



New genus and species of lithistid demosponges from submarine caves in Nuku Hiva (Marquesas Islands) and Tahiti Iti (Society Islands), French Polynesia

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Abstract

Lithistid demosponges are well known from limestone caves of karstic origin in the Mediterranean Sea. However, they have never been reported from submarine caves of volcanic origin in the South Pacific. Here, we describe and provide DNA barcodes for four new lithistid demosponges including one new genus. All species grew on basaltic rocks inside lava tubes on Nuku Hiva Island (Marquesas Islands) and Tahiti Iti peninsula on Tahiti Island (Society Islands) in French Polynesia. Three of the species have rhizoclone desmas as choanosomal skeletons and belong to the family Scleritodermidae (*Microscleroderma miritatarata* sp. nov. and *Microscleroderma lava* sp. nov.) and Siphonidiidae (*Gastrophanella basaltica* sp. nov.). The new genus *Levispongia* gen. nov. belongs to the family Corallistidae. The new species *Levispongia meyeri* gen. nov. sp. nov. has dicranoclone desmas, complex dichotrianes with strongly spinose upper surfaces of the cladome and microstyles as the only microscleres. Phylogenetic relationships of these new species are discussed and compared with other material from the Caribbean and Central to the West Pacific Ocean.

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Keywords: Cave sponges, lithistid demosponges, DNA barcoding, relict fauna, French Polynesia

Introduction

Submarine caves share several ecological features which often resemble that of deep-sea habitats including darkness, hydrodynamic, geochemical and faunal compositions (Harmelin & Vacelet 1997). Although differences in pressure, temperature and habitat sizes exist (Moldovan et al. 2019), these submarine caves are often colonized by deep-sea invertebrates like gastropods, annelids, crustaceans and sponges (Bussotti et al. 2006; Gerovasileiou et al. 2015; Culver & Pipan 2019). In particular, the abundance of demosponges represents an important element of submarine cave communities (Bibiloni et al. 1989; Gerovasileiou &

Voultsiadou 2012). Since most of these caves are accessible by SCUBA diving, they provide a unique opportunity to study various aspects of deep-sea sponge biology and systematics (Vacelet 1996). However, we still know little about the diversity and connectivity of sponges from different cave systems around the world, especially how many of these species are cryptic or relict, present as a living fossil. Sponge cave biodiversity has been well studied in the Mediterranean Sea (e.g. Gerovasileiou et al. 2016). The Mediterranean submarine caves are all of karstic origin (limestones) and are a large biodiversity reservoir of sponge species that are otherwise only recorded

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from the deep-sea (Gerovasileiou & Voultsiadou 2012). In particular, the occurrence of a polyphyletic group of demosponges historically called lithistids (Pisera & Lévi 2002a; Schuster et al. 2015) seems to be highly abundant and thrive in these cave systems (Pérez et al. 2004; Manconi et al. 2006; Manconi & Serusi 2008; Pisera & Vacelet 2011; Pisera & Gerovasileiou 2018). Lithistids are characterized by an articulated choanosomal skeleton composed of siliceous desmas. Molecular systematics placed the majority of these desma-bearing sponges into the order Tetractinellida Marshall 1876 (Schuster et al. 2015). In oceans today, lithistids are normally found in deep-waters of the tropics (Carvalho et al. 2015; Schuster et al. 2021), however, some species are also found in shallow waters (Pomponi et al. 2001). It is postulated that the majority of these sponges were originally shallow water sponges that moved into deeper waters as silica concentrations decreased in shallow water (Pisera 2004). Few records exist of lithistid cave fauna occurring outside the Mediterranean Sea (Gerovasileiou et al. 2016; Gómez et al. 2021). Some lithistids were described from shallow crevices in coral reefs of Madagascar (Vacelet & Vasseur 1965), from the central western Atlantic in Belize and Fernando de Noronha (Muricy & Minervino 2000), and a few more were observed in a large submarine cave on Palawan in the Philippines, which represents the only known record of cave lithistids so far in the Pacific Ocean (Pisera & Vacelet 2006). In all investigated caves, the dominant lithistid species seem to belong to rhizomorphine families like Scleritodermidae Sollas, 1888, Azorizidae Sollas, 1888 Siphonidiidae Von Lendenfeld, 1903 and dicranoclone family Corallistidae Sollas, 1888. All of which are usually recorded from deep-waters. The observed morphological features from all these various cave lithistids show high affinities to those of the Mesozoic of Europe (Łukowiak et al. 2014; Frisone et al. 2016; Świerczewska-Gładysz 2016), which would suggest that most of these species represent a relict fauna with probable Tethys origin as already predicted for other non-cave lithistids (Reid 1967; Manconi 2011) and recently tested with molecular clocks for the lithistid genus *Vetulina* Schmidt, 1879 (Sphaerocladina Schrammen 1924) (Schuster et al. 2018).

In this integrative taxonomy study, we describe for the first time four new lithistid demosponges and one new genus from two shallow submarine caves in French Polynesia: Ekamako Cave at the southern coast of Nuku Hiva (Marquesas Islands) and Te Pari Cave on Tahiti Iti peninsula (Tahiti island, Windward Islands, Society Islands) (Figure 1). In contrast to the above-mentioned limestone caves, the Polynesian cave systems are formed by large lava

flows and are of volcanic origin. This is an important finding not only because they grow on these basaltic volcanic rocks inside lava tubes, but also due to the fact that the new genus and species described herein represent the first records of lithistids from this extreme isolated archipelago in French Polynesia. Thus, our results will be of profound interest for further biogeographical and systematic studies on this evolutionary important demosponge group.

Material and methods

Specimen collection and morphological investigations

Lithistid sponges from Marquesas were collected by SCUBA diving in the 80 m long lava tube called Ekamako, on Nuku Hiva southern shore (Marquesas Islands) (Figure 1(b,c)): Research Vessel (R/V) called Alis, cruise BSMPF-1 (Debitus 2009), site MNH03, 8°56.173'S, 140°05.593'W, 11 m, 29/08/2009 (Figure 1). They grew from 10 meters (m) distance from the entrance of the cave and continued to appear deeper into the cave (Pérez et al. 2012). Other sponges in this cave were the non-lithistid demosponges *Xestospongia* sp. (6–10 m), *Dactylospongia elegans* (6–10 m distance from the entrance), *Suberea* sp. (6–10 m distance from the entrance), *Epipolasis* sp. (6–10 m distance from the entrance) and *Cinachyrella* sp. (8 m distance from the entrance), some of them probably represent new species too, but await formal description.

The sponges from Tahiti Iti peninsula were also collected by SCUBA diving from a lava tube inside the Te Pari Cave (Tahiti Island, Windward Islands, Society Islands) (Figure 1 D,E). For more details on the cruise see Debitus (2013). The entrance of this cave is about 10 m wide and its sandy bottom lies at 12 m depth. It forms a right angle 25 m after the cave mouth and is another 180 m long (measured with a hand depth sounder). It is a regular 6–8 m wide cylinder, that narrows and rises towards the end. The sides and bottom (after the turn) are formed of irregular basaltic rocks. The cave ends in a narrow, rocky, chaotic pipe, inaccessible for divers. The roof at the end of the cave is characterized by an air pocket as it is above sea level. The presence of a few dead leaves indicated freshwater inflows, probably during heavy rains. The top water column temperature in the cave was around 26°C, while the lower bottom was warmer around 28°C, and the open sea temperature was 30°C. This cooler top water temperature would confirm the inflow of freshwater, thus keeping the upper layer of the cave water cooler. Further indication for freshwater inflow is given by the observation of some cave

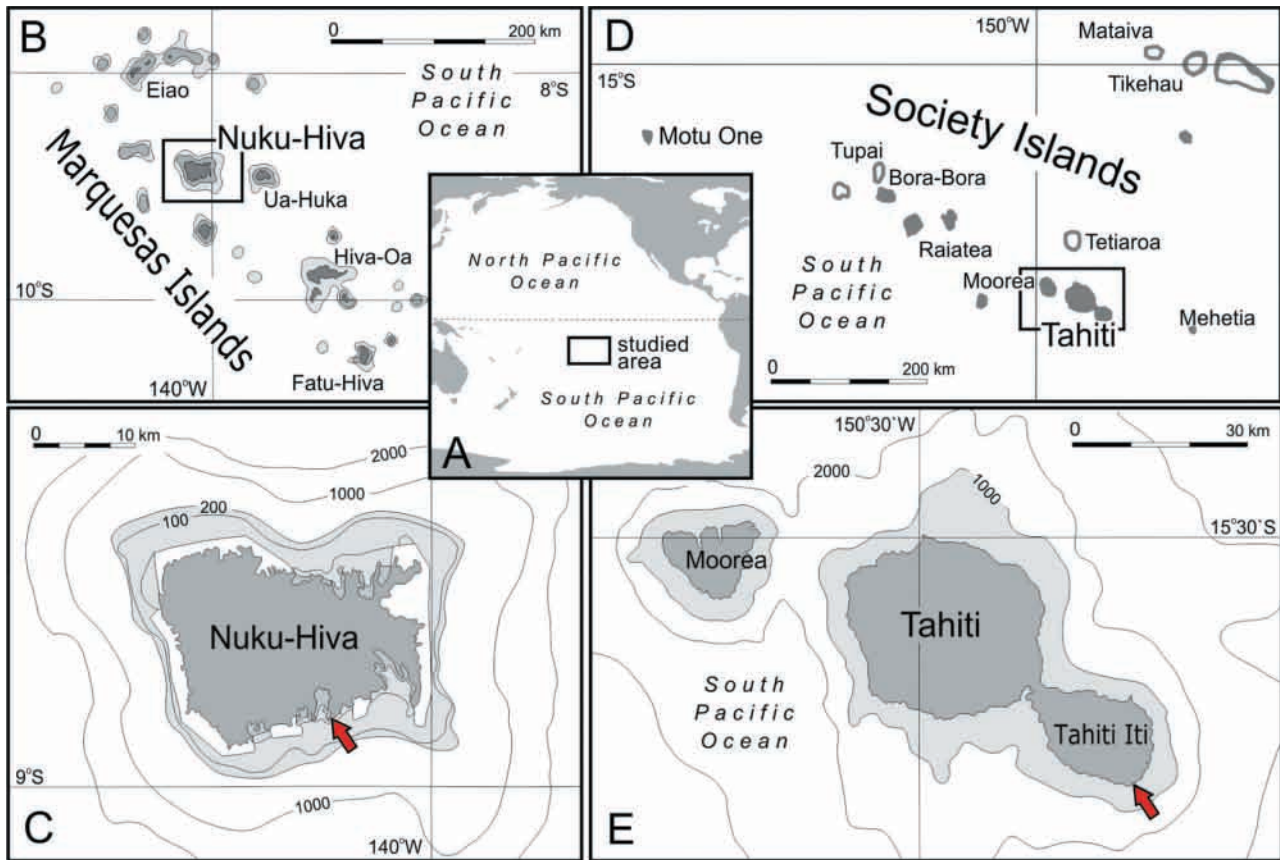


Figure 1. Map of sampling sites. (a): Overview of French Polynesia in the South Pacific Ocean. (b,c): Sampling site at Nuku Hiva Island (Marquesas Islands). (d,e): Sampling site at Tahiti Iti peninsula. Red arrows indicate the position of caves where lithistids were collected.

openings that are close to trails where locals observed salty water coming out during rough seas and killing the surrounding plants, however, no light could be observed inside the cave. Moreover, the water at the surface in the back (end) of the cave tasted less saline than throughout the rest of the cave, which again indicates the inflow of freshwater from the surrounding environments. This cave represents a hot spot of diversity of sponges in Tahiti and concentrates almost half of the total observed species in our surveys (26 species including lithistids, most of them new to science) (personal observation by the author C. Debitus).

