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First record of sea urchin-associated *Epizoanthus planus* from Japanese waters and its morphology and molecular phylogeny

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Abstract: The species *Epizoanthus planus* is the only known described zoantharian with an association with echinoderms, and it is known to live on the spines of living sea urchins from the family Cidaridae. This species has been reported from 741 to 1019 m in the Indian Ocean and the East China Sea. However, diagnostic characters are lacking in both the original description and subsequent studies. The present study reports the first record of *E. planus* from Japanese waters (300–400 m) based on a newly collected specimen, and this record slightly extends the species distribution range in the northwest Pacific Ocean. This new record increases the number of *Epizoanthus* species in Japanese waters to at least five species. Although many taxonomy and diversity studies have focused on specimens from SCUBA-based collections in Japanese waters, few studies have focused on zoantharians in deeper waters below SCUBA diving limits. The results of the present study highlight the importance of examining specimens from deeper waters to better understand the overall diversity of the order Zoantharia.

Key words: zoantharian, deep sea, distribution, echinoderms, substrate association

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Introduction

The genus *Epizoanthus* Gray, 1867 (Hexacorallia: Zoantharia: Epizoanthidae) contains primarily deep-sea species, with approximately 83 valid species at present (Reimer & Sinniger 2018). Many *Epizoanthus* species are associated with various marine invertebrates such as shells inhabited by either hermit crabs or gastropods, eunicid worms, the stalks of glass sponges, and antipatharians (Reimer et al. 2010b; Kise & Reimer 2016; Carreiro-Silva et al. 2017), while some other species are not epizoic and are attached directly to the seafloor (e.g., *E. scotinus* Wood, 1957 from western Canada; Reimer & Sinniger 2010). The species *Epizoanthus planus* Carlgren, 1923 was described from 741 to 1019 m in the Indian Ocean, and it is the only described zoantharian species with a known association with echinoderms. A subsequent study by Pei (1998) also reported *E. planus* based on specimens collected from the East China Sea. Although the results of Carlgren (1923) and Pei (1998) suggest that this species is widely distributed in the Indo-Pacific Ocean, only these two reports have been published due to difficulty in specimen collection and observation as the species is found well below safe depth limits for SCUBA diving. Additionally, diagnostic characters are lacking in both the original description of two colonies by Carlgren (1923) and 15 colonies by Pei (1998). Moreover, this species incorporates high levels of sand and siliceous particles into its mesoglea, making histological analyses difficult (Reimer et al. 2010a).

In this study, we document the first record of *E. planus* from Japanese waters based on a newly collected specimen, and this discovery slightly extends its distribution range in the Pacific Ocean. Additionally, we provide morphological and molecular phylogenetic data associated with this species.

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Materials and Methods

Collection. A single specimen consisting of 10 polyps was collected at a depth of 300 to 400 m via dredging on the vessel *Daisan Idoinkyo-maru* off Jogashima, Sagami Bay, Japan (35°4′50.0″N, 139°35′53.0″E) by Jun Hirose on October 29, 2015. After observation of the living specimen, the specimen was fixed in 5–10% seawater formalin and was later preserved in 70% ethanol for morphological analyses. A subsample was preserved in 99.5% ethanol for molecular analyses. The specimen was deposited in the Molecular Invertebrate Systematics and Ecology Laboratory (MISE) collection at the University of the Ryukyus, Nishihara, Okinawa, Japan.

Morphological analyses. Morphological data were collected from photographs and histological sections. The lengths and diameters of individual polyps, polyp dimensions (oral disk diameter and polyp height), tentacle lengths and numbers, polyp colors, and diameters of oral disks were measured using photographs of the living specimen. Regarding mesentery arrangement and number as well as the location and shape of the marginal muscle, histological sections of 8 to 10 μm thickness were made and stained with hematoxylin and eosin. Cnidae analyses were conducted using undischarged nematocysts from tentacles, columns, actinopharynx, and mesenterial filaments of polyps (n=2) using a Nikon Eclipse80i stereomicroscope (Nikon, Tokyo). Cnidae sizes were measured using ImageJ v1.45s (Rasband 2012). The reported frequencies are the relative amounts based on numbers from all slides in cnidae analyses.

