HANS JØRGEN HANSEN

ELECTRON-MICROSCOPICAL STUDIES ON THE ULTRASTRUCTURES OF SOME PERFORATE CALCITIC RADIATE AND GRANULATE FORAMINIFERA

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Synopsis

The ultrastructures of the shells of six species of forminifera are described. Within the group of optically radiate/ultrastructurally radiate species (viz. *Nodosaria latejugata* Gümbel; *Polymorphina* sp.; *Bulimina midwayensis* Cushman & Parker; *Bulimina marginata* d'Orbigny) the crystal units of the wall are composed of single crystals each of which is enveloped by an organic membrane. In the boundaries between secondary lamels are concentrations of spongy organic material which is intimately connected with the organic pore-tubes. Locally the secondary lamels were found to be constructed of primary lamels. The calcite crystals of the wall are generally elongated in direction of the optical c-axis which is orientated perpendicular to the shell surface.

In the granulate *Melonis scaphum* (Fichtel & Moll) the crystal units are constructed of single crystals which are deliminated by organic membranes. The crystal units in *Heterolepa* cf. *subhaidingeri* (Parr) are composite but united by an organic membrane. The crystal units are build of tiny plates of calcite each of which is surrounded by an organic membrane which is much more delicate than the one surrounding the whole crystal unit.

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INTRODUCTION

The present study is a continuation of a previous work by the present author (Hansen, 1968a) in which the crystallographic orientation of the calcite crystals in a radiate and a granulate foraminifer was investigated by X-ray diffraction.

It was concluded that in the radiate form the calcite crystals are orientated with their basal pinacoid parallel to the shell surface. This corroborates the observations by Wood (1949) who arrived at the same conclusion using a polarizing microscope.

In the granulate form the crystallographic face parallel to the shell surface was shown to be the cleavage rombohedron as suggested in a hypothesis by Towe & Cifelli (1967).

The question as to the morphology of the calcite elements in these two types of wall structure naturally rises. This study is an attempt to clarify the ultrastructures of the shells of some radiate and granulate foraminifera.

The choice of species for electron-microscopical studies was largely determined by the forms used in the X-ray diffraction work.

When describing radiate wall structures it would appear necessary to distinguish between, on one hand, optically radiate/ultrastructurally radiate, and on the other hand optically radiate/ultrastructurally non-radiate walls in view of the investigations by Pessagno & Miyano (1968), Reiss & Schneidermann (1969), and by Hansen, Reiss & Schneidermann (1969).

The radiate *Polymorphina* sp. has a thick shell. This also applies to the species *Nodosaria latejugata*. The former was earlier used for X-ray diffraction studies while the surface ultrastructures of the latter were briefly described by Hay, Towe & Wright (1963).

In contrast to *Polymorphina* sp., *Nodosaria latejugata* possesses ornamental costae of the inflational type and shows a very distinct secondary lamination. The Paleocene *Bulimina midwayensis* has a relatively thin wall and is ornamented with spines in the older part of the test. The closely related recent species *Bulimina marginata* (the type species of the genus) was studied with respect to concentration of organic matrices as these were not prominent in the fossil *Bulimina midwayensis*.

In the granulate *Melonis scaphum* the wall is extremely thin and is therefore well suited for combined studies in light microscope and electron microscope, especially so, as the distal face of the final chamber is constructed of only one layer of crystal units. By contrast, the species *Heterolepa cf. subhaidingeri* was chosen to represent thick shelled granulate forms. This species was investigated earlier by HANSEN, REISS & SCHNEIDERMANN (1969) in their study of the nature of the bilamellar septa.

Both types of wall structures represented in the present study are illustrated by forms which beyond any doubt can be referred to either the radiate or the granulate structural type by aid of a polarizing microscope.

The aragonitic species have been omitted from consideration as a thorough investigation of a representative of the *Robertinacea*, viz. *Hoeglundina elegans*, was published recently by REISS & SCHNEIDERMANN (1969).

In the following the abbreviations SEM and TEM are used for scanning electron microscope and transmission electron microscope respectively.

Acknowledgements

Professor Z. REISS, The Hebrew University, Israel, kindly placed specimens of Heterolepa cf. subhaidingeri at the author's disposal.

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TECHNIQUE

Preparation of Specimens for the Scanning Electron Microscope

The specimens studied in the SEM were mounted, plated and if necessary cleaned again according to the technique described by HANSEN (1968b). The SEM micrographs shown in the present work were made in a Stereoscan Mk. IIa scanning electron microscope housed in the Geological Institutes of the University of Copenhagen.

Preparation of Specimens for the Transmission Electron Microscope

All sections of specimens studied in the TEM were prepared according to the technique described by HANSEN (1967, 1969) involving embedding in araldit, sectioning by frosted glass plates, polishing with MgO-powder prior to etching.

The author also applied the method described by KRINSLEY & BÉ (1965) but found a replication with collodium dissolved in pentylacetate more convenient.

Replicas of etched and un-etched outer and inner surfaces were made of specimens embedded in araldit. In order to obtain replicas of inner surfaces the chosen specimen was embedded with the chambers air-filled. The aperture was sealed with gum tragantum prior to embedding to prevent the embedding medium from flowing into the empty chambers. After hardening of the araldit the specimen was ground half way down with a frosted glass-plate leaving the specimen like a series of hemispheres. Before etching the specimen was replicated one or several times to remove the inner organic membrane and grinding dust. The specimen was then etched with an EDTA-solution (EDTA = ethylene-diamine-tetra-acetate) and washed in distilled water. After etching the specimen was cleaned by being replicated one or several times to remove the free-etched organic matrices.

The specimen does not necessarily have to be perfectly clean when this technique is used.

As fossil specimens often have sediment particles adhering to the surface even after careful washing it was necessary to find a technique by which it was possible to replicate the surface several times without loosing the specimen.

The specimens were laid on a glass plate, which had been covered in the centre with a small drop of araldit. The drop was spread to a very thin film using a needle and a dry test was placed in the araldit in the desired position. If a lenticular specimen was to be orientated vertically (i.e. standing on the periphery) it was first mounted on a clean glass plate with a very small amount of gum tragantum and afterwards the araldit was placed around it with a needle. Specimens with heavy ornamentation, reticulate surface or larger pores may cause some difficulty as the embedding medium creeps along the uneven structures and covers the specimen. This can be avoided by using only very little embedding material. By this method the surface of a specimen can be studied in an un-etched and later in an etched state.

The replicas were shadowed in an Hitachi vacuum evaporator. The author found it most convenient to use only carbon shadowing. Shadow casting with gold or platinum veiled the very faint differences in electron density between the organic membranes and the pure carbon film. The combination of a carbon replica with adhering organic material is in the following called replica-pseudoreplica.

In replicas of some specimens shadowed with carbon-platinum, striation with a spacing of 30–40 Å was found (pl. 2, fig. 1). The striation is orientated in two directions cutting each other at an angle of about 30°.

According to Reimer (1967) the resolution power of a collodium replica should at its best be about 60 Å. The striae are thus probably an artefact representing the structure of the replication material and do not refer to any structure in the replicated specimen.

Two-stage replicas have mainly been used. All micrographs made in the TEM show inverted relief.

The transfer of the shadowed replicas to cut-out grids has previously been described by the author (Hansen, 1967).

The technique used by Hansen (1969) was applied for preparation of specimens for combined light microscope and electron microscope studies.

In this work three different transmission electron microscopes have been used, viz. Hitachi HU-11-C, Akashi transcope and Philips EM-75. The former two are housed in the Geological Institutes of the University of Copenhagen, while the latter is now housed in the Department of Metallurgy, the Royal Danish Technical University.

Species with Radiate Wall Structure

Nodosaria latejugata Gümbel, 1868.

Pls. 1–8.

The material of this species originates from the Lower Selandian sediments in the Copenhagen area.

Thin section studies under light microscope between crossed nicols showed a very distinct radiate extinction. The extinction of the ornamental costae gave the

impression of a fan-shaped orientation of the crystals while the adjacent part of the shell showed the normal radiate extinction.

The test is distinctly lamellar (pl. 1, figs. 1–2). One specimen consisting of 11 chambers was cut, and a thin section of each chamber was prepared. The sections illustrated here represent chambers 7 and 8 of this series. When the nicols of the microscope were orientated parallel a faint lamination of the costae in some sections could be observed.

In the wall itself the youngest secondary lamels are considerably thinner than the older ones. The glassy appearance of the costae is due to the lack of pores which are abundant in the adjacent chamber wall. The abundant slender pores led early workers to introduce the term fibrous when describing this kind of wall structure. It later caused some difficulty as the term was considered synonymous with the term optically radiate and should accordingly be avoided (for discussion see Towe & Cifelli, 1967).

The boundaries between the secondary lamels are clearly seen on replicas of etched sections studied in the TEM. At the boundaries organic matrices were found. The boundaries are found on both strongly and slightly etched sections (pl. 1, fig. 3; pl. 2, fig. 2).

In deeply etched sections the secondary lamels were locally found to be constructed of primary lamels (pl. 3, figs. 1–2; pl. 4, fig. 1). The primary lamels are not as pronounced and distinct as the secondary ones. This is possibly due to the thicker organic matrices found between the secondary lamels.

The calcite crystals of the wall are elongated in the direction of the optical c-axis (pl. 3, figs. 1–2; pl. 5, fig. 2; pl. 7, fig. 2). The reason why there is a primary lamination in certain areas of the shell, while this structure seems untraceable in other areas is problematic. In most cases a distinct columnar structure indicative of continuous growth within each secondary lamel was found (pl. 5, figs. 1–2).

On replicas of etched inner surfaces the boundaries between the crystal units are distinct (pl. 6, figs. 1–2). Pores are found distributed both along the boundaries and inside the crystal units. The pores are circular to slightly elliptical in cross section and have a diameter of about 0.2 μ. Their diameter is thus smaller than the resolution power of a normal light microscope.

In the boundaries of the crystal units are organic matrices enveloping each of the units (pl. 6, fig. 1). The replica-pseudoreplica shadowed at right angles to the surface showed the delicate nature of the membranes.

Hay, Towe & Wright (1963) studied the ultrastructures of the surface of specimens of *Nodosaria affinis* from the basal part of the Kincaid Formation, Texas, U.S.A. combining electron microscope investigations of one-stage surface replicas and light microscope studies of thin sections. They wrote, concerning the ornamental costae: "Where the test is thickened by the ornamental ribs, the pores are discontinuous . . . The pores appear to have originally been continuous, but have later been filled in with calcite. . . . the ribs behave like a few large crystals of calcite which

extinguish in different orientations from the adjacent perforate wall. It is not certain whether this is due to recrystallization or whether it is an original feature".

Specimens of *Nodosaria latejugata* GÜMBEL (= ? HAY et al.'s *Nodosaria affinis*) from the basal part of the Kincaid Formation from the collection of the Mineralogical Museum of the University of Copenhagen were studied in TEM by the author. The structures found in these specimens are identical with the ones present in the Danish material but were different from those of HAY et al. It therefore would seem likely that the specimens studied by HAY et al. were recrystallized in view of their remarks on the extinction of the costae compared to the adjacent chamber wall.

Replicas of sectioned specimens cut at righ angles to the long axis of the test clearly demonstrated that the pores are not discontinuous at the ornamental ribs (pl. 4, fig. 1) and that they follow the general direction of the crystal units. The latter show a fan-shaped striation indicative of the optical orientation of the crystals.

If pores had been present in the ornamental ribs they should be traceable on etched surfaces. Replicas of etched surfaces of ornamental ribs did not show any trace of pores (pl. 7, fig. 3; pl. 8, fig. 2) while they were abundant in the areas between i.e. the un-ornamented chamber wall (pl. 7, fig. 1 & 3; pl. 8, fig. 1).

Polymorphina sp.

Pls. 9–11.

The material of this recent species originates from a sample collected by the author at a locality situated in the Kattegat east of Læsø at a depth of 56 m. Specimens of the same species were earlier investigated by the author by X-ray diffractometry.

Both sections and crushed specimens showed a distinct radial extinction when studied between crossed nicols under the light microscope.

The specimens used for electron microscopy were embedded air-filled in araldit and sectioned to the median plane. They were replicated to remove the inner membrane, etched for 2 minutes with EDTA and replicated again. After shadowing a replica-pseudoreplica was obtained. TEM stereo micrographs (pl. 9, figs. 1–2) showed that the organic membranes adhere for some distance to the free etched pore-tubes. A generalized model of the relation between the pore-tubes and the organic membranes is shown Fig. 1. This model is comparable with the micrograph shown on pl. 10, fig. 1.

To obtain a further proof of the presence of organic material in the wall the following technique was used. Specimens were embedded so that a small area was left free of embedding material. To clean the surface it was replicated several times to remove the organic material. Afterwards it was etched for 45 seconds with EDTA. After washing in distilled water the specimens were shadowed at a low angle. After this, collodium was put on top and left to dry. Instead of pulling off the replica it was only lifted a little at one side in order to expose a small area of the shell. The specimen with adhering replica was then transferred to 5 % HCl. When the specimen was dissolved the replica was pulled off and washed in distilled water.

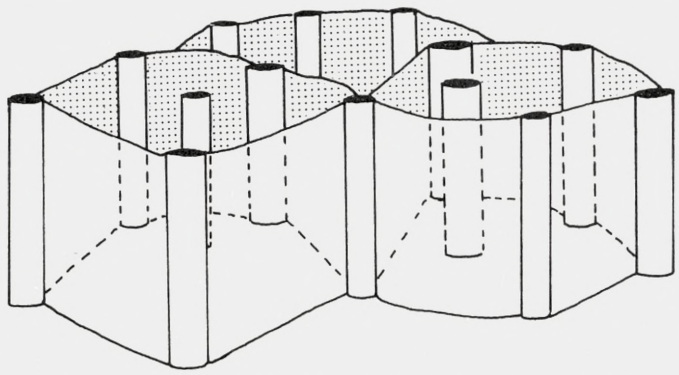

Fig. 1. Generalized model of the relation between the organic membranes enveloping the crystal units and the organic pore-tubes.

Where organic membranes are present they will cause shadow and they will remain in their original position in the carbon film; when using a two-stage replica technique the organic membranes often flow away from their original position during the dissolution of the collodium.

The organic matrices enveloping the crystal units are clearly exposed by this method (pl. 11, fig. 1).

Bulimina midwayensis CUSHMAN & PARKER, 1936.

Pls. 12–16; pl. 17, fig. 1.

The material of this species originates from the Lower Selandian deposits exposed in the gorge of the streamlet Lellinge å south of Copenhagen.

Thin sections studied under the light microscope between crossed nicols show a radiate extinction indicative of an optical radiate arrangement of the crystals where the c-axis are perpendicular to the surface of the test. Secondary lamination of the older part of the test could also be observed.

A section of *Bulimina midwayensis* studied in TEM was published by HANSEN (1967). On replicas of etched polished sections the lamination connected with the addition of new chambers is distinct. The secondary lamels found in the older part of the test have an almost constant thickness of about 3 μ. There is, however, a slight thickening of the lamels in the inflational spines and especially of the oldest lamels (pl. 12, fig. 1).

