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On iridescent shells—Part I. Introductory

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1. Introduction

The study of the iridescence of nacreous shells is of importance from various points of view. The employment of the material in decorative art and for other useful purposes gives the subject some practical interest and invests it with an appeal even for the layman. Students of physical optics had long been familiar with Sir David Brewster's pioneer investigations on the origin of the colours of mother-of-pearl, references to which were to be found in most treatises on light, and were apt to imagine that the subject had been fully elucidated. This impression was dispelled by the more recent studies of A H Pfund[1] and of Lord Rayleigh[2] which served to draw attention to the subject and revealed some features overlooked by Brewster. The present investigation indicates that the subject has so far been only very imperfectly explored and offers much scope for further research.

To the chemist and the crystallographer, the structure of the nacreous substance offers problems of peculiar interest. The periodic stratifications which are characteristic of the material depend on the presence, distributed through the volume of the substance, of a small proportion of an organic compound—conchyolin—which serves to hold the particles of calcium carbonate together and gives strength and elasticity to the structure. These facts have led colloid chemists to postulate that mother-of-pearl is essentially analogous to the periodic precipitates in gels studied by Leduc,[3] Liesegang and others. It has even been claimed that by slow precipitation of calcium carbonate by diffusion in a gelatinous medium, structures resembling mother-of-pearl in their structure and optical properties have been synthesised.[4] One of the remarkable features of

[1] A H Pfund, *Franklin Inst. J.*, 1917, **183**, 453.
[2] Lord Rayleigh, *Proc. R. Soc.* (*A*), 1923, **102**, 674.
[3] Leduc, *Alexander's Colloid Chemistry*, New York, 1928, **2**, 72.
[4] Clement and Riviere, *Alexander's Colloid Chemistry*, New York, 1932, **4**, 503.

mother-of-pearl is that the calcium carbonate is present in the form of aragonite instead of the commoner crystalline variety calcite. Optical and X-ray examination indicates that in many cases the crystals of aragonite are laid down with considerable regularity so as to build up the laminated structure of nacre. It may be remarked that the foliated structures containing calcite present in certain shells, e.g., the *Anomiidae*, though sometimes faintly iridescent, do not show the characteristic properties of nacre. Why the aragonitic form of calcium carbonate is preferred and what determines the size and orientation of the crystals in nacre are problems still awaiting solution.

To the zoologist, the nature of the nacreous substance in molluscan shells is part of the general problem of the structure of calcareous shells and the manner of their formation and growth from the secretions of the animal which they enclose, on which subjects there has been a great output of literature. Owing to the kindness of the present Director of the Zoological Survey of India who is himself a specialist in this field of research, I have obtained access to the most recent zoological publications on the structure of calcareous shells. Detailed references to the literature will be found later in the course of this paper. It will be sufficient here to mention the name of W J Schmidt who is very generally regarded as the principal authority in this field and whose book is an invaluable work of reference.[5] A very complete account of Schmidt's latest work is contained in a monograph on bivalves by F Haas.[6]

If anything were needed to add to the fascination attaching to the subject of the iridescence of mother-of-pearl, it is the connection between it and the study of the pearls (natural or cultured) found in association with it in molluscan shells.[7] It is known that the structure of pearls presents many points of analogy with that of mother-of-pearl[8] and the optical characters of the two substances are therefore very intimately related.

2. Material for the study

According to Boggild,[9] the nacreous substance is rather common among the three main groups of the molluscs, the Pelecypoda, the Gastropoda and the Cephalopoda, while it is never found outside the molluscs. The shell structure of the molluscs is elaborately described in Boggild's memoir and the families in which a nacreous layer is to be found are enumerated. It will be sufficient for our

[5] W J Schmidt, *Die Bausteine Des Tierkorpers in Polarisertem Lichte*, F Cohen, Bonn. 1924.
[6] F Haas, *Bronn's Klassen und Ordnungen Des Tierreichs*, 3, iii, 3, Akad. Verlag. Leipzig, 1931.
[7] L Boutan, *La Perle. Gaston Doin*, Paris, 1925.
[8] F Haas, *Bau und Bildung Der Perlen*, Akad. Verlag. Leipzig, 1931.
[9] O B Boggild, *Mem. R. Acad. Copenhagen*, 1930, 2, 235.

purpose to mention some of the material available which is specially suitable for the purpose of optical study.

