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Together till the end: endosymbiosis of the annelid *Haplosyllides floridana* in the giant barrel-shaped sponge *Xestospongia muta* throughout the Tropical Atlantic

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Abstract

The symbiotic relationship between the syllid polychaete, *Haplosyllides floridana* Augener, 1922, and the barrel-shaped sponge *Xestospongia muta* (Schmidt, 1870), originally documented solely in the Caribbean, is presumed to be species-specific. Recently, the host sponge has been found as a single species distributed across approximately 8000 km (from 26°N to 22°S). Herein we addressed new spatial and bathymetric population records of *H. floridana* to question the persistence of the association with *X. muta*, and whether, in the case of an association, the polychaete remains as a single species throughout this extensive distribution. Our findings change the restricted distribution of *H. floridana*, revealing a remarkable association with *X. muta* from Tropical north-western to south-western Atlantic including records in the Fernando de Noronha Archipelago and the Almirante Saldanha Seamount, at 270 m deep. The populations analysed in this study are morphologically consistent. The study underscores the need for further investigations into the connectivity of *Xestospongia* species, the presence of *Haplosyllides* in other ocean basins, and the shared evolutionary history between *Xestospongia* and *Haplosyllides*. The observed life cycle completion of *H. floridana* within the host sponge suggests a potential co-evolutionary relationship, offering insights into the intricate dynamics of symbiotic associations in marine ecosystems.

Introduction

The family Syllidae Grube, 1850 stands out as the most diverse and intricate group within marine annelids, encompassing approximately 1100 valid species and 79 genera (San Martín and Aguado, 2014; Pamungkas *et al.*, 2019; Martin *et al.*, 2021). Integration of morphological and molecular data has led to the establishment of a monophyletic family with five subfamilies, along with the classification of certain genera as ‘Incertae sedis’ (Aguado *et al.*, 2012; San Martín and Aguado, 2014). Syllids can be found in abundance in several marine habitats as part of the soft bottom macro- and meiofauna, and in association with algae and other marine animals (San Martín, 2003; Martin *et al.*, 2021), especially corals and sponges, with 36 and 59 documented relationships, respectively (Martin and Britayev, 2018).

These symbiotic relationships require some phenotypic modification of the Syllidae species. For instance, the evolution of simple chaetae from compound ones in some genera, such as *Alcyonosyllis* Glasby & Watson, 2001, *Haplosyllides* Augener, 1922, *Haplosyllis* Langerhans, 1879, *Parahaplosyllis* Hartmann-Schröder, 1990, *Trypanoseta* Imajima & Hartman, 1964, and some species of *Syllis* Savigny in Lamarck, 1818, is interpreted as an adaptation to facilitate symbiotic associations with other organisms (Glasby and Watson, 2001; San Martín, 2003; Aguado and San Martín, 2009; Martin and Britayev, 2018).

The genus *Haplosyllides* is strictly symbiotic (Martin *et al.*, 2009). Initially considered monotypic, the genus underwent revision by Martin *et al.* (2009), leading to the identification of three distinct species: *Haplosyllides floridana* Augener, 1922, the previously recognized species, *Haplosyllides aberrans* (Fauvel, 1939), proposed as a new combination, and a third species, *Haplosyllides ophiocomae* Martin, Aguado & Britayev, 2009. These three valid species were described in association with different host organisms: *H. aberrans* was described associated with the crustacean *Platycaris latirostris* Holthuis, 1952; *H. ophiocomae*, with the ophiuroid *Ophiocoma pumila* Lütken, 1856; and *H. floridana*, uniquely found as an endosymbiont of the barrel-shaped sponge *Xestospongia muta* (Schmidt, 1870) only in the Caribbean region (Martin *et al.*, 2009; Martin and Britayev, 2018).

The type locality of *H. floridana* is in Florida, USA (Figure 1A), and its host sponge species *X. muta* is distributed across approximately 8000 km in the Tropical north- to south-western Atlantic ecoregions: from South Florida, Cuba (San Martín *et al.*, 1997), Guyana, Suriname, to Brazil (from the states of Amapá to Bahia, and in the Fernando de Noronha Archipelago) and extending to the



