the occurrence of this group in the eastern and central Pacific and in the western Indian Ocean, gives credence to the possibility that this group of mollusks, once thought to be extinct, may be fairly widely distributed in the abyssal depths of the world's oceans.

JOSEPH ROSEWATER

Division of Mollusks, U.S. National Museum of Natural History, Washington, D.C. 20560

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Microarchitecture and Deposition of Gastropod Nacre

Abstract. *The microarchitecture of gastropod nacre reveals deposition of aragonite in the form of crystal stacks and differs markedly from the characteristic microstructure of pelecypod nacre. The structure permits direct observation of both organic and mineral phases of deposition on a growth surface topography that is ideal for the study of processes of mollusk shell calcification. The stack mode of deposition is functionally useful to the animal because it increases the number of crystals which can form and develop on the growth surface at one time.*

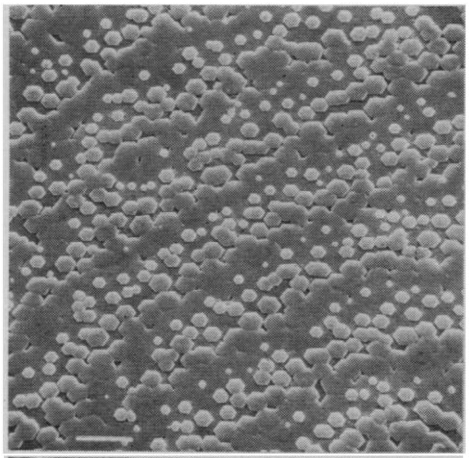
Mother-of-pearl (nacre) (*1*), an organic material of unusual luster, iridescence, and economic importance, has long been an object of microscopic study (*2*). Investigations by transmission electron microscopy have elucidated its submicroscopic appearance in pelecypods and cephalopods and have provided evidence in support of the epitaxial theory of shell calcification (*3*); however, the microarchitecture of gastropod nacre has received little study. A preliminary investigation of the gastropod *Cittarium pica* (*4*) revealed crystals of nacre deposited on growth surfaces in tall vertical stacks formed coeval with a system of expansive organic membranes. I show here that mineral deposition in crystal stacks is the characteristic pattern of calcification in gastropod nacre. This deposition produces a microarchitecture distinguishable from that most commonly observed in pelecypod nacre and forms a growth surface topography ideal for the study of the deposition of both organic and mineral phases of shell.

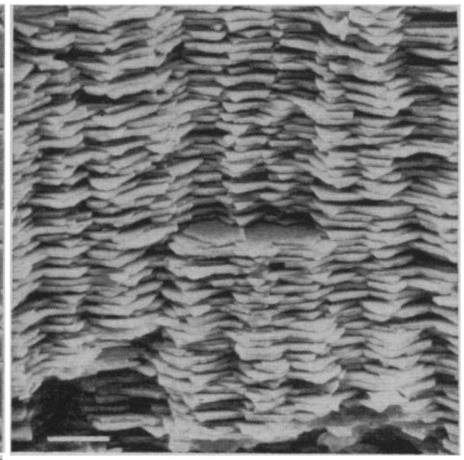
Specimens representing all superfamilies of Recent gastropods secreting mother-of-pearl, including *Haliotis rufescens, Astrea caelata, Turbo castanea, Tegula funebralis, Callistoma ligatum, Margarites pupilles, Norrisia norrisi*, and additional specimens of *Cittarium pica*, have been studied by scanning electron microscopy. Preparation techniques have been described (*4*). In all specimens the growth surface of the nacreous layer was covered by tall, evenly spaced conical stacks (see cover). Incipient aragonite crystals form at the tops of the stacks and then expand laterally with growth as more crystals form on top. Continued lateral growth of older crystals maintains the conical shape of the stacks and produces flat tabular crystals similar to those observed in the nacre of pelecypods and cephalopods. Lateral expansion ultimately brings crystals of adjacent stacks into contact; these crystals then coalesce to form the broad mineral laminae which characterize the nacre of all mollusks. This mode of deposition is quite different from that observed in most pelecypods. The nacre of bivalves typically exhibits an imbricate growth surface topography composed of mineral laminae which overlap in a steplike pattern (Fig. 1). New crystals are deposited at the margin of each step; they expand laterally with growth and eventually merge with the laminae to extend the structure.

