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Isozoanthus antumbrosus, a new species of zoanthid (Cnidaria: Anthozoa: Zoanthidea) symbiotic with Hydrozoa from the Caribbean, with a key to hydroid and sponge-symbiotic zoanthid species

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Abstract

Isozoanthus antumbrosus, a new species of zooxanthellate zoanthid, is described. Colonies associate with the arborescent hydroid *Dentitheca dendritica* in the Caribbean Sea at 1–60 m. The coenenchyme, column, and oral disk are seal brown. The tentacles are golden brown and number 30–38. The coloration of the oral disk and tentacles recalls an annular solar eclipse. Polyps are 4.1–8.9 mm long and 2.2–4.3 mm in diameter. Genetic, morphological, and ecological characters differentiate this species from other hydroid-symbiotic zoanthids. Assignment to the genus *Isozoanthus* is based on morphology, with the acknowledgment that the currently accepted genera may not reflect evolutionary relationships.

Key words: cryptic species, Coelenterata, Macrocnemina, Parazoanthidae, symbiosis

Introduction

Zoanthids are cnidarians belonging to class Anthozoa and order Zoanthidea (also referred to as Zoantharia or Zoanthiniaria). Members of the zoanthid suborder Macrocnemina form symbioses (*sensu* Saffo 1992) with members of at least five invertebrate phyla in most major benthic habitats from the sublittoral to the deep sea. Caribbean macrocnemic zoanthids living shallower than 60 m include six sponge-symbiotic and two hydroid-symbiotic species delineated by phylogenetic analysis of nuclear DNA sequences (Swain *in press*). Nuclear DNA data indicating two hydroid-symbiotic species are consistent with analyses of mitochondrial DNA (16S, Swain *in press*; combined 12S and 16S, Sinniger *et al.* 2005) and morphological characters (Swain *in press*). The morphology of one hydroid-symbiotic species is consistent with the original description of *Parazoanthus tunicans* Duerden, 1900 (Swain *in press*). That of the second is consistent with one specimen (USNM 50878), but not five others (USNM 17218, 50354, 50777, 50778, 52526), in the United States National Museum labeled with a *nomen nudum* (Swain *in press*). In the absence of a valid description, a new species, *Isozoanthus antumbrosus*, is described here.

Material and methods

Zoanthid colonies associated with the arborescent hydroid *Dentitheca dendritica* (Nutting 1900) were observed and photographed on coral reefs of Panamá (Bocas del Toro), Dominica, Tobago, and Curaçao. Standardized photographs for morphological measurements were taken in Panamá and Tobago. Specimens for histological and molecular analysis were collected manually in Dominica and Curaçao. Each specimen was split into two fragments and preserved in 100% ethanol for molecular analysis or 4% zinc formalin followed by 70% ethanol for histological study.

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Morphological data were collected from photographs and histological sections; molecular data were culled from Swain (*in press*) and GenBank. Column height and width, oral disk diameter, and tentacle basal diameter and length were measured from photographs with Image-J 1.40 (U.S. National Institutes of Health). Individual polyps dissected from colonies were decalcified for 4 h in Formical-4™ (Decal Chemical Corporation; Tallman, NY) and desilicified for 4 h in 20% hydrofluoric acid, then stored in 70% ethanol. Polyps were dehydrated in ethanol, cleared with xylene, embedded in paraffin, and sectioned at the Florida State University Histology Facility. Serial 13-µm longitudinal and cross sections of polyps were stained with Harris' hematoxylin and eosin Y. Type specimens were deposited at the U.S. National Museum of Natural History, Washington, DC, USA (USNM).

Description

Suborder Macrocnemina Haddon and Shackleton, 1891a

Family Parazoanthidae Delage & Hérouard, 1901

Genus *Isozoanthus* Carlgren in Chun, 1903

Isozoanthus antumbrosus new species

Synonymy. *Parazoanthus tunicans* "black" *sensu* Sinniger *et al.*, 2005
Parazoanthus tunicans sensu Reimer *et al.*, 2008
Isozoanthus sp. nov. *sensu* Swain, *in press*

