

**Figure 7.** *Clypeosectus delectus*, shell and external anatomy of specimens from Galapagos Rift. Anterior at top in dorsal and ventral views. A-E. USNM 859970, holotype. Alvin dive 984. Length 5.2 mm. A. Exterior surface with black mineral deposits. B. Interior, showing forward extension of muscle scar produced by pallial attachment scar. C. Right side showing elevated slit-border. D. Ventral view showing right tentacle projecting through slit. E. Oblique view from right side. F-H. LACM 2360, paratype. Alvin dive 991. Length 4.5 mm. F. Exterior, surface encrusted with black mineral deposits. G. Ventral view with body attached. H. Oblique view of right side.

late, three posterior pairs in *Clypeosectus*, four posterior pairs plus two anterior pairs in *Pseudorimula*. In *Clypeosectus* both sexes with small genital process at ventral base of right cephalic tentacle and ciliated band along right neck (Haszprunar, 1989). Foot with double anterior edge marking opening of pedal gland. Paired ctenidia bipectinate, right ctenidium smaller than left. Operculum lacking at maturity. Shell muscle without hooks.

For anatomical characters see Haszprunar (1989).

**Radula.** Radular ribbon nearly symmetrical. Rachidian tooth with long, tapering overhanging tip, edges with strongly projecting serrations; shaft of rachidian broad at base. Lateral teeth five to nine pairs, overhanging tips decreasing gradually in size away from rachidian, similar in morphology to rachidian, with strongly projecting serrations; shafts of laterals long and narrow, outermost laterals with

longer, more sinuous shafts. Enlarged outer lateral tooth lacking. Marginal teeth numerous, with spatulate tips, edges finely and sharply serrated, serrations similar to those of laterals. Marginals and outer laterals with one long denticle on outer edge of shaft near overhanging tip. Marginals tending to be fused along shaft bases. Tip of each marginal in *Clypeosectus* with long, filamentous process (lacking in *Pseudorimula*).

**REMARKS.** This new family is created for the new genus *Clypeosectus*, with two species from the eastern Pacific hydrothermal vents, and the new genus *Pseudorimula*, with one species from the western Pacific Mariana Back-Arc vents. Despite substantial differences in shell morphology and configuration of epipodial tentacles, the radular morphology of the two genera fits the same plan and confirms their affinity. Although shells of both genera resemble those of fissurellids, they differ in lacking the shell pits or pores that characterize fissurellids. The well-defined pedal gland of both genera is unknown in fissurellids.

Anatomical evidence for the establishment of a new family is given by Haszprunar (1989). Radular characters are sufficiently unique to suggest the need for a new family on this basis alone. The symmetrical radular ribbon distinguishes the clypeosectids from all fissurellids. There is no trace of the enlarged outer lateral tooth characteristic of fissurellids, which results in radular asymmetry in fissurellids. In addition, most fissurellids do not have the tendency toward similar morphology of rachidian, lateral, and marginal teeth that is exhibited by clypeosectids. The long denticle on the outer edge of the shaft of the outer lateral and marginal teeth is unique to clypeosectids. Scissurellid radulae differ principally in having a large rachidian tooth that is unlike the adjacent lateral teeth.

Due to the tendency of lateral and marginal teeth to have a similar morphology, it is difficult to distinguish between them in SEM views, and in views in which the marginals overlie the position of the laterals, it is not always possible to be certain how many lateral teeth characterize each species. Radular preparations for *C. delectus* (Figs. 8A-E) show nine pairs of lateral teeth, but only six pairs could be verified for *C. curvus* (Fig. 8F). The ninth lateral of *C. delectus* appears to be attached to a basal element that serves as a lateromarginal plate.

## KEY TO GENERA

Shell with open slit; three posterior pairs of epipodial tentacles ..... *Clypeosectus*  
 Slit closed at margin; two anterior pairs and four posterior pairs of epipodial tentacles .....  
 ..... *Pseudorimula*

### *Clypeosectus* new genus

**TYPE SPECIES.** *Clypeosectus delectus* new species.

**DESCRIPTION.** Slit strongly deflected to right in dorsal view; slit-borders raised, nearly in contact at anterior end. Apex posterior, deflected to right, but not overhanging posterior margin. Protoconch length 200  $\mu\text{m}$ , surface with finely pitted sculpture. Shell surface with thin periostracum, sculpture chiefly radial (spiral). False muscle scar produced by scar of pallial attachment extending close to border of slit anteriorly.

