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## Description of a new species of *Leiopathes* (Antipatharia: Leiopathidae) from the Hawaiian Islands

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### Abstract

The Hawaiian antipatharian coral previously identified as *Leiopathes glaberrima* (Esper, 1792) and *Leiopathes* sp. is described using polyp morphology, skeletal spine morphology and *in situ* photographs, and assigned the new name of *Leiopathes annosa* sp. nov. The species is characterized by tall (1 m or more), fan-shaped colonies, with thick, sometimes overlapping branches, and tissues that are colored bright orange when alive. Skeletal spines are smooth, hemispherical, often times multi-lobed, and typically 75 µm tall, but range between 30–225 µm. Polyps are of variable size (0.88–3.35 mm) and arranged on all sides of the corallum on thicker branches, and uniserially on terminal branches. *Leiopathes annosa* sp. nov. differs from all other nominal species of *Leiopathes* by having a generally flabellate corallum with thick branches and conspicuous skeletal spines that are multi-lobed and hemispherical. The biogeographical distribution of species within the monogeneric family Leiopathidae is presented and discussed.

**Key words:** Anthozoa, black coral, biogeography, cold-water coral, deep-sea, *Leiopathes annosa* sp. nov.

### Introduction

Antipatharians, commonly known as black corals, are a taxonomic order within the anthozoan subclass Hexacorallia characterized by (1) proteinaceous skeletons that are covered with minute skeletal spines, (2) polyps with six unbranched tentacles that are non-retractile, (3) six primary mesenteries, and (4) being exclusively colonial (reviewed by Wagner *et al.* 2012; Brugler *et al.* 2013). The antipatharian order currently encompasses over 235 described species, which are divided into 42 genera and seven families (Wagner *et al.* 2012). Among these families, the Leiopathidae Haeckel, 1896, is fairly distinctive from the remaining Antipatharia in that all species have poorly developed skeletal spines, particularly on the thickest branches and stem, and possess polyps with twelve mesenteries (six primary and six secondary), whereas all other antipatharians have either six (six primary and no secondary) or ten (six primary and four secondary) (Opresko 1998). Due to these substantial morphological differences, the Leiopathidae may even merit higher taxonomic status (Opresko 1998; Brugler *et al.* 2013). In fact, the family may be the most primitive in the antipatharian order, as indicated by an unpublished phylogeny based on 16S, 18S and 28S sequences by the CnidToL Working Group that placed the Leiopathidae as a sister to all other black coral families with strong node support (as cited in Brugler *et al.* 2013).

The family Leiopathidae consists of a single genus, *Leiopathes* Haime, 1849, which currently contains eight described species (Molodtsova 2011): *L. glaberrima* (Esper, 1792), *L. expansa* (Johnson, 1899), *L. grimaldii* (Roule, 1905), *L. valdiviae* (Pax, 1915) *L. acanthophora* Opresko, 1998, *L. secunda* Opresko, 1998, *L. bullosa* Opresko, 1998, and *L. montana* Molodtsova, 2011. Additionally, several undescribed and unidentified *Leiopathes* spp. have been reported from around the globe. In the Hawaiian Islands, the genus *Leiopathes* is common and abundant at depths below 300 m (Grigg and Opresko 1977; Grigg 1988; Chave and Malahoff 1998; Parrish 2006; Parrish and Baco 2007; Baco 2007). In particular, *L. glaberrima*, a species originally described from the Mediterranean Sea (Esper 1792; Grasshoff 1991; Opresko and Baron Szabo 2001), has been reported from around the Hawaiian Archipelago (Grigg and Opresko 1977; Grigg 1988; Chave and Malahoff 1988; Roark *et al.* 2006;

Parrish and Baco 2007), although none of the Hawaiian specimens were ever compared to *L. glaberrima* specimens from the type locality. The purpose of this study was to compare Hawaiian *Leiopathes* specimens to those of described congeners from around the globe using (1) skeletal spine morphology, (2) polyp morphology, and (3) published colony photographs and illustrations.

## Material and methods

A total of 21 specimens stored at both the National Museum of Natural History, Smithsonian Institution in Washington, D.C. (USNM), and the Bernice P. Bishop Museum in Honolulu, Hawai'i (BPBM) were examined (Table 1). Examined specimens included 17 specimens from Hawaiian waters, type material of *L. acanthophora*, *L. bullosa* and *L. secunda*, as well as a topotype of *L. glaberrima* (Table 1). Samples of all specimens were prepared for scanning electron microscopy (SEM) by rinsing branches in commercial bleach for 1–2 min to remove remaining tissue, and then transferred to 95% ethanol for 1 h. Samples were air dried, gold-palladium coated using a Cressington 108 Auto Sputter Coater adjusted to 30 nm thickness with a Cressington MTM 20 Thickness Controller, and viewed under a Leica Stereoscan 440 SEM at the USNM. Skeletal features were measured from SEM photomicrographs using the image analysis software ImageJ (Wayne Rasband, National Institute of Health). Spine heights were measured between the apex and the center of the base of spines, and spine widths were measured at the base of spines along the proximal-distal axis. Polypar features were mostly measured from sample BPBM D1871 (the holotype), because the polyps in all other specimens were poorly preserved. Polyps were photographed under a Nikon PFX binocular microscope, and polypar features were measured from photographs as described above. Polyp transverse diameters were measured between the proximal edge of the proximal lateral tentacles to the distal edge of the distal lateral tentacles. Polyp spacing was measured between the centers of the mouths of two adjacent polyps. For specimens collected by the Hawai'i Undersea Research Laboratory's (HURL) manned submersibles (see Table 1), *in situ* photographs were retrieved from HURL archives.

## Results and discussion

### Order Antipatharia Milne Edwards, 1857

### Family Leiopathidae Haeckel, 1896

### Genus *Leiopathes* Haime, 1849

#### *Leiopathes annosa* sp. nov.

(Fig. 1a–e, 2a–d, 3a–h, 4a–o, 5a, 6a–d)

not *Leiopathes glaberrima*, (Esper 1972) (and later authors; see Opresko and Baron-Szabo, 2001 for synonymy)

*Leiopathes glaberrima*, Grigg and Opresko, 1977: 242–261, fig. 7.

*Leiopathes glaberrima*, Grigg 1988: 142.

*Leiopathes glaberrima*, Chave and Malahoff, 1998: 40, fig. 93.

*Leiopathes glaberrima*, Roark *et al.*, 2006\*: 1–14.

*Leiopathes glaberrima*, Parrish and Baco, 2007\*: 186.

*Leiopathes* sp. Roark *et al.* 2009\*: 5204–5208.

*Leiopathes* sp. Wagner *et al.*, 2011: 211–225, fig. 1k, 2d.

*Leiopathes* sp. Wagner *et al.*, 2012: 76, 80, 84, 88, 90.

*Leiopathes* sp. P4-227-2 Brugler *et al.*, 2013: 325, 327, 335, fig. 2–3.

*Leiopathes* USNM1070976 Brugler *et al.*, 2013: 335, fig. 2–3.

\* Re-identification based on *in situ* photographs in HURL archives only. For all others, both specimens and *in situ* photographs were examined.

**Type locality.** South of Ni'ihau Island, Main Hawaiian Islands, 21°49'21"N 160°6'37"W, 382 m.

**TABLE 1.** *Leiopathes* specimens examined as part of this study (\* = type material; NR = not reported; <sup>1</sup> molecular sequence data for specimen BPBM D1871 (as P4-227-2) was reported in Brugler et al. (2013) and is available from GenBank under accession numbers KF054599, KF054665 and KF054466; <sup>2</sup> molecular sequence data for specimen USNM1070976 was reported in Brugler et al. (2013) and is available from GenBank under accession numbers KF054593, KF054663 and KF054467).

