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New *Hamacantha* from Peru and resurrection of *Zygherpe* as subgenus (Demospongiae, Poecilosclerida, Hamacanthidae)

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Abstract

Two species of *Hamacantha* with tylostyles are reported here for the Peruvian coast, namely *H. desmacelloides* **sp.nov.** and *H. hyaloderma*. The former is the first species in the genus with apically microspined sigmas, similar to those known to occur in *Neofibularia*, and recently reported from genera *Biemna*, *Desmacella*, *Rhabderemia* and *Sigmaxinella*. *Hamacantha hyaloderma* was previously known from Mexico to Canada, and is here reported for the first time from the south east Pacific. The finding of a second species with tylostyles led us to reinstate subgenus *Hamacantha* (*Zygherpe*). The possible phylogenetic significance of apically microspined sigmas is discussed in view of recent findings on the basis of molecular data.

Key words: taxonomy, marine biodiversity, Porifera, southeastern Pacific, micromorphology, spicules

Introduction

The South East Pacific is a notoriously undersampled and understudied region as regards its sponges (Phylum Porifera; van Soest, 1994; Willenz *et al.*, 2009). Although several studies on the Chilean sponge fauna have been published in recent years (Hajdu *et al.*, 2006; Carvalho *et al.*, 2007, in press; Esteves *et al.*, 2007; Hajdu & Desqueyroux-Faúndez, 2008; Azevedo *et al.*, 2009; Willenz *et al.*, 2009), the rest of the South American coast has been relatively neglected. The few species recorded from Peru, mostly originated from deeper waters, with the consequence that shallow subtidal species, albeit more accessible, are less well known. With this perspective in mind, 2007 saw the launching of a concerted effort to extend the taxonomic inventory of South-eastern Pacific sponges into Peruvian waters. Nearly 900 samples were collected by SCUBA, snorkeling, wading at low tide, or even bought from beachfront artisans selling marine curios. Most samples were photographed *in situ* and studied using scanning electron microscopy (SEM), taxonomic descriptions of many have been started. Preliminary results of this concerted effort were published by Hooker (2008) and Aguirre *et al.* (2011).

In this article we describe a new species of *Hamacantha*, as well as redescribe and considerably extend the geographic range of *H. hyaloderma* de Laubenfels, 1932 along the coast of South America.

Material and methods

Eight specimens were collected by SCUBA diving on several localities along the Peruvian coast (Fig. 1). They were all photographed *in situ* and preserved in ethanol usually no longer than 2h after the end of the dive. Specimens were each split into four fragments, for deposition of similar materials at the Universidad Peruana

Cayetano Heredia (UPCH), the Royal Belgian Institute of Natural Sciences (RBINS), the Museu Nacional of Universidade Federal do Rio de Janeiro (MNRJ) and the Museum d'Histoire Naturelle de Genève (MHNG). Every specimen has been studied under SEM in a FEI/Philips XL30 ESEM TMP Microscope at the RBINSc. Dissociated spicules and thick anatomy sections (embedding in epoxy resin) were obtained according to procedures outlined in Hajdu *et al.* (2011) and Aguirre *et al.* (2011), respectively.

