Bryozoa from Costa Rica¹

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ABSTRACT: Twenty-three species of cheilostomes and one cyclostome from two localities on the Atlantic and Pacific sides of Costa Rica are described and illustrated. Two-thirds (16) of the species are considered poorly understood taxonomically. The bryozoan fauna of tropical America is probably less well understood than the literature suggests. Discussions of special interest are those of the genera *Membranipora*, *Parellisina*, *Labioporella*, *Schizoporella*, *Escharina*, *Cigclisula*, and *Rhynchozoon*, and of the higher taxa Bryozoa, Ectoprocta, Gymnolaemata, Eurystomata, Anasca, Ascophora, and Cyclostomata.

TAXA CONSIDERED

Phylum Bryozoa 384 Class Gymnolaemata 385 Subclass Eurystomata 385 Order Cheilostomata—anascans 385 Suborder Malacostega Family Membraniporidae 385 Genus Membranipora 385 Membranipora tuberculata (Bosc) 385 Membranipora arborescens (Canu & Bassler) 387 Family Alderinidae 388 Genus Parellisina 388 Parellisina latirostris Osburn 388 Suborder Cellularina 389 Family Scrupocellariidae 389 Genus Scrupocellaria 389 Scrupocellaria bertholleti (Audouin) 389 -Suborder Coilostega Family Steginoporellidae 390 390 Genus Labioporella Labioporella sinuosa Osburn 390 Family Thalamoporellidae 391 Genus Thalamoporella Thalamoporella californica Levinsen 391 Order Cheilostomata—ascophorans 392 Family Cribrilinidae Genus Cribrilaria 392 Cribrilaria flabellifera (Kirkpatrick) 392

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Family Exechonellidae 394 Genus Tremogasterina 394 Tremogasterina mucronata (Smitt) 394
Family Microporellidae 395
Genus Microporella 395
Microporella umbracula (Audouin) 395
Family Schizoporellidae 395
Genus Schizoporella 395
Schizoporella ?serialis (Heller) 395
Genus Escharina 399
Escharina porosa (Smitt) 399
Family Stomachetosellidae 400
Genus Cigclisula 400
Cigclisula turrita (Smitt) 400
Cigclisula aviculifera (Canu & Bassler) 402
Family Sertellidae 403
Genus Rhynchozoon 403
Rhynchozoon sp. 1 403
Rhynchozoon sp. 2 404
Rhynchozoon sp. 3 405
Family Lageniporidae 407 Genus <i>Teuchopora</i> 407
Genus <i>Teuchopora</i> 407 <i>Teuchopora</i> , undescribed sp. 407
Family Smittinidae 408
Genus Parasmittina 408
Parasmittina crosslandi (Hastings) 408
Genus Rhamphostomella 409
?Rhamphostomella sp. 410
Family Hippoporinidae 412
Genus Hippoporella 412
Hippoporella costulata Canu & Bassler 412
Family Hippopodinidae 412
Genus Hippopodina 413
Hippopodina feegeensis (Busk) 413
Family Adeonidae 414
Genus Reptadonella 414
Reptadonella violacea (Johnston) 414
Family Cycloporidae 415
Genus Cyclocolposa 415
Cyclocolposa ?parva (Marcus) 415
Class Stenolaemata 416
Subclass Cyclostomata 416
Superfamily Articulata 416
Family Crisiidae 416 Genus <i>Crisia</i> 416
Crisia sp. cf. elongata Milne-Edwards 416
Crisia sp. ci. ciongana Minic-Lawards 410

THE BRYOZOAN FAUNA of tropical America is diverse, but has been studied relatively little. A literature survey by Schopf (1973:267) re-

cords 278 species from the tropical Atlantic continental shelf alone. This report deals with less than a tenth of that fauna. At first sight,

our faunal list offers few surprises; nearly all the specimens identified seem to be typical representatives of the American tropical and subtropical bryozoan fauna. This observation, however, is misleading. Close study of the 24 species considered here indicates that two-thirds (16) are badly confused taxonomically. Many vary so much over their ranges as to arouse doubts about their genetic continuity.

The major collections described from the Caribbean are the following: Curação (Osburn 1927), Puerto Rico and the Virgin Islands (Osburn 1940, Schopf 1974), Panama (Canu and Bassler 1918, Hastings 1930, Powell 1971), and Venezuela [Weisbord 1967 (fossils)]. Some general collections in the Caribbean area were described by Osburn (1947) and by Canu and Bassler [1919, 1928a (fossils)]; other occasional small collections have been described, but these descriptions are scattered widely in the works of Levinsen, Waters, Hastings, Harmer, Marcus, Hincks, and others. Perhaps 130 or so species have been described in the area. The sampling on the Atlantic side of Panama, Costa Rica, Nicaragua, and Colombia has been sparse. On the Pacific side of Central America, Canu and Bassler [1918, 1919 (fossils)], Hastings (1930), and Powell (1971) reported on Bryozoa from western Panama. Canu and Bassler [1919 (fossils)] and especially Osburn (1950, 1952, 1953) described collections from the tropical eastern Pacific, and some of our knowledge of the area comes from studies of the Galapagos (Canu and Bassler 1930a, Hastings 1930, Osburn 1950, 1952, 1953) and Cocos Island, which is politically part of Costa Rica, although it is not geographically (Soule 1963).

This paper reports on two collections of marine Bryozoa from Costa Rica—one on the Atlantic and one on the Pacific side. To our knowledge, only two authors have described collections from the mainland of Costa Rica: Canu and Bassler (1919) and Osburn (1950, 1952, 1953). Canu and Bassler's material was of Tertiary and Quaternary fossils; Osburn's was from a few stations of the *R/V Velero III*.

MATERIALS AND METHODS

All material was air-dried. Methods used for mounting the material are described elsewhere (Banta et al. 1973). Photographs were made of NH₄ Cl-coated material prepared according to Kier et al. (1965). Material is retained in the senior author's collection for eventual deposit in the National Museum of Natural History, Washington, D.C.

Measurements were taken with an eyepiece reticle at $\times 90$. Averages were taken by measuring a few individuals estimated to be about average in size. Where appropriate, the range (given in parentheses) was taken by measuring extremely large or extremely small individuals, with respect to the variate measured. We have compared figures derived in this manner to those based on averages and ranges of hundreds of zoids in each of several cheilostome species, and find that the averages agree within 1 or 2 percent, the ranges within 10 percent. Scales on figures were made by measuring features on photographed specimens after the plates were made; they are reliable to about $+15 \mu$.

Synonyms given are from works containing records from the Costa Rica area, extensive synonomies, and major nomenclatural changes or observations of special interest. Although later revisions were made, most of the work for this paper was complete in 1975; subsequent findings are not included.

Portete (Figure 1) refers to station C3-64, collected by the senior author on 18-19 August 1964. Portete is located about 2 km south of Limon, on the Atlantic side of Costa Rica. Collecting was done by snorkeling with a rock hammer. Two environments were collected: a small coral reef consisting of staghorn coral, fire coral (Millepora), encrusting coral (Porites), and coral rubble; and a reef flat dominated by turtle grass (Thallasia). Dominant algae were Sargassum polyceratium, Thallasia testudinum, Bryothamnion sp., ?Acanthophora sp., Hynea musciformis, Caulerpa racemosa, Caulterpa sertularoides, Sargassum sp., Dichtyoptera sp., Gaulaxaura oblongata, Dichtyoa sp., Codium isthmocladium, Galaxaura marginata,

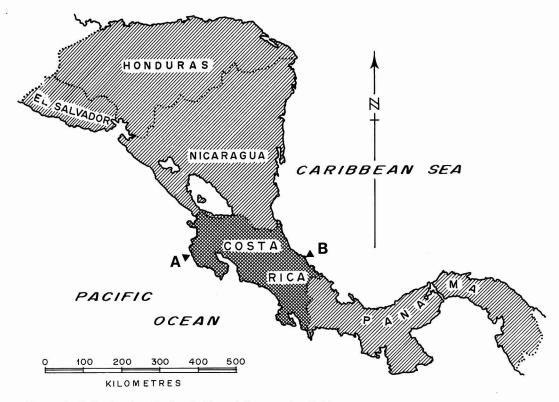


FIGURE 1. Collecting sites. Station A, Playa el Coco; station B, Limon.

Gymogongrus sp., Halimeda opuntia, Padina peridusiata, Fosliella sp., and Rhizoclonium sp. Identifications were checked by Dalton Harrington in 1964. Animals were abundant but except for Bryozoa, were not recorded.

Playa el Coco (Figure 1) refers to station D1-64, collected 4 August 1964 by the senior author. Playa el Coco (Pacific) is located on the Nicoya Peninsula in Guanacasta, Costa Rica. The rocky intertidal and subtidal were collected; the subtidal was collected by snorkeling. The temperature at the time of collecting was above 22° C. Algae were relatively uncommon; Isactis plana (splash zone), Caulothrix crustacea (splash zone), Callithamnion sp., Chactomorpha, Chlorodesmis, Monostroma sp., Thuretia burneti, Hydroclathurus sp., Enteromorpha lingulata, Padina sp., Dichtyota, Spatoglossum, and Amphiroa. Identifications were checked by Dalton Harrington in 1964. Fishes were abundant,

especially *Girella* sp. Also common were an oyster (*Ostrea* sp.), on ophiuroid (*Opiocoma* sp.), a gastropod (*Acanthina* sp.), two corals (one a *Porites*), some sponges, holothurians, nudibranchs, hydroids, and polyclads.

PHYLUM BRYOZOA EHRENBERG, 1831 Polyzoa Thompson, 1830 Ectoprocta Nitsche, 1869

The phylum name still is controversial. A good summary of the various viewpoints is found in J. D. Soule and D. F. Soule (1968). We agree with British authors that "Polyzoa" has priority, but "Bryozoa" is well established. Bryozoa Ehrenberg, 1831 did not originally include entoprocts; this group was added by Nitsche (1869:13–36), who divided the Bryozoa into two classes, Entoprocta and Ectoprocta. Hatschek (1877) later elevated

both to the phylum level and dropped "Bryozoa." This was accepted by Hyman (1959) and many subsequent authors (mostly Americans). Hatschek's action seems undesirable because it disrupts stability of zoological nomenclature. An example applied to another taxon is useful. The Mollusca originally included the barnacles; are we to change the phylum name Mollusca because barnacles subsequently were removed from it?

Some authors have argued that knowing whether an author uses "Bryozoa" or "Ectoprocta" tells us whether that author considers entoprocts included in the phylum. Here, another example is useful. Graptolites have been variously included in the Hemicordata or the Coelenterata without causing difficulty. Do we ask graptolite specialists to use one phylum name if they include graptolites among coelenterates and another if they do not? Some zoologists believe entoprocts to belong in the Bryozoa (see, for example, Nielsen 1971). Are we to subject phylum names to change in the face of inevitable changes in our understanding of systematic relationship? Viewed in this light, the case for Ectoprocta only repeats a controversy that already has been settled in other groups. Names of phyla should be considered as permanent, and controversies about their relationships should not involve them.

CLASS GYMNOLAEMATA ALLMAN, 1856:10 Infundibulata Gervais, 1837 Stelmatapoda Van der Hoeven, 1846 Pyxibryozoa Cuffey, 1973:558 (part)

We use this class in Allman's original sense to include the marine Bryozoa (stenolaemates and eurystomes). Some authors break this class into two classes: Stenolaemata and Gymnolaemata (Borg 1926, Ryland 1970:77, Boardman and Cheetham 1973:122). Our usage reflects our evaluation that stenolaemates and eurystomes resemble each other more closely than either resemble the remaining class of Bryozoa, the Phylactolaemata.

SUBCLASS EURYSTOMATA MARCUS, 1938 Cheilo-ctenostomata Silén, 1942 Gymnolaemata auctt. Order Cheilostomata Busk, 1852*a*

Most authors follow Levinsen (1909:203) in dividing cheilostomes into anascans and ascophorans. We use this convenient arrangement, but avoid Levinsen's formal suborders (Anasca and Ascophora) because of the probability that both are polyphyletic and represent only grades of evolution rather than separable evolutionary lines (Silén 1942:58, Banta 1970:55).

ANASCAN CHEILOSTOMES

Suborder Malacostega Levinsen, 1909:91

Family Membraniporidae Busk, 1854:55 Biflustridae Smitt, 1872 Acanthodesiidae Vigneaux, 1949 Electrinidae Lagaaij, 1952

Genus Membranipora de Blainville, 1830:411 Nichtina Canu, 1900 Nitscheina auctt.

Type species: Flustra membranacea Linnaeus, 1791:3830, designated by Norman (1903:585). See discussion by Brown (1952:44).

Membranipora tuberculata (Bosc)

Figure 2A.

Flustra tuberculata Bosc, 1802:143; Atlantic. Nichtina tuberculata (Bosc) (Canu 1900:380). M. tuberculata (Bosc) (Robertson 1908:265, Pl. 15, Figs. 16, 17; Pl. 16, Fig. 18); California.

M. tuberculata (Bosc) (Osburn 1914:193); Tortugas.

Nichtina tuberculata (Bosc) (Harmer 1926: 208, Pl. 13, Fig. 10); Celebes.

Nitscheina [sic] tuberculata (Bosc) (Canu and Bassler 1928b:18); Florida.

Nichtina tuberculata (Bosc) (Hastings 1930: 706, Pl. 3, Figs. 9, 10); Galapagos.

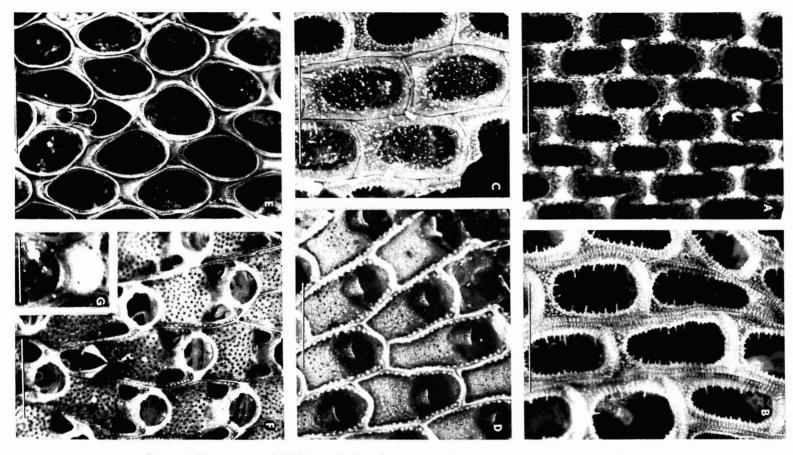


FIGURE 2. Frontal views of KOCl-coated colony fragments. Scales, 500 μ except G, 250 μ . A, Membranipora tuberculata (Bosc); Portete (Atlantic). B, Membranipora arborescens (Canu & Bassler); Playa el Coco. C, The same, treated lightly with KOCl to preserve the frontal membrane and its spinules. D, Labioporella sinuosa Osburn; Portete. E, Parellisina latirostris Osburn; Portete. Avicularium below center. F, Thalamoporella californica Levinsen; Playa el Coco. Avicularium lower right. G, Parellisina latirostris Osburn; Portete. Ovicell.

