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# CONTRIBUTIONS IN SCIENCE

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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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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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JAMES H. McLEAN<sup>1</sup> AND DANIEL L. GEIGER<sup>2</sup>

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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: *Manganeosepta* and *Profundisepta*. All described species previously assigned to *Fissurisepta* are tentatively assigned among these genera.

New species described here are *Manganeosepta 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 leviniae* 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 *Fisurella* 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 ge-

neric 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 Massachusetts; 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 *Manganesepsta* and *Profundisepta*, all species of which are reviewed.

One other genus having a septum and retaining the protoconch is not included in the analysis: *Vaccerrena* 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-

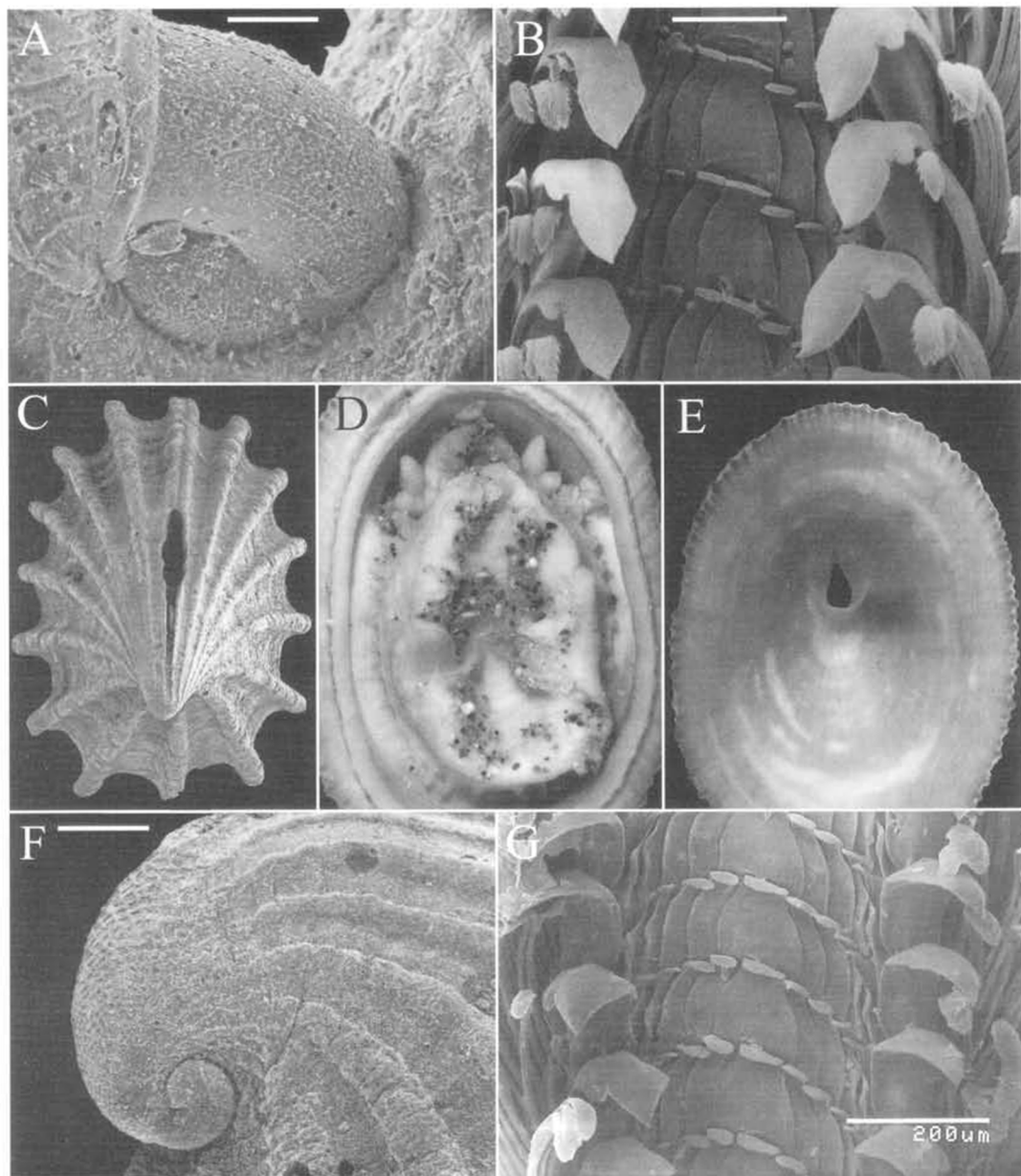


Figure 1A–G. Illustrations of plesiomorphic character states in *Emarginula*, *Cranopsis*, and *Puncturella*. A. Protoconch of *Emarginula superba* Hedley and Petterd, 1906 (scale bar = 40  $\mu$ m). B. Radula of *Cranopsis decorata* (Cowan and McLean, 1968) (scale bar = 100  $\mu$ m). C. Doubled anterior 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  $\mu$ m). G. Radula of *P. solis* (scale bar = 200  $\mu$ m). [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 proto-

conchs 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 noachima* 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 *Manganesepa*, new genus

Figure 2

Type species: *Manganesepa 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.** *Manganesepa* 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

