

NEW SLIT-LIMPETS (SCISSURELLACEA AND  
FISSURELLACEA) FROM HYDROTHERMAL VENTS.  
PART 1. SYSTEMATIC DESCRIPTIONS AND  
COMPARISONS BASED ON  
SHELL AND RADULAR CHARACTERS

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**ABSTRACT.** Six new species of slit-limpets endemic to the deep-sea hydrothermal-vent habitat have similar shells and similar external anatomy, but are placed in two families in separate superfamilies: Scissurellacea and Fissurellacea.

Taxonomic innovations for Scissurellacea (raised from family level by Haszprunar [1989]) include the recognition of four subfamilies in Scissurellidae: new subfamily *Temnocinclinae* with two new genera having open slits: *Temnocinclis*, monotypic for *T. euripes* new species from the Juan de Fuca Ridge, and *Temnozaga*, monotypic for *T. parilis* from 21°N on the East Pacific Rise; new subfamily *Sutilizoninae*: *Sutilizona* new genus with a closed slit, monotypic for *S. theca* from 12°N on the East Pacific Rise. Non-hydrothermal-vent scissurellids are retained in the new subfamily *Anatominiae* and the typical subfamily *Scissurellinae*. Subfamilies are defined on the basis of shared protoconch, radular, and gill characters.

Taxonomic innovations for Fissurellacea are the new family *Clypeosectidae* with two new genera: *Clypeosectus* with an open slit, and *Pseudorimula* with a closed slit and a unique, tripartite shell muscle. *Clypeosectus* has two new species, type species *C. delectus* from the Galapagos Rift and the East Pacific Rise at 13°N and 21°N, and *C. curvus* from the Juan de Fuca Ridge and the Explorer Ridge. *Pseudorimula* is monotypic for *P. marianae* new species from the Mariana Back-Arc Basin vents.

Study of anatomy by Haszprunar (1989) confirms the need for the new higher taxa, which are based on anatomical characters as well as shell and radular characters. As in all other scissurellids, there are no reproductive specializations in the new vent-associated scissurellid limpets. Clypeosectids have such fissurellacean characters as a reduced left kidney and anal gland, but differ in having a unique radula and a pedal gland, and lacking muscle hooks and pits on the early teleoconch; they further differ in being specialized for internal fertilization.

The new genera of both superfamilies lack the enlarged outermost lateral teeth that characterize the non-vent associated genera. This is interpreted as a convergent loss possibly due to a more easily processed food source of bacterial films in the hydrothermal-vent habitat.

As previously hypothesized for other hydrothermal-vent limpets, these groups may have entered the hydrothermal-vent habitat in the early Mesozoic, at the same time their superfamilies appeared and diversified in shallow water.

## INTRODUCTION

The recently discovered hydrothermal-vent community has produced a number of unusual new mollusks, among which gastropods of limpet form are exceptionally well represented. At latest summary (McLean, 1988b), seven superfamilies (four endemic) and eight families (seven endemic) were represented by 27 species.

Radulae characteristic of some of the hydrothermal-vent limpet groups have been illustrated (Hickman, 1983) prior to their formal descriptions. Except for the slit-limpets, brief preliminary notes on external features of the new groups of hydrothermal-vent limpets have been given by McLean (1985). Protoconchs and immature shells of many of the limpets, including two species of slit-limpets, have also been illustrated (Turner et al., 1985), although not identified to family or species.

To date, five new families of limpets from hydrothermal vents have been described: Neomphalidae in the new superfamily Neomphalacea (McLean, 1981), anatomy by Fretter et al. (1981); Pyropeltidae in the existing superfamily Lepetellacea (McLean and Haszprunar, 1987); Lepetodrilidae and Gorgoleptidae in the new superfamily Lepetodrilacea (McLean, 1988a), anatomy by Fretter (1988); and Peltospiridae in the new superfamily Peltospiracea (McLean, 1989), anatomy by Fretter (1989).

Slit-limpets from the hydrothermal-vent community were first noted by Turner (1980), who illustrated a shell of the species from the Galapagos Rift that is here described as *Clypeosectus delectus*. Other illustrations of shells of slit-limpets from the Galapagos Rift and from the East Pacific Rise at 21°N have been given by Lutz et al. (1984), Turner

and Lutz (1984), and Turner et al. (1985), who also included a species from 21°N identified as an "unnamed *Rimula*(?)," which is here described as *Temnozaga parilis*.

The caption to Turner's (1980) first figure of a slit-limpet (the species here described as *Clypeosectus delectus*) stated that "it is probably a living representative of a genus known in the fossil record from the Upper Jurassic to the Eocene." That allusion surely alluded to *Loxotoma* Fischer, 1885, a fissurellid that had a markedly asymmetrical slit (see Knight et al., 1960, fig. 141-7). On shell characters, however, the slit-limpets lack the pits that characterize the early teleoconch sculpture of all fissurellids (e.g., see Bandel, 1982, pl. 11, fig. 11). Hickman (1983) figured the radula of the same species from the Galapagos Rift, noting that it is unlike that of fissurellids, and concluded that the species is but "questionably allied to the Fissurellidae."

Although shells of the six species described here may suggest (except for the lack of pits) that these are fissurellid limpets, the first impression derived from the external morphology suggests that all are scissurellids, because all have a large anterior pedal gland (which is lacking in fissurellids) and all have relatively few epipodial tentacles (as in scissurellids, not fissurellids). In view of the unique radula previously figured by Hickman (1983), a study of the internal anatomy was necessary to establish relationships. Anatomy of these species is treated by Haszprunar (1989) in Part 2. His investigation of anatomy has indicated that a new family related to Fissurellidae should be erected for three species in two genera having the bizarre radular type originally figured by Hickman, and that limpets of the family Scissurellidae are also present in the hydrothermal-

vent community. The new scissurellids, however, have modified scissurellid radulae.

MATERIALS AND METHODS

Slit-limpets were found when the deep-sea hydrothermal-vent biological community was discovered in 1979 along the Galapagos Rift by the Woods Hole submersible *Alvin* (Corliss et al., 1979; Hessler and Smithey, 1983). In 1979, slit-limpets were again collected by the *Alvin* at the Galapagos Rift and at the East Pacific Rise at 21°N (Spiess et al., 1980; Hessler et al., 1985). In 1982, the limpets were collected at 13°N on the East Pacific Rise by a French expedition using the submersible *Cyana* (Desbruyeres et al., 1982; Desbruyeres and Laubier, 1983). Two additional species described here were first collected in 1983 with the submersible *Pisces IV* on the Juan de Fuca Ridge by a Canadian expedition (Chase et al., 1985; Tunnicliffe et al., 1985). Jones et al. (1985) give station data for all dives made by these submersibles through 1985.

Yet another species was discovered with the *Alvin* in 1987 at the Mariana Back-Arc Basin vents in the western Pacific (Hessler et al., 1988). The most recently discovered species was collected with the *Alvin* in March, 1988, on the East Pacific Rise at 12°N.

Hydrothermal-vent sites investigated by the *Alvin* that have not yielded slit-limpets are the Guaymas Basin, first visited in 1982, and the Florida Escarpment, first visited in 1984.

Mollusks were collected as part of the sampling program on most dives made by submersibles at hydrothermal-vent sites (for details of collecting procedures see Turner et al., 1985). Many of the limpets were collected along with samples of vestimentiferan tube worms by the mechanical arms of the submersibles. Specimens were dead on reaching the surface and were originally fixed for 24 hours in 5% seawater formalin buffered with sodium borate, washed in freshwater, and transferred to 70% ethanol.

Unlike all other newly described limpet groups from hydrothermal vents, none of the slit-limpets was abundant. For most species the number available was barely sufficient for description and, in some cases, not enough to provide specimens of both sexes for sectioning. Station data and numbers of specimens for dives yielding slit-limpets are summarized in Table 1. Measurements and disposition of all examined specimens are given in Table 2.

Except for Figures 4B,C and 9A-F, which have previously been published by Turner et al. (1985), and Figure 11A, previously published by Hickman (1983), the illustrations in this paper result from photographic and SEM work at the Natural History Museum of Los Angeles County.

Type material is placed in the Natural History Museum of Los Angeles County (LACM), the Museum of Comparative Zoology, Harvard University, Cambridge (MCZ), the Museum National d'Histoire Naturelle, Paris (NMNH), and the National Museum of Natural History, Washington, D.C. (USNM).

SYSTEMATICS

Order ARCHAEOGASTROPODA  
Thiele, 1925

Suborder VETIGASTROPODA  
Salvini-Plawen, 1980

Recent authors (Salvini-Plawen, 1980; Salvini-Plawen and Haszprunar, 1987; Haszprunar, 1988a,

1988b; Hickman, 1988) have discussed the problems inherent in the archaeogastropod concept, pointing out that the order Archaeogastropoda, as traditionally constituted (Thiele, 1925; Knight et al., 1960), represents a grade. Although Hickman (1988) has redefined and limited Archaeogastropoda to cover those superfamilies now treated by Salvini-Plawen and Haszprunar (1987) as the suborder Vetigastropoda (in so doing making Vetigastropoda a synonym of Archaeogastropoda), I have elected to follow Haszprunar (1988a, 1988b) in a classification scheme that allows Archaeogastropoda as an "orthophyletic grade" and Vetigastropoda as a clade.

Superfamily SCISSURELLACEA  
Gray, 1847

Justification for the removal of Scissurellidae from the Pleurotomariacea and elevation to superfamilial status is given by Haszprunar in (1989). As the superfamily contains but a single living family, the diagnosis that follows serves for that of the superfamily and family.

Family SCISSURELLIDAE  
Gray, 1847

**DESCRIPTION.** Coiled or limpetlike, interior nacre lacking, with shell slit, two shell muscles, and operculum. Protoconch finely reticulate (sometimes finely pitted), or with strong collabral ridges. Eyes (if present) with closed vesicles. Operculum retained in all genera. Rachidian tooth broad, base of shaft with lateral projections; overhanging cusp broad with one main denticle and smaller lateral denticles; lateral teeth narrow, cusps with several sharp denticles, shafts with laterally directed elbow; enlarged outer lateral present or absent; marginal teeth numerous.

**REMARKS.** Herbert (1986) has reviewed the systematics of Scissurellidae and discussed the shell and protoconch characters upon which the relatively few genera in the family have been based. Two groups were apparent, based on protoconch sculpture. The genera *Anatoma* Woodward, 1859, and *Sukashitrochus* Habe and Kosuge, 1964, have a finely reticulate protoconch, whereas the genera *Scissurella* d'Orbigny, 1824, and *Sinezona* Finlay, 1927, have strong collabral sculpture on the protoconch (Fig. 6C; see also Batten, 1975; Yaron, 1980; Bandel, 1982; Herbert, 1986). Here I add *Incisura* Hedley, 1904, to those with strong collabral sculpture (Fig. 6E). All of these genera have a basic radular plan in common: a broad, multicuspoid rachidian tooth, three lateral teeth of similar morphology, and an enlarged outer lateral tooth with numerous cusps (Figs. 6F,G).

The three new scissurellid genera from the hydrothermal-vent habitat (*Temnocinclis*, *Temnozaga*, and *Sutilizona*) do not have the collabral sculpture on the protoconch and share certain features

Table 1. Station data and number of specimens from dives yielding slit-limpets.