Although cnidae classification generally followed England (1991) and Ryland & Lancaster (2004), basitrichs and microbasic *b*-mastigophores were considered the same type of nematocyst based on studies by Schmidt (1974), Hidaka et al. (1987), and Hidaka (1992); therefore, these two types were pooled together.

Molecular phylogenetic analyses. The specimen's DNA was extracted using the guanidine method, following the protocol by Sinniger et al. (2010). Mitochondrial marker 16S ribosomal DNA (16S-rDNA) was amplified utilizing a HotStarTaq Master Mix Kit Plus (Qiagen, Hilden, Germany) and the primers 16Sant1 and 16SbmH (Sinniger et al. 2005). PCR products were cleaned using shrimp alkaline phosphate (SAP) and Exonuclease I (Takara Bio, Shiga, Japan). All PCR products were sequenced in both directions by Fasmac (Kanagawa, Japan), and the obtained sequences were initially assembled and edited using Geneious 10.2.3 (Kearse et al. 2012). The novel sequence (713 bp) generated in this study was deposited in GenBank. In the present study, 19 *Epizoanthus* sequences from GenBank were downloaded to compare to our obtained sequences. Therefore, a total of 20 *Epizoanthus* sequences were used for molecular phylogenetic analyses (Table 1).

Table 1. GenBank accession numbers used for phylogenetic analyses.

Taxon/ID name	16S-rDNA
Epizoanthidae	
Epizoanthus couchii	AB247343
Epizoanthus aff. *arenaceus*	GQ464862
Epizoanthus arenaceus Marseille	AY995926
Epizoanthus cf. *arenaceus* MED 65	GQ464863
Epizoanthus beriber HK127	KU175733
Epizoanthus incrustatus	GQ464865
Epizoanthus illoricatus	AY995929
Epizoanthus inazuma	KU175736
Epizoanthus aff. *illoricatus*	GQ464866
Epizoanthus cf. *balanorum*	GQ464869
Epizoanthus scotinus WA166/MISE	GQ464870
Epizoanthus sp. 'Sub-Antarctic'	EF687815
Epizoanthus sp. 'Deep Mediterranea' 1	EF687817
Epizoanthus sp. E EK10	HM040881
Epizoanthus sp. C EK01	HM040882
Epizoanthus paguricola FS171	AY995928
Epizoanthus lindhali	EF687816
Epizoanthus fiordicus Chile 1	EF687813
Epizoanthus ramosus	GQ464864
Epizoanthus planus HK195	MH453965
Microzoanthidae	
Microzoanthus occultus	HQ912860
Parazoanthidae	
Isozoanthus giganteus	GQ464867
Isozoanthus cf. *giganteus*	GQ464868

All sequences for each marker were aligned using MUSCLE with default settings and were then manually edited using Geneious 10.2.3 (Kearse et al. 2012). *Microzoanthus* and *Isozoanthus* species were selected as outgroup sequences. A 16S-rDNA alignment of 23 sequences representing 839 sites with hypervariable regions was generated for phylogenetic analyses, and the shortest and longest sequences were 354 bp and 777 bp, respectively. The alignment is available upon request from the corresponding author.

The 16S-rDNA alignment was analyzed using maximum likelihood (ML) and neighbor joining (NJ) methods. ML phylogenetic reconstruction was performed using PhyML (Guindon & Gascuel 2003) with 1000 bootstrap replicates, and the analysis used an input tree generated by BIONJ (Gascuel 1997) with models suggested by jModelTest (Posada 2008) (GTR+G) under Akaike Information Criterion (AIC), which include eight gamma-categories of substitution rates. Missing data were treated as N. NJ phylogenetic reconstruction was performed using Geneious 10.2.3 (Kearse et al. 2012) with default settings under HKY85 model with 1000 bootstrap replicates.

