

Zoanthid (Cnidaria: Anthozoa: Hexacorallia: Zoantharia) species of coral reefs in Palau

James Davis Reimer · Doris Albinsky · Sung-Yin Yang · Julien Lorion

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Abstract Palau is world famous for its relatively pristine and highly diverse coral reefs, yet for many coral reef invertebrate taxa, few data exist on their diversity in this Micronesian country. One such taxon is the Zoantharia, an order of benthic cnidarians within the Class Anthozoa (Subclass Hexacorallia) that are commonly found in shallow subtropical and tropical waters. Here, we examine the species diversity of zoanthids in Palau for the first time, based on shallow-water (<35 m) scuba surveys and morphological identification to create a preliminary zoanthid species list for Palau. Our results indicated the presence of nine zoanthid species in Palau (*Zoanthus sansibaricus*, *Z. giganteus*, *Palythoa tuberculosa*, *P. mutuki*, *P. heliodiscus*, *Palythoa* cf. *toxica*, *Epizoanthus illoricatus*, *Parazoanthus* sp., *Microzoanthus kagerou*), apparently slightly more than have been recently observed in nearby Guam, Saipan, and the Ogasawara Islands. Additionally, it appears that some zoanthid species that have been observed to be co-occurring in the fringing reefs of Okinawa may inhabit different locations in the better developed reefs of Palau.

Keywords Benthos · Biodiversity · Brachycnemina · Macrocnemina · Micronesia · Pacific Ocean

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J. D. Reimer (✉) · D. Albinsky · S.-Y. Yang · J. Lorion
Molecular Invertebrate Systematics and Ecology Laboratory,
Graduate School of Engineering and Science, University of the
Ryukyus, Senbaru 1, Nishihara, Okinawa903-0213, Japan
e-mail: jreimer@sci.u-ryukyu.ac.jp

J. Lorion
Palau International Coral Reef Center, P.O. Box 7086, Koror 96940,
Palau

Introduction

Palau is located at the southwestern corner of Micronesia, and is just outside the Coral Triangle, the region with the highest marine biodiversity in the world (Hoeksema 2007). Thus, Palau is an important link between the central Indo-Pacific and the Pacific Islands, and diversity and distribution data of marine organisms from Palau can help us to understand the evolutionary and biogeographical history of the region. Because of Palau's combination of a high habitat diversity with a close proximity to the Coral Triangle, it has the most diverse marine flora and fauna in Micronesia (Yukihira et al. 2007).

Despite the importance of an understanding of the Palauan marine fauna in inferring links between the Coral Triangle and the rest of Micronesia and the Pacific Islands, relatively little research has been performed on most of Palau's coral reef invertebrates. The diversity of hard corals (Kawaguti 1940, 1941, 1942; Maragos et al. 1994; Randall 1995; Golbuu 2000; Yukihira et al. 2007) and many fish species (Myers 1999) are quite well understood, and faunistic research has also been performed on some other taxa, including octocorals (e.g. Bayer 1974; van Ofwegen 2008), sponges (Kelly-Borges and Valentine 1995), bivalves and marine snails (Hiro 1936). However, for the majority of coral reef taxa in Palau, little or no diversity information exists (Colin 2009).

One such taxon for which very few data exist in Micronesia are the zoanthids (Cnidaria: Anthozoa: Zoantharia) (Colin 2009; Reimer and Fujii 2013). Zoanthids comprise an order of benthic cnidarians most closely related to the sea anemones (Actiniaria) (Fujii and Reimer 2011; Kayal et al. 2013), and are common in shallow subtropical and tropical waters of the world (Karlson 1980; Swain 2010; Irei et al. 2011). Despite their ubiquity, particularly on coral reefs, the taxonomy of zoanthids has been confused due to a combination of a lack of diagnostic characters and intraspecific morphological variation (Burnett et al. 1997; Reimer et al. 2004). Over the past

two decades, molecular techniques have brought about a reassessment of zoanthid species (Burnett et al. 1997; Reimer et al. 2004, 2012) and higher-level taxonomy (Sinniger et al. 2005, 2010, 2013; Reimer et al. 2006b; Fujii and Reimer 2011). Combined with newly acquired distributional data for many regions of the world (e.g. Sinniger 2006; Reimer 2007; Reimer and Todd 2009), the diversity of this group is gradually becoming clearer.