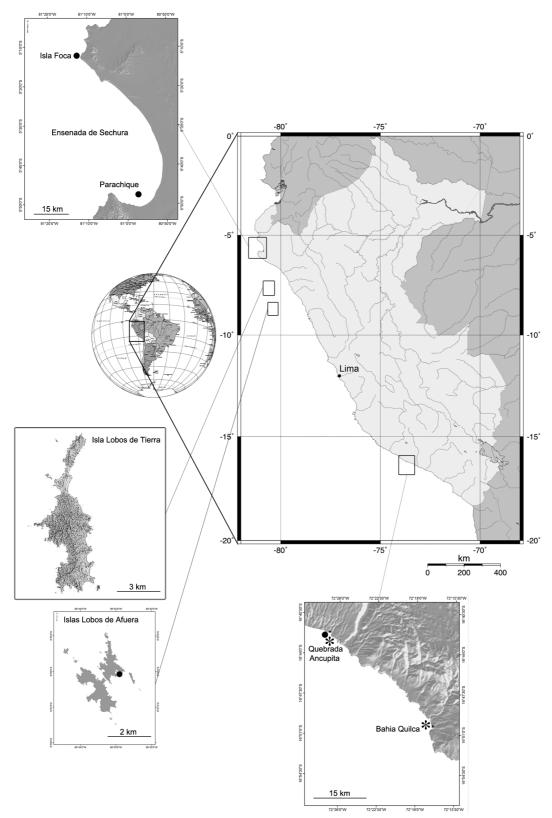


FIGURE 1. Schematic representation of the Peruvian coast, showing collecting localities in detail.

Systematics section

Phylum Porifera Grant, 1836

Class Demospongiae Sollas, 1885

Order Poecilosclerida Tospent, 1928

Family Hamacanthidae Gray, 1872

Genus Hamacantha Gray, 1867

Subgenus Zygherpe de Laubenfels, 1932 (revalidated)

Diagnosis. *Hamacantha* with tylostyles and encrusting habit. Type species—*Zygherpe hyaloderma* de Laubenfels, 1932: 65.

Remarks. De Laubenfels (1932) erected *Zygherpe* for encrusting sponges bearing tylostyles and diancistras. With a single species known, Hajdu (1994) argued that the occurrence of tylostyles per se was not a solid character on which to diagnose a new genus for sponges with diancistras and proposed the synonymy of *Zygherpe* with *Hamacantha*. Subsequently, Hajdu (2002) proposed to assign species with diactinal megascleres to subgenus *Hamacantha*, and those with monactinal megascleres to subgenus *Vomerula*. The finding of a second species sharing relevant morphologic features with *Hamacantha hyaloderma* suggests it is worth reinstating de Laubenfels' genus *Zygherpe*, here assigned to subgenus level, to further discriminate species with tylostyles from those with styles. The shared occurrence of encrusting habit, tylostyles and sigmas, as well as the overlapping distribution of *H. (Z.) desmacelloides* sp.nov. and *H. (Z.) hyaloderma* is remarkable.

Subgenera in Porifera are currently used as a convenient classification rank (Hooper, 2002; van Soest, 2002a, b; van Soest & Hajdu, 2002), with no general claim for monophyly. Most of these are former genus names, downgraded to subgeneric rank as a consequence of suspicion (or even confirmation) of their non-monophyly. It is beyond the scope of this contribution to debate whether or not these assemblages should be kept in use or abandoned altogether. Rather, the decision taken here aims to undo a possibly unjustified taxonomic decision taken by Hajdu (1994, 2002), when *Zygherpe* was synonymized with *Hamacantha*. The main argument used for the proposed synonimization was the redundancy of recognition of higher taxa for single species (which renders genus and species diagnoses the same). This argument collapsed after a second species with tylostyles was found by us in Peru. We had to choose between resurrecting *Zygherpe*, which we preferred, or to assign both species with tylostyles to either *Hamacantha (Hamacantha)* or *H. (Vomerula)*. The dichotomy between monactines and diactines suggested by the Systema Porifera classification for hamacanthids need not be entirely meaningful in evolutionary terms, and above all, there is no real evidence that species with tylostyles are possibly closer to those with styles than to others with oxeas. For this reason, we deemed convenient to take advantage of de Laubenfels' taxon, which is resurrected here to keep both species with tylostyles, until further evolutionary evidence convincingly points in an alternative direction.

Hamacantha (Zygherpe) desmacelloides sp. nov.

Figs 2A, 3, Table 1

Holotype. CZA 13661 (fragments from holotype MNRJ 13661, RBINS 13661, MHNG INVE 76156), Parachique (05°47'35.30" S–80°57'08.70" W), Bahía de Secchura, Peru, 7.4 m depth, coll. Y. Hooker, 07.xii.2009.