Material examined. *Isozoanthus antumbrosus*: Atlantic Ocean, Caribbean Sea, Netherlands Antilles, Curaçao, Spaanse Water Baai channel, 12°3′55″ N, 68°51′10″ W, 10 m, 1 December 2007, associated with *Dentitheca dendritica*, preserved in 4% formalin, stored in 70% ethanol, USNM 1113090, holotype. A second individual was collected at the same location and time, USNM 1113091, paratype. Atlantic Ocean, Caribbean Sea, Dominica, Salisbury, Whale Shark Reef, 15°26′24″ N, 61°27′26″ W, 21 m, 12 November 2003, preserved in 70% ethanol, consumed in analyses, paratype. USNM 50878. Morphological measurements from photographs taken in Panamá and Tobago. DNA sequences culled from GenBank: EU418275 (Curaçao), EU418276 (Dominica), EU418277 and EU828761 (Panamá), and AY995940 (*Parazoanthus tunicans* "black" *sensu* Sinniger *et al.* 2005, Honduras). Unidentified anthozoans: USNM 17218, 50354, 50777, 50778, 52526. *Parazoanthus tunicans*: Atlantic Ocean, Caribbean Sea, Netherlands Antilles, Curaçao, Spaanse Water Baai channel, 12°3′55″ N, 68°51′10″ W, 10 m, 1 December 2007, associated with *Dentitheca dendritica*, preserved in 4% formalin, stored in 70% ethanol, USNM 1113089. Morphological measurements from photographs taken in Panamá and Tobago. DNA sequences culled from Genbank: EU418339 (Curaçao), EU418340 (Dominica), EU418341 and EU828760 (Tobago), and AY995941 (*Parazoanthus tunicans* "white" *sensu* Sinniger *et al.* 2005, Honduras).

Diagnosis. Zooxanthellate Parazoanthidae symbiotic with *Dentitheca dendritica*. Expanded polyps dichromatic; coenenchyme, column, and oral disk seal brown with 30–38 golden tentacles. Coloration of oral disk and tentacles recalls an annular solar eclipse. Largest expanded polyp columns 8.9 mm long, 4.3 mm in diameter; oral disk diameter 4.8 mm. Contracted polyps monochromatic, with 15–19 distinct capitular ridges.

Colony. Coenenchyme thin and encrusting, completely enveloping the central and secondary axial branches of *D. dendritica* colonies; usually not covering the finest pinnate branches, where the hydroid zooids are located (Fig. 1). Coenenchyme usually seal brown (but can appear dark olive green or nearly black) and densely infiltrated with calcareous sediment and siliceous spicules (and therefore appearing "flecked" with white).

Polyp. Fully expanded polyps dichromatic: capitulum and oral disk seal brown, tentacles translucent

golden; color most saturated at the bases of tentacles (Fig. 1). Column 4.1–8.9 mm long, 2.2–4.3 mm in diameter, and infiltrated with calcareous sediments and siliceous spicules in a gradient that diminishes toward the bases of tentacles. Oral disk 2.7–4.8 mm in diameter, concave with obvious ridges corresponding to tentacles and internal mesenteries; a central, oval protrusion bears a slit-like mouth. Tentacles 30-38, in two cycles (alternating tentacles directed toward and away from the coenenchyme), 1.9–5.0 mm long and 0.4–0.7 mm in diameter at the point of insertion in the oral disk, and gradually tapered to rounded, nearly white tips.

Polyps at intervals of approximately 1.5–2.5 polyp diameters, often in an orthogonal or distichous (on the finest hydroid branches) arrangement with oral disks nearly parallel to the plane of pinnate hydroid branches. Tentacles of adjacent polyps nearly touching at tips but not interdigitating (Fig. 1).