Sample number	Species	Collection date	Locality	Collection depth (m)	Latitude	Longitude
USNM 99402*	<i>Leiopathes acanthophora</i>	July 31, 1988	East of Cape Arid, Western Australia	1011–1020	34°03'00"S	125°31'00"E
USNM 99409*	<i>Leiopathes bullosa</i>	April 14, 1990	Southwest of Cape Adieu, South Australia	522–910	33°29'00"S	130°33'00"E
USNM 1099249	<i>Leiopathes glaberrima</i>	December 31, 2003	Capraia Island, Italy, Mediterranean Sea	361–404	43°13'34"N	9°36'19"E
USNM 99404*	<i>Leiopathes secunda</i>	February 11, 1990	East of South East Cape, Tasmania	890–1020	43°58'00"S	150°22'00"E
BPBM D1871* <sup>1</sup>	<i>Leiopathes annosa</i>	December 2, 2009	South of Ni'ihau Island	382	21°49'21"N	160°06'37"W
BPBM 910	<i>Leiopathes annosa</i>	October 17, 1982	Hilo Harbor disposal site, Puna Canyon, Hawai'i Island	347	19°30'00"N	155°00'W
BPBM 1017	<i>Leiopathes annosa</i>	October 15, 1982	Off Hilo, Mauna Kea Ledge, Hawai'i Island	347	NR	NR
BPBM 970	<i>Leiopathes annosa</i>	April 7, 1983	Off Makapuu, O'ahu Island	366	21°18'30"N	157°33'42"W
BPBM 982	<i>Leiopathes annosa</i>	January 19, 1984	Off Makapuu, O'ahu Island	411	NR	NR
USNM 1070976 <sup>2</sup>	<i>Leiopathes annosa</i>	October 5, 2004	Off Lanikai, O'ahu Island	403	21°24'22"N	157°38'33"W
USNM 1071416	<i>Leiopathes annosa</i>	October 5, 2004	Off Lanikai, O'ahu Island	470	21°24'22"N	157°38'33"W
USNM 1071417	<i>Leiopathes annosa</i>	October 6, 2004	Off Lanikai, O'ahu Island	431–536	21°24'23"N	157°38'00"W
USNM 77082	<i>Leiopathes annosa</i>	March 8, 1972	Kaua'i Island	295–432	21°56'44"N	159°44'51"W
USNM 99497	<i>Leiopathes annosa</i>	March 8, 1972	Kaua'i Island	295–432	21°56'44"N	159°44'51"W
USNM 99500	<i>Leiopathes annosa</i>	March 8, 1972	Kaua'i Island	295–432	21°56'44"N	159°44'51"W
USNM 99501	<i>Leiopathes annosa</i>	March 8, 1972	Kaua'i Island	295–432	21°56'44"N	159°44'51"W
USNM 99496	<i>Leiopathes annosa</i>	August 23, 1971	Brooks Bank	398–412	23°57'30"N	166°40'30"W
USNM 1129919	<i>Leiopathes annosa</i>	August 23, 1971	Brooks Bank	399–412	23°57'30"N	166°40'30"W
USNM 1071405	<i>Leiopathes annosa</i>	October 3, 2003	Salmon Bank, South of Midway Island	472	27°01'10"N	176°31'33"W
USNM 77480*	<i>Leiopathes annosa</i>	October 15, 1976	Necker Island	457	NR	NR
USNM 52278	<i>Leiopathes</i> sp.	June 12, 1902	Kaua'i Island	966	22°15'50"N	159°29'55"W

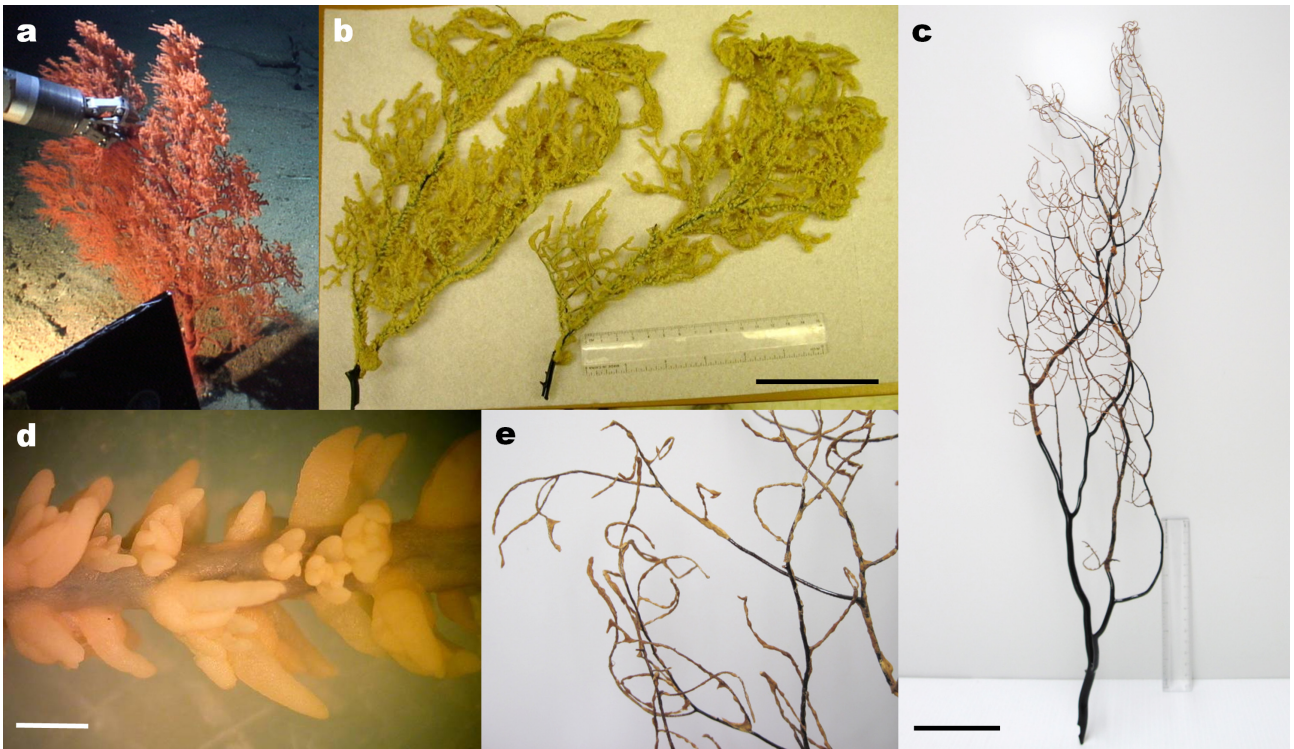
**Diagnosis.** Colonies are up to 1 m in height or more, with most branches located in an approximately single plane like a fan (Fig. 1a–c, 3a–h). In some colonies, branches overlap considerably producing a rather thick corallum that is still planar, whereas in others all the branches are in a single plane (Fig. 1a–c, 3a–h). Most of the smaller branches are directed distally relative to the branches from which they arise, as well as upwards towards the top of the corallum. Branching is mostly irregularly bilateral, but uniserial in some places, with the branches tending to be directed vertically. The highest order branches are typically 1.5–6 cm in length, 1.4 mm in diameter at their midpoint with tissue (range = 1.0–1.8 mm), and on average spaced 0.8 cm apart (range = 0.4–1.7 cm). Polyps are variable in size (0.88–3.35 mm), arranged irregularly on all sides of the corallum on thicker branches and uniserially on terminal branches with adjacent polyps spaced 1.2–3.2 mm apart, resulting in 5–6 polyps/cm (Fig. 1). Spines are typically 75  $\mu$ m tall (range = 30–225  $\mu$ m) and 140  $\mu$ m wide at the base (range = 35–315  $\mu$ m). On the terminal branchlets (~0.07 mm in diameter excluding the spines), the spines can be hemispherical, balloon-shaped, irregularly knobby or with one or more round or misshapen lobes (Fig. 2d, 4a–o). On such terminal branchlets, 3–5 spine rows are visible in lateral view (Fig 2d, 4a–o). On thicker branches (0.15 mm in diameter excluding spines), the spines are more hemispherical to mound-like with fewer, but larger round lobes, and the spine arrangement in rows becomes obscured (Fig. 2b–c). On branches thicker than 0.27 mm in diameter excluding the spines, the spines become smaller and more knob-like or somewhat conical to deltoid in shape, with little remaining evidence of lobes (Fig 2a). The living tissues are colored bright orange (Fig. 1a, 3a–h).

**Material examined.** Holotype (BPBM D1871), south of Ni‘ihau Island, Main Hawaiian Islands, 21°49’21”N 160°6’37”W, 382 m, HURL submersible *Pisces IV*, dive P4-227, specimen 2, 2 December 2009, ethanol. Paratype (USNM 77480), bank north of Necker Island, Northwestern Hawaiian Islands, no coordinates recorded, 457 m, *R/V Townsend Cromwell*, cruise 76-06-73, fish trawl, 15 October 1976, dry. For all other non-type material examined as part of this study see Table 1.

