# TOPOGRAPHY OF THE ORGANIC COMPONENTS IN MOTHER-OF-PEARL

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PLATES 251 TO 257

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It has been known for a long time (1–4), that mother-of-pearl, forming the innermost layer of various shells, consists of numerous mineral leaves or lamellae, disposed parallel to the inner surface of the shell, and piled upon each other horizontally. Each leaf or lamella is composed of microscopical crystals of aragonite (1) in which calcium carbonate is crystallized in a rhombic lattice[1]. The crystals, which have a long axis weakly developed (1–4) and therefore a tabular shape, are disposed side by side in a single layer within each leaf, and appear, in tangential view of a lamella, as polygonal slabs in a flagging.

The organic components of mother-of-pearl (so called conchiolin) are traditionally described (26, 25, 13, 24, 23, 1–4) as consisting of extremely thin parallel sheets, which alternate with the mineral lamellae in the horizontally stratified nacreous configuration. These parallel sheets are united by transverse bridges of the same organic substance, which cross the lamellae at right angles between the crystals of aragonite. The whole system appears in the figures recorded by light microscopy as an extremely thin linear network, resembling the concrete in a brick wall (22), but without any other detail of structure (1).

After decalcification of mother-of-pearl, the organic residue consists of soft transparent stratified membranes. As shown previously (5, 6), ultrasonic vibrations may be used to cleave and break the organic membranes of decalcified mother-of-pearl into thinner pellicles and fragments of leaflets. In the electron microscope, these pellicles, collapsed by desiccation on to a formvar background, appear perforated by openings, the size, shape, and distribution of which vary with the groups and species of molluscs investigated. These details of structure were measured in twenty-seven species of Pelecypods and fifteen species of Gastropods. The results suggested that the differences recorded in the patterns of the leaflets were statistically characteristic at a high level (class) of the taxonomic hierarchy. Within the same class, the differences in the patterns were not, or were questionably significant at a lower level (genus, species).

[1] In the inner layer of the shells, in which calcium carbonate is crystallized in a rhombohedric lattice, there is no mother-of-pearl. The results of a study of this so called subnacreous layer, or calcitostracum, will be reported later.

Owing to the procedures used for preparing these pellicles, no information could be collected in these studies about their transversal structure or their location within the nacreous texture.

Preservation of the topographical connections between organic and mineral components requires the use of methods such as thin sectioning or replication of the figures of corrosion induced by etching in fragments of mother-of-pearl variously orientated. The latter procedure, which was selected for the present work, has already been used on shell material. However, in the papers available (7, 8) the organic structures have been, but incidentally, investigated.

## *Material and Methods*

*Material.*—The shells from the following species have been used:

*Cephalopoda: Nautilus macromphalus* Sowerby.

*Gastropoda: Turbo* sp. (*Turbinidae*); *Umbonium giganteum* Lesson (*Umboniidae*).

*Pelecypoda: Pinctada* (*Pteria, Meleagrina*) *margaritifera* Linné; *Pinctada* (*Pteria, Meleagrina*) *vulgaris* (*fucata*) Gould; *Pinctada galtsoffi* Bartsch (*Aviculidae*). *Mytilus edulis* Linné, *freshly collected specimens from 19 mm. to 45 mm. of shell length* (*Mytilidae*). *Anodonta cygnaea* Linné; *Anodontites trapezialis* Lamarck (*Nayadidae, Unionidae*).

In all these species, the innermost layers of the shells are composed of true mother-of-pearl (9), in which calcium carbonate appears in the form of crystals of aragonite.

Replicas were made, before and after etching, from the inner surface of the shells, from cleavage patterns of mother-of-pearl obtained by fracture, and from polished surfaces of fragments orientated tangentially and transversally to the nacreous stratification. Replicas were also prepared from crystals of aragonite polished along the two main axes corresponding to those of the shell crystals and etched in the same conditions as the shell material.

*Polishing.*—The fragments of shells were embedded, at a temperature not exceeding 19°C., in a transparent hardening plastic (10, 11), and roughly polished with several grades of emery powder of decreasing coarseness. Then they were finely polished on ragwheels impregnated with chromium oxide and with two grades of alumine, until disappearance of most of the scratches, controlled in the metallographic microscope.

*Etching.*—Hydrochloric, acetic, and formic acids, traditionally used as etchants and decalcifiers in previous investigations of shells of molluscs by light microscopy (12, 13, 1–4, 14), were tried on the present material. At the electron microscope level, these acids, even when employed at concentrations ten to twenty times lower than those indicated in the literature, disorganized the delicate structures unmasked during decalcification.

In most of the preparations of the present study, etching was performed by saturated aqueous solutions of the disodium salt of ethylene-diamine tetra-acetic acid (sequestrene NA 2, Alrose Chemical Corporation, Providence, Rhode Island, at pH 5.0 and pH 9.0; titriplex III, Merck, Darmstadt, Germany). This organic chelating agent preserves better than acids the organic structures of the hard mineralized tissues (15). The surfaces were flooded with the etchant during various lengths of time (between 1 and 21 minutes) and the degree of corrosion followed under a binocular microscope. The surfaces were rinsed with tap and with distilled water, dried, and covered with the moulding solution.

Artifacts of desiccation were controlled by using water soluble plastics, immediately after rinsing, for the first intermediate replica.

*Replicas.*—Positive replicas were prepared before and after etching by the double stage method, following the conventional procedures reported in the literature (16, 17) and mostly by the carbon replica technique (18).

With films of uniform thickness such as the metallic films (19) interpretation of three-dimensional effects is difficult (20), especially at low magnification. In the present study, owing to modifications of the specimen stage of the electron microscope, a stereoscopic device could not be used. The inequalities in the levels have therefore been checked by shadow casting the final positive carbon replicas with palladium, at angles varying from 18° to 27.5°, and by preparing simultaneously for the same material shadow-cast formvar replicas (0.75 per cent solutions of formvar in ethylene dichloride).

The preparations, mounted on copper screens, were examined with a R.C.A., E.M.U. electron microscope, without objective aperture. The illustrations in this paper are micrographs (negative prints) of final, positive, postshadowed replicas, and reproduce the actual appearance of the original surfaces.

## RESULTS

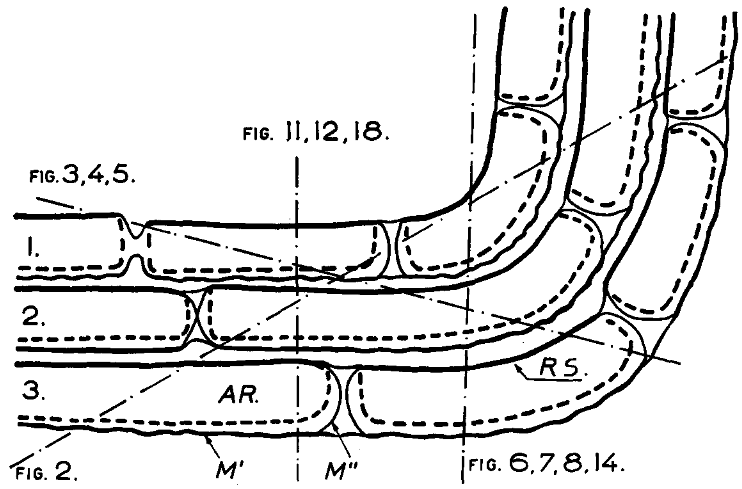
*Unetched Material.*—Positive replicas of the inner nacreous surface of the shells and of surfaces of cleavage induced by fracture inside mother-of-pearl, show successive nacreous lamellae superimposed in a terrace-like disposition (Fig. 20). On each lamella, linear shallow grooves or streaks delimit polygonal fields, which correspond to the upper surface of the tabular crystals of aragonite involved in the lamellar structure. These surfaces are smooth or finely granular, except in areas where thin perforated leaflets, exhibiting a lace-like pattern, occasionally overlap them (Fig. 20, bottom left). A similar pattern is visible in the pits sometimes left in the terraces after removal of splinters during fracture of the shell (Fig. 21). Veil-like, flaky shreds appear sandwiched between consecutive lamellae (Fig. 20), or protrude upwards in the regions of fracture (Fig. 20, thin white lines).