The bivalves include the following families in which a nacreous layer is present:

Aviculidae, Pinnidae, Pernidae, Vulsellidae, Mytilidae, Nuculidae, Nayadidae, Trigonidae, Anatinidae.

The large family of the *Aviculidae* is of great interest to Indian students, for in the waters of the Indian Ocean[10] are found some of the best known representatives; they include the Pearl-Oyster (*Margaritifera*), the Wing-shells (Aviculids proper) and the Hammer-Oyster (*Malleus*). The Indian and Ceylon Pearl-Oyster (*Margaritifera vulgaris*) is amongst the smallest of its kind and compares unfavourably in size with the huge Gold-lip Pearl-Oyster from Mergui and the South seas, a species with shell large enough for a dinner-plate. The larger Black-lip Oyster (*M. Margaritifera*) is also occasionally found in the Indian seas, and is a handsome stoutly-built shell with a thick layer of nacre. Figure 8 in the plate represents a carved shell of pearl-oyster exhibiting a beautiful lustre and iridescence. The Aviculids proper, the true Wing-shells, have often very curious shapes (e.g., *Pteria castanea, Pteria semisagitta*), and include some larger forms (*Pteria macroptera*) displaying plenty of iridescent nacre. The *Pinnidae* are represented in Indian waters by several species of which the commonest is *Pinna bicolor*, a big wedge-shaped shell often a full foot in length, and *Pinna fumata* which is shorter and stouter. *Vulsella rugosa*, a deep oblong shell without ears is the chief Indian representative of the *Vulsellidae*. The *Mytilidae* form a large family, the three common genera in Indian seas being *Mytilus*, *Modiola* and *Lithodomus*. Deserving of special mention is the very handsome green mussel (*Mytilus viridis*) widely distributed round the South Indian Coast and readily recognised because of the striking green colouration of the horny membrane or periostracum investing the exterior surface of its valves. This shell can be found in fairly large sizes and displays a beautiful and characteristic iridescence in its nacreous layer. Amongst the numerous fresh-water bivalves of India,[11] the mussel *Lamellidens marginalis* is a conspicuous species. It has a thick layer of nacre which, however, exhibits little colour.

The gastropods, according to Boggild, include the following families in which a nacreous layer is present:

Pleurotomariidae, Haliotidae, Stomatidae, Turbinidae, Delphinulidae, Trochidae, Umboniidae.

This group of molluscs includes some of the most gorgeously iridescent shells known, amongst which should be mentioned particularly the *Haliotidae*, the

[10] J Hornell, *The Common Molluscs of South India*, Govt. Press, Madras, 1924.

[11] H B Preston, *Fauna of British India: Freshwater Molluscs*, London, 1915.

Turbinidae and the *Trochidae*. A common Indian species among the Ear-shells is *Haliotis varia*, which, however, is quite a small one, seldom exceeding $1\frac{1}{2}$ inch in length—a poor representative of the family. Much larger specimens of the *Haliotidae* are to be found in the waters around France, Japan, New Zealand and California, attaining lengths from 4 to 6 inches and displaying a vivid colouration of the mother-of-pearl lining of the shell. The Californian specimens of the *Haliotidae*, known locally as the abalone, are the most remarkable in this respect. At least three distinct species of abalone are known which differ greatly in their optical characters, as will be described more fully later. The polished convex surfaces of the shells of two species of abalone are illustrated in figures 1 and 2. Other species of *Haliotidae* of large size are known which differ from the abalone in being far more translucent to light. The *Turbinidae* and the *Trochidae* include numerous species and are some of the commonest shells to be met with on the South Indian littoral, but usually only in relatively small sizes. Very large specimens of *Turbo* and *Trochus* are, however, available from the vicinity of the Andaman and Laccadive islands, and when cleaned and polished externally make a remarkable display of lustre and iridescence. One such shell of *Turbo* (not of specially large size) is illustrated in figure 3. *Trochus* shells in large sizes also make beautiful and lustrous objects when the nacreous layer is exposed, though the colours are less vivid than with *Turbo* shells. One such shell of *Trochus* from which the periostracum and prismatic layer had been brushed out with dilute hydrochloric acid is illustrated in four different positions in figures 4, 5, 6 and 7. The conical form, the spiral structure, the sculpturing on the ridges and the lines of growth on the nacre are all beautifully seen.