Paratypes. CZA 11342 (fragments MNRJ 11342, RBINS 11342, MHNG INVE 76155), Bahia Ladron (06°56'0.59" S–80°42'58.7" W), Islas Lobos de Afuera, Peru, 11.1 m depth, coll. Ph. Willenz & Y. Hooker, 04.x.2007. CZA 12167 (fragments MNRJ 12167, RBINS 12167, MHNG INVE 76162), small cove to the north of Quilca (16°42'06.10" S–72°26'54.0" W), Peru, 2.6 m depth, coll. Y. Hooker & M. Vilchez, 01.xii.2008. CZA 13690 (fragments MNRJ 13690, RBINS 13690, MHNG INVE 76157), Bajo Norte I (05° 12' 02.80" S–81° 12' 31.30" W), Isla Foca, Peru, 13.9 m depth, coll. Y. Hooker & M. Rios, 11.xii.2009. CZA 13699 (fragments MNRJ

13699, RBINS 13699, MHNG INVE 76158), Bajo Norte II (05°12'06.08" S-81°12'29.70" W), Isla Foca, Peru, 9.1 m depth, coll. Y. Hooker & M. Rios, 13.xii.2009.

Additional material. CZA 14501 (fragments MNRJ 14501, RBINS 14501), Islote Norte, Islas Lobos de Tierra, Peru, 8 m depth, coll. Y. Hooker & A. Gonzales, 14.ix.2010.

Diagnosis. This is the only encrusting *Hamacantha* with tylostyles, cyrtancistra-like diancistras and two categories of sigmas, both apically microspined.

Description (Fig 2A). The holotype covered over 10 x 5 cm in area, and now consists of two small fragments, the largest of which has 25 mm in maximum diameter and 2–3 mm maximum thickness. It is the thickest specimen found, all the remaining ones were no thicker than 1 mm, and were encrusting on rocky surfaces. The largest one, CZA 11342 covered ca. 15 x 7 cm in area. The sponge is light-yellow alive, and becomes beige in ethanol. A clear ectosomal reticulation is visible in the *in situ* photos of CZA 12167, and subectosomal canals were visible in CZA 12167, 13661 and 13699, but less obvious in CZA 11342. The consistency is fragile and the texture mostly reflects the underlying substratum.

TABLE 1. Comparative micrometric spicular data for the type series of *Hamacantha (Zygherpe) desmacelloides* sp.nov. and the Peruvian specimens of *H. (Z.) hyaloderma* (de Laubenfels, 1932). Comparative data for the latter was taken from the literature. Data presented as minimum length (standard deviation)–mean length–maximum length / minimum width–mean width–maximum width (n, when not 25), in micrometers.

	Tylostyles	Diancistras	Sigmas
H. (Z.) desmacelloides s	p. nov.		
holotype, 13661	138–276.8–426 / 5–6.4–10	162–190.6–219	I, 16–19.7–26 II, 8–11.2–14
paratype, 11342	211-304.4-502 / 5.4-12.4	148–176.8 –204	I, 18.6–24.8 II, 9.3–12.4
paratype, 12167	166-313.8-472 / 5-8.6-13	154–174.8–187	I, 20–26 II, 8.7–13.5
paratype, 13690	188–307.3–511 / 5–7.8–12	177-192.5-216	I, 17–20.8–23 II, 9.3–11.6–14.7
paratype, 13699	170-298.5-428 / 4-7.3-10	165–198.0–217 (x7)	I, 19–22.1–26 II, 9.3–10.4–14
14501	230-332.9-453 / 6-8.0-10	171-188.5-201	I, 17–20.3–23 II, 9–10.3–14
H. (Z.) hyaloderma			
12146	180-197.9-218 / 4.4-6.1	28-32.7-37	I, 31–62.0–87 II, 14–16.5–22
12160	149-177.7-201 / 5.2-5.8	26–30.7–34	I, 30–62.6–89 (x7) II, 14–20.5–23
12162	167–193.7–240 / 5.5	28-32.9-38	I, 33–49–76 II, 16–19.0–22
<i>sensu</i> de Laubenfels (1932), California	150 / 5	similar to length of sigmas (inferred from illustration)	25–50
type remeasured	173-195.7-230 / 6.5-7.9	29–32.8–37	I, 40–52.3–66 (x6) II, 23–25.9–32
s <i>ensu</i> Bakus (1966), Washington	146–253 / 3–8	26–41	I, 15–46
sensu Lee et al. (2007), California	142-227 / 5-7	23–41	I, 12–65
sensu Austin (unpubl.), measured here	149–176.9–199 / 5.8–8.9	33–36.1–40	I, 46–72 (x3) II, 13–16.5–23
sensu Gómez ¹	138–205 / 2.6–5.2	23–35	I, 36–61 II, 10.5–24.9