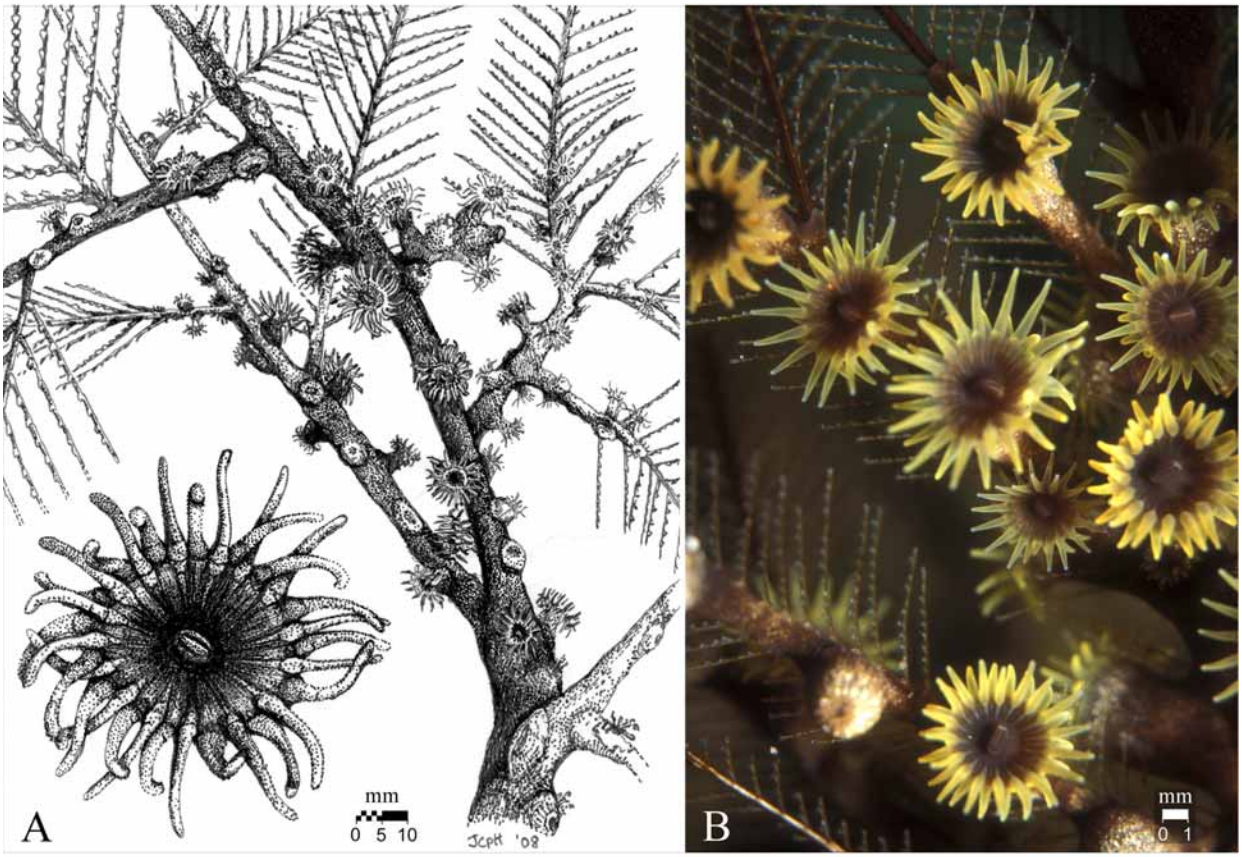

FIGURE 1. A. Line drawing showing *Isozoanthus antumbrosus* colonized *Dentitheca dendritica*. Scale bar is solid for colony and checkered for polyp detail inset. Drawing by J. Putnam H. of Florida State University. **B.** *In situ* macrophotograph of *Isozoanthus antumbrosus* with *Dentitheca dendritica* zooids visible in background.

Contracted polyps seal brown, mammiform, 2.2–4.2 mm in diameter and extending 3.3–9.9 mm above surrounding coenenchyme. Capitulum bearing 15–19 distinct ridges.

Internal Anatomy. Mesenteries 30–38, in typical macrocnemic arrangement (fifth mesentery complete; Fig. 2). Retractor muscles and mesoglea of macrocnemes minimal. Mesenterial filaments present. Marginal sphincter muscle endodermal and diffuse (Fig. 2). Ectoderm and mesoglea of column with many lacunae left behind by dissolved calcareous and siliceous particles (Fig. 2). Encircling sinus usually imperceptible.

Distribution. Found on coral reefs or rocky substrata at 1–60 m in Honduras, Panamá, Colombia, Curaçao (Netherlands Antilles), Tobago (Trinidad and Tobago), Suriname, and Dominica. Not observed free of *D. dendritica* colonies, which are found throughout the Caribbean but rarely dominate the benthic invertebrate community except in areas of consistently high current (*e.g.*, channel between Trinidad and Tobago).