At the lamel boundaries are found concentrations of organic material. The organic material is, however, not prominent in *Bulimina midwayensis*. The systematically closely related recent species *Bulimina marginata* had more organic material and is described below. Fossilisation may have caused a shrinkage of the organic material in *Bulimina midwayensis* and accordingly no attention has been paid to the organic material in the test of this species.

The optical radiate arrangement of the calcite crystals is also seen in the crystal morphology. The boundaries between the crystal units are found to run perpendicular

to the test surface (pl. 12, fig. 2; pl. 13, fig. 1). It was found that the crystal units are interrupted at the lamel boundaries (pl. 13, fig. 2).

Areas with more irregular boundaries between crystal units were found as well (pl. 14, fig. 1), mainly where new chambers are added.

On etched inner surfaces of the chambers the crystal unit boundaries are distinct (pl. 15, fig. 1; pl. 16, fig. 1). There would seem to be some difference between the construction of the wall of the proloculus and that of the younger chambers. The two figured chambers (pl. 15, fig. 1; pl. 16, fig. 1) showing the proloculus and the third chamber have been exposed to the same etching for the same period of time. The boundaries in the proloculus are more deeply etched than those of the younger chamber. This is possibly due to thicker organic matrices between the crystal units in the proloculus than in the younger chambers. The boundaries between crystal units in the proloculus seem to be more irregular than in the younger chambers.

The pattern of the boundaries between the crystal units gives the impression of a simple jig-saw puzzle. In end view the crystal units show a lobate configuration. In the calcite small pits are seen where the crystalline matter has been more strongly attacked by the EDTA. This may possibly be explained as areas of dislocation or some other disorder in the crystal structure. That they do not represent planes of twinning or crystal intergrowth is indicated by their irregular distribution. The etch pits are found both in the basal pinacoid (parallel to the surface of the test) and in sections at right angles to the wall surface (pl. 17, fig. 1).

The transition from an etched hollow chamber to the adjacent sectioned chamber wall is shown in pl. 14, fig. 2. The crystal unit boundaries stand out like mountain ranges and it is evident that these boundaries are the ones found running perpendicular to the wall surface when studied in sections. As on pl. 16, fig. 1, the boundaries between crystal units are more regular than the boundaries in the proloculus.

Bulimina marginata D'Orbigny, 1826.

Pl. 17, fig. 2; pl. 18.

Specimens recently collected from the Kattegat were embedded, sectioned, polished, etched and replicated. The first replica after etching was used to study the free etched organic material. The replica-pseudoreplica was shadowed with about 75 Å carbon at a very high angle. The true replica is found as a background on which the organic membranes and pore tubes are lying. There are some difficulties in obtaining resonably well-focused electron micrographs of this kind of specimens as the organic matter gives a very high relief. In the sections was found a high concentration of organic material both on the inner and outer surface of the test as well as in the boundaries between secondary lamels (pl. 18, figs. 1–2).

A replica-pseudoreplica of an etched inner surface showed the crystal unit boundaries as dark irregular bands which are relatively thick and also the free etched organic membranes which lay within the replica while it was shadowed. The mem-

branes have probably floated out of position during the dissolution of the replica and have shrunk in such a way that they are now found as dark bands running concordant with the crystal unit boundaries (pl. 17, fig. 2).

Species with Granulate Wall Structure

Melonis scaphum (Fichtel & Moll, 1798).

Pls. 19–21.

The material of this species was recently sampled from the Kattegat by the author.

A micrograph of a crushed specimen observed under the light microscope between crossed nicols showing extinction indicative of a granulate wall structure was previously published by Hansen (1968a). When studying flat fragments under the light microscope between crossed nicols the question of the delimitation of crystal units arises. When rotating the microscope stage the jig-saw puzzle pattern of dark lines constituting the boundaries between optical crystal units disappear and reappear.

In thin sections of radiate calcitic forms the lamel boundaries are clearly seen when the boundaries are orientated at right angles to the polarizing direction of the nicols (especially so when both nicols are orientated parallel). It would appear that the same phenomenon to a certain extent applies to the boundaries between the optical crystal units in *Melonis scaphum*.

As *Melonis schaphum* has a lamellar test, only the central part of the relatively plane apertural faces of the septa have been used, as this part is non-lamellar, so that a possible optical phenomenon, superimposed from one crystal upon another, could be avoided. The apertural face provided a flat fragment of the shell apparently constructed of only one layer of crystals as in *Chilostomella* (see Towe & Cifelli, 1967). The central part of the apertural face of several specimens was broken off and embedded floating on a small drop of half-hardened araldit on a glass slide. The same fragment could in this way be studied under the light microscope and could also be replicated for electron microscope study.

In the TEM a slightly etched apertural face showed the presence of organic material delimiting the crystal units and lying along the boundaries (pl. 19, figs. 1–2.)

Pores are present both inside the crystal units and along the boundaries between them (pl. 20, fig. 1). The organic material is of a spongy nature and is intimately connected with the pore-tubes (pl. 20, fig. 2). On one of the specimens a correlation between the light microscope picture and the electron microscope observations could be achieved. Pl. 21, figs. 1–3 shows the same area seen in both types of microscope. It is evident from these micrographs that one *optical* crystal unit consists of only one *morphological* single crystal. This also corroborates the observation of the crystal units of the optically and morphologically radiate forms. In these a crystal unit consists of only one crystal which is indicated by the lack of any organized etch figures that are to be expected along lines of crystal intergrowth and lines between crystallographic twins.

When studied in thin section between crossed nicols the test was found to be lamellar. The secondary lamels are very thin but can be seen in the older thickened walls. In these the optical crystal units were found to extinguish across the lamel boundaries. As, however, the wall is very thin, even in the older part, observational difficulties made it impossible to correlate light microscope and electron microscope observations of the same specimen.

Heterolepa cf. subhaidingeri (PARR, 1950).

Pls. 22–26.

The specimens of this form originate from off New Zealand. The were kindly placed at the author's disposal by Professor Z. REISS, Israel.

In thin section this species shows a very pronounced secondary lamination. The extinction between crossed nicols is of the granulate type as described by WOOD (1949). Micrographs of the species were published by HANSEN, REISS & SCHNEIDERMANN (1969). The extinction demonstrates optical units extinguishing across the boundaries between secondary lamels. The shapes of the extinguishing units may vary somewhat, but are in general elongated in a direction perpendicular to the shell surface. These optical units are of the order of size of 20–30 μ in length while their width is about 3–5 μ. The boundaries between them studied in thin sections only are not as well defined as in *Melonis scaphum*. Crushed specimens studied between crossed nicols showed an indistinct extinction.

On replicas of etched and polished sections studied in TEM was found a pronounced division of the calcite into plates each of which have a thickness of about 0.3 μ (pl. 22, fig. 1). The calcite plates are grouped as morphologically uniformly orientated piles surrounded by a thick organic membrane (pl. 22, fig. 2; pl. 23, fig. 1). Also between the plates which lie within the thick organic membrane are found organic matrices (pl. 23, fig. 2) which, however, are much more delicate than those mentioned above.

The boundaries between secondary lamels are marked by a concentration of organic material easily seen on replicas of etched specimens (pl. 24, fig. 2). It is not as thick as that found in the septa (pl. 24, fig. 1).

While each of the crystal units in *Melonis scaphum* consists of an optical and morphological single crystal of calcite (in the septa) the crystal units in *Heterolepa cf. subhaidingeri* are composed of a group of plates which all have the same optical and morphological orientation. Analogous to the radiate forms and the granulate *Melonis scaphum* the delimiting factor of the crystal unit is the thicker organic membrane surrounding the optical unit.

The same orientation of the calcite plates continues across the boundaries between the secondary lamels (pl. 24, fig. 2). In contrast to this the crystal plates are interrupted at the lamel boundaries (pl. 25, figs. 1–2).

The pores have a diameter of about 15 μ. Prominent constrictions are found where the pores cross the boundaries between the secondary lamels. Besides the

strong constrictions corresponding to these lamels are found less pronounced constrictions (pl. 26, fig. 1). The lamels corresponding to these latter constrictions could not be traced in the SEM and TEM. The slight constrictions are supposed to represent primary lamination analogous to the one observed in some of the radiate forms. The minor constrictions are not found in all pores (pl. 26, fig. 2).

In the septa (pl. 24, fig. 1) are found the same piles of calcite plates with alternating directions as in the chamber wall and in the secondary lamels. The orientation of the plates is not identical on both sides of the thick organic matrix constituting the dark dividing line in the septum. This may explain the indistinct extinction of the septa when studied in crushed specimens between crossed nicols.

CONCLUSIONS AND DISCUSSION

In the present work mainly optically radiate/ultrastructurally radiate species have been investigated. These forms show both in their optical properties and in their ultrastructures that the calcite of the wall is columnar and elongated in direction of the c-axis arranged perpendicular to the wall surface. In these forms the crystal units are composed of single crystals which are interrupted at the boundaries between the secondary as well as at the primary lamels. The interruption of crystals at lamel boundaries was mentioned earlier by Hansen (1968 c), Reiss & Schneidermann (1969) and by Hansen, Reiss & Schneidermann (1969).

Two granulate species have been investigated. The one shows, that an optical crystal unit consists of a morphologically single crystal, while it in the other form is composed of a series of thin plates with identical morphological orientation.

The question of single crystals, aggregates etc. in the description of mineral matter in the test of foraminifera was discussed by Towe & Cifelli (1967). They concluded that it would be nonsense to measure parameters like crystal diameter. As, however, single crystals or aggregates of crystals are delimited by organic membranes, and, as these are easily traceable on etched specimens studied in the TEM, it is possible to discern crystal units. *A crystal unit is thus here defined as one or more crystals with identical optical orientation enveloped by a membrane; the membrane is regarded as the delimiting factor.*

In the investigated species the pores are situated both inside and along the boundaries between crystal units. In *Heterolepa cf. subhaidingeri* the author did not succeed in observing the position of the pores in relation to the crystal unit boundaries.

The presence of pores within the crystal units conflicts with the statement by Loeblich & Tappan (1964) that the pores pass between crystals in the hyaline radiate forms.

In the sectioned specimens concentrations of organic material are prominent in the boundaries between the secondary lamels. Hansen, Reiss & Schneidermann (1969) demonstrated the continuity of the organic spongy material in the bilamellar septum with the spongy organic material found at the inner boundary of the corresponding secondary lamel (i.e. lying at the inner surface of the outer lamella).

Towe & Cifelli proposed a model of calcification in foraminifera. They suggested an epitaxial growth of crystals from an active-passive membrane. The passive membrane, being thick, carries the active compounds responsible for the nucleation of the calcite which, when initiated, grows on outwards.

This model fits to a certain extent to the observation of calcification in *Spiroloculina hyalina* published by Arnold (1964). The crystallization takes place in the wall close to its inner surface. In the later stages of mineralisation the outer part of the organic wall is calcified. It was found that the wall of *Spiroloculina hyalina* was formed

as an organic matrix prior to calcification. As, however, the calcification takes place in a series of isolated spots also in the middle and upper part of the primary organic matrix there must be several more points of nucleation than those found close to the passive innermost membrane.

Towe & Cifelli did not stress the importance of the organic matrices enveloping the crystals or crystal units. Accordingly their model of calcification does not encompass these structures.

All observations point to the presence of an organic three-dimensional framework probably of spongy nature intimately connected with the organic pore-tubes in the wall of foraminifera prior to calcification. Moreover, the crystal interruption at lamel boundaries would imply that renewed nucleation of calcite takes place on the other side of the lamel boundary. The crystal unit boundaries in *Heterolepa cf. subhaidingeri* were found to be independent of the secondary lamination. In contrast to the crystal units the small plates comprising the crystal units are interrupted at the boundaries, while their direction is un-altered. In spite of the crystal plate interruption at the lamel boundaries the orientation from an older to a younger lamel persists.

The problem of primary lamination needs a thorough study but already with the few available observations (Gerke, 1957; de Civrieux & Dessauvagie, 1965; Reiss & Schneidermann, 1969; Hansen, Reiss & Schneidermann, 1969) it appears that the model of calcification proposed by Towe & Cifelli needs modification, as pointed out by Lynts & Pfister (1967).

The solution to this problem lies within the field of study of living specimens rather than in the study of tests of dead foraminifera as clearly demonstrated by the work of Arnold (1964), and Angell (1967).

РЕЗЮМЕ

В данной работе описаны ультраструктуры раковин шести видов фораминифер. В группе оптически радиально-лучистых — ультраструктурно радиально-лучистых видов (Nodosaria latejugata Gümbel; Polymorphina sp.; Bulimina midwayensis Cushman & Parker; Bulimina marginata d'Orbigny) кристаллические единицы стенок состоят из единичных кристаллов, каждый из которых покрыт органической мембраной. На границах между вторичными пластинками развито губчатое органическое вещество, непосредственно связанное с органическими поровыми трубками. Местами вторичные пластинки оказываются сложенными первичными. Кальцитовые кристаллы, слагающие стенку, обычно удлинены в сторону оптической оси "c", которая направлена перпендикулярно к поверхности раковины.

У гранулированной Melonis scaphum (Fichtel & Moll) кристаллические единицы состоят из единичных кристаллов, разделенных тонкими органическими мембранами. Кристаллические единицы у Heterolepa cf. subhaidingeri (Parr) являются сложными, но также окруженными органической мембраной. Каждая единица сложена тонкими пластинами кальцита, каждая из которых покрыта органической мембраной, намного тоньше той, которая покрывает всю пачку.

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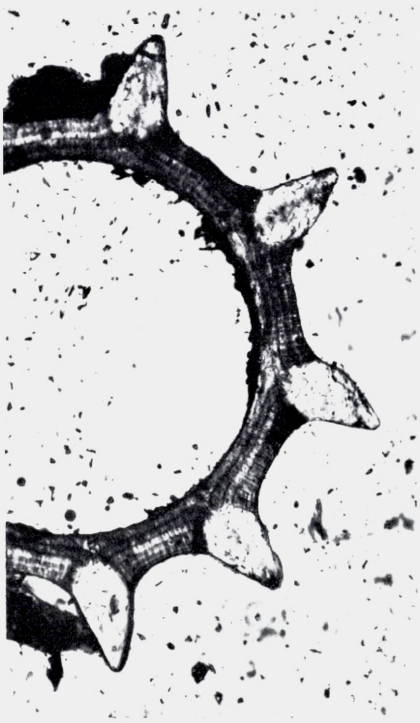
PLATES

PLATE 1

Figs. 1–2. *Nodosaria latejugata* Gümbel.
Transverse thin section of chambers 7 and 8 respectively, showing secondary lamination. 2 nicols parallel.

