

SHELL ULTRASTRUCTURE
OF THE ATLANTIDAE
(HETEROPODA, MESOGASTROPODA)
OXYGYRUS AND *PROTATLANTA*, WITH
COMMENTS ON *ATLANTA INCLINATA*

ROGER L. BATTEN AND MICHAEL P. DUMONT

BULLETIN
OF THE
AMERICAN MUSEUM OF NATURAL HISTORY
VOLUME 157 : ARTICLE 4 NEW YORK : 1976

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BULLETIN OF THE AMERICAN MUSEUM OF NATURAL HISTORY

Volume 157, article 4, pages 263-310, figures 1-60

Issued September 13, 1976

Price. \$2.90

ISSN 0003-0090

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ABSTRACT

The purpose of the present study is to describe and interpret the wall ultrastructure of three atlantid heteropod species for phylogenetic and taxonomic analysis; they are *Oxygyrus keraudreni*, *Protatlanta souleyeti*, and *Atlanta inclinata* found in shallow waters of subtropic and tropic oceanic regions. Whereas most other members of predominantly thick-shelled, benthic mesogastropod families have three or more calcified crossed-lamellar layers termed here "normal," the exceedingly thin-walled planktonic atlantids have highly modified, crossed-lamellar layers termed here "Type-2." This "Type-2" structure was perhaps derived from the normal mesogastropod type structure as a result of thinness of the wall, as this structure has been observed in unrelated thin-shelled taxa, such as pteropods (opisthobranchs), scissurellids (archaeogastropods), and early embryonic stages of fissurellids (archaeogastropods). An important variation is that both the first-order lamellae and the second-order rods may be rigid "Type-2," sigmoidal, or curved so that a layer may resemble helical structure. A new type of prismatic layer, asymmetric prismatic, is de-

scribed and distinguished from simple prismatic, apertural prismatic, and myostracal structure. Variations of ultrastructure within samples of *Oxygyrus keraudreni* from the same population were found to have variant patterns identical with those of distant populations. Ornamented and unornamented embryonic *Protatlanta souleyeti* were found within populations in about the same ratio. The wall structure among *Oxygyrus keraudreni*, *Protatlanta souleyeti*, and *Atlanta inclinata* is distinct, with variations that can be used to distinguish each species. Embryonic variations of ultrastructure are characterized by changing thickness of wall structure during growth, whereas adult variations of ultrastructure are characterized by morphologic changes within a specific wall unit type.

A study of heteropod material from plankton tows and bottom dredges failed to establish any recognizable difference in alteration of ultrastructure by selective solution in deep sea sediments. Both types of samples displayed about the same degree of alteration, implying that factors either biological or chemical are operating on individuals even during their life cycle.

INTRODUCTION

The Atlantidae belong to the superfamily Atlantacea (=Heteropoda) and are taenioglossate, pectinate Mesogastropoda. They are unrelated to the opisthobranch pteropods, with which they were originally associated. Thiriot-Quiévreux (1973) wrote an excellent review of the status and characteristics of the heteropods. The Atlantidae are composed of genera that have fully developed shells. Other families either have vestigial or reduced internal shells or are naked. The members of the superfamily can be arranged in order of decreasing shell protection and increasing size and nakedness. For example, in the Atlantidae the animal is fully retractable into the shell and there is an operculum, whereas the Pterotracheidae lack even a vestigial shell.

The purpose of the present paper is to report our observations and interpretations of the ultrastructure of *Oxygyrus keraudreni* (Lesueur,

1817) and *Protatlanta souleyeti* (Smith, 1888), with comparative remarks on *Atlanta inclinata* Souleyet, 1852. Certain external morphological features, particularly of the embryonic shells not previously described are also included in the discussion. *Oxygyrus keraudreni* was selected for study because it is more strongly bilaterally symmetrical than other species of the family. The ultrastructure in asymmetrical shells is much more difficult to interpret geometrically than planispiral or limpet-shaped shells. The adult stage of *O. keraudreni* is not calcified and is considered by Richter (1961) to be at one end of an atlantid morphocline, which is partially constructed on the basis of gradual decalcification of the shell.

Protatlanta souleyeti is the next species in the morphocline and displays more calcification than *O. keraudreni*. *Atlanta inclinata* occupies a posi-

tion near the opposite end of the cline; it is one of the largest sized species but has a rather thin shell. Because the shell thickness of the adult whorls in each of the species is approximately the same, we selected them so that differences or similarities among the three species would be more easily interpreted.

The shelled atlantids, in spite of the restriction of possessing a shell, are active carnivores living in shallow waters of the subtropic to tropic open ocean water masses. The pteropods have a wider geographic distribution and are found in deeper water; they also appear to migrate diurnally (Van der Spoel, 1972, p. 558). Hence, there is a broader adaptive zone available to the pteropods, with the possibility of increasing speciation. Van der Spoel (1972, p. 559) has shown that the heteropods are gonochorists; and he believes that there is a reduced gene flow. The atlantids are fast swimmers compared with the pteropods, and this may have a bearing on the selection for streamlining and bilateral symmetry of the heteropod shell. Most atlantid adult shells are quite similar and very conservative between species, consisting of an almost planispiral whorl that is flattened and possesses a stabilizing keel. The pteropod shell, by contrast, does not exhibit any obvious adaptive feature to suggest rapid motion.

The number of shelled pteropod species are about the same as the atlantids (Van der Spoel, 1972) but in terms of absolute numbers of specimens found at a given locality, the pteropods are far more common. For example, in a dredge haul taken 25 miles southwest of Arena Point, Luzon, less than 20 percent of the total number of shells representing the two groups are atlantids. There may be a collecting bias, due to the thin heteropod shells that may not survive transport to the bottom or the conditions on the bottom. In plankton tows most collectors have noted that the pteropods are more plentiful than the heteropods. Bé (personal commun.) has suggested that since the fast-swimming heteropods escape capture, and the less active pteropods are more likely to be caught in tow nets, there results a collecting bias.

Increased collecting activity over the past several decades has resulted in a number of papers detailing the anatomy, classification, and

zoogeography of the pteropods and heteropods. Tesch, 1949; Richter, 1968, 1972; Van der Spoel, 1972; and Thiriot-Quiévreux, 1973; and others have been particularly active. They have established that the opercula, pigmentation, tentacle size, eye shape, and embryonic shell characters are particularly important in systematics and phylogeny. Richter (1961) has constructed a most convincing morphocline, based on an arrangement of radular forms and he relates shell features to this trend. He has demonstrated that most atlantid species can be recognized (with some problems) on the basis of their embryonic shells and, to some degree, the post-embryonic stages. Thiriot-Quiévreux (1973) also has recognized the importance of the early shell. These observations imply that most variation occurs in the embryonic stages. This may be in response to unstable or rapid chemical changes during embryonic growth, a phenomenon noted in other groups.

With the exceptions noted above, most recent reports on the pteropods and heteropods are the result of expeditions or localized collecting trips. These reports are valuable and usually include anatomical and distribution studies (Tesch, 1949; Frontier, 1966; Thiriot-Quiévreux, 1967; Richter, 1968; and many others). Most papers include SEM micrographs of embryonic whorls for identification of species. We shall follow this means of identification.

The purpose of the study is to describe the ultrastructure of heteropod shells with a view to possible determination of relationships between species using this feature. This would contribute an additional morphological dimension, which would be potentially valuable in the systematic analysis and phylogeny of the family, and determine whether it might be possible to recognize heteropod species from fragments of shells in deep-sea sediments.

In a subsequent paper we shall detail the ultrastructure of seven relatively common species of *Atlanta* and the vestigial shell of *Carinaria lamarcki* (Carinariidae, Heteropoda).

ACKNOWLEDGMENTS

We thank Drs. Allan Bé, Niles Eldredge, and Copeland MacClintock for their useful comments

and stimulating discussions. We are particularly grateful to Drs. S. Van der Spoel and Gotthard Richter for their patience, help, guidance, and prompt replies to our letters over the years of this study. Mr. Robert J. Koestler of the American Museum of Natural History provided much skill and technical advice in the operation of the scanning electron microscope.

We are grateful to Dr. Frank D. Ferrari, Supervisor for Plankton at the Smithsonian Oceanographic Sorting Center, Smithsonian Institution, for the assistance he gave in reviewing material and for specimens of the atlantids; to Dr. John Taylor of the British Museum (Natural History) for access to collections and for specimens of *Protatlanta souleyeti* and *Atlanta fusca*; and to Dr. T. S. S. Rao, Officer-in-Charge, Indian Ocean Biological Centre, South India, for specimens of *Oxygyrus keraudreni*.

This study was initiated by the authors and Dr. Allan W. H. Bé of Lamont-Doherty Geological Observatory, and continues as a part of a joint project to investigate the characteristics of planktonic foraminifera, Pteropoda, and Heteropoda. Support for this study was received from the National Science Foundation as grant GA 14,777.

MATERIALS AND METHODS

For the most part, samples for this study were recovered from dredge and plankton tow material collected by the R. V. *Vema* of Lamont-Doherty Geological Observatory. The samples are circumglobal and range between latitude 40° N and latitude 40° S. Although there was abundant material available, the thin calcareous shells were mostly destroyed owing to long storage time and the method of preservation employing formalin. Because of the scarcity of well-preserved material, fewer localities were used than were planned or desired for this study. We have examined more than 600 plankton tows and 400 dredge hauls. Of these only about 150 contained well-preserved material.

It is interesting to note that more than half of both tow or dredge samples from a given locality was invariably affected by infaunal or infloral infestation of the shell and surprisingly, to a

much greater degree than was expected, in the tow samples.

Two methods of preparing the shells for study were used, depending on the origin of the sample: 1) Tow material was cleaned in dilute laundry bleach to remove the organic tissues (except in the case of adult *Oxygyrus keraudreni*, which retains a cartilaginous body whorl and keel). These samples were then repeatedly washed in distilled water to remove the residue, and finally placed in laboratory alcohol in an ultrasonic cleaner for 15 seconds to dislodge any remaining tissues and detritus (diatoms, coccoliths, etc.). The specimens were air-dried on filter paper in petri dishes and sorted according to species with a vacuum pick, which is faster than tweezers and causes less damage to the keels and thin shells. 2) Dredged material was washed in distilled water and placed in an ultrasonic cleaner, and sorted in a similar fashion to the tow material.

Aside from the vagaries of preservation, a major problem was encountered in obtaining controlled cut sections from the thin shells, gross average thickness being less than 50 μm . We tried embedding the specimens in epoxy and microtoming the shells, but either the thin shells crumbled or the microtome blade left artifacts (gouges) on the crystals of the shell material, thus obscuring the ultrastructure. Acid etching and polished sectioning also proved unsatisfactory, as there was not enough control of the cutting action. The most successful technique employed was careful orientation prior to controlled fracturing of the thin shells with a tempered, sharpened insect pin mounted in a pin vise. The specimens were then prepared using standard SEM techniques. Five large mosaics of *Oxygyrus keraudreni* were assembled to aid in the interpretation of wall ultrastructure changes and transformations. Some of the figures included in this paper are abstracted from the mosaics, and their position in the sequence is noted in the figure captions. The mosaics are available for study in the Department of Fossil and Living Invertebrates at the American Museum of Natural History. The "H-000" notation in the figure captions is a code number for localities of a given specimen. The locality register is given in Appendix.

ATLANTID ULTRASTRUCTURE—GENERAL REMARKS

TYPE-2 CROSSED-LAMELLAR LAYER

Most members of mesogastropod families are predominantly thick-shelled benthic forms, which usually have three or more calcified crossed-lamellar layers (here termed "normal"), as described by Bøggild (1930), Philippon (1974), and many others. The atlantids, being planktonic with exceedingly thin walls, may also have a basic pattern of three calcified, but highly modified, crossed-lamellar layers that we term "Type-2"; see Batten, 1975, p. 12 and figure 4b. It is possible that this structure is simply a variant of the normal mesogastropod type, perhaps resulting from the thinness of the wall. Type-2 structure has been observed in unrelated thin-shelled taxa, such as the pteropods (opisthobranchs), the scissurellids (archaeogastropods), and the early embryonic stages of the fissurellids (archaeogastropods).

The term "crossed-lamellar" in the Type-2 structure is, in a sense, a misnomer, since the second- and third-order elements are rarely lamellar. Even the first-order lamellae are not

always rigid plates but may be fan-shaped or domal (fig. 1).

The second-order units are usually rods, as opposed to the sheetlike lamellae of the normal crossed-lamellar type. The first- and second-order units are highly variable, in contrast to the normal crossed-lamellar structure. The third-order unit is only relatively invariant, consisting of rhomboidal tablets with the boundaries at right angles or at high angles to the second-order rods; in fact, they are usually normal to the inner or outer surface (fig. 2; Batten, 1975, pp. 13-14).

The adult whorl of thin-shelled species of atlantids appears to be quite flexible, based on some rather crude experiments. It may be that the development of the third-order tablets with boundaries essentially normal to the shell surfaces may aid in flexing. Bé, MacClintock and Currie (1972) speculated that the helical structure found in the pteropods may have a flexing function. Interestingly, the rods of the helical structure and the tablets composing the rods in pteropods are identical with the second-order

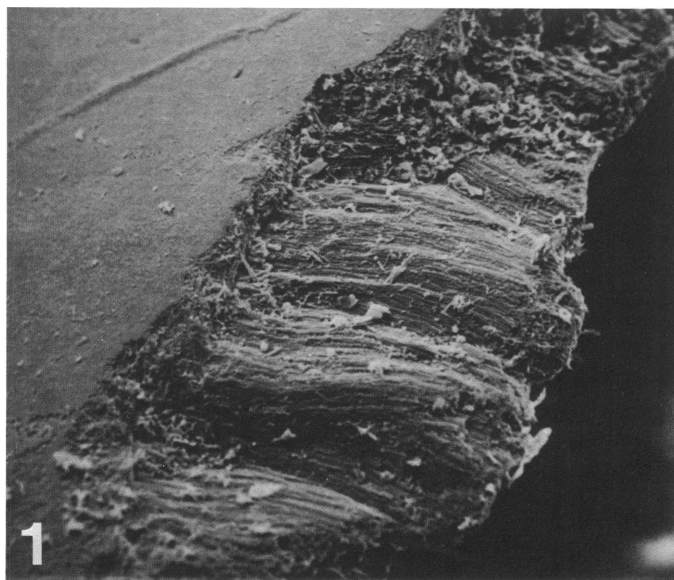
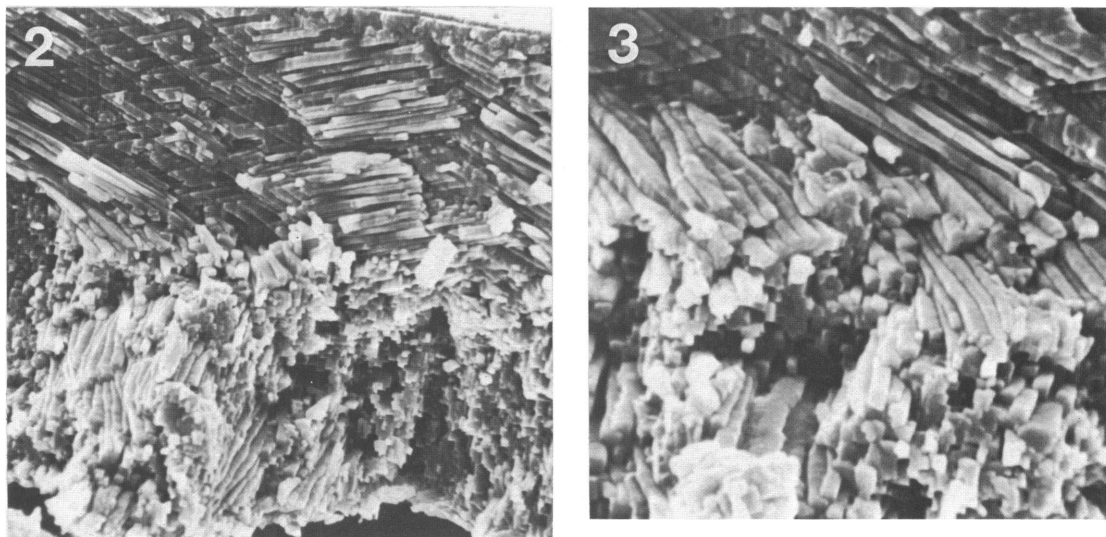


FIG. 1. *Oxygyrus keraudreni* (Lesueur, 1817). AMNH 32000: H-80 (see loc. register). Broken apertural edge of seventh growth stage. Middle crossed-lamellar layer is composed of overlapping bundles of second-order rods. $\times 650$.



FIGS. 2, 3. *O. keraudreni*. 2. AMNH 32001: H-5. Broken fragment normal to apertural edge. Note middle crossed-lamellar layer composed of rigid second-order rods. Third-order tablet boundaries are essentially normal to the axis of second-order elements, micrograph no. 1a from mosaic H-5 (bis B). $\times 3400$. 3. AMNH 32001: H-5. A section near figure 2. Middle layer at top, outer layer below, showing transformation of rigid middle layer rods to curved outer layer structure that resembles helical structure in the pteropods at this site, micrograph no. 7a from mosaic H-5 (bis B). $\times 6400$.

rods and third-order tablets in the Type-2 crossed-lamellar structure; see their figure 3, pl. 6, and compare with our figure 3, except in size. Type-2 tablets average $0.07 \mu\text{m}$ in width, whereas helical tablets average $0.02 \mu\text{m}$.

