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Filling gaps in the Webbnesia marine diversity: The madeiran sponge fauna

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ABSTRACT

Despite few pioneering works in the late XIX and early XX century, the poriferan fauna of Madeira has remained mostly unexplored until today, Madeira being one of the least studied eastern Atlantic archipelagos in terms of its sponge diversity. After a thorough analysis of both new material collected by SCUBA diving as well as a literature research, 140 sponge species are known to occur in the Madeira archipelago. From the 56 species identified by both collected material and pictures, approximately 60% (34 species) are new records for the Archipelago. These 34 new records were found associated with littoral rocky substrates and, to a lesser extent, caves, rhodolith beds and wrecks, within a depth range of 10–35 m depth. Our records also contain several Mediterranean species that have not been previously recorded in the North Atlantic, several North-east Atlantic species whose presence in Madeira marks their southernmost limit of occurrence, as well as elements from the subtropical West African fauna. Amongst the new additions to its sponge fauna there are the first records of Homomscleromorpha, with at least three *Oscarella* species noted, as well as a new species of *Hemimycale* (Demospongiae, Poecilosclerida). Yet, this is still an underestimation of Madeira's real sponge diversity. Data on Madeiran sponge fauna is still skewed towards shallow and littoral habitats, with other less accessible environments, such as caves, rhodolith beds or the deep sea, remaining largely unexplored. Similarly, complex poriferan groups (e.g. calcareans, haplosclerids, tetractinellids, hymedesmids) have only been partially studied, and their true diversity remains unknown. Finally, due to a lack of prior baseline it is difficult to conclude if some newly recorded species are non-indigenous, range-expanding or simply previously overlooked native species. However, it is now clear that two previously thought non-indigenous species, *Mycale* (*Carmia*) *senegalensis* and *Prosuberites longispinus* are in fact native to the Archipelago, their prior status as non-indigenous arising from the lack of prior confirmation of their presence outside of port facilities.

1. Introduction

Coastal marine habitats and associated biodiversity are exposed to multiple threats (Crain et al., 2009; Barbier, 2017) and consequently are among the most vulnerable ecosystems worldwide (Kolar and Lodge, 2001; Hochberg and Gotelli, 2005). Furthermore, islands, which harbour a big portion (one-fifth) of the world's biodiversity, sustained by a profusion of endemic species, contain the most threatened ecosystems (Kier et al., 2009; Lagabrielle et al., 2009), being particularly prone to ecological damages. In addition, oceanic islands, such as Madeira, are structurally more vulnerable to disturbances, because their small size and isolation reduces spatial options for persistence of biodiversity (Martín-García et al., 2015). This situation exacerbates the need to develop biodiversity assessments and monitoring programmes in many regions around the world and particularly in insular systems, as the Madeira archipelago, where knowledge gaps regarding marine biodiversity have been highlighted (e.g. Pestana et al., 2018; Ribeiro and Neves, 2020; Neves et al., 2021) and still persist.

With 9639 sponge species considered as valid nowadays (de Voogd et al., 2024), sponges constitute a dominant group in hard-bottom benthic communities, both in terms of biomass and species richness, but it is thought that the real number of extant species is at least twice this number (van Soest et al., 2012a). Yet, as a consequence of their difficult identification, sponges have been historically overlooked in

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community or ecosystem studies (Bell et al., 2017), even in fairly accessible areas. In this regard, while the Atlanto-Mediterranean region is considered worldwide amongst the best studied in terms of poriferan diversity (van Soest et al., 2012a), the Madeira archipelago might be considered, alongside the African coast, one of its biggest gaps of knowledge (van Soest et al., 2013, 2014; Pestana et al., 2018), and one of the least studied areas of the Webbnesia region (a new ecoregion, comprising the archipelagos of Madeira, Selvagens and the Canary Islands. Designated in the new biogeographical classification proposed by Freitas et al., 2019) and of the 'Macaronesian region' (the 'wider', historically recognized grouping of oceanic archipelagos, which included the Azores, Madeira, Selvagens, Canary and Cabo Verde islands). Most of the aforementioned archipelagos have had a long-lasting story of sponge research spanning over a century (e.g. Topsent, 1891, 1904, 1928; Levi and Vacelet, 1958; de Groot, 1980; Boury-Esnault and Lopes, 1985; Moss, 1992; van Soest, 1993; Sarà and Bavestrello, 1998; Cruz, 2002; van Soest et al., 2012b, 2013, 2014; Xavier et al., 2021) with Azores and Cape Verde recognized as hotspots of sponge biodiversity (Xavier and van Soest, 2012). In this sense, while old accounts mentioned the existence of a rich and diverse sponge fauna on Madeira already over a century ago (Greeff, 1872; Vandelli, 1885; da Silva and de Meneses, 1921), it has never been properly studied, with most works relaying on specimens collected either accidently or by research vessels in sporadic expeditions (e.g., Johnson, 1863, 1899; Topsent, 1904, 1928). Moreover, the existent information is mostly fragmented (e.g., van Soest et al., 2014; Carvalho et al., 2015, 2020; Pestana et al., 2018), and much of it has not yet been published (Reed & Pomponi, 1992; van Soest et al., 2013, 2014). This lack of data regarding the sponge fauna poses constraints for conservation and marine spatial planning in the archipelago, and the lack of a reliable baseline hinders the recognition of marine biodiversity changes (Ribeiro and Neves, 2020), including the detection of Non-Indigenous Species (NIS) that might arrive to the archipelago.

In this context, this work intends to fill the gaps regarding the knowledge on the littoral marine biodiversity of Madeira archipelago, particularly sponges by: (I) providing an exhaustive account of the known sponge fauna of the Madeira archipelago, with emphasis on (II) rare, new or faunistically relevant species, as well as (III) a critical review on NIS sponges on the island, with the aim of providing a reliable and robust baseline for future monitoring of benthic communities in the area.

2. Material and methods

2.1. Study area

The archipelago of Madeira (Portugal) is of volcanic origin and comprises two inhabited islands, Madeira (742 km^2) and Porto Santo (43 km^2) and the uninhabited islands of Desertas (14 km^2). The former two are home to 250,769 people (DREM, 2021), whereas Desertas is a protected area (Costa Neves, 1998). The archipelago is located in the subtropical North-eastern Atlantic, within the 32–33°N latitude and 16–17.5°W longitude (Fig. 1). The islands are surrounded by oceanic waters and characterized by reduced shelf and shallow subtidal seabeds (0–20 m depth) that are dominated by rocky reefs (Ribeiro, 2008; Friedlander et al., 2017; Ribeiro et al., 2023). The dominant oceanic currents are the Portuguese, Azores, and Canary currents, all part of the eastern anticyclonic North Atlantic subtropical gyre (Sala et al., 2013) which result in a high salinity, high temperature and low-nutrient regime waters system (Johnson and Stevens, 2000; New et al., 2001). The climate in the Madeira archipelago is generally mild and conservative, but exposed to the seasonal oscillations of the Azores, Portugal, and Canary Currents (Caldeira et al., 2002).

2.2. Sampling

Since 2016, SCUBA-diving surveys have been conducted to monitor the benthic subtidal habitats in several locations of Madeira archipelago (Fig. 2; Supp. Mat. 1). The surveys provided detailed and quantitative observation of seabed habitats that allowed the inventory and discovery of new marine biodiversity to the archipelago (e.g., Ribeiro et al., 2019, 2023; Wirtz and Zilberberg, 2019; Wirtz and Machado, 2022), as well habitat mapping and communities characterisation (e.g. Ribeiro and Neves 2020; Neves et al., 2021; Lourenço et al., 2022; Ribeiro et al., 2022). During many of these SCUBA-diving surveys across the archipelago, sponges were observed within a depth range of 1–35 m in natural rocky reefs, crevices, caves and artificial reefs, their presence being documented by photography. When possible, a representative piece of the species was collected for its posterior identification. Samples were preserved in 96% ethanol.

2.3. Species identification

In most cases, both photographic material and a representative piece of the specimens was available. Yet, due to dive-related limitations or constraints, not all sponges photographed could be always sampled. For those species that were just identified in the photographic census but no

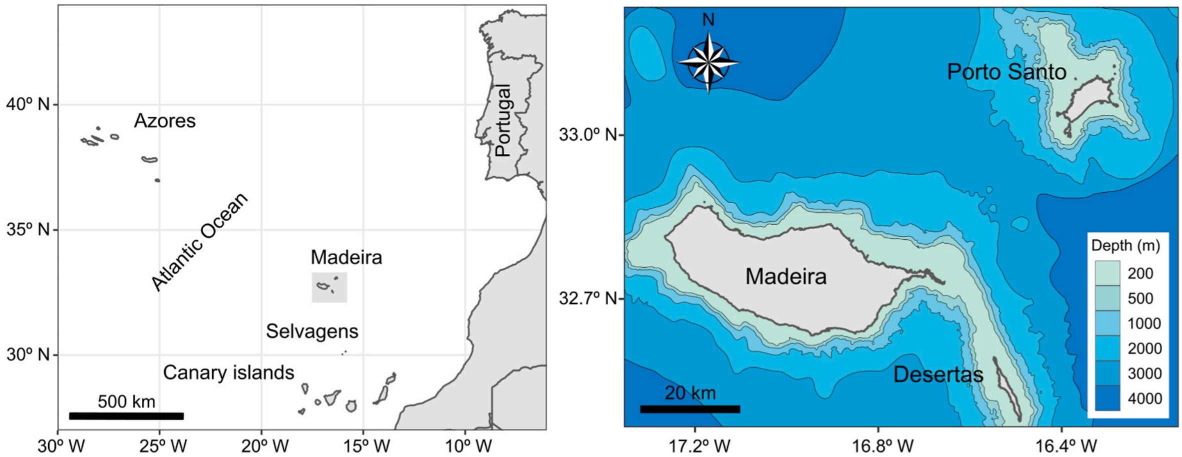

Fig. 1. Map of the study area. *Left*: location of the Madeira Archipelago (grey rectangle) on the North Atlantic area; *Right*: Madeira, Porto Santo and Desertas islands. CRS: WGS84/Pseudo-Mercator (EPSG 3857).

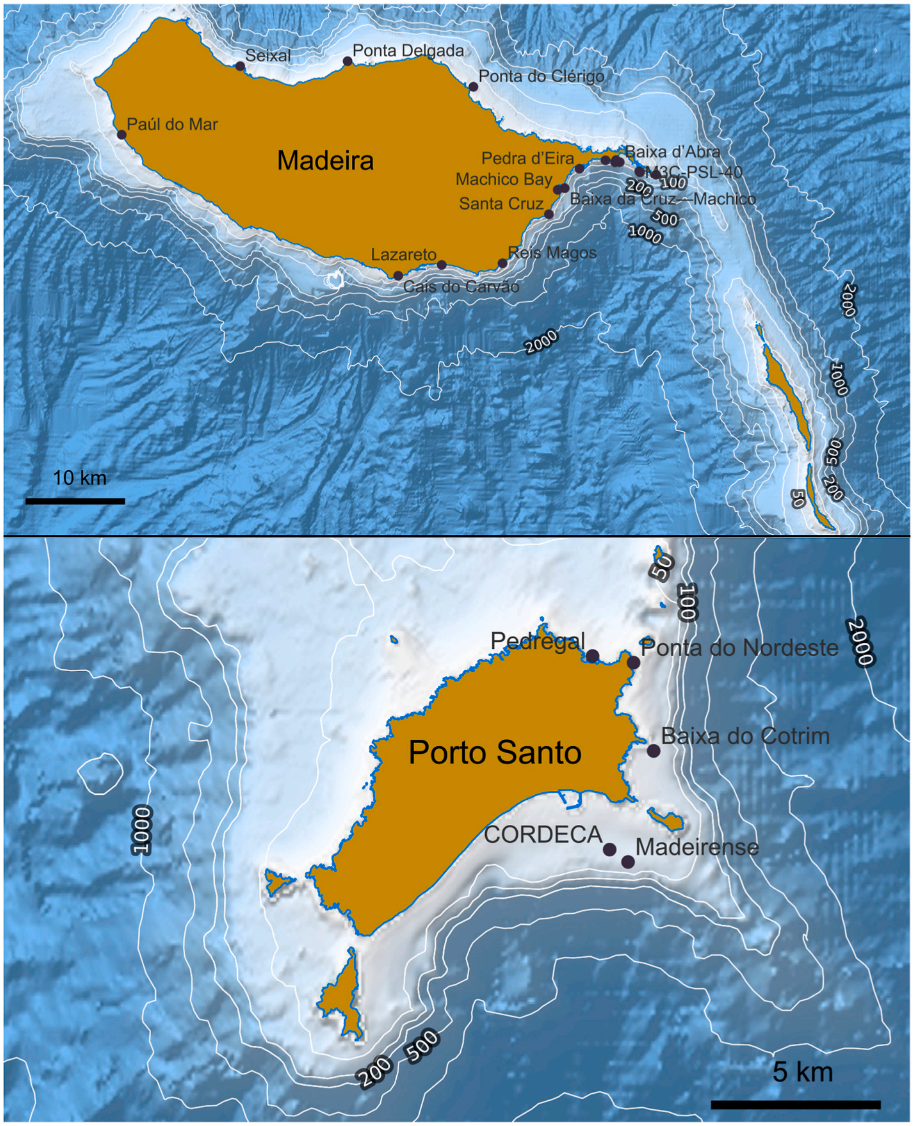

Fig. 2. Locations of the collection sites in the Madeira Archipelago. CRS: WGS84/Pseudo-Mercator (EPSG 3857). Names correspond with those shown in Supp. Mat. 1.

sample was available, identification was attempted to the lowest taxonomic level when possible, yet it is kept as tentative until samples can be analysed (Table 1). For all collected samples, initial identifications were made by examining teased preparations of fragments, made with industrial bleach for both calcareous and siliceous species, and H_2O_2 for keratose sponges. Similarly, in order to analyse the skeletal arrangement of both ectosome and choanosome, several sections were cut for each specimen and treated with xylene, as described in Cristobo et al. (1993). To obtain spicule preparations for both optical and scanning electron microscopy (SEM), fragments of the sponges were dissolved with nitric acid (HNO_3) following the procedures described in Cristobo et al. (1993) and Uriz et al. (2017a). The SEM observations were conducted through a HITACHI S-3500 N scanning electron microscope from the Institut de Ciències del Mar (ICM-CSIC), at 5 KeV. Spicule dimensions are given as maximum and minimum length and width for each spicule category with the average values being given in between in italics followed by ± the Standard Deviation (i.e. MIN. – $\underline{\textit{MEAN}}$ ± SD – MAX.). Unless stated otherwise, all spicule measurements were based on 40 spicules. All the new material examined has been labelled and deposited in the Funchal Natural History Museum (MMF) collections with the same acronyms used to identify each sample along the text (Supp. Mat. 1). This paper follows the currently proposed classification for sponges in the World Porifera Database (de Voogd et al., 2024).

2.4. Literature review

To provide an account of the historical records regarding the sponge fauna of the area, a careful examination of the literature was conducted in search for any relevant data regarding the occurrence of sponges in the Madeiran Archipelago (including the Madeira, Porto Santo and Desertas islands and nearby seafloor). This systematic literature search was conducted using the biographic database Web of Science (WoS) in August 2022. Additionally, 'historical papers' likely to contain relevant information were checked regardless of whether or not they were retrieved by the search engine, as WoS is known to offer an incomplete coverage of old literature (Marx, 2012). Historical papers were recovered from the Biodiversity Heritage Library (https://www.biodiversitylibrary.org/; Gwinn and Rinaldo, 2009), the World Porifera Database (https://www.marinespecies.org/porifera/; de Voogd et al., 2024), requested to colleagues, as well as the authors own private libraries.

Table 1
Synoptic table including all known sponge species recorded for the Madeira Archipelago. Acronyms following species names: TL, original description of the species, with Madeira as type locality; *dr*, dubious record in need of confirmation; NIS, Non-Indigenous species; RG, range-expanding species; SC, species complex; Ms, misapplication; Is, *Incertae sedis*; P, Species reported in this study only from photographic records (at the time being); new records for the area appear in **bold**. Numbers in **bold** indicate publications for which a description of the specimens was provided, whereas roman typeface indicates that the species was recorded from the area, but no description was provided.