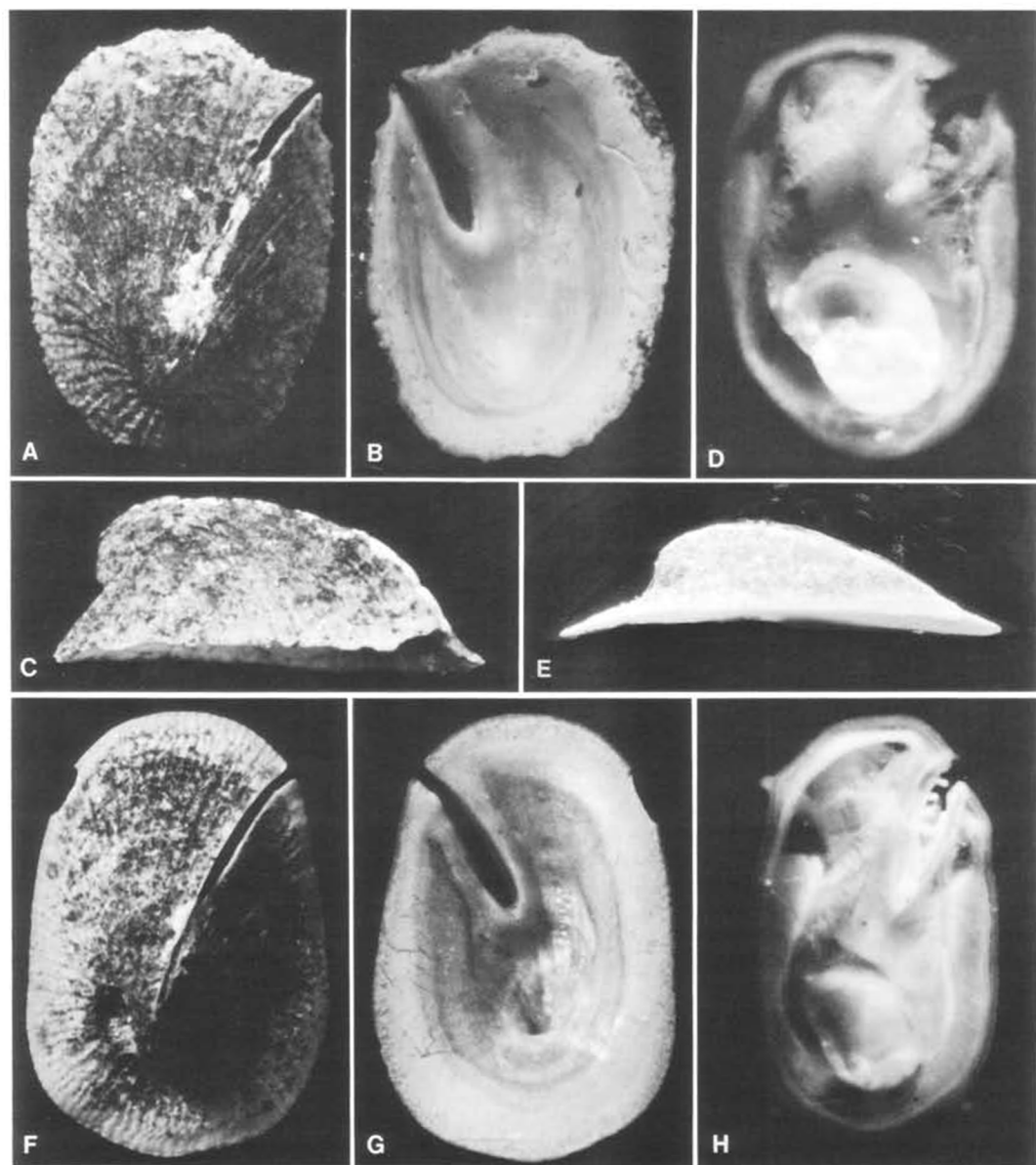
**External Anatomy.** Anterior end of foot broad, its tip with double anterior edge marking opening of pedal gland; foot posterior obtusely pointed; sole of foot with broad mid-ventral depressed area. Cephalic tentacles relatively long (preserved, contracted condition), the right seeming to project through slit; base of tentacle slightly enlarged in normal position of eyes. Three posterior pairs of epipodial tentacles, on body wall midway between foot edge and thick border of mantle margin. Mantle skirt deeply emarginate corresponding to slit, edge of emargination with tentaculiform appendages. Mantle skirt above head thin, nearly transparent. Shell muscle without hooks, extending anteriorly equal distances on both sides, approximately two-thirds body length. Both sexes with small genital process at ventral base of right cephalic tentacle and ciliated band along right neck. Right ctenidium smaller than left.

**Radula.** Rachidian tooth with long, tapered, overhanging tip, edges with strongly projecting serrations; shaft of rachidian broad at base. Six to nine pairs of lateral teeth, overhanging tips decreasing gradually in length away from rachidian, similar in morphology to rachidian, with strongly projecting serrations; shafts of lateral teeth long and narrow, outermost lateral with longer, more sinuous shafts. Marginal teeth numerous, with spatulate tips, edges finely and sharply serrated, serrations similar to those of lateral teeth. Marginal tooth and outer lateral tooth with one long denticle on outer edge of shaft near overhanging tip. Marginals tending to be fused along shaft bases. Tips of marginals with single long, filamentous process.

**REMARKS.** The false muscle scar produced by the anterior pallial attachment scar is more pronounced in this genus than it is in *Pseudorimula*, making the interior aspect of the shell completely unlike that of any fissurellid limpet. The radula differs from that of *Pseudorimula* in having longer, more tapered overhanging cusps, and the filamentous tip of the marginals is unique to *Clypeosectus*.

Two species are known from eastern Pacific hydrothermal vents: the type species, *Clypeosectus delectus*, from the Galapagos Rift and the East Pacific Rise at 13°N and 21°N, and *C. curvus*, known only from the Juan de Fuca Ridge. The two species are distinguished by differences in outline (elongate in *C. delectus*, oval in *C. curvus*), elevation (low in *C. delectus*, high in *C. curvus*), and position of apex (posteriormost in *C. curvus*).

**ETYMOLOGY.** The generic name is a Latin



**Figure 8.** *Clypeosectus delectus*, shell and external anatomy of specimens from East Pacific Rise. Anterior at top in dorsal and ventral views. A–D. MNHN, uncatalogued, shell margin decalcified and broken back. East Pacific Rise at 13°N, *Cyana* dive 82-36. Length 3.2 mm. A. Shell exterior, showing scattered black mineral deposits. B. Interior, showing extended muscle scar produced by pallial attachment scar. C. Right side. D. Detached body, dorsal view, showing bipectinate ctenidia. E–H. LACM 2361a. East Pacific Rise at 21°N, *Alvin* dive 1221. Length 3.9 mm. E. Right side. F. Exterior view. G. Interior view. H. Detached body, dorsal view, showing bipectinate ctenidia.

compound of *clypeus*, shield, and *sectus*, cut. Gender: masculine.

