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Microarchitecture and Mode of Formation of Nacre (Mother-of-Pearl) in Pelecypods, Gastropods, and Cephalopods

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ABSTRACT

Variations in the mode of calcification of the nacreous layer of mollusc shells impress patterns on the internal microarchitecture of the shells which have taxonomic significance.In gastropods crystals are deposited in tall vertical stacks which differ markedly from the imbricate and row-stack patterns observed in pelecypods. Internal vertical structures in gastropod and cephalopod nacre (parallel cylindrical stacks) are more highly ordered than analagous features in pelecypods (*Vertikalschichtung*, *Treppen*, lenticular nacre) but differ from each other in the orientation of the tabular aragonite crystals which form the mineral laminae. The stacked mode of deposition provides gastropods with a definite functional advantage in calcifying shell because it allows more crystals to form and develop on the growth surface at one time. This mode of deposition appears to be a primitive trait among molluscs which has been lost by degrees in pelecypods during their evolution of a new (bivalve) shell form. Results indicate that microarchitectural patterns in the nacre can be correlated with evolutionary tendencies and ecological adaptations of the major groups of molluscs, and that shell microstructures and substructures will serve as useful indices in studies of molluscan phylogeny as more data become available from scanning electron microscope investigations.

CONTENTS

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1. INTRODUCTION

Because of its importance to pearl fisheries as well as its existence in its own right as a substance of unusual beauty and luster, nacre (mother-of-pearl) has been studied more intensely by modern workers than any other molluscan shell structure. In gross morphology, nacre consists of a succession of mineral laminae interleaved with thin lace-like organic membranes. Each mineral lamina is composed of tabular shaped crystals of organically deposited calcium carbonate in the form of aragonite. The organic matrices are composed of several fibrous and nonfibrous proteins collectively referred to as "conchiolin." GRÉGOIRE and his associates (GRÉGOIRE, et al., 1949, 1950, 1955; GRÉGOIRE, 1957, 1959) have distinguished structural patterns in the organic matrices which are taxonomically indicative at the Class level. In the case of pelecypods, statistically significant differences have been recorded at the Family level (GRÉGOIRE, 1958, 1960, 1967). If (as is commonly believed) the organic matrix is elaborated by the mantle epithelium prior to mineralization (WADA, 1961; WILBUR, 1964; BEVELANDER & NAKAHARA, 1969), and if it influences the nucleation and growth of crystals of nacre, one might then expect to find organic matrices of different structural configuration associated with different arrangements of crystals in nacre. Indeed, GRÉGOIRE (1962) has confirmed by electron microscopy the presence of a strictly ordered and persistent columnar stacking of crystals in cephalopod nacre. Similar structures have rarely been reported in pelecypods. Differences in the internal structures of gastropod and pelecypod nacre were also reported by AHRBERG (1935), but these were not discerned in early submicroscopic studies (WADA, 1961). Recently, however, it has been maintained (WISE, 1969a, 1969b, 1970; MUTVEI, 1969) that taxonomically significant differences do exist in the internal structure and in the mode of formation of the nacre in these two groups. The purposes of this report are 1. to present the evidence on which such claims have been made by this writer, and 2. to discuss the importance these differences may have to phylogeny and functional morphology. To better understand the taxonomic differences, it will be helpful to relate the mode of formation of each variety of nacre (as observed on growth surfaces) to the resultant microarchitectural pattern observed in sections through the mature nacre.

2. MATERIALS AND METHODS

Specimens used in this study are of Recent age and were collected on the East and West Coasts of North America and from the South Pacific Ocean. Except for the gastropod *Turbo castanea* and one specimen of *Haliotis rufescens*, all material was collected live; soft parts were removed at the time of collection either manually or after boiling.

Specimens and localities are:

PELECYPODA: *Amblema costata* (RAFINESQUE), Danville, Illinois; *Lampsilis ventricosa*, Danville, Illinois; *Pinctada radiata* LEACH, Bimini, Bahamas; *Mytilus edulis* (LINNÉ), locality unknown; *Pinna carnea* GMELIN, Bimini, Bahamas; *Nucula proxima* (SAY), Woods Hole, Massachusetts.

GASTROPODA: *Turbo castanea* GMELIN, Bimini, Bahamas; *Astraea americana* (GMELIN), Pigeon Key, Florida; *Astraea caelata* (GMELIN), Bimini, Bahamas; *Cittarium* *pica* (LINNÉ), Bimini, Bahamas; *Haliotis rufescens* SWAINSON, California; *Tegula funebralis* A. ADAMS, California; *Margarites pupillus* GOULD, Puget Sound, Washington; *Callistoma ligatum* GOULD, US West Coast; *Norrisia norrisi* SOWERBY, California.

CEPHALOPODA: *Nautilus pompilius* LINNÉ, South Pacific Ocean.

All micrographs in this report are scanning electron micrographs with the exception of Plate X, Figure 6. As explained in WISE & HAY (1968b), all sections of shells are oriented with the proximal direction up (at the top of the micrograph). Detailed instructions for preparing molluscan shell material for examination via scanning electron microscopy have appeared in previous reports (WISE & HAY, 1968a, 1968b) and will not be redescribed here; however, additional comments will be made concerning the preparation of fracture sections.

The vertical arrangements of crystals which occur in the nacre of certain groups of molluscs are best displayed on vertical fracture surfaces. In some pelecypods, however, it may be necessary to induce *radial* vertical fractures (i.e., fractures parallel to the ribs) to expose vertical structures. Fractures are controlled 1. by sawing grooves in the specimen to guide the break, and 2. by fracturing the specimen over an appropriately placed fulcrum (toothpicks are often convenient in size and shape to use as fulcrums). To assure a clean fracture surface free from contaminants, specimens which have been sawed are rinsed and *dried* before fractures are made.

Vertical fractures through inner shell growth surfaces are induced by sawing, along the exterior of the shell, a groove penetrating to within a half millimeter of the inner surface. The fulcrum is placed on the exterior side of the shell so that the growth surface will not be damaged when pressure is applied.

The crystallographic orientations of the tabular aragonite crystals composing the mineral laminae of nacre were studied by single crystal X-ray diffraction techniques (precession method). The orthorhombic *c* axes of the crystals are always perpendicular to their tabular faces and are therefore parallel to each other in the laminar structure (SCHMIDT, 1923; WADA, 1961). WADA (1961) found that the *a* and *b* axes are parallel in pelecypod nacre, and believed that there is a tendency for these axes to be aligned in all classes of molluscs. The purpose of the present X-ray study is to test this hypothesis in the case of both gastropods and cephalopods. To determine whether or not the *a* and *b* axes are aligned, a sample of nacre must be irradiated parallel to the *c* axes of the crystals (i.e., perpendicular to the mineral laminae). WADA's preparations consisted of thin sections cut parallel to the mineral laminae and polished to thicknesses of 0.2, 0.5, and 1.0 mm. Because the laminae are not actually parallel to the inner shell surface in gastropods and nautiloids (the growth lines are oblique to the inner shell surface), it is difficult to cut thin sections exactly parallel to the laminar structure. A more reliable method than thin sectioning is cleaving the laminae into thin plates. This is accomplished by crushing the nacre in a mortar and pestle. Because the principal plane of weakness in nacre is parallel to the laminae, thin flakes are liberated when blocks of nacre are struck parallel to the laminae with the pestle. Flakes about one millimeter in breadth which appear perfectly flat in the light microscope are picked out by hand and their thicknesses are measured using the SEM. Specimens 150–300 μ thick are then selected and mounted in a precession camera set at a mu angle of 30° and irradiated for 23 hours.

3. RESULTS AND DISCUSSION

3.1 Mode of formation and microarchitecture of pelecypod and gastropod nacre

3.11 Growth surface configurations and Backsteinbau, Treppen, and lenticular patterns in pelecypod nacre

Although skeletal structures of mollusc shells had been studied microscopically for over one hundred years, it was not until the publication of W. J. SCHMIDT's authoritative account (SCHMIDT, 1923) that enough data were available to resolve several long-standing disagreements concerning the structure of pelecypod nacre. Particularly troublesome had been: 1. disagreement over the configuration of the growth surface, and 2. conflicting reports of various vertical structures in the mother-of-pearl layer of certain species. Although previous authors had based their investigations on similar forms, their conclusions varied widely. SCHMIDT's unifying work is of such accuracy and detail that his conclusions have been little modified by subsequent work.

Transmission electron microscopy by WATABE (1954, 1955) and WADA (1957a, 1957b, 1960, 1961) confirmed SCHMIDT's conception of the developmental growth surface of pelecypod nacre. As illustrated in Plate I, Figure 1, the tabular crystals of aragonite form thin mineral laminae (called *Elementarlamellen* by SCHMIDT) which overlap on the growth surface to form an imbricate or step-like pattern. New crystals are deposited at the margins of each lamina on top of the underlying step. These expand laterally with growth, eventually filling the intervening spaces and merging evenly with the laminae to extend the structure. This is the characteristic mode of formation of nacre in pelecypods. SCHMIDT (1923) found it developed in all of the pelecypods he studied, a total of 24 species representing 14 genera. Another striking feature of Figure 1 is that all of the crystals have the same orientation, a trait WADA (1961) noted in the pelecypods he studied.

In etched polished sections cut perpendicular to this structure, crystals forming the laminae appear to be fitted together like bricks in a wall laid in the common "running bond" or "stretcher bond" pattern of brickmasonry (Pl. I, Fig. 2). This configuration of crystals in cross section is referred to as the *Backsteinbau* or "brick wall" pattern (EHRENBAUM, 1885; SCHMIDT, 1923). It has long been regarded as being the most common and characteristic pattern developed in pelecypod nacre, and is a direct consequence of the imbricate mode of growth. SCHMIDT found it in all of the families of pelecypods he studied by thin section. Its existence has been confirmed numerous times by transmission electron microscopists in a large number of lamellibranchs (see GRÉGOIRE, 1957; WADA, 1961; KOBAYASHI, 1964; HUDSON, 1968; TOWE & HAMILTON, 1968a, 1968b). In a few instances, SCHMIDT (1923) observed a vertical stairstep pattern in the nacre of pelecypods which he called *Treppen* (Pl. I, Fig. 3). The progressive shift in the position of each crystal in the *Treppen* structure is thought to reflect a systematic shift in the loci of deposition of new crystals on the growth surface. A third pattern observed by SCHMIDT, the *Vertikalschichtung*, will be dicussed later in this report.

In the *Backsteinbau*, the distribution of crystals in the vertical direction is essentially random; therefore, vertical fractures through this structure are irregular and follow no particular plane of reference (Pl. II, Fig. 1). As shown in Plate II, Figure 2, fractures pass indiscriminately through as well as around individual crystals and no vertical structures are evident.

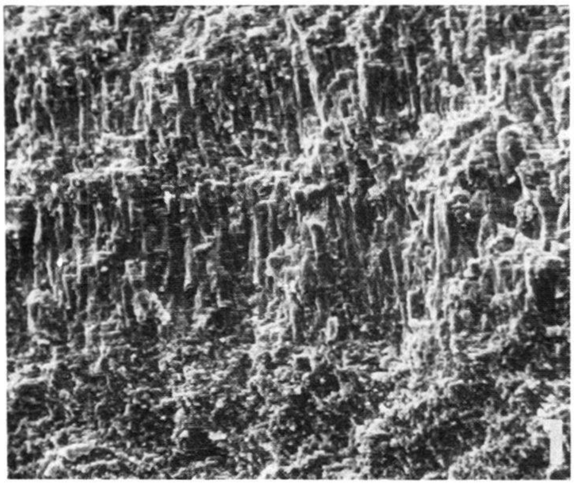
Recently, TAYLOR et al. (1969) introduced the terms "sheet nacre" and " lenticular nacre" to describe patterns within the nacre of pelecypods. Although these authors did not reconcile their terminology with that of SCHMIDT, it is apparent from their usage of the terms that "sheet nacre" is synonymous with the term *Backsteinbau*. They noted that "sheet nacre" is best developed in the inner nacreous layer of pelecypods which have two distinct nacreous layers separated by pallial myostracum. The term" lenticular nacre" is applied to patterns described by SCHMIDT under the names *Vertikalschichtung* and *Treppen*, and also to a "lenticular" structure in the outer nacreous layer of the Unionacea. This last pattern was not described by SCHMIDT; however, because it is closely related to *Backsteinbau* and *Treppen*, it will be discussed in the present section.

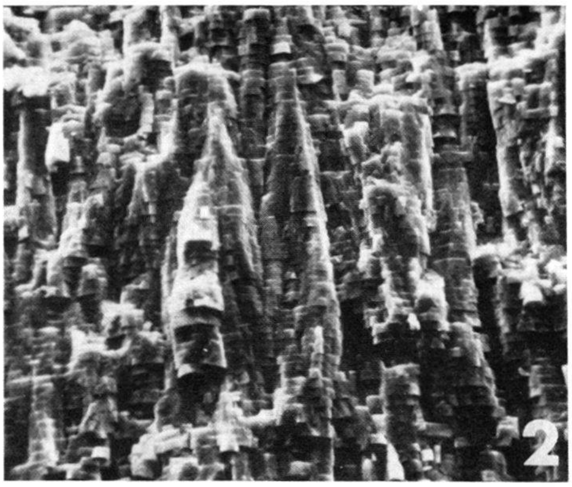
TAYLOR et al. (1969, p. 28) defined "lenticular nacre" as a structure consisting of columns of up to fifteen tabular crystals,

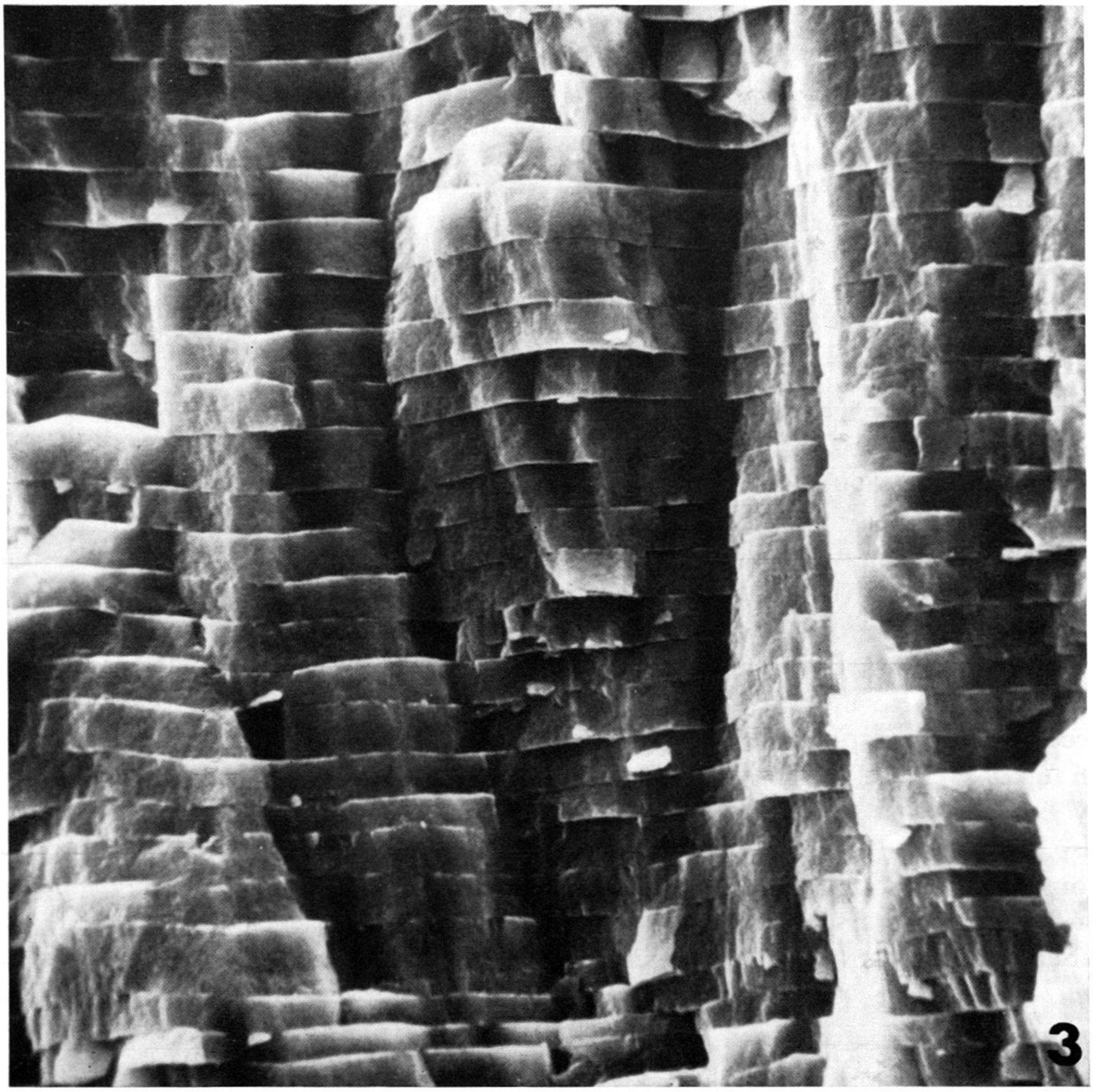
> with the columns approximately 20–30 microns high. Within columns, tablets are of rather similar dimensions in the central part but decrease in size at either end to give the lenticular shape ... Columns usually end in a single crystal, although the apparent size of this clearly depends on the relation of the plane of the section to the axis of the column. Adjoining columns vary in width sympathetically and form a solid structure.