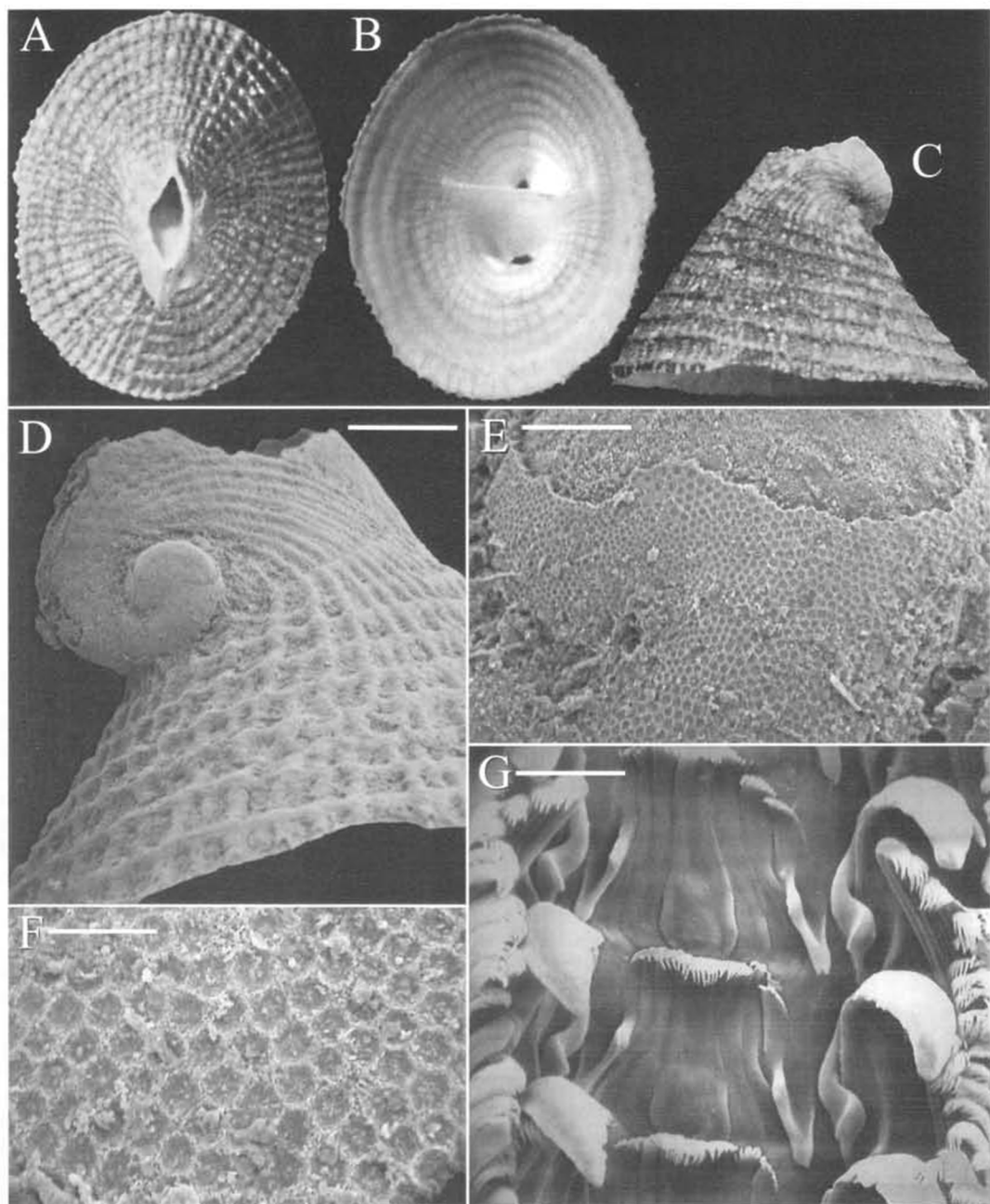


Figure 2A–G. *Manganesepta bessleri* new species. A–C. LACM 2785, holotype; 4500 m, on manganese nodules, North Equatorial Pacific, NW of Clipperton Island (14°37–42'N, 125°22–27'W). Length 2.6, width 2.2, height 1.6 mm. A. Exterior, showing clathrate sculpture and apical whorl posterior to foramen. 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  $\mu$ m). E. SEM enlargement of protoconch sculpture (scale bar = 40  $\mu$ m). F. SEM enlargement of hexagonal protoconch sculpture (scale bar = 10  $\mu$ m). G. SEM view of radula, showing deeply serrate tip of rachidian and laterals (scale bar = 10  $\mu$ m).

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.

*Manganeosepta* 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 *Manganeosepta* 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.

### *Manganeosepta 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 expansion 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 profunda* Jeffreys, 1877.

The following diagnosis is based on the type species *Profundisepta profunda*, 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 *Manganeosepta*. The posterior pedal tentacle of *Manganeosepta* 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 profunda* (Jeffreys, 1877)

Figure 3A–G

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

*Fissurisepta profunda*.—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).

