

Shallow-Water Brachycnemic Zoanthids (Cnidaria: Hexacorallia) from Taiwan: A Preliminary Survey

James D. Reimer^{1,2,*}, Masami Obuchi¹, Yuka Irei³, Takuma Fujii³, and Yoko Nozawa⁴

¹Molecular Invertebrate Systematics and Ecology Laboratory, Rising Star Program, Transdisciplinary Research Organization for Subtropical Island Studies (TRO-SIS), Univ. of the Ryukyus, Senbaru 1, Nishihara, Okinawa 903-0213, Japan

²Marine Biodiversity Research Program, Institute of Biogeosciences, Japan Agency for Marine-Earth Science and Technology (JAMSTEC), 2-15 Natsushima, Yokosuka, Kanagawa 237-0061, Japan

³Molecular Invertebrate Systematics and Ecology Laboratory, Graduate School of Marine Science, Univ. of the Ryukyus, Senbaru 1, Nishihara, Okinawa 903-0213, Japan

⁴Biodiversity Research Center, Academia Sinica, Nankang, Taipei 115, Taiwan

(Accepted December 9, 2010)

James D. Reimer, Masami Obuchi, Yuka Irei, Takuma Fujii, and Yoko Nozawa (2011) Shallow-water brachycnemic zoanthids (Cnidaria: Hexacorallia) from Taiwan: a preliminary survey. *Zoological Studies* 50(3): 363-371. Zoanthids are benthic cnidarians commonly seen in shallow coral reef and subtropical marine ecosystems, and are increasingly being utilized as research subjects for marine products and biodiversity studies. However, their distributions and overall species diversity remain relatively unknown except for in a few regions of the world, including southern Japan. Here, for the 1st time, the shallow-water diversity of zoanthids of the suborder Brachycnemina, which primarily includes zooxanthellate species, was examined in Taiwanese waters. Species diversity surveys conducted at coral reef (Kenting and Lyudao) and non-reefal (Keelung) locations revealed 12 zoanthid species (*Acrozoanthus australiae*, *Isaurus tuberculatus*, *Zoanthus gigantus*, *Z. kuroshio*, *Z. sansibaricus*, *Z. aff. vietnamensis*, *Palythoa heliodiscus*, *P. mutuki*, *P. tuberculosa*, *Palythoa* sp. tokashiki, unknown *Palythoa* spp., and another unknown zoanthid), most of which are new records for Taiwan. All 3 locations had totals of 7-10 species present, with the 2 coral reef locations resembling locations with coral reefs in Okinawa (e.g., by the presence of *Z. kuroshio*, *P. heliodiscus*, *Palythoa* sp. tokashiki), while the zoanthid community at Keelung was more similar to zoanthids observed at subtropical Shikoku, Japan (e.g., by the presence of *Z. aff. vietnamensis* and large *Z. gigantus* colonies). It is possible that the unknown *Palythoa* specimens constitute 1 or more species new to science, and further investigation of these zoanthids is needed. It is hoped that the species lists provided in this study will help provide a basis for future zoanthid research in Taiwan. <http://zoolstud.sinica.edu.tw/Journals/50.3/363.pdf>

Key words: Taiwan, Kuroshio Current, Biodiversity, Zoanthid.

Zoanthids are a hexacorallian order (Zoantharia, Zoanthidea) of benthic cnidarians characterized by having 2 rows of tentacles, and are usually colonial, with individual polyps connected by a coenenchyme, or common tissue, similar to many hard coral species. Additionally, most zoanthids have sand and/or other detritus encrusted within their mesoglea to help provide strength and structure, an unusual strategy

unique to zoanthids. Zoanthids are found in most environments from shallow tropical coral reefs (Burnett et al. 1997) to cold seeps in the deep sea (Reimer et al. 2007).

Although often common in many ecosystems, the taxonomy of zoanthids has historically been chaotic due to difficulty in correct identification, caused by large amounts of intraspecific variation (Burnett et al. 1997, Reimer et al. 2004), a lack of

*To whom correspondence and reprint requests should be addressed. Tel: 81-98-8958542. Fax: 81-98-8958577. E-mail: jreimer@sci.u-ryukyu.ac.jp

viable morphological characteristics that are easily examined, and difficulty in internal examinations due to sand encrustation (Reimer et al. 2010b). Thus, knowledge of the diversity and biogeography of zoanthids is relatively scant compared to related hexacorallian orders such as hard corals (Scleractinia) and anemones (Actinaria).

Shallow-water tropical and subtropical zoanthids of the suborder Brachycnemina are ubiquitous in coral reef ecosystems, and often form large colonies on intertidal and shallow reef crests (Karlson 1980). This suborder is distinguished from the other zoanthid suborder, Macrocnemina, by the status of the 5th mesentery from the dorsal directive, which is complete in Macrocnemina and incomplete in Brachycnemina (see figure 2 in Reimer et al. 2010b). The Brachycnemina includes 3 families. The family Sphenopidae is sand-encrusted, and includes the colonial zooxanthellate *Palythoa*, and the unitary *Sphenopus* known only from a handful of species. Neozoanthidae is monogeneric and monospecific and known only from Madagascar, although other unidentified specimens point to a Pacific distribution (Reimer 2010). The 3rd family, the Zoanthidae, is the only zoanthid taxa that does not utilize encrustation, and includes 3 genera, *Acrozoanthus*, *Isaurus*, and *Zoanthus*. *Palythoa* and *Zoanthus* in particular are the most speciose genera, are quite common on coral reefs, and are popular items in the pet industry, as well as subjects for research into palytoxin (*Palythoa*) (Moore and Scheuer 1971) and fluorescent proteins (*Zoanthus*) (Labas et al. 2002).

