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PRELIMINARY SURVEY OF ZOOXANTHELLATE ZOANTHID DIVERSITY (HEXACORALLIA: ZOANTHARIA) FROM SOUTHERN SHIKOKU, JAPAN

by

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Abstract

Zooxanthellate members of the order Zoantharia (Anthozoa: Hexacorallia) previously reported from Japan consist of the genera *Zoanthus* and *Isaurus* in the family Zoanthidae as well as the genus *Palythoa* in the family Sphenopidae. In particular, *Zoanthus* and *Palythoa* are common in shallow tropical and sub-tropical waters from the southern limits of Japan in Okinawa to their northern limits in the Izu Islands (Miyakejima Island). Previous studies have documented the occurrence of zooxanthellate zoanthids in Okinawa, the Nansei Islands, Kyushu, mid-Honshu (Wakayama), and the Izu Islands, but until now no formal survey of zoanthids occurring in the waters of Shikoku has been conducted. The area surveyed in this study was divided into two regions: zooxanthellate zoanthid diversity was higher (8 species) along the southern Pacific Coast region of Kochi, and lower in waters of the Bungo Strait region (5 species). The majority of observed species listed here were found below the extreme low tide line to depths of approximately 5 m. *Zoanthus* and *Palythoa* were found in most sites surveyed, while *Isaurus* was limited to sites on the Pacific coast. Zooxanthellate zoanthids in southern Shikoku are most abundant in shallow hard substrate marine habitats with a well-developed coastal terrace, and consistent high amounts of wave activity, current, and light levels.

Introduction

In recent years, research has begun to investigate the diversity of zooxanthellate zoanthids (Anthozoa: Hexacorallia: Zoantharia) from Japanese waters. Distribution of the genera *Zoanthus*, *Isaurus* (Family Zoanthidae) and *Palythoa* (Sphenopidae) roughly follows the course of the Kuroshio Current, which brings warm tropical waters from Okinawa and the east coast of Taiwan to high latitudes of the Pacific coast of Japan (Fig. 1a). While the genus *Isaurus* has only been previously reported from a few sites in Japan (including the Danjo Islands, Tatsukushi, and Otsuki – Nishidomari-Matsubae; F. Iwase, personal communication; also see Fig. 1b), there are numerous documented samples of *Zoanthus* and *Palythoa* spp. from Okinawa, the Nansei Islands, Kyushu, mid-Honshu, and the Izu Islands (see Uchida 2001; Reimer *et al*. 2006a; Reimer *et al*. 2006d; Fig. 1a). However, until now there has been no investigation into the diversity of zooxanthellate zoanthids from the waters of Shikoku, representing a critical gap in the reported distributions of these cnidarians in Japan.

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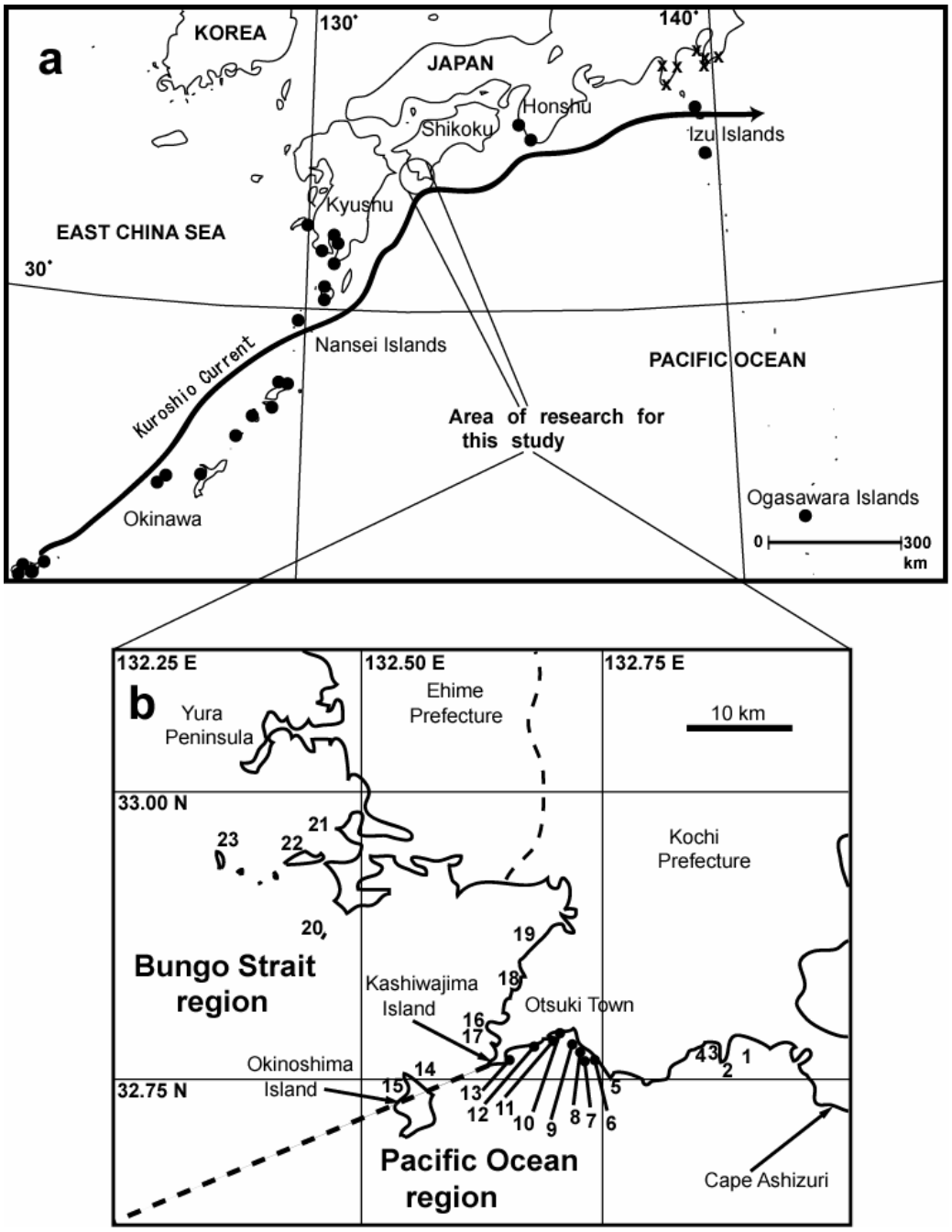

Fig. 1. a) Map of previous zooxanthellate zoanthid sampling sites in Japan with area of this study. Black closed circles represent areas where zooxanthellate zoanthids have previously been found, and crosses areas that were previously investigated but no zooxanthellate zoanthids found; b) map of sampling sites investigated in this study. The dotted line represents the border between the two regions of this study. Numbered sites correspond to site numbers as given in Table 2.

The area investigated in this study (from Cape Ashizuri, Kochi to Yura Peninsula, Ehime; see Fig. 1b) can be geographically divided into two regions. The Pacific Coast region (Cape Ashizuri to Kashiwajima) features frequent waves and has a well-developed coastal terrace, while the region from Kashiwajima to Yura Peninsula is somewhat more protected from open ocean waves, and has steep rocky cliffs that extend underwater (Iwase 2004) (Table 1). Both regions are strongly influenced by the Kuroshio Current. Additionally, both regions have several marine parks and Marine Protected Areas (MPAs) (Iwase 2004), with detailed species lists for many groups of marine organisms. Unfortunately, few if any zoanthid species appear on such lists despite their presumed presence in the parks and MPAs.

