CONTRIBUTIONS IN SCIENCE

NEW SLIT-LIMPETS (SCISSURELLACEA AND FISSURELLACEA) FROM HYDROTHERMAL VENTS. PART 2. ANATOMY AND RELATIONSHIPS

GERHARD HASZPRUNAR
The scientific publications of the Natural History Museum of Los Angeles County have been issued at irregular intervals in three major series; the issues in each series are numbered individually, and numbers run consecutively, regardless of the subject matter.

- Contributions in Science, a miscellaneous series of technical papers describing original research in the life and earth sciences.
- Science Bulletin, a miscellaneous series of monographs describing original research in the life and earth sciences. This series was discontinued in 1978 with the issue of Numbers 29 and 30; monographs are now published by the Museum in Contributions in Science.
- Science Series, long articles and collections of papers on natural history topics.

Copies of the publications in these series are sold through the Museum Book Shop. A catalog is available on request.

The Museum also publishes Technical Reports, a miscellaneous series containing information relative to scholarly inquiry and collections but not reporting the results of original research. Issue is authorized by the Museum's Scientific Publications Committee; however, manuscripts do not receive anonymous peer review. Individual Technical Reports may be obtained from the relevant Section of the Museum.

Scientific Publications Committee

Craig C. Black, Museum Director
Daniel M. Cohen
John M. Harris, Committee Chairman
Charles L. Hogue
George L. Kennedy
Joel W. Martin
Robin A. Simpson, Managing Editor

Natural History Museum of Los Angeles County
900 Exposition Boulevard
Los Angeles, California 90007

Printed at Allen Press, Inc., Lawrence, Kansas
ISSN 0459-8113
NEW SLIT-LIMPETS (SCISSURELLACEA AND FISSURELLACEA) FROM HYDROTHERMAL VENTS. PART 2. ANATOMY AND RELATIONSHIPS

GERHARD HASZPRUNAR

ABSTRACT. The anatomy of the slit-limpets from the deep-sea hydrothermal-vent communities belonging to the Scissurellidae and Fissurellacea, which are described by McLean (1989b), is presented.

Temnocinclus euripes and Temnozaga parilis have scissurellid anatomy, but differ from other scissurellids in sharing largely symmetrical shells, equally shaped and structured monopunctate ctenidia, smooth cephalic and epipodial tentacles, diagnostic radial features and statocysts, and in lacking eyes. Both are therefore united in the subfamily Temnocinclinae. Stuttziona theca also has scissurellid anatomy, differing from other scissurellids in having diagnostic protoconch sculpture, a peculiar gland at the anterior left pallial roof, monopunctate ctenidia, unusually large gonads, diagnostic radial features, a single pair of radial cartilages only, and vestigial eyes.

Clypeosectus delectus, C. curvis, and Pseudorimula mariana exhibit fissurellacean characters (vestigial left kidney, gonoduct opening in right renopericardial duct, anal gland). In contrast to the fissurellid condition they are characterized by an asymmetrical shell and mantle cavity, lack of shell-muscle hooks, a diagnostic type of epipodium, diagnostic radula, and by lack of a radial caecum and of eyes. In addition, males are equipped with a prostate and a copulatory organ, and females with a receptaculum seminis, both indicating internal fertilization. Based on all these characters, the species are united in a separate family Clypeosectidae in the Fissurellacea.

The reproductive features of the new groups are briefly discussed and compared with other members of the respective superfamilies. The Pleurotomariacea are regarded as a grade and are split into Scissurellacea, Haliotacea, and Pleurotomariacea sensu stricto; the latter are most closely related to the Trochacea.

INTRODUCTION

Although the close relationship between Pleurotomariidae and Trochinae has been recognized for nearly a century (e.g., Pelseneer, 1899; Bourne, 1919), authors usually have united the Pleurotomariacea and Fissurellacea within the "Zygobranchia." This was based mainly on the presence of paired ctenidia, the common retention of the shell slit or hole, and on the "Scissurella-stage" in fissurellid ontogeny. The latter argument, however, is no longer valid (see McLean, 1989b). The paired ctenidia mentioned above represent a common primitive character, not directly relevant for tracing the relationships of the included groups.

Moreover, until recently, anatomical comparisons between the Scissurellidae and Fissurellidae (Pelseneer, 1899; Bourne, 1919; Fretter and Graham, 1962, 1976) have revealed little affinity between the two families. Scissurellidae have been considered to be part of the evolutionary sequence trending from Pleurotomariacea to Trochacea, in which the foot has a double anterior edge marking the opening of the anterior pedal gland, an asymmetrical mantle cavity, and a well-developed left kidney, a papillary sac. In contrast, adult Fissurellidae never have the foot with a pedal gland, and the left kidney is reduced.

Salvini-Plawen (1980) proposed the suborder "Vetigastropoda" to include the Fissurellacea, Pleurotomariacea, Trochacea, and (tentatively) the Cocculinacea. The last superfamily has more recently been treated as another suborder, the Cocculiformia (Haszprunar, 1988b). Salvini-Plawen and Haszprunar (1987) have redefined the Vetigastropoda as a clade, restricting the taxon to Fissurellacea, Pleurotomariacea (sensu lati), and Trochacea. In contrast to Hickman (1988), who favored a restricted use of "Archaeogastropoda" replacing Vetigastropoda, I still use "Archaeogastropoda" (a grade) and Vetigastropoda (a clade including also the Lepetodrilacea; see Haszprunar, 1988a).