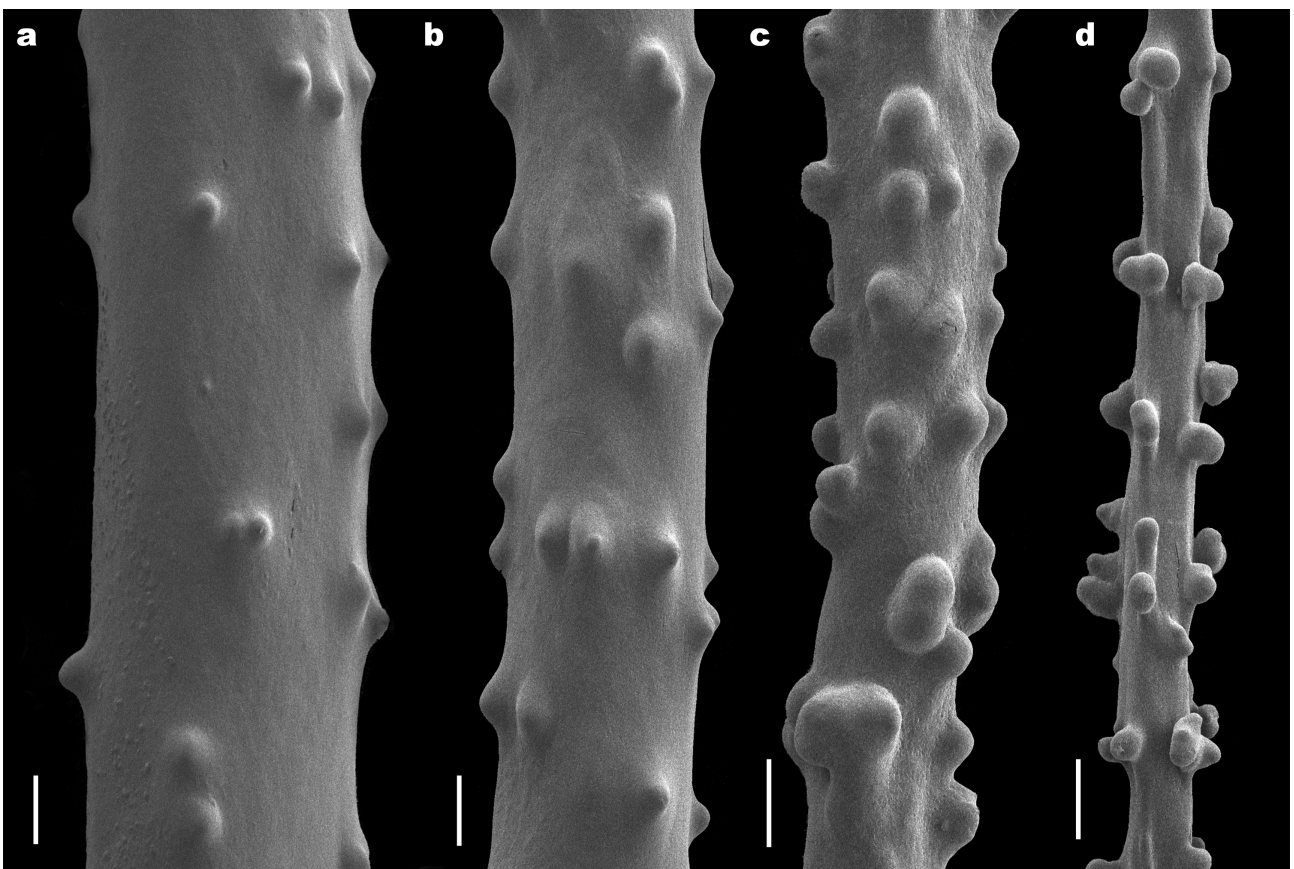
**Description of holotype.** The holotype (BPBM D1871) consists of two separate ethanol-preserved fragments collected from the distal part of a colony (Fig. 1a–b). The colony from which the holotype fragments were collected, branches sparsely towards the center of the corallum, and becomes more dense and irregular distally, with multiple orders of branching (Fig. 1a–b, 3a). The first holotype fragment has a basal branch diameter of 5 mm and is approximately 31 cm long and 16 cm wide, whereas the second fragment has a basal branch diameter of 6 mm, measures 33 cm in length and 18 cm in width. On both fragments polyps are arranged irregularly on all sides of the axis on the main branch and larger branches, and uniserially on the terminal branches. Polyps are 0.88–3.35 mm in transverse diameter, and spaced 1.2–3.2 mm apart on the terminal branches, resulting in 5–6 polyps/cm. Terminal branches are typically 3–4 cm in length (range = 1.5–6 cm), 1.4 mm in width at their midpoint with tissue (range = 1.0–1.8 mm) and 280  $\mu$ m in width without tissue (range = 165–400  $\mu$ m). On the terminal branches, 3–4 spine rows are visible in lateral view; however, on thicker branches the spine arrangement in rows becomes obscured (Fig. 2a–b). Spines are smooth and typically hemispherical, but spines with multiple lobes occur often (Fig. 2c–d). On terminal branches spines are generally 70  $\mu$ m tall (range = 30–100  $\mu$ m) and 145  $\mu$ m wide (range = 70–310  $\mu$ m). On thicker branches (width = 400–810  $\mu$ m without tissue), spines range between 30–110  $\mu$ m in height and 130–315  $\mu$ m in width (Fig. 2a).

**Description of paratype.** The paratype (USNM 77480) consists of a dried colony that is 63 cm tall, 17 cm wide, 8 mm in basal diameter and was broken off above the base (Fig. 1c, e). The branching is sparse towards the center of the corallum, and becomes more dense and irregular distally, with nine orders of branching (Fig. 1c). Most of the smaller branches are directed distally relative to the branches from which they arise, as well as upwards towards the top of the corallum (Fig. 1c, e). Branching is mostly irregularly bilateral, but uniserial in some places, with the branches tending to be directed vertically (Fig. 1c, e). Branches coming off the main axis range between 3–5 mm in diameter. The terminal branches are 1.5–6 cm long, tend to be curved distally, and measure 400–650  $\mu$ m at their midpoint with remaining tissue. On portions without remaining tissue, terminal branches measure 280–440  $\mu$ m at their midpoint. Despite being preserved as a dry specimen, polyp remnants remain on a few terminal branchlets of the paratype (Fig. 1e) and measure 2–2.5 mm in diameter. On the terminal branches, 4–5 spine rows are visible in lateral view; however, on thicker branches the spine arrangement in rows becomes obscured. Spines on terminal branches are smooth and range between hemispherical, balloon-shaped and irregularly knobby. On terminal branches (250–400  $\mu$ m at their midpoint without spines), spines are 55–140  $\mu$ m tall and 75–240  $\mu$ m wide at their base. On thicker branches (width = 450–675  $\mu$ m without tissue), spines range between 50–120  $\mu$ m in height, 120–260  $\mu$ m in width and tend to be mound-like, conical or deltoid in shape.



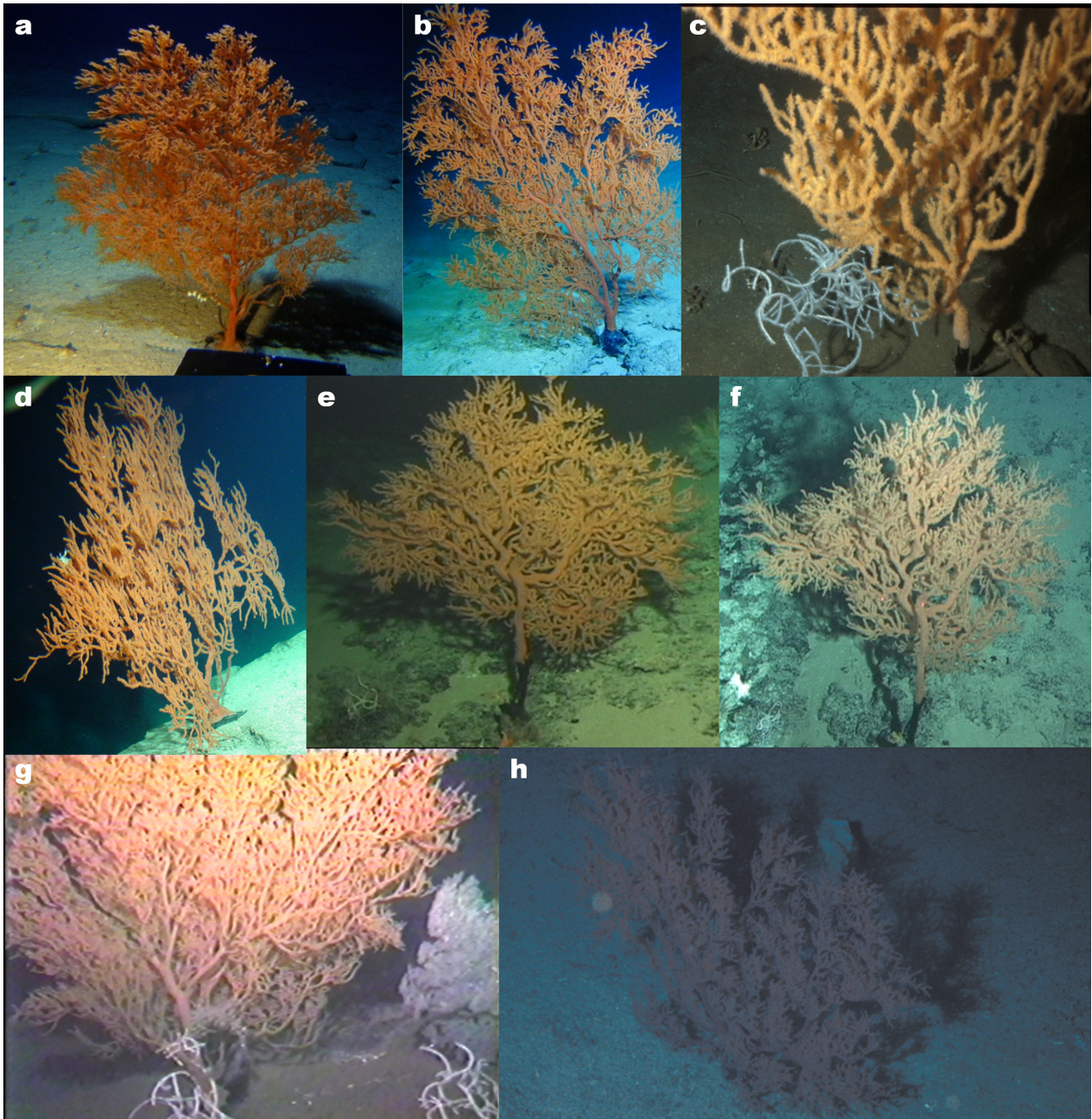


**FIGURE 1.** *Leiopathes annosa* sp. nov. type material. **a.** holotype (BPBM D1871) *in situ*, **b.** preserved specimen of holotype (BPBM D1871), **c.** dry specimen of paratype (USNM 77480). **d.** polyps of holotype (BPBM D1871) under light microscopy, **e.** distal branches of paratype (USNM 77480) (scale bars: b = 8 cm; c = 8 cm; d = 2 mm).



