

STUDIES ON DEEP-SEA PROTOBRANCHIA (BIVALVIA);¹ THE FAMILIES SILICULIDAE AND LAMETILIDAE

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ABSTRACT. Two new families are erected, the Siliculidae and the Lametilidae. Both are characterized by laterally elongate hinge teeth, but each having a suite of distinguishing features. Two new species of *Silicula* are described and one species each of the new genera *Lametila* and *Prelametila*.

It is argued that the elongate, laterally compressed form of *Silicula* and the anteriorly directed and well-developed foot are features of a fast-burrowing animal and are in direct contrast to the globular lametilids with their ventrally directed foot.

While the two species of the family Lametilidae are totally abyssal, the species of *Silicula* range from upper slope depths to the abyss.

Unlike other protobranch families (*e.g.*, Pristiglomidae), in the Siliculidae and Lametilidae sexes are separate. Males are larger than females and *Lametila* is probably protogynous. This may well be of considerable importance in sparse abyssal faunas, that maximum sperm density is achieved through the large size of the adult.

The present paper forms part of the continuing investigation on the deep-water Protobranchia of the Atlantic Ocean. The objectives together with the specific consideration of the Family Pristiglomidae are given in the previous contribution of this series (Sanders and Allen, 1973). In this

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study we turn our attention to those nuculanacid protobranchs that may lack the chevron-shaped taxodont teeth, the supposed hallmark of the protobranchiate bivalve, and have instead elongate teeth running obliquely parallel to the dorsal edge of the shell on either side of the umbo. Despite the fact that four of the nuculanacid species collected in our samples share such a tooth configuration, while a fifth has taxodont teeth as well, they separate sharply into two categories that differ decisively in a considerable number of morphological features. Therefore, we propose that two new families, the Siliculidae and the Lametilidae, be erected to include these species.

The basis for creating two rather than one family for this assemblage is as follows:

- (1) Shell shape
Siliculidae—elongate and laterally compressed
Lametilidae—rounded and somewhat tumid
- (2) Ligament
Siliculidae—internal, elongate, obliquely opisthodontic
Lametilidae—internal, oblong, amphidetic
- (3) Elongate teeth
Siliculidae—at least four elongate teeth on the posterior and three elongate teeth on the anterior hinge plate
Lametilidae—no more than two

- elongate teeth on either the posterior or the anterior hinge plate
- (4) Gut
Siliculidae—never more than one loop to the right and left of the body, gut penetrates deep into the foot
Lametilidae—two or more loops to the left and the right of body, gut does not penetrate deep into foot
- (5) Palp
Siliculidae—large and elongate
Lametilidae—smaller and broader and more anterior in position
- (6) Palp proboscides
Siliculidae—very long and narrow
Lametilidae—large but not elongate
- (7) Foot
Siliculidae—very large and elongate, no posterior projection from the heel of foot
Lametilidae—short and square, a triangular posterior projection from the heel of foot
- (8) Ctenidium
Siliculidae—outer gill plates half the size of the inner; frontal and laterofrontal cilia are exceptionally long and dense
Lametilidae—outer and inner gill plates of the same size; frontal and laterofrontal cilia not exceptionally long or dense
- (9) Inhalent current
Siliculidae—through an inhalent aperture
Lametilidae—through an inhalent siphon
- (10) Tentacle
Siliculidae—fine and attenuated
Lametilidae—stout
- (11) Visceral ganglion
Siliculidae—below the level of the posterior adductor muscle
Lametilidae—level with the posterior adductor muscle
- (12) Kidney
Siliculidae—short
Lametilidae—elongate

- (13) Body axis
Siliculidae—bent through 90°
Lametilidae—vertical

Family SILICULIDAE new family

Nuculanid protobranchs with fragile, smooth, laterally flattened, posteriorly elongate and gaping shell; hinge weak and elongate; teeth elongate; umbo small, hardly raised above the dorsal margin of the shell; lunule and escutcheon absent; ligament internal, elongate, opisthodontic, slanting posteroventrally; inhalent aperture not complete but formed by the dorsal and ventral adhesion of the mantle edges; outer gill plate half the size of the inner, frontal and laterofrontal cilia exceptionally long and dense; mouth set well back from anterior adductor muscle; pedal ganglion exceptionally large.

Genus *Silicula* Jeffreys, 1879

Type species (by monotypy): *Silicula fragilis* Jeffreys

Hinge teeth relatively few in number, 4–8 on the posterior and 3–5 on the anterior hinge plate, elongate and parallel or obliquely parallel to the hinge; posterior dorsal margin of the shell either straight or convex.

The available evidence from hard-part anatomy of shell structure, hinge line, umbo size and ligament suggests that *Silicula* probably is most closely related to the genus *Propeleda* Iredale (see Thiele, 1935) and, perhaps to a lesser degree, to *Poroleda* Tate. Iredale (1924) separated *Propeleda* from *Poroleda* on the basis of the former having fewer elongate, overlapping teeth, parallel or obliquely parallel to dorsal shell margin (as in *Silicula*) rather than numerous short teeth set diagonally across hinge plate and which do not, or just barely, overlap. Both *Propeleda* and *Poroleda* are more extended posteriorly and more rostrate than *Silicula* and have the posterior dorsal margin concave rather than straight or convex. *Silicula mcalesteri* (page 278) begins to approach the condition present in

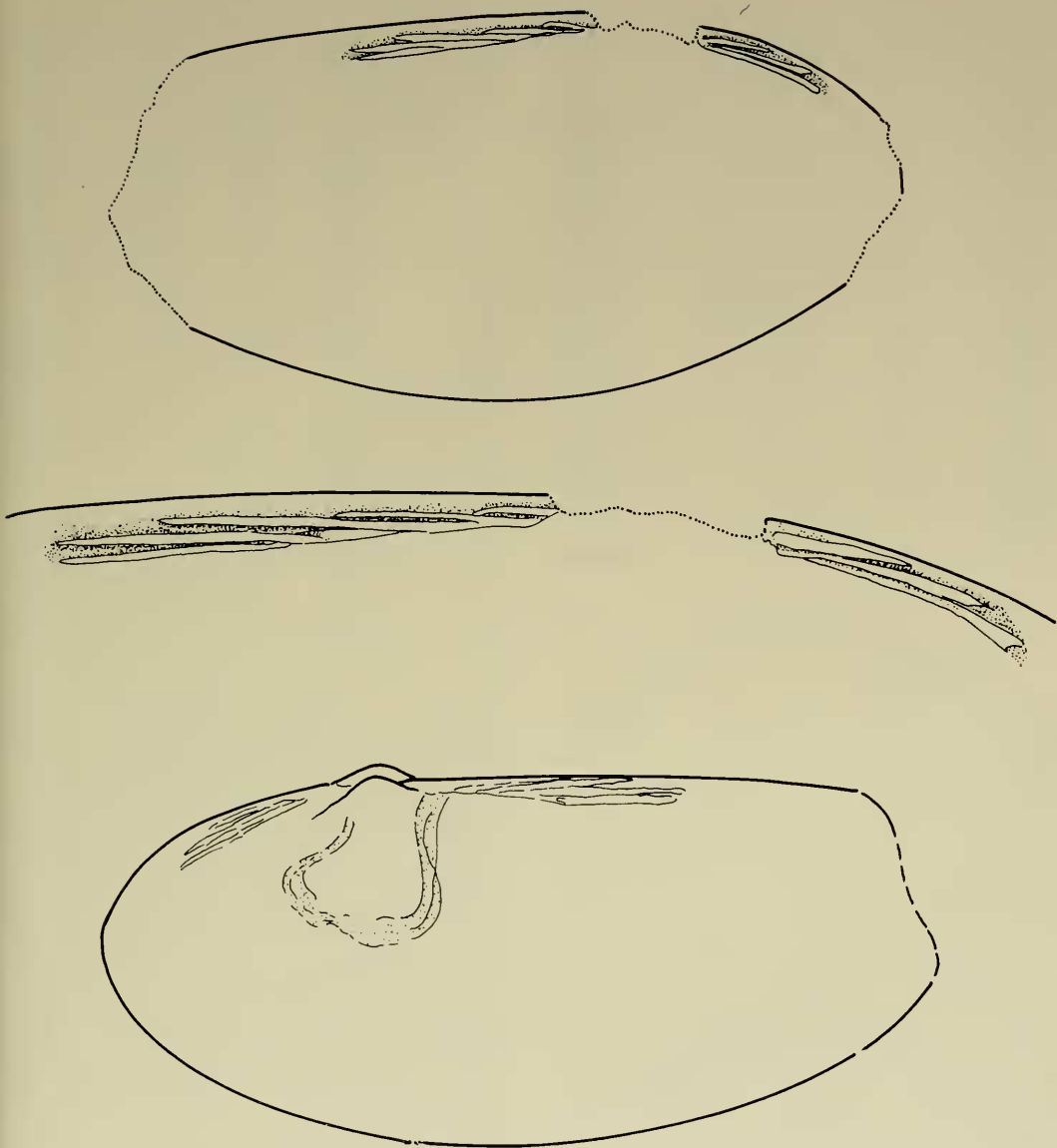


Figure 1. *Silicula fragilis* Jeffreys. Internal view of the left valve, with hinge detail in enlargement and view of right side of intact holotype (U.S. Nat. Mus. No. 197405).

Propeleda for it is both more elongate and more rostrate than the other species of *Silicula*; however, the posterior dorsal margin is convex rather than concave. Until there is information about the soft anatomy of *Propeleda* we cannot determine whether that genus can be legitimately separated

from *Silicula*. We can, therefore, only tentatively place *Propeleda* and *Poroleda*, together with *Silicula*, as distinct genera within the family Siliculidae.

The nomenclature of the genus *Silicula* is not clear. Monterosato (1875) gave a brief description of a new genus which he

called *Phaseolus*. Authors (e.g., Dall, 1908; Dell, 1956) have overlooked this description by Monterosato (1875, Vol. 4) and considered *Phaseolus* a *nomen nudum* (Dall, 1908; Bowden and Heppell, 1966) and dated the genus *Phaseolus* from Seguenza (1877), *P. ovatus* Seguenza being the type (Thiele, 1935). Jeffreys (1879) considered the name *Phaseolus* to be preoccupied in botanical nomenclature and substituted the name *Silicula*, citing *S. fragilis* Jeffreys as the type species. Jeffreys (1879) mentions the existence of *Phaseolus ovatus* in the same paper and said that this fossil possibly belongs to the same genus. Nevertheless, the use of *Phaseolus* in both zoological and botanical nomenclature is no reason for substituting a new name. Later, Verrill and Bush (1897), having examined specimens

of both *Silicula fragilis* and *Phaseolus ovatus*, proposed that because of the considerable differences in shell character both names should be retained. This conclusion was disputed by Dall (1908), who was of the opinion that until all the characters of the two species were known *Silicula* could hardly rank higher than a subgenus, particularly as he thought "it highly likely that species of intermediate character would be found." We have retraced these steps and have examined the holotype of *Silicula fragilis* from the Jeffreys collection in the U.S. National Museum (No. 197405) and also *Phaseolus ovatus* from the type locality in the same collection (No. 197406). We believe that Verrill and Bush (1897) were correct and that the two species are grossly different and belong to different genera. The specimen of *Phaseolus ovatus* corresponds to the descriptions of Monterosato (1875) and Seguenza (1877) and exactly with the figures of the type of this species (e.g., fig. 791, Thiele, 1935). We are supported in our findings by Thiele (1935) himself as he too separates the two species. The present work shows that there are at least two distinct groups having elongate lamellar hinge teeth, one of which is typified by *Silicula fragilis*. We believe that *Phaseolus* may be included in our second group comprising the new genera *Lametila* and *Prelametila*.

It must be pointed out also that the genus *Phaseolus* has been misapplied by authors (Belyaev, 1972; Knudsen, 1970) and it is doubtful that *P. faba* (Knudsen, 1970) belongs to the genus.

Silicula filatovae new species

Figures 3-11

Type locality: ATLANTIS II, Cruise 17, Station 93, in 5007 m. Holotype: MCZ 271977. Depth range = 3826-5042 m. Records: Table I.

Shell laterally compressed, smooth, glossy, iridescent, almost transparent, fragile, with fine concentric lines; elongate oval in outline and without a pronounced posterior extension; dorsal margin long, curving al-

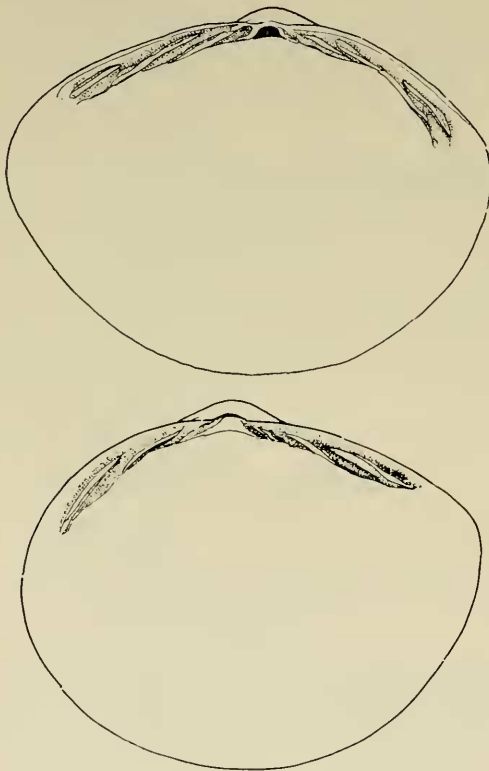


Figure 2. Internal views of left and right valves of *Phaseolus ovatus* Seguenza (U.S. Nat. Mus. No. 197406) from type locality—Fierazzi, Bougnone, Sicily.

TABLE I. RECORDS FOR *Silicula flatovae* NEW SPECIES.

Cruise	No.	Sta.	Depth (m)	Speci- mens	Latitude	Longitude	Gear	Date
NORTH AMERICAN BASIN								
Chain	50	78	3826	10	38°0.8'W	69°18.7'W	ES	30.6.65
Chain	50	85	3834	55	37°59.2'N	69°26.2'W	ES	5.7.65
Chain	50	84	4749	7	36°24.4'N	67°56.0'W	ES	4.7.65
Chain	58	100	4743- 4892	1	33°56.8'N	65°47.0'W	ES	1.5.66
Atlantis II	24	125	4825	1	37°24.0'N- 37°26.0'N	65°54.0'W- 65°50.0'W	ES	23.8.66
Chain	50	80	4970	9	34°49.8'N	66°34.0'W	ES	2.4.65
Chain	50	83	5000	2	34°46.5'N	66°30.0'W	ES	3.4.65
Atlantis II	17	93	5007	1	34°39.0'N	66°26.0'W	ES	14.12.65
Chain	50	81	5042	2	34°41.0'N	66°28.0'W	ES	8.4.65
CAPE VERDE BASIN								
Atlantis II	31	149	3861	1	10°30.0'N	18°18.0'W	ES	7.2.67
ANGOLA BASIN								
Atlantis II	42	197	4565- 4595	25	10°29.0'S	9°04.0'E	ES	21.5.68
Atlantis II	42	196	4612- 4630	1	10°29.0'S	9°04.0'E	ES	21.5.68
Atlantis II	42	198	4559- 4566	13	10°24.0'S	9°09.0'E	ES	21.5.68

most imperceptibly downwards away from the umbo; posterior margin broad and smoothly rounded; anterior margin narrow and sharply, though evenly, rounded, anterodorsal margin slightly shorter than anteroventral margin, ventral margin long but gradually and smoothly curved; umbos very small, hardly interrupting the contour of the dorsal shell margin, posteriorly directed and slightly anterior in position, the antero-posterior umbonal ratio being about 45/55; shell gaping anteriorly and, more so, posteriorly with the valves separated along much of the dorsal margin (Fig. 3).

Hinge plate long, narrow, slanting away from dorsal edge of shell distally, with an oblong opisthodontic internal ligament which is ventroposteriorly directed. Four elongate, narrow, slightly convex teeth insert one above the other behind umbo, diverge distally, and occupy much of the ventral side of the posterior hinge plate; dorsal tooth shortest and narrowest, terminating almost at the level of the posterior adductor muscle, each of the more ventral teeth progressively more elongate, with the

second reaching the distal edge of the posterior adductor muscle, the third and fourth terminating beyond the adductor muscle, close to dorsal edge of the posterior shell margin; ventral tooth forming the ventral edge of the hinge plate, very thin proximally where it is almost hidden by the overlying tooth but thicker distally in the region of posterior adductor muscle. Anterior hinge plate with three elongate, narrow teeth curved slightly to the ventral side; these teeth are almost as long as the posterior series, lying one above the other and diverging slightly; all teeth reach the level of the anterior adductor muscle, dorsal tooth shortest, the two ventral teeth thicker than the dorsal, each longer than the one dorsal to it, terminating beyond the adductor muscle where they approach the dorsal edge of the anterior shell margin; ventral tooth forming the ventral edge of the hinge plate and partially hidden proximally by the overlying tooth. Shells range in size from 1.65 mm to 5.20 mm, the height-to-length ratio changing slightly with size and ranging from .559 in the smallest

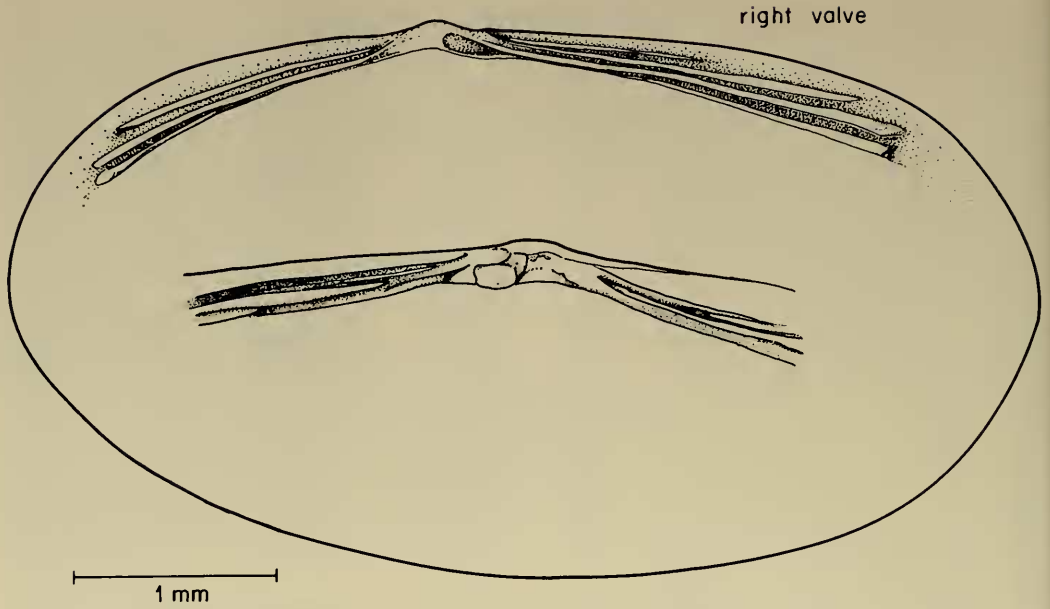


Figure 3. *Silicula filatovae* Allen and Sanders. Internal view of right valve, with hinge detail of left valve.

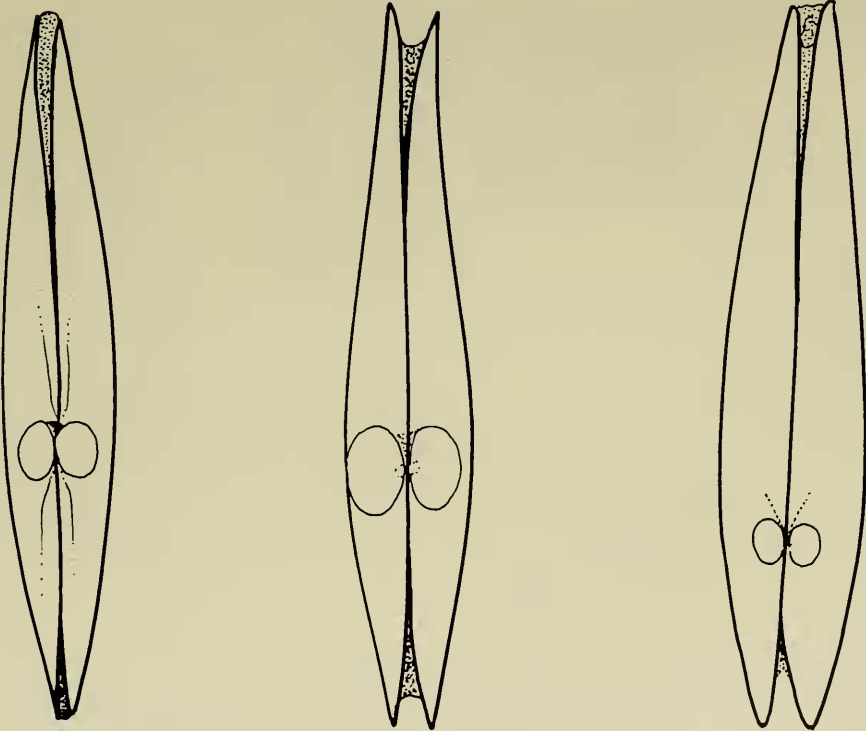


Figure 4. Lateral views of a series of specimens of *Silicula filatovae* to show changes of shape with increasing size. Features of the soft-part anatomy, seen through the shell, are indicated.

to .491 in the larger specimens (Figs. 4, 11). The width-to-length ratio is only about .17, reflecting their very flattened form (Figs. 5, 11). The prodissoconch varies from about $290\ \mu$ – $310\ \mu$, suggesting that development is direct (Ockelmann, 1965).

