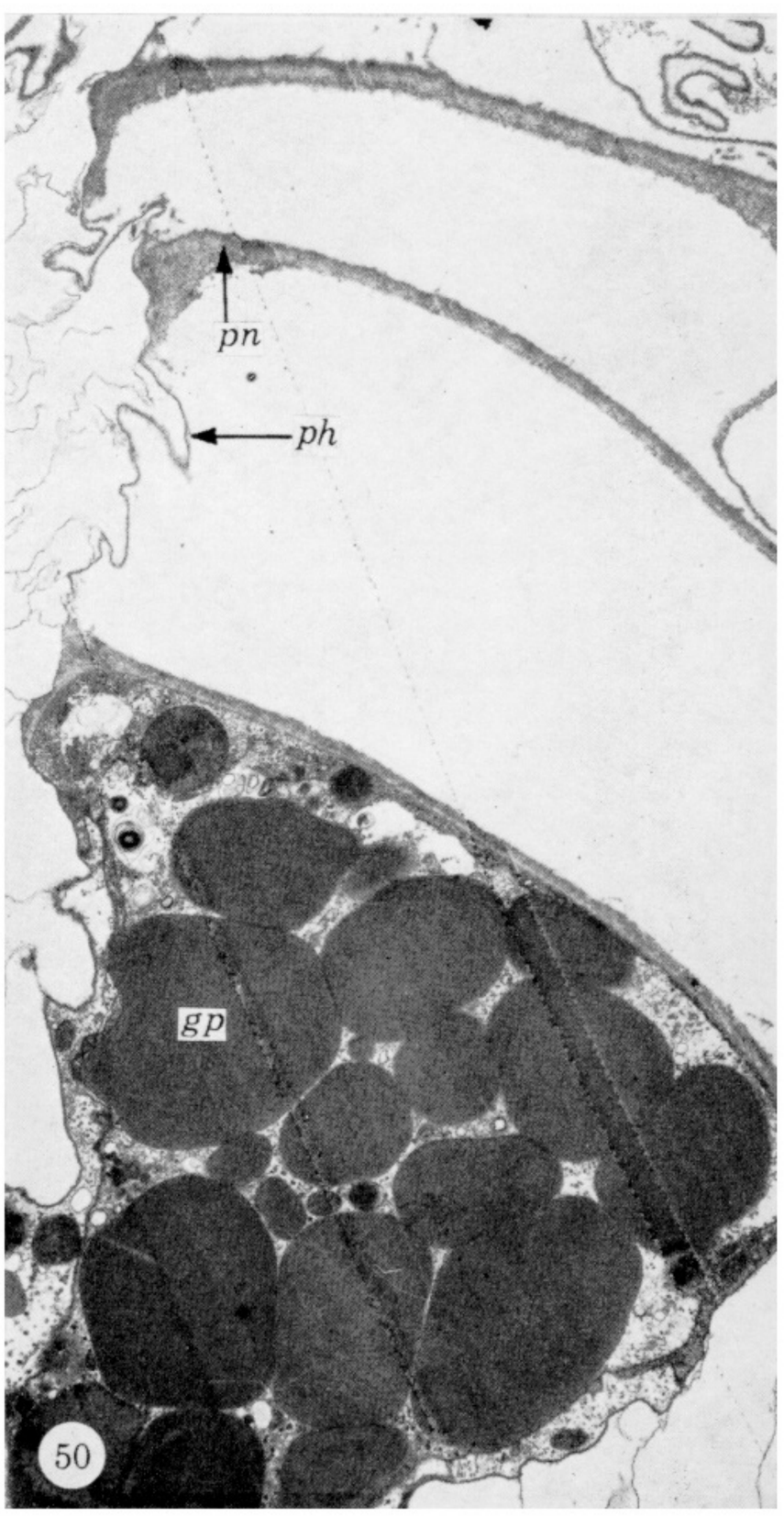

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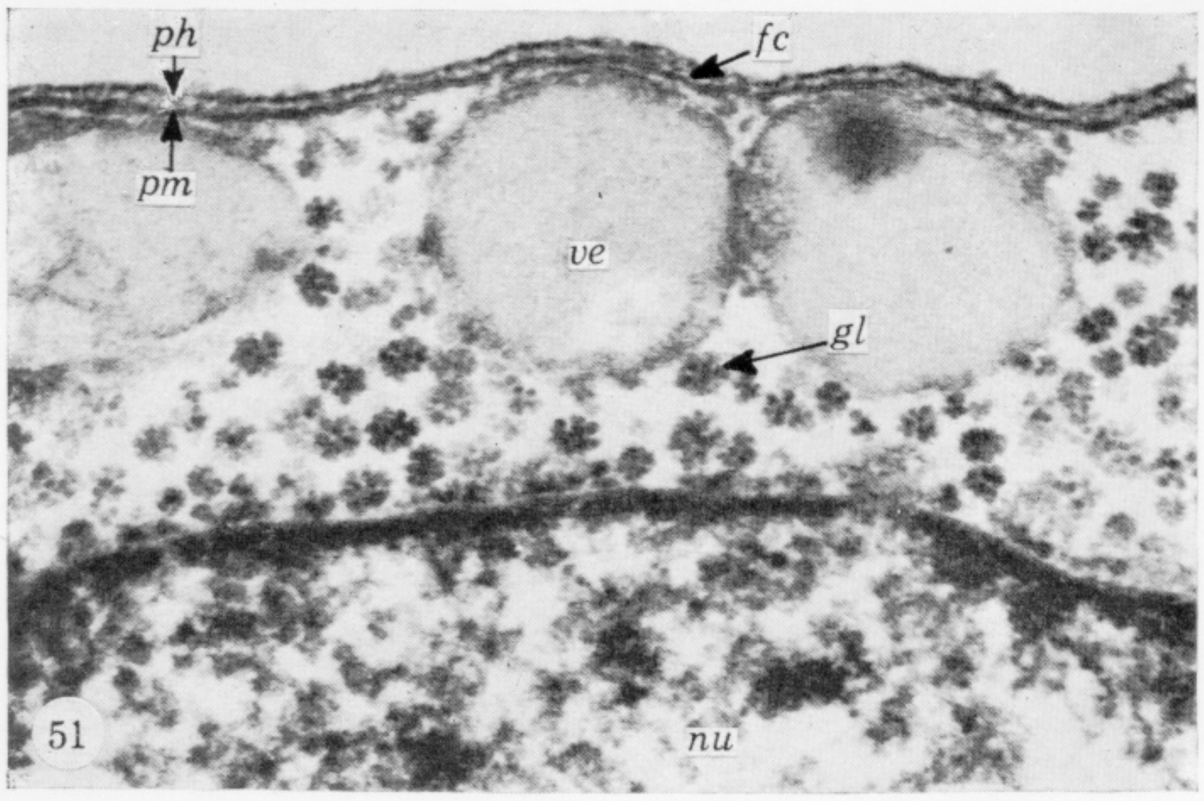
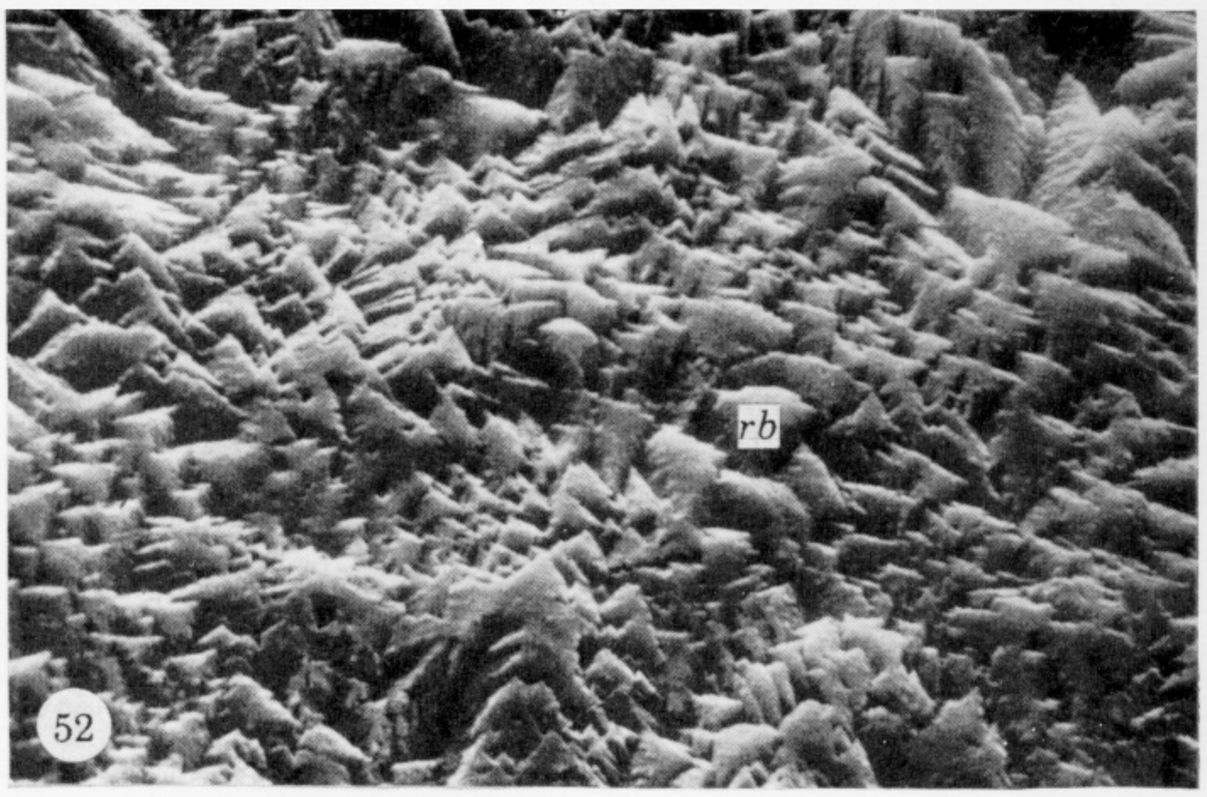
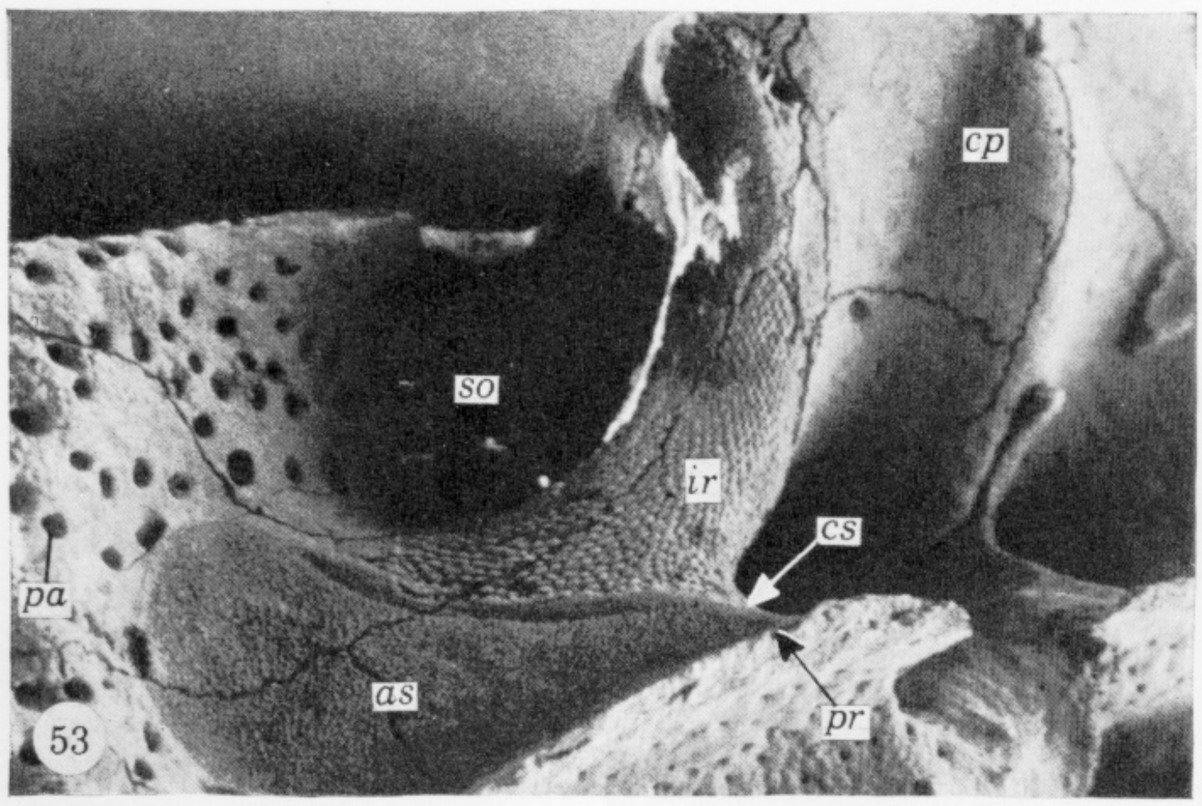
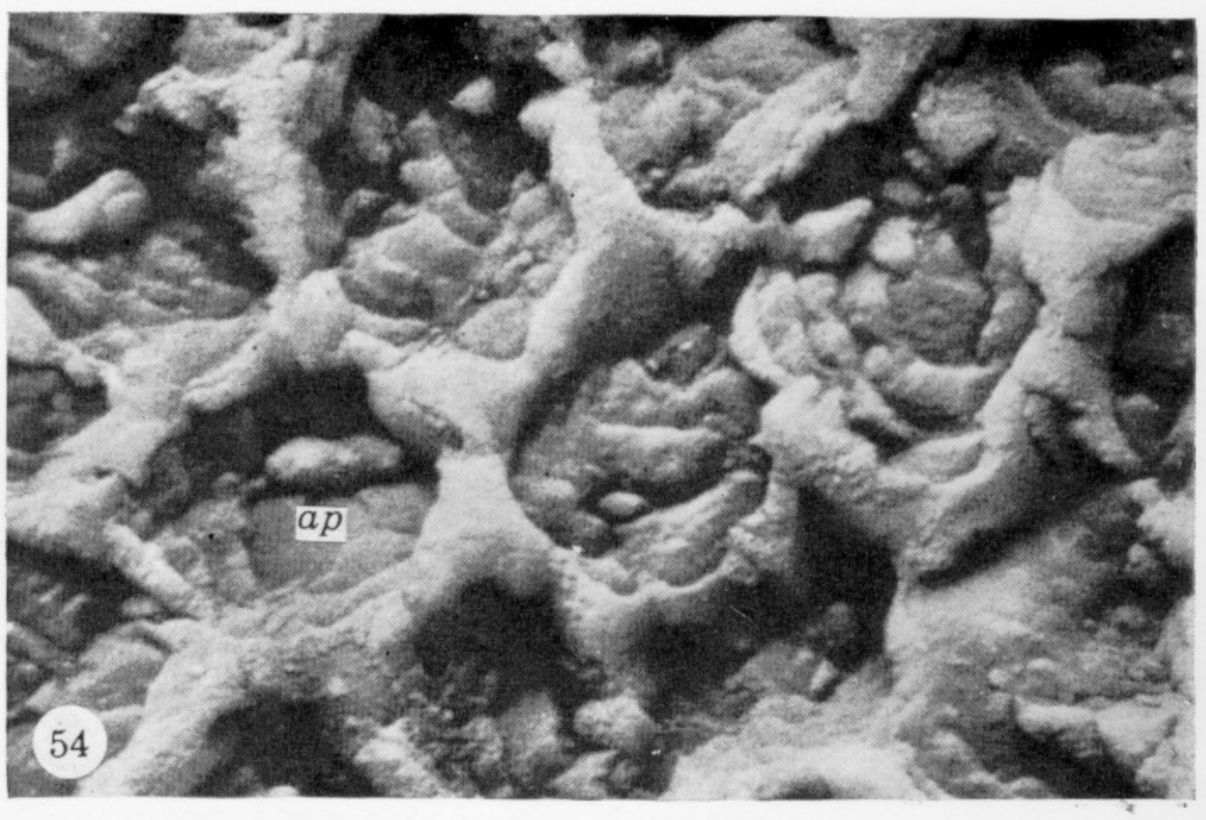
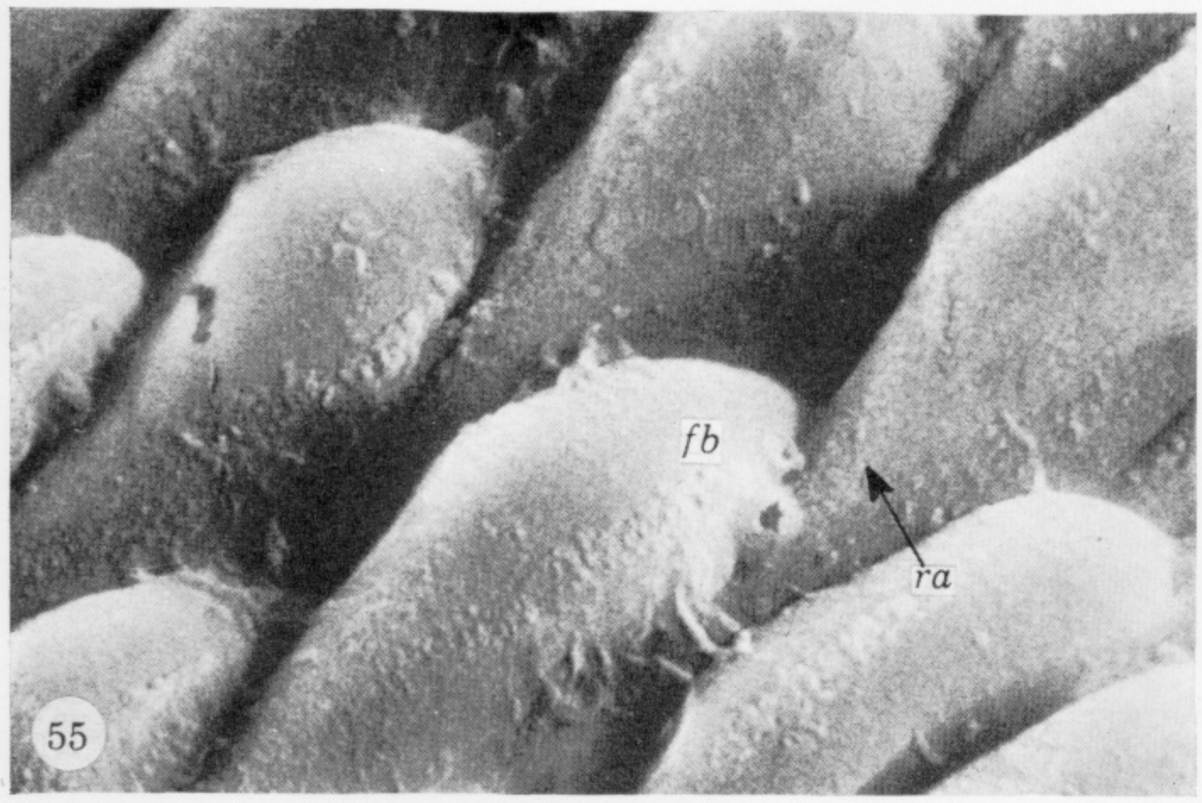
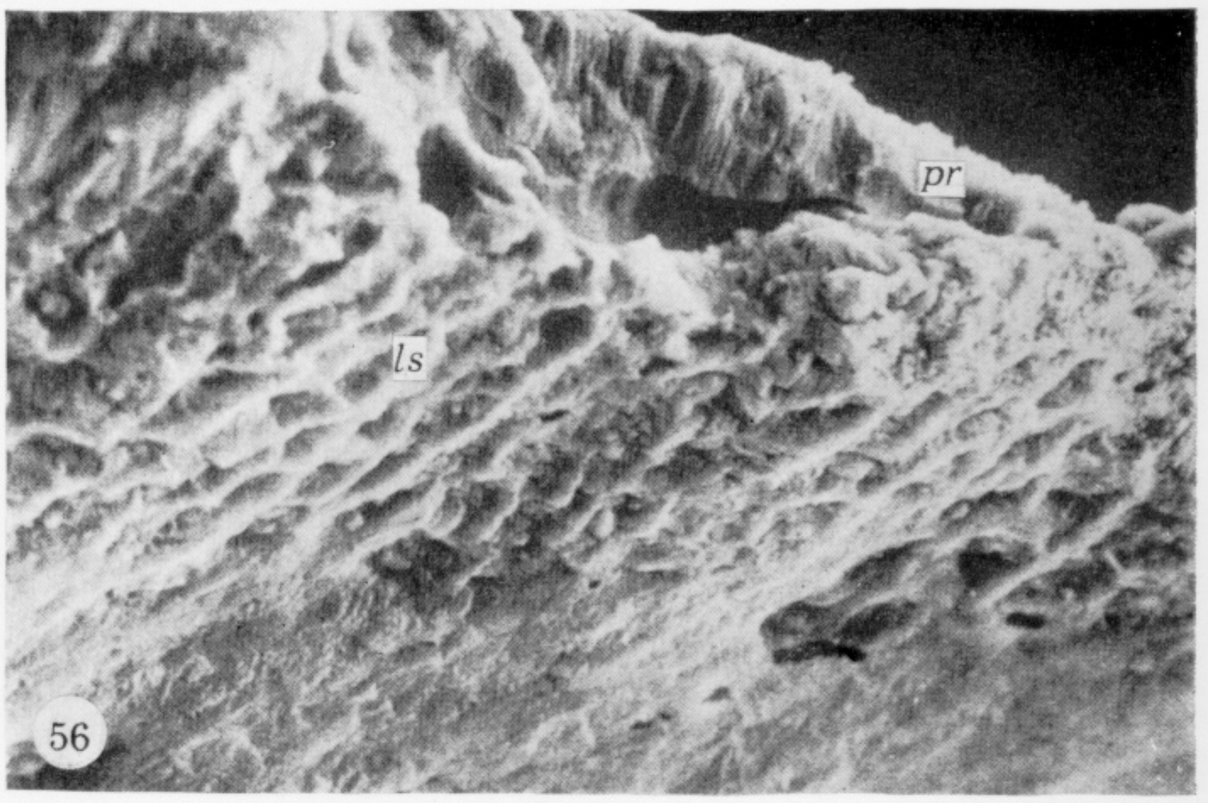