Species	Publications
Class DEMOSPONGIAE	
Order AGELASIDA	
Family HYMERHABDIIDAE	
Prosuberites longispinus Topsent, 1893	52; 56; 59
Order AXINELLIDA	
Family AXINELLIDAE	
Axinella damicornis (Esper, 1794)	30; 58; 59
***Axinella dissimilis* (Bowerbank, 1866)**	59
***Axinella guiteli* Topsent (1896)**	**59**
Axinella polypoides Schmidt, 1862 P	19; 59
***Axinella verrucosa* (Esper, 1794)**	59
Family HETEROXYIDAE	
Alloscleria tenuispinosa Topsent (1927) TL	**18**; **19**
Family RASPAILIIDAE	
Eurypon lacazei **(**Topsent, 1891**)**	21; **50**; 59
Raspailia (Raspailia) viminalis Schmidt, 1862	**19**
Family STELLIGERIDAE	
Paratimea duplex (Topsent, 1927) TL	**18**; **19**
Order BUBARIDA	
Family BUBARIDAE	
Bubaris vermiculata (Bowerbank, 1866)	**19**
Family DICTYONELLIDAE	
Acanthella acuta Schmidt, 1862	30; 59
***Dictyonella incisa* (Schmidt, 1880)**	**59**
Dictyonella madeirensis (Topsent, 1928) TL	**19**; 23
***Dictyonella pelligera* (Schmidt, 1864)**	**59**
Order CHONDROSIIDA	
Family CHONDROSIIDAE	
Chondrosia plebeja Schmidt, 1868	16
Chondrosia reniformis Nardo, 1847	25; 30; 50; 55; 59
Order CLIONAIDA	
Family CLIONAIDAE	
Cliona celata Grant, 1826 SC	**39; 50;** 59
Cliona viridis (Schmidt, 1862) SC	**19**; 59
Spiroxya spiralis (Johnson, 1899) TL	**9**
Family SPIRASTRELLIDAE	
Spirastrella cunctatrix Schmidt, 1868	**6**
Order DENDROCERATIDA	
Family DARWINELLIDAE	
Aplysilla sulfurea Schulze, 1878 P	**50**; 59
Family DICTYODENDRILLIDAE	
Spongionella depressa Topsent, 1928 *dr* (I)	21
Order DESMACELLIDA	
Family DESMACELLIDAE	
Desmacella informis (Stephens, 1916)	**19**
Order DICTYOCERATIDA	
Family DYSIDEIDAE	
Dysidea fragilis (Montagu, 1918) *dr*	**19**
Dysidea spp.	**19**; 59
Family IRCINIIDAE	
Ircinia fasciculata sensu Vacelet (1959)	31; 59
Ircinia dendroides (Schmidt, 1862)	**19**; 50
Ircinia variabilis (Schmidt, 1862)	**19**; 59
Sarcotragus spinosulus Schmidt, 1862	**19**
Family SPONGIIDAE	
Hyattella obscura Lendenfeld (1889) TL	**9**
Spongia (Spongia) excavata (Lendenfeld, 1889) Is, TL	**9**
Spongia (Spongia) hispida Lamarck, 1814 Ms (II), TL	**9**
Spongia (Spongia) virgultosa (Schmidt, 1868)	**19**
Family THORECTIDAE	
***Cacospongia mollior* Schmidt, 1862**	59
***Fasciospongia cavernosa* (Schmidt, 1862)** P	59
Hyrtios collectrix (Schulze, 1880)	**19**
Order HAPLOSCLERIDA	
Family CALLYSPONGIIDAE	
***Callyspongia (Callyspongia)* sp.**	59
Callyspongia (Callyspongia) burtoni van Soest & Hooper, 2020	**26**; 30; 59
***Siphonochalina* sp.**	59
Family CHALINIDAE	
***Chalinula limbata* (Montagu, 1814)**	59
***Chalinula nigra* Boury-Esnault and Lopes (1985)** CG/NIS	**59**
Chalinula parasimulans Lévi (1959) *dr*	43
***Dendroxea lenis* (Topsent, 1892)**	59
Haliclona (Flagellia) porosa (Fristedt, 1887)	**19**
Haliclona (Gellius) angulata (Bowerbank, 1866)	**6**; **26**
***Haliclona (Halichoclona) fistulosa* (Bowerbank, 1866)**	59
***Haliclona* (*Haliclona*) sp.**	59
Haliclona (Haliclona) simulans (Johnston, 1842)	**19**
Haliclona (Reniera) cinerea (Grant, 1826)	**19**
Haliclona (Rhizoniera) indistincta (Bowerbank, 1866)	43
Haliclona (Soastrella) implexa (Schmidt, 1868)	**26**
Family NIPHATIDAE	
Gelliodes fayalensis Topsent, 1892 TL	**19**
Family PHLOEODICTYIDAE	
Siphonodictyon infestum (Johnson, 1889) TL	**9**
Siphonodictyon insidiosum (Johnson, 1889) TL	**9**
Family PETROSIIDAE	
***Petrosia (Petrosia)* cf. *clavata* (Esper 1794)**	59
Petrosia (Petrosia) ficiformis (Poeiret, 1789)	**26**; 30; 32; 53; 55; 59
Order MERLIIDA	
Family HAMACANTHIDAE	
Hamacantha (Hamacantha) johnsoni (Bowerbank, 1864) TL	**4**; **19**
Hamacantha (Vomerula) azorica Topsent (1904)	**19**
Hamacantha (Vomerula) falcula **(**Bowerbank, 1874**)** *dr* (I)	21
Family MERLIIDAE	
Merlia normani Kirkpatrick, 1908 P	13; 14; 17; 22; 27; 37; 59
Order POECILOSCLERIDA	
Family CLADORHIZIDAE	

(*continued on next page*)

Table 1 (*continued*)

Species	Publications
Chondrocladia (Chondrocladia) virgata Thomson, 1873 *dr* (1)	21
Cladorhiza abyssicola Sars, 1872	**15**; 19
Nullarbora grimaldii (Topsent, 1909) TL	**15**; 19
Family CHONDROPSIDAE	
Batzella inops (Topsent, 1891)	30; 31; 50; 55; 59
Family COELOSPHAERIDAE	
Forcepia (Leptolabis) brunnea (Topsent, 1904) TL	**10**; **19**
Family CRAMBEIDAE	
Crambe crambe (Schmidt, 1862) NIS	34; 59
Family CRELLIDAE	
Crella (Crella) elegans (Schmidt, 1862)	**19**; 59
Family ESPERIOPSIDAE	
Ulosa jullieni (Topsent, 1892)	42
Family HYMEDESMIIDAE	
Hemimycale columella (Bowerbank, 1934) P	**19**; 59
***Hemimycale funchalensis* sp. nov.**	**59**
***Hymedesmia (Hymedesmia)* sp.**	59
***Hymedesmia (Hymedesmia) senegalensis* Lévi (1956)**	**59**
Hymedesmia (Hymedesmia) storea Lundbeck, 1910	**19**
Hymedesmia (Stylopus) coriacea (Fristedt, 1885)	**19**
Phorbas fictitius (Bowerbank, 1866)	40; 50; 55; 59
Family MICROCIONIDAE	
Antho (Antho) mediterranea (Babiç, 1922)	**44**
Antho (Antho) morisca (Schmidt, 1868)	**19**
Antho (Antho) paradoxa (Babiç, 1922)	**44**
Clathria (Clathria) coralloides sensu Boury-Esnault and Lopes (1985)	**50**
***Clathria (Microciona)* cf. *gradalis* sensu Cruz (2002)**	59
Clathria (Microciona) haplotoxa (Topsent, 1928) TL	**19**
Family MYCALIDAE	
***Mycale (Carmia)* sp.**	59
Mycale (Carmia) cf. *macilenta* (Bowerbank, 1866)	**50**; 59
Mycale (Carmia) senegalensis **Lévi (1952)**	43; 48; 52; 56; 57; **59**
Family MYXILLIDAE	
Myxilla (Myxilla) rosacea (Liberkühn, 1859)	**19**
Family TEDANIIDAE	
Tedania (Tedania) anhelans (Vio in Olivi, 1792)	**50**; 58
Order POLYMASTIIDA	
Family POLYMASTIIDAE	
Spinularia sarsii (Ridley and Dendy, 1886)	**19**
Order SUBERITIDA	
Family HALICHONDRIIDAE	
***Axinyssa digitata* (Cabioch, 1968)**	59
***Ciocalypta penicillus* Bowerbank, 1862 P**	59
Epipolasis spissa (Topsent, 1892) *dr* (I)	21
***Spongosorites* cf. *cavernicola* Bibiloni (1993)**	**59**
Family SUBERITIDAE	
Aaptos aaptos (Schmidt, 1864)	29; **36**; 50; 55
Suberites carnosus (Johnston, 1842)	31; 50
Order TETHYIDA	
Family HEMIASTERELLIDAE	
Hemiasterella sp.	31

Table 1 (*continued*)

Species	Publications
Family TETHYIDAE	
***Tethya* spp.** P	59
Order TETRACTINELLIDA	
Family AZORICIDAE	
Leiodermatium lynceus Schmidt, 1870	21; **46**
Leiodermatium pfeifferae (Carter, 1873) TL	**7**
Family CORALLISTIDAE	
Corallistes masoni (Bowerbank, 1869) TL	**5**; **46**
Neophrissospongia nolitangere (Schmidt, 1870)	**46**
Neoschrammeniella bowerbankii (Johnson, 1863)	**2**; **3**; **12**; **46**
Family GEODIIDAE	
Calthropella (Calthropella) geodioides (Carter, 1876) *dr* (I)	21
cf. *Erylus* sp.	59
cf. *Erylus* sp. 2	59
Erylus deficiens Topsent (1927) TL	**18**; 38; 41
Erylus listeri (Bowerbank, 1858) Is (III)	1
Geodia megastrella Carter, 1876	**19**
Geodia nodastrella Carter, 1876	**19**; **45**
Penares candidatus (Schmidt, 1868)	29
Family PACHASTRELLIDAE	
Pachastrella monilifera Schmidt, 1868	**19**; 58
Pachastrella ovisternata Lendenfeld, 1894	35
Family PHYMARAPHINIIDAE	
Exsuperantia archipelagus Carvalho and Pisera (2019) (IV)	**46**; **51**
Family THENEIDAE	
Annulastrella schmidti Maldonado (2002) (V)	19; **35**
Thenea muricata (Bowerbank, 1858)	19
Family THEONELLIDAE	
Discodermia verrucosa Topsent (1928)	**46**; 54
Family THOOSIDAE	
Alectona verticillata (Johnson, 1899) TL	**9**
Family VULCANELLIDAE	
Poecillastra schulzei (Sollas, 1886) Ms (I; VI)	21
Vulcanella gracilis (Sollas, 1888)	**19**
Order TRACHYCLADIDA	
Family TRACHYCLADIDAE	
Trachycladus minax (Topsent, 1888)	**19**
Order VERONGIIDA	
Family APLYSINIDAE	
Aplysina aerophoba (Nardo, 1833)	25; 30; 32; 33; 50; 55; **59**
Family IANTHELLIDAE	
***Hexadella* sp.** P	59
Class CALCAREA	
Order LEUCOSOLENIDA	
Family AMPHORISCIDAE	
Paraleucilla dalmatica Klautau, Imesek, Azevedo, Plese, Nikolic & Cetkovic, 2016	49
Paraleucilla magna Klautau, Monteiro & Borojevic, 2004 NIS	43; 47; 48; 52; 56; 57; 59
Family LEUCOSOLENIIDAE	
Leucosolenia variabilis Haeckel, 1870	25

(*continued on next page*)

Table 1 (*continued*)

Species	Publications
Family GRANTIIDAE	
***Ute glabra* Schmidt, 1864**	59
Family SYCONIDAE	
Sycon caminatum Thacker, 1908	49
Sycon ciliatum (Fabricius, 1780)	48; 52; 56; 57
***Sycon humboldti* Risso, 1827**	59
***Sycon raphanus* Schmidt, 1862**	59
Order CLATHRINIDA	
Family CLATHRINIDAE	
***Borojevia* cf. *cerebrum* (Haeckel, 1872)**	59
***Clathrina* sp.**	59
Clathrina cf. *clathrus* (Schmidt, 1864) *dr*	42; 52; 56
Clathrina lacunosa (Johnston, 1842)	4
Class HOMOSCLEROMORPHA	
Order HOMOSCLEROPHORIDA	
Family OSCARELLIDAE	
Oscarella balibaloi Pérez, Ivanisevic, Dubois, Pedel, Thomas, Tokina & Ereskovsky, 2011 P	**59**
***Oscarella* sp. 1**	59
***Oscarella* sp. 2** P	59
Class HEXACTINELLIDA	
Order AMPHIDISCOSIDA	
Family HYALONEMATIDAE	
Hyalonema (Cyliconemaoida) lusitanicum Barboza du Bocage, 1864	24
Order LYSSACINOSIDA	
Family ROSSELLIDAE	
Asconema setubalense Kent, 1870	58
Order SCEPTRULOPHORA	
Family APHROCALLISTIDAE	
Aphrocallistes beatrix Gray, 1858 *dr* ^(I)^	20
Family EURETIDAE	
cf. *Chonelasma* sp. *dr* ^(VII)^	**19**
Family FARREIDAE	
Farrea foliascens Topsent (1906)	**11; 19**
Farrea cf. *occa* Bowerbank, 1862 SC	**19**
TOTAL	140

1. Bowerbank (1858); 2–3. Johnson (1863, 1864); 4. Bowerbank (1864); 5. Bowerbank (1869); 6. Bowerbank (1872); 7. Carter (1873); 8. Lendenfeld (1889); 9. Johnson (1899); 10. Topsent (1904); 11. Topsent (1906); 12. Lendenfeld (1907); 13. Kirkpatrick (1908) 14. Kirkpatrick (1909); 15. Topsent (1909); 16. Kirkpatrick (1910a); 17. Kirkpatrick, 1910b, 1911); 18–19. Topsent (1927, 1928); 20. Burton (1954); 21. Burton (1956); 22. Vacelet (1967); 23. Cabioch (1968); 24. Wolff (1971); 25. Augier (1985); 26. de Weerdt (1986); de Weerdt and Van Soest (1986); 27. Vacelet and Uriz (1991); 28. Carballo et al. (1996); 29. Pascual et al. (1996, 2000, 2001a, 2001b, 2002a; 2002b); Pascual & Nuñez (1999a; 1999b); Pascual (2009); 30. Nike-Bianchi et al. (1998); 31. Arújo et al. (1999); 32. Wirtz (1999); 33. Malaquias et al. (2001); 34. Duran et al. (2002, 2004a, 2004b; 2004c); 35. Maldonado (2002); 36. van Soest et al. (2002); 37. Hajdu & van Soest et al. (2002); 38. Cárdenas et al. (2010); 39. Xavier et al. (2010a); 40. Xavier et al. (2010b); 41. Cárdenas et al. (2011); 42. van Soest et al. (2012b) 43. Canning-Clode et al. (2013a, 2013b); 44. Van Soest et al. (2013); 45. Cárdenas and Rapp (2015); 46. Carvalho et al. (2015); 47. Guardiola et al. (2016); 48. Gestoso et al. (2017); 49. Alvizu et al. (2018); 50. Pestana et al. (2018); 51. Carvalho and Pisera (2019); 52. Ramalhosa et al. (2019); 53. Riesgo et al. (2019); 54. Carvalho et al. (2020); 55. Ribeiro and Neves (2020); 56. Png-Gonzalez et al. (2021); 57. Chebaane et al. (2022). 58. Braga-Henriques et al., 2022 59. *Present study.*

(I) Burton (1956) mentions several species as part of the Madeiran fauna without verifiable previous records or further rationale in the manuscript for their inclusion; (II) *Spongia hispida* is an Indo-Pacific sponge, its presence in Madeira being most likely a misapplication of the former by Lendenfeld (1889); (III) Boury-Esnault and Lopes (1985) and Cárdenas et al. (2007) transferred the species from *Pachymatisma* to *Erylus*, yet it remains insufficiently known; (IV) originally reported as *Exsuperantia* sp.; (V) *Poecillastra schulzei* was described by Sollas (1886) from the Macdonald Islands, hence the presence of the species in the area seems unlikely; (VI) Originally recorded as *Sphinctrella annulata* (Schmidt, 1880) by Topsent (1928); (VII) Topsent (1928) attributed some broken fragments from Madeira to *Chonelasma* Schulze, 1886 with hesitation, yet it noted that the poor conservation state of the material hindered its description. Until further material arises, the record should be considered as dubious.

