# Diversity, Distribution and Phylogenetic Relationships of Deep-Sea Lithistids (Porifera, Heteroscleromorpha) of the Azores Archipelago

Joana R. Xavier[1,2]*, David J. Rees[2], Raquel Pereira[3], Ana Colaço[4,5], Christopher K. Pham[4,5] and Francisca C. Carvalho[2,6]

[1] CIIMAR – Interdisciplinary Centre of Marine and Environmental Research, University of Porto, Matosinhos, Portugal, [2] Department of Biological Sciences, University of Bergen, Bergen, Norway, [3] Systematic Biology, Department of Organismal Biology, Evolutionary Biology Centre, Uppsala University, Uppsala, Sweden, [4] Okeanos – Instituto de Investigação em Ciências do Mar, Universidade dos Açores, Horta, Portugal, [5] IMAR – Instituto do Mar, Horta, Portugal, [6] Section of Taxonomy and Evolution, Department of Natural History, University Museum of Bergen, University of Bergen, Bergen, Norway

Lithistid sponges are globally distributed in temperate and sub-tropical areas, constituting an important component of deep-sea benthic communities where they form structurally complex and vulnerable marine ecosystems (VMEs). In this study, we assess the diversity and investigate the spatial and bathymetric distribution of the lithistid sponges of the Azores archipelago (North Atlantic) based on historical records and examination of samples accidentally collected during deep-sea longline fishing operations in the region. Eleven lithistid species are recognized to occur in the Azores, including *Leiodermatium tuba*, recently described from material collected in several Northeast Atlantic seamounts that is hereby reported for the first time to the archipelago. We provide molecular barcodes (mtDNA COI and rRNA 28S) for seven of these species, including *Discodermia ramifera*, *Macandrewia azorica*, and *Exsuperantia archipelagus*, for which the Azores constitutes the type locality. We further discuss the phylogenetic and biogeographic affinities of the Azorean lithistids in the context of the Porifera classification, and the wider Northeast Atlantic upper bathyal fauna. Our study also warrants the addition of some lithistid species to the list of VME indicators for the Northeast Atlantic in support of the sustainable management and conservation of these species and habitats, as well as the ecological functions they deliver.

Keywords: bathyal, rock sponges, oceanic islands, seamounts, biodiversity, biogeography, vulnerable marine ecosystems, conservation

## INTRODUCTION

Lithistids are a polyphyletic group of demosponges, distributed across three orders and 13 families, which share the presence of a hypersilicified skeleton formed by an intricately articulated spicule type called desmas (Pisera and Lévi, 2002). They are found distributed globally in temperate and sub-tropical areas largely in the upper bathyal zone, and seem to be particularly prevalent in oceanic

(island and seamount) environments (e.g., Schlacher-Hoenlinger et al., 2005; Carvalho et al., 2015, 2020; Schuster et al., 2018). Knowledge of the diversity, ecology and phylogenetic affinities of these sponges has greatly increased in recent years, with new species and habitats described for understudied areas (Carvalho et al., 2015, 2020; Maldonado et al., 2015; Schuster et al., 2018; Ríos et al., 2020), (phylo)diversity and distribution patterns assessed (Pomponi et al., 2001; Kelly et al., 2007; Schuster et al., 2021), and considerable changes proposed regarding their placement within the poriferan classification system proposed (Cárdenas et al., 2011; Morrow and Cárdenas, 2015; Schuster et al., 2015).

Recently, lithistid sponges were found forming structural habitats, aggregations and reef-like formations, in the upper bathyal in the western Mediterranean (Maldonado et al., 2015) and the northeast Atlantic (Ríos et al., 2020), possibly analogous to reef habitats which developed and thrived during the Mesozoic in shallower waters (Kauffman et al., 2000). While the ecological role of lithistid aggregations is yet to be investigated, sponge habitats dominated by other groups (e.g., such as geodiids and hexactinellids) were shown to serve as habitat for numerous invertebrate and fish species (e.g., Hawkes et al., 2019), also performing numerous functions in bentho-pelagic coupling and nutrient recycling (Cathalot et al., 2015; Maldonado et al., 2020; Rooks et al., 2020).

Sponge habitats meet several of the vulnerability criteria, viz. uniqueness or rarity, functional significance, fragility, low recovery potential, and structural complexity, defined for vulnerable marine ecosystems (VMEs) by the Food and Agriculture Organization within the scope of the International Guidelines for the Management of Deep-Sea Fisheries in the High Seas (FAO, 2009, ICES, 2020). Therefore, uncovering their distribution patterns is critical to inform the development of appropriate conservation measures to ensure long-term sustainability and minimize the impacts of the various anthropogenic activities operating over the deep seafloor.

In the Northeast Atlantic, the Azores archipelago constitutes the region for which the lithistid fauna has been most comprehensively investigated. Since the description of the first lithistid for the area (*Macandrewia azorica* Gray, 1859), nine species were reported to the archipelago largely thanks to the studies by the French sponge taxonomist Émile Topsent, resulting from the historical expeditions of Prince Albert I of Monaco between 1885 and 1915 onboard the vessels Princesse Alice I and II and Hirondelle I and II (Topsent, 1892, 1898, 1904, 1928; see also Porteiro, 2009). However, it was not until recent that new data and samples became available as a result of an increase of the exploration efforts toward the deeper environments of this archipelago. These, alongside recent studies describing the lithistids of the Macaronesian archipelagos of Madeira and Selvagens (Carvalho et al., 2015) and seamounts off the Iberian margin and South of the Azores (Carvalho et al., 2020), allow for the first time a comparison of the lithistid assemblages of the Lusitanian and Mediterranean marine provinces.

Thus, the main aims of this study were to: (i) investigate the patterns of spatial and bathymetric distribution of the lithistid sponges throughout the Azores archipelago from the integration of historical records and newly obtained data and samples; (ii) assess their diversity and phylogenetic relationships; and (iii) explore the biogeographic affinities of the species occurring on the Azores in the context of the wider Northeast Atlantic and Mediterranean bathyal fauna.
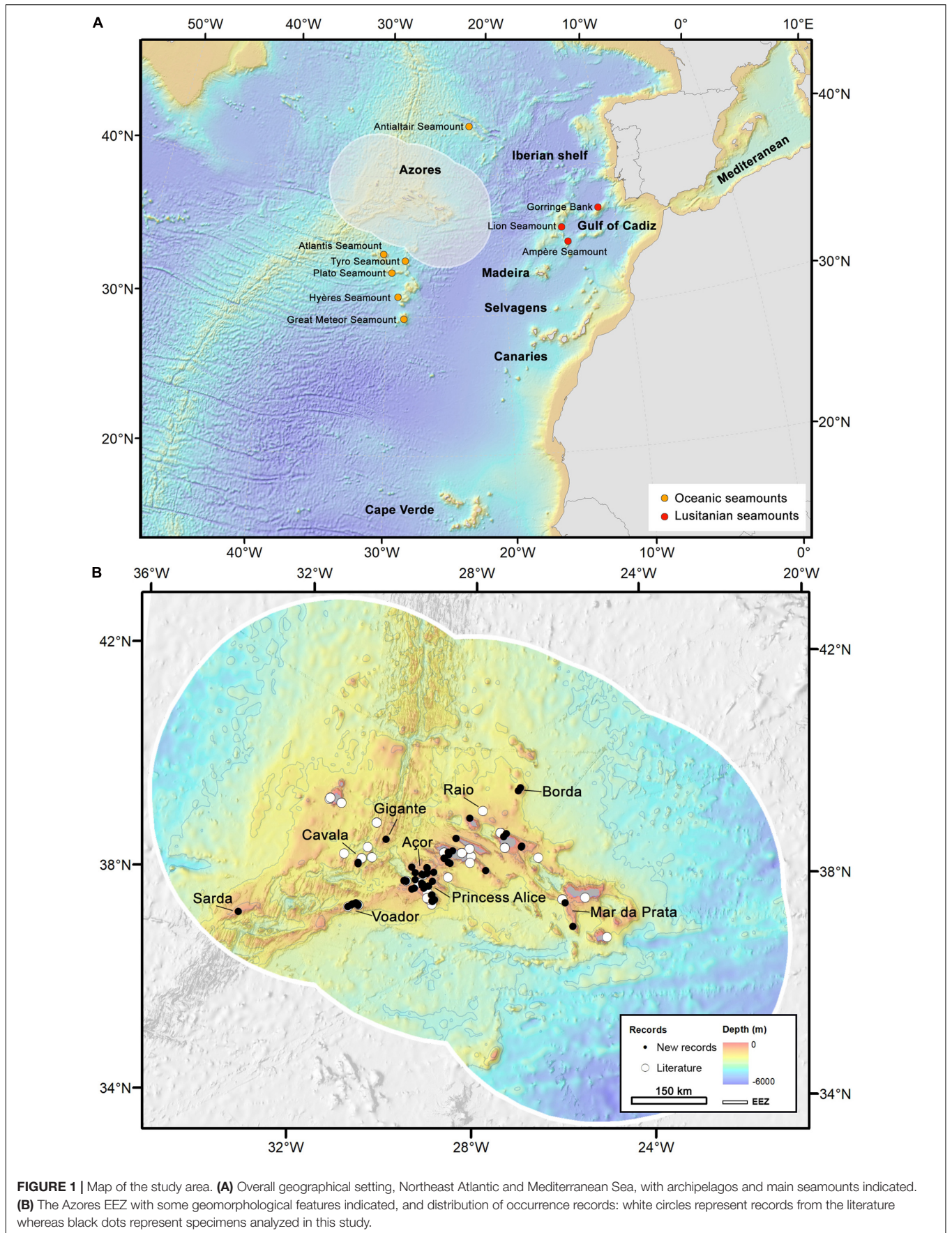
## MATERIALS AND METHODS

### Study Area

The Azores is an oceanic volcanic archipelago that lies above the Mid-Atlantic Ridge in the North Atlantic Ocean. The seafloor is mostly deep, but a large number of seamounts, a fraction of the Mid-Atlantic Ridge, and the slopes of the islands compose the shallowest parts (Perán et al., 2016). Underwater it is characterized by the presence of numerous seamounts, isolated or associated with the Mid-Atlantic ridge (Morato et al., 2008), that host a wide variety of open-ocean and deep-sea organisms. The region is considered a biodiversity hotspot for several groups of organisms, from cetaceans and other megafauna (Silva et al., 2014; Afonso et al., 2020) to benthic corals (Braga-Henriques et al., 2013; Sampaio et al., 2019). A convergence of oceanographic processes manifests in the Azores Archipelago, designated as a confluence zone between the west and the east North Atlantic. Different dominant oceanographic processes affect the west and the east groups not only by the water mass composition but also in their nutrient (climatological) profiles (Caldeira and Reis, 2017). Various water masses, e.g., the Eastern North Atlantic Central Water (ENACW), the Mediterranean Outflow Water (MOW), and the North Atlantic Deep Water (NADW) are found in the region at different depths (Bashmachnikov et al., 2015 and references therein). The Azores region is located in oligotrophic waters where primary production and carbon flux to the seafloor are lower than other Atlantic areas (Abell et al., 2013). Seafloor environmental conditions show high spatial and temporal (seasonal/inter-annual) variability (Amorim et al., 2017).

