

# A new species of *Zanclaea* (Cnidaria: Hydrozoa) associated with scleractinian corals from Okinawa, Japan

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*The new species of Zanclaea sango sp. nov. is described from Okinawajima Island, Ryukyu Archipelago, south-western Japan. The new hydrozoan species is associated with at least three scleractinian corals (Pavona divaricata, P. venosa and Psammocora contigua). Zanclaea sango sp. nov. is a polymorphic hydroid and the hydrorhiza grows between the coral skeleton and calicoblastic ectoderm. The hydrocaulus and hydrorhiza are surrounded by perisarc. Newly released medusae are almost spherical, with four perradial exumbrellar nematocyst pouches including stenoteles, and two long marginal tentacles with cnidophores containing macrobasic euryteles. Zanclaea sango sp. nov. is allied to Zanclaea gilii Boero et al., 2000 and Zanclaea margaritae Pantos & Bythell, 2010, but it is distinguished by its cnidome, the presence of a perisarc around hydrorhiza, and lower host-specificity. According to a hypothetical Zanclaea phylogeny, the ancestral species of Zanclaea had an opportunistic association with some benthic organisms, such as algae or bivalves, and its hydrorhiza was covered by a perisarc. Later, some species established specific associations with benthic animals, after which the hydrorhiza lost the perisarc and became directly covered with host tissue. Among Zanclaea inhabiting corals, the present species, with multiple coral host species and a perisarc around the hydrorhiza, seems to retain more ancestral character states than Z. gilii and Z. margaritae, which have specific coral host species and no perisarc around the hydrorhiza.*

**Keywords:** Cnidaria, Hydrozoa, new species, perisarc, Scleractinia, symbiosis

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## INTRODUCTION

Many hydroids are associated with other marine organisms such as algae, seagrasses, sponges, cnidarians, bryozoans, polychaetes, molluscs, crustaceans, echinoderms, tunicates, and fish (e.g. Gili & Hughes, 1995; Boero & Bouillon, 2005; Puce *et al.*, 2008a). The polyps are involved in associations ranging from simple epibiosis to strict symbioses (from mutualism to parasitism). The best-known mutual symbiosis is that of hydroids on the shells of hermit crabs: the hermit crab gives hydroids access to food and the hydroid protects the hermit crab from predators (e.g. Christensen, 1967; Brooks & Mariscal, 1985).

Sessile organisms are often inhabited by various hydroids. Many hydroid species of more than five families have been found on the surfaces or inner walls of the canal systems of sponges (Puce *et al.*, 2005): the hydroids increase the sponges' food supply owing to the water currents produced by the host sponge and may use toxins contained in the sponge tissue to avoid predators such as nudibranchs. The relationship between sponges and hydroids is classified into three types: (1) the hydranth protrudes from the sponge surface and cannot retract into it; (2) the hydranth protrudes from the sponge surface but can retract into the host sponge;

and (3) the hydrorhizal system is embedded in the sponge tissue and hydranths do not come out of the sponge (Puce *et al.*, 2005). The last case represents the closest relationship between hydrozoans and sponges. Bryozoans also harbour symbiotic hydrozoans including the six genera *Hydranthea*, *Cytaeis*, *Octotiarra*, *Halocoryne*, *Zanclaea* and *Zanclella* (Puce *et al.*, 2007, 2008a), and show as wide a range of mutuality levels as sponges.

Although some genera are generalists that live in association with different unrelated groups, almost entire genera or even families are associated with specific groups (Puce *et al.*, 2008a). The family Zanclaeidae Russell, 1953, comprises three genera (*Halocoryne* Hadzi, 1917, *Zanclaea* Gegenbaur, 1857 and *Zanclella* Boero & Hewitt, 1992) and all species live in association with other benthic organisms. All species of *Halocoryne* and *Zanclella* are associated with bryozoa (Boero *et al.*, 2000; Puce *et al.*, 2002, 2008a). Most *Zanclaea* species are also associated with bryozoa (*Z. bomala*, *Z. divergens*, *Z. exposita*, *Z. giancarloii*, *Z. hirohitooi*, *Z. polymorpha*, *Z. protecta*, *Z. retractilis*, *Z. sessilis* and *Z. tipis*), although *Z. alba* live on algae, *Z. costata* and *Z. fanella* live on bivalve shells, *Z. timida* live on octocoral, and *Z. gilii* and *Z. margaritae* are associated with scleractinian corals (Gegenbaur, 1857; Hastings, 1930; Calder, 1988; Schuchert, 1996; Boero *et al.*, 2000; Puce *et al.*, 2002, 2008b; Pantos & Bythell, 2010).

Boero *et al.* (2000) described *Z. gilii* from Papua New Guinea as living in corals, although they did not give a clear description or identification of the coral host species. Recently, Pantos & Bythell (2010) described *Z. margaritae*,

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inhabiting the scleractinian coral *Acropora muricata* (= *A. formosa*) on the Great Barrier Reef, and this hydroid was not found on any other coral species. From the Sesokojima Island in Okinawa Islands, the southernmost islands in Japan, Yamada & Kubota (1987) reported *Zanclaea* sp. attached to the living stony coral *Porites rus* and some other coral species at depths of a few metres. However, the details of the hydroid were not described, and no medusa buds were found on the hydroids.

