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NEW GENERA AND SPECIES HAVING THE *FISSURISEPTA* SHELL FORM, WITH A GENERIC-LEVEL PHYLOGENETIC ANALYSIS (GASTROPODA: FISSURELLIDAE)

JAMES H. MCLEAN AND DANIEL L. GEIGER

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New Genera and Species Having the *Fissurisepta* Shell Form, with a Generic-Level Phylogenetic Analysis (Gastropoda: Fissurellidae)

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ABSTRACT. Six genera having an interior septum and an apical or subapical foramen are defined on characters of shell sculpture, shell profile, radula, epipodium, and ctenidial structure. Four genera obliterate the protoconch by expansion of the foramen at maturity: *Altrix* Palmer, 1942, *Fissurisepta* Seguenza, 1862, and the new genera *Clathrosepta* and *Cornisepta*. Two new genera retain the protoconch at maturity: *Manganesepta* and *Profundisepta*. All described species previously assigned to *Fissurisepta* are tentatively assigned among these genera.

New species described here are *Manganesepta hessleri* on manganese nodules from the north equatorial Pacific near Clipperton Island, 4500 m; *Clathrosepta depressa* from Volcano 5, Eastern Pacific Rise at 13°N, 1160 m; *Clathrosepta becki* from hot vents at Manus Basin, east of Papua New Guinea, 2494 m; *Cornisepta levinae* from Volcano 6, Eastern Pacific Rise at 13°N, 1775 m; and *Cornisepta verenae* from Axial Seamount, Juan de Fuca Ridge, 1530 m.

A hypothesis for the evolution of these genera is offered, based on a cladistic analysis of morphological characters. Outgroup genera are the scissurellid genus *Anatoma* Woodward, 1859, and the fissurellid genus *Emarginula* Lamarck, 1801, which is first recorded from the Middle Triassic. Additional genera included in the analysis are *Cranopsis* A. Adams, 1860, and *Puncturella* Lowe, 1827, in which the apical whorl is retained, and *Diodora* Gray, 1821, in which the septum is reduced to a truncate callus.

Analysis of 22 characters for 10 genera produced a single most parsimonious tree. The traditional sequence of *Emarginula, Cranopsis, Puncturella,* and *Diodora* is confirmed. The genera *Clathrosepta, Fissurisepta,* and *Cornisepta* showed the highest number of derived character states.

INTRODUCTION

The concept of the deep-sea fissurellid genus *Fissurisepta* Seguenza, 1862, has traditionally been based on a shell form like that of the genus *Puncturella* Lowe, 1827, in which there is an interior septum that separates the dorsal, excurrent region of the mantle cavity from the most dorsal part of the visceral mass but differing in having the foramen at the summit of the shell, rather than on the anterior slope. The protoconch and apical portion of the shell is obliterated with growth, as in the shallow-water genera *Diodora* Gray, 1821, and *Fissurella* Bruguière, 1789. Shells of profiles ranging from moderately elevated to very high and exhibiting various kinds of sculpture have been referred to the genus *Fissurisepta,* although the relationships of the diverse assortment of species assigned to that genus can now be questioned.

Radular characters, of primary importance to generic definitions in fissurellids (Thiele, 1929), have been known for very few species of the deep sea, due to the difficulty of obtaining material from the continental slope and abyssal depths in which most species treated here have been recorded.

Here we redefine and increase the number of genera in which there is an apical foramen and septum (the *Fissurisepta* group), based on characters of external anatomy, gill and radula, and on shell characters of relative height, structure of the septum, and type of sculpture.

Boutan (1885), an early student of fissurellids, described an evolutionary progression of genera leading from *Emarginula* to *Puncturella* and *Diodora,* but the present work represents the first attempt to examine this relationship and that of the *Fissurisepta* group using cladistic methodology.

In previous reviews of the genus *Fissurisepta,* Pilsbry (1890) copied original descriptions and illustrations of species then known, as did Thiele

(1919), who translated them to German. Farfante (1947) placed three western Atlantic species in *Fissurisepta* (as a subgenus of *Puncturella*). Clarke (1962) provided a catalog of the abyssal gastropods of the world, in which four species were assigned to *Fissurisepta,* again as a subgenus of *Puncturella.* Cowan (1969) first described a monopectinate state for the paired ctenidia in *Fissurisepta pacifica* Cowan, 1969, which provided an argument that the genus should be considered distinct from *Puncturella.* Taviani (1974) discussed the type species of *Fissurisepta, F. papillosa* Seguenza, 1862, and the related species *F. granulosa* Jeffreys, 1882. Ghisotti and Giannini (1983) provided a catalog of 16 species previously assigned to the genus. Lateral views in silhouette and height-to-length ratios were given based on original descriptions and illustrations. Ugorri and Troncosa (1995) reiterated most of the names proposed in the genus *Fissurisepta.* Di Geronimo and La Perna (1997) figured fossil specimens of both *F. papillosa* and *F. rostrata* Seguenza, 1862. Some species treated by these authors are here assigned to the new genera *Clathrosepta* and *Cornisepta.*

MATERIALS AND METHODS

This account is based on recently collected material from various sources, particularly specimens collected by deep-sea submersibles. It includes four new species from the hydrothermal-vent habitat or vents on the flanks of submarine volcanoes.

Examination of the radula, protoconch, and surface sculpture was done with a scanning electron microscope (SEM). Although radular material is available only for some of the species treated in this paper, we have attempted to reallocate all species previously assigned to *Fissurisepta.* This is done on the basis of shell characters that can be correlated with those of species for which the external anatomy and radula are known. Reassigned species are treated only briefly here; more detailed treatments should be sought by reference to the original descriptions.

The species used for character state coding are mentioned ahead of the diagnosis for each genus. Depths given originally in fathoms have been converted to the nearest meters.

For the phylogenetic analysis we use two outgroups, the scissurellid genus *Anatoma* Woodward, 1859, and the fissurellid genus *Emarginula* Lamarck, 1801. *Emarginula* lacks the defining characters of the ingroup (the foramen and septum), instead having a slit at the margin of the shell. *Emarginula* dates from the Middle Triassic, which represents the earliest appearance of the family. The analysis includes other genera of fissurellid limpets with a septum but having the foramen on the anterior slope: *Cranopsis* A. Adams, 1860, and *Puncturella* Lowe, 1827. Also included in the analysis is *Diodora* Gray, 1821, in which the apex is obliterated and the septum is reduced to truncate callus bordering the posterior end of the foramen.

Cladistic analysis was performed with the program PAUP 3.1 (Swofford, 1993). The character states of the genera were coded in agreement with the species included in the respective genera to the extent that the material allowed observation of the characters. Multistate characters were treated as unordered. Binary characters were polarized through outgroup comparison. All characters were equally weighted. Uninformative characters were excluded from the analysis and calculations of tree statistics. Exhaustive searches using ACCTRAN and DELTRAN optimizations were performed. Skewness (g_1) was calculated from all trees in the exhaustive search with an interval width of 1.

Museum abbreviations: LACM, Natural History Museum of Los Angeles County; MCZ, Museum of Comparative Zoology, Harvard University, Cambridge Massachussetts; MNHN, Muséum National d'Histoire Naturelle, Paris; NHMW, Natural History Museum, Vienna; SMNH, Swedish Museum of Natural History, Stockholm; USNM, National Museum of Natural History, Washington.

SYSTEMATICS

Family FISSURELLIDAE Fleming, 1822

Subfamily EMARGINULINAE Gray, 1834

All genera included in the analysis are diagnosed in this section. Genera are arranged in the order of increasing numbers of apomorphic states (Table 1), as revealed by subsequent phylogenetic analysis.

Plesiomorphic genera

Plesiomorphic genera are here considered as those that retain the protoconch at maturity. Three are speciose and well represented in shallow water and the upper continental shelf: *Emarginula, Cranopsis,* and *Puncturella.* Subgenera have been defined for each of these groups, but these are not treated here nor are species treated. References are given to recent papers that illustrate the characters discussed in the phylogenetic analysis.

Two of the new genera also retain the protoconch: the monotypic *Manganesepta* and *Profundisepta,* all species of which are reviewed.

One other genus having a septum and retaining the protoconch is not included in the analysis: *Vacerrena* Iredale, 1958, which is small-shelled and occurs in shallow water. It has a peculiar autapomorphic sculpture of oblong granules; nothing is known of its anatomy and radula (Kilburn, 1978: 448).

Genus *Emarginula* Lamarck, 1801
Figure 1A

Emarginula Lamarck, 1801:69. Type species (M): *E. conica* Lamarck, 1801. Eastern Atlantic.

DIAGNOSIS. Shell height moderate; anterior slope broadly convex; apical whorl overhanging posterior slope; posterior slope concave; protoconch with linear and concentric sculpture; foramen represented by deep anterior slit, its position in earlier growth stages marked by a long selenizone. Sculpture radial and concentric; radial sculpture marked by primary and secondary ribs.

Mantle skirt slit corresponding to shell slit; epipodial tentacles of similar size, numerous. Ctenidia bipectinate, gill axis free.

Rachidian tooth broad, inner lateral teeth nar-

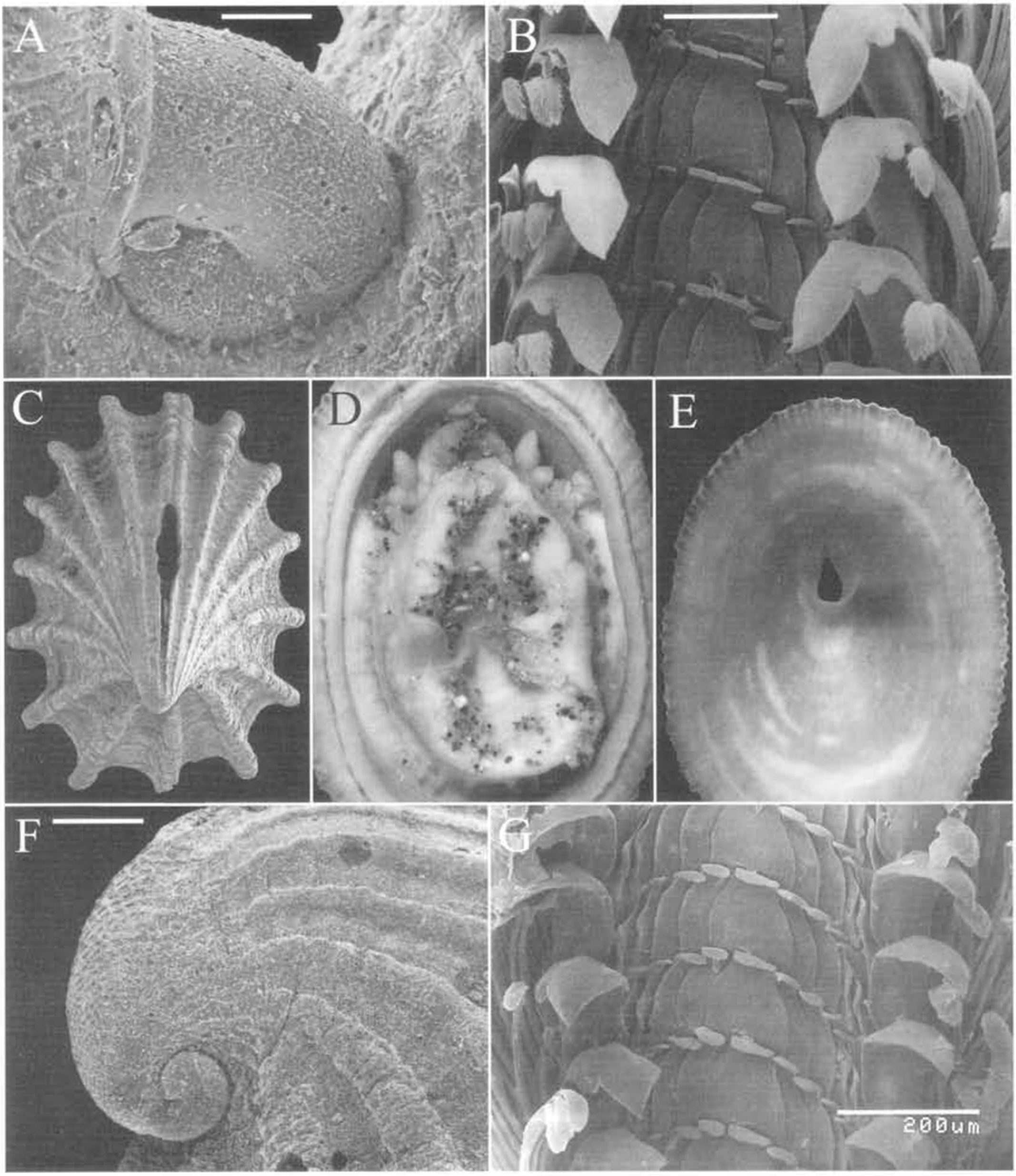

Figure 1A–G. Illustrations of plesiomorphic character states in *Emarginula, Cranopsis,* and *Puncturella*. **A.** Protoconch of *Emarginula superba* Hedley and Petterd, 1906 (scale bar = 40 μm). **B.** Radula of *Cranopsis decorata* (Cowan and McLean, 1968) (scale bar = 100 μm). **C.** Doubled anterior rib and long selenizone of *Cranopsis cucullata* (Gould, 1846) (shell length 4.4 mm). **D.** Numerous epipodial tentacles of *Puncturella solis* (Beck, 1996) (shell length 20.3 mm). **E.** Curved septum of same. **F.** Protoconch and unique earliest teleoconch sculpture of *C. cucullata,* showing scattered pits in teleoconch (scale bar = 200 μm). **G.** Radula of *P. solis* (scale bar = 200 μm). [Illustrations of *P. solis* by L. Beck.]

row; pluricuspid tooth massive, with inner and outer secondary cusps.

REMARKS. The protoconch of *Emarginula superba* Hedley and Petterd, 1906, is illustrated here (Fig. 1A). SEM illustrations of radulae and protoconchs of other *Emarginula* species were provided by Herbert and Kilburn (1986).

Emarginula is the oldest fissurellid known, with a Middle Triassic origin (Keen, *in* Knight et al., 1960:226); we therefore assume that all characters considered here for *Emarginula* are plesiomorphic. The genus includes approximately 80 species (Thiele, 1929).

Genus *Cranopsis* A. Adams, 1860
Figure 1B, C, F

Cranopsis A. Adams, 1860. Type species (M): *C. pelex* A. Adams, 1860. Japan.

DIAGNOSIS. Shell height moderate; anterior slope broadly convex; apical whorl overhanging posterior slope; posterior slope concave; protoconch with linear and concentric sculpture; foramen on anterior slope of shell, its position in earlier growth stages marked by strong selenizone. Anterior slope in advance of foramen marked by doubled anterior rib and seam on interior surface. Foramen bordered posteriorly on inner surface by low, curved septum. Sculpture usually radial and concentric, radial sculpture marked by primary and secondary ribs.

Mantle skirt slit extending to position of foramen. Epipodial tentacles numerous. Ctenidia bipectinate, gill axis free.

Rachidian tooth usually narrow, inner lateral teeth narrow; pluricuspid tooth massive, with inner and outer secondary cusps.

REMARKS. Illustrated here are the radula of *Cranopsis decorata* (Cowan and McLean, 1968) (Fig. 1B) and the juvenile shell of *C. cucullata* (Gould, 1846) (Fig. 1C, D), a species unusual in lacking secondary ribs and concentric sculpture. SEM illustrations of radulae and protoconchs of *Cranopsis* species were provided by Herbert and Kilburn (1986).

This genus is characterized by the doubled anterior rib in advance of the selenizone; although this might seem to be a superficial shell character, the mantle skirt is correspondingly split, like the mantle in *Emarginula*. Thiele (1929) estimated 10 species, but additional species have subsequently been described.

Genus *Puncturella* Lowe, 1827
Figure 1D, E, G

Puncturella Lowe, 1827; type species (M): *Patella noachina* Linnaeus, 1771. Arctic and northern seas.

DIAGNOSIS. Shell height moderate; anterior slope broadly convex; apical whorl overhanging posterior slope; posterior slope concave; protoconch with linear and concentric sculpture; foramen on anterior slope of shell, position in earlier growth stages marked by strong selenizone. Anterior slope in advance of foramen not marked by doubled anterior rib. Foramen bordered posteriorly on inner surface by low, curved septum. Sculpture radial and concentric, radial sculpture marked by primary and secondary ribs.

Mantle skirt intact anteriorly, perforated only to correspond to position of foramen. Epipodial tentacles numerous. Ctenidia bipectinate, gill axis free.

Rachidian tooth usually narrow, inner lateral teeth narrow; pluricuspid tooth massive, with inner and outer denticles.

REMARKS. Illustrated here are the epipodial tentacles, septum, and radula of *Puncturella solis* Beck, 1996, a species from 1492 m in a sulfide habitat at Edison Seamount, east of Papua New Guinea, western Pacific. SEM illustrations of radulae and protoconchs of *Puncturella* species were provided by Herbert and Kilburn (1986). Additionally, SEM illustrations of radulae for recently described species were given by Okutani et al. (1993) and Beck (1996).

Puncturella differs from *Cranopsis* in lacking the doubled anterior rib and in not having the split mantle skirt anteriorly. The genus includes approximately 30 species (Thiele, 1929).

Genus *Manganesepta*, new genus
Figure 2

Type species: *Manganesepta hessleri,* new species.

The following diagnosis is based on the monotypic type species *M. hessleri,* new species.

DIAGNOSIS. Shell small, profile moderately high, one apical whorl retained in teleoconch before expansion to limpet shell form. Apical whorl marked by radial sculpture only; juncture between apical whorl and limpet form marked by constriction. Protoconch with pointed tip, retained in adult shell on right side of apical whorl. Microsculpture of protoconch of raised circular ridges. Foramen subapical, outline of foramen elongate-triangular, selenizone greatly reduced, septum straight, high. Mature shell sculpture coarsely clathrate, concentric sculpture overriding radial sculpture.

Epipodial tentacles one posterior pair; posterior pedal tentacle present. Gill characters unknown (single preserved specimen is immature).

Rachidian tooth with long shaft and broader base; overhanging tip deeply serrate; first two laterals similar to rachidian; third lateral shorter, bearing similar cusps, its shaft expanded to fit the fourth lateral, which has a thick, sinuous base; pluricuspid large, with long acutely tapered overhang, larger outer denticle, and with flange to articulate with fourth lateral.