In mother-of-pearl polished tangentially to the lamellae, the terrace-like stratification of the successive lamellae, levelled by the polishing process, has disappeared, and the linear limits of the crystals of aragonite are the only structures to appear on the smooth surfaces.

In polished transversal sections of mother-of-pearl, the smooth levelled surfaces are crossed by parallel straight shallow grooves, which are the limits of the successive lamellae cut obliquely or at right angles. These parallel grooves are crossed at distances by transversal streaks. Both systems of linear depressions divide the polished surfaces into square areas, which correspond to the sections or to the edges of the crystals of aragonite.

*Figures of Corrosion Induced by Etching.*—Owing to the shell curvatures and to the undulating configuration of the nacreous stratified lamellae, orientation of the polishing planes, in apparently perfect tangential and transversal direction with regard to the inner shell surface, provided in most instances all gradations of obliquity (Text-fig. 1).

In every orientation of the surfaces of mother-of-pearl, erosion starts in the grooves, which separate the lamellae and which surround the margins of the crystals of aragonite. The etchant deepens and enlarges these grooves and exposes between the lamellae and around the crystals thin membranes, or sheets,




TEXT-FIG. 1. Topography of the organic (membranes or sheets) and mineral (crystals of aragonite aligned in rows, forming the lamellae) components in mother-of-pearl of various shells (tentative).

This schematic drawing was constructed on the basis of information from 500 micrographs of positive replicas of nacreous surfaces polished in various orientations. The drawing incorporates the various configurations of the intercrystallinic sheets (*M''*) observed in the material.

*1*, *2*, and *3* represent three consecutive parallel lamellae in a region of curvature of the shell. The lamellae are shown in section transverse to their surface and to the tabular surface of the individual crystals of aragonite (*AR*, silhouettes in interrupted lines) aligned in rows in each lamella. In this drawing, the curvature has been shortened and the crystals curved. The interlamellar spaces have been broadened. The thickness of the crystals varies with the species of mollusc, the region of mother-of-pearl (local variations), and the orientation of the planes of polishing.

*RS* marks the location of the lace-like reticulated sheet unequivocally detected at the base of the crystals of aragonite. This area is a fraction of the organic membranes which run in continuous sheets in between consecutive lamellae. In some preparations of *Nautilus* (not reported in the plates), the reticulum was tighter and denser in the part of the organic membranes topographically in close contact with one side of the crystals than in the other areas of the organic systems, including *M''* (intercrystallinic membranes, crossing the lamellae at the margins of the crystals) and *M'* (membranes running in the interlamellar spaces, duplicating *RS*). However, in other preparations of *Nautilus* (Fig. 6) and in other shells, such as *Umbonium* (Figs. 7 and 8), *Anodonta* (Fig. 18), and *Pinctada* (Fig. 23), local differences of texture were not detected, and the organic interlamellar sheets appeared homogeneous in their various parts.

Lines of dashes alternating with points indicate the approximate orientation in mother-of-pearl of the planes of polishing, illustrated in the corresponding micrographs. For comparison with Fig. 2, reverse the picture by 180 degrees. The lines of orientation of the planes of polishing parallel or nearly tangential to the tabular surface of the crystals (Figs. 1, 10, 16, 17, and 19) have not been represented.

The preferential planes of cleavage in mother-of-pearl appear to be primarily along the membranes sandwiched between the consecutive lamellae, secondarily, within each lamella, in the bridges between the crystals.

which appear in the negative prints of the shadow-cast replicas, as whitish or snow white veils, variously folded or collapsed (Figs. 2 to 4, 6 to 8, 12, 14, and 18).

In mother-of-pearl polished tangentially to the inner surface of the shells, the planes of polishing either coincide exactly with the tabular surfaces of the crystals of aragonite (Figs. 1, 7, 10, 17), or cross these surfaces at various angles (Figs. 3 to 5, 16, and 19).

Etching reveals progressively on the tabular surfaces, originally smooth or finely granular, a lace-like reticulated sheet, which protrudes from the still mineralized background. The patterns of this structure vary with the species examined. In *Nautilus macromphalus*, (Figs. 1, 3 to 5), the reticulum is coarse, with relatively broad, elongated lozenge-shaped openings, frequently of irregular outlines. The trabeculae of the fabric are relatively sturdy (30/35 m$\mu$). In the Gastropods *Umbonium giganteum* (Fig. 7) and *Turbo* sp. (Figs. 9, 10, and 14), the reticulum is tighter than in *Nautilus* and the openings are round or polygonal. The trabeculae here are more delicate than in *Nautilus*. In Pelecypods (Figs. 16 and 17), the reticulum is characterized by a texture which is still tighter and more condensed than in *Nautilus* and in Gastropods, and by the extremely small size of the openings. In the genus *Pinctada*, however, larger circular holes, similar in their size and in their shape to those recorded in *Turbo* and in *Umbonium*, but scarcer in number, are scattered in the typical condensed reticulated sheet of Pelecypods (Figs. 19, 22, and 23).

In the shadow-cast replicas, the trabeculae appear as knobby cords, resembling frequently the rhizomes of the garden iris. This shape is especially evident in *Nautilus* (Figs. 2 to 5), and in Gastropods (Figs. 9, 10, 14, and 15). It may also be observed in Pelecypods (Fig. 19, top left; Figs. 21 and 22). The trabeculae are frequently sprinkled with hemispherical protuberances or polygonal tuberosities of various sizes (Figs. 4, 5, 9, 15, 17, 19, 21, 23).

In incidental depressions of the etched surfaces, in which the structures were protected from the incoming vaporized palladium by overhanging obstacles, these cords are discernible in the shadows, on the obscure background, as transparent, cylindrical elements.

After heavy etching, lace-like reticulated sheets were exposed over large areas and appeared to run as continuous structures collapsed on to the underlying adjacent nacreous lamella. In some preparations from *Nautilus*, observed in tangential orientation, the fabric was looser and the openings were broader in the intercrystallinic areas than in those in close contact with the tabular crystal surface.

In several preparations, especially in those of tangential orientation, crystals of aragonite, at various stages of disintegration, were removed from the etched surfaces of the objects, along with the intermediate negative replicas, and adhered to the subsequent positive metallic replicas (Figs. 10, 13). In these crystals (pseudoreplicas, 21), erosion coincides incidentally with the planes of the crystallographic pattern, or takes place at random. A replica of the corroded surface of mother-of-pearl (*Turbo*) shown in Fig. 13, illustrates both the characteristic lace-like reticulated sheet of this species, and the surface of a corroded crystal of aragonite, with erect rod-like fragments. These fragments seem to coincide occasionally with the location of the openings in the perforated sheet, as if the rods were caught in its meshes.

In preparations of mother-of-pearl sectioned and polished transversally to the inner shell surface, the stratified lamellae and their rows of crystals were revealed in the plane of polishing, either transversally (Figs. 6 to 8, 12, 14, 18) or at various degrees of obliquity (Figs. 2, 11, 14, and Text-fig. 1).

Etching of surfaces polished at right angles to the stratification of the lamellae deepens the furrows which limit these lamellae, and, within each lamella, those which separate the crystals aligned in rows. During these progressive alterations, the well known "brick wall" appearance (22) of mother-of-pearl is progressively unmasked (Figs. 8, 11, 12, 18).

At the beginning of the corrosion, each crystal appears in cross-section as a rectangular ridge, with a smooth or finely granular texture of its surface. Heavier etching discloses folded, collapsed, or protruding membranes, which run without discontinuity along the furrows separating the parallel lamellae or rows of crystals. Bridges in these membranes cross the spaces between the crystals. Each crystal seems to be wrapped within a membrane as though inside a bag (Figs. 7, 8, 12, 18). Progressive etching reveals, on one side of the square area of the crystal section, pads (Fig. 12) or strands (Figs. 2, 6, 11, 14). These formations represent, viewed transversally or obliquely, the part of the lace-like reticulated wrapping, in contact with the base of the crystals and described above in tangential preparations (compare Fig. 2 to Fig. 1; Fig. 11 and Fig. 14 to Fig. 10).