During an ecological study of scleractinian corals on Okinawajima Island, in the Ryukyu Archipelago, we found *Zanclaea* hydroids associated with several scleractinian corals on a shallow reef. Here, we describe this *Zanclaea* species as a new species and discuss an evolutionary trend among coral-symbiotic *Zanclaea* spp. compared to bryozoan-symbiotic species.

## MATERIALS AND METHODS

### Specimens

Small pieces (3–5 cm long) of *Pavona divaricata* were collected from reef flats (0.5–1 m) at Bise, Okinawajima Island (26°42'31"N 127°52'58"E) on 9 July 2009. Small pieces of *P. divaricata*, *Pavona venosa* and *Psammocora contigua* were then collected from the same site on 28 June and 8 July 2010. Small pieces of *P. venosa* and *P. contigua* were collected from reef flats (0.5–1 m) at Zanpa, Okinawajima Island (26°26'18"N 127°42'40"E) on 24 June and 12 July 2010. Small pieces of *P. divaricata*, *P. venosa* and *P. contigua* were collected from reef flats (0.5–1 m) at Odo, Okinawajima Island (26°05'20"N 127°42'31"E) on 26 July 2010. Each specimen was brought to the laboratory in 300-ml plastic bottles filled with seawater. To collect newly released medusae, each coral species with hydranths was incubated separately in 500-ml plastic jars filled with 0.45- $\mu$ m-pore filtered seawater (FSW) at room temperature (27–29°C).

Type specimens were deposited in the National Museum of Nature and Science, Tokyo.

### Microscopy

Live specimens were used to observe and measure cnidocytes and medusae. Ten or more medusae detached from each coral host species at every collection site were measured within 16 hours after detachment from the parent hydranth. For some photomicrographs, several images were combined to increase the depth of field by using the image post-processing software Helicon Focus Pro 3.79 (Helicon Soft). The capsule size of each cnidocyte and the diameters of medusae were measured from the digital images using ImageJ 1.41 (rebweb.nih.gov).

### Histological observation

Small pieces of *P. divaricata* with *Zanclaea* polyps were fixed in 2.5% glutaraldehyde/0.1 M cacodylate/0.45 M sucrose and stored at 4°C. Specimens were then rinsed with 0.1 M cacodylate/0.45 M sucrose and post-fixed in 1% osmium tetroxide/0.1 M cacodylate for 1.5 hours. After a brief rinse with 50% ethanol, coral skeletons were decalcified with 2.5% acetic acid in FSW. Following dehydration through a graded ethanol series, specimens were embedded in styrene resin.

They were sectioned to about 1  $\mu$ m thickness and stained with 1% toluidine blue for light microscopy. Serial sectioning continued until the desired structures were exposed, after which the resin was removed by soaking in acetone (three times for 1 hour in fresh solvent). After a brief rinse with ethanol, the specimens were immersed in *t*-butanol and freeze-dried, sputter-coated with gold-palladium, and examined under a scanning electron microscope (SEM; JEOL JSM-6060LV).

## RESULTS

### SYSTEMATICS

Order CAPITATA Kühn, 1913  
Family ZANCLEIDAE Russell, 1953  
Genus *Zanclaea* Gegenbaur, 1857  
*Zanclaea sango* sp. nov.  
(Figures 1–3)

### TYPE MATERIAL

Holotype: gono-gastrozooids associated with *Pavona divaricata*, Bise (26°42'31"N 127°52'58"E; Okinawajima Island, Ryukyu Archipelago); water depth ~0.3 m at lowest tide; [NSMT-Co1538]. Collected by M. Hirose, 28 June 2010.

Paratypes: newly released medusa collected on release from parent colony associated with *P. divaricata* at Bise, 28 June 2010, [NSMT-Co1539]. Collected by M. Hirose, 29 June 2010. Gono-gastrozooids associated with *Pavona venosa*, Bise (26°42'31"N 127°52'58"E; Okinawajima Island, Ryukyu Archipelago); water depth ~0.3 m at lowest tide; [NSMT-Co1540]. Collected by M. Hirose, 28 June 2010.

Paratypes: newly released medusa collected on release from parent colony associated with *P. venosa* at Bise, 28 June 2010, [NSMT-Co1541]. Collected by M. Hirose, 29 June 2010. Gono-gastrozooids associated with *Psammocora contigua*, Bise (26°42'31"N 127°52'58"E; Okinawajima Island, Ryukyu Archipelago); water depth ~0.3 m at lowest tide; [NSMT-Co1543]. Collected by M. Hirose, 28 June 2010.

Paratypes: newly released medusa collected on release from parent colony associated with *P. contigua* at Bise, 28 June 2010, [NSMT-Co1544]. Collected by M. Hirose, 29 June 2010.

### TYPE LOCALITY

Bise, Okinawajima Island, Ryukyu Archipelago.