Dive	Depth (m)	Position	Date	Number
<i>Temnocinclis euripes</i>				
Alvin dives, Endeavour Segment, Juan de Fuca Ridge				
1447	2213	47°57.0'N, 129°06.0'W	03 Sep 1984	2
1452	2208	47°57.0'N, 129°0.60'W	07 Sep 1984	2
Pisces IV dive, Axial Seamount, Mid-Juan de Fuca Ridge				
1726	1575	45°59.5'N, 130°03.5'W	27 Jul 1986	4
Alvin dive, Southern Juan de Fuca Ridge				
1463	2250	44°39.2'N, 130°22.0'W	24 Oct 1984	3
<i>Temnozaga parilis</i>				
Alvin dives, East Pacific Rise at 21°N				
1226	2616	20°50.0'N, 109°06.0'W	10 May 1982	1
1229	2615	20°50.0'N, 109°06.0'W	14 May 1982	1
<i>Sutilizona theca</i>				
Alvin dive, East Pacific Rise at 12°N				
2003	2715	11°46.0'N, 103°47.0'W	25 Mar 1988	3
<i>Clypeosectus delectus</i>				
Alvin dives, Galapagos Rift				
733	2496	00°47.3'N, 86°07.8'W	16 Mar 1977	1
880	2493	00°47.6'N, 86°06.4'W	21 Jan 1979	1 + 1 juv.
884	2482	00°48.1'N, 86°07.0'W	25 Jan 1979	8 juv.
890	2447	00°48.9'N, 86°13.3'W	15 Feb 1979	1
895	2482	00°47.9'N, 86°09.3'W	20 Feb 1979	2 + 1 juv.
896	2460	00°48.2'N, 86°13.6'W	21 Feb 1979	3 juv.
984	2451	00°48.0'N, 86°13.0'W	01 Dec 1979	3
989	2482	00°48.0'N, 86°09.0'W	06 Dec 1979	1
991	2490	00°48.0'N, 86°09.0'W	08 Dec 1979	1
Cyana dive, East Pacific Rise at 13°N				
82-36	2633	12°48.6'N, 103°56.7'W	13 Mar 1982	4
Alvin dives, East Pacific Rise at 21°N				
1221	2618	20°50.0'N, 109°06.0'W	04 May 1982	2
1222	2614	20°50.0'N, 109°06.0'W	06 May 1982	1
1223	2616	20°50.0'N, 109°06.0'W	07 May 1982	1
1226	2616	20°50.0'N, 109°06.0'W	10 May 1982	10 + 8 juv.
<i>Clypeosectus curvus</i>				
Pisces IV dive, Explorer Ridge				
1494	1818	49°45.6'N, 130°16.1'W	01 Jul 1984	1
Alvin dive, Endeavour Segment, Juan de Fuca Ridge				
1447	2213	47°57.0'N, 129°06.0'W	03 Sep 1984	1
Pisces IV dives, Axial Seamount, Mid-Juan de Fuca Ridge				
1729	1575	45°59.5'N, 130°03.5'W	30 Jul 1986	1
1730	1575	45°59.5'N, 130°03.5'W	31 Jul 1986	5
1733	1575	45°59.5'N, 130°03.5'W	03 Aug 1986	2
<i>Pseudorimula marianae</i>				
Alvin dives, Mariana Back-Arc Basin				
1836	3660	18°10.95'N, 144°43.2'E	27 Apr 1987	4
1843	3640	18°12.6'N, 144°42.4'E	04 May 1987	1

of the external anatomy (monopectinate ctenidia, loss of eyes, cephalic tentacles lacking micropapillae). Additionally, they have a radular distinction in common: all lack the enlarged fourth lateral tooth. However, *Sutilizona* stands apart from *Temnocinclis* and *Temnozaga* in radular and protoconch characters. Because a number of shared characters can now be limited to groups of genera in Scissurellidae, it is necessary to recognize four groups at the subfamily level:

1. Anatominae, new subfamily for *Anatoma* and *Sukasitrochus*. Shell coiled, protoconch finely reticulate, radula with enlarged fourth lateral tooth, ctenidia bipectinate.

2. Scissurellinae, typical subfamily for *Scissurella*, *Sinezona*, and *Incisura*. Shell coiled or of limpet form, protoconch with strong axial ribs, radula with enlarged fourth lateral tooth, ctenidia bipectinate.

3. Temnocinclinae, new subfamily for the new genera *Temnocinclis* and *Temnozaga*. Shell of limpet form, protoconch finely reticulate, radula lacking enlarged fourth lateral tooth, ctenidia monopectinate.

4. Sutilizoninae, new subfamily for new genus *Sutilizona*. Shell of markedly asymmetrical limpet form, protoconch reticulate with deep pits, radula lacking enlarged fourth lateral tooth, marginal teeth similar to lateral teeth, ctenidia monopectinate.

The two new subfamilies (Temnocinclinae and Sutilizoninae) restricted to the hydrothermal-vent community are treated below in greater detail.

Waren and Bouchet (1989) illustrated a fragmentary specimen from *Alvin* dive 1214, East Pacific Rise near 21°N, identified as *Sinezona* sp., representing a scissurellid genus from shallow water. That record needs further confirmation before a species of *Sinezona* can be admitted to the hydrothermal-vent fauna.

TEMNOCINCLINAE new subfamily

TYPE GENUS. *Temnocinclis* new genus.

DESCRIPTION. Shell of limpet form, nearly symmetrical; slit remaining open at maturity, slit-borders with interlocking projections; protoconch finely reticulate, lacking collabral ridges. Radula lacking enlarged fourth lateral tooth. Ctenidia monopectinate, of equal size and position; cephalic tentacles non-papillate, eyes lacking.

For anatomical characters see Haszprunar (1989).

REMARKS. Two new genera (*Temnocinclis* and *Temnozaga*) known only from the hydrothermal-vent habitat share the above characters. Both genera are monotypic. The two species are unusually large-sized members of the family. Unique characters of this subfamily are the finely reticulate protoconch and the interlocking edges of the slit-borders, particularly near the anterior tip. The monopectinate ctenidia, the lack of eyes, and the lack of sensory papillae on the cephalic and epipodial tentacles are shared with the new subfamily Sutilizoninae.

Investigation by Haszprunar (1989) shows that

the internal anatomy of Temnocinclinae closely corresponds to that of shallow-water Scissurellidae, with no reproductive specializations, making this and the Sutilizoninae the only groups of hydrothermal-vent limpets not requiring the erection of a new family.

The limpet form in Scissurellidae is also known in *Incisura lytteltonensis* (E.A. Smith, 1894) (Figs. 6B,E,G), a species common in the intertidal zone in New Zealand. *Incisura* has a maximum length of 1.3 mm, which is about one-third the length of *Temnocinclis* and *Temnozaga*. *Incisura* continues to be erroneously assigned to Fissurellidae (e.g., by Powell, 1979:37, who had missed Bourne's (1910) study of the anatomy and radula). *Incisura* has an axially ridged protoconch (Fig. 6E) like that of *Sinezona* (Fig. 6C) and *Scissurella*. It lacks the sculptural elements of the teleoconch of other scissurellids and the slit-borders are not raised; it has an extremely short slit and selenizone (Fig. 6B). However, as in *Temnocinclis*, there is a reduction in the epipodial tentacles, compared to those of other scissurellids.

The extremely long slits of both *Temnocinclis* and *Temnozaga* are very different from the short slit of *Incisura* and appear to represent structural liabilities in the shell; yet, some stability and rigidity may result from the interlocking projections along the slit-borders (Figs. 1G, 2B).

The radula of temnocincline genera (Figs. 5A-D) agrees with that of other scissurellid genera in having little asymmetry between the left and right sides of the radular ribbon. Temnocincline genera lack the enlarged outer lateral tooth of other scissurellid genera, but the morphology of the rachidian and inner lateral teeth is clearly comparable to the condition in other scissurellid genera.

KEY TO GENERA

- Apical whorl overhanging posterior end of shell . . . . . *Temnocinclis*
- Apical whorl not overhanging shell posterior . . . . . *Temnozaga*

*Temnocinclis* new genus

TYPE SPECIES. *Temnocinclis euripes* new species.

DESCRIPTION. Shell elongate, relatively high; apical whorl posterior to apertural margin, not raised above it. Protoconch sculpture unknown (all specimens heavily coated with mineral deposits). Sculpture sharply clathrate; slit-borders raised, with interlocking projections in contact at anterior end. Broad band of periostracum stretched posteriorly across excavated columellar region of shell.

External Anatomy. Cephalic tentacles and ctenidia as diagnosed for subfamily. Three posterior pairs of epipodial tentacles; operculum small, multispiral, early volutions with raised edges.

Radula. Rachidian tooth broad, multicuspid; lat-

Table 2. Dive numbers, figure numbers, museum catalog numbers of holotypes and paratypes, dimensions, and condition of slit-limpet specimens. Except where indicated as dry, most specimens are maintained in alcohol because shells are decalcified at the margins. Dimensions are given in the order: length, width, and height.

Dive	Figure	Museum no.	Dimensions (mm)			Condition
<i>Temnocinclis euripes</i>						
1447a	—	USNM 859962	2.9 × 2.0 × 1.6	Shell decalcified at margin, body intact		
1447b	1E,F	LACM 2351	— — —	Shell fragmented, body sectioned (female)		
1452	5A,B	USNM 859963	3.7 × 2.3 × 1.6	Shell decalcified at margin, radula used		
1726a	1A-C	USNM 859964	3.8 × 2.4 × 1.5	Holotype, shell dry, body sectioned (male)		
1726b	1G,H	LACM 2352a	4.0 × 2.7 × 1.8	Shell decalcified at margin, body intact		
1726c	4A	LACM 2352b	2.5 × 1.6 × —	Shell dry, scanned, body intact		
1726d	—	USNM 859965	1.8 × 1.3 × 0.7	Shell decalcified at margin, body intact		
1463a	1D	LACM 2353a	3.8 × 2.4 × 1.7	Shell decalcified at margin, body intact		
1463b	—	LACM 2353b	— — —	Shell crushed, body intact		
1463c	—	MCZ 297060	3.8 × 2.5 × 1.7	Shell decalcified at margin, body intact		
<i>Temnozaga parilis</i>						
1226	2A-F, 4B,C	USNM 859966	4.1 × 3.0 × 1.7	Holotype, Turner et al., 1985, fig. 11		
1229	2G,H, 5C,D	LACM 2354	— — —	Shell missing, radula used, operculum intact		
<i>Sutilizona theca</i>						
2003a	4D-F,3C	USNM 859967	1.3 × 0.9 × 0.5	Holotype, shell scanned, body sectioned		
2003b	3A,B	LACM 2355a	1.3 × 0.9 × 0.5	Shell broken, body sectioned		
2003c	E,F	LACM 2355b	— — —	Shell in fragments, radula used		
<i>Clypeosectus delectus</i>						
—	9A-C	— —	1.9 × 1.4 —	Turner et al., 1985, fig. 9		
733	11A	— —	— — —	Hickman, 1983, fig. 5, radula		
880a	—	LACM 2356a	— — —	Shell broken (ca. 3 mm), no body		
880b	—	LACM 2356b	— — —	1 decalcified juvenile under 1 mm		
884	—	USNM 859968	— — —	8 decalcified juveniles under 1 mm		
890	—	USNM 859969	1.8 × 1.3 × 0.4	Shell decalcified at margin, body intact		
895a	—	MCZ 297601	4.2 × — × 1.0	Shell sides broken, margin decalcified, body intact		
895b	—	LACM 2357a	4.6 × — × 1.5	Shell sides broken, margin decalcified, body intact		
895c	—	LACM 2357b	— — —	1 decalcified juvenile under 1 mm		
896	—	MCZ 297062	— — —	3 decalcified juveniles under 1 mm		
984a	7A-E	USNM859970	5.2 × 3.7 × 1.2	Holotype, shell dry, body sectioned (female)		
984b	—	USNM 859971	4.5 × — × —	Shell sides and apex broken, body intact		
984c	11B	LACM 2358	4.0 × 3.0 × 1.3	Shell broken, radula used		
989	—	LACM 2359	— — —	Shell only, broken		
991	7F-H	LACM 2360	4.5 × 3.0 × 1.0	Shell margin decalcified, body intact		
82-36a	8A-D, 11C-E	MNHN —	3.2 × 2.3 × 1.2	Shell dry (4 separate bodies, radula used)		
82-36b	—	MNHN —	— — —	Shell dry, anterior end broken		
82-36c	—	MNHN —	— — —	Shell fragmented, dry		
1221a	8E-H	LACM 2361a	3.9 × 2.7 × 0.8	Shell intact, body intact		
1221b	—	LACM 2361b	1.8 × 1.3 × 0.6	Shell intact, body intact		
1222	—	USNM 859972	1.6 × 1.2 × 0.6	Shell intact, body intact		
1223	—	USNM 859973	— — —	Juvenile, shell decalcified		
1226a	9D-F	— —	0.9 × 0.7 × —	Turner et al., 1985, fig. 10		
1226b	—	LACM 2362a	3.6 × 2.8 × 1.1	Shell and body intact		
1226c	—	LACM 2362b	— — —	Shell and body crushed, ca. 4 mm long		
1226d	—	LACM 2362c	2.5 × 1.9 × 0.7	Shell decalcified, body intact		
1226e	—	LACM 2362d	— — —	2 small crushed, 2 decalcified juveniles under 1 mm		
1226f	—	USNM 859974a	3.2 × 2.2 × 1.1	Intact, partially decalcified at margin		
1226g	—	USNM 859974b	2.6 × 2.0 × 1.0	Intact, partially decalcified at margin		
1226h	—	USNM 859974c	2.5 × 1.8 × 0.8	Intact, partially decalcified at margin		
1226i	—	USNM 859974d	1.8 × 1.3 × 0.5	Intact, partially decalcified at margin		
1226j	—	USNM 859974e	1.7 × 1.2 × 0.5	Intact, partially decalcified at margin		
1226k	—	MCZ 297063a	3.1 × 2.3 × 0.9	Intact, partially decalcified at margin		
1226l	—	MCZ 297063b	2.3 × 1.5 × 0.7	Intact, partially decalcified at margin		
1226m	—	MCZ 297063c	2.0 × 2.6 × 0.6	Intact, partially decalcified at margin		

Table 2. Continued.