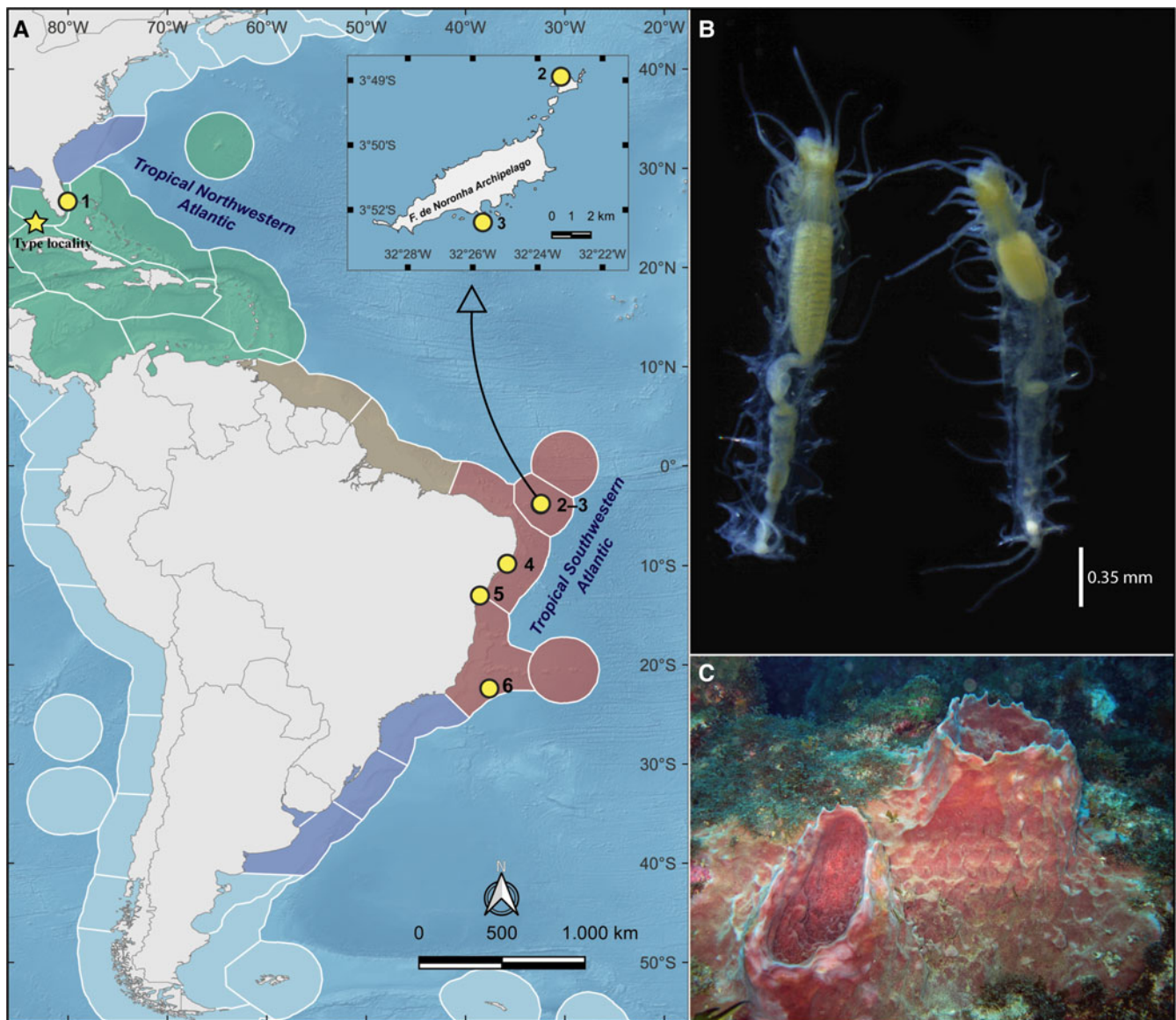


Figure 1. (A) Known distribution of *Haplosyllides floridana* off the Tropical north- and south-western Atlantic, with type locality (★), and new records (-): 1: Palm Beach, 2–3: Fernando de Noronha Archipelago (Ponta das Caracas and Cagarras, respectively), 4: state of Alagoas, Marechal Deodoro (Cabeço do Arpão), 5: state of Bahia (Todos os Santos Bay), 6: state of Rio de Janeiro (Almirante Saldanha Seamount). (B) Dorsal view of long proventricled, toothless specimen, and short specimen, with tooth and shorter proventricled. (C) The host barrel sponge *Xestospongia muta*.

Almirante Saldanha Seamount (at 270 m depth) off the coast of the state of Rio de Janeiro (Figure 1A) (Rocha *et al.*, 2021). Recently subjected to morphological revision throughout its distribution, *X. muta* has retained its status as a single species (Rocha *et al.*, 2021). Considering the vast spatial and bathymetric range, as well as the biogeographical barriers between the northern and southern extremes of its distribution, questions arise about the persistence of the association between *X. muta* and *H. floridana*, and whether, in the case of an association, the latter remains a single species throughout this extensive distribution. To address these questions, we combined the search for specimens of *H. floridana* in vouchers of the host sponges deposited in the Porifera collection at the Museu Nacional do Rio de Janeiro, Brazil, with new samples of *X. muta*.

Materials and methods

Study area

The examined specimens were obtained from populations throughout the Atlantic Ocean (Figure 1A). In the Tropical

north-western Atlantic, specimens were collected in Florida, Palm Beach, relatively close to the species' type locality, Dry Tortugas (Figure 1A). We also examined specimens from populations distributed across the majority of the Tropical south-western Atlantic, including the Fernando de Noronha Archipelago (Ponta das Caracas and Cagarras), Alagoas (Cabeço do Arpão), and Bahia (Farol da Barra), which are three localities in north-eastern Brazil, as well as from the Almirante Saldanha Seamount, in south-eastern Brazil (Figure 1A).

