THE POST-ECDYSIAL DEVELOPMENT OF THE CUTICLE AND THE EYE OF THE DEVONIAN TRILOBITE *PHACOPS RANA MILLERI* STEWART 1927

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(*Communicated by Sir Frederick Stewart, F.R.S.* – *Received* 30 *March* 1979 – *Revised* 22 *June* 1979)

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Specimens of the Devonian trilobite *Phacops rana milleri* Stewart 1927 from the Silica Shale of Ohio are sometimes preserved in the early stages of the post-ecdysial cycle. Individuals that died in this early stage have pale, thin and wrinkled cuticles; in later stages the cuticle became rigid as it thickened and darkened. The post-ecdysial development of the cuticle and the schizochroal compound eye has been studied in a suite of specimens representing various stages, culminating in the intermoult condition.

Scanning electron microscope studies on etched specimens, supplementing cathodoluminescence and light microscopy, have enabled primary structures to be distinguished from secondary diagenetic effects, and have been used to elucidate diagenetic changes.

In our earliest post-ecdysial cuticle the 10 μm thick outer prismatic layer is already formed and the principal layer below this is only about 25 μm thick. The later thickening of the cuticle affects the principal layer alone. In subsequent development there is a division into three zones with a variety of vertical canals. The final intermoult cuticle can be up to 500 μm thick.

In the developing eye, each of the post-ecdysial lenses has initially the form of a small, simple calcite cone hanging from the lower surface of the cornea. In later stages this lens spreads to the full width of the lens capsule, losing its conical form, taking on

a Huygensian shape, and eventually acquiring its mature form in which there is a central core of massive texture and, proximally, a thin intralensar bowl, of much the same appearance as the core. The upper unit of the lens consists of thin calcite lamellae, radially arranged around the *c*-axis, each lamella consisting of palisade-like fibres, parallel in the lower part of the lens, but radiating outwards where they meet the convex outer lens surface. When the lens is mature, a ring of scleral material forms on the inside of the cylindrical wall of the lens capsule, together with an annular girdle of fine-grained material at the junction of lens and sclera.

Some suggestions are made regarding function in the developing eye, and the need for complete replacement of calcium carbonate at each ecdysis is discussed.

1. Introduction

Like modern arthropods, trilobites shed their exoskeletons periodically to accommodate changes in size and shape produced by their growth. Palaeontologists have, therefore, long been aware that the majority of trilobite remains represent cast-off shields or exuviae and not dead animals. The moulting process in trilobites has twofold significance for palaeontology. First, there are considerable implications to follow from a knowledge of where, when and how trilobites moulted. Certain trilobites have left undisturbed associations of dorsal shield components in characteristic and consistent configurations. These occurrences are similar to those produced by modern crustaceans and are considered to represent exuvial assemblages reflecting distinctive types of moulting behaviour (Miller, in press). Henningsmoen (1975) has provided a comprehensive review of this aspect of moulting in relation to trilobite morphology.

The second field where moulting is of importance is that of trilobite biology. Little or no evidence, beyond studies of the number of moult stages accumulating during ontogeny (Hunt 1967), has, so far, been forthcoming in this field. It is now recognized that the various stages in the arthropod moulting cycle are more or less continuous, the recovery from one moult being followed by renewed storage of metabolic reserves in preparation for the next. Ecdysis itself is a period of considerable physiological stress, accounting for a large percentage of arthropod mortality. Trilobite cuticle is exceptional in arthropods, being composed almost entirely of calcite, and, until now, no clear evidence has been available to suggest how trilobites regrew their cuticles after ecdysis.

In this paper, we describe a suite of specimens of *Phacops rana milleri* Stewart 1927 from the Middle Devonian of Ohio (Eldredge 1972). These are preserved in various stages of the early post-ecdysial cycle and have allowed us to determine how much cuticle carbonate was removed and renewed during moulting, how the layers of cuticle were built up post-ecdysially and how specialized cuticular organs, especially the schizochroal eyes, were reconstructed immediately after exuviation. We make some attempt to consider how the solution of some problems facing trilobites in moulting reflects on studies of their functional morphology in particular and their evolutionary history in general.

2. Material and methods

(*a*) *Location of material*

The specimens of *Phacops rana milleri* are all from the Middle Devonian Silica Shale and were collected from the north quarry of the Medusa Portland Cement Company, Silica, Ohio. They include a uniquely informative slab collected by Mr Mullard Widener of Tulsa,

Oklahoma, and registered AMNH 29282 (American Museum of Natural History). Other material was donated by Dr N. Eldredge and Dr R. Levi-Setti, and is deposited in the Royal Scottish Museum (R.S.M.). Cuticle and eye fragments of *P. rana africanus* Burton & Eldredge 1974 from the Eifelian of the Spanish Sahara, together with those from *P. rana crassituberculata* and *P. rana rana* from the Silica Shale, were also examined for comparative purposes. Professor A. D. Wright, Queen's University of Belfast (Q.U.B.), provided an early post-ecdysial specimen of *Cheirurus* sp. from the Silurian Wenlock Limestone of Dudley, England.

(*b*) *Description of post-ecdysial specimens*

(i) AMNH 29282 (figure 5†)

A 7 cm square slab of pale grey calcareous mudstone with an outstretched intaglio (complete specimen) of *P. rana milleri* having a pale honey-coloured cuticle that is extremely thin (30 μm) and transparent. Almost at right angles to this individual lie the exoskeletal parts of another *P. rana milleri*, with dark brown cuticle of thickness typical of intermoult stage (300–500 μm). On the right is the thoracopygon (term defined by Henningsmoen 1975, p. 182), with the pygidium inclined at 45° to the horizontal. A small, inverted fragment of hypostome lies between the thoracopygon and the intaglio, and the cephalon partly underlies the left side of the intaglio. Most of the hypostome appears to have been removed in the preliminary preparation of the specimen.

(ii) RSM GY 1979.11.1 (figures 8, 9) (This specimen was figured intact by Levi-Setti (1975, p. 13, pl. 5).)

An intaglio 4.6 cm long, with pale translucent brown-grey cuticle 40 μm thick; dark areas due to disseminated pyrite. Immediately underlying the pygidium of this intaglio is a partial thoracopygon of a slightly narrower specimen with its anterior 180° opposed to the intaglio. The cuticle of the thoracopygon is dark brown and of typical intermoult thickness.

(iii) RSM GY 1979.11.2.

A damaged specimen; thorax, 2.6 cm width, but asymmetrically compacted; cuticle, light brown, semi-translucent.

(iv) RSM GY 1979.11.3 (figure 7)

An almost complete specimen 6.6 cm long, undistorted by compaction. Cuticle glossy, pale brown and translucent; 135 μm thick.

(v) RSM GY 1979.11.4 (figure 10)

An intaglio 3 cm long, somewhat compacted, left eye missing. Cuticle very thin (20 μm), pale honey colour, opaque, not glossy.

(vi) RSM GY 1979.11.5

An enrolled specimen from which many preparations have been made. Cuticle thin (30 μm), mid-brown, highly glossy.

† Figures 5–47 appear on plates 1–7.

(vii) QUB 2732 (figure 6)

A specimen of *Cheirurus centralis* Salter from the Silurian Wenlock Limestone of Dudley, England, preserved in light olive coloured calcareous mudstone; cuticle light to medium brown, semitransparent and very thin (20 μm). No visual surface preserved. It is figured here to show a comparable developmental stage in a different taxon.

(*c*) *Other material*

Numerous preparations have been made for scanning electron microscopy (Grant Institute: Gr I 46150-61) and cathodoluminescence (Museum of Paleontology, Michigan: MPM 27063a), all from mature intermoult specimens.

(*d*) *Interpretation of specimens*

All the specimens of *P. rana milleri* described above have an unusually thin, fragile and light-coloured cuticle compared with the typical intermoult cuticle, which is dark brown and ranges in thickness from 250–500 μm (Miller 1976). Only the disarticulated exoskeletal material underlying the intaglio of AMNH 29282, and that of RSM GY 1979.11.1 have the character of fully developed intermoult cuticle. Therefore, those specimens with pale thin cuticles appear to be in various stages of cuticle calcification and thickening following ecdysis, and probably themselves represent the remains of animals that died before post-ecdysial development was complete. The conclusion that the individuals with thin cuticles are in immediate post-ecdysial condition is supported both by our detailed studies on cuticle structure and by the development of the schizochroal eye as described in §§ 4–6.

In both AMNH 29282 and RSM GY 1979.11.1 it seems reasonable to suppose that the trilobite died shortly after completing exuviation and rests partly upon its own exuviae. The cephalon–hypostome–thoracopygon configuration of AMNH 29282 is within the typical range shown by Salterian moulting (N. Eldredge, personal communication; Henningsmoen 1975, p. 192). Bearing in mind the larger degree of compaction undergone by the very thin and apparently flexible cuticle of the intaglio, and the fact that aquatic arthropods rapidly swallow water once free of the old exoskeleton to increase their size, the relative sizes of the exuviae and the adjacent 'paper-shell' individuals are compatible. It has, unfortunately, not proved possible to count accurately the number of lens files on the intaglio of AMNH 29282 owing to considerable flattening and distortion of the eyes. Thus we were not able to verify Clarkson's (1966*a*) suggestion that a new lens row is injected at every moult in *Phacops* holaspids.

(*e*) *Methods*

For studies of the cuticle structure, fragments of exoskeleton were removed both from intaglios and from exuviae, broken cleanly across to give transverse sections. These were etched in saturated solutions of EDTA (disodium salt) before mounting for scanning electron microscopy (s.e.m.). Etching was controlled by observation under a high power binocular microscope. Etch times varied between 5 and 35 min. Fragments of visual surface from post-ecdysial eyes were similarly treated, but in one the cuticle was entirely dissolved away and the internal mould examined (figures 46, 47). Whole eyes were removed from intermoult specimens. They were then trimmed into small blocks with a diamond blade of 1 cm radius. Vertical sections were made by grinding flat faces passing vertically through one of the dorso-ventral files;

horizontal sections were made with the line of section cutting through lenses at different levels (cf. Clarkson 1967, text-figs 1, 2) and passing tangentially, parallel with the principal plane of each lens.

Final smoothing of the cut faces was done with 1000 grade carborundum, and, after rinsing, the specimens were etched in EDTA as described above. Distilled water and, finally, absolute alcohol were used for gentle washing after etching. The specimens, after coating in gold–palladium, were scanned, on the s.e.m., from one end of the cut face to the other. A series of overlapping photographs were taken to provide a large scale montage (see, for example, figure 19), facilitating examination of the eye as a whole. Tilting specimens in the s.e.m. enabled three-dimensional correlation of cut planes at various angles with the outer lens surfaces.

Slides from a serially sectioned, enrolled *P. rana milleri* were used for cathodoluminescence microscopy. The trilobite was embedded in Araldite before slicing, and sections were polished on both sides and were attached to the slides with Araldite. Slices passing through the eyes were examined in a Nuclear Enterprises Inc. Luminoscope, with cold cathode discharge at 18 kV and 0.35 mA, at low pressure. Paired photographs were made by transmitted light and cathodoluminescence (see, for example, figures 42, 43), with exposures of 1 s for transmitted light and 5 s for luminescence, on Ilford FP4 film uprated by development to ASA 200. The Luminoscope proved invaluable in revealing structural details in preparations where little was visible optically, and also gave significant information about diagenesis.

3. Diagenetic modification of the cuticle and eye structure

All the specimens examined by us had undergone some degree of diagenesis, which wholly or partially obliterated the primary structure. Neomorphic replacement of primary calcite appears to have been the major process involved. In several instances, indications of primary microstructure are revealed in the arrangement of neomorphosed calcite crystallites, which were based on an organic matrix (cf. Sandberg 1975). In others, neomorphic replacement has been very coarse, obliterating any primary microstructure. Using relatively unaltered specimens as a reference, we have charted the different degrees of alteration that lenses in our material had suffered (figure 1).

The main problem in interpretation of the primary structures is that, while the etching process greatly clarifies the internal organization of the lens, it also partially dissolves it. Hence, cleavage planes in the calcite are highly accentuated, and so are the primary voids that may exist in the calcite of the lens, but it is not very clear what the *in vivo* dimensions of the latter actually were.

However, the various internal zones of both cuticle and eyes, as revealed by textural differences in etched specimens, were also confirmed by luminescence microscopy. Sommer (1972*b*) has shown that invertebrates with calcareous skeletons incorporate trace amounts of Mn^{2+} into their calcite, which produces a characteristic red luminescence under electron excitement. Structures and layers grown at different times and of different constructions can luminesce more or less brightly according to their manganese content. The iron content of the calcite also affects luminescence; increasing iron quenches the red manganese luminescence. It appears that, during neomorphism, manganese ions in the calcite lattice retain their relative concentrations, so that, even in highly crystallized material, primary structures can still be revealed by luminescence microscopy (figures 35–37, 42, 43). There is thus no doubt that the structural

elements observed in the visual apparatus, as well as finer architectural details such as lamination, were originally present and are not artefacts produced either by diagenesis or preparation.

Neomorphism has affected all cuticle calcite, but is most noticeable in the eye lenses. Lens crystallites were optically well oriented, providing preferential sites for epitaxial cement overgrowths which occluded the small intercrystallite spaces, probably at a very early stage in diagenesis. The excellent optical orientation of the lens calcite is further indicated by later large syntaxial cement crystals growing into sublensar cavities, where they have successfully competed with other cements (figure 36).

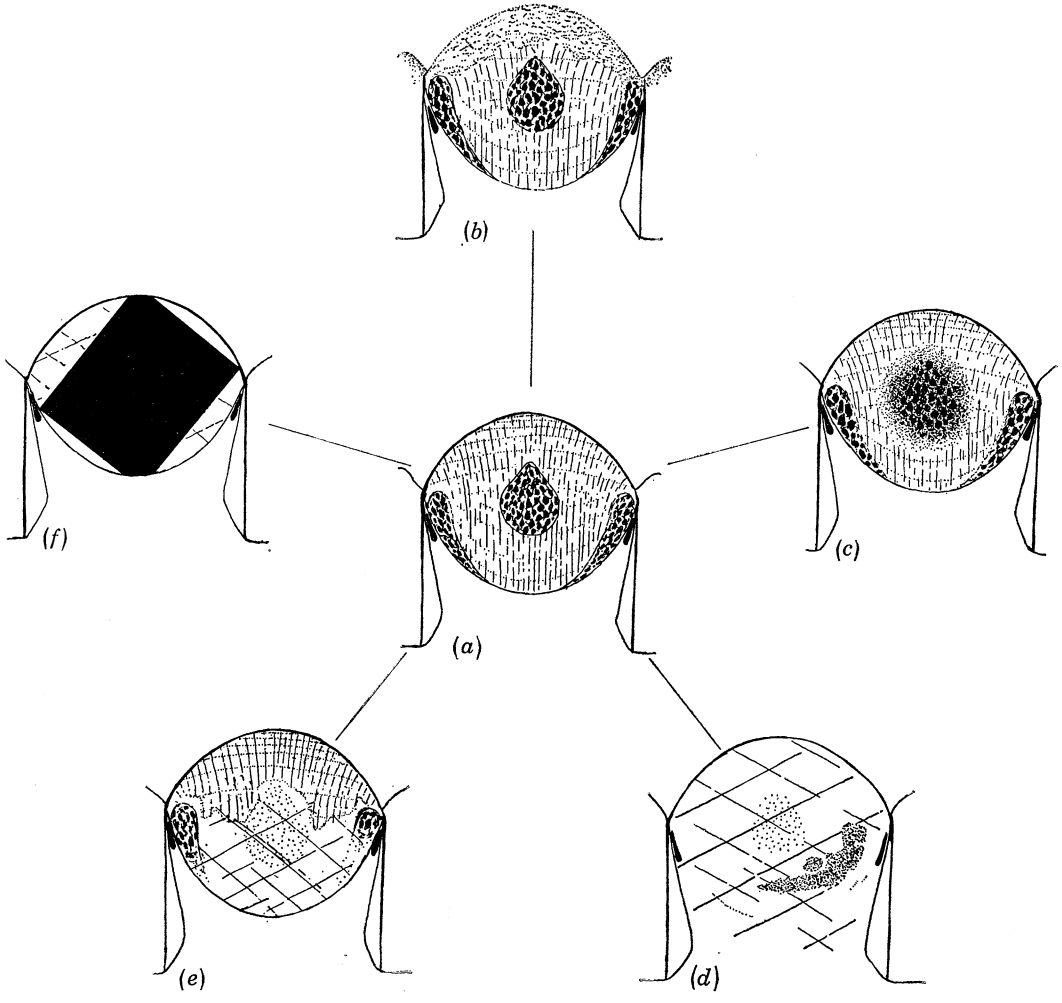


FIGURE 1. Diagenetic changes that have been observed in the eyes of *Phacops rana milleri* Stewart 1927 from the Silica Shale of Ohio. (*a*) Intact lens with bowl and core; (*b*) micritization of the outer part by endolithic algae; (*c*) apparent expansion of core by outward migration of core material; (*d*) complete recrystallization of lens and sublensar alveolus involving neomorphism and occlusion of primary voids by epitaxial cements; (*e*) recrystallization of part of lens; (*f*) partial or complete pyritization, in this case replacement of calcite by a large single pyrite crystal.

4. The structure and the post-ecdysial development of the intermoult cuticle

(*a*) *Terminology*

The terms used herein to describe the *P. rana milleri* cuticle are those suggested by Dalingwater & Miller (1977), who recognized an outer prismatic layer and an inner principal layer, the latter composed of three texturally distinct zones. Terminology of accessory (sensory) structures in the cuticle follows Miller (1976).

(*b*) *Intermoult cuticle* (figures 14–16)

A general description of intermoult cuticle has been given by Miller (1976) for several subspecies of *P. rana*. Fragments of thoracic pleura from the exuvial thoracopygon of AMNH 29282 (figure 5) show similar features to other *P. rana milleri* cuticle samples, whether from isolated exuviae or from enrolled individuals, and are also typical of intermoult cuticles in all other subspecies of *P. rana* so far examined.

The cuticle ranges between 300 and 500 μm in thickness and is heavily pigmented brown or almost black. Its glossy surface is due to the presence of a thin outer layer, possibly analogous to an epicuticle. The 10 μm thick prismatic layer is not readily seen in etched preparations because it etches back far more rapidly than the other layers or zones. Electron microprobe scans across the thickness of cuticle failed to reveal any significant differences in chemical composition between prismatic and principal layers, and this consistent response to EDTA etching may probably be attributed to the larger size and coherent *c*-axis normal orientation of the prismatic layer calcite crystallites.

The principal layer, comprising the bulk of cuticle thickness, is clearly divided into three distinct zones. The innermost and outermost zones are composed of finely textured calcite crystallites and show traces of narrow laminae about 10–20 μm apart, while the central zone crystallites are very much coarser and there are only a few, widely spaced laminae. The triple zonation is present throughout most of the cuticle but is lost at the doublure and at the intersegmental articulations (figure 16). Scleral cuticle also shows the triple zonation, but its laminate character is far more marked than that elsewhere (figure 19). Much of the upper zone in the scleral region has been lost by etching, but this and the lower zone show a finely laminate, compact arrangement of calcite crystallites (figure 26). Laminae of the lower zone appear to continue across the corneal membrane bounding the lens capsule, passing into the alveolar ring; on either side of the membrane, the laminae become steeply divergent in a distal direction. The middle zone of the scleral areas is more coarsely laminated than is cuticle elsewhere. The scleral cuticle appears to lack the characteristic widely spaced 'major' laminar boundaries seen in non-specialized cuticle, and a general impression is gained that the scleral organization is differentiated for its function in support and regeneration of the visual complex (see § 6).

Both scleral and non-scleral cuticle are richly supplied with vertical elements opening into surface pits. These have been described in detail by Miller (1976, pp. 346–353), and are considered to represent the sites of former sensory setae varying in size, strength and flexibility.

Pseudotubercles (Miller 1976, p. 351) are local raised thickenings of cephalic cuticle, which contain mushroom-like bundles of ducts. They are considered to be differentiated sensory organs, possibly with a long distance chemoreceptory (olfactory) function.

Close comparisons of cuticles from enrolled *P. rana milleri* (which may be presumed to represent dead intermoult-stage animals), with isolated ecdysed cephala and pygidia have revealed no detectable differences in their layering, zonation, or thickness. In particular, the exuvial cuticle of AMNH 29282 is indistinguishable from the cuticle of a comparably sized enrolled individual. Intermoult and ecdysed cuticles from *P. rana rana*, *P. rana crassituberculata* and *P. rana africanus* are also identical, as far as can be determined. It must be concluded that during moulting these trilobites shed the entire intermoult exoskeleton without significant prior resorption of carbonate. This conclusion is borne out by our study of the *Phacops* visual system and its post-ecdysial regeneration, and, as discussed in the final section, has considerable implications for the biology of trilobites.

(*c*) *Post-ecdysial cuticle* (figures 4*a*, 11–13)

Apart from their being considerably thinner, the post-ecdysial cuticles are comparable to intermoult cuticles in possessing a well developed epicuticle and prismatic layer; they have, however, a very much thinner principal layer. The epicuticle is illustrated in figure 12; its appearance under s.e.m. is that of a somewhat fibrous film with small embedded calcite crystals. It burns away rapidly in the electron beam above 10 kV potential, especially if the beam is directed on one particular spot.

Beneath the epicuticle is a prismatic layer of typical trilobite type and of normal thickness (10 μm) for *P. rana milleri*. The large calcite crystallites are arranged with their *c*-axes normal to the surface, and the surface shows an even and regular crystal texture (figure 13).

The principal layer varies in thickness from 25 to 500 μm in the suite of post-ecdysial specimens. Its calcite crystallites are smaller and lack the uniform orientation of the prismatic layer. No traces of laminar organization have been observed, nor is there any indication of zonation in the principal layer at this early stage.

Vertical ducts opening into pits are present in all the post-ecdysial cuticles (figures 12, 13); the typical intermoult size ranges of duct appear, and surface socket pits and fossettes are distributed exactly as in intermoult cuticles. However, the pseudotubercles are undifferentiated; they are represented by inflated areas without cuticular thickening and without the differentiated mushroom bundle of ducts characteristic of final intermoult stages.

The thinnest cuticles in the suite of post-ecdysial specimens have all been wrinkled as the trilobites were subject to post-mortem compaction. In many instances, double folds have been developed, especially near the eyes (figure 44, 45). Some brittle fracture of the cuticle has occurred, but it seems that in the early stages the cuticle was essentially flexible, as would be expected if calcification was incomplete. Later stages (e.g. RSM GY 1979.11.1) are nearly undistorted and have cuticles with comparatively thicker principal layers, though still thinner overall than in the intermoult stage. This supports the contention that trilobite cuticles developed their strong calcification on a matrix or template of organic matter (Dalingwater 1973; Dalingwater & Miller 1977).

(*d*) *Post-ecdysial development of the cuticle*

Prior to ecdysis the new epicuticle and prismatic layer must have been formed above the hypodermis and the moulting split must have occurred between the neo-epicuticle and the proximal margin of the old principal layer. Presumably, as in modern crustaceans, sensillae,

ducts etc. were already formed within the new cuticle, and, in the same way, setae were probably everted by friction during shedding of the exuviae.

It is impossible to be certain if any of the principal layer was laid down before ecdysis, although evidence from the eye (pp. 474–478) might suggest that only the epicuticle and prismatic layer were complete at ecdysis. The subsequent development of the cuticle must have involved the inward progress of calcification, thickening of the principal layer and development of the characteristic intermoult zones.

5. The mature eye and its lens structure

The gross morphology of the eye of many phacopacean and dalmanitacean trilobites has been described (Lindström 1901; Rome 1936; Clarkson 1966*a*,*b*, 1967, 1969, 1979; Campbell 1975) and needs little further comment. In all schizochroal eyes the lenses are separate (figures 3, 4*b*) and each has its own corneal membrane which leaves the periphery of the lens to plunge through the interlensar sclera as a cylindrical ring (intrascleral membrane). The lens is evidently compound, with an 'intralensar bowl', whose function has recently been interpreted (Clarkson & Levi-Setti 1975; Clarkson 1979) as an optical correcting element, within it. In dalmanitacean trilobites the sclera is normally thinner than the lenses (Clarkson 1975), but in phacopaceans it is thick, so that the lens is set at the top of a cylindrical cavity, the sublensar alveolus.

Our new information contributes to the understanding of the microstructure of the cuticular intralensar sclera, which is broadly comparable with that of the rest of the cuticle, and to the minute structure of the lenses.

(i) *The lens capsule*

The lens, the corneal membrane and its prolongation, and the intrascleral membrane, together with the scleral material lying within the intrascleral membrane, all form parts of a developmentally discrete structure, here termed the lens capsule. It is only through the study of the post-ecdysial development of the lenses that this has become clear (*q.v.*), for in the mature eye it is solely apparent in the real discontinuity of the laminae within and without the intrascleral membrane.

(ii) *The structure of the lens in* P. rana milleri *as shown by s.e.m. and cathodoluminescence microscopy* (*figures* 3 *and* 4)

Much has been written about the structure of the mature lenses in adult phacopacean trilobites, but interpretations, by various authors, of intralensar structures have tended to be contradictory and sometimes confusing. This is almost entirely because of diagenetic modification of primary structure. Indeed, such alteration has often gone so far that virtually all trace of primary structure has disappeared (see, for example, figure 34 compared with figure 41). To disentangle the primary from the secondary elements it has been necessary to use new techniques. We have found that the EDTA etching process, previously applied to the study of trilobite cuticle by Miller (1975, 1976), is highly satisfactory, and, together with luminescence microscopy, has helped to resolve not only what the primary structures are, but also the various diagenetic pathways that lead to interpretative problems. In previous work (Lindström 1901; Clarkson 1966*a*, *b*, 1967, 1968, 1969; Clarkson & Levi-Setti 1975) the existence of the intralensar bowl in many phacopid species was established.

Towe (1973) made thin sections of the eyes of *P. rana milleri* and found no trace of intralensar bowls. But, as shown later, one diagenetic pathway leads from a highly structured lens with real internal differentiation to an altered lens of clear or cloudy calcite, crystallographically syntaxial with the original structure and looking deceptively primary in origin.

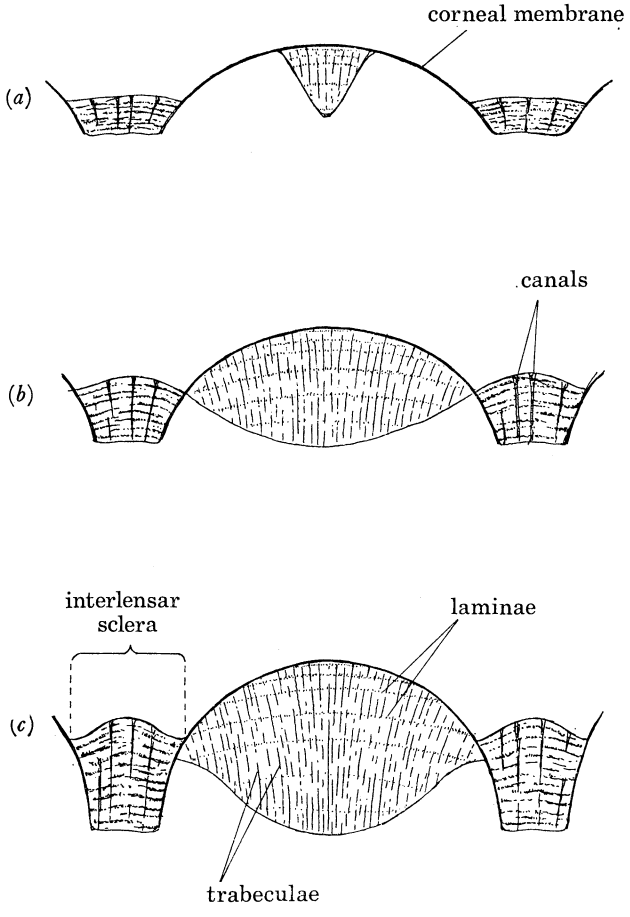


FIGURE 2. *Phacops rana milleri* Post-ecdysial development of the lens. (*a*) Initial conical lens (cf. figure 39, plate 6; figures 46, 47, plate 7); (*b*) thin biconvex lens (cf. figure 18, plate 3); (*c*) Huygens lens, before the differentiation of the core and addition of the intralensar bowl (cf. figure 20, plate 3).