3. Results

3.1. Systematic description

A total of 89 sponge specimens were analysed, accounting for a total of 67 different species, 56 of which were identified at least to genus level; 34 are new records for Madeira archipelago, and one new species (Table 1; Supp. Mat. 1). Present records also contain several Mediterranean species that have not been previously recorded in the North Atlantic. Three out of the four existing Porifera classes (Calcarea, Demospongiae, Homoscleromorpha) were present within the samples collected (Figs. 3 and 4). Calcarea and Homoscleromorpha were represented by five and three species respectively, while the remaining samples corresponded to Demospongiae, with Poecilosclerida, Suberitida, Haplosclerida and Axinellida being the most diverse orders encountered (Table 1). Following is the description of some species deemed rare, faunistically relevant or new to science.

Class HOMOSCLEROMORPHA Bergquist, 1978

Order HOMOSCLEROPHORIDA Dendy, 1905

Family OSCARELLIDAE Lendenfeld, 1887

Genus *Oscarella* Vosmaer, 1884

3.1.1. *Oscarella balibaloi* Pérez, Ivanisevic, Dubois, Pedel, Thomas, Tokina & Ereskovsky, 2011

Material examined: Pictures taken (Fig. 4E), but no material was collected for the species.

Comparative material: unregistered *Oscarella* sp. (Fig. 4F) collected growing over an octocoral in Baixa da Cruz, Machico, Madeira Island (32°46′58.7″N 16°47′58.1″W), Madeira Archipelago, 30 m depth, May 16, 2022 [coll. Wirtz, P.]

Description. Soft and slimy encrusting sponge, loosely attached to the substratum and with an intense, uniform orange coloration. Its surface is covered by numerous small lobes, somewhat irregularly elongated, becoming smaller and more densely packed close to the conspicuous oscular tubes, which are slightly elevated and with wide openings (Fig. 4E).

Geographic distribution. The species was so far only known from the Mediterranean Sea, where occurs within cave and other sciaphilous environments (Pérez et al., 2011; Grenier et al., 2018), as it is common for most homoscleromorphs (van Soest et al., 2012a). This record for Madeira Island would be its first finding outside Mediterranean waters.

Remarks. Oscarella species (as well as most Homoscleromorpha) have been historically considered almost indistinguishable at species level due to lack of skeletal features. This resulted in single species within the genus, *O. lobularis*, being recorded from around the globe for almost 100 years, considered a cosmopolitan species with a high morphological polymorphism (Boury-Esnault et al., 1992; Muricy et al., 1996).

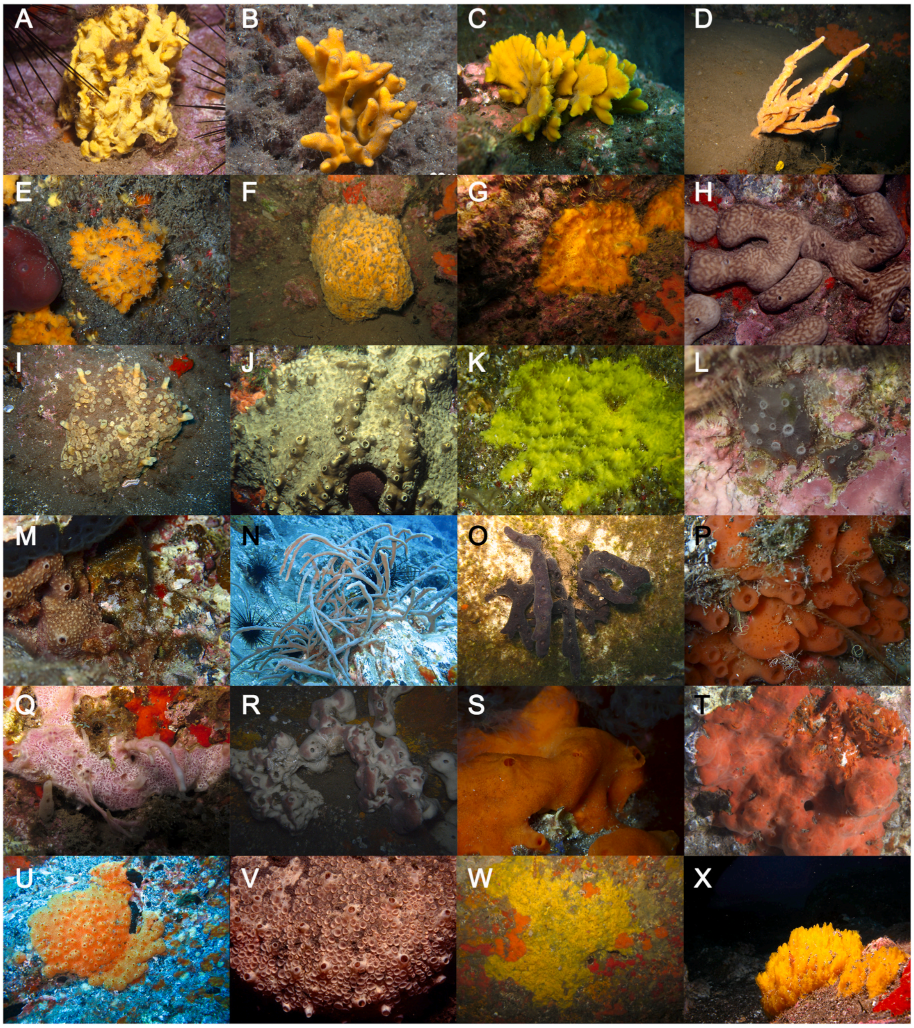

Fig. 3. Some of the common Demospongiae (excluding Tethyida and Verongiida) within the Madeiran archipelago shallow waters: A) *Axinella damicornis* (Esper, 1794); B) *Axinella verrucosa* (Esper, 1794); C) *Axinella dissimilis* (Bowerbank, 1866); D) *Axinella polypoides* Schmidt, 1862; E) *Acanthella acuta* Schmidt, 1862; F) *Dictyonella incisa* (Schmidt, 1880); G) *Dictyonella pelligera* (Schmidt, 1864); H) *Chondrosia reniformis* Nardo, 1847; I) *Cliona celata* Grant, 1826; J) *Cliona viridis* (Schmidt, 1862); K) *Aplysilla sulfurea* Schulze, 1878; L) *Fasciospongia cavernosa* (Schmidt, 1862) in association with the scyphozoid *Nausithoe* sp. (Cnidaria); M) *Ircinia* sp. N) *Callyspongia* (*Callyspongia*) *burtoni* van Soest & Hooper, 2020; O) *Chalinula nigra* Boury-Esnault and Lopes (1985); P) *Chalinula limbata* (Montagu, 1814); Q) *Haliclona* (*Halichoclona*) *fistulosa* (Bowerbank, 1866); R) *Petrosia* (*Petrosia*) *ficiformis* (Poiret, 1789); S) *Batzella inops* (Topsent, 1891) T) *Crambe crambe* (Schmidt, 1862); U) *Crella* (*Crella*) *elegans* (Schmidt, 1862); V) *Hemimycale columella* (Bowerbank, 1874); W) *Hymedesmia* (*Hymedesmia*) *senegalensis* Lévi (1956); X) *Axinyssa digitata* (Cabioch, 1968).

Nevertheless, the development of new technological advances as well as a holistic approach to the genus (e.g. combination of molecular and chemical markers, histology, cytology and ecology) demonstrated that, in fact, the genus was far more diverse than originally thought (Boury-Esnault et al., 2013), with 15 species having been described since the 1990s from around the globe (Muricy et al., 1996; Pérez et al., 2011; Gazave et al., 2013). From these, six have been described from Atlantic and Mediterranean waters, with the additional revival of *Oscarella tuberculata* (Schmidt, 1868) as a separate species from *O. lobularis* (Boury-Esnault et al., 1992). While coloration might vary within any given species, it is still considered the main external distinguishing feature for Atlantic *Oscarella*, alongside consistency and overall external appearance. In this sense, *O. balibaloi* Pérez et al. (2011) is close to *Oscarella imperialis* Muricy et al. (1996) and *Oscarella bergenensis* Gazave et al. (2013) in terms of coloration, while its external morphology might resemble that of *Oscarella microlobata* Muricy et al., 1996. Nevertheless, the combination of a homogenous orange coloration, soft consistency and densely lobated surface (Fig. 4E) is unique to the species (Pérez et al., 2011) and tells it apart from other Atlantic and Mediterranean *Oscarella* as well as from other unidentified *Oscarella* spp. occurring in Madeira (Fig. 4F and G). While, all considered, points towards the probable presence of *O. balibaloi* in Madeira, this record should nevertheless remain tentative until proper material can be collected and analysed by means of histological and molecular techniques.

Class DEMOSPONGIAE Sollas, 1885

Order AXINELLIDA Lévi, 1953

Family AXINELLIDAE Carter, 1875

Genus *Axinella* Schmidt, 1862

3.1.2. *Axinella guiteli* Topsent, 1896

Material examined. Axinella guiteli MMF50230 [332CR] collected on rocks in Pedra d'Eira, Caniçal, Madeira Island (32°42′47.7″N 16°44′05.0″W), Madeira Archipelago, 16 m depth, October 31, 2017 [coll. Ribeiro, C., & Neves, P.].

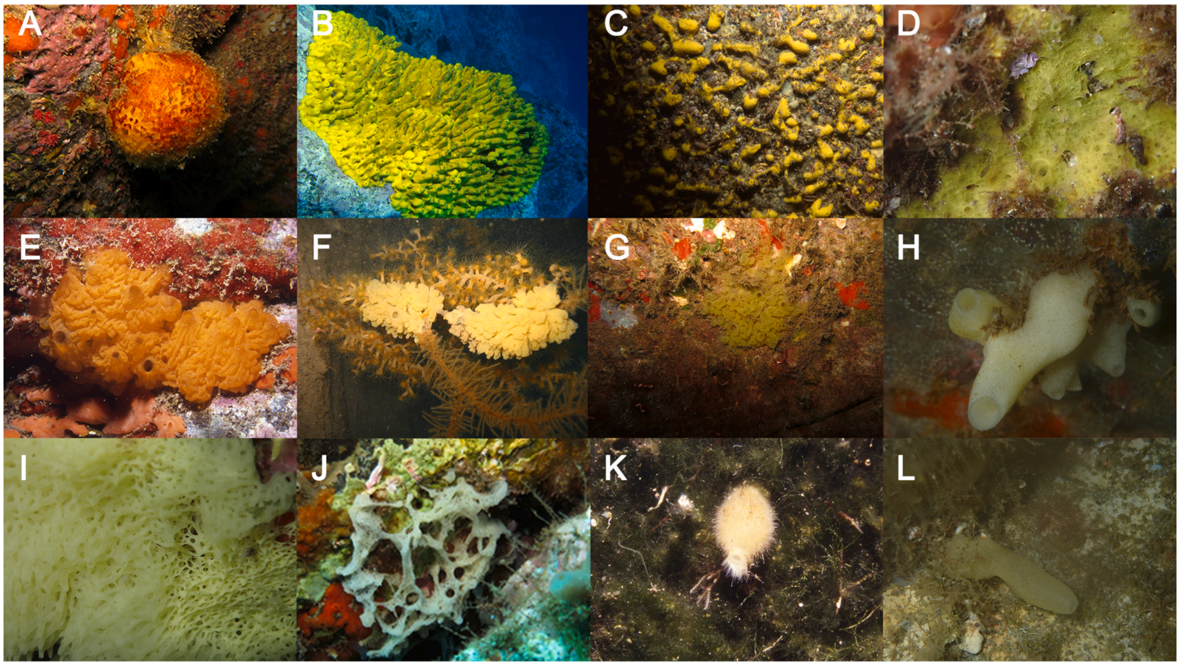

Fig. 4. Some of the common Demospongiae (Tethyida and Verongiida), Homoscleromorpha and Calcarea within the Madeiran archipelago shallow waters: A) *Tethya* sp. B) *Aplysina aerophoba* (Nardo, 1833); C) *Aplysina* cf. *aerophoba*, cave morphotype; D) *Hexadella* sp.; E) *Oscarella* cf. *balibaloi* Pérez et al. (2011); F) *Oscarella* sp. 1; G) *Oscarella* sp. 2; H) *Paraleucilla magna* Klautau, Monteiro & Borojevic, 2004; I) *Clathrina* sp. (Schmidt, 1864); J) *Borojevia* cf. *cerebrum* (Haeckel, 1872); K) *Sycon raphanus* Schmidt, 1862; L) *Ute glabra* Schmidt, 1864.

Comparative material examined. *Axinella damicornis* MMF50191 [333CR] collected on rocks in Pedra d'Eira, Caniçal, Madeira Island (32°42′47.7″N 16°44′05.0″W), Madeira Archipelago, 16 m depth, October 31, 2017 [coll. Ribeiro, C., & Neves, P.]; MMF50225 [06_2022] collected on rocks in Pedra d'Eira, Caniçal, Madeira Island (32°42′47.7″N 16°44′05.0″W), Madeira Archipelago, 15 m depth, March 06, 2022 [coll. Ribeiro, C., & Neves, P.]; MMF50199 [57_2022] collected on rocks in Baixa d'Abra, Baía d'Abra, Madeira Island (32°44′42.2″N 16°41′51.6″W), Madeira Archipelago, 20 m depth, June 14, 2022 [coll. Wirtz, P.]

Axinella verrucosa MMF50205 [56_2022] collected on rocks in Baixa d'Abra, Baía d'Abra, Madeira Island (32°44′42.2″N 16°41′51.6″W), Madeira Archipelago, 20 m depth, June 14, 2022 [coll. Wirtz, P.]

Description. The specimen is an erect with anastomosing ramose-foliose branches, being attached to the substrate by short peduncle. The branches are all located in the same plane and axially compressed, resulting in thin fan-shaped lamina (1–2 mm in width) pierced here and there, with an irregular lobate contour. Surface of the sponge is microhispid upon close examination. Colour in spirit is brown to ochre.

Skeleton. The peduncle is composed of ascending oxea and short styles. In the laminae, tracts become progressively loose, being organized in plumose fashion, being composed of both oxea and short styles, with longer styles commonly occurring in an echinating position.

Spicule complement. Two categories of styles and one category of oxea (Fig. 5).

Style I (Fig. 5A): Long, smooth styles, usually slightly bent on its entirety, more rarely straight. They become progressively thinner towards its tip, which is clearly acerate. Occasional subtilostyle modifications might occurs (Fig. 5F).

Size range: 665.5–*792.8* ± 101.9–1016.8 μm x 3.6–*5.6* ± 1.7–9.1 μm.

Style II (Fig. 5B): Short smooth styles, with an acerate tip (Fig. 5E). They possess the same width along the entirety of its shaft except for the tip, giving them and sturdier appearance than the style I category. They are bent once, the twist being located between the middle of the shaft and the style's head.

Size range: 192.6–*237.2* ± 49.4–356.2 μm x 4.1–*5.8* ± 1.2–7.5 μm.

Oxea (Fig. 5C): Commonly bent in a characteristic anisodimaetric fashion. With sharp ends (Fig. 5D), which might become slightly blunt with increasing thickness of the spicule.

Size range: 216.5–*299.7* ± 54.8–410 μm x 1.9–*4.9* ± 2–9.1 μm.

Geographic distribution. The species appears to be relatively common within Mediterranean sciaphilous environments, mostly caves (Vacelet, 1969; Pansini, 1984) and mesophotic communities of the continental shelf (Santín et al., 2018; Idan et al., 2021). Outside the Mediterranean the species had so far been recorded from the continental Portuguese coast, located in caves in the Algarve region (Boury-Esnault et al., 2001) and the Canary Islands (Cruz, 2002), this being the first record for Madeira.