A generalized wall in the atlantids consists of a dominant middle Type-2 layer with two thinner outer layers of prismatic structure, or with either the inner or outer layer of Type-2 crossed-lamellae. The first-order lamellae of the middle layer are usually arranged collaterally (parallel to the aperture), whereas the first-order lamellae of the outer layers (where present) are spirally arranged (with some exceptions noted below). Thus, the Type-2 layers are at right angles to each other, just as in the normal crossed-lamellar layers. The second-order rods of one layer are usually contiguous with the adjacent rods of the next crossed-lamellar layer (fig. 4a, or 4b). One might infer that these layers are simply a different orientation of a single layer. This has been suggested for normal crossed-lamellae by MacClintock, 1967, and has been called by him "pseudolayers." Alternatively, contiguity of rods

or lamellae between layers does not necessarily imply per se a single layer concept.

The first-order Type-2 lamellae may be similar to those found in the normal crossed-lamellar layer, that is, straight or linear. They are composed of uniform groups of second-order rods, which are usually evenly formed and rigid (figs. 2, 5). This is the prevailing pattern in the middle layer, but it also may appear in the outer layers as well. However, near the sutures or at changes in the topology of the shell, even this uniformity changes so that the layer might form sheet prismatic structure (figs. 6, 7), or some other modification.

Two important variations should be mentioned here in order to interpret properly random views of the shell structure in the heteropods. One is that the first order lamellae may display variation in the number and shape of second-order rods that compose them. Figures 8 and 9 show 50 or more second-order rods in a single first-order lamella. The second variation is that both the first-order lamellae and the second-order rods may be either curved or sigmoidal (fig.

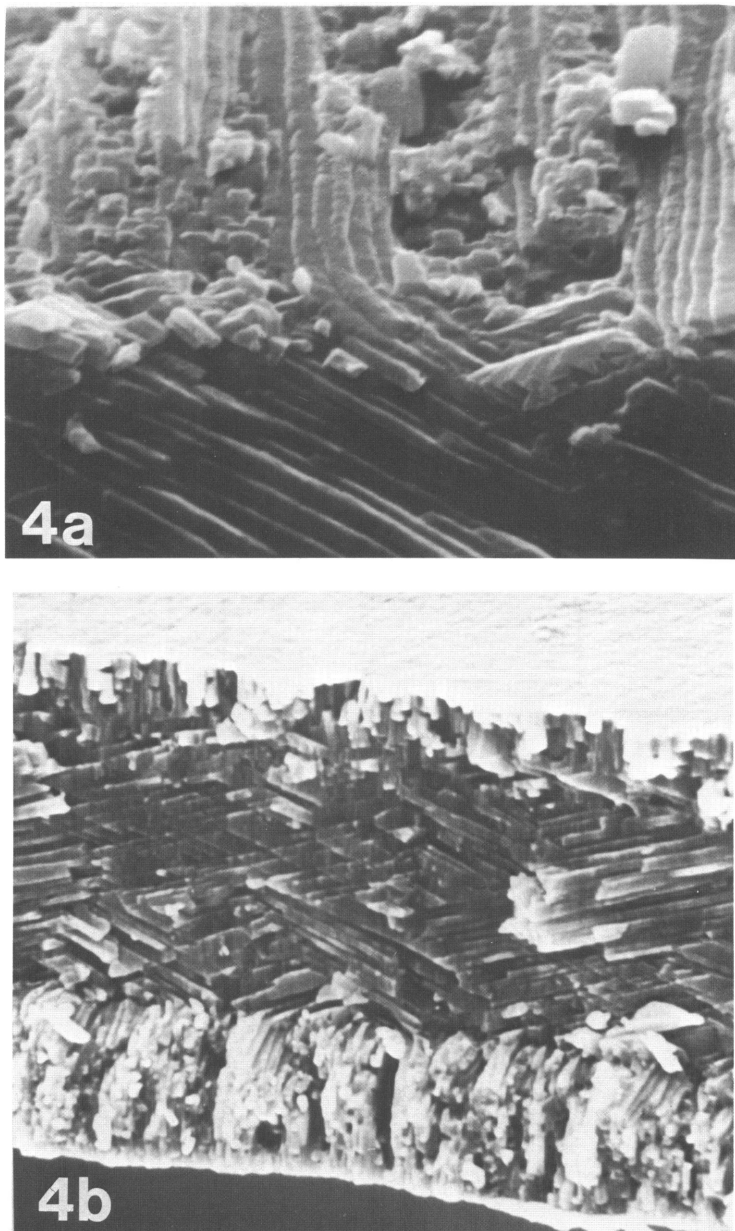
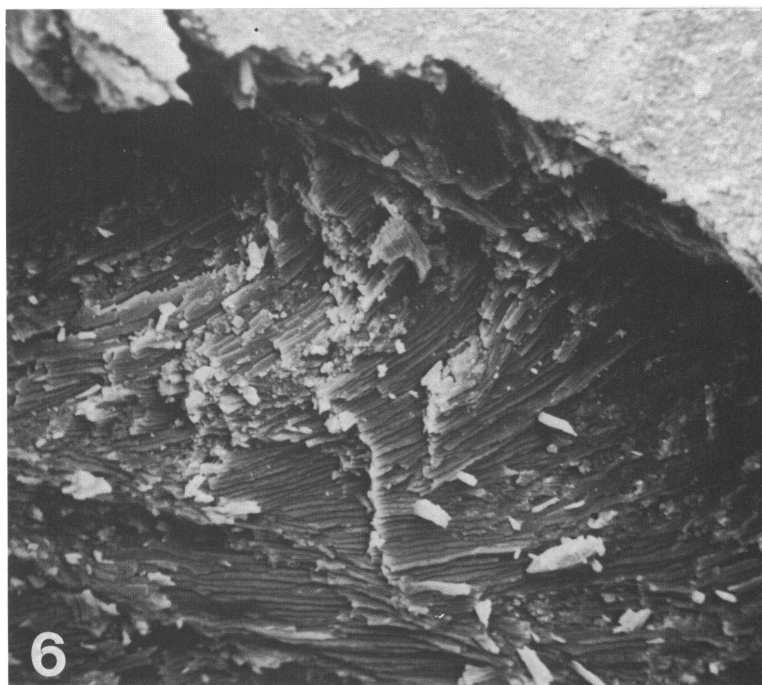
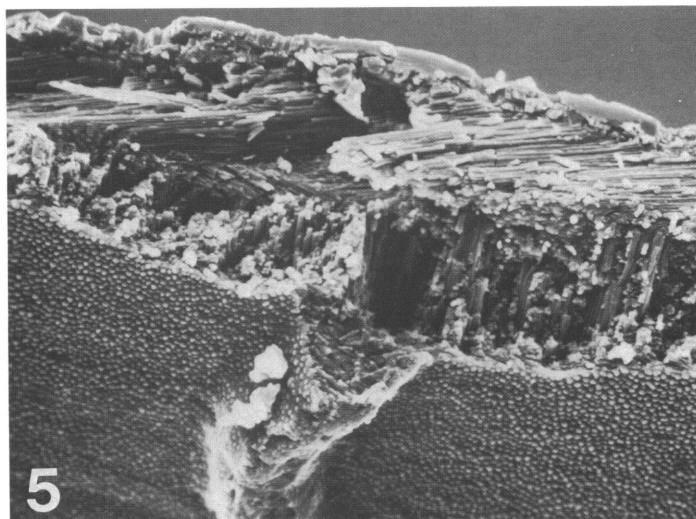
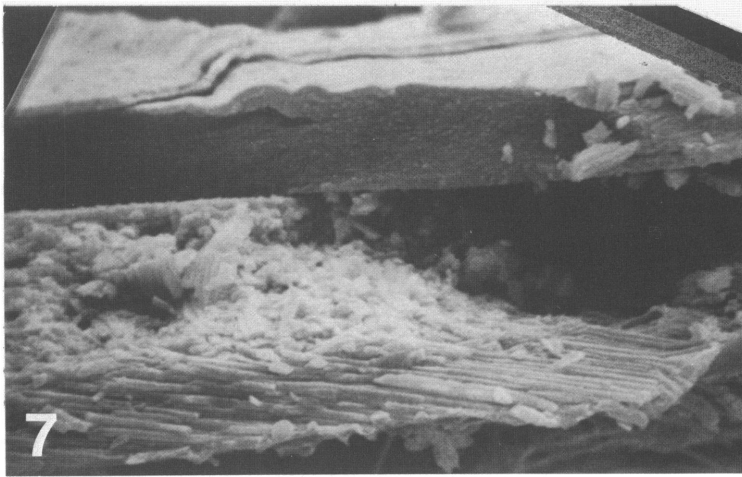


FIG. 4. *O. keraudreni*. AMNH 32001: H-5. a. A section near figure 2 of boundary of the inner crossed-lamellar layer at top and middle layer below. Note continuity of rods and irregular nature of inner layer second-order rods. $\times 11000$. b. Same section as figure 2, but near umbilicus. Note asymmetric prismatic inner layer at top of section and criss-cross pattern on inner shell surface. Curved second-order rods of outer layer are normal to the outer surface, micrograph no. 14, from mosaic H-5. $\times 5100$.



FIGS. 5, 6. *O. keraudreni*. AMNH 32002: H-42. Broken apertural edge from upper pustulose surface of sixth stage. Note evenly formed, rigid Type-2 crossed-lamellar outer and middle layers. Second-order rods in cross section of ridge in center of micrograph are normal to the outer ridge surface. $\times 2200$. 6. *O. keraudreni*. AMNH 32000: H-80. Section at right angle to aperture, near suture of seventh stage. Suture just off micrograph at right; note sheet prismatic structure at right becoming crossed-lamellar at left. $\times 2500$.



FIGS. 7, 8. *O. keraudreni*. AMNH 32002: H-6. Section normal to aperture at the very end of the calcified shell. Lower layer is composed of sheet prismatic structure and the layer is the same as the middle layer in earlier stages. The upper layer is the cartilaginous layer that forms the final adult stage. $\times 5000$. 8. *O. keraudreni*. AMNH 32000: H-80. Seventh stage apertural section showing curved, numerous second-order rods forming first-order units in middle cross-lamellar layer. $\times 1250$.

8). In one layer there may be a combination of both forms (fig. 10). When second-order rods are curved, the cross-lamellar aspect becomes obscure and the layer could be interpreted as

being either helical or overlapping rounded sheets (fig. 9). In any event, this curved condition has, to our knowledge, no counterpart in any published work on molluscan ultrastructure. It is

interesting to note that the second-order rods in the curved or sigmoid types have irregular boundaries, but in the more rigid Type-2 layers, which usually have regular boundaries, the second-order rods may also have an irregular aspect (fig. 4a).

We shall offer examples to illustrate that the layers, at least in some cases, are separate. In figure 11, the middle layer consists of straight rods with sharply defined boundaries, but the inner layer is composed of prisms that are not continuous with the middle layer elements. Figure 12 shows a transformation of an outer simple prismatic layer to a crossed-lamellar one, with no contiguity with any elements of the middle layer. Further, although the middle layer retains its conservative aspect, the inner and outer layers become thicker, thinner, or become transformed from crossed-lamellar to several types of prismatic layers, or they may suddenly

wedge out. The outer layers become very thin (representing perhaps no more than 10% to 20% of the wall thickness) particularly where the wall is thin, near the umbilici and in early or very late ontogeny. The outer layers in those cases become prismatic but of a special form discussed below.

Throughout most of this report, except where noted, discussion of wall structure variation is based on observations of the middle whorl or in the area near the plane of symmetry.

ASYMMETRIC PRISMATIC LAYER

As an outer Type-2 layer begins to thin, the second-order rods become progressively shorter owing to the smaller distance between the inner and outer surfaces of the layer. In the final stages of this progression, the rods are converted to prisms that are asymmetrical in cross section, with the largest face contiguous with the second-

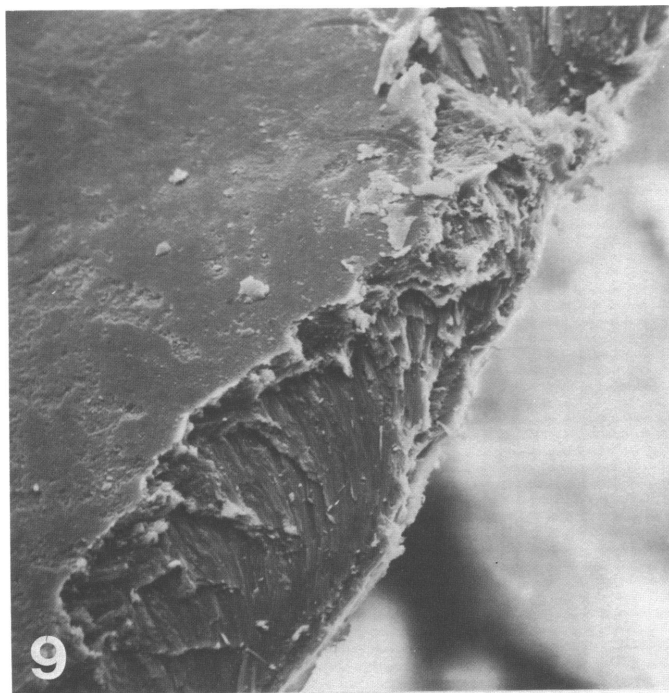
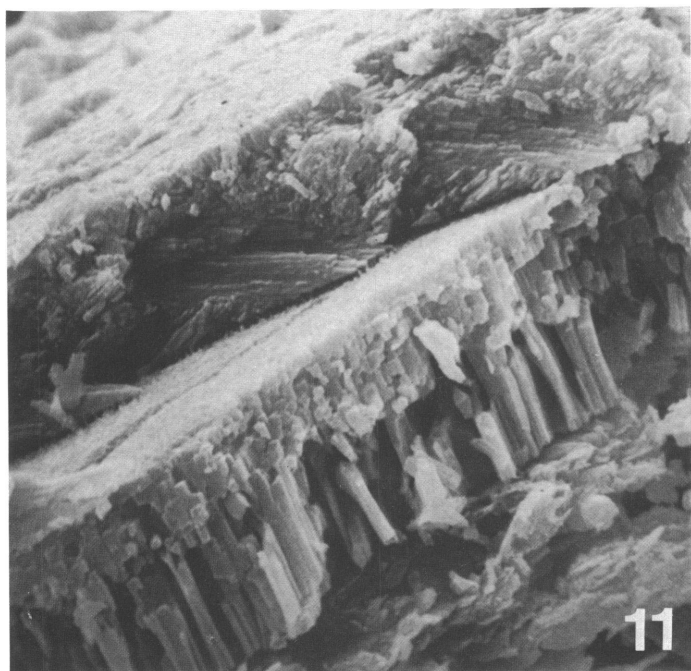
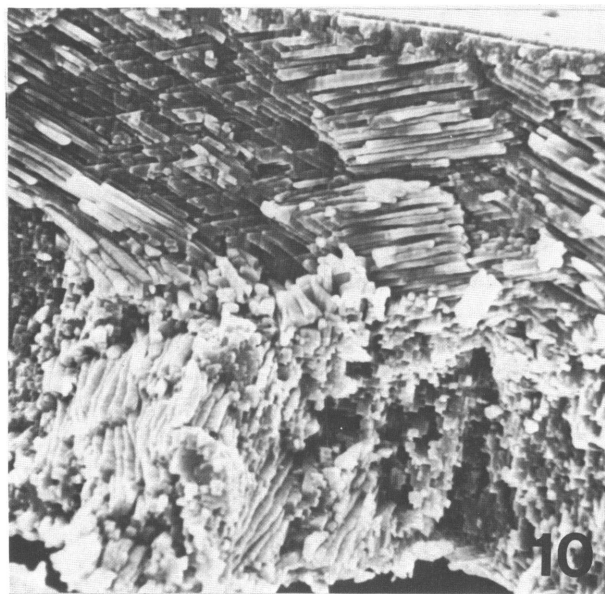


FIG. 9. *O. keraudreni*. AMNH 32000: H-80. Seventh stage, basal apertural section one-third distance from umbilicus to plane of symmetry. Middle crossed-lamellar layer with multiple curved second-order rods giving appearance of helical structure. Diagonal ridges near bottom of micrograph and straight rods near top of section indicate traces of opposing first-order lamellae. $\times 550$.



FIGS. 10, 11. *O. keraudreni*. AMNH 32001: H-5. Apertural section of seventh stage near umbilicus. Inner layer at top of micrograph. Note curved and sigmoid second-order rods in outer layer (lower part of illustration). These rods usually have irregular boundaries, micrograph no. 6a from mosaic H-5 (bis B). $\times 3400$. 11. *Protatlanta souleyeti* (Smith, 1888). AMNH 32004: H-43. Base of fourth stage. Rigid Type-2 middle layer rests on inner (lower) layer, with no continuity between second-order units of middle layer and elements of inner layer. Note thick inner asymmetric prismatic layer. $\times 4500$.

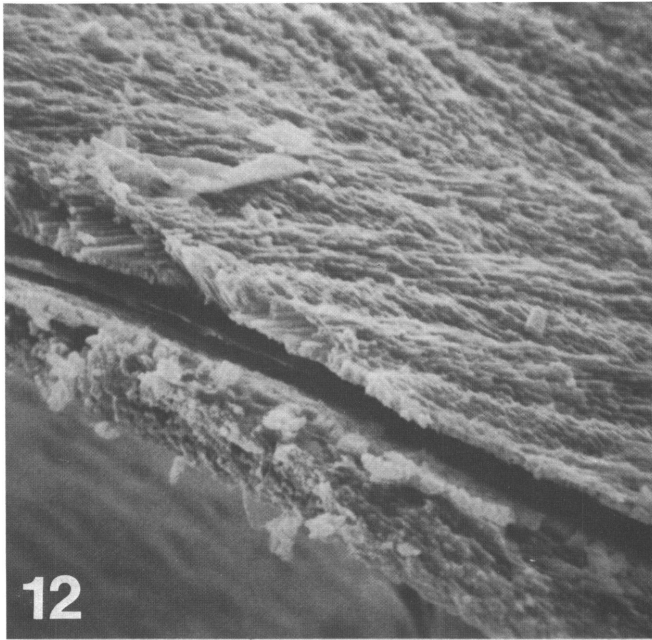


FIG. 12. *O. keraudreni*. AMNH 32005: H-112. Apertural section of late third stage one-third distance from umbilicus to plane of symmetry. Thin outer prismatic layer at right is transformed to a Type-2 crossed lamellar layer at left. $\times 5600$.