Here, in order to provide detailed information on zooxanthellate zoanthid diversity and distribution in Shikoku, we have conducted surveys of numerous locations in southern Kochi and western Ehime prefectures (Fig. 1b). We provide a species list, a morphological dichotomous key for all zooxanthellate zoanthids observed, and also discuss some of their ecological characteristics.

Table 1. Description of environment and fauna in the two regions of southern Shikoku investigated in this study.

Region	General description	Maximum ocean temperature[1]	Minimum ocean temperature[1]	Average ocean temperature[1]	Commonly observed benthos[2]
Pacific Coast	Directly on open ocean, strong Kuroshio influence, ocean terraces, points and bays interspersed	28.62 °C	14.72 °C	21.74 ± 3.67 °C	*Acropora* spp., *Pavona* spp., other hermatypic corals.
Bungo Strait	More sheltered from open ocean, strong Kuroshio influence, steep complex cliffs that continue into ocean	29.12 °C	16.15 °C	22.01 ± 3.46 °C	*Acropora* spp., *Tubastraea* spp., Alcyonacea

[1]Temperature data from HOBO Water Temp Pro (Onset Computer Corporation, Bourne, MA, USA) sensors recording at one hour intervals, for the period from March 29, 2005 to March 15, 2006 (n=8348). Pacific Coast region sensor placed at Nishidomari site (depth = 6 m), Bungo Strait region sensor at Tachinbanaura site (depth = 10 m).
[2]From Iwase (2004).

Materials and methods

Samples: Zooxanthellate zoanthid species and their relative abundance were noted at 23 locations (Fig. 1, Table 2) in southern Shikoku between January and October 2006 by SCUBA and/or snorkeling. Other data recorded included depth and colony size. *In situ* photographs were taken to assist in further analyses (oral disk color, tentacle number, etc.) in the laboratory. Samples of each species were collected from all locations in Kochi Prefecture, and have been deposited in JDR's zoanthid collection at the Japan Agency for Marine-Earth Science and Technology (JAMSTEC; Yokosuka, Japan) or at the Biological Institute at Kuroshio (BIK; Otsuki, Japan). No samples were collected in Ehime Prefecture due to prefectural sampling restrictions, but it is hoped samples can be obtained in the future. Samples were preserved

Table 2. Abundance of zooxanthellae Zoantharia species in southern Shikoku by location.

Region / site[1] (with number of species in area)	Site type[2]	Wave/ current activity	*Zoanthus sansibaricus*[3]	*Zoanthus gigantus*	*Zoanthus vietnamensis*	*Zoanthus kuroshio*	*Isaurus tuberculatus*	*Isaurus* sp. B	*Palythoa tuberculosa*	*Palythoa mutuki*
Pacific Coast (8 species)			★	★	★	★	★	★	★	★
1. Mizushima	Outside	High	◎	◎	◎	X	○	X	◎	○
2. Omurabae	Outside	High	◎	◎	◎	X	X	X	◎	○
3. Tatsukushi-Bentenjima	Outside	Medium	●	●	●	X	X	X	◎	○
4. Obae	Outside	Medium	◎	◎	◎	X	X	X	◎	○
5. Hozaki	Outside	High	○	○	○	X	◎	X	○	○
6. Nishidomari-Matsubae	Outside	High	●	●●	●●	◎	○	1	●●	○
7. Nishidomari	Bay	Medium	◎	●	●●	X	X	X	●●	○
8. Nishidomari South	Outside	High	○	●	●	X	X	X	●	◎
9. Kashinoura-Bentenjima	Outside	High	○	◎	◎	X	○	X	◎	X
10. Shirigai-Matsubae	Outside	High	◎	●	●	X	◎	1	●	○
11. Oshirigai	Bay	Medium	○	◎	◎	X	○	X	●	○
12. Odo North	Outside	High	◎	◎	◎	X	○	X	◎	X
13. Odo South	Outside	High	◎	◎	◎	X	○	X	◎	X

Table 2. continued

Region / site[1] (with number of species in area)	Site type[2]	Wave/ current activity	*Zoanthus sansibaricus*[3]	*Zoanthus gigantus*	*Zoanthus vietnamensis*	*Zoanthus kuroshio*	*Isaurus tuberculatus*	*Isaurus* sp. B	*Palythoa tuberculosa*	*Palythoa mutuki*
Bungo Strait (5 species)			★	★	★				★	★
14. Torinokubi	Outside	High	●	●	●●	X	X	X	●●	X
15. Oura	Bay	Medium	X	◎	◎	X	X	X	●	X
16. Futatsubae	Sheltered	Medium	X	X	X	X	X	X	○	X
17. Komo	Sheltered	Medium	X	X	X	X	X	X	X	X
18. Tachibanaura Harbor	Harbor	Low	X	X	1	X	X	X	X	X
19. Shirozaki	Sheltered	Low	X	◎	◎	X	X	X	◎	X
20. Jinoiso	Outside	High	●	●	●	X	X	X	●	X
21. Kurobae	Sheltered	High	X	X	X	X	X	X	X	X
22. Kashima	Sheltered	Low	◎	◎	●●	X	X	X	◎	X
23. Yokoshima	Sheltered	High	◎	◎	◎	X	X	X	◎	○

[1]Site numbers correspond to site numbers in Figure 1b.

[2]Outside=exposed to open ocean, Bay=exposed to open ocean but partially sheltered, Sheltered=largely protected from open ocean waves and more sheltered than "Bay", Harbor=within breakwaters, no waves.

[3]★=species present in region. Abundance symbols: ●●=abundant, ●=common, ◎=uncommon, ○=rare, **1**=single colony present, X=not present.

in 99.5 % ethanol at –30 °C for future DNA analyses (as in Reimer *et al*. 2004; 2006a; 2006c; etc.) or in 10 % formalin seawater for future morphological analyses (as in Ono *et al*. 2005).

Regions and locations: The sampling area in southern Shikoku was divided into two regions (Pacific Coast and Bungo Strait) based on observed differences in environment and predominant benthos within region (see Iwase 2004) (Fig. 1b, Table 1). Each location within each region's "ocean exposure" was classified as either "outside" (directly exposed to the open ocean), "bay" (somewhat sheltered from open ocean), "protected" (non-"bay" but sheltered from open ocean), or "harbor" (completely sheltered from open ocean). Additionally, wave and tidal current activity at each location was assessed by a combination of high wave lines onshore and local diving guide information combined with previous references into three categories ("high", "medium", or "low").

Species Identification: Species were identified *in situ* using previously reported morphological characteristics (*Zoanthus* – see Reimer *et al*. 2006a; Reimer *et al*. 2006b; *Palythoa* – see Reimer *et al*. 2006c; *Isaurus* – see Uchida 2001). In addition, some samples had their identities further confirmed by DNA sequencing (data to appear elsewhere).

Species diversity analyses: After collection of samples and field data, zooxanthellate zoanthid species diversity was analyzed by comparing species numbers between regions between locations classified by ocean exposure classes ("outside" vs. all "sheltered" classes), and between locations classified by wave and current classes.