### Literature and Database Review

An extensive review of the sponge taxonomic literature (e.g., Gray, 1859; Topsent, 1892, 1898, 1904, 1928; Lévi and Vacelet, 1958) as well as biodiversity data portals (e.g., OBIS, GBIF) was performed and all records of lithistid sponges contained within the Azores EEZ were compiled in an excel spreadsheet following Darwin Core (DwC) data standards (Wieczorek et al., 2012). Five specimens, collected outside the EEZ, on the Irving and Plato seamounts located southern of the archipelago were also included for completeness. For each record, information on expedition (vessel, year), location (station no., coordinates and depth), sampling gear (e.g., trawl, longline), and taxonomic identification (as reported and currently accepted) was assembled (see **Supplementary Material 1**). Collection data of the specimens examined here and occurrences, both historical and recent, are publicly available in the PANGAEA data repository[1], and in the

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[1] https://doi.pangaea.de/10.1594/PANGAEA.921772

**FIGURE 1 |** Map of the study area. **(A)** Overall geographical setting, Northeast Atlantic and Mediterranean Sea, with archipelagos and main seamounts indicated. **(B)** The Azores EEZ with some geomorphological features indicated, and distribution of occurrence records: white circles represent records from the literature whereas black dots represent specimens analyzed in this study.

SponGIS data portal[2] developed in scope of the H2020 SponGES project[3].

## Sampling and Identification

New material and information were collected during several scientific expeditions (2006–2008; 2010–2011; 2017), experimental fishing surveys and bycatch monitoring through fisheries observers in the course of various projects and programs, both past and ongoing in the region, such as SponGES, MERCES, Discardless, CoralFish (see also section "Acknowledgments"). Sampling was performed according to national Portuguese laws and approved by the Azorean Directorate of Sea Affairs of the Azores Autonomous region through the CCPI 03/2017/DRCT for the samples collected during the SponGES project.

Specimens were identified from analyses of external and/or internal morphological characteristics such as habitus, texture, consistency, surface ornamentation and oscula distribution, skeletal arrangement and spicular composition, following standard methods (Boury-Esnault and Rützler, 1997). Detailed morphological descriptions are not provided in this study as taxonomic studies of neighboring areas (Madeira and Selvagens archipelagos, Northeast Atlantic seamounts), including many of the species herein reported, were recently presented (Carvalho et al., 2015, 2020; Carvalho and Pisera, 2019).

## DNA Extraction and Sequencing

Genomic DNA was extracted from small pieces of choanosomal tissue using a DNeasy Blood and Tissue kit (QIAGEN), following the instructions of the manufacturer. The Folmer region of the mitochondrial cytochrome *c* oxidase subunit I (COI), and the C1–D2 region of the nuclear ribosomal 28S gene were amplified and sequenced. The COI and 28S fragments were amplified using the primer pairs LCO1490 and HCO2198 (Folmer et al., 1994) or dgLCO1490 and dgHCO2198 (Meyer et al., 2005), and C1'ASTR and D2 (Lê et al., 1993; Cárdenas et al., 2010), respectively. The polymerase chain reaction conditions used follow the protocols as in Schuster et al. (2015). Obtained amplicons were purified with a solution of Exonuclease 1 (EXO, 10 U μL-1) and shrimp alkaline phosphatase (SAP, 10 U μL-1 USB®), and Sanger sequenced in both directions 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). Generated sequences were deposited in GenBank under accession nos. MW006490– MW006541 for rRNA 28S (C1–D2) and MW000672– MW000696 for mtDNA COI (see **Supplementary Material 2**).

## Phylogenetic Reconstructions

Obtained sequences were verified using the Basic Local Alignment Search Tool (BLAST) available at http://www.ncbi. nlm.nih.gov/BLAST/. Sequence quality checks, assembly and editing were performed in Geneious v.10.0.9[4] (Kearse et al., 2012)

and aligned using Muscle (Edgar, 2004). Several sequences of the orders Tetractinellida Marshall, 1876 and Sphaerocladina Schrammen, 1924 were downloaded from GenBank and used in these alignments (see **Supplementary Material 2**, also deposited in PANGAEA[5]) according to the new classification of Demospongiae Sollas, 1885 (Morrow and Cárdenas, 2015). Sequences belonging to the order Sphaerocladina were used as outgroups. The final datasets comprise 192 sequences for mtDNA COI and 212 sequences for rRNA 28S, of which 25 and 48, respectively, are new. Phylogenetic reconstructions were performed for the individual markers under Bayesian Inference, as implemented in MrBayes v3.2 (Ronquist et al., 2012) and Maximum Likelihood as implemented in RaxML v.8 (Stamatakis, 2014) via the CIPRES Science Gateway V.3.3[6]. Reconstructions under Bayesian Inference were obtained under two runs and four Metropolis-coupled Markov chains (MCMC) over 100 million generations, sampled every hundredth generation and with a burnin of 0.25, and the best-fitting model for both genes (GTR + G + I) as estimated by jModelTest v.2.1.7 (Darriba et al., 2012) calculated under the Akaike Information Criterion (AIC). For the Maximum Likelihood analysis, the GTRGAMMAI model was used and 1000 rapid bootstrapping replicates performed. The obtained phylogenetic trees were visualized in FigTree v.1.4.4[7] and edited in Adobe® Illustrator® (2019).

## Biogeographic Affinities

To examine the biogeographic affinities of the lithistid fauna in the context of the wider Northeast Atlantic and Mediterranean we built a presence/absence data matrix based on literature records and our own data for five oceanic archipelagos (Azores, Madeira, Selvagens, Canaries, and Cape Verde), two seamount groups (the oceanic seamounts located south of the Azores, and the Lusitanian seamounts off the Southwestern European shelf), as well as for the continental slopes of the Iberian margin, the Gulf of Cadiz and the Mediterranean Sea. This species × area matrix was then used to build a pairwise similarity matrix using the Bray-Curtis coefficient as implemented in PRIMER 7 (Clarke and Gorley, 2015).

## RESULTS

A total of 47 individual records, representing 10 species, seven genera, distributed across seven families and two orders (Tetractinellida and Bubarida Morrow and Cárdenas, 2015), were compiled from the literature for the region. Detailed information on such records, including nomenclatural changes as verified in the World Porifera Database (Van Soest et al., 2021), can be found in **Supplementary Material 1**. In addition, 82 specimens collected as bycatch from bottom longline fishing operations were examined and assigned to seven species. Combined, the two datasets, elevate to 11 the total number of lithistid species reported from the Azores archipelago (see systematic

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list below, and following sections) (**Figures 1**, **2**). Of these, *Neophrissospongia nolitangere* (Schmidt, 1870) and *Macandrewia azorica* Gray, 1859 were the most commonly captured, with 22 and 20 individuals collected, followed by *Leiodermatium* spp. (*N* = 25, collectively) and *Exsuperantia archipelagus* Carvalho and Pisera (2019) (*N* = 12) (**Supplementary Material 1**). Specimens within the genus *Leiodermatium* Schmidt, 1870 could not be assigned with full confidence to the two species previously reported for the Azores archipelago, i.e., *Leiodermatium lynceus* Schmidt (1870) and *Leiodermatium pfeifferae* (Carter, 1873), either because we did not find consistency in the characters traditionally used to distinguish the two species, i.e., location of the inhalant and exhalant openings (ostia and oscula), the thickness of the plate and the hispidity of its margin; or, in some instances, because we only had access to small fragments which prevented such analyses. These were therefore retained as *L.* cf. *lynceus* and *L.* cf. *pfeifferae* when they seemed more similar to one of the species, and as *Leiodermatium* sp. *indet.*, following the open nomenclature standards proposed by Sigovini et al. (2016) and Horton et al. (2021), when they appeared somewhat intermediate or only small fragments were available.

## Systematic List

Phylum PORIFERA Grant, 1836
Class DEMOSPONGIAE Sollas, 1885
Subclass HETEROSCLEROMORPHA Cárdenas et al., 2012
Order TETRACTINELLIDA Marshall, 1876
Suborder ASTROPHORINA Sollas, 1877
Family CORALLISTIDAE Sollas, 1888
Genus *Neophrissospongia* Pisera and Lévi, 2002
Species **Neophrissospongia nolitangere** (Schmidt, 1870)
Family THEONELLIDAE Lendenfeld, 1903
Genus *Discodermia* du Bocage, 1869
Species **Discodermia ramifera** Topsent, 1892*
Family MACANDREWIIDAE Schrammen, 1924
Genus *Macandrewia* Gray, 1859
Species **Macandrewia azorica** Gray, 1859*
Species *Macandrewia ramosa* Topsent, 1904*
Species *Macandrewia robusta* Topsent, 1904*
Family PHYMARAPHINIIDAE Schrammen, 1924
Genus Exsuperantia Özdikmen, 2009
Species **Exsuperantia archipelagus** Carvalho and Pisera, 2019*
Suborder SPIROPHORINA Bergquist and Hogg, 1969
Family AZORICIDAE Sollas, 1888
Genus *Leiodermatium* Schmidt, 1870
Species **Leiodermatium (cf.) lynceus** Schmidt, 1870
Species **Leiodermatium (cf.) pfeifferae** (Carter, 1873)
Species **Leiodermatium tuba** Carvalho and Xavier, 2020
Family SIPHONIDIIDAE Lendenfeld, 1903
Genus *Siphonidium* Schmidt, 1879
Species *Siphonidium ramosum* (Schmidt, 1870)
Order BUBARIDA Morrow and Cárdenas, 2015
Family DESMANTHIDAE Topsent, 1893
Genus *Petromica* Topsent, 1898
Subgenus *Petromica* (*Petromica*) Topsent, 1898
Species **Petromica (Petromica) grimaldii** Topsent, 1898*

Highlighted in bold font are species found in the present study; * denote species for which the type-locality is in the Azores archipelago.