The width of these formations is related to the degree of obliquity of the plane of polishing (transversal section: Figs. 2, 12, and 14 bottom; oblique section: Figs. 11 and 14 top). The exposed surface of crystal section (not covered by these structures) exhibits a finely granular homogeneous background.

Alkaline (pH 9.0) saturated aqueous solutions of sequestrene NA 2 induced slower etching effects than unbuffered solutions (pH 5.0), without essential difference of aspect in the figures of corrosion.

## DISCUSSION

The above observations are illustrated schematically in Text-fig. 1.

1. Corrosion of surfaces of mother-of-pearl reveals in between the mineral lamellae (Figs. 2, 3, 6, 12, 14, 18, 20, and Text-fig. 1 (*RS*, $M'$) and between the individual crystals of aragonite aligned in rows in these lamellae (Figs. 7, 8, 12, 18, and Text-fig. 1, $M''$) a system of soft membranes or sheets, which resist erosion by the chelating agent. This system corresponds topographically

to the organic linear network detected formerly (1, 22, 32) in mother-of-pearl with the light microscope.

2. The interlamellar membranes consist of one (Text-fig. 1, *RS*), or more than one (Text-fig. 1, *RS*, *M′*) sheet. These sheets run as continuous formations in between consecutive mineral lamellae. In these sheets, especially in those parts in close contact with the base of the crystals of aragonite, a lace-like reticulum has been detected with the electron microscope.

3. The structural pattern of this reticulum varies with the species of mollusc. In the corresponding species, the reticulum exhibits the same morphological features[2] as the perforated organic leaflets of decalcified mother-of-pearl, cleaved by ultrasonic waves, and studied formerly (5, 6) after collapse by desiccation on to a formvar background. The present studies have shown that these leaflets are fragments of the interlamellar membranes.

4. A reticulated pattern is not discernible in all the pictures of the membranes or sheets belonging to the system of interlamellar (Text-fig. 1, *M′*) and especially of intercrystallinic (Text-fig. 1, *M″*) sheets. These differences might suggest dissimilarities of structure between different parts of the organic phase in

[2] This coincidence suggests that the reticulated sheets which resist erosion in the present preparations, may reasonably be identified with the organic matrix (conchiolin) of mother-of-pearl.

In an attempt to collect additional information on the identity of the lace-like structures, surfaces of mother-of-pearl polished transversally (*Pinctada*) were covered during one to several days, at room temperature, with a 10 per cent solution of potassium hydroxide, an agent traditionally used (1, 2, 13, 24) for selective destruction of conchiolin. On the replicas of this material, the parallel streaks which run on the polished surfaces and in which the interlamellar membranes are located, appeared deepened into furrows. Small spherical bodies were scattered all over the preparations.

Similarly, surfaces of mother-of-pearl (*Nautilus*), on which the lace-like sheet had been previously exposed by heavy etching, were submitted to the same procedure, and as a result, the reticulated sheet disappeared from large areas of the crystal surfaces, unscreening the mineral background. In other regions of the surfaces, the reticulum persisted, but was variously disorganized. Swellings and dissociation of the cords into spherical bodies were the characteristic alterations. Small whitish flecks, floating in the solutions bathing the nacreous surfaces, were collected on to formvar-coated screens, and shadow-cast with palladium. This material appeared in the electron microscope as the ghosts of the partly dissolved reticulum detached from the surfaces.

Inorganic crystals of aragonite were polished and etched in the same conditions as the crystals of mother-of-pearl, along the corresponding axes. Owing to the greater hardness of this inorganic material, contact of the polished surfaces with the etchant was increased in several preparations. As shown in Figs. 24 and 25, the figures of corrosion differed from those recorded in crystals of mother-of-pearl. Interpretation of these micrographs is left to competent crystallographers. Some of the details of structure exposed by erosion in these inorganic crystals resemble figures obtained by von Ebner (27) in his investigations on corrosion of crystals of aragonite induced by formic acid. In older observations, performed at much lower magnifications with the light microscope, Rose (28) reported identical figures of corrosion in aragonite crystals and in mother-of-pearl, a result which von Gümbel (29) did not find convincing, on the basis of his own studies.

mother-of-pearl. Previous observations (5, 6) do not support such interpretation: the samples from suspensions of organic material of mother-of-pearl, dissociated by ultrasonic waves after decalcification, consistently contained only perforated leaflets of the same pattern. Shrinkages of these soft and extremely thin pellicles projected without support above the etched surfaces, are among the factors which might possibly account for their amorphous appearance.

### *Ultrastructure of the Trabeculae in the Reticulated Sheets*

As described above, the trabeculae of the organic lace-like structures appear, in shadow-cast positive replicas of the figures of corrosion, as knobby cords, frequently studded with hemispherical protuberances of various sizes (from 2 to 4 m$\mu$). Identical rugosities were recorded formerly, and were specially visible in shadow-cast material, on the dissociated organic leaflets (5, 6). In the present material, these tuberosities were found exclusively on the trabeculae. Their size is distinctly different from that of the thin granulations characterizing the background of other surfaces. These differences seem to exclude the possibility that they represent a contamination such as an adsorbed film of oil, collected into droplets. Such a film would cover uniformly all the structures (30, 31). In parts of the replicas protected from the vaporized palladium, these tuberosities are no more discernible. This fact seems to rule out the possibility that these structures correspond to pseudoreplicas of highly electron-scattering material, such as small fragments of microcrystals of aragonite. The protuberances seem rather to correspond to actual elevations or to bloats in the structures. Their significance, discussed previously (6), is still unknown.

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## SUMMARY

1. The topography of the organic components (conchiolin) has been investigated on positive, postshadow-cast, formvar, and carbon replicas of mother-of-pearl from shells of a Cephalopod, of two Gastropods, and of six Pelecypods. All these shells are characterized by a true nacreous inner shell layer.

2. The material included normal shell surfaces, fragments of cleavage obtained by fracture, and surfaces polished tangentially and transversally to the inner surface of the shells. Replicas of these surfaces were prepared before and

after etching of graded heaviness, induced by a chelating agent (sequestrene NA 2, titriplex III). Micrographs of the successive steps of the process of corrosion have been recorded.

3. Corrosion unmasked, on the nacreous surfaces, organic membranes or sheets, running as continuous formations in between adjacent mineral lamellae, and separating the individual crystals of aragonite which are aligned in rows and constitute each lamella.

4. The interlamellar sheets of material exhibit a reticulated structure, which is especially visible in preparations orientated tangentially to the lamellae and to the tabular surface of the aragonite crystals. The pattern of this lace-like structure, different in the various species studied, appeared in the same species as closely similar to that reported previously in leaflets of thoroughly decalcified mother-of-pearl, dissociated by ultrasonic waves. The present results support former conclusions with regard to the existence of taxonomic differences between Cephalopods, Gastropods, and Pelecypods in the morphological organization of the organic phase within mother-of-pearl.

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## EXPLANATION OF PLATES

Micrographs of positive, formvar or carbon replicas, of regions of fracture inside the nacreous layer, before (Figs. 20 and 21) and after etching (Figs. 22 and 23), and of surfaces of mother-of-pearl (Figs. 1 to 19), polished in various orientations, and subsequently corroded with saturated aqueous solutions of sequestrene NA 2 at pH 5.0 (unless otherwise indicated) and of titriplex III, during various lengths of time (indicated in brackets). All the replicas were shadow-cast with palladium, at angles varying from 18 to 27.5°. Negative prints. Scale, 1 $\mu$; in Fig. 15, 0.1 $\mu$.

## Plate 251

*Nautilus macromphalus* Sowerby (Cephalopoda).

Fig. 1. Plane of polishing tangential to the tabular surface of a crystal of aragonite. Etched with sequestrene (10 minutes) Carbon replica.