In this study, we report on the preliminary field identification of shallow-water zoanthids in Palau from surveys conducted in 2012 and 2013. We also discuss our findings compared to the shallow-water zoanthid species of nearby Guam and Saipan (Paulay et al. 2003), and of the Ogasawara (Bonin) Islands (Reimer et al. 2011a). The data from these surveys should serve as a baseline species list to provide a foundation for future work on zoanthids in Palau and surrounding regions.

Materials and methods

Zoanthids were searched for and collected (Table S1) in August and November 2012, and by snorkeling and SCUBA in March, July and August 2013, from 12 sites in Palau (Table 1) as part of a preliminary survey of the coral reefs of Palau for the Science and Technology Research Partnership for Sustainable Development (SATREPS) Program implemented by Japan and Palau. In situ observations and identification were performed following Reimer (2010) and Reimer et al. (2011b) unless otherwise noted, with in situ images taken before specimen collection. Colonies or portions of colonies collected were very small (<5 cm²) and were frozen at the

Palau International Coral Reef Center (PICRC), Koror, and then stored in −20 °C. In future, specimens from this study will be deposited at the Belau National Museum, Koror, once a marine invertebrate collection is established. Specimens are currently housed at PICRC under specimen numbers PICRC-SATREPS #1–125.

Results

During the surveys, 125 zoanthid specimens (=colonies) were collected from 12 sites. Sites are shown in Fig. 1 with GPS localities given in Tables 1 and S1. Specimens were identified as belonging to nine species, as detailed below. In this section, the site numbers in parentheses after site names correspond to Table 1 site numbers.

Suborder Brachycnemina Haddon & Shackleton, 1891
Family Zoanthidae Rafinesque, 1815

1. *Zoanthus sansibaricus* Carlgren, 1900

Figs. 2a, S1

Specimens: PICRC-SATREPS 1–8, 10–12, 18–31, 33–48, 57–60, 92, 96–122, 124, 125, I–XI (Roman numerals).
Sites: Jake Seaplane (1), Nikko Bay Site XXIX (2), Ngerchaol Site 172 (5), Peleliu West Coast Site 176 (9), Ngeruktabel Site 178 (11). **Depth:** intertidal–16 m.

Notes: This species was by far the most common zoanthid at some sites, particularly in shallow intertidal sheltered areas under limestone overhangs (Nikko Bay, Ngerchaol Site 172), where it was the dominant benthos species at some sites. This species is known as a “generalist” (Kamezaki et al. 2013), able to inhabit a variety of shallow and deep (to 52 m in Okinawa,

Table 1 Sites in Palau investigated in this study, their GPS coordinates, and other information; numbers correspond to sites shown in Fig. 1

Site name	Latitude	Longitude	Depths investigated (m)	Environment type	Water current regime ^b
1. Jake Seaplane	7°22'08.0"N	134°26'53.9"E	12–16	Reef lagoon	Medium
2. Nikko Bay Site XXIX	7°19' 32.6"N	134°29' 38.0"E	Intertidal–20	Inner bay	Low
3. Short Dropoff	7°15'49.0"N	134°31'11.1"E	5–22	Dropoff, reef wall	High
4. Lighthouse Channel	7°17'43.0"N	134°27'22.0"E	8–17	Channel	High
5. Ngerchaol Site 172	7°20'25.4"N	134°25'45.9"E	Intertidal–15	Inner bay	Low
6. Siaes Tunnel	7°17'45.6"N	134°14'16.6"E	9–30	Dropoff, reef wall	High
7. Ulong Channel	7°17'00.6"N	134°14'40.9"E	8–11	Channel	High
8. Peleliu West Coast Site 175	7°02'00.2"N	134°14'15.4"E	9–34	Dropoff, reef wall	High
9. Peleliu West Coast Site 176	7°03'11.8"N	134°14'32.9"E	12–19	Dropoff, reef wall	Medium
10. Ngergong Site 177	7°06'42.3"N	134°22'10.7"E	6–10	Reef flat at edge of dropoff, with sea grass	Low
11. Ngeruktabel Site 178	7°17'40.1"N	134°26'41.5"E	5–16	Inner bay	Low
12. Palau Mariculture Demonstration Center ^a	7°19'43"N	134°27'1"E	Several cm	Artificial, outflow pipe	High