Results

A list of zooxanthellate zoanthid species by location is shown in Table 2, with representative *in situ* photographs of zooxanthellate zoanthid species in Fig. 2. Overall, *Zoanthus vietnamensis* Pax & Mueller and *Palythoa tuberculosa* Delage & Herouard were seen to be the most widely found zooxanthellate zoanthids (20/23 locations investigated), with *Zoanthus kuroshio* Reimer & Ono and an unidentified *Isaurus* species (designated *Isaurus* species B here) found at only one location each (Tables 2 & 3). No zooxanthellate zoanthids were found at two locations, both in the Bungo Strait region (Table 2).

Table 3. Frequency of occurrence of zooxanthellate zoanthid species at investigated sites in southern Shikoku.

Pacific Coast region species diversity

Species	Pacific Coast region site occurrences (13 total sites)	Bungo Strait region site occurrences (10 total sites)	Total site occurrences (23 total sites)
Zoanthus sansibaricus	13	4	17
Zoanthus gigantus	13	6	19
Zoanthus vietnamensis	13	7	20
Zoanthus kuroshio	1	0	1
Isaurus assymetricus	8	0	8
Isaurus sp. B	2	0	2
Palythoa tuberculosa	13	7	20
Palythoa mutuki	10	1	11

13 sites were investigated along the Pacific Coast region (Fig. 1b, Table 2). At all sites *Zoanthus sansibaricus* Carlgren (Pl. 1), *Zoanthus gigantus* Reimer and Tsukahara (Pl. 2), *Zoanthus vietnamensis* sensu Uchida (2001) (Pl. 3 A-C), and *Palythoa tuberculosa* (Pl. 6) were found in varying abundances. Additionally, *Palythoa mutuki* Carlgren (Pl. 7) and *Isaurus tuberculatus* Gray (Pl. 4) were found in most locations surveyed (10 and 8 sites, respectively – Table 2). *Zoanthus kuroshio* (Pl. 3 D-E) was only observed at the Nishidomari-Matsubae site in tide pools above the extreme low tide line. Additionally, single colonies of a potentially undescribed species of *Isaurus* (to be reported elsewhere) (Pl. 5) were observed and sampled from the Shirigai-Matsubae and Nishidomari-Matsubae sites.

Bungo Strait region species diversity

A total of ten sites were investigated in the Bungo Strait region, with a total of five zooxanthellate zoanthid species present (Fig. 1b, Table 2).

Two sites were investigated at Okinoshima Island. On the north coast of the island at the Torinokubi site, the species *Z. sansibaricus*, *Z. gigantus*, *Z. vietnamensis* and *P. tuberculosa* were common, while on the northeast coast at the Oura site, only *P. tuberculosa* was common, with occasional colonies of *Z. gigantus* and *Z. vietnamensis* observed.

Four sites were investigated in the Otsuki Town portion of the Bungo Strait, and only three species observed. The Ostuki – Bungo Strait coastline sites are characterized by being much more sheltered from the open ocean than the other sites in this study. Despite numerous dives at the four sites in Ostuki – Bungo Strait, only three zooxanthellate species were confirmed to be present, and all in low abundances; *Z. gigantus*, *Z. vietnamensis*, and *P. tuberculosa*. No zoanthids were observed at the Komo site.

Additionally, four sites were investigated in Ehime on the Bungo Strait, and five species of zooxanthellate zoanthids observed. *Z. sansibaricus*, *Z. gigantus*, *Z. vietnamensis* and *P. tuberculosa* were abundant at the Jinoiso site. At Kashima, *Z. vietnamensis* was particularly abundant. *P. mutuki* was confirmed only at the Yokoshima site. No zoanthids were observed at the Kurobae site.

Species diversity analyses results

Zooxanthellate zoanthid species numbers at Pacific Coast region sites (average 5.5 ± 0.8, n = 13) were higher than species numbers at non-Pacific Coast region sites (average 2.5 ± 2.2, n = 10). Species numbers of sites with “outside” exposure were also significantly higher (average 5.3 ± 0.9, n = 13) than species numbers at “sheltered” sites (average 2.7 ± 2.1, n = 13). Additionally, the average number of species per site as classified by the three classes of wave and current activity were also different (high 4.9 ± 1.8, n = 13; medium 3.7 ± 2.4, n = 7; low 2.6 ± 1.5, n = 3).

List of zooxanthellate zoanthids found in southern Shikoku

I. Family Zoanthidae

The family Zoanthidae is the only family within the Order Zoantharia to not be sand-encrusted. All three genera (*Zoanthus*, *Isaurus*, *Acrozoanthus*) in Zoanthidae are zooxanthellate and found worldwide in shallow tropical and sub-tropical waters.

A. Genus *Zoanthus*

The genus *Zoanthus* can be distinguished from most other zoanthid genera by its lack of sand and/or detritus uptake. Although *Isaurus* spp. (also Family Zoanthidae) similarly do not incorporate detritus into their tissue, unlike *Isaurus* species' polyps that usually have tubercules *Zoanthus* polyps are uniformly smooth on the outer surface. *Zoanthus* spp. can also often be distinguished from the other species and genera observed in this study by often having brightly colored oral disks, although green and brown forms (similar to *Palythoa* spp.) do exist. The external surface of polyps and the coenenchyme is mainly light to dark purple, although pale green polyp colors are sometimes observed.

Zoanthus species are quite common along southern Shikoku shorelines, and are usually found in locations with high wave or current activity and high light levels. All *Zoanthus* species noted in southern Shikoku are attached to hard substrate, usually large rocks, but also occasionally dead hard corals. Four species have been confirmed to exist in the study area, with three of the species (*Z. sansibaricus*, *Z. gigantus*, *Z. vietnamensis*) quite common. The four species of *Zoanthus* described here were found from depths ranging from the lower intertidal zone to approximately 5 m.

1. *Zoanthus sansibaricus* Carlgren, 1900 (Plate 1)

Brief description: As described in Reimer *et al*. (2006a), *Z. sansibaricus* often forms large colonies with "liberae" polyps well clear and free of the coenenchyme (see Pax 1910). Adult polyps 3-12 mm in diameter, up to 20 mm in length. External polyp surface light to dark purple, no markings, generally uniform in color, may be slightly paler around edge of oral disk. 40-58 tentacles, 48-54 mesenteries. Wide variation in oral disk color (orange, red, green, brown, purple, white, blue, yellow), often fluorescent.

Remarks: *Z. sansibaricus* has previously been shown using genetic data to consist of many different color morphotypes (Reimer *et al*. 2004; 2006a), and similar to previous studies here many different color morphotypes (oral disks green, orange, blue, white etc) of *Z. sansibaricus* were observed. However, compared to *Z. gigantus* and *Z. vietnamensis*, *Z. sansibaricus* appears to be not as common in terms of colony numbers in the area examined here, and much less common than observed at Sakurajima, Kagoshima, Japan (Reimer *et al*. 2006a; Ono *et al*. 2007). In all other areas examined in Japan to date (see Fig. 1a), *Z. sansibaricus* is the most common *Zoanthus* species. We can offer no explanation for the relative lack of *Z. sansibaricus* abundance in southern Shikoku, and reasons for this remain to be investigated. As has been previously noted in other Japanese locations (Kagoshima, Wakayama, Hachijojima,

Miyakejima), *Z. sansibaricus* is exclusively found below the extreme low tide line. This species appears to have undergone reticulate evolution with another unknown *Zoanthus* species some time in the past (Reimer *et al*. 2007).