Schmidt (*2*) observed the imbricate growth surface pattern in all of the pelecypods he studied, a total of 24 species representing a wide variety of freshwater and marine forms. He also noted that in vertical cross section the individual crystals of pelecypod nacre are usually arranged like bricks of a wall laid in the common "running bond" configuration, and that this arrangement is a direct consequence of the imbricate mode of deposition. Schmidt called this pattern the *backsteinbau* and found it to be a typical and recurring phenomenon in all the pelecypod families he investigated. In contrast, my study reveals that vertical sections through gastropod nacre exhibit a striking columnar appearance (Fig. 2) which results from the crystal stack mode of deposition. This stacked pattern can be detected in thin sections and fragmented particles by light microscopy and sometimes in replicas of polished and etched sections prepared for transmission electron microscopy. It is best displayed, however, in vertical fracture sections viewed with the aid of the scanning electron microscope. Such sections are easy to prepare because vertical fractures tend to follow the planes of weakness which parallel the stacks.

Stacks of crystals like those shown in Fig. 2 have been photographed in all gastropod species I examined, and no other construction has been observed. A similar columnar structure is reported in cephalopods (*5*). Out of all the pelecypods that Schmidt investigated (*2*), he found a vertical pattern developed only in the nacre of *Pinna* and in some specimens of the nut clam *Nuclea nuclea* (*6*). It is evident, therefore, that the microarchitecture of gastropod nacre differs significantly from the familiar *backsteinbau* construction found in most pelecypods. This information, if used with discretion (in view of the two exceptions mentioned above), can be helpful to sedimentologists and paleontologists in the analysis of fragmentary shell remains.

Expansive organic membranes were present on growth surfaces of all the specimens I observed (Fig. 3). In an earlier study it was not possible to determine the configuration and number of membranes present because of distortion produced when specimens were cleaned by boiling (*4*). The specimen shown in Fig. 3, however, was collected live and cleaned manually. At least three separate horizontal membranes or cohering sets of membranes are visible. In the background of the figure a thick organic sheet covered with debris generated when the shell was sectioned appears to be draped over the tops of the stacks; it was removed from the foreground by stripping the specimen with cellulose acetate peels (*4*). A second sheet, free of debris, crosses the stacks at mid-height. The hole in this sheet (center of figure) was opened thermally by concentrating the electron beam at this spot, thus revealing a third sheet near the bottom of the hole. Remnants of another possible membrane stretch between crystal stacks in the foreground. In another specimen treated ultrasonically, four or five closely spaced membranes were stretched between the higher crystals of two neighboring stacks. These observations indicate that numerous membranes were originally deposited on the growth surface but have since dried together into the three or four thick sheets seen now.





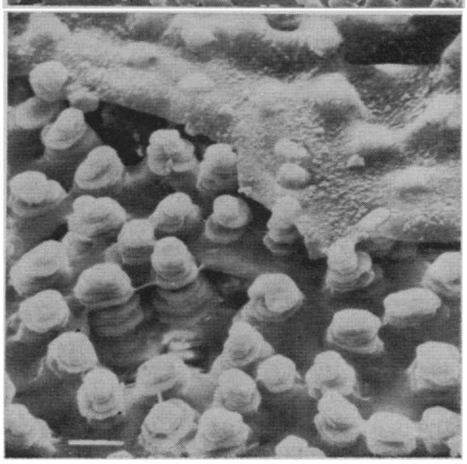


Fig. 1 (top left). Growth surface of the nacreous layer in *Pinctada radiata* (pelecypod). New crystals form at the margins of the overlapping mineral laminae (scale, 10 μm). Fig. 2 (top right). Vertical fracture surface through the nacre in *Haliotis rufescens* (gastropod), showing the columnar stacking of crystals in the pattern characteristic of gastropod nacre (scale, 5 μm). Fig. 3 (bottom left). Growth surface of the nacreous layer in *Cittarium pica* (gastropod). Several horizontal organic membranes or cohering sets of membranes stretch between crystal stacks (scale, 5 μm).