Unique amongst the Cephalopods is the well known *Nautilus pompilius*, shells of which are a familiar sight on tropic beaches. Many text-books on Zoology contain figures of the remarkable internal architecture of this shell containing a series of septa with a perforation running through them. In the natural state, the shell is covered externally with a thin white enamel-like layer ornamented with brown stripes. When this is brushed off with dilute acid, the beautiful nacreous substance is exposed which exhibits bands of colour following the visible lines of growth on the shell. One such specimen, unfortunately incomplete, is illustrated in figure 9. The septa which may be exposed by sawing the shell in two also consist wholly of nacre. It may be mentioned that the septa of the beautiful little *Spirulidae* are nacreous but are not iridescent.

3. Structure of iridescent shells

The shell structures of molluscs generally, and in particular, the structures of the various layers in iridescent shells have been the subject of elaborate investigation by zoologists. Accounts of the subject are given by W J Schmidt in his book, by Boggild in the memoir already quoted, and a detailed review with numerous illustrations in F Haas's monograph on the bivalves. The subject has been studied mainly by the examination under the polarisation microscope of thin sections of the shell cut in one or another of three perpendicular directions, namely parallel to the surface of the shell, transverse to the surface and either parallel or perpendicular to the lines of growth on it. Many photographs under low magnifications of such sections illustrate Boggild's monograph. It appears that the nacreous structure is only one of the numerous forms which the calcareous substance in shells can assume. Boggild describes no fewer than eight different modes of aggregation, the four commonest according to him being "the homogeneous", "the prismatic", "the crossed lamellar" and "the nacreous" structures. A fifth kind namely "the foliated structure" is of special interest as it also exhibits a pearly lustre and appears in certain families, namely in the *Ostreidae, Pectinidae, Spondylidae* and the *Anomiidae*; it differs however from the nacreous structure in being less regular and in being composed of calcite instead of aragonite.

In all iridescent shells, we have at least three layers, the first and outermost being the periostracum which is a thin layer of organic material known as conchin or conchyolin. This is followed by a second layer which in most bivalve shells is prismatic in structure, but in certain others, e.g., the *Mytilidae*, the *Stomatidae*, the *Turbinidae* and the *Trochidae*, is "homogeneously prismatic" and in the *Haliotidae* "homogeneously grained". This second layer is followed by the nacreous substance which save in a very few cases is the innermost or final layer.[12] The outer layers namely, the periostracum and the prismatic layer, may be removed mechanically, or alternatively by brushing with dilute hydrochloric acid which acts upon them more readily than upon the nacreous substance. The latter which is thus exposed may then be ground and polished in order the more effectively to display its optical properties.