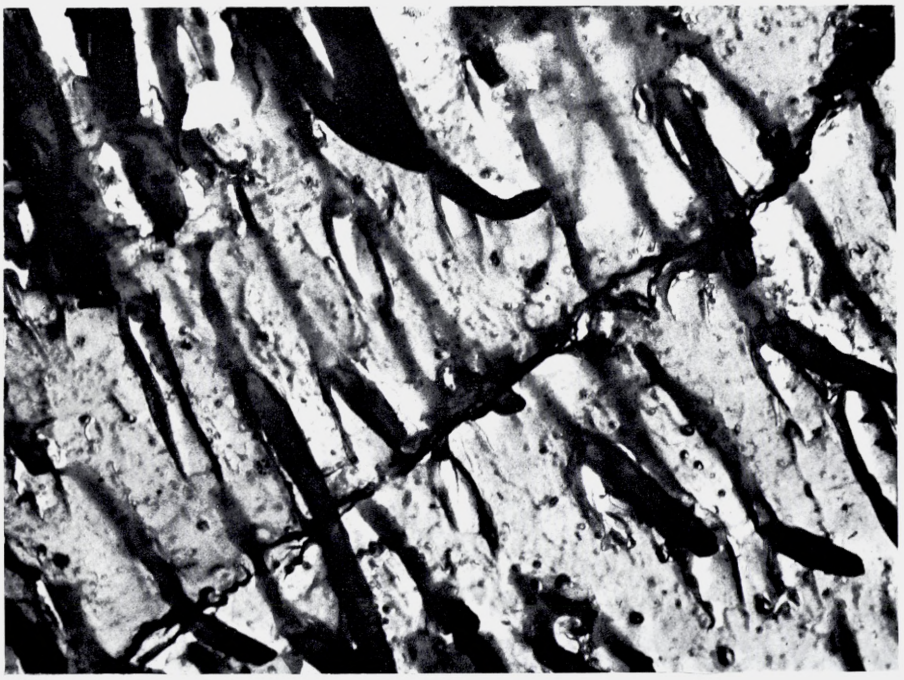
Fig. 3. *Nodosaria latejugata* Gümbel.
Carbon shadowed replica of etched transverse section showing the boundary between two secondary lamels with a sheet of organic material. TEM.



1

100 μ

2



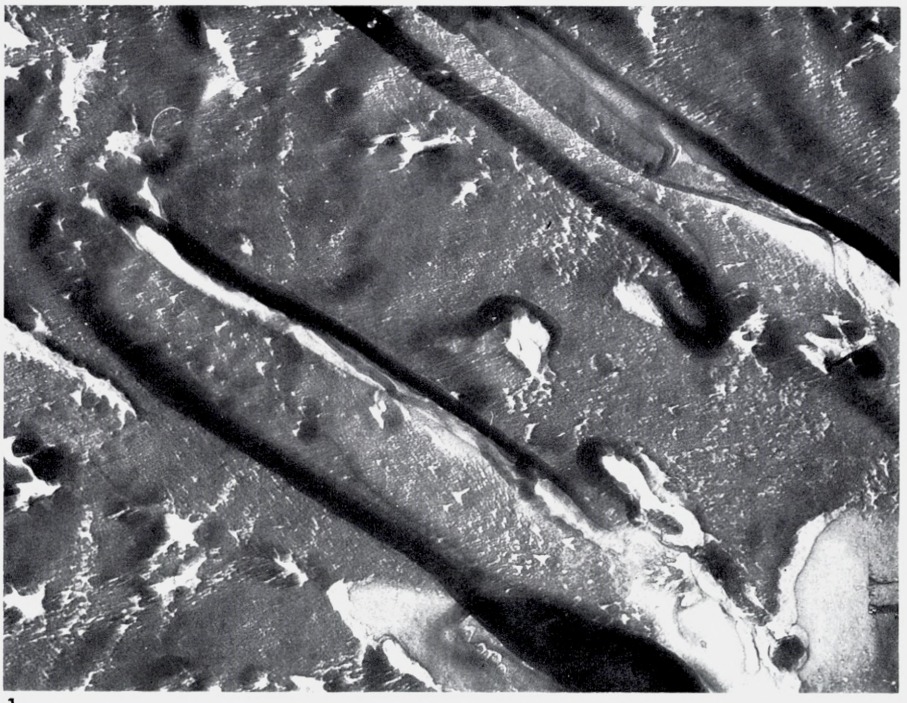
1 μ

3

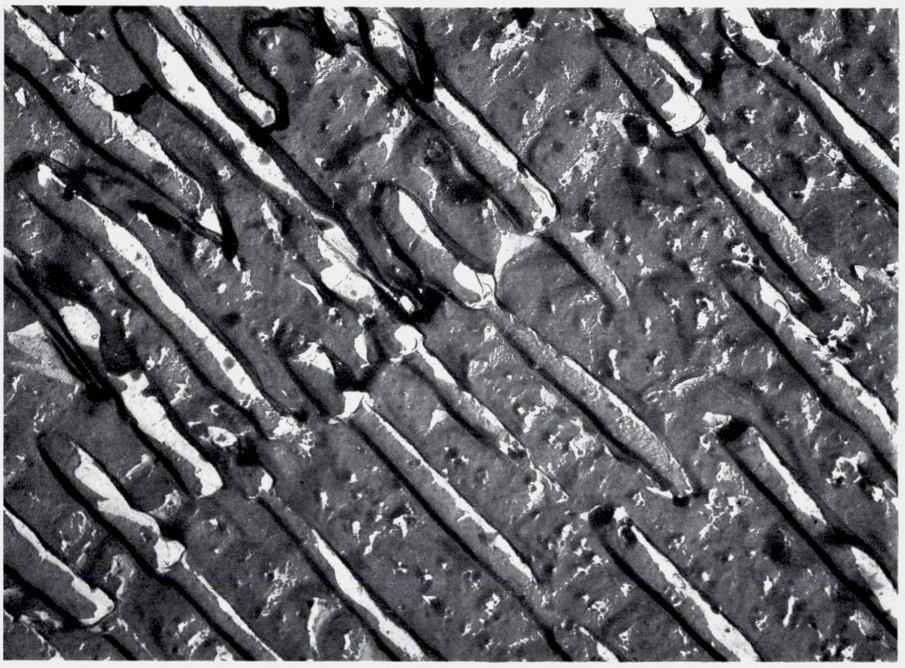
PLATE 2

Fig. 1. *Nodosaria latejugata* Gümbel.
Carbon-platinum shadowed collodium replica of etched transverse section of chamber wall. The micrograph shows in two directions (with an angle of ca. 30°) striae with a distance of 30–40 Å representing the structure of the collodium. TEM.

Fig. 2. *Nodosaria latejugata* Gümbel.
Carbon-platinum shadowed replica of slightly etched transverse section of the chamber wall with a boundary between two secondary lamels at which the pore-tubes show slight constrictions. TEM.



1

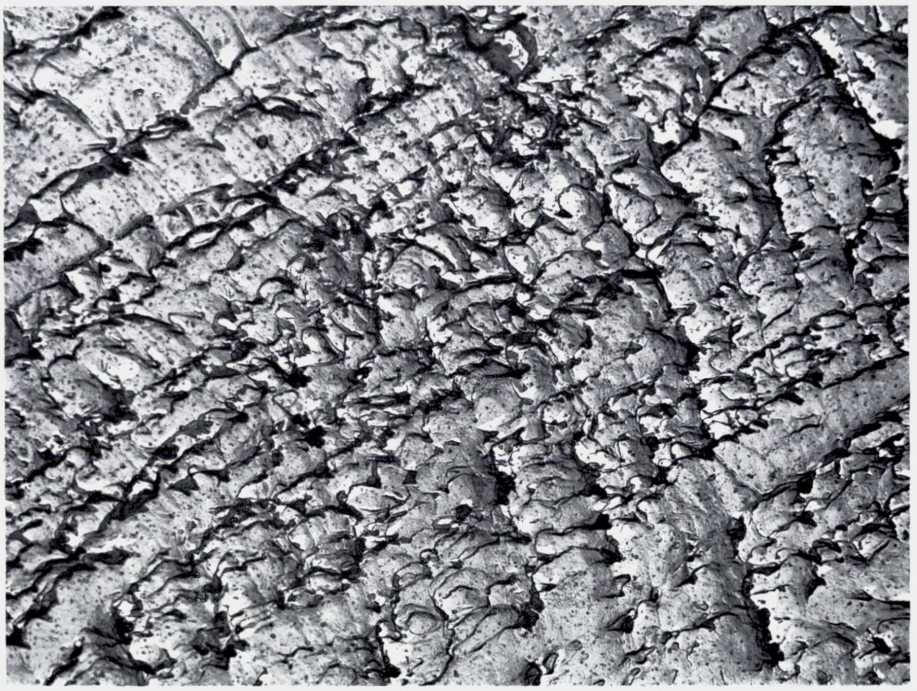


2

PLATE 3

Fig. 1. *Nodosaria latejugata* Gümbel.
Carbon shadowed replica of etched transverse section of ornamental costa showing primary lamination. Shell surface in upper right direction. TEM.

Fig. 2. Detail of fig. 1. The primary lamels are seen to be constructed of columnar calcite crystals about 1 μ long and enveloped by delicate organic membranes. TEM.

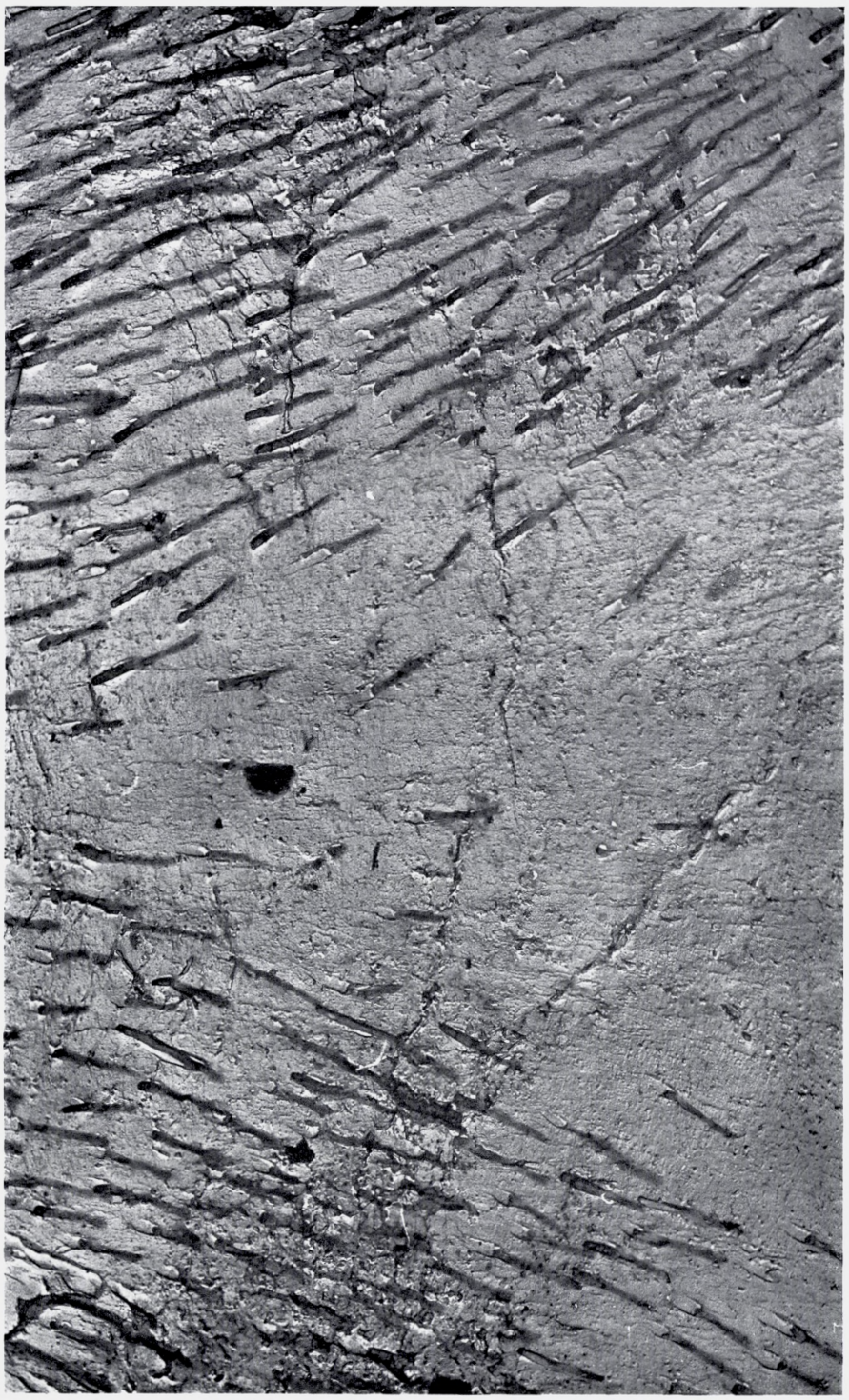


1

2

PLATE 4

Fig. 1. *Nodosaria latejugata* Gümbel.
Carbon shadowed replica of slightly etched transverse section showing the base of an ornamental costa. In the costa is seen slight striation of a fan-shaped arrangement indicating the morphological orientation of the calcite identical to the optical orientation. The pores are seen to follow the general direction of the calcite crystals and are not present within the costa itself. In the upper part of the micrograph are seen traces of primary lamination. TEM.

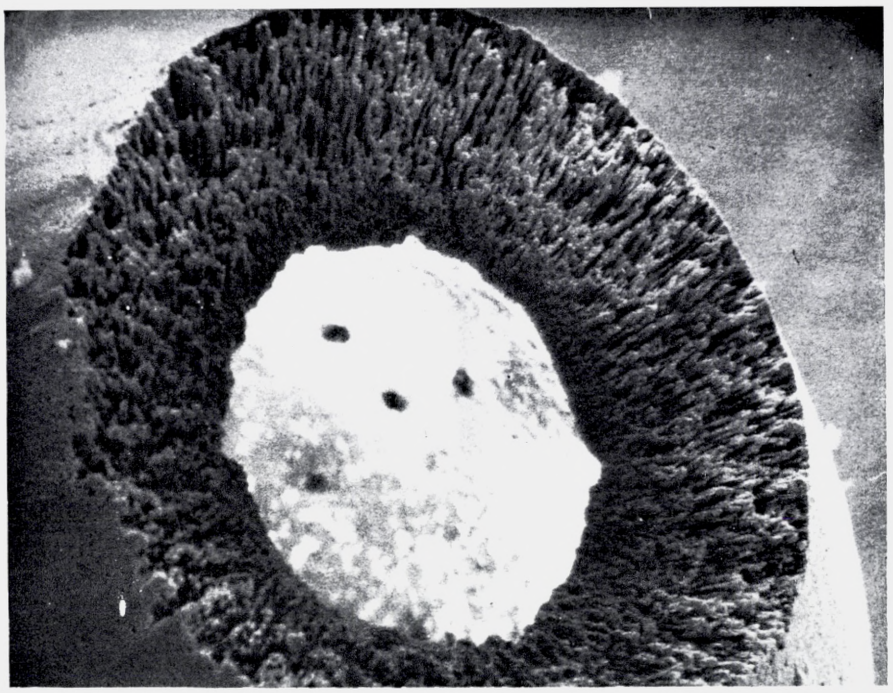


1

PLATE 5

Fig. 1. *Nodosaria sp.* Hvorslev, Denmark. Middle Oligocene.
Fractured and naturally corroded apertural part, showing the columnar nature of the calcite. SEM.

