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Notes on Shell Morphology and Classification of the Siliquariidae (Gastropoda) The Protoconch and Slit of *Siliquaria* *squamata* Blainville

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INTRODUCTION

More than 100 individuals of the curious slit worm-snail *Siliquaria squamata* Blainville were found embedded in a single sponge dredged from a depth of 300–400 fathoms in waters southeast of St. David's Light, Bermuda, on July 12, 1964. These specimens, including several that have retained the previously undescribed protoconch of the genus, represent the first reported occurrence of *Siliquaria* in waters near Bermuda. Dall (1889, p. 260) doubted that *S. squamata* lives in sponges, but the Bermuda specimens affirm earlier suspicions of a sponge habitat. A specimen of *S. squamata*, showing characteristic slit length and erratic coiling, is shown in figure 1.

ACKNOWLEDGMENTS

Specimens were kindly made available to me by Dr. F. Mackenzie of the Bermuda Biological Station (*S. squamata*) and Dr. W. K. Emerson of the American Museum of Natural History (six other siliquariid species in the collection of the Department of Living Invertebrates of the Ameri-

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CONVERGENCE IN MESOGASTROPOD UNCOILING

Older typological classifications placed all erratically uncoiled mesogastropods in the family Vermetidae. Subsequent investigations have demonstrated the heterogeneity of this group which, in its broad sense, included representatives of three families. Morton (1951) took the Siliquariidae (*Stephopoma*, *Pyxipoma*, and *Siliquaria*) from the vermetid complex and placed *Vermicularia* in the Turritellidae (Morton, 1953). These changes leave a restricted family Vermetidae with phylogenetic coherence (Keen, 1961).

The broad similarity of shell form among uncoiled mesogastropods is best viewed as an incidence of evolutionary convergence attendant on the assumption of a sessile mode of life. Morton (1955, p. 3) noted that well-developed cilia and mucous tracts of the pallial cavity, which are presumed to be ancestrally functional as cleansing mechanisms, are excellently preadapted for the development of filter feeding which in turn implies sessility. If coiling in the Gastropoda be considered primarily as an adaptation for compactness in long-bodied, mobile, benthic forms, then the advantages thus conferred are lost in derived immobile species (which may gain adaptive benefit from uncoiling). The turritellid *Vermicularia spirata* which, in waters near Bermuda, cements itself almost exclusively to the tree coral *Oculina* (personal observation) is enabled by its erratic coiling habits to grow around obstacles provided by the copious branching of its preferred host. Uncoiling in the rock-clinging, intertidal, true vermetids provides a greater surface area for cementation, a clear advantage in the surf environment. (It may be significant for the general argument that other sessile forms, the Capulidae and the Calyptraeidae, demonstrate another type of deviation from normal gastropod coiling—a rapidly expanding generating curve which precludes the formation of more than a very few whorls and leads to the limpet shape.)

FORMAL ASPECTS OF SILIQUARIID TAXONOMY

Mörch (1860) noted that, although earlier naturalists had figured slit worm-snails, Martin Lister was the first to comment on the fissure which had previously been overlooked or regarded as accidental. Linnaeus (1758, p. 787) placed *Siliquaria* in his overextended genus *Serpula*, finding the slit of sufficient significance for specific distinction as *Serpula anguina*. Blainville (1827) first suggested molluscan affinities. Previous authors,

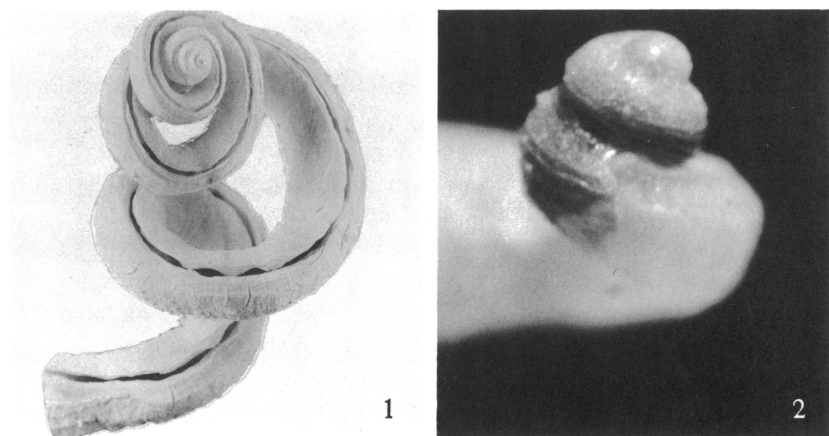


FIG. 1. *Siliquaria squamata* Blainville, dredged from 300–400 fathoms in waters off St. David's Light, Bermuda. Actual length of specimen, 3.9 cm.