### DIAGNOSIS

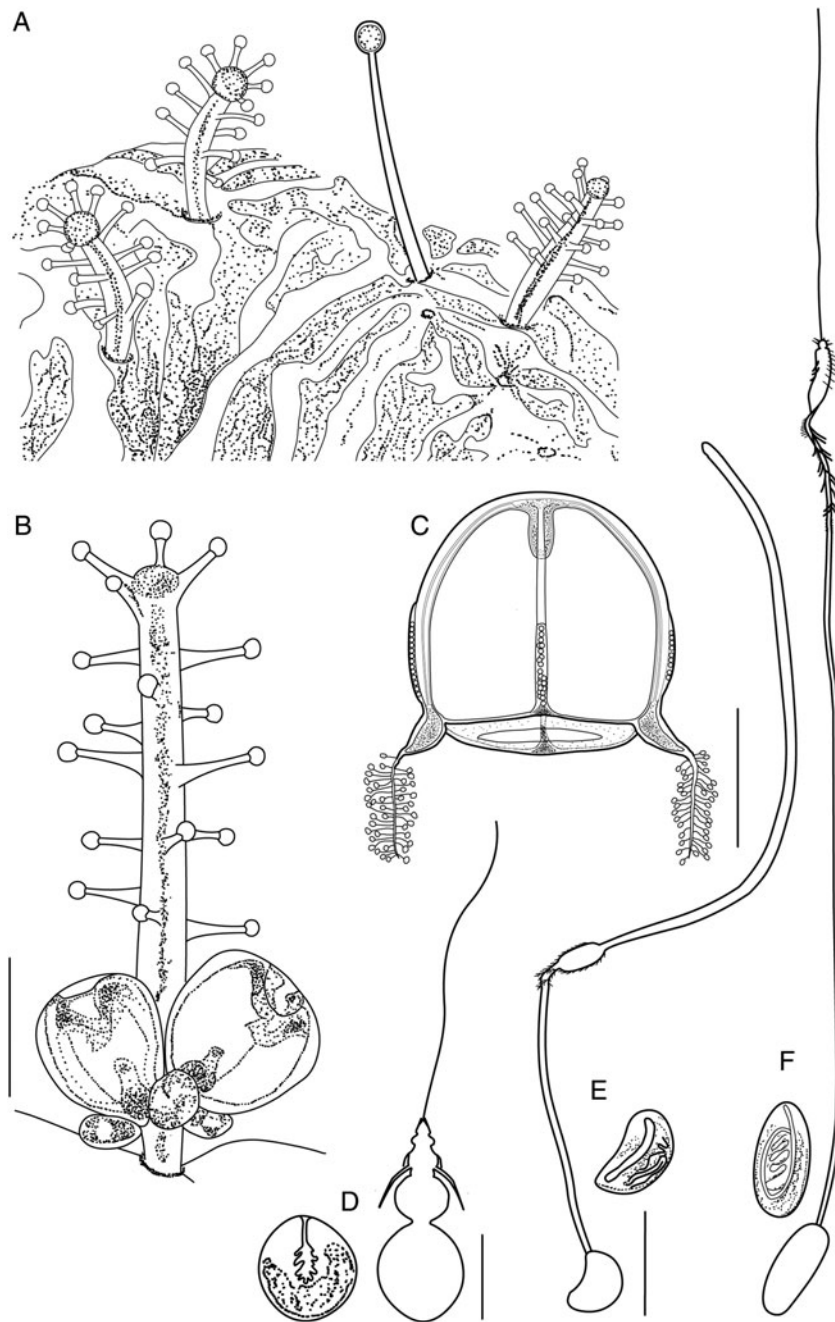
Polymorphic *Zanclaea* species associated with living scleractinian coral (*Pavona divaricata*, *P. venosa* and *Psammocora contigua*). Hydrorhiza are surrounded by a perisarc, and grow between the coral skeleton and calicoblastic ectoderm. Newly released medusae are almost spherical, with four perradial exumbrellar nematocyst pouches including stenoteles, and two long marginal tentacles with cnidophores. Nematocyst complement consists of two sizes of stenotele and macrobasic euryteles (both in the hydranth and newly released medusa) and apotrichous euryteles in the cnidophores of the tentacles of newly released medusae.