¹material from Carreón-Palau et al. (2003).



FIGURE 2. Hamacantha spp. from Peru, in situ. A, H. (Zygherpe) desmacelloides sp. nov., holotype. B, H. (Z.) hyaloderma (de Laubenfels, 1932), MNRJ 12160.

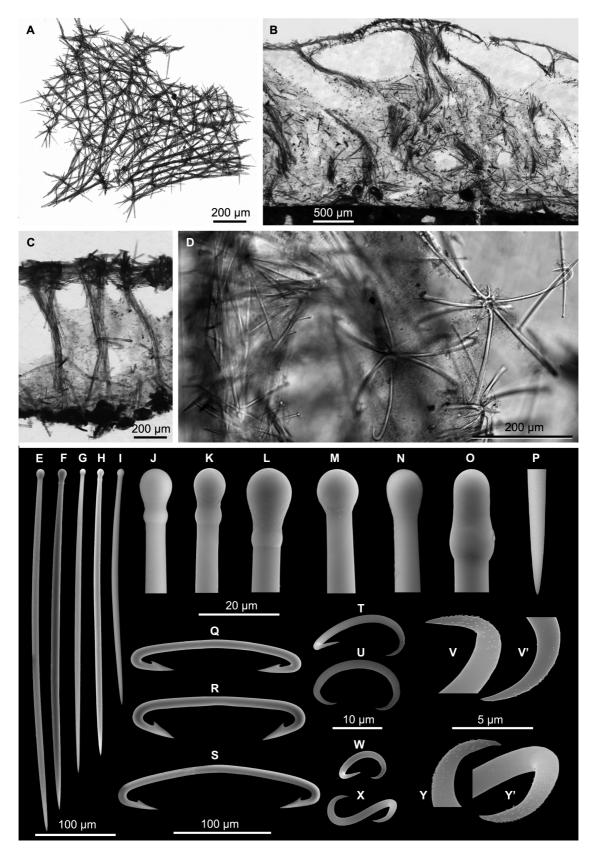


FIGURE 3. *Hamacantha (Zygherpe) desmacelloides* **sp. nov.** A, ectosomal architecture in tangential view. B–C, choanosomal architecture in transverse view. D, diancistras in rosettes. E–I, tylostyles. J–O, bases of tylostyles. P, apex of tylostyle. Q–S, diancistras. T–U, sigmas I (larger). V–V', terminal spination on sigmas I. W–X, sigmas II (smaller). Y–Y', terminal spination on sigmas II. (MNRJ 11342 = K, Q, V–V', X–Y'. MNRJ 12167 = F, H, L–M, O, R and W. MNRJ 13661 = E, G, J, T–U. MNRJ 13699 = I, N, P and S).