## Diversity and Distribution

Of the seven species identified from the material collected as bycatch from longline fisheries in the Azores, one (*Leiodermatium tuba*) constitutes a new record for the archipelago. Similarly, the specimens DOP 5850 and DOP 5853 collected at 461–501 m depth in the Plato seamount constitute the first record of *Neophrissospongia nolitangere* in this group of oceanic seamounts, thereby extending the known distribution of the species.

Overall, both historical and recent records are widely distributed across the archipelago, on island slopes and offshore seamounts, but are mostly concentrated in the central island group, south of the islands of Faial and Pico (**Figures 1**, **3**). Except for the five specimens collected from the Plato and Irving seamounts, all specimens were collected on the Azores plateau and within the EEZ. The genus *Macandrewia* (family Macandrewiidae) is the most widely distributed, with the species *Macandrewia azorica* being found on all islands' groups. In the Eastern island group, no records were found for *N. nolitangere*, *Discodermia ramifera*, *Siphonidium ramosum,* and *Petromica* (*Petromica*) *grimaldii*. On the other hand, in the Western island group only *P.* (*P.*) *grimaldii, M. azorica, M. ramosa,* and *Exsuperantia archipelagus* have been recorded. Several species of *Leiodermatium* spp., *M. azorica*, *E. archipelagus*, *D. ramifera,* and *S. ramosum* are also recorded in the topographic highs of the Mid-Atlantic Ridge between the Western and Central island groups (**Figure 3**).

With regards to bathymetric distribution, the majority of the records (*N* = 82) and species (*S* = 9) were found in the upper bathyal between 200–800 m depth, peaking at 300–400 m depth. Comparatively, the number of records and species for the circalittoral zone above 200 m or for the lower bathyal zone below 800 m depth were much lower, with 14 records (*S* = 6) for the former, and 13 records (*S* = 5) for the latter. The shallowest record is that of *D. ramifera* recorded at 98 m depth east of the Açor bank, and the deepest of *M. azorica* found at 1495 m depth in the deep slope east of Santa Maria Island. The species *N. nolitangere*, *D. ramifera*, *M. azorica,* and *L.* (cf.) *lynceus* were found to be restricted to depths above 800 m, whereas *E. archipelagus*, *L.* (cf.) *pfeifferae,* and *P. grimaldii* further extend to deeper areas (down to 1250 m, depending on the species). *Macandrewia ramosa* and *M. robusta* (family Macandrewiidae) are the only two lithistid species exclusively found in the deeper zones (>1100 m depth), whereas *L. tuba* and *S. ramosum* were only found in the upper bathyal, between 622–723 m and 349–793 m depth, respectively (**Figure 4** and **Supplementary Material 1**).

## Phylogenetic Relationships

In total, we obtained 25 mtDNA COI and 48 partial rRNA 28S sequences representing four and seven species, respectively (**Supplementary Material 2**). Phylogenetic trees obtained separately for the mtDNA COI and the 28S rRNA regions
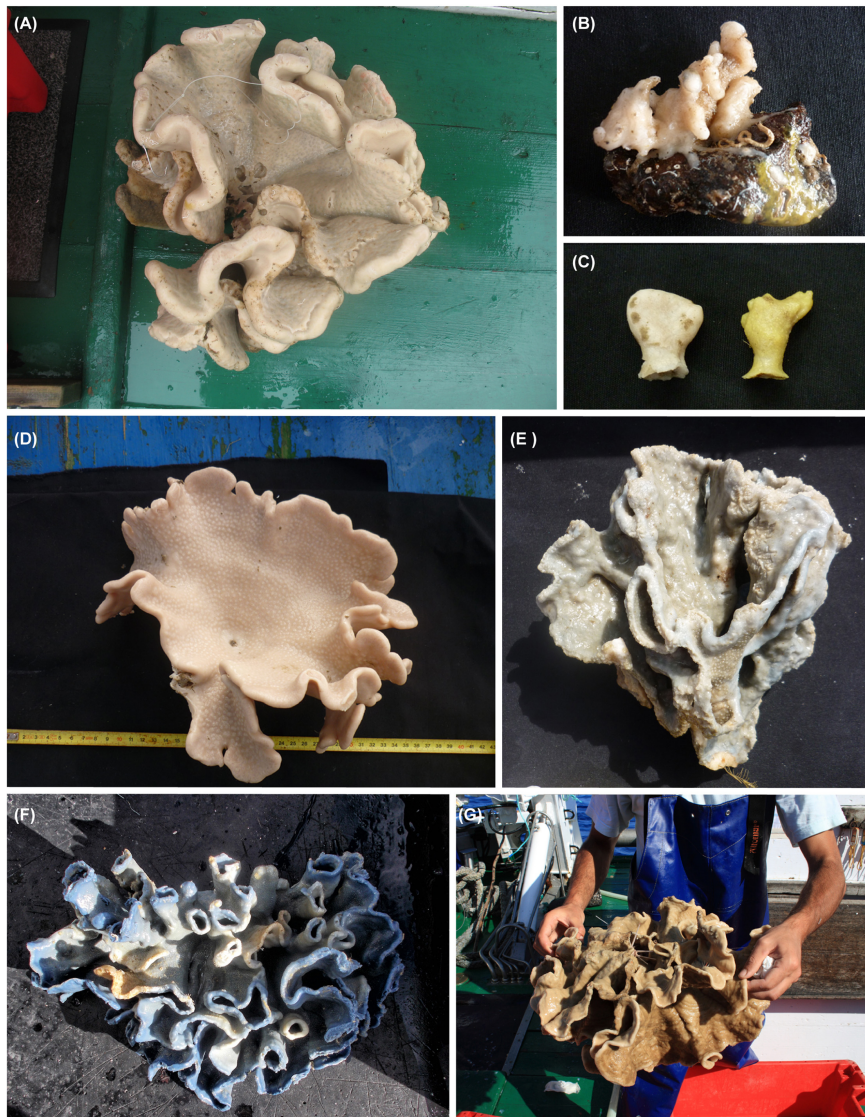
**FIGURE 2 |** Example of lithistid sponges of the Azores, collected and analyzed in the present study. **(A)** *Neophrissospongia nolitangere* (DOP 5323), **(B)** *Discodermia ramifera* (DOP 6477), **(C)** *Exsuperantia archipelagus* (DOP 6212), **(D)** *Macandrewia azorica* (DOP 6601), **(E)** *Leiodermatium* cf. *lynceus* (DOP 6429), **(F)** *Leiodermatium* cf. *pfeifferae* (DOP 11102), **(G)** *Leiodermatium tuba* (DOP 2975).

were largely congruent, both in overall topology as well as with high support at species and genus levels with a decrease in support toward deeper (family level) nodes (**Figures 5**, **6** and **Supplementary Material 3**).

Within the family Macandrewiidae, all specimens assigned to *Macandrewia azorica* formed a clade with maximum support with a single rRNA 28S sequence of *M. rigida* Lévi and Lévi (1989), from the Solomon Islands, available on GenBank ($PP_{28S} = 1$; $BS_{28S} = 100$) (**Figure 6**). In the COI tree, the clade comprising all of the Azorean specimens was retrieved with only moderate support ($PP_{COI} = 0.77$; $BS_{COI} = 62$), sister to a clade formed by two sequences of unidentified *Macandrewia* spp. from South Africa, within a highly supported *Macandrewia* sp. clade ($PP_{COI} = 1$; $BS_{COI} = 79$). Within the Azorean *Macandrewia*

clade, two sequences (DOP 2866 and DOP 6249) formed a separate but only moderately supported sub-clade ($PP_{COI} = 0.80$, $BS_{COI} = 64$) (**Figure 5**).