Results

Systematics

Order Zoantharia Rafinesque, 1815

Suborder Macrocnemina Haddon & Shackleton, 1891
Family Epizoanthidae Delage & Hérouard, 1901
Genus *Epizoanthus* Gray, 1867

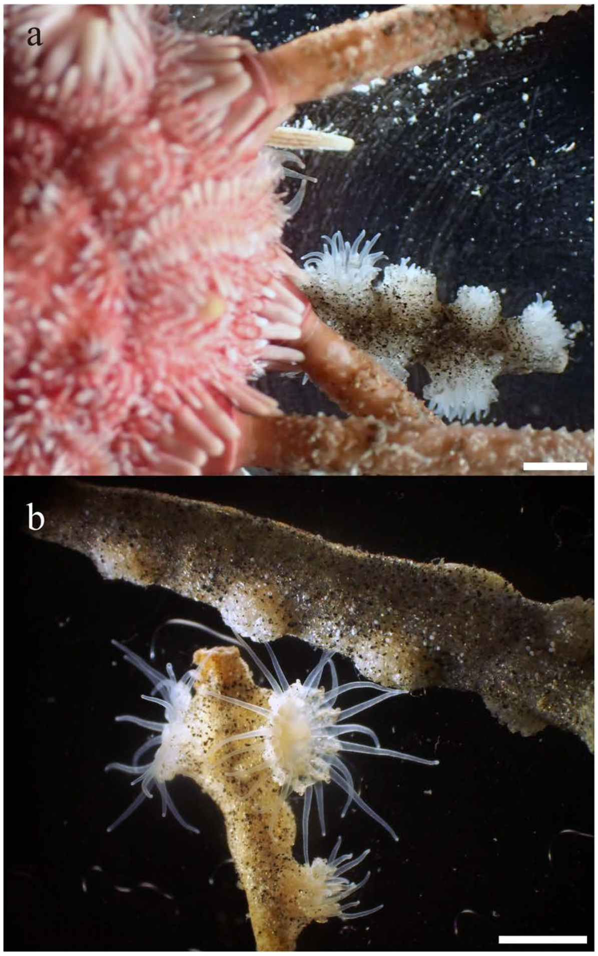

Fig. 1. Polyp images of *Epizoanthus planus*. a, Colony connected by heavily encrusted coenenchyme; b, close-up image of polyp on Cidaridae sea urchin. Scale bars: 10 mm.

Epizoanthus planus Carlgren, 1923
Figures 1 and 2, Table 2

Material examined. Voucher number MISE-HK195, collected from off Jogashima, Sagami Bay, Japan (35°4′50.0″N, 139°35′53.0″E) at a depth of 300–400 m via dredging by Jun Hirose, October 29, 2015.

Description. External morphology: Colony consists of 10 polyps connected by well-developed dark grey coenenchyme on two spines of a sea urchin (family Cidaridae Gray, 1825). Oral disk brown to brownish in coloration, with the number of oral furrows the same as the number of tentacles. The number of tentacles of each polyp in this study 20 to 22, transparent in coloration. Tentacles arranged in two rows, as long as the expanded oral disk diameter. Tips of tentacles usually cream in coloration. Height of living polyps approximately 2 to 4 mm, and oral disk 10 to 15 mm in diameter when polyps expanded. Preserved, contracted polyps approximately 3–5 mm in diameter and approximately 1–3 mm in height from coenenchyme. Contracted preserved polyps only rise a little from the coenenchyme and very flat. Ectoderm of polyps and coenenchyme heavily encrusted with numerous and various sizes of sand particles. Encrustation also appears at exterior edge of oral disk but decreases toward the mouth. Capitular ridges 10–12 in number, although not often clearly visible due to heavily encrustation. Preserved polyps and coenenchyme dark grey in coloration.

Cnidom: Basitrichs and microbasic *b*-mastigophores, microbasic *p*-mastigophores, holotrichs, and spirocysts (see Figure 2 and Table 2).

Internal morphology: Zooxanthellae absent. Fine sand particles and silica encrusted into ectoderm and mesoglea. Mesenterial filaments present.

