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The Interstitial Bryozoan Fauna from Capron Shoal, Florida

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ABSTRACT

A unique fauna of interstitial bryozoans has been found encrusting sand substrata on a high-energy shoal off the Atlantic coast of Florida. This fauna includes juveniles of two species of free-living cupuladriids, as well as nine new species (one new genus) apparently adapted to interstitial conditions and characterized by small size, simplified colony structure, and very early reproduction. Other species known from larger substrata were also found encrusting interstitial sand and shell grains at Capron Shoal. The "interstitial refuge" may be important in explaining the broad species distributions of encrusting bryozoans along mostly sandy continental shelves.

INTRODUCTION

Large expanses of the continental shelves of the world's oceans are composed of sandy sediments. These areas are known to support abundant faunas of rooted and free-living bryozoans (Maturo, 1968; Cook and Chimonides, 1978, 1981), but the unstable nature and extremely small size of sand substrata have been assumed to prevent colonization by encrusting bryozoans. Recently, however, during a study of the population biology of two species of free-living bryozoans, *Cupuladria doma* and *Discoporella umbellata depressa,* we discovered a number of encrusting species, utilizing sand and shell-gravel grains as substrata, in an interstitial habitat on a high-energy shoal located on the Atlantic coast of Florida (Håkansson and Winston, 1986).

In this paper we describe the 33 encrusting species found thus far, including nine new species and one new genus. We also discuss morphological variation occurring in interstitial colonies of species which are also found on larger substrata. The species found at Capron Shoal are characterized by the small sizes of zooids and colonies, precocious sexual reproduction, presence of spines and tubercles, and lack of avicularia. The study clearly demonstrates the importance of these character-

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istics and of morphological plasticity in the exploitation of stressed environments previously thought to be depauperate.

STUDY AREA

Capron Shoal is located on the Atlantic coast of Florida, off South Hutchinson Island, about 7 km south of Fort Pierce Inlet. It is one of a series of linear sand shoals distributed along this section of the Florida coast (Duane et al., 1972; Gallagher, 1977). The shoal trends roughly north-south and extends for approximately 6 km, with a minimum depth along its crest of 6 m, falling off to 17 m toward the coast and eventually to 40 m offshore.

Capron Shoal was probably built up as a consequence of the northeast storm-generated hydraulic regime (Gallagher, 1977), which causes southward trending storm currents. In summer months, wind and current conditions may be mild, but during the rest of the year they are often severe, with breaking waves marking the shoal crest. Sedimentological conditions change with each storm, and even in fine weather some sediment shifting occurs on the shoal crest.

The shoal sediment is a well-sorted, medium coarse biogenic sand, with a 15–30 percent quartz fraction. The biogenic portion is composed chiefly of mollusk shell fragments and barnacle plates. The finest sand is found at the shoal crest, with a tendency toward downslope coarsening; sediments of the trough lying between the shoal and the beach include shell-gravel and shell-hash in places (Gallagher, 1977). At some times of the year pockets of shell-gravel and shell fragments are common on the landward side of the shoal.

Salinities in the area are generally between 34 and 38‰, but surface salinities, at least, may be diluted by freshwater outflow through Fort Pierce Inlet. Water temperatures range between 15 and 30°C, with occasional rapid warming and cooling during summer months caused by upwelling (Smith, 1981).

The macrofauna on these shoals is less diverse than in the trough shell-hash substrata. At nearby offshore stations studied during ecological monitoring for the Florida Power and Light Company's St. Lucie Plant (Applied Biology, 1976), 431 macrofaunal invertebrate taxa were identified. Of these, 50 percent were annelids, 20 percent mollusks, and 5 percent echinoderms and minor phyla.

At Capron Shoal the most noticeable macroinvertebrates are the sand dollars *Encope michelini* and *Mellita quinquesperforata.* Also common are starfish (especially *Luidia clathrata*), sea pansies, crabs, mantis shrimp, brittle stars (*Ophiolepis elegans*), gastropods (e.g., *Oliva sayana, Murex fulvascens, Phalium granulatum*), bivalves (especially *Dinocardium robustum*), and the lancelet, *Branchiostoma virginiae.* Bottom-dwelling fishes include lizard fish, a flatfish, and a sea-robin.

Meiofauna have not been surveyed at Capron Shoal, but surveys at Pierce Shoal, 9 km further south, found nematodes, gastrotrichs, kinorhynchs, halocarids, and harpacticoid copepods to dominate (Applied Biology, 1976).

METHODS

At each census (April 1983, August 1983, January 1984, July–August 1984, November 1984, and January 1985) samples of sand (250–600 ml) were sorted under the dissecting microscope. The species described here were all found encrusting sand and shell grains in these samples.

Photographs of living specimens were taken in the laboratory and observations were made whenever possible on morphology of living colonies with regard to color, size, surface condition, presence of embryos, etc. Ctenostome and entoproct species were preserved in formalin. Some of the cheilostomes were fixed in formalin and preserved in 70 percent alcohol, but most cheilostome colonies were rinsed in fresh water and allowed to dry.

Measurements were made on one to five colonies of each species. Measurements (in mm) given following species descriptions include standard characters: Lz, Wz (zooid length and width); Lo, Wo (orifice length and width); Lop, Wop (opesia length and width); Lov, Wov (ovicell length and width); Lav, Wav (avicularium length and width); plus other measurements relevant to particular species. At least one specimen of each species was examined by SEM. Specimens were prepared for scanning by treatment with bleach to remove tissue and chitinous parts, ultrasonic cleaning, and sputter coating with gold. In a few cases air-dried specimens were coated without bleaching to illustrate characterisics of opercula or avicularian mandibles. Illustrated specimens and type material are deposited in the Department of Invertebrates, American Museum of Natural History, New York (AMNH).

Synonymies have been restricted to publications of major importance for recognition of the species and those that deal with western Atlantic and Caribbean records for the species. They include only papers having illustrations and descriptions, not checklists, with the exception of Maturo's (1968) checklist of species from the S.E. Atlantic continental shelf which was used in compiling species ranges. The classification used follows Brood (1972) for Stenolaemata and Gordon (1984) for Gymnolaemata.

In individual species descriptions the characteristics described in the "description" section refer to Capron Shoal specimens. Any morphological differences between our specimens and those from other areas are noted in the "discussion" section.

SPECIES LIST

ECTOPROCTA
- STENOLAEMATA
  - TUBULIPORATA
    - Family Lichenoporidae
      - *Disporella plumosa*, new species
- GYMNOLAEMATA
  - CTENOSTOMATA
  - Suborder Stolonifera
  - Superfamily Terebriporoidea
    - Family Spathiporidae
      - cf *Spathipora brevicauda*
  - Suborder Carnosa
  - Superfamily Alcyonidioidea
    - Family Alcyonidiidae
      - *Alcyonidium capronae*, new species
  - CHEILOSTOMATA
  - Suborder Anasca
  - Superfamily Membraniporoidea
    - Family Membraniporidae
      - *Membranipora triangularis*, new species
      - *Membranipora arborescens*
      - *Membranipora savartii*
    - Family Calloporidae
      - *Antropora leucocypha*
      - *Alderina smitti*
      - *Retevirgula caribbea*
      - *Vibracellina laxibasis*
    - Family Cupuladriidae
      - *Cupuladria doma*
      - *Discoporella umbellata* subspecies *depressa*
  - Superfamily Microporoidea
    - Family Microporidae
      - *Cymulopora uniserialis*, new genus, new species
    - Family Onychocellidae
      - *Floridina parvicella*
  - Superfamily Buguloidea
    - Family Beaniidae
      - *Beania klugei*
  - Suborder Ascophora
  - Superfamily Cribrilinoidea
    - Family Cribrilinidae
      - *Cribrilaria innominata*
      - *Cribrilaria parva*, new species
      - *Bellulopora bellula*
      - *Reginella repangulata*, new species
  - Superfamily Hippothoöidea
    - Family Hippothoidae
      - *Hippothoa balanophila*, new species
      - *Trypostega venusta*
  - Superfamily Schizoporelloidea
    - Family Schizoporellidae
      - *Schizoporella rugosa*
      - *Escharina pesanseris*
    - Family Smittinidae
      - *Parasmittina nitida*
      - *Parasmittina signata*
    - Family Microporellidae
      - *Microporella umbracula*
    - Family Phylactellidae
      - *Phylactella ais*, new species
  - Superfamily Celleporoidea
    - Family Celleporidae
      - *Trematooecia psammophila*, new species
    - Family Cleidochasmatidae
      - *Cleidochasma porcellanum*
      - *Cleidochasma angustum*, new species
      - *Aimulosia pusilla*
      - *Aimulosia uvulifera*
    - Family Sertellidae
      - *Drepanophora torquata*, new species

ENTOPROCTA
Family Pedicellinidae
Barentsia minuta, new species

PHYLUM ECTOPROCTA

CLASS STENOLAEMATA BORG, 1926

ORDER TUBULIPORATA JOHNSTON, 1847

FAMILY LICHENOPORIDAE SMITT, 1866

GENUS *DISPORELLA* GRAY, 1848

Disporella plumosa, new species
Figures 1, 2

DIAGNOSIS: Neotenous *Disporella* in which colonies become sexually mature while still fan shaped and never become circular in shape.

HOLOTYPE: AMNH 628.

PARATYPES: AMNH 629, 630, 631.

ETYMOLOGY: The species name, taken from the Latin *plumosa* = feathery, refers to the tufted appearance of the colonies.

DESCRIPTION: Colonies are white and encrusting, forming a spiny tuft or fan. A colony is initiated by a hemispherical ancestrula which develops into the first tubular encrusting zooid. Unlike other members of the genus, which rapidly become discoidal, colonies of *Disporella plumosa* become sexually mature while still fan shaped. At the edge of the colony is a peripheral growing zone or common bud; as the colony grows outward it expands, increasing the number of partitions to form new zooid tubes. The white upper surface of the zooid tubes is roughened by a series of spiny projections; the tubes end in pointed spines. The entire colony surface, including the common bud and brood chamber, is speckled by small calcareous pustules and pseudopores. The brood chamber is a flask-shaped bulge between two central zooids, opening in the flared lip of the ooeciostome.

MEASUREMENTS

	RANGE	MEAN	N
Lz	0.144–0.252	0.208	15
Wz	0.090–0.144	0.113	15
Lo	0.054–0.108	0.076	15
Wo	0.054–0.072	0.058	15

OCCURRENCE: The species was found at Capron Shoal in all seasons. Live specimens were found in August 1984.

CLASS GYMNOLAEMATA

SUBORDER STOLONIFERA EHLERS, 1876

SUPERFAMILY TEREBRIPOROIDEA D'ORBIGNY, 1847

FAMILY SPATHIPORIDAE POHOWSKY, 1978

GENUS *SPATHIPORA* FISCHER, 1866

Spathipora brevicauda Pohowsky, 1978
Figures 3, 4

Spathipora brevicauda Pohowsky, 1978, p. 104.

DESCRIPTION: Colonies make shallow borings in shells, most frequently with zooids opening on the concave side. Usually all that remains are traces of the narrow branched or unbranched stolon from which zooids have budded off laterally, leaving elongate seed-shaped autozooidal scars. Globular, pedunculate polymorphs, "sac zooids," may also occur.

MEASUREMENTS

	RANGE	MEAN	N
Lz	0.180–0.378	0.311	15
Wz	0.036–0.072	0.059	15
W stolon	0.018	0.018	5

OCCURRENCE: No living colonies of this species were found, but bored shells were collected at each census.

DISTRIBUTION: The species was described by Pohowsky (1978) from the Miocene of France.

SUBORDER CARNOSA GRAY, 1841

SUPERFAMILY ALCYONIDIOIDEA JOHNSTON, 1838

FAMILY ALCYONIDIIDAE JOHNSTON, 1838

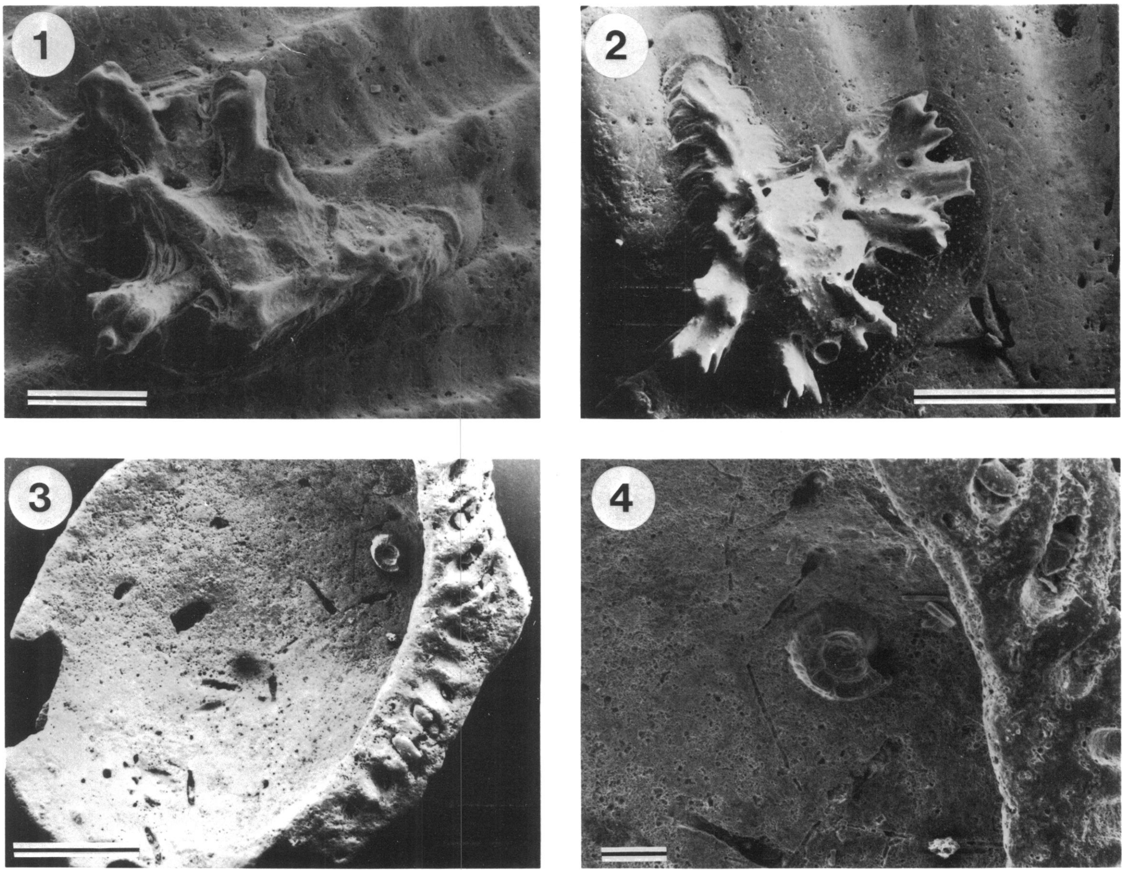
GENUS *ALCYONIDIUM* LAMOUROUX, 1813

Alcyonidium capronae, new species
Figures 5–7

DIAGNOSIS: *Alcyonidium* with baggy erect zooids, forming small clusters on colonies of *Cupuladria doma.* Polypides with 11–15 tentacles.

HOLOTYPE: AMNH 633.

PARATYPES: AMNH 634, 635.



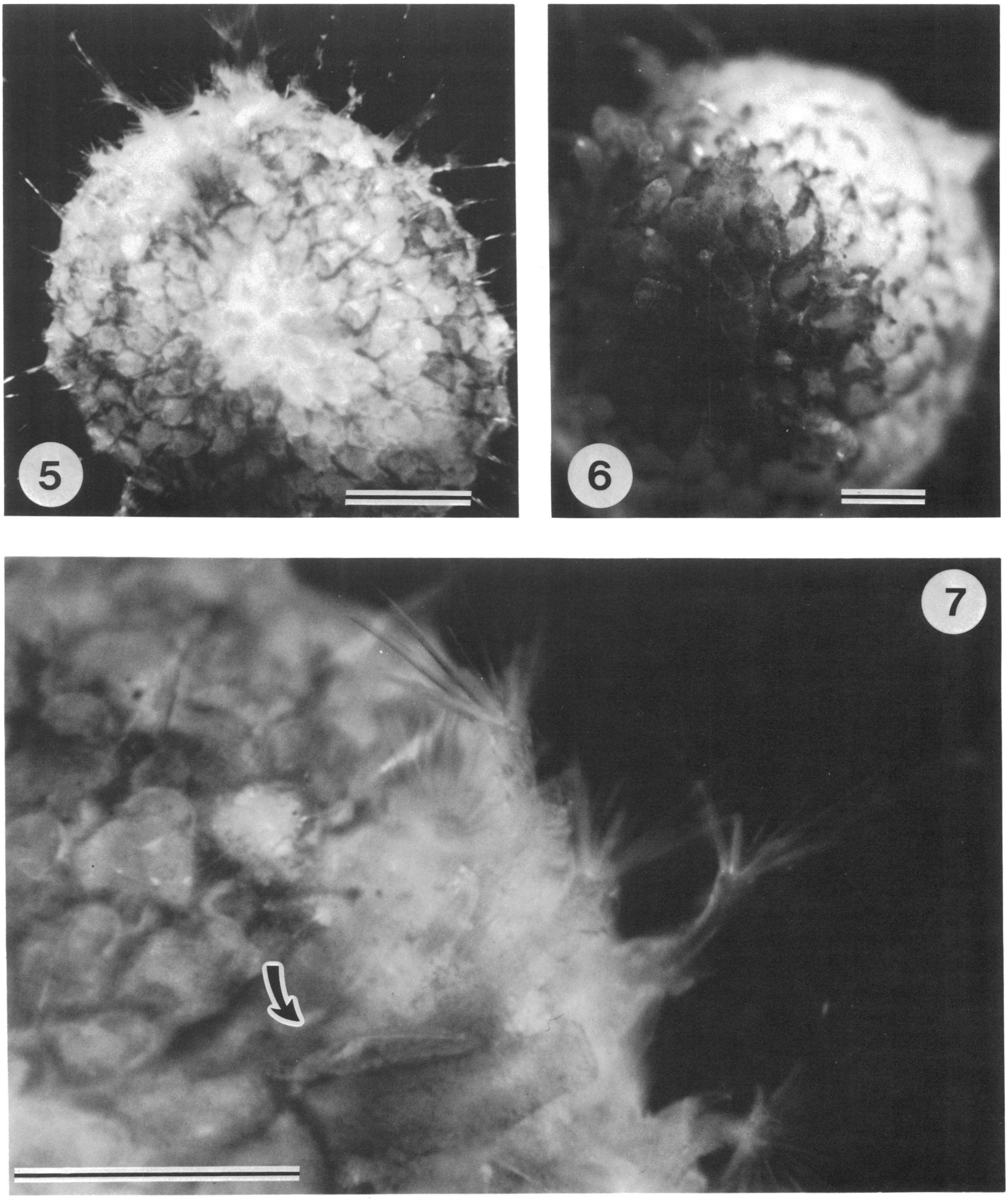
Figs. 1–4. **1.** *Disporella plumosa* (AMNH 628), young colony. Scale bar = 200 μm. **2.** *Disporella plumosa* (AMNH 629), mature colony with brood chamber. Scale bar = 400 μm. **3.** *Spathipora brevicauda* (AMNH 632), zooid and stolon borings on bivalve shell. Scale bar = 1 mm. **4.** *Spathipora brevicauda,* close-up of borings. Scale bar = 200 μm.

ETYMOLOGY: Named after Capron Shoal where the species was discovered. In the 19th century the military trail called the Capron Trail, linking Fort Brooke (now Tampa) with Fort Capron, north of the present Fort Pierce, was the only road between the east and west coasts of Florida.

DESCRIPTION: Colonies are encrusting on those of *Cupuladria doma.* Zooids are baggy and semierect, the saclike basal portion adherent to the substratum, the erect, tubular, and wrinkled distal portion ending in a squared tip. These zooids occur either in clusters on the upper surfaces of the *Cupuladria* colony, or spaced in the crevices between the zooids of its lower edge. Zooid color ranges from transparent (in newly formed zooids) to a mottled reddish brown in old zooids (due to adherent diatoms). Partially expanded zooids show the fringe of the setigerous collar. Polypides are transparent, with 11–15 tentacles and a straight to slightly belled lophophore. An intertentacular organ is present in breeding zooids.

MEASUREMENTS

	RANGE	MEAN	N
Retracted Lz	0.324–0.396	0.360	4
Wz	0.126–0.180	0.153	4
Expanded Lz	0.396–0.486	0.444	3
Wz	0.144–0.180	0.168	3
Wo	0.090–0.108	0.094	5
Lophophore diameter	0.288–0.342	0.317	5
Tentacle length	0.180–0.306	0.234	5
Mouth diameter	0.036	0.036	1



Figs. 5–7. **5.** *Alcyonidium capronae* (AMNH 633) (only lophophores visible) on surface of *Cupuladria doma.* Scale bar = 1 mm. **6.** *Alcyonidium capronae,* retracted zooids on *Cupuladria doma.* Scale bar = 500 μm. **7.** *Alcyonidium capronae,* close-up of zooids (speckled with diatoms) and actively scanning lophophores. Scale bar = 500 μm.

DISCUSSION: This species was found only on living colonies of *Cupuladria doma.* Zooids were attached directly to the cuticle of the *Cupuladria* zooids. In a *Cupuladria* colony bearing a ctenostome colony, vibraculae protruded between ctenostome zooid tips, but their movement did not dislodge the *Alcyonidium* colony, or even cause its lophophores to retract.

OCCURRENCE: The species occurred year-round. Specimens with intertentacular organs on lophophores and 3–4 white eggs in coeloms were found in August 1983 and November 1984.

ORDER CHEILOSTOMATA BUSK, 1852

SUBORDER ANASCA LEVINSEN, 1909

SUPERFAMILY MEMBRANIPOROIDEA BUSK, 1854

FAMILY MEMBRANIPORIDAE BUSK, 1854

GENUS *MEMBRANIPORA* BLAINVILLE, 1830

Membranipora triangularis, new species
Figures 8–10

DIAGNOSIS: Biserial, sand-encrusting *Membranipora* zooids with a triangular cross section due to low outer wall, a proximally beaded cryptocyst, and a large proximal tubercle.

HOLOTYPE: AMNH 636.

PARATYPES: AMNH 637, 638, 639.

ETYMOLOGY: The species name is from the Latin *triangularis,* forming three angles.

DESCRIPTION: Colonies are biserial, encrusting sand grains, typically forming bidirectional chains capable of "jumping" from grain to grain via a noncalcified tubular connection. Zooids are elongate, rounded distally, and somewhat narrowed proximally alternating or in pairs. The distal part of the frontal surface is membranous, the proximal part is underlain by a beaded cryptocyst with a slightly denticulated edge. Inner lateral walls are high and outer walls are minimal; thus zooids are triangular in cross section. They typically have a large tubercle on the inner proximal edge. Polypides are transparent, with 12 tentacles. There are no ovicells or avicularia.