The slit-limpets described here exhibit new combinations of characters among the Vetigastropoda. This necessitates a general reconsideration of the interrelationships of the vetigastropod subgroups. Also the aberrant limpet genus Neomphalus (McLean, 1981; Fretter et al., 1981) and the recently described superfamly Lepetodrilacea (McLean, 1988; Fretter, 1988) are to be reconsidered with respect to their vetigastropod affinities. However, in the light of rapid increase of knowledge by means of EM-studies (e.g., Healy, 1988) and several papers

1. Institut für Zoologie der Universität Innsbruck, Technikerstraße 25, A-6020 Innsbruck, Austria.

Contributions in Science, Number 408, pp. 1-17.
Natural History Museum of Los Angeles County, 1989
Figure 1. *Temnocinclis euripus*, sections of holotype (USNM 859964), all frontal view. A. At line of statocysts. Scale bar = 500 \( \mu m \). B. At mouth opening. Scale bar = 200 \( \mu m \). C. At heart. Scale bar = 200 \( \mu m \). D. Epipodium (arrow marks ESO). Scale bar = 100 \( \mu m \). E. Statocysts with tiny statocones embedded in matrix. Scale bar = 100 \( \mu m \).

Lettering: au, auricle; ca1,2, radular cartilages (anterior, posterior); ct, ctenidium; e, epipodial tentacle; f, intestine; hg, hypobranchial gland; ho, horizontal muscle; mg, midgut gland; oe, oesophagus; os, osphradial ganglion; pc, pericardium; pg, pedal ganglion; r, rectum; rk, right kidney; s, stomach; sg, salivary gland; sm, shell muscle; st, statocysts; t, tentacular nerve; te, testis; ugo, urinogenital opening; ve, ventricle.
MATERIAL AND METHODS

The specimens investigated anatomically are listed by McLean (1989b: table 2). The preservation of specimens was good, and the anatomy could be reconstructed with sufficient certainty despite the low number of specimens investigated.

Histological section series were prepared at the Universities of Vienna and Innsbruck (see Acknowledgments). Specimens of Sutilizona theca were embedded in araldit, serially sectioned at 2 μm, and stained with Redaud's fluid. Specimens of all other species were embedded in paraformaldehyde, serially sectioned at 5-10 μm, and stained with azan (Heidenhain's method).

Anatomy of the scissurellid species will be treated further by Marietta Strassoldo (University of Vienna), who has a comparative study on the anatomy and ontogeny of the family Scissurellidae in preparation.

SCISSURELLACEA—SCISSURELLIDAE

DIAGNOSIS

(see also McLean [1989b] and Discussion)

Coiled or limpet-like Vetigastropoda, shell with shell slit or foramen, interior nacre lacking, protoconch of variable sculpture. Two shell muscles lacking hooks. Operculum retained in adults of all genera. Two bi- or monopunctate ctenidia, often of unequal shape and position. Left kidney as papillary sac, the larger right kidney ramifying between viscera, with an urninogenital opening. Never with organs for internal fertilization. Eye-vesicles (if present) closed. Several pairs of epipodial and single pair of separated epipodial sense organs (ESO)-tentacles or several ESO-tentacles alone. Diagnostic radula features (see McLean, 1989b).

ANATOMY OF TEMNOCINCLIS EURIPES AND TEMNOZAGA PARILIS

Both species are very similar in anatomy; therefore, a common description is given. Differences between species are mentioned where they occur.

The pedal sole is totally ciliated, and a large pedal gland is present. The mantle border is smooth and contains large blood-sinususes. The monopunctate ctenidia have no free axis, both are of equal length. Only a single skeletal rod is present in the axis, whereas the skeletal elements are paired in the leaflets. The latter are provided with bursicles. The right hypobranchial gland (Fig. 1C: Hg') is much larger than the left, which is limited in its extent by the heart.

The heart is situated somewhat to the left (Fig. 1C) and is functionally diotocardian, the pericardium is large and the auricles are of equal size but not of equal shape (as in Clypeosectus, see Figs. 1C, 3: au, au').

The left kidney is a papillary sac and is smaller than the right one. The right kidney forms a large coelomic system and is fused with the vas deferens (or oviduct, respectively) near their common opening. The species are gonochoristic. In both sexes the gonad occupies the entire left side of the body and posteriorly surrounds the stomach. The sperm cells have very short flagellae or even lack flagellae, thus the appearance of the testis is "granular" (as in Pseudorimula). The proximal vas deferens contains a dense mass of ripe sperm cells and obviously has the function of a vesicula seminalis. In the female of Temnocinclis euripes (a female of Temnozaga parilis has not been investigated anatomically) the ovary contains large yolk-rich eggs, the oviduct is ciliated and non-glandular.

The jaws are massive, the salivary glands are simple and pouclike (Fig. 1B: sg). There are two radial cartilages (Fig. 1A: ca1, ca2) and the radular sheath is long, making two loops. Compared with the Clypeosectidae the anterior oesophagus lacks a specialized ventral tract and does not encircle the radular sheath. The oesophagus pouches are rather small. In Temnocinclis euripes they lack papillae, whereas in Temnozaga parilis they are papillate (as in Clypeosectus, see Fig. 4D). The posterior oesophagus enters the stomach between the two openings of the midgut glands (as in Clypeosectus, see Fig. 5C). The stomach is provided with a gastric shield and protostyle, the caecum is small. The intestine makes several loops, having a distinct groove (as in Clypeosectus, see Fig. 5A). The stomach and the intestine contain detritus. The ventricle encircles the reeumen, and in contrast to the Clypeosectidae (see below) an anal gland is generally lacking.

