

AMERICAN MUSEUM *Novitates*

PUBLISHED BY
THE AMERICAN MUSEUM
OF NATURAL HISTORY

CENTRAL PARK WEST AT 79TH STREET
NEW YORK, N.Y. 10024 U.S.A.

NUMBER 2567 FEBRUARY 20, 1975

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Number 2567, pp. 1-29, figs. 1-37, 1 diagram

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The Scissurellidae—Are They Neotenuously Derived Fissurellids? (Archeogastropoda)

ROGER L. BATTEN¹

ABSTRACT

Comparative anatomical studies have been made of the families Scissurellidae, Pleurotomariidae, and Fissurellidae. Shared primitive characters such as paired organs and shared derived characters like epipodial tentacles, indicate that the Scissurellidae should be removed from the Pleurotomariacea, despite nearly identical external morphology, and placed in the Fissurellacea. The only available pleurotomariaceans when the scissurellids appeared in Early Cenozoic time are the haliotids and the Pleurotomariidae. Neither family has as many shared characters as the scissurellids and the fissurellids. A study of the ultrastructure of the scissurellids further justifies this decision. Ultrastructure normally is

quite conservative in major taxa. The pleurotomarians have a complex prismatic-nacreous wall, whereas the scissurellids have a simple prismatic—"type-2 crossed-lamellar" wall. This latter wall type is found in the embryonic stage only of the fissurellids; in adults the wall is complex crossed-lamellar-crossed-lamellar. The early embryonic stages of the fissurellids are similar or nearly identical with all growth stages in the scissurellids. This observation suggests that the scissurellids might have been neotenuously derived from the fissurellids. The scissurellids are remarkably convergent on several genera of the Upper Paleozoic Eotomariidae and the Triassic Temnotropidae in external morphology.

INTRODUCTION

I first became interested in the systematics of the family Scissurellidae when I discovered that *Scissurella (Anatoma) crispata* Fleming, 1832, has a crossed-lamellar principle ostracal layer (Batten, 1972, p. 34). I attributed this major discontinuity (all known pleurotomariaceans have a nacre-prismatic wall structure) to the fact that some taxa in a related group, the bellerophonitids, also have crossed-lamellar walls. Hence, the pleurotomariaceans had the genetic potential

to produce such a wall. During the course of my study, it became obvious that the scissurellids very probably are not pleurotomariaceans.

Besides offering some new evidence regarding the taxonomic position of the Scissurellidae, together with a description of ontogenetic sequences, the purpose of this study is to review the relationship of other groups that possess shared characters. These groups include the Fissurellidae, Haliotidae, Pleurotomariidae and

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Trochidae. In the present paper, I shall primarily confine my statements to the position that the scissurellids occupy in relation to the fissurellids and Pleurotomariacea.

D'Orbigny (1824) who first described the genus *Scissurella* placed it in the family Pleurotomariidae and recent classifications (Knight et al., 1960, vol. 1; Taylor and Sohl, 1962) have followed this traditional scheme. *Scissurella* is based on such conchological attributes as a trochoid shell, slit, selenizone, type of ornamentation, etc. However, Fischer and Bernardi (1856, p. 162) believed that as the scissurellids did not have a nacreous layer among other features that the family should be considered trochoids. Jeffreys (1865, p. 282) observed an inner nacreous layer and also considered them trochoids. Thiele (1912, p. 1) on the other hand, using general shell characters, saw a closer relationship with the fissurellids. Perhaps the most interesting suggestion was that of Sowerby (1824, p. 255), who believed that the scissurellids were simply the early ontogenetic stages of *Haliotis* and *Fissurella*. This idea is obviously an oversimplification, because he apparently only considered the superficial shell characteristics. However, he may have been partly correct; my conclusion is that the scissurellids might have originated as neotenous fissurellids.

The scissurellids are a small but interesting group of primitive Archeogastropoda because they are quite variable in shell features within and between species, for the cosmopolitan distribution of some species, and they possess an array of primitive pleurotomariid characters and derived features shared with the Fissurellacea, Haliotidae, and Trochacea.

These tiny species are predominantly found below the euphotic zone but are known from a wide range of depths and latitude. Thorson (1941, p. 4) for example, found *S. (A.) crispata* in 8 m. of water in Oslo Fjord and in 2020 m. off the coast of France. Most species appear to prefer colder waters. Adams (1859, p. 439), however, did find *S. indicus* living in a surficial sargassum community and McLean (1967, p. 404) stated that some species are known from sublittoral faunas. If *Incisura* Hedley, 1904, is included in the family, then the range should include the littoral zone as well. Species appear to be

adapted to a broad range of substrate, they are moderately common in soft muds, globigerine oozes, sands, and coarse-mixed gravels. The most commonly encountered member of the family seems to be *S. (A.) crispata*, and there are many reports of dredge hauls containing specimens from Japan to the eastern Pacific (McLean, 1967, p. 405), most of the North Atlantic, and the Mediterranean.

One great difficulty encountered in this study was to obtain sufficiently well-preserved material. For example, of more than 40 specimens of *Scissurella*, only 12 possessed shells that were not riddled with infloreal and infaunal infestations. Most of the 12 that were prepared and examined proved to be considerably altered and this was also true of specimens of the fissurellids. The early whorls are invariably the most altered because they were exposed the longest to the environment; thin-shelled forms are particularly vulnerable.

The recrystallization process begins by the solution of crystal faces so that the structural elements are exaggerated (fig. 1). Then, what is probably calcite begins to precipitate as a micritic envelope around the elements (see fig. 2) until finally the wall structure is all but obliterated. Chave (1964, p. 384), suggested that aragonite inversion to calcite may occur by chemical action on the sea floor before burial. Most research on aragonite inversion has been in connection with diagenetic changes in sediments and have shown that in situ inversion can occur either during lithification or when the rock comes in contact with fresh or connate water. Undoubtedly, there is a whole spectrum of alteration sequences possible but we now know that alteration and inversion may occur during the lifetime of the animal.

In the current study it seemed, at first, that recrystallization was initiated at sites of borings or fractures, but in some shells, alteration was complete where no evidence of outside access was noted. The process by which this occurs is difficult to assess as it appears that it is an in situ nonbiological diagenesis. The assumption that fossil molluscan shells were altered before, during, or after lithification cannot be made until an analysis indicates that the altered shell and the medium or matrix contain the same or different trace elements. Further, the problem of how wall

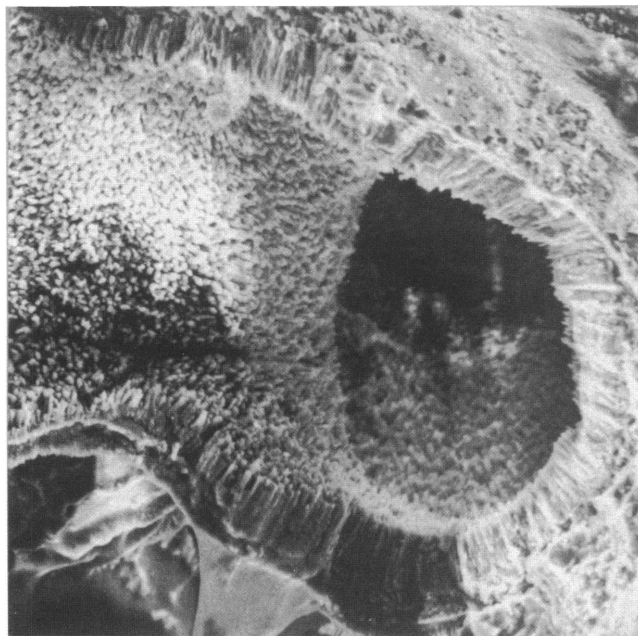


FIG. 1. *Scissurella* (*Scissurella*) *declinans* Watson, 1886. AMNH 29303; loc. D5601. From 765 m., 20.7 miles N of Limbe Island (Philippines), latitude $1^{\circ}13'N$, longitude $125^{\circ}17'E$, Albatross Expedition. Fragment of protoconch in lower portion and beginning of first whorl in upper portion of micrograph. Single layer of simple prisms has been eroded so that crystal boundaries are exaggerated. X1200.

structure is preserved as far back as the Pennsylvanian is made even more difficult.

Acknowledgments

I thank Mr. Michael P. Dumont and Dr. Niles Eldredge of the American Museum of Natural History for their comments and suggestions which improved this paper. Mr. Dumont was of great help in the technical aspects of this study and I am particularly grateful for his patience in sorting large numbers of samples to recover very few specimens. Mr. Robert Koestler also of the American Museum provided much technical advice and skill during the examination procedures.

I am deeply appreciative of the following people for their cooperation and generous contributions of rare study specimens: Dr. Allen Bé of

Lamont-Doherty Geological Observatory for permission to sample the large deep-water collections in the Oceanography Division; Dr. Frank Climo, Dominion Museum, Wellington, New Zealand, for providing specimens of *Incisura*; Dr. James McLean, Los Angeles County Museum, for specimens of *Sinezona*; Dr. Donald Moore, Rosenstiel School of Marine and Atmospheric Science, Miami, Florida, for fissurellid species from the Bahamas and Florida; Dr. George Radwin, Natural History Museum of San Diego, for fissurellid material from California; and Dr. Joseph Rosewater, National Museum of Natural History, Smithsonian Institution, for rare specimens of fissurellids from the Caribbean and Ascension Island. Much of the material they sent was recovered from deep dives or dredge hauls representing a considerable effort and expense;

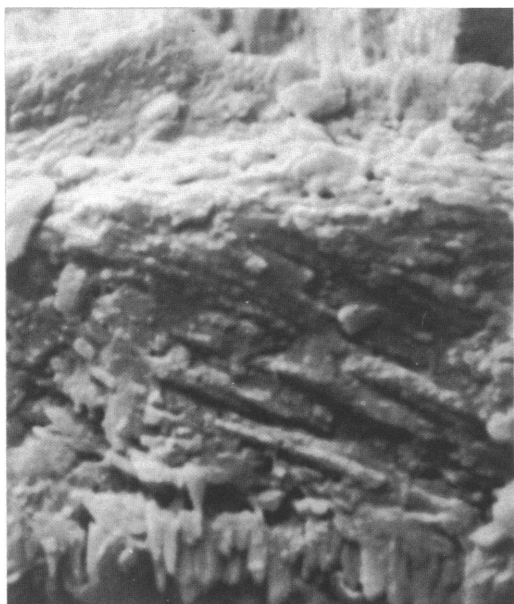


FIG. 2. *Scissurella* (*Scissurella*) *costata* d'Orbigny, 1823. AMNH 29304; loc. D5601. Cross section of second whorl midway between suture and selenizone. Both inner prismatic layer (lower layer in fig.) and middle crossed-lamellar layer have been eroded and coated by a calcitic micrite film obscuring detail. X650.

therefore I am doubly grateful for their willingness to fulfill my requests.