2. *Z. gigantus* Reimer & Tsukahara, 2006 (Plate 2)

Brief description: Polyps "liberae" and extend from poorly developed coenenchyme. Often polyps less crowded together than *Z. sansibaricus*. Polyps up to 25+ mm in diameter, up to 40 mm in length, larger in diameter towards oral opening than at base, appear "swollen" when closed. External surface of polyps purple with white or pale striped vertical markings on upper half. 42-60 tentacles, approximately 62 mesenteries. Oral disk color may vary (orange, red, brown, pink, gray, blue), often with fluorescent green oral opening. Colonies vary widely in size (< 50 polyps to thousands of polyps).

Remarks: *Z. gigantus* was relatively abundant at many sites in this study, particularly along the Pacific coast. In the original description of *Z. gigantus*, colonies of this species were described as relatively small (< 100 polyps) (Reimer *et al*. 2006a), but unlike in other areas of Japan examined thus far, often colonies of *Z. gigantus* along the Pacific coast of Ostuki are very large (thousands of polyps). Additionally, colonies of different color morphotypes were often observed interspersed with each other at sites investigated in this study, a phenomenon seen previously with *Z. sansibaricus* and also between *Z. sansibaricus* and *Z. vietnamensis* (see Fig. 1 in Reimer *et al*. 2006b), but not previously observed in *Z. gigantus*. The most commonly observed oral disk color morphotypes of *Z. gigantus* were orange (Pl. 2 B, C & E) and mint green (Pl. 2 F). Similar to *Z. sansibaricus*, *Z. gigantus* is found only below the extreme low tide line in southern Shikoku.

Z. gigantus has only recently been described, and no common Japanese name exists for this species. We would like to designate a Japanese name of "budo-mamesunaginchaku" (ブドウマメスナギンチャク) for *Z. gigantus* in reference to its large, "swollen" appearance compared to other *Zoanthus* species in Japan ("budo" means "grape" in Japanese).

3. *Z. vietnamensis* Pax & Müller, 1957 (Plate 3 A-C)

Brief description: As described in Uchida (2001) and Reimer *et al*. (2006b), *Z. vietnamensis* forms small colonies (less than 100 polyps). However, in this study many large colonies (thousands of polyps) were observed. Polyps up to 30 mm in length, up to 20 mm in diameter. Polyps "liberae". Oral disk always pale to dark pink, often with white oral opening. 55-64 tentacles.

Remarks: *Z. vietnamensis* is the most abundant *Zoanthus* species in southern Shikoku, often forming large colonies (thousands of polyps) below the extreme low tide line. Like *Z. sansibaricus* and *Z. gigantus*, *Z. vietnamensis* was most common in areas of high wave or current activity, but was also occasionally found in very sheltered areas. For example, a large colony of *Z. vietnamensis* was found in very sheltered Tachibanaura Harbor surrounded by *Acropora* colonies. *Z. vietnamensis*, *Z. sansibaricus*, and *Z. gigantus* often occur sympatrically in many sites examined here.

4. *Zoanthus kuroshio* Reimer & Ono, 2006 (Plate 3 D & E)

Brief description: Similar to *Z. vietnamensis, Z. kuroshio* usually with pale pink oral disk, although white and pale blue varieties observed. 42-48 mesenteries, 50-64 tentacles. Polyps "immersae", deeply embedded, barely extend from coenenchyme. Oral disk 6-12 mm in diameter expanded. Polyps narrower in diameter towards oral opening than at base. Edge of coenenchyme "tongue-like" in form. Colonies often intertidal and in tide pools on wave-exposed shoreline, can be very large and encrusting, forming a "mat" over substrate (rock or dead coral).

Remarks: *Z. kuroshio* was found only at one site examined in this study. Unlike the other three *Zoanthus* species examined, *Z. kuroshio* was found above the extreme low tide line, in tidepools facing the ocean at Nishidomari-Matsubae. This is similar to *Z. kuroshio* as observed on Yakushima (Reimer *et al*. 2006a). Based on molecular data, there is some question as to whether *Z. kuroshio* is only a morphotype of *Z. vietnamensis* (Reimer *et al*. 2006b), but we have included this species here as its morphology is clear and distinct from *Z. vietnamensis* and other *Zoanthus* species.

Similar to *Z. gigantus*, *Z. kuroshio* has only recently been described, and no common Japanese name exists for this species. We would like to designate a Japanese name of "kuroshio-mamesunaginchaku" (クロシオマメスナギンチャク) for *Z. kuroshio* in reference to its distribution along the Kuroshio Current in Japan.

B. Genus *Isaurus*

Isaurus differs from *Zoanthus* by having recumbent polyps (in daytime) that are generally closed during the daytime, becoming open and upright at night. Additionally, some species or individuals have small, rough tubercules on the exposed upper surface of their polyps. While the genus *Isaurus* is now well-established, historically there has been some confusion about whether or not this genus is truly separate from *Zoanthus* (see Muirhead and Ryland [1985] for a description of this), as although *Isaurus* species are distinguishable from *Zoanthus* spp. by the morphological traits listed above, other morphological traits (no sand-encrustation, generally colonial, zooxanthellate, "liberae" polyps) as well as their ecology (found in shallow tropical and sub-tropical waters) very closely resemble *Zoanthus*.

5. *Isaurus tuberculatus* Gray, 1828 (Plate 4)

Brief description: As described in Uchida (2001) and Muirhead and Ryland (1985), polyps recumbent in daytime, with many tubercules on upward surface of polyps. Some polyps may lack tubercules. Crown tubercules well-formed, clearly delineating oral disk area from capitulum. Body tubercules often in longitudinal series. Tubercules green, white, or gray, sometimes fluorescent. Polyp surface coloration cryptic and varies with environment (white, gray, red, purple), often reflecting surrounding sea weed and corals. Polyps average approximately 2 cm in length, though smaller and larger polyps common. Base of polyps and coenenchyme often with white or pale in color. Colonies small (usually < 50 polyps).

Remarks: Until now, *Isaurus* was known only from a few sites in Japan – including two

investigated here (Tatsukushi and Nishidomari) as well as the Danjo Islands in Nagasaki, and believed to be very rare. While *Isaurus* is undoubtedly less frequently encountered than *Zoanthus* and *Palythoa* species, this survey reveals *I. tuberculatus* colonies to be much more common than previously believed, at least along the Pacific Coast of Kochi. We have added six new sites to the known distribution of *I. tuberculatus* in Japan, and additional data (JDR, not shown) that will be presented elsewhere expands the distribution of *I. tuberculatus* to the Nansei Islands in Kagoshima. Uchida (2001) lists this *Isaurus* sp. in Japan as *I. assymetricus* (originally described from Australia in Haddon and Shackleton [1891]), but the original binomen of this species is *I. tuberculatus* (Gray 1828, unknown origin) according to Muirhead and Ryland (1985), and we have followed their suggestions in this study. Further studies should clarify the status of *Isaurus* species diversity.