^a As reported in Reimer and Fujii (2013)

^b Based on tidal currents and waves

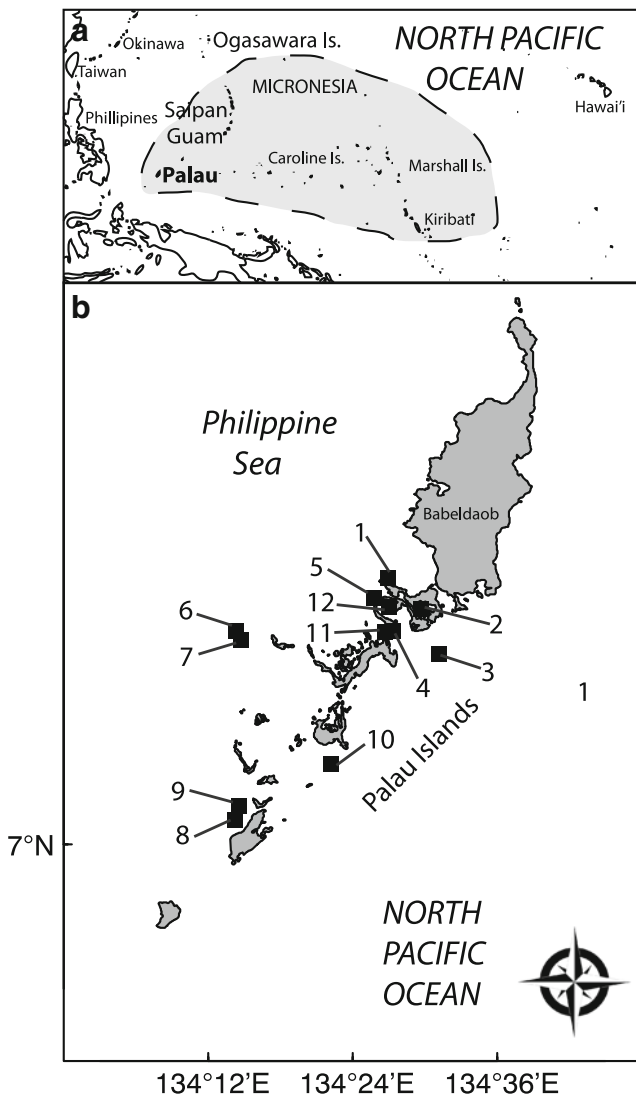


Fig. 1 **a** Location of Palau and Micronesia (in grey) with other areas mentioned in the text also shown. **b** Sites surveyed during this study (black squares). Numbers correspond to sites detailed in Table 1

Japan) coral reef environments, and has a semi-flexible association with *Symbiodinium* spp. (Reimer et al. 2006c, 2007b, 2011a; Kamezaki et al. 2013).

The oral disc coloration of this species has been reported from Japan to be quite variable (Reimer et al. 2004), and this was also observed in Palau. A wide variety of oral disc phenotypes were found in Palau (Fig. S1).

This species is known from Guam (Paulay et al. 2003, identified as *Z. vietnamensis* Pax & Mueller, 1957), Saipan (Reimer, unpublished data) and Ogasawara (Reimer et al. 2011a), and it is likely to be found in other Micronesian sites, as *Z. sansibaricus* is widespread in the Indo-Pacific (e.g. at least from its type locality in Zanzibar to the Galapagos; Reimer and Hickman 2009).