## Description

### HYDROID

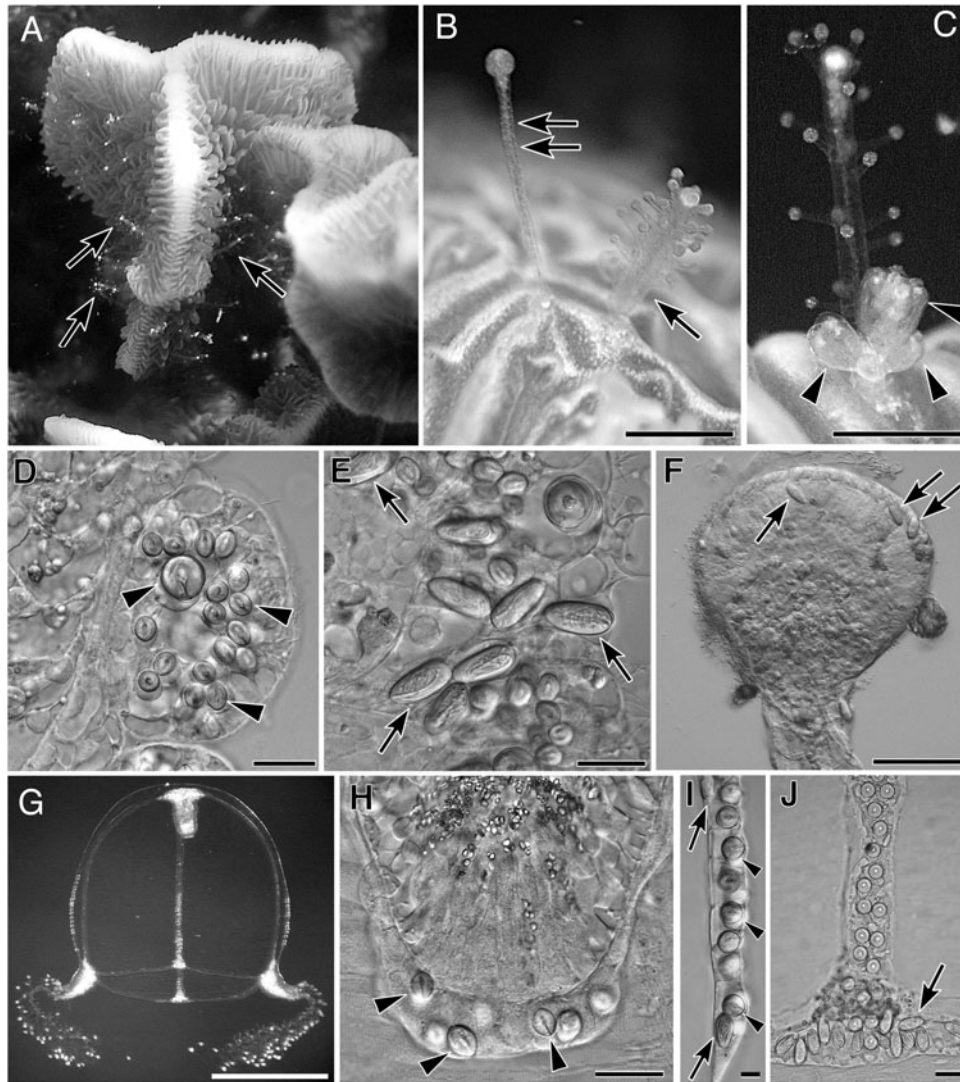
Polymorphic colonies inhabit the tissues of the scleractinian coral *Pavona divaricata* (Figures 1 & 2A). The hydrorhiza grows between the coral skeleton and the calciblastic ectoderm (Figure 5A–D). The hydrocaulus and hydrorhiza are surrounded by a perisarc (Figure 5A–D, arrowheads). Gono-gastrozoid hydranths are cylindrical and 0.8–1.9 mm long and 0.1–0.2 mm wide (without capitate tentacles). Five to six oral capitate tentacles on the whitish hypostome surround the mouth, and about 11–22 capitate tentacles in 3–5 rows cover the rest of the hydranth body

(Figures 1A–B & 2B–C). Highly retractile dactylozooids (Figure 2B), ~1.2 mm long when fully extended have apical knobs (100–140  $\mu\text{m}$  in diameter) with few apotrichous macrobasal euryteles and many glandular tissues (Figure 2F). One to six medusa buds are found on a single gono-gastrozoid. The medusa buds are on the basal part of the gono-gastrozoid hydranth (Figure 2C). In a nearly matured medusa, the manubrium turns pink and the bell begins pulsating while the medusa is still attached to the hydranth. Following maturation, four exumbrellar pouches become discernible. Large pulsating medusae (about 400  $\mu\text{m}$  in diameter) are sometimes found with small, immature medusae (less than 120  $\mu\text{m}$  in diameter) on the same hydranth (Figure 2C).



**Fig. 1.** *Zanclea sango* sp. nov. (A) Gastrozooids and dactylozooid emerging from the scleractinian coral *Pavona divaricata*; (B) gono-gastrozoid; (C) newly released medusa; (D) undischarged and discharged large stenotele from hydroid; (E) undischarged and discharged apotrichous macrobasal eurytele from cnidophores; (F) undischarged and discharged apotrichous macrobasal euryteles from hydroid. Scale bars: (B & C) 0.5 mm; (D, E & F) 10  $\mu\text{m}$ .





**Fig. 2.** Colony, polyps, and newly released medusae of *Zanclea sango* sp. nov. (A) Field photograph of the hydroid. Many polyps (arrows) emerging from the tissues of the scleractinian coral *Pavona divaricata*; (B) a gastrozoid (arrow) and dactylozoid (double arrow) on the same coral colony; (C) gono-gastrozoid with medusae at several developmental stages (arrowheads); (D) two sizes of stenoteles (arrowheads) found in the capitulate tentacle of the gono-gastrozoid; (E) apotrichous macrobasic euryteles (arrows) found around the mouth; (F) apical knob of dactylozoid (fixed specimen). Arrows indicate apotrichous macrobasic euryteles; (G) newly released medusa; (H) stenoteles (arrowheads) found around mouth; (I) exumbrella pouches containing stenoteles (arrowheads) and apotrichous macrobasic euryteles (arrows); (J) apotrichous macrobasic euryteles (arrow) in the bell margin. Scale bars: (B, C & G) 0.5 mm; (F) 100  $\mu\text{m}$ ; (D, E, H & J) 20  $\mu\text{m}$ ; (I) 10  $\mu\text{m}$ .