MEASUREMENTS

	RANGE	MEAN	N
Lz	0.360–0.504	0.422	15
Wz	0.198–0.288	0.246	15
Lo	0.072–0.090	0.087	6
Wo	0.090–0.108	0.096	6
Lop	0.108–0.270	0.211	15
Wop	0.144–0.180	0.163	15

DISCUSSION: This species is referred to *Membranipora* on the basis of its cryptocystal calcification. What appear to be ancestral zooids are double (the proximal two zooids of a chain are side by side as in fig. 9), a diagnostic character for *Membranipora,* but because of the tendency of this species to form tubular uncalcified connections between grains, detaching portions of colonies from each other, many of these may be pseudoancestrulae rather than ancestrulae. The species is listed as membraniporid n. sp. A in Håkansson and Winston (1985).

OCCURRENCE: Capron Shoal. Specimens collected at each census. Living colonies were present in August 1984.

Membranipora arborescens
(Canu and Bassler), 1928
Figures 11, 12

Biflustra savartii Smitt, 1873, p. 20. Not *Flustra savartii* Audouin.

Acanthodesia arborescens Canu and Bassler, 1928a, p. 15.

Conopeum commensale Marcus, 1937, p. 35; 1938a, p. 16; 1939, p. 126; 1941, p. 16; 1955, p. 30. Maturo, 1957, p. 37. Lagaaij, 1963, p. 166. Shier, 1964, p. 610. Not *Conopeum commensale* Kirkpatrick and Metzelaar.

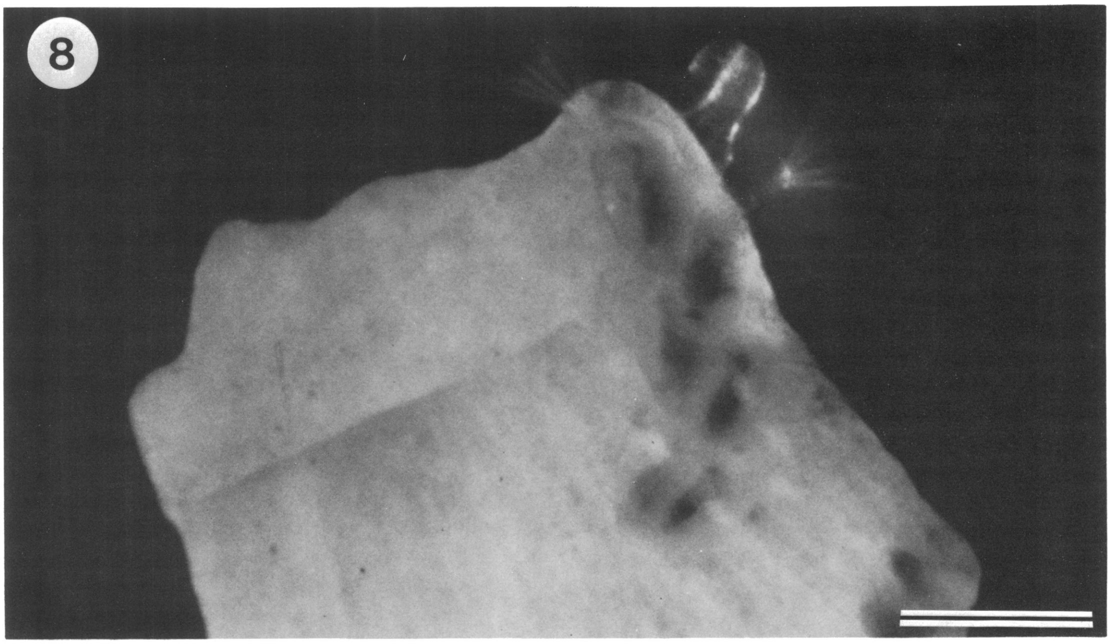
Membranipora arborescens Cook, 1968a, p. 138; 1968b, p. 121. Winston, 1982, p. 117.

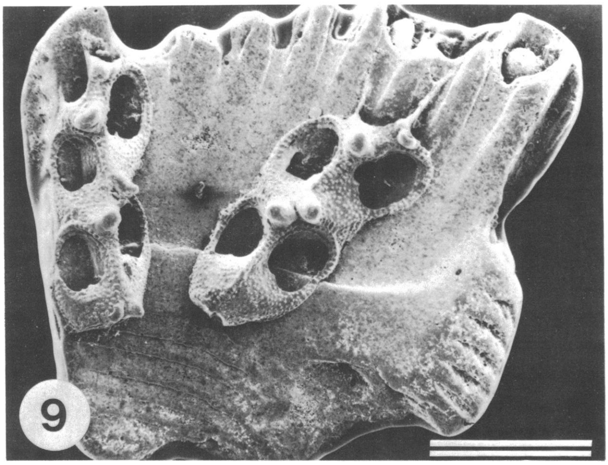
DESCRIPTION: Colonies are white, multiserial, and encrusting. Zooids are rectangular, with an oval membranous frontal area and two stout, smooth tubercles at the distal end and commonly a similar tubercle at the proximal end. There is a narrow raised mural rim and a narrow shelf of beaded cryptocyst in the proximal portion of the zooid. No avicularia or ovicells occur. Eggs are broadcast into the sea where they are fertilized and develop into feeding larvae.

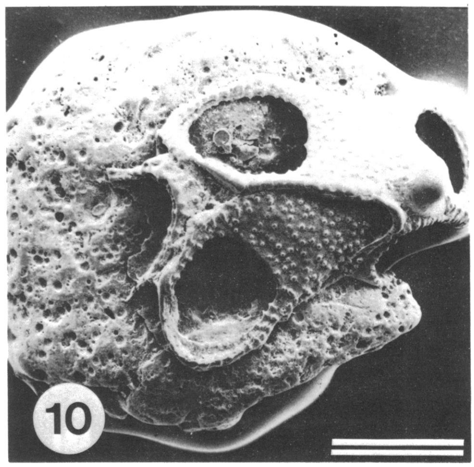
MEASUREMENTS

	RANGE	MEAN	N
Lz	0.252–0.450	0.325	15
Wz	0.180–0.306	0.223	15
Lo	0.036–0.054	0.053	15
Wo	0.072–0.108	0.092	15
Lop	0.144–0.288	0.209	15
Wop	0.108–0.216	0.166	15

DISCUSSION: Colonies settled on Capron Shoal sand grains, like those of *M. savartii,* grow multiserially, encrusting the entire grain.







Figs. 8–10. **8.** *Membranipora triangularis,* living colony on barnacle plate grain; note uncalcified bud extending from grain surface. Scale bar = 500 μm. **9.** *Membranipora triangularis* (AMNH 636), two colonies on barnacle plate grain. Scale bar = 500 μm. **10.** *Membranipora triangularis,* colony on small grain. Scale bar = 200 μm.

OCCURRENCE: Colonies were collected at Capron Shoal in April 1983, August 1983, April 1984, August 1984, November 1984, and January 1985. None of the colonies collected were living.

DISTRIBUTION: Cape Hatteras to Brazil. Gulf of Mexico. West Africa. Eastern Pacific: Mexico to Ecuador.

Membranipora savartii (Audouin), 1826

Figure 13

Flustra savartii Audouin, 1826, p. 240.

Biflustra denticulata Smitt, 1873, p. 18.

Ancanthodesia savartii Canu and Bassler, 1928b, p. 14. Marcus, 1937, p. 40. Osburn, 1940, p. 352.

Membranipora savartii Osburn, 1950, p. 27. Maturo, 1957, p. 35. Shier, 1964, p. 670. Long and Rucker, 1970, p. 19. Winston, 1982, p. 119.

DESCRIPTION: Colonies are multiserial, white, and are encrusting on sand and shell fragments. Zooids are rectangular, with a beaded and variably denticulated cryptocyst extending under the proximal part of the frontal membrane. There is a raised mural rim (broad and worn in these specimens) and a distinct groove between zooids. There may be a single raised proximal tubercle. No ovicells or avicularia occur.

	MEASUREMENTS		
	RANGE	MEAN	N
Lz	0.450–0.630	0.520	15
Wz	0.234–0.450	0.305	15
Lop	0.144–0.270	0.224	15
Wop	0.144–0.306	0.200	15

DISCUSSION: *Membranipora savartii* was one of the most common species found on large shell fragments at Capron Shoal (Winston, 1982) and was collected on shell and beach rock substrata at coastal stations as well. In sand grain collections multiserial sheetlike colonies were found on substrata less than 2 square mm in size, which they almost completely covered. Thus, although the species is somewhat similar in zooid morphology to *M. triangularis,* there is a clear distinction in colony morphology.

OCCURRENCE: Colonies were found at Capron Shoal in April and August 1983, January, April, August, and November 1984, and January 1985. None were alive at the time of collections.

DISTRIBUTION: Cosmopolitan in subtropical and tropical waters. Western Atlantic: Beaufort to Brazil. Caribbean. Gulf of Mexico.

FAMILY CALLOPORIDAE NORMAN, 1903

GENUS *ANTROPORA* NORMAN, 1903

Antropora leucocypha (Marcus), 1937

Figures 14–16

Crassimarginatella leucocypha Marcus, 1937, p. 46; 1938a, p. 20. Cheetham and Sandberg, 1964, p. 1017.

Conopeum reticulum (in part) Osburn, 1940, p. 351.

Antropora leucocypha Shier, 1964, p. 613. Winston, 1982, p. 123

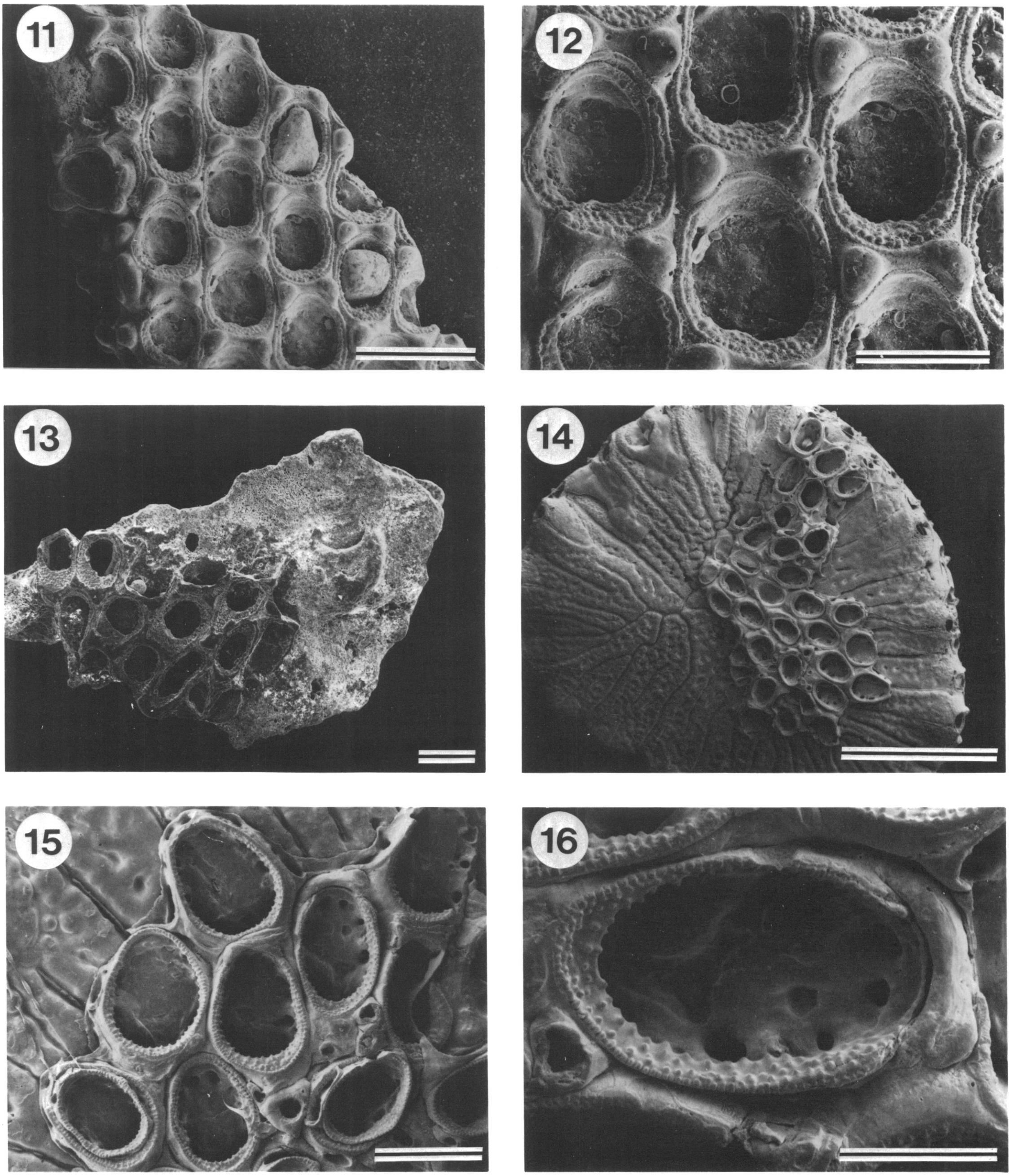
DESCRIPTION: Colonies are encrusting on the bases of live *Cupuladria doma* colonies. Zooids are irregularly oval, somewhat narrowed distally, with a smooth-textured gymnocyst, a beaded crenulated cryptocyst that broadens proximally, and an irregularly oval to subtriangular opesia. The species is characterized by polygonal kenozooids which develop between zooids. When open they have an inner rim of beaded cryptocyst, but many are solid tubercles of relatively smooth gymnocyst.

Also striking are the thick-walled pore chambers that can be seen in zooids at the growing edge (fig. 14), and the thick, rough-textured interior calcification which results in the interior sides of the communication pore being sunken in deep cavities. Ovicells are endozooidal, marked by a solid crescent-shaped pillow of calcification at the distal end of the fertile zooid (fig. 15). Capron Shoal colonies had polypides with 10 transparent tentacles and a yellow-orange gut. In larger colonies from other substrata in the area the mean tentacle number is 12.

	MEASUREMENTS		
	RANGE	MEAN	N
Lz	0.252–0.306	0.271	12
Wz	0.180–0.234	0.199	12
Lo	0.036–0.054	0.046	12
Wo	0.054–0.090	0.078	12
Lov	0.036	0.036	2
Wov	0.108	0.108	2
Lop	0.162–0.216	0.192	12
Wop	0.126–0.180	0.142	12
Lkz	0.036–0.108	0.077	10
Wkz	0.036–0.090	0.050	10

DISCUSSION: Though colonies of this species can become large and multilaminar, comparison of our specimens with young (fig. 36, Winston, 1982) and old (fig. 37, Winston, 1982) colonies from the Indian River area indicated that ovicelled zooids are found in the younger colonies. In the colony from Capron Shoal illustrated here, reproduction was initiated 7–8 generations from the ancestrula.

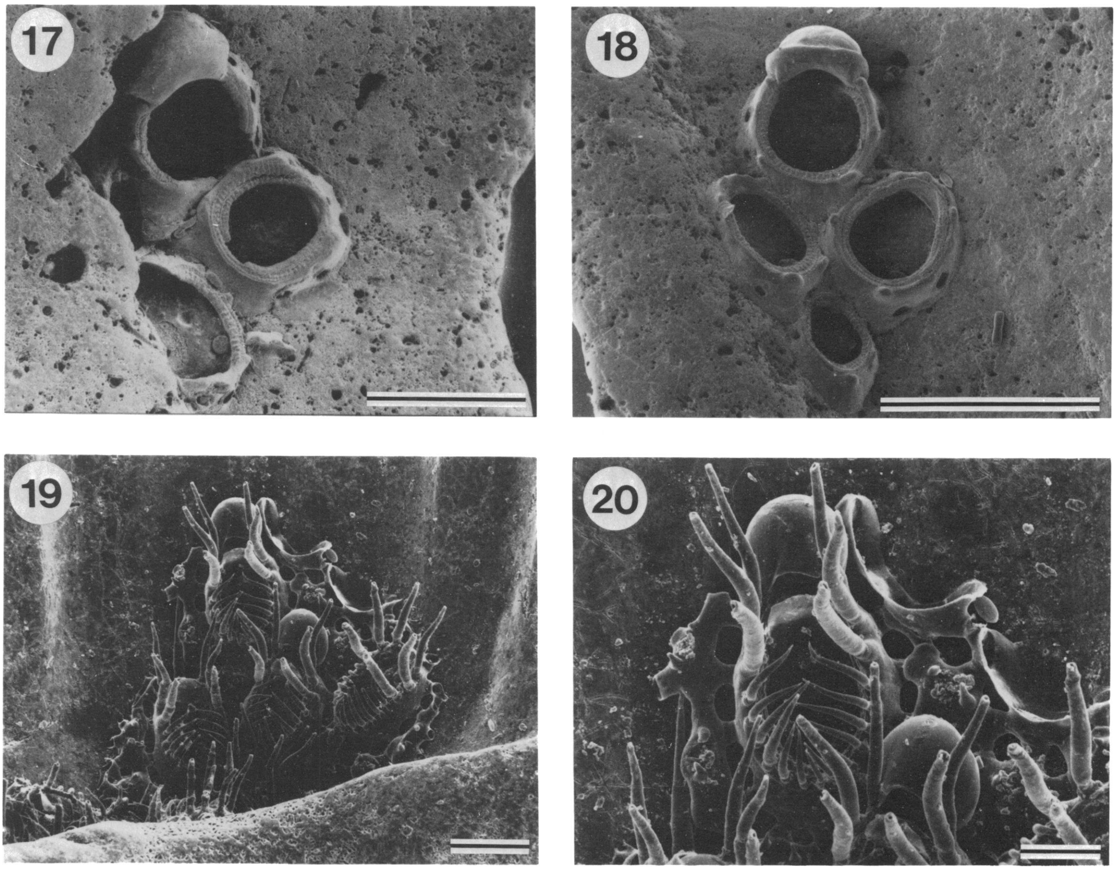
OCCURRENCE: Capron Shoal, collected live in November 1984 and January 1985. Also common year-round at Indian River coastal



Figs. 11–16. **11.** *Membranipora arborescens* (AMNH 640), showing multiserial growth pattern. Scale bar = 400 μm. **12.** *Membranipora arborescens,* close-up of zooids. Scale bar = 200 μm. **13.** *Membranipora savartii* (AMNH 641), worn colony. Scale bar = 400 μm. **14.** *Antropora leucocypha* (AMNH 642), encrusting underside of *C. doma* colony. Scale bar = 1 mm. **15.** *Antropora leucocypha,* zooids and kenozooids. Scale bar = 200 μm. **16.** *Antropora leucocypha,* close-up of ovicelled zooid. Scale bar = 100 μm.

zone stations (Winston, 1982), chiefly on shells of *Thais haemostoma floridana.*

DISTRIBUTION: Cape Hatteras to Brazil. Caribbean. Gulf of Mexico.



Figs. 17–20. **17.** *Alderina smitti* (AMNH 643) colony on shell grain. Scale bar = 400 μm. **18.** *Alderina smitti* (AMNH 644), close-up of ovicelled colony. Scale bar = 400 μm. **19.** *Retevirgula caribbea* (AMNH 645), colony in crevice of barnacle plate. Scale bar = 200 μm. **20.** *Retevirgula caribbea,* close-up of ovicelled zooid. Scale bar = 100 μm.

GENUS *ALDERINA* NORMAN, 1903

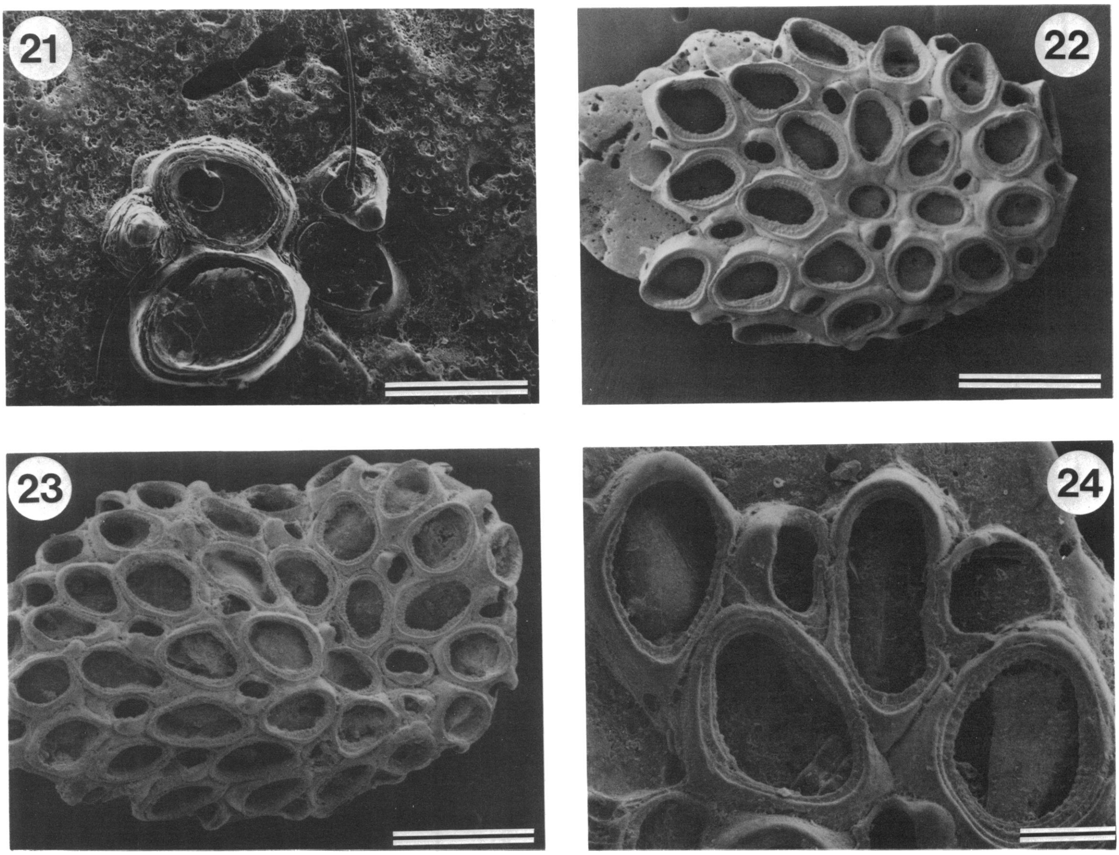
Alderina smitti Osburn, 1950
Figures 17, 18

Membranipora irregularis Smitt, 1873, p. 8. Osburn, 1914, p. 194.
Alderina irregularis Canu and Bassler, 1920, p. 142; 1928b, p. 27. Hastings, 1930, p. 708. Osburn, 1940, p. 363.
Alderina smitti Osburn, 1950, p. 59.

Description: Colonies are encrusting, single-layered, and glass-white. Zooids are very small, oval to pyriform, with an oval or pyriform opesia bordered by one to three rows of finely beaded cryptocyst, edged by a smooth textured gymnocyst on which small raised tubercles may be scattered. Large pore chambers (diatellae) are visible on the outer zooids of the colony. There are no avicularia and no lateral spines, although small distal spines have been noted on a few zooids. Ovicells are thick transversely elongated cushions of calcification. Polypides have 11 tentacles.