Recently, much research focused on the distribution of brachycnemid zoanthids in Japan (Reimer 2007 2010, Ono et al. 2008), and knowledge of their diversity and biogeography for this region, while far from complete, exists at basic levels. However, data from surrounding regions remain scarce. Taiwan is located directly to the south of the Ryukyu/Nansei chain of islands in southern Japan, and the east coast of this island is also influenced by the warm Kuroshio Current.

Historically, there is almost no information or records in the literature on zoanthids from Taiwan, except for an excellent examination of *Sphenopus* by Soong et al. (1999) and an examination of nitrogen fixation-utilizing *P. tuberculosa* collected from Kenting (Shieh and Lin 1992), and there are no data on zoanthid species diversity. However, coral reef and non-reefal coral communities were described at many sites in Taiwan (Chen 1999, Chen and Shashank

2009), and thus it very likely that many zoanthid species are present in these areas. As a neighbor to Japan and connected by the Kuroshio Current, an understanding of brachycnemid zoanthid diversity in Taiwan is critical to achieving a more complete understanding of their biodiversity and biogeography in the northwestern Pacific. Thus, a survey of brachycnemid zoanthid biodiversity was cooperatively carried out by the Univ. of the Ryukyus (UR), Japan and the Biodiversity Research Center, Academia Sinica, Taipei, Taiwan at 3 different locations in Taiwan (2 coral reefs and 1 non-reef coral community) to create a preliminary species list. Herein, we report on the initial results of that survey.

MATERIALS AND METHODS

Surveys of zoanthids in Taiwan were carried out in Sept. 2009-Sept. 2010 by snorkeling and scuba diving. Three different locations were investigated (Fig. 1): (1) Wanlitung, Tiaoshi, and at Kenting, southern Taiwan (sampling permission #989094/1400), which are coral reef ecosystems; (2) Gueiwan, Gongguan, Shihlang, Dabaisha, and Matichao at Lyudao (also known as Green I., off the southeastern coast of Taiwan) which are coral reef ecosystems; and (3) Yehliu and Bitouchiao at Keelung, northeastern Taiwan, which are primarily subtropical non-reefal coral communities (Chen 1999, Chen and Shashank 2009).

Specimens were photographed *in situ* prior to collection, and images were used to characterize external morphological features. Species were identified primarily following Reimer (2010), with *Acrozoanthus* specimens identified following Ryland (1997). Specimens were preserved in 70% or 99.5% ethanol, and examined at the UR. Currently, specimens are deposited at the 1st author's laboratory at the UR, but once molecular examinations are completed, specimens will be deposited in the National Museum of Natural Science (NMNS), Taichung, Taiwan.

RESULTS

Results of the surveys are summarized in table 1. A dichotomous key to the majority of the species found in Taiwan is given in Reimer (2010). Nomenclature used is *sensu* Reimer (2010) unless otherwise noted.

Species diversity by location

At Kenting (coral reef) in southern Taiwan, 7 brachycnemic zoanthid species were recorded (Table 1), and specimens were collected for 6 of these. The presence of *Zoanthus sansibaricus*, *Z. kuroshio*, *Acrozoanthus australiae* (detailed in Reimer et al. 2010a), *Isaurus tuberculatus* (images only), *P. tuberculosa*, *P. mutuki*, and *Palythoa* sp. tokashiki was confirmed in this area.

Similarly, at both Lyudao (coral reef) and Keelung (non-reefal), 7-10 species of zoanths were confirmed from images and sampling (Table 1). At Lyudao, *Z. sansibaricus*, *Z. kuroshio*, *Z. aff. vietnamensis*, *Z. gigantus*, *A. australiae*, *P. tuberculosa*, *P. mutuki*, *P. heliodiscus*, *Palythoa* sp. tokashiki, and 1 or 2 potentially undescribed *Palythoa* species were noted; while at Keelung *Z. sansibaricus*, *Z. aff. vietnamensis*, *Z. gigantus*, *I. tuberculatus* (images only), *P. tuberculosa*, *P.*

