The Shell Structure and Mineralogy of *Chama pellucida* Broderip

BY

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(Plates 61 to 64; 6 Text figures)

The calcified shell of the bivalvia is normally built up of two forms of calcium carbonate, aragonite and calcite. Shells may be wholly aragonitic, or may contain both aragonite and calcite, always in separate monomineralic and structurally distinct layers.

Amongst extant bivalves, calcite is confined to 7 superfamilies of the subclass Pteriomorphia (classification after Newell, 1965) and a single member of the Heterodonta. This species is *Chama pellucida* Broderip, 1835.

Primary calcite was also present in an extinct heterodont group, the rudists (Hippuritacea; Kennedy & Taylor, 1968).

The distribution in living bivalves is:

	superfamilies	
Palaeotaxodonta:	Nuculacea	aragonite only
	Nuculanacea	aragonite only
Cryptodonta:	Solemyacea	aragonite only
Pteriomorphia:	Arcacea	aragonite only
	Limopsacea	aragonite only
	Mytilacea	aragonite only or aragonite + calcite
	Pinnacea	aragonite + calcite
	Pteriacea	aragonite + calcite
	Pectinacea	aragonite + calcite
	Anomiacea	aragonite + calcite
	Limacea	aragonite + calcite
	Ostreacea	aragonite + calcite
Palaeoheterodonta:	Unionacea	aragonite only
	Trigonacea	aragonite only
Heterodonta:	All superfamilies	wholly aragonite, so far as is known, except for *Chama pellucida.*
Anomalodesmata:	All	wholly aragonitic

The single occurrence of calcite in *Chama pellucida,* outside the Pteriomorphia, is therefore of considerable interest. This fact was first reported by Lowenstam (1954a, 1954b) and confirmed subsequently by him (Lowenstam, 1963, 1964) and by our present work.

In bivalve superfamilies where calcite and aragonite occur together in the same shell, Lowenstam (1954a, 1954b, 1963, 1964) and Dodd (1963, 1964) have shown that in some cases the proportion of aragonite is related to temperature. Species living in warmer water tend to have a higher proportion of aragonite in their shells than species living in temperate or cold waters.

Chama pellucida is a West American species ranging from Peru to California. It thus extends into cooler waters well outside the normal range of the Chamacea, which are otherwise more or less confined to the tropics and subtropics. Lowenstam (1954b, 1963, 1964) was thus able to use *Chama pellucida* to illustrate the temperature effect on mineralogy. That is, calcite appears in a species which inhabits cooler waters than the other wholly aragonitic members of the superfamily. Furthermore, he illustrated (Lowenstam, 1963, plate iv) the microstructure of the shell, stating that the outer aragonitic layer of the shell in warm water species of *Chama* is transformed to an outer calcitic layer in *Chama pellucida.* This layer has a distinct and different microstructure.

During a general survey of the mineralogy and microstructure of the Bivalvia (Taylor, Kennedy & Hall, in press), we have found this interpretation to be incorrect. In view of the exceptional nature of *Chama pellucida* we present this more detailed study.

METHODS

Mineralogical determinations were carried out by X-ray diffraction on samples of the shell layers of 29 species of

Chamacea. The microstructure of the shell was examined at optical level by use of acetate peels prepared from polished, etched sections (methods after KUMMEL & RAUP, 1965). Petrographic thin sections were also examined. Fine structure was studied on shell interiors and on polished and E. D. T. A. etched sections with a Cambridge Instrument Company (U. K.) 'Stereoscan' scanning electron microscope. Two-stage formvar, gold palladium shaded replicas were studied by transmission electron microscopy (techniques from KAYE, 1964).

OBSERVATIONS

The shell of most Chamacea consists of two layers, an outer, crossed-lamellar layer and an inner, complex crossed-lamellar layer (terminology from BØGGILD, 1930, TAYLOR, KENNEDY & HALL, in press). These two layers are separated by a thin layer of a blocky prismatic aragonite. This is the pallial myostracum (OBERLING, 1964), and represents the trace of mantle attachment at the pallial line, being deposited below the pallial muscles. It is the 'pellucid layer' of Japanese workers (i. e. KOBAYASHI, 1964), the hypostracum of JAMESON (1912), LOWENSTAM (1964) and others, and the 'helle Schicht' of many workers. When sections are cut through the muscle scars, thick pads of similar myostracal prisms are seen, forming thick adductor myostraca. Small areas of myostracal prisms occur elsewhere in the shell, and are discussed below. These relations are summarised in Text figure 1.