	MEASUREMENTS		
	RANGE	MEAN	N
Lz	0.234–0.306	0.276	15
Wz	0.180–0.306	0.226	15
Lo	0.054–0.072	0.059	4
Wo	0.072–0.126	0.092	15
Lov	0.090–0.126	0.108	5
Wov	0.144–0.180	0.169	5
Lop	0.180–0.216	0.203	15
Wop	0.126–0.198	0.155	15

Discussion: Sexually mature colonies on sand grain substrata are very small, often consisting of the ancestrula, one or two au-



Figs. 21–24. **21.** *Vibracellina laxibasis* (AMNH 646), showing ancestrula and early growth pattern. Scale bar = 200 μm. **22.** *Vibracellina laxibasis* (AMNH 647), showing growth pattern. Scale bar = 400 μm. **23.** *Vibracellina laxibasis* (AMNH 648), colony completely encrusting sand grain. Scale bar = 400 μm. **24.** *Vibracellina laxibasis,* close-up showing ovicelled zooid (upper left). Scale bar = 100 μm.

tozooids, and a single ovicelled zooid (e.g., fig. 18).

Occurrence: Found in collections from each census. Living colonies were found in August 1984 and January 1985.

Distribution: Western Atlantic: Cape Hatteras to Florida. Gulf of Mexico. Caribbean. Eastern Pacific: Southern California to the Galapagos.

Genus *Retevirgula* Brown, 1948

Retevirgula caribbea (Osburn), 1947
Figures 19, 20

Pyrulella caribbea Osburn, 1947, p. 15.
Retevirgula flectospinata Shier, 1964, p. 64.

Description: Colonies are encrusting, multiserial, and single layered, with zooids separated from each other by a series of tubes. Zooids are oval with a membranous frontal wall protected by 16–17 spines. The distal three pairs of spines are long and thick and curve upward, while the remaining lateral and proximal spines are more delicate and curve inward over the frontal membrane.

From each zooid a series of tubules extends outward. These connect to an irregular tube of calcification which produces other tubules that in turn bud new zooids. These elongated intrazooidal tubes also produce occasional, vertically projecting, thornlike spines; the short tubules connecting to the zooids do not have spines. Polypides are transparent white and have 10 tentacles. The ovicell is helmet shaped and imperforate, with a shallow longitudinal groove. Ovicelled zooids occurred within two generations of the ancestrula.

MEASUREMENTS

	RANGE	MEAN	N
Lz	0.216–0.288	0.252	15
Wz	0.162–0.234	0.187	15
Lo	0.036–0.054	0.050	15
Wo	0.054–0.090	0.067	15
Lov	0.090–0.108	0.100	7
Wov	0.108–0.162	0.139	7

DISCUSSION: Several species of *Retevirgula* have been described from the Caribbean. Lagaaij (1963) discussed the characteristics of *R. tubulata* and *R. periporosa.* The Capron Shoal species best fits the description of *R. caribbea* described by Osburn (1947) from Aruba. *Retevirgula flectospinata,* described by Shier (1964) from northwest Florida, appears to be synonymous with *R. caribbea,* sharing with it the three pairs of enlarged and curved distal spines. His specimens also had "small round punctations surrounded by a low rim," apparently corresponding to the bases of the interzooecial spines described above, as they are visible in this condition in worn Capron Shoal specimens. Our specimens differ from Osburn and Shier's specimens in lacking interzooecial avicularia and are somewhat smaller.

OCCURRENCE: Colonies found April 1983 (live), August 1983, April 1984, August 1984, November 1984, and January 1985.

DISTRIBUTION: Florida (Atlantic and Gulf coasts). Caribbean.

GENUS *VIBRACELLINA* CANU AND BASSLER, 1917

Vibracellina laxibasis Canu and Bassler, 1928

Figures 21–24

Vibracellina laxibasis Canu and Bassler, 1928b, p. 23.

Vibracellina caribbea Osburn, 1947, p. 11.

DESCRIPTION: Colonies are encrusting and single layered, forming a lacy meshwork that may completely enclose, but does not project outward from, a grain. Zooids are oval, with a membranous frontal wall underlain by a narrow lateral cryptocyst.

Interzooecial vibracula are budded distolaterally from zooids, and are round with a raised tubercle at the end nearest the budding point, a figure-eight shaped opening, and long curved vibracular setae which hinge upon the condyles marking the waist of the figure eight. Ovicells are endozooidal, visible only as a thickened gymnocystal cap at the distal end of the zooid, covering the narrow distal cryptocyst and giving a hooded appearance to the fertile zooid.

MEASUREMENTS

	RANGE	MEAN	N
Lz	0.198–0.342	0.319	15
Wz	0.162–0.234	0.204	15
Lo	0.036–0.072	0.047	13
Wo	0.072–0.090	0.089	15
Lop	0.162–0.216	0.191	15
Wop	0.108–0.144	0.136	15
Lov	0.036	0.036	15
Wov	0.072–0.108	0.086	15
Lavz	0.108–0.180	0.139	15
Wavz	0.090–0.144	0.124	15
Lav-op	0.054–0.126	0.095	15
Wav-op	0.054–0.090	0.060	15

OTHER SPECIMENS EXAMINED: (NMNH), USNM 70868, *Vibracellina laxibasis,* Pliocene, Minnitimmi Creek, Bocas Is., Almirante Bay, Panama, cotypes. *Vibracellina caribbea* USNM 208837, 2 slides, cotype and paratype.

DISCUSSION: Note: this species was listed as *Setosellina ?goesi* in Håkansson and Winston (1986). Living *Vibracellina* colonies can use vibracular motion to rock sand grains but apparently are not able to unbury themselves from sediment as cupuladriids can (Håkansson and Winston, 1986). Unlike cupuladriid colonies, they never appeared on the surface of sediment samples maintained in the laboratory.

OCCURRENCE: Living colonies were found at Capron Shoal in August 1983 and August 1984. Colonies were collected at all times of the year.

DISTRIBUTION: Cape Hatteras to Florida. Gulf of Mexico. Caribbean.

FAMILY CUPULADRIIDAE LAGAAIJ, 1952

GENUS *CUPULADRIA* CANU AND BASSLER, 1919

Cupuladria doma (d'Orbigny), 1851

Figures 25, 27, 29

Discoflustrellaria doma d'Orbigny, 1851, p. 561.

Cupularia doma Smitt, 1873, p. 15. Canu and Bassler, 1923, p. 77; 1928a, p. 64.

Discoporella doma Osburn, 1940, p. 374. Maturo, 1957, p. 41. Cheetham and Sandberg, 1964, p. 1022. Shier, 1964, p. 621.
Cupuladria doma Gautier, 1962, p. 54. Cook, 1965, p. 216; 1968a, p. 145. Prenant and Bobin, 1966, p. 314. Winston, 1982, p. 122.

DESCRIPTION: Living colonies are pink to brownish red, conical, subtriangular or shaped like drumlins, their basal surfaces flat to convex, glistening white, with radial grooves and tubercles. They may reach 6 mm in length. Larvae settle on a sand grain, metamorphosing into an ancestrular triad of zooids (fig. 26). The colony grows around the sand grain completely and becomes free living on and between sand grains. Zooids are rhomboidal, small in size, and regularly arranged. The opesia is subtrifoliate, the opercular area spade shaped to semicircular; the proximal portion has a lacy cut-out shape due to inward denticulate projections of the granular cryptocyst.

In older colonies central and peripheral zooids are closed by continuous granular calcification. A vibraculum with a strong, slightly curved mandible occurs distal to each zooid. Those around the colony periphery are largest; their zooids give a scalloped edge to still-growing colonies. In completely mature colonies there is a double row of those vibracula, and the interstices between them are filled in by colonial basal calcification, making the basal rim smooth rather than scalloped. Polypides have 11–13 tentacles and are a pale translucent pink. Embryos are brooded internally. Larvae are pinkish orange, becoming rapidly geopositive after release from adult colonies.

MEASUREMENTS

	RANGE	MEAN	N
Lz	0.270–0.432	0.346	15
Wz	0.180–0.252	0.196	15
Lo	0.072–0.108	0.092	15
Wo	0.090–0.126	0.104	15
Lav	0.054–0.108	0.080	15
Wav	0.054–0.090	0.074	15

OCCURRENCE: Living colonies were found year-round at Capron Shoal. Live recently settled juveniles were found in April 1983, August 1983 and 1984, and November 1984. This is the most abundant lunulitiform species occurring on the continental shelf of the southeastern United States (Maturo, 1968; Knowles, personal commun.), where it is an important component of sand-bottom communities.

DISTRIBUTION: Subtropical and tropical Atlantic. Western Atlantic: Cape Hatteras to Florida. Gulf of Mexico. Caribbean.

GENUS *DISCOPORELLA* D'ORBIGNY, 1851

Discoporella umbellata subspecies *depressa* (Conrad), 1841

Figures 26, 28, 30

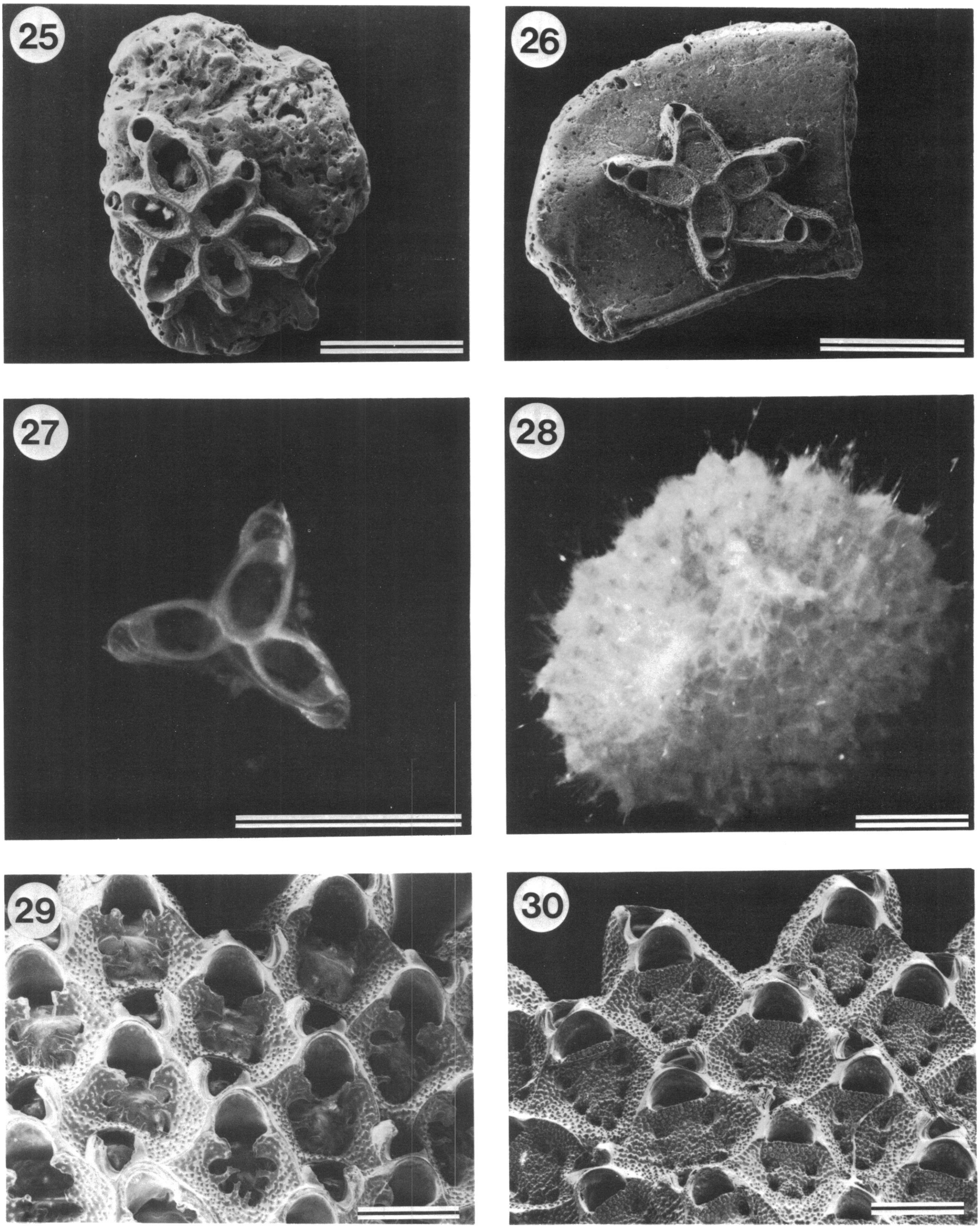
Lunulites depressa Conrad, 1841, p. 348.
Cupularia umbellata Smitt, 1873, p. 14. Canu and Bassler, 1928a, p. 64. Hastings, 1930, p. 718.
Cupularia lowei Osburn, 1914, p. 194.
Discoporella umbellata Osburn, 1940, p. 374; 1950, p. 113. Maturo, 1957, p. 41. Shier, 1964, p. 621. Cheetham and Sandberg, 1964, p. 1022. Soule and Soule, 1964, p. 10.
Discoporella umbellata subspecies *depressa* Cook, 1965, p. 180. Winston, 1982, p. 122.

DESCRIPTION: Living colonies are pink to brownish red, shaped like flattened cones or bowls, with concave (rather than flat) basal surfaces, and reach 9.5 mm. Like those of *C. doma,* larvae settle and metamorphose on sand grains; adults are free living among the sand grains. Zooids are rhomboidal and regularly arranged. The frontal surface consists of a distal semicircular opesia and a proximal granular calcified area, made up of fused cryptocystal processes, pierced by six to eight opesiules. Vibracula with long curved mandibles occur at the distal end of each zooid. Polypides have an average of 13 tentacles, a mean lophophore diameter of 0.453 mm, and are rose pink. Embryos are brooded in zooids.

MEASUREMENTS

	RANGE	MEAN	N
Lz	0.342–0.468	0.400	15
Wz	0.198–0.324	0.258	15
Lo	0.072–0.126	0.096	15
Wo	0.090–0.162	0.110	15
Lav	0.072–0.126	0.100	15
Wav	0.072–0.108	0.091	15

DISCUSSION: The larger and flatter colonies of this species undergo more fragmentation by physical and biological agents than those of *Cupuladria doma,* and regenerated asexually produced colonies are more common than those developed from settled larvae.



Figs. 25–30. **25.** *Cupuladria doma* (AMNH 649), young colony. Scale bar = 1 mm. **26.** *Discoporella umbellata depressa* (AMNH 652), young colony. Scale bar = 1 mm. **27.** *Cupuladria doma* (AMNH 650), ancestral triad produced by metamorphosis of settled larva. Scale bar = 900 μm. **28.** *Discoporella umbellata depressa* (AMNH 653), large asexually produced colony with lophophores expanded. Scale bar = 1 mm. **29.** *Cupuladria doma* (AMNH 651), zooids and vibracula. Scale bar = 200 μm. **30.** *Discoporella umbellata depressa* (AMNH 654), zooids and vibracula. Scale bar = 200 μm.

OCCURRENCE: Living colonies were collected year-round at Capron Shoal. Recently settled juveniles were collected in April and August 1983 and April 1984. This species is less abundant than *Cupuladria doma* in the Capron Shoal area and apparently over the entire southeastern continental shelf (Maturo, 1968; Knowles, personal commun.).

DISTRIBUTION: Western Atlantic: Cape Hatteras to Florida. Gulf of Mexico. Caribbean. Also found in the eastern Pacific from Point Concepcion, California, to Ecuador.

SUPERFAMILY MICROPOROIDEA GRAY, 1848

FAMILY MICROPORIDAE GRAY, 1848

***CYMULOPORA*, NEW GENUS**

TYPE SPECIES: *Cymulopora uniserialis.*

DIAGNOSIS: Zooids pyriform, with proximally elongate gymnocyst, a smooth to radially striated cryptocyst, and triangular to bell-shaped opesia. Ovicell endozooidal, inconspicuous. Avicularia absent.

ETYMOLOGY: The genus name is taken from the Latin *cymula,* diminutive of *cyma,* young shoot or sprout.

DISCUSSION: We have placed the genus in the Microporidae because of similarities with other genera in that family, particularly *Mollia,* which resembles *Cymulopora* in the bell-shaped opesia and the small immersed, pillow-shaped ovicell. Yet, in *Mollia* species and in species of the other microporid genera, the cryptocyst is rough, granular, or beaded in texture, never showing the concentric striations found in *Cymulopora.*

Cymulopora uniserialis, new species
Figures 31–36

DIAGNOSIS: As for genus.

HOLOTYPE: AMNH 655.

PARATYPES: AMNH 656, 657, 658.

ETYMOLOGY: The species name is from the Latin *unus* (one) and *series* (row)—because zooids are arranged in a single series.

DESCRIPTION: Colonies are encrusting, made up of short and bidirectional chains of zooids. Avicularia are lacking. Zooids are elongate, pyriform, the lateral walls with smooth transversely wrinkled calcification raised high centrally around the ovoid frontal surface and tapering proximally. The frontal wall, surrounded by the raised mural rim, is slightly concave and covered by a faintly roughened calcification showing concentric growth rings.

The opesia is bell shaped, with shallow opesiular indentations and a smooth, slightly bowed proximal margin. The ancestrular zooid, which is morphologically similar to other zooids, but lacks the elongated proximal portion, produces first a distal and then a proximal bud from large pore chambers. The ovicell is a very small gymnocystal tubercle consisting of an ovoid cap of calcification interrupting the mural rim at its distal end. Polypides have eight transparent white tentacles.

MEASUREMENTS

	RANGE	MEAN	N
Lz	0.180–0.270	0.211	15
Wz	0.126–0.180	0.167	15
Lo	0.072–0.108	0.089	15
Wo	0.072–0.090	0.084	15

DISCUSSION: The taxonomic affinities of this unique species are not certain. The raised lateral walls and straggling uniserial growth of *C. uniserialis* are reminiscent of the shootlike early stages of some erect forms (hence the genus name) and suggest that this species may be neotenously derived from an erect ancestor. Perhaps it is significant that the only other species we have observed with a similar concentrically striated cryptocyst is *Nellia tenella,* a primitive erect species of anascan (Winston and Cheetham, 1984).

OCCURRENCE: Colonies were collected at Capron Shoal in April 1983 (live), August 1983 (live), January 1984, August 1984, and January 1985 (live).

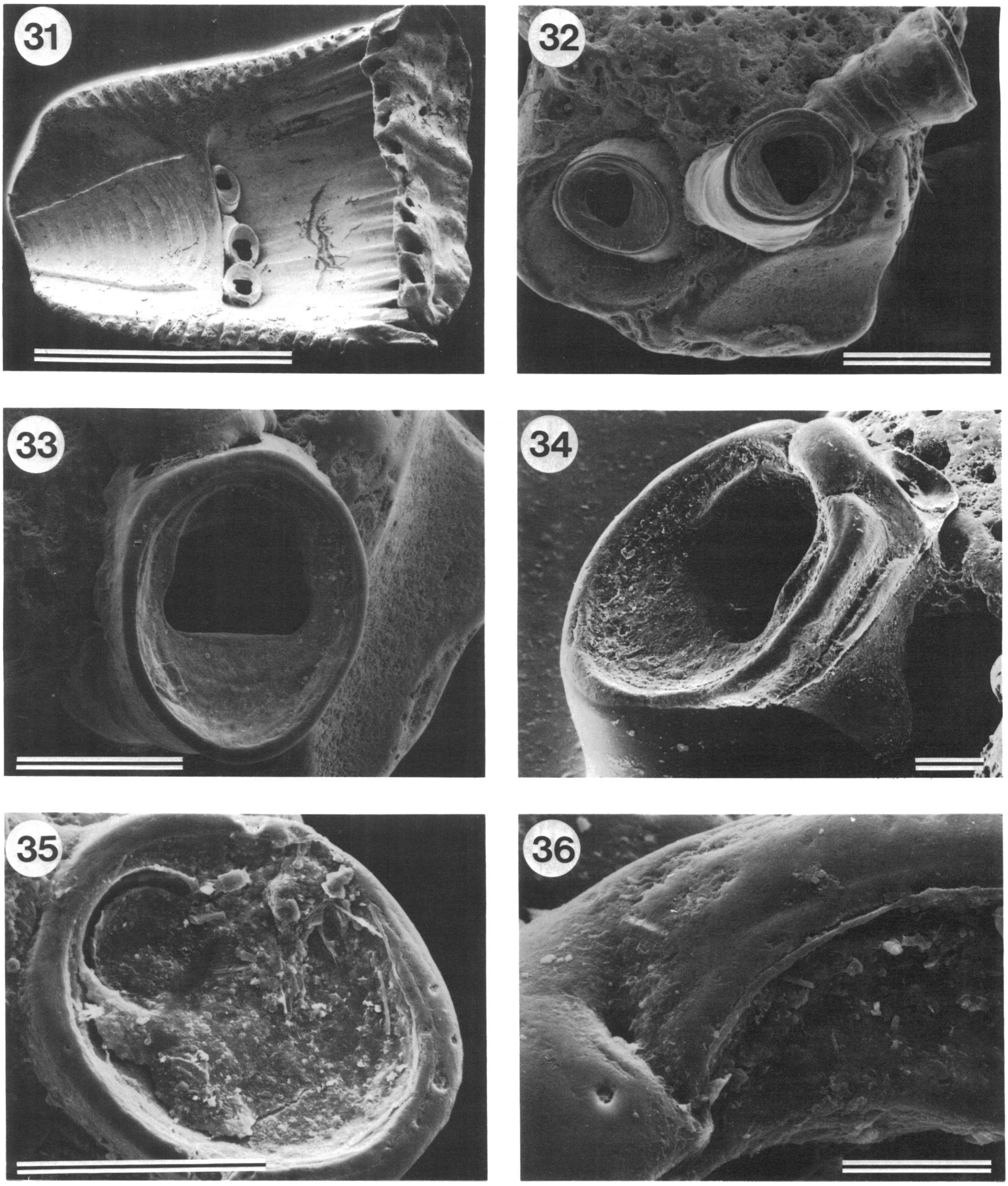
FAMILY ONYCHOCELLIDAE JULLIEN, 1882

GENUS *FLORIDINA* JULLIEN, 1882

Floridina parvicella
Canu and Bassler, 1923
Figures 37, 38

Floridina parvicella Canu and Bassler, 1923, p. 57. Lagaaij, 1963, p. 177.