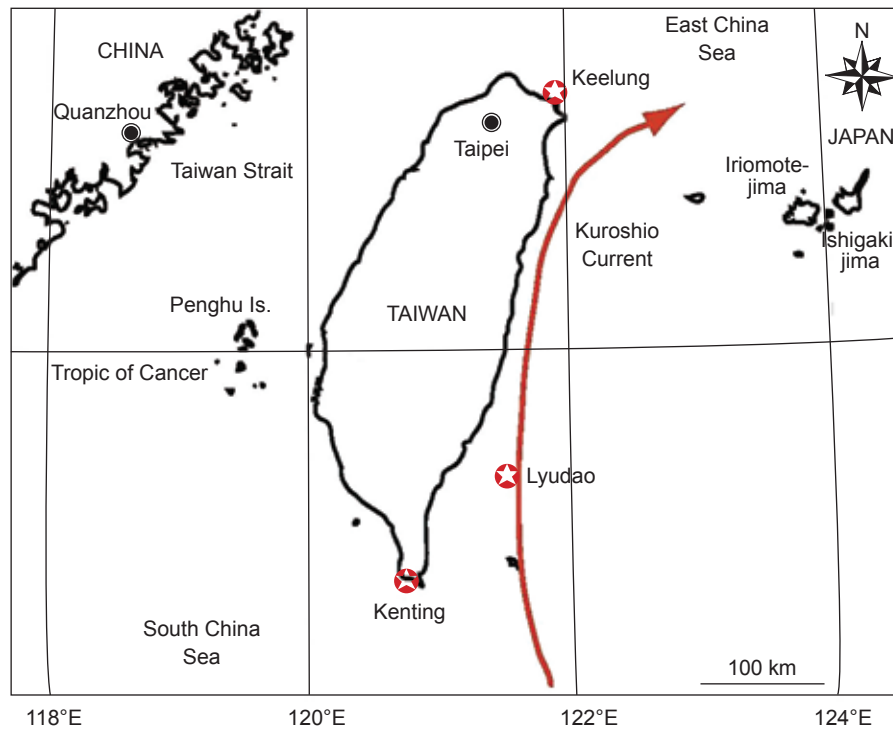


Fig. 1. Map of Taiwan showing the locations where zoanthid species diversity was investigated in this study (red stars). The Kuroshio Current is indicated by the red line and arrow. Note the relative proximity of islands in Japan to northern Taiwan, and their connection by the Kuroshio Current.

Table 1. Brachycnemic zoanthid species and their occurrence in Taiwan

Family	Genus/species	Kenting (coral reef, S. Taiwan)	Lyudao (coral reef, island off E. Taiwan)	Keelung (nonreefal, N. Taiwan)
Zoanthidae	<i>Zoanthus kuroshio</i>	+	+	
	<i>Zoanthus aff. vietnamensis</i>			+
	<i>Zoanthus gigantus</i>		+	+
	<i>Isaurus tuberculatus</i>	+*		+*
	<i>Acrozoanthus australiae</i>	+	+	
Sphenopidae	<i>Palythoa tuberculosa</i>	+	+	+
	<i>Palythoa mutuki</i>	+	+	+
	<i>Palythoa heliodiscus</i>		+	
	<i>Palythoa</i> sp. tokashiki	+	+	
	Unknown <i>Palythoa</i> spp.		+	+
unknown	Unknown zoanthid			+*

*Only images of these species, no specimens collected.

mutuki, an unknown *Palythoa* species, and an undescribed small zoanthid (images only) were found.

**Brachycnemic zoanthid species list Family
Zoanthidae Gray 1840**

***Zoanthus sansibaricus* Carlgren 1900
(Fig. 2A)**

This species of zoanthid is common throughout the Pacific (Reimer and Hickman 2009), and was only found in very shallow areas (intertidal to shallow subtidal depths of < 3 m) on the tops of reefs exposed to waves and currents in all 3 areas. Polyps generally stand clear of the coenenchyme (“liberae” in Pax 1910). Most observed morphotypes in Kenting had green, yellow, or cream-colored oral discs, and at Keelung most colonies were subtidal and had green oral discs, in line with the large amounts of color variation observed at Lyudao and previously in this species (Reimer et al. 2004). Colonies at all locations were generally small (< 50 polyps) and somewhat hidden in cracks and fissures in the coral reef substrate, but some large colonies (> 1 m²) were observed at Lyudao. Oral disc diameters were approximately 0.4-0.8 cm for fully grown polyps.

***Zoanthus kuroshio* Reimer and Ono 2006
(Fig. 2B)**

Unlike *Z. sansibaricus*, *Z. kuroshio* polyps are embedded or only partially clear of a well-developed coenenchyme (“immersae” or “intermediae” in Pax 1910). In this study, they were observed at Kenting and Lyudao, where *Z. kuroshio* colonies were found in the shallow subtidal to depths of approximately 2 m, and were generally slightly deeper than *Z. sansibaricus* colonies. Oral discs were fluorescent-pink (slightly brighter than the light pink morphotype often seen in the Ryukyu Is.) or light-green, and 0.4-1.2 cm in diameter. Colonies were generally larger than *Z. sansibaricus* colonies, and formed patches on the outside of reefs in areas exposed to waves and currents.

***Zoanthus aff. vietnamensis* Pax and Mueller
1957, (sensu Uchida 2001)
(Fig. 2C)**

This species was noted at Keelung and Lyudao, where it was often abundant in shallow subtidal areas at depths of < 3 m. Colonies were often very large at Keelung, covering more than 1 m² of substrate. Polyps were “liberae” (Pax 1910), stood clear of the coenenchyme, and were much larger (with oral disc diameters up to almost 2 cm) than *Z. sansibaricus* or *Z. kuroshio* polyps, and almost as big as *Z. gigantus* polyps (see below). The outside of the polyps was lighter in color than observed in *Z. sansibaricus* or *Z. gigantus*, and oral discs were usually pale pink, with white, green, gray, or light pink tentacles. Previously, it was demonstrated that this species may be conspecific with *Z. kuroshio*, based on molecular data, but morphological data clearly separate these into different groups (Reimer et al 2006a).