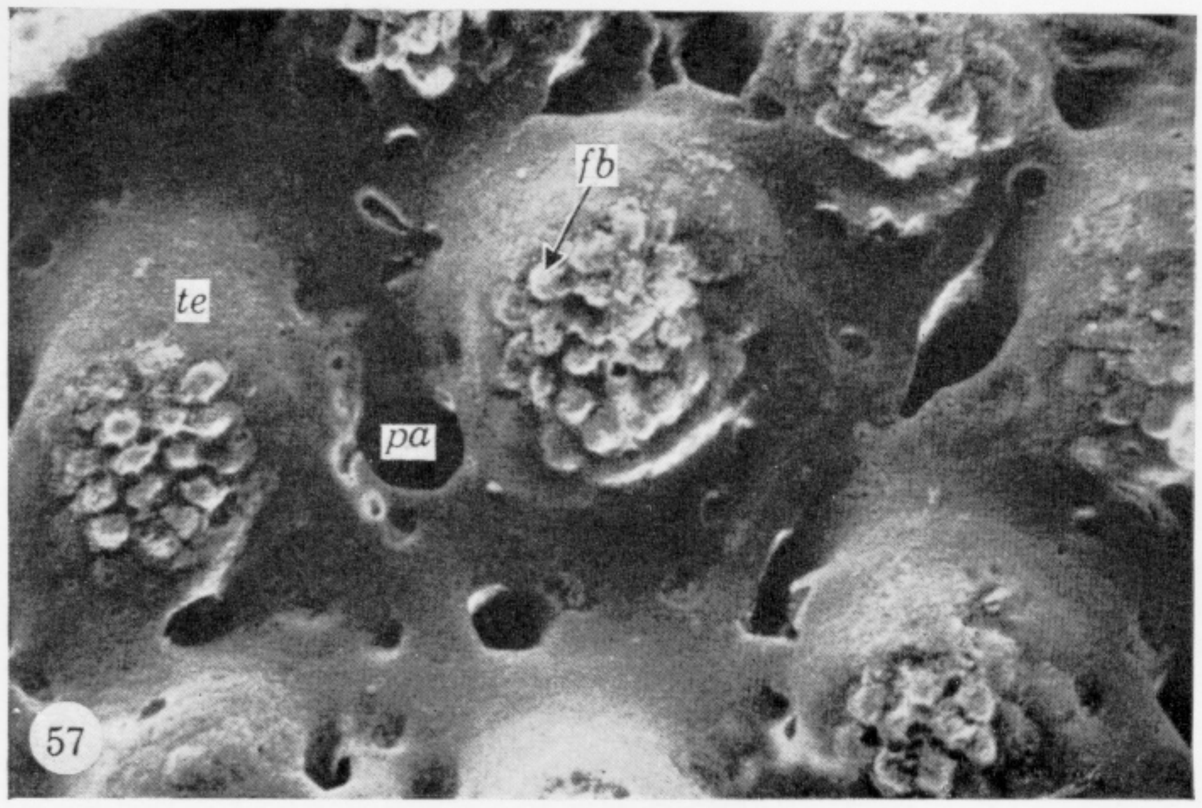


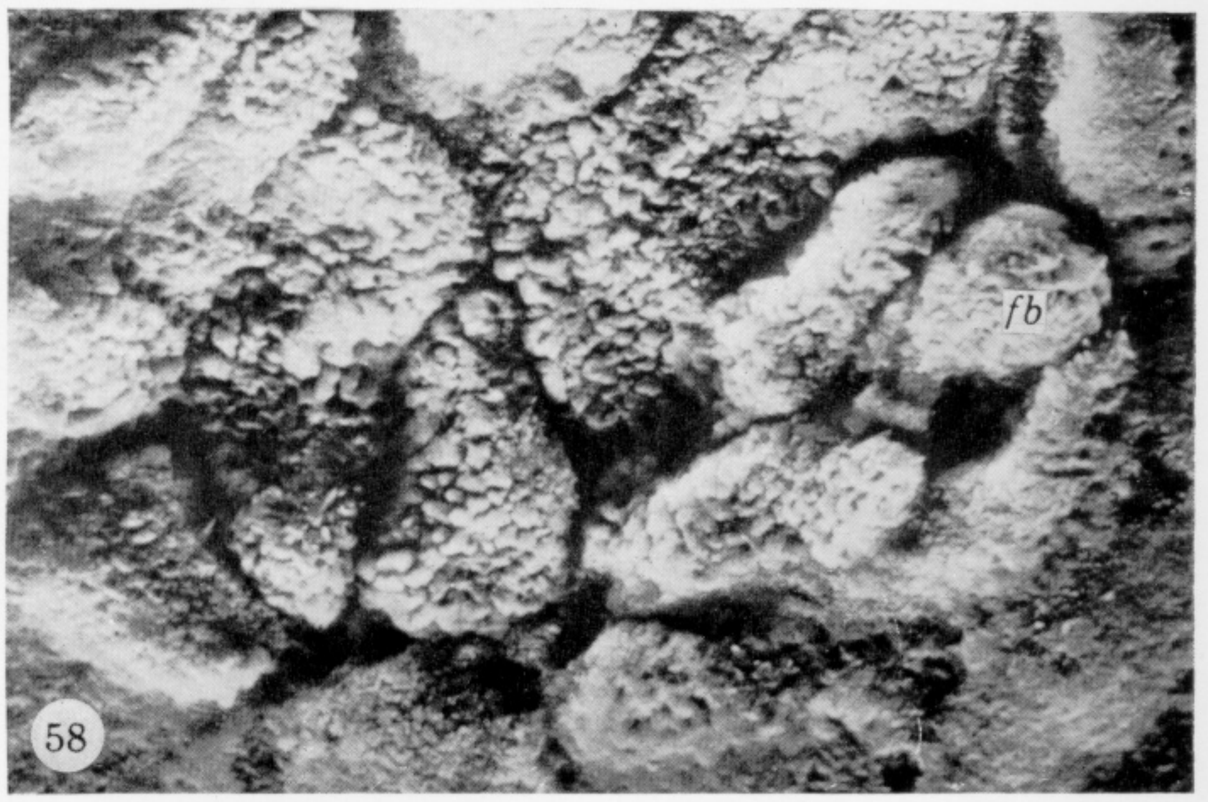




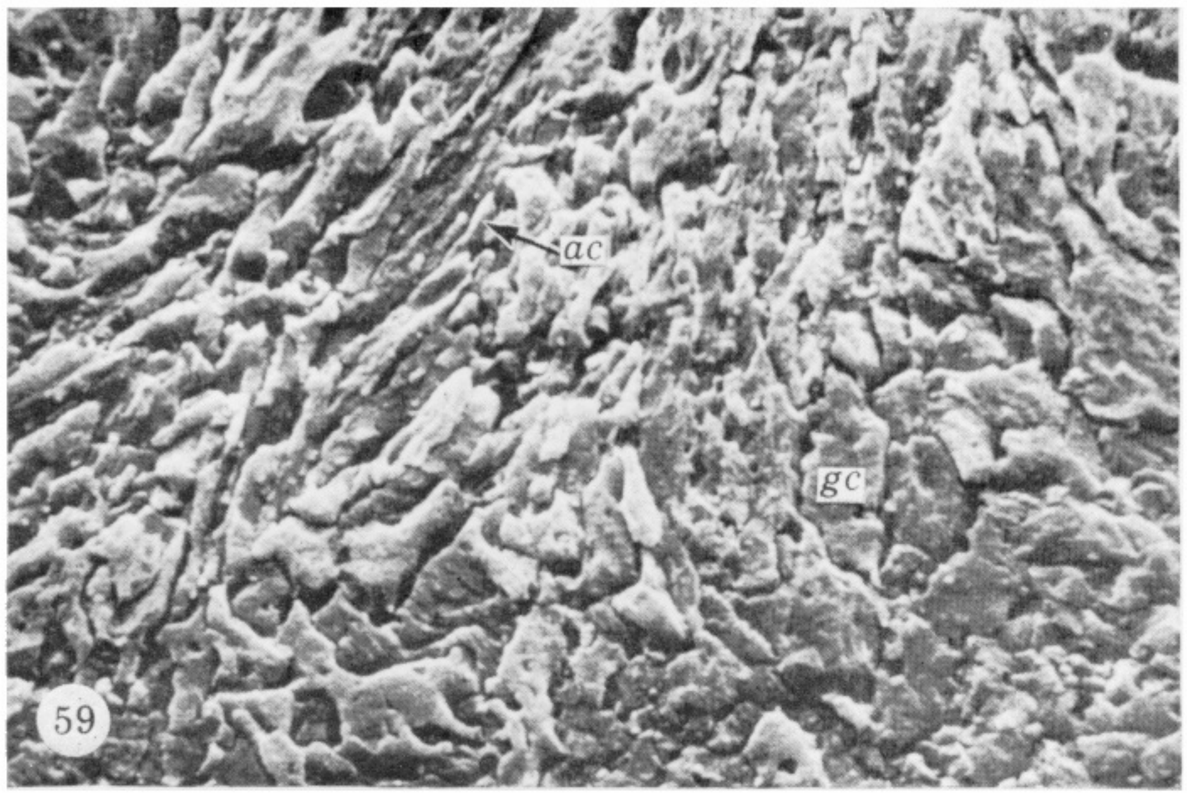


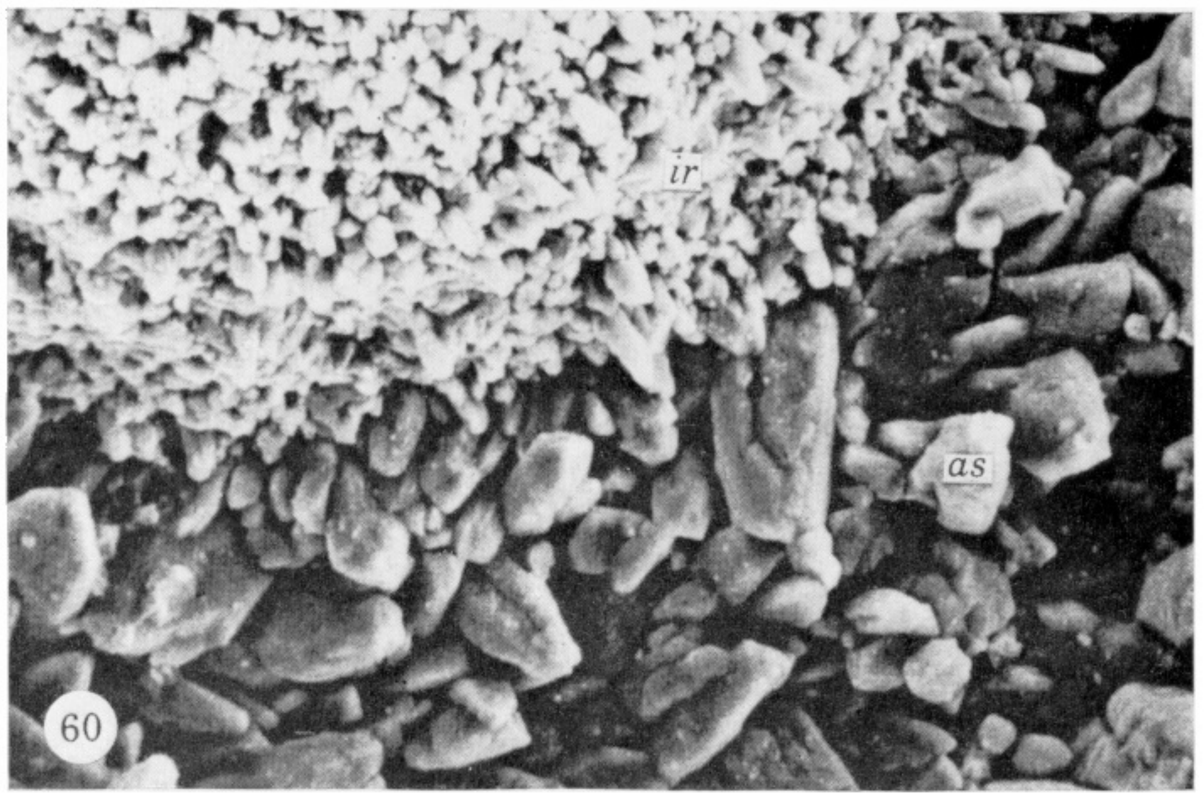


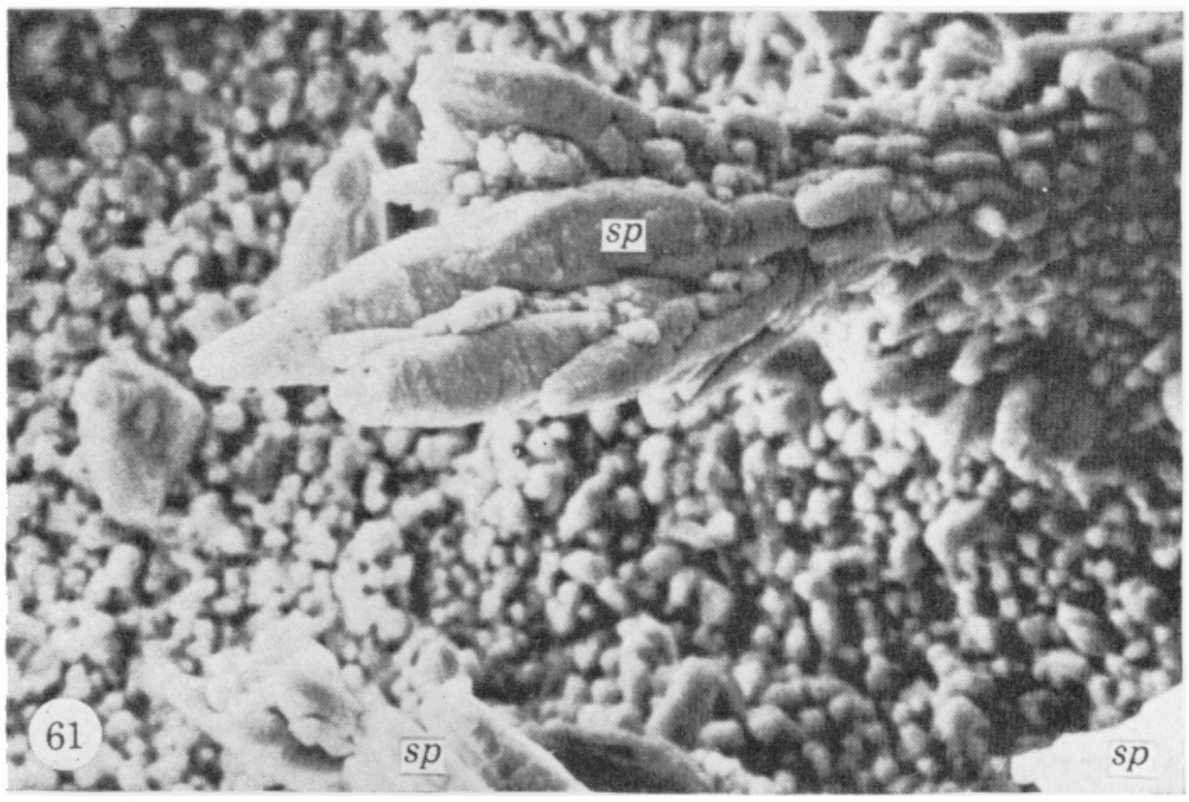


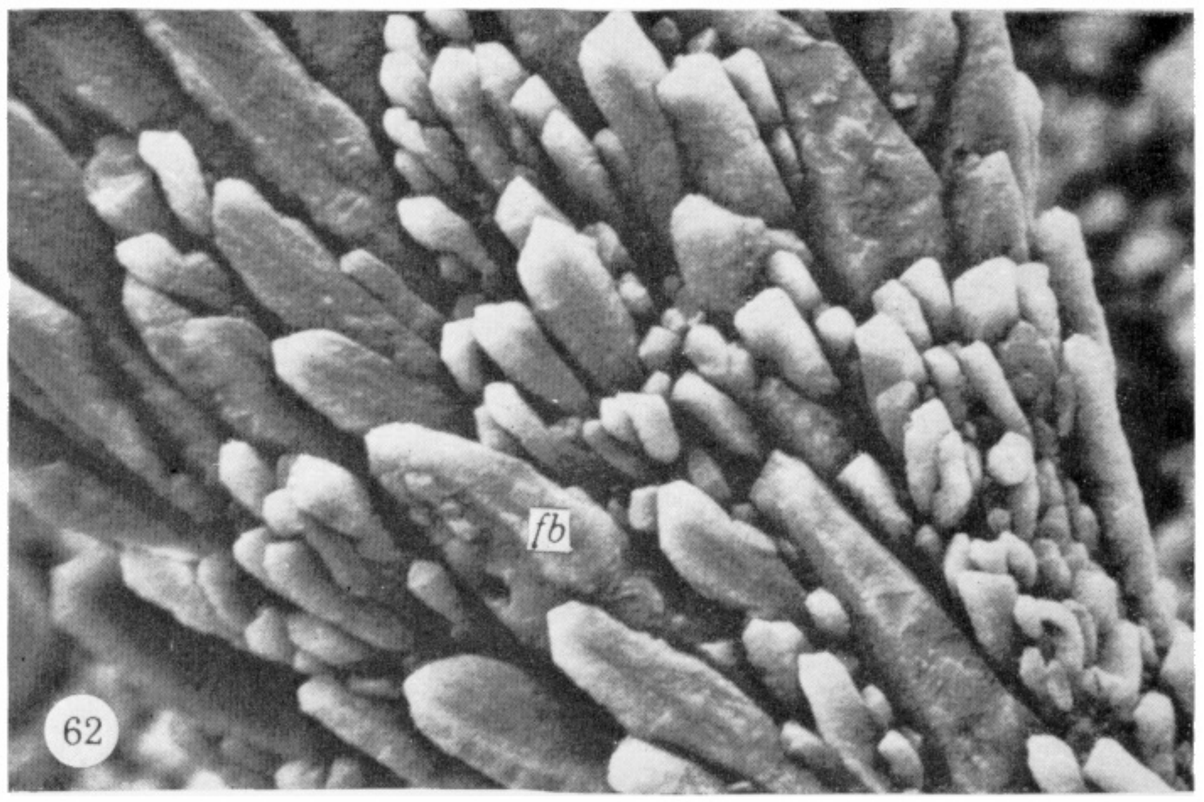


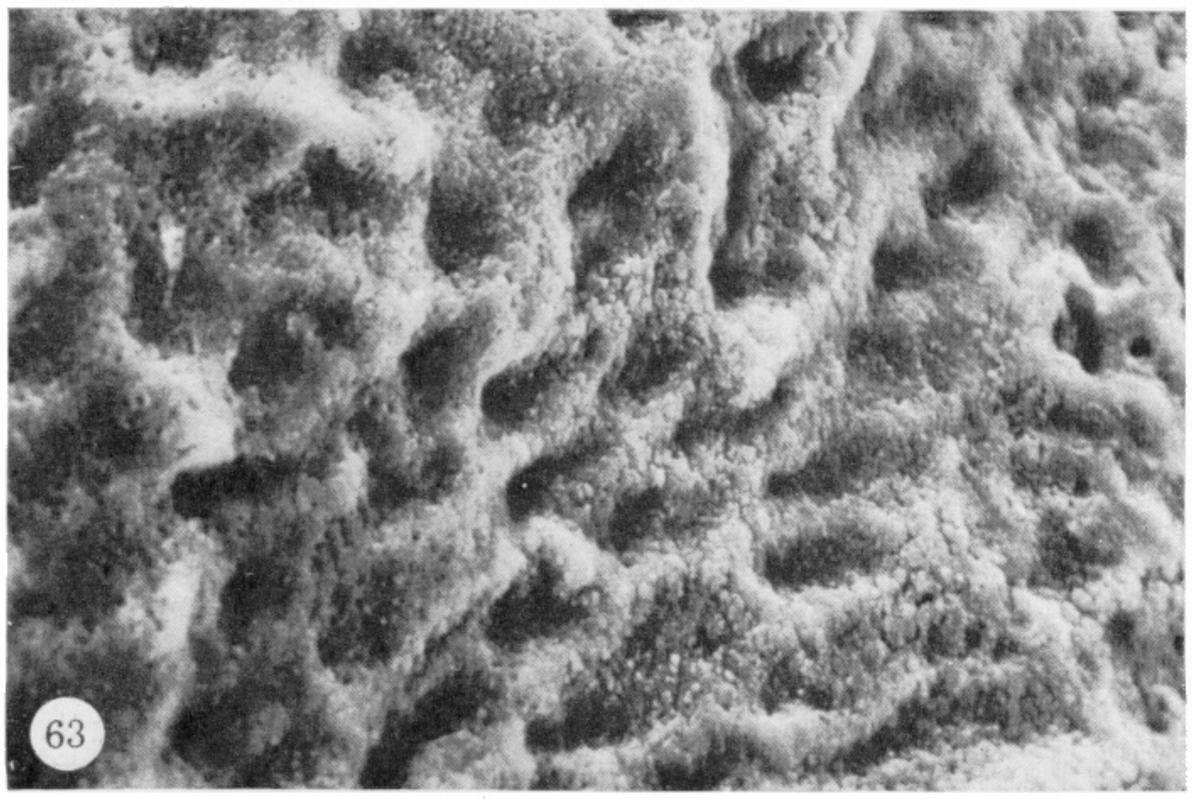
FIGURES 51 TO 58. For legends see facing page.