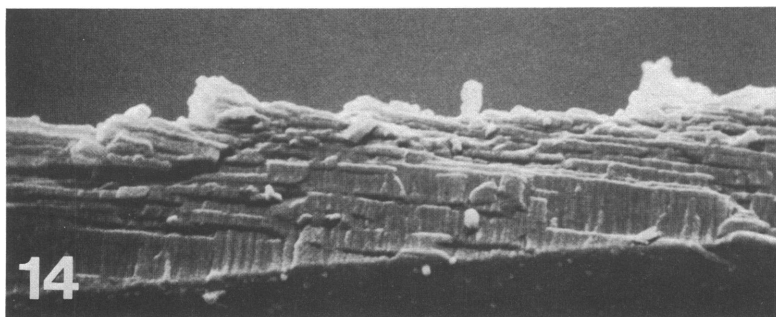
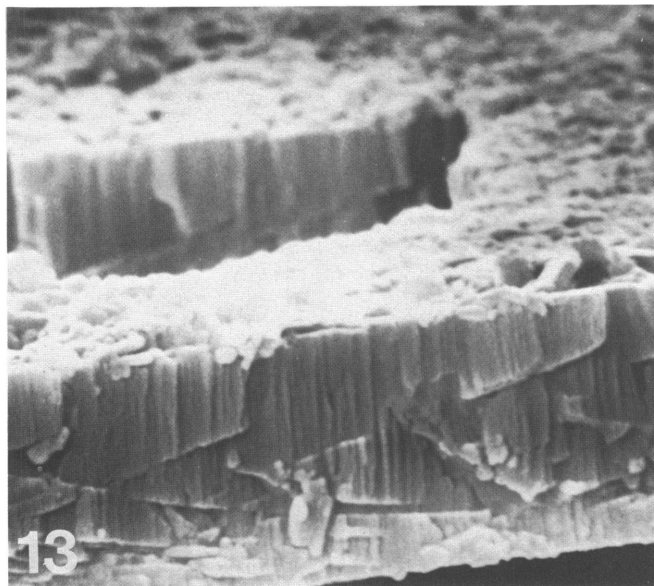
order rods of the middle layer (fig. 4b). Alternate prisms have this enlarged face in apposition, probably reflecting their crossed-lamellar origin. On the shell surface, these prisms form a criss-cross pattern (fig. 4b). This layer might be interpreted as being composed of the upturned ends of middle layer second-order rods forming a solid outer, or inner, shell surface. But since we can trace the above transformation, we doubt that this interpretation is correct in the above example of progressive change. In cases where the outer layers are consistently asymmetric prismatic, we believe that they are upturned elements of the middle layer. In any event, we wish to distinguish this type of layer from the simple prismatic layer, which is also found in the atlantids; hence the name asymmetric prismatic.

The above observations and interpretations were based mostly on a study of numerous specimens of *Oxygyrus keraudreni*. Another interesting set of observations of asymmetric prismatic structure can be seen in *Protatlanta souleyeti* (fig. 11). The inner layer is very thick in most

locations of the shell and is composed mainly of fine elongated prisms, which we assume represent an asymmetric prismatic layer. In various parts of the shell and apparently unrelated to the proximity of any change in shell geometry or location, such as near the suture or near the plane of symmetry, the characteristics of the layer may change either abruptly or progressively. Within the layer, fine demarcation lines may appear diagonally and at opposing angles giving the appearance of incipient crossed-lamellar (figs. 13, 45). These lines may be patchy with no further development.

In other areas the incipient elements become progressively stronger until second-order rods are formed and Type-2 crossed-lamellar structure is developed (fig. 14). It should be noted in the crossed-lamellar mode that the prisms appear to lose their asymmetry, and their boundaries assume the appearance of third-order tablets of the Type-2 structure.

At first glance, the layer under discussion appeared remarkably homologous to the



FIGS. 13, 14. *P. souleyeti*. AMNH 32004: H-43. Apertural section near center of whorl at end of third stage. Inner asymmetric prismatic layer showing incipient development of Type-2 crossed-lamellar structure. Other two layers not preserved at this site. $\times 5100$. 14. *P. souleyeti*. AMNH 32006: H-118. Apertural section near periphery of third stage. Crossed-lamellar inner layer is fully formed and beginning to be further transformed to sheet prismatic structure. $\times 6100$.

apertural prismatic and columellar myostracal layers described in a pteropod (*Cuvierina*) by Bé, MacClintock and Currie (1972, pp. 53-54). They attributed the formation of these layers to pallial and muscle attachments. These layers are associated with helical structure and they show traces of helical rods within the layers (see fig. 3, pl. 14). They stated that "the tablets of the helical rods give rise to the elongate prisms by the simple process of extension." (Page 53.)

When we first encountered this layer in *Protatlanta* we assumed that it was a myostracal

layer because of the very fine and uniform prisms. Further investigation demonstrated that the layer is uniform in thickness over much of the shell and may be about the same uniform thickness as the dominant middle crossed-lamellar layer, a condition not observed in most gastropods involving myostracal deposits. We have not observed second-order rods of the middle layer as extensions or connected to the prisms of the inner layer; indeed, the prisms are usually much smaller than the second-order rods. Further, when incipient crossed-lamellar traces

appear in some cases, they are directed toward the inner surface of the shell. If the prisms were extensions of the middle layer one would expect incipency adjacent to the middle layer. In our opinion the prisms differ from pteropod layers and from the normal pallial myostracum in being asymmetrical. When this layer is converted to

Type-2 structure, first-order lamellae are oriented essentially parallel to the middle layer lamellae, in sharp contrast to the usual condition, see page 270. We conclude that this prismatic layer is separate and unlikely to be formed by either the mantle or muscles.

CHARACTERISTICS OF THE SPECIES

Oxygyrus keraudreni (Lesueur, 1817)

EXTERNAL MORPHOLOGY

As in most other snails, the protoconch is globular but differs somewhat by being compressed abaperturally (fig. 15). The surface is pustulose, as a result of the external expression of terminal prisms of the shell structure. Rising above this surface are fairly evenly spaced tubercles, composed of clusters of raised prisms the same as those forming the pustulose surface (fig. 15). These clusters do not show any regular pattern and become widely spaced by the beginning of the first whorl.

The first whorl resembles a cone shell, having an elongate base and a narrow aperture. The second and third whorls become progressively more elongate, with the fourth whorl completely enveloping the earlier portions of the shell (fig. 16). These asymmetrical whorls form the

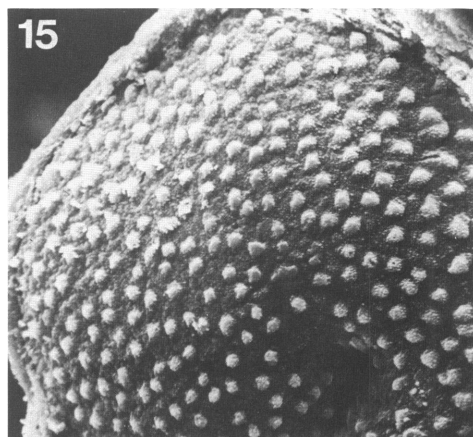


FIG. 15. *O. keraudreni*. AMNH 32007: H-25. Protoconch showing evenly spaced tubercles and pustulose surface. $\times 2000$.

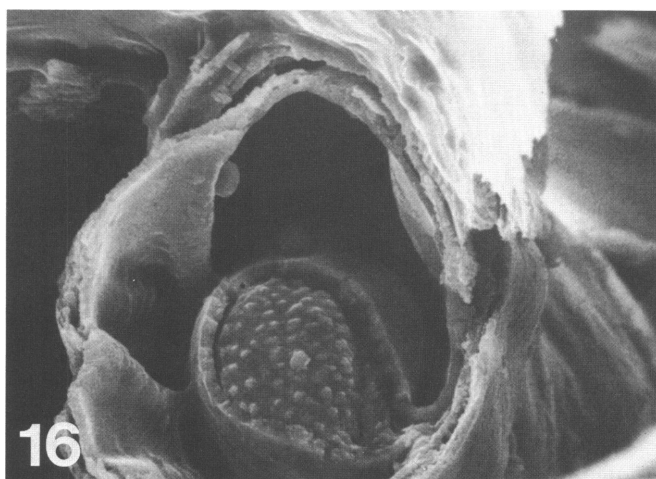


FIG. 16. *O. keraudreni*. AMNH 32008: H-63. Broken columella showing the first three tightly coiled whorls that completely obscure the protoconch in the completed shell. $\times 1050$.

columella with their extremities serving as sites for the umbilici of the fourth, fifth, and sixth whorls, which are markedly inflated. These later whorls appear to be nearly bilaterally symmetrical and planispiral (fig. 17). To indicate the marked degree of asymmetry not apparent in later ontogeny, the protoconch occupies a position in the columella near the upper umbilicus (fig. 18). The first four whorls are smooth with rather faint growth lines visible. Near the end of the fifth whorl faint sinuous lines appear which gradually become stronger. There is an abrupt margin marking the beginning of the Bellerophina stage surface ornament (fig. 19). Richter (1968, p. 365) has illustrated some of these early asymmetric stages. Figure 21 is a reconstruction of the first six whorls of *Oxygyrus keraudreni*.

The Bellerophina stage (sixth whorl) was so-named because of its resemblance to the primitive archaeogastropod bellerophontids, which are bilaterally symmetrical with inflated planispiral coiling and with two umbilici (fig. 20). The bellerophontids, only, possess bilateral symmetry in such features as the selenizone, in apertural features, and musculature. As we have shown, *Oxygyrus* is asymmetrical in early ontogeny but becomes progressively more symmetrical into the adult stage. Additionally, the selenizone is below midwhorl, and the slit is moderately shallow. The selenizone is flush with the surface and is bordered by lira with scalloped ornament facing away from the selenizone. There are two sinuous, flat-topped ridges on the selenizone, and the surface of the selenizone is pustulose with scattered tubercles. The aperture is asymmetrical and narrower at the base where the inhalant siphon (?) is moderately well formed. At the upper apertural lip the exhalant siphon (?) is rounded.

The Bellerophina stage, as in comparable stages in other atlantids, is the most highly ornamented. The dominant ornament consists of from 20-24 sinuous, flat-topped spiral ridges (fig. 20). As in earlier whorls, the surface is pustulose and growth lines are faint. However, both umbilical areas are devoid of pustules, whereas growth lines are exaggerated. Completion of this whorl may indicate completion of the veliger larval stage.

As growth proceeds into the nepianic stage, the selenizone migrates to the plane of bilateral symmetry and the slit becomes deeper (fig. 22). The slit then gradually becomes shallow. Within one-quarter of a whorl a wide flangelike keel is formed, and the slit abruptly narrows and continues as an open slit, dividing the keel for its entire length to termination in the adult (fig. 23). In this stage the surface is smooth, glassy, and translucent with faint growth lines. In a search through the literature we have not been able to discover the function of the slit.

The Bellerophina ornament abruptly terminates at the completion of the sixth whorl, and the post-Bellerophina shell is smooth with prominent growth lines (fig. 23). In addition, the calcified wall progressively thins.

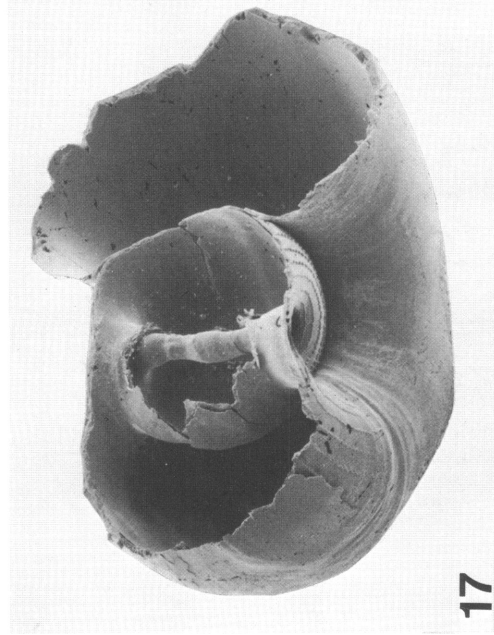
The final "adult" stage is about one-half whorl in length and is also bilaterally symmetrical. It is unique among the gastropods in lacking calcification (fig. 24). Tesch (1949), and others have described the wall as being cartilaginous, and the same tissue also covers the entire early shell during life (fig. 25). We have been unable to discover the chemical composition of this cartilaginous material but, in any event, it serves as the periostracum.

The cartilaginous shell and the keel have observable growth lines and are ornamented by fine spiral striations. These striations are irregularly spaced and may be interrupted by growth lines (fig. 24).

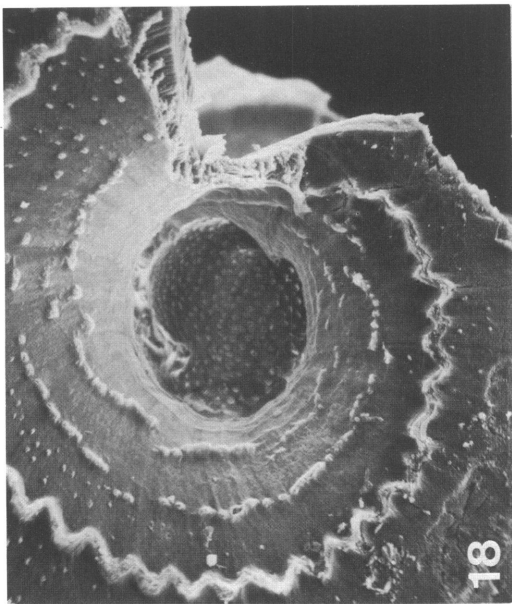
As much of the adult whorl is either biodegradable or very thin, it is not surprising to note that essentially all of *O. keraudreni* specimens recovered from dredge hauls are in the Bellerophina stage, in which the wall is thickest. Other atlantids are usually found as adults.

ULTRASTRUCTURE

Protoconch. As is true in most thin-shelled snails, protoconchs are not well preserved. However, the wall appears to be composed of an outer simple prismatic and an inner rodlike prismatic layer about 4.0 μm thick. The outer layer has prisms oriented normal to the outer surface and probably are of the same thickness as the size of the pustules on the surface. Most



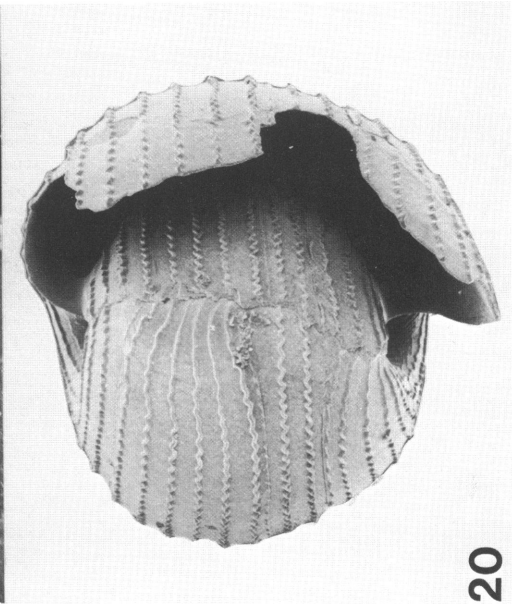
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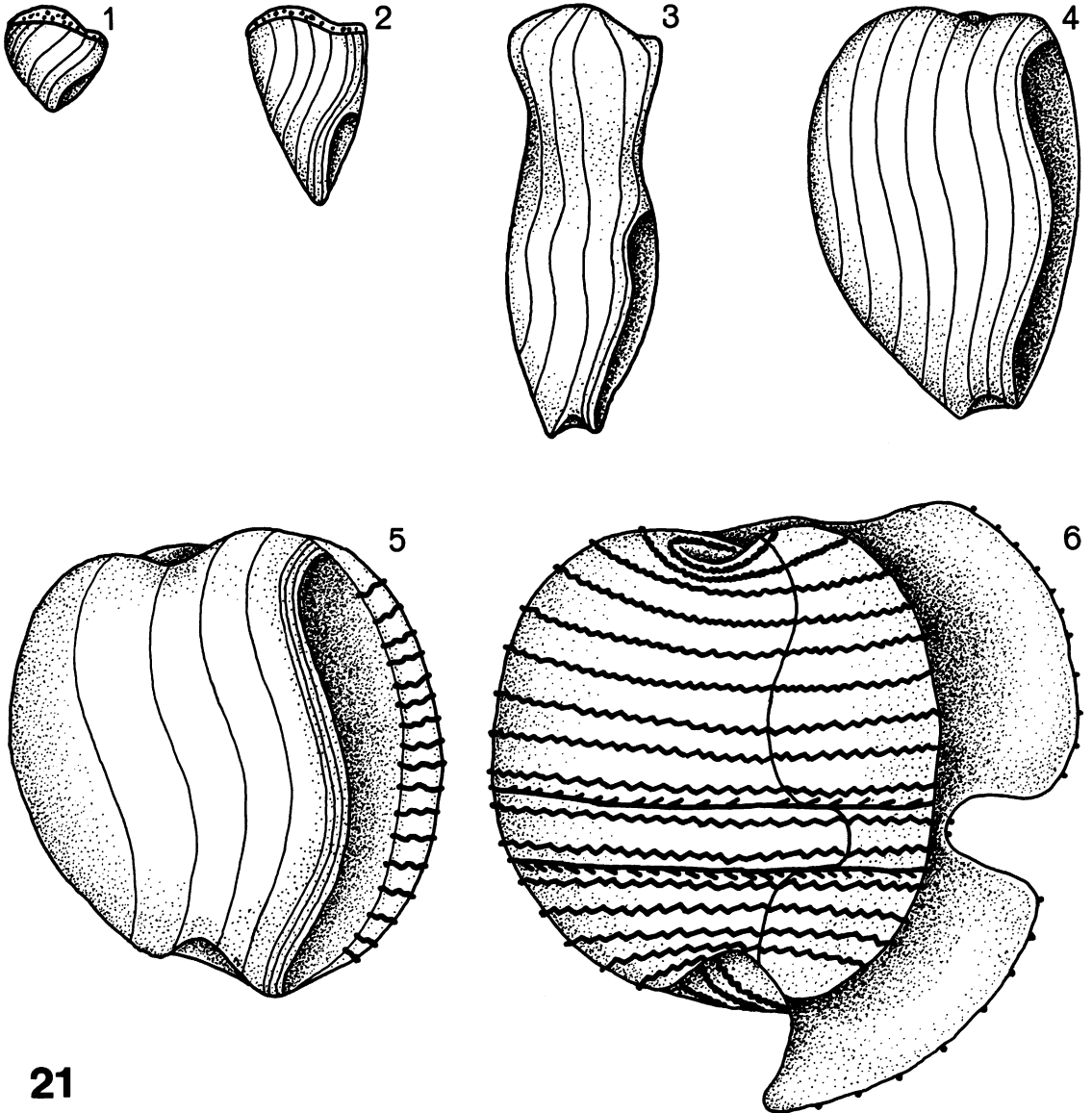
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FIGS. 17-20. *O. keraudreni*. 17. AMNH 32009:H-24. Oblique view of columella and expanded and inflated stages through stage 6. $\times 38$. 18. AMNH 32010 H-52. Umbilical view of shell top showing protoconch near columella. $\times 380$. 19. AMNH 32010:H-52. Top lateral view of beginning adult stage, showing abrupt change from Bellerophina stage. $\times 175$. 20. AMNH 32011:H-48. Apertural view of Bellerophina stage. $\times 80$.

specimens examined show broad bladelike prisms, which may represent recrystallization (fig. 26).