Posterior exhalant siphon, formed by the fusion of the inner muscular folds of the mantle, can be completely retracted within the mantle/shell; siphonal embayment shallow and almost nonexistent, the pallial line being set back from the posterior shell edge so that the inner muscular fold of the mantle is distant from the middle sensory fold, the retracted siphon lying within this space posterior to the posterior adductor muscle within the space so formed. Pos-

terior adductor muscle set forward within the mantle cavity below the posterior limit of the hinge teeth; siphonal retractors poorly developed, extending anteriorly and ventrally below the posterior adductor; posterior inhalant aperture formed by the apposition of the somewhat extended inner muscular folds of the mantle immediately ventral to the exhalant siphon and at a point close to the posteroventral mantle/shell edge; inhalant region broad, occupying the whole of the posterior margin below the level of the posterior adductor muscle (Fig. 6); sensory lobe minutely papillate in the inhalant region, but elsewhere a simple fold; inhalant aperture may extend beyond the shell edge but clearly not to the same



Silicula filatovae

10 x 25

Silicula fragilis

10 x 25

Silicula mcalesteri

10 x 12

Figure 5. Comparative figures of the dorsal view of specimens of *Silicula filatovae*, *S. fragilis*, and *S. mcalesteri*.

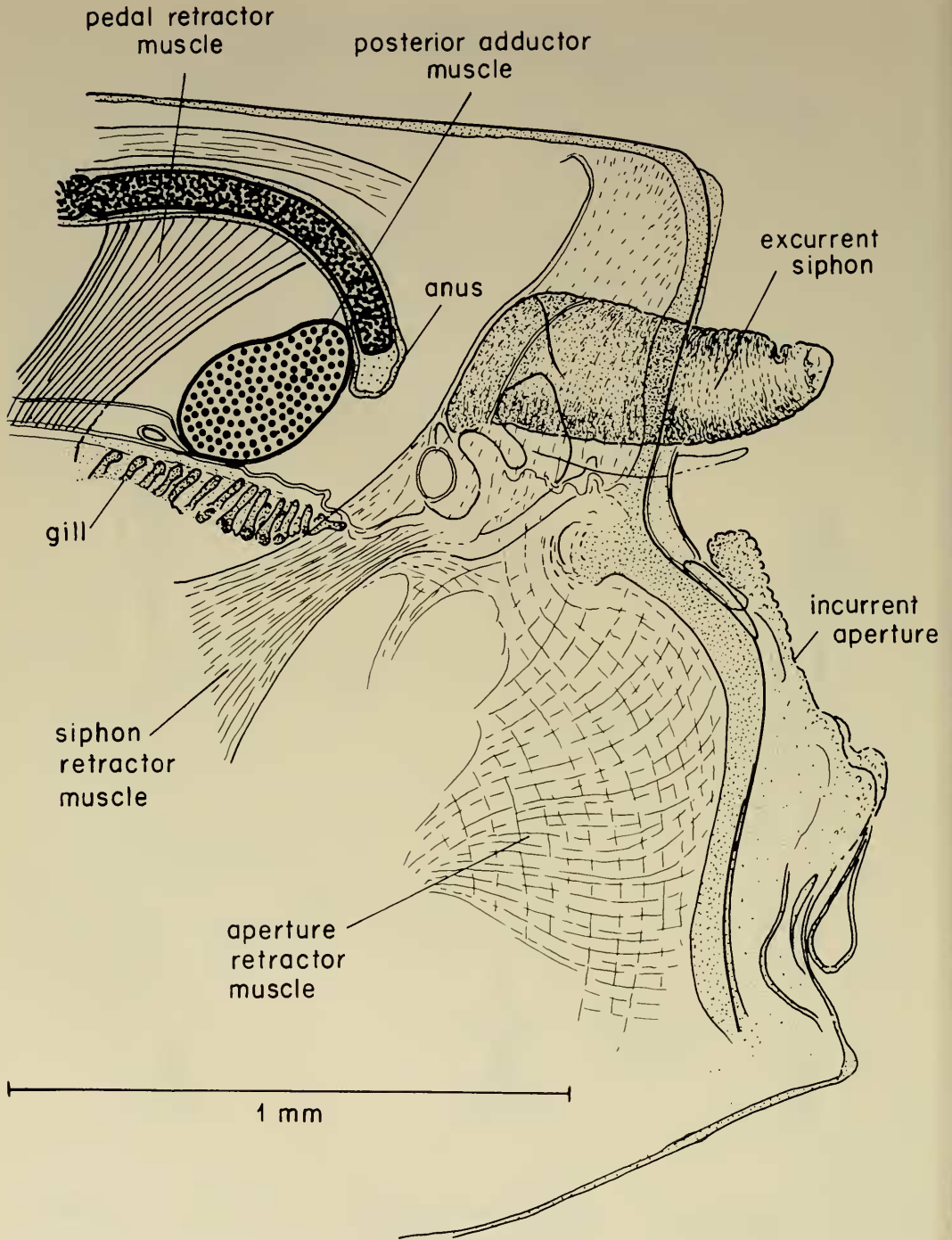


Figure 6. Siphonal region of *Silicula filotovae* as seen from the left side.

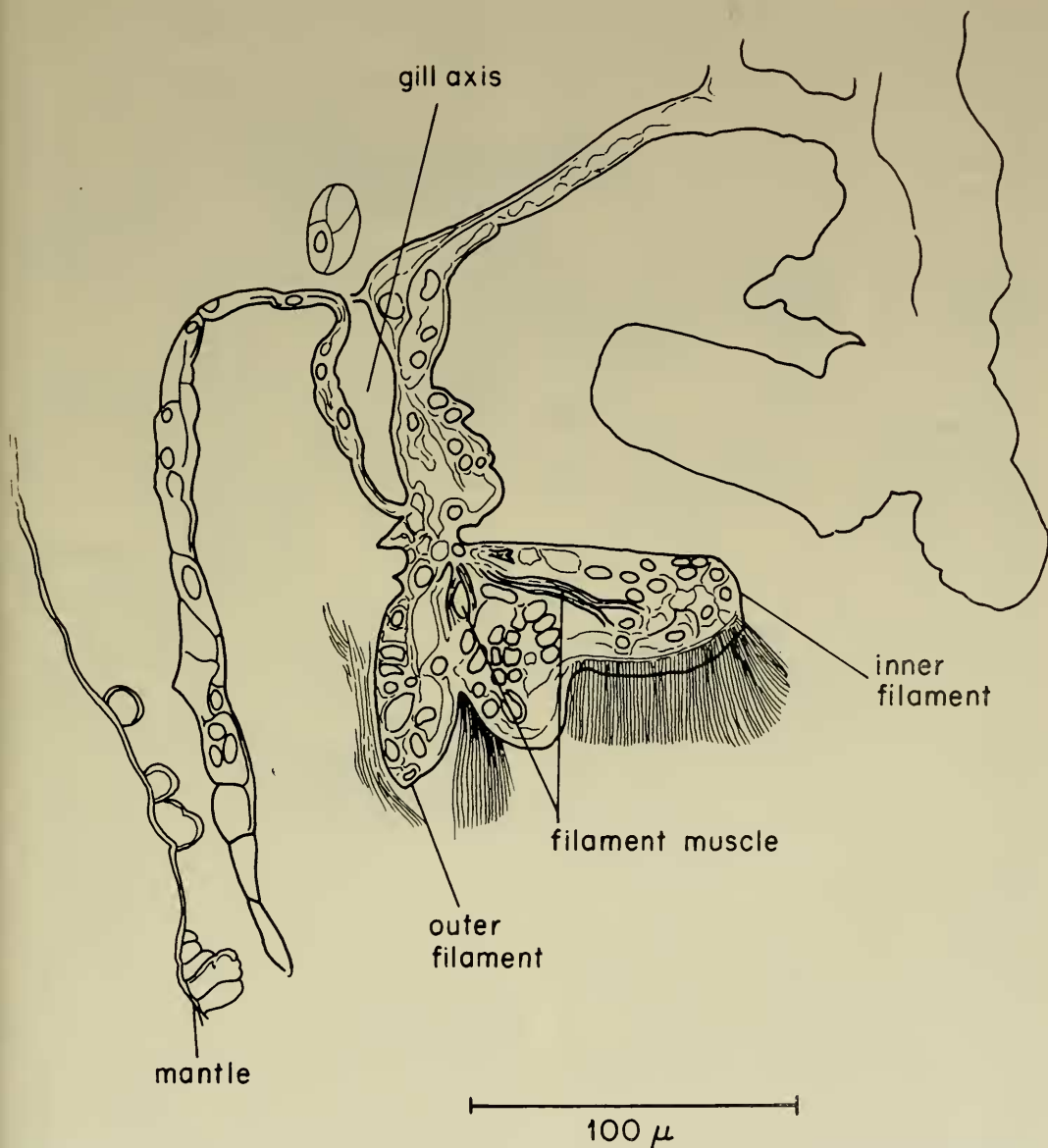


Figure 7. *Silicula filatovae* Allen and Sanders. Transverse section through a gill axis and filament of the left side.

extent as the exhalent siphon; fine retractor muscle fibers extend anteriorly into the mantle tissue behind the inhalent aperture, and numerous epithelial gland cells are present in the mantle epithelium internal to the aperture.

Anterior mantle sense organ located below the level of the anterior adductor mus-

cle and is formed by a moderately elongate, swollen section of the middle sensory fold with an increase in the number of overlying epithelial layers and gland cells.* Single posterior, very fine, attenuate tentacle on

* The detailed consideration of the histology of the anterior sense organ will be deferred to a later paper.

the right side, its point of origin between the base of the siphon and the dorsal limit of the inhalant aperture. Adductor muscles equal in size, both elongate although the anterior muscle is more rounded than the posterior, the long axes approximate to the anteroposterior axis of the body, "quick and catch" sections distinct.

Gill axis horizontal and parallel to anteroposterior axis of shell and extends from the ventral side of the exhalent siphon to a position one-third the distance across the body; axis attached along its whole length to the body wall and, posterior to the body, it is also attached to the mantle where there is no free posterior process as in the *Pristiglomidae* (Sanders and Allen, 1973); gill filaments 12–44, the number depending on the size of the animal, set alternately on either side of the axis as in *Nuculana* (Yonge, 1939); gill filaments short, the outer series half the length of the inner (Fig. 7); shorter, outer filaments make ciliary junctions with the mantle whereas the inner filaments, behind the foot, are joined by tissue adhesion. Thus, the gills separate a hypobranchial cavity from the rest of the mantle cavity. Frontal and laterofrontal cilia exceptionally long and dense, longer than the filament is deep (oral-aboral dimension); abfrontal cilia very sparse. Suspensory part of the gill axis is without muscle fibers; however, two or three bundles are present in the gill filament. The latter muscles radiate out from the dorsal side of the filament close to the axis in a fashion similar to those in other protobranchs, but are not so well defined (Atkins, 1936; Yonge, 1939).

Palps and palp proboscides relatively narrow and very elongate, even in the contracted state; palp ridges vary in number from 24–30 and, in the contracted state, the most posterior ridges fan out so that the proximal ridge lies parallel to gill axis. Mouth *not* adjacent to the anterior adductor muscle but posterior to and far removed from it (Figs. 8, 9), and thus the palp also

is posterior in position within the mantle cavity.

Body and foot together take up much of the shell's space; foot deeply cleft in the sagittal plane, the peripheral papillae of the sole numerous and varying in size. "Byssal" gland* very large with a conspicuous spherical cavity which is, typically, filled with a hyaline substance, the cavity is partially divided in the sagittal plane by a tongue of tissue. Foot greatly extended posteriorly but lacking the large hooked heel found in the *Pristiglomidae* (Sanders and Allen, 1973). Body axis curved anteriorly through 90° so that the foot is extended anteriorly. Pedal retractors, particularly the posterior, very powerful and consist of 1 posterior and 3 anterior pairs.

The course of the gut follows the basic pattern of the Protobranchia; thus, the oesophagus, somewhat displaced to the right, leads dorsally and posteriorly to a large stomach and the combined style sac and midgut; from the latter, the hindgut makes a single loop to the right side before passing dorsally and posteriorly over the posterior adductor muscle to the anus. Stomach simple, very large, occupying much of the available dorsal body space with a broad, nonridged sorting area, dorsal hood, and an extensive chitinous lining over much of dorsal side. Digestive gland with 3 ducts (2 left and 1 right). Long axis of stomach and style sac anteroposterior. Hindgut elongate, proximally penetrating deep into the foot where it curves posterior to and then ventral to the pedal ganglion (Fig. 8) before turning dorsally alongside the proximal section and then passing to the right side of the body. Before it turns to the right there is a characteristic U-shaped bend posterior to the style sac. The loop on the right side passes forward to the posterior edge of the anterior adductor and then turns posteriorly and middorsally to the anus, thus outlining the digestive gland

* The form and function of the protobranch "byssal" gland will be discussed in a later paper.

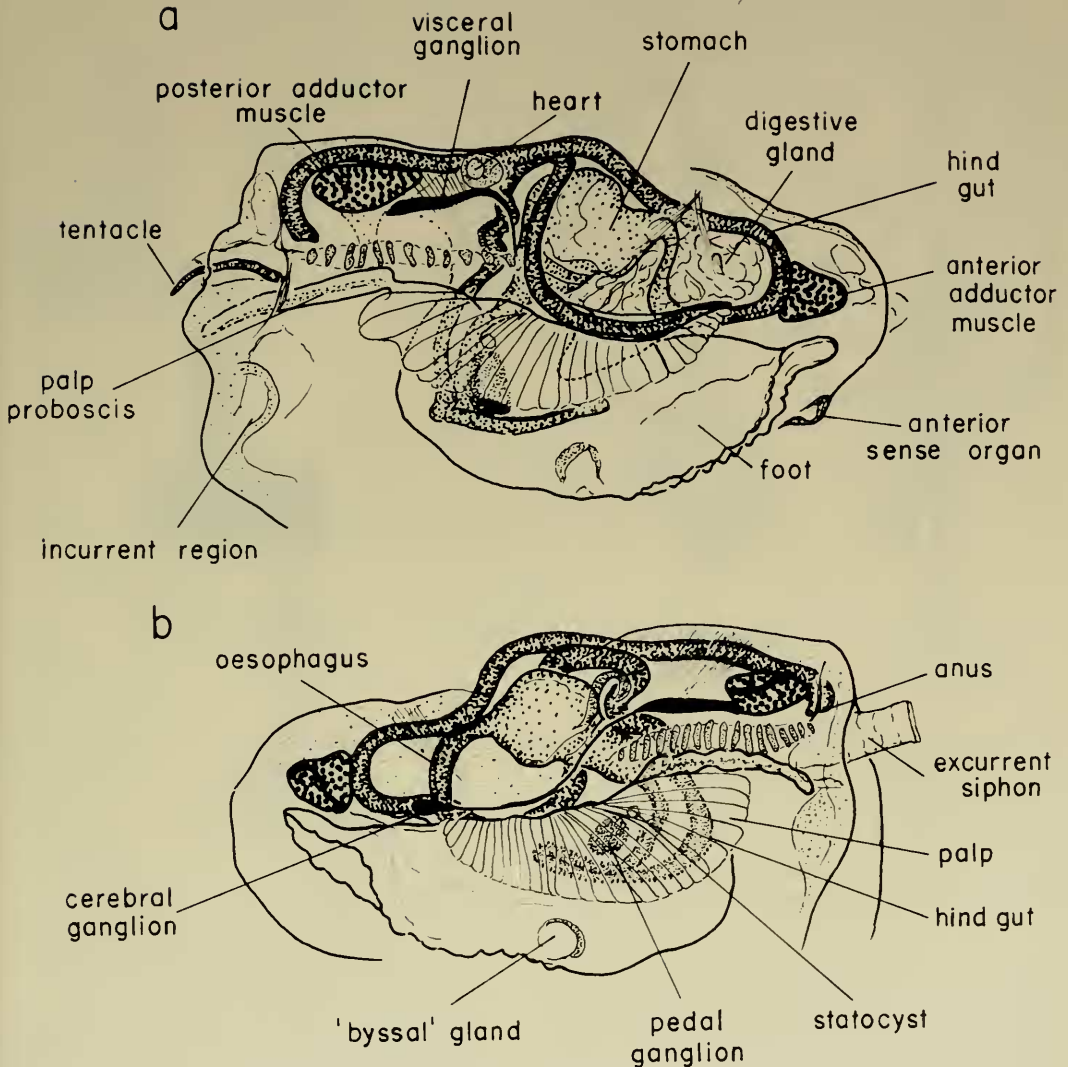


Figure 8. *Silicula filatovae* Allen and Sanders. a) Right and b) left lateral, semidiagrammatic views of the body and mantle organs.

and stomach. Lumen of hindgut relatively large, being 0.6 mm diameter in a specimen 4.0 mm total length.

Sexes separate; immature gonads lie ventral to the digestive gland and with increasing maturity extend dorsally to cover the sides of the visceral mass. Main part of the kidney, because of the anterior position of the posterior adductor muscle, compressed

anteroposteriorly between well-developed posterior pedal retractors and the posterior adductor. In compensation there is an anterior extension of the kidney into the posterior part of the body cavity. Nervous system characterized by huge paired pedal ganglia each with an associated statocyst. Visceral ganglia cylindrical, elongate and, like the cerebral ganglia, relatively small.

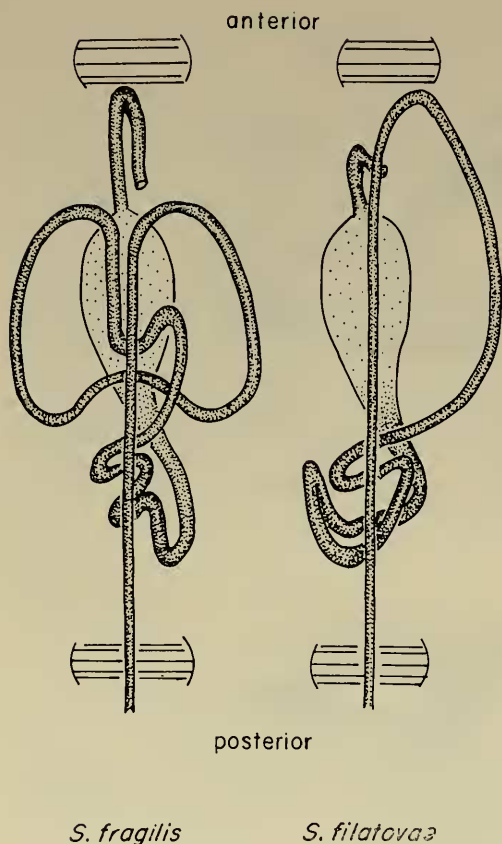


Figure 9. Diagrammatic comparison of the guts of *Silicula fragilis* and *S. filatovae* as seen from the dorsal side.

This species is named for Dr. Z. A. Filatova of the Institute of Oceanology, Academy of Sciences, U.S.S.R., an esteemed friend and colleague, in recognition of her important ecological and malacological contributions to the understanding of the deep-sea benthos.

Because the shell is transparent, we were able to appraise the state of maturity of *S. filatovae* at Station 85. Animals without gonadal development (11) varied in length from 1.89 to 3.40 mm, those with incipient gametogenesis (10) ranged from 2.80 to 3.79 mm, and those with obvious gonad development (23) were 3.40 to 5.20 mm long (Table II and Fig. 10). The larger speci-

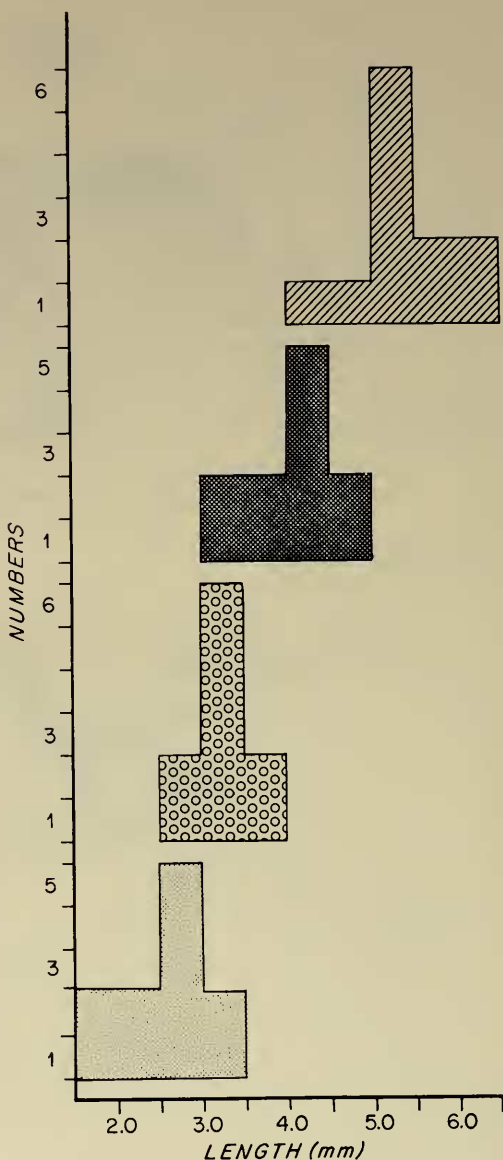


Figure 10. Size/frequency distribution of specimens of *Silicula filatovae* collected from Station 85, sorted according to sex and gonadal development.

mens were all mature, the smaller specimens immature, and both categories overlap, there being an intermediate size group that had incipient gonad development. Our interpretation of these findings is given later (p. 307) in the discussion.

