



Revision of the genus *Exsuperantia* Özdikmen, 2009 (Tetractinellida: Phymaraphiniidae) with description of a new species from the Atlantic Ocean

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Abstract

Phymaraphiniidae Schrammen 1924 (Porifera: Astrophorina) is a family of lithistid demosponges that has received little attention in the past decades. The systematic problems within this family have not been addressed for a long time due to the absence of new records and material. The genus *Exsuperantia* Özdikmen 2009 was first described by Schmidt (1879) as *Rimella* to allocate the species *Rimella clava*, found in the Caribbean. In 1892, Topsent found what he thought to be the same species described by Schmidt in the Azores, and synonymized it with *Racodiscula clava*, as he thought this species belonged to the family Theonellidae Lendenfeld 1903. However, *Rimella* and *Racodiscula* belong to distinct families: *Rimella* to Phymaraphiniidae, and *Racodiscula* to Theonellidae. Due to the fact that the genus *Rimella* was already preoccupied by a gastropod, it was renamed as *Exsuperantia*. In result of the poor preservation of Schmidt's material and the absence of new specimens, the attribution of Topsent's specimens to the family level remained obscure. Here, we review the genus *Exsuperantia* based on the analysis of new material recently collected during various research expeditions in the northeast Atlantic Ocean. The comparison of these new specimens with Schmidt's and Topsent's type material, allowed us to assign Topsent's specimens to a new species, *Exsuperantia archipelagus* **sp. nov.**, and confirm its attribution to the family Phymaraphiniidae (not Theonellidae). Phylogenetic reconstructions using newly generated sequences of the cytochrome subunit (COI) marker also support the assignment of the new species to the family Phymaraphiniidae (not Theonellidae).

Key words: Porifera, lithistids demosponges, Macaronesian islands, new species

Introduction

Lithistid demosponges are a polyphyletic group of sponges (*e.g.* Pisera & Lévi 2002a; Morrow & Cárdenas 2015; Schuster *et al.* 2015) that share the possession of an interlocked and rigid skeleton of siliceous spicules—desmas. The current distribution of these sponges is mainly restricted to tropical and warm temperate deep waters (*e.g.* Schmidt 1870, 1880; Topsent 1898; Lévi & Lévi 1983, 1988; Pomponi *et al.* 2001; Kelly 2007). Nevertheless, they can also be found in shallow waters, and in caves and reef tunnels (Vacelet & Vasseur 1965; Manconi *et al.* 2006; Manconi & Serusi 2008; Pisera & Vacelet 2011).

Lithistids are a sponge group with a rich fossil record, as a result of the high fossilization potential of interlocked desmas (Finks 1970; Rigby 1991; Pisera 2002). The fossil record dates back to the lower/middle Cambrian—513 Mya—and they have been repeatedly considered to be much more diverse and abundant in the Upper Cretaceous—66 to 100 Mya—when compared with the extant diversity (Reid 1967; Lévi 1991). However, based on our current knowledge, we now know that the contemporary diversity of these sponges is very similar to the past one (Pisera, unpublished). Lithistid sponges have been allocated in three distinct orders—Tetractinellida Marshall, 1876, Sphaerocladina Schrammen, 1924 and Bubarida, Topsent 1894—and comprise over 200 species distributed across 13 families and 42 genera (*e.g.* Cárdenas *et al.* 2011; Morrow & Cárdenas 2015; Schuster *et al.* 2015).

Phymaraphiniidae Schrammen, 1924 is a poorly known and a rare family of fossil and extant sponges characterized by the possession of trider-type desmas (Pisera & Lévi 2002b). The placement of Phymaraphiniidae within Tetractinellida was first suggested by morphology (Pisera & Lévi, 2002b) and later confirmed by molecular markers (Cárdenas *et al.*, 2011). Currently three genera, *Exsuperantia* Özdikmen, 2009, *Kaliapsis* Bowerbank,

1869, and *Lepidothenea* de Laubenfels, 1936, and five species, are assigned to this family. However, in the case of *Lepidothenea*, which has no desmas, and only ectosomal discs and microscleres, such assignment is questionable. *Lepidothenea* was designated a new genus (*Lepidospongia* Dendy, 1924 was preoccupied) and assigned to the family Kaliapsidae Laubenfels (1936) due to the presence of phyllotrias. Since Kaliapsidae was erected without a diagnosis, Pisera & Lévi (2002b) suggested to abandon this family and to include its members in *Kaliapsis* (Phymaraphiniidae). However, the placement of *Lepidothenea* is not established, and it remains *incertae sedis* due to its resemblance with Neopeltidae Sollas, 1888 (Kelly, 2007), Theonellidae Lendenfeld, 1903 (Bergquist, 1968) and Phymaraphiniidae. *Kaliapsis* and *Lepidothenea* are known from the Indian and Pacific Oceans, respectively, while *Exsuperantia* is exclusively known from the North Atlantic (Schmidt 1879; Topsent 1892, 1904, 1928; Laubenfels 1936; Vacelet & Vasseur 1971). Little is known about the distribution and type of habitat of these species due to short and incomplete earlier descriptions (Bowerbank 1869; Schmidt 1870, 1879). Furthermore, there are no recent records of *Kaliapsis* and *Lepidothenea*. Contrastingly, *Exsuperantia* has a recent record from the Azores (Cárdenas *et al.* 2011), but *E. clava* (Schmidt, 1870) is its only species known to date.

Fossil phymaraphiniids are well known from the Cretaceous rocks of Europe (Aptian to Maastrichtian), and are assigned to seven genera and numerous species (Reid 2004). Undescribed Eocene species (at least two different ones) have been found in SW Australia (Gammon *et al.* 2000; Pisera unpublished). Desmas in fossil species are typical regular tridiers, and ectosomal spicules, if present, are phyllotrias or discotrias with incised margins. No microscleres have been reported, but in our opinion, this is likely a taphonomic effect.

Here we present a systematic revision of *Exsuperantia* based on Topsent's (1892, 1904, 1928) and Schmidt's (1879) materials and recently collected specimens in the Macaronesian archipelagos (Azores, Madeira and Canaries). A new species from the Azores is hereby described, and the phylogenetic affinity of the family inferred using molecular methods.

Material and methods

In order to make a revision of *Exsuperantia* we examined the type material of *Rimella clava* (Schmidt) and *Exsuperantia clava* (Topsent), available at the Museum of Comparative Zoology at Harvard University (MCZ), and at the Muséum National d'Histoire Naturelle (MNHN) in Paris, respectively; as well as specimens recently collected at the Macaronesian islands and seamounts of the Azores exclusive economic zone (EEZ) (see table 1 for more detailed information). Schmidt's material consists of four different deciduous dry specimens, and Topsent's material is a dry specimen. The recent material was collected during scientific surveys of the Department of Oceanography and Fisheries of the University of Azores (DOP) and the Harbour Branch Oceanographic Institute (HBOI). The new material is represented by entire specimens, preserved in ethanol upon collection. Data regarding the collection of specimens examined here are available at the PANGAEA data repository (<https://doi.pangaea.de/10.1594/PANGAEA.896251>).