2. *Zoanthus gigantus* Reimer & Tsukahara, 2006a

Fig. 2b

Specimens: PICRC-SATREPS 9. **Sites:** Jake Seaplane (1). **Depth:** 12 m.

Notes: This species was only observed at one site, Jake Seaplane, which is within the well-developed lagoon of Palau. In a previous study in Okinawa, Japan, this species was shown to be most common on coral reef edges in the shallow subtidal zone. Despite examining similar environments during this survey, no colonies of this species were found in such sites. Further searching in other sites may reveal additional colonies, but for now, we consider *Z. gigantus* to be potentially uncommon in Palau. Furthermore, no records of this species exist in Guam, Saipan, or the Ogasawara Islands. Aside from the type locality in southern Japan, this species has been reported from Taiwan (Reimer et al. 2011b).

This species may be the same as *Z. pacificus* Walsh and Bowers, 1971, which was described from Hawai'i and also reported from American Samoa and Tahiti, based on similar external striped patterns of polyps (Walsh and Bowers 1971: pl. 6), but this is not yet clear.

Family Sphenopidae Hertwig, 1882

3. *Palythoa mutuki* (Haddon & Shackleton, 1891)

Fig. 2c

Specimens: PICRC-SATREPS 14–17, 32, 61, 79, 82, 85, 89. **Sites:** Nikko Bay Site XXIX (2), Ngerchaol Site 172 (5), Sias Tunnel (6; not collected), Peleliu West Coast Site 175 (8), Peleliu West Coast Site 176 (9). **Depth:** intertidal–15 m.

Notes: This species was found sporadically in Palau. In shallow waters, it was often in the same microenvironment (shaded overhangs) as *Z. sansibaricus*, albeit much less common. As seen in Japan, oral discs may be green or brown (e.g. Reimer et al. 2006b), and polyps are 'liberae' (e.g. free-standing above the coenenchyme; sensu Pax 1910). This species is also known from the Ogasawara Islands (Reimer et al. 2011a), and therefore is likely to be present in Guam and Saipan, although it is not listed in Paulay et al. (2003). Originally described from the Great Barrier Reef, it has also been reported from Japan (e.g. Reimer et al. 2006b), Taiwan (Reimer et al. 2011b), New Caledonia (Sinniger 2006), and the Galapagos (Reimer and Hickman 2009).

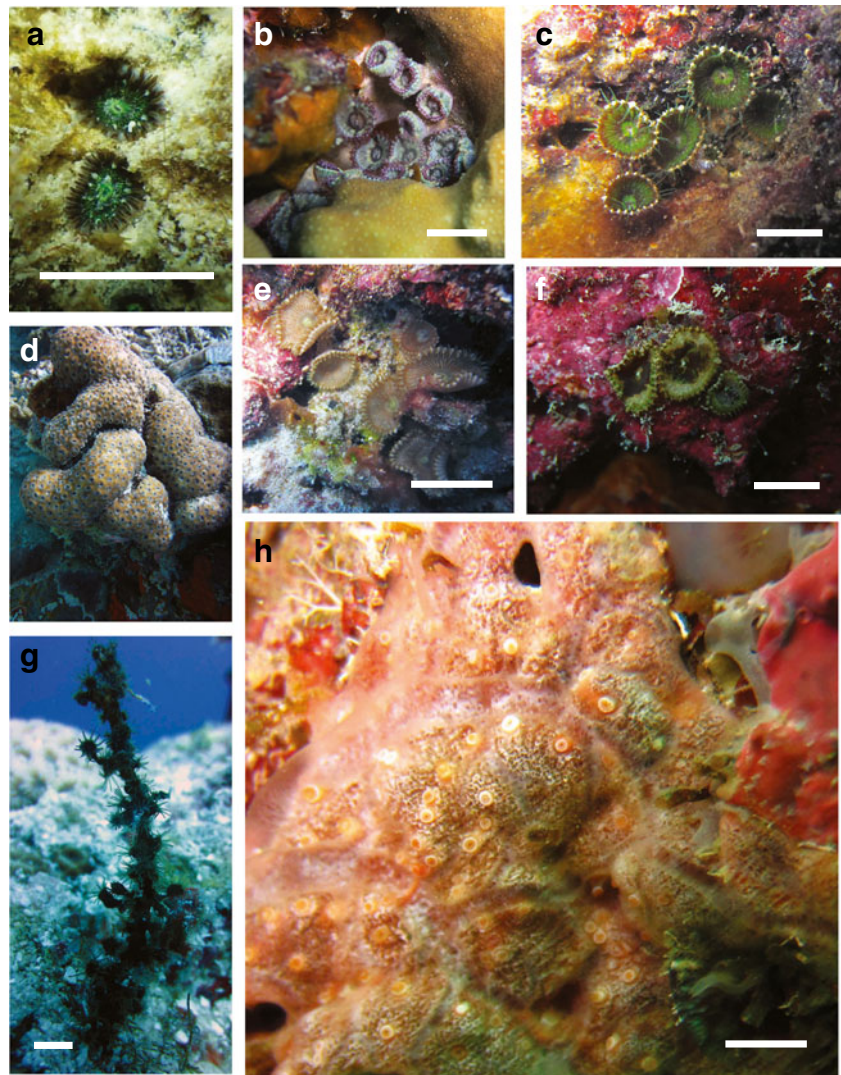
4. *Palythoa tuberculosa* (Esper, 1805)