Skeleton (Figs. 3A–D). Ectosomal architecture (Fig. 3A) with a loose reticulation of tylostyles, either single or in paucispicular tracts. Pores (31–56 µm diameter) are seen in the meshes, and microscleres are abundant. Diancistras are mostly arranged in loose rosettes. Choanosomal architecture (Figs 3B–C) consists of short, sinuous, wispy longitudinal paucispicular tracts of tylostyles supporting the tangential ectosomal architecture. Scattered megascleres are common, as well as diancistras, the latter frequently disposed in rosettes around the longitudinal tracts (Figs 3C–D). The choanosomal framework arises from a discontinuous and variably thick tangential basal layer of megascleres and diancinstras.

Spicules (Figs 3E–Y', Table 1).

Megascleres. Tylostyles (Figs 3E–P), smooth, slender, mostly slightly curved with well pronounced heads, $138-511 / 5-13 \mu m$. Variations are straight shafted and subtylostylote forms, the latter with elliptical, sub-terminal heads. Microscleres. Diancistras (Figs 3Q–S), cyrtancistra-like, large, smooth, never notched, fimbriae restricted to the inner surfaces of hooks, which may project slightly off the plane of the main shaft, $104-219 \mu m$. Sigmas I (Figs T–V'), relatively stout, mostly contorted, apically microspined, $18-26 \mu m$. Sigmas II (Figs W–Y'), relatively stout, mostly contorted, microspined on both apical thirds or fourths, $8-16 \mu m$.

Distribution and ecology. The species was recorded between 2.6 and 13.9 m depth, and its distribution range stretches from 05°12' to 16°42' S. Water temperature in the collecting sites ranged from 13 to 21°C. The following species were observed in the underwater images obtained from the studied specimens: barnacles, brachiopods, bryozoans, ophiuroids, polychaetes, shrimps, and other sponges.

Etymology. The species name "*desmacelloides*" recognizes its similarity to some *Desmacella* spp., where the combination of tylostylote megascleres and sigma microscleres is a recurrent occurrence.

Remarks. The diancistras in the new species resemble the cyrtancistras of *Pozziella* (Hajdu, 1994; Díaz-Agras, 2008). We preferred to restrict the use of the term cyrtancistra to the gigantic sigmoid microscleres of the latter genus(103–760 μ m long), which are most often of considerably hemispherical morphology, were not yet reported to form rosettes, and come next to exotyles. These are generally larger than the megascleres co-occurring in the same species, which is not the case in the new species described here, nor on additional *Hamacantha* spp. with somewhat similar diancistra morphology [e.g. *H. popana* (de Laubenfels, 1935)].

The only other *Hamacantha* known to possess tylostyles and an encrusting habit, *H. hyaloderma* (see below), can be easily differentiated from the new species through the latter's possession of cyrtancistra-like diancistras which are over three times larger and of a different morphology, as well as two categories of apically microspined sigmas, in contrast to two or three smooth categories in *H. hyaloderma*. All other species of *Hamacantha* have either diactinal or styloid monactinal megascleres, when sigmas are present, these were not reported to be apically microscpined, and in general they are not thinly encrusting. The new species appears to us well differentiated from all *Hamacantha* spp.

Hamacantha (Zygherpe) hyaloderma (de Laubenfels, 1932)

Figs 2B, 4, Table 1

Material studied. CZA 12146 (fragments deposited in MNRJ 12146, RBINS 12146, MHNG INVE 76161), Quebrada Ancupita (16°50'13.3" S–72°17'28.3" W), Matarani, Peru, 3.7 m depth, coll. Y. Hooker & U. Zanabria, 27.xi.2008. CZA 12160 (fragments deposited in MNRJ 12160, RBINS 12160, MHNG INVE 76163), Bahia Quilca (16°42'06.10" S–72°26'54.0" W), Quilca, Peru, 10.4 m depth, coll. Y. Hooker & M. Vilchez, 30.xi.2008. CZA 12162 (fragments deposited in MNRJ 12162, RBINS 12162, MHNG INVE 76160), Bahia Quilca (16°42'06.10" S–72°26'54.0" W), Quilca, Peru, 8.0 m depth, coll. Y. Hooker & M. Vilchez, 30.xi.2008.