Sequences obtained for *Discodermia ramifera* were retrieved in a highly supported clade ($PP_{28S} = 1$; $BS_{28S} = 93$; $PP_{COI} = 1$, $BS_{COI} = 98$) with the Mediterranean species *D. polymorpha* Pisera and Vacelet (2011) in an equally monophyletic *Discodermia* spp. clade ($PP_{28S} = 1$, $BS_{28S} = 93$; $PP_{COI} = 1$; $BS_{COI} = 98$), sister to *Theonella* spp. Similarly, all sequences of *Exsuperantia archipelagus* were grouped into a clade with maximum support ($PP_{28S} = 1$; $BS_{28S} = 100$; $PP_{COI} = 1$; $BS_{COI} = 100$) together with sequences (available in GenBank) previously obtained for this archipelago and the seamounts located south of the Azores. In the COI tree, some sub-structuring was observed
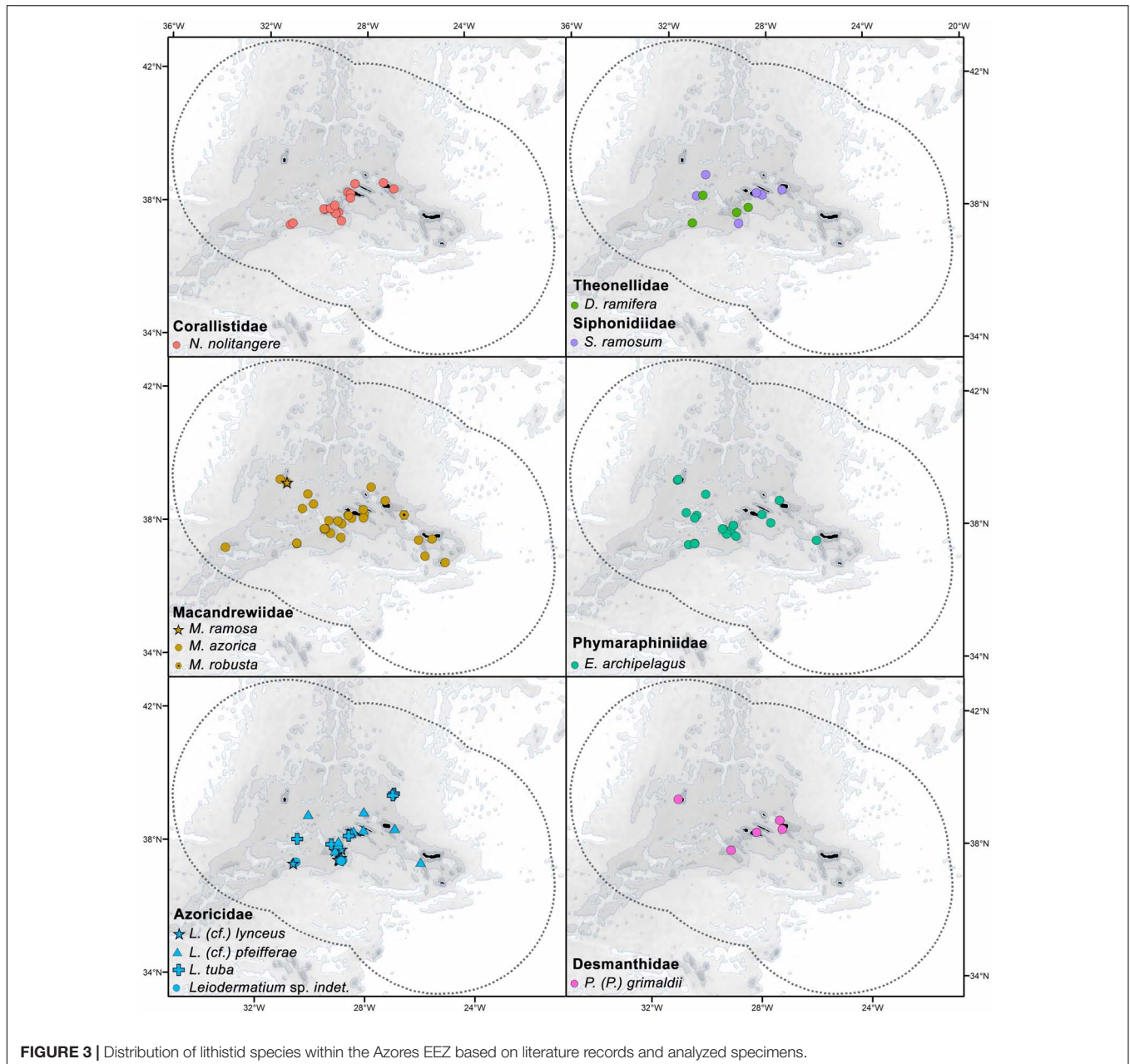
**FIGURE 3 |** Distribution of lithistid species within the Azores EEZ based on literature records and analyzed specimens.

with two sequences, presenting 1 bp difference to the remaining ones, forming a sub-clade strongly supported in the Bayesian analysis (PP$_{COI}$ = 0.97) and moderately supported by maximum likelihood (BS$_{COI}$ = 64) (**Figures 5, 6**).

In the COI tree, all specimens of *Neophrissospongia nolitangere* collected in the Azores archipelago formed a highly supported clade (PP$_{COI}$ = 0.98, BS$_{COI}$ = 99) sister to *N. galapagoensis* Schuster, 2018 from the Galapagos islands (**Figure 5**). However, in the 28S tree and with the addition of two sequences of *Neophrissospongia* spp. from Western Australia, the Azorean clade is not supported (PP$_{28S}$ = 0.53, BS$_{28S}$ = 78) (**Figure 6**). This *Neophrissospongia* spp. clade is retrieved as sister to a larger clade comprising the genera *Herengeria* Lévi and Lévi (1988),

*Corallistes* Schmidt (1870), *Neoschrammeniella* Pisera and Lévi (2002), and *Isabella* Schlacher-Hoenlinger et al. (2005) within family Corallistidae.

For the Spirophorina suborder we were only able to obtain 28S sequences and all attempts at amplifying the mtDNA COI marker failed. Within this suborder, our reconstructions show all our sequences of *Leiodermatium* spp. in a highly supported clade (PP$_{28S}$ = 1; BS$_{28S}$ = 97), within which two groups are found: one clade grouping specimens identified as *L.* cf. *pfeifferae*, *L.* cf. *lynceus* and *Leiodermatium* sp. (PP$_{28S}$ = 0.98, BS$_{28S}$ = 85) and one group with specimens identified as *L. tuba* (DOP 4862, DOP 11254, DOP 11445) only strongly supported in the maximum likelihood analysis (PP$_{28S}$ = 0.55,
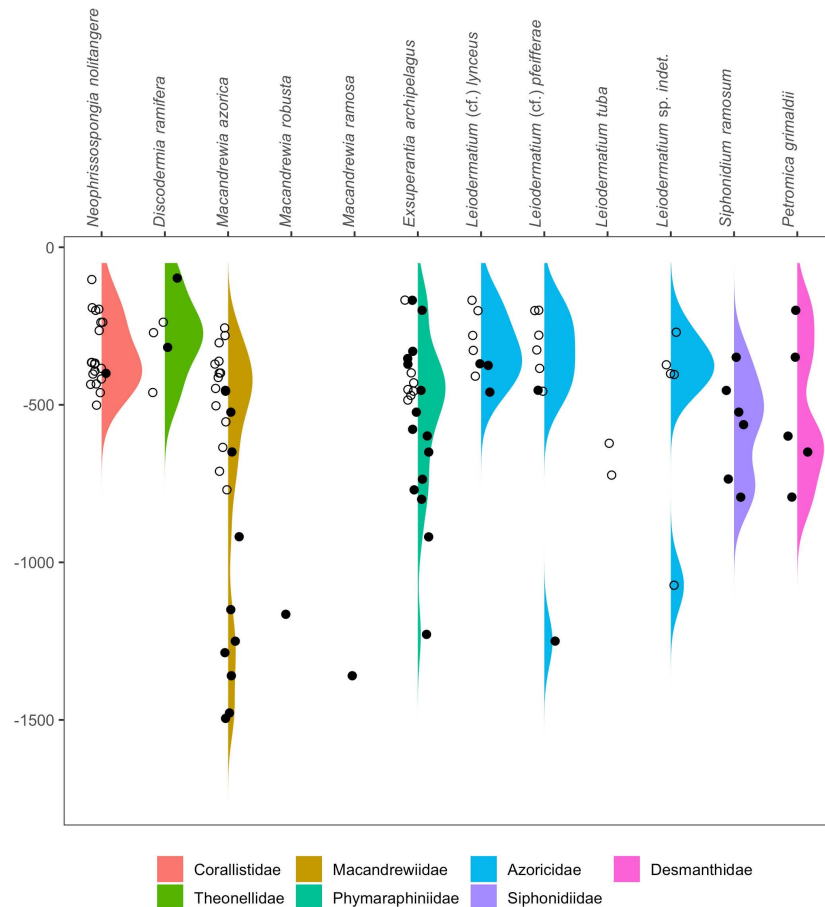
**FIGURE 4 |** Ridge plots of bathymetric distribution records for each individual species based on georeferenced literature records (closed circles) and analyzed specimens (open circles). Colors correspond to each individual family.

$BS_{28S}$ = 84). *Leiodermatium* spp. is found as sister to *Aciculites* spp., but only with moderate to low support ($PP_{28S}$ = 0.83, $BS_{28S}$ = 59). A monophyletic clade comprising representatives of the genera *Leiodermatium* (family Azoricidae) and *Aciculites* Schmidt, 1879 + *Scleritoderma* Sollas, 1888 + *Microscleroderma* Kirkpatrick (1903) (family Scleritodermidae Sollas, 1888) is retrieved with maximum support in our Bayesian analysis ($PP_{28S}$ = 1) but only moderately supported in the maximum likelihood analysis ($BS_{28S}$ = 69) (**Figure 6**). Unfortunately, no specimens, and therefore no sequences were obtained for *Macandrewia robusta* and *M. ramosa* (family Macandrewiidae), *Siphonidium ramosum* (family Siphonidiidae) or *Petromica* (*Petromica*) *grimaldii* (family Desmanthidae), all known to occur in the archipelago.

## Biogeographic Affinities

Examining the faunal similarities across the Northeast Atlantic and the Mediterranean Sea, we found the Azores lithistid assemblage to be most similar (51.9%) to the one occurring in the oceanic seamounts located to the south of the archipelago with seven species shared. This was followed by the Canaries and Madeira archipelagos, with 45.5 and

44.4% (five and four species shared), respectively. The lowest levels of similarity were found between the Azores and Iberian slope (no species shared) and the Cape Verde archipelago with which it only shares *Leiodermatium pfeifferae* (**Figure 7**, **Table 1**, and see also **Supplementary Material 4**). Of the 38 lithistid species occurring in the Northeast Atlantic and Mediterranean Sea, only one (*Macandrewia ramosa* Topsent, 1904) has been exclusively reported in the Azores (**Table 1**).

## DISCUSSION

### Diversity

From the integration of historical records and newly obtained data and samples we expanded considerably our knowledge of the diversity and spatial distribution of an important and vulnerable group of deep-sea sponges (lithistid demosponges) in the Azores archipelago. *Leiodermatium tuba*, recently described from material collected on various oceanic seamounts located South of the Azores as well as on the Gorringe Bank and the Canaries (Carvalho et al., 2020), is reported here for the

first time raising to 11 the number of lithistids in the Azores archipelago. When compared with other areas of the Atlanto-Mediterranean region this diversity is the third highest, only lower than that found in the oceanic seamounts (16 species) and the Mediterranean Sea (14 species) and similar to the richness found in the Canaries. Together, the Azores and the oceanic seamounts harbor 20 species, i.e., 54% of all lithistid species of this region, and may therefore be considered a lithistid diversity hotspot of the central North Atlantic. However, such diversity is still modest when compared with the tropical Western Atlantic, a region where latest estimates suggest the occurrence of at least 88 lithistid species (Schuster et al., 2021) and that is also

recognized by its high Poriferan richness overall (Van Soest et al., 2012). Considering that the Azores harbor an additional 270+ (non-lithistid) deep-sea sponge species (Topsent, 1904, Xavier et al. unpublished data), as well as a rich cold-water coral fauna (Braga-Henriques et al., 2013; Sampaio et al., 2019) further emphasizes the value of this region as a reservoir of deep-sea biodiversity.