The most recent work on the fine structure of phacopacean lenses is that of Campbell (1975), who worked on *P. rana milleri*, *Phaciphacops raymondi*, and other North American Devonian Phacopacea. This valuable study has given much new detail of lens structure, as well as confirming previous work. The techniques used by Campbell included examination of the surfaces of silicified specimens where the outer cornea has broken away revealing the internal structures, and also the preparation and examination of thin sections and polished surfaces, which were observed under oil.

The important elements distinguished by Campbell were the intralensar bowl 'formed of calcite with many inclusions', below which is a basal layer of 'clear, randomly oriented microcrystalline calcite', and a large pear-shaped central core, sometimes in contact with the basal layer, at other times located well above it, and always with its *c*-axis parallel with the lens axis.

In the upper unit the *c*-axes of the more peripheral calcite crystals turn outwards fanwise, so as to make a lesser angle with the external surface than if they had been horizontal. Within the upper unit there are laminations, probably organic in nature, and with a somewhat lesser curvature than the outer lens surface. The outer cornea appeared to Campbell to be multilayered and probably with random crystallographic orientation.

The observations that we have made with our etching technique largely confirm Campbell's studies on the eyes of *P. rana milleri*, but extend them so that for the first time it is possible to

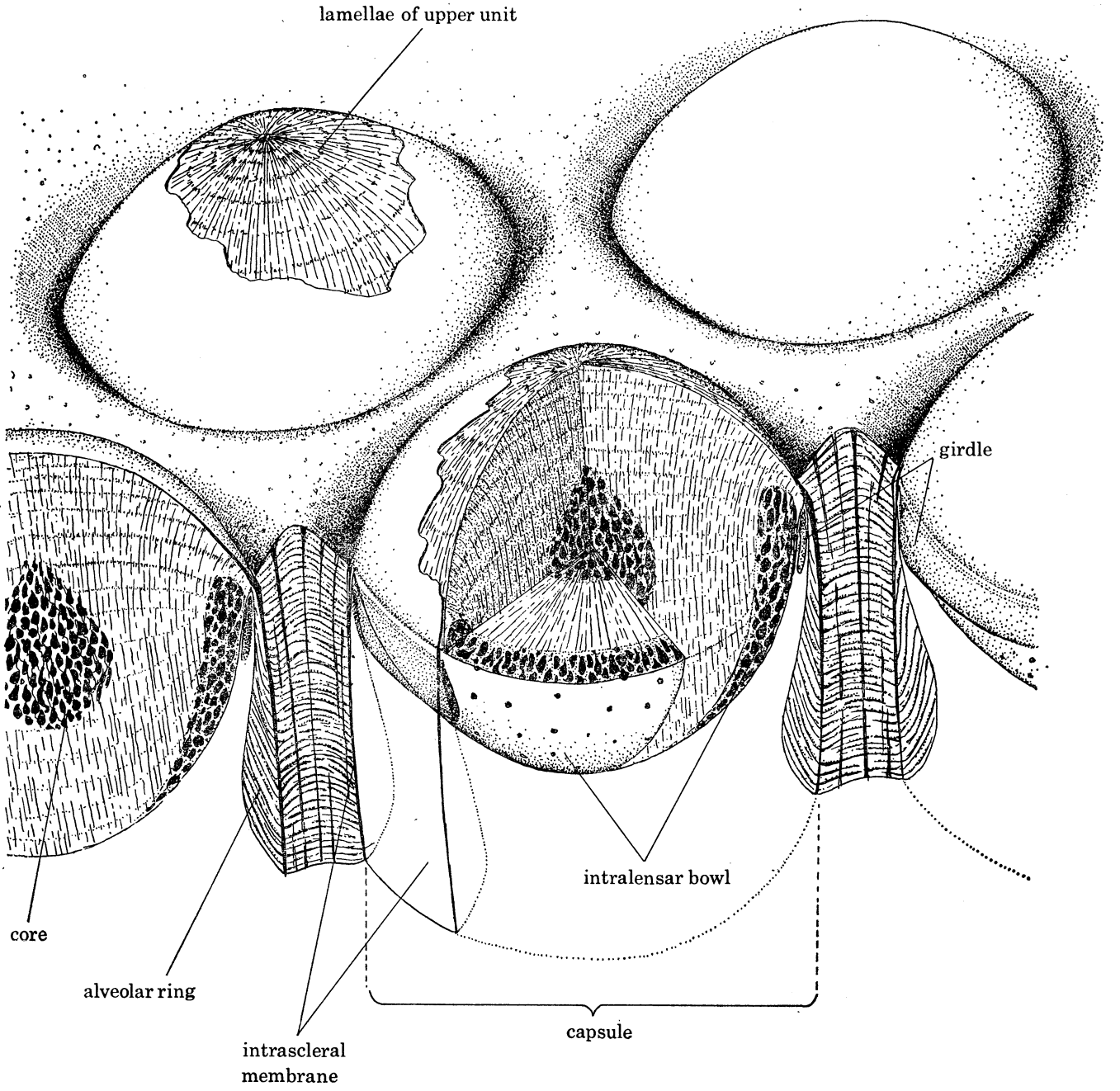


FIGURE 3. Diagrammatic representation of the mature eye of *Phacops rana milleri*, with lenses dissected to show internal structure. Details of corneal structure have been omitted for clarity.

visualize the lens as a three-dimensional structure and to determine its detailed micro-organization.

The elements of lens structure are broadly as Campbell described them, and the core, bowl and laminae in the upper unit are all confirmed as real internal parts, regarding which the s.e.m. reveals a wealth of detail.

A new and important fact to emerge from the study of tangential sections is that the whole lens, like that of the holochroal eye (Clarkson 1979), is constructed of calcitic plates arranged radially round the central axis (shown vertical in standard orientation). This radial appearance shows most clearly in sections cut normal to the axis and parallel with the principal plane of the lens, and in external elements exposed when the cornea is stripped off. All other internal elements within the lens relate in some way to this radial organization, which is here described in detail for the first time. It has hitherto been tacitly assumed that schizochroal lenses were constructed as simple, single crystals of calcite since they behaved optically in this way. We now realize that their open mesh construction is analogous to that of echinoderm ossicles and plates, presumably reflecting a similar strategy of economy in fabrication combined with functional efficiency.

(*a*) *The cornea*

Campbell (1975, p. 174) described this as the 'outer layer', and correctly indicated that it is composite. He describes it as three-layered, with a central dark layer sandwiched between two clear layers, of which the inner one thickens peripherally and interdigitates with the distal part of the upper unit. He regards it as being continuous with the basal layer of the lens. Our s.e.m. preparations also show that there are three layers, indicated on figure 4 together with their correspondences to scleral layers. The cornea (figures 4*b*, 22, 23) consists of an outermost organic epicuticle which covers both lens and sclera, below which is the corneal layer, continuous with and homologous to the cuticular prismatic layer. The corneal layer does not continue into the lens capsule (figure 4*b*) but wedges downwards at the periphery of the lens.

Below the cornea is a corneal membrane (continuous with the intrascleral membrane), which plunges through the scleral pillar and bounds the lens capsule (figure 26). There is a marked change in orientation of cuticular laminae in the sclera on either side of the intrascleral membrane.

(*b*) *The upper unit*

In tangential section the radial structure of the upper unit is very clear. In the specimen shown in figures 31 and 32 there has been an incipient diagenesis; nevertheless, the radial plates are visible, especially in the outer part of the eye. This slice is cut just above the level of the intralensar bowl, but goes through the core, which has been expanded through diagenesis. The appearance here is like a lacy meshwork with the radial lamellae being dominant; these seem to retain constant thickness, but new radial lamellae were intercalated between them as the lens grew. In a vertical slice (figures 19, 33, 34) the same kind of meshwork is evident, but the main elements are more or less vertical (parallel to the lens principal axis), though turning out in a fanlike structure just below the cornea. Hence, the radial plates seen in transverse section are not solid, but more like individual net curtains, with a generally vertical pattern. The calcite needles of which they are formed (trabeculae) are parallel with the lens axis in the lower part of the lens, but veer outwards towards the top so as to make an angle of some 70° to the upper lens surface at its periphery. This accords with Campbell's description of the

arrangement of the calcitic axial structure, which he deduced from the study of extinction patterns between crossed nicols.

The upper unit, like the core of the lens, is traversed by well marked subconcentric laminae, which become increasingly closely spaced towards the cornea (figure 19), and which are shown clearly by cathololuminescence (figures 35–38). These laminae are bounded by deeply etched slots, which were observed during etching to contain a thin, fragile, translucent membrane, presumably organic in composition. These observations are closely comparable to those made for laminar units of *Asaphus* cuticle (Dalingwater & Miller 1977), and the membranes are probably laminar membranes. Such laminae have been described in *Reedops bronni* (Clarkson 1969, p. 196–8, text-fig. 5; pl. 3, figs 5–6) and, by Campbell, in various phacopids (1975, p. 175, pl. B, fig. 6). Campbell's most striking photograph shows a specimen of *Phaciphacops birdsongensis* (Delo) (Campbell 1975, pl. 5, fig. 3), having silicified laminae through which the top of the central core projected.

The laminated region of the upper unit corresponds to an inverted bowl-like region in the lens of *P. latifrons* (Clarkson 1967, pl. 99, fig. 5; text-fig. 2*g*, where it is marked as 'x'), suggesting that the latter is a diagenetically modified version of the same structure bounded by the lowermost lamina. Some of Campbell's figures show a similarly accentuated laminar zone (Campbell 1975, pl. B, figs 3, 4), which may seem to be disproportionately pronounced in abaxial sections, not because of a real difference in composition, but by virtue of the change in direction of the calcite crystallites within the upper unit. The organic interfaces of the laminae seem, in addition, to have acted as centres of diagenesis modifying the structure further.

(*c*) *The core*

The pyriform core of Campbell is probably equivalent to the 'proximal nucleus' described by Clarkson (1967). But, since diagenesis had modified the original structure of the *Ananaspis* specimens upon which the original term was based and since Campbell's concise term 'core' refers to an apparently unmodified and real structure, Campbell's term is to be preferred. The core consists of very dense ferroan calcite (figures 19, 24, 25), clearly distinct from that of the upper unit. When subjected to longer periods of EDTA treatment than normal, it is etched into cavities, but whether or not there were original cavities within it is unknown. The reconstruction (figures 3, 4*b*) shows such cavities, since they appear in most of our preparations. There is a striking equivalence in the appearance of the calcite of the core and that of which the ferroan calcite intralensar bowl is constructed. Campbell (1975, pl. B, fig. 7) illustrates a core and bowl of similar dimensions to those of our material. In other sections, however, the core seems to be appreciably larger. We have noticed a similar effect in several of our thin sections and also on a few of our etched tangential faces. The excess dimensions of the core appear to be related to a diagenetic front growing out from the core and enlarging it preferentially, with calcite cements epitaxially growing and occluding primary void fabric (figure 1). The dimensions of the core given in our reconstruction appear to us to be in keeping with its shape and size in unaltered material. Laminae passing through the core are seen by cathodoluminescence microscopy (figure 37), though these are less evident in s.e.m. preparations.

(*d*) *The intralensar bowl*

In schizochroal lenses the bowl is one of the constant structures to be found in nearly all preparations. In *P. rana milleri* the upper rim of the bowl is thick and rounded, but below this lip the bowl becomes much thinner, almost vanishing centrally below the core (figures 17, 19, 26, 34, 37, 38). Such a bowl structure seems to be a little unusual in Phacopina, though in *Reedops* species the bowl may also be reduced in thickness axially. The bowl in the species under discussion is very deep, rising high up the sides of the lens. Such morphology contrasts strongly with the much flatter bowl of the Dalmanitacea, which has been the subject of independent study elsewhere (Clarkson & Levi-Setti 1975).

The similarity in its texture and composition to that of the core has already been noted. Both bowl and core may be coarsely recrystallized high ferroan replacements, perhaps of original high magnesium calcite structures. Richter & Füchtbauer (1978) have suggested such replacements to be common in former high magnesium skeletal calcites. Electron microprobe studies show that *P. rana* cuticles are presently low in magnesium, but magnesium is lost during neomorphism and it is not otherwise possible to determine if all cuticle and intralensar structures were originally rich in magnesium or if the bowl and core were differentiated in this respect. Certainly, were the calcite composition of both bowl and core different in this way, this might give the required shift in refractive index to enable them to function as correcting elements as discussed on page 478. No lamination of the bowl has been observed with the s.e.m., but cathodoluminescence microscopy shows very clear concave laminae in the bowl (figure 38).

(*e*) *The girdle* (*figures* 26, 40, 41)

This constant feature of phacopid lenses has hitherto escaped description. It is an annulus of very fine-grained calcite crystallites encircling the lens parallel with its principal plane and just below its widest part, at the junction of the lens with the sclera. It appears dense, whitish or pale grey in thin section. It consistently etches far more rapidly than other lens elements. The girdle is always present, and, though not part of the lens itself, is apparently an integral component of the visual system, as it lies within the lens capsule. Its function, however, can only be speculated on.

(*f*) *Sublensar cylinders*

In one specimen of *P. rana africanus* wherein the lens was incomplete (in that the bowl had not been added), a pair of symmetrical calcitic horns are seen projecting from the bottom of one of the lenses into the matrix (figure 41). These must be part of a downwardly flaring cylinder, whose upper aperture seems to be attached to the curving lower surface of the lens, though well within its circumference. The symmetry would suggest that this is an original part of the visual complex, though, in the absence of other evidence, it cannot be fully substantiated. No such structures have so far been seen in *P. rana milleri*.

6. Post-ecdysial development of the lenses

Enough material has been available for us to have been able to trace the nearly complete development of the lens from a very early post-ecdysial stage to maturity.

(*a*) The earliest stage in post-ecdysial development (figures 2*a*, 39, 46, 47) is shown by the newly moulted intaglio of AMNH 29282. Here, the cornea was apparently flexible, as the

wrinkling of the eye surface shows. Where the cornea is translucent the embryonic upper unit of the lens can be seen through the transparent cornea as a clear, small, dark circle, 150 μm across in the centre of the lens. The whole corneal surface is about 650 μm across and the lens hangs suspended from the proximal surface of the cornea. At this stage the lens forms a steep-sided cone whose proximal point lies in approximately the same plane as the lower surface of the sclera.

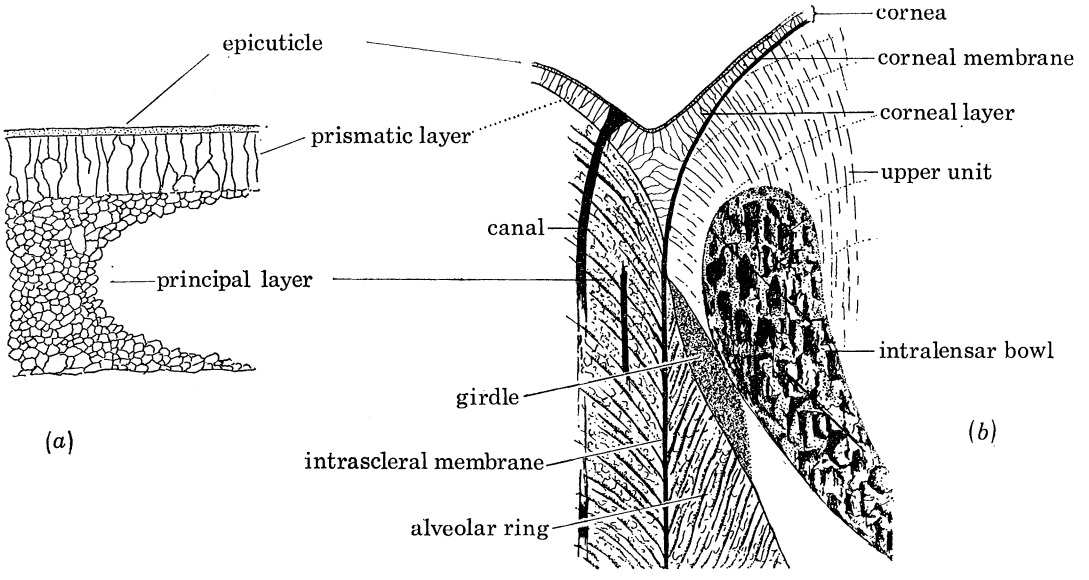


FIGURE 4. (*a*) Structure of thin (30 μm) post-ecdysial cuticle of *Phacops rana milleri* (cf. figure 11, plate 2); (*b*) structure of edge of mature lens and sclera, showing terminology and relation of the various parts.

The true shape of the early post-ecdysial lens has been determined by removing a fragment of the eye of AMNH 29282 and dissolving out the lens so that the internal mould could then be photographed (figures 46, 47). The sides of the cone are slightly incurved and the tip truncated. In addition, the form of the lens shows up, though not so clearly , in a s.e.m. photograph of an etched surface of part of RSM GY 1979.11.5 (figure 39). As the specimen is severely recrystallized, however, the shape is less evident and nothing can be made of the internal structure of the lens. This early stage in the development of the lens must have been constructed on a radial plan, however, as it is retained in the mature intermoult lens as the small central 'aster' (figures 29, 30).

(*b*) The next stage in development is shown by figures 2*b*, 18. Here the lens has grown right to the periphery of the cornea and has lost its conical form, becoming biconvex, the lower surface being slightly more curved, as in the olenids (Clarkson 1973). The lowermost part of the lens still lies in approximately the same plane as the proximal edge of the sclera. In our material, unfortunately, all examples displaying this stage in development have been slightly recrystallized.

(*c*) A little later, the lens has become thicker, as has the sclera, and the proximal surface of the lens has assumed a Huygensian form (figures, 2*c*, 20). In some of our specimens at this stage there are good indications of curved laminations in the upper part of the lens, even though there has been some degree of recrystallization.

Description of plates 1–3

Plate 1

Phacops rana milleri Stewart 1927, Middle Devonian, Silica Shale, Ohio.

Figures 5, 7–10. Mature and post-ecdysial specimens in various stages of development.

Figure 5. A large, thin-cuticled (30 μm), recently ecdysed individual (left) overlies an exuvial cephalon, and (right) thoracopygon (AMNH 29282). Magn. × 1.7.

Figure 7. Thick-cuticled (135 μm) and nearly completed intermoult intaglio (RSM GY 1979.11.3). Magn. × 1.35.

Figure 8. Specimen with cuticle of intermediate thickness (40 μm), showing patches of darker material. Right eye now removed. Specimen figured by Levi-Setti (1975, p. 13, pl. 5) (RSM GY 1979.11.1). Magn. × 1.5.

Figure 9. Left eye of same. Magn. × 6.

Figure 10. Thin-cuticled (20 μm), post-ecdysial intaglio, indifferently preserved (RSM GY 1979.11.4). Magn. × 1.5.

Figure 6. *Cheirurus centralis* Salter 1853, Wenlock Limestone, Dudley. Thin-cuticled (20 μm) specimen shown for comparative purposes; cf. Lane 1971, pl. 5, figs 1–6, 8–12 (QUB 2732). Magn. × 1.5.

Plate 2

Phacops rana milleri. Structure of post-ecdysial and mature cuticle.

Figure 11. Broken fracture surface of thin post-ecdysial cuticle, 35 μm thick, showing outer prismatic layer and thicker principal layer (AMNH 29282). Magn. × 650.

Figure 12. External surface of cuticle of same specimen, etched with EDTA and showing calcite crystallites of the prismatic layer; openings of 10 μm wide setal canals partially overlain by thin organic epicuticle (AMNH 29282). Magn. × 650.

Figure 13. External surface of unetched intermoult cuticle showing calcite crystallites of outer prismatic layer with a setal pit (AMNH 29282). Magn. × 2000.

Figure 14. Ground and etched section of intermoult cuticle showing etched outer prismatic layer (above), setal canals filled with secondary calcite, and triple layering (Gr I 46150). Magn. × 65.

Figure 15. Polished and etched section through intermoult cuticle, 300 μm thick, showing deeply etched outer prismatic layer and triple layering in the principal layer (Gr I 46151). Magn. × 45.

Figure 16. Similar section through intersegmental articulation of pleura showing loss of triple zonation (Gr I 46151). Magn. × 45.

Plate 3

Phacops rana milleri.

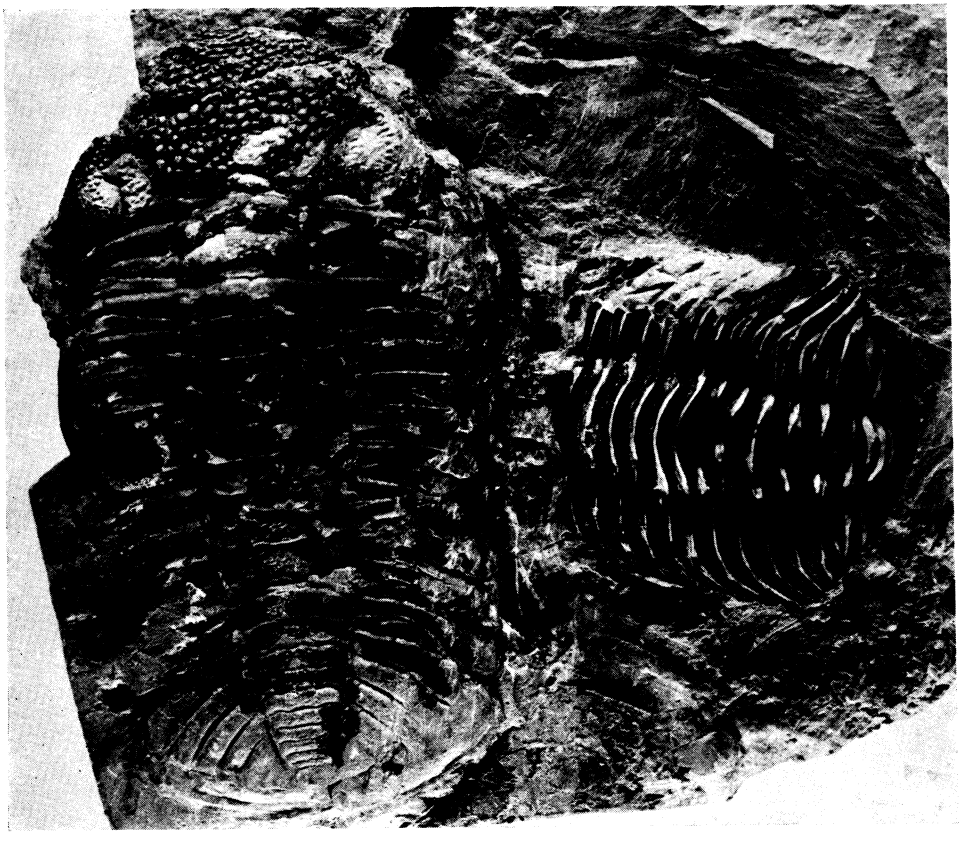
Figure 17. A single, etched, unaltered lens, cut obliquely off centre, showing radial lamellae of the upper unit, and bowl partially obscured by matrix (Gr I 46153). Magn. × 100.

Figure 18. Post-ecdysial lens of biconvex form equivalent to stage 2 of figure 2*b*, somewhat micritized, cuticle 20 μm thick (RSM GY 1979.11.4). Magn. × 45.

Figure 19. Montage scanning a slightly oblique vertical section etched with EDTA, through four adjacent lenses of a single dorso-ventral file. This specimen has suffered very little diagenetic alteration. Lens A is grazed at the edge, showing the more massive texture of the intralensar bowl and the finer texture of the upper unit (see also figure 5 and plate 4). Lens B, cut almost centrally, shows the core (c.), intralensar bowl (i.b.), and upper unit (see also figure 26*j*). Deeply etched cleavage planes show the crystallographic structure of the calcite. Lens C, cut off centre, shows the bowl and the upper unit; only the edge of the bowl in lens D is present (Gr I 46152). Magn. × 100.

Figure 20. Post-ecdysial lens of Huygensian shape equivalent to stage 3 of figure 2*b*, somewhat altered, but with traces of laminae still present; cuticle, 50 μm thick (Gr I 46162).

Figure 21. Partially altered and recrystallized lens, which still retains traces of the bowl and pronounced laminae (Gr I 46154). Magn. × 100.



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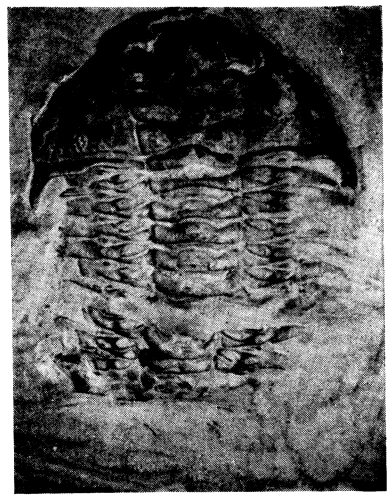

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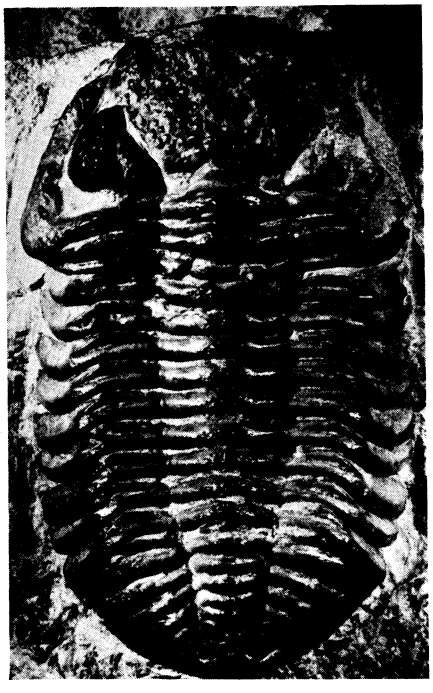

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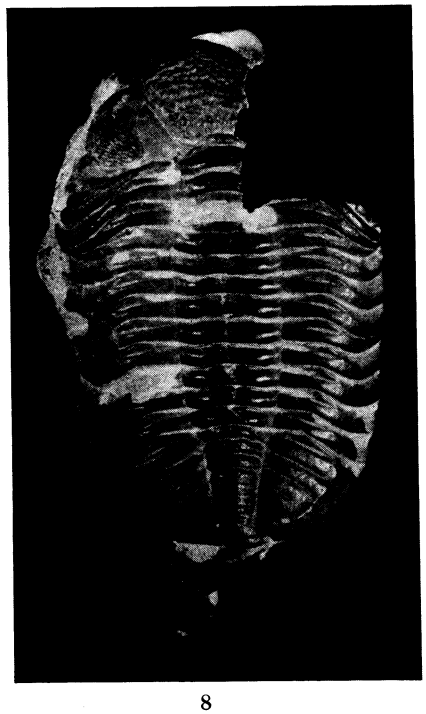

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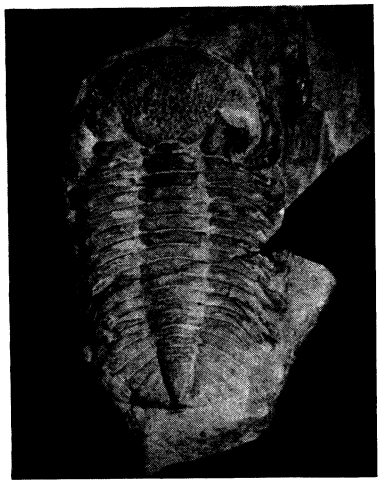

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FIGURES 5–10. For descriptions see opposite.