Lace-like reticulated sheet with elongated lozenge-shaped meshes, exposed on the finely granular background of the crystal. In the lower part of the crystal surface, the structures, with the exception of two parallel cords, were probably detached from the mineral. The pattern of the sheet resembles closely that described previously (references 5 and 6, Plates III and IV) in decalcified leaflets of mother-of-pearl from *Nautilus*, cleaved by ultrasonic waves.

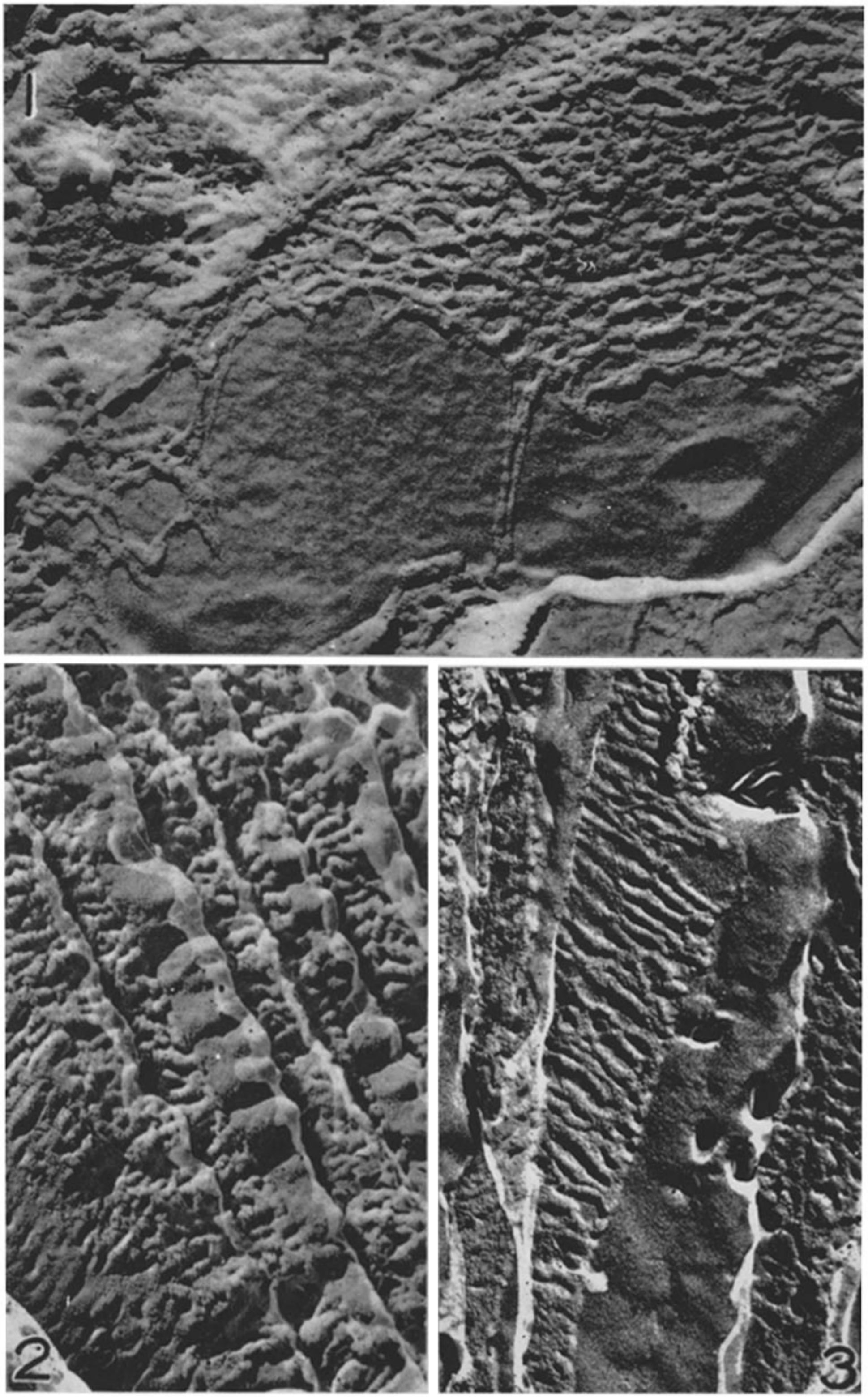
Top left, on an adjacent crystal, organic reticulated sheet still partly embedded in mineral substance and possibly covered by fragments of crystals (pseudoreplicas), transferred through the intermediate to the final positive replica. Bottom right, in succession downward: falling slope (shadow) of the crystal of aragonite, a white thick cord corresponding to a folded intercrystallinic membrane, the margin of another crystal surmounted by fragments of organic sheet. ×27,000.

Fig. 2. Plane of polishing transversal oblique to the surface of the lamellae. Etched with sequestrene (10 minutes). Carbon replica.

The corroded edges of successive parallel lamellae are shown. In between adjacent lamellae, the lace-like sheet exposed by corrosion is abruptly interrupted by the plane of polishing. Fragments of apparently amorphous membranes are collapsed on to the contiguous crystals. These membranes belong, together with the reticulated sheets, to the system of interlamellar organic structures (*M'* and *RS* in Text-fig. 1). ×27,000.

Fig. 3. Plane of polishing slightly oblique to the surface of the lamellae. Etched with titriplex III (8 minutes) Carbon replica.

The edges of consecutive imbricated mineral lamellae, alternating with interlamellar organic reticulated sheets, are shown. These edges, involved in the plane of polishing, correspond to Schmidt's "Niveaulinien" (1). A patch of reticulated sheet characterizing *Nautilus*, is exposed in the centre of the picture. ×27,000.



(Grégoire: Organic components in mother-of-pearl)

## Plate 252

*Nautilus macromphalus* Sowerby (Cephalopoda).

Fig. 4. Plane of polishing slightly oblique to the surface of the lamellae. Etched with sequestrene (10 minutes). Carbon replica.