### *Clypeosectus delectus* new species

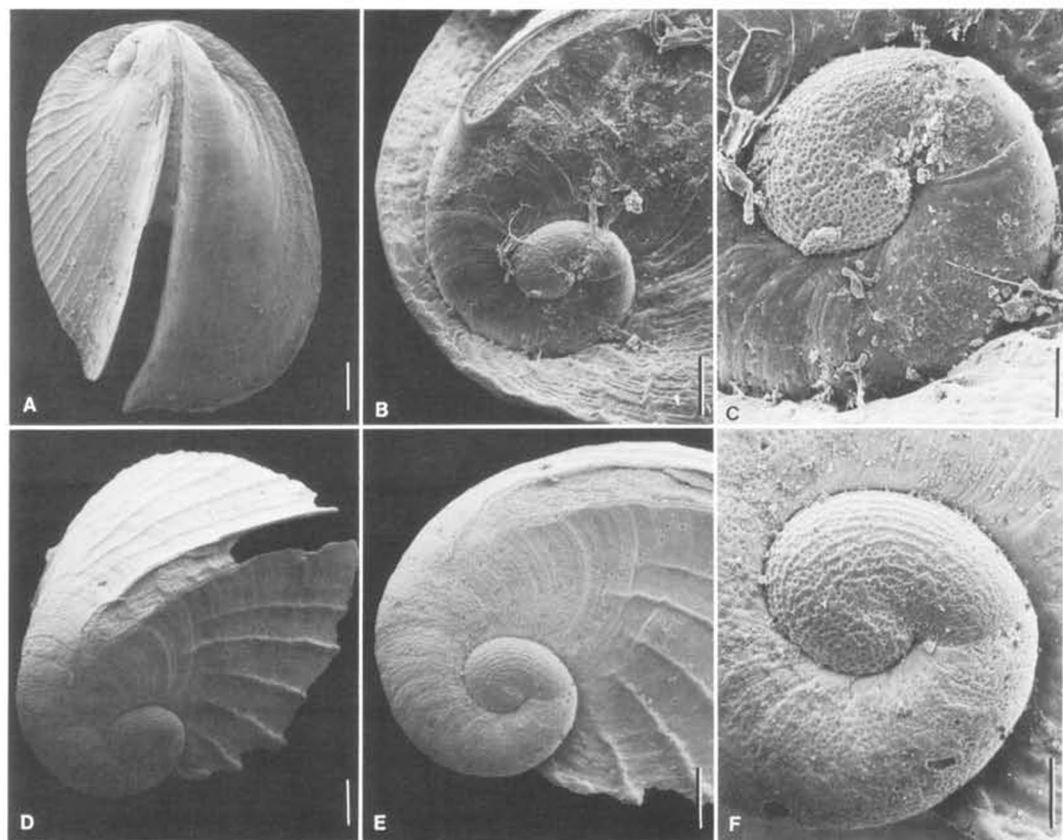
Figures 7A–H, 8A–H, 9A–F, 11A–E

Unnamed slit-limpet; Turner, 1980, fig. 1; Hickman, 1983:75, fig. 5 [radula]; Lutz, Jablonski, and Turner, 1984, fig. 1a; Turner, Lutz, and Jablonski, 1985, figs. 9a,b [juvenile shell and protoconch

from Galapagos Rift], figs. 10a–c [juvenile shell and protoconch from East Pacific Rise at 21°N].

**DIAGNOSIS.** Outline elongate, profile low, sculpture of narrow radial ribs, apex at three-fourths shell length from anterior margin.

**DESCRIPTION.** Shell (Figs. 7A–H, 8A–C, E–G, 9A–F) small, but relatively large for genus, maximum length 5.2 mm, thin; periostracum thin, pale yellow-brown; outline of aperture elongate oval,



**Figure 9.** *Clypeosectus delectus*, juvenile shells and protoconchs (after Turner et al., 1985, figs. 9, 10). A–C. Galapagos Rift, *Alvin* dive unknown. A. Dorsal view, anterior at bottom. Scale bar = 200  $\mu\text{m}$ . B. Posterior lateral view, showing protoconch and selenizone. Scale bar = 100  $\mu\text{m}$ . C. Enlarged view of protoconch, showing ridges and deep pitting. Scale bar = 50  $\mu\text{m}$ . D–F. East Pacific Rise at 21°N, *Alvin* dive 1226. D. Posterior dorsal view. Scale bar = 100  $\mu\text{m}$ . E. Lateral view. Scale bar = 100  $\mu\text{m}$ . F. Enlarged view of protoconch, showing ridges and deep pitting. Scale bar = 50  $\mu\text{m}$ .

either end may be broader than the other; margin of aperture in same plane; apical whorl at three-fourths shell length from anterior margin; highest elevation of shell at about half its length. Profile low, height of holotype 0.23 times length. Protoconch diameter 200  $\mu\text{m}$ ; protoconch sculpture of fine pitting (Figs. 9C,F); first teleconch whorl smooth, rounded, not descending below level of protoconch. Slit arising at position of three-fourths whorl in first teleconch whorl, at which stage aperture expands to produce limpet form through one-half whorl of additional rotation. Slit open one-half shell length in dorsal view, directed to right at angle of approximately 30 degrees off mid-dorsal line. Slit-borders sharply raised, slit open at edge of shell. Selenizone depressed below slit-border; additions to selenizone U-shaped. Sculpture of fine, sharply raised ribs (spiral cords); concentric (axial) sculpture weak, of fine growth lines only. Additional ribs arise in interspaces and assume equal prominence so that pattern of primary and secondary ribs not apparent. Shell edge thin. Muscle scar

deeply impressed, continuous anteriorly with broad pallial attachment scar extending almost to slit on both sides (extent of forward position of muscle discernible on preserved specimens). Shell interior transparent at muscle scar, through which exterior sculpture visible; shell interior outside pallial line with frosted surface; slit bordered by heavy deposition of callus along inner side.

**External Anatomy** (Figs. 7D,E,G, 8D,H). As described for genus.

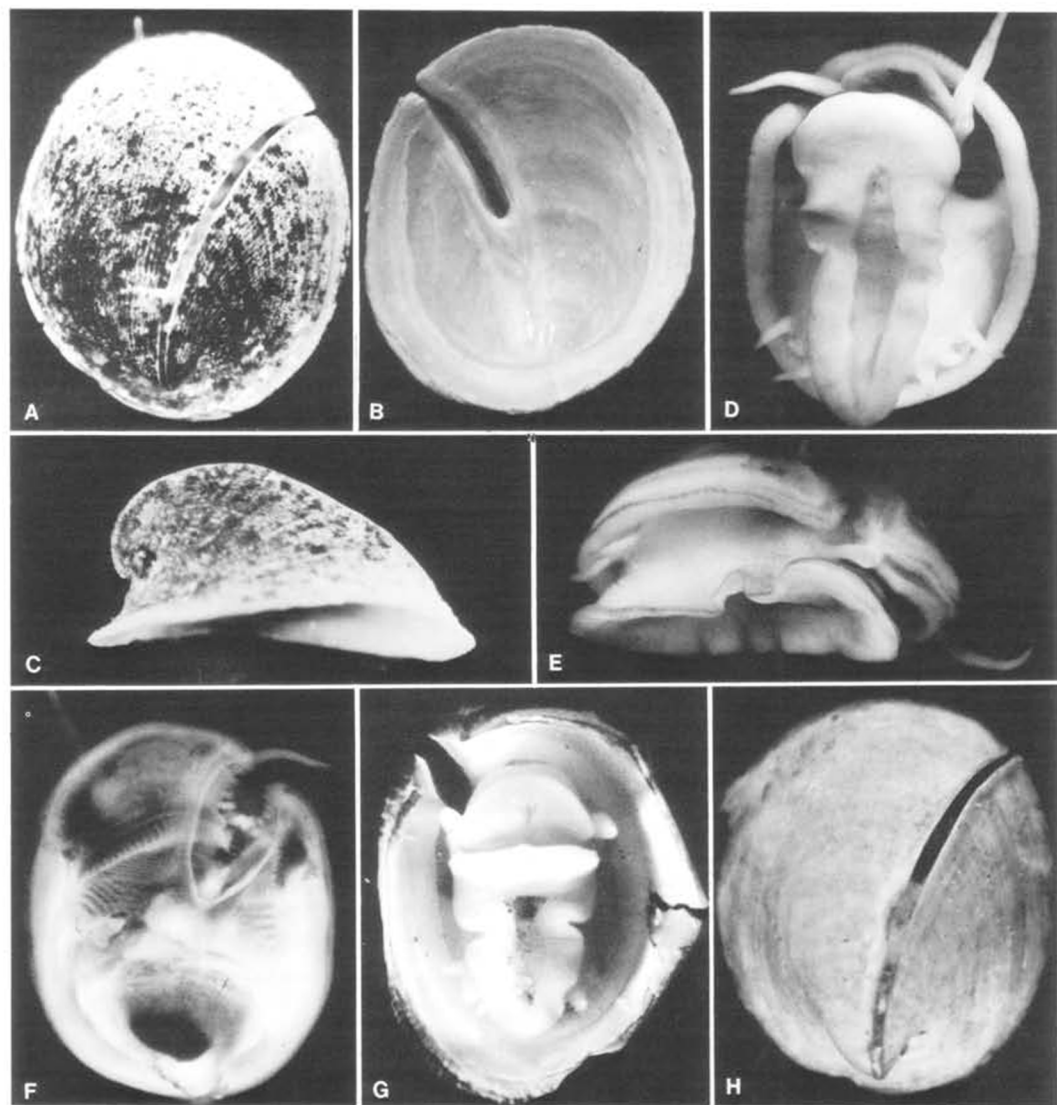
**Internal Anatomy.** Described by Haszprunar (1989).

