

***Epitonium millecostatum* and *Coralliophila clathrata*:
Two Prosobranch Gastropods Symbiotic with Indo-Pacific *Palythoa*
(Coelenterata: Zoanthidae)¹**

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ABSTRACT: Two little known prosobranch gastropods, the wentletrap *Epitonium millecostatum* (Pease 1860–1861) and the muricacean *Coralliophila clathrata* (A. Adams 1854), are both obligate symbionts of the colonial zoanthid sea anemone *Palythoa*. Data are given on the taxonomy of both gastropods, and on their symbioses in the Maldive Islands, Sri Lanka (Ceylon), and the Great Barrier Reef, Australia. Neither species had been reported previously from any of these regions, and the known range of *C. clathrata* is also extended to Zanzibar and the Marquesas Islands. *Coralliophila sugimotoi* Kuroda 1930 is shown definitely to be a synonym of *C. clathrata*.

Palythoa sloughs off nematocysts and zooxanthellae in its mucus, and both gastropods ingest this; they do not ingest the *Palythoa* tissue or polyps, which contain sand grains. The feces of the *Epitonium* consist chiefly of discharged nematocysts, while those of the *Coralliophila* consist chiefly of remnants of zooxanthellae. Both species presumably digest the mucus. The *Epitonium* also digests the zooxanthellae, thereby being in part herbivorous, and the *Coralliophila* apparently also digests the nematocysts. Both species have small eggs and a planktotrophic larval stage lasting about a month or more. The larvae of the two species must have well-developed settlement responses to *Palythoa*, which is sparsely and patchily dispersed in shallow water. Frequencies of the adult gastropods with *Palythoa* are low.

DESPITE THEIR NEMATOCYSTS, many kinds of coelenterates are host to symbiotic prosobranch and opisthobranch gastropods that feed on their tissues or mucus. One such host is the colonial zoanthinarian sea anemone or soft coral *Palythoa* (family Zoanthidae). *Palythoa* is a tropical genus that occurs around the world in shallow water, forming small to large incrustations on hard substrates. *Palythoa* has zooxanthellae, sand grains, and three kinds of nematocysts (Hyman 1940) embedded in its tissues, and extracts from some species are highly toxic

when injected into mammals (Moore and Schæfer 1971).

Three kinds of gastropods have been reported as symbionts with *Palythoa*: a nudibranch, a group of architectonicids, and various coralliophilids (muricaceans). The nudibranch is the specialized eolid *Aeolidiopsis ransonii* Pruvot-Fol (1956), reported only from the Tuamotu archipelago (Polynesia). According to Pruvot-Fol (1956) it feeds on the tissues of *Palythoa* and has sand grains in its gut.

The architectonicid genus *Heliacus* is obligately symbiotic with zoanthinarians (Robertson 1967). A *Heliacus* feeds by everting its long acrembolic proboscis and making a deep hole in its host. *Heliacus* feces contain zooxanthellae and sand grains. Their larvae are planktotrophic.

The first gastropod reported to have been

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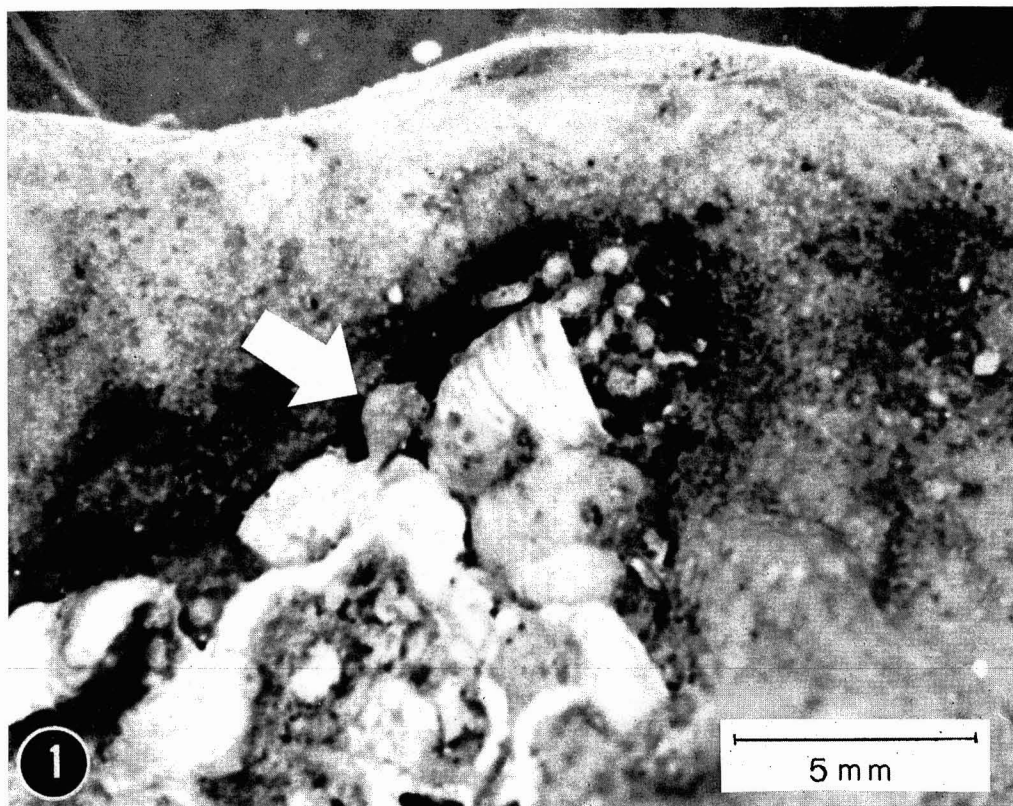


FIGURE 1. Specimen 29 and specimen 30 (arrow) of *Epitonium millecostatum* with egg capsules on underside of edge of incrustation of *Palythoa*. Great Barrier Reef, Australia.

found with *Palythoa* (as *Corticifera*, a synonym) was *Coralliophila sugimotois* Kuroda (1930, 1931) [= *C. clathrata* (A. Adams 1854)], described from Japan. The association apparently is a true symbiosis, i.e., the occurrence of this *Coralliophila* with *Palythoa* is consistent (Sugimoto 1929). The same seems to be true of *C. squamosissima* (E. A. Smith 1876), the synonymy of which was treated by Kilburn (1977). Kuroda (1931) recorded this second *Coralliophila* with *Corticifera* (= *Palythoa*) in Japan (as *C. stearnsii* Pilsbry 1895), and Kilburn (1972) recorded it with *Palythoa* in South Africa [as *C. meyerdorffi* (Calcara)]. Also, the Academy of Natural Sciences of Philadelphia has two specimens of *C. squamosissima* (ANSP 302792) embedded in a piece of *Palythoa* from Okinawa. In the tropical western Atlantic, *C. aberrans* (C. B. Adams

1850) is another *Palythoa* symbiont (Mendonça de Oliveira 1971; ANSP collection).