Worth mentioning is that the first 25 m into the cave (before the turn) concentrate most of the non-lithistid sponge species of which some are already described and published such as the calcareous *Leucetta chagosensis* Dendy, 1913 and *Ascandra* cf. *crewsi* (Klautau *et al.* 2020) and many more demosponge species that await formal descriptions (*Chondrosia corticata*, *Psammocinia* sp., *Suberea ianthelliformis*, *Spirastrella* sp., *Chondrosia* sp., *Tedania* sp., *Hyatella* sp., *Dysidea* sp., *Psammoclema*

sp., *Haliclona* spp., *Halichondria* sp., *Chondrilla* sp., *Cinachyrella* sp., *Luffariella* sp., *Rhabdastrella* sp.). The lithistids were found further inside the cave on the walls and roof of the cave, with *Microscleroderma lava* sp. nov. first, after which *Gastrophanella basaltica* sp. nov. and *Levispongia meyeri* gen. nov. sp. nov. followed further inside the cave with a few other demosponges on the rocky blocks on the cave floor (*Suberea* sp., *Halichondria* sp., *Dysidea* sp., *Haliclona* sp., *Tedania* sp., *Plakinastrella* sp.).

All lithistid specimens were preserved in 70–80% ethanol and are deposited within the “Zoothèque” of the Natural History Museum in Paris (MNHN). SEM stubs and small pieces of the holotypes and paratypes are stored at the Polish Academy of Sciences, Institute of Paleobiology in Warsaw, Poland (ZPAL). In addition, DNA samples are available at the Bavarian State Collection for Palaeontology and Geology (BSPG) in Munich, Germany. DNA barcodes are registered at the Sponge Barcoding Database (SBD) <https://www.spongebarcoding.org/> and new sequences (28S, C1-D2 region) from this study are deposited at the National Center for Biotechnology Information (NCBI).

New species are registered in ZooBank (<http://zoobank.org/urn:lsid:zoobank.org:pub:844E385C-9A92-4F1B-B85C-9C1E319CD13F>.)

Morphological features of the specimens were analyzed through Scanning Electron Microscopy (SEM). In detail, pieces of the ectosome and choanosome of the sponges were cut and either directly mounted on stubs or digested in nitric acid (HNO₃) first, in order to remove any organic material, followed by several washing steps with distilled water and twice 70–80% ethanol before a final fixation in 99% ethanol (Pisera & Pomponi 2015). Dried spicules, zygosid skeletons and chemically untreated surfaces were mounted on stubs using Carbon-Leit-C (PLANO, Germany) and covered with platinum for examination on a Philips L-20 SEM at the Institute of Paleobiology in Warsaw, Poland.

Molecular Systematics

For the assessment of the molecular relationships of the new species and the new genus *Levispongia* gen. nov. among other lithistids, we performed two separate phylogenetic analyses. One for the family Corallistidae where the new genus belongs to, and another for the suborder Spirophorina Bergquist & Hogg, 1969 that includes all new rhizomorine species from this study. In detail, we used the C1-D2 region of the 28S rDNA gene (~800 bp) that has been shown in previous studies to resolve relationships on species level (see Schuster et al. 2015, 2018). For *Microscleroderma lava* sp. nov. (LR656090) and the two *Microscleroderma miritatarata* sp. nov. (LR656088, LR656089) 28S sequences already exist and were extracted from Schuster et al. (2021). For *Gastrophanella basaltica* sp. nov. and *Levispongia meyeri* gen. nov. sp. nov., new sequences of the same gene were obtained following the molecular barcoding protocol in Schuster et al. (2015, 2021).

For a better overview, we reduced the sequence alignment of Schuster et al. (2021) to the family Corallistidae which includes representative species from all six valid genera (*Awhiozhio* Kelly, 2007, *Corallistes* Schmidt, 1870, *Herengeria* Lévi & Lévi, 1988, *Isabella* Schlacher-Hoenlinger, Pisera & Hooper, 2005, *Neophrissospongia* Pisera & Lévi, 2002b and *Neoschrammeniella* Pisera & Lévi, 2002b) and aligned to this the new sequence *Levispongia meyeri* gen. nov. sp. nov. using AliView v.1.26 (Larsson 2014). A reduced alignment from Schuster et al. (2021) including Scleritodermidae, Siphonidiidae and Azoricidae was used to calculate the phylogenetic tree. Since in this study the new *Microscleroderma* species were already included, only

Gastrophanella basaltica sp. nov. was added using the same program as above.

Bayesian inference (BI) of phylogenies was executed separately for each dataset using the MrBayes 3.2.2 plugin on the CIPRES Science gateway (Miller et al. 2010). The best fit evolutionary model (GTR + G + I) was selected according to the results of JModelTest2 (Darriba et al. 2012) plugin using the CIPRES Science Gateway v.3.3 (Miller et al. 2010). Two concurrent runs of four Metropolis-coupled Markov-chains Monte Carlo (MCMC) for 100,000,000 generations were run and stopped when the average standard deviation of split frequencies reached below 0.01. The first 25% of the sampled trees were discarded as burn-in for further analyses. FigTree v1.4.2 (Rambau 2009) and Inkscape 1.0 was used to visualize the trees.

Unfortunately, we could not sequence the independent mitochondrial barcoding marker COI for *Gastrophanella basaltica* sp. nov. and *Microscleroderma miritatarata* sp. nov., most likely because of the presence of intronic regions within COI. These intronic regions seem to be widespread among rhizomorine taxa (see Schuster et al. 2017) and it was detected in the new species *Microscleroderma lava* sp. nov. (COI = LT628364, synonym *Microscleroderma* sp.3, in Schuster et al. 2017). In fact, this species harbors two intron insertions (ORF 723 and ORF 870) within its most conserved COI barcoding region. Therefore, we suspect that also *Microscleroderma miritatarata* sp. nov., contain such an intron, which awaits to be sequenced in a follow-up study.

Results

Species descriptions

Porifera Grant, 1836

Class Demospongiae Sollas, 1885

Subclass Heteroscleromorpha Cárdenas et al., 2012

Order Tetractinellida Marshall, 1876

Suborder Astrophorina Sollas, 1887

Family Corallistidae Sollas, 1888

Genus *Levispongia* gen. nov.

Etymology. This genus name is given to honor Prof. Claude Lévi for his achievements in sponge science.

Type species: *Levispongia meyeri* gen. nov. sp. nov.

Diagnosis. Massive to fan-shaped corallistid with complex dichotrianes that show a strongly spinose upper surface of their cladome and microscleres that are microstyles and microrhabds; no streptaster of any kind.

Remarks. The new genus is close to *Neophrissospongia* as it shares very similar desmas with a central core, complex dichotriaenes with spinose or tuberculated upper surface of the cladome and microstyles among microscleres. However, it lacks any kind of streptasters, but instead has two types of spinose microrhabds. Also, the habitus of this new species is different from most, but not all *Neophrissospongia* species, which are vase or foliose in shape. Such differences usually are treated to characterize different genera (see for example *Racodiscula*; Zittel, 1878 and *Theonella*; Gray, 1868; (Pisera & Lévi 2002c)). The only other close corallistid species, attributed earlier to *Neophrissospongia*, is *N. microstylifera* Lévi & Lévi, 1983 from New Caledonia, as a result we propose to transfer this species from the genus to the new genus *Levispongia* gen. nov.

***Levispongia meyeri* sp. nov.**

(Figures 2–4)

Diagnosis. Massive to fan-shaped sponge composed of cylindrical units that are more or less fused; dichotriaenes are complex and have strongly spinose upper surface of cladome; desmas are dicranoclones with central core and are strongly tuberculated; larger tubercles are ornated by small tubercles; microscleres as spinose microstyles and two types of spinose microrhabds; one is thin, long and curved, the second is short, massive and often irregular.

Type material. **Holotype:** MNHN-IP-2019-2 (field number P515/1), Tahiti Island, Society Islands, French Polynesia, basaltic lava tube on island fall, Station 30, 17°52.657'S, 149°09.330'W, 6 m, SCUBA, Coll. Cécile Debitus, Merrick Ekins 14/04/2013. **Paratypes:** MNHN-IP-2019-3, MNHN-IP-2019-4, MNHN-IP-2019-5, MNHN-IP-2019-6 (field numbers P515/2, P515/3, P515/4 and P516A respectively), same collection details as the holotype.

Type locality. Tahiti Iti peninsula, Tahiti Island, Society Islands, French Polynesia (Figure 1(a,d,e)).

Distribution. Only known from type locality.

Habitat. Lava tube cave, attached to basaltic rocks.

Description. **Morphology,** the examined sponges have the shape of cylindrical almost erected subunits that are fused and evenly anastomosing along most of their length, each with its own osculum (Figure 2). The body plus side growths of the largest sponge (holotype, MNHN-IP-2019-2) is 13 cm wide x 10 cm high and about 2 cm thick, Figure 2(c–e)). The individual cylinders are up to 10 cm long and

about 0.5–1 cm in diameter. The top of cylinders is rounded with a small 1–3 mm centrally located osculum. There are about seven of such cylindrical subunits present in the holotype (Figure 2(c–e)) with numerous outgrowths on sides at the base. At the base of the fan, those cylindrical subunits have an irregular orientation, are shorter and only partly fused (Figure 2(d,e)). The two smaller paratypes (Figure 2(a,b)) are of the same growth form but smaller in size (6 cm wide x 3.5 cm height and are 1–1.5 cm thick, and 7 x 5 cm and 1 cm thick). The smallest specimen is just 2 x 1.5 in size and formed by the partial fusion of only three cylinders. **Texture,** stony and hard. **Surface,** even, but not entirely smooth due to the rugged surface of the choanosomal skeleton protruding in many places from below the ectosome. The external surface of the paratype (MNHN-IP-2019-6) is covered very sparsely by inhalant rounded openings that are about 200 µm in diameter; the other internal side is covered with very densely distributed slit to rounded openings that are evenly distributed over the whole surface. These openings are separated only by dichotriaene branches. **Colour,** is cream white in life, beige in ethanol preservative. **Ectosomal skeleton,** contains rhabd microscleres and the cladome part of the dichotriaene megascleres. The cladomes are strongly spinose on the upper surface with 184–218 µm in diameter. The rhabdomes of the dichotriaene are 218–358 µm long and 33.8–48.1 µm in diameter and penetrate into the choanosome (Figure 4(n–r)). **Choanosomal skeleton** composed of zygosid dicranoclone desmas (Figure 3) and microstyles. **Megascleres,** desmas that are massive arched shaped with a central core from which several arms (four to six) branch from the underside of the arch and both the core and the arms are strongly covered with irregular tubercles (Figure 3). Young dicranoclone desmas are less tuberculated than mature ones (Figure 3(f)). **Microscleres,** in the holotype are spined microstyles that occur in the choanosome and that are 77.6–93.6 µm long and 3.09–4.56 µm in diameter at the top (Figure 4(k–m)); short and thick microrhabds that are concentrated in the ectosome and that are 24.4–32.7 µm long and 11.3–17.3 µm in diameter (Figure 4(a–c); (h–j)), as well as longer slightly curved rhabds that are 47.1–53.6 µm long and 6.73–9.83 µm in diameter (Figure 4(d–g)).