They also found that lenticular nacre is best developed in the *outer* nacre of pelecypods having two distinct nacreous layers. In Textfigure 1, which shows a radial fracture section through the nacre of the fresh water clam *Lampsilis ventricosa*, the structure is developed in an irregular columnar pattern which in places exhibits indications of a "lenticular" pattern (Textfig. 2). Although the lenticular nature of the pattern is not consistently developed throughout the layer, it is apparent that some planes of weakness in the vertical direction do exist which influence the trend of the fracture. These planes of weakness probably reflect coincidences in the vertical direction of boundaries of the tabular crystals in successive mineral laminae. In pelecypods this occurs on a limited scale because of a tendency for new crystals to be deposited on top of previously formed crystals of the underlying laminae (a phenomenon noted by BEVELANDER & NAKAHARA, 1969). A weakly developed *Treppen* pattern might also give a lenticular appearance to fractured and etched sections of various orientations. The most important detail to note on the fracture surface through the *Lampsilis* shell is that the fracture passes indiscriminately through as well as around individual tabular crystals (Text fig. 3) in the same manner that fractures do through *Backsteinbau*.

Six-sided crystals are the most common euhedral forms in pelecypod nacre. On the growth surface these merge along their prism and lateral faces to form mineral laminae. Outlines of mature crystals are seen in the laminae of *Mytilus edulis* (LINNÉ) exposed by a fracture (Pl. II, Fig. 3). These crystals also show concentric bands which possibly represent periodic growth increments of a daily or diurnal cycle. Growth







Figs. 1–3 *Lampsilis ventricosa* (pelecypod), radial fracture through nacreous layer.
Fig. 1 Crudely developed vertical structures within the "lenticular nacre" alternate with sublayers of *Treppen* and *Backsteinbau*. × 110.
Fig. 2 Some of the vertical structures exhibit a tapered or "lenticular" appearance. ×470.
Fig. 3 Detail from Figure 1 (above). The fracture surface passes through as well as around individual tabular crystals and leaves the surface of the vertical features relatively smoothly sculptured. ×2550.

bands have also been observed on the growth surface of *Pinna carnea* GMELIN (Pl.II, Figs. 4 and 5). These indicate that the growth of the tabular crystals of nacre is both uniform and concentric. Because the overgrowths are uniform, each individual crystal behaves as a coherent optical unit [2]).

Considerable discussion has arisen in the literature over the possible existence of *intra*crystalline membranes within individual tabular crystals (WATABE, 1963, 1965; TOWE & HAMILTON, 1968a, 1968b). On the basis of the evidence in Plate II, Figure 3, it has been suggested that the presence of intracrystalline conchiolin may be attributed, at least in part, to growth banding of crystals. It is interesting to note that in MUTVEI's diagrammatic representation of crystals in nautiloid cephalopods and gastropods (MUTVEI, 1969, Fig. 1), the intracrystalline membranes and vertical conchiolin accumulations are disposed more or less concentrically near the margins of the crystals. Some of the more prominent growth bands in Plate II, Figure 3 are also developed in this fashion. On the other hand, the growth bands in *Pinna* (Pl. II, Fig. 5) are spaced evenly, $^1/_2$–1 μ apart. Because the growth bands parallel the geometric outlines of the orthorhombic crystals, it is unlikely that any accumalations of conchiolin associated with the bands (if such accumulations do exist) are anything more than either 1. residual accumulations of conchiolin settled from the extrapallial fluid during periods of non-deposition, or 2. material pushed ahead of the advancing mineral front during active growth (BEVELANDER & NAKAHARA [1969] have detected particulate organic matter suspended in the extrapallial fluid surrounding growing crystals).

Also shown in Plate II, Figure 4 is an unusual row pattern which is superimposed on the imbricate growth surface configuration of the nacre of pelecypods of the family Pinnidae (SCHMIDT, 1923). Crystals merge end-to-end to form long strips; new crystals are spaced along the tops of the strips while at depth the strips merge laterally to form the broad laminae which characterize nacreous structure. Such strips of crystals will be called "row-stacks" in this report.

3.12 Crystal stacks in Gastropod nacre.

Because the imbricate growth surface pattern of pelecypods has been reported in the literature by numerous light and transmission microscopists, WISE & HAY (1968b) were somewhat surprised to find the configuration shown in Plate III, Figure 1 developed over the nacre of the gastropod *Cittarium pica* (LINNÉ). This topography, which is reminiscent of a lollobrigidian landscape, is formed by the deposition of crystals in tall vertical stacks. New crystals form at the tops of the stacks and expand laterally with growth as more crystals are deposited on top, thus maintaining the conical shapes of the stacks (WISE & HAY, 1968b). As seen in Plate III, Figure 2, lateral growth brings crystals near the bottoms of adjacent stacks into contact. At this point the manner in which the laminae are formed becomes apparent. Very precisely, crystals at the

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[2]) The word "crystal" is used quite loosely throughout this discussion to denote the smallest crystalline units which can be discerned in a given structure by scanning electron microscopy. It is assumed that each such unit arises from a single nucleation site and maintains optical continuity throughout its growth. For a complete discussion of the meaning of the word "crystal" as it applies to electron microscopy of organically deposited crystalline material, see TOWE & CIFFELI (1967).

same level in adjacent stacks contact and merge laterally to form continuous sheets of crystals which, when completed, are indistinguishable from those observed in pelecypods. Often crystals contact in a staggered sequence (center, Pl. III, Fig. 2) assuring a tighter bond between stacks and adding strength to the structure.

Crystal stacks cover the entire growth surface of the nacre of gastropods and give it a granular appearance when viewed at low magnification (Pl. III, Fig. 3). The density of stacks is normally between twenty and thirty thousand stacks per square millimeter of growth surface area.

It is reasonable to assume that some form of organic control is responsible for the precision by which crystals in countless stacks over the growth surface merge evenly to form broad continuous mineral laminae. WISE & HAY (1968b) did observe poorly preserved organic membranes on the growth surface of the gastropod *Cittarium pica*. However, the model of calcification proposed by TSUJII et al. (1958), which so well explains crystal formation in the calcitostracum of *Crassostrea virginica*, could not readily be applied to explain the formation of nacre in gastropods. Instead of seed crystals being nucleated at random over an expansive organic membrane as in *Crassostrea*, each site of nucleation in gastropods is precisely positioned at the top of a stack. However, in view of the fact that nacre differs from calcitostracum in both mineralogy and structure[3]), it is not surprising that the mechanics of calcification may differ somewhat in the two systems.

A major breakthrough in understanding the mechanism of calcification in pelecypod nacre was achieved by BEVELANDER & NAKAHARA (1969) who demonstrated the relationship between the organic matrices and the developing aragonite crystals as they exist on the growth surface during calcification. Their sectioned material shows the mantle, the pallial space, and the inner part of the nacre in their normal relationship. It is apparent that the organic matrices separating the imbricated mineral laminae are elaborated over the growth surface in advance of mineralization. Within the "compartments" formed by the organic matrices, the proper environment for crystallization is established, and crystal nucleation occurs. In pelecypods the nucleation sites appear to be distributed at random within the compartments except that "the formation of new crystals occurs in contact with, or in close proximity to, a formed crystal in an adjacent layer separated only by a 'perforated' lamella. This situation suggests an induction mechanism" (BEVELANDER & NAKAHARA, 1969, p. 91).

It is quite easy to envision a similar model of calcification for gastropod nacre. A succession of "compartments" would be formed over the growth surface by organic matrices; the last formed compartments would be suspended in the pallial fluid above the tops of the crystal stacks. The "induction mechanism" (the nature of which is presently unknown) would pinpoint the sites of nucleation at the tops of the stacks. Crystals would expand laterally with growth, and all crystals within the same compartment would eventually merge to form a continuous mineral lamina. In support of this hypothesis, WISE (1970) determined that in gastropods, multiple membranes are present on the growth surface and that they are disposed horizontally.

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[3]) Nacre is aragonite and has a more regular laminar structure than calcitostracum (BØGGILD, 1930). Calcitostracum is calcitic and organic matrices occur infrequently, only between every thirty or so calcite laminae (WATABE & WILBUR, 1961).

Two possible mechanisms that may influence or control the formation of crystals in stacks have been suggested to this writer by persons who have examined the micrograph shown in Plate III, Figure 1. Prof. FERNANDEZ MORAN and Dr. JOHAN DE VILLIERS both suggested independently (1969, personal communication) that a screw dislocation mechanism may be involved in the development of the stacks. Dr. HANS J. HANSEN (1970, personal communication) suggested that each individual stack may be secreted by a single cell of the mantle epithelium. Although an assessment of these ideas is beyond the scope of this paper, both suggestions merit further investigation.

In order to observe the mineral structure of the growth surface in gastropods, the organic lamellae must be stripped away with cellulose acetate peels (WISE & HAY, 1968b). All specimens shown in Plate III were prepared in this manner. In Plate IV, Figure 1, however, only the topmost lamellae have been stripped away, and more organic membranes are exposed beneath. Only the tops of the crystal stacks are visible, and the spaces between are covered by horizontal organic sheets.

Developing crystals of gastropod nacre are sometimes elongated in various directions (Pl. IV, Fig. 2), the only consistency being that the direction of elongation appears to be constant within any given stack. However, no preferential direction exists between stacks. Six-sided euhedral crystals have been observed in *Astrea caelata* (GMELIN) (Pl. IV, Fig. 3), and the direction of elongation in these crystals is also constant within a given stack, but random between stacks. Thus it appears that the anhedral crystals are elongated along a definite crystallographic direction, and that this direction is *not* constant over the growth surface as it is in pelecypods (compare Pl. IV, Figs. 2, 3 with Pl. I, Fig. 1). This suggests that in gastropods, an inductive mechanism not only controls the site of nucleation, but also the crystallographic orientation of the crystal anlages. Apparently the individual stacks are so isolated during growth that neither control by the organic matrix nor the influence of neighboring crystals is sufficient to maintain a uniform alignment of crystals over the growth surface.

In most pelecypods, the random distribution of new crystals at the margins of the mineral laminae produces a random or irregular vertical distribution of crystals in the mature nacre. However, in gastropods, the formation of crystals in tall vertical stacks produces a most conspicuous vertical distribution of crystals throughout the layer. In fractures intersecting the growth surface of *Cittarium pica* (Pl. IV, Figs. 4, 5), individual stacks can be traced from the growth surface directly down into the mature nacre. The columnar arrays of crystals give the nacre a pseudoprismatic appearance in cross section which obscures the horizontal layering of the mineral laminae. The fundamental horizontal lamination of nacre is always present in gastropod mother-of-pearl, and is evidenced by the specimen of *Haliotis* in Plate IV, Figure 6. The stacks have been completely removed from the inner surface by abrasion, and on the eroded upper surface several horizontal laminae of mature nacre are exposed. The crystals which form the laminae have merged just as evenly as those forming pelecypod nacre; however, the positions of the stacks are still visible on the fracture surface (lower portion of the figure).

Crystal stacks are visible throughout the nacre of gastropods and no other pattern has been observed in the species studied. These include *Haliotis rufescens* SWAINSON, *Astraea americana* GMELIN, *A. caelata* (GMELIN), *Turbo castanea*, *Cittarium pica*, *Tegula funebralis* A. ADAMS, *Margarites pupillus* GOULD, *Callistoma ligatum* GOULD, and *Norrisia norrisi* SOWERBY.

The vertical fracture in Plate V, Figure 1 exposes the entire thickness of the shell of *Tegula funebralis*. The nacre is the thickest layer, bounded on top by a thin inner layer and by a massive distal layer below. The stacks are nearly straight, but may curve slightly. Individual stacks may persist long distances through the layer. One stack in Plate V, Figure 2 can be traced from the bottom of the figure to a point near the center where it bifurcates; the two stacks can then be traced continuously to the top of the figure, a total distance of about 350 μ.

Vertical fractures through gastropod nacre follow the planes of weakness offered by the boundaries of the stacks. Adjacent stacks tend to "pull apart" rather than shatter; perhaps this parting is aided by the presence of the thick "vertical conchiolin accumulations" MUTVEI (1964, 1969) observed at the crystal margins. By contrast, vertical fractures through pelecypod nacre pass indiscriminately through as well as around individual crystals. Because stack boundaries serve as a plane of reference for the passage of vertical fractures, the position of each stack is clearly delineated on fracture surfaces (Pl. V, Figs. 3, 4; Pl. VI, Figs. 1, 2). Because the stacks are essentially cylindrical, it does not matter how the fractures are oriented with respect to the rest of the shell as long as they are perpendicular to the horizontal laminae. Therefore, in the SEM vertical fractures through gastropod nacre are readily distinguished from those through pelecypod nacre constructed in the *Backsteinbau*, *Treppen*, and lenticular patterns.

The parting of crystals of gastropod nacre along stack boundaries leaves gaps which alternate with the crystals on the fracture surface (Pl. V, Fig. 4). This is particularly noticeable where crystals of adjacent stacks have merged in an interlocking sequence (as seen in Pl. III, Fig. 2). Thus the surface of the fracture is not smoothly scalloped as is the fracture through the *Lampsilis* shell (Text fig. 3).

In gastropods, stack boundaries also stand out sharply on etched sections cut parallel to their lengths. The micrographs of *Haliotis rufescens* (Pl. VI, Figs. 3, 4) display the offset pattern of interlocking crystal margins. Judging from these figures, it appears that the section published by WADA (1961, Fig. 34) of the nacre of *Turbo colnutus* shows such a boundary intersected at a slightly oblique angle.

Although the structure of gastropod nacre (particularly the growth surface configuration) was not well known before the advent of scanning electron microscopy, a survey of the literature reveals that WILLIAM CARPENTER (1848) did observe certain gross aspects of the layer. CARPENTER was one of the first light microscopists to systematically survey molluscan shell structures. He noted in the nacreous layer of *Haliotis* indications of a cellular structure which he had not observed in bivalve nacre. His interpretation of the structure is given in a composite diagram (Pl. VII, Fig. 1) in which *a* is the appearance "which the cells present when the section passes through them transversely; at *b* the section has traversed them obliquely; and at *c* are shown their natural terminations, where they crop out upon the surface of the shell" (CARPENTER, 1848, p. 115; Pl. XIII, Fig. 56). The diameter of the cells was reported to be not more than one five thousandth of an inch (i.e., 5 μ), and they were also observed in the nacre of the gastropods *Turbo*, *Trochus*, and *Delphinula*.

CARPENTER could not resolve individual crystals in the cellular units, but in every other respect his descriptions fit those of the stacks shown in the present report. Unfortunately CARPENTER's constant reference to the word "cell" in describing the units denotes his basic misunderstanding of their significance. He believed, as did several other investigators of his time (BOWERBANK, 1844; QUEKETT, 1854; WOODWARD, 1866), that shell formation occurred through the mineralization of tissue cells which were dispersed over the inner shell surface and calcified in place[4]). Cell nuclei were even reported in the large prisms of the pelecypod *Pinna* (CARPENTER, 1844). The result was that while later investigators did sometimes note the presence of vertical lineations in gastropod nacre (FRANK, 1914), little or no consideration was given CARPENTER's discovery. BØGGILD's comment revealed his confusion on reading CARPENTER's account: "A description of the shell of *Haliotis* has been given by CARPENTER (1847, p. 115). I must confine myself to a reference to this description as I have not been able to find the horny plates mentioned or the different forms of 'cells' described and drawn" (BØGGILD, 1930, p. 300).

AHRBERG (1935), a student of W. J. SCHMIDT, was able to resolve the individual crystals forming gastropod nacre and did perceive the presence of vertical stacks of crystals in thin sections. These he illustrated by figures and excellent light micrographs. He also photographed crystal stacks on the growth surface of *Trochus adriaticus* (AHRBERG, 1935, Pl. I, Fig. 3), but lacking sufficient resolving power and depth of field, he erroneously interpreted these stacks as being single crystals scattered about the growth surface. Working with museum specimens which apparently had been worn, damaged, or eroded, he thought he detected imbricated mineral laminae on the growth surface similar to those observed in pelecypods (AHRBERG, 1935, Pl. II, Figs. 8–13). He concluded that the mode of calcification in gastropods is essentially the same as that observed by SCHMIDT (1923) in pelecypods, i.e., the deposition and coalescence of crystals along the margins of the imbricated *Elementarlamellen*.

AHRBERG's descriptions are complicated by the fact that he included photographs from the innermost shell layer of *Trochus adriaticus* which he considered to be a second layer of nacre. Although the inner layer of prosobranch gastropod shells often does have a pearly luster, it is not necessarily nacre. For instance, the thin pearly veneer inside the shell of *Cittarium pica* has a prismatic structure (WISE & HAY, 1968b). The inner layer of *Turbo castanea* has an analogous structure, but is thicker and has a scattering of large crystals over the growth surface (WISE, 1968, unpublished) which are similar to those shown by AHRBERG in his figures 5 and 6 on Plate II (AHRBERG, 1935). No two-fold division of the nacreous layer such as that found in the pelecypods *Nucula* (SCHMIDT, 1922) and *Margaritana* (RUBBEL, 1911) exists in gastropods.

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[4]) The origin of this general theory of shell calcification is revealed in the following comment by WOODWARD (1866, p. 250): "Drs. BOWERBANK and CARPENTER have advocated the views taken by botanists and anatomists, namely that the hard tissues of shells are formed by deposits of lime in cells, or upon layers of membrane ... We have every reason to believe that the cells are formed *first*, and then that lime is deposited in them afterwards, just as the hard tissues of seed-vessels, the albumen of the vegetable ivory, and the silicious cuticle of grain is formed." This theory persisted in the literature throughout the nineteenth century, and was advocated as late as 1896 by OGILVIE to explain calcification of stony corals (OGILVIE, 1896).

