

Isozoanthus primnoidus, a new species of zoanthid (Cnidaria: Zoantharia) associated with the gorgonian *Callogorgia verticillata* (Cnidaria: Alcyonacea)

M. Carreiro-Silva^{1*}, A. Braga-Henriques¹, I. Sampaio¹, V. de Matos¹, F. M. Porteiro¹, and O. Ocaña²

¹Department of Oceanography and Fisheries, University of the Azores, 9901-862 Horta, Portugal

²Departamento de Biología Marina, Fundación Museo del Mar, Autoridad Portuaria de Ceuta, Muelle Cañonero Dato s/n 51001, Ceuta (North Africa), Spain

*Corresponding Author: M. Carreiro-Silva, tel: +351 292 200 400; fax: +351 292 20 0411; e-mail: mcsilva@uac.pt

Carreiro-Silva, M., Braga-Henriques, A., Sampaio, I., de Matos, V., Porteiro, F. M., and Ocaña, O. *Isozoanthus primnoidus*, a new species of zoanthid (Cnidaria: Zoantharia) associated with the gorgonian *Callogorgia verticillata* (Cnidaria: Alcyonacea). – ICES Journal of Marine Science, doi:10.1093/icesjms/fsq073.

Received 31 August 2009; accepted 11 April 2010.

In the Azores, Northeast Atlantic, an undescribed epizoan zoanthid is often found in association with the cold-water gorgonian *Callogorgia verticillata* at 110–800 m depth. This zoanthid was identified as a new species, *Isozoanthus primnoidus* sp. nov., based on morphological and anatomical characters of the polyps and type of cnidae. The distinguishing features of *I. primnoidus* are coenenchyme, column, and oral disc light brown, with short, translucent tentacles. Contracted polyps have column diameter up to 3 mm and height up to 2 mm. Ectoderm and outer mesogloea are densely encrusted with mineral particles and gorgonian sclerites. Capitulum bears a maximum of 14 distinctive ridges. *Isozoanthus primnoidus* was associated with 17% of *C. verticillata* colonies studied, and covered $14 \pm 5\%$ of the gorgonian colony. There was strong evidence of a parasitic relationship whereby *I. primnoidus* progressively eliminates gorgonian tissue and uses the gorgonian axis for structure and support, and sclerites for protection.

Keywords: cold-water corals, deep-sea, Gorgonacea, octocoral, parasitism, Parazoanthidae, Primnoidea, symbiosis, zoanthid.

Introduction

Zoanthids are a group of cnidarians that form symbiosis with octocorals in shallow and deep-water environments (Ryland *et al.*, 2004). Several zoanthid species have been reported to grow as pseudocolonies on different gorgonians in the North Atlantic (Storm, 1901; Dons, 1944; Carlgren, 1945, Buhl-Mortensen and Mortensen, 2004). The zoanthid *Epizoanthus norvegicus* (Koren and Danielssen, 1877) has been observed as a commensal of *Paragorgia arborea* (Dons, 1944) and *Primnoa resedeaformis* on the Norwegian coast (Carlgren, 1945). In the Northeast Channel, an unidentified species of the genus *Epizoanthus* has been described as a parasite of *Primnoa resedeaformis* (Buhl-Mortensen and Mortensen, 2004; Mortensen *et al.*, 2005).

Zoanthids are one of the least studied groups of cnidarian. The paucity of standardized morphological characters and difficulties in examining internal morphology has challenged discrimination among species (Sinniger *et al.*, 2005; Sinniger and Häussermann, 2009) and required the use of genetic techniques. Recent molecular phylogenetic analyses show disagreement on taxonomic relationship among genera and species inferred from morphological characters and molecular data (Reimer *et al.*, 2004, 2006; Sinniger *et al.*, 2005; Swain, 2009a). However, phylogenetic studies on zoanthids have often overlooked important morphological characters (e.g. cnidom, internal anatomy of the musculature, and mesenterial arrangement) and this may be in part responsible for the disagreement between classical taxonomic studies and molecular genetics studies.

In the Azores, *Callogorgia verticillata* (Pallas, 1766) is a common gorgonian species on seamounts and island slopes. It belongs to the family Primnoidea, having a fan-shaped, branching morphology. Epizoan zoanthids have often been observed attached to colonies of *C. verticillata*, but the identity of this zoanthid and the nature of the relationship between the two species have never been established. The objectives of this study were (i) to identify this undescribed zoanthid using different morphological characters (polyp morphology, internal anatomy, and type of cnidae), and (ii) to investigate the nature of this association.

Material and methods

Callogorgia verticillata colonies and associated zoanthids were observed and photographed *in situ* in the Azores, Northeast Atlantic, 38°30'N 28°37'W, depth 350 m, on 9 September 2008. Photographic quality did not allow a close enough view of the zoanthid polyps for precise measurements of column and tentacles. Specimens used for determination of the prevalence of association, gorgonian area covered by zoanthids, as well as morphological and histological analysis were obtained from bycatch material from longline fishing cruises with RV “Arquipélago” (ARQDAÇO campaigns) and from the local longline fleet. We analysed 53 *C. verticillata* colonies collected at depths between 110 and 800 m from 12 locations in the Azores region (Figure 1). Each zoanthid specimen was split into two fragments and preserved in 10% formalin for histological analysis and 70–95% ethanol for future molecular studies.