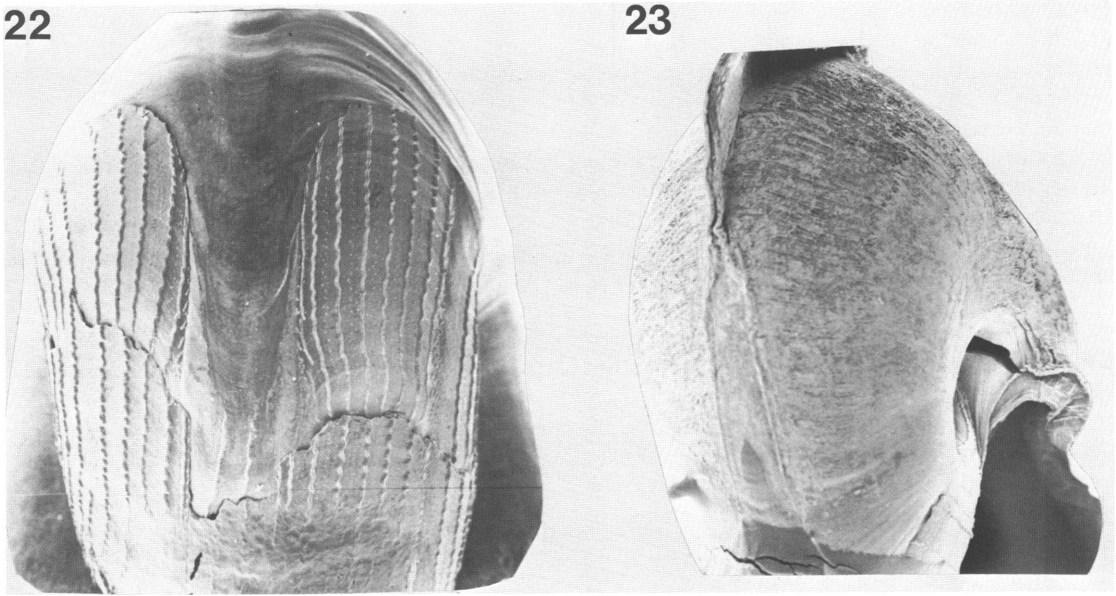
The inner layer is composed of fine, elongated

prisms (and probably is incipient Type-2 crossed-lamellar structure), which are parallel or at a low angle to the inner surface. This layer is thinner than the outer one but increases to become the



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FIG. 21. A reconstruction of the first six whorls of *O. keraudreni*. Note enlargement of apertures at each stage. Protoconch is surrounded by inflation of whorls after stage two. Stage three has open umbilici and forms major portion of columella. Stage four through six shows rapid expansion of inflated whorls. Note asymmetrically placed selenizone and constricted "inhalant siphon" at base of aperture. Not drawn to scale. (Numbers on figures represent stages.)



FIGS. 22, 23. *O. keraudreni*. AMNH 32012: H-13. Top view of late Bellerophina stage showing shift of selenizone to plane of symmetry, note deep slit. The smooth surface of adult stage is cartilaginous tissue. $\times 75$. 23. *O. keraudreni*. AMNH 32013: H-14. Posterior view of young adult stage. Note narrowing of selenizone and formation of a keel with a very narrow slit. Faint growth lines of calcareous shell show through abraided cartilaginous cover. Keel is entirely composed of such tissue. $\times 38$.

dominant layer, $3.0\ \mu\text{m}$ thick, near the junction of the first whorl. Interestingly, the inner surface of the protoconch is also pustulous, with the terminal ends of the inner prisms at an angle to the surface (fig. 27).

Postprotoconch Embryonic Stages. At the beginning of the first whorl, the inner prismatic layer is converted to a Type-2 structure (fig. 28), to become eventually the dominant middle layer. At the second whorl, the wall thickens by the addition of an inner prismatic layer equal in thickness to the outer layer. The crystals of this inner layer are normal to the inner surface, are asymmetric and finer than those of the outer layer, and are about the same size as the second-order rods of the middle Type-2 layer (fig. 29).

During the growth of the third whorl, the inner asymmetric prismatic layer is gradually converted to a Type-2 layer and gradually thickens. As in the usual case, the first-order lamellae of this layer are essentially at right angles to the opposing lamellae of the middle crossed-lamellar layer. During this growth stage,

the outer layer prisms progressively thicken to about the size of the second-order rods of the middle layer. Total wall thickness is $7\ \mu\text{m}$. By the end of the third growth stage, these outer prisms bend to form sheet prismatic structure and by the beginning of the fourth growth stage this layer is converted to Type-2 structure (fig. 30).

At the beginning of the fourth whorl, the middle layer is still dominant but with the outer layer becoming thick (fig. 31). By the completion of the fourth growth stage, the inner crossed-lamellar layer has increased in thickness to $6.0\ \mu\text{m}$ along with the outer layer ($6.0\ \mu\text{m}$), so that all three layers are about equal in development. Total thickness is $20.0\ \mu\text{m}$ (fig. 32).

The Bellerophina stage displays a very wide range of ultrastructure variation. The sinuous ridges on the surface of the Bellerophina stage are composed of rigid Type-2 structure. Interestingly, the angle of opposing second-order rods is such that they are normal to the surface of the ridge. The pustulose surface is due to the up-

turned second-order rods of the outer layer. Both the ridges and the tubercles appear to be anchor points for the thin covering tissue (periostacum?). As in other growth stages, the middle crossed-lamellar layer is more rigid and conservative with one exception noted below. The outer layer is not so well organized with most changes involving the composition and ordination of second-order rods composing first-order lamellae. This condition is even more noticeable in later growth stages (fig. 2).

All three layers vary considerably in thickness with the outer layers particularly changeable. For example, the two outer layers may be thin rinds ($4.0\text{ }\mu\text{m}$) compared with the middle layer ($22.0\text{ }\mu\text{m}$ thick) (fig. 33). Because the wall appears to be of uniform thickness at this stage in all specimens examined, we suspect the layers change to compensate for this uniformity.

It is important to note that there is much variation even within samples from the same tow or haul. In a sample from off the Marianas (H-119) two specimens have a thin inner asymmetric prismatic layer; the middle and outer in one of the specimens are equal in thickness, whereas in

the other specimens the middle is dominant. In two other specimens there is no inner layer, with middle and outer layers the same as in the previous described specimens.

In a haul from off the coast of Florida the same variant pattern was observed. In contrast, all specimens from a sample (H-120) from north-east of Madagascar have the outer layer very thin and a massive middle layer. Off the Brazilian coast in the South Atlantic (H-122), specimens have ultrastructure composed of a very thin outer layer and a middle layer showing a marked curving of the second-order rods of the middle layer. The inner layer is absent from both the Madagascar and South Atlantic sample. All specimens examined from these last two localities do not display any variation in the layering; however, in the South Atlantic sample the second-order rods of the middle layer vary somewhat in the degree of curvature (fig. 34). It is quite unexpected to find virtually identical variant patterns in populations that clearly can have no gene flow; i.e., the Marianas population and the Florida population. *Oxygyrus*, as noted elsewhere, is limited in its latitudinal range, and there could not have been population mixing since mid-Cenozoic time. We must therefore lean toward a mechanical explanation based on the very limited range of morphological possibilities. Geological range information is sketchy, but *O. keraudreni* has probably existed since at least Eocene time.

The Adult Stage. In the seventh growth stage, three basic wall structure variant patterns were observed. The most conservative pattern begins with the outer layers of rigid Type-2 structure, the same as that of the middle layer (fig. 35). These layers are thinner ($14.0+ \mu\text{m}$) than the middle layer ($30.0+ \mu\text{m}$). Both outer layers thin appreciably toward the adult calcified aperture, with the inner layer wedging out about one-fourth whorl back of the aperture. Near the end of the calcified shell the outer layer is about $1.0\text{ }\mu\text{m}$ thick and the middle layer $20.0\text{ }\mu\text{m}$ thick (fig. 36). Essentially this pattern is a continuation and rational projection of the development seen in the *Bellerophina* stage.

The next pattern involves variations of Type-2 structure in the outer layer. In specimens from near the Marianas, at the beginning of the adult

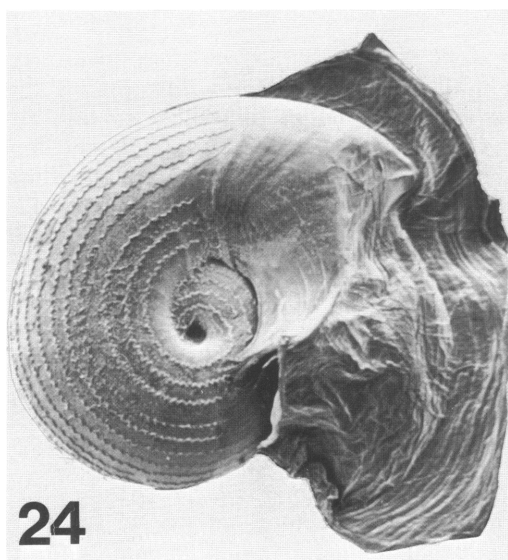


FIG. 24. *O. keraudreni*. AMNH 32003: H-6. Side view of an entire specimen. Note collapsed cartilaginous whorl and end of calcified shell. Tissue of whorl and keel have fine spiral and collabral striations. $\times 50$.

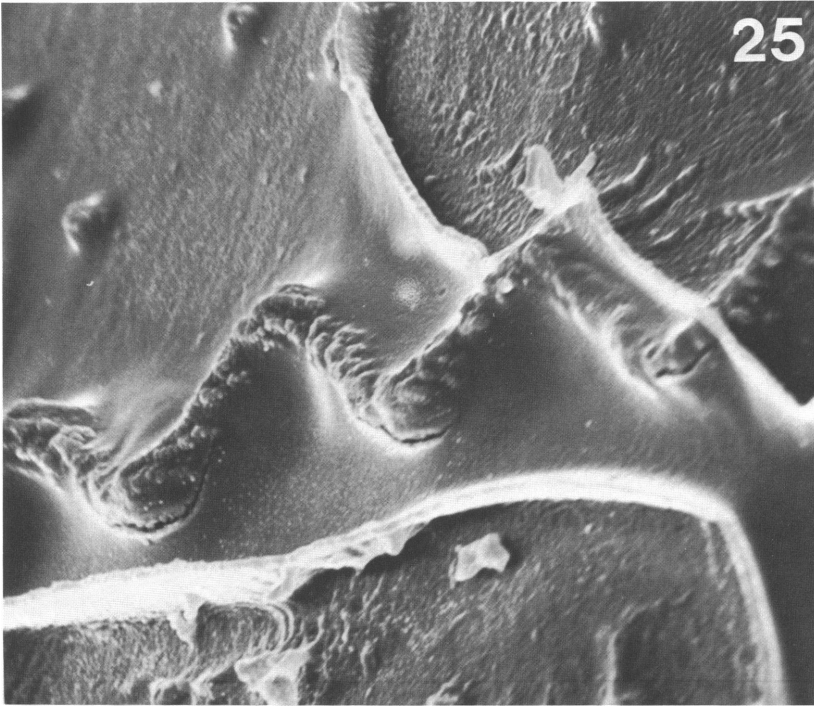


FIG. 25. *O. keraudreni*. AMNH 32003: H-6. Dorsal view of Bellerophina stage, showing peeling of tissue that covers entire shell. $\times 2100$.

stage the inner layer remains thin asymmetric prismatic, about $1.0\ \mu\text{m}$ thick. The middle rigid Type-2 layer is about $8\ \mu\text{m}$ thick, but the outer layer rapidly thickens from $6.0\ \mu\text{m}$ to more than $12\ \mu\text{m}$ within a one-fourth whorl. The first-order lamellae are turned downward toward the inner surface (fig. 37) in such a manner that the crossed-lamellar aspect is lost or difficult to recognize. The outer layer then appears to consist of a parallel series of curved second-order rods, the ends of which are normal or at an angle to the outer surface (fig. 4b). The rods are transformed units of the middle layer (fig. 3). The first-order lamellae may be single units or units consisting of a few second-order rods, or they may be composed of multiple units of second-order rods.

In passing, it should be noted that the inner layer is a conservative layer in *O. keraudreni*, being either thin prismatic, asymmetric prismatic, or Type-2 crossed-lamellar. In one

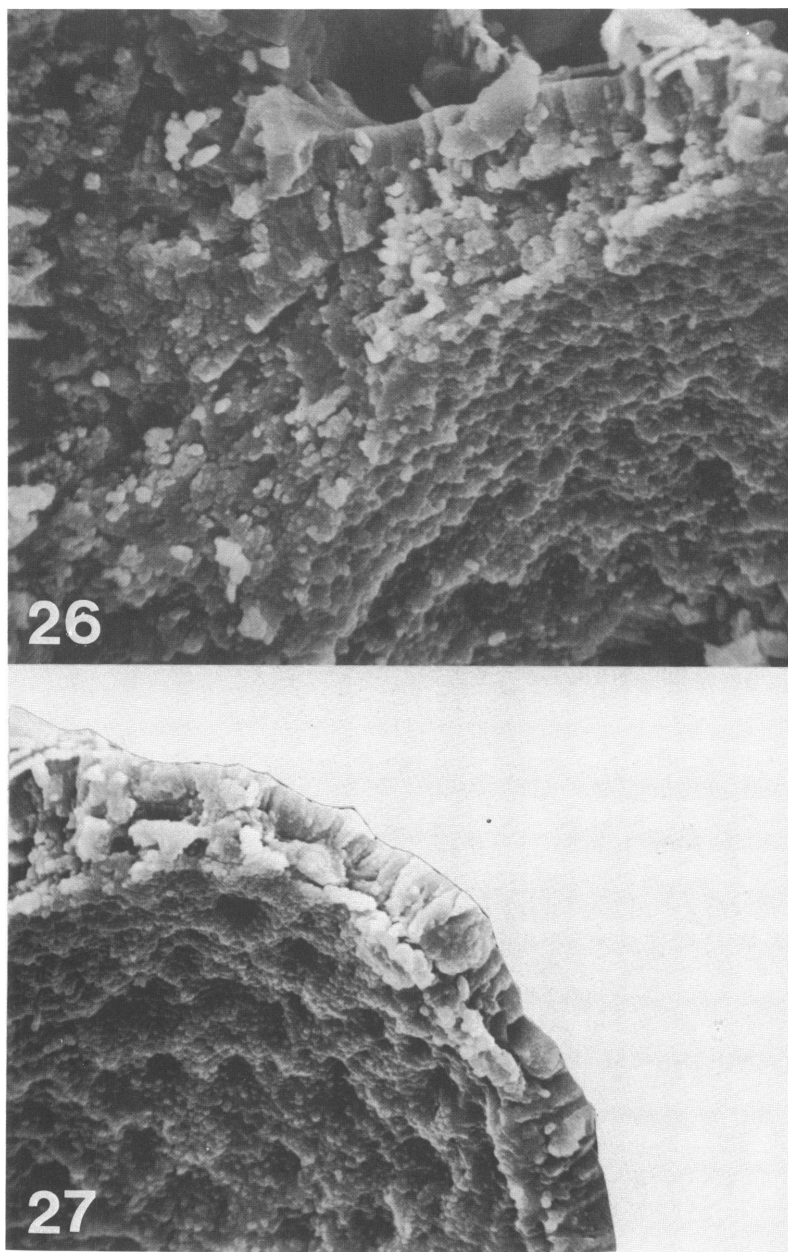
instance, we noted a slight curving of second-order rods or transformations into prismatic sheets.