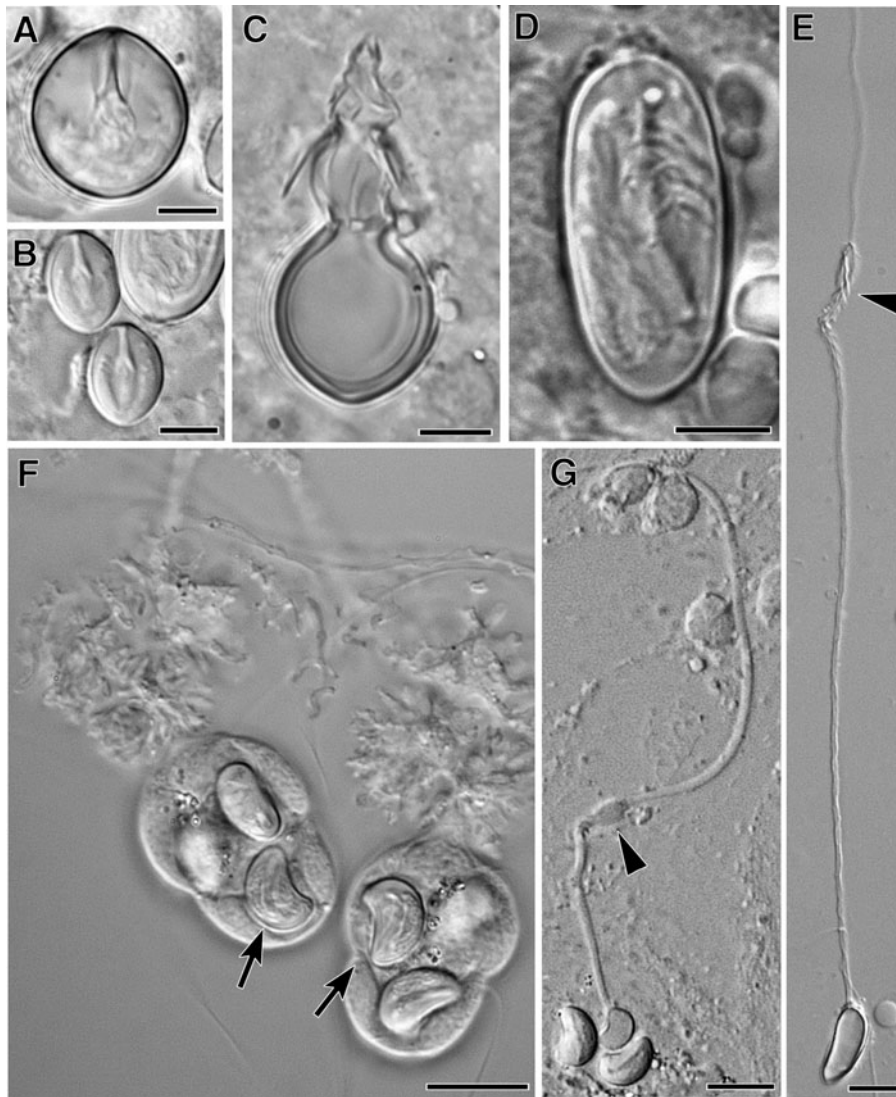
The cnidomes of living specimens were examined to identify cnidocyst types. Two sizes of stenoteles (undischarged  $\sim 14 \times 13 \mu\text{m}$  and  $8.5 \times 6.5 \mu\text{m}$ ) are found in the capitulum of the tentacles (Figures 2D & 3A, B). The size of discharged large stenotele capsule was about  $12 \times 11 \mu\text{m}$  and shaft ( $\sim 12.5 \mu\text{m}$  long) dilated with three well developing spines (stylets,  $\sim 6.3 \mu\text{m}$  long) (Figure 3C). Apotrichous macrobasic euryteles with the shaft coiled along the main capsule axis (undischarged  $\sim 18 \times 7.5 \mu\text{m}$ ) are also found in a circle around the mouth and sometime in the ectodermal layer of the basal part of the hydranth (Figures 2E & 3D). The size of discharged capsule was about  $16 \times 6.5 \mu\text{m}$  and the dilating end of the long shaft ( $\sim 140 \mu\text{m}$  long) is ornamented with spines and a thread protrudes from it (Figure 3E).

#### NEWLY RELEASED MEDUSAE

Newly released medusae ( $526.6\text{--}778.0 \mu\text{m}$  in diameter) are almost spherical, with four perradial exumbrellar nematocyst

pouches and four marginal bulbs at the bases of the nematocyst pouches. Two large white conical tentacular bulbs are covered with about 30 cnidophores; the two smaller bulbs have no tentacles. The manubrium with white oral region is contractile and  $\sim 200 \mu\text{m}$  in length when extended (Figures 2G & 3G).

Newly released medusae possess stenoteles of two sizes; small stenoteles are found around the mouth (undischarged  $\sim 8.5 \times 6.5 \mu\text{m}$ ; Figure 2H), and large stenoteles are present in exumbrellar nematocyst pouches (undischarged  $\sim 11 \times 10 \mu\text{m}$ ; Figure 2I). Each exumbrellar nematocyst pouch contains 20–30 stenoteles. Apotrichous macrobasic euryteles (undischarged  $\sim 18 \times 8 \mu\text{m}$ ) are distributed in exumbrellar nematocyst pouches and bells (Figure 2I, J). Bean-shaped apotrichous macrobasic euryteles (undischarged  $\sim 8 \times 5 \mu\text{m}$ ) are present in the cnidophores of the tentacles (Figure 3F). The size of discharged capsule was about  $6.6 \times 4.0 \mu\text{m}$  and shaft dilated distally (Figure 3G).



**Fig. 3.** Nematocyst of *Zanclea sango* sp. nov. (A) Large undischarged stenotele from hydroid; (B) small undischarged stenotele from hydroid; (C) large discharged stenotele from hydroid; (D) undischarged apotrichous macrobasic euryteles from hydroid; (E) discharged apotrichous macrobasic euryteles. The dilating end of the long shaft is ornamented with spines (arrowheads) and a thread protrudes from it; (F) cnidophores including undischarged bean-shaped apotrichous macrobasic euryteles (arrows); (G) discharged bean-shaped apotrichous macrobasic euryteles. Arrowhead indicates dilatation of shaft. Scale bars: (A, B, C & D) 5  $\mu\text{m}$ ; (E, F & G) 10  $\mu\text{m}$ .