In this study, *I. tuberculatus* seems to prefer areas of shoreline with large rock walls and high current and wave activity, but not directly exposed to waves, and is often found in the "corners" of small bays behind points and headlands. Often colonies are attached to cracks in large rocks just below the extreme low tide line.

6. *Isaurus* sp. B undescribed (Plate 5)

Brief description: Unlike *I. tuberculatus*, colonies large (thousands of polyps), with small green polyps less than half the length (approximately 1 cm) of *I. tuberculatus*. Tubercules purple, more rounded than *I. tuberculatus*, and not arranged in the longitudinal fashion as often seen in *I. tuberculatus*. Base of polyps and coenenchyme often with white or pale in color.

Remarks: Only two colonies of this potential new species have been found in the study area; one colony each at Shirigai Matsubae and Nishidomari Matsubae sites. An *Isaurus* sample from the Danjo Islands (nominally named *Isaurus brevia* by Uchida, personal communication) appears to have very similar morphology to the two *Isaurus* sp. B samples from this study. The molecular phylogeny of these samples and *I. tuberculatus* are currently being investigated and will be presented elsewhere. It remains to be seen whether these samples are conspecific with *I. tuberculatus* or not, as both Larson and Larson (1982) and Muirhead and Ryland (1985) note that *I. tuberculatus* has high levels of polyp morphological variation.

In this study, the two colonies were both found in shallow water (< 3 m), and similar to *I. tuberculatus*, in areas with high current but not direct exposure to waves.

II. Family Sphenopidae

This family differs from Zoanthidae in that it is sand-encrusted. Sphenopidae includes the zooxanthellate colonial genus *Palythoa* with many species worldwide, as well as the solitary zoanthid genus *Sphenopus*.

A. *Palythoa* species

Palythoa species (Family Sphenopidae) can be distinguished from the other two zooxanthellate genera present in southern Shikoku by the fact that they take up sand and detritus to help form their structure. Unlike *Zoanthus* species, *Palythoa* species of southern

Shikoku do not have a wide variety of oral disk color variation; usually with either green or brown coloration. Similarly, colony and polyp tissues are usually tan or brown, although patchy bleaching is sometimes observed in larger *P. tuberculosa* colonies. *Palythoa* species in southern Shikoku appear to prefer the same general high wave/current, high light levels and hard substrate conditions as *Zoanthus* and *Isaurus*, and often occur sympatrically with these two genera.

1. *Palythoa tuberculosa* Delage & Herouard, 1901 (Plate 6)

Brief description: As described in Uchida (2001) and Reimer *et al*. (2006c), polyps "immersae", barely extending above large, well-developed coenenchyme. Oral disks up to 20 mm in diameter, though often closed in day time Coenenchyme white to dark brown, generally uniform in color although some patchiness often observed. Colonies small to large (see remarks below). Like *Z. kuroshio*, colonies encrust substrate.

Remarks: *Palythoa tuberculosa* was the most common zooxanthellate zoanthid at the sites examined in this study. *P. tuberculosa* has been previously noted for its ability to exist in environments that are often more "marginal" than many other colonial cnidarians (see Reimer *et al*. 2006d). At the sites examined here, *P. tuberculosa*, like most other zooxanthellate zoanthids, was found below the extreme low tide line. However, *P. tuberculosa* was often found extending to deeper depths than the other zooxanthellate species found in southern Shikoku. An example of this was seen at the Futatsubae site, where *P. tuberculosa* colonies were noted at depths to 9 m, and no other zoanthids were found at this site. Similarly, *P. tuberculosa* at Nishidomari has been observed to depths of 8 m (J. Reimer, personal observation) and east of Omurabai at 16 m (J. Reimer, personal observation), as well as in other areas of Japan (Yakushima) as deep as approximately 10 m (Reimer *et al*. 2006c).

P. tuberculosa appears to have at least two major growth forms. One form is a "massive encrusting" colony form, in which a single colony can cover several square meters of hard substrate (Pl. 6 C). Examples of this form were in particular noted at Torinokubi and Tatsukushi-Bentenjima sites. The other, and most common form in southern Shikoku, are "small, rounded" colonies usually no more than 30 cm in diameter (for example, see Pl. 6 F). It remains to be determined if there are any distinctive genetic differences between these two forms.

2. *Palythoa mutuki* Carlgren, 1937 (Plate 7)

Brief description: As described in Ryland and Lancaster (2003) and Reimer *et al*. (2006c), polyps "liberae" in form, up to 40 mm in length. Oral disk diameter up to 30 mm, oral disk color green or brown. Radii often visible (white, pale brown). Colonies generally small (<100 polyps).

Remarks: In the area investigated in this study, *P. mutuki*, although found at most sites, was only encountered uncommonly, and not with the frequency of *P. tuberculosa*. Often *P. mutuki* was found on rock walls in areas somewhat shaded, and almost never in areas with very high light levels (on tops of rocks, etc.) that *Zoanthus* spp. seem to prefer. Previous studies have suggested *P. mutuki* consists of at least two to four clades based on genetic data (Reimer *et al*.

2006c), but here we included all *P. mutuki* morphotypes as one species as phylogeny within this "species group" remains to be clarified. *P. mutuki* has been further shown to be closely related to *P. tuberculosa*, and may have undergone reticulate evolution with *P. tuberculosa* at some point in the past (Reimer *et al*., unpublished data).

Morphological dichotomous key to zooxanthellate zoanthids in southern Shikoku.

1. Polyps sand-encrusted – go to 3 and 4.
2. Polyps not sand-encrusted – go to 5 and 6.
3. Polyps barely free of coenenchyme ("immersae") – *Palythoa tuberculosa*.
4. Polyps free and clear of coenenchyme ("liberae") – *Palythoa mutuki*.
5. Polyps upright – go to 7 and 8.
6. Polyps recumbent – go to 12 and 13.
7. Polyps barely free of coenenchyme ("immersae") – *Zoanthus kuroshio*.
8. Polyps free and clear of coenenchyme ("liberae") – go to 9, 10, and 11.
9. Polyps pale to dark purple, with pale or white oral disk – *Zoanthus vietnamensis*.
10. Polyps with vertical white or pale stripes on upper half when closed – *Zoanthus gigantus*.
11. Polyps with no vertical stripes on outside surface, with oral disks not pale to dark purple – *Zoanthus sansibaricus*.
12. Colonies small (< 50 polyps), polyps up to 2 or 3 cm in length – *Isaurus tuberculatus*.
13. Colonies large (thousands of polyps), polyps <1.5 cm in length – *Isaurus* sp. B.

Discussion

While the main purpose of this investigation was to list the species of zooxanthellate zoanthids between Cape Ashizuri and the Yura Peninsula, it became obvious during the course of the survey that the numbers and frequency of species along the Pacific Coast region were higher than at Bungo Strait locations. As shown in our statistical analyses, it appears that zooxanthellate zoanthids prefer locations on the open ocean with high amounts of wave activity and/or current. However, these results must be interpreted with caution. As shown in Table 1, the Pacific Coast region is geographically characterized by a well-developed coastal terrace. On the other hand, the Bungo Strait region has steep underwater cliffs and a dearth of coastal terraces in shallow waters. Thus, the Pacific Coast region's high zoanthid species diversity and numbers may be not necessarily due to wave and current action, but due to the relatively greater amount of preferable habitat for zooxanthellate zoanthids inherent to the Pacific Coast region. Clearly, investigations over a wider area, including locations on the open ocean with little or no coastal terrace, are necessary to draw conclusions on the environmental factors influencing zooxanthellate zoanthid species diversity.