Fig. 2. Detail of fig. 1. Columnar calcite crystals indicative of continuous growth with slight etch lines indicative of the cleavage rombohedron. *Note* that the crystals are uninterrupted, suggesting that no primary lamination is present. SEM.



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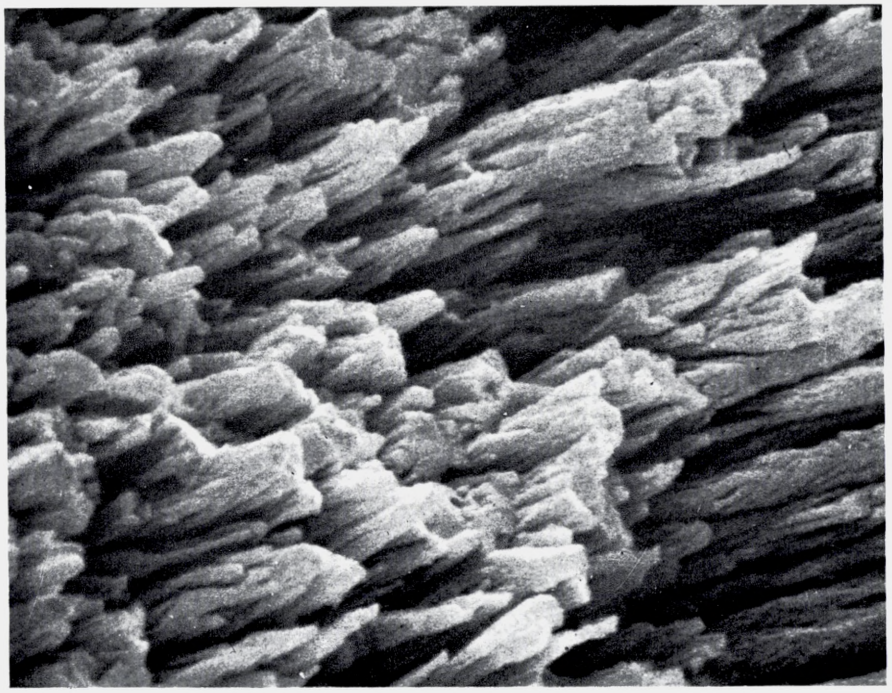


2

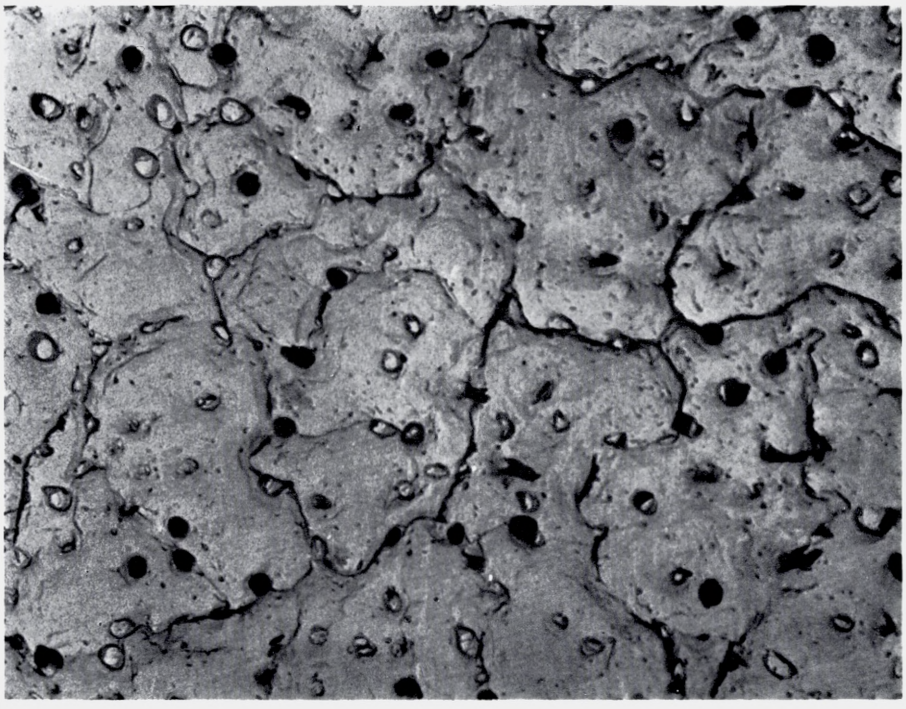
PLATE 6

Fig. 1. *Nodosaria latejugata* Gümbel.
First replica of inner etched surface. Carbon shadowing at right angles to the surface showing organic membranes between crystal units as well as organic pore-tubes. TEM.

Fig. 2. *Nodosaria latejugata* Gümbel.
Third replica of inner etched surface shadowed with carbon at right angles to the surface showing pores along the crystal unit boundaries and within the crystal units. TEM.

1 μ

1



0,5 μ

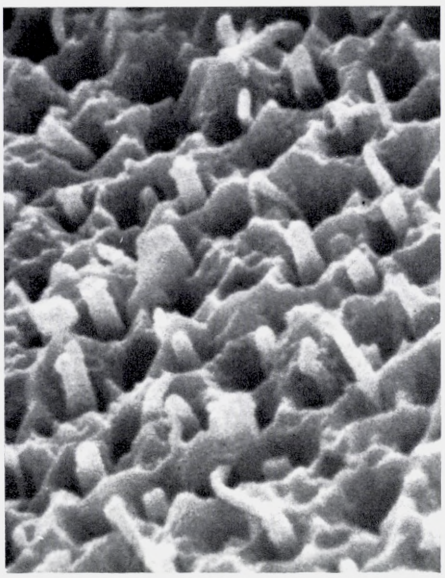
2

PLATE 7

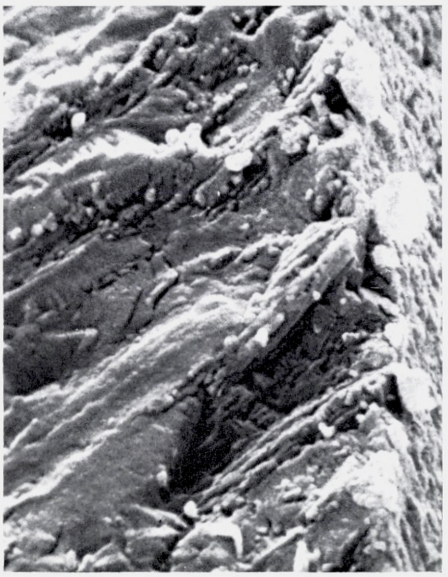
Fig. 1. *Nodosaria latejugata* Gümbel.
Slightly etched outer surface of chamber wall with pore-tubes etched free. SEM.

Fig. 2. *Nodosaria latejugata* Gümbel.
Fractured wall showing the columnar nature of the calcite crystals. SEM.

Fig. 3. *Nodosaria latejugata* Gümbel.
Slightly etched outer surface showing transition from a pore-free costa (left) to porous chamber wall (right). SEM.



1 1μ



2 10μ

5μ

3

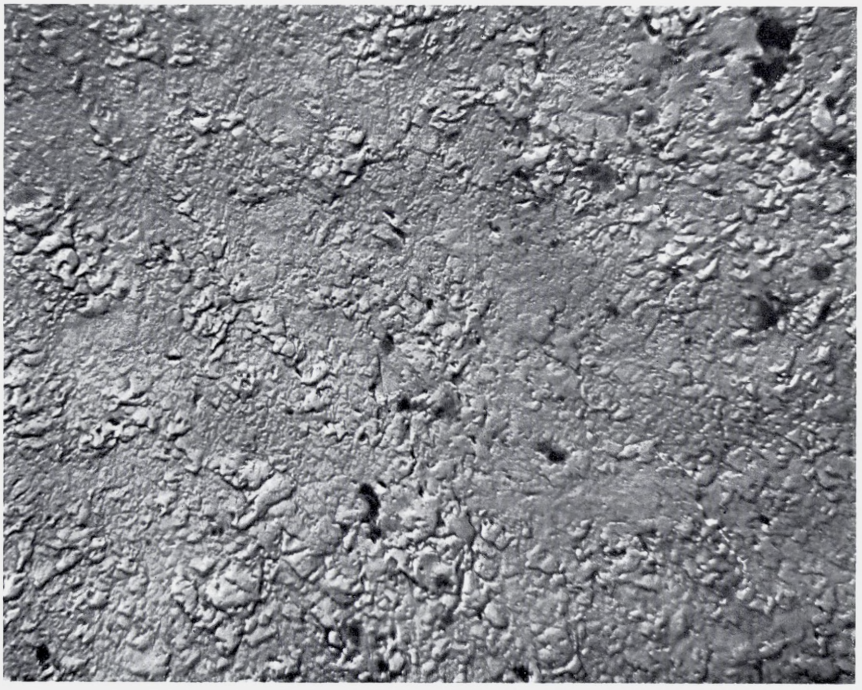
PLATE 8

Fig. 1. *Nodosaria latejugata* Gümbel.
Carbon shadowed replica of un-etched surface of porous chamber wall. TEM.

Fig. 2. Same specimen as fig. 1.
Non-porous costa. TEM.

5 μ

1



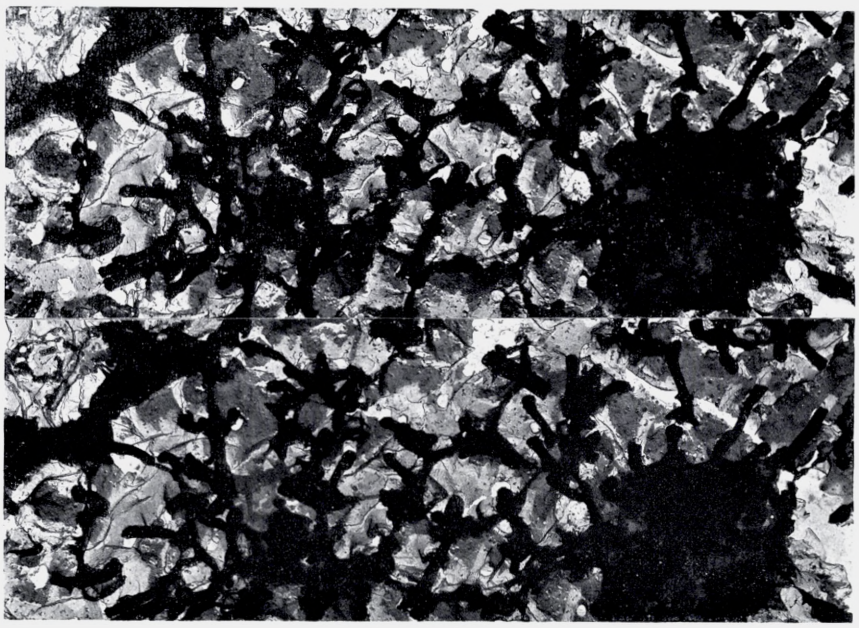
5 μ

2

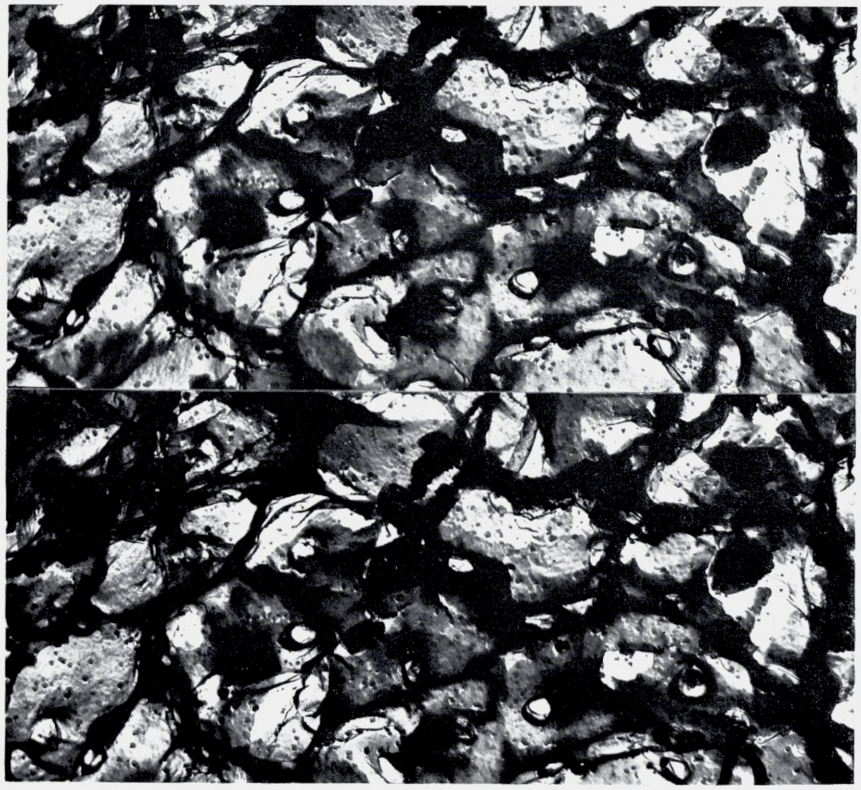
PLATE 9

Fig. 1. *Polymorphina sp.*
Carbon shadowed replica of etched inner surface with organic pore-tubes and adhering membranes. Stereopair. TEM.

Fig. 2. Same specimen as fig. 1.
Pores are found both along the boundaries between crystal units and within the crystal units. Stereopair. TEM.