Etymology. Named after Jean-Yves Meyer, research delegate of French Polynesia and an active conservation biologist in French Polynesia who helped in various logistical and administrative ways during our sampling field trips.

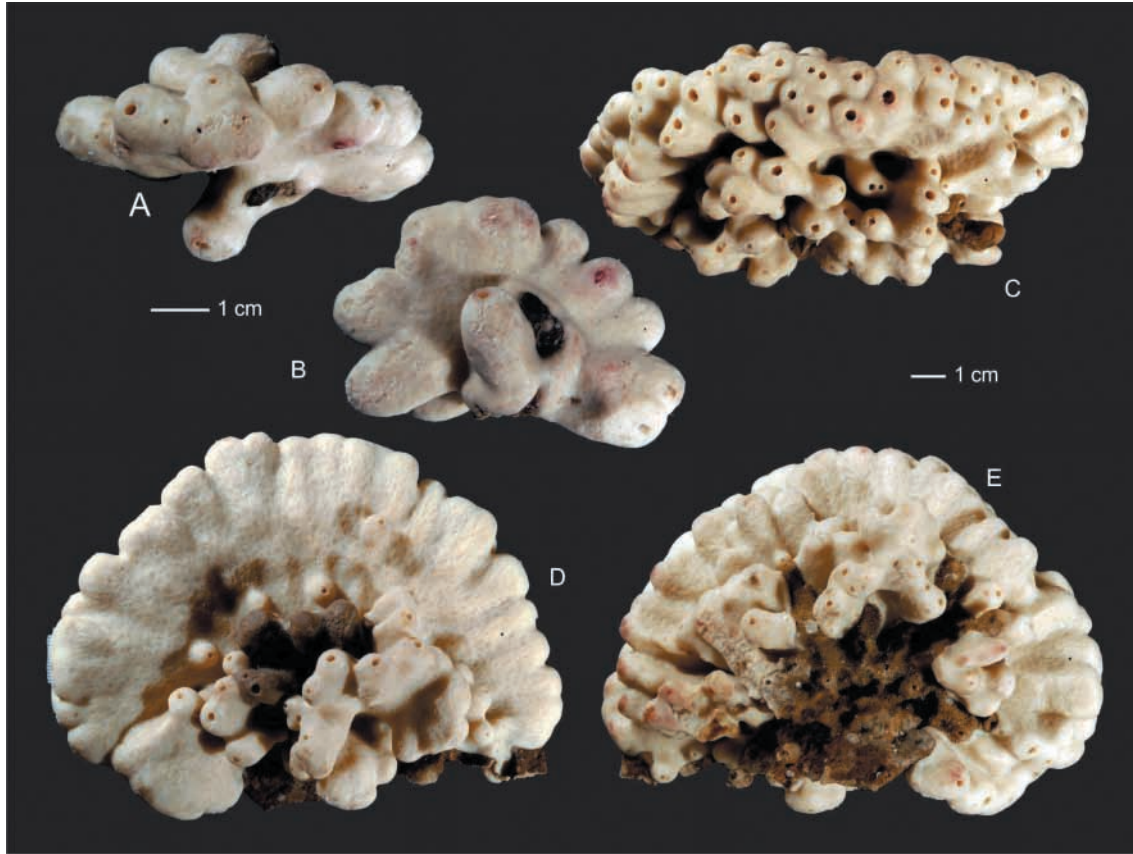


Figure 2. *Levispongia meyeri* gen. nov. sp. nov. (a,b): Paratype specimen MNHN-IP-2019-3; (a): lateral view; (b): top view. (c–e): Holotype specimen MNHN-IP-2019-2; (c): top view, (d,e): lateral views.

DNA barcodes. We sequenced partial 28S (C1-D2 region ~800 bp) of the holotype. GeneBank accession number: MZ313226, Sponge Barcoding Project (SBP) number: 2323.

Remarks. Habitus of this new species is unique within the family Corallistidae, in addition to the set of microscleres that contains no streptasters. The only other described corallistid species that lacks streptasters is *Neophrissospongia microstylifera* from New Caledonia. The species *N. microstylifera* differs by having only microstyles and microstron-gyles. It differs also in growth form by being massive conical. On the other hand, we are aware of an undescribed lithistid sponge from Western Australia (WAM Z35946, LR656117, Figure 14) that has a similar set of microsclere characters (pers. observation A. Pisera) and is molecularly sister (3 bp difference) to the new *Levispongia* gen. nov. species (Figure 14). We therefore suggest to synonymize the species WAM Z35946 (LR656117) with the new genus *Levispongia* gen. nov. sp. (Figure 14). Due to major differences in the composition of

microscleres and the species specific habitus, we assign the new described species *L. meyeri* sp. nov. and *L.* gen. nov. sp. (WAM Z35946) together with *N. microstylifera* to the new genus *Levispongia* that is sister to the genus *Neophrissospongia* (Figure 14). The species *N. microstylifera* (OCDN7083-J, LR656096) will be *N.* cf. *microstylifera* until further investigations and comparison.

Suborder Spirophorina Bergquist & Hogg, 1969

(Note: status change and disused)

Family Siphonidiidae Von Lendenfeld, 1903

Genus *Gastrophanella* Schmidt, 1879

Type species. *Gastrophanella implexa* Schmidt, 1879

Diagnosis. Following Pisera & Lévi, 2002d, clavate to cylindrical to globular to massive lobate to vase- to ear-shaped sponge. No special ectosomal spicules; desmas are rhizoclones. Choanosomal spicules are smooth staples and/or exotylostyles with ornamented to smooth heads.

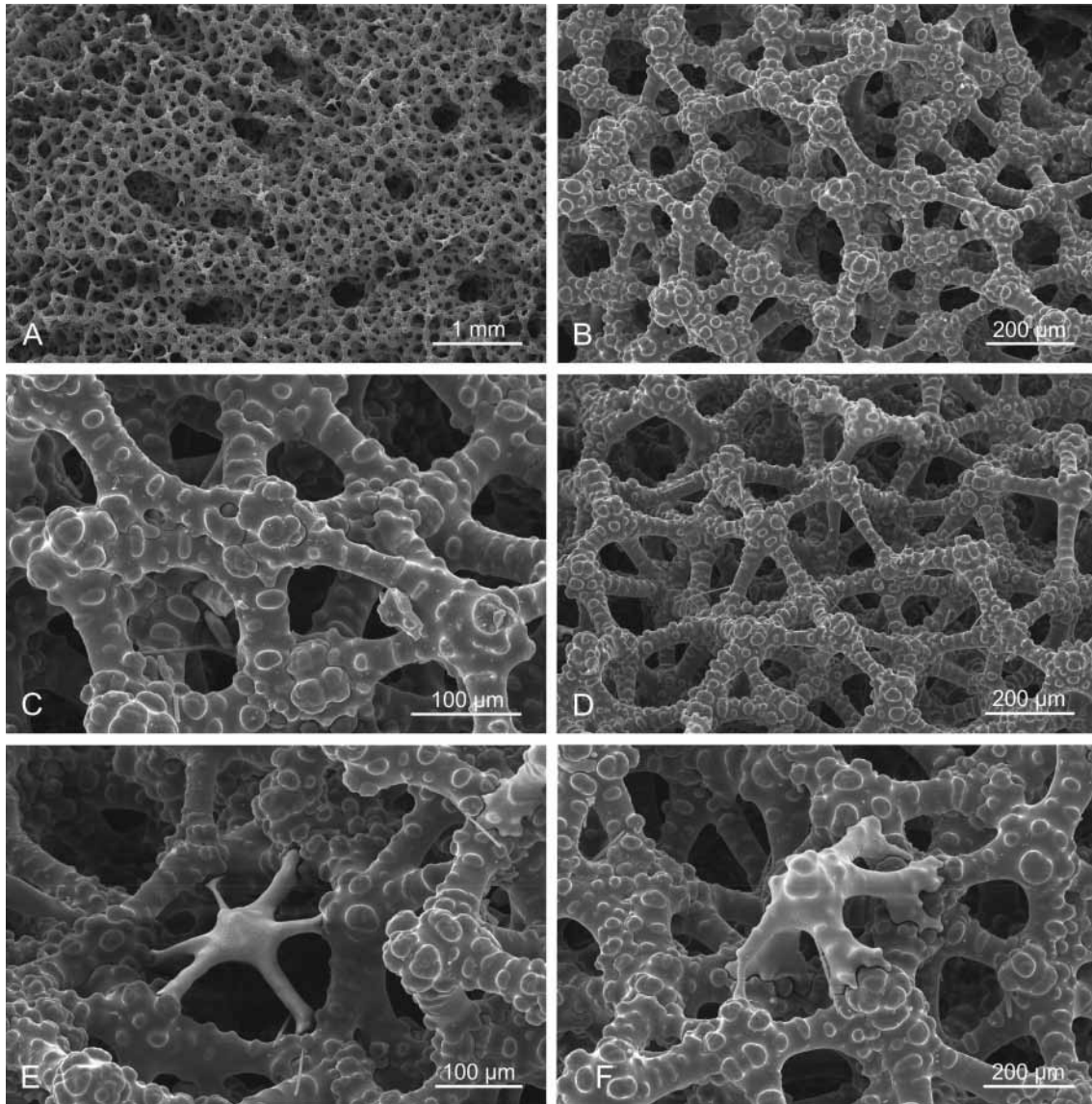


Figure 3. Choanosomal desma skeleton of the holotype *Levispongia meyeri* gen. nov. sp. nov. (MNHN-IP-2019-2). (a–d): Details of choanosomal desmas skeleton formed by tuberculated dicranoclones. (e–f): details of the desma skeleton with young and less tuberculated spicules inserted.

***Gastrophanella basaltica* sp. nov.**
(Figures 5(d–h), 6,7)

Diagnosis. Irregular mass of cylindrical subunits with additional lateral tubes or curved shallow ear-shaped fan with two clearly different surfaces. Microscleres are exotylostyles in the ectosomal part of the sponge and densely distributed and oriented perpendicularly to the surface.

Type material. **Holotype** specimen MNHN-IP-2019-7 (field number P516/2), Tahiti Iti peninsula, Tahiti Island, Society Islands, French Polynesia,

Station 30, 17°52.657'S, 149°09.330'W, 6 m, basaltic Te Pari lava tube on Island fall, SCUBA, Coll. Cécile Debitus, Merrick Ekins 14/04/2013.

Paratypes: specimen MNHN-IP-2019-8 (field number P533) same collection details as the holotype; paratype specimen MNHN-IP-2019-9 (field number P554), basaltic Te Pari lava tube on Tahiti Iti peninsula, Tahiti Island, Society Islands, French Polynesia, Station 30, Coll. Cécile Debitus, 15/12/2015.

Type locality. Te Pari lava tube cave, Tahiti Iti Peninsula, Tahiti island, Society Islands.