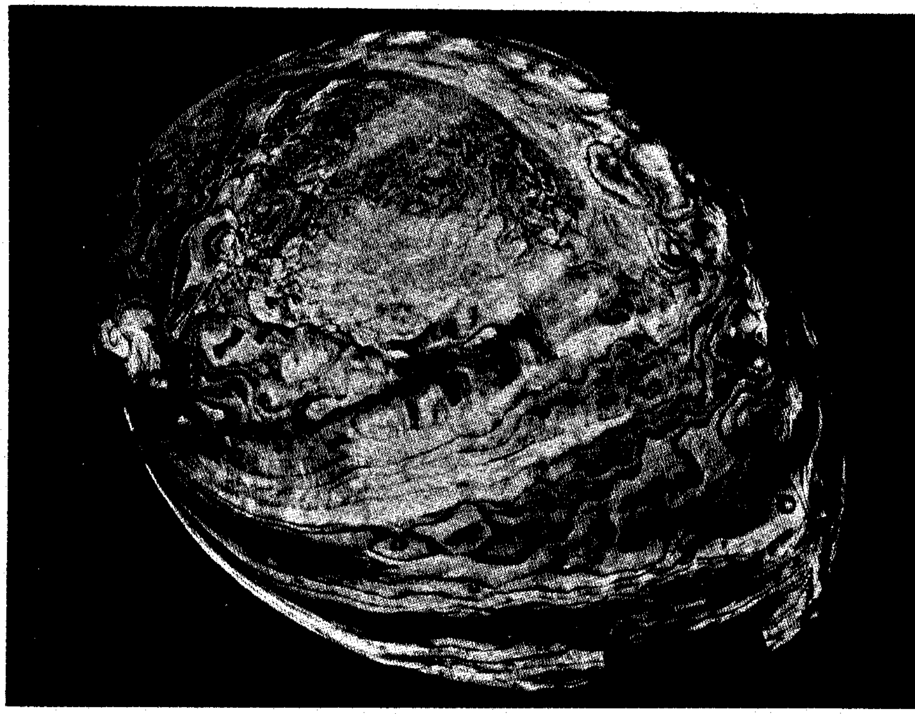
The chemical and physical nature of the nacreous substance has been elaborately investigated and described by W J Schmidt and illustrated by numerous diagrams and photographs. We may here quote Schmidt's definition of the nacreous substance. "Mother-of-pearl consists of microscopically small, tablet-shaped crystals of aragonite formed along the basis, the so-called platelets of mother-of-pearl,—which are regularly arranged in positions parallel to the surface of the shell and are cemented together by an organic substance, the so-called conchin or conchyolin." The platelets so held together form elementary laminae and these are in their turn superposed on one another in great numbers and cemented together by immeasurably thin layers of the same organic substance. The individual platelets of aragonite are about 10μ in diameter; they are sometimes rounded in form (for instance in *Meleagrina* and *Pinna*), sometimes

[12] "The Helle Schicht" or "Hypostrakum" which appears on the shell at the regions of attachment to it of the muscles of the animal is regarded by Schmidt as merely a modification of the nacreous layer, but this is a disputed point.

bounded by straight edges (e.g., in *Mytilus*) and may also assume other shapes. The thickness of the elementary laminae corresponds to that of the platelets of which they are composed, and is of the order of magnitude 1μ but may vary between the extreme limits 0·5 and 2μ in different species. According to Schmidt, the statement often found in the older text-books that mother-of-pearl consists of alternate and equally thick layers of calcareous and organic material is definitely erroneous. (This erroneous statement is, strangely enough, repeated by Boggild in his memoir quoting Schmidt as his authority.) That the actual thickness of the organic layers is immeasurably small compared with that of the aragonite layers has been inferred by Schmidt from his observations of the cross-sections of mother-of-pearl under the highest available magnifications.

From his studies of cross-sections of mother-of-pearl under the polarisation microscope, as also of the tiny crystalline platelets separated by digesting the material with alkali, Schmidt drew important conclusions regarding the optical characters of the substance. According to him, mother-of-pearl is an aggregate of crystals, which both in the individual elementary laminae and also in neighbouring ones are arranged essentially parallel to one another. This regular arrangement of innumerable single crystals explains the more or less complete optical homogeneity of the substance, as shown by the more or less uniform extinction and axial picture which is determined by the aggregate effect of the regularly-arranged ultimate units. The transverse cross-sections have their extinction parallel to the laminae and always behave as optically negative with reference to the normal to the laminae. The parallel sections have their extinction parallel to the lines of growth on the shell and generally behave as positive (rarely as negative) with reference to this direction. The normal to the laminae is the first middle line of the axial picture seen in the parallel section. The c-axis is therefore normal to the elementary laminae, and the lines of growth lie in the axial plane and are parallel to the macro-axis. (In rare cases, the axial plane and the lines of growth cross each other, and the latter then correspond to the brachy-axis.) The form and arrangement of the platelets determine the structure of the substance, and the intimate connection between the morphological structure and the optical properties is thus explained. Smaller and larger disturbances of the regularity of the structure show themselves in the incompleteness and irregularity of the extinctions and the varying values of the axial angles.