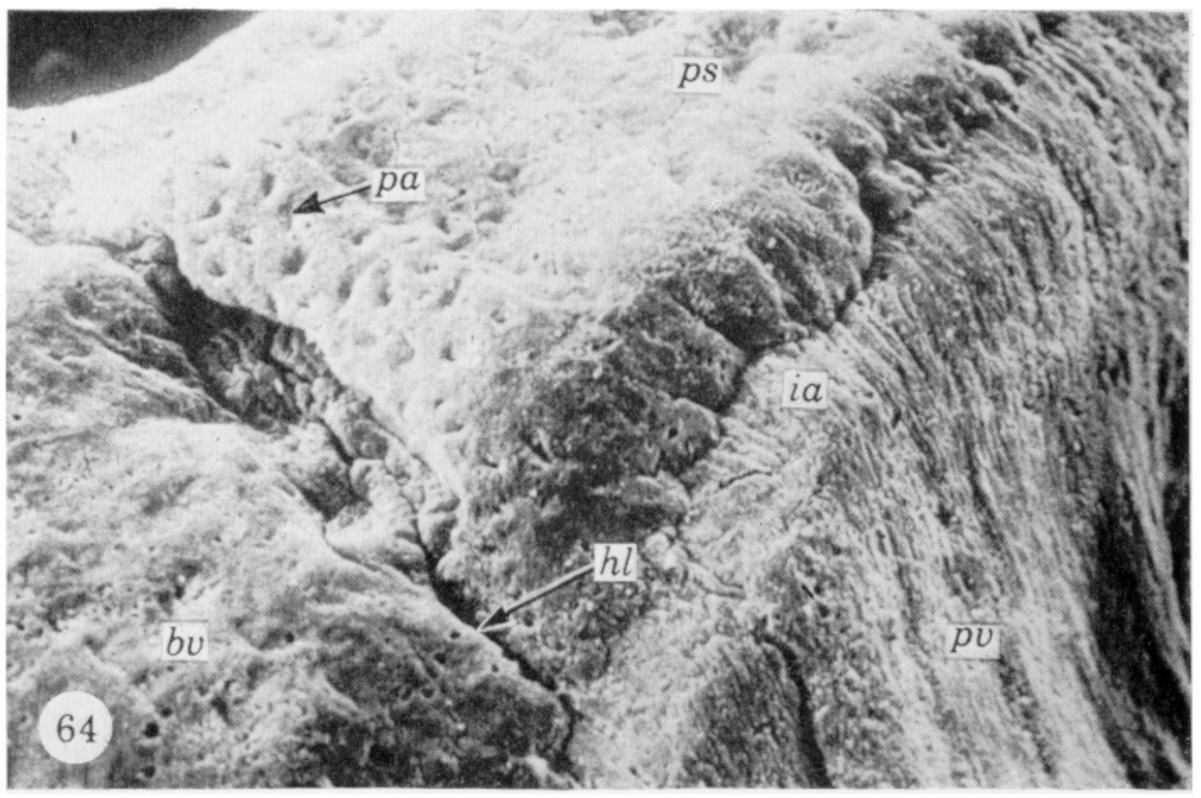


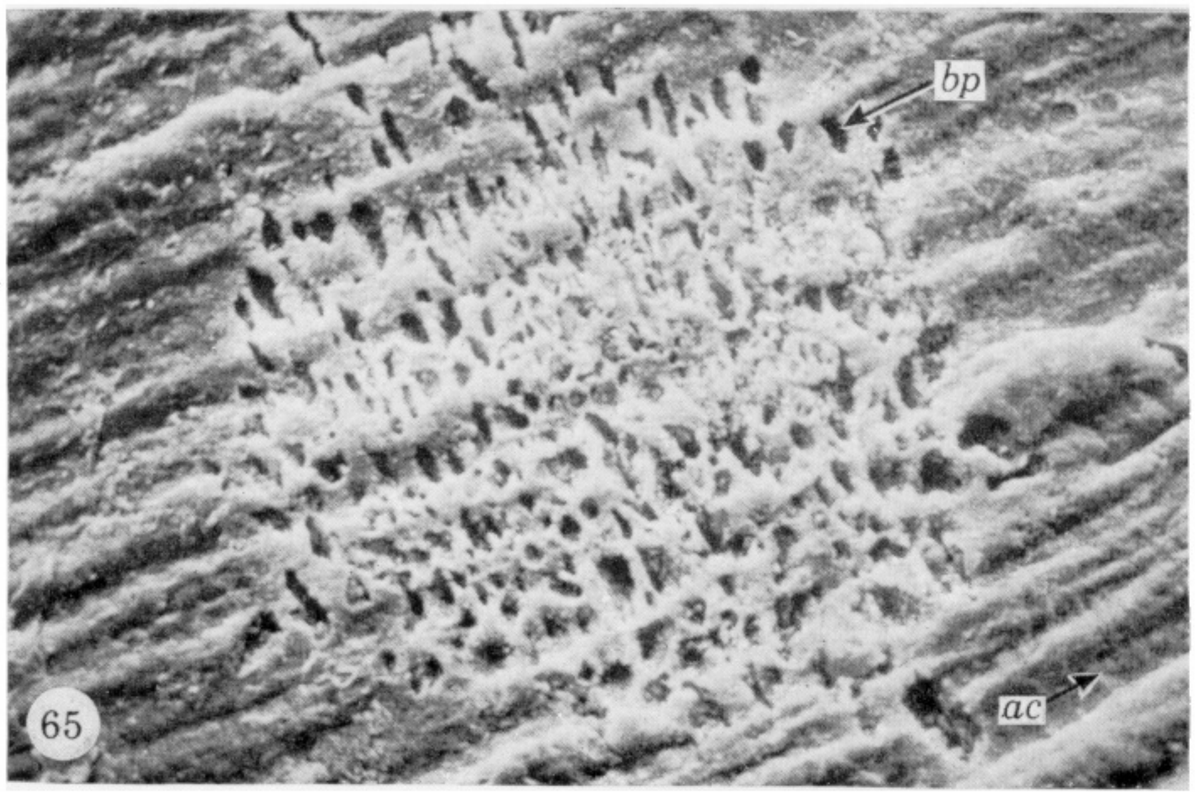


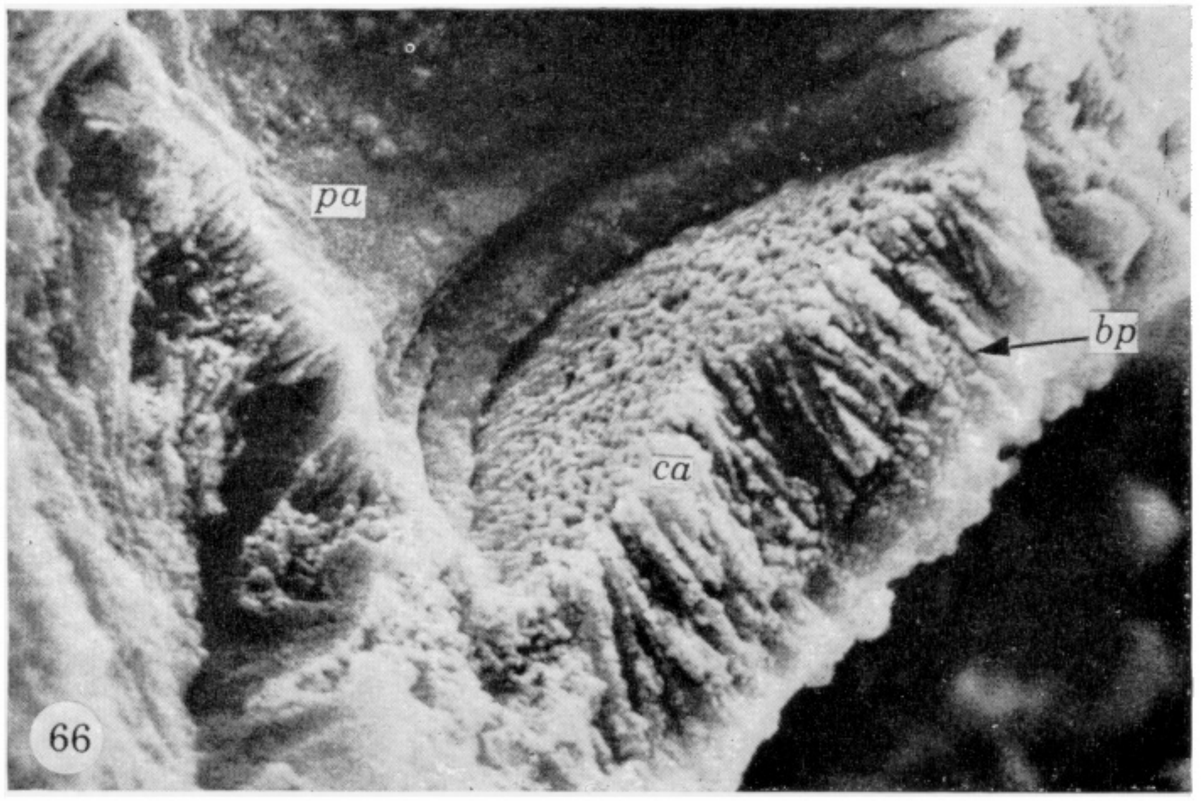




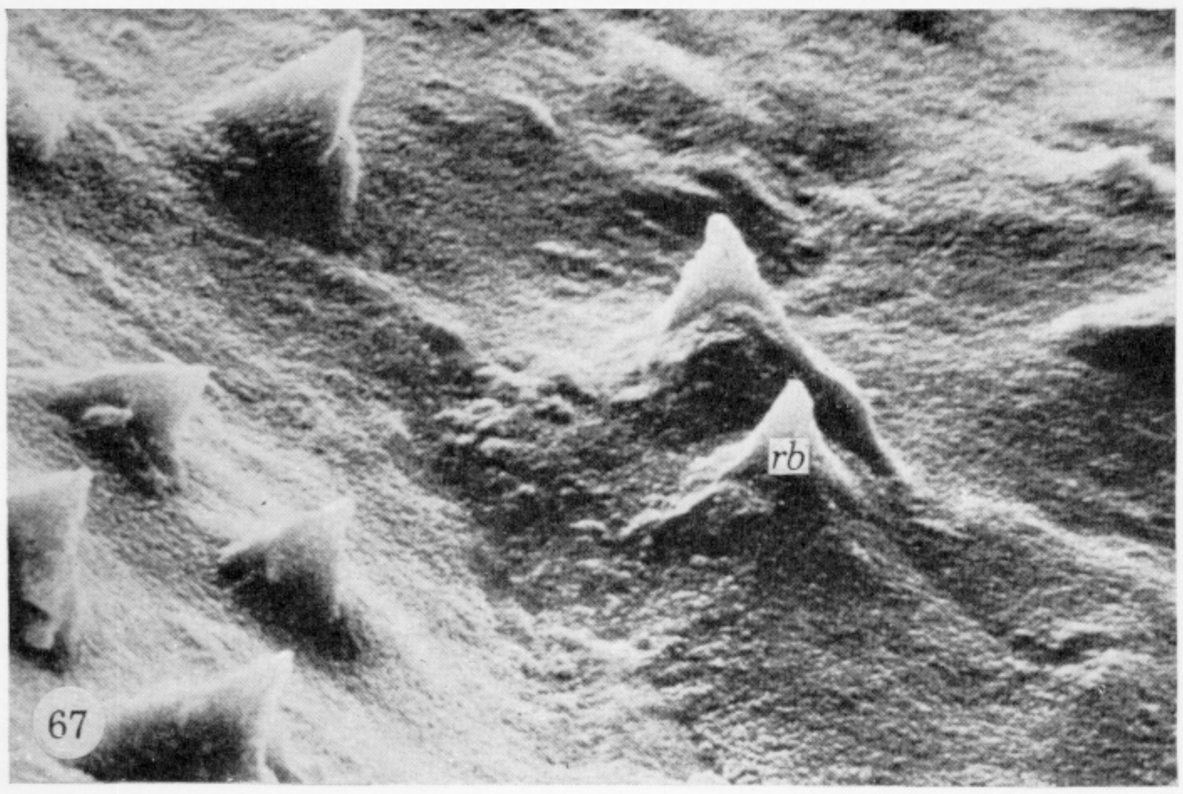


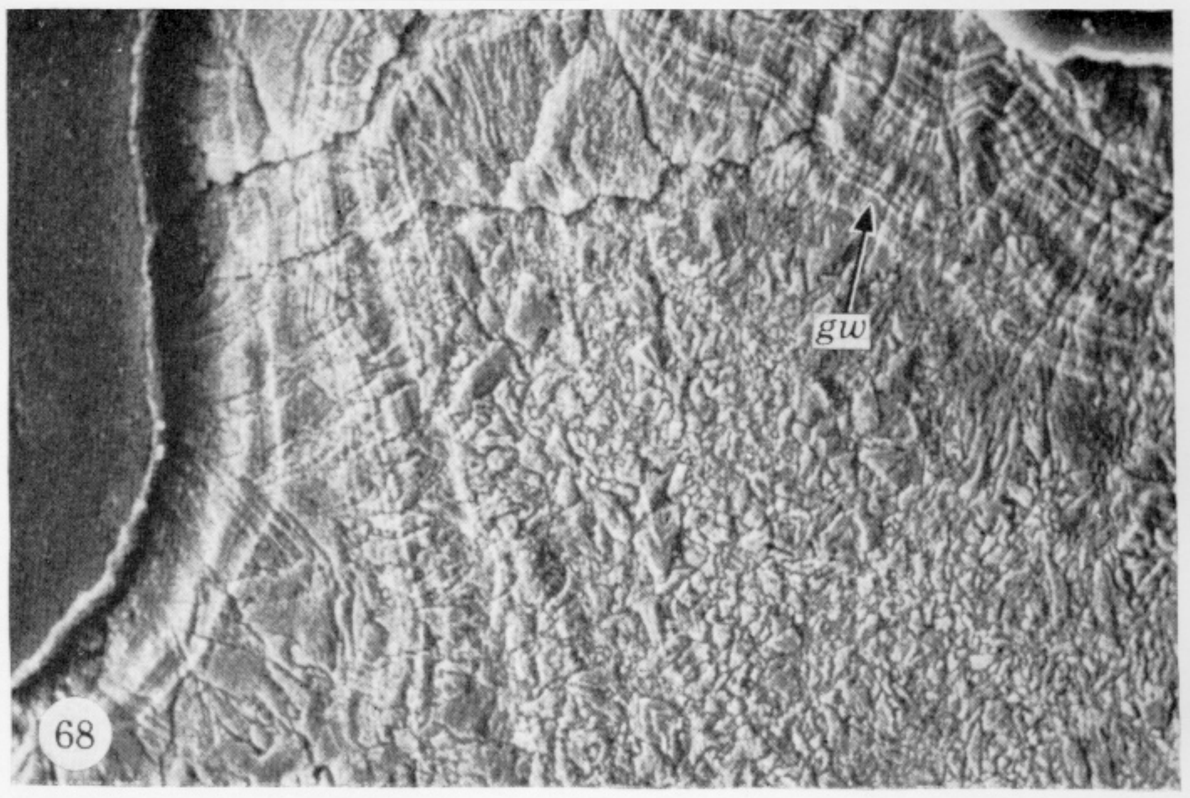


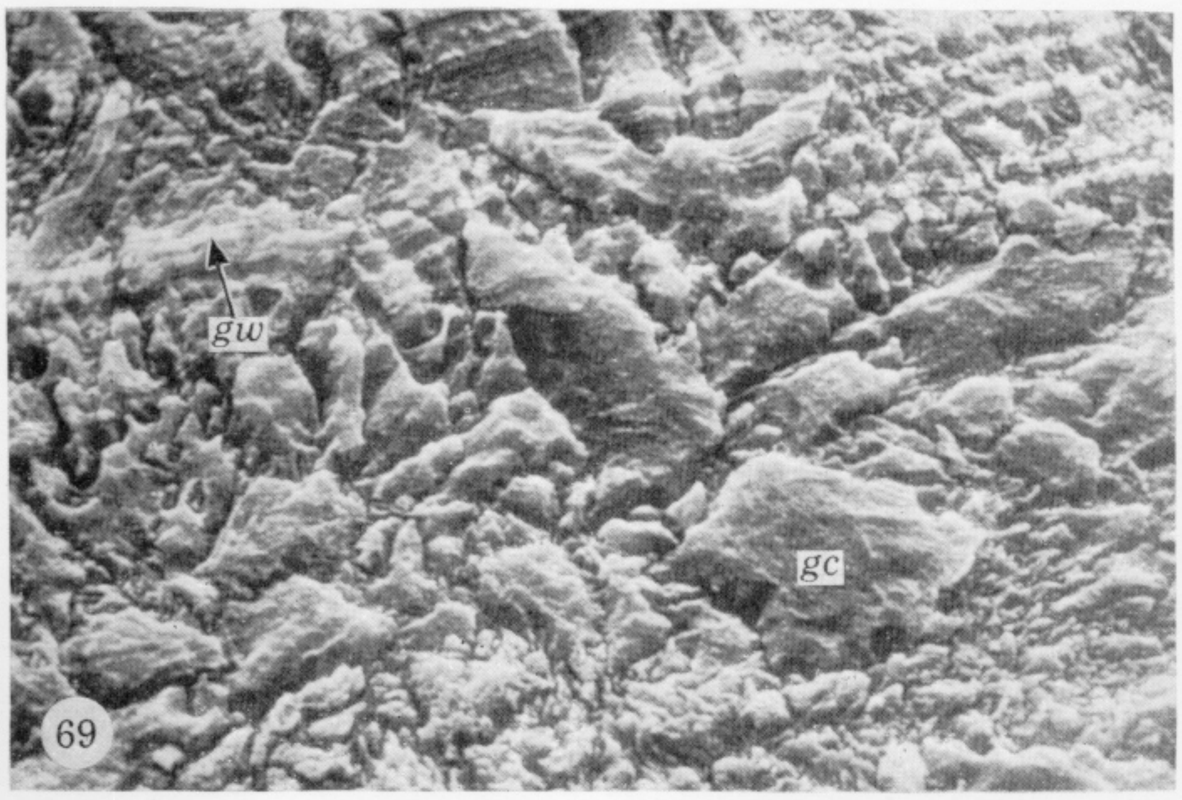


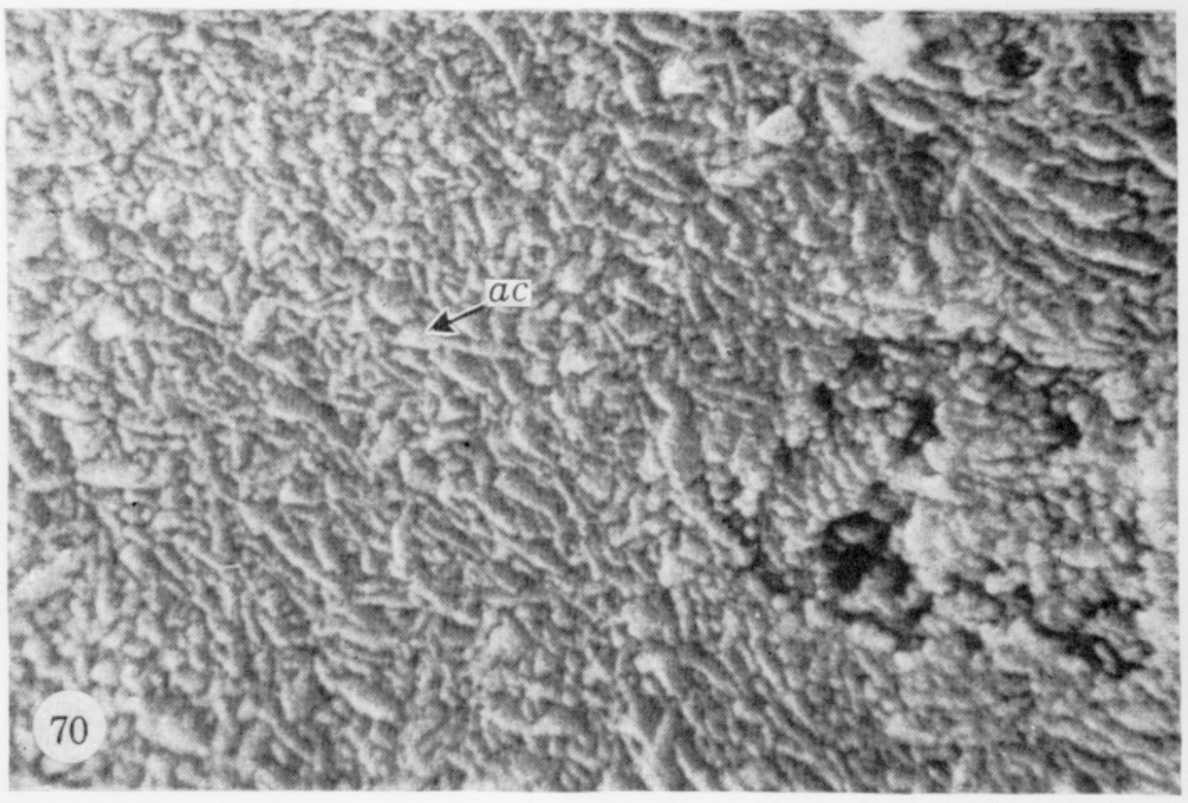


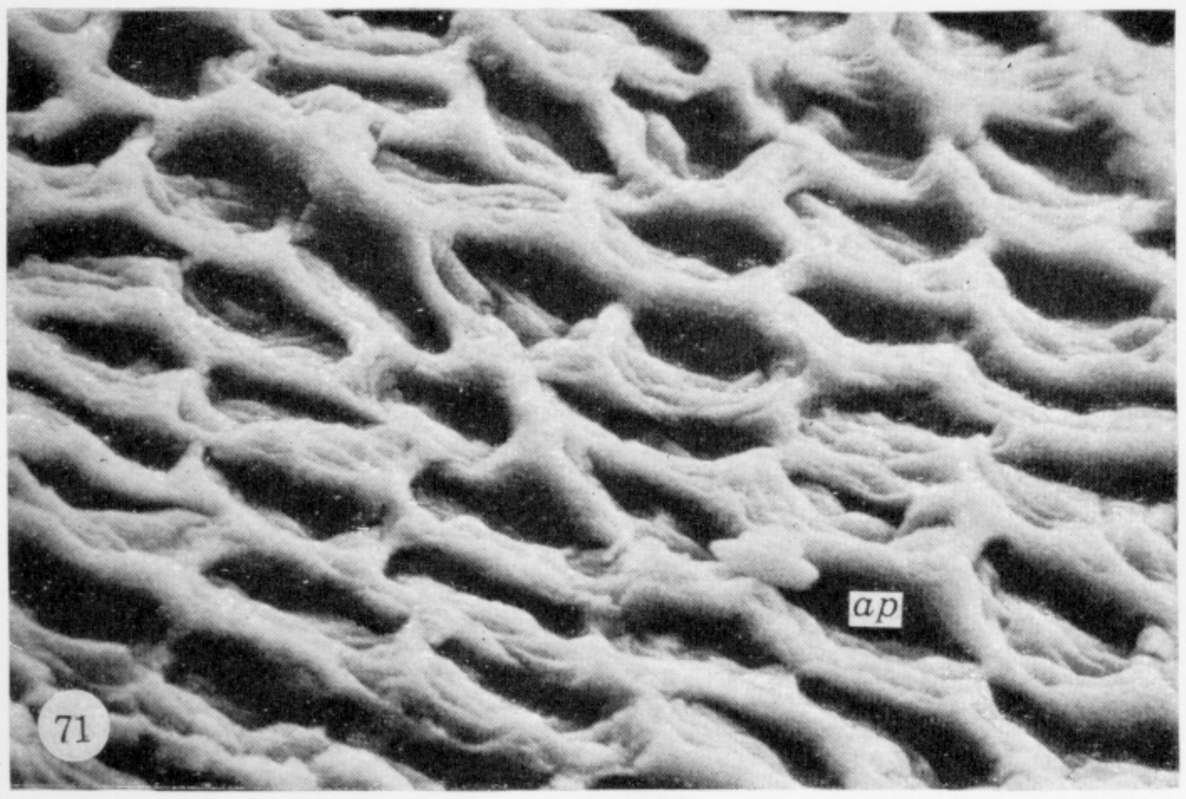