Identifications were made from the analyses of skeletal structures under optical microscopy. Cross sections and spicules slides were prepared using standard procedures (Boury-Esnault & Rützler 1997), and Canada balsam as selected mounting medium. In addition, some specimens were observed under scanning electron microscopy (SEM). For this purpose, small pieces of the sponges were digested in nitric acid, rinsed several times with distilled water and fixated in ethanol. Stubs containing desmas and loose spicules were prepared separately and coated with gold-palladium or platinum. Spicules measurements were also taken for different individuals in order to assess intraspecific variation.

Samples originally preserved in ethanol were subjected to DNA extractions using the DNeasy blood and tissue kit (QIAGEN) following the instructions of the manufacturer. Barcodes of the mtDNA COI gene (658 bp) were amplified using the LCO1490 and HCO2198 primers (Folmer *et al.* 1994). The polymerase chain reaction conditions used are the following: 5 min/94°C; 5 cycles [30 s/94°C, 1 min/45°C, 1min/72°C]; 30 cycles [30 s/94°C, 1min/50°C, 1min/72°C]; 7 min/72°C. The PCR products were further purified with a solution of Exonuclease 1 (EXO, 10 U μL^{-1}) and shrimp alkaline phosphatase (SAP, 10 U μL^{-1} USB®). Sanger Sequencing was performed with Big Dye® Terminator v3.1, on a capillary-based Applied Biosystem 3730XL Analyzer. The molecular work was carried out at Biodiversity Laboratories (BDL, DNA Section) at the Department of Biological Sciences (University of Bergen) and the obtained sequences are deposited in GenBank (table 2) and Sponge Barcoding Project webpage

(SBP) (<https://www.spongebarcoding.org/>). Due to the preservation mode of the type material from Schmidt's and Topsent's collections, we were not able to generate DNA sequences for these specimens.

Sequences were checked by searches in BLAST (the Basic Local Alignment Search Tool—<https://blast.ncbi.nlm.nih.gov/Blast.cgi>), edited in Geneious v.10.0.9 (Kearse *et al.* 2012) and aligned using Muscle (Edgar 2004). The final dataset is composed of 68 nucleotide sequences (including outgroups) with 691 characters, of which 438 are constant, 37 are parsimony uninformative and 216 are parsimony informative. All families of the suborder Astrophorina were included in the dataset—following the new classification of Demospongiae (Morrow & Cárdenas 2015)—except Thrombidae Sollas, 1888 due to the absence of mtDNA COI sequences available. Of the 68 sequences seven were newly generated for this study. Members of Tetillidae Sollas, 1886 were designated as outgroup.

A phylogenetic reconstruction under Bayesian Inference was implemented using Mr. Bayes v. 3.2 (Ronquist *et al.*, 2012). The best fitting model for our dataset was GTR+I+G, as estimated in JModeltest (Posada 2008; Darriba *et al.* 2012) according to the Akaike Information Criterion (AIC). The analysis was performed in three runs of four Metropolis-coupled Markov chains (MCMC). Chains ran for 5,000,000 generations or were stopped when the standard deviation of split frequencies of runs fell below 0.01. The initial 25% sampled trees were discarded for burn in.

The Maximum Likelihood (ML) analysis was run with RAxML v. 8 (Stamatakis 2014) using the model GTRGAMMAI and 1000 rapid bootstrapping replicates. The produced phylogenetic trees were visualized and compared in FigTree (<http://tree.bio.ed.ac.uk/software/figtree/>).

Results

Systematics

Class Demospongiae Sollas, 1885

Subclass Heteroscleromorpha Cárdenas, Pérez & Boury-Esnault, 2012

Order Tetractinellida Marshall, 1876

Suborder Astrophorina Sollas, 1887

Family Phymaraphiniidae Schrammen, 1924

Genus *Exsuperantia* Özdikmen, 2009

Synonymy. *Rimella* Schmidt, 1879: 21 (preoccupied); *Racodiscula* sensu Topsent, 1892 (Topsent 1904, 1928) (wrong generic assignment).

Type species. *Rimella clava* Schmidt, 1879: 21.

Diagnosis. Phymaraphiniidae with a clavate shape, and phyllotriaenes as ectosomal spicules (Pisera & Lévi 2002b).

Description. Clavate to columnar sponges; ectosomal spicules are smooth phyllotriaenes; choanosomal macroscleres are subtylostyles to tylotes, and desmas are triders with smooth and/or tuberculated tubercles; microscleres are acanthomicroxeas, acanthorhabds and amphiasters (emended from Pisera & Lévi 2002b).

Remarks. Schmidt (1879) described a new genus from the Gulf of Mexico with the type species *Rimella clava*. However, *Rimella* was already preoccupied by a gastropod defined by Agassiz (1840), turning *Rimella* Schmidt into a junior synonym of *Rimella* Agassiz (Özdikmen 2009). More recently, the original Schmidt material (1879) was redescribed and reillustrated by Pisera & Lévi (2002b).

TABLE 1. List of *Exsuperantia* specimens examined in this study with information of museum's voucher codes, sampling sites, depth, collection year, collection gear, campaign, preservation mode of the material and institution where it is deposited.

Species	Code	Locality	Latitude	Longitude	Depth (m)	Collection year	Vessel/ship	Collection gear	Campaign	Preservation	Institution
<i>E. archipelagus</i> sp. nov.	MNHN DT-782/1*	Azores	38° 52' 50"N	27° 23' 05"W	599	1896	Princesse-Alice	Dredge	Prince de Monaco (1889-1905)	Dry	MNHN
<i>E. archipelagus</i> sp. nov.	MNHN DT-782/2**	Azores	38° 52' 50"N	27° 23' 05"W	599	1896	Princesse-Alice	Dredge	Prince de Monaco (1889-1905)	Dry	MNHN
<i>E. archipelagus</i> sp. nov.	DOP1976**	Azores	38° 05' 59"N	29° 08' 59"W	168–594	2007	Manuel Arriaga	Bottom longline	–	90% Ethanol	DOP
<i>E. archipelagus</i> sp. nov.	DOP5883	Azores	37° 59' 13"N	29° 31' 48"W	371	2011	Mestre Bobicha	Bottom longline	–	90% Ethanol	DOP
<i>E. archipelagus</i> sp. nov.	DOP6212	Azores	37° 29' 13"N	30° 50' 45"W	353	2010	R/V Arquipélago	Bottom longline	CoralFishD-33-V10	90% Ethanol	DOP
<i>E. archipelagus</i> sp. nov.	DOP6248	Azores	37° 31' 22"N	30° 36' 28"W	770	2010	R/V Arquipélago	Bottom longline	CoralFishD-33-V11	90% Ethanol	DOP
<i>E. archipelagus</i> sp. nov.	DOP6255	Azores	37° 31' 30"N	30° 36' 28"W	578	2010	R/V Arquipélago	Bottom longline	CoralFishD-33-V12	90% Ethanol	DOP
<i>E. archipelagus</i> sp. nov.	HBOM 003:02023 (BMR 29-V-91-3-003)	Madeira	33° 01' 90"N	16° 26' 27"W	563	1991	R/V Seward Johnson	Johnson-Sea-Link I submersible	Eastern Atlantic Expedition	90% Ethanol	HBOI
<i>E. archipelagus</i> sp. nov.	HBOM 003:00660 (BMR 09-VI-91-4-008)	Canaries	28° 18' 00"N	16° 56' 10"W	408	1991	R/V Seward Johnson	Johnson-Sea-Link I submersible	Eastern Atlantic Expedition	90% Ethanol	HBOI
<i>E. clava</i> (Schmidt, 1879)	MCZ 6436	Gulf of Mexico	–	–	534	–	–	–	–	–	MCZ

DOP—Department of Oceanography and Fisheries of the University of Azores; HBOI—Harbour Branch Oceanographic Institute; MCZ—Harvard Natural History Museum; MNHN—Muséum National d'Histoire Naturelle, Paris. The specimen marked by * is the holotype and the other two specimens marked with ** are the paratypes of *Exsuperantia archipelagus* sp. nov.