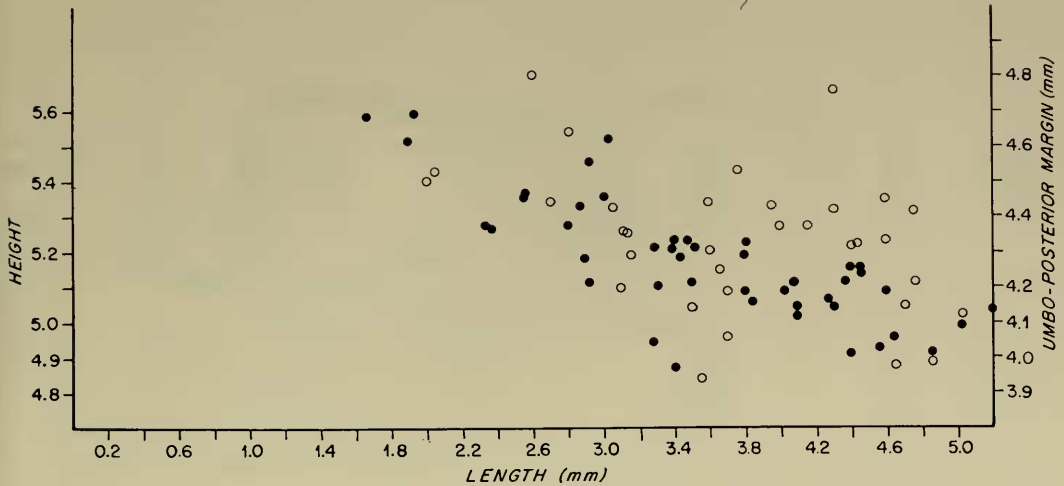


Figure 11. *Silicula flatovae* Allen and Sanders. Graph showing height/total length (●) and umbo to posterior margin/total length (○) plotted against total length.

TABLE II. INDEX OF BODY SPACE OCCUPIED BY THE GONAD FOR 192 INDIVIDUALS BELONGING TO SPECIES OF *Silicula* AND *Lametila*. NOTE ALL SPECIES NEED NOT HAVE THE SAME PROPORTION OF BODY SPACE OCCUPIED WHEN SEXUALLY MATURE.

	0	1	2	3	4	5	6	7	8	spent	Station No.
Gonad stages	0	1	2	3	4	5	6	7	8	spent	
<i>S. mcalesteri</i>	1	1	2	4	9	3	10	9	8	—	280
<i>S. fragilis</i>	11	6	2	—	—	—	—	—	—	—	85
	26	3	3	4	2	3	1	2	—	—	126
<i>S. flatovae</i>	21	4	7	8	3	1	—	—	—	—	85
<i>L. abyssorum</i>	4	10	3	10	6	2	1	1	—	1	64

Silicula fragilis Jeffreys, 1897

Figures 1, 5, 12-17

Silicula fragilis Jeffreys, 1879: 574 (Type locality: PORCUPINE Expedition, 1869, Station 16; type specimen: U.S. National Museum no. 197405).

Previous records. Depth range in Clarke (1962) = 1493-2223 m. West Europe Basin, 2 stations (1493 and 2223 m).

Present records. Depth range = 1922-4402: Table III.

A few supplemental remarks can be added to the original description by Jeffreys (1879) of *Silicula fragilis*, for the positioning of the teeth is not elaborated in detail in the text and the illustration shows some artistic license. We have examined the type specimen carefully and find a number of

major differences. The posterior teeth are much shorter than figured, they do not extend upwards to reach the dorsal margin but, instead, are straight and relatively parallel to it. The distal tooth does not remotely approach the posterior margin of the shell. Similarly, the anterior teeth are shorter, they do not reach the anterior shell margin and, rather than being somewhat concave as figured, they are slightly convex. In each of these respects, our material agrees with the holotype (Figs. 1, 12).

The basic detail of the mantle, mantle fusion, tentacle, anterior sense organ and mantle glands is similar to that of *S. flatovae* (Fig. 13). The adductor muscles are relatively smaller than in *S. flatovae* with the anterior more circular in outline, and

TABLE III. RECORDS FOR *Silicula fragilis* JEFFREYS.

Cruise	No.	Sta.	Depth (m)	Specimens	Latitude	Longitude	Gear	Date
NORTH AMERICA BASIN								
Atlantis II	12	64	2891	1	38°46.0'N	70°06.0'W	ES	21.8.64
Atlantis II	24	126	3806	41	39°37.0'N— 39°37.5'N	66°47.0'W— 66°44.0'W	ES	24.8.66
Chain	50	85	3834	39	37°59.2'N	69°26.2'W	ES	5.7.65
WEST EUROPE BASIN								
Sarsia		S-65	1922	2	46°15.0'N	04°50.0'W	ES	25.7.67
ARGENTINE BASIN								
Atlantis II	60	259a	3305— 3317	5	37°13.3'S	52°45.0'W	ES	26.3.71
Atlantis II	60	242	4382— 4402	1	38°16.9'S	51°56.1'W	ES	13.3.71

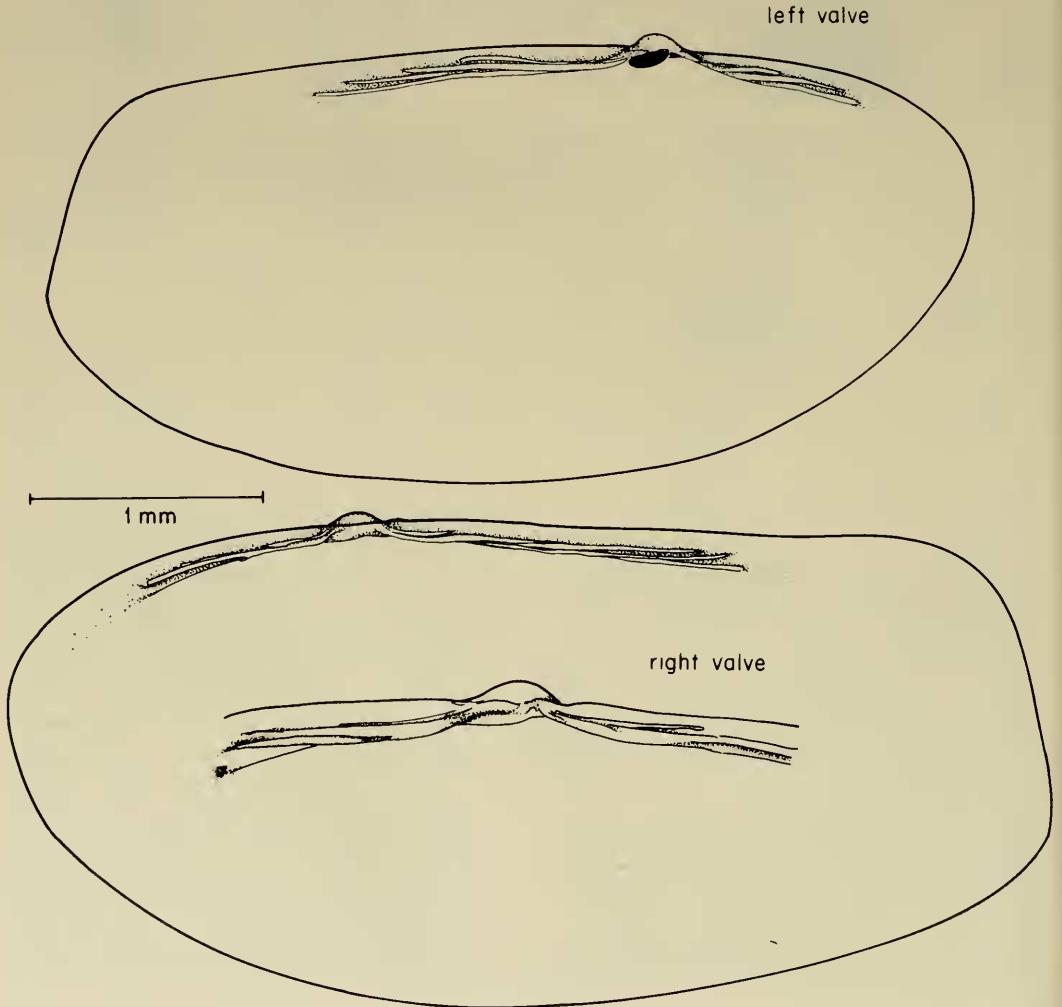


Figure 12. *Silicula fragilis* Jeffreys. Internal views of left and right valves, with enlarged hinge detail of right valve.

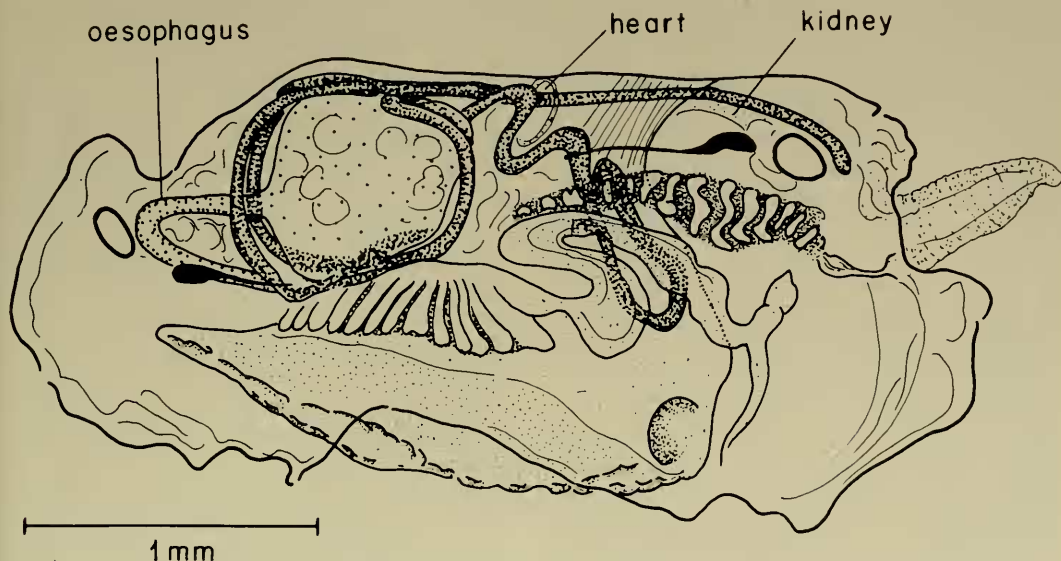


Figure 13. *Silicula fragilis* Jeffreys. Left lateral, semidiagrammatic view of the body and mantle organs.

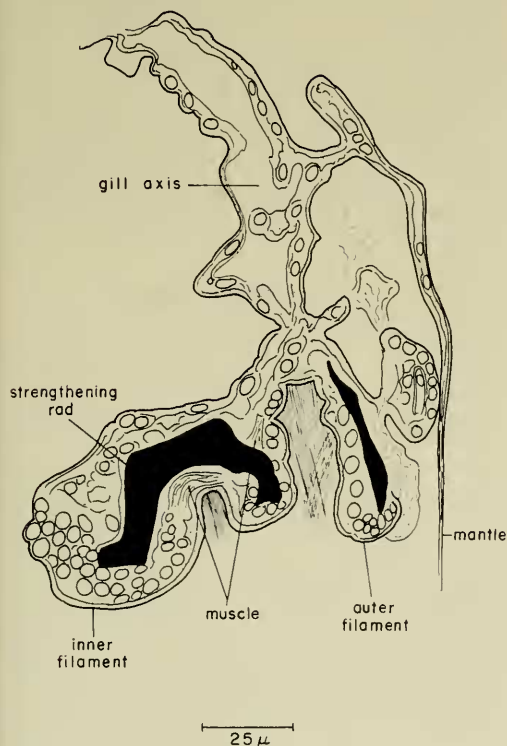


Figure 14. *Silicula fragilis* Jeffreys. Transverse section through a gill axis and filament of the right side.

the posterior set well forward within the mantle cavity. The gills are also similar in position and form; however, there are only 11–13 gill filaments and the gill does not extend as far across the body as it does in *S. filatovae*. The suspensory membrane is not muscular but there are one or two radiating muscles within the gill filament. The skeletal elements of the inner filaments are very broad (Fig. 14). The palps and palp proboscides are exceptionally attenuated, being much narrower than those of *S. filatovae* and with 14–18 palp ridges. Attenuation is accentuated because the mouth is somewhat closer to the anterior adductor muscle than it is in *S. filatovae* and because of the greater posterior extension of the mantle cavity.

In the form and arrangement of the gut *S. fragilis* differs markedly from *S. filatovae* as well as from *S. rouchi* and *S. mcalesteri*. The mouth is closer to the anterior adductor muscle and the oesophagus extends forward as far as the posterior limit of the muscle before it turns dorsally and posteriorly towards the stomach and style sac (Fig. 9). The latter are orientated in an

anteroposterior direction. The hindgut is very elongate and loops to the left as well as to the right side of the body. From its junction with the midgut, the hindgut extends posterior to the pedal ganglion, but does not curve forward below the ganglion, instead it turns dorsally behind the style sac where it forms two U-bends before passing forward to the *right* of the dorsal midline. Opposite the point where the oesophagus joins the stomach, the hindgut turns to the left side of the body and forms a single loop before returning to the right-hand side dorsal to the stomach. A single loop is formed on the right side and this leads to the final middorsal posterior section which ends at the anus. The right and left loops outline the periphery of the stomach and style sac. Note, in the case of both loops, the material in the gut is passing counter-clockwise when viewed from the side. The loops do *not* extend as far as the anterior adductor muscle and the diameter of the lumen is relatively smaller than in *S. filatovae*. The pedal ganglion is huge. The "byssal" gland is relatively smaller than that in *S. filatovae*.

Remarks. *Silicula fragilis* can be separated readily from *S. filatovae* by the elongate rectangular shell shape (not elongate oval); the anterior position of the umbo; the straight dorsal margin behind the umbo which is not gently and smoothly convex; the broad and obliquely truncate posterior margin that slants posteriorly and ventrally rather than being smoothly rounded; the shorter, less robust teeth that parallel the dorsal margin rather than diverge from it; the presence of five rather than four teeth in the posterior series and four rather than three in the anterior series; the shell is even more fragile than in *S. filatovae*; the gut loops on both sides of the body, rather than being confined to the right side; the posterior adductor muscle and pallial line are well anterior to the posterior shell margin.

Beside the suite of familial features, *S. fragilis* shares with *S. filatovae* a shell that

gapes both anteriorly and posteriorly and valves that are separated along part of the dorsal margin (Fig. 5).

Within the size range of 1.25 mm–5.09 mm, the height-to-length ratio changes with increasing length from .634 to .436 (Figs. 15, 16). The thickness-to-length ratio is only about .16, reflecting the very flattened form of *S. fragilis* (Fig. 15). The prodissoconch appears to be about 200 μ long, suggesting a lecithotrophic mode of development. Some gonad development was observed in specimens as small as 2.09 mm but the appraisal of gametogenesis is rendered difficult because the shells of many of our specimens are opaque. At Station 126, 17 of the 36 specimens available were opaque. Of the remaining 19 individuals, nine showed some development of the gonad and ten did not (Table 1 and Fig. 17). The latter group varied in length from 1.25 mm–3.03 mm while the former ranged from 2.09 mm–5.09 mm. At Station 85 where 20 specimens were available for analysis, one was opaque, ten varying in length from 2.47 mm–4.17 mm showed no gametogenesis, and eight, with a range in sizes from 2.90 mm–4.60 mm, were mature or maturing (Table II and Fig. 17). Our interpretation of these data is given in the discussion section (p. 307).

Silicula mcalesteri new species

Figures 5, 18, 20–22

Type locality: ATLANTIS II, Cruise 60, Station 280, in 275–305 m. Holotype: MCZ 271974. Depth range = 275–305 m. Records: Table IV.

The shell, elongate in outline with the posterior margin considerably extended, smooth, glossy, iridescent, straw-yellow, semitransparent and somewhat laterally compressed with fine concentric lines; dorsal margin long; umbo small, barely rising above the dorsal margin of the shell and placed far forward at a position about 25 to 29 percent of the distance between anterior and posterior edges; shell highest in the region of the umbo and gradually and continuously tapering posteriorly (Fig. 18);

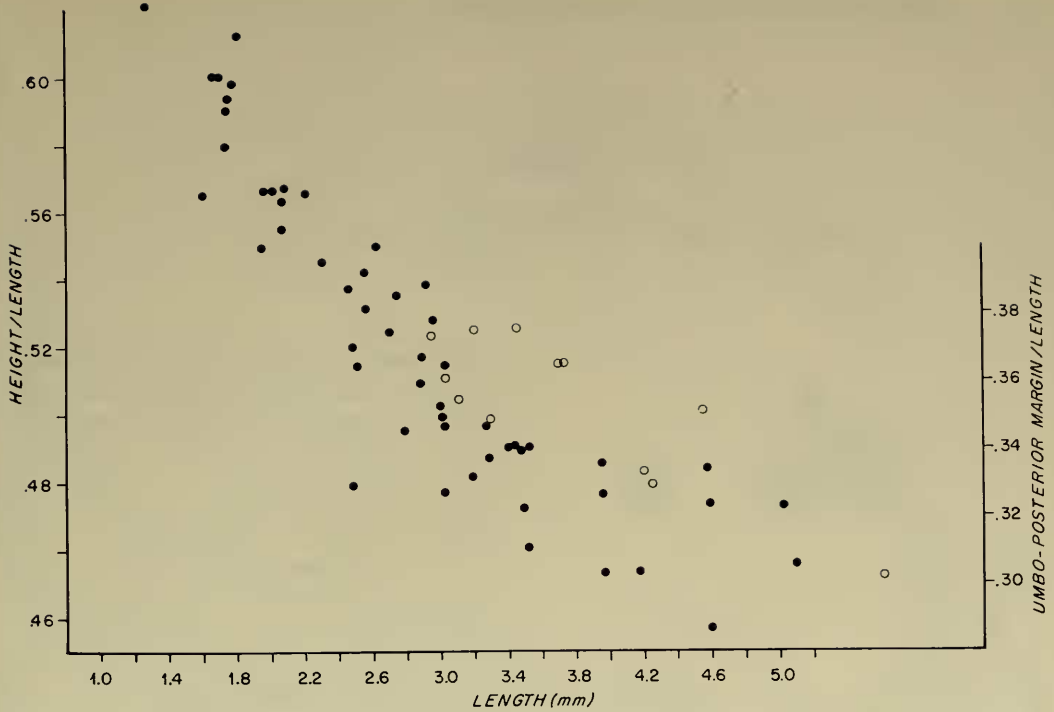


Figure 15. *Silicula fragilis* Jeffreys. Graph showing height/total length (●) and umbo to posterior margin/total length (○) plotted against total length.

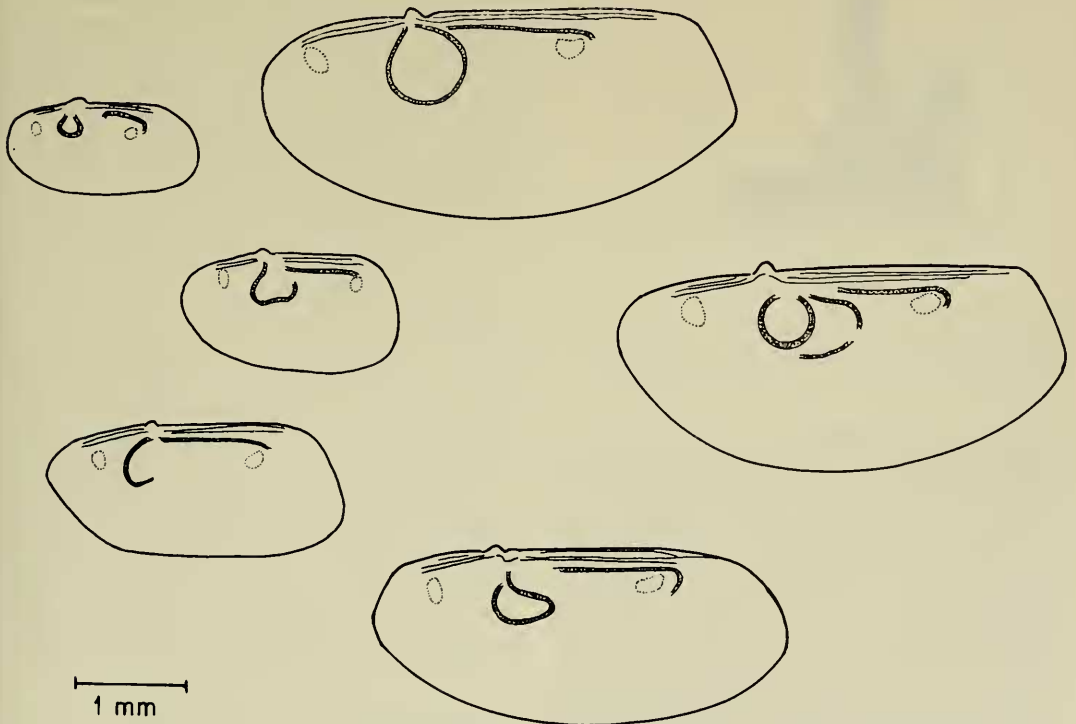


Figure 16. Lateral views of a series of specimens of *Silicula fragilis* to show changes in shape with increasing size.