Dive	Figure	Museum no.	Dimensions (mm)	Condition
1226n	—	MCZ 297063d	1.6 × 1.1 × 0.4	Intact, partially decalcified at margin
1226o	—	MCZ 297063e	1.3 × 1.0 × 0.3	Intact, partially decalcified at margin
<i>Clypeosectus curvus</i>				
1494	—	USNM 859975	4.1 × 3.2 × 1.8	Shell chipped, body used for radular attempt
1447	10G, 11F	LACM 2363	2.4 — —	Shell fragmented, body used for radula
1729	—	MCZ 297064	4.8 × 3.7 × 2.0	Shell only, chipped near slit
1730a	10A-F	USNM 859976	4.6 × 4.0 × 2.0	Holotype, shell dry, body intact
1730b	10H	LACM 2364a	4.0 × 3.5 × 2.0	Shell dry, body sectioned (female)
1730c	—	LACM 2364b	4.4 × 3.8 × 2.0	Shell dry, chipped, body sectioned (male)
1730d	—	LACM 2364c	— — —	Shell fragments, radular attempt
1730e	—	LACM 2364d	3.4 × 2.4 × 1.6	Shell only, edges chipped
1733	—	LACM 2365	2.3 × 1.9 × 0.6	Shell margin decalcified, body intact
<i>Pseudorimula marianae</i>				
1836a	12A-E, 13C,D	USNM 859977	6.4 × 5.2 × 2.4	Holotype, shell dry, radula used, body sectioned (female)
1836b	12F	LACM 2366a	8.6 × 7.1 × 3.3	Shell dry, edges broken, body sectioned (male)
1836c	—	USNM 859978	6.1 × 4.9 × 2.5	Shell dry, body intact
1836d	12G,H	LACM 2366b	4.1 × 3.1 × 1.7	Shell in good condition, body intact
1843	13A,B	LACM 2367	2.7 × 2.0 × 0.8	Shell scanned, body intact

eral teeth three pairs, each with four denticles; basal part of shafts of laterals and inner marginal teeth fading into basal membrane of ribbon.

**REMARKS.** This genus is based on a single, previously unfigured species from the hydrothermal vents of the Juan de Fuca Ridge.

**ETYMOLOGY.** The generic name is a Greek compound of *temno*, to cut, and *kinklis*, lattice, suggested by the sculpture and deeply cut slit. Gender: feminine.

*Temnocinclis euripes* new species

Figures 1A-H, 4A, 5A,B

Split limpet; Tunnicliffe, 1988:353.

**DIAGNOSIS.** Shell asymmetrical, apical whorl projecting posteriorly, sculpture clathrate.

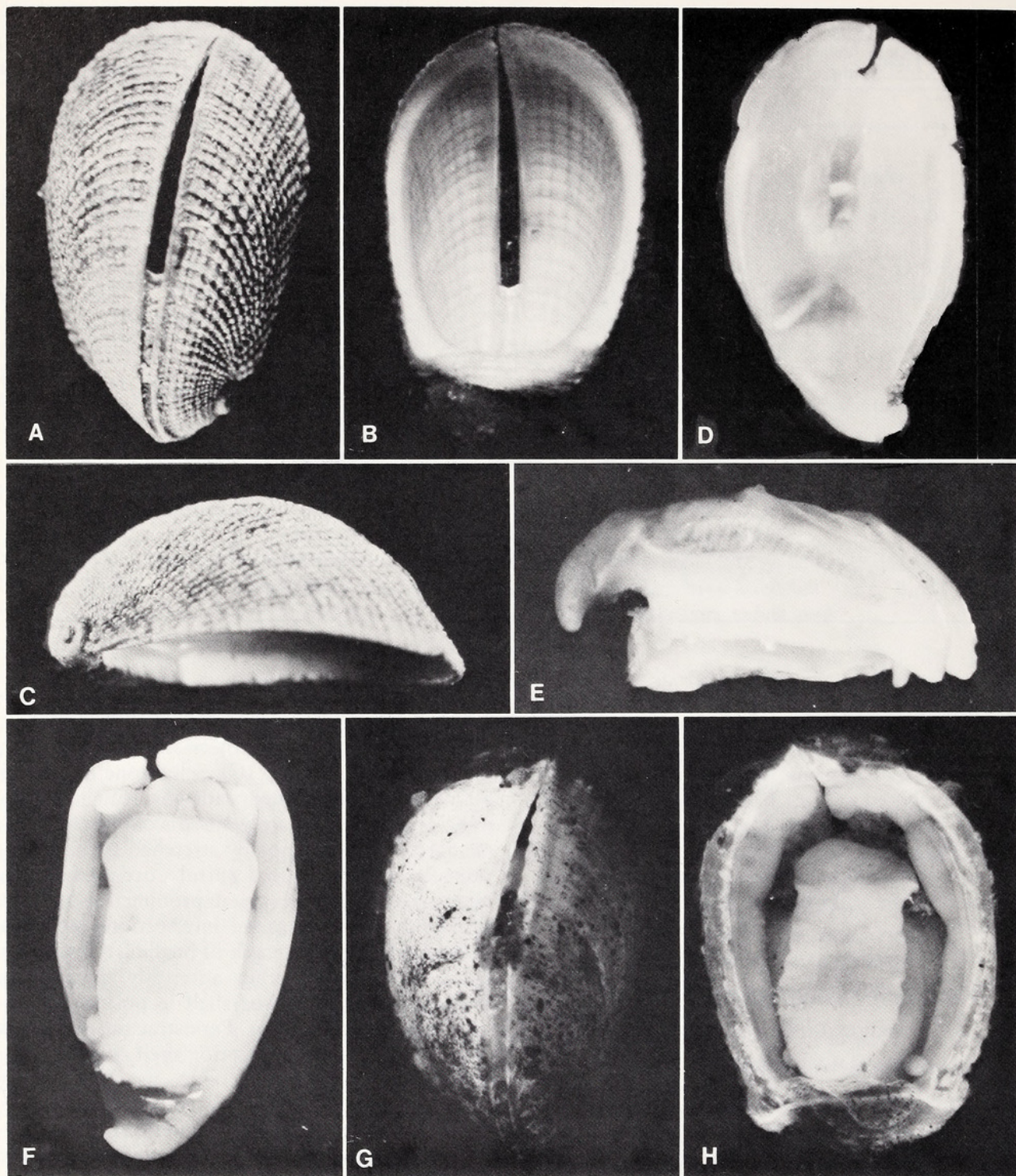
**DESCRIPTION.** Shell (Figs. 1A-C,G,H, 4A) large for family (maximum length 4.0 mm), thin; periostracum thick, light brown; outline of aperture elongate oval, anterior broader than posterior, margin of aperture in same plane; apical whorl (first whorl of teleoconch) projecting posteriorly. Profile relatively high; height of holotype 0.39 times length. Protoconch diameter 250 μm, surface sculpture unknown (all specimens coated, Fig. 4A). First whorl of teleoconch rounded, descending below protoconch; sculpture weak, both axial and spiral. Slit arising at position of three-fourths growth of first teleoconch whorl, at which stage aperture expands to produce limpet form through one-half whorl of additional rotation. Slit open more than half length of shell in dorsal view, dividing shell into nearly equal areas, its position only slightly deflected to

right in dorsal view. Slit-borders sharply raised, edges enveloped by periostracum; left and right sides of shell with interlocking projections along anterior termination of slit (Fig. 1G). Selenizone depressed below slit-borders, filled with fine lamellar additions. Sculpture of sharply raised axial ribs and spiral cords, forming laterally stretched beads at intersections. Additional spiral cords arising in interspaces, assuming equal prominence so that overall number of beaded intersections increases with growth while strength of beading remains the same. Apertural lip thin anteriorly, posteriorly forming broad, depressed shelf in position corresponding to columella. Periostracum stretched across depression of posterior shelf (Figs. 1B,H). Muscle scar barely detectable, its terminations rounded, extending anteriorly to position equal to greatest breadth of shell. Shell interior highly transparent, revealing exterior clathrate sculpture except near margin, where surface is somewhat opaque. Slit-border and previous positions of septum not marked by heavy deposition of interior callus.

**External Anatomy** (Figs. 1D-F,H). Cephalic tentacles non-papillate, thick, short (contracted condition); three posterior pairs of non-papillate epipodial tentacles. Shell muscle horseshoe-shaped, solid, muscle terminations rounded. Two monopectinate ctenidia, left slightly larger than right. Foot with double anterior edge marking opening of pedal gland; operculum attached to metapodium, multispiral with early volutions raised (Figs. 1F,H).

Internal anatomy is described by Haszprunar, (1989).

**Radula** (Figs. 5A,B). Radular ribbon nearly symmetrical. Rachidian tooth broad, with strong lateral



**Figure 1.** *Temnocinclis euripes*, shell and external anatomy. Anterior at top in dorsal and ventral views. A–C. USNM 859964, holotype. Axial Seamount, Juan de Fuca Ridge, *Pisces IV* dive 1726. Length 3.8 mm. A. Exterior view. B. Interior, showing band of periostracum across posterior margin. C. Right side. D. LACM 2353a, body of paratype, dorsal view. Southern Juan de Fuca Ridge, *Alvin* dive 1463. Length 3.4 mm. E, F. LACM 2351, body of paratype, prior to sectioning. Endeavour Segment, Juan de Fuca Ridge, *Alvin* dive 1447. E. Right side showing monopectinate right ctenidium. F. Ventral view, showing operculum attached to metapodium. G, H. LACM 2352a, paratype with attached body, showing less pronounced sculpture and decalcification at margin. Axial Seamount, Juan de Fuca Ridge, *Alvin* dive 1726. Length 4.0 mm. G. Dorsal view. H. Ventral view, showing attached operculum.

projections, overhanging edge with sharp pointed central cusp, flanked by five to six pairs of smaller pointed cusps. Three pairs of lateral teeth with similar morphology, overhanging cusps with four sharp denticles, decreasing in size from large innermost cusp; shafts of laterals with elbows corresponding

to lateral projections of rachidian; shafts below elbow fading into basal membrane of ribbon. Enlarged outer lateral and lateromarginal plate lacking. Marginal teeth numerous, cusps of similar size and with four pointed denticles like those of laterals; shafts of innermost marginals short, fading

into basal membrane in manner like that of laterals; shafts of outer marginals long, not clearly separated at base from those of adjacent marginals.