In an abstract, Robertson (1966) lists "*Epitonium* sp." and "*Coralliophila* cf. *C. sugimotois* Kuroda, 1930-31" as symbiotic with *Palythoa* in Ceylon and the Maldives.

The present paper treats the taxonomy, zoogeography, and some aspects of the ecology and life history of two prosobranch symbionts of *Palythoa* in the Indo-Pacific: the wentletrap *Epitonium millecostatum* (Pease 1860-1861) (Figure 1) and the muricean *Coralliophila clathrata*.

MATERIALS AND METHODS

Palythoa was torn up in search for prosobranchs when general collections of mollusks were made in Sri Lanka and the Maldives

Islands during the International Indian Ocean Expedition in 1964. More intensive investigations were made during a visit to the Lizard Island Research Station, Great Barrier Reef, northern Queensland, Australia, from 30 May to 13 June 1979. At Lizard Island the epitoniums were at depths between about 0.5 and 2 m below mean low water, except for specimen 42, which was an empty shell embedded in *Palythoa*, found by Ian Loch while scuba diving at a depth of 5 m. Loch also found the single Lizard Island specimen of *Coralliophila clathrata* while scuba diving at a depth of 10 m.

The Indian Ocean prosobranchs were dropped unrelaxed into 70 percent ethyl alcohol. The Great Barrier Reef prosobranchs were relaxed with $MgCl_2$ and then preserved. Three of the epitoniums were fixed in Bouin's solution, which dissolved the shells and enabled me to sex the specimens. (Epitoniid spermatozeugmata and oocytes can readily be distinguished in the gonads even with a dissecting microscope.) Other specimens, preserved in alcohol, were sexed either by crushing the shells or by boiling them to loosen the attachment of the columellar muscle and removing the body with a pin. Radulae were extracted (or in the case of the *Coralliophila*, searched for) from whole bodies with Clorox (5.25 percent sodium hypochlorite). Eggs and veligers were studied, measured, and drawn with the aid of a compound microscope. Feces of both species were collected from the outer edge of the operculum.

Sample specimens of *Palythoa* are retained along with the gastropods in the malacology collections of the Academy of Natural Sciences of Philadelphia and the Australian Museum, Sydney, Australia. Museum abbreviations used in the text are: AMS, Australian Museum; ANSP, Academy of Natural Sciences of Philadelphia; BMNH, British Museum (Natural History); SDSNH, San Diego Society of Natural History.

PALYTHOA

Palythoa taxonomy is in such chaos that it is presently impossible to identify the Lizard

Island host or hosts to species. More than one species may be present. Thus, the two gastropods associated with *Palythoa* at Lizard Island may or may not be host-specific. The *Palythoa* specimens range in color from reddish or yellowish brown through tan, sometimes with a greenish tinge.³ The polyps do not project much above the coenenchyme. The septa per average-sized polyp range from 40 to 46 (four counts; mean 42). The Indian Ocean species possibly is the same species as that at Lizard Island.

Palythoa ranges from the lower intertidal zone down to at least 15–16 m off North Point, Lizard Island (*vide* Ian Loch). Most of the *Palythoa* torn up was in 0.5–2 m of water. No large incrustations such as occur in Sri Lanka and the Maldives were seen. Old colonies split up into clusters of daughter colonies about 5–10 cm in diameter. The prosobranchs seemed mainly to be with small, isolated colonies of the anemones.

SUPERFAMILY EPITONIACEA (= PTENOGLOSSA) FAMILY EPITONIIDAE

Epitonium millecostatum (Pease 1860–1861)

SYNONYMY:

Scalaria millecostata Pease (1860–1861: 400, unfigured [Sandwich (Hawaiian) Islands]). Holotype (BMNH) discussed and illustrated by Kay (1965: 42–43, pl. 6, figs. 5–6).

Scala millecostata (Pease). E. A. Smith (1901: 109, pl. 1, fig. 5).

Epitonium millecostatum (Pease). Pilsbry (1921: 377) and Kay (1979: 155, fig. 54H).

SHELL (Figure 2): An all-white *Epitonium* attaining a length of 9.7 mm and an (exceptional) width of 7.1 mm, with about $6\frac{3}{4}$ teleoconch whorls. Thin and fragile. Pro-

³The same or a similar Great Barrier Reef *Palythoa* has been well illustrated in color (as *P. caesia*) by Gillett and McNeill (1959); the polyps are shown closed.

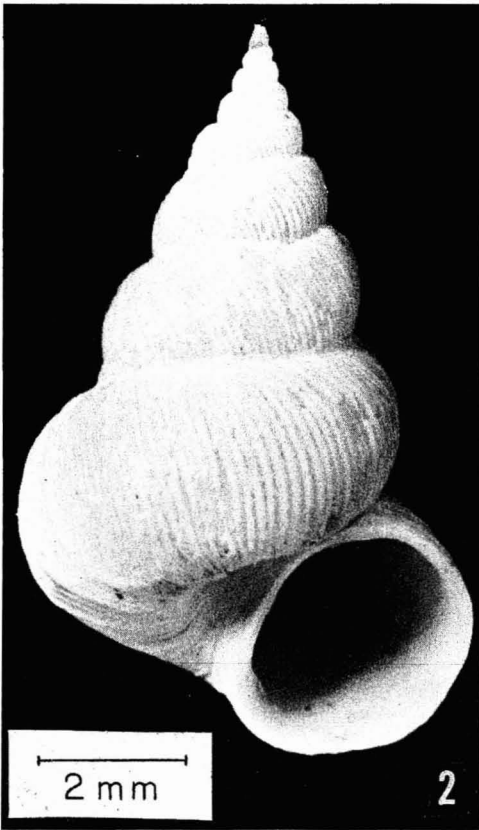


FIGURE 2. Shell of *Epitonium millecostatum* (specimen 28). Great Barrier Reef, Australia.

toconch high conic, about 2.7 whorls,⁴ about 0.5 mm high (immersed), smooth (micro-sculpture probably present), terminated by a varix. Teleoconch outline triangularly ovate. Spire angle 45–55° (exceptionally 60°). Spire outline usually concave. Whorls joined. Axial ribs numerous, prosocline, increasing in number per whorl with increasing shell size, 60–80 on last whorl of average-sized specimens and up to about 100 on largest specimens. Axial ribs thin and wrinkly where not coalesced, crests rolled over away from aperture, forming tubes. Spiral threads between axial ribs on early whorls, occasion-

⁴Kay (1965) was incorrect in stating that “the protoconch consists of one and one half . . . whorls.” Later, Kay (1979) stated that it had “four . . . whorls.”