#### ETYMOLOGY

The specific name is derived from *sango*, meaning coral in Japanese, because the hydrozoan colonies are associated with several scleractinian coral species.

#### REMARKS

This hydrozoan belongs to the genus *Zanclea* Gegenbaur, 1857, based on the following characters: colonial hydroid, cylindrical gono-gastrozoid with an oral whorl of capitate tentacles and numerous aboral capitate tentacles scattered or in several whorls over the column, medusa buds at the base of the gastrozoid, bell-shaped medusa with four periradial exumbrellar pouches including stenoteles, and two long marginal tentacles with cnidophores containing macrobasic euryteles.

The genus *Zanclea* currently includes 19 species (Boero *et al.*, 2000; Puce *et al.*, 2002, 2008b; Pantos & Bythell, 2010). Thirteen *Zanclea* species have monomorphic hydroids,

five species have polymorphic hydroids and the hydroid of *Z. dubia* is unknown. Three of the five polymorphic species are associated with bryozoans. *Zanclea sango* sp. nov. is a polymorphic hydroid inhabiting corals, and these features are shared with *Zanclea gilii*, Boero, Bouillon & Gravili, 2000 and *Z. margaritae* Pantos & Bythell, 2010. Moreover, the two aforementioned species and the present new species have dactylozooids lacking capitate tentacles.

Differences of the character states among the three species are summarized in Table 1. *Zanclea margaritae* specifically inhabits *Acropora muricata* (Anthozoa: Scleractinia) on the Great Barrier Reef (Pantos & Bythell, 2010); Boero *et al.* (2000) did not identify the coral host species in their original description of *Z. gilii*. In contrast, colonies of *Z. sango* sp. nov. were found on at least three scleractinian coral species (*Pavona divaricata*, *P. venosa* and *Psammocora contigua*) in Okinawa. The cnidome of *Z. sango* sp. nov. is different from those of *Z. gilii* and *Z. margaritae*. Additionally, *Z. sango* sp. nov. does not contain microbasic mastigophores or

**Table 1.** Character states of *Zanclaea sango* sp. nov. and the other *Zanclaea* species associated with hard corals.

	<i>Z. gillii</i> Boero <i>et al.</i> , 2000	<i>Z. margaritae</i> Pantos & Bythell, 2010	<i>Z. sango</i> sp. nov.
Locality	Papua New Guinea	Great Barrier Reef	Okinawa
Host coral	Unidentified coral	<i>Acropora muricata</i> (= <i>A. formosa</i> ) specific	<i>Pavona divaricata</i> , <i>Pavona venosa</i> and <i>Psammocora contigua</i>
Hydroid (Gastrozooid)			
Oral tentacles	Up to 6	5–6	5–6
Aboral tentacles	11–30, in 2–3 whorls and scattered below	5–17, in rows (up to 5–6)	11–22, in rows (3–5)
Perisarc around hydrorhiza	Absent	Absent	Present
Stenotele (large and small)	Mainly in the tentacular capitula	In the tentacular capitula	In the tentacular capitula
Macrobasal euryteles	In a circle around the mouth	Absent	In a circle around the mouth and base of the gono-gastrozooid
Microbasal mastigophore	Absent	In the tentacular capitula	Absent
Basitrichous isorhizas	Absent	In the base of the gono-gastrozooid	Absent
Hydroid (Dactylozooid)			
Nematocysts	Present (details undescribed)	Present (details undescribed)	Apotrichous macrobasal eurytele
Newly released medusae			
Bell diameter	About 1 mm*	0.4–0.6 mm	536.6–778.0 $\mu\text{m}$ (643.5 $\pm$ 53.3 $\mu\text{m}$ (average $\pm$ SD))
Cnidophore	About 20	Present (number unknown)	About 30
Large stenotele	In the exumbrellar chambers and around mouth	In the exumbrellar chambers	In the exumbrellar chambers
Small stenotele	In the exumbrellar chambers and around mouth	In the exumbrellar chambers	Around mouth
Macrobasal euryteles	Absent	Absent	In the exumbrellar chambers and bell margin
Microbasal mastigophore	Absent	In the exumbrellar chambers	Absent
Bean-shaped apotrichous macrobasal euryteles	In the cnidophores	In the cnidophores	In the cnidophores

\*, estimation by Pantos & Bythell (2010).

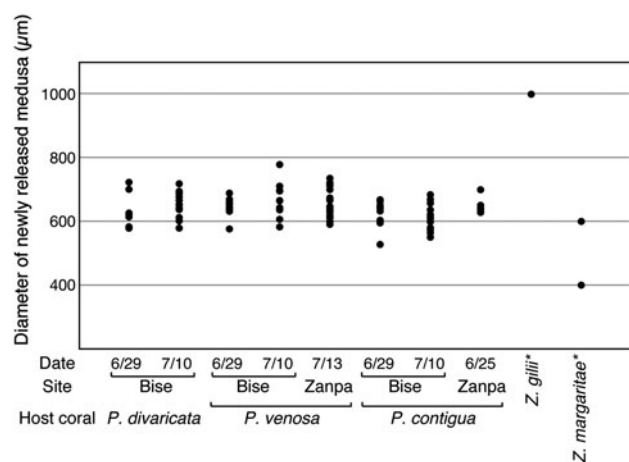
basitrichous isorhizas in hydroids or newly released medusae, while macrobasal euryteles are found in newly released medusae. The bell diameter of newly released *Z. margaritae* is 0.4–0.6 mm, approximately half that of *Z. gillii* (Pantos & Bythell 2010). The bell size of newly released *Z. sango* sp. nov. medusae is 643.5  $\pm$  53.3  $\mu\text{m}$  (average  $\pm$  SD, N = 91), with maximum and minimum sizes of 778.0  $\mu\text{m}$  and 536.6  $\mu\text{m}$ . In the present species, bell size did not differ significantly among specimens from different coral host species or collection sites (Kruskal–Wallis test,  $P > 0.05$ ; Figure 4).