1



2

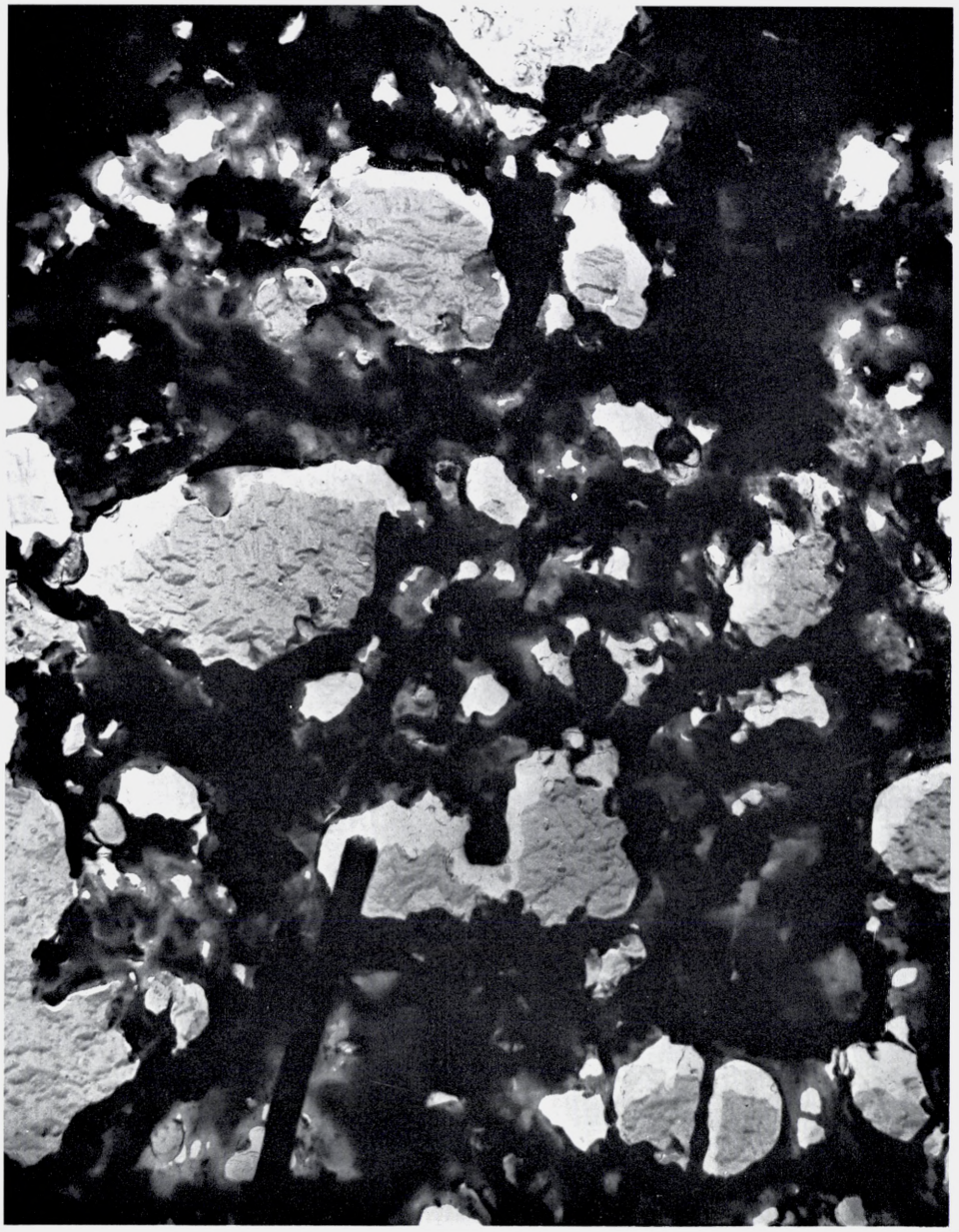
PLATE 10

Fig. 1. *Polymorphina sp.*
Replica of etched inner surface shadowed with carbon showing pore-tubes and organic membranes. TEM.

1

PLATE 11

Fig. 1. *Polymorphina sp.*
One-stage carbon replica of etched surface showing organic membranes and crystal units. TEM.



2 μ

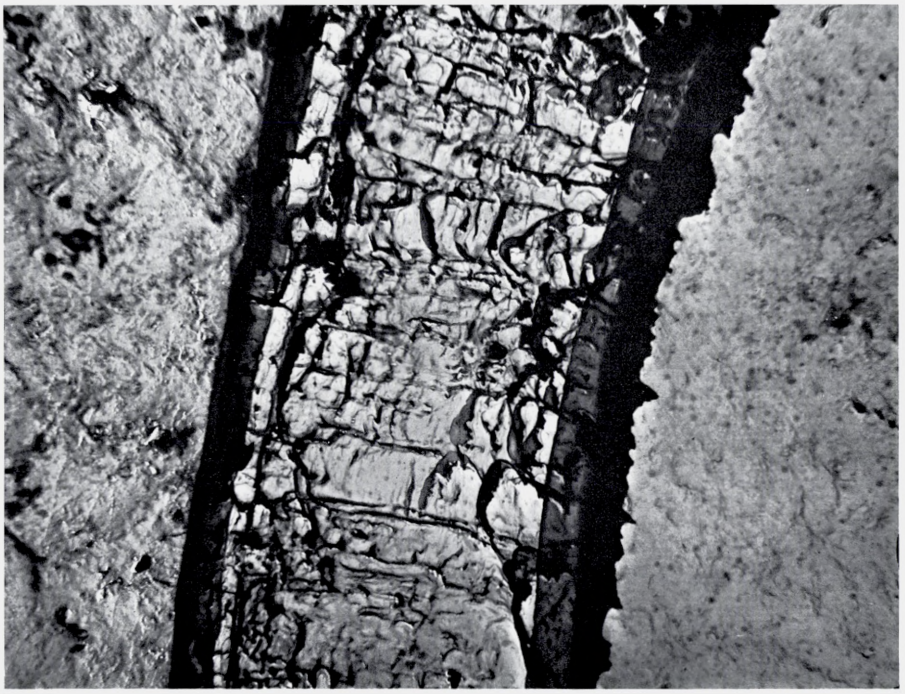
1

Plate 12

Fig. 1. *Bulimina midwayensis* Cushmann & Parker.
Carbon shadowed replica of etched section showing lamination of spine of proloculus. TEM.

Fig. 2. Same specimen as fig. 1.
Showing columnar orientation of the crystal units. TEM.

1



2

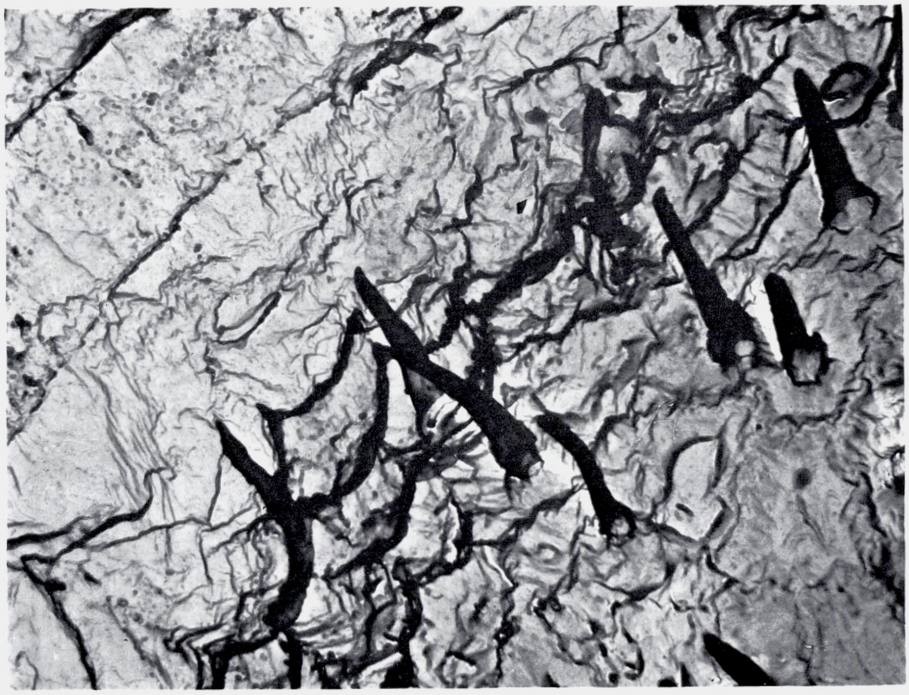
PLATE 13

Fig. 1. *Bulimina midwayensis* Cushman & Parker.
Carbon shadowed replica of polished, etched section of chamber wall showing columnar orientation of the crystal units. TEM.

Fig. 2. *Bulimina midwayensis* Cushman & Parker.
Carbon shadowed replica of etched longitudinal section with hollow chambers. The area shown is transitional between the inner surface with torn-out pore-tubes and boundaries between crystal units and a cross section of the laminated chamber wall. TEM.

3μ

1



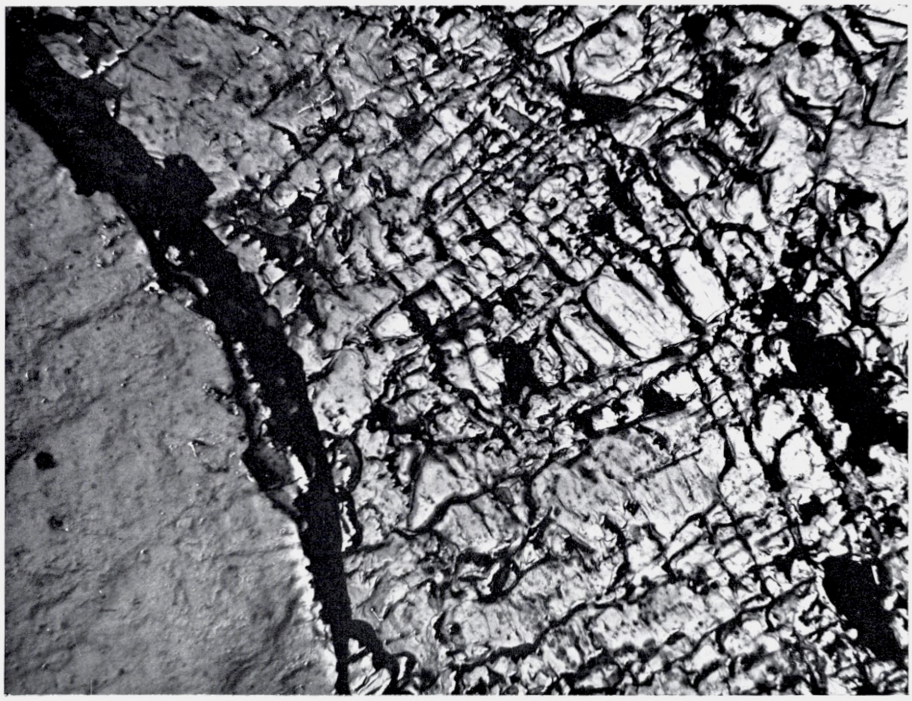
3μ

2

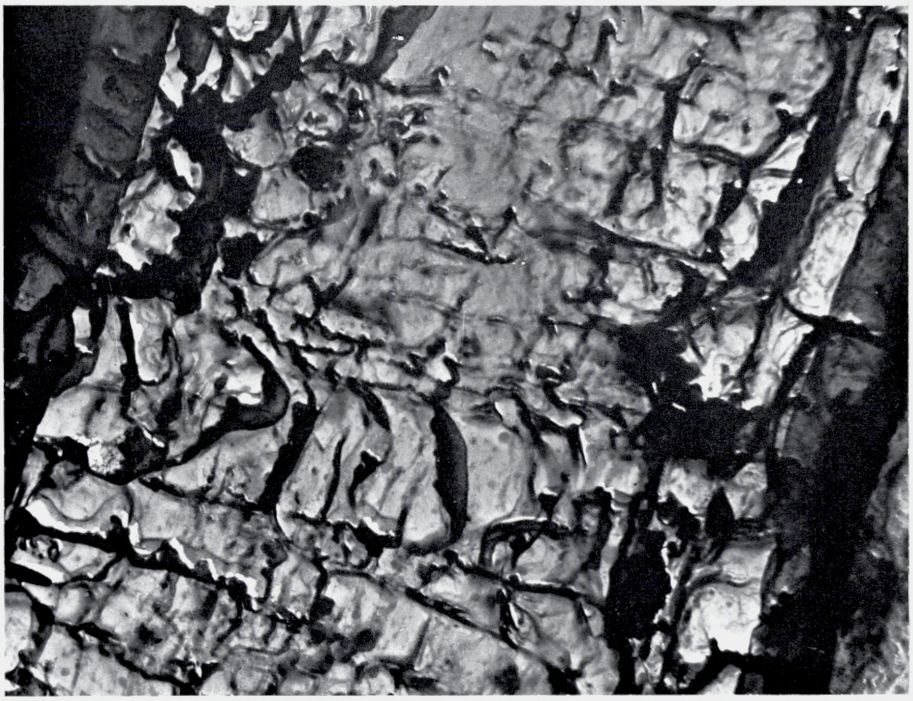
PLATE 14

Fig. 1. *Bulimina midwayensis* Cushman & Parker.
Carbon shadowed replica of polished, etched longitudinal section showing irregular crystal units at the junction between the walls of two chambers. TEM.

Fig. 2. Same as fig. 1.
In the right side of the micrograph are seen crystal units interrupted at a lamel boundary. TEM.