REMARKS. *Manganesepta* displays a mix of plesiomorphic characters (one apical whorl, protoconch with pointed tip, retention of protoconch, radula plan) but has a number that are apomorphic (small size, reduced selenizone, straight and high septum, reduced epipodial tentacles, and posterior pedal tentacle) and that have the autapomorphic character state of the protoconch sculpture of circular ridges. The apomorphic characters, particularly the posterior pedal tentacle and the ridged protoconch sculpture, justify the proposal of a separate genus.

The single whole specimen of *M. hessleri,* on

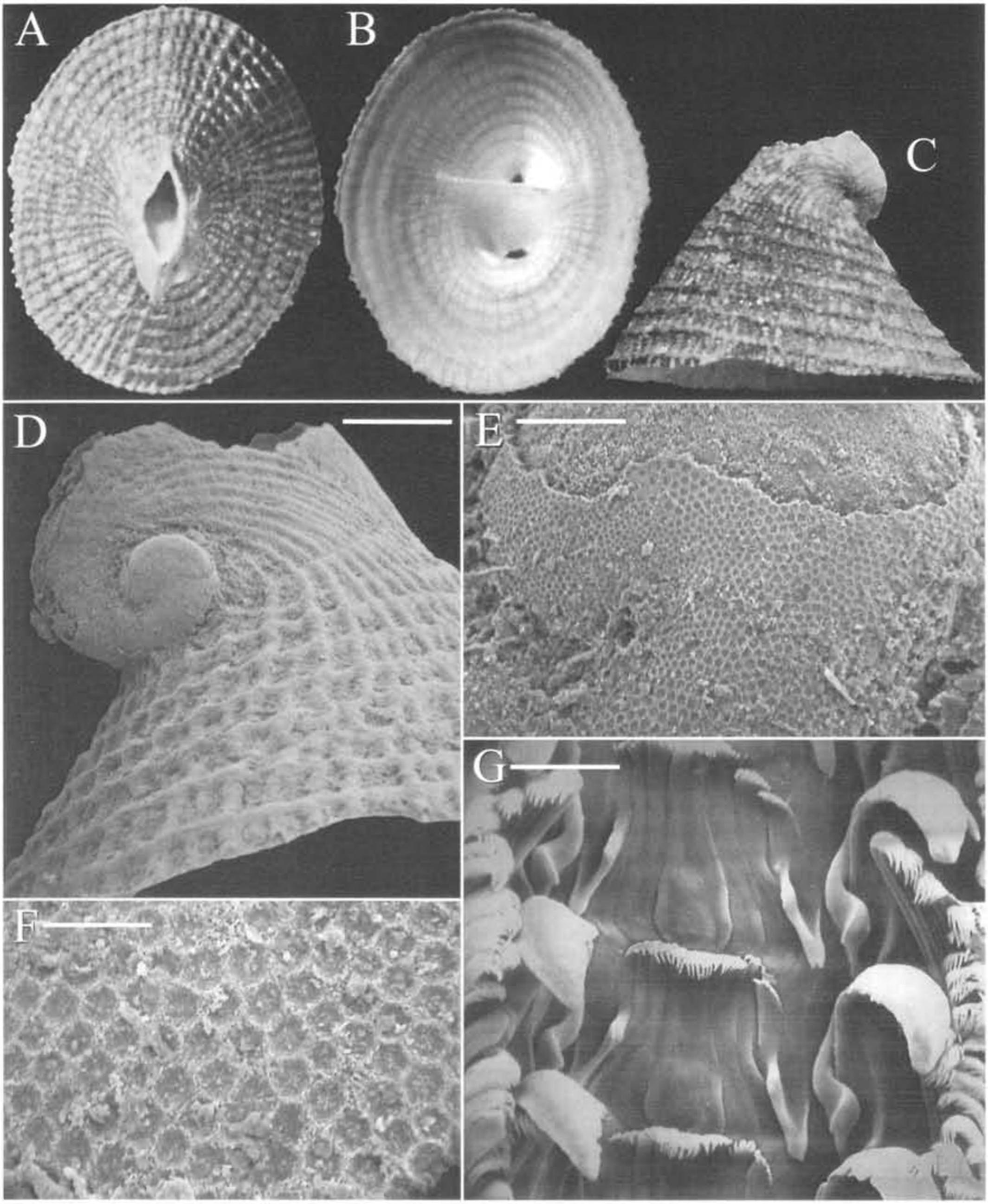

Figure 2A–G. *Manganesepta hessleri* new species. **A–C.** LACM 2785, holotype; 4500 m, on manganese nodules, North Equatorial Pacific, NW of Clipperton Island (14°37–42′N, 125°22–27′W). Length 2.6, width 2.2, height 1.6 mm. **A.** Exterior, showing clathrate sculpture and apical whorl posterior to foramen. **B.** Interior, showing straight, high septum. **C.** Left side, showing foramen at summit of shell with apical whorl retained. **D.** SEM view of right side showing coiled first teleoconch whorl and early teleoconch sculpture of spiral elements only (scale bar = 200 µm). **E.** SEM enlargement of protoconch sculpture (scale bar = 40 µm). **F.** SEM enlargement of hexagonal protoconch sculpture (scale bar = 10 µm). **G.** SEM view of radula, slowing deeply serrate tip of rachidian and laterals (scale bar = 10 µm).

which the anatomical description is based, is about 1 mm in length and is clearly immature for the species. Four gill filaments are present, but the full complement of leaflets on the gill of mature specimens cannot be established.

Manganesepta and *Clathrosepta* share certain apomorphies (clathrate sculpture, the posterior pedal tentacle, few epipodial tentacles, and a similar radula). However, the differences (size, apical whorl in *Manganesepta* but not *Clathrosepta,* height and shape of foramen) are sufficient to eliminate the possibility that *M. hessleri* could simply be a juvenile stage of a species of *Clathrosepta,* for which small specimens are unknown.

Manganesepta hessleri, new species

Figure 2

DESCRIPTION. Shell small, high, retaining one apical whorl; protoconch retained, protoconch lip not evident, protoconch sculpture hexagonal. Foramen subapical, positioned in first teleoconch whorl, elongate-triangular, selenizone short, extending posterior to foramen in apical whorl. Sculpture clathrate, radial ribs all of similar strength, not marked as primary and secondary ribs; radial ribs approximately 75 in holotype; concentric sculpture stronger than radial ribs, nearly lacking on apical whorl, approximately 10 strong, but narrow rings appearing abruptly on final expanse of shell. Shell interior transparent, revealing exterior sculpture, muscle scar not apparent. Septum high, extending straight across.

External anatomy and radula as for genus, above.

Dimensions. Length 2.6, width 2.2, height 1.6 mm (holotype).

TYPE LOCALITY. North Equatorial Pacific, NW of Clipperton Island (14°37–42′N, 125°22–27′W), 4500 m, on manganese nodules. Details of the habitat and method of collection were given by Speiss et al. (1987).

TYPE MATERIAL. Holotype LACM 2785, three paratypes LACM 2786. Four specimens, Echo I expedition, Scripps Institution of Oceanography, R/V *Melville,* June 1983.

REMARKS. To our knowledge, no limpets of any families have been recorded or described from manganese nodule habitats in abyssal depths.

ETYMOLOGY. The name honors Robert Hessler of Scripps Institution of Oceanography, who forwarded the specimens to us.

Genus *Profundisepta,* new genus

Figures 3, 4

Type species: *Puncturella* profundi Jeffreys, 1877.

The following diagnosis is based on the type species *Profundisepta profundi,* the only species for which the protoconch sculpture, epipodium, ctenidium, and radula are known.

DIAGNOSIS. Shell small, profile moderately high, one-half apical whorl retained in teleoconch before expansion to limpet shell form. Apical whorl nearly smooth. Protoconch bulbous, retained in adult shell on right side of apical whorl. Protoconch microsculpture of deep, closely spaced pits, visible only under high magnification. Foramen subapical, outline of foramen broadly triangular; selenizone greatly reduced, septum straight, high. Mature sculpture finely clathrate, with low beads at intersections (in most species).

Epipodial tentacles reduced, consisting of one large posterior pair, one smaller lateral-posterior pair, and one smaller posterior pair (Fig. 3E). Gill bipectinate with free axis (Fig. 3F).

Rachidian tooth with long shaft and broader base; overhanging tip deeply serrate; shafts and cusps of lateral teeth similar to those of rachidian; cusps of fourth lateral reduced; pluricuspid large, with acutely tapered tip and inner and outer cusps near bend.

REMARKS. *Profundisepta* has characters of protoconch form, protoconch sculpture, and early whorl that differ from those of *Manganesepta.* The posterior pedal tentacle of *Manganesepta* is lacking. The pitted microsculpture of the protoconch is unique among the genera treated here. The bulbous form of the protoconch is shared with that of *Fissurisepta,* although the apex is unlike that of *Fissurisepta,* in which the apical whorl is lost in mature specimens. Shell sculpture differs among the species assigned to the genus.

Profundisepta profundi (Jeffreys, 1877)

Figure 3A–G

Puncturella profundi Jeffreys, 1877:232.—Jeffreys, 1883:675, pl. 50, fig. 10.—Watson, 1883:35.—Dautzenberg and Fischer, 1896:491.—Thiele, 1919:152, pl. 17, figs. 8–11.—Dall, 1927:111.—Clarke, 1962:7 [listed].—Abbott, 1974:22 [listed].—Bandel, 1982, pl. 11, figs. 9, 12, pl. 12, fig. 9.

Puncturella (*Cranopsis*) *profundi.*—Watson, 1886:47.—Pilsbry, 1890:243, pl. 27, figs. 73, 74.—Dautzenberg and Fischer, 1896:491.—Dautzenberg, 1927:224.—Nordsieck, 1968:12, pl. 1, fig. 03.21.

Puncturella (*Puncturella*) *profundi.*—Farfante, 1947:129, pl. 56, figs. 1–5.

Fissurisepta profundi.—Warén, 1980:14.—Warén, 1991:55, fig. 1D.

REMARKS. SEM illustrations of the shell and protoconch of this species were previously published by Bandel (1982) and Warén (1991). Warén (1980, 1991) provisionally placed this species in *Fissurisepta,* pending knowledge of its radula and anatomy. The mature sculpture is clathrate with beads at intersections, not the curved rows of beads of *Fissurisepta.*

Dimensions. Length 5, width 4, height 2.5 mm (Farfante, 1947). Length 4.2, width 3.0, height 3.7 mm (Fig. 3A).

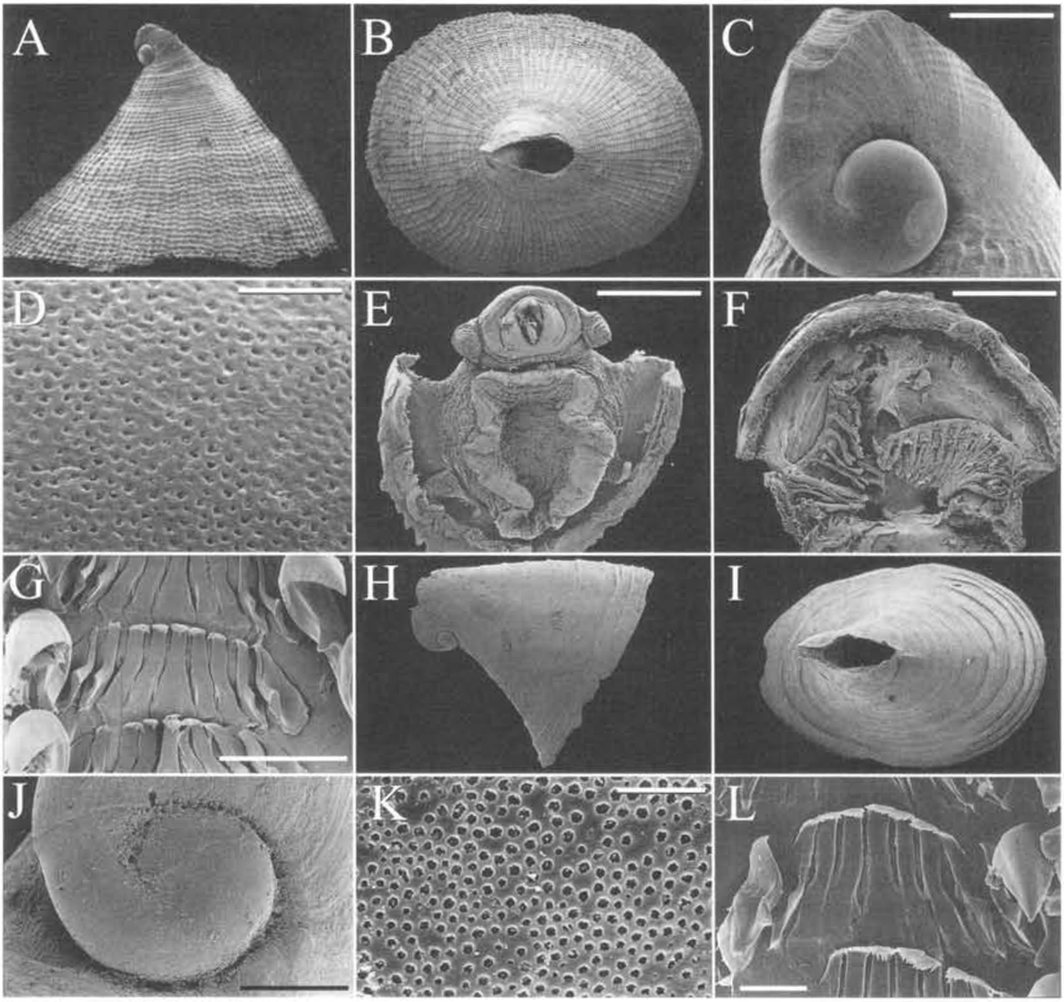

Figure 3A–L. Two species of *Profundisepta*. A–G. *P. profundi* (Jeffreys, 1877). SMNH, Bioice sta. 2692, off Iceland (no coordinates). Length 4.2, width 3.0, height 3.7 mm. A. Right side of shell. B. Dorsal view of shell, anterior at right. C. Apex, showing protoconch and selenizone (scale bar = 200 μm). D. Pitted microsculpture of protoconch (scale bar = 10 μm). E. Ventral view of body, showing paired posterior epipodial tentacles (scale bar = 600 μm). F. Ventral view of excised mantle skirt, showing paired, bipectinate ctenidia with free tips (scale bar = 500 μm). G. Radula of specimen from 1110 to 1125 m, Galicia Bank (42°50.9′N; 11°53.1′W) (scale bar = 50 μm). H–L. *P. alicei* (Dautzenberg and Fischer, 1896). MNHN; 1530 m, Iberian–Moroccan Gulf, BALGIM Expedition, sta. DW64 (35°30′N, 07°46′N). Length 1.7, width 1.1, height 1.5 mm. H. Right side of shell. I. Dorsal view of shell, anterior at right. J. Protoconch (scale bar = 100 μm). K. Pitted microsculpture of protoconch (scale bar 10 μm). L. Radula (scale bar = 10 μm). [All SEM photos by A. Warén.]

Occurrence. Northeastern and western Atlantic (Farfante, 1947), 500–2500 m.

Profundisepta alicei (Dautzenberg and Fischer, 1897)
Figure 3H–L

Puncturella (*Cranopsis*) *alicei* Dautzenberg and Fischer, 1897:180, pl. 4, figs. 23, 24.

Puncturella alicei.—Thiele, 1919:153, pl. 17, figs. 12, 13.

REMARKS. This species is more slender than *P. profundi,* and the shell is nearly smooth, but the generic assignment is confirmed by the protoconch sculpture of fine pits (Fig. 3K). Mature sculpture was described as having a chagrinée (finely granular) surface. The apical whorl and protoconch are posterior and below the foramen. There is no indication of the doubled anterior rib of *Cranopsis.*

A new record of this species in the eastern Atlantic is reported here: Iberian–Moroccan Gulf (35°30′N; 07°46′W), 1530 m, BALGIM expedi-

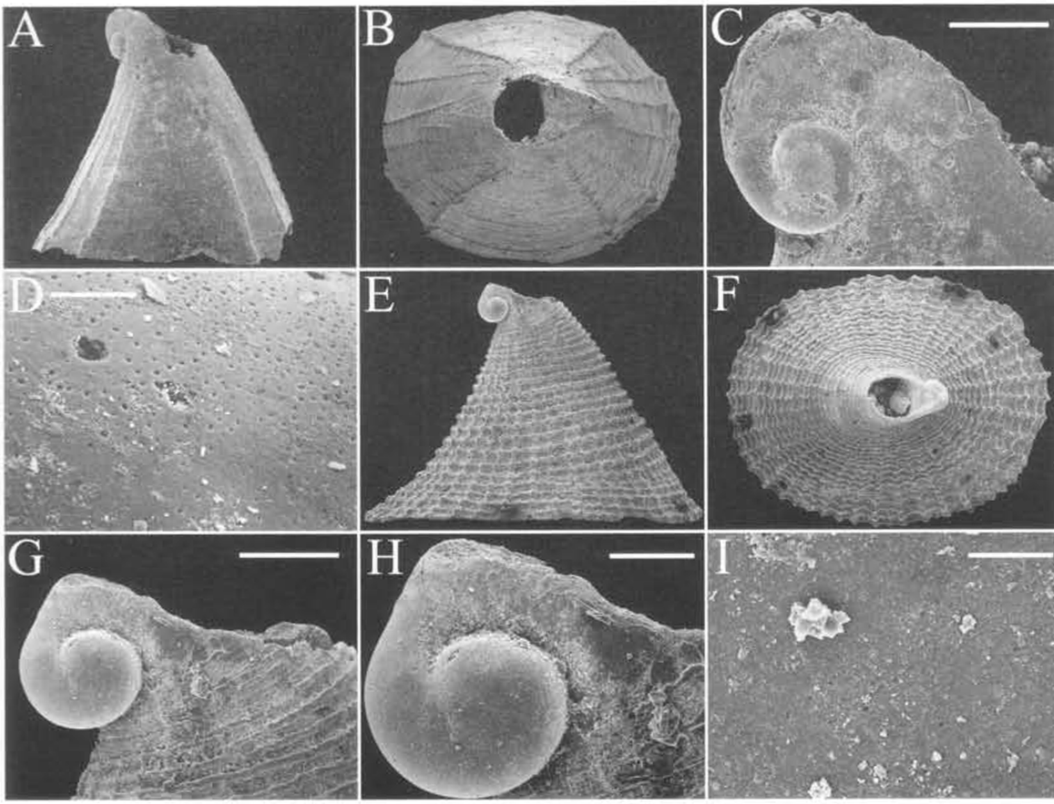

Figure 4A–I. Two species of *Profundisepta*. A–D. *P. borroi* (Farfante, 1947). MCZ 160525, Atlantis station 2993; off Bahia Cardenas, Matanzas, Cuba (23°N, 80°44′W). Length 2.4, width 1.9, height 2.3 mm. A. Right side. B. Dorsal view, anterior at left. C. Apex, showing eroded protoconch (scale bar = 200 μm). D. Pitted microsculpture of protoconch (scale bar = 10 μm). E–I. *P. sportella* (Watson, 1883). MCZ 160521, *Atlantis* station 3459; off Sagua la Grande, Santa Clara, Cuba (23°21′N, 80°36′W). Length 2.85, width 2.15, height 1.7 mm. E. Right side of shell. F. Dorsal view of shell, anterior at left. G. Apex of shell (scale bar = 200 μm). H. Protoconch (scale bar = 100 μm). I. Pitted miscrosculpture of protoconch (scale bar = 10 μm).

tion, R/V *Cryos*, sta. DW64, 4 June 1984 (two specimens, MNHN).