This interpretation, previously considered unlikely (*4*), is quite reasonable in view of Bevelander and Nakahara's recent demonstration of the existence of "membrane envelopes" on the growth surface of the pelecypod *Pinctada radiata* (*3*). Conclusive proof of an episodic deposition of organic membranes alternating with mineral deposition in gastropod nacre would support the epitaxial theory and would explain the precision by which crystals of adjacent stacks merge to form horizontal mineral laminae. It may be possible to determine more precisely the actual configuration of the membranes by one or other of two methods developed recently: (i) scanning electron microscopy of freeze-dried and ion-etched specimens (*7*); and (ii) transmission electron microscopy of ultrathin sections cut perpendicular to the growth surface by the microtomy techniques of Bevelander and Nakahara (*3*).

Deposition of nacre in the form of tall crystal stacks is functionally advantageous to the animal. It permits more crystals to form and develop within a given amount of growth surface area, thus increasing the amount of shell which can be deposited in a given amount of time. This is particularly significant in the case of gastropods because in most forms the growth surface of the nacreous layer is very limited in that it consists of a narrow band a few millimeters wide located just inside the aperture. The stacked mode of deposition permits a relatively thick layer of nacre to be deposited within this narrow growth zone. At the same time the layer itself can be extended in the apertural direction at the same rate as the other layers of the shell. In most pelecypods the growth surface of the nacre covers a much broader area of shell in proportion to the thickness of the layer, and the stacked mode of deposition is not necessary for the construction of a thick layer. As seen in *Pinctada*, the developmental surface of the nacre covers the entire inner area of the shell, thus making it possible for further deposition to augment the thickness of the layer throughout the life of the animal.

Differences between gastropod and pelecypod nacre were not more apparent to earlier microscopists because of the inherent limitations in the light microscope and in the carbon replica technique used for transmission electron microscopy. In addition, there was little attempt to synthesize and verify existing data. Simroth (*8*), in a review of prosobranch gastropods, did mention that gastropod nacre appeared more prismatic; however, because of a lack of suitable examples, he cited descriptions of *Mytilus* and *Pinna* to explain the structure. Frank (*9*) observed closely spaced vertical lineations in cross sections of *Gibbula cineraria*, and Ahrberg (*2*) noted the systematic columnar stacking of individual crystals in cross sections of *Trochus adriaticus* and *Turbo ticaonicus*. However, Ahrberg erroneously concluded that the mode of formation of nacre in *Trochus* and *Turbo* followed the model described by Schmidt (*2*) for pelecypods. From the evidence I have presented, it is apparent that Carpenter (*10*) did observe the broad outlines of crystal stacks in *Haliotis splendens*. Although individual crystals could not be resolved, his composite drawing published in 1847 shows the crystal stacks as tubular structures in section and as rounded mounds on the growth surface. This remarkable illustration was largely ignored by later investigators, possibly because of confusion resulting from Carpenter's adherence to the cell theory of shell calcification. He believed that shell was formed by the deposition of calcium carbonate in animal cells which covered the inner shell surface (*11*). Supposedly, cell outlines could be detected in cross sections of shell, and cell nuclei were even reported in the prisms of *Pinna*. Carpenter quite naturally labeled the crystal stacks "cells." Bøggild (*1*), however, who was mystified by Carpenter's report, was unable to find "cells" in *Haliotis*; this statement closed the discussion on Carpenter's discovery until the present study.

SHERWOOD W. WISE, JR.

Department of Geology, University of Illinois, Urbana 61801

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11. This idea was held by J. S. Bowerbank [*Trans. Microsc. Soc. London* **1**, 123 (1844)] and later subscribed to by J. Quekett [*Lectures on Histology* (Bailliere, London, 1854, vol. 2] and by S. P. Woodward [*Intellectual Observ.* **10**, 241 (1866)].
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Magnetometer Evidence of a Structure within the La Venta Pyramid