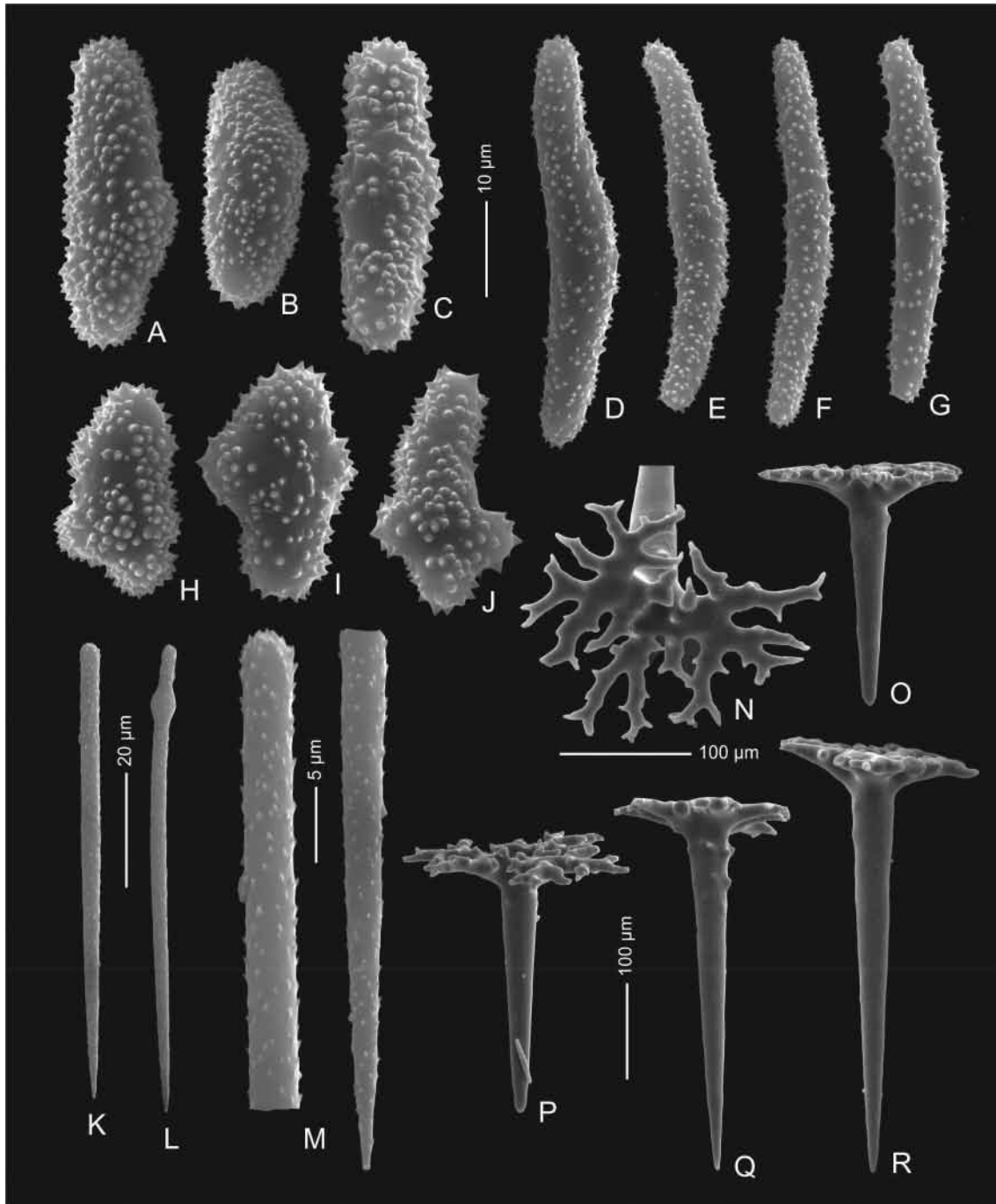


Figure 4. Mega- and microscleres of holotype *Levispongia meyeri* gen. nov. sp. nov. (MNHN-IP-2019-2). (a–c) & (h–j): short thick spined microrhabds. (d–g): long slightly curved and spined microrhabds. (k–m): microstyles. (n–r): dichotriaenes in various views.

Distribution. Only known from type locality Tahiti Iti Island.

Habitat. On basaltic rocks in lava tube caves.

Description. **Morphology** of the holotype (specimen MNHN-IP-2019-7) is an irregular mass of cylindrical

subunits (or fan-like with additional lateral tubes). Each tube is fused at the base or along most of its length and has an apical osculum of 1 to 3 mm in diameter (Figure 5(g,h)). The sponge is 6 cm wide and 4.5 cm high and has about 20 tubes ranging from 3 mm to 10 mm in diameter (Figure 5(g,h)). **Texture**, stony and hard. **Color** in life is cream white and beige

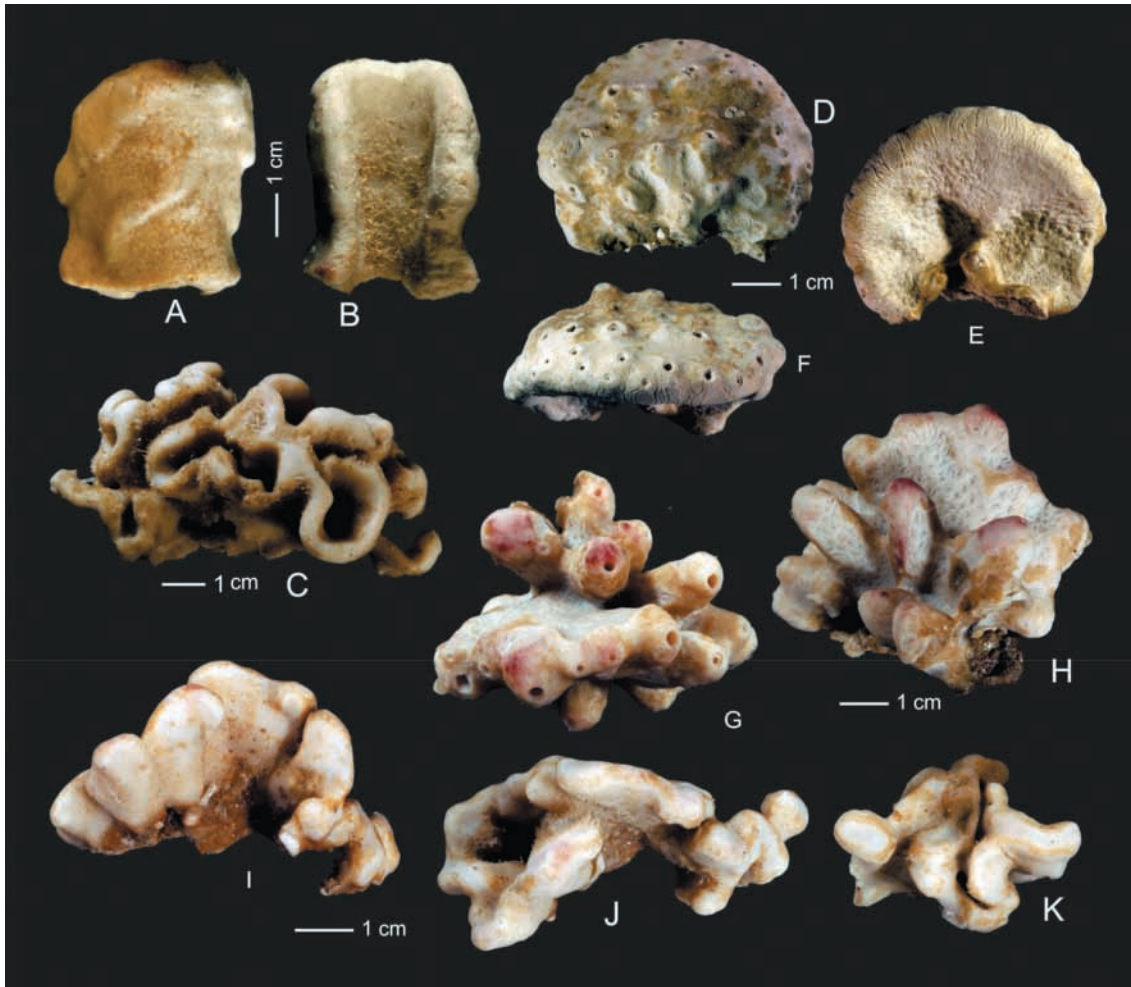


Figure 5. Outer growth form of new rhizomorine lithistids. (a,b): Paratype (MNHN-IP-2019-12) of *Microscleroderma miritatarata* sp. nov. (c): Holotype (MNHN-IP-2019-11) of *Microscleroderma miritatarata* sp. nov. (d–f): Paratype (MNHN-IP-2019-9) of *Gastrophanella basaltica* sp. nov. (g,h): Holotype (MNHN-IP-2019-7) of *Gastrophanella basaltica* sp. nov. (i–k): Holotype (MNHN-IP-2019-10) of *Microscleroderma lava* sp. nov.

to light brownish in ethanol. **Surface**, mostly inhalant; these areas are separated by narrow, slightly elevated flat ridges that are smooth. Short sinuous subdermal canals are visible on the surface that run from the top of tubes downward. Inhalant areas are rough on the surface of the narrow, short skeletal ridges that run in all directions; between them are sparsely distributed depressions with ostia. This entire surface is hispid as it is covered with very short protruding microsclere spicules. One of the paratype specimens (MNHN-IP-2019-9, Figure 5(d–f)) differs considerably in morphology by being a curved shallow ear-shaped fan with two clearly different surfaces, one is concave, has a lot of irregularities and is rough with subdermal short skeletal ridges visible

on the surface (the same as inhalant areas in the holotype MNHN-IP-2019-7) between each ridge membranes ostia are visible that measure about 0.05–0.1 mm in diameter. This concave side has exotylostyles that are densely distributed and oriented perpendicularly to the surface. The other side that is convex bears numerous (about 30) raised oscula that are 1–2 mm in diameter. The oscula are located on low (up to 5 mm high) conical outgrowths. Oscula approaches the upper margin of the sponge from the convex side. The oscula membrane is armed with tangentially embedded exotylostyles. Ectosomal skeleton, with exotylostyles that are densely distributed and oriented perpendicularly to the surface (Figure 6(a)). On the concave side, the margin bears numerous sinuous subdermal furrows that are visible