**Radula** (Figs. 11A–E). As described for genus. Nine pairs of lateral teeth, outermost attached to lateromarginal plate. Marginal teeth with extremely long, filamentous cusps (Figs. 11B,E).

**DIMENSIONS.** Length 5.2, width 3.7, height 1.2 mm (holotype).

**TYPE LOCALITY.** Hydrothermal vents of Galapagos Rift (00°48.0'S, 86°13.0'W), 2451 m.

**TYPE MATERIAL.** Holotype and two paratypes from *Alvin* dive 984, 1 December 1979. Ho-



**Figure 10.** *Clypeosectus curvus*, shell and external anatomy. Anterior at top in dorsal and ventral views. A-C. USNM 859977, holotype shell, Axial Seamount, Juan de Fuca Ridge, *Pisces IV* dive 1730. Length 4.6 mm. A. Exterior, surface encrusted with black mineral deposits. B. Interior. C. Right side. D-F. Body of holotype. D. Ventral view, showing three posterior pairs of epipodial tentacles. E. Right side. F. Dorsal view, showing bipectinate ctenidia and retracted pallial tentacles bordering slit. G. LACM 2363, paratype, ventral view with body attached, showing decalcification at margin. Endeavour Segment, Juan de Fuca Ridge, *Alvin* dive 1447. Length 2.4 mm. H. LACM 2364a, paratype, exterior view, surface free of mineral deposits. Axial Seamount, Juan de Fuca Ridge, *Pisces IV* dive 1730. Length 4.0 mm.

lotype, USNM 859970 (body sectioned). Paratypes from this and other *Alvin* dives at the Galapagos Rift in 1979 are distributed as specified in Tables 1 and 2.

The holotype (Figs. 7A-C) is the largest and best-preserved specimen from the Galapagos Rift. There are only six specimens of 4.0 mm in length or larger and most are now in damaged or broken condition. Most specimens are decalcified at the margin.

**DISTRIBUTION.** Hydrothermal-vent habitat at Galapagos Rift and at 13°N and 21°N on the East Pacific Rise.

**REMARKS.** This species is the largest of the two members of the genus and has the lowest profile.

Radial sculpture in *C. delectus* is variable in strength. The holotype (Figs. 7A,C) has rather fine sculpture compared to other specimens from the Galapagos Rift (Figs. 7F,H) and the East Pacific Rise



**Figure 11.** SEM views of radulae of *Clypeosectus* species. A. *C. delectus*, rachidian and laterals (courtesy C. Hickman). Galapagos Rift, *Alvin* dive 733. Scale bar = 30  $\mu\text{m}$ . B. *C. delectus*, showing filamentous tips of marginals folded over central field. LACM 2358. Galapagos Rift, *Alvin* dive 984. Scale bar = 10  $\mu\text{m}$ . C-E. *C. delectus*. MNHN. East Pacific Rise at 13°N, *Cyana* dive 83-36. C. Central field, showing rachidian and marginals on right side. Scale bar = 20  $\mu\text{m}$ . D. Full width of ribbon, showing marginals of left side folded over and those of right side folded back. Scale bar = 40  $\mu\text{m}$ . E. Enlarged view of base of marginals, showing fusion at base and filamentous tips. Scale bar = 20  $\mu\text{m}$ . F. *C. curvus*, rachidian laterals and marginals. LACM 2363. Endeavour Segment, Juan de Fuca Ridge, *Alvin* dive 1447. Scale bar = 20  $\mu\text{m}$ .

at 13°N (Figs. 8A-C) and 21°N (Figs. 8E-F). There is little doubt that a single, highly variable species is represented. Radular characters of specimens from the Galapagos Rift (Fig. 11A) agree with those from 13°N (Figs. 11C-E). Protoconchs of specimens from the Galapagos Rift (Figs. 9A-C) compare well with those from 21°N (Figs. 9D-F).

**ETYMOLOGY.** The name is a Latin adjective meaning delightful.

### *Clypeosectus curvus* new species

Figures 10A-H, 11F

Slit-limpet; Tunnicliffe, 1988:353.

**DIAGNOSIS.** Outline broadly oval, profile high; apex more posterior and sculpture finer than that of *C. delectus*.

**DESCRIPTION.** Shell (Figs. 10A-C,G,H) small,

but moderately large for genus, maximum length 4.8 mm; periostracum thin, pale yellow-brown; outline of aperture broadly oval, nearly circular, neither end broader than other; margin of aperture not in same plane, sides raised relative to ends; apical whorl at nine-tenths shell length from anterior margin; highest elevation of shell at about two-thirds shell length from anterior margin. Profile high, height of holotype 0.43 times that of length. Protoconch sculpture unknown (coated on all specimens). First teleoconch whorl rounded, slightly descending below level of protoconch. Slit arising at position of three-fourths whorl in first teleoconch whorl, at which stage aperture expands to produce limpet form through one-half whorl of additional rotation. Slit open nearly half length of shell in dorsal view, directed to right in smooth, even curve, its position at lip at about 40 degrees off mid-dorsal line. Slit-borders sharply raised, slit open at edge of shell. Selenizone depressed below slit-border, additions to selenizone U-shaped. Radial sculpture of fine ribs; ribs arise in interspaces and assume equal prominence with original ribs so that pattern of primary and secondary ribs not apparent. Shell edge thin, easily broken. Muscle scar impressed, continuous anteriorly with broad pallial attachment scar extending anteriorly almost to slit on both sides (extent of forward position of muscle discernible from preserved specimen). Shell interior opaque, tending to be more transparent at muscle scar. Slit bordered by heavy deposition of callus on interior surface.