Etymology. "Antumbra" is the astronomical term for the region from which an occulting body appears surrounded by the light source producing an annular eclipse. Coloration of the oral disk and tentacles recalls

the appearance of an annular solar eclipse. From the Latin noun *umbra*, feminine, meaning shadow; used here as the masculine adjective, *antumbrosus*, to agree with the Latinized *Isozoanthus*, masculine, from the Greek *anthos*, neuter, meaning flower.

Differential Diagnosis. Although colonies of *P. tunicans* and *I. antumbrosus* both associate with *D. dendritica* colonies, distinct morphological and molecular differences separate them (Swain *in press*). *Isozoanthus antumbrosus* polyps have darker colored column and coenenchyme; significantly greater (t = 23.4, df = 190, $p = 8.2 \times 10^{-58}$, n_{polyps} = 192, $n_{colonies}$ = 37) numbers of tentacles and capitular ridges (Fig. 3); significantly longer (t = 2.1, df = 28, $p = 5.3^{-4}$, n_{polyps} = 30, $n_{colonies}$ = 17) and wider (t = 2.1, df = 20, $p = 6.2^{-5}$, n_{polyps} = 22, $n_{colonies}$ = 16) polyp columns; and significantly larger (t = 2.0, df = 30, $p = 4.4^{-8}$, n_{polyps} = 32, $n_{colonies}$ = 20) oral disk diameters. Twelve nucleotide substitutions within the first internal transcribed spacer (ITS1) nuclear gene (Table 1) and seven nucleotide substitutions (and one deletion) within the 16S mitochondrial gene (Table 2) consistently differentiate *I. antumbrosus* from *P. tunicans*. No substitutions or deletions occur within 16S sequences between *P. tunicans* "white" *sensu* Sinniger *et al.* (2005) and *P. tunicans* or between *P. tunicans* "black" *sensu* Sinniger *et al.* (2005) and *I. antumbrosus* (Table 2).

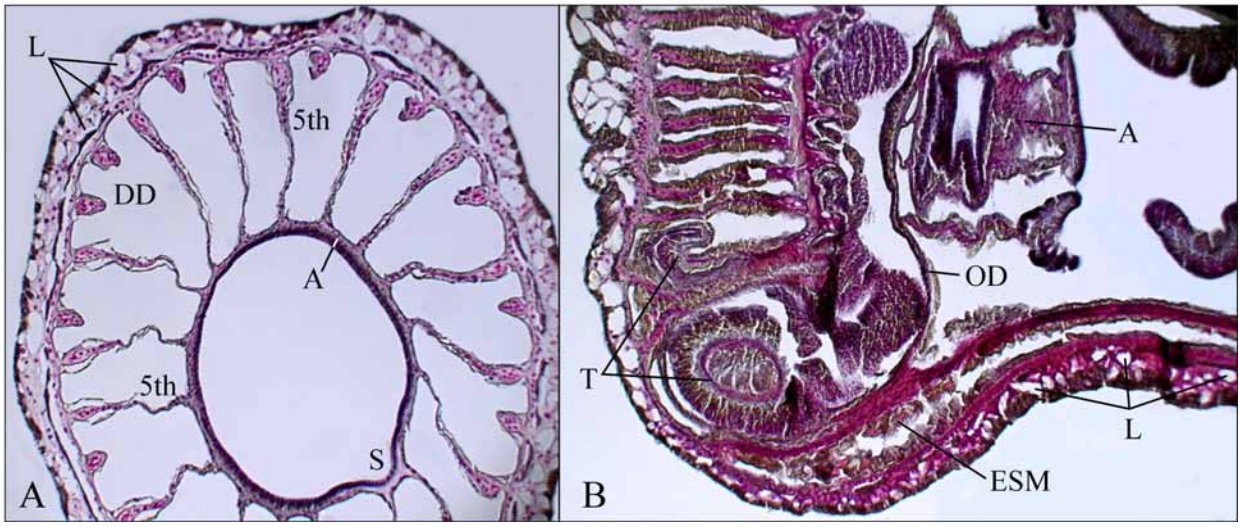

FIGURE 2. A. Cross-section of *Isozoanthus antumbrosus* polyp at the region of the actinopharynx (A) showing the dorsal directives (DD), siphonoglyph (S) and the macrocnemic (complete) fifth mesenteries (5th). Note the abundant lacunae (L) in the mesoglea and ectoderm. **B.** Longitudinal section of contracted *Isozoanthus antumbrosus* polyp at the region of the capitulum showing the endodermal sphincter muscle (ESM), actinopharynx (A), oral disk (OD) and tentacles (T). Note the abundant lacunae (L) in the mesoglea and ectoderm.