Dimensions. Length 2.2, width 1.5, height 2 mm (original description); length 1.7, width 1.1, height 1.5 mm (Fig. 3H).

Occurrence. Azores (type locality) and Iberian–Moroccan Gulf, 1165–1600 m.

Additional species of *Profundisepta*

The species that follow are known from archibenthal or abyssal depths. The radula of each is unknown. All are small and retain an apical spur and in some cases the protoconch on the apical spur just posterior to the foramen. The list is exhaustive and is derived from examination of literature records of species described in *Puncturella*.

Profundisepta borroi (Farfante, 1947)
Figure 4A–D

Puncturella borroi Farfante, 1947:132, pl. 57, figs. 5–7.—Clarke, 1962:7 [listed].—Abbott, 1974: 22 [listed].

REMARKS. Sculpture consists of scattered radial ribs. Fine pits on the protoconch of the holotype (Fig. 4D) confirm the generic assignment.

Dimensions. Length 4.25, width 3, height 3.25 mm.

Occurrence. Off eastern Cuba, 410–1860 m.

Profundisepta sportella (Watson, 1883)
Figure 4E–I

Puncturella sportella Watson, 1883:37.—Watson, 1886:45, pl. 4, fig. 9.—Thiele, 1919:154, pl. 18, figs. 11–14.—Abbott, 1974:22 [listed].

Puncturella (*Puncturella*) *sportella*.—Pilsbry, 1890: 235, pl. 26, figs. 42–45 [copy Watson, 1886].—Farfante, 1947:133, pl. 58, figs. 1–4.

REMARKS. This species has clathrate sculpture beaded at intersections. The fine pits of the protoconch (Fig. 4I) are not as dense as those of the species above but are taken as evidence of the generic assignment.

Dimensions. Length 4.5, width 3, height 3.5 mm.
Occurrence. Georgia to West Indies, 530–710 m (Farfante, 1947).

Profundisepta circularis (Dall, 1881)

Puncturella circularis Dall, 1881:75.—Dall, 1889: 403, pl. 23, figs. 7, 7b.—Dall, 1890:356.—Pilsbry, 1890:236, pl. 25, fig. 1.—Dall, 1927:112.—Farfante, 1947:130, pl. 57, figs. 1–4.—Clarke, 1962:7 [listed].

REMARKS. This species is characterized by sculpture dominated by radial ribs. Farfante (1947: pl. 57, fig. 2) illustrated a specimen that retains the protoconch.
Dimensions. Length 6.5, width 5.25, height 4 mm (Farfante, 1947).
Occurrence. Florida to Tobago, 690–1060 m (Farfante, 1947).

Profundisepta gemmata (Schepman, 1908)

Puncturella gemmata Schepman, 1908:87, pl. 7, fig. 3.—Thiele, 1919:155, pl. 19, figs. 9–11.

REMARKS. Sculpture radial and concentric, with radial sculpture strongest, finer concentric sculpture forming beads at intersections. The protoconch is shown in the original illustration.
Dimensions. Length 6, width 5, height 3.5 mm.
Occurrence. Indonesia, 1244 m.

Apomorphic genera

Apomorphic genera are those that lose the protoconch and apical whorl with the expansion of the foramen at maturity. Except for the cosmopolitan, shallow-water genus *Diodora,* all described species of the established genera *Altrix* and *Fissurisepta* are treated as well as those of the new genera *Clathrosepta* and *Cornisepta,* with justifications given for their revised generic assignment.

Genus *Diodora* Gray, 1821
Figure 5A–C

Diodora Gray, 1821. Type species (M): *Patella apertura* Montagu, 1803 [=*Patella graeca* Linnaeus, 1758]. Europe.
Glyphis Carpenter, 1857. Type species: *Fissurella aspera* Rathke, 1833 [not *Glyphis* Agassiz, 1843].

DIAGNOSIS. Shell height moderate; anterior slope short, sometimes concave; protoconch and short selenizone present only on juvenile shell posterior to foramen; protoconch with linear and concentric sculpture; expansion of foramen obliterates protoconch with growth. Foramen bordered posteriorly on inner surface by a broad, truncated callus. Sculpture radial and concentric, radial sculpture marked by primary and secondary ribs.

Mantle skirt intact anteriorly. Epipodial tentacles numerous, of similar size. Ctenidia bipectinate, gill axis free.

Rachidian tooth broad to narrow, inner lateral teeth narrow; pluricuspid tooth massive.

REMARKS. Illustrated here are the juvenile shell, protoconch, and radula of *Diodora aspera* (Rathke, 1833) (Fig. 5A–C). Pernet (1997) illustrated the early foramen of *D. aspera,* a species of *Diodora* in which there is no selenizone in the early stage.

In this genus the septum is reduced to a posteriorly truncate ridge of callus. It also differs from other genera treated here in having the anterior slope rather than the posterior slope shorter and sometimes concave, although this is shared with *Altrix.*

Subgenera of *Diodora* are not treated here. The genus contains approximately 100 species.

Genus *Altrix* Palmer, 1942
Figure 5D–F

Folia Palmer, 1937:29 [as section of *Puncturella,* subgenus *Fissurisepta*]. Type species (OD): *Fissurella altior* Meyer and Aldrich, 1896. Claibornian, Middle Eocene, Alabama. Not *Folia* Lohman, 1892.
Altrix Palmer, 1942:674 [new name for *Folia* Palmer].
Esmeria Olsson, 1964:200 [as subgenus of *Puncturella*]. Type species (OD): *Puncturella (Esmeria) palmerae* Olsson, 1964. Lower Pliocene, beds of Onzole Formation, Esmeraldas Province, Ecuador.

The following diagnosis is based on the Neogene species *Altrix trifolium* (Dall, 1881), which has yet to be collected alive but is known from fresh appearing mature shells (Fig. 5E–G).

DIAGNOSIS. Shell large (maximum length 27 mm), profile high; all slopes slightly concave; sculpture of strong radial and concentric ribs; radial sculpture of secondary ribs forming between primary ribs; beads formed at intersections of radial and concentric ribs. Foramen relatively small, at summit of mature shell; circular in exterior view, tripartite in interior view, tripartite condition emphasized by three projecting tubercles, two lateral and one posterior; septum small, thick, low, anterior edge bearing tubercle that forms the most posterior of three tubercles. Juvenile shell and protoconch unknown, no evidence of early coiled whorl.

Anatomy and radula unknown.

REMARKS. Palmer (1937) assigned Dall's *Puncturella trifolium* to her genus *Folia,* which she later renamed *Altrix,* because *Folia* is preoccupied. The type species of *Esmeria* Olsson, 1964, differs from the type species of *Altrix* only in its lesser development of the tubercles that border the foramen on the inner side. Olsson (1964) also assigned Dall's *trifolium* to his genus *Esmeria.*

Sohl (1992:420) treated *Altrix* as a subgenus of *Puncturella* and extended the origin of the genus to the Upper Cretaceous. He described one new species (see below) and identified another only to genus.

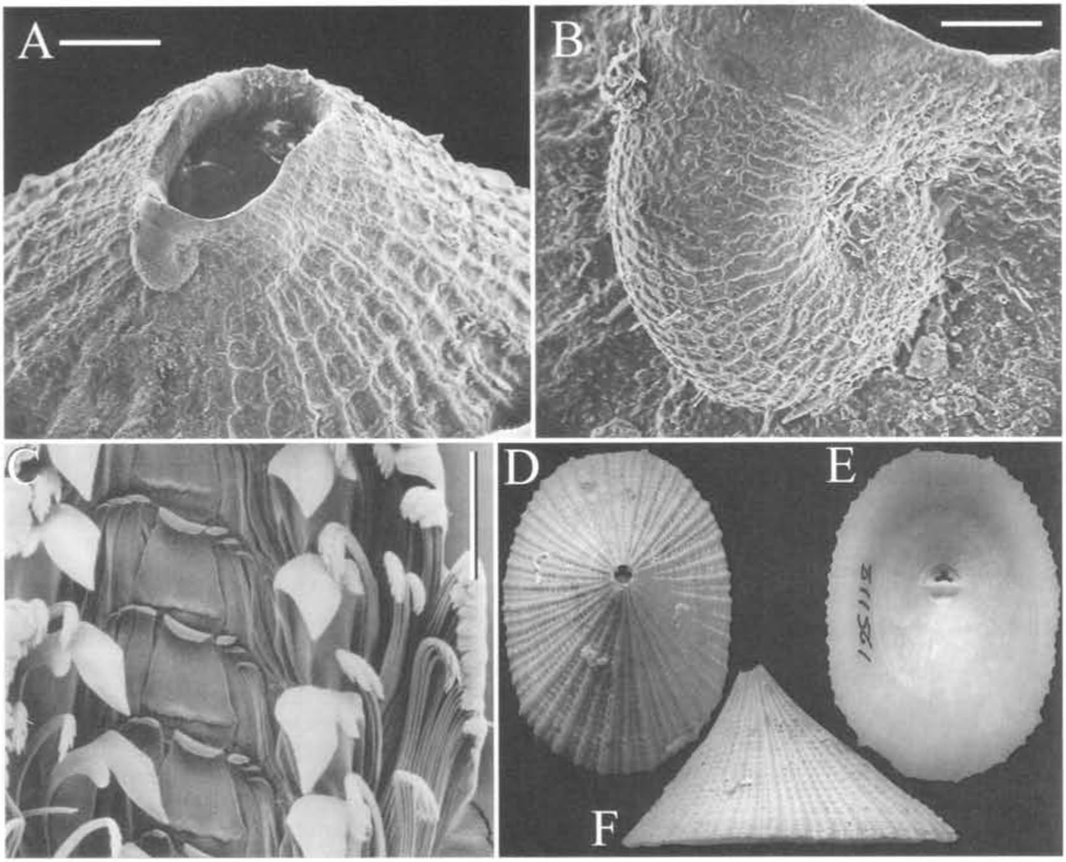

Figure 5A–G. Illustrations to show character states of *Diodora* and *Altrix*. **A, B.** *Diodora aspera* (Rathke). **A.** Oblique posterior view showing foramen of juvenile shell with protoconch attached (scale bar = 200 μm). **B.** Protoconch with plesiomorphic sculpture (scale bar = 40 μm). **C.** Radula of *D. aspera* (scale bar = 100 μm). **D–F.** *Altrix trifolium* (Dall, 1881). LACM 66-264.1, ex USNM 811561; 165 m, 80 miles NW of Bridgetown, Barbados (13°41′N, 60°53′W). Length 27.1, width 19.0, height 14.1 mm. **D.** Exterior showing alternating primary and secondary ribs. **E.** Interior, showing low septum and tripartite foramen, bordered by two anterior-lateral tubercles and one posterior tubercle attached to septum. **F.** Left side, showing concave anterior profile.

Species grouped here in *Altrix* have the radial ribs differentiated into primary and secondary ribs as in many species of *Puncturella,* as well as a strong, relatively small, curved septum as in *Puncturella* but differ in having the apex obliterated in the mature shell, as in *Diodora,* with its highly reduced septum, and *Fissurella,* which has lost the septum entirely. Shells are generally larger than those of *Clathrosepta, Fissurisepta,* and *Cornisepta* and the septum is smaller.

The occurrence of the living species *A. trifolium* at moderate depths and the occurrence of the fossil species in facies of moderate depth indicates that this genus is characteristic of moderate depths, in contrast to the continental slope and abyssal depths for *Clathrosepta, Fissurisepta,* and *Cornisepta.*

The lack of knowledge of the juvenile shell, protoconch, radula, and gill of *Altrix* is a major gap. The high profile and concave slopes of *Altrix* would lend a functional advantage to having a reduced, monopectinate ctenidium, but whether the monopectinate gill occurs in *Altrix* awaits examination of living material. *Altrix* could prove to be a link to *Fissurisepta* should the gill condition prove to be monopectinate; or, if the gill condition proves to be the plesiomorphic bipectinate condition, it would serve as the link to *Diodora,* in which the septum is reduced to a posterior truncation of the interior callus ring that borders the foramen. Like *Diodora, Altrix* has the anterior slope shorter and more concave.

Altrix trifolium (Dall, 1881)
Figure 5D–F

Puncturella trifolium Dall, 1881:76.—Dall, 1889: 403, pl. 26, fig. 8, 8b.—Thiele, 1919:165, pl. 20, figs. 8, 9 [copy of original illustrations].—Abbott, 1974:23, fig. 86.—Pilsbry, 1890:237, pl. 27, figs. 50, 51 [copy of original illustrations].

Puncturella (Fissurisepta) trifolium.—Farfante, 1947:144, pl. 63, figs. 4–7.
Fissurisepta trifolium.—Ghisotti and Giannini, 1983:28 [listed only].

REMARKS. The generic description above applies to this species.

Dimensions. Length 14, width 10.5, height 7 mm (holotype); length 27.1, width 19.1, height 14.5 mm (Fig. 5E–G).

Occurrence. Yucatan Strait, 1170 m (type locality); off Barbados, 165 m (USNM 811561 and LACM 66-264.1).

Other species of *Altrix*

To our knowledge, the following four additional species include all that have been assigned to *Altrix* or the synonymous *Esmeria*.

Altrix altior (Meyer and Aldrich, 1886)

Fissurella altior Meyer and Aldrich, 1886:41, pl. 2, fig. 16, 16a, 16b.
Glyphis altior.—Pilsbry and Johnson, 1892:113 [listed only].
Puncturella (Fissurisepta) [section *Folia*] *altior*.—Palmer, 1937:30, pl. 3, figs. 1, 3, 6, 8.

REMARKS. This is the type species of the genus. Radial ribs are differentiated into primary and secondary ribs.

Dimensions. Length 19, width 13, height 18 mm (Palmer, 1937).

Occurrence. Claibornian, Middle Eocene, Alabama.

Altrix leesi (Sohl, 1992)

Puncturella (Altrix) leesi Sohl, 1992:420, figs. 6.1–6.7.

REMARKS. Radial ribs are differentiated into primary and secondary ribs.

Dimensions. Length 8.2, width 6.3, height 7.8 mm.

Occurrence. Maastrichtian, Upper Cretaceous, Puerto Rico.

Altrix pacifica (Squires and Goedert, 1996)

Puncturella (Altrix) pacifica Squires and Goedert, 1996:230, figs. 8–9.

REMARKS. This is the smallest species yet assigned to *Altrix*.

Dimensions. Length 3, width 3, height 2.8 mm.

Occurrence. Lower Eocene, Crescent Formation, Washington.

Altrix palmerae (Olsson, 1964)

Puncturella (Esmeria) palmerae Olsson, 1964:201, pl. 33, fig. 8–8c.

REMARKS. This is the type species of *Esmeria* Olsson, 1964, which is here placed in synonymy of *Altrix*. Olsson also assigned the Neogene species *A. trifolium* to his genus and it is not clear why he proposed *Esmeria*. The foramen has a tripartite outline in the interior view, as does *A. trifolium*. Primary and secondary ribs are well developed. In shell size this species is comparable to *A. trifolium*.

Dimensions. Length 27.2, width 20.4, height 15.1 mm.

Occurrence. Esmeraldas beds of Onzole Formation, Lower Pliocene, Esmeraldas Province, Ecuador.

Genus *Clathrosepta*, new genus

Figures 6, 7

Type species: *Clathrosepta depressa*, new species.

The following diagnosis for shell characters is based on the four species here assigned to the genus, whereas the description of the epipodium and radula is based on the type species and on *Clathrosepta becki* new species.

DIAGNOSIS. Shell of moderate size for family (maximum length 13.1 mm), height low to moderately high; all slopes straight to slightly convex. Juvenile shell and protoconch unknown. Foramen at summit of mature shell; triangular in outline (at least when viewed from interior); septum small, thick, slightly bowed posteriorly; anterior edge with weak pustule. Sculpture finely clathrate, beads formed at intersections of numerous radial and concentric ribs.

Epipodial tentacles three pairs, one reduced anterior pair and two pairs of longer tentacles posteriorly. Posterior pedal tentacle present (Figs. 6E, 7B). Ctenidia paired, bipectinate, leaflets numerous (Fig. 6F).

Radula. Rachidian elongate, base slightly broader than tip; shaft edges nearly straight, with tapered overhanging cusp with main projecting denticle and fine serrations on both edges of overhang; laterals four pairs, two innermost similar to rachidian, third shorter and lacking overhang; fourth with curved lower shaft that articulates with flange of pluricuspid tooth. Lateromarginal plate obstructed by pluricuspid. Pluricuspid large, with large tapered overhang and smaller cusps near bend; inner edge grooved to accommodate fourth lateral tooth, outer edge grooved to accommodate marginal teeth. Marginal teeth numerous, overhanging tips finely denticulate.

REMARKS. Although juvenile shells and protoconchs are unknown, the low profile of the type species would preclude the existence of a coiled early teleoconch whorl like that of *Puncturella*.

Shell sculpture differs from that of *Puncturella*, *Cranopsis*, and *Altrix* in being finely clathrate, with no distinction between primary, secondary, and tertiary ribs remaining at the growing edge of mature shells.

The four abyssal species that are assigned to the genus are smaller than the species of *Altrix*, but their size is much larger than known in the more apomorphic genera *Fissurisepta* or *Cornisepta*.