In the future, more surveys and sampling in Ehime Prefecture and on the open ocean side of Okinoshima Island, as well as preliminary surveys northwards along the Pacific Coast of Shikoku should help complete the picture of zooxanthellate zoanthid distribution in Shikoku.

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Explanation of Plates

PLATE 1

Zoanthus sansibaricus

Various morphotypes *in situ* at A) Nishidomari-Matsubae, depth 1 m, B) Jinoiso, 2.5 m, C) Nishidomari, 1.5 m, D) Nishidomari-Matsubae, 0.5 m and E) Nishidomari-Matsubae, 1.5 m, respectively.

PLATE 2

Zoanthus gigantus

Various morphotypes *in situ* at A) Nishidomari-Matsubae, depth 1.5 m, B) Mizushima, 2 m, C) Obae, 1.5 m, D) Nishidomari-Matsubae, 2 m, E) Nishidomari-Matsubae, 2 m and F) Nishidomari-Matsubae, 3.5 m, respectively.

PLATE 3

Zoanthus vietnamensis

Various morphotypes *in situ* at A) Jinoiso, depth 1.5 m, B) Kashima, 0.5 m and C) Yokoshima, 1.5 m, respectively.

Zoanthus kuroshio

Various morphotypes *in situ* at D) Sangohama, Kurio, Yakushima, Kagoshima, depth + 0.5 m above extreme low tide line and E) Sangohama, Kurio, Yakushima, Kagoshima, 0 m, respectively. Colonies of *Z. kuroshio* observed at Nishidomari-Matsubae of very similar form and coloration, but due to their location in tide pools exposed to high wave activity, no *in situ* images were able to be obtained.

PLATE 4

Isaurus tuberculatus

Various morphotypes *in situ* at A) Hozaki, depth 1.5 m, B) Hozaki, 4 m, C) Hozaki, 1.5 m, D) Mizushima, 0.5 m, E) Mizushima, 0.5 m and F) two polyps from different colonies at Shirigai-Matsubae in a tank at BIK, respectively.

PLATE 5

***Isaurus* sp. B**

A) and B) colony from Shirigai-Matsubae *in situ*, depth 2 m. C) and D) polyps from same colony in a tank at BIK.

PLATE 6

Palythoa tuberculosa

Various morphotypes *in situ* at A) Shirozaki, depth 1 m, B) Nishidomari South, 0.5 m, C) Torinokubi, 4.5 m, D) Mizushima, 1.5 m, E) Shirozaki, 1 m, F) Shirozaki, 1 m and G) Torinokubi, 3 m, respectively.

PLATE 7

Palythoa mutuki

Various morphotypes *in situ* at A) Odo South, depth 2 m, B) Tatsukushi-Bentenjima, 2 m, C) Nishidomari South, 2 m and D) Tatsukushi-Bentenjima, 0.5 m, respectively.


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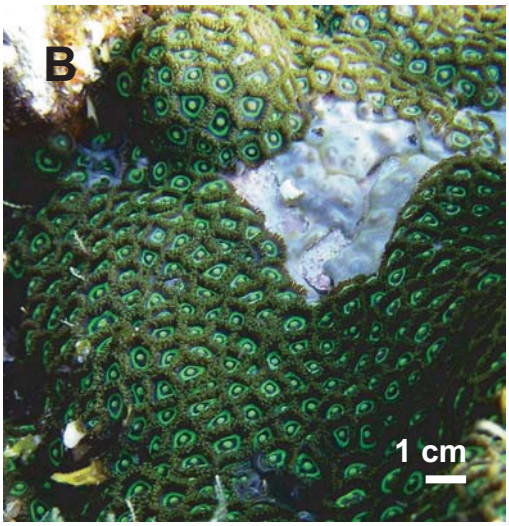
1 cm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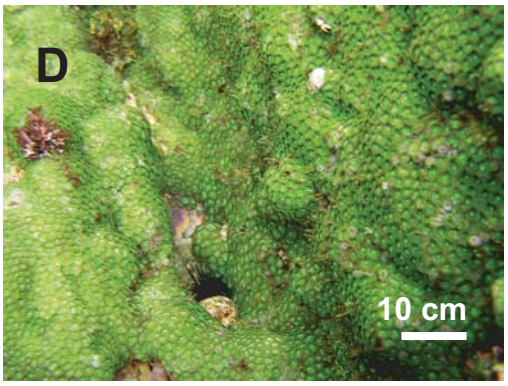
C
1 cm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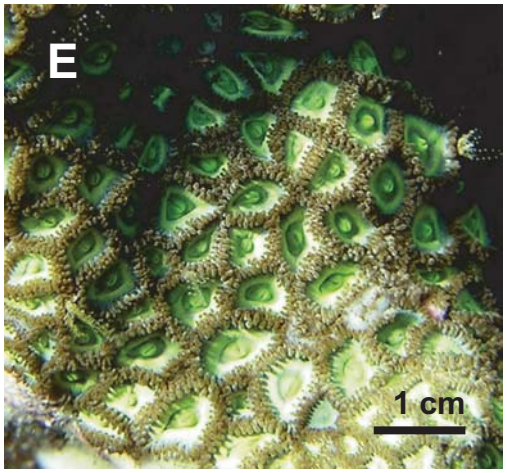
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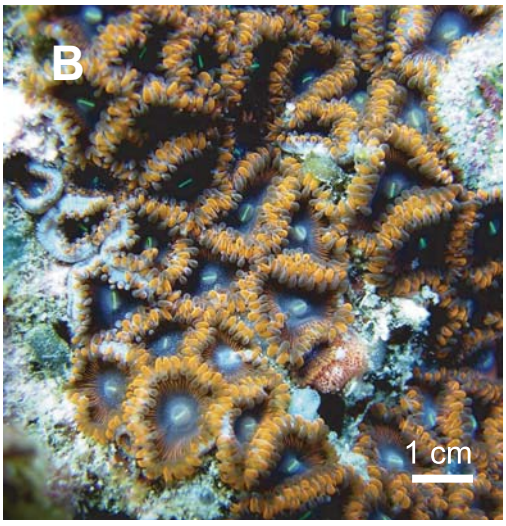