THE SCISSURELLIDAE

The Scissurellidae as classified in Knight et al. (1960, p. i221) consists of three genera and four subgenera. *Scissurella* d'Orbigny, 1824, possesses an open slit which generates a selenizone and is divided into two subgenera based on the relative position of the selenizone. *Scissurella* (*Scissurella*) tends to develop strong collabral or axial ribbing during at least a portion of its ontogeny. The upper whorl face usually is flattened and the selenizone is at the junction of the upper and outer whorl faces. *Scissurella* (*Anatoma*) Woodward, 1859 (fig. 3), has a trochoid shell with finer ornament than in *S.* (*Scissurella*) (fig. 4), and the selenizone is about midwhorl. *Scissurella* (*Anatoma*) is the more commonly encountered and more widely distributed member of the family, and there are more than 20 described species ranging from the

Paleocene to Recent. A cursory examination of illustrations of these species and others of the family suggests that a taxonomic revision is overdue. Fortunately, McLean (1967) has modernized and revised the classification of the Pacific species of *Scissurella*.

Incisura Hedley, 1904, is an auriform, haliotid-like genus with a very short slit and a selenizone situated just above midwhorl (fig. 5). *Incisura* (*Incisura*) and *I.* (*Scissurona*) Iredale, 1904, appear to be separated by the possession of fine ornament in the latter subgenus. The genus is restricted to New Zealand-Australasia and is known only from the Recent. *Sinezona* Finlay, 1927, has a variable, but usually trochoid shell shape. The critical generic feature is the formation of a foramen which results from the closing of the slit during late maturity (see fig. 6). The position of the foramen in relation to the outer lip apparently is variable between species. The genus is widespread throughout the oceans and ranges in age from Pliocene to Recent. *Scissurella* (*Scissurella*) is also cosmopolitan and first appears in the Paleocene.

Nearly all adult scissurellid shell features can be found within the families of the Pleurotomariacea but not embryonic features. In fact, some species have analogs among pleurotomarian genera. For example, *S.* (*A.*) *crispata* has many of the shell features found within the Paleozoic genus *Glabrocingulum*, whereas *S.* (*S.*) *costata* d'Orbigny has attributes of the Triassic *Temnotropis*. *Scissurella* first appeared in the Danian (Lower Paleocene) of western Europe.

By Cretaceous time, the major periods of adaptive radiation of the Pleurotomariacea had ended and the rather cohesive family Pleurotomariidae was the sole surviving group, and is extant. The all-important selenizone complex displays a modest amount of variability in the Cretaceous (Cox, 1960; see pls. 45-59). The basic plan of the complex involves a selenizone that is conformable with, or slightly convex and raised above, the whorl surface. The surface of the selenizone reflects the general whorl ornament, but may subdue or exaggerate it in some species. The selenizone varies somewhat in position on the whorl depending on the whorl shape, but basically it is at or slightly below midwhorl. The selenizone margin is defined by a narrow shallow

trough; however, it also may be a barely discernible line or a slightly rounded lira. An alveozone is rarely developed; one is present in the genus *Bathrotomaria* Cox, 1956. The three living genera and most Cretaceous and Cenozoic species are quite large in size compared with those in earlier pleurotomarian families.

The scissurellid selenizone resembles that found in the embryonic stages of the fissurellids (see fig. 25) having a concave selenizone with well-developed selenizone margins with lunulae and with or without an alveozone. On this basis and also considering ornament patterns, radically different ontogenetic sequences, wall structure, and size, I cannot find any likely source or compelling reasons to believe that the scissurellids could have been derived from the Pleurotomariidae.

Scissurella (Anatoma) crispata Fleming, 1832

This is perhaps the best known species of the family and I therefore use it to develop my thesis that the family should be treated as a member of the Fissurellacea. Most adult specimens have about five whorls, and the width-height range is about 3 to 6 mm. (see fig. 3). For a diagnosis see McLean (1967, p. 405). The most obvious inter-specific variability involves width-height ratios, ornament pattern, sutural placement on the

whorl, and modifications of the selenizone margin. Little is known about its life habits, but Fretter and Graham (1962, p. 488) observed a live specimen rasping food particles off hard substrate. Specimens living in soft muds must graze on shells or other relatively small surface areas.

Comparative Anatomy and Its Implications

The most recent and detailed dissection of *S. (A.) crispata* was accomplished by Fretter and Graham (1962) using the specimen mentioned above. Dr. Vera Fretter in a letter dated January 22, 1972, most generously detailed the anatomy of *Scissurella* compared with the pleurotomariids, haliotids, trochids, and fissurellids. I am taking the liberty of abstracting her comparisons and including some of my own observations; most importantly, I am making interpretations based on her statements and take full responsibility for the conclusions drawn.

The following characters appear to be derived and shared by the scissurellids and the fissurellids: epipodial tentacles, the oesophageal-caecal groove, a similar radular train, subocular tentacles, a subreticulate protoconch, the spiral caecum, a simple-prismatic inner and outer protoconch wall, the development of type 2 crossed-lamellar walls (defined on pp. 13-14) with a concomitant gradual percentage reduction of outer

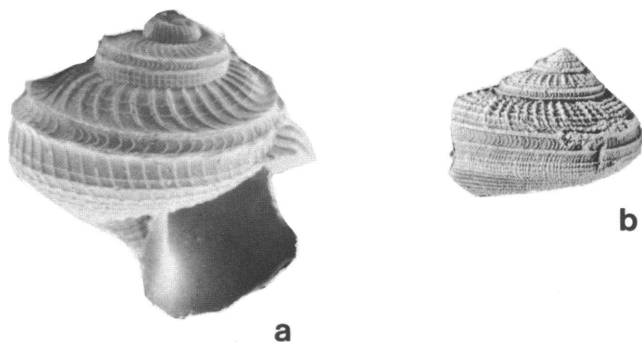
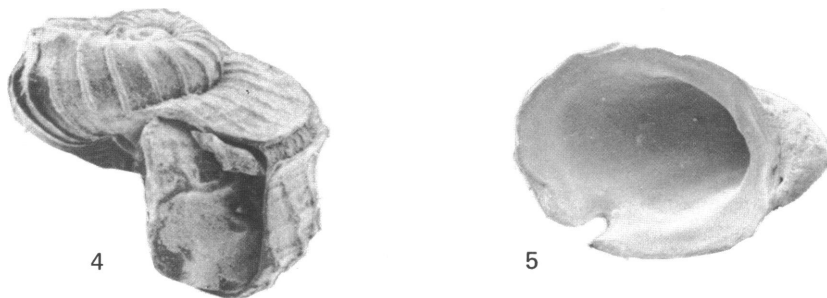


FIG. 3. a. *Scissurella (Anatoma) crispata* Fleming, 1832. AMNH 29305; loc. D5601. An oblique side view. This species is convergent on *Eirlysia* Batten, 1956, belonging to the Paleozoic family Eotomariidae. X20. b. *Eirlysia reticulata* Batten, 1958. AMNH 28058; loc. AMNH 502. Cherry Canyon Formation (Permian), Guadalupe Mountains, Texas. X4.



FIGS. 4, 5. 4. *Scissurella* (*Scissurella*) *costata*. AMNH 29304; loc. D5601. An oblique apertural view. Convergent in a number of features, such as placement of selenizone, on Triassic *Temnotropis* Laube, 1870. X52. 5. *Incisura* (*Incisura*) *lytteltonensis* (Smith), 1894. AMNH 29306. Intertidal rock pool, Lyttelton Harbor, South Island, New Zealand. An apertural view. X22. Collected by Dr. Frank Climo.

and inner wall thickness with growth and the development of a slit, selenizone, and ornament at approximately the same position on the embryonic whorls.

Features shared by the scissurellids and the living pleurotomariids include: a radular caecum, a well-developed left kidney, papillate tentacles, and poorly developed eyestalks. It is unclear to me and probably very difficult to be sure if these represent primitive or derived characters; one can speculate that the enlarged left kidney is probably derived, for example. However, such paired pallial organs as the bipectinate ctenidia, paired shell muscles and paired (but unequally-sized) kidneys, and the presence of a slit and selenizone in adult specimens seem to be shared, primitive features. The presence of exhalant re-entrants in other groups such as in the haliotids also most probably are primitive character states. In rare cases, the slit and selenizone may be highly specialized, derived characters in such advanced groups as *Siliquaria* Bruguière, 1789. This type of convergence is easily recognized when the entire morphological design is analyzed. Finally, *Scissurella* has a rectal gland that is unique to the genus.

Based on Fretter's detailed anatomical comparisons, along with additional ultrastructure and ontogenetic evidence which is detailed below, I offer a tentative scheme of relationship involving groups under discussion with shared characters (diagram 1).

Ontogenetic Considerations

Surficial Features. The most impressive shell feature that sharply sets apart the scissurellids and fissurellids from the related pleurotomariaceans, haliotids, and trochids is the variable early ontogenetic sequence which may be initiated by a unique reticulate protoconch (see fig. 8). In the latter three groups, the usual embryonic shell progression begins with a smooth and polished, globose protoconch usually without

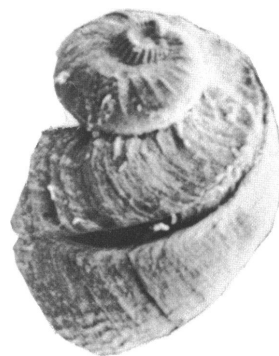


FIG. 6. *Sinezona rimuloides* (Carpenter), 1865. AMNH 29037. Shallow water along the Southern California coast. Oblique side view. Note foramen terminating selenizone in this young adult specimen. X50. Collected by Dr. James McLean.

any growth increments. There tends to be a boundary between the protoconch and the beginning of the first whorl, represented by the first growth element. Within the next whorl in these groups either an upper whorl surface spiral feature may appear or the first flexure of growth lines that initiate the slit (except for the holostomous Trochacea). Just beyond the second whorl, there is a progression of shell feature development leading to the adult condition, usually attained by the fifth whorl in the Archeogastropoda. This generalized sequence has been observed in many groups, for example, in *Perotrochus midas*, Bayer, 1965 (a pleurotomariid). I have examined thousands of specimens from

virtually all pleurotomarian families and many trochids without observing much variation of this conservative ordering. Some trochid genera, however, do show a reticulate protoconch. Another type of variation in these primitive groups can be seen in *Perotrochus midas*; as the ornament first appears it becomes as strongly developed as in the adolescent shell, giving the appearance of an additional embryonic stage. But very soon the ornament becomes wider spaced and normal progression occurs. Many other prosobranchs tend to grow in a similar manner, whereas others show a more complicated sequence such as Knight illustrated in his monographic treatment of the Pseudozygopleuridae (1930) and that

