



# Tropical Eastern Pacific Amphoriscidae Dendy, 1892 (Porifera: Calcarea: Calcaronea: Leucosolenida) from the Peruvian coast

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Received: 19 March 2018 / Revised: 12 October 2018 / Accepted: 18 February 2019 / Published online: 19 March 2019  
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## Abstract

Two new species of Amphoriscidae Dendy, 1892 (Porifera Grant, 1836: Calcarea Bowerbank, 1862: Leucosolenida Hartman, 1958) from the northern coast of Peru, Tropical Eastern Pacific, are described integrating molecules and morphology. *Leucilla mancoraensis* sp. nov. is a tube-shaped sponge with apical osculum, sylleibid aquiferous system, and a skeleton composed of cortical triactines and giant tetractines, thick subatrial triactines, and atrial tetractines with short apical actines. *Paraleucilla tarazonai* sp. nov. is the first record of *Paraleucilla* Dendy, 1892 for the Eastern Pacific and presents a skeleton formed of cortical microdiactines, diactines, triactines, and tetractines, subatrial triactines, and atrial triactines and tetractines. These two species are provisionally endemic to the northern coast of Peru (Guayaquil ecoregion). Our phylogenetic analysis, which included the largest number of Amphoriscidae species, was congruent with previous studies. The family Amphoriscidae including an *Amphoriscus* Haeckel, 1870 species as well as the genera *Leucilla* Haeckel, 1872 and *Paraleucilla* were recovered as non-monophyletic groups. Despite being polyphyletic, information on species distribution of this family is relevant for diversity studies; consequently, we present the geographic distribution of each genus of Amphoriscidae.

**Keywords** *Amphoriscus* · *Leucilla* · *Paraleucilla* · C-region of LSU · Tropical East Pacific province · Guayaquil ecoregion

*Leucilla mancoraensis* sp. nov. is registered in ZooBank under urn:lsid:zoobank.org:act:F7BA6F47-9205-4F93-950B-43A96970DDFD  
*Paraleucilla tarazonai* sp. nov. is registered in ZooBank under urn:lsid:zoobank.org:act:03448075-D3C5-445B-AFC5-5DCA800EE07E

Communicated by D. Janussen

This article is registered in ZooBank under urn:lsid:zoobank.org: pub: 2E7AA716-8B23-41B5-AA63-EDB985C4E5F0

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## Abbreviations

GW	Gert Wörheide
IRB	Institut Ruđer Bošković, Zagreb, Croatia
MNRJ	Museu Nacional of Universidade Federal do Rio de Janeiro, Brazil
PMR	Prirodoslovni Muzej Rijeka, Croatia
QM	Queensland Museum, Australia
RMNH	Rijksmuseum van Natuurlijke Historie Leiden, Netherlands
SAM	South Australian Museum, Australia
UFRJPOR	Porifera collection of the Biology Institute of Universidade Federal do Rio de Janeiro, Brazil
WAMZ	Zoological collection of the Western Australian Museum, Perth, Australia
ZMA.POR	Zoologisch Museum, Instituut voor Systematiek en Populatiebiologie, Amsterdam, The Netherlands

## Introduction

The Eastern Pacific harbours a great variety of coastal ecosystems and submarine habitats with different sea currents and comprises the entire Tropical Eastern Pacific realm and the Eastern sides of the Temperate Northern Pacific and the Temperate South America realms (Spalding et al. 2007). Despite several sampling campaigns in this large area, subsequent published inventories (Breitfuss 1898; Wilson 1904; Thiele 1905; Lendenfeld 1910a, b, 1915; de Laubenfels 1930; Austin 1996; Azevedo et al. 2009, 2015; Willenz et al. 2009; Hajdu et al. 2013), and sponge species descriptions (Desqueyroux-Faúndez and Van Soest 1996; Díaz et al. 2005; Aguirre et al. 2011; Hajdu et al. 2015; Fernández et al. 2016; Lehnert and Stone 2017; Carballo et al. 2018; Gómez et al. 2018), the Eastern Pacific is still one of the least studied marine regions in terms of diversity and distribution of sponges of the class Calcarea (Porifera: Calcarea) (Van Soest et al. 2012).

Up to date, only 34 species of Calcaronea Bidder, 1998 (Porifera, Calcarea) are known from the Eastern Pacific, 11 from the Temperate Northern Pacific (Lambe 1893; Urban 1902, 1906; de Laubenfels 1930; Duplessis and Reisinger 2000; Lehnert and Stone 2017), three from the Tropical Eastern Pacific (Hôzawa 1940), and 20 from the Temperate South America (Haeckel 1872; Ridley 1881; Breitfuss 1898; Tanita 1942; Azevedo et al. 2009). The low number of species reported from the Tropical Eastern Pacific may not reflect the real diversity of the subclass Calcaronea in that area, but instead the lack of sampling effort and taxonomy expertise.

Amphoriscidae comprises Calcaronea diagnosed as “Leucosolenida with syconoid, sylleibid or leuconoid organisation, and a distinct cortex supported by tangential tetractines with centripetal apical actines crossing the outer part, or the whole choanosome. Tangential triactines and small tetractines may be also present in the cortex. The choanoskeleton is typically inarticulate, composed of the apical actines of cortical tetractines, and the unpaired actines of subatrial spicules. In species with a thick wall, scattered triactines and/or tetractines may also be present, either in the inarticulate choanoskeleton, or forming a distinct subatrial layer. An atrial skeleton is always present” (Borojević et al. 2002). Although molecular phylogenies reject the monophyly of this family (Voigt et al. 2012; Alvizu et al. 2018; Córdor-Luján et al. 2018), it is still accepted in the systematics of Calcarea, as an alternative system could not yet been established (Hooper and Van Soest 2002).

Amphoriscidae comprises three genera, *Leucilla* Haeckel, 1872, *Paraleucilla* Dendy, 1892, and *Amphoriscus* Haeckel, 1870 (Borojević et al. 2002), and includes 45 species distributed worldwide (Van Soest et al. 2018). Among those species, only *Leucilla nuttingi* (Urban, 1902) had been recorded from the Eastern Pacific (Temperate Northern Pacific, California).

In a previous study (Azevedo et al. 2015), we reported five new species and three new records of Calcinea (Porifera, Calcarea) from Peru, all of them from the Temperate South America and the Tropical Eastern Pacific realms. In this work, we present two new Amphoriscidae from the Tropical Eastern Pacific province (Guayaquil ecoregion).

## Material and methods

### Sample collection

All samples analysed in this study were collected in the northern coast of Peru, Guayaquil ecoregion, in the Tropical Eastern Pacific province. Specimens were collected in five localities (Fig. 1) at depths varying from the intertidal to 15 m, from 2007 to 2009, during the expeditions of projects ESPER (Esponjas del Perú) and EsponjAS (Esponjas da América do Sul).

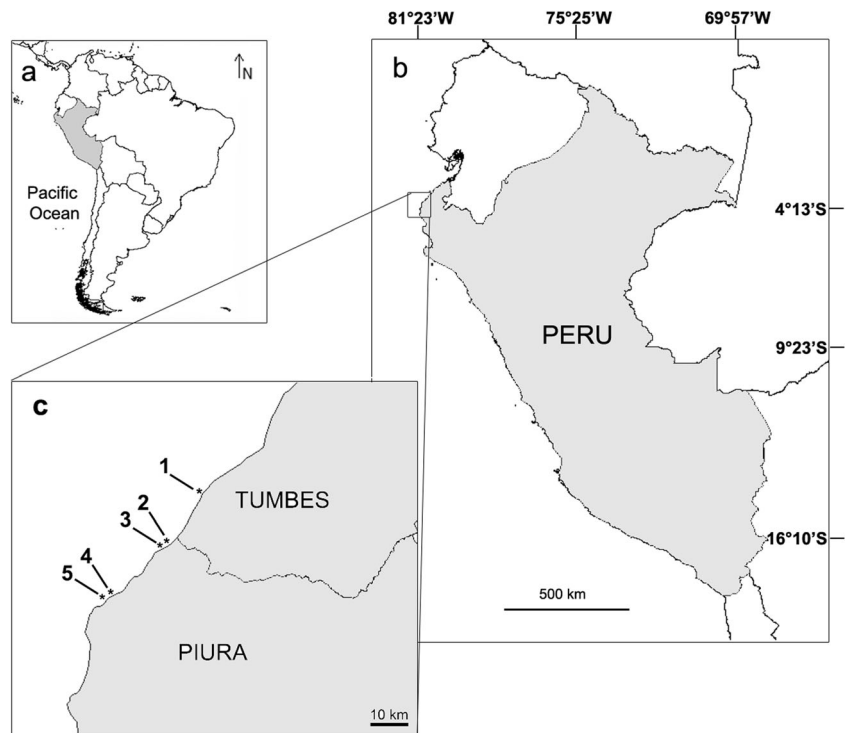
All specimens were preserved in ethanol 96% and were deposited in the sponge collections of the Museu Nacional of the Universidade Federal do Rio de Janeiro (MNRJ), Brazil; Colección de Zoología Acuática, Laboratorio de Biología Marina/Universidad Peruana Cayetano Heredia (CZA), Peru; and the Royal Belgian Institute of Natural Sciences (RBINS), Belgium.

### Morphological analyses

The external morphology and the internal anatomy of each specimen were assessed. Characteristics of the surface, presence of oscula, consistency, texture, and colour were analysed on the preserved specimens under a stereomicroscope and complemented with information retrieved from the in situ pictures and field notes.

Preparations of spicules and sections followed standard procedures (Wörheide and Hooper 1999; Klautau and Valentine 2003). To illustrate the species descriptions, micrographs were taken with a digital camera AxioCam MRC5 coupled to a Zeiss Imager A2 microscope. Additional spicule preparations were made for scanning electron microscopy (SEM) following procedures detailed in Azevedo et al. (2015). SEM micrographs were recorded at the Royal Belgian Institute of Natural Sciences on a FEI/Philips XL30 ESEM at 20 to 30 kv, or at the Institute of Biology of Universidade Federal do Rio de Janeiro (UFRJ) on a JSM-6510. Spicule measurements were made using an ocular micrometre. The length and width at the base of the actines of each spicule category were taken ( $n = 20$ ). Identifications followed the Systema Porifera (Hooper and Van Soest 2002) and other appropriate literature (e.g. Cavalcanti et al. 2014; Córdor-Luján et al. 2018).