Another recurring pattern involves variations of the middle layer. In the simplest form, the first-order lamellae composed of relatively few second-order rods develop a curve but still preserve the crossed-lamellar structure (fig. 38). The curving is confined to a single direction; that is, it is concave to the right when the wall is viewed aperturally (to the right of the plane of symmetry). A variation of the arcuate pattern is shown in figure 8, where the second-order rods of one first-order lamella are curved in the opposite direction to the opposing first-order lamella. We have observed this only in the middle layer, where the first-order lamellae are composed of one or several second-order rods.

The extreme development of the arcuate pattern is represented by the apparent loss of the crossed-lamellae, so that the layer seems to be

composed of curved second-order rods that are parallel to the outer surfaces (fig. 9). We must again emphasize that these patterns we are

describing frequently are gradational from Type-2 structure. In the above pattern where the first-order lamellae are not readily apparent, the



FIGS. 26, 27. *O. keraudreni*. AMNH 32014: H-68. Cross section of protoconch, showing outer simple prismatic layer, inner layer of prisms appears to be at an angle to inner surface. $\times 5200$. 27. AMNH 32014: H-68. Inner surface of protoconch, showing pitted, pustulose surface. $\times 5000$.

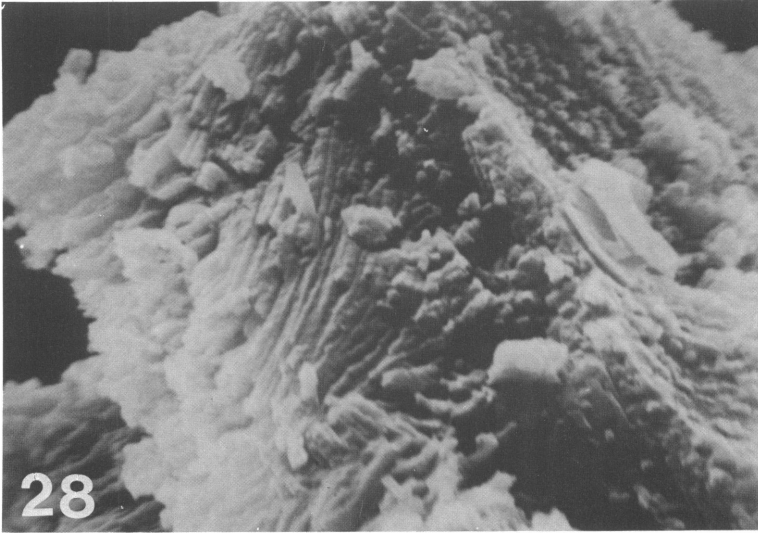


FIG. 28. *O. keraudreni*. AMNH 32015: H-70. Cross section of beginning of first whorl. Note that inner layer is crossed-lamellar, other layers not preserved. $\times 5500$.

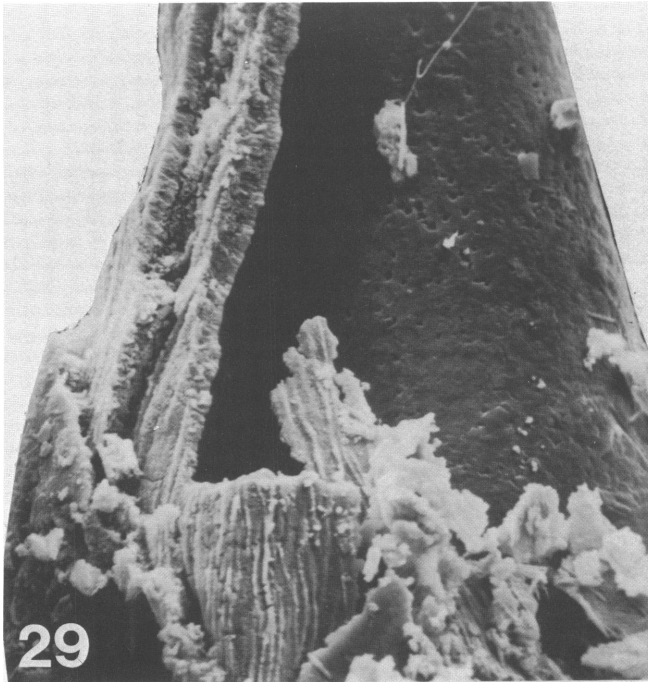


FIG. 29. *O. keraudreni*. AMNH 32016: H-87. Cross section near end of second whorl. Wall composed of three layers, two outer prismatic layers and a middle crossed-lamellar layer. $\times 1900$.

pattern was derived from curved crossed-lamellar structure. A single observation led us to believe that the middle layer was either helical or spiral. This was falsified by the subsequent construction of mosaics of several specimens.

Yet another middle layer variant pattern involves first-order lamellae composed of bundles of second-order lamellae. Adjacent bundles overlap each other and the second-order lamellae are either sigmoid or curved downward (fig. 1).

Within an eighth of a whorl from the end of the calcified adult aperture, the outer layers (if present; that is, if they have not wedged out earlier) disappear. The middle Type-2 layer thins and is converted at the edge of the shell into a sheet prismatic layer about $2.0\text{ }\mu\text{m}$ thick, dipping toward the inner surface (fig. 7). The cartilaginous layer, which becomes thicker in the adult stage, is about $30.0\text{ }\mu\text{m}$ thick at the end of the calcified shell.

Protatlanta souleyeti (Smith, 1888)

EXTERNAL MORPHOLOGY

Protatlanta souleyeti has been considered a transitional morphologic form between *Oxygyrus keraudreni* and the other atlantids by Tesch (1949, p. 13). This is based on the presence of a cartilaginous keel and pigmentation of the gonads, among other common, presumably derived features shared by both *O. keraudreni* and *P. souleyeti*. Aside from the cartilaginous

keel character, *O. keraudreni* possesses a cartilaginous body whorl, whereas the other atlantids and *P. souleyeti* are calcified through all whorls. As mentioned above, Richter (1963, pp. 144-145) observed a trend in the atlantids toward decalcification, and he placed *P. souleyeti* and *O. keraudreni* as end members of a morphocline. *Protatlanta souleyeti* is allied with the other atlantids in most other characters, such as an

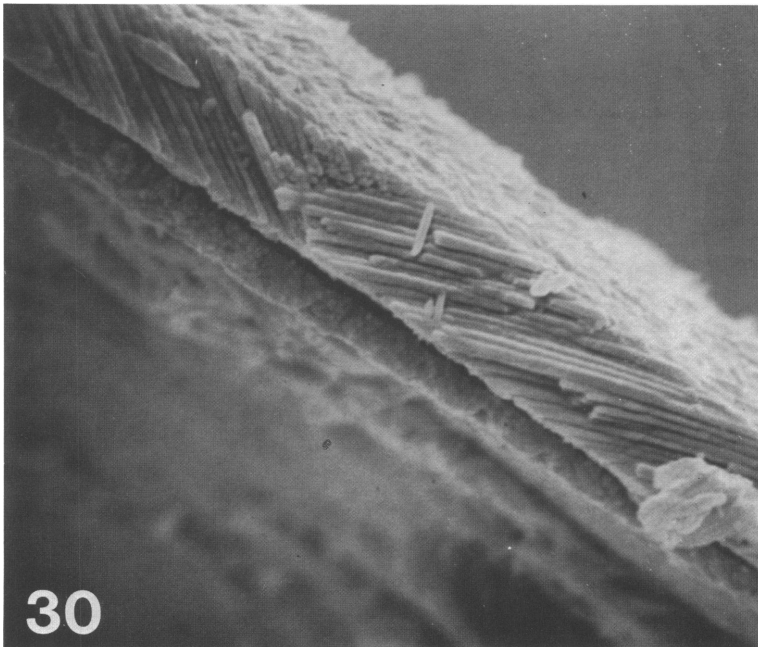
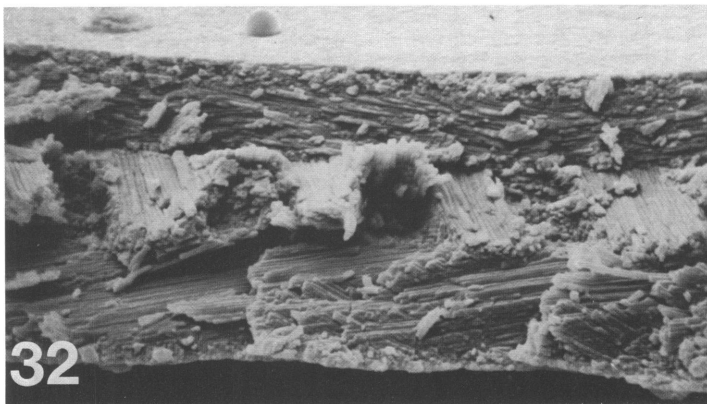
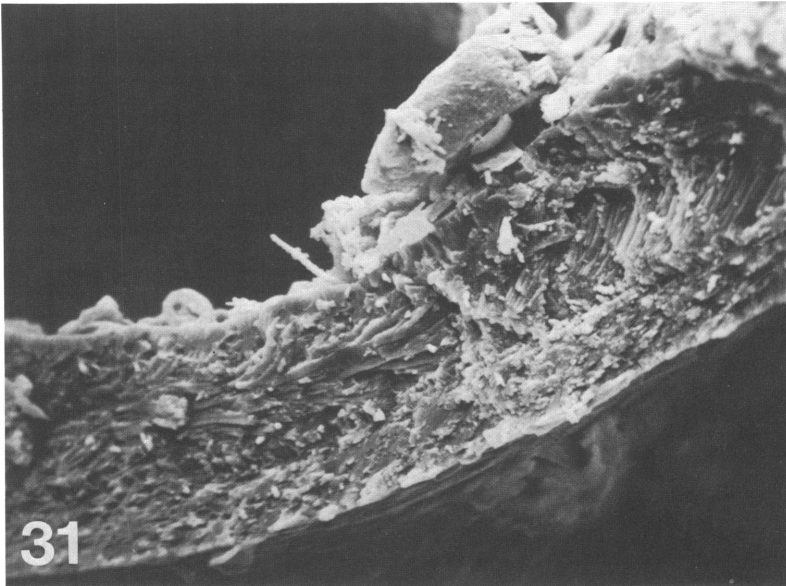


FIG. 30. *O. keraudreni*. AMNH 32017: H-54. Cross section at end of third stage. Outer layer prisms are at an angle to surface at right. At left the outer prismatic layer has converted to a crossed-lamellar structure, micrograph no. 1 from mosaic H-54. $\times 6000$.



FIGS. 31, 32. *O. keraudreni*. AMNH 32018: H-79. Cross section at the beginning of the fourth stage. Note thickened outer wall (bottom layer) and curving of middle Type-2 layer. $\times 2500$. 32. *O. keraudreni*. AMNH 32014: H-68. Cross section at completion of fourth stage. Note that all three layers are about the same thickness. $\times 2400$.

asymmetric embryonic stage, similar opercula, and similar radula. The species is small, less than 5 mm. in diameter compared with other atlantids.

Published SEM micrographs by Richter (1974, pl. 3, fig. 16) and Thiriôt-Quévieux (1973, fig. 1B) of the embryonic whorls of *Protatlanta souleyeti* seem to show that the upper whorl surfaces are unornamented. The adult whorl as illus-

trated by Thiriôt-Quévieux (1973, fig. 1B) appears to have numerous spiral elements with lirae nearer the suture and rows of tubercles toward the outer portions of the adult whorl. Tesch and others have noted that the adult whorl of *P. souleyeti* is more inflated than in most other species in the family, except *Atlanta helicinoides*.

We have examined specimens of *Protatlanta*

souleyeti identified by Smith in the British Museum collections and material gathered by us from the *Vema* cruises, and have found an ornamented embryonic variant. A sample from the *Vema* (V15-SBT 158) has shown that the two variants (ornamented and unornamented) occur within a population of *P. souleyeti* in about the same ratio (fig. 39).

The protoconch and first whorl of the two variants is unornamented and has the typical atlantid feature of a pustulous surface (fig. 15). The ornamented variety has developed, on the early part of the second whorl, two spiral lirae evenly spaced on the upper whorl face near the suture. Additional lirae may appear from under the suture late in the second whorl and gradually strengthen into spiral ribs on the third whorl (fig. 40). In consequence, the whorl profile is angulate. On the shell surface in the area between the spiral ornament, faint, spirally aligned tubercles are developed that gradually disappear late in the third whorl.

Richter (personal commun.) has suggested that perhaps this ornamented embryonic stage may be a variant of *A. helicinoides*. But the closely spaced, well-developed spiral ribbing of *A. helicinoides* and the evenly inflated whorls suggest too large a morphologic discontinuity to the ornamented form under discussion for us to believe it to be within the range of that atlantid species.

Strongly developed collabral ribbing appears early in the first whorl, gradually becomes less prominent late in the second whorl, and cannot be distinguished from growth lines by the beginning of the third whorl (fig. 39). A sinus is developed on the third whorl just below the periphery. A slit and selenizone forms and continues through the fourth whorl adult stage. The inflated adult whorl is essentially smooth with distinct growth lines and a few randomly spaced and scattered tubercles and a slit that is not in the plane of symmetry.

The unornamented embryo is completely

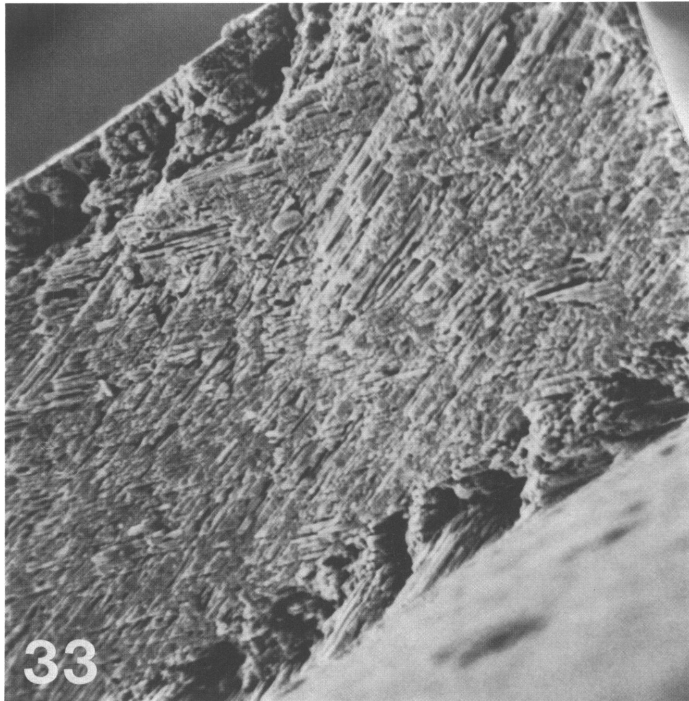
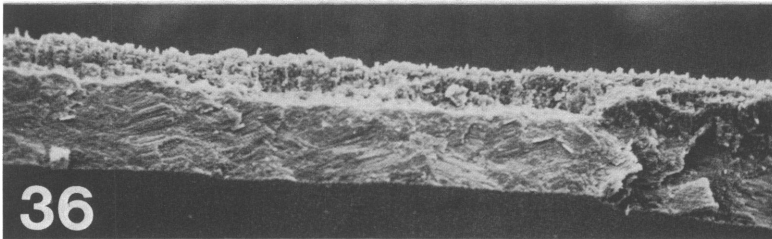
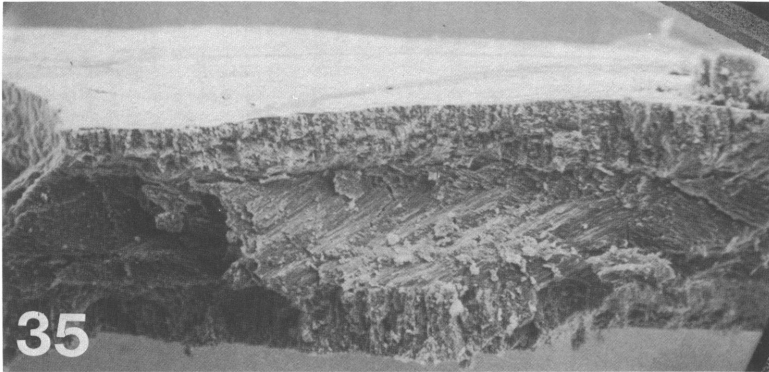
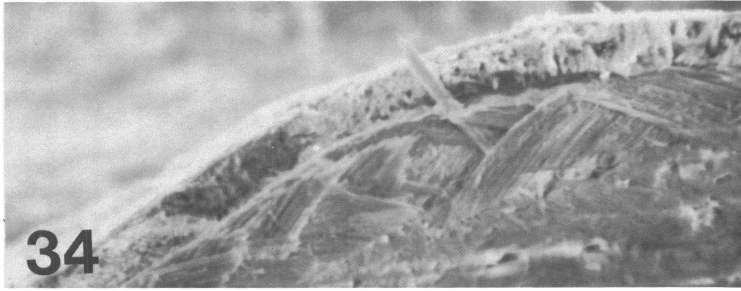


FIG. 33. *O. keraudreni*. AMNH 32028: H-121. Cross section of Bellerophina stage showing very thin outer layers. $\times 2400$.