**FIGURE 2.** Scanning electron micrographs of skeletal spines on various branches of the holotype of *Leiopathes annosa* sp. nov. (BPBM D1871; scale bars = 100  $\mu$ m).

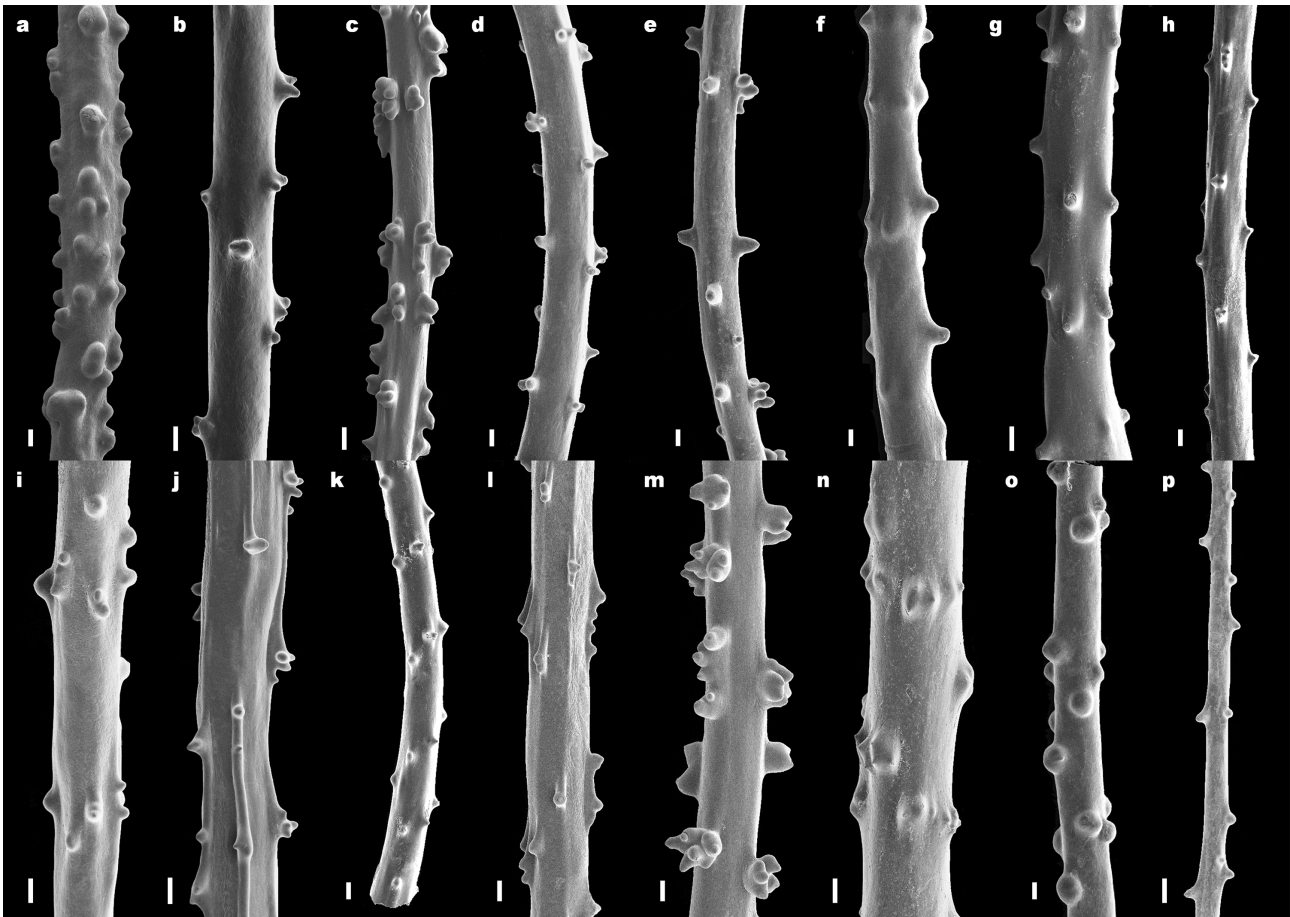




**FIGURE 3.** *In situ* photographs of *Leiopathes annosa* **sp. nov.** colonies examined as part of this study. **a.** BPBM D1871, **b.** USNM 1071417, **c.** BPBM 910, **d.** USNM 1071405, **e.** USNM 1071416, **f.** USNM 1070976, **g.** BPBM 1017, and **h.** BPBM 982 (photographs courtesy of HURL).

**Intraspecific variability and a unique morphotype.** The holotype and paratype of *Leiopathes annosa* **sp. nov.** both have skeletal spines that are smooth, hemispherical, often times multi-lobed, 30–225  $\mu\text{m}$  in height and 35–310  $\mu\text{m}$  in width. In the examination of the 14 additional specimens assigned to this species (see Table 1), skeletal spine morphology ranged widely even within the same specimen, and varied from hemispherical, balloon-shaped, irregularly knobby, multi-lobed, mound-like, conical and deltoid (Fig. 4a–o). However, spines with multiple lobes were present on all specimens assigned to *L. annosa* **sp. nov.** (see Table 1). Similar to skeletal spine morphology, the dimensions of skeletal spines varied between the 16 specimens assigned to *L. annosa* **sp. nov.** (Table 1), and ranged from an average height of 55  $\mu\text{m}$  and average basal width of 125  $\mu\text{m}$  for specimen USNM 1071417, to an average height of 95  $\mu\text{m}$  and average basal width of 190  $\mu\text{m}$  for specimen USNM 99500. However, the skeletal spines of all specimens assigned to *L. annosa* **sp. nov.**, ranged between 30–225  $\mu\text{m}$  in height and 35–

310  $\mu\text{m}$  in width at the base. In contrast, one specimen from Hawaiian waters (*Leiopathes* sp.; USNM 52278) was unique in that its skeletal spines were (1) much smaller (average = 40  $\mu\text{m}$ ; range = 20–65  $\mu\text{m}$ ), (2) narrower (average = 90  $\mu\text{m}$ ; range = 30–160  $\mu\text{m}$ ), and (3) had almost no multi-lobed spines (Fig. 4p). Additionally, while the polyp spacing of specimen USNM 52278 (1.2–3.05 mm) is similar to those of the specimens assigned to *L. annosa* sp. nov. (1.2–3.2 mm), its polyps are smaller (0.70–2.10 mm vs. 0.88–3.35 mm). Furthermore, the 16 Hawaiian specimens assigned to *L. annosa* sp. nov. were all collected at depths ranging between 295–536 m, whereas specimen USNM 52278 was collected in much deeper waters (966 m; Table 1). Based on these substantial differences, specimen USNM 52278 represents a distinct species that is morphologically more similar to *L. montana* and *L. glaberrima*. However, a more detailed study, ideally using both morphological and molecular markers, will be needed to determine the taxonomic identity and affinities of specimen USNM 52278.