Remarks. Although it was noted that *E. planus* is associated with sea urchins and octocorals in the original description by Carlgren (1923), the species was described based on characters of the sea urchin-associated speci-

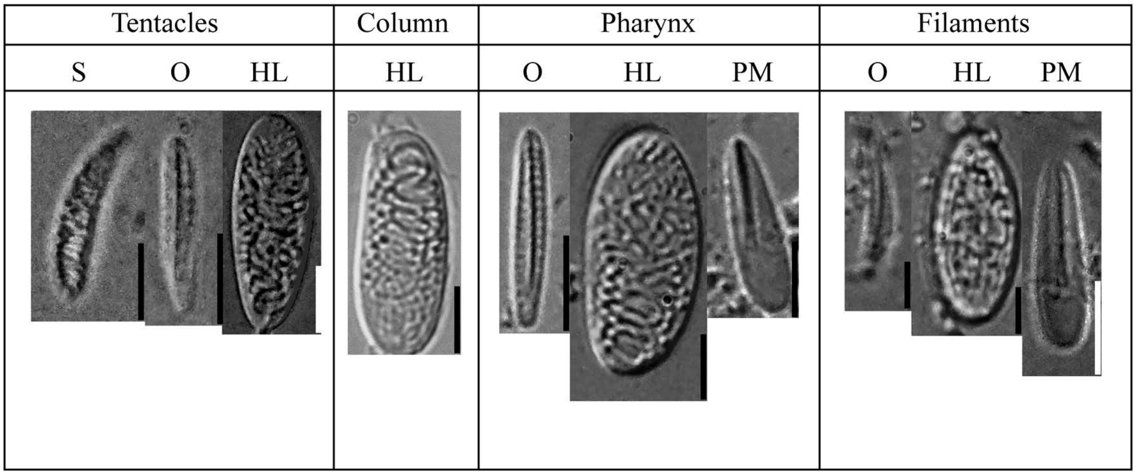

Fig. 2. Cnidae in the tentacles, column, pharynx, and filaments of *Epizoanthus planus*. Abbreviations: HL, holotrich large; O, bastrichs or microbasic *b*-mastigophores; P, microbasic *p*-mastigophores; S, spirocysts. Scale bars: 50 μm.

Table 2. Cnidae types and sizes observed in *Epizoanthus planus*. Frequency: relative abundance of cnidae type in decreasing order; numerous, common, occasional, rare (n = number of cnidae).

		Length (min–max, average)	Width (min–max, average)	n	Frequency
Tentacles	Spirocysts	11–25, 16.6	1–6, 3.2	152	Numerous
	Holotrichs (L)	24–33, 28.0	9–13, 11.3	12	Common
	Bastrichs and microbasic b-mastigophores	11–25, 15.9	1–5, 2.9	117	Numerous
	Microbasic p-mastigophores	—	—	—	—
Column	Spirocysts	—	—	—	—
	Holotrichs (L)	24–27, 26.0	8–10, 9.3	3	Rare
	Bastrichs and microbasic b-mastigophores	—	—	—	—
	Microbasic p-mastigophores	—	—	—	—
Pharynx	Spirocysts	—	—	—	—
	Holotrichs (L)	28–36, 31.6	13–16, 14.8	6	Rare
	Bastrichs and microbasic b-mastigophores	16–22, 19.6	1–4, 3.0	26	Common
	Microbasic p-mastigophores	15–20, 17.3	4–5, 4.6	9	Occasional
Mesenteries	Spirocysts	—	—	—	—
	Holotrichs (L)	25	13	1	Rare
	Bastrichs and microbasic b-mastigophores	17–19, 18.0	3–5, 4.0	2	Rare
	Microbasic p-mastigophores	16–21, 18.6	4–7, 5.2	18	Common