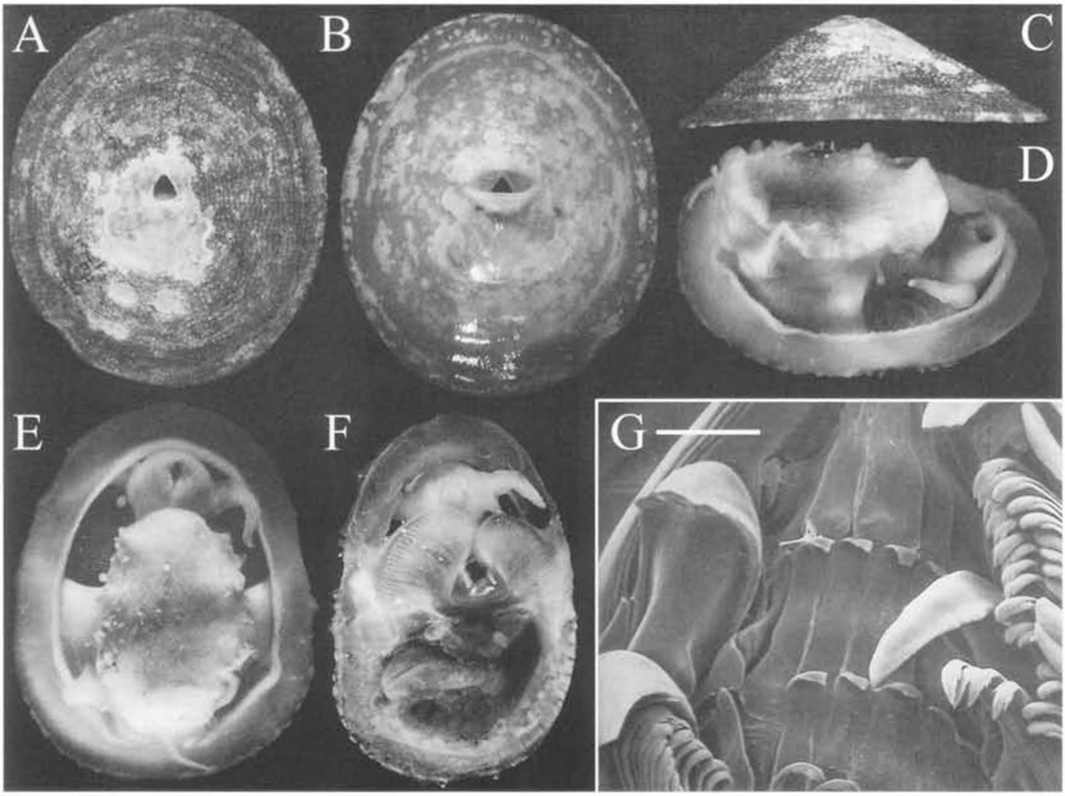

Figure 6A–G. *Clathrosepta depressa* new species. LACM 2784, holotype; 1160 m, eastern slope of Volcano 5, Eastern Pacific Rise at 13°N (12°58.0′N, 103°26.0′W). Length 13.1, width 11.0, height 3.8 mm; length of preserved retracted body 7 mm. **A.** Exterior showing fine clathrate sculpture and triangular outline of foramen. **B.** Interior, showing low, curved septum. **C.** Left side of shell. **D.** Body removed from shell, oblique view of left side, showing one short anterior epipodial tentacle, two longer posterior epipodial tentacles, and the single projecting posterior pedal tentacle. **E.** Ventral view of body, showing the projecting posterior pedal tentacle. **F.** Dorsal view of body showing paired bipectinate gills with detached axis. **G.** SEM view of radula, showing large pluricuspid teeth; tips of rachidian and laterals finely denticulate (scale bar = 40 μm).

Although the ctenidia are similar to those of *Puncturella,* the reduced number of epipodial tentacles and the presence of a posterior pedal tentacle are characters unlike those of *Puncturella.* In *Clathrosepta* the actual count of anterior and posterior tentacles differs in the two species, but there are too few specimens to be certain of the pattern.

The radula of *Clathrosepta* is close to that of the basic emarginuline plan, hardly differing from that of *Puncturella.* As in some species of *Puncturella,* the rachidian is relatively narrow.

Clathrosepta exhibits an unexpected combination of plesiomorphic character states (size, profile, curved septum, low septum, ctenidium, radula) and apomorphic character states (loss of apical whorl, apical foramen, posterior pedal tentacle, reduced epipodial tentacles). Further understanding of this genus awaits the description of the protoconch and juvenile shell. We consider it unlikely that *Clathrosepta* would have a coiled phase comparable to that of *Profundisepta.* More likely it would be like *Diodora* in lacking the coiled phase in the juvenile that might still retain the protoconch.

The type species from an eastern Pacific seamount and *C. becki* from the western Pacific are clearly associated with hydrothermal vent habitats. The habitat requirements of the other two species assigned to this genus is unknown; both were described before hydrothermal habitats were discovered. Anatomical data to confirm their assignment would be of great interest in order to establish that species of this genus can live in normal habitats as well as the sulfide-rich hydrothermal habitat.

Clathrosepta depressa, new species

Figure 6

DESCRIPTION. Shell thin, periostracum light brown, adherent, profile low, length 3.4 times height. Shell of holotype eroded around foramen and posteriorly, where it is thickened from within. Radial ribs at shell length of 5 mm approximately

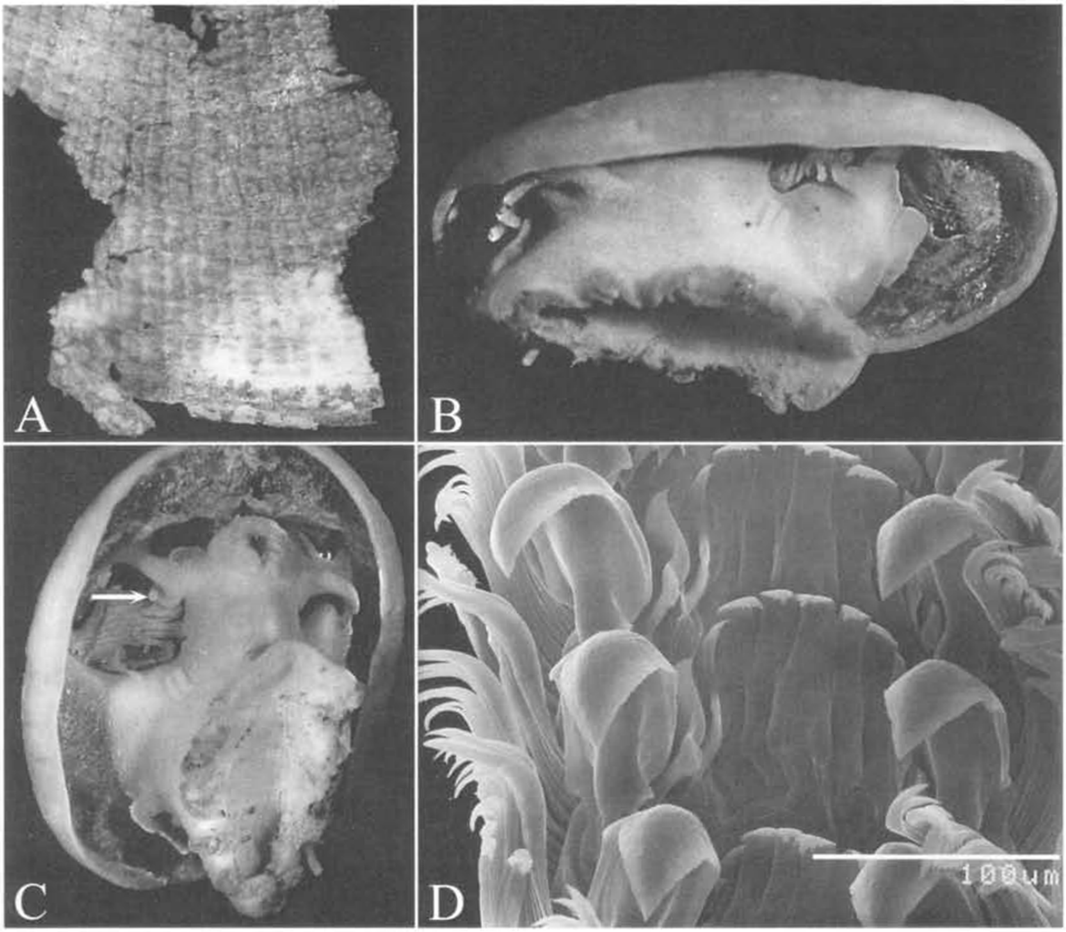

Figure 7A–C. *Clathrosepta becki* new species. Holotype NHMW 88.218; 2494 m, Manus Basin, Vienna Woods hydrothermal field, South Equatorial Pacific (3°9.86′S, 150°16.80′E). Preserved, retracted body length 6.0 mm. **A.** Periostracal fragment, retaining fine clathrate sculpture (scale bar = 1 mm). **B.** Right lateral view of body, showing two short anterior epipodial tentacles, two longer posterior epipodial tentacles, and the single upturned posterior pedal tentacle. **C.** Oblique ventral view of body, showing free axis of right gill and two short anterior epipodial tentacles. Arrow shows right suboptic tentacle. **D.** SEM view of radula (scale bar = 100 μm). [All photos by L. Beck.]

60, and at margin approximately 150, emerging secondary ribs quickly becoming as strong as primary ribs. Concentric sculpture of same strength and spacing as radial ribs, forming square clathrations and producing raised beads at intersections, interspaces of approximately same width as beads. Foramen proportionally very small (length 0.8 mm), triangular; septum low, ends curved anteriorly, anterior surface with weak tubercle. Muscle scar horseshoe-shaped, thin, not strongly indicated. Interior surface transparent, revealing exterior scars and markings.

Epipodial tentacles, posterior pedal tentacle, gill and radula as described under the genus.

Dimensions. Length 13.1, width 11.0, height 3.8 mm (holotype).

TYPE LOCALITY. On eastern slope of Volcano 5, Eastern Pacific Rise at 13°N (12°58.0′N, 103°26.0′W), 1160 m. The site is reported to be composed of pillow basalt at a hydrothermal mound topped with red crust (Lisa Levin, pers. comm.).

TYPE MATERIAL. Holotype LACM 2784. *Alvin* dive 1401, 15 June 1984, a single specimen received from Lisa Levin.

REMARKS. This species has the lowest profile of the species assigned to this genus.

Clathrosepta becki, new species

Figure 7

DESCRIPTION. Shell not preserved except for brown periostracal fragments, which show pattern of fine clathrate and beaded sculpture. Interspaces between radial ribs relatively broad, at least two times broader than ribs. Interspaces between concentric rings equal to rings. Cancellations are therefore rectangular rather than square.

Posterior pedal tentacle, epipodial tentacles, gill, and radula as described under genus.

Dimensions. Preserved, retracted body length 6.0 mm.

TYPE LOCALITY. Vienna Woods hydrothermal field, Manus Basin, east of Papua New Guinea, south equatorial Pacific (3°9.86′S, 150°16.80′E), 2494 m, on base of active "black smoker" sulfide chimney.

TYPE MATERIAL. Holotype NHMW 88.218. OLGA II, 18 May 1990, a single specimen lacking the shell except for periostracal fragments, received from Lothar Beck.

REMARKS. Although collected alive, the thin shell of the holotype specimen was apparently lost to an overly long initial preservation in unbuffered formalin. Despite the absence of a shell, the characters provided by the periostracal remnants, body, and radula make the generic assignment certain. Further collecting at the western Pacific vents will undoubtedly produce this species, and it is prudent to name it at this time.

The body and radula of the specimen are so similar to those of *C. depressa* that it could be regarded as the same species, although the preserved body is not as compressed as that of *C. depressa,* which suggests that *C. becki* should have a higher shell profile. There are no differences in the radula. Both species have the prominent posterior pedal tentacle. The arrangement and count of the epipodial tentacles is similar (two pairs of long posterior tentacles), except for the pair of short anterior tentacles, for which the difference is that in the holotype of *C. becki* the right tentacle consists of two separate tentacles instead of the one in *C. depressa.* More specimens would have to be compared to determine whether this difference is significant.

The major difference between the two species is in the detail of the sculpture. In *C. becki* (Fig. 6B) the radial ribs are much further apart and the interspaces broader than those of *C. depressa.*

Finally, the geographic distance between the Eastern Pacific Rise and the Manus Basin vents in the western Pacific suggests that speciation would have occurred. Although genera of vent mollusks may occur at both the eastern and western Pacific sites, there are no known instances of the same species occurring in two such widely separated sites.

ETYMOLOGY. This species is named after Lothar Beck, who allowed us to describe the species.

Other species of *Clathrosepta*

The following two species were originally allocated to *Fissurisepta,* although no anatomical or radular descriptions were provided. They are assigned to the new genus *Clathrosepta* because they have nearly straight septa and prominent clathrate sculpture and are larger than known for *Fissurisepta* or *Cornisepta.* As noted above, neither of the following two species was recorded from hydrothermal vent habitats.

Clathrosepta agulhasae (Clarke, 1961)

Puncturella (Fissurisepta) agulhasae Clarke, 1961: 347, pl. 1, fig. 3; pl. 2, fig. 9.—Clarke, 1962:7.
Fissurisepta agulhasae.—Ghisotti and Giannini, 1983:29.

REMARKS. This species resembles *C. depressa,* but has a higher profile. The foramen is triangular in interior view. Although the specimen was "alive when collected" (Clarke, 1961), the soft parts are no longer retained with the holotype shell at the MCZ. The size is much larger than usual in the genera *Fissurisepta* or *Cornisepta.*

Dimensions. Length 8.5, width 7.5, height 5.5 mm.

Occurrence. Agulhas Basin, 1000 miles west of Capetown, South Africa, 3670 m.

Clathrosepta undulata (Okutani, 1964)

Puncturella (Fissurisepta) undulata Okutani, 1964: 378, pl. 1, fig. 11.
Fissurisepta undulata.—Ghisotti and Giannini, 1983:29.

REMARKS. The sculpture is finely clathrate and the foramen was originally described as "subtriangular."

Dimensions. Length 7.9, width 5.65, height 3.65 mm.

Occurrence. Off Torishima Island, Japan, 2280 m, known only from holotype.

Genus *Fissurisepta* Seguenza, 1862
Figures 8, 9

Fissurisepta Seguenza, 1862:83. Type species (SD Woodring, 1928:454): *Fissurisepta papillosa* Seguenza, 1862. Plio-Pleistocene, Sicily, Italy.

The following diagnosis is based on shells of *F. granulosa* Jeffreys, 1882 (LACM 151946), descriptions of the epipodium of that species given by Warén (1972), and notes provided on an additional preserved specimen (Warén, pers. comm.), the SEM illustration of the radula by Hickman (1983), as well as the SEM illustrations of the radula and juvenile shell of *F. enderbyensis* (Powell, 1958) provided by S. Hain.

DIAGNOSIS. Shell small, height low to moderate; all slopes flat-sided. Apical whorl lacking, protoconch retained in young shells until shell length of 2 mm; protoconch sculpture rugose. Foramen apical, obliterating protoconch in mature shell, of weakly tripartite outline. Selenizone lacking. Septum relatively small, straight across, thin, low. Sculpture of raised pustules aligned in radial rows.

Epipodial tentacles 6–8 pairs, of differing lengths, with shorter tentacles between longer ones; posterior pedal tentacle present. Ctenidia monopectinate.

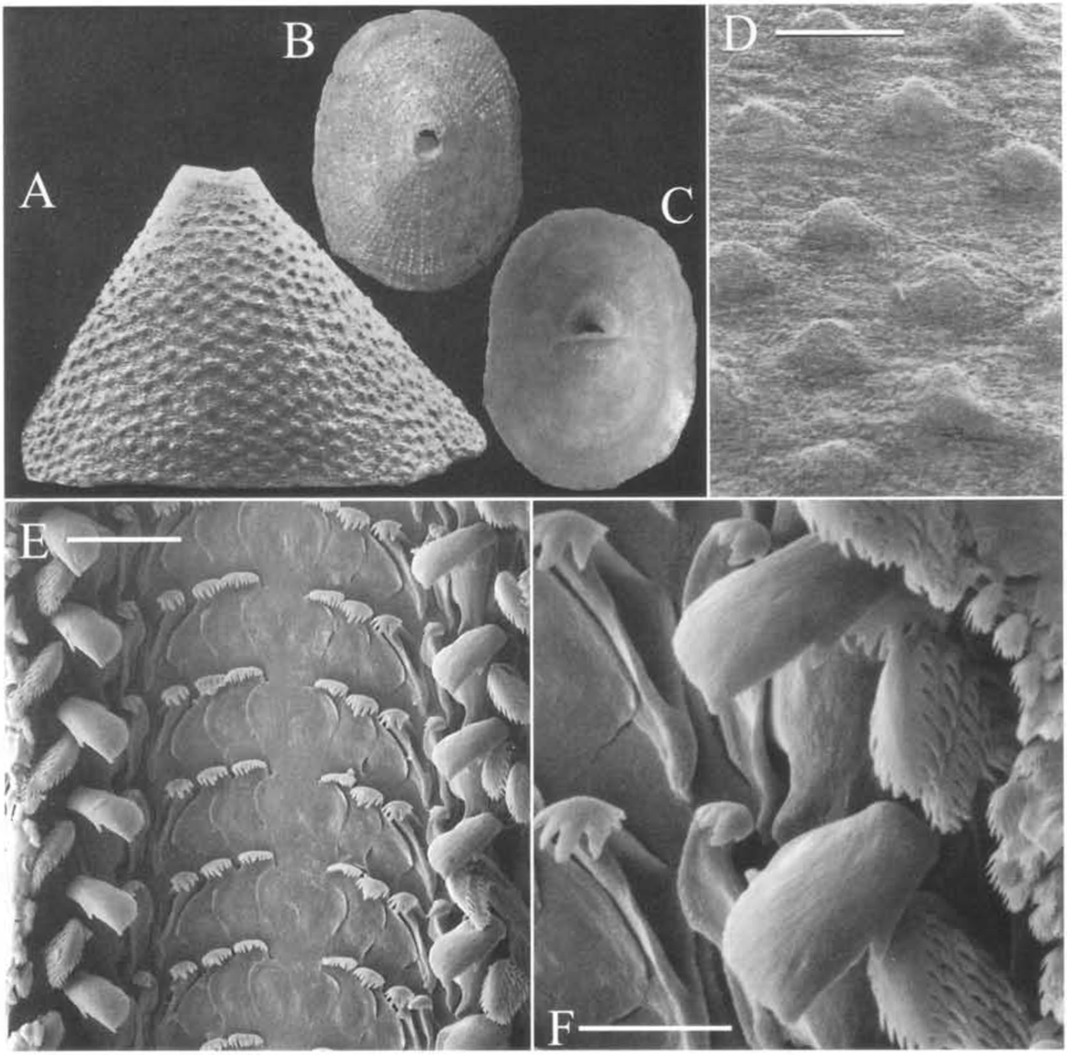

Figure 8A–F. *Fissurisepta granulosa* Jeffreys, 1882. LACM 151946, ex A. Warén; 100–180 m, E of Brattholmen, Hjeltefjord, SW Norway (60°24.5′N, 05°07′E). **A.** SEM view, left side of shell; specimen of high profile, showing pustules in radial rows (shell length 3.2, width 2.5, height 1.8 mm). **B.** Exterior view of shell of low profile, showing pustules in radial rows (shell length 4.3, width 3.3, height 1.7 mm). **C.** Interior view of same shell as in C, showing low septum and tripartite outline of foramen. **D.** Same specimen as A; SEM view of pustules (scale bar = 100 μm). **E.** SEM view of radula (scale bar = 10 μm). **F.** SEM view of radula showing teeth associated with the large pluricuspid tooth of right side (scale bar = 40 μm). [E, F by C. Hickman.]