In *Chama pellucida* there is an additional, outer layer, built of prismatic calcite. Within this there is a middle, crossed-lamellar layer, and an inner, complex crossed-lamellar layer, bordered by the trace of the pallial myostracum. These relationships are summarised in Text figure 2. *Chama pellucida* thus possesses an additional layer, not, as LOWENSTAM (1964) states, a layer which replaces the outer layer of wholly aragonitic species. The middle layer of *C. pellucida* is equivalent to the outer layer of other species of *Chama*.

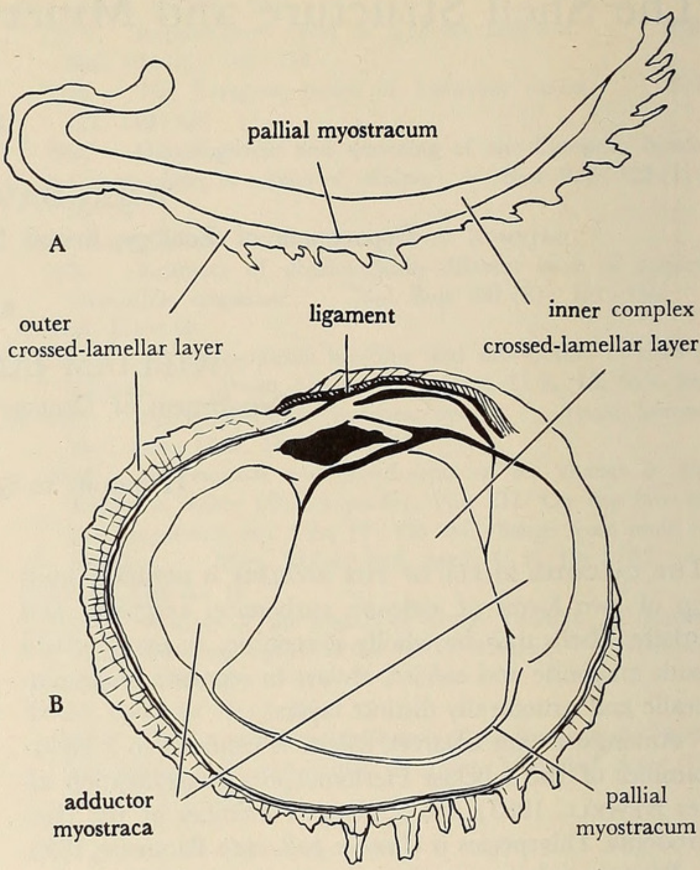


Figure 1

Distribution of shell layers in *Chama macerophylla*
A – section B – shell interior

Explanation of Plate 61

Figure 1: The contact of the middle crossed-lamellar layer and the adductor myostracum of *Chama radians*. Acetate peel of a radial section. × 100

Figure 2: Radial section of the inner layer of *Chama lamellosa* showing complex crossed-lamellar structure and thin sheets of 'myostracal type' prisms. Acetate peel. × 100

Figure 3: Transverse section of the outer, prismatic calcite layer of *Chama pellucida* showing the large irregularly prismatic blocks with much finer units within. Acetate peel. × 100

Figure 4: Planar section of the outer prismatic, calcite layer of *Chama pellucida*. Sub-parallel finely prismatic units and growth bands are visible. Acetate peel. × 100

Figure 5: Contact of the outer prismatic layer (above) and the middle crossed-lamellar layer (below) in *Chama pellucida*. Growth bands are continuous between layers. Crossed-lamellar structure is seen in the lower right hand corner of the picture, the transition zone between the layers is homogeneous and rich in organic matrix. Acetate peel. × 100

Figure 6: The inner complex crossed-lamellar layer of *Chama pellucida* showing myostracal pillars. Acetate peel. × 100

Figure 7: Myostracal pillars in the inner complex crossed-lamellar layer of *Chama radians*. Acetate peel of a radial section. × 100

Figure 8: Planar section through the adductor myostracum of *Chama lazarus*. Acetate peel. × 100