M. tuberculata (Bosc) (Osburn 1947:9); Venezuela.

M. tuberculata (Bosc) (Osburn 1950:23, Pl. 2, Figs. 4, 5, 6); eastern Pacific.

M. tuberculata (Bosc) [Prenant and Bobin 1966:115 (synonomy), Fig. 29]; France.

M. tuberculata (Bosc) (Moyano 1966:8, Pl. 1, Figs. A, B); Chile.

M. tuberculata (Bosc) (Cook 1968:120, Pl. 2, Figs. C, D, text Fig. 1); West Africa.

M. tuberculata (Bosc) (Schopf 1974:355); Virgin Islands, shallow.

Several samples of unilaminar colonies were found encrusting algae and Thallasia in the subtidal at Portete (Caribbean). Autozoids are rectangular in outline, arranged in neat quincunx. The gymnocyst is represented by a pair of prominent calcareous knobs or tubercles about 50 μ in diameter located at the proximolateral corners of each zoid. They are sometimes connected by a strap of gymnocyst running along the top of the transverse wall. The cryptocyst is well developed proximally, usually about 90 μ wide. It is decorated by about 20 hemispherical calcareous tubercles 10 to 25 μ in diameter. The cryptocyst narrows abruptly along lateral walls, where it is represented only by a single row of tubercles similar to those on the proximal cryptocyst. The distal cryptocyst varies from a row of scattered tubercles to a short shelf about 20 μ wide.

A pair of calcareous spines, sometimes comblike, may project basally into the coelom from the basal side of the proximal cryptocyst. Similar structures have been described by Waters (1898:664), Robertson (1908:265), and Kluge (1914:664). Their function is unknown.

There are no spines, avicularia, or ovicells. *Measurements*: Zoid length, 500 μ (410–550 μ); width, 200 μ (190–250 μ).

Of the membranimorph Bryozoa commonly encrusting seaweeds, the only species likely to be confused with it are those of the *Membranipora membranacea* group (*M. membranacea*, *M. isabelleana*, and others; see Osburn 1950:21, Moyano 1966:11, Cook 1968:120). *Membranipora tuberculata* is readily distinguished from members of the

M. membranacea group by its prominent tubercles, but it is possible that M. tuberculata may intergrade with the M. membranacea group. Membranipora tuberculata usually encrusts algae, but occasional instances are known when it settles on hard substrates (Osburn 1950:21, Cook 1968:121) and sea snakes (Krompach and Soule 1973). Cuffey (1971) reported a similar species, Electra cf. angulata, from the sea snake Pelaonis platurus in Golfo Dulce, Costa Rica.

Membranipora tuberculata is widely distributed in tropical, subtropical, and temperate waters throughout the world. It is characteristic of floating Sargassum in the Sargasso Sea. In the eastern Pacific, it ranges from southern Chile to Vancouver; in the western Atlantic, from Patagonia to Massachusetts (Prenant and Bobin 1966:118).

Membranipora arborescens Canu & Bassler, 1928c

Figure 2B, C.

Acanthodesia arborescens Canu & Bassler, 1928c:15, Pl. 1, Figs. 2-5; Atlantic coast of Morocco.

M. arborescens (Canu & Bassler) [Cook 1968: 121, Pl. 1, Figs. C, D; Pl. 2, Fig. 3E; text Fig. 2 (synonomy)]; West Africa.

M. aborescens (Canu & Bassler) (Powell 1971: 768); Panama.

Several colony fragments were found encrusting unknown substrates from Playa el Coco (Pacific). Zoids are regularly rectangular, but are sometimes distorted in shape. The cryptocyst is oval and provided with a series of tubercles that give it a serrated appearance (Figure 2B). Most specimens possess one to many calcareous spinules about 35 μ long; these project from the cryptocyst into the opesium, but they are sometimes absent. Zoids are surrounded by a brown line, presumably representing a zone where the frontal membrane dips basally into the calcareous walls. The frontal membrane is usually provided with about 30 cuticular "spinules" approximately 40 μ long (Figure 2C). In some zoids, however, spinules are

completely lacking, and in others there may be only one or two. Zoids with many, few, or no spinules may occur on the same colony.

Measurements: Zoid length, 630 μ (520–720 μ); width, 360 μ (250–520 μ).

There is probably no bryozoan taxon more difficult to work with than the Membranipora savartii complex. All the species with this general morphology are highly variable, and there are many cases where zoids on the same colony could be referred to different species, genera, or in some cases different families. It appears that many species in the families Electrinidae and Membraniporidae intergrade without morphological discontinuity, and that a large rassenkreis may be involved. Until a thorough morphological study is undertaken, we shall operate under the premise that it is safer to split than to group and follow Cook (1968:121) in calling specimens with this morphology M. arborescens "encrusting phase."

The species most easily confused with *M. arborescens* in the Panama area are *M. tenuis* (Desor 1848:66), *M. annae* Osburn, 1953: 774, and *M. savartii* (Audouin 1826:240); the species also intergrades extensively with the West African form *M. commensale* (Kirkpatrick and Metzelaar 1922:985). A brief digest of the characters used by Cook (1968) to distinguish these species from *M. arborescens* is given below, but accurate assignments are, in practice, difficult.

M. tenuis: Cryptocyst sometimes asymmetrical; one lateral denticle may be larger than the others; tubercles occasionally present on the gymnocyst.

M. annae: Denticles and spinules long, regularly spaced; large vicarious avicularia sometimes present.

M. savartii: A median proximal denticle is present; variously developed.

M. commensale: Gymnocyst usually provided with tubercles; cryptocyst without denticles or spinules; cuticular spinules on frontal membrane rare; West African.

In view of the taxonomic uncertainties involved, it seems useless to discuss the distribution of *M. arborescens*. However, the *M. savartii* complex appears to be circumglobal in warm and temperate waters.

Family Alderinidae Canu & Bassler, 1927:3 Genus *Parellisina* Osburn, 1940:360

Parellisina latirostris Osburn, 1940

Figure 2E, G.

- P. latirostris Osburn, 1940:361, Pl. 4, Figs. 33, 34; Puerto Rico, 7 to 27 f.
- P. latirostris Osburn (Osburn 1949: 5, Fig. 4); eastern and northwestern Gulf of Mexico.
- P. latirostris Osburn (Lagaaij 1963:175, Pl. 8, Fig. 3); eastern and northwestern Gulf of Mexico, to 50 f.
- P. latirostris Osburn (Maturo 1968:278); "Cape Hatteras, south."
- P. latirostris Osburn (Long and Rucker 1970:19, Fig. 2:4); Ft. Lauderdale, Florida, shallow.
- P. latirostris Osburn (Schopf 1974:355); U.S. Virgin Islands, shallow.

Material examined: Holotype USNM 11844, Puerto Rico.

Three colony fragments were found encrusting coral rubble from Portete (Atlantic). Colonies are unilaminar; autozoids are arranged in regular quincunx. The gymnocyst is smooth, translucent, and broadest in corners between zoids. The cryptocyst is narrow and equally broad except at the distal tip of the zoid, where the aperture opens. The cryptocyst is provided with numerous minute conical tubercles a few microns in diameter. The opesium is broad, oval, and slightly more pointed proximally than distally.

Interzoecial avicularia are rare; there are only five among the hundreds of zoid examined. The distally directed rostrum is broad, rounded, and symmetrical (Figure 2E). There is a small pair of cardelles and a tiny proximal cryptocyst in the postmandibular field. Each avicularium is associated with a peculiar arrow-shaped kenozoid just distal to it. The wall between them is perforated by scattered uniporous pore plates similar to those between autozoids. The avicularia are usually proximolateral daughter zoids at bifurcations of zoid rows, but not in the specimen illustrated (Figure 2E).

Ovicells are prominent, and slightly embedded in the gymnocyst of the next distal



FIGURE 3. Scrupocellaria bertholleti (Audouin): part of an internode with three ovicells. See text for scale.

zoid (Figure 2G). The ovicell appears to be quite spacious, but this is deceptive because it is flattened (only half as deep as broad). Its surface is imperforate and decorated with the same minute tubercles as the cryptocyst. There is a proximal lip; the junction between the lip and body of the ovicell looks like the drawstring on an old-fashioned bonnet.

There are no spines, knobs, or other decorations of the cuticle or zoecia.

Measurements: Length of zoids, 470 μ (280–550 μ); width, 300 μ (190–440 μ). Operculum width, 120 μ . Ovicell length, 150 μ ; width, 200 μ . Avicularium length, 240 μ ; width, 160 μ .

Parellisina latirostris seems to be indistinguishable from Alderina smitti Osburn, 1950:8 [= A. irregularis (Smitt 1873)] unless avicularia are present. Since avicularia are frequently absent (Lagaaij 1963:175), it may be that these two species sometimes have been confused. It is also possible that the species are identical, and that A. smitti is a name given to colonies of P. latirostris in which avicularia happen to be absent. The situation is further confused because the eastern Pacific representatives of A. smitti have a broader and more coarsely granular

("crenulated") cryptocyst (Osburn 1950, Pl. 6, Fig. 2) than other *A. smitti*. The Pacific form may be a different species.

Parellisina latirostris is known from Puerto Rico (Osburn 1940), southern Florida (Long and Rucker 1970), and the eastern and northwestern Gulf of Mexico (Lagaaij 1963). Maturo (1968) gives a range "from Cape Hatteras, south." We have obtained one specimen from Galeta, Panama (on a fouling plate at 25 ft), sent to us by Charles Birkeland. Its range is probably the southeastern United States, the Gulf of Mexico, and the Caribbean. The deepest record is 50 f (Lagaaij 1963).

Suborder Cellularina Smitt, 1867:279

Family Scrupocellariidae Levinsen, 1909:89 Cellulariidae auctt.

Genus Scrupocellaria van Beneden, 1845:26
Cellarina (part) van Beneden, 1848:70
(not Cellarina d'Orbigny, 1851:181)
Licornia van Beneden, 1849:656
Crisina van Beneden, 1850:656 (not
Crisina d'Orbigny, 1853)
Savignella van Beneden, 1849:656 (not
Savignyella Levinsen, 1909:274)

Type species by original designation: Sertularia scruposa Linnaeus, 1758:815.

Scrupocellaria bertholleti (Audouin)

Figure 3.

Acamarchis bertholleti Audouin, 1826:241, Pl. 11, Fig. 3; Red Sea.

- S. bertholletii (Audouin) (Hastings 1930: 703, Pl. 1, Fig. 105); Pacific—Colombia, Galapagos.
- S. bertholetti [sic] (Audouin) (Osburn 1950: 133, Pl. 15, Figs. 7, 8, Pl. 21, Fig. 8); eastern Pacific including Panama, Costa Rica.
- S. bertholleti (Audouin) (Soule and Soule 1964:11); Baja California.
- S. bertholleti (Audouin) (Maturo 1968: 279); Atlantic; "ranging from Cape Hatteras, south."
- S. bertholletii (Audouin) (Powell 1971:770); Pacific—Panama.

S. bertholletti [sic] (Audouin) (Schopf 1974: 355); Virgin Islands.

Numerous colony fragments were found attached to unknown substrate from Guanacaste (Pacific). Colonies are yellowish, erect, branched, and jointed, forming tufts over 3 cm in height. There are about 7 (5–9) autozoids per internode, an uncalcified cuticular joint transverses the opesium of the most proximal zoid in each internode. The branching is of Type 8 of Harmer (1923:357).

The opesium occupies about one-fourth of the length of the frontal surface. There is no cryptocyst; all the walls except pore plates on ordinary autozoids are external. Some probably inactive zoids may seal off the opesium or restrict it to a small opening by development of a cryptocyst. There are no skeletal pores on the animals except on some ovicells and on multiperforate pore plates with about a dozen communication pores. There are about 5 (4-8) spines on the gymnocystal wall surrounding the distal half of the opesium; there are 3(3-5) outer spines and 3(2-5) inner spines, counting the scutum. The spines are hollow, jointed at the base, and measure about 100μ long. They are usually lost during KOCl cleaning, leaving spine bases. The scutum is attached on the inner side of the opesium near its center. The scutum is much branched (2-9 points), and covers most of the opesium. Rare paddleshaped scuta occur on a few zoids.

Frontal avicularia are developed on the proximal gymnocyst of about a quarter of the autozoids. Most have a tiny (25 μ) pointed rostra directed laterally, but a few large avicularia, resembling small ones except for size (125 μ), occur. Lateral avicularia are present on the outer distal angle of most autozoids; the rostrum is pointed, directed laterally, and measures about 100 μ long. Basal vibracula are present on every zoid just medial to lateral avicularia. A radicle pore about 50 μ in diameter perforates the vibracular chamber; radicles of great length are frequent, attaching the branches to the substrate. The vibraculum slit is transverse; the flagellum is about 300 μ long, pointed, directed laterally and distally. There is one axial vibraculum.

Ovicells are remarkable because two kinds

occur. Both are globular, distal swellings probably developed by enlargement of distal spines. The frontal and lateral lips are smoother than the other parts of the ovicell. One type of ovicell is perforated by about 15 minute pores 50μ in diameter; the second type is imperforate or sparsely perforate and is decorated by irregular knobs of calcium carbonate. Both forms occur on the same colony.

Measurements: Autozoid length measured as proximal–distal distance between lateral avicularia, 330 μ (250–380 μ); width, 200 μ (170–220 μ). Internode length, 1 mm (0.5–3 mm). Rostrum, frontal avicularia, 25 μ (25–400 μ); lateral avicularia, 50 μ . Length vibraculum chamber, 150 μ ; width, 150 μ . Length ovicell, 140 μ (130–170 μ); width, 165 μ (165–200 μ).

Scrupocellaria bertholleti closely resembles S. panamensis Osburn 1950:141, but the latter species has bifurcating spines, a relatively shorter vibracular chamber, and lacks "giant" avicularia. The two species are difficult to distinguish in practice, and may be synonymous.

Scrupocellaria bertholleti is circumtropical to subtropical in distribution (Powell 1971: 770), ranging in the Pacific from California to the Galapagos (Osburn 1950:133).

Suborder Coilostega Levinsen, 1902:2

Family Steginoporellidae Bassler, 1952: G171

Steganoporellidae Hincks, 1884*b*:358 Labioporellidae Harmer, 1926:280

Genus Labioporella Harmer, 1926:281 Labiopora Levinsen, 1909:174 (not Labiopora Moseley 1879:476 or Labiopora Moisisovics 1878)

Genotype by original designation: Labiopora crenulata Levinsen, 1909:174.

Labioporella sinuosa Osburn, 1940

Figure 2D.