TABLE 2. List of mtDNA COI sequences used in the phylogenetic analysis with their corresponding GenBank accession numbers.

Systematics	Accession number
ANCORINIDAE Schmidt, 1870	
<i>Ancorina</i> sp.	HM592744
<i>Ecionemia robusta</i> (Carter, 1883) ¹	HM592724
<i>Rhabdastrella cordata</i> Wiedenmayer, 1989	HM592727
<i>Rhabdastrella globostellata</i> (Carter, 1883)	HM592746
<i>Stelletta clarella</i> de Laubenfels, 1930	HM592736
<i>Stelletta fibrosa</i> (Schmidt, 1870)	FJ711643
<i>Stelletta lactea</i> Carter, 1871	HM592752
<i>Stelletta normani</i> Sollas, 1880	EU442193
CORALLISTIDAE Sollas, 1888	
<i>Herengeria</i> sp.	LN624190
<i>Isabella harborbranchi</i> Carvalho, Pomponi & Xavier, 2015	KM185728
<i>Isabella mirabilis</i> Schlacher-Hoenlinger, Pisera & Hooper, 2005	KR270646
<i>Isabella tanoa</i> Ekins, Erpenbeck, Worheide & Hooper, 2016	KX267963
<i>Neoschrammeniella castrum</i> Schlacher-Hoenlinger, Pisera & Hooper, 2005	LN624191
<i>Neoschrammeniella fulvodesmus</i> (Lévi & Lévi, 1983)	KR270685
GEODIIDAE Gray, 1867	
<i>Erylus discophorus</i> (Schmidt, 1862)	HM592692
<i>Erylus granularis</i> Topsent, 1904	HM592729
<i>Erylus mamillaris</i> (Schmidt, 1862)	EU442207
<i>Erylus topsenti</i> Lendenfeld, 1903	HM592733
<i>Geodia atlantica</i> (Stephens, 1915)	HM592695
<i>Geodia barretti</i> Bowerbank, 1858	EU442194
<i>Geodia cydonium</i> (Linnaeus, 1767)	HM592738
<i>Geodia gibberosa</i> Lamarck, 1815	EU442209
<i>Geodia megastrella</i> Carter, 1876	HM592731
<i>Geodia vosmaeri</i> (Sollas, 1886)	HM592722
<i>Pachymatisma johnstonia</i> (Bowerbank in Johnston, 1842)	EF564338
<i>Pachymatisma normani</i> Sollas, 1888	EF564329
ISORAPHINIIDAE Schrammen, 1924	
<i>Costifer</i> sp.	LN624196
NEOPELTIDAE Sollas, 1888	
<i>Calipelta</i> sp.	LN624197
<i>Triptolemma intextum</i> (Carter, 1875)	HM592710
CALTHROPELLIDAE Lendenfeld, 1907	
<i>Calthropella (Calthropella) geodioides</i> (Carter, 1876) ²	HM592705
PLEROMIDAE Sollas, 1888	
<i>Anaderma rancureli</i> Lévi & Lévi, 1983	LN624205
<i>Pleroma menoui</i> Lévi & Lévi, 1983	LN624206
PHYMARAPHINIIDAE Schrammen, 1924	
<i>Exsuperantia</i> sp. (= <i>E. archipelagus</i>) ³	HM592730
<i>Exsuperantia archipelagus</i> sp. nov. DOP1976	MK214739*
<i>Exsuperantia archipelagus</i> sp. nov. DOP5883	MK214740*
<i>Exsuperantia archipelagus</i> sp. nov. DOP6212	MK214741*
<i>Exsuperantia archipelagus</i> sp. nov. DOP6248	MK214742*
<i>Exsuperantia archipelagus</i> sp. nov. DOP6255	MK214743*

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TABLE 2. (Continued)

Systematics	Accession number
<i>Exsuperantia archipelagus</i> sp. nov. HBOM 003:00660 (BMR 09-VI-91-4-008)	MK214744*
<i>Exsuperantia archipelagus</i> sp. nov. HBOM 003:02023 (BMR 29-V-91-3-003)	MK214745*
PHYMATELLIDAE Schrammen, 1910	
<i>Neoaulaxinia clavata</i> (Lévi & Lévi, 1983)	KR270693
<i>Neoaulaxinia</i> sp.	LN624198
<i>Neoaulaxinia zingiberadix</i> Kelly, 2007	KR270723
<i>Reidispongia coerulea</i> Lévi & Lévi, 1988	LN624203
TETILLIDAE Sollas, 1886	
<i>Antarctotetilla grandis</i> (Sollas, 1886)	KT124325
<i>Antarctotetilla leptoderma</i> (Sollas, 1886)	KT124318
<i>Antarctotetilla sagitta</i> (Lendenfeld, 1907)	KT124320
<i>Cinachyra antarctica</i> (Carter, 1872)	KT124315
<i>Cinachyra barbata</i> Sollas, 1886	KT124312
<i>Cinachyrella</i> sp.	JQ236881
<i>Paratetilla</i> sp.	JQ236883
Tetillidae sp.	KT124313
THENEIDAE Carter, 1883	
<i>Thenia abyssorum</i> Koltun, 1964	HM592712
<i>Thenia levis</i> Lendenfeld, 1907	HM592717
<i>Thenia schmidti</i> Sollas, 1886	HM592737
THEONELLIDAE Lendenfeld, 1903	
<i>Discodermia polymorpha</i> Pisera & Vacelet, 2011	HM592686
<i>Discodermia proliferans</i> Lévi & Lévi, 1983	KJ494347
<i>Theonella</i> cf. <i>cupola</i> Burton, 1928	KJ494352
<i>Theonella</i> cf. <i>cylindrica</i> Wilson, 1925	KJ494353
<i>Theonella deliqua</i> Hall, Ekins & Hooper, 2014	KJ494355
<i>Theonella maricae</i> Hall, Ekins & Hooper, 2014	KJ494356
<i>Theonella mirabilis</i> (de Laubenfels, 1954)	LN624208
<i>Theonella swinhoei</i> Gray, 1868	HM592745
<i>Theonella xantha</i> (Sutcliffe, Hooper & Pitcher, 2010)	KJ494375
VULCANELLIDAE Cárdenas, Xavier, Reveillaud, Schander & Rapp 2011	
<i>Vulcanella aberrans</i> (Maldonado & Uriz, 1996)	HM592699
<i>Vulcanella gracilis</i> (Sollas, 1888)	HM592702
INCERTAE SEDIS	
<i>Characella pachastrelloides</i> (Carter, 1876)	HM592749
<i>Neamphius huxleyi</i> (Sollas, 1888)	HM592682

*Sequences generated in this study; ¹As in Cárdenas *et al.*, (2011); ²In GenBank as *Calthropella geodioides*; ³In GenBank as *Exsuperantia* sp. however is the same species here described.