In the Azores, the spatial patterns of distribution, with a considerably higher number of records southwest of Faial and Pico islands (central island group) reflect collection efforts. This area has a complex topography and comprises several seamounts (e.g., Açor and Princesse Alice banks) which were
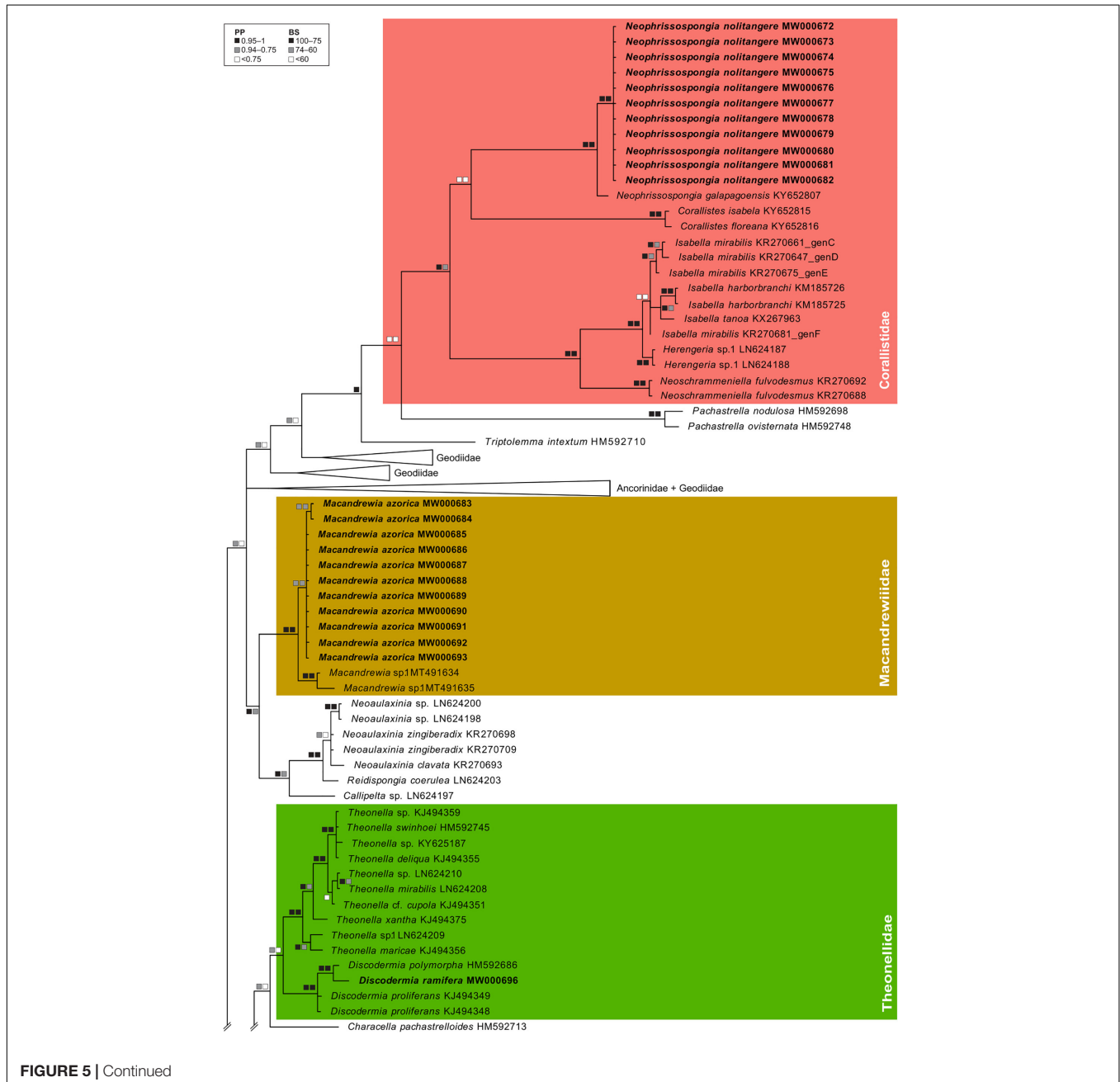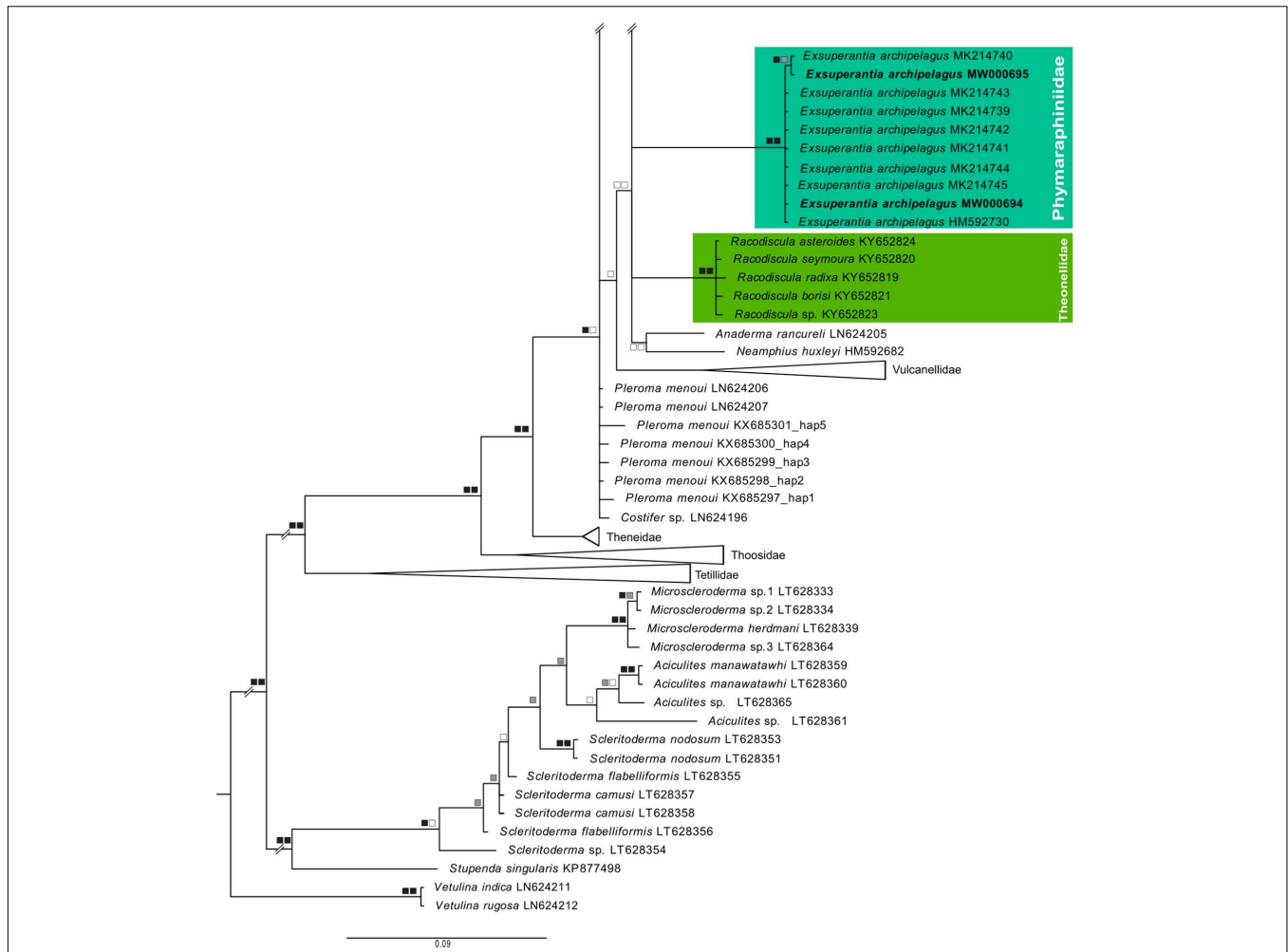


**FIGURE 5 |** Continued

**FIGURE 5 |** Phylogenetic reconstruction of the mtDNA COI gene for lithistids recorded in the Azores archipelago. Bayesian posterior probabilities (PP, left square) and maximum likelihood bootstrap support (BS, right square) values are provided on the branches. If only one square is shown, it means the clade was not retrieved in the Maximum Likelihood analysis. Sequences generated in this study are in bold. Families encompassing lithistid species found in the present study are highlighted in color.

surveyed during historical expeditions and are traditionally used as fishing grounds of the small-scale longline fisheries fleet in the region.

## Bathymetric Distribution

The Azorean lithistid fauna is composed of a mix of steno- and eurybathic species, mostly overlapping in upper bathyal depths between 200 and 600 m. In general, distribution ranges observed for the various species in the Azores are similar to those reported for other northeast Atlantic archipelagos and seamounts (e.g., Carvalho et al., 2015, 2020, see also **Table 1**). However, it is important to note the uneven number of records for some species (e.g., only two records for *Macandrewia ramosa* and *M. robusta* below 1100 m in the literature), as well as some uncertainty regarding the taxonomic identification of some specimens both examined in this and previous studies (e.g., *Leiodermatium* spp. and *M. azorica*), which may be confounding observed spatial and bathymetric ranges.

The highest species diversity and number of records found in the upper bathyal (200–800 m) suggests that oceanographic conditions may be optimal at this depth range for lithistids. The pattern here observed for lithistids agrees well with previous findings of highest diversity of cold-water corals between 300 and 900 m in the archipelago (Braga-Henriques et al., 2013). However, this pattern may also partly result from considerably higher collection efforts in this depth range targeted by the fisheries from which the specimens of both studies have been obtained.