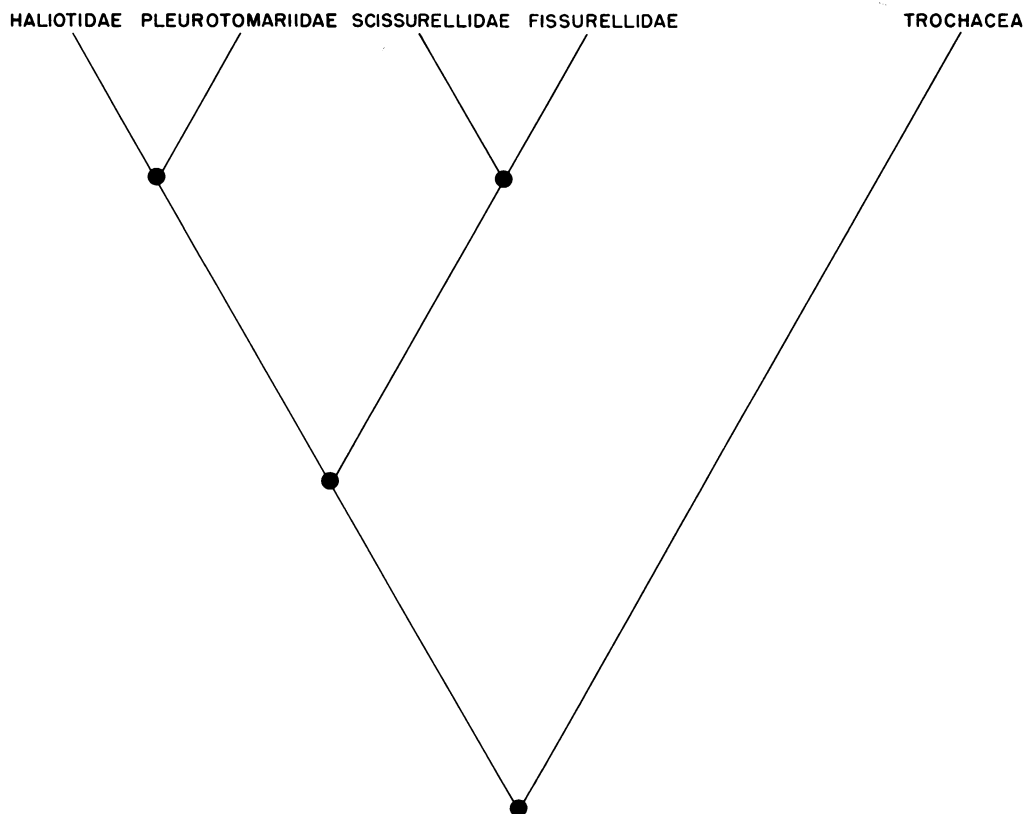


DIAGRAM 1. Cladogram representing a tentative scheme of relationships among some zeugobranch archeogastropods. The basis for this arrangement is the number of shared primitive and shared derived characters between the groups.

described in *Fusus* by Grabau (1904). Fretter and Pilkington (1971) described variation patterns in surficial and shell structure characters of embryonic whorls of some unrelated prosobranchs. They conclude that external features are distinctive enough so that they can be used to identify larval shells. The two surface patterns (reticulate and smooth) appear to be unrelated to whether the larvae were free-swimming or encapsulated, and further, appear to be randomly distributed within groups of prosobranchs. (See also Robertson, 1971.)

Since the reproductive cycle of the scissurellids is unknown, we can only speculate that they produce egg cases, as do the fissurellids. Garstang (1929, p. 85) has shown that reticulate larval forms settle to a hard substrate directly from the egg case in fissurellids and shortly thereafter the protoconch is absorbed.

In the scissurellids the surface of the protoconch is variable among species and even within populations. Basically, the pustulose surface is formed by terminal prism ends of the outer shell layer (see fig. 7). Superimposed on this surface is a pattern of ridges which may meander without any particular pattern, but usually intersect to form an irregular network (see fig. 8). In this

type of pattern, the ridges are tapered and their summits may be quite uneven (fig. 9). In some specimens there may be a more regular pattern in which case the ridges tend to be wider and truncated (fig. 7). Most specimens of *S. (A.) crispata* are of the first type, whereas *S. (S.) costata* tends to display the latter type indicating interspecific variation in this feature. In *Sinezona rimuloides* the protoconch is entirely pustulose.

In *S. (A.) crispata*, the protoconch surface persists for approximately one-half whorl of the embryonic shell. Gradually, the ridges become flattened and enlarged. While still sinuous they do not intersect each other, but rather are arranged more or less parallel to the aperture (see fig. 8). Just beyond the first whorl there is an abrupt change in the character of the shell surface. There is a sharply defined and raised lamella (see fig. 8) which separates the embryonic shell from the next developmental stage. It is at this juncture that, in all probability, the individual emerged from the egg case.

The surface of the next, probably post-torsional, stage is relatively smooth and without pustules; instead, the surface is marked with growth increments. Rather widely spaced, even, collabral ribs appear which at first are flat-topped

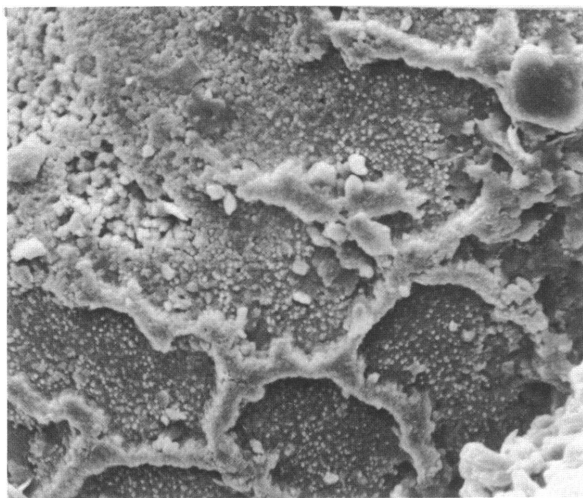


FIG. 7. *Scissurella (Scissurella) costata*. AMNH 29304; loc. D5601. Side view of protoconch. Note flattened ridges and pustulose surface between them. X1990.

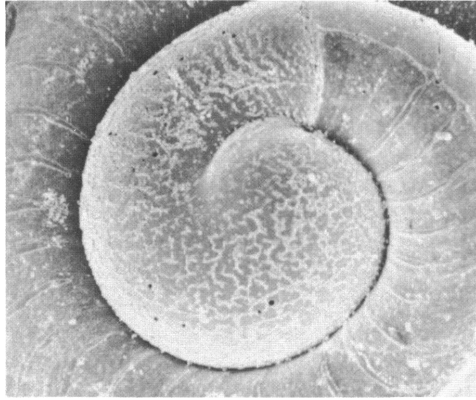


FIG. 8. *Scissurella (Anatoma) crispata*. AMNH 29308. East of the Mariana Islands, 760 m., latitude $17^{\circ}56'S$, longitude $154^{\circ}8'W$, Vema Expedition, 1962. Top view. Note irregular reticulate pattern on protoconch and early whorl and lack of growth lines. The protoconch is terminated by a reflection of the aperture. $\times 180$.

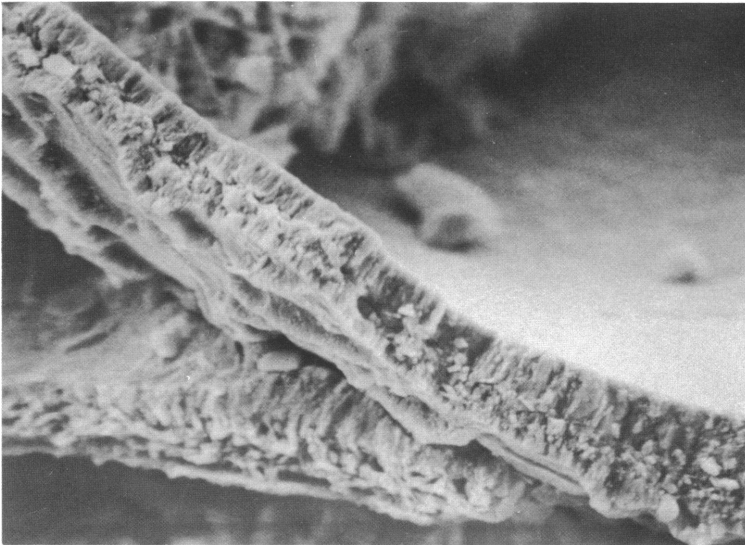


FIG. 9. *Scissurella (Anatoma) crispata*. AMNH 29309. West of the Canary Islands, 1080 m., latitude $26^{\circ}27'N$, longitude $28^{\circ}15'W$, Vema Expedition, 1959. Fragment near juncture of protoconch and first whorl. Note uneven and tapered ridges in cross section near bottom of micrograph; outer surface is down. $\times 5752$.

and possibly homologous to the sinuous ridges of the later embryo shell. Within one-fourth of a whorl these ribs become rounded and persist into the adult shell as the strongest ornamental feature (fig. 8). Just above midwhorl, a flat-topped spiral rib appears but does not become as organized as the collabral ribs. This rib persists for about one-fourth of a whorl and marks the precise site where the slit is to form. Growth lines during this stage are collabral but at about half whorls, the growth lines abruptly swing back above the spiral rib and forward just below the rib to form a V-shaped sinus. Within a distance of two collabral ribs the growth lines swing back and become parallel-sided to form a true slit (see fig. 10). It is at this point that the larva has completed its veliger stage and has settled to the bottom. From this position on the shell abapically, characters are added rapidly until the adult features are fully formed, usually by the fourth whorl.

It is interesting that in the three species of *Scissurella* available for this study, the post-

torsional sequence differs, an unusual occurrence in the Archeogastropoda. In *S. (S.) costata* the end of the torsional stage is marked by an unusually large rib (see fig. 11). From this point forward, rounded and evenly spaced collabral ribs become progressively stronger until the completion of the veliger stage when the selenizone is formed, followed by a rapid and progressive weakening of the ribs (fig. 12). One unusual character in this species is the presence of about eight evenly spaced and formed, overlapping lamellae between ribs with dip slopes toward the protoconch (see fig. 11). It is assumed that these represent growth increments. Strong ribbing persists throughout growth.

In *S. (S.) declinans* (fig. 13), the collabral ribs begin as sharp ridges, gradually rounding until about the third whorl when they suddenly become muted and more closely spaced during the remainder of ontogenetic growth. In *Sinezona rimuloides* (Carpenter), 1865, ribbing begins at the end of the protoconch. The collabral ribbing is closely spaced and terminates with



FIG. 10. *Scissurella (Anatoma) crispata*. AMNH 29310; loc. D5601. Oblique side view showing abrupt formation of selenizone. X250.