L. sinuosa Osburn, 1940:377, Pl. 5, Figs. 40, 41; 1947:109, Pl. 11, Fig. 12; Tortugas, 23 meters.

L. sinuosa Osburn (Shier 1964:619); Florida.

L. sinuosa Osburn (Soule and Duff 1957:98); Pleistocene, California.

Types examined: Labioporella sinuosa Osburn, 1940. Holotype nmnh 11832. Siphonoporella granulosa Canu & Bassler, 1928b:69. Holotype nmnh 7593, Florida.

Several colony fragments were found encrusting coral rubble from Portete (Atlantic). The colorless or yellowish zoids are arranged in quincunx and have a thick hyaline cryptocystal frontal wall that slopes downward toward a large distal opesium. The opesium occupies about one-third of the length of the zoid. The cryptocyst is perforated by about 20 small pores approximately 5μ in diameter. Lateral walls are tuberculated frontally; distal walls are relatively smooth. The polypide tube, usually complete, projects into the opesium and is not appreciably more tuberculated than the remainder of the cryptocyst. Zoids are widest at the level of the opesium. No spines, ovicells, avicularia.

Measurements: Zoid length, 500 μ (500–800 μ); greatest width, 300 μ (250–390 μ); length of opesium, 190 μ (180–270 μ); width of opesium, 210 μ (165–260 μ).

The only species occurring in the area likely to be confused with Labioporella sinuosa are species possessing avicularia. Avicularia are rare on the holotype of Siphonoporella granulosa Canu & Bassler, 1928:69, a species otherwise indistinguishable from L. sinuosa. It may be that L. sinuosa is synonomous with S. granulosa, and that the name is applied to specimens lacking avicularia. Siphonoporella granulosa fits better in the genus Labioporella (Cheetham and Sandberg 1964:1023). Cook (1968) discusses these and other genera.

Labioporella sinuosa apparently is an uncommon but widely distributed tropical American species.

Family Thalamoporellidae Levinsen, 1902:21

Genus Thalamoporella Hincks, 1887:164

Type species by original designation: Flustra rozieri Audouin, 1826:239.

Thalamoporella californica Levinsen, 1909

Figure 2F.

- T. rozieri (Audouin) var. E. (californica) Levinsen, 1909, Pl. 6b, Figs. 2a-d; California.
- T. californica Levinsen (Hastings 1930:716, Pl. 10, Figs. 47–53; Pl. 11, Figs. 56, 57); Galapagos.
- T. californica (Levinsen) [Soule 1959:33 (synonomy)]; California and Gulf of California
- T. californica (Levinsen) (Soule and Soule 1964b:196); California.

Two unilaminar colony fragments were found encrusting algae from Playa el Coco (Pacific) (Figure 2F). Autozoids are arranged in quincunx and are roughly quadrangular in shape. The hyaline frontal wall in the proximal half of the zoid is perforated by about 70 pores approximately 12 μ in diameter, evenly arranged. The distal third of the frontal wall is imperforate. Just behind and lateral to the aperture are a pair of large opesiules. The proximal borders of the opesiules are formed by the frontal wall dipping nearly perpendicularly. On one side, but not both, the frontal wall inserts on the basal wall. The gymnocyst is decorated with small, widely spaced conical tubercles 10 to 15 μ in diameter. The anter of the aperture is approximately hemispherical. The poster is shaped like a broad U; a pair of barely recognizable, triangular cardelles is frequently present. Coelomic spicules were not examined because adequate material was not available for sacrifice (Soule and Soule 1970:14).

Lateral walls possess about 5 (3–6) annular multiporous pore plates near the base of the lateral wall; there is a U-shaped cluster of communication pores at the bottom and sides of the transverse wall. We have only one interzoidal avicularium; it is the first zoid in a new zoid row. The mandible represents about half the length of the avicularium; it is shaped like the head of an arrow. There are no spines; our specimens possess no ovicells, but they are described as very large, hemispherical, and smooth (Soule 1959:33).

Measurements: Autozoid length, 600 μ (500-690 μ); width, 350 μ (270-410 μ).

Aperture length, 200 μ (180–210 μ); width, 190 μ (180–200 μ). Avicularium length, 330 μ ; width, 190 μ .

Thalamoporella californica is found in the eastern Pacific from Point Conception in California to Gorgona, Colombia (Osburn 1950:112).

ASCOPHORAN CHEILOSTOMES

Despite attempts, no usable subdivision of ascophoran cheilostomes has been proposed above the level of family. Perhaps the best approaches have been those of Silén (1942), Harmer (1957), and others, who group ascophorans on the basis of frontal wall morphology. Despite the view expressed elsewhere by one of us (Banta 1970, 1971), we found it preferable to avoid even tentative formal taxa above the family level, partly because the morphology of frontal walls still is poorly understood in most ascophorans, and partly because of the finding of Cook (1973) that apparently similar cheilostomes may have quite different methods of frontal wall formation. In the absence of a rationale other than convention, we have attempted to arrange ascophoran families into groupings of more or less similar overall appearance. Our inclusion of Cribrilaria among ascophorans is arbitrary.

Family Cribrilinidae Hincks, 1880:182 [=Costulae Jullien, 1888 and the families Myagroporidae, Otoporidae, Ctenoporidae, Thoracoporidae, Taractoporidae, Lagynoporidae, Calpidoporidae, Discheloporidae, Rhadheoporidae, Andrioporidae, and Pelmatoporidae of Lang (1916)]

Larwood (1962) has discussed the systematics of cretaceous cribrimorphs. In our opinion, present information on variation within the suborder does not permit recognition of more than one large family.

Genus Cribrilaria Canu & Bassler, 1928b:27

Type species by original designation:

Cribrilina radiata Moll, 1803:63. Brown (1958:54) presented strong evidence for the validity of this generic name.

Cribrilaria flabellifera (Kirkpatrick 1888)

Figure 4A.

Cribrilina radiata var. flabellifera (Kirkpatrick 1888:75, Pl. 10, Fig. 4); Indian Ocean.

Cribrilina radiata, var. flabellifera Kirkpatrick (Thornely 1912:144); Indian Ocean.

Puellina radiata flabellifera (Kirkpatrick) (Canu and Bassler 1929b:239, Pl. 22, Fig. 2); Philippines.

Colletosia radiata flabellifera (Kirkpatrick) (Soule 1959:48); Baja California.

Colletosia radiata (Kirkpatrick) [Harmer 1926:475 (part), Pl. 24, Fig. 18]; New Guinea.

Cribrilaria flabellifera (Kirkpatrick) (Harmelin 1970:94, text Fig. 1, n, o). Mediterranean.

One unilaminar colony was found encrusting coral rubble from Portete (Atlantic). Autozoids are arranged in quincunx and are rhomboidal or kite-shaped in outline. The entire frontal wall is formed of about 14 (12– 24) costae, which run from margins to the center of the frontal wall. Between costae are about 7 (3-12) minute pores (lacunae). The first pair of costae is larger than the others, and may form a semicular umbo proximal to the aperture. The aperture is hemispherical. the proximal border is straight and transverse. The distal and lateral borders of the aperture are formed of prominent spines, usually 6 (5–8) in number. Avicularia are interzoecial, with elongate rostra. The avicularium chamber is smooth, without pores or costae. Ovicells are smooth, imperforate and longitudinally keeled. The keel is sometimes developed into a low central umbo.

Measurements: Zoid length, 330 μ (270–410 μ); width, 270 μ (220–300 μ). Aperture length, 45 μ ; width, 70 μ . Ovicell length, 150 μ ; width, 140 μ . Total length of avicularium chamber and rostrum, 220 μ ; greatest width, 120 μ .

Our specimens agree well with the excellent

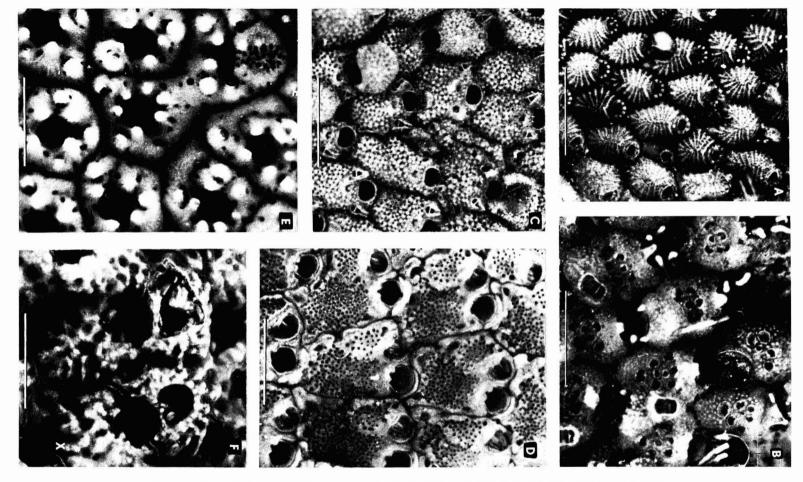


FIGURE 4. Frontal views of KOCl-treated colonies. Scales, 500 μ . A, Cribrilaria flabellifera (Kirkpatrick 1888); Portete. Ovicells at upper center and middle left; avicularia at upper center and middle right. B, Tremogasterina mucronata (Smitt); Portete. Complete ovicell below and left of center. C, Microporella umbracula (Audouin); Playa el Coco. Ovicells at left center, lower left, and upper right. D, Escharina porosa (Smitt); Portete. E, Cigclisula turrita (Smitt); Portete. Ovicell upper left. F, Cigclisula aviculifera (Canu & Bassler); Portete. Both zoids have ovicells.

description of Harmelin (1970:94), with these differences: (1) our specimens have slightly larger and proportionately less elongate autozoids [length of Mediterranean material, $296 \mu (262-367 \mu)$; width, $193 \mu (170-210 \mu)$]; (2) our material is more variable in the number of costae, and may possess nearly twice as many as the maximum number in Mediterranean material [11 (10-13) according to Harmelin 1970:95]; (3) the plateau of frontal wall between the first pair of costae and the aperture does not contain a median lacuna larger than the others, as is the case in Mediterranean material.

Cribrilaria flabellifera is closely related to C. crenulata Harmelin 1970:91, which is also from the Mediterranean.

Family Exechonellidae Harmer, 1957:651 [= Arachnopusiidae (part) Jullien, 1888]

Genus Tremogasterina Canu, 1911:256

Type species by original designation: Tremogasterina problematica Canu, 1911:256.

Tremogasterina mucronata (Smitt, 1873)

Figure 4B.

Escharipora(?) mucronata Smitt, 1873:24, Pl. 5, Figs. 113–115; Tortugas.

T. truncatorostris Canu & Bassler, 1923:244, Pl. 47, Fig. 6; Miocene, Santo Domingo.

T. grunulata Canu & Bassler, 1928b:45, Pl. 13, Fig. 34; Pl. 33, Fig. 2, text Figs. 6B-6F; Pliocene, Panama.

T. ventricosa Canu & Bassler, 1928b:47, Pl. 13, Figs. 1, 2; Atlantic, off Georgia.

T. malleolus Canu & Bassler, 1928b:48,Pl. 13, Figs. 5–8;Pl. 33, Fig. 8;Gulf of Mexico, Caribbean, Pliocene of Panama.

T. sparsipora Canu & Bassler, 1928b:50, Pl. 33, Fig. 3; Pliocene, Panama.

T. mucronata (Smitt) [Powell and Cook 1967: 9, Pl. 1, Figs. a, b (synonomy)]; Caribbean. Material examined: Tremogasterina truncatorostris NMNH holotype 68685; T. granulata NMNH holotype 7603; T. ventricosa NMNH holotype 7601; T. malleolus NMNH syntypes

7602; T. sparsiporosa NMNH holotype 70865. A unilaminar colony fragment was found

encrusting coral rubble from Portete (Atlantic). Autozoids are arranged in quincunx and are rhomboidal in shape. The translucent frontal wall is nearly smooth when first developed, but soon becomes covered by tiny round tubercles about 25 μ in diameter. The margins of the wall are perforated by 5 to 20 marginal pores 10 to 40 μ in diameter, sometimes becoming occluded in older zoids. A multiporous pore plate can be seen at the base of each marginal pore, so they almost certainly are true areolae. The central part of the wall is perforated by a cluster of about 5 (3-10) pores of varying shapes. The most usual form is kidney-shaped, with the hilum directed medially. The pores, probably ascopores, measure about 50 μ (10–80 μ) along their broadest axis.

Just behind the aperture of most zoids is a prominent spikelike umbo or mucro pointing frontally and slightly distally. About 6 (2–8) prominent spines are present around the distal and lateral borders of the aperture. Ovicells are prominent, imperforate, and decorated with the same pattern of tiny tubercles as the frontal wall. The rim of the opening of the ovicell is imperforate; it is not closed by the operculum. The calcium carbonate of the ovicell appears to be continuous with the frontal wall of the next distal zoid. Nearly every ovicell is surmounted by an avicularium, and few avicularia occur elsewhere. The mandible is rounded at the tip. Ovicell avicularia are perched at the distallateral edge of the ovicell, and communicate basally with areolae of adjacent zoids. There are a few adventitious avicularia located between autozoids. They appear superficially to be interzoidal (vicarious), but they are confluent with areolae of zoids surrounding them, sometimes with zoids belonging to different zoid rows.

Measurements: Autozoid length, 700 μ (550–950 μ); width, 410 μ (270–550 μ). Aperture length, 140 μ (100–165 μ); width, 140 μ (90–170 μ). Ovicell length, 190 μ ; width, 270 μ . Avicularium length, 140 μ (130–190 μ); width, 95 μ (80–110 μ).

The synonomy given is that according to Powell and Cook (1967:9), who examined much of the relevant type material and found

that variation within this species group is extreme, and that overlap or potential overlap between species is common. Our observations of type material are in agreement with this finding.

The species appears to be limited to the Gulf of Mexico and the Caribbean, and ranges from the Miocene to Recent (Powell and Cook 1967:9).

Family Microporellidae Hincks, 1879:156 Genus *Microporella* Hincks, 1877b:526

Type species by original designation: Lepralia ciliata Pallas, 1766:38.

Microporella umbracula (Audouin, 1826)

Figure 4C.

Flustra umbracula Audouin, 1826:239, Pl. 9, Figs. 1–7.5; Red Sea.

M. ciliata var. corunata (Audouin) (Hastings 1930:727); Panama.

M. coronata (Audouin) (Osburn 1952:386, Pl. 45, Fig. 1); Galapagos.

M. umbracula (Audouin) (Harmer 1957: 964).

M. umbracula (Audouin) (Powell 1971:772). Panama.

Five colony fragments were found encrusting shells from Playa el Coco (Pacific). Zoids are arranged in quincunx and are irregularly rectangular in shape. The frontal wall is slightly inflated, tuberculated, and perforated by about 100 evenly distributed pores approximately 10 μ in diameter. About 50 μ proximal to the aperture is a median, crescent-shaped ascopore about 40 μ wide. Behind the ascopore, there is usually a low umbo. The aperture is straight proximally, rounded distally; 2-5 short spines may be present in young zoids, but old zoids show little trace of them. A pair of avicularia with long pointed mandibles is usually present on each side of the zoid at the level of the imperforate area between the ascopore and aperture. Ovicells are thick-walled, tuberculated, and evenly perforated by minute (5 μ) pores about half the diameter of frontal wall pores.