The anterior nervous system is hypothroid in forming a pleuropedal complex. The labial lobes of the cerebral ganglia are large, but no labial commissure could be detected. The visceral loop is streptoneurous with distinct visceral ganglia. Eyes and optical nerves are completely lacking. In Temnocinclis euripes the epipodial tentacles are of different types, the second one bears an epipodial sense organ (Fig. 1D). Temnozaga parilis, in contrast, has uniform epipodial tentacles, each of which is provided with an epipodial sense organ. In contrast to other vetigastropods a subradular organ is lacking in both genera. The statocysts contain many statocones, each of which is embedded in a small vacuole (Fig. 1E).

ANATOMY OF SUTILIZONA THECA

The mantle slit is to the right, oblique, and is provided with a single tentacle. The mantle cavity is asymmetrical, and deeper at the right side. The two
Figure 2. *Sutilizona theca* (USNM 859967, LACM 2355). Semi-thin sections of certain organs, all frontal view. A. Mantle margin near anterior end of right shell muscle. Note positions of osphradial ganglion and of the single ctenidial skeletal rod. Scale bar = 50 μm. B. Statocysts with statoconia. Scale bar = 25 μm. C. Mantle roof near anterior end of left shell muscle with pallial gland. Note positions of osphradial ganglion and of the single ctenidial skeletal rod. Scale bar = 100 μm. D. Voluminous anterior oesophagus with large dorsal folds, pleuropedal complex. Scale bar = 100 μm. E. Stomach with gastric shield filled with grit. Scale bar = 50 μm.

Lettering: b, buccal ganglion; df, dorsal oesophageal fold; ms, mantle sinus; os, osphradial ganglion; oe, lumen of anterior oesophagus; p, pedal ganglion; pa, pallial gland; pl, pleural ganglion; sk, skeletal rod of ctenidial axis; sm, shell muscle.
monoplectinate ctenidia are unequal in several respects: The left gill reaches backwards to the anterior line of the pericard, its leaflets are rather long. Anteriorly left there is a prominent gland (Fig. 2C: pa). The right ctenidium is much smaller than the left one and occupies only the anterior half of the mantle cavity. The gill's axis is situated inwards of the right shell muscle and not at the mantle roof (Fig. 2A: sk), its leaflets are half as long as those of the left ctenidium, and the most anterior leaflets form a brush. The right ctenidial/ophradial ganglion (Fig. 2A: os) is situated to the right of the anterior end of the right shell muscle, whereas the left ganglion occupies the usual position inwards of the anterior end of the left shell muscle (Fig. 2C: sm). Each ctenidial leaflet bears a bursicle. Only the right hypobranchial gland is present, continuing the ctenidium backwards, and fills the free space of the right posterior mantle roof.

The diotoocardian heart occupies the central and left mantle roof, its ventricle encloses the rectum. The left kidney lies in the pallial roof and has a simple opening to the left of the anus. The right kidney is much larger than the left one and forms large lobes centrally and to the left between the viscera. It contains many tiny excretory granules; the urogenital opening is situated more posteriorly.

The species is gonochoristic; the male investigated is juvenile, the female investigated contains ripe eggs. In both sexes the gonad is very large and occupies the central body cavity, posteriorly it is situated at the left side. The appearance of the massive (not lobular) testis is granular, all stages of sperm development except ripe sperm cells are present. Late spermatocytes lack flagella. The vas deferens surrounds the stomach posteriorly, runs forward at the right dorsal side, and has a common opening with the right kidney. The ovary contains very large (max. 200 μm), yolky eggs in all stages of development. The course of the simple oviduct is as described for the vas deferens.

The jaws are massive and toothlike. The salivary glands are tubular and simple. A single pair of radial cartilages is present, the radial sheath is very long and makes an S-like loop. The anterior oesophagus (Fig. 2D: oe) is very broad, its dorsal folds and its glandular pouches are very large. The posterior oesophagus runs backward at the ventral right side and enters the stomach between the openings of the two unequal (the left one is smaller) midgut glands. The stomach is provided with a gastric shield (Fig. 2E) and sorting area, a caecum is not present. Like the intestine, which makes many loops, it is filled with grit and detritus (Fig. 2E).

The central nervous system of Sutlib zones affixed by the brain and connectives to the cardinal ganglia. Generally all ganglia are very large, according to the connectives and commissures are short. The cephalic tentacles are smooth, a single pair of ESO-tentacles is present. The eyes are vestigial, consisting of a small vesicle lacking pigment, the optic nerve is still present. The statocysts contain many statocones that are hollow (Fig. 2B).

**FISSURELLACEA**

**DIAGNOSIS**

Vetigastropod limpets with shell slit or hole and two shell muscles, operculum present only in larval stage. Two ctenidia, hypobranchial glands restricted to the mantle-slit/hole area. Left kidney reduced; gonoduct opening into renopericardial duct of right kidney. Salivary glands enlarged, forming several tube like pouches. Anal gland may be present. Epipodial sense organs (ESO) at tips or at ventral sides of smooth tentacles. Eyes (if present) with closed vesicles.