(*Facing p.* 476)

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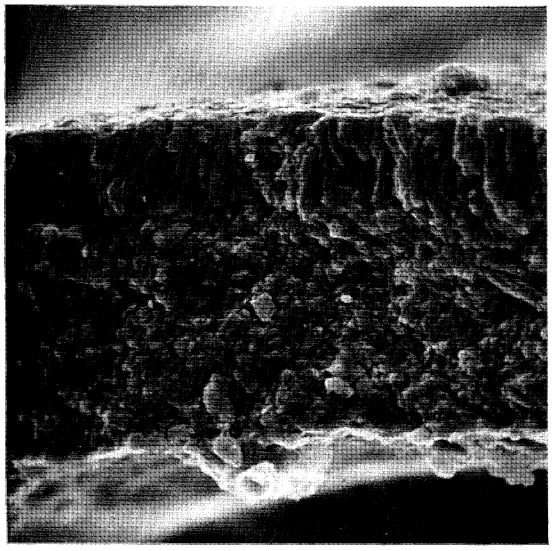

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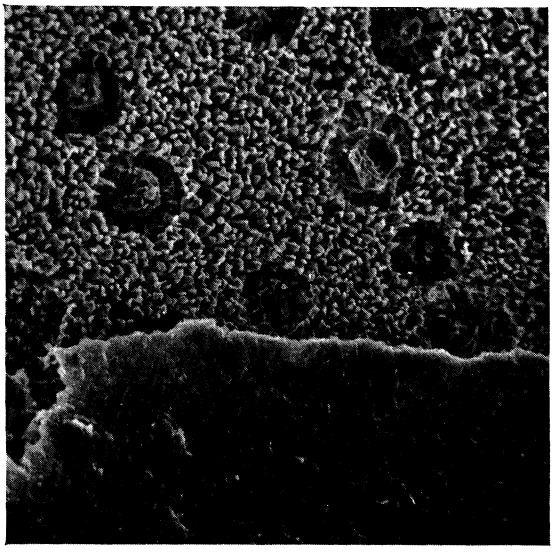

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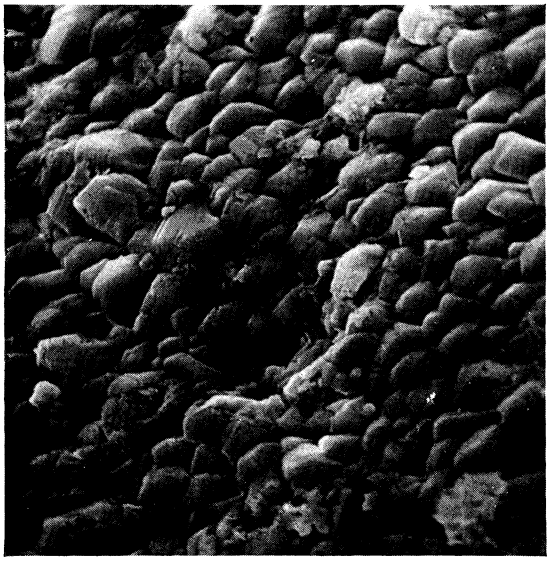

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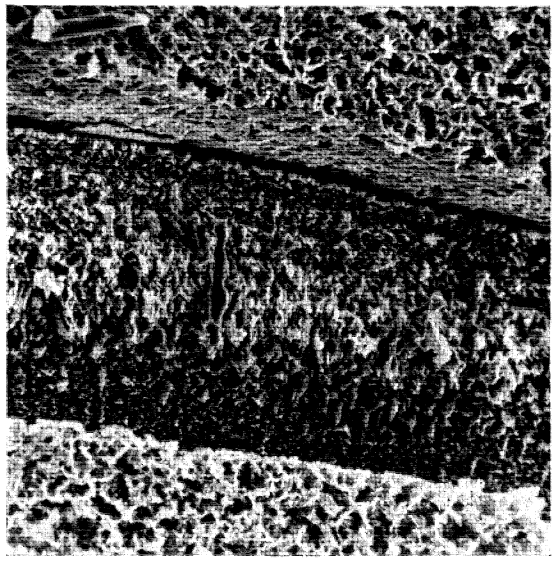

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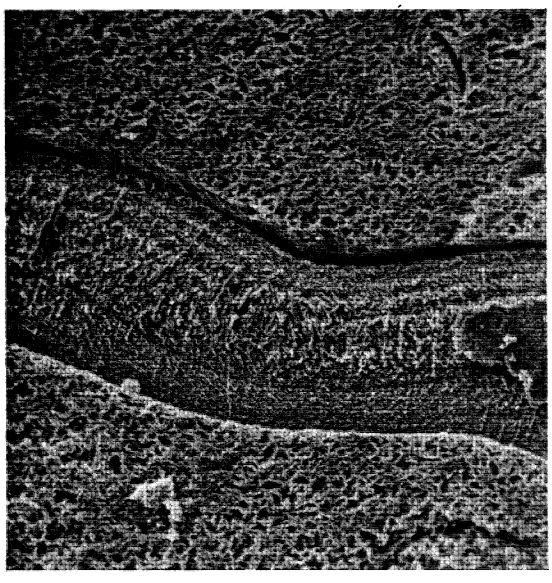

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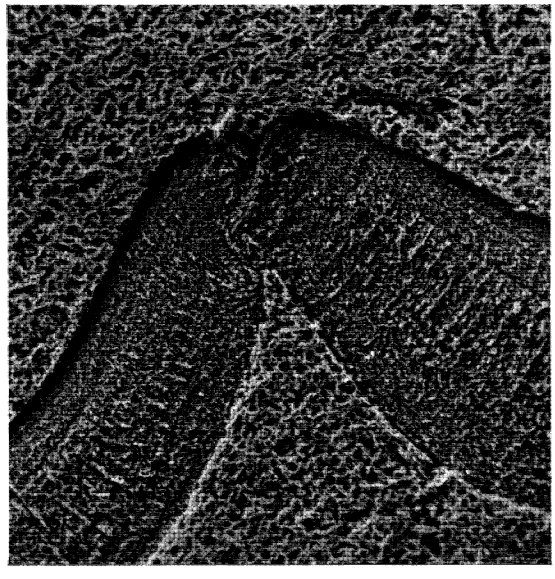
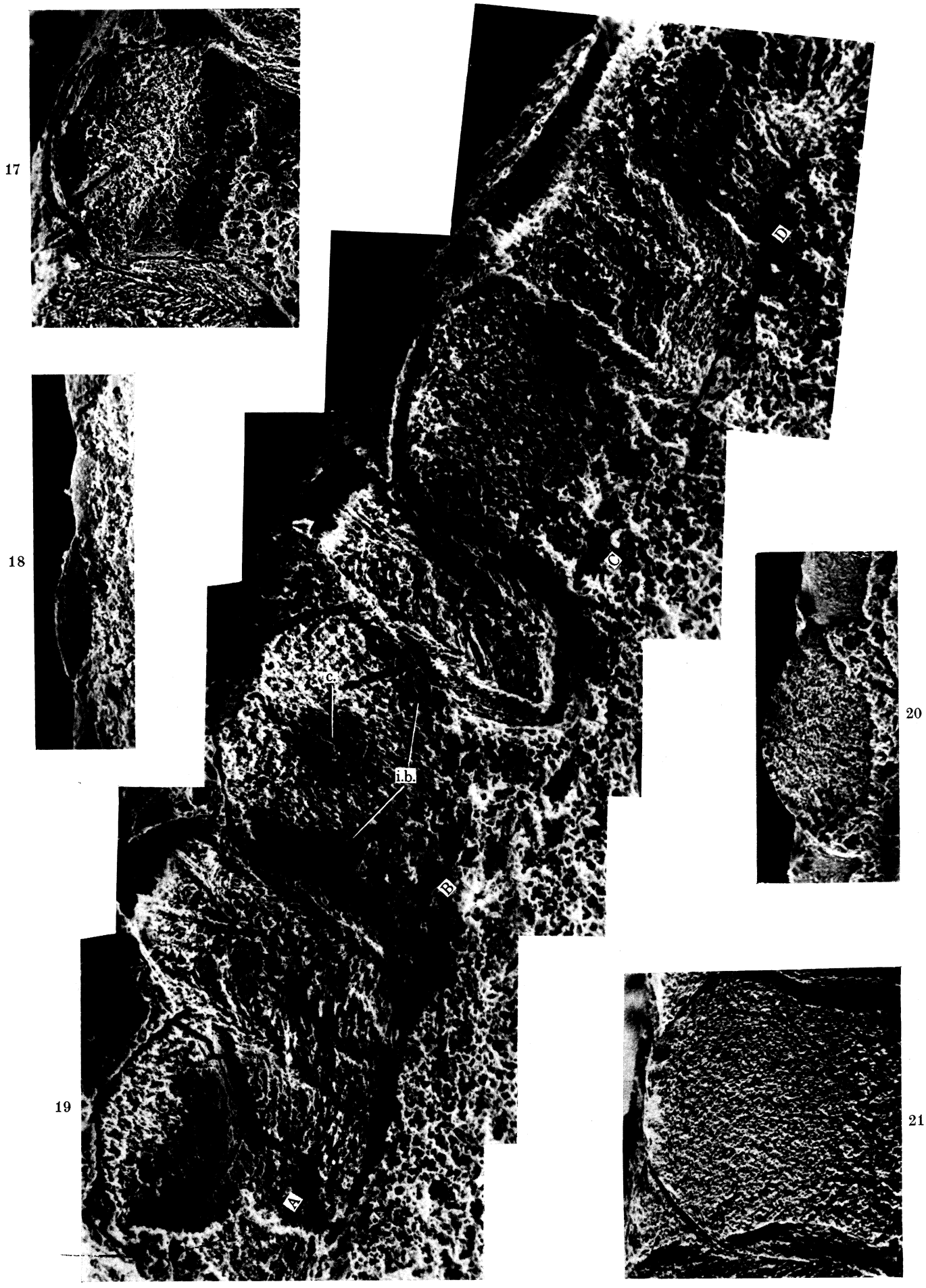


FIGURES 11–16. For description see page 476.



FIGURES 17–21. For description see page 476.

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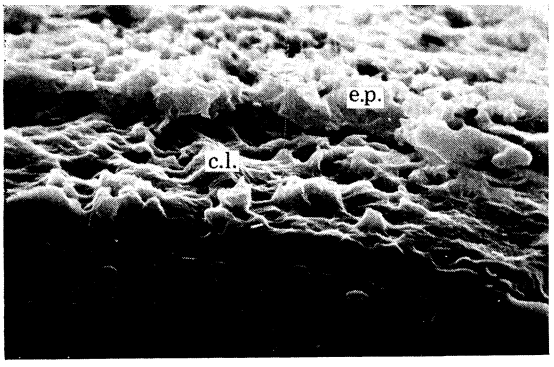

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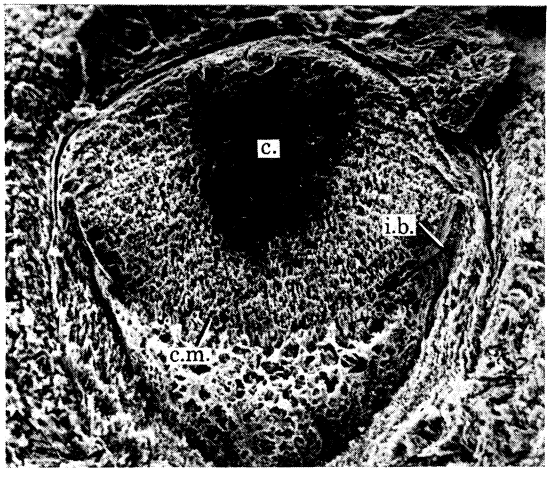

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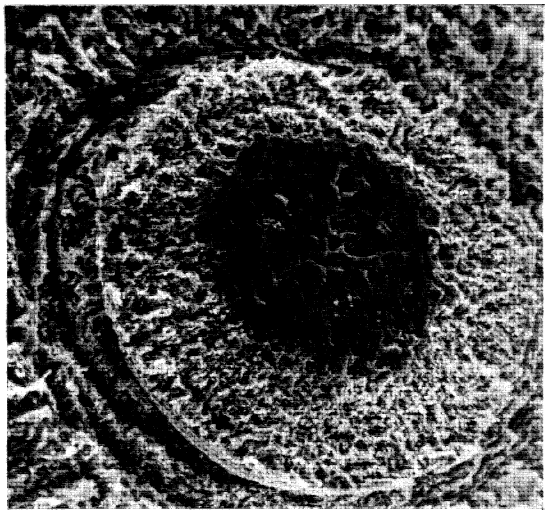

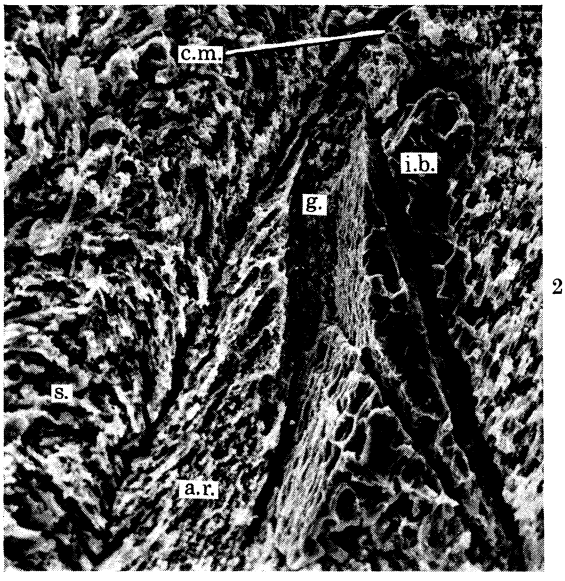

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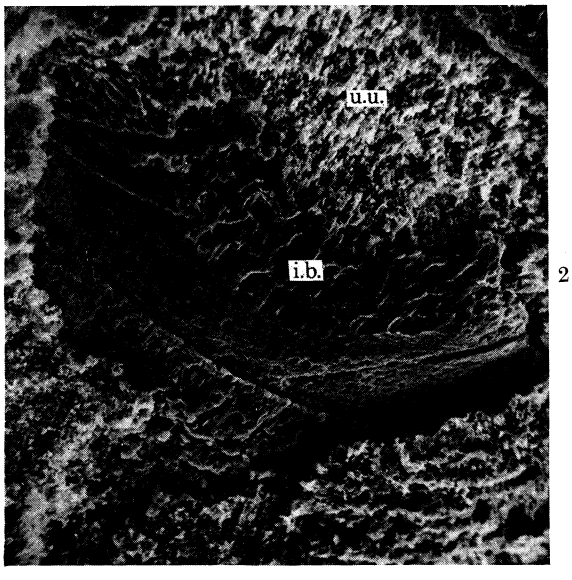

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FIGURES 22–28. For descriptions see opposite.

Description of plate 4

Phacops rana milleri.

Figures 22 and 23. Oblique view of outer surface of vertically sectioned and etched lens, showing epicuticle (ep.), with surface of corneal layer (cl.) below lying above slightly recrystallized upper unit (Gr I 46155). Figure 22 magn. × 1800; figure 23 magn. × 435.

Figure 24. Single lens, cut obliquely and etched showing core (c.), slightly enlarged by diagenesis, radial lamellae, laminae, thin edges of intralensar bowl (i.b.), and, below, matrix filling of alveolus and corneal membrane (c.m.) (Gr I 46156). Magn. × 100.

Figure 25. Section cut in principal plane of lens, showing core, probably expanded by incipient diagenesis, slightly altered radial lamellae of upper unit, intralensar bowl (crescent on left hand side) and deeply etched ring of corneal membrane (Gr I 46157). Magn. × 100.

Figure 26. Left hand edge of lens B in figure 19, plate 3, with well marked calcitic bowl (i.b.) and upper unit traversed by a deeply etched cleavage plane; girdle (g.), sclera (s.), corneal membrane (c.m.) and alveolar ring (a.r.) (Gr I 46152). Magn. × 200.

Figure 27. Same lens showing etched trabeculae of upper unit in vertical section (Gr I 46152). Magn. × 400.

Figure 28. Enlargement of obliquely cut and etched lens A in figure 19, plate 3, showing junction of massive textured bowl (i.b.), and more open textured upper unit (u.u.) (Gr I 46152). Magn. × 200.

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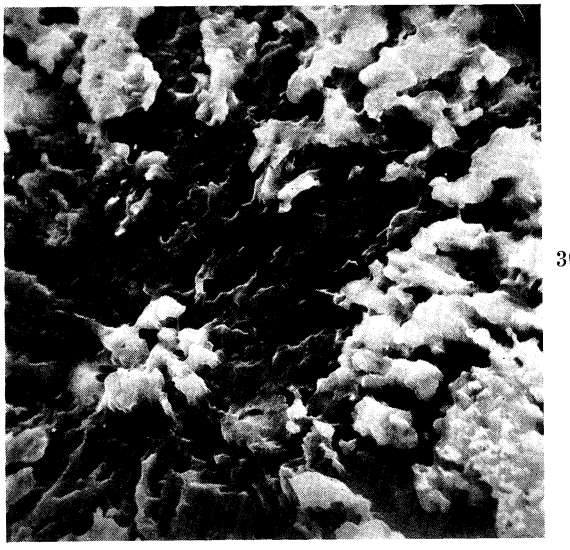

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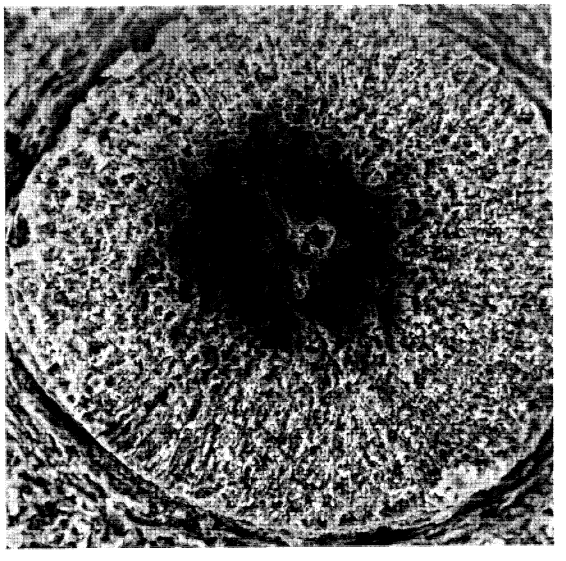

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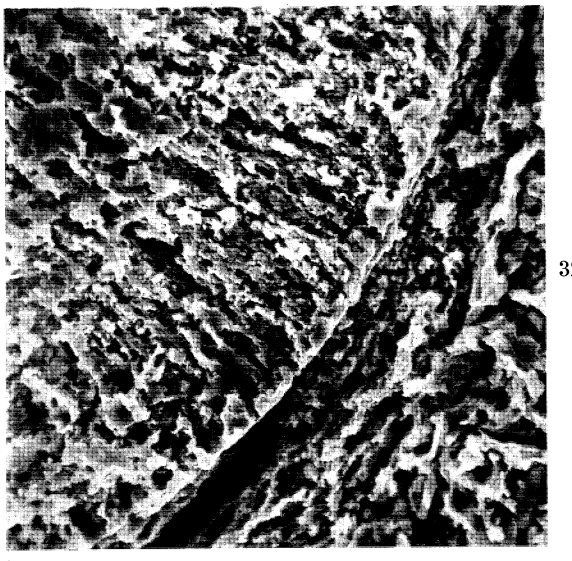

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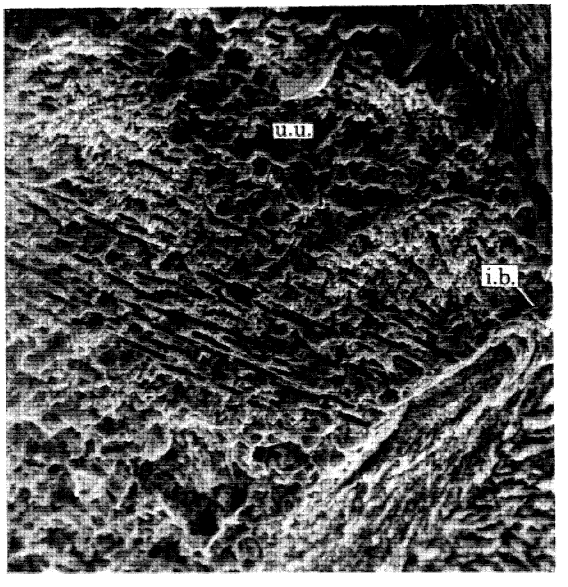

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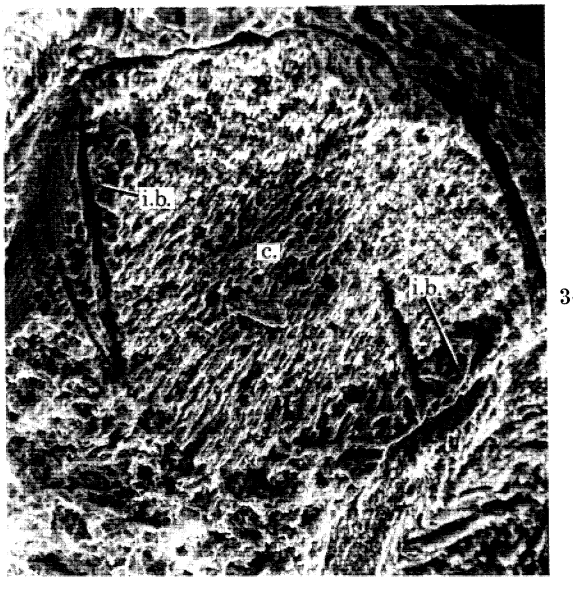

FIGURES 29–34. For description see page 477.

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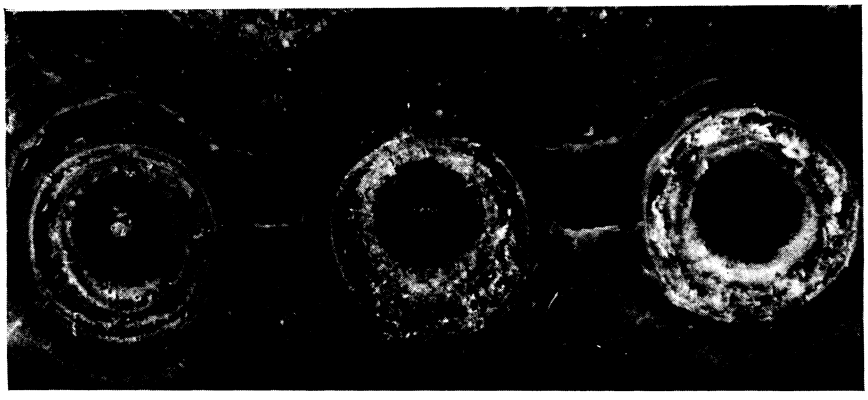

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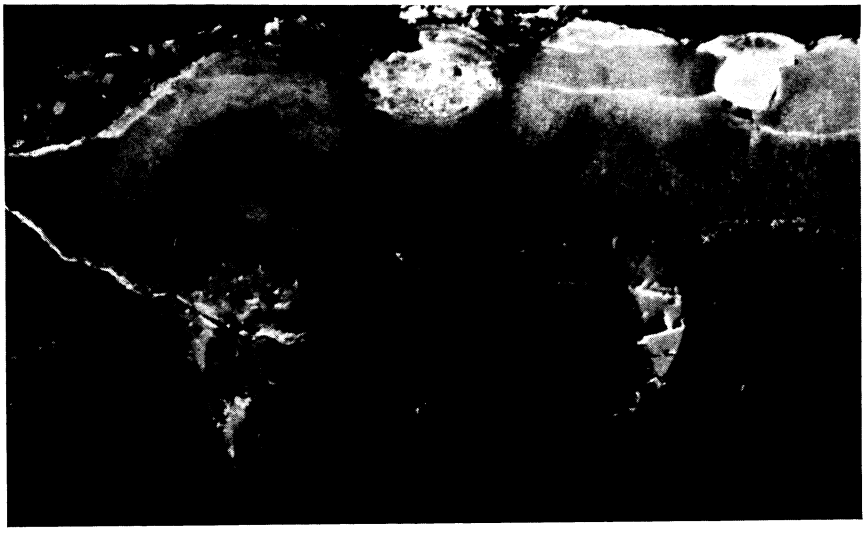

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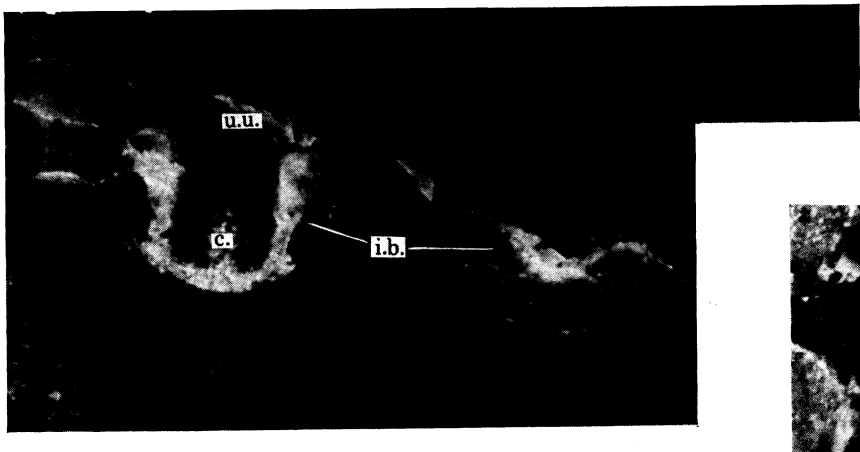

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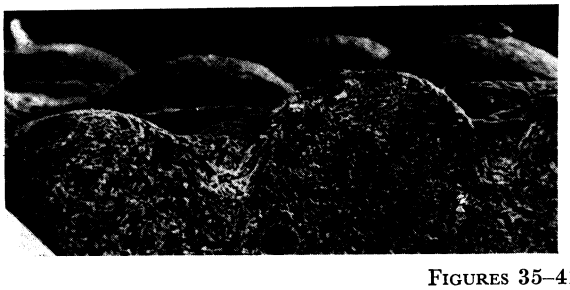

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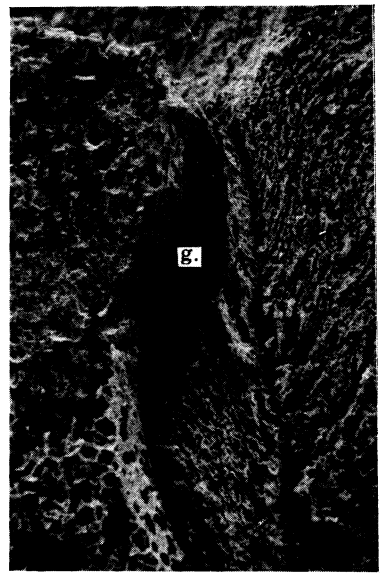

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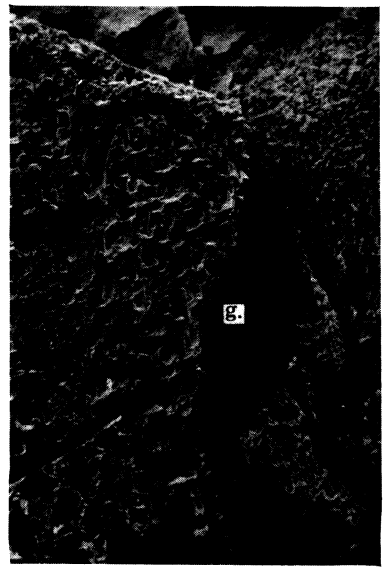

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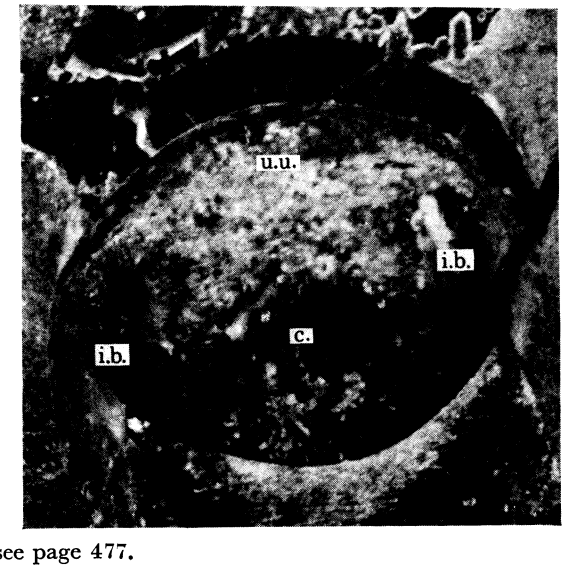

FIGURES 35–41. For description see page 477.