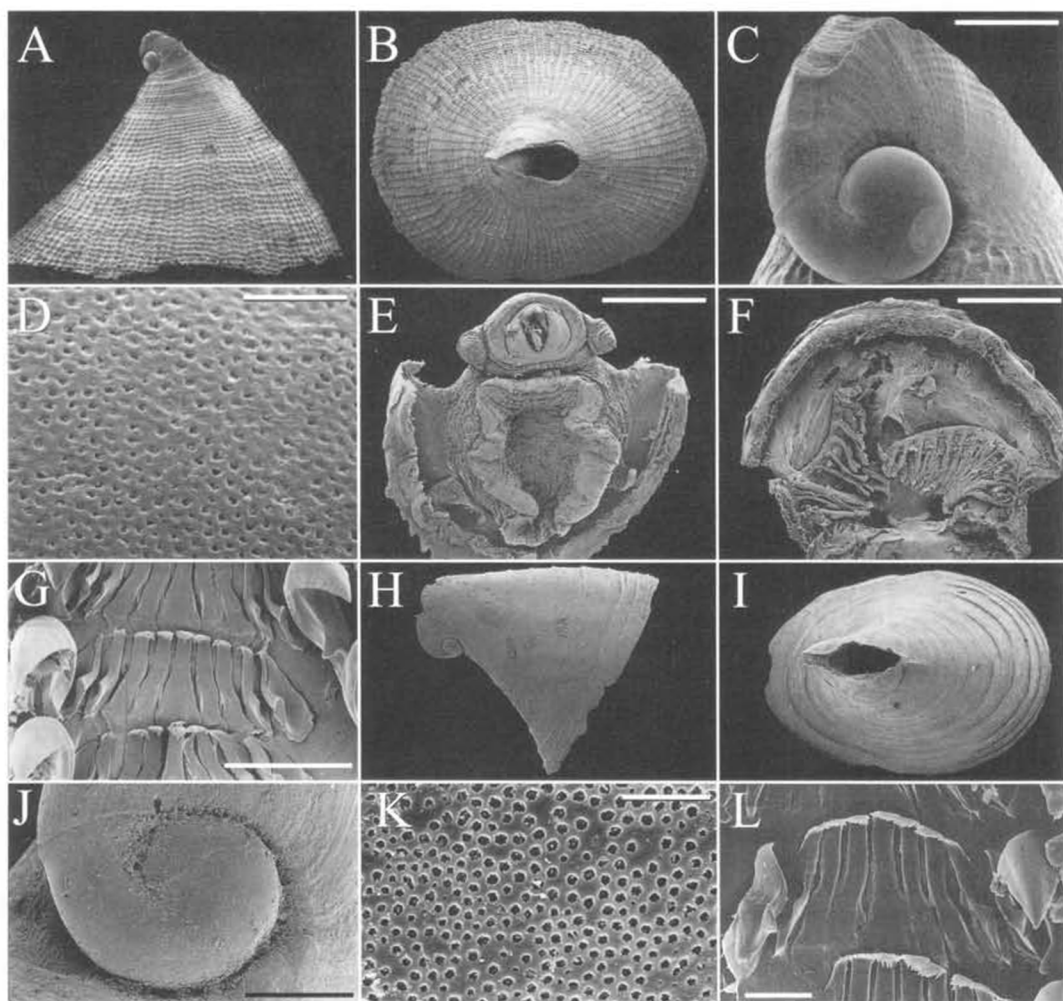


Figure 3A-L. Two species of *Profundisepta*. A-G. *P. profundus* (Jeffreys, 1877). SMNH, Bioice sta. 2692, off Iceland (no coordinates). Length 4.2, width 3.0, height 3.7 mm. A. Right side of shell. B. Dorsal view of shell, anterior at right. C. Apex, showing protoconch and selenizone (scale bar = 200  $\mu$ m). D. Pitted microsculpture of protoconch (scale bar = 10  $\mu$ m). E. Ventral view of body, showing paired posterior epipodial tentacles (scale bar = 600  $\mu$ m). F. Ventral view of excised mantle skirt, showing paired, bipectinate ctenidia with free tips (scale bar = 500  $\mu$ m). G. Radula of specimen from 1110 to 1125 m, Galicia Bank (42°50.9'N; 11°53.1'W) (scale bar = 50  $\mu$ m). 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  $\mu$ m). K. Pitted microsculpture of protoconch (scale bar 10  $\mu$ m). L. Radula (scale bar = 10  $\mu$ m). [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. profundus*, 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-