Measurements: Autozoid length, 440 µ

(250–550 μ); width, 250 μ (200–350 μ). Aperture length, 90 μ (87–110 μ); width, 110 μ (85–140 μ). Ovicell length, 220 μ (200–250 μ); width, 290 μ (220–390 μ). Length of avicularium calcareous parts, 110 μ (95–120 μ).

Harmer (1957:964) synonomized M. coronata (Audouin 1826) with M. umbracula (Audouin 1826), picking the latter name because it was better characterized. The only species in the area likely to be confused with M. umbracula are M. ciliata (Pallas 1766), which usually has only one avicularium per autozoid, and M. californica (Busk 1855a), which is larger (600–700 μ long, 400–500 μ wide; aperture, 120 μ long, 160 μ broad; ovicell, 260–300 μ wide) (Osburn 1952).

The species has a "worldwide distribution in warmer waters" (Osburn 1952:387).

Family Schizoporellidae Jullien, 1882:527

Genus Schizoporella Hincks, 1877b:527 Schizopodrella Canu & Bassler, 1917:40

Schizoporella ?serialis (Heller, 1867)

Figures 5F, 6A, B

Lepralia spinifera Johnston, 1847 [Busk 1854: 69 (part), Pl. 91, Figs. 1, 2]; Europe. Lepralia serialis Heller, 1867:104.

Lepralia errata stadium Hemeschara Waters, 1879: 39, Pl. 10, Fig. 5; Naples, Cape of Good Hope.

S. errata (Waters) (Calvet 1927:17); Monaco. S. errata (Waters) (Gautier 1961:149, Text fig. 14); Mediterranean.

?S. violacea Canu & Bassler, 1930b; Tunisia. ?S. violacea Canu & Bassler (Pouyet 1971: 190, Pls. 13–14); Tunisia.

S. errata (Waters) (Powell 1970: 1848, Fig. 4); Israel

Four multilaminar colony fragments were found encrusting unknown substrates from Playa el Coco (Pacific). Most of the exposed zoids are adventitious (frontally budded), but there is a small fragment of a primogenial subcolony (see Banta 1972 for terminology). Adventitious and primogenial layers will be discussed separately.

Adventitious zoids are oriented randomly, that is, the anter may be directed in any

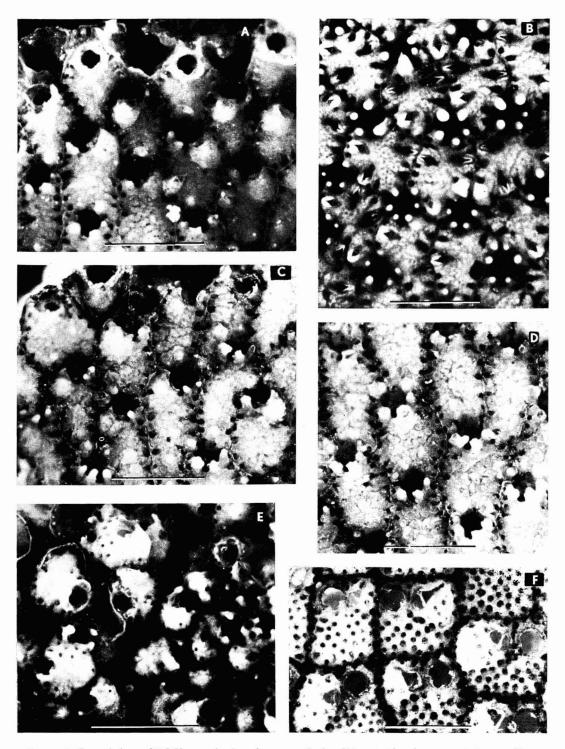


FIGURE 5. Frontal views of KOCl-treated colony fragments. Scales, 500μ . A, Rhynchozoon sp. 1; Portete. Young primogenial buds. B, The same; older primogenial zoids; extreme ontogenetic change is evident. C, Rhynchozoon sp. 2; Portete. Young primogenial zoids. D, The same; older primogenial zoids. E, Rhynchozoon sp. 3; Playa el Coco. Adventitious zoids. F, Schizoporella ?serialis (Heller, 1867); Playa el Coco. Adventitious zoids.

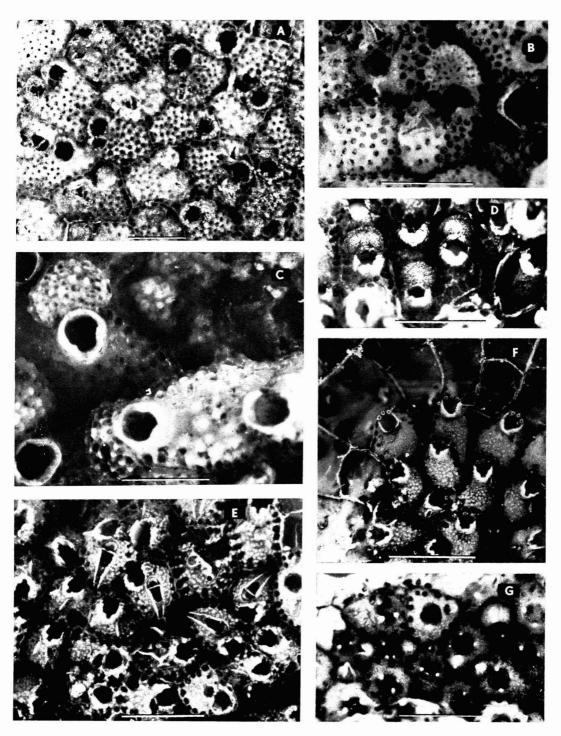


FIGURE 6. Frontal views of KOCl-treated stained colony fragments coated with NH₄Cl. Scales, 500 μ . A, Schizoporella ?serialis (Heller, 1867); Playa el Coco. Adventitious zoids. B, The same, ovicell. C, Teuchopora, undescribed sp.; Portete. Ovicells at left. D, Parasmittina crosslandi (Hastings); Playa el Coco. Ovicells. E, The same, adventitious layer with large avicularia. F, The same, developing primogenial zoids. G, Hippoporella costulata Canu & Bassler; Playa el Coco. Adventitious zoids; ovicell at upper right.

direction, without orientation to the center or margin of the colony. The frontal wall is thick and roughened, hyaline to opaque. There is usually a row of variously developed areolae at the very margin of the zoid. In some young zoids, areolae are slitlike in frontal view; their inner ends are closed by a nearly vertical circular plate, probably a multiporous pore plate. In older zoids, the areolae are carried frontally with the thickening of the frontal wall and become rounder and more prominent. In some cases, some, but never all, of the areolae become occluded with calcium carbonate. The remainder of the frontal wall, except for a small area immediately proximal to the aperture, is perforated by evenly distributed circular pseudopores. The size and number is variable, but there are typically about 40 pores 30 μ in diameter. Pores are seldom, if ever, more than 30 μ . Smaller pores (down to less than 10 μ) appear mainly on older zoids; therefore, they are probably 30 μ when formed, and are made smaller by increasing calcification. Pseudopores are frequently occluded completely, especially in zoids ready to produce a frontal bud (recognized by a prominent vertical wall rising from the intercalary cuticle between zoids).

With advancing calcification, the aperture may become surrounded by a low peristome. There is no noticeable tendency to form an umbo proximal to the aperture.

The aperture shape may vary somewhat, but there is always a well-defined sinus. The anter is always nearly perfectly hemicircular, between 120 and 150 μ in greatest width. The poster is likewise hemicircular, but formed from a circle of variable diameter, from onethird to one-half the diameter of the circle forming the hemicircular anter. The poster, therefore, varies in appearance from a wide U shape to a narrow U shape. A pair of cardelles is present just distal to the junction of the anter and poster. The junctions of the margins of the anter and poster may form a pair of triangular false cardelles, especially when the poster is small. This may give rise to the appearance of having two pairs of cardelles, one proximal to the other.

One avicularium is almost always present

on each autozoid, but they are sometimes absent. The avicularium is located just proximal and lateral to the aperture; it may be oriented distolaterally, laterally, or proximolaterally. The rostrum varies in shape from equilaterally triangular to enlongate or hastate. The distal tip of the rostrum may be an open notch, indicating that the mandible may have projected far beyond the end of the rostrum as a setose or filiform structure. We have no cuticular parts left on any specimen: thus, the mandible may have projected far beyond the end of the rostrum as a setose or filiform structure. The avicularia vary greatly in size (see measurements below). Occasional interzoidal avicularia occur. They resemble ordinary adventitious avicularia, but are developed on what appears to be an aborted autozoid.

The ovicell is globular, prominent, and roughly hemispherical. Its calcium carbonate appears to be continuous with frontal walls of adjacent zoids. It is pierced by numerous irregularly shaped pores, smaller $(5-20 \mu)$ than pseudopores of autozoids.

There are no spines.

Primogenial zoids are arranged in zoid rows, but there is no apparent tendency toward a quincunx pattern. The autozoids are approximately square in outline. The aperture is located in a distolateral corner instead of the distal end, as is usual in encrusting cheilostomes. A distolaterally directed avicularium is located in the second distolateral corner. The other superficial characters are the same as those of adventitious zoids.

Measurements: Length of primogenial zoids, 500 μ (440–600 μ); width, 450 μ (380–500 μ). Length of adventitious zoids, 500 μ (400–710 μ); greatest width, including avicularium chamber, 500 μ (400–700 μ). Length of aperture of primogenial and adventitious zoids, 140 μ (120–170 μ); width, 150 μ (120–170 μ). Length of avicularium opesium (including rostrum), 190 μ (110–280 μ); greatest width, 95 μ (55–110 μ). Ovicell length, 250–270 μ ; width, 330 μ (270–410 μ).

The taxonomy of the *Schizoporella* complex is extremely confusing; many of the "species" involved are variable and seem to intergrade. Our specimens most closely re-

semble *S. errata* Waters and its likely synonym, *S. violacea* (Canu & Bassler). Unfortunately, the familiar name, *S. errata*, is almost undoubtedly a junior synonym of *S. serialis* Heller. Heller designated as the type of his new species, a specimen figured by Busk (1854, Pl. 91, Figs. 1, 2) and described by him as *Lepralia spinifera* Johnston. Waters (1879:39) states his conviction that the same specimen is conspecific with his new *S. errata*. There seems to be little doubt he was correct, so Heller's name must stand.

Schizoporella serialis seemingly differs from S. floridana Osburn 1914: 205 in having autozoids with nearly square outlines, compared to the rectangular outlines of S. floridana. Osburn (1914, Figs. 17, 18) shows avicularia distal to the aperture, but he says they are "occasionally behind the orifice." Giant adventitious avicularia are present, and the ovicell is smooth and imperforate. Schizoporella floridana Osburn may well be a species distinct from the S. floridana of American authors (references in Weisbord 1967:82). The latter form rarely, if ever, possesses avicularia distal to the aperture, giant adventitious avicularia are rare or absent, and the ovicell is rough and finely perforate. If the species are distinct, the next available name for the common American Schizoporella seems to be Schizopodrella (=Schizoporella) pungens Canu & Bassler, 1928b:95. The situation is further confused by the fact that S. pungens closely resembles S. violacea and S. serialis and may be synonymous with one or both.

Schizoporella serialis appears to be widely distributed in warm waters, and may be circumglobal (Powell 1970:1848). The confused taxonomy, however, makes this conclusion suspect.

Genus *Escharina* Milne-Edwards, 1836:231

= Herentia (part) Gray, 1848:122 Mastigophora Hincks, 1877b:527 Schizolavella Canu & Bassler, 1920:358 Mastigophorella Bassler, 1953:G220

Genotype by original designation: Eschara

vulgaris var. alpha Moll, 1803:55 (Harmer 1957:997).

Escharina porosa (Smitt, 1873)

Figure 4D.

Hippothoa porosa Smitt, 1873:41, Pl. 7, Fig. 158; Tortugas Island.

Mastigophora porosa (Smitt) (Canu and Bassler 1928b:134, Pl. 19, Figs. 8, 9); Gulf of Mexico.

Mastigophora porosa (Smitt) (Canu and Bassler 1928a: 38, Pl. 9, Fig. 10); Brazil, 128 meters.

Mastigophora porosa (Smitt) (Osburn 1952: 480, Pl. 58, Fig. 4); Colombia.

Escharina porosa (Smitt) (Cheetham and Sandberg, 1964:1032, Fig. 33); Northern Gulf of Mexico.

Not Escharina porosa Verrill, 1879: 193; New York.

Not *Hippoporina porosa* (Verrill) (Maturo and Schopf 1968:48, Fig. 12a).

Material examined: Mastigophora porosa. NMNH hypotype 7547 (Canu and Bassler 1928b); NMNH hypotype 8577 (Canu and Bassler 1928a).

Two colony fragments were found encrusting coral rubble from Portete (Atlantic). The rhomboidal-shaped zoids are arranged in quincunx. Each zoid possesses a nearly level frontal wall perforated by approximately 100 small pores, probably pseudopores, measuring less than 5 μ in diameter. The peripheral part of the frontal wall is provided with 4 to 8 much larger pores, probably areolae, which measure 25 to 50 μ in diameter. The aperture is nearly round except for a small V-shaped poster. In one lateral corner of each autozoid is a large interzoecial (vicarious) vibraculum with a long seta 1 mm or more in length and about 30 μ in diameter. The wall separating the vibraculum chamber from the autozoid is perforated by 5 to 10 uniporous nonannular septulae. The pores between autozoids are multiporous; septulae in lateral walls are probably annular, but this could not be confirmed.

Autozoids are surrounded by a groove, probably marking the place where cuticle (epitheca) descends into the calcareous wall.

No such groove is seen between autozoids and vibracula. This and the observation that the septulae are nonannular indicates that this wall is probably a simple interior wall.

There are no spines, ovicells, or avicularia. Measurements: Length of autozoid, 640 μ (450–700 μ); width, including vibraculum, 550 μ (320–700 μ). Aperture length, including poster, 140 μ (120–160 μ); width, 140 μ (120–160 μ). Length vibraculum chamber, 400 μ (250–550 μ), greatest width, 250 μ (160–

330 μ). Length vibraculum aperture, 110 μ (80–110 μ); width, 110 μ (70–130 μ).

Escherina porosa (Smitt) is a secondary homonym of Escherina porosa Verrill. The International Congress of Zoology (1961: Art. 59) allows individual authors to decide whether the homonym is likely to cause confusion, and if so, to rename the junior homonym. In our opinion, the two species belong in widely different genera, and are unlikely to be combined in the same genus again. The benefits of the nomenclatural stability seem to outweigh the potential problems of confusion, so we chose to let both names stand.