Abstract. *The pyramid at La Venta, Tabasco, Mexico, was surveyed in May 1969 with a high-sensitivity difference magnetometer. The general pattern of the magnetic map is one of low (10-gamma) radial anomalies, which reflect the ridge and gully topography of the pyramid, with a larger magnetic high area (+30 gammas) centered 25 meters south and 10 meters east of the center of the pyramid. The anomalous region near the top has been interpreted with the aid of computer-calculated anomalies from three-dimensional rectangular blocks. The major high is probably associated with a basalt structure that rises to within 1 to 2 meters of the surface. A possible form for this structure was found to be a 10-meter-square horizontal platform with walls along its northern and eastern margin.*

The La Venta pyramid (Fig. 1), although the largest single structure at the important Olmec ceremonial center in lowland Tabasco, has until recently received scant attention from researchers at the site. Investigations there by M. W. Stirling and P. Drucker in 1940–42 centered around the unique art style embodied in the large carved stone monuments and the problems of ceramic stratigraphy (*1*). The large-scale explorations of Drucker and Heizer in 1955 concentrated on the unexpected complexities of complex A (*2*). Although the entire site was mapped, the pyramid (also referred to as complex C) was covered with a dense growth of jungle cover and was incorrectly reported by the party surveyor to be a somewhat elongated rectangle. Drucker and Heizer found in 1967 that the pyramid was actually a fluted cone or, more technically, a conoidal frustum (*3, 4*). Ten alternating valleys and ridges were seen to run up and down the structure's 100-foot elevation, spaced at roughly equal intervals around its circular basal plan. In 1968 a University of California field party completed a detailed topographic map of the entire pyramid structure that constitutes complex C (*5, 6*).

This new information, as well as providing new facts and fresh insights into the history of Olmec culture (*4, 6*), has generated a certain interest in the unique structure itself (*7, 8*). Much of this interest, of course, revolves around the possible function of the great mound and the question of what it might contain. The 1969 magnetometer survey was conceived in the hope of providing partial answers to these questions. It was known that most of the large Olmec carved monuments, as well as the natural basalt columns that were used to border the plaza or "ceremonial court" and the "tomb" in complex A, were of a highly magnetic basalt secured from the Tuxtla Mountains, some 100 km to the west (*9*). Samples of clays from the site were tested and found to be effectively nonmagnetic. Thus it was felt that, had the Olmecs buried any large stone monuments or built any structures of basalt within the pyramid, they could be detected by a sensitive magnetometer. This hope was encouraged by the successful magnetometer survey in 1968 at San Lorenzo, about 31 km from the La Venta site (*7*).

Test calculations before the survey indicated that the increased sensitivity of a difference magnetometer would be required to detect significant basalt monuments within the pyramid. The principles of operation of such a magnetometer, which employs two Varian alkali vapor sensors, have been described (*10*). For the La Venta survey we borrowed a cesium sensor and leased a rubidium sensor from Varian Associates. The sensitivity of the magnetometer for the system used at La Venta was $\pm 0.0325\ \gamma$. (The earth's total magnetic field at La Venta is approximately 43,000 γ.)

To facilitate carrying the roving sensor with its dragging cable, the pyramid was cleared of the dense plant growth. Survey lines were then laid out radially with heavy white string that was marked off in 3-m intervals. Readings were taken at each 3 m out on one line, the line was then swung approximately 6 m in chord distance at the 60-m radius, and the line was surveyed again. Intermediate values between lines at large radii were filled in by estimating position.

Azimuth readings were taken periodically, and topographic features were noted on the survey lines so that the data could later be fitted accurately to the plan map of the pyramid.

The values at each station were recorded directly on radially scaled graph paper, a procedure that allowed preliminary contouring of data in the field. All the data were later digitized, the mean was removed, and the values were accurately machine-contoured in levels of 5 γ. The final magnetic contour map is presented in Fig. 2.

The large magnetic anomaly to the south of the center of the pyramid, contained within the inner rectangle of Fig. 2, is the feature of main interest in the survey. The pattern of this anomaly is complex, although it may conveniently be broken into two parts. The first is the broad high contained within the 10-γ contour, with an associated belt of lows roughly outlined by the zero contour, which runs from the southeast across the top of the pyramid and off to the northwest. Superimposed on this general high-low pattern is a further region of high values confined within the 20-γ contour. The very high gradient along the northern and eastern margin of the broad high suggests an origin near the surface, whereas the ex-