***Zoanthus gigantus* Reimer and Tsukahara 2006
(Fig. 2D)**

In this study, *Z. gigantus* was found at Lyudao and Keelung. Like the other *Zoanthus* species described above, *Z. gigantus* was found in shallow waters. At Lyudao, this species was found in both small (< 50 polyps) and large colonies, while at Keelung, it often formed very large colonies, similar to *Z. aff. vietnamensis*. Oral discs were up to 2.0 cm in diameter, and were seen to have a variety of colors, often with a fluorescent-green mouth, similar to that previously described (Reimer et al. 2006b). The outer surface of the polyps around the oral end had the characteristic white “stripes” common to this species. Polyps were “liberae” (Pax 1910) and up to 2 cm in height.

***Acrozoanthus australiae* Saville-Kent 1893
(Fig. 2E)**

This species was found in both coral reef environments, Kenting and Lyudao, and was exclusively on the outside of eunicid worm tubes (detailed in Reimer et al. 2010a). The worm tubes were usually found protruding from giant *Porites* colonies (Kenting) or on worm tubes directly attached to the reef substrate (Lyudao) at depths of approximately 8-12 m. Polyps were 5-

10 mm in height, with a very reduced stoloniferous coenenchyme, or occasionally unitary (solitary). The outer surface of the polyps was light purple or pale brown. Oral discs were 2-6 mm in diameter, and colored brown or pale purple often with fluorescent mint-green markings. Tentacles were comparatively much longer than those of other brachycnemic zoanthid species, and up to twice the oral disc diameter in length. Tentacles were pale brown, purple, or fluorescent mint-green.

***Isaurus tuberculatus* Gray 1828**
(Fig. 2F)

This species was not directly observed during the surveys, but its distribution in Kenting and Keelung was confirmed through previously acquired digital images (CA Chen, G Hsu, pers. commun.). *Isaurus tuberculatus* is noted for its unusual appearance, with recumbent (not erect) polyps with tubercles (small bumps) on the outer surface of the polyps. Polyps are generally closed during the daytime, and often are very cryptic in appearance, with coloration similar to

the surrounding substrate. As no specimens were collected during this survey, dimensions of this species are not given here, but it is expected from digital images that Taiwanese specimens are similar in size and appearance to those from southern Japan (Reimer et al. 2008b).

Family Sphenopidae

***Palythoa tuberculosa* Klunzinger 1877**
(Fig. 3A)

This species was found at all 3 sites, and from the shallow intertidal to depths of approximately 10 m. It was most common at depths of 3-6 m at Keelung and Kenting, and in the lower intertidal at Lyudao. The overall appearance of this species was as seen in Japan (Reimer 2007), with “immersae” polyps (Pax 1910) in a well-developed coenenchyme and color from pale to dark brown, often with yellowish-green fluorescence. Polyps had short tentacles approximately 1/2 the oral disc diameter. Colonies were most generally 5-

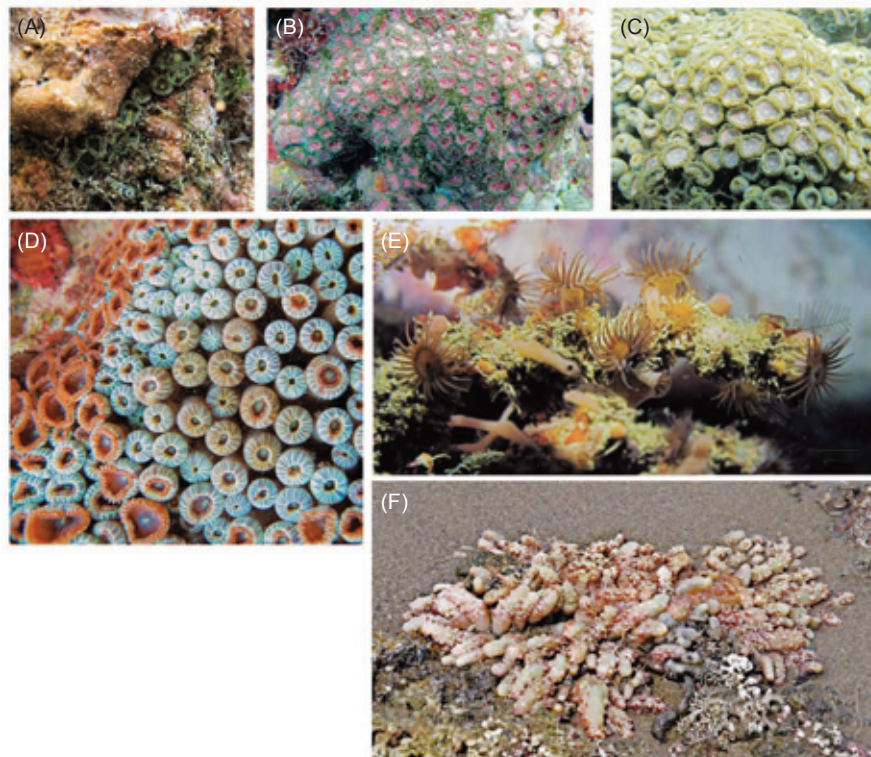


Fig. 2. Brachycnemic zoanthids from the family Zoanthidae from Taiwan. (A) *Zoanthus sansibaricus* at Wanlitung, Kenting, depth = 0.7 m; (B) *Z. kuroshio* at Wanlitung, Kenting, 1.5 m; (C) *Z. aff. vietnamensis* at Bitouchiao, Keelung, 2.1 m; (D) *Z. gigantus* at Yehliu, Keelung, 1.9 m; (E) *Acrozoanthus australiae* at Houbihu, Kenting, 10.3 m; (F) *Isaurus tuberculatus* at Taidong, eastern Taiwan, intertidal (image courtesy of G. Hsu 2004).