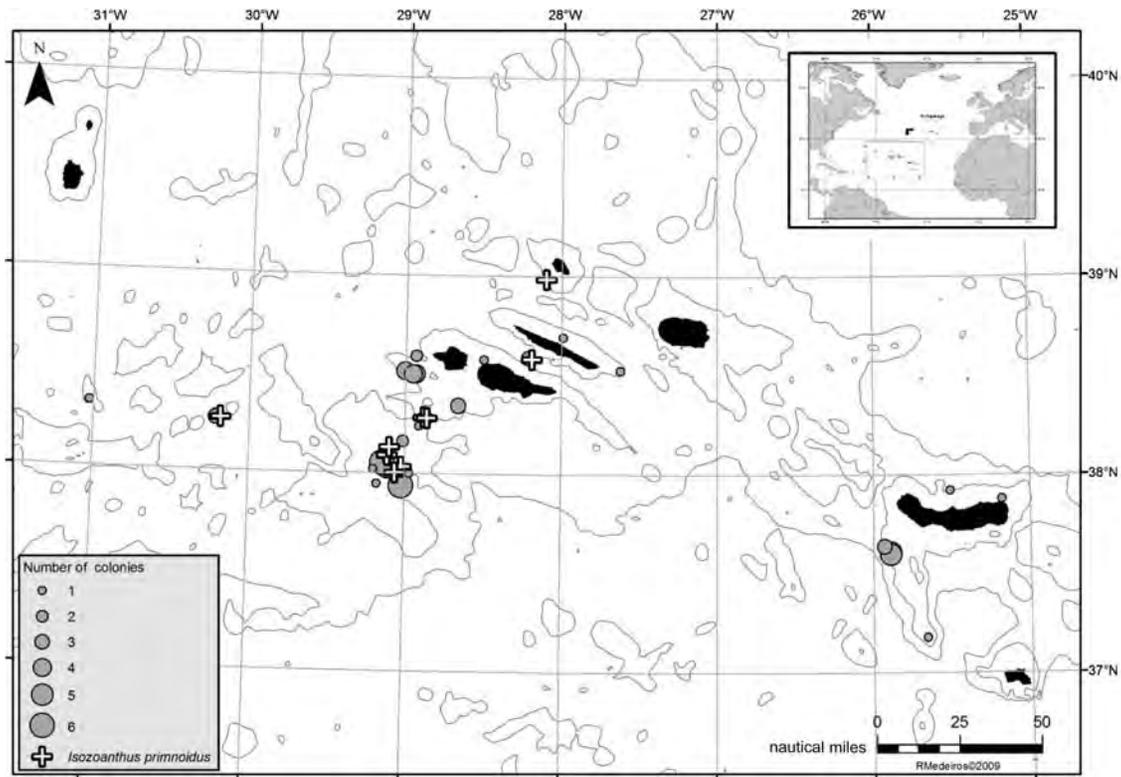


Figure 1. Geographic location of *Callogorgia verticillata* collection sites. Crosses indicate locations where the zoanthid *Isozoanthus primnoidis* was found on *C. verticillata*; circles indicate locations where *C. verticillata* was found, but no *I. primnoidis* was present. The size of the circles is proportional to the number of colonies obtained in each location.

Morphological data were obtained from photographs and histological sections. Observations of zoanthid colonies were made using a dissecting microscope Leica MZ 16FA, and measurements taken using Image-J 1.40 software (US National Institutes of Health). The tissue of the gorgonian host *C. verticillata* was also examined. Observed sclerites within the zoanthid specimens were compared with gorgonian sclerites after tissue removal using a sodium hypochlorite solution. Individual polyps dissected from zoanthid colonies were decalcified for 4 h with RDF Mild Decalcifier (CellPath Ltd, UK) and desilicified for 2 h in 20% hydrofluoric acid, then washed in distilled water. Polyps were dehydrated in ethanol, cleared with xylene, embedded in paraffin, and sectioned. Serial 8- μ m longitudinal and cross sections of polyps were stained with Mallory Trichrome. Cross sections were cut transversely across the column, at the level of the actinopharynx. Longitudinal sections were cut across the marginal sphincter muscle.

Undischarged nematocysts were identified and measured in squashed tissue preparations from the tentacles, column, pharynx, and mesenterial filaments of three preserved specimens using light microscopy ($\times 1000$, oil immersion). Cnidae were classified according to the terminology used by Ryland and Lancaster (2004).

Results

Zoanthid taxonomical description

Suborder Macrocnemina Haddon and Shackleton (1891)

Family Parazoanthidae Delage and Hérouard (1901)

Genus *Isozoanthus* Carlgren in Chun (1903)

Isozoanthus primnoidis new species.

Material examined

Holotype. Atlantic Ocean, Condor seamount, 38°32'N 29°06'W, depth 293 m, 26 June 2008, associated with *C. verticillata*, DOP-804. Paratypes. Atlantic Ocean, Condor seamount, 38°08'N 29°05'W, depths 274–293 m, 17 September 2006, associated with *C. verticillata*, DOP-3243; Atlantic Ocean, Açor Bank, 38°17'N 28°52'W, depth 368 m, 11 September 2007, associated with *C. verticillata*, DOP-3051. Type specimens were deposited in the reference collection of the Department of Oceanography and Fisheries, University of the Azores.

Description

Colony morphology

Colonial zoanthid found at the surface of *C. verticillata* (Figure 2a). In life, capitulum and oral disc light brown with short translucent tentacles (Figure 2b). In preserved samples, polyps light brown connected by thin coenenchyme growing over the gorgonian axis (Figure 2c and d). Polyps occur at intervals of approximately 1–1.5 polyp diameters, often in an orthogonal arrangement.