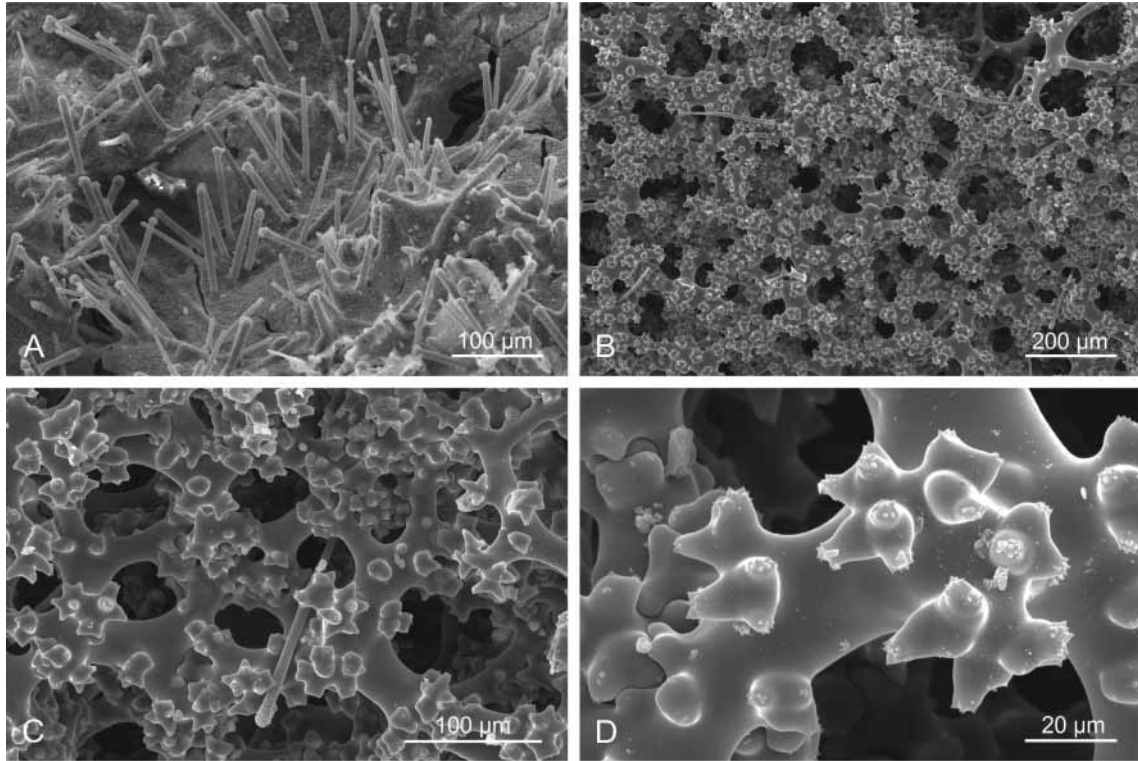


Figure 6. Ectosomal surface and choanosomal skeleton of *Gastrophanella basaltica* sp. nov., (holotype MNHN-IP-2019-7). (a): Ectosomal natural surface with protruding exotylostyles. (b–d): details of choanosomal rhizomorine desmas.

through the dermal membrane. Choanosomal skeleton is composed of a very dense network of rhizocone desmas with blunt outgrowths bearing tiny spines

(Figure 6). Megascleres are rhizocone desmas only. Microscleres are exotylostyles that are 207–249 μm long with spinose heads (Figure 7(a–d)). The head of

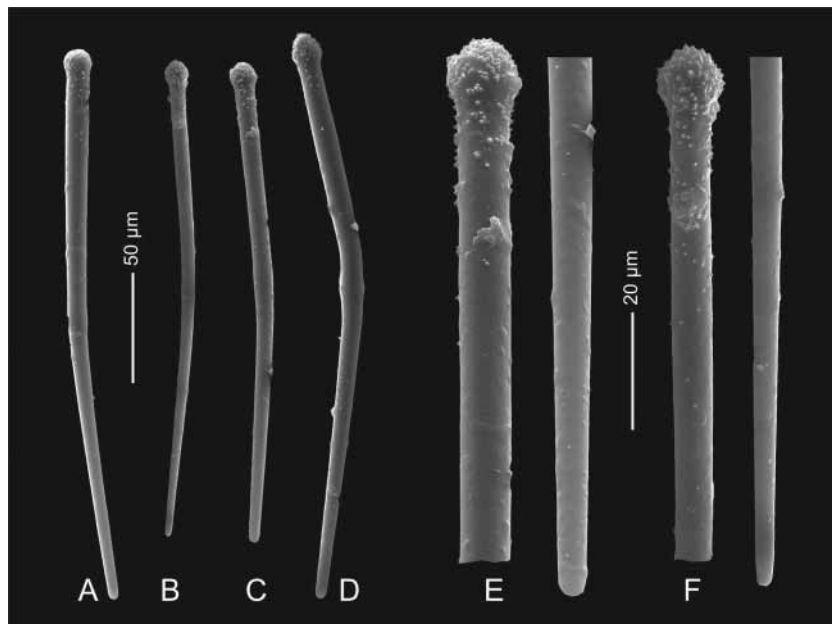


Figure 7. Microscleres of *Gastrophanella basaltica* sp. nov. (holotype MNHN-IP-2019-7). (a–d): exotylostyle microscleres. (e,f): details of spinose heads of exotylostyles.

the exotylostyles are 10.9–14.2 μm long and 12.3–14.3 μm in diameter, whilst the rhabd is 9.41–11.1 μm in diameter at the top (Figure 7(e,f)).

Etymology. named after the basaltic rocks on which it grows inside lava tube cave.

DNA barcodes. We sequenced partial 28S (C1-D2 region ~800 bp) of the holotype. GeneBank accession number: MZ313225, Sponge Barcoding Project (SBP) number: 2324.

Remarks. Gross morphology of the sponge resembles that of *Levispongia meyeri* gen. nov. sp. nov., for which it could be mistaken for in the field, however, it has different spicules: rhizoclonas instead of dicranoclonas, and microscleres as spiny exotylostyles. To date, three *Gastrophanella* species are known from the Atlantic namely *G. implexa* Schmidt, 1879, *G. cavernicola* Muricy & Minervino, 2000 and *G. stylifera*; Mothes & Silva, 1999, however, the latter one might be likely a junior synonym of *G. implexa* (see Pisera & Lévi 2002d). One species is known from a cave in the Mediterranean Sea *G. phoeniciensis* Perez, Vacelet, Bitar & Zibrowius, 2004 and another one *G. mammilliformis* Burton, 1929 was recorded from South African waters, with no precise location given (Burton 1929). Until now, the only known *Gastrophanella* from the central Eastern Pacific coast of Mexico was *G. primore* Gómez, 1998. Our new species *Gastrophanella basaltica* sp. nov. will add the second species of this genus in the Pacific. Its habitus is similar to *G. cavernicola* from Fernando de Noronha, Brazil because both species form a mass of cylindrical tubes, but *G. cavernicola* is rather massive while our species is rather fan shaped. Another similar species from the Atlantic (Brazil) is *G. stylifera* Mothes and Silva, 1999 which is tube shaped thus also similar. Molecularly (28S C1-D2, Figure 15) *G. basaltica* sp. nov. is closely related (2 bp difference) to species from Honduras and Curacao (Figure 15) that were first considered to belong to the genus *Siphonidium* in Schuster et al. (2021). Based on our current morphological and molecular barcodes of the *G. basaltica* sp. nov. in this study we propose the reallocation of all species (LR656148, LR656147, LR656145, LR656146, LR656150) to the genus *Gastrophanella* (Figure 15).

Family Scleritodermidae Sollas, 1888
Genus *Microscleroderma* Kirkpatrick, 1903

Diagnosis. Adopted from Pisera and Lévi 2002. This genus can be vase or foliate in shape with hairy oxeas

protruding from the ectosome; Microscleres are sigmaspires.

Type species. *Microscleroderma hirsutum* Kirkpatrick, 1903

***Microscleroderma lava* sp. nov.**
(Figures 5(i–k), 8–9)

Synonymy. *Microscleroderma* sp. 3 (Schuster et al. 2017, 2019).

Diagnosis. *Microscleroderma* with laminar folded slightly compressed growth morphology. Surface covered with long hair-like oxeas; microscleres as thick spinose sigmaspires.

Type material. Holotype MNHN-IP-2019-10 (field number P498 composed of several fragments of various size), Tahiti Iti peninsula, Tahiti Island, Society Islands, French Polynesia, 17°52.657'S, 149°09.330'W, 6 m, Station 30, basaltic lava tube Te Pari on Island fall, SCUBA, Coll. Cécile Debitus, Merrick Ekins, 14/04/2013.

Comparative material. *Microscleroderma miritatarata* sp. nov. MNHN-IP-2019-10 and MNHN-IP-2019-11 (see below).

Type locality. Tahiti-Iti peninsula, Tahiti Island

Distribution. French Polynesia

Habitat. On basaltic rock in lava tube cave Te Pari

Description. **Morphology**, three larger and three very small fragments of the same laminar sponge were examined. The larger fragments show several folds that are slightly compressed (Figure 4(a,b)). The size of the largest fragment is about 4 cm long, 2.5 cm in wide and 3 cm high. The thickness of the folds is 3 to 5 mm. Ectosomal **surface** is even and strongly hispid on both sides; there are evenly and densely occurring depressions with ostia openings that are about 0.4–0.5 mm in diameter. **Choanosomal skeleton**, is evenly and densely covered by canal openings that are 200–300 μm in diameter and contains rhizoclone desmas. **Megascleres** are dense heavily spined rhizoclonas (Figure 8(c,f)), where the spines are divided many times. On the surface, long hair-like oxeas are visible (Figure 8(a,b)). **Microscleres** as relatively thick spinose sigmaspires that are 13.0–16.0 μm long and 2.02–2.76 μm in diameter (Figure 9(a–h)).

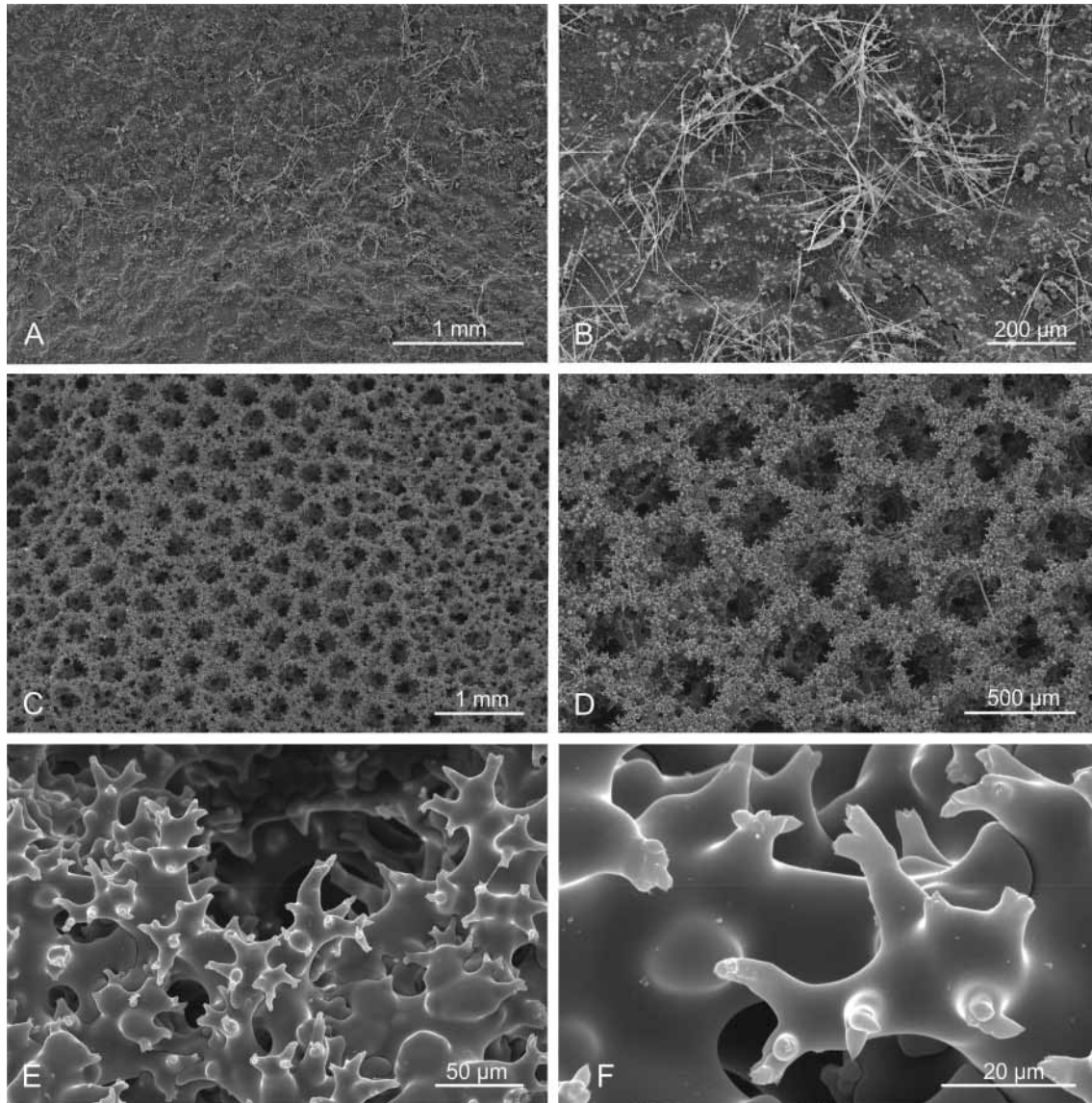


Figure 8. *Microscleroderma lava* sp. nov. (holotype MNHN-IP-2019-10). (a,b): natural surface with ectosomal hair-like oxoas randomly distributed. (c–f): Details of the choanosomal skeleton composed of rhizoclone desmas forming a dense network.