Escherina porosa is apparently a warmwater species of the Atlantic and eastern Pacific. It is known from the Gulf of Mexico, Florida, and Guinea coast of Africa, and in the Pacific, near Colombia (Cheetham and Sandberg 1964:1032).

Family Stomachetosellidae Canu & Bassler, 1917:44

Genus Cigclisula Canu & Bassler, 1927:6, 26

Trematooecia Osburn, 1940:457 Cigclisula Canu & LeCointre, 1925:10 is a nomen nudum

Type species by original designation: Escharoides occlusa (Busk 1884:150).

Cigclisula turrita (Smitt, 1873)

Figures 4*E*, 7. *Lepralia turrita* Smitt, 1873:65, Pl. 11, Figs. 226–228; Florida, 26 to 44 f.



FIGURE 7. Cigclisula turrita (Smitt). Operculum. Scale, 200 μ .

Holoporella turrita (Smitt) (Canu and Bassler 1923:179, Pl. 46, Fig. 1); Pleistocene, United States.

Holoporella turrita (Smitt) (Canu and Bass-1928b:145, text Fig. 33); Gulf of Mexico, 24 to 143 f.

Holoporella turrita (Smitt) (Hastings 1930: 732, Pl. 12, Fig. 73); Galapagos.

?Cigclisula turrita (Smitt) [Harmer 1957: 1059, Pl. 69, Figs. 21–24, 27 (synonymy)]; Indonesia.

Trematooecia turrita (Smitt) (Powell 1971: 773); Panama.

Cigclisula turrita (Smitt) (Maturo, 1968: 277); Cape Hatteras, south.

Material examined: Trematooecia protecta Osburn, 1940:459, NMNH syntype 11831, Puerto Rico; Holoporella turrita (Smitt) (Canu and Bassler 1923:179), NMNH hypotype 68708, Pleistocene, Panama.

Four colony fragments were found encrusting coral rubble from Portete (Atlantic). The colonies are unilaminar, colorless to light yellow when dry. Even newly formed autozoids are hexagonal in shape, and as deep or deeper than the diameter of the frontal surface. The aperture is at the center of the frontal surface; its orientation is random, that is, the anter may point in any direction without regard to distal or proximal. The frontal wall is thick and opaque. There appear to be two kinds of pores: (1) Marginal pores, probably areolae, are located very near the junction between zoids. Each zoid has about 20 of these, approximately 10 μ in diameter. Avicularia seem to develop in association with these pores through a tubule, even though avicularia may be located near the aperture. (2) More central pores, sometimes blind, shallow pits

in the calcareous wall, occur almost anywhere on the frontal wall, but tend to cluster around the aperture. Blind pits must be pseudopores, but some complete central pores may be areolae (Banta 1973). Central pores vary greatly in size, but are never smaller than about $10~\mu$. Interzoidal communication pores are scattered on the wall and are uniporous. We observed no frontal budding.

The aperture is slightly oval and elongated along the anter-poster axis. There is a pair of strong triangular cardelles. The operculum (Figure 7) possesses narrow proximal and distal sclerites and a pair of strong sclerites connecting the porta to the points of articulation with the cardelles.

The aperture is surrounded by 4 (3–6) tubercles or spikes typically flattened and granulated at the tip. Adventitious avicularia occur anywhere on the frontal wall. There are no giant interzoidal avicularia. True (hollow) spines are absent.

Ovicells are prominent and hemispherical. In most cases (9) the ovicell is smooth laterally and perforated by a median longitudinal band of pores 10 to 30 μ in diameter. In one case, there is only one central pore that is about 50 μ in diameter. All ovicells are on the same colony fragment.

Measurements: Diameter of hexagonal zoids, 510 μ (450–560 μ); length of aperture, 190 μ (180–210 μ); width, 160 μ (140–170 μ); width of avicularia, 55 μ (40–85 μ); length of ovicell, 330 μ (320–350 μ); width, 390 μ (380–490 μ).

Trematooecia turrita is the type species of the genus Trematooecia Osburn, 1940:457, which was named for the structure of the ovicell. According to Osburn (1940:458), the ovicell is perforated by a single pore covered by a cuticular membrane. This contradicts the description of Smitt (1873:65), who states that the "median frontal part above the aperture [is] perforated [by] pores" (loose translation from Latin). Our finding that both morphologies occur on the same colony indicates that the ovicell is more variable than previously recognized. It is possible, however, that more than one species is involved.

Osburn (1940:458) states that West Indian material is vellowish pink to brick red; our specimens are colorless or light vellow in the dry state. The length he gives for autozoids (90 mm, a typographical error for 0.9 mm) are much larger than the 0.56 mm maximum for our material: the same is true for the aperture (160–200 μ , compared to our 140– 170 μ). Osburn mentioned that "large spatulate avicularia" are "frequent" in addition to small frontal avicularia on tubercles; no large avicularia are present on our material. The ovicell Osburn describes (see above) is quite different from the usual ovicell in our specimens. Osburn's T. turrita, therefore, is not the same as ours, but it does closely resemble the description given below for C. aviculifera.

Smitt's (1873:65) description of C. turrita indicates that it differs from our material in three ways. His material is a little larger (autozoid length, 750 μ compared to our 510 μ). Adventitious avicularia, absent in Smitt's material, are present in ours; interzoecial spatulate avicularia are present in Smitt's specimens, but not in ours. In view of the known variability of the group, we conclude these differences are small enough to assign tentatively our specimens to Smitt's species. Osburn's material, however, seems to be distinct from both Smitt's and our specimens and probably is better assigned to C. aviculifera until types can be examined.

The nature of Osburn's specimens would seem to be critical to the definition of the genus *Trematooecia*, but its importance is negated if one agrees, as we do, with Harmer (1957:1059), Maturo (1968:277), and others, who believe *Trematooecia* to be a subjective junior synonym of *Cigclisula* Canu & Bassler, 1927:6.

We examined syntypes (NMNH 11831) of *Trematooecia protecta* Osburn, 1940:459. Unfortunately, the only ovicell on the five colony fragments is broken, but Osburn's figure (1940: Pl. 8, Fig. 67) shows a single median pore. The species is close to our *C. turrita*, but differs from it in two main ways: (1) avicularia are much less common in Osburn's material than in ours (about one avicularium per zoid, compared to three per

zoid in our specimens), and (2) frontal budding occurs in Osburn's material, but not in ours. We conclude that our specimens are probably distinct from *T. protecta*, but closely related.

A number of specimens have been assigned to *C. turrita* from all over the world (synonomy in Harmer 1957:1059). Most differ in detail from Smitt's description.

Cigclisula turrita may be easily confused with C. osburni (Marcus 1955:311), C. cheethami (Weisbord 1967:106), C. hexagonalis (Canu and Bassler 1930a:38), C. protecta (Osburn 1940:459), and others. We are unable to be of help in sorting them out. It seems likely that the taxonomy of C. turrita and its relatives will not be untangled until many specimens are examined from all over the world and more is known about variability of American material, at least.

If all the records are to be believed, *C. turrita* is an equatorial species (Powell 1971: 773).

Cigclisula aviculifera (Canu & Bassler, 1923)

Figure 4F.

Holoporella aviculifera Canu & Bassler, 1923: 179, Pl. 46, Fig. 2; Canal Zone, Pleistocene. Holoporella turrita (Smitt) (Osburn 1914: 217); Florida.

Holoporella turrita (Smitt) (Osburn 1927: 131); Caribbean.

Trematooecia turrita (Smitt) (Osburn 1940: 458, Pl. 8, Fig. 72); Puerto Rico.

Trematooecia aviculifera (Canu & Bassler) (Powell 1971:773); Atlantic, Panama.

Probably distinct, but related: Porella rogickae Soule, 1961:31, Fig. 1; Gulf of California. Porella rogickae Soule (Soule and Soule 1964:24, Fig. 7); Baja California.

Material examined: Holoporella aviculifera Canu & Bassler, 1923:179, NMNH holotype 68709. Trematooecia turrita (Smitt) (Osburn 1940:458, 1927:131), NMNH hypotypes 208837.

Fragments of a single brick-colored colony were found encrusting coral rubble from Portete (Atlantic). Zoids are at first arranged in regular quincunx, but later the appearance

becomes irregular because of frontal budding of adventitious layers. Primogenial zoids vary from rectangular to hexagonal; the aperture faces obliquely, frontally, and distally at the distal end of the zoid. The frontal wall is thick and opaque; around its margin are about 20 pores, probably areolae, measuring approximately 25 μ in diameter. A few additional pores about the same size may be present near the center of the wall. The aperture is shaped like a thumb nail; rounded distally, the lateral margins straight, diverging proximally, the proximal border straight, transverse. There are no cardelles or apertural spines, but a few pointed knobs may be present around the aperture, especially in adventitious zoids.

Avicularia are of two kinds, apertural and giant. Apertural avicularia are present inside the peristome just proximal to the aperture in almost every autozoid. They have rounded mandibles directed laterally. Giant avicularia are represented by only one individual in our collections. It is located between adventitious autozoids and possesses a large oval mandible. Ovicells are thick-walled and partially embedded in the frontal wall of the next distal zoid. The frontal surface is perforated by a large pore about 190 μ wide. The pore is hemicircular or crescent-shaped and is plugged by a cuticular membrane, sometimes calcified.

Measurements: Autozoid length, 800 μ (560–900 μ); width, 550 μ (510–620 μ); aperture length, 160 μ ; width, 180 μ ; width of frontal avicularia, 70 μ ; length of giant interzoecial avicularium, 350 μ ; width, 190 μ ; ovicell length, 350 μ (330–400 μ); width, 490 μ .

The holotype of Canu and Bassler's (1923: 179) *Holoporella aviculifera* is a small colony growing on coral; there are no ovicells, but two avicularia are present on adventitious layers. The morphology indicates it is conspecific with our material. We also examined Osburn's (1927:131; 1940:458) types of *Trematooecia turrita* and conclude it is conspecific with *H. aviculifera*. The difference between Osburn's material and typical *C. turrita* is discussed in our description of that species.

Family Sertellidae Jullien & Calvet, 1903:56 Reteporidae Smitt, 1867

Harmer (1933:618) pointed out that the genus *Retepora* is based on the unrecognizable species *Millepora cellulosa* Linnaeus, 1767 (non M. cellulosa Linnaeus, 1758), so both the genus and family names must be discarded. The next available names are *Sertella* Jullien & Calvet, 1903:57 and Sertellidae Jullien & Calvet, 1903:56. These authors indicated that their joint 1903 work should be considered the work of separate authors, so the genus, for example, can be cited *Sertella* Jullien in Jullien and Calvet, but if this is done, a work by Jullien and Calvet does not exist. To avoid bibliographic confusion, we disregard the authors' wishes.

Genus *Rhynchozoon* Hincks, 1895:v *Rhynchopora* Hincks, 1877*b*:528 *Strophiella* Jullien & Calvet, 1903:66

Type species by Hincks' indirect designation: Lepralia bispinosa Johnston, 1847:326. The validity of this well-known name is slightly questionable because it was introduced in the index of a collection of papers reprinted from the Quarterly Journal of Microscopical Science (Harmer 1957:1062). Hincks there substituted Rhynchozoon for Rhynchopora, preoccupied (Brachiopoda), so the type species is clear, even though it was designated earlier (1877b:528) for Rhynchopora.

Rhynchozoon Hincks, 1895:v Strophiella Jullien and Calvet, 1903:66

Genotype by original designation: Lepralia bispinosa Johnston, 1847:326.

Rhynchozoon sp. 1

Figures 5A, B, 8A.

Thirty-two unilaminar colony fragments were found encrusting coral rubble and unknown substrates from Portete (Atlantic). When first developed the zoids can be seen to be arranged in regular quincunx. The

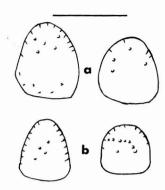


FIGURE 8. Ovicell plates. A, Rhynchozoon sp. 1; B, Rhynchozoon sp. 3. Scale, 200 μ .

individuality of zoids quickly becomes obscured, however, by secondary thickening, so young zoids differ greatly from older ones (Jullien 1881a:210). Newly formed zoids are easier to study and seem to vary less than older ones. The frontal wall is at first smooth and relatively hyaline. There are about 25 marginal "pores" about 20 μ in diameter occluded by an apparent pore plate perforated by a central pore a few microns in diameter; the pores are probably areolae. The anter of the aperture is hemicircular in outline, beaded by 20 to 30 minute tubercles.

The poster is V- or U-shaped; its maximum width is about half that of the anter. A pair of cardelles is present just distal to the junction of the anter and the poster. The poster is never beaded. The aperture is soon surrounded by a low, thin flaring peristome (apertural collar), but this rapidly becomes buried in, probably continuous with, the calcium carbonate of the thickening of its own frontal wall and those of adjacent zoids. A large avicularium with long triangular, hooked rostrum soon develops immediately proximal and lateral to the aperture. The rostrum is always directed laterally and slightly frontally relative to the operculum; it is tilted slightly frontally along its long axis. The frontal wall thickens rapidly until it is more than ten times its original thickness. At first interargolar buttresses (costae) are present, but they soon become obscured. Areolae are carried frontally with the frontal wall; their outer ends enlarge to

30 to 50 μ in diameter. Some areolae must become occluded or united with others, because older zoids have only about 10 exterior areolae, compared with about 30 in young ones. Frontal avicularia, with triangular long-pointed mandibles soon appear on the frontal wall, developing from areolae. At about the same time, conical tubercles or spikes about 60 μ in diameter, and 20 to 100 μ long appear on the frontal wall, especially around the aperture. There are typically two tubercles proximolateral and two distolateral to the aperture, but this is highly variable; there may be as few as two or as many as seven, variously positioned. By this time, the primary aperture has become completely obscured in frontal view, and can be seen only by tilting the colony to look down into the secondary aperture. In some colonies, the apertural avicularium becomes similarly hidden; in others it remains visible.

Ovicells develop after the thickening of the frontal wall has begun. They quickly become embedded in the thickening walls of surrounding zoids, opening into the secondary aperture of the zoid immediately proximal to it. The frontal surface is thick-walled. translucent, and smooth, sometimes supporting a low median proximal umbo. Its proximal side, the face opening into the secondary aperture, is a thin hyaline plate contrasting distinctly with the rest of the ovicell (Figure 8A). The aperture of the ovicell opens almost directly basally behind the plate. The plate is shaped like the operculum of a Schizoporella (no homology with an operculum is implied, however). Its poster is pointed basally. The distal border of its anter is minutely decorated with tiny tubercles about 10 μ in diameter; the remainder of the plate is relatively smooth.

This species apparently never produces frontal buds. If colonies are more than one-layered, it is because one primogenial colony has overgrown the other. Oral spines are lacking, even in very young zoids.