External anatomy

In preserved specimens, contracted polyps, 1.8–3.0-mm diameter and extending 1.0–2.1 mm above the coenenchyme; proximal part of the polyp slightly broader than distal part (Figure 3a). Ectoderm and outer mesogloea densely encrusted with mineral particles, gorgonian sclerites, foramineferan tests, and sponge spicules, and therefore appearing “flecked” with white (Figure 3a and b); sclerites were confirmed to be from *C. verticillata* (Figure 3b and c).

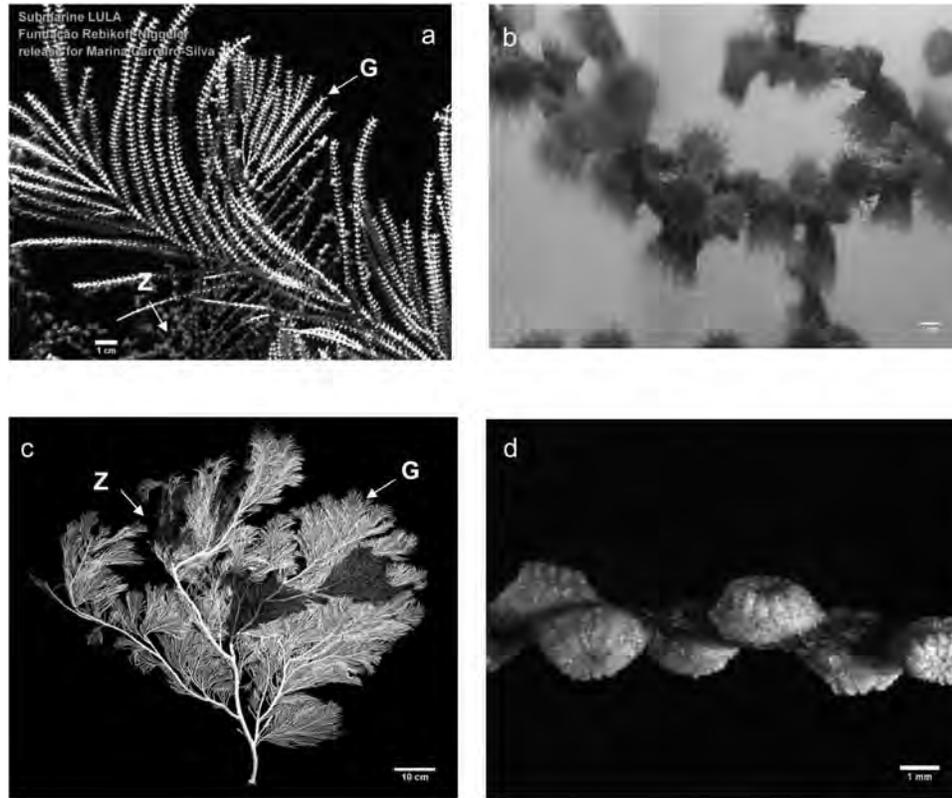


Figure 2. (a–d) *Isozoanthus primnoides* (Z) on *Callogorgia verticillata* (G) colonies. (a) *In situ* photograph of living colonies; (b) close-up of living *I. primnoides*; (c) preserved colony of *C. verticillata* colonized by *I. primnoides*; (d) close-up of preserved *I. primnoides* on the gorgonian axis.

Capitulum bearing 12–14 distinct ridges. Thin cuticle present in contact areas with the gorgonian.

Internal anatomy

Mesenteries in macrocnemic arrangement, but the state of retraction did not allow us to confirm the number. Musculature poorly developed; retractor muscles not present in mesenteries; parieto-basilar muscles are weak, forming very small pennons (Figure 4a); stronger ectodermal musculature in tentacles (Figure 4b). Sphincter is endodermal but short and concentrates in the upper part of the column, forming a wide sinus (Figure 4c); siphonoglyph conspicuous and prominent. Absence of lacunae canals system and encircling sinus. Mesogloea of the body wall presents a large number of lacunae left behind by dissolved mineral particles and host sclerites (Figure 4d). Lacunae are less numerous and larger in the connected coenenchyme (Figure 4e). Gonads associated with mesenterial filaments, with ova and spermatozooids (Figure 4f). No zooxanthellae.

Cnidae

Cnidom spycysts, basitrichs, holotrichs, microbasic b-mastigophores, and microbasic p-mastigophores appear in Figure 5. See Table 1 for sizes and distributions. Large holotrichs (holotrich 1) were the most characteristic nematocyst observed in this species, and were very common in the ectoderm of the body wall.

Ecology and distribution

Found on the surface of *C. verticillata* colonies at depths between 110 and 800 m in the Azores region, Northeast

Atlantic (Figure 1), with ocean temperatures ranging from 10°C to 15°C.

Etymology

Species named for type species association with a living gorgonian of the family Primnoidea. The origin of the word primnoidea comes from the Greek name Prynno, feminine, one of the Oceanids, daughters of the Greek mythological god Oceanus, used here as the masculine adjective, *primnoides*, to agree with the Latinized *Isozoanthus*, masculine, from the Greek *anthos*, neuter, meaning flower.

Characterization of the association

Isozoanthus primnoides was associated with 17% of *C. verticillata* colonies studied (9 zoanthid-bearing colonies/53 total colonies), and covered $14 \pm 5\%$ (mean \pm s.d., $n = 6$) of the gorgonian colony. The largest concentration of zoanthid-bearing *C. verticillata* occurred on Açor Bank and Princesse Alice Bank.