FIGS. 34-36. *O. keraudreni*. AMNH 32029: H-122. Cross section showing the middle layer second-order rods curving. $\times 1100$. 35. *O. keraudreni*. AMNH 32019: H-99. Cross section of the adult stage, micrograph no. 1 of mosaic H-99. $\times 550$. 36. AMNH 32019: H-99. Cross section normal to aperture and near edge of calcified shell. Note absence of inner layer, which wedged out just to the left of the micrograph, micrograph no. 40 of mosaic H-99. $\times 550$.

devoid of such surface features as spiral lirae and ribbing. The spirally aligned tubercles are also absent. Early in the first whorl there are collabral lirae developed, which become weaker by the early second whorl, where they become indistinguishable from growth lines (fig. 41). The whorl profile is evenly inflated. The second and third whorls are basically featureless, except for a sinus and selenizone, which develop in a similar way to the ornamented variant. Both the

ornamented and nonornamented varieties of *P. souleyeti* possess a cartilaginous keel, beginning just posterior to the apertural lip that extends over half the circumference of the adult whorl. The cartilaginous keel and the markedly inflated adult stage distinguish *P. souleyeti* from all other atlantid species, except for *A. helicinoides*, which may lack a keel or the keel may be reduced. *Atlanta helicinoides* is similar to *P. souleyeti* in its small size, inflated body wall and distinct

sculpture of the early whorls (Richter, personal commun.). In fact, Richter (1974, p. 69) believed that *A. helicinoides* is allied with *Protatlanta*.

ULTRASTRUCTURE

The sequential development of the wall ultrastructure of *Protatlanta souleyeti* is considerably different than that of *Oxygyrus keraudreni*. However, the middle layer is similar to that of *O. keraudreni* in that it is rigid Type-2 crossed-lamellar structure. The early outer asymmetric prismatic layer of *P. souleyeti* appears to be homologous to the early prismatic wall of *O. keraudreni*. The early part of the first whorl is composed of an inner layer of blocky, asymmetric prismatic structure overlain by a

thin, finely crystallized asymmetric prismatic layer (see fig. 42). By mid first whorl, the inner asymmetric prismatic layer forms an incipient Type-2 crossed-lamellar wall structural unit, and the outer fine asymmetric prismatic layer gradually begins to thicken. The inner wall gradually becomes more organized to form a blocky Type-2 crossed-lamellar wall by the end of the first whorl and the beginning of the second whorl (fig. 43). The outer fine asymmetric prismatic layer, which started to thicken at mid first whorl, has lost the fine crystal aspect at the end of the first whorl and the beginning of the second and becomes blocky.

During the growth of the second whorl, the outer asymmetric prismatic layer evolves into blocky, alternating prisms. The middle Type-2 crossed-lamellar layer appears to have

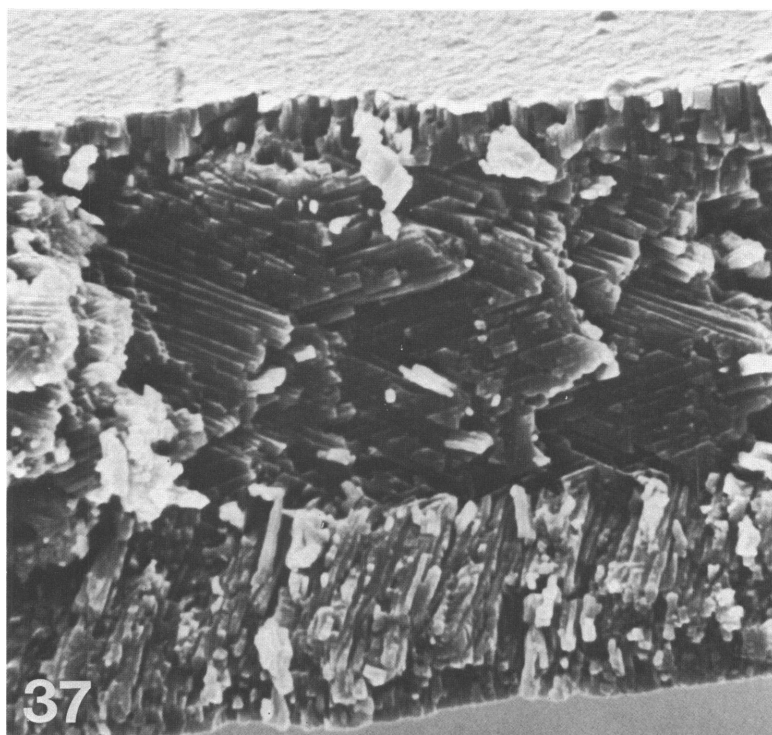


FIG. 37. *O. keraudreni*. AMNH 32001: H-5. Cross section of adult stage. Note outer (lower) layer with second-order rods curved down. First-order lamellae are obscured by irregular boundaries of second-order elements. Continuity with middle layer rods can be seen at right of micrograph, micrograph no. 21 of mosaic H-5. $\times 5100$.

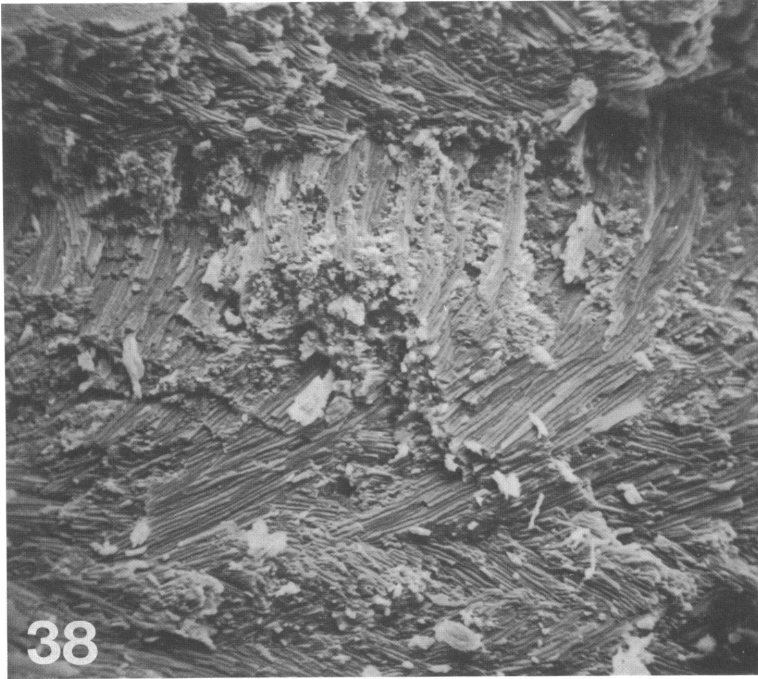


FIG. 38. *O. keraudreni*. AMNH 32000: H-80. Cross section normal to aperture of the adult stage. Note development of curved second-order rods of the middle layer. $\times 2300$.

imperceptibly gained in thickness, whereas a more dramatic change occurs within the inner layer. The inner layer rapidly thickens, and by the third whorl it is composed of very fine polygonal prisms that resemble the apertural prismatic layer and the columellar myostracum described by Bé, MacClintock, and Currie, 1972, but it is actually asymmetric prismatic (fig. 44).

The ultrastructure of the third whorl of *P. souleyeti* is dramatically different from that of *O. keraudreni*. The middle, low angle crossed-lamellar layer appears to thin slightly, as does the outer asymmetric prismatic layer. The overall width of the shell is maintained by a thickening of the inner asymmetric prismatic layer to the extent that it becomes the massive, dominant structural unit of the wall (fig. 11). The third whorl fixes this ultrastructural pattern through the fourth and body whorl. The outer asymmetric prismatic layer remains fairly constant in thickness from the third whorl onward. However, there are some changes in thickness of

the massive, inner asymmetric prismatic layer in the late growth stage of the adult whorl.

In the adult whorl (adult body whorl), the inner asymmetric prismatic layer thins to become almost equal in thickness to the middle Type-2 crossed-lamellar wall unit, with the exception of the area adjacent to the suture where it remains the dominant wall type. The outer layer thins slightly, and the prisms appear to be at an angle to the outer surface of the shell rather than being normal to the surface (fig. 45).

In the adult whorl, the middle and outer layers thicken. The outer layer appears to have been converted into a rigid Type-2 crossed-lamellar unit; however, we cannot substantiate this due to the poor preservation of material (fig. 46).

It is in the adult whorl that we encounter a most interesting divergence in wall ultrastructural type between the ornamental and unornamented variants. The variety that has a smooth embryo may have collabral lirae until the early second

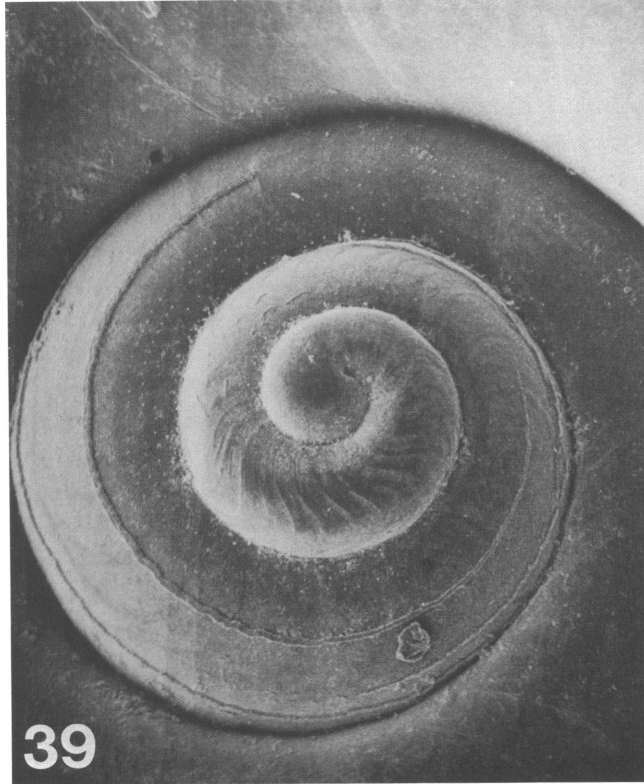


FIG. 39. *Protatlanta souleyeti* (Smith, 1888). AMNH 32029: H-1 14. Top view of embryonic stages of ornamented variant. Note strong collabral ornament on first whorl. $\times 220$.



FIG. 40. *P. souleyeti*. AMNH 32021: H-45. Oblique side view of embryonic stages. Note appearance of third lira on second whorl. $\times 210$.

whorl and lacks the inner asymmetric prismatic layer in the late adult stage (fig. 47). The other variety, with a spirally ornamented embryo, retains the inner asymmetric prismatic layer in the late adult stage of the body whorl (fig. 46). This relationship of embryonic characters to the adult wall characters is quite consistent within

the specimens examined. Hence, if a portion of an inflated adult shell minus the embryonic stage is available, the two varieties can be identified.

Alternatively, it is possible that we have confused two species. The only species with features similar to *P. souleyeti* is *Atlanta helicinoides*. The main difference is that *A. helicinoides* does not

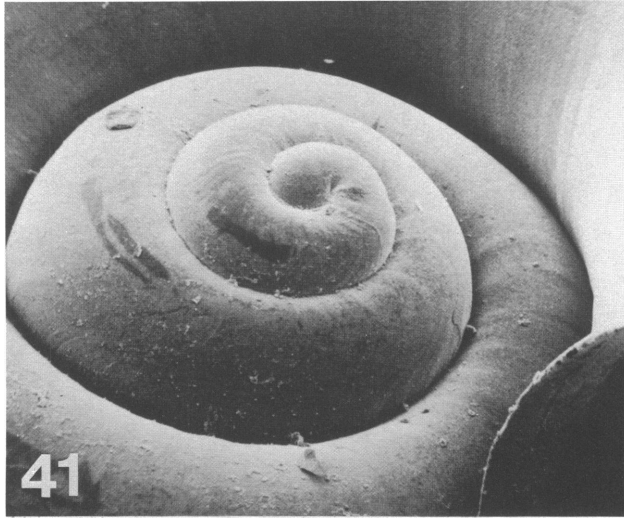


FIG. 41. *P. souleyeti*. AMNH 32022: H-116. Oblique side view of embryonic stages of unornamented variant. $\times 240$.

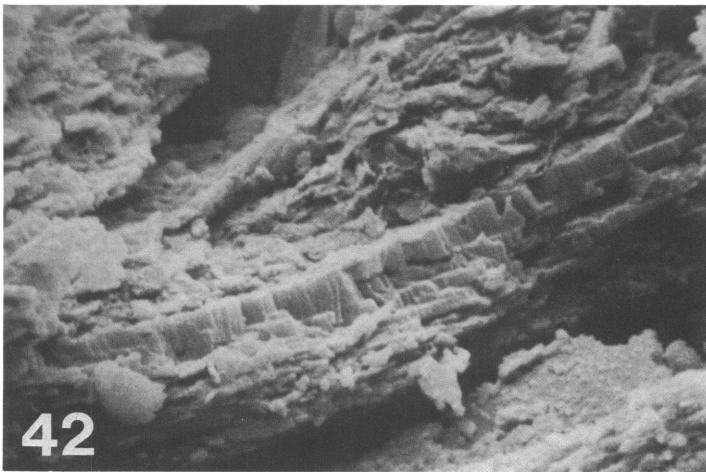
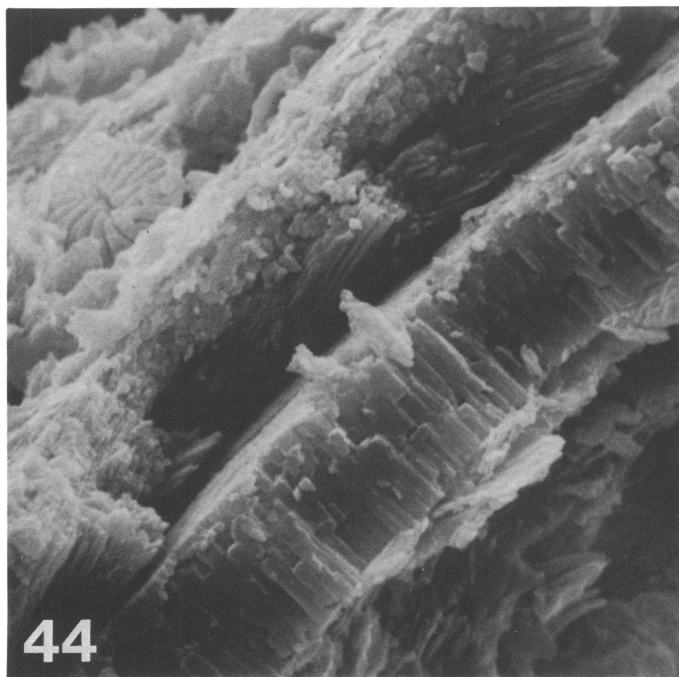
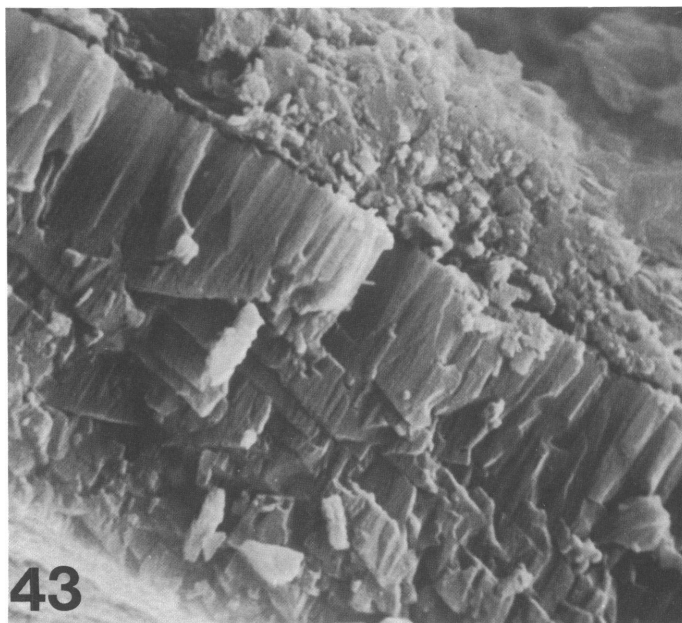


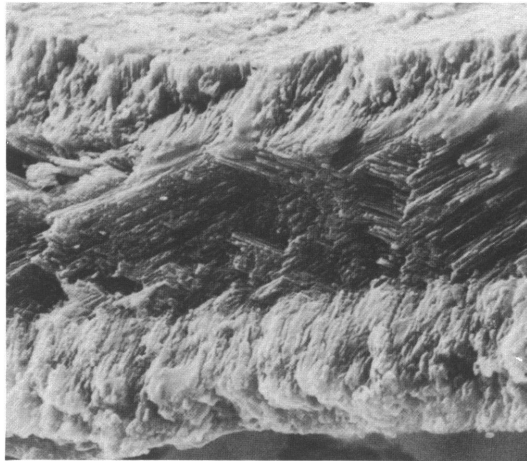
FIG. 42. *P. souleyeti*. AMNH 32004: H-43. Cross section at shoulder of first whorl. Inner (upper) layer is composed of blocky asymmetric prisms. Lower layer is composed of fine asymmetric prisms being transformed into crossed-lamellar structure. $\times 4600$.



FIGS. 43, 44. *P. souleyeti*. AMNH 32004: H-43. A cross section near the base of the early third whorl. Note blocky Type-2 structure in transition toward a prismatic structure of inner layer; other layers not preserved. $\times 5250$. 44. AMNH 32004: H-43. A cross section of a slightly later growth stage of third whorl. Note that inner layer is dominant and has been converted completely to an asymmetric prismatic structure composed of relatively fine prisms. $\times 4800$.

develop a keel until the late adult stage. However, the external ornament, shape, and height of the embryonic whorls are strikingly different. Hence, we do not believe, at this point, that the

variant we have described can be accommodated in that species. Lacking the operculum or internal morphology of the ornamented variant we are not in a position to test this idea further.



FIGS. 45, 46. *P. souleyeti*. AMNH 32004: H-43. A cross section of the fourth whorl. Note that inner (lower) layer is about the same thickness and that there is no apparent continuity between elements of the layers. Note further that inner asymmetric prismatic layer shows a few prisms suggesting incipient crossed-lamellar structure. $\times 4500$. 46. AMNH 32004: H-43. Cross section of fifth whorl. Middle layer is dominant and inner (lower) appears to have converted back to a Type-2 layer. Poor preservation prevents documentation. $\times 2100$.