Measurements: Length of young autozoids, 440 μ (410–550 μ); width, 330 μ (270–380 μ); proximal-distal distance between edges of secondary apertures of old zoids,

330 μ (260–440 μ); length of primary aperture, 100 μ (95–110 μ); width, 100 μ (100–110 μ); length of apertural avicularia (measured as the length of the rostrum plus postmandibular field), 110 μ (95–140 μ); length of frontal avicularia, 110 μ (70–140 μ); width of ovicell plate (other ovicell measurements are almost impossible to take consistently), 170 μ (150–180 μ).

Rhynchozoon sp. 2

Figure 5C, D.

A single unilaminar colony fragment was found with several hundred zoids encrusting a shell and another bryozoan (unrecognized) from Portete (Atlantic). Autozoids are arranged in quincunx and remain distinct. They do not undergo nearly such drastic changes with age as do the other Costa Rican species of Rhynchozoon. The frontal wall is roughened by tubercles about 30 μ in diameter, even when first laid down. The margin of the young frontal wall is provided with 20 to 25 pores about 30 μ in diameter. Each pore is occluded by a calcareous plate pierced by a tiny pore about 5 μ in diameter; they are clearly areolae. As the frontal wall thickens, areolae remain relatively constant in size at 30 μ , and unlike other species of Rhynchozoon, the number of areolae seen frontally does not diminish with age.

Apertures are almost vertical at the distal end of the zoid, and cannot be seen from a frontal view, even in very young zoids; the colony must be tilted to see it. The anter is hemicircular, beaded by about 20 minute tubercles. Its width is always slightly smaller than those of other Costa Rican species of *Rhynchozoon*. The nonbeaded poster is V-shaped; its width is always less than half that of the anter—usually about a third or less. There is a pair of minute triangular cardelles just distal to the junction of the anter and the poster. Autozoids communicate with neighboring zoids through about 15 to 20 uniporous pore plates.

Apertural avicularia are uncommon; fewer than one zoid in 20 was seen to bear one, but the number may be higher because they are sometimes obscured by tubercles. They are developed from areolae pores and are situated just proximal and lateral to the aperture; the long-pointed rostrum is directed laterally and frontally. Frontal avicularia are even less common; there are only a few on the colony. They develop from areolae and resemble apertural avicularia.

As the frontal wall thickens, tubercles become larger and more prominent, up to 100 μ in diameter. In the oldest zoids, the tubercles become engulfed in smaller tubercles about 10 μ in diameter and appear granular. Apertural tubercles become prominent early in development. They first appear as a completely developed peristome developed from the frontal wall of the zoid bearing the aperture. As this half-peristome lengthens, it becomes lobulated into about 3 (2-4) tubercles approximately 60 μ in diameter and of varying length (to 100 μ). Meanwhile, tubercles of the same morphology develop on zoids distal and lateral to the aperture, so that each aperture becomes surrounded by about 6 (5-8) tubercles. One difference between the fully developed zoids in this species and in Rhynchozoon sp. 1 is that the frontal wall does not thicken nearly as much (up to only about 120 μ).

The colony has no fully developed ovicells. There are no traces of apertural spines.

Measurements: Autozoid length of old and young autozoids, 550 μ (400–700 μ); width, 320 μ (250–400 μ). Proximal–distal distance between secondary aperture of fully developed zoids (measured from base of spiramen to distal aperture of proximal zoid), 410 μ (320–550 μ). Primary aperture length, 100 μ (95–110 μ); width, 100 μ , with no variation in 12 zoids measured. Length of apertural avicularia (rostrum plus postmandibular field), 100 μ (50–120 μ); length of frontal avicularia, 120 μ .

Rhynchozoon sp. 3

Figures 5E, 8B.

Two multilaminar colony fragments were found encrusting shell and unknown substrates from Playa el Coco (Pacific). Young zoids thicken quickly to the adult appearance, in much the same way as *Rhynchozoon* sp.

1, but the situation rapidly becomes complicated by the fact that this species undergoes extensive frontal budding, making the colony surface even more irregular-looking.

The frontal wall of the newly budded autozoids is translucent and slightly roughened. There are less than 20 marginal pores about 15 μ in diameter, and occasional more central pores, presumably pseudopores, that sometimes become lost during secondary calcification. The aperture is tilted to an angle of about 45° to the long axis of the zoid, and can be seen only when the colony is tilted. The anter is variable in shape, hemicircular, transversely oval, or nearly round in outline. Its border is decorated with 30 or more minute beads or denticles. The poster is also variable; it is V-shaped or occasionally U-shaped and varies from a quarter to half the width of the anter. It is not beaded. Cardelles are less conspicuous than in the other Costa Rican species of Rhynchozoon. A peristome soon develops around the aperture, but it is only seldom complete distally. The peristome of very young zoids should not be confused with the secondary aperture formed from thickening frontal walls of adjacent zoids. The peristome is formed entirely from the calcium carbonate of the zoids to which the aperture belongs. (See the description of *Rhynchozoon* sp. 1.)

An apertural avicularium develops soon after formation of the peristome. The avicularium forms lateral and immediately proximal to the aperture. Its rostrum is directed laterally and frontally. It is usually tilted slightly basally (toward the aperture) relative to the aperture along its long axis. (This character does not hold in frontally budded zoids; see below.) A single (rarely double) calcareous spicule develops from the peristome on the side of the aperture opposite the avicularium. It is hook-shaped; the tip is directed slightly frontally and medially, forming a spiramenlike notch between the spicule and the avicularium. Occasionally, low tubercles of low spikes form the frontal walls of adjacent zoids, but these are always low, irregular, and poorly developed compared to those of the other Costa Rican species of Rhynchozoon.

As the frontal wall thickens, interareolar buttresses may form, giving an irregular ribbed (costae) appearance to many zoids; the costate appearance is always more marked than in *Rhynchozoon* sp. 1. In older primogenial zoids the frontal wall becomes roughened by irregular low knobs and bulges.

Occasional frontal avicularia, resembling apertural avicularia, develop from areolae. Their mandibles tend to be directed proximally.

Almost as soon as primogenial zoids are completely developed, the colony undergoes extensive frontal budding of adventitious layers. Adventitious zoids resemble primogenial zoids, with the following differences: (1) even the first adventitious zoids are irregular, oriented without regard to the center or edge of the colony; (2) the rhomboidal shape becomes lost, and the zoids tend toward a hexagonal shape, if any; (3) peristomes are most likely to be complete distally; and (4) apertural avicularia are more prone to be tilted outward, that is, they tend more often to be tilted frontally along their long axis relative to the aperture. This makes apertural avicularia easier to see in adventitious zoids than in primogenial zoids.

We have only a few ovicells and all are on adventitious zoids. They are like ovicells of *Rhynchozoon* sp. 1, but the ovicell plate (Figure 8*B*) tends to be tilted more frontally, and is slightly narrower than those of *Rhynchozoon* sp. 1 (140 μ , compared to 170 μ).

Measurements: Length of primogenial zoids, 350 μ (250–410 μ); width, 250 μ (210–330 μ). Aperture length of primogenial and adventitious zoids, 95 μ (80–110 μ); width, 100 μ . Length of apertural avicularia (rostrum plus postmandibular field measured on primogenial and adventitious zoids), 100 μ (80–150 μ); length of frontal avicularia on primogenial and adventitious autozoids, 140 μ (110–170 μ). Width of ovicell plate (on adventitious zoids only), 140 μ (110–150 μ); ovicell length, 200 μ (160–220 μ); width, 200 μ . The distance between secondary apertures was not measured because adventitious layers soon obscure older primogenial

layers and because the measurement is useless in adventitious layers.

DISCUSSION OF SOME AMERICAN SPECIES OF RHYNCHOZOON

Rhynchozoon is one of many difficult genera that have drawn complaints from a number of authors. As Osburn (1952:454) put it, they "try men's souls," mostly because of their exasperating variability. The literature of the genus suffers from inadequate description, unconscionable lumping, and inadequate illustration.

The three Costa Rican species are distinguished as follows: species 3 (Pacific) buds frontally, even in relatively young colonies; species 2 and 3 (Caribbean) apparently never do so; species 3 undergoes extensive thickening of the frontal wall and possesses numerous avicularia; species 2 does not thicken its frontal wall appreciably, and avicularia are uncommon. Other differences are provided in the species descriptions and illustrations.

The Pacific species (species 3) is probably identical to Rhynchozoon (Lepralia) rostratum (Busk 1856:4). We have examined many specimens from the northern Gulf of California and can find no consistent differences between these specimens and Rhynchozoon sp. 3. The type locality for R. rostratum is Mazatlan, near the mouth of the Gulf, so identity is probable. Rhynchozoon rostratum auctt., from southern California, differs appreciably from more southern material. Our specimens collected there undergo extensive frontal budding, as in R. sp. 3, but the apertures are much larger (about 150 µ compared with 90 μ), avicularia are larger, and the frontal is more ribbed (costate). There are other differences as well (Banta, unpublished). Soule and Soule (1964:33) synonymized Rhynchozoon (Schizoporella) tumulosum (Hincks 1882:252), a Canadian species, with R. rostratum, presumably based largely on Californian forms and specimens from the Pacific coast to Baja California. This conclusion seems valid; they are at least closely related. The problem is that Californian specimens are probably not conspecific with *R. rostratum* (Busk). Perhaps the northern form belongs to *R. tumulosum*, whereas the more southern form is *R. rostratum*.

Rhynchozoon rostratum appears to have been frequently confused with Rhynchozoon (Cellepora) verruculata (Smitt 1873:50), and probably with other species of the genus. Hastings (1930: 728) pointed out a number of differences between R. rostratum and R. verruculata. She states that her specimens of R. rostratum from Panama and the Galapagos have a thick epitheca "faintly greenish in color," the same color as Busk's type. Smitt (1873:50) refers to a vitreous blue color. Presumably all specimens concerned were preserved or dry when examined. Our specimens of Rhynchozoon sp. 3 are colorless to light yellow. Soule and Soule (1964:34) indicate that "color appears to vary considerably, depending on local conditions, in many species." The taxonomic value of color in the group is unknown. Smitt's (1873: Pl. 8, Fig. 93) figure of R. verruculatum lacks a "triangular area on the ovicell," presumably referring to what we call the ovicell plate. Canu and Bassler (1928c:88) referred to the type and state that the area is missing in Smitt's species. Thus, R. verruculatum auctt. of the American Atlantic and Caribbean may be another species. Rhynchozoon verruculatum auctt. of the Mediterranean certainly is (Hastings 1930:728). The situation is further complicated by Osburn's (1952:456) synonymizing of R. verruculatum with R. rostratum. This view, followed by Maturo (1957:57), Shier (1964: 640), and others, seems unlikely.

The American species of *Rhynchozoon* are clearly in need of much more study.

Family Lageniporidae Jullien, 1882: 526

Phylactellidae Canu & Bassler, 1917
 Perigastrellidae Vigneaux, 1949
 Phylactelliporidae Bassler, 1953:217
 Teuchoporidae Harmer, 1957:896

The family and its genotype are discussed by Harmer (1957:821, 899). In our opinion,

none of the families cited above as synonyms are based on genera sufficiently different from *Lagenipora* to justify separation. The type species of *Lagenipora*, usually given as *Lagenipora socialis* Hincks, 1877a:214, is actually *Celleporella lepralioides* Norman, 1868:222 (Harmer 1957:822).

Genus *Teuchopora* Neviani, 1895*b*:66 = *Coleopora* nom. nud. Canu & LeCointre, 1925:10

Coleopora Canu & Bassler, 1927:6

Type species by original designation: Alecto castrocarensis Manzoni, 1875:40.

Teuchopora, undescribed sp.

Figure 6*C*. ?*Holoporella* (?) *tubulosa* Canu & Bassler, 1928*b*:147, Pl. 24, Figs. 1–6, text Fig. 33a.

Three colony fragments were found encrusting coral rubble from Portete (Atlantic). The colonies are unilaminar, uniserial to biserial, and grow into nooks in the rock, making them difficult to observe. The frontal wall is a thick, minutely granular layer when first laid down. The only perforations at this stage are about 30 marginal pores approximately 30 μ in diameter. In young zoids, these pores can be seen to be multiporous pore plates, so marginal pores are almost certainly true (septular) areolae. The aperture soon becomes elongated into a tubular peristome or apertural collar of varying length (up to 0.6 mm). These long peristomes sometimes give the colony the appearance of a small cyclostome colony. Advancing secondary calcification almost immediately changes the appearance of the young frontal wall.

The secondary calcareous layer is shiny and translucent, contrasting distinctly with the granular primary layer. It first appears at areolae, progressing medially. The areolae soon become elongated frontally, because the outer ends are larger (50 μ) than the pore plate at the inner end. Secondary pores appear near the center of the frontal wall as it thickens. Some of these can be seen to be

mere blind pits, while others seem to go down to the primary layer. Many zoids lack central pores completely. In either case, fully developed frontal walls are garnished with about 25 hemispherical knobs up to $100~\mu$ in diameter, evenly distributed over the frontal wall. The primary layer probably corresponds to the "olocyst" of Canu and Bassler (1920:47), and the secondary layer is probably a "pleurocyst" or "tremocyst," but these terms are avoided for reasons given elsewhere (Banta 1970:45).

The primary aperture, the true aperture covered by the operculum, is difficult to see because of the elongated peristomes, but it is oval, longer than wide, and without cardelles.

Ovicells open through a hemispherical opening into the base of the peristome. The peristome continues growing frontally above the ovicell, maintaining its round opening. The ovicell is prominent, globular, and slightly wider than long. It is provided with numerous, evenly distributed hemispherical tubercles of varying size $(20-60~\mu)$. Between tubercles are apparent pores 10 to 30 μ in diameter, but they may be only blind pits, like median pores in the frontal wall.

There are no spines, avicularia, or traces of any of these.

Measurements: Autozoid length, 830 μ (700–1280 μ); width, 640 μ (520–880 μ). Aperture length, 220 μ ; width, 190 μ . Ovicell length, 330 μ ; width, 520 μ .

Teuchopora sp. most closely resembles Coleopora granulosa Canu & Bassler (1928b: 82) from the Pliocene of Panama, but differs from it in the following respects: (1) Teuchopora sp. is smaller than C. granulosa. Canu and Bassler's measurements are zoid length. 1150 to 1250 μ ; width, 750 to 850 μ ; aperture length, 200 μ ; width, 250 μ . (2) The aperture of C. granulosa is broader than long, the opposite of Teuchopora sp. (3) C. granulosa is multiserial. (4) There are more perforations on the frontal wall of C. granulosa than in Teuchopora sp. (Canu and Bassler 1928b: Pl. 33, Fig. 9). Canu and Bassler (1928b:82) state that C. granulosa "approaches very closely Coleopora minutipora Canu & Bassler from the Philippines," but as Marcus (1949:

19) points out, this name is an apparent nomen nudum. In the same paper, Marcus discusses other members of the genus *Coleopora* (= *Teuchopora*), none of which are likely to be confused with *Teuchopora* sp.