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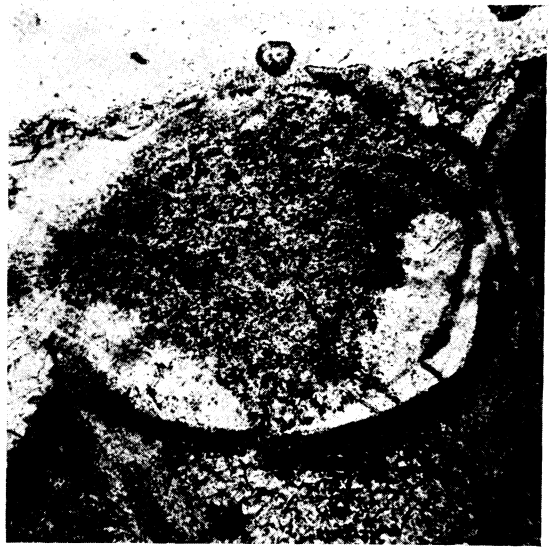

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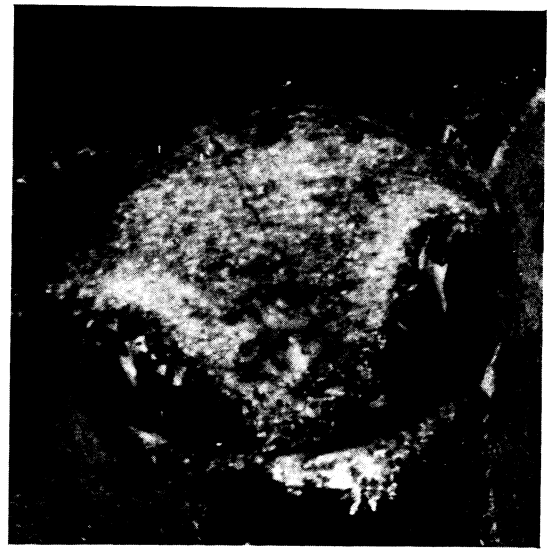

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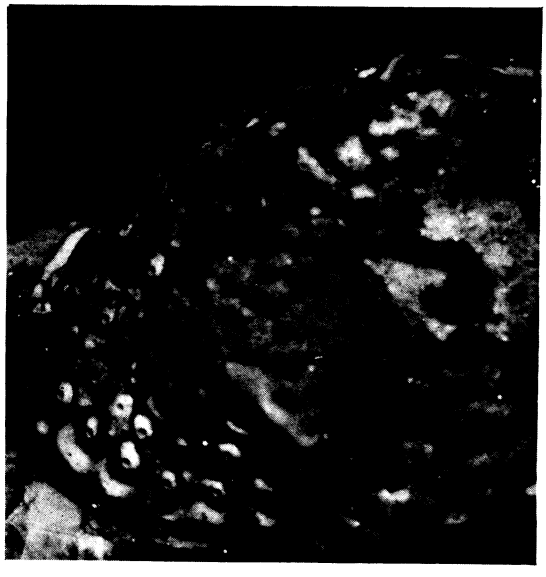

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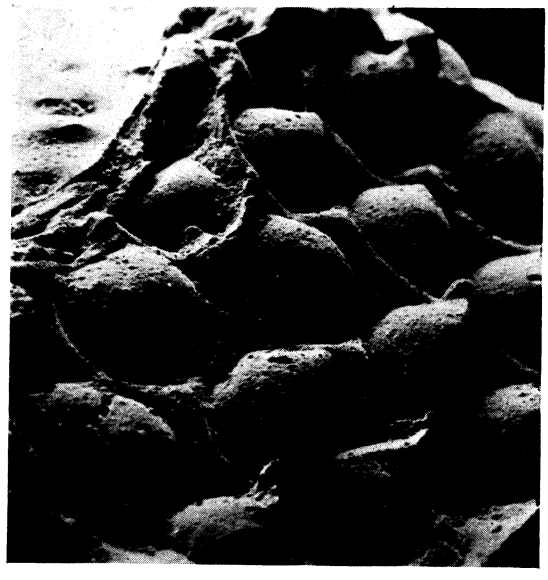

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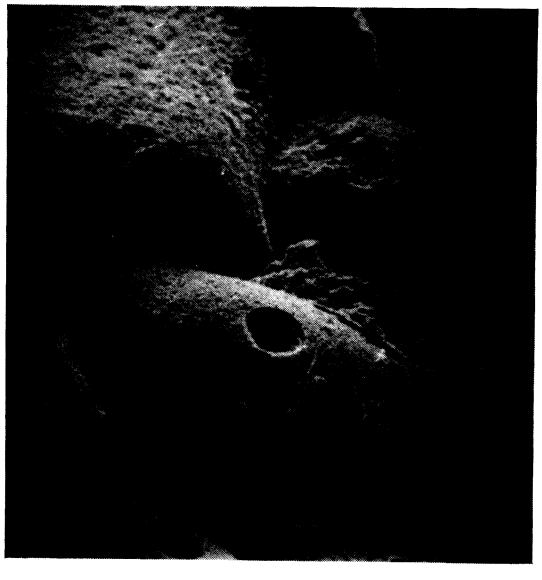

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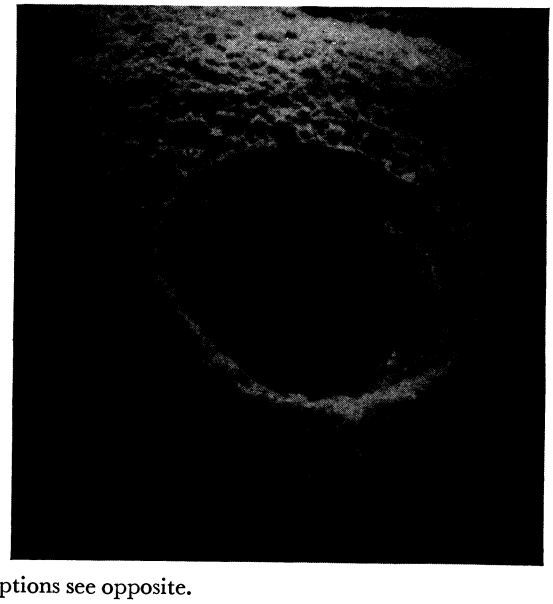

FIGURES 42–47. For descriptions see opposite.

Description of plates 5–7

Plate 5

Phacops rana milleri.

Figure 29. Etched upper surface of lens showing radial subcorneal structure and evidence of growth of upper unit in concentric zones (Gr I 46158). Magn. × 450.

Figure 30. Similar preparation of another lens (Gr I 46159). Magn. × 900.

Figure 31. Etched section of lens, cut parallel to principal plane, above the intralensar bowl. Core evidently expanded through diagenesis, but radial lamellae of the upper unit unaffected (Gr I 46160). Magn. × 180.

Figure 32. Radial lamellae of the same lens. Magn. × 450.

Figure 33. Substantially altered lens, cut tangentially, parallel with axis and etched. Intralensar bowl (i.b.) still discernible peripherally, but largely replaced below by recrystallizing calcite with pronounced cleavage planes. Upper unit (u.u.) also largely recrystallized (Gr I 46161). Magn. × 480.

Figure 34. Lens B of plate 3, figure 19, enlarged, showing unaltered bowl (i.b.), core (c.), trabeculae and laminae. The etching has opened up the cleavage planes in the calcite. Magn. × 180.

Plate 6

Phacops rana milleri.

Figures 35–38. Lens structure revealed by cathodoluminescence microphotography.

Figure 35. Section parallel with principal plane of three lenses, showing core, upper unit, bowl, alveolar ring, corneal membrane and sclera in sequence away from the centre. A neomorphic calcite crystal is growing in the left hand lens (MPM 27063a). Magn. × 45.

Figure 36. Vertical section through cuticle with setal canals and zoned syntaxial crystals of secondary calcite cement below lenses (the latter out of the plane of section) (MPM 27063a). Magn. × 45.

Figure 37. Altered lenses in vertical section, which still retain parts of the bowl (i.b.), altered core (c.), dark central structure and upper unit (u.u.). Note intralensar laminae (MPM 27063a). Magn. × 15.

Figure 38. Single lens (MPM 27603a), cut in oblique vertical section, showing altered bowl (i.b.), part of core (c.) and laminations in upper unit (u.u.). Magn. × 80.

Figure 39. Post-ecdysial lenses in earliest stage of development, cut in vertical section and etched, showing initial conical shape of lens and thin cuticle, with only slight diagenetic alteration (RSM GY 1979.11.5). Magn. × 45.

Figures 40–41. *Phacops rana africanus* Burton & Eldredge, Devonian, Spanish Sahara.

Figure 40. Vertical section of edge of etched lens, partially recrystallized, with possible original trabeculae and bowl. The girdle (g.) is very distinct (BMNH 5687696). Magn. × 160.

Figure 41. Edge of another etched lens completely recrystallized and penetrated by borings, showing girdle and one of a pair of sublensar 'horns' seemingly continuous with the original lens structure and presumably forming a conical ring (BMNH 5687696). Magn. × 160.

Plate 7

Phacops rana milleri.

Figures 42 and 43. A tangential vertically sectioned lens, photographed in plane polarized light (figure 42) and with cathodoluminescent microphotography (figure 43), showing neomorphic partial replacement of the bowl and laminations in the upper unit. The core is mainly out of the plane of section (MPM 27063(a)). Magn. × 80.

Figures 44–47. The earliest stages in post-ecdysial development (all AMNH 29282).

Figure 44. Left eye, slightly crushed, photographed under alcohol. The dark spot seen through the transparent cornea is the early conical lens. Magn. × 9.

Figure 45. Wrinkled surface of right eye of same specimen. Magn. × 42.

Figure 46. Etched surface showing moulds of small conical lenses which have been dissolved out with EDTA. Magn. × 95.

Figure 47. Detail of a single etched conical lens. Magn. × 450.

Figures 45–47 are scanning electron micrographs.

(*d*) The mature lens (figures 3, 19, 34) has a properly developed intralensar bowl, and a central core. It is much thicker than in stage (*c*), but, for the first time, the sclera has thickened greatly so that its proximal surface lies well below the base of the lens. At all previous stages of development the lens capsule has been bounded internally by the inner face of the corneal cylinder, but in the mature lens both the girdle and the alveolar ring have grown inside the cylinder and are clearly very late-stage developments. Though all these new developments apparently happened quite rapidly, it has not been possible for us to tell from the material at hand whether they took place in a particular sequence or developed more or less simultaneously.

The post-ecdysial development of the lenses is therefore a process involving several stages of growth. There seems to be little change in the curvature of the upper surface of the lens, but new material, as would be expected, is accreted exclusively on the lower part of the lens and on the inner wall of the lens capsule.

7. Function in the developing eye

It seems pertinent to consider whether the conical shape of the immediately post-ecdysial lens was a functional adaptation or was merely a record of the only way in which the lens could grow. An analysis of the optics of the different developmental stages is beyond the scope of this paper, but one or two points seem clear. First, the optical function of the lens optimized as the lens developed and as the components within it differentiated. The eye must have reached maximum efficiency only when the cuticle had achieved its full thickness. The time scale of this process is not known, but the thickness of the cuticle is such that it must have been some time, perhaps even several days after ecdysis, before visual acuity could be returned to an optimal level. This seems to have been, at least to some extent, a limitation on trilobite organization to add to those occasioned by ecdysis itself.

The conical shape of the early lenses apparently was retained only during the period while the cuticle was flexible, so that the trilobite would not have been capable of much movement. In this state the animal probably had to hide, as do many newly ecdysed arthropods. Though there is not an exact equivalence, these conical lenses resemble the parabolic exocones of *Limulus* described by Levi-Setti *et al.* (1975) as ideal light concentrators. For a recently moulted trilobite, which needed to keep out of sight (possibly either by partial burial or by timing ecdysis at night-time), there would be a great value in having eyes highly sensitive to light for detection of potential enemies. The conical lenses could therefore have been optimized, at this early and most critical stage, for the best possible vision given their incomplete formation. The early lens shapes were certainly neither constructively the simplest nor the most economical of material. In the later stages of development the change in optical function is reflected in the change in shape of the lens.

8. The cuticular carbonate metabolism of *P. rana milleri*

Trilobites are exceptional among arthropods in their high degree of cuticular calcification (Dalingwater & Miller 1977). Crustaceans, the other major group to use calcification as a method of strengthening cuticle, rely on a combination of a histochemically tanned organic matrix impregnated with calcite and calcium phosphate in varying concentrations.

Considerable amounts of metabolic energy are expended in accumulating inorganic ions from the external environment and secreting them as cuticle deposits. Most crustaceans maximize efficiency by reducing loss of these materials in their cast exoskeleton through pre-ecdysial resorption of inorganic salts (Passano 1960). The resorbed calcium is added to newly acquired material for redeposition in early post-ecdysial calcification stages.

In *P. rana milleri*, *P. rana rana*, *P. rana crassituberculata* and *P. rana africanus* the entire calcified visual apparatus was shed along with the rest of the cuticle and was completely reformed after each ecdysis. Such a complete periodic renewal of a relatively thick calcite cuticle must have demanded considerable metabolic effort on the part of these trilobites, contributing considerably to the high physiological stress of their ecdysial cycle. If it is shown that most trilobites failed to resorb their cuticular carbonate, then we may speculate that the inefficiencies of this system might have put trilobites at a selective disadvantage compared with crustaceans competing for the same niches. Further, the demands of this high-turnover calcium carbonate metabolism could also have influenced both local (ecological) and stratigraphic (evolutionary) distribution of trilobites according to fluctuations in calcium availability and/or partial pressure of carbon dioxide. Further investigations along these lines could shed new light on the evolutionary biology of trilobites.

We are indebted to Dr N. Eldredge, Dr R. Levi-Setti and Professor A. D. Wright for donating specimens upon which this study is based. Dr J. E. Dalingwater provided much useful discussion on cuticular matters. S.e.m. photography was carried out at the Institute of Terrestrial Ecology, Bush, Midlothian, where Lynn Lamont gave valuable technical assistance. Mr D. Ince helped with macrophotography, and Mrs Janette Brunton typed the manuscript.

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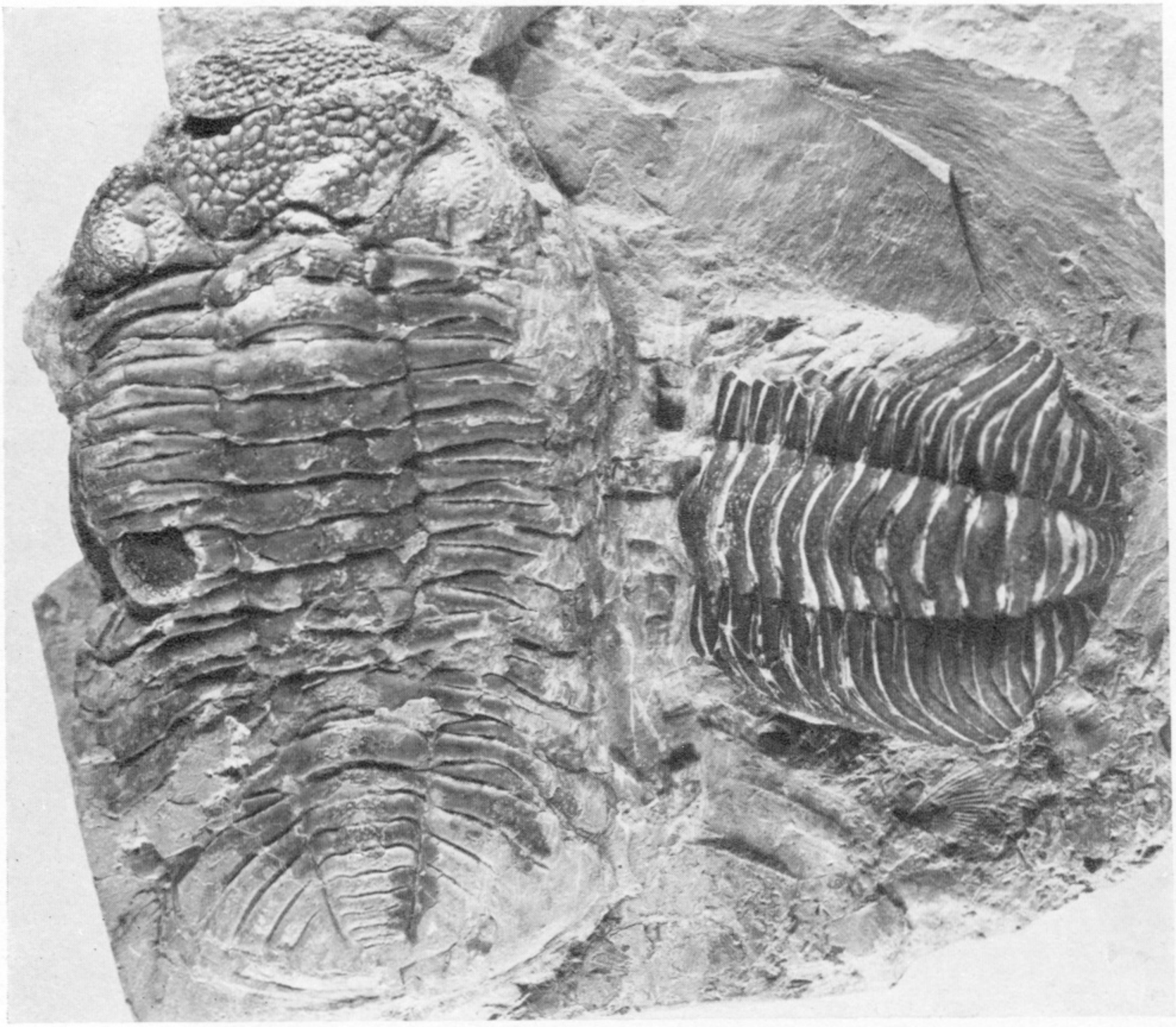

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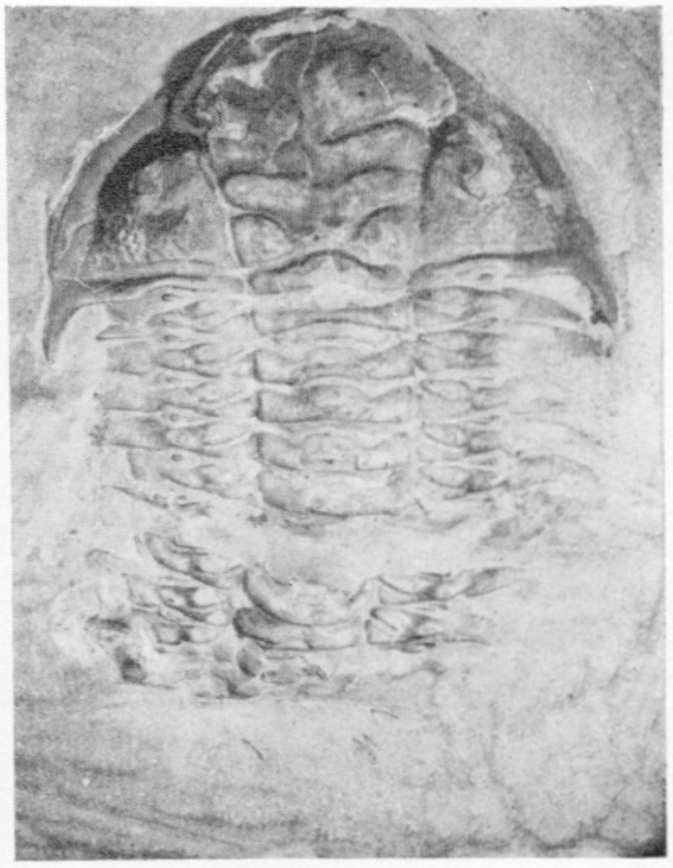

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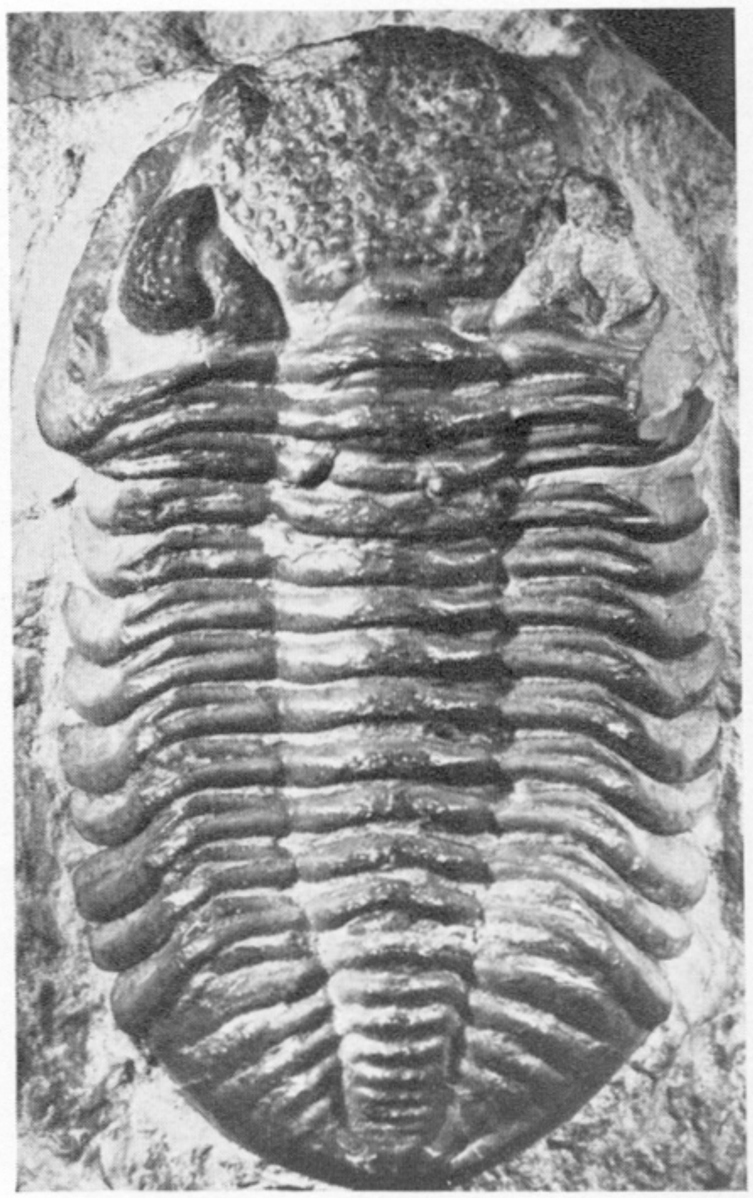

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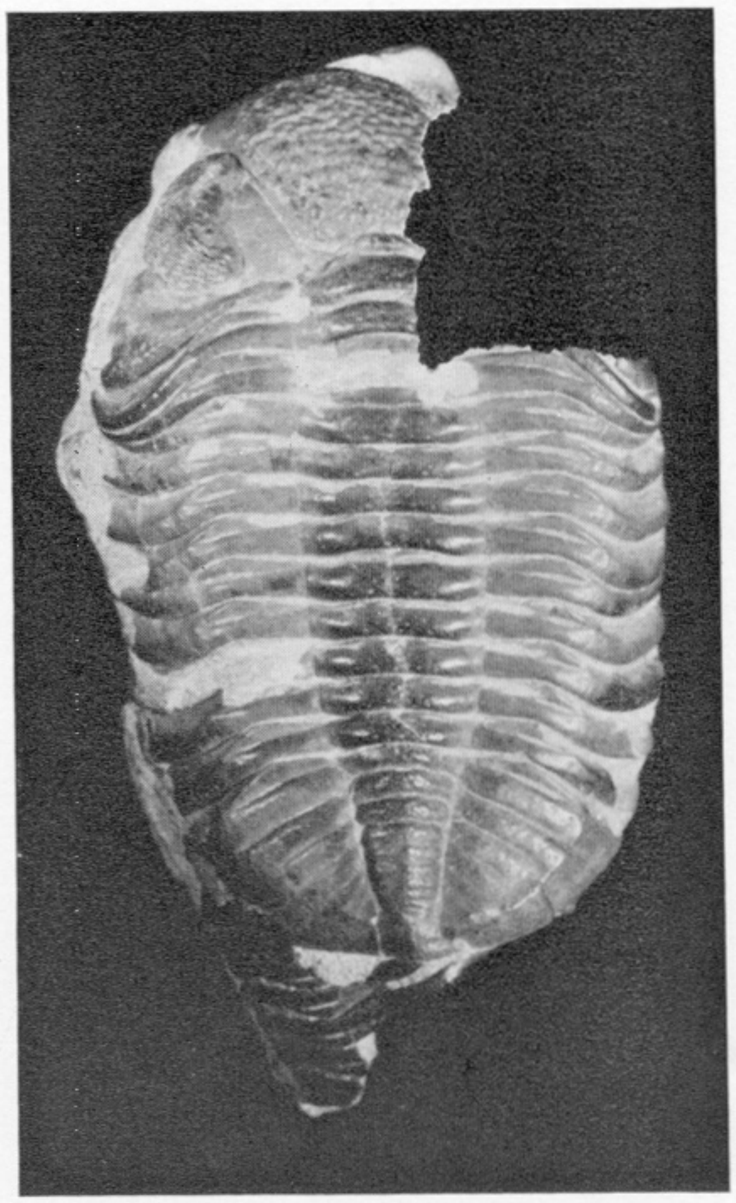

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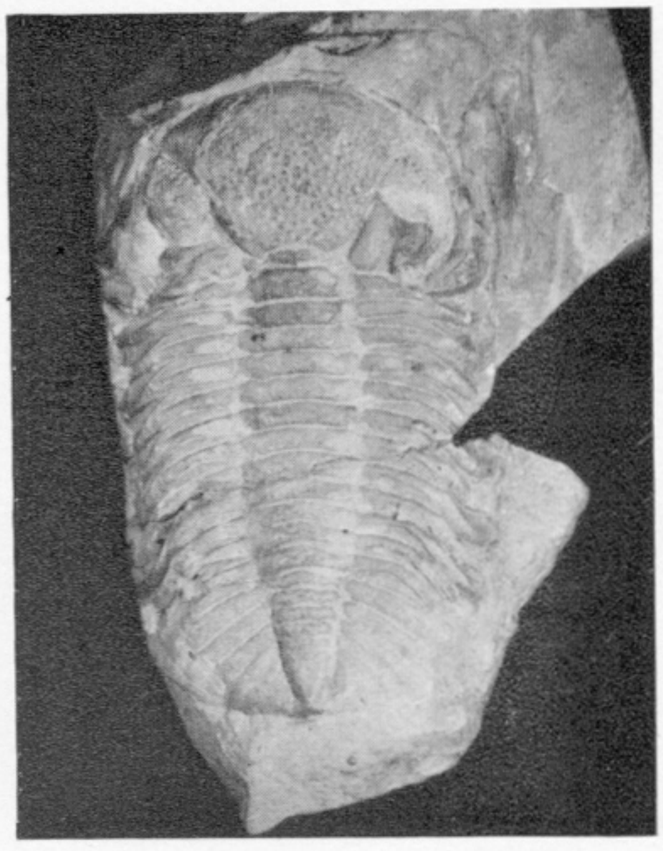

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FIGURES 5–10. For descriptions see opposite.