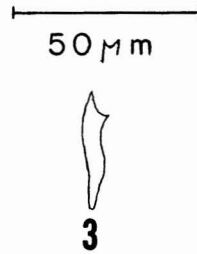


FIGURE 3. Representative radular tooth of *Epitonium millecostatum*.

ally also on later whorls of large shells. Axial ribs not prominent at shoulder. No basal spiral cord. Aperture round; umbilicus small.

The shells of *Epitonium millecostatum* have far more axial ribs than any other epitoniid; the rolled over axial ribs are also characteristic.

APPEARANCE AND HABITS: Coloration of body contrasts with that of *Palythoa*: translucent yellowish cream, with yellowish white superficial mottling on the dorsal front end of the foot; subsurface white granules medial and posterior to each eye; pigmented mantle organ purple-red with a little orange-yellow. Large individuals crawl with difficulty, the foot being folded transversely. A mucous thread is continuously secreted from the pedal pore; the thread attaches the *Epitonium* to its host. A cuticularized esophageal tube like those illustrated by Clench and Turner (1952) is present. A representative tooth from the one radula studied is shown in Figure 3.

The feces are uncompacted, cream white, consisting almost entirely of nematocysts (Figure 4), all holotrichous isorhizas, most of them discharged; no sand grains or orange-brown pigment present.

The egg capsules (Figure 5) occur in clusters near the apertures of the adults, connected to one another and to the adult foot by an elastic mucous thread which is commonly bunched up. The capsules are elliptical in outline, with irregular projections; detritus sometimes attached but no sand grains. Dimensions (five measurements of each): length 1.24–1.48 mm (mean 1.40);

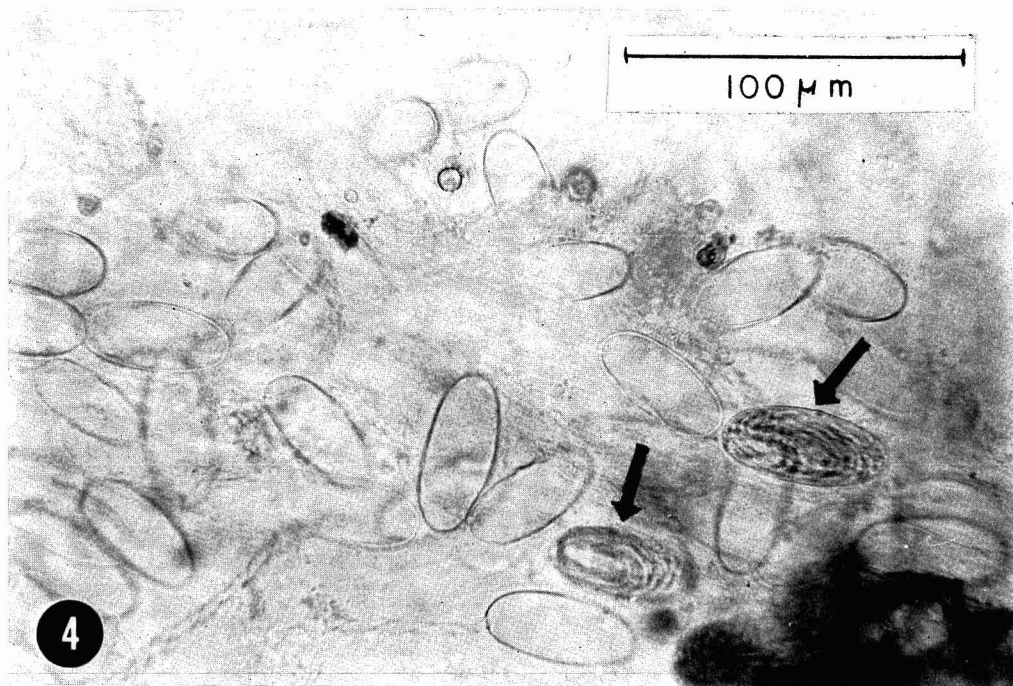


FIGURE 4. Photomicrograph of some feces from *Epitonium millecostatum*, showing the *Palythoa* nematocysts. All are holotrichous isorhizas, and all but the two marked with arrows are discharged. Note the spiny nematocyst tubes.

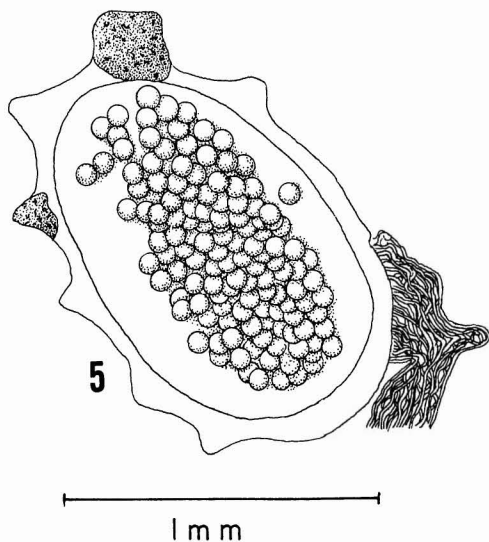


FIGURE 5. Egg capsule of *Epitonium millecostatum*.

width 0.79–0.90 mm (mean 0.87); thickness 0.61–0.80 mm (mean 0.72). The smallest capsule came from the smallest specimen with egg capsules (specimen 36, 6.1 mm long). The largest number of capsules came from specimen 42, 7.4 mm long (with 59 empty and 32 egg-bearing capsules). Eggs per capsule: 149–185 (mean from three counts, 165). The largest number of eggs came from specimen 36 (6.1 mm long), the smallest specimen with egg capsules.

Uncleaved egg diameter: 71–76 μm (mean from ten measurements, 73 μm). The newly hatched veliger (Figure 6) has two small velar lobes with long velar cilia. Shell with $1\frac{1}{4}$ whorls, transparent, planispiral but slightly orthostrophic; no beak on outer lip. Statocysts prominent. Eyes present. Right tentacle a low dome; left tentacle narrower, smaller. Foregut pale pinkish brown. Pigmented mantle organ oblong, on right side, dark purple-brown. Head-foot, stomach and diges-

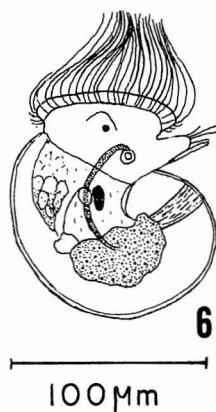


FIGURE 6. Newly hatched veliger of *Epitonium millecostatum*.

tive gland pale greenish cream. Maximum shell diameter 119–126 μm (mean from ten measurements, 124 μm); shell height 82–86 μm (mean from six measurements, 84 μm).

This *Epitonium* is symbiotic with *Palythoa* sp. or spp., under the edges of incrustations. Small individuals are free-living; large individuals are virtually immobile.