While we lack high-resolution data to investigate which environmental factors drive the distribution of the various species or the assemblage as a whole, it is accepted that availability and diversity of geomorphological features with steep slopes and limited sedimentation (island slopes, near shore banks and offshore seamounts) play an important role in providing the hard substrate needed for lithistid settlement and growth (Pomponi et al., 2001; Kelly et al., 2007). Investigating the

role of other factors such as depth, temperature, salinity, and nutrients shown to be important predictors for the distribution of deep-sea sponge species and communities (e.g., Knudby et al., 2013; Howell et al., 2016; Alvarez et al., 2017; Murillo et al., 2018) will be critical to better understand the ecology of this important group.

## Phylogenetic Relationships

Phylogenetic reconstructions based on two molecular markers traditionally used in the group, i.e., the mitochondrial COI and the ribosomal 28S, confirmed our morphology-based assignments, corroborated previous findings regarding the classification and phyletic status of some groups (e.g.,
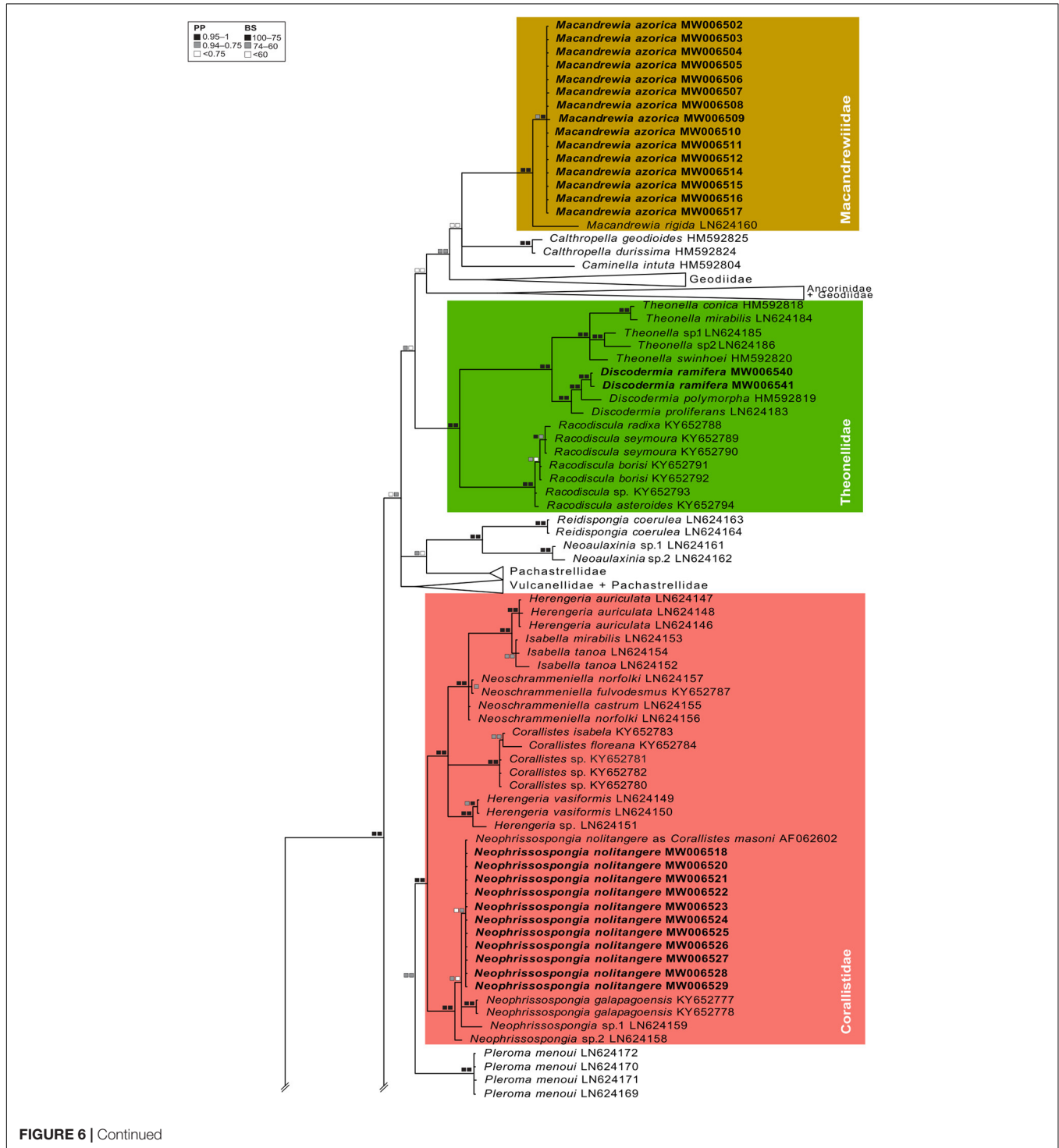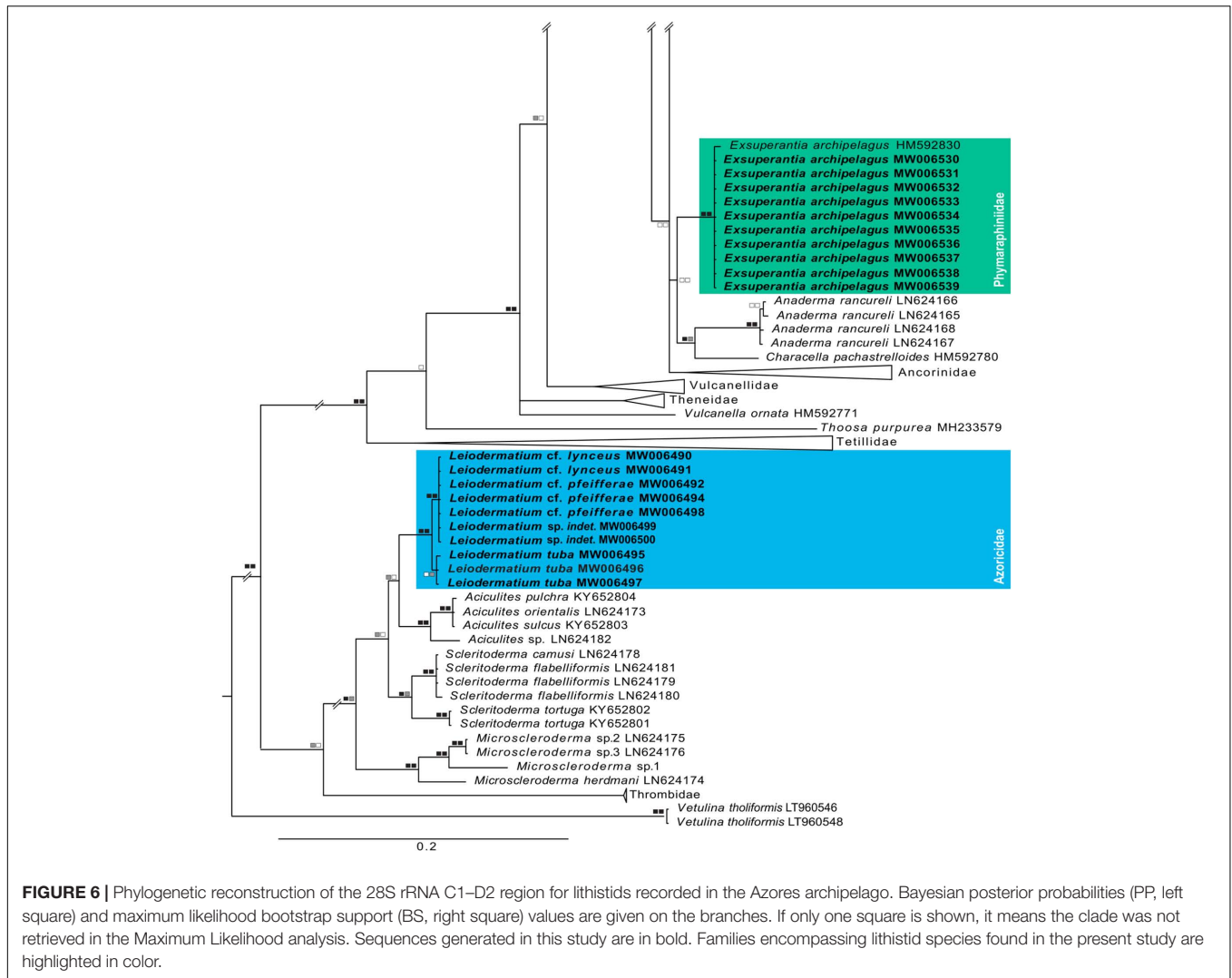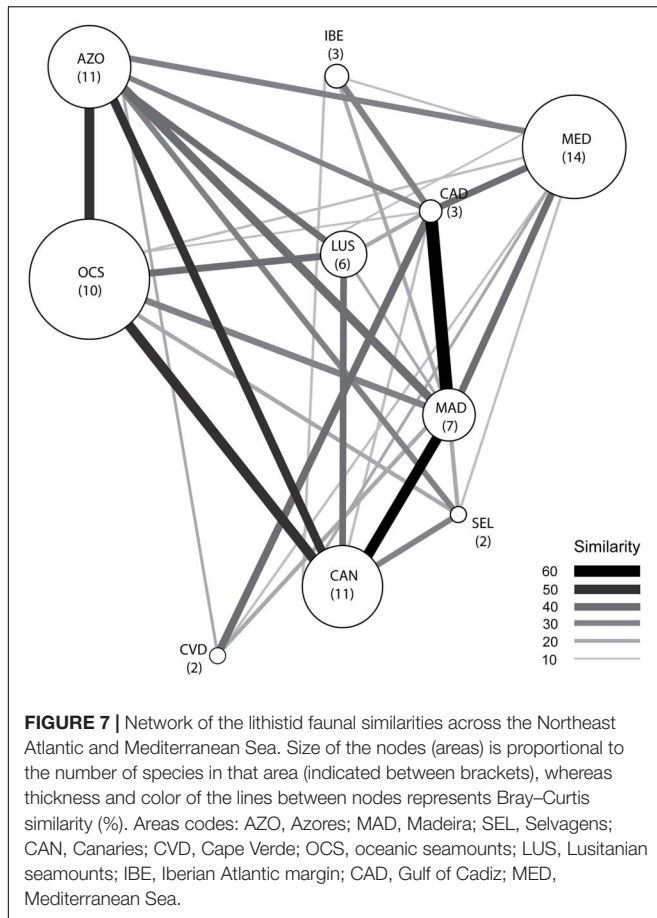


**FIGURE 6 |** Continued

**FIGURE 6 |** Phylogenetic reconstruction of the 28S rRNA C1–D2 region for lithistids recorded in the Azores archipelago. Bayesian posterior probabilities (PP, left square) and maximum likelihood bootstrap support (BS, right square) values are given on the branches. If only one square is shown, it means the clade was not retrieved in the Maximum Likelihood analysis. Sequences generated in this study are in bold. Families encompassing lithistid species found in the present study are highlighted in color.