DESCRIPTION: Colonies are single layered and encrusting on shell grains. Color of living colonies is a shining white, invisible against white shell background except for the golden trefoils of opesiae and opercula. Zooids are



Figs. 31–36. **31.** *Cymulopora uniserialis* (AMNH 655), whole colony in crevice of barnacle plate. Scale bar = 1 mm. **32.** *Cymulopora uniserialis* (AMNH 656), another colony showing high lateral walls. Scale bar = 200 μm. **33.** *Cymulopora uniserialis,* close-up of zooid. Scale bar = 100 μm. **34.** *Cymulopora uniserialis,* close-up of ovicelled zooid. Scale bar = 40 μm. **35.** *Cymulopora uniserialis* (AMNH 657), unbleached colony to show operculum and frontal membrane. Scale bar = 100 μm. **36.** *Cymulopora uniserialis,* close-up to show attachment of frontal membrane; portion of an ovicell is visible at lower left. Scale bar = 20 μm.

ovoid to subhexagonal. The opesia is trifoliate, with two narrow opesiular indentations and a large rounded operculum filling in the center. The rest of the frontal surface is underlain by a granular cryptocyst, which curves concavely inward from the mural rim and is raised convexly at the proximal edge of the opesia. Junctions between adjacent zooids are marked by the development of rounded tubercles (fig. 37).

No ovicells. Vicarious avicularia occur occasionally between autozooids in some, but not all, Capron Shoal colonies. When present they are of elongated ovoid shape, with a figure-eight shaped opesia, a cryptocystal surface texture similar to that of autozooids, and a pair of condyles for the support of the avicularian mandible.

MEASUREMENTS

	RANGE	MEAN	N
Lz	0.270–0.378	0.301	15
Wz	0.180–0.288	0.230	15
Lo	0.090–0.126	0.110	15
Wo	0.229–0.144	0.121	15
Lavz	0.216–0.324	0.262	7
Wavz	0.162–0.180	0.172	7
Lav	0.108–0.162	0.121	7
Wav	0.054–0.072	0.064	7

DISCUSSION: This species was described by Canu and Bassler (1923) as a Pliocene fossil from South Carolina, but living specimens have since been found in the Gulf of Mexico (Lagaaij, 1963).

OCCURRENCE: Specimens were present in all of the censuses. Living colonies were collected at Capron Shoal in January 1985.

DISTRIBUTION: Cape Hatteras to Florida. Gulf of Mexico.

SUPERFAMILY BUGULOIDEA GRAY, 1848

FAMILY BEANIIDAE CANU AND BASSLER, 1927

GENUS *BEANIA* JOHNSTON, 1840

Beania klugei Cook, 1968

Figure 39

Beania intermedia Osburn, 1914, p. 189; 1940, p. 398. Hastings, 1930, p. 705. Shier, 1964, p. 624. Maturo, 1966, p. 579.
Beania klugei Cook, 1968a, p. 164. Winston, 1982, p. 131.

DESCRIPTION: Colonies are uniserial and straggling, attached to the substratum by radicles. Zooids are ovoid, with a flattened frontal membrane, and a rounded, lightly calcified abfrontal surface. Zooids narrow proximally into the tubes by which they were budded from previous zooids. At the distal end of the zooid, above the operculum, there are two pointed distal projections. On either side of the operculum is a short-stalked bird's head avicularium. There are no lateral spines or ovicells.

MEASUREMENTS

	RANGE	MEAN	N
Lz	0.270–0.360	0.316	15
Wz	0.144–0.270	0.220	15
Lo	0.036–0.054	0.052	15
Wo	0.054–0.090	0.074	15
Lov	0.126–0.144	0.138	3
Wov	0.144	0.144	3

OCCURRENCE: The one specimen collected at Capron Shoal (August 1983) was a living two-zooid colony attached to a vibraculum of a *Cupuladria doma* colony.

DISTRIBUTION: Tropical and subtropical. Western Atlantic: Cape Hatteras to Florida. Gulf of Mexico. Caribbean.

SUBORDER ASCOPHORA LEVINSEN, 1909

SUPERFAMILY CRIBRILINOIDEA HINCKS, 1879

FAMILY CRIBRILINIDAE HINCKS, 1879

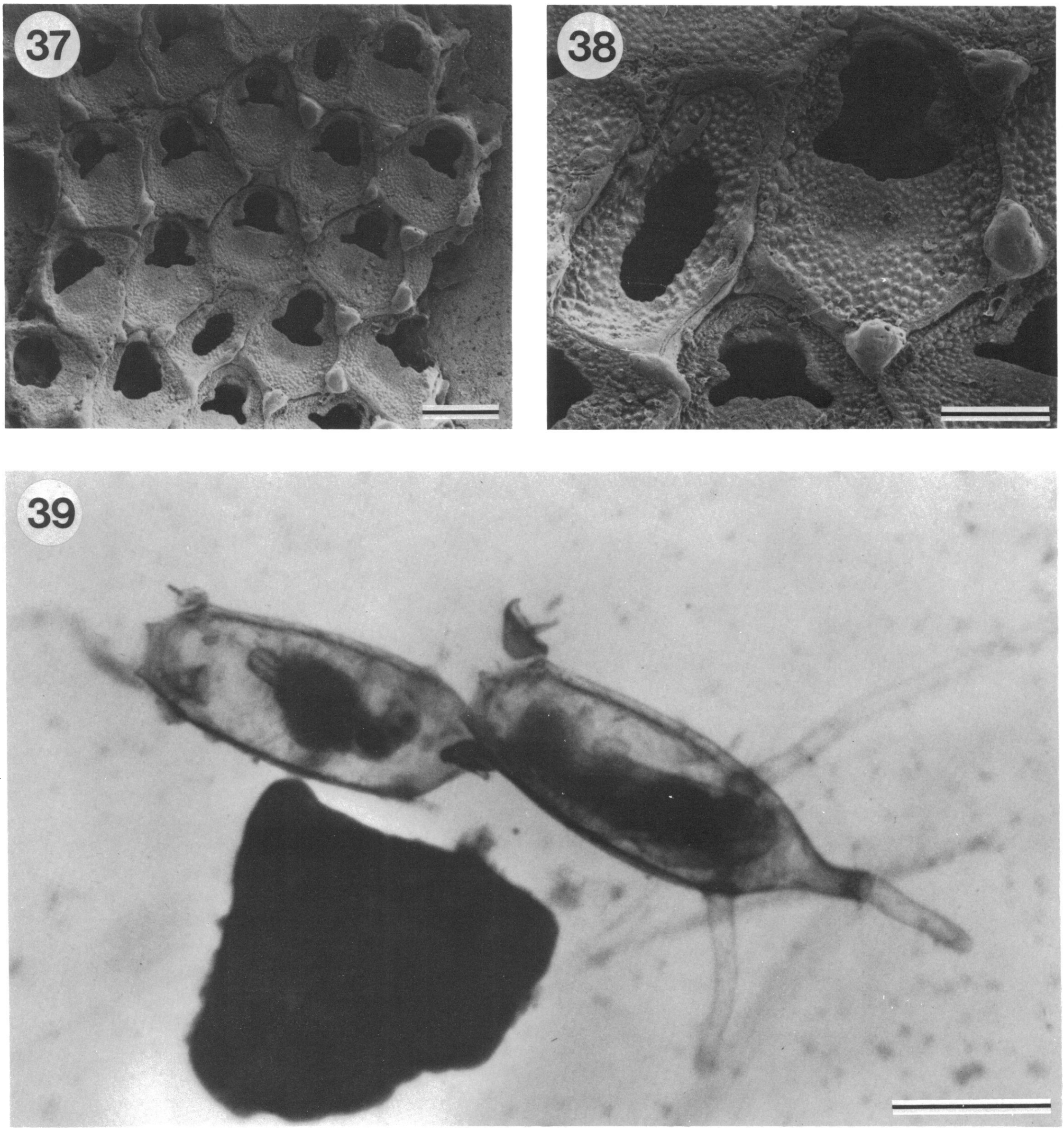
GENUS *CRIBRILARIA* CANU AND BASSLER, 1928

Cribrilaria innominata (Couch), 1844

Figures 40, 42, 44

Lepralia innominata Couch, 1844, p. 114.
Cribrilina innominata, Smitt, 1873, p. 22.
Puellina innominata, Canu and Bassler, 1928b, p. 73.
Colletosia radiata, Marcus, 1937, p. 73 (in part; fig. 39). Maturo, 1957, p. 48. Shier, 1964, p. 625.
Colletosia innominata Prenant and Bobin, 1966, p. 589.
Cribrilaria radiata, Long and Rucker, 1970, p. 19. Winston, 1982, p. 133.
Cribrilaria innominata Harmelin, 1970, p. 84. Hayward and Ryland, 1979, p. 64.

DESCRIPTION: Colonies are encrusting, biserial to multiserial. Zooids are small, ovoid to egg-shaped and separated from each other by deep grooves. The orifice is semicircular



Figs. 37–39. **37.** *Floridina parvicella* (AMNH 659), portion of multiserial colony. Scale bar = 200 μm. **38.** *Floridina parvicella,* close-up of zooid and avicularium. Scale bar = 100 μm. **39.** *Beania klugei* (AMNH 660), colony detached from *Cupuladria doma* vibraculum. Scale bar = 300 μm.

with five spines around its distal margin (four in ovicelled zooids). The frontal wall is formed by the fusion of pairs of ribs or costae (five or six pair in these specimens) with radiating rows of pores between them and a larger pore just below the orifice.

In these specimens the outer ends of costae are noticeably thickened and rise into tubercles, while the two costae surrounding the suboral pore form a raised triangle. Pore chambers are clearly visible in lateral walls of outer zooids. Ovicells are imperforate, helmet shaped, and have a raised central keel. Ovicelled zooids may occur within five generations of the ancestrula. The ancestrula has 9–10 spines. Polypides have eight tentacles and are transparent white in color.

MEASUREMENTS

	RANGE	MEAN	N
Lz	0.270–0.360	0.316	15
Wz	0.144–0.270	0.220	15
Lo	0.036–0.054	0.052	15
Wo	0.054–0.090	0.074	15
Lov	0.126–0.144	0.138	3
Wov	0.144	0.144	3

DISCUSSION: Colonies of *Cribrilaria innominata* encrusting small sand grains often have a runnerlike growth form with only two or three zooids in a row. Interzooecial avicularia with long pointed mandibles usually occur in this species, but were lacking in sand-grain encrusting colonies.

Cribrilaria innominata was the more common of the two species of *Cribrilaria* found at Capron Shoal and is one of the few species that makes the transition from sand-size grains to larger shell substrata. According to Hayward and Ryland (1979) it is most abundant on shell banks in shallow continental shelf waters. For a long time the species was regarded as a variety of *C. radiata,* but is now recognized as distinct. Marcus (1937) synonymized the two species, and Osburn (1940) questioned their distinction, thus creating confusion in tropical western Atlantic records. Five or six species of *Cribrilaria* occur in this region, most of them apparently distinct from the European species described so far. Only a thorough study will resolve the taxonomic confusion that now exists, but we have attempted to include in the synonymy above the records that (either from illustrations or examination of specimens) appear to pertain to *C. innominata.*

OCCURRENCE: Colonies were found at Capron Shoal at each census. Living colonies were found in August 1984 and January 1985.

DISTRIBUTION: Cosmopolitan in temperate to tropical waters. Southwestern England to Mediterranean. Western Atlantic: Cape Hatteras to Brazil. Gulf of Mexico. Caribbean.

Cribrilaria parva, new species

Figures 41, 43, 45

DIAGNOSIS: Extremely small *Cribrilaria* with six oral spines and five to six rows of costae, the second row raised and enlarged to form a curved or V-shaped ridge. Suboral lacuna not enlarged. No avicularia.

HOLOTYPE: AMNH 662.

PARATYPES: AMNH 663, 664, 665.

ETYMOLOGY: The species name is taken from the Latin *parvus,* or little.

DESCRIPTION: Colonies are encrusting on sand grains and small shells. Zooids are ovoid and even smaller than those of *C. innominata* from the same habitat. The frontal wall consists of a narrow border of gymnocyst and a frontal shelf made up to 5–6 pairs of costae. Tubercles at outer ends of costae, if they occur, are smaller and less prominent than those of the preceding species.

The central suboral pore is not enlarged, but the second pair of costae is enlarged on most zooids, forming a curved bar or ridge across the frontal surface. The orifice is semicircular, its distolateral margin bearing six oral spines. Ovicells are imperforate, with laterally ridged calcification raised into a bump or keel centrally. Ovicells may occur within two generations of the ancestrula. Only four spines are visible on ovicelled zooids. There are no avicularia. The ancestrula is tatiform with 12 spines.

MEASUREMENTS

	RANGE	MEAN	N
Lz	0.180–0.270	0.232	15
Wz	0.144–0.216	0.185	15
Lo	0.036–0.054	0.037	15
Wo	0.054–0.072	0.061	15
Lov	0.090–0.126	0.102	6
Wov	0.108–0.144	0.123	6

OCCURRENCE: Colonies were found at Capron Shoal at each census.

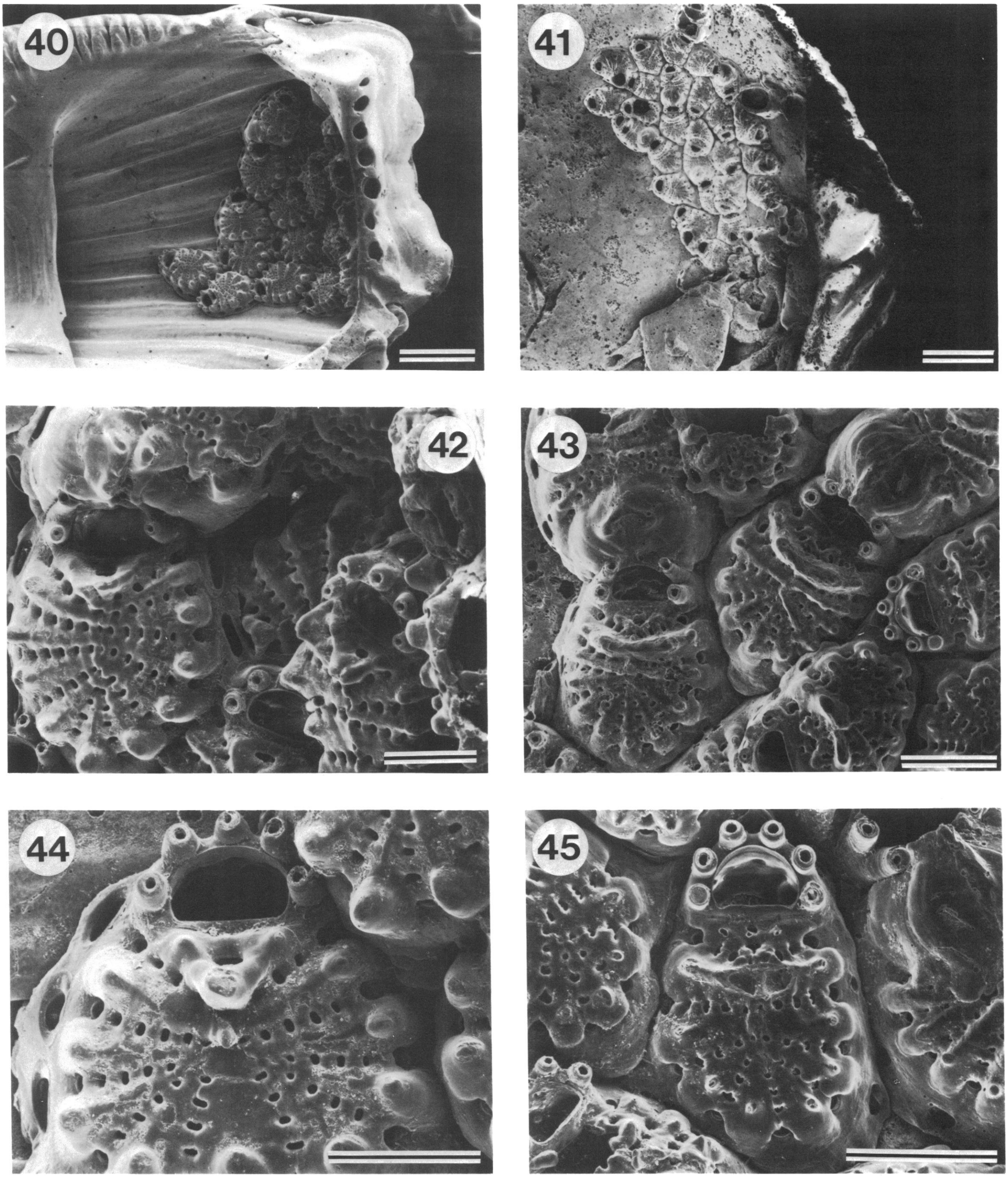
GENUS *BELLULOPORA* LAGAAIJ, 1963

Bellulopora bellula (Osburn), 1950

Figures 46, 47

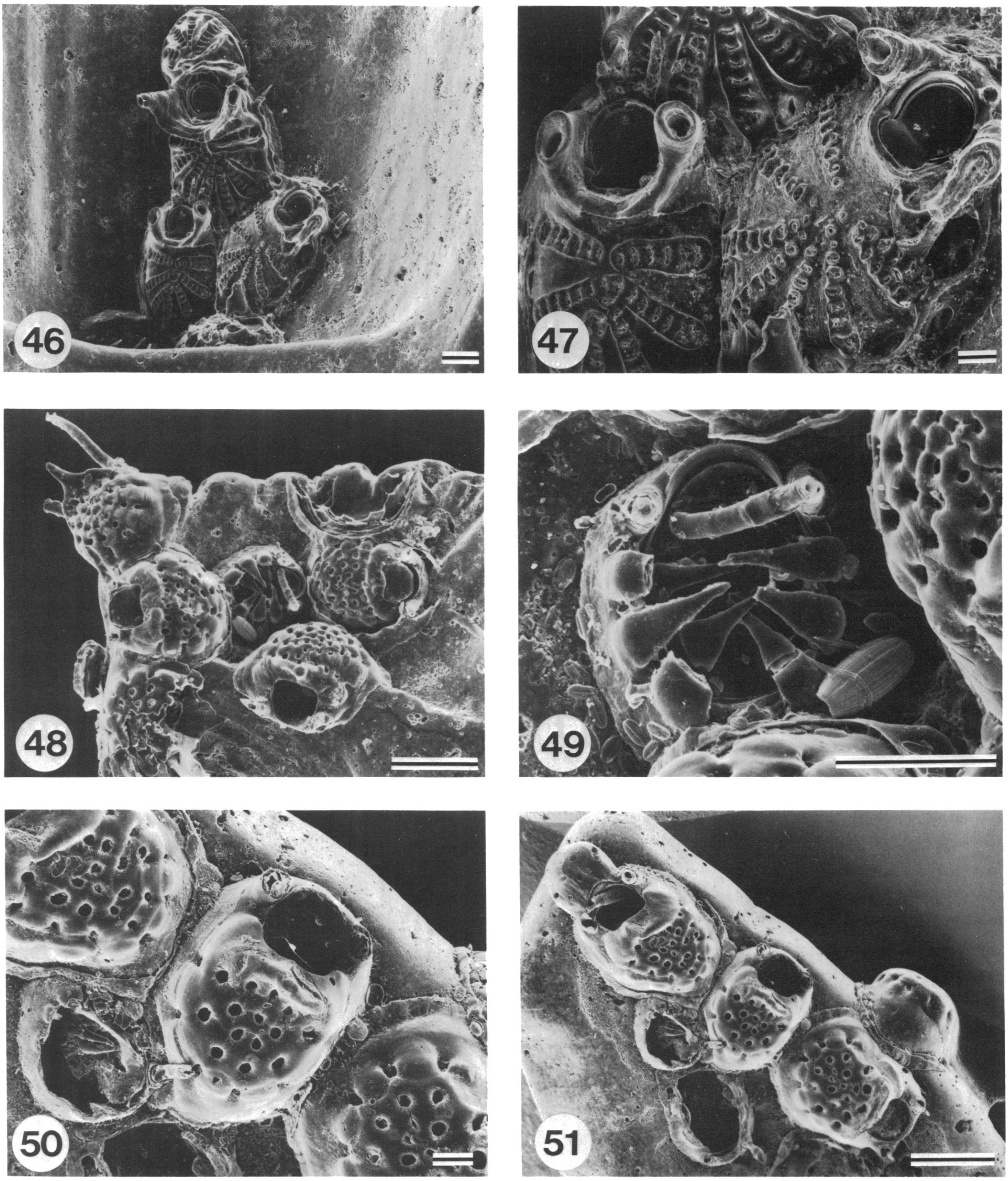
Colletosia bellula Osburn, 1950, p. 188.
Bellulopora bellula Lagaaij, 1963, p. 183. Winston, 1982, p. 134.

DESCRIPTION: Colonies are encrusting and unilaminar. Zooids are ovoid, separated by deep grooves, the frontal surface composed of six or seven radiating pairs of costae with rows of slitlike lacunae between them and a variously developed proximal oval shield.



Figs. 40–45. **40.** *Cribrilaria innominata* (AMNH 661), whole colony on barnacle plate grain. Scale bar = 400 μm. **41.** *Cribrilaria parva* (AMNH 662), whole colony on shell at same magnification as previous figure. Scale bar = 400 μm. **42.** *Cribrilaria innominata,* zooids and ovicells. Scale bar = 100 μm. **43.** *Cribrilaria parva,* zooids and ovicells. Scale bar = 100 μm. **44.** *Cribrilaria innominata,* zooid orifice and oral spines. Scale bar = 100 μm. **45.** *Cribrilaria parva,* zooid orifice and oral spines. Scale bar = 100 μm.

The orifice is keyhole shaped. The ovicell is small relative to the size of the zooid, hemispherical, and carinate, with the same pattern of radiating rows of costae as the zooids. Ovi-



Figs. 46–51. **46.** *Bellulopora bellula* (AMNH 666). Scale bar = 100 μm. **47.** *Bellulopora bellula,* close-up of zooids. Scale bar = 40 μm. **48.** *Reginella repangulata* (AMNH 667), whole colony, showing long oral spines. Scale bar = 200 μm. **49.** *Reginella repangulata,* ancestrula. Scale bar = 100 μm. **50.** *Reginella repangulata.* Scale bar = 100 μm. **51.** *Reginella repangulata,* same colony tilted to show ovicell and raised, barlike structure of first pair of costae. Scale bar = 200 μm.

cells occur in the third generation of zooids. The ancestrula has nine delicate spines, the second zooid has two distal spines above the large hollow spines.

	MEASUREMENTS		
	RANGE	MEAN	N
Lz	0.288–0.378	0.342	15
Wz	0.162–0.306	0.211	15
Lo	0.054–0.090	0.082	15
Wo	0.054–0.108	0.074	15
Lov	0.126–0.198	0.173	15
Wov	0.162–0.234	0.198	5

DISCUSSION: Pedicellate avicularia adjacent to the orifice have been described in this species, but no avicularia occurred in Capron Shoal specimens. The two hollow spines which bear the avicularia do occur, but their ends are membranous.

OCCURRENCE: Live colonies were collected at Capron Shoal in April and August 1983 and January 1985. The only time the species was not collected was January 1984. The species was also collected from offshore shell (60–90 m) in the Sebastian Pinnacle area (Winston, 1982).

DISTRIBUTION: Western Atlantic: Cape Hatteras to Florida. Also reported from the Gulf of California and the Galapagos.

GENUS *REGINELLA* JULLIEN, 1886

Reginella repangulata, new species

Figures 48–51

DIAGNOSIS: *Reginella* with elongate unbranched distal spines and a frontal shield composed of 7–11 fused costae, the topmost pair raised to form a suborificial bar. No avicularia. Ovicell with scattered pores.