**Fig. 1** Collection sites of Amphoriscidae in Peru. **a** Location of Peru in South America (grey); **b** Detail of Peru indicating the study area; **c** Sampled localities: (1) Punta Sal Resort, Tumbes; (2) Máncora Beach, Piura; (3) Máncora Pier, Piura; (4) El Ñuro site 4, north of Quebrada Verde, Piura; (5) El Ñuro site 7, south of Quebrada Verde, Piura



## Molecular analyses

The C-region of LSU (28S rDNA) was amplified using the primers fwd: 5'-GAAAAGCACTTTGAAAAGAGA-3' (Voigt and Wörheide 2016) and rv: 5'-TCCG TGTTTCAAGACGGG-3' (Chombard et al. 1998). DNA extraction, amplification, and sequencing followed Córdor-Luján et al. (2018).

Sequences used in recent phylogenies (Van Soest and de Voogd 2015; Klautau et al. 2016; Voigt and Wörheide 2016; Alvizu et al. 2018; Córdor-Luján et al. 2018) were retrieved from the GenBank database and are listed in Table 1, as well as those generated in this study. Sequences were aligned through the MAFFT v.7 online platform (Katoh and Standley 2013) using the strategy Q-INS-i (Katoh and Toh 2008). The nucleotide substitution model that best fitted the alignment was indicated by the Bayesian Information Criterion in MEGA 6 (Nei and Kumar 2000; Tamura et al. 2013): TN93 + G.

Phylogenetic reconstructions were performed under two approaches: Bayesian inference (BI) and maximum likelihood (ML). BI analyses were executed in MrBayes 3.1.2 (Huelsenbeck and Ronquist 2001; Ronquist and Huelsenbeck 2003) under  $10^6$  generations and a 25% burn-in, generating a consensus tree of majority with clades supported with posterior probability values. ML analyses were conducted in MEGA 6 using an initial NJ tree (BIONJ) and bootstrap analysis of 1000 pseudo-replicates. To estimate the genetic interspecific distances, we calculated the uncorrected

p-distance in MEGA 6. The obtained molecular phylogeny and p-distance values were used to confirm species identifications.

## Results

### Morphology

Phylum Porifera Grant, 1836

Class Calcarea Bowerbank, 1862

Subclass Calcaronea Bidder, 1898

Order Leucosolenida Hartman, 1958

Family Amphoriscidae Dendy, 1892

Genus *Leucilla* Haeckel, 1872

Diagnosis: Amphoriscidae with sylleibid or leuconoid organisation. Choanoskeleton formed primarily by apical actines of giant cortical tetractines, and unpaired actines of subatrial triactines or tetractines. Dispersed spicules may occur, but typical articulated choanoskeleton is always absent (Borojevic et al. 2002, emend.)

Type species: *Leucilla amphora* Haeckel, 1872 (by subsequent designation; Dendy and Row 1913)

*Leucilla mancoraensis* sp. nov. (Figs. 2 and 3, Table 2)

Diagnosis: *Leucilla* with tubular to ovoid body, apical osculum, sylleibid aquiferous system, and skeleton composed of cortical triactines and giant tetractines, subatrial triactines with

**Table 1** Species names, locality where the specimen was collected, voucher numbers, and GenBank accession numbers used in this study

Species	Locality	Voucher number	GenBank accession number
<b>In-group</b>			
<i>Amphoriscus pedunculatus</i>	Brazil	UFRJPOR 6004	MH028217*
<i>Anamixilla torresi</i> (T)	Australia	-	AY563536
<i>Anamixilla singaporensis</i>	Singapore	RMNH.POR.9350	MF686073
<i>Breitfussia schulzei</i>	West Greenland	FB61	MH385228
<i>Grantia compressa</i> (T)	France	-	AY563538
<i>Grantiopsis heroni</i>	Australia	QMG313670 (H)	JQ272261
<i>Grantiopsis cylindrica</i> (T)	Australia	GW973	JQ272263
<i>Heteropia minor</i>	Indonesia	RMNH.POR.1872	MF686070
<i>Kebira tetractinifera</i>	South Africa	ZMA.POR.15245 (H)	MF872786
<i>Kebira uteoides</i> (T)	Red Sea	RMNH.POR.9563	MF872784
<i>Leucandra ananas</i>	Norway	SA136	MH385249
<i>Leucandra aspera</i>	France	-	AY563535
<i>Leucandra falakra</i>	Adriatic Sea	PMR13748	KT447560
<i>Leucandra</i> cf. <i>gausapata</i>	Antarctic	HT15	MH385252
<i>Leucandra mozambiquensis</i>	Mozambique	ZMA.POR.22408b	MF872766
<i>Leucandra nicolae</i>	Australia	QMG313672 (H)	JQ272268
<i>Leucandra penicillata</i>	West Greenland	FB40	MH385253
<i>Leucandra pilula</i>	Seychelles	ZMA.POR.10528 (H)	MF872767
<i>Leucandra spinifera</i>	Adriatic Sea	IRBSG3	KT447561
<i>Leucandra</i> sp.	Coral Sea	QMG316285	JQ272265
<i>Leucascandra caveolata</i> (T)	Australia	QMG316057	JQ272259
<i>Leucandrilla</i> sp.	Galapagos	GAL2017	MF872768
<i>Leucandrilla quadriradiata</i>	Curaçao	UFRJPOR 6705 (H)	MF472618
<i>Leucilla antillana</i>	Curaçao	UFRJPOR 6768 (H)	MF472615
<i>Leucilla mancoraensis</i> sp. nov.	Peru	MNRJ 12967 (P)	MH028214*
<i>Leucilla micropilosa</i>	Curaçao	UFRJPOR 6755 (H)	MF472621
<i>Paragrantia waguensis</i>	Japan	RMNH.POR.9317	KT277668
<i>Paraleucilla dalmatica</i>	Adriatic Sea	PMR-13747	KT447565
<i>Paraleucilla dalmatica</i>	Portugal	PT03	MH385276
<i>Paraleucilla dalmatica</i>	Madeira Island	PT05	MH385277
<i>Paraleucilla erpenbecki</i>	Mozambique	ZMA.POR.22409C (P)	MF872728
<i>Paraleucilla magna</i>	Brazil	GW824	JQ272267
<i>Paraleucilla magna</i>	Adriatic Sea	IRB-P14	KT447564
<i>Paraleucilla magna</i>	Portugal	PT06	MH385279
<i>Paraleucilla magna</i>	St. Helena	SA84	MH385282
<i>Paraleucilla perlucida</i>	São Pedro e São Paulo Archipelago	UFRJPOR 6515	MH028215*
<i>Paraleucilla tarazonai</i> sp. nov.	Peru	MNRJ 11448 (H)	MH028216*
<i>Paraleucilla</i> sp. 1	St. Helena	SA83	MH385283
<i>Paraleucilla</i> sp. 2	St. Helena	SA85	MH385284
<i>Sycon ancora</i>	Adriatic Sea	IRB SD12	KT447568
<i>Sycon caminatum</i>	Madeira Island	PT02	MH385301
<i>Sycon carteri</i>	Australia	SAM-PS0143	JQ272260
<i>Sycon conulosum</i>	Curaçao	UFRJPOR 6707 (H)	MF472620
<i>Sycon magnapicale</i>	Curaçao	UFRJPOR 6748 (H)	MF472622
<i>Sycon scaldiense</i>	North Sea	ZMA.POR.21237	MF686095
<i>Sycon spinispiculum</i>	Norway	SA36	MH385312
<i>Sycon villosum</i>	Norway	AA05	MH385313
<i>Teichonopsis labyrinthica</i> (T)	Australia	SAM-PS0228	JQ272264
<i>Ute ampullacea</i>	Australia	QMG313669 (H)	JQ272266
<b>Out-group</b>			
<i>Eilhardia schulzei</i>	Australia	QMG316071	JQ272256
<i>Leuconia nivea</i>	-	-	AY563534
<i>Petrobiona massiliana</i> (T)	Mediterranean Sea	GW1729	JQ272307

“-” means no data available

T type species of the genus, H holotype, P paratype

\*Sequences generated in the present study

thick actines (10–40  $\mu\text{m}$ ), and atrial tetractines with short apical actines (18–65  $\mu\text{m}$ ). Trichoxeas can be added to the cortex.

**Etymology:** named after its type locality.

**Type locality:** Máncora Beach, Piura

**Type material:** (Holotype/ethanol): MNRJ 12948; Máncora Beach, Piura, Piura Region, Peru (04° 06' 20.50" S–81° 03' 34.00" W); collected by Y. Hooker, F. Menendez, and Ph. Willenz; intertidal; 17 November 2009. (Paratypes/ethanol): MNRJ 12967; Máncora Pier, Piura, Piura Region, Peru (04° 06' 35.65" S–81° 04' 02.41" W); collected by Y. Hooker, F. Menendez, and Ph. Willenz; 2.9 m depth; 18 November 2009. MNRJ 13075; Punta Sal Resort, Tumbes Region, Peru (03° 59' 02.70" S–80° 59' 11.40" W); collected by Y. Hooker and Ph. Willenz; intertidal; 2 December 2009

**Additional material examined:** MNRJ 12988; El Ñuro site 7, south of Quebrada Verde, Piura Region, Peru (04° 13' 30.40" S–81° 12' 31.60" W); collected by Y. Hooker and F. Menendez; 15.0 m depth; 19 November 2009. MNRJ 21304 and MNRJ 21305; El Ñuro site 4, north of Quebrada Verde, Piura Region, Peru (04° 13' 22.30" S–81° 12' 24.10" W); collected by Y. Hooker, M. Rios, and Ph. Willenz; 4.0–5.0 m depth; 14 October 2007

**Colour:** yellowish-beige in life (Fig. 2a) and white in ethanol (Fig. 2b)

**Morphology and anatomy:** sponge with a tubular to ovoid body with an apical osculum (Fig. 2a, b) supported by sagittal tetractines and with a feeble crown of trichoxeas (Fig. 2c). The holotype (MNRJ 12948) measures  $1.5 \times 4.5 \times 4.0$  mm (Fig. 2a, b). Surface rough and consistency friable. Aquiferous system sylleibid with several spherical chambers ranging, in the largest diameter, from 110 to 176  $\mu\text{m}$  (Fig. 2d)

**Skeleton:** osculum ornamented with short, delicate trichoxeas, imperceptible under the stereomicroscope. Oscular margin composed only of tetractines (Fig. 2c). Cortical skeleton formed of triactines, the basal system of giant tetractines and few scattered trichoxeas. Triactines and tetractines are tangentially distributed on the cortex (Fig. 2e), whereas trichoxeas are arranged perpendicularly (Fig. 2f). Choanosomal skeleton inarticulate, formed by the apical actine of the giant cortical tetractines and the unpaired actine of the subatrial triactines (Fig. 2g). Apical actine of the tetractines crosses the choanosome. Atrial skeleton formed by tetractines bearing a very short apical actine projected into the atrium (Fig. 2h).