FIGURES 59 TO 66. For legends see facing page.

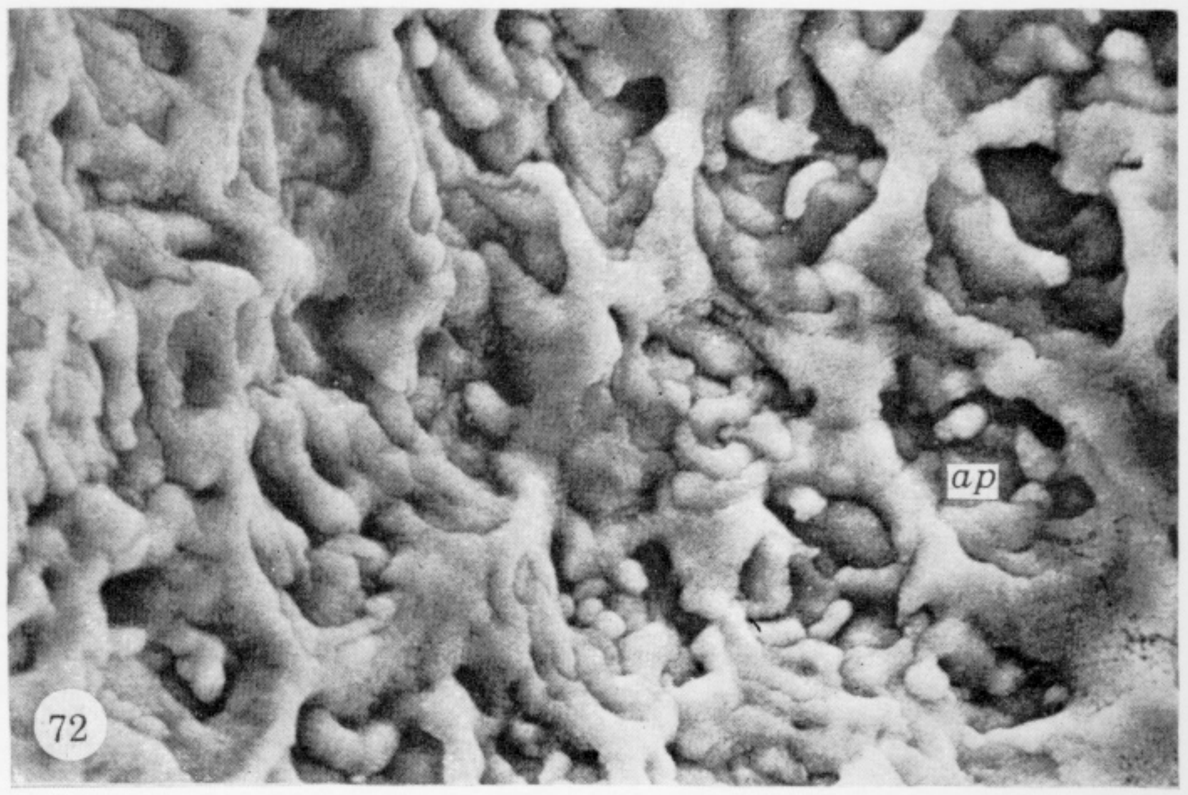


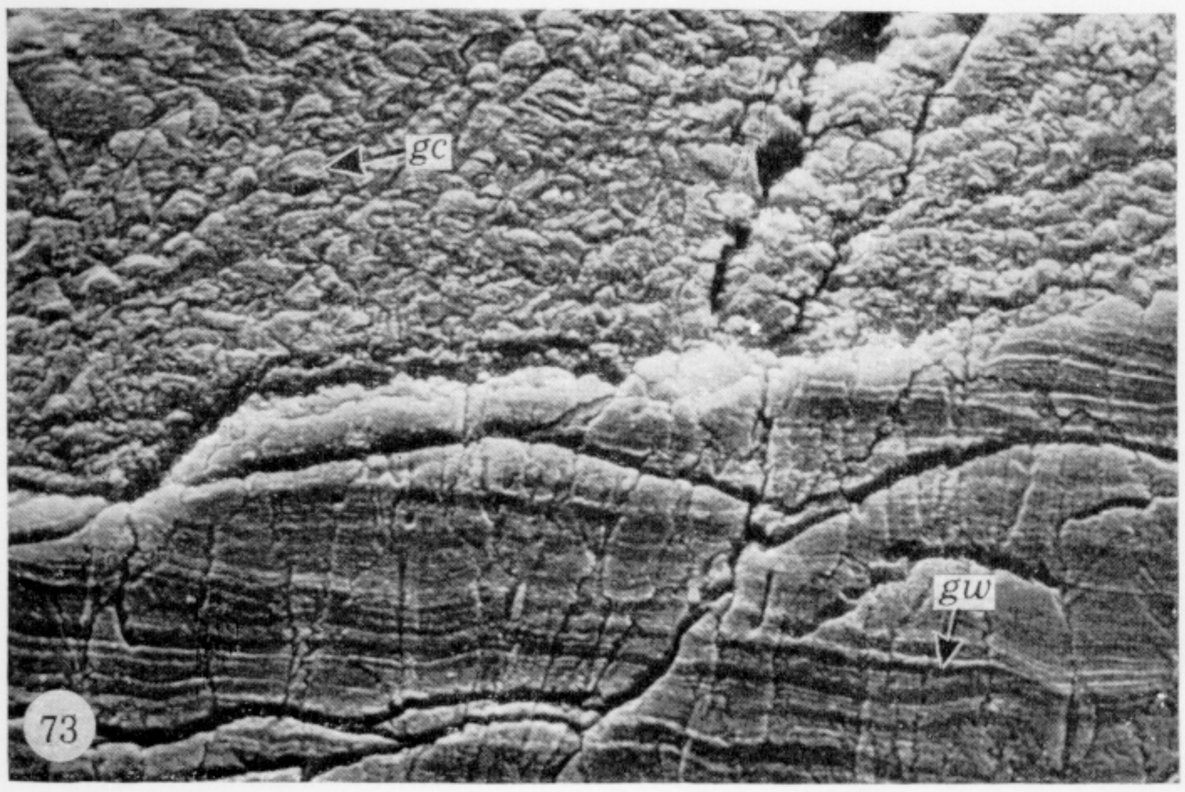












FIGURES 67 TO 74. For legends see facing page.

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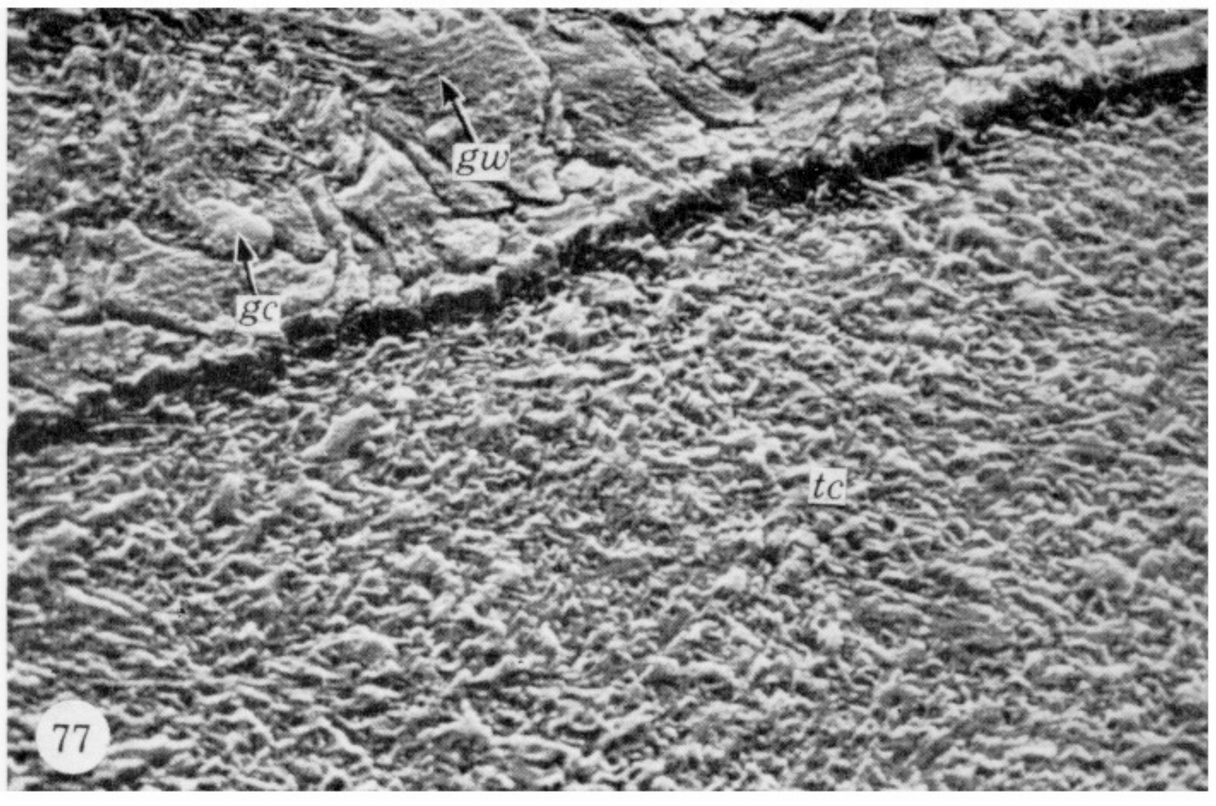
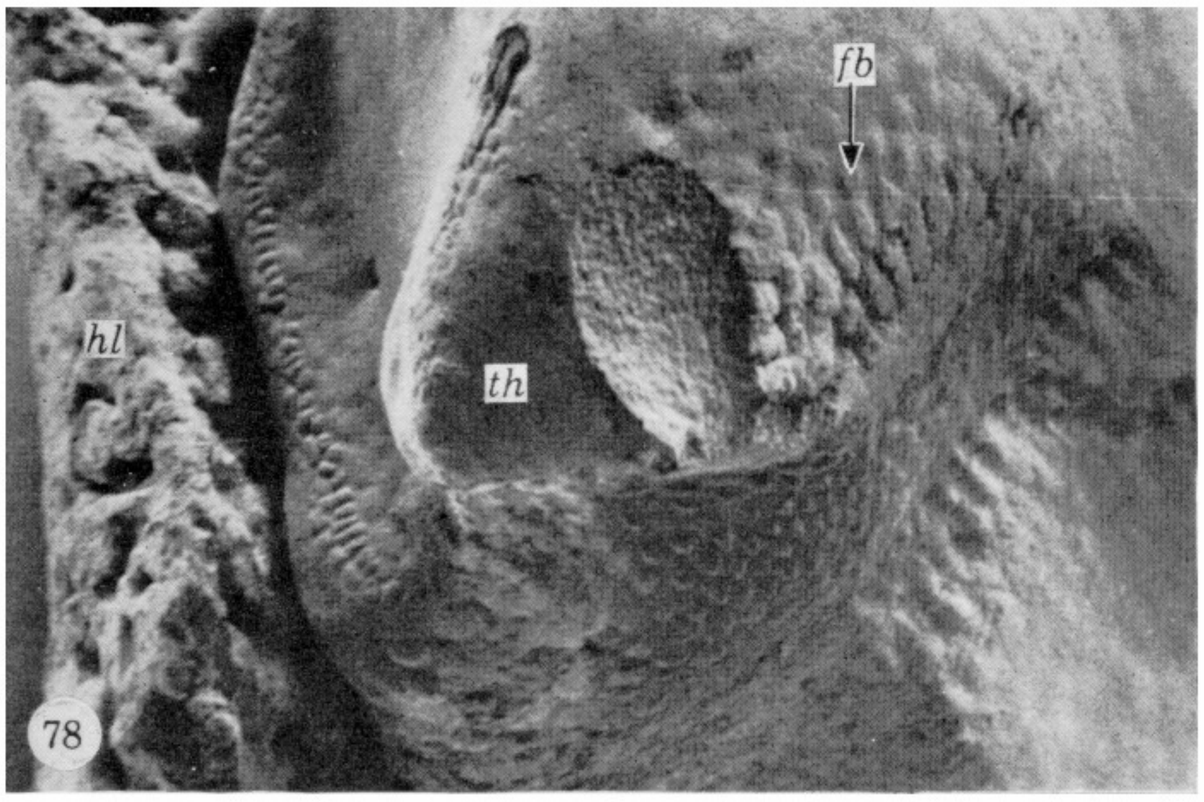
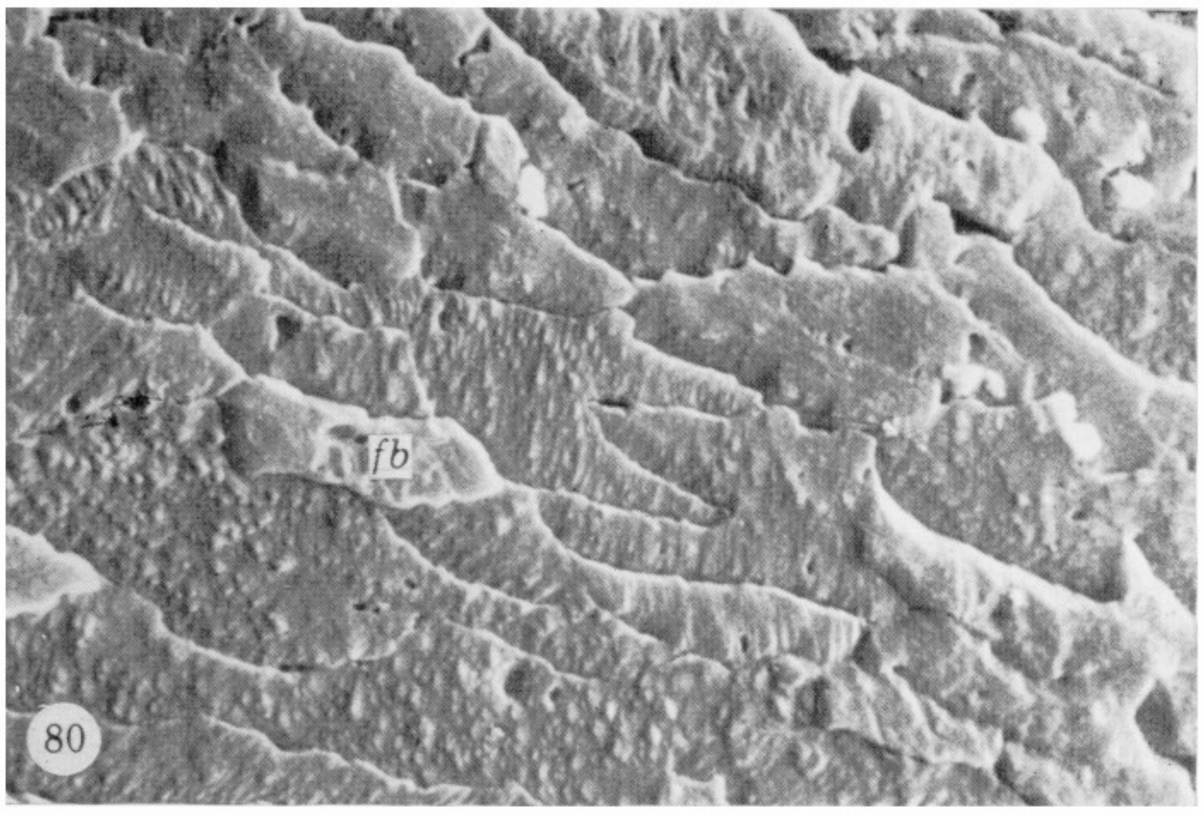