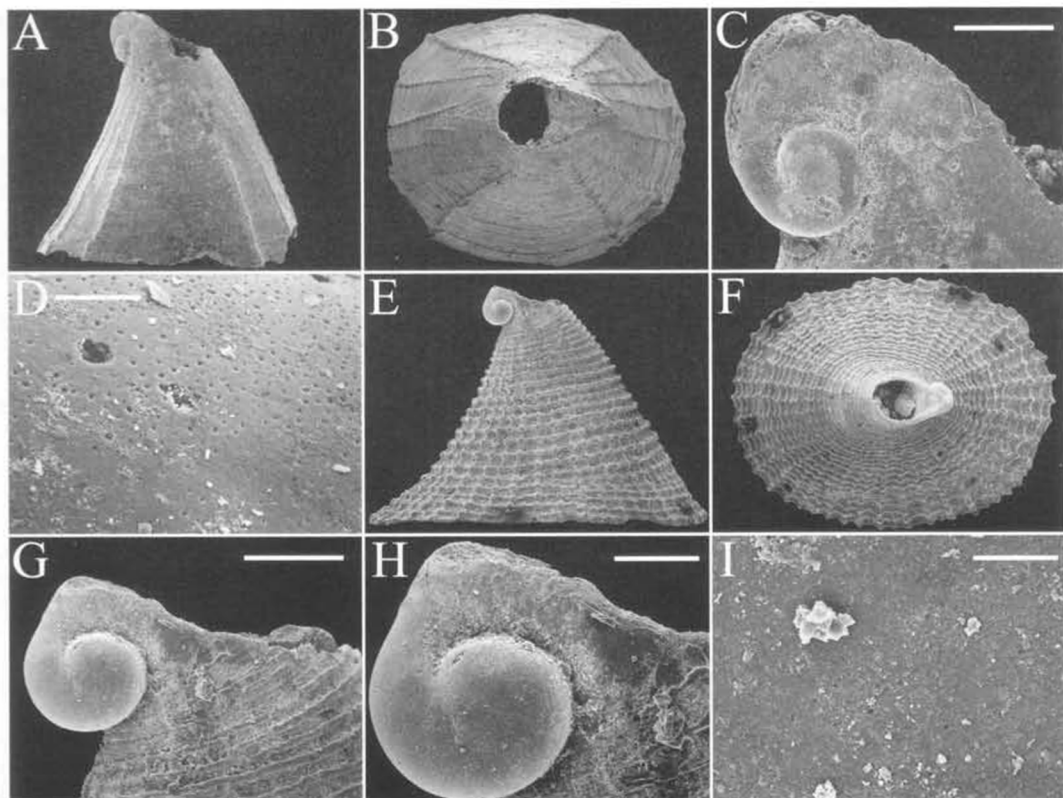


Figure 4A-I. Two species of *Profundisepta*. A-D. *P. borroi* (Farfante, 1947). MCZ 160525, Atlantis station 2993; off Bahia Cardenas, Matanzas, Cuba (23°N, 80°44'W). Length 2.4, width 1.9, height 2.3 mm. A. Right side. B. Dorsal view, anterior at left. C. Apex, showing eroded protoconch (scale bar = 200  $\mu$ m). D. Pitted microsculpture of protoconch (scale bar = 10  $\mu$ m). 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  $\mu$ m). H. Protoconch (scale bar = 100  $\mu$ m). I. Pitted microsculpture of protoconch (scale bar = 10  $\mu$ m).

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 archibenthic 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.