FIG. 11. *Scissurella* (*Scissurella*) *costata*, AMNH 29311; loc. D5601. Note large rib which terminates embryonic phase of shell growth and imbricating growth increments between ribs. X600.

a large rib; presumably this ribbing is restricted to the torsional stage of development (see fig. 14).

Incisura lyttletonensis (Smith), 1894, has a pustulose protoconch which is followed by lightly ribbed whorls; there are no abrupt early stages and the selenizone does not form until the final whorl.

A review of the other species of *Scissurella* shows growth patterns reflecting the two major types outlined above. One group has a strong ornament pattern which abruptly changes in early ontogeny to subdued, but perhaps more complicated patterns, as in *S. (S.) declinans*. The other group, which also has abrupt early ornament, changes but retains strong ornament throughout growth as in *S. (S.) costata*. It is these patterns together with other anatomical characters and the ultrastructure that have compelled me to remove the scissurellids from the Pleurotomariacea.

The Ultrastructure. The protoconch wall in all specimens of *Scissurella*, *Sinezona*, and *Incisura* is essentially the same, consisting of a single layer

of prisms that are normal to the inner and outer surfaces. The exception is in the reticulate ridges where the prisms do not fan out to maintain normality as is the case in most ridges and ribs of molluscs (see fig. 9). The prisms are elongate with irregularly developed faces and a polygonal cross section, closely resembling the orthorhombic, accicular pyramidal habit of inorganic



FIG. 12. *Scissurella* (*Scissurella*) *costata*, AMNH 29304; loc. D5601. Top view showing progressive weakening of ribs. X45.

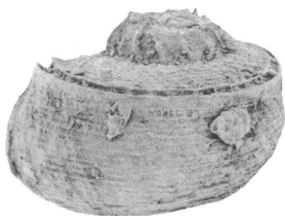


FIG. 13. *Scissurella* (*Scissurella*) *declinans*. AMNH 29303; loc. D5601. Oblique side view showing ontogenetic change in ornament. X25.



FIG. 14. *Sinezona rimuloides*. AMNH 29312. Shallow water along Southern California Coast. Top view showing ontogenetic changes. Compare with figure 25. X75. Collected by Dr. James McLean.

aragonite. The crystal terminations at the outer surface of the protoconch may be either blunt or sharply formed, but they are flattened to form a smooth inner surface (see figs. 7, 9). There is some variation in the thickness of the protoconch wall of *S. (A.) crispata* (fig. 9); compare *Sinezona rimuloides* (fig. 15). The prisms are particularly subject to corrosion which begins on the inner surface so that they may become needle-like (fig. 1).

Near the juncture of the protoconch and the beginning of the first whorl, the prismatic wall separates into two layers of equal thickness in *S. (A.) crispata*; in other species either the outer or inner layer will be thicker (see fig. 9). The point of separation also varies between species; in *S. (S.) declinans* it occurs later in the first whorl

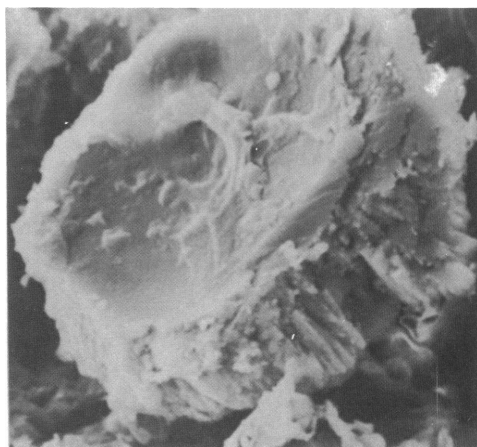


FIG. 15. *Sinezona rimuloides*. Same specimen as figure 14. Broken fragment of protoconch. Inner surface is up. Note elongate bladelike prisms of wall. X1250. Collected by Dr. James McLean.

(this species has a thinner outer layer). Within the first whorl, or by the beginning of the second whorl, depending on the species, an inner crossed-lamellar layer forms as a wedge between the two prismatic layers and rapidly thickens until it becomes the dominant wall element (fig. 16). Usually, the outer prismatic layer remains constant in thickness throughout growth, but the inner layer may thin rapidly so that the inner surface represents terminal ends of the crossed-lamellar layer (fig. 17). In several specimens, a very thin myostracal layer was observed on the inner surface of the penultimate whorl near the junction of the whorls.

The crossed-lamellar wall structure in the scissurellids, and in at least the early ontogeny of some fissurellids, is quite distinct from the classical crossed-lamellar layer of most gastropods and bivalves. The structure is so different that it quite possibly is formed by a different physiological process; in consequence, I shall refer to the scissurellid layer as "type-2" crossed-lamellar structure. I am reluctant to coin a new name until more is known of its formation and characteristics.

The typical molluscan crossed-lamellar wall consists of first order lamellae which are blade-like and typically normal to the shell surface.

They are composed of second order lamellae which dip at a sharp angle from the top surface of the first order lamellae and the degree of dip usually varies from group to group. Adjacent first order elements have their second order lamellae dipping in opposite directions, thus producing angular differences greater or less than 90 degrees; again the angular differences depend on the particular group; see MacClintock (1967) for illustrations and a detailed description. The third order lamellae make up the second order lamellae and are the smallest unit of this wall type. Actually these elements are not lamellae (*Lamella*—Latin for plate or blade) but rather are rodlike or beadlike and arranged parallel to the axis of the second order lamella (see fig. 18).

In addition to variations in angular differences between opposing second order lamellae among groups of molluscs, the base or top of first order lamellae may abruptly change direction in relation to an apparent adjacent crossed-lamellar layer. As MacClintock (1967, pp. 41, 45) has shown, the interface zone is gradational and involves the twisting of the second order lamellae (see fig. 19). He is of the opinion that the two

apparently separate layers are, in fact, a single layer and calls the tandem unit "pseudolayers." The first order elements may be inclined at an angle to the outer surface to the degree that they may parallel it. Usually this condition occurs at the periphery of the shell, at major ornamental features or at whorl contacts. There are several other variations (see Uozumi, Iwata, and Togo, 1972) involving the first order lamellae but the relationship of second and third order lamellae remains fairly constant in relation to each other.

Type-2 crossed lamellar structure is found in the scissurellids, fissurellids, in the mesogastropod group—the atlantids—and in a few other unrelated taxa. This structure is usually associated with thin-walled shells. It has the superficial appearance of the typical molluscan form discussed above, but it is more variable (even within a single shell) and is morphologically distinctive in several respects. The first order lamellae are usually composed of second order rods which dip in opposite directions in alternate first order lamellae (see fig. 17). The second order rods are variable in shape and in the number of rows that make up a first order unit.

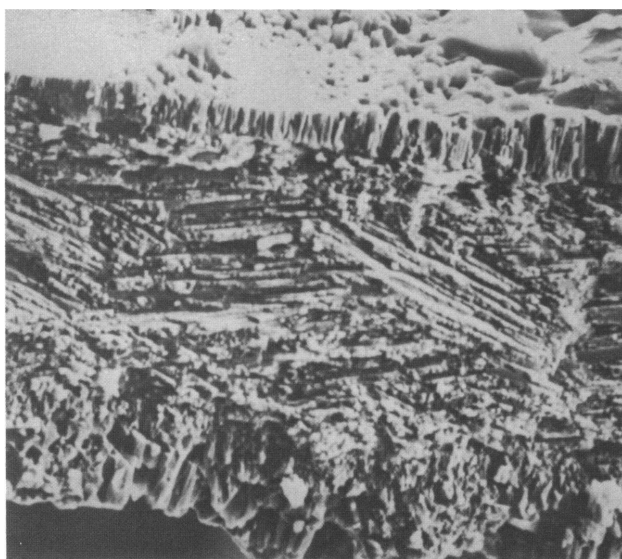


FIG. 16. *Scissurella (Anatoma) crispata*. AMNH 29303; loc. D5601. Cross section near beginning of second whorl showing moderately thick prismatic layers separated by the type-2 crossed-lamellar layer. $\times 2450$.

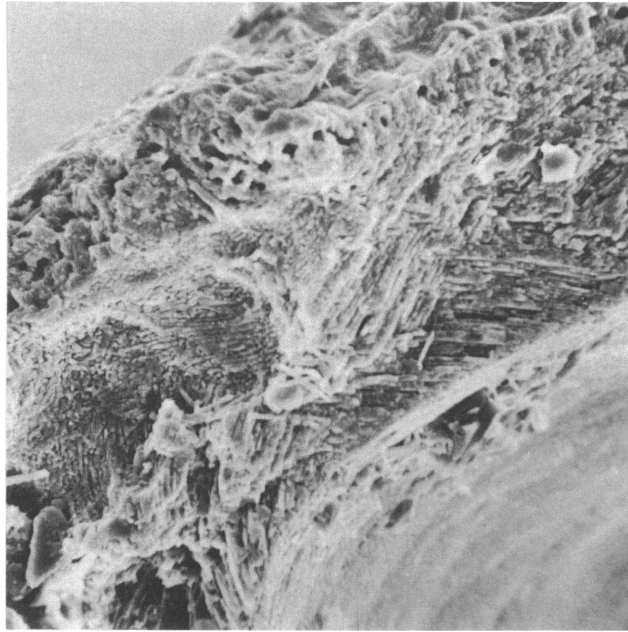


FIG. 17. *Scissurella (Anatoma) crispata*. AMNH 29308. East of Mariana Islands, 760 m., latitude $17^{\circ}56'S$, longitude $154^{\circ}8'E$. Vema Expedition, 1962. Cross section from an adult whorl showing curved second order rods of the type-2 crossed-lamellar layer. Note absence of inner prismatic layer. $\times 1810$.

There may be but a single row (see fig. 20) or a number of rows (the usual condition in the normal molluscan type, fig. 21). Further, the second order elements may curve (fig. 17). The most striking feature of the type-2 wall is that the crossed-lamellar aspect may suddenly disappear so that alternating angular relationships of second order orientation may be converted into a series of parallel rods forming sheets (see figs. 22, 37). This condition is also found in the fissurellids and is partly related to changes in external morphology. However, in the scissurellid species studied, when this change was observed it was randomly distributed and did not appear to be related to any particular character of the shell.

Perhaps the most fundamental difference between the two crossed-lamellar wall types is the nature of the third order elements that make up the second order rods of the type-2 layer. In contrast to the normal molluscan third order lamellae, the elements are composed of rectangular or rhomboid tablets; (fig. 23). Usually, these

tablets are arranged so that their boundaries are essentially perpendicular to the axis of the second order rods, but they may be at an angle. In some areas of the shell, the tablets in opposing sets of second order rods may be arranged in parallel and are apparently normal to the inner surface of the shell (see fig. 23).