Note—The photographs illustrating this paper were taken by Mr C S Venkateswaran to whom my best thanks are due. To Dr Baini Prashad, Director of the Zoological Survey of India who furnished me with valuable specimens and loaned a collection of zoological literature I am greatly indebted. Dr H Srinivasa Rao, of the Zoological Survey, has also very kindly presented to me a collection of *Trochus* and *Turbo* shells from the Andamans. The scientific results of the study of the material placed at my disposal by these and other friends will be reported upon in the subsequent instalments of the paper.



(1)

(2)

Figures 1 and 2. Abalone shell (*Haliotis* Sp.).

Plate I

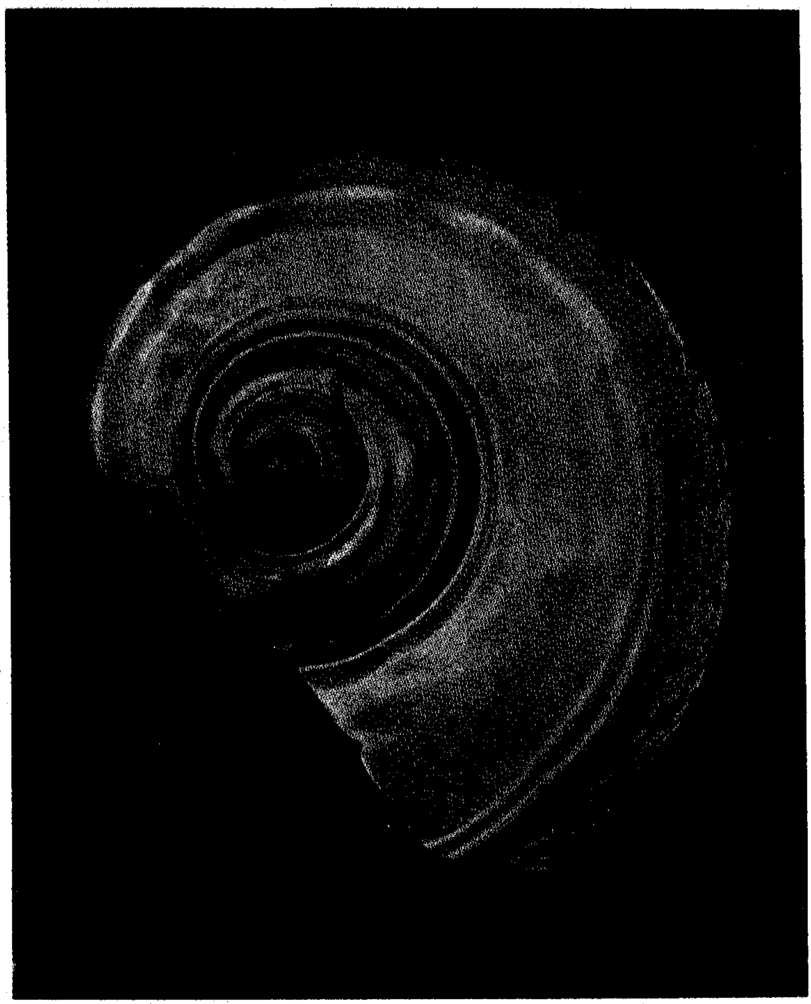
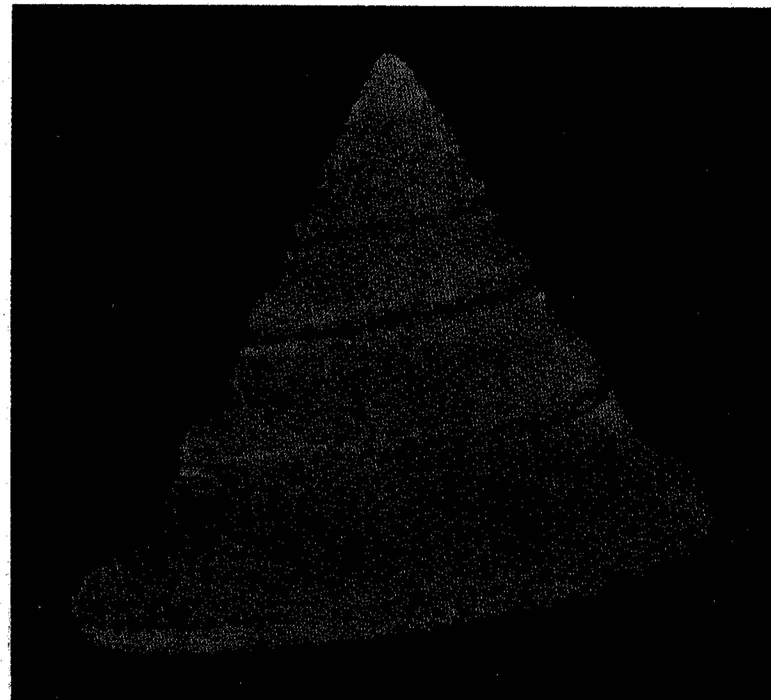