10 cm in diameter, although smaller and larger (of several square meters) colonies were occasionally observed.

***Palythoa mutuki* Haddon and Shackleton 1891**
(Fig. 3B)

Colonies of *P. mutuki* were observed at all 3 sites. This species was found in shallow intertidal to subtidal (10-m) depths, where it often formed small patches on hard substrates. Occasionally, large colonies (> 50 cm in diameter) were observed at Keelung. "Intermediae" or "liberae" polyps (Pax 1910) were connected by a coenenchyme. Sometimes polyps were tightly crowded together, while in other colonies, polyps were somewhat regularly spaced apart. *Palythoa mutuki* oral disks were up to 2.0 cm in diameter, but rarely observed to be fully opened, and were instead often partially closed (Fig. 3B). The external coloration was brown, with green and/or brown oral disks. Tentacles were generally short (< 1/2 of the oral disk diameter).

***Palythoa heliodiscus* Ryland and Lancaster 2003**
(Fig. 3C)

Palythoa heliodiscus was only observed at Lyudao, at 12.9 m, and other specimens that could possibly be this species were observed and collected at Lyudao, although they had different oral disc coloration (Figs. 3E, H). The confirmed *P. heliodiscus* colony was very large (over 1 m long), similar to that seen at similar depths in Okinawa, Japan. Polyps were "liberae" (Pax 1910), with brown external coloration and brown oral disks up to 2.0 cm in diameter. This species is characterized by its relatively plain oral disc, with clearly visible septae, and numerous (up to approximately 80) very short tentacles. It was commonly found on ledges and the upper sides of channels and drop-offs.

***Palythoa* sp. tokashiki sensu Reimer 2010**
(Fig. 3D)

This undescribed species was observed at Okinawa I. and the Yaeyama Is. in Japan, and was found at both Kenting and Lyudao in Taiwan. In both cases, similar to as in Japan, it was found in completely shaded cracks, crevices, and small caves. Colonies were generally very small (< 10 polyps), and polyps were "liberae" (Pax 1910)

and somewhat recumbent, angled towards the opening of the crack or crevice. Oral disks were up to 1.2 cm in diameter. Like other *Palythoa* species, the external coloration was whitish-tan or brown. Tentacles were striped black and creamy-white, and generally longer than the oral disk diameter.

Unknown *Palythoa* species
(Figs. 3E, F, H)

Several specimens of *Palythoa* from Lyudao and Keelung did not fit with current descriptions of any known species. Some specimens were "liberae" (Pax 1910) and resembled *P. heliodiscus* or *P. mutuki* in general morphology but differed in the oral disk coloration or habitat (i.e., deeper than expected for *P. mutuki*-like specimens; with different coloration than *P. heliodiscus*) (Figs. 3E, H).

One exceptional specimen was unattached to the substrate, and had formed a large (size) colony that was rolling loose on the substrate (Fig. 3F). Polyps of this specimen were "intermediae" (Pax 1910), and although the colony somewhat resembled *P. mutuki*, such a growth form has not been recorded for this species. Additionally, polyps were larger (size) than those of *P. mutuki*, and oral discs were completely brown and plainer than those of most *P. mutuki* specimens (Fig. 3F).

Unknown zoanthid
(Fig. 3G)

This as yet unidentified zoanthid was only observed in 1 image from Keelung, but closely resembles unidentified zoanthids from Japan (T. Fujii, pers. comm.). The polyps were very small (approximately 1 mm in diameter), encrusted with relatively large pieces of sand and detritus, and had a reduced, stoloniferous coenenchyme. These zoanthids had little coloration of their own, and tentacles were long and almost transparent. It is unknown whether this zoanthid belongs to Brachycnemina or Macrocnemina, but is included here as it is often found in shallow coral reef environments in the Pacific (T. Fujii, pers. obs.).

DISCUSSION

Diversity at different locations

Overall levels of zoanthid species diversity

did not differ much by location, with 7-10 species found at each location. However, there were differences as far as the species found at the different locations. Such results are not surprising, given what is known about zoanthid species' biogeography from southern Japan (Reimer et al. 2008a). In southern Japan, 6 or 7 brachycnemic species are commonly present, with diversity decreasing in areas where ocean temperatures fall below 15-16°C in winter (Reimer et al. 2008a). However, it is somewhat surprising that the diversity observed in colder (Chen 1999), non-reefal Keelung (7 species) was almost as high as that at coral reef locations (7-10 species) in Taiwan. This suggests that at least some species of zooxanthellate zoanthids are relatively tolerant of slightly colder waters, especially compared to some other coral reef/coral community fauna. For example, in a study examining the diversity of photosymbiotic ascidians conducted at the same time and at the same locations as the current study, no photosymbiotic ascidians species were seen at Keelung, despite their presence at both

Lyudao and Kenting (Hirose and Nozawa 2010).

Location by location, zoanthid diversity at both Kenting and Lyudao coral reefs resembled coral reefs of Okinawa I. and the Yaeyama Is., with generally similar species (e.g., *P. heliodiscus*, *Palythoa* sp. tokashiki, and *Z. kuroshio*) and similar morphologies present. The marine environments of coral reefs in Taiwan and Okinawa are similar, with similar temperature regimes, and are connected by the Kuroshio Current (Fig. 1), so this finding is not surprising. The only major difference noted was the unexpected finding of *Acrozoanthus australiae* at both locations; this species had not been noted outside of Indonesia and Australia until these Taiwanese surveys (Reimer et al. 2010a).