Sampling and taxonomic procedures

The specimens of *Haplosyllides floridana* (Figure 1B) from all populations were extracted from fragments of the barrel sponge *Xestospongia muta* (Figure 1C). Most of the material examined came from the Porifera collection of the Museu Nacional do Rio de Janeiro – MNRJ (Rio de Janeiro, Brazil), except for the populations from the state of Alagoas and the Fernando de Noronha Archipelago. The collections were carried out at

different opportunities from 2002 to 2013 and generally fixed and conserved in ethanol 92%. The *H. floridana* specimens were carefully examined and measured using a Zeiss Stemi SV11 stereomicroscope and a Zeiss Axio Lab A1 microscope. Additionally, a subset of specimens underwent further examination using scanning electron microscopy (SEM). For SEM analysis, the specimens were subjected to dehydration in a graded series of ethanol concentrations (up to 100%). Subsequently, critical point-drying was performed, followed by coating with approximately 30 nm of gold. The specimens were then examined and photographed at the Laboratório de Imagem em Microscopia Óptica e Eletrônica (LABIM-UFRJ). Precise line drawings were created

from slide-mounted specimens, with the assistance of a drawing tube, and digital images. The length of the specimens was measured from the tip of the palps to the tip of the pygidium, excluding the anal cirri. Width measurements were taken at the proventricular level, excluding parapodia. The material was deposited in the Museu Nacional do Rio de Janeiro at the Universidade Federal do Rio de Janeiro (MNRJ), Brazil.

Results

We found 73 specimens of *Haplosyllides floridana* associated with *Xestospongia muta* considering all populations examined,