Figure 3. Shell of *Turbo* Sp.

Plate II



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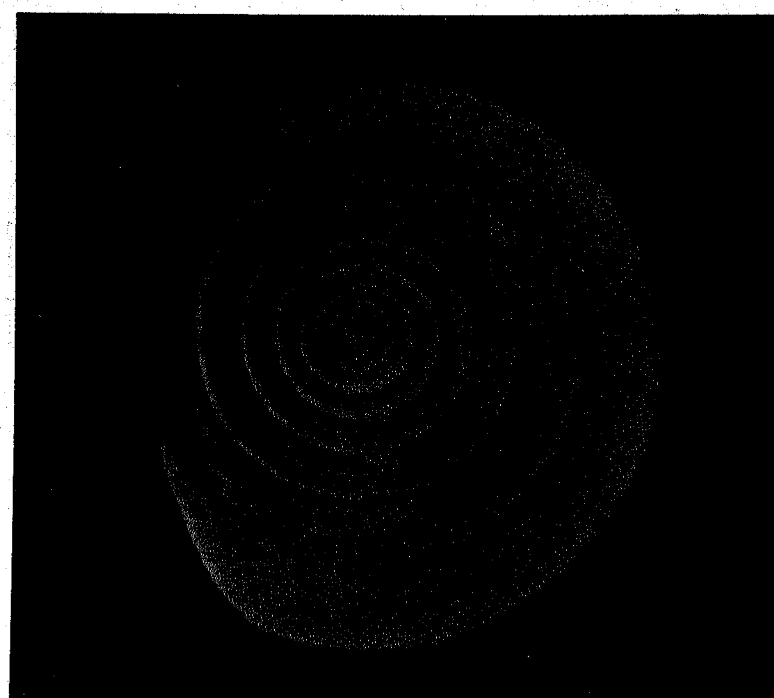
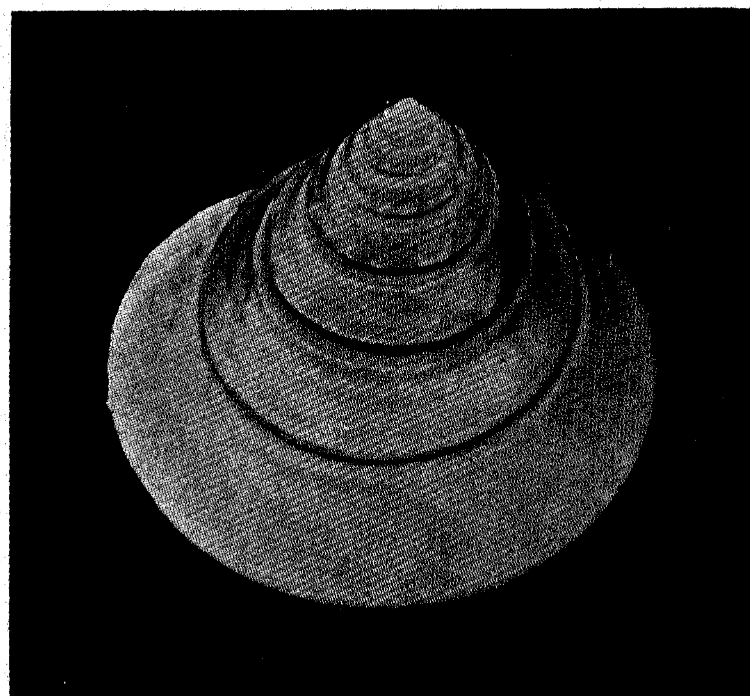