However, zoanthid diversity in non-reefal locations at Keelung more closely resembled locations previously examined in subtropical/temperate Shikoku, Japan (see Reimer 2007) in terms of the species present and their morphology, distribution (subtidal), etc. For example, large colonies of *Z. gigantus* and *Z. aff. vietnamensis* were seen in both regions, and were not seen in

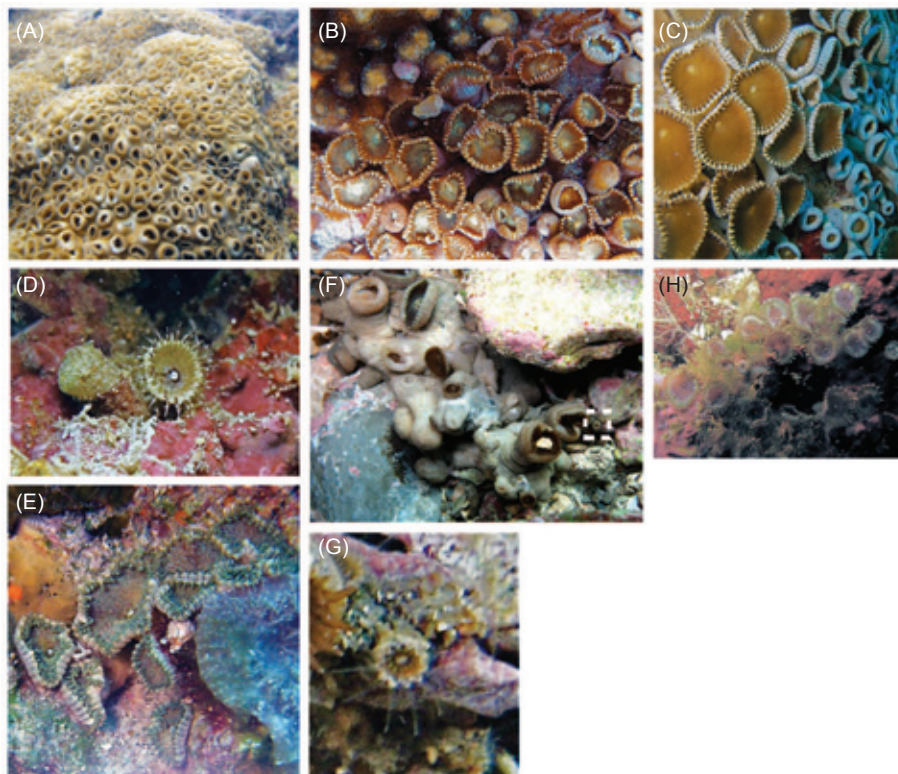


Fig. 3. Brachycnemic zoanthids from the family Sphenopidae (unless otherwise noted) from Taiwan. (A) *Palythoa tuberculosa* at Bitouchiao, Keelung, depth 1.6 m; (B) *P. mutuki* at Yehliu, Keelung, 1.5 m; (C) *P. heliodiscus* at Matichiao, Lyudao, 12.9 m; (D) *Palythoa* sp. tokashiki at Wanlitung, Kenting, 3.7 m; (E) unknown *Palythoa* sp. at Dabaisha, Lyudao, 10.8 m; (F) unknown *Palythoa* sp. at Yehliu, Keelung, 2.0 m, with dotted box indicating location of 3G; (G) unknown zoanthid (family also unknown), information as in F; (H) unknown *Palythoa* sp. at Shihlang, Lyudao, 9.1 m.

coral reef locations in Taiwan or Japan. Further research into other aspects of zoanthid biology (e.g., zooxanthellae clades and spawning timing) may reveal additional common points between northern Taiwan and the Pacific coast of southern mainland Japan.

Species' biogeography

When examining data from this study combined with previous (Reimer et al. 2008a) data, it was apparent that some species of zooxanthellate zoanthids are less tolerant of colder environments than others. In particular, *P. heliodiscus* has not been found north of the middle of the Ryukyu/Nansei Archipelago (Okinoerabu I. in Reimer et al. 2008a, Tokunoshima I. from recent expeditions; JD Reimer, data not shown), and it is theorized that this species does not inhabit areas where the ocean temperature falls below 20°C (Ono et al. 2008). Similarly, in this study, *P. heliodiscus* was found at Lyudao but not at Kenting or Keelung. At Kenting and Lyudao ocean temperatures may reach a minimum of 19°C, but in northern Taiwan the Kuroshio Current veers to the east, and subsequently winter temperatures may reach 16°C, resulting in a non-reefal coral community (Veron 1995, Chen 1999). Additionally, it appears that *A. australiae* may be limited to warmer waters as it was only seen at the 2 coral reef sites in this study.

Thus, with combined data from Japan and Taiwan, preliminary speculation about different zoanthid species' temperature tolerances can be made. Based on observations, some species (*P. heliodiscus*, *Palythoa* sp. tokashiki, *A. australiae*, and *Z. kuroshio*) appear to prefer warmer (> 20°C) waters, while *Z. aff. vietnamensis* prefers colder waters, as it was primarily only found in Keelung (with small numbers only found at Lyudao, Taiwan), and Kagoshima and Shikoku in Japan (Reimer et al. 2008a). The remaining described species (*Z. sansibaricus*, *Z. gigantus*, *P. tuberculosa*, *P. mutuki*, and *I. tuberculatus*) appear to be much more "generalist" in terms of temperature preference.