FIG. 2. Protoconch of *Siliquaria squamata* Blainville. Note differing ornament types above and below whorl periphery and the sinuous aperture with salient at the whorl periphery and re-entrant above in the area of nepionic slit formation. The salient is overlain with a thin wash of nepionic shell material. Actual height of protoconch, 0.27 mm.

Lamarck in particular (1818, p. 337), had ranked it among the Annelida: "Quoique l'on ne connaisse pas encore l'organisation de l'animal des siliquaires, on ne saurait douter qu'il appartienne à la classe des annelides."

Two synonyms, *Tenagodus* (Guettard, 1770) and *Siliquaria* (Bruguière, 1789), are used with about equal frequency in recent literature as designations for the genus to which the Bermudian specimens belong. Since Guettard, at least in his 1770 work, did not use the Linnaean system, Bruguière's name should be adopted. Guettard's (1770, p. 129) non-binomial designation for the type species *S. anguina* is: "*Tenagode à tuyau relevé de côtes hérissées de mamelons pointus et à spirale irrégulière, et dont les pas sont éloignés.*"

Further confusion attaches to authorship of the family name Siliquariidae. Although both Schaufuss (1869, p. 9, spelled as Siliquariadae) and Morton (1951, p. 39) proposed Siliquariidae as the designation of a new taxon, I have traced authorship to Chenu (1859, p. 321). Paetel's (1873, p. 9) elaboration of Schaufuss' work correctly ascribed authorship to Chenu.

THE PROTOCONCH OF *SILIQUARIA*

Of the three extant siliquariid genera, protoconchs are known and

have been described only for *Stephopoma* and *Pyxipoma*. In these genera, variation is confined to the details of ornament; the basic size and shape are identical. The protoconch is slightly more than 1 mm. in diameter and consists of one and one-half planispiral whorls. The description of *Stephopoma mamillatum* (Morton and Keen, 1960, p. 29) is typical: "The embryonic shell is wide-mouthed and nautiloid, almost planispiral, of $1\frac{1}{2}$ whorls. It is shiny, distinct brown in colour, scarcely translucent. The aperture is almost circular, its peristome distinctly effused, so that the thicker, unsculptured juvenile tube appears to spring from a narrow trumpet mouth. The first apical whorl is lighter brown and smooth, after which the nucleus becomes studded with large wart-like mamillae regularly spaced and arranged in rows corresponding to the growth striae."

Pyxipoma weldii (Morton, 1951) differs only in that the sculpture is composed of finely granulated spiral striae. Measurements of major and minor protoconch diameters of three species of *Stephopoma* are presented in table 1.

TABLE 1
MEASUREMENTS (IN MILLIMETERS) OF MAJOR AND MINOR PROTOCONCH
DIAMETERS IN THREE SPECIES OF *Stephopoma*

Species	Locality	Major Diameter	Minor Diameter
<i>S. mamillatum</i>	Senegal	1.3	0.8
<i>S. pennatum</i>	West Panama	1.2	0.9
<i>S. myrakeenae</i>	East Panama	1.1	0.9

Based on similarities of soft anatomy, radula, and operculum, the coherence of the Siliquariidae as a natural phylogenetic taxon is well established. Since these characteristics offer little aid to the conchologist and none to the paleontologist, Morton (1951) felt the desirability of using a shell feature, the protoconch, as the defining familial character: "The principal diagnostic feature is the embryo shell which is exactly alike in shape in *Stephopoma* and *Pyxipoma*, consisting of $1\frac{1}{2}$ whorls coiled in an almost plane spiral of nautiloid or limacinid shape. The mouth is wide, circular and trumpet-shaped, with the peristome projecting freely around the inception of the adult shell" (Morton, 1951, p. 38).