Rachidian short, broad, cuspless, with shaft edges laterally projecting; four pairs of laterals having broad, short, laterally projecting, overlapping shafts, tips with narrow overhanging edges with up to seven cusps, but no serrations on lateral edges of shaft; fourth lateral with socket for articulation with flange of pluricuspid; pluricuspid with broad, inwardly directed flange, overhanging tip with short acute tip; marginals numerous, tips finely divided.

REMARKS. The type species of *Fissurisepta* is based on a fossil taxon, but the assumption has been made by previous authors and accepted here that it is closely related to the living species *F. granulosa,* for which the radula has been illustrated by Hickman (1983:fig. 2). The same radular plan occurs in the Antarctic *F. enderbyensis* (Powell, 1958), as illustrated here (Fig. 9E). The pluricuspid tooth of the two species is not entirely similar (compare Figs. 8F, 9E), although the differences may be a matter of differing orientation.

A drawing of the protoconch of *F. granulosa* still retained on a juvenile shell was provided by Warén (1972:fig. 1A); it agrees with the juvenile of *F. enderbyensis* illustrated here (Fig. 9B).

We have not examined a preserved specimen. Ac-

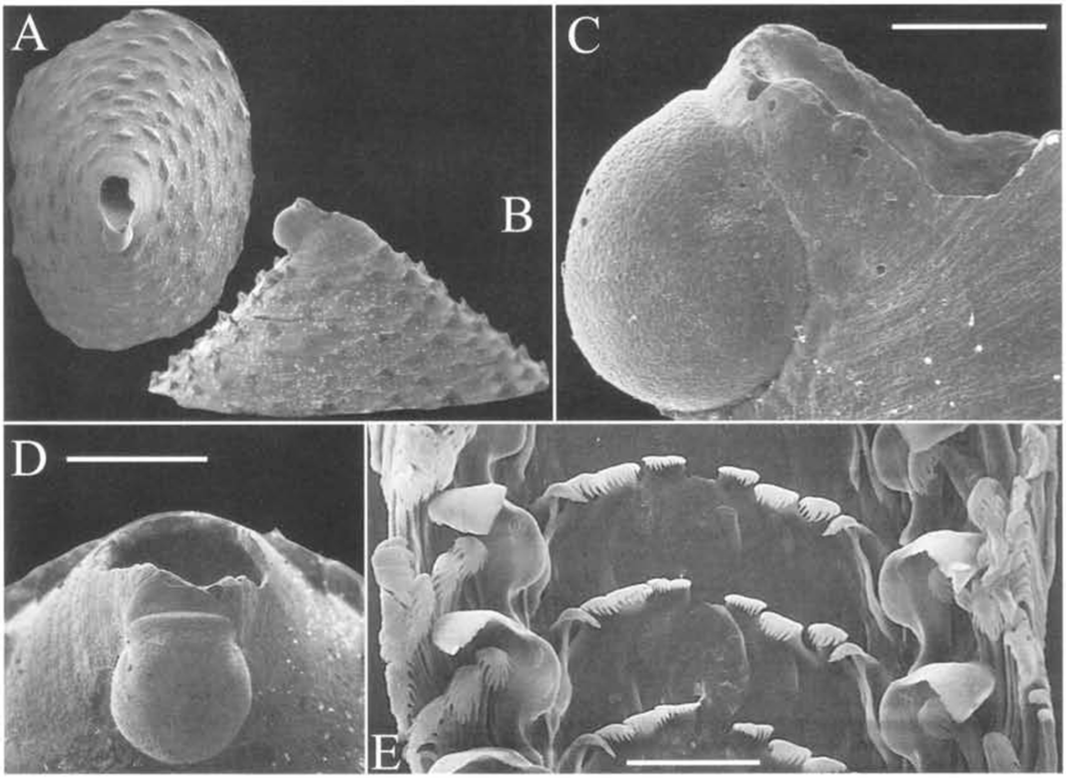

Figure 9A–E. *Fissurisepta enderbyensis* (Powell, 1958). LACM 152291, ex S. Hain; Weddell Sea, Antarctica (71°12.0'S, 013°15.4'W), 402–412 m. Length 2.2, width 1.4 , height 1.0 mm. **A.** SEM, dorsal view of shell. **B.** SEM, right side of juvenile shell with intact protoconch. **C.** SEM, right lateral view of protoconch and foramen (scale bar = 100 μm). **D.** SEM, posterior view of protoconch (scale bar = 200 μm). **E.** SEM, radula (scale bar = 20 μm). [All photos by S. Hain.]

cording to Warén (1972:19), the foot of *F. granulosa* "has six epipodial tentacles on each side, of which the two midmost ones are much smaller than the anterior and posterior pairs." A second specimen recently examined by Warén (pers. comm.) has on both sides "one long, then four short, one long, one short, one long and finally one unpaired short." The "unpaired short" is here regarded as homologous with the posterior pedal tentacle of *Manganesepta* and *Clathrosepta.*

A drawing of the juvenile animal of *F. enderbyensis* provided by S. Hain shows a single pair of posterior epipodial tentacles and one tentacle midway on the left side; however, the juvenile condition of this species is probably not indicative of mature characters.

Fissurisepta is apomorphic in most character states, except for having a relatively low septum.

Fissurisepta granulosa Jeffreys, 1883
Figure 8

Fissurisepta granulosa Jeffreys, 1883:675, pl. 50, fig. 9.—Warén, 1972:17, fig. 1A–D.—Taviani, 1974:40, pl. 1, fig. 2a–b.—Warén, 1980:14, pl. 2, figs. 19, 20.—Hickman, 1983:72, fig. 2 [radula].—Ghisotti and Giannini, 1983:28, pl. 1, figs. 1–4; pl. 2, figs. 1–4.—Warén, 1991:54, fig. 1C.

Puncturella (Fissurisepta) granulosa.—Pilsbry, 1890:246, pl. 27, figs. 71, 72 [copy of original figure].

REMARKS. According to Jeffreys (1883), this species "is more delicate, the sculpture is much finer, with regular and close-set striae which are studded with far more numerous and minute tubercles. The foramen is circular in the present species, and triangular in *F. papillosa.*" Although Warén (1972) placed the two taxa in synonymy, Taviani (1974) illustrated both *F. granulosa* and *F. papillosa,* showing finer pustules in *F. granulosa,* so the two taxa are separated here.

Warén (1972) confirmed that the ctenidium of this species agrees with that described and illustrated by Cowan (1969) for the species here treated as *Cornisepta pacifica.*

Fissurisepta granulosa is highly variable in height, as illustrated by Warén (1972:figs. C and D). Although we have not examined a preserved specimen, the epipodium has been described by

Warén (see generic description above). The radular illustration used here was first published by Hickman (1983).

Dimensions. Length 4.3, width 3.4, height 1.6 mm (Fig. 8C, D), a specimen of low profile. Length 3.1, width 2.4, height 1.6 mm, a specimen of high profile (both LACM 151946).

Occurrence. Mediterranean and northeastern Atlantic, 50–500 m.

Fissurisepta enderbyensis (Powell, 1958)
Figure 9

Puncturella enderbyensis Powell, 1958:180, pl. 2, figs. 1, 2.—Dell, 1990:273 [listed].

REMARKS. Previously unpublished SEM work on the radula (Fig. 9E) done by S. Hain shows that the rachidian and lateral teeth are like those of *F. granulosa* in having short, bulging shafts and a cuspless rachidian. The pluricuspid tooth differs as noted above, however. The single specimen collected by Hain still retained the protoconch (Fig. 9A–D). Mature shells were evidently not obtained. Other shell characters that agree with *Fissurisepta* are the low profile and the pustules aligned in radiating rows.

Dimensions. Length 2.2, width 1.4, height 1.0 mm (Fig. 8).

Occurrence. Enderbyland, Antarctica, 300 m (type locality); Weddell Sea, Antarctica, 402–412 m (Fig. 8).

Other species of *Fissurisepta*

With the exception of the first species below, the following species that were originally described or subsequently allocated in *Fissurisepta* have shell profiles in agreement with the here more restricted definition of *Fissurisepta*. The number of species retained in *Fissurisepta* is smaller than previously. Other species previously treated in *Fissurisepta* are transferred in this paper to the new genera *Clathrosepta* and *Cornisepta*.

Fissurisepta oxia (Watson, 1883)

Puncturella oxia Watson, 1883:36.—Watson, 1886:44, pl. 4, fig. 8a–e.—Pilsbry, 1890:235, pl. 26, figs. 46–49 [copy of original illustrations].—Thiele, 1919:154, pl. 18, figs. 15–17.—Dall, 1927:111.—Farfante, 1947:134, pl. 58, figs. 5–7.

REMARKS. This species has a low profile and pustules in curved rows. If this species is correctly assigned to *Fissurisepta*, it represents an extreme for the genus in which the apex is retained after a shell length of 4 mm. The sculpture of pustules in curved rows allows placement only in the genus *Fissurisepta*. However, this needs to be verified by radular evidence.

Dimensions. Length 4, width 3, height 2.25 mm (Farfante, 1947).

Occurrence. Georgia and St. Thomas, Virgin Islands, 530–740 m (Farfante, 1947).

Fissurisepta manawatawhia (Powell, 1937)

Puncturella manawatawhia Powell, 1937:177, pl. 48, fig. 8.
Fissurisepta manawatawhia.—Powell, 1979:39, fig. 3.7.—Ghisotti and Giannini, 1983:29.

REMARKS. The protoconch is retained in the immature holotype specimen, as noted by Ghisotti and Giannini (1983). The low profile and pustules in radiating rows make this species readily assignable to *Fissurisepta*.

Dimensions. Length 1.5, width 1.15, height 0.8 mm (holotype).

Occurrence. Three Kings Islands, New Zealand, 260 m.

Fissurisepta papillosa Seguenza, 1862

Fissurisepta papillosa Seguenza, 1862:84, pl. 4, fig. 2a, 2b.—Jeffreys, 1870:443.—Jeffreys, 1883: 675.—Taviani, 1974:40, pl. 1, fig. 1a–b.—Ghisotti and Giannini, 1983:28, fig. 1A–C [copy of original figs.], pl. 1, fig. 5; pl. 2, fig. 8.—Di Geronimo and La Perna, 1997:395, pl. 1, figs. 1–3.
Puncturella (Fissurisepta) papillosa.—Pilsbry, 1890: 245, pl. 64, figs. 16–18 [copy of original figs.].—Clarke, 1962:8 [listed].

REMARKS. This is the type species of the genus. Taviani (1974) illustrated a Plio-Pleistocene specimen showing coarser pustules than those he figured for *F. granulosa*. A recently collected fossil specimen was illustrated by Di Geronimo and La Perna (1997).

Dimensions. Length 2.8, width 1.9, height 2 mm (Seguenza, 1862).

Occurrence. Plio-Pleistocene of Sicily, Italy, but treated as a living species by Ghisotti and Giannini (1983).

Fissurisepta tenuicula (Dall, 1927)

Puncturella tenuicula Dall, 1927:112.
Puncturella (Fissurisepta) tenuicola [sic].—Farfante, 1947:147, pl. 64, figs. 4–6.
Fissurisepta tenuicola [sic].—Ghisotti and Giannini, 1983:23, pl. 2, fig. 9.

REMARKS. The sculpture according to Dall consists of almost microscopic radial granulations. Allocation to *Fissurisepta* is based on the low shell profile.

Dimensions. Length 3, width 2, height 1.75 mm (Farfante, 1947).

Occurrence. Off Cumberland Island, Georgia, 538 m.

Genus *Cornisepta*, new genus
Figures 10–14

Type species: *Fissurisepta antarctica* Egorova, 1972.

The following diagnosis is based on *Cornisepta antarctica*, *C. rostrata* (Seguenza, 1862), *C. pacifica*

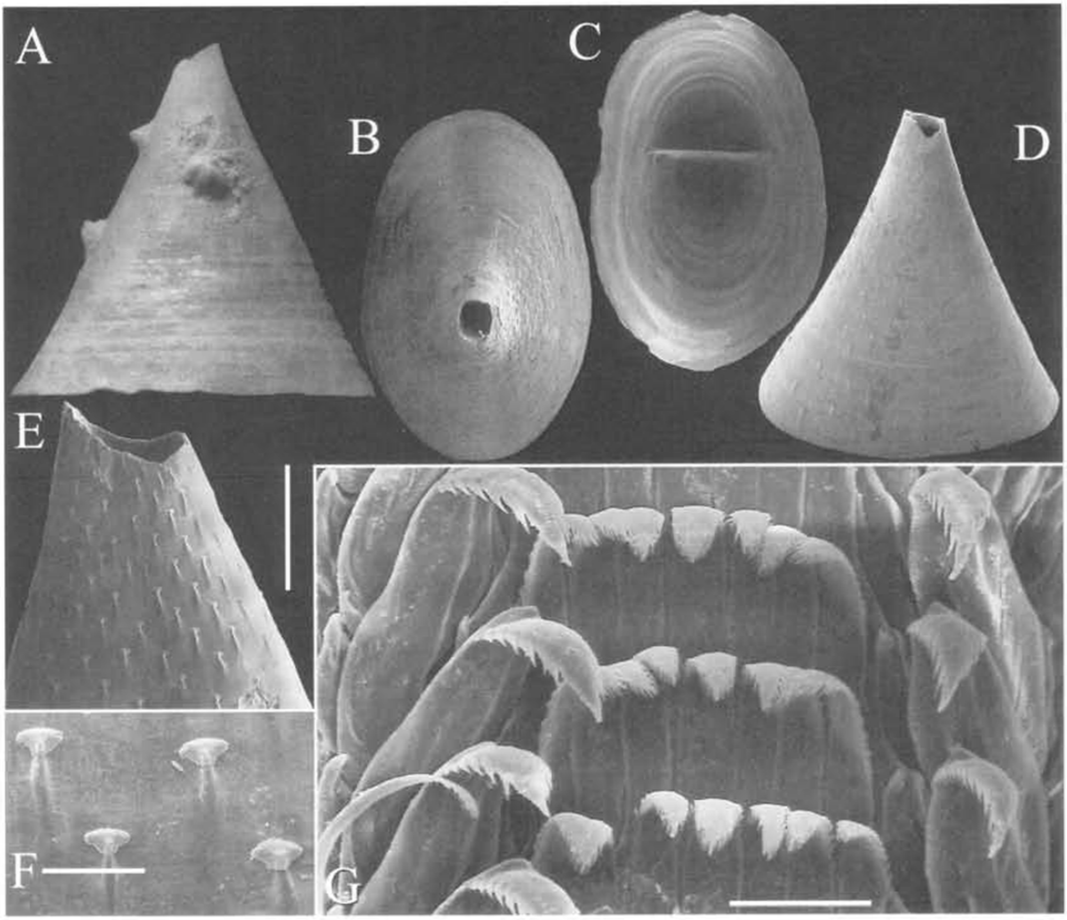

Figure 10A–E. *Cornisepta antarctica* (Egorova, 1972). LACM 151947; 620–640 m, Weddell Sea, Antarctica (74°43′S, 61°13′W), 620–640 m. **A.** Largest specimen, left side of shell with attached sessile foraminifera; length 7.1, width 5.0, height 6.8 mm. **B.** Smallest specimen, dorsal view; length, 3.0, width 2.0, height 3.5. **C.** Interior view of another specimen; length 4.8, width 3.2, height 5.3 mm. **D.** Oblique lateral view of right side of another specimen; length 5.9, width 4.0, height 5.8 mm. **E.** Enlargement of pustules on early shell; same specimen as in D (scale bar = 500 μm). **F.** Detail of pustules, same specimen (scale bar = 100 μm). **G.** SEM view of radula, showing pinnate form of all teeth (scale bar = 25 μm). [All photos by S. Hain.]

(Cowan, 1969), *C. verenae*, new species, and *C. levinae*, new species.

DIAGNOSIS. Shell height high to very high; anterior slope convex to straight, posterior slope concave. Apical whorl lost, juvenile shell and protoconch unknown. Foramen at summit of mature shell; septum high, straight across, thin. Sculpture of raised pustules aligned in curved rows.

Epipodial tentacles two posterior pairs (Figs. 11C, 12E, 13B, 14D); posterior pedal tentacle lacking. Ctenidium monopectinate (Figs. 11D, 13C).

Radula. Rachidian tooth and three pairs of pinnate lateral teeth of similar morphology, with long shafts and tapered, overhanging tips; tips and shaft edges deeply and finely serrate; pluricuspid tooth large, overhanging tip tapered, sides of overhang with five strong denticles away from tip; shaft edges of pluricuspid not serrate; marginals numerous, pinnate, tips and sides deeply serrate.

REMARKS. The radula of *Cornisepta* (Figs. 10G, 11E, 12F, 13F, 14F) is unlike that of the European *F. granulosa,* a species closely similar to the fossil type species of *Fissurisepta.* The differences (compare the slender, pinnate rachidian and laterals of *Cornisepta* to the short, overlapping laterals of *Fissurisepta*) are so extreme that placement in the same genus is precluded. On shell characters, the species of *Cornisepta* differ in having the profile higher, the posterior slope concave, and the septum higher.