Overall, *Z. sansibaricus* and *P. tuberculosa* were by far the most common reef zoanthids in Taiwan, and were commonly found in most locations. Similarly, *P. tuberculosa* was previously shown to have "generalist" zooxanthellae and live in a wide variety of habitats (Reimer et al. 2006c), while *Z. sansibaricus* is flexible in its zooxanthella associations, which may allow this

species to inhabit different environments (Reimer et al. 2006d). Furthermore, it appears that *Z. sansibaricus* is more tolerant of desiccation than other zoanthid species, as it was found highest in the intertidal zone at Kenting, similar to results from Japan (Reimer et al. 2008a, Reimer 2008). On the other hand, *P. mutuki*, while found at all 3 locations and tolerant of both hot and cold temperatures, seems to be most common on reef flats, was found in lower numbers, and is somewhat more of a niche specialist than *Z. sansibaricus* and *P. tuberculosa*. Thus, aspects of zooxanthellate zoanthid species' distributions should be considered from both their temperature tolerances and their preferred habitats.

Isaurus tuberculatus was not located during surveys in this study, but digital images confirmed the presence of this species in Kenting, Keelung, and at Taidong on the southeastern coast of Taiwan. Such results are reminiscent of a study from Japan (Reimer et al. 2008b), which found *I. tuberculatus* to be widespread, albeit at low densities. The overall "cryptic" appearance of this species also contributes to difficulty in locating specimens in the field, and it is likely that this species is also present at Lyudao.

Future zoanthid work in Taiwan

It is hoped that this work will provide a basis for further examination of zoanthids in Taiwan in the future. As a region linked to both colder-temperate waters and the warmer subtropical/tropical Kuroshio Current, Taiwan may have much undiscovered marine biodiversity. As a complement to this study, an examination of the diversity of macrocnemic zoanthids, similar to those conducted in New Caledonia (Sinniger 2006) and the Galapagos (Reimer et al. 2008c), would help establish a clearer overall picture of zoanthid species diversity. Indeed, during our study, at least 2 species of macrocnemic zoanthids (*Parazoanthus* aff. *puertoricense* sensu Uchida 2001 and *Hydrozoanthus gracilis*) were confirmed at Lyudao, and it is very likely more species exist in the waters of Taiwan.

Acknowledgments: The authors thank Dr. C.A. Chen (Biodiversity Research Center, Academia Sinica (BRCAS), Taipei, Taiwan) and members of his laboratory for invaluable assistance in the field. G. Hsu (BRCAS) kindly provided images of *I. tuberculatus*. Prof. E. Hirose (Univ. of the Ryukyus, Okinawa, Japan) also greatly assisted

with sample collection. The 1st author was funded by a grant-in-aid from the Japan Society for the Promotion of Science (Wakate B no. 21770089), and the Rising Star Program at the Univ. of the Ryukyus. This is contribution no. 6 of the Green I. Reef Laboratory, Biodiversity Research Center, Academia Sinica.