TABLE IV. RECORDS FOR *Silicula mcalesteri* NEW SPECIES.

Cruise	No.	Sta.	Depth (m)	Specimens	Latitude	Longitude	Gear	Date
ARGENTINE BASIN								
Atlantis II	60	280	275–305	39	36°18.0'S–36°19.0'S	53°24.5'W	ES	29.3.71



Figure 17. Size/frequency distribution of specimens of *Silicula fragilis* collected from Stations 126 and 85 and sorted according to sex and gonadal development.

dorsal margin behind the umbo convex in front of the umbo, slanting abruptly downwards to the anterior limit of the shell, such that the dorsal and ventral margins merge in a smooth curve; shell margin, immediately anterior and posterior to the umbo forming small concavities; posterior margin narrowly truncate; anterior margin sharply and evenly rounded; ventral margin long and gently curving; shell gaping anteriorly and posteriorly, the valves separated along part of the dorsal margin (Figs. 5, 18).

Hinge plate long, thin, and weak; posterior hinge plate long, straight, and paralleling the dorsal shell margin; anterior hinge plate short, straight and angled ventro-anteriorly. Opisthodontic ligament large, elongate, originating below the umbo and directed transversely in a ventroposterior direction. Posterior hinge plate with 6–8 very narrow, elongate teeth, only the largest specimens having 7 and 8 teeth; the most proximal tooth small, being readily overlooked, and rising from the thickened hinge plate immediately behind the umbo and above the ligament; the second tooth is also small, but three times the length of the first, and positioned on the hinge plate immediately below and behind the first, above the distal end of the ligament, and slanting posteriorly and dorsally away from the hinge line towards the dorsal margin; remaining teeth considerably longer, and continuously overlapping, on hinge line and, excepting the distal tooth, directed slightly anteriorly towards the dorsal shell margin; the terminal tooth forms the distal hinge line; in specimens with 6 teeth, 1 to 5 are sequentially more elongate, teeth 4 and 5 extending more than half the length of the posterior hinge plate, and tooth 6 half the length of tooth 5; anterior hinge plate with 5 overlapping teeth which arise from the anterior hinge line and are considerably shorter than all but the two most proximal of the posterior hinge series; teeth 1–4 diverge from the hinge line, tooth 5 forms the distal hinge line, the most proximal tooth is smallest and slightly concave; teeth 3 and 4 are longest and slightly convex, pallial line present and with a pronounced embayment below the posterior adductor muscle scar.

The 49 specimens of *S. mcalesteri* from Station 280 varied from 3.55 mm–11.38 mm

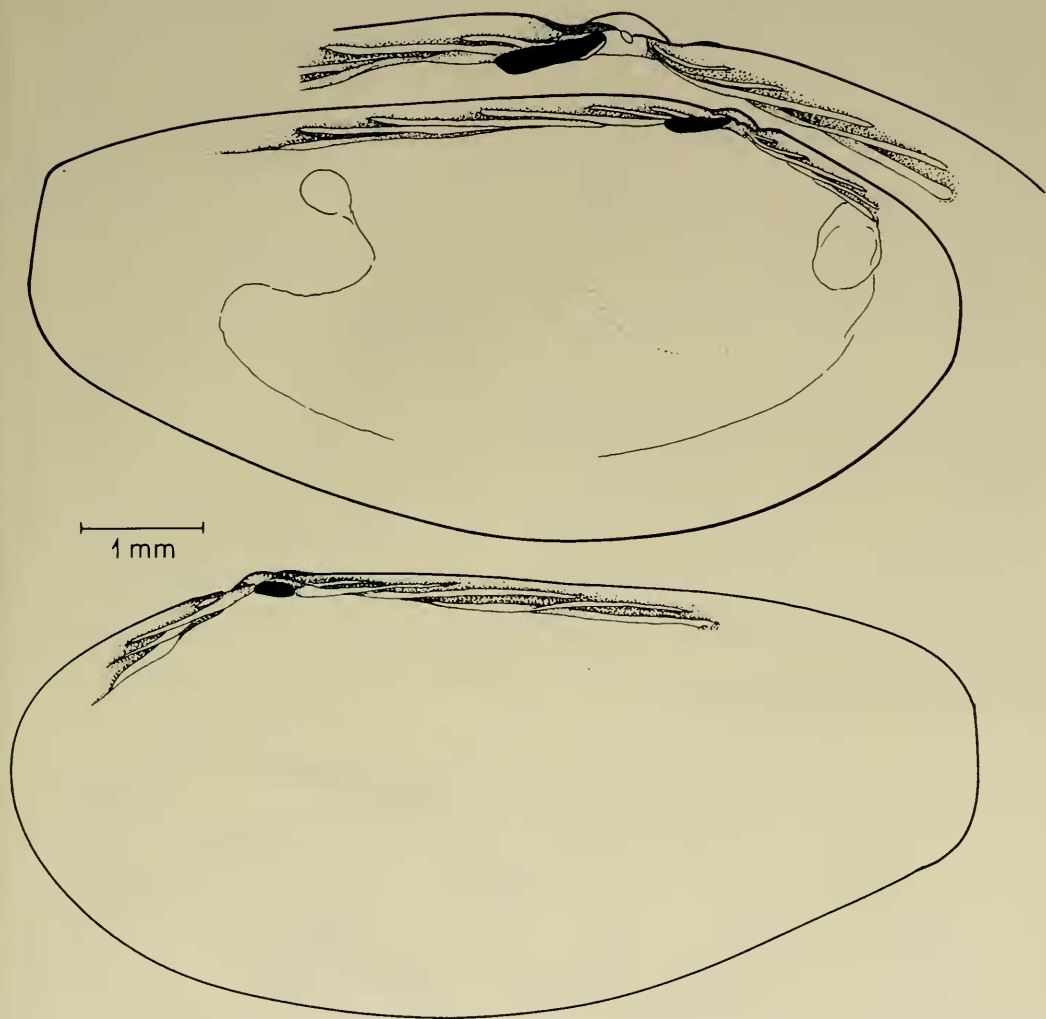


Figure 18. *Silicula mcalesteri* Allen and Sanders. Internal views of the left and right valves, with enlarged hinge detail of the left valve.

in length. Within the length range of 4.0 mm–11.38 mm, the height-to-length ratio remains relatively constant, 0.43–0.48. The two smallest specimens, less than 4 mm, have a height-to-length ratio of 0.56 and 0.52 (Figs. 19, 20). With a width-to-length ratio of 0.27, *S. mcalesteri* does not have the extreme flattened form of either *S. filatovae* (0.17) or *S. fragilis* (0.16).

S. mcalesteri exhibits the greatest posterior elongation of the mantle/shell of the species described. Exhalant siphon very

well developed with a well-defined siphonal embayment; siphonal retractor muscles form 5–6 bundles. Similarly, the muscular inner fold of the mantle edge in the region of the inhalant aperture is particularly well developed. Anterior sense organ small but well defined. Both adductor muscles small, but the posterior muscle is somewhat smaller than the anterior, and, as in the other species, is set far forward in mantle cavity, where it still stands opposite the end of the hinge plate.

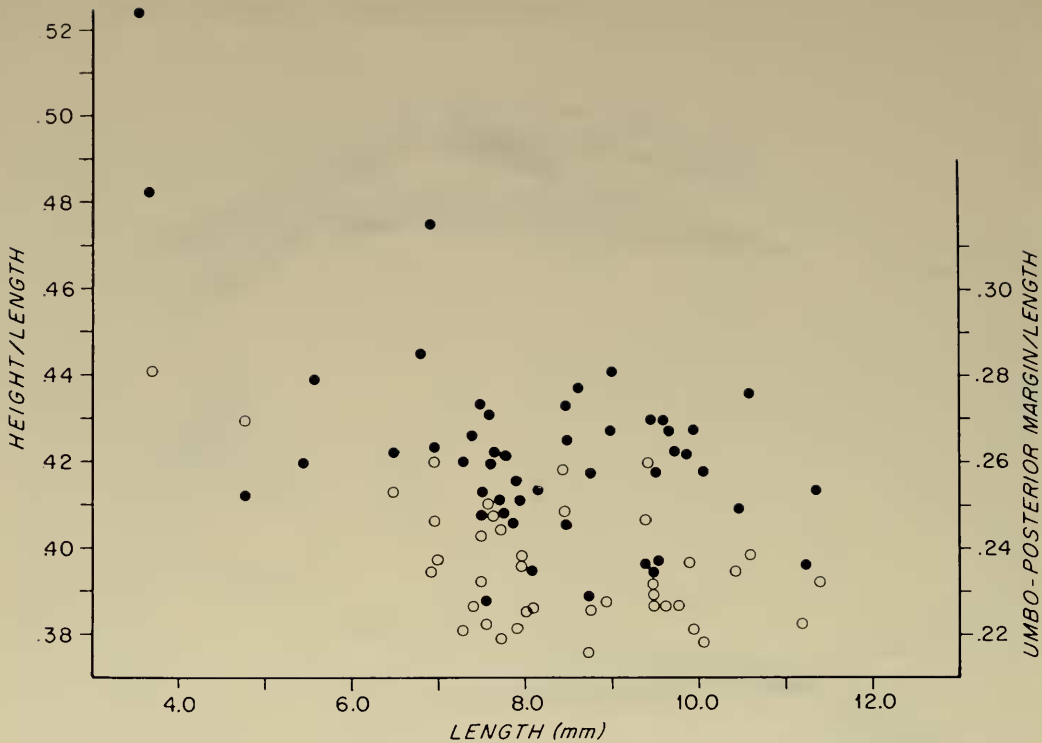


Figure 19. *S. mcalesteri* Allen and Sanders. Graph showing height/total length (●) and umbo to posterior margin/total length (○) plotted against total length.

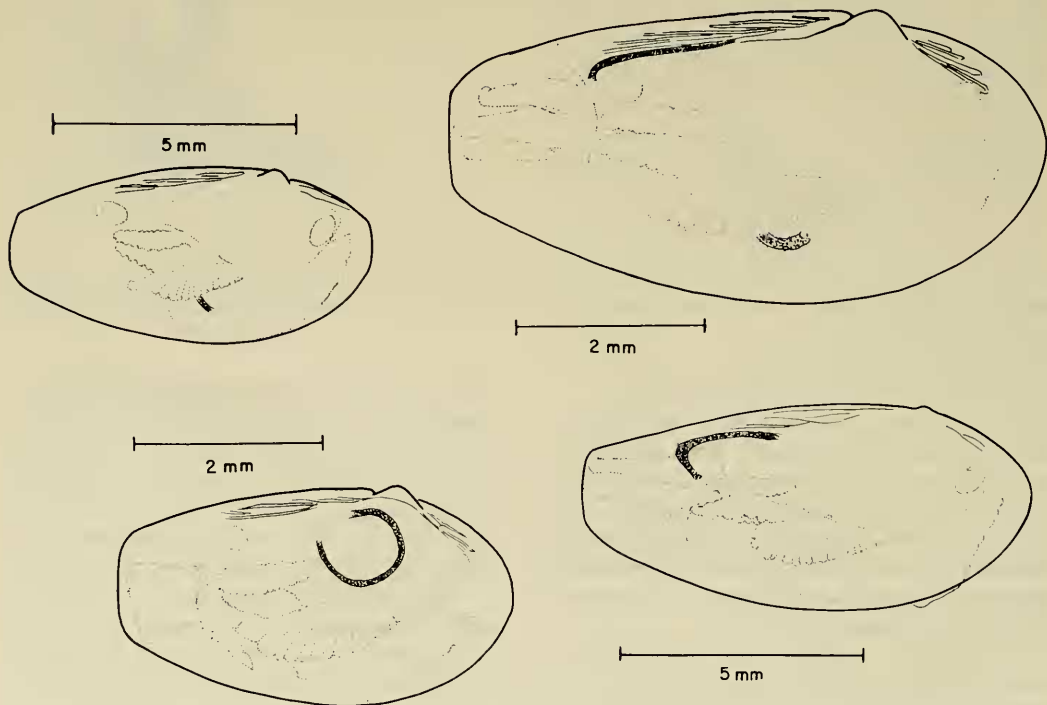


Figure 20. Lateral views of a series of specimens of *S. mcalesteri* to show changes in shape with increasing size.

Gills well developed with 27–35 plates to each side of the axis, and extend along the body to a position opposite the posterior limit of the stomach; no muscles in the suspensory part of the axis and in sectioned specimens the axial blood space is exceptionally large (Fig. 22). Palps, bearing about 35 ridges, centrally located in the mantle cavity and lie relatively close to the ventral edge of the shell. Body and foot large, the dorsoventral axis turned through 90°. “Byssal” gland moderately large and the fringing papillae of the foot variable but relatively small in size.

Mouth set far back from the anterior adductor muscle; the oesophagus extends diagonally anteriorly and dorsally towards the anterior adductor; however, unlike *S. fragilis*, it turns short of the posterior edge of the muscle towards the stomach. Stomach large, but proportionately smaller than in other species of *Silicula*. Combined style

sac and midgut large and elongate, the long axis oriented in a more dorsoventral direction than in the previous two species. Hindgut curving downwards anteriorly towards the pedal ganglion before passing dorsally to the right side of the body where it forms a single, small loop. There is no U-bend in the hindgut behind the style sac. Both cerebral and visceral ganglia small, elongate and cylindrical in shape. Kidney more extensive than in *S. filatovae* and *S. fragilis*, invading the body behind the stomach (Fig. 21).

Remarks. *Silicula mcalesteri* is possibly conspecific with *Silicula patagonica* (Dall). We have examined the type specimen of *S. patagonica* (U.S. Nat. Mus. No. 96914; Fig. 23) and the single valve lacks the umbonal region together with the proximal parts of the anterior and posterior hinge plates. In addition, the posterior shell margin is badly eroded, and the anterior shell

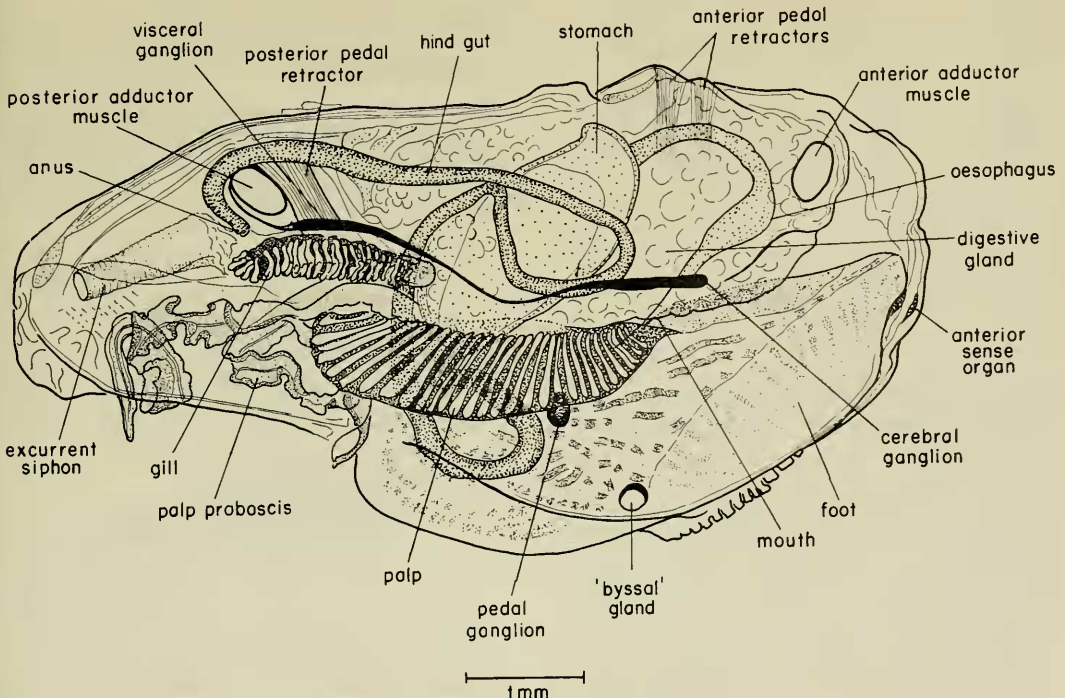


Figure 21. *Silicula mcalesteri* Allen and Sanders. Right lateral, semidiagrammatic view of the body and mantle organs.

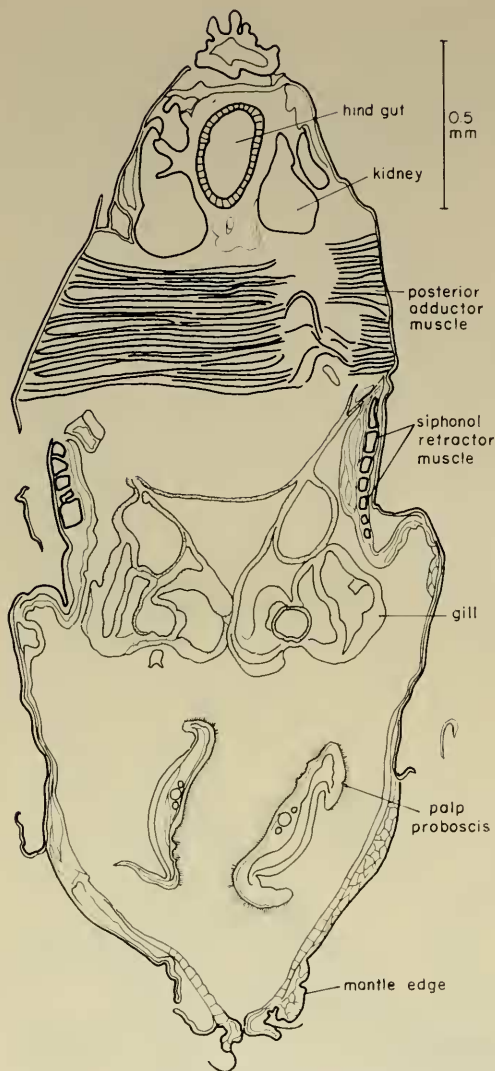


Figure 22. *Silicula mcalesteri* Allen and Sanders. Transverse section through posterior adductor muscle, gills and palp proboscides.

margin is not intact. Though the type is reminiscent of *S. mcalesteri* the teeth appear thicker and, because *S. patagonica* is from the eastern Pacific, we decided to consider these as separate entities.

The present species is named in honour of Dr. A. Lee McAlester, Department of Geology and Geophysics, Yale University, for his keen and perceptive contributions to

the evolutionary history of the protobranch bivalves.

The shell of this species is sufficiently transparent for us to appraise the state of maturity and sex of the animals in our sample. Only the two specimens smaller than 4 mm were not mature; one was immature and the other showed incipient gonad development. The sexes are separate and present in our sample in essentially equal numbers, 23 females and 24 males. In the region of broad overlap, 6.5 mm–10.0 mm, males and females were equally abundant (Fig. 24). The three mature specimens smaller than 6.5 mm were females and each of the five individuals larger than 10.0 mm were males, suggesting a possible size differential in the sexes. The mature egg is small (90 μ) for a protobranch and according to the criteria of Ockelmann (1965) this size would make it barely lecithotrophic. We estimate that about 1,000 ripe eggs were present in the one specimen examined.

Silicula rouchi Lamy, 1910

Figures 25–27

Silicula rouchi Lamy, 1910: 394 (Type locality: Alexander Island, Antarctica; type specimen: Mus. natl. Hist. nat., Paris); 1911: 30. Hedley, 1916: 18. Soot-Ryen, 1951: 6. Carcelles, 1953: 208. Powell, 1958: 171; 1960: 171. Dell, 1964: 147. Nicol, 1966: 15. Dell, 1969, folio 11.

Although this species is not represented in our collections, we include it since it completes the known species of the genus. Through the kindness of John Taylor we were able to borrow preserved material of *S. rouchi* from the British Museum of Natural History (B.M. No. 196526W) and study the soft-part anatomy.