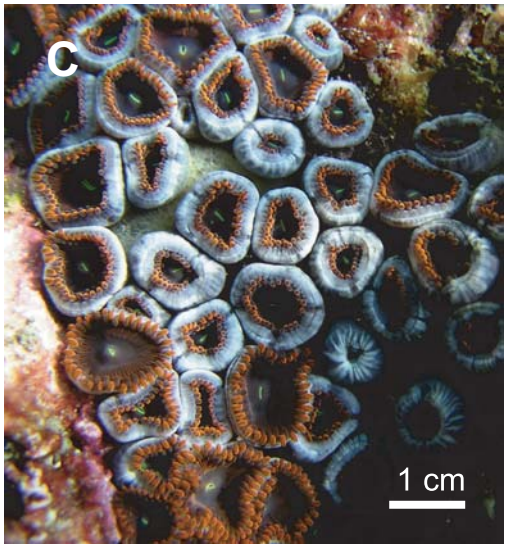

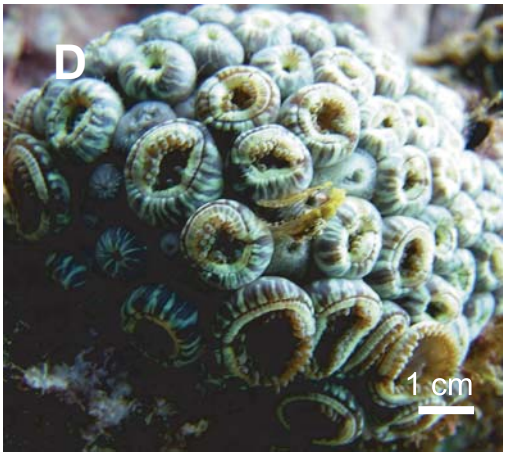

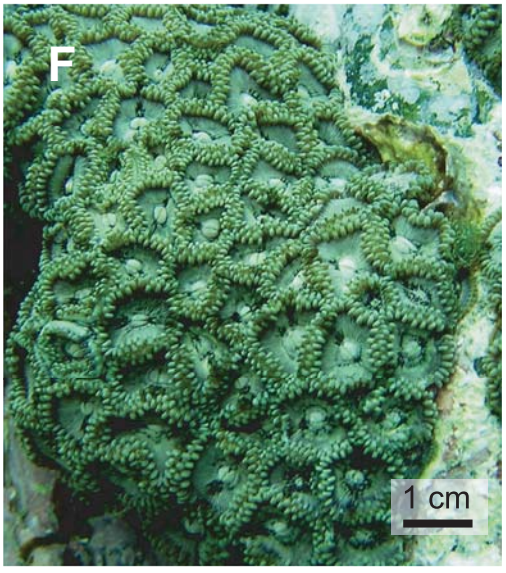


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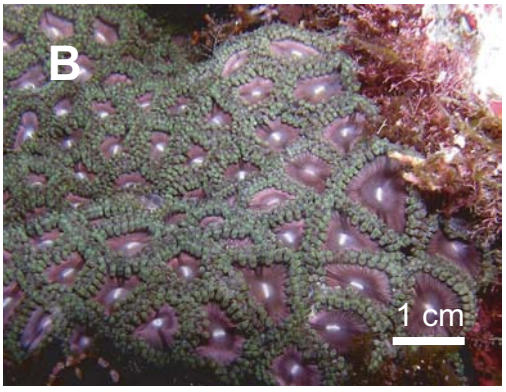
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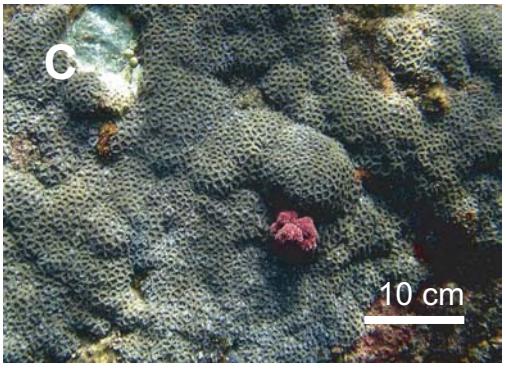
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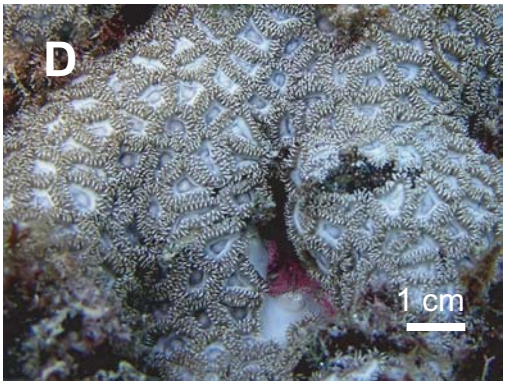
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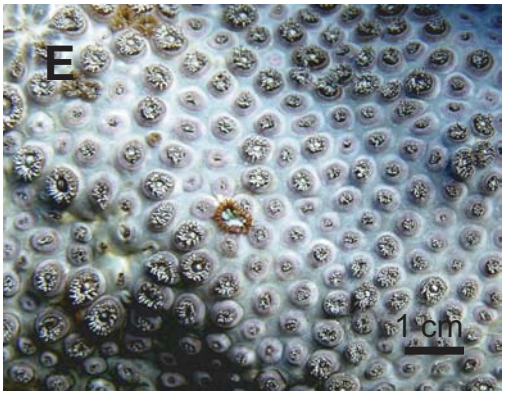
E
1 cm

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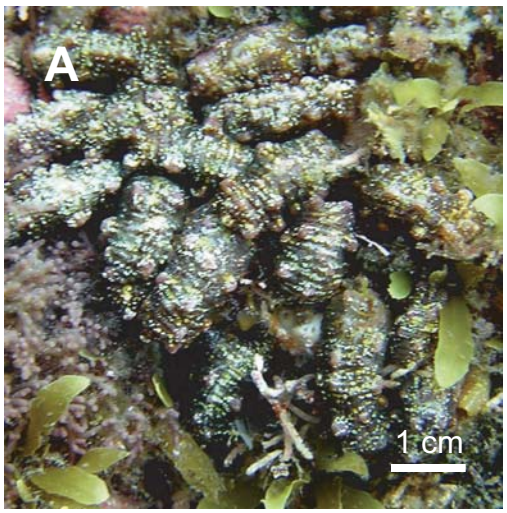