FIG. 47. *P. souleyeti*. AMNH 32022: H-116. A cross section of the late adult stage. Outer shell surface at top. Note thick middle rigid Type-2 layer and absence of an inner layer. Specimen is an unornamented variant of the species. $\times 6100$.

Atlanta inclinata Souleyet, 1852

INTRODUCTION

It is our intention in a subsequent paper to describe the variations encountered in the external morphology and ultrastructure of the common species of *Atlanta* from the *Vema* cruise samples. For reasons of comparison, we are including in this study some observations on the morphology and the ultrastructure of a selected species, *Atlanta inclinata*.

In general, atlantid species can be distinguished by the embryonic shells, which are quite variable. In the case of *Atlanta inclinata*, the embryonic whorls are inflated and relatively high-spined, with the sutural contact high on the whorl. The surface of the embryo, as well as the

adult, is ornamented by a series of closely packed tubercles lined up in a spiral fashion. A rather deep slit forms a selenizone at the base of the whorls (see fig. 48). The embryonic whorls are inclined at an angle to the plane of symmetry of the adult. As in most other atlantids, the adult whorl is flattened so the aperture is ovoid. On the adult whorl, a wide keel is composed of two sheets of wall, which are separated by a gap forming a slit that closes near the end of the whorl. Although Tesch and others have noted that *Atlanta inclinata* is one of the larger of the species of *Atlanta*, our preliminary observations indicate that the wall of the shell is consistently thin, reflecting the problem of being a shelled

carnivorous planktonic gastropod where weight could be a disadvantage.

ULTRASTRUCTURE

In contrast to the two other species in this study, the wall of the embryonic stage of *A. inclinata* is considerably thinner. In the earlier stage of the embryo there are three layers; a middle rigid Type-2 layer is dominant. In contrast to equivalent stages of *O. keraudreni* and *P. souleyeti*, the outer layer is about half the thickness of the middle layer and is composed of a rigid Type-2 structure which is approximately at right angles to the middle layer. The inner layer of *A. inclinata* is composed of thin asymmetric prismatic structure. This combination is not found in any of the stages of the two genera under discussion. By the third whorl, the inner layer is converted into Type-2 structure. At this growth stage, the second-order rods of the middle layer are gently curved. Both the inner and outer layers thin, and by the end of the embryonic growth they are about equal in thickness (outer layer about 2.0 μm , the inner 4.5 μm , whereas the middle layer is 7.0 μm , see fig. 49). In most embryonic growth there are changes in the wall

thickness, usually in the form of progressive thickening. In many gastropods, the wall layers thicken where there are changes in shell topography, near sutures, at a sharp periphery, or beneath large ornament features. In the atlantids the same observation can be made, but, additionally, the wall layers may change almost at random, for example, at the base of the sixth whorl.

The expanded adult stage begins at the sixth whorl. The wall thickens to about 40.0 μm and is composed of the usual dominant middle layer with a somewhat thicker outer layer and thinner inner layer. Near the suture the inner layer is dominant, with the middle layer about 30 percent and outer layer less than 20 percent of the wall thickness (fig. 50).

All the adult specimens in our collections have seven whorls, as do those in the illustrations in Tesch (1949) and other authors. None of our specimens show an unbroken aperture. Hence, we cannot make a statement regarding the nature of the growing edge of *A. inclinata* or the formation of the primary layer produced by the organic matrix. In the heteropods we would regard the first calcified layer produced by the extrapallial fluid as the most conservative one. We believe that such is the case in *O. keraudreni*, where the first calcified layer produced was the conservative rigid, middle Type-2 one, with the outer layers being variable.

Since we are unable to observe the succession of layer additions at the point of growth, we will illustrate the layer sequence from near the suture of the seventh whorl to the periphery, in which there is progressive thinning. The rationale for this is found in the sequence in *O. keraudreni* from the thick center of the whorl to the thin margin near the umbilici. This is similar to the sequential development of the layers from the apertural growth edge to the point where all layers are formed.

The wall of the seventh whorl is thickest near the suture and is composed of the same proportionate layer arrangement as described for the sixth whorl. At the center of the upper whorl surface, the outer and middle Type-2 layer are about the same thickness, whereas the inner layer is relatively thin (fig. 51). The outer and middle

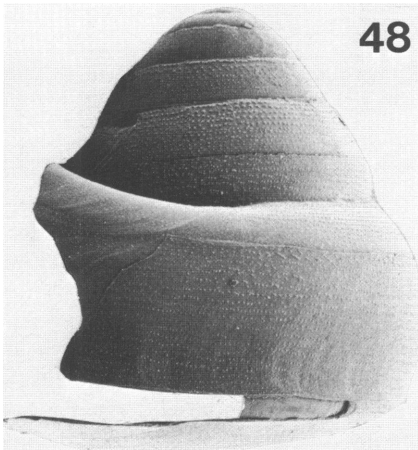
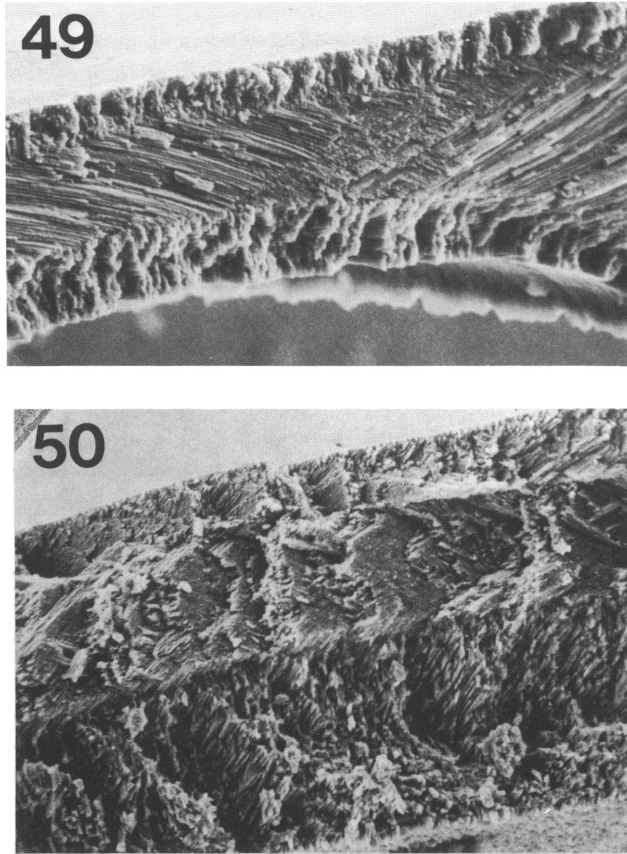


FIG. 48. *Atlanta inclinata* Lesueur, 1817. AMNH 32023: H-36. Side view of embryonic shell and a portion of an adult stage. Note basal selenizone and deep slit. Whorls are inflated and ornamented by rows of tubercles. $\times 65$.



FIGS. 49, 50. *A. inclinata*. AMNH 32024: H-111. Cross section of third whorl near suture. Note that inner and outer (upper) layers are about same thickness. $\times 2200$. 50. *A. inclinata*. AMNH 32015: H-110. Cross section of base of sixth stage. Note dominant inner (lower) layer. $\times 1050$.

layer progressively thins toward the periphery (fig. 52). Although the inner layer rapidly thickens at the periphery only the inner Type-2 layer remains. This layer changes at the keel from a rigid structure composed of even, second-order rods to a more irregular layer in which the second-order rods become enlarged and the third-order tablets become dominant (fig. 53). In at least one case, the middle layer becomes sheet prismatic structure as it wedges out near the end of the wall at the periphery (fig. 54). We, therefore, make the assumption that the primary layer is the inner one in *A. inclinata*, in contrast to the primary middle layer in *O. keraudreni*. This description is based on sections of the adult stage

that parallel the aperture and follows the termination of the front edge of the keel, figure 55.

KEEL ULTRASTRUCTURE

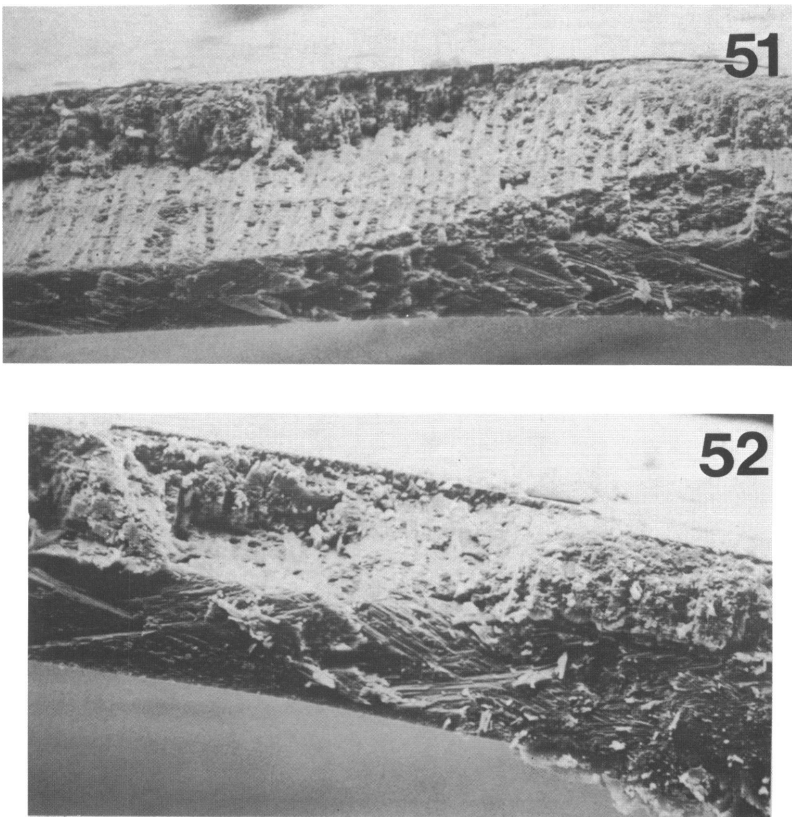
Unlike *Oxygyrus keraudreni* and *Protatlanta souleyeti*, which are the end members of the Richter morphocline, *Atlanta inclinata* (along with all the other *Atlanta* species) has a calcified keel. The construction, variations, and ultrastructure of the calcified keel in the atlantids will be detailed in a subsequent paper. However, we include a description of the keel ultrastructure of *Atlanta inclinata* here, as an additional example

of rapid ultrastructural changes within a wall. The wall adjacent to the keel differs from the above description of the seventh whorl, which was based on a later growth stage. At about one-third the distance from the proximal edge of the keel, the wall structure changes from a dominant middle layer, with two relatively minor outer Type-2 walls to one with a thicker outer layer. At this point an additional inner layer appears, composed of blocky crossed-lamellae with dominant third-order tablets. This rigid "inner" layer thickens at the expense of the middle layer (fig. 57).

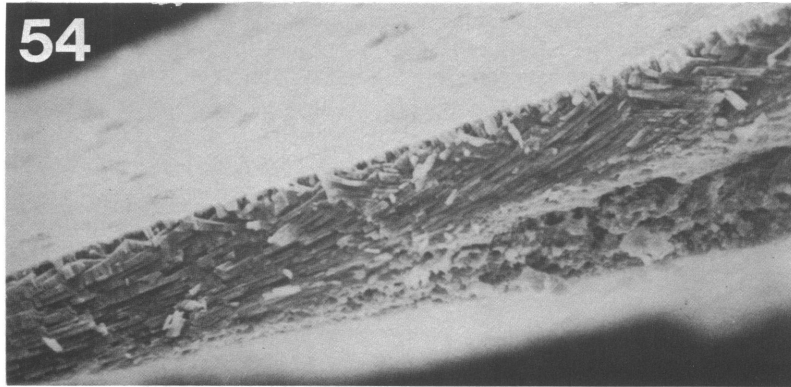
Near the edge of the keel, an additional thin asymmetric prismatic layer forms above what

was the regular outer Type-2 layer. The regular outer layer changes from low-angled second-order rods to high-angled rods. An additional middle layer appears and rapidly thickens. In brief, a sequence of lateral intercalations results in essentially a double wall at the keel, but with the proportions of the layers different from the adult wall (fig. 58).

Thus the keel at its proximal edge may be composed of a thin outer asymmetric prismatic layer, a middle dominant Type-2 layer, and an inner Type-2 layer. The whorl wall beneath the keel is composed of an outer and middle crossed-lamellar layer and an inner asymmetric prismatic



FIGS. 51, 52. *A. inclinata*. AMNH 32026: H-38. A cross section of adult whorl near center. At left, outer (upper) and middle layers are about equal in thickness (middle layer appears thicker owing to oblique fracture). At right, outer layer is very thin and the inner layer rapidly thickens. $\times 1200$. 52. AMNH 32026: H-38. Cross section adjacent and to the right of that in figure 51 (toward periphery). Note dominance of inner (lower) layer composed of rigid Type-2 structure. Outer layer is a thin rind. $\times 1200$.



FIGS. 53, 54. *A. inclinata*. AMNH 32026: H-38. Cross section at edge of shell at slit. Same cross-section as in figure 51. Outer and middle layers have wedged out. $\times 2400$. 54. *A. inclinata*. AMNH 32025: H-110. Cross section of a specimen in same position as that in figure 53. Note that outer and middle layers are wedging out and crossed-lamellar inner layer is transformed into sheet prismatic structure near edge of section at right. $\times 2000$.

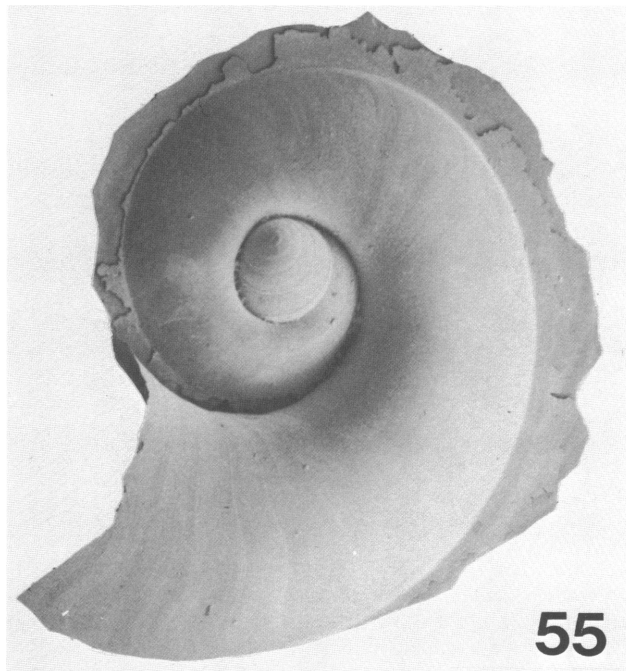


FIG. 55. *A. inclinata*. AMNH 32027: C-6. Top view of a specimen similar to H-38. Figures 51-53 were taken along aperture at a similar break on H-38. Figures 56-59 were taken after shell had been broken back one-third of a whorl on H-38 where keel is fully developed, approximately on a line continued out from coiling axis of embryonic shell. $\times 23$.

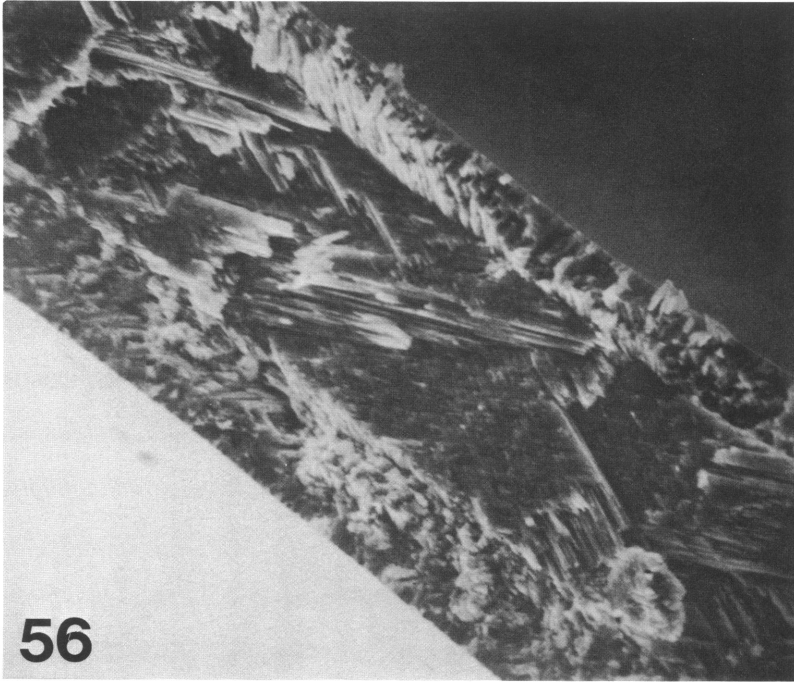


FIG. 56. *A. inclinata*. AMNH 32026: H-38. Cross section about one-third distance from proximal edge of keel toward center of shell. Note middle layer is dominant. $\times 2100$.

layer (fig. 59). At this point on the shell (about one-third of the whorl back from the aperture), the slit has been filled in, presumably with the same ultrastructural arrangement as in the adjacent adult wall under the keel. The poor state of preservation of this portion of the shell and the curved surface with its attendant geometric complexities, prevent detailing of this area (fig. 59). Beyond the keel region, the wall ultrastructure again assumes the normal configuration as seen in figure 56.