Remarks. From all described east Atlantic *Axinella* species, the current material would be closer to either *Axinella guiteli* Topsent (1896) or *Axinella vaceleti* Pansini (1984). Both species were originally described from the Mediterranean Sea (Topsent, 1896; Pansini, 1984) and appear to be close in external appearance and spiculation, which has led to confusion over their identity (Pansini, 1984). While oxeas were not observed on *A. guiteli*'s original description, upon reexamination of its type material Topsent concluded it possessed true oxeas and strongyles, the later possibly resulting from style II modifications (Topsent, 1934). Posterior descriptions of the species noted a considerable variability on both external appearance (presence/absence of a penduncle, laminate to foliose appearance) and spicular complement (absence/presence of a secondary category of styles and/or strongyles) (Table 2), these differences being attributed to the possible aberrant morphology of *A. guiteli*'s holotype (Vacelet, 1969).

As so, *A. vaceleti* was later on erected to distinguish those individuals with both oxea and styles as main megascleres and possessing an external pedunculated-laminate morphology (Pansini, 1984),

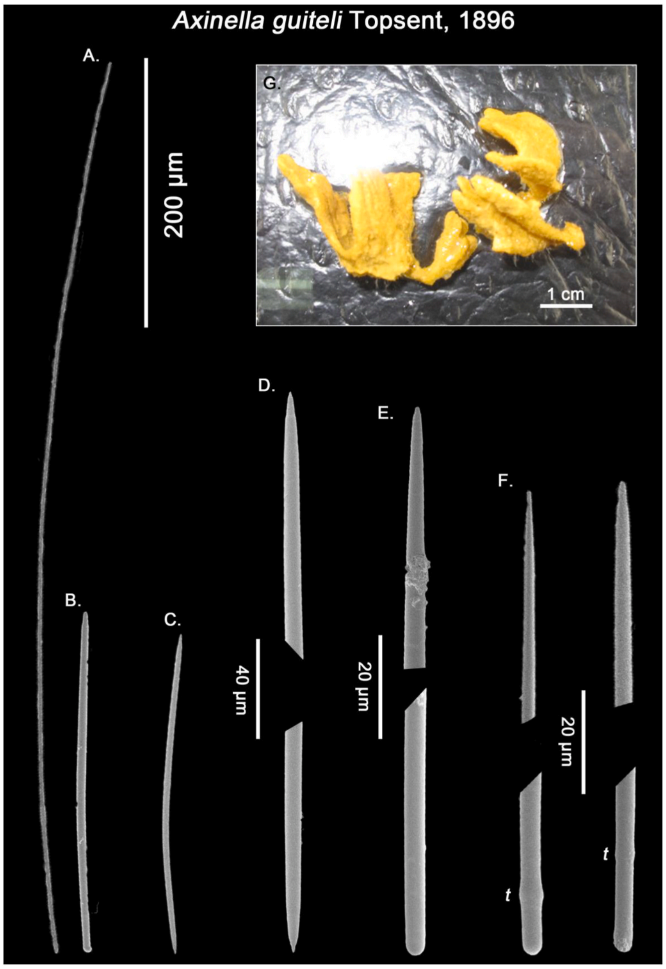

Fig. 5. SEM imaging of *Axinella guiteli* Topsent (1896) spicular set. A. Style I; B. Style II; C. Oxea; D. Close up of the head and tip of the oxea; E. Close up of the head and tip of the Style II; scale bar for A-C. 200 µm, scale bar for D. 40 µm and E-F. 20 µm.

reassigning all records of *A. guiteli* other than the original description (Vacelet, 1969; Boury-Esnault, 1971) to *A. vaceleti*. Yet, both species were still acknowledged to be close, being the peculiar external morphology of *A. guiteli* (without a peduncle, and with anastomosing foliose branches) the main distinguish characteristic between both species (Pansini, 1984). Since then, while most records of *A. vaceleti* refer to a laminate sponge (e.g. Pansini, 1984; Santín et al., 2018), others have described the species with foliose anastomosing branches (Idan et al., 2021) as in *A. guiteli*. In fact, the current examined material matches well with *A. guiteli* in external appearance (ramose-foliose), but its skeletal features conform with *A. vaceleti* both in terms of spiculation (styles, often modified to sybtylostyles and oxea) and dimensions (Table 2). In this sense, additional *A. guiteli* records from the Mediterranean coasts of Spain (Bibiloni and Uriz, 1979; Uriz, 1982) and the Canary Islands (Cruz, 2002) also mention a pedunculated ramose-foliose external morphology in combination with both oxeas and styles as main megascleres, further blurring the line between both species.

Both species are described as having characteristically thin laminae (1.5 mm in width) with conspicuous exhalant channels and a microhispid surface with fringed contours and irregular piercing, while additionally both possessing a bright orange coloration when *in vivo* (Topsent, 1896; Pansini, 1984). In this sense, laminae's width, contour and external coloration has been noted to be rather conservative in *Axinella* species, and are considered diagnostic at species level (Sitjà and Maldonado, 2014; Idan et al., 2021), leaving the anastomose-foliose vs. lamellate morphology as the only remaining external difference between both species. Yet, while some external characteristic might be rather conservative, axinellids are also known to display a considerable amount of external morphological plasticity (Alvarez and Hooper, 2009; Santín et al., 2019), with 'aberrant' morphologies being commonly described (Siribelli, 1961; Pansini, 1984). Similarly, axinellids are also quite variable in terms of spicule dimensions and composition, with oxea and style modifications being a common within *Axinella* species (Pansini, 1984; Ackers et al., 1992; Alvarez and Hooper, 2009). Thus, in view of accumulating evidence, and lacking clear diagnostic characteristic that can currently tell both species apart, it is here proposed to follow a more conservative approach and, until a proper in-depth review of the genus can be performed, to place both species into synonymy under *A. guiteli* Topsent, 1896, with *A. vaceleti* Pansini (1984) as its junior synonym (ICZN Principle of Priority).

Order BUBARIDA Morrow and Cárdenas, 2015

Family DICTYONELLIDAE van Soest, Díaz & Pomponi, 1990

Genus *Dictyonella* Schmidt, 1868

3.1.3. *Dictyonella incisa* (Schmidt, 1880)

Material examined. MMF50250 [#02] collected on rocks in Seixal, Madeira Island (32°49′35.2″N 17°06′27.1″W), Madeira Archipelago, 16 m depth, August 28, 2017 [coll. Ribeiro, C., & Neves, P.]; MMF50179 [#21] collected on rocks covered with sand in Paúl do Mar, Madeira Island (32°45′30.8″N 17°13′55.0″W), Madeira Archipelago, 19 m depth, August 25, 2017 [coll. Ribeiro, C., & Neves, P.]; MMF50245 [#091] collected on rocks in Baixa do Cotrim, Porto Santo Island (33°04′32.0″N 16°17′13.9″W), Madeira Archipelago, 14 m depth, June 26, 2017 [coll. Ribeiro, C., & Neves, P.].

Description. Encrusting massive to massive oval sponge with a smooth, densely conulose surface. *In vivo* the sponge shows a characteristic bright egg-yolk coloration (Figs. 3F and 6B-D) which is lost after preservation in spirit, becoming dull orange. Ostia are not visible, while oscules are scarce and located at the surface of the sponge, between the conules (Figs. 3F and 6B-D). Ectosome firmly attached to the choanosome, which comes off as flakes when peeled, as characteristic for the genus.

Skeleton. Paucispiculate ascending tracts of megascleres reinforced with spongin which divide an anastomose without any clear pattern, ending at the surface of the sponge with little to no hispidation. Ectosome without spicules.

Spicule complement. Styles (Fig. 6A): Almost straight to flexuous styles, most of them just being slightly bent on its entirety, with characteristic long tapering acerate tips and rounded heads, sometimes with a slight subterminal constriction. Modifications include typical acerate ends to blunt terminations, the later giving them the appearance of strongyles, which may be relatively abundant in certain individuals.

Size range: 626–*1005.3* ± 266.7–1569 µm x 3.5–*9.6* ± 2.9–15.3 µm.

Geographic distribution. A common species within the Mediterranean basin, it has mostly been signalled from shallow to circalittoral bottoms, usually in association with shady hard substrates. Its known presence in the Atlantic is more restricted, having only been found prior in the Portuguese coast (Naveiro-Millán, 2002), and the Canary and Cape Verde islands (van Soest, 1993; Cruz, 2002). In Madeira, it appears to be relatively abundant, though it was not noticed until the present study. Thus, the species appears to be more common in the Lusitanian region than previously reported.

Table 2
Known descriptions of *Axinella guiteli* and *Axinella vaceleti*, including the locality (Loc.) and depth of the sample, external morphology (Morph.), colour when alive (Col.), as well as the measurement of their spicular complement. * indicates the holotype's description. ***Nr***: not recorded. (**St**): strongyles.

Species	Loc./Depth	Morph./Col.	Style I	Style II	Oxea
Axinella guiteli	Cap l'Abeille[a]*/ 25–40 m	Ramose-foliose/Orange	800–1000 µm × 11 µm	200–300 µm x 3–10 µm	-
	Re-examination of the former[b]	Ramose-foliose/Orange	800–1300 µm × 11 µm (**St**) 415–550 µm x 20–22 µm	250–300 µm x 3–10 µm (**St**) Same size range	95–155 µm x 6–7 µm
	Cassidaigne Canyon[c]/ 130 m	Laminate-pedunculated/ ***nr***	400–1050 µm x 7.5–12 µm (**St**) 415–550 µm x 20–22 µm	250–350 µm x 6–10 µm (**St**) Same size range	250–350 µm x 6–10 µm
	Catalan coast[d]/ 40–100 m	Laminate-pedunculated/ Orange	1500–1900 µm × 10 µm (St) 415–550 µm x 20–22 µm	–	470–600 µm x 10–12 µm
	Canary Islands[e]/ Circalittoral	Ramose-foliose-pedunculated/Yellow	500–1500 µm x 4–7 µm	200–400 µm x 3–6 µm	200–400 µm x 3–6 µm
	Madeira[f]/16 m	Ramose-foliose-pedunculated/Orange	665.5–*792.8* ± 101.9–1016.8 µm x 3.6–*5.6* ± 1.7–9.1 µm	192.6–*237.2* ± 49.4–356.2 µm x 4.1–*5.8* ± 1.2–7.5 µm	216.5–*299.7* ± 54.8–410 µm x 1.9–*4.9* ± 2–9.1 µm
Axinella vaceleti	Iîle Plane[3]/45 m	Laminate-pedunculated/ Orange	850–1300 µm x 5–12 µm	130–270 µm x 11–12.5 µm (**St**) Same size range	230–400 µm x 5–8 µm
	Ligurian Sea[g]*/5–30 m	Laminate-pedunculated/ Orange	270–1450 µm x 2.5–14 µm	–	250–370 µm x 2–12 µm
	Balearic archipelago[h]/***nr***	Ramose-foliose-pedunculated/Orange	840–1400 µm x 10–12 µm	Present (**St**) Present	370–600 µm x 12–16 µm

[a] Topsent (1896).
[b] Topsent (1934).
[c] Vacelet (1969) [*A. vaceleti* is reported as an undescribed *Axinella* alongside *A. guiteli*'s description].
[d] Uriz (1982).
[e] Cruz (2002).
[f] *Present study*.
[g] Pansini (1984).
[h] Bibiloni (1990).

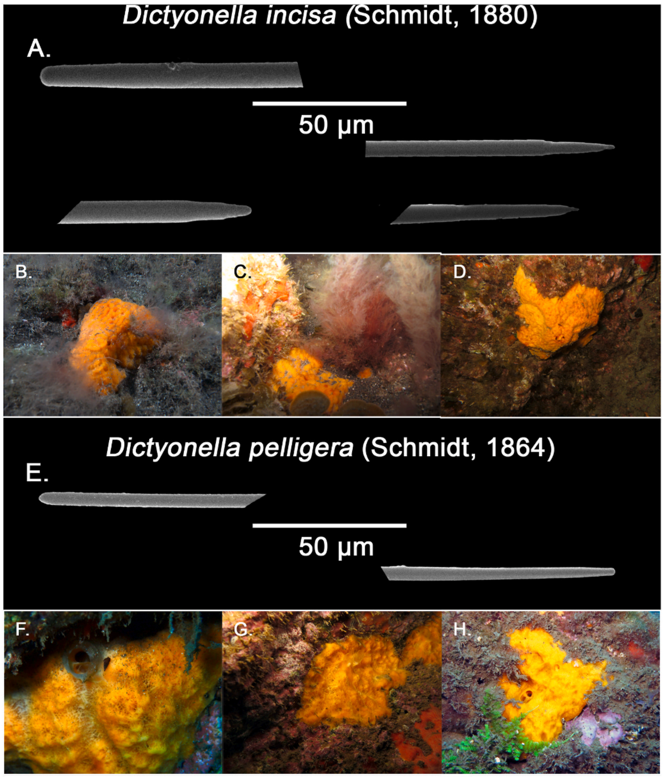

Fig. 6. SEM and *in situ* imaging of *Dictyonella incisa* and *Dictyonella pelligera* spicular set. A. Head and tips of the styles of *D. incisa*. B-D, *in situ* images of #02, #21 and 60_2022 respectively. E. Head and tips of the styles of *D pelligera.* F–H, *in situ* images of 05_2022, 30_2022, 38_2022 respectively. Scale bar for A and E, 25 µm.

Remarks. See remarks for *Dictyonella pelligera* (Schmidt, 1864).

Dictyonella pelligera (Schmidt, 1864)

Material examined. MMF50228 [#05_2022] collected on rocks in Pedra d'Eira, Caniçal, Madeira Island (32°42′47.7″N 16°44′05.0″W), Madeira Archipelago, 18 m depth, March 06, 2022 [coll. Ribeiro, C., & Neves, P.]; MMF50194 [30_2022] collected on a cave wall in Ponta de São Lourenço, Madeira Island (32°44′27.8″N 16°42′00.8″W), Madeira Archipelago, 1 m depth, May 03, 2022 [coll. Wirtz, P.]; MMF50215 [38_2022] collected on rocks in Machico Bay, Madeira Island (32°42′50.4″N 16°45′48.4″W), Madeira Archipelago, 12 m depth, May 20, 2022 [coll. Wirtz, P.].

Description. Encrusting sponge firmly attached to the substrate, with a conulose surface. *In vivo* the sponge shows a variable bright egg-yolk colour, varying in shades in some areas of the sponge (Figs. 3G and 6F–H). Ectosome is translucid and firmly attached to the choanosome, which in some areas shows multiple grooves and choanosomal spaces. Usually with one or two oscules, rarely more, which are located atop of translucid ectosomal papillae (Fig. 6F–H).

Skeleton. As in other *Dictyonella*, it is composed of loose paucispiculate ascending tracts of megascleres reinforced with spongin, ending at the surface of the sponge. Ectosome without spicules.

Spicule complement. Styles (Fig. 6E): Straight styles with rounded tips, giving them the appearance of anisostrongyles: sometimes they are not modified, still possessing a more or less acerate end.

Size range: 491.4–*563.8* ± 65.1–681.2 µm x 2.7–*4.6* ± 1.1–6.2 µm.

Geographic distribution. Similarly to *D. incisa*, the species has mostly been reported from the Mediterranean basin, with a single record from the Atlantic coming from the Celtic Seas, at the French coast (Cabioch, 1968), being this its first report to Madeira archipelago and from the Lusitanian region.