TABLE 1. Comparison between *Isozoanthus antumbrosus* and *Parazoanthus tunicans* of nucleotide sequences of the first internal transcribed spacer region of the ribosomal RNA nuclear gene (ITS1). Nucleotides that are identical to the first sequence are indicated by dots (·), missing data are indicated by question marks (?), and ambiguous nucleotides are indicated by standard letter code (M = A or C, K = G or T).

Species and collection location	ITS1 nucleotide position and identity													
	216	244	255	269	273	280	304	328	349	356	358	380	385	386
Parazoanthus tunicans Tobago	G	C	T	C	G	T	C	G	G	T	G	M	K	T
Parazoanthus tunicans Dominica	·	·	·	·	·	·	·	·	·	·	·	T	A	?
Parazoanthus tunicans Curaçao	·	·	·	·	·	G	·	·	·	·	·	G	A	·
Isozoanthus antumbrosus Dominica	A	T	G	T	A	·	T	A	A	A	A	A	A	C
Isozoanthus antumbrosus Panamá	A	T	G	T	A	·	T	A	A	A	A	A	A	C
Isozoanthus antumbrosus Curaçao	A	T	G	T	A	·	T	A	A	A	A	A	A	C

TABLE 2. Comparison between *Isozoanthus antumbrosus* and *Parazoanthus tunicans* of the nucleotide sequences of the 16S ribosomal RNA mitochondrial gene (16S). Nucleotides that are identical to the first sequence are indicated by dots (·), missing data are indicated by question marks (?), and gaps in the alignment are indicated by dashes (—).

Species and collection location	16S nucleotide position and identity							
	14	194	358	504	513	515	538	625
Parazoanthus tunicans Tobago	A	T	T	C	G	A	C	G
"*Parazoanthus tunicans* 'white'" Honduras	?	·	·	·	·	·	·	·
"*Parazoanthus tunicans* 'black'" Honduras	?	C	C	T	A	G	T	—
Isozoanthus antumbrosus Panamá	G	C	C	T	A	G	T	—

Other similar species. Swain (*in press*) demonstrated a strong tendency for closely related zoanthids (regardless of current taxonomy) to form symbioses with closely related host species (phylogenetic conservatism) and presented morphological and genetic evidence for a transoceanic distribution of some species. Therefore, any macrocnemic zoanthid species that forms associations with hydroids representing *Dentitheca* and its relatives must be differentiated. Members of *Parazoanthus gracilis* (Lwowsky 1913) form associations with hydroids of the genus *Plumularia* (*D. dendritica* was originally described as a *Plumularia*) in Japan but have tentacles numbering 36–42 (Lwowsky 1913) and distinct 16S and COI DNA sequences (Reimer *et al.* 2008). Members of *Parazoanthus dichroicus* Haddon & Shackleton, 1891b have 18 capitular ridges and form associations with hydroids of the genus *Plumularia* in the Torres Straits (Australia) but have polyps measuring 2.5 × 1.5 mm that are dichromatic when contracted (capitulum yellow) and have a "dichroic effect" on preserving alcohol (Haddon & Shackleton 1891b). Members of *Parazoanthus douglasi* Haddon & Shackleton, 1891b form associations with hydroids in the Torres Straits but are uniform sandy brown in color, have indistinct capitular ridges, and are facultative symbionts (Haddon & Shackleton 1891b). Members of *Parazoanthus elongatus* McMurrich, 1904 form associations with hydroids in Chile but have a distinct cuticle and thick mesoglea, mesenteries numbering 28–32, and polyps measuring 15–20 mm in length (McMurrich 1904). Members of *Epizoanthus patagonichus* Carlgren, 1899 form associations with hydroids in Chile and Argentina (Cutress & Pequegnat 1960) and have polyps measuring 5–6 mm in length and 4.5–5.0 mm in diameter with 32 mesenteries but have rust-red tentacles and are facultative symbionts (McMurrich 1904).