Figs. 2d, S2

Specimens: PICRC-SATREPS 52–56, 63–67, 70, 72–74, 76, 80, 81, 83, 84, 88, 90. **Sites:** Short Dropoff (3; not collected), Lighthouse Channel (4), Sias Tunnel (6), Ulong Channel (7), Peleliu West Coast Site 175 (8), Peleliu West Coast Site 176 (9), Ngeregong Site 177 (10; not collected). **Depth:** 8–34 m.

Notes: This species, along with *Z. sansibaricus*, is the most common shallow water zoanthid in Okinawa (Irei et al. 2011), and this also appears to be the case in Palau. Like *Z. sansibaricus*, this species encompasses many different morphotypes (Burnett et al. 1997; Hibino et al. 2013), and colonies observed in Palau varied in external color from

Fig. 2 Shallow water coral reef zoanthids of Palau in situ. **a** *Zoanthus sansibaricus* at Nikko Bay Site XXIX, depth 0 m (intertidal zone); **b** *Z. giganteus* at Jake Seaplane, depth 13 m; **c** *Palythoa mutuki* at Nikko Bay Site XXIX, depth 0 m (intertidal zone); **d** *P. tuberculosa* at Lighthouse Channel, depth 8 m; **e** *P. heliodiscus* at Peliliu West Coast Site 175, depth 20 m; **f** *Palythoa* cf. *toxica* at Ulong Channel, depth 11 m; **g** *Epizoanthus illoricatus* at Short Dropoff, depth 22 m; **h** *Parazoanthus* sp. at Nikko Bay Site XXIX, depth 3 m. All scale bars approximately 1 cm, with no scale for **(d)**, in which the colony is approximately 20–25 cm in width



pale cream to brown to fluorescent green/yellow, and from having polyps immersed in a well-developed coenenchyme (=‘immersae’; sensu Pax 1910) to having polyps protruding from the coenenchyme (=‘intermediae’; sensu Pax 1910) (Fig. S2).

Recent research has also indicated that *P. caesia* Dana, 1846 and *P. tuberculosa* are the same species, and thus *P. caesia* from Guam in Paulay et al. (2003) is almost certainly *P. tuberculosa* (Hibino et al. 2013). This species has also been reported from Saipan (Reimer et al. 2007c) and the Ogasawara Islands (Reimer et al. 2011a). Originally described from India and redescribed with material from the Red Sea (Klunzinger 1877), it has also been reported from Japan (e.g. Reimer et al. 2006b), Taiwan (Reimer et al. (2011b), New Caledonia (Sinniger 2006), and Hawai’i (Walsh and Bowers 1971).