HOLOTYPE: AMNH 667.

PARATYPES: AMNH 668, 669, 670.

ETYMOLOGY: The species name is taken from the Latin *repangulata,* meaning barred or bolted, in reference to the shape of the suborificial pair of costae.

DESCRIPTION: Colonies are encrusting and single layered. The ancestrula is tatiform with narrow lateral spines and two stout distal spines. Zooids are ovoid to subhexagonal, convex, and set off from each other by deep grooves. The frontal wall is a raised frontal shield formed by the coalescence of 7 to 11 costae, with rounded lacunae marking their fusion.

The topmost pair of costae is clasped like a pair of hands across the proximal border of the orifice, forming a raised and centrally pointed bar. The orifice is subrectangular, edged distolaterally by a pair of spines. Ovicells are helmet shaped and heavily calcified, with a few scattered pores and often a flattended central keel. Embryos are shell pink. Polypides are glassy and transparent, with 11 tentacles.

	MEASUREMENTS		
	RANGE	MEAN	N
Lz	0.252–0.396	0.347	15
Wz	0.198–0.324	0.266	15
Lo	0.054–0.108	0.089	15
Wo	0.090–0.108	0.098	15
Lov	0.126–0.162	0.138	6
Wov	0.162–0.216	0.174	6

DISCUSSION: Costae are more smoothly fused than in *Cribrilaria* and concentric growth lines may make a stronger pattern than the radial lines between adjacent costae. This species appears to fit the description of *Reginella* (Jullien, 1886) as given by Osburn (1950). Examination of the superficially similar West Coast species described by Canu and Bassler (1923) as *Metracolposa mucronata* (USNM 68530) showed that species to have much larger zooids with more numerous costae and with less gymnocyst visible around the zooid edge. In *R. mucronata* the first pair of costae has fused into a flattened bifid mucro below the orifice, whereas in *R. repangulata* they have become enlarged, but remain rounded and one overlaps the other. *Reginella mucronata* also lacks the distolateral oral spines. *Figularia contraria* (Lagaaij, 1963) appears superficially similar from his illustration (pl. IV, fig. 1), but examination of his specimen (USNM 648027) showed it to be a true *Figularia,* with typical pores on the ovicells and with a larger number of costae. *Reginella floridana* has been collected from deeper water in the area (Winston, 1982), but differs from *R. repangulata* in having trifid distal spines and flattened lateral spines arching over the orifice, as well as a larger zooid size.

OCCURRENCE: Living specimens were found at Capron Shoal in April 1983, November 1984, and January 1985. Specimens were collected at each census except January 1984.

SUPERFAMILY HIPPOTHOOIDEA FISCHER, 1866

FAMILY HIPPOTHOIDAE FISCHER, 1866

GENUS *HIPPOTHOA* LAMOUROUX, 1821

Hippothoa balanophila, new species
Figures 52–55

DIAGNOSIS: Uniserial *Hippothoa* with very small keeled autozooids, no zooeciules, female zooids smaller than autozooids and closely attached to them. Distally sloping orifice with raised rim and moderately deep U-shaped sinus with a double set of condyles.

HOLOTYPE: AMNH 671.

PARATYPES: AMNH 672, 673, 674.

ETYMOLOGY: The species name is taken from the Greek *balanus* = barnacle and *philia* = friendly love, because of the preference of the species for the grooved inner surfaces of barnacle plates.

DESCRIPTION: Straggling uniserial colonies are found encrusting shell grains, particularly barnacle plates. They are usually oriented along grooves or concavities in the grain (fig. 51). Autozooids are pyriform, with a flat tubular proximal portion and an ovoid, raised, commonly keeled, distal portion. They are imperforate, with a smooth or slightly wrinkled texture to the calcification. Autozooid orifices are rounded distally and have a moderately deep U-shaped proximal sinus (figs. 53, 54). Female zooids are short, with a smoothly calcified helmet-shaped ovicell, often bearing a single central bump. Female zooid orifices are also rounded distally and convex proximally, with a very shallow sinus (fig. 53).

MEASUREMENTS

	RANGE	MEAN	N
Lz	0.144–0.288	0.221	15
Wz	0.090–0.144	0.114	15
Lo	0.018–0.054	0.040	15
Wo	0.036–0.054	0.040	15
Lov	0.090	0.090	2
Wov	0.090–0.108	0.099	2

DISCUSSION: Colonies on sand grain substrata are more compact than those of *Hippothoa flagellum* from larger shell and coral substrata; the tubular portions of zooids, which may be a millimeter or more in length in *H. flagellum* colonies from *Oculina* substrata (see fig. 84 in Winston, 1982) are shortened or absent; the female zooids are closely adherent to autozooids. This species is most similar to *H. flagellum* Manzoni (reviewed in Ryland and Gordon, 1977) and *H. peristomata* Gordon (1984). Autozooids differ from those of *H. flagellum* in their smaller size, frontal keel, and relatively larger orificial sinus. They are also smaller than those of *H. peristomata.* That species also lacks a raised longitudinal keel and has an orifice with a shallower sinus. Female zooid orifices lack the proximal tubercles shown by *H. peristomata.* They are similar to those of *H. flagellum,* but the distal end of the ovicell is never pointed, as it sometimes is in *H. flagellum*; ovicells often have a large central bump.

OCCURRENCE: Colonies were found at Capron Shoal in April 1983 (live), April 1984, August 1984, November 1984, and January 1985.

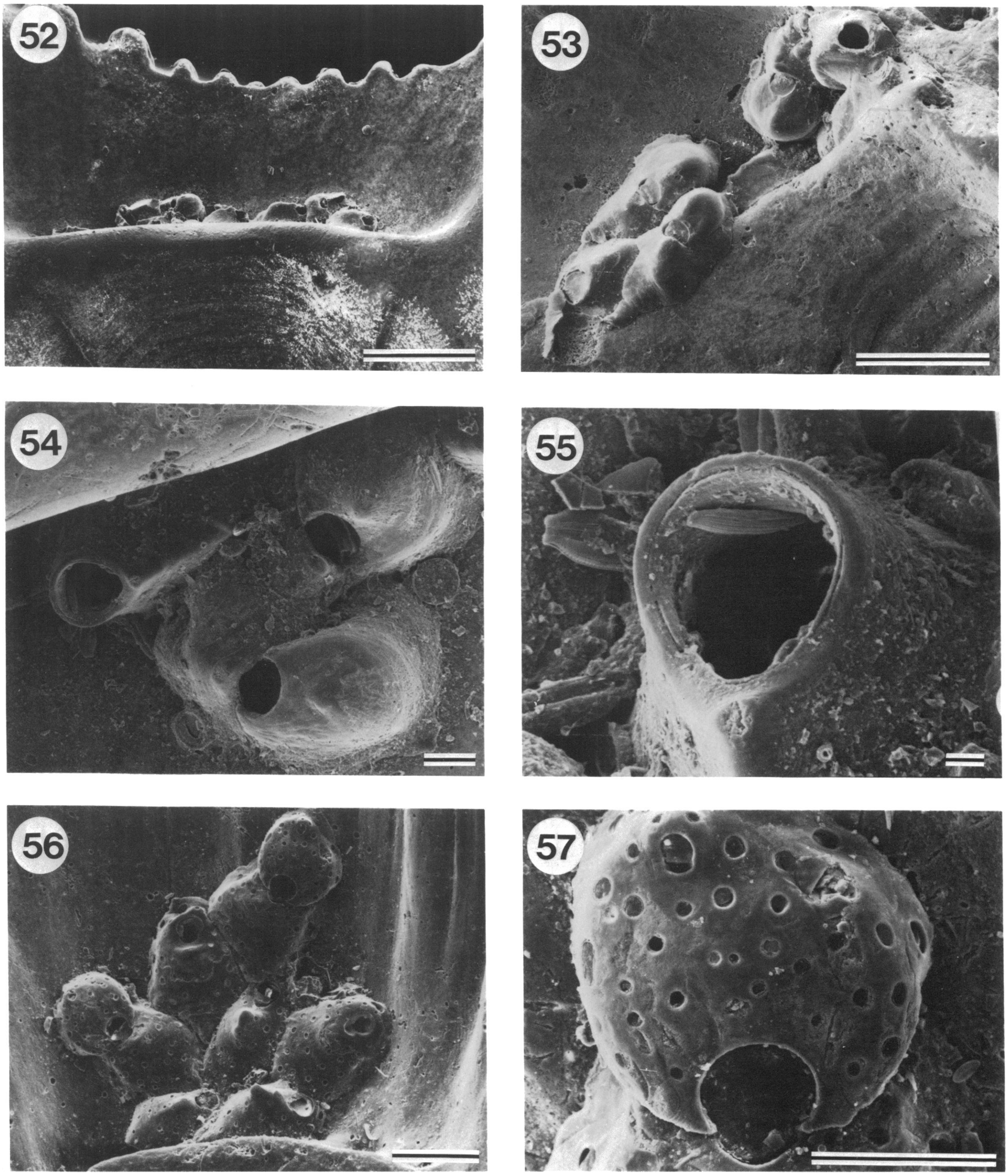
GENUS *TRYPOSTEGA* LEVINSEN, 1909

Trypostega venusta (Norman), 1864
Figures 56, 57

Lepralia venusta Norman, 1864, p. 84.
Gemellipora glabra forma *striatula* Smitt, 1873, p. 37.
Trypostega venusta Osburn, 1914, p. 198; 1940, p. 409; 1952, p. 280. Canu and Bassler, 1928b, p. 77. Marcus, 1938a, p. 35. Shier, 1964, p. 627. Cook, 1968a, p. 177. Winston, 1982, p. 151; 1984, p. 18.

DESCRIPTION: Colonies are encrusting and single layered, with a smooth, glassy, transparent surface, spangled by glittering pores. Zooids are rhomboidal. Small pores are scattered evenly over the frontal surface. Transverse lines and faint longitudinal striations may also be present. Autozooids are interspersed with dwarf zooids or zooeciules, which ordinarily are found at the distal end of each autozooid.

Autozooid orifices are keyhole shaped, circular distally, and have proximally directed condyles and a proximal V-shaped sinus. Sometimes there is a small umbo proximal to the orifice. Zooeciule orifices are simple, but also rounded distally, with a moderate sinus proximally. In living specimens the operculum is a very pale gold. Ovicells are



Figs. 52–57. **52.** *Hippothoa balanophila* (AMNH 671), colony in crevice of barnacle plate. Scale = 400 μm. **53.** *Hippothoa balanophila,* female zooids. Scale bar = 200 μm. **54.** *Hippothoa balanophila* (AMNH 672), showing orifices of female zooids. Scale bar = 40 μm. **55.** *Hippothoa balanophila,* close-up of autozooid orifice. Scale bar = 10 μm. **56.** *Trypostega venusta* (AMNH 675), whole colony on barnacle plate grain. Scale bar = 200 μm. **57.** *Trypostega venusta,* close-up of ovicell and associated zooeciule. Scale bar = 100 μm.

embedded, covered with the same small evenly spaced pores, and cover the proximal portions of zooeciules. Polypides are transparent white. Embryos are pinkish red.

MEASUREMENTS	RANGE	MEAN	N
Lz	0.234–0.378	0.329	15
Wz	0.126–0.324	0.228	15
Lo	0.054–0.090	0.071	15
Wo	0.054–0.072	0.065	15
Lov	0.108–0.198	0.138	6
Wov	0.180–0.234	0.195	6
Zooeciules			
Lz	0.144–0.234	0.185	4
Wz	0.126–0.216	0.171	4
Lo	0.018	0.018	4
Wo	0.018	0.018	4

DISCUSSION: Zooids of sand grain colonies are considerably smaller than those of colonies from large substrata from Florida, Jamaica, and Belize that we have examined and have fewer pores. They also reproduce at a very small size. (Figure 56 shows a colony with seven zooids, two of them ovicelled; maximum diameter of this colony is about 0.9 mm.) This is very unlike Jamaican cryptic reef colonies, for example, which did not reproduce until they were at least 2 cm maximum diameter (Winston, unpub. data). This species is given as *Trypostega* sp. in Håkansson and Winston (1985).

OCCURRENCE: Living colonies occurred at Capron Shoal in August and November 1984. Colonies were found in each census.

DISTRIBUTION: Cosmopolitan in warmer waters. Western Atlantic: Cape Hatteras to Brazil. Gulf of Mexico. Caribbean.

SUPERFAMILY SCHIZOPORELLOIDEA JULLIEN, 1883

FAMILY SCHIZOPORELLIDAE JULLIEN, 1883

GENUS *SCHIZOPORELLA* HINCKS, 1887

Schizoporella rugosa (Osburn), 1940

Figures 58–60

Stephanosella rugosa Osburn, 1940, p. 423.

DESCRIPTION: The colony is biserial, encrusting on a shell grain. Zooids are very small, ovoid to subhexagonal, and convex. The wall is perforated by numerous small pores, many of them not round, but irregularly shaped. As secondary calcification proceeds the frontal surface becomes covered by irregular ridges which more or less rim the orifice and come to cover most of the pores.

The orifice is semicircular to almost circular distally, with two small rounded condyles and a broad V-shaped sinus proximally. A small bluntly pointed avicularium is located on a raised umbo below and to one side of the orifice. Ovicells have an outer layer of imperforate calcification and a semicircular to band-shaped inner layer, with faint radiating ribs and a row of marginal pores.

MEASUREMENTS	RANGE	MEAN	N
Lz	0.270–0.360	0.313	5
Wz	0.162–0.306	0.238	5
Lo	0.054–0.108	0.076	5
Wo	0.054–0.108	0.068	5
Lov	0.126	0.126	2
Wov	0.126–0.144	0.135	2
Lav	0.072	0.072	1
Wav	0.036	0.036	1

DISCUSSION: The species was described by Osburn from Puerto Rico and Bermuda. The present location of his specimens is unknown, but we were able to examine specimens from Venezuela (Jackson collection). The sand grain specimens are somewhat warped and irregular in comparison with these and with Osburn's illustration (pl. 8, fig. 57), but we have no doubt they belong to Osburn's species. Like other species which also occur on larger substrata, the Capron Shoal colony of *S. rugosa* is not multiserial and has reproduced at a very small size. In contrast to most other interstitial species, however, characteristic avicularia occur and appear to have been functional.

OCCURRENCE: Found at Capron Shoal in April 1983 and April and August 1984.

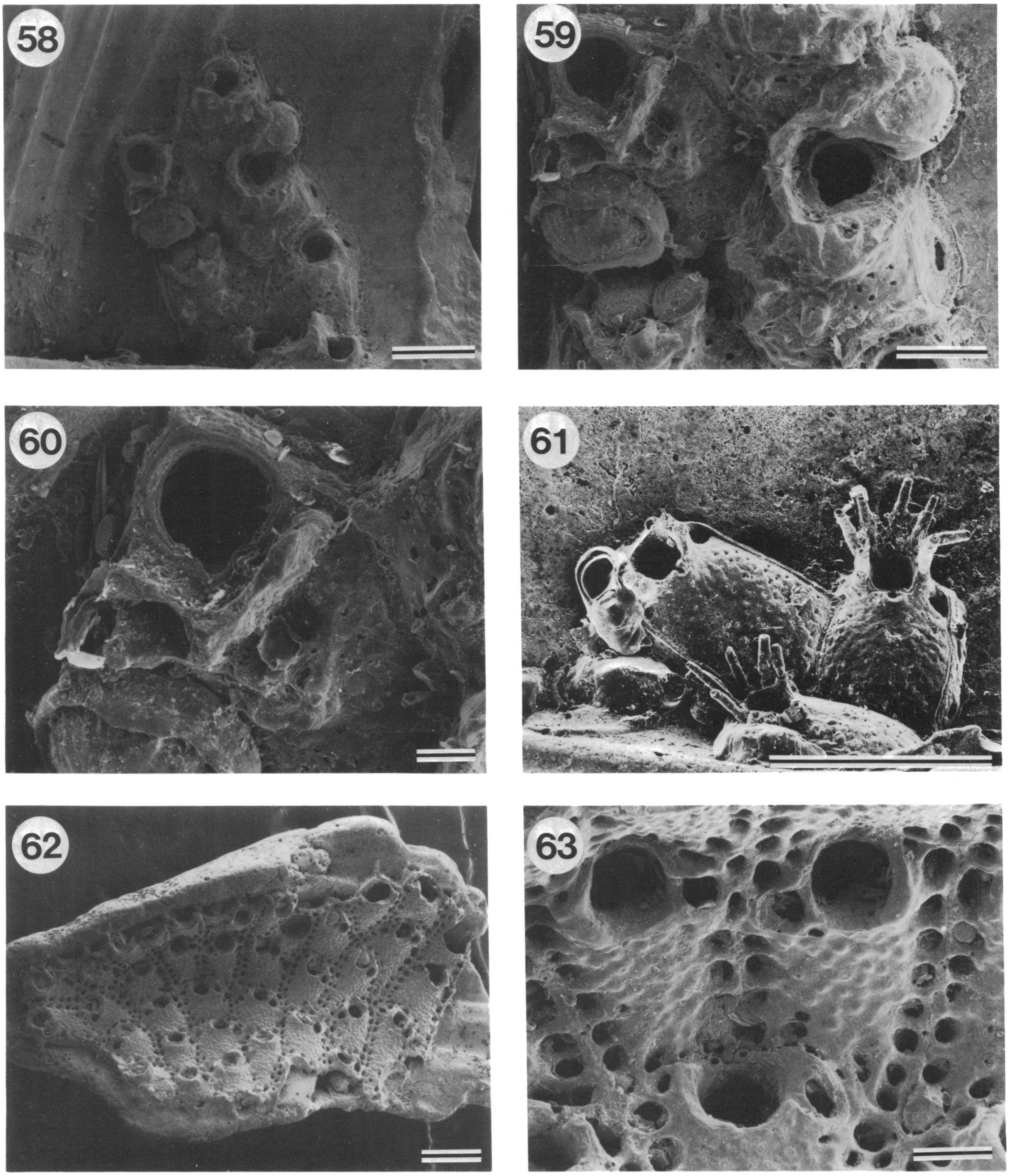
DISTRIBUTION: Bermuda. Cape Hatteras to Florida. Caribbean.

GENUS *ESCHARINA* MILNE-EDWARDS, 1838

Escharina pesanseris (Smitt), 1873

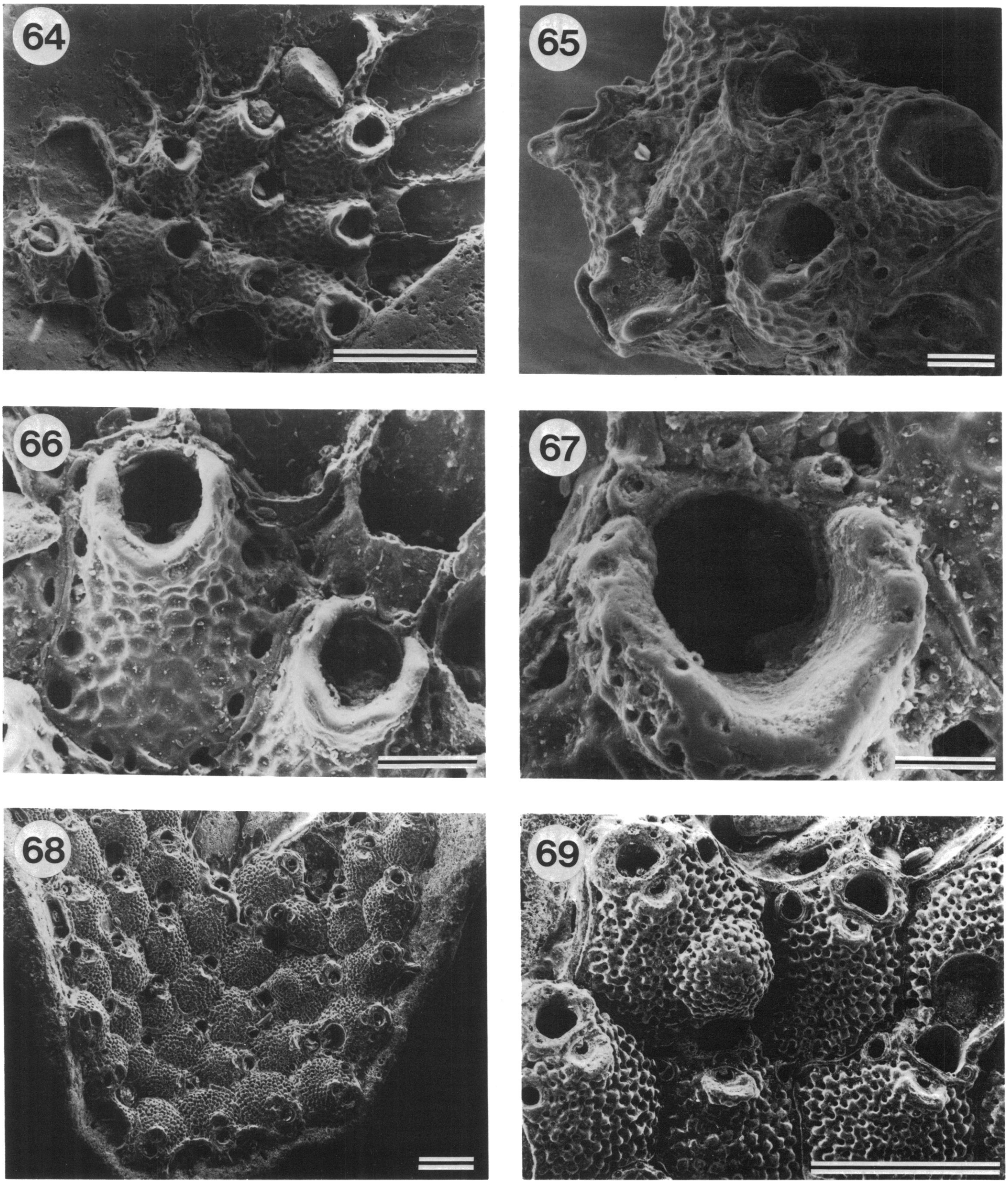
Figure 61

Hippothoa pesanseris Smitt, 1873, p. 43.
Escharina pesanseris Osburn, 1914, p. 207.
Mastigophora pesanseris Osburn, 1927, p. 130; 1940, p. 452; 1952, p. 479. Canu and Bassler, 1928b, p. 133. Hastings, 1930, p. 722. Marcus, 1939, p. 142.
Escharina pesanseris Cook, 1968a, p. 195. Long and Rucker, 1970, p. 19. Winston, 1982, p. 145; 1984, p. 26.



Figs. 58–63. **58.** *Schizoporella rugosa* (AMNH 676). Scale bar = 200 μm. **59.** *Schizoporella rugosa,* showing ovicelled zooids. Scale bar = 100 μm. **60.** *Schizoporella rugosa,* close-up of orifice and irregular pores. Scale bar = 40 μm. **61.** *Escharina pesanseris* (AMNH 677) and *Hippothoa balanophila.* Scale bar = 400 μm. **62.** *Parasmittina nitida* morphotype B, whole colony on shell grain (AMNH 678). Scale bar = 400 μm. **63.** *Parasmittina nitida* morphotype B, close-up of zooids. Scale bar = 100 μm.