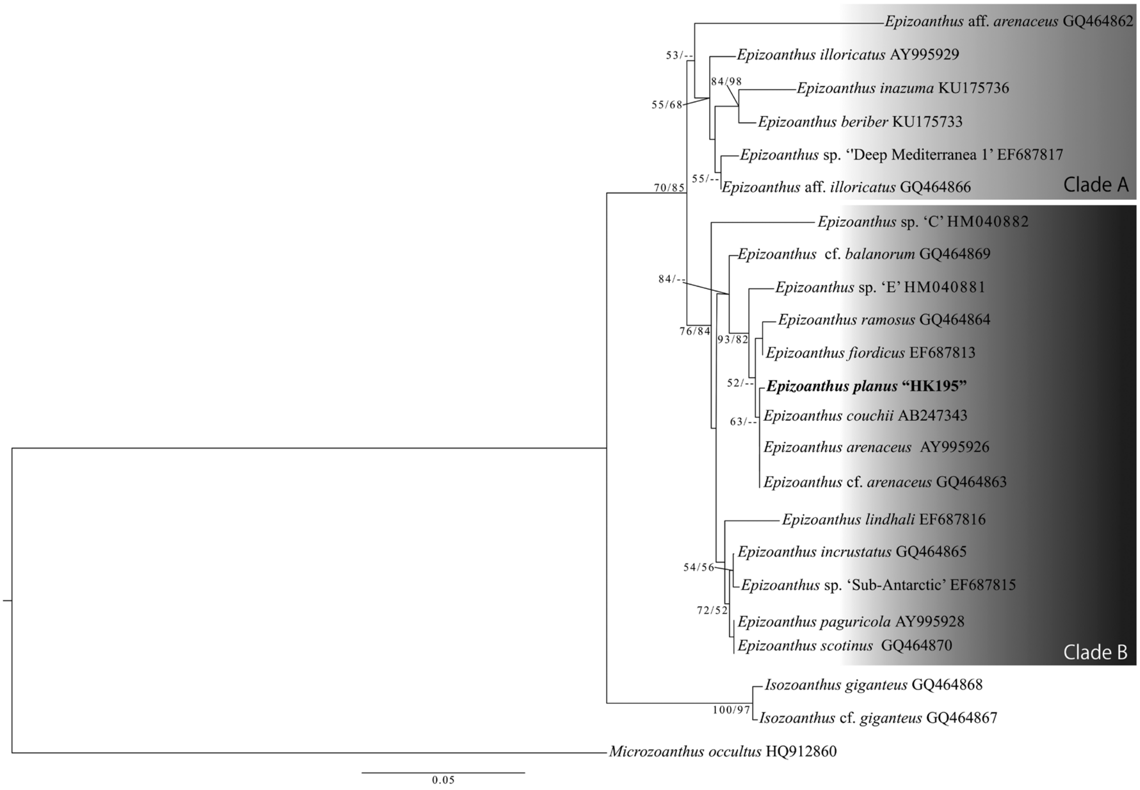

Fig. 3. Maximum likelihood (ML) tree based on 16S-rDNA. Numbers on nodes represent ML bootstrap values and NJ bootstrap values (>50% are shown for both), respectively. The specimen examined in this study is highlighted in bold.

mens; however, there is little information given with regard to the octocoral-associated specimens. Therefore, it is questionable if the octocoral associated-specimens truly correspond to *E. planus* as stated in the original description. Additionally, the marginal muscle shapes of *Epizoanthus* species are similar to those of species in the genus *Terrazoanthus* (family Hydrozoanthidae), which are known to be octocoral-associated (Bo et al. 2012; Swain et al. 2015). Further research is needed to determine if octocoral-associated *E. planus* corresponds to the genus *Terrazoanthus* or not.

Phylogeny. Based on the 16S-rDNA phylogeny, *Epizo-*

anthus sequences formed two main clades (Figure 3). *E. planus* sequences were located within clade B, which also contained sequences of *E. arenaceus* (Delle Chiaje, 1823), *E.* cf. *arenaceus*, *E. couchii* (Johnston in Couch, 1844), *E. fiordicus* Sinniger & Haussermann, 2009, *E. lindhali* Carlgren, 1913, *E. scotinus* Wood, 1957 (all non-epizoic species), *E.* cf. *balanorum* (Thoracica-associated), and *E. incrustatus* (Düben & Koren, 1847) (=*E. papillosus*), *E. paguricola* Roule, 1900, *E. ramosus* Carlgren, 1936, *Epizoanthus* sp. C sensu Reimer et al. (2010), and *Epizoanthus* sp. E sensu Reimer et al. (2010) (all hermit crab-associated species) with moderate nodal support (ML=76%; NJ=84%).