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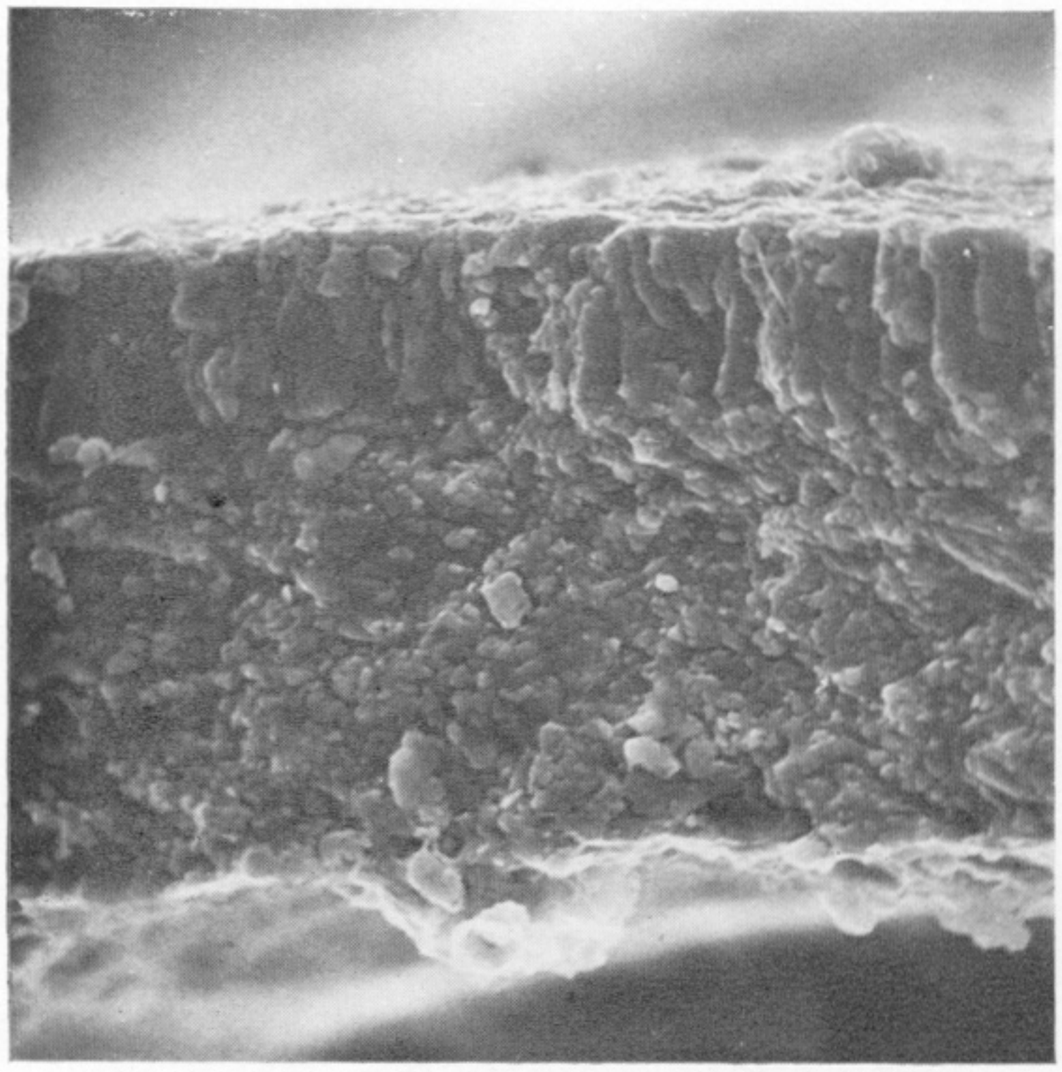

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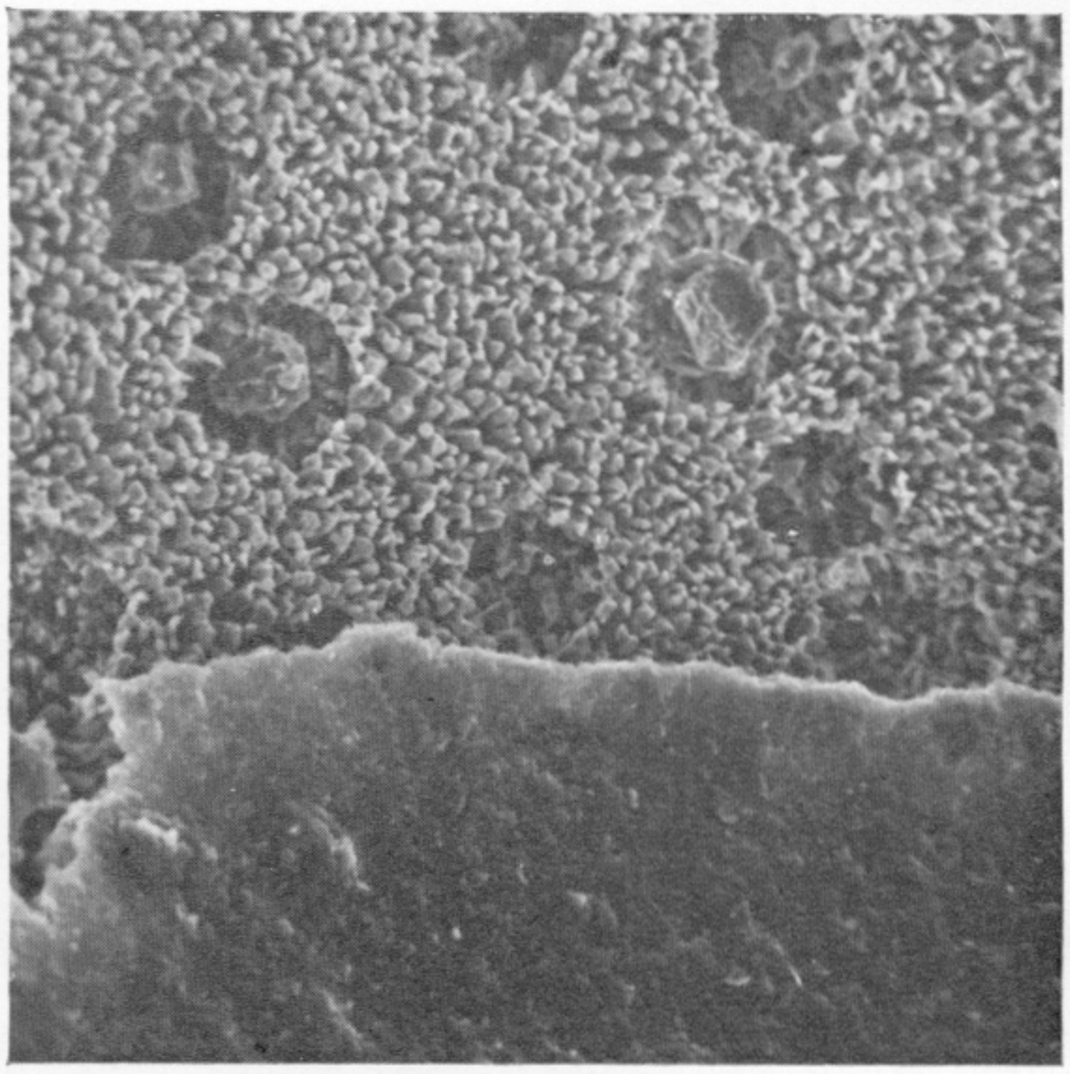

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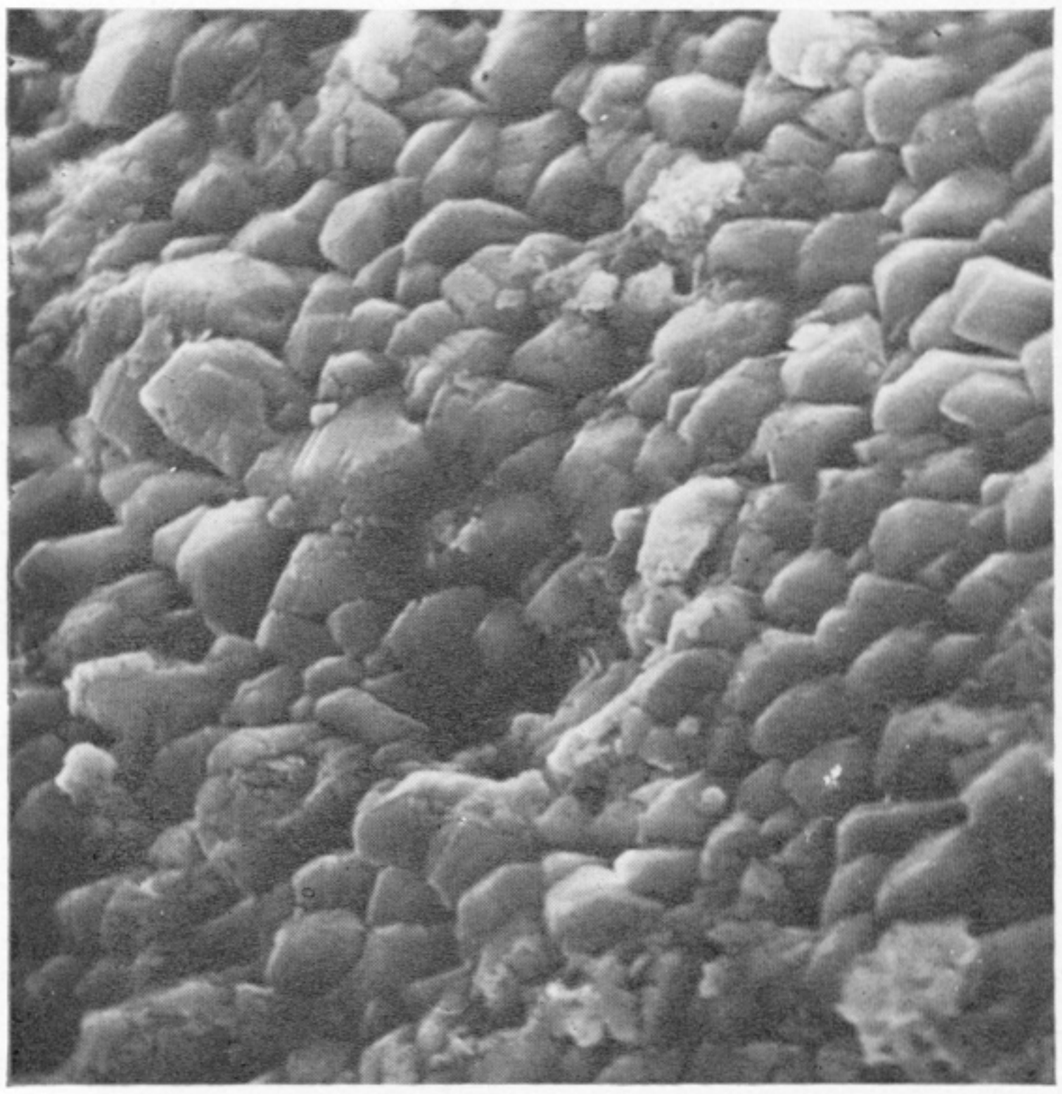

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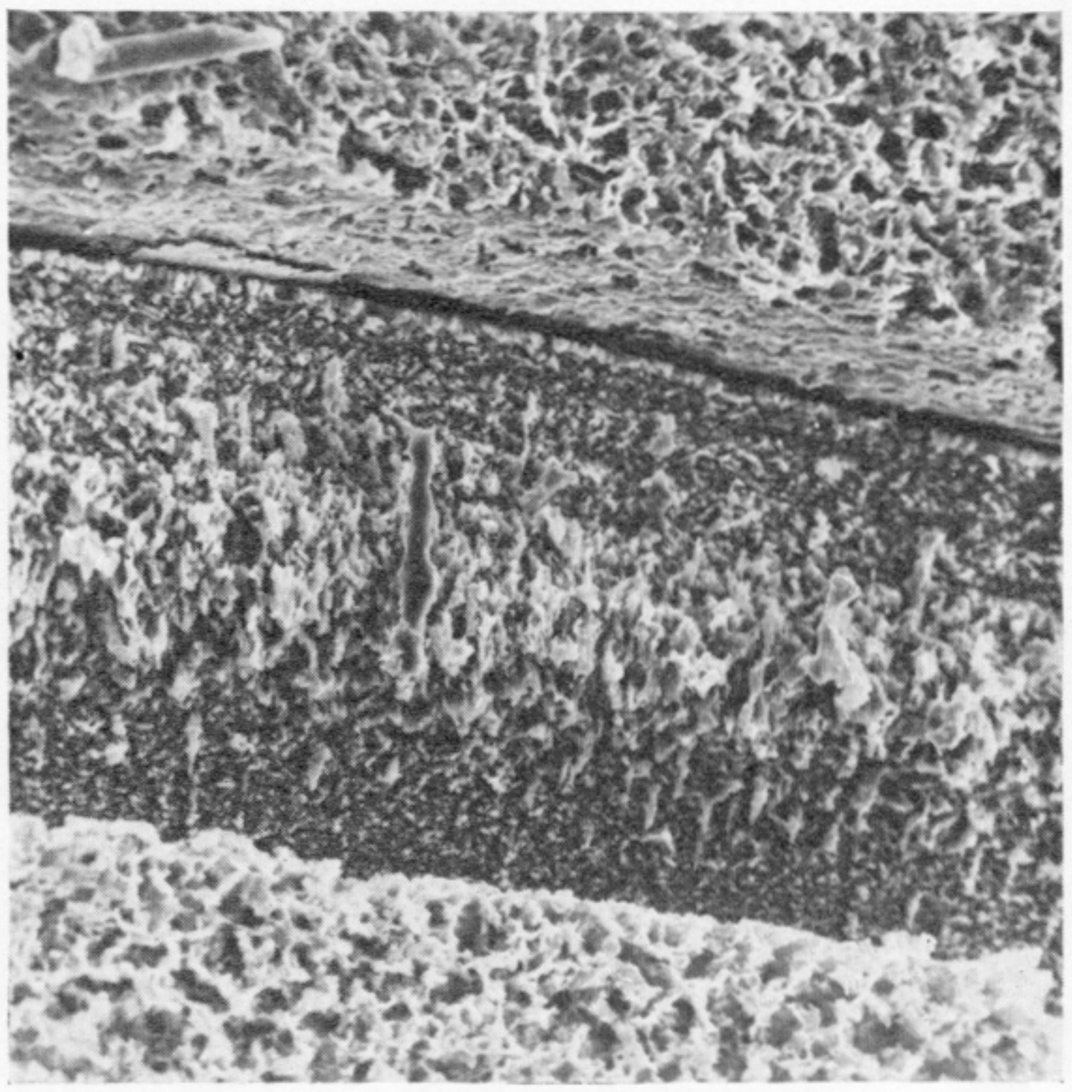

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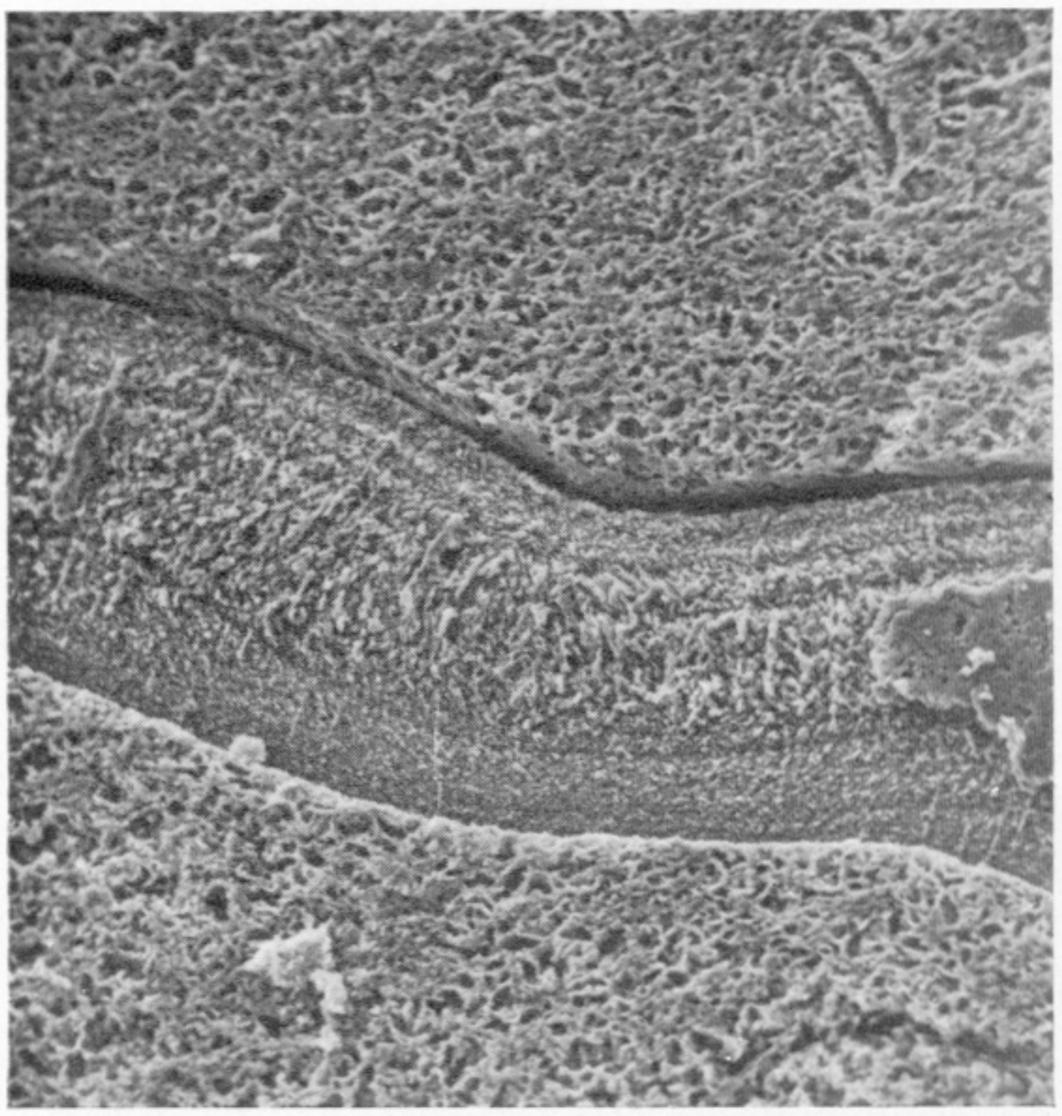

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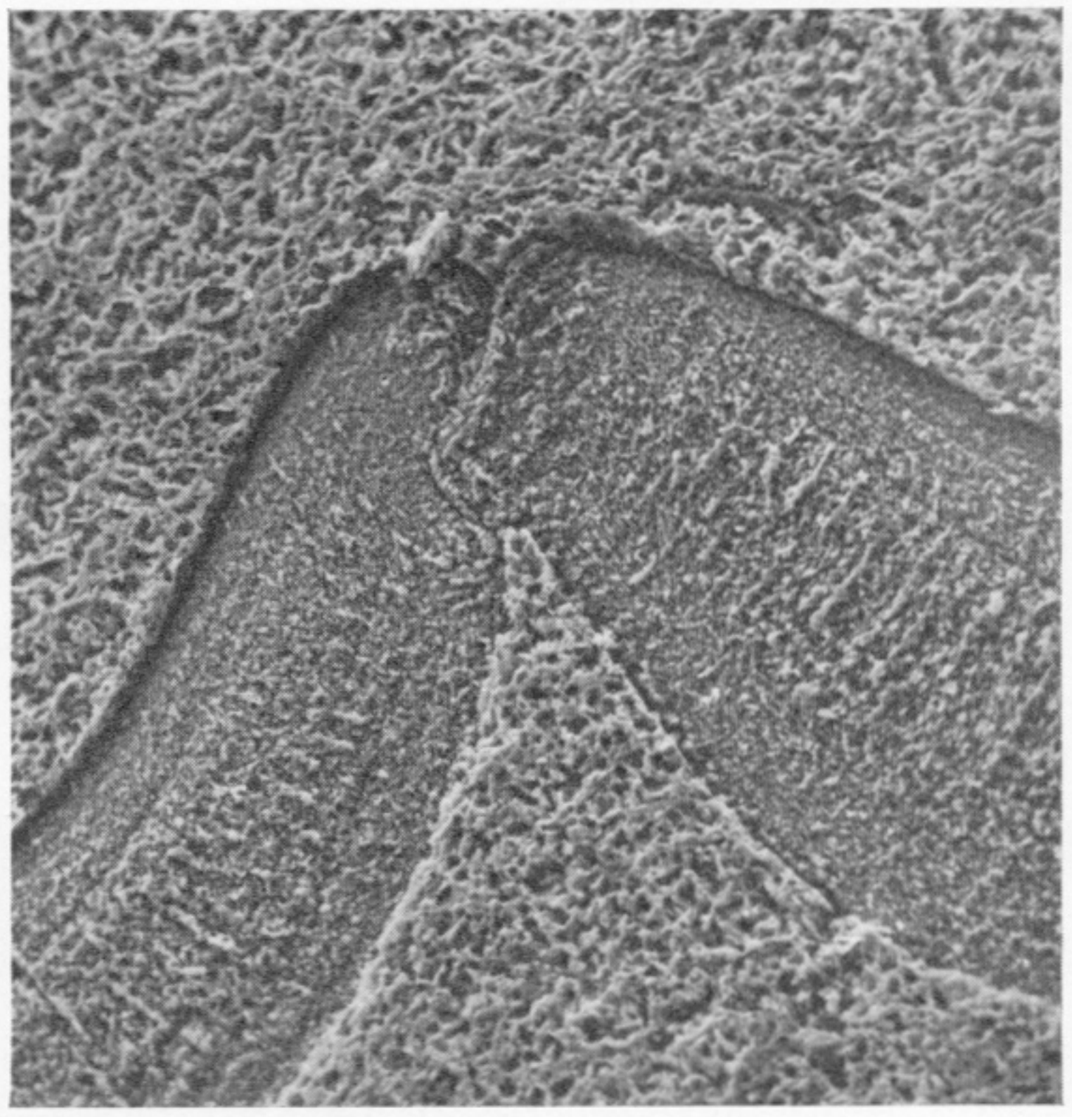
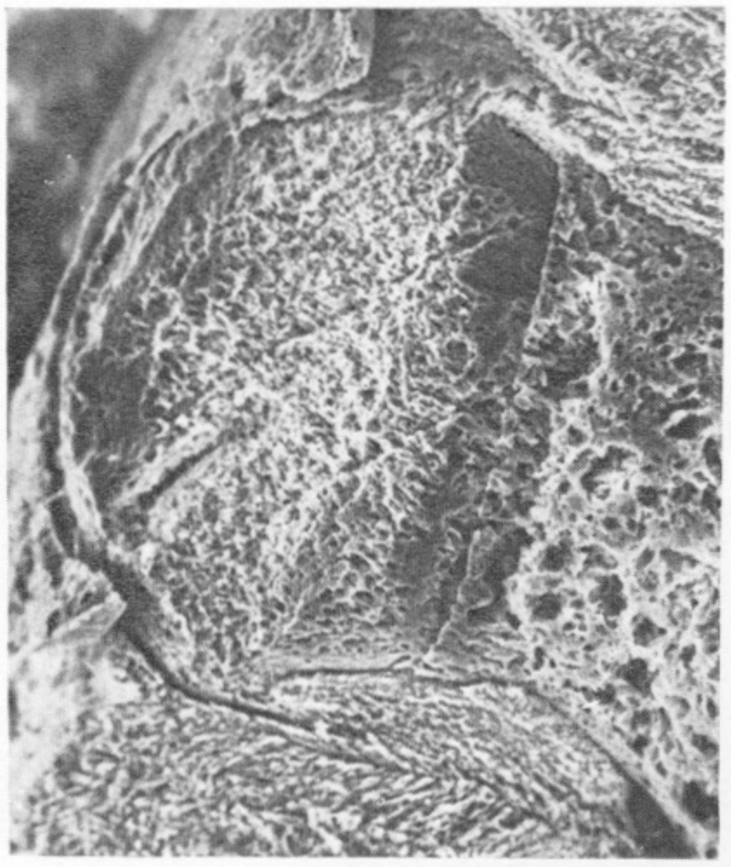


FIGURES 11–16. For description see page 476.



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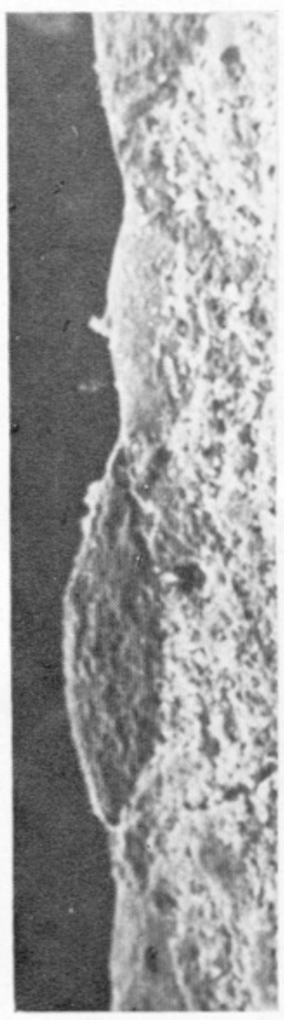

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FIGURES 17–21. For description see page 476.