### Interaction with host

The hydrorhiza of *Z. sango* sp. nov. grows under the calicoblastic ectoderm of scleractinian corals and is completely covered by host tissues. The base of the hydrocaulus is surrounded by a raised collar of tissue derived from the host coral (Figure 5A, B). At the point where the hydrocaulus passes into the coral tissue, the hydrozoan tissue comes close to the coral epidermal tissue. Inflammatory responses and abnormal growth were not recognized in the tissues of either species in histological examinations. The epidermal layer of the hydrorhiza was thicker (10–15  $\mu\text{m}$ ) than that of the hydranth (~8  $\mu\text{m}$ ), while the endodermal cells of the hydrorhiza were smaller (10–15  $\mu\text{m}$ ) than those of the hydranth (20–40  $\mu\text{m}$ ). There were many small particles and much debris in the gastrovascular cavities of gastrozooids (Figure 5E, F). There were some gastrozooids in which the coelenteron (gastrovascular cavity) was expanded by ingested food items (Figure 5G).

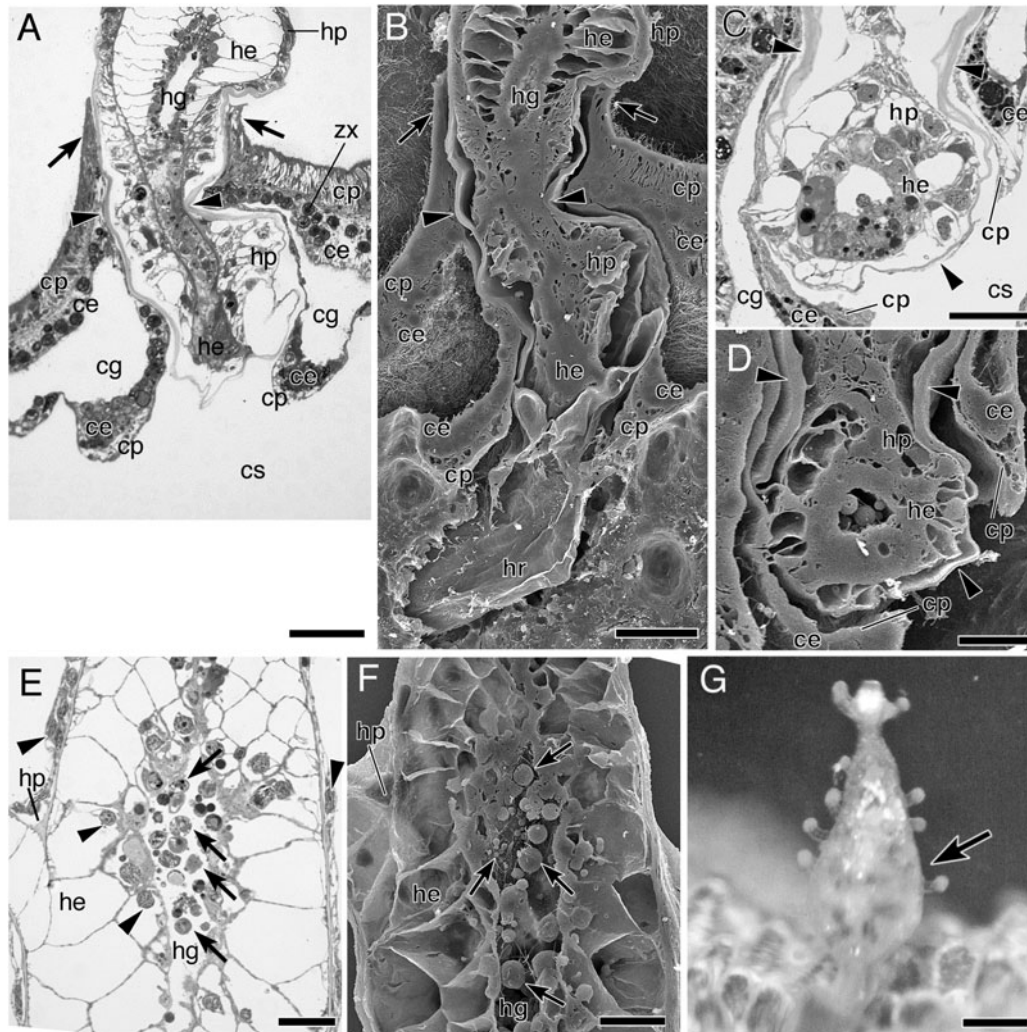
### DISCUSSION

Most species of the genus *Zanclaea* live in association with bryozoans, while some species inhabit algae (*Z. alba*), bivalve shells (*Z. costata* and *Z. fanella*), octocorals (*Z. timida*) and hard corals (*Z. gillii* and *Z. margaritae*). Boero *et al.* (2000) proposed an evolutionary scenario for the transition of zancleid hydroids from non-symbiotic species to symbiotic hydroids



**Fig. 4.** Variation in diameter of newly released medusae in *Zanclaea sango* sp. nov. Bell size of *Z. gillii* and *Z. margaritae* are cited from Pantos & Bythell (2010). In *Z. sango* sp. nov., differences in bell sizes were not significant among specimens from different coral host species or different collection sites (Kruskal–Wallis test,  $P > 0.05$ ).