***Exsuperantia archipelagus* sp. nov.**

Figures 1–4; Table 3

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Synonymy. *Racodiscula clava sensu* Topsent (1892, 1904, 1928); *Exsuperantia* sp. Carvalho *et al.* (2015).

Type locality. Terceira island, Azores archipelago, Portugal.

Type material. Holotype. MNHN DT-782/1 (dry specimen), locality: Terceira island, Azores archipelago, Por-

tugal (38°52'50"N, 27°23'05"W), depth: 599 m. Paratypes. MNHN DT-782/2 (dry specimen), locality: Terceira island, Azores archipelago, Portugal (38°52'50"N, 27°23'05"W) depth: 599 m; DOP1976 (specimen preserved in 90% ethanol), locality: Azores Bank, Azores archipelago, Portugal (38°05'59"N, 29°08'59"W), 168–594 m depth.

Additional material. *Exsuperantia archipelagus* sp. nov.: DOP 5883/6212/6248/6255, Azores archipelago; HBOM 003:02023 (BMR 29-V-91-3-003), Madeira, HBOM 003:00660 (BMR 09-VI-91-4-008), Canaries (see table 1 for more details).

Comparative material examined. *Exsuperantia clava* Schmidt 1879—Syntype MCZ 6436 (orig. 275), Gulf of Mexico.

External morphology. Columnar to ficiform sponges, that can possess lateral protuberances or branches (Fig. 1). Small, 20–30 mm tall and 10–20 mm thick, attached to the substrate by the entire base. Surface is smooth, with marked water canals on the surface of the choanosomal skeleton. Oscules or pores are not visible to the naked eye. Color is beige to whitish in ethanol and when dry.



FIGURE 1. Habitus of *Exsuperantia archipelagus* sp. nov. A: Holotype MNHN DT 782/1, B: Paratype MNHN DT 782/2, C: Paratype: DOP1976 (scale 1 cm).

Skeleton. The ectosome is composed by a layer of overlapped phyllotriaenes (Figs. 2A–B), numerous acanthomicroxeas and acanthorhabds, and some amphiasters. Pores are surrounded by these microscleres. The choanosome has regular trider-type desmas with smooth and/or tuberculated tubercles; the sculpture of the tubercles is related to the stage of formation of the desma: smooth tubercles in earlier stages and tuberculated when older; the extremities of the desmas also varies, spine-like and smooth when young, or with a tubercle on the top when older (Figs. 2C–H, Fig. 3). Subtylostyles to tylotes are transverse to the surface, and cross both parts of the skeleton. Acanthorhabds and acanthomicroxeas are very abundant and spread through the entire skeleton; amphiasters are few and dispersed.

In addition, we have found some spicules with a strange appearance in the lower part of the sponge in the paratype DOP1976 (Fig. 3D). They resemble irregular disco- to phyllotriaenes with a strong sculpture that have been developed in the lower part and merged with the desma skeleton. This skeleton formation, previously observed in other lithistid demosponges, may have the purpose of consolidating the basal skeleton of the sponge.

Spicules

1. Trider-type desmas: robust, 409–693 μm in maximum diameter, 52–98 μm thick arms, with tubercles mainly distributed in the extremities of the desma; tubercles are large, 26–74 μm in diameter, and can protrude slightly from the arm (Figs. 2C–H, 3A–F; table 3).
2. Phyllotriaenes: cladome is smooth, large, with long clads, 640–890 μm in diameter; rhabdome has a conical shape with a rounded tip, 229–320 μm long and 71 μm wide (Figs. 2A–B, 4A–C; table 3).
3. Subtylostyles to tylotes: smooth, often curved, very variable in length and shape, 260–1114 μm long and 3–38 μm wide (Figs. 4J–M; table 3).