Cornisepta is the most apomorphic of the genera treated here, having the highest shell profile and the most modified radula, in which all of the teeth are pinnate, autapomorphies for this suite of charac-

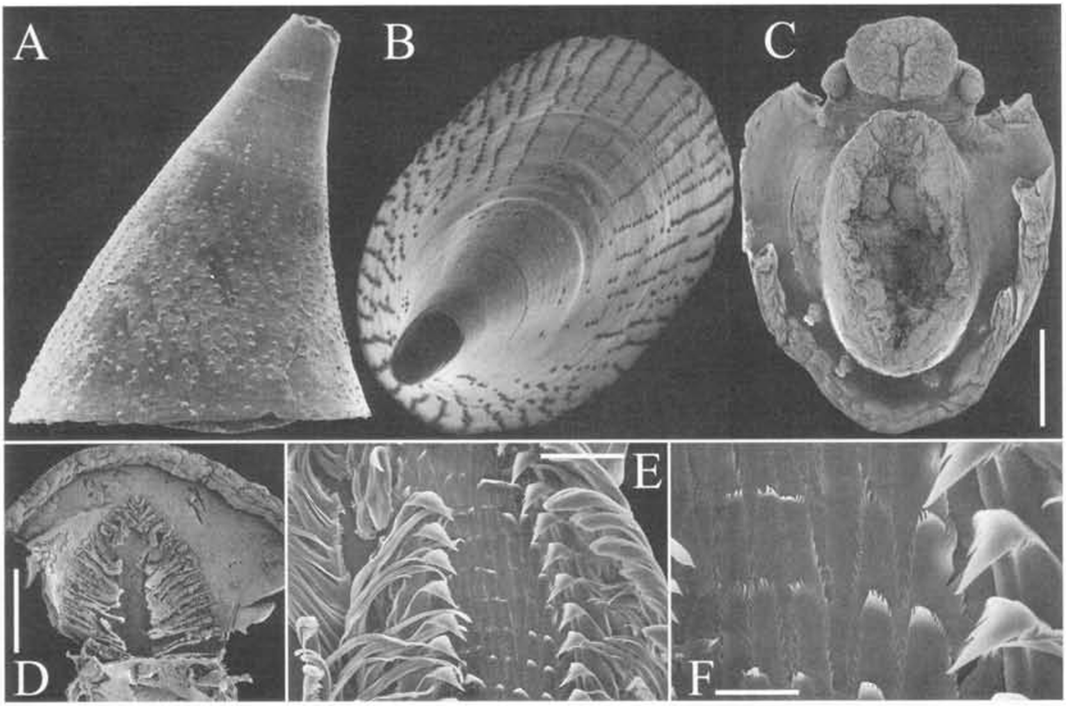

Figure 11A–F. *Cornisepta rostrata* (Seguenza, 1862). MNHN; off western France, 1035–1080 m, Thalassa station Z409 (47°43′N, 08°02′W). Length 3.5, width 2.4, height 4.2 mm. **A.** Left side of shell, anterior at left. **B.** Dorsal view of shell, anterior at right. **C.** Ventral view of body (critical point dried) showing paired, posterior epipodial tentacles (scale bar = 800 μm). **D.** Paired monopectinate ctenidia attached to roof of mantle cavity (scale bar = 700 μm). **E.** Full width of radula (scale bar = 60 μm). **F.** Half row of radula (scale bar = 20 μm). [All SEM photos by A. Warén.]

ters. There is considerable interspecific variability in shell height and the size, spacing, and morphology of the pustules, as is evident among the four species illustrated here.

Protoconchs are unknown for all species, which suggests that they must be shed at a very early stage. The smallest specimen known in the genus (1.6 mm length) is the holotype of *C. verenae*, which lacks the protoconch. Knowledge of the type of protoconch sculpture in this genus is a significant gap.

Hain (1990) reported that the gut contents of two individuals of *C. antarctica* (as *Fissurisepta*) were exclusively benthic diatoms of various genera. This suggests that the highly modified radula of *Cornisepta* is adapted to sweeping that food source. It further suggests that the food of all species of *Cornisepta* will prove to be the same.

Cornisepta antarctica is made the type of the genus because it is represented by the largest amount of material, including two preserved bodies, that can be made available on loan for future work, as was Hain's intention in placing the material in the LACM collection.

ETYMOLOGY. The name derives from the Latin noun for horn, suggested by the high profile.

Cornisepta antarctica (Egorova, 1972)

Figure 10

Fissurisepta antarctica Egorova, 1972:384, fig. 1a,b.—Hain, 1990:34, pl. 10, fig. 6a,b [drawings of shell]; pl. 28, fig. 8 [SEM view of radula].

REMARKS. This species is the largest known member of *Cornisepta*. The pustular sculpture of this species can easily be missed, as it is not readily apparent, even under magnification with a dissecting microscope. The pustules are T-shaped under SEM examination, aligned in diagonal rows, and becoming fewer in later growth stages. Size of the pustules increases only slightly with growth of the shell.

Hain (1990) illustrated the radula of this species but did not compare it to the illustration of the radula of *Fissurisepta* provided by Hickman (1983). Other citations of Egorova in the synonymy of this species cited by Hain are repetitive of the original description.

Dimensions. Length 7.0, width 4.9, height 6.7 mm (LACM 151947, Fig. 10A).

Occurrence. Weddel Sea, Antarctica, 280–700 m.

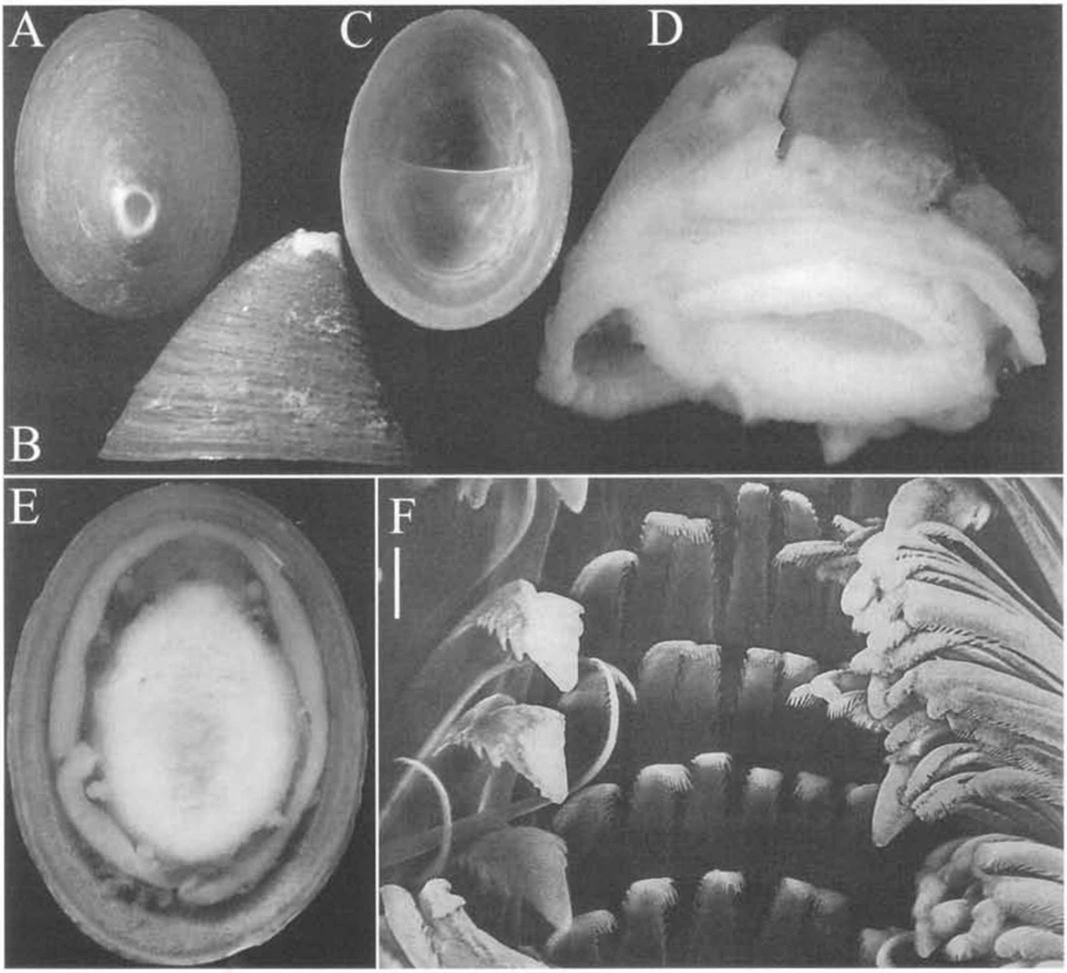

Figure 12A–F. *Cornisepta pacifica* (Cowan, 1969). LACM 77-285.1; 444–500 m, NW slope of Santa Cruz Basin, S of Santa Cruz Island, California (33°46.0′N, 119°49.2′W). Length 4.8, width 3.5, height 3.6 mm. **A.** Exterior, anterior at top. **B.** Left side showing weakly developed pustular sculpture and concave posterior slope. **C.** Interior showing high septum, anterior at top. **D.** Left side of body removed from shell, showing monopectinate gill by transparency on left and deep cleft left by position of septum. **E.** Ventral view of body before removal from shell showing reduced epipodial tentacles. **F.** Radula (scale bar = 20 μm).

Cornisepta rostrata (Seguenza, 1862)
Figure 11

Fissurisepta rostrata Seguenza, 1862:84, pl. 5, fig. 3a–c.—Jeffreys, 1883:675.—Ghisotti and Giannini, 1983:28, fig. 2A, B, C [copy of original figs.], pl. 2, fig. 15.—Di Geronimo and La Perna, 1997:395, pl. 1, figs. 4, 5.

Puncturella (*Fissurisepta*) *rostrata*.—Watson, 1886: 48, pl. 4, fig. 10.—Pilsbry, 1890:245, pl. 25, fig. 25, pl. 64, figs. 30, 31.—Clarke, 1962:8 [listed].

Fissurisepta rostrata var. *elata* Seguenza, 1862:84, fig. 3d.—Ghisotti and Giannini, 1983:26, fig. 2D [copy of original figs.].

REMARKS. The high shell elevation is indicative of *Cornisepta*.

Dimensions. Length 5, width 3.5, height 4.6 mm (Seguenza). Length 3.5, width 2.4, height 4.2 mm (Fig. 11A).

Occurrence. Northeastern Atlantic and Mediterranean, 1000–2000 m.

Cornisepta pacifica (Cowan, 1969)
Figure 12

Fissurisepta pacifica Cowan, 1969:24, figs. 1, 2 [head and ctenidia], 3 [shell fragments].—Warén, 1972:19 [discussed].—Abbott, 1974:23 [listed only].—Ghisotti and Giannini, 1983:29 [listed only].

REMARKS. The holotype shell was damaged in transit before it was illustrated and the radula of

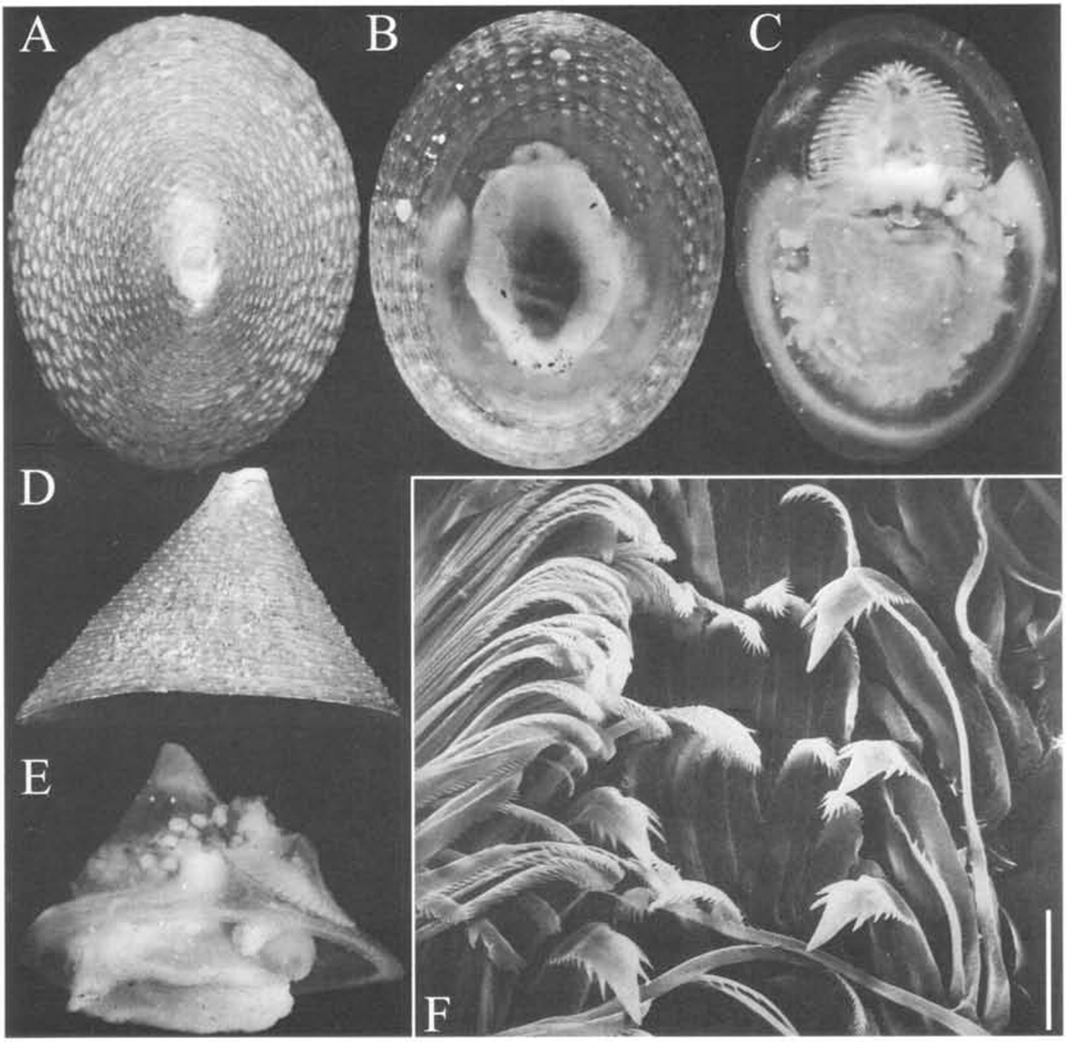

Figure 13A–F. *Cornisepta levinae* new species. LACM 2788, holotype; 1775 m, summit of Volcano 6, Eastern Pacific Rise at 13°N (12°44.0′N, 102°33.0′W). Length 5.2, width 4.1, height 3.5 mm. **A.** Exterior, anterior at top. **B.** Ventral view of retracted animal in shell. **C.** Left side of shell showing pustules in curved rows and concave posterior slope. **D.** Body in dorsal view, showing paired monopectinate ctenidia by transparency. **E.** Body from right side, showing right ctenidium and ooccytes by transparency. **F.** SEM view of radula showing pinnate form of all teeth (scale bar = 10 μm).

the holotype was not originally figured. However, three specimens from southern California as well as two from Alaska and one from Oregon are now known. The shell (Fig. 12A–C) and radula (Fig. 12F) are here illustrated. Warén (1972:19) noted that Cowan had incorrectly identified the first pair of epipodial tentacles as a second pair of cephalic tentacles.

Dimensions. Length 4.8, width 3.5, height 3.6 mm (Fig. 10A–D).

Occurrence. Kiska, Aleutian Islands, Alaska, San Clemente Island, California. Records from Sitka, Alaska, to southern California have a depth range of 440–880 m; the single shell from Kiska, Aleutian Islands, was recorded at 168 m.

Cornisepta levinae, new species

Figure 13

DESCRIPTION. Shell of moderate size for genus, profile moderately high (75% of length in holotype); anterior slope nearly straight, posterior slope slightly concave. Juvenile shell and protoconch unknown. Foramen oval in outline, septum deep and straight across (broken in holotype). Sculpture of thin, elongate, projecting pustules, in

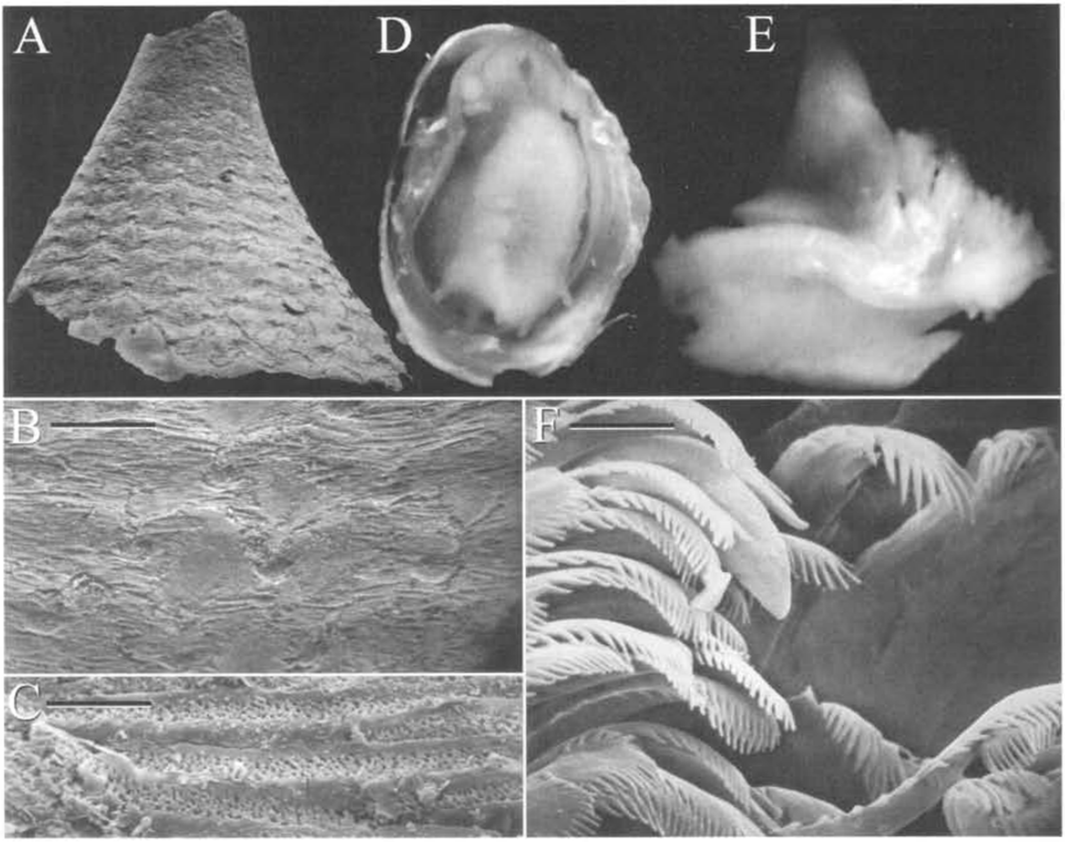

Figure 14A–F. *Cornisepta verenae* new species. LACM 2787, holotype; 1530 m, Axial Seamount, Juan de Fuca Ridge, vent no. 1 (45°56.2′N, 130°04′W). Length 1.6, width 1.3, height 1.3 mm. **A.** SEM, left side of shell, posterior slope concave. **B.** Enlargement of surface showing detail of periostracum and weakly projecting pustules (scale bar = 100 μm). C. Further enlargement showing pits in periostracum (scale bar = 10 μm). **D.** Preserved body before removal from shell showing posterior epipodial tentacles. **E.** Right side of body after removal from shell, showing depth penetrated by septum. F. SEM of radula, showing pinnate form of all teeth, tips of marginals on left, tip of pluricuspid among marginals, and laterals at right in dark shadow (scale bar = 4 μm).

radial rows during early growth and continuing in straight rows anteriorly, rows becoming disorganized on sides. In profile view the pustules appear organized along the lines of growth.