**ANATOMY OF CLYPEOSECTUS DELECTUS, C. CURVUS, AND PSEUDORIMULA MARIANAE**

**Mantle Cavity**

The mantle cavity is deep, more or less asymmetrical, and has a posterior, broad, triangular pouch at left and right (Fig. 3C: mc). In both *Clupeosectus* species the two bipectinate ctenidia are provided with long afferent and efferent membranes; anteriorly a short free axis is present, however. In *Pseudorimula* the ctenidial membranes are shorter so that the free portion is as long as the fused one. In both genera, each ctenidial filament has paired skeletal rods and a bursicle (Fig. 4G); the ctenidial axis also has paired skeletal rods corresponding to its bipectinate structure (compare with Temnocinclinae). An oesophagus is situated inwards of the efferent membrane and at the free efferent axis of each ctenidium.

Conditions of the hypobranchial glands differ: In both sexes of *Clupeosectus* and in males of *Pseudorimula* these are small and are restricted to the mantle-slit area, whereas females of *Pseudorimula* lack a hypobranchial gland.

**Heart and Excretory System**

Whereas *Clupeosectus* species have a vestigial and isolated left kidney, this organ is lacking in *Pseudorimula*. Generally the right kidney is large and ramifications between the viscera, especially at the right side (Figs. 3C, 5A, C: rk). Both kidneys have their openings beneath the anus.

The heart is functionally diotoocardian; the pericardium is very large. The auricles are of equal size but differ in shape (Figs. 3A–C: au, au').

**Genital System**

Clupeosectids are gonochoristic. The gonad is voluminous and occupies the posterior ventral part
Figure 3. Clypeosectus curvus, female (LACM 2364a). A. Dorsal view of an intact specimen, shell removed. B. Section of the same specimen as marked in A. C. Reconstruction of mantle cavity and coelomic system of same specimen as in A and B. Scale bars = 500 μm.

Lettering: ag, anal gland; as, afferent ctenidial sinus; au, auricle; ct, ctenidium; es, efferent ctenidial sinus; h, head; i, intestine; lk, left (vestigial) kidney; mc, posterior end of mantle cavity; mg, midgut gland; o, ovary; od, oviduct; oe, oesophagus; os, osphradial ganglion; p, pedal cord; pc, pericardium; pd, reno-pericardial duct; r, rectum; rk, right kidney; rs, seminal receptacle; sm, shell muscle; t, cephalic tentacle; ugo, urinogenital opening; ve, ventricle.
of the visceral mass. In both sexes the gonoduct opens into the right renopericardial duct, which meets the right kidney near its opening (Fig. 3C: ugo).

The heads of the spermatozoa of Clypeoscutus are about 6 μm long and filiform (Fig. 6B). In males these are found in great number in the proximal vas deferens, which is enlarged to form a fucional vesicula seminalis. Ripe sperm cells also have been found freely in the mantle cavity of one female (Fig. 6B). In Clypeoscutus a single, specific “prostate” gland (Fig. 5B: pr) is present, the epithelium of which is very high (50 μm) and consists of mucous cells and ciliated cells. It starts around the urinogenital opening. Here the right hypobranchial gland, which has a lower (30 μm), less ciliated epithelium, is enlarged and forms a distinct pocket. Posteriorly, the hypobranchial gland disappears and the prostate (Fig. 5C: pr) also forms a large pocket in the posterior right corner of the mantle cavity. From the anterior ventral prostate pocket a small but distinct ciliary band runs forward and over the right neck to the ventral base of the right cephalic tentacle, where the penis emerges. The latter has no groove or duct, but is densely ciliated. However, these structures are also present in the females of Clypeoscutus. Here the ciliated band leads backwards to an otherwise isolated receptaculum seminis (Fig. 3C: rs), which opens into the most posterior extent of the mantle cavity on the right. Whereas the duct of the receptaculum has strong longitudinal folds (Fig. 4B: rs), the vesicle lacks folds and is filled with sperm (Fig. 4C). The heads of these (probably allo-) spermatozoa are directed to the wall of the receptaculum vesicle (Fig. 4C). The oviduct is wide (100 × 35 μm) but depressed, and is simply ciliated. In the ovary all stages of egg development are present; ripe eggs are large (diameter 200 μm) and contain much yolk.

In males of Pseudorinula the prostate gland (Fig. 9C: rs) is paired and has the same histology as that of Clypeoscutus. The left prostate gland forms a large pocket situated dorsally of the pericardium; the right prostate forms a larger pocket at the posterior right corner of the mantle cavity, as in Clypeoscutus. Here ripe sperm cells have been found that are in close contact with mucous droplets (Fig. 9C: md) of the prostate gland. Near this contact zone the droplets change their shape. The sperm cells (Fig. 9C: sp) have a round head (diameter about 4
µm) and a rather short tail. Males of *Pseudorimula* lack a penis and the seminal groove.

The single investigated female of *Pseudorimula mariana* lacks a penis and a seminal groove, as well as a receptaculum. The conditions of oviduct and eggs are as described above for *Clupeosectus* (Fig. 3C); the ovary (Fig. 7: o) also fills the free space between the main muscle bundles.

**Alimentary Tract**

The jaws of *Clupeosectus* are delicate, whereas those of *Pseudorimula* are massive (Fig. 8A: j), as in the
Tennocinclinae. Whereas the salivary glands of *Clypeosectus* are enlarged and form several tubelike pouches (Fig. 4A: sg), those of *Pseudorimula* form simple grooves (Fig. 8A: sg) continuing into the dorsal longitudinal folds of the oesophagus. In contrast to *Clypeosectus*, in which the posterior pair of radular cartilages is vestigial, these structures are well developed in *Pseudorimula* (Fig. 9A: ca1, ca2).
The radial sheath is short and straight and a radial caecum is lacking.