Concerning the shell, little needs to be added to the descriptive information provided by Lamy (1910), Dell (1964), and Nicol (1966). In shell morphology, tooth structure, and shape, it is more similar to *S. fragilis* than the other species. However, *S. rouchi* differs from *S. fragilis* by having a relatively smaller and more anteriorly placed umbo, an anterior dorsal margin

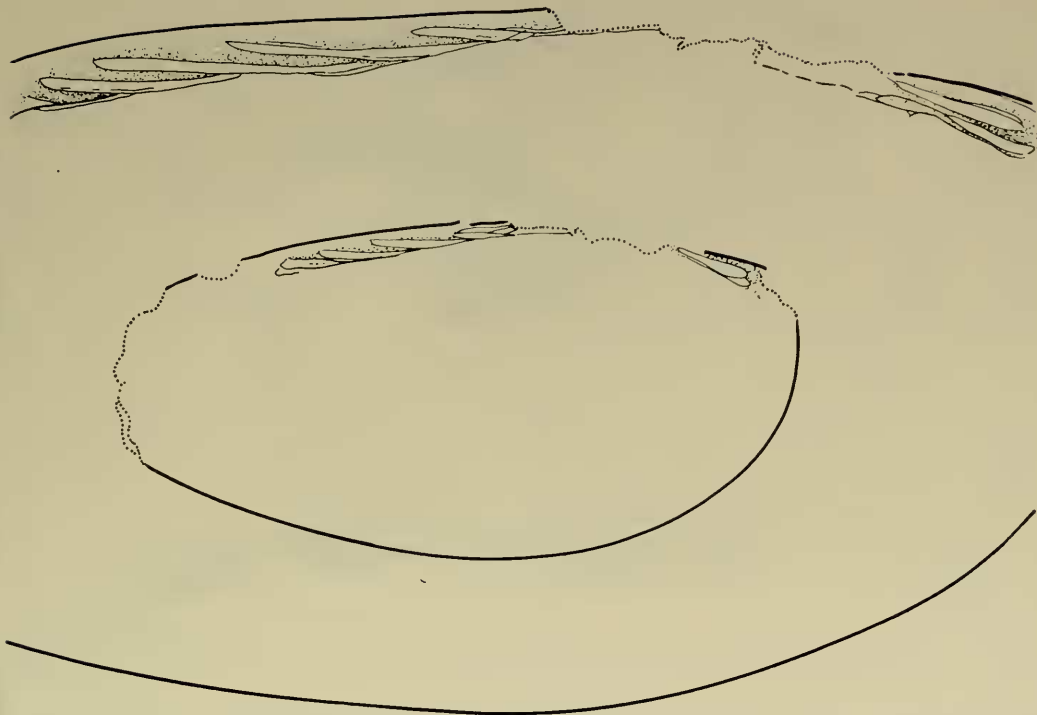


Figure 23. Two lateral views (left valve), one an enlargement of holotype of *Silicula patagonica* Dall. (U.S. Nat. Mus. No. 96914, Station 2783, west coast of Patagonia.)

which initially curves dorsally in front of the umbo rather than being straight, and an

anterior hinge that is shorter and more ventrally curved which bears shorter though thicker teeth (Figs. 25, 27).

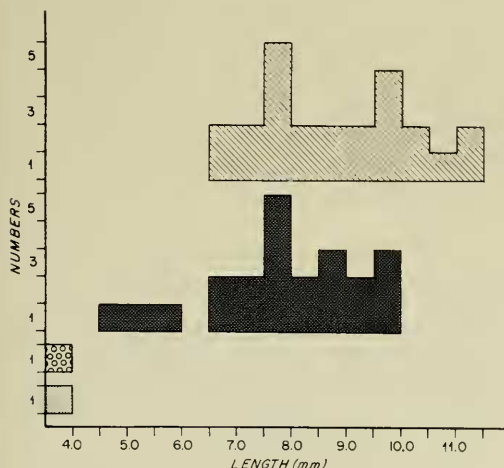


Figure 24. Size/frequency distribution of specimens of *S. maclesteri* collected from Station 280, and sorted according to sex and gonadal development.

The soft parts are very similar to *S. filatovae*, with differences being a matter of degree. The adductor muscles are relatively large, ovoid, and equal in size. The long axis of the anterior adductor muscle is dorsoventral, that of the posterior approximately anteroposterior. The exhalent siphon is well developed with a slight but noticeable siphonal embayment. The inhalent aperture, as in all species of the genus, is formed by the apposition of the inner muscular mantle layers, but involves no fusion. A single tentacle on the right side is inserted between the inhalent aperture and the exhalent siphon. The gill is horizontal with 35-40 gill filaments to each side of the axis of each demibranch, the outer filaments being half the size of the inner. The palps, with approximately 18 ridges, are relatively

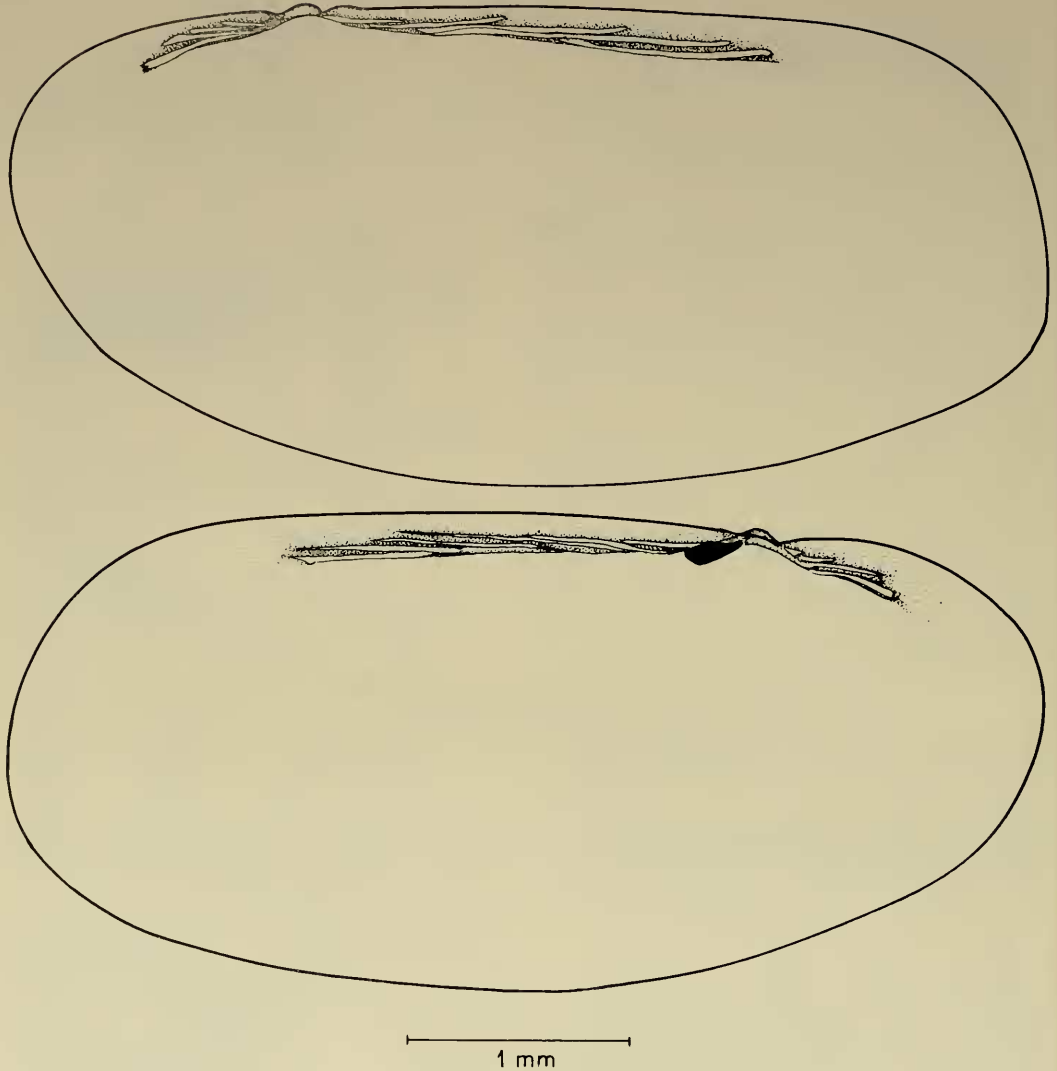


Figure 25. *Silicula rouchi* Lamy. Internal views of left and right valves.

shorter and narrower than those of other species and barely extend across the length of the body. Because the mouth is set so far posterior to the anterior adductor muscle, the palps occupy a central position within the mantle cavity. The palp proboscides are exceptionally long, reflecting the increased posterior extension of the mantle cavity. The foot is relatively small and the body axis is not turned anteriorly to the same extent as in the previous species. How-

ever, the foot remains very muscular with powerful anterior and posterior retractor muscles.

The mouth is positioned about one-third the length of the body posterior to the anterior adductor and, as in *S. fragilis*, the course of the oesophagus is forward to the anterior adductor muscle before turning posteriorly towards the stomach. The stomach is not as large as in the other members of the genus, nor does it take up as much

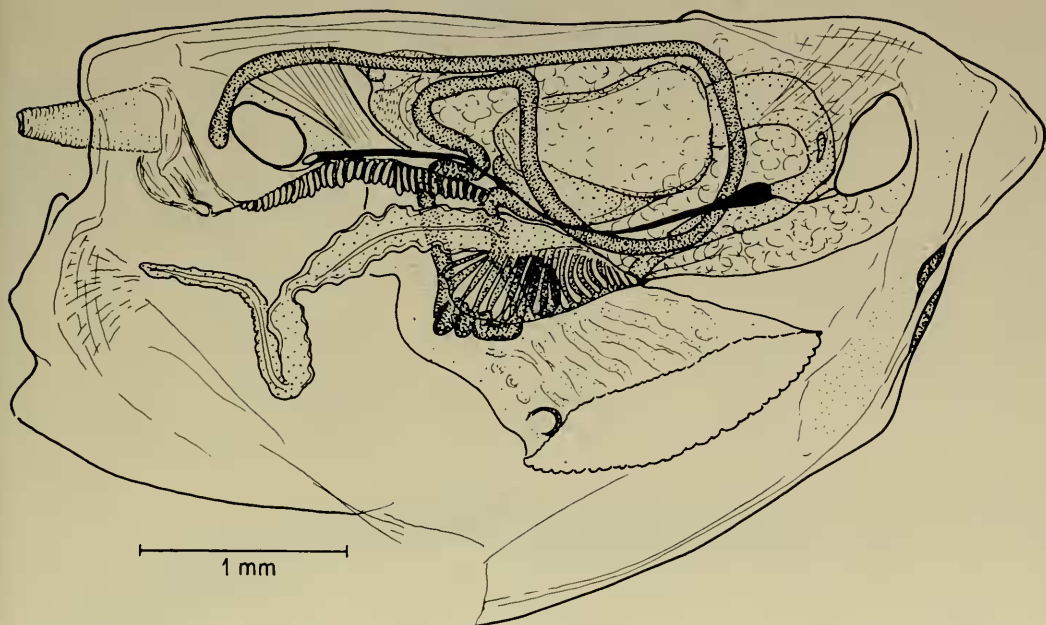


Figure 26. *Silicula rouchi* Lamy. Right lateral, semidiagrammatic view of the body and mantle organs.

of the body space. It has seven or eight broad sorting ridges, and the combined style sac and midgut is relatively short. The hindgut does not penetrate the foot ventral to the pedal ganglion; however, there is one U-bend posterior to the style sac and before the single loop to the right side of the body. The loop does *not* extend as far as the anterior adductor. The pedal ganglion is very large and the visceral ganglia are elongate and cylindrical, while the cerebral ganglia are set forward of the mouth close to the oesophagus between the mouth and the anterior adductor muscle (Fig. 26).

Family LAMETILIDAE new family

Nuculanacid protobranchs with smooth, somewhat tumid shells and rounded in outline; hinge weak, always with elongate teeth which are never more than two in number on either the anterior or the posterior hinge plate, taxodont teeth present or absent; umbo low and relatively elongate; lunule and escutcheon absent; ligament internal, oblong, and amphidetic; in-

halent siphon present but not fused on the ventral side; gill filaments broad and leaf-like; hindgut complex, with loops to the right and left sides of the stomach that connect both dorsally and ventrally behind stomach and ventrally in front of stomach; foot relatively square in outline with a small, triangular, posteriorly directed heel.

Genus *Lametila* new genus

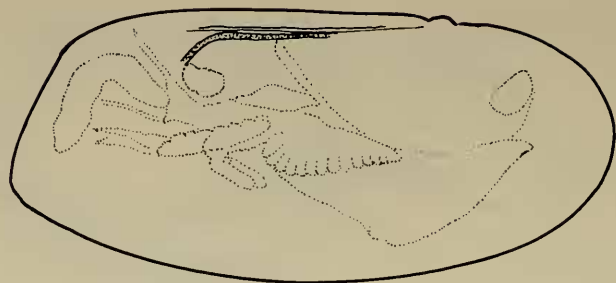
Type species: *Lametila abyssorum* Allen and Sanders new species

Teeth exclusively of elongate type; adductor muscles equal in size; viscera occupy only the dorsal half of the shell cavity; hindgut with two loops on the right hand side of body, posterior edge of the foot square. Characters that differentiate the genus *Lametila* from the other genus of the family (*Prelametila*) are given on p. 296.

Lametila abyssorum new species

Figures 28–35

Type locality: ATLANTIS II, Cruise 12, Station 24, in 2891 m. Holotype: MCZ 271978. Depth range = 2496–3834 m. Records: Table V.

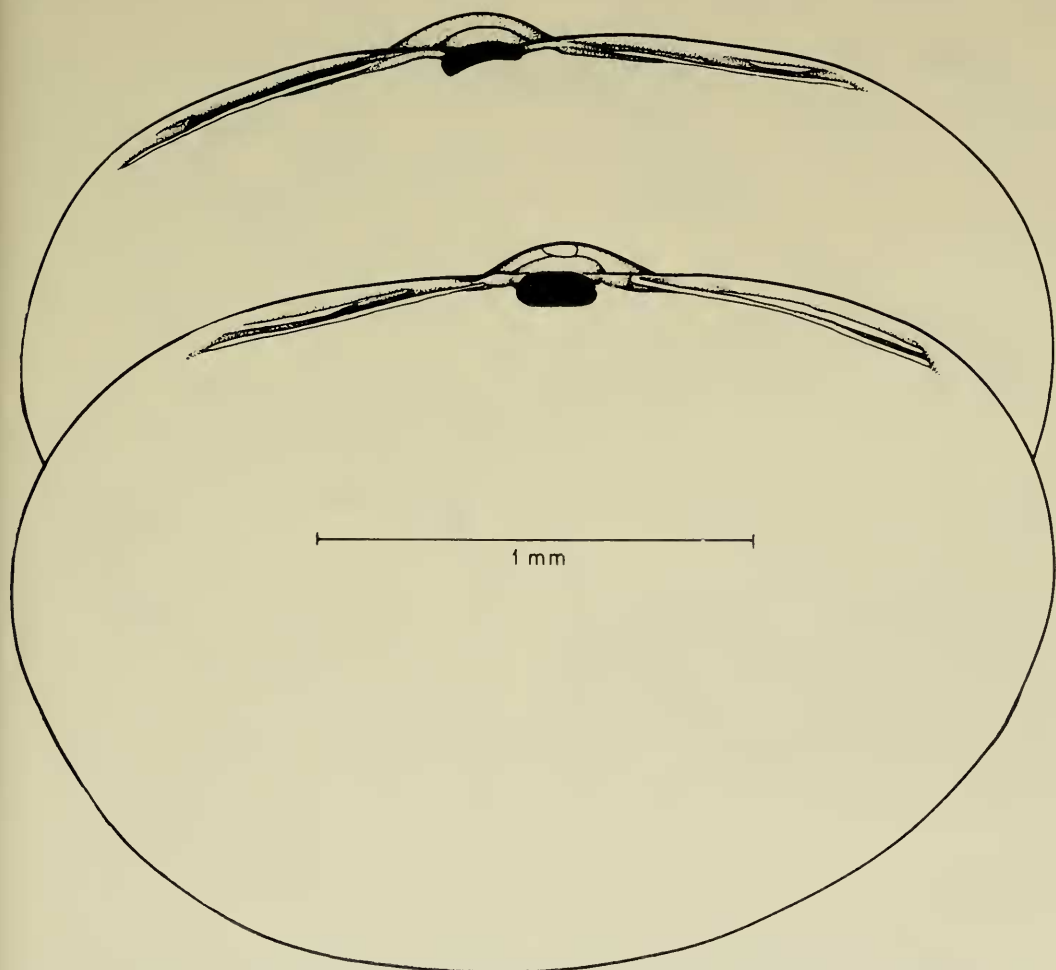


1 mm

Figure 27. Lateral views of three specimens of *S. rouchi* to show changes in shape with increasing size.

TABLE V. RECORDS FOR *Lametila abyssorum* NEW SPECIES.

Cruise	No.	Sta.	Depth (m)	Speci- mens	Latitude	Longitude	Gear	Date
NORTH AMERICA BASIN								
Atlantis II	12	62	2496	2	39°26.0'N	70°53.0'W	ES	21.8.64
Atlantis II	12	72	2864	18	38°16.0'N	71°47.0'W	ES	24.8.64
Atlantis II	12	64	2891	60	38°46.0'N	70°06.0'W	ES	21.8.64
Atlantis II	24	126	3806	6	39°37.0'N— 39°37.5'N	66°47.0'W— 66°44.0'W	ES	24.8.66
Chain	50	85	3834	60	37°59.2'N	69°26.2'W	ES	5.4.65
BRAZIL BASIN								
Atlantis II	31	156	3459	46	00°46.0'S— 00°46.5'S	29°28.0'W— 29°24.0'W	ES	14.2.67
Atlantis II	31	155	3730— 3783	3	00°63.0'S	27°48.0'W	ES	13.2.67

Figure 28. *Lametila abyssorum* Allen and Sanders. Lateral views of the inside of left and right valves.

Shell small, less than 3.5 mm in length; smooth, almost transparent, fragile and with fine concentric striae; height measurement about 0.4 times length (Fig. 34); oblong and rounded in outline; dorsal margin of intermediate length, gently rounded, curving gradually ventrally from the umbonal region and forming raised crests both behind and before the umbo; posterior crest longer than the anterior; posterior margin broad and smoothly rounded with the ventroposterior margin longer than the dorso-posterior; anterior margin narrow and sharply, though evenly, rounded; ventral edge smoothly rounded; umbos small, low,

relatively elongate, medially directed with, characteristically, a more opaque medial and ventral region (Fig. 28); umbos central (50%) of the distance along dorsal margin in smaller specimens, but more anterior (45%) in larger individuals (Figs. 29, 34); shell with small gap at the posterior end of dorsal margin (Fig. 31).

Hinge plate long, narrow, weak, with a short section under the umbo straight and parallel to the dorsal margin; anterior and posterior to the umbo the hinge line slopes slightly ventrally; ligament internal, large, amphidetic, at least twice as deep dorso-ventrally as long, somewhat bean-shaped in

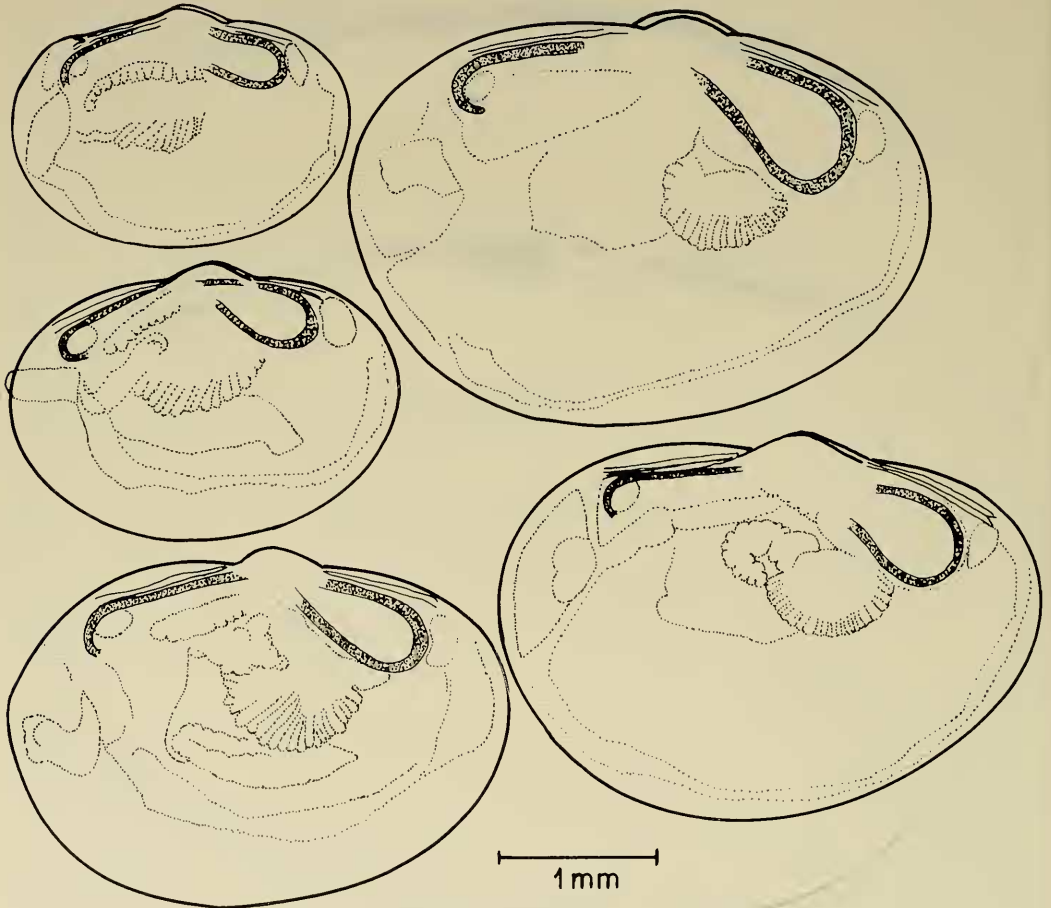


Figure 29. Lateral views of a series of specimens of *Lametila abyssorum* to show changes in shape with increasing size.

outline but wedge-shaped in cross section; two elongate teeth on both the anterior and the posterior hinge plate parallel to or confluent with hinge line; ventral tooth very long, inserted on the thickened medial portion of the hinge plate and angled distally across proximal plate to form the distal 2/3 to 3/4 of the hinge line, terminating above the adductor muscles; dorsal teeth of left and right valves shorter than the ventral teeth; dorsal tooth of left valve relatively elongate and paralleling the distal 70 to 75 percent of the ventral tooth; dorsal tooth on the posterior hinge plate diverges distally from the ventral tooth, the terminal end converging again and forming a crescent-shaped cavity between the teeth; distal divergence of the dorsal tooth on anterior hinge plate less marked and more continuous; dorsal teeth of right valve much smaller; the larger, on posterior hinge plate, about 1/4 the length of the ventral tooth and just medial and parallel to the distal end of the ventral tooth; the smaller dorsal tooth on the anterior hinge plate a thin low ridge, only 1/8 the length of ventral tooth and 1/8 the distance medially from its distal tip.