**DIMENSIONS.** Length 3.8, width 2.4, height 1.5 mm (holotype).

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

**TYPE MATERIAL.** Holotype and three paratypes from *Pisces IV* dive 1726, 27 July 1986. Holotype, USNM 859964 (Figs. 1A–C). Paratypes from this dive and other dives from the Endeavour Segment, Juan de Fuca Ridge, and other sites on the southern Juan de Fuca Ridge are distributed as indicated in Tables 1 and 2.

The holotype shell is the only specimen in good condition; it is preserved dry and the body has been sectioned. All specimens except the holotype exhibit some decalcification at the margin. No juvenile specimens smaller than a length of 1.8 mm are known.

**DISTRIBUTION.** Hydrothermal-vent community at Juan de Fuca Ridge, from northern Endeavour Segment (47°57.0'N) to southern section (44°39.2'N).

**REMARKS.** Sculpture ranges from sharply clathrate (holotype, Figs. 1A,C) to very weak (Fig. 1G). Of the present material, the holotype has the best-developed sculpture.

**ETYMOLOGY.** The specific name of the type species, from Greek *euripos*, means strait, or channel, referring to the slit.

### *Temnozaga* new genus

**TYPE SPECIES.** *Temnozaga parilis* new species.

**DESCRIPTION.** Shell elongate, relatively high; apical whorl close to apertural margin. Protoconch sculpture smooth with fine reticulations. Sculpture predominantly radial, concentric sculpture of raised lamellae. Slit-borders raised, with interlocking projections in contact at anterior end. Columella with angular posterior ridge.

**External Anatomy.** Cephalic tentacles and ctenidia as diagnosed for subfamily. Four posterior pairs of epipodial tentacles. Operculum small, multispiral, edges of early volutions raised. Ctenidia monopectinate.

**Radula.** Rachidian broad, overhanging tip narrow, with three main cusps, three pairs of lateral teeth, each with four denticles; basal part of shafts of laterals and inner marginals fading into basal membrane of ribbon.

**REMARKS.** This genus is based on a single, previously figured species from hydrothermal vents at 21°N on the East Pacific Rise.

*Temnozaga* and *Temnocinclis* share a number of features, including relatively large size for the family, the interlocking projections of the shell edge along the anterior contact, and similar opercular morphology. There are, however, two major dif-

ferences: the position of the apex, posterior to the shell margin in *Temnocinclis*, but not in *Temnozaga*, and, of more importance, the excavated posterior rim in *Temnocinclis*, over which the periostracum extends. There is no comparable structure in *Temnozaga*, which has a smooth posterior rim. There are also major differences in the radula: the rachidian and lateral teeth of *Temnocinclis* have more secondary cusps than those of *Temnozaga*, *Temnozaga* has a much narrower overhanging cusp on the rachidian tooth, and the innermost marginal teeth of *Temnozaga* have longer shafts than those of *Temnocinclis*.

**ETYMOLOGY.** The generic name is a Greek compound of *temno*, to cut, and part of zig-zag, with reference to the deeply cut slit and the interlocking projections of the shell along the slit margin anteriorly. Gender: neuter.

### *Temnozaga parilis* new species

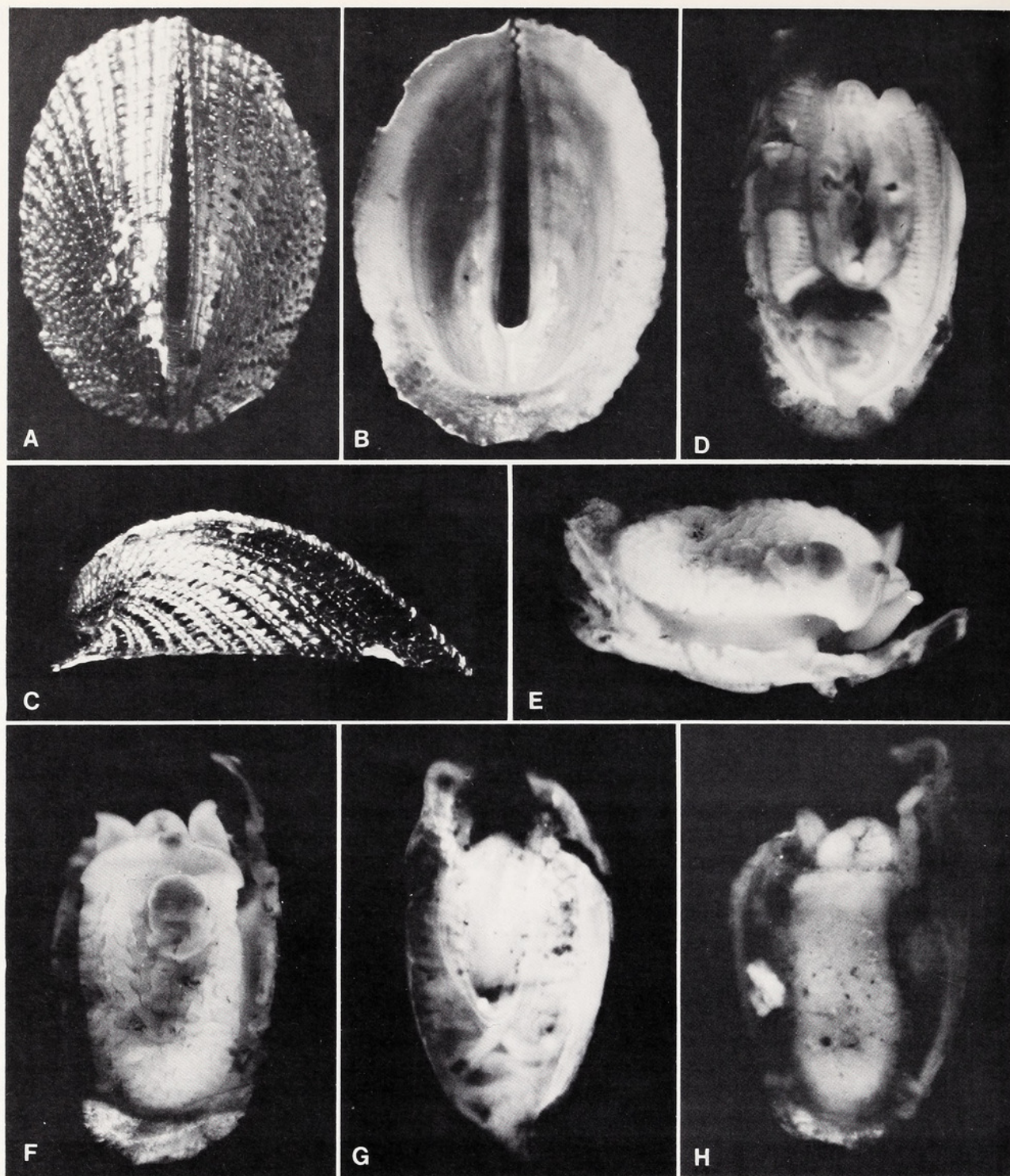
Figures 2A–H, 4B,C, 5C,D

Unnamed *Rimula*(?); Turner, Lutz, and Jablonski, 1985, figs. 11a–c (juvenile shell and protoconch).

**DIAGNOSIS.** Shell nearly symmetrical, apical whorl not projecting.

**DESCRIPTION.** Shell (Figs. 2A–C, 4B,C) relatively large for family (maximum length 4.0 mm); periostracum thick; outline of aperture elongate-oval, broader anteriorly. Margin of aperture nearly in same plane, sides raised slightly relative to ends. Highest elevation of shell at half its length. Profile moderately high, height of holotype 0.41 times length. Apical whorl nine-tenths shell length from anterior end, deflected to right. Protoconch diameter 170  $\mu$ m; protoconch surface smooth; first teleconch 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 teleconch whorl, at which stage expansion of aperture produces limpet form through one-half whorl of additional rotation. Slit open nearly three-fourths length of shell in dorsal view, not deflected to right. Slit-borders sharply raised, bearing alternating, interlocking projections in contact anteriorly. Selenizone depressed below slit-border, additions to selenizone slightly curved, projecting farther anteriorly on left side. Sculpture of about 30 strong primary ribs with one to three secondary and tertiary ribs arising in interspaces. Concentric sculpture of fine growth lines, raised into sharp lamellar scales on crossing primary radial ribs. Shell margin finely crenulated by ribs. Apertural lip thin anteriorly, forming angulate ridge posteriorly in position corresponding to columella. Shell interior opaque white, muscle scar barely detectable, its terminations rounded. Slit bordered by slightly raised callus deposition.

**External Anatomy** (Figs. 2D–H). Body nearly bilaterally symmetrical; cephalic tentacles thick, tapered, short (contracted condition); four posterior pairs of epipodial tentacles (strongly contracted),

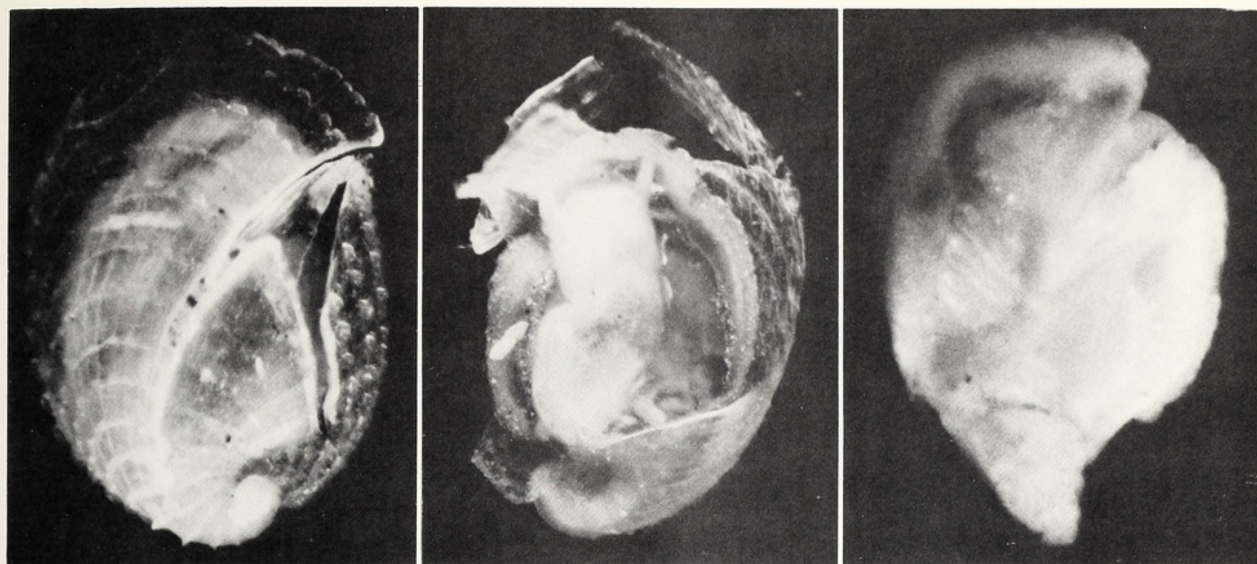


**Figure 2.** *Temnozaga parilis*, shell and external anatomy. East Pacific Rise at 21°N. Anterior at top in dorsal and ventral views. **A–C.** USNM 859966, holotype shell, photographed subsequent to gold coating for scanning and loss of pieces of periostracum. *Alvin* dive 1226. Length 4.0 mm. **A.** Exterior view. **B.** Interior view. **C.** Right side. **D–F.** Body of holotype prior to sectioning, mantle skirt torn away anteriorly. Length 2.5 mm. **D.** Dorsal view, showing paired monopectinate ctenidia by transparency through mantle skirt. **E.** Left side, showing folded operculum. **F.** Ventral view, showing inner side of iridescent operculum. **G,H.** LACM 2354, body of paratype (shell lost), prior to extraction of radula. *Alvin* dive 1229. Length 1.0 mm. **G.** Dorsal view, showing paired monopectinate ctenidia by transparency through mantle skirt. **H.** Ventral view, showing operculum and paired epipodial tentacles at posterior end of foot.

decreasing in size posteriorly, all tentacles non-papillate. Shell muscle horseshoe-shaped, of similar width throughout; muscle terminations rounded. Two monopectinate ctenidia of equal size, 27 leaflets visible on left ctenidium (right ctenidium damaged). Foot with double anterior edge marking

opening of pedal gland. Operculum 1.3 mm in diameter, at least six volutions, edges of early volutions raised (Figs. 2E,F).