77



78

79



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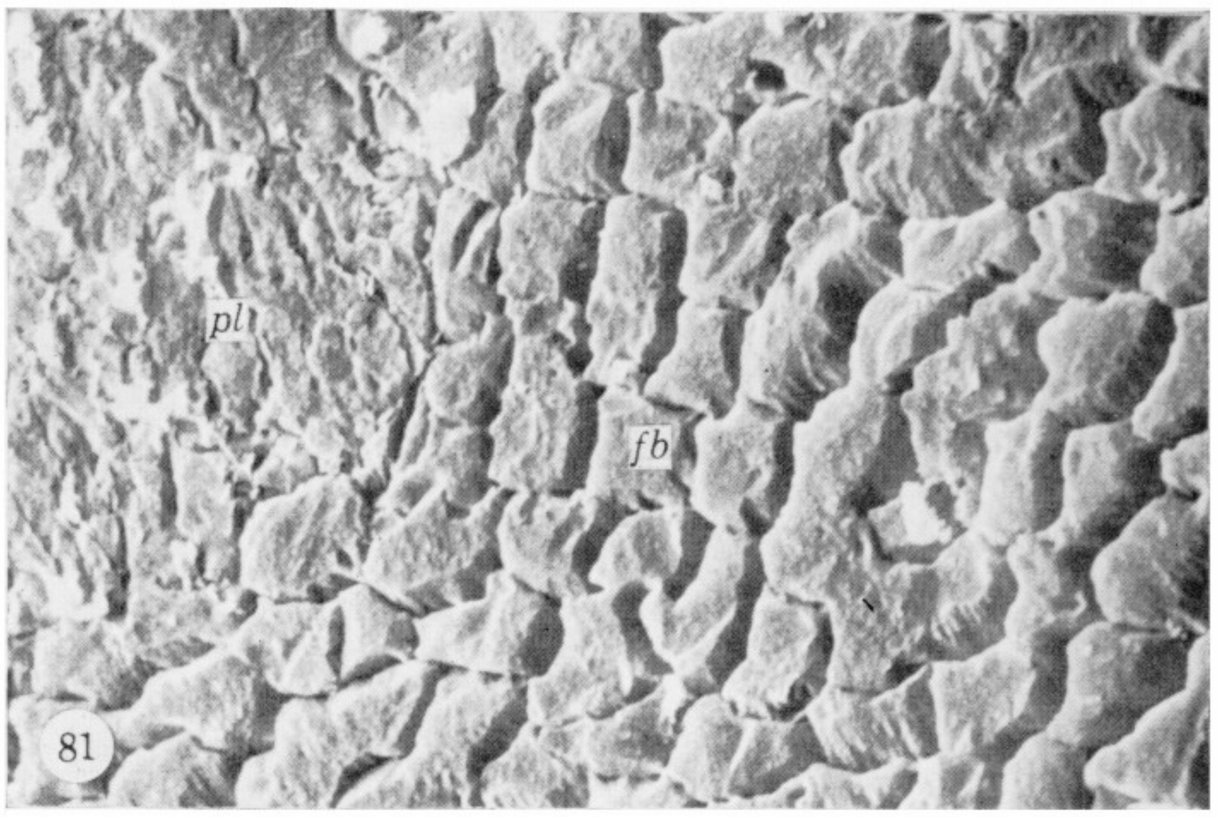
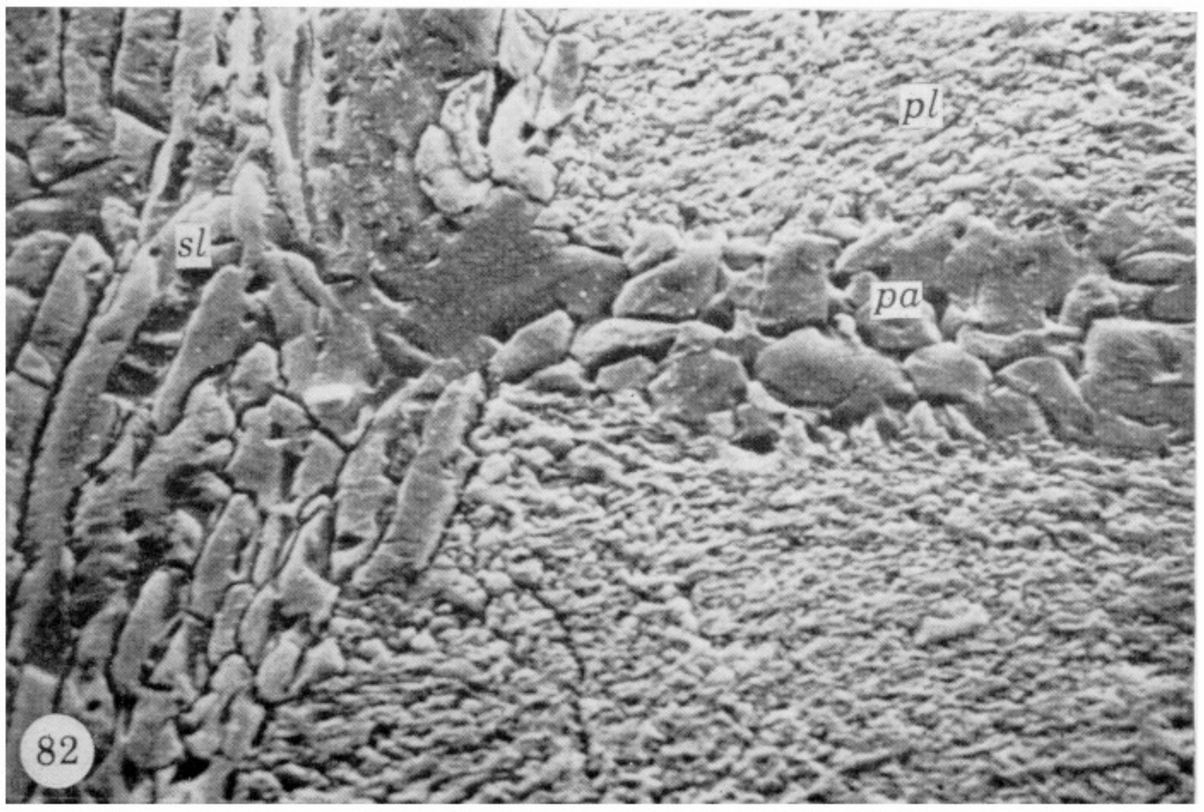
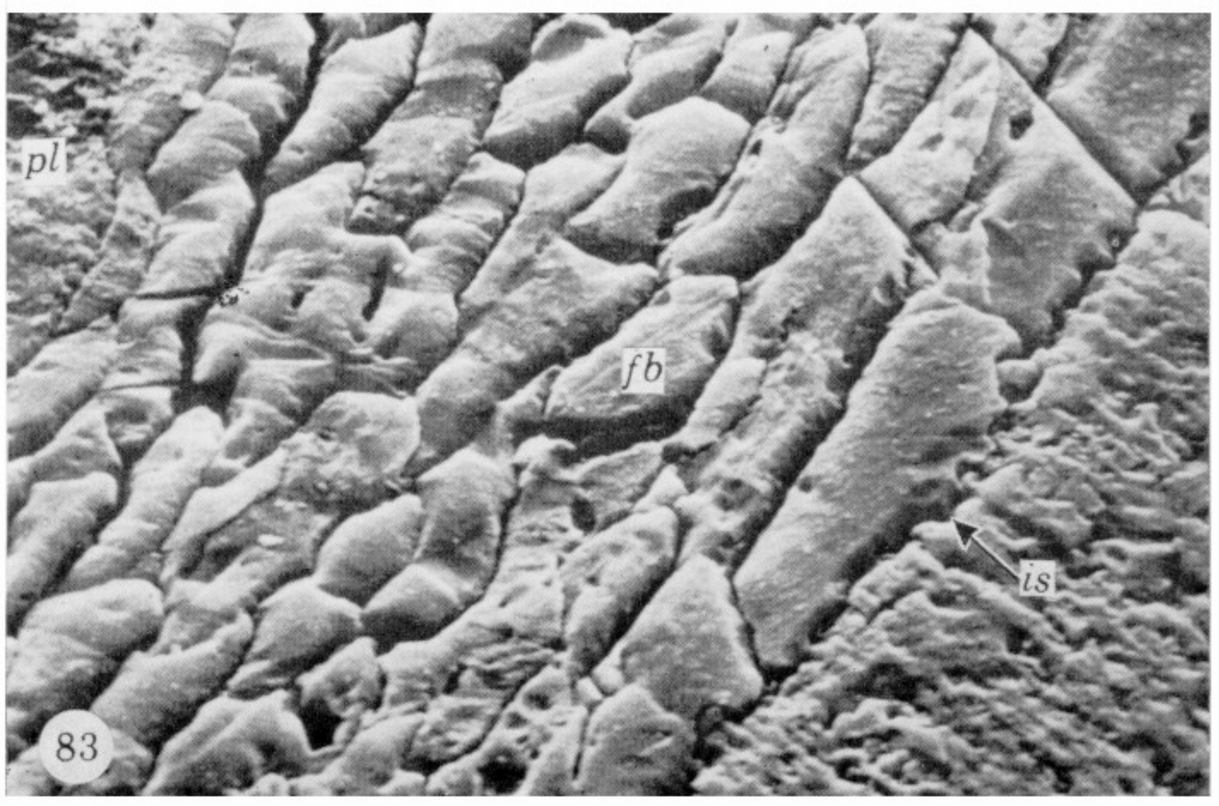