**External Anatomy** (Figs. 10D–G). As described for genus.

**Internal Anatomy.** Described by Haszprunar (1989).

**Radula** (Fig. 11F). As described for genus. Six pairs of lateral teeth, outermost lateral originating from basal unit regarded as lateromarginal plate; serrations of marginal teeth more numerous and more closely spaced than those of lateral teeth. Marginal teeth with filamentous distal tips.

**DIMENSIONS.** Length 4.6, width 4.0, height 2.0 mm (holotype).

**TYPE LOCALITY.** Hydrothermal vents near summit of Axial Seamount, Juan de Fuca Ridge off Washington (45°59.5'N, 130°03.5'W), 1575 m.

**TYPE MATERIAL.** Holotype and four paratypes from *Pisces IV* dive 1730, 31 July 1986. Holotype, USNM 859976. Additional paratypes from Axial Seamount and from Explorer Ridge near 50°N and Endeavour Segment, Juan de Fuca Ridge (Tables 1, 2). The holotype body remains wet-preserved; two paratype bodies were sectioned. Most of the specimens show some decalcification at the margin, although for the most part the material is in better condition than that of *C. delectus*. No juvenile specimens of *C. curvus* are known; the smallest known specimen has a length of 2.3 mm.

**DISTRIBUTION.** Hydrothermal-vent community of Explorer Ridge (49°45.6'N) and Juan de Fuca Ridge. On the Juan de Fuca Ridge known

from Endeavour Segment (47°57.0'N) and Axial Seamount (45°59.5'N) (Table 1).

**REMARKS.** This species differs from *C. delectus* in having an oval, nearly circular outline. The apical whorl is more posterior, the slit is more deflected to the right, the profile is higher, and the radial sculpture is finer than that of *C. delectus*.

**ETYMOLOGY.** The specific name is Latin for curved, calling attention to the curve of the selenizone in dorsal view.

### *Pseudorimula* new genus

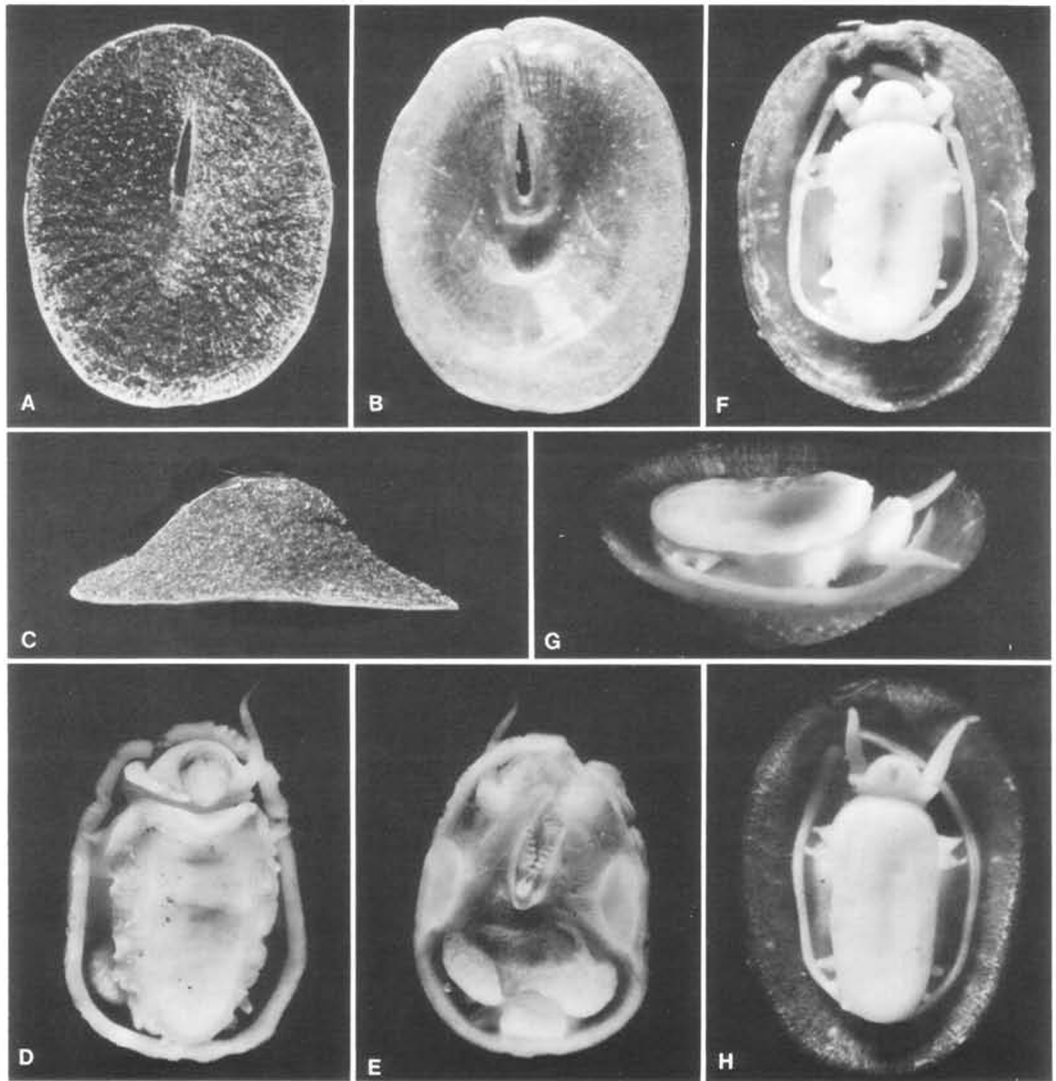
**TYPE SPECIES.** *Pseudorimula marianae* new species.