Remarks. The genus *Dictyonella* is rather small, with 12 species recorded from temperate seas across the world, six of which occur in the eastern Atlantic Ocean and Mediterranean Seas (van Soest et al., 2002; de Voogd et al., 2024). Externally, most of these species might appear similar (Sarà and Siribelli, 1960; Carballo et al., 1996), having an orange coloration and an encrusting-massive morphology (Table 4). Additionally, the sole possession of styles (with a wide variability in length in most species) as main megascleres, which in combination might hamper species determination (Carballo et al., 1996). From these, *Dictyonella obtusa* (Schmidt, 1862), *Dictyonella incisa* (Schmidt, 1880) and *Dictyonella marsilli* (Topsent, 1893) all have a similar external appearance, but while *D. marsilli* and *D. obtusa* display considerable amount of variation in their style's length (Sarà and Siribelli, 1960)*, D. incisa* styles are constant between 800 and 1300 μm and possess tapering tips, the combination of both characters considered species specific (Pulitzer-Finali, 1983). *Dictyonella pelligera* on the other hand is the least known of all Mediterranean *Dictyonella* species (Sarà and Siribelli, 1960) and, while it is characterized by a more encrusting nature, it could still be externally confused with the aforementioned species. Nevertheless, its styles are considerably shorter than in most other species (Table 4) and usually end in rounded tips, with only *Dictyonella alonsoi* Carballo, Uriz and García-Gómez, 1996 possessing styles in the same size range (Carballo et al., 1996). Yet, given their contrasting morphologies, with *D. alonsoi* possessing a pear like to digitiform morphology and yellow coloration (Carballo et al., 1996; Santín et al., 2019), confusion between both is unlikely.

Order HAPLOSCLERIDA Topsent, 1928

Family CHALINIDAE Gray, 1867

Genus *Chalinula* Schmidt, 1868

3.1.5. *Chalinula nigra* Boury-Esnault and Lopes (1985)

Material examined. MMF50118 [#23] collected on rocks in Reis Magos, Madeira Island (32°38′49.3″N 16°49′26.9″W), Madeira Archipelago, 12 m depth, June 10, 2017 [coll. Ribeiro, C., & Neves, P.]; MMF50217 [03_2022] collected on rocks in Pedra d'Eira, Caniçal, Madeira Island (32°42′47.7″N 16°44′05.0″W), Madeira Archipelago, 17 m depth, March 06, 2022 [coll. Ribeiro, C., & Neves, P.], MMF50195 [22_2022] collected on rhodolith in Ponta de São Lourenço, Madeira Island, Madeira Archipelago, 20 m depth, May 02, 2022 [coll. Ribeiro, C., & Neves, P.], MMF50239 [42_2022] collected on rocks in Cais do Carvão, Funchal, Madeira Island (32°38′08.9″N 16°56′10.9″W), Madeira Archipelago, 8 m depth, March 06, 2022 [coll. Ribeiro, C., & Neves, P.].

Description. With slender oxeas with acerate ends, in a 90–135 × 1.4–3.5 μm size range (96.2–*124.5* ± 11–134.6 + 1.4–2.1 ± 0.6–3.4 μm, MMF50118; 94.2–*116.9* ± 9.5–131.3 + 1.6–*2.3* ± 0.8–3.3 μm, MMF50217; 90.8–*112.7* ± 10.7–131.2 + 1.6–*2* ± 0.6–3.6 μm, MMF50195; 96.2–*108.3* ± 12.3–129.5 + 1.5–*2.3* ± 0.5–3.4 μm, MMF50239); arranged in dense tracts embed in spongin fibres, which are disposed in a ladder like fashion. Ultimately, the species most characteristic feature is its external appearance, it being that of an erect branching sponge with a dark coloration (Fig. 3O), with clearly visible oscula located across the branches, usually on its upper face.

Geographic distribution. The species was originally described from the Azores (Boury-Esnault and Lopes, 1985) later being also reported from the Atlantic side of the strait of Gibraltar (Carballo and Garcia-Gómez, 1994). Nevertheless, in recent years the sponge has been expanding through the Alboran Sea both in the Moroccan (Santín et al., 2021a) and the Andalusian coasts (Sánchez-Tocino *pers. comm.*). Despite it being certainly conspicuous, the species had not been previously reported from Madeira.

Remarks. All the analysed specimens match well both the original (Boury-Esnault and Lopes, 1985) and posterior re-description (Santín et al., 2021a) of the species. A strikingly similar species in external appearance to *C. nigra*, *Chalinula parasimulans* (Lévi, 1959), was presumably also recorded in the Madeira from a marina (Canning-Clode et al., 2013a), yet none of the material collected during this study could be referred to the later. A rather ill-known species, *C. parasimulans* is only known from the Senegalese coasts and the Canary Islands. Yet, specimens from the later (Cruz, 2002) differ greatly from both *C. parasimulans* original description (Lévi, 1959) as well as the current material, with the status and relationships regarding *C. parasimulans* and *C. nigra* being in need of further research (Santín et al., 2021a). Interestingly, an unidentified shrimps of the genus *Periclimenaeus* Borradaile, 1915 has been recorded associated with *C. nigra* at Madeira Island (Wirtz, 2020).

Order POECILOSCLERIDA Topsent, 1928

Family HYMEDESMIIDAE Topsent, 1928

Genus *Hemimycale* Burton, 1934

3.1.6. *Hemimycale funchalensis Santín & Ribeiro sp. nov*

LSID urn:lsid:zoobank.org:pub:36,965,911-35CF-4EC6-8A1E-BA652F315BE4.

Holotype: MMF50218 [14_2022] collected on a rhodolith in Pedra d'Eira, Caniçal, Madeira Island (32°42′47.7″N 16°44′05.0″W), Madeira Archipelago, 20 m depth, April 13, 2022 [coll. Ribeiro, C., & Neves, P.].

Paratype: MMF50234 [59_2022] collected on rocks in Porto Novo, Madeira Island (32°39′31.2″N 16°48′29.1″W), Madeira Archipelago, 15 m depth, June 18, 2022 [coll. Wirtz, P.].

Description. Thinly encrusting sponge growing attached to rocky substrates, surface smooth with a few, slightly elevated oscules, around which the aquiferous channels are more clearly visible. Pore sieves are conspicuous, barely elevated and with a well-defined rim. When *in vivo*, the sponge exhibits a characteristic dark green coloration that is lost after preservation in spirit, turning grey (Fig. 7C–H).

Skeleton. Paucispiculated plumose tracts of tylotes perpendicular to the

Table 3

Known records of *Hymedesmia* (*Hymedesmia*) *senegalensis*, including the locality (Loc.) and depth of the sample, as well as the measurement of their spicular complement. * indicates the holotype's description. ***Nr***: not recorded.

Author	Loc./Depth	Tornotes	Acanthostyles	Chelae	Sigmas
Lévi (1956)*	Senegalese coast/ ***nr***	130 μm x 3–4 μm	75–210 μm × 10 μm	**(I)** 15 μm **(II)** 8 μm	26–28 μm
Carballo (1994)	Gibraltar Strait/ 3–12 m	128–*148* ± 8.8–161 μm	**(I)** 190–*219* – 252 μm **(II)** 73–*89* – 99 μm	**(I)** 19–*21* – 25 μm **(II)** 10–*10* – 12 μm	20–*32* – 37 μm
Present study	Madeira/17 m	131.1–*146.5* ± 8.8–161.8 μm x 1.4–*2.2* ± 2.9–0.4 μm	**(I)** 142.8–*176.2* ± 14.8–198 μm x 5.1–*7.1* ± 1.3–9.5 μm **(II)** 70.4–*82.7* ± 6.6–88 μm x 2–*5* ± 1.9–7.6 μm	**(I)** 16.7–*21.4* ± 2.9–25 μm **(II)** 8–*10.1* ± 1.2–12.45 μm	**(I)** 29.3–*34.3* ± 3.4–40.3 μm **(II)** 9.5–*21.1* ± 5–28.4 μm

Table 4
Comparison between East Atlantic *Dictyonella* species, including the locality (Loc.) and depth of the sample, coloration (Col.) and external morphology (Mor.) as well as the measurement of their spicular complement. * indicates the holotype's description. ***Nr***: not recorded; (S): Styles; (O): Oxeas; (St): strongyles.

Species	Loc./Depth	Col./Mor.	Megascleres
Dictyonella incisa	Canary Islands[a]/ Littoral to 50 m	Orange/ Massive-oval	**(S)** 600–1200 µm x 3–12 µm
	Naples[b]/***nr***	Orange/ Massive	**(S)** (1000) 1200–1400 (2000) µm x (5) 12–15 (20) µm
	Gibraltar Strait[c]/ Infralittoral	Orange/ Encrusting-massive	**(S)** 962–1265 µm x 9–12 µm
	Italian waters[d]/ 2–35 m	Orange/ Massive-oval	**(S)** 800–1350 µm x 8–17 µm
	Madeira[e]/16 m	Orange/ Massive oval	**(S)** 756–*882* ± 105.3–1079.3 µm x 2.1–*9* ± 1.3–12.8 µm
	Madeira[e]/17 m	Orange/ Massive oval	**(S)** 626–*1005.3* ± 266.7–1569 µm x 3.5–*9.6* ± 2.9–15.3 µm **(St)** In the same size range
Dictyonella madeirensis	Canary Islands[a]/ Circalittoral	Yellow/ Arborescent	**(S)** 500–1040 µm **(O)** 624–1100 µm
	Gibraltar Strait[c]/ 15 m	Yellow/Massive arborescent	**(S)** 390–735 µm x 5–35 µm **(St)** 390–735 µm x 5–35 µm
Dictyonella alonsoi	Gibraltar Strait[c]*/4–14 m	Dull yellow/ Erect-conulose	**(S)** 590–880 µm x 9–20 µm
Dictyonella marsillii	Naples[b]/***nr***	***nr***/Massive	**(S)** 1500–2130 µm × 12 µm
	Banyuls[b]/***nr***	***nr***/Massive	**(S)** 1400–1890 µm × 12 µm
	Cap-d'Ail[d]/50 m	***nr***/Erect	**(S)** 750–1200 µm x 6–11.5 µm
	Naples[f]/10–100 m	Brown yellowish/ Encrusting	**(S)** 900–1140 µm x 7–10.5 µm
			(S) 680–1275 µm x 7–10.5 µm
Dictyonella obtusa	Banyuls[b]/***nr***	Salmon/Erect-foliose	**(S)** 1600–2200 µm x 17–23 µm
	La Calle[b]/***nr***	Salmon/Erect-foliose	**(S)** 1545–2050 µm x 23–25 µm
	Gibraltar Strait[c]/ 20 m	Brown-orangish/ Massive	**(S)** 1845–2336 µm x 10–30 µm
	Off Calvi[d]/ 117–160 m	Salmon/Erect-foliose	**(S)** 1500–2600 µm x 15–29 µm
Dictyonella pelligera	Adriatic[b]/***nr***	***nr***/Encrusting	**(S)** 580–665 µm × 13 µm
	Roscoff[g]/75 m	***nr***	**(S)** 440–630 µm x 3–10 µm
	Croatia[d]/47 m	***nr***/Encrusting	**(S)** 490–690 µm × 13 µm
	Naples[f]/1–10 m	Yellowish/ Encrusting	**(S)** 544–763 µm × 7 µm
	Naples[f]/1–10 m	Yellowish/ Encrusting	**(S)** 610–680 µm x 7–10.5 µm
	Naples[f]/1–10 m	Yellowish/ Encrusting	**(S)** 332–765 µm x 3.3–7 µm
	Naples[f]/1–10 m	Yellowish/ Encrusting	**(S)** 385–867 µm x 3.5–10.5 µm
	Naples[f]/1–10 m	Yellowish/ Encrusting	**(S)** 544–789 µm x 3.5–10.5 µm
	Naples[f]/1–10 m	Yellowish/ Encrusting	**(S)** 476–714 µm x 3.5–7 µm
	Naples[f]/1–10 m	Yellowish/ Encrusting	**(S)** 510–816 µm x 3.5–7 µm
	Naples[f]/1–10 m	Yellowish/ Encrusting	**(S)** 425–687 µm x 3.5–7 µm
	Naples[f]/1–10 m	Yellowish/ Encrusting	**(S)** 374–799 µm x 3.5–7 µm
	Naples[f]/1–10 m	Yellowish/ Encrusting	**(S)** 510–816 µm x 3.5–7 µm
	Madeira[e]/18 m	Orange yellowish/ Encrusting	**(S)** 491.4–*563.8* ± 65.1–681.2 µm x 3.1–*5.8* ± 0.9–6.8 µm µm
	Madeira[e]/18 m	Orange yellowish/ Encrusting	**(S)** 401.4–*503.9* ± 79.6–756.5 µm x 2.7–*4.6* ± 1.1–6.2 µm
	Madeira[e]/12 m	Orange yellowish/ Encrusting	**(S)** 510–816 µm x 3.5–*5.5* ± 1.7–7 µm

[a] Cruz (2002).
[b] Topsent (1925).
[c] Carballo (1994) for *D. incisa* and *D. obtusa* and Carballo et al. (1996) for *D. alonsoi* and *D. madeirensis*.
[d] Pulitzer-Finali (1983).
[e] *Present study*.
[f] Sarà and Siribelli (1960).
[g] Cabioch (1968).

sponge surface in the choanosome, whereas the ectostome is made of a tangential mat of spicules. Spicule density in the ectosome is usually low and varies between individuals, increasing in density only close to the pore sieves rims.

Spicule complement. Strongylotylote (Fig. 7A): Mostly straight to slightly flexuous, with unequally and slightly inflated terminal ends. The tips' end in a usually long, thin tyle, with just a slight contraction on its base (Fig. 7B). Modifications are not frequent but present, including shorter tyles to true strongyles and very rarely, acerate tips.

Size range: 171.5–*192.9* ± 11–210.6 µm x 1.1–*1.7* ± 0.5–2.5 µm.

Geographic distribution. So far, the species has only been recorded in Madeira, where it is frequent on shallow, moderately sciaphilous hard substrates, especially rhodolith beds and coralligenous concretions

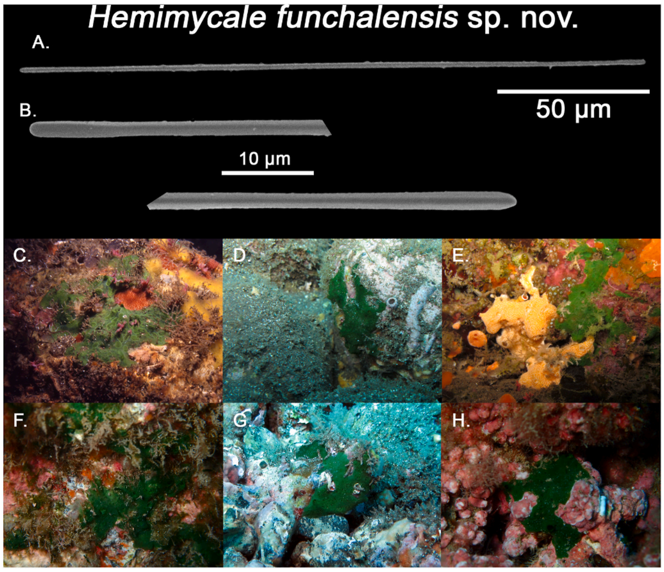

Fig. 7. SEM and *in situ* imaging of *Hemimycale funchalensis* sp. nov. spicular set. A. Strongylotylote; B. Close up of the tyles; scale bar for A 50 µm and scale bar for B. 10 µm; C–H. *In situ* images of several individuals, including the holotype (H) and paratype (G).

(Fig. 7C–H).

Etymology. The species is named *funchalensis* (from the word 'funcho', fennel in Portuguese, which is the root word to Madeira's capital, Funchal) in recognition of the work done by the Museu de História Natural do Funchal during this past century in order to map, catalogue and preserve Madeira's biodiversity.

Remarks. Externally, most Hymedesmiidae and Crellidae genera might strikingly resemble one another due to their encrusting nature and the presence of conspicuous pore sieves (van Soest, 2002b). Nevertheless, while similar in appearance, all genera possess clear cut differences in spiculation and skeletal organization, with *Hemimycale* being the only one to possess exclusively smooth diactinal megascleres without chelae (Uriz et al., 2017a, 2017b) which are presumed to have been secondary lost (Huguenin et al., 2018). In this sense, *Hemimycale funchalensis* sp. nov could be externally confused with *Hymedesmia* (*Hymedesmia*) *paupertas* (Bowerbank, 1866), yet said species almost always has blue tonalities (Ackers et al., 1992) and never attains such an intense green coloration as in *Hemimycale funchalensis* sp. nov. (Fig. 7C–H), which is a rare colour for marine Porifera overall.