Carvalho and Pisera, 2019; Schuster et al., 2021) and further shed light into some long-standing species-level taxonomic problems. In the majority of cases, specimens assigned to a given species formed species-level monophyletic clades or clustered with GenBank sequences of other congeneric species. This was the case for *Neophrissospongia nolitangere*, *Macandrewia azorica*, *Discodermia ramifera*, and *Exsuperantia archipelagus*.

In *N. nolitangere*, all specimens had identical (COI) or near-identical (28S) sequences and formed a robust clade with the Pacific *N. galapagoensis*. In the future it is important to compare the Azores specimens with the two new, as yet undescribed, species found in the Caribbean (Schuster et al., 2021) as these may prove much more closely related. Similarly, all our *M. azorica* specimens form a clade consistent with a species level relationship, although the phylogenetic support was only moderate in the COI tree. The 1 bp difference found in COI for two specimens (DOP 2866 and DOP 6249) is likely to reflect some intraspecific genetic variability associated with the depth at which the specimens were found (635 and 711 m), considerably deeper than most other specimens. The 1 bp difference found in

COI for one specimen of *E. archipelagus* confirms the variability previously reported for this species by Carvalho and Pisera (2019). In this case, no distinctive patterns were found in relation to spatial or bathymetric distribution. Such small levels of intraspecific genetic variability, while not commonly reported, have been previously found in other tetractinellid sponges, such as *Geodia barretti* Bowerbank, 1858 (Cárdenas et al., 2013). Comparatively higher levels of variation in COI were also found in the genus *Isabella* from the Norfolk Ridge (off New Caledonia), warranting the description of a new species (*Isabella tanoa* Ekins et al., 2016) and the recognition of a morphologically cryptic species complex for *Isabella mirabilis* Schlacher-Hoenlinger et al. (2005; Ekins et al., 2016).

A close relationship of *Discodermia ramifera* with the Mediterranean *D. polymorpha* was strongly supported, in comparison to another congener from the southwest Pacific (*D. proliferans* Lévi and Lévi, 1983). Unfortunately, no sequences were available of other *Discodermia* spp. from the Northeast Atlantic [*D. arbor* Carvalho and Xavier, 2020, *D. kellyae* Carvalho and Xavier 2020, *D. polydiscus* (Bowerbank, 1869)

**FIGURE 7 |** Network of the lithistid faunal similarities across the Northeast Atlantic and Mediterranean Sea. Size of the nodes (areas) is proportional to the number of species in that area (indicated between brackets), whereas thickness and color of the lines between nodes represents Bray–Curtis similarity (%). Areas codes: AZO, Azores; MAD, Madeira; SEL, Selvagens; CAN, Canaries; CVD, Cape Verde; OCS, oceanic seamounts; LUS, Lusitanian seamounts; IBE, Iberian Atlantic margin; CAD, Gulf of Cadiz; MED, Mediterranean Sea.

and *D. verrucosa* Topsent, 1928] which would allow to better understand their phylogenetic and biogeographic relationships.

An important finding of our study was the fact that neither through morphological examination nor molecular data we were able to confidently assign our *Leiodermatium* specimens to the two species – *Leiodermatium lynceus* and *Leiodermatium pfeifferae* (see section "Results") – long reported to occur in the region (Topsent, 1892, 1904; Lévi and Vacelet, 1958) and throughout the Northeast Atlantic and Mediterranean Sea. In fact, all specimens which morphologically seemed most similar to *L. pfeifferae* or *L. lynceus*, and those which we could not assign to either species (*Leiodermatium* sp. *indet.*), grouped in a strongly supported clade in our 28S tree. Similar to previous studies, we failed to obtain COI sequences for any of our *Leiodermatium* specimens, further corroborating the hypothesis that a type I intron, similar to those found in other genera of the family Scleritodermidae (Schuster et al., 2017) may also be present in this genus as also suggested by Schuster et al. (2021).

Our results suggest that the Azorean *Leiodermatium* sp. *indet.* specimens, and possibly other records previously assigned in the literature to *L. pfeifferae* and *L. lynceus*, may represent either (i) a single species of *Leiodermatium* with some morphological variability; (ii) a complex of species where reduced genetic differentiation and morphological plasticity hamper unequivocal species-level discrimination, or (iii) a case of hybridization

or incomplete lineage sorting between closely related species. If the former hypothesis is confirmed, *L. pfeifferae* would become a junior synonym of *L. lynceus*, type-species of the genus, following the priority principle (Article 23) of the International Code of Zoological Nomenclature (ICZN, 1999). However, a detailed taxonomic revision including examination of additional specimens collected from both species' type-localities (Portugal mainland slope for *L. lynceus* and Madeira island for *L. pfeifferae*), and other Northeast Atlantic localities, as well as an improved molecular dataset including other mitochondrial and nuclear markers, would be needed to support this or other nomenclatural act(s). A future comparison, both morphological and molecular, with the eight *Leiodermatium* species recently proposed by Schuster et al. (2021) for the tropical western Atlantic would further allow a complete review of the systematics and biogeography of this genus in the Atlantic.

## Biogeographic Affinities

The Azores lithistid fauna is largely composed of species with a broader northeast Atlantic or Atlanto-Mediterranean distribution, and very low endemism (one single species). This is in accordance with previous findings both for sponges (Xavier and Van Soest, 2012) and other taxonomic groups in shallow waters (Freitas et al., 2019), as well as for cold-water corals in which a putative endemism of 14–15% was observed in the region (Braga-Henriques et al., 2013; Sampaio et al., 2019). Comparably low endemism levels have also been reported for the New Zealand lithistid assemblages at similar spatial scales (Kelly et al., 2007).

The highest similarity found between the Azores and the oceanic seamounts lithistid assemblages was expected given the geographical proximity and similar environmental conditions (temperature, salinity, oxygen and major nutrients) observed at the seafloor (Amorim et al., 2017). The occurrence of *Leiodermatium tuba* in the Azores and of *Neophrissospongia nolitangere* on these oceanic seamounts, herein reported for the first time, further suggests that as surveys and taxonomic efforts increase, more species will be found to be shared between these two regions, and possibly other, as previously posited by Carvalho et al. (2020).

The upper bathyal (200–1000 m depth) of the area comprising the Azores archipelago and the oceanic seamounts, where the vast majority of the lithistid records are found, is dominated by the North Atlantic Central Water, which presents a salinity of 35.2 – 36.7 PSU, temperatures between 8.5°– 19°C and high median concentration of oxygen (94%) (Palma et al., 2012; Bashmachnikov et al., 2015). Below this depth there is only a limited influence of Subarctic Intermediate Water and Mediterranean Outflow Water below this depth (Bashmachnikov et al., 2015).

The major North Atlantic water masses and current pathways have been shown to structure the diversity and distribution of deep-sea sponges and corals, as well as the habitats they form (Puerta et al., 2020; Roberts et al., 2021). The large-scale circulation of the temperate northeast Atlantic is dominated

**TABLE 1 |** Spatial and bathymetric distribution of lithistid sponges (Porifera, Demospongiae, Heteroscleromorpha) across the Northeast Atlantic and Mediterranean Sea.

| Family/Species | Oceanic archipelagos | | | | | Seamounts | | Continental slope | | |
|---|---|---|---|---|---|---|---|---|---|---|
| | AZO | MAD | SEL | CAN | CVD | OCS | LUS | IBE | CAD | MED |
| CORALLISTIDAE Sollas, 1888 | | | | | | | | | | |
| *Corallistes elegantior* Schmidt, 1870 | | | | | | | | data n.a. | | |
| *Corallistes masoni* (Bowerbank, 1869) | | 480–610 | | 415–417 | | | | | | |
| *Corallistes microtuberculatus* Schmidt, 1870 | | | | | data n.a. | | | | | |
| *Isabella harborbranchi* Carvalho et al., 2015 | | | | 133–366 | | | | | | |
| *Neophrissospongia endoumensis* Pisera and Vacelet, 2011 | | | | | | | | | | 5[c] |
| *Neophrissospongia nana* Manconi and Serusi, 2008 | | | | | | | | | | 6[c] |
| *Neophrissospongia nolitangere* (Schmidt, 1870) | 102–501 | 317 | 358 | 10–20[c]; 295–450 | | 461–501 | | | | 313-352 20–22[c] |
| *Neophrissospongia radjae* Pisera and Vacelet, 2011 | | | | | | | | | | data n.a.[c] |
| *Neoschrammeniella bowerbankii* (Johnson, 1863) | | 113–669 | | | | | | 486–672[aff.] | 530–912 | 12–30[c]; 400–640 |
| *Neoschrammeniella inaequalis* Carvalho and Xavier, 2020 | | | | | | | 460–675 | | | |
| *Neoschrammeniella piserai* Carvalho and Xavier, 2020 | | | | | | 695 | | | | |
| *Neoschrammeniella pomponiae* Carvalho and Xavier, 2020 | | | | | | 480 | | | | |
| *Neoschrammeniella* sp. | | | | | | 580–610 | | | | |
| THEONELLIDAE Lendenfeld, 1903 | | | | | | | | | | |
| *Discodermia arbor* Carvalho and Xavier, 2020 | | | | | | 330 | | | | |
| *Discodermia kellyae* Carvalho and Xavier, 2020 | | | | | | 580 | | | | |
| *Discodermia polydiscus* (Bowerbank, 1869) | | | | 10–20[c] | | | | data n.a. | | |
| *Discodermia polymorpha* Pisera and Vacelet, 2011 | | | | | | | | | | 3–30[c]; 60–360 |
| *Discodermia ramifera* Topsent, 1892 | 98–318 | | | | | 300–461 338–520[cf.] | | | | |
| *Discodermia verrucosa* Topsent, 1928 | | 476–497 | | 303–400 | | 338–520 | | | | |
| *Discodermia* sp. | | | | | | 304 | | | | |
| *Theonella annulata* | | | | 146 | | | | | | |
| MACANDREWIIDAE Schrammen, 1924 | | | | | | | | | | |