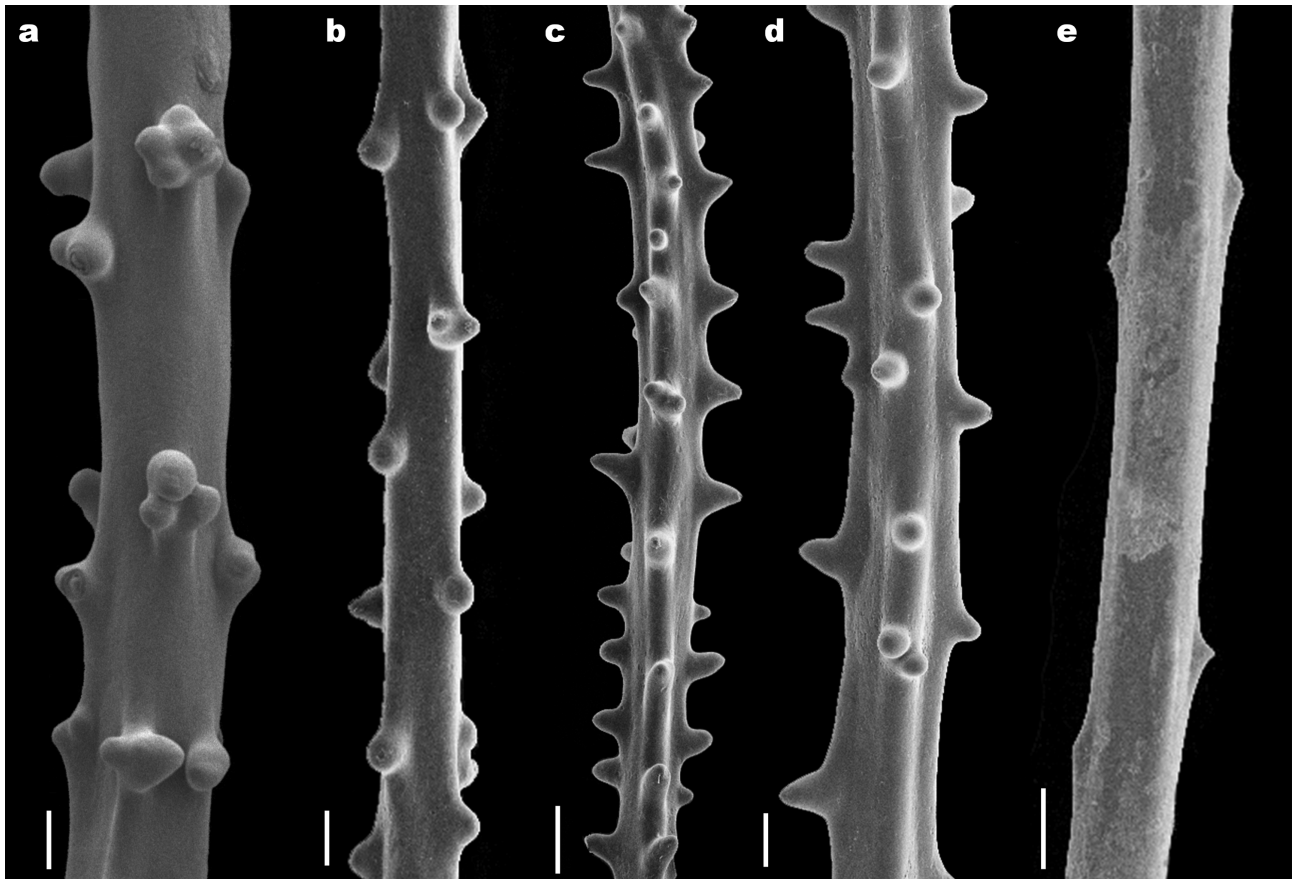


**FIGURE 4.** Scanning electron micrographs of skeletal spines of Hawaiian *Leiopathes* specimens examined as part of this study, assigned to *L. annosa* sp. nov. (a–o) and *Leiopathes* sp. (p). **a.** BPBM D1871, **b.** BPBM 910, **c.** BPBM 970, **d.** USNM 77082, **e.** USNM 77480, **f.** USNM 99500, **g.** USNM 99497, **h.** USNM 99496, **i.** USNM 1071405, **j.** USNM 1071416, **k.** USNM 1071417, **l.** USNM 1070976, **m.** USNM 1070976, **n.** USNM 1129919, **o.** USNM 99501 and **p.** USNM52278 (scale bars = 100  $\mu\text{m}$ ).

**Comparisons.** In Hawaiian waters, *Leiopathes annosa* sp. nov. has previously been referred to as *Leiopathes* sp. (Roark *et al.* 2009; Wagner *et al.* 2011; Wagner *et al.* 2012; Brugler *et al.* 2013) and *L. glaberrima* (Grigg and Opresko 1977; Grigg 1988; Chave and Malahoff 1988; Roark *et al.* 2006; Parrish and Baco 2007). As part of this study, we reexamined *in situ* photographs and specimens referenced in those previous studies, and as a result re-assigned those records to *L. annosa* sp. nov. The previous misidentification of the Hawaiian specimens as *L. glaberrima* was due to: (1) Hawaiian specimens were not compared to specimens from other geographic locations, and (2) diagnostic characters of *L. glaberrima* were largely unknown because Esper's (1792) original species description was quite brief and type material remained without further reexamination until recently (Opresko & Baron-Szabo 2001). The recent redescription of *L. glaberrima* has established the diagnostic characters of this species which include (1) triangular, simple and smooth spines which are 20–60  $\mu\text{m}$  tall, (2) polyps that are up to 1



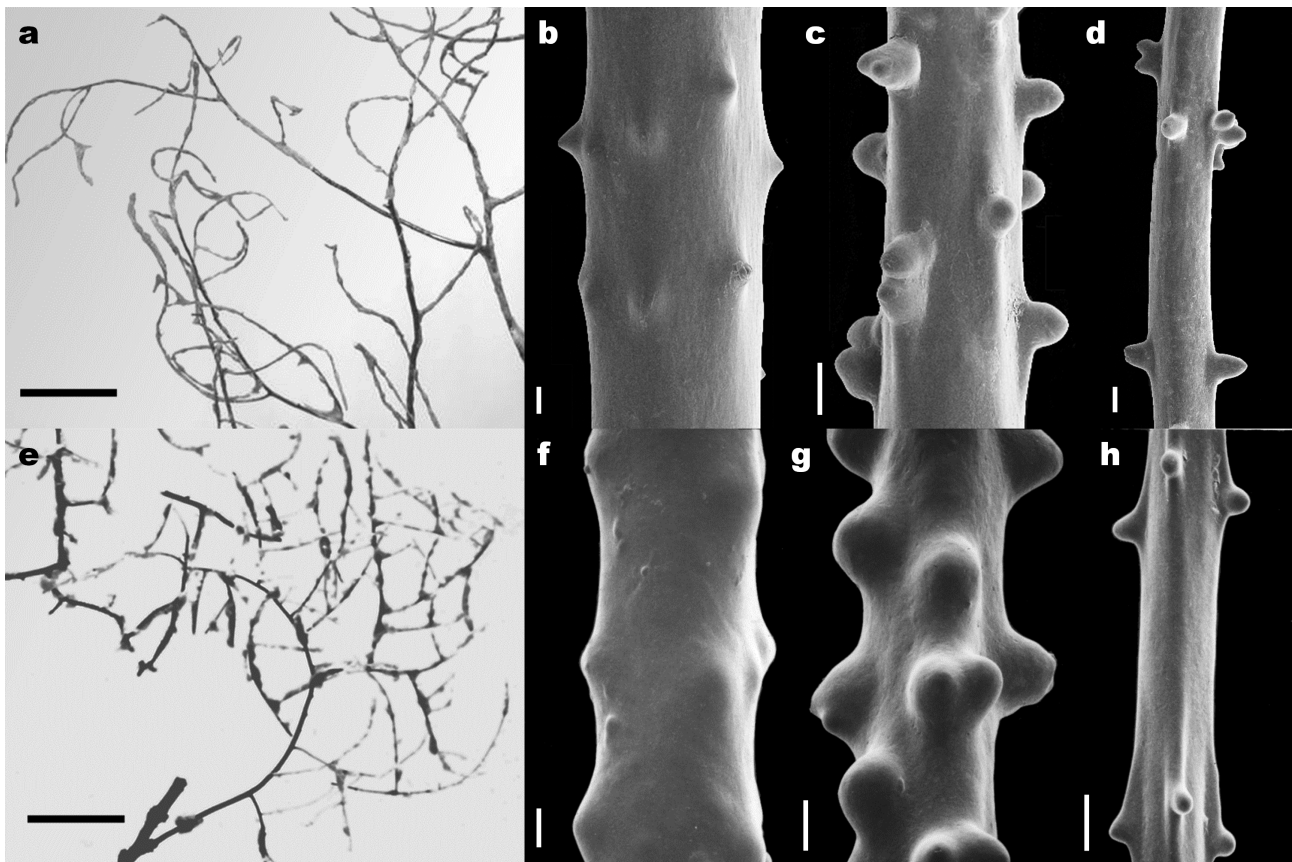
mm in diameter, (3) terminal branches with a length of 1–2 cm, and (4) an irregularly branched corallum (Opresko & Baron-Szabo 2001). *Leiopathes annosa* **sp. nov.** differs from *L. glaberrima* in that its spines are hemispherical and frequently multi-lobed, and substantially larger (30–225  $\mu\text{m}$ ) (Fig. 5a–e). Additionally, polyps of *L. annosa* **sp. nov.** reach a larger maximum size (3.35 mm) than those in *L. glaberrima* (1 mm), and its terminal branches are longer (< 6 cm). Finally, *L. annosa* **sp. nov.** colonies are fan-like and bright orange *in situ* (Fig. 1a, 3a–h), whereas living colonies of *L. glaberrima* are grayish-white, white, pale orange or bright orange, and branched irregularly (Bo 2008; Vertino *et al.* 2010; Mastrototaro *et al.* 2010; Bo *et al.* 2015). *Leiopathes glaberrima* has been reported to occur at depths as shallow as 37 m in the Gulf of Mexico (Opresko 2009) and as deep as 1532 m off Morocco (Grasshoff 1989), whereas *L. annosa* **sp. nov.** has a limited bathymetric range (295–536 m).



**FIGURE 5.** Scanning electron micrographs of skeletal spines of various *Leiopathes* spp. including **a.** *L. annosa* **sp. nov.** (BPBM D1871), **b.** *L. bullosa* (USNM 99409), **c.** *L. secunda* (USNM 99404), **d.** *L. acanthophora* (USNM 99402), and **e.** *L. glaberrima* (USNM 1099249) (scale bars = 100  $\mu\text{m}$ ).