Combined exhalent and inhalent siphons formed in part from the fusion dorsally and medially of the inner muscular lobes of the posterior mantle edge; inhalent siphon not fused ventrally and the siphonal channel is completed by the adhesion of the ventral edges; although the siphon can be contracted into a very shallow siphonal embayment, there is no obvious development of siphonal retractor muscles from the base of the siphons extending anteriorly within the mantle; retraction appears to be entirely the concern of the internal siphonal musculature. Posteroventrally there is further development of the inner muscular layer into two rather broadly curving pads; these are almost certainly opposed in life and delimit a "feeding aperture" through which the palp proboscides and the tentacle extend. Tentacle large, single, inserted on the right side of the mantle ventral to the base of the

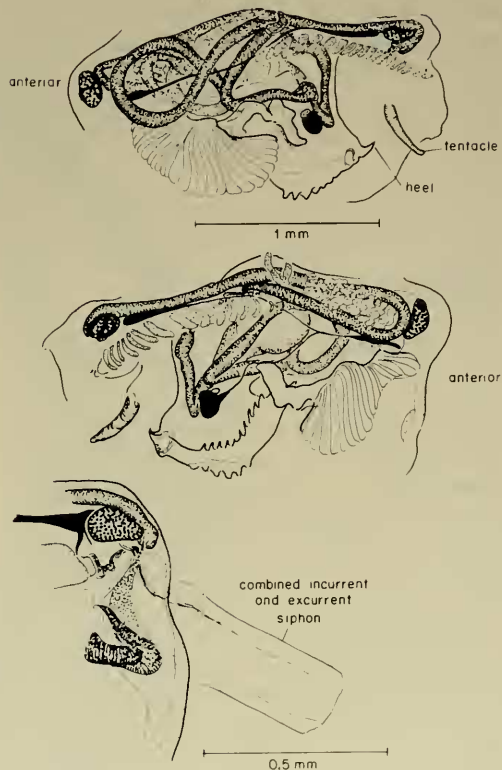


Figure 30. *Lametila abyssorum* Allen and Sanders. Right and left lateral, semidiagrammatic views of the body and mantle organs, with enlarged detail of the siphonal region.

siphons (Fig. 30). Anterior mantle sense organs small, but well defined. Very few gland cells are present except above the muscular pads. A well-defined ciliated tract is present between the pad and the gland cells, and probably corresponds to the site of formation of pseudofeces. Adductor muscles are equal in size, elongate and very small, and inserted close to the dorsal anterior and posterior limits of the mantle/shell; long axis of the posterior adductor muscle anteroposterior and that of the anterior muscle dorsoventral.

Gills horizontal to the anteroposterior body axis, both inner and outer gill filaments are broad, deep, and equal in size; posteriorly the axes join the septum dividing the exhalent from the inhalent si-

phon. Hypobranchial gland cells line the posterior part of the cavity laterally and overlie the posterior adductor muscle close to the base of the exhalent siphon. Gills without dense and long frontal cilia as in *Silicula* but are similar to those described for *Lembulus* (Yonge, 1939), having between 17 and 22 filaments on either side of each axis, depending on the size of the animal.

Palps relatively small, placed far anterior; mouth, although not abutting the anterior adductor muscle, is close to its ventroposterior edge. Palps, with 21–26 ridges, do not extend as far posteriorly as the junction of the foot-body, with the result that the palp proboscides are relatively long and narrow. Foot short, somewhat square in outline, its junction with the body far posterior and, in preserved specimens, lying clearly posterior to the palps with the heel frequently close to the aperture through which the palp proboscides are extended; sole of foot short with relatively few (14–16) fringing papillae. As in all protobranchs, the foot is divided. However, in preserved specimens, the two halves of the sole are open and form a flat ventral surface. There is a series of mucus glands at the edge of the foot, just medial to the papillae. "Byssal" gland well developed and just anterior to the short, pointed, posteriorly directed heel.

Oesophagus relatively short, it does not follow an anterior course towards the anterior adductor, but curves dorsally and posteriorly to the large stomach and combined style sac and midgut. Stomach simple with a shallow dorsal hood and nonridged sorting area; three broad ducts lead to the digestive diverticula. The course of the hindgut has no parallel within the protobranchs; it extends from the midgut to the anus passing from one side of the body to the other, several times, in front, behind, below and above the stomach. Essentially there are two loops on each side of the body (Fig. 31). From the junction with the midgut, the hindgut passes dorsally, forming a shallow U-bend behind the stomach before

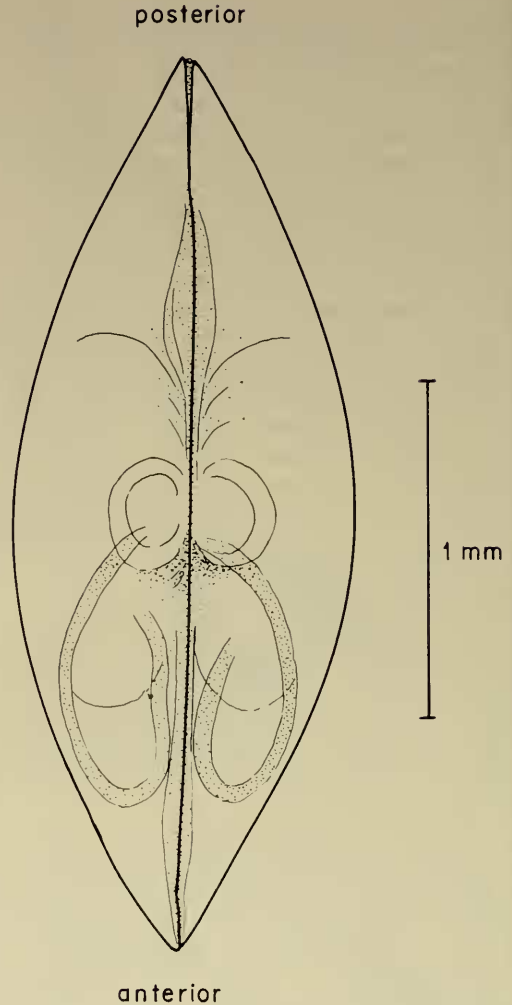


Figure 31. Dorsal view of a specimen of *Lometilo abyssarum*, showing the limits of the prodissoconch and anterior loops of the hindgut.

passing to the left side of the body. There it makes a short loop and then crosses to the right side of the body below the stomach to make a second loop that curves dorsally forward as far as the oesophagus before turning ventrally and returning to the left side below the stomach but anterior to the first cross, over from left to right. A third loop (the second on the left) is formed and extends forward as far as the anterior adductor muscle before turning back and

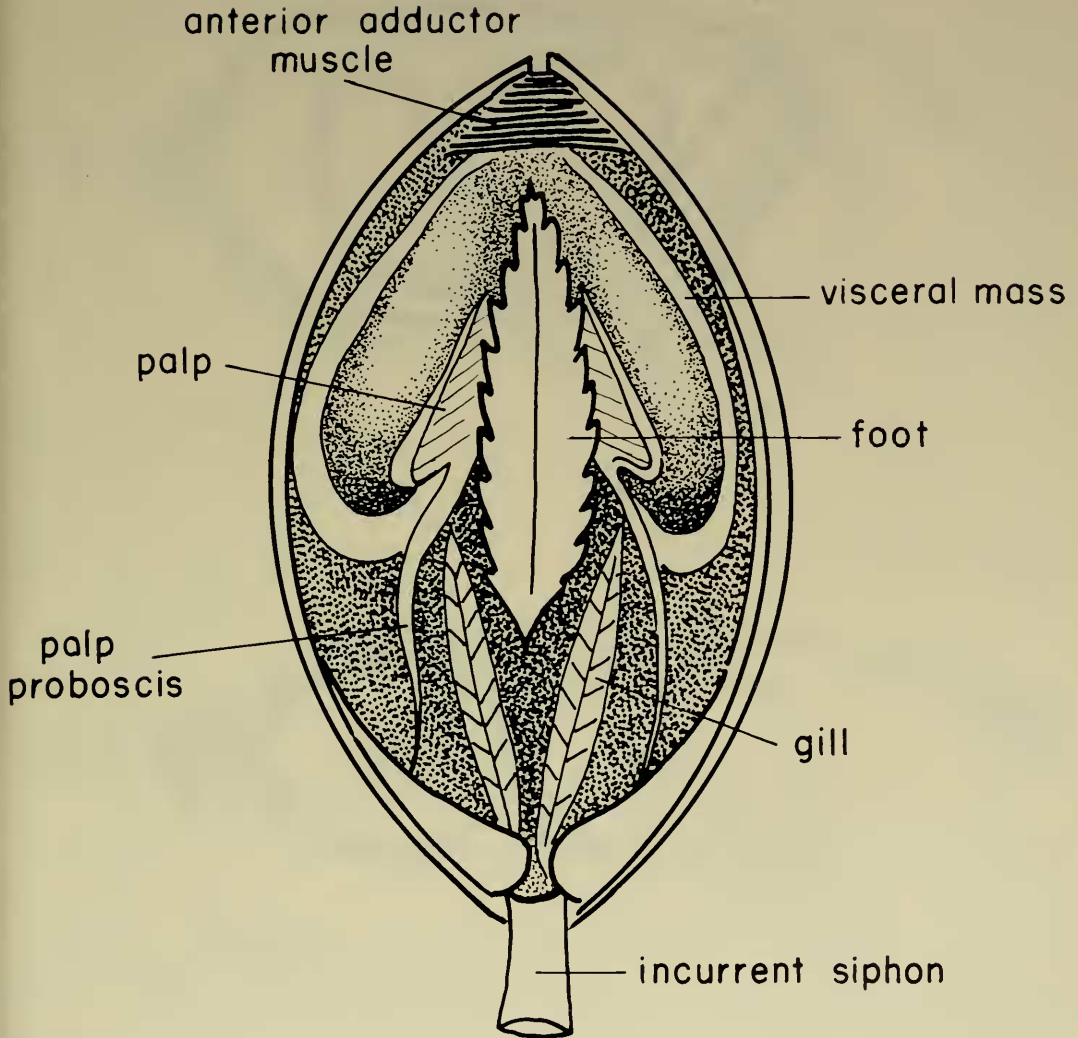


Figure 32. Diagrammatic ventral view of body and mantle organs of *Lametila abyssorum*.

taking a diagonal course from the ventral to the dorsal side of the body. The hindgut crosses again to the right side of the body where it forms the fourth (the second on the right) and last loop, which also passes forwards as far as the anterior adductor muscle before turning dorsally and medially to the anus (Fig. 33). The displacement of the mouth a short distance posterior to the anterior adductor muscle is no doubt a result of the two hindgut loops passing adjacent to the muscle. The globular stomach

and the lateral loops of the gut which have a relatively wide-diameter lumen (0.08 mm in a specimen 2.80 mm long) is reflected in the lateral extensions of the body and in the totally different body proportions as compared to *Silicula* (Fig. 32).

Nervous system characterized by elongate and cylindrical cerebral and visceral ganglia; large pedal ganglion positioned high in foot and has an associated pair of statocysts. Sexes separate; gonads lateral and peripheral within body.

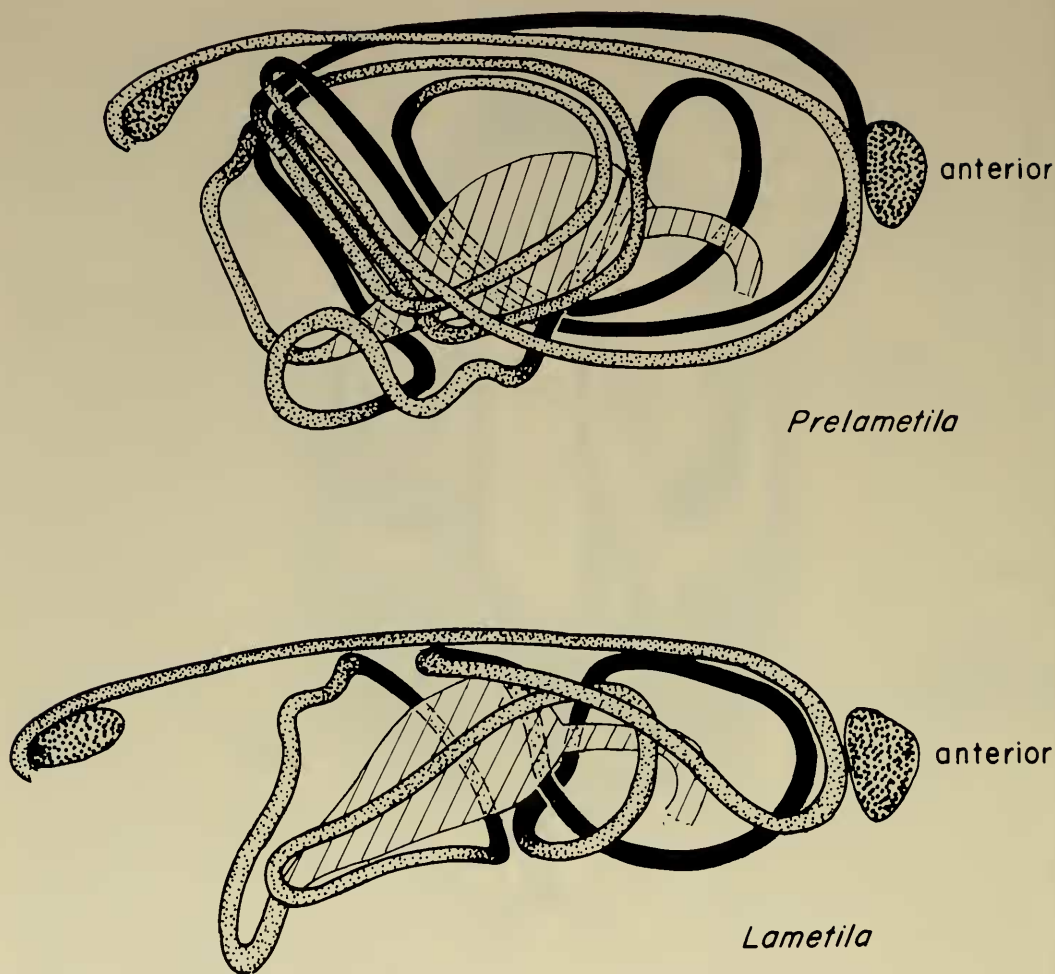


Figure 33. Comparison of the guts of *Lametila abyssorum* and *Prelametila clarkei*. Stippled section on right, and black sections on left of the stomach.

The 38 intact specimens of *Lametila* from Station 64 varied in length from 1.70 mm to 3.25 mm. Within this length range, there is no obvious height/length ratio change with increasing size and most values fall between 0.67 and 0.72 (Fig. 34). However, there is an obvious relationship between the position of the umbo along the dorsal shell margin and the shell length (Fig. 29). Measuring from the anterior end, among the smaller specimens, the umbo is slightly more than halfway to the posterior edge. With increasing size, the position of the umbo becomes progressively more anterior

so that, in the largest specimens, it is positioned less than halfway to the posterior margin. This is probably the result of a tangential component of shell growth (Owen, 1952) and thus, although the height/length proportion remains relatively constant with increasing size, differential growth is reflected in the progressively more anterior positioning of the umbo on the dorsal shell margin.

The valves of *L. abyssorum* usually are sufficiently transparent to sex the specimens and approximate their state of maturity. Sexes are separate. Three groupings (the

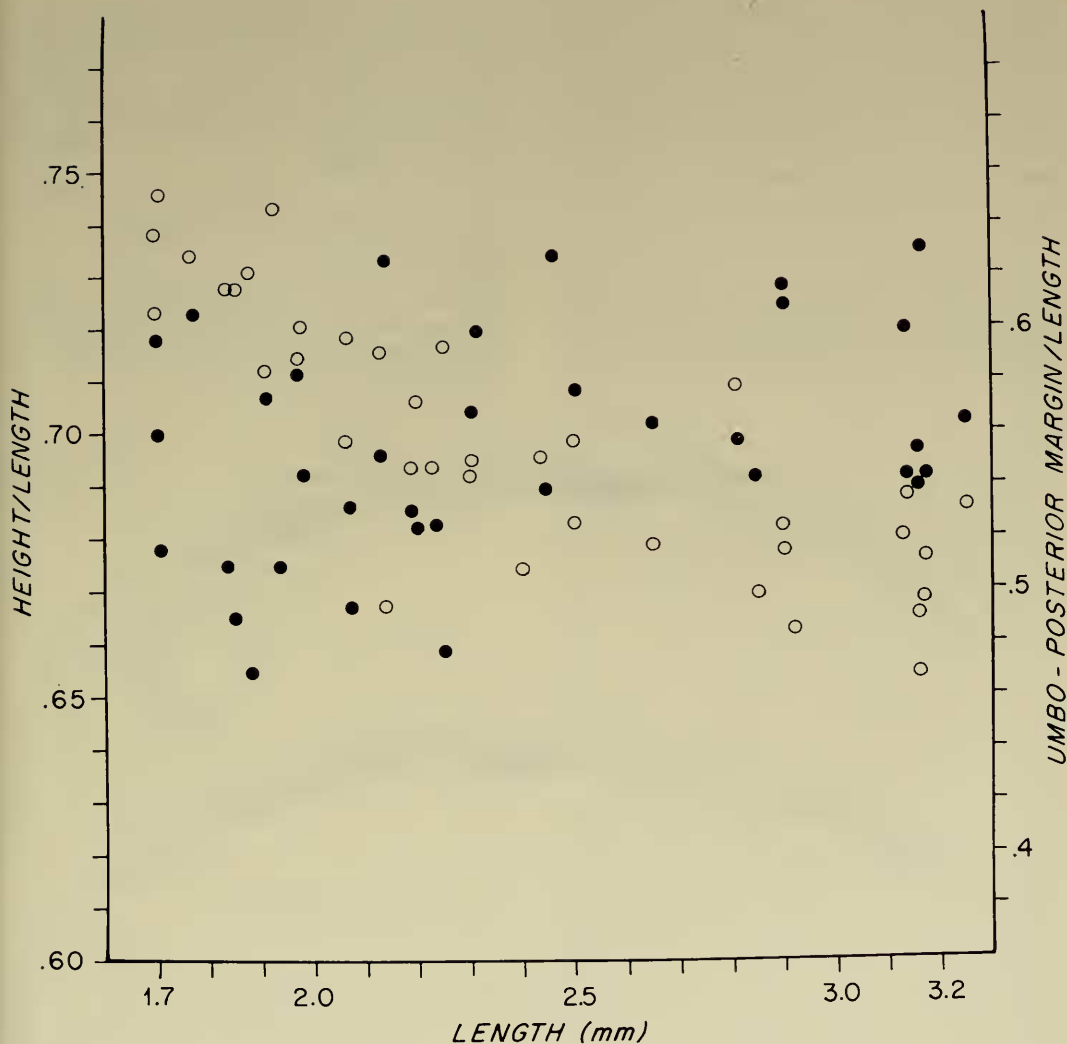


Figure 34. *Lametila abyssorum* Allen and Sanders. Graph showing height/total length (●) and umbo to posterior margin/total length (○) plotted against total length.

immature and incipiently matures, the females, and the males) can be separated with relatively little overlap (Fig. 35). The immature-incipiently mature category (10 individuals) are mostly less than 2.0 mm in length. The females form the numerically most abundant group, 20 individuals, with but three specimens smaller than 2.0 mm and two specimens greater than 3.0 mm. There are only six males in our sample, yet they are among the largest representatives; four specimens exceed 3.0 mm while two

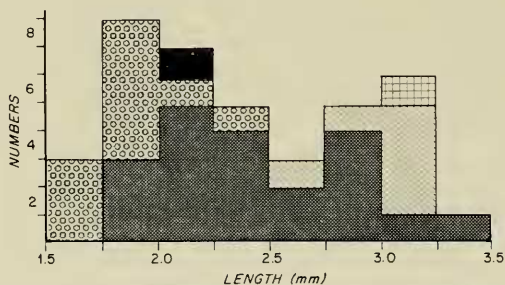


Figure 35. Size frequency distribution of specimens of *Lametila abyssorum* sorted according to sex and gonadal development.

are smaller. Two specimens cannot be categorized, a single larger spent individual (3.13 mm) whose sex is indeterminate and a specimen (2.07 mm) whose shell is too opaque to discern the soft parts within.