Comparative material: Holotype, USNM 22060, Point Lobos (California, USA), 13.vii.1930, det. M.W. de Laubenfels. MNRJ 3428, Kanuka Bay (San Juan Island, Washington, USA), 25.iv.1959, det./leg. G.J. Bakus. MNRJ 14504, Samsun Narrrows opposite Bold Bluff (British Columbia, Canada), 06.v.2008, det./leg. W.C. Austin. CNPGG 363, Bahía Tortugas (Baja California Sur, Mexico), 15.iv.1997, det. P. Gómez.

Diagnosis. This is the only encrusting *Hamacantha* with tylostyles, regular diancistras and two categories of smooth sigmas.

Description (Fig. 2B). All three specimens collected were encrusting over granitic boulders, and were about 1 mm thick. The largest one, CZA 12162 covered approximately 20 x 10 cm in area. The sponge is yellow (CZA 12146) or orangy-yellow (CZA 12162) alive, and becomes beige in ethanol. Its surface bears conspicuous

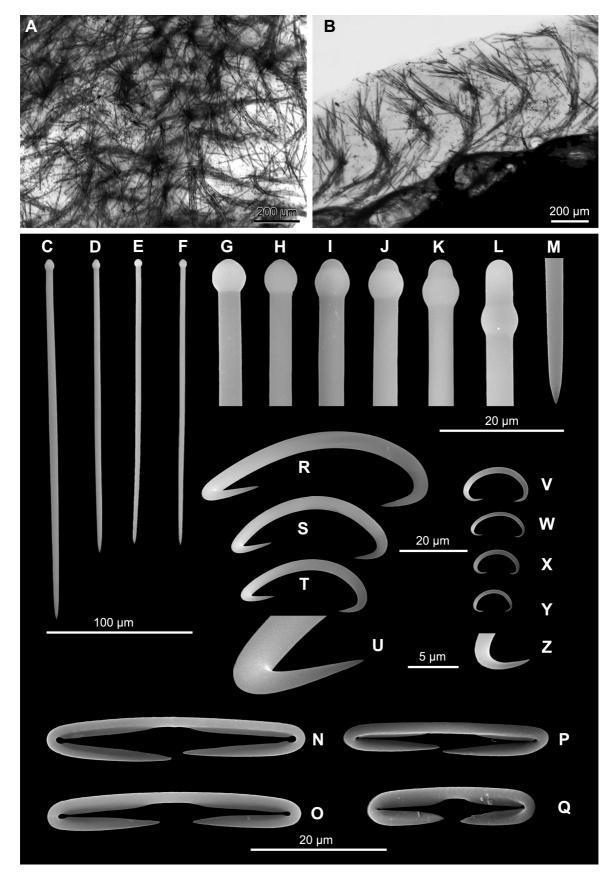


FIGURE 4. *Hamacantha (Zygherpe) hyaloderma* (de Laubenfels, 1932), Peruvian specimens. A, ectosomal architecture in tangential view. B, choanosomal architecture in transverse view. C–F, tylostyles. G–L, bases of tylostyles. M, apex of tylostyle. N–Q, diancistras. R–T, sigmas I (larger). U, smooth end of sigma I. V–Y, sigmas II (smaller). Z, smooth end of sigmas II. (MNRJ 12146 = D–H, J, K–M, R–Z. MNRJ 12162 = C, I, N–Q).