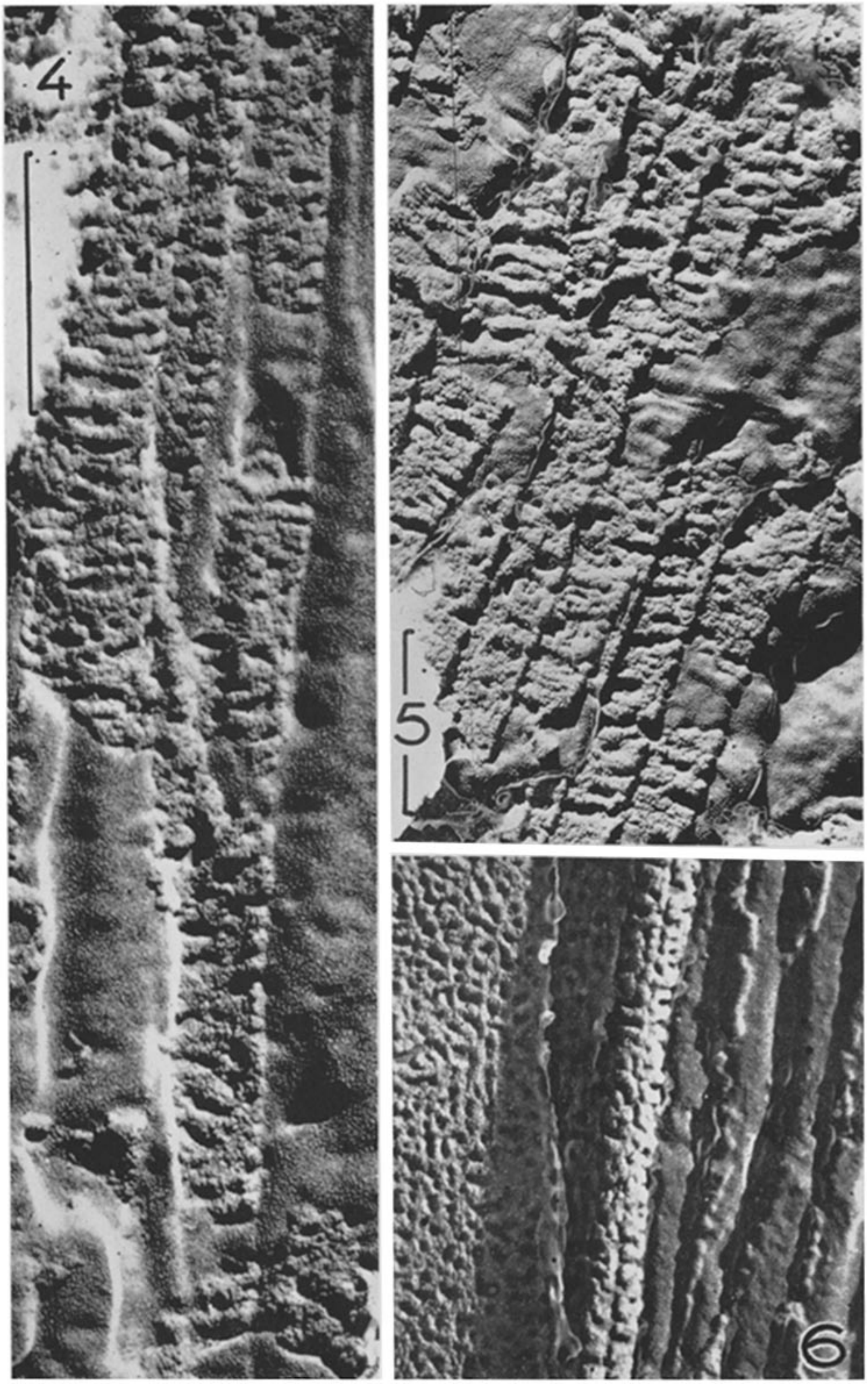
The wave-like edges ("Niveaulinien", Schmidt, 1) of approximately four successive mineral lamellae and of the interlamellar organic reticulated sheets sandwiched between these lamellae appear in the plane of polishing. At the lower left of the picture, fragments of reticulum were possibly detached during rinsing, leaving exposed the underlying mineral lamella. The blurred white traces at the edges of the lamellae correspond probably to fragments of membranes belonging to the interlamellar organic system (*M'* in Text-fig. 1). The trabeculae of the reticulated sheet appear studded with spherical blisters or protuberances, of various sizes. Absence of similar tuberosities on the finely granular surface of the mineral lamellae excludes the possibility of a general contamination of the surfaces by oil vapours during shadow casting. × 39,000.

Fig. 5. Plane of polishing oblique to the surface of the lamellae. Etched with sequestrene (10 minutes). Carbon replica.

Approximately seven imbricated organic sheets are shown. Their trabeculae are sprinkled with protuberances as in Fig. 4. With the exception of scattered areas with a finely granular surface, the mineral lamellae alternating with these sheets are either hidden by the superimposed organic structures or have been partly dissolved by etching, leaving the organic leaves piled upon each other. ×27,000.

Fig. 6. Plane of polishing transversal to the surface of the lamellae. Etched with titriplex III (4 minutes). Carbon replica.

Owing to curvature in the shells and to incidental variations in the stratified configuration of the lamellae, crystals of aragonite orientated at right angles to each other may be found in close contiguity. Fig. 6 represents one of these variations of structure. From left to right: (1) tangential view of a reticulated sheet with the *Nautilus* texture; (2) shadowed region, with the same sheet in the obscure background and thin membranes projecting upwards; (3) a structure crossing vertically the centre of the picture, with a fabric (brightly "illuminated") consisting of small horseshoe-like trabeculae; this structure represents probably the curved or folded edge of one or of two lace-like sheets, cut transversally; (4) four parallel lamellae, with a finely granular texture, separated by membranes visible as folded white lines in the furrows. These lamellae are shown in transversal orientation, at right angles with the crystal surface, on the left. ×27,000.




(Grégoire: Organic components in mother-of-pearl)

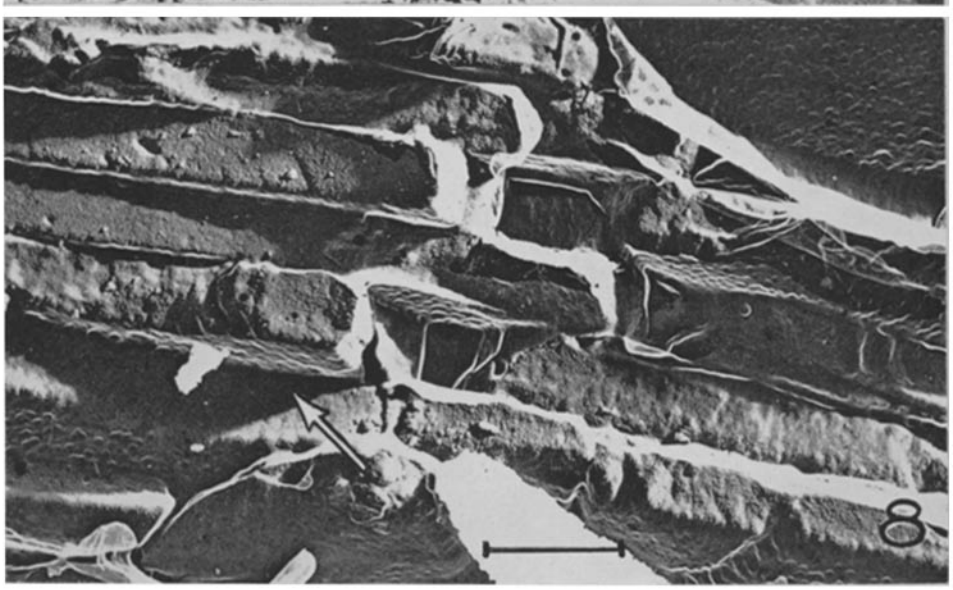
## Plate 253

*Umbonium giganteum* Lesson (Gastropoda, *Umboniidae*).

In this region of mother-of-pearl, crystals orientated at right angles are shown in close vicinity of each other. Etched with sequestrene (13 minutes). Carbon replicas.

Fig. 7. From top to bottom: (1) The edges (snow white) of four successive lamellae are viewed tangentially and slightly obliquely. In the triangular area of the lowest lamella, the tabular surfaces of three partly broken (artifact) crystals of aragonite, separated by furrows, are covered by a lace-like reticulated sheet, revealed by corrosion, and characteristic of *Umbonium* (compare with reference 6, in decalcified leaflets of mother-of-pearl dissociated by the ultrasonic waves: Plate X, Figs. 4 and 6; Plate XIII, Figs. 1 and 2). (2) Three stratified mineral lamellae, seen in transversal section, with interlamellar and intercrystallinic organic membranes (snow white undulating lines) clearly visible. At the border line between the crystals in tangential orientation and the first lamella in transversal orientation (bottom left of the picture), the reticulated sheet seems to continue into a latticework which protrudes like a roof (oblique shadows) over the abruptly falling edges of the crystals cut transversally. Right below, a similar latticework appears between the first and the second lamellae seen in transversal section (bottom left). The picture suggests that these latticeworks and the reticulated sheets appearing in tangential orientation belong to identical structures. ×18,000.

Fig. 8. Another field of the same preparation. The crystals from several superimposed lamellae are shown in transverse orientation, wrapped in organic membranes. In the lower left centre of the micrograph, a latticework, projecting obliquely, overhangs and shadows (see arrow) the corroded edge of a crystal belonging to the next lamella below. The fabric of this latticework corresponds to that of the reticulated sheets viewed tangentially (Fig. 8, top right; Fig. 7, see above). Two other similar lattices are shown in the centre and to the right of the picture. ×18,000.


(Grégoire: Organic components in mother-of-pearl)

## PLATE 254

*Turbo* sp. (Gastropoda, *Turbinidae*).

FIG. 9. Plane of polishing transverse to the surface of the lamellae. Etched with sequestrene (8 minutes). Formvar replica.