Interestingly, the rectangular outline of the tablets (fig. 24) and the general appearance of the second order rods are virtually identical with those seen in the helical structure in the pteropod *Cuvierina columella* (Rang) described and illustrated by Bé, MacClintock, and Currie (1972, pl. 6).

The rectangular second order rods may be modified in outline so that they are either ovoid or bladelike (see fig. 37). Usually these changes occur in regions where the crossed-lamellar aspect is lost.

THE FISSURELLIDAE

The Fissurellidae consist of three subfamilies,

the Emarginulinae, the Diodorinae, and the Fissurellinae. The last two subfamilies are more closely related in that they share a number of features, such as an anal perforation at or very near the apex. They are dominantly conical, ovoid, and bilaterally symmetrical and tend to have radial ornament.

Early appearing genera tend to have a higher conical shape and this can be observed also in Recent Emarginulinae, suggesting that the lower conical shape with an anal perforation at the apex is a derived feature.

The Emarginulinae are much more varied in shell features. In only several genera is the anal perforation near the apex (as in *Puncturellopsis* Haber, 1932). In a few genera there is no perforation present (as in *Scutus* Monfort, 1810), whereas in others there may be an elongate trema in the line of symmetry of the adult shell (as in *Rimula* DeFrance, 1827) or there may be a slit followed by a selenizone as in *Emarginula* (*Entomella*) Cossmann, 1888. Some genera are conical

and bilaterally symmetrical and others are coiled with rapidly expanded spiral growth.

The most comprehensive and classic study of the ontogeny of the fissurellids is that of Boutan, 1885. He was the first to observe the considerable amount of variation in the embryonic stages between the fissurellid groups. It was from his illustration of *Fissurella reticulata* Forbes and Hanley, 1849, that I perceived an additional link between the scissurellids and the fissurellids (fig. 25), and his illustration provides an outstanding example of convergence (compare figs. 14 and 25).

The coiled embryonic shell varies between species in the subfamily Fissurellinae, a relatively uncommon phenomenon in the gastropods. It may have a slit or notch as in *F. reticulata* or show no evidence of any exhalant re-entrant as in *F. nubecula* Linné, 1758 (fig. 26). In the latter species growth lines in the earliest stage of the nepionic shell also show no reflection and the anal perforation apparently forms abruptly. As

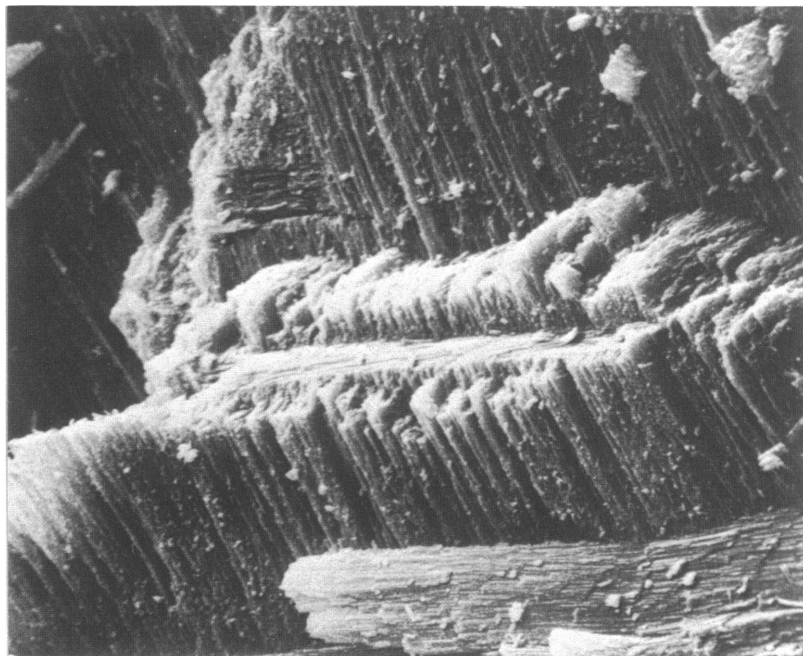


FIG. 18. *Strombus pugilis* Linné, 1758. AMNH 29314. Key Biscayne, Florida. Fragment of base of outer lip showing several second order lamellae composed of third order lamellae parallel to axes of second order. X1100.



FIG. 19. *Cerithium* sp. AMNH 29313. Locality unknown. Polished and etched cross section taken from upper portion of final whorl near sutural contact. Note 90-degree twist of first order lamellae of the outer crossed-lamellar layer, forming two "pseudo-layers." Upper part of layer (outer surface is to right) is cross section of first order lamellae and next "layer" is tangential section. X475.

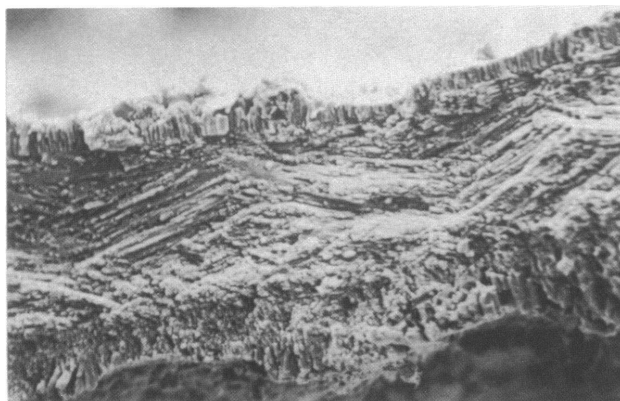


FIG. 20. *Scissurella (Anatoma) crispata*. AMNH 29305; loc. D5601. Cross section of first whorl taken at periphery; inner surface at top. Section is broken back at an angle. Note that first order lamellae are composed of single rows of second order rods. X1400.

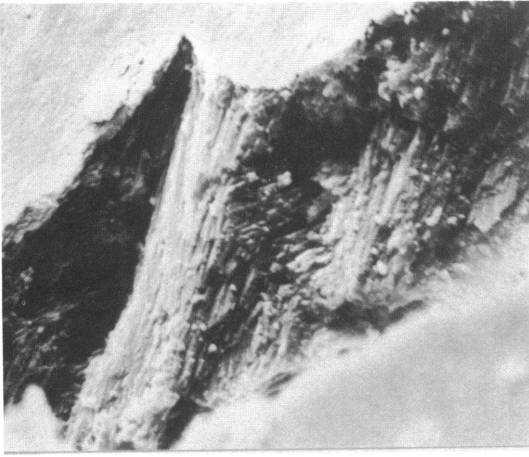


FIG. 21. *Scissurella (Anatoma) crispata*. AMNH 29305; loc. D5601. Fracture on inner surface of final whorl showing first order lamellae composed of a number of second order rods. $\times 1500$.

seen in figures 25 and 26, the ornament also is variable. The other two subfamilies show more conservatism in early ornament pattern. The possibility exists that species that have functional shell slits or notches (reflecting the mantle perforation complex) represent free swimming veliger

larvae. Those without slits may have remained in the egg case until the completion of the veliger stage. I have not been able to substantiate this from a literature search.

Embryonic Shell Comparisons

Protoconch External Morphology. The protoconch in the three subfamilies is irregularly reticulate. In *Fissurella*, the ridges that are responsible for the reticulation are thick, flat-topped, and occupy most of the surface. The surface between the ridges is pustulose, reflecting the underlying prismatic layer. This condition persists through the veliger stage which terminates in a slightly raised ridge. This is similar to that observed in some species of the scissurellids. The conical nepionic shell in *F. nubecula* has irregular bifurcating and beaded ribs that radiate outward from the margin of the veliger terminus (see fig. 26). When the individual has grown to about 0.3 mm., an anal perforation is formed in the line of bilateral symmetry and when it is about 0.5 mm. in size, the adult radial ribbing begins to form. Resorption of the embryonic and nepionic shell does not take place until the perforation has migrated to the adult position at or near the apex of the shell. The mechanism by which the metamorphosis occurs is unknown.

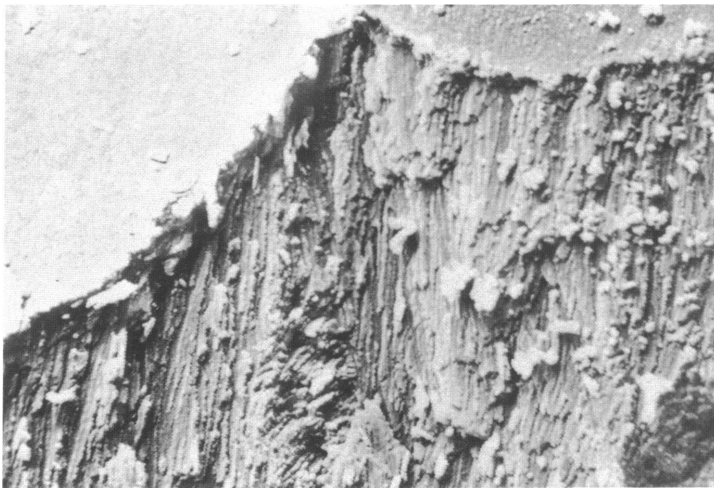


FIG. 22. *Scissurella (Anatoma) crispata*. AMNH 29305; loc. D5601. Oblique fracture of inner surface of final whorl showing loss of crossed-lamellae and formation of sheets of second order rods. Micrograph taken near area shown in figure 21. $\times 2200$.

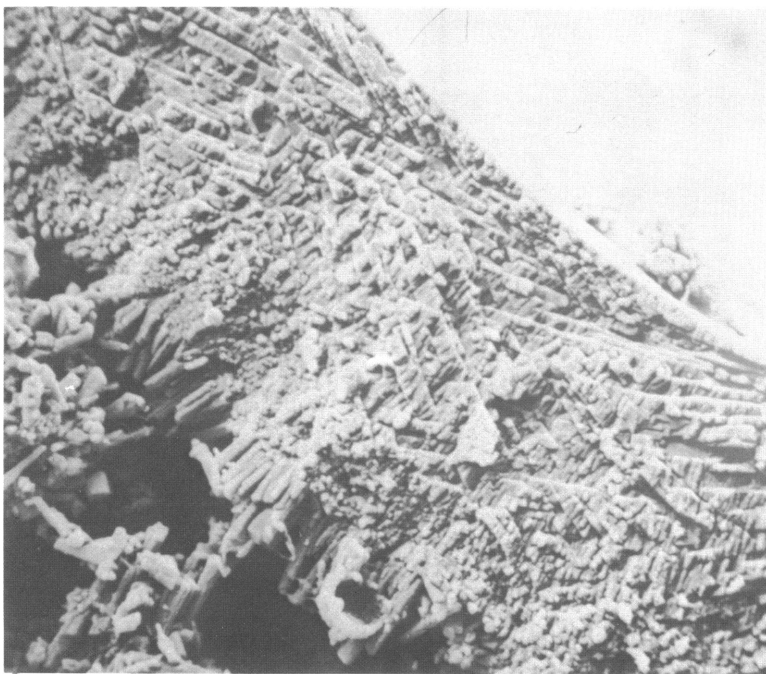


FIG. 23. *Scissurella (Anatoma) crispata*. AMNH 29305; loc. D5601. Cross section of final whorl showing third order tablets; their boundaries are parallel to inner surface at right and normal to second order rod axes to left. X2850.