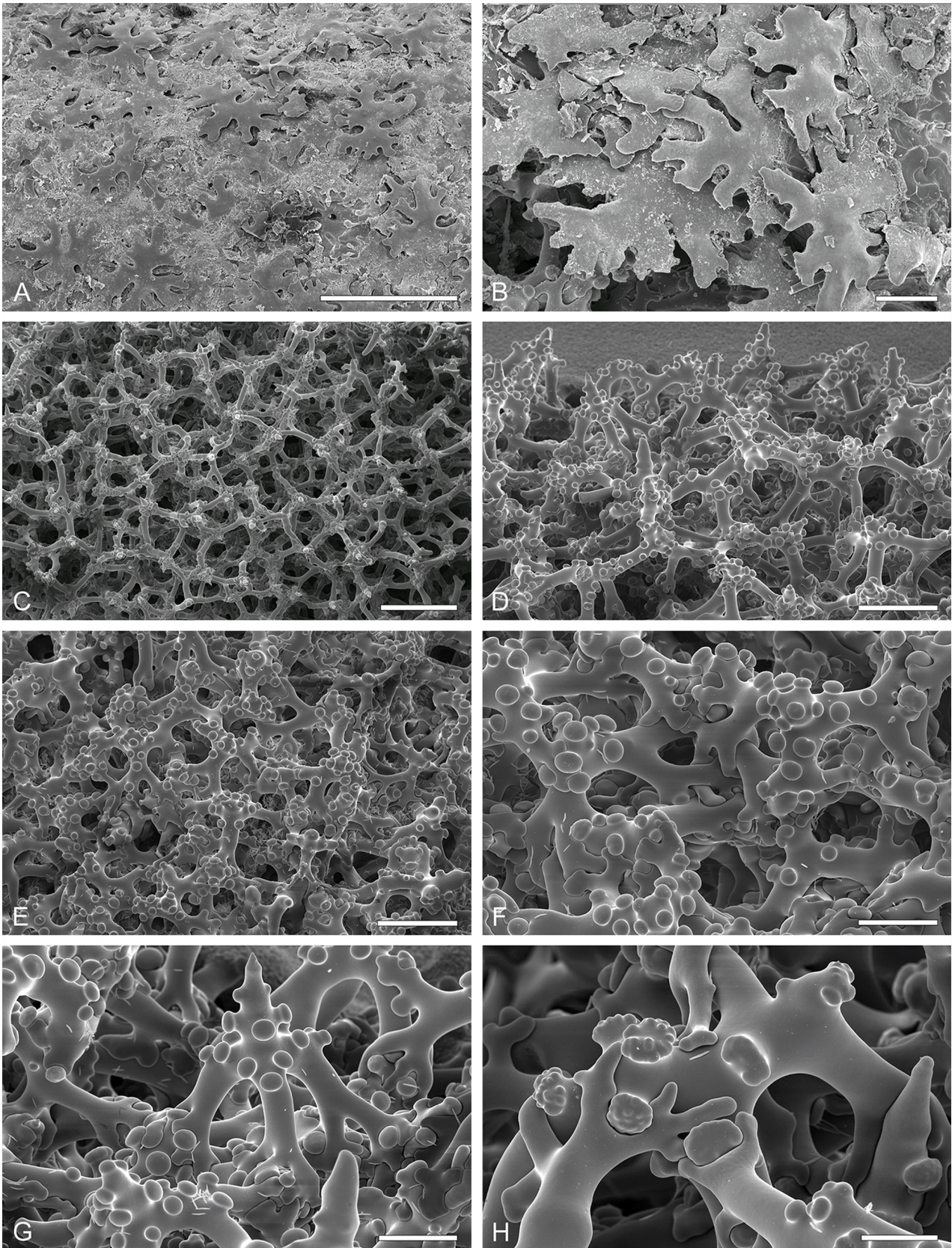


FIGURE 2. *Exsuperantia archipelagus* sp. nov. Holotype MNHN DT 782/1, from Azores. A: Top surface of the sponge with phyllotriaenes (scale 1 mm), B: details of overlapping phyllotriaenes in the ectosome (scale 200 μ m), C–D: upper surface of the choanosomal skeleton composed of triders located in the upper part/top of the sponge (growing edge) (scale 1mm and 200 μ m, respectively), E–F: choanosomal triders located in the lower part/or near the base of the sponge (scale 500 μ m and 200 μ m, respectively), G: young trider desma with smooth tubercles (scale 200 μ m), H: old trider with distinct tuberculation of the tubercles and detail of the zygone (articulation) (scale 100 μ m).

4. Acanthomicroxeas: thin, evenly covered with spines, with sharp tips, 31–47 μm long and 2.9–4.2 μm wide (Figs. 4D–E; table 3).
5. Acanthorhabds: robust, fully covered by spines, 18–24 μm long and 2.3–4.1 μm wide (Figs. 4F–G; table 3).
6. Amphiasters: regular, slender with several spinous arms, 15–19 μm long and 1.2–1.7 μm thick arms (Figs. 4 H–I; table 3).

Distribution. This species is known from its type locality (Azores, 168–770 m depth) and also from other Macaronesian islands (Madeira, 563 m depth, and Canaries, 403 m depth). It was previously recorded as *Racodiscula clava* sensu Topsent (1892, 1904, 1928) and *Exsuperantia* sp. (Cárdenas *et al.* 2011; Carvalho *et al.* 2015) for the Northeast Atlantic.

Etymology. Named for the locations where the species has been found, several Macaronesian archipelagos (Azores, Madeira and Canaries).

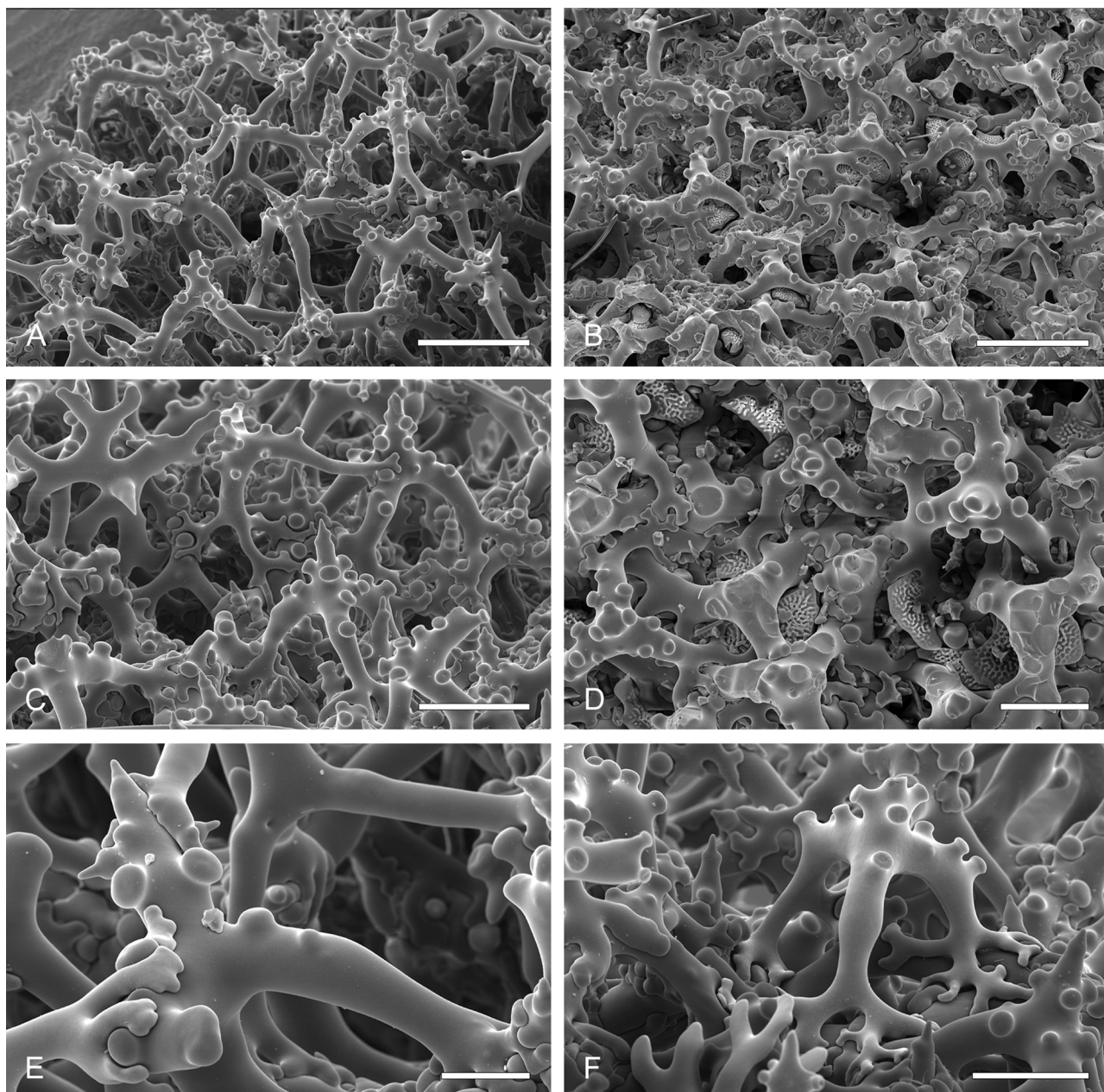


FIGURE 3. *Exsuperantia archipelagus* sp. nov. Paratype DOP 1976, from Azores. A: surface of the choanosomal skeleton from the top of the sponge (scale 500 μm), B: surface of the choanosomal skeleton from the base of the sponge (scale 500 μm), C: young trider (lower part), and a phyllotriaene (upper left) (scale 200 μm), D: surface of the choanosomal skeleton with irregular triders in the basal part of the sponge (scale 220 μm), E: detail of young and less regular trider and its zygome (scale 100 μm), F: detail of older trider (scale 200 μm).