RECORDS—SPECIMENS FOUND WITH *Palythoa* (Figure 7): Sri Lanka (Ceylon): Specimens 1–3 (live-collected and dead); between Beruwala Point and Palli Gala (6°27' N, 79°58' E), southwest coast, 28 February 1964, Sta. RO10; ANSP 305992 (dry) and A7951 (in alcohol with hosts). Shells 4.5–7.3 mm long; specimen 6.9 mm long embedded in *Palythoa* but live when collected and with one empty egg capsule. Specimens 4–19 (live-collected and dead); Point de Galle and vicinity (6°01' N, 80°12' E), southwest coast, 4–6 March 1964, Sta. RO11; ANSP 305891 (dry) and A7952 (with hosts in alcohol). Shells 2.7–9.7 mm long. Largest specimen with a large mass of egg capsules, another with 35 capsules; one specimen with apex of shell projecting through the upper surface of the *Palythoa*.

Maldive Islands: Specimens 20–25 (live-collected and dead); Imma Island and vicinity (4°18'30" N, 73°33'30" E), southeast side North Male Atoll, 21 March 1964, Sta. RO14; ANSP A7953 (in alcohol with hosts). Shells 4.0–8.7 mm long. Specimen 8.7 mm

long embedded in *Palythoa* but live-collected, with numerous egg capsules. Specimen 26 (dead); islet 3½ mi northeast of Feridu Island (4°06'05" N, 72°44'30" E), Ari Atoll, 22 April 1964, Sta. RO26; ANSP 305712 (dry) and A7961 (host in alcohol). Shell 6.1 mm long. Specimen 27 (live-collected); northwest tip of Gan and vicinity (0°41' S, 73°9' E), Addu Atoll, 27 April to 5 May 1964, Sta. RO29; ANSP A7954 (with host in alcohol). Shell 3.9 mm long.

Great Barrier Reef: Specimens 28–30 (live-collected and dead); Mermaid Cove, north end Lizard Island (14°40' S, 145°28' E), 31 May 1979; ANSP 350062 (dry) and A7955 (with host in alcohol). Shells 2.5–9.7 mm long (Figure 2). Specimens 2.5 and 7.7 mm long together, with 13 egg capsules (Figure 1); former specimen fixed in Bouin's; immature. Specimen 31 (dead); northeast of Lizard Head, east coast Lizard Island, 2 June 1979; AMS C116675. Shell about 6 mm long. Specimens 32 and 33 (dead); near Leong Creek, west coast Lizard Island, 3 June 1979; ANSP A7956 (with host in alcohol) and AMS C116674. Shells about 5.3 mm long. Specimen 34 (live-collected); Second Beach, southwest coast Lizard Island, 6 June 1979; ANSP A7957 (in alcohol). Shell 4.1 mm long. Specimen fixed in Bouin's; immature. Specimens 35 and 36 (live-collected and dead); Third Beach, southwest coast Lizard Island, 8 June 1979; ANSP A7958 (with host in alcohol). Shells about 6.8 and 6.1 mm long. Live specimen 6.1 mm long with egg capsules (14 empty, 23 containing eggs). Specimens 37–41 (live-collected and dead); First Beach, southwest coast Lizard Island, 8–9 June 1979; ANSP A7959 (with hosts in alcohol). Shells 4.6–8.6 mm long. Specimen about 4.6 mm long fixed in Bouin's; males together with female specimen 7.0 mm long with egg capsules (2 empty and 29 containing eggs). Specimen 8.6 mm long with 17 empty and 25 egg-bearing capsules; specimen 7.0 mm long with 22 empty and 14 egg-bearing capsules; these last two specimens found without associated males. Second specimen 7.0 mm long also female. One group of egg capsules (57 empty and 31 with eggs) found without associated *Epito-*

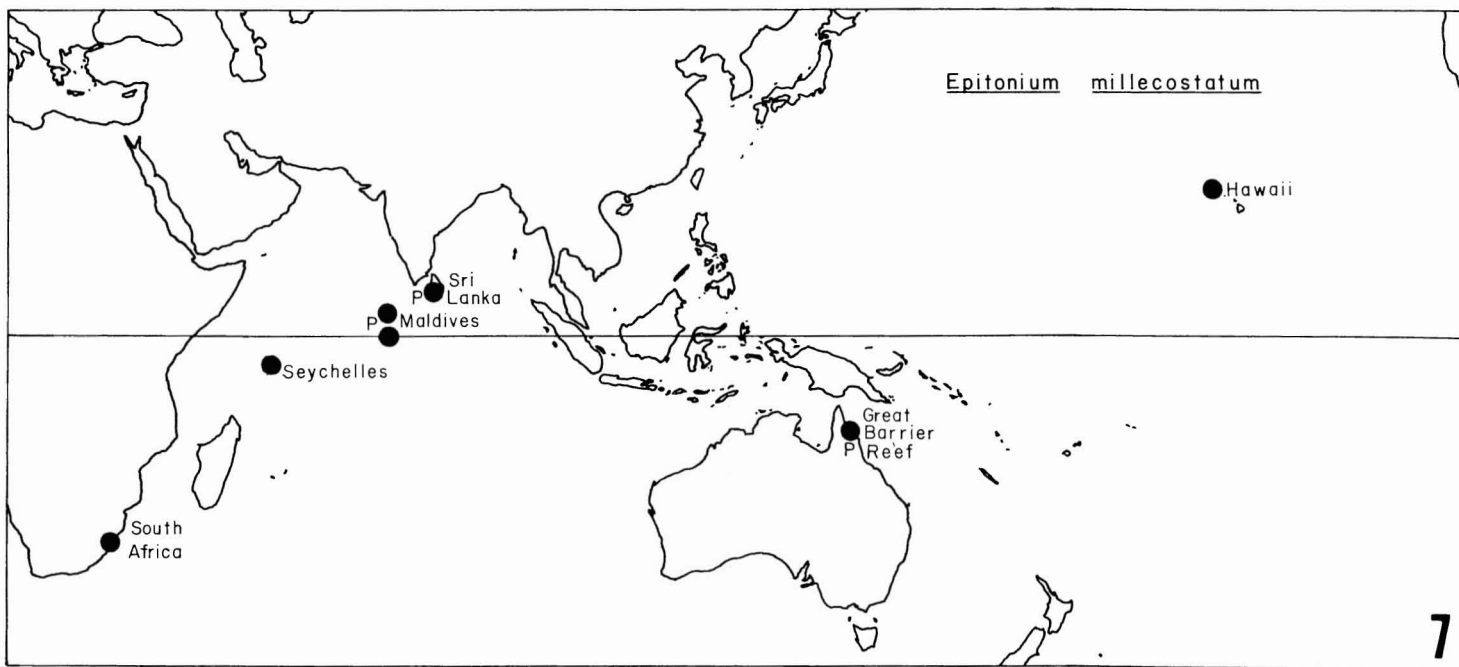


FIGURE 7. Geographic records of *Epitonium millecostatum*; P indicates localities where the species is known to occur with *Palythoa*.