81



82



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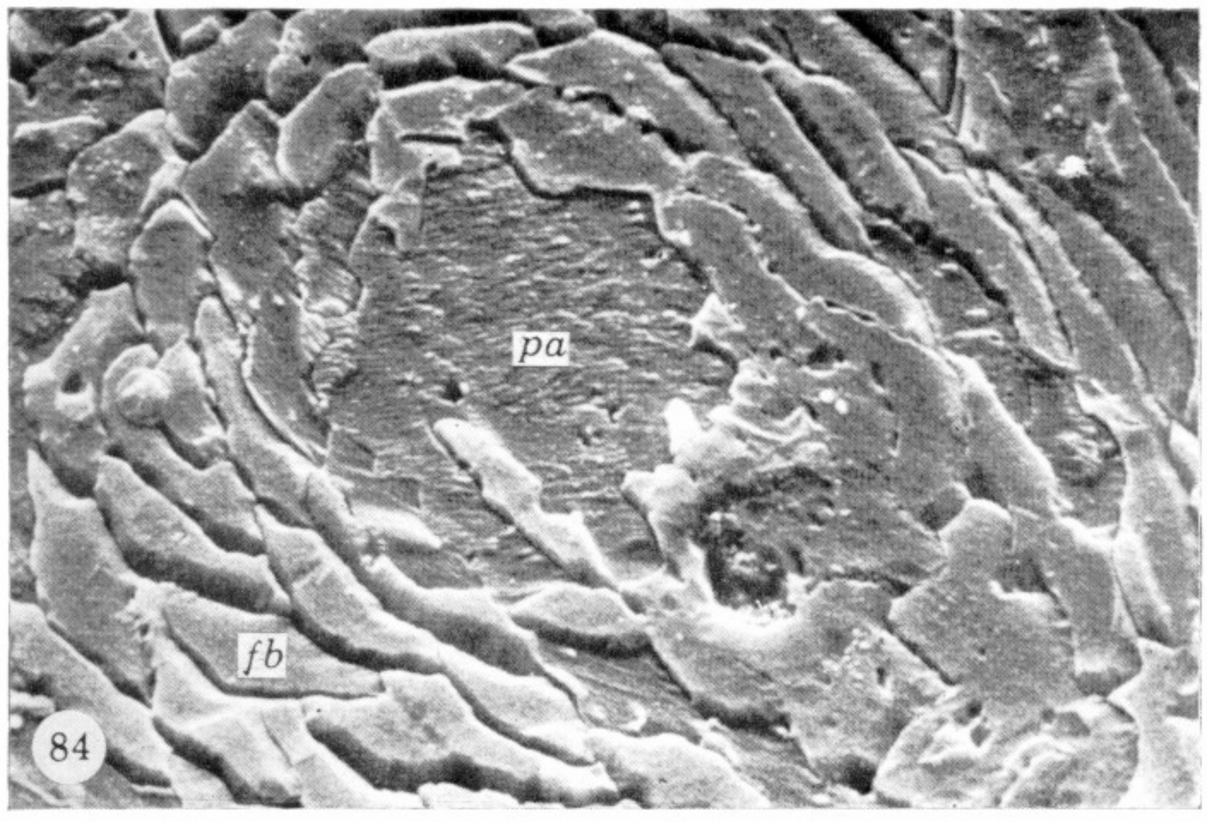
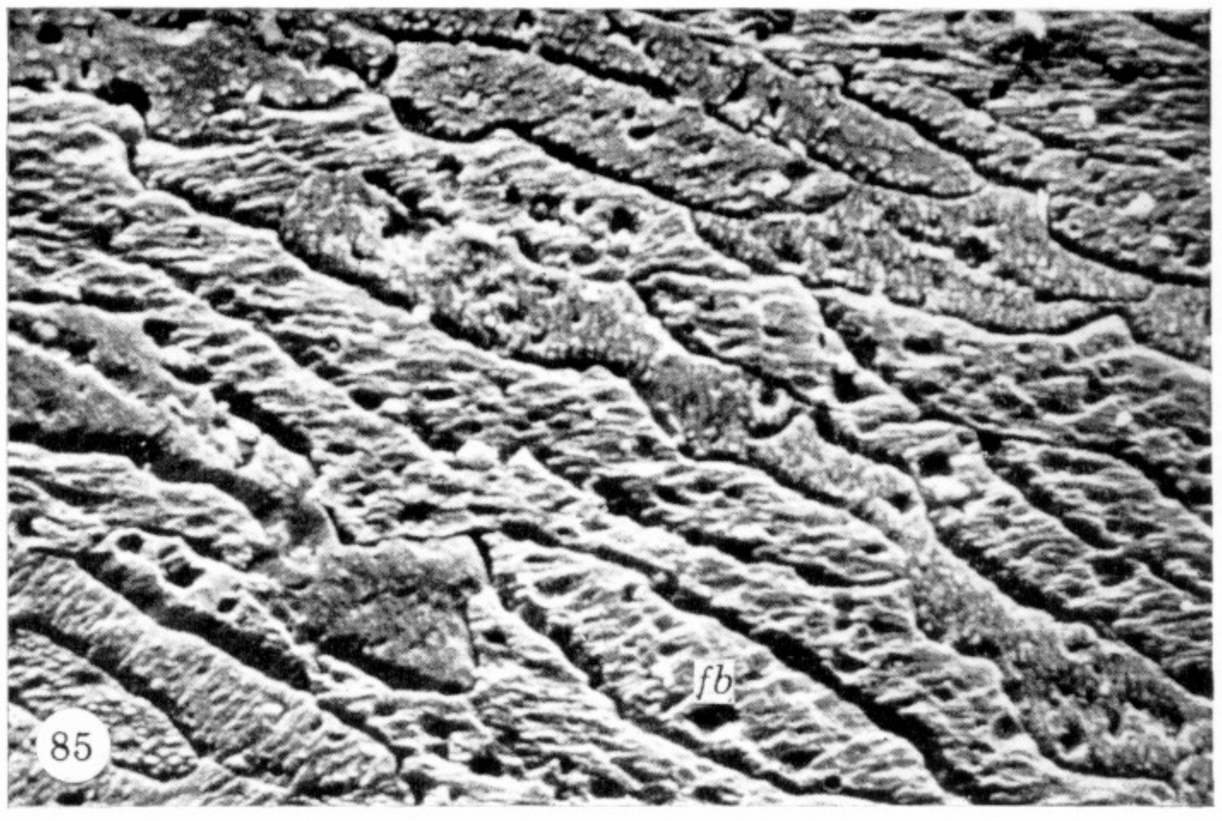
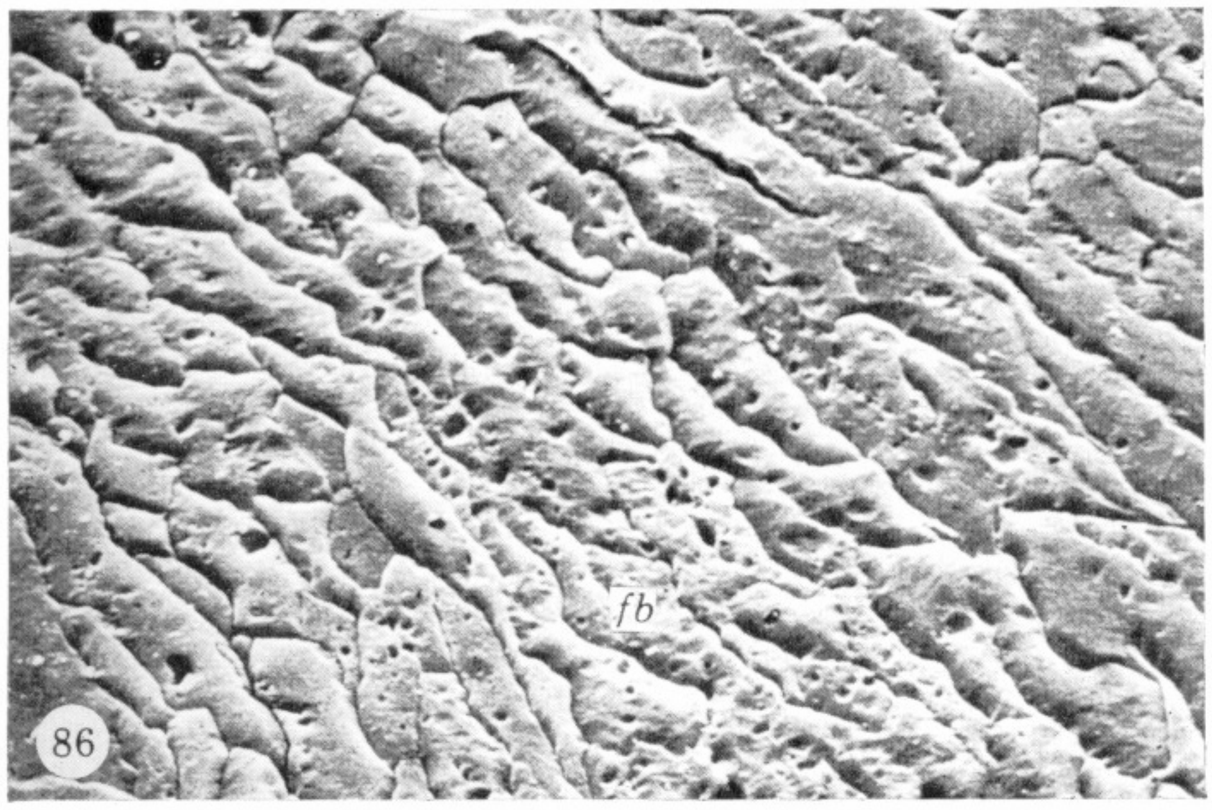
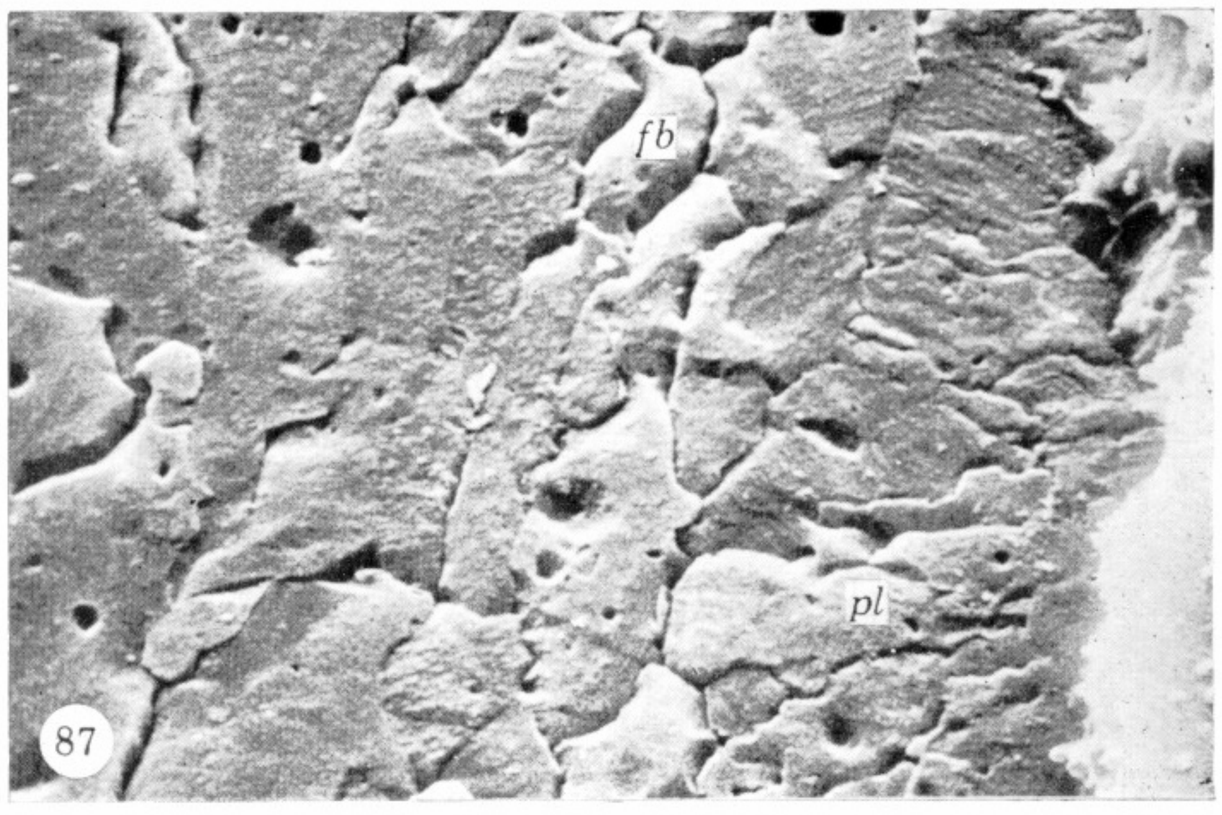
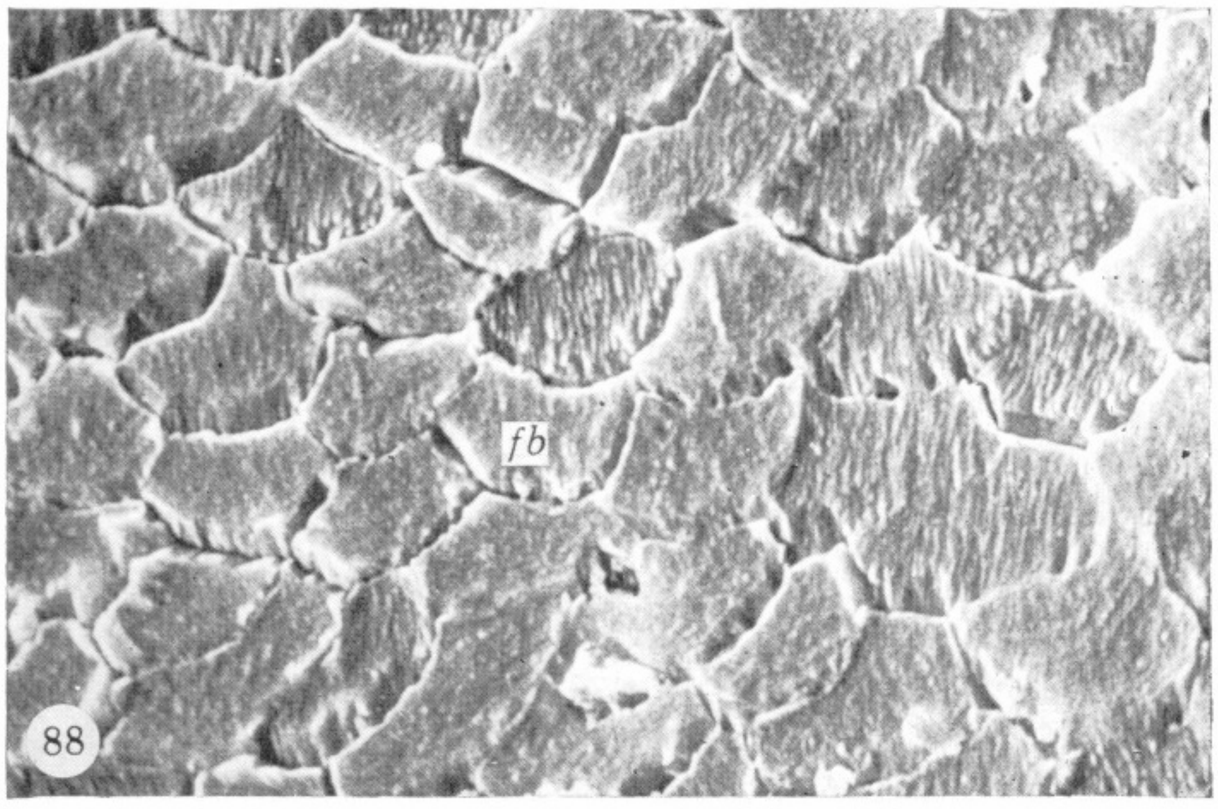
FIGURES 76 TO 83. For legends see facing page.