Epipodial tentacles, gill, and radula as described under the genus.

Dimensions. Length 5.2, width 4.1, height 3.5 mm.

TYPE LOCALITY. Summit of Volcano 6, Eastern Pacific Rise at 13°N (12°44.0′N, 102°33.0′W), 1775 m. According to the field notes for dive 1389, the site was under hydrothermal influence, with orange and green mud and orange crusty material on the pahoehoe lava, with a 1-mm-thick manganese coating (Lisa Levin, pers. comm.).

TYPE MATERIAL. Holotype LACM 2788, *Alvin* dive 1389, 3 June 1984. A single specimen received from Lisa Levin.

REMARKS. This species differs from *C. pacifica* in its straighter anterior slope and denser configuration of more laterally compressed pustules.

ETYMOLOGY. This species is named after Lisa Levin who collected the holotype.

Cornisepta verenae, new species

Figure 14

DESCRIPTION. Shell small (possibly immature), profile high (81% of length in holotype); protoconch unknown. Foramen oval, septum high, straight across. Pustules weakly projecting, appearing to be linked in chains that encircle the slopes of the shell; similar chains above and below alternate in filling space. Pustules increasing in number but not size with growth, pustules 50 μm in diameter. Shell covered with light-colored periostracum that forms minute ridges, the ridge interspaces deeply pitted (Fig. 14C).

Epipodium (Fig. 14D) and radula (Fig. 14F) as in generic description.

Dimensions. Length 1.6, width 1.3, height 1.3 mm (holotype).

TYPE LOCALITY. Axial Seamount, Juan de Fuca Ridge, eastern area, vent no. 1 (45°56.2'N, 130°04'W), 1530 m. This species lives in or near the sulfide-rich hydrothermal habitat.

TYPE MATERIAL. Holotype LACM 2787. *Pisces* dive 1730–1431, 31 July 1986, a single specimen collected by V. Tunnicliffe.

REMARKS. The growing margin of the holotype was received in broken condition. The shell was extremely thin but was mounted for SEM examination (Fig. 14A–C). The shell shattered during the attempt to reposition it on the stub; consequently the holotype now consists of the body with the radula extracted.

This species adds a new dimension to the kinds of pustule morphology possible in *Cornisepta*, as similar sculpture of pustules in low, interlocking chains is otherwise unknown in the genus.

ETYMOLOGY. The name honors Verena Tunnicliffe, who collected the specimen.

Other species of *Cornisepta*

On the basis of the high shell profile, most of the remaining species usually treated in *Fissurisepta* Seguenza, 1862, are probable members of *Cornisepta* and are here transferred to this new genus. Seven further species are noted here.

Cornisepta acuminata (Watson, 1883)

Puncturella (*Fissurisepta*) *acuminata* Watson, 1883: 38.—Farfante, 1947:145, pl. 64, figs. 1–3.

Fissurisepta acuminata.—Abbott, 1974:22, fig. 71.—Ghisotti and Giannini, 1983:28, pl. 2, figs. 12–14.

Fissurisepta triangulata Dall, 1889:404.—Dall, 1890:357.—Dall, 1927:112.—Ghisotti and Giannini, 1983:28.

Puncturella (*Fissurisepta*) *rostrata* var. *triangulata*.—Pilsbry, 1890:245.

REMARKS. Some authors recognize two species, *acuminata* and *triangulata*, but they are synonymized here. Assignment to *Cornisepta* is certain because of the high elevation and dense pustules in curving rows.

Dimensions. Length 5, width 3.5, height 4 mm (Farfante, 1947).

Occurrence. Georgia to Yucatan and the Caribbean, 290–710 m.

Cornisepta crossei (Dautzenberg and Fischer, 1896)

Fissurisepta crossei Dautzenberg and Fischer, 1896: 492, pl. 22, fig. 15.—Dautzenberg and Fischer, 1897:181.—Dautzenberg, 1927:225, pl. 7, fig. 17.—Ghisotti and Giannini, 1983:29, pl. 2, fig. 17.

Puncturella (*Fissurisepta*) *crossei*.—Thiele, 1919, pl. 20, fig. 19 [copy of original illustrations].

REMARKS. The very high profile is indicative of *Cornisepta*.

Dimensions. Length 3, width 2, height 5 mm.

Occurrence. Azores, 1022 m.

Cornisepta festiva (Crozier, 1966)

Fissurisepta festiva Crozier, 1966:46, fig. 18.—Powell, 1979:39, fig. 3.8.—Ghisotti and Giannini, 1983:29, pl. 2, fig. 18.

REMARKS. The high profile and scattered pustules are indicative of *Cornisepta*.

Dimensions. Length 5.1, width 3.2, height 5.3 mm.

Occurrence. Off Three Kings Islands, New Zealand, 805 m.

Cornisepta fumarium (Hedley, 1911)

Puncturella fumarium Hedley, 1911:100, pl. 18, figs. 13, 14.

Fissurisepta fumarium.—Cotton, 1930:222.—Cotton, 1959:68, fig. 31.—Ghisotti and Giannini, 1983:29, pl. 2, fig. 11.

Puncturella (*Fissurisepta*) *fumarium*.—Cotton and Godfrey, 1934:55, pl. 1, fig. 14.

REMARKS. The high profile suggests that of *Cornisepta*. The original depth is unusually shallow for the genus.

Dimensions. Length 2.15, width 1.35, height 1.85 mm.

Occurrence. Off Cape Wills, Australia, 180 m.

Cornisepta microphyma (Dautzenberg and Fischer, 1896)

Fissurisepta microphyma Dautzenberg and Fischer, 1896:492, pl. 22, fig. 14.—Ghissoti and Giannini, 1983:29, pl. 2, fig. 16.

Puncturella (*Fissurisepta*) *microphyma*.—Thiele, 1919, pl. 20 [no text].

REMARKS. The high profile is indicative of *Cornisepta*.

Dimensions. Length 6, width 4, height 5 mm.

Occurrence. Azores, 861–1202 m.

Cornisepta onychoides (Herbert and Kilburn, 1986)

Fissurisepta onychoides Herbert and Kilburn, 1986:24, figs. 87–89.

REMARKS. This recently described species has pustules in curved rows and a high profile and is a probable member of *Cornisepta*.

Dimensions. Length 4.5, width 3.2, height 5.3 mm.

Occurrence. Natal and Transkei, South Africa, 250–430 m.

Cornisepta soyoae (Habe, 1951)

Fissurisepta soyoae Habe, 1951:116, pl. 17, figs. 9, 10.—Habe, 1964:4, fig. 15.—Kuroda, Habe, and Oyama, 1971:8, pl. 106, fig. 7.—Ghisotti and Giannini, 1983:29, pl. 2, fig. 10.

REMARKS. The high profile and pustules in curving rows are indicative of *Cornisepta.*

Dimensions. Length 3.6, width 2.4, height 2.3 mm.

Occurrence. Sagami Bay, Japan, 120–270 m.

Species removed from the *Fissurisepta* group

Puncturella granitesta (Okutani, 1968)

Fissurisepta granitesta Okutani, 1968:26, pl. 3, fig. 1.

REMARKS. Although described originally in *Fissurisepta,* this species is relatively large and elongate, having well-differentiated primary and secondary ribs. The illustration of the single holotype specimen suggests a species of *Puncturella* in which the entire apical area had been worn away.

Dimensions. Length 14, width 8, height 6 mm.

Occurrence. Off Miyake Island, Japan, 1080–1205 m.

Diodora vetula (Woodring, 1928)

Puncturella (*Fissurisepta*) *vetula* Woodring, 1928: 455, pl. 39, figs. 21, 22; pl. 40, fig. 1.

REMARKS. In *Diodora* species of high profile, the truncate callus at the posterior border of the foramen projects slightly, although not to the extent that it does so in *Altrix.* This species resembles the small species *Diodora pusilla* Berry, 1959, which is common in shallow water in the Panamic Province.

Dimensions. Length 3.5, width 2.2, height 2.9 mm (holotype).

Occurrence. Pliocene of Jamaica, shallow-water facies.

Family Pseudococculinidae Hickman, 1983

Tentaoculus eritmeta (Verrill, 1884)

Puncturella (*Fissurisepta*) *eritmeta* Verrill, 1884: 204, pl. 32, fig. 19.—Clarke, 1962:8.

Puncturella eritmeta.—Pilsbry, 1890:238, pl. 27, figs. 60, 61 [copy of Verrill].

Tentaoculus eritmeta.—McLean and Harasewych, 1995:27, figs. 76, 78.

REMARKS. McLean and Harasewych (1995) illustrated type material with SEM and assigned this northwestern Atlantic species to the pseudococculinid genus *Tentaoculus,* in which there is a small, low septum that does not separate the viscera from the mantle cavity. A worn apical area was originally misinterpreted as a foramen, which explains how it was wrongly assigned to the Fissurellidae.

CHARACTER ANALYSIS

Characters used in the analysis are discussed below by character number as scored in the matrix (Table 1). Polarity is based on outgroup comparison to the scissurellid genus *Anatoma* and the fissurellid genus *Emarginula.* Character state determinations for *Anatoma* are based on treatment of the genus in McLean (1989). All character states of *Emarginula* are considered to be plesiomorphic for the family, as in the Systematic section. We use the terms plesiomorphic and apomorphic in the descriptions of the character states to refer to the states as determined in the subsequent parsimony analysis; all characters were treated as unordered.

Illustrations in the present paper are cited in this section for each character discussed below.

Characters not included in the analysis

Species of all genera have cephalic tentacles and a right suboptic tentacle (*Clathrosepta,* Fig. 7C), but no modifications providing apomorphic states have been noted. Some of the species examined show that the earliest teleoconch sculpture corresponding to a shell length of 400–600 μm represents a separate growth stage having sculpture less complex than that which follows, usually of spiral elements that lack the concentric elements of later stages (*Manganesepta,* Fig. 5D). In *C. cucullata* (Fig. 1D), however, there are broad depressions that are unlike mature sculpture. Too little is known about this character to include it in the analysis.

General shell characters (1–5)

1. **Anterior profile.** The anterior slope can be convex: *Emarginula, Cranopsis, Puncturella, Cornisepta*; straight: *Manganesepta* (Fig. 2C), *Profundisepta* (Fig. 3A), *Clathrosepta* (Fig. 6C), *Fissurisepta* (Fig. 8A); or concave: *Diodora, Altrix* (Fig. 5G).

Three states: convex (0), straight (1), and concave (2).

2. **Posterior profile.** The posterior slope can be convex: *Diodora, Altrix* (Fig. 5G), straight: *Manganesepta* (Fig. 2C), *Clathrosepta* (Fig. 6C), *Fissurisepta* (Fig. 8A); or concave: *Emarginula, Cranopsis, Puncturella, Profundisepta* (Fig. 3A), *Cornisepta* (Fig. 11A).

Three states: convex (0), straight (1), and concave (2).

3. **Shell pits.** Pores or pits in the early teleoconch are found in the plesiomorphic genera: *Emarginula, Cranopsis, Puncturella, Diodora, Altrix*; whereas these are missing (presumed lost) in all of the remaining, apomorphic genera.

Two states: pits present (0) and pits absent (1).

4. **Apical whorl.** Plesiomorphic genera have a coiled stage of about ⅔ or more whorl (more than 225°) between the protoconch and apertural expansion that leads to the limpet form: *Emarginula* (Fig. 1A), *Cranopsis* (Fig. 1F), and *Puncturella.* In *Man-*

ganesepta (Fig. 2D) the plane of the lip of the protoconch is about 270° away from the plane of the aperture. In *Diodora* (Fig. 5A) there is a whorl of about 135° in the juvenile shell. In *Profundisepta* (Fig. 3A) the coiled stage ranges from 120° to 210°. In *Fissurisepta* (Fig. 9C) the plane of the lip of the protoconch is about 120° away from the plane of the aperture. Although the protoconch and any evidence of a coiled stage in *Cornisepta* is unknown, the coiled stage can certainly be interpreted as minimal or completely lost. Apertural expansion may proceed directly in the early teleoconch (Fig. 10E).

Three states: coiled stage of ⅔ or more of whorl, more than 225° (0); coiled stage of about ½ to ⅓ of whorl, 210° to 120° (1); coiled stage minimal or less than 90° (2).

5. **Mature shell sculpture.** Plesiomorphic shell sculpture in fissurellids has strong radial ribs with defined primary and secondary ribs as well as concentric rings: *Emarginula, Cranopsis, Puncturella, Diodora* (Fig. 5A), *Altrix* (Fig. 5E), and some species of *Profundisepta* (Fig. 3A). Apomorphic sculpture can be clathrate with no distinction between primary and secondary ribs: *Manganesepta* (Fig. 2A) and *Clathrosepta* (Fig. 6A); or pustular: *Fissurisepta* (Fig. 8A) and *Cornisepta* (Fig. 11A).

Three states: with both primary and secondary ribs or primary ribs alone (0), evenly clathrate (1), and with pustules (2).

Protoconch characters (6–9)

Protoconchs are unknown for *Altrix, Clathrosepta,* and *Cornisepta.*

6. **Retention of protoconch in adult shell.** *Emarginula* (Fig. 1A), *Cranopsis* (Fig. 1F), *Puncturella, Manganesepta* (Fig. 2D), and *Profundisepta* (Fig. 3C) retain the protoconch in the adult shell. In other genera it may be present in the juvenile but is obliterated as the foramen expands: *Diodora, Altrix* (Fig. 5E), *Clathrosepta* (Fig. 6A), and *Cornisepta* (Fig. 10E).

Two states: protoconch retained in adult (0) and protoconch lost in adult (1).

7. **Retention of protoconch on juvenile shell to shell length of 2 mm.** Although juvenile shells of some genera treated here are unknown (*Altrix, Clathrosepta, Cornisepta*), the genera *Diodora* (Fig. 5A) and *Fissurisepta* (Fig. 9A–D) retain it on the early juvenile but lose it after the shell attains a length of about 2 mm.

Two states: protoconch retained in early juvenile of about 2 mm length (0) and protoconch lost by shell length greater than 2 mm (1).

8. **Protoconch form.** Bandel (1982) recognized two kinds of fissurellid protoconchs: the plesiomorphic condition with pointed tip: *Emarginula* (Fig. 1A), *Cranopsis* (Fig. 1F), *Puncturella, Diodora* (Fig. 5B), *Manganesepta* (Fig. 2D); and round with bulbous tip: *Profundisepta* (Fig. 3C), *Fissurisepta* (Fig. 9C). The protoconch with pointed tip has a compressed appearance with one quarter whorl more than the bulbous type.

Two states: pointed (0) and bulbous (1).

9. **Protoconch sculpture.** Plesiomorphic genera have linear, ladderlike spiral sculpture with scattered granules (*Emarginula,* Fig. 1A). That of *Diodora* (Fig. 5B) is more organized in a clathrate pattern but is considered to be of the same type. Some species in these genera can also have a finely rugose pattern. The finely rugose pattern has also been detected in *F. enderbyensis* (Fig. 9C). Two additional states for protoconch sculpture are first described here, the hexagonal pattern of *M. hessleri* (Fig. 2F), and the extremely minute pitted pattern of *Profundisepta,* which can only be seen under 2000 times magnification (Fig. 3D).

Three states: linear-rugose (0), hexagonal (1), and pitted (2).

Shell characters related to foramen (10–14)

10. **Position of foramen in adult.** The outgroup *Emarginula* has an open slit at the anterior margin; the foramen appears in *Cranopsis* (Fig. 1C) and *Puncturella* and is positioned on the anterior slope. In *Manganesepta* (Figs. 2C, D) and *Profundisepta* (Fig. 3B) it is subapical, slightly below the highest point on the shell. In *Diodora* (Fig. 4A), *Altrix* (Fig. 5E), *Clathrosepta* (Fig. 6A), *Fissurisepta* (Fig. 8B), and *Cornisepta* (Fig. 10B) it is apical and obliterates the apical whorls and protoconch.

Four states: at margin (0), on anterior slope (1), subapical (2), and apical (3).

11. **Outline of foramen.** The plesiomorphic outline of the foramen is elongate: *Cranopsis* (Fig. 1C), *Puncturella,* and *Manganesepta* (Fig. 2A). Additional states include short triangular or oval: *Profundisepta* (Fig. 3B) and *Cornisepta* (Fig. 10B). In *Altrix* (Fig. 5E), there is a marked tripartite outline produced by bulging tubercles on the interior callus within the foramen; the posterior of these tubercles is attached directly to the septum. A similar, though less pronounced arrangement of tubercles is detectable in *F. granulosa* (Fig. 7C). It is faint in *Clathrosepta* (Fig. 6A), in which the septal tubercle shows as a bulge, looking dorsally through the foramen. Some species of *Diodora* have a constricted foramen; others have an oval outline (*Diodora* is scored as oval, as in the majority of species).

Four states: slit (0), elongate triangular (1), oval or short triangular (2), and tripartite with tubercles (3).

12. **Retention of selenizone in adult shell.** The selenizone (slit band) indicates previous positions of the foramen during earlier growth stages. It is well developed in the plesiomorphic genera *Emarginula, Cranopsis* (Fig. 1C), and *Puncturella,* present in reduced form in *Manganesepta* (Fig. 2A) and *Profundisepta* (Fig. 3B). It is not seen in mature shells of *Diodora, Altrix, Clathrosepta, Fissurisepta,* and *Cornisepta,* although it might have been present in earliest juveniles.

Three states: long (0), short (1), and lost at maturity (2).

13. **Septal height.** Low in *Cranopsis, Puncturella* (Fig. 1E), *Altrix* (Fig. 5F), *Profundisepta, Clathrosepta* (Fig. 5B), as well as *Fissurisepta* (Fig. 7C), reduced to truncate posterior callus in *Diodora,* or high in *Manganesepta* (Fig. 2B) and *Cornisepta* (Fig. 10C).