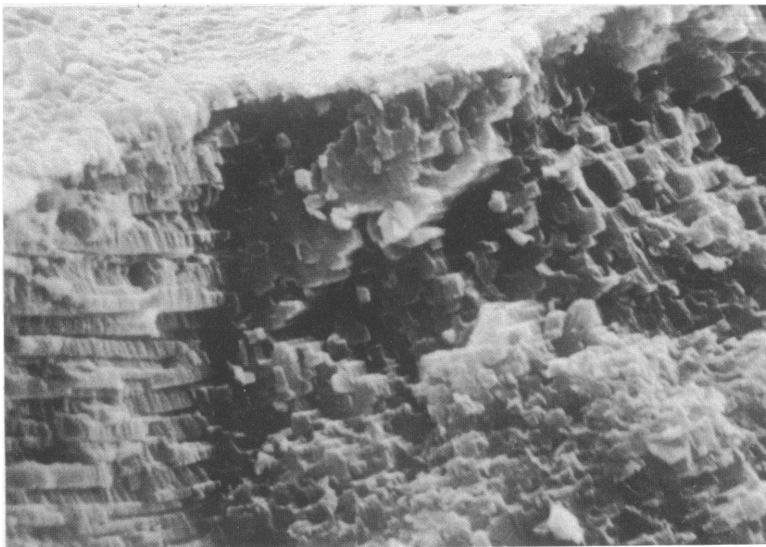


FIG. 24. *Scissurella (Anatoma) crispata*. AMNH 29305; loc. D5601. Fragment of adult whorl showing rectangular outline of third order tablets. X5000.

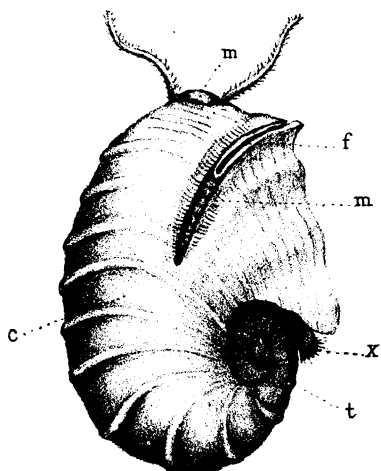


FIG. 25. *Fissurella reticulata* Forbes and Hanley, 1849. Copy of plate 42, figure 5 of Boutan, 1885. Compare with figure 14. No magnification given by Boutan.

In spite of strikingly different adult shells, the Diodorinae and Emarginulinae have several embryonic features in common, in particular, the smooth post-protoconch coil. In *Diodora*, the protoconch and first whorl have a very fine, but irregular reticulate pattern with V-shaped ridges. The shell is smooth between the ridges, which occupy only a small portion of the entire surface, in contrast to that observed in *Fissurella*. *Emarginula* has an embryonic stage essentially identical with that of *Diodora*. *Diodora* (fig. 27) has a narrower whorl diameter, which in *Emarginula* expands rapidly (fig. 28). The final embryonic stage in both genera expands rapidly and culminates in either an oval anal perforation (*Diodora*) or a slit, which generates a selenizone (*Emarginula*). Additionally, *Emarginula* at this stage has fine, regular radial threads, whereas *Diodora* is smooth (due to what appears to be a secondary outer deposit).

Protoconch Shell Structure. The inner and outer walls or the single wall of the protoconch in the three subfamilies are composed of simple

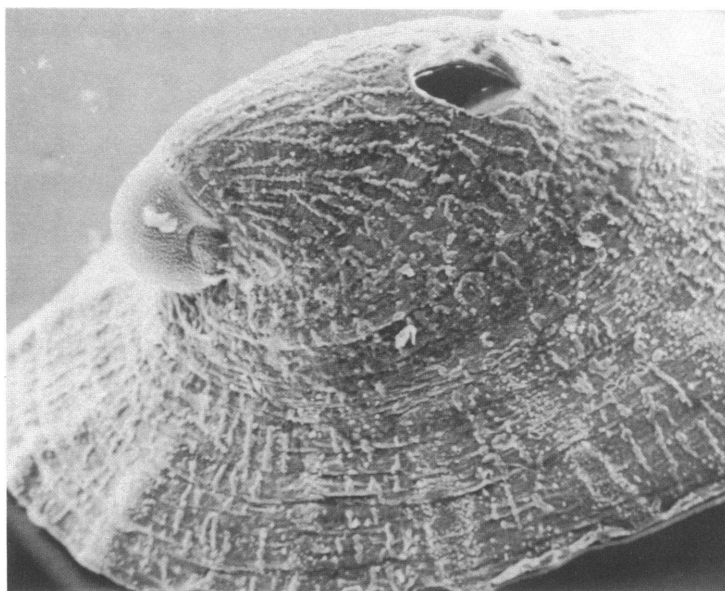


FIG. 26. *Fissurella nubecula* Linné, 1758. AMNH 29314. Collyer Point, Ascension Island. Oblique view of coiled embryonic stage and the larval limpet stage. Adult radial ribbing just beginning to form near aperture. Note lack of slit or selenizone in the coiled stage compared to *F. reticulata*. X125. Collected by R. B. Manning.



FIG. 27. *Diodora minuta* Lamarck, 1801. AMNH 29315. Port Royal, Jamaica. Note reticulate protoconch and smooth coiled embryonic shell. X120.

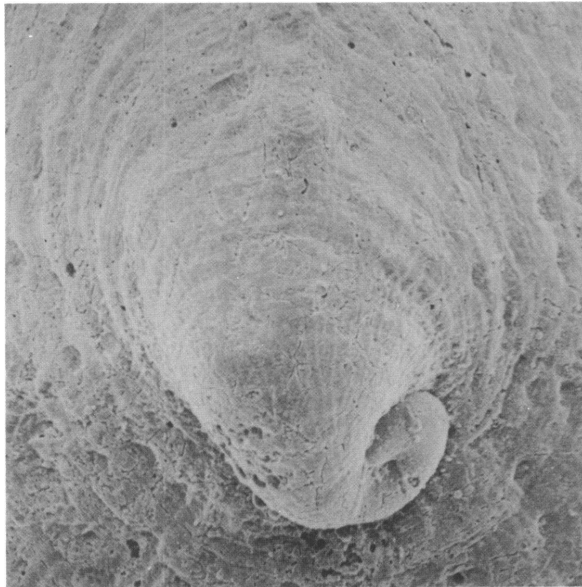


FIG. 28. *Emarginula pumila* Adams, 1851. AMNH 29316. Glover's Reef, 14 m., British Honduras (Belize). Note rapid expansion and ornament of embryonic shell. X115. Collected by D. Marszalek.



FIG. 29. *Diodora minuta*. AMNH 29317. Glover's Reef, 14 m., Belize. Cross section of protoconch, inner surface at top. X5250. Collected by D. Marszałek.

aragonite prisms. In *Diodora* the prisms are elongate and bladelike with the crystal terminals forming the inner and outer surface of the single layer which forms the protoconch (fig. 29). At the beginning of the first whorl, a second layer may form either as a separately deposited unit or by the bifurcation of the primary layer. By comparison, the wall in *Fissurella* consists of an inner and outer simple prismatic layer each about $4\ \mu$ thick. The prisms are polygonal and much shorter than those in *Diodora*, giving a robust appearance (fig. 30). These two layers are separated by the principal layer, which is about $25\ \mu$ thick. This layer is composed of elongated rods parallel to the surfaces of the protoconch.

The protoconch of *Emarginula* has a somewhat more complicated protoconch. Recrystallization of the material available prevents an accurate description (see fig. 31). There appears to be a thin prismatic outer layer about $3\ \mu$ thick underlain by one that seems to have elongate elements paralleling the outer surface. This layer is approximately $4\ \mu$ thick, and it is probable that the layer is composed of the same type of rods noted in the other groups. The next layer, $8\ \mu$ thick, is composed of simple bladelike prisms, followed by a type-2 crossed-lamellar layer about $40\ \mu$ thick. The innermost layer is prismatic but recrystallization prevents a description, and thickness measurements would be meaningless. The principal crossed-lamellar layer is the same as in the other groups.

In both the emarginulines and diodorines there is a progressive filling of the embryonic stage with growth until it is completely filled. Only in a few fissurellids was any "secondary" deposition noted in this stage. It is most puzzling that the diodorines completely fill in the early coiled stages, as they are resorbed in the early adult.

The Post-protoconch Coiled Shell and Its Structure. As mentioned above there are differences in the protoconch between the three sub-families. The coiled embryos also display dissimilarities. In *Fissurella*, the inner and outer prismatic layers retain their thickness but the crossed-lamellar layer rapidly thickens to become the dominant one. At the beginning of the first whorl the parallel rectangular rods become re-oriented to form this dominant layer (which seems to be identical in all details with that found in the scissurellids). The first order lamellae consist of a variable number (sometimes more than 20) of second order rods. The third order tablet boundaries are at an angle to second order axes as in *Diodora* (see fig. 32).

In the uncoiled, bilaterally symmetrical (limpet) portion of the larval shell in the fissurellines, the inner and outer prismatic layers gradually thin so that by the early adult stage only the crossed-lamellar layer forms the wall. I emphasize again that when the anal perforation

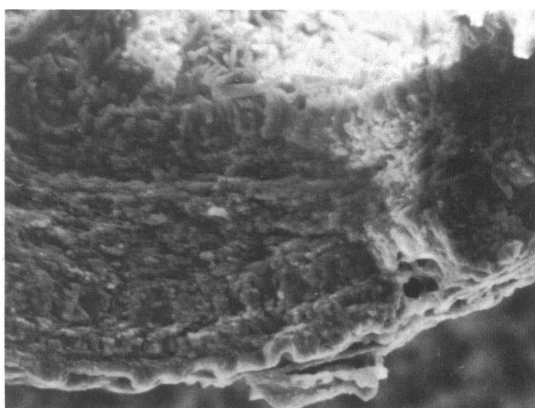


FIG. 30. *Fissurella nubecula*. AMNH 29320. Collyer Point, Ascension Island. Cross section of protoconch showing robust, polygonal prisms of inner layer. Corrosion has altered layer. X2012.