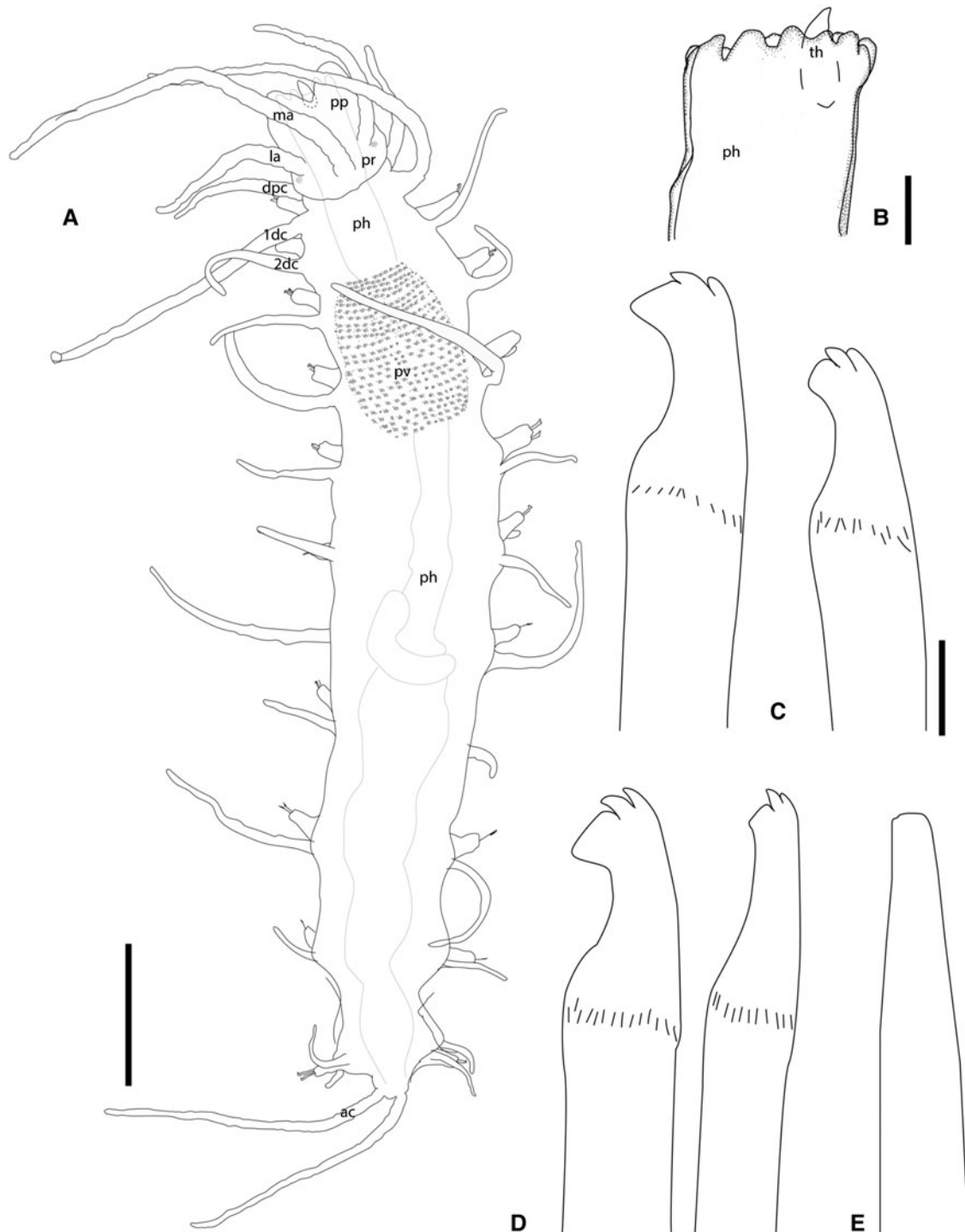


Figure 2. (A) Hand drawing of *H. floridana*, whole specimen, dorsal view; (B) anterior end of pharynx showing papillae and tooth; (C, D) anterior and posterior chaetae, respectively; (E) acicula. Scale bars: (A) 0.33 mm; (B) 20 μ m; (C–E) 5 μ m. pp, palps; pr, prostomium; ma, median antenna; la, lateral antenna; dpc, dorsal peristomial cirri; 1dc, dorsal cirri of chaetiger 1; 2dc, dorsal cirri of chaetiger 2; ph, pharynx; pv, proventricle; th, tooth; ac, anal cirri.

representing new occurrence records throughout the Tropical north-western and south-western Atlantic (USA and Brazil), including records of the specific association in the Fernando de Noronha Archipelago and the Almirante Saldanha Seamount, also expanding the bathymetric range to 270 m depth.

Taxonomy

Family SYLLIDAE Grube, 1850
Genus *Haplosyllides* Augener, 1922
Haplosyllides floridana Augener, 1922
(Figures 1–4)

Examined material

Atlantic Ocean, Tropical north-western Atlantic, USA

Florida, Palm Beach, Bath and Tennis Reef (26°40'31"N, 80°02'01"W), 16 m depth, in *X. muta*: 9 specimens (MNRJP 007877), coll. E. Hadju, 6 August 2011.

Atlantic Ocean, Tropical south-western Atlantic, Brazil

Pernambuco, Fernando de Noronha Archipelago, Ponta das Caracas (3°52'33"S, 32°25'31"W), 1 m depth, in *X. muta*: 9 specimens (MNRJP 007872), coll. F. Moraes, 21 November 2003; Cagarras (3°48'30"S, 32°23'21"W), 15 m depth, in *X. muta*: 5 specimens (MNRJP 007873), coll. G. Muricy, 8 November 2003; 20 m depth, in *X. muta*: 18 specimens (MNRJP 007874), coll. G. Muricy, 13 November 2003. Alagoas, Marechal Deodoro, Cabeço do Arpão (9°48.395'S, 35°47.184'W), 20 m depth, in *X. muta*: 10 specimens, coll. M. D. Correia. Bahia, Salvador, Todos os Santos Bay, Farol da Barra (13°00'38"S, 38°32'05"W), 15.8 m depth, in *X. muta*: 10 specimens (MNRJP 007875), coll. E. Hadju and C.C. Branco, 3 June 2009. Rio de

Janeiro, Almirante Saldanha Seamount, Estação Y2 (22°22'55"S, 37°35'17"W), 270 m depth, in *X. muta*: 15 specimens (MNRJP 007876) coll. 12 June 2002.

Morphological characterization

Small-sized body, longest complete specimen examined 2.2 mm long, 0.33 mm wide, with 14 segments; body translucent, without pigmentation in fixed specimens (Figure 1B). Palps fused, through most of their length, with bilobed appearance, fused to prostomium (Figure 2A). Prostomium oval, with only one pair of eyes, at midline; median antenna inserted posteriorly to pair of eyes, very long, usually surpassing posterior edge of proventricle, 3.5 times longer than palps and prostomium together; lateral antennae inserted almost in front of pair of eyes, 1.5 times longer than palps and prostomium together (Figure 2A). Peristomium shorter than following segments, with two pairs of peristomial cirri; dorsal peristomial cirri slightly shorter than lateral antennae (Figure 2A), ventral peristomial cirri with 1/3 length of dorsal ones. Antennae, peristomial, and dorsal cirri smooth to rugose, unarticulated, slender to filiform. Dorsal cirri of chaetiger 1 long, but shorter than median antenna, about 3 times longer than width of correspondent chaetiger; on chaetigers 2 and 3, slightly shorter than chaetigers width; remaining dorsal cirri alternating long (longer than body width), and two subsequent short (shorter than body width) (Figures 1B & 2A); dorsal cirri becoming shorter posteriorwards; same pattern seems to be present in juvenile specimens (Figure 3C). Ventral cirri digitiform, distally rounded, shorter than or about same length of parapodial lobes (Figure 3D). Parapodial lobes conical. Two simple chaetae per parapodium, one broader than the other, with three distal teeth, one triangular, enlarged, and two smaller; chaetae with a subdistal constriction, with chaetae apex slightly wider on broader chaetae