The interlamellar reticulated sheet, collapsed in the centre of the picture, exhibits the structural pattern found previously in decalcified dissociated leaflets of *Turbo* (reference 6, Plate IX to XI). This fragment of sheet does not seem to be a pseudoreplica of a leaflet deposited at random on the still mineralized background. The other interlamellar membranes (white crests on parallel ridges) are still embedded in the mineral substance. The picture suggests differences in the hardness of contiguous structures in mother-of-pearl, resulting in variations in the effects of corrosion. ×27,000.

FIG. 10. Plane of polishing parallel to the tabular surface of a crystal of aragonite. Etched with sequestrene (8 minutes). Formvar replica.

The *Turbo* pattern of an interlamellar sheet is visible through an incidental window left by partial dissolution of a crystal of aragonite (pseudoreplica), adhering to the positive replica. ×27,000.

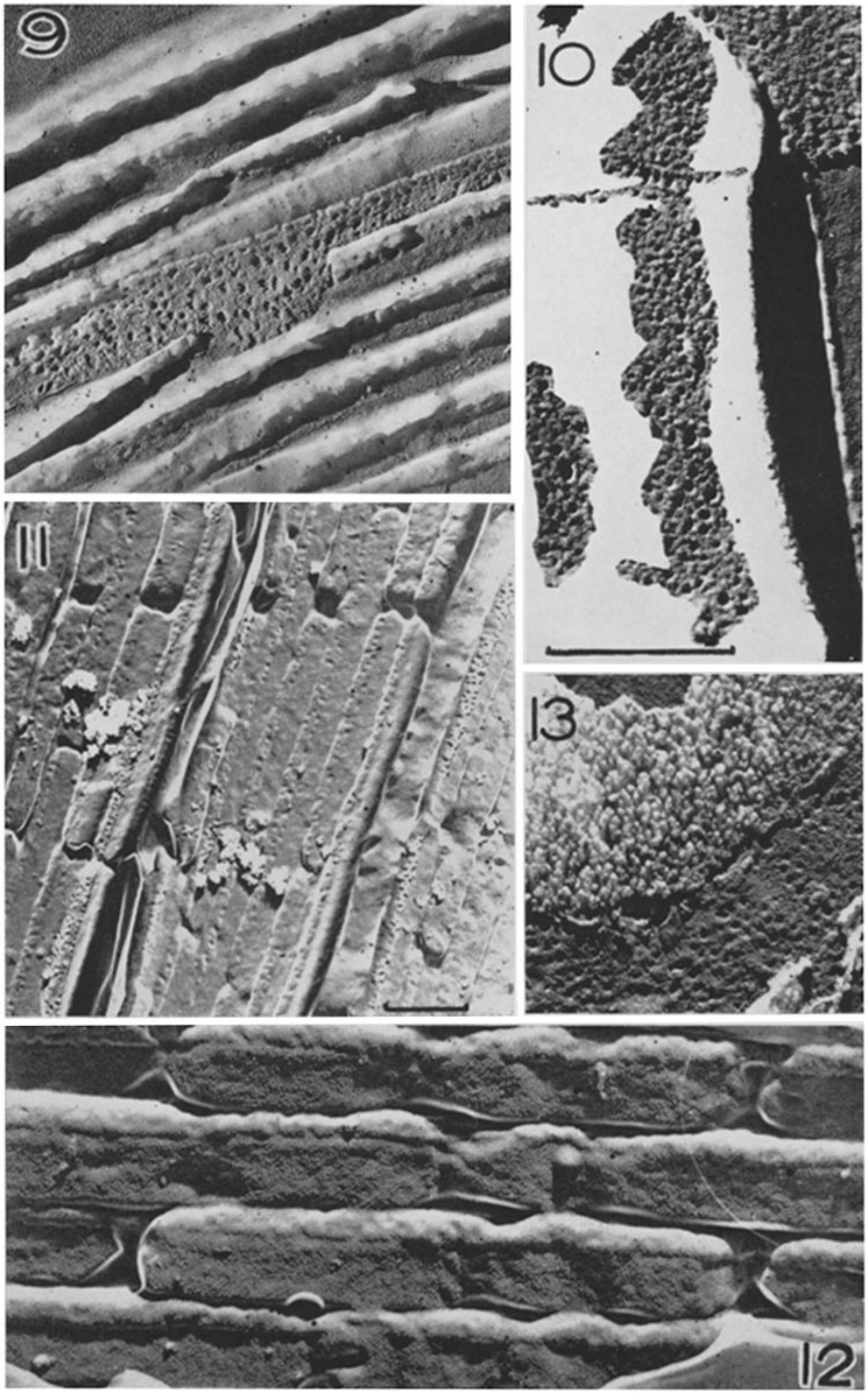
FIG. 11. Plane of polishing transverse (slightly oblique) to the surface of the lamellae. Etched with sequestrene (4 minutes). Carbon replica.

Brick wall appearance. Approximately sixteen lamellae are visible in transverse orientation. The organic sheets alternating with the lamellae, appear as perforated bands on one side of the transversal surface of the crystals. The region of mother-of-pearl used for the present preparation showed a periodical alternation of one protruding lamella consisting of thicker crystals, and of six lamellae consisting of thinner crystals. One of these periods is seen in the centre of Fig. 11. ×12,000.

FIG. 12. Plane of polishing transverse to the surface of the lamellae. Etched with sequestrene (4 minutes). Carbon replica. (Compare with Text-fig. 1). Brick wall appearance. Organic sheets (Text-fig. 1, *RS*) appear as snow crests on the upper part of the crystals, where their actual thickness might be increased by some degree of folding, and run along the crystals arranged in lamellae. These sheets are connected with, or send bridges into the intercrystalline spaces (Text-fig. 1, $M''$). Between consecutive lamellae, there may be more than one organic sheet (Text-fig. 1, $M'$, parallel to *RS*). ×27,000.

FIG. 13. Plane of polishing parallel to the surface of the lamellae. Etched with sequestrene (8 minutes). Formvar replica.

The replica of an organic sheet exhibiting the typical *Turbo* pattern is shown together with a pseudoreplica of a disintegrating crystal of aragonite. Rod-like fragments appear erect on the surface of this crystal. ×27,000.




(Grégoire: Organic components in mother-of-pearl)

## Plate 255

Fig. 14. *Turbo* sp. Plane of polishing transverse to the surface of the lamellae. Etched with sequestrene (11 minutes). Carbon replica.

A band of a lace-like organic sheet with the *Turbo* pattern overhangs the crystal cut obliquely by the plane of polishing (upper half of the micrograph). The membrane wrapping the crystal, variously torn and collapsed, is partly visible. In the lower half of the micrograph, the edges of three lamellae were heavily etched, and appear covered by collapsed organic structures. Undulating white strings correspond to interlamellar membranes cut transversally. ×27,000.

Fig. 15. *Turbo* sp. Plane of polishing parallel to the surface of the lamellae. Etched with sequestrene (8 minutes). Formvar replica.

The trabeculae of an organic sheet appear sprinkled with hemispherical protuberances. "Iris rhizome" aspect. ×174,000.

Fig. 16. *Anodonta cygnaea* Linné (Pelecypoda, *Nayadidae-Unionidae*). Plane of polishing parallel or slightly oblique to the surface of the lamellae. Etched with titriplex III (8 minutes). Carbon replica.