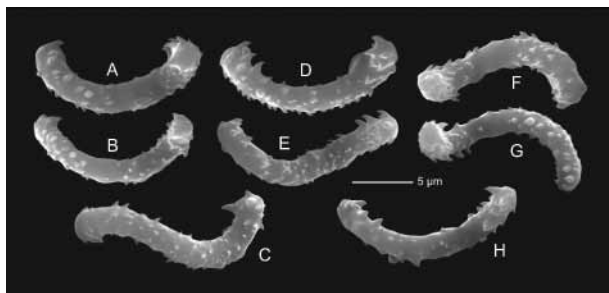


Figure 9. Sigmaspire microscleres of *Microscleroderma lava* sp. nov. (holotype MNHN-IP-2019-10).

Etymology. Named after its occurrence in caves formed by lava flows.

DNA barcode. 28S (C1-D2 region): LR656090 (Schuster et al. 2021); CO1: LT628364, intron ORF 723 + 870 (Schuster et al. 2017).

Remarks. This species is most similar to *Microscleroderma lamina* Perez, Vacelet, Bitar & Zibrowius, 2004 from the submarine cave in Lebanon (Eastern Mediterranean Sea), however, its desmas are rather tuberculated than spinose, sig-

maspires are more S-shaped and spiral, as well as much smaller and less thick than in *M. lava* sp. nov.

In habitus *M. lava* sp. nov. resembles also *M. novaeselandiae* Kelly, 2007 from New Zealand, but its outer wall is considerably thicker and rhizoclone desmas are different. The sizes of the sigmaspires are similar, albeit being slightly smaller and less thick (stout). The differences mentioned here between our Tahiti material and the one from New Zealand, as well as their geographical distance between them, support the morphological difference that they are different species. Notable that features of *M. novaeselandiae* are not well illustrated in detail, making any closer comparison difficult. Molecularly these two species differ by 28 bp difference in the 28S C1-D2 region (Figure 15).

***Microscleroderma miritatarata* sp. nov.**
(Figures 5(a–c), 10–13)

Synonymy. *Microscleroderma* sp. 1 LR656088, LR656089 (Schuster et al. 2021)

Diagnosis. *Microscleroderma* with a complex mass of folded laminae, microoxeas in the choanosomal

part, long hair-like oxeas partly bundled on top of the surface.

Type material. **Holotype** specimen MNHN-IP-2019-11 (field number P112), Nuku Hiva Island, Marquesas Islands, French Polynesia, 8°46.173'S, 140°05.593'W, 6 m, Station MNH03, Expedition BSMPF-1, long Ekamako cave, sandy bottom, SCUBA, Coll. Eric Folcher, 29/08/2009; **Paratype** specimen MNHN-IP-2019-12 (field number P109) same collection details as the holotype.

Comparative material. *Microscleroderma lava* sp. nov. MNHN-IP-2019-10 (see above).

Distribution. Nuku Hiva Island, Marquesas Islands, French Polynesia.

Habitat. Deep inside caves, sandy bottom.

Description. **Morphology**, the holotype (MNHN-IP-2019-11) is a complex mass of folded laminae that is 7.5 cm large and about 4 cm wide and 3 cm high. The laminae are 5–6 mm wide and have rounded margins (Figure 3(a–c)). **Surfaces**, both inner and

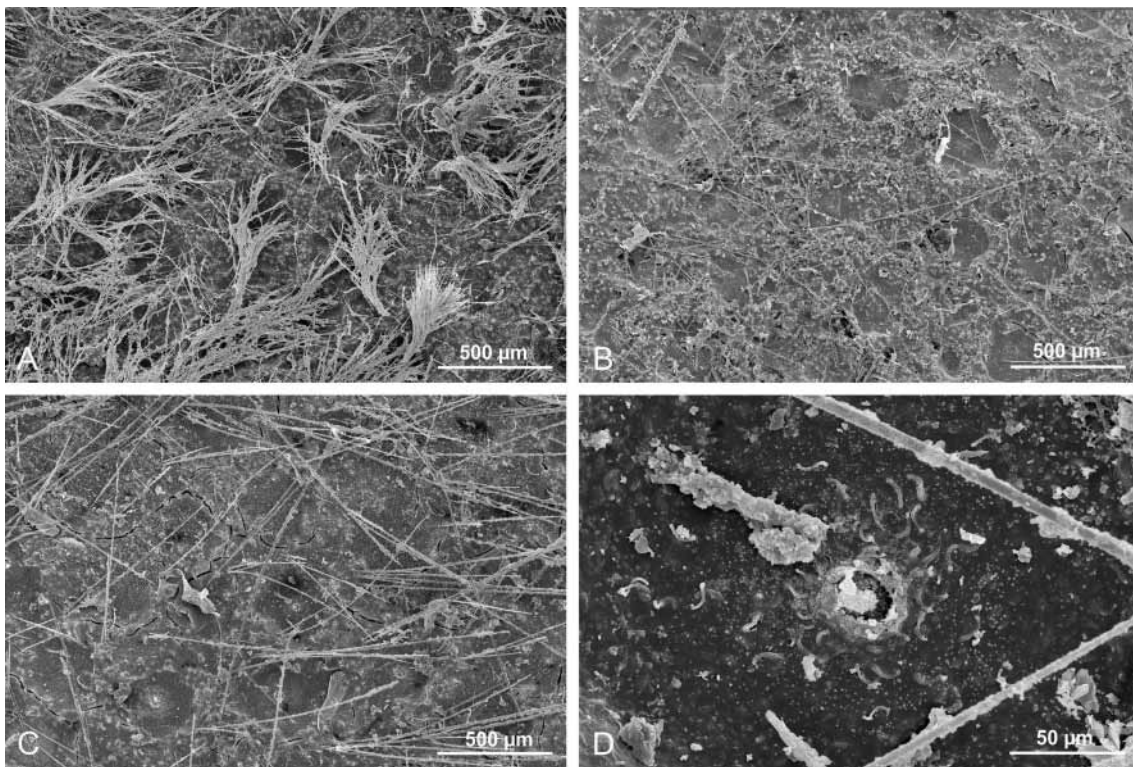


Figure 10. Surface of *Microscleroderma miritatarata* sp. nov. (a,b): Holotype specimen MNHN-IP-2019-11. (c,d): Paratype specimen MNHN-IP-2019-12 with D showing the membrane around ostium with several sigmaspire microscleres embedded.

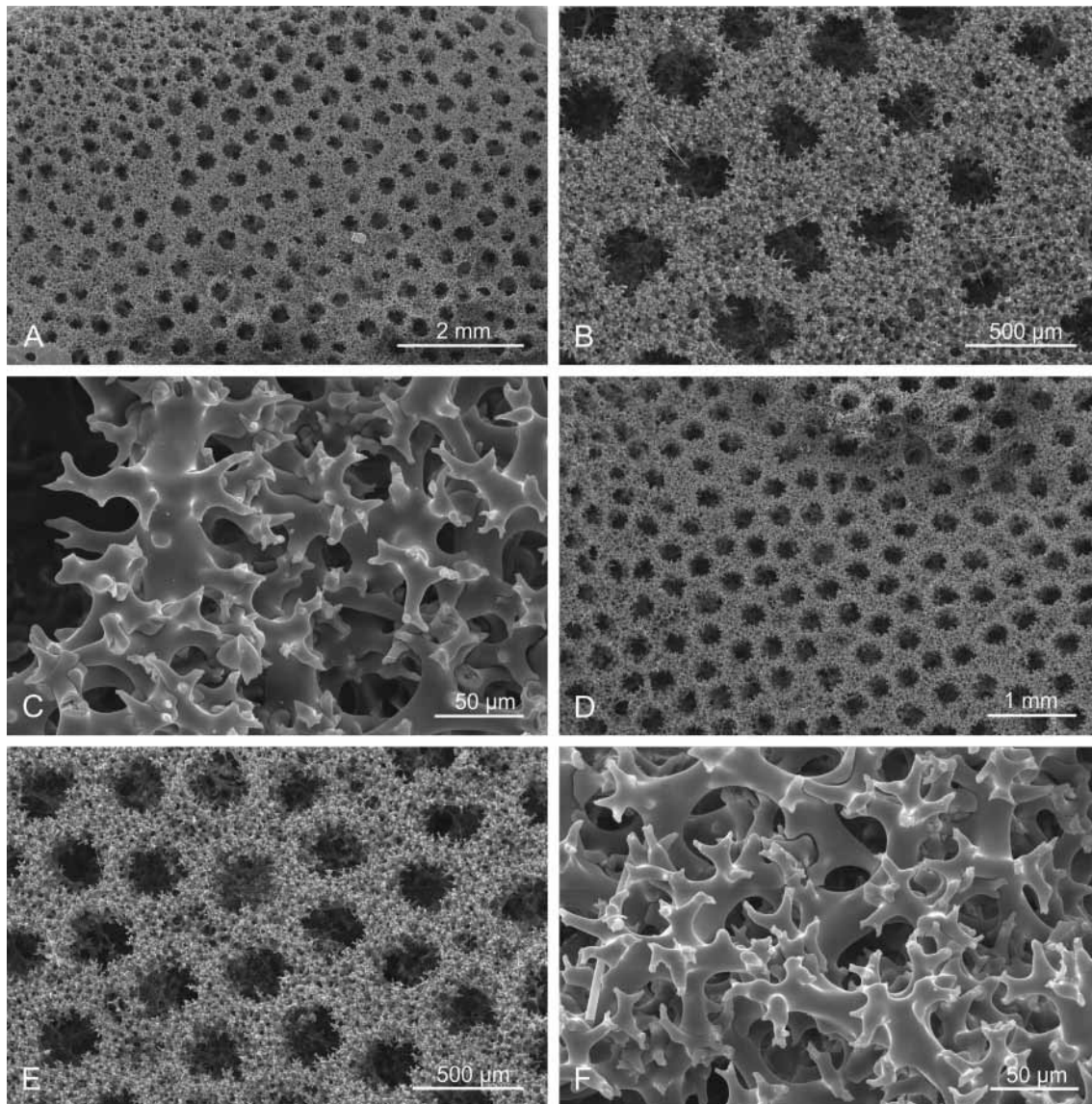


Figure 11. Choanosomal skeleton of *Microscleroderma miritatarata* sp. nov. Details of rhizocone desmas of the holotype specimen MNHN-IP-2019-11. (a–c): represent one side of the surface. (d–f): represents the opposite side of the surface.