**Spicules:**

**Cortical triactines:** sagittal. Actines are conical, straight with sharp tips. Paired actines can be longer than the unpaired ones (Fig. 3(a–d)). Size: 130–378/11–32  $\mu\text{m}$  (paired) and 118–410/11–27  $\mu\text{m}$  (unpaired)

**Cortical tetractines:** sagittal. Actines are conical, straight with sharp tips. The apical actine is the longest actine, and it can be distally undulated (Fig. 3(e–g)). Size: 140–583/16–54  $\mu\text{m}$  (paired), 313–658/11–54  $\mu\text{m}$  (unpaired), and 184–994/16–54  $\mu\text{m}$  (apical)

**Subatrial triactines:** sagittal. Actines are conical, straight with sharp tips. The unpaired actine is frequently longer than the paired ones (Fig. 3(h–l)). Size: 118–389/11–43  $\mu\text{m}$  (paired) and 238–616/11–43  $\mu\text{m}$  (unpaired)

**Atrial tetractines:** sagittal. Actines are conical with sharp tips. Paired actines are often shorter than the unpaired ones, and they are curved (Fig. 3(m)). Size: 84–227/10–18  $\mu\text{m}$  (paired) and 103–284/10–19  $\mu\text{m}$  (unpaired) and 19–59/7–12  $\mu\text{m}$  (apical)

**Ecology:** this species was found living from the intertidal down to 15 m depth. Some specimens (MNRJ 11448 and 12948) were associated with bryozoans and algae, in a highly silted area.

**Geographical distribution:** provisionally endemic to the northern coast of Peru (Piura and Tumbes regions). Corresponding MEOW: Guayaquil ecoregion, Tropical East Pacific Province (TEP)

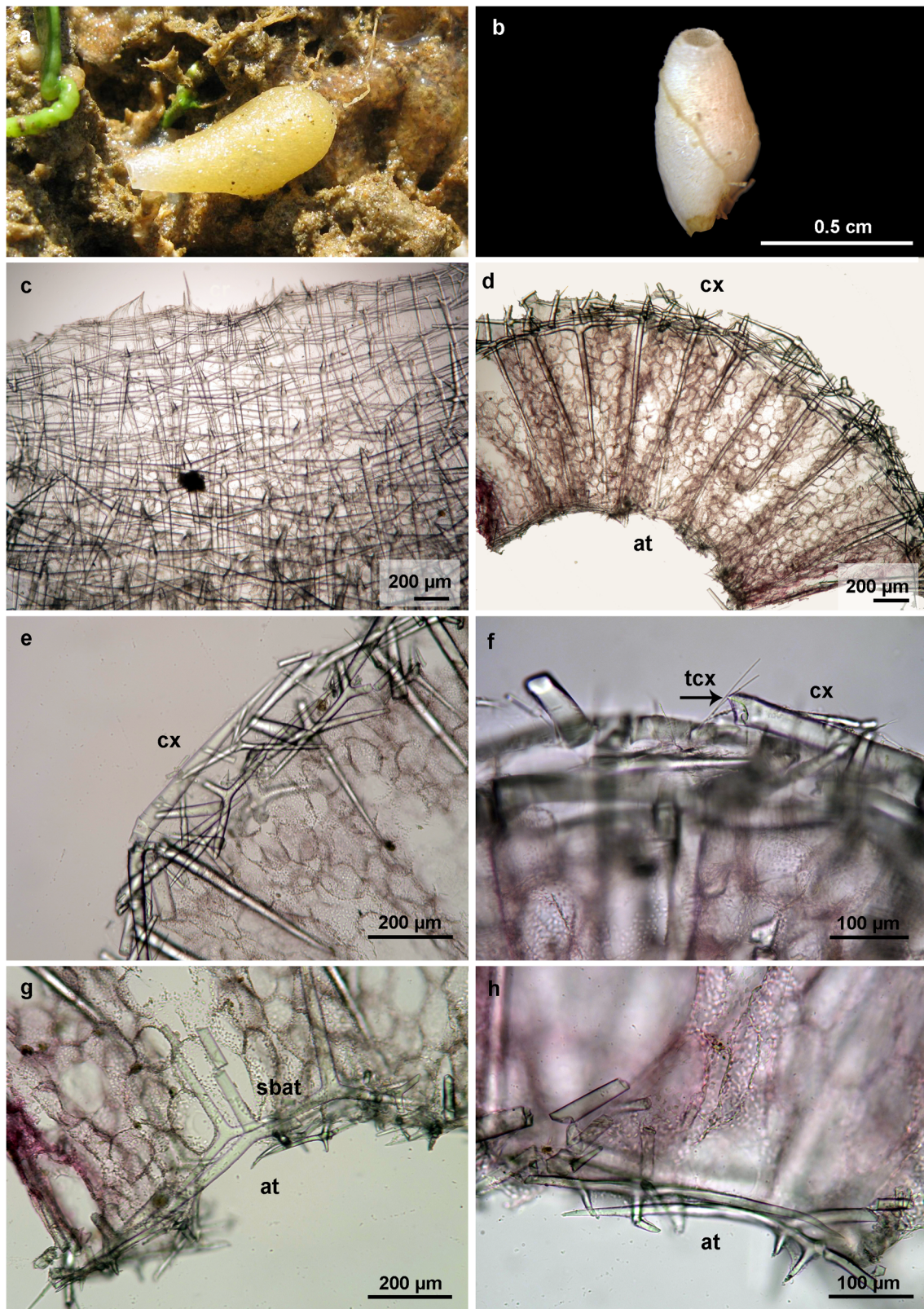
**Remarks:** the species that most resemble *Leucilla mancoraensis* sp. nov. are *L. micropilosa* Córdor-Luján, Louzada, Hajdu & Klautau, 2018 from Curaçao and *L. nuttingi* from California, as they have sylleibid aquiferous system and share similar spicule composition (cortical triactines and tetractines, subatrial triactines, and atrial tetractines). Although Lanna et al. (2017) had showed that specimens of *Leucilla* could be young paraleucillas, *Leucilla mancoraensis* sp. nov. has sylleibid aquiferous system, a type of aquiferous system known only in *Leucilla*.

*Leucilla micropilosa* is well-characterised by the presence of cortical microdiactines, which are absent in *L. mancoraensis* sp. nov. In addition, the skeleton of the new species present thicker subatrial triactines (26–28  $\mu\text{m}$ ) compared to *L. micropilosa* (14  $\mu\text{m}$ ).

Unlike *L. mancoraensis* sp. nov., *L. nuttingi* has a stem and microdiactines protruding through the cortex. Moreover, in *L. nuttingi*, the cortical triactines and tetractines have similar width (40  $\mu\text{m}$ ) and are located in the same layer (see Urban 1902, Plate XIV, Fig. 2), whereas in *L. mancoraensis* sp. nov. (holotype measurements), the cortical triactines (14  $\mu\text{m}$ ) are thinner than the tetractines (31–37  $\mu\text{m}$ ), which are located in a subjacent layer.

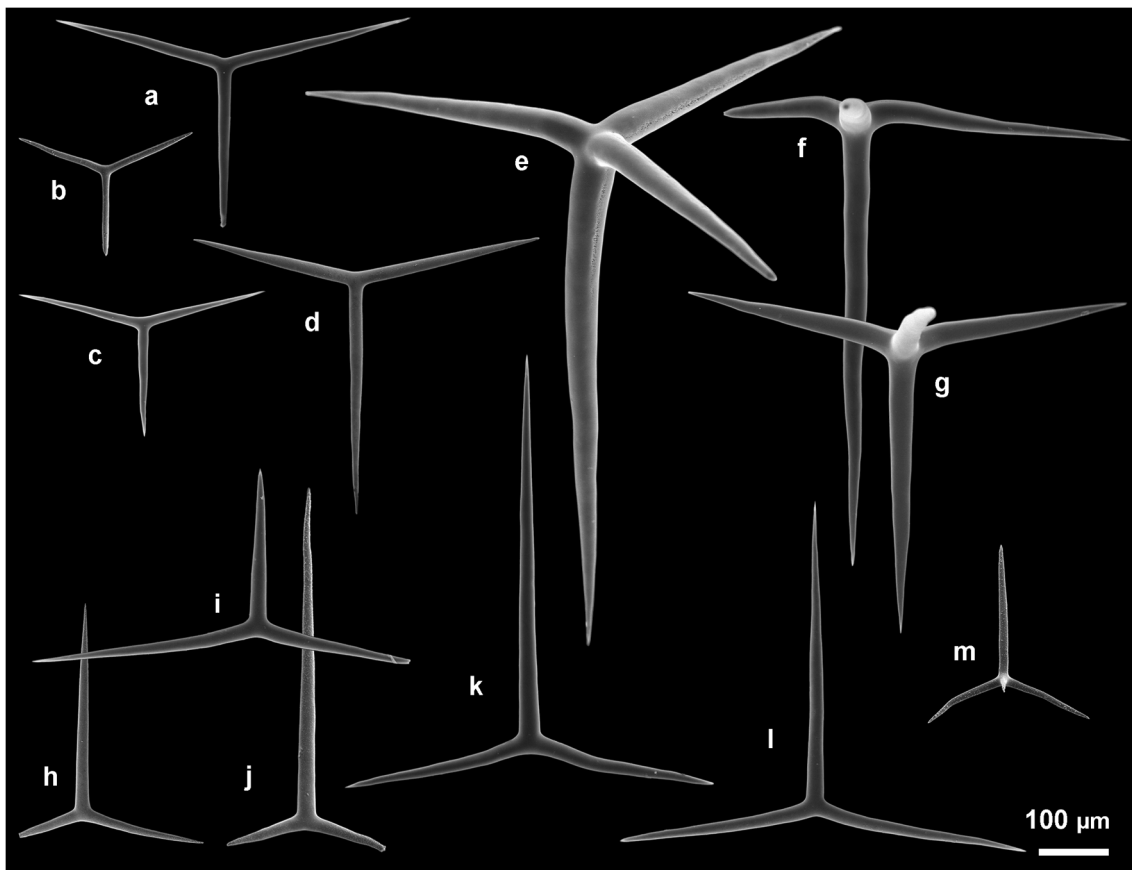
**Genus *Paraleucilla* Dendy, 1892**

**Diagnosis:** “Amphoriscidae with leuconoid organisation. The thick wall is divided into two regions. The outer region is supported by the skeleton, which remains essentially inarticulate, with the apical actines of cortical tetractines pointed inwards, and a layer of triactines and/or tetractines with the unpaired actine pointed outwards. The inner region of the choanoskeleton is intercalated between the original subatrial skeleton and the atrial one, and it is supported by large triactines and/or tetractines, that are scattered in disarray, and whose form is similar to the spicules found in the outer layer of the choanoskeleton, or inside the atrial skeleton. Because the original subatrial layer still remains in the outer part of the