**DESCRIPTION.** Elevation moderate, apex deflected to right, posterior to center, not overhanging posterior margin. Foramen not curving to right in dorsal view; foramen sealed anteriorly. Mature shell nearly symmetrical; sculpture of raised lamellar elements aligned with strong radial ribs. Muscle scar consisting of three nearly equal elements: two lateral and one posterior elements.

**External Anatomy.** Anterior end of foot broad, foot tip with double anterior edge marking opening of anterior pedal gland; foot posterior rounded. Cephalic tentacles relatively long (preserved, contracted condition). Four posterior pairs of epipodial tentacles, on body wall midway between foot edge and thick border of mantle margin; two anterior pairs, with thick, joined bases, each with narrow projecting tips. Mantle skirt deeply emarginate, corresponding to foramen and seam in shell, edge of emargination with projecting papillae. Mantle skirt above head thin, nearly transparent. Shell muscles without hooks, macroscopically separate posteriorly; third muscle present posteriorly. Ctenidia of nearly equal size, right ctenidium slightly smaller.

**Radula.** Radular ribbon nearly symmetrical. Rachidian tooth with long, rounded, overhanging tip, edges serrated; shaft of rachidian broad at base. Five pairs of lateral teeth, similar in morphology to rachidian, outer edges with fine serrations, inner edges smooth; size of overhanging tips decreasing gradually away from rachidian, shafts of laterals increasing in length away from rachidian. Fifth lateral continuous with basal element regarded as lateromarginal plate; enlarged outer lateral lacking. Marginal teeth numerous, with spatulate tips, edges finely and sharply serrated, serrations similar to those of laterals. Marginals and outer laterals with one long denticle on outer edge of shaft near overhanging tip.

**REMARKS.** Unlike *Clypeosectus*, *Pseudorimula* has the slit sealed anteriorly, producing a shell that is stronger than that of *Clypeosectus*, many shells of which are broken in the present material. In this aspect it is convergent with shell morphology of the fissurellid genus *Rimula* DeFrance, 1827, which is a structural improvement over the design of *Emarginula* Lamarck, 1801. The greater symmetry of *Pseudorimula* also trends toward the condition



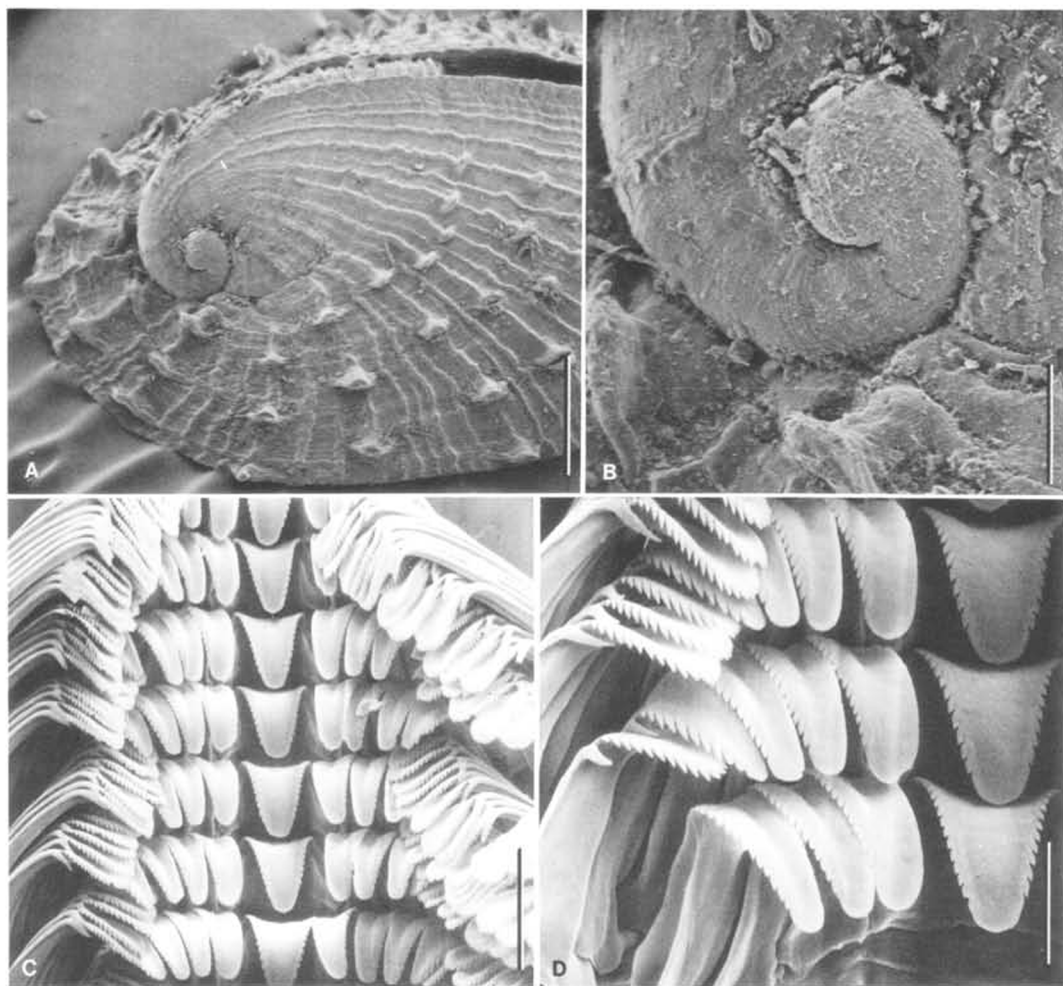
**Figure 12.** *Pseudorimula marianae*, shells and external anatomy. All from Mariana Back-Arc Basin, *Alvin* dive 1836. Anterior at top in all dorsal and ventral views. A–C. USNM 859977, holotype. Length 6.4 mm. A. Exterior, with thick coat of black mineral deposits. B. Interior. C. Left side. D,E. Body of holotype prior to sectioning. D. Ventral view, specimen with radula projecting. E. Dorsal view, showing posterior shell muscle and bipectinate ctenidia. F. LACM 2366a, paratype with body attached, ventral view. Length 6.1 mm. G,H. LACM 1366b, immature paratype specimen with body attached. Length 4.2 mm. G. Right side. H. Ventral view.

of nearly complete symmetry of fissurellids. The sculpture of *Pseudorimula* is also more characteristic of fissurellids in having primary and secondary ribs that increase in prominence with growth.

The muscle configuration, in which there is an irregular posterior element, is highly unusual, and is unknown in other limpet families. *Pseudorimula* has more pairs of epipodial tentacles than does *Clypeosectus*, thereby approaching the fissurellid condition to a greater extent than the latter genus. *Pseudorimula* further differs in lacking the genital process of *Clypeosectus*.