Considered a monotypic genus for decades (van Soest, 2002b), in recent years several new species have been discovered or moved to the genus, for a total of 10 recognized *Hemimycale* species nowadays (Ilan et al., 2004; Moraes, 2011; Uriz et al., 2017a, 2017b; Huguenin et al., 2018; Sim-Smith et al., 2021). From these, *Hemimycale funchalensis* sp. nov. clearly differs from all other species in its bright, dark green coloration, which is unusual within Hymedesmiidae, as well as its spicular complement, as no other species possesses long tylote modifications as main megascleres, which additionally are relatively small when compared with most species of the genus (Uriz et al., 2017a, 2017b; Huguenin et al., 2018; Sim-Smith et al., 2021).

Genus *Hymedesmia* Gray, 1858

3.1.7. *Hymedesmia (Hymedesmia) senegalensis* Lévi (1956)

Material examined: MMF50180 [#08] collected on a cave wall in Ponta do Clérigo, Madeira Island (32°48′27.2″N 16°51′13.9″W), Madeira Archipelago, 17 m depth, August 30, 2017 [Ribeiro, C., & Neves, P.].

Description. Tightly encrusting yellow sponge, slightly hispid, growing attached to rocky substrates. It possesses a translucid ectosome with patent subectosomal channels, yet with no visible oscules (Fig. 3W).

Skeleton. In a hymedesmoid fashion i.e. with acanthostyles erect on the substrate, with their heads embedded in a basal layer of spongin. Ectosomal tornotes might in some instances form spicule tracks that penetrate into the choanosome. Microscleres abundant, and scattered in both the ectosome and choanosome, albeit they occur in higher abundance alongside the acanthostyle's heads.

Spicule complement. Tornotes, two categories of acanthostyles, two categories of chelae and two categories of sigma (Fig. 8).

Tornotes (Fig. 8A): Straight, with unequally inflated terminal ends, their appearance range from that of tornotes (abruptly pointed ends) to tornotylotes (with mucronated ends; Fig. 8D).

Size range: 131.1–*146.5* ± 8.8–161.8 μm x 1.4–*2.2* ± 2.9–0.4 μm.

Acanthostyle I (Fig. 8B): Straight to slightly bent, with a subtle head, almost the same with as the shaft, which narrows towards an acerate tip. Spination is hook-like in appearance, with sharp to blunt ends, the latter more common towards the head and the former towards the tip (Fig. 8E–F). The spination looks downwards along the shaft, and upwards close to and along the head (Fig. 8E–F). They are not dense, yet are equally distributed along the shaft, from the tip to the head.

Size range: 142.8–*176.2* ± 14.8–198 μm x 5.1–*7.1* ± 1.3–9.5 μm.

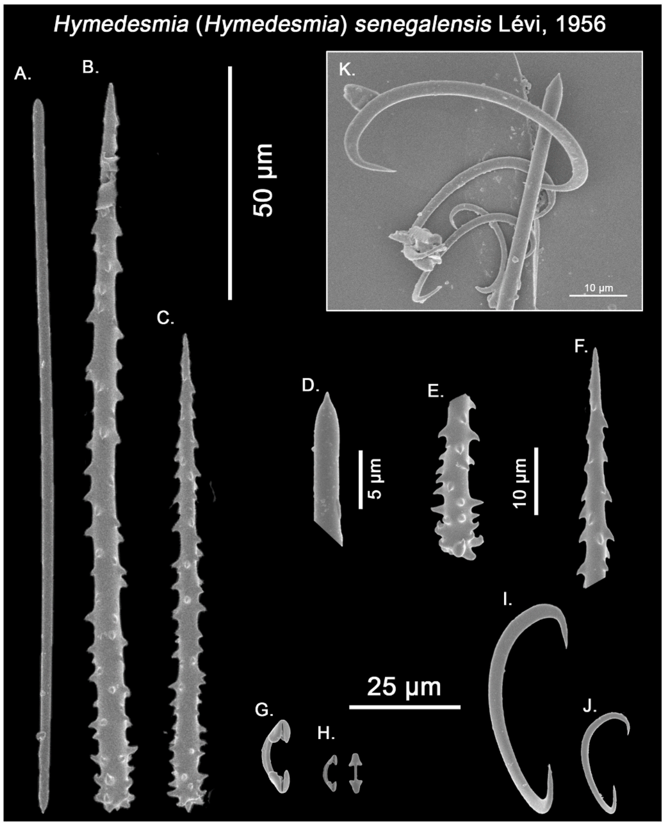

Fig. 8. SEM imaging of *Hymedesmia* (*Hymedesmia*) *senegalensis* spicular set. A. Tornote; B. Acanthostyle I C. Acanthostyle II; D. Close up of the tip of the tornotes; E. Close up of the head of the acanthostyles I; F. Close up of the tip of the acanthostyles II.; G. Chelae I; H. Chelae II, lateral and frontal view; Scale bar for A-C, 25 μm, scale bar for D, 5 μm, scale bar for E-F, 10 μm and scale bar for G-H, 25 μm (scaled in regards to as for A-C).

Acanthostyle II (Fig. 8C): Similar to acanthostyles I category, but smaller in size. They appear slightly more spinose, again with spines equally along the shaft.

Size range: 70.4–*82.7* ± 6.6–88 μm x 2–*5* ± 1.9–7.6 μm.

Isochelae I (Fig. 8G): Robust, with an arcuate shaft and three alae with smooth, rounded terminations, presenting a prominent fusion between the lateral alae and the shaft.

Size range: 16.7–*21.4* ± 2.9–25 μm.

Isochelae II (Fig. 8H): The smallest of the chelae categories, its alae are sometimes partially fused at their base.

Size range: 8–*10.1* ± 1.2–12.45 μm.

Sigma I (Fig. 8I): Both C and S shaped, with C-shaped ones being the most common and usually showing unequal ends, one more gently curved and the other more abruptly straight ending. Very abundant.

Size range: 29.3–*34.3* ± 3.4–40.3 μm.

Sigma II (Fig. 8J): The smallest of the sigma categories, both C and S shaped. Very abundant. Differences in morphology between both sigma categories are minimal and could be in fact considered a single one, but due prevalence of two clear size categories (ca. 30 μm and ca. 20 μm) amongst them, they have been treated as two (Fig. 8K).

Size range: 9.5–*21.1* ± 5–28.4 μm.

Geographic distribution. An uncommon species, it appears to be restricted to the north-western coasts of Africa and nearby areas in the Lusitanian region, having only been recorded from Senegal (Lévi, 1956) and Gibraltar (Carballo and García-Gómez, 1994) prior to this study. So far, it has only been recorded from shallow sciaphilous hard substrates.

Remarks. *Hymedesmia* might be amongst the most diverse genera within the order Poecilosclerida, if not Porifera as a whole (Goodwin and Picton, 2009; Goodwin et al., 2011) and, while its skeletal ("hymedesmiid skeleton") and spicular composition (ectosomal tornotes, acanthostyles as choanosomal megascleres, chelae) appears to be relatively stable, just about 30 species of *Hymedesmia* are known to have sigmas, from which just only 5 possess two categories of chelae (Cárdenas and Thollesson, 2016). From these, *Hymedesmia* (*Hymedesmia*) *velata* Topsent (1928), *Hymedesmia* (*Hymedesmia*) *mucronata* (Topsent, 1904), *Hymedesmia* (*Hymedesmia*) *lindstroemae* Cárdenas and Thollesson (2016) all possess megascleres and microscleres that far exceed in length those of the current material, whereas as for *Hymedesmia* (*Hymedesmia*) *zetlandica* Bowerbank (1864), it has a unique, reduced chelae type (van Soest, 2002b) not seen in the current specimen. On the contrary, the current material appears to be identical with *Hymedesmia (Hymedesmia) senegalensis* Lévi (1956), an ill known species described from the coasts of Senegal (Lévi, 1956), which is mostly told apart from other *Hymedesmia* species by the possession of mucronated tornotes in combination with two categories of fully spinnated acanthostyles, two chelae categories and sigmas (Carballo and García-Gómez, 1994). The only distinction between the current material with prior descriptions of the species would be the presence of two sigma categories against a single one (Table 3), yet the overall shape and size range of the sigmas remains almost the same with previous descriptions, and it wouldn't justify considering the current material as a separate species.

Family MYCALIDAE Lundbeck, 1905

Genus *Mycale* Gray, 1867

3.1.8. *Mycale (Carmia) senegalensis* Lévi (1952)

Material examined. Material examined: MMF50192 [#96] collected on a wreck (Madeirense), Porto Santo Island (33°03′22.9″N 16°18′50.1″W), Madeira Archipelago, 20 m depth, July 02, 2017 [coll. Ribeiro, C., & Neves, P.]; MMF50232 [11_2022] collected on a wreck (CORDECA) in Porto Santo Island (33°02′49.9″N 16°19′07.8″W), Madeira Archipelago, 22 m depth, April 02, 2022 [coll. Ribeiro, C., & Neves, P.]; MMF50204 [48_2022] collected on rocks in Cais do Carvão, Funchal, Madeira Island (32°38′08.9″N 16°56′10.9″W), Madeira Archipelago, 8 m depth, June 11, 2022 [coll. Ribeiro, C., & Neves, P.]; MMF50213 [49_2022] collected on rocks in Cais do Carvão, Funchal, Madeira Island (32°38′08.9″N 16°56′10.9″W), Madeira Archipelago, 10 m depth, June 11, 2022 [coll. Ribeiro, C., & Neves, P.].

Description. Encrusting sponge with a thin, translucid ectosome and a characteristic bluish to purplish, choanosome with bright red to orange areas (sometimes the entire sponge being almost red) visible through the ectosome (Fig. 9A–D). It possesses conspicuous excurrent channels can be seen converging on its oscules (Fig. 9A–C), a characteristic common in many *Mycale* species (Ackers et al., 1992). The ectosome is devoid of spicules, being supported by a loose plumorticulate skeleton of mycalostyles with elongated heads (Fig. 9D), always in a 200–260 × 2–4 μm size range. Microscleres include a single chelae (16–21 μm) and sigma (25–42 μm) categories, both being particularly scant or absent in most specimens.

Geographic distribution. The species was originally described from the Senegal (Lévi, 1952), and has since then only been reported from east Atlantic Oceanic Islands, including Ascension, Madeira and the Canary Islands (Cruz, 2002; van Soest et al., 2014). In Madeira, the sponge had previously been reported from inside a marina (Canning-Clode et al., 2013a), having been considered since then as an invasive species on the island. However, based on our study *M. senegalensis* appears to be present in most littoral habitats across the Madeiran archipelago, occurring mainly on rocks but also in wreckages or artificial substrates, and its first detection from a marina most likely arose from the islands' incomplete sponge inventorying rather than a real absence of the species prior to it.

Remarks. At least three different *Mycale* species are suspected to occur from Madeira from collected material (Table 1; Supp. Mat. 1). Yet, in most specimens, microscleres occurred in very low numbers or were even absent hindering species identification, a common problem already reported for *Mycale* species in the area (van Soest et al., 2014). It was only due to the vast collection of *M. senegalensis* specimens that its entire

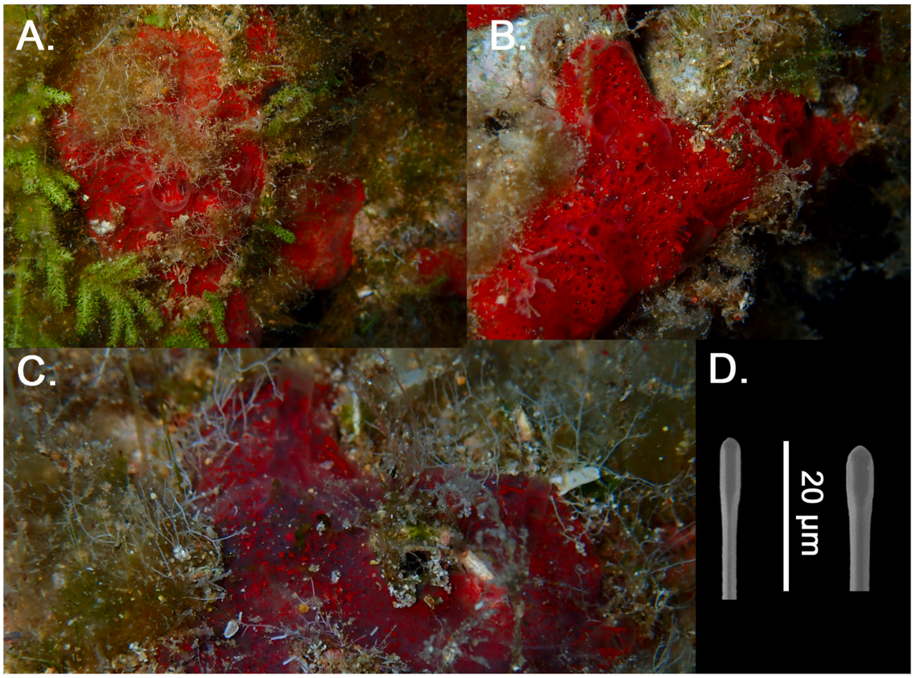

Fig. 9. A-E) *In situ* images of *Mycale* (*Carmia*) *senegalensis* from different locations across the Madeiran Archipelago. F) SEM imaging details and variations amongst *M. senegalensis* mycalostyles' heads; scale bar 20 μm.

spicular set could be reliably identified, with Madeiran individuals matching well the species redescription (van Soest et al., 2014). Yet, while microscleres might be scant in most individuals, *M. senegalensis* can still be recognized from other Madeiran *Mycale* based on the combination of its external features and coloration, paired with the presence of a single category of sigma, chelae and mycalostyle, the later always with characteristic, elongated heads (Fig. 9D).

Order SUBERITIDA Chombard and Boury-Esnault, 1999

Family HALICHONDRIIDAE Gray, 1867

Genus *Spongosorites* Topsent, 1896

3.1.9. *Spongosorites cf. cavernicola* Bibiloni (1993)

Material examined: MMF50189 [#07] collected on a cave wall in Ponta do Clérigo, Madeira Island (32°48′27.2″N 16°51′13.9″W), Madeira Archipelago, 16 m depth, August 30, 2017 [Ribeiro, C., & Neves, P.].

Description. Massive lumpy sponge with irregular, interconnected branching processes of varying size and shape. Oscules are numerous and located everywhere around the sponge, but are more prevalent on the top of the protuberances. It has a smooth appearance, with a clear white coloration (Fig. 10E). The sponge possesses a thin, translucid ectosome, firmly attached to the choanosome, and can only be peeled off as flakes. The choanosome is cavernous, with several openings of varying size. The sponge is hardly compressible. Colour in spirit, grey.

Skeleton. The ectosome is made of a dense layer of oxeas, parallel to the sponge's surface and without a clear organization. The choanosome on the other hand is of a 'halichlonoid' nature, cavernous in nature and densely packed with oxas and strongyloxeas, which occur in a rather confused manner, without a clear direction.

Spicule complement. Strongyloxea and oxea (Fig. 10).

Strongyloxeas (Fig. 10A): Robust oxeas with slightly acerate to blunt terminations (Fig. 10C), which gives them appearance of strongyloxeas. They are mostly straight to slightly bent, and possess the same width across the spicule except for its terminations, which end in short, sometimes tapering blunt to acerate tips.

Size range: 99–*156.3* ± 27.8–252.5 μm x 3–*5.2* ± 1.3–7.8 μm.

Oxeas (Fig. 10B): Oxeas slightly bent in the middle with acerate terminations, sometimes with blunts tips (Fig. 10D). They are tighter at the centre, gently decreasing in width towards the ends.

Size range: 37.5–*73.5* ± 31.9–152 μm x 1.4–*1.9* ± 0.6–4 μm.