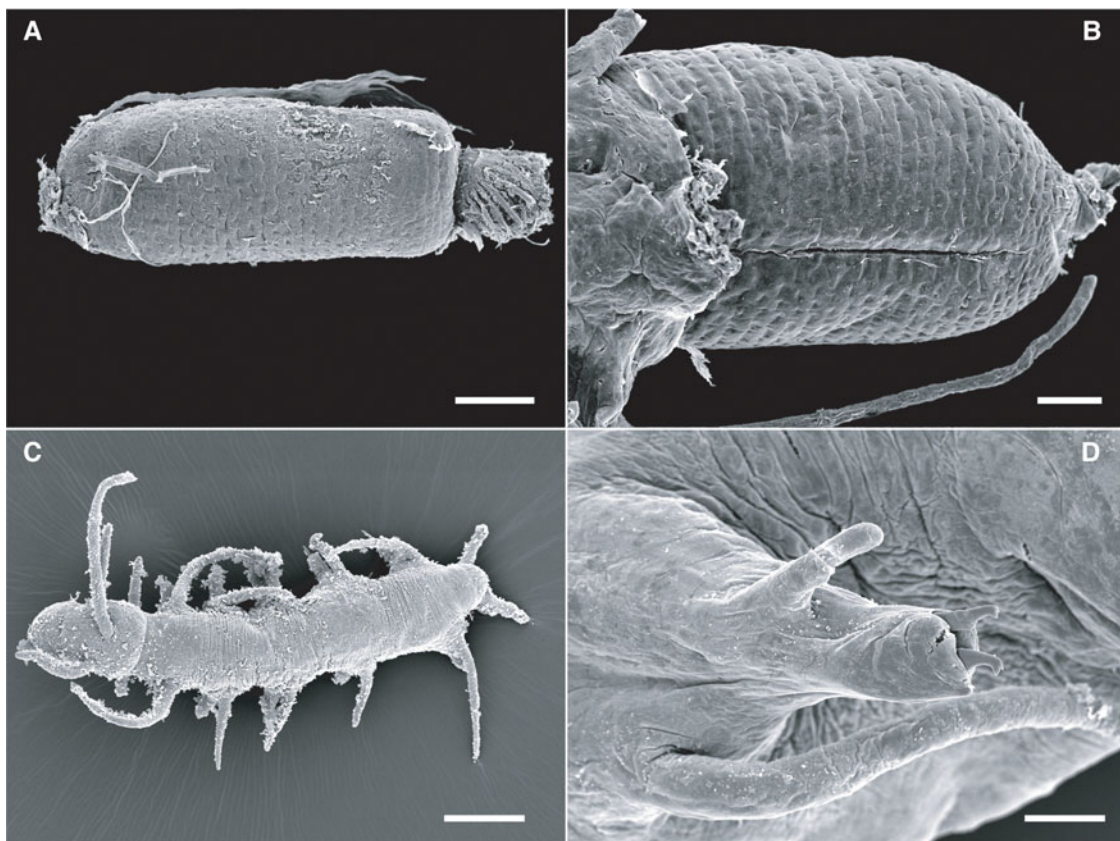


Figure 3. *H. floridana*, SEM: (A, B) Large and small proventricles of two specimens from Almirante Saldanha Seamount; (C) juvenile specimen, dorsal view; (D) midbody parapodial lobe, ventral view. Scale bars: (A) 100 μ m, (B) 50 μ m, (C) 100 μ m, (D) 20 μ m.