5. *Palythoa heliodiscus* (Ryland & Lancaster, 2003)

Fig. 2e

Specimens: PICRC-SATREPS 78. **Sites:** Short Dropoff (3; not collected), Peleliu West Coast Site 175 (8). **Depth:** 20–23 m.

Notes: This species was only seen twice during this survey, and appears to be much less common in Palau than in Okinawa, Japan, where it is often the most common shallow-water zoanthid deeper than 5 m. This species can be distinguished by its brown oral discs with radiating pale lines, and very short tentacles (Ryland and Lancaster 2003). Similar to *P. mutuki*, this species has a ‘liberae’ polyp/colony morphology (sensu Pax 1910). In Japan, *P. heliodiscus* has a more southern northern limit than other zooxanthellate zoanthid species (Ono et al. 2008). Similarly, while this species is now known from Palau, and previously reported from Guam (Paulay et al. 2003, as “*Protopalythoa* sp. 1”) and Saipan (Reimer et al. 2007c), it has not been found in the Ogasawara Islands (Reimer et al. 2011a). This species was originally described from Fiji and has also been reported from Australia (Ryland and Lancaster 2003), New Caledonia (Sinniger 2006), Japan (e.g. Reimer et al. 2006b) and Taiwan (Reimer et al. 2011b).

6. *Palythoa* cf. *toxica* Walsh & Bowers, 1971

Fig. 2f

Specimens: PICRC-SATREPS 51, 69, 71, 75, 77, 91. **Sites:** Short Dropoff (3), Siaes Tunnel (6), Ulong Channel (7), Peleliu West Coast Site 175 (8), Peleliu West Coast Site 176 (9). **Depth:** 9–30 m.

Notes: The identity of these specimens is still somewhat unclear. Morphologically similar specimens have been reported from Singapore (Reimer and Todd 2009, as *Palythoa* sp. “singapura”), Taiwan (Reimer et al. 2011b) and Okinawa (Nishimura and Reimer, unpublished), and they strongly resemble *P. toxica* originally described from Hawai’i by Walsh and Bowers (1971). The validity of *P. toxica* is in question, as Ryland and Lancaster (2003) mentioned that it may not be distinct from *P. mutuki*. However, mitochondrial DNA sequences from specimens in Singapore and Okinawa were identical to those of *P. heliodiscus*, and thus this species is closely related to *P. heliodiscus*. Final identity of this species requires phylogenetic comparison with the *P. toxica* holotype, and thus for now we designate this species as *P. cf. toxica*. Regardless of its true identity, this species appears to be somewhat common in Palau, and was more common than *P. heliodiscus* in this survey, opposite to what has been seen in other sites. It has not been reported from other Micronesian sites, nor from the Ogasawara Islands.

These specimens can be distinguished from *P. heliodiscus* by the slight green or purple coloration of the oral disc, and they have a distinct internal transcribed spacer region of ribosomal DNA sequence (ITS-rDNA) from *P. heliodiscus*.

Suborder Macrocnemina Haddon & Shackleton, 1891

Family Microzoanthidae Fujii and Reimer, 2011

7. *Microzoanthus kagerou* Fujii and Reimer, 2011

Figure: see Reimer and Fujii 2013

Specimens: PICRC-SATREPS 94, 95 (reported in Reimer and Fujii 2013). **Sites:** Palau Mariculture Demonstration Center (12).

Notes: This species was initially reported from Palau in Reimer and Fujii (2013), and has only been found at this one, artificial site. As species of the genus *Microzoanthus* are among the smallest zoanthids, and only recently described, there are few data on their distribution in the central Pacific Ocean, although it is speculated to be widespread, as it has been reported from numerous locations across the Pacific, including Okinawa, mainland Japan, Singapore, Thailand, Australia, and the Galapagos (Fujii and Reimer 2011). Until further surveys are conducted in other regions of Micronesia and the Ogasawara Islands, it is impossible to speculate on its distribution in this region.