Despite the distinctiveness of our specimens, we hesitate to describe the species as new because of the small number of our specimens and because the present confusion of genera among these forms makes it easy to miss species descriptions made under other generic names.

Family Smittinidae Levinsen, 1909:335 Smittidae Jullien, 1888b:52 Mucronellidae Levinsen, 1902 Phoceanidae Vigneaux, 1949 Rhamphostomellidae Kluge, 1962:534

Jullien's Smittidae was based on *Smittia* Hincks, 1879:160, preoccupied by *Smittia* Holmgren, 1874 (Diptera). Levinsen's Mucronellidae, based on *Mucronella* Hincks, 1877b, is invalid if one agrees, as we do, with the view of Ryland (1963:19) that *Mucronella* is a junior synonym of *Escharella* Gray, 1848:125 (non *Escharella* d'Orbigny, 1851': 218, a junior homonym).

Genus Parasmittina Osburn, 1952:411

Type species by original designation: Lepralia jeffreysi Norman, 1876:208. The genus has been recently monographed by Menon (1972) and Soule and Soule (1973).

Parasmittina crosslandi (Hastings) Pl. IV, Figs. 24–25.

Lepralia trispinosa Johnston (Busk 1855:3); Gulf of California.

Smittina crosslandi Hastings, 1930:726, Pl. 13, Figs. 75–79; Pl. 17, Fig. 122; Galapagos, Panama.

Parasmittina crosslandi (Hastings) (Osburn 1952:418, Pl. 48, Fig. 12) (part); eastern Pacific.

Parasmittina crosslandi (Hastings) [J. Soule 1961:37 (part)]; Gulf of California.

Parasmittina crosslandi (Hastings) (Soule and Soule 1964:27); western Baja California.

Parasmittina crosslandi (Hastings) (Soule and Soule 1973:382, Figs. 2E, F); eastern Pacific.

Parasmittina crosslandi (Hastings) (Powell 1971:722); Pacific, Panama.

Not *P. crosslandi* (Hastings) (Canu and Bassler, 1930a: 37, Pl. 4, Figs. 1–5). Galapagos. Not *P. crosslandi* auctt. from southern California.

Parasmittina crosslandi (Hastings) (Powell 1971:722); Panama.

Seven colony fragments were found encrusting unknown substrates from Playa el Coco (Pacific). The colonies are multi-laminar; the layer above the first, or primogenial layer, is produced by frontal budding of adventitious zoids or by overgrowth of older zoids by secondary primogenial layers produced by frontally budded pseudoancestrulae.

Autozoids are arranged in quincunx in primogenial layers, but the arrangement may be distorted in spots, probably due to irregularities on substrate or other microenvironmental effects. Zoids vary in shape from rectangular to hexagonal; the latter are more common. The frontal wall is thick, smooth or slightly granular, and somewhat transparent when first laid down. The granulations become fused into minute tubercles a few microns in diameter in older zoids. Each zoid is nearly surrounded by about 25 (15– 30) presumed areolae approximately 25 μ in diameter. Areolae are absent just distal to the aperture, where they are replaced with 3 (2-5) hollow apertural spines, which become rapidly lost. In older zoids, the spines are represented only by spine bases or are buried beneath ovicells. Each areola is occluded basally by a tiny pore plate perforated by several communication pores.

A peristome begins to develop almost as soon as the frontal wall is fully calcified. It is a thick semicircular area of calcium carbonate about $100~\mu~(50-150~\mu)$ high on the lateral and proximal sides of the aperture; it is absent distally where spines are located. In young zoids, there is a notch about $30~\mu$ wide in the proximal part of the peristome; the notch resembles the spout of a cream pitcher. In some older zoids, the notch (a

spiramen) becomes lost and the proximal peristome may rise up into an umbolike spike.

The aperture is nearly round. A prominent pair of proximally directed cardelles is present just proximal to the middle of the lateral border of the aperture. There is a median proximal lyrule about 35 μ wide; it is almost square in outline, but is usually widest at its distal edge.

Adventitious avicularia vary greatly in size $(59-300 \mu)$, but all have pointed or (rarely) blunt mandibles and are oriented so that the proximal end is located lateral to the proximal part of the aperture. Rostra are always directed proximally or proximolaterally. A complete hinge bar is invariably present. The avicularia do not originate from areolae (Banta 1973:214; D. Soule 1973:498), but the former reference was based on a misidentified specimen of another species. There is usually only one avicularium per zoid, but very rarely there may be two small ones.

Measurements: Primogenial zoids are smaller than adventitious; the former measure 330 μ (270–390 μ) long, 230 μ (160–280 μ) wide; the latter are 380 μ (280–500 μ) long by 300 μ (200–400 μ) wide. Aperture length, 100 μ (95–100 μ); width, 90 μ (85–330 μ) long, larger on adventitious zoids. Ovicells are 180 μ (140–200 μ) long by 190 μ (130–220 μ) wide.

Parasmittina crosslandi apparently is an exclusively Pacific tropical to subtropical form, common from the Gulf of California to Colombia (Osburn 1952:418; Soule and Soule 1973:383).

Genus Rhamphostomella Lorenz, 1886:93

Type species, designated by Norman (1903: 125): Eschara scabra Fabricius, 1780. The type usually is given as Rhamphostomella costata Hincks, 1889:426, designated by Canu and Bassler (1917:52), apparently unaware of Norman's previous designation. Authors have followed the opinion of Harmer (1957:1102), who preferred Canu and Bassler's designation because R. scabra was

"insufficiently described by Fabricius." There seems to be no question, however, that it is recognizable (Kluge 1962:536), so we follow the opinion of Kluge in considering *R. scabra* the type species.

?Rhamphostomella sp.

Figure 9E, F.

Two fragments of a single colony were found encrusting coral rubble from Portete (Atlantic). The dry colony is coarse, but regular in appearance and pale tan in color. Autozoids are unusually large, over 1 mm in length, and undergo frontal budding, which disrupts the regular quincunx arrangement seen in primogenial layers. Primogenial zoids are roughly rectangular in outline, separated by thin vertical walls perforated by about 25 pore plates perforated by a single communication pore approximately 20 μ in diameter. Pore plates occur anywhere on the wall, but are concentrated along the basal wall, where they may be separated by inconspicuous buttresses. Even in young autozoids, vertical walls are extended above the frontal wall as an interzoidal ridge that eventually forms the vertical walls of an adventitious zoid when the primogenial zoid buds frontally.

The slightly translucent frontal wall is moderately inflated, minutely granular, and perforated by 100 to 150 pores about 25 μ in diameter. The region immediately behind the aperture is left imperforate, perhaps owing to the attachment of the ascus roof to the frontal wall. Because frontal budding occurs, some or all the frontal pores probably are areolae. The primary aperture, located at the extreme distal end of the zoid, is about as long and is inconspicuously divided into a distal, almost hemispherical anter and a broadly V-shaped poster. The anter, which occupies about two-thirds of the apertural length, is widest at its proximal end. The operculum, the same shape as the aperture, possesses a thin distal marginal sclerite and heavy paired sclerites at the lateral margins of the porta. The vanna lacks obvious decoration.

The aperture soon becomes surrounded by

a thick, nodular peristome. The distal third of the peristome apparently is formed from the skeleton of the next distal zoid and sometimes is composed of vertical rods of carbonate recalling the spinous peristomes of cribrimorphs. The proximal two-thirds of the peristome is formed by a high calcareous ridge and a conspicuous apertural avicularium separated by a deep, proximal spiramen (notch) placed just to one side of the midline. The apertural avicularium, which develops from 1 to 3 marginal pores, is oval in outline and possesses a strong hinge bar at the base of the broad mandible. The tip of the rostrum is tilted upward and directed distolaterally. A narrow, finely beaded cryptocyst sometimes is present in both the rostrum and post-mandibular field. The avicularium chamber is perforated by 5 to 10 pores similar to those of the frontal. The peristome opposite the avicularium on the other side of the spiramen usually is elaborated into a sharp, hooklike spike directed toward the avicularium.

Three of the approximately 200 zoids in our specimens possess remarkably distinct giant apertural avicularia with curved, blunt mandibles (Figure 9F). Giant avicularia are about three times as long as ordinary avicularia and slightly broader. The body of the mandible is directed laterally, but the distal third curves proximally. They develop in the same way as ordinary avicularia.

Ovicells are lacking in our specimens, but two zoids show depressions in the frontal walls of their distal neighbors; presumably they are in preparation for development of hyperstomial ovicells.

Adventitious zoids are similar to primogenial zoids except that their orientation is more irregular. Our colony is small but possesses at least two adventitious layers in central parts.

Measurements: Autozoid length, 1000 μ (770–1370 μ); width, 700 μ (400–1100 μ). Length of primary aperture, 220 μ (210–250 μ); width, 220 μ . Length of ordinary avicularia, 160 μ (110–250 μ); width, 110 μ (80–160 μ). Length of giant avicularia (N=3), 550 μ (550–630 μ); width, 140 μ (80–160 μ).

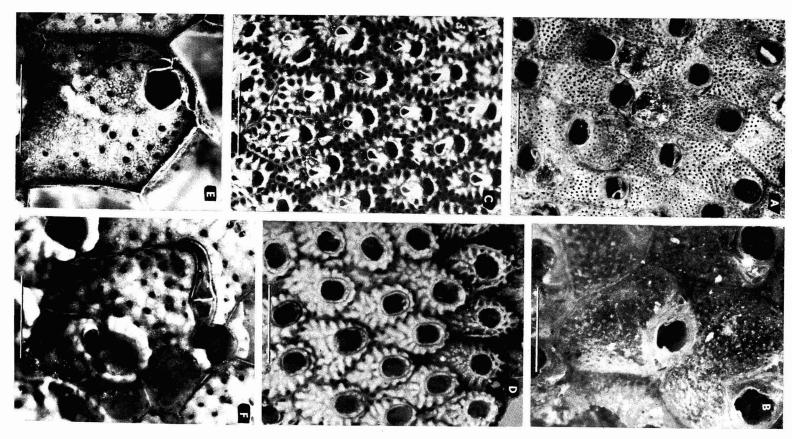


FIGURE 9. Frontal views of KOCl-treated stained colony fragments coated with NH₄Cl. Scales, 500 μ. A, Hippopodina feegeensis (Busk); Playa el Coco. Ovicell below and right of center. B, The same, from Portete. C, Reptadonella violacea (Johnston); Playa el Coco. D, Cyclocolposa ?parva (Marcus); Playa el Coco. E, Rhamphostomella sp.; Portete. Developing zoid. F, The same. Avicularia at upper left and below and right of center.

Family Hippoporinidae Bassler, 1935 = Hippozeugosellidae Vigneaux, 1949

Genus Hippoporella Canu, 1917b:36 = Hippoporella Canu & Bassler, 1920:377

Genotype designated by Canu (1917b:36): Lepralia hippopus Smitt, 1868:99. Canu and Bassler (1920:377) later designated Hippoporella perforata Canu & Bassler, 1920:377. Harmer (1957:1096) accepts the latter name on the basis of ambiguity in Canu's original designation, but Canu's intent seems clear. The family is frequently cited as Hippoporella Canu & Bassler, 1920:377, because these authors said it was a new genus, apparently forgetting Canu's earlier erection of the same group.

Hippoporella costulata Canu & Bassler, 1923

Figure 6G.

Hippoporella costulata Canu & Bassler, 1923: 133, Pl. 45, Fig. 14; Pleistocene, Canal Zone, Panama.

Two multilaminar colony fragments were found encrusting unknown substrates at Playa el Coco (Pacific). We have only adventitious (frontally budded) layers; therefore, zoids are directed at random. The colony surface appears chaotic and nodular. Zoids are typically elongate hexagonal in shape, covered by a thick, translucent frontal wall perforated marginally by about 15 or 20 pores, probably areolae, approximately 20 μ in diameter. The aperture is shaped roughly like a thumb nail; the distal border is rounded, the sides gently diverge proximally, the proximal margin is slightly convex. There is a pair of short cardelles about a third of the way from the proximal to distal edge of the aperture. A marginal sclerite surrounds the operculum; it is thickest just distal to the cardelles. The aperture may be surrounded by 0 to 4 knobs or (rarely) spikes of varying length. Avicularia are usually present, developed from marginal pores. The mandible is triangular or short-pointed. Ovicells are hemispherical with a V-shaped notch at the proximal side. The notch is partially filled

with a cuticular membrane. The ovicell is smooth, imperforate and partially embedded in the next distal zoid. There are no oral spines, even on young (adventitious) zoids.

Measurements: Length of autozoids (adventitious), 440 μ (280–500 μ); width, 300 μ (160–360 μ). Length of aperture, 100 μ (80–100 μ); greatest width, 100 μ (90–110 μ). Length of avicularia, 85 μ (55–100 μ). Ovicell length, 280 μ ; width, 200 μ .

Hippoporella costulata was described from the Pleistocene of Mount Hope, Canal Zone. Our specimens differ from Canu and Bassler's description in having slightly larger zoids and smaller apertures, and in lacking a costate (ridged) frontal wall. Canu and Bassler gave zoid length as 450 to 500 μ , width as 350 to 450 μ , and aperture length and width equal at 120 μ .

Hippoporella costata resembles the following species: Hippoporidra spiculifera (Canu & Bassler, 1930a:43); Aimulosia uvulifera (Osburn, 1914:210); Hippoporella gorgonensis Hastings, 1930:723; Hippoporella rimata (Osburn, 1952:351); and Trematooecia cheethami Weisbord, 1967:106. Hippoporella costata lacks oral spines even in young zoids; this distinguishes it from all but H. spiculifera and possibly T. cheethami, Hippoporella spiculifera lacks spines, but usually has erect, massive colonies and avicularia with long, thin mandibles (Canu and Bassler 1930:43). Trematooecia cheethami is poorly described. but may be synonomous with *H. costata*. The placement of these six described morphotypes in five different genera illustrates the unsatisfactory present arrangement and understanding of the genera.

As far as is known, the distribution is limited to the Pleistocene of the Canal Zone (Panama) and the Pacific side of Costa Rica.

Family Hippopodinidae Levinsen, 1909:353

Genus Hippopodina Levinsen, 1909:353 = Cosciniopsis (part) Canu & Bassler, 1929b:276

Type species by original designation: Lepralia feegeensis Busk, 1884:144.

Hippopodina feegeensis (Busk, 1884)

Figure 9A, B.

Lepralia feegeensis Busk, 1884:144, Pl. 22, Figs. 9–96; China.

H. feegeensis (Busk) (Levinsen 1909:353, Pl. 24, Figs. 3a-f); Singapore.

Cosciniopsis fallax Canu & Bassler, 1929b: 276; Australia.