DESCRIPTION: Colonies are encrusting and very small. Zooids are polygonal, the frontal surface slightly convex and covered with fine pores, which may become occluded by secondary calcification. The orifice is semicircular, its proximal border straight, with a nar-



Figs. 64–69. **64.** *Parasmittina signata* (AMNH 679), colony on shell grain. Scale bar = 400 μm. **65.** *Parasmittina signata,* showing high peristomes. Scale bar = 100 μm. **66.** *Parasmittina signata,* close-up of zooid. Scale bar = 100 μm. **67.** *Parasmittina signata,* close-up of orifice, showing oral spines. Scale bar = 40 μm. **68.** *Microporella umbracula* (AMNH 680), multiserial colony on large grain. Scale bar = 400 μm. **69.** *Microporella umbracula,* showing ovicelled zooids and avicularia. Scale bar = 400 μm.

row, deep sinus. The peristome forms a raised rim around the distal portion of the orifice. It bears six to eight thick spines. Distally directed avicularia occur on one or both sides of the orifice; they have a fin-shaped "duck-foot" mandible. Ovicells are small, globular, and imperforate.

	MEASUREMENTS		
	RANGE	MEAN	N
Lz	0.378–0.504	0.438	6
Wz	0.180–0.360	0.267	6
Lo	0.090–0.126	0.096	6
Wo	0.072–0.108	0.090	6

OCCURRENCE: Living colonies found at Capron Shoal in January 1985. The species has also been collected from larger shell and coral substrata at Capron Shoal and on the offshore *Oculina* pinnacles (Winston, 1982).

DISTRIBUTION: Circumtropical. Western Atlantic: Cape Hatteras to Brazil. Caribbean. Gulf of Mexico.

FAMILY SMITTINIDAE LEVINSEN, 1909

GENUS *PARASMITTINA* OSBURN, 1952

Parasmittina nitida morphotype B Maturo and Schopf, 1968

Figures 62, 63

DESCRIPTION: Colonies are encrusting and multiserial. Zooids are rectangular, with a coarsely granular frontal wall and a single row of marginal pores. The primary orifice is rounded distally, with short blunt condyles and a broad proximal lyrula. The orifice is surrounded by a short orificial collar, and there are two distal oral spines (often broken or overgrown). No ovicells were present in interstitial colonies. Ovicells in this species are prominent and rounded, the distal rim and sides covered with granular calcification, the center penetrated by two rows of large pores (Winston, 1982, fig. 71). Avicularia are variable in shape, one to three per zooid. Those of interstitial specimens lacked cross-bars and appeared to be vestigial.

	MEASUREMENTS		
	RANGE	MEAN	N
Lz	0.324–0.540	0.384	15
Wz	0.198–0.360	0.268	15
Lo	0.090–0.126	0.100	15
Wo	0.090–0.108	0.100	15
Lav	0.036–0.090	0.066	9
Wav	0.036–0.054	0.046	9

DISCUSSION: *Parasmittina nitida* morphotype B was one of the most common specimens on subtidal beach rock in the area. It has also been found on larger shell substrata at Capron Shoal (Winston, 1982).

OCCURRENCE: Colonies were collected at Capron Shoal in April and August 1983, April 1984, November 1984, and January 1985.

DISTRIBUTION: New England to Brazil.

Parasmittina signata (Waters), 1889

Figures 64–67

Smittina signata Waters, 1889, p. 17.
Schizoporella horsti Osburn, 1927, p. 127.
Rimulostoma ? *signata* Cheetham and Sandberg, 1964, p. 1038.
Parasmittina signata Lagaaij, 1963, p. 197.

DESCRIPTION: Colonies are encrusting, forming small irregular patches on sand grains. Zooids are ovoid to subhexagonal, with a wavy, rugose frontal wall, perforated only by marginal areolae. Distally the frontal surface rises to a thick and scalloped peristomial collar around the lateral and proximal sides of the orifice. The peristome dwindles at the distal end of the orifice where a smooth rim bears two or three oral spines. The orifice is semicircular distally, with two elongate condyles defining a small U-shaped proximal sinus. No ovicells or avicularia occurred on our specimens.

	MEASUREMENTS		
	RANGE	MEAN	N
Lz	0.270–0.468	0.376	12
Wz	0.198–0.306	0.231	12
Lo	0.072–0.144	0.095	12
Wo	0.072–0.126	0.093	12
Lov	0.180–0.198	0.189	2
Wov	0.180–0.216	0.198	2

OCCURRENCE: Collected at Capron Shoal in August 1983, August 1984, November 1984, and January 1985.

DISTRIBUTION: Cosmopolitan in warm water. Western Atlantic: Cape Hatteras to Florida. Caribbean. Gulf of Mexico.

FAMILY MICROPORELLIDAE HINCKS, 1880

GENUS *MICROPORELLA* HINCKS, 1877

Microporella umbracula (Audouin), 1826

Figures 68, 69

Flustra umbracula Audouin, 1826, p. 239.
Microporella ciliata var. *coronata* Hastings, 1930, p. 727.
Microporella coronata Osburn, 1952, p. 386.
Microporella umbracula Harmer, 1957, p. 964. Powell, 1971, p. 772. Banta and Carson, 1977, p. 395. Winston, 1982, p. 150.

DESCRIPTION: Colonies encrusting, unilaminar, pink to orange when alive, with short, dark green spines. Zooids are polygonal and variable in size. The surface is inflated, with roughened calcification perforated by small pores. Zooids are separated from each other by a depression.

The orifice is semicircular, with four to six spines occurring around its distal margin, usually becoming broken off. A crescent-shaped ascopore, edged with a row of fine teeth, is found under the orifice. In sand grain specimens the area below the ascopore is greatly thickened and raised into an umbo. Distolaterally directed avicularia with very pointed mandibles occur on one or both sides of the ascopore. The ovicell is large, globular, porous, and closed by the zooidal operculum.

MEASUREMENTS

	RANGE	MEAN	N
Lz	0.432–0.630	0.521	15
Wz	0.306–0.504	0.372	15
Lo	0.072–0.108	0.094	15
Wo	0.090–0.126	0.107	15
Lov	0.234–0.252	0.243	2
Wov	0.270	0.270	2
Lav	0.036–0.090	0.173	15
Wav	0.036–0.054	0.032	15
Lasc	0.018–0.036	0.021	14
Wasc	0.018–0.036	0.031	14

DISCUSSION: This species (which was found only on larger grains) is always multiserial. Ovicells appear to form earlier than in colonies from larger substrata; in the colony illustrated in figure 68 they are developing on zooids in the third generation from the ancestrula.

OCCURRENCE: Living colonies were found at Capron Shoal in August 1983 and January 1985. Colonies were found at each census. *Microporella umbracula* is also found on larger shell substrata at Capron Shoal, Walton Rocks, and further offshore on the *Oculina* pinnacles (Winston, 1982).

DISTRIBUTION: Circumtropical. Western Atlantic: Florida. Caribbean.

FAMILY PHYLACTELLIDAE CANU AND BASSLER, 1917

GENUS *PHYLACTELLA* HINCKS, 1879

Phylactella ais, new species

Figures 70–75

DIAGNOSIS: Uniserial *Phylactella,* with blunt condyles but no lyrula, and with a prominent flared peristome which comes to a point proximally. No avicularia. Prominent ovicell with scattered pores.

HOLOTYPE: AMNH 681.

PARATYPES: AMNH 682, 683, 684, 685.

ETYMOLOGY: The species is named for the Indian tribe that once inhabited the shores of South Hutchinson Island.

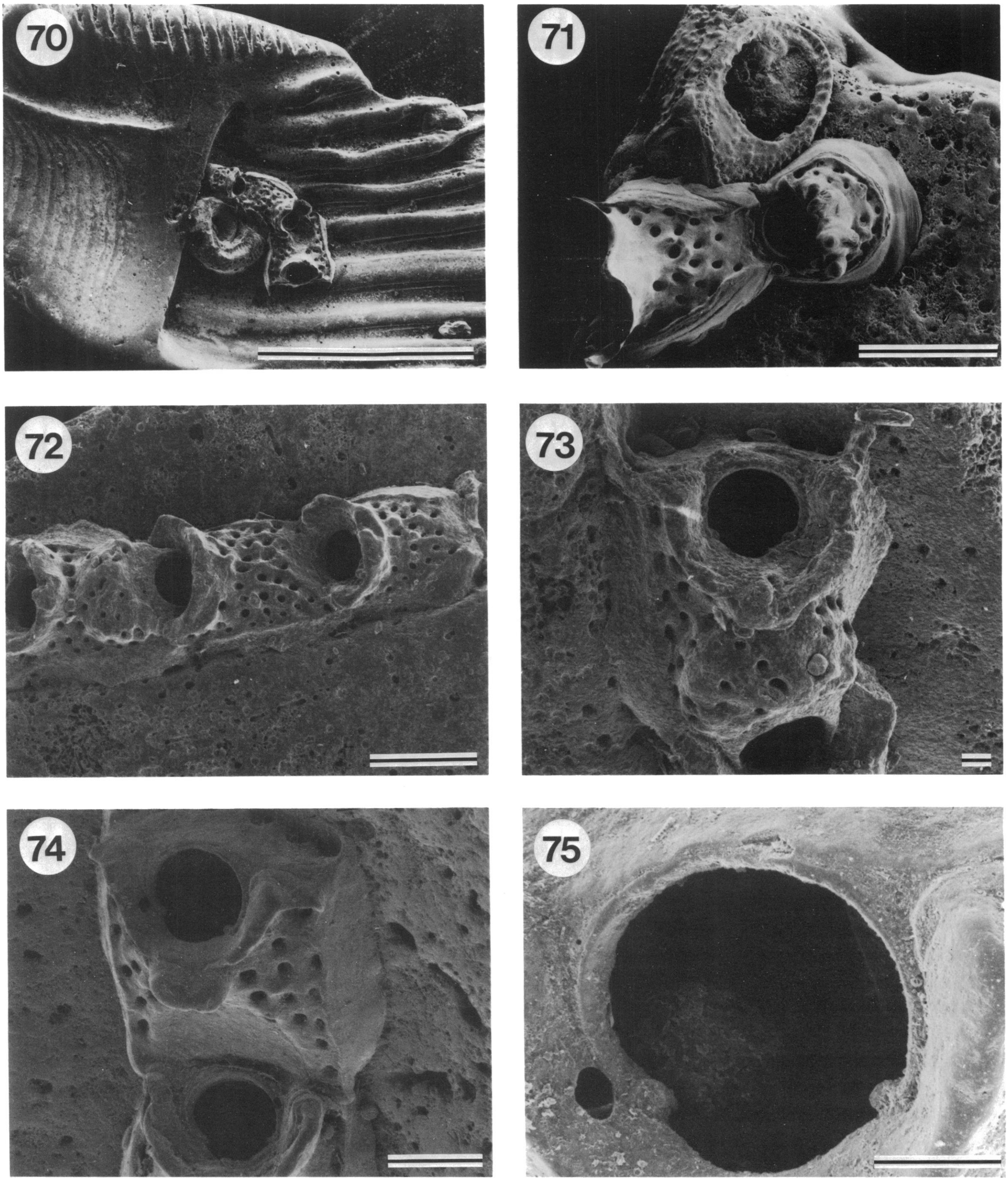
DESCRIPTION: Colonies are white, encrusting, sometimes branching in uniserial rows. Zooids are rectangular in shape; the frontal wall convex, rough textured and punctured by large round, evenly spaced, sunken pores. The primary orifice is semicircular anteriorly, with blunt lateral condyles and a shallowly curved proximal margin. The orifice is surrounded laterally and proximally by a broad raised peristomial collar which comes to a central point proximally.

The ancestrula is not tatiform. Its frontal wall is heavily calcified with a few pores; it lacks the orificial collar of other zooids and possesses two distolateral spines. Ovicells are helmet shaped, with scattered pores (smaller and fewer than those of zooids) and can be found in the first generation from the ancestrula. Embryos are orange-yellow. Polypide has 12 pale-orange tentacles and displays *Schizoporella*-type writhing behavior.

MEASUREMENTS

	RANGE	MEAN	N
Lz	0.216–0.324	0.278	12
Wz	0.144–0.306	0.228	14
Lo	0.072–0.090	0.082	14
Wo	0.072–0.108	0.089	14
Lov	0.108–0.126	0.114	3
Wov	0.180–0.216	0.198	3

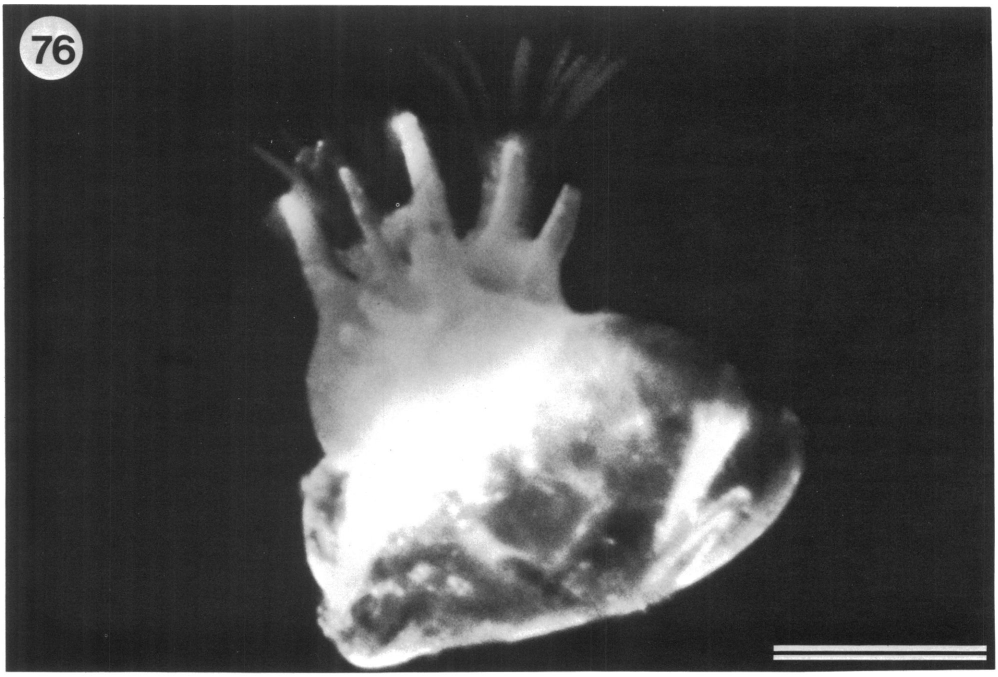
OCCURRENCE: Colonies were found at Capron Shoal in April 1983 (live), August 1983,



Figs. 70–75. **70.** *Phylactella ais* (AMNH 681), colony on barnacle plate grain. Scale bar = 1 mm. **71.** *Phylactella ais* (AMNH 682), showing ancestrula (also visible is a zooid of *Membranipora triangularis*). Scale bar = 200 μm. **72.** *Phylactella ais* (AMNH 682), colony with ovicelled zooid. Scale bar = 200 μm. **73.** *Phylactella ais*, close-up of ovicelled zooid. Scale bar = 40 μm. **74.** *Phylactella ais*, showing flared peristome. Scale bar = 100 μm. **75.** *Phylactella ais*, close-up of orifice. Scale bar = 40 μm.

August 1984, November 1984, and January 1985.

DISTRIBUTION: Capron Shoal, Atlantic coast of Florida.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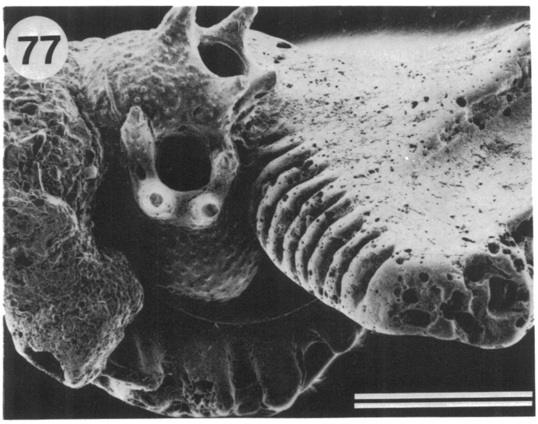
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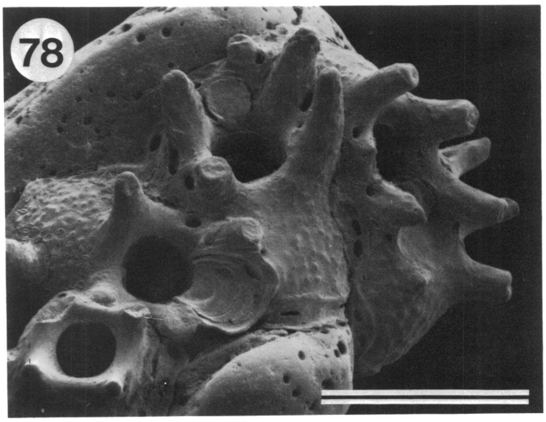
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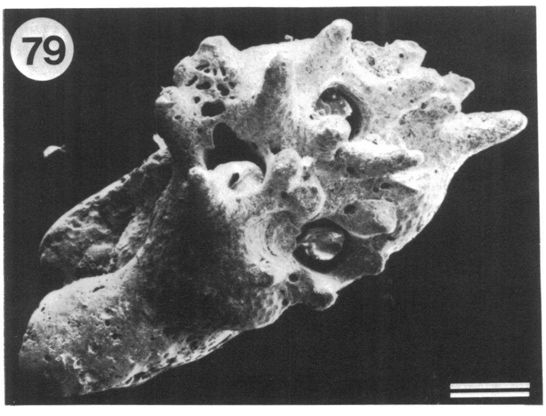
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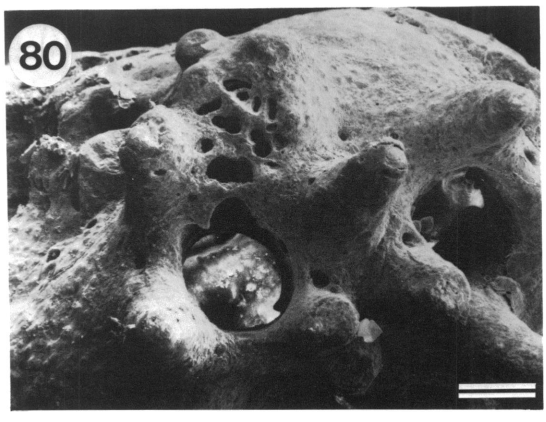
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SUPERFAMILY CELLEPOROIDEA LAMOUROUX, 1821

FAMILY CELLEPORIDAE BUSK, 1852

GENUS *TREMATOOECIA* OSBURN, 1940

Trematooecia psammophila, new species
Figures 76–80

Diagnosis: *Trematooecia* with colony encrusting sand grains. Zooids with 4–5 marginal spines and with marginal pores only. Ovicell frontal area with about 8–12 pores. No avicularia.

Holotype: AMNH 686.

Paratypes: AMNH 687, 688, 689.

Etymology: The species name, *psammophila,* is taken from the Greek *psammos* (sand) and *philia* (love) in recognition of its preference for small grains as substrata.

Description: Colonies are encrusting, unilaminar, and pale pink when alive. Zooids are erect, covered by a thick tubercular calcification that is penetrated only by a few marginal pores. The primary orifice is centrally located, circular anteriorly with a short pointed condyle, convex posteriorly, and surrounded by four or five (usually four) thick, solid, tapering spines, also covered by the same minute tubercles. There are no avicularia. The ovicells, which may be initiated in colonies with only three to five zooids, are buried in the surface calcification between the two distal spines. The ovicell has a lacy, porous central area and an arched opening above the zooidal operculum. Embryos are red. Lophophores have a translucent peach coloration.

MEASUREMENTS

	RANGE	MEAN	N
Lz	0.270–0.486	0.413	15
Wz	0.252–0.450	0.336	15
Lo	0.126–0.162	0.143	15
Wo	0.090–0.162	0.132	15
Lov	0.216	0.216	1
Wov	0.180	0.180	1

Discussion: The ancestrula of this species most frequently occurs in a hollow or crevice of a grain, but unlike most sand grain species, *T. psammophila* colonies are most commonly found encrusting convex surfaces of grains or protruding from them (Håkansson and Winston, 1985). They are found most often on very small grains (fig. 76), but they have also been observed to cement two grains together (fig. 77).

This species is very similar to *Trematooecia turrita* (Smitt), which is found on larger substrata in the area. It differs from *T. turrita* in its smaller colony and zooid size (zooids of Florida specimens average about 0.50 mm in length and width; zooids of Belize specimens about 0.54 in length and 0.52 in width). *T. turrita* zooids also have pores scattered over the frontal surface, rather than limited to zooid margins and have ovoid adventitious avicularia of two size classes, smaller ones with a serrated frontal rostrum, and larger ones with a smooth, scoop-shaped rostrum. In addition, the ovicells of *T. turrita* have fewer (4–8), and larger pores than those of *T. psammophila.* (The species is listed as *Cigclisula* cf. *turrita* in Håkansson and Winston, 1985.)

Occurrence: Colonies were collected at Capron Shoal during each census and found alive in the following censuses: April 1983, August 1984, and January 1985.