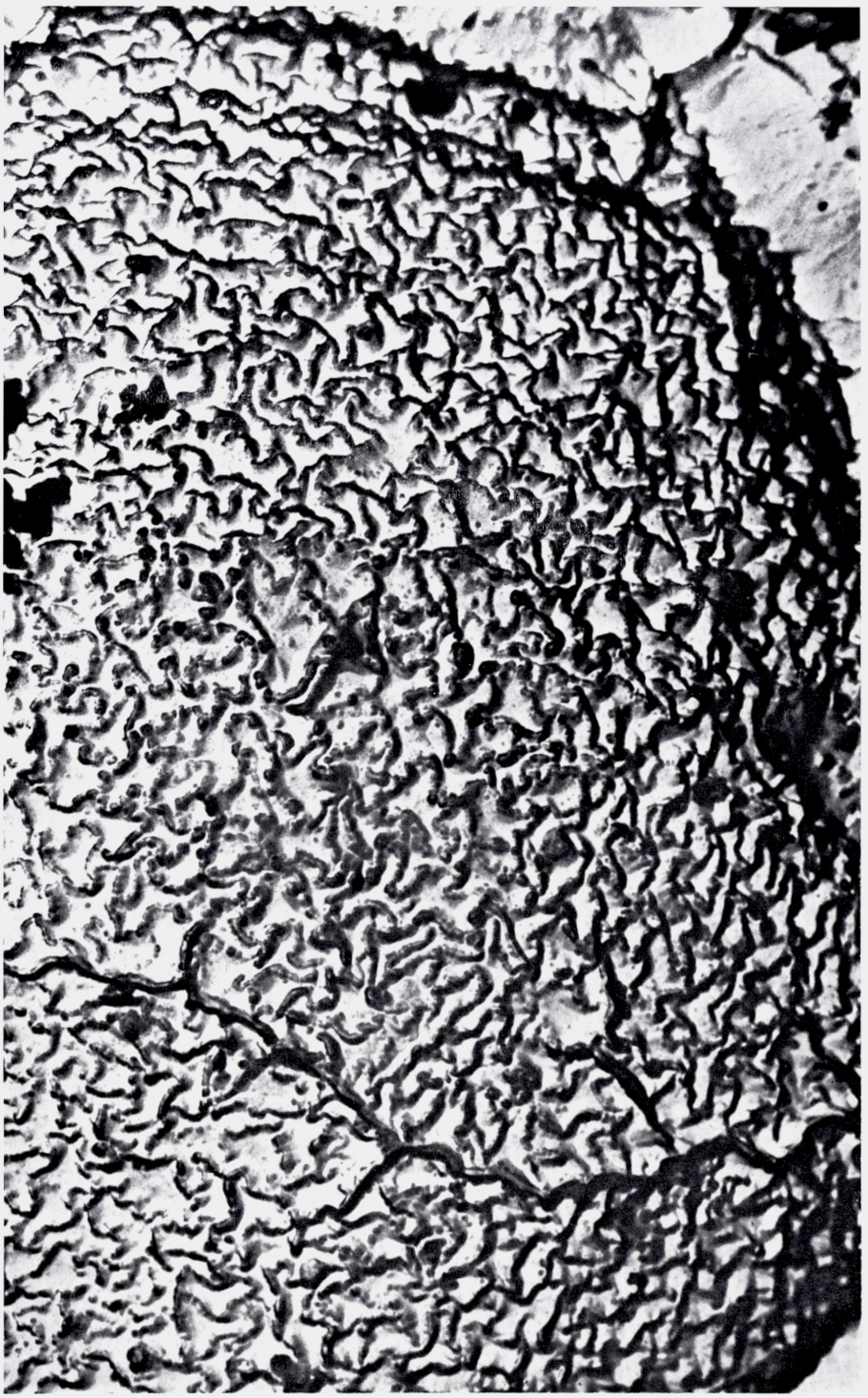
1



2

PLATE 15

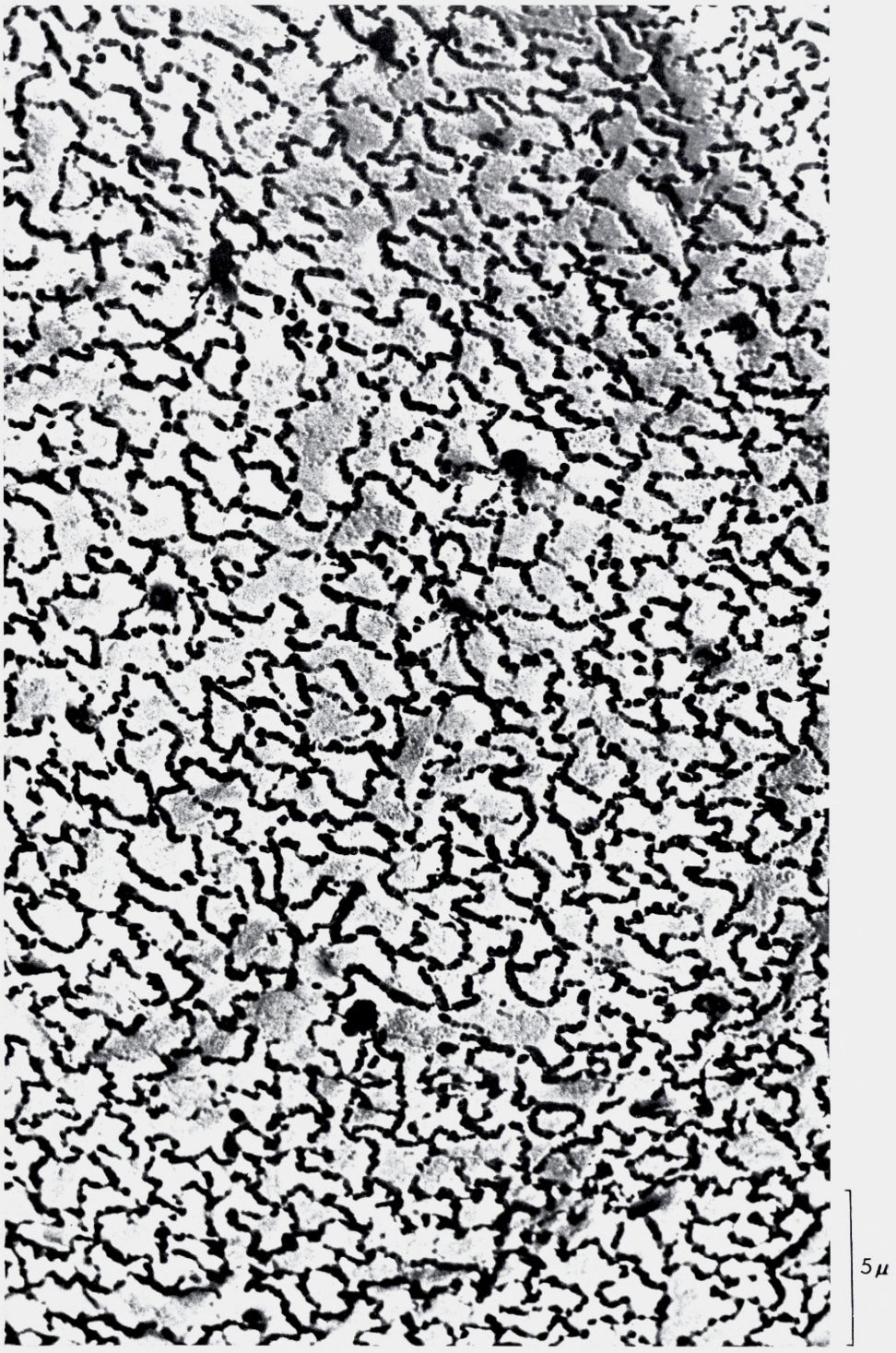
Fig. 1. *Bulimina midwayensis* Cushman & Parker.
Second carbon shadowed replica of etched inner surface of proloculus of megalospheric specimen showing irregular boundaries between crystal units. TEM.



1

PLATE 16

Fig. 1. *Bulimina midwayensis* Cushman & Parker.
Second carbon shadowed replica of etched inner surface of the oldest-but-two chamber of megalospheric specimen showing irregular boundaries between crystal units. In spite of the same duration of etching the boundaries are less deepened than in the proloculus (compare pl. 15, fig. 1). TEM.

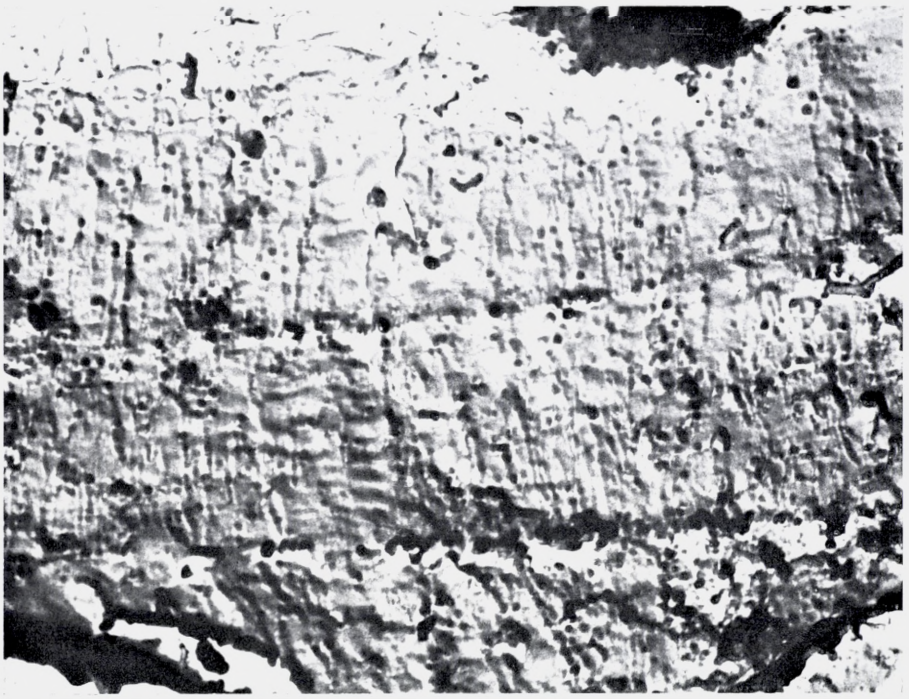


1

PLATE 17

Fig. 1. *Bulimina midwayensis* Cushman & Parker.
Carbon shadowed replica of polished, etched section of lamellar chamber wall. Etch pits are found along lamel boundaries and at places with supposed disorder in the crystal structure. TEM.

Fig. 2. *Bulimina marginata* d'Orbigny.
High angle carbon shadowed replica of inner etched surface showing pore-tubes and boundaries between crystal units. In the right side of the micrograph are seen delicate organic membranes running inside the crystal unit boundaries and roughly following the direction of the boundaries. The shrinkage of the membranes, the original position of which was in the boundaries, is thought to be caused by the dissolution of the collodium replica. TEM.



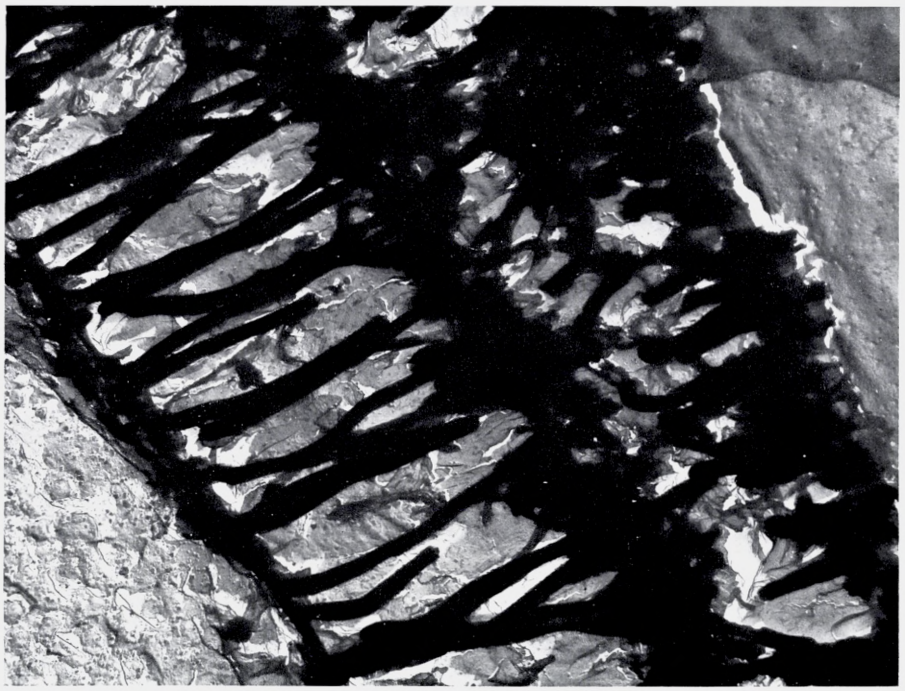
1

2

PLATE 18

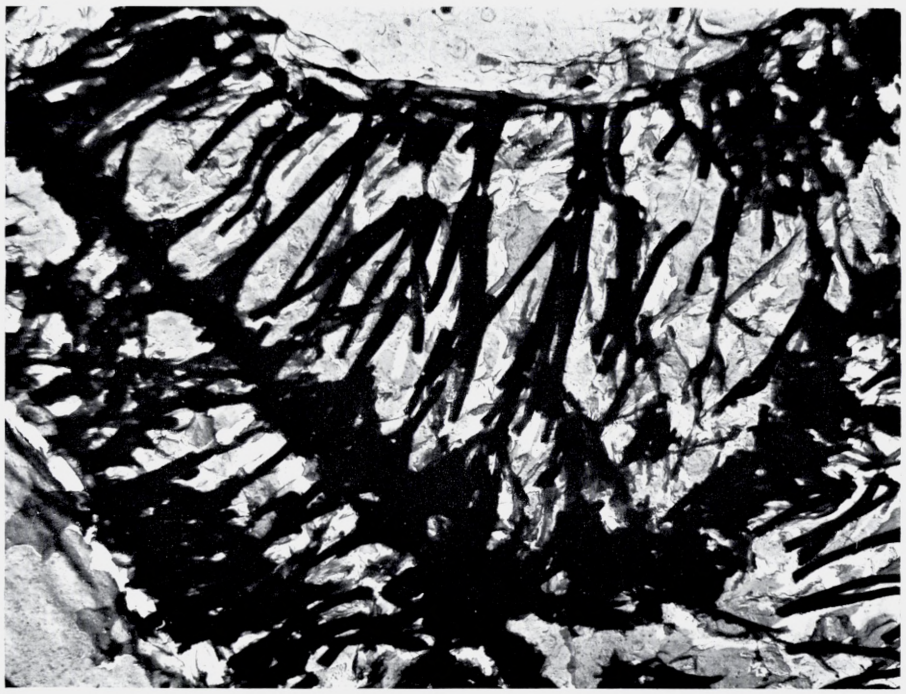
Fig. 1. *Bulimina marginata* d'Orbigny.
Replica-pseudoreplica of etched section of laminated wall of youngest-but-one chamber, showing concentration of organic material in the lamel boundary intimately connected with the pore-tubes. TEM.

Fig. 2. Same as fig. 1.
In left side of the micrograph are seen organic membranes adhering to pore-tubes and high concentrations of organic material in the lamel boundaries. TEM.



3μ

1



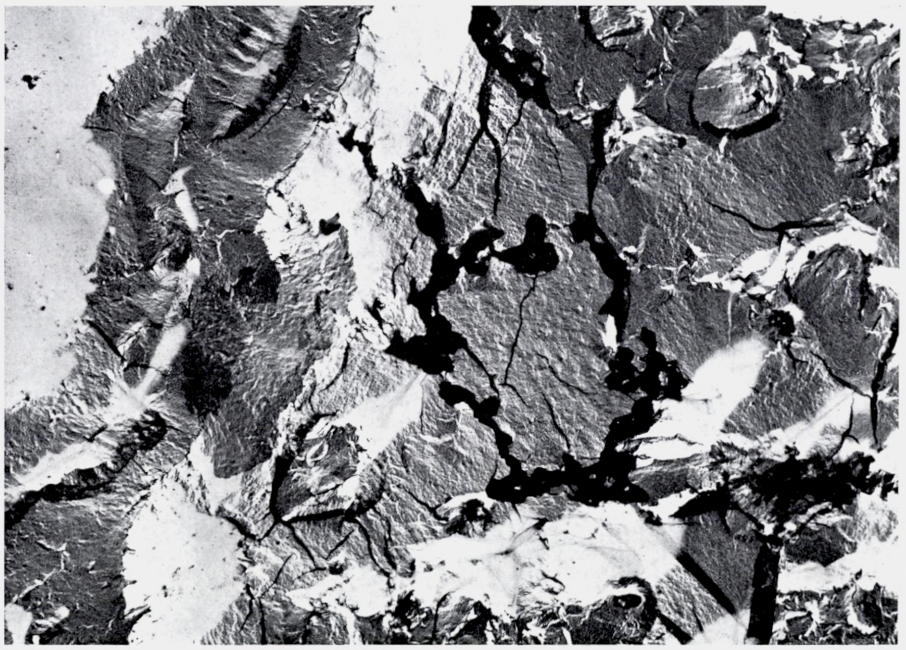
5μ

2

PLATE 19

Fig. 1. *Melonis scaphum* (Fichtel & Moll).
Replica-pseudoreplica of outer etched surface of central part of apertural face showing delimitation of a crystal unit by organic spongy material. TEM.