TABLE 3. Measurements of the different spicule types of *Exsuperantia archipelagus* sp. nov. specimens analyzed in this study in comparison with *E. clava* (Schmidt, 1879). Spicule measurements of *E. clava* were taken from the redescription of the species in Pisera & Lévi (2002b). Minimum and maximum values are given.

Species	Trider	Phyllostriaenes	Subtylostyles to tylotes	Acanthomicroxeas	Acanthorhabds	Amphiasters	Locality
<i>E. archipelagus</i> sp. nov. MNHN DT-782/1	409–693 x 52–98 µm.	Cladome 640–890 µm in diameter; rhabdome 229–320 x 71 µm. (n=10).	260–1114 x 3–38 µm (n=12).	31–47 x 2.9–4.2 µm (n=9).	18–24 x 2.3–4.1 µm (n=9).	15–19 x 1.2–1.7 µm (n=3).	Azores.
<i>E. archipelagus</i> sp. nov. DOP1976	295–485 x 30–68 µm (n=9).	Cladome 364–673 µm in diameter; rhabdome 75–184 x 25–55 µm. (n=12).	469–1102 x 9.4–21.0 µm (n=30).	21.8–40.9 x 1.9–4.9 µm (n=30).	10.4–29.2 x 2.1–3.8 µm (n=30).	6.4–17.1 µm (n=30).	Azores.
<i>E. archipelagus</i> sp. nov. HBOM 003:02023 (BMR 29-V-91-3-003)	355–751 x 30–87 µm (n=21).	Cladome 169–458 µm in diameter; rhabdome 91–108 x 20–36 µm (n=15).	585–879 x 11.3–19.3 µm (n=11).	36.8–54.1 x 1.9–4.5 µm (n=20).	11.1–19.5 x 2.1–3.8 µm (n=20).	6.9–12.5 µm (n=12).	Madeira.
<i>E. archipelagus</i> sp. nov. HBOM 003:00660 (BMR 09-VI-91-4-008)	352–599 x 30–76 µm (n=17).	Cladome 210–667 µm in diameter; rhabdome 46–145 x 12–37 µm (n=16).	546* x 6.9–10.1 µm (n=6).	32.4–65.1 x 1.8–3.4 µm (n=20).	11.5–25.5 x 1.6–3.2 µm (n=20).	3.9–13.9 µm (n=20).	Canaries.
<i>Exsuperantia clava</i> (Schmidt, 1879)	230–320 µm.	–	–	–	–	–	Cuba.

* – indicates that there is no information; *all subtylostyles to tylostyles were broken, thus 546 µm represents the minimum length obtained.

Comments. The new *Exsuperantia* species described here, although very similar in habit to *Exsuperantia clava* Schmidt, 1879, differs on the desmas' morphology and sculpture (Figs. 2, 3 and 5). *E. clava* triders are more widely tuberculated, i.e. tubercles are spread through the desmas' arms, while in *Exsuperantia archipelagus* **sp. nov.**, the tubercles are more concentrated near the zygoxis or the tip of the trider. Another distinct characteristic is the sculpture and ornamentation of the tubercles. In *E. archipelagus* **sp. nov.** the tubercles are in general smooth, with very few presenting rugosity (Figs. 2G and 2H), whereas in *E. clava* the tubercles are all finely rugose. Therefore, based in our detailed analyses we consider the Macaronesian material as non-conspecific to Schmidt's *E. clava*, reason for which we describe *E. archipelagus* as a new species, the second within *Exsuperantia*.

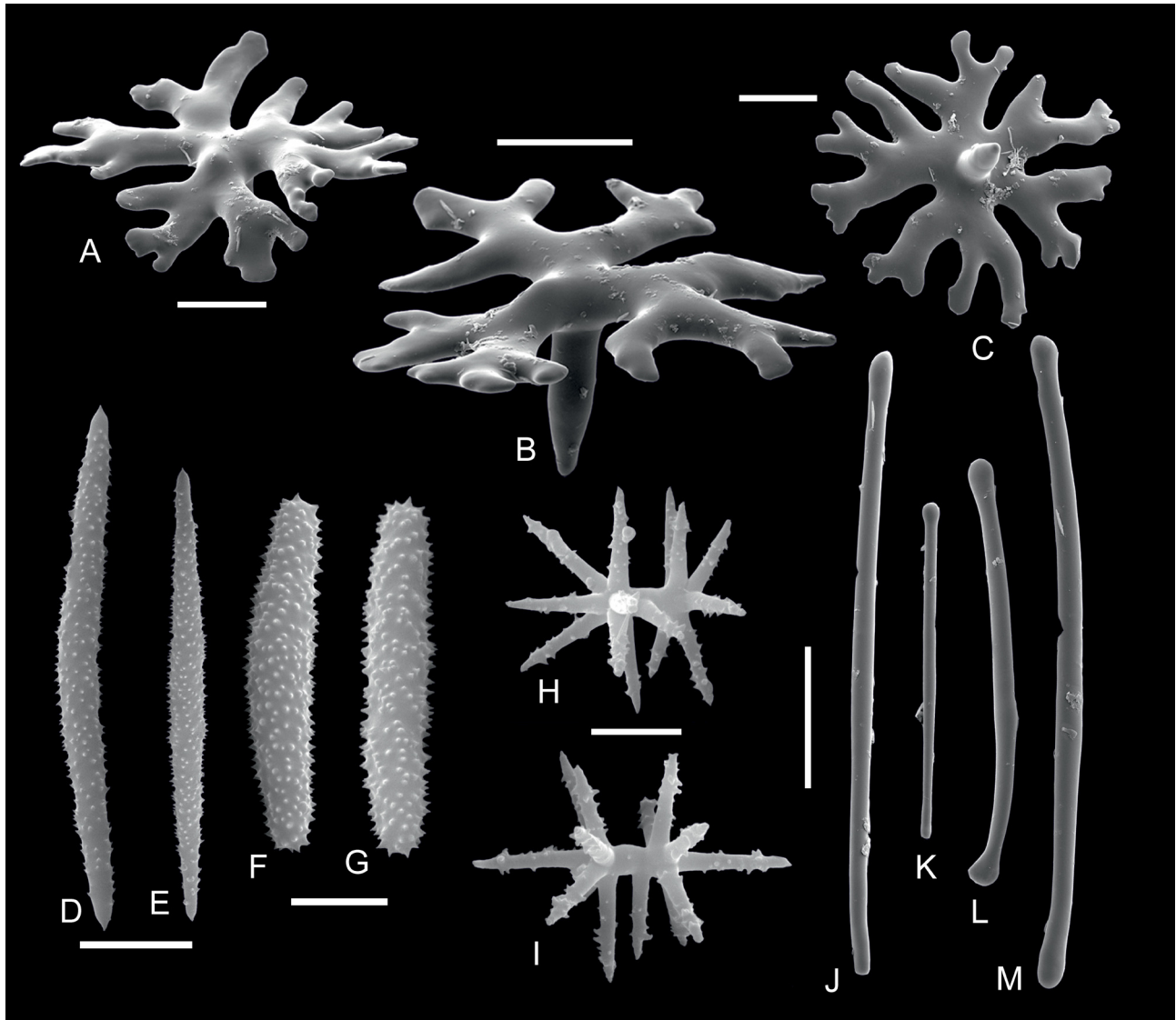


FIGURE 4. *Exsuperantia archipelagus* **sp. nov.** Holotype MNHN DT-782/1, A–B: top view of ectosomal phyllotriaenes (scale 200 µm), C: ectosomal phyllotriaene from below (scale 200 µm), D–E: acanthomicroxeas (scale 10 µm), F–G: acanthorhabds (scale 5 µm), H–I: amphiasters with long rays (scale 5 µm), J–M: subtylostyle to tyloles, (scale 200 µm).