The first-order crossed-lamellae of the middle layer parallel growth lines in the adult whorl, whereas the crossed-lamellae of the outer layer

(when present) are normal to growth. The growth lines of the keel swing back sharply, paralleling the anterior edge of the keel. The keel growth lines, in part, are almost normal to those of the adult whorl. This is reflected in the wall structure as well, the middle layer first-order lamellae parallel the growth of the keel (fig. 60). Hence, a cross section of the adult whorl and keel cut essentially parallel to the aperture would show the first-order lamellae lying parallel to the lamellae in the whorl, and at the middle layer of the keel it would show the cut edges of the alternating lamellae (fig. 60).

SUMMARY AND CONCLUSIONS

1. We have shown that the wall structure composition is unique in all three species. Both the embryonic and adult walls are assembled and constructed differently in each of the species. In spite of the fact that a particular layer may

change its characteristics at given sites in the shell wall, it is possible that fragments of the wall can be used to identify species, but this has yet to be tested.

2. An important observation made was the

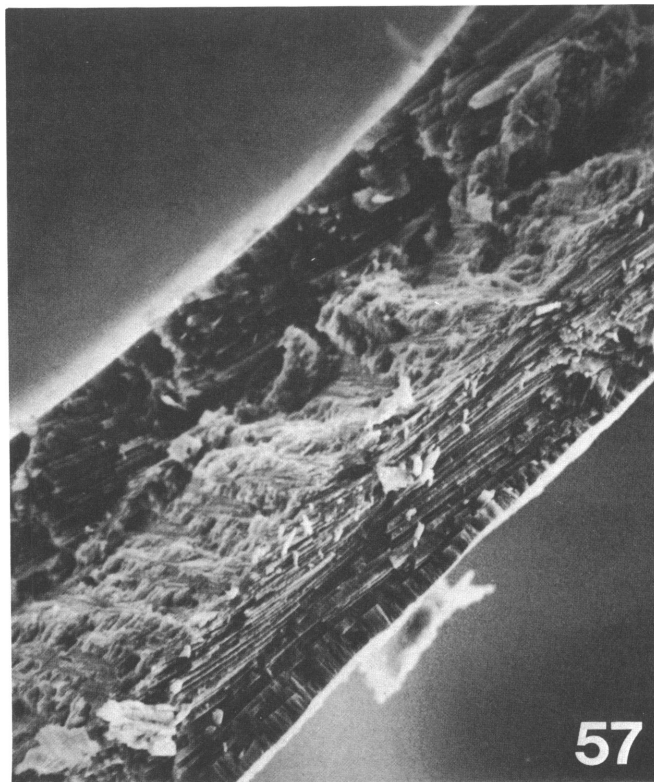


FIG. 57. *A. inclinata*. AMNH 32026: H-38. Cross section just adjacent and proximal to figure 56. An additional inner layer is present, and an asymmetric outer prismatic layer (upper part of wall micrograph). $\times 2100$.

striking variation in the ultrastructure, both in the larval and adult shells, even within a single population. Further, many of these changes appear to be random and may be subtle or large. One would assume that this variation is ecologically controlled, but the species are cosmopolitan and restricted only by the properties of large water masses in which they are found.

3. The principal modification of the wall involves relative changes in thickness (and consequent structural modifications), particularly of the outer layers. These changes are partially related to ontogenetic growth and to areas where the shell thins, for example near the umbilicus. A second but equally important modification is in the structural transformation of one wall type to another within a single layer.

4. The Type-2 crossed-lamellar structure is

more variable than any other type that we have encountered in the molluscs, based on our experience and a review of the literature. The Type-2 ranges from a single second-order rod configuration making up a first-order lamella to a sequence of over 50 rods. Curved or bundled second-order rods are common and often obscure the crossed-lamellar aspect of the structure. Therefore, it is important to make several observations of a curved structure before identification can be made. In the variant patterns that depart from a rigid "normal" appearing Type-2 crossed-lamellar structure, the second-order rods are frequently irregular in thickness and shape. The second- and third-order elements are remarkably similar to those found in the helical structure of the pteropods, which is believed by Bé, MacClintock, and Currie, 1972, to have a flexing

function. Since the Type-2 structure is found in very thin-shelled molluscs, we believe that its function is to provide flexibility to the wall.

5. The alternating typical crossed-lamellar layers of the heteropods are probably not always a single layer composed of pseudolayers described by MacClintock but may be formed separately. This judgment is based on sudden and rapid transformations within a layer, with no apparent continuity with elements of an adjacent layer. Further, the layer may thicken, thin or wedge out completely, with no topologically related change to the shell. It is difficult to imagine that such changes could transpire during shell formation at the mantle lobe site, although this process cannot be ruled out.

6. We recognized another hereto undescribed wall structure type which we term *asymmetric prismatic*. It consists of alternating simple prisms that are asymmetrical with the largest face in apposition to adjacent prisms. The layer is

usually, but not always, thin and forms only the outer or inner layer. In the majority of cases, the prisms are continuous with elements of the middle layer, but at a different angle (less than 90 degrees). The layer was thought to be simply a thinning of a crossed-lamellar layer, and it is probable that this might be the usual case. However, the layer may appear abruptly as a lenticle, with no apparent relationship to adjacent layers.

In *P. souleyeti* the inner layer is very thick and composed of fine elongate prisms, much like that of a myostracum; these prisms are also asymmetric. Dramatically, this layer may suddenly or progressively change by developing fine diagonal lines at opposing angles. These lines become dominant, forming a crossed-lamellar structure with the fine prisms being replaced by blocky third-order tablets; one of the best examples of transformation we have seen. As in other cases of wall structure transformation, there does not appear to be any relationship with

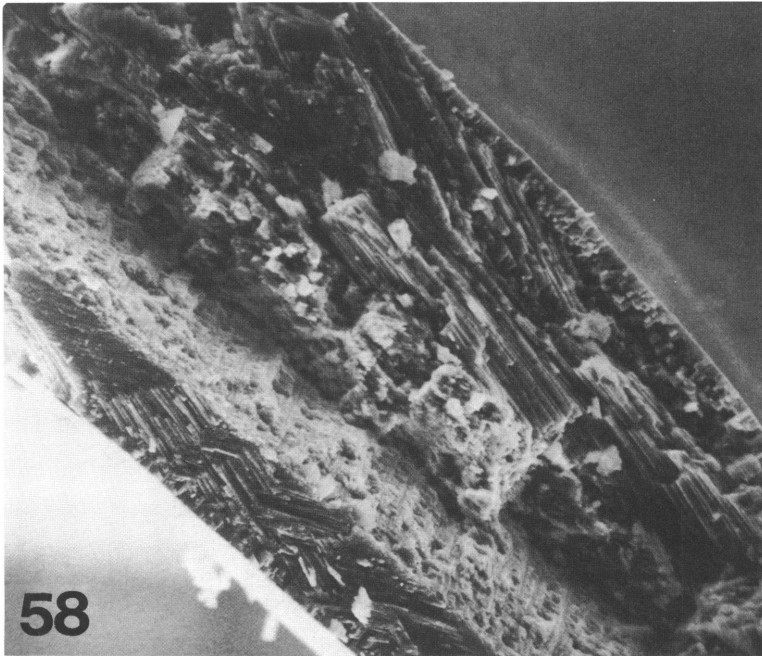


FIG. 58. *A. inclinata*. AMNH 32026: H-38. Cross section at keel showing double wall. The outer (upper) wall is the keel, consisting of an outer asymmetric prismatic layer and a middle and inner Type-2 layer. Lower wall is shell at the keel consisting of an inner and middle Type-2 layer and an outer (lower) asymmetric prismatic layer. $\times 2100$.

shell geometry changes or at particular sites such as near the suture or keel.

7. The only shell characteristics of *O.*

keraudreni bellerophina stage that retain asymmetry are the asymmetrically placed slit and selenizone, plus a slight constriction at the base

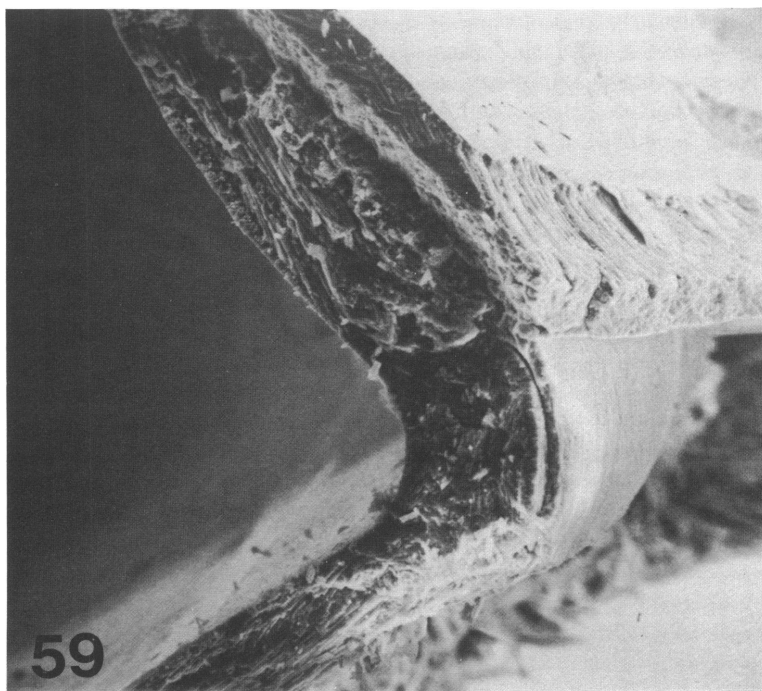


FIG. 59. *A. inclinata*. AMNH 32026: H-38. Cross section at keel, showing broken keel at top and curved cross section of selenizone. $\times 1050$.

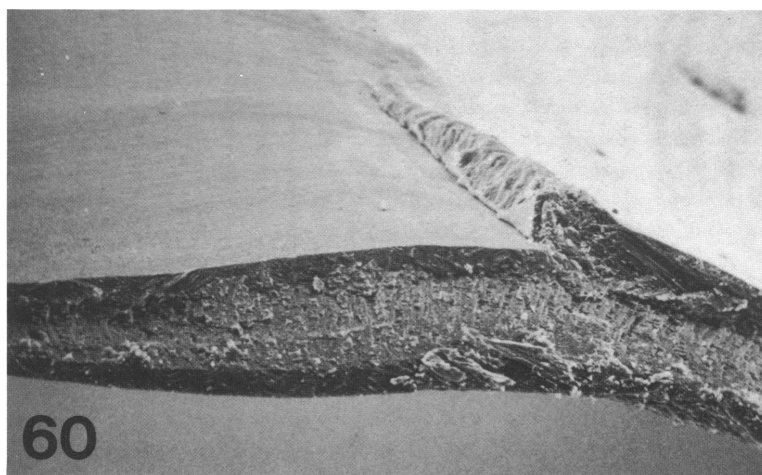


FIG. 60. *A. inclinata*. AMNH 32024: H-111. Cross section at junction of shell wall (upper right) and keel, showing middle layer first-order lamellae at right angles. $\times 550$.

of the columellar lip, where in most mesogastropods the inhalant siphon is located. In terms of the shell, *O. keraudreni* seems to us the most advanced species of the atlantids in developing general bilateral symmetry while still in the early (veliger?) growth stage and in the decalcification of the shell. On completion of our studies of other atlantids and the carinariidae, we shall attempt to analyze the groups for apomorphic and plesiomorphic characters.

8. *Protatlanta souleyeti* is easily recognized by the cartilaginous keel and the whorl profile that is more inflated than in other species of the family. Published illustrations show an unornamented, inflated embryonic shell. But in examining specimens with the SEM, we noted a number that possessed a few spiral lirae which changed the appearance of the early stages. In other characters they are identical with *P. souleyeti*, and from the literature we cannot place the ornamented specimens in any other species. A specimen from the hypodigm of *P. souleyeti* described by Smith from the *Challenger* Expedition is of this form. There are differences in the wall structure, so that we considered the two groups as separate entities. Until living specimens of the ornamented variant are captured, the taxonomic position of them cannot be resolved; however, we are tempted to consider them as separate species.

9. The wall structure is quite different in *A. inclinata* compared with the other two species. Basically, the outer crossed-lamellar layer of the embryonic stage is nearly equally developed as the middle layer, with the inner layer usually thin and of the asymmetric prismatic type, this a combination not found in the embryonic stages of *P. souleyeti* and *O. keraudreni*. In the adult the three layers are of about the same thickness, but toward the periphery or keel the inner layer

becomes dominant at the expense of the other layers. The keel is formed by the gradual intercalation of additional layers, resulting in a double wall at the proximal end of the keel; the keel then has three layers.

10. One of the most puzzling aspects of this study was the large number of specimens, that had recrystallized walls. Some walls were clearly destroyed by floral and/or faunal infestations. However, almost as many specimens from the plankton hauls were affected as those found in bottom dredges, so that diagenetic changes occur in the shell wall of planktonic forms during life. Houck, Buddemeier, and Chave, 1975, have reported calcite crystals in the aragonitic skeleton of *Porites lobata* with no evidence of boring, and they believe the calcite is biogenic. They suggest it may be an alternative form of calcification. We suspect, however, that the recrystallization involves aragonite alone in the heteropods.

We were unable to establish any pattern of selective solution of heteropod ultrastructure, thus far, in deep-sea sediments (we have not yet examined specimens from cores). Although abundant material was available, preservation employing formalin rendered most of those thin, calcareous shells useless for ultrastructural studies. Therefore, fewer localities were used than were planned or desired for this study.

11. Of the three species examined, representing three genera, there does not appear to be any correlation involving relationships using ultrastructure alone. However, ultrastructure of each is distinct and can be used for identification.

12. Finally, we believe that it is of benefit to recognize a primary layer as a standard of reference to assay ultrastructure variation in the heteropods.

APPENDIX

Heteropod Localities: *Oxygyrus keraudreni* (Lesueur, 1817)

Specimen No.	Sample No.	Latitude	Longitude	Depth	Date
H-5	V 24-IK 10	18° 39'N	133° 25'E	47 m.	19-V-67
H-6	V 29-04 # 39	19° 43'S	51° 32'E	0-10 m.	20-II-72
H-13	V 15- SBT 158	26° 27'N	78° 15'W	1090-1069 m.	24-VI-59
H-14	V 15- SBT 158	26° 27'N	78° 15'W	1090-1069 m.	24-VI-59
H-24	V 15- SBT 4 LGO 89	27° 17'N	77° 08'W	1316 m.	1-XI-58
H-25	V 15- SBT 4 LGO 89	27° 17'N	77° 08'W	1316 m.	1-XI-58
H-42	V 15- SBT 4 LGO 89	27° 17'N	77° 08'W	1316 m.	1-XI-58
H-48	V 15- SBT 4 LGO 89	27° 17'N	77° 08'W	1316 m.	1-XI-58
H-50	V 15- SBT 4 LGO 89	27° 17'N	77° 08'W	1316 m.	1-XI-58
H-52	V 15- SBT 4 LGO 89	27° 17'N	77° 08'W	1316 m.	1-XI-58
H-54	V 15- SBT 4 LGO 89	27° 17'N	77° 08'W	1316 m.	1-XI-58
H-63	V 15- SBT 4 LGO 89	27° 17'N	77° 08'W	1316 m.	1-XI-58
H-68	V 15- SBT 4 LGO 89	27° 17'N	77° 08'W	1316 m.	1-XI-58
H-70	V 14- T 53	39° 05'N	12° 11'E	2801 m.	16-VII-58
H-79	V 15- SBT 4 LGO 89	27° 17'N	77° 08'W	1316 m.	1-XI-58
H-80	V 15- SBT 4 LGO 89	27° 17'N	77° 17'W	1316 m.	1-XI-58
H-87	V 15- SBT 4 LGO 89	27° 17'N	77° 08'W	1316 m.	1-XI-58
H-99	V 14- T 53	39° 05'N	12° 11'E	2801 m.	16-VII-58
H-112	V 15- SBT 4 LGO 89	27° 17'N	77° 08'W	1316 m.	1-XI-58
H-119	V 18- BBD # 2	17° 56.5'S	154° 08'W	730-769 m.	10-IX-62
H-120	V 14- T 53	39° 05'N	12° 11'E	2801 m.	16-VII-58
H-121	V 15- SBT 158	26° 27'N	78° 15'W	1090-1069 m.	24-VI-59
H-122	V 17- 104 SBT	26° 40'S	40° 55'W	2703 m.	1-VII-61

Heteropod Localities: *Protatlanta souleyeti* (Smith, 1888)

Specimen No.	Sample No.	Latitude	Longitude	Depth	Date
H-43	British Museum (Natural History) Reg. No.: 1888.8.17.134 South Atlantic Challenger Expedition				
H-45	V 15- SBT 158	26° 27'N	78° 15'W	1090-1069 m.	24-VI-59
H-114	V 15- SBT 158	26° 27'N	78° 15'W	1090-1069 m.	24-VI-59
H-116	V 15- SBT 158	26° 27'N	78° 15'W	1090-1069 m.	24-VI-59
H-117	V 15- SBT 158	26° 27'N	78° 15'W	1090-1069 m.	24-VI-59
H-118	V 15- SBT 158	26° 27'N	78° 15'W	1090-1069 m.	24-VI-59

Heteropod Localities: *Atlanta inclinata* Souleyet, 1852

Specimen No.	Sample No.	Latitude	Longitude	Depth	Date
H-36	V 15- SBT 4 LGO 89	27° 17'N	77° 08'W	1316 m.	1-XI-58
H-38	V 14- 42	21° 07'N	38° 07'E	2231 m.	22-VI-58
H-110	V 15- SBT 4 LGO 89	27° 17'N	77° 08'W	1316 m.	1-XI-58
H-111	V 15- SBT 4 LGO 89	27° 17'N	77° 08'W	1316 m.	1-XI-58
C-6	V 15- SBT 4 LGO 89	27° 17'N	77° 08'W	1316 m.	1-XI-58

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