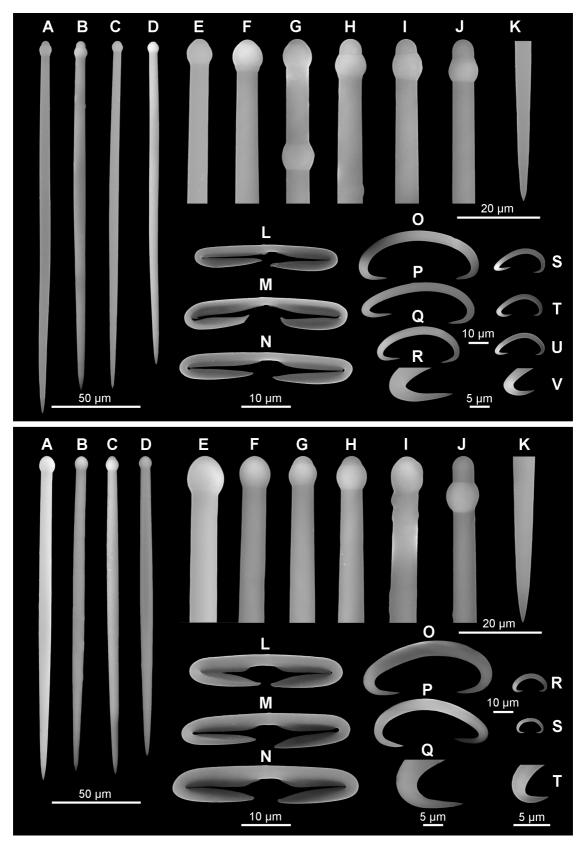


FIGURE 5. *Hamacantha (Zygherpe) hyaloderma* (de Laubenfels, 1932). Holotype (USNM 22060), on top (A–V). A–D, tylostyles. E–J, bases of tylostyles. K, apex of tylostyle. L–N, diancistras. O–Q, sigmas I (larger). R, smooth end of sigma I. S–U, sigmas II (smaller). V, smooth end of sigmas II. Canadian specimen, below (A–T). A–D, tylostyles. E–J, bases of tylostyles. K, apex of tylostyle. L–N, diancistras. O–P, sigmas I (larger). Q, smooth end of sigma I. R–S, sigmas II (smaller). T, smooth end of sigmas II.

meandering subectosomal canals, leading to a few scattered oscula up to 1 mm in diameter. Texture is smooth, and consistency somewhat fragile.

Skeleton (Figs 4A–B). Ectosomal architecture unspecialized. Only scattered microscleres occur, and the wispy terminations of ascending choanosomal tracts (Fig. 4A). Choanosomal architecture with sinuous ascending wispy tracts of megascleres (Fig. 4B).

Spicules (Figs 4C–Z, Table 1). Megascleres. Tylostyles (Figs 4C–M), smooth, mostly slender and straight, heads well pronounced, usually spherical, frequently subterminal, $149-240 / 4.4-6.1 \mu m$. Microscleres. Diancistras (Figs 4N–Q), small, smooth, mostly contorted, with conspicuous notches, hooks run parallel to axis which has fimbriae on both apical thirds, 26–38 μm . Sigmas I (Figs 4R–U, uncommon), relatively stout, smooth, contorted, 30–89 μm . Sigmas II (Figs 4V–Z, abundant), relatively stout, smooth, contorted, 14–23 μm .

Distribution and ecology. Specimen CZA 12162 was partly epibiotic over a gastropod, and several cirripeds and polychaete tubes. In Peru the species was found between 3.7 and 10.4 m depth, between Matarani (16°42'S) and Quilca (16°50'S). Water temperature in the collecting sites was 14-15°C. The species appeared to be one of the dominant members of the community in shaded habitats in the Quebrada Ancupita. This species was reported by Goddard (1983) to be common in Oregon and one of the preferred items in the diet of the opisthobranch mollusc *Montereina nobilis* MacFarland, 1905.