Only a single radular preparation for the type species was possible. As in *Clypeosectus*, there is difficulty in distinguishing between lateral and marginal teeth, which have similar morphology. The radula is very similar to that of *Clypeosectus*, including the presence of the long denticle on the outer edge of the shaft of the outer laterals and marginals, and the tendency of laterals and marginals to have a similar appearance. There is, however, no indication of the filamentous tip that is characteristic of the marginals of *Clypeosectus*. The radula further differs from that of *Clypeosectus* in





**Figure 13.** *Pseudorimula marianae*, juvenile shell, protoconch and radula. All from Mariana Back-Arc Basin, *Alvin* dive 1836. **A,B.** LACM 2367, immature shell. **A.** Oblique posterior-lateral view of apical area. Scale bar = 400  $\mu\text{m}$ . **B.** Protoconch. Scale bar = 100  $\mu\text{m}$ . **C,D.** USNM 859977, radular ribbon from holotype. **C.** Rachidian, laterals, and marginals. Scale bar = 40  $\mu\text{m}$ . **D.** Enlarged view of rachidian and laterals. Scale bar = 20  $\mu\text{m}$ .

having a less elongate shaft to the rachidian, a broader cusp with a more rounded tip, the laterals being serrate on the outer edges only, and fewer lateral teeth. There are at least five pairs of lateral teeth in *Pseudorimula marianae*, compared to nine in *C. delectus* and six in *C. curvus*.

*Pseudorimula* is monotypic for *P. marianae*, from the Mariana Back-Arc vents, western Pacific.

**ETYMOLOGY.** The generic name means false *Rimula*, owing to its resemblance to the fissurellid genus *Rimula* DeFrance, 1827. Gender: feminine.

### *Pseudorimula marianae* new species

Figures 12A–H, 13A–D

**DIAGNOSIS.** Outline oval, height moderate, sculpture radial with sharp imbrications, apex at two-thirds shell length from anterior margin, fo-

ramen one-half length of anterior slope, directed toward right.

**DESCRIPTION.** Shell (Figs. 12A–C, F–H, 13A, B) relatively large for family, maximum length 8.7 mm. Periostracum yellowish brown, tightly adhering, projecting slightly past shell margin and enveloping edge. Outline of aperture oval, slightly broader anteriorly; margin of aperture not in same plane, sides raised relative to ends; highest elevation of shell at about one-half its length. Profile moderately high, height of holotype 0.37 times length. Apical whorl at two-thirds shell length from anterior end, deflected to right; protoconch length 200  $\mu\text{m}$ , surface finely reticulate (Fig. 13B), first teleoconch whorl smooth, rounded, slightly descending below level of protoconch; slit arising three protoconch diameters away at position of one-half whorl of growth in first teleoconch whorl, at which stage

expansion of aperture produces limpet form through one-half whorl of additional rotation. Slit open one-half length of anterior slope, slightly deflected to right. Borders of foramen slightly raised, except anteriorly, where slit sealed and its trace slightly depressed. Selenizone weakly depressed below slit-border, additions to selenizone extending straight across. Sculpture of about 22 sharply defined primary ribs with one to three secondary ribs of equal prominence arising in interspaces. Concentric sculpture of fine growth lines, raised into sharp lamellar scales on crossing primary ribs. Muscle scars three, anterior-lateral scars rounded anteriorly, not joined to form horseshoe-shaped posterior element, but represented posteriorly by large irregular muscle scar. Anterior pallial attachment scars faint. Position of muscles more readily determined from comparison with preserved specimens. Thick seam of interior callus strengthens shell anterior to slit; interior further strengthened by transverse callus posterior to apical pit. Shell interior somewhat transparent, especially in region of muscle scars.

**External Anatomy** (Figs. 12D–H). As described for genus.

**Internal Anatomy.** Described by Haszprunar (1989).

**Radula** (Figs. 13C,D). As described for genus, with at least five pairs of lateral teeth.

**DIMENSIONS.** Length 6.4, width 5.2, height 2.4 mm (holotype).

**TYPE LOCALITY.** Snail Pit vents, Mariana Back-Arc Basin (18°10.95'N, 144°43.2'E), 3660 m.

**TYPE MATERIAL.** Holotype and three paratypes from *Alvin* dive 1836, 27 April 1987. Holotype USNM 859977. The holotype had the radula protruding, from which a piece was removed for the SEM preparation. One additional paratype (smallest specimen) from Alice Springs vent, Mariana Back-Arc Basin, *Alvin* dive 1843, 4 May 1987. For measurements and disposition of paratypes see Tables 1 and 2.

The three largest specimens are coated with black mineral deposits that partially obscure the sculpture. The two smallest specimens are relatively free of encrustations and show the periostracum.

**REMARKS.** The smallest shell (Figs. 13A,B) (length 2.7 mm) has a relatively longer foramen than that of the larger specimens, indicating that the foramen does not enlarge proportionally with increase in shell length.

**ETYMOLOGY.** The name refers to the type locality.

## DISCUSSION

Haszprunar shows in Part 2 (1989) that the slit-limpets represent two different anatomical plans that differ at the superfamily level, but which may be accommodated within existing superfamilies, the Scissurellacea (separated from Pleurotomariacea by Haszprunar) and the Fissurellacea. One group, the Clypeosectidae, differs sufficiently, particularly in its

reproductive anatomy, to warrant the establishment of a new family within the Fissurellacea. In the Scissurellacea, however, there are not sufficient differences in the internal anatomy to warrant the establishment of a separate family for the hydrothermal-vent genera, although there are radular and protoconch differences, as well as differences in anatomical details that justify the erection of two new subfamilies for these genera. Here I discuss the shell and radular characters that support the recognition of new suprageneric taxa in both superfamilies.

## CHARACTER STATES

### Protoconch

Sculpture of strong collabral ridges on the protoconch of *Scissurella*, *Sinezona* (Fig. 6C), and *Incisura* (Fig. 6E) is an apomorphy within Scissurellidae, limited to the most derived subfamily Scissurellinae. Lack of such sculpture in both the Temnocinclinae and the Clypeosectidae is clearly primitive, as it is unknown elsewhere among fossil and Recent archaeogastropods.

The finely ridged and deeply pitted protoconch of *Sutilizona* (Figs. 4D–F) is comparable to that of *Clypeosectus* (Figs. 9A–F). This evidently represents convergence between unrelated genera in different superfamilies.