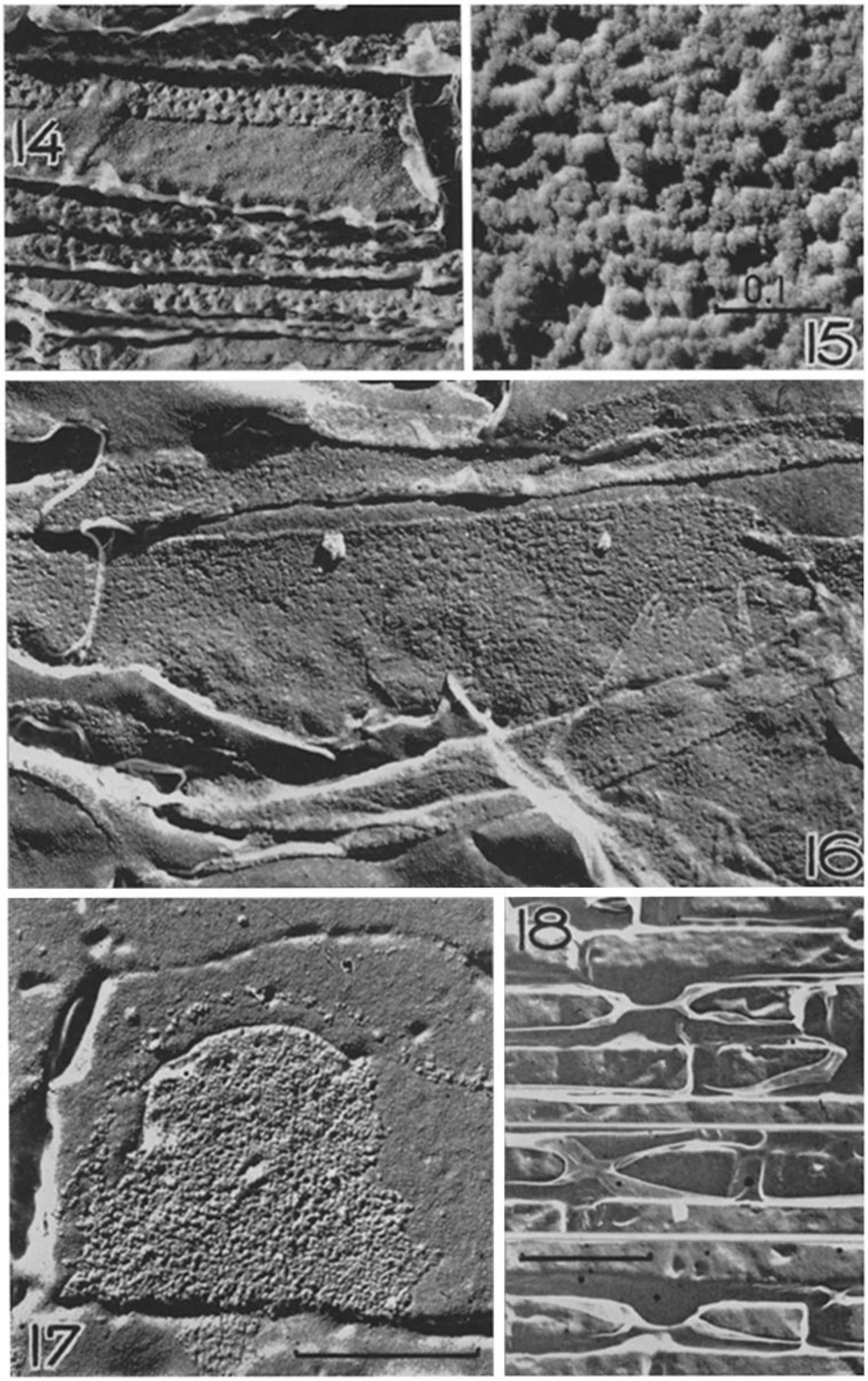
Typical Pelecypod pattern of a reticulated sheet (compare with reference 6, Plate XVI), dense and tight, with numerous tiny openings and a few larger holes irregularly scattered. Lower right, possibly a pseudoreplica of a displaced membrane, detached from the etched surface and adhering to the final replica. ×27,000.

Fig. 17. *Anodonta cygnaea* Linné. Plane of polishing parallel to the surface of the lamellae. Etched with sequestrene (pH 9.0; 15 minutes). Carbon replica.

Fragment of the typical reticulated sheet surmounting the tabular surface of a crystal of aragonite, and anchored to a depression in this surface. Other parts of the sheet were probably detached from the background. Pseudoreplicas of the same structures were collapsed on other regions of the surfaces. ×27,000.

Figs. 18 *a*, *b*, and *c*. *Anodonta cygnaea* Linné. Plane of polishing transverse to the surface of the lamellae. Etched with sequestrene (pH 9.0; 15 minutes). Carbon replica.

Brick wall appearance. Membranes wrap the crystals of aragonite. The lace-like pattern is not visible on that micrograph. ×19,000.




(Grégoire: Organic components in mother-of-pearl)

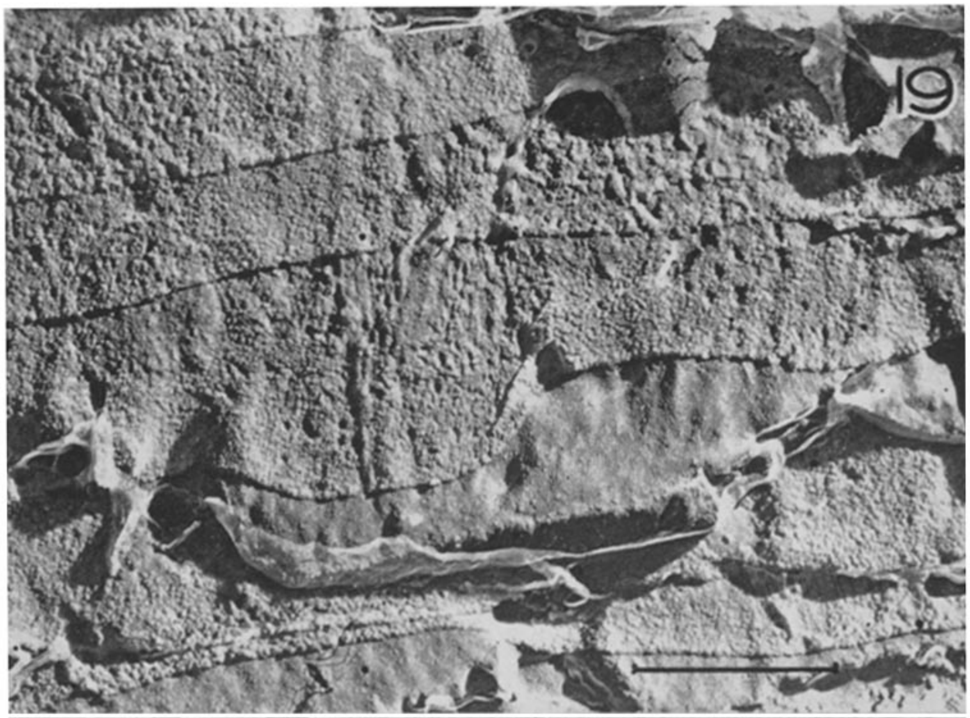
## PLATE 256

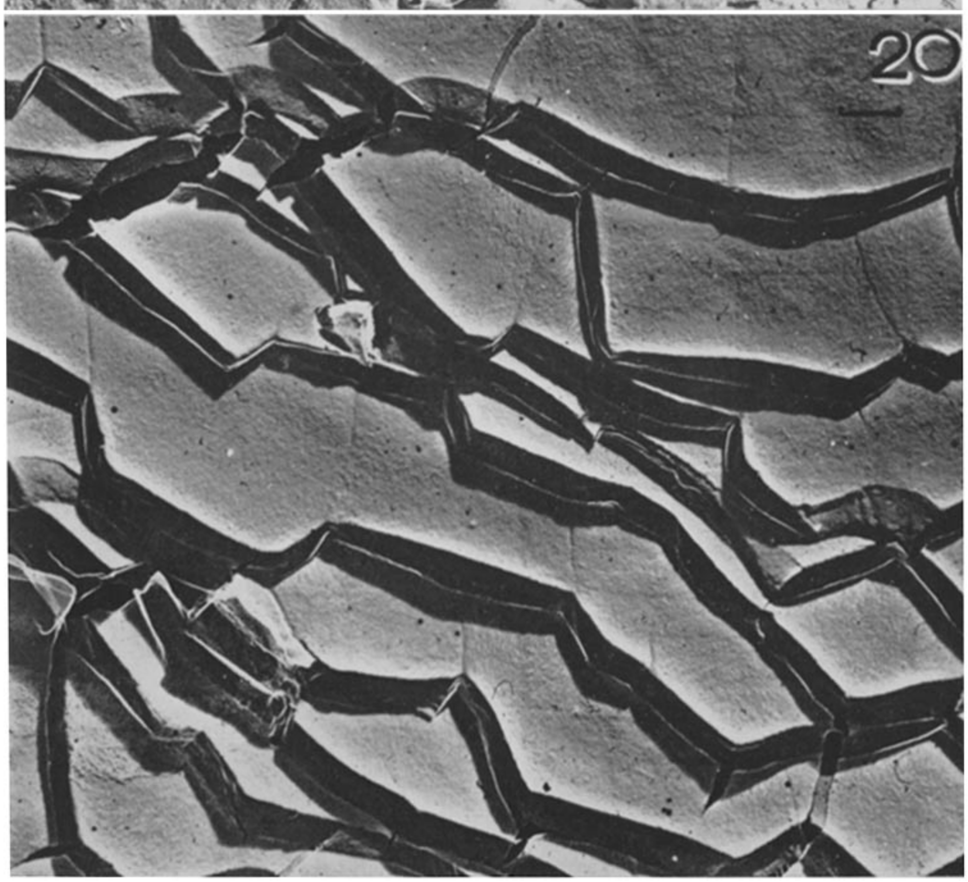
FIG. 19. *Pinctada galtsoffi* Bartsch (Pelecypoda, *Aviculidae*). Plane of polishing tangential to the surface of the lamellae. Etched with titriplex III (9 minutes). Carbon replica.