**Fig. 5.** Interaction between host coral (*Pavona divaricata*) and *Zanclea sango* sp. nov. (A, B) Image pair showing longitudinal section through a gastrozooid emerging from coral tissue (A, resin section; B, scanning electron microscopy (SEM)). The hydrocaulus emerges through a collar of coral (arrows). The base of the hydrocaulus and hydrorhiza are covered by a perisarc (arrowheads); (C, D) image pair showing transversal section of hydrorhiza (C, resin section; D, SEM). Arrowheads indicate perisarc; (E, F) image pair showing longitudinal section of mid-region of gastrozooid (E, resin section; F, SEM). There are many small particles and debris (arrows) in the gastrovascular cavity. Arrowheads indicate the nuclei of the hydrozoan cells; (G) a gastrozooid. The hydranth is expanded by the ingested food items (arrow). ce, coral endodermis; cg, coral gastrovascular cavity; cs, coral skeleton; cp, coral epidermis; he, hydrozoan endodermis; hg, hydrozoan gastrovascular cavity; hp, hydrozoan epidermis; hr, hydrorhiza; zx, zooxanthella. Scale bars: (G) 0.5 mm; (A & B) 50  $\mu$ m; (C, D, E & F) 20  $\mu$ m.

with advanced integration with the host. They presumed that *Z. alba*, which lives on algae, is the most basal species of *Zanclea* based on its absence of macrobasal euryteles, less specialized features of the hydroids and medusae, and hydrorhiza creeping on the substrate. Furthermore, Puce *et al.* (2002) pointed out the importance of the presence or absence of a perisarc around the hydrorhiza. The hydrorhiza is covered by a perisarc in several species that live on algae (*Z. alba*) and bivalve shells (*Z. costata* and *Z. fanella*) (Boero *et al.* 2000). Ten *Zanclea* species are known to associate with bryozoa: six species lack a perisarc and their hydrorhiza is directly covered by the bryozoan skeleton, three species have a perisarc and their hydrorhiza is covered by the skeleton, and *Z. exposita* is the only species that lacks a perisarc and whose hydrorhiza grows on the bryozoan skeleton (Hastings, 1930; Schuchert, 1996; Boero *et al.*, 2000; Puce *et al.*, 2002). Puce *et al.* (2002) hypothesized that the ancestral species of *Zanclea* had opportunistic associations with some benthic organisms, such as algae or bivalves,

and that its hydrorhiza was covered by a perisarc. Later, some species established specific associations with bryozoans, and then the hydrorhiza was lost and directly covered by the bryozoan skeleton. Integration with bryozoans may induce the loss of the perisarc around the hydrorhiza.

Fifteen hydroid species are known to be associated with anthozoans. Among them, three *Zanclea* species (*Z. gili*, *Z. margaritae* and *Z. sango* sp. nov.) inhabit scleractinian corals; the other species (*Ptilocodium repens* Coward, 1909; *Hydrichthella epigorgia* Stechow, 1909; *Sarsia medelae* Gili *et al.*, 2006; *Ralpharia magnifica* Watson, 1980; *Ralpharia coccinea* Watson, 1984; *Ralpharia neira* Petersen, 1990; *Ralpharia gorgoniae* Petersen, 1990; *Ralpharia sanctisebastiani* da Silveira & Migotto, 1984; *Ralpharia parasitica* Korotneff, 1887; *Asyncoryne philippina* Hargitt, 1924; *Pteroclava kremphi* Billard, 1919; and *Zanclea timida* Puce *et al.*, 2008b) are associated with octocorals. Most of the hydroids that inhabit octocorals have a perisarc-covered hydrorhiza that separates the coenosarc

from the host tissue, while *Ptilocodium repens*, *Z. timida* and *Hydrichthella epigorgia*, associated with the gorgonian *Anthoplexaura dimorpha*, lack a distinct perisarc sheath (see Gili *et al.*, 2006; Puce *et al.*, 2008b). Among species that inhabit scleractinian corals, the hydrorhizae of *Z. gili* and *Z. margaritae* are completely embedded in coral tissue and lack perisarc (Boero *et al.*, 2000; Pantos & Bethyll, 2010), while that of *Z. sango* sp. nov. has a perisarc. If advanced integration with the host may induce the loss of the perisarc (Puce *et al.*, 2002), then *Z. sango* sp. nov. may be a more basal species among the three *Zanclaea* species that inhabit hard corals. The host specificity of these *Zanclaea* also supports this scenario: *Z. sango* sp. nov. is associated with at least three coral host species, while *Z. margaritae* has a specific host, *Acropora muricata*. On the other hand, *Z. gili* lives in unidentified, non-acroporid corals. In the lineage of *Zanclaea* species that inhabit hard corals, the ancestral species is predicted to have been a generalist with a perisarc, whereas advanced species established specific associations with particular host species and lost their perisarc, following the development of the symbiotic relationship.

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