### Teleoconch Sculpture

All previously known scissurellids other than *Incisura* (Fig. 6B) have strong axial (collabral) elements on the early teleoconch, a trait that is also shared with the new genera in the Temnocinclinae and Sutilizoninae (Figs. 4A–F). In contrast, fissurellids have strong spiral sculpture on the early teleoconch, never showing strong collabral sculpture at this stage of growth. The early sculpture of *Clypeosectus* (Figs. 9A–F) and *Pseudorimula* (Figs. 13A,B) is spiral, and comparable to that of fissurellids, except that the transition to the first teleoconch whorl does not include a sudden increase in diameter, as is frequent for fissurellids (e.g., McLean, 1985, fig. 7B).

In fissurellids the basic pattern of sculpture consists of primary radial (spiral) ribs that increase in size with growth, between which secondary and tertiary ribs appear and remain discernible. In *Anatoma* the secondary spiral cords attain the strength of the primary cords and become indistinguishable so that sculptural elements increase in number, not size. This is true also of *Temnocinclis*. However, *Temnozaga* has primary and secondary ribs that remain distinct, which implies a closer affinity of the latter genus to the Fissurellidae, but is more likely due to convergence.

The punctations that form pits on the early teleoconch sculpture of fissurellids are not present in any scissurellid or in the clypeosectids. Herbert and Kilburn (1986:1, figs. 1–6) showed that processes

of the mantle penetrate through pores in the shell and reach the exterior pits in fissurellids. Bandel (1982) suggested these processes to be homologous with aesthetes of chitons. If so, it would be an ancestral, plesiomorphic character. However, the polarity of this character is not clear, as it is limited to only a single archaeogastropod family.

### Slit

The slit in fissurellids may start early, almost in contact with the protoconch lip (e.g., *Nesta candida* H. Adams, 1870, figured by Bandel, 1982, pl. 10, fig. 3, and *Puncturella voraginosa* Herbert and Kilburn, 1986, fig. 68), or, more commonly, it may arise at one or more protoconch diameters away (e.g., *P. capensis* Thiele, 1919, figured by Herbert and Kilburn, 1986, fig. 65). In all scissurellids and in clypeosectids it starts three-fourths to one whorl away from the protoconch lip. An early start in some fissurellids is likely a convergent, derived character.

A sharply raised border to the slit and a depressed selenizone is a trait of all scissurellids and clypeosectids, but not of such fissurellid genera as *Emarginula* and *Rimula*. In the Fissurellacea this character is diagnostic for clypeosectids.

Among zeugobranchs, an open slit is primitive, whereas a closed slit is a convergent, derived character. Polarity in this character is evident from study of the fossil record of many zeugobranchs. Most groups, including three of the scissurellid subfamilies, as well as the clypeosectids and fissurellids, have representative genera with both conditions. The closed slit imparts obvious mechanical strength to the shell.

### Shell Muscle Scars

Emarginuline fissurellids (the oldest and most primitive members of the family) have unique hook-shaped terminations to the muscles and scars (e.g., MacClintock, 1963; McLean, 1984). The genera of the youngest fissurellid subfamily (Fissurellinae) and the two genera of clypeosectids lack the hooks. The apparent hook-shaped process of the left muscle scar of *Clypeosectus delectus* in Figure 7B is actually made by an extension of the pallial attachment muscle. Absence of hooks is a diagnostic, apomorphic character for Clypeosectidae.

Among scissurellids, the shell muscle of *Incisura* lacks hooks and is not joined posteriorly. *Temnocinclis* and *Temnozaga* are the first known scissurellid limpets with horseshoe-shaped muscles. Hook-shaped muscles are unknown in scissurellids.

The unusual shell muscle configuration of *Pseudorimula*, in which there are two lateral muscles and a single posterior muscle, is unlike that of all other limpets among diverse families. It is surprising that only one of the two clypeosectid genera has this condition. The evolutionary advantage of this tripartite pattern is unknown. Systematists who base their classifications on shell muscle conditions should take note of this apparently unique case.

### Radular Morphology

In the Scissurellidae, the temnocincline radula and the sutilizonine radula differ from those of anatominine and scissurelline scissurellids in lacking the enlarged fourth lateral that heretofore had been considered a hallmark of the family. There is a similar comparison within the Fissurellacea. The presence of an enlarged tooth is a hallmark of the Fissurellidae. Although clypeosectids are unique in having a relatively large number of lateral teeth (5 to 9 pairs), the chief distinctive feature of the clypeosectid radula is the lack of an enlarged outer lateral tooth. Thus, temnocinclines, sutilizonines, and clypeosectids are comparable in lacking enlarged outer laterals.

Character polarity for the lack of an enlarged lateral in the hydrothermal-vent slit-limpets is not clear. Lack of such a tooth could be primitive in both superfamilies or, more likely, it may represent a convergent loss, possibly due to less need for feeding specialization in the hydrothermal-vent habitat. Feeding by browsing on the bacterial films that are ubiquitous in the hydrothermal-vent habitat may not require the strongly developed outer lateral teeth. In fissurellids, the enlarged outer lateral teeth are the most functional, working teeth. However, food sources in shallow-water environments are more diverse and tougher in composition, including sponges, the principal food of emarginuline fissurellids.

Asymmetry in the rhipidoglossate radula has been discussed by Hickman (1981, 1983, 1984a). Asymmetry is unknown in scissurellid radulae, whereas most fissurellids have a moderately to highly asymmetrical radula. In fissurellids the asymmetry is correlated with the greatly enlarged fifth lateral and the necessity to stagger the placement of this element when the ribbon is folded. Although the anatominine and scissurelline scissurellids have an enlarged fourth lateral, it is not sufficiently large to require staggering of the opposing elements when this ribbon is enrolled; consequently, the scissurellid radula remains symmetrical. The clypeosectid radula is also symmetrical at least partly due to the lack of an enlarged outermost lateral tooth.

### FOSSIL RECORD OF SCISSURELLIDAE

Although the first appearance of Scissurellidae is cited as Cretaceous (Knight et al., 1960), K. Bandel (pers. comm. to G. Haszprunar) reports a Triassic record of the family.

Batten (1975) and Bourne (1910) argued that scissurellids were neotenuously derived from fissurellids, basing their arguments in large part on the depiction by Boutan (1885, pl. 42, fig. 5) of a scissurellid juvenile purported to represent a stage in fissurellid development. The supposed "*Scissurella*-stage" in fissurellid ontogeny was based on a misidentification of that figure, as separately noted by both Bandel (1982) and further detailed by McLean (1984, caption to fig. 6).