FIGURES 8, 9. Beachworn shell of *Coralliophila clathrata* (specimen 35). Philippines. Lectotype of *Rapana* (*Rhizochilus*) *clathrata* A. Adams (1854).

nium. Specimen 42 (dead); at 5 m, northwest of Palfry Island, south of Lizard Island, 9 June 1979; AMS C116676. Specimens 43–45 (live-collected and dead); Carter Reef, 9 mi northeast of Lizard Island, 12 June 1979; ANSP A7960 (in alcohol with hosts). Shells 7.4 and about 5 mm long. Specimens together, with egg capsules (59 empty, 32 egg-bearing).

RECORDS—SPECIMENS EXAMINED WITH NO HABITAT DATA (Figure 7): Seychelles: Specimen 46 (dead); Port Ternay, northwest Mahé, 15–40 ft, sand and grass, 9 February 1966, Sta. Sy 20; ANSP 311092. Shell 7.0 mm long. Specimen 47 (dead); channel south of St. Anne Island, northeast Mahé, 18 ft, sand, shell, sparse grass, 31 January and 5 or 14 February 1966, Sta. Sy 12; ANSP 311549. Shell fragment 2.9 mm long.

Hawaii: Specimen 48 (dead); Haena, Kauai; ANSP 127826. Shell 6.3 mm long.

PUBLISHED GEOGRAPHIC RECORDS (Figure 7): South Africa: Isipingo, Natal (E. A. Smith 1901).

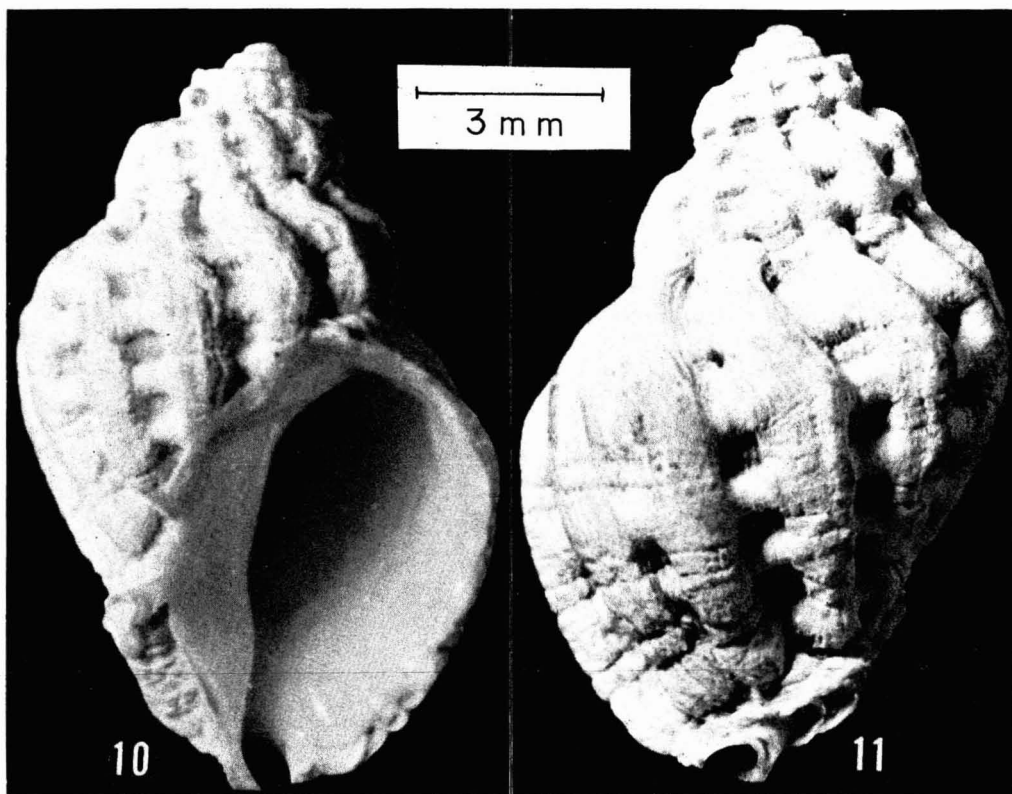
Hawaii: Pease (1860–1861), Pilsbry (1921), and Kay (1965, 1979); Kay (1979) says “Living animals are uncommonly found on reef flats and shells have been found embedded in the ‘soft coral,’ *Zoanthus*.” Could *Palythoa* be meant, or does the species live with both genera?

SUPERFAMILY MURICACEA
FAMILY CORALLIOPHILIDAE (=RAPIDAE,
MAGILIDAE)

Coralliophila clathrata (A. Adams 1854)

SYNONYMY:

Rapana (*Rhizochilus*) *clathrata* A. Adams (1854: 97–98, unfigured [Philippines]).
Lectotype here selected BMNH 1979 189



FIGURES 10, 11. Live-collected shell of *Coralliophila clathrata* (specimen 30). Great Barrier Reef, Australia.

(Figures 8, 9); two paralectotypes BMNH 1979 190.

Coralliophila clathrata (A. Adams). Tryon (1880:211, unidentified); Hidalgo (1904:176, listed); and Faustino (1928:268, listed).

Coralliophila sugimotois "Kuroda" Sugimoto (1929:140 [*nomen nudum*]); Kuroda (1930, pl. 1, figs. 5–7, name and figures only) and Kuroda (1931:316–318, Okinoshima, Tosa, Japan). Holotype figured 1930, fig. 5.

Quoyula sugimotois (Kuroda). Yokoyama (1931:46).

Coralliobia sugimotois (Kuroda). Yen (1935:260–261, pl. 11, fig. 13); Kuroda (1941:113); Kira (1955:51, pl. 25, fig. 5); and Shikama and Horikoshi (1963:77, pl. 117, fig. 1).

(?) *Coralliobia* sp. Barnard (1969:637–638, fig. 17c, Chaka's Rock, Natal,

South Africa). See Kilburn (1972).

Coralliophila (*Latimurex*) *clathrata* (A. Adams). Kilburn (1972:414, fig. 9a, b, not 10, various localities in Natal, South Africa).

Coralliophila (*Pseudomurex*) *clathrata* (A. Adams). Kilburn (1977:189, Mozambique).