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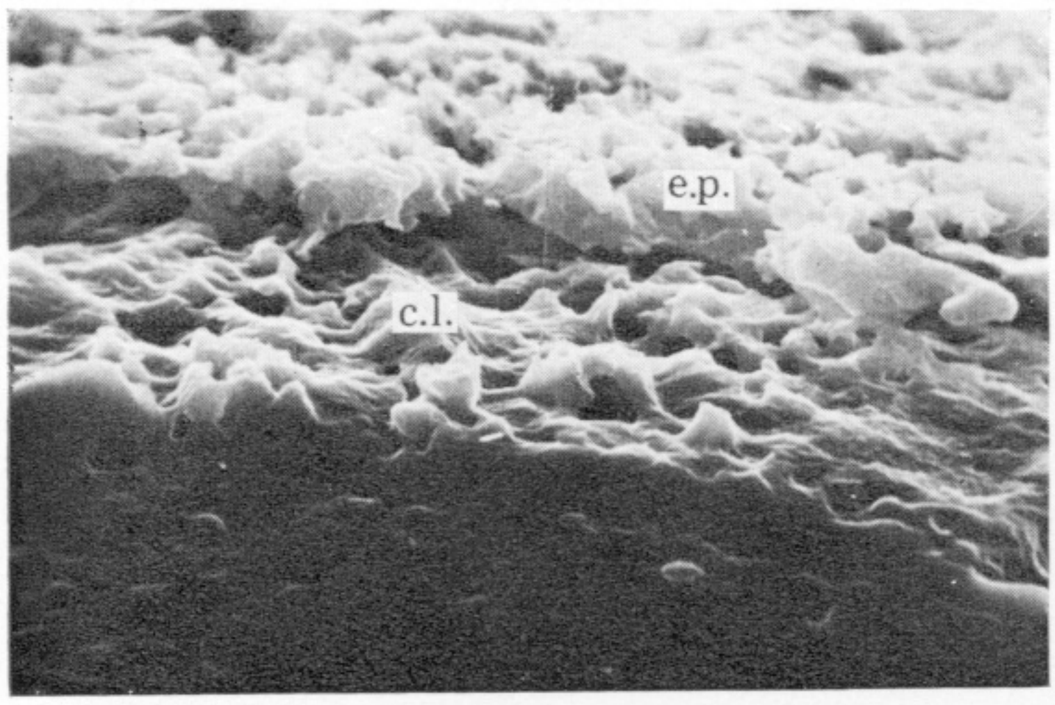

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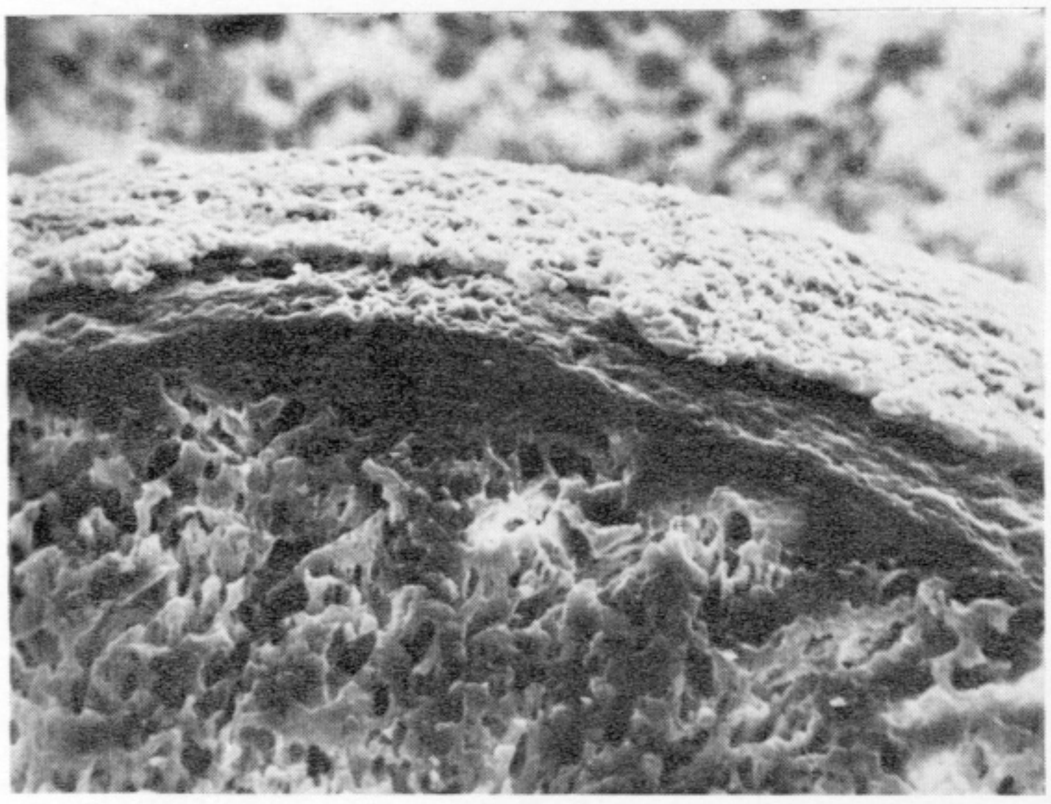

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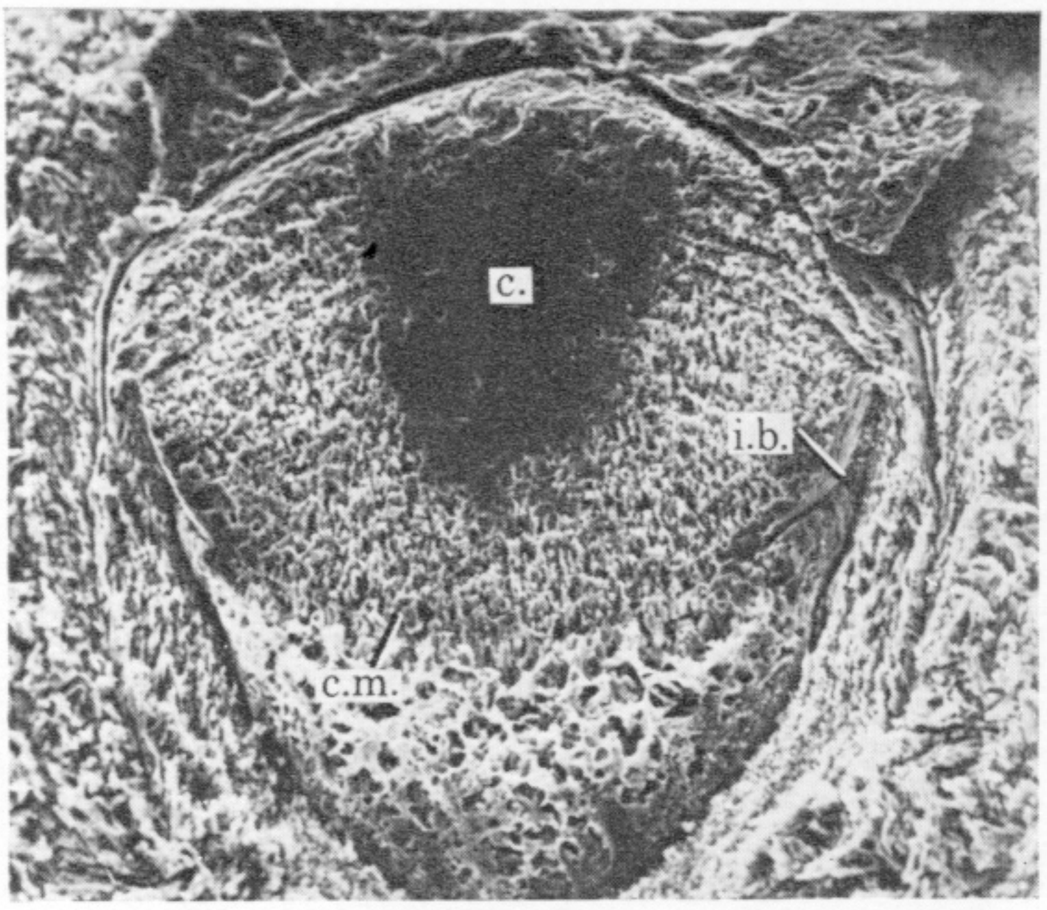

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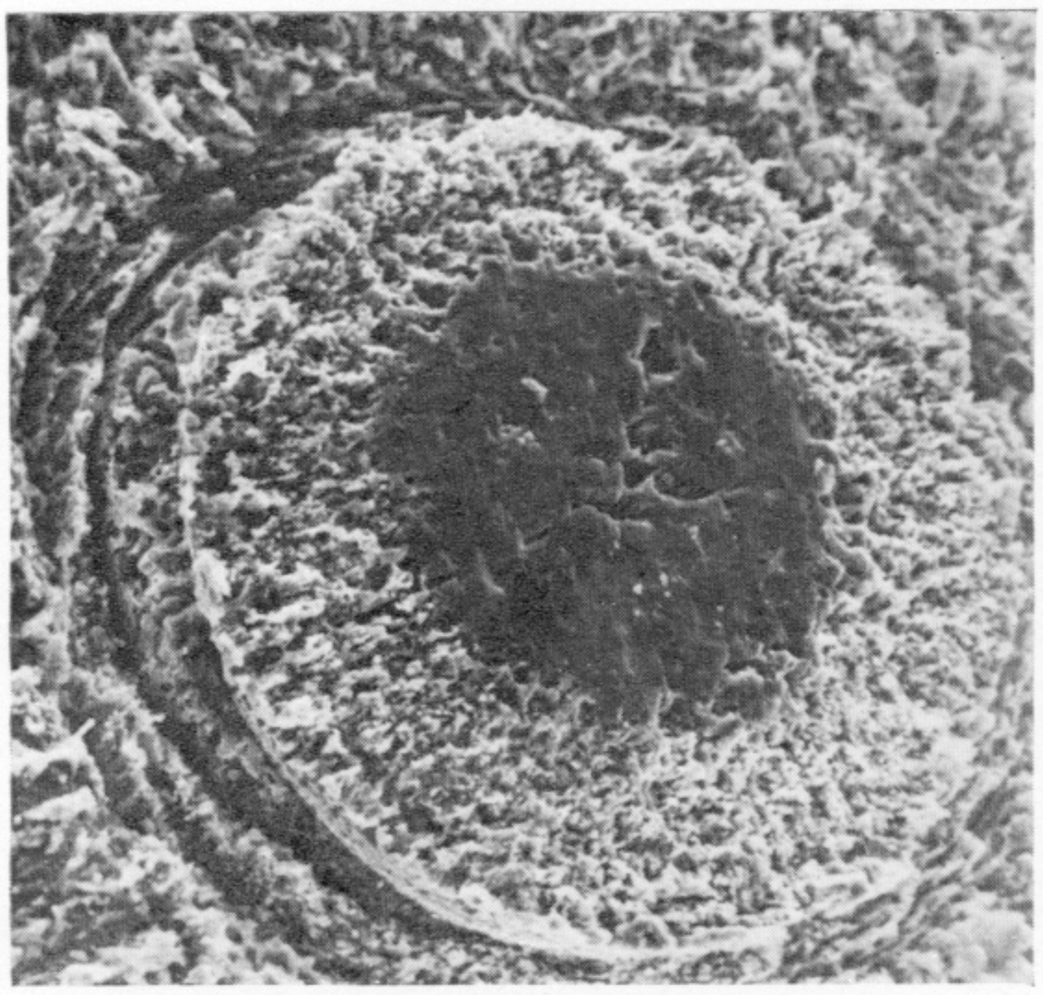

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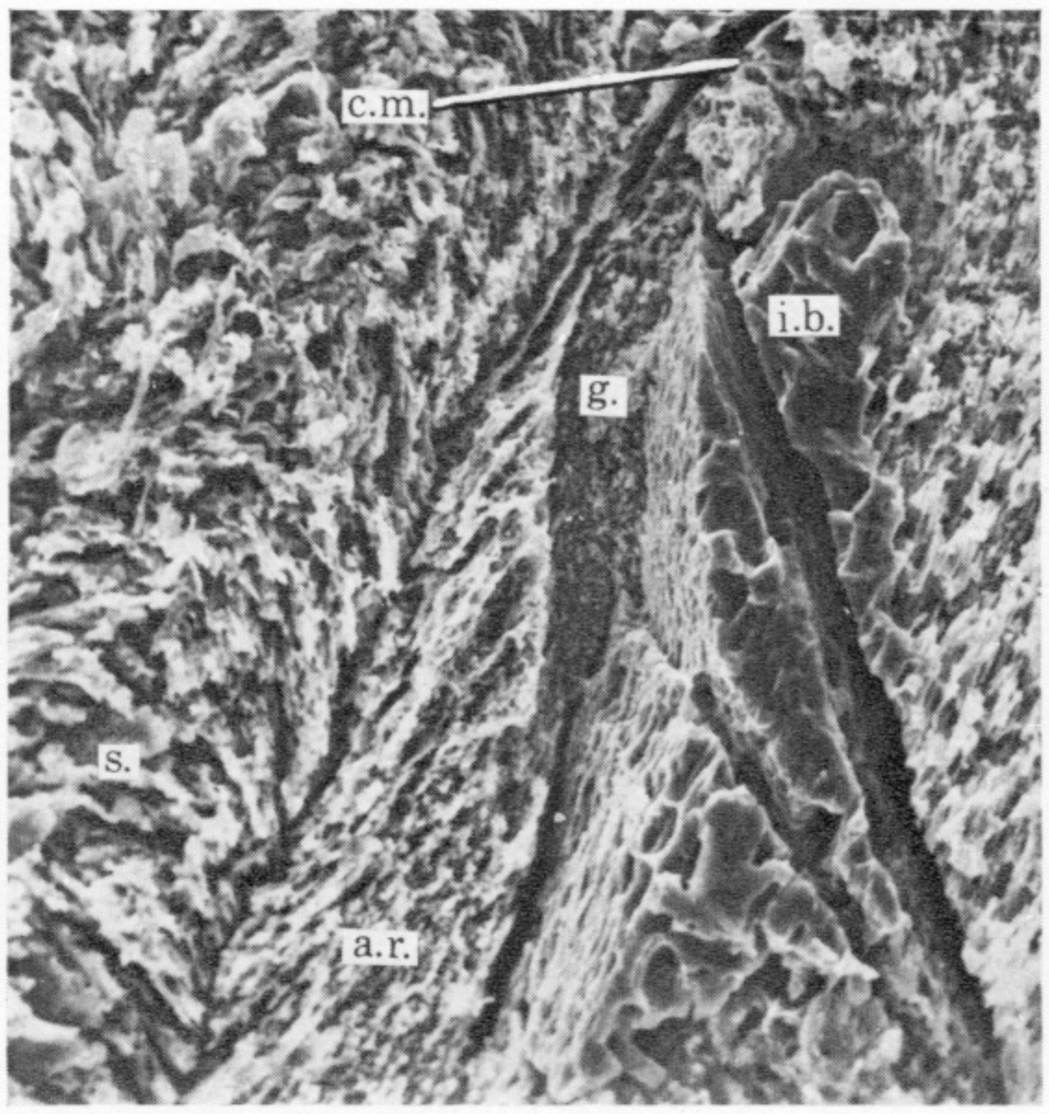

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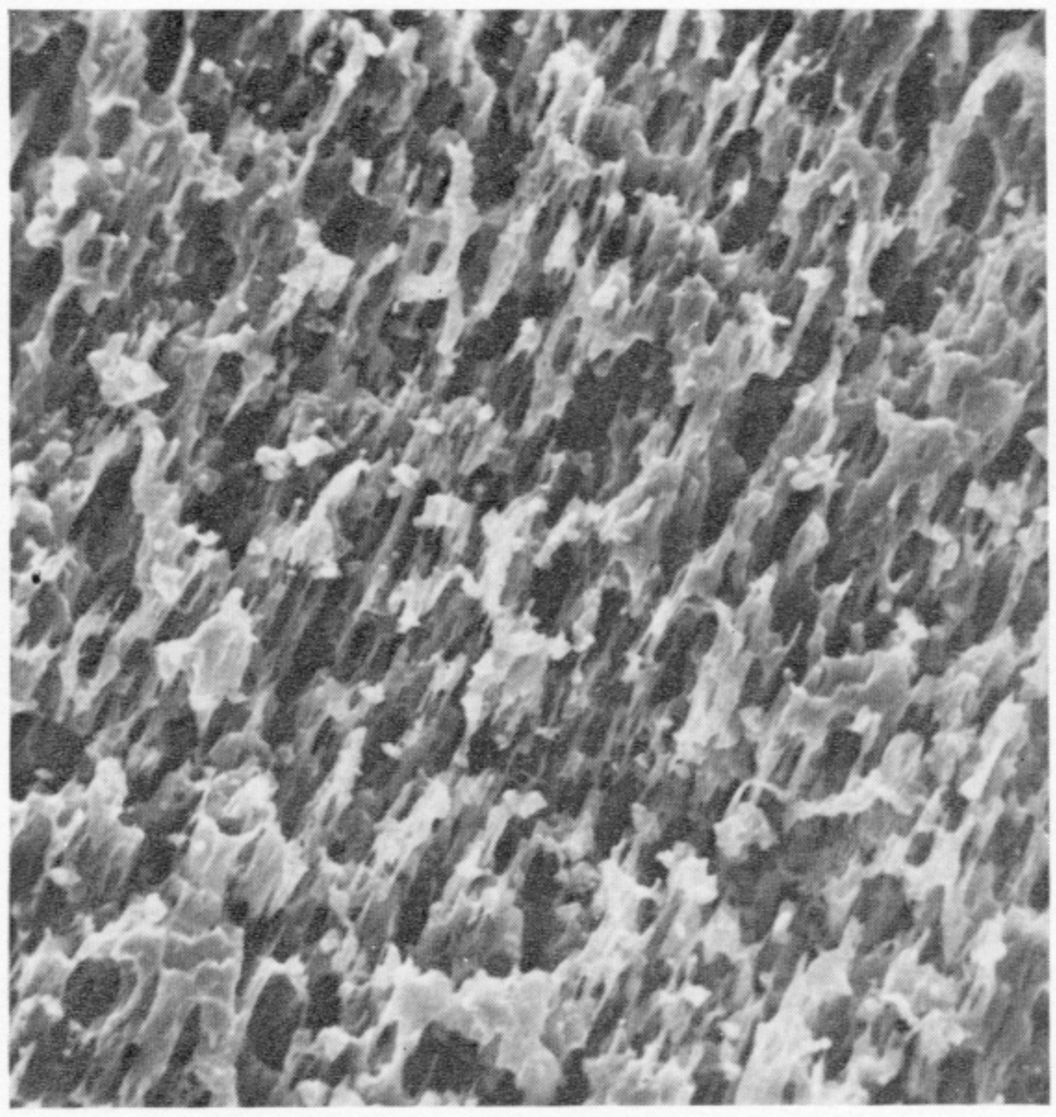

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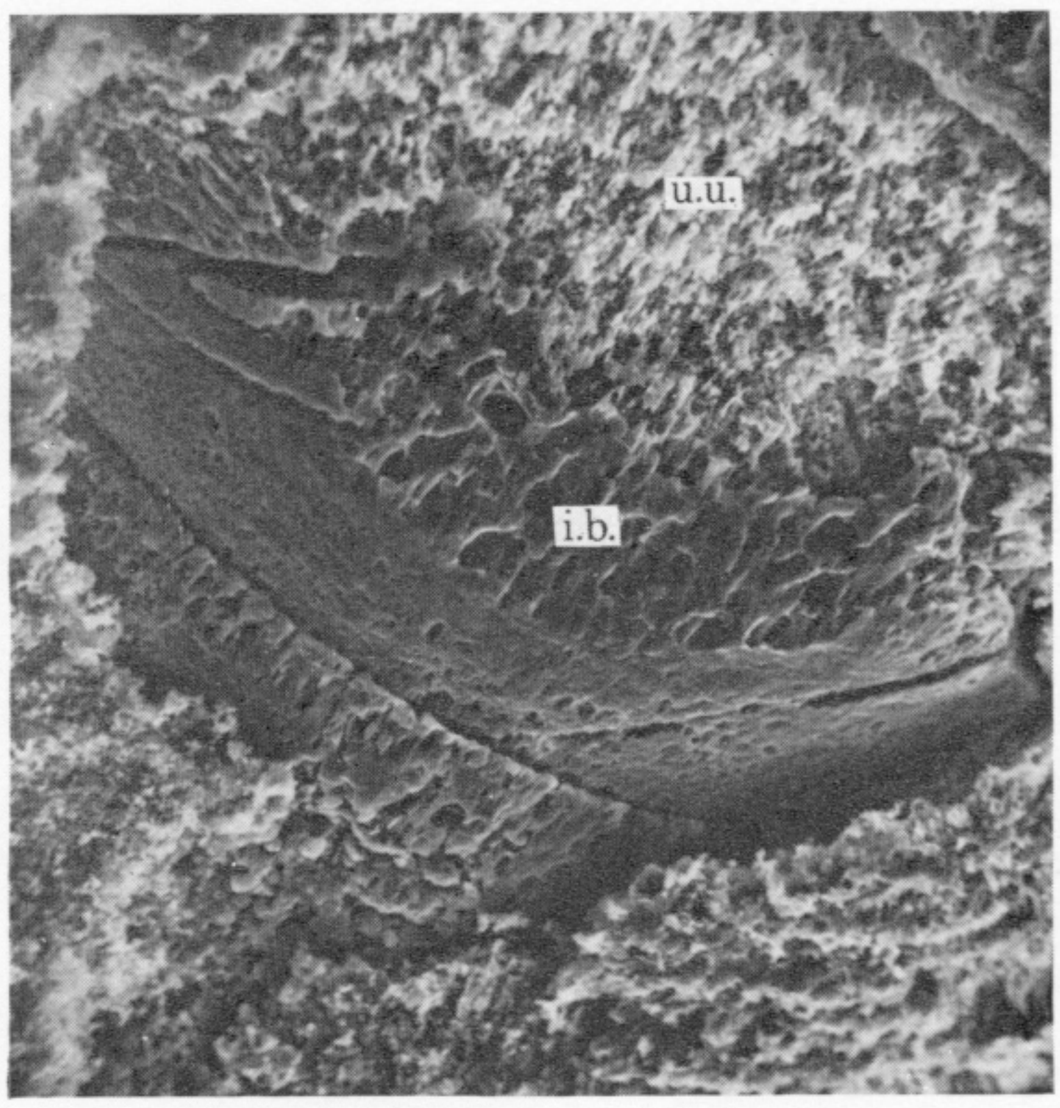

FIGURES 22–28. For descriptions see opposite.

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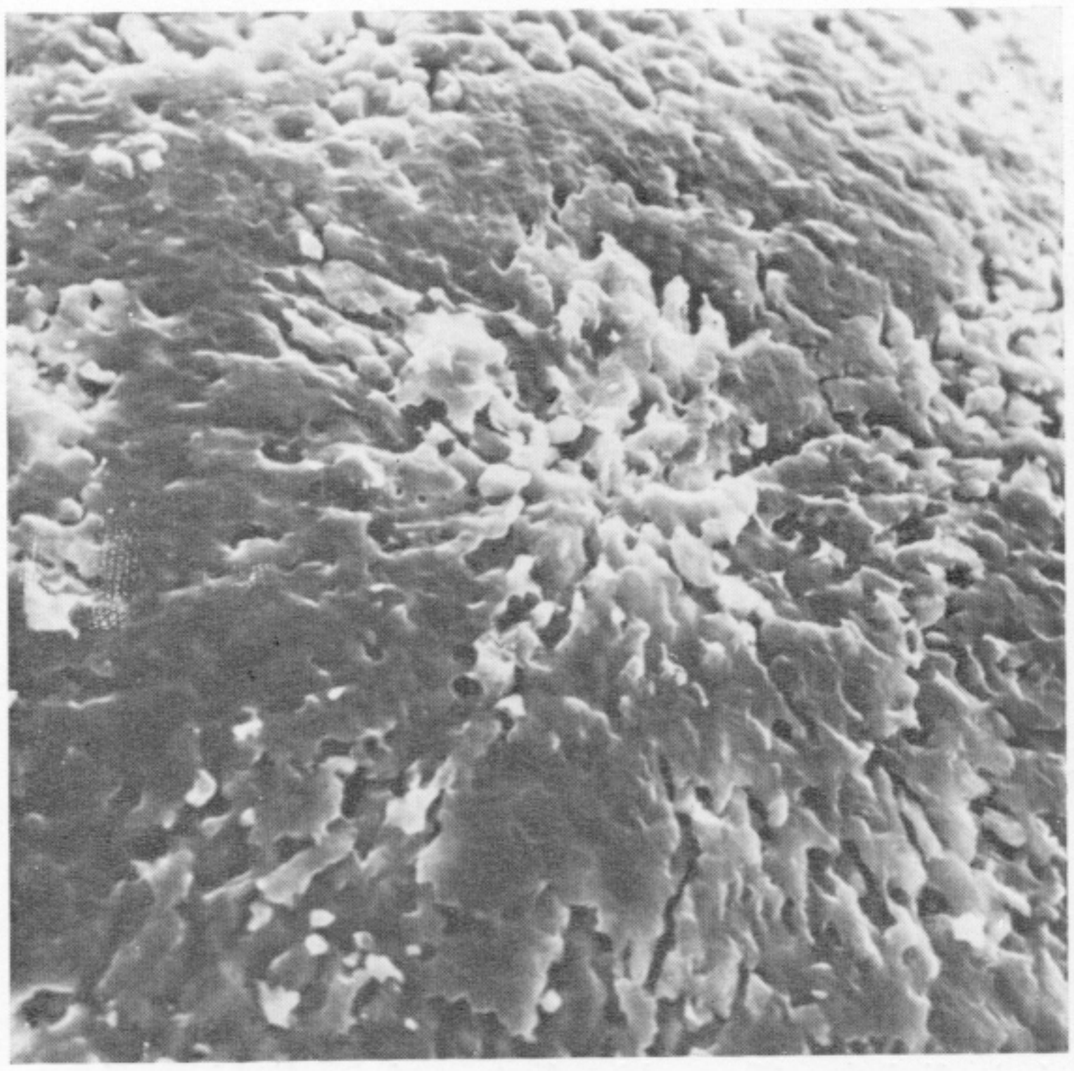

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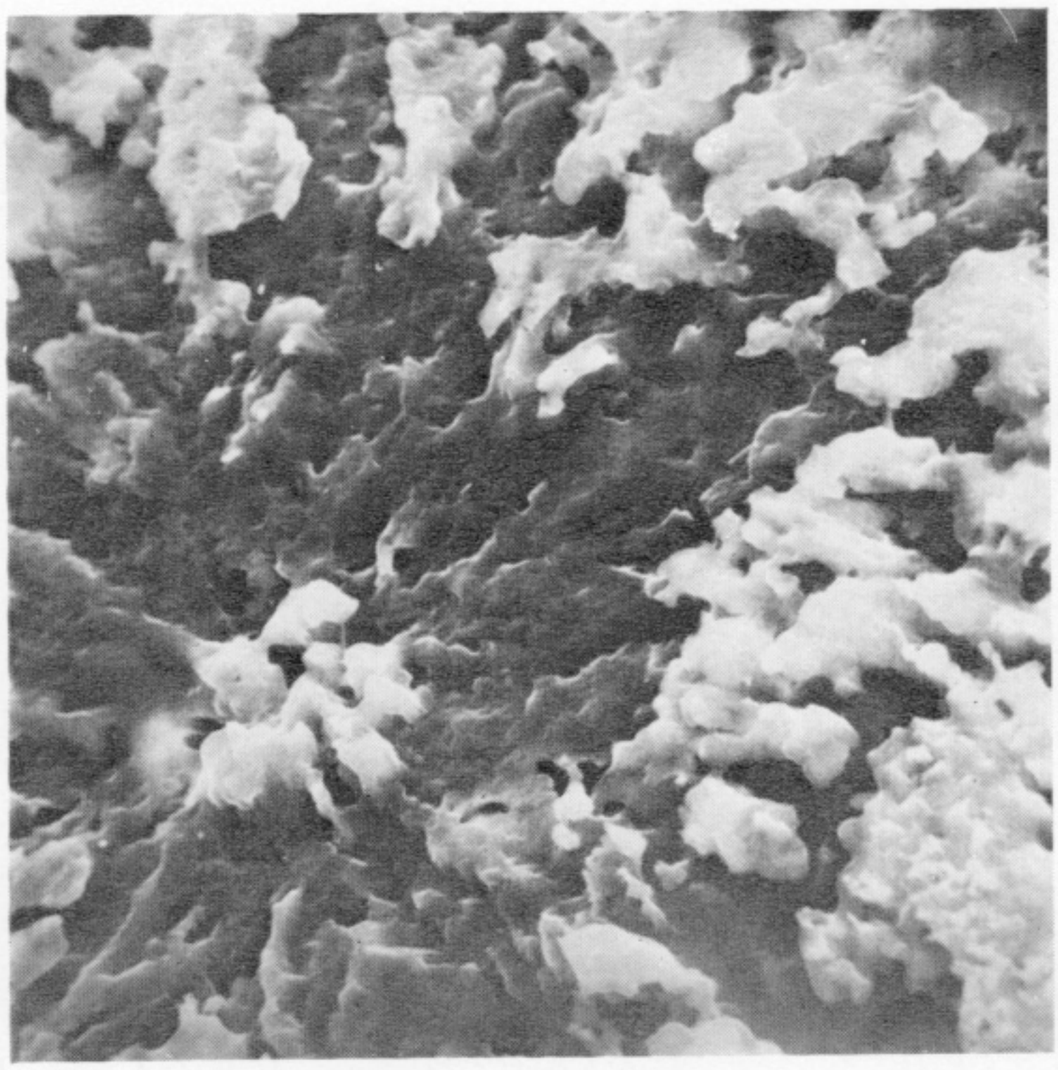