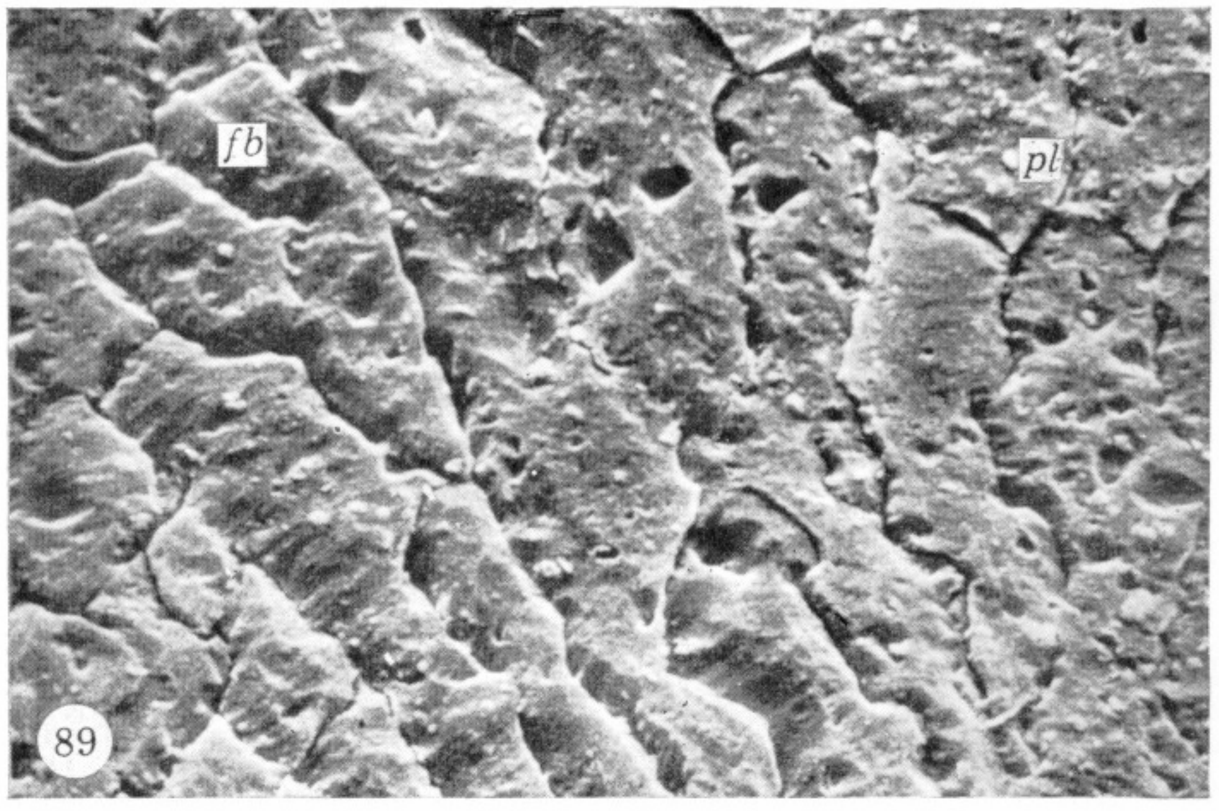


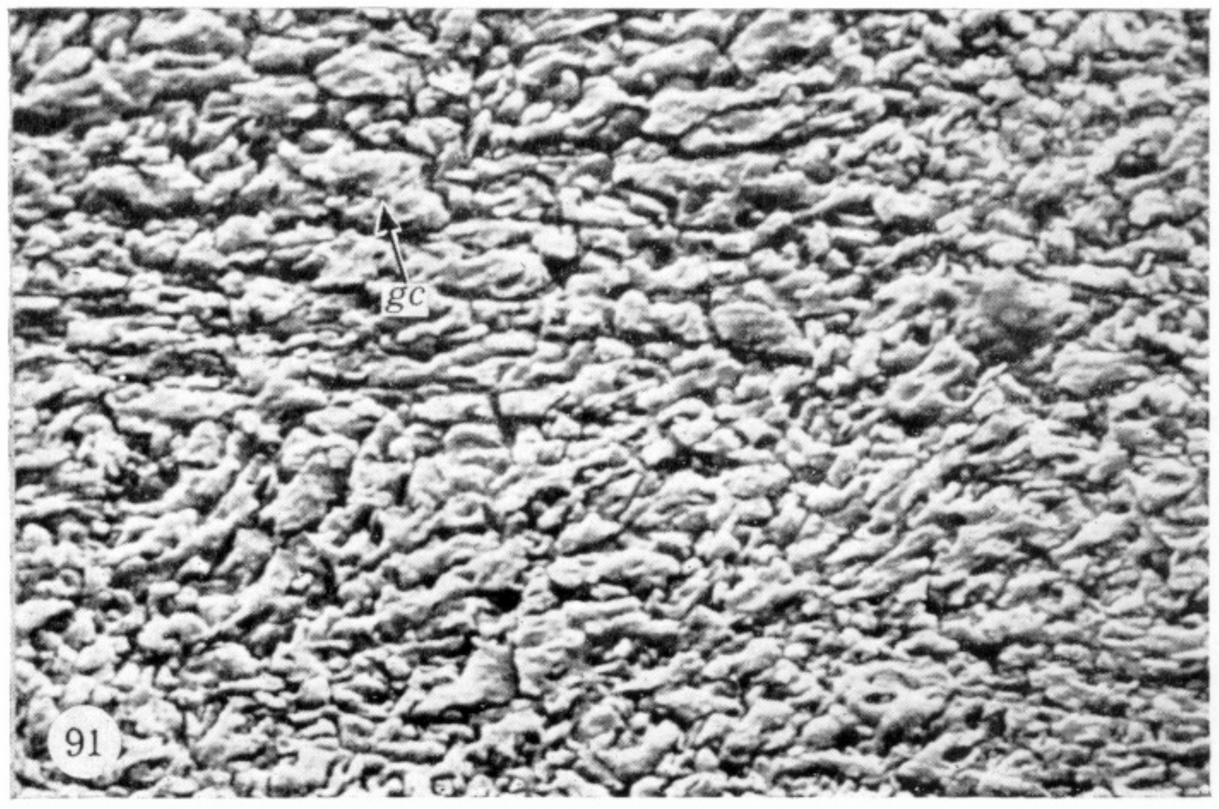




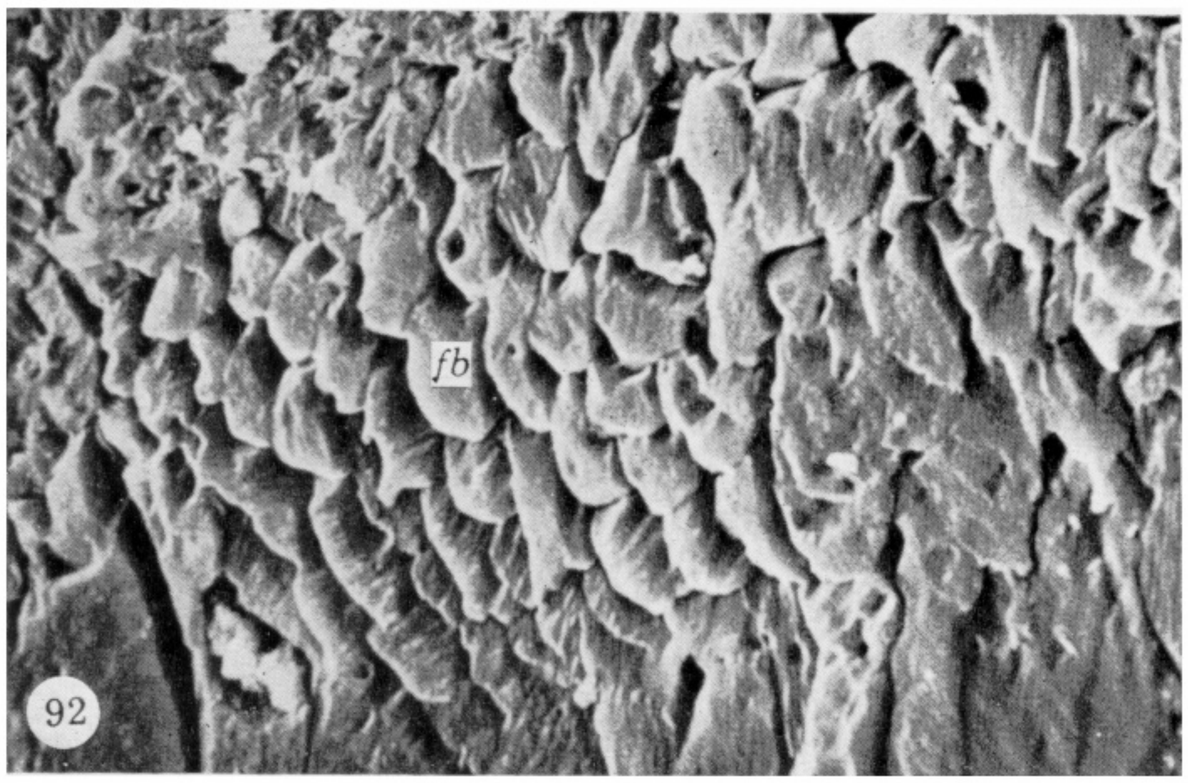


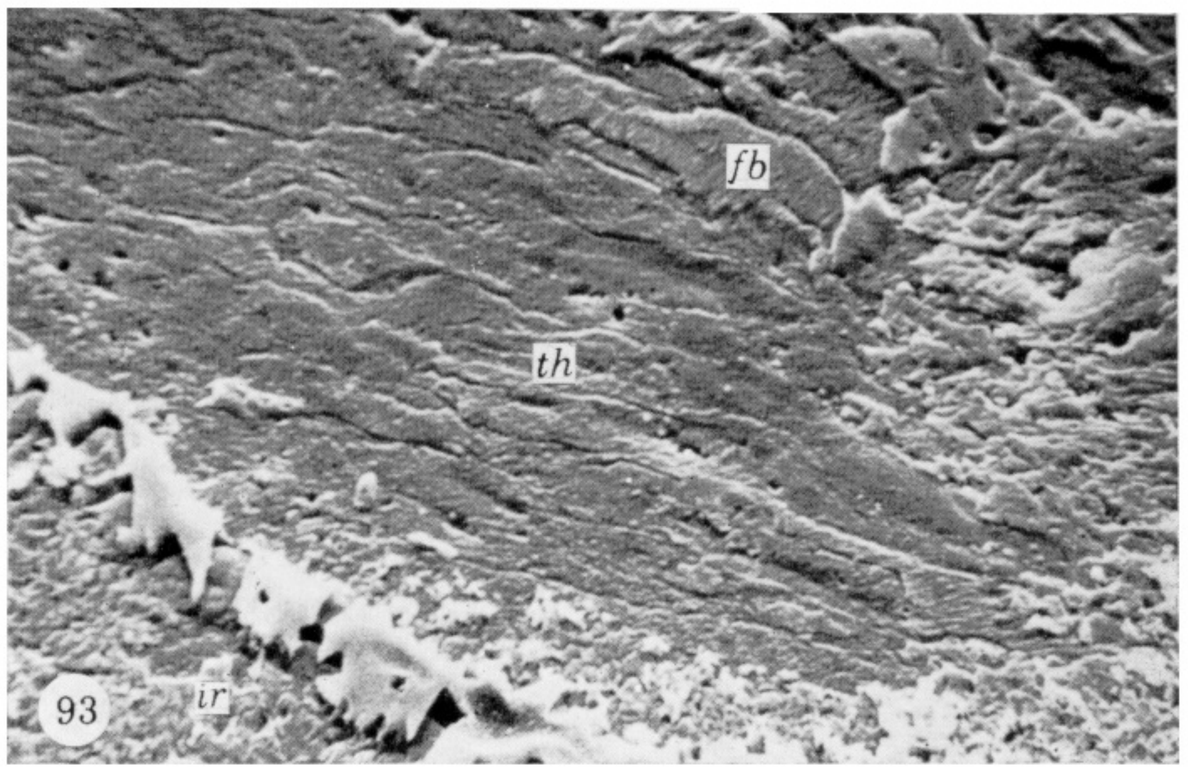


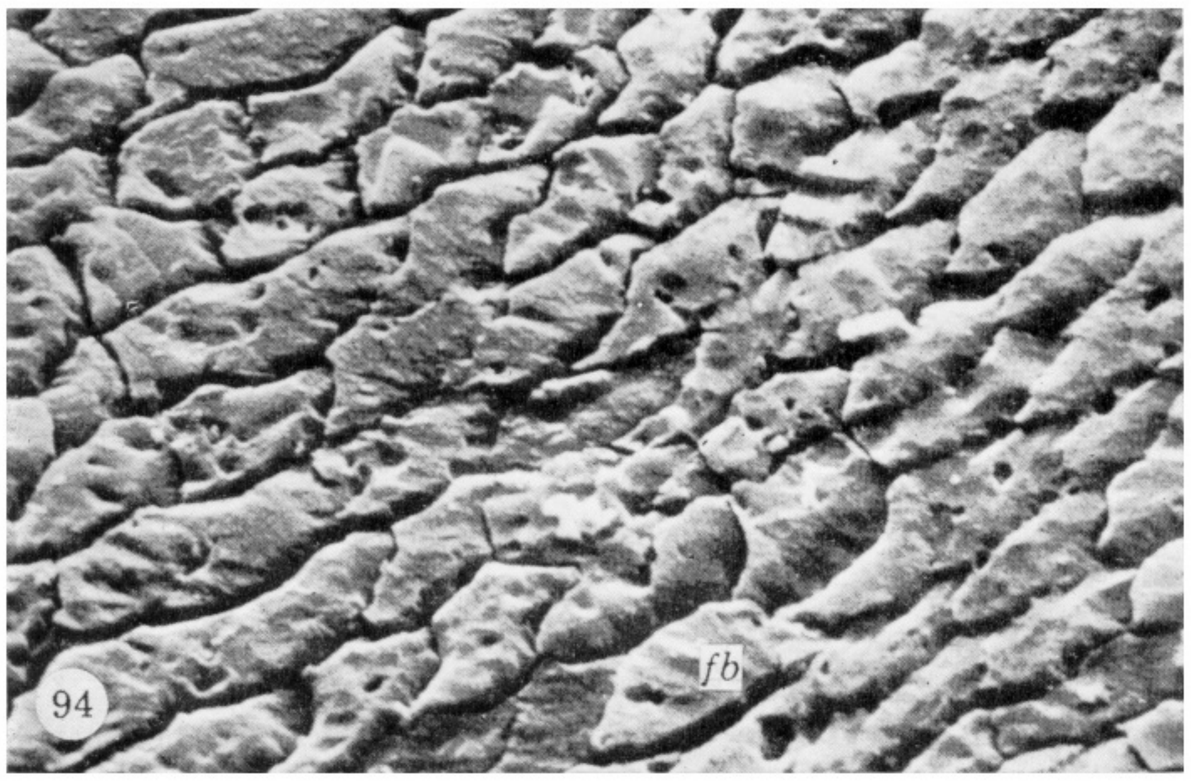


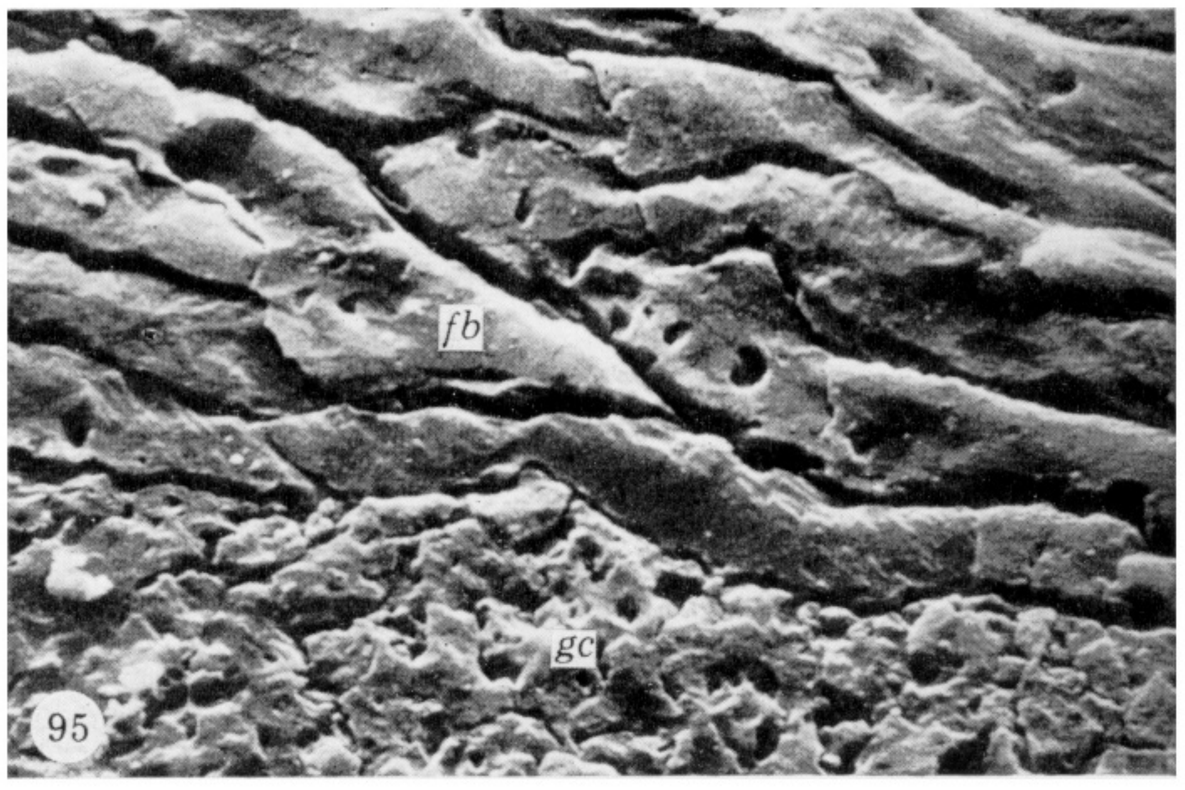


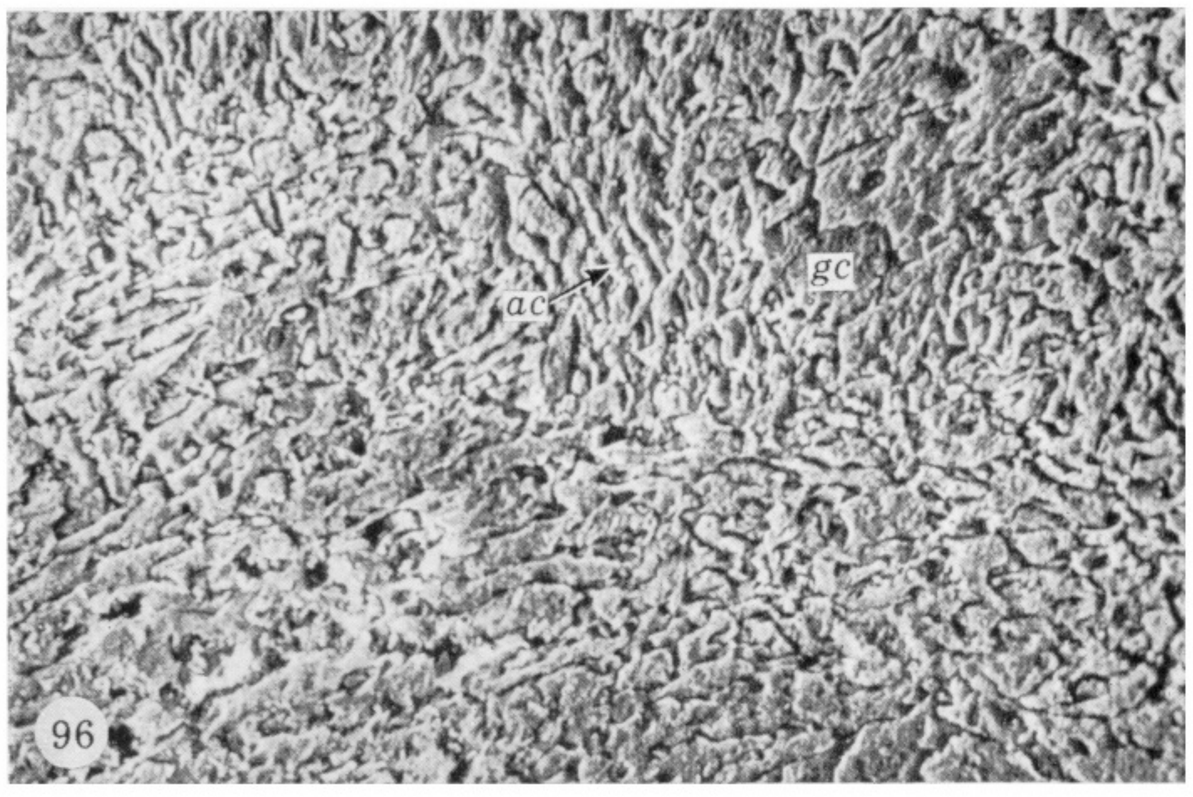
FIGURES 84 TO 91. For legends see facing page.