The anterior oesophagus has a specialized ventral tract; the oesophageal pouches more or less encircle the radula sheath and are papillate (Figs. 4D, 9A: pa). In *Clypeoscalus* there is a continuous change into the posterior oesophagus, whereas in *Pseudorimula* the posterior oesophagus starts more abruptly, forming a dorsally positioned fold. The posterior oesophagus enters the stomach adjacent to the openings of the paired midgut gland (Fig. 5C: mg). The stomach itself is provided with a thick gastric shield; a protostyle and a spiral caecum could not be detected. The intestine makes several loops; like the stomach it has a distinct groove formed by a very thin epithelium. The rectum runs through the ventricle obliquely. In both genera these structures are filled with detritus, including iron sulphide particles, which destroyed several sections. In *Clypeoscalus* a small anal gland (Fig. 4F: ag) opens adjacent to the right of the anus. In *Pseudorimula* an anal gland was not detected, but this is possibly due to some folds in the respective sections.

**Nervous System**

The clypeoscalid nervous system resembles that of the Scissurellidae (e.g., Bourne, 1910) or the Fissurellidae (e.g., Pelseneer, 1899). The anterior system is hypoarthroid in having adjacent pleural and pedal ganglia (Figs. 4D, 9B: pg, pl). The cerebral ganglia are situated laterally at the bases of the cephalic tentacles and are interconnected by a very long commissure (Fig. 4A: cc). The labial lobe is small in *Clypeoscalus*, large in *Pseudorimula*; a labial commissure could not be detected. There are pedal cords with several commissures. The visceral loop is streptoneurous and has distinct visceral ganglia. Two osphradial ganglia are present, corresponding to the number of ctenidia. As usual in archaeogastropods, the length of the visceral loop and the position of the visceral ganglion correspond to the depth of the mantle cavity (Haszprunar, 1988a).

**Sense Organs**

Eyes are lacking. Whereas *Clypeoscalus* species have retained an optical nerve, this is lacking in *Pseudorimula marianae*. Both genera show a dimorphism of epipodial tentacles (more appropriately ESO-tentacles). In the posterior (two or three) epipodial tentacles the ESO are situated at the tip (Fig. 8B), whereas the anterior (one or two) tentacles have them ventrally situated (Fig. 4F).

The paired osphradia are situated at the efferent ctenidial axes. A subradular organ is not present. The statocysts contain statoconia (Fig. 9B: st).

**DISCUSSION**

**INFERRED MODE OF REPRODUCTION**

**Scissurellidae**

The scissurellid species described here anatomically are the only archaeogastropod inhabitants of the hydrothermal-vent habitat lacking all features of internal fertilization. Only the group-C limpets (Hickman, 1983; i.e., the "symmetrical" limpets of McLean, 1985) also lack a penis or receptacula. Copulatory organs in males and/or receptacula in females have been described in all other archaeogastropods from the hydrothermal-vent habitat (McLean, 1981, 1985, 1988, 1989b; Fretter et al.,
1981; Fretter, 1988; Warén and Bouchet, 1989; McLean and Haszprunar, 1987; Haszprunar, 1988a). Nevertheless, because of the small size of the animals, the obvious rarity of the animals (see McLean, 1989b), the structure of the sperm cells (lacking long flagella), and the low number of eggs, it is likely that fertilization takes place in the female mantle cavity. This might likewise be correct for other scissurellid species; however, the mode of sperm transfer is completely unknown in the Scissurellidae.

Obviously, males of the rii-vent scissurellid species occur as close as is possible to 50% (3 of 5 determined specimens). This is in contrast to certain shallow-water species, where males are very rare (Incisura: Bourne, 1910: 16; Scissurella: Marietta Strassoldo, pers. comm., July 1988). Possibly facultative parthenogenesis takes place in such species. As a whole, fertilization biology of the Scissurellidae may be much more complex than previously thought.

Clypeosectidae
As far as is known, Clypeosectus is the only zeugobranch genus with internal fertilization via a penis. Based on anatomy, the probable route of
Figure 8. *Pseudorimula marianaec*, histological sections, all frontal views. All scale bars = 100 μm. A. Buccal cavity and mouth opening of male (LACM 2366a). B. Posterior epipodial tentacle of holotype (female, USNM 859977) with ESO (arrow) at tip. C. Cerebral ganglia and anterior oesophagus of holotype (female).

Lettering: c, cerebral ganglion; ca1, anterior radular cartilage; dfc, dorsal food channel; j, jaw; oe, oesophagus; oep, oesophageal pouch; ra, radula; rs, radular sheath; sg, salivary gland.
gametes in Clypeosectus is as follows: Ripe spermatozoa are stored in the seminal vesicle, then pass via the vas deferens and the right renopericardial duct, and finally are released through the urino-genital opening into the mantle cavity. The mucus of the prostate gland probably packs the sperm cells together; they are transferred via the seminal groove and the penis into the mantle cavity of the female. There the sperm cells are stored in the receptaculum seminis. When eggs are released via the oviduct,
renopericardial duct, and urinogenital opening, sperm cells become free and fertilization takes place in the mantle cavity of the female. Brood protection may occur, as in many Cocculiniformes (see Haszprunar, 1988b), but is unknown at present.