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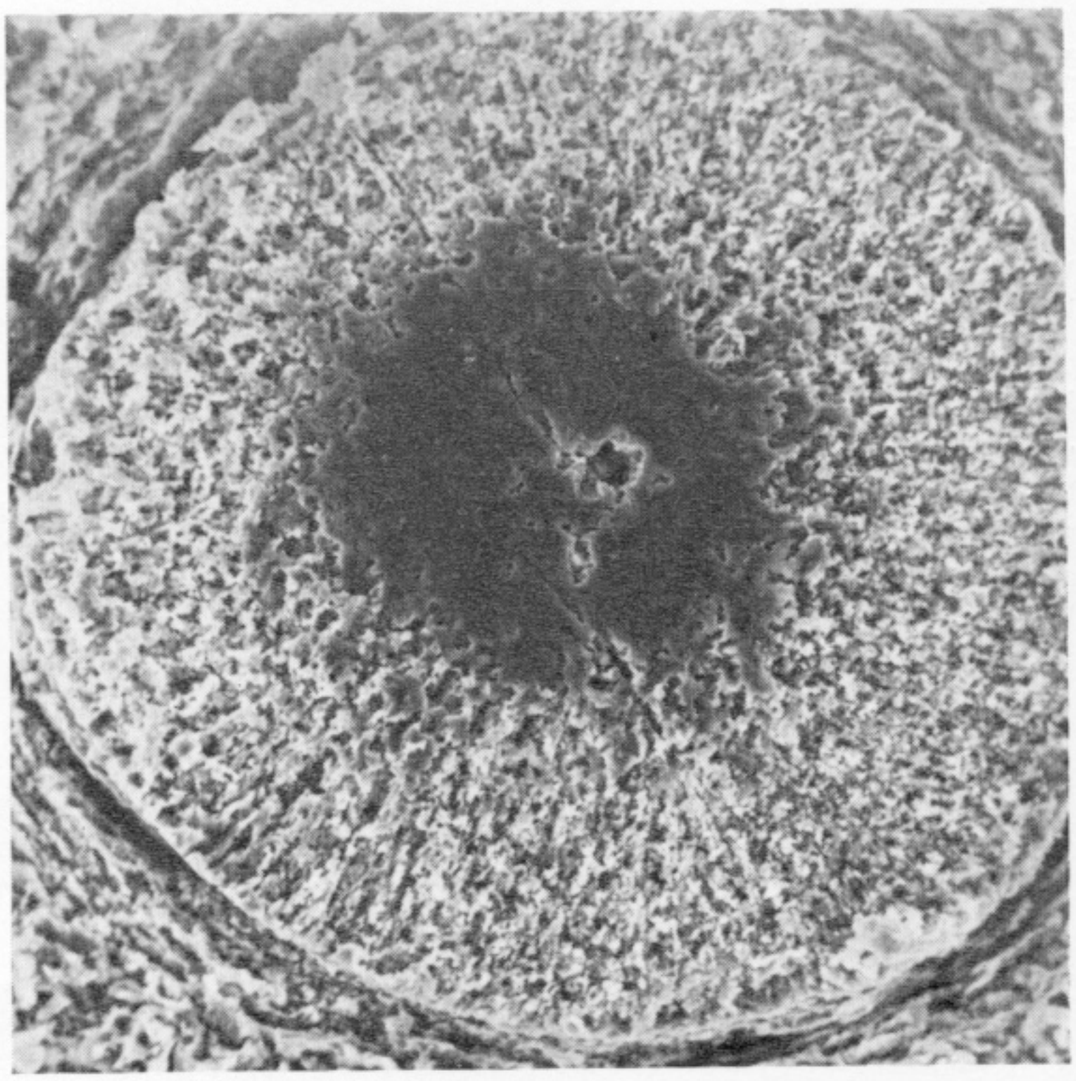

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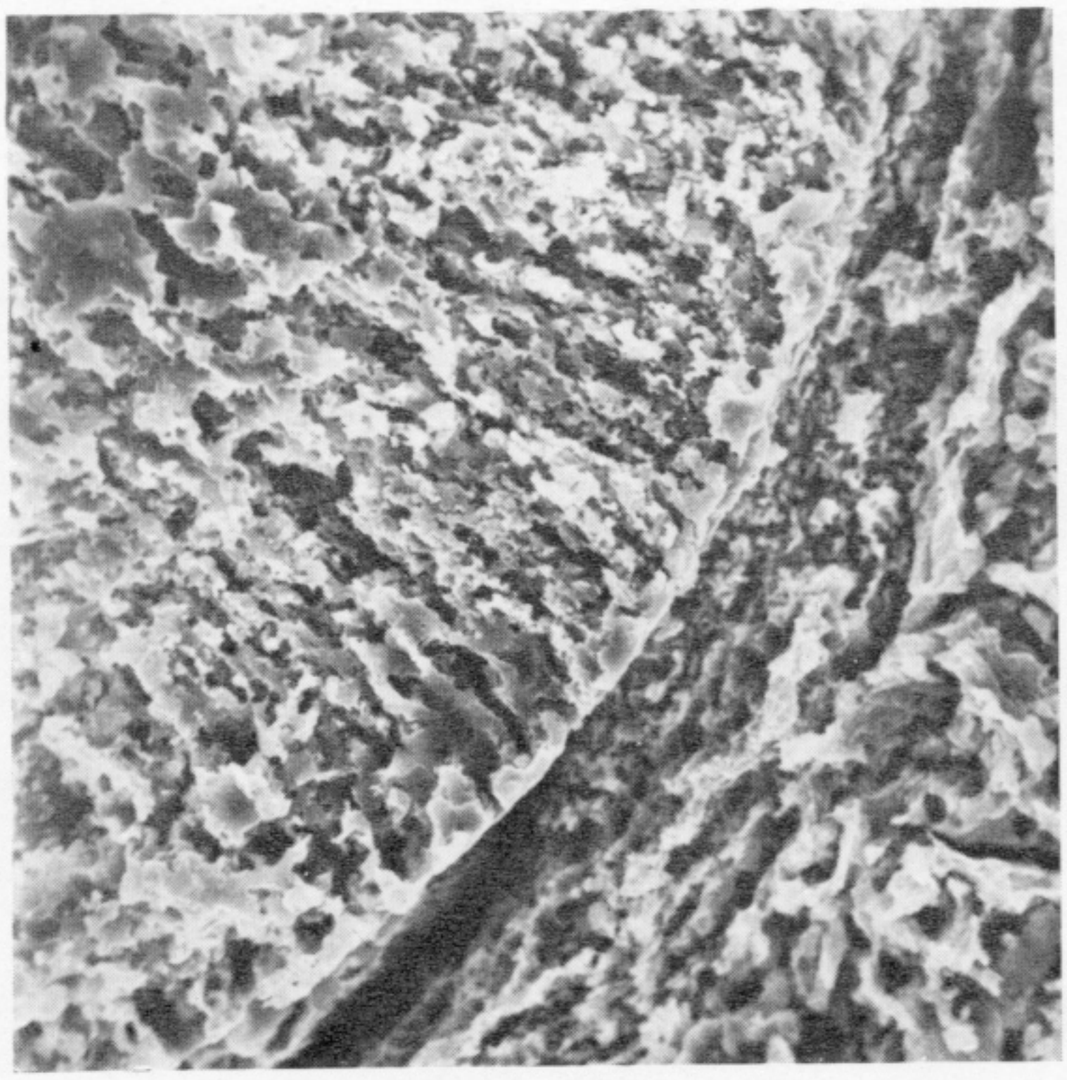

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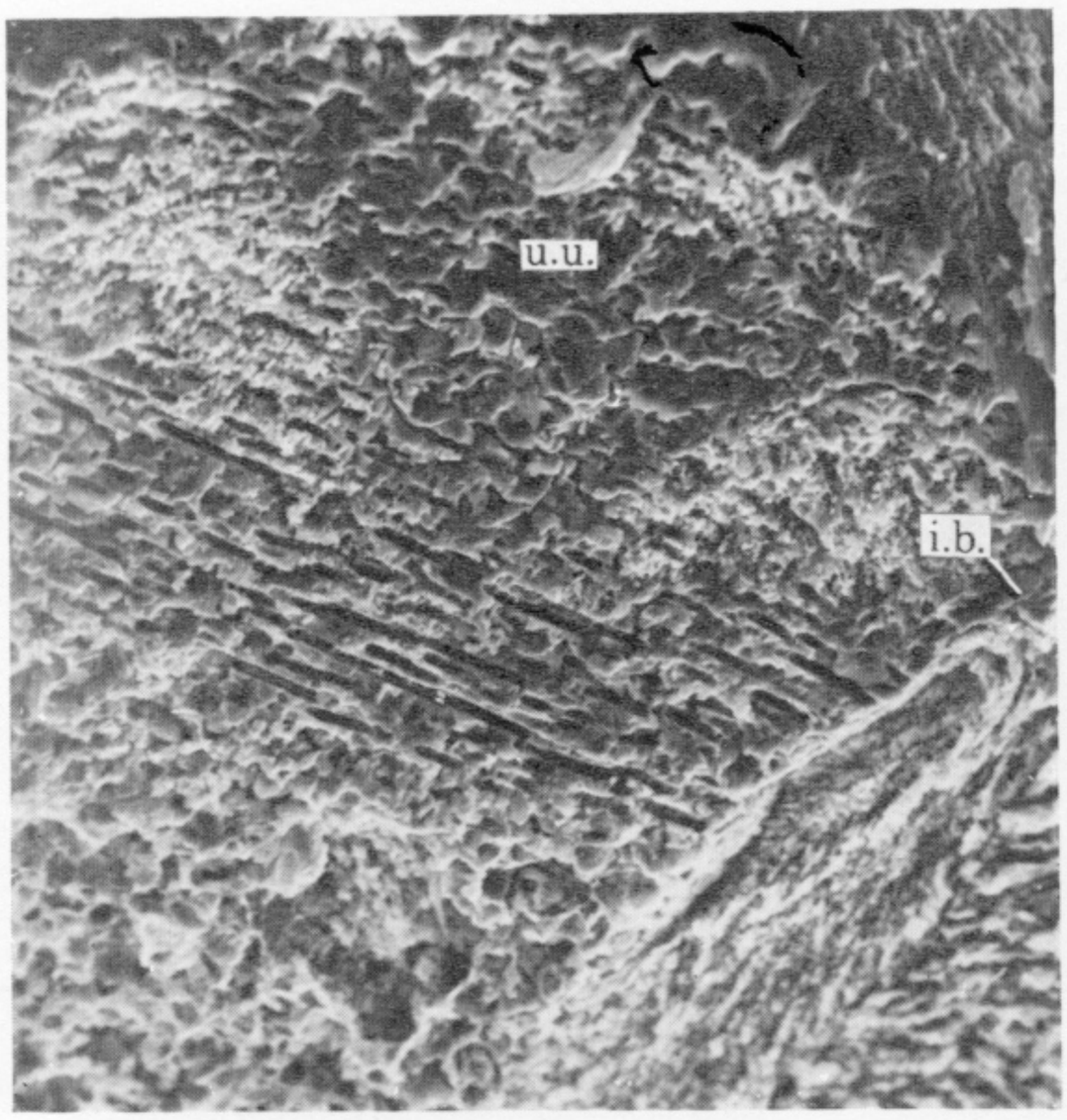

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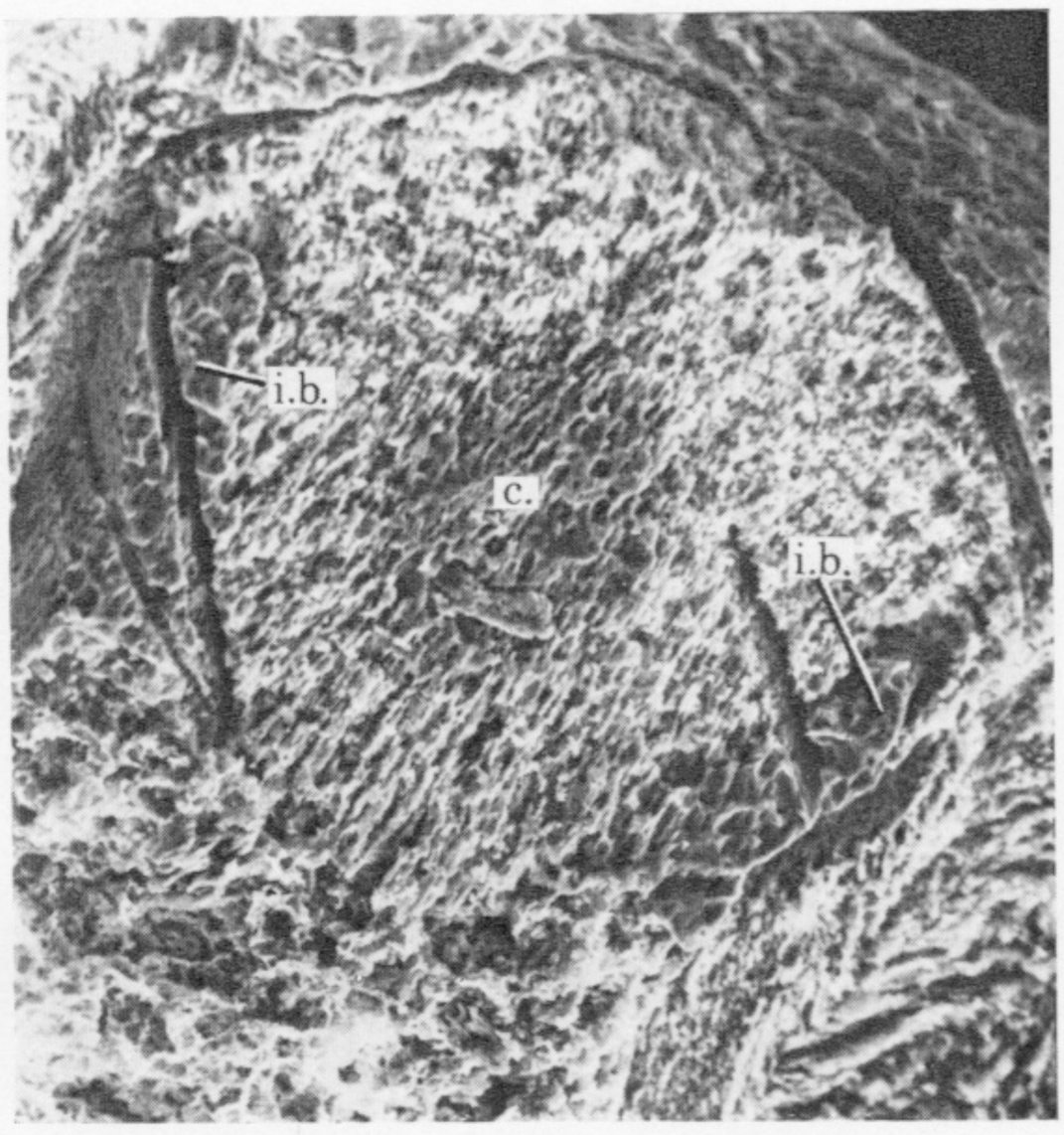

FIGURES 29–34. For description see page 477.

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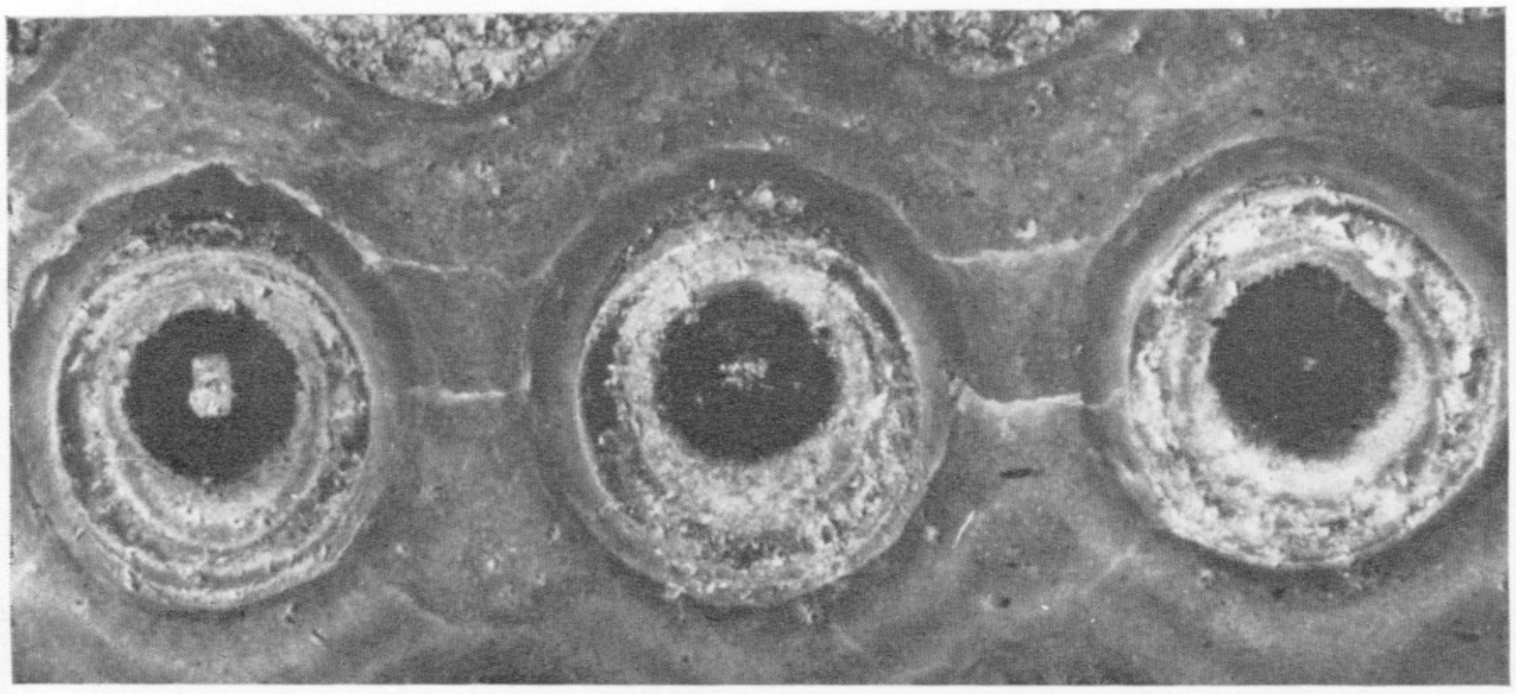
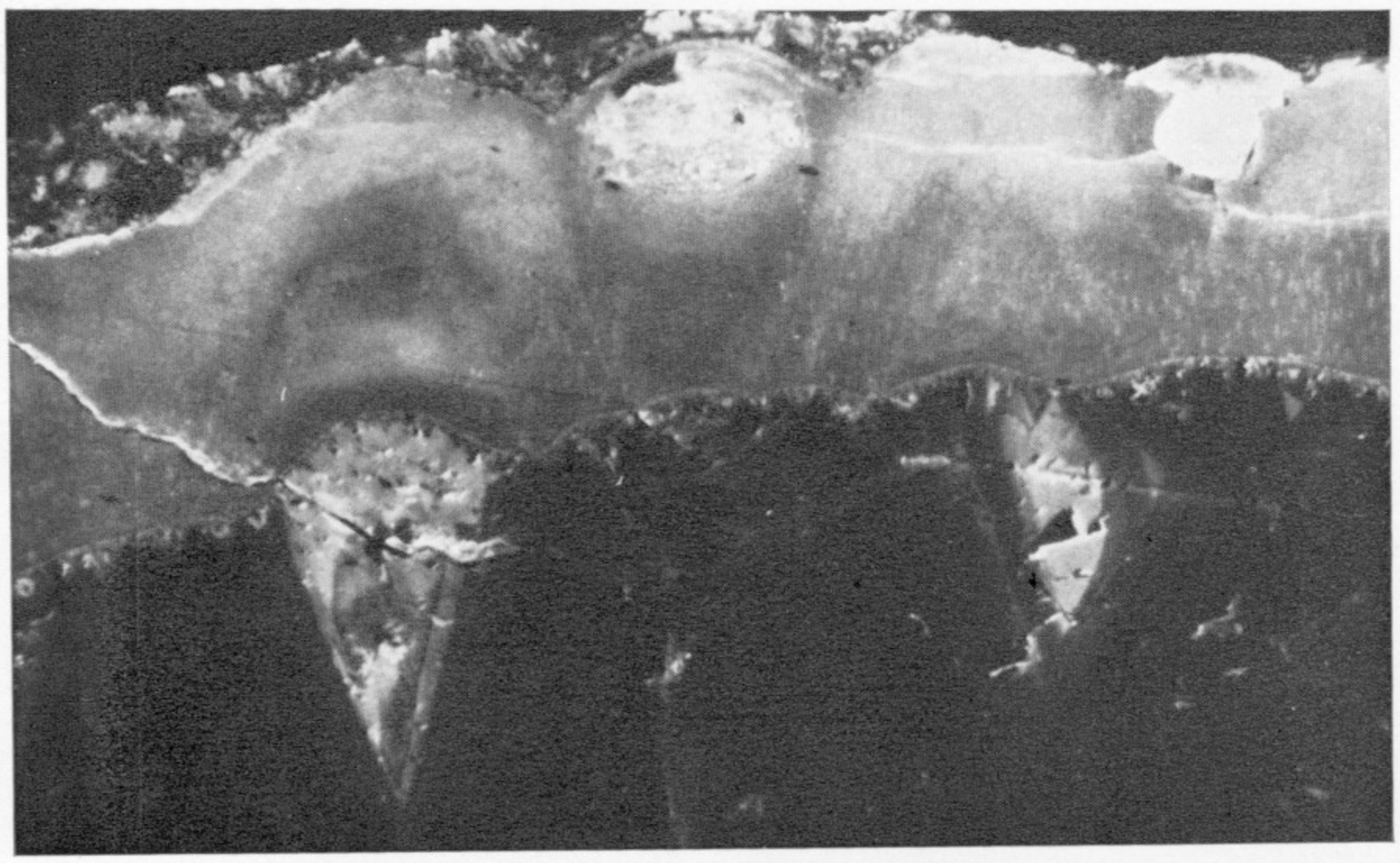
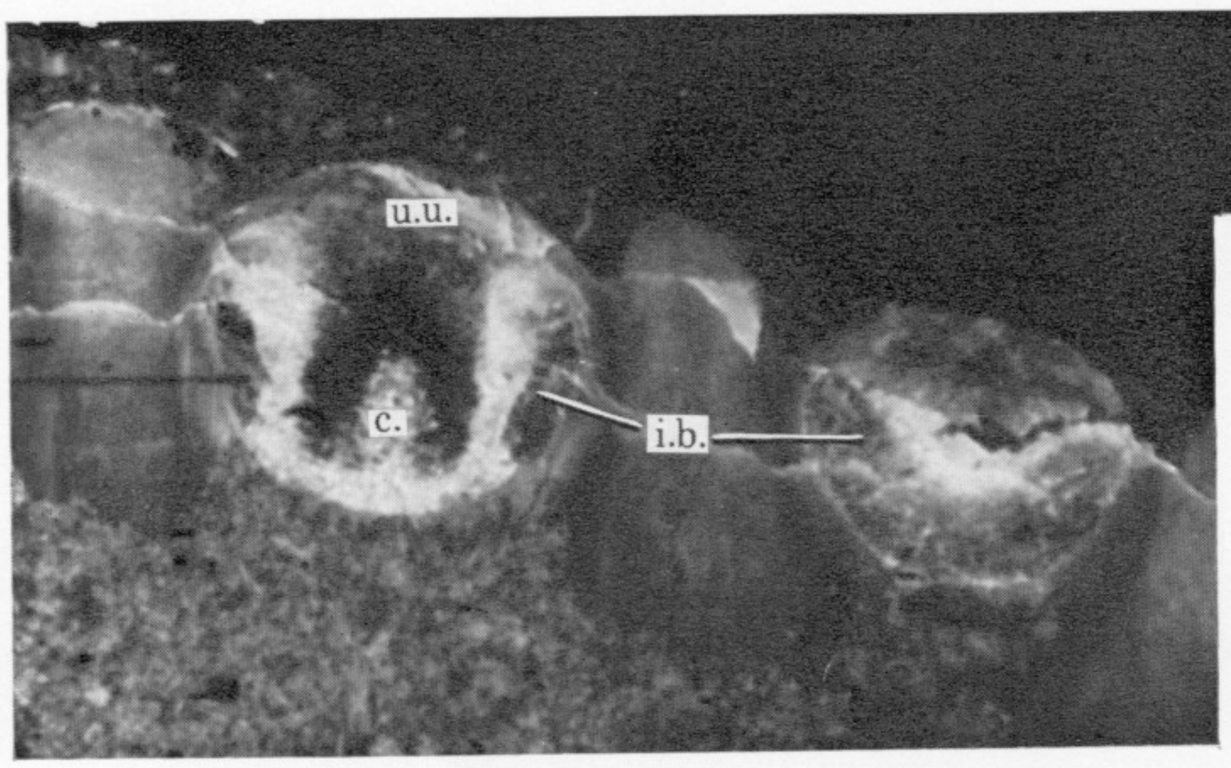