Molecular results

The best trees obtained by both phylogenetic analyses (ML and BI) of the COI have a congruent topology. These analyses show a strongly supported clade (posterior probability 1, bootstrap 100) containing all of our sequences and a sequence of *Exsuperantia* sp. (which we confirm to be *E. archipelagus* **sp. nov.**) obtained from a specimen collected on the seamounts south of the Azores (Cárdenas *et al.* 2011). This clade appears inside a larger polytomic clade which includes Pleromidae Sollas, 1888, Isoraphiniidae Schrammen, 1924, Phymatellidae Schrammen, 1910, Pachastrellidae Carter, 1875, Theneidae Carter, 1883, Geodiidae Gray, 1867, Calthropellidae Lendenfeld, 1907,

Vulcanellidae Cárdenas, Xavier, Reveillaud, Schander & Rapp, 2011, Ancorinidae Schmidt, 1870 and Corallistidae Sollas, 1888, sister to a poorly supported Theonellidae clade (posterior probability 0.83, bootstrap 56). An intra-specific variation of 0.02% (equivalent to 1 base pair) among *Exsuperantia* specimens was found and is shown by slightly longer branch in the specimen DOP5883 (see Fig. 6).

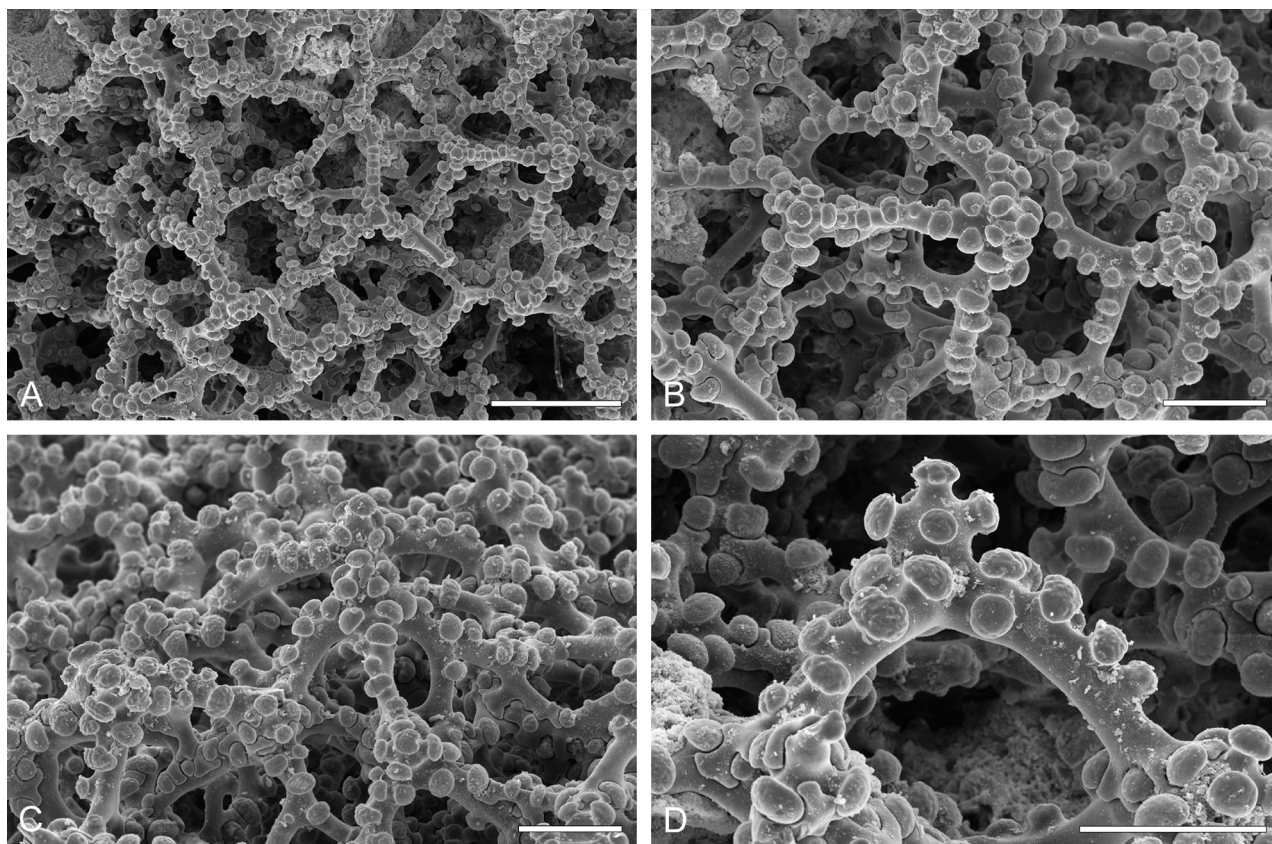


FIGURE 5. *Exsuperantia clava* (Schmidt, 1879), Syntype MCZ 6436 (orig. 275), from Gulf of Mexico. A: choanosomal skeleton strongly tuberculate (scale 500 µm), B–C: trider-like desmas with large and tubercles covered with smaller tubercles (scale 200 µm), D: detail of trider and articulation (scale 200 µm).

Discussion

In 1879, Schmidt erected *Rimella* to accommodate *R. clava* from specimens collected in the Caribbean Sea, in the vicinity of Havana, at 534 m depth. In his monographs, Topsent (1892, 1904, 1928) assigned several specimens from the Azores and Canary Islands to *Racodiscula clava* and synonymized *Rimella* with *Racodiscula* due to the law of priority—*Racodiscula* was first established with *R. asteroides* Zittel, 1878. However, the species described by Schmidt does not belong to the same family, i.e., *Rimella* belongs to Phymaraphiniidae (trider-type desmas) while *Racodiscula* belongs to Theonellidae (tetraclones desmas). Later on, Pisera & Lévi (2002b) re-identified Topsent's material as belonging to a similar yet undescribed species of *Rimella* (family Phymaraphiniidae). Schmidt's *Rimella* was in the meantime found to be a pre-occupied genus and thus changed to *Exsuperantia* (Özdkimen 2009).