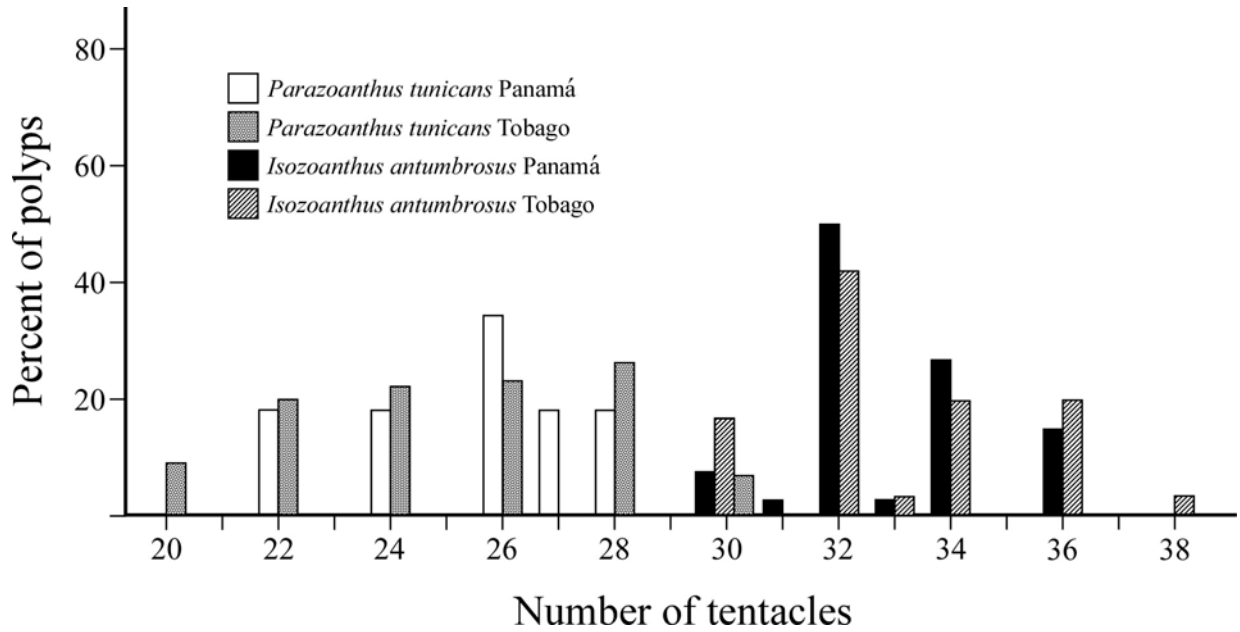

FIGURE 3. Comparison of tentacle numbers observed on polyps of *Isozoanthus antumbrosus* (n_{polyps} = 80, $n_{colonies}$ = 18) and *Parazoanthus tunicans* (n_{polyps} = 112, $n_{colonies}$ = 19) in Panamá and Tobago.

Remarks. Symbiosis with *D. dendritica* dominates the life history of *I. antumbrosus*. Although the position of a symbiotic relationship along the parasitism–mutualism continuum cannot be decided on the basis of one-time observations, examination of many holobionts may provide clues (*e.g.*, Beaulieu 2001) that can help shape future experiments. Of more than 200 observed associations, in only one did an *I. antumbrosus* colony completely cover a *D. dendritica* colony. Usually the coenenchyme of *I. antumbrosus* colonies envelops the central and secondary axial branches of *D. dendritica* colonies but not the finest pinnate branches, where the hydroid zooids are located (Nutting 1900). Repeated observations of associations with live hydroid colonies that do not cover the critical zooid supporting branches suggest that the *I. antumbrosus*-*D. dendritica* symbiosis is not parasitic, but the definitive experiments have not yet been completed. By comparison, *P. gracilis* colonies associated with hydroids in Izu, Japan, seem to be aggressive parasites, as five years of repeated photographs show hydroid zooids steadily disappearing beneath the coenenchyme of *P. gracilis* (pers. comm., J. Reimer).