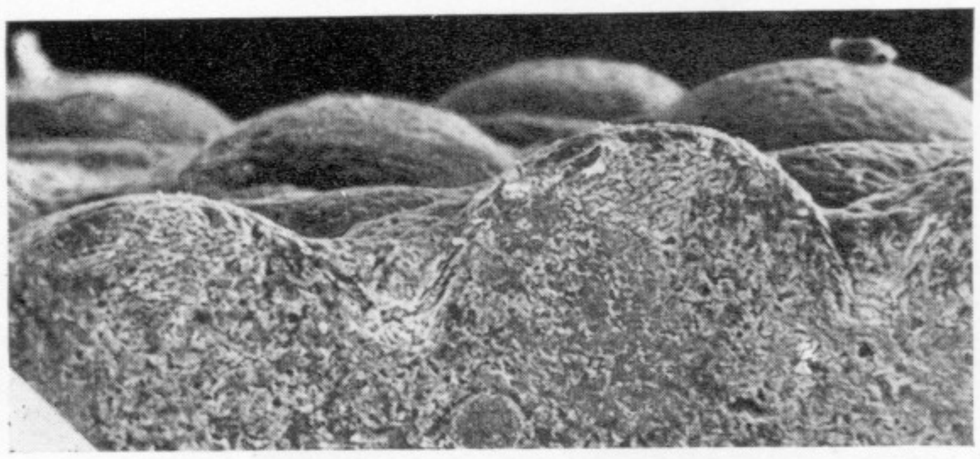
36



37



39



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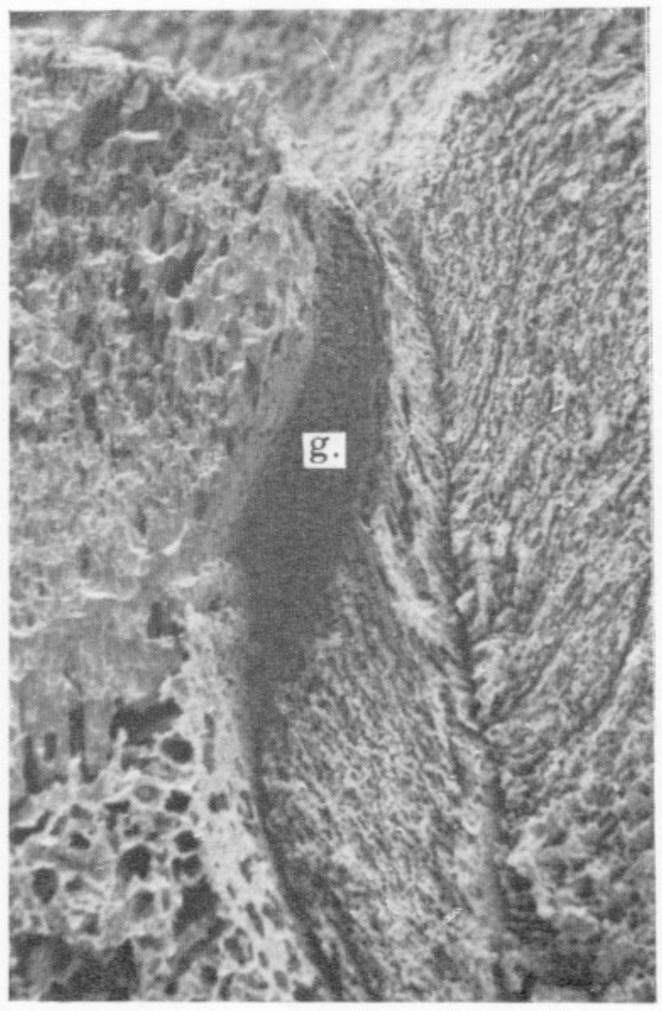
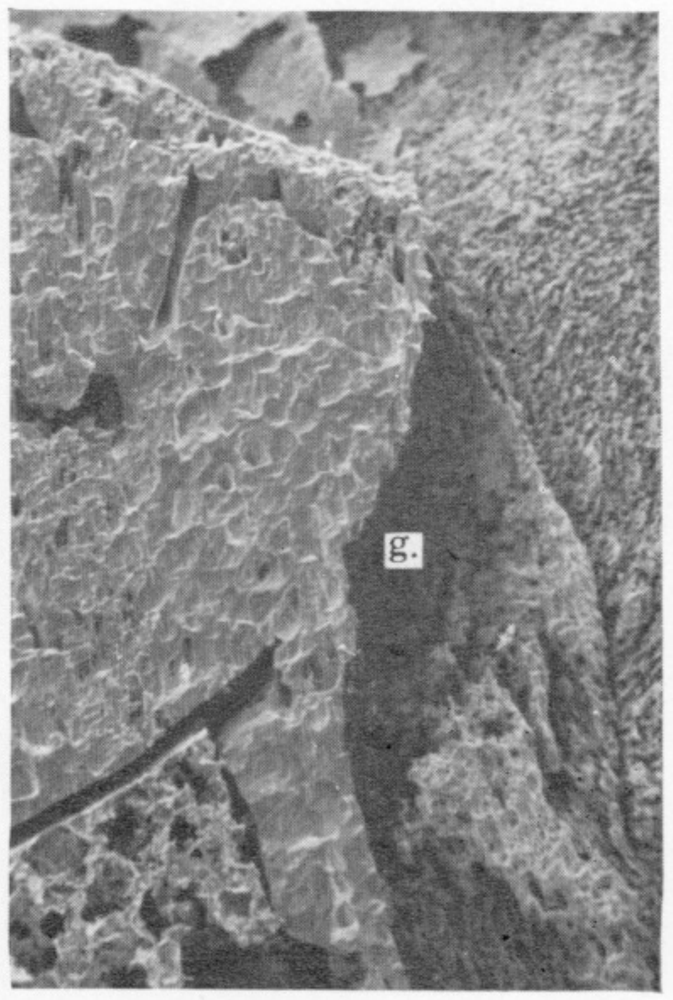
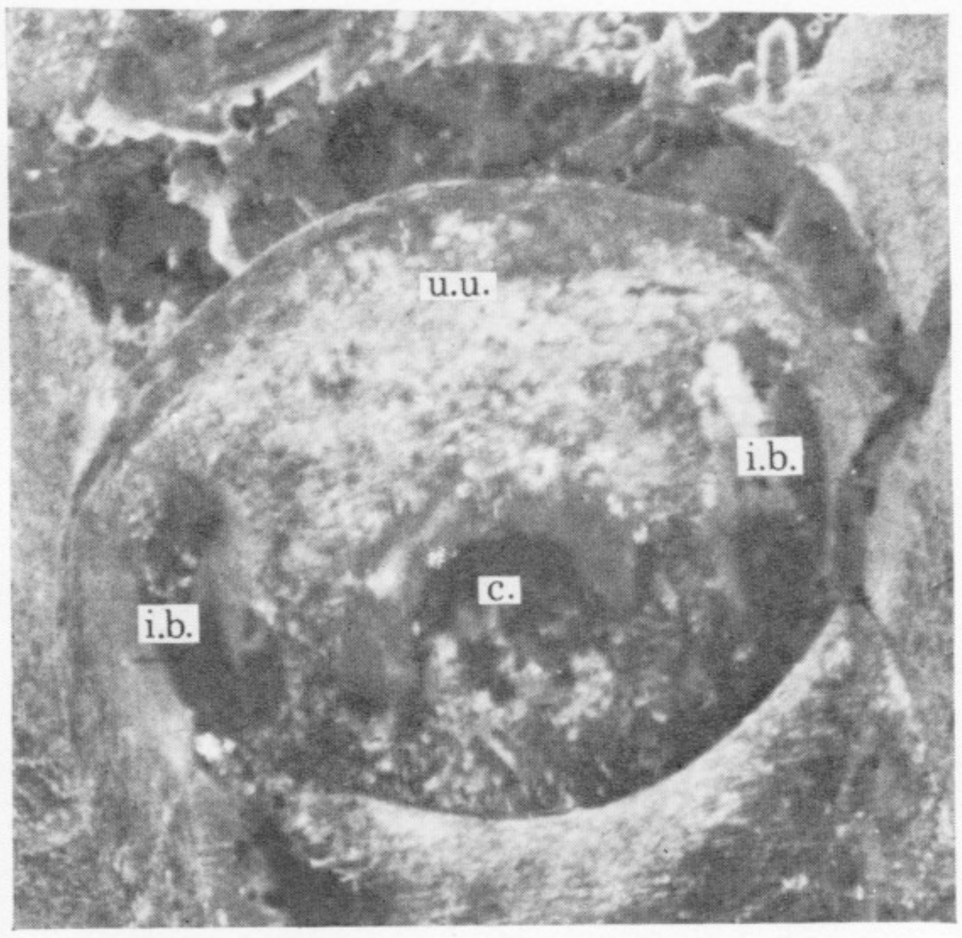


41



38



FIGURES 35–41. For description see page 477.

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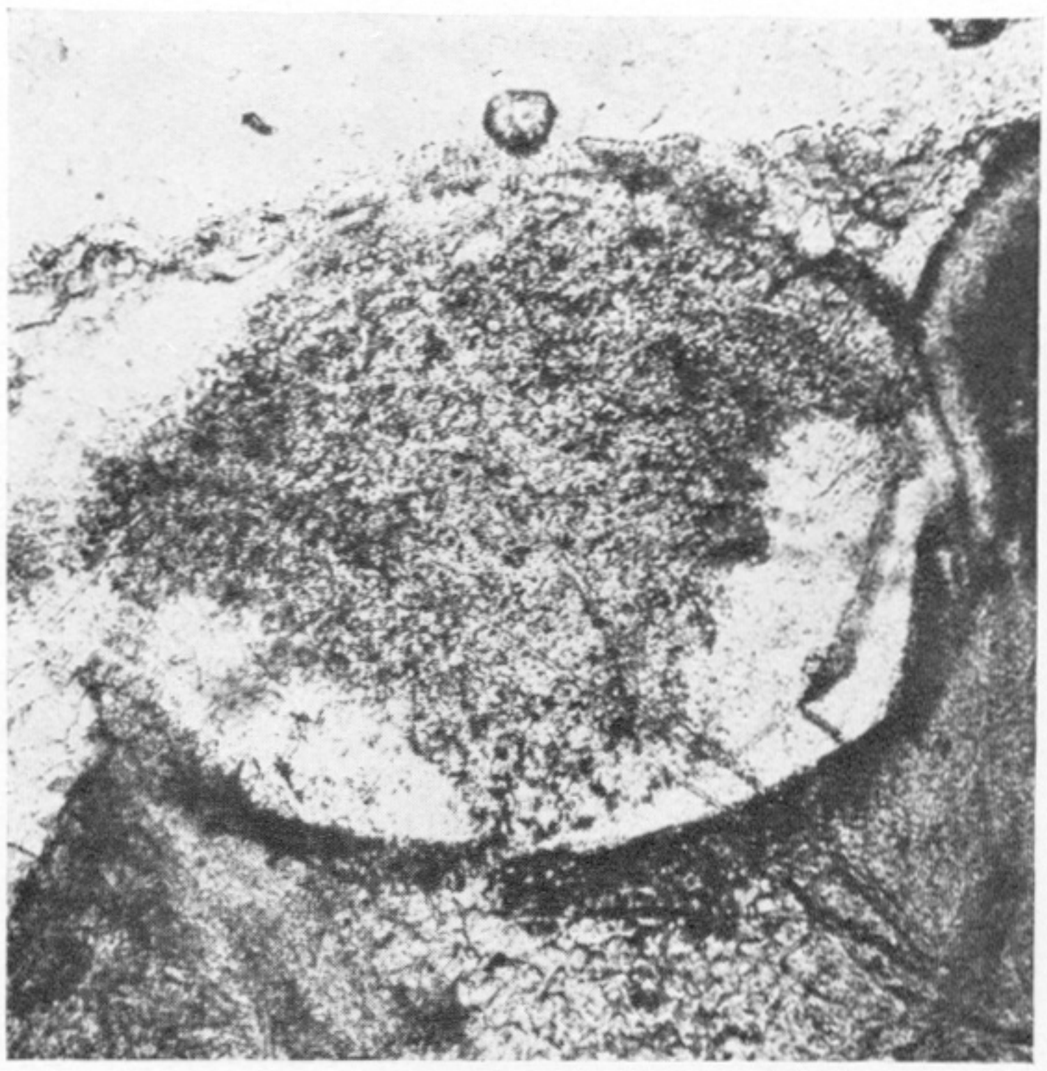
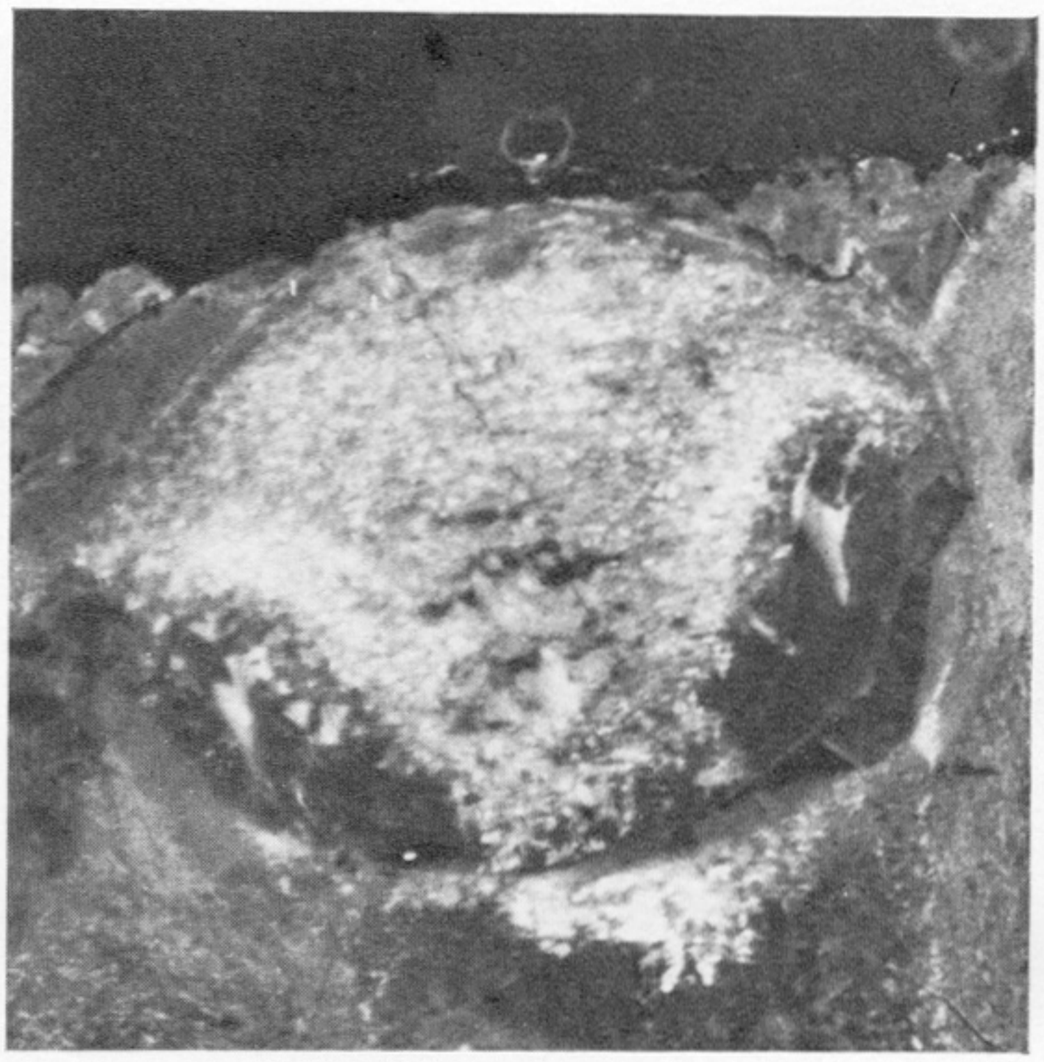
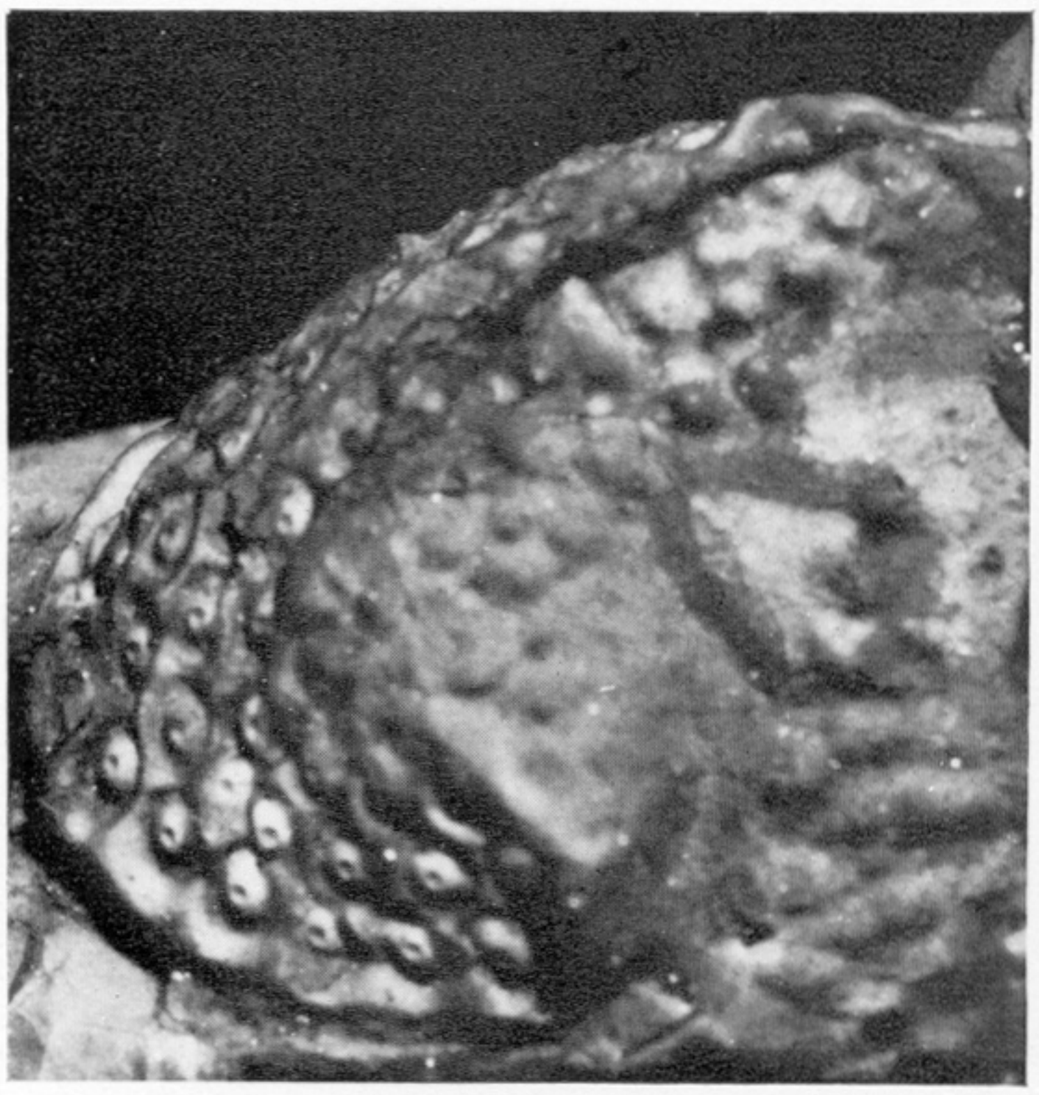


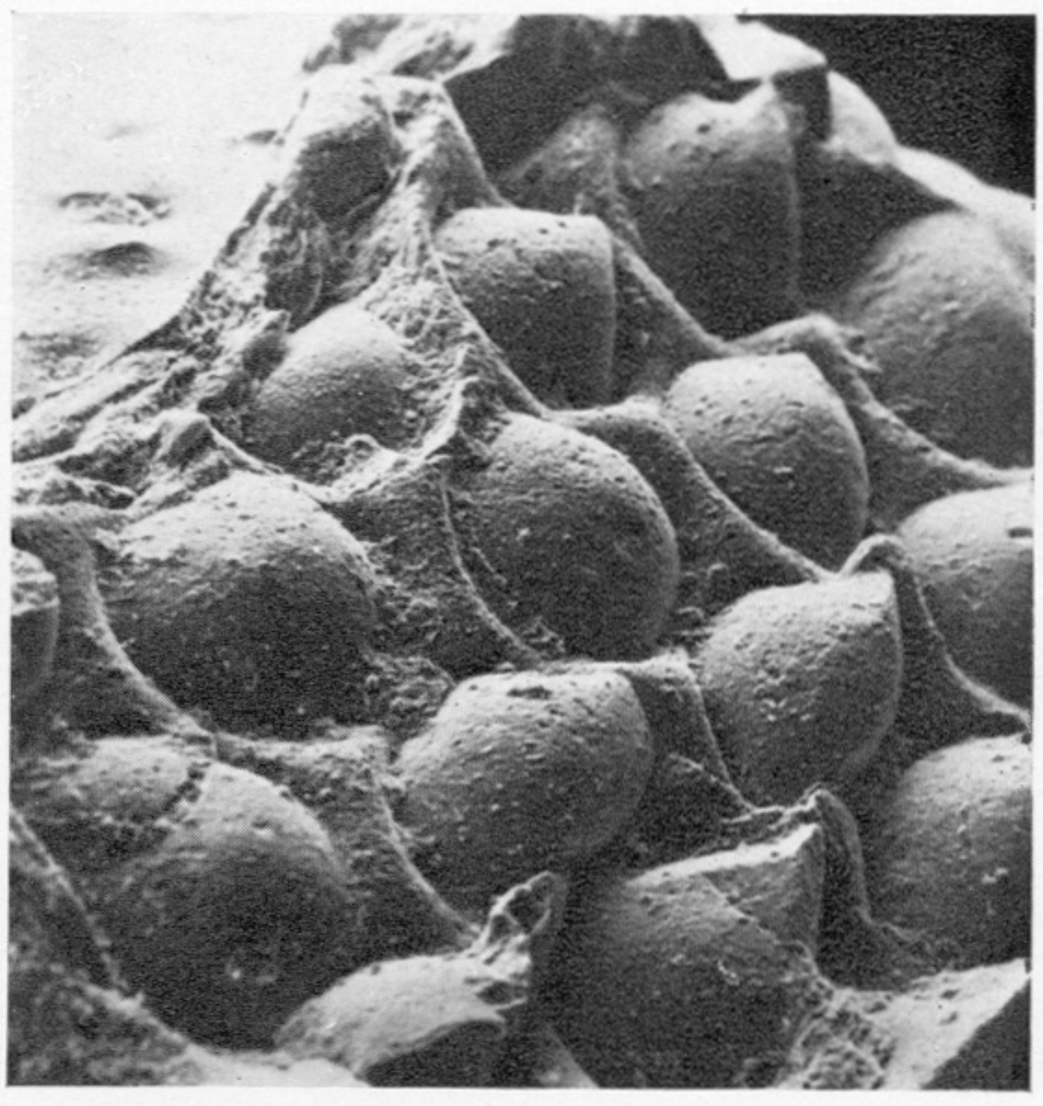
43



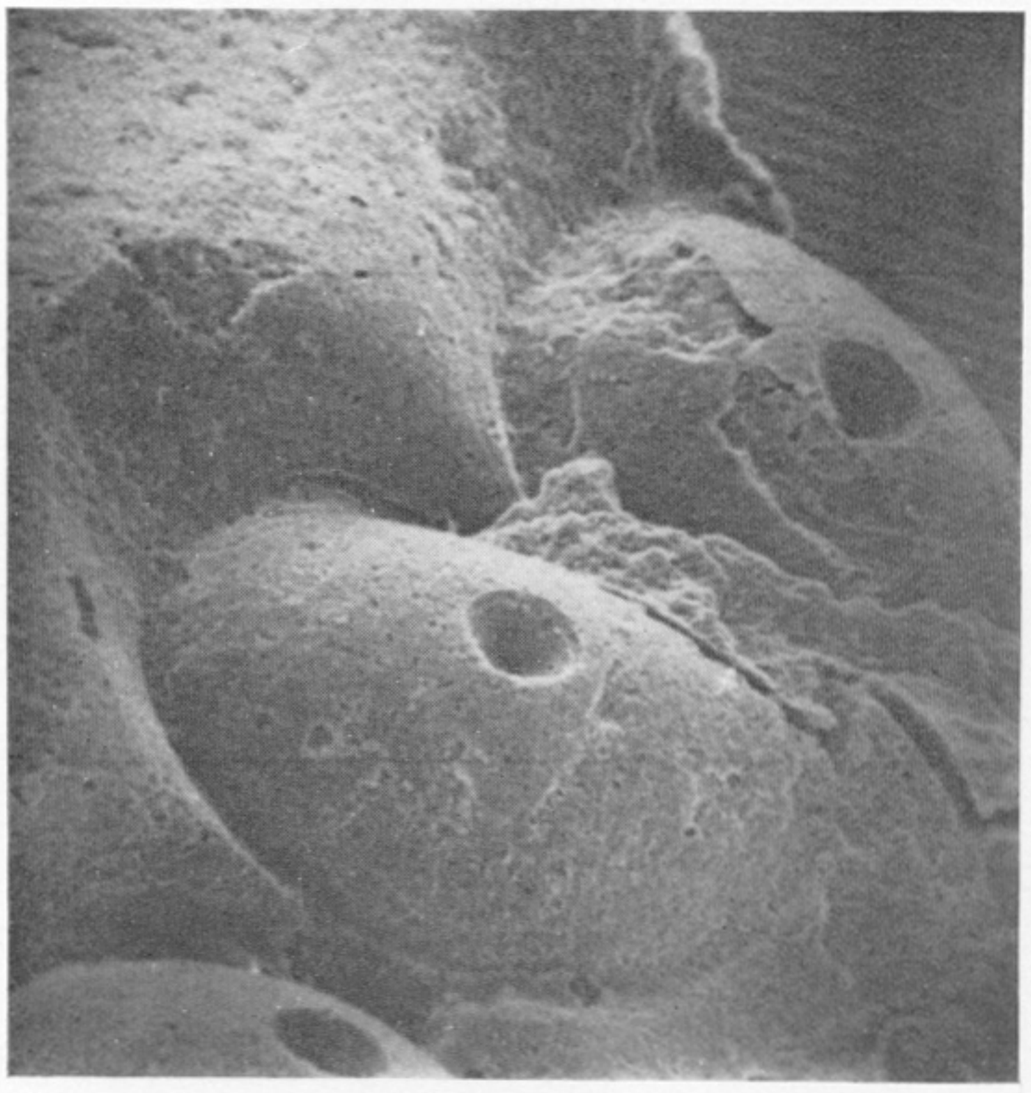
44



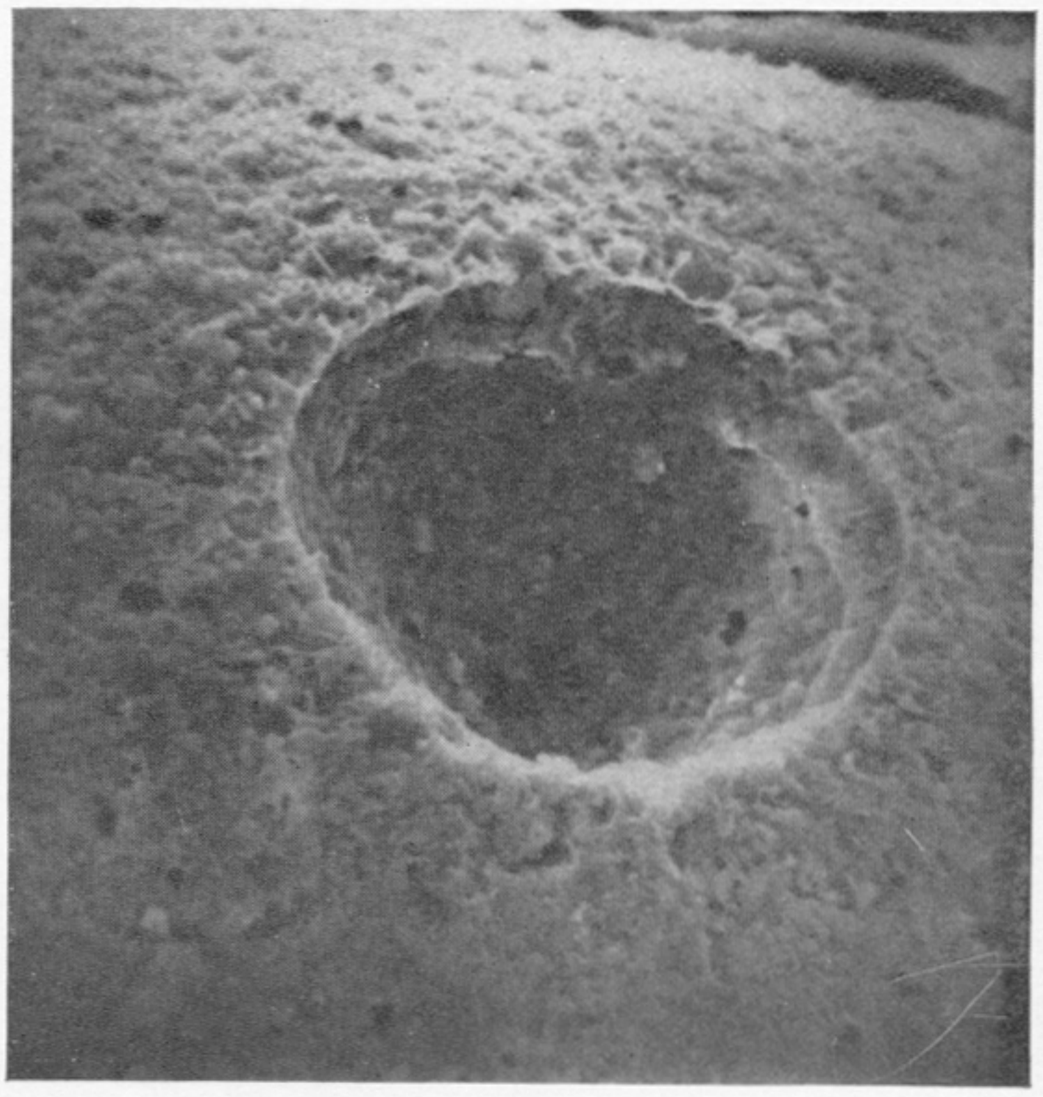
45



46



47



FIGURES 42–47. For descriptions see opposite.