Family Epizoanthidae Delage & Hérouard, 1901

8. *Epizoanthus illorricatus* Tischbierk, 1930

Fig. 2g

Specimens: PICRC-SATREPS 49, 50, 62. **Sites:** Short Dropoff (3), Siaes Tunnel (6). **Depth:** 20–30 m.

Notes: This species was observed below 20 m in Palau, and is often seen at deeper mesophotic depths (e.g. approximately

80 m at Osprey Reef, Australia; Lindsay et al. 2012). Easily identifiable as it lives solely as an epibiont on the outer surface of eunicid worm tubes, this species was found only on outer reef walls. Although only three specimens were collected during the course of this study, it is expected that this species is common given the high prevalence of steep and deep outer reef walls in Palau (Colin 2009).

This species has not been reported from other sites in Micronesia or the Ogasawara Islands, but is described from the Philippines (Tischbierk 1930), and is also known from Australia (Lindsay et al. 2012), New Caledonia (Sinniger 2006), Taiwan (Reimer et al. 2012), and Japan (Reimer et al. 2010), and appears to have a wide Pacific distribution.

Family Parazoanthidae Delage & Hérouard, 1901

9. *Parazoanthus* sp.

Fig. 2h

Specimens: none, images only. **Sites:** Nikko Bay Site XXIX (2; not collected). **Depth:** 5 m.

Notes: This species was only seen once, during preliminary dives in August 2012, and not collected. Polyps were embedded within an orange and white encrusting sponge, and very small (diameter of expanded polyps < 3 mm). The sponge was located in a crack within a small overhang, in a shaded site.

Currently, only a few sponge-associated species have been described from the Pacific Ocean, and none from tropical waters in the West Pacific, making it highly likely that this is an undescribed species. Collection and formal description along with phylogenetic analyses are needed to properly place this species within the zoanthids.

A similar species has been reported from Guam and Saipan (Paulay et al. 2003), where it is found on *Astrosclera willejana* Lister, 1900 coralline sponges. No *Parazoanthus* spp. have been reported from the Ogasawara Islands (Reimer et al. 2011a).

Discussion

The biodiversity of Palauan coral reef invertebrates is expected to be higher than that of the remainder of Micronesia, but lower than that of the Philippines, as Palau is the closest Micronesian region to the Coral Triangle (Colin 2009). Even though the numbers of shallow water zoanthids identified in this and similar research papers (Paulay et al. 2003; Reimer et al. 2011a) are low, the patterns from the current study and previous reports appear to support this hypothesis. From the combined sum of this and previous studies, we estimate that there are six to nine brachycnemic zoanthid species in Palau (Table 2), as opposed to the three to seven that are found in Guam, Saipan, and the Ogasawara Islands.

Furthermore, there are very few data on shallow water zoanthids from the Philippines or other regions of the Coral

Table 2 Status of knowledge of distribution of zoanthid species in Micronesia and the Ogasawara Islands

● specimens and/or DNA sequences, documented records; ○ photographs and/or anecdotal reports; × not yet found or reported; ×(?) not yet found or reported, but likely present given the species' distribution and habitat preferences

^a Colin (2009)

^b Reimer and Fujii (2013)

^c This study

^d Paulay et al. (2003)

^e Reimer et al. (2007c)

^f Reimer, unpublished data

^g Reimer et al. (2011a)

^h Total species numbers for Macrocnemina not given, as data are almost certainly far from complete (see "Discussion")