Upon collection of new material of *Exsuperantia* in the Macaronesian islands, it was finally possible to compare and ascertain the status of the species within this genus. The new specimens were found to be conspecific with those of *Racodiscula clava* sensu Topsent, and to be significantly different in desma morphology and sculpture from Schmidt's *Exsuperantia clava* (Figs. 2, 3 and 5). It is important to mention that the type material of *E. clava* is deciduous (see Pisera & Lévi 2002b) and a redescription of the species, particularly with regards to the microscleres, is needed when new material becomes available. The geographical distribution—*E. clava* in Northwest and *E. archipelagus* **sp. nov.** in the Northeast Atlantic—also supports the distinction of these two species. In fact, only a small proportion of all North Atlantic lithistids are common to both sides of this basin (e.g. Pomponi *et al.* 2001; Manconi & Serusi 2008; present authors' unpublished data).

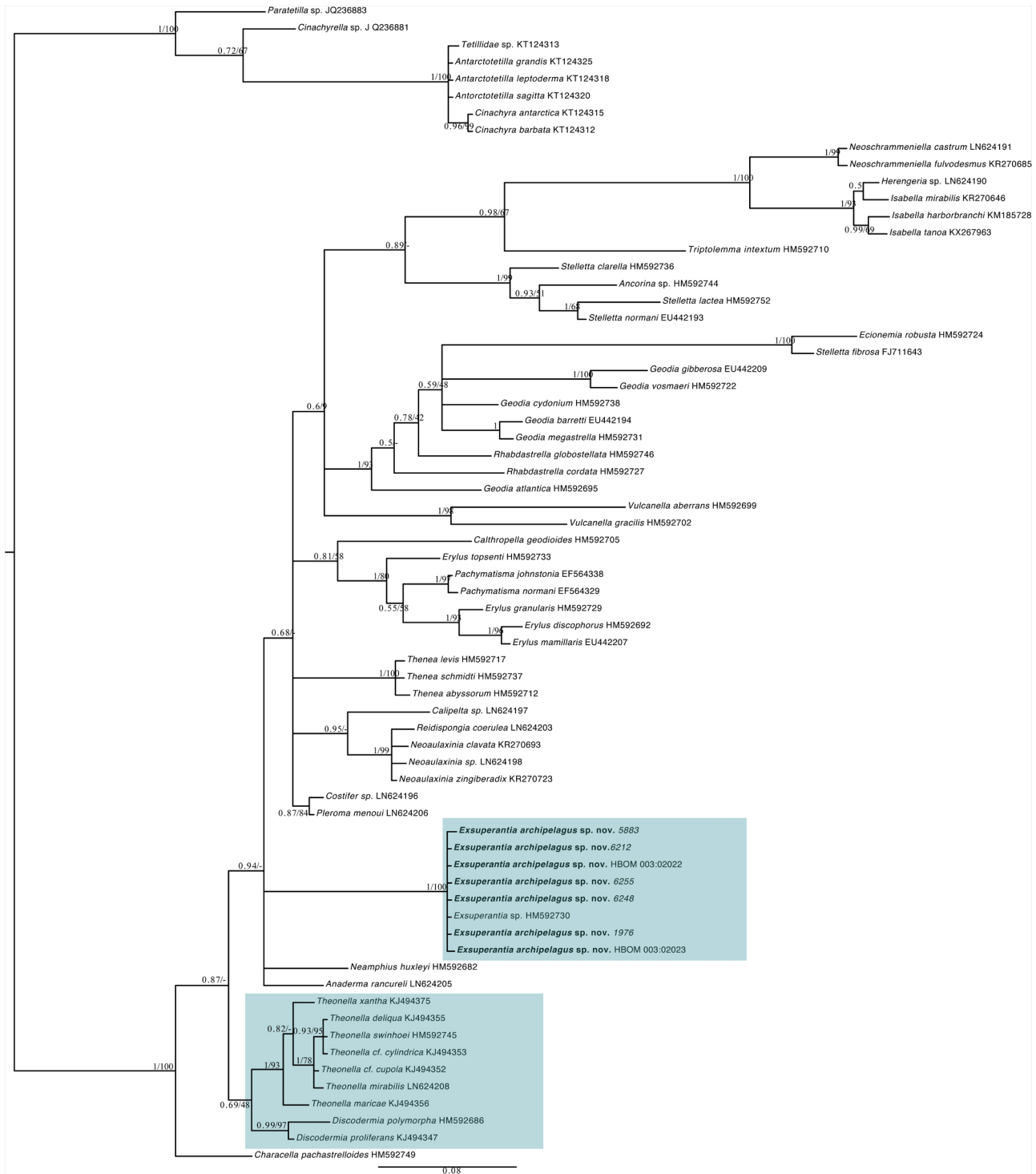


FIGURE 6. Bayesian phylogeny of the mtDNA COI gene (MrBayes, model GTR+I+G) of some astroporinids' families with emphasis on the affinities of Phymaraphiniidae and Theonellidae. Numbers at the nodes correspond to posterior probabilities. The values next to the Bayesian posterior probability correspond to RAXML bootstrap values ("-" means the clade was not retrieved in ML analysis).

Our morphological examinations and phylogenetic reconstructions support what was previously suggested by Pisera & Lévi (2002b), i.e. that the species assigned by Topsent to *Racodiscula clava* (now *E. archipelagus* sp. nov.) does not belong to the Theonellidae (tetraclone desmas), but instead to Phymaraphiniidae (trider desmas). Our sequences of *E. archipelagus* sp. nov. are recovered in a well-supported clade, apart from representatives of the Theonellidae (*Theonella* spp. and *Discodermia* spp.) as previously observed (Cárdenas *et al.* 2011; Schuster *et al.* 2015). In order to avoid misidentifications in the future, it is important to note that the types of free spic-

ules are very similar between *Exsuperantia* (Phymaraphiniidae) and *Racodiscula* (Theonellidae). The similarity of spicules between these two families are the presence of phyllostriaenes (*Racodiscula* has phyllo— to discotriaenes, fossil phymaraphiniids also have both phyllo— and discotriaenes), acanthorhabds and amphiasters as microscleres. However, *Exsuperantia* additionally has acanthomicroxeas, whereas *Racodiscula* has two types of acanthorhabds (Pisera & Lévi 2002b, 2002c). This high level of spicule homoplasy has been found to occur in Tetractinellida, and this is even more prevalent in microscleres than in megascleres (*e. g.* Cárdenas *et al.* 2011; Schuster *et al.* 2015). Thus, the morphological character most easily differentiating these sponges are choanosomal desmas, tetracloones in *Racodiscula*, and triders in *Exsuperantia*. One has to keep in mind, that the desmas type of *Exsuperantia* can be misinterpreted (Figs. 2–3) if the observation is done only from the interior, and/or the base of the sponge (where desmas can be broken and/or strongly modified). For a better analysis of desmas, one should observe the desmas from the surface of the sponge.

In this paper, we have shown that the species previously described as *Racodiscula clava* by Topsent (1892, 1904, 1928) is in fact a species new to science. At the time of this study, ethanol-preserved material of the other phymaraphiniid genera was not available, preventing us from investigating the phylogenetic relationships within the family, or testing if *Lepidothenea* belongs to Phymaraphiniidae or to Neopeltidae, as suggested by Pisera (in Kelly 2007).

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