*Leiopathes annosa* **sp. nov.** can be easily differentiated from all but one of the remaining seven described species of *Leiopathes* on the basis of the morphology of its skeletal spines (Fig. 5a–e). In *L. expansa*, *L. grimaldi*, *L. valdiviae*, *L. secunda*, *L. acanthophora* and *L. montana*, the spines are predominantly conical, subdeltoid or relatively tall (height greater than width at the base) with a rounded apex. In none of these seven species are the spines hemispherical or multi-lobed (see summary of species characteristics as given on Table 1 in Molodtsova 2011). Hemispherical spines are, however, found in *L. bullosa* (Fig. 5b, 6f–h). The major morphological difference between *L. annosa* **sp. nov.** and *L. bullosa* is the fact that in the former the spines, especially those on the terminal branches, can be multi-lobed (Fig. 4a–o, 6c–d), whereas in *L. bullosa* multi-lobed spines have not been reported (Fig. 6f–h). Other differences between the two species exist in the maximum thickness of the terminal branches (0.2 mm in *L. bullosa* and 0.4 mm in *L. annosa* **sp. nov.**), maximum length of the terminal branches (2 cm in *L. bullosa* and 6 cm in *L. annosa* **sp. nov.**), maximum size of the spines (140  $\mu\text{m}$  in *L. bullosa* and 225  $\mu\text{m}$  in *L. annosa* **sp. nov.**), arrangement of the spines (clearly in rows in *L. bullosa*, and not in discernable rows in *L. annosa* **sp. nov.**), maximum size of the polyps (2 mm in *L. bullosa* and 3.35 mm in *L. annosa* **sp. nov.**), and in the density of the polyps (3–5/cm in *L. bullosa* and 5–6/cm in *L. annosa*). *L. annosa* **sp. nov.** forms colonies that are large,

flabellate, with relatively thick branches (Fig. 1a, 3a–h). In comparison, the branches of *L. bullosa* are much thinner, and even though individual clusters of branches of the holotype were described as being somewhat planar, the holotype consists of small fragments, and therefore the size, shape, and branching pattern of intact colonies of *L. bullosa* are unknown.



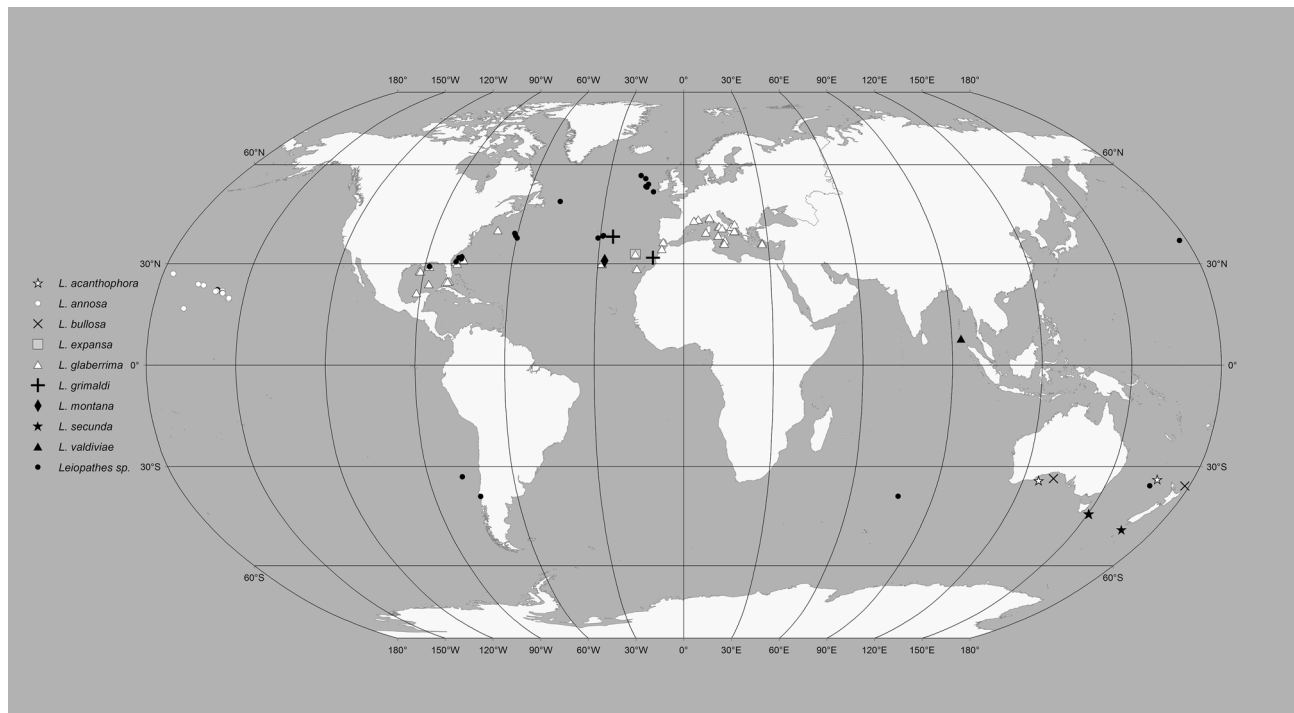
**FIGURE 6.** Comparison of branching pattern and skeletal spine morphology between **a–d.** *L. annosa* **sp. nov.** (USNM 77480), and **e–h.** *L. bullosa* (USNM 99409) (scale bars: a and e = 2 cm; b–d and f–h = 100 µm).

**Previous studies in Hawai‘i.** Several studies have reported on different ecological aspects of *L. annosa* **sp. nov.** in Hawai‘i (identified at the time as *L. glaberrima* or *Leiopathes* sp.), including on its: (1) growth rate and longevity (Roark *et al.* 2006; Roark *et al.* 2009), (2) population density (Grigg 1988), (3) associated fish assemblages (Parrish 2006), and (4) sexual reproduction (Wagner *et al.* 2011). Roark *et al.* (2006, 2009) used high-resolution skeletal radiocarbon measurements and estimated average radial growth rates of 5–13 µm/year for this species, corresponding to longevities ranging between 350–4,265 years, thus making this the longest living marine organism studied to date. Furthermore, Roark *et al.* (2009) concluded that growth rates are not uniform throughout the lifespan of this species, with faster initial growth rates that gradually decrease with age. Grigg (1988) examined the population densities of various dominant deep-water corals (365–400 m) off O‘ahu Island, and noted average densities of 0.002–0.003 colonies/m<sup>2</sup> for this species. Parrish (2006) studied fish assemblages within deep-water corals (300–500 m) across various Hawaiian Islands, and noted that various fish occasionally use taller colonies of *L. annosa* **sp. nov.** as shelter. Wagner *et al.* (2011) used histological techniques to study the reproductive anatomy of eight Hawaiian antipatharian species, including a sample of the *L. annosa* **sp. nov.** holotype, and noted that it had both previtellogenic and vitellogenic oocytes within its primary mesenteries. Finally, as part of a study on the evolutionary history of the order Antipatharia, Brugler *et al.* (2013) provided mitochondrial and nuclear DNA sequence data for two specimens (USNM 1070976 and BPBM D1871 as P4-227-2) that are assigned to *L. annosa* **sp. nov.** here (see Table 1 for GenBank accession numbers). Molecular sequences of these two specimens had identical sequences in the intergenic region between *nad5* and *nad1*, and between *cox3-cox1*, but did differ in a single position in the intergenic region between *trnW* and *nad2* (Brugler *et al.* 2013). Future studies will need to include a molecular component in order to determine whether the morphological analysis presented in this study

holds up, as well as to elucidate the taxonomic relationships among the various species within the genus *Leiopathes*.

**Etymology.** From the latin ‘*annosa*’ (long-lived) in reference to the extreme longevity estimates reported for this species (350–4,265 years; Roark *et al.* 2006; Roark *et al.* 2009).

**Distribution.** Under the name *L. glaberrima* or *Leiopathes* sp., *L. annosa* sp. nov., has previously been reported throughout the Hawaiian Islands (Grigg & Opresko 1977; Chave & Malahoff 1998; Parrish and Baco 2007; Roark *et al.* 2006; Roark *et al.* 2009; Wagner *et al.* 2011; Wagner *et al.* 2012; Brugler *et al.* 2013), as well as from Johnston Atoll (Chave & Malahoff 1998) at depths between 300–500 m. Specimens examined as part of this study were collected throughout the Hawaiian Archipelago from Hawai’i Island (19°30’00”N 155°00’00”W) to Salmon Bank (27°01’10”N 176°31’33”W) at depths between 295–536 m (Table 1).



**FIGURE 7.** World distribution of black coral species in the genus *Leiopathes*.

**Leiopathidae biogeography.** Within the monogeneric family Leiopathidae, seven species have been recorded from a limited geographic region, including (1) *L. expansa* from Madeira (Johnson 1899), (2) *L. montana* from the Great Meteor Seamount (Molodtsova, 2011), (3) *L. grimaldi* from two locations in the northeastern Atlantic (Roule 1905), (4) *L. valdiviae* from the Nicobar Islands (Pax 1915; Pax 1922), (5) *L. secunda* from Tasmania and New Zealand (Opresko 1998; Cairns *et al.* 2009), (6) *L. acanthophora* from South Australia and New Zealand (Opresko 1998; Cairns *et al.* 2009), and (7) *L. bullosa* from South Australia and New Zealand (Opresko 1998; Cairns *et al.* 2009), (Fig. 7). In contrast, *L. glaberrima* has been recorded from widespread geographic locations, including from throughout the Mediterranean (Gray 1857; Opresko & Baron-Szabo 2001; Bo 2008; Carlier *et al.* 2009; Sinniger & Pawlowski 2009; Deidun *et al.* 2010; Vertino *et al.* 2010; Mastrototaro *et al.* 2010; D’Onghia *et al.* 2012; Brugler *et al.* 2013; Angeletti *et al.* 2014; Bo *et al.* 2014a, 2014b, 2015; Fabri *et al.* 2014; Ingrassia *et al.* in press), the northeastern Atlantic (Johnson 1899; Grasshoff 1985, 1989; Brito & Ocaña 2004), the northwestern Atlantic and Caribbean (Brook 1889; Cairns *et al.* 1993; Williams *et al.* 2006, 2007; Opresko 2009) (Fig. 7). To the eight previously described species of *Leiopathes*, we here add *L. annosa* sp. nov. from the Hawaiian Archipelago and Johnston Atoll (Fig. 7). In addition to the described *Leiopathes* fauna, several undescribed and unidentified *Leiopathes* spp. have been reported from around the globe, including from the coasts off Chile (Häussermann & Försterra 2007; Yañez *et al.* 2009), the southeastern United States (Fernholm & Quattrini 2008; Ross & Quattrini 2009; Brugler *et al.* 2013), eastern Canada (Murillo *et al.* 2010), Ireland (Roberts *et al.* 2006; Wienberg *et al.* 2008; Le Guilloux *et al.* 2010), Saint Paul Island (Guerriero *et al.* 1988), Azores (Carreiro-Silva *et al.* 2013), New Zealand (Cairns *et al.* 2009) and Hawai’i (Parrish & Baco 2007; Baco 2007; Brugler *et al.* 2013; this report) (Fig.