Heretofore, the protoconch of the type genus *Siliquaria* has not been described. A form named *Helix incisa*, described in the non-binomial work of Chemnitz (1786, pp. 129-130) as "*eine der wunderbarsten Erdschnecken*" turned out to be a young *Siliquaria* (Sowerby, 1822), but the

specific name itself indicates that the juvenile slit whorls, not the protoconch, were involved, and the generic allocation demonstrates the inadequacy of an antiquated typology. Dall (1881–1882, 1889), who worked extensively on the American species of *Siliquaria*, never saw a protoconch: "The most perfect spires I have seen showed no sign of a regularly spiral nucleus" (Dall, 1889, p. 260). I have been able to find only two uninformative references to *Siliquaria* protoconchs. Mörch (1860, p. 401) stated: "The foetal shell is wanting in all the specimens I have seen, except in

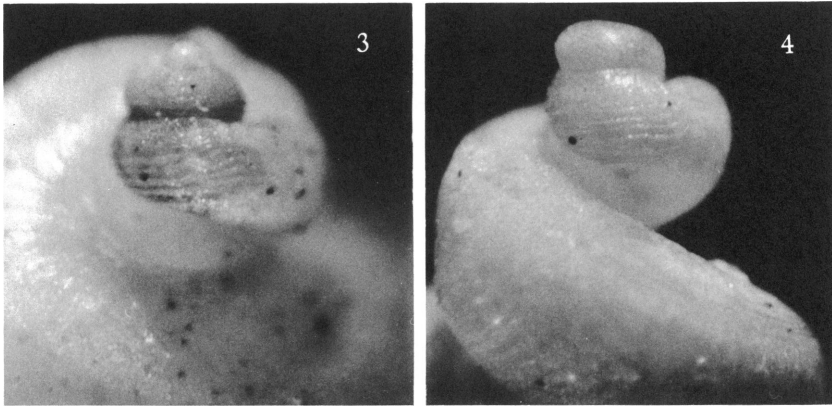


FIG. 3. Protoconch of *Siliquaria squamata* Blainville. Actual height of specimen, 0.27 mm.

FIG. 4. Protoconch of *Siliquaria bernardi* (A.M.N.H. No. 49739), in orientation similar to that of figure 3. Note difference in whorl number and color. Actual height of specimen, 0.27 mm.

Siliquaria lactea, where it had the form of *Ampullaria*, the under part of the outer lip being produced, and of a brown color." Powell (1940, p. 231) described the protoconch as "a small callus blob." A brown amorphous dot appears at the apex of a specimen of *Siliquaria anguina* in one of Clessin's (1904) plates, but, with no accompanying textual commentary, it could just as well represent a printer's flaw.

The Bermudian specimens of *Siliquaria squamata* therefore furnish the first evidence of protoconch morphology in the type genus of the Siliquariidae. The protoconch is so small and fragile that recovery of specimens still embedded in the sponges in which they lived may be essential for preservation. That these specimens seem to be the first ever described from sponge material may explain the previous lack of recovery.

The protoconch of *S. squamata* (figs. 2 and 3) is approximately 0.25

mm. wide and equally high; it is helically coiled and consists of two and a quarter whorls. The apex of the protoconch is low and bulbous, largely immersed in the succeeding whorl (fig. 2). Whorls are broadly rounded, increasing rather slowly in height and diameter. The first two-thirds whorl is whitish brown and smooth as in *Stephopoma* and *Pyxipoma*. The remainder is light golden brown in color and ornamented on the upper whorl faces with five to eight rows of very small and indistinct nodes (similar to but weaker than those of various *Stephopoma* species). The lower whorl faces are ornamented with finely granulated spiral striae as in *Pyxipoma*. Contact between the two types of ornament at the whorl periphery is fairly sharp. Ornamentation does not decrease in strength on the last half whorl as in some *Stephopoma* species. The aperture is strongly sinuous, deeply embayed on the upper whorl surface at the point of contact with the beginning nepionic slit (fig. 2). A fairly wide, parallel-sided salient extends over the nepionic shell below the slit in the area of the whorl periphery (fig. 3); a second re-entrant is present on the under side of the whorl. This sinuosity contrasts markedly with the circular aperture of *Stephopoma* and *Pyxipoma*. Furthermore, although the protoconch often overlaps the following nepionic shell deposition, it is not distinctly effused over it in trumpet-mouth fashion as in *Stephopoma* and *Pyxipoma*. (Moreover, I have noted in two specimens that the salient of the protoconch aperture is overlain by nepionic shell material; fig. 2.) The height and width measurements of 10 specimens are presented in table 2.