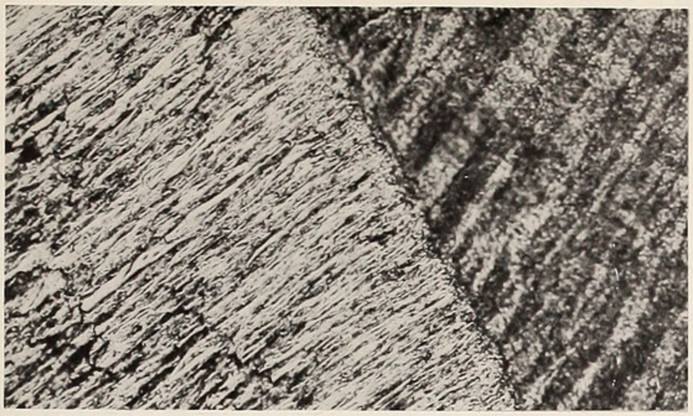


Figure 1

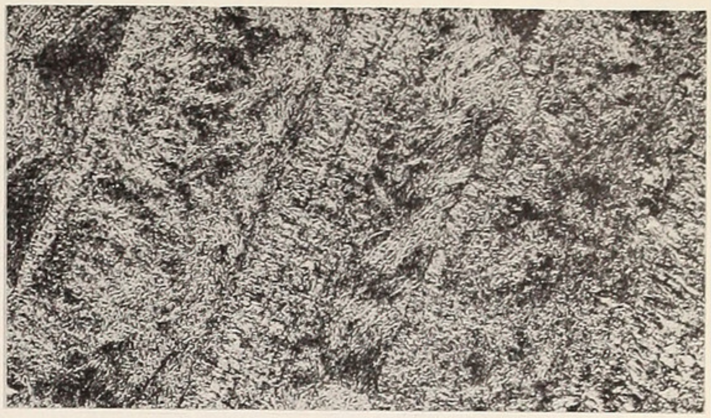


Figure 2

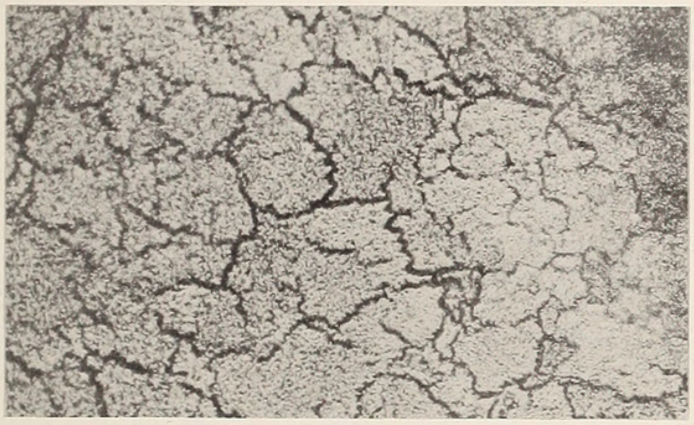


Figure 3

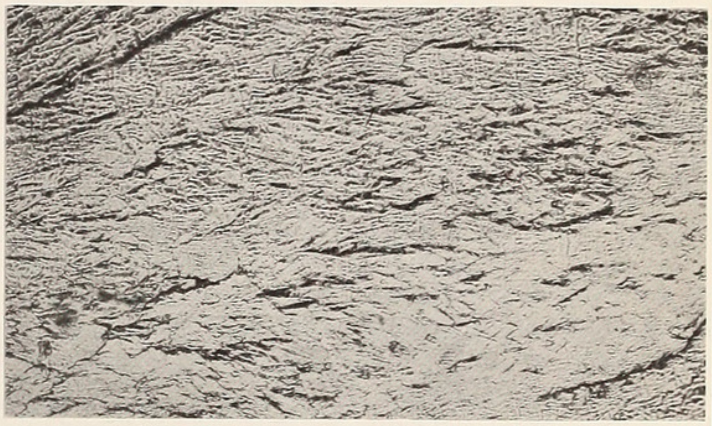


Figure 4

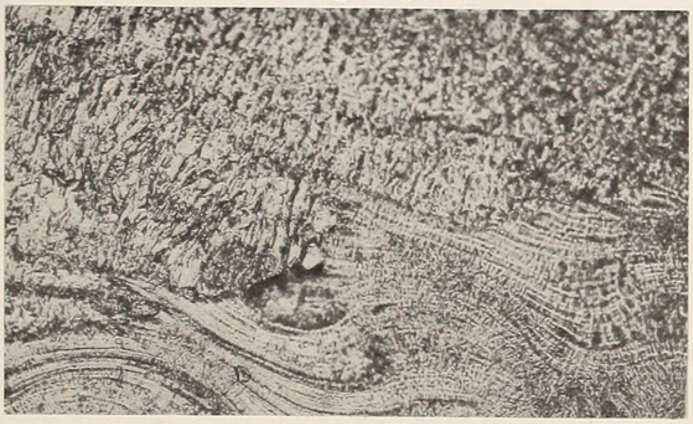