Fig. 2. *Melonis scaphum* (Fichtel & Moll).
Replica-pseudoreplica of outer etched surface of central part of apertural face showing free-etched organic limitations of the crystal units. The crystalline matter has been dissolved prior to replication. TEM.



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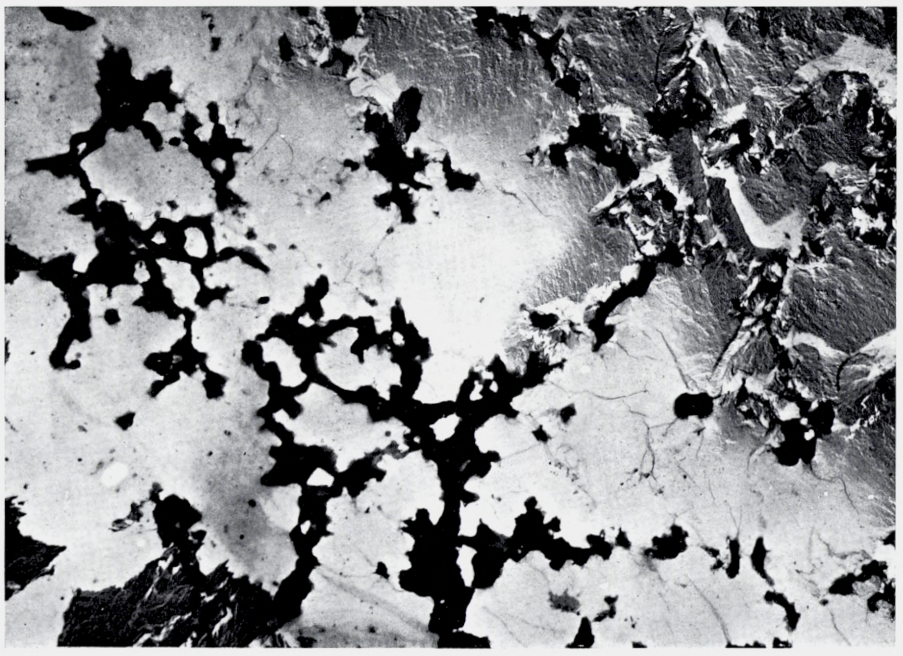
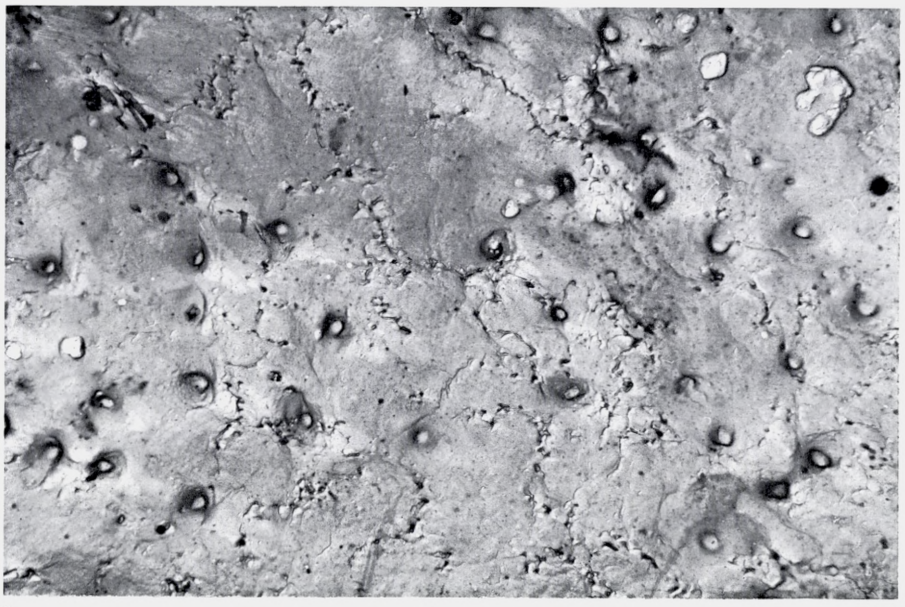


2

PLATE 20

Fig. 1. *Melonis scaphum* (Fichtel & Moll).
Second carbon shadowed replica of inner surface of central part of apertural face showing pores both inside the crystal units and along the boundaries. TEM.

Fig. 2. *Melonis scaphum* (Fichtel & Moll).
First carbon shadowed replica of strongly oblique section of wall of the youngest chamber after etching with EDTA for 20 secunds. Note the intimate relationship between the spongy organic material bounding the crystal units and the pores. TEM.



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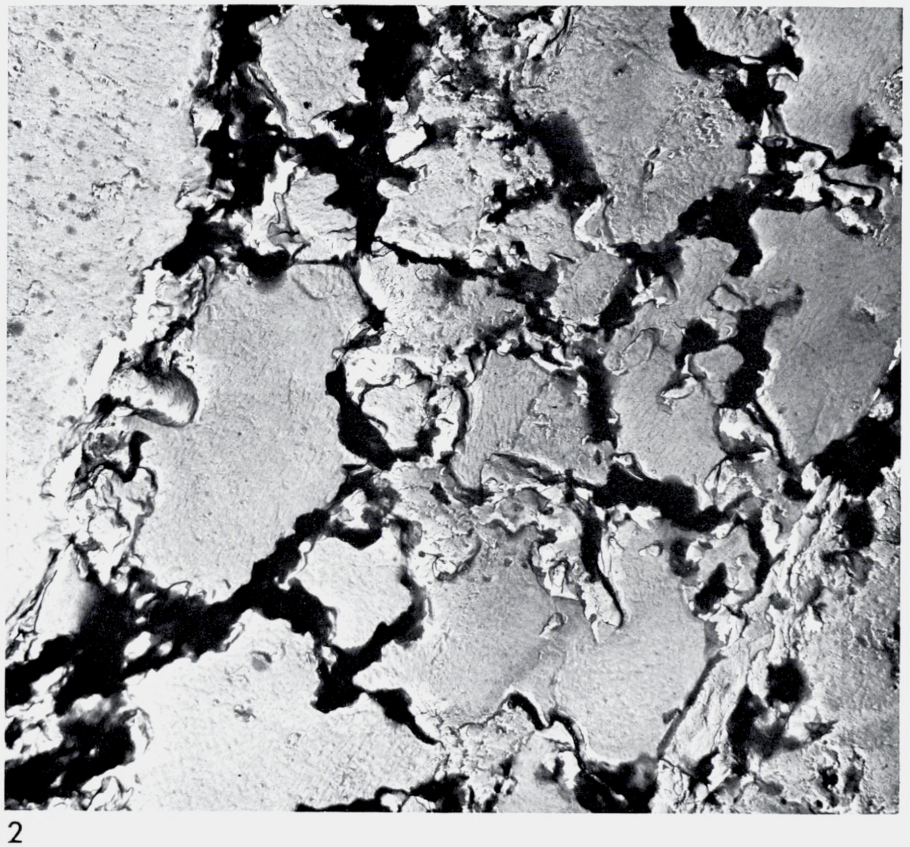


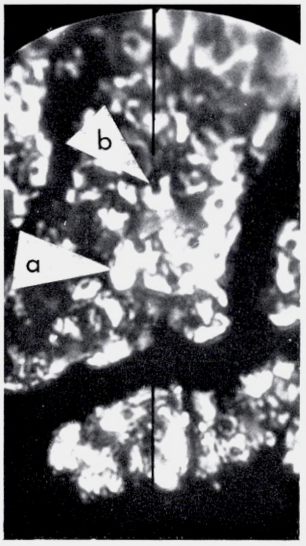
2

PLATE 21

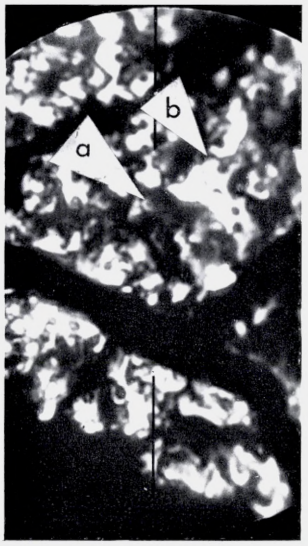
Fig. 1. *Melonis scaphum* (Fichtel & Moll).
Photomicrograph of central part of fractured apertural face. Crossed nicols.

Fig. 2. Same as fig. 1.
Specimen rotated 40° relative to fig. 1. Crossed nicols.

Fig. 3. Same as fig. 1.
Carbon shadowed replica of the same area (slightly etched). (a) the single crystal unit which in fig. 2 shows extinction. (b) the crystal unit which in fig. 1 has just passed the extinction point. TEM.

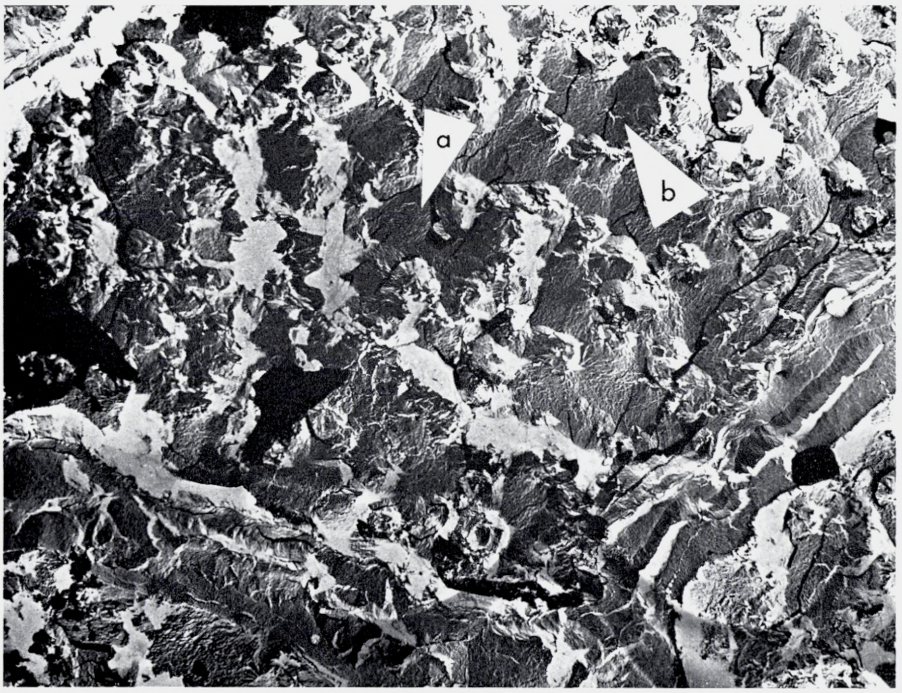


1



25μ

2



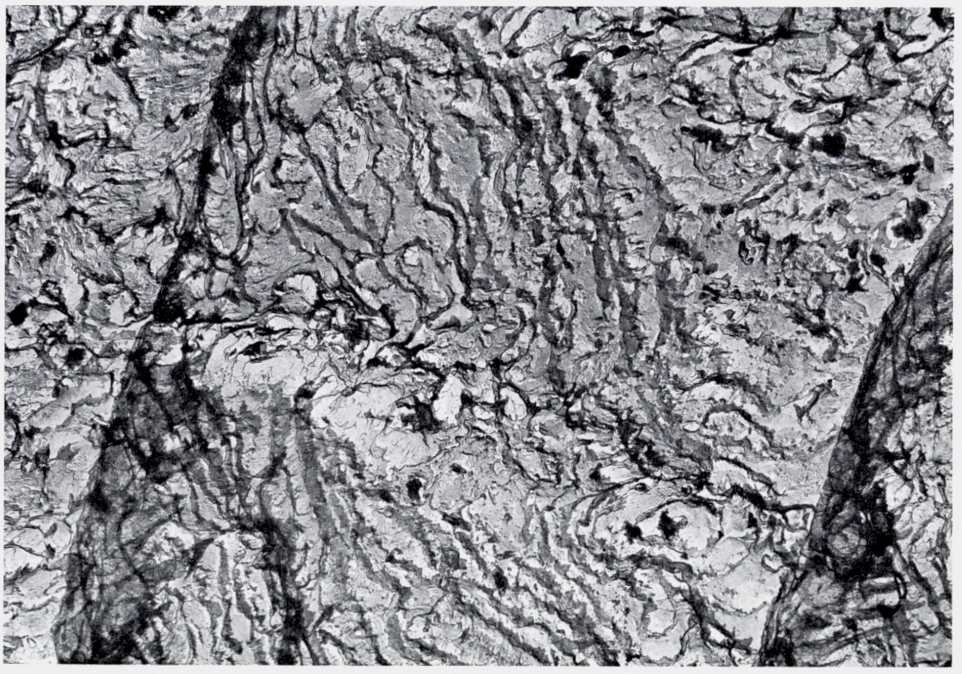
5μ

3

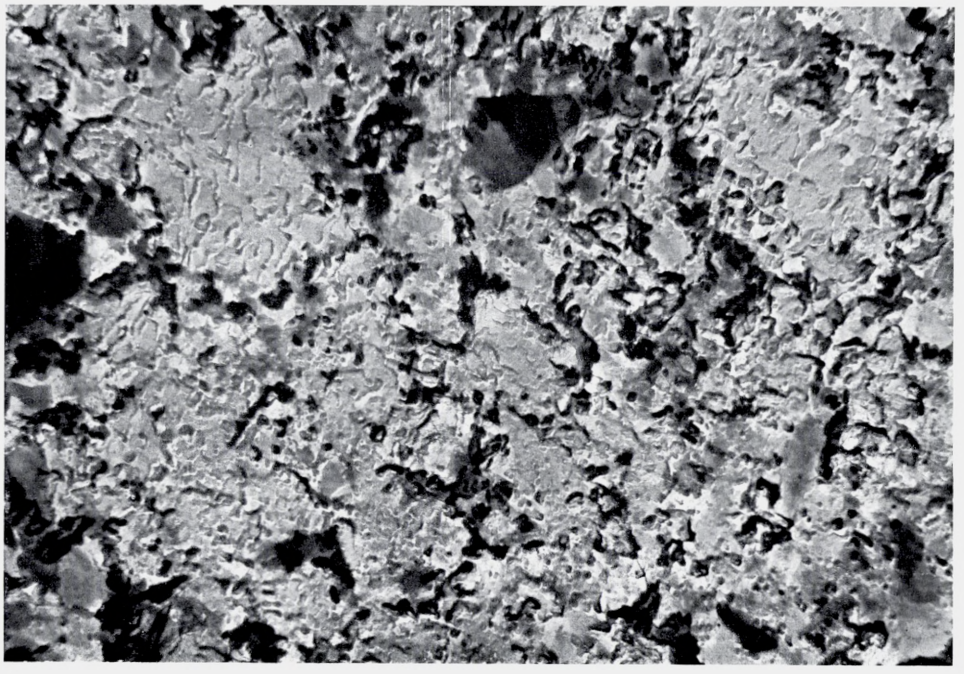
PLATE 22

Fig. 1. *Heterolepa cf. subhaidingeri* (Parr).
Third two-stage replica of polished, etched section showing platy nature of calcite constituting crystal units in a secondary lamel. The furrow from left center to lower right represents the boundary between two crystal units. TEM.