Genus *Prelametila* new genus

Type species: *Prelametila clarkei* Allen and Sanders new species

Hinge teeth composed of both elongate and taxodont types; adductor muscles unequal in size; body occupying much of the mantle cavity; hindgut forming 4 loops on

the right side of the body; the posterior end of the foot rounded. This genus differs from *Lametila* in the possession of taxodont teeth, more than two hindgut loops on the right side of the body, and by its heteromyarian condition.

***Prelametila clarkei* new species**

Figures 36–38

Type locality: ATLANTIS II, Cruise 60, Station 247, in 5209–5227 m. Holotype: MCZ 271975.

Depth range = 4382–4405 m to 5209–5227 m.

Records: Table VI.

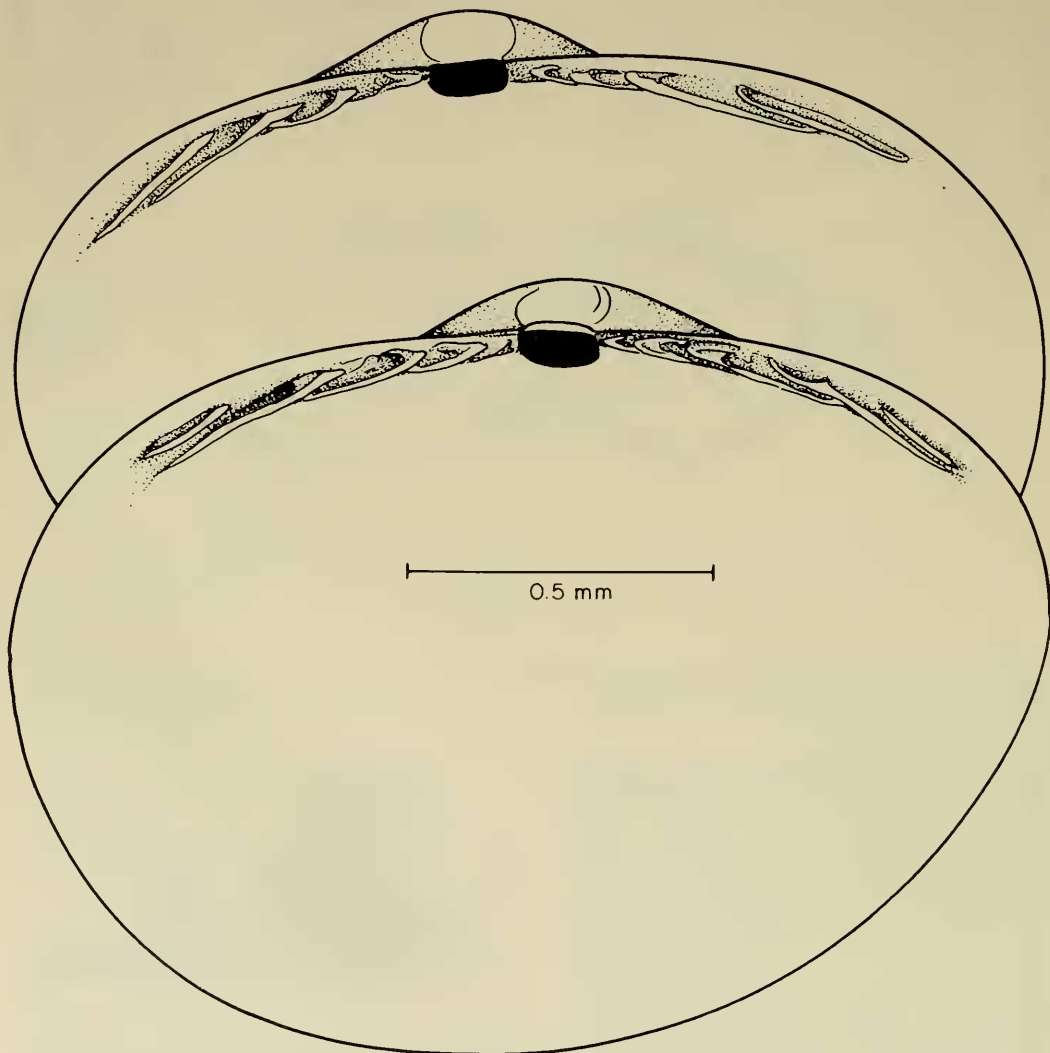


Figure 36. *Prelametila clarkei* Allen and Sanders. Internal views of left and right valves.

TABLE VI. RECORDS FOR *Prelametila clarkei* NEW SPECIES.

Cruise	No.	Sta.	Depth (m)	Specimens	Latitude	Longitude	Gear	Date
ARGENTINE BASIN								
Atlantis II	60	247	5209– 5227	239	43°34.6'S– 43°33.0'S	48°58.0'W– 48°51.1'W	ES	17.3.71
Atlantis II	60	242	4382– 4405	29	38°16.9'S	51°56.1'W	ES	13.3.71

Shell small, less than 2.5 mm in length, smooth, semitransparent, not markedly fragile and with fine concentric striae; height about 0.43 times length (Figs. 36, 37); subovate and smoothly rounded in outline; the proportionately short dorsal margin gently rounded behind and more strongly curved in front of the umbo and forming raised crests along both the an-

terior and the posterior dorsal midline, posterior crest longest; posterior margin broad and smoothly rounded with the ventro-posterior margin longer than the dorsoposterior; anterior shell margin is narrow and strongly curved, ventro-anterior margin longer than the dorso-anterior; ventral margin not long, but strongly curved; umbo moderately large, elongate with a flattened medially directed beak; umbo just anterior of the midline being between 47 to 49 percent of the length distance from the anterior edge of the valves; shell gape not visible from the dorsal margin; shell height greatest immediately behind umbo.

Hinge plate long and moderately thick; posterior hinge line curving gently downwards, that of the anterior hinge plate more precipitous; ligament internal, amphidetic, oblong and large, but proportionately smaller than in *L. abyssorum*. Hinge teeth of both elongate lateral and taxodont types with gradation between the 2 forms; most proximal 2 teeth typically taxodont, proportionately small and with the dorsal arm nearly as long as the ventral; next most distal tooth the longest, its dorsal arm much reduced, the ventral arm elongate and extending laterally to occupy the entire hinge line below the terminal tooth on the left valve and half the hinge line under the terminal tooth of the right valve; distal tooth elongate, lacking a dorsal arm, and obliquely parallel to the hinge line; distal tooth on the right valve about 1.6 times longer than that on the left.

The four specimens of *P. clarkei* that were picked from the sample aboard ship vary from 1.96 mm to 2.09 mm in total length. The height/length ratio is 0.72–0.74 and the width/length ratio, 0.43; the posi-

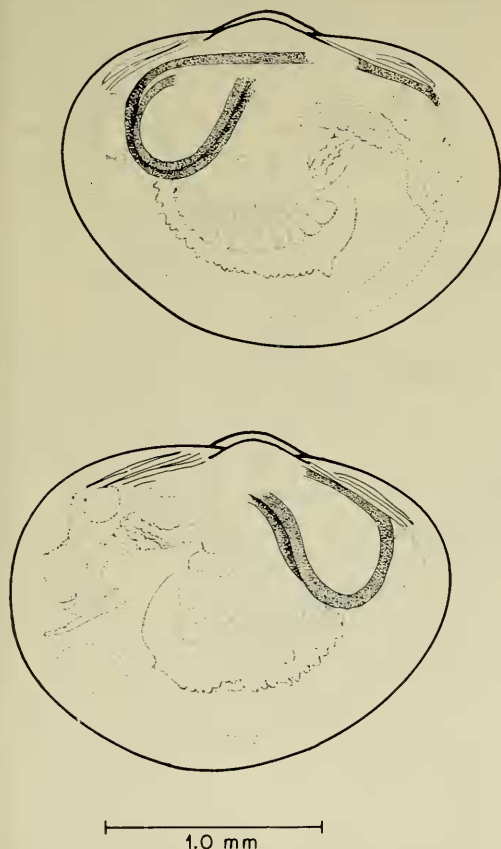


Figure 37. *Prelametila clarkei* Allen and Sanders. Right and left lateral view of an intact specimen.

tion of the umbo is between 46.8 to 48.8 percent of the total length measurement from the anterior edge.

Inhalent and exhalent siphon combined and can be retracted into a shallow siphonal embayment, similar to *Lametila*; inhalent siphon not fused ventrally. Ventral and posterior paired extensions of inner muscular layer separate a posterior feeding aperture through which the palp proboscides and tentacle extend. Tentacle placed to the right and more slender and pointed than that of *Lametila*. Small but well-defined anterior mantle sense organs present. Adductor muscles somewhat larger than those of *Lametila*; they differ in size, the anterior being approximately twice as large as the posterior. Gills similar in position and extent to those of *Lametila* but with only 10 filaments on each side of the axis. Palps fan shaped, relatively broad, lying somewhat further back in the mantle cavity than in *Lametila*, because the mouth itself is further from the anterior adductor muscle; 15 palp ridges present in each of the four specimens comprising our collection (Fig. 38).

Course of gut similar to that of *Lametila*; however, it differs in having two additional loops formed by the hindgut on the right-hand side of the body, giving a configuration that is the most complex so far encountered in the protobranchs. The characteristic first section of the hindgut passes dorsally behind the stomach forming a single U-bend; the hindgut then returns to the ventral side of the style sac via the right side of the body, making a single posterior loop before passing to the left-hand side of the body ventral to and in front of the stomach. The posterior loop is not as large as that in *Lametila* but the basic course is, nevertheless, the same. The two additional loops that are present on the right-hand side in *Prelametila* are penultimate to the final loop on the *left* side which extends forward to the anterior adductor muscle. The two additional loops to the right encircle the stomach but do not pass close to the

adductor (Fig. 33). As in *Lametila*, the last loop of the hindgut is on the right-hand side of the body and extends forward to the posterior edge of the anterior adductor.

Nervous system similar to *Lametila*. Foot, which has a very small, posteriorly pointing triangular heel, carried more anterior than in *Lametila* and somewhat extended posteriorly as in, but not to the same extent as, *Silicula*. "Byssal" gland moderately small.

There are too few specimens to determine sex ratios, gametogenesis, egg size, and egg numbers.

This species is named in honor of Dr. Arthur H. Clarke, Jr., of the National Museum of Canada, student of the deep-sea Mollusca, for his contributions to this field.

On the basis of shell morphology (e.g., amphidetic ligament, rounded subovate shape and elongate, oblique, lateral teeth [Fig. 2]), *Phaseolus ovatus* might best be included as a separate genus within the Lametilidae. However, in the absence of any knowledge of the soft parts, we prefer to defer making a decision (see p. 266).

FUNCTIONAL MORPHOLOGY OF THE SOFT PARTS OF THE SILICULIDAE AND LAMETILIDAE

From consideration of the form of the soft parts of *Silicula*, and deductions about its habits, it is clear that the following morphological features are of great functional significance: 1) the elongate and extremely slender shape, 2) the tubular exhalent siphon, 3) the inhalent aperture formed by the apposition of the somewhat extended inner muscular lobe, 4) the extremely elongate palp proboscides which, in many preserved specimens, extend out of the *inhalent* aperture, 5) the elongate and deeply cleft foot with extremely well-developed retractor muscles, 6) the curvature of the body/foot axis anteriorly through 90°, 7) the posterior extension of the foot and body, 8) the displacement of the mouth posteriorly, 9) the anterior position of the posterior adductor muscle, 10) the heavy ciliation of the frontal surface of the gill, and 11) the posi-

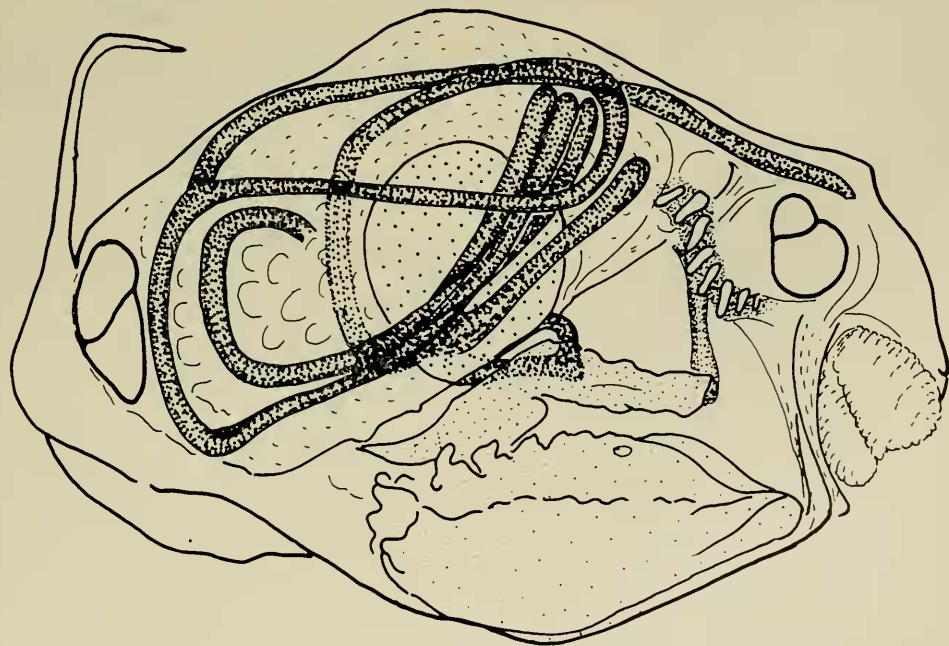
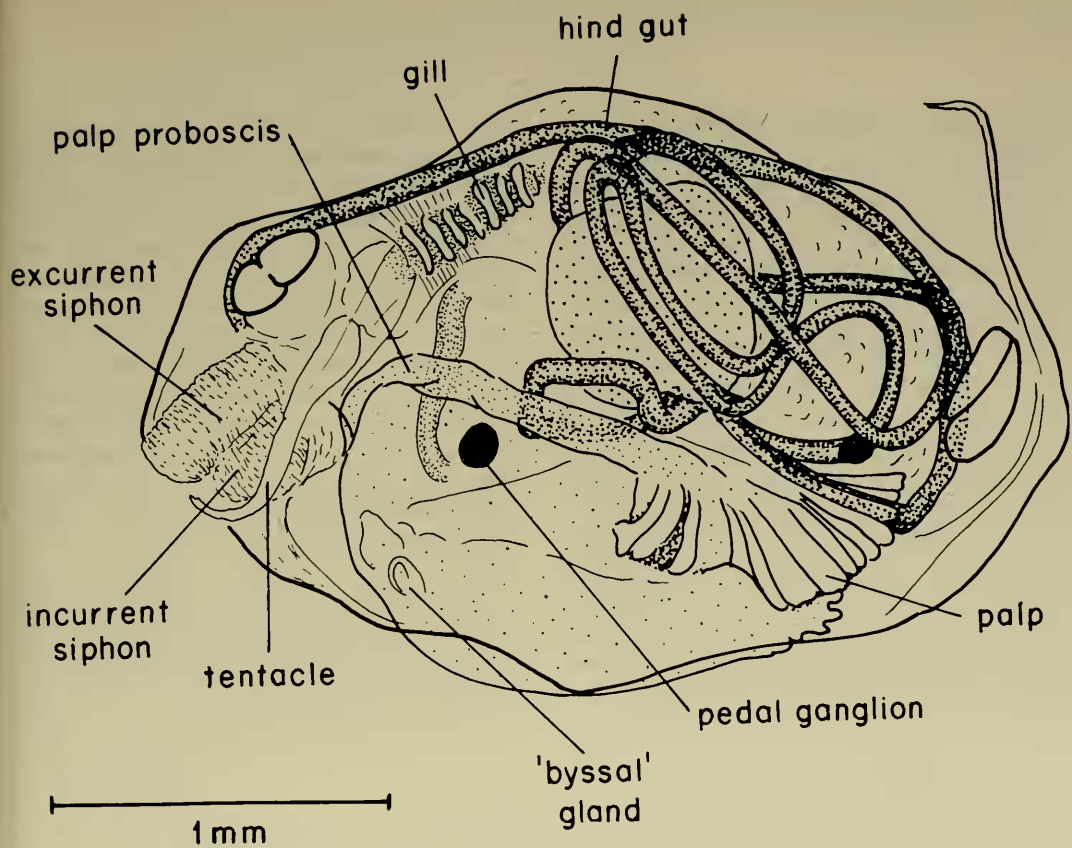


Figure 38. *Prelametila clarkei* Allen and Sanders. Right ventrolateral and left dorsolateral, semidiagrammatic views of the body and mantle organs.

tion of the stomach. Conclusions to be drawn from this array are that *Silicula* can burrow rapidly; that they orientate within the sediment so that the anteroposterior axis is vertical; that, when feeding, the posterior rim of the extended inhalent aperture is level with the sediment surface and the palp proboscides pass through the aperture; and, that the exhalent siphon can be extended at least as far as the limits of extension of the palp proboscides—there is no evidence of coprophagy so the fecal rods probably are deposited beyond the range of the palp proboscides (Fig. 39).

By correlating form and habit and comparing the morphology of the *Silicula* species, it is possible to draw some conclusions as to evolution in the genus. Progressive, posterior elongation of the body has occurred, the extremes being *S. flatovae* on

the one hand and *S. mcalesteri* on the other. The more elongate the species the better defined is the exhalent siphonal embayment. We believe that the animal takes up a vertical position* in the sediment, and that this relates to the form and disposition of the foot. Elongation of the foot and the interior turn of its axis through 90° tends to limit the amount of body space available for the gut, digestive diverticula, and the gonads. This limitation compensates the posterior extension of the body/foot. In addition, lateral compression of the body itself limits the available space for body organs. The very shortened gill filaments (the outer

* Note that the hinge line is straight. In other elongate genera, e.g., *Poroleda* and *Propeleda*, with a concave posterior dorsal margin, the anteroposterior axis of the shell may well be diagonal to the sediment surface (Fig. 39).

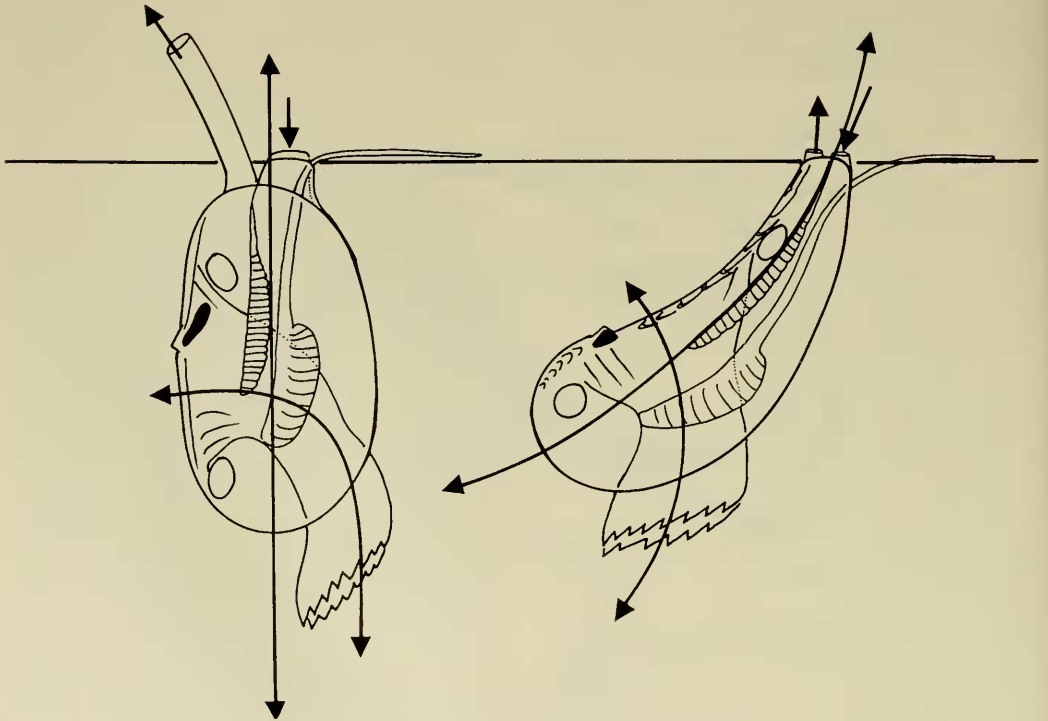


Figure 39. Comparison of hypothetical attitude in life of *Silicula* and *Propeleda*. Arrows indicate anteroposterior and body axes.

filaments being half the size of the inner) are modifications to the thinness of the body. The foot, when retracted, lies in the anterior part of the mantle cavity and this may be related to the posterior position of the mouth. However, there is functional reason in the mouth being posterior in position in an elongate animal in which the food arrives posteriorly. In this context the densely ciliated gills should be mentioned, for although a protobranch, it is likely that these convey food material towards the mouth. It is also significant that, although abyssal, these species appear to be selective feeders and, in most animals examined, the stomach and the digestive diverticula are packed with whole diatom frustules of a similar size. The morphology of *Silicula*, in fact, parallels other dimyarian bivalves that are elongate and very active burrowers within soft sediments, e.g., *Pharella* (Owen, 1959), *Pharus* (Yonge, 1959), and *Siliqua* (Yonge, 1952).