H. feegeensis (Busk) (Hastings 1930:729); Panama

H. feegeensis (Busk) (Osburn 1940:412, Figs. 54, 55); Puerto Rico.

H. feegeensis (Busk) (D. Soule and J. Soule 1968:212, Fig. 3); Baja California.

H. feegeensis (Busk) (Long and Rucker 1969:62, Fig. 1); Japan.

H. feegeensis (Busk) (Powell 1971:771); Panama.

H. feegeensis (Busk) (Eitan 1972:27, Fig. 1); Mediterranean, Israel.

The Atlantic and Pacific material in our collections differ in morphology and will be described separately.

Pacific Material (Playa el Coco). Figure 9A

Fragments of several colonies were found encrusting unknown substrates. Zoids are arranged in quincunx and are lightly calcified and hyaline. The frontal wall is evenly perforated by about 80 pores 30 μ in diameter. There is a pair of prominent hinge teeth (cardelles); the proximal border of the poster varies from convex proximally to nearly transverse. Ovicells are round, flattened, and immersed in a concavity of the frontal wall of the next distal zoid. The ovicell is usually considered hyperstomial, but this term is poorly defined (Brown 1952: 36). Our impression from examining dry material is that the hypostegal coelom of the ovicell is broadly confluent with that of the next distal zoid. If so, it seems probable that some of the marginal zoecial pores are areolae (Banta 1973) and that nutrients for cells depositing the calcium carbonate of the ovicell are supplied in whole or in part by the zoid distal to the ovicelled zoid. Similar situations are known elsewhere (Woollacott and Zimmer 1972). Apertures of ovicelled

zoids resemble those of ordinary autozoids, but are very slightly wider. One or two short-pointed avicularia are located distal and lateral to the aperture of a few zoids. They are straight and are directed medially and distally. There are no spines. Reparative budding occurs occasionally, but there is no sign of frontal budding.

Measurements: Length of zoid, 830 μ (720–1100 μ); width of zoid, 390 μ (360–550 μ); aperture length ordinary autozoid, 180 μ ; width, 175 μ ; aperture length ovicelled zoids, 180 μ ; width, 190 μ . Ovicell length, 580 μ (500–650 μ); width, 500 μ (500–650 μ).

Atlantic Material (Portete). Figure 9B

Two colony fragments were found encrusting coral rubble. Zoids differ from those of Pacific material in the following respects: (1) autozoids are larger and relatively broader (compare measurements); (2) pores are more numerous (about 200, compared to 80 in Pacific specimens) and smaller (20 μ diameter compared to 30 μ); (3) the poster (sinus) of the aperture is relatively larger; (4) avicularia are much more common, occurring on all zoids, usually bilaterally; and (5) avicularia are much longer, setiform instead of shortpointed, and oriented medially and proximally instead of distally. Each zoid possesses two avicularia, one slightly larger than the other.

Measurements: Length of zoids, 1100 μ (970–1380 μ); width, 830 μ (700–970 μ); aperture length, 250 μ ; width, 250 μ . No ovicells present. Larger avicularium, 410 μ ; smaller, 320 μ .

The Atlantic and Pacific specimens differ greatly, especially in size and avicularian morphology, but *H. feegeensis* is extemely variable in these features. It may be that two or more species are involved, but a study of many specimens from all over the world seems necessary before a decision can be reached. *Hippopodina feegeensis* seems related to *Cosciniopsis ambita* Hayward, 1974: 390 (*Cosciniopsis* sp. of Harmelin 1968: 1206) from the Mediterranean. This species differs principally from our Atlantic material in possessing one instead of two avicularia, and

lacking frontal pores (pseudopores) and pores on the ovicells. *Cosciniopsis ambita* certainly belongs as well or better in *Hippopodina* than in *Cosciniopsis* Canu & Bassler, 1927:6. The type of that genus, *C. coelatus* Canu & Bassler, 1927:9 lacks avicularia and possesses a perforate frontal.

Hippopodina feegeensis has been reported widely in warmer waters. The species was originally described from the Philippines, not the Fiji Islands (Harmer 1957:975). Powell (1969:161) discussed and mapped the distribution of the animal in recent seas and as fossils. The species seems to be circumtropical and restricted within 21° C isotherms. The animal may be a fouling pest (D. Soule and J. Soule 1968:212, Powell 1971:771).

Family Adeonidae Jullien & Calvet, 1903:53 Adeoneae Busk, 1884:177

The systematics of the family are discussed well by Cook (1973:246).

Genus Reptadonella Busk, 1884:178 Multiporina Gabb & Horn, 1862 (preoccupied, Multiporina d'Orbigny, 1851) Reptoporellina (part) d'Orbigny, 1851:476 Heckelia Neviani, 1895a:82, 106

Type species by monotypy: Lepralia violacea Johnston, 1847:325. Bassler (1935: 186) designated the type of Reptoporellina as Cellepora heckeli Reuss, 1847:85, which is regarded by most authors as a synonym of L. violacea. Since the designation was made subsequent to the establishment of Reptadonella, the later genus has precedence (Harmer 1957:814).

Reptadonella violacea (Johnston, 1847)

Figure 9C.

Lepralia violacea Johnston, 1847:325; England.

R. violacea (Johnston) (Busk 1884:180). Adonea heckeli Canu & Bassler, 1923:158,

Pl. 24, Figs. 1, 2; Miocene, Jamaica, southern United States.

?A. violacea (Johnston) (Hastings 1930:728).

?Not A. violacea (Johnston) (Osburn 1952: 441, Pl. 58, Figs. 6, 7); Eastern Pacific.

?R. violacea (Johnston) (Soule 1963:233); Cocos Island, Costa Rica.

R. violacea (Johnston) (Powell 1971:773);

Our specimens encrusted unknown substrates from Playa el Coco (Pacific). Zoids are arranged in quincunx. The thick frontal wall is opaque, granular, and perforated by about 24 marginal pores approximately 25 μ in diameter and by a central oval pore about 50 μ wide and 10 to 20 μ long. The central pore is considered to represent an ascopore. The aperture is wider than long, hemicircular to oval without observed cardelles.

Apertures of brooding zoids are said to be larger than ordinary autozoids, but aperture sizes in our specimens intergrade evenly with each other. A median suboral avicularium without observed connection with marginal pores is always present and is directed distally. The ascopore is immediately proximal to the avicularium, not separated from it. There is a low peristome that does not reach distally to the level of the distal transverse wall. There are no spines or external ovicells.

The absence of observed connections between marginal pores and avicularia, and the absence of external pores on the avicularium, suggests that there may be an areolar pore between the avicularium and autozoid (Banta 1973). If so, the ascus must not immediately underlie the frontal wall.

Measurements: Zoid length, 440 μ (360–520 μ); width, 300 μ (220–300 μ). Avicularium length, 120 μ (110–140 μ); width, 70 μ (59–95 μ). Aperture length, 85 μ (55–90 μ); width, 110 μ (100–120 μ).

Cheetham and Sandberg (1964:1039) have discussed the complex taxonomy of the many species of *Reptodonella* frequently lumped under *R. violacea*. The species in tropical America most likely to be confused with it is *R. hastingsae*. Cheetham & Sandberg (1964:1039) (Figure 10). In the latter species, the ascopore is "well removed" from the avicularium, and the peristome is "somewhat elongate . . . reaching the distal margin of the zoecium." Avicularia are "directed obliquely distally." Because of apparent



FIGURE 10. Reptadonella hastingsae. Cheetham & Sandberg. After Cheetham and Sandberg (1964:1042).

lumping, the distribution of the species of *Reptadonella* is difficult to sort out. The type locality of *R. violacea* is in Great Britain, but it is usually regarded primarily as a circumglobal warm-water form (Powell 1971: 773).

Family Cycloporidae Hincks, 1884:129

Genus *Cyclocolposa* Canu & Bassler, 1923:135

= Cyclocolposa Canu & Bassler, 1923:123, nom. nud.

Type species by original designation: Cyclocolposa perforata Canu & Bassler, 1923: 135.

Cyclocolposa ?parva (Marcus, 1938)

Figure 9D.

Hippodiplosia otto-mülleriana (Moll) var. parva Marcus, 1938:39, Pl. 9, Figs. 22A, C; Pl. 10, Fig. 22B; Brazil.

Hippodiplosiatto-mulleriana [sic] var. parva Marcus (Marcus 1941:24, Fig. 20); Brazil. ?Schizoporella costulata Canu & Bassler, 1929b:317, Pl. 36, Figs. 10, 11); Philippines.

Five unilaminar colonies were found encrusting basaltic rock from Playa el Coco (Pacific). Autozoids are arranged in irregular quincunx and resemble *Cryptosula pallasiana*. The single-layered frontal wall is at first hyaline, but later becomes opaque. The margin of each zoid is perforated by about 15 to 20 marginal pores approximately $10~\mu$ in diameter; they are presumably areolae. As the wall thickens, buttresses (costae) appear between the pores, giving the frontal wall a

costate appearance. The central part of the wall may be provided with large irregular hemispherical tubercles about $100~\mu$ in diameter. There are no pseudopores. The walls between zoids are provided with about 20 dietellae, which are difficult to see except in developing zoids. Areolae appear to open into dietellae instead of the perigastric coelom.

The aperture is oval and longer than it is wide. There is a pair of cardelles at about the center of the aperture.

There are no spines, avicularia, or ovicells. No cuticular parts remain in our material.

Measurements: Zoid length, 410 μ (330–550 μ); width, 300 μ (190–410 μ); aperture length, 150 μ (110–170 μ); width, 120 μ (110–130 μ).

Our specimens closely resemble Hippodiplosia otto-mülleriana parva Marcus, 1938: 39 from Brazil, Marcus does not mention or figure marginal pores, but they are inconspicuous in our material. Marcus states that secondary calcification takes place, so areolae are probably present. According to Marcus (1938:40), there are about 12 multiporous pore plates, not dietellae as in our specimens. The dietellae, however, are inconspicuous because they become buried in the wall. which looks like an ordinary wall without dietellae until broken or unless very young zoid buds are examined. The rosette plates figured by Marcus (Pl. 10, Fig. 22B, r) are almost certainly dietellae.

This species obviously does not belong in Hippodiplosia Canu, 1916:328. This genus possesses an evenly perforated frontal wall. suboral avicularia, and hyperstomial ovicells (Lagaaij 1952:80). Hippodiplosia otto-mülleriana (Moll 1803:60) has oral spines, median avicularia, globular ovicells, and an evenly perforated frontal wall. Clearly, Marcus' form deserves specific rank. The type of species of Cyclocolposa, C. perforata, resembles C. parva in all the characters usually used at the generic level, except that C. perforata possesses ovicells, whereas none are known in C. parva. Cyclocolposa perforata lacks cardelles, has a double row of areolae (variable in their figures), and has nearly round apertures (Canu and Bassler 1923:135). Cyclocolposa spinifera Canu & Bassler, 1923:136 resembles C. parva, but the former has apertual spines, ovicells, and an occasional median suboral avicularium. Schizoporella costulata Canu & Bassler, 1929b:317, which probably belongs in Cyclocolposa, lacks cardelles and may lack dietellae, although this is doubtful. The species is known only from Brazil and Costa Rica.

Class Stenolaemata Borg, 1926:490

Subclass Cyclostomata Busk, 1852a:346 = Stenostomata Marcus, 1938:116

Marcus (1938:116) has pointed out that the term Cyclostomata is almost homonymous with class Cyclostoma Curvier (Vertebrata). A century of experience, however, has shown that confusion has been minimal, so there seems to be no reason to change the familiar name Cyclostomata. Marcus intended his Stenostomata to replace Stenolaemata Borg, as well as Cyclostomata Busk. Marcus' concept of the Stenostomata seems to be closest to Cyclostomata Busk.

Superfamily Articulata Busk, 1859:92 Family Crisiidae Johnston, 1838:260

Genus Crisia Lamouroux, 1812:183

Type species: Sertularia eburnea Linnaeus, 1758.

Crisia sp. cf. elongata Milne-Edwards, 1838

Figure 11.

- C. elongata Milne-Edwards, 1838:203, Pl. 7, Fig. 2; Red Sea.
- C. eburnea form denticulata Smitt, 1872:4, Fig. 5; Florida.
- C. elongata Milne-Edwards [Harmer 1915: 96, Pl. 8, Figs. 1–8 (synonymy)]; East Indies.
- C. elongata Milne-Edwards (Osburn 1953: 684, Pl. 71, Fig. 9); Gulf of California.
- C. elongata Milne-Edwards (Maturo 1957: 31, Fig. 21); North Carolina.

A few colony fragments were found at Playa el Coco (Pacific). The colony size and

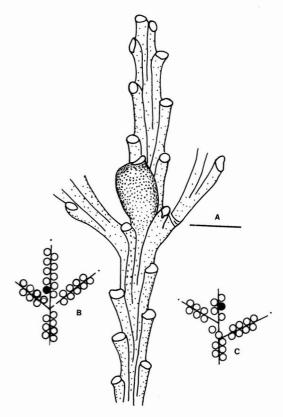


FIGURE 11. Crisia sp. cf. elongata Milne-Edwards, 1838. A, Frontal view of colony; scale, 300μ . B, diagram of the same colony; the darkened circle represents the ovicell; conventions after Ryland (1967). C, The same, another colony fragment.

substrate are not known. The dry fragments are yellowish white, erect and branching, provided with irregularly spaced yellow joints separating internodes of about 8 (7-13)hyaline autozoids. Fertile internodes (those possessing oecia) have 16 to 18 autozoids. Autozoids are mostly arranged biserially, but a very few triserial regions are present just before branches (Figure 11). Autozoids are mostly cylindrical, with gradually tapering proximal ends. Peristomes range from short to moderately long (250 μ), directed frontally. Each autozoid is uniformly perforated by about 100 tiny pores, presumably pseudopores, approximately 15 μ in diameter. There appears to be no basis rami; proximal ends of autozoids abut directly

against one another. Occasional stolons about 50 μ originate from the basal side of branches; they are perforated in the same manner as autozoids.

Oecia are developed near bases of branches; they are inflated, shaped like teardrops, and have the aperture located apically, basally, and adnate to the autozoid next distal to it on the oecium's side of the branch. There is no oecial peristome. The oecium is more densely perforate than autozoids.

Measurements: Length of autozoids, measured on the basal side as the distal-proximal distance between bases of peristomes, 320 μ (210–400 μ). Diameter of autozoid aperture, 80 μ . Length of oecium, measured from aperture to base of swollen portion of the zoid, 550 μ . Length and width of oecial aperture, 60 μ .

Our specimens appear to fall within the range of variation of *C. elongata* auctt., but the species or species complex is extraordinarily variable. It may be that more than one species is involved, but examination of much more material will be necessary to settle the matter.

If all the material recorded under this name and its subjective synonyms is conspecific, the species is circumtropical. As far as we are aware, the only previous record from the western Pacific is that of Osburn (1953:684) from the Gulf of California.

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