TABLE 2

HEIGHT AND WIDTH MEASUREMENTS (IN MILLIMETERS) OF *Siliquaria* PROTOCONCHS

	<i>S. squamata</i> Bermuda	<i>S. bernardi</i> Senegal
Mean height	0.276	0.268
Observed range of height	0.261-0.289	0.257-0.284
Mean width	0.263	0.263
Observed range of width	0.257-0.275	0.257-0.272
Mean ratio: height to width	1.05	1.02
Observed range of ratio: height to width	1.00-1.10	0.96-1.07
Number of specimens	10	7

Seven protoconchs of the Senegalian species *Siliquaria bernardi* were recovered from an excellent group of more than 100 individuals em-

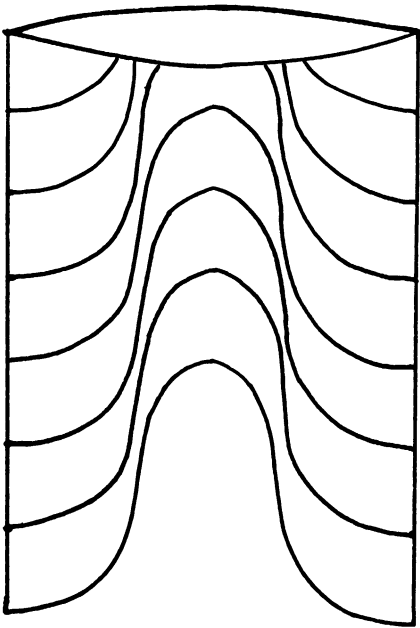


FIG. 5. Hypothetical slit of slit-bearing archaeogastropod, showing deployment of the incremental striae.

bedded in a sponge (A.M.N.H. No. 49739). (No specimen of five other *Siliquaria* species in the American Museum of Natural History collection has retained its protoconch, and no other specimen remains embedded in a sponge.) They correspond almost exactly in size and shape to protoconchs of *S. squamata*, but consist of only one and a half whorls. Paler color and weaker sinuation of the apertural margin constitute the only other consistent differences from protoconchs of *S. squamata*. A specimen corresponding in orientation to that of *S. squamata* in figure 3 is shown in figure 4; the height and width measurements of the seven protoconchs are presented in table 2.

Although ornamental patterns of protoconchs of *Siliquaria* show similarities to those of *Stephopoma* and *Pyxipoma*, the differences of general form and size are startling for a feature proposed as sufficiently invariant to serve as the major diagnostic family character. The protoconch of *Siliquaria* is one-quarter of the width of that of other siliquariids, and completely different in shape (in plane of coiling and features of the apertural margin), thus demonstrating once again that adaptation is a process operating at all stages of ontogeny.

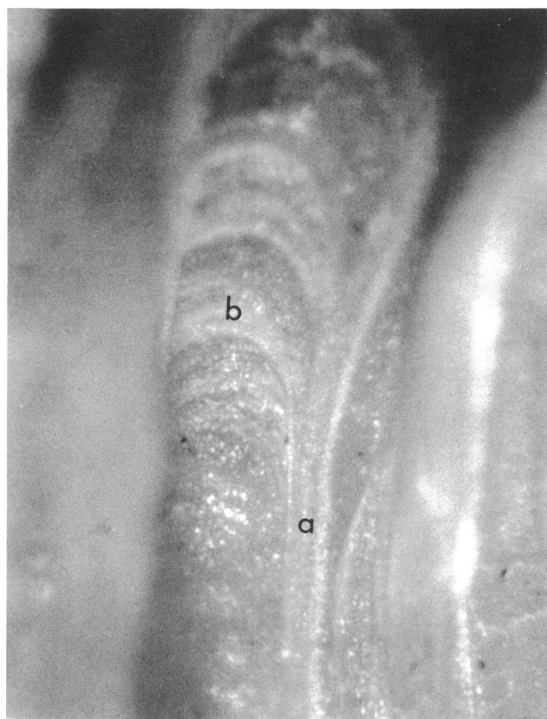


FIG. 6. Slit healing in *Siliquaria squamata* Blainville. Lunulae of depressed slit-healing lamina bordered on each side by (blurred) shell surface at the slit margin. Specimen tilted toward the right so that the vertical wall connecting the slit-healing lamina with the shell surface can be seen directly to the right of the lamina. An increment, running along the vertical wall just to the left of a, passes across the slit at b, adding a lunule to the slit-healing lamina. Actual width of slit, 2.1 mm.