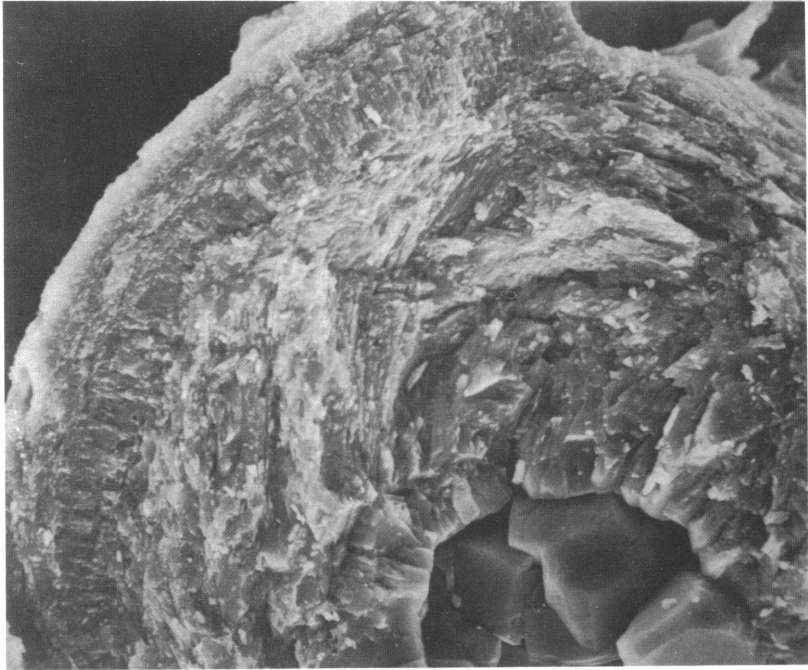


FIG. 31. *Emarginula pumila*. AMNH 29321. Glover's Reef, Belize. Cross section of protoconch showing thick type-2 crossed-lamellar layer. Inner layer is recrystallized and incompletely filled. X1300.

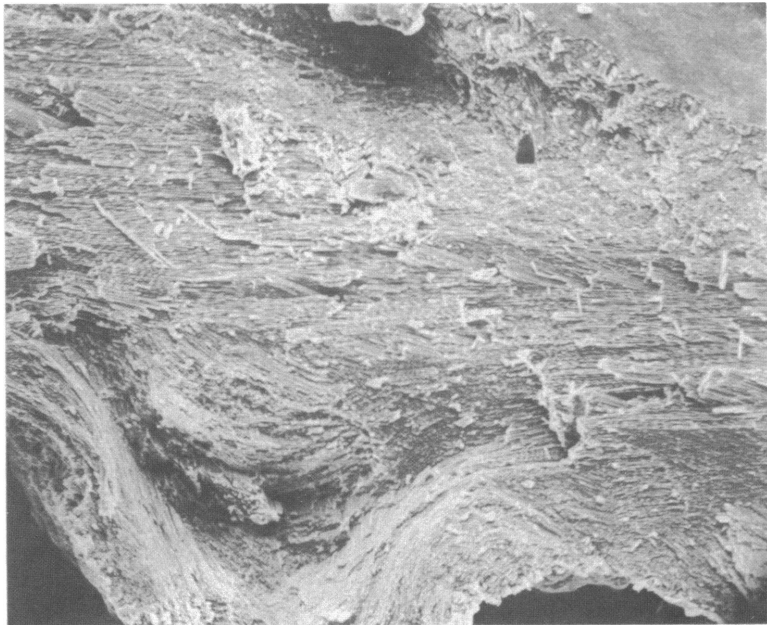


FIG. 32. *Emarginula pumila*. Same specimen as figure 31. Cross section of larval limpet stage showing part of wall and a rib; outer surface is down. Note third order tablet boundaries on second order rods in center of micrograph. Second order rods parallel and rhomboid in outline. X460.

migrates to the axis in early adulthood, the entire larval shell is resorbed. A brief investigation of the post-larval shell of *F. barbadensis* (Gmelin), 1791 (not illustrated) seems to indicate that there is a wedge-shaped inner complex crossed-lamellar layer extending from the apical callus and terminating at the pedal muscle scar. It comprises more than half the wall at the apical portion. The outer wall is a normal molluscan crossed-lamellar type with third order elements parallel to the axes of second order lamellae.

In *Diodora* the first whorl prismatic layers thicken so that they are equal in thickness to the middle type-2 crossed-lamellar layer. As noted above, the entire embryonic shell is completely filled by crystalline material. This is accomplished by lengthening the prisms of the inner layer and by the addition of type-2 crossed-lamellar fill (see fig. 33). The wall of the larval limpet stage is defined by an inner prismatic layer and by an outer, thicker prismatic layer. Again, as in *Fissurella* the principal layer is the

type-2 crossed-lamellar layer. Both prismatic layers are absent in the adult shell. The presence of crossed-lamellar structure in the coiled embryonic wall is in sharp contrast to that seen in *Fissurella* where rectangular rods are parallel to the outer surface.

The adult shell of *Diodora* consists, as in *Fissurella barbadensis*, of the typical molluscan crossed-lamellar structure that forms the outer layer (see fig. 34), and a wedge-shaped complex crossed-lamellar inner layer (see fig. 35). In both *F. barbadensis* and *Diodora minuta* Lamarck, 1801, the outer layer thickens at the same rate as the inner layer thins, to maintain constant wall thickness.

In *Emarginula pumila* (Adams), 1851, the prismatic layers in the coiled shell are absent and the entire coiled shell is composed of elongated rods as in the protoconch. These rods are longer and more uniform owing to the increased space available. As in *Diodora* the entire coiled shell is completely filled, but in this case by elongate

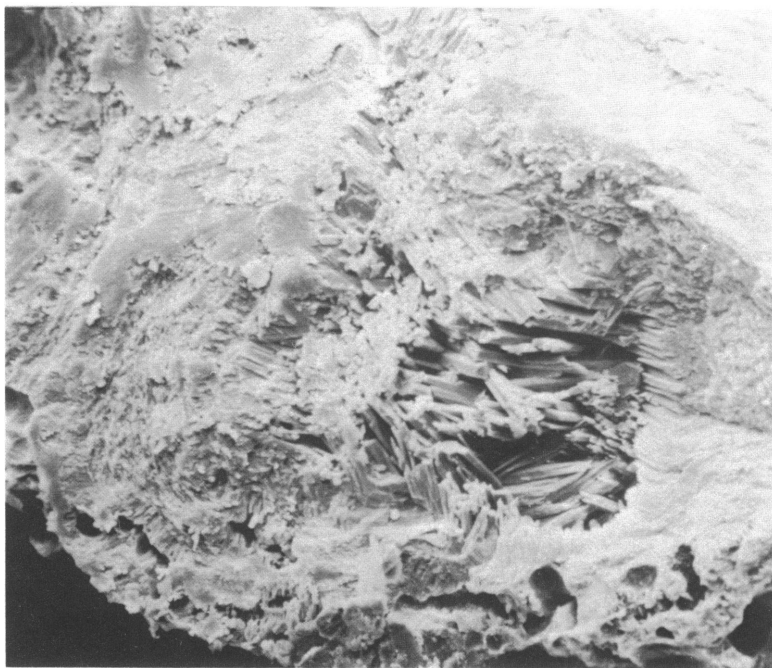


FIG. 33. *Diodora minuta*, AMNH 29384. One mile E of Wax Cut, 3 m., Andros Island, Bahamas. Cross section of protoconch showing elongate prisms of inner layer and type-2 crossed-lamellar "fill." Specimen has been partially recrystallized. X655. Collected by Donald Moore.

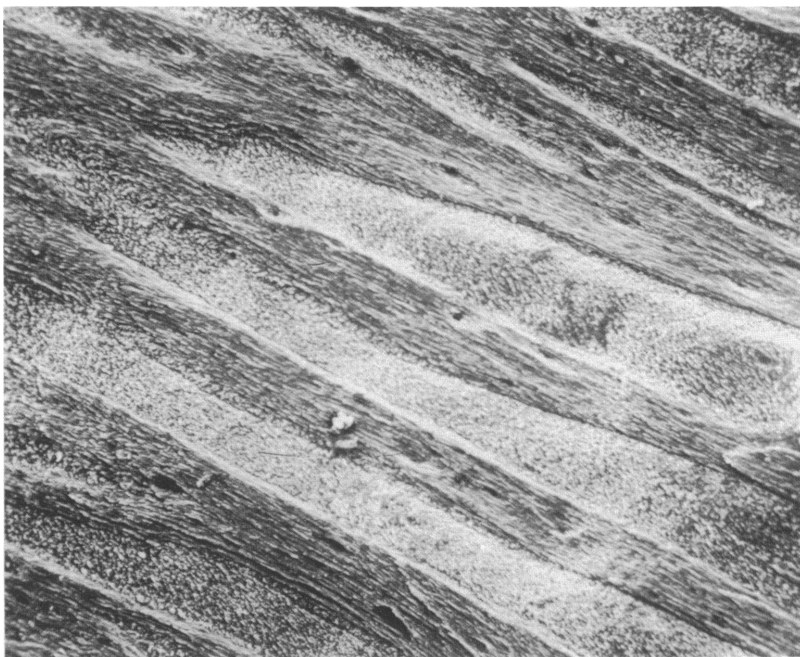


FIG. 34. *Diodora listeri* d'Orbigny, 1823. AMNH 29385. Bear Cut, Key Biscayne, Florida. Polished and etched inner shell surface in plane of symmetry near margin of an adult specimen, showing normal molluscan crossed-lamellar structure. X600.

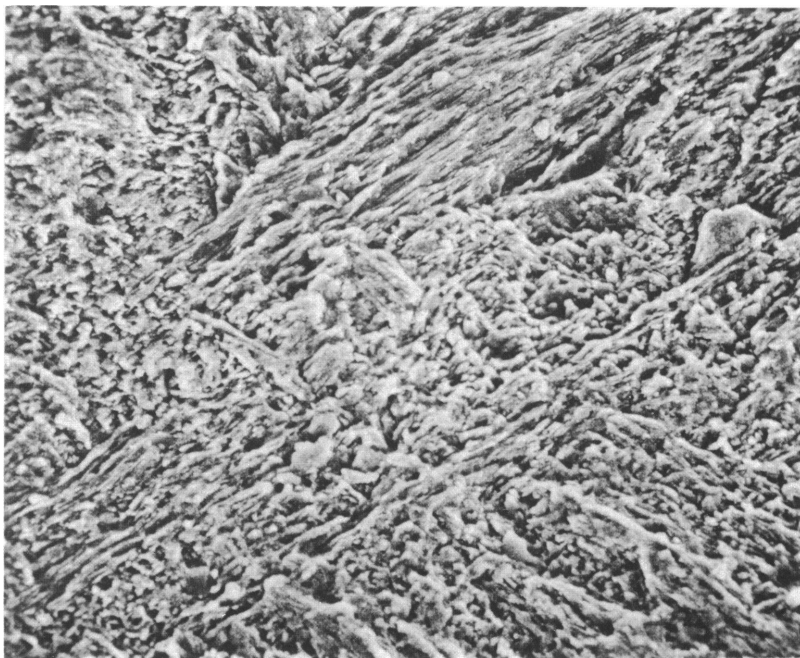


FIG. 35. *Diodora listeri*. Same specimen as figure 34. Cross section of adult specimen in plane of symmetry, polished and etched, showing complex crossed-lamellar structure. X1300.

rods. At the beginning of the larval limpet stage these rods convert to the type-2 crossed-lamellar structure (see fig. 36). As discussed in the section on *Fissurella*, this type of structure is easily converted from being crossed to sheets of rods. The conversion can occur at random or where shell shape changes, such as at rib sites (see fig. 37). In almost every instance where the conversion is made to sheets, the rods appear to alter becoming ovoid in outline; also the third order tablet boundaries become normal to the axes of the rods.