**Fig. 2** *Leucilla mancoraensis* sp. nov. (MNRJ 12948, holotype). **a** Specimen in vivo; **b** Specimen after fixation; **c** Ocular margin supported by tetractines; **d** Cross section of the skeleton; **e** Cortex with

triactines and tetractines; **f** Cortex with trichoxeas; **g** Subatrial triactines; **h** Atrium with apical actines of tetractines. *cx* cortex, *at* atrium, *tcx* trichoxea, *sbat* subatrial triactine



**Fig. 3** Spicules of *Leucilla mancoraensis* sp. nov. (MNRJ 12948, holotype). **a–d** Cortical triactines; **e–g** Cortical tetractines; **h–l** Subatrial triactines; **m** Atrial tetractine

choanosome, facing the cortical tetractines, there are no typical subatrial spicules adjacent to the atrial skeleton” (Borojevic et al. 2002).

Type species: *Leucandra cucumis* Haeckel, 1872 (by monotypy)

*Paraleucilla tarazonai* sp. nov. (Figs. 4 and 5, Table 3)

Diagnosis: *Paraleucilla* with massive body, osculum without crown, skeleton composed of rare large diactines ( $> 1100/27 \mu\text{m}$ ), cortical spined thin microdiactines ( $54\text{--}189/1\text{--}3 \mu\text{m}$ ), cortical triactines and tetractines, subatrial triactines, and atrial triactines and tetractines with short apical actines ( $33\text{--}135 \mu\text{m}$ )

Etymology: named after the ecologist Juan Tarazona Barboza who greatly contributed to the understanding of the Peruvian marine ecosystem

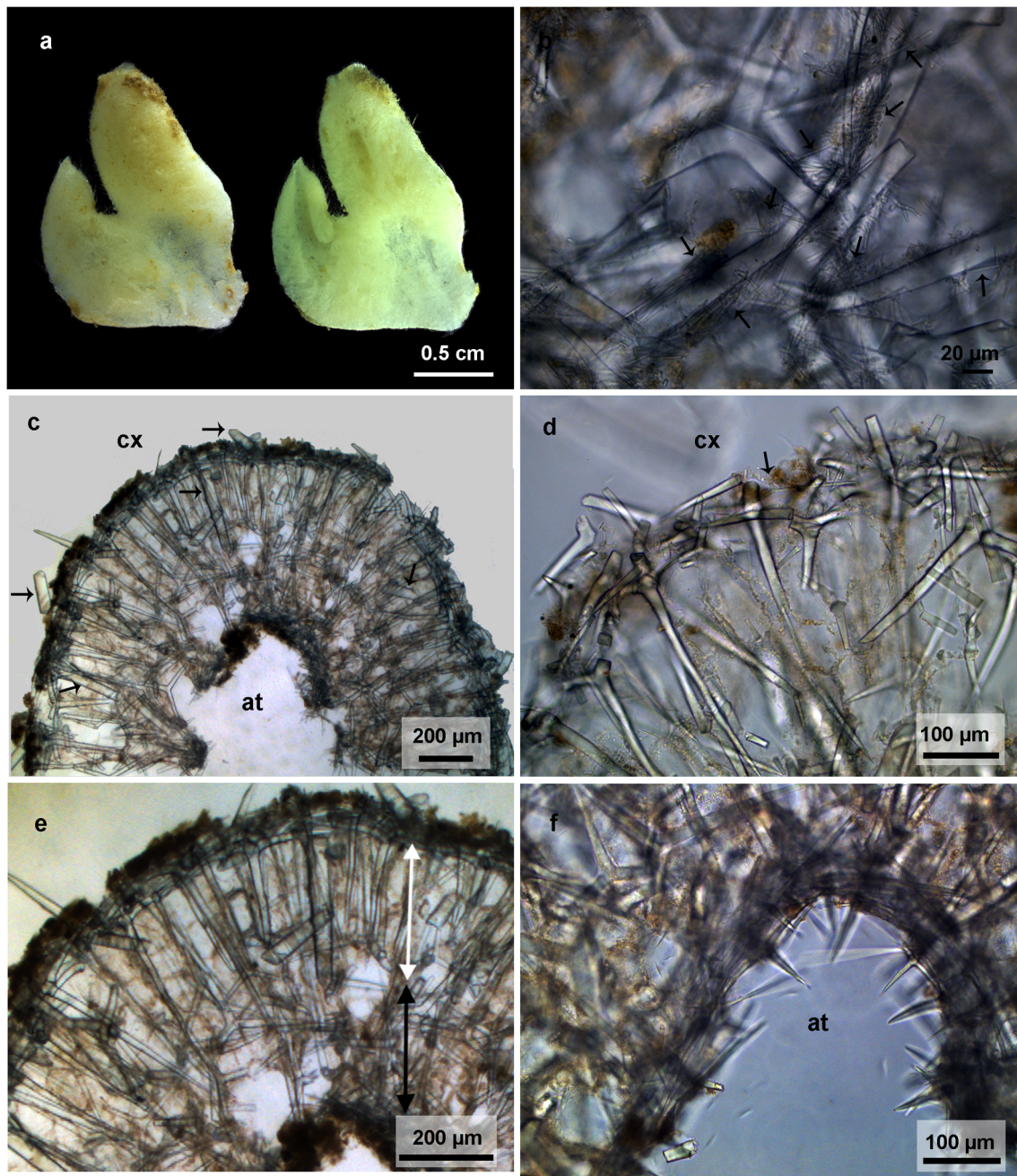
Type locality: El Ñuro site 4, north of Quebrada Verde, Piura.

Type material: (Holotype/ ethanol): MNRJ 11448; El Ñuro site 4, north of Quebrada Verde, Piura Region, Peru ( $04^{\circ} 13' 22.30'' \text{S}\text{--}81^{\circ} 12' 24.10'' \text{W}$ ); collected by Y. Hooker, M. Rios, and Ph. Willenz; 4.0–5.0 m depth; 14 October 2007. (Paratypes/ethanol): MNRJ 21306 and MNRJ 21307; same data as the holotype

Colour: unknown in life and beige in ethanol (Fig. 4a).

Morphology and anatomy: the holotype (MNRJ 11448) is massive and ramified, with two oscula without crown. It measures  $12.0 \times 10.0 \times 4.0 \text{ mm}$  (Fig. 4a). Consistency firm but friable. Osculum supported by sagittal triactines and tetractines, the same spicules as the body wall. Surface rough and scarcely hispid because of the presence of few diactines. Aquiferous system leuconoid with subspherical choanocyte chambers, ranging from 98 to  $130 \mu\text{m}$ .

Skeleton: cortical skeleton composed of microdiactines, few large diactines, rare triactines, and a basal system of tetractines. Microdiactines and diactines are perpendicular to the cortex. The microdiactines are frequently organised in tufts (Fig. 4b) and the diactines can cross the choanosome (arrows in Fig. 4c). The triactines and the basal system of the tetractines lay tangentially to the surface (Fig. 4d). Choanosomal skeleton typical of the genus, being inarticulate near the surface (outer region) and without organisation below the subatrial skeleton (inner region). The outer region is formed by the diactines, the apical actine of the cortical tetractines, and the unpaired actine of subatrial triactines (Fig. 4e). The apical actine of the cortical tetractines crosses the choanosome and can even reach



**Fig. 4** *Paraleucilla tarazonai* sp. nov. (MNRJ 11448). **a** Specimen after fixation; **b** Cortical microdiactines (*arrows*); **c** Cross-section (*arrows* = broken diactines); **d** Cortical triactines (*arrow*) and tetractines; **e** Cross-

section showing the outer (*white arrowheads*) and inner regions (*black arrowheads*); **f** Atrium with the apical actine of the tetractines. *cx* cortex, *at* atrium

the atrium. The inner region is evident only when the body wall of the sponge is thick. Triactines similar to those of the subatrial skeleton and subregular triactines are scattered in this region. Atrial skeleton formed by triactines and tetractines. The apical actine of the atrial tetractines is not conspicuous (Fig. 4f).