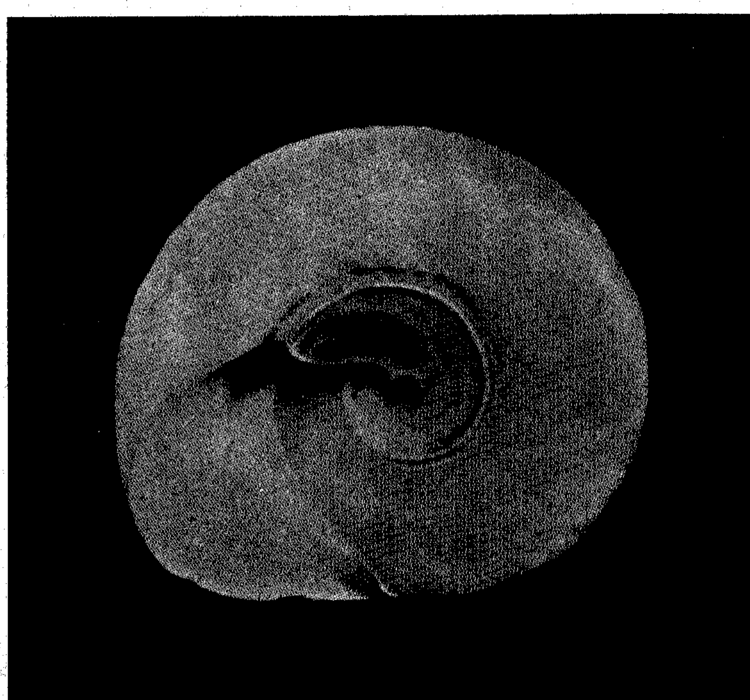
(5)

Figures 4 and 5. Shell of *Trochus* Sp.

Plate III



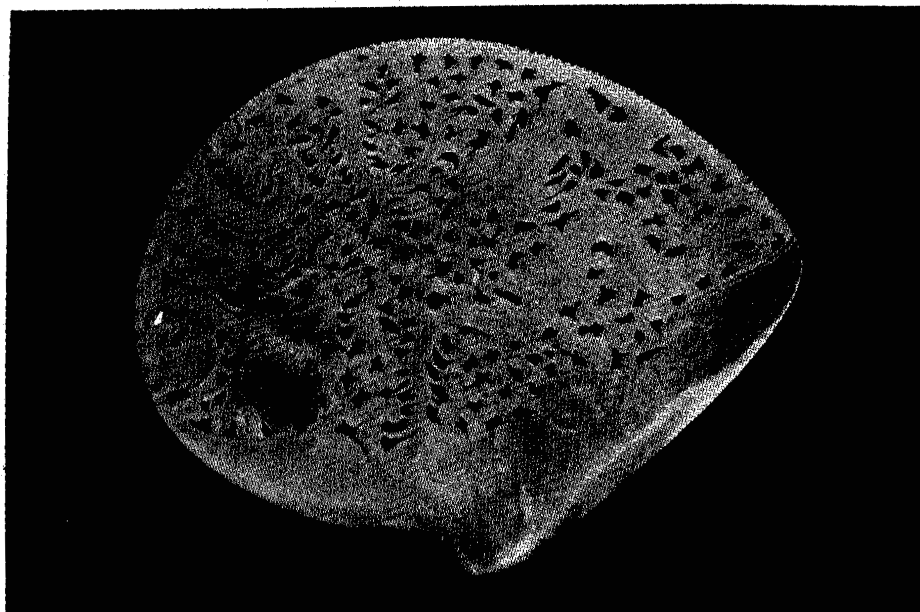
(6)



(7)

Figures 6 and 7. Shell of *Trochus* Sp.

Plate IV



(8)

(9)

Figures 8 and 9. 8. Shell of *Margaritifera*. **9.** Shell of *Nautilus pompilius*.

Plate V