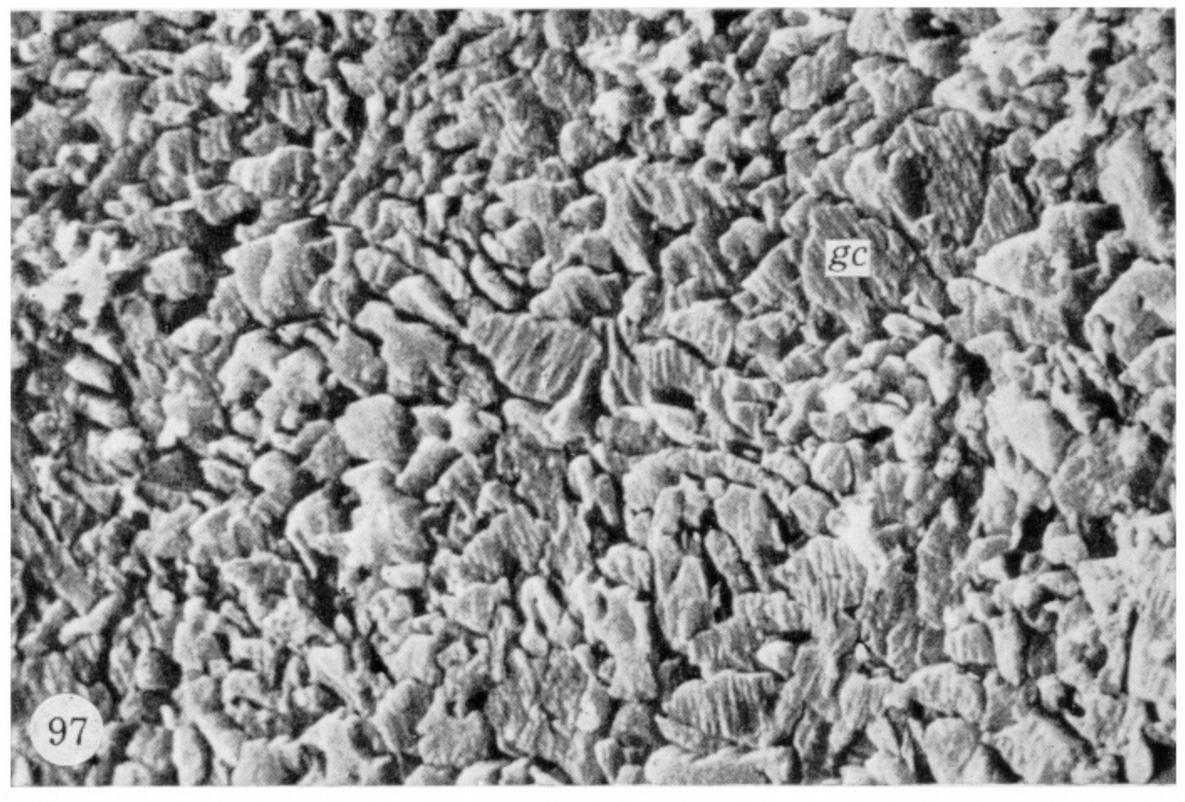


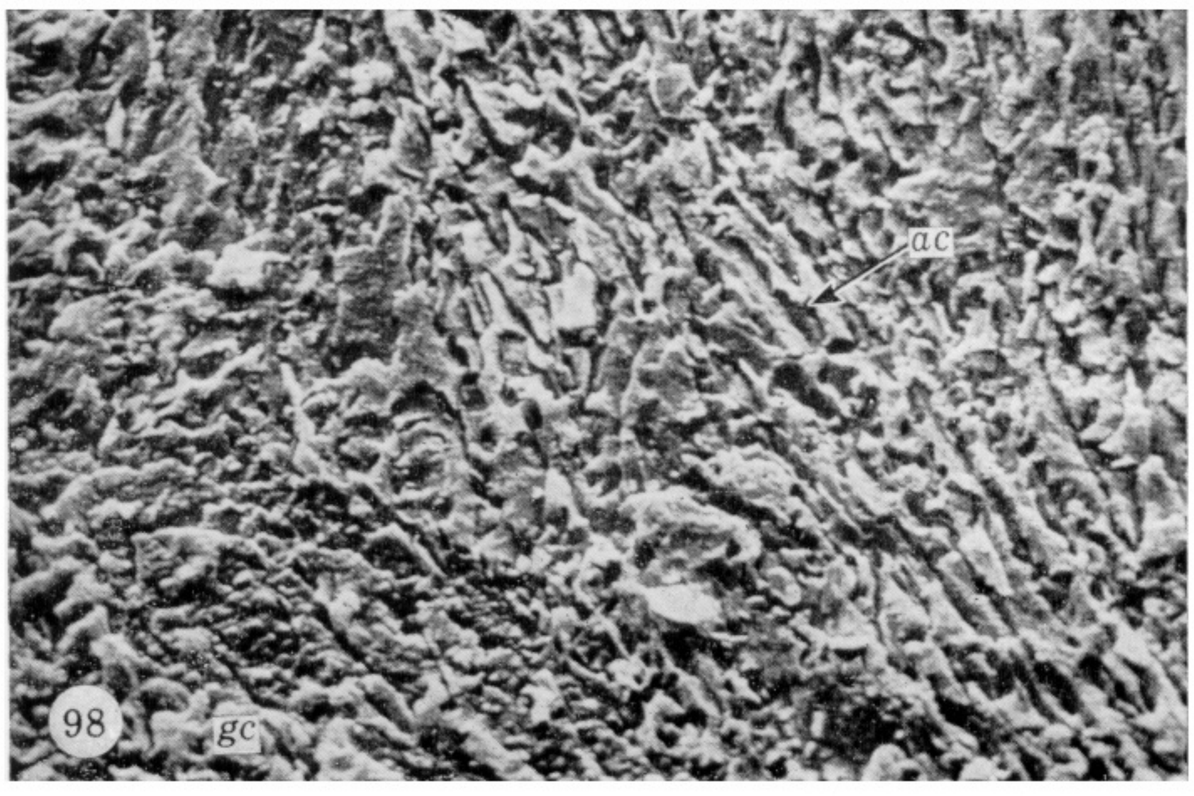


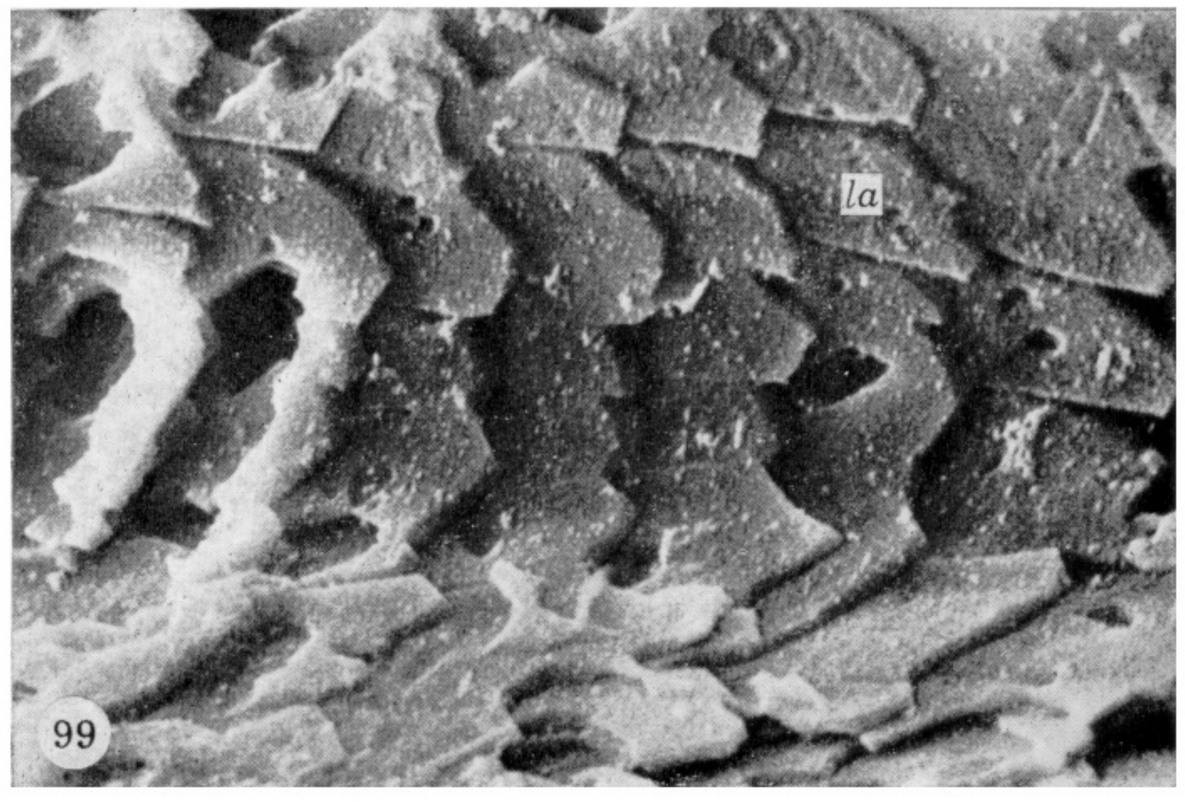




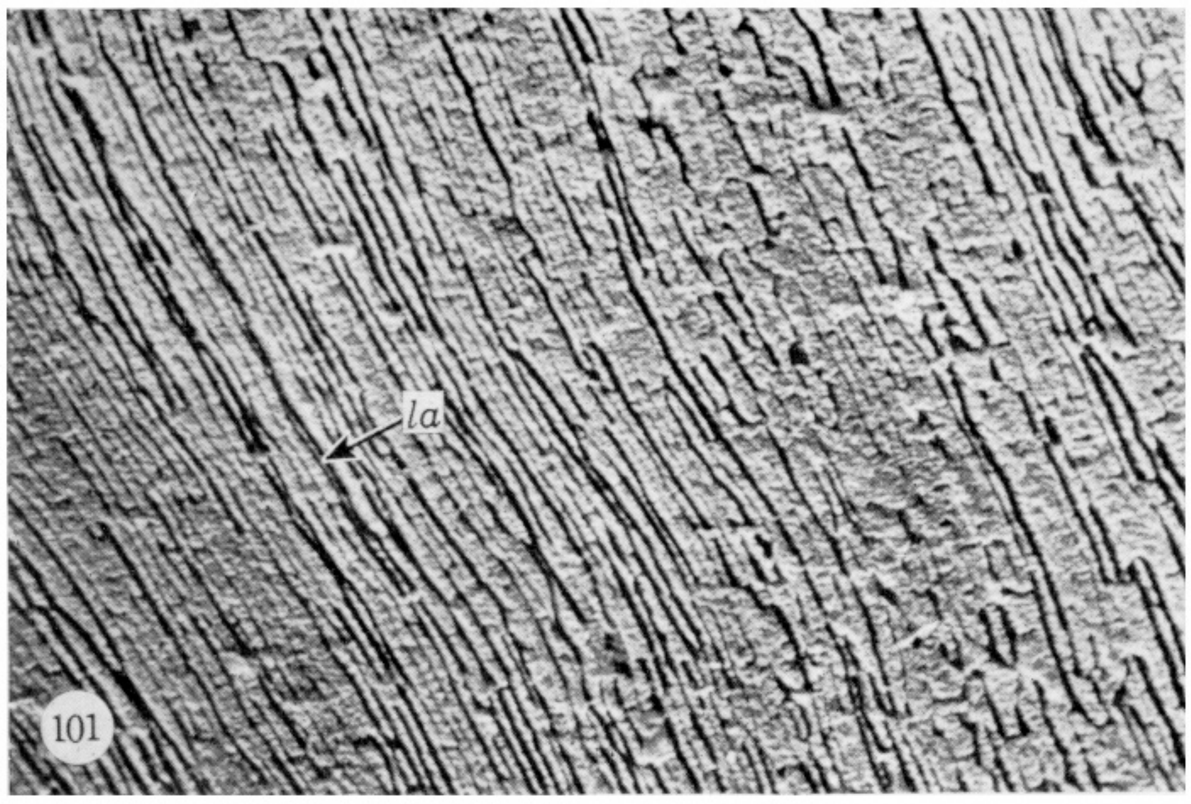


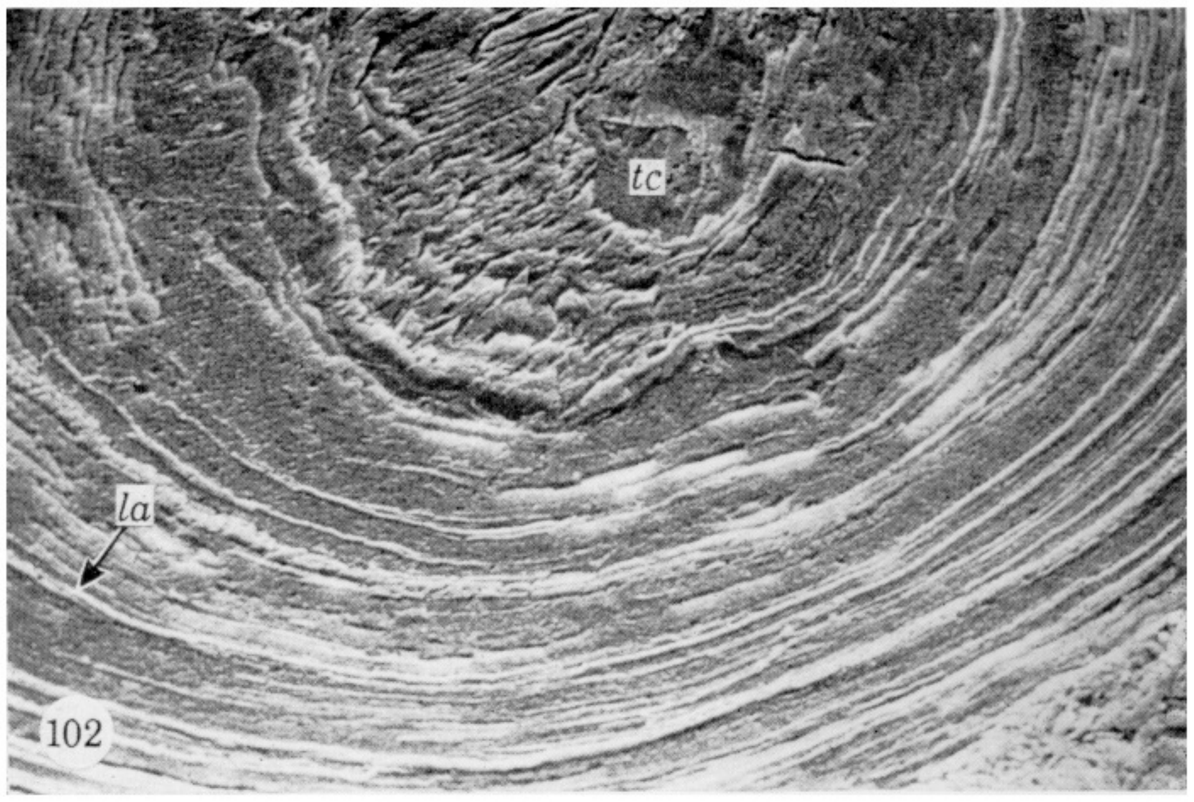


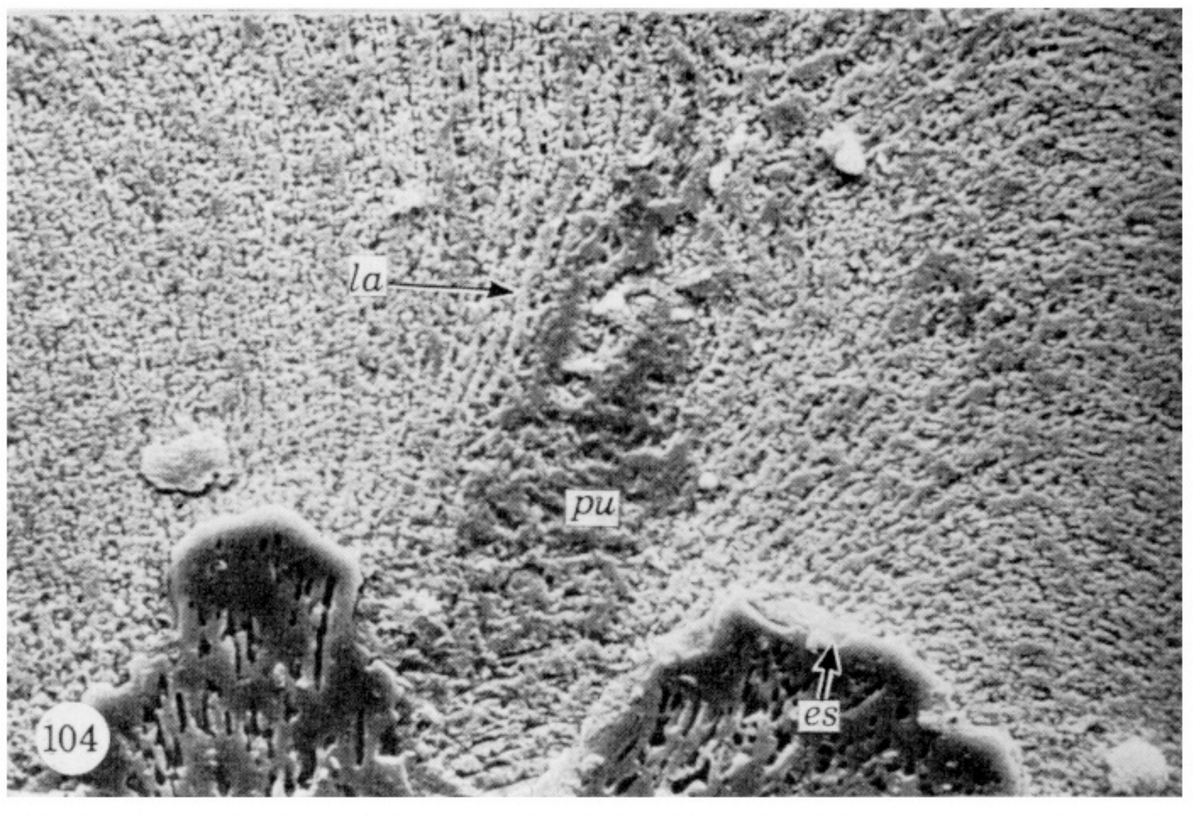


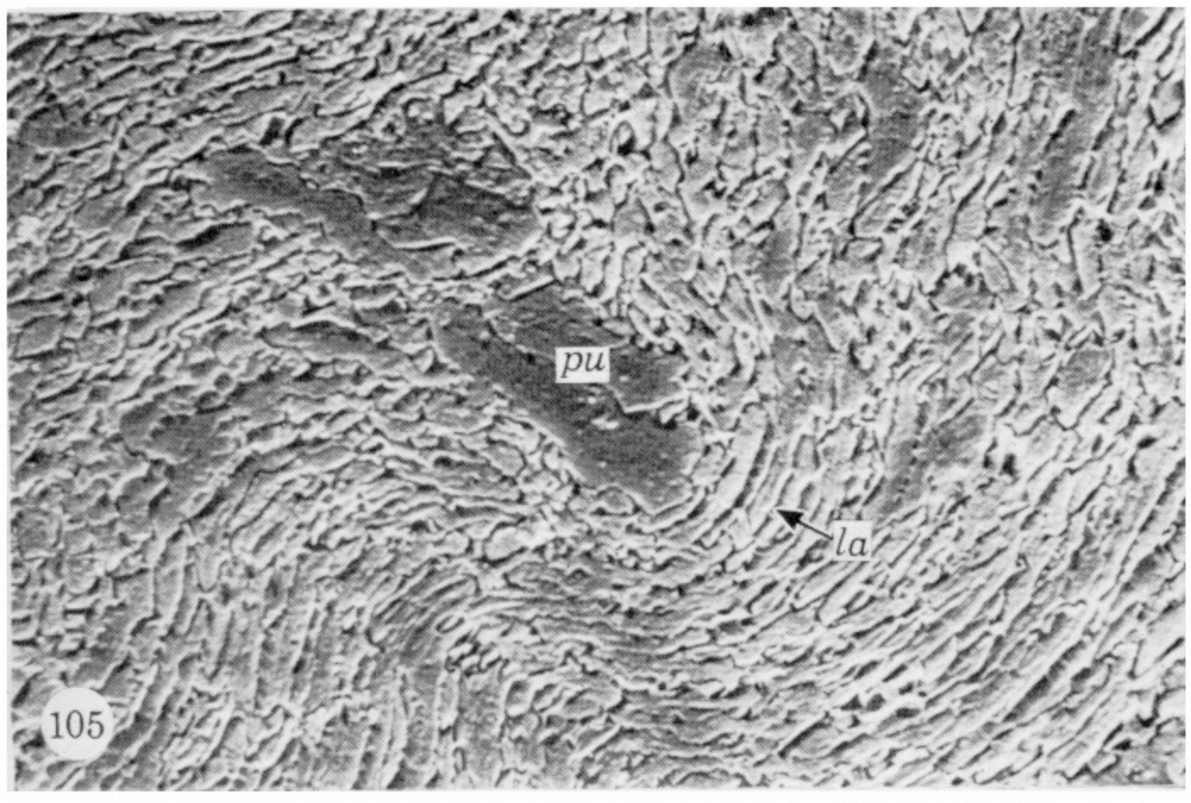


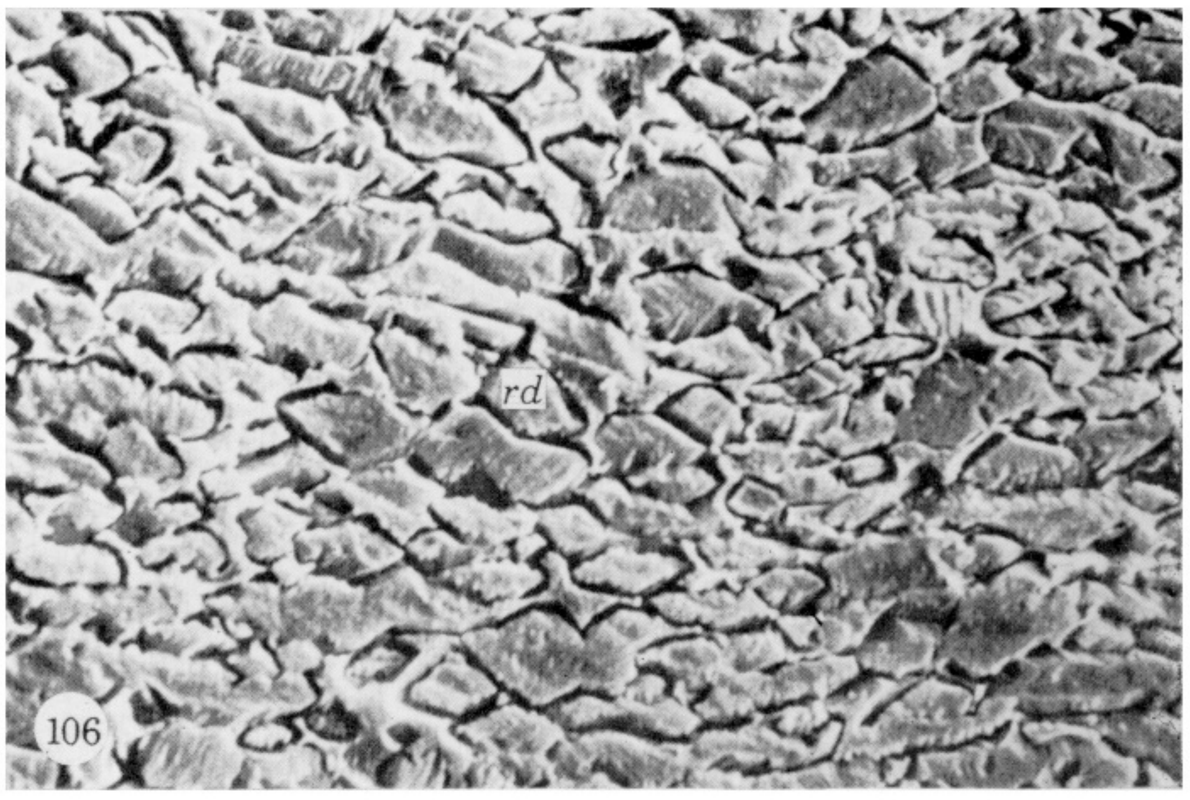
FIGURES 92 TO 99. For legends see facing page.

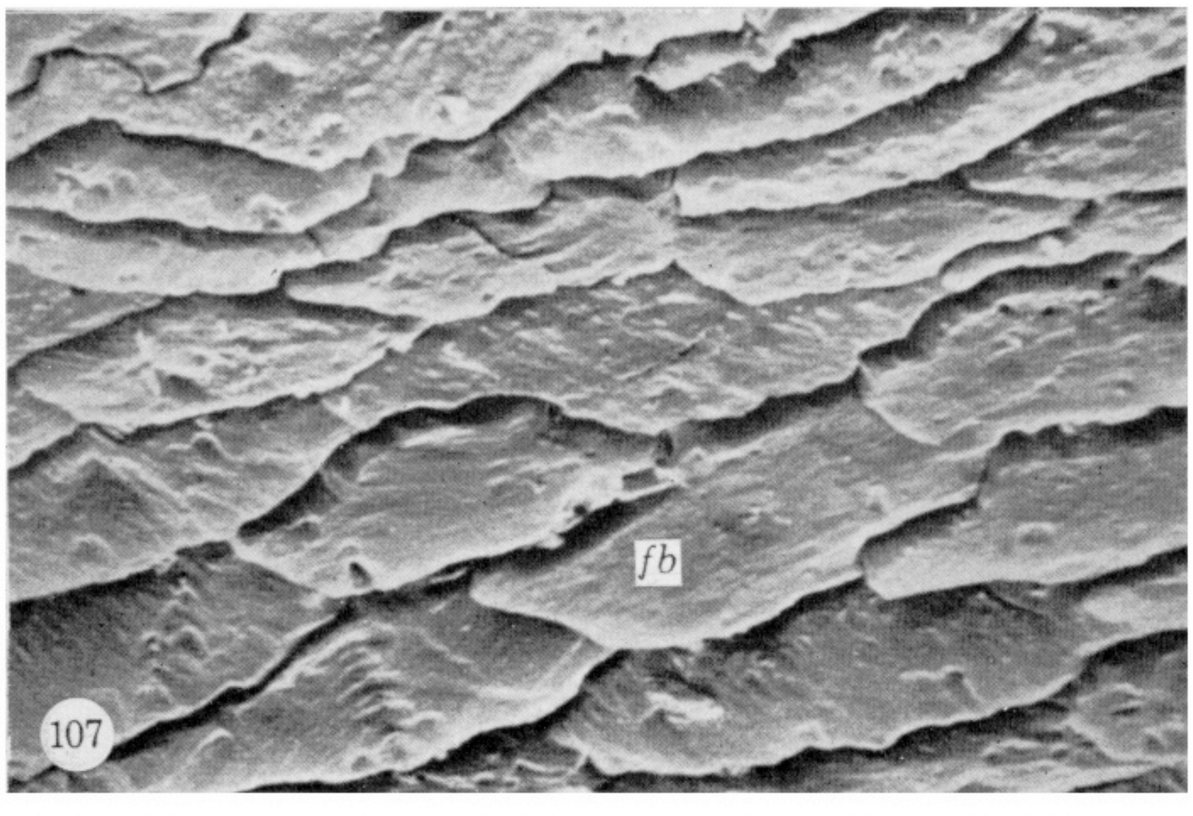


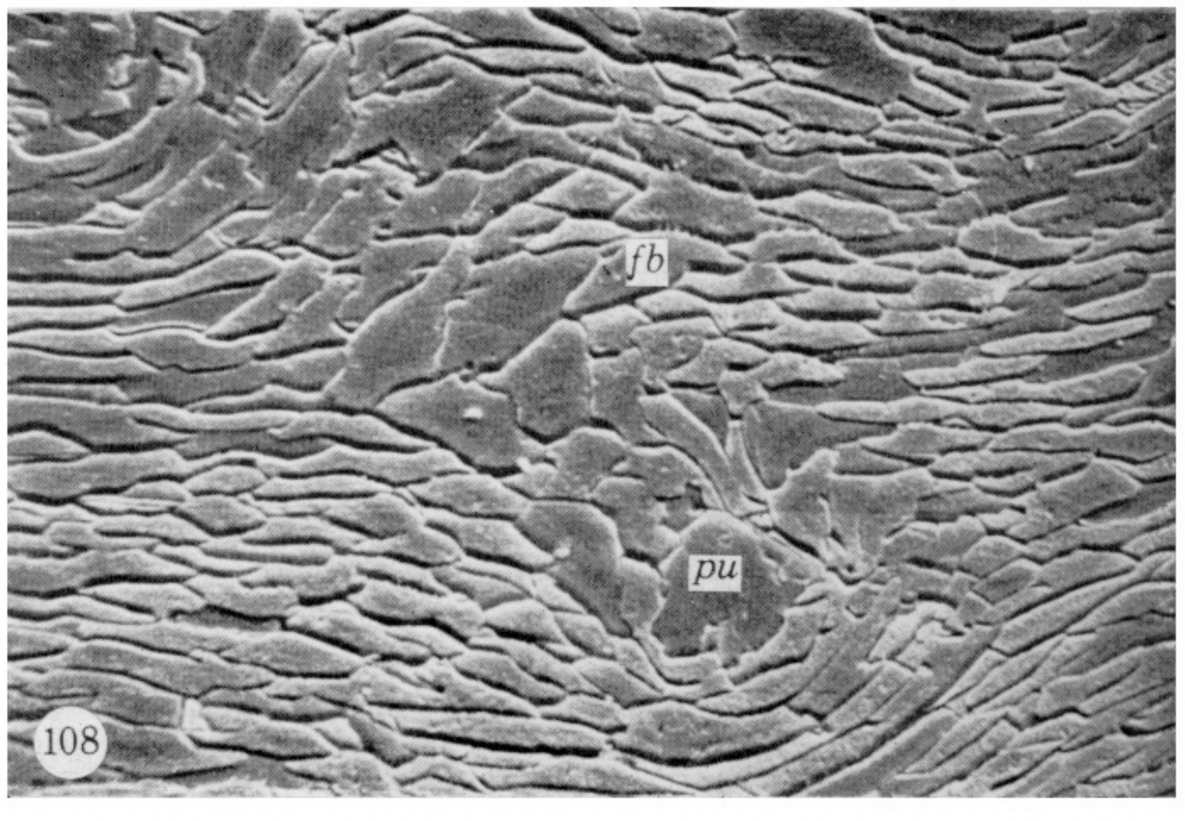












FIGURES 101 TO 108. For legends see facing page.