NOMENCLATURE: Kilburn (1972) was the first to suggest that *Coralliobia sugimotois* (Kuroda 1930) might be a junior synonym of *Rapana* (*Rhizochilus*) *clathrata* A. Adams 1854. Examination of the three syntypes of *Rapana clathrata* at the British Museum (Natural History) shows them to be beachworn specimens of the same species (Figures 8–11). *Coralliophila clathrata* does not quite fit the definition of a *nomen oblitum*, having been used twice in the last 50 years (both times by Kilburn); and *C. sugi-*

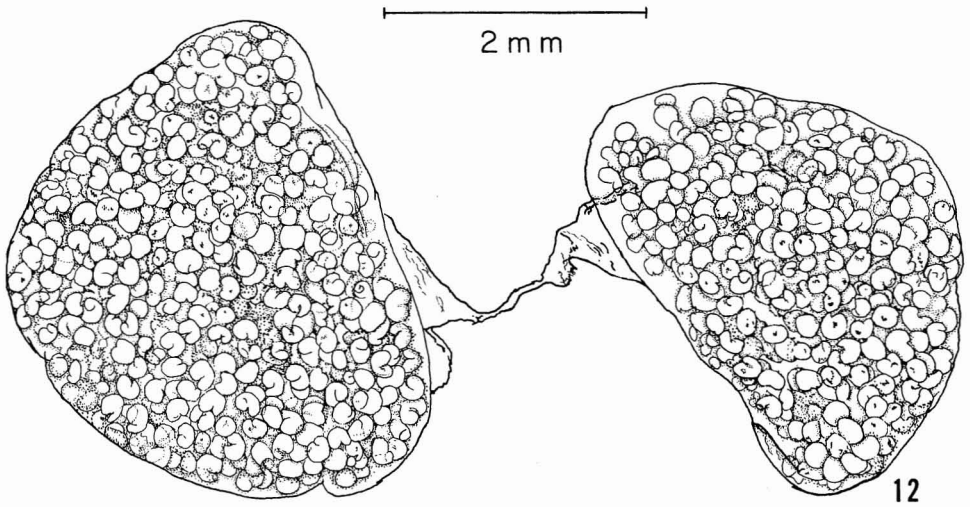


FIGURE 12. Two egg capsules of *Coralliophila clathrata* containing veligers ready to hatch (from specimen 31).

motonis has been used fewer than ten times in the last 50 years (eight times by six different authors). *Coralliophila clathrata* is therefore the valid name for the species.

SHELL (Figures 8–11): An all-white *Coralliophila* attaining a length of 21.5 mm and a width of 13.2 mm, with about five teleoconch whorls. Protoconch high conic, with about four whorls, about 0.7 mm high (immersed), spirally carinate and with fine axial plicae, terminated by a varix. Teleoconch outline ovate, whorls slightly shouldered. Spire angle 55–65°. Sculpture consisting of strong axial and fairly strong spiral ribs, creating a coarse lattice. Shell thin where pitted between ribs (occasionally worn through). Seven to twelve axial ribs on last whorl, varying in width, sometimes partly coalesced. Two (rarely three) spiral ribs above the suture, and five (rarely six) major, squamose ones on the last whorl (excluding the siphonal fasciole). Each sulcus between the major spirals may have in it one (rarely two or three) small cords; these are most prevalent and largest anteriorly. Sculpture subdued near outer lip of large shells. Aperture ovate. Outer lip of large shells flared. Margin of outer lip irregular. Columellar callus thin. Siphonal canal short recurved.

The five (rarely six) major spiral ribs and

the seven to twelve less major axial ribs are characteristic, forming a coarse lattice. The shell characters and lack of a radula place *Coralliophila clathrata* in the Coralliophilidae. The genera or subgenera *Quoyula*, *Coralliobia*, *Latimurex*, and *Pseudomurex* are poorly defined, so the species is retained in *Coralliophila*, *sensu lato*.

APPEARANCE AND HABITS: Coloration of body contrasts with that of *Palythoa*; translucent cream-white; tentacles, head, and siphon mottled superficially with opaque cream-white. The animals crawl readily, but probably are sedentary with *Palythoa* (specimen 31 has an oyster on the anterior end of the shell that would have impeded locomotion). No mucous thread like that of *Epitonium* is present, and there is no radula. The feces are uncompact, flocculent, with bright orange-brown pigment in fine granules; no nematocysts or sand grains were present. Specimen 31 had two egg capsules (Figure 12) in the mantle cavity. The capsules were connected together with a thread, but were not attached to the body. One of the capsules contained 907 veligers nearly ready to hatch, the other, 676. In the veligers a pigment spot is present behind the eyes. The shells are about $1\frac{1}{4}$ whorls and amber in color. The outer lips are rostrate, and the outer surfaces minutely tuberculate. Range

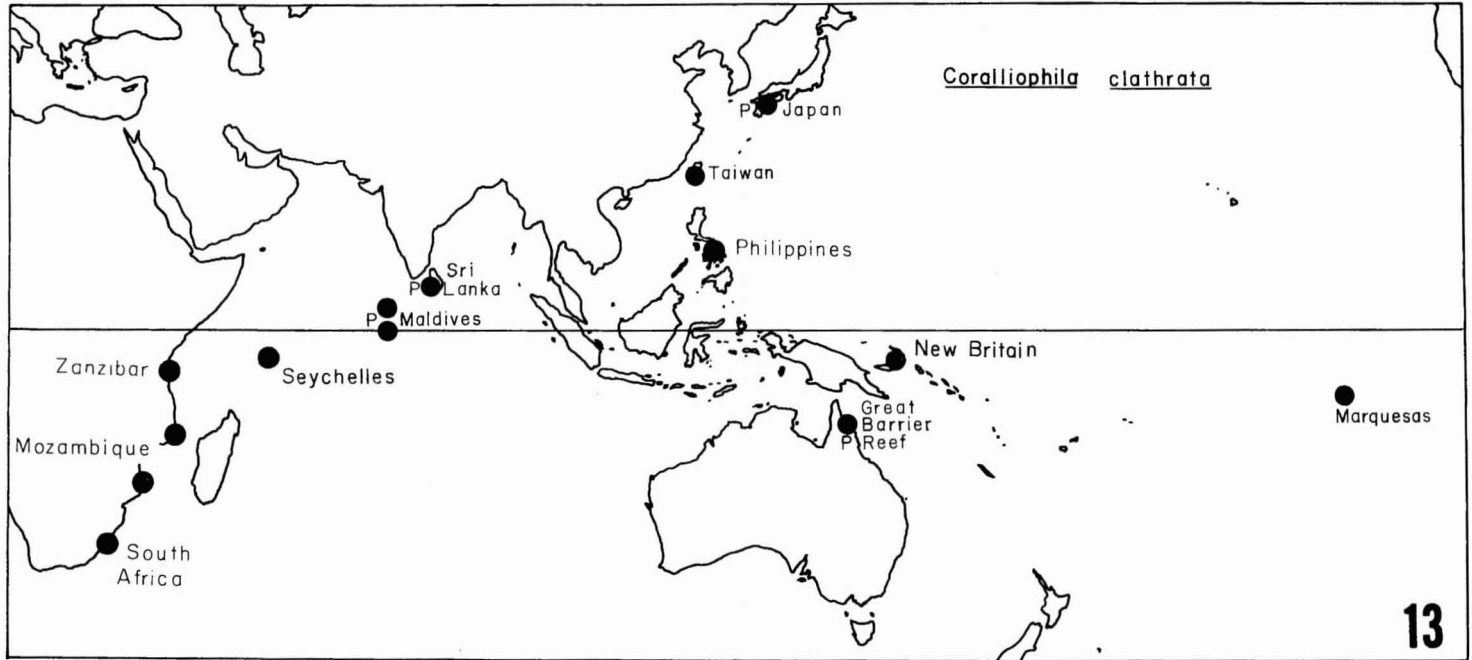


FIGURE 13. Geographic records of *Coralliophila clathrata*; P indicates localities where the species is known to occur with *Palythoa*.

in maximum shell diameter (approximately the width) is 190–213 μm (mean from 20 measurements, 204 μm); height about 185 μm (several approximate measurements).