Common Japanese name. Ousama-yadori-sunaginchaku

Distribution. *E. planus* may be distributed around the Indo-Pacific Ocean as the species has been found offshore of southeastern Somalia (Carlgren 1923), in the South China Sea (Pei 1998), and in the Pacific Ocean.

Discussion

Epizoanthus planus has been previously reported from the Indian Ocean and the East China Sea at depths ranging from 420 to 1019 m (Carlgren 1923; Pei 1998). Additionally, unidentified sea urchin-associated *Epizoanthus* specimens were found at 500 m in the Caribbean (Ryland & Ward 2016) and in the Azores (Richald 1902; Barel & Kramers 1977). Thus, *Epizoanthus*-sea urchin associations may be relatively common, occurring throughout the world's oceans.

The specimen in this study is the first record of this species from Japan. This new record increases the confirmed number of *Epizoanthus* species in Japanese waters to at least five species: *E. parasiticus* (Verrill, 1864), *E. indicus* (Lwowsky, 1913), *E. illoricatus* Tieschbierek, 1930, *E. ramosus* Carlgren, 1936, and *E. inazuma* Kise & Reimer, 2016. The species diversity of order Zoantharia is comparatively high in waters around Japan (see Reimer & Fujii 2017), although sampling bias is undoubtedly present. Additional potentially undescribed *Epizoanthus* species have also been found in Japanese waters (e.g. Reimer et al. 2010b), even though the species diversity of other zoantharians has been relatively well studied in this region. Until now, many taxonomic and diversity studies in this region have focused on specimens from SCUBA-based collections (<50 m depth), with the notable exception of some deep-sea species (e.g., Hertwig 1882; Reimer et al. 2007, 2008). Although historical deep-sea expeditions such as the Challenger Expedition were conducted around Japanese waters, very few zoantharians were described from collected specimens (but see Wassilieff 1908).

Recently, some deep-sea zoantharian species have been formally described from various locations, including Hawaii (Sinniger et al. 2013) and the Eastern Atlantic (Carreiro-Silva et al. 2017). These studies demonstrate the importance of collecting and examining specimens from deeper waters to better understand the overall diversity of the order Zoantharia. Although many deep-sea species belong to the genus *Epizoanthus*, studies focused on their taxonomy and diversity are limited, particularly those combining morphological and molecular phylogenetic analyses. Moreover, many described *Epizoanthus* species have not been found or examined since their original descriptions were published (e.g., *E. valdivae* Carlgren, 1923).

Based on data in the present study and Reimer et al. (2010b), *Epizoanthus* species may not have strict substrate relationships such as those that are often seen in the family Parazoanthidae whose members form monophyletic clades (and often genera) based on the type of associated substrate (Sinniger et al. 2005, 2010). On the other hand, such associations have not been observed within *Epizoanthus*. This phenomenon could be a consequence of the deep-sea environments where many *Epizoanthus* species are found, which are muddy environments that may be uninhabitable for sessile anthozoans. Moreover, *Epizoanthus* species may adapt to a variety of substrates and therefore not share evolutionary histories associated with specific substrates under such conditions. However, only a few potentially opportunistic *Epizoanthus* species with a wide range of substrate organisms have been recognized to date, including hermit crab-*Epizoanthus* associations (Williams & McDermott 2004). The present study highlights that there are still many questions remain to be answered, and that both further taxonomic work and observations of substrate preferences in controlled laboratory settings should be conducted. Answering these questions about the genus *Epizoanthus* will result in a better understanding of the diversity and evolution of substrate associations in deep-sea environments.

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