REFERENCES

- Burnett WJ, JAH Benzie, JA Beardmore, JS Ryland. 1997. Zoanthids (Anthozoa, Hexacorallia) from the Great Barrier Reef and Torres Strait, Australia: systematics, evolution and a key to species. *Coral Reefs* **16**: 55-68.
- Chen AC. 1999. Analysis of scleractinian distribution in Taiwan indicating a pattern congruent with sea surface temperatures and currents: examples from *Acropora* and *Faviidae* corals. *Zool. Stud.* **38**: 119-129.
- Chen AC, K Shashank. 2009. Taiwan as a connective stepping-stone in the Kuroshio Triangle and the conservation of coral ecosystems under the impacts of climate change. *Kuroshio Sci.* **3**: 15-22.
- Hirose E, Y Nozawa. 2010. Photosymbiotic ascidians from Kenting and Lyudao in Taiwan. *Zool. Stud.* **49**: 681-687.
- Karlson RH. 1980. Alternative competitive strategies in a periodically disturbed habitat. *Bull. Mar. Sci.* **30**: 894-900.
- Labas YA, NG Gurskaya, YG Yanushevich, AF Fradkov, KA Lukyanov, SA Lukyanov, MV Matz. 2002. Diversity and evolution of the green fluorescent protein family. *Proc. Natl. Acad. Sci. USA* **99**: 4256-4261.
- Moore RE, PJ Scheuer. 1971. Palytoxin: a new marine toxin from a coelenterate. *Science* **172**: 495-498.
- Ono S, JD Reimer, J Tsukahara. 2008. Survey of zooxanthellate zoanthid diversity in Kagoshima, Japan. *Kuroshio Biosph.* **4**: 1-16.
- Pax F. 1910. Studien an westindischen Actinien. In JW Spengel, ed. *Ergebnisse einer Zoologischen Forschungsreise nach Westindien von Prof. W. Kukenthal und Dr. R. Hartmeyer im Jahre, 1907*. Jena, Germany: G. Fischer, *Zoologische Jahrbucher Supplement* 11, pp. 157-330.
- Reimer JD. 2007. Preliminary survey of zooxanthellate zoanthid diversity (Hexacorallia: Zoantharia) from southern Shikoku, Japan. *Kuroshio Biosph.* **3**: 1-16 + 7 pls.
- Reimer JD. 2008. Implications for different diversity levels of *Symbiodinium* spp. (Dinophyceae, Suessiales) within closely related host genera: zoanthids (Cnidaria: Hexacorallia: Anthozoa) as a case study. *Galaxea* **10**: 3-13.
- Reimer JD. 2010. Key to field identification of shallow water brachycnemid zoanthids (Order Zoantharia: Suborder Brachycnemina) present in Okinawa. *Galaxea* **12**: 23-29.
- Reimer JD, C Hickman. 2009. Preliminary survey of zooxanthellate zoanthids (Cnidaria: Hexacorallia) of the Galápagos and associated symbiotic dinoflagellates (*Symbiodinium* spp.). *Galápagos Res.* **66**: 14-19.
- Reimer JD, S Hirano, Y Fujiwara, F Sinniger, T Maruyama. 2007. Morphological and molecular characterization of *Abyssoanthus nankaiensis*, a new family, new genus and new species of deep-sea zoanthid (Anthozoa: Hexacorallia: Zoantharia) from a northwest Pacific methane cold seep. *Invertebr. Syst.* **21**: 255-262.
- Reimer JD, SA Ishikawa, M Hirose. 2010a. New records and molecular characterization of *Acrozoanthus* (Cnidaria: Anthozoa: Zoanthidae) from Taiwan. *Mar. Biodivers.* DOI 10.1007/s12526-010-0069-5.
- Reimer JD, S Nakachi, M Hirose, E Hirose, S Hashiguchi. 2010b. Using hydrofluoric acid for morphological investigations of zoanthids (Cnidaria: Anthozoa): a critical assessment of methodology and necessity. *Mar. Biotechnol.* **12**: 605-617.
- Reimer JD, S Ono, A Iwama, J Tsukahara, T Maruyama. 2006a. High levels of morphological variation despite close genetic relatedness between *Zoanthus* aff. *vietnamensis* and *Zoanthus kuroshio* (Anthozoa: Hexacorallia). *Zool. Sci.* **23**: 755-761.
- Reimer JD, S Ono, A Iwama, J Tsukahara, K Takishita, T Maruyama. 2006b. Morphological and molecular revision of *Zoanthus* (Anthozoa: Hexacorallia) from southwestern Japan with description of two new species. *Zool. Sci.* **23**: 261-275.
- Reimer JD, S Ono, F Sinniger, J Tsukahara. 2008a. Distribution of zooxanthellate zoanthid species (Zoantharia: Anthozoa: Hexacorallia) in southern Japan limited by cold temperatures. *Galaxea* **10**: 57-67.
- Reimer JD, S Ono, K Takishita, Y Fujiwara, J Tsukahara. 2004. Reconsidering *Zoanthus* spp. diversity: molecular evidence of conspecificity within four previously presumed species. *Zool. Sci.* **21**: 517-525.
- Reimer JD, S Ono, J Tsukahara, F Iwase. 2008b. Molecular characterization of the zoanthid genus *Isaurus* (Anthozoa: Hexacorallia) and its zooxanthellae (*Symbiodinium* spp.). *Mar. Biol.* **153**: 351-363.
- Reimer JD, F Sinniger, C Hickman. 2008c. Zoanthid diversity (Anthozoa: Hexacorallia) in the Galapagos Islands: a molecular examination. *Coral Reefs* **27**: 641-654.
- Reimer JD, K Takishita, T Maruyama. 2006c. Molecular identification of symbiotic dinoflagellates (*Symbiodinium* spp.) from *Palythoa* spp. (Anthozoa: Hexacorallia) in Japan. *Coral Reefs* **25**: 521-527.
- Reimer JD, K Takishita, S Ono, J Tsukahara, T Maruyama. 2006d. Latitudinal and intracolony ITS-rDNA sequence variation in the symbiotic dinoflagellate genus *Symbiodinium* (Dinophyceae) in *Zoanthus sansibaricus* (Anthozoa: Hexacorallia). *Phycol. Res.* **54**: 122-132.
- Ryland JS. 1997. Budding in *Acrozoanthus* Saville-Kent, 1893 (Anthozoa: Zoanthidea). In JC den Hartog, ed. *Proceedings of the 6th International Conference on Coelenterate Biology*. Leiden, Netherlands: Nationaal Natuurhistorisch Museum, pp. 423-428.
- Shieh WY, YM Lin. 1992. Nitrogen fixation (acetylene reduction) associated with the zoanthid *Palythoa tuberculosa* Esper. *J. Exp. Mar. Biol. Ecol.* **163**: 31-41.
- Sinniger F. 2006. Zoanthids of New Caledonia. In C Payri, B Richier de Forges, eds. *Compendium of marine species from New Caledonia*. Noumea, French Polynesia: IRD Editions, pp. 127-128.
- Soong K, YS Shiau, CP Chen. 1999. Morphological and life history divergence of the zoanthid, *Sphenopus marsupialis*, off the Taiwanese coast. *Zool. Stud.* **38**: 333-343.
- Uchida H. 2001. Sea anemones in Japanese waters. Tokyo: TBS Britannica. (in Japanese)
- Veron JEN. 1995. *Corals in space and time*. Sydney, Australia: Univ. of New South Wales Press.