This *Coralliophila* is symbiotic with *Palythoa* sp. or spp., under the edges of incrustations; all individuals are free-living, but probably sedentary.

RECORDS—SPECIMENS FOUND WITH *Palythoa* (Figure 13): Sri Lanka (Ceylon): Specimens 1–7 (live-collected and dead); between Beruwala Point and Palli Gala (6°27' N, 79°58' E), southwest coast, 28 February 1964, Sta. RO10; ANSP A7964A (in alcohol). Shells 4.6–8.1 mm long.

Maldive Islands: Specimens 8–10 (live-collected); Imma Island and vicinity (4°18'30" N, 73°33'30" E), southeast side North Male Atoll, 21 March 1964, Sta. RO15; ANSP A7964B (in alcohol). Shells 6.0–9.0 mm long. Specimens 11 and 12 (live-collected); between Mafilefuri and Maro Islands (5°21'30" N, 73°25'10" E), Fadiffolu Atoll, 23–25 March 1964, Sta. RO17; ANSP 305710 (dry). Shells 5.5 and 8.3 mm long. Specimens 13–16 (live-collected); north end and northwest of Ongu Island (5°40'35" N, 73°0'05" E), North Malosmadulu Atoll, 21 April 1964, Sta. RO24; ANSP A7964C (in alcohol). Shells 7.5–10.8 mm long. One loose egg capsule 2.5 × 2.0 × 1.3 mm containing congealed eggs. Specimens 17–19 (live-collected); islet 3½ mi northeast of Feridu Island (4°06'05" N, 72°44'30" E), Ari Atoll, 22 April 1964, Sta. RO26; ANSP 305711 (dry) and A7961 (host in alcohol). Shells 7.4–8.5 mm long. Specimens 20–29 (live-collected and dead); northwest tip of Gan and vicinity (0°41' S, 73°09' E), Addu Atoll, 27 April to 5 May 1964, Sta. RO29; ANSP A7963 (host in alcohol). Shells 3.6–8.4 mm long.

Great Barrier Reef: Specimen 30 (live-collected); at 10 m, near entrance to Blue Lagoon, Lizard Island (14°40' S, 145°28' E), 6 June 1979; AMS C117042 (dry) and G15057 (host in alcohol). Shell 11.9 mm long (Figures 10, 11). Female; no egg capsules. Specimen 31 (live-collected); at 1 m, Carter Reef, 9 mi northeast of Lizard Island, 12 June 1979; ANSP 350061 (dry) and A7962

(host in alcohol). Shell 13.1 mm long with an oyster on the anterior end. Female; two egg capsules in mantle cavity (Figure 12).

RECORDS—SPECIMENS EXAMINED WITH NO HABITAT DATA (Figure 13): Zanzibar: Specimen 32 (dead); SDSNH 71571. Shell 21.5 mm long.

Seychelles: Specimen 33 (live-collected); Anse Boileau, Mahé, December 1938; R. Winckworth Collection BMNH. Shell 12.2 mm long. Specimen 34 (live-collected); Glacis, Mahé, November 1938; R. Winckworth Collection BMNH. Shell 19.8 mm long.

Philippines: Specimens 35–37 (dead); H. Cuming, leg.; lectotype (BMNH 1979 189) and paralectotypes (BMNH 1979 190). Shells 8.1–11.7 mm long (Figures 8, 9).

Japan: Specimens 38–40 (live-collected); Okinoshima, Tosa, T. Kuroda, 1929; ANSP 149893. Paratypes of *Coralliophila sugimotois*. Shells 12.4–17.9 mm long. Specimens 41–46 (live-collected); Tosa, R. Sugimoto, leg.; ANSP 224852. Shells 11.1–13.8 mm long. Specimens 47–49 (live-collected); Tosa; ANSP 241373. Shells 11.8–13.5 mm long.

New Britain: Specimens 50–53 (live-collected); Nonga, Rabaul, 15 April 1975, "in sand on the rocks"; AMS C117043. Shells 5.2–8.3 mm long.

Marquesas Islands: Specimens 54 and 55 (live-collected); Atuona, Hiva-oa, 1968; ANSP 314061. Shells 11.1 and 11.7 mm long.

PUBLISHED GEOGRAPHIC RECORDS (Figure 13): South Africa: Scottburgh, Umkomaas, Isipingo (all Kilburn 1972); Chaka's Rock, all Natal [Barnard 1969, as (?) *Coralliobia* sp.; see Kilburn 1972].

Mozambique: Bazaruto Island ("on underside of green soft coral"), Conducia Bay (both Kilburn 1977).

Taiwan: Ryukyu-syo (Kuroda 1941, as *Coralliobia sugimotois*).

Japan: Okinoshima, Tosa (Kuroda 1931, as *Coralliophila sugimotois*).

DISCUSSION AND CONCLUSIONS

Forty-five of the forty-eight available museum specimens of *Epitonium millecos-*

tatum (all those with habitat data) were collected with *Palythoa*; the three others are empty shells that probably were in sand (one is badly broken). *Epitonium millicostatum* therefore seems to be an obligate symbiont on *Palythoa*. It is the third epitoniid to be reported with zoanthinarians, two Japanese species of "*Graciliscala*" having been reported with *Epizoanthus* by Masahito and Habe (1976).

It is not surprising that *Epitonium millicostatum* should live with and feed on a coelenterate. The hypothesis that many epitoniids live with coelenterates and that all are adapted to feed on coelenterates or their mucus (Thorson 1957, Robertson 1963) is consonant with subsequent findings (Bosch 1965, DuShane and Bratcher 1965, Fager 1968, Morton and Miller 1968, Albergoni et al. 1970, Guinther 1970, Robertson 1970, Hochberg 1971, Masahito and Habe 1976, Raeihle 1976, Kendrick 1977, Salo 1977, C. R. Smith 1977, J. B. Taylor 1977, Beu 1978, Perron 1978, Kay 1979).

Different species of epitoniids have differently shaped radular teeth (Thiele 1928, Clench and Turner 1952). Those of *Epitonium millicostatum* (Figure 3) conform in a general way with those illustrated, but there are the usual specific differences. There is no unusual development of the radula of *E. millicostatum* for feeding on *Palythoa*.