In contrast to the Caribbean sponge-symbiotic zoanthids, which have largely nonoverlapping suites of host sponge species (Swain & Wulff 2007), the Caribbean hydroid-symbiotic zoanthids share the same single host species (Swain *in press*), and colonizations by *I. antumbrosus* and *P. tunicans* are observed on the same individual host. Contact regions between the two species often include a bare zone of exposed hydroid axial skeleton and reduced, damaged, or contracted zoanthid polyps. Competition among sponge-symbiotic zoanthids has only been documented in a single study, and the outcome of that competitive bout was decidedly uncertain; different outcomes were observed at different times across different regions of the zoanthid colonies (West 1979).

The genera of Macrocnemina are currently uncertain and include distinct subdivisions within genera (Sinniger *et al.* 2005, Reimer *et al.* 2008, Swain *in press*) and close evolutionary relationships among some species currently assigned to separate genera (Swain *in press*). The morphology of *I. antumbrosus* is consistent with the genus *Isozoanthus* (fifth mesentery complete, marginal sphincter muscle endodermal, and mesogloeal ring-sinus inconspicuous), but molecular phylogenetics (Sinniger *et al.* 2005, Reimer *et al.* 2008, Swain *in press*) indicates that the closest known relatives are representatives of the genus *Parazoanthus* (fifth mesentery complete, marginal sphincter muscle endodermal, and mesogloeal ring-sinus conspicuous). Sinniger *et al.* (2005), Reimer *et al.* (2008), and Swain (*in press*) indicate that the clade of zoanthids that includes *I. antumbrosus* is distinct from the clade of zoanthids that includes the type species of the genus *Parazoanthus* (*Parazoanthus sensu stricto*: Reimer *et al.* 2008), suggesting that *I. antumbrosus* is not a representative of *Parazoanthus*. Because the inconsistency between morphological and molecular data cannot be resolved with currently available data, I accept the morphological definition of *Isozoanthus* here, with the stipulation that it will probably change to a different (not yet described) genus in the future.

Key to hydroid and sponge-symbiotic zoanthids of the greater Caribbean region

(1) Host associations:
- Sponges 2
- Hydroids..... 3

(2) Color:
- Red/maroon polyps and coenenchyme 4
- Golden-brown polyps and coenenchyme..... 5
- Orange, yellow, salmon, or off-white polyps and coenenchyme..... 6

(3) Color:
- White coenenchyme with golden-brown tentacles 7
- Seal-brown coenenchyme with golden-brown tentacles 8

(4) Tentacles and mesenteries number to 24 and capitular ridges number to 12, polyps single or in small groups of 2–3. Symbiont of sponges representing the orders Halichondrida or Agelasida ..... *Parazoanthus puertoricense*

(5) Colony morphology:
- Polyps consistently single or in small groups of 2–3 9

- Polyps form chains early in ontogeny of the colony but may fragment into single polyps or small groups of 2–3 polyps in older colonies 10
- Coenenchyme stolon-like and buried beneath surface of host sponge. Polyps able to retract completely beneath surface of host sponge..... 11

(6) Polyp morphology:

- Tentacles and mesenteries number to 26 and capitular ridges to 13. Symbiont of sponges representing the orders Agelasida, Halichondrida, or Poecilosclerida ..... *Parazoanthus swiftii*
- Tentacles and mesenteries number to 32 and capitular ridges to 16. Symbiont of sponges representing the order Halichondrida ..... *Parazoanthus axinellae*

(7) Tentacles and mesenteries number to 30 and capitular ridges to 15. Symbiont of the hydroid *Dentitheca dendritica* ..... *Parazoanthus tunicans*

(8) Tentacles and mesenteries number to 38 and capitular ridges to 19. Symbiont of the hydroid *Dentitheca dendritica* ..... *Isozoanthus antumbrosus*

(9) Tentacles and mesenteries number to 28 and capitular ridges to 14. Symbiont of sponges representing the orders Haplosclerida or Hadromerida ..... *Parazoanthus parasiticus*

(10) Tentacles and mesenteries number to 20 and capitular ridges to 10. Symbiont of sponges representing the order Haplosclerida ..... *Parazoanthus catenularis*

(11) Tentacles and mesenteries number to 12 and capitular ridges to 12. Symbiont of sponges representing the order Haplosclerida ..... *Epizoanthus cutressi*

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