Fig. 2. *Heterolepa cf. subhaidingeri* (Parr).
Second replica of slightly etched shell surface (umbilical side) showing calcite plates (upperleft) and organic matrices marking the boundaries of crystal units. TEM.



1



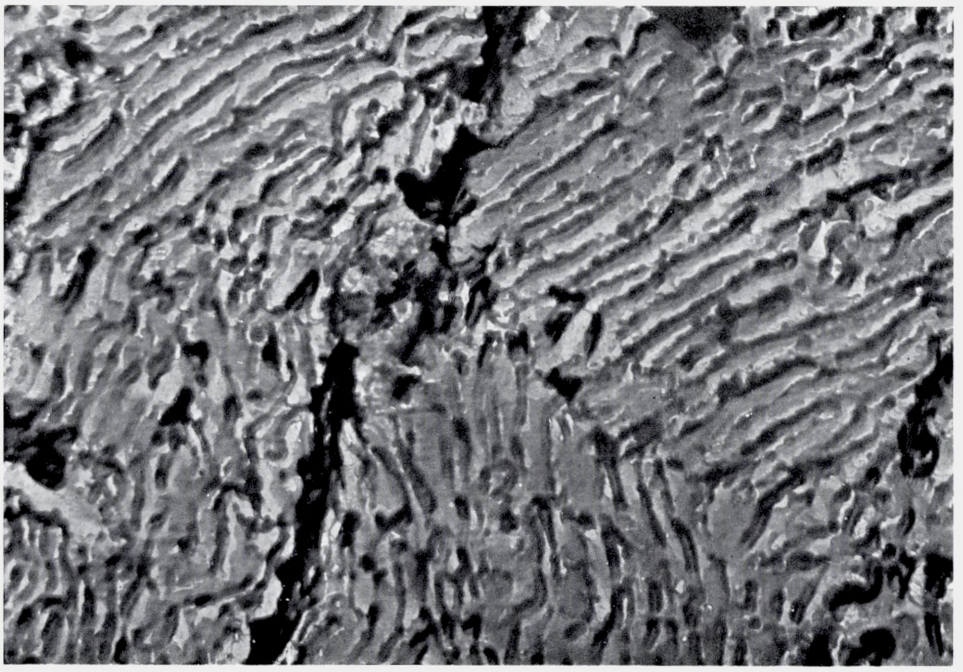
2

PLATE 23

Fig. 1. *Heterolepa cf. subhaidingeri* (Parr).
First two-stage replica of polished, etched section showing delicate organic membranes enveloping the small crystal plates constituting crystal units. A crystal unit boundary is seen running from bottom to top of the micrograph slightly right of center. TEM.

Fig. 2. *Heterolepa cf. subhaidingeri* (Parr).
Second two-stage replica of polished, etched section showing secondary lamels. The orientation of the calcite plates constituting the crystal units is seen to continue across the lamel boundary. The boundary between two crystal units (upper left to lower right) is slightly irregular. TEM.

1

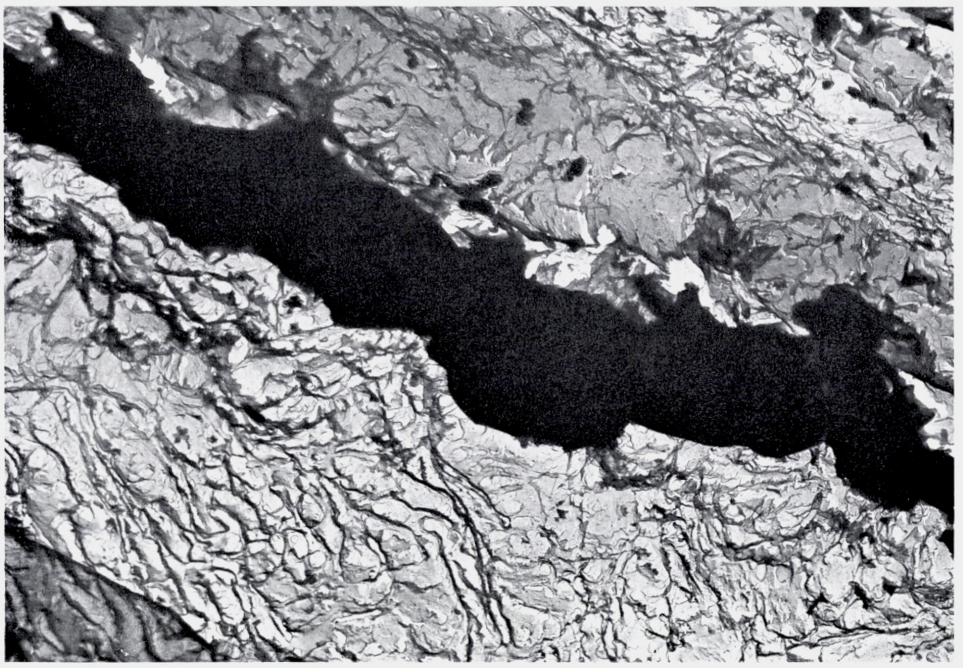


2

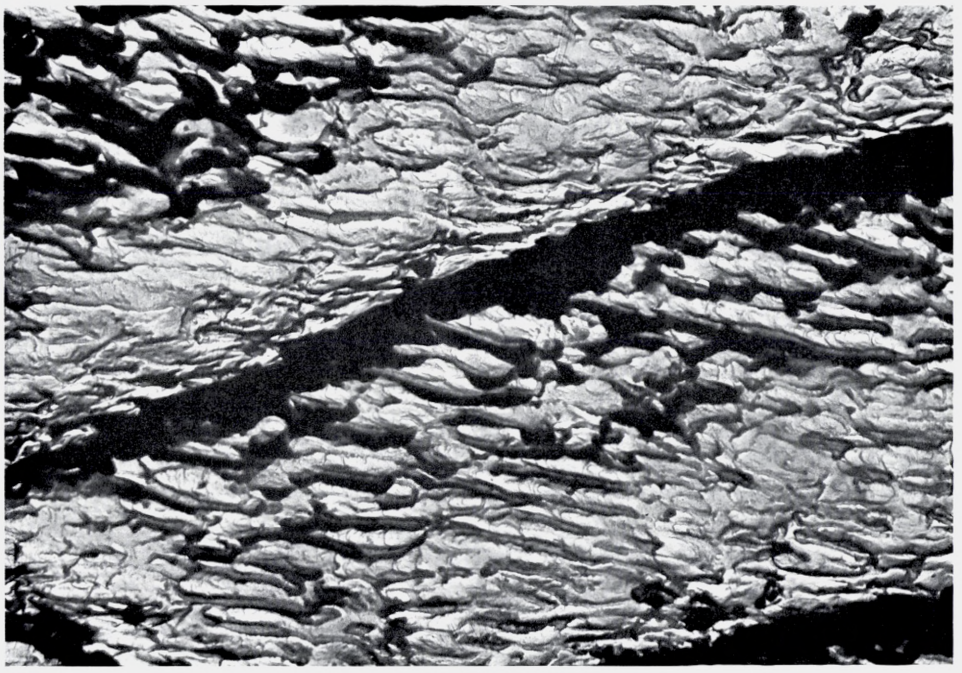
PLATE 24

Fig. 1. *Heterolepa cf. subhaidingeri* (Parr).
Second two-stage replica of polished, etched section of septum showing concentration of spongy organic material between outer lamel (lower left) and inner lamel (upper right). The directions of the calcite plates are not identical in the inner and outer lamel. TEM.

Fig. 2. *Heterolepa cf. subhaidingeri* (Parr).
First two-stage replica of polished, etched section of chamber wall demonstrating identical orientation of calcite plates across boundary between two secondary lamels. In the lamel boundary is seen concentration of organic material of a spongy appearance. TEM.



1

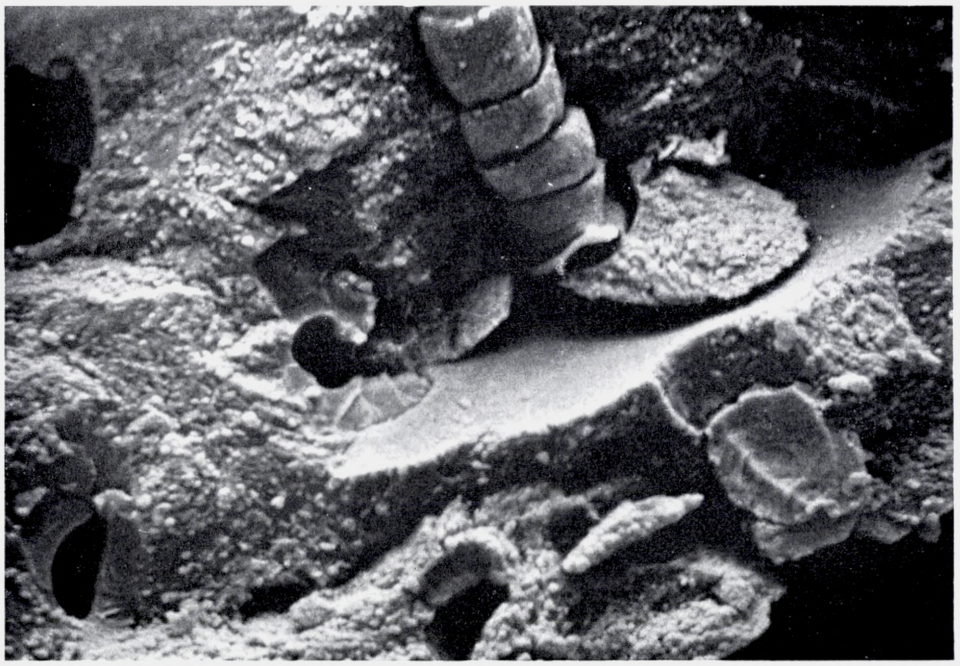


2

PLATE 25

Fig. 1. *Heterolepa cf. subhaidingeri* (Parr).
Fractured outer wall (umbilical side) showing secondary lamination with corresponding pore constrictions. Pore-tubes fully or partly filled in with embedding medium. SEM.

Fig. 2. Detail of fig. 1, showing boundary floor between two secondary lamels. The direction of the plates is at right angles to the plane of the picture. On the floor is seen the concentration of organic material. The crystal plates are seen to be interrupted at the lamel boundary. SEM.



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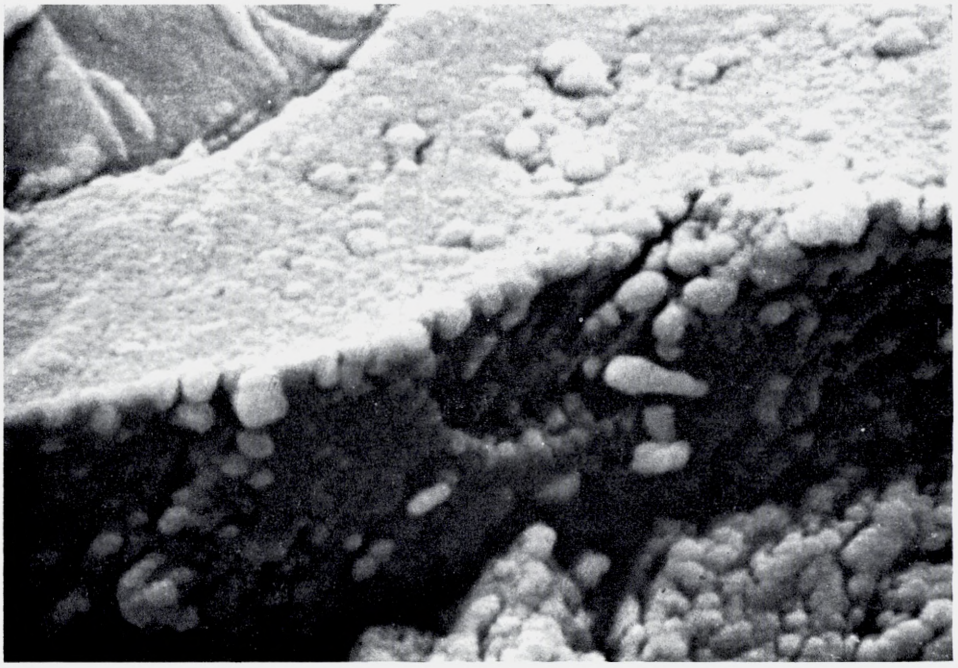
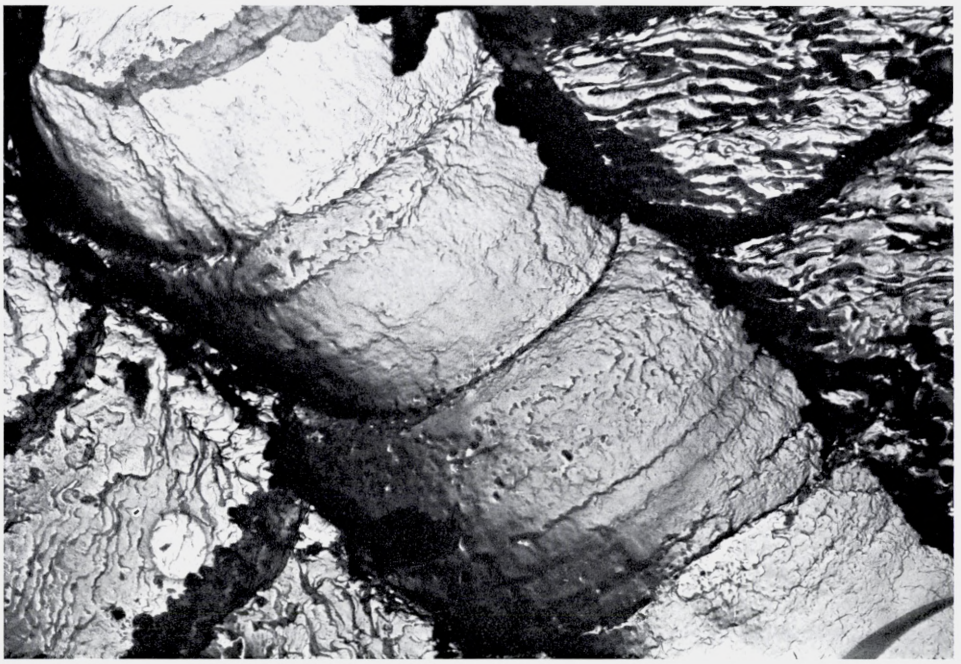


2

PLATE 26

Figs. 1–2. *Heterolepa cf. subhaidingeri* (Parr).
Second two-stage replica of polished, etched section of outer chamber wall showing concentrations of organic material in the boundaries between secondary lamels with corresponding pore constrictions. Remains of the organic inner lining of the pores are seen along the sides of the pores. Between the constrictions of the pore shown in fig. 1 are seen smaller constrictions supposed to represent primary lamination. In fig. 2 such finer constrictions are missing. TEM.



1

2

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