The zoanthid coenenchyme often covered the central and secondary branches of colonies up to the finest pinnate branches (Figure 2c). Gorgonian tissue was completely absent from most areas covered by the zoanthid. However, on partially colonized gorgonian branches, we observed “older” areas where gorgonian tissue was absent (Figure 2d), and more recently colonized areas where zoanthid polyps overgrew gorgonian polyps (Figure 3d). Unusual agglomerations of gorgonian polyps along the axis were observed next to areas overtaken by zoanthids (Figure 3e).

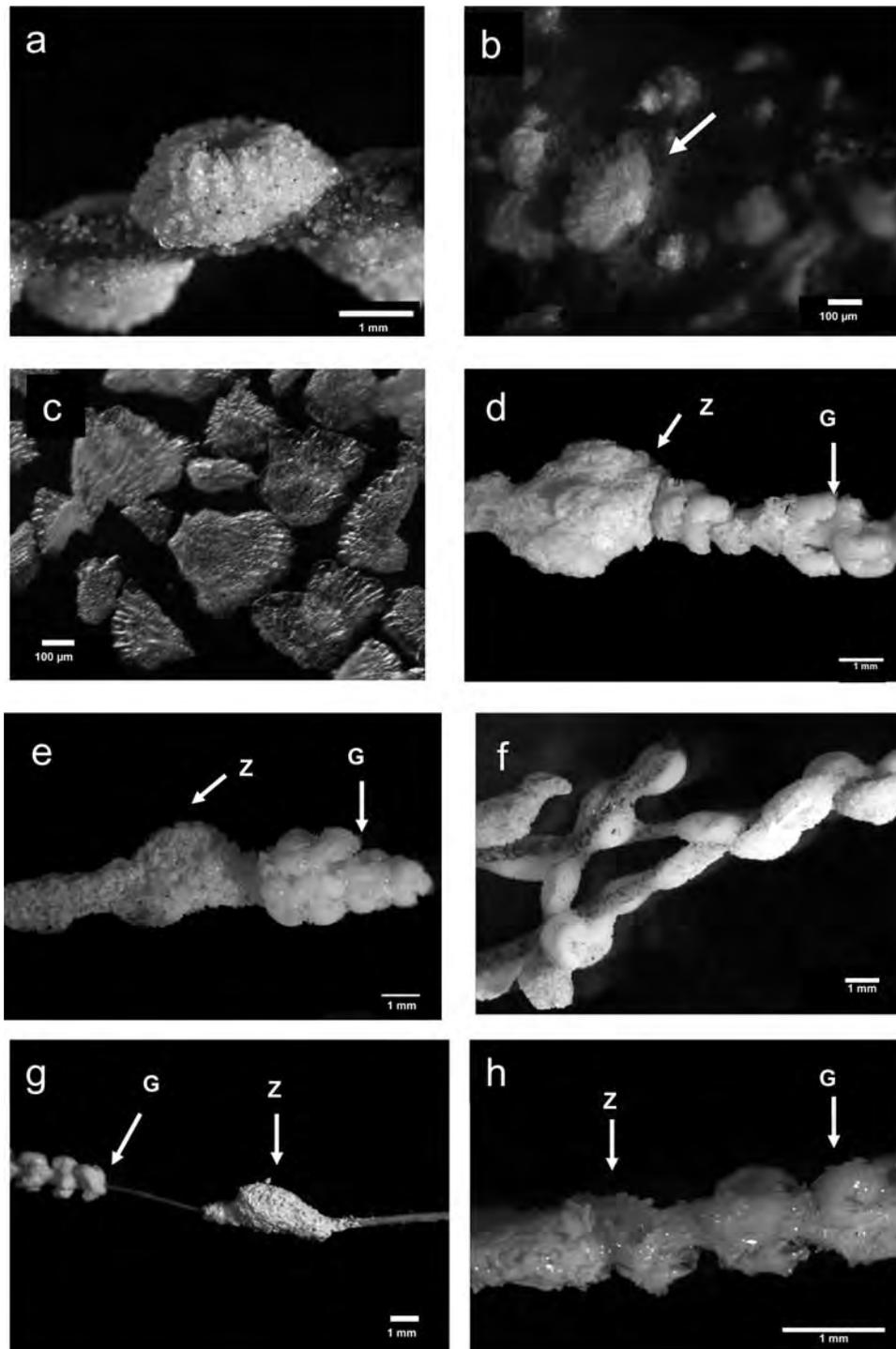


Figure 3. (a–h) Details on the association between *Isozoanthus primnoides* (Z) and the gorgonian *Callogorgia verticillata* (G). (a) Encrustations in *I. primnoides* coenenchyme; (b) close-up of *I. primnoides* coenenchyme showing *C. verticillata* sclerites (arrow); (c) sclerites of *C. verticillata* for comparison with (b); (d) zoanthid polyp overgrowing gorgonian polyps; (e) atypical concentration of gorgonian polyps in the area next to the zoanthid polyp; (f) anastomosis of gorgonian branches produced by *I. primnoides* coenenchyme; (g) area of the gorgonian axis without coenenchyme showing a zoanthid polyp; (h) juvenile *I. primnoides* among *C. verticillata* polyps.

Discussion

Taxonomy

Based on histological analysis, this new zoanthid species was placed in the family Parazoanthidae because of the position of the sphincter muscle in the endoderm. In contrast, in the family

Epizoanthidae, the sphincter muscle is mesogloal (Delage and Hérouard, 1901).