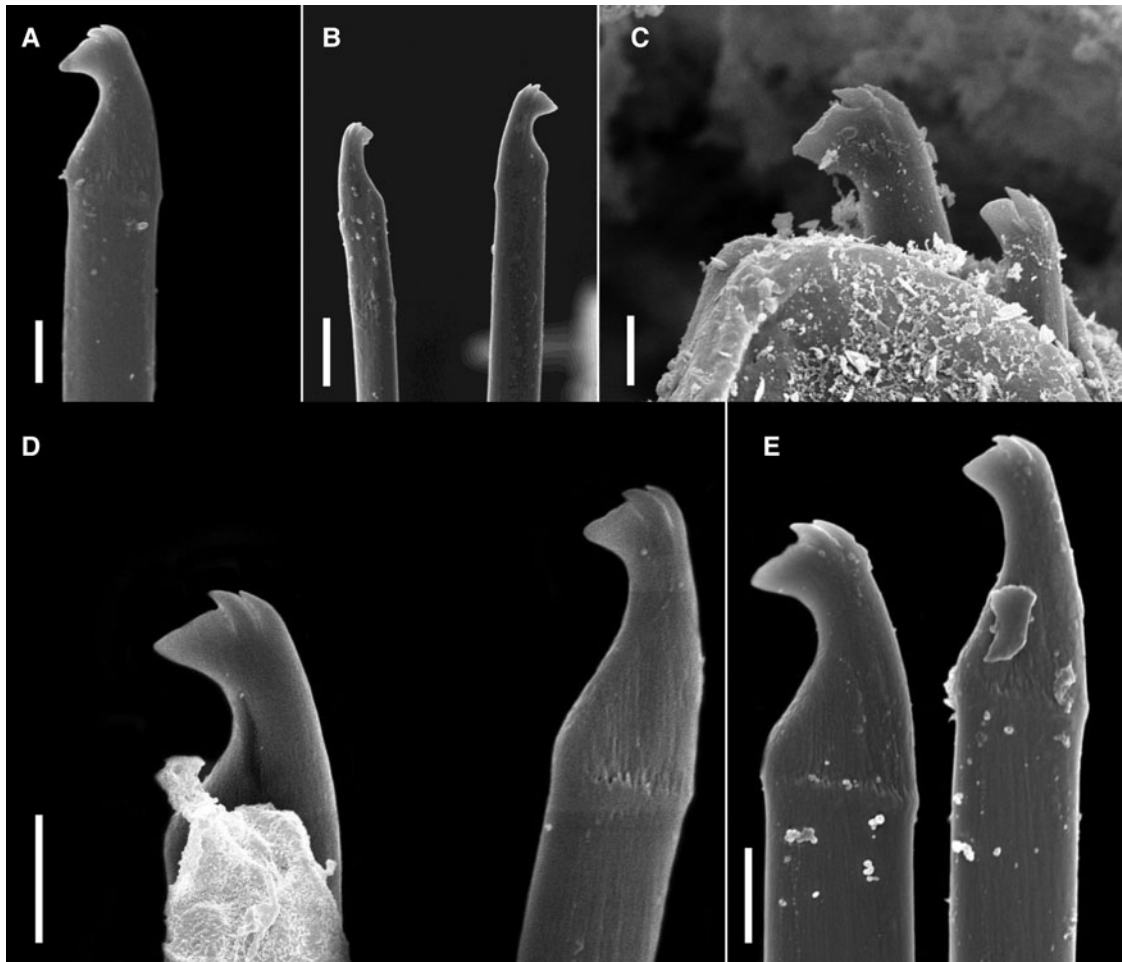


Figure 4. *H. floridana*, SEM: (A–C) anterior body chaetae from Florida, Bahia, and Almirante Saldanha Seamount specimens, respectively; (D, E) posterior body chaetae from Bahia and Florida specimens, respectively. Scale bars: (A, B, E) 5 μ m, (C) 1 μ m, (D) 2 μ m.

(Figures 2C, D & 4D, E); distance between the chaetal tip and subdistal constriction similar on the two chaetae of anterior parapodia (Figures 2C & 4A, B), on posterior parapodia, the distance between the chaetal tip and subdistal constriction longer in the slender chaetae (Figures 2D & 4D, E). Chaetae frequently emerging in different angles, which may lead to misinterpretations of length and angles between teeth. Only one acicula per parapodium throughout, about the same thickness of chaetae, straight, distally tapering, with tips flattened to truncated (Figure 2E). Pygidium small, rounded, with two anal cirri similar in shape and length to long dorsal cirri (Figure 1A). Pharynx variable, through 4–5 segments (Figures 1B & 2A), frequently everted, with crown of 11–12 soft papillae (Figure 2B); pharyngeal tooth located anteriorly on the margin of the pharynx, long, conical (Figure 2B), absent more frequently on specimens with larger proventricle (Figure 1B). Proventricle variable, relatively long, extending through 3–4 chaetigers and 25–27 rows of muscle cells (Figures 1B & 3A), or short, extending through 2–3 chaetigers and 23–24 rows muscle cells (Figures 1B, 2A & 3B).

Reproduction

Reproduction by schizogamy, developing tricerous stolons; with three eyes ventrally directed, and three small antennae (San Martín, 1997). Some juveniles were found, which may indicate that the species has its complete life cycle within the sponge canals; the juveniles were similar to the adults, not showing signs of regeneration, which may reinforce that the species was

reproducing sexually as in the case of some *Haplosyllis* species found by Lattig and Martin (2011).

Habitat

Coastal; insular; great range of bathymetry, 1–270 m depth; until now, only found in *X. muta*.

Type locality

Dry Tortugas, Florida.

Distribution

Atlantic Ocean: Florida, Cuba. New records for South Atlantic: Fernando de Noronha archipelago, north-eastern Brazil (states of Alagoas and Bahia), south-eastern Brazil (Almirante Saldanha Seamount).

Discussion

The species *Haplosyllides floridana* was originally described from Dry Tortugas (Florida) inhabiting the giant barrel sponge *Xestospongia muta*. We examined 73 specimens of *Haplosyllides* associated with *X. muta* from various locations spanned from 26° N to 22°S, mainly in the Tropical south-western Atlantic (Fernando de Noronha Archipelago, Alagoas, Bahia and on the Almirante Saldanha Seamount). We also examined a population (16 specimens) from the Tropical north-western Atlantic (off West Palm Beach, Florida, USA), close to the type locality but outside the Gulf of Mexico. The remarkable endosymbiosis of *H. floridana*

in *X. muta* was observed across all these localities, covering more than 8000 km from the Tropical south- to north-western Atlantic marine provinces and with a remarkable bathymetric distribution from 1 to 270 m deep. Consequently, we broaden the known geographic and bathymetric distribution of *H. floridana* and its association with *X. muta* to the south-western Atlantic coast.