#### Spicules:

*Diactines*: fusiform with sharp tips (Fig. 5(a)). Size: > 1100/27  $\mu\text{m}$

*Cortical microdiactines*: straight, spined, with one sharp and one lanceolated tip (Fig. 5(b)). Size: 54–189/1–3  $\mu\text{m}$

*Cortical triactines*: sagittal. Actines are conical, straight, with sharp tips (Fig. 5(c, d)). Size: 70–170/4–12  $\mu\text{m}$  (unpaired) and 86–265/4–14  $\mu\text{m}$  (paired)

*Cortical tetractines*: sagittal. Basal actines are slightly conical to conical, straight, with sharp tips. The apical actine is slightly undulated and longer than the other actines (Fig. 5(e,



**Table 2** Spicule measurements of *Leucilla mancoraensis* sp. nov. Values are shown in micrometres, as minimum (Min), mean, standard deviation (SD), maximum (Max), and sample size (*N*)

Specimen	Spicule	Actine	Length				Width				<i>N</i>
			Min	Mean	SD	Max	Min	Mean	SD	Max	
MNRJ 12948, holotype	Cortical tetractine	Paired	205.2	365.4	84.7	583.2	16.2	31.5	7.9	54	30
		Unpaired	324.0	481.7	69.0	648.0	32.4	37.4	6.2	54	25
		Apical	324.0	534.6	168.0	993.6	16.2	31.0	7.0	54	30
	Cortical triactine	Paired	162.0	243.4	43.2	324.0	10.8	14.0	4.0	21.6	30
		Unpaired	194.4	286.2	60.2	410.4	10.8	13.9	3.9	27.0	30
	Subatrial triactine	Paired	129.6	246.2	63.4	388.8	10.8	26.6	8.4	43.2	30
		Unpaired	259.2	97.1	97.1	471.2	10.8	28.3	8.5	43.2	30
	Atrial tetractine	Paired	86.4	150.5	32.5	226.8	10.8	12.8	2.1	17.6	30
		Unpaired	113.4	197.7	37.7	283.5	9.5	13.5	2.5	18.9	30
Apical		18.9	34.3	7.2	54.0	6.8	8.3	1.2	10.8	30	
MNRJ 12967, paratype	Cortical tetractine	Paired	291.6	373.8	58.0	507.6	27.0	32.7	5.4	43.2	18
		Unpaired	334.8	403.9	65.0	540.0	10.8	34.0	8.8	43.2	10
		Apical	259.2	565.2	144.6	810.0	21.6	36.5	8.1	54.0	30
	Cortical triactine	Paired	162.0	268.3	58.6	378.0	16.2	21.6	6.6	32.4	13
		Unpaired	162.0	275.0	65.8	356.4	16.2	19.9	4.6	27.0	13
	Subatrial triactine	Paired	162.0	224.2	41.7	356.4	10.8	20.5	4.7	32.4	25
		Unpaired	259.2	388.4	80.7	615.6	16.2	22.7	4.1	32.4	25
	Atrial tetractine	Paired	94.5	143.4	29.8	194.4	9.5	12.8	2.0	16.2	16
		Unpaired	113.4	177.0	41.1	248.4	9.5	13.2	2.1	16.2	16
Apical		27.0	41.2	8.1	59.4	5.4	9.1	1.6	12.2	30	
MNRJ 13075, paratype	Cortical tetractine	Paired	183.6	259.2	65.4	356.4	16.2	23.1	7.5	32.4	7
		Unpaired	194.4	345.6	82.6	475.2	16.2	27.0	5.7	32.4	10
		Apical	270.0	510.8	111.3	680.4	16.2	25.4	5.3	32.4	20
	Cortical triactine	Paired	153.9	180.4	33.4	232.2	9.5	14.0	2.8	16.2	5
		Unpaired	151.2	187.9	43.2	261.9	8.1	14.6	3.6	16.2	5
	Subatrial triactine	Paired	64.8	101.9	40.4	153.9	10.8	13.2	2.3	16.2	4
		Unpaired	145.8	219.4	66.3	302.4	10.8	14.9	3.5	18.9	4
	Atrial tetractine	Paired	89.1	138.2	35.6	172.8	10.8	13.3	2.8	16.2	6
		Unpaired	116.1	156.2	40.1	207.9	10.8	15.8	4.0	18.9	6
Apical		21.6	44.8	11.4	64.8	5.4	8.1	1.0	10.8	20	

f). Size: 32–230/11–27  $\mu\text{m}$  (unpaired actine); 118–400/11–43  $\mu\text{m}$  (paired); and 178–745/13–65  $\mu\text{m}$  (apical)

*Subatrial triactines*: sagittal. Actines are conical, straight, with sharp tips. Paired actines are shorter than the unpaired one (Fig. 5(g–k)). Size: 150–535/11–38  $\mu\text{m}$  (unpaired) and 89–300/11–38  $\mu\text{m}$  (paired)

*Atrial triactines*: sagittal. Actines are slightly conical, with sharp tips. Size: 78–338/4–12  $\mu\text{m}$  (unpaired) and 103–262/7–13  $\mu\text{m}$  (paired)

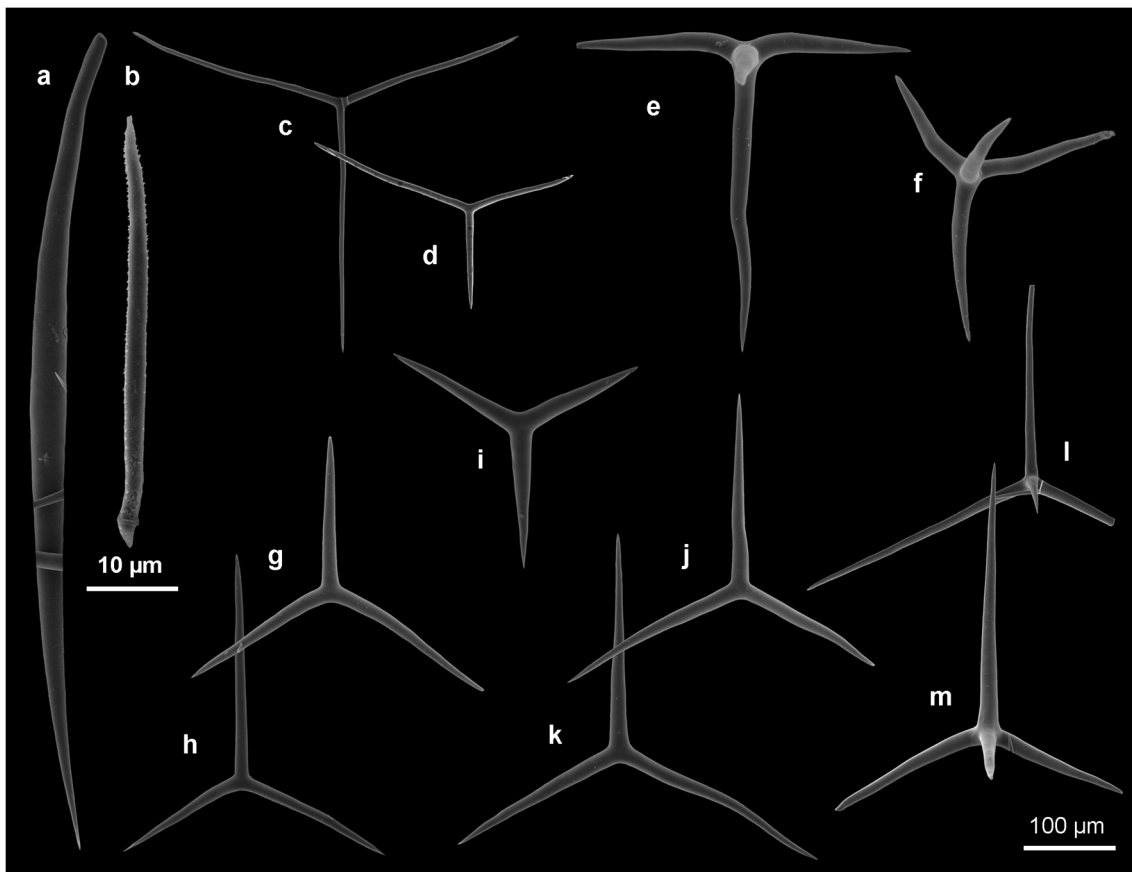
*Atrial tetractines*: sagittal. Actines are conical, straight with sharp tips. The apical actine is the shortest one (Fig. 5(l, m)). Size: 127–263/5–16  $\mu\text{m}$  (unpaired), 89–300/5–16  $\mu\text{m}$  (paired), and 33–135/5–11  $\mu\text{m}$  (apical)

Ecology: the specimens were found on an oyster shell at 4–5 m depth.

Geographical distribution: provisionally endemic to the northern coast of Peru (Piura region). Corresponding MEOW: Guayaquil ecoregion, Tropical East Pacific Province (TEP)

Remarks: *Paraleucilla* comprises 13 species (Van Soest et al. 2017). Among them, *P. crosslandi* (Row, 1909) from the Red Sea and *P. proteus* (Dendy, 1913) from the Indian Ocean present a similar skeleton composition as that of *P. tarazonai* sp. nov. The skeleton of these three species is composed of triactines and tetractines in the cortex, triactines in the inner region, and triactines and tetractines in the atrium. However, differently from the new species, *P. crosslandi* and *P. proteus* do not have diactines, nor microdiactines.

As a juvenile *Paraleucilla* can be easily misidentified as *Leucilla* (see *P. magna*, Lanna et al. 2017), we compared our



**Fig. 5** Scipules of *Paraleucilla tarazonai* sp. nov. (MNRJ 11448). **a** Diactines; **b** Cortical microdiactines; **c**, **d** Cortical triactines; **e**, **f** Cortical tetractine; **g–i** Subatrial triactines of the inarticulate skeleton; **j**, **k** Subatrial triactines adjacent to the atrium; **l**, **m** Atrial tetractines

specimens also with other *Leucilla* species with similar skeleton composition. Among them, the skeleton of *P. tarazonai* sp. nov. most resembles *L. endoumensis* Borojevic & Boury-Esnault, 1986 from the Mediterranean Sea, *L. oblata* Row & Hôzawa, 1931 from Western Australia, and *L. schauinslandi* (Preiwisch, 1904) from the Chatham Islands (New Zealand). Nonetheless, they can be easily distinguished by the absence of diactines in the latter three species. Additionally, *L. oblata* possesses tetractines in the subatrial skeleton, and *L. schauinslandi* has tetractines scattered in the choanosome, whereas *P. tarazonai* sp. nov. lacks tetractines in those regions.

*Paraleucilla tarazonai* sp. nov. is the first *Paraleucilla* reported from the Eastern Pacific and can be easily distinguished from the other *Paraleucilla* and *Leucilla* species because of its unique skeleton composition (diactines, microdiactines, triactines, and basal system of tetractines in the cortex, subatrial triactines, and triactines and tetractines supporting the atrium).