Four states: no septum (0), low (1), truncate (2), and high (3).

14. **Septal curvature.** The septum is not present in either outgroup, hence septal curvature is scored as inapplicable. It is curved in the plesiomorphic genera: *Cranopsis* and *Puncturella* (Fig. 1E), as well as in the more advanced *Clathrosepta* (Fig. 5B) and straight in the more apomorphic genera: *Manganesepta* (Fig. 2B), *Profundisepta, Fissurisepta* (Fig. 8C), and *Cornisepta* (Fig. 10C). In small shells of high profile, the straight septum is logically an effective means of strengthening the shell. In *Diodora* it is reduced to a low truncate callus, and in *Altrix* (Fig. 5F) it is reduced to a lesser extent; both are scored as straight.

Two states: inapplicable (–), curved (0), and straight (1).

Characters of external anatomy (15–18)

External anatomy is completely unknown only in *Altrix.*

15. **Anterior mantle skirt.** In the most plesiomorphic fissurellid genera (*Emarginula, Cranopsis*) the mantle skirt is split to correspond with the slit or foramen on the anterior slope of the shell (Fig. 1C). The apomorphic condition has the mantle skirt sealed anteriorly with no seam on the shell exterior: *Puncturella, Diodora, Manganesepta* (Fig. 2A), and *Profundisepta, Clathrosepta,* and *Fissurisepta.* This distinction separates *Cranopsis* with its split mantle skirt and *Puncturella* with its sealed skirt. The character can be scored on the shell alone, as the shell seam correlates with the split or sealed mantle skirt.

Two states: split (0) and sealed (1).

16. **Epipodial tentacles.** The plesiomorphic condition is that of numerous epipodial tentacles of similar size: *Emarginula, Cranopsis, Puncturella* (Fig. 1D), and *Diodora.* In *Fissurisepta* there are 6–8 tentacles, including those that are relatively long and those much shorter. More apomorphic genera have the epipodial tentacles greatly reduced: *Manganesepta, Profundisepta* (Fig. 3E), *Clathrosepta* (Fig. 6E), *Fissurisepta,* and *Cornisepta* (Fig. 11C). The scissurellid outgroup *Anatoma* also has a reduced number of epipodial tentacles.

Three states: numerous (0), 6–8, unequal (1), and fewer than six pairs (2).

17. **Posterior pedal tentacle.** The posterior pedal tentacle is absent in the plesiomorphic genera but present in *Manganesepta, Clathrosepta* (Figs. 6D, E, 7B), and *Fissurisepta.*

Two states: absent (0) and present (1).

18. **Ctenidium.** The plesiomorphic condition for the paired fissurellid ctenidia is bipectinate, with the gill axis free and bearing leaflets on both sides: *Emarginula, Cranopsis, Puncturella, Diodora, Profundisepta* (Fig. 3F), and *Clathrosepta* (Fig. 6F). Cowan (1969) first described the apomorphic condition in which the axis is lost and a single row of filaments is attached to the mantle skirt: this is known in both *Fissurisepta* and *Cornisepta* (Fig. 11D). In present material of *M. hessleri* we could find only four monopectinate leaflets and regard this as a juvenile condition; it is therefore scored here as indeterminate (?).

Two states: bipectinate (0) and monopectinate (1).

Radular characters (19–22)

There are three basic kinds of radulae that provide four characters. The plesiomorphic radula is seen in the outgroup *Emarginula, Cranopsis* (Fig. 1B), *Puncturella* (Fig. 1G), and *Diodora* (Fig. 5C), with some modification in the more apomorphic genera *Manganesepta* (Fig. 2G), *Profundisepta* (Fig. 3G), and *Clathrosepta* (Fig. 6G). Two different kinds of radulae are seen in *Fissurisepta* (Fig. 8E) and *Cornisepta* (Fig. 10G). The radula is unknown only in *Altrix.*

19. **Rachidian tooth.** The plesiomorphic rachidian tooth of the fissurellid radula is broad (*Cranopsis,* Fig. 1B; *Puncturella,* Fig. 1G). A variation of this is the form with narrow shaft and more pronounced comblike denticles: *Manganesepta* (Fig. 2G), *Profundisepta* (Fig. 3G), and *Clathrosepta* (Fig. 6D). Apomorphic states include the bulging, cuspless rachidian of *Fissurisepta* (Fig. 7E), and the pinnate form of all teeth in the row for *Cornisepta* (Fig. 10G), for which fine denticles occur on the edges of the shaft as well as the tips.

Four states: broad (0), narrow (1), short and broad with cusps lost (2), and pinnate (3).

20. **Inner lateral teeth.** The plesiomorphic fissurellid lateral tooth is narrow: *Emarginula, Cranopsis* (Fig. 1B), *Puncturella* (Fig. 1G), *Diodora* (Fig. 5C), *Manganesepta* (Fig. 2G), *Profundisepta* (Fig. 3G), and *Clathrosepta* (Fig. 6D). Apomorphic conditions have the lateral teeth short and bulging laterally (*Fissurisepta,* Fig. 8E) or pinnate with projecting denticles on the sides of the shafts (*Cornisepta,* Fig. 10F). In the outgroup *Anatoma* the lateral teeth have a projecting elbow (McLean, 1989: fig. 6F).

Four states: narrow (0), bulging (1), pinnate (2), and with elbow (3).

21. **Pluricuspid tooth.** The plesiomorphic condition of the enlarged outermost lateral tooth (the pluricuspid tooth) is massive, flanged on both sides, and has a large, acute median cusp with two lateral cusps: *Emarginula, Cranopsis* (Fig. 1B), *Puncturella* (Fig. 1G), *Diodora* (Fig. 5C), *Manganesepta* (Fig. 2G), *Profundisepta* (Fig. 3G), and *Clathrosepta* (Fig. 6G). Apomorphic states are that of *Fissurisep-*

Table 1. Characters and their states used in the analysis (see Character Analysis). Outgroups are the scissurellid *Anatoma* and the fissurellid *Emarginula*. Characters 1 and 2 are not applicable for *Anatoma* because it is not of limpet form.

	1111111111222
	1234567890123456789012
Anatoma	--10000000000-02000330
Emarginula	020000000000-00000000
Cranopsis	0200000001101000000000
Puncturella	0200000001101010000000
Diodora	2001011003222110000000
Altrix	200101???332111???????
Manganesepta	111010001211311 21?1000
Profundisepta	1210000122211112001000
Clathrosepta	111111???3321012101000
Fissurisepta	1111211103321111112110
Cornisepta	021221???3223112034221

ta (Fig. 9E) with a very broad inwardly directed flange, and that of *Cornisepta* (Fig. 10G), pinnate with numerous denticles on the edges of the overhanging tip. The pluricuspid differs in the two species of *Fissurisepta* illustrated here (compare Figs. 8F and 9E), but both are scored as flanged. In the outgroup *Anatoma,* both edges of the overhanging cusp are deeply serrate (McLean, 1989:fig. 6F)

Four states: tricuspid (0), flanged (1), pinnate (2), and serrate (3).

22. **Denticles of marginal teeth.** The plesiomorphic fissurellid marginal teeth are slender with deeply indented comblike denticles at the tip: *Emarginula, Cranopsis* (Fig. 1B), *Puncturella* (Fig. 1G), *Diodora* (Fig. 5C), *Manganesepta* (Fig. 2G), *Profundisepta,* and *Clathrosepta* (Fig. 7G). The marginals of *Cornisepta* (Fig. 9G) are pinnate, with long projecting denticles on the shafts as well the tips.

Two states: denticles at tip (0) and pinnate (1).

RESULTS OF CLADISTIC ANALYSIS

The data matrix (Table 1) contains 22 characters for 11 genera, of which 18 characters are informative and four are uniformative (protoconch sculpture, and three of four radular characters). A single most parsimonious tree of 46 steps was produced from an exhaustive search by PAUP (Fig. 15). The consistency index (CI) is 0.696, the retention index 0.798, the rescaled consistency index 0.493, and skewness (g_1) is -0.589, with uninformative characters excluded. No differences in character state transitions were found between ACCTRAN and DELTRAN character state optimizations. None of the data types (shell, protoconch, anatomy, radula) showed more homoplasy than another.

Figure 15 shows the phylogenetic hypothesis of the fissurellid genera retaining the protoconch (plesiomorphic group) and those of the apomorphic genera that have lost the protoconch and apical whorl in the adult. Outgroups are the scissurellid *Anatoma* and the plesiomorphic fissurellid genus *Emarginula,* which has a slit rather than a foramen. The ingroup (Plesiomorphic Groups plus Apomorphic Groups) is supported by three synapomorphies with a CI of 1: foramen on anterior slope, elongate triangular septum, and truncate septum.

The second, strongly supported clade is ((*Altrix* + *Diodora*) + ((*Cornisepta*) + (*Clathrosepta* + *Fissurisepta*))), or the Apomorphic Groups (Fig. 15). It is supported by five synapomorphies with a CI of 1: coiled stage ½ to ⅓ whorls, protoconch lost in adults, protoconch lost at shell length of 2 mm, apical foramen, and selenizone lost at maturity.

The clade (*Manganesepta*) + ((*Profundisepta*) + (Apomorphic Groups)) is supported by eight synapomorphies of which three have a CI of 1: the subapical foramen, the foramen tripartite, and the short selenizone. The other monophyletic groups are less well supported with zero or one synapomorphy with a CI of 1 and zero to four additional synapomorphies. Although the Apomorphic Groups form a clade, the Plesiomorphic Groups do not constitute a natural group but a paraphyletic assemblage.

DISCUSSION

Here we discuss the inferred character evolution, starting with the position of the selenizone and its influence on the structure of the mantle skirt and the condition of the gill. In the scissurellid outgroup and the fissurellid outgroup *Emarginula,* there is an open slit and a corresponding slit in the mantle skirt. In *Cranopsis* the shell is sealed at the anterior margin and the seam remains on the anterior slope of the shell, corresponding to the split mantle skirt; the foramen is positioned on the anterior slope. In *Puncturella,* and all of the more apomorphic genera, the shell seam and the split mantle are lost. The foramen stays on the anterior slope in *Manganesepta* and *Profundisepta* but shifts to a fully apical position in the Apomorphic Groups.

In the septum a trend from curved to straight can be observed, but the septal height is variable; the very high septum shared by *Manganesepta* and *Cornisepta* has arisen as a parallelism in the two genera.

The shell sculpture progresses from primary ribs only in the Plesiomorphic Groups and (*Diodora* + *Altrix*) to a condition with pustules shared by *Fissurisepta* and *Cornisepta.* It is most like the condition of *Clathrosepta,* in which there are numerous raised pustules produced by the intersections of fine radial and concentric sculpture. Note that the clathrate condition in *Clathrosepta* and *Manganesepta* is inferred as having arisen as a parallelism from two different character states: in *Manganesepta* from the plesiomorphic conditions with only ra-

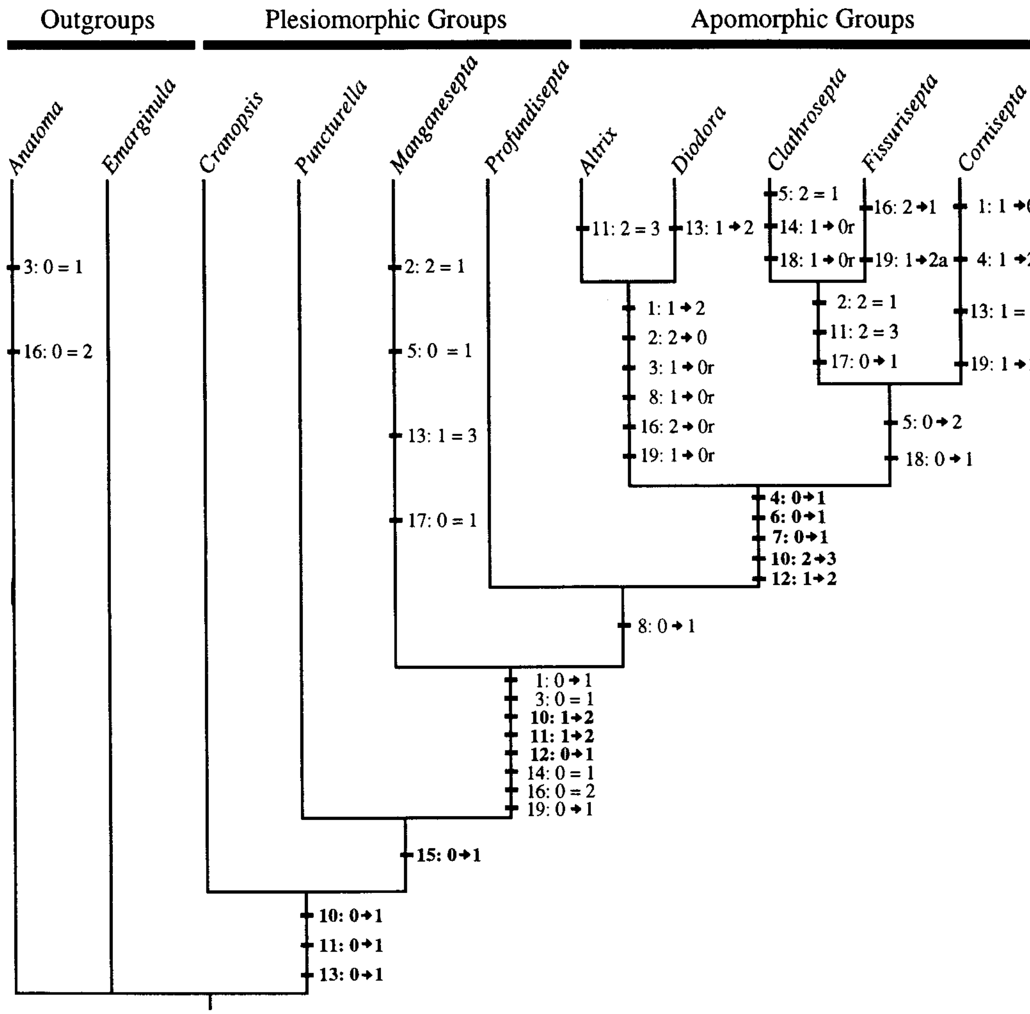

Figure 15. Cladogram showing hypothesis for the phylogeny of fissurellid genera with the *Fissurisepta* shell form. Tree length = 46 steps, consistency index (CI) = 0.696, retention index = 0.798, rescaled consistency index = 0.493, and autapomorphies excluded. Character state changes of all 18 informative characters are plotted. Bold type face: synapomorphy with CI of 1; plain type face: character state change with subsequent reversal; equal sign: parallelism; a: autapomorphy; r: reversal.

dial ribs, in *Clathrosepta* from the derived pustules. Pustular sculpture can be considered to be remnants of the beads formed at the intersections of the clathrate sculpture. The pustular sculpture of *Fissurisepta,* in most species of which it is in radial rows, is simpler than that of *Cornisepta.* The curved rows of beads in all species of *Cornisepta* are probably more apomorphic. This sculpture has a number of differing expressions at the specific level within *Cornisepta.*

Although the loss of the shell pits in all of the highly apomorphic genera may seem to be a noninformative character, the pits are present in juvenile shells of *Diodora* and in the early stages of *Altrix,* which supports a less derived interpretation for these two genera within the Apomorphic Groups.

The emarginuline radula changes very little among the genera, except for the width of the rhomboidal rachidian tooth. However, this may not be of phylogenetic importance because the rachidian can have little functional significance in its cuspless condition. The massive pluricuspid teeth are the strongest teeth and the primary ones used in rasping (Märkel, 1966). Variation in the width of the rachidian may mean little more than the application of a developmental device to separate the asymmetrically aligned pluricuspid teeth during enrollment of the flexoglossate radula when it is retracted (Märkel, 1966; Hickman, 1981).

The evolution of the gill is not as clear as the associated shell characters, in part because the condition in *Altrix* is unknown. The monopectinate gill with six or more leaflets is found only in two of the most highly apomorphic genera. This condition can be interpreted as an adaptation to the very high shell profile—particularly in *Cornisepta*—with a much more narrow mantle cavity. The mature condition in *Manganesepta* is unknown. *Profundisepta* has the plesiomorphic, bipectinate gill, but the number of leaflets is greatly reduced, compared to genera of larger size.

Radula characters of *Fissurisepta* and *Cornisepta* seem to have diverged in opposite directions, both of which differ from the plesiomorphic condition. Functionally, the radula of *Fissurisepta* is not so different from the plesiomorphic type because the pluricuspid teeth are well developed, but the autapomorphic radula of *Cornisepta* represents a more profound departure. Hain (1990) reported the gut of *C. antarctica* to be filled with diatoms, and it is likely that the feathery teeth of all species of *Cornisepta* are designed for such a diet and that those of other fissurellids are not. Carnivorous grazing on sessile invertebrates is known in most fissurellids (Miller, 1968; Ghiselin et al., 1975) other than *Fissurella,* which grazes on algae (Ward, 1966; Franz, 1989). The plesiomorphic radula with the strong pluricuspid teeth is well designed for grazing.

The position of *Altrix* within the Apomorphic Groups must still be considered largely unresolved due to the missing information on its anatomy and radula. There is a remote possibility that the radula may turn out to be similar to that of *Fissurisepta,* but it is more likely to be of a less apomorphic state. *Altrix* can be interpreted as either an intermediate in the sequence leading from *Puncturella* to *Diodora* in which the septum is but partially transformed to that of *Diodora*; or it can be regarded as a morphological extreme of *Diodora,* characterized by its extremely high profile and higher septum. The fact that *Altrix* and *Diodora* share the concave anterior slope (unlike all other genera treated here) suggests the latter interpretation. Another possibility is that *Altrix* might have the monopectinate gill as a correlate to the high profile. If the monopectinate gill can be demonstrated to occur in *Altrix,* the genus could serve as a link to *Fissurisepta* and *Cornisepta.* The septal tubercle of *Fissurisepta* is shared with *Altrix.*

The genera in the Plesiomorphic Groups show straight character state transitions leading as stepping stones to the Apomorphic Groups. The traditional progression of *Emarginula, Cranopsis, Puncturella,* and *Diodora* as originally proposed by Boutan (1885) is confirmed here using cladistics. The Apomorphic Groups then underwent a radiation resulting in five genera, as well as additional genera that are not part of the analysis.

Some cells in the data matrix are still not filled. The anatomy of *Altrix* and the condition of the protoconch in *Cornisepta* are still unknown. Until these gaps are filled, the evolutionary sequence of the radula, ctenidium, and protoconch in the Apomorphic Groups is not satisfactorily resolved.

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