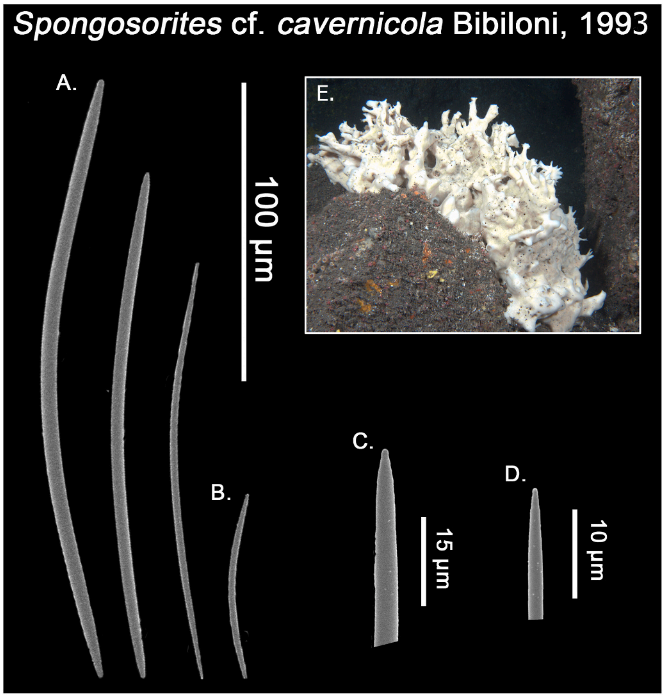

Fig. 10. SEM imaging of *Spongosorites* cf. *cavernicola* spicular set. A. Strongyloxea. B. Oxea C. Tip of the strongyloxea D. rounded tip of an oxea; E. *In situ* picture of *S.* cf. *cavernicola*. Scale bar for A and B, 100 μm, C. 15 μm and D. 10 μm.

Geographic distribution. The species was only known from a single specimen from '*La Catedral*' cave (Cathedral cave), located in the southwest area of Cap des Freu in Mallorca Island (Balearic Archipelago, Western-Mediterranean Sea). This record represents not only the second finding of the species, but the first outside of the Mediterranean Sea.

Remarks. Species differentiation with *Spongosorites* is hazardous, as it mostly relies on subtle differences in the spicules (Santín et al., 2021b), while confusion with other aligned genera, such as *Topsentia*, are possible (Bertolino et al., 2015). Regarding the current material, it has been assigned to *Spongosorites* due to the possession of exclusively bent oxeas smaller than 600 μm and the presence of a smooth surface (van Soest, 2002a). In this sense, from all *Spongosorites* species described in the north Atlantic, only three possess two categories of oxeas, namely *Spongosorites cavernicola* Bibiloni (1993), *Spongosorites dendyi* (Topsent, 1927) and *Spongosorites placenta* (Topsent, 1896). From these, the current material differed with *S. dendyi* in the lack of centrotylotism in its smaller oxea category and overall smaller length of its oxea categories (van Soest, 2002a). Regarding *S. placenta* and *S. cavernicola*, both have two oxea categories in the same size range, but *S. placenta* is said to possess oxeas with clear acerated tips and an encrusting nature (van Soest, 2002a), whereas *S. cavernicola* has bluntly-terminated oxeas and shows a more massive-lobate morphology (Bibiloni, 1993), for which the present material is assigned to the later. An ill-known species, *S. cavernicola* was described from a cave in the Mediterranean Sea, and had never been reported again. In this sense, while *S. cavernicola* is indubitably the closest described species to the collected material some differences still persist, mainly in the oxeas size being larger (Table 5) and the strongyloxeas being bent twice rather than once in the holotype (Bibiloni, 1993). Unfortunately, the holotype of the species appears to be lost (Díaz-Lorca, *pers. comm.*) and, given the scarce information provided in the original description, it would seem prudent to retain the current material as *S.* cf. *cavernicola* rather than erecting a new species until additional material can be collected.

Order VERONGIIDA Bergquist, 1978

Family APLYSINIDAE Carter, 1875

Genus *Aplysina* Nardo, 1834

3.1.10. *Aplysina cf. aerophoba* Nardo (1833)

Material examined: MMF50236 [32_2022] collected on a cave wall in Ponta de São Lourenço, Madeira Island (32°44′27.8″N 16°42′00.8″W), Madeira Archipelago, 1 m depth, May 03, 2022 [coll. Wirtz, P.].

Description. Small encrusting sponge (Fig. 4C), somewhat between slightly rounded to lumpy, and of an intense yellow colour. It usually occurs localized but in high numbers, commonly occurring as several slight elevations located near each and being more or less interconnected by thin, encrusting filaments. Oscules are clearly visible and located at the top of each mass, never on the interconnecting tissue.

Geographic distribution. Aplysina aerophoba is widely distributed across the Mediterranean basin and its nearby areas, being amongst the most common shallow sponges in the Webbnesia region (Cruz, 2002),

Table 5

Comparative table between *Spongosorites* with two oxea categories, including the locality (Loc.) and depth of the sample, as well as the measurement of their spicular complement. Size range outliers are marked between brackets (.). Numbers after Locality indicate the reference for each sample; * indicates this is the holotype of the species; (So) strongyloxeas.

Species	Loc./Depth	Oxeas
Spongosorites cavernicola Bibiloni (1993)	Mallorca[a]*/5 m (cave)	**(I)** 150–350 × 4–15 μm **(II)** 150–200 × 4–6 μm
	Madeira[b]/16 m (cave)	**(I)** 99–*156.3* ± 27.8–252.5 μm x 3–*5.2* ± 1.3–7.8 μm (**So**) **(II)** 37.5–*73.5* ± 31.9–152 μm x 1.4–*1.9* ± 0.6–4 μm
Spongosorites dendyi (Topsent, 1927)	Cape Verde[c]*/ 91 m	**(I)** (300) 500 × (5) 16–21 μm **(II)** 45–145 × 7 μm
Spongosorites placenta (Topsent, 1896)	Azores[3]/550 m	**(I)** 300–330 (470) x 5–6 μm **(II)** 70–120 μm

[a] Bibiloni (1993).

[b] *Present study*.

[c] Topsent (1928).

including Madeira (Augier 1985, Fig. 4B). Nevertheless, its encrusting ‘morphotypes’ are far less common, so far having only been reported from caves on the Ligurian and Ionian Seas, in the Mediterranean Basin (Costa et al., 2020) and, in the continental Portuguese coast, the Basque country and the Madeira Archipelago in the east Atlantic (Chevaldonné and Lejeusne, 2006).

Remarks. Currently *Aplysina aerophoba* (Schmidt, 1862) and *Aplysina cavernicola* (Vacelet, 1959) are the only accepted *Aplysina* representatives in the eastern North Atlantic. Despite their striking morphological similarities both species can be told apart by their contrasting ecologies, with *A. aerophoba* presenting budding digitations and being located in rather shallow and photophilous environments, whereas the *A. cavernicola* never shows such buddings and occurs associated with sciaphilous environments, such as caves or mesophotic environments (Vacelet, 1959). Nevertheless, both species have been shown to possess considerable morphological plasticity in response to environmental factors (Díaz et al., 2019; Costa et al., 2020), are known to hybridize and cannot be reliably distinguished by molecular markers (Heim et al., 2007). Hence, the line between both species is somewhat diffuse, especially in the Aegean (Voultsiadou-Koukoura, 1987) or the Adriatic Sea (Klöppel et al., 2009), where differentiation between both species becomes increasingly difficult.

So far, only *A. aerophoba* has been recorded outside the Mediterranean Sea. Yet, another encrusting *Aplysina* appears to dwell within cave environments of the Madeira Island, and potentially Azores (Moss, 1992). Recent works in the Mediterranean have concluded, based on molecular markers, that these cave encrusting *Aplysina* might in fact just be an ecotype of *A. aerophoba*, which would be adapted to cave environments (Costa et al., 2020). Nevertheless, said study did not include cave-encrusting *Aplysina* from the Atlantic, while prior unpublished data supports that East Atlantic encrusting *Aplysina* specimens might in fact be a separated species from both *A. aerophoba* and *A. cavernicola* (Chevaldonné and Lejeusne, 2006). Hence, based on the current available data the present material is here considered as *A.* cf. *aerophoba* cave morphotype, yet more data is needed before a conclusion can be reached on whether or not the Atlantic encrusting *Aplysina* represent just and ecotype of *A. aerophoba* or a distinct, separate species.

4. Discussion

4.1. State of the art and knowledge gaps on the madeiran sponge fauna

While Madeira was the first of the North Atlantic oceanic islands where any given sponge species was described (viz. *Erylus listeri*; Bowerbank, 1858) its sponge fauna has remained mostly unexplored until nowadays (Pestana et al., 2018), and could be considered one of the least studied phyla among the Madeiran archipelago marine fauna. Indeed, other marine groups such as cnidarians, crustaceans, tunicates and fish have been more extensively studied in the archipelago, with new records, species descriptions, updated checklists and ecological and behavioural data being reported (e.g. Wirtz, 1998, 1999, 2007; Pascual et al., 2000; 2000b, 2001a, 2001b; Wirtz et al., 2008; Biscoito et al., 2018; Png-Gonzalez et al., 2021; Castro et al., 2022; Godinho et al., 2022). In comparison, Topsent's (1928) monograph on the North Atlantic Mediterranean Sea sponge fauna (which contained 33 new records for the island of Madeira out of the 47 reported species; Table 1) still remains the biggest contribution regarding Madeiran sponges until the present (Table 1; Fig. 11). In fact, since Topsent's contribution only a single study has exclusively dealt with the Madeiran sponge fauna (Pestana et al., 2018), while most other additional records correspond to occasional mentions of species in articles of diverse topics (Table 1; Figs. 11 and 12), such as chemical compounds (Araújo et al., 1999), broader faunistic studies (e.g. Augier 1985; Nike-Bianchi et al., 1998; Xavier et al., 2010b; Ribeiro and Neves, 2020), sponges as hosts for other phyla (e.g. Pascual et al., 1996, 2000, 2001a; Wirtz, 1999, 2020), or as part of wider taxonomic works regarding certain sponge families or genera across the North Atlantic waters (e.g. van Soest et al., 2012b, 2013, 2014; Carvalho et al., 2015; Alvizu et al., 2018). Despite its relative accessibility and proximity to the continental shore and other nearby well-studied archipelagos (Azores, Canary Islands and Cape Verde), the study of the Madeiran sponge fauna rather resembled that of isolated, oceanic islands such as the Ascension Island (approximately 1600 km to the nearest major mainland; Goodwin et al., 2021). Both share a limited and patchy historical research regarding Porifera, with several dubious or unverifiable records (Table 1) and, if it were not for Topsent's work (Topsent 1904, 1906, 1909, 1927, 1928), they would have a similar account of species (65 species for Madeira, Table 1; 47 potential species for Ascension Island, Goodwin et al., 2021).

Commonly, the taxonomic inventory of any given area begins with a rapid increase in recorded species fuelled by the account of its more conspicuous and abundant taxa, with the number of new additions decreasing once most of these have been accounted, paired with a gradual shift in focus towards its more cryptic fauna (Salani et al., 2022). In this sense, after this work the total number of species for the islands has increased by ca. 25% to a total of 140 (Fig. 11), with the bulk of these new records corresponding to well-known and/or conspicuous taxa (e.g. *Axinella damicornis* (Fig. 3A), *Axinella verrucosa* (Fig. 3B), *Axinella dissimilis* (Fig. 3C), *Axinyssa digitata* (Fig. 3X), *Chalinula limbata* (Fig. 3P), *Borojevia* cf. *cerebrum* (Fig. 4J), *Hexadella* sp. (Fig. 4D), *Sycon raphanus* (Fig. 4K) or *Tethya* spp. (Fig. 4A)). Our records also contain several Mediterranean species that have not been previously recorded in the North Atlantic (viz. *Oscarella* cf. *balibaloi* (Fig. 4E), *Spongosorites* cf. *Cavernicola* (Fig. 10E), *Petrosia* cf. *Clavata* (Esper, 1794)), several north-east Atlantic species whose presence in Madeira marks their southernmost limit of occurrence (viz. *Dictyonella pelligera* (Fig. 3G; Fig. 6F–H), *Borojevia* cf. *cerebrum* (Fig. 4J), *U. glabra* (Fig. 4L), *Axinella dissimilis*, *Chalinula nigra* (Fig. 3O) or *Axinyssa digitata*) as well as elements from the subtropical west African fauna (viz. *Hymedesmia* (*H.*) *senegalensis* (Fig. 3W) and *Mycale* (*C.*) *senegalensis* (Fig. 9A–C)). This close relation with the Mediterranean had been previously observed in the nearby Canary Islands (Cruz, 2002), and it might be related to the influx of Mauritanian species into the Mediterranean following the Messinian Salinity Crisis ca. 5.3 Ma (Maldonado and Uriz, 1995). Additionally, it has been speculated that during glacial periods connectivity within the Webbnesian region (Canary Selvagens and Madeira islands – *sensu* Freitas et al., 2019) and with the continent might be facilitated by certain oceanic seamounts becoming islands and acting as stepping stones for marine organisms (Freitas et al., 2019). Thus, the presence of Lusitanian and Senegalian elements in the current Madeira sponge fauna would reflect the alternating glacial and interglacial Quaternary migrations (Maldonado and Uriz, 1995). Regarding any

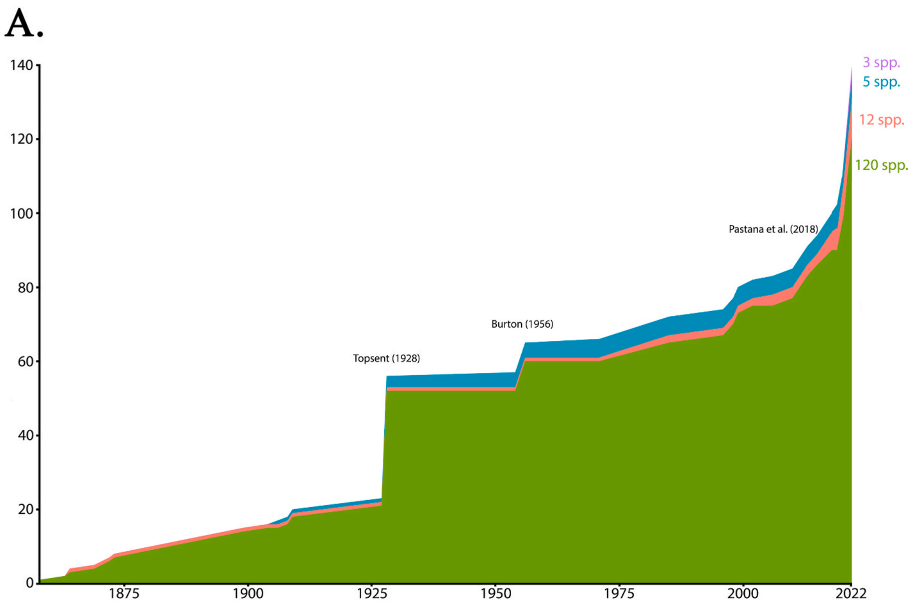

Fig. 11. A) Cumulative timeline of the total number of sponge species in the Madeiran archipelago by class: Demospongiae (green), Calcarea (red), Homoscleromorpha (purple) and Hexactinellida (blue). Articles mentioned refer to the main prior contributions to the Madeiran sponge fauna and whose focus was primary on sponges.

possible recent changes in the island's sponge fauna composition, some of the most common sponges found during this study (Table 1, Supp. Mat. 1) have barely or not been recorded previously on the island (viz. *Axinella damicornis*, *Cliona celata* (Fig. 3I), *Cliona viridis* (Fig. 3J), *Axinyssa digitata*), amongst many others). They have most likely gone unnoticed until recently due to previous limited reporting, hindering the detection of previous faunal changes over time, and making it harder to distinguish of newly arrived non-indigenous species (NIS) (Castro et al., 2022). While certainly dozens of additional species will be added as the more conflicting samples are sorted out (e.g. calcareous or homoscleromorph sponges), it could be considered that the most common and abundant shallow (0–30 m depth) sponge fauna of Madeira is now relatively identified. Nevertheless, there are still specific habitats within the archipelago that remain largely unexplored, with potentially dozens of additional unknown sponges to Madeira to be described.