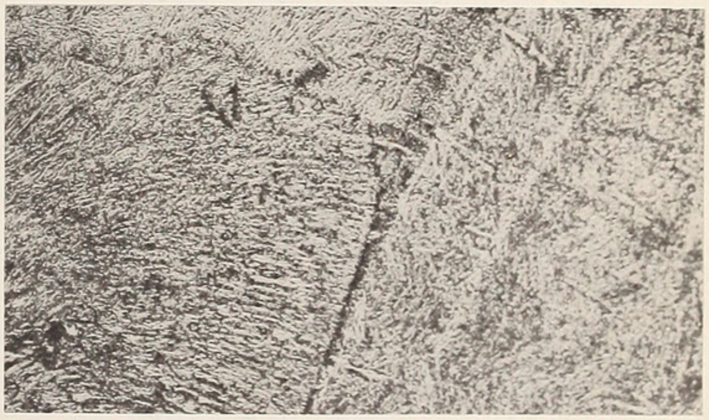


Figure 5



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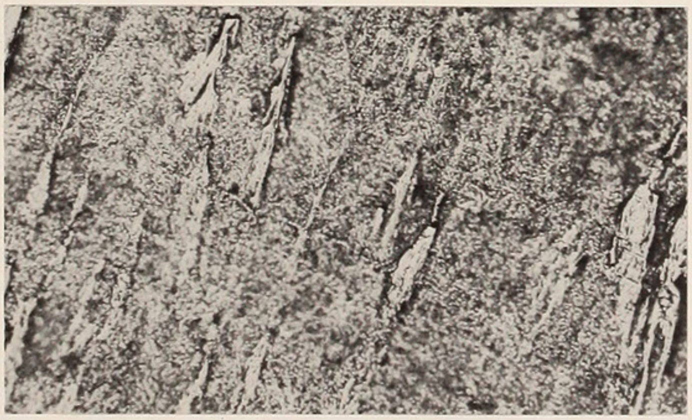

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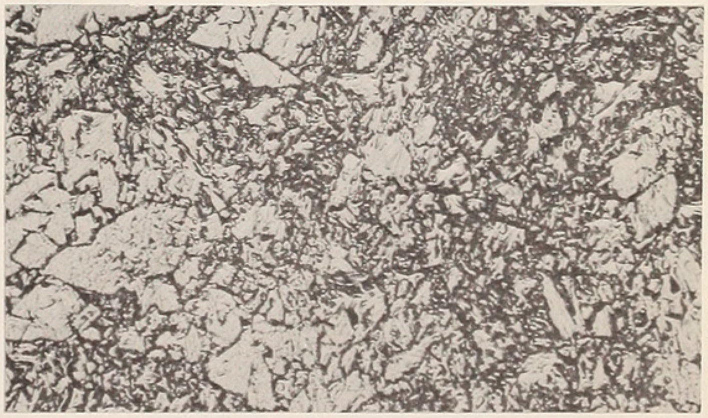