Species of the family Parazoanthidae frequently form symbiotic associations with other marine invertebrates (Sinniger and Häussermann, 2009). Well-established species in the genus

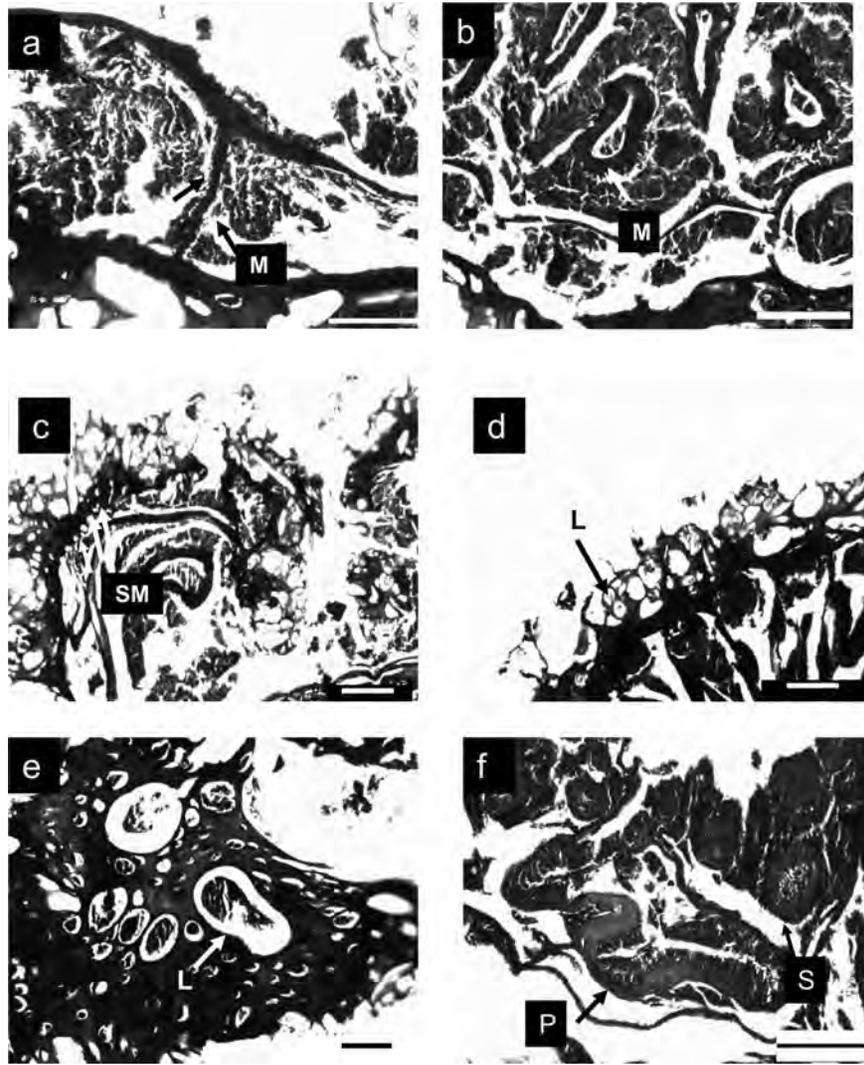


Figure 4. (a–f) Histological sections of *Isozoanthus primnoidus*. (a) Mesenterial musculature (M) forming very small pennons (arrow); (b) tentacles musculature (M); (c) endodermal sphincter muscle (SM) forming a wide sinus; (d) lacunae in the wall of the polyp (L); (e) lacunae in the coenenchyme (L); (f) pharynx (P) and male gonads (S). Cross sections of contracted polyps are shown in (a), (b), (d), and longitudinal sections in (c), (e), and (f). Scale bar = 100 μm .

Parazoanthus are known to be associated with sponges (Swain and Wulff, 2007). Another genus, *Gerardia* (*Savalia*), can be parasitic on gorgonians, black corals, and even hydroids, and the damage against the host is quite evident (see Ocaña and Brito, 2004). *Isozoanthus* is an encrusting genus not generally considered as parasitic (Carlgren, 1913, 1927; Swain, 2009b).

In contrast to members of the genus *Gerardia*, the zoanthid examined in this study does not secrete its own scleroprotein axis (see Ocaña *et al.*, 2004, 2007). In addition, the lack of lacunae canal systems and encircling sinus placed the studied specimens in the genus *Isozoanthus* (members of the genus *Parazoanthus* have these two morphological characters).

There are marked differences in morphological features and cnidom characters between *I. primnoidus* and rocky or shell-encrusting species belonging to the genus *Isozoanthus* (described in Carlgren, 1913, 1927). The great dimensions of the ectoderm nematocysts and the morphological structure of the body wall distinguishes *I. primnoidus* from most species of *Isozoanthus*. Other non-parasitic bathyal species have large

nematocysts in the body wall (e.g. *I. multinsulosus* Carlgren, 1913, *I. ingolfti* Carlgren, 1913, *I. valdiviae* Carlgren, 1924, *I. arenosus* Carlgren, 1924, and *I. africanus* Carlgren, 1924) but do not have the peculiar mesogloae structure found in *I. primnoidus*. The zoanthid *Isozoanthus antumbrosus* Swain (2009b) found in association with the hydroid *Dentitheca dendritica* is a shallow-water species living in tropical Atlantic waters, but with a polyp shape similar to that of *I. primnoidus* (Swain, 2009b). Despite differences in polyp dimensions, the two species have a similar way of growing along the host and similar polyp aggregations (see Swain, 2009b, Figure 1). The internal anatomy indicates a stronger sphincter muscle in *I. primnoidus* than in *I. antumbrosus*, but similar mesogloae structure of the body wall.