**Radula** (Figs. 5C,D). Radular ribbon slightly asymmetrical. Rachidian tooth broad, its basal area expanded, neck of overhanging tip narrow, with



**Figure 3.** *Sutilizona theca*, shell and external anatomy. East Pacific Rise at 12°N. Anterior at top in dorsal and ventral views. **A,B.** LACM 2355a, paratype with body attached, prior to sectioning. *Alvin* dive 2003. Length 1.3 mm. **A.** Dorsal view. **B.** Ventral view. **C.** USNM 859966, holotype body prior to sectioning, showing monopectinate ctenidia by transparency, the left larger than the right. *Alvin* dive 2003. Length 1.2 mm.

sharp pointed central cusp, flanked by one relatively large cusp on either side, sometimes with smaller cusps between. Three pairs of similar lateral teeth, overhanging edge with one major cusp and one or two minor cusps; shafts of laterals with elbows corresponding to basal projections of rachidian; shafts below elbow fading into basal membrane of ribbon. Enlarged outer lateral and lateromarginal plate lacking. Marginal teeth numerous, cusps of similar size and with denticles like those of laterals, shafts with strong indentation near tip; shafts of all marginals long, those of outermost marginals not clearly separated from those of adjacent marginals.

**DIMENSIONS.** Length 4.1, width 3.0, height 1.7 mm (holotype).

**TYPE LOCALITY.** East Pacific Rise at 21°N (20°50.0'N, 109°06.0'W), 2616 m.

**TYPE MATERIAL.** Holotype from *Alvin* dive 1226, 10 May 1982. Holotype, USNM 859966. The shell had been coated with gold for SEM by R. Lutz (Figs. 4B,C) prior to photography (Figs. 2A–C), which accounts for its present metallic appearance. The holotype body (Figs. 2D–F) has been sectioned by Haszprunar; the operculum remains intact. Paratype (LACM 2354, Figs. 2G,H) from *Alvin* dive 1229, single body 1.0 mm long of which the anterior end was used for the radular preparation; the posterior part of the body with operculum attached remains.

**DISTRIBUTION.** Hydrothermal-vent habitat of East Pacific Rise at 21°N.

**REMARKS.** The imbricate sculpture on the radial ribs resembles that of the clypeosectid *Pseudorimula marianae* new species, but that represents convergence in shell characters between two families in different superfamilies. Differences from *Temnocinclis euripes* are treated above.

**ETYMOLOGY.** The specific name is Latin for equal, denoting the symmetry of the teleoconch shell.

### SUTILIZONINAE new subfamily

**TYPE GENUS.** *Sutilizona* new genus.

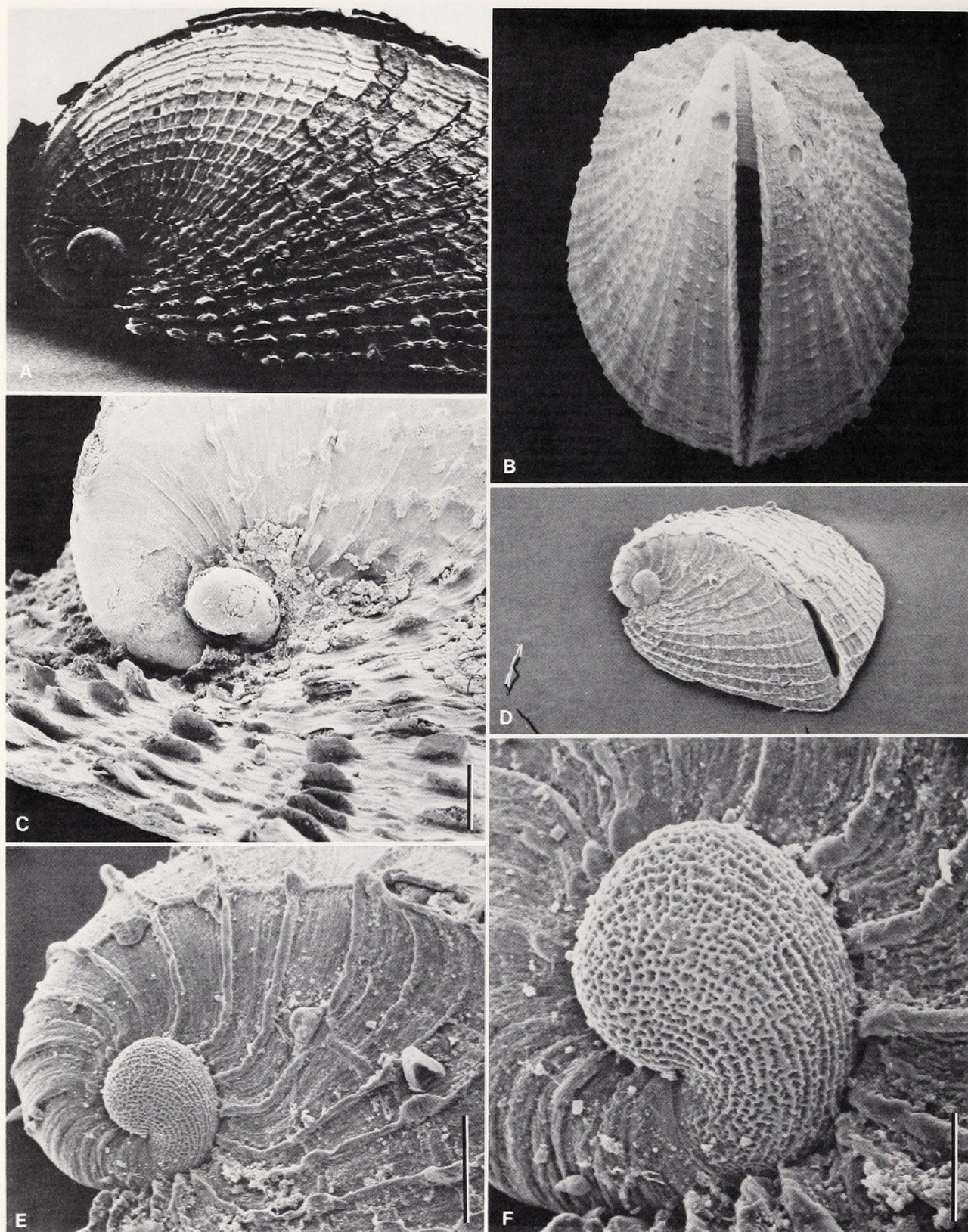
**DESCRIPTION.** Shell of strongly asymmetrical limpet form, retaining a coiled portion; slit closed (fused) at maturity. Protoconch reticulate with deep pits. Radula lacking enlarged fourth lateral tooth, marginal teeth similar to lateral teeth. Ctenidia monopectinate, of unequal shape and position; cephalic and epipodial tentacles non-papillate, eyes lacking.

For anatomical characters see Haszprunar (1989).

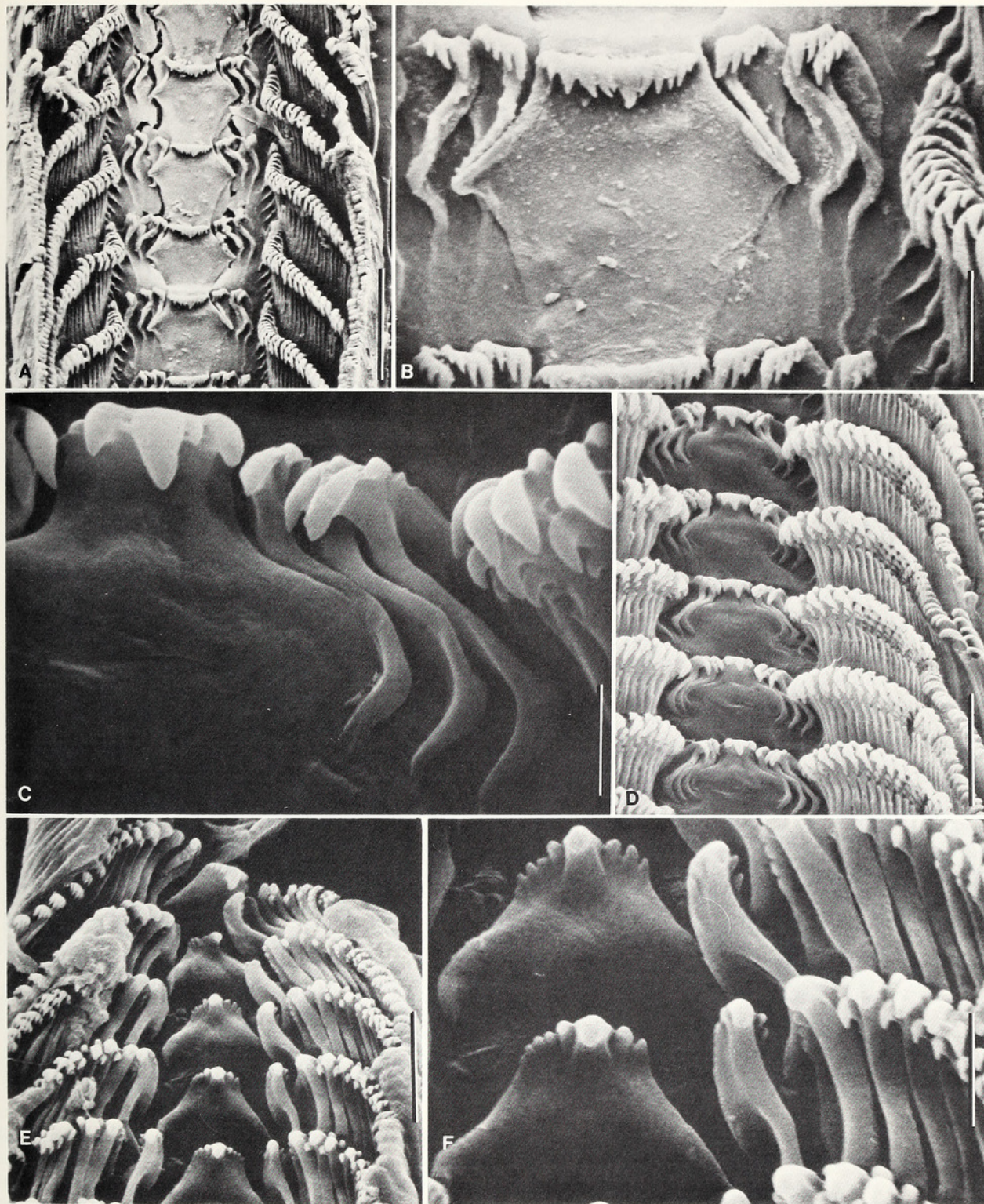
**REMARKS.** Although the new genus *Sutilizona* has monopectinate ctenidia, as do both genera of the new subfamily Temnocinclinae, additional characters of the protoconch and radula are unique to it, and are not represented in any other genus of Scissurellidae. Haszprunar (1989) finds further justification for separating this genus at the subfamily level.

In shell characters *Sutilizona* is unlike *Temnocinclis* and *Temnozaga* in having no posterior ridge for muscle insertion on the shell interior, in retaining a posterior coiled portion visible on the interior side, and in having the slit sealed anteriorly in mature specimens. The anteriorly sealed slit is a character shared with the shallow-water scissurellid genera *Sinezona* (subfamily Scissurellinae) and *Sukashitrochus* (subfamily Anatominae), each of which is assigned to a different subfamily on the basis of radular and protoconch characters.