A puzzling question concerns the "copulatory" process and a "seminal" groove that is also present in females of Clypeoscoletus. These structures could be used in egg-laying, as assumed for the neritic genus Phenacolepas Pilsbry, 1891, by Fretter (1984), or may simply be the result of genetic interference (expression of male genes in females) between the sexes. Protrandric hermaphroditism is very unlikely, considering that the single male is fully mature. Correspondingly, a similar condition occurs in the Lepetodrilidae (Fretter, 1988, and pers. obs.), in which females have a copulatory process that is smaller, as well as a groove in the position of the seminal groove of males.

Obviously the conditions in Pseudorimula (lack of copulatory process in males, and lack of receptaculum seminis in females) are less specialized and more primitive. However, the presence of quite aberrant sperm and of a large prostate gland also suggest internal fertilization in this genus. The exact influence of the prostate on the sperm cells and the mode of sperm-transfer (via mobil spermatophores?) is completely unknown at present. Medem (1943) reported sperm in the mantle cavity of Fissurella nubecula (Linnaeus, 1758) (see also Fretter and Graham, 1962:324) and this condition may be typical for the Fissurellacae, as there is as yet no report on external (free water) fertilization of any fissurellid. Thus, fissurellids and both clypeoscoletid genera seem to reflect a step by step process toward internal fertilization via a penis.

GENERAL REMARKS ON PHYLOGENETICS

The following considerations are based on an assumed vetigastropod archetype (= stem species), which is characterized as follows (for reasoning see Haszprunar, 1988a, and in prep.): Shell small (2–4 mm), coiled, with few whorls and slit; protoconch 1 (= embryonic shell) with more or less regular sculpture. Operculum in adults present, a single pair of cephalic and few pairs of epipodial tentacles provided with papillae, a single pair of (smooth) tentacles with ESO. Mantle cavity deep; two bicipitate ctenidia (left one slightly larger) with long efferent and short afferent axial membranes, the leaflets provided with bursicles; two osphradia; two hypobranchial glands. Heart diotocardian, auricles of equal size and of different shape, the ventricle encircles the rectum. Two kidneys with different structure and function, the left one at the pallial roof, the right one ramifying between the viscera, both connected with the pericardium. Sexes separate, the ciliated gonoduct (vas deferens or oviduct) and the right renopericardial duct have a common urinogenital opening. Sperm of the primitive type, eggs large and lecithotrophic, external fertilization.

Paired jaws consisting of numerous teeth, salivary glands are simple pouches. Radula rhipidoglossate, symmetrical; two pairs of cartilages and a radular diverticulum present. Anterior oesophagus of the polyplacophoran type, with papillate pouches, more or less encircling the buccal apparatus, showing torsion. Stomach provided with gastric shield, protostyle, and simple caecum; paired midgut gland; intestine with few loops; rectum through heart. Nervous system hypothaloid, long cerebral commissure, with labial ganglia and commissure, pedal cords interconnected by several commissures, visceral loop streptoneurous. Eyes open, with lens; statocysts with several statocones.

ANATOMICAL COMPARISON OF SCISSURELLID SPECIES

The anatomies of Temnocinclis euripes and Temnozaga parilis are very similar. Aside from shell and radula characters (see McLean, 1989b), both species differ only in the anterior oesophagus (papillate or not) and in epipodial features. Obviously both genera are closely related. In contrast, Sutilizona theca is quite different in anatomy and radula and thus not closely related to either.

The scissurellid nature of all three species is founded on the characters of shell, radular, epipodial, and sperm conditions. According to the assumed vetigastropod archetype (see above), most of these characters are primitive for Vetigastropoda (shell slit, symmetrical radula, epipodium with few epipodial and a single pair of ESO-tentacles), or might be due to convergence (lack of nacre, derived sperm cells). Thus, the scissurellid nature of Temnocinclinae and Sutilizoninae is poorly founded, nevertheless it is the most probable solution. Further studies on shell structure (see Batten, 1975) or sperm ultrastructure (see Healy, 1988) should substantiate the present classification.

Although the extent of anatomical variation is poorly known in the Scissurellidae, differences from other scissurellids can be summarized as follows:

(1) Temnocinclis euripes and Temnozaga parilis differ from other scissurellids (including Sutilizona theca) in having a nearly symmetrical shell and mantle cavity, diagnostic radular features (McLean, 1989b), two monopectinate ctenidia of equal shape and position, lack of eyes, and in the particular structure of the statocyst. Further common characters (although not unique among the Scissurellidae) are the smooth cephalic and epipodial tentacles, the presence of both hypobranchial glands, the type of salivary glands, and the unusual sperm cells. According to these common characters of Temnocinclis and Temnozaga both genera are united in a new subfamily Temnocinclinae among the Scissurellidae (McLean, 1989b).

(2) Sutilizona theca differs from other Scissurellidae (including the Temnocinclinae) in having a unique protoconch sculpture, a diagnostic radula (McLean, 1989b), a single pair of radular cartilages, a very broad anterior oesophagus, a multi-looped
intestine, the left pallial gland, the large gonads (otherwise restricted to the left body cavity; e.g., Bourne, 1910), and vestigial eyes. Further diagnostic (but not unique among the Scissurellidae) features are the monopodial ctenidia, the single (right) hypobranchial gland, the type of salivary glands, and the sperm cells. In accordance with McLean (1989b), I regard the differences mentioned above as important enough to place Sutiliza theca in its own subfamily, Sutilizinae. The occurrence of a single pair of ES0-tentacles might be explained by the immaturity of the specimens studied (see McLean, 1984: fig. 6), although McLean (1989b) noted that the foramen is closed, which is indicative of maturity. Thus, Sutiliza theca may exhibit a paedomorphic condition in this respect.