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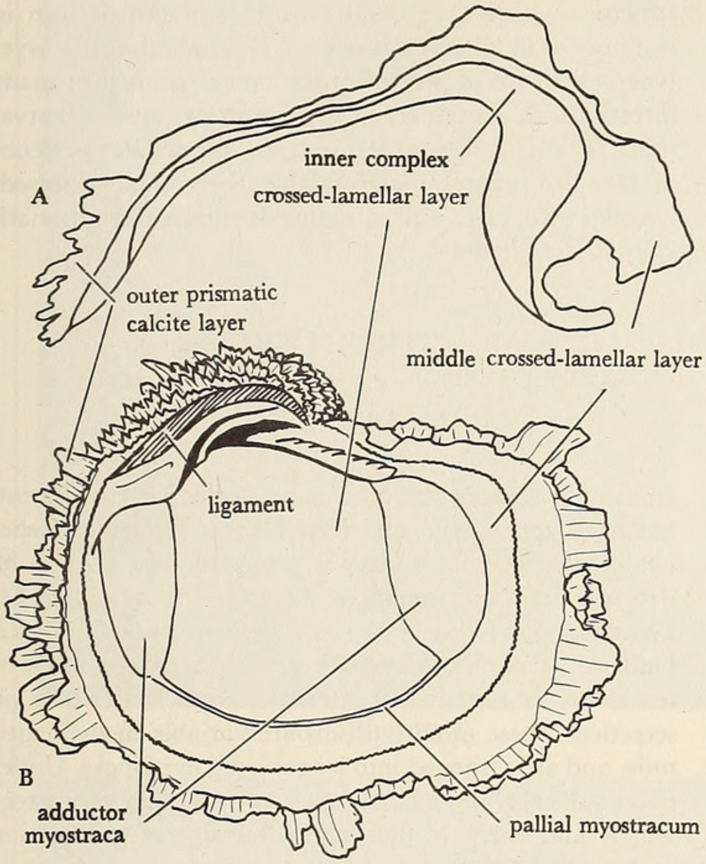

Figure 2

Distribution of shell layers in *Chama pellucida*
A – section B – shell interior

The structure of the various parts of the shell is described below.

STRUCTURE
OF THE
CROSSED-LAMELLAR LAYER

Conventional microscopy shows the inner surface of this layer as a series of elongate, branching and interdigitating lenses. These are arranged with their long axes running concentrically, parallel to the shell margins. These lenses are the first order lamels of Bøggild (1930). In sections, these lamels run normal to the inner surface of the shell layer, although often bending and turning towards the outer surface of the shell. They often branch and interdigitate, producing a strong interlocking structure (Plate 64, Figures 20, 21).

Thin sections and peels of this layer show a very striking colour pattern, with adjacent first order lamels being either straw or red-brown in colour.

Lamels may be up to several millimeters long, and are usually of the order of 0.5 mm wide. Sections of the umbonal region show a characteristic pattern of diverging primary lamels.

Internal structures of first order lamels are not easily resolved at optical level. It can be seen, however, that each first order lamel is built of second order lamels which are inclined to the shell interior, with opposed directions of inclination in adjacent first order lamels. Each second order lamel appears to be built of smaller laths, joined in side-to-side contact. Becke line studies reveal that the whole of the crossed-lamellar layer is an intergrowth of aragonite crystals in only two crystallographic orientations.

These observations are confirmed and extended by electron microscopy (Plate 62, Figure 12). These results are summarised in Text figure 3. Thus the whole layer can be seen to be built of minute laths, lying parallel within each first order lamel, and joined into sheets. These laths are up to 1μ in diameter, and some tens of

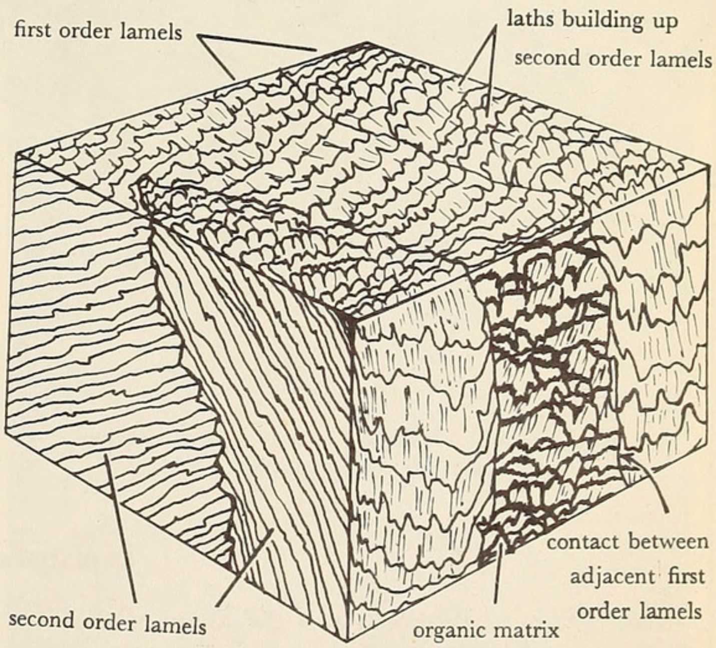

Figure 3

Block diagram of crossed-lamellar structure,
based on electronmicrographs

microns long. Etching reveals the presence of lace-like membranes within the crossed-lamellar layer; these correspond to the proteinaceous organic matrix well known in molluscan nacre and prisms. (GRÉGOIRE, 1967, with references.)