The radula of *Sutilizona* is more similar to that of *Temnozaga* than to *Temnocinclis* in having a



**Figure 4.** SEM views of early sculpture and protoconchs of scissurellids from hydrothermal vents. **A.** *Temnocinclis euripes*. LACM 2352b, right lateral view of paratype, in which surface of protoconch has exfoliated. Axial Seamount, Juan de Fuca Ridge, *Pisces IV* dive 1726. Length 2.7 mm. **B,C.** *Temnozaga parilis*. USNM 859966, holotype shell (after Turner et al., 1985, figs. 11a,b). East Pacific Rise at 21°N, *Alvin* dive 1226. Length 4.0 mm. **B.** Exterior view, anterior at bottom. **C.** Enlarged view of apical area showing lamellar sculpture and eroded protoconch. Scale bar = 100  $\mu$ m. **D-F.** *Sutilizona theca*. USNM 859967, holotype shell. East Pacific Rise at 13°N, *Alvin* dive 2003. Length 1.3 mm (anterior end broken). **D.** Oblique view of entire shell from left side (anterior end broken to left of foramen). Scale bar = 400  $\mu$ m. **E.** Protoconch and early teleoconch sculpture. Scale bar = 100  $\mu$ m. **F.** Enlarged view of protoconch showing pits. Scale bar = 40  $\mu$ m.



**Figure 5.** SEM views of radulae of hydrothermal-vent scissurellids. **A,B.** *Temnocinclis euripes*. USNM 859963. Endeavour Segment, Juan de Fuca Ridge, *Alvin* dive 1452. **A.** Full width of radular ribbon. Scale bar = 40  $\mu$ m. **B.** Rachidian, three pairs of laterals, and inner marginals. Scale bar = 10  $\mu$ m. **C,D.** *Temnozaga parilis*. LACM 2354. East Pacific Rise at 21°N, *Alvin* dive 1229. **C.** Rachidian, laterals, and tips of inner marginals. Scale bar = 4  $\mu$ m. **D.** Half width of ribbon. Scale bar = 20  $\mu$ m. **E,F.** *Sutilizona theca*. LACM 2355b. East Pacific Rise at 13°N, *Alvin* dive 2003. **E.** Full width of ribbon. Scale bar = 10  $\mu$ m. **F.** Rachidian, laterals, and inner marginals. Scale bar = 4  $\mu$ m.

narrower overhanging cusp and relatively few secondary cusps on the rachidian and lateral teeth. It differs primarily in the lack of morphological distinction between lateral and marginal teeth, making it unclear whether there are two or three pairs of

lateral teeth. Marginal teeth of *Temnozaga* (Fig. 5C) may be distinguished from lateral teeth in having a significant indentation high on the shaft, but there is no indentation on the marginals of *Sutilizona*.



**Figure 6.** SEM views (except B) of shells, protoconchs, and radulae of non-hydrothermal vent scissurellids. **A.** Shell of *Anatomia lyra* (Berry, 1947). LACM 82-64. Cordell Bank, California, 50 m. Height 0.8 mm. **B.** Shell of *Incisura lytteltonensis* (E.A. Smith, 1894). LACM 47-3. Stewart Island, New Zealand. Length 1.3 mm. **C.** Shell of *Sinezona rimuloides* (Carpenter). LACM 66-57. Carmel, California. Height 0.8 mm. **D.** Protoconch of *Anatomia lyra*, showing smooth surface with irregular reticulation. Same specimen as in Figure 6A. Scale bar = 100  $\mu$ m. **E.** Protoconch of *Incisura lytteltonensis*, showing strong axial ridges. Same lot as Figure 6B. Scale bar = 100  $\mu$ m. **F.** Radula of *Anatomia crispata* (Fleming, 1832), showing rachidian (right center) and four pairs of laterals, the enlarged outermost (at left) with pointed tip and serrations on inner side. Scale bar = 20  $\mu$ m. **G.** Radula of *Incisura lytteltonensis*, showing rachidian (at left) and four pairs of laterals, the enlarged outermost (at right) with numerous strong serrations on inner side. Scale bar = 10  $\mu$ m.

### *Sutilizona* new genus

**TYPE SPECIES.** *Sutilizona theca* new species.

**DESCRIPTION.** Shell oval and relatively low; apical whorl sharply offset to right and directly above

posterior margin. Protoconch with deep pits. Sculpture predominantly concentric, radial sculpture suggested by linear alignment of raised lamellae. Slit-borders not raised, slit sealed anteriorly. Shell interior retains coiled portion at posterior.

**External Anatomy.** Cephalic and epipodial tentacles non-papillate, epipodial tentacles one posterior pair. Operculum small. Ctenidia monopectinate, unequal.

**Radula.** Rachidian tooth broad at base, overhanging tip narrow; with one prominent and two to four smaller cusps; lateral teeth at least two pairs, of similar morphology as marginal teeth.

**REMARKS.** This genus is based on a single species from hydrothermal vents at 12°N on the East Pacific Rise.

**ETYMOLOGY.** The generic name is a compound of the Latin *sutilis*, sewn together, and Latin *zona*, belt, referring to the sealed selenizone of mature specimens. Gender: feminine.

### *Sutilizona theca* new species

Figures 3A–C, 4D–F, 5E,F

**DIAGNOSIS.** Slit closed at maturity, shell retaining coiled portion.

**DESCRIPTION.** Shell (Figs. 3A,B, 4D–F) small for family (possibly immature), maximum length 1.3 mm; periostracum thin; outline of aperture oval, broader anteriorly. Apical whorl deflected to right and overhanging posterior margin; protoconch diameter 250  $\mu$ m; protoconch sculpture drawn into elongate rows with deep pits. First teleoconch whorl rounded, with strong collabral (axial) ribs; slit arising two protoconch diameters away at position of three-fourths whorl of growth in first teleoconch whorl, at which stage expansion of aperture produces limpet form. Slit sealed anteriorly at shell length of 0.9 mm, open only one-fourth length of shell in dorsal view, slit and selenizone strongly curved to right. Slit-borders not sharply raised; selenizone not depressed below slit-border. Spiral sculpture weak except for one strong rib arising at one-half whorl of growth in first teleoconch whorl and extending to slit-band. Concentric sculpture strong, producing raised lamellar scales on crossing weak radial sculpture. Apertural lip thin and fragile. Shell interior transparent, muscle scar not deeply impressed, slit and selenizone bordered by raised ridges of callus. Shell interior retaining coiled portion posteriorly.

**External Anatomy** (based on 1.3 and 1.1 mm bodies; Figs. 3B,C). Body asymmetrical; cephalic tentacles slender, moderately long (contracted condition); one posterior pair of epipodial tentacles. Shell muscle horseshoe-shaped, longer on left side, muscle terminations expanded inwardly. Left ctenidium monopectinate, up to seven leaflets visible through transparent mantle skirt in larger specimen, four in smaller specimen. Right gill not visible through mantle. Foot with double anterior edge marking opening of pedal gland. Operculum small, nearly transparent, diameter about 0.5 mm in larger specimen.

Internal anatomy is described by Haszprunar (1989).

**Radula** (Figs. 5E,F). Radular ribbon symmetrical. Rachidian tooth broad, its basal area expanded, neck of overhanging tip narrow, with sharp pointed central cusp, flanked by two to four smaller irregular cusps. Lateral teeth at least two pairs, each with large main cusp and one to two smaller cusps on each side; first lateral with depression on front surface to fit edge of rachidian; second lateral similarly shaped to fit against first lateral. Shafts of lateral teeth and marginal teeth long, their bases concealed by cusps of row below. Third and subsequent teeth in row not clearly distinguishable as either laterals or marginals.

**DIMENSIONS.** Length 1.1 (shell anterior broken, projected length 1.3), width 0.9, height 0.5 mm (holotype).

**TYPE LOCALITY.** On sulfide mounds at base of inactive chimney, East Pacific Rise near 12°N (11°46'N, 103°47'W), 2715 m.

**TYPE MATERIAL.** Holotype and two paratypes from *Alvin* dive 2003, 25 March 1988. Holotype, USNM 859967; two paratypes, LACM 2355 (Tables 1, 2). All specimens are in damaged condition. The holotype (Figs. 4D–F) has been coated for SEM and the body removed for sectioning. One paratype (Figs. 3A,B), initially broken, has been separated from the shell for sectioning, resulting in further breakage. The third paratype was initially so decalcified that nothing but shell fragments remain; the body was used for radular extraction.

**DISTRIBUTION.** Hydrothermal vents of East Pacific Rise near 12°N.

**REMARKS.** It is possible that the present specimens are immature, considering that their ctenidia are so poorly developed: one specimen showed seven leaflets and the other four on the left ctenidium. However, the closed slit seems to suggest that the specimens may be mature. In *Sinezona* (subfamily Scissurellinae) the slit is open during most of the growing phase and is closed only at maturity.

**ETYMOLOGY.** The specific name *theca* is Latin, sheath, a feminine noun in apposition referring to the coiled portion of the shell that is retained in the interior (ventral) view.

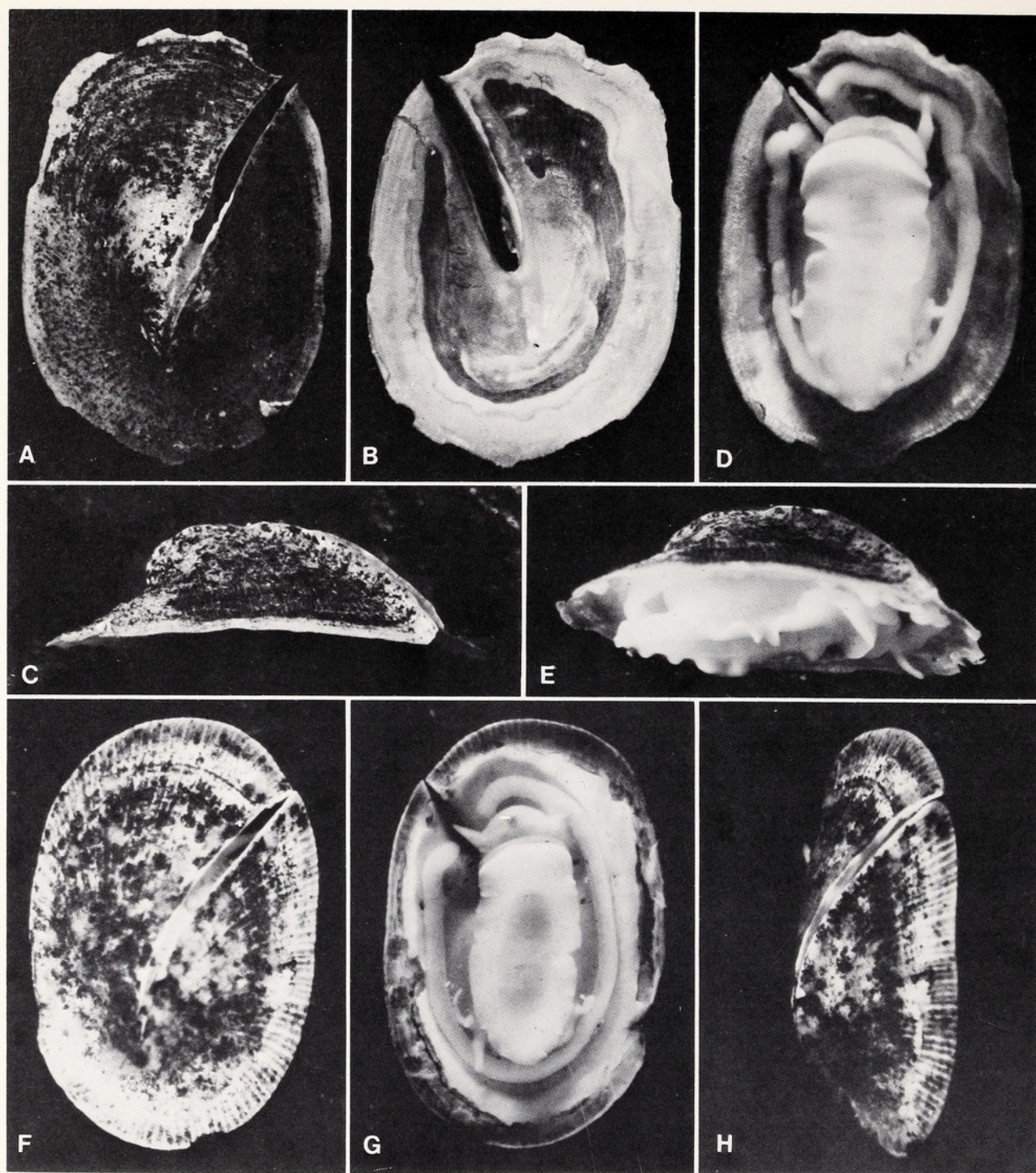
## Superfamily FISSURELLACEA Fleming, 1822

### CLYPEOSECTIDAE new family

**TYPE GENUS.** *Clypeosectus* new genus.

**DESCRIPTION.** Shell of limpet form with deep, asymmetrical slit or foramen; slit-borders raised, nearly in contact or sealed at anterior end. Apex deflected to right, not overhanging posterior margin. Shell lacking pits (or pores) on early teleoconch. Muscle scar without inturned hooked-process of fissurellids; anterior extension of pallial attachment scar producing false muscle scar.