In seeking a possible explanation for these differences, we note that reproduction in the Siliquariidae is ovoviviparous. Though the anatomy of *Siliquaria* is not well understood, I assume that space requirements for embryonic incubation are stringent. The helical shape is a poor space filler and, given limited room, forms of that configuration might have to be quite small. If a larger protoconch proved advantageous, the exigencies of space limitation might require a more economical shape. The planispiral form of larger siliquariid protoconchs may be a result of conformity to space limitations of the parental brood pouch. Although the correlation of observed shape with absolute size seems reasonable, we are left with no clue as to the adaptive advantage of the sizes involved.

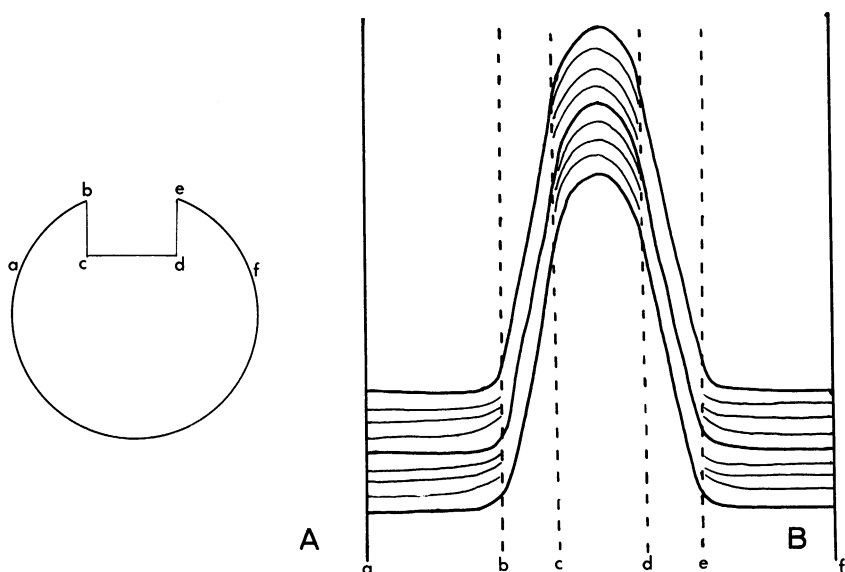


FIG. 7. A. Cross section through *Siliquaria* whorl in the area of slit healing. Line c-d represents the depressed level of the slit-healing lamina. B. Slit healing in *Siliquaria*. Letters a through f correspond to those of A. To reconstruct, fold along dotted lines, up on lines c and d, then down on lines b and e to obtain configuration of A in three dimensions. To avoid confusion, only a few growth increments are shown, illustrating both means by which *Siliquaria* prevents lateral filling of the slit. Discontinuous increments show areas of non-deposition on vertical walls b-c and d-e; continuous increments run longitudinally along the vertical walls. Highly diagrammatic; in actual specimens the apertural stria and its corresponding lunule are separated by many times the distances shown.

Some relation to varying modes of dispersal after hatching and assumption of sessility (a completely uninvestigated aspect of siliquariid ecology) seems probable.

SLIT MORPHOLOGY IN *SILIQUARIA*

Although the slit was the chief conchological character of earlier classifications, it is present in only two of the three siliquariid genera (absent from *Stephopoma*), and is not a defining familial feature. In *Siliquaria*, it is initiated directly after the termination of protoconch deposition and persists throughout teloconch ontogeny. The slit may, however, become closed or annulated by ingrowth and fusion of shell material on either side.

Many archaeogastropods, including pleurotomarians, bellerophontids, murchisonids, and emarginellids, possess a slit presumably functioning, since the anus is at the apical terminus of the slit, as a mechanism to prevent fouling of water at the aperture. Since the siliquariid anus is situated, as in most gastropods, near the shell aperture, similar reasoning cannot be invoked to explain its adaptive significance. Earlier authors, including Lamarck (1818, p. 337), Sowerby (1822), and Chenu (1859, p. 322) suggested that the slit functioned in respiration as a path of water influx or gill protrusion. More recently, Morton (1951, pp. 33-34) maintained that it probably serves for the passage of an exhalant current, either as "an adaptation for the rapid expulsion of waste in a ciliary feeder dependent upon a pallial water current" or "for the rapid expulsion of water when the head and trunk are sharply retracted into the pallial cavity."