Recent molecular analyses have shown a strong phylogenetic conservatism in the evolution of host associations with symbiotic zoanthids (Sinniger *et al.*, 2005; Swain, 2009a), and substratum specificity has been suggested as an additional taxonomic criterion (Sinniger *et al.*, 2005; Reimer *et al.*, 2008). *Isozoanthus*

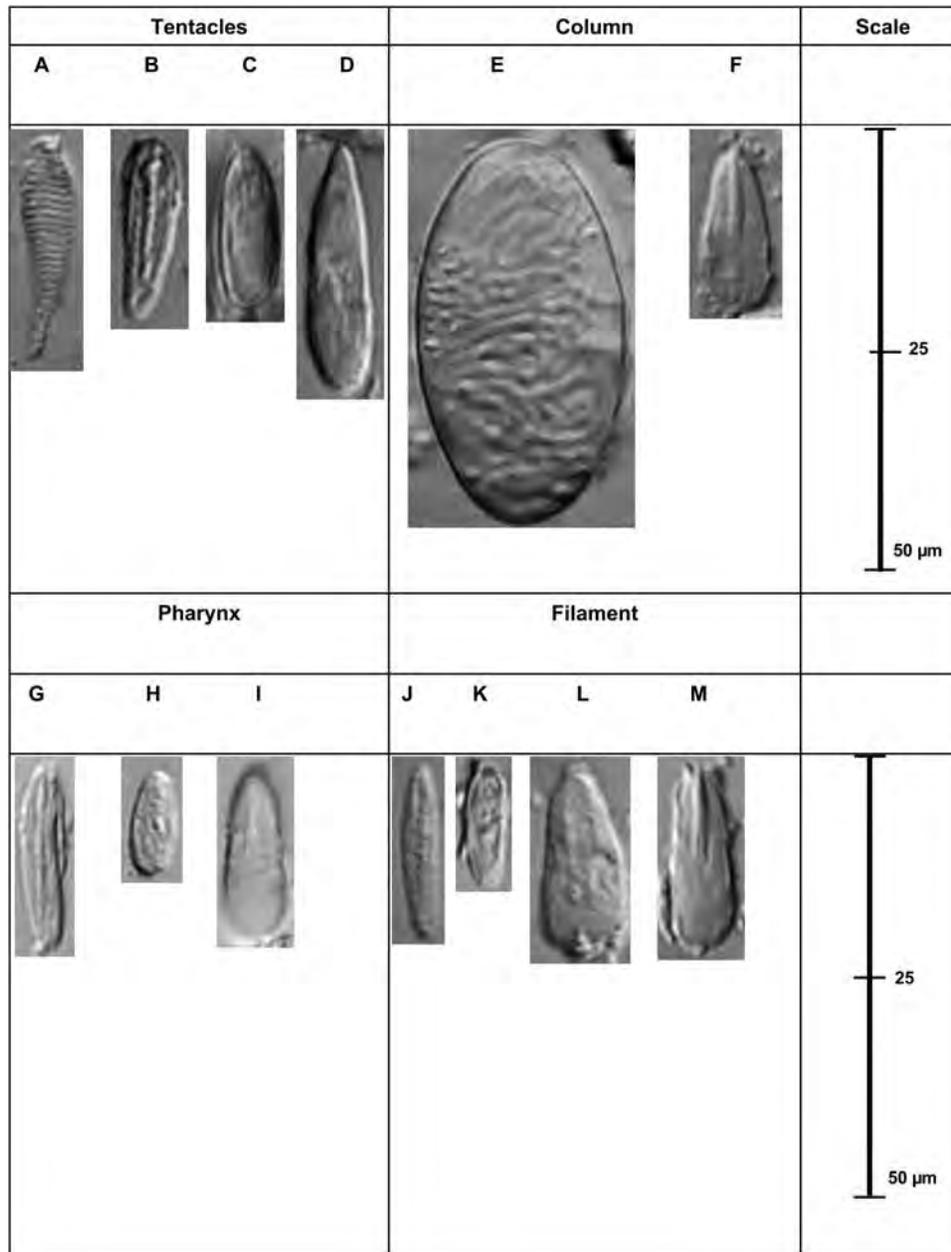


Figure 5. Cnidae in the tentacles, column, pharynx, and mesenterial filaments of *Isozoanthus primnoidus*; letters correspond to cnidae listed in Table 1.

primnoidus is not the first record of parasitic zoanthid on primnoidae gorgonians. However, the zoanthid identified as *Epizoanthus* sp., recorded on *Primnoa resedaeformis* (Buhl-Mortensen and Mortensen, 2004; Mortensen et al., 2005) displays important shape and size differences from our material. Its colour and larger size makes it closer to *Epizoanthus norvegicus*, a well-known *Primnoa*- and *Paragorgia*-encrusting species. Nevertheless, the species awaits detailed taxonomic study and has some resemblance to the species *Mesozoanthus fossii* (Sinniger and Häussermann, 2009) from Chile, which can grow on dead *Primnoella chilensis* (see Sinniger and Häussermann, 2009), and *Parazoanthus lucificum* from California, which grows on *Muricea californica* Aurivillius, 1931 (Cutress and Pequegnat, 1960). Future molecular analysis will help to clarify the

phylogenetic relationship between the species described here and other zoanthid species.

Symbiotic association

The term “symbiosis” is used here to refer to different organisms living together (Saffo, 1992). The term “parasitism” is used to describe a relationship where the symbiont benefits but the host is harmed.