outer surface are strongly hispid, especially in protected areas in the folds. **Colour**, *in situ* is light yellowish beige and beige with light brownish spots in ethanol. **Megascleres**, in the exposed areas (i.e. ectosomal outer part of the sponges) the protruding oxeas are either absent or very sparsely distributed (Figure 10). All thin, long hair-like oxeas observed in our preparations were broken and thus not measured. **Microscleres** are spinose sigmaspires that are 11.6–12.6 long and 1.64–2.12 μm thick (Figure 13(a–e)). **Morphology** of the paratype (MNHN-IP-2019-12) represents an ear shaped

fragment, probably from a larger folded massive specimen (Figure 3(a,b)) that is 4 cm high and 3.5 cm wide with walls about 8 mm thick and rounded margins. Both **surfaces** are even and covered with small depressions that are densely and evenly distributed over the entire surface. On the outer site of the sponge these depressions are up to 0.4 mm in diameter and separated by a very narrow skeletal band; on the inner side of the sponge body they are also 0.4 mm in diameter, but slightly less depressed; this inner side has a hispid surface due to the numerous very long (mm scale) oxeas

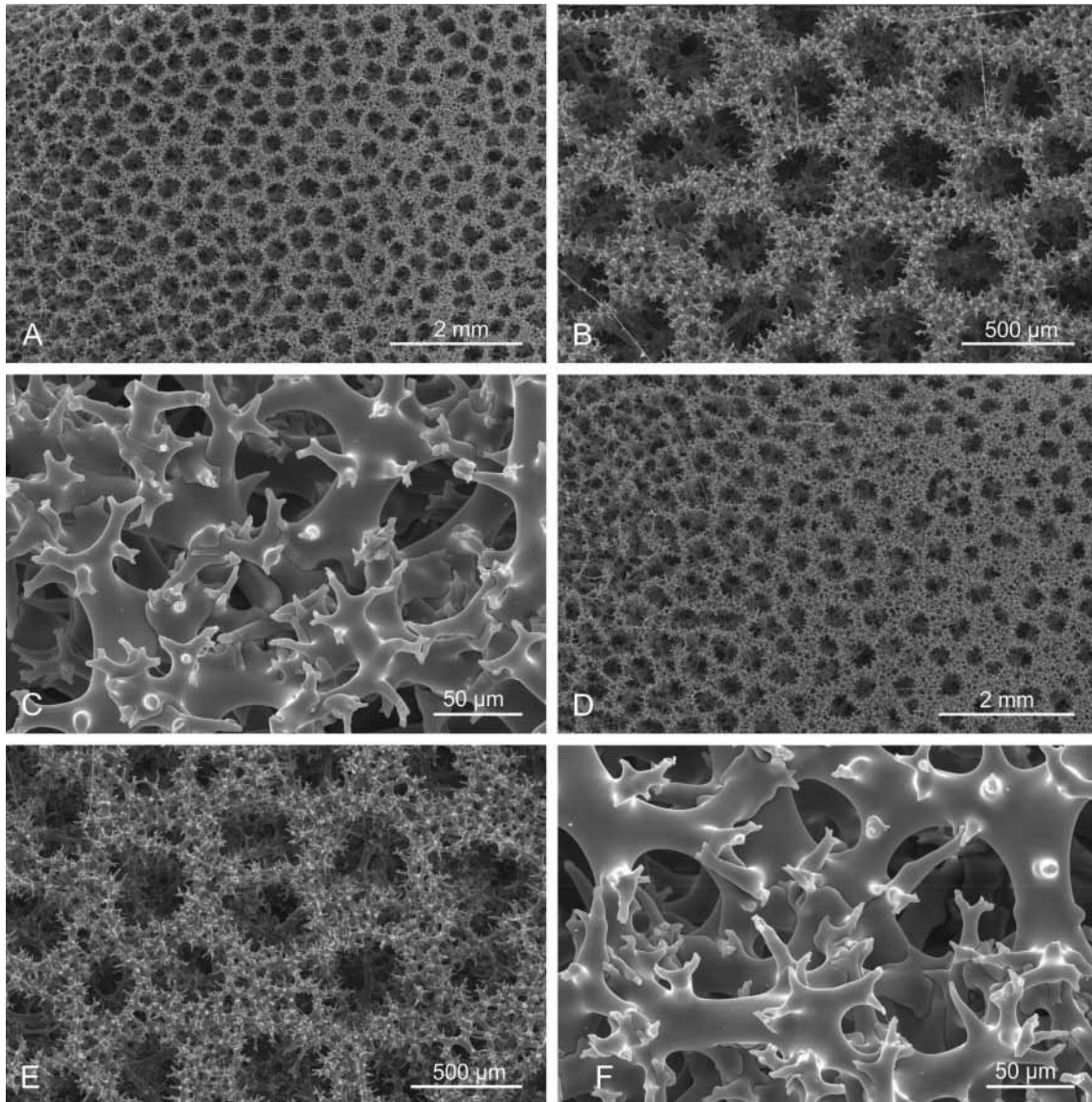


Figure 12. Choanosomal skeleton of *Microscleroderma miritatarata* sp. nov. Details of rhizoclone desmas of the paratype specimen MNHN-IP-2019-12. (a–c): represent one side of the surface. (d–f): represents the opposite side of the surface.

protruding from the surface. The bottom of these depressions is covered with a membrane into which numerous sigmaspires (**microscleres**) are embedded. The surface of the **choanosomal skeleton** on both sides is densely and regularly pierced by round openings which correspond to the depressions on the surface of the ectosome that are 200–300 µm in diameter and slightly larger on one side. The choanosomal skeleton further consists of rhizoclones desmas. Megascleres are zygosid rhizoclone desmas. **Microscleres** of the paratype are spinose sigmaspires that are 13.9–15.1 µm long and 1.2–

1.73 µm in diameter (Figure 13(f–Figure f)); thin oxeas 1–2 µm in diameter and 1–2 mm long were also observed in our spicule preparations.

Etymology. Named after Miri Tatarata, the head of the environment department in French Polynesia.

DNA barcodes. 28S (C1–D2 region): LR656088, LR656089 (Schuster et al. 2021).

Remarks. This species is most similar to the new species *Microscleroderma lava* sp. nov. from Tahiti Iti,

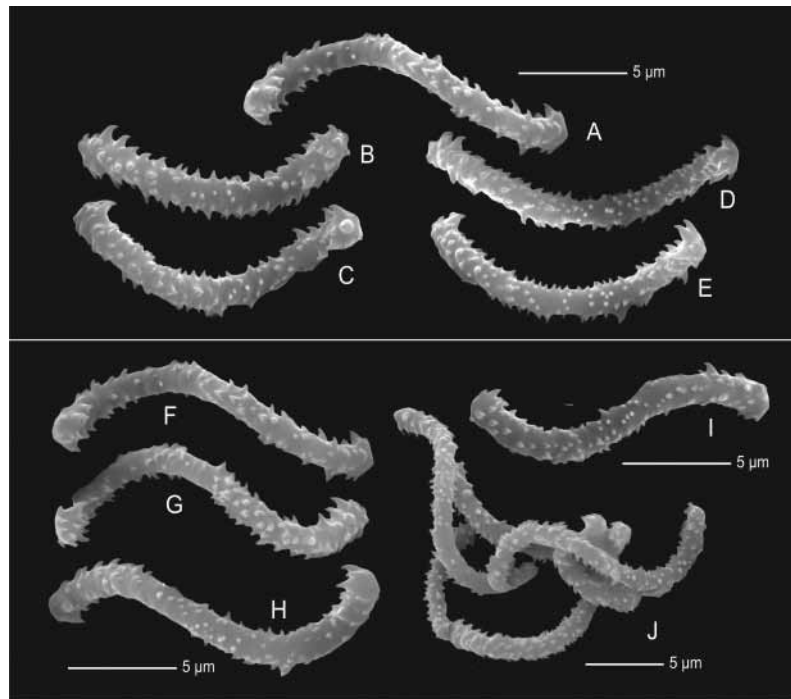


Figure 13. Sigmaspires of *Microscleroderma miritatarata* sp. nov. (a–e): Sigmaspires of holotype specimen MHNH-IP-2019-11. (f–j): Sigmaspires of paratype specimen MHNH-IP-2019-12.

however, it differs in having longer, thinner and more spined sigmaspires. It also differs in the gross morphology. Another morphologically close species is *M. lamina* from the Lebanon coast of the Mediterranean Sea (Pérez et al. 2004), but their geographic distance makes their con-specificity very unlikely. Molecularly our new species *M. miritatarata* sp. nov. is sister to *Microscleroderma* sp. 1 (LR656087) from Martinique (Figure 15).

Discussion and summary

In this study, we report for the first time the occurrence of lithistids in French Polynesia and subsequently increase the current knowledge on Pacific lithistids. Three new species of rhizomorphines were described i.e. *Microscleroderma lava* sp. nov., *Microscleroderma miritatarata* sp. nov. and *Gastrophanella basaltica* sp. nov. One new corallistid species *Levispongia meyeri* gen. nov. sp. nov., which is also a new genus based on the morphological and the phylogenetic species concept, was also described.

Microscleroderma miritatarata sp. nov. was found in the cave Ekamako on Nuku Hiva Island (Marquesas

Islands) (Figure 1), characterized by its rhizoclones desmas and sigmaspire microscleres. The three other lithistid species were found in a longer submarine cave at Te Pari on Tahiti Iti peninsula (Tahiti Island, Windward Islands, Society Islands) (Figure 1). *Microscleroderma lava* sp. nov. is very similar to *M. miritatarata* sp. nov. from Nuku Hiva, but differs morphologically and molecularly (33 bp difference). Organic extracts of *M. miritatarata* sp. nov. displayed antifungal properties related to the presence of microsclerodermins, as described in other species from the Western Pacific deep waters and from a shallow water species from Mauritius, *Microscleroderma herdmanni*, Dendy, 1905; (Bewley et al. 1994; Qureshi et al. 2000). Previous to this study, only three species of *Microscleroderma* were described from the Indo-Pacific namely *M. hirsutum*, *M. herdmanni* and *M. stonae* Lévi & Lévi, 1983, however, none of these species were recorded in caves. So far, the only cave species (*Microscleroderma lamina* Pérez, Vacelet, Bitar & Zibrowius) was found in the Eastern Mediterranean Sea (Pérez et al. 2004). The new *Microscleroderma* species from Marquesas and Tahiti are most similar in morphology and spiculation to the Mediterranean