All of the fractures shown so far in this chapter are vertical fractures, i.e., perpendicular to the horizontal lamination of the nacre. Such fractures are easy to induce in gastropod nacre because they tend to follow the plane of least resistance offered by the stack boundaries. Even when gastropod nacre is pulverized into small particles using a mortar and pestle, fractures tend to pass either parallel or perpendicular to the mineral laminae. When fractures do pass obliquely through the laminar structure (Pl. VII, Fig. 2), each consecutive lamina is exposed sequentially, so that it is impossible to detect the vertical structure of the crystal stacks. Therefore, it is impossible to distinguish the stacked structure of gastropods from the *Backsteinbau* of pelecypods on the basis of such micrographs (compare Pl. VII, Fig. 2 with: GRÉGOIRE, 1957, Fig. 20; WADA, 1957b, Fig. 15; WADA, 1961, Fig. 39). Other differences do exist, however, namely the orientation of the *a* and *b* crystallographic axes of the tabular crystals composing the laminae. As noted both visually and optically (WADA, 1961; Pl. I, Fig. 1 this report), these crystallographic axes are closely aligned in pelecypod nacre. This alignment has also been noted in X-ray diffraction patterns (Laue photographs) produced by thin sections 0.2–1.0 mm thick cut parallel to the lamination of the nacre (WADA, 1961). Because the *c* axes of the aragonite crystals are perpendicular to their tabular face, specimens irradiated perpendicular to the plane of the mineral laminae give X-ray patterns representing the *a* and *b* lattice planes. WADA's data was confirmed by undistorted lattice images (Pl. VII, Fig. 3) obtained by irradiating thin plates of nacre from the pelecypod *Pinctada radiata* using the precession camera. The discreteness of the spots (Pl. VII, Fig. 3) indicates an alignment of *a* and *b* axes within about 35 degrees.

WADA (1961) obtained, with some difficulty and no degree of consistency, X-ray patterns from *Haliotis* and *Turbo* which he interpreted as indicating a tendency for the tabular crystals of gastropod nacre to align in a manner similar to those of pelecypod nacre. Visual observations using the SEM (Pl. IV, Figs. 2, 3) indicate that no such alignment exists, and X-ray diffraction patterns using the precession method support these observations (Pl. VII, Fig. 4). The continuous circular rings indicate a random orientation of the tabular crystals. The pattern shown is from a sample of *Cittarium pica* 300 μ thick. Identical patterns have been obtained from samples of *Haliotis rufescens* 150 μ thick. When the sample in Figure 4 was rotated 90 degrees and irradiated perpendicular to the *c* axes, the expected pattern indicating the parallel alignment of the *c* axes was obtained (Pl. VII, Fig. 5), thus proving the consistency of the method.

These results show differences within the microarchitecture of the mineral elements of gastropod and pelecypod nacre which are just as striking as those detected in structures of the organic matrices. At least two groups of pelecypods, however, do show a reasonably well ordered vertical pattern within the nacre. The similarities and differences between these structures and the crystal stacks of gastropod nacre will now be discussed.

3.13 Vertikalschichtung in pelecypod nacre

It was noted in Plate II, Figure 4 that crystals on the growth surface of *Pinna* are arranged in a series of parallel row-stacks which SCHMIDT (1923) found to be singularly characteristic of the group. The large euhedral crystals in the *Pinna* shells were first observed by ROSE (1858) and later by SCHMIDT (1923), who described in great detail the many crystal forms which occur on a single specimen. SCHMIDT (1923) and WADA (1961) noted that in the narrow transition zone where the myostracum deposited by the adductor muscle overrides the nacre, crystals of the row-stacks are very large and are stacked to heights of six to eight crystals or more. The transition zone of *Pinna carnea* GMELIN is shown in Plate VII, Figure 6. Toward the myostracum (M), the row-stacks become progressively larger in size. They are eventually covered by a smooth deposit of myostracum, and the boundaries between row-stacks are obliterated. A close-up of the area bounded by the white rectangle shows the exaggerated stacking which occurs within the transition zone (Pl. VIII, Fig. 1). These stacks differ from those in gastropods by their large size (up to 80μm long and 40μm wide), elongated outlines, and parallel orientation. Vertical fracture sections oriented perpendicular to the row-stacks (Pl. VIII, Figs. 2, 3) show the vertical alignment of crystals in successive laminae (*Vertikalschichtung*) described and figured by SCHMIDT (1923). The vertical persistence of the row-stacks is evident both in the vertical portion of the fracture and also in the shallow oblique portion in the foreground of Figure 2. Fractures parallel to the row-stack structure do not show *Vertikalschichtung* because crystals are distributed more randomly up and down the rows (this may explain why TAYLOR et al. [1969] did not observe *Vertikalschichtung* in the *Pinna* shells they studied).

The other pelecypod in which SCHMIDT (1922, 1923) found *Vertikalschichtung* is *Nucula*. The outer layer has composite prismatic structure (BØGGILD, 1930) and the inner layer is nacre which, on the growth surface, is divided into an inner and outer sublayer by the pallial line. The growth surface pattern of the inner nacre is like that of the inner portion of *Pinctada*, replete with growth spirals (see WADA, 1961, 1966). SCHMIDT (1922) found that the *Vertikalschichtung* is developed in the outer nacre; however, his examination of the inner surface revealed no pattern other than the imbricate pattern seen in other pelecypods .This pattern is seen in Plate VIII, Figure 4. This is a view of the outer sublayer of the nacre of *Nucula proxima* SAY as it appears viewed toward the ventral margin of the shell. The crenulated or ribbed margin of the shell is seen at the top of the figure. Arrow D indicates the dorsal direction. The most striking feature immediately apparent is that the imbricate mineral laminae overlap toward the dorsum, just opposite from those of other pelecypods studied (compare with micrographs which show the ventral margin of the nacre in *Pinctada*, e.g., WADA, 1961, Fig. 12; WISE, 1969c, Figs. 1, 2). In *Nucula*, then, the primary zone of accretion for the outer nacre is in the ribbed area. There laminae form and then grow inward toward the dorsum until they are overridden by the myostracum at the pallial line. In *Pinctada*, the primary zone of accretion is in the dorsal portion of the nacre where laminae form in the complex system of growth pyramids. Along the ventral margin of the layer, the laminae grow outwards in the ventral direction along parallel growth fronts.

The nacre between the ribs in Fig. 4 appears granular. Turning the specimen around and viewing the area between two ribs where the nacre meets the composite prismatic layer (Pl. VIII, Fig. 5, dorsal direction indicated by arrow), it is apparent that the granularity is produced by crude stacks three to four crystals high. Such stacks are prevalent in the ribbed area of some specimens but nearly lacking in others. Plate IX, Figure 1 shows particularly well-developed stacks in the area just dorsal to the ribs in another specimen. These crystals are elongated and aligned in row-stacks. The rows are parallel to the ventral margin. Their development is similar to the row-stacks in *Pinna*, although they are certainly not as strictly aligned. The parallel orientation and elongation of the crystals differentiate them from the crystal stacks of gastropods.

Radial fractures through the shell pass through the row structure at a right angle and show the *Vertikalschichtung* where it is developed. Plate IX, Figure 2 is a radial fracture through the entire thickness of the shell of *Nucula proxima* showing 1. irregular parting through the inner nacre (*Backsteinbau*, upper portion of figure), 2. columnar stacking in the outer nacre (*Vertikalschichtung*, upper center), 3. folded laminae marking the position of a rib, and 4. the composite prismatic layer below. The crystals of the stacks of the outer nacre are smoothly fractured and are about 10 μ wide (Pl. IX, Fig. 3).

The account of the structure of *Nucula* given by Taylor et al. (1969) agrees closely with that given in Schmidt (1923) and the present report. However, because the columnar development in the outer nacre is more regular and persistent in *Nucula* than in the Unionacea, Schmidt's designation of the structure in *Nucula* as *Vertikalschichtung* seems appropriate for purposes of description and is followed in this report. The "lenticular" nature of the structure indicated by Plate 11, Figure 5 of Taylor et al. (1969) occurs where the columns of crystals bend out of the plane of the section. The diminution in size of the crystals at the extremities of the "lenses," therefore, is an apparent phenomenon and not an actual feature of the structure.

3.2 Microarchitecture of nacre in cephalopods

The microarchitecture of the nacre of the pearly *Nautilus* has been well studied and known for many years. Carpenter noticed that it had a markedly "cellular" appearance, "the cells being very minute, and bearing a strong resemblance to those of the nacreous layer in *Haliotis* and *Turbo*" (Carpenter, 1848, p. 116). It was later recognized that the prismatic appearance of the nacre in vertical cross section was due to the columnar stacking of crystals in successive laminae, and this has been observed on many occasions in the Recent *Nautilus* (Nathusius-Königsborn, 1877; Biedermann, 1902; Schmidt, 1924; Ahrberg, 1935; Grégoire, 1962; Mutvei, 1964, 1969; Stenzel, 1964; Erben et al., 1968, 1969; Wise, 1969c). Crystal stacking has also been observed in fossil ammonoids (Grégoire, 1966; Mutvei, 1967; Erben et al., 1969). In vertical fracture section, stacks in the nacre of *Nautilus* resemble those in gastropods (Pl. IX, Fig. 4, upper layer), and one might expect to find the same arrangement of conical stacks on the growth surface as well. Unfortunately, satisfactory observations have never been made of the growth surface of the nacreous layer of the outer shell wall. This growth surface is located along the apertural margin of the living chamber. However, as Mutvei (1964) pointed out, in adult specimens it is covered by a deposit of semi-prismatic material; therefore, if true stacks of nacre are present there, they are buried. Deposits of semi-prismatic material have frustrated attempts to observe stacks in this region. In one specimen studied, however, a fracture through the outer shell wall did reveal ledges in the nacre where the stacks are not only well defined, but are somewhat isolated because the tabular crystals did not completely merge into continuous laminae (Pl. IX, Fig. 5; Pl. X, Fig. 1). Viewing the ledge from above (Pl. X, Fig. 2), the crystals appear discrete and euhedral.

Another possible growth surface to search for crystal stacks is along the dorsal surface of the living chamber where nacre is deposited on the black organic mat which coats the outer surface of the previous whorl. On the specimens available for study, the crystals are formed in stacked aggregates, but their edges appear ragged and may have been etched after the death of the animal (Pl. X, Fig. 3). The concave surface of the penultimate and earlier formed septa may be covered by euhedral crystals in aligned or non-aligned orientations (GRÉGOIRE, 1962; WISE, 1969 c); however, no septa have been observed which were in the process of being formed at the time the animal was collected. The orientations of the last formed crystals on mature septal surfaces (Pl. X, Fig. 4) may not necessarily reflect the true growth surface configuration during active calcification. Therefore, at the present time a valid comparison cannot be made between cephalopods and other classes of molluscs as far as the growth surface configuration and mode of formation of the nacre are concerned. Although the development of a prominent stacked structure is evident in the mature nacre, it is not possible to say whether tall vertical stacks, row-stacks, or another type of stack characterizes the various growth surfaces of *Nautilus*.

X-ray data do reveal one fundamental difference between gastropod and cephalopod nacre. Despite the non-oriented appearance of the immature crystals seen on the ledge in Plate X, Figure 2, samples of mature nacre from the outer shell wall consistently show a parallel alignment of *a* and *b* axes (Pl. X, Fig. 5). This is not surprising in view of the fact that the intrabecular areas ("pores") in the organic matrices of cephalopods are elongated ellipses aligned in the same general direction (GRÉGOIRE et al., 1950, 1954; MUTVEI, 1969). GRÉGOIRE found that the ellipses tend to be aligned in the direction of the *a* axes of the tabular crystals (GRÉGOIRE, 1962).

Basic data concerning the mode of formation and the internal structural patterns in the nacre of pelecypods, gastropods, and cephalopods are summarized in Table 1. This includes observations recorded in the present study and data gathered from literature sources such as SCHMIDT, 1923; WADA, 1961; MUTVEI, 1964, 1969; GRÉGOIRE, 1966; TOWE & HAMILTON, 1968a; ERBEN et al., 1969; TAYLOR et al., 1969. Taxonomic names given in footnote *a* are those originally used by the authors cited.

3.3 Possible significance of microarchitectural variations to phylogeny and functional morphology

The consistent development of well ordered crystal stacks which persist throughout the nacreous layer in gastropods and cephalopods and the near absence or incomplete development of this phenomenon in pelecypods is striking. Two possible explanations are offered to account for this disparity: 1. stacking represents a relatively primitive condition in gastropods and cephalopods which has been lost by most pelecypods in their evolution of a new (bivalve) shell form; 2. the stacked mode of deposition is functionally advantageous in calcifying shells with limited growth surface areas because it allows more crystals to form and develop on the growth surface at one time.

Table 1. Comparison of mode of formation and internal structure pattern of nacre in pelecypods, gastropods and cephalopods.

	PELECYPODS		GASTROPODS	CEPHALOPODS[b]
	PINNIDAE NUCULA	OTHER PELECYPODS[a]		
GROWTH SURFACE CONFIGURATION	imbricate laminae row stacks	imbricate laminae	tall conical crystal stacks	crystal stacks?
VERTICAL PATTERN IN MATURE NACRE	Backsteinbau Vertikal-schichtung	Backsteinbau Treppen "lenticular nacre"[c]	cylindrical crystal stacks	cylindrical crystal stacks
ALIGNMENT OF *a* AND *b* AXES OF TABULAR CRYSTALS	parallel	parallel	random	parallel

[a] Included in this category are: *Unio tuberculatus, U. grayanus, U. ambiguus, U. complanatus, Anodonta anserian, A. angulata, A. castelnaudi, Margaritana margaritifera, M. complanata, Barbula plicatula, Hyria subviridis, Pleiodon ovatus, Pandora trilineata, P. higgensoni, Avicula radiata, Meleagrina margaritifera, Crenatula undata, Malleus vulgaris, Mytilus (edulis) galloprovincialis, M. smaragdinus, M. dunkeri* (Schmidt, 1923); *Hyriopsis schlegeli, Quadrula undata, Unio margaritifera, Pinctada margaritifera, P. martensii* (Wada, 1961); *Elliptio complanatus, Brachidontes recurvus* (Towe & Hamilton, 1968a); *Pinctada* sp., *Mytilus edulis, Anodonta* sp. (Mutvei, 1969); *Amblema costata, Pinctada radiata, Lampsilis ventricosa* (present study); see also Tables 6, 7, and 15 of Taylor et al. (1969) for lists of additional species.

[b] Only cephalopods having an external shell are considered.

[c] Applied here only to members of the order Unionacea.

The first hypothesis is supported by the fact that crystal stacks are present in the most primitive class of molluscs having a nacreous layer, the monoplacophorids (Erben et al., 1968). The crystal stacks of *Pilina unguis* are similar to those of gastropods and cephalopods except that the tabular crystals are larger. Unfortunately, in the only surviving genus of this Class (*Neopilina*), the nacre is so thin that published photographs of the layer (Schmidt, 1959; Erben et al., 1968) fail to reveal evidence of stacking.

It should be noted that the presence of stacks in the nacre of the prosobranch gastropods is in keeping with the low taxonomic position assigned that group within the Gastropoda. As a corollary of the first hypothesis, it may also be said that the stacked mode of deposition in both gastropods and cephalopods indicates a relatively close taxonomic link between the two classes. This contention is supported on geologic and paleontologic grounds by EASTON (1960, p. 427) who relates that "it is generally believed that cephalopods arose from some gastropodlike molluscan ancestor, within or near the gastropods, although no intermediate stages are known, either living or extinct." These phylogenetic relationships have also been constructed independently by DEGENS and his associates who used a computer to draw up a phylogenetic tree of the Mollusca (DEGENS et al., 1967). They analyzed the amino acid sequences in the organic matrices of shells and used factor analysis to determine evolutionary trends in evolving proteins. According to their analysis, the pelecypods branch off early from the primitive stock while the gastropod and cephalopod lineages divide at a later time.

Among living pelecypods the nuculids are considered the most primitive (see DEGENS et al., 1967), and the presence of low conical stacks and row-stacks in their mother-of-pearl layer could be considered a trait held over from a more primitive ancestry. Among the more highly developed pelecypods having mother-of-pearl layers (with the exception of the Pinnidae; see discussion below), the tendency for stacking is less pronounced or absent altogether. A complete transition is seen in the outer nacreous layer beginning with the primitive *Nucula* in which the stacking is pronounced enough to classify as *Vertikalschichtung*. In the Trigonacea (a group considered less primitive than the Nuculacea) the stacks are somewhat less strictly aligned in straight vertical columns (WISE, 1969, unpublished; see also descriptions by SCHMIDT, 1923), while in the Unionacea, the degree of ordering is reduced to the levels of *Treppen*, lenticular nacre, and finally *Backsteinbau*. In *Pinctada*, the entire outer nacre is *Backsteinbau* with only traces of a vertical component (TAYLOR et al., 1969), while in other pelecypods (e.g., *Mytilus edulis*), the outer nacre has atrophied until only a vestige of the layer is left (see WISE, 1969c, Fig. 7). Sufficient data are not available at the present time to allow the construction of evolutionary schemes for pelecypods based in part on the microstructure of the nacre. However, enough indices are available which can be used as tracers (e.g., growth surface configuration; microarchitectural pattern within the layer; number, type, and extent of nacreous layers present in a shell, etc.) to warrant further study of this problem.

On the other hand, it is acknowledged that the Pinnidae cannot be fit readily into any simply constructed evolutionary scheme partially based on shell microstructure. Members of this group have many unique features of structure as well as a specialized mode of life peculiar to themselves (YONGE, 1953). They hold a more highly advanced taxonomic position than the nuculids, and differ from them in having only one discernible nacreous layer on which is developed a more extensive and more strictly aligned system of row-stacks. Because of these differences, it is possible that the development of row-stacks in pen shells is a secondarily acquired characteristic rather than the continuance of a primitive trait.

The analysis of DEGENS et al. (1967) is based on the amino acid content of entire shells. A more rigorous test of the first hypothesis would be a similar analysis based only on protein extracted from the nacreous layer. Unfortunately, very few chemical analyses of any kind have been made on single layers of shells.The results of such analyses, however, could be far more rewarding than those based on whole multi-layered specimens.