7). Based on all available records, the Leiopathidae are currently known from tropical latitudes around the Nicobar Islands (7.80°N; Pax 1915; Pax 1922) to temperate latitudes off the coasts of Ireland (56.50°N; Wienberg *et al.* 2008) and New Zealand (48.80°S; Opresko 1998). The conspicuous absence of this family from polar regions (Fig. 7) may suggest that the geographic distribution of the Leiopathidae is limited by oceanographic or environmental conditions. Alternatively, the absence of Leiopathidae records from polar regions may be due to lower sampling efforts in these areas, and future collections in these regions will be needed to determine whether this is the case.

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## References

- Angeletti, L., Taviani, M., Canese, S., Fogliani, F., Mastrototaro, F., Argnani, A., Trincardi, F., Bakran-Petricioli, T., Ceregato, A., Chimentini, G., Macic, V. & Poliseo, A. (2014) New deep-water cnidarian sites in the southern Adriatic Sea. *Mediterranean Marine Science*, 15, 1–11.
- Baco, A.R. (2007) Exploration for deep-sea corals on North Pacific seamounts and islands. *Oceanography*, 20, 108–117. <http://dx.doi.org/10.5670/oceanog.2007.11>
- Bo, M. (2008) Taxonomy and ecology of Antipatharians. *Ph.D. Dissertation in Marine Biology and Ecology, Università Politecnica Delle Marche, Ancona, Italy*, 212 pp.
- Bo, M., Cerrano, C., Canese, S., Salvati, E., Angiolillo, M., Santangelo, G. & Bavestrello, G. (2014a) The coral assemblages of an off-shore deep Mediterranean rocky bank (NW Sicily, Italy). *Marine Ecology*, 35, 332–342.
- Bo, M., Bava, S., Canese, S., Angiolillo, M., Cattaneo-Vietti, R. & Bavestrello, G. (2014b) Fishing impact on deep Mediterranean rocky habitats as revealed by ROV investigation. *Biological Conservation*, 171, 167–176.
- Bo, M., Bavestrello, G., Angiolillo, M., Calcagnile, L., Canese, S., Cannas, R., Cau, A., D'Elia, M., D'Orlando, F., Follesa, M.C., Quarta, G. & Cau, A. (2015) Persistence of pristine deep-sea coral gardens in the Mediterranean Sea (SW Sardinia). *PLoS ONE*, 10, e0119393. <http://dx.doi.org/10.1371/journal.pone.0119393>
- Brito, A. & Ocaña, O. (2004) *Corales de las Islas Canarias*. Francisco Lemus: La Laguna, 477 pp.
- Brook, G. (1889) Report on the Antipatharia. Report of the scientific results of the voyage of the H.M.S. Challenger. *Zoology*, 32, 1–222.
- Brugler, M.R., Opresko, D.M. & France, S.C. (2013) The evolutionary history of the order Antipatharia (Cnidaria: Anthozoa: Hexacorallia) as inferred from mitochondrial and nuclear DNA: implications for black coral taxonomy and systematics. *Zoological Journal of the Linnean Society*, 169, 312–361. <http://dx.doi.org/10.1111/zoj.12060>
- Cairns, S.D., Opresko, D.M. & Hopkins, T.S. (1993) New records of deep-water Cnidaria (Scleractinia & Antipatharia) from the Gulf of Mexico. *Northeast Gulf Science*, 13, 1–11.
- Cairns, S.D., Gershwin, L.A., Brook, F.J., Pugh, P., Dawson, E.W., Ocaña, O., Vervoort, W., Williams, G., Watson, J.E., Opresko, D.M., Schuchert, P., Hine, P.M., Gordon, D.P., Campbell, H.J., Wright, A.J., Sanchez, J.A. & Fautin, D.G. (2009) The Phylum Cnidaria, Corals, Medusae and Hydroids. In: *New Zealand Inventory of Biodiversity*, volume 1. Kingdom Animalia, Canterbury University Press, Christchurch, New Zealand, pp. 59–101.
- Carlier, A., Le Guilloux, E., Olu, K., Sarrazin, J., Mastrototaro, F., Taviani, M. & Clavier, J. (2009) Trophic relationships in a deep Mediterranean cold-water coral bank (Santa Maria di Leuca, Ionian Sea). *Marine Ecology Progress Series*, 397, 125–137. <http://dx.doi.org/10.3354/meps08361>
- Carreiro-Silva, M., Andrews, A.H., Braga-Henriques, A., de Matos, V., Porteiro, F.M. & Santos, R.S. (2013) Variability in

- growth rates of long-lived black coral *Leiopathes* from Azores. *Marine Ecology Progress Series*, 473, 189–199.  
<http://dx.doi.org/10.3354/meps10052>
- Chave, E.H. & Malahoff, A. (1998) *In deeper waters: photographic studies of Hawaiian deep-sea habitats and life-forms*. University of Hawai'i Press: Honolulu, 136 pp.
- Deudin, A., Tsounis, G., Balzan, F. & Micallef, A. (2010) Records of black coral (Antipatharia) and red coral (*Corallium rubrum*) fishing activities in the Maltese Islands. *Marine Biodiversity Records*, 3, 1–6.
- D'Onghia, G., Maiorano, P., Carlucci, R., Capezzuto, F., Carluccio, A., Tursi, A. & Sion, L. (2012) Comparing deep-sea fish-fauna between coral and non-coral “megahabitats” in the Santa di Leuca cold-water province (Mediterranean Sea). *PLoS ONE*, 7, e44509.
- Esper, E.J.C. (1792) *Die Pflanzenthiere in Abbildungen nach der Natur mit Farben erleuchtet nebst Beschreibungen*. Vol. 2. Nürnberg: 133–164.
- Fabri, M.C., Pedel, L., Beuck, L., Galgani, F., Hebbeln, D. & Freiwald, A. (2014) Megafauna of vulnerable marine ecosystems in French Mediterranean submarine canyons: spatial distribution and anthropogenic impacts. *Deep-Sea Research II*, 104, 184–207.  
<http://dx.doi.org/10.1016/j.dsr2.2013.06.016>
- Fernholm, B. & Quattrini, A.M. (2008) A new species of hagfish (Myxinidae: Eptatretus) associated with deep-sea coral habitat in the western North Atlantic. *Copeia*, 1, 126–132.  
<http://dx.doi.org/10.1643/CI-07-039>
- Grasshoff, M. (1985) Die Gorgonaria und Antipatharia der Großen Meteor-Bank und der Josephine-Bank (Cnidaria: Anthozoa). *Seckenbergiana Maritima*, 17, 65–87.
- Grasshoff, M. (1989) Die Meerenge von Gibraltar als Faunen-Barriere: Die Gorgonaria, Pennatularia und Antipatharia der BALGIM-Expedition (Cnidaria: Anthozoa). *Seckenbergiana Maritima*, 20, 201–223.
- Grasshoff, M. (1991) Die von E. J. C. Esper 1788-1809 beschriebenen Anthozoa (Cnidaria). *Seckenbergiana Biologica*, 71, 325–368.
- Gray, J.E. (1857) Synopsis of the families and genera of axiferous zoophytes or barked corals. *Proceedings of the Zoological Society of London*, 25, 278–294.  
<http://dx.doi.org/10.1111/j.1096-3642.1857.tb01242.x>
- Grigg, R.W. (1988) Recruitment limitation of a deep benthic hard-bottom octocoral population in the Hawaiian Islands. *Marine Ecology Progress Series*, 45, 121–126.  
<http://dx.doi.org/10.3354/meps045121>
- Grigg, R.W. & Opreško, D.M. (1977) Order Antipatharia, black corals. In *Reef and Shore Fauna of Hawai'i. Section 1: Protozoa through Ctenophora.* (Eds. D.M. Devaney and L.G. Eldredge), Honolulu: Bishop Museum Press, pp. 242–261.
- Guerriero, A., D'Ambrosio, M. & Pietra, F. (1988) Leiopathic acid, a novel optically active hydroxydocosapentaenoic acid, and related compounds, from the black coral *Leiopathes* sp. of Saint Paul Island (S. Indian Ocean). *Helvetica Chimica Acta*, 71, 1094–1100.  
<http://dx.doi.org/10.1002/hlca.19880710523>
- Haeckel, E. (1896) *Systematische Phylogenie der wirbellosen Thiere (Invertebrata)*. Berlin. Verlag von Georg Reimer, 720 pp.  
<http://dx.doi.org/10.1515/9783111443935>
- Haime, J. (1849) Sur le polypieroides d'un *Leiopathes glaberrima*. *Annales des Sciences Naturelles*, 12, 224–226.
- Häussermann, V. & Försterra, G. (2007) Large assemblages of cold-water corals in Chile: a summary of recent findings and potential impacts. In: *Conservation and adaptive management of seamount and deep-sea coral ecosystems*, George, R.Y. & Cairns, S.D. (Eds.), Miami, FL: Rosenstiel School of Marine and Atmospheric Science, University of Miami, pp. 1–324.
- Ingrassia, M., Macelloni, L., Bosman, A., Chiocci, F.L., Cerrano, C. & Martorelli, E. (in press) Black coral (Anthozoa, Antipatharia) forest near the western Pontine Islands (Tyrrhenian Sea). *Marine Biodiversity*, pp. 195–207.
- Johnson, J.Y. (1899) Notes on the antipatharian corals of Madeira, with descriptions of a new species and a new variety, and remarks on a specimen from the West-Indies in the British Museum. *Proceedings of the Zoological Society of London*, 53, 813–824.  
<http://dx.doi.org/10.1111/j.1469-7998.1899.tb07913.x>
- Le Guilloux, E., Hall-Spencer, J.M., Söffker, M.K. & Olu, K. (2010) Association between the squat lobster *Gastroptychus formosus* and the cold-water corals in the North Atlantic. *Journal of the Marine Biological Association of the United Kingdom*, 90, 1363–1369.  
<http://dx.doi.org/10.1017/S0025315410000524>
- Mastrototaro, F., D'Onghia, G., Corriero, G., Matarrese, A., Maiorano, P., Panetta, P., Gherardi, M., Longo, C., Rosso, A., Sciuto, F., Sanfilippo, R., Gravili, C., Boero, F., Taviani, M. & Tursi, A. (2010) Biodiversity of the white coral bank off Cape Santa Maria di Leuca (Mediterranean Sea): an update. *Deep Sea Research Part II: Topical Studies in Oceanography*, 57, 412–430.  
<http://dx.doi.org/10.1016/j.dsr2.2009.08.021>
- Milne-Edwards, H. (1857) *Histoire Naturelle des Coralliaires*. Vol. 1. Paris, 326 pp.
- Molodtsova, T.N. (2011) A new species of *Leiopathes* (Anthozoa: Antipatharia) from the Great Meteor seamount (North Atlantic). *Zootaxa*, 3138, 52–64.