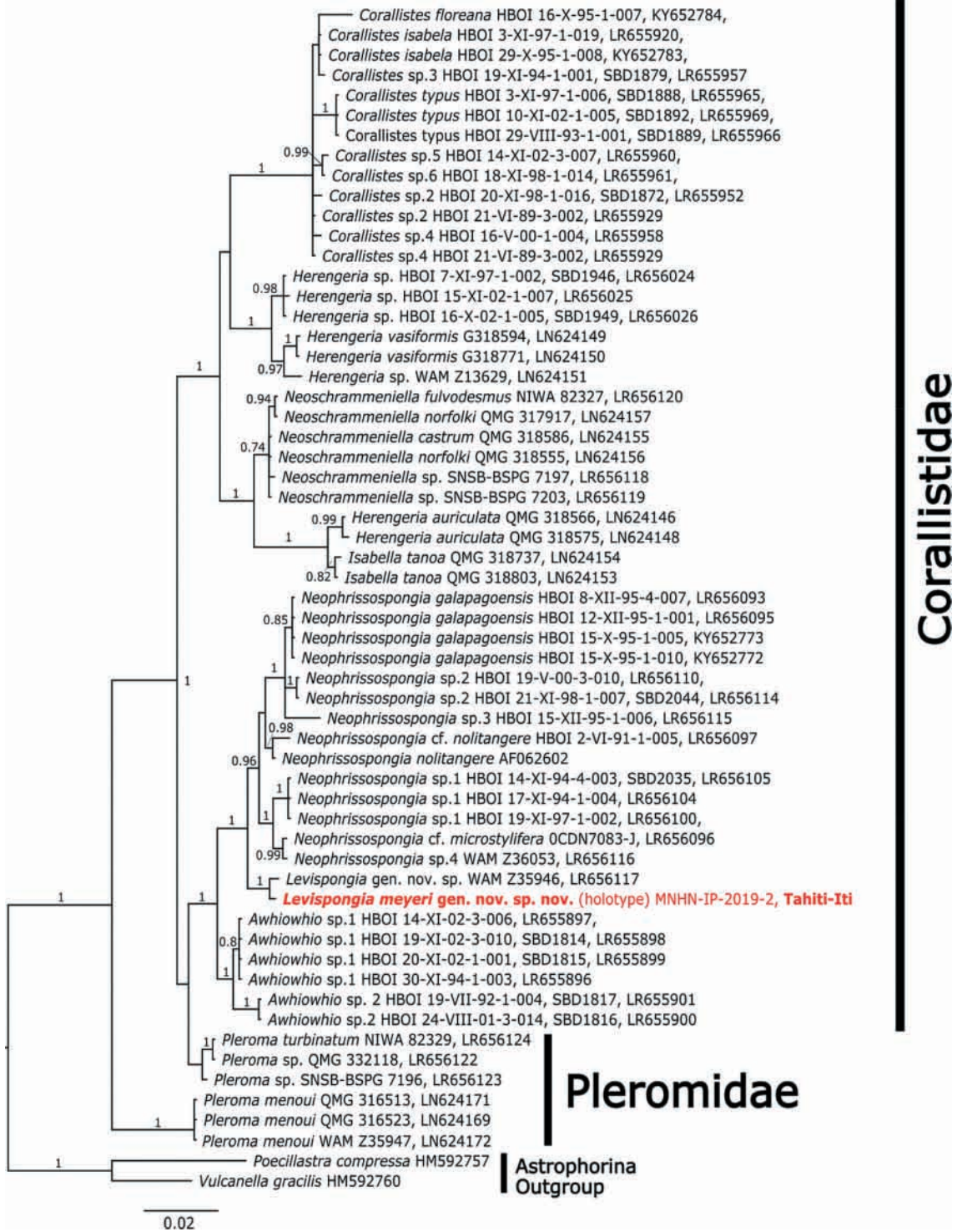


Figure 14. Bayesian inference (BI) reconstruction of the 28S rDNA gene (C1-D2 region) showing the relationship of *Levispongia meyeri* sp. nov. (in red) to other genera within the family Corallistidae. Bayesian posterior probability values are indicated for clades >0.75 otherwise not given. Numbers following the taxon names are collection numbers or NCBI Genbank accession numbers.

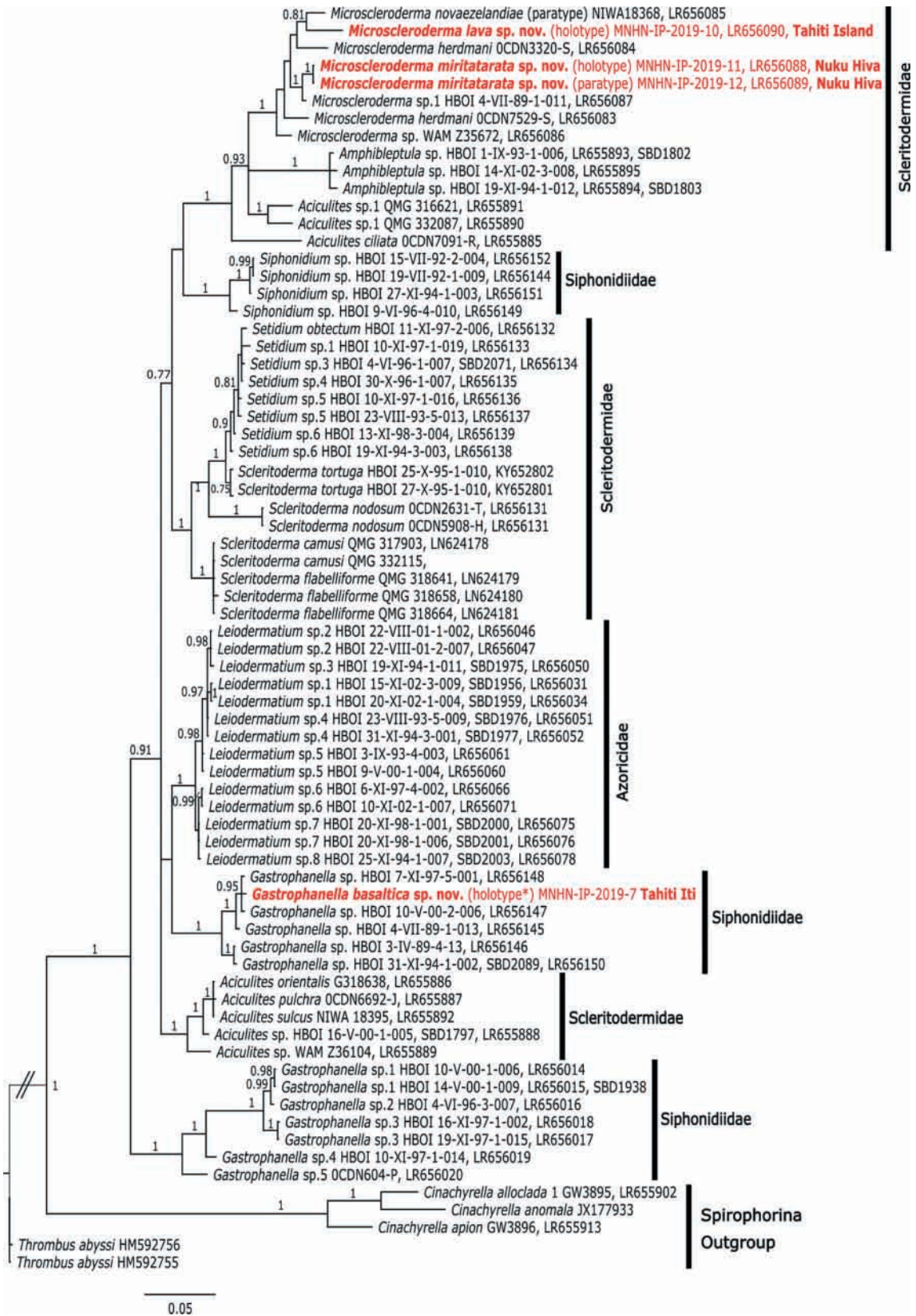


Figure 15. Bayesian inference (BI) reconstruction of the 28S rDNA gene (C1-D2 region) showing the relationship of the new species (in red) to other spirophorin species. Bayesian posterior probability values are indicated for clades >0.75 otherwise not given. Numbers following the taxon names are collection numbers or NCBI Genbank accession numbers.

cave species *M. lamina* due to their hair-like oxeas, which were not reported in the other *Microscleroderma* species. Unfortunately, no sequences of *M. lamina* exist to date, making any additional molecular comparison impossible. Nevertheless, our 28S gene tree indicates that *M. lava* sp. nov. is sister to *M. novaezelandiae* from New Zealand although with a low support value (PP = 0.81, Figure 15), both species group in a clade (not supported) with *M. herdmani* from the Philippines (Figure 15). In contrast, *M. miritatarata* sp. nov. is sister (PP = 1.0) to *Microscleroderma* sp.1 from the Caribbean Sea (Martinique) (Figure 15). The other rhizomorine lithistid species have exotylostyles as microscleres and belongs to the genus *Gastrophanella*. This genus is relatively rare, but is reported from all oceans (WPD, Van Soest et al. 2019) and here for the first time from the Central Pacific. A very similar species (*Gastrophanella phoeniciensis* Pérez, Vacelet, Bitar & Zibrowius, 2004) was found in the submarine cave in the Eastern Mediterranean (Pérez et al. 2004). Molecularly, our new species groups in a highly supported clade (PP = 1.0) with other *Gastrophanellas* from the Caribbean Sea (Figure 15). The third species belongs to the family of Corallistidae (desmas as dicranoclones) and has dichotriaenes with spinose/tuberculated surface of the caldome, and acanthorhabds and spine styles as microscleres. Based on morphological and molecular characters it represents a new genus. The 28S gene indicates its sister-relationship (PP = 1.0) to *Levispongia* gen. nov. sp. (LR656117) from the Western Australian Imperieuse Reef. Among all corallistid genera, the new genus is sister to the monophyletic *Neophrissospongia* genus (Figure 14). The desmas of this new genus are very similar to typical sphaeroclones known in some lithistids from the Mesozoic of Europe (see Pisera 2002).

Overall, the Tahiti lithistid fauna with three new species belonging to three different families seems to be more diverse than the Marquesas with only one species. However, compared to the observed diversity in the Western Pacific (unpublished data A. Pisera and M. Ekins) and Eastern Pacific e.g. the Galapagos Archipelago (Schuster et al. 2018) and Cocos Island (unpublished data A. Schuster) both faunas show a much lower diversity. This finding would fit well with the general pattern of decreasing diversity from the West and East continental areas towards the Central Pacific (Zezina 1997, 2001; Bitner 2006). In addition, the Marquesas Islands and Tahiti are one of the most isolated archipelagos in our oceans with no additional islands in between that would facilitate

dispersal of organisms. Also, water current patterns, which play an essential role in dispersal of marine organisms, are generally further away from this archipelago (Springer 1982; Richer De Forges et al. 1999). Interestingly, a very similar assemblage of lithistids (*Microscleroderma*, *Gastrophanella* and corallistids) was reported from a submarine cave in the Philippines (Pisera & Vacelet 2006). In conclusion, this study provides the first to investigate the cave lithistid fauna in one of the most remote marine areas, the French Polynesian Archipelago by providing descriptions and barcodes of this unique cave specimens. Our phylogenetic analyses (Figures 14 and 15) including other material from the Caribbean, Atlantic, Central and West Pacific support the hypothesis that most of these sponges are endemic to this region, however, further sampling from other areas of the French Polynesian Archipelago and the Eastern Pacific is needed to get a more complete biogeographic picture on their distribution patterns in Pacific Ocean.

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Disclosure statement

No potential conflict of interest was reported by the author(s).

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