It is uncertain whether Temnocinclinae and Sutilizinae are sister-groups (for their scissurellid nature see above), and whether or not both groups have invaded the hydrothermal-vent habitat independently. The similarities of both subfamilies (reduction of eyes, monopodial ctenidia, smooth tentacles) might be due to convergence, because all these characters are also found in other deep-water or hydrothermal-vent vestigastropods. The lack of the enlarged forth lateral tooth might be a common derived character (McLean, 1989b); however, the buccal apparatus of Sutiliza theca differs considerably from that of the Temnocinclinae and other scissurellids. Moreover, the remaining anatomy of both subfamilies differs considerably. Therefore a sister-group relationship of Temnocinclinae and Sutilizinae is possible but not yet ascertained.

STATUS OF SCISSURELLIDAE (SCISSURELLACEA)

Until now the Pleurotomariacea (sensu lato) have been exclusively defined by primitive characters, suggesting that the group represents a grade rather than a clade.

Pleurotomariidae and Trochacea are closely allied by sharing the oviductal gland (Bourne, 1910; Fretter, 1966). The Haliotidae stand closer to both families than to Scissurellidae in also having a posteriorly elongated mantle cavity and a spiral caecum of the stomach. As noted by Bourne (1910:31): “Not only are the Scissurellidae distinct from the Pleurotomariidae, but they are clearly less closely related to them than the Haliotidae or even than the Trochidae and Turbonidae [sic], for the last-named families, although they have lost the labral incision in the shell, as also the right ctenidium and the structures correlated to it, have retained many anatomical features which find their counterpart in Pleurotomaria.” In addition, the Scissurellidae exhibit a quite different and advanced sperm ultrastructure, whereas the Pleurotomariidae and Haliotidae have sperm of the primitive type (Healy, 1988; this paper).

These considerations suggest that the “Pleurotomariacea” (comprised of Pleurotomariidae, Haliotidae, and Scissurellidae) very probably represents what Haszprunar (1986) has called a multidimensional paraphyletic group (i.e., a grade with two or several emerging lines not included), because the Fissurellacea and Trochacea, and possibly also the Lepetodrilacea (see Haszprunar, 1988a), are here considered to have branched off at different points along the “pleurotomariacean” line. As outlined in detail by Haszprunar (1986), such groups must be dissolved, otherwise the hypothesized phylogenetic relationships cannot be expressed unequivocally in a classification. Superfamilial status for the Haliotidae has already been proposed by Golikov and Starobogatov (1975), so that only the Scissurellidae remain to be removed from the Pleurotomariacea. Accordingly, the family Scissurellidae is elevated to superfamilial level in this paper. This is well founded, considering the numerous differences summarized by Bourne (1910:30) and outlined herein.

The restriction of Pleurotomariacea to the Pleurotomariidae does not take into account 20 extinct Paleozoic and Mesozoic taxa treated by paleontologists at the family level within the Pleurotomariacea, all of which have conispiral shells with slits or hole series, differing in size and other characters of shell morphology from the Pleurotomariidae (see Knight et al., 1960). Living Pleurotomariidae have a rhipidoglossate radula unlike that of other vestigastropods (see Hickman, 1984a,b), differing to the extent that some authors designate it as “hystrichoglossate” rather than rhipidoglossate. In contrast, the radulae of Haliotidae and Scissurellidae are more typical of other vestigastropods. The hystrichoglossate radula may well be a novelty of the family Pleurotomariidae, which dates from the Mesozoic, as do the Haliotidae and Scissurellidae. It is much more likely that the ancestors of the latter two families were conispirally coiled “pleurotomariaceans” with typical kinds of rhipidoglossate radulae, rather than that the ancestors had the hystrichoglossate radula. Accordingly, it is much more likely that some or all of the extinct families might have had the basic features of scissurellacean organization, except for such derived features as an advanced shell structure that includes loss of nacre. It is likely that anatomy of the extinct families would therefore place them in the Scissurellacea, rather than in the Pleurotomariacea (sensu strico).

According to Knight et al. (1960) the Scissurellidae first appeared in the fossil record during the Cretaceous. Earlier fossils from the Triassic have been recently discovered (K. Bandel, pers. comm., Sept. 1988), placing the origin of Scissurellidae early in the Mesozoic. The scissurellid body plan, however, is likely to have had a Paleozoic origin.

ANATOMICAL COMPARISONS OF CLEFTYPOSECTID SPECIES

Several characters of Pseudorimula differ from those of Clypeosectus both in external and internal organization. Differences concern external shape, presence of copulatory processes, shell muscle,
length of the ctenidial membranes, genital system, salivary glands, radular cartilages, oesophagus, size of labial lobe, presence of optic nerve, and number of ESO-tentacles. The phylogenetic significance of these differences is treated further below.

Inclusion of the Clypeosectidae in the Vetigastropoda is based on the shell slit, the presence of epipodial sense organs, the number (two) and type of ctenidia (bipectinate with skeletal rods and bursicles), and the oesophageal conditions (papillate pouches encircling the radular sheath).