**External Anatomy.** Eyes lacking, cephalic tentacles not papillate. Epipodial tentacles not papil-



**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  $\mu$ 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.

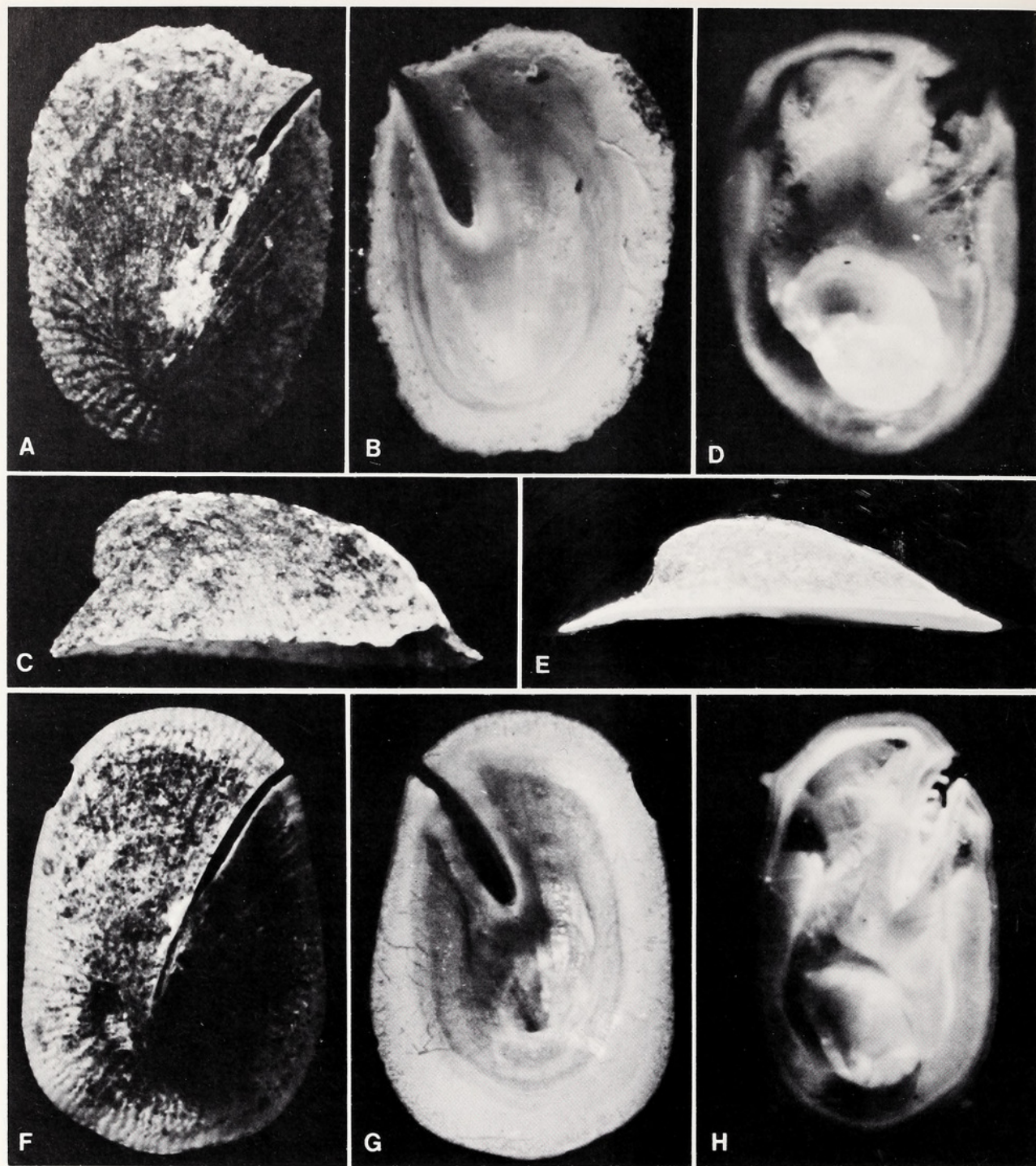
**External Anatomy.** Anterior end of foot broad, its tip with double anterior edge marking opening of pedal gland; foot posterior obtusely pointed; sole of foot with broad mid-ventral depressed area. Cephalic tentacles relatively long (preserved, contracted condition), the right seeming to project through 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

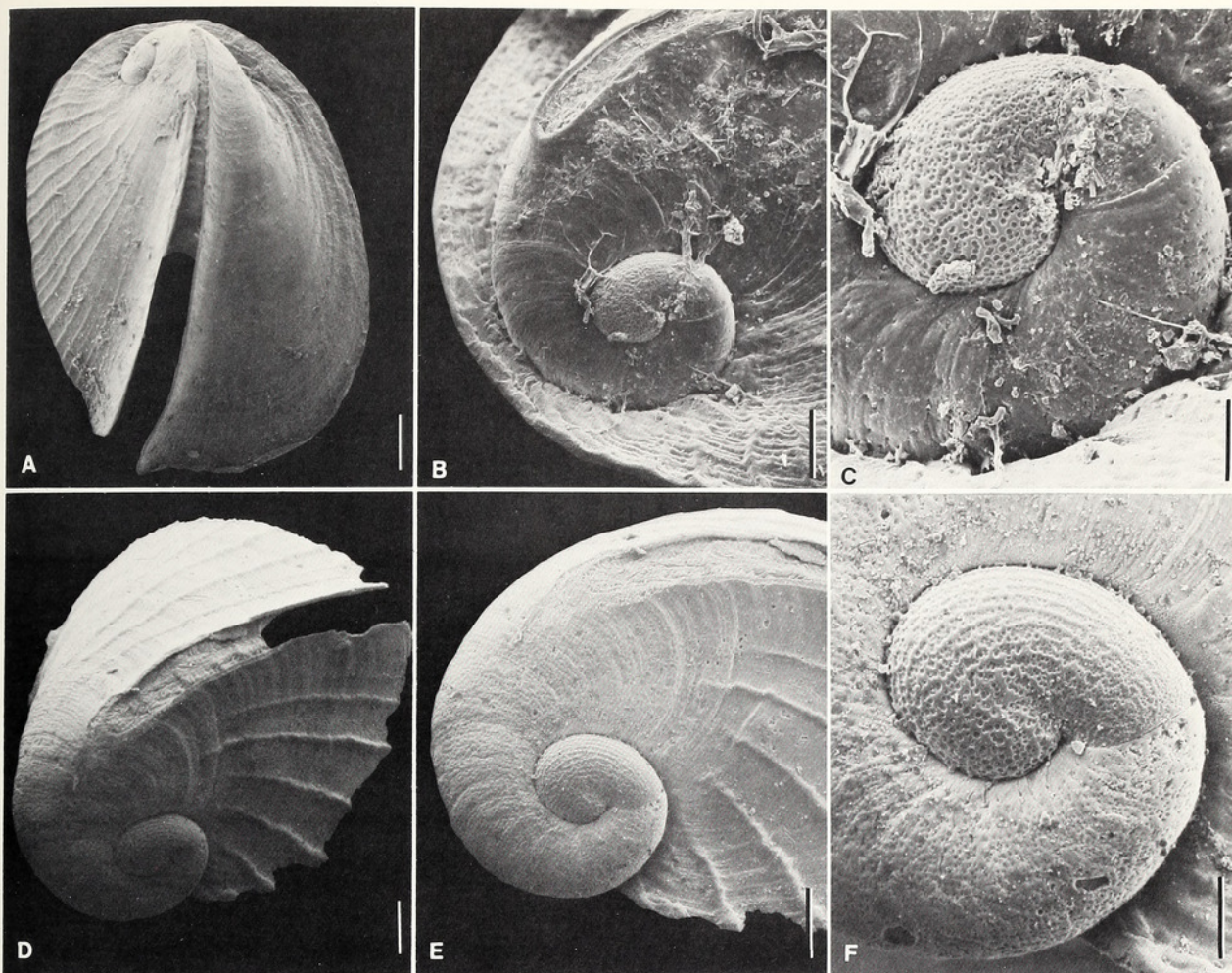
Figures 7A-H, 8A-H, 9A-F, 11A-E

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  $\mu$ m. B. Posterior lateral view, showing protoconch and selenizone. Scale bar = 100  $\mu$ m. C. Enlarged view of protoconch, showing ridges and deep pitting. Scale bar = 50  $\mu$ m. D–F. East Pacific Rise at 21°N, *Alvin* dive 1226. D. Posterior dorsal view. Scale bar = 100  $\mu$ m. E. Lateral view. Scale bar = 100  $\mu$ m. F. Enlarged view of protoconch, showing ridges and deep pitting. Scale bar = 50  $\mu$ 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  $\mu$ 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.

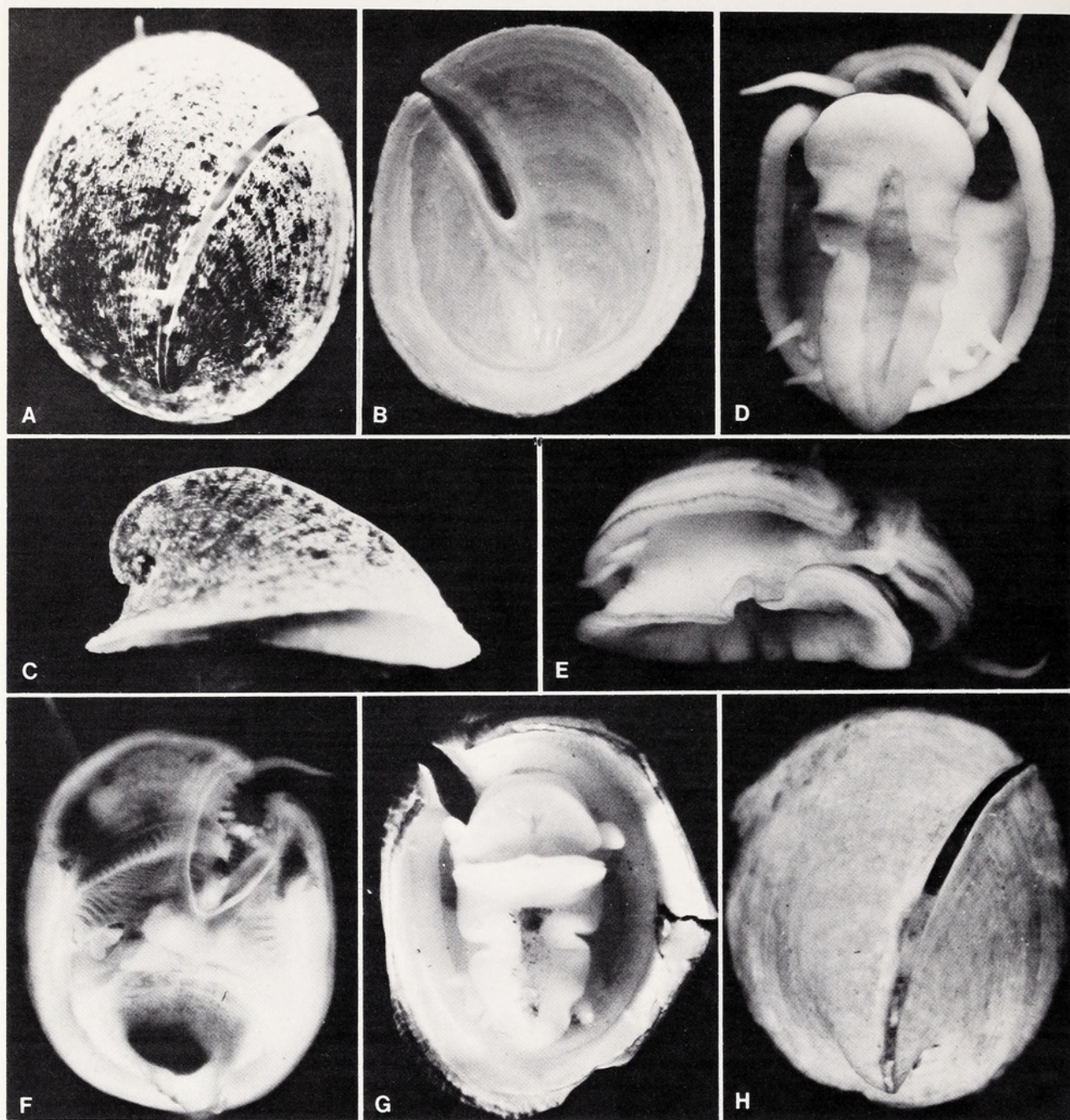
**Internal Anatomy.** Described by Haszprunar (1989).