The populations analysed in this study are consistent in morphological terms with the redescription provided by Martin *et al.* (2009). The chaetae exhibit a striking similarity; however, in the posterior parapodia, slender chaetae may show a slightly longer distance between the subdistal constriction and the chaetae tip. This distinction is considered an intraspecific variation, appearing randomly throughout the populations.

The population of *H. floridana* from Cuba exhibits two morphotypes: a non-reproductive type with a long body, lacking pharyngeal tooth and featuring a long proventricle, and a shorter reproductive type with stolons, a pharyngeal tooth, and a relatively small proventricle (San Martín *et al.*, 1997). While we also observed intrapopulation variability in our material, the lack of specimens with stolons makes it challenging to attribute the presence of tooth solely to the reproductive status of the specimens. Aguado and San Martín (2009) also noted significant plasticity in the morphology of pharyngeal structures in the specimens of the genera *Trypanoseta* and *Haplosyllis*. The presence and absence of pharyngeal teeth within the same population have been documented in *Trypanosyllis* species, which have pharyngeal teeth as juveniles but lose them as adults, retaining only the trepan (San Martín, 2003; San Martín *et al.*, 2008). In some populations examined, the absence of pharyngeal teeth was more frequent in longer specimens with larger proventricles. Given the proventricle's role as a muscular suction structure, one could imagine that the loss of teeth might induce hypertrophy of the proventricle, resulting in a more robust shape.

In Brazilian waters, the genus *Haplosyllides* included the species *H. aberrans* (reported as *Haplosyllis*) recorded off the coast of Recife (north-eastern Brazil) at a depth of 33 m on calcareous algae (Rullier and Amoureux, 1979). However, Martin *et al.* (2009) considered this a doubtful record due to differences in substrate association and biogeographical inconsistency. They noted that the type locality of *H. aberrans* is in Indochina, making its occurrence on the Brazilian coast unlikely. In addition, the Brazilian population lacks a detailed description, demanding a complete morphological reevaluation, which is out of the scope of the present study. Herein, we reestablish the presence of this genus along the Brazilian coast.

We looked for *Haplosyllides* in a different species of *Xestospongia* collected in Bahia (sponge det. by André Bispo). However, all the examined species of Syllidae found there corresponded to the genus *Haplosyllis*. This finding may strengthen the hypothesis that *H. floridana* is a strict endosymbiont of *X. muta*.

Notably, major biogeographic barriers, such as the Amazon and the São Francisco River's plumes, as well as open ocean expanses and isolation by distance that typically hinder dispersal for oceanic island species, do not appear to impede the dispersion of *X. muta* and *H. floridana*. Future research should (1) investigate the genetic connectivity of Brazilian *Xestospongia* with Caribbean lineages, (2) investigate the presence of *Haplosyllides* associated with barrel sponges in other ocean basins, and (3) investigate whether *Xestospongia* and *Haplosyllides* share a similar evolutionary history (co-evolution) and speciation pattern. We observed juveniles of *H. floridana* in the host sponge, which indicates that the species completes its life cycle in the sponge, reinforcing the possibility of a shared evolutionary history between the host and the commensal.

Data Availability. All data used are available throughout the manuscript.

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Author contributions. R. L. N.: conceptualization, sample collection and processing, analysis, led the original draft, write – reviewing and editing; A. B.: conceptualization, sample collection and processing, original draft, write – reviewing and editing; M. V. F.: analysis, write – reviewing and editing, supervision; K. P.: sample collection and processing, analysis, write – reviewing and editing; P. C. P.: write – reviewing and editing, supervision. All authors contributed critically to the manuscript and gave final approval for publication.

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Competing interests. None.