FAMILY CLEIDOCHASMATIDAE CHEETHAM AND SANDBERG, 1964

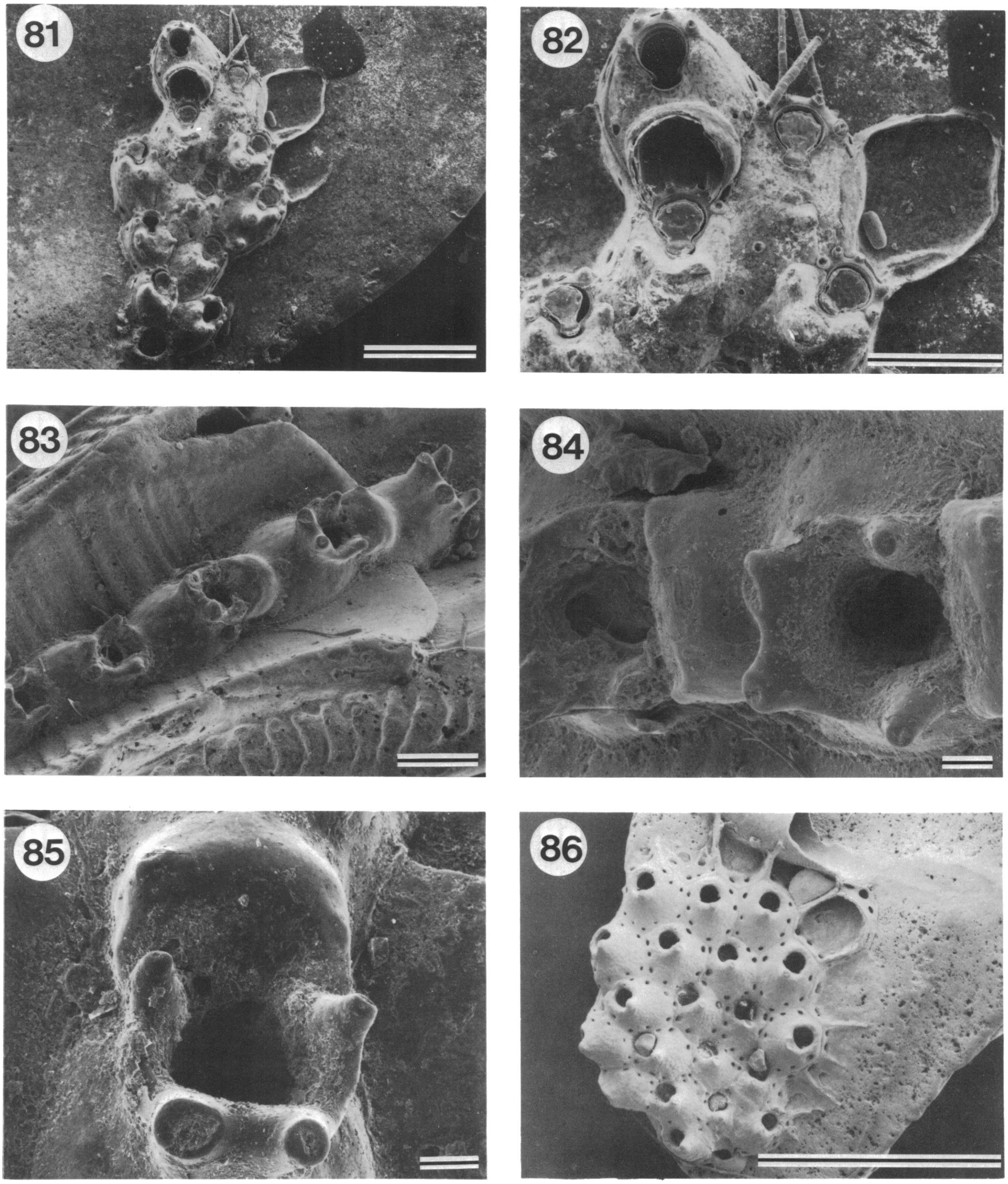
GENUS *CLEIDOCHASMA* HARMER, 1957

Cleidochasma porcellanum (Busk), 1860
Figures 81, 82

Lepralia porcellana Busk, 1860, p. 283.
Lepralia cleidostoma Smitt, 1873, p. 63.
Hippoporina cleidostoma Canu and Bassler, 1928b, p. 104.

←

Figs. 76–80. **76.** *Trematooecia psammophila,* live colony on quartz grain. Scale bar = 300 μm. **77.** *Trematooecia psammophila* (AMNH 685), colony welding two sand grains together. Scale bar = 400 μm. **78.** *Trematooecia psammophila* (AMNH 687), colony on edge of grain, showing developing ovicell. Scale bar = 400 μm. **79.** *Trematooecia psammophila* (AMNH 688). Scale bar = 200 μm. **80.** *Trematooecia psammophila,* close-up of ovicell and orifice. Scale bar = 100 μm.



Figs. 81–86. **81.** *Cleidochasma porcellanum* (AMNH 690), whole colony on shell grain. Scale bar = 400 μm. **82.** *Cleidochasma porcellanum,* close-up of zooids. Scale bar = 200 μm. **83.** *Cleidochasma angustum* (AMNH 691), colony on barnacle plate grain. Scale bar = 200 μm. **84.** *Cleidochasma angustum,* close-up of orifice. Scale bar = 40 μm. **85.** *Cleidochasma angustum,* close-up of orifice. Scale bar = 40 μm. **86.** *Aimulosia pusilla* (AMNH 695), whole colony on shell grain. Scale bar = 1 mm.

Hippoporina porcellana Hastings, 1930, p. 721. Marcus, 1937, p. 96. Osburn, 1940, p. 428; 1952, p. 344. Shier, 1964, p. 633.

Cleidochasma porcellanum Cheetham and Sandberg, 1964, p. 1032. Cook, 1964, p. 11; 1968a, p. 198. Long and Rucker, 1970, p. 19. Powell, 1971, p. 771. Winston, 1982, p. 148; 1984, p. 28.

DESCRIPTION: Colonies are encrusting, multiserial, unilaminar, and porcellanous white, distinguishable from the white of their shell grain substrata only by their golden-colored opercula. The ancestrula is tatiform with eight spines. Subsequent zooids are hexagonal, the frontal surface granular, often with a large suboral and two lateral umbos, and several marginal pores.

The orifice is keyhole shaped, its distal portion circular, with proximally directed cardelles and with a posterior sinus which varies from narrow to broad. There are four to five spines around the orifice. In this species avicularia are triangular, with trifoliate openings; their size and position can vary considerably. No avicularia were present in sand grain specimens. Ovicells are hyperostomial and imperforate, prominent on young zooids (as in the developing ovicell of fig. 82). Away from the growing edge they may be increasingly embedded in calcification.

	MEASUREMENTS		
	RANGE	MEAN	N
Lz	0.216–0.306	0.257	15
Wz	0.126–0.234	0.185	15
Lo	0.072–0.108	0.097	15
Wo	0.054–0.090	0.070	15
Developing ovicells			
Lov	0.126–0.162	0.149	4
Wov	0.126–0.198	0.162	4

DISCUSSION: Though not as precocious as other sand grain species, these colonies reproduced early in comparison to Jamaican colonies of *Cleidochasma porcellanum*. Ovicells occurred in the fourth generation from the ancestrula (fig. 81). Morphological variation in *C. porcellanum* has been discussed by Cook (1964). Most zooids in our specimens have mamillated, rather than smooth-textured, frontal walls, the orifice surrounded distally by long spines and proximally by the lateral and suboral umbos. The proximal sinus of the orifice and the proximal portion of the operculum display the wide intercolony variation described by Cook (1964). Capron Shoal specimens differ from other specimens from Florida and the Caribbean in lacking avicularia and having four or five rather than the three spines described by Cook (1964).

OCCURRENCE: Living colonies were found at Capron Shoal in April 1984. Dead colonies were found in November 1984 and January 1985.

DISTRIBUTION: Circumtropical. Western Atlantic: Cape Hatteras to Brazil. Gulf of Mexico. Caribbean.

Cleidochasma angustum, new species

Figures 83–85

DIAGNOSIS: *Cleidochasma* with uniserial encrusting colony. Zooid orifice surrounded by four thick spinous processes. Ovicell imperforate, with a granular semicircular frontal area. No avicularia.

HOLOTYPE: AMNH 691.

PARATYPES: AMNH 692, 693, 694.

ETYMOLOGY: The species is named from the Latin *angustus*, narrow, because of its uniserial growth habit.

DESCRIPTION: The colony is uniserial, encrusting sand grains. Zooids are ovoid, the entire frontal surface imperforate and smooth textured. The orifice is keyhole shaped, circular anteriorly, with a U-shaped proximal sinus. It is surrounded by a thick peristome ending in four tubby tapering spines. The ovicell also is smooth walled and imperforate, but has a semicircular frontal area with more granular calcification. There are no avicularia.

	MEASUREMENTS		
	RANGE	MEAN	N
Lz	0.252–0.360	0.289	12
Wz	0.144–0.270	0.216	12
Lo	0.054–0.072	0.061	12
Wo	0.054–0.072	0.061	12
Lov	0.108–0.126	0.117	2
Wov	0.144–0.162	0.153	2

DISCUSSION: Members of the genus *Cleidochasma* show a tendency to produce minute "sand fauna" colonies or species (see Cook, 1966; Harmelin, 1977; Hayward and Cook, 1979).

OCCURRENCE: Living colonies were found at Capron Shoal in April 1983. Dead colonies were found in August 1984 and January 1985.

GENUS *AIMULOSIA* JULLIEN, 1888

Aimulosia pusilla (Smitt), 1873
Figures 86–89

Discopora albirostris forma *pusilla* Smitt, 1873, p. 70.
Holoporella pusilla Osburn, 1914, p. 215.
Hippoporella pusilla Cook, 1964, p. 10; 1968a, p. 190.

DESCRIPTION: Colonies are encrusting, multiserial, and unilaminar. Zooids are hexagonal, convex, and outlined by a single row of large marginal pores. The rest of the frontal surface is covered by thick roughened calcification, rising to a peak in the suboral umbo. The orifice is large relative to zooid size and hoof shaped, with a circular anterior portion and a broad shallow proximal portion. The anterior portion is bordered by four oral spines which may become broken and obscured with age. The ancestrula is tatiform, with a circular frontal membrane and eight oral spines. Ovicells have a concave lower rim, large marginal pores, and a roughened surface, sometimes with a projecting central tubercle.

MEASUREMENTS

	RANGE	MEAN	N
Lz	0.180–0.360	0.268	15
Wz	0.162–0.270	0.217	15
Lo	0.054–0.108	0.074	15
Wo	0.072–0.126	0.084	15
Lov	0.090–0.162	0.126	4
Wov	0.162–0.180	0.176	4

OCCURRENCE: This species was collected at Capron Shoal at each census.
DISTRIBUTION: Florida. West Africa.

Aimulosia uvulifera (Osburn), 1914
Figures 90–92

Lepralia uvulifera Osburn, 1914, p. 210; 1940, p. 427.
Aimulosia uvulifera Osburn, 1947, p. 35; 1952, p. 352. Maturo, 1957, p. 52. Soule, 1961, p. 20. Shier, 1964, p. 634. Soule and Soule, 1964, p. 19.

DESCRIPTION: Colonies are encrusting and very small. Zooids are small and subhexagonal. The frontal surface is heavily calcified except for a very few marginal pores and is smooth textured; it rises distally into a projecting pointed umbo, so that the primary orifice lies sunken within a peristome. The orifice is rounded distally, with straight sides, and arcuate proximally. Six marginal spines (four in ovicelled zooids) border the orifice. The ancestrula is tatiform with eight to nine oral spines. The ovicell is globose and imperforate and broader than long, with a scalloped proximal margin and a central projecting point.

MEASUREMENTS

	RANGE	MEAN	N
Lz	0.198–0.270	0.240	15
Wz	0.144–0.216	0.190	15
Lo	0.054–0.072	0.062	15
Wo	0.054–0.072	0.065	15
Lov	0.090–0.108	0.099	4
Wov	0.108–0.144	0.126	4

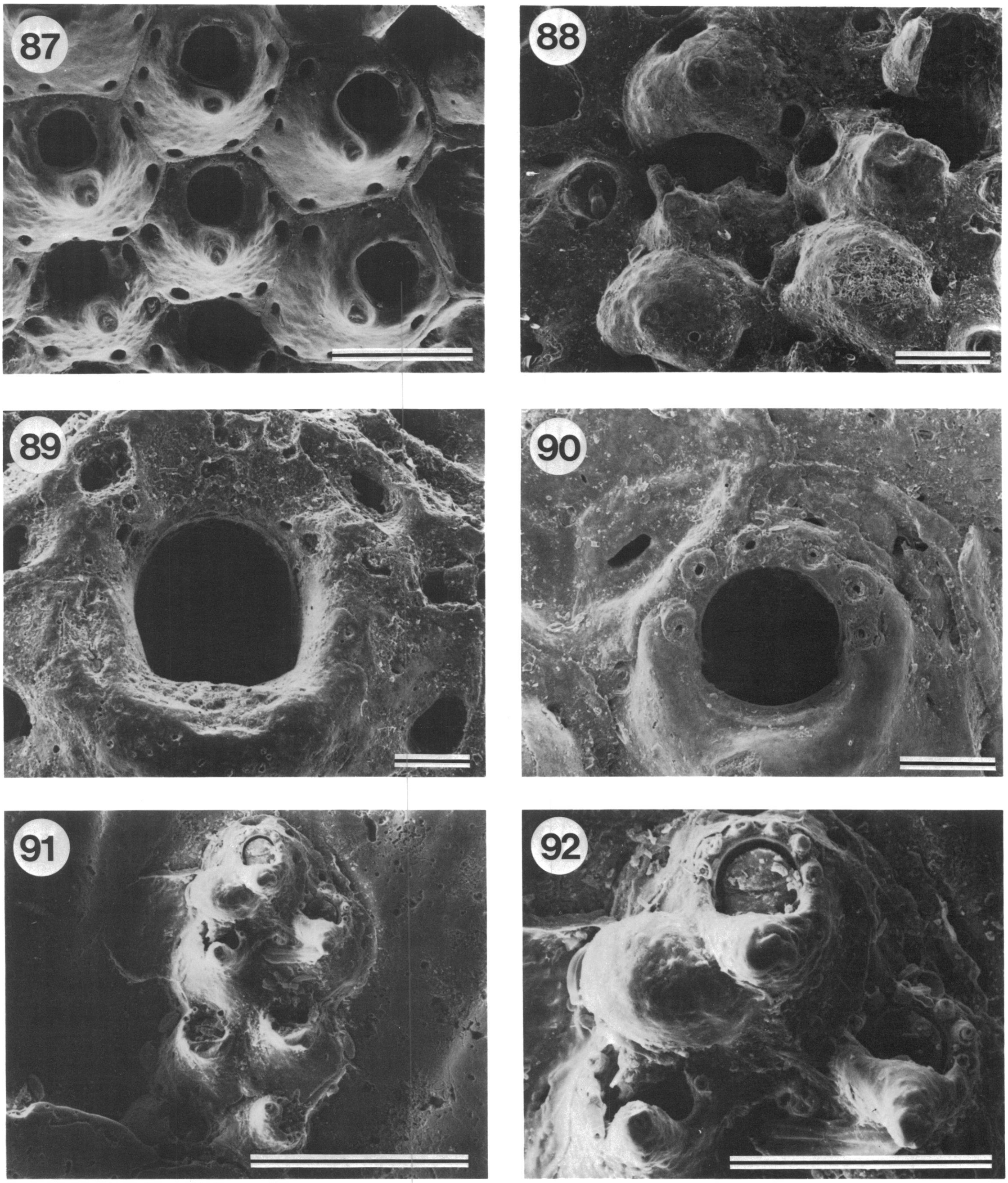
DISCUSSION: A trifid end to the umbo has been described (Osburn, 1914), but umbos of sand grain specimens end in a single point. A small triangular avicularium may occur lateral to the orifice, but no avicularia were found in sand grain specimens. Soule and Soule (1964) have discussed the confusion of this species with *Hippoporella gorgonensis*.
OCCURRENCE: The species was collected at Capron Shoal in April 1983 (live), August 1983, January 1984, and August 1984.
DISTRIBUTION: Beaufort, N.C. to Florida. Gulf of Mexico. Caribbean. Gulf of California and tropical E. Pacific.

FAMILY SERTELLIDAE JULLIEN, 1903

GENUS *DREPANOPHORA* HARMER, 1957

Drepanophora torquata, new species
Figures 93–96

DIAGNOSIS: Uniserial *Drepanophora*, with tubular peristome and curved orificial process, but no peristomial avicularium. Ovicells globose, lateral pores large.
HOLOTYPE: AMNH 699.
PARATYPES: AMNH 700, 701, 702.
ETYMOLOGY: From the Latin *torquatus*, meaning adorned with a necklace or collar.
DESCRIPTION: Colonies are primarily uniserial, rarely loosely pluriserial, arising from an 8?-spined tatiform ancestrula, with a gymnocystal area as large as the opesia. Zooids



Figs. 87–92. **87.** *Aimulosia pusilla.* Scale bar = 200 μm. **88.** *Aimulosia pusilla* (AMNH 696), close-up of ovicells. Scale bar = 100 μm. **89.** *Aimulosia pusilla,* close-up of orifice. Scale bar = 40 μm. **90.** *Aimulosia uvulifera* (AMNH 697), close-up of orifice and oral spines. Scale bar = 40 μm. **91.** *Aimulosia uvulifera* (AMNH 698), whole colony. Scale bar = 400 μm. **92.** *Aimulosia uvulifera,* close-up of ovicells. Scale bar = 200 μm.

are ovoid, the frontal surface convex proximally and rising distally into a thick-walled tubular peristome. The frontal wall is imperforate except for marginal pores, and rough textured, with many small tubercles. Some zooids may have an umbo developed below the peristome.

The secondary orifice is irregularly subtriangular, the distal part broad, the proximal part tapering. A thin curved process or denticle is located near the proximal end of the secondary orifice and projects into it, but there is no associated peristomial avicularium. Ovicells are globose, wider than long, with a thick outer covering and two large lateral pores. In some colonies the peristome of ovicellate zooids becomes transversely elongated and fluted. Polypides have 12 tentacles and a pale orange coloration.

MEASUREMENTS

	RANGE	MEAN	N
Lz	0.198–0.360	0.278	15
Wz	0.162–0.270	0.229	15
Lo	0.072–0.144	0.106	15
Wo	0.090–0.126	0.102	15
Lov	0.072–0.144	0.108	4
Wov	0.144–0.234	0.180	4

DISCUSSION: This species can be assigned to *Drepanophora* on the basis of the peristomial denticle and the two lateral pores in the ovicell. In zooidal characters it most closely resembles two of the species described by Thornely (1905) from Ceylon as *Rhyncopora* [sic] *incisor* and *Rhyncopora corrugata.* Harmer (1957) pointed out that the basal denticle is actually the tip of an acute triangular projection of the avicularium. From Harmer (1957) it is apparent that of the specimens of *D. corrugata* he examined many had "incomplete" or "undeveloped" avicularia, thus had only basal denticles. The species also resembles *Drepanophora tuberculatum,* but that species has a shorter peristome and the ovicell is completely calcified, with a thickened proximal rim, the lateral pores obvious only on young ovicells.

OCCURRENCE: Living specimens were collected at Capron Shoal in August 1984 and January 1985. Dead colonies were collected at each census.

DISTRIBUTION: Capron Shoal, Atlantic coast of Florida.

PHYLUM ENTOPROCTA NITSCHE, 1869

FAMILY PEDICELLINIDAE JOHNSTON, 1847

GENUS *BARENTSIA* HINCKS, 1880

Barentsia minuta, new species

Figure 97

DIAGNOSIS: Very small *Barentsia* with colonies epizooic on those of *Cupuladria doma.*

HOLOTYPE: AMNH 703.

PARATYPE: AMNH 704.

ETYMOLOGY: The species name is from the Latin *minutus,* meaning little.

DESCRIPTION: Colonies consist of creeping stolons with clusters of cup-shaped individuals on upright stalks spaced along them. The stolon is flexible and thin-walled, with a septum perforated by a central pore just above its muscular barrel-shaped base. Septa also occur between the pedicel base and the stolon. The cuplike calyx holds the internal organs. It ends in 12–13 short tentacles. The size of individuals varies with age.

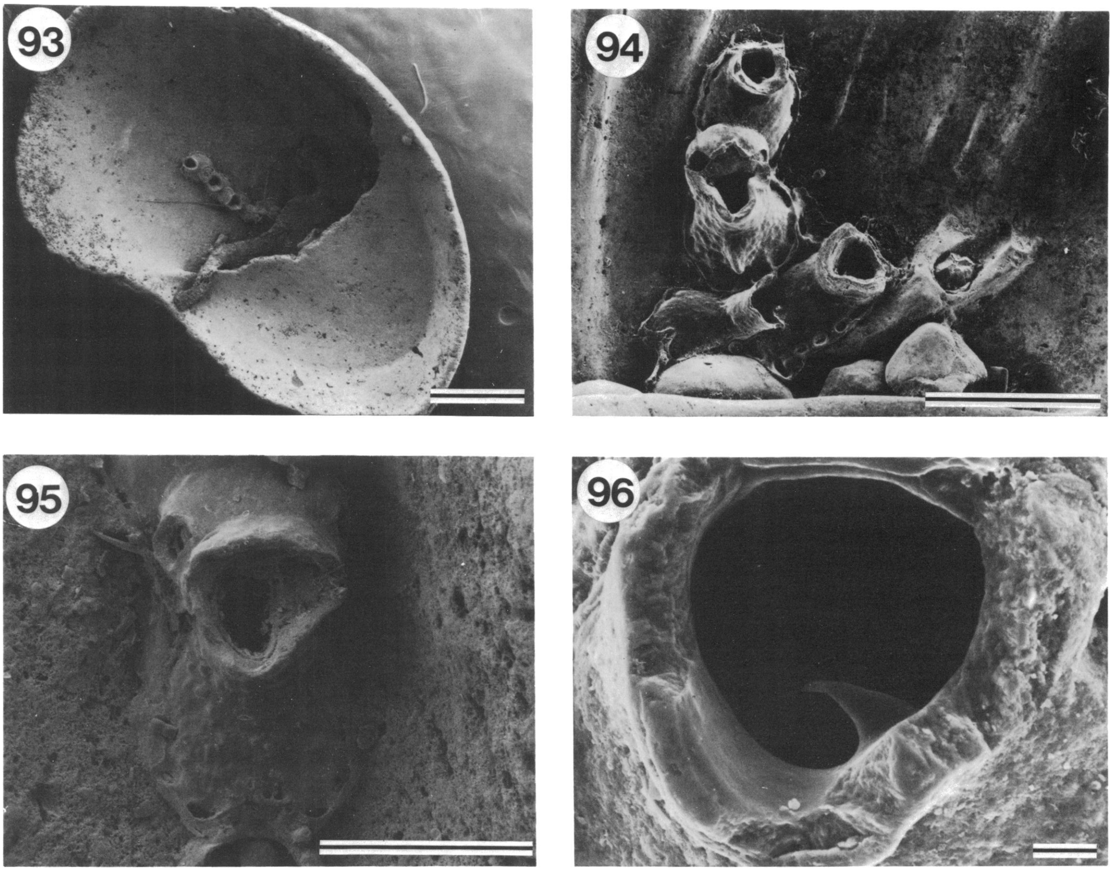
MEASUREMENTS

	RANGE	MEAN	N
Calyx L	0.126–0.315	0.171	8
W	0.105–0.315	0.171	8
Pedicel heights	0.420–0.630	0.321	7
Diameter	0.042–0.063	0.046	5
Basal enlargement			
L	0.168–0.231	0.210	5
W	0.063–0.105	0.084	5

DISCUSSION: Entoproct species seem to be extremely plastic in their morphology, varying both in quantitative characters like size, and in qualitative characters such as presence or absence of spines, pores, joints, etc. The presence of the muscular basal enlargement of the pedicel establishes this species as *Barentsia. Barentsia gracilis* is probably the closest relative of this species, but the extremely small size range of our specimens, plus their commensal habit, resulted in a decision to describe them as a new species.

OCCURRENCE: Found attached to *Cupuladria doma* colonies at Capron Shoal. Entoprocts were noted in all samples. In April samples many of the individuals consisted only of pedicels—the calyces had been lost or shed during the winter months. January 1985 samples showed white embryos in calyces of some individuals.

DISTRIBUTION: Capron Shoal, Atlantic coast of Florida.