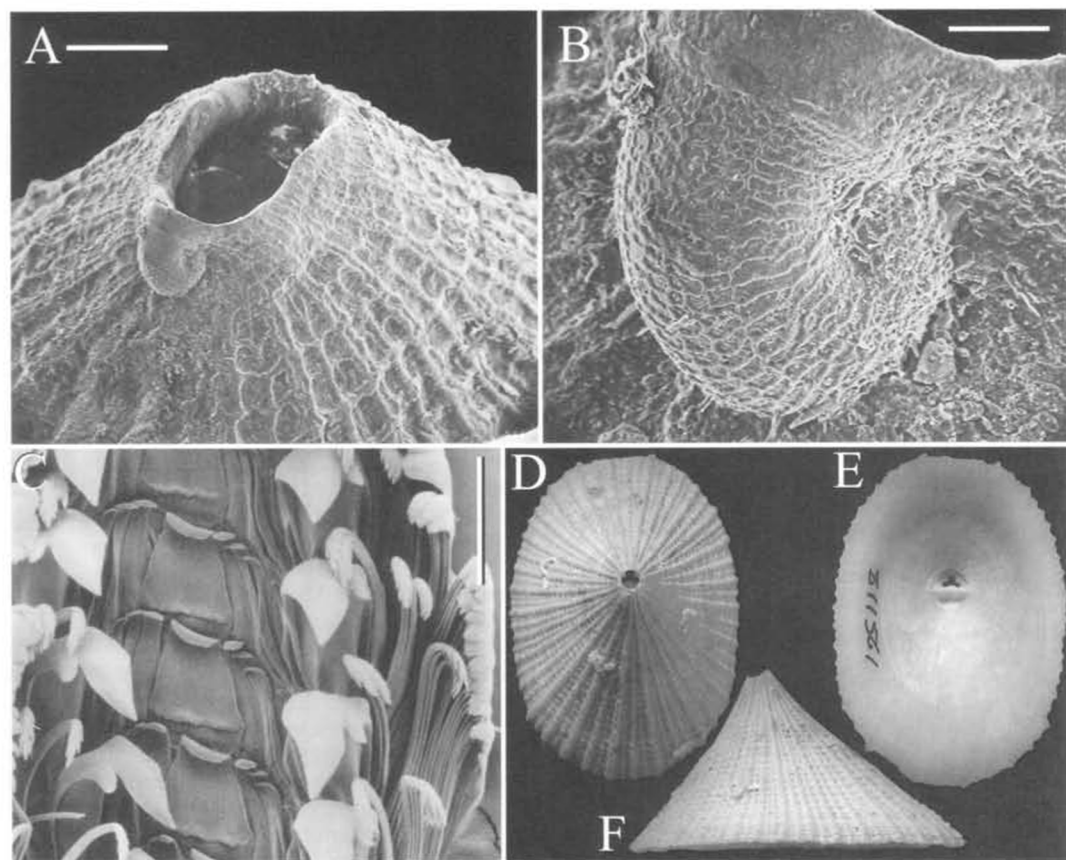


Figure 5A–G. Illustrations to show character states of *Diodora* and *Altrix*. A, B. *Diodora aspera* (Rathke). A. Oblique posterior view showing foramen of juvenile shell with protoconch attached (scale bar = 200  $\mu$ m). B. Protoconch with plesiomorphic sculpture (scale bar = 40  $\mu$ m). C. Radula of *D. aspera* (scale bar = 100  $\mu$ m). 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*.