All the specimens of *Epitonium millicostatum* were under the edges of *Palythoa* incrustations. Small specimens are free-living and may forage, but most of those longer than 5 mm were wedged tightly in concavities in the *Palythoa* conforming with the shape of the shell. Few living animals were actually embedded in the *Palythoa* tissue, but nearly all the empty shells were. Somehow most living specimens avoid being embedded. Nevertheless, they are more or less stationary, as shown in one case by a sponge growing over a shell and connecting it with the *Palythoa*. As an *E. millicostatum* grows in its confined space it must somehow be able to rotate its shell, keeping the aperture in the same relative position, so that the body can extend from the aperture.

Epitoniids are believed to be protandric hermaphrodites (Ankel 1926), though in one

species sex reversal is said to take place at each breeding season (Ankel 1936). *Epitonium millicostatum* appears to be protandric and not to change back to a male after it has reached the female stage. Of the few specimens sexed, the 2.5- and 4.1-mm animals were immature, the 4.6-mm animal was male, and the two 7.0-mm animals were females. All Lizard Island individuals longer than 6.1 mm were found with egg capsules.

The egg capsules found with *Epitonium millicostatum* were both egg-bearing and empty. The capsules are connected to one another by an elastic mucous thread, and even after they have released veligers the capsules are durable and are retained. The number of capsules per adult *Epitonium* varies considerably: the maximum number was found with specimen 43 (7.4 mm long), which had 59 empty and 32 egg-bearing capsules. Assuming that the average number of eggs per capsule was 165, there had been or were about 15,000 eggs in these capsules. It is not clear whether the capsules had been deposited during the entire lifetime of the *Epitonium*, or whether they had been spawned in all or part of one breeding season.

Coralliophilids are like epitoniids in having hosts that are all coelenterates (Gohar and Soliman 1963, Ward 1965, Spada 1968, Robertson 1970, Albergoni and Spada 1972, Ott and Lewis 1972, J. D. Taylor 1976). Thirty-one of the fifty-five available museum specimens of *Coralliophila clathrata* (nearly all those with habitat data) were collected with *Palythoa*. The 12 specimens from Japan probably were also with *Palythoa*, but their habitat data have been lost. The new data substantiate Sugimoto's (1929) claim that this *Coralliophila* is an obligate *Palythoa* ("*Corticifera*") symbiont.

Epitonium millicostatum and *Coralliophila clathrata* have not been found alive together on the same *Palythoa* colony. Frequencies of the two species are low, but were not quantified.

The long acrembolic proboscis of the *Epitonium* was not seen everted, and feeding was not observed in either *Epitonium* or *Coralliophila*. However, it is possible to make inferences about feeding from the

TABLE 1
CONTENTS OF THE GUTS OR FECES OF GASTROPODS SYMBIOTIC WITH *Palythoa*

	SAND GRAINS	ZOOXANTHELLAE	DISCHARGED NEMATOCYSTS	REFERENCE
<i>Epitonium millecostatum</i>	—	—	+	This paper
<i>Heliacus</i> spp.	+	+	—	Robertson (1967)
<i>Coralliophila clathrata</i>	—	+	—	This paper
<i>Aeolidiopsis ransoni</i>	+	?	?	Pruvot-Fol (1956)

feces. Sand grains were not found in the feces of either species, and thus neither species ingests the sand-containing *Palythoa* tissue. In this they are unlike *Heliacus* and *Aeolidiopsis* (Table 1). Nor do *Epitonium* and *Coralliophila* make feeding holes in *Palythoa*; no lesions were observed.

The sand grains in *Palythoa* are confined to the coenenchyme and to the basal parts of the polyps (Rudman, *in litt.*). Conceivably, species feeding on *Palythoa* and lacking sand grains in their feces might ingest the upper parts of the polyps. This seems not to be the case with *Epitonium millecostatum* and *Coralliophila clathrata*, however, because both species live under the edges of *Palythoa* colonies where *Coralliophila* is probably sedentary and *Epitonium* is definitely stationary (except when juvenile) and thus out of proboscis reach from the polyps.

It seems likely that the *Epitonium* and the *Coralliophila* feed on and digest *Palythoa* mucus. Mucus is sloughed off copiously and contains mixed zooxanthellae and nematocysts (personal observations). Robertson (1963) reports another *Epitonium* feeding in part on sea anemone mucus, and Hadfield (1976) discusses the probable importance of coelenterate mucus as food for symbiotic prosobranchs.

As recorded earlier, holotrichous isorhizas were the only nematocysts found in the feces of the *Epitonium* (Figure 4). It is not known whether these nematocysts are localized in *Palythoa*, but if they are, finding them in the feces would be good evidence as to their provenance.

The *Epitonium* and the *Coralliophila* process the zooxanthellae and nematocysts differently. The *Epitonium* defecates the nema-

tocysts (Figure 4), while the *Coralliophila* defecates remnants of the zooxanthellae (bright orange-brown granules). Thus, the *Epitonium* digests zooxanthellae, thereby being partly herbivorous, and the *Coralliophila* apparently digests nematocysts.

Little information is available about epitioid and coralliophilid egg capsules, eggs, and veligers. The major papers are Thorson (1946) and Richter and Thorson (1975) on epitioids, and Gohar and Soliman (1963) and Wells and Lalli (1977) on coralliophilids.

Evidence that both *Epitonium millecostatum* and *Coralliophila clathrata* have planktotrophic larvae comes from the small size of the eggs of the *Epitonium*, and from the hatching veligers of both species being much smaller than the protoconchs on the respective adults. The uncleaved eggs of *E. millecostatum* average 73 μm in diameter. According to Thorson (1952), no lecithotrophic prosobranch is known with an egg less than 150 μm in diameter. Shells of newly hatched veligers of *E. millecostatum* average 84 μm in height, with $1\frac{1}{4}$ whorls. Protoconchs of the *Epitonium* are about 500 μm high (immersed), with about 2.7 whorls. Although it has not yet been measured, the egg of *C. clathrata* is also small, the shells of the hatching veligers being about 185 μm high, with $1\frac{1}{4}$ whorls. Protoconchs of the *Coralliophila* are about 700 μm high (immersed), with about 4 whorls. It is uncertain whether a sinusigerous lip, an indicator of a long pelagic stage, is present in *C. clathrata*; one is present on the *Coralliophila* protoconchs illustrated by Hedley (1903) and Richter and Thorson (1975) but not on the one illustrated by Barnard (1959).

It is evident that larvae of both species

grow substantially while they are in the plankton. I estimate that the planktonic larval stage of each of the species lasts about a month and possibly longer. Scheltema (1971) mentions *Coralliophila* as being a genus that includes teleplanic species. It is of interest how symbiotic species with planktotrophic (even teleplanic) larvae find their hosts. They presumably have well-developed settlement responses.

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