STRUCTURE OF THE COMPLEX CROSSED-LAMELLAR LAYER

Peels and thin sections (Plate 61, Figures 2, 6, 7) show that this layer is built up of the same basic elements as crossed-lamellar structure, i. e., laths arranged into second order lamels. These are not arranged into lenticular first order lamels, but form irregular interdigitating blocks, with lamel attitudes similar within blocks, but opposed in adjacent blocks. Sections show areas of granular appearance between blocks which have a distinct lamel structure within them, and since this pattern is seen in sections cut in all orientations, we conclude that this layer type is built up of second order lamels inclined in many directions. Electronmicroscopy confirms these observations (Plate 62, Figure 9), and also shows the presence of lace-like organic matrix within the complex crossed-lamellar structure. This structure is shown diagrammatically in Text figure 4.

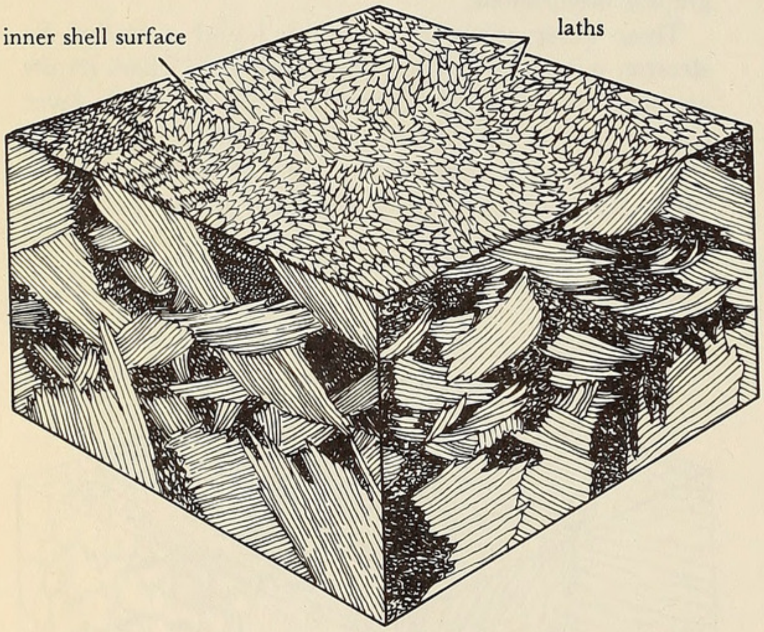

Figure 4

Block diagram of complex crossed-lamellar structure, based on electronmicrographs

STRUCTURE OF THE PRISMATIC LAYER

In hand specimens, this layer has a distinctive translucent, 'pellucid' appearance, and gives *Chama pellucida* its specific name. The outer layer is projected into a series of irregular folia and squamae. At optical level (Plate 61, Figures 3, 4, 5) this layer has a grey appearance, and is built up of minute blade-like prisms, arranged more or less normally to the shell interior margin at the time of secretion. These minute prisms are variable in their attitude, and are arranged into longer irregular blocks. Under polarised light, these blocks go into extinction very irregularly, and there is thus no uniformity of orientation within the blocks.

This structure is markedly different from that of the calcite prismatic layer of most other bivalves, in that thick conchiolin walls are not developed between prisms.

There is a variable relationship at the contact between the prismatic layer and the crossed-lamellar layer. The inner surface of the prismatic layer shows irregular corrugations arranged radially from the umbo which are impressions of radial musculature of the mantle. Over wide areas of the contact there is a marked discontinuity with a zone of fine-grained aragonite, rich in organic matrix (Plate 64, Figures 21, 22, 23). This fills up the underlying grooves in the corrugated surface. Elsewhere, minute angular calcite crystals project into the outer part of the aragonite crossed-lamellar layer (Plate 64, Figure 22).