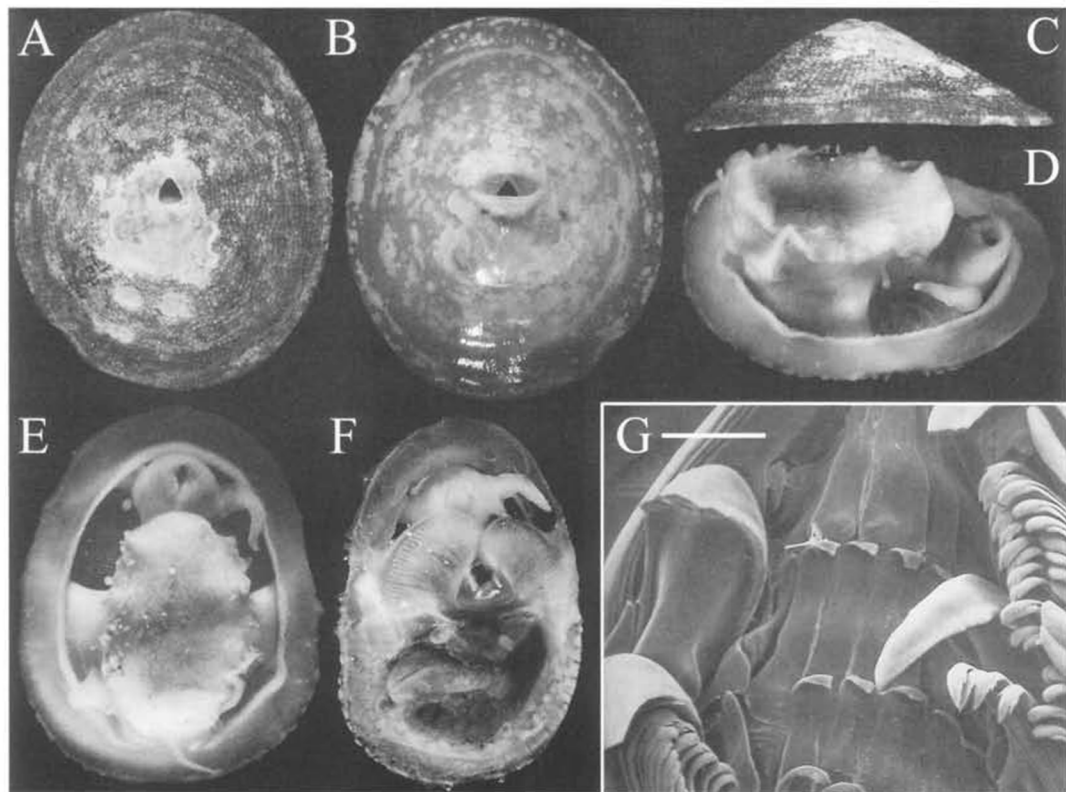


Figure 6A–G. *Clathrosepta depressa* new species. LACM 2784, holotype; 1160 m, eastern slope of Volcano 5, Eastern Pacific Rise at 13°N (12°58.0'N, 103°26.0'W). Length 13.1, width 11.0, height 3.8 mm; length of preserved retracted body 7 mm. A. Exterior showing fine clathrate sculpture and triangular 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  $\mu$ m).

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