Figs. 93–96. **93.** *Drepanophora torquata* (AMNH 699), colony inside *Crepidula* shell, partially overgrown by sponge. Scale bar = 1 mm. **94.** *Drepanophora torquata* (AMNH 700), another colony. Ovicelled zooid with large hole bored on left side. Scale bar = 400 μm. **95.** *Drepanophora torquata* (AMNH 701), close-up of ovicelled zooid. Scale bar = 200 μm. **96.** *Drepanophora torquata,* close-up of peristomial denticle. Scale bar = 20 μm.

DISCUSSION

The Interstitial Existence

Almost every invertebrate phylum is represented in interstitial faunas, and some whole groups, such as the Gnathustomulida, Gastrotricha, Kinorhyncha, and the most recently described phylum, the Loricifera (Kristensen, 1983), are entirely interstitial. However, most studies on interstitial meiofauna have been carried out in intertidal sand or mud habitats. Much less work has taken place in subtidal habitats like that at Capron Shoal.

The sediment in our study area was primarily a well-sorted, medium-coarse biogenic sand, with very little silt and a low organic content, grading in places to coarse sand and shell gravel. The internal surface area of such a sand, composed of the surfaces of all the grains, is vast in extent, providing an enormous habitat for microbial populations: bacteria and (near the surface) sessile diatoms (Jansson, 1971). Many sand dwellers utilize bacteria or diatoms as a food source. Thus, a rich fauna may be present even when the organic content is low. Detritus may also be a food source, but can be detrimental as well, because detritus particles may restrict pore space.

In fact, pore space, rather than grain size, appears to be what limits distribution of at least the larger interstitial organisms (Jansson, 1971; Williams, 1971). Interstitial or-

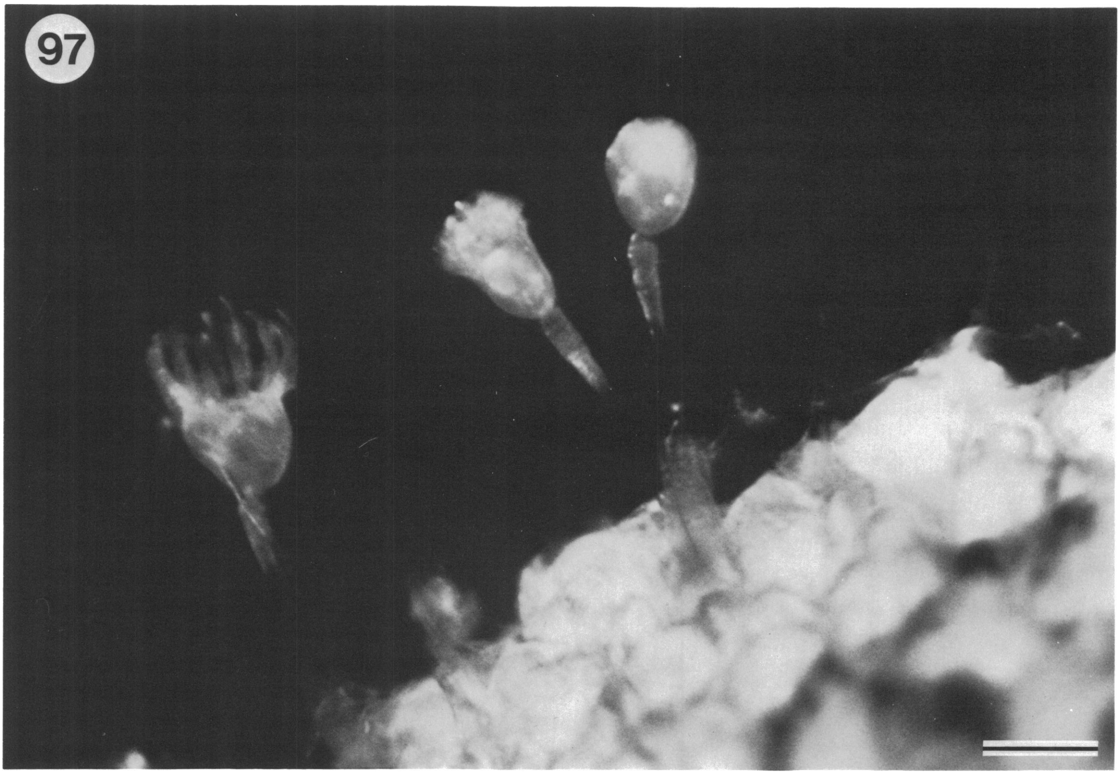


Fig. 97. *Barentsia minuta* (AMNH 703), living colony on upper surface of a *Cupuladria* colony. Scale bar = 200 μm.

ganisms live in an array of channels formed by the spaces between sediment grains. Through these channels water flows in a viscous manner; in them the animals move or feed. As Vogel (1981) put it, for us to imagine the physical world of these animals is to imagine "slithering through moving glop between boulders while blindfolded."

Other factors affecting meiofaunal distributions are temperature, salinity, oxygen, and water movement. Subtidal communities are buffered from the abrupt changes of temperature and salinity experienced in the intertidal zone. Coarse subtidal sand like that at Capron Shoal acts like a giant aquarium filter, the action of waves and currents causing a constant flow of oxygenated water to pass through the sediment; oxygen is not a problem due to the effects of this subtidal pump (Riedl et al., 1972). The reducing layer is situated well below the sediment–water interface, and, in comparison with the intertidal, meiofaunal organisms can live many centimeters into the sand. Preliminary analyses of cores taken at Capron Shoal in August 1984, for example, showed live encrusting bryozoans occurring 16 cm into the substratum (Håkansson, unpub. data).

Effects of wave and current action are more important in shallow areas like Capron Shoal than in deeper waters. Fifty meter SCUBA transects carried out at the Capron Shoal study site in August 1983 showed sediment patterns to consist of ripple marks, 3 crests per meter, about 20 cm in relief, arranged parallel to the long axis of the shoal. Such ripple marks were again observed during dives made the following August. No large-scale transition in grain size was observed over the transects; all the variation was microvariation on or between ripples. Thus, sediment grains of different sizes, weights, and shapes were not evenly distributed, but aggregated in patches due to their differential behavior with regard to wave surge (larger shell fragments seem to drift to the top of the sediment) and the action of burrowing animals, chiefly the sand dollars, *Encope* and *Mellita*. This microvariation is obliterated in dredged samples subjected to sediment analysis, but may be important in regulating the distribution of the interstitial fauna.

No quantitative meiofaunal surveys have been undertaken at Capron Shoal. In our samples, the most common motile organisms were ciliates, copepods, nematodes, ostracodes, flatworms, archiannelids, polychaetes, small gastropods, scaphopods, juvenile bivalves, and *Amphioxus*.

The bryozoans, of cousre, are not part of this motile fauna. They are, instead, an important component of the encrusting meiofauna, a category which seems to have been almost totally neglected by meiofaunal ecologists. At Capron Shoal the encrusting meiofauna included the following groups: foraminiferans, serpulid and spirorbid tubeworms, hydroids, sponges, turbellarian and other egg cases, and fungi. Fungal and algal borings were also common, as were the borings produced by ctenostome bryozoans. The foraminiferans encrusted the largest percentage of grains, followed by the tubeworms and bryozoans; the other encrusting organisms were much rarer. This community is illustrated in figure 98.

Characteristics of Interstitial Bryozoans

Morphological and ecological characteristics of the noncupuladriid bryozoans are shown in table 1.

All meiofaunal organisms share certain adaptations to the interstitial existence. These include small body size, elongate form, simplified body organization relative to noninterstitial relatives, development of adhesive organs, neoteny, small number of eggs or embryos, and brooding or nonplanktonic development.

Eleven of the noncupuladriid species found at Capron Shoal are only known from sand or gravel-sized sediments. Our previous study (Håkansson and Winston, 1985) showed that several of these species have specific grain size preferences, indicating that they are adapted to the interstitial life.

Preliminary studies of a series of grains ranging from sand to whole shells (Winston, unpub.) showed also that species diversity is bimodal. Diversity is high on the sand and fine gravel fraction (those species described in this paper). It declines considerably on small whole shells (6–10 mm in length) to less than a dozen species with *Cribrilaria innominata, Bellulopora bellula, Trypostega venusta,* and *Alderina smitti* dominating. On larger shells the number of species climbs again, but in addition to the 17 species listed (table 1), includes an additional suite of species not found on smaller grains (Winston, unpub. data).

Other characteristics also adapt Capron Shoal species to live in interstitial sand.

Transparency: Most interstitial organisms are transparent. Their invisibility against the shiny grains on which they dwell may render them less susceptible to predation. The bryozoans in our sample showed few exceptions to this rule. As exemplified by the colony of *Membranipora triangularis* shown in figure 8, living colonies are almost impossible to photograph—only the guts of the polypides (which had been fed with dark-colored flagellates) can be seen against the light-colored barnacle plate grain. Transparency may, in fact, be common among most shell-dwelling bryozoans, as all but two of the other encrusting cheilostomes were unpigmented.

Small Size: Interstitial species are also characterized by the small size of zooids and colonies. Such colonies exhibit paedomorphosis, becoming sexually mature at a juvenile stage. Zooids of the entire colony remain neanic (in the sense of Ryland, 1970), the colony never reaching the zone of astogenic repetition found in most encrusting species.

Colony structure is simplified in that there is little or no investment in nonfeeding polymorphs like avicularia. All the nonlunuliti-form species that were restricted to small grains lacked avicularia. Moreover, colonies of five of the species also found on larger substrata either lacked avicularia entirely or had nonfunctional avicularia, lacking mandibles. This parallels the situation in social insects, in which colonies are initiated by nanitic workers, small in size and timid in behavior, and larger workers and defensive castes appear later, once the colony has achieved a certain population size (Oster and

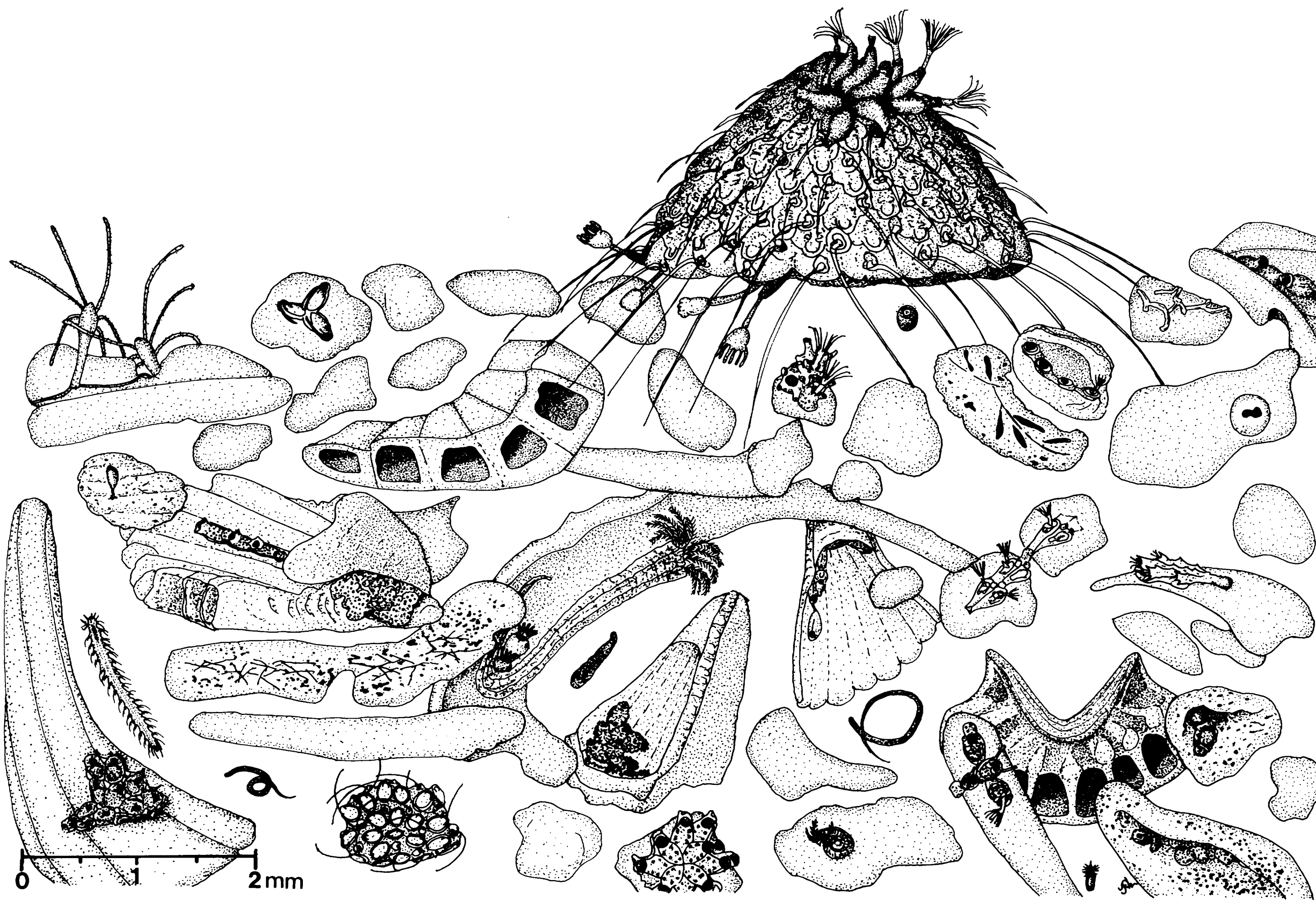


Fig. 98. A cross-sectional view of the interstitial habitat at Capron Shoal. At the sediment surface is an adult colony of *Cupuladria doma* with epizoic *Alcyonidium* and *Barentsia* colonies attached. A *Cupuladria* larva is visible below the adult. Other grains bear colonies of interstitial bryozoans, including juveniles of cupuladriids, and other encrusting fauna: tubeworms, forams, egg cases, hydroids, etc. Motile meiofauna occupy the water-filled spaces between the grains (sand grains and pore space drawn to scale from a resin-embedded sample).

TABLE 1
Characteristics of Sand Fauna Species

Species	Sand fauna only	Larger substrata	Cape Hatteras-Caribbean only	Other areas also	Uniserial	Bi-triserial	Multiserial	Spines	Tubercles, umbo, etc.	Avicularia	Size at repro-duction	Color of zooid/ polypide
Disporella plumosa	X		X				X		X		6Z	W/T[b]
Membranipora triangularis	X		X								NB[a]	W/T
Vibracellina laxibasis	X		X				X		X	X	15–20	W/T
Cymulopora uniserialis	X		X		X						3Z	W/T
Cribrilaria parva	X		X			X		X	X		12	W/T
Reginella repangulata	X		X		X			X	X		3Z	W/T
Hippothoa balanophila	X		X		X				X		6Z	W/T
Phylactella ais	X		X		X				X		3Z	W/pale orange
Trematooecia psammophila	X		X			X			X		4–5Z	pale pink/ peach pink
Cleidochasma angustum	X		X		X				X		3Z	W/?
Drepanophora torquata	X		X		X				X		3Z	W/T
Membranipora arborescens		X		X			X		X		NB	W/T
Membranipora savartii		X		X			X		X		NB	W/T
Alderina smitti		X		X		X			X		3Z	W/T
Antropora leucocypha		X		X			X				20	W/T
Retevirgula caribbea		X	X				X	X	X		6Z	W/T
Beania klugei		X		X	X			X		X	?	tan/tan
Floridina parvicella		X		X			X		X	X	20	W/T
Cribrilaria inominata		X		X		X	(X)	X	X	—[c]	12	W/T
Bellulopora bellula		X		X		X		X		—[c]	5Z	W/T
Trypostega venusta		X		X		X	(X)		X		4Z	W/T
Schizoporella rugosa		X	X			X	(X)		X	X	3Z	W/T
Escharina pesanseris		X		X			(X)	X		X	?	W/?
Microporella umbracula		X		X			X	X	X	X	15–20	pink-orange/ pink
Cleidochasma porcellanum		X		X		X	(X)	X	X	—[c]	10	W/T
Aimulosia pusilla		X		X			X	X	X	?	24	W/?
Aimulosia uvulifera		X		X		X		X	X	—[c]	3Z	W/?
Parasmittina signata		X		X		X	(X)	X	X	—[c]	?	W/?

[a] NB = nonbrooding.
[b] W = white; T = transparent.
[c] Nonfunctional.

Wilson, 1978). As in the social insects, a newly founded colony should attempt to maximize number of workers (autozooids) and their initial survival rate, on the basis of the limited energy available to the founder (queen or metamorphosed larva). And, as in the shorter-lived social insects, in the interstitial bryozoans, only two castes are produced, workers and reproductives.

REPRODUCTIVE PRECOCITY: Sexual reproduction takes place very early. It is not possible to indirectly assess reproductive state in nonbrooding species (four species in this study), but the presence of ovicells in brooding species shows the reproductive status reached even by colonies dead when collected. Ovicelled zooids occurred in the first three zooids of five of the species limited to small substrata and three of the species also found on larger substrata. Six more species were capable of initiating reproduction with colonies six zooids in size. Of the species restricted by substratum size, *Cribrilaria parva* and *Vibracellina laxibasis* produced the greatest number of zooids before reproducing, 12 zooids and 15–20 zooids, respectively.

But perhaps more interesting is the flexibility shown by species which also occur on larger substrata. Of the 14 species which produce ovicells, 12 had colonies with ovicells in our sample; all of these had reproduced with colonies of 24 or fewer zooids. Colonies of the same species from other habitats (e.g., *Cleidochasma porcellanum* and *Trypostega venusta* are both common in cryptic reef communities in Jamaica) reproduce at a much larger colony size. If colonies from other environments really are conspecific (and it must be stressed that we can only judge this on morphological criteria) then it appears that at least some bryozoans show a remarkable plasticity in the onset of sexual reproduction, and that onset seems to be triggered by environmental cues rather than a threshold colony size.

PROJECTIONS AND SPINES: One of the most striking features of most of these species is the presence of numerous projecting umbos, tubercles, and spines (e.g., *Membranipora triangularis*, fig. 9; *Reginella repangulata*, fig. 50; *Phylactella ais*, fig. 71). These may be important in the interstitial environment, where physical damage may be a greater problem than predation. Nevertheless, predation does occur in the interstitial fauna. A large percentage of motile forms are predators. A number of these, such as flatworms and gastropods (e.g., see drilled hole in the *Drepanophora* ovicells, fig. 94) may prey on bryozoans. Colonies are also damaged by boring organisms (e.g., holes in *Phylactella ais*, figs. 74, 75). But the effects of abrasion are more noticeable (e.g., figs. 13, 37, 41, 48, 56–58, 64, 88). Skeletal abrasion is very common in dead colonies, but many living colonies also showed evidence of regeneration and repair of abraded zooids, indicating that much damage takes place during life. Although flow of water through undisturbed sediment occurs in a viscous manner, and this viscosity may protect grains, preventing them from touching and abrading their encrusting fauna, physical processes in shallow water environments such as Capron Shoal may become violent. The polished, rounded surfaces of many grains indicate that much grinding of grain against grain does occur; this grinding may be enhanced by the intermixture of the small, hard, sharper-edged quartz grains which make up 15–30 percent of the sediment. The abrasion probably takes place primarily during the periods of heavy seas or storm conditions that are more common during winter months.

SHORT LIVES: We have no data on the lifespan of the interstitial encrusting species, but their early reproduction, the presence of a large number of skeletons for every living colony (averaging about 20 to 1), and the large amount of partial mortality and repair noted, suggest that colonies of these species are ephemeral. Population data on cupuladriids indicate that colonies of *Cupuladria doma*, whose juveniles are among the most common interstitial bryozoans, were primarily annual, with the greatest mortality taking place between January and April when weather conditions are most severe. Colonies of the larger *Discoporella umbellata depressa*, which reproduced primarily by fragmentation, appeared to be longer lived (Winston and Håkansson, unpub. data).

MORPHOLOGICAL PLASTICITY

The degree to which a species can exhibit changes in zooid or colony morphology under varied environmental conditions has long been a subject of speculation among bryozoan workers because of its taxonomic implications. If morphological plasticity is high, then we run the risk of splitting morphotypes that belong within the same species. If it is low, we may be lumping several similar species together. Growth form seems more plastic than zooid form. We know that some species can vary their growth from encrusting, to erect, to tubular or bilaminate and platy, depending on substratum and environmental conditions (e.g., Cook, 1968a; Ryland, 1970). But can a species vary its growth pattern from uniserial to multiserial according to its substratum?

Sixteen of the species we collected are known also from larger substrata. On such substrata they grow as multiserial sheets. Six species retain this growth pattern even on small grains, which they generally cover almost completely (e.g., *Membranipora arborescens,* fig. 11; *Microporella umbracula,* fig. 68). Other species show a biserial-triserial fanlike growth pattern on sand grains (e.g., *Cribrilaria innominata,* fig. 40; *Aimulosia uvulifera,* fig. 91). Young colonies of these species often exhibit similar growth on large substrata; they may also be multiserial. No species we studied varied from uniserial to multiserial. Plasticity in growth form appears real, but moderate.

Plasticity in zooid form is more restricted. The chief differences between sand grain specimens and those from larger substrata appear to be the strong development of skeletal projections in sand grain species and a slightly smaller, overall zooid size.

As pointed out in the previous section, onset of reproduction shows great plasticity. The situation with regard to other types of polymorphism—the development of avicularia, kenozooids or zooeciules—is more ambiguous. It does appear that at least half the species which have avicularia on larger substrata lack them in sand grain specimens. In interstitial colonies of *Trypostega venusta,* which normally have zooeciules between zooids, they are present only on ovicells (fig. 56).

Biogeographic Significance of Interstitial Habitat

The fact that two-thirds of the species found interstitially also occur on larger substrata has important implications for bryozoan biogeography. Fourteen of these species have relatively broad distributions, occurring in at least two tropical or subtropical regions. Ecologists and biogeographers have struggled to explain such distributions in animals like bryozoans, with nonfeeding larvae which spend a very short period of time (less than 24 hours) in the plankton. The idea of vicariance, the distribution of animals via drift of the continental plates themselves, has great appeal for such animals. The idea of dispersal by rafting has also recently been revived (Jokiel, 1984; Jackson, in press).

Unlike these two hypotheses, the interstitial refuge cannot explain dispersal across deep water, but it can help explain distributions along shallow shelves. On continental shelves like that off the southeastern United States, encrusting bryozoans have been assumed to be limited to the scattered occurrences of hard substrata: fossil reef, shell debris, ballast deposits, etc. (Maturo, 1968). The fact that a number of encrusting species can grow and reproduce on very small grains indicates that distributions may not be that patchy. It is true that living colonies are sparsely distributed. In Capron Shoal samples the average abundance of living encrusting (nonlunuliti-form) species was 0.75 per cm^3 of sediment. Thus, one square meter of sediment 1 cm in depth would contain 7500 living colonies. For the inner continental shelf off Florida alone this would yield a population of about 1.3×10^{12} colonies, and this estimate is conservative, as living colonies are known to occur much deeper than 1 cm into the sediment. In fact, the interstitial refuge may be an important factor in maintaining distributions of encrusting species, acting almost like the seed bank for populations of plants, by buffering the effects of physical and biological perturbations and lowering the chances of local extinction.

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