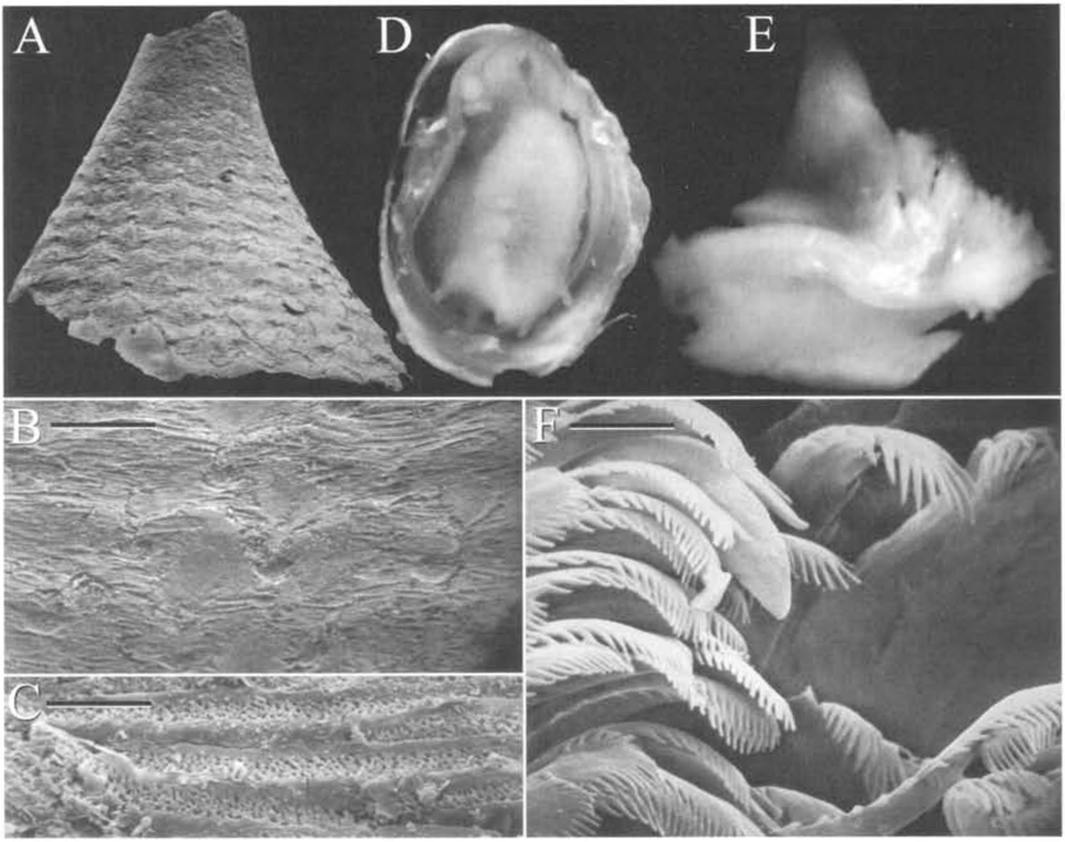

Figure 14A–F. *Cornisepta verenae* new species. LACM 2787, holotype; 1530 m, Axial Seamount, Juan de Fuca Ridge, vent no. 1 (45°56.2′N, 130°04′W). Length 1.6, width 1.3, height 1.3 mm. **A.** SEM, left side of shell, posterior slope concave. **B.** Enlargement of surface showing detail of periostracum 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	11101000121131121?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-

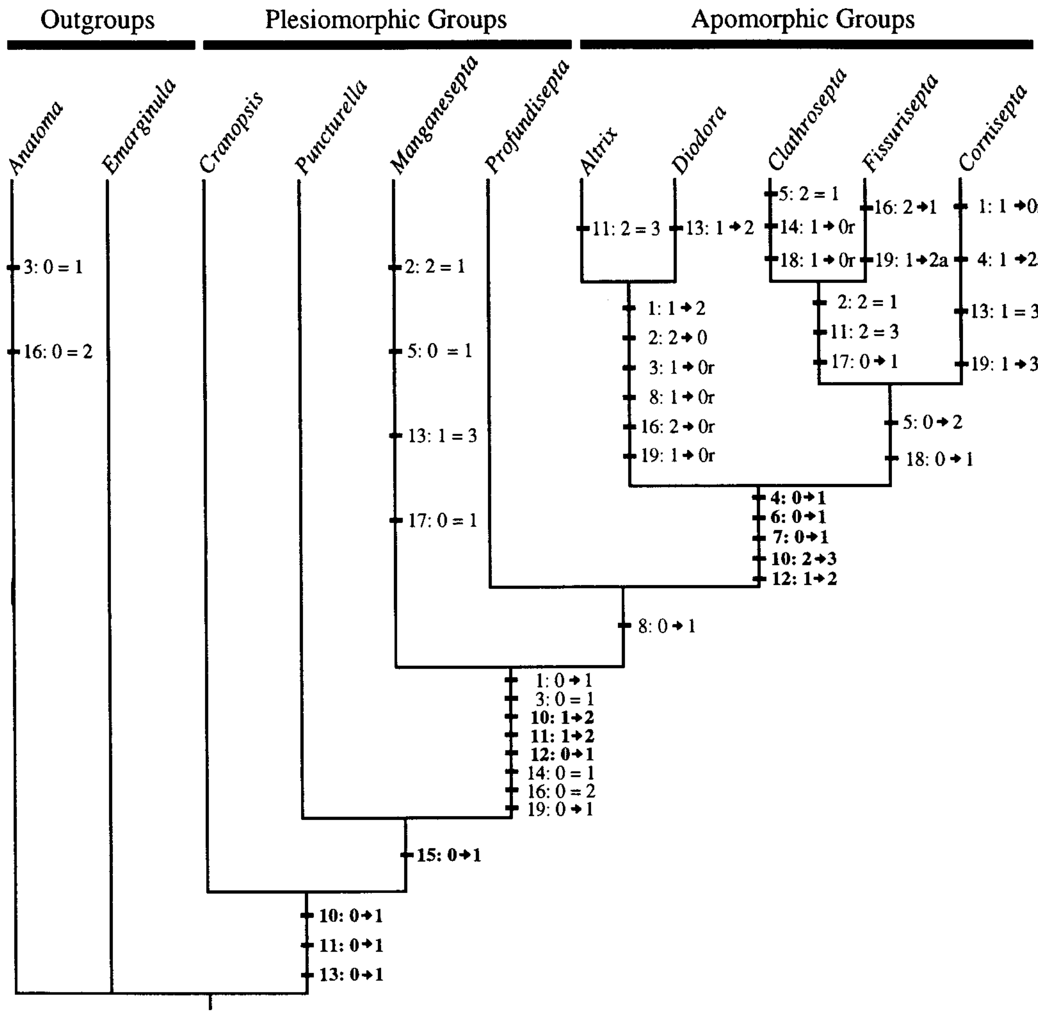

Figure 15. Cladogram showing hypothesis for the phylogeny of fissurellid genera with the *Fissurisepta* shell form. Tree length = 46 steps, consistency index (CI) = 0.696, retention index = 0.798, rescaled consistency index = 0.493, and autapomorphies excluded. Character state changes of all 18 informative 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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