Several imbricated interlamellar organic sheets, with the pattern characterizing the genus *Pinctada* (especially top left; compare with reference 6, Plate XX), are collapsed on to the mineral background. ×27,000.

FIG. 20. *Pinctada* (*Pteria*, *Meleagrina*) *margaritifera* Linné (Pelecypoda, *Aviculidae*). Mother-of-pearl cleaved by fracture. Unetched. Carbon replica.

Eleven superimposed consecutive lamellae in terrace-like arrangement are shown. The irregular edges of the broken lamellae appear as steep or as vertical cliffs intensely shadowed. Fragments of organic membranes are visible as thin flaky shreds (white lines) projecting between the lamellae. On the surfaces of the lamellae, shallow grooves delimit the crystals of aragonite. The surfaces of the terraces are finely granular, except where fragments of a lace-like reticulated sheet are lying on the surface of the two lowermost terraces (bottom left). ×8,000.




(Grégoire: Organic components in mother-of-pearl)

PLATE 257

FIG. 21. *Pinctada margaritifera* Linné. Region of fracture (white bands) in three superimposed lamellae (terraces). Unetched. Carbon replica.

Removal of an incidental splinter of fracture in the two terraces left, has exposed at the bottom of the pit, a plane of fracture which coincides with the organic interlamellar sheet characterizing the Pelecypods (tight and dense pattern). Overhanging the upper part of this region, there is a floating organic membrane. Note the rugosities on the terraces. These inequalities might correspond to the traces of moulding, left on the surface of the crystals of aragonite by the surmounting interlamellar organic sheet removed after fracture together with the shell fragment. ×27,000.

FIG. 22. *Pinctada margaritifera* Linné. Region of fracture. Etched with titriplex III (3 minutes). Carbon replica.

The picture illustrates the progressive unfolding of the *Pinctada* pattern in an organic interlamellar reticulated sheet (compare with reference 6, Plates XX and XXI) on the surface of a terrace similar to that shown in Fig. 21. Heavier corrosion on the left of the picture. ×27,000.

FIG. 23. *Pinctada margaritifera* Linné. Region of fracture. Etched with titriplex III (3 minutes). Carbon replica.

The organic sheet, possibly still partly embedded, appears in a tortuous pit left by removal of a splinter. Membranes (snow white) appear erect (shadows) or collapsed on to the uneven background. ×27,000.

FIGS. 24 and 25. Two aspects of the image of corrosion induced in inorganic crystals of aragonite polished at right angles to their long axis, a plane of polishing which corresponds to the tabular surface of the nacreous crystals.

Fig. 24: etched with sequestrene (100 minutes). Carbon replica. ×4400.

Fig. 25: etched with sequestrene (21 minutes). Carbon replica. ×8,000.

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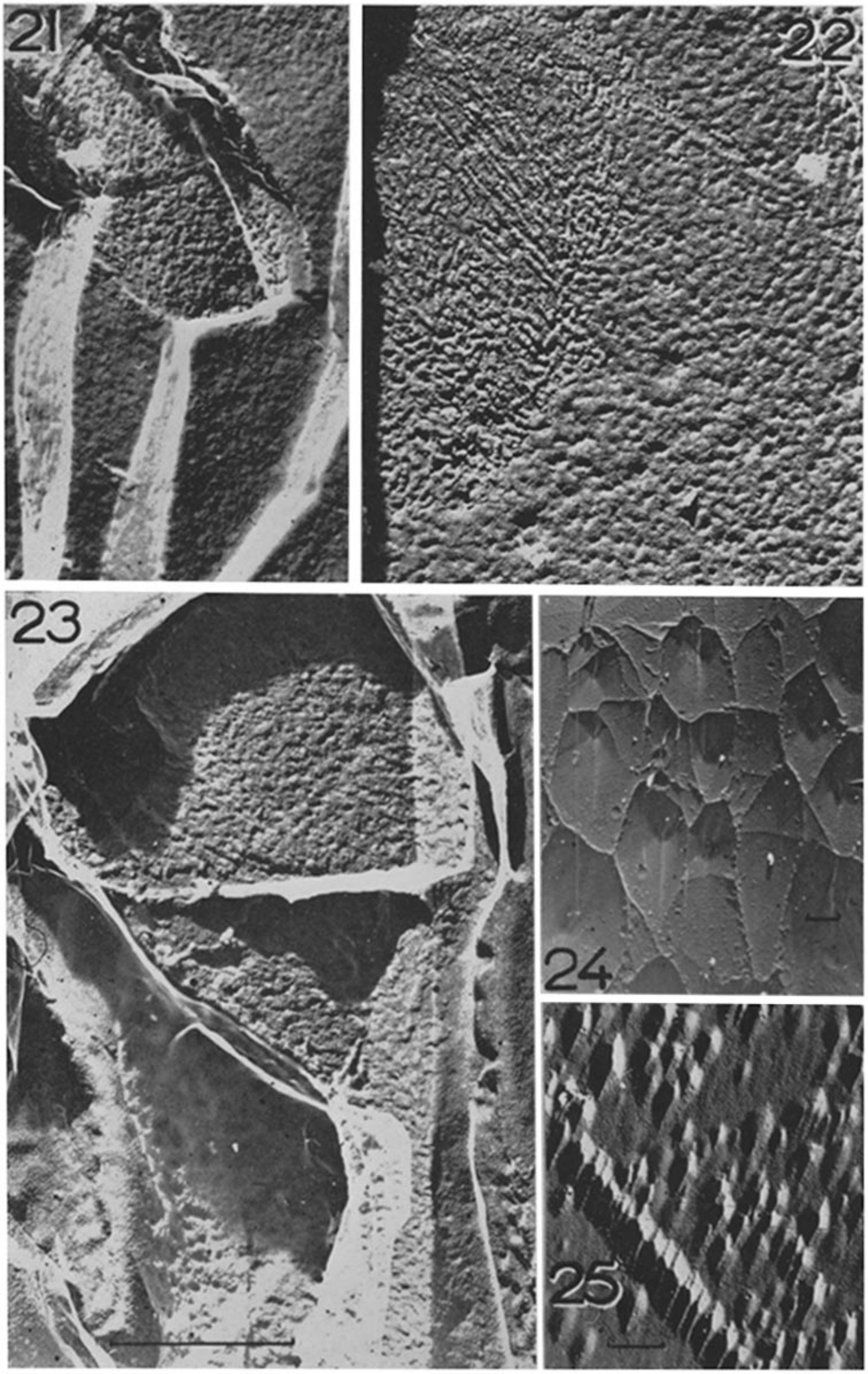
PLATE 257
VOL. 3




(Grégoire: Organic components in mother-of-pearl)