Species	Palau ^{a,b,c}	Guam ^d	Saipan ^{d,e,f}	Ogasawara ^{f,g}
Suborder Brachycnemina				
<i>Zoanthus sansibaricus</i>	●	●	○	●
<i>Zoanthus gigantus</i>	●	×	×	×
<i>Zoanthus kuroshio</i>	× (?)	×(?)	×(?)	●
<i>Isaurus tuberculatus</i>	× (?)	●	× (?)	○
<i>Palythoa tuberculosa</i>	●	●	●	●
<i>Palythoa mutuki</i>	●	×(?)	×(?)	●
<i>Palythoa heliodiscus</i>	●	●	●	×
<i>Palythoa</i> cf. <i>toxica</i>	●	×	×	×
<i>Palythoa</i> sp. "sakurajimensis"	×	×	×	●
<i>Sphenopus marsupialus</i>	×(?)	●	×(?)	×
Suborder Macrocnemina ^h				
<i>Microzoanthus kagerou</i>	●	×	×	×
<i>Epizoanthus illoricatus</i>	●	×	×	×
<i>Epizoanthus</i> sp.	○	×	×	×
<i>Parazoanthus</i> sp.	○	○	○	×
Parazoanthidae sp.	×	×	×	●
Total spp.	8+5(?)	5+3(?)	3+5(?)	7

Triangle, and acquisition of species diversity data is critically needed to more completely understand zoanthid diversity patterns in the Pacific Ocean. It should also be noted that the species numbers we report here are preliminary, and we expect to find more brachycnemic zoanthids from Palau and other Micronesian regions. One potential example is *Isaurus tuberculatus* Gray, 1828 (family Zoanthidae). This species is cryptic and occurs in very low numbers (Muirhead and Ryland 1985; Reimer et al. 2008), and has been reported from both Guam (Paulay et al. 2003) and Ogasawara (Reimer, unpublished data). However, with a wide subtropical and tropical distribution, this species is also likely present in Palau and Saipan. Other species not reported from one or more of Palau, Guam, Saipan, or Ogasawara, but likely to be present in all four regions, include *Zoanthus kuroshio*, *Palythoa mutuki* and *Sphenopus marsupialus* (Gmelin, 1791) (Table 2).

Additionally, there are probably many more macrocnemic zoanthids to be found in Palau and Micronesia. Colin (2009) includes an image of an unidentified zoanthid in a tunnel that is epizootic on mussel shells, which is likely an *Epizoanthus* species (p. 255), and also mentions "epizotic zoanthids are often found living in sponges, on hydroids and dead gorgonians, and in deep water (>90 m) are found on dead ahermatypic corals and covering gastropod shells" (p. 363), suggesting that much remains to be discovered regarding macrocnemic zoanthid diversity in Palau. Even deeper regions may also harbour other Macrocnemina spp., as the deep sea has recently been shown to include potentially high levels of zoanthid diversity (Reimer et al. 2007a; Sinniger et al. 2013).

One noticeable difference between the results of the zoanthid survey in Palau and previous surveys in Okinawa, Japan, where the majority of recent zoanthid research has been performed, was with regards to the sites where some *Zoanthus* and *Palythoa* spp. were found. In this study, while *Z. sansibaricus* and *P. tuberculosa* were the most commonly seen species, similar to Okinawa (Irei et al. 2011), the sites of these two species were different. In Okinawa, *Z. sansibaricus* has been shown to be most common on reef crests, while *P. tuberculosa* was most common on both reef crests and outer reef slopes (Irei et al. 2011). In Palau, *Z. sansibaricus* was found primarily in shaded, shallow overhang environments, or at other areas in the large coral lagoon of Palau (e.g. Jake Seaplane), and was not seen on the outer reef slopes often (Table S1). On the other hand, *P. tuberculosa* was not seen very often within the lagoon, and was more common on outer reef slopes. The differences between results in Palau and Okinawa may have to do with structural or environmental differences between reefs in Okinawa (=Okinawa-jima Island) and Palau. Most reefs surveyed in Okinawa by Irei et al. (2011) are fringing reefs, with a small moat or lagoon of a few hundred meters at most, while the reef of Palau includes a well-developed lagoon on the scale of tens of kilometers. While both *P. tuberculosa* and *Z. sansibaricus* are known to be generalist species, it may be that the reefs of Okinawa are compact enough so that there is considerable overlap in their habitats, while in Palau the expanded scale of reefs results in little habitat overlap for these two species. The present study did not employ a methodological assessment of zoanthid colony numbers, unlike Irei et al. (2011), and hence

the next logical step in assessing zoanths in Palau would be to conduct abundance surveys.

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