For *I. primnoidus* and its gorgonian hosts, several pieces of evidence indicate that the presence of the zoanthid causes harm to the host. First, there is evidence that *I. primnoidus* can cover gorgonian polyps and coenenchyma and change the position of gorgonian polyps along the axis, resulting in the elimination of the gorgonian tissue. Second, *I. primnoidus* incorporates gorgonian sclerites in its

Table 1. Types, relative abundances, and sizes of cnidae of *Isozoanthus primnoidus*.

Tissue	Cnidae type	N	n	Size
Tentacles	vc; spirocysts (A)	3/3	15	15–25 × 3–4
	vc; basitrichs (B)	3/3	30	15–18 × 3–4
	rc; p-mastigophore (C)	3/3	20	16–24 × 5–6
	r; b-mastigophore (D)	1/3	1	30 × 6
Column	vc; holotrich 1 (E)	3/3	30	30–40 × 15–20
	r; p-mastigophore (F)	1/3	1	17 × 6
Pharynx	c; basitrich (G)	3/3	30	15–17 × 3–4
	uc; holotrich 2 (H)	3/3	10	9–11 × 3–4
Filament	rc; p-mastigophore (I)	3/3	20	15–20 × 5–6
	c; basitrich (J)	3/3	20	13–19 × 3–3.5
	uc; holotrich 2 (K)	3/3	10	9–12 × 3–4
	rc; b-mastigophore (L)	3/3	20	14–20 × 6–7
	vc; p-mastigophore (M)	3/3	30	15–20 × 5–7

N, ratio of the number of individuals examined having a particular type of cnidae to the total number examined; n, the number of measured capsules. Measurements, in μm , are given as a range of length × width. Capital letters refer to images in Figure 5. Lower-case letters indicate the relative abundance: vc (very common); c (common); rc (rather common); uc (uncommon); r (rare).

tissue. These observations suggest that *I. primnoidus* progressively eliminates gorgonian tissue and uses the gorgonian axis for structure and support, and sclerites for protection. Reaching the organic axis is the final colonization effect reported for other zoanthids or actinarians associated with gorgonians, pennatularians, or antipatharians (Ocaña *et al.*, 1995; Ocaña and Brito, 2004).

Isozoanthus primnoidus appears to expand and progressively colonize the gorgonian branches by asexual colony multiplication. We commonly observed the anastomosis (i.e. branch fusion) of neighbouring gorgonian branches produced by the coenenchyma of the zoanthid colony (Figure 3f), which suggests that this may be a mechanism used by the zoanthid to progress the colonization of the gorgonian.

Our observations do not allow us to determine the ingestion of gorgonian tissue or the adsorption of substances from the host by the zoanthid, but there is substantial evidence of harm done by the zoanthid to the host. Therefore, we feel that parasitism best describes this association. Further sample collection and aquarium observations will help clarify the nature of this association.

A similar parasitic relationship between a zoanthid and a deep-sea gorgonian has been described for *Epizoanthus* sp. and the gorgonian *P. resedeaformis* in the Northern Channel (Buhl-Mortensen and Mortensen, 2005; Mortensen *et al.*, 2005). Those authors observed *Epizoanthus* sp. gradually overgrowing and killing *P. resedeaformis*. Mortensen *et al.* (2005) suggested that the degree of incidence of this zoanthid is related to gorgonian damage by fishing, with *Epizoanthus* sp. colonizing tissue-abraded areas and taking over large parts of the gorgonian skeleton. From our data, we cannot determine whether a similar relationship exists between gorgonian damage caused by fishing and the degree of colonization by *I. primnoidus*. All *C. verticillata* specimens were collected within fishing grounds, so we have no comparison with areas outside fishing areas. We did observe zoanthid polyps colonizing areas of the gorgonian axis with no tissue (Figure 3g), possibly indicating that damaged gorgonian branches may be more susceptible to colonization by zoanthids. Nevertheless, we also observed a juvenile stage of *I. primnoidus* between two clusters of *C. verticillata* polyps (Figure 3h),

suggesting that they can also colonize areas of the colony that are not damaged, probably by sexual reproduction. Future studies comparing number of colonized *C. verticillata* colonies inside and outside fishing areas will help to clarify the effect of fisheries on the degree of colonization by zoanthids.

Acknowledgements

This study was supported by the EU-funded CoralFISH project (FP7-ENV-2007-1 213144), Fundação para a Ciência e a Tecnologia (M. C-S, SFRH-BPD-34634–2007) and Direcção Regional para a Ciência e a Tecnologia (AB-H, M3.1.2/F/016/2008). We thank bottom longline fishers. In particular Jorge Gonçalves, and the chief scientists (Gui Menezes and Diana Catarino) of ARQDAÇO campaigns for providing specimens. We are also grateful to Department of Oceanography and Fisheries technicians, Ricardo Medeiros for map elaboration and Domitilia Rosa for her help with the histological techniques. The Rebikoff-Niggeler Foundation is gratefully acknowledged for permission to use their photographs.