References

- Aguado MT and San Martín G (2009) Phylogeny of Syllidae (Polychaeta) based on morphological data. *Zoologica Scripta* **38**, 379–402.
- Aguado MT, San Martín G and Siddall MT (2012) Systematics and evolution of syllids (Syllidae, Annelida). *Cladistics* **28**, 234–230.
- Augener H (1922) Über litorale polychäten von Westindien. *Sitzungsberichte der Gesellschaft Naturforschende Freunde zur Berlin* **1922**, 38–53.
- Fauvel P (1939) Annélides Polychètes de l'Indochine recueillies par M. C. Dawidoff. Commentationes. Pontificia Academia Scientiarum, Ann. III, 3, 243–368.
- Glasby CJ and Watson C (2001) A new genus and species of Syllidae (Annelida: Polychaeta) commensal with octocorals. *The Beagle, Records of the Northern Territory Museum of Arts and Sciences* **17**, 43–51.
- Grube AE (1850) Die Familien der Anneliden. *Archiv für Naturgeschichte* **16**, 249–364.
- Hartmann-Schröder G (1990) Teil 15. Die Polychaeten der subtropisch-tropischen und tropischen Ostküste Australiens zwischen Lake Macquarie (New South Wales) im Süden und Gladstone (Queensland) im Norden. *Mitteilungen aus dem Hamburgischen Zoologischen Museum und Institut* **87**, 41–87.
- Holthuis LB (1952) The Decapoda of the Siboga Expedition. Part XI. The Palaemonidae collected by the Siboga and Snellius expeditions with remarks on other species II. Subfamily Pontoniinae. *Siboga Expeditie Monographs* **39**, 1–253.
- Imajima M and Hartman O (1964) The polychaetous annelids of Japan. *Occasional Papers of the Allan Hancock Foundation* **26**, 1–452.
- Lamarck JB (1818) *Histoire Naturelle des animaux sans vertèbres, présentant les caractères généraux et particuliers de ces animaux, leur distribution, leurs classes, leurs familles, leurs genres, et la citation des principales espèces qui s'y rapportent; précédées d'une introduction offrant la détermination des caractères essentiels de l'animal, sa distinction du végétal et des autres corps naturels, enfin l'exposition des principes fondamentaux de la zoologie*, vol. 5. Paris: Deterville.
- Langerhans P (1879) Die Wurmfauuna von Madeira [part I]. *Zeitschrift für wissenschaftliche Zoologie* **32**, 513–592.
- Lattig P and Martin D (2011) Two new endosymbiotic species of *Haplosyllis* (Polychaeta: Syllidae) from the Indian Ocean and Red Sea, with new data on *H. djiboutiensis* from the Persian Gulf. *Italian Journal of Zoology* **78**, 112–123.
- Lütken CF (1856) Bidrag til kundskab om Slangestjernerne. II. Oversigt over de vestindiske Ophiurer. *Videnskabelige Meddelelser fra Dansk Naturhistorisk Forening i Kjøbenhavn* **7**, 1–19.
- Martin D, Aguado MT and Britayev T (2009) Review of the symbiotic genus *Haplosyllides* (Polychaeta: Syllidae), with a description of a new species. *Zoological Science* **26**, 646–655.
- Martin D and Britayev G (2018) Symbiotic polychaetes revisited: an update of the known species and relationships (1998–2017). *Oceanography and Marine Biology: An Annual Review* **56**, 371–448.
- Martin D, Aguado MT, Fernández Álamo MA, Britayev TA, Böggemann M, Capa M, Faulwetter S, Fukuda MV, Helm C, Petti MAV, Ravara A and Teixeira MAL (2021) On the diversity of Phyllocodica (Annelida:

- Errantia), with a focus on Glyceridae, Goniadidae, Nephtyidae, Polynoidae, Sphaerodoridae, Syllidae and the holoplanktonic families. *Diversity* **13**, 131.
- Pamungkas J, Glasby CJ, Read GB, Wilson SP and Costello MJ** (2019) Progress and perspectives in the discovery of polychaete worms (Annelida) of the world. *Helgoland Marine Research* **73**, 4.
- Rocha L, Moraes F, Salani S and Hajdu E** (2021) Taxonomy of Petrosiidae Van Soest, 1980 (Haplosclerida, Porifera) from Brazil. *Zootaxa* **5004**, 251–287.
- Rullier F and Amoureux L** (1979) Annélides Polychètes. *Annales de l'Institut Oceanographique* **55**, 145–206.
- San Martín G** (2003) Annelida Polychaeta II: Syllidae. In Ramos MA (ed.), *Fauna Ibérica*, vol. **21**. Madrid: Museo Nacional de Ciencias Naturales, CSIC, pp. 1–544.
- San Martín G and Aguado MT** (2014) Family Syllidae. Phyllococida: Nereidiformia. In Westheide W and Purschke G (eds), *Handbook of Zoology Online, Annelida: Polychaeta*. Berlin: De Gruyter, pp. 1–52.
- San Martín G, Ibarzábal DR, Jiménez M and López E** (1997) Redescription of *Haplosyllides floridana* Augener, 1924 (Polychaeta, Syllidae, Syllinae), with notes on morphological variability and comments on the generic status. *Bulletin of Marine Science* **60**, 364–370.
- San Martín G, Hutchings P and Aguado MT** (2008) Syllinae (Polychaeta, Syllidae) from Australia. Part. 1. Genera *Branchiosyllis*, *Eurysyllis*, *Karroonsyllis*, *Parasphaerosyllis*, *Plakosyllis*, *Rhopalosyllis*, *Tetrapalpia* n. gen., and *Xenosyllis*. *Records of the Australian Museum* **60**, 119–160.
- Schmidt O** (1870) *Grundzüge einer Spongien-Fauna des atlantischen Gebietes*. Leipzig: Wilhelm Engelmann.