As the inner region of the skeleton of *Paraleucilla* is only evident when the wall is thick enough, specimens with thin wall (i.e. in early stages of growth) can be erroneously identified as a *Leucilla* (Lanna et al. 2017). Thus, descriptions of new *Paraleucilla* and *Leucilla* must be made with caution. To avoid

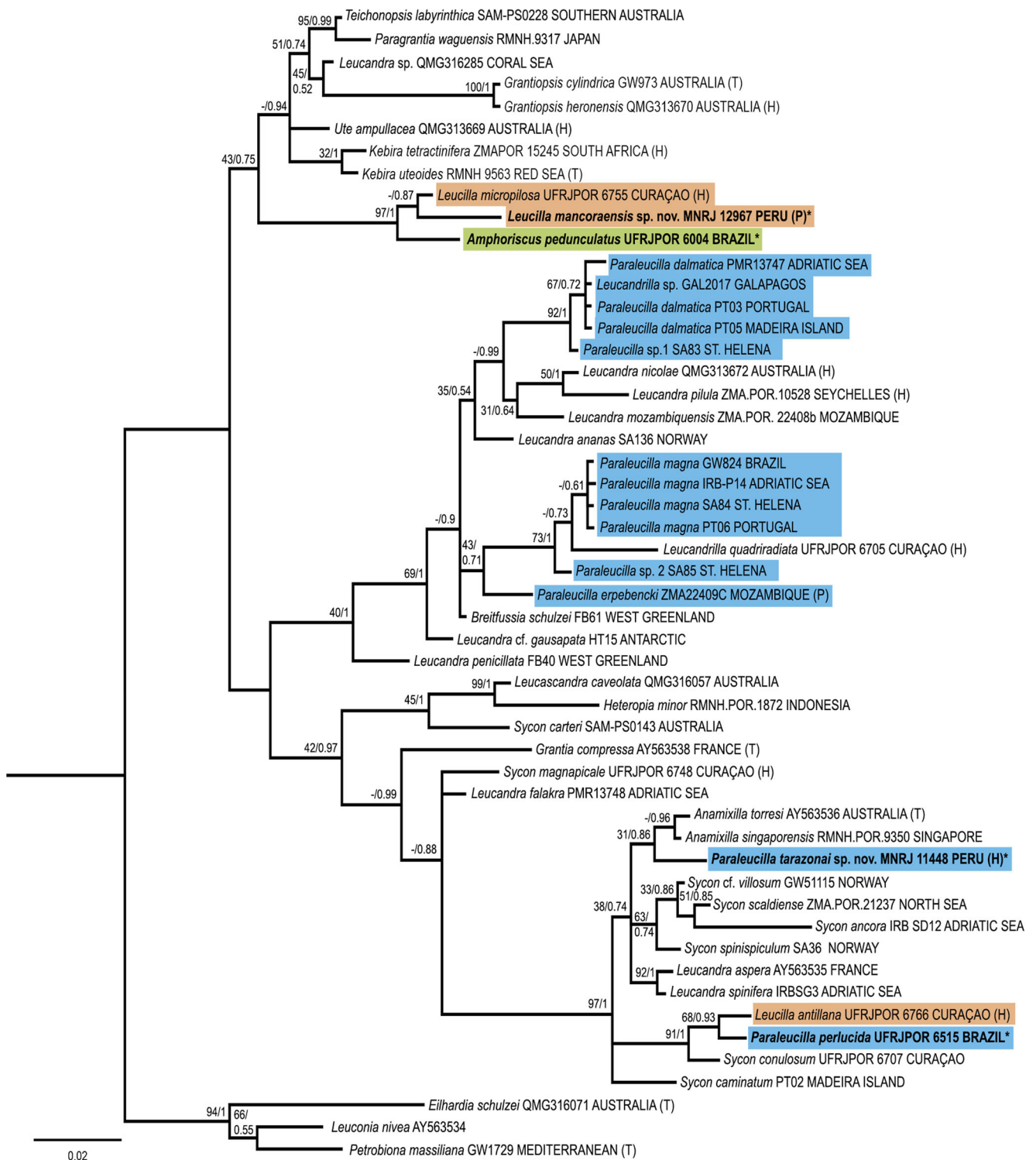
misidentifications, the study should be based, when possible, in more than one specimen of different ages (or sizes). In this study, it was possible to analyse specimens of *L. mancoraensis* sp. nov. and *P. tarazonai* sp. nov. with different growth stages, which allowed us to unequivocally allocate these specimens in the correct genera.

### Molecular taxonomy

In this study, we provide sequences for the new species *Leucilla mancoraensis* sp. nov. and *Paraleucilla tarazonai* sp. nov., as well as for two known Amphoriscidae species, *Amphoriscus pedunculatus* Klautau, Cavalcanti & Borojevic, 2017 and *P. perlucida* Azevedo & Klautau, 2007.

The final alignment included 52 sequences (Table 1) and had a total length of 430 bp (including gaps), 262 conservative sites, 140 variable sites, and 31 singletons.

Both phylogenetic methods (BI and ML) recovered trees with similar topologies. The obtained ML tree is shown in Fig. 6. Neither Amphoriscidae nor *Leucilla* or *Paraleucilla* were recovered as monophyletic, instead Amphoriscidae sequences appeared in three different clades.



**Fig. 6** Bayesian phylogenetic tree obtained from the sequences of the C-region of LSU. Support values (bootstrap/posterior probability) are indicated on the branches. Asterisk indicates sequences produced in this study. T type species of the genus, H holotype, P paratype

*Leucilla mancoraensis* sp. nov. appeared as sister species of *L. micropilosa*, with a p-distance of 2.2% and branch support of 0.87 (BI). Both species grouped with another Amphoriscidae, *Amphoriscus pedunculatus*, with high support (1 in BI and 97%

in ML analyses). *Paraleucilla tarazonai* sp. nov. grouped with a clade formed by *Anamixilla torresi* and *A. singaporensis*, with p-distances of 1.8% and 1.4%, respectively, and supported by 0.86 in BI and 55% in ML analyses.

**Table 3** Spicule measurements of *Paraleucilla tarazonai* sp. nov. Values are shown in micrometres, as minimum (Min), mean, standard deviation (SD), maximum (Max), and sample size (*N*). “-” means measurement not taken

Specimen	Spicule	Actine	Length				Width				<i>N</i>	
			Min	Mean	SD	Max	Min	Mean	SD	Max		
MNRJ 11448, holotype	Microdiactine		-	-	-	-	-	-	-	-	-	
	Diaactine		> 1100	-	-	-	25	27.0	2.9	30	03	
	Cortical triactine	Unpaired		70.2	90.9	18.0	102.6	4.1	6.8	2.3	8.1	03
		Paired		86.4	156.2	57.6	264.6	4.1	7.9	2.9	13.5	07
	Cortical tetractine	Unpaired		32.4	131.8	54.1	229.5	10.8	18.9	5.1	24.3	10
		Paired		117.5	156.0	30.9	217.5	12.5	16.1	2.9	20.0	11
		Apical		177.5	245.8	44.6	335.0	12.5	18.9	3.0	25.0	28
	Subatrial triactine	Unpaired		150.0	257.6	38.7	350.0	12.5	18.3	2.3	22.5	30
		Paired		125.0	203.0	34.5	300.0	12.5	17.8	3.1	23.8	30
	Atrial triactine	Unpaired		91.8	217.4	78.5	283.5	8.1	10.4	1.4	12.2	06
		Paired		167.4	223.3	31.9	261.9	8.1	10.0	1.1	10.8	07
	Atrial tetractine	Unpaired		137.5	202.8	48.6	262.5	5.0	9.5	2.2	11.3	08
		Paired		170.0	238.5	44.5	300.0	5.0	9.8	1.9	12.5	15
		Apical		32.5	51.2	17.0	77.5	5.0	7.0	1.1	8.8	08
	MNRJ 21306, paratype	Microdiactine		54.0	56.7	2.7	59.4	1.4	1.8	0.8	2.7	20
Diaactine			248.4	450.0	174.9	561.6	16.2	25.2	8.2	32.4	03	
Cortical triactine		Unpaired		75.6	119.7	68.3	170.1	4.1	9.0	4.3	12.2	09
		Paired		121.5	171.9	46.6	213.3	5.4	9.5	3.6	12.2	09
Cortical tetractine		Unpaired		129.6	173.9	37.8	216.0	5.4	17.8	8.5	27.0	07
		Paired		172.8	270.0	77.1	399.6	10.8	23.9	9.8	43.2	20
		Apical		226.8	442.8	181.9	745.2	16.2	35.8	16.8	64.8	20
Subatrial triactine		Unpaired		267.3	349.1	73.2	534.6	10.8	22.0	6.2	37.8	20
		Paired		89.1	183.7	58.4	270.0	10.8	20.9	6.0	37.8	20
Atrial triactine		Unpaired		140.4	212.3	63.9	337.5	6.8	9.5	2.3	12.2	08
		Paired		170.1	205.2	21.0	229.5	6.8	10.0	2.2	12.2	08
Atrial tetractine		Unpaired		126.9	163.6	23.9	213.3	8.1	12.4	2.2	16.2	20
		Paired		89.1	114.2	16.7	153.9	8.1	11.5	2.6	16.2	20
		Apical		48.6	68.9	11.2	81.0	5.4	6.9	1.4	8.1	20
MNRJ 21307, paratype		Microdiactine		148.5	168.8	28.6	189.0	-	2.7	0	-	02
	Diaactine		> 885.6	-	-	-	30.2	37.4	4.1	43.2	05	
	Cortical triactine	Unpaired		72.9	75.6	3.8	78.3	5.4	6.8	1.9	8.1	02
		Paired		108.0	114.8	9.5	121.5	5.4	6.1	1.0	6.8	02
	Cortical tetractine	Unpaired		162.0	183.6	30.5	205.2	-	21.6	0	-	02
		Paired		183.6	234.9	28.4	313.2	10.8	234.9	3.5	21.6	20
		Apical		216.0	325.6	50.9	421.2	10.8	18.6	3.3	21.6	20
	Subatrial triactine	Unpaired		183.6	304.4	54.1	378.0	10.8	12.2	2.4	16.2	16
		Paired		140.4	195.4	27.5	226.8	10.8	12.3	2.5	16.2	11
	Atrial triactine	Unpaired		78.3	123.5	49.1	226.8	4.1	6.5	1.3	8.1	11
		Paired		102.6	161.0	36.5	210.6	6.8	10.0	2.0	13.5	08
	Atrial tetractine	Unpaired		162.0	202.5	40.5	243.0	8.1	9.0	1.6	10.8	03
		Paired		-	75.6	-	-	-	8.1	-	-	01
		Apical		62.1	94.8	17.4	135.0	5.4	7.6	1.5	10.8	20