References

- Buhl-Mortensen, L., and Mortensen, P. B. 2004. Symbiosis in deep-water corals. *Symbiosis*, 37: 33–61.
- Buhl-Mortensen, L., and Mortensen, P. B. 2005. Distribution and diversity of species associated with deep-sea gorgonian corals off Atlantic Canada. *In* Cold-water Corals and Ecosystems, pp. 849–879. Ed. by A. Freiwald, and J. M. Roberts. Springer, Berlin. 1244 pp.
- Carlgren, O. 1913. Zoantharia. The Danish Ingolf Expedition, vol. 5, part 4, pp. 1–65.
- Carlgren, O. 1927. Actinaria and Zoantharia. *In* Further Zoological Results of the Swedish Antarctic Expedition 1901–1903, under the direction of Dr. Otto Nordenskjöld, 2: 1–102.
- Carlgren, O. 1945. Polyptydyr (Coelenterata). III. Koraldyr. Danmarks Fauna, 51 BD. Kobenhavn. 168 pp.
- Chun, C. 1903. Aus den Tiefen des Weltmeeres. Schilderungen von der Deutschen Tiefsee-Expedition. von Gustav Fisher, Jena. 592 pp.
- Cutress, C. E., and Pequegnat, W. E. 1960. Three new species of zoantharia from California. *Pacific Science*, 14: 89–100.
- Delage, Y., and Hérouard, E. 1901. Traité de Zoologie Concrète, vol. II. Les Coelentérés. Reinwald, Paris. 848 pp.
- Dons, C. 1944. Norges korallrev. Det Kongelige Norske Videnskabers Selskabs Forhandling, 16: 37–82.
- Haddon, A. C., and Shackleton, A. M. 1891. A Revision of the British Actinariae. Part II: The Zoanthae. *Scientific Transactions of the Royal Dublin Society*, 4: 609–672.
- Mortensen, P. B., Buhl-Mortensen, L., Gordon, D. C., Fader, G. B. J., McKeown, D. L., and Fenton, D. G. 2005. Effects of fisheries on deepwater gorgonian corals in the Northeast Channel, Nova Scotia. *In* Benthic Habitats and the Effects of Fishing, pp. 369–382. Ed. by B. W. Barnes, and J. P. Thomas. American Fisheries Society Symposium, 41.
- Ocaña, O., and Brito, A. 2004. A review of Gerardiidae (Anthozoa: Zoantharia) from the Macaronesian Islands and the Mediterranean Sea with the description of a new species. *Revista de la Academia Canaria de Ciencias*, 3–4: 159–189.
- Ocaña, O., Brito, A., González, G., and Herrera, R. 2007. Additions in relation to Gerardiidae from the Macaronesian waters and the Mediterranean Sea (Anthozoa: Zoantharia). *Vieraea*, 35: 163–168.
- Ocaña, O., Brito, A., Núñez, J., and Bacallado, J. J. 1995. Redescrición de *Gerardia savaglia* (Bertoloni, 1819) (Anthozoa: Zoantharia: Gerardiidae). *Vieraea*, 24: 153–164.

- Ocaña, O., den Hartog, J. C., and van Ofwegen, L. P. 2004. Ring sea anemones, an overview (Cnidaria, Anthozoa, Actiniaria). *Graellsia*, 60: 143–154.
- Reimer, J. D., Nonaka, M., Sinniger, F., and Iwase, F. 2008. Morphological and molecular characterization of a new genus and new species of parazoanthid (Anthozoa: Hexacorallia: Zoantharia) associated with Japanese red coral. *Coral Reefs*, 27: 935–949.
- Reimer, J. D., Ono, S., Fujiwara, Y., Takishita, K., and Tsukahara, J. 2004. Reconsidering *Zoanthus* spp. diversity: molecular evidence of conspecificity within four previously presumed species. *Zoological Science*, 21: 517–525.
- Reimer, J. D., Ono, S., Iwama, A., Takishita, K., Tsukahara, J., and Maruyama, T. 2006. Morphological and molecular revision of *Zoanthus* (Anthozoa: Hexacorallia) from southwestern Japan with description of two new species. *Zoological Science*, 23: 261–275.
- Ryland, J. S., Brasseur, M. M., and Lancaster, J. E. 2004. Use of cnidae in taxonomy: implications from a study of *Acrozoanthus australiae* (Hexacorallia, Zoanthidea). *Journal of Natural History*, 38: 1193–1223.
- Ryland, J. S., and Lancaster, J. E. 2004. A review of zoanthid nematocyst types and their population structure. *Hydrobiologia*, 530/531: 179–187.
- Saffo, M. B. 1992. Coming to terms with a field: words and concepts in symbiosis. *Symbiosis*, 14: 17–31.
- Sinniger, F., and Häussermann, V. 2009. Zoanthids (Cnidaria: Hexacorallia: Zoantharia) from shallow waters of the southern Chilean fjord region, with descriptions of a new genus and two new species. *Organisms Diversity and Evolution*, 9: 23–36.
- Sinniger, F., Montoya-Burgos, J. L., Chevaldoné, P., and Pawlowski, J. 2005. Phylogeny of the order Zoantharia (Anthozoa, Hexacorallia) based on mitochondrial ribosomal genes. *Marine Biology*, 147: 1121–1128.
- Storm, V. 1901. Oversigt over Thronheimsfjordens fauna (med et kort). Trondhjems Biologiske Station, Meddelelser fra stationsanleggets arbeidskomite, H. Moe's Bog and Accidentstrykkeri, Trondhjem. 20 pp.
- Swain, T. D. 2009a. Phylogeny-based species delimitations and the evolution of host associations in symbiotic zoanthids (Anthozoa, Zoanthidea) of the wider Caribbean region. *Zoological Journal of the Linnean Society*, 156: 223–238.
- Swain, T. D. 2009b. *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. *Zootaxa*, 2051: 41–48.
- Swain, T. D., and Wulff, J. L. 2007. Diversity and specificity of Caribbean sponge-zoanthid symbioses: a foundation for understanding the adaptive significance of symbioses and generating hypotheses about higher-order systematics. *Biological Journal of the Linnean Society*, 92: 695–711.