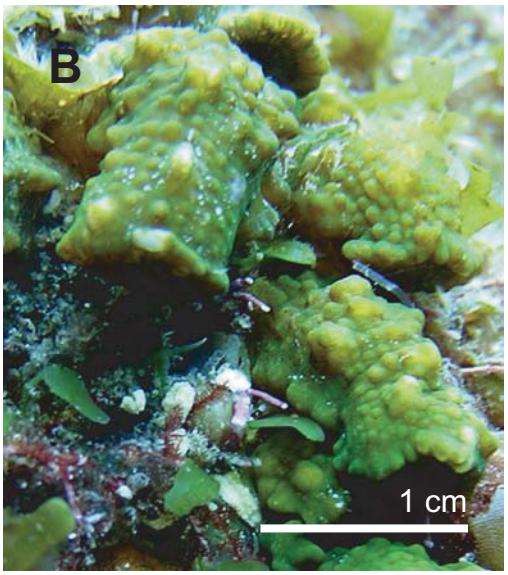

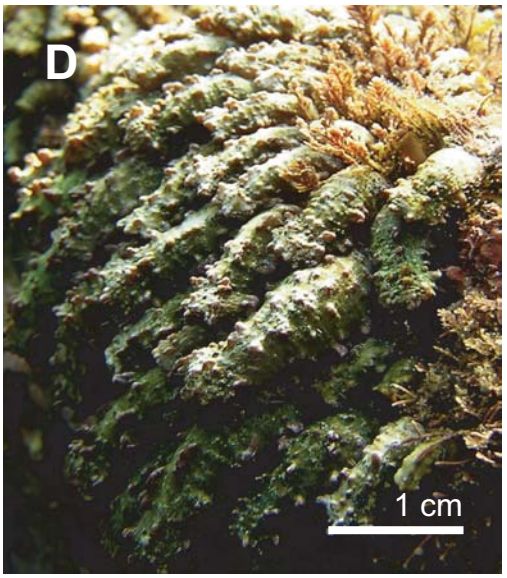

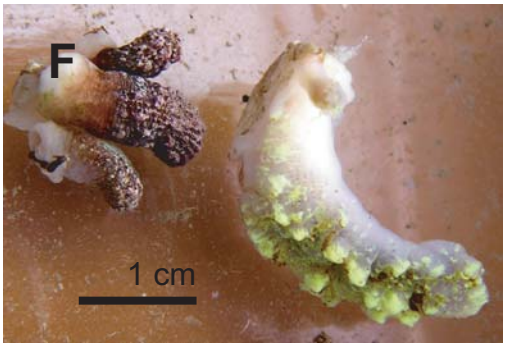

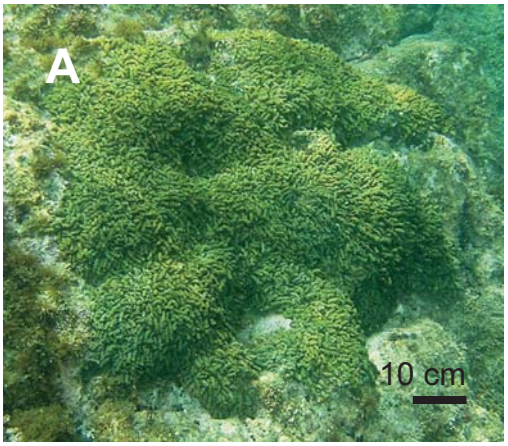
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B
1 cm


C
1 cm

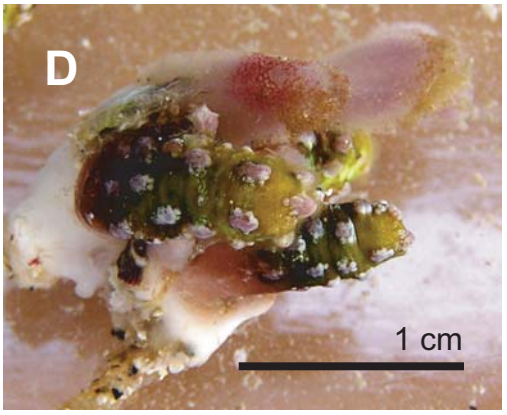
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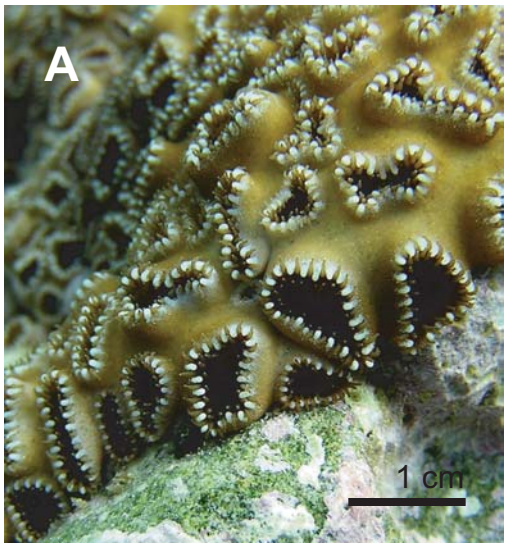
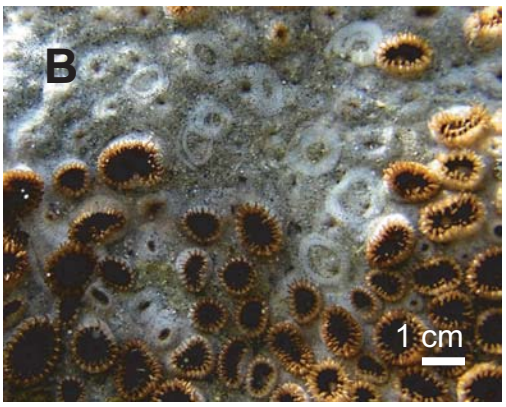
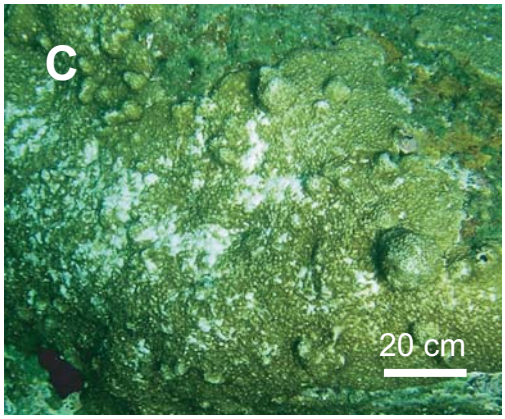
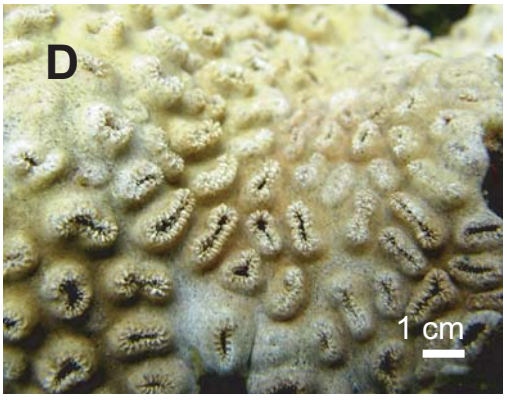
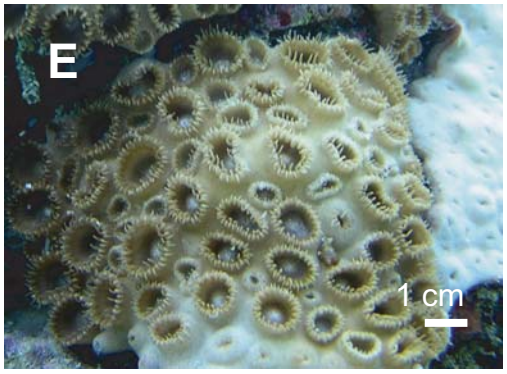
PLATE 6







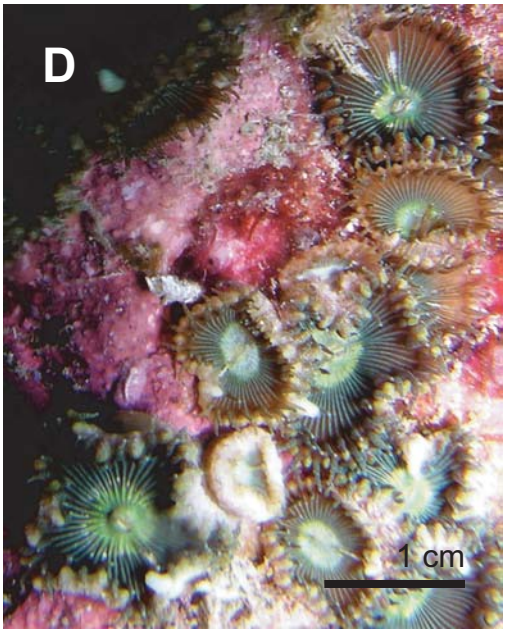





A
1 cm


B
1 cm


C
1 cm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