## Discussion

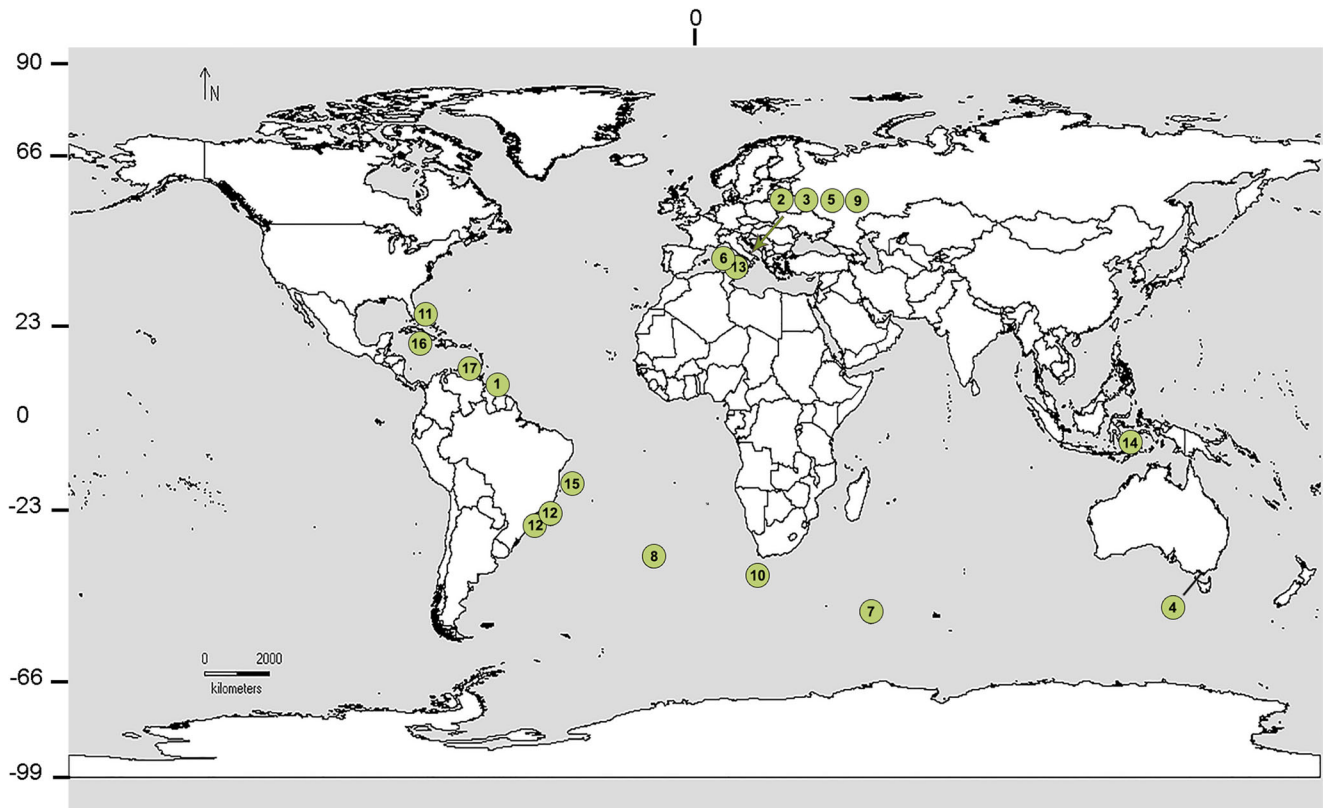
### Phylogenetic affinities in Amphoriscidae

This is the first study that included all the available sequences of the three accepted Amphoriscidae genera, *Amphoriscus*, *Leucilla*, and *Paraleucilla*, in a molecular tree. As observed in previous studies (Voigt et al. 2012; Alvizu et al. 2018; Córdor-Luján et al. 2018), Amphoriscidae was not recovered as a monophyletic group. Moreover, *Leucilla* and *Paraleucilla* were polyphyletic, as recently shown by Córdor-Luján et al. (2018) and Alvizu et al. (2018), respectively.

Although not being monophyletic in our molecular tree species of *Leucilla* with similar skeleton composition (cortical triactines and tetractines, subatrial triactines and atrial tetractines) and sylleibid aquiferous system, *L. mancoraensis* sp. nov. and *L. micropilosa* grouped in a monophyletic clade. Interestingly, *L. antillana*, which presents different skeleton composition (cortical tetractines, subatrial triactines, and atrial tetractines) and leuconoid aquiferous system, appeared in another clade. Whether skeleton composition and type of aquiferous system are characters with phylogenetic/evolutionary signal in certain species of *Leucilla* should be revised in future studies.

Klautau et al. (2016) obtained a highly supported clade formed by two species of *Paraleucilla* (*P. magna* and *P. dalmatica*); however, this genus was recovered as polyphyletic in further molecular analyses (Alvizu et al. 2018; Córdor-Luján et al. 2018). Herein, we added new sequences of *Paraleucilla* (*P. erpenbecki* and *P. tarazonai* sp. nov.) and our results supported again the non-monophyly of this genus.

Recently, Klautau et al. (2017) pointed out the possible phylogenetic signal of attachment structures after describing *A. pedunculatus*, an Amphoriscidae with peduncle. Those authors suggested that certain Calcaronean species provided with peduncle or root-like structures could be congeneric as they appeared in a monophyletic group within a molecular phylogeny. In our analysis, *A. pedunculatus*, *Leucilla micropilosa*, and *L. mancoraensis* sp. nov., which present similar skeleton composition, formed a monophyletic group. However, differently from *A. pedunculatus* and *L. mancoraensis* sp. nov., *L. micropilosa* does not bear any peduncle. Considering that convergent evolution and secondary loss can have a relevant role in the evolutionary history of Calcaronea (Alvizu et al. 2018), the absence of peduncle in *L. micropilosa* could be a case of secondary loss.



**Fig. 7** World distribution of *Amphoriscus*. (1) *A. ancora*; (2) *A. buccichii*; (3) *A. chrysalis*; (4) *A. cyathiscus*; (5) *A. cylindricus*; (6) *A. dohrni*; (7) *A. elongatus*; (8) *A. gastrorhabdifer*; (9) *A. gregorii*; (10) *A. kryptoraphis*; (11)

*A. oviparus*; (12) *A. pedunculatus*; (13) *A. salfi*; (14) *A. semoni*; (15) *A. synapta*; (16) *A. testiparus*; (17) *A. urna*

Nonetheless, an ecological response cannot be discarded. While *L. mancoraensis* sp. nov. and *A. pedunculatus* were found attached to organisms, *L. micropilosa* was collected underneath boulders. Considering this, the attachment structures may be related to the sponge habitat more than to ancestry, as previously suggested by Klautau et al. (2017). Although very incipient, our results may be the starting point to understand the evolution of attachment structures within Amphoriscidae.

Until now, the 28S (including the C-region of LSU) is being a good marker for alpha systematics in Calcaronea (e.g. Klautau et al. 2016; Alvizu et al. 2018; Córdor-Luján et al. 2018). However, the phylogenetic relationships among genera are not yet clearly solved. We agree with previous authors (e.g. Klautau et al. 2016; Alvizu et al. 2018) that it is necessary to find an additional molecular marker to really unveil the phylogeny of this subclass.

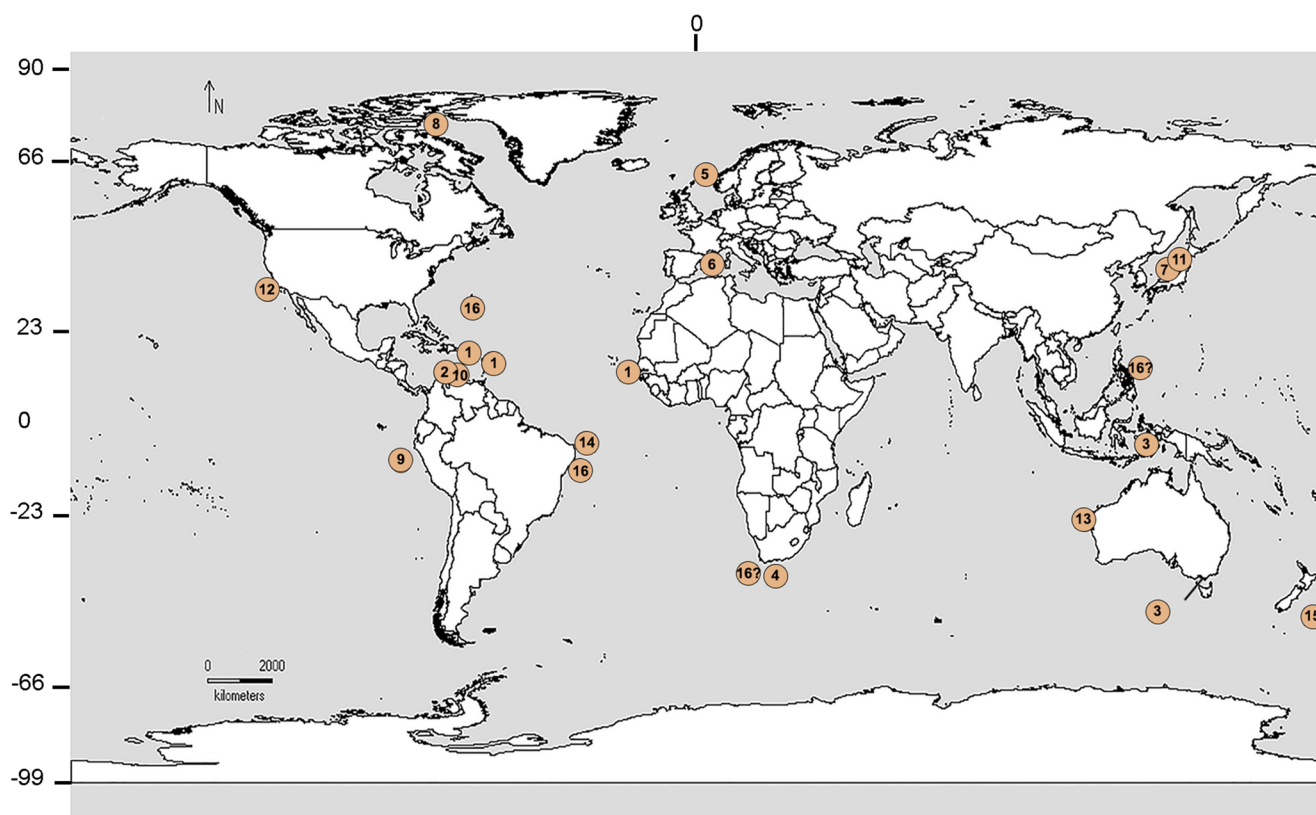
### Geographic distribution of *Amphoriscus*, *Leucilla*, and *Paraleucilla*

Although the three genera of Amphoriscidae are probably not monophyletic, as our and others' results showed (Alvizu et al. 2018; Córdor-Luján et al. 2018), they are

still considered valid. Therefore, we show here their geographic distribution.

*Amphoriscus* comprises 17 accepted species (Van Soest et al. 2018). Among them, 13 were recorded from tropical or subtropical waters (Atlantic Ocean, Mediterranean Sea, and Indo-Pacific) and four from temperate waters (South Atlantic and sub-Antarctic) (Fig. 7). Until now, *Amphoriscus* has not been reported from the Eastern Pacific, probably because of the poor sampling effort on Calcareia in this region.

With this work, *Leucilla* now includes 16 valid species. Six species are exclusive of temperate waters (East Pacific, North Atlantic, South Atlantic, and Indo-Pacific), seven occur in tropical or subtropical waters (Atlantic, Caribbean, Mediterranean, East Pacific, and Indo-Pacific), two are found in both temperate and tropical waters, and only one is present in cold waters (Arctic) (Fig. 8). *Leucilla uter* shows a wide geographic range, being found in both sides of the Atlantic (Poléjaeff 1883; Borojevic 1967; Muricy et al. 2011) and in the Indo-Pacific (Poléjaeff 1883). *Leucilla mancoraensis* sp. nov. is the second species recorded from the Eastern Pacific, and it constitutes the first record of this genus for the Southeastern Pacific.

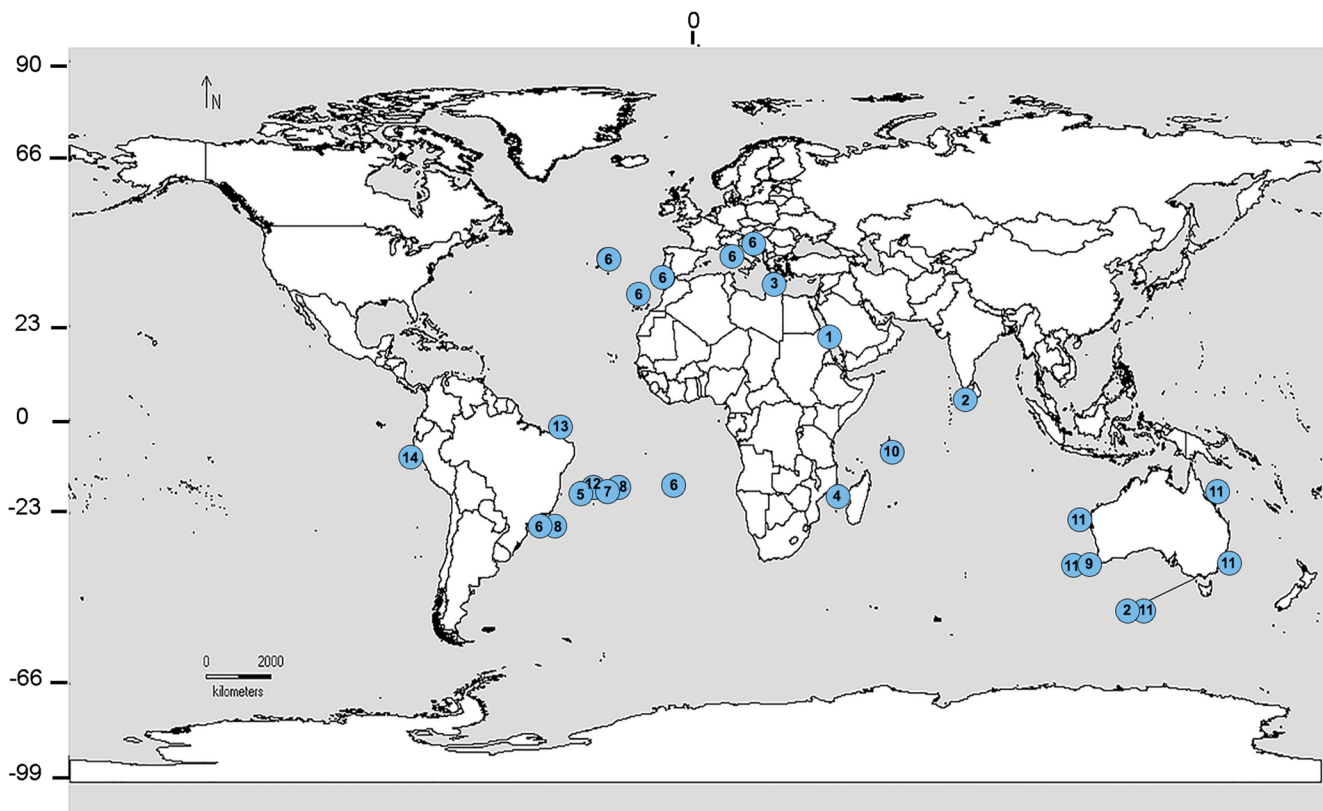


**Fig. 8** World distribution of *Leucilla*. (1) *L. amphora*; (2) *L. antillana*; (3) *L. australiensis*; (4) *L. capsula*; (5) *L. echina*; (6) *L. endoumensis*; (7) *L. hirsuta*. (8) *L. leuconoides*; (9) *L. mancoraensis* sp. nov.; (10) *L. micropilosa*; (11) *L. minuta*; (12) *L. muttingi*; (13) *L. oblata*; (14) *L. sacculata*; (15) *L. schauinslandi*; (16) *L. uter*

*Paraleucilla* groups now 14 valid species. Nine of them were recorded exclusively from tropical or subtropical waters (East Pacific, Western Atlantic, Mediterranean Sea, Red Sea, and Indo-Pacific). Three species are present in both tropical and temperate waters, and only one occurs exclusively in temperate waters (Fig. 9). *Paraleucilla magna* is one of the most widespread species of this genus. This species was described from the tropical Atlantic, although it is probably not originally from that region (Klautau et al. 2004). Some years later, it was registered from the Eastern Atlantic and from different parts of the Mediterranean Sea, mainly in harbours and mussel farms (Longo et al. 2007; Dailianis et al. 2016; Klautau et al. 2016; Topaloğlu et al. 2016; Gerovasileiou et al. 2017; Mačić and Petović 2017). Most recently, it was found in St. Helena Island in the South Atlantic and in the southern coast of Portugal (Alvizu et al. 2018). *Paraleucilla magna* has been categorised an alien-invasive species because of its ability to rapidly colonise different environments and for being responsible for economic losses in mussel farms in the Mediterranean Sea (Longo et al. 2007). *Paraleucilla cucumis* and *P. saccharata* also present wide distributions, being recorded throughout the Indo-Pacific (Cavalcanti et al. 2014).

### Distributional patterns of calcareous sponges from Peru

Azevedo et al. (2015) described three biogeographical patterns for Peruvian species belonging to the subclass Calcinea: (1) endemic to the northern part of Peru, (2) widespread, and (3) discontinuous. The new Calcaronean species, *Leucilla mancoraensis* sp. nov. and *Paraleucilla tarazonai* sp. nov., may also be restricted to the northern coast of Peru as they have not been found in southernmost localities so far. However, the presence of some demosponges originally reported from Peru (*Clathria aculeofila* Aguirre, Hooker, Willenz & Hajdu, 2011 and *Acarinus peruanus* Van Soest, Hooper & Hiemstra, 1991) in localities farther north, in Ecuador and Mexico (personal observations and Aguilar-Camacho et al. 2014, respectively), suggests that provisionally endemic Peruvian calcareous species may also turn out in those latitudes from the Tropical Eastern Pacific, once these get enhanced taxonomic effort. The widespread distribution of *Hamacantha hyaloderma* (de Laubenfels, 1932), which occurs from British Columbia (Austin et al. 2012) down to Peru (Hajdu et al. 2015), also supports this hypothesis.



**Fig. 9** World distribution of *Paraleucilla*. (1) *P. crosslandi*; (2) *P. cucumis*; (3) *P. dalmatica*; (4) *P. erpenbecki*; (5) *P. incomposita*; (6) *P. magna*; (7) *P. oca*; (8) *P. perlucida*; (9) *P. princeps*; (10) *P. proteus*; (11) *P. saccharata*; (12) *P. solangeae*; (13) *P. sphaerica*; (14) *P. tarazonai* sp. nov.

**Acknowledgements** We thank the field staff (F. Menendez and M. Rios) for assistance in collecting samples. We also thank Gisele Lôbo-Hajdu (UERJ), students, and biologists from both Peru and Brazil (B. Ibañez, F. Menendez, M. Rios, C. Segami, and W. Vieira) for assistance in collecting samples on different expeditions.

**Funding information** ESPER Project granted to RBINS was funded by the Global Taxonomy Initiative from the Belgian Development Cooperation (ESPER Project, 2419JVG2, 2431JVG2, and 2433FRK2); Proyecto EsponjAS was funded by the National Council of Technological and Scientific Development (CNPq/PROSUL –490425/2007-0; CNPq/Universal 476558/2012-3; CNPq/Universal 476597/2013-7) and by the Coordination for the Improvement of Higher Education Personnel (CAPES/Protax – 561782/2010-5). The collection of samples was performed thanks to RBINS diving gear. BCL and FA received scholarships from CAPES. PhW was supported by travel grant #18834 from the FNRS (Fonds National de la Recherche Scientifique) to conduct part of this study at MNRJ and UFRJ. YH obtained travel funds from the GTIBDC. MK received a fellowship from CNPq (302459/2014-6) and CAPES (440628/2015-6).

## Compliance with ethical standards

**Conflict of interest** The authors declare that they have no conflict of interest.

**Ethical approval** All applicable international, national, and/or institutional guidelines for the care and use of animals were followed by the authors.

**Sampling and field studies** All necessary permits for sampling and observational field studies have been obtained by the authors from the competent authorities.

**Data availability** The datasets generated during and/or analysed during the current study are available in the GenBank repository, <https://www.ncbi.nlm.nih.gov/genbank/>

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