In addition to ingrowth from the sides, the siliquariid slit can become closed in quite a different and more regular manner. It is progressively healed, in all species that I have examined, by the growth of a thin lamina precisely analogous in form to that of slit-bearing archaeogastropods. The lamina is smooth save for a series of incremental lunulae, convex toward the apex, representing progressive fusion of the previously slit mantle edges. (The etymology of "selenizone," the term used to describe analogous structures of slit-bearing archaeogastropods, indicates the conspicuous nature of this crescentic ornament.) In slit-bearing archaeogastropods, each lunule corresponds to an incremental growth line at the aperture. At the slit, this apertural growth line curves sharply, whence it can usually be traced passing apically along the slit margin, crossing the slit with addition of a lunule to the slit-healing lamina, and passing down the other border of the slit toward the aperture (fig. 5).

The siliquariid slit is markedly longer than that of any archaeogastropod I have seen, usually open for about two-thirds of the adult length (fig. 1). Given such an open length, if each incremental stria were to run longitudinally along the slit margin externally to its predecessor, the slit would soon be filled by crowding and fusion of shell material forming the striae, which indeed does happen in some forms that annulate or close the slit. In *Siliquaria*, this potential difficulty is solved in two ways (diagrammatically depicted in fig. 7).

1. By non-deposition along mantle edges bordering the slit: Most apertural striae curve sharply at the slit but do not run longitudinally along it for any great distance. They soon abut against the edge of the slit and can be traced no farther. Nonetheless, similar spacing of incremental striae at the aperture and on the slit-healing lamina suggest a one-to-

one correspondence even though non-deposition along mantle edges bordering the slit precludes actual continuity of an apertural stria with its corresponding lunule. (This phenomenon is also noted in archaeogastropods possessing an unusually long slit; see, for example, Horný, 1963, fig. 8, p. 68.)

2. The few striae that can be continuously traced from aperture to lunule do not run along the slit margin externally and in the same surface as preceding striae (fig. 5). Rather, they pass underneath and in the same vertical plane as their predecessors and are thereby constituted in a manner that avoids lateral filling of the slit (fig. 7). The plane of slit healing is therefore depressed below the level of the external surface (fig. 7A). A continuous stria, departing from the external shell surface at the aperture passes progressively deeper as it runs longitudinally along the sides of the slit until it intersects the plane of slit healing (fig. 7), at which point it adds an incremental lunule to the slit-healing lamina. The configuration of a continuous stria represents, of course, the position of the mantle edge at the time of its deposition. In figure 6, a growth increment can be seen passing from the vertical slit-bordering wall across the plane of slit healing.

As a consequence of this type of growth, shell thickness at the slit margin is minimal at the aperture and greatest at the point of slit healing (where maximal vertical piling of the continuous striae occurs). A specimen of *Siliquaria bernardi* (A.M.N.H. No. 49739), 0.02 mm. thick at the aperture, increases 14-fold to 0.28 mm. at the point of slit healing 5 cm. toward the apex (the entire specimen is 12 cm. long). None of the *S. squamata* specimens have preserved the delicate aperture, but the most complete individual has a shell 0.13 mm. thick at the abapical extremity, increasing within 2.5 cm. to 0.5 mm. at the point of slit healing.

SUMMARY

More than 100 specimens of *Siliquaria squamata*, previously unrecorded from waters near Bermuda, were found embedded in a sponge dredged from a depth of 300 to 400 fathoms. The Siliquariidae are one of three mesogastropod families, the uncoiling representatives of which were once classed together as the Vermetidae. Shell uncoiling is now viewed as an evolutionary convergence developed among forms in which the ciliary mode of feeding favored a sessile existence. The generic name *Siliquaria* should replace Guettard's earlier non-binomial *Tenagodus*; Chenu first established the family Siliquariidae in 1859. The protoconch of *Siliquaria*, described for the first time, is 0.25 mm. wide, helically coiled, and has a sinuous aperture, whereas that of the other two siliquariid genera is 1 mm.

wide and planispiral, with a circular aperture. Protoconch form can no longer be used as the chief diagnostic familial characteristic as proposed by Morton (1951). The siliquariid slit is analogous in form, but not in function, to the selenizone of slit-bearing archaeogastropods. Since the siliquariid slit is much longer than that of archaeogastropods, the morphology of slit healing differs. To prevent lateral filling of the slit by growth increments running longitudinally along the slit toward the slit-healing lamina, such increments are either not deposited or else run underneath, rather than in the same surface, as in their predecessors.

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