Remarks. *Hamacantha hyaloderma* was originally reported from California (de Laubenfels, 1932; Lee *et al.*, 2007), and subsequently found in Washington (Bakus, 1966), Oregon (Goddard, 1983) and British Columbia (Austin *et al.*, 2012), thus suggesting the species to be of cold temperate affinity. The exception to this was Carreón-Palau *et al.*'s (2003) record from Lower California. Surprisingly, given the large geographic gap, we were able to find this species in southern Peru. In the absence of molecular data to show the contrary, we are confident to determine both SE and NE Pacific specimens as conspecific. Table 1 compares micrometric measurements obtained from the materials studied here and those available in the literature (or re-evaluated), and together with Fig. 5, shows how similar SE and NE Pacific materials are in terms of spicule dimensions. On the other hand, the morphologic variability compiled for NE Pacific specimens might be hiding an underlying genetic structure. For instance, the British Columbia specimen analyzed has abundant small sigmas (13–23 μ m), and exceedingly rare large ones (> 46 μ m). This is markedly distinct from what is observed in the species' holotype, where rather small sigmas (< 23 μ m) appear to be absent. If there is a hidden species complex, the Peruvian specimens might quite likely pertain to a new species given their apparent isolation.

Discussion

The new species is peculiar in several respects, noteworthy among these, the possession of apically microspined sigmas. This character was restricted to the poecilosclerid families Desmacellidae Ridley & Dendy, 1886 and Rhabderemiidae Topsent, 1928. Recent reshuffling of demosponge classification based on 18S, 28S and CO1 sequencing (Morrow *et al.*, 2012, 2013; Redmond *et al.*, 2013) resulted in its current distribution in two order-level clades. One of these, the newly proposed Biemnida Morrow, 2013 [not yet uptaken in the World Porifera Database classification (van Soest *et al.*, 2014) which is adopted here], as a consequence of these sigmas occurring in *Biemna, Neofibularia, Rhabderemia* and *Sigmaxinella*. The other, the Poecilosclerida, if Desmacellidae is maintained in this order, albeit its basal phylogenetic position.

The phylogenetic position of Hamacanthidae has been discussed by Hajdu (1994) who argued that it was close to Mycalidae on the basis of the shared occurrence of rosettes and true toxas. The striking similarity between diancistras and clavidiscs [*Merlia* spp, Kirkpatrick (1908)] was argued to possibly reflect the symplesiomorphic occurrence of sigmancistra derivatives in these sponges. On the other hand, Hajdu (2002) noticed that the fossil record for diancistras and clavidiscs is much older, dating back to the lower Jurassic (Mostler, 1990), while that for anisochelae dates back to the lower Cretaceous only (Gruber & Reitner, 1991; Wiedenmayer, 1994). This is indicative that from an evolutionary perspective, a close relationship between *Hamacantha* and *Merlia* is actually a sound hypothesis. The latter relationship was also recently recovered in a morphological phylogenetic study of genera contained in the Mycalina Hajdu, van Soest & Hooper, 1994 (Hajdu *et al.*, 2013), but awaits double checking via molecular tools. As yet there are no published sequences of *Hamacantha*, but complete 18S sequences point to *Merlia* being at the base of the poecilosclerid clade (Redmond *et al.*, 2013). This brings us back

to the issue of whether terminally microspined sigmas are monophyletic or not. Morrow *et al.* (2013) proposed a new order, Biemnida Morrow, 2013, to accommodate the Biemnidae Hentschel, 1923 and Rhabderemiidae Topsent, 1928, at the base of the Tetractinellida Marshall, 1876. The terminally microspined sigmas known from *Biemna, Desmacella, Neofibularia, Sigmaxinella*, and recently reported from *Rhabderemia* (Cedro *et al.*, 2013), are argued here as being possibly homologous to the sigmaspires of Spirophorida Bergquist & Hogg, 1969, in a transformation series as previously proposed for sigmancistras, cyrtancistras/diancistras and clavidiscs (Hajdu, 1994). One would then expect *Hamacantha*, on account of its terminally microspined sigmas reported in this study, and by extrapolation, *Merlia*, to group in the Biemnida too. Thus far, this scenario has not been retrieved in phylogenetic analyses of any sort. For this reason, Hamacanthidae is here still treated within the Poecilosclerida.

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