*(Continued)*

**TABLE 1 |** Continued

| Family/Species | Oceanic archipelagos | | | | | Seamounts | | Continental slope | | |
|---|---|---|---|---|---|---|---|---|---|---|
| | AZO | MAD | SEL | CAN | CVD | OCS | LUS | IBE | CAD | MED |
| *Macandrewia azorica* Gray, 1859 | 256–1495 | | 361 | 480[cf.] 1340–1530 | | 420– 1000[cf.] | | | | |
| *Macandrewia minima* Carvalho and Xavier, 2020 | | | | | | 615 | | | | |
| *Macandrewia ramosa* Topsent, 1904 | 1360 | | | | | | | | | |
| *Macandrewia robusta* Topsent, 1904 | 1165 | | | | | 705 | | | | |
| *Macandrewia schusterae* Carvalho and Xavier, 2020 | | | | | | 520–805 | 605–675 | | | |
| *Macandrewia* sp. | | | | | | 225–280 | 900 | | | |
| PHYMARAPHINIIDAE Schrammen, 1924 | | | | | | | | | | |
| *Exsuperantia archipelagus* Carvalho and Pisera, 2019 | 168–1229 | 563 | | 408–1530 | | 280–1000 | | | | |
| *Exsuperantia levii* Carvalho and Xavier, 2020 | | | | | | 480 | | | | |
| AZORICIDAE Sollas, 1888 | | | | | | | | | | |
| *Leiodermatium lynceus* Schmidt, 1870 | 370–460 201–594 [cf.] | 402–741 | | 281–1530 | | 480 | 305–320 | | 948 | 207–700 430–469[cf.] |
| *Leiodermatium pfeifferae* (Carter, 1873) | 454–1250 200–457[cf.] | data n.a. | | | 183–234 | | | | 704–734 | 615–890 |
| *Leiodermatium tuba* Carvalho and Xavier, 2020 | 622–723 | | | 660 | | 330–710 | 805–1035 | | | |
| *Leiodermatium* sp. *indet*. | 270–1073 | | | | | | | | | |
| SCLERITODERMIDAE Sollas, 1888 | | | | | | | | | | |
| *Aciculites mediterranea* Manconi et al., 2006 | | | | | | | | | | 8[c] |
| *Microscleroderma lamina* Pérez et al., 2004 | | | | | | | | | | 2[c] |
| *Microscleroderma spirophora* Lévi, 1960 | | | | | 18–107 | | | | | |
| SIPHONIDIIDAE Lendenfeld, 1903 | | | | | | | | | | |
| *Gastrophanella phoeniciensis* Pérez et al., 2004 | | | | | | | | | | 2[c] |
| *Siphonidium elongatus* Carvalho and Xavier, 2020 | | | | 470 | | 480–545 | 460–675 | | | |
| *Siphonidium ramosum* (Schmidt, 1870) | 349–793[?] | | | | | | | | | 20–1000[?] |
| DESMANTHIDAE Topsent, 1893 | | | | | | | | | | |
| *Desmanthus incrustans* (Topsent, 1889) | | | | | | | | | | 2-40 |
| *Petromica (Petromica) grimaldii* Topsent, 1898 | 200–914 | | | | | | 255–265 | | | |

*(Continued)*

**TABLE 1** | Continued

| Family/Species | Oceanic archipelagos | | | | | Seamounts | | Continental slope | | |
|---|---|---|---|---|---|---|---|---|---|---|
| | AZO | MAD | SEL | CAN | CVD | OCS | LUS | IBE | CAD | MED |
| *Sulcastrella tenens* (Vacelet, 1969) | | | | | | | | | | 210–240 |
| Total no. of species in each region (no. of species shared with the Azores) | 11 | 7 (4) | 2 (2) | 11 (5) | 3 (1) | 16 (7) | 6 (3) | 3 (0) | 3 (2) | 14 (4) |
| No. of potential endemic species (% in relation to all northeast Atlantic and Mediterranean species) | 1 (2.6) | 0 (0) | 0 (0) | 2 (5.3) | 3 (7.9) | 6 (15.7) | 0 (0) | 1 (2.6) | 0 (0) | 9 (23.7) |

*Bathymetric ranges presented in meters. Oceanic archipelagos: AZO, Azores; MAD, Madeira; SEL, Selvagens; CAN, Canaries (including the Saharan upwelling ecoregion); CVD, Cape Verde (including the Sahelian upwelling ecoregion); Seamounts: OCS, oceanic seamounts, include the Antialtair, Atlantis, Tyro, Plato, Hyères, and the Great Meteor seamounts; LUS, Lusitanian seamounts, include Lion, Gorringe, and Àmpere seamounts. Continental slope: IBE, Iberian Atlantic margin; CAD, Gulf of Cadiz; MED, Mediterranean Sea. Data n.a., depth data not available.*
*[c]Indicates species occurring in submerged caves, [cf.]and [aff.]correspond to records with some degree of species-level uncertainty, and [?] correspond to records of doubtful validity for the area (see discussion).*
*Sources of records: this study, Carvalho et al. (2015, 2020) (and references therein), Maldonado et al. (2015); Carvalho and Pisera (2019), Sitjà et al. (2019); Ríos et al. (2020), and Pisera and Gerovasileiou (2021).*

by the Azores Current (AzC) that flows eastwards toward the Iberian margin (Carracedo et al., 2014). Importantly, the AzC southward and eastward branches have been identified as an important transport pathway between the Azores archipelago and the oceanic seamounts of the Great Meteor complex and the Lusitanian seamounts, respectively (Lima et al., 2020). The AzC therefore provides the physical connectivity needed for the dispersal of sponge larvae between these regions. However, the considerably largest distances between the Azores, the Lusitanian seamounts and Iberian shelf, over abyssal areas is likely to limit successful dispersal of the generally short-lived and lecitotrophic larvae typical of sponges, resulting in a much lower similarity between these regional assemblages.

Our results suggest that the complex and dynamic oceanographic circulation patterns of the northeast Atlantic, as well as a rich topography with numerous seamounts provide the conditions for these typically bathyal species to disperse and maintain regional-scale distributions and low endemism. This has in fact been observed in other tetractinellid groups (Cárdenas et al., 2013; Cárdenas and Rapp, 2015) and cladorhizids (Hestetun et al., 2015, 2017) with similar depth distributions.

## Conservation
In our study, the vast majority (87%) of the lithistid records obtained as a result of bycatch of longline fisheries corresponded to large and potentially habitat-building species (*Neophrissospongia nolitangere*, *Macandrewia azorica*, and *Leiodermatium* spp.). This finding suggests that sponge species attaining large sizes, with a more complex morphology and with a dense hypersilicified skeleton may be more vulnerable to this activity than smaller species (*Discodermia ramifera*), or those with looser or softer skeletal structure [*Petromica* (*Petromica*) *grimaldii*]. These results concur with previous studies which showed that although bottom longline fishing has a reduced impact on deep-sea corals (another VME-indicator taxon

when compared to bottom trawling, the removal rates were significantly higher in corals with more complex morphology (Sampaio et al., 2012; Pham et al., 2014).

Notably, deep-sea sponges are presumed to exhibit slow growth rates and high longevity (Leys and Lauzon, 1998; Fallon et al., 2010; Kahn et al., 2016), which renders them particularly vulnerable to both environmental and anthropogenic disturbances. An age between 135 and 160 years was established for a specimen of *Corallistes undulatus* Lévi and Lévi (1983) (family Corallistidae), roughly 30 cm in diameter, collected on the Norfolk Ridge (Ellwood et al., 2007). Accidental longline capture of specimens of similar and larger sizes, thus possibly centennial in age, in the Azores is not uncommon. So, while the impact of bottom longline fisheries may be negligible in terms of the number of individuals removed from the seafloor, over time its selectivity for larger/older individuals may cause shifts in community composition and population structure and consequently alter or compromise the function(s) of the ecosystem at local scales.

Taking such considerations into account, our results further support the recent addition of lithistid tetractinellids, particularly those in the genera *Leiodermatium*, *Neophrissospongia*, *Neoschrammeniella,* and *Macandrewia* to the list of VME indicators for the Northeast Atlantic (ICES, 2020), and their proposed inclusion in Annex III of the EU deep-sea access regulations (EU Reg. 2016/2336) toward preventing significant adverse impacts on these VMEs (EU, 2016).

Whether these lithistid species form dense habitats as those found dominated by *Leiodermatium pfeifferae* on seamounts in the Western Mediterranean (Maldonado et al., 2015), and suspected for *M. azorica* on the Hyères seamount (Carvalho et al., 2020) requires verification using *in situ* observation systems such as remotely operated or autonomous underwater vehicles (ROVs/AUVs), and cameras.

Larger scale investigations, currently underway, of the patterns of diversity and distribution of lithistids across the entire North Atlantic, as well as their underpinning ecological and evolutionary drivers will allow to coordinate efforts toward conservation of these species, habitats and the ecological functions they deliver.

## DATA AVAILABILITY STATEMENT

The datasets generated and analyzed in this study can be found in the PANGAEA data repository (https://doi.pangaea.de/10.1594/PANGAEA.921772 and https://doi.pangaea.de/10.1594/PANGAEA.929934), and in the SponGIS data portal (www.spongis.org). Sequences are deposited in GenBank under accession nos. MW006490–MW006541 for rRNA 28S (C1–D2) and MW000672–MW000696 for mtDNA COI gene fragments.

## AUTHOR CONTRIBUTIONS

JX and FC designed the study. JX, RP, and FC identified the samples. DR and FC generated the sequence data. JX, RP, CP, and FC analyzed the data. AC and CP contributed the samples and data. JX wrote the draft of the manuscript. JX, RP, CP, and FC prepared the figures and tables. All the authors contributed the text and reviewed the manuscript.

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## SUPPLEMENTARY MATERIAL

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