GENERAL REMARKS ON THE FISSURELLIDS

The above discussion is based on the examination of 18 embryonic shells, six of *Diodora*, eight of *Fissurella*, and four of *Emarginula*. Only eight specimens were undamaged by infloral

infestation. Since larval shells are usually resorbed (except in the emarginulines) they are rare in museum collections. This has prevented any attempt to work out details of variant patterns and to make comparisons. Nonetheless, I believe there is an unusual amount of larval shell variation between species, particularly in the fissurellines, and between subfamilies. This is a rare phenomenon in the archeogastropods where larval development within and between groups is usually conservative.

None of the adults within the family were examined systematically and this should be done in order to ascertain if there is comparable variation of shell structure as in the larvae.

Another purpose in making these difficult larval stage comparisons was to illustrate that larval variation was derived during the course of evolution in the fissurellacea and reflects expansion into high energy environments. Further,

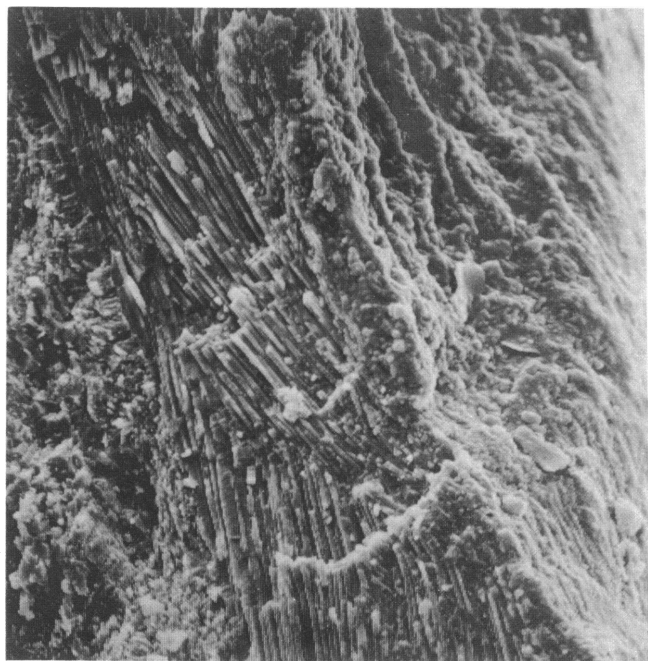


FIG. 36. *Emarginula pumila*. Same specimen as figure 32. Cross section of juncture of protoconch and first whorl. At lower margin of micrograph, second order rods are parallel to outer surface of protoconch. Just above, layer at beginning of first whorl is converted to type-2 crossed-lamellar structure. X2400.

the larval characteristics of *Scissurella* probably represent the primitive condition in the Superfamily Fissurellacea.

The shell shapes in the emarginulines, the earliest appearing subfamily (Triassic), are dominantly coiled with a smaller apertural-shell height ratio in the Mesozoic. By Jurassic time *Puncturellopsis*, a high conical group with an anal perforation at the apex, had appeared. At the same time the earliest diodorine *Pseudofisurella* is found and both are very similar in a number of features, suggesting that they had evolved into the intertidal zone. By Cretaceous time the diodorines were all low conical shells with a perforation at the apex; the Fissurellinae were probably derived from the diodorines in Paleocene time. The primitive emarginulines are confined to offshore rocky bottoms, whereas the other two subfamilies tend to be found in the rocky intertidal to sublittoral zones.

Because the Fissurellidae have few shared

derived features with any pleurotomariacean group, no likely ancestors are now known.

SUMMARY AND CONCLUSIONS

This study has demonstrated to my satisfaction that the family Scissurellidae should be removed from the Pleurotomaricea and placed in the Fissurellacea as a sister group of the Fissurellinae. Based solely on a brief examination of the distinctive wall ultrastructure of the three subfamilies of the Fissurellidae (Fissurellinae, Diodorinae, and the Emarginulinae), it seems desirable to raise the subfamilies to family rank. This would be logical if the scissurellids are included in a superfamily that contains but a single family.

My primary evidence used in concluding that the scissurellids are fissurellaceans is the ontogenetic development of the embryonic shell and its wall ultrastructure. To my knowledge, the

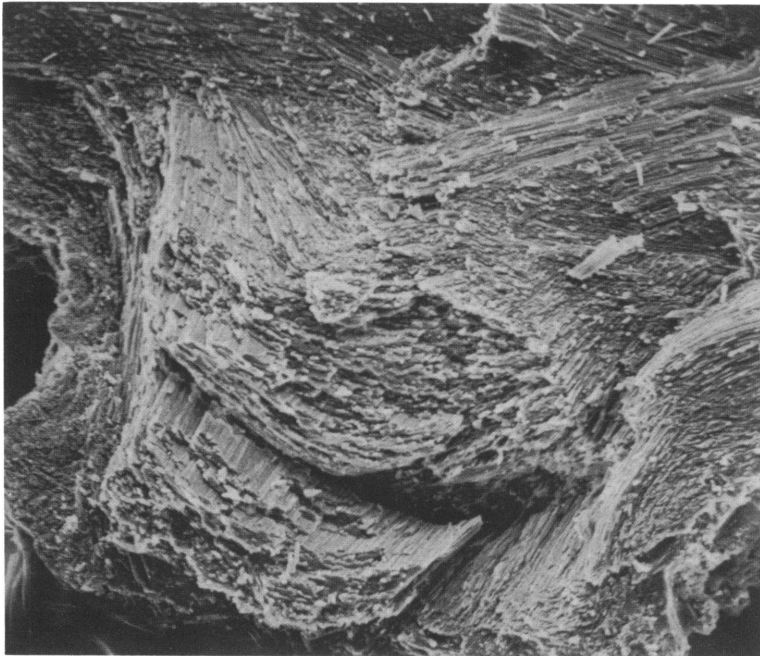


FIG. 37. *Emarginula pumila*. Same specimen as figure 32. Cross section of outer portion of wall and a rib. Outer shell surface is down. Note in upper right, type-2 crossed-lamellar layer and its conversion to sheets formed of ovoid second order rods at base of rib. X940.

Pleurotomariacea without exception have a nacreous-composite prismatic wall. The embryonic fissurellaceans have a variable wall composed of a simple prismatic-type-2 crossed-lamellar wall combination, essentially identical to the scissurellids.

However, the decision to transfer the scissurellids was not based on wall structure alone. Most importantly, the internal anatomy of the haliotids, pleurotomariaceans, fissurellids, and trochaceans has been detailed by Fretter (personal commun.). From this analysis it became clear that the scissurellids share primitive characters of the haliotids and pleurotomariaceans. The majority of shared derived characters are found in the scissurellids and fissurellids. This comparison was made using adults of all groups, but Boutan (1885) showed that the late embryonic stage of *Fissurella reticulata* has already developed the critical features needed for this comparison.

The diodorines and emarginulines have more closely shared early ontogenetic features, in particular, a filled embryonic shell, which was not observed in the fissurellines investigated.

In spite of simpler embryonic walls in the scissurellids and fissurellines, there are some differences. The scissurellid protoconch is composed of a single or double layer of simple prisms, with a middle type-2 crossed-lamellar layer appearing at the beginning of the first whorl. In the fissurelline protoconch, two simple prismatic layers are separated by a middle layer of rods that parallel the outer surface. This layer becomes a type-2 crossed-lamellar layer at the beginning of the first whorl. The difference between the two protoconch walls might be attributed to the difference in habitat. The fissurellines generally live in a high energy environment, whereas the scissurellids live in quiet, deep water. This might not have been true, however, in early Cenozoic time, when both groups appeared.

Additionally, the ontogenetic sequence involving external morphologic features is similar or nearly identical to the fissurellines. Both groups appear at the base of the Cenozoic, an additional point in favor of their being sister taxa. The close similarity in external shell morphology, ultra-structure, and internal anatomy of the embryonic fissurellids and the complete ontogeny of the

scissurellids suggests that the latter group may have been derived neotenously from the fissurellines.

Adult fissurellaceans (post-larval limpet stage) have normal molluscan crossed-lamellar layers and in some genera (*Diodora*, for example) have an inner complex crossed-lamellar layer. Hence, the embryonic shells are radically different, sharing simple prismatic-type-2 crossed-lamellar wall with the scissurellids. This difference cannot be over-emphasized in assessing the relationship between the two groups and the likelihood of a neotenous derivation. The rationale behind this statement is the fact that ultra-structure is very conservative within major taxa and, in most cases, does not change types during embryonic-adult transition other than wall thickness progression.

One further statement is required at this point. The type-2 crossed-lamellar structure is found in several unrelated major taxa, in particular, the Atlantacea (Order Mesogastropoda) and Spirallacea (Order Thecosomata). These taxa, as well as those discussed in this report, are all thin-shelled suggesting that type-2 structure may have formed in response to mechanical requirements. Nonetheless, assessment of the entire suite of morphological complexes in the scissurellids and fissurellids does not, in my opinion, diminish the importance of type-2 structure as a part of the genetic regime.

In terms of the general shell morphology of the scissurellids, it would be rational to seek an ancestor in the Pleurotomariacea. However, the only available groups in the late Cretaceous or early Cenozoic are the Haliotidae and the Pleurotomariidae. The haliotids have none of the shared derived characters and possess a complex prismatic-nacreous wall. The Pleurotomariidae are composed of dominantly turbiniform shells with a selenizone at mid-whorl, flush with the whorl. The selenizone margins are weakly formed and frequently invaginated. Most shells are an order of magnitude larger than the trochiform scissurellids, thus external shell shape and size alone precludes their consideration.

Finally, the scissurellids are of interest because of their convergence on the Paleozoic pleurotomarian family Eotomariidae and the

Triassic family Temnotropidae, providing some of the best examples of homeomorphy I have seen in the gastropods.

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