**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  $\mu$ m. **B.** *C. delectus*, showing filamentous tips of marginals folded over central field. LACM 2358. Galapagos Rift, *Alvin* dive 984. Scale bar = 10  $\mu$ 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  $\mu$ m. **D.** Full width of ribbon, showing marginals of left side folded over and those of right side folded back. Scale bar = 40  $\mu$ m. **E.** Enlarged view of base of marginals, showing fusion at base and filamentous tips. Scale bar = 20  $\mu$ m. **F.** *C. curvus*, rachidian laterals and marginals. LACM 2363. Endeavour Segment, Juan de Fuca Ridge, *Alvin* dive 1447. Scale bar = 20  $\mu$ 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

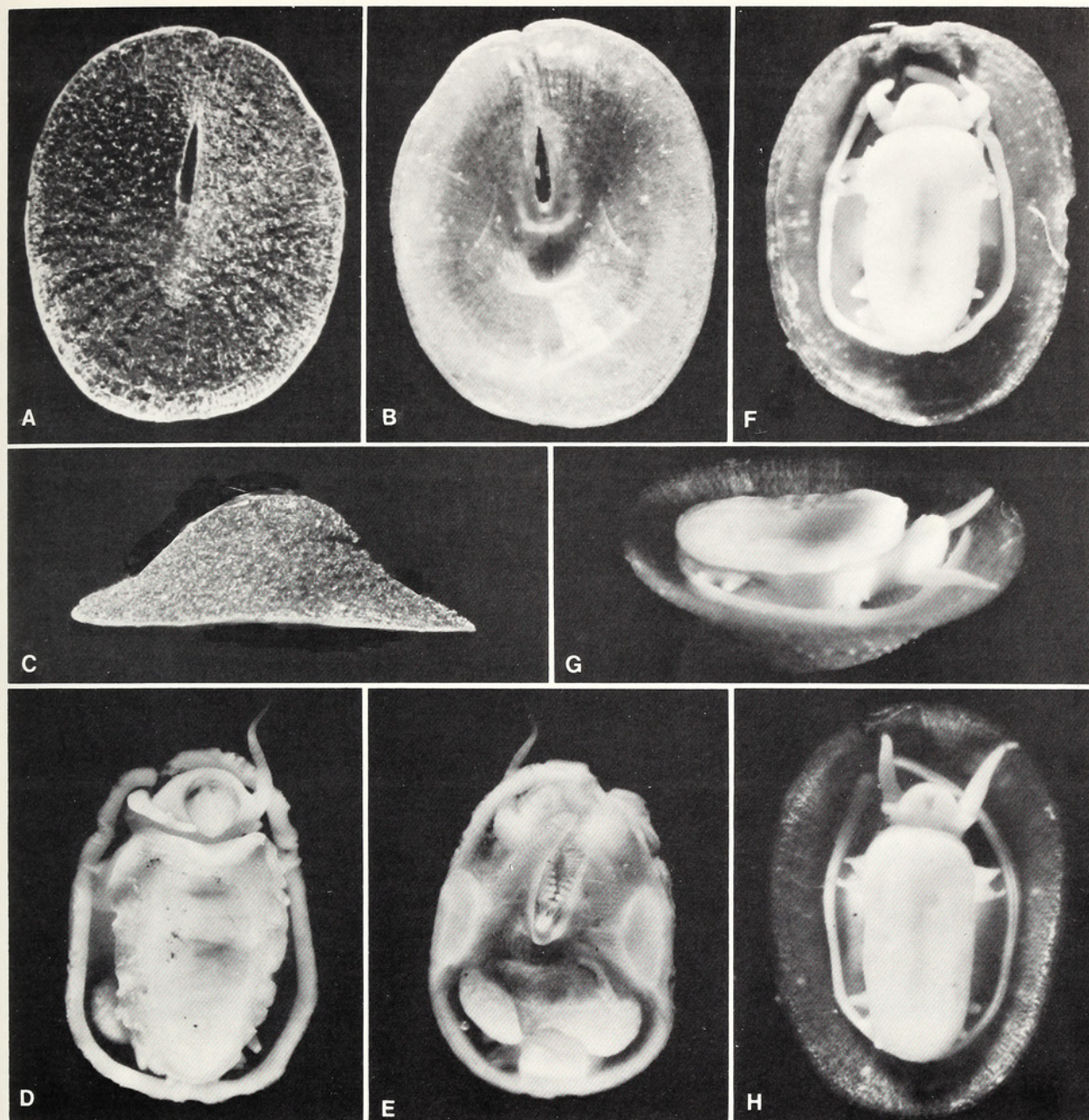
**TYPE SPECIES.** *Pseudorimula marianae* new species.

**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

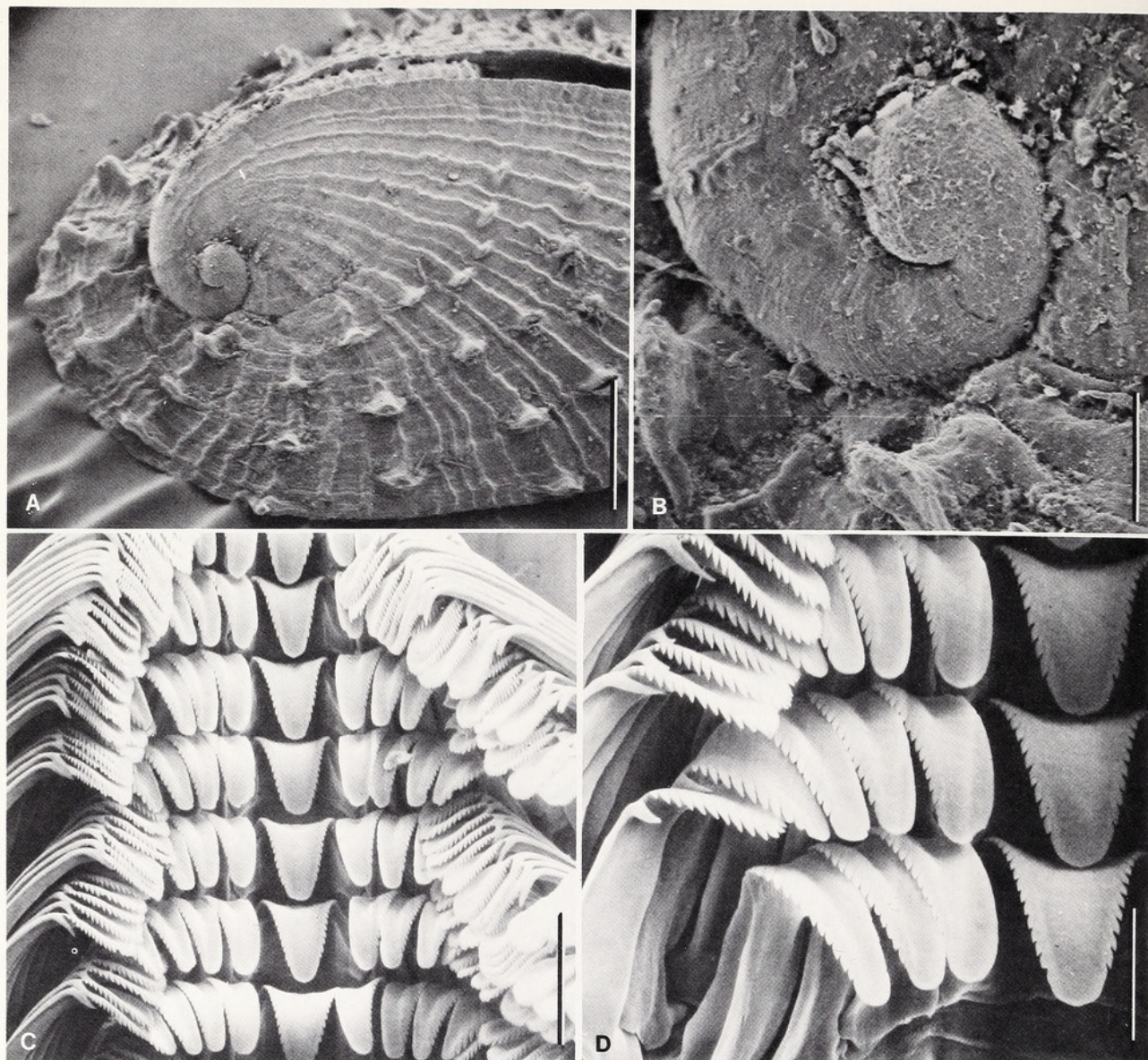


**Figure 12.** *Pseudorimula marianae*, shells and external anatomy. All from Mariana Back-Arc Basin, *Alvin* dive 1836. Anterior at top in all dorsal and ventral views. **A–C.** USNM 859977, holotype. Length 6.4 mm. **A.** Exterior, with thick coat of black mineral deposits. **B.** Interior. **C.** 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 anatomine 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 anatomine 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 neotenously 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).

FOSSIL RECORD OF FISSURELLIDAE

The Fissurellidae are traceable to the Middle Triassic and underwent a substantial radiation in the Jurassic (Knight et al., 1960; McLean, 1984).

Earlier (McLean, 1984) I presented arguments in support of the scenario that fissurellids were derived from Paleozoic bellerophonaceans, developing an idea proposed originally by Golikov and Starobogatov (1975). No further evidence in support of this theory has been offered. Two primary objections remain: there is asymmetry in the ontogeny of all fissurellids, and the punctations or pores in the early teleoconch of fissurellids have not been detected in bellerophonaceans. As noted most recently by Hickman (1988), the question of bellerophonacean affinities remains as controversial as ever.

TIME OF ENTRY TO THE  
HYDROTHERMAL-VENT COMMUNITY

Earlier (McLean, 1985, 1988a, 1988b, 1989), I hypothesized that the newly described families and superfamilies of archaeogastropod limpets (Neomphalacea, Lepetodrilacea, Peltospiracea) from the hydrothermal-vent community entered this community by the early Mesozoic, the time of divergence and origin of other living archaeogastropod superfamilies, and a time in which archaeogastropods were the dominant gastropods in shallow seas. Fissurellaceans and scissurellaceans had an early Mesozoic origin and there is no reason to disallow a Mesozoic origin for temnocincline and sutulizone scissurellids and the clypeosectid fissurellaceans. The argument, however, is less compelling than for the other newly described superfamilies because the rank of endemism (see Newman, 1985), i.e., the hierarchical level of new taxa, is below the superfamily level for the slit-limpets.

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