It has been shown in the genus *Abra* (Allen and Sanders, 1966), of which there is a series of species showing vertical zonation, that those species from deep water have much longer hindguts than those in shallow water. In general *Silicula* is similar, thus *S. rouchi* and *S. mcalesteri* have much shorter hindguts than *S. fragilis* and *S. filatovae*. It might be expected that *S. fragilis* with its twice-looped gut would occur in water deeper than that in which *S. filatovae*, with one loop, occurs. However, the reverse appears to be the case. It may be that size also has to be taken into account, that small species have relatively larger hindguts than larger species of the same genus at the same depth range. It is true that tiny abyssal protobranchs have exceptionally long hindguts—*vide* *Pristigloma* and *Microgloma* (Sanders and Allen, 1973), and that the relatively longer hindgut of *S. fragilis*, as compared with *S. filatovae*, is but a reflection of size difference.

The exhalent siphon and inhalent aperture are extended by hydrostatic pressure,

and retracted by longitudinal musculature. The siphon is constructed as two cylinders of circular collagen fibers with a lumen between divided into compartments by transverse fibers, thus forming elongate channels approximately rectangular in cross section. Within the channels run longitudinal muscle fibers on the inner peripheral faces. No major nerves pass up the siphon; innervation presumably is brought about by fine fibers close to the walls of the channels. It appears that the palp proboscides are extended and contracted in a similar way, for there is a similar system of muscles, collagen fibers and spaces; however, here there is a very large nerve passing medially along the length of each palp proboscis (Fig. 22).

On morphological grounds it seems likely that the habits of *Lametila* are very different from those of *Silicula*. 1) In *Lametila* and *Prelametila* the respiratory and feeding activities appear to be completely separate, whereas in *Silicula* they are combined. 2) *Silicula* is laterally compressed, elongate, and designed for rapid vertical burrowing, yet it can remain in contact with the surface through the use of the extended inner muscular folds of the posterior inhalent aperture. However, *Lametila*, being more globose, is not especially designed for rapid burrowing and, because it has an inhalent siphon, need not necessarily maintain a vertical position. There is no evidence that the mantle edge of the feeding aperture can be extended, even though it can open separately to the pedal gape and thus allow the palps and tentacle to be extended into the substratum. 3) In the Lametilidae the palps are far anterior and there is no evidence that the gills are associated with the palp proboscides in any way. 4) The foot in *Lametila* and *Prelametila* is totally different in shape, position, and attitude to that in *Silicula*. It is broad, posteriorly situated, and the two halves of the sole are separated to form a flat sole. The body axis is vertical and the foot is, no doubt, extended ven-

trally and is designed for horizontal progression.

FUNCTIONAL MORPHOLOGY OF THE HARD-PART ANATOMY OF THE SILICULIDAE AND LAMETILIDAE

a) Siliculidae

The light-shelled, razor-thin, elongate form of the Siliculidae together with its large, powerful foot are indicative of an actively burrowing mode of life. The extensive gape along the dorsal shell margin, a feature unique among the protobranchs, permits greater flexibility in the opening and closing of the valves. Such opening and closing phases, when repeated rhythmically, form a pumping activity. Because the water volume between the valves is small in these markedly flattened forms, it is readily expelled as the valves come together during the excurrent phase. On the alternate separating or incurrent phase, water is drawn in by the resulting vacuum, which additionally creates considerable suction that greatly enhances burrowing activity.* The dorsal gape itself is made possible by the characteristic siliculid elongate teeth paralleling the hinge plate rather than by the more typical series of smaller taxodont teeth relatively perpendicular to the dorsal shell margin of most protobranchs. The proportionately anterior position of the posterior adductor muscle is another requisite for the pronounced dorsal gape. With contraction and expansion of the adductors, the elongate teeth roll against one another like the hinges of a door. There is one potential weakness in the system. The tooth configuration on the weak hinge plate is such that it might be displaced as a result of strong pumping activities and cause shearing of the two valves. We believe that the stability imposed by a large internal ligament is an effective countermeasure. The elongate shape of the siliculid ligament and its epis-

* Such pumping activity could also assist in feeding. However, we have no evidence for this.

thodetic form are logical responses to the greatly inequilateral shape of the valve (*i.e.*, most of the animal is posterior to the umbo) brought about by the extension of the shell posteriorly.

b) Lametilidae

The relatively equilateral shell, the more inflated form, and small foot cumulatively demonstrate that the Lametilidae, unlike Siliculidae, are not active burrowers. Rather, they are relatively sedentary forms possibly lying in a horizontal or near horizontal position close to the sediment surface. The posterior adductor muscle, as compared to *Silicula*, is close to the posterior margin of the shell with the result that the dorsal gape is very small in *Lametila* and restricted to the most posterior part of the dorsal margin. There is no gape in *Prelametila*. The small adductor muscles, as in *Pristigloma alba* (Sanders and Allen, 1973), can be related to the combination of a fragile shell, more tumid form, weak hinge plate, and lamellar, or elongate, teeth. Despite the similarly fragile shell, the proportionately larger adductor muscles in *Silicula* are possible because the flattened shell and reduced lateral mantle space are structurally stronger than the inflated one. Furthermore, since pumping activities are probably more critical in *Silicula*, its adductor muscles must be larger.

Unlike *Silicula*, the tooth configuration in *Lametila* differs in the two valves. The dorsal tooth on both the anterior and the posterior hinge plate of the left valve is very small and is situated distally. The same tooth on the right valve is considerably longer, arising about one-third the distance from the medial point of the hinge plate and extending distally. Unlike that in *Silicula*, it lies flush against the ventral tooth except at the distal hinge margin where it diverges, slightly on the anterior hinge plate and somewhat more extensively on the posterior hinge plate, to accommodate the dorsal tooth of the opposite valve. Thus only the ventral teeth are capable of

rolling against each other, while the dorsal teeth tend to lock the valves together.

With a weak hinge plate and shallow, elongate teeth (as well as weak taxodont teeth in *Prelametila* which are confined medially on the hinge plate), there is a tendency of the valves to shear. Rigidity and prevention of possible shear is achieved through the elaboration of a large ligament. The shell of *Lametila* is equilateral, and the ligament is internal and amphidetic. The ligament is bean-shaped in outline and wedge-shaped in cross section, being correlated with the more tumid form of the shell. Because of the relatively massive ligament size, the short, medial portion of the hinge plate supporting it is appreciably thickened.

Only the distal teeth of *Prelametila* approximate the *Lametila* tooth configuration. The gradual transition from medial taxodont to distal elongate teeth imposes a somewhat different set of relationships among the components comprising the hard-part morphology. The proximal chevron-shaped taxodont teeth lock the two valves together (Fig. 36) and the small dorsal gape that persists in *Lametila* is absent in *Prelametila*—only the distal elongate teeth are able to roll against one another. The tendency of the valves to shear is thus reduced. In relation to this, the oblong, amphidetic internal ligament, although relatively large in *Prelametila*, is proportionately smaller than in *Lametila*. Similarly, the larger adductor muscles may be a direct response to the less fragile and heavier shell of *Prelametila*.

DISTRIBUTION PATTERNS

The two deep-water siliculids in our collections are either predominantly or exclusively abyssal. On the well-collected Gayhead-Bermuda transect in the North America Basin, *Silicula fragilis* has been taken at three stations, two from depths between 3800 and 3900 meters and one (single specimen) at nearly 2900 meters. Elsewhere in the Atlantic we have col-

lected this species at a depth of 1922 m in the West Europe Basin and in the Argentine Basin at 3305–3317 m. Earlier records for *S. fragilis* are from two further stations in the West Europe Basin (Jeffreys, 1879) at 1493 and 2223 m. Thus *S. fragilis* appears to be an Atlantic species of the deeper slope and abyssal rise depths.

A single large specimen of a siliculid that corresponds closely to *S. fragilis* was taken from a depth of between 4469–4476 m in the Argentine Basin. This was picked from the Epibenthic Sled soon after it came aboard. The samples from the cruise are yet to be processed and we choose for now tentatively to exclude this specimen from the species *S. fragilis* until additional representatives are available for a careful appraisal. Our equivocation is due to a reluctance either to dissolve the shell to study the soft-part anatomy or, alternatively, destroy the soft parts with sodium hypochlorite to study the inner shell morphology. Further reasons for caution are that the specimen is more than twice as large as any known representative of *S. fragilis*, and that it comes from a depth that is 640 m greater than any known record of the species.

Silicula filatovae is a deeper-dwelling species than *S. fragilis*. On the Gayhead-Bermuda transect, its shallowest record is from 3826 m. *S. filatovae* was present in 9 of the 17 stations from that depth to 5042 m and overlaps *S. fragilis* at the shallow end of its range. Both species were taken at Station 85 at a depth of 3834 m. Other than the Gayhead-Bermuda transect, our records for *S. filatovae* are from a single station in the Cape Verde Basin at 3861 m, and three stations in the Angola Basin at 4559–4566 m to 4612–4630 m. These records suggest that *S. filatovae* is broadly distributed throughout the abyssal depths of the Atlantic.

At no station where the quantitative assessment has been completed does *S. filatovae* or *S. fragilis* form a significant percentage of the protobranch fauna. *S. filatovae* contributes almost 4 percent to

the protobranch fauna at one station and 1 percent or less at the remaining six. Similarly, at the four stations where it was found, *S. fragilis* comprises 8.5 percent of the protobranchs at one station and 1.0 percent at the other three.

The third representative, *Silicula mcalesteri*, is found at much shallower depths. We have taken it at only one locality in 275–305 m off Uruguay. *S. mcalesteri* is an upper slope and possibly an outer shelf species of the Southwest Atlantic. Despite the fact that the sample from which the present specimens were extracted has yet to be processed, the obvious abundance of *S. mcalesteri* in that sample clearly indicates that it will be an important numerical constituent of the protobranch fauna.

Both representatives of the Family Lametilidae in our collections are totally abyssal. *Lametila abyssorum* has a sharply defined depth range. On the Gayhead-Bermuda transect it is found from approximately 2500–3900 m and is a species constituent at five of the seven stations from that depth interval. The two remaining records for the species are in the eastern Brazil Basin near the mid-Atlantic ridge at depths of 3459 and 3730–3783 m. When *L. abyssorum* is present in a sample, it is often one of the most abundant species. At the seven recorded stations, the bivalve formed 61.33, 31.0, 13.04, 7.76, 1.25, 0.94 and 0.72 percent of the protobranch fauna.

Prelametila clarkei was present at the two deepest stations on the Argentine Basin transect in 4382–4405 m and 5209–5227 m. Thus, *P. clarkei* may be categorized as a lower abyssal species of the Argentine Basin.*

IMPLICATIONS FOR THE FOSSIL RECORD

The protobranchs appeared early in the fossil record during the mid-Cambrian together with another, supposedly nonprotobranch, bivalve group, the Actinodonta. The latter had either radiating cardinal teeth in the region of the umbo or elongate lateral teeth parallel to the hinge line, or both, in various combinations, rather than the chevron-shaped taxodont teeth of the nuculoids. The modern, but enigmatic, family Nucinelidae typically has both cardinal and lateral teeth. Yet, on the basis of soft-part anatomy, they are protobranchs whose nearest known living relatives are the Solemyidae (Allen and Sanders, 1969). We have included them with the Solemyidae within the order Solemyoidea of the subclass Protobranchia (Sanders and Allen, 1973). Furthermore, lamellar, elongate, and overlapping rather than taxodont teeth are present in at least one species of nuculacid protobranch, *Pristigloma alba* (Sanders and Allen, 1973). In the present paper, we have shown that within the remaining major protobranch grouping, the superfamily Nuculanacea, two of its constituent families bear elongate, overlapping teeth parallel to the hinge plate rather than exclusively chevron-shaped taxodont teeth. Yet, another form, the Pliocene fossil *Phaseolus ovatus* Seguenza also had elongate and overlapping teeth on both the anterior and posterior hinge plate (Fig. 2). Modern specimens that have been included under this name are clearly not the same species. They lack the elongate teeth and instead have a few taxodont teeth that are very small and rounded or oblong in shape, not unlike the microglomids (see Sanders and Allen, 1973).

On the basis of such accumulating information, it is becoming increasingly evident that the paleontologist must interpret the early bivalve fossil record with considerable caution. Lack of taxodont teeth *per se* can no longer be used as the prime cri-

* We have recently found a second species of *Prelametila* in three samples from the Argentine Basin that ranged in depth from 3305–3317 to 4382–4405 m. The same species has also been recovered from a sample collected at 4592–4597 m depth in the Angola Basin. A description of this new form will be included in a later paper in the series.

terion for excluding fossil bivalves from the subclass Protobranchia. In fact, there is no way of demonstrating that the early actinodonts could not have been protobranchs.

For example, the Silurian actinodont, *Actinodonta cuneata* (Phillips and Salter, 1848), was strikingly similar to the extant Siliculidae (Fig. 40). Both have the elongate and apparently flattened shell form, a similar small, low umbo, and, to judge from the hinge plate configuration under the umbo, *A. cuneata* must have had a siliculid-like internal ligament that was opisthodontic and elongate.

Pertinent to this discussion are observations of Vogel (1962) that the oldest toothed bivalves, from the base of the mid-Cambrian of Spain, did not have taxodont but instead had elongate teeth parallel to the hinge plate. These were bivalves with an equilateral shell and either one or two elongate teeth on both the anterior and the posterior hinge plates. Vogel (1962) created the actinodont genus *Lamellodonta* to include them. From such forms he derived the remaining actinodonts and, eventually, the other major bivalve taxa. The modern analogue to the *Lamellodonta* is *Lametila abyssorum*, for it has the same transversely oval shell and two elongate teeth on both the anterior and posterior hinge plate that are parallel to the hinge line.

It must be clearly stated, however, that we are not claiming extreme primitiveness for the Lametilidae and Siliculidae. We

cannot provide the evidence for a suite of primitive soft-part characteristics that can be associated with the elongate teeth. Instead, the soft-part anatomy shows that both the Siliculidae and Lametilidae are typical nuculanacids.

Yet, even in the distant Cambrian, the protobranchs (and actinodonts) radiated, diverged, and diversified so that they may have been hardly more "primitive" than their modern descendants. In the absence of the later-evolving major bivalve taxa, there were numerous habitats to exploit, a strong impetus for evolutionary change. For example, *Actinodonta cuneata*, with its siliculid morphology, including a probable razor-thin shape and large powerful foot, may well have been an active burrower. Alternatively, the rounded, massive-shelled taxa were relatively immobile surface or near surface forms. A modern analogue is the nonsiphonate *Tindaria*.

Elongate teeth were derived more than once from taxodont teeth or *vice versa*. The presence of the elongate tooth configuration among representatives of both the orders Solemyoidea and Nuculoidea as well as the two superfamilies composing the Nuculoidea provide unequivocal evidence for its multiple and independent origin. Such a tooth pattern might be derived merely by the elongation of one arm of a chevron tooth and the reduction of the other. Alternatively, the elongate tooth can give rise to a taxodont tooth by developing a process and then foreshortening the main axis. The teeth on the posterior hinge plate of *Pristigloma nitens* represent a possible transitional stage (Sanders and Allen, 1973). Of even greater relevance is the documentation in the present paper of the tooth pattern in *Prelametila clarkei* which represents an almost ideal intermediate stage. The medial teeth are taxodont, the distal teeth elongate, and the teeth in-between have a greatly foreshortened dorsal and a considerably elongated ventral arm.

This constant progression distally from the taxodont to the elongate tooth config-



Figure 40. *Actinodonta cuneata* Phillips. Lateral view of inside of left(?) valve. Redrawn from Phillips and Salter (1848).

uration is even more continual if we consider the teeth on both valves together. Since any given tooth on the right valve inserts more medially than its counterpart on the left valve, *i.e.*, tooth 2 on right ($T_2R.V.$) as compared to tooth 2 on left valve ($T_2L.V.$), it is slightly more taxodont in structure. Beginning with the distal elongate tooth on the right valve, the constant trend medially towards the taxodont morphology is as follows: $T_4R.V. \rightarrow T_3L.V. \rightarrow T_3R.V. \rightarrow T_2L.V. \rightarrow T_2R.V. \rightarrow T_1L.V.$ (see Fig. 36).

SHELL DIMENSION RELATIONSHIPS

We have observed that the shell shape of many species of deep-sea protobranchs changes as the animal grows, and *Silicula* is no exception. While there is much individual variation, when height/length ratio is plotted against length, there is a continuous shift to lower ratios with increasing length, *i.e.*, the shell elongates as it grows. This is least apparent in *S. filatovae*, and it is significant that this species is the least extended posteriorly with the umbo relatively central in position. *S. fragilis* and *S. mcalesteri* show much greater elongation with increasing size, particularly *S. fragilis* (Fig. 5). In both cases the small umbo is anterior in position and, when the ratio—distance from the anterior shell margin to the umbo/length—is plotted against length, there is a comparable shift to lower ratio values with increasing length, confirming that much of the elongation is due to posterior growth.

Similar measurements taken for *Lametila* show a different picture (Fig. 34). The height/length relationship of this species shows little change with increasing size; if anything there is a slight tendency for the ratio value to increase with increasing length. In contrast the umbo/length to length plot is very similar to that in *Silicula*. We believe that the change in position of the large umbo relative to length is a consequence of a relatively large tangential component of shell growth (Owen, 1952)

in association with a large umbo and globular form (a relatively high value for the angle of the logarithmic spiral).

These changes in shape are what might be expected if our conclusions on the functional morphology and habits of these animals are correct.

REPRODUCTION

Unlike the condition found in the Pristiglomidae (Sanders and Allen, 1973), sexes are separate in the Siliculidae and Lametiliidae. As many of the shells are transparent we were able to determine the degree of development of the gonad and, from experience, found it convenient to adopt a scale of maturity (0–8), the limits being (0), immature specimens in which no development of the gonads could be seen in lateral view by means of a stereo binocular, and (8), fully ripe animals in which the whole of the body organs were overlain (laterally) with mature gametes. (We have no evidence that the scale of maturity represents an arithmetic progression.) In all species of the Siliculidae and Lametiliidae the gonads develop ventrolaterally along a narrow band in the body below the digestive gland and lower sections of the hindgut and also below the heart. With increasing maturity the gonads enlarge and extend dorsally until all available space within the body is occupied (Table II).

In all three species of *Silicula* in which gonads were examined, males and females were in approximately equal numbers. However, it is evident that, although the sizes overlap, males are on an average larger than females and the larger specimens have the more mature gonads. The overall picture of maturity differed according to species. In the shallow-water representative *S. mcalesteri* (Sta. 280, 1971), of 49 specimens examined only one individual showed no sign of gonadal development and in one other it was impossible to sex the animal from external examination (classified as incipient (1)). The 47 remaining specimens were maturing, several

TABLE VII. EGG AND PRODISOCONCH SIZE AND EGG NUMBER FOR 5 SPECIES OF PROTOBRANCHS.

	Max. Egg Size (μ)	Prod. Size (μ)	Egg Number
<i>S. filatovae</i>	70	290-310	c2000 (4 mm t.l.)
<i>S. fragilis</i>	70	200	c1000 (4 mm t.l.)
<i>S. mcalesteri</i>	90	580	c1000 (8 mm t.l.)
<i>L. abyssorum</i>	70	370	260 (2.5 mm t.l.)
<i>P. clarkei</i>	?	190	? —

being fully ripe; furthermore, the largest specimens were more mature than the smallest.

In the case of *S. fragilis* where specimens from two samples were available, less than half of those from Station 85 showed any trace of gonad development and of those maturing none were more than one-fourth mature. A similar picture was obtained at Station 126, 13 1/2 months later, although here there were a few with more advanced gonad development. The relationship between size and sex is similar both in *S. mcalesteri* and *S. fragilis*, with males being on average larger than the females.

Gonad development of *S. filatovae*, from Station 85, is similar to *S. fragilis* at the same station, though those specimens of *S. filatovae* with developing gonads were in a somewhat more advanced state of maturity.

In all three species there is a wide overlap in the length of the maturing males and females. Although the males are on average longer than the females, there is no evidence of protogyny.

Gonadal development in specimens of *Lametila* from Station 64 is somewhat different from that in *Silicula*. The largest specimens are males and there is little size overlap with the smaller females. The sex ratio is approximately one male to three maturing females. There is a relatively wide range of gonadial stages in the sample. While there is no evidence of sex change in *Silicula*, it would appear, from our limited data, that *Lametila* is protogynous.

That males are larger than females, and that in *Lametila* the female phase precedes the male phase, would appear to have considerable advantage in the deep sea where

animal density is low. Larger animals produce more gametes and sperm density is maximized. There is no evidence of brooding in any species discussed in this paper. Egg size is relatively small in all species; however, prodissoconch size varies considerably and, with the exception of *Prelametila*, is relatively large.

In the light of the data presented by Ockelmann (1965) for lamellibranchs, it would seem to be a paradox in that egg size would indicate planktotrophic/lecithotrophic development whereas prodissoconch size would indicate lecithotrophic/direct development (see Table VII).

Ockelmann (1965) does not give information about the Protobranchia and it may well be that their development, involving a "barrel-shaped" larva, does not conform to the general rule applying to the Lamellibranchia.

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