Marine caves are considered relatively inaccessible environments as well as diversity hotspots, commonly harbouring rare, cryptic or relict species, as well as species with bathyal affinities (Vacelet et al., 1994; Gerovasileiou and Bianchi, 2021). Among invertebrate taxa found in caves, Porifera dominate in terms of species richness, spatial coverage, and biomass, as the absence of light and the disappearance of space-competing macroalgae favours the development of rich sponge communities (Gerovasileiou and Voultsiadou, 2012). Yet, there is barely any information regarding cave fauna in temperate regions, including Madeira (Bell, 2002). While still poorly explored, Madeiran caves are known to harbour rare and new species to science (Pascual et al., 1996; Wittmann and Wirtz, 1998; Wirtz, 1998; Opresko, 2001; Calado et al., 2004), yet no sponges have previously been reported from these environments. Similarly, rhodolith beds (free-living calcareous algae, with a worldwide distribution, from polar to tropical regions - Foster, 2001; Riosmena-Rodríguez et al., 2017) support very high biodiversity levels (Barbera et al., 2003; Sordo et al., 2020). These habitats provide shelter and settlement ground for attached flora and sessile fauna and have been highlighted for hosting unique sponge communities due to the presence of different microhabitats within the nodules (Sciberras et al., 2009; Calcinai et al., 2013; Santín et al., 2018, 2019; Longo et al., 2020). The present study is the first one reporting and identifying sponges from Madeiran caves (9 spp.) and rodolith beds (8 spp.) and, while several rare (e.g. *Spongosorites cavernicola*; caves) and new species (e.g. *Hemimycale funchalensis* sp. nov.; rodolith beds) are here reported from these habitats they still represent a small fraction of all sponges observed and potentially occurring in said habitats.

With roughly 5% of the ocean's seafloor properly mapped (Wölfl, et al., 2019), continental shelfs, slopes, abyssal plains and other deep-sea ecosystems (e.g. seamounts, trenches, hydrothermal vents) around the globe became the new frontier to ocean exploration (Robison, 1999). Since the increased accessibility to deep benthic environments provided by ROV and other imaging technologies, a multitude of unique benthic ecosystems have been discovered in recent years (Rozwadowski, 2005). Yet, we currently know very little about these communities, that contain a high diversity of species (e.g. Navarro-Barranco et al., 2023). Sponges are known to be particularly abundant in mesophotic and deep-sea environments (e.g. Bertolino et al., 2015; Santín et al., 2018; Idan et al., 2021), and old accounts mention the existence of a rich and diverse sponge fauna dwelling within the deep-sea waters of the Madeiran archipelago (da Silva and de Meneses, 1921). Moreover, there are recent findings of rich sponge grounds in deep waters off Madeira, which were recognized as local diversity hotspots (Braga-Henriques et al., 2022). However, most deep-sea sponge material from the archipelago remains largely unpublished (Reed and Pomponi, 1992; van Soest et al., 2013, 2014), with sporadic published records that mostly correspond to conspicuous (e.g. *Asconema setubalense*) species, with the bulk of the fauna still to be properly assessed (Braga-Henriques et al., 2022, Fig. 12).

4.2. *Introduced sponge species in madeira*

The Temperate Northern Atlantic is one of the most affected ecoregions by invasive species and, while knowledge concentrates towards European North Atlantic and Mediterranean coasts (Molnar et al., 2008; Tsiamis et al., 2019; Zenetos et al., 2022), the presence of NIS has been known in Madeira for decades (Table 1; Fig. 13). Furthermore, new NIS are being detected almost yearly on the archipelago (Canning-Clode et al., 2013a, 2013b; Gestoso et al., 2017; Png-Gonzalez et al., 2021). Regarding Porifera, prior to this study, four sponge species (*Prosuberites longispinus* Topsent, 1893, *Mycale* (*Carmia*) *senegalensis* Lévi, 1952, *Paraleucilla magna* Klautau, Monteiro & Borojevic, 2004 and *Crambe crambe* (Schmidt, 1862)) were considered as NIS for the Madeiran waters. A potential fifth species, *Chalinula nigra* Boury-Esnault and Lopes

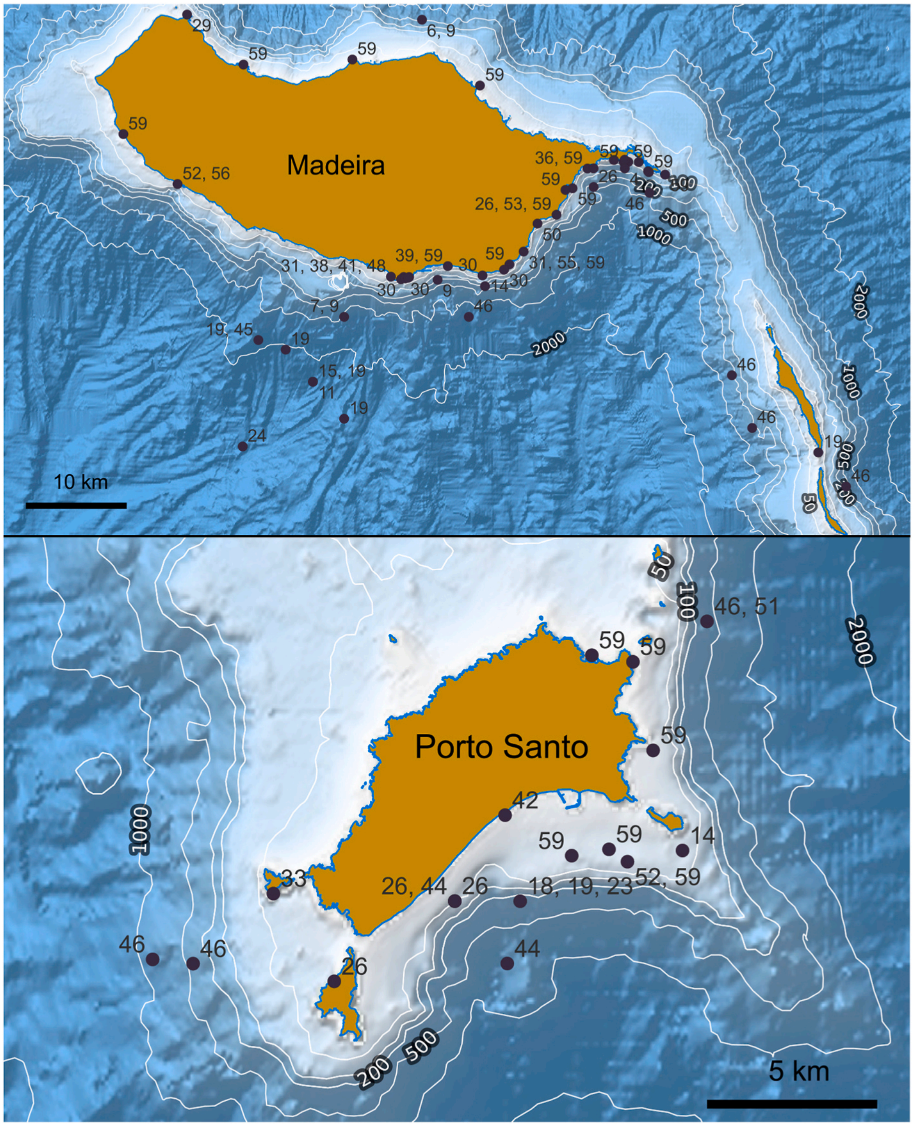

Fig. 12. Map with all historical sampling stations which had reported sponges in the Madeiran archipelago. Numbers indicate the publications as in Table 1; current study corresponds to 59. CRS: WGS84/Pseudo-Mercator (EPSG 3857).

(1985) is now being added to this list by this study. While this might seem like a low number of NIS, especially if compared to other marine taxa, such as Bryozoans or Rhodophytes (16 and 17 NIS respectively, Tsiamis et al., 2019), it represents ca. 25% of all known NIS sponges in the EU MSFD marine subregions, being second only to the great North Sea EU MSFD, with 11 NIS (Tsiamis et al., 2019).

Among all the Madeiran NIS sponges, *P. magna* is perhaps the most recognized of all invasive sponges worldwide (Fig. 4H). With an uncertain native range, the species was first observed from Brazilian coasts in the nineties, yet remained undescribed until 2004. By the time of its descriptions, it had already become one of the most abundant sponges in Rio de Janeiro State's coasts, where it was deemed to be invasive (Klautau et al., 2004). Paralel to its description from Brazil in 2004, the species was found for the first time in the Mediterranean coasts of Italy in the same year (Longo et al., 2007). Since then, the species has expanded across the entire Mediterranean basin (Longo et al., 2007; Guardiola et al., 2016), and made its way to Madeiran and the Azorean archipelagos (Castro et al., 2022). Contrary to *P. magna*, whose native range is unknown, *C. crambe* is a characteristically shallow orange sponge native to the Mediterranean basin, detected for the first time in Madeira in 1998 (Duran et al., 2002; Castro et al., 2022). Both species are suspected to have been introduced in the area via maritime transport (Duran et al., 2004a; Canning-Clode et al., 2013a), now appearing to be widespread across the island, and being amongst the most common sponges in some areas (Fig. 13).

Regarding *M. senegalensis*, the species is known to possess a wide distribution across the Atlantic, being recorded from Ascension Island (van Soest et al., 2014), Senegal (Lévi, 1952) and the Webbnesian archipelago of the Canaries since at least the early 2000s (Cruz, 2002; van Soest et al., 2014). However, in Madeira it was considered a NIS after its initial detection at Quinta do Lorde Marina (QLM) growing over PVC plates, where it rapidly became one of the dominant species, a trait that is commonly attributed to invasive species (Canning-Clode et al., 2013a; Png-Gonzalez et al., 2021; Chebaane et al., 2022). Similarly, *P. longispinus* was originally found alongside *M. senegalensis* at the same Marina, and it considered as having a NIS status on the island by some authors (Canning-Clode et al., 2013a; Png-Gonzalez et al., 2021). In this sense, *P. longispinus* is a common Mediterranean species, and its presence on the Atlantic is known from the Celtic Seas, Azores (Boury-Esnault and Lopes, 1985) and the Canary Islands (Cruz, 2002). During the course of this study, *P. longispinus* was observed in Porto Novo (Madeira Island), attached to the same rocks as the paratype of *H. funchalensis* sp. nov.

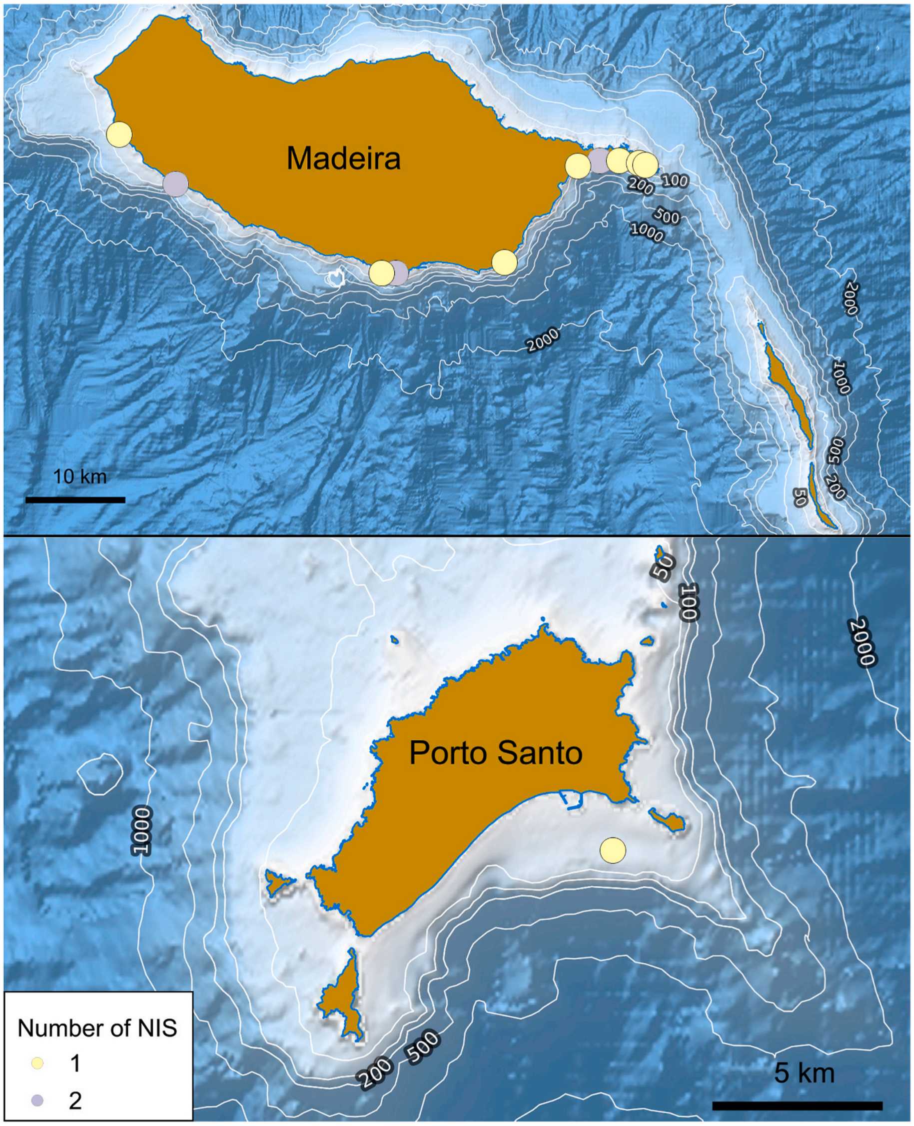

Fig. 13. Presence of poriferan NIS in Madeira. Yellow dots indicate one species, whereas purple-grey ones, two species present. CRS: WGS84/Pseudo-Mercator (EPSG 3857).

(sample MMF50234), whereas *M. senegalensis* was amongst the most common species reported from littoral areas of the Madeira Archipelago (see results). Thus, currently there is not enough evidence to support a NIS status for either species in Madeira, which should be rather considered as native to the island.

Finally, during the current study *C. nigra* has been found to be particularly abundant in Madeira, yet its presence has only been noticed on the island recently by researchers who have been SCUBA diving there for more than 30 years (Wirtz and Ribeiro *pers. obvs*.). Thus, given its conspicuous, distinctive external morphology, recent detection, and the fact that the species is experiencing a range expansion across its distribution (Santín et al., 2021a), *C. nigra* appears to be of, at least, a crypto-expanding species on Madeira.

Hence, after revision, two out of four previously considered NIS sponge species in Madeira are, in fact, native to the area, with *C. nigra* being range-expanding and only *C. crambe* and *P. magna* having enough support to be considered as NIS. In this sense, studies of port facilities in poorly studied areas might reveal native species that have not yet been reported elsewhere (Castro et al., 2022), highlighting the importance for proper inventorying of marine biodiversity to avoid hindering of future conservation efforts.

5. Conclusions

The present article provided the first comprehensive insight on the littoral sponge fauna of the Madeira Archipelago in almost a century, with the description of a new species, several new records and rare species. Interestingly, Madeiran sponge fauna seems to be a mixture of both Tropical Atlantic and Temperate Northern Atlantic fauna, which could point towards the Webbnesian region being a potential hotspot for sponge diversity. While we provide the first reliable baseline for future monitoring of sponge species in Madeira, the limited historical records hinder the detection of any possible species turnover that might have occurred over time. Overall, this highlights the need for a quantitative and objective faunal baseline regarding diversity, distribution, population size structures and vulnerabilities to anthropogenic stressors of the islands' sponge species in order to support the implementation of effective management and monitoring measures over time. The present study is a contribution towards that goal.

CRediT authorship contribution statement

A. Santín: Writing – review & editing, Writing – original draft,

Visualization, Validation, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **P. Wirtz:** Writing – review & editing, Validation, Resources, Methodology, Investigation, Conceptualization. **P. Neves:** Writing – review & editing, Visualization, Supervision, Software, Resources, Project administration, Methodology, Funding acquisition, Data curation. **C. Ribeiro:** Writing – review & editing, Validation, Supervision, Resources, Project administration, Methodology, Investigation, Funding acquisition, Data curation, Conceptualization.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.csr.2024.105230.

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