Explanation of Plate 62

Figure 9: Scanning electronmicrograph of a fractured section of the inner complex crossed-lamellar layer of *Chama macerophylla*. Parts of three blocks of parallel laths are shown, the inclination of laths in each block is different. × 550

Figure 10: Scanning electronmicrograph of a polished, HCl-etched section of the crossed-lamellar layer of *Chama pellucida* showing sheets of fenestrate organic matrix. × 1 400

Figure 11: The inner surface of a myostracal pillar in the inner layer of *Chama macerophylla*. Note the irregular form of the myostracal pillars and grooves between the prisms. Scanning electronmicrograph. × 2 200

Figure 12: Fractured section of the crossed-lamellar layer of *Chama macerophylla*. The contact of two first order lamels is shown, the second order lamels and laths of each first order lamel are inclined in opposed directions. Scanning electronmicrograph. × 1 100

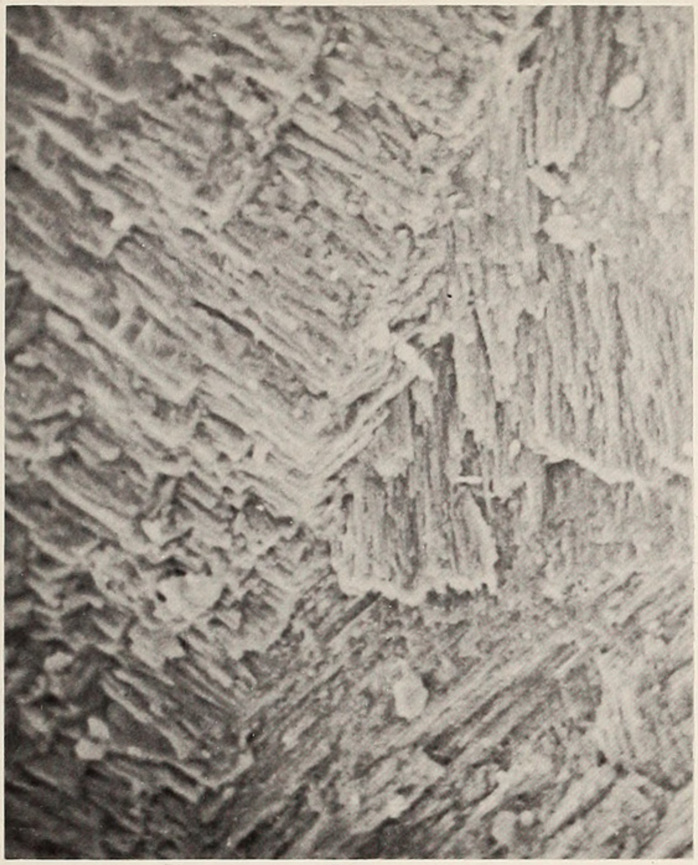

Figure 9

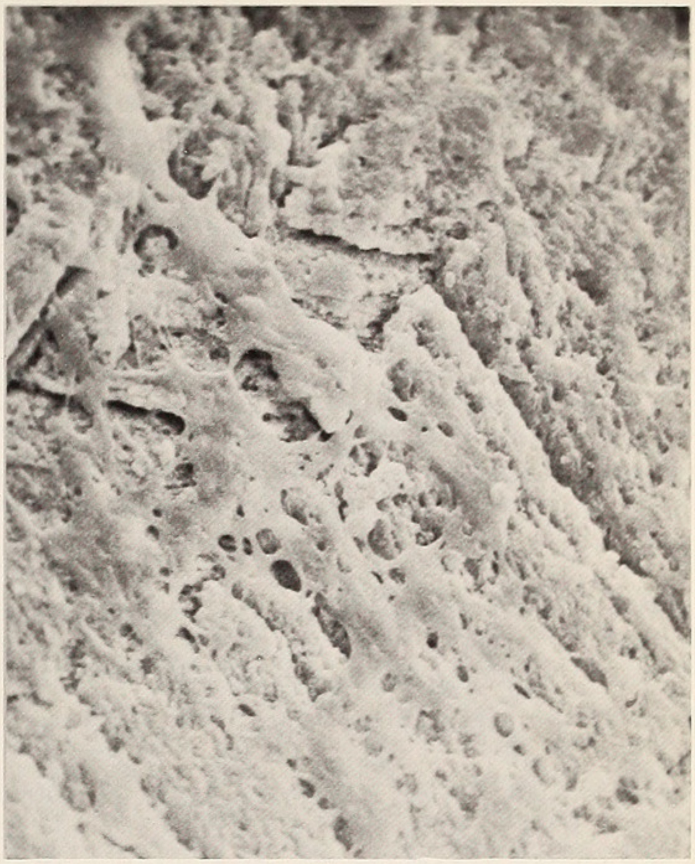

Figure 10

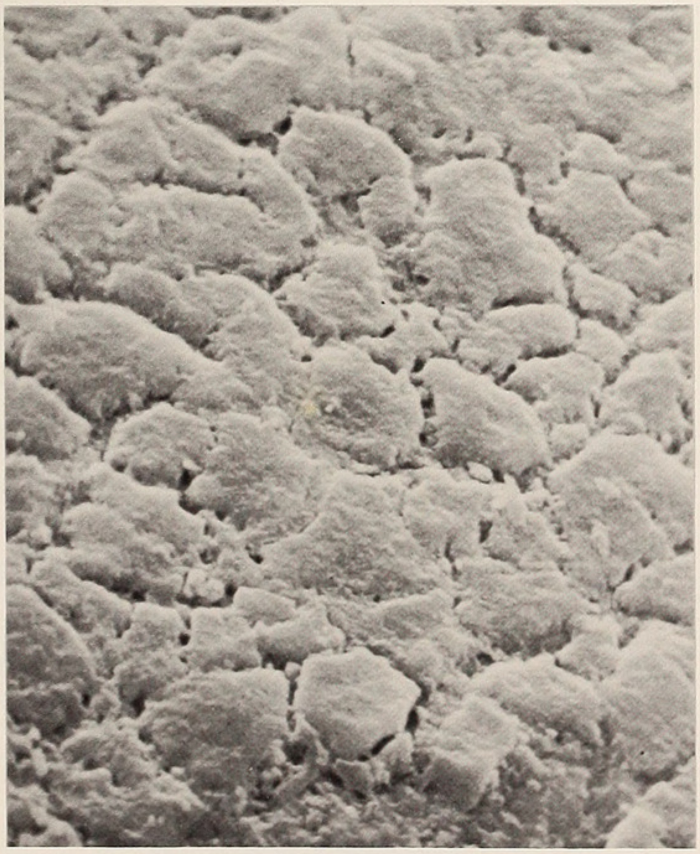

Figure 11

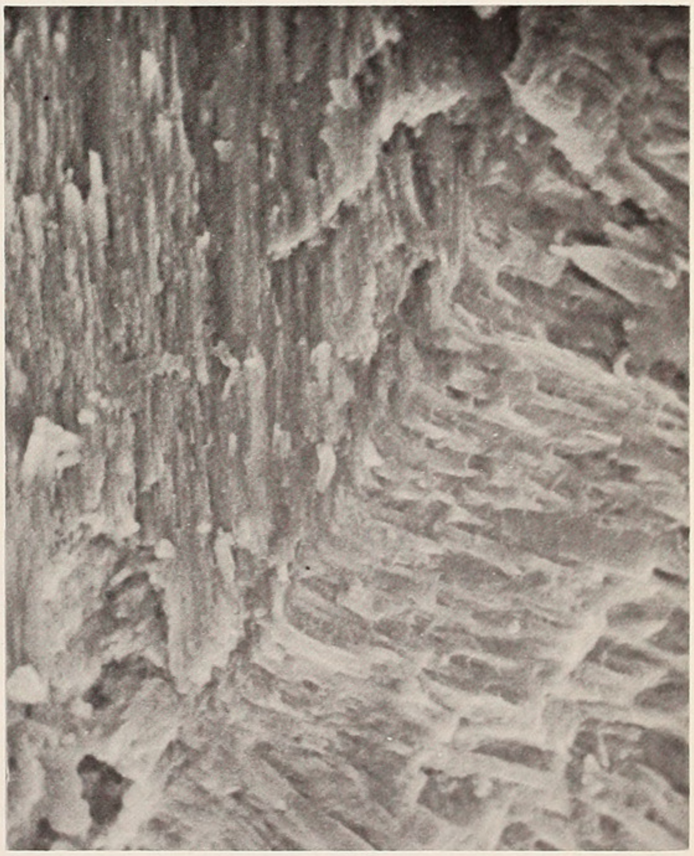

Figure 12