The fissurellacean affinity of Clypeosectidae is based upon essential features in the excretory, reproductive, and digestive systems. The vestigial left kidney is a basic feature of the Fissurellidae, otherwise known only in the leptetellacean family Pyropeltidae (McLean and Haszprunar, 1987). In the genital system, the gonoduct opens into the reno-pericardial duct, reaching the right kidney near its opening, which is a basic character of the Fissurellidae, although present in the Leptetodrilacea (Fretter, 1988). In Clypeosectus, the salivary glands consisting of several pouches, and the presence of an anal gland, are typical fissurellacean characters that are not found in any other archaeogastropod group. Moreover, the ESO are situated at the ventral base of the epipodial tentacles as in fissurellids, a condition otherwise known only in Haliotidae. In addition, the rather small hypobranchial glands are restricted to the shell-slit area, as in fissurellids.

Differences from the Fissurellidae include the shell shape (more markedly asymmetrical), lack of shell pores, double anterior edge of foot marking pedal gland (absent in adult Fissurellidae), shell muscle (no hooks), cephalic tentacles (smooth), epipodium (few tentacles instead of many), internal fertilization (unknown in Fissurellidae), and particularly the radular characters (symmetrical plan, no enlarged fifth lateral as in Fissurellidae), lack of radular caecum, and the lack of a subradular organ.

Clypeosectids resemble the Temnocinclinae in having three posterior pairs of epipodial tentacles, the double anterior edge to the foot, and similar transparency to the shell. However, clypeosectids lack an operculum, the epipodial and cephalic tentacles are longer than those of the Temnocinclinae, and the additional genital process in both sexes is lacking in the latter. Whereas the similarities are regarded as common primitive characters for the Vetigastropoda (see above), the differences in anatomy indicate that the Temnocinclinae and the Clypeosectidae belong to different superfamilies.

STATUS OF CLYPEOSECTIDAE

The status of the Clypeosectidae as a clade appears well founded by several peculiarities of the family. The most important are the common aberrant radula type, the common modifications of the male genital system (prostate gland), and the shared epipodial condition. Accepting this view, all similarities shared by only one genus with the Fissurellidae must be due to convergence, or reflect a common basal condition in the Fissurellacea.

Such similarity is found in the salivary glands. Whereas Clypeosectus has several pouches as in the Fissurellidae, Pseudorimula has only simple ridges. Among archaeogastropods reduction of the salivary glands has been reported in the Cocculinidae and certain genera of the Pseudococculinidae (Haszprunar, 1988b). In contrast, the condition of Clypeosectus and the Fissurellidae is unique. It is thus more likely that the salivary gland of Pseudorimula represents the advanced state among the Fissurellacea.

A second case is the symmetry of shell and mantle cavity in Pseudorimula and Fissurellidae. One could speculate that this genus represents an intermediate level between the marked asymmetry of Clypeosectus and the nearly perfect symmetry in the Fissurellidae. However, this idea would imply that Clypeosectidae is a grade rather than a clade and that the above-mentioned peculiarities of the family are convergences or primitive ones. That they are both is highly improbable. The logical conclusion is therefore that the symmetrical conditions of Pseudorimula and Fissurellidae have been convergently evolved. This is much more likely because there are several cases of secondary symmetry known among gastropods (see Yonge, 1947).

Comparison with the vetigastropod archetyp (see above) indicates that within the Clypeosectidae, Clypeosectus is more advanced with respect to the following characters: copulatory processes in both sexes, the asymmetry of the prostate glands, the presence of a receptaculum in females, the larger degree of fusion of the ctenidial axis, the reduction of the posterior pair of radular cartilages, and the smaller labial lobe. In Pseudorimula the general symmetry, the sperm cells, the salivary glands and oesophageal conditions, and the loss of the optical nerve are advanced characters.

STATUS OF FISSURELLACEA

The Fissurellacea clearly represent a clade (Haszprunar, 1986, 1988a). Shared derived characters are the excretory system with a reduced left kidney and the anal gland. Also the genital system, in which the gonoduct opens directly into the reno-pericardial duct, is distinctly modified from the primitive condition. This condition, however, also occurs in the Leptetodrilacea (pers. obs.). In addition, the salivary glands typically form several pouches. Finally the operculum has been lost in the adult, although this is correlated with limpet life. Modifications of the epipodium are of minor importance, as a similar position of the ESO-tentacles also occurs in Haliotidae (see Crofts, 1929).

In still having an asymmetrical shell and mantle cavity and a pedal gland, Clypeosectus stands close to a hypothetical fissurellacean ancestor. Specialization concerns the radular type, lack of eyes, and internal fertilization. In contrast, the Fissurellidae have developed a special caecum of the radular sheath (Fretter and Graham, 1962: fig. 96: pm), lost the pedal gland in adults, and developed a more symmetrical shell and mantle cavity.
ACKNOWLEDGMENTS
Specimens were sectioned by B. Ruthensteiner (University of Vienna) and W. Salvenmoser (University of Innsbruck). I am indebted to Ms. Marietta Strassoldo (University of Vienna) and Klaus Bandel (University of Hamburg) for valuable information on reproduction and paleontology of the Scissurellidae. I thank Luifried v. Salvini-Plawen (University of Vienna), Richard S. Houbrick (Smithsonian Institution, Washington), and David R. Lindberg (University of California, Berkeley) for helpful commentary and review of the manuscript. I am grateful to James H. McLean for making it possible for me to treat the anatomy of these limpets. He and George L. Kennedy (LACM) have also expended much effort in editing the manuscript.

LITERATURE CITED


Haszprunar: New Slit-Limpets ■ 17