The second hypothesis is not incompatible with the first explanation offered, and explains why most pelecypods have evolved a new internal microarchitecture of the nacre while evolving a new shell form. The position and areal extent of the growth surface of the nacre in gastropods and cephalopods[5]) is fundamentally different from the situation developed in pelecypods. A view of the aperture of the gastropod *Cittarium pica* (Pl. X, Fig. 6) shows the growth surfaces of the four layers of the shell. These growth surfaces form narrow bands parallel to the apertural lip. The thin outermost layer of the shell (distal layer, position indicated by arrow D) forms the leading edge of the aperture inside of which is deposited the composite prismatic layer (CP). These two outer layers comprise the pigmented portions of the shell. The growth surface of the nacreous layer (N) forms a light colored band 5–6 mm wide. The innermost layer, the oblique prismatic (OP), is deposited as a thin veneer over the nacre (see Wise & Hay, 1968b for a detailed description of the shell layers of *C. pica*). During shell growth, each layer is extended in the apertural direction at the same rate, and each layer overrides the layer beneath as calcification proceeds. The growth surface of the nacre is never more than a few millimeters wide because as it is extended in the apertural direction, the oblique prismatic layer is extended concurrently. Although the nacre is one of the thickest layers of prosobranch shells (see Pl. V, Fig. 1), its growth surface is relatively narrow. Therefore, deposition must be quite rapid to allow it to be extended in the apertural direction at the same rate as the other layers of the shell. Rapid deposition is facilitated by the deposition of crystals in tall vertical stacks. This not only allows a closer spacing of crystal anlages than is possible on imbricate growth surfaces, it also allows each crystal to expand laterally while more crystals are deposited at the same spot on the growth surface. By this method, fifteen to twenty-five crystals can develop simultaneously in a stack which occupies no more than 100 sq μ of growth surface area. This is several times the number of crystals which can develop within the same amount of area on the imbricate growth surface of pelecypods. Compare the number of crystals developing on the growth surface of the gastropod *Turbo castanea* (Pl. IV, Fig. 2) and the pelecypod *Pinctada radiata* (Pl. I, Fig. 1). Both figures are printed at nearly the same magnification. Assuming there are 17 crystals in each stack in *Turbo*, and correcting for the difference in magnification between the photographs, the ratio of crystals (gastropod to pelecypod) is 4:1. Text figure 4 also allows an appreciation of the rate at which nacre accumulates in gastropods. This micrograph shows the leading edge of the growth surface of the nacre (right) at the boundary along which it overrides the distal layer. Note how quickly the stacks are built up. The rise in slope to the right indicates a rapid accumulation of nacre.

The fact that many more crystals can be deposited on the growth surface of gastropod nacre explains why such a thick layer of nacre can be formed within such a narrow growth surface area. It is assumed that a similar mechanism would operate to form the outer shell wall of cephalopods.

In pelecypods the growth surface of the nacre usually covers the entire innermost portion of the shell (e.g., *Pinctada*). The thickness of the layer is augmented throughout the life of the animal, so that there is no need for the entire layer to be deposited

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[5]) For purposes of the present discussion, only the outer shell wall of cephalopods having an external shell is considered.

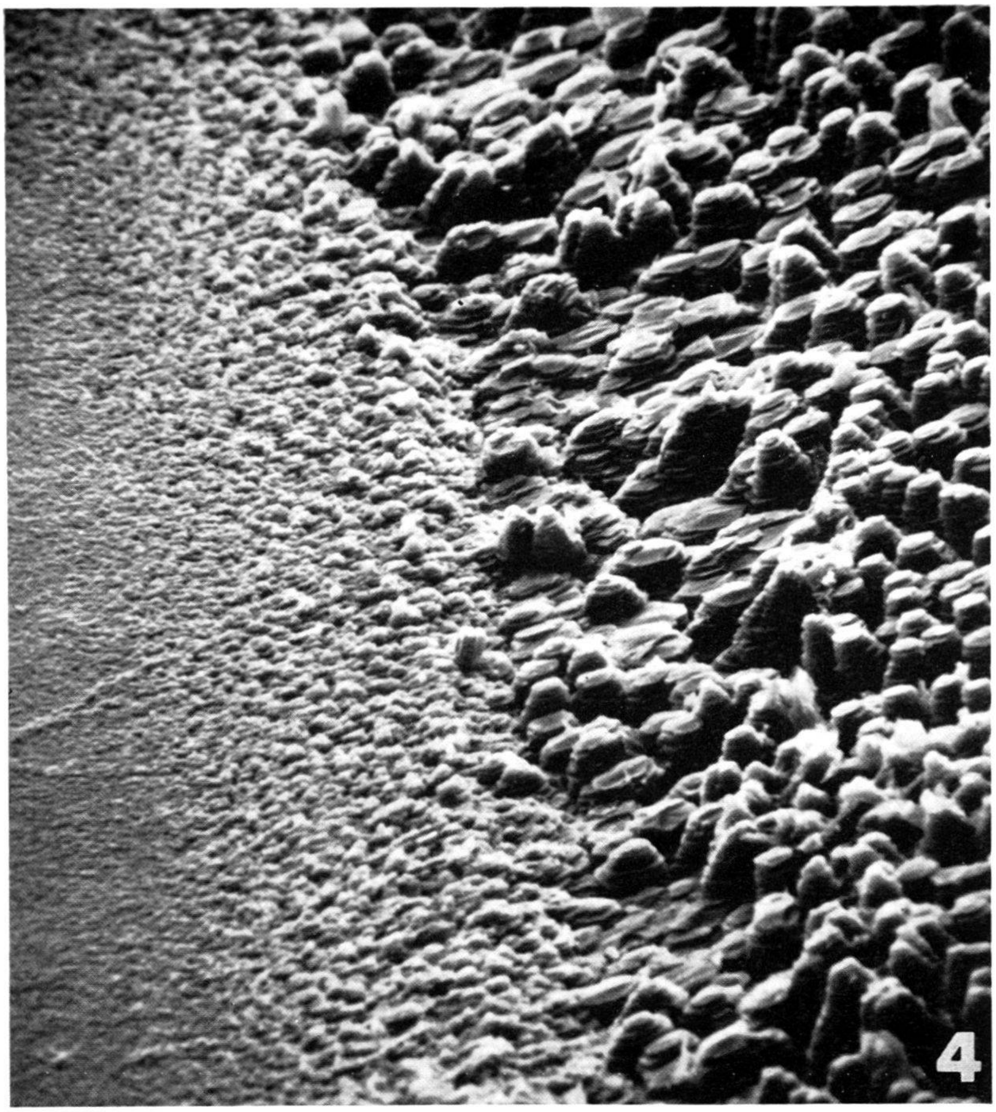

Fig. 4. *Turbo castanea* (gastropod). Inner shell surface showing growth surface of nacre (right) at boundary along which it overrides distal layer (left). Although some stacks of nacre were removed when the specimen was stripped with acetate peels, it is evident how quickly nacre builds up from incipient crystals (center of figure) to fully developed stacks (right). The rise in slope of the surface toward the right also indicates rapid accumulation of nacre. × 950.

within a narrow growth zone. Therefore the stacked mode of growth is not necessary and a structure can be fashioned which will give more strength to the layer. The "running bond" pattern of the *Backsteinbau* has no planes of weakness in the vertical direction and would tend to resist crushing or hammering blows directed against the exterior of the shell. Thus it is well suited to line the saucer shaped shells of pelecypods which live in high energy environments, e.g., *Mytilus*, *Pinctada*, *Unio*, *Amblema*, etc.

The low conical stacks and row-stacks in *Nucula*, when developed, form along the outer nacre in a zone of rapid mineral deposition. Their usefulness in this region is analogous to that of the high conical stacks in gastropods. For this reason it is suggested that the stacks in *Nucula* represent a primitive trait retained in modified form to fulfill a specialized function. As noted above, this trait is lost by degrees in more highly advanced pelecypods although it is maintained in some form wherever a thick outer nacreous layer is found. TAYLOR et al. (1969) noted that all of the features they described under the term lenticular nacre represent growth normal to the marginal area. Even the "lenticular" nacre observed in the Unionacea, therefore, can be considered functionally reminiscent of the *Vertikalschichtung* in *Nucula* despite the fact that the regularity of the lenticular structure has been much reduced during evolution.

Pelecypods which have lost totally or in part the ability to calcify shell efficiently and rapidly utilizing the stack mode of crystal formation compensate for this loss by developing other mechanisms of calcification. In the nacre of *Pinctada*, as in the inner nacre of *Nucula*, the zone of highest accretion is at the site of growth pyramids (WADA, 1966). Growth pyramids, therefore, provide a mechanism for a more rapid accumulation of nacre in pelecypods where the ability to form stacks has been sacrificed during the evolution of a new shell form.

It is interesting to note that in the evolution of more advanced forms of pelecypods, the aragonite mother-of-pearl layer has been replaced by the calcitic foliated layer (calcitostracum) (NEWELL, 1954). Animals secreting calcitostracum form multiple laminae between each secretion of organic matrix (TSUJII et al., 1967; WATABE & WILBUR, 1961), and in so doing, increase the rate at which they can calcify the shell. The efficiency of this mode of calcification is evidenced by *Ostrea titan* and *Ostrea gravitesta* (Late Miocene) which attained lengths of 60 cm (EASTON, 1960).

Although gastropods, cephalopods, and nuculid pelecypods appear to derive a definite functional advantage from the formation of stacked structures in the nacre, the presence of row-stacks in the Pinnidae remains an enigma. The nacre in *Pinna* is much reduced in area, and forms only a thin deposit within the visceral region of the shell. The prevalence of euhedral crystals suggests a slow rate of calcification (WADA, 1961), indicating little need for a stacked structure. Perhaps a different advantage exists which is not apparent at the present time.

The data presented in this report are based in part on some of the early studies of mollusc shells made with the aid of the scanning electron microscope. It is hoped that as more data become available as a result of investigations utilizing this instrument, closer correlations can be made between 1. modes of calcification and microarchitectural patterns of mollusc shells, and 2. the evolutionary tendencies and ecological adaptations of the various lineages within the phylum.

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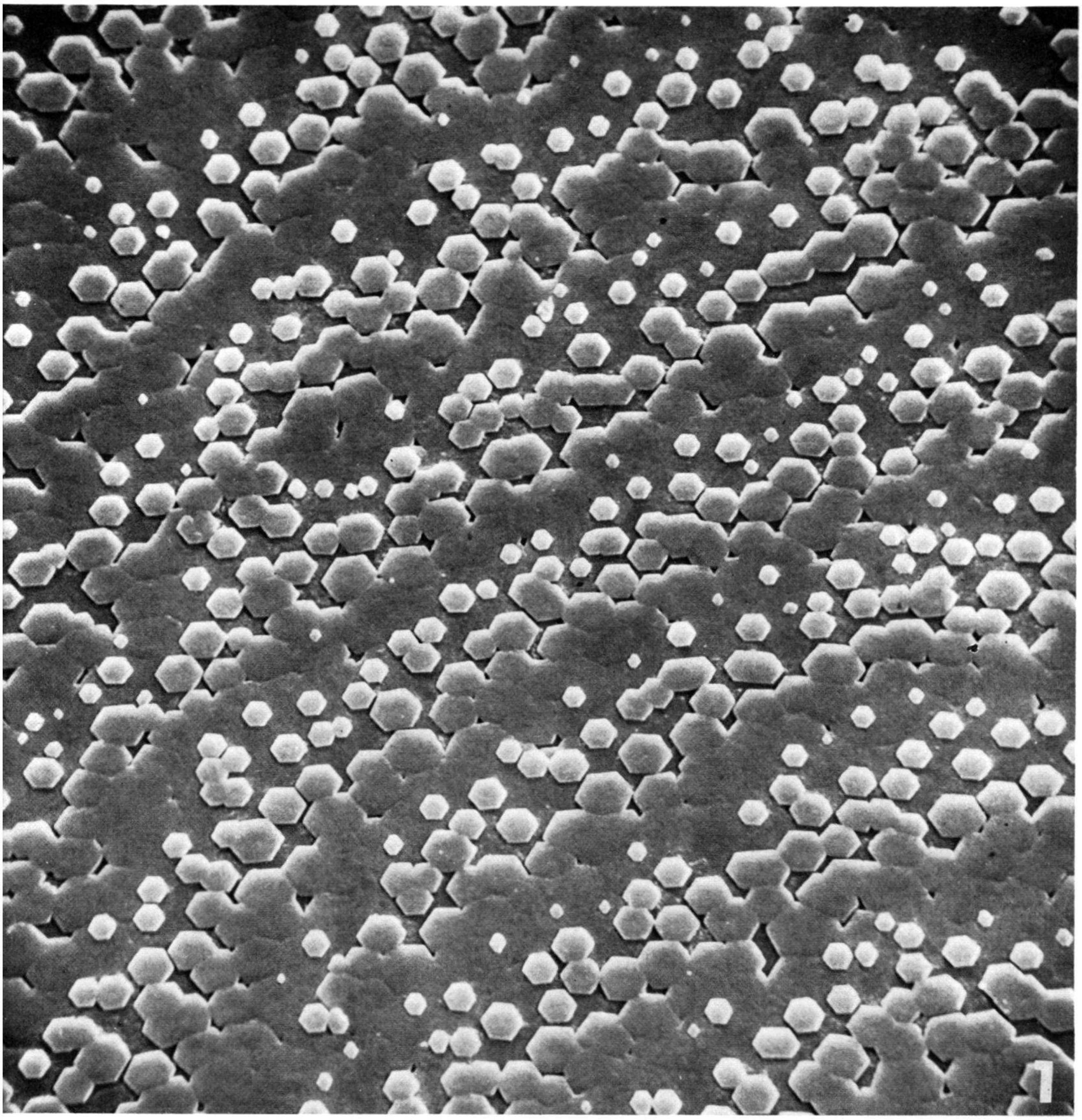
Plate I

Fig. 1 *Pinctada radiata* LEACH (pelecypod). Developmental growth pattern characteristic of pelecypod nacre. Pattern formed by the imbrication of thin horizontal mineral laminae at the surface. New crystals form at the margins of each lamina. × 1,600. (WISE, 1970)

Fig. 2 *Amblema costata* (pelecypod). Typical "brick wall" pattern (*Backsteinbau*) observed in vertical cross sections through pelecypod nacre. × 2,200.

Fig. 3 *Amblema costata*. Stair-step pattern (*Treppen*) sometimes observed in nacre of pelecypods. × 2,900.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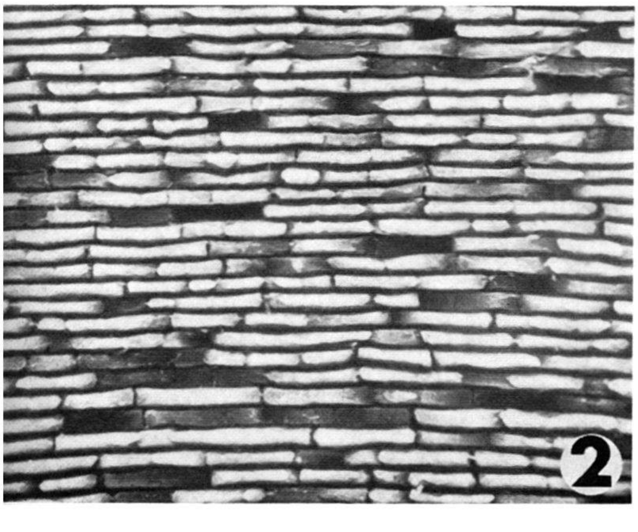
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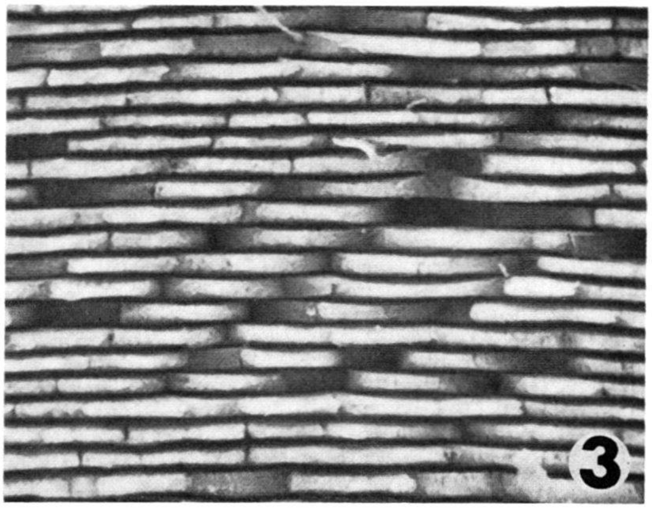
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Plate II

Fig. 1	*Amblema costata* (pelecypod). Vertical fracture section through the nacre revealing no discernible vertical ordering of crystals composing horizontal laminae. × 680.
Fig. 2	*Amblema costata*. Vertical fracture section passing through individual crystals of nacre arranged in *Backsteinbau* pattern. × 2,000.
Fig. 3	*Mytilus edulis* (Linné) (pelecypod). Ledge exposed by fracture section revealing mature six-sided crystals which have merged evenly to form mineral laminae. Uniform orientation of crystals reflects alignment at time of formation (compare with Plate I, Fig. 1). Prominent growth banding may indicate daily cycle of mineral deposition. × 3,500. (Wise, 1969c).
Fig. 4	*Pinna carnea* Gmelin (pelecypod). Growth surface of nacreous layer displaying row-stack pattern of crystal deposition. Crystals are uniformly aligned end-to-end with incipient crystals forming new rows directly on top of older rows. × 900.
Fig. 5	*Pinna carnea*. Detail of Figure 4 (above) showing prominent growth banding of crystals. × 2,200.


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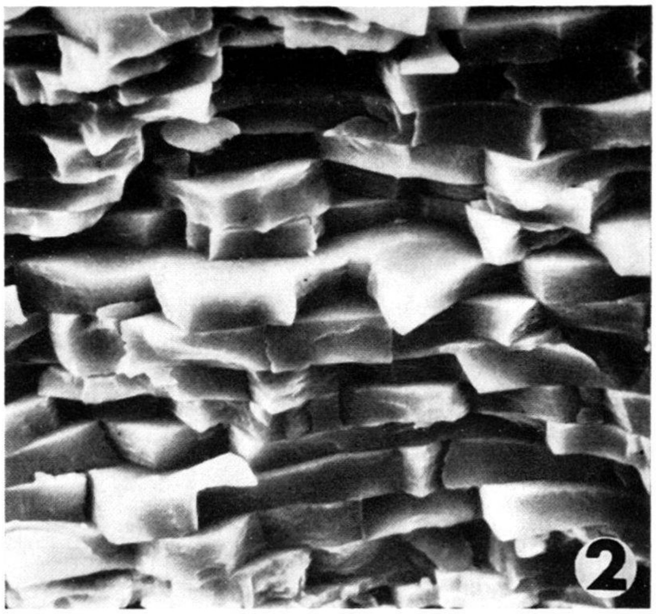
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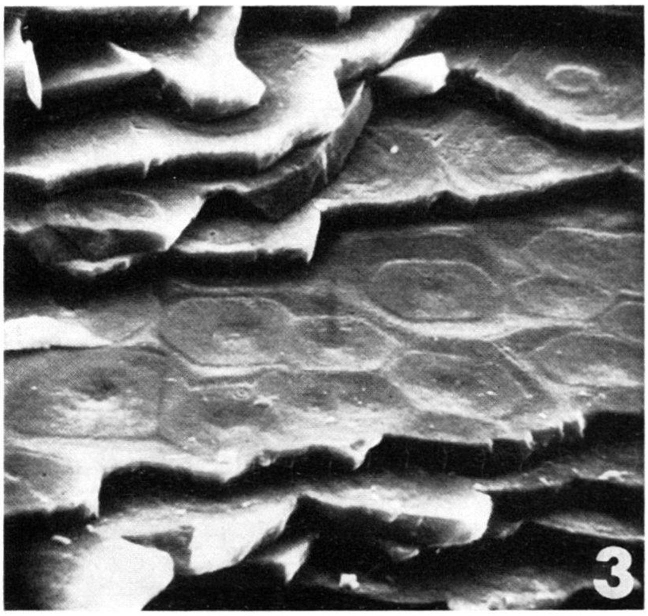
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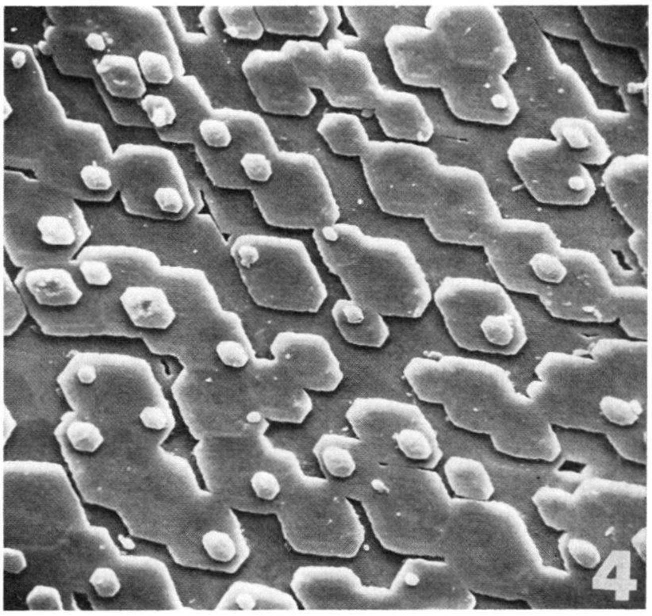
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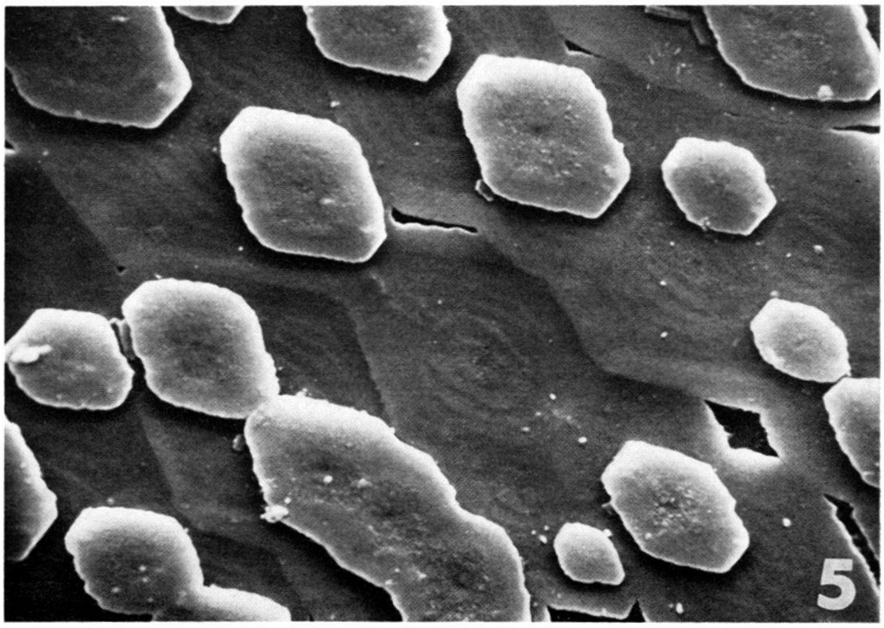
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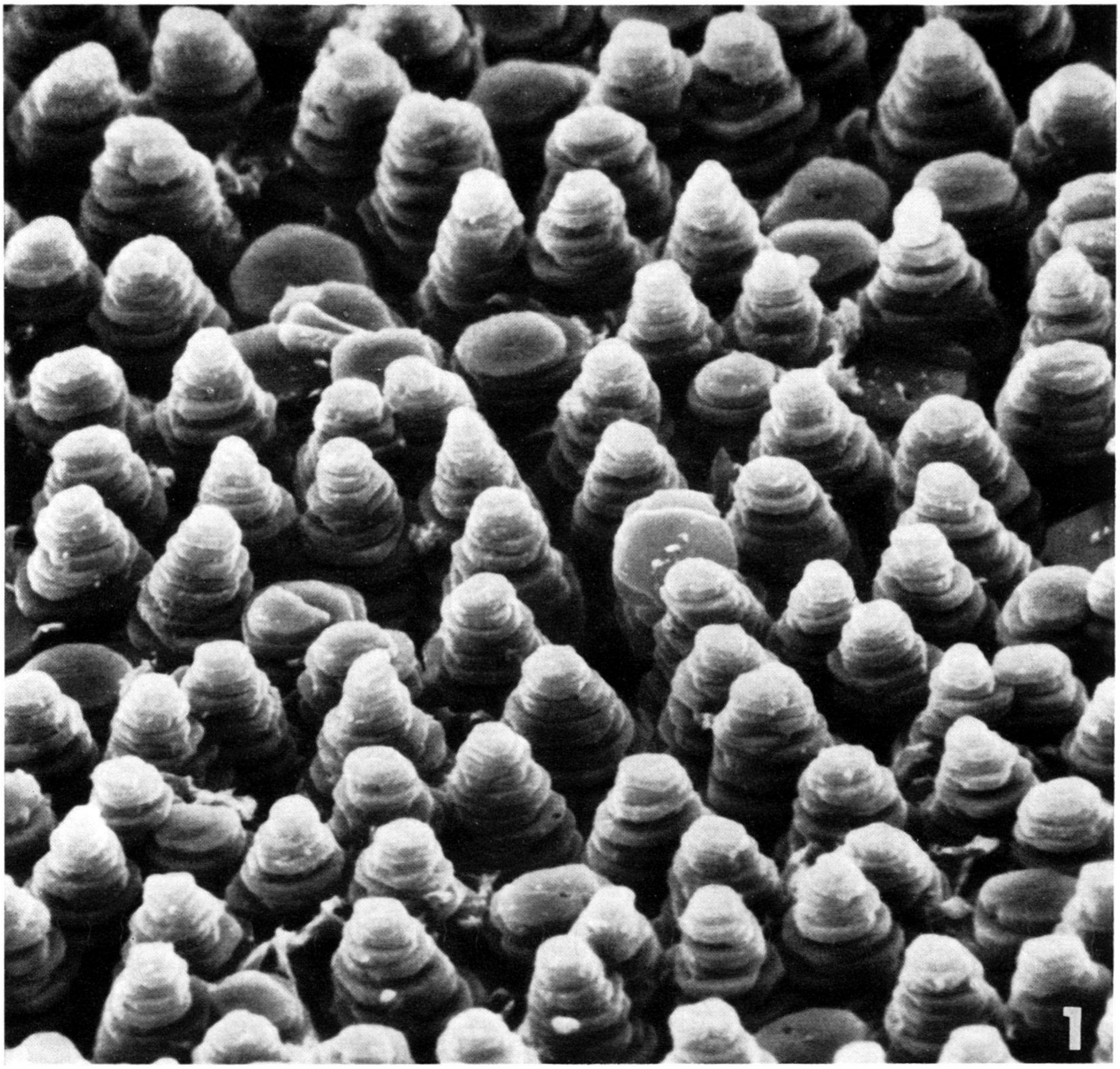
Plate III

Fig. 1 *Turbo castanea* GMELIN (gastropod), oblique view. Developmental growth surface of nacreous layer formed by the deposition of crystals in tall vertical stacks. This pattern is characteristic of gastropod nacre. × 2,800.

Fig. 2 *Turbo castenea*, oblique view of growth surface of nacreous layer. Developing crystals expand laterally with growth and merge evenly with crystals of adjacent stacks to form horizontal mineral laminae. Crystals of neighboring stacks frequently overlap at their margins in the offset interlocking pattern seen in the center of the figure. × 5,000.

Fig. 3 *Turbo castanea*, vertical view of growth surface of nacreous layer. In gastropods the entire growth surface of the nacre is covered by crystal stacks which give the surface a granular appearance at low magnification. × 180.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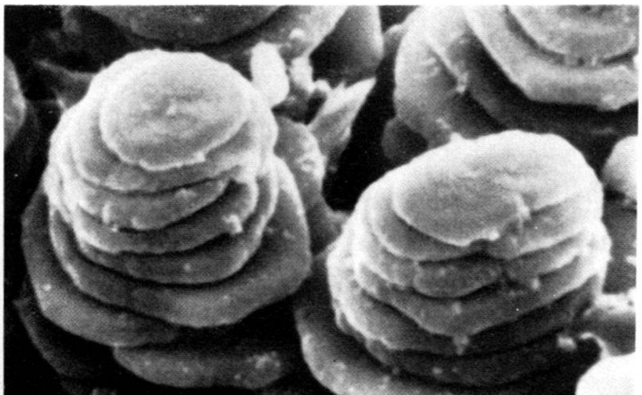
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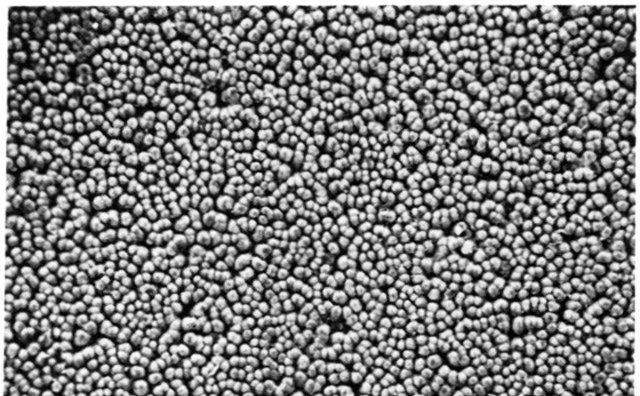
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Plate IV

Fig. 1 *Astrea americana* (GMELIN) (gastropod). Vertical view of growth surface of nacreous layer from which the topmost organic membranes have been removed by acetate peels. Only tops of crystal stacks are visible; spaces between them are filled by horizontal sheets of conchiolin. × 850.

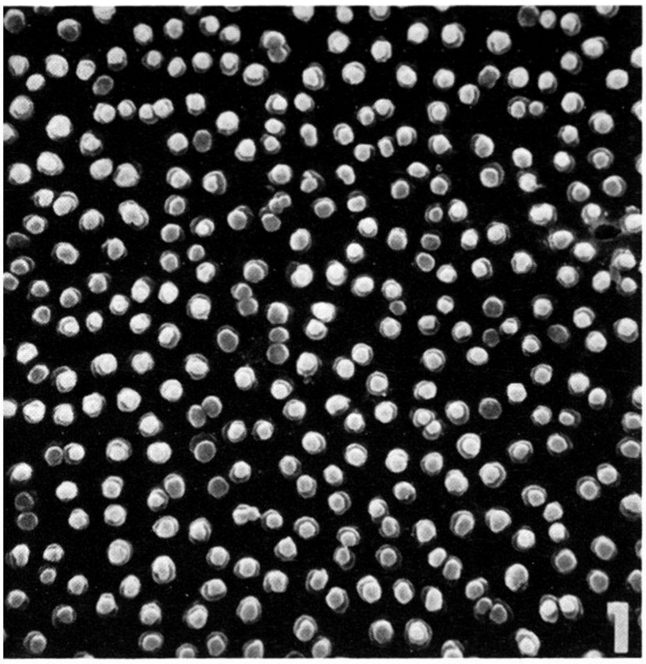
Fig. 2 *Turbo castanea* (gastropod). Growth surface from which all organic membranes have been removed. Crystals of the stacks are preferentially elongated in one direction. The direction of elongation is usually constant within any given stack, but no systematic alignment exists between stacks. × 1,500.

Fig. 3 *Astraea caelata* (GMELIN). Growth surface of nacreous layer. Although partially obscured by organic matrices, these stacks composed of euhedral six-sided crystals show the same crystal to stack relationships observed in Figure 2 (above). This suggests that the anhedral crystals observed in Figure 2 are elongated preferentially along crystallographic axes. × 1,100.

Fig. 4 *Cittarium pica* (LINNÉ) (gastropod). Oblique view of vertical fracture intersecting growth surface (upper portion of figure). Deposition of crystals in stacks on growth surfaces produces columnar arrays of crystals which give the mature nacre of gastropods a pseudoprismatic appearance in cross section. × 530.

Fig. 5 *Cittarium pica*. Vertical fracture intersecting growth surface. Vertical ordering of crystals on the growth surface can be traced directly down into the mature nacre. In fracture sections the columnar pattern obscures the horizontal layering of the mineral laminae. X 1,050.

Fig. 6 *Haliotis rufescens* SWAINSON (gastropod). Oblique view of a vertical fracture surface intersecting the inner surface of a beach worn specimen. The fundamental horizontal lamination of gastropod nacre is evidenced by this specimen in which the crystal stacks have been completely removed from the inner surface by abrasion. The uneven erosion of the growth surface has exposed several horizontal mineral laminae of mature nacre (top portion of figure) while the vertical fracture diplays an unmistakable columnar stacking of crystals. × 850.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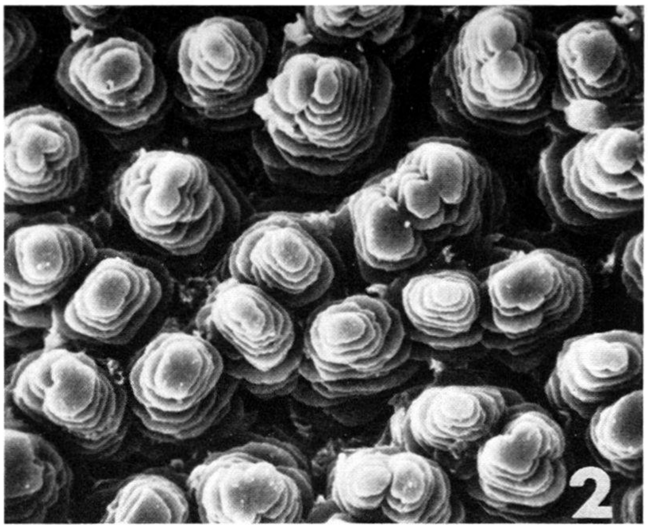
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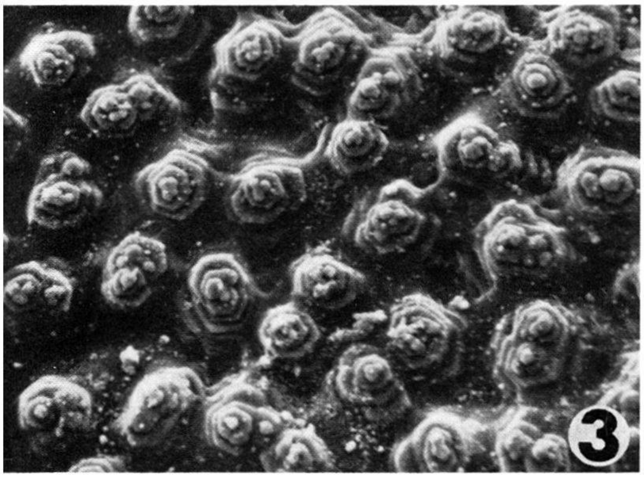
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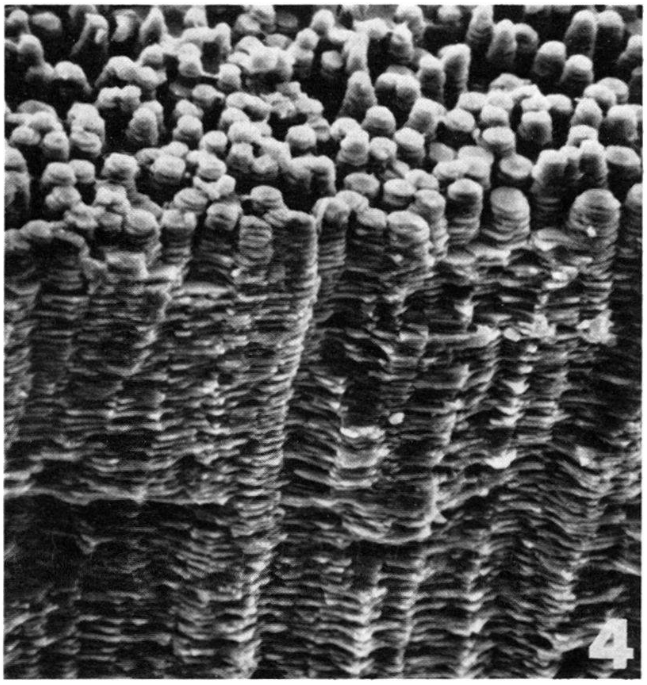
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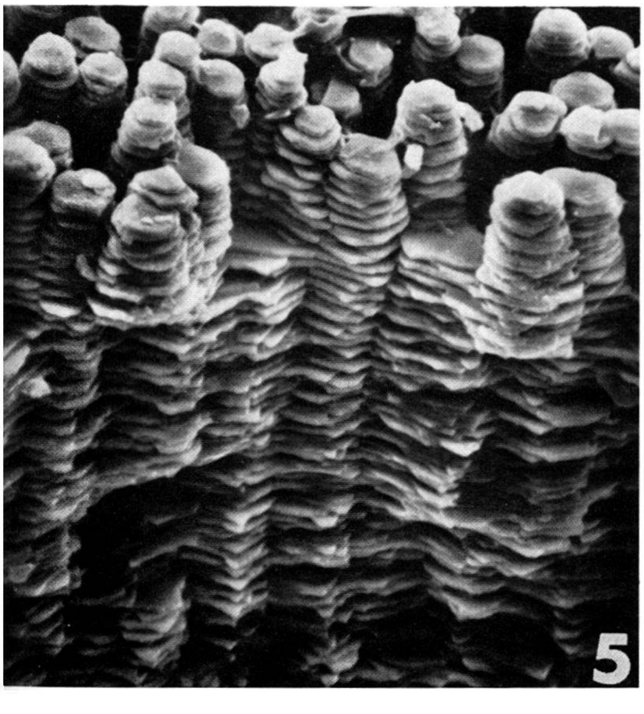
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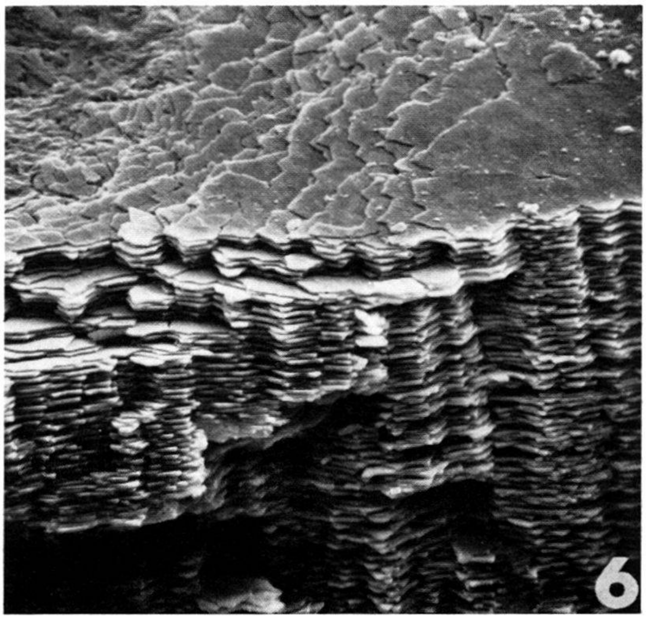
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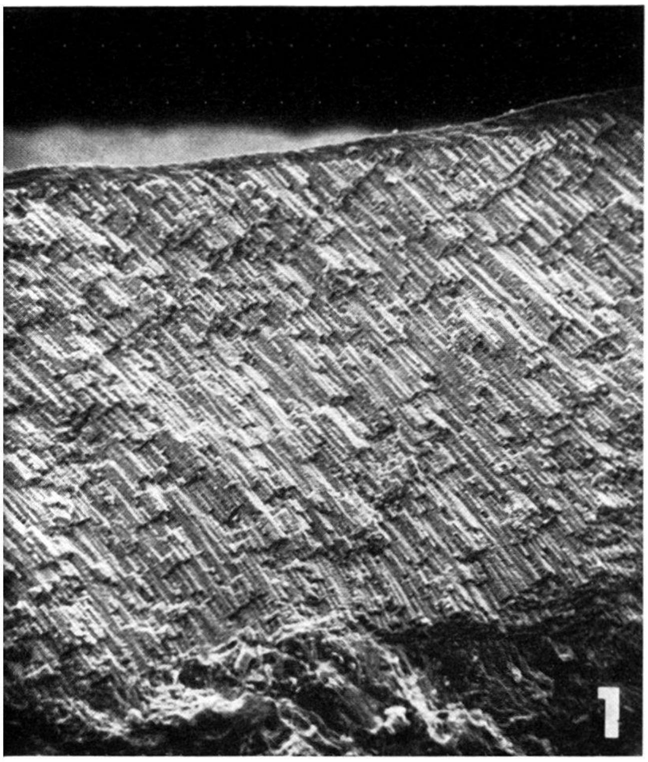
Plate V

Fig. 1	*Tegula funebralis* A. ADAMS (gastropod). Vertical fracture through the entire thickness of the shell. The nacreous layer (middle layer in figure) is usually the thickest in prosobranch shells; the coin-like stacks of crystals may curve slightly through the layer. × 95.
Fig. 2	*Tegula funebralis*, detail of section in Figure 1 (above). Individual stacks may be traced long distances through the layer. × 290.
Figs. 3 and 4	*Haliotis rufescens* (gastropod). Vertical fracture surface. Vertical fractures through gastropod nacre tend to part along the boundaries between stacks, clearly delineating the position of each stack. Fig. 3 × 1,200; Fig. 4 × 2,400. (WISE, 1970)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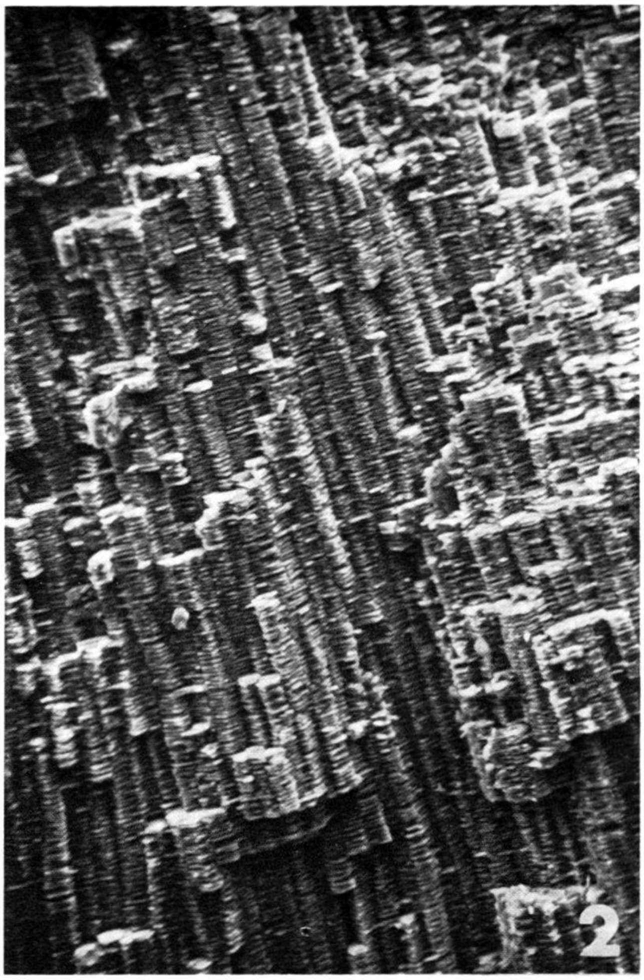
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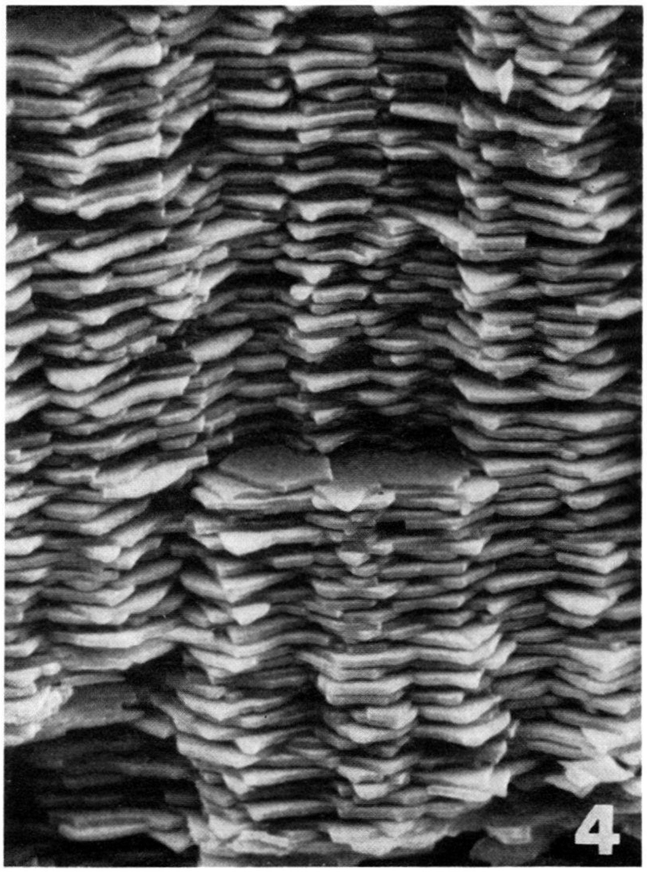
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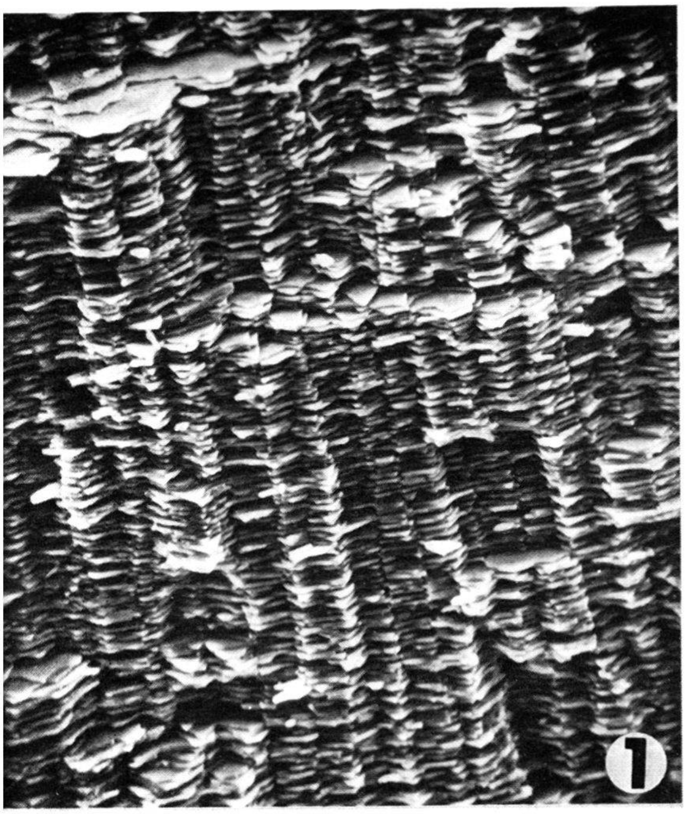
Plate VI

Fig. 1 *Turbo castanea* (gastropod). Vertical fracture through the nacrous layer. × 570.

Fig. 2 *Cittarium pica* (gastropod). Vertical fracture through the nacreous layer. × 260.

Fig. 3 *Haliotis rufescens* (gastropod). Vertical cross section (polished and etched) through the nacreous layer. About ten stacks can be discerned in this section which was cut parallel to the length of the columns. × 1,400.

Fig. 4 *Haliotis rufescens*, view of a portion of Figure 3 (above) at higher magnification. Four adjacent stacks exhibit offset pattern of interlocking crystal margins at stack boundaries. × 2,800.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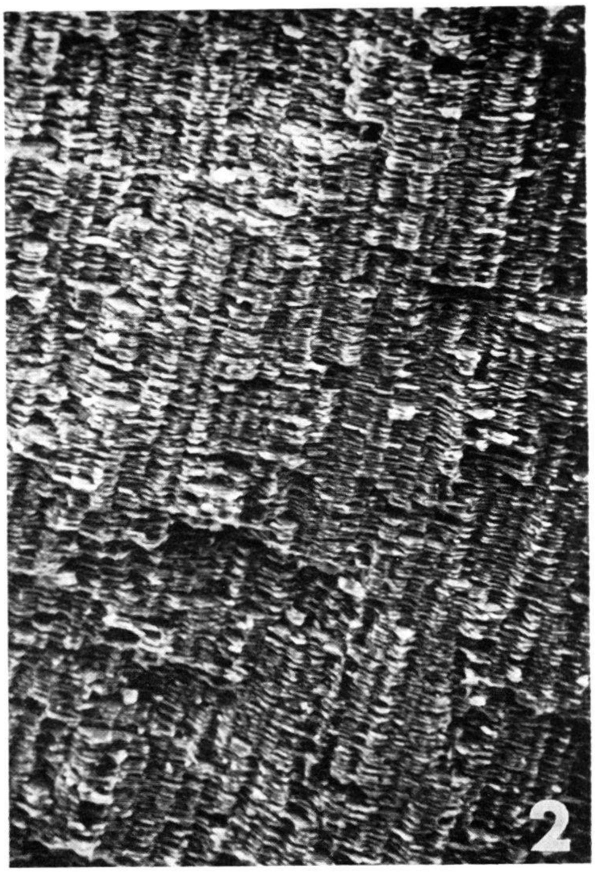
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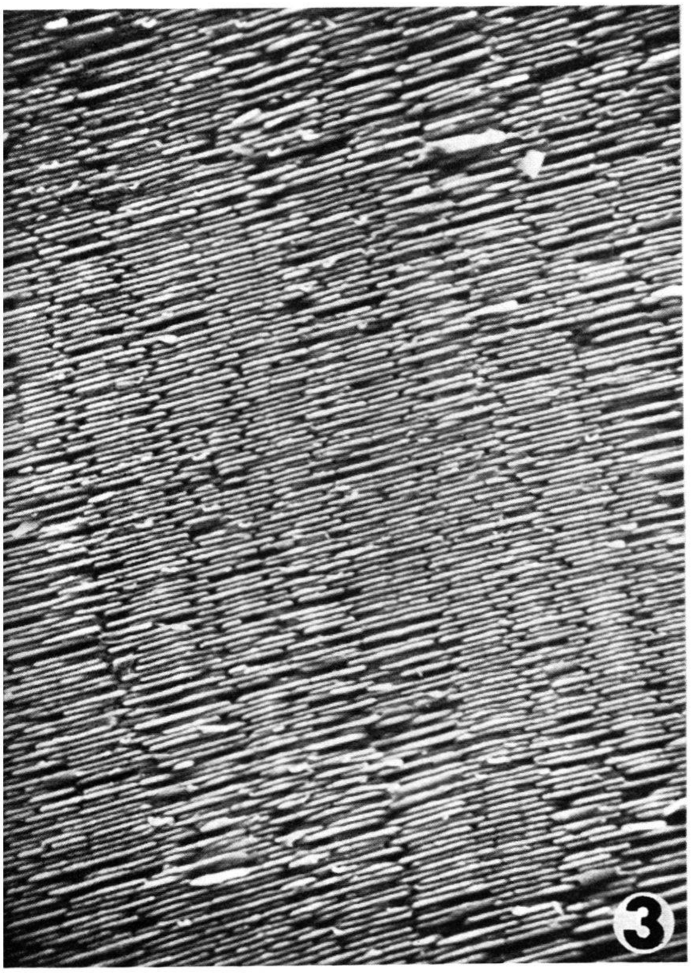
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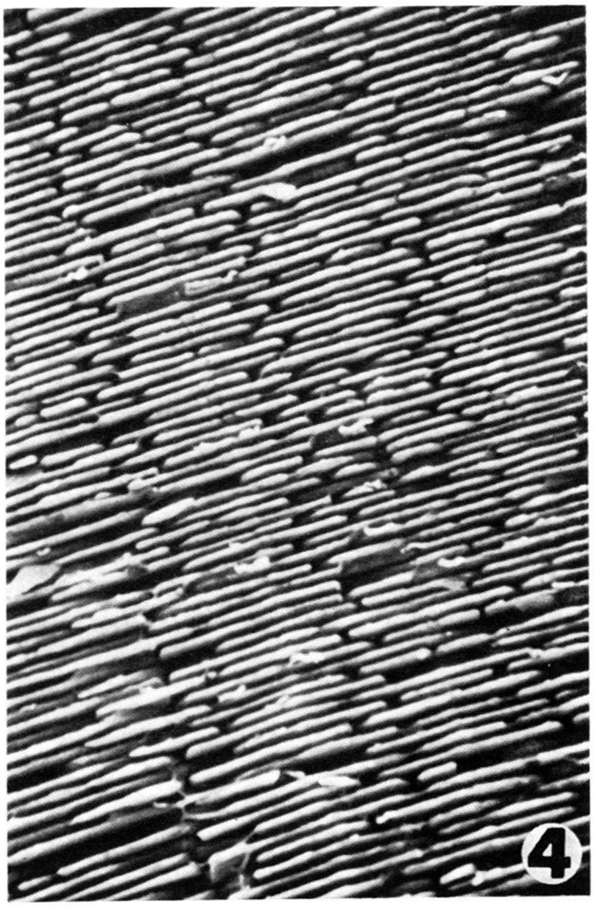
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Plate VII

Fig. 1 Idealized composite diagram by CARPENTER (1848) portraying "cells" (i.e., stacks) in nacre of *Haliotis splendens* (gastropod) observed in three views: a) section normal to the long axes of the columns; b) section somewhat oblique to their lengths; and c) their terminations at the growth surface.

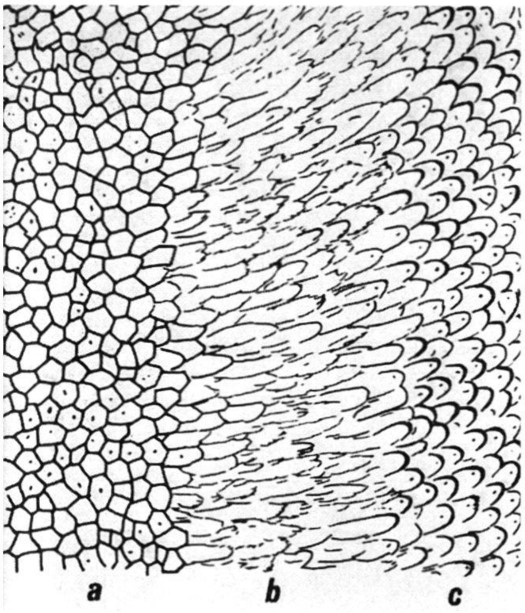
Fig. 2 *Haliotis rufescens*. Fracture section oblique to the horizontal laminae of nacre, revealing laminae in a step-like series. Oblique fractures do not display vertical stack structure. × 870.

Fig. 3 *Pinctada radiata* (pelecypod). X-ray pattern (precession method) produced by nacre with laminae oriented perpendicular to beam (i.e., *c* axis of the tabular crystals parallel to beam). Pattern indicates a parallel orientation of *a* and *b* axes of the individual crystals throughout the sample area.

Fig. 4 *Cittarium pica* (gastropod). X-ray pattern given by nacre oriented as in Figure 3 (above). Pattern indicates a random orientation of *a* and *b* axes of crystals throughout the sample area.

Fig. 5 *Cittarium pica*. X-ray pattern given by same sample as in Figure 4 oriented with the mineral laminae parallel to beam (crystallographic *c* axis perpendicular to the beam). Pattern reveals parallel alignment of the *c* axes of the crystals in the sample area.

Fig. 6 *Pinna carnea* (pelecypod). Inner shell surface at boundary between growth surface of the nacreous layer and the myostracum (M, upper left corner of figure). In the narrow transition area between the two layers. the tabular crystals of nacre broaden to form extremely large units (up to 80 μ in length) which are eventually covered by the deposition of myostracum. × 115.



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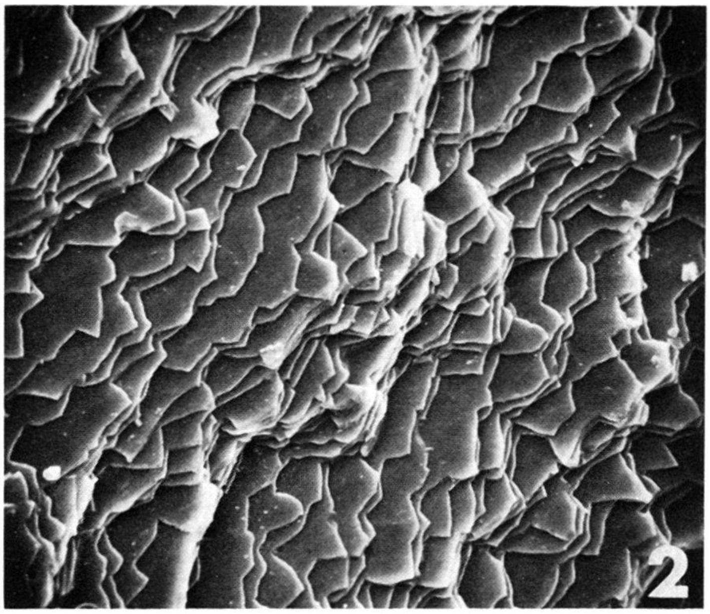
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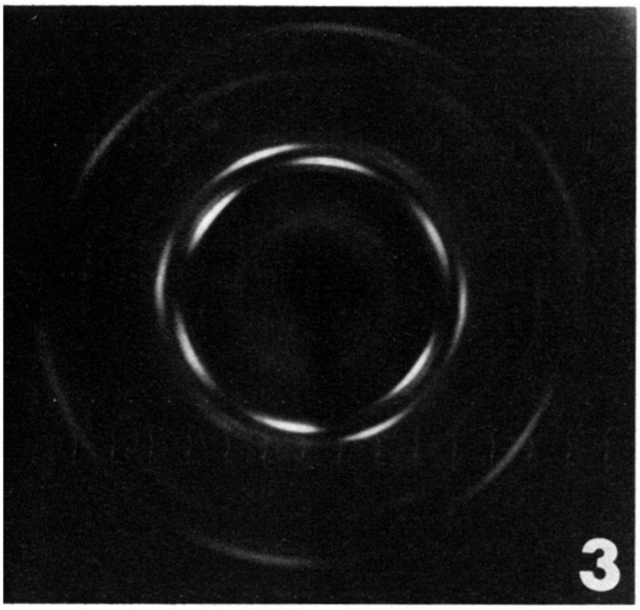
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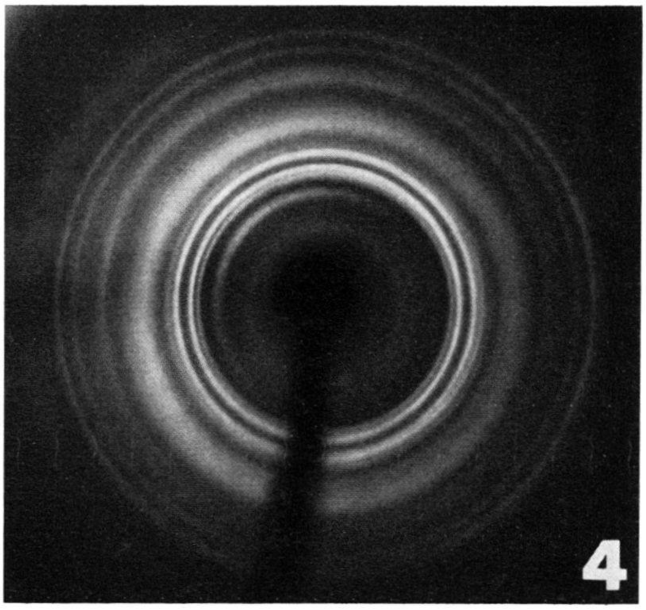
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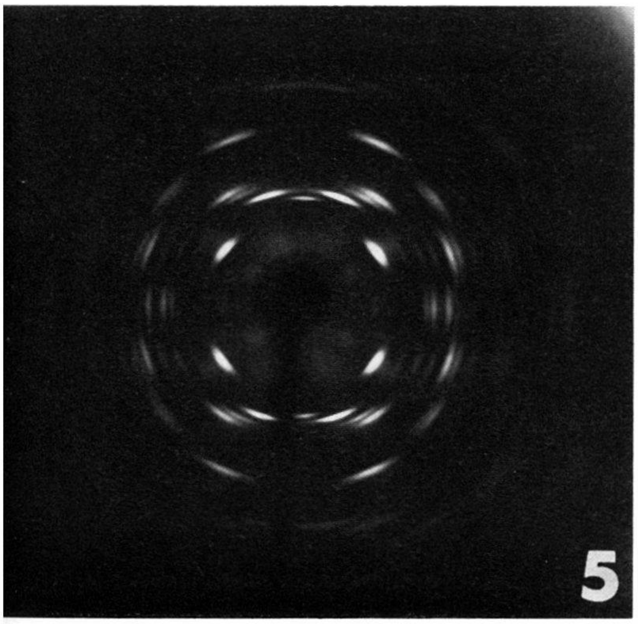
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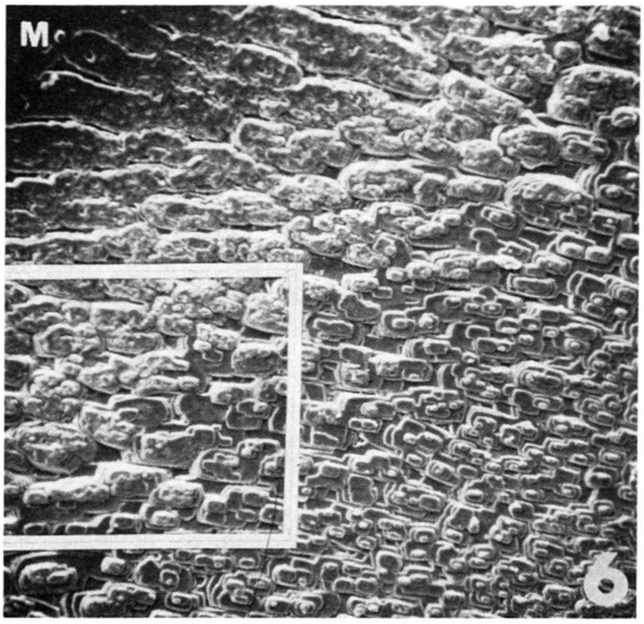

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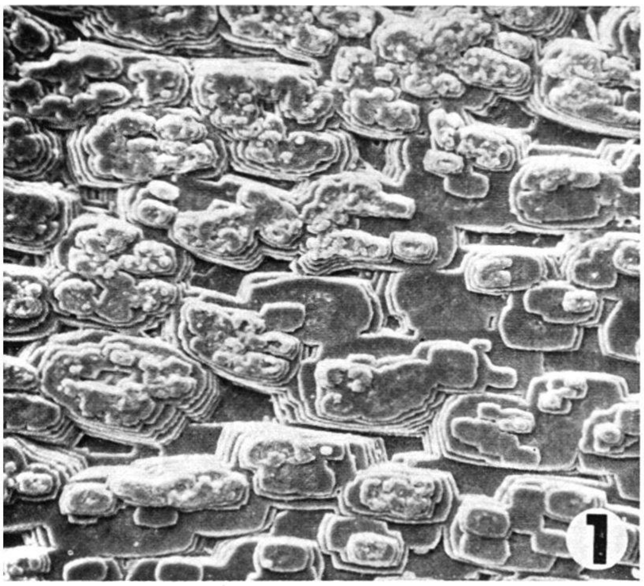
Plate VIII

Fig. 1	*Pinna carnea*, area outlined by white rectangle on Figure 6, Plate VII. Broadening of row-stacks produces large elongate units composed of six or seven stacked plates. × 260.
Fig. 2	*Pinna carnea.* Fracture surface oriented perpendicular to the inner surface of nacre in center of the figure becoming sub-parallel to surface in bottom portion of figure. Vertical fracture perpendicular to trend of row-stacks on growth surface. × 490.
Fig. 3	*Pinna carnea.* Detail of the vertical fracture surface in Figure 2 (above) revealing vertical ordering (*Vertikalschichtung*) of row-stacks. To observe *Vertikalschichtung*, sections must be cut nearly perpendicular to the length of the row-stacks. × 900.
Fig. 4	*Nucula proxima* SAY (pelecypod). View of inner shell surface showing outer nacreous layer and three ribs or crenulations along ventral margin. Unlike other pelecypods observed, the imbricated laminae of nacre ventral to the pallial line overlap in the dorsal direction (i.e., toward the beak [arrow D]). × 140.
Fig. 5	*Nucula proxima.* Area between two ribs of specimen shown in Figure 4 (above) viewed from ventral margin looking toward the dorsum (direction of arrow D). Surface of composite prismatic layer in lower third of figure; nacre in upper portion. Stacks three or four crystals high developed in nacre just above boundary. × 720.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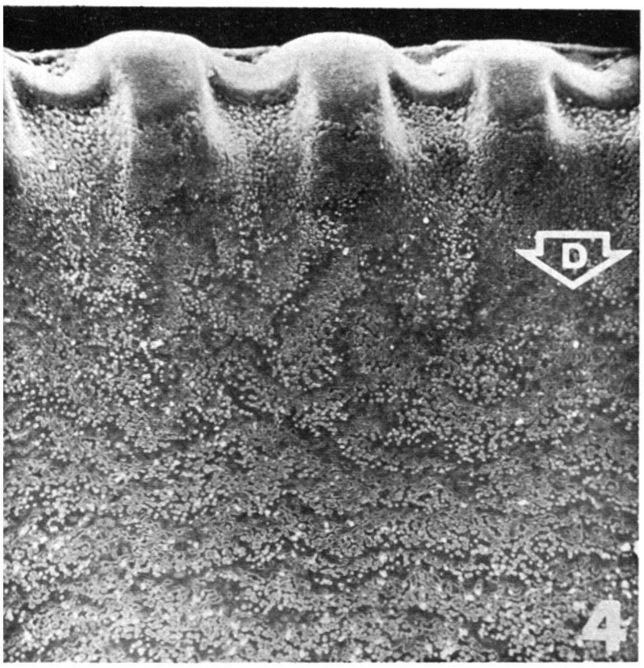
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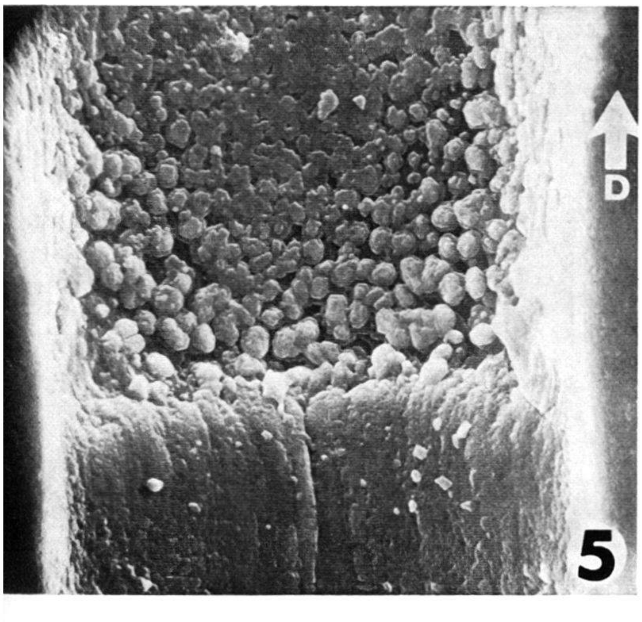
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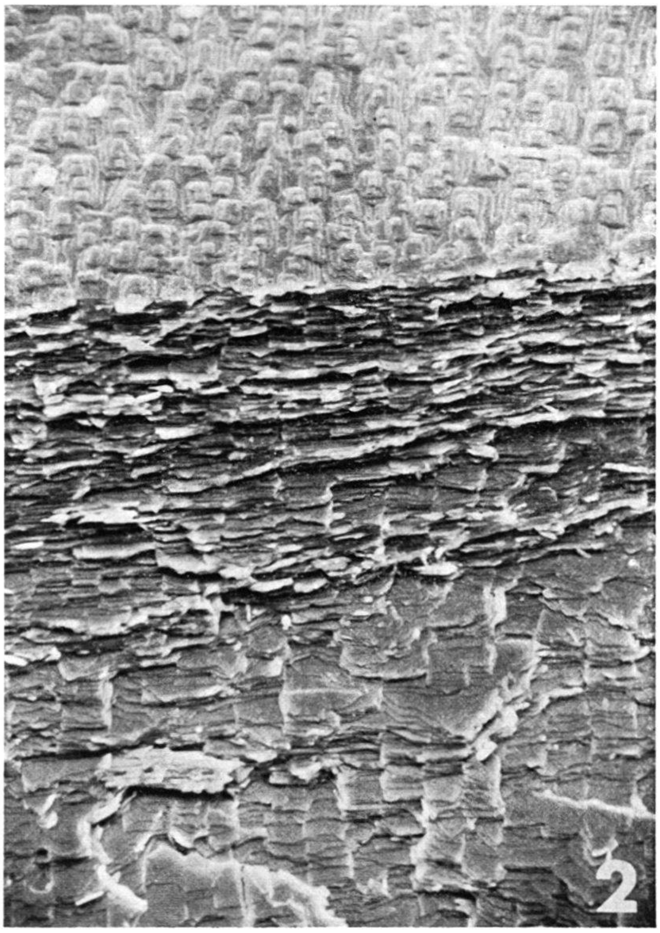
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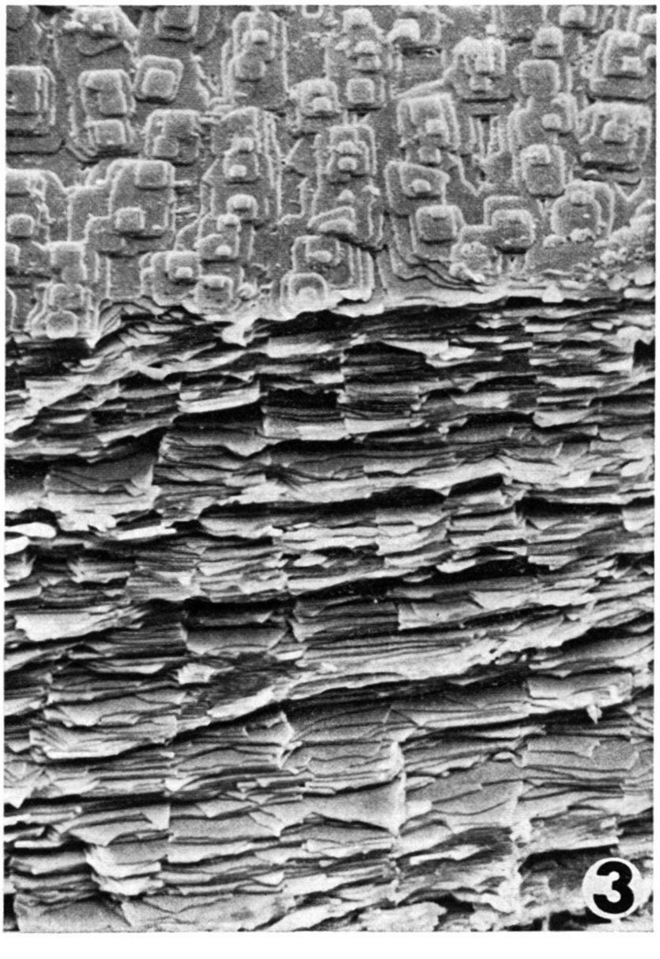
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Plate IX

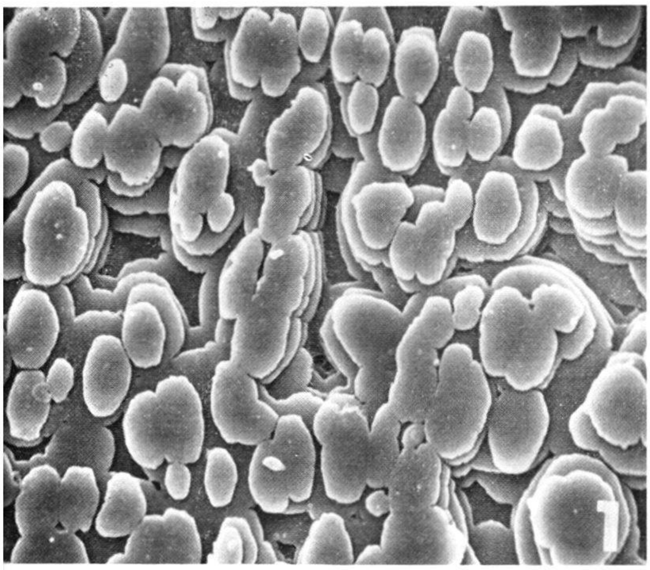
Fig. 1 *Nucula proxima* (pelecypod). In some specimens, row-stacks five or six crystals high are developed on growth surface of the nacre near the crenulated ventral margin. Row-stacks are parallel to the ventral margin. × 1,400.

Fig. 2 *Nucula proxima*. Composite photograph of radial fracture section through entire thickness of the shell. Upper portion of nacre developed in *Backsteinbau* pattern; central portion is columnar (*Vertikalschichtung*); folded portion marks position of a rib. Lowermost layer is composite prismatic. × 160.

Fig. 3 *Nucula proxima*. Close-up of the columnar portion of the nacre. × 770.

Fig. 4 *Nautilus pompilius* LINNÉ (cephalopod). Vertical fracture section through outer shell wall of living chamber showing boundary between nacreous layer (above) and spherulitic-prismatic layer (below). Note columnar stacking in nacre. × 1,000.

Fig. 5 *Nautilus pompilius*. Fracture surface through boundary shown above (Fig. 4). Ledge in the nacreous layer parallel to horizontal stratification. × 500.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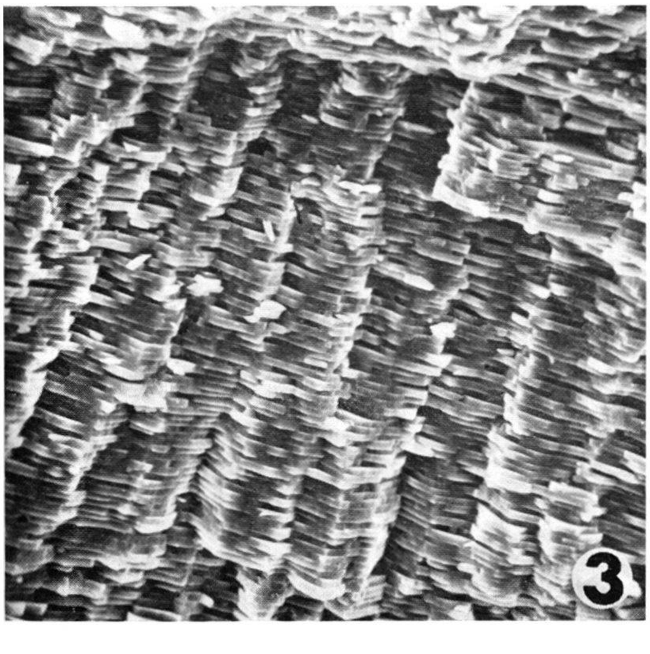
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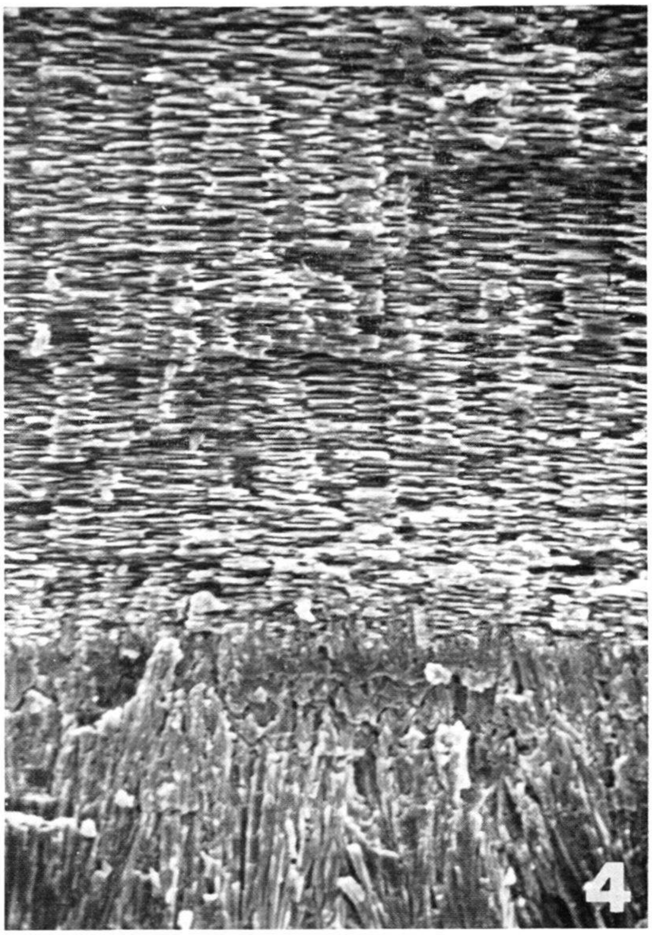
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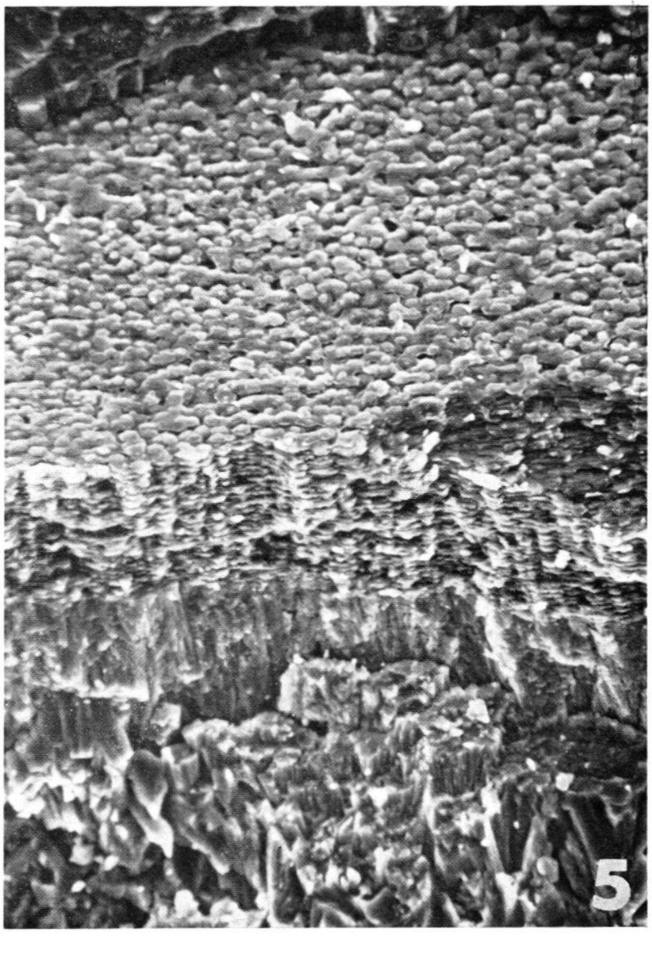
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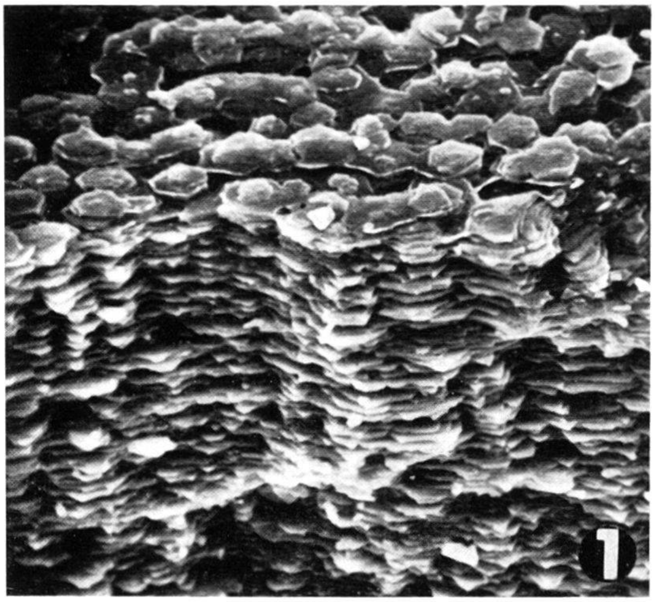
Plate X

Figs. 1–5.	*Nautilus pompilius* (cephalopod).
Fig. 1	Detail of fracture in Pl. IX, Fig. 5 showing vertical stacks in nacre. × 1,500.
Fig. 2	Vertical view of horizontal ledge in Pl. IX, Fig. 5. Crystals are immature and do not form continuous laminae between stacks. × 1,800.
Fig. 3	Growth surface of nacre deposited on dorsal surface of the living chamber. × 1,400. (Wise, 1969c)
Fig. 4	Crystals of nacre deposited on the concave surface of a mature septum. × 750.
Fig. 5	X-ray pattern produced by nacre with laminae oriented perpendicular to beam. Pattern indicates a parallel orientation of *a* and *b* axes of the tabular crystals.
Fig. 6	*Cittarium pica* (gastropod), light micrograph of the aperture of the shell. Growth surfaces of the four shell layers form parallel bands inside the apertural lip. The thin outermost or distal layer (position indicated by arrow D) forms the leading edge of the aperture over which is deposited the composite prismatic layer (P), the nacreous layer (N), and the oblique prismatic layer (OP) which forms a thin veneer on the inside of the shell. × 1.2.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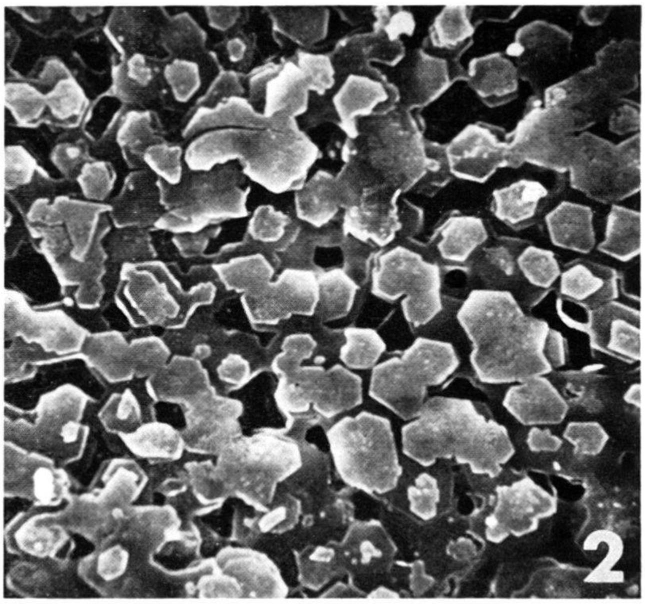
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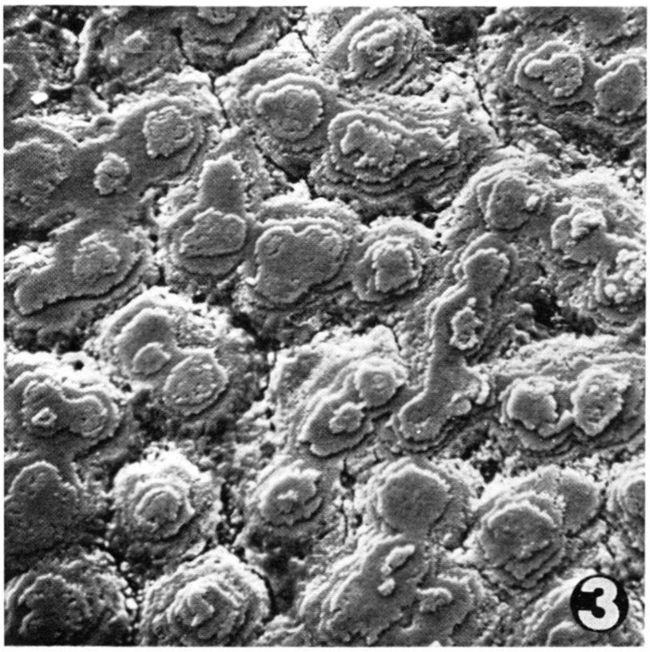
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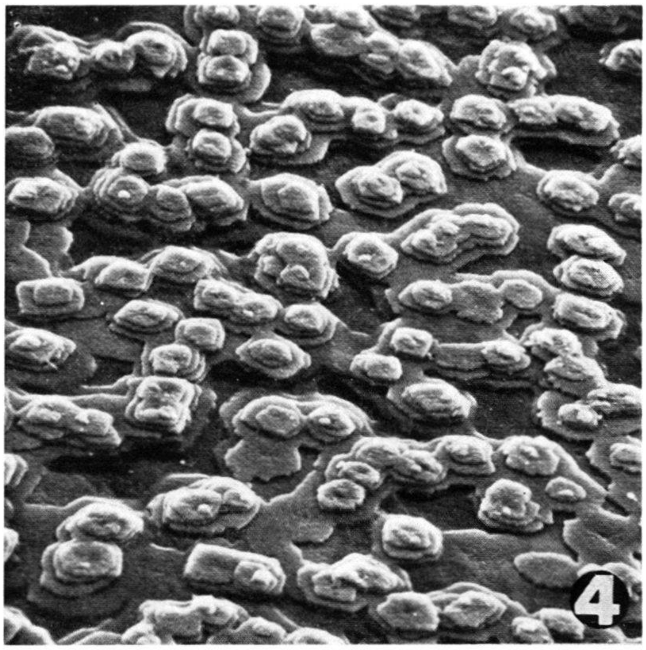
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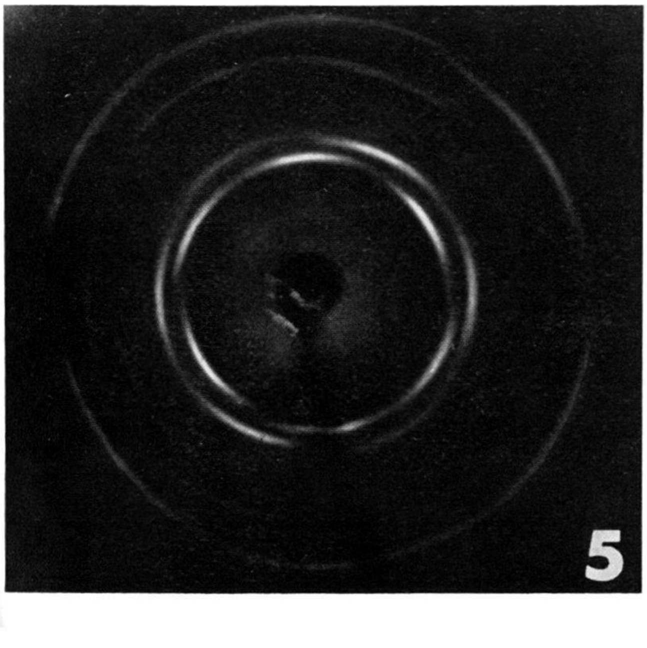
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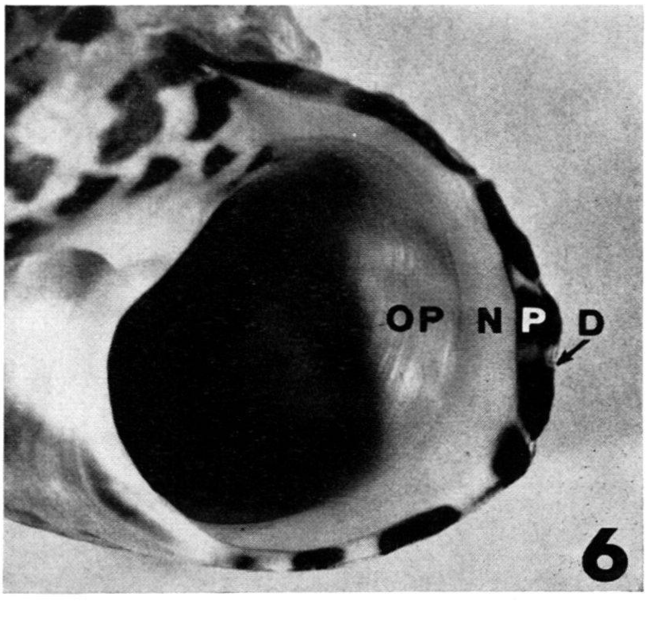

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