- Murillo, F.J., Duran Muñoz, P., Altuna, A. & Serrano, A. (2010) Distribution of deep-water corals of the Flemish Cap, Flemish Pass, and the Grand Banks of Newfoundland (Northwest Atlantic Ocean): interaction with fishing activities. *ICES Journal of Marine Science*, 68, 319–332.  
<http://dx.doi.org/10.1093/icesjms/fsq071>
- Opresko, D.M. (1998) Three new species of *Leiopathes* (Cnidaria: Anthozoa: Antipatharia) from southern Australia. *Records of the South Australian Museum*, 31, 99–111.
- Opresko, D.M. (2009) Antipatharia (Cnidaria) of the Gulf of Mexico. In: *Gulf of Mexico origin, waters, and biota. Vol. 1, Biodiversity*, Tunnell, J.W. Jr., Felder, D.L. & Earle, S.A. (Eds.), pp. 1385. Corpus Christi, TX: Texas A&M University Press, pp. 359–363.
- Opresko, D.M. & Baron-Szabo, R.C. (2001) Re-descriptions of the antipatharian corals described by E. J. C. Esper with selected English translations of the original German text (Cnidaria, Anthozoa, Antipatharia). *Seckenbergiana Biologica*, 81, 1–21.
- Parrish, F.A. (2006) Precious corals and subphotic fish assemblages. *Atoll Research Bulletin*, 543, 425–438.
- Parrish, F.A. & Baco, A.R. (2007) State of deep coral ecosystems: in the U.S. Pacific Islands region: Hawaii and the U.S. Pacific territories. In: *The state of deep coral ecosystems in the United States*, Lumsden, S.E., Hourigan, T.F., Bruckner, A.W. & Dorr, G. (Eds.), pp. 365. Silver Spring, MD: NOAA Technical Memorandum CRCP – 3, pp. 159–194.
- Pax, F. (1915) Diagnosen neuer Antipatharien. *Zoologische Anzeiger*, 45, 598–601.
- Pax, F. (1922) Die Antipatharien der Deutschen Tiefsee-Expedition. *Deutsche Tiefsee-Expedition, 1898–1899*, 3–5. Roark, E.B., Guilderson, T.P., Dunbar, R.B. & Ingram, B.L. (2006) Radiocarbon-based ages and growth rates of Hawaiian deep-sea corals. *Marine Ecology Progress Series*, 327, 1–14.  
<http://dx.doi.org/10.3354/meps327001>
- Roark, E.B., Guilderson, T.P., Dunbar, R.B., Fallon, S.J. & Mucciarone, D.A. (2009) Extreme longevity in proteinaceous deep-sea corals. *Proceedings of the National Academy of Sciences of the United States of America*, 106, 5204–5208.  
<http://dx.doi.org/10.1073/pnas.0810875106>
- Roberts, J.M., Wheeler, A.J. & Freiwald, A. (2006) Reefs of the deep: the biology and geology of cold-water coral ecosystems. *Science*, 312, 543–547.  
<http://dx.doi.org/10.1126/science.1119861>
- Ross, S.W. & Quattrini, A.M. (2009) Deep-sea reef fish assemblage patterns on the Blake Plateau (Western North Atlantic Ocean). *Marine Ecology*, 30, 74–92.  
<http://dx.doi.org/10.1111/j.1439-0485.2008.00260.x>
- Roule, L. (1905) Description des Antipathaires et Cérianthaires recueillis par S.A.S. le Prince de Monaco dans L'Atlantique nord. Fascicule XXX. Monaco.
- Sinninger, F. & Pawlowski, J. (2009) The partial mitochondrial genome of *Leiopathes glaberrima* (Hexacorallia: antipatharia) and the first report of the presence of an intron in COI in black corals. *Galaxea, Journal of Coral Reef Studies*, 11, 21–26.  
<http://dx.doi.org/10.3755/galaxea.11.21>
- Van Pesch, A.J. (1914) *The Antipatharian of the Siboga Expedition. Siboga-Expeditie*, 17. Leyden: E.J. Brill.
- Vertino, A., Savini, A., Rosso, A., Di Geronimo, I., Mastrototaro, Sanfilippo R., Gay, G. & Etiope, G. (2010) Benthic habitat characterization and distribution from two representative sites of the deep-water SML Coral Province (Mediterranean). *Deep Sea Research Part II: Topical Studies in Oceanography*, 57, 380–396.  
<http://dx.doi.org/10.1016/j.dsr2.2009.08.023>
- Wagner, D., Brugler, M.R., Opresko, D.M., France, S.C., Montgomery, A.D. & Toonen, R.J. (2010) Using morphometrics, *in situ* observations and genetic characters to distinguish among commercially valuable Hawaiian black coral species; a redescription of *Antipathes grandis* Verrill, 1928 (Antipatharia: Antipathidae). *Invertebrate Systematics*, 24, 271–290.  
<http://dx.doi.org/10.1071/IS10004>
- Wagner, D., Luck, D.G. & Toonen, R.J. (2012) The biology and ecology of black corals (Cnidaria: Anthozoa: Hexacorallia: Antipatharia). *Advances in Marine Biology*, 63, 67–132.  
<http://dx.doi.org/10.1016/b978-0-12-394282-1.00002-8>
- Wienberg, C., Beuck, L., Heidkamp, S., Hebbeln, D., Freiwald, A., Pfannkuche, O. & Monteys, X. (2008) Franken Mound: facies and biocoenoses on a newly-discovered "carbonate mound" on the western Rockall Bank, NE Atlantic. *Facies*, 54, 1–24.  
<http://dx.doi.org/10.1007/s10347-007-0118-0>
- Williams, B., Risk, M.J., Ross, S.W. & Sulak, K.J. (2006) Deep-water antipatharians: proxies of environmental change. *Geology*, 34, 773–776.  
<http://dx.doi.org/10.1130/G22685.1>
- Williams, B., Risk, M.J., Ross, S.W. & Sulak, K.J. (2007) Stable isotopes data from deep-water antipatharians: 400-year records from the southeastern coast of the United States of America. *Bulletin of Marine Science*, 81, 437–447.
- Yañez, E., Silva, C., Vega, R., Espindola, F., Alvarez, L., Solva, N., Palma, S., Salina, S., Menschel, E., Häussermann, V., Soto, D. & Ramirez, N. (2009) Seamounts in the southeastern Pacific Ocean and biodiversity on Juan Fernandez seamounts, Chile. *Latin American Journal of Aquatic Research*, 37, 555–570.