

Sponges of Western Mediterranean seamounts: new genera, new species and new records

Julio A. Díaz^{1,2}, Sergio Ramírez-Amaro^{1,3} and Francesc Ordines¹

¹ Instituto Español de Oceanografía, Centre Oceanogràfic de Balears, España, Palma, Spain

² Interdisciplinary Ecology Group, Biology Department, Universitat de Les Illes Balears, Palma, Spain

³ Laboratori de Genètica, Biology Department, Universitat de Les Illes Balears, Palma, Spain

ABSTRACT

Background: The seamounts Ses Olives (SO), Ausias March (AM) and Emile Baudot (EB) at the Mallorca Channel (Balearic Islands, western Mediterranean), are poorly explored areas containing rich and singular sponge communities. Previous works have shown a large heterogeneity of habitats, including rhodolith beds, rocky, gravel and sandy bottoms and steeped slopes. This diversity of habitats provides a great opportunity for improving the knowledge of the sponges from Mediterranean seamounts.

Methods: Sponges were collected during several surveys carried out by the Balearic Center of the Spanish Institute of Oceanography at the Mallorca Channel seamounts. Samples were obtained using a beam-trawl, rock dredge and remote operated vehicle. Additional samples were obtained from fishing grounds of the Balearic Islands continental shelf, using the sampling device GOC-73. Sponges were identified through the analysis of morphological and molecular characters.

Results: A total of 60 specimens were analyzed, from which we identified a total of 19 species. Three species and one genus are new to science: *Foraminospongia balearica* **gen. nov. sp. nov.**, *Foraminospongia minuta* **gen. nov. sp. nov.** and *Paratimea massutii* **sp. nov.** *Heteroxya* cf. *beauforti* represents the first record of the genus *Heteroxya* in the Mediterranean Sea. Additionally, this is the second report of *Axinella spatula* and *Haliclona* (*Soestella*) *fimbriata* since their description. Moreover, the species *Petrosia* (*Petrosia*) *raphida*, *Calyx* cf. *tufa* and *Lanuginella pupa* are reported for the first time in the Mediterranean Sea. *Petrosia* (*Strongylophora*) *vansoesti* is reported here for the first time in the western Mediterranean Sea. *Haliclona* (*S.*) *fimbriata* is reported here for the first time in the north-western Mediterranean Sea. *Hemiasterella elongata* is reported here for the second time in the Mediterranean Sea. The species *Melonanchora emphysema*, *Rhabdobaris implicata*, *Polymastia polytylota*, *Dragmatella aberrans*, *Phakellia ventilabrum* and *Pseudotrachya hystrix* are reported for first time off Balearic Islands. Following the Sponge Barcoding project goals, we have sequenced the Cytochrome Oxidase subunit I (*COI*) and the 28S ribosomal fragment (C1–D2 domains) for *Foraminospongia balearica* **sp. nov.**, *Foraminospongia minuta* **sp. nov.**, *H.* cf. *beauforti* and *C.* cf. *tufa*, and the *COI* for *Paratimea massuti* **sp. nov.** We also provide a phylogenetic analysis to discern the systematic location of *Foraminospongia* **gen. nov.**, which, in accordance to skeletal complement, is placed in the Hymerhabdiidae

Submitted 15 April 2021

Accepted 7 July 2021

Published 26 August 2021

Corresponding author

Julio A. Díaz, julio.diaz@ieo.es

Academic editor

Jörg Oehlmann

Additional Information and
Declarations can be found on
page 55

DOI 10.7717/peerj.11879

© Copyright

2021 Díaz et al.

Distributed under

Creative Commons CC-BY 4.0

OPEN ACCESS

family. A brief biogeographical discussion is provided for all these species, with emphasis on the sponge singularity of SO, AM and the EB seamounts and the implications for their future protection.

Subjects Biodiversity, Biogeography, Marine Biology, Taxonomy, Zoology

Keywords Biodiversity, Sponges, New genus, New species, DNA barcoding, Seamounts, Mediterranean Sea

INTRODUCTION

Seamounts are structures of high ecological and biological interest (*Carvalho et al., 2020; Morato et al., 2013; Rogers, 2018*), which provide excellent habitat for a rich communities of filter-feeding animals, such as corals, crinoids and sponges (*Samadi, Schlacher & De Forges, 2007*). These organisms are favored by enhanced currents, scarcity of fine sediment, accidented topography and predominance of hard substrata, features that characterize seamounts (*White & Mohn, 2004*). Sponges are ubiquitous on seamounts, where they tend to form dense and diverse aggregations that provide habitat and refuge to other animals like crustaceans, mollusks and fishes (*Samadi, Schlacher & De Forges, 2007*). Also, they are involved in benthic-pelagic coupling and recycling of nutrients, both processes of utmost importance in oligotrophic areas like the Mediterranean Sea, where they may contribute to the maintenance of higher trophic levels (*De Goeij et al., 2013*).

Despite their importance, very little is known about sponges of the Mediterranean seamounts, which is in contrast to the vast number of studies on sponge taxonomy available in other domains like the continental shelf or the submarine canyons (e.g. *Vacelet, 1961, 1969; Pulitzer-Finali, Hadromerida & Poecilosclerida, 1978; Pulitzer-Finali, 1983; Boury-Esnault, Pansini & Uriz, 1994; Pansini, Manconi & Pronzato, 2011; Bertolino et al., 2015; Longo et al., 2018; Manconi et al., 2019; Enrichetti et al., 2020*). However, in recent years the increase in the use of Remote Operated Vehicles (ROV) has facilitated the access and study of seamounts. Currently, information on sponges is available from the Erathostenes seamount in the Levantine Sea (*Galil & Zibrowius, 1998*), the Vercelli seamount in the northern Tyrrhenian Sea (*Bo et al., 2011*), the Ulisse and Penelope seamounts in the Ligurian Sea (*Bo et al., 2020*), the Avempace, Alboran Ridge, Seco de los Olivos and Cabliers seamounts in the Alboran Sea (*Boury-Esnault, Pansini & Uriz, 1994; Pardo et al., 2011; Sitjà & Maldonado, 2014; De la Torre et al., 2018; Corbera et al., 2019*), and the Stone Sponge, Ses Olives, Ausias March and Emile Baudot seamounts in the Balearic Sea (*OCEANA, 2011; Aguilar et al., 2011; Maldonado et al., 2015*). However, most of these works address the sponges at a community level, focusing on a general habitat characterization. Nonetheless, the studies addressing taxonomy have revealed that the Mediterranean seamounts are habitats for rare, poorly-known, or new species. For example, *Aguilar et al. (2011)* reported the carnivorous sponge *Lycopodina hypogea* (*Vacelet & Boury-Esnault, 1996*) at the Ausias March seamount, representing the first sighting of this species outside littoral caves. A singular reef formed by the Lithistid

Leiodermatium pfeifferae (Carter, 1873) was recorded at the Stone Sponge seamount, being the first report of this species in the Mediterranean Sea (Maldonado et al., 2015).

Determining which species are present on a given seamount, and hence the seamount's biodiversity is a first step towards the development of management plans to protect these habitats. It is also crucial to understand seamounts' biocenosis, their structure and dynamics, how they can be affected by human disturbances, and to monitor potential biological invasions and long-term community changes (Clark et al., 2012; Danovaro et al., 2020).

Sponges are problematic as they are difficult to identify, which may lead to incorrect or underestimated biodiversity values. The use of molecular markers, a powerful tool to help in sponge identification, has shown that this group is much more speciose than previously thought, and cryptic species are very common (Cárdenas, Perez & Boury-Esnault, 2012). Thus, detailed morphological descriptions supported by a complete genetic database are crucial for future studies.

The objective of this work was to improve the taxonomic knowledge on the sponges at three seamounts of the Mallorca Channel in the Balearic Islands: Ses Olives, Ausias March and Emile Baudot. Currently, these seamounts are being assessed for inclusion in the Natura 2000 network, under the scope of the LIFE IP INTEMARES project. One of the goals of this project is to improve the scientific knowledge of areas of ecological interest that harbor rich, vulnerable and protected habitats and species, which is necessary knowledge for the development of management plans. High abundance and diversity of invertebrates were observed during several surveys carried out in 2018, 2019, and 2020 at these seamounts, highlighting sponges as the dominant group. In the present paper we provide detailed descriptions of 18 demosponges and one hexactinellida, including a new genus and three new species, together with new descriptions and records of poorly-known taxa. For the new and dubious species, the sequences of two most used barcoding genes, the mitochondrial Cytochrome Oxidase subunit I (COI) and the nuclear 28S ribosomal fragment (C1-D2 domains), are also provided.

MATERIALS AND METHODS

Study area

The Mallorca Channel is located in the Balearic Promontory (western Mediterranean Sea), between the islands of Mallorca and Ibiza. The area harbors three seamounts: Ses Olives (SO; 1°58'58.8"N, 38°57'36"E) and Ausias March (AM; 1°49'4.8"N, 38°44'49.2"E) located east of Ibiza and Formentera islands, and Emile Baudot (EB; 2°30'0"N, 38°43'55.2"E) located south of Mallorca and east of Ibiza-Formentera (Fig. 1). The seamounts SO, AM and EB are 375, 264 and 600 m high, respectively and 10 to 17 km long, with tabular summits elongated in NE-SW trends and located at 225–290, 86–115 and 94–150 m depth, respectively. SO and AM are of orogenic origin, emerging from depths around 900 and 600 m in their eastern sides and being separated from Ibiza and Formentera islands by depths around 600 and 400 m. By contrast, EB is a guyot of volcanic origin, which in its western side emerges from a plain around 900 m deep, with numerous fields of pockmark type depressions, located between SO and AM. At the eastern side

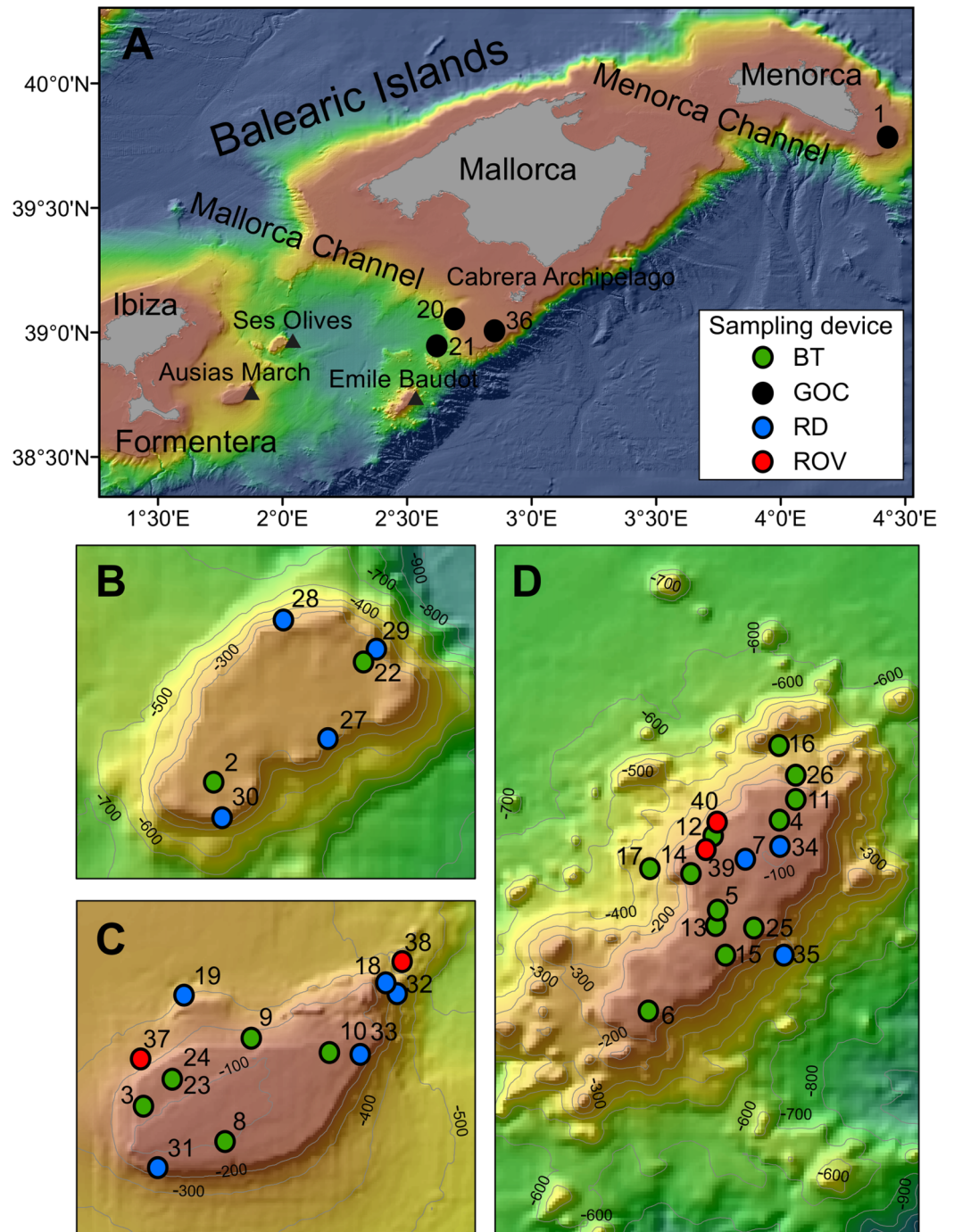


Figure 1 Map of the studied area showing the location of the sampling stations of beam trawl (BT), bottom trawl type GOC73 (GOC), rock dredge (RD) and remote operated vehicle (ROV). The characteristics of these sampling stations are shown in Table 1. (A) General view of the Balearic Islands. (B) Detail of Ses Olives. (C) Detail of Ausias March. (D) Detail of Emile Baudot.

Full-size  DOI: [10.7717/peerj.11879/fig-1](https://doi.org/10.7717/peerj.11879/fig-1)

Table 1 Details of the sampling stations.

R _{survey}	R _{study}	Year	Sampling device	Depth (m)	Coordinates		Area	Seabed characteristics
					Initial	Final		
206	1	2017	GOC-73	135	39°47'37.2"N 4°26'15.4"E	39°47'37.2"N 4°26'15.4"E	E Me	Fishing ground, sedimentary bottom
20	2	2018	BT	275	38°56'6"N 1°57'58.3"E	38°56'6"N 1°57'43.9"E	SO	Detrital bed of muddy sand
22	3	2018	BT	105	38°44'30.5"N 1°46'5.9"E	38°44'30.5"N 1°45'53.3"E	AM	Rhodolith bed with invertebrates
51	4	2018	BT	128	38°44'53.9"N 2°30'41.4"E	38°44'58.9"N 2°30'54.7"E	EB	Coarse sand with dead rhodoliths
60	5	2018	BT	138	38°43'13.1"N 2°29'29.4"E	38°43'5.5"N 2°29'20.4"E	EB	Coastal detrital with sand
66	6	2018	BT	146	38°41'13.9"N 2°28'11.3"E	38°41'7.1"N 2°28'1.9"E	EB	Coastal detrital with sand and small dead rhodoliths
52	7	2018	RD	109	38°44'13.2"N 2°30'3.6"E	38°44'12.5"N 2°30'12"E	EB	Rhodolith bed
50	8	2019	BT	102	38°43'33.6"N 1°48'12.6"E	38°43'34.7"N 1°48'23.4"E	AM	Rhodolith bed with invertebrates
99	9	2019	BT	131	38°46'20"N 1°48'54.7"E	38°46'29.3"N 1°49'36.1"E	AM	Coastal detrital with sand and sponges
104	10	2019	BT	118	38°45'57.6"N 1°51'2.5"E	38°46'4.8"N 1°51'8"E	AM	Coastal detrital
124	11	2019	BT	152	38°45'19.1"N 2°31'0.5"E	38°45'20.9"N 2°31'8.4"E	EB	Detrital border
135	12	2019	BT	169	38°44'42.7"N 2°29'25.8"E	38°44'21.2"N 2°29'15.8"E	EB	Detrital border with sand
136	13	2019	BT	147	38°44'42.7"N 2°29'25.8"E	38°43'13.1"N 2°29'21.5"E	EB	Detrital border with gross black sand
166	14	2019	BT	433	38°44'3.1"N 2°28'12.7"E	38°43'44.4"N 2°28'1.2"E	EB	Detrital mud
167	15	2019	BT	151	38°42'21.6"N 2°29'37.3"E	38°42'12.6"N 2°29'29.4"E	EB	Detrital border with sand
175	16	2019	BT	410	38°46'21"N 2°30'44.3"E	38°46'31.1"N 2°31'5.9"E	EB	Detrital mud
177	17	2019	BT	156	38°43'57.7"N 2°28'54.1"E	38°43'47"N 2°28'53.4"E	EB	Detrital border with sand
95	18	2019	RD	275–220	38°47.8'0"N 1°52.6'0"E	38°47.7'0"N 1°52.4'0"E	AM	Rocky slope
103	19	2019	RD	302–231	38°47.4'0"N 1°47.2'0"E	38°47.3'0"N 1°47.2'0"E	AM	Rocky slope
224	20	2019	GOC-73	252	39°3'3.6"N 2°42'2.9"E	39°5'15.7"N 2°42'13.3"E	SW Ca	Fishing ground, sedimentary bottom
225	21	2019	GOC-73	754	38°57'11.5"N 2°37'54.1"E	39°0'2.9"N 2°38'33"E	SW Ca	Fishing ground, bathyal mud
1	22	2020	BT	289	38°58'0.5"N 2°0'22.7"E	38°58'14.9"N 2°0'0"E	SO	Detrital with encrusting sponges and small crustaceans

(Continued)

Table 1 (continued)

R _{survey}	R _{study}	Year	Sampling device	Depth (m)	Coordinates		Area	Seabed characteristics
					Initial	Final		
17	23	2020	BT	113	38°45'15.5"N 1°46'53.4"E	38°45'4.7"N 1°46'36.1"E	AM	Rhodolith bed with invertebrates
18	24	2020	BT	114	38°45'15.5"N 1°46'53.4"E	38°45'16.2"N 1°46'54.1"E	AM	Rhodolith bed with invertebrates
45	25	2020	BT	147	38°42'51.8"N 2°30'13.7"E	38°42'28.1"N 2°29'24"E	EB	Coarse sand and gravel with crustaceans and sponges
52	26	2020	BT	320	38°45'47.5"N 2°31'0.5"E	38°45'56.9"N 2°30'37.1"E	EB	Organogenic sediments, shells rests and gravel with sponges
3	27	2020	RD	288–318	38°56'4.7"N 1°59'48.1"E	38°56'44.5"N 1°59'46.3"E	SO	Rocks and rests of fossil Ostreids
7	28	2020	RD	325–255	38°58'41.9"N 1°59'2.4"E	38°58'33.6"N 1°59'8.5"E	SO	Rocks, rests of fossil Ostreids and fossil corals
8	29	2020	RD	315–295	38°58'11.3"N 2°0'30.6"E	38°58'12"N 2°0'25.2"E	SO	Rocks and rests of fossil Ostreids
14	30	2020	RD	325–270	38°55'33.6"N 1°58'5.6"E	38°55'45.1"N 1°58'1.2"E	SO	Mud, rocks and fossil Ostreids
20	31	2020	RD	104–138	38°42'51.1"N 1°46'28.2"E	38°43'14.5"N 1°46'27.5"E	AM	Rhodolith bed with sponges
27	32	2020	RD	222–195	38°47'31.2"N 1°52'43.7"E	38°47'28.7"N 1°52'31.8"E	AM	Carbonated rocks with encrusting sponges and gravels
28	33	2020	RD	135–140	38°45'56.5"N 1°51'51.5"E	38°46'3.7"N 1°51'45.7"E	AM	Rhodolith bed and rocks with sponges
43	34	2020	RD	118–116	38°44'25.1"N 2°30'40.3"E	38°44'26.9"N 2°30'33.5"E	EB	Rhodolith bed and rocks with sponges
46	35	2020	RD	280–306	38°42'21.6"N 2°30'44.3"E	38°42'31.3"N 2°30'42.5"E	EB	Basaltic rocks and fossil Ostreids with encrusting sponges
94	36	2020	GOC-73	142	39°1'13.8"N 2°51'2.5"E	39°2'16.8"N 2°49'43.7"E	SW Ca	Fishing ground, sedimentary bottom
07_1	37	2020	ROV	249–122	38°45'44.7"N 1°46'0.8"E	38°45'22.3"N 1°46'22.1"E	AM	Sedimentary slope and rhodolith bed with sponges
13	38	2020	ROV	465–352	38°48'22.3"N 1°52'57"E	38°48'26.3"N 1°52'39.4"E	AM	Rocky slope with large sponges
23	39	2020	ROV	133–169	38°44'27.6"N 2°29'15"E	38°44'40.2"N 2°29'43.4"E	EB	Rocky slope, rhodolith bed with sponges and corals
24	40	2020	ROV	150–134	38°44'46"N 2°29'28.3"E	38°44'57.5"N 2°29'54.2"E	EB	Rocky slope and summit, rhodolith bed with sponges and corals

Note:

(R_{survey}) reference number in the survey. (R_{study}) correspondent reference in the present study. (GOC-73) experimental bottom trawl net. (BT) beam trawl. (DR) rock dredge. (ROV) Remote Operated Vehicle Liropus 2000. (SO) Ses Olives. (AM) Ausias March. (EB) Emile Baudot. (E Me) eastern Menorca. (SW Ca) south-western Cabrera Archipelago.

of EB there is the so-called Emile Baudot scarpment, which descend down to 2,600 m deep and connects the EB to the abyssal plain of the Algerian sub-basin (between the Balearic Islands and the Algerian coast) (*Acosta et al., 2004*).

The Algerian sub-basin hydrodynamics are mainly affected by density gradients, receiving warm and less saline Atlantic waters (*Pinot, López-Jurado & Riera, 2002*). These

surface waters have high seasonal temperature variation, ranging from 13 °C during winter to 26 °C during summer, when a strong vertical temperature gradient is established between 50 and 100 m deep. The water column below this depth shows fewer variations than in other parts of the western Mediterranean Sea, being mainly influenced by the Levantine Intermediate Water (LIW). This water mass, originated in the eastern Mediterranean, has temperature and salinity around 13.3 °C and 38.5 ppt, respectively, and is situated approximately between 200 and 700 m deep, just above the Western Mediterranean Deep Water, which is located in the lowest part of the water column (*Monserrat, López-Jurado & Marcos, 2008*). The western Mediterranean Intermediate Water, characterized by lower temperature (~12.5 °C) because it is formed during winter in the Gulf of Lions by deep convection when sea-air heat flux losses are high enough, is found at 100–300 m deep, but does not reach the Mallorca Channel every year (*Monserrat, López-Jurado & Marcos, 2008*).

Within the general oligotrophy of the Mediterranean, the southern Balearic Islands waters in the Algerian sub-basin show more pronounced oligotrophy than waters of the Balearic sub-basin located north of the Archipelago, and above all than the adjacent waters off the Iberian Peninsula and the Gulf of Lions (*Estrada, 1996; Bosc, Bricaud & Antoine, 2004*). The lack of supply of nutrients from land runoff and the lower influence of shelf/slope fronts flowing along the Iberian Peninsula and the northern insular shelf edge could explain these differences (*Massutí et al., 2014*; and references cited therein).

Sampling

Sponge samples were collected at SO, AM and EB seamounts with a Jennings type beam trawl (BT) of 2 and 0.5 m horizontal and vertical openings, respectively, and a 5 mm mesh size cod-end, a rock dredge (RD) and the Remote Operated Vehicle (ROV) Liropus 2000 with an extensible arm. Sampling was performed during INTEMARES research surveys carried out in 2018, 2019 and 2020 on board of the R/Vs *Angeles Alvariño* and *Sarmiento de Gamboa* (*Fig. 1*). Additional samples from trawl fishing grounds of the continental shelf off Mallorca and Menorca were collected during the MEDITS research surveys carried out in 2017, 2019 and 2020 using the bottom trawl net GOC-73 of 2.5–3 and 18–22 m vertical and horizontal openings, respectively and a 10 mm mesh size cod-end, on board the R/V *Miquel Oliver* (*Fig. 1*). The sampling strategy of the MEDITS surveys is detailed in *Bertrand et al. (2002)* and *Spedicato et al. (2019)*. BT and GOC-73 have been shown effective for sampling macro-benthic species of the epibenthic and nektobenthic communities of sedimentary bottoms, respectively (*Reiss, Kröncke & Ehrlich, 2006; Fiorentini et al., 1999; Ordines & Massutí, 2009*). The SCANMAR and MARPORT systems were used to control the deployment and retrieval of both gears to the bottom. By contrast, RD and ROV were used for sampling rocky bottoms and steep slopes. A summary of sampling stations used in the present work can be found in *Table 1*.

On board, specimens were photographed and stored in absolute EtOH. External morphology, color and texture were annotated prior to conservation. Spicule preparations and histological sections were made according to the standard methods described by *Hooper (2003)*. All the specimens were deposited in the Marine Fauna Collection (<http://www.ma.ieo.es/cfm/>) based at the Centro Oceanográfico de Málaga (Instituto

Español de Oceanografía), with the numbers from CFM7356 to CFM7417 and CFM7450-CFM7451 (Table S1).

The electronic version of this article in Portable Document Format (PDF) will represent a published work according to the International Commission on Zoological Nomenclature (ICZN), and hence the new names contained in the electronic version are effectively published under that Code from the electronic edition alone. This published work and the nomenclatural acts it contains have been registered in ZooBank, the online registration system for the ICZN. The ZooBank LSIDs (Life Science Identifiers) can be resolved and the associated information viewed through any standard web browser by appending the LSID to the prefix <http://zoobank.org/>. The LSID for this publication is: (urn:lsid:zoobank.org:pub:47EC2384-A88C-4654-8425-A7A46BC47AC5). The online version of this work is archived and available from the following digital repositories: PeerJ, PubMed Central and CLOCKSS.

Morphological descriptions

Spicules were observed with a Nikon S-Ke optical microscope and photographed with a CMOS digital camera. Images were processed using the Fiji software ([Schindelin et al., 2012](#)). Whenever possible, at least 30 spicules per spicule type were measured. Spicules measures are written as length: min-average-max × thickness: min-average-max μm. Tangential and transversal thick sections were made with a scalpel and, if necessary, dehydrated with alcohol, mounted in DPX and observed under a compound microscope. Aliquots of suspended spicules were transferred onto foil, air dried, sputter coated with gold and observed under a HITACHI S-3400N scanning electron microscope (SEM).

Molecular analysis

DNA was extracted from a piece of choanosomal tissue (~2 cm³) using the DNeasy Blood and Tissue Extraction kit (QIAGEN). Polymerase chain reaction (PCR) was used to amplify the Cytochrome C Oxidase subunit I (COI; DNA barcoding) and the C1-D2 domains of the 28S ribosomal gen, with the universal primers LCO1490/HCO2198 ([Folmer et al., 1994](#)) and C1' ASTR/D2 ([Vân Le, Lecointre & Perasso, 1993](#); [Chombard, Boury-Esnault & Tillier, 1998](#)), respectively. PCR was performed in 50 μl volume reaction (34.4 μl ddH₂O, 5 μl Mangobuffer, 2 μl DNTPs, 3.5 MgCl₂, 1 μl of each primer, 1 μl BSA, 0.1 μl TAQ and 2 μl DNA). The PCR thermal profile used for COI amplification was (94 °C/5 min; 37 cycles (94 °C/15 s, 46 °C/15 s, 72 °C/15 s); 72 °C/7 min). 28S amplification was carried out as detailed in [Chombard, Boury-Esnault & Tillier \(1998\)](#). PCR products were visualized with 1% agarose gel, purified using the QIAquickR PCR Purification Kit (QIAGEN) and sequenced at MacroGen Inc. (South Korea).

Sequences were imported into BioEdit 7.0.5.2. ([Hall, 1999](#)) and checked for quality and accuracy with nucleotide base assignment. Sequences were aligned using Mafft ([Katoh et al., 2002](#)). The resulting sequences were deposited in the GenBank database (<http://www.ncbi.nlm.nih.gov/genbank/>) under the following accession numbers: MW858346–MW858351 and MZ570433 for COI sequences and MW881149–MW881153 for 28S sequences; Table S1.

To assess the phylogeny of *Foraminospongia balearica* sp. nov. and *Foraminospongia minuta* sp. nov., two different approaches were used: Bayesian Inference (BI) and Maximum likelihood (ML). Here, we selected closely related sequences belonging to the orders Agelasida, Axinellida, Scopalinida and Biemnida, obtained after a BLAST search (Altschul et al., 1990). Additionally, two sequences belonging to the order Suberitida were used as outgroup. A complete list of the used sequences is available at Table S1. BI and ML analyses were performed with the CIPRES science gateway platform (<http://www.phylo.org>; Miller, Pfeiffer & Schwartz, 2010) using Mr Bayes version 3.6.2 (Ronquist et al., 2012) and RAxML (Stamatakis, 2014). For Mr Bayes, we conducted four independent Markov chain Monte Carlo runs of four chains each, with 5 million generations, sampling every 1000th tree and discarding the first 25% as burn-in, while RAXML was performed under the GTRCAT model with 1000 bootstrap iterations. Convergence was assessed by effective sample size (ESS) calculation and was visualised using TRACER version 1.5. Genetic distance (p-distance) and number of base differences between pair of DNA sequences were estimated with MEGA version 10.0.5 software (Kumar et al., 2018).

RESULTS

A total of 60 specimens belonging to two classes, nine orders, 13 families, 15 genera and 19 species were analyzed. All these species were collected at the Mallorca Channel seamounts, while three of them (*Phakellia robusta* Bowerbank, 1866, *Petrosia* (*Petrosia*) *raphida* Boury-Esnault, Pansini & Uriz, 1994 and *Hemiasporea elongata* (Topsent, 1928)) were also found at the continental shelf around Mallorca and Menorca. *In situ* images of some of these sponges, obtained with ROV from the seamounts of the Mallorca Channel, are shown in Fig. 2.

Systematics

Phylum PORIFERA Grant, 1836

Class DEMOSPONGIAE Sollas, 1885

Suborder HETEROSCLEROMORPHA Cárdenas, Perez & Boury-Esnault, 2012

Order AGELASIDA Hartman, 1980

Family HYMERHABDIIDAE Morrow, Picton, Erpenbeck, Boury-Esnault, Maggs & Allcock, 2012

Genus *Foraminospongia* gen. nov.

(Figs. 2B, 2F, 2H, 3, 4, 5, 6; Table 2)

Type species

Foraminospongia balearica sp. nov.

Diagnosis

Hymerhabdiidae with massive, massive-tubular or bushy growth form, with styles, subtylostyles, tylostyles, and rhabdostyles. Besides, curved or angulated oxeas may be present. Ectosome with an aspicular dermal membrane supported by a plumoreticulated skeleton of styles, subtylostyles and tylostyles. Pores grouped into inhalant areas. Choanosome confusedly plumoreticulated.

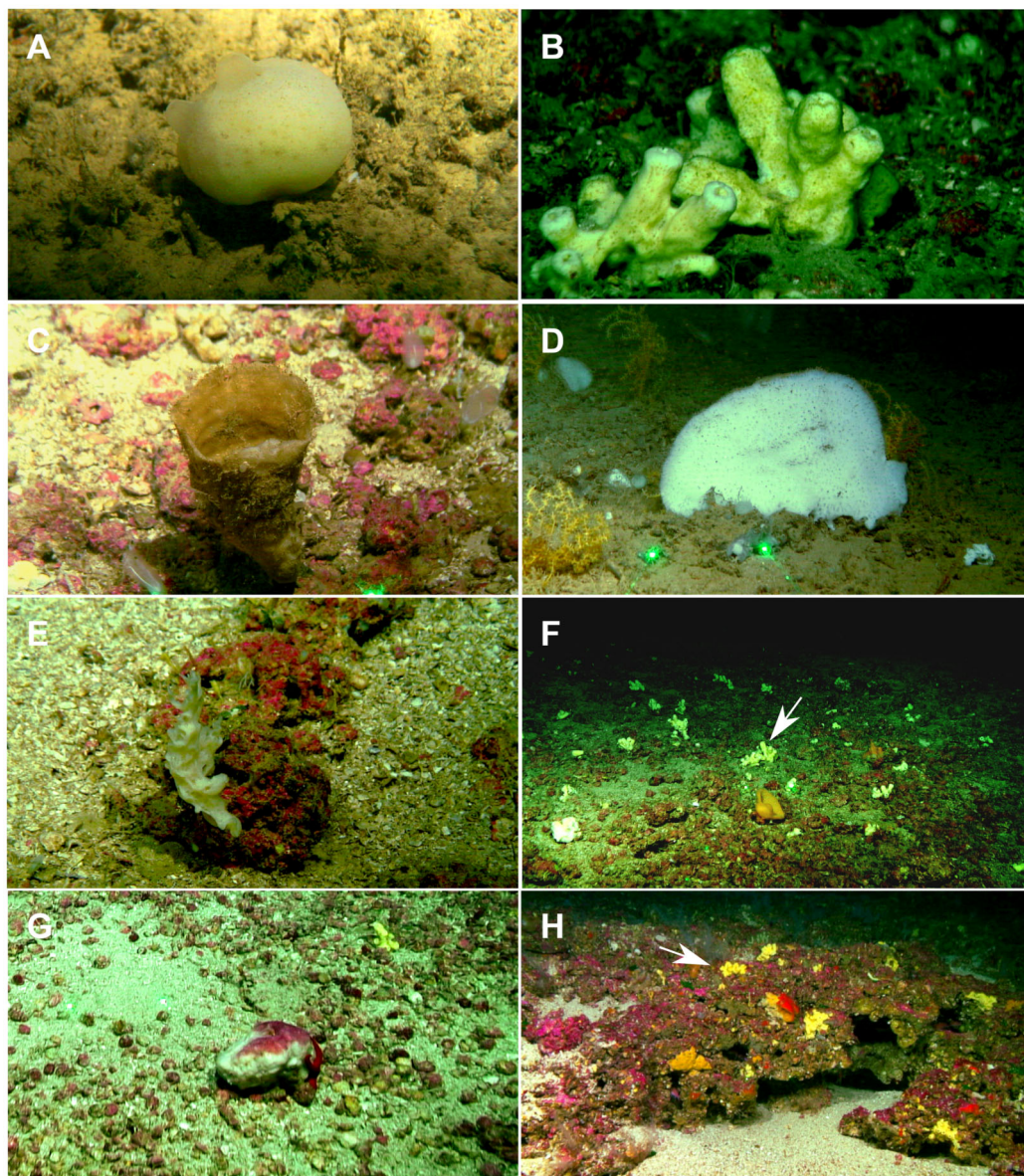


Figure 2 Remote Operated Vehicle (ROV) images of the sponge fauna from the seamounts of the Mallorca Channel, Ses Olives (SO), Ausias March (AM) and Emile Baudot (EB). (A) Specimen of *Polymastia polytylota* collected at 409 m depth in AM. (B) Holotype of *Foraminospongia balearica* sp. nov. collected at 129 m depth in the AM summit. (C) Specimen of *Phakellia ventilabrum* collected at 132 m depth in the EB summit. (D) Uncollected specimen of *Phakellia* sp. at 374 m depth in the north knoll of AM. (E) Specimen of *Haliclona (soestella) fimbriata* collected at 131 m depth in the EB. (F) Rhodolith bed at 110 m depth in the summit of AM, with different sponge species, including *F. balearica* sp. nov. (arrow), (G) uncollected specimen of *Calyx* cf. *tufa* at 106 m depth in the summit of AM, (H) coralligenous bottom at 97 m depth in the summit of AM, with several sponges, including *F. balearica* sp. nov. (arrow). [Full-size !\[\]\(1663bb69f307a960345edb0e712f8c02_img.jpg\) DOI: 10.7717/peerj.11879/fig-2](https://doi.org/10.7717/peerj.11879/fig-2)

Etymology

From the Latin *foramen* (pores) and *spongia* (sponge). The name refers to the fact that in both species, their skin has areas where pores are grouped, giving a characteristic macroscopical appearance.

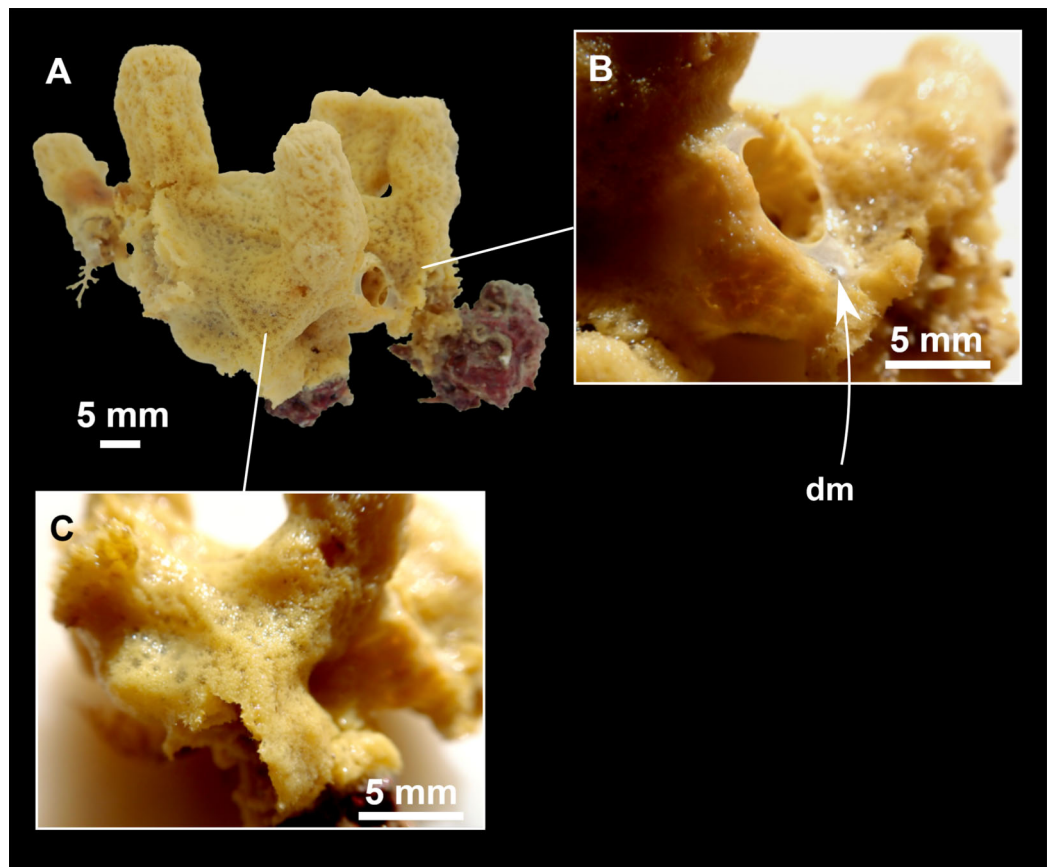


Figure 3 *Foraminospongia balearica* sp. nov. (A) Habitus of CFM-IEOMA-7356/i802 (holotype) in fresh state, with (B) Detail of the oscula and the dermal membrane (dm) and (C) Macroscopic view of the grooves at the skin. [Full-size](#) DOI: 10.7717/peerj.11879/fig-3

Foraminospongia balearica sp. nov.

(Figs. 2B, 2F, 2H, F3, 4, 5; Table 2)

Diagnosis

Massive-tubular to bushy *Foraminospongia*, with styles, rhabdostyles and oxeas.

Etymology

The name refers to the Balearic Islands, the area where the species has been collected.

Material examined

Holotype: CFM-IEOMA-7356/i802, St 37, AM, ROV.

Paratypes: CFM-IEOMA-7357/i144, St 4, EB, BT; CFM-IEOMA-7358/i293_1, St 9, AM, BT; CFM-IEOMA-7359/i239 (not described), St 8, AM, BT; CFM-IEOMA-7360/i745 (not described), St 26, EB, BT; CFM-IEOMA-7361/i824_4, St 39, EB, ROV.

Specimens observed but not sampled: St 12, EB, BT; St 14, EB, BT.

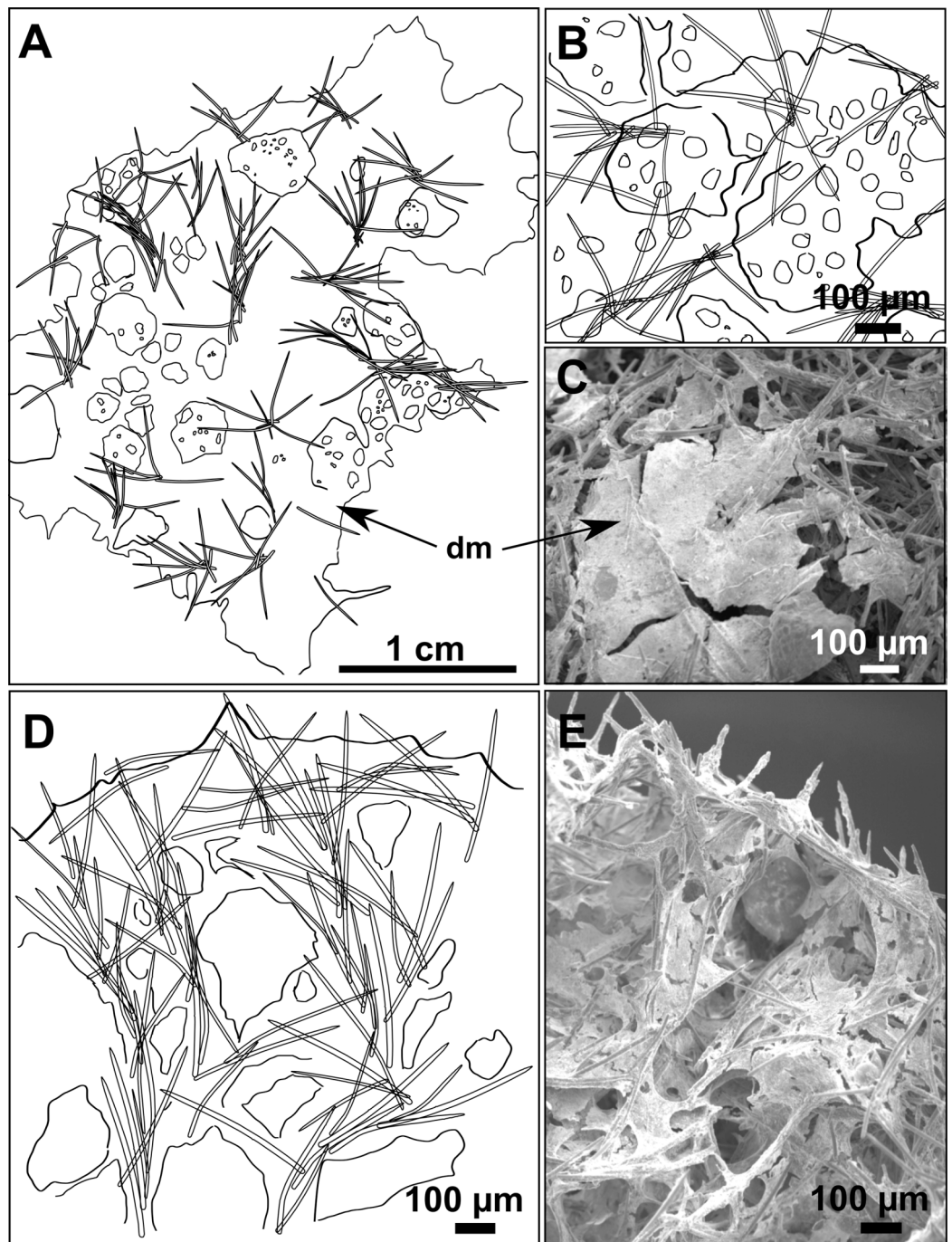


Figure 4 Skeletal arrangement of *Foraminospongia balearica* sp. nov., CFM-IEOMA-7356/i802 (holotype). (A–C) Tangential images of the surface, showing the dermal membrane (dm). (D–E) Transversal sections. [Full-size !\[\]\(5f471a71b78d7676bc356df190b88ab4_img.jpg\) DOI: 10.7717/peerj.11879/fig-4](https://doi.org/10.7717/peerj.11879/fig-4)

Comparative material

Foraminospongia minuta sp. nov.: CFM-IEOMA-7362/i439, St 27, RD, SO; CFM-IEOMA-7363/i474, St 29, SO, RD.

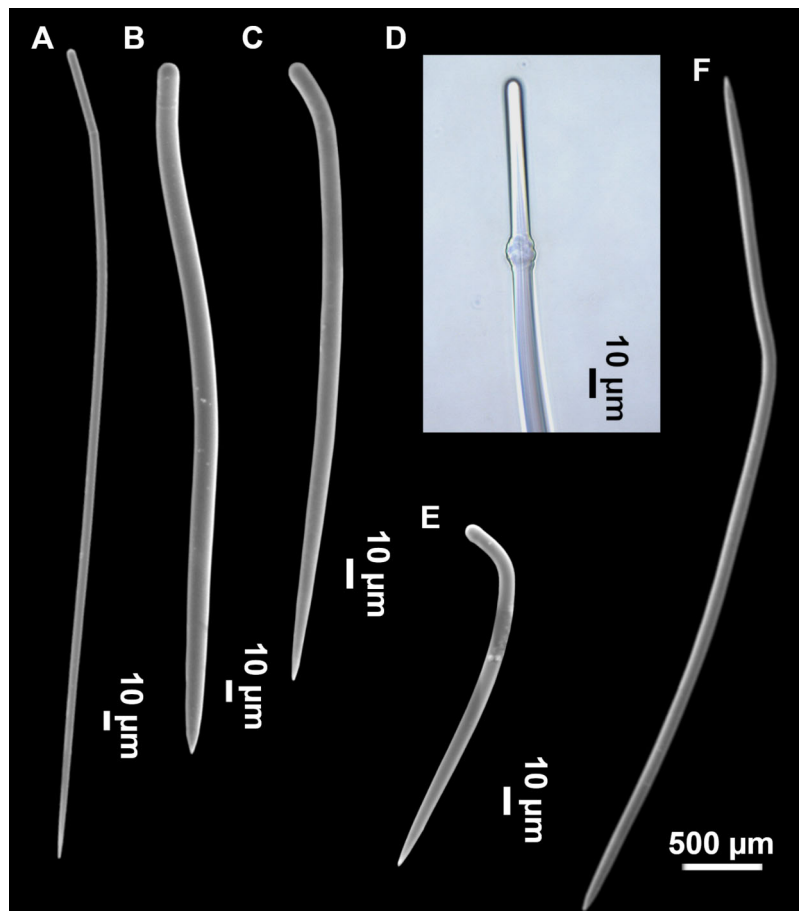


Figure 5 SEM images of the spicules from *Foraminospongia balearica* sp. nov. CFM-IEOMA-7358/i293_1 (paratype). (A–D) Styles. (E) Rhabdostyles. (F) Oxea.

Full-size  DOI: [10.7717/peerj.11879/fig-5](https://doi.org/10.7717/peerj.11879/fig-5)

Rhabderemia sp.: CFM-IEOMA-7415/i729_1 (only a slide deposited at the CFM-IEOMA), St 35, EB, RD.

Description

Massive-tubular or bushy sponges (Figs. 2B, 2F, 2H and 3A). Largest specimens up to 6 cm in diameter. When present, tubes are 2–3 cm in height and 1 cm in diameter. Sometimes several tubes are fused on another of its sides. Consistency slightly elastic, brittle, easily broken when manipulated. Surface smooth, rough to the touch. Color in life golden yellow, tan after preservation in EtOH. A translucent membrane is present, more evident near the oscula (Fig. 3B). Subdermal grooves forming a visible pattern (Fig. 3C). Circular oscula 0.3–0.6 cm. In most cases, oscula are placed at the end of tubes, however, the holotype also has a large osculum in the main body (Fig. 3B).

Skeleton

Ectosome characterized by a plumoreticulated tangential skeleton and a dermal membrane (Figs. 4A, 4B and 4C). In some areas of the dermal membrane there are small

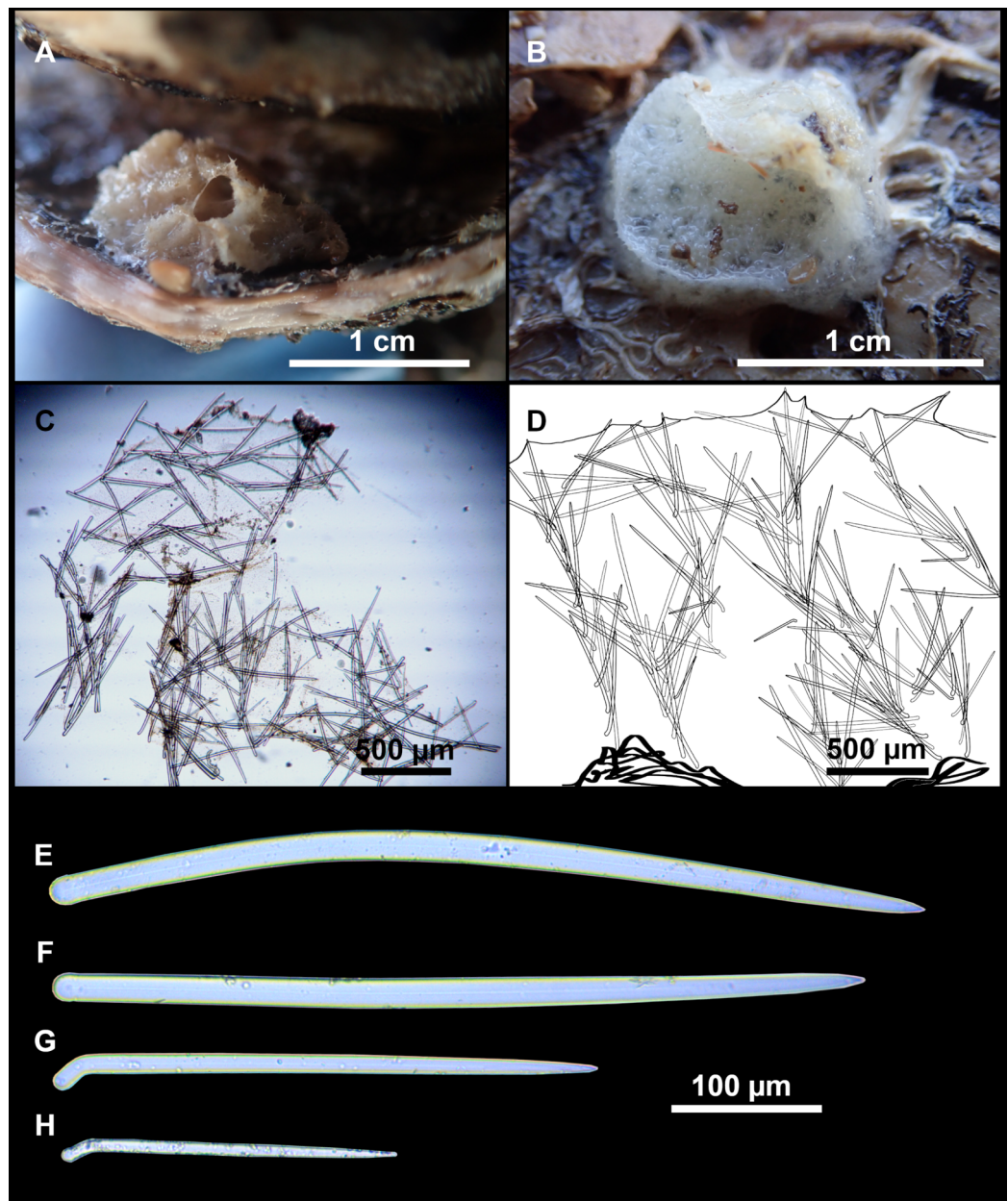


Figure 6 *Foraminospongia minuta* sp. nov. (A) Habitus of CFM-IEOMA-7362/i439 (holotype) on fresh state. (B) On deck image of CFM-IEOMA-7363/i474 (paratype). (C) Optic microscope image of the tangential skeleton of the holotype. (D) Schematic illustration of the choanosome of the holotype. (E–F) Styles. (G–H) Rhabdostyles. [Full-size !\[\]\(1679558f37f6db0dd8360a2a7e913e90_img.jpg\) DOI: 10.7717/peerj.11879/fig-6](https://doi.org/10.7717/peerj.11879/fig-6)

pores gathered. These porae areas correspond to the grooves that are perceptible to the eye. Choanosome, confusedly plumoreticulated with extensive spaces and ascending spicule tracts of 2–5 styles, sometimes protruding the surface. The tracts contain abundant spongin. In between the tracts transversal spicules are abundant (Figs. 4D–4E).

Table 2 Comparative characters of *Foraminospongia balearica* sp. nov. and *Foraminospongia minuta* sp. nov.

Specimen	Style	Rhabdostyle	Oxea	Depth	Area
<i>Foraminospongia balearica</i> sp. nov.					
CFM-IEOMA-7356/i802 Holotype	188– <u>378</u> –492 × 6– <u>11</u> –14	90–179 × 4–7 (<i>n</i> = 9)	456–609 × 9–11 (<i>n</i> = 3)	249–122	AM St 13
CFM-IEOMA-7357/i144 Paratype	197– <u>378</u> –501 × 4– <u>9</u> –12	108–164 × 3–5 (<i>n</i> = 5)	249– <u>493</u> –656 × 4– <u>8</u> –12 (<i>n</i> = 15)	128	EB St 4
CFM-IEOMA-7358/i293_1 Paratype	179– <u>356</u> –516 × 3– <u>8</u> –14	138–179 × 3–6 (<i>n</i> = 5)	328– <u>527</u> –763 × 3– <u>8</u> –13	127	AM St 9
CFM-IEOMA-7361/i824_4 Paratype	177– <u>403</u> –634 × 5– <u>9</u> –13	92–165 × 3–6 (<i>n</i> = 9)	600 × 9 (<i>n</i> = 1)	133–169	EB St 39
<i>Foraminospongia minuta</i> sp. nov.					
CFM-IEOMA-7362/i439 Holotype	283– <u>509</u> –658 × 9– <u>14</u> –21	175–262 × 7–9 (<i>n</i> = 7)	np	318–288	SO St 26
CFM-IEOMA-7363/i474 Paratype	244– <u>416</u> –555 × 10– <u>14</u> –20	147–232 × 7–9 (<i>n</i> = 4)	np	315–295	SO St 28

Note:

Depth (m), area (SO, Ses Olives; AM, Ausias March; EB, Emile Baudot) and sampling station (St; see *Rstudy* in Table 1) where these specimens were collected are also shown. Spicule measures are given as minimum-mean-maximum for total length × minimum-mean-maximum for total width. A minimum of 30 spicules per spicule kind are measured, otherwise it is stated. All measurements are expressed in μm . Specimen codes are the reference numbers of the CFM-IEOMA/and author collection. np, not present.

Spicules

Styles (Figs. 3A–3D): Fusiform, most gently curved, but sometimes abruptly curved once or twice. When the curvature is in the last portion of the spicule, they may resemble rhabdostyles. Roundish heads and sharp tips, sometimes telescoped, strongylote forms present. Swellings may happen at the head or below, sometimes barely visible, sometimes more patent, rarely tuberculated (Fig. 3D). Size range constant between specimens, not influenced by depth nor area (Table 2). They measure 177–375–634 × 3–9–14 μm . Rhabdostyles (Fig. 3E): Uncommon. Abruptly curved below the head. Stylote, subtylote and tylote modifications present. Round head and acerated tips. They measure 90–143–179 × 3–5–7 μm . Oxeas (Fig. 3F): specimens Curved or bent, with one, two or several curvatures, sometimes slightly sinuous. Tips acerated or telescoped. They measure 249–520–763 × 3–8–13 μm . Their abundance varies between specimens.

Genetics

Two *COI* Folmer fragment sequences were obtained for the Holotype (CFM-IEOMA-7356/i802) and for one paratype (CFM-IEOMA-7358/i293_1) (Genbank id's MW858346 and MW858347, respectively). Besides, we obtained a 28S sequence (C1-D2 domains) for the Holotype (GenBank id MW881153).

Ecological notes

The species is very abundant on the EB and AM, between 100 and 169 m (Table 2). It can be mainly found on rhodolith beds and sedimentary bottoms with gravel, together with other sponges like *Poecillastra compressa* (Bowerbank, 1866), *Axinella* spp.,

Halichondria spp. or some Haplosclerids, as well as with a very broad number of crustaceans and echinoderms. It was also collected down to 433 m (St 14).

***Foraminospongia minuta* sp. nov.**

(Fig. 6; Table 2)

Diagnosis

Small, massive-encrusting and greyish in color *Foraminospongia*, with only styles and rhabdostyles as spicules.

Etymology

The name refers to the small size of the two collected specimens.

Material examined

Holotype: CFM-IEOMA-7362/i439, St 27, SO, RD.

Paratype: CFM-IEOMA-7363/i474, St 29, SO, RD.

Comparative material

Foraminospongia balearica sp. nov.: CFM-IEOMA-7357/i144, St 4, EB, BT; CFM-IEOMA-7358/i293_1, St 9, AM, BT; CFM-IEOMA-7356/i802, St 37, AM, ROV; CFM-IEOMA-7361/i824_4, St 39, EB, ROV.

Rhabderemia sp.: CFM-IEOMA-7415/ i729_1, St 35, EB, RD.

Description

Small massive-encrusting sponge (Figs. 6A and 6B), about 1.5 cm in diameter and 0.5 cm in height. Consistency: compressible and slightly crumbly. Velvety surface. The holotype was brownish due to mud, the paratype was greyish, both in life and after preservation in EtOH. Translucent membrane that can be peeled off is present, with grooves forming a distinguishable pattern (Fig. 6B). A single, circular oscule is present on the holotype.

Skeleton

The ectosome consists of a tangential reticulation of styles (Fig. 6C), and some loose rhabdostyles.

The choanosome is a plumoreticulated net of styles, with some loose rhabdostyles (Fig. 6D).

Spicules

Styles (Figs. 6E and 6F): Fusiform, gently curved or straight. Heads roundish and swelled in most cases. Sharp tips. Most are tylota. Size range variable between the holotype and the paratype (Table 2). They measure 244–465–658 × 9–14–21 μm.

Rhabdostyles (Figs. 6G and 6H): Uncommon. Abruptly curved below the head, most with roundish, tylota modifications at the head and sharp tips. They measure 147–209–262 × 7–8–9 μm.

Genetics

Sequences of *COI* Folmer fragment and 28S C1-D2 domains were obtained for the holotype and deposited in Genbank under accession numbers [MW858348](#) and [MW881151](#), respectively.

Ecological notes

Both specimens were found at SO, between 288 and 318 m deep, associated to hard bottoms with fossil ostreids reefs.

Remarks on *F. balearica* sp. nov. and *F. minuta* sp. nov.

Regarding the interspecific variability of *F. balearica* sp. nov., the spicules of the studied specimens are in the same size range, except for the styles of the specimen from AM (CFM-IEOMA-7358/i293_1), which are shorter and thinner than those of the specimens from EB. Also, specimen CFM-IEOMA-7358/i293_1 has much more abundant oxeas than the others.

Regarding *F. minuta* sp. nov., the features of this species support the differential diagnostic characters of the genus *Foraminospongia* (plumoreticulated choanosomal skeleton, ectosome formed by a reticulation of spicules, dermal aspicular membrane with poral areas, presence of large styles and small rhabdostyles), but differs from *F. balearica* sp. nov. in its external morphology, being much smaller and massive-encrusting compared to massive-tubular or bushy and of a greyish color instead of golden yellow in the latter. Also, the spicular complement is different: *F. minuta* sp. nov. lacks oxeas and has longer and thicker styles and rhabdostyles. The differences in the size of the styles between the holotype and the paratype are notable, considering that both were collected at similar depths and habitats. These differences could suggest intraspecific variability for the spicule size within the species; however, more specimens are needed to corroborate this statement.

The morphological differences between the two species are backed by genetic results. The phylogenetic reconstructions for *COI* and 28S fragments show well-supported separation between the two *F. balearica* sp. nov. sequences and the *F. minuta* sp. nov. sequence. Between the two species, the differences in bp and p-distance (in percentage) for *COI* Folmer and the 28S fragments were 1 bp/0.2% and 1bp/0.1%, respectively.

Remarks on the genus *Foraminospongia*

The family Hymerhabdiidae was recently erected to include the genera *Hymerhabdia*, *Prosuberites* and some species of the polyphyletic genus *Axinella* and *Stylissa* ([Morrow et al., 2019](#)). Here, we propose *Foraminospongia* as a new hymerhabdiid genus. The main differences between *Foraminospongia* gen. nov. and both *Hymerhabdia* and *Prosuberites* are the growing habit, with *Foraminospongia* gen. nov. being massive, massive-tubular or bushy against encrusting. Also, it differs from *Prosuberites* in the presence of rhabdostyles and oxeas. However, the presence of rhabdostyles and oxeas is shared with *Hymerhabdia*, but the genetic differentiation between *Foraminospongia* and *H. typica* (type species of *Hymerhabdia*) is clear ([Fig. 7](#)). In addition, the ectosome with a dermal membrane and grouped pore areas of *Foraminospongia* is not present in any

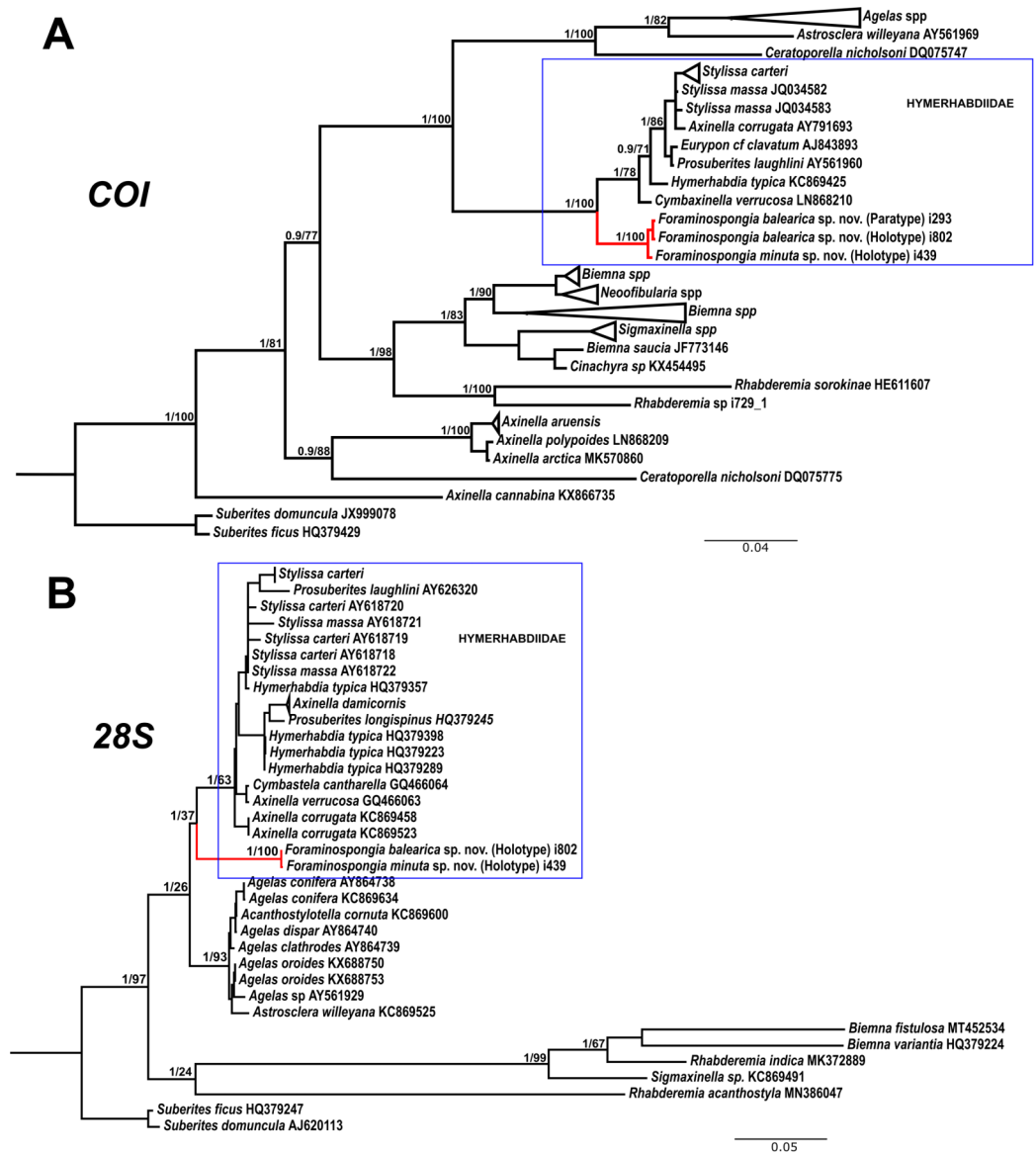


Figure 7 Phylogenetic tree topology for specimens of *Foraminospongia balearica* sp. nov., *Foraminospongia minuta* sp. nov. described in the present study and other related Agelasids. The tree was constructed with Maximum likelihood and Bayesian inference, based on COI (A) and 28S (B) fragments. Posterior probabilities and bootstrap support values are shown at the nodes. A sequence of *Suberites domuncula* and *Suberites ficus* are used as outgroups in both trees.

Full-size DOI: 10.7717/peerj.11879/fig-7

Hymerhabdia apart *Hymerhabdia oxecta* (Dendy, 1924) that has a dermal membrane, although neither Dendy nor the re-examination done by Van Soest & Hooper (1993) described pore areas. Therefore, *H. oxecta* could represent an intermediate stage between genuine *Hymerhabdia* and *Foraminospongia* species. However, the last statement is only speculative and must be checked in future works.

As stated before, there are species of *Axinella* and *Stylissa* that are grouped inside Hymerhabdiidae. Although currently all these species are kept in Axinellida and

Suberitida, respectively (Van Soest et al., 2021), they are phylogenetically related to *Foraminospongia* (see Fig. 7). To resolve this relatedness, we have included in the phylogenetic analysis sequences of *A. damicornis* (Esper, 1794), *A. verrucosa* (Esper, 1794), *A. corrugata* (George & Wilson, 1919), *S. carteri* (Dendy, 1889) and *S. massa* (Carter, 1887) used by Morrow et al. (2012) to define Hymerhabdiidae. The resulting trees show that those species are clearly different from *Foraminospongia*, which is corroborated by their morphology (Pansini, 1984; Hooper & Van Soest, 2002).

The genus *Rhabderemia* (Order Biemnida, family Rhabderemiidae) resembles *Foraminospongia* in having rhabdostyles and possessing a plumoreticulated choanosomal skeleton. However, most *Rhabderemia* also have peculiar rugose microscleres (thraustoxeas, spirosigmata, thraustosigmata, microstyles). To clarify the potential relatedness of *Rhabderemia* and *Foraminospongia*, we have included in the phylogenetic analyses the species *Rhabderemia sorokinae* Hooper, 1990, *R. indica* Dendy, 1905 and *R. destituta* Van Soest & Hooper, 1993. Moreover, we included in the COI tree one sequence of an encrusting *Rhabderemia* sp. (CFM-IEOMA-7415/ i729_1; Genbank ID MZ570433) collected at the EB, with spined rhabdostyles, toxas and spirosigmata (Fig. 7B). Other sequences of Biemnida available at the genbank have also been included (see Table S1).

The sequence of *Rhabderemia* sp. (CFM-IEOMA-7415/ i729_1; Genbank ID MZ570433) clustered together with *R. sorokinae*, a Great Barrier Reef sponge which also has spined rhabdostyles, toxas and spirosigmata, in addition to microspined microstyles, a fact that confirms that archetypical rhabderemids are not related to *Foraminospongia*. However, microscleres are lacking in *R. mona* (de Laubenfels, 1934) and *R. destituta*, so they resemble *Foraminospongia*. *Rhabderemia mona* is a Caribbean sponge described from bathyal depths off Puerto Rico, used to erect the genus *Stylospira* for “sponges having no spicules other than peculiar spirally twisted styles” (de Laubenfels, 1934). This single specimen was later studied by Van Soest & Hooper (1993) on a revision of the genus, who concluded that *Stylospira* should be considered a subgenus of *Rhabderemia*. Van Soest & Hooper (1993) also described *R. destituta* from the Galapagos Islands, a second species matching de Laubenfels’ diagnosis. Interestingly, apart from the lack of any kind of microscleres (even though de Laubenfels reported raphides for *R. mona*, not found by Van Soest & Hooper, 1993), both species had smooth rhabdostyles, just as *Foraminospongia*, which is in contrast to most of the other *Rhabderemia* spp. Among the 30 known species of the genus, only *R. stellata* (Bergquist, 1961), *R. spirophora* (Burton, 1931), *R. gallica* (Van Soest & Hooper, 1993), *R. profunda* (Boury-Esnault, Pansini & Uriz, 1994), *R. africana* Van Soest & Hooper, 1993, *R. prolifera* Annandale, 1915 and *R. meirimensis* Cedro, Hajdu & Correia, 2013 have smooth rhabdostyles.

Unfortunately, there are no sequences available for *R. mona* nor *R. destituta*, so their potential relatedness with *Foraminospongia* cannot be addressed. However, it should be noted that both species have only rhabdostyles as megascleres, which is in contrast to the heterogeneous set of megascleres shown by *Foraminospongia* (styles, tylostyles, subtylostyles, rhabdostyles and oxeas). This seems a strong argument against congeneric relatedness with *Foraminospongia*. However, this issue should be properly addressed in the future when sequences of *R. mona* and *R. destituta* become available.

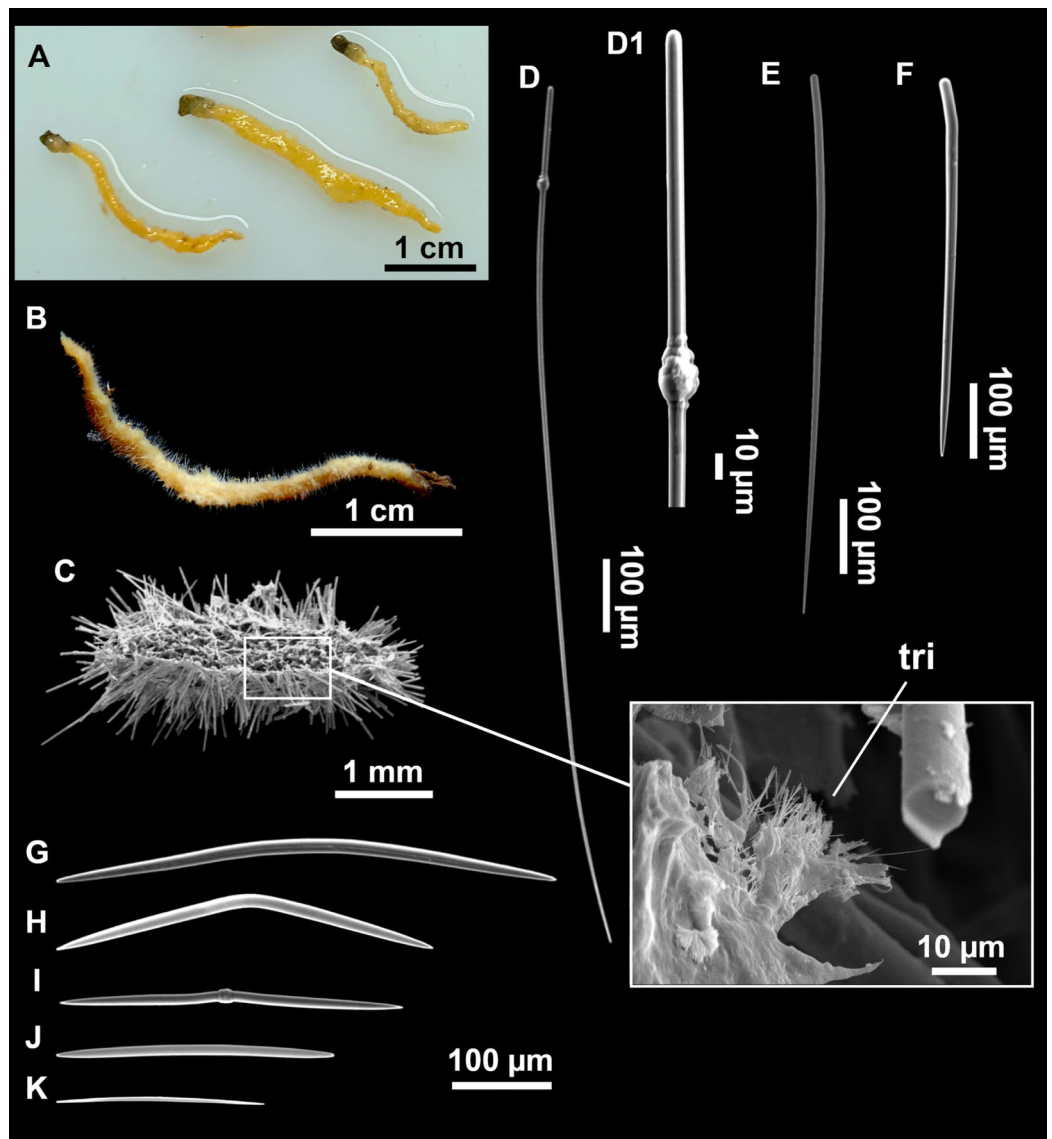


Figure 8 *Axinella spatula* Sitjà & Maldonado, 2014. (A) Photograph of fresh material deposited under CFM-IEOMA-7364-7366/i338_1A-1C. (B) Habitus of CFM-IEOMA-7366/i338_1C preserved in EtOH. (C) SEM images of the skeletal structure of CFM-IEOMA-7366/i338_1C with detail of the inner ectosomal layer, with trichodragmata (tri). (D) Long styles with (D1) subterminal swelling. (E) Regular shaped style. (F) Style with rhabdose modification. (G) Oxea asymmetrically curved. (H) Oxea centrocurved. (I) Oxea centrotylota. (J-K) Small oxeas. [Full-size !\[\]\(5f471a71b78d7676bc356df190b88ab4_img.jpg\) DOI: 10.7717/peerj.11879/fig-8](https://doi.org/10.7717/peerj.11879/fig-8)

Order AXINELLIDA Lévi, 1953

Family AXINELLIDAE Carter, 1875

Genus *Axinella* Schmidt, 1862

Axinella spatula Sitjà & Maldonado, 2014

(Fig. 8; Table 3)

Table 3 Comparative characters of the collected specimens of *Axinella spatula* Sitjà & Maldonado, 2014, and those reported for the type material (Sitjà & Maldonado, 2014).

Specimen	Styles	Oxeas	Trichodragmata	Color	Depth	Area
MNCN-Sp145-BV33A <i>Sitjà & Maldonado (2014)</i> Holotype	165–1050 × 3–15	180–520 × 2.5–15	25–30 × 5–8	Beige after EtOH	134–173	Alboran Island
MNCN-Sp188-BV41A <i>Sitjà & Maldonado (2014)</i> Paratype	119–1400 × 4–15	190–750 × 5–20	25–35 × 5–8	Beige after EtOH	102–112	Alboran Island
MNCN-Sp57-BV21B <i>Sitjà & Maldonado (2014)</i> Paratype	245–1225 × 8–18	120–432 × 9–12	25–30 × 6–10	Black after EtOH	93–101	Alboran Island
CFM-IEOMA-7364/i338_1A This work	349– <u>613</u> –1161 × 7– <u>13</u> –16 (<i>n</i> = 20)	187– <u>374</u> –507 × 5– <u>11</u> –16	32– <u>39</u> –47 × 5– <u>7</u> –10	Orange in life orange beige after EtOH	152	EB St 11
CFM-IEOMA-7365/i338_1B This work	248– <u>900</u> –1304 × 11– <u>17</u> –26 (<i>n</i> = 17)	219– <u>377</u> –485 × 7– <u>11</u> –16	36– <u>45</u> –56 × 5– <u>7</u> –8 (<i>n</i> = 9)	Orange in life orange beige after EtOH	152	EB St 11
CFM-IEOMA-7366/i338_1C This work	332– <u>638</u> –1265 × 4– <u>12</u> –17 (<i>n</i> = 23)	247– <u>332</u> –493 × 7– <u>10</u> –16	32– <u>39</u> –52 × 5– <u>7</u> –11	Orange in life orange beige after EtOH	152	EB St 11

Note:

Depth (m), area (EB, Emile Baudot) and sampling station (St; see *Rstudy* in Table 1) where these specimens were collected are also shown. Spicule measures are given as minimum-mean-maximum for total length × minimum-mean-maximum for total width (or as they appear in the cited texts). A minimum of 30 spicules per spicule kind are measured, otherwise it is stated. All measurements are expressed in μm . Specimen codes are the reference numbers of the CFM-IEOMA/and author collection for the Balearic specimens and the reference numbers of Invertebrate Collection of the National Museum of Natural Sciences (MNCN) of Madrid for *Sitjà & Maldonado (2014)* specimens.

Material examined

CFM-IEOMA-7364/i338_1A, CFM-IEOMA-7365/i338_1B and CFM-IEOMA-7366/i338_1C, St 11, EB, BT.

Description

Small, erect, cylindrical, and slightly flattened sponges, up to 3 cm height and 2–3 mm width (Figs. 8A–8C). Very hispid all along the body. Orange in life (Fig. 8A) and orange beige after preservation in EtOH (Fig. 8B).

Skeleton

As in *Sitjà & Maldonado (2014)*.

Spicules**Megascleres**

Styles (Figs. 8D–8F): with a wide size range, rounded ends and sharp tips. Straight or slightly curved. The largest ones may be slightly sinuous, sometimes with subterminal swellings (Fig. 8D1). Rhabdostyle modifications are present in small and intermediate intermediate stages (Fig. 8F). They measure 248–722–1304 × 4–14–17 μm .

Oxeas: curved or bent, sometimes centrotlyote (Figs. 8G–8K), with the curvature point at the center or displaced towards one of the extremities. Tips acerated. They measure 187–357–507 × 5–11–16 μm .

Microscleres

Raphides in trichodragmata (Fig. 8C, detail), abundant and of the same morphology in all specimens. They measure 32–40–56 × 5–7–11 μm .

Ecology notes

Found only on the north-eastern part of EB, at 152 m deep, on gravel bottoms with dead rhodoliths and with a large abundance of sponges such as *P. (Petrosia) ficiformis* (Poiret, 1789), *P. (Petrosia) raphida* Boury-Esnault, Pansini & Uriz, 1994, *P. (Strongylophora) vansoesti* Boury-Esnault, Pansini & Uriz, 1994 and several Tetractinellida.

Remarks

The specimens match well with those originally described from the Alboran Sea. Balearic specimens are smaller (maximum height of 3 cm against maximum height of 10 cm in alboran specimens). Also, the size range of their styles and oxeas are not as wide as in Alboran specimens and trichodragmata of our specimens were always longer (Table 3).

Sitjà & Maldonado (2014) described two phenotypes, according to the color acquired after preservation in EtOH (black or beige). Also, they found skeletal variations linked to each group, corresponding to a higher or lower presence of short styles, the morphology of the trichodragmata or the skeletal arrangement. The specimens collected here correspond only to the beige phenotype.

With the present record, the species distribution widens towards the north-western Mediterranean Sea, since previously it was known only for the type's location, at the Alboran Island (*Sitjà & Maldonado, 2014*).

***Phakellia robusta* Bowerbank, 1866**

Synonymised names.

Phacellia robusta (Bowerbank, 1866) (misspelling of genus name)

Material examined

CFM-IEOMA-7367/i347_2, St 12, EB, BT; CFM-IEOMA-7368/i405 and CFM-IEOMA-7369/i409, St 15, EB, BT; CFM-IEOMA-7370/i414_2, St 16, EB, BT; CFM-IEOMA-7371/i417, St 17, EB, BT; CFM-IEOMA-7372/i712, St 25, EB, BT; CFM-IEOMA-7373/i731, St 35, EB, RD; CFM-IEOMA-7374/POR760, St 20, south-western Cabrera Archipelago, GOC-73; CFM-IEOMA-7375/POR762, St 21, south-western Cabrera Archipelago, GOC-73.

Ecology notes

The species was frequent at the studied area, being found in a broad depth range (150–750 m) on both rocky and sedimentary bottoms. In the trawl fishing grounds of the continental shelf around Mallorca and Menorca it was mostly found below 300 m deep, where most of the collected specimens were larger. In the seamounts of the Mallorca Channel, the species was common on gravel bottoms 150–170 m deep, where specimens tended to be very small (1.5–3 cm in height) and in rocky outcrops and vertical walls, where sizes were intermediate (4–12 cm in height) and large (20–35 cm in height).

Remarks

The species is reported for the first time in the Mallorca Channel, being its second record at the Balearic Islands, where it was previously recorded by *Santín et al. (2018)* from

the Menorca Channel. In the Mediterranean, it is also known from the Gulf of Lions ([Vacelet, 1969](#)), the Tyrrhenian Sea ([Topsent, 1925](#)), the Alboran Sea ([Maldonado, 1992](#)), the Strait of Sicily ([Calcinai et al., 2013](#)) and the Adriatic Sea ([D'Onghia et al., 2015](#)). Besides, the species has been reported from several localities of the North Atlantic including the Gulf of Cadiz ([Sitjà et al., 2019](#)), the Azores Islands ([Topsent, 1904](#)), the Cantabrian Sea ([Ferrer Hernández, 1914](#)) and the North Sea ([Bowerbank, 1866](#)).

***Phakellia ventilabrum* (Linnaeus, 1767)**

Synonymised names

Halichondria ventilabrum (Linnaeus, 1767)

Phacellia ventilabrum (misspelling of genus name)

Phakellia ventilabra (ruling of ICZN)

Spongia strigose Pallas, 1766 (genus transfer & junior synonym)

Spongia venosa Lamarck, 1814 (genus transfer & junior synonym)

Spongia ventilabra Linnaeus, 1767 (genus transfer & incorrect spelling)

Spongia ventilabrum Linnaeus, 1767 (genus transfer)

Material examined

CFM-IEOMA-7376/i822_1, St 39, EB, ROV.

Ecology notes

The single specimen was collected on a rhodolith bed in the summit of the EB at 132 m deep ([Fig. 2C](#)) where, according to preliminary analysis of ROV videos, it seems to be a rare species.

Remarks

This is the first report of the species at the Balearic Islands. The species has been widely reported in the North Atlantic (e.g. [Alvarez & Hooper, 2002](#)), to Greenland ([Lundbeck, 1909](#); [Hentschel, 1929](#)) and Canada ([Lambe, 1900](#)). In the Mediterranean, it has been reported northern of the Iberian Peninsula ([Uriz, 1984](#)), in the Alboran Sea ([Maldonado, 1992](#)) and Corsica ([Vacelet, 1961](#)).

***Phakellia hirondellei* Topsent, 1890**

Synonymised names

Axinella hirondellei Topsent, 1890 (reverted genus transfer)

Phakellia robusta var. *Hirondellei* (Topsent, 1890) (status change)

Tragosia hirondellei (Topsent, 1890) (reverted genus transfer)

Material examined

CFM-IEOMA-7377/i353, St 13, EB, BT; CFM-IEOMA-7378/i623, St 33, AM, RD.

Ecology notes

The species was found at two stations of similar depth (135–147 m) in AM and EB. Both stations are located at the border of the summit, an area that may be affected by enhanced water current and an increase in nutrient and food supply ([Samadi, Schlacher & De Forges, 2007](#); [Rogers, 2018](#)). This could explain the common presence of large erect

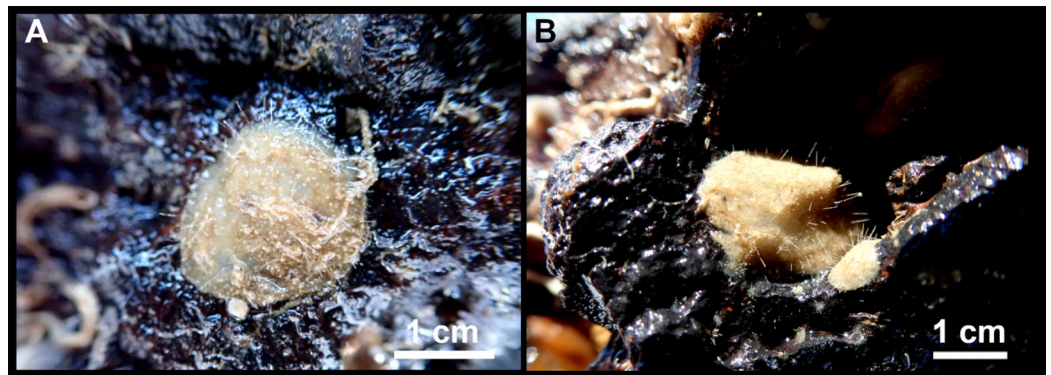


Figure 9 *Heteroxya cf. beauforti*. (A) Habitus of CFM-IEOMA-7380/i726 in fresh state. (B) Habitus of CFM-IEOMA-7382/i461 in fresh state (large patch). [Full-size](#) DOI: [10.7717/peerj.11879/fig-9](https://doi.org/10.7717/peerj.11879/fig-9)

sponges such as *Poecillastra compressa* (Bowerbank, 1866) on stations located at these areas (personal observations).

Remarks

The species is reported for the first time in the Mallorca Channel, being its second record at the Balearic Islands, where it was previously recorded by Santín *et al.* (2018) from the Menorca Channel. In the Mediterranean Sea, it is also known in the north of the Balearic Sea (Uriz, 1984) and in the Gulf of Lions, the Ligurian Sea and Corsica (Fourt *et al.*, 2017) and the Alboran Sea (Boury-Esnault, Pansini & Uriz, 1994).

Family HETEROXYIDAE Dendy, 1905

Genus *Heteroxya* Topsent, 1898

Heteroxya cf. beauforti

(Figs. 9, 10 and 11; Table 4)

Material examined

CFM-IEOMA-7381/i444, St 27, SO, RD; CFM-IEOMA-7382/i461, St 28, SO, RD;
CFM-IEOMA-7450/i487, St 30, SO, RD; CFM-IEOMA-7380/i726, St 35, EB, RD;
CFM-IEOMA-7379/i727, St 35, EB, RD.

Description

Small encrusting patches, circular or irregular, up to 2 cm in diameter (Figs. 9A and 9B). Body less than 1 mm thick. Consistency hard and slightly flexible. Hispidation visible to the naked eye. Greyish in life and after preservation in EtOH. No pores observed.

Skeleton

A basal spongin layer adheres to the substrate and allows the whole body to be peeled-off with a scalpel. Just upon this layer there are Oxea II running parallel to the substrate. The choanosome has low spicule content. Choanosomal chambers are relatively well developed in the thicker parts of the sponge (Figs. 10A and 10B). Thick areas also have ascending tracts of Oxea II, with Oxea II placed in between. The choanosomal tracts are not present in the thinner areas (Fig. 10C). The basal layer and the choanosome have

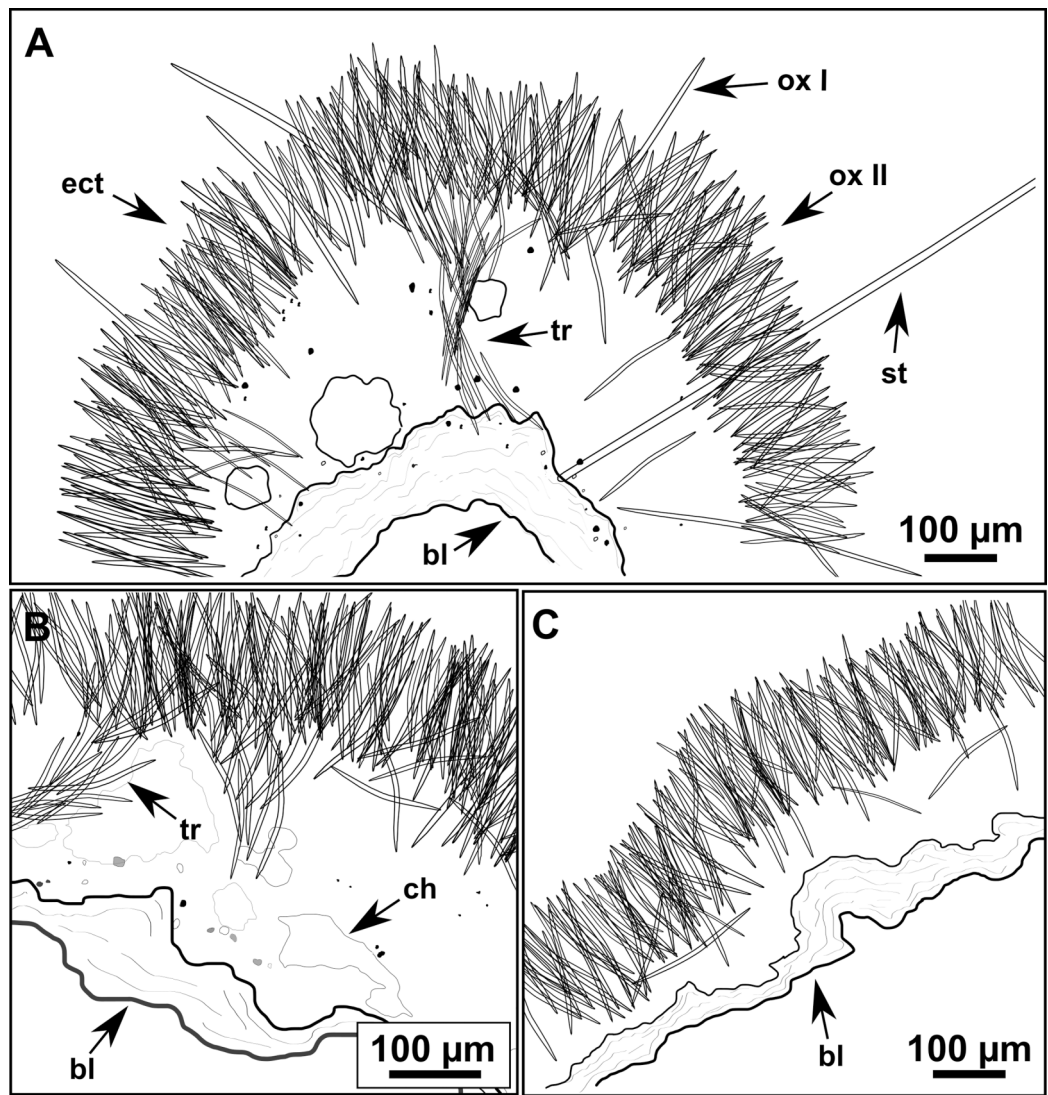


Figure 10 Schematic illustration of *Heteroxya* cf. *beauforti* skeleton in transversal section. (A) General view. (B) Body arrangement on a thick area. (C) Body arrangement on a thin area. (ox I) oxea I. (ox II) oxea II. (bl) basal lamina. (ect) ectosome. (ch) choanosome. (tr) spicule tracks.

Full-size [DOI: 10.7717/peerj.11879/fig-10](https://doi.org/10.7717/peerj.11879/fig-10)

abundant circular bodies 3-9 μm in diameter, dark or transparent (Fig. 10B). The ectosome is constructed by a dense palisade of Oxea II, perpendicular to the surface, with Oxea I placed in the same perpendicular position, emerging towards the exterior. Long styles are found here and there outcrossing the ectosome and causing the hispidation.

Spicules

Oxeas I (Fig. 11A): may be gently curved or bent in the middle, with sharp tips. They measure 319–482–623 \times 7–10–15 μm .

Oxeas II (Figs. 11B): gently curved, curved or bent in the middle. Some stylote modifications present. Many with teratogenic parts like bifid tips, swellings or poliaxonal modifications (Figs. 11C and 11D). They measure 104–198–293 \times 3–7–10 μm .

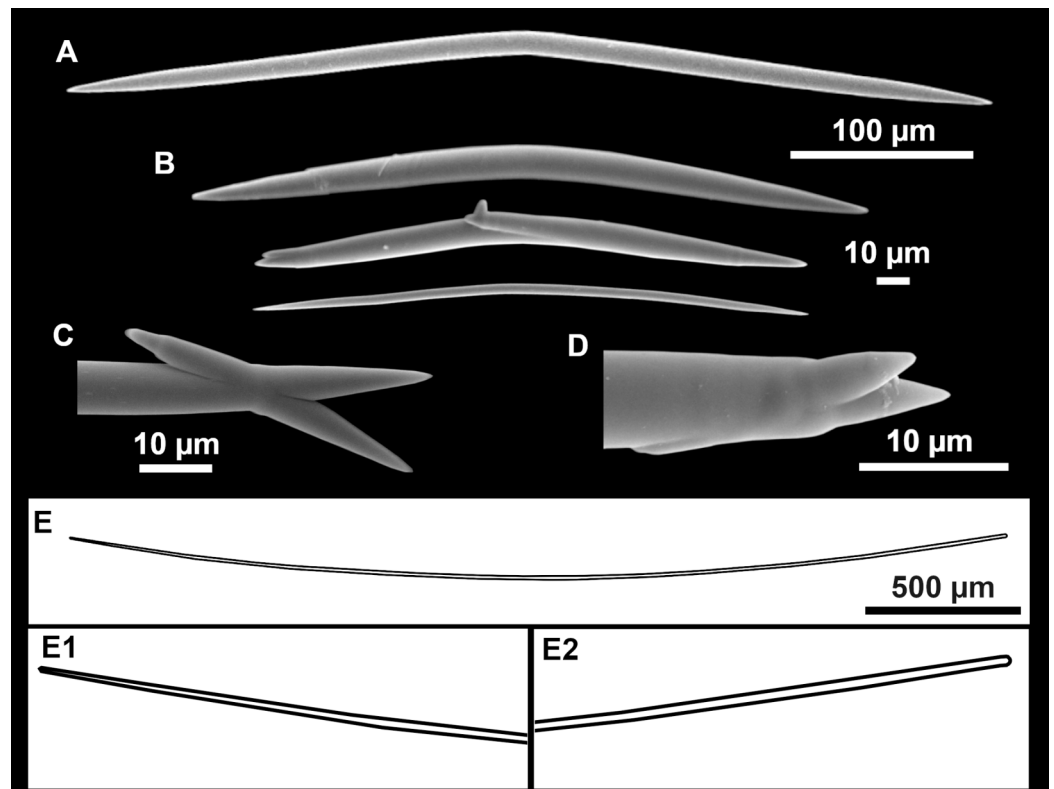


Figure 11 Scicules of *Heteroxya cf. beauforti*. (A) Large oxeas I. (B) Small oxeas II. (C–D) Detail of polyactinal teratogenic modifications of oxeas II. (E) Drawing of a style with details of the tip (E1) and the head (E2).
Full-size [DOI: 10.7717/peerj.11879/fig-11](https://doi.org/10.7717/peerj.11879/fig-11)

Hispidating styles (Figs. 11E–11E2): very long and thin, curved, with round ends and sharp tips. Most broken, only three complete from specimen CFM-IEOMA-7381/i444, measuring $1151\text{--}3502 \times 8\text{--}14 \mu\text{m}$ ($n = 3$).

Ecological notes

The species has been collected on smooth basaltic rocks between 270 and 325 m deep at SO and EB, where it seems to be rather common. Mostly associated with other minute encrusting sponges like *Hamacantha* spp. or *Bubaris* spp.

Genetics

Sequences of *COI* Folmer fragment and the 28S C1–D2 domains were obtained from the specimen CFM-IEOMA-7380/i726. Both sequences were deposited at the Genbank, under the accession numbers [MW858350](https://www.ncbi.nlm.nih.gov/nuclseq/MW858350) and [MW881150](https://www.ncbi.nlm.nih.gov/nuclseq/MW881150), respectively.

Remarks

The genus *Heteroxya* contains two species, *H. corticata* [Topsent, 1898](#) and *H. beauforti* [Morrow, 2019](#). *Heteroxya corticata* is the type of the genus, known only from deep waters (1,200–1,600 m) of the Azores Archipelago. The species has two categories of oxeas, both microspined, and lacks styles. Conversely, *H. beauforti* is known from slightly shallower waters of Ireland (630–1,470 m), has smooth oxeas and possesses long hispidation

Table 4 Comparative characters of species of the genus *Heteroxya*.

Specimen	Oxea I	Oxea II	Style	Depth	Area
<i>Heteroxya corticata</i>					
<i>Topsent</i> , (1898) Syntypes redescribed by <i>Morrow et al.</i> (2019)	1600–1700–2000 × 26–32–37, Microspined ends	235–310–420 × 12–23 Pronounced spination (more at the tips)	np	1165–1240	Azores
<i>Heteroxya beauforti</i>					
<i>Morrow et al.</i> (2019) Holotype	622–1030–1385 × 10–16–21 Smooth	207–280–370 × 11–14–16 Smooth	5000–5650–6300 × 23–25–27	629–1469	Celtic Seas
<i>Heteroxya cf. beauforti</i>					
CFM-IEOMA-7380/i726	434–569 × 7–13 (<i>n</i> = 7) Smooth	107–180–287 × 4–6–9 Smooth	Broken	280–306	EB St 35
CFM-IEOMA-7381/i444	319–467–580 × 6–10–14 (<i>n</i> = 23) Smooth	104–171–257 × 4–6–8 Smooth (<i>n</i> = 23)	1151–3502/8–14 (<i>n</i> = 3)	288–318	SO St 27
CFM-IEOMA-7382/i461	327–460–586 × 6–10–15 Smooth	167–233–286 × 3–7–9 Smooth	Broken	255–325	SO St 28
CFM-IEOMA-7379/i727	420–530–623 × 9–12–15 (<i>n</i> = 18) Smooth	142–192–293 × 6–8–10 Smooth	Broken	280–306	EB St 35
CFM-IEOMA-7450 /i487	nm	nm	nm	270–325	SO St 30

Note:

Depth (m), area (SO, Ses Olives; EB, Emile Baudot) and sampling station (St; see *Rstudy* in Table 1) where these specimens were collected are also shown. Spicule measures are given as minimum-mean-maximum for total length × minimum-mean-maximum for total width. A minimum of 30 spicules per spicule kind are measured, otherwise it is stated. All measurements are expressed in μm . Specimen codes are the reference numbers of the CFM-IEOMA/author collection. np, not present; nm, not measured.

styles (Table 4). The genus was reviewed by *Morrow et al.* (2019), that sequence the COI of both holotypes. They found no differences between the COI of *H. corticata* and *H. beauforti* but conclude that morphological differences were enough to consider both as different species.

Morphologically, our material is more related to *H. beauforti* due to the absence of microspined oxeas and the presence of hispidation styles. We have found circular bodies embedded in the choanosome and the basal layer, which can be equivalent to the spherulous cells found in *H. beauforti* (*Morrow et al.*, 2019). However, oxea I, oxea II and styles are markedly shorter and thinner in our material than those of *H. beauforti*. Those differences may be a result of depth, nutrient, or temperature differences. On the other hand, the COI sequence of our material is identical to the sequences of *H. corticata* and *H. beauforti*. We have sequenced the 28S C1-D2 domains, but there are no published sequences to compare. Considering the lack of genetic differences and the affinity of our material to *H. beauforti*, here we believe that erecting a new species is not justified. Future works using other markers will clarify if *H. cf. beauforti* and *H. beauforti* are conspecific, or if *H. cf. beauforti* is a different species.

Heteroxya cf. beauforti represents the first record of a species belonging to the genus *Heteroxya* in the Mediterranean Sea.

Family STELLIGERIDAE Lendenfeld, 1898

Genus *Paratimea* Hallmann, 1917

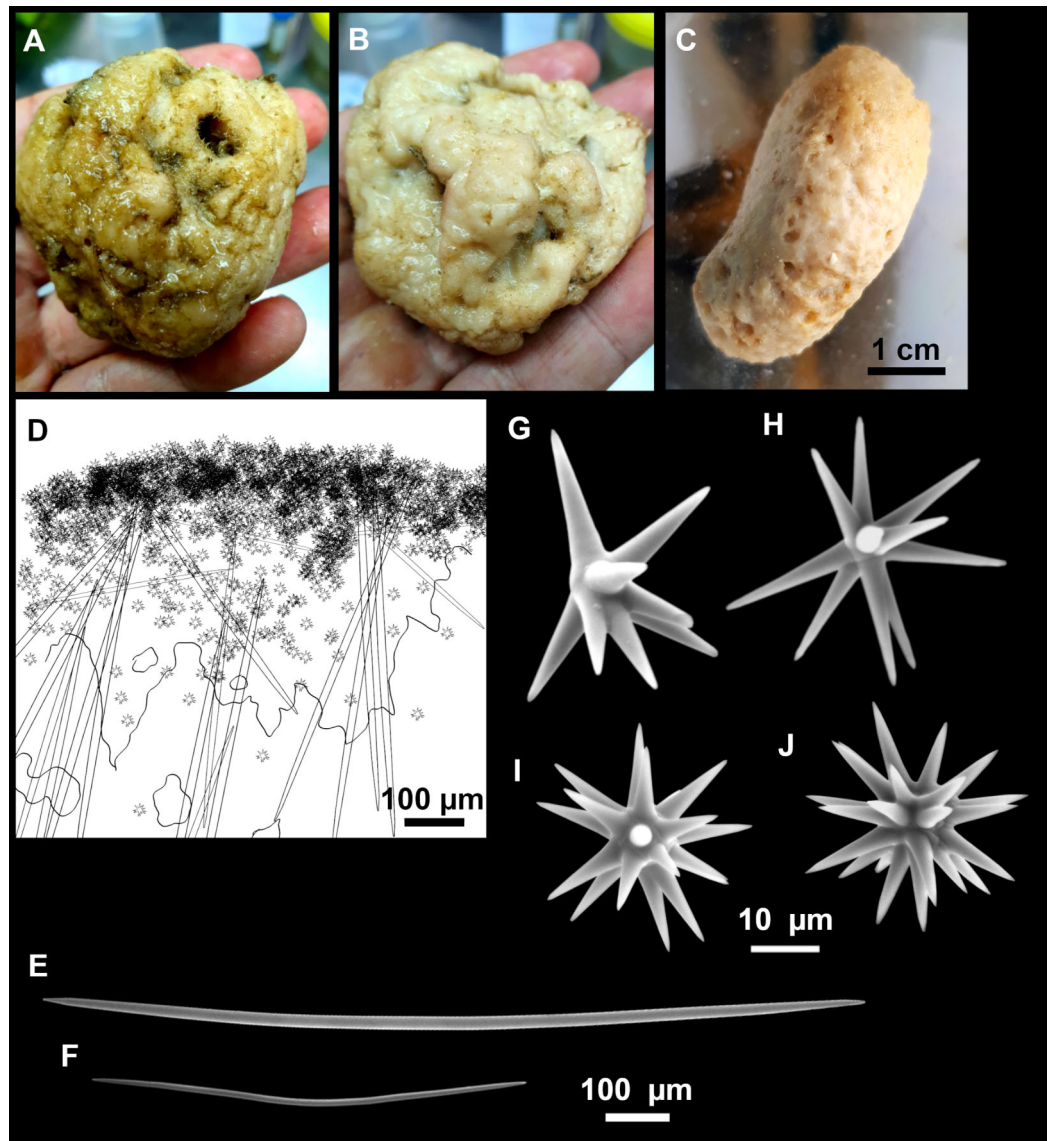


Figure 12 *Paratimea massutii* sp. nov. (A–B) Habitus of the holotype CFM-IEOMA-7383/i403 in fresh state, on its upper (A) and lower (B) sides. (C) Habitus of the paratype CFM-IEOMA-7384/i420 preserved in EtOH. (D) Schematic illustration of a transversal section of the holotype. (E–J) SEM images of the Holotype. (E) Oxea I, (F) Oxea I (auxiliar spicule). (G–J) Oxyasters (all with same bar scale).

Full-size  DOI: [10.7717/peerj.11879/fig-12](https://doi.org/10.7717/peerj.11879/fig-12)

Paratimea massutii sp. nov.

(Fig. 12; Table 5)

Diagnosis

Massive ovoid sponge with oxeas as megascleres and oxeas as auxiliary spicules. Centrotlyotism occasionally present in both. Oxyasters smooth.

Etimology

Dedicated to Professor Enric Massutí, for his contribution to the knowledge of the benthic communities of the Balearic Islands.

Table 5 Comparative characters of *Paratimea* spp. from the Mediterranean and the north-eastern Atlantic, including *Paratimea massuttii* sp. nov.

Species/specimen	Megascleres	Accessory oxeas	Oxyaster	Other spicules	External morphology	Depth	Area
<i>Paratimea massuttii</i> sp. nov.							
CFM-IEOMA-7383/ i403	Oxeas 910–1419–1711 × 16–24–33 (n = 17)	469–681–827 × 3–8–10 (n = 7)	Smooth, 25–36–45 9–25 rays	np	Massive, lobate surface, whitish with diatom brownish on the upper side	151 m	EB St 15
Holotype							
CFM-IEOMA-7384/ i420	Oxeas 1130–1374–1561 × 11–20–28	556–755–862 × 3–6–8	Smooth, 27–39–57 7–20 rays (occasionally 2 rays)	np	same as i403	156 m	EB St 17
Paratype							
<i>Paratimea oxeata</i> Pulitzer-Finall, (1978)							
Holotype	1000–1450 × 14–24	250–650 × 3–7	40–60	np	Thickly encrusting, up to 4 × 5 × 0.4 cm, drab color in life, white after formalin and EtOH	60 and 100–110 m	Bay of Naples
<i>Bertolino et al. (2013)</i>							
Holotype	810–961–1200 × 15–18–25	300–547–700 × 3–5–5	25–42–60	np	Very small (0.5 cm ²) insinuating sponge, grey colored in dry state.	35 m	Ligurian Sea
<i>Morrow et al. (2019)</i>							
Holotype	1000–1500 × 14–24	250–650 × 3–7	20–40 but up to 60 when reduced rays 4–12 rays	np	Massive lobose, surface conulose, oscules arranged on top of raised humps, Pale yellow- cream	Caves, 15–20 m	Gulf of Lion
<i>Paratimea loricata</i> (Sarà, 1958a)							
Holotype	Oxeas, poliaxonic and aberrant terminations. Mostly non- centrotylota. 320–420 × 5–7 (most common) and 600 × 15 (n = 1)	Centrotylote 105–180 × 2–3	Large: 40–50 Small (uncommon): 12–20	Tylostyles, trilobated head 130–170 × 4–7	Encrusting, elastic but friable, whitish-yellow after EtOH	Not specified, infralittoral	Ligurian Sea
<i>Paratimea pierantonii</i> (Sarà, 1958b)							
Holotype and paratypes	Styles and Subtylostyles: 1530–2550/12–18	650–1175 × 4–10, centrocurved, non-centrotylote	15–25	np	Cushion shaped with papillae. Hispid, smooth to the touch. Orange yellow at the surface, brownish inside.	30 cm, tidal cave	Tyrrhenian Sea

(Continued)

Table 5 (continued)

Species/specimen	Megascleres	Accessory oxaeas	Oxyaster	Other spicules	External morphology	Depth	Area
<i>Paratimea arbuscula</i> (Topsent, 1928) Holotype	Curved or flexuous, centrotyle. Some modified to styles. 560–1000 × 5–12	nr	Without centrum, with conical, acanthose actines, 15–60 most with 12 rays	np	Small arbuscular sponge, up to 1 cm in height, 1 mm in width, hispid. Whitish. Asters concentrated at the periphery	650–914 m	Azores
<i>Paratimea duplex</i> (Topsent, 1927) Reproduced from the redescription in Morrow et al. (2019)	Centrotyle oxaeas 2000–2600 × 20–40, styles to subtylostyles 1600–1800 × 25–35	Weakly centrotyle 360–770 × 7–9	Without centrum, smooth rayed, 50–100 10–15 rays	np	cushion shaped, 3 mm thick, with a conulose surface	240–2165 m	North Atlantic Ocean
<i>Paratimea constellata</i> (Topsent, 1904) Holotype, reproduced from Morrow et al. (2019)	Long, slender tylostyles 2500–3000 × 13–14	Centrotyle oxaeas 379–670–900 × 8–10	Smooth-rayed euasters 14–30–46	np	Cushion shaped, 2–3 mm thick, yellow gold	40 m	Roscoff, Celtic seas
<i>Paratimea loenbergi</i> (Alander, 1942) Reproduced from the redescription of the Holotype in Morrow et al. (2019)	1350–3000 × 10–13–15 (n = 4); head, 16–20–27	Slightly bent, 530–712–930 × 5–5–6 (n = 7)	Smooth 22–28–36	Small category of tylostyles not found by Morrow et al. (2019) but mentioned in the original description, measuring 180–225 × 12–15	Thin, hispid crust, pale yellow.	60 m	Väderöfjord, Sweden
<i>Paratimea hoffmannae</i> Morrow & Cárdenas, 2019 Holotype, original description	Large, curved oxaeas, occasionally centrotyle 2056–2187–2250 × 25–26–28	Rare, bent, occasionally centrotyle 353–446–520 × 3–4–5	Asymmetric 42–60–81 μm 7–18 smooth, tapering rays	np	Massive, subspherical. Holotype is ~7 in diameter. Surface covered in large conules, 1–4 mm in height. Creamish white.	328 m (Holotype) 1500 m (Paratype)	Norway (Holotype) Ireland (Paratype)

Note:

Depth, area (EB, Emile Baudot) and sampling station (St; see *Rstudy* in Table 1) where these specimens were collected are also shown. Spicule measures are given as minimum-mean-maximum for total length × minimum-mean-maximum for total width. A minimum of 30 spicules per spicule kind are measured, otherwise it is stated. All measurements are expressed in μm. Specimen codes are the reference numbers of the CFM-IEOMA/author collection. np, not present; nr, not reported.

Material examined

Holotype: CFM-IEOMA-7383/i403, St 15, EB, BT.

Paratype: CFM-IEOMA-7384/i420, St 17, EB, BT.

Description

Both specimens are massive, subspherical, the largest (holotype, CFM-IEOMA-7383/i403; Fig. 12A) measuring about 5 cm in diameter, having a lobose surface with grooves and humps. Skin of a leathery touch, hispid only in the grooves. Color in life differing between the upper and the lower faces, the former having the first a brownish tinge while the latter a whitish to beige shade (Figs. 12A and 12B). After preservation in EtOH the whole body turns homogeneous vanilla cream (Fig. 12C). Both specimens have 4–6 circular oscula, 1–2 mm in diameter, scattered throughout the body. However, the holotype also has a main large and circular osculum, about 1 cm in diameter, on the upper side. Both specimens expelled a considerable amount of mucus when collected.

Skeleton

Ectosome not separable from the choanosome, formed by a dense crust of oxyasters and tangential principal and auxiliary oxeas. Choanosome composed of irregularly arranged oxeas and oxyasters, although radial bundles of large oxeas are present in the periphery, supporting the ectosome (Fig. 12D).

Spicules

Megascleres

Oxea I (Fig. 12E): robust and fusiform, some double bent, sometimes slightly centrotylote. They measure 910–1390–1711 × 11–21–33 μm.

Auxiliary spicules

Oxea II (Fig. 12F): uncommon. Bent or slightly sinuous, sometimes centrotylote. They measure 469–746–1088 × 3–7–10 μm.

Microscleres

Oxyasters (Figs. 12G–12J): with long, smooth and sharp rays. About 7–25 rays, occasionally less. Smaller ones tend to have more rays than larger ones, measuring 25–38–57 μm. Occasionally, some two-rayed oxyaster present.

Ecological notes

Found at two stations on calcareous gravel bottoms on the summit of EB (155 and 167 m deep), which was dominated by sponges such as *Hexadella* sp., *Phakellia robusta* and different species of the order Tetractinellida. A large number of the brachiopod *Gryphus vitreus* (Born, 1778) and echinoderms were also recorded.

Genetics

Sequences of COI Folmer fragment was obtained from the Holotype (CFM-IEOMA-7383/i403) and deposited at Genbank under the accession number MW858351.

Remarks (see Table 5 for a detailed comparison with other *Paratimea* spp.)

Morphologically, the species resembles *Paratimea oxeata* Pulitzer-Finali, Hadromerida & Poecilosclerida, 1978, a Mediterranean species reported at rocky and muddy bottoms, at 35–60 and 110 m deep, respectively (Pulitzer-Finali, Hadromerida & Poecilosclerida, 1978; Bertolino et al., 2013), and at submarine caves at 15–20 m deep (Morrow et al., 2019). However, *P. massutii* sp. nov. is massive, a feature only shared with the cave specimen (S153) reported by Morrow et al. (2019). Notwithstanding, in *P. massutii* sp. nov. oxeas I are thicker, oxeas II longer and oxyasters slightly larger and with more actines (2–25 vs. 4–12). A comparison of the COI sequences between the holotype of *P. massutii* sp. nov. and the cave specimen confirms those morphological differences, with 15 bp differences and a *p*-distance of 2%. On the other side, both the holotype and the specimens studied by Bertolino et al. (2013) differ from *P. massutii* sp. nov. in being cushion shaped or encrusting and having smaller oxeas. Unfortunately, no sequences of Bertolino et al. (2013) specimens are available to compare. *Paratimea massutii* sp. nov. is also similar to *P. hoffmannae* Morrow et al. (2019), a North Atlantic species found in Norway and Ireland that is also massive and subspherical and has oxeas as both megascleres and auxiliary spicules. However, the large oxeas are much larger and thicker than in *P. massutii* sp. nov., in contrast to the auxiliary spicules, which are shorter and thinner. Also, the oxyasters of *P. hoffmannae* are larger and with less actines. As for *P. oxeata*, COI sequences between *P. hoffmannae* and *P. massutii* sp. nov. are notably distant, with 13 bp differences and a *p*-distance of 2%. A similar case happens with *P. lalori* Morrow, 2019 from Ireland. This species is also massive-sub spherical with oxeas as main megascleres and auxiliary spicules. Just as in *P. hoffmannae*, megascleres of *P. lalori* are longer and thicker than those of *P. massutii* sp. nov., auxiliary spicules are shorter and thinner and oxyasters slightly larger and with fewer actines.

Paratimea massutii sp. nov. also differs from the other Mediterranean *Paratimea* spp. as follows: *P. loricata* (Sarà, 1958a) is encrusting, has much smaller oxeas I and oxeas II and two categories of oxyasters, and bears tylostyles; *P. pierantonii* (Sarà, 1958b) is cushion-shaped, has styles and subtylostyles as megascleres, longer, thicker, and never centrotylote oxeas II and smaller oxyasters.

Also, *P. massutii* sp. nov. differs from North-eastern Atlantic *Paratimea* spp. as follows: *P. constellata* is cushion shaped, has tylostyles and smaller oxyasters; *P. arbuscula* (Topsent, 1928), is arbustive, lacks auxiliary spicules and has smaller, acanthose oxyasters; *Paratimea duplex* (Topsent, 1927) is cushion shaped, has much larger oxeas I, bears styles, subtylostyles, and two categories of oxyasters; *P. loennbergi* (Alander, 1942) is thinly encrusting, has tylostyles and smaller oxyasters.

This is the first report of the genus *Paratimea* in the Balearic Islands, and the deepest record in the Mediterranean Sea.

Order BUBARIDA Morrow & Cárdenas, 2015

Family BUBARIDAE Topsent, 1894

Genus *Rhabdobaris* Pulitzer-Finali, 1983

***Rhabdobaris implicata* Pulitzer-Finali, 1983**

Synonymised names

Cerbaris implicatus ([Pulitzer-Finali, 1983](#))

Material examined

CFM-IEOMA-7385/i338_2_1, St 11, EB, BT; CFM-IEOMA-7386/i698, St 34, EB, RD.

Ecological notes

Uncommon sponge found at two stations on the EB summit at 117 and 152 m deep, growing on living rhodoliths. Both stations were rich in massive demosponges, including large Tetractinellids, *Petrosia* (*Petrosia*) *ficiformis* and *P. (Strongylophora) vansoesti*.

Remarks

This is the third time that the species is recorded, previously only known from the holotype collected in Corsica ([Pulitzer-Finali, 1983](#)) and the neotype collected at the Alboran Island ([Sitjà & Maldonado, 2014](#)).

Order DESMACELLIDA Morrow & Cárdenas, 2015

Family DESMACELLIDAE [Ridley & Dendy, 1886](#)

Genus *Dragmatella* Hallman, 1917

Dragmatella aberrans ([Topsent, 1890](#))

([Fig. 13](#); [Table 6](#))

Material examined

CFM-IEOMA-7387/i52_b1, St 2, SO, BT; CFM-IEOMA-7388/i175, St 5, EB, BT.

Description (modified from [Hooper & Van Soest, 2002](#))

Small hollow sponge encrusting on stones or corals. Up to 2 cm in diameter. Whitish grey in life and after preservation in EtOH. Surface smooth, but provided with long thin, pointed fistules ([Figs. 13A](#) and [13B](#)).

Skeleton

Ectosome composed of parallel tight tracts of styles, disposed in 4–5 layers of 30–50 μm in thickness ([Fig. 13C](#)). The raphides, sometimes grouped in trichodragmata, are scattered in the ectosomal and choanosomal tracts. Choanosome is cavernous ([Fig. 13D](#)), with tracts of styles, about 200 μm long, verging from a basal layer towards the ectosome.

Spicules*Megascleres*

Styles ([Figs. 13E](#) and [13E1](#)) fusiform, tapering towards the head, slightly or abruptly bent. They measure 349–546–676 \times 6–10–15 μm .

Microscleres

Raphides ([Figs. 13F](#) and [13F1](#)) abundant, straight, with an irregular shaft and one end hook-shaped, occasionally with central swellings. They measure 162–195–222 \times 1–2–3 μm .

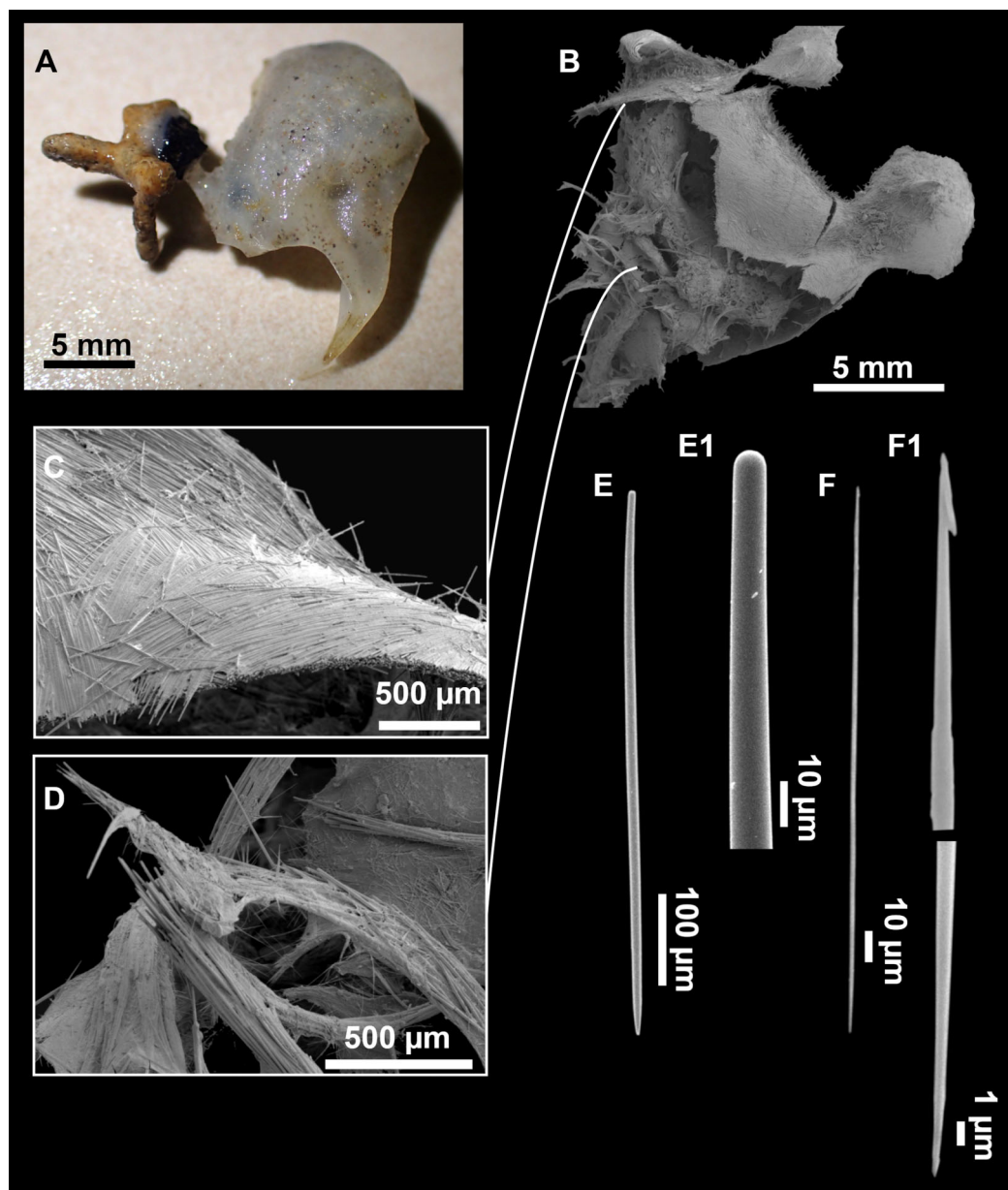


Figure 13 *Dragmatella aberrans* (Topsent, 1890). (A) Habitus of CFM-IEOMA-7388/i175 preserved in EtOH. (B–D) SEM images of the skeletal structure of CFM-IEOMA-7388/i175. (B) General view of the skeletal arrangement. (C) Detail of the ectosome. (D) View of the ascending choanosomal tylostyle tracks. (E–E1) Mycalostyles. (F) Raphides with (F1) Detail of the hook-shaped ends and central irregularities.

Full-size [DOI: 10.7717/peerj.11879/fig-13](https://doi.org/10.7717/peerj.11879/fig-13)

Ecological notes

Abundant species on sedimentary bottoms, with rests of calcareous shells and corals, found in SO, AM and EB and, to a lesser extent, on trawl fishing grounds of the continental shelf off Mallorca (between 138 and 362 m deep). On the same bottoms other small encrusting sponges such as *Hamacantha* spp. or *Bubaris* spp., the pedunculated

Table 6 Comparative characters of representative reports of *Dragmatella aberrans*.

Specimen	Styles	Raphides	Depth	Area
<i>Topsent (1892)</i>	600	180	135–134	Cantabric Sea
<i>Topsent (1928)</i>	600–800 × 9–11.5	70–200 × 12–20	552–1262	Cap Sines (Portugal)
<i>Vacelet (1969)</i>	350–600 × 6–13	150–210	250–324	Cassidaigne (Gulf of Lion)
<i>Pulitzer-Finali (1983)</i>	400–600 × 6–14	200	128–150	Off Calvi (Corsica)
<i>Boury-Esnault, Pansini & Uriz, 1994</i>	315– <u>571</u> –631 × 5– <u>11</u> –16	95– <u>207</u> –260 × 0.4– <u>2</u> –3	485 (Atlantic) 195 (Mediterranean)	Atlantic and Alboran Sea
CFM-IEOMA-7387/i52_b1 This work	349– <u>555</u> –676 × 6– <u>9</u> –13	162– <u>197</u> –222 × 1– <u>2</u> –3	275	SO St 2
CFM-IEOMA-7388/i175 This work	351– <u>539</u> –651 × 8– <u>11</u> –15	163– <u>193</u> –214 × 1– <u>2</u> –3	138	EB St 5

Note:

Depth (m), area (SO, Ses Olives; EB, Emile Baudot) and sampling station (St; see *Rstudy* in Table 1) where these specimens were collected are also shown. Spicule measures are given as minimum-mean-maximum for total length × minimum-mean-maximum for total width. A minimum of 30 spicules per spicule kind are measured, otherwise it is stated. All measurements are expressed in μm . Specimen codes are the reference numbers of the CFM-IEOMA/author collection.

Rhizaxinella pyrifer (*Delle Chiaje, 1828*) and *Thenia muricata* (*Bowerbank, 1858*), the brachiopod *Gryphus vitreus* (*Born, 1778*) and small crustaceans are to be found.

Remarks

The species is easily distinguished by its hollow body and the possession of both styles and raphides. The latter have singular hook-shaped ends, a feature that had not been recorded before, and that is similar to the raphides found in some species of the genus *Dragmaxia* (Order Axinellida) (*Hooper & Van Soest, 2002*). No molecular data are available for *Dragmatella*, but a phylogenetic relationship with *Dragmaxia* is unlikely, given the possession of styles and the skeletal arrangement of both genera. Therefore, hook-shaped raphide are probably homoplastic.

This is the first report of the species in the Balearic Islands. In the Mediterranean Sea it has been recorded at the Gulf of Lions (*Vacelet, 1969*), Corsica (*Pulitzer-Finali, 1983*) and the Alboran Sea (*Boury-Esnault, Pansini & Uriz, 1994*; *Sitjà & Maldonado, 2014*). In the North Atlantic Ocean, this species has been recorded at several locations, including the coast of Portugal (*Topsent, 1895*), the Josephine Bank (*Topsent, 1928*) and the Cantabric Sea (*Topsent, 1890*).

Order HAPLOSCLERIDA *Topsent, 1928*

Family CHALINIDAE Gray, 1867

Genus *Haliclona* Grant, 1841

Subgenus *Soestella* De Weerdt, 2000

Haliclona (Soestella) fimbriata Bertolino & Pansini, 2015

Material examined

CFM-IEOMA-7389/i825_1, St 40, EB, ROV.

Ecological notes

The species was spotted regularly at the rhodolith beds of the EB summit, between 134 and 150 m deep. However, it was less abundant and not forming patches, as occurs in

some areas of the Gulf of St. Eufemia in the Tyrrhenian Sea, where [Bertolino et al. \(2015\)](#) reported densities of 7.4 ± 0.7 specimens/m².

This is the second report of the species, previously recorded only at the Gulf of St. Eufemia (southern Tyrrhenian Sea; [Bertolino et al., 2015](#)), expanding its distribution range towards the westernmost part of the Mediterranean Sea.

Family PETROSIIDAE Van Soest, 1980

Genus *Petrosia* Vosmaer, 1885

Subgenus *Strongylophora* Dendy, 1905

Petrosia (Strongylophora) vansoesti [Boury-Esnault, Pansini & Uriz, 1994](#)

Material examined

CFM-IEOMA-7390/i192_A and CFM-IEOMA-7391/i192_B, St 6, EB, BT; CFM-IEOMA-7392/i313_P and CFM-IEOMA-7393/i313_G, St 11, EB, BT; CFM-IEOMA-7394/i351, St 13, EB, BT; CFM-IEOMA-7395/i694, St 34, EB, RD.

Ecological notes

Large amounts of *P. (S) vansoesti* were collected from various stations in the summit of the EB, suggesting that it is an important species inhabiting Mediterranean seamounts and probably a habitat builder that confers three-dimensionality to the seafloor. The species was found from 116 to 152 m deep, on stations with living and dead rhodoliths and gravels, associated with large sponges such as *P. (P.) ficiformis* and some tetractinellids and halichondrids. Many groups of invertebrates, such as small crustaceans and echinoderms, were also observed at these stations.

Remarks

This is the first record of the species in the western Mediterranean. The type locality is the Gulf of Cadiz, in the north-eastern Atlantic. In the Mediterranean it has been recorded in marine caves at both the Ionian Sea ([Costa et al., 2019](#)) and the Aegean Sea ([Gerovasileiou & Voultziadou, 2012](#)). It has been also recorded at the Levantine Sea, living on rocks at depths shallower than 3 m ([Evcen & Çinar, 2012](#)). On the Balearic Islands, the species has only been collected in EB.

Subgenus *Petrosia* Vosmaer, 1885

Petrosia (Petrosia) raphida [Boury-Esnault, Pansini & Uriz, 1994](#)

([Fig. 14](#); [Table 7](#))

Material examined

CFM-IEOMA-7396/POR406, St 1, south-east of Menorca, GOC-73; CFM-IEOMA-7397/i178_3, St 5, EB, BT; CFM-IEOMA-7451/i242 and CFM-IEOMA-7398/i254_2, St 8, AM, BT; CFM-IEOMA-7399/i305, St 10, AM, BT; CFM-IEOMA-7400/i312, St 11, EB, BT.

Description

Massive sponges, the largest collected specimen measuring about 4.5 cm in diameter and 2.5 cm in height ([Fig. 14A](#)). Whitish in life, beige after preservation in EtOH.

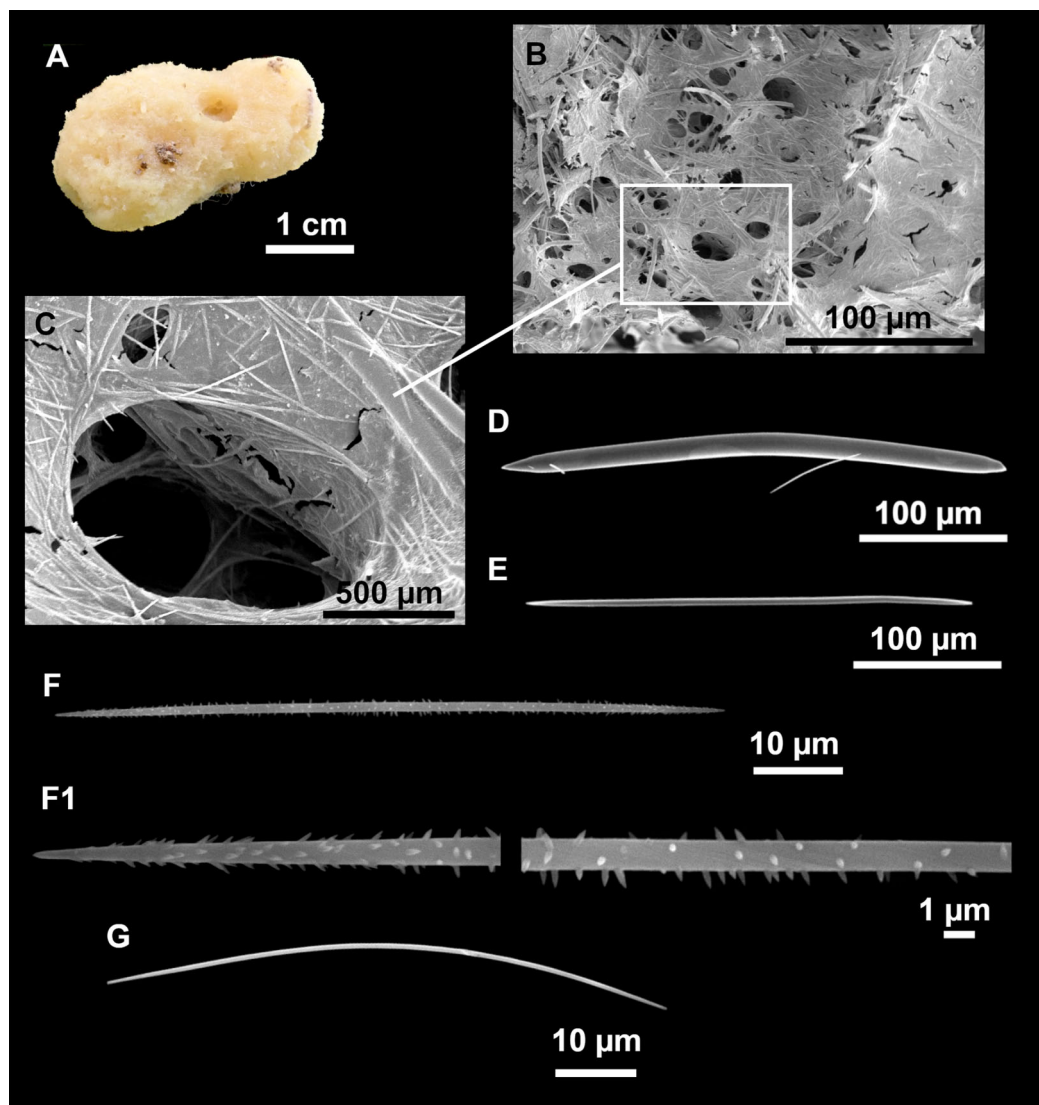


Figure 14 *Petrosia (Petrosia) raphida* Boury-Esnault, Pansini & Uriz, 1994. (A) Habitus of CFM-IEOMA-7451/i242, preserved in EtOH. (B) SEM image of the choanosome. (C) Detail of a choanosomal chamber. (D) Oxeas. (E) Young stages of oxeas. (F–F1) Acanthoses raphides. (G) Smooth raphides.

Full-size DOI: [10.7717/peerj.11879/fig-14](https://doi.org/10.7717/peerj.11879/fig-14)

Consistency hard, slightly crumbly. Surface rough due to minute conules, although in some specimens this is less obvious. There are 1 to 6 circular oscules of 2–5 mm diameter.

Skeleton

Ectosome forming a detachable crust not evident to the naked eye, tightly adhering to the choanosome, and made of irregular net of polygonal to triangular meshes. Meshes are constituted by one or two spicules. Spongin is present and fully embedded with raphides.

Table 7 Comparative characters from published records of *Petrosia (Petrosia) raphida* Boury-Esnault, Pansini & Uriz, 1994 and present work.

Specimen	Oxeas	Raphides	Depth	Area
<i>Boury-Esnault, Pansini & Uriz (1994)</i> Holotype	354– <u>449</u> –499 × 26– <u>32</u> –36 (strongyles)	81– <u>95</u> –108 × 1	580	Gibraltar
<i>Sitjà et al. (2019)</i>	290–500 × 20–25 (rarely as short as 7.5)	75–100 × 1 (some without spines)	530–573	Volcano of Gulf of Cadiz (Pipoca)
CFM-IEOMA-7396/POR406 This work	271– <u>369</u> –432 × 9–13–16	62– <u>78</u> –91 × 1– <u>1</u> –2	134	South-east of Menorca St 1
CFM-IEOMA-7397/i178_3 This work	242– <u>378</u> –450 × 10– <u>16</u> –19	72– <u>80</u> –89 × 2– <u>3</u> –4	138	EB St 5
CFM-IEOMA-7451/i242 This work	268– <u>333</u> –380 × 11– <u>14</u> –17	70– <u>80</u> –91 × 1– <u>2</u> –2	101	AM St 8
CFM-IEOMA-7398/i254_2 This work	300– <u>378</u> –426 × 9– <u>15</u> –19	66– <u>75</u> –86 × 1– <u>2</u> –2	101	AM St 8
CFM-IEOMA-7399/i305 This work	242– <u>346</u> –394 × 9– <u>15</u> –19	65– <u>75</u> –88 × 1– <u>2</u> –2	118	AM St 10
CFM-IEOMA-7400/i312_1 This work	349– <u>403</u> –453 × 8– <u>15</u> –19	70– <u>79</u> –95 × 1– <u>2</u> –2	152	EB St 11

Note:

Depth (m), area (SO, Ses Olives; AM, Ausias March; EB, Emile Baudot) and sampling station (St; see *Rstudy* in Table 1) where these specimens were collected are also shown. Spicule measures are given as minimum-mean-maximum for total length × minimum-mean-maximum for total width. A minimum of 30 spicules per spicule kind are measured, otherwise it is stated. All measurements are expressed in μm . Specimen codes are the reference numbers of the CFM-IEOMA/author collection.

Choanosome (Figs. 14B and 14C) with an isotropic net of pauci-spicular spicule tracts covered by spongin, forming roundish meshes. These meshes are abundantly embedded by raphides. The tracts tend to condense towards the surface, supporting the ectosome.

Spicules

Oxeas (Figs. 14D and 14E): curved, with mucronated ends. Some polyaxonal modification in the shaft and ends may be present. They measure 242–372–450 × 9–15–19 μm , although underdeveloped stages (196–368/3–8 μm) are present. Styles and strongyles of the same length and width as the oxeas, present but scarce.

Raphides (Figs. 14F and 14F1): slightly curved, most minutely spined, although smooth ones are also present (Fig. 14G). They measure 62–77–95 × 1–2–2 μm .

Ecological notes

This species is very common in both AM and EB at the 101–152 m bathymetric range, and has been also found at the same depths off the southern coast of Menorca (Table 7). It can be found as a free-living sponge or growing attached to small fragments of calcareous sediments. However, it is also commonly found as an epibiont of other sponges and rhodoliths. The species seems to prefer massive specimens of *Hexadella* sp. and *Halichondria* sp. as substrate.

Remarks

The species is easily recognized due to the presence of characteristic spined raphides, added to other Petrosid features such as the skeletal architecture and the morphology of the oxeas. Remarkably, the specimens described in this study differ from the two

previous reports in having much smaller oxeas (see below in brackets). This could be explained by the scarcity of nutrients in waters around the Balearic Islands, the bathymetric range in which the specimens were collected and/or differences in water temperature, seasonal variability and population phenotypes (Simpson, 1978; Valisano *et al.*, 2012). These variables could also be the cause of differences in the morphology of the megascleres already noted by Sitjà *et al.* (2019) when comparing their material with the holotype. In the specimens from the Gulf of Cadiz (north-eastern Atlantic), strongyles were rare. Instead, megascleres consisted mostly of oxeas with stepped tips and some occasional stylote or strongylote modifications. This last feature is shared with specimens of the Balearic Islands but not with the holotype, whose spicules have mostly strongylote extremities. These differences may be related to variations in nutrient regimes between the Balearic Islands and these areas (Santinelli, 2015).

This is the first record of the species in the Mediterranean, but at a considerably shallower depth (101–152 m) than in the north-eastern Atlantic, where the species was reported at 580 m deep in the Strait of Gibraltar (Boury-Esnault, Pansini & Uriz, 1994) and at 530–575 m deep in the Gulf of Cadiz (Sitjà *et al.*, 2019) (Table 7).

Family PHLOEODICTYIDAE Carter, 1882

Genus *Calyx* Vosmaer, 1885

Calyx cf. *tufa*

(Fig. 15; Table 8)

Material examined

CFM-IEOMA-7403/i525, St 24, AM, BT; CFM-IEOMA-7401/i75, St 3, AM, BT; CFM-IEOMA-7402/i515, St 23, AM, BT.

Description

Large, massive and semicircular sponges, up to 15 cm in diameter and 5 cm in height (Fig. 15A). Surface smooth to the touch; consistency stony hard and uncompressible. Choanosome slightly friable and cavernous. Color in life beige, with pink tints in the upper side of the body and whitish beige in the lower. It became homogeneous brownish beige after preservation in EtOH. A total of Two to three large and circular oscula are located in the upper side of the body, measuring 1.3 cm in diameter. Ostia grouped in poral areas of the ectosome (Fig. 15B).

Skeleton

The ectosome (Fig. 15C) is formed by a crust of tangential spicules, forming triangular paucispicular meshes that become less dense at the poral areas. Spongin present but not abundant, with a granular appearance due to the presence of spherulous cells filled with granules (Fig 15C, arrow).

The choanosome (Figs. 15D and 15E) is mostly composed of a rather isotropic, unispicular net of spicules.

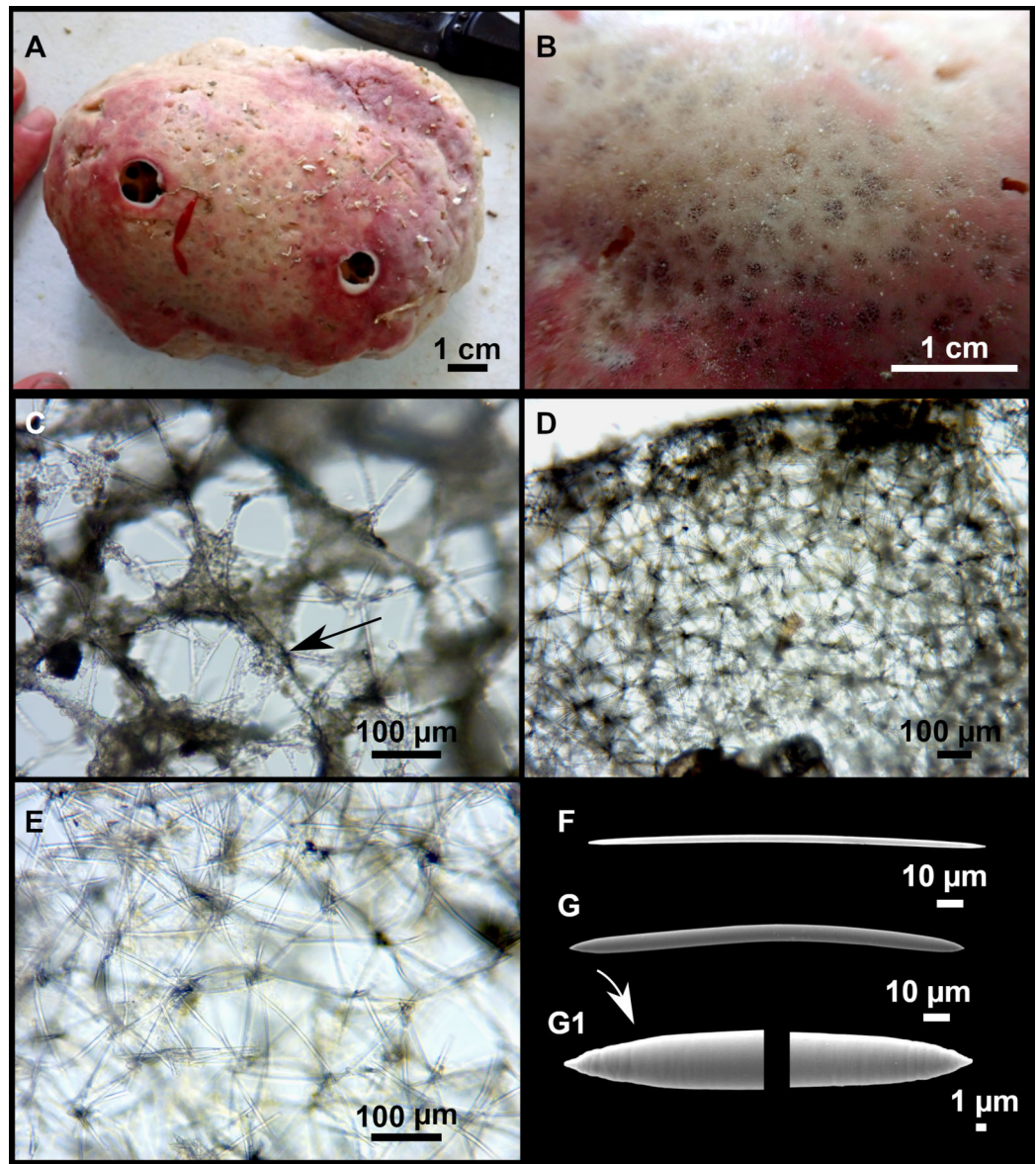


Figure 15 *Calyx cf. tufa*. (A) Habitus of CFM-IEOMA-7403/i525 in fresh state. (B) Detail of the ectosome with poral areas. (C) View of a poral area of the ectosome with spherulous cells (arrow). (D) Transversal section of the choanosome. (E) Detail of the reticulation of the choanosome. (F–G) Immature and mature oxeads, with (G1) Detail of the tips of (G).

Full-size [DOI: 10.7717/peerj.11879/fig-15](https://doi.org/10.7717/peerj.11879/fig-15)

Spicules

Oxeads (Figs. 15F and 15G): slightly curved, with stepped or slightly mucronate points (Fig. 15G1) and rarely bent in the middle. They measure $132\text{--}173\text{--}206 \times 4\text{--}7\text{--}9 \mu\text{m}$.

Genetics

Sequences of COI Folmer and 28S C1–D2 domains were obtained from the specimen CFM-IEOMA-7403/i525 and deposited in Genbank under the accession numbers [MW858349](https://www.ncbi.nlm.nih.gov/nuccore/MW858349) and [MW881149](https://www.ncbi.nlm.nih.gov/nuccore/MW881149), respectively.

Table 8 Comparative characters from *Calyx* cf. *tufa* and *Calyx tufa* Ridley & Dendy, 1886.

Specimen	Oxeas	External morphology	Depth	Area
<i>Calyx</i> cf. <i>tufa</i>				
CFM-IEOMA-7403/i525 This work	146– <u>170</u> –189 × 6– <u>7</u> –8	Large, massive, roundish. Surface smooth. Stony hard and uncompressible. Ectosomal crust present. Beige with pink tints at the upper side. Whitish beige after EtOH	114	AM St 24
CFM-IEOMA-7402/i515 This work	140– <u>171</u> –205 × 4– <u>7</u> –9	As the holotype	113	AM St 23
CFM-IEOMA-7401/i75 This work	132– <u>178</u> –206 × 4– <u>6</u> –9	As the holotype	105	AM St 3
<i>Calyx tufa</i> Ridley & Dendy (1886) holotype	200 × 10	Massive, cake-like. Firm, almost stony, but brittle. Surface smooth but uneven. Dermal membrane (=ectosomal crust) readily peeling off. Vents rather small, circular, flush. Greyish yellow.	219	St Lago, Cape Verde
<i>Topsent</i> (1892)	nr	Firm but crumbly. Without ectosomal crust due to damaging. Light brown.	300	Cantabrian Sea

Note:

Depth (m), area (AM, Ausias March) and sampling station (St; see *Rstudy* in Table 1) where these specimens were collected are also shown. Spicule measures are given as minimum-mean-maximum for total length × minimum-mean-maximum for total width. A minimum of 30 spicules per spicule kind are measured, otherwise it is stated. All measurements are expressed in μm . Specimen codes are the reference numbers of the CFM-IEOMA/and author collection. nr, not reported.

Ecological notes

The species was found only at the summit of AM between 105 and 114 m deep, associated with rhodolith beds. It has also been found amongst with diverse set of sponges, including large Tetractinellids and other sponges such as *Hexadella* sp., *Axinella* spp. or *P. (P.) raphida*, as well as among many other invertebrates typically inhabiting the rhodolith beds, like small crustaceans and echinoderms. The pink coloration of its upper skin is probably caused by symbiotic cyanobacteria, as commonly happens in other Haplosclerids (Rützler, 1990).

Remarks

There are only two reported species of *Calyx* from the north-eastern Atlantic and the Mediterranean: *Calyx nicaeensis* (Risso, 1827) and *C. tufa* (Ridley & Dendy, 1886). The first is the type species of the genus, which is a well-known species characterized by its growing habit (vasiform), blackish color and large size. This species has been widely reported at both the western and eastern Mediterranean in infralittoral and circalittoral bottoms at 3–50 m deep (Trainito, Baldaconi & Mačić, 2020). *Calyx* cf. *tufa* clearly differs from *C. nicaeensis* in morphology (massive vs. vasiform, respectively), genetics (COI: 11 bp difference; 28S: 43 bp difference) and bathymetry (105–114 vs. 3–50 m, respectively). *Calyx tufa* is only known from its type locality at Cape Verde (Dendy, 1886) and from the Cantabrian Sea (Topsent, 1892). The species that we studied shares many characteristics with *C. cf. tufa*, including external morphology, consistency, and skeletal architecture. Unfortunately, the only description available is the one provided by Dendy (1886), which is

too general and matches with the characters of many other *Calyx* spp. (e.g., *Calyx podatypa* de Laubenfels 1934; *Calyx magnoculata* Van Soest, Meesters & Becking, 2014; *Calyx nyaliensis* Pulitzer-Finali, 1983). The large distances between the reports of *C. tufa* and *C. cf. tufa*, the strong genetic barriers that separate the two records (the Strait of Gibraltar and the Almeria-Oran front), the generalized low dispersive potential of some sponge species (Riesgo et al., 2019; Griffiths et al., 2021) and the difference of habitats, are reasons that may suggest that the species that we report here is different from *C. tufa*. Moreover, no intermediate geographical findings have been reported, which would be expected if there was conspecificity (Topsent, 1928; Maldonado, 1992; Boury-Esnault, Pansini & Uriz, 1994; Sitjà & Maldonado, 2014; Sitjà et al., 2019). It should be noted that *C. cf. tufa* is a very large, massive, and easily recognizable sponge, which cannot be easily go unnoticed. However, considering that we did not study the holotype and that no genetic sequences of *C. tufa* are available, the possible conspecificity of *C. cf. tufa* with *C. tufa* cannot be completely assessed. Therefore, future work comparing the holotype of *C. tufa* may be needed to determinate if both species are different or conspecific. Considering the mentioned lack of data, here we use the more conservative choice by assigning the present record to *C. cf. tufa*.

Order POECILOSCLERIDA Topsent, 1928

Family MYXILLIDAE Dendy, 1922

Genus *Melonanchora* Carter, 1874

Melonanchora emphysema (Schmidt, 1875)

(Fig. 16)

Synonymised names

Desmacidon emphysema Schmidt, 1875 (genus transfer)

Material examined

CFM-IEOMA-7404/i573, St 31, AM, RD.

Description

Hollow sponge with a detachable, smooth and paper-like ectosome provided with fistulas (Fig. 16A). About 2 cm in diameter. The choanosome is loose and includes sediment. Greyish white in life and after preservation in EtOH.

Skeleton

As in the previous records of the species (Schmidt, 1785; Vacelet, 1969; Pulitzer-Finali, 1983).

Spicules

Megascleres

Tylotes (Figs. 16B and 16C) slightly curved, with roundish ends. Their length tends to be inversely related to their thickness. They measure 359–446–556 × 5–8–11 μm.

Microscleres

Spheranchoras (Figs. 16D and 16E) of usual morphology, but uncommon. They measure 36–40–46 × 14–19–23 μm ($n = 11$).

Arcuate isochela I (Fig. 16F) with well-developed fimbriae and spatulated and bifid alae. They measure 29–42–47 μm.

Arcuate isochela II (Fig. 16G) similar to isochela I, but with rounded alae. They measure 14–18–21 μm.

Ecological notes

The single specimen was found in AM, on a rhodolith bed between 104 and 138 m deep. It was growing upon a large rhodolith, which was extensively epiphyted by encrusting, massive-encrusting or pedunculated sponges (like *Hamacantha* sp. or *Jaspis* sp.) or pedunculated Axinellids.

Remarks

The specimen matches well with the previous records of the species, both in external morphology, spicules and skeletal arrangement. This is the third record of this species in the Mediterranean, where it was recorded in the canyon de Cassidaigne in the Gulf of Lions (Vacelet, 1969) and Corsica (Pulitzer-Finali, 1983). In the North-Atlantic, it has been reported at several localities: the type locality at Norway (Schmidt, 1875), the east Greenland shelf (Lundbeck, 1905), the Faroe Plateau (Hentschel, 1929) and the north coast of the Iberian Peninsula (Solórzano, 1990). The vast distances between the Mediterranean and the North Atlantic reports (being the closest off northern Iberian Peninsula), and the lack of intermediate reports in well-studied areas such as the Alboran Sea, may indicate that Mediterranean and North Atlantic *M. emphysema* are different species, as already discussed by Vacelet (1969).

Order POLYMASTIIDA (Morrow & Cárdenas, 2015)

Family POLYMASTIIDAE (Gray, 1867)

Genus *Polymastia* (Lamarck, 1815)

***Polymastia polytylota* Vacelet, 1969**

(Fig. 17; Table 9)

Material examined

CFM-IEOMA-7405/i810, St 39, AM, ROV.

Description

Rounded sponge, 2 cm high and wide, with two conical papillas (0.5 cm high and 3 mm wide) placed on the upper side of the body (Figs. 17A and 17B). Consistency hard and slightly compressible. Surface smooth to the touch, but microhispid under the stereomicroscope. Cream color before and after preservation in EtOH, with a darker choanosome. The specimen suffered a contraction after collection. *In situ* the sponge was 4.5 cm in height and 4 cm in width, being looser and with its surface full of visible ostia (Fig. 2A).

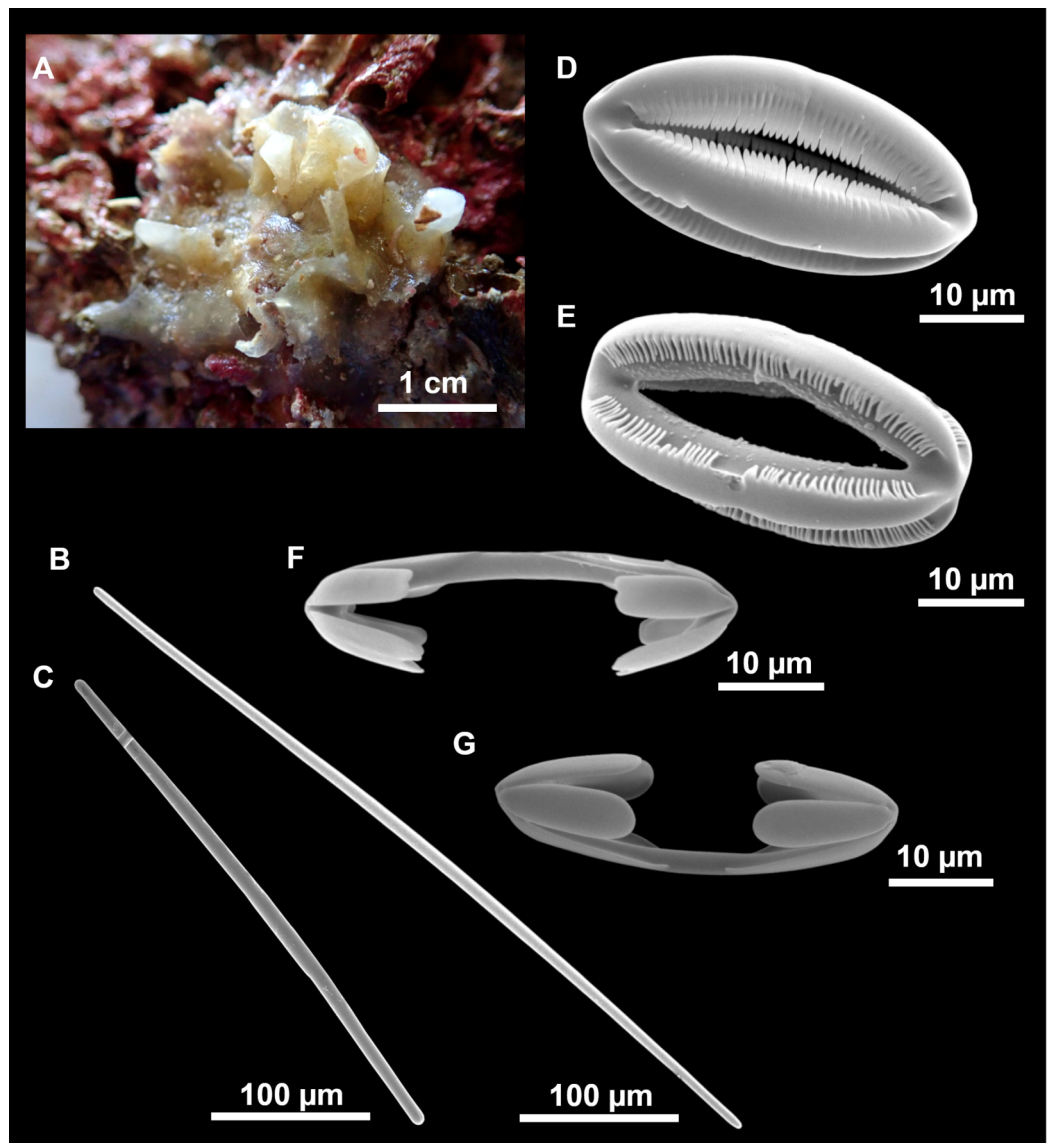


Figure 16 *Melonanchora emphysema* (Schmidt, 1875). (A) Habitus of CFM-IEOMA-7404/i573 on fresh state, attached to a rodolith. (B–C) Tylotes. (D–E) Spheranchoras. (F) Anchorate isochela I. (G) Anchorate isochela II. [Full-size !\[\]\(5f471a71b78d7676bc356df190b88ab4_img.jpg\) DOI: 10.7717/peerj.11879/fig-16](https://doi.org/10.7717/peerj.11879/fig-16)

Skeleton

As in the previous reports of the species (Vacelet, 1969; Pulitzer-Finali, 1983; Boury-Esnault, 1987; Boury-Esnault, Pansini & Uriz, 1994).

Spicules

Principal tylostyles (Figs. 17C and 17C1): straight and fusiform, with several tyloles in the proximal half part of the shaft. They measure $438\text{--}909\text{--}1154 \times 8\text{--}11\text{--}15 \mu\text{m}$.

Intermediary tylostyles (Figs. 17D and 17D1): fusiform, with a rounded head, often showing a vesicle. They measure $308\text{--}443\text{--}586 \times 6\text{--}7\text{--}9 \mu\text{m}$.

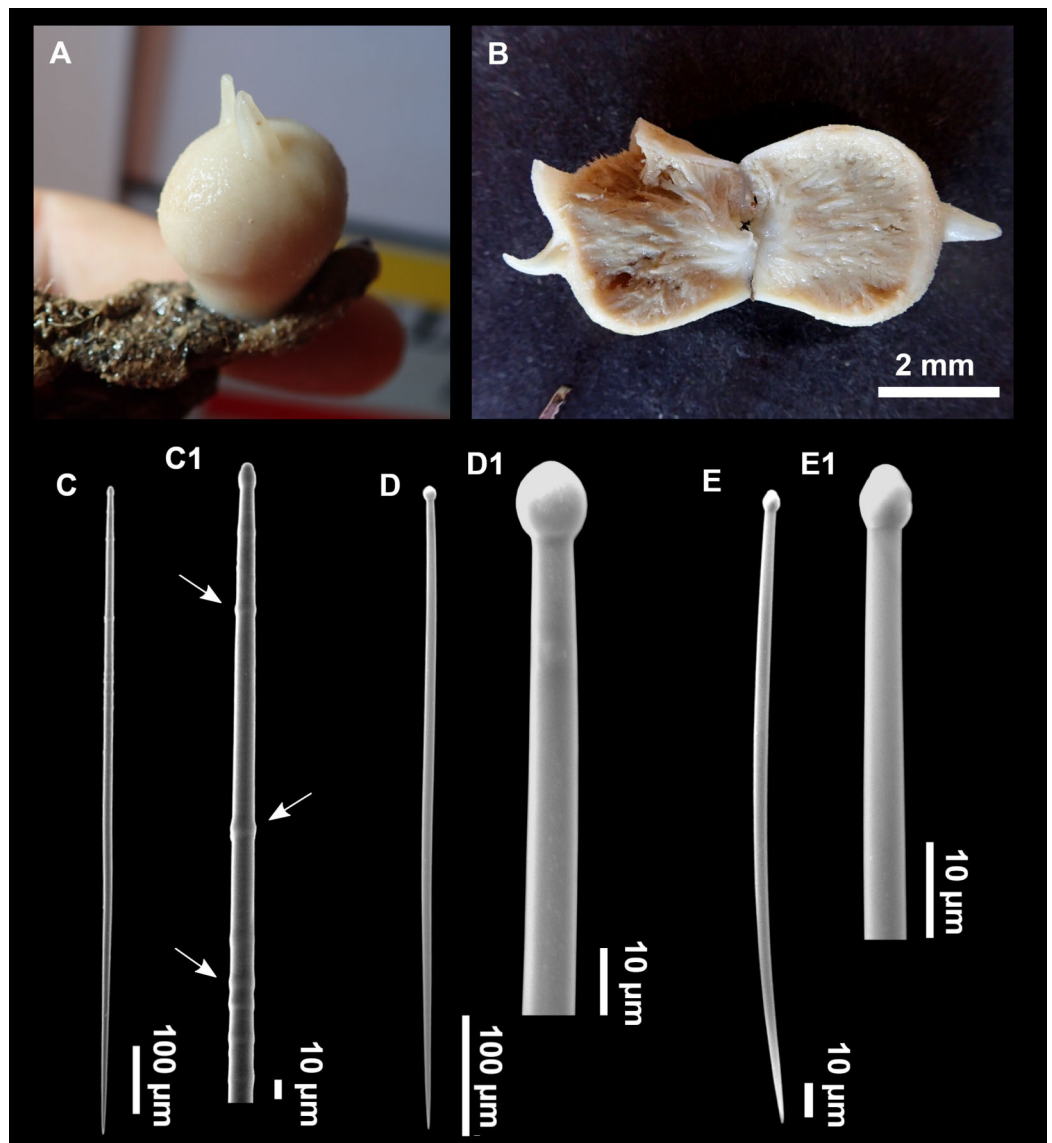


Figure 17 *Polymastia polytylota* Vacelet, 1969. (A–B) Habitus of CFM-IEOMA-7405/i810, on fresh state (A), and preserved in EtOH (B). (C–C1) Principal subtylostyles with detail of the tyles in the shaft (arrows). (D) Intermediary tylostyles with (D1) detail of the head. (E) Ectosomal tylostyles with (E1) Detail of the head. [Full-size !\[\]\(b345a1c4255362eec3746050dd71ccac_img.jpg\) DOI: 10.7717/peerj.11879/fig-17](https://doi.org/10.7717/peerj.11879/fig-17)

Ectosomal tylostyles (Figs. 17E and 17E1): slightly curved. They measure $121\text{--}166\text{--}200 \times 2\text{--}3\text{--}5 \mu\text{m}$.

Ecology notes

Only one specimen collected in the northern part of the AM, between 352 and 465 m deep, on a rocky bottom characterized by enhanced water movement, with several large *Phakellia* spp, *Pachastrella* spp and *Poecillastra compressa*, as well as other *Polymastia* cf. *polytylota*. Although the present specimen was the only collected, its easy identification

Table 9 Comparative characters from *Polymastia polytylota* Vacelet, 1969.

Specimen	Principal tylostyles	Intermedium tylostyles	Ectosomal tylostyles	Depth	Area
<i>Boury-Esnault, (1987)</i> Redescription of the Holotype	650–990 × 10–13	210–490 × 7–10	70–180 × 2–5	165–270	Toulon, but also in Corsica
<i>Boury-Esnault, Pansini & Uriz (1994)</i>	668–854–1108 × 5–13–16	276–403–509 × 5–11–13	94–115–143 × 3–3–4	Alboran:480 Atl: 362–485	Alboran Sea and North Atlantic
<i>Pulitzer-Finali (1983)</i>	650–810 × 10–13	210–490 × 7–10	80–120 × 2–3	117	North of Corsica
CFM-IEOMA-7405/i810 This work	438–909–1154 × 8–11–15	308–443–586 × 6–7–9	121–166–200 × 2–3–5	352–465	AM St 3

Note:

Depth (m), area (AM, Ausias March) and sampling station (St; see *Rstudy* in Table 1) where these specimens were collected are also shown. Spicule measures are given as minimum-mean-maximum for total length × minimum-mean-maximum for total width. A minimum of 30 spicules per spicule kind are measured, otherwise it is stated. All measurements are expressed in μm . Specimen codes are the reference numbers of the CFM-IEOMA/and author collection.

and the other sightings during ROV transects may suggest that this sponge is quite common in some areas of the Mallorca Channel.

Remarks

The present specimen matches with the previous descriptions of the species in external morphology, skeletal architecture and spicule morphometrics. The only difference is that our specimen has two papillae instead of one. The Fig. 2A shows the first *in-situ* image of this species.

This is the first record of this species at the Balearic Islands. In the Mediterranean it is known from the type locality at the Gulf of Lions (Vacelet, 1969), the Ligurian Sea (Vacelet, 1969; Pulitzer-Finali, 1983) and the Alboran Sea, while it has been also reported at the Gulf of Cadiz in the north-eastern Atlantic (Boury-Esnault, Pansini & Uriz, 1994).

Genus *Pseudotrachya* Hallmann, 1914

Pseudotrachya hystrix (Topsent, 1890)

(Fig. 18; Table 10)

Material examined

CFM-IEOMA-7406/i303_A, St 19, AM, RD; CFM-IEOMA-7407/i613, St 32, AM, RD.

Description

Roundish and pad-like encrusting sponge, up to 2 cm diameter and 3 mm in height (Fig. 18A). Coloration beige in life and whitish after preservation in EtOH. Very hispid surface. Consistency hard and only slightly compressible. No papillae, oscula and ostia inconspicuous.

Skeleton (modified from Plotkin, Gerasimova & Rapp, 2012)

Single layered cortex (palisade of microxeas). Main choanosomal skeleton of principal anisoxeas radially arranged, echinating the surface and auxiliary choanosomal skeleton of microxeas (Figs. 18B and 18B1).

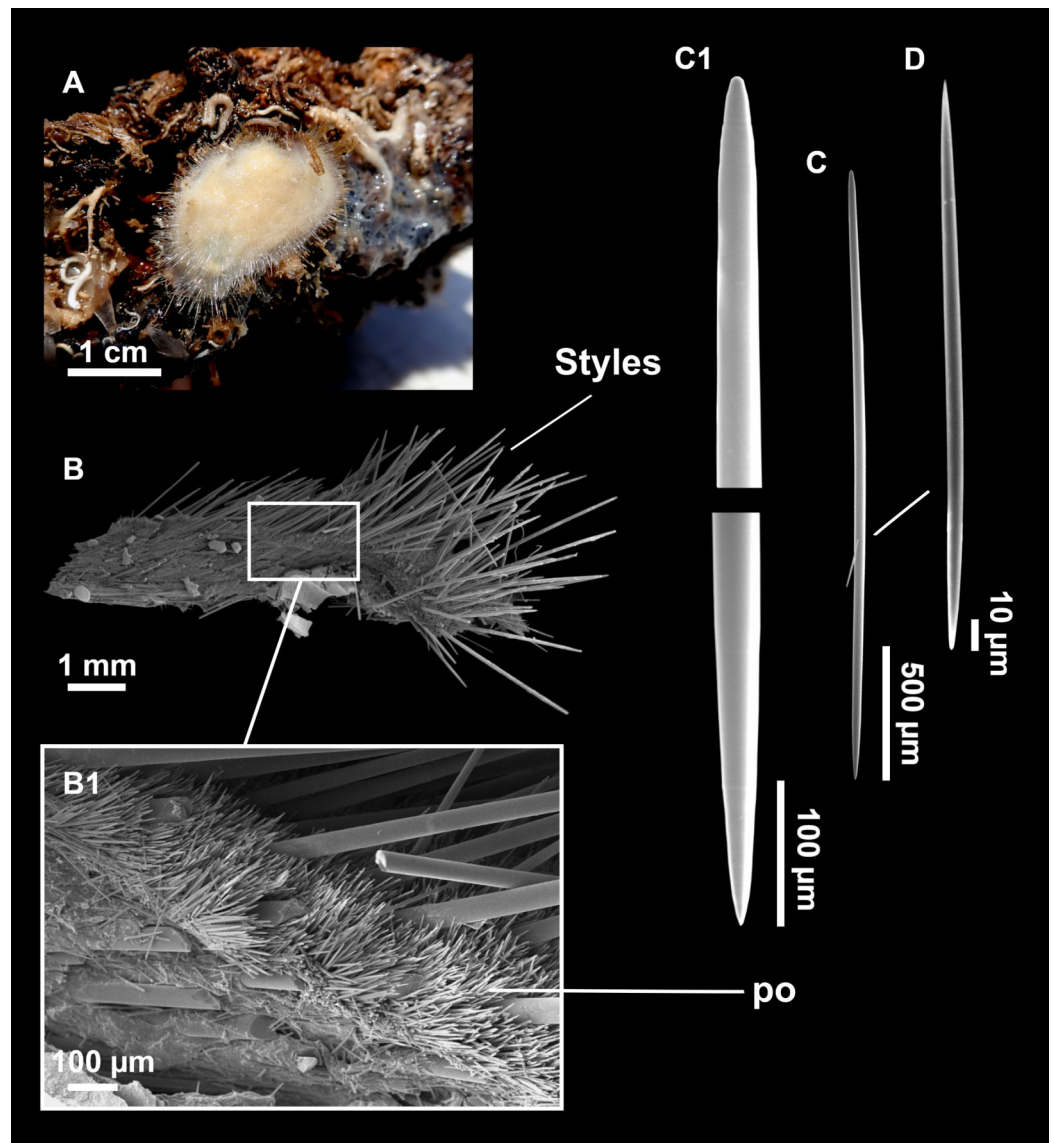


Figure 18 *Pseudotrachya hystrix* (Topsent, 1890). (A) Habitus of CFM-IEOMA-7407/i613 on fresh state. (B–B1) SEM images of the skeletal structure. (po) Palisade of oxeads. (C–C1) Anisoxeads. (D) Microxeads. [Full-size !\[\]\(fd7fe780e8fd8eece60268c87d0c3e04_img.jpg\) DOI: 10.7717/peerj.11879/fig-18](https://doi.org/10.7717/peerj.11879/fig-18)

Spicules

Anisoxeads (Figs. 18C and 18C1): straight and robust, with stepped ends. Intermediary stages between oxeads and styles present. Anisoxea size differs between specimens, measuring 834–1689–3358 × 10–25–42 μm in specimen i303 and 768–2088–3402 × 18–32–45 μm in specimen i613. Small and immature anisoxeads also present, but very scarce, about 500/10 μm.

Microxeads (Fig. 18D): fusiform and measuring 156–185–217 × 4–5–6 μm in specimen i303 and 152–203–270 × 3–5–6 in specimen i613.

Table 10 Comparative characters from *Pseudotrachya hystrix* (Topsent, 1890).

Specimen	Anisoxeas	Microxeas	Depth (m)	Area
<i>Topsent</i> (1892) holotype	up to 7,000 × 70	185 × 6	318 and 454	Azores
<i>Topsent</i> (1928)	nr	nr	650–914	Azores
<i>Sarà</i> (1959)	4,000–5,000 × 35–45	150–240 × 3–5	100	Tyrrhenian sea
<i>Boury-Esnault, Pansini & Uriz</i> (1994)	2,000–3,400–4,300 × 18–44–63	200–235–330 × 5–6–7	153–568	Alboran Sea,
<i>Vacelet</i> (1969) (Various specimens)	St15: 1,000–1,250 × 22–30 St23: >2,000 × 30–35 St34: 1,600–6,600 × 18–40 St46: 1,100–4,500 × 20–60	110–320 × 3–5 Stylote modifications	St 15: 180 St 23: 210–240 St 34: 270 St 46: 450–550	St 15: Cassidaigne St 23: Corse St 34: Cassidaigne St 46: Cassidaigne
CFM-IEOMA-7406/i303_A This work	834– <u>1,689</u> –3,358 × 10– <u>25</u> –42	156– <u>185</u> –217 × 4– <u>5</u> –6	231–302	AM St 19
CFM-IEOMA-7407/i613 This work	768– <u>2,088</u> –3,402 × 18– <u>32</u> –45	152– <u>203</u> –270 × 3– <u>5</u> –6	195–222	AM St 32

Note:

Depth (m), area (AM, Ausias March) and sampling station (St; see *Rstudy* in Table 1) where these specimens were collected are also shown. Spicule measures are given as minimum-mean-maximum for total length × minimum-mean-maximum for total width. A minimum of 30 spicules per spicule kind are measured, otherwise it is stated. All measurements are expressed in μm . Specimen codes are the reference numbers of the CFM-IEOMA/and author collection. nr, not reported.

Ecology notes

In addition to the two specimens described above, several other *P. hystrix* were collected from rocky slopes of AM and EB, between 195 and 302 m deep, suggesting that this species could be quite common in the Mallorca Channel seamounts. The species is found at rocky slopes, together with other small encrusting sponges such as *Hamacantha* spp., *Bubaris* spp. and the Hexactinellid *Tretodyctium* sp.

Remarks

This is a well-known species, characterized by their enormous megascleres with unequal tips (oxeote to stylote), and their small microxeas. Variations in the size of megascleres have been previously documented and may be related to ecological factors such as depth, nutrient availability, or temperature (*Maldonado et al., 1999*). However, due to their size, the largest megascleres were mostly broken, which could be a reason for the lack of reports on sizes 5,000–7,000 μm (Table 10).

This is the first record of the species in the Balearic Islands, expanding its geographical distribution in the Mediterranean, where it was previously reported at the Tyrrhenian Sea (*Sarà, 1959*), the Ligurian Sea (*Pulitzer-Finali, 1983*), the Gulf of Lions (*Vacelet, 1969*) and the Alboran Sea (*Boury-Esnault, Pansini & Uriz (1994)*).

Order TETHYIDA Morrow & Cardenas, 2015

Family HEMIASTERELLIDAE Lendenfeld, 1889

Genus *Hemiasterella* Carter, 1879

Hemiasterella elongata *Topsent, 1928*

Material examined

CFM-IEOMA-7408/i149_4, St 7, EB, RD; CFM-IEOMA-7409/i337, St 11, EB, BT;
CFM-IEOMA-7410/i531, St 24, AM, BT; CFM-IEOMA-7411/POR1066, St 36,
south-western Cabrera Archipelago, GOC-73.

Ecological notes

This species was found at mesohypoclimatic bottoms, between 109 and 152 m deep, generally associated with rhodolith beds, or areas with dead rhodoliths on the summits of EB and AM, but also sporadically at the same depths on trawl fishing grounds of the continental shelf of Mallorca.

Remarks

This is the third record of the species and the third for the Mediterranean, where it was only known from the Alboran Sea (*Sitjà & Maldonado, 2014*). It is also the third report worldwide, considering the type locality at Cabo Verde in the eastern Atlantic (*Topsent, 1928*).

Class HEXACTINELLIDA *Schmidt, 1870*

Subclass HEXASTEROPHORA Schulze, 1886

Order LYSSACINOSIDA Zittel, 1877

Family ROSSELLIDAE Schulze, 1885

Subfamily LANUGINELLIDAE Gray, 1872

Genus *Lanuginella* *Schmidt, 1870*

Lanuginella pupa *Schmidt, 1870*

([Fig. 19](#); [Table 11](#))

Material examined

CFM-IEOMA-7412/i286_1, CFM-IEOMA-7413/i286_2 and CFM-IEOMA-7414/i286_3, St 18, AM, RD.

Description

Tubular (CFM-IEOMA-7412/i286_1) to calyx-like (CFM-IEOMA-7413/i286_2 and CFM-IEOMA-7414/i286_3) sponges ([Fig. 19A](#)), up to 4 cm high and 2 cm in diameter. Surface smooth, but slightly hispid at localized areas. Fragile consistency and soft touch. Dirty white color in life and white after preservation in EtOH. All the three specimens present a single, circular oscule at the upper part of the body. One of the calyx-like specimens (CFM-IEOMA-7413/i286_2) has a minute and short peduncle.

Skeleton

As usual for the species (see *Ijima, 1904*; *Tabachnick, 2002* and *Sitjà et al., 2019* for detailed descriptions)

Spicules

Choanosomal diactines ([Fig. 19B](#)): long and slim, slightly sinuous, with four vestigial tubercles in the center ([Fig. 19B1](#)), which may have swellings all over the shaft and spines on their tips. They measure $245\text{--}1611 \times 3\text{--}15 \mu\text{m}$.

Choanosomal hexactines ([Fig. 19C](#)): with actines of different lengths, sometimes sinuous. They measure $349\text{--}983 \times 10\text{--}25 \mu\text{m}$ ($n = 12$).

Hypodermal pentactines ([Fig. 19D](#)): with a ray reduced to a stump or absent. Proximal ray much larger than the others and perpendicularly arranged. Rays are smooth or slightly

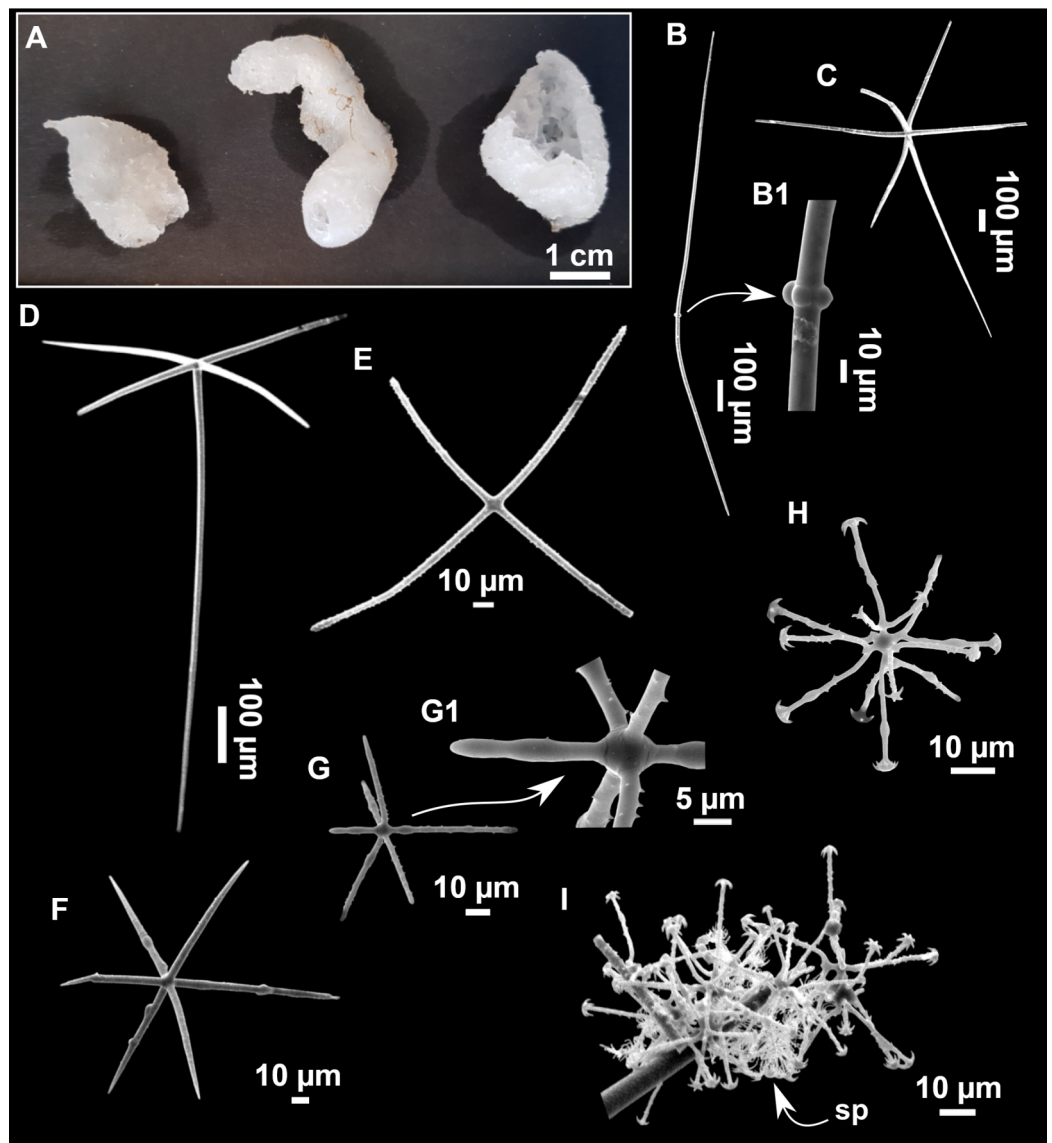


Figure 19 *Lanuginella pupa* Schmidt, 1870. (A) Habitus of CFM-IEOMA-7413/i286_2 (left), CFM-IEOMA-7412/i286_1 (middle), i286_3/CFM-IEOMA-7414 (right) preserved in EtOH. (B–I) SEM images of spicules from CFM-IEOMA-7412/i286_1. (B) Choanosomal diactine with (B1) detail of the four central tubercles. (C) Choanosomal hexactine. (D) Hypodermal pentactine. (E) Stauractine. (F–G) Atrial hexactines with (G1) Detail of the spines of (G). (H) Discohexaster. (I) Agglomeration of discohexasters, with a strombiloplumicome (sp) beneath. [Full-size !\[\]\(1663bb69f307a960345edb0e712f8c02_img.jpg\) DOI: 10.7717/peerj.11879/fig-19](https://doi.org/10.7717/peerj.11879/fig-19)

rugose. Proximal ray measuring $242\text{--}950 \times 7\text{--}19 \mu\text{m}$ ($n = 8$) and perpendicular rays measuring $137\text{--}850 \times 4\text{--}20 \mu\text{m}$ ($n = 28$).

Stauractines (Fig. 19E): with four actines perpendicularly arranged one another in the same plane. They are straight or slightly curved, strongly spined, with roundish tips. They measure $61\text{--}111 \times 3\text{--}5 \mu\text{m}$ ($n = 23$).

Dermal hexactines (not shown): uncommon. Rugose, with the proximal ray slightly longer than the distal one. Overall measures: proximal rays $151 \times 7 \mu\text{m}$ ($n = 1$), distal rays $105 \times 6 \mu\text{m}$ ($n = 1$) and perpendicular rays $68\text{--}110 \times 2\text{--}6 \mu\text{m}$ ($n = 3$).

Table 11 Comparative characters from *Lanuginella pupa* Schmidt, 1870.

Specimen	Parenchymalia		Dermalia		Other	Gastralia		Hexasters		Depth	Area
	Choanosomal Diactine	Choanosomal Hexactine	Hypodermal Pentactine	Stauractines		Atrial hexactine	Discohexaster	Strombiplumicomes			
<i>Schmidt (1870)</i> holotype	nr		nr	Stauractines: 160–200	nr					201	Cape Verde (Atlantic Ocean)
<i>Schulze (1897)</i>	nr	nr	nr	Stauractines: rarely tauctines, 220–330 (average length) × 7	220–330 × 7			32–80–100	40	183–572	Little Ki Island (Banda Sea)
<i>Ijima (1904)</i> Several specimens	up to 4,000 × 22	variable in size, up to 2,000 × 30 (as oxyhexactine)	1,000 × 34					40–90	34–76		Dōketsba, Okinose, Mochiyama (Japan), Vries Island (Vries Strait, Pacific Ocean)
<i>Okada, 1932</i>	3,500–5,000 × 100	3,000 × 60	nr	nr	nr			45–80	50	180	Kagoshima Gulf (Eastern China Sea)
<i>Burton, 1956</i>	nr			Abundant stauractines, scarce pentactins, tauctins and hexactins 43–140 × 2–6	46–150 × 2–6			30–70	nf	690	Gulf of Cadiz (Mud volcano, North Atlantic Ocean)
<i>Sitjà & Maldonado (2014)</i>	325–3,000 × 4–7	250–850 × 6–13	Perp: 170–850 × 4–10 Prox: 242–950 × 8–12					43–57–70 (n = 12)	20–38 (n = 5)	220–275	AM St 18
CFM-IEOMA- 7412/1286_1 This work	586–1,900 × 7–14 (n = 6)	664–983 × 10–25 (n = 3)	Perp: 175–343–435 × 6–13–20 (n = 13) Prox: 323–777 × 7–19 (n = 3)				Prox: 108–113 × 5–6 (n = 2) Dist: 70–95 × 4–7 (n = 2) Perp: 101 × 6 (n = 1) Prox: 151 × 7 (n = 1) Dist: 105 × 6 (n = 1) Paratractactins: 77–4 (n = 1)	49–76 (n = 7)	nf	220–275	AM St 18
CFM-IEOMA- 7413/1286_2 This work	245–1,726–2,586 × 3–9–12 (n = 19)	492–920 × 16–20 (n = 4)	Perp: 242–519 × 8–15 (n = 7)				Prox: 107 × 4 (n = 1) Dist: 97 × 5 (n = 1) Perp: 83–145 × 3–6 (n = 7)	49–76 (n = 7)	nf	220–275	AM St 18
CFM-IEOMA- 7414/1286_3 This work	528–1,533–2,611 × 3–9–15	349–926 × 10–19 (n = 5)	Perp: 137–437 × 9–17 (n = 8) Prox: 516–831 × 11–14 (n = 5)				Prox: 119–159 × 4–6 (n = 5) Dist: 79–102 × 4–6 (n = 5) Perp: 70–96 × 4–6 (n = 5)	45–53–62 (n = 10)	20 (n = 1)	220–275	AM St 18

Note:

Depth (m), area (AM, Ausias March) and sampling station (St; see [Retstudy](#) in [Table 1](#)) where these specimens were collected are also shown. Spicule measures are given as minimum–mean–maximum for total length × minimum–mean–maximum for total width. A minimum of 30 spicules per spicule kind are measured, otherwise it is stated. All measurements are expressed in μm. Specimen codes are the reference numbers of the CFM-IEOMA and author collection. nr, not reported; nf, not found.

Paratetractin: only a single spicule observed, measuring $77/4$ ($n = 1$).

Atrialia hexactines (Figs. 19F and 19G): common. Slightly rough to smooth. Overall measures: proximal rays $107\text{--}159 \times 4\text{--}6 \mu\text{m}$ ($n = 8$), distal rays $70\text{--}102 \times 4\text{--}7 \mu\text{m}$ ($n = 8$) and perpendicular rays $70\text{--}150 \times 3\text{--}7 \mu\text{m}$ ($n = 22$).

Discohexasters (Fig. 19H): rather uncommon. Some with underdeveloped, twisted rays. They measure $43\text{--}76 \mu\text{m}$ ($n = 29$).

Strobiloplumicomis (Fig. 19I): very rare and not found in specimen CFM-IEOMA-7413/i286_2. They measure: $20\text{--}38 \mu\text{m}$ ($n = 6$).

Ecological notes

Species found only at one station located in a rocky slope at SO, between 220 and 275 m deep. It was associated with fossil ostreid reefs and carbonated rocks, together with other encrusting sponges like *Hamacantha* sp., *Bubaris* sp., and *Jaspis* sp.

Remarks

This poorly-known species is the single representative of the genus *Lanuginella*, reported at several distant locations around the world: Kagoshima Gulf at the Sea of China (Okada, 1932), Ki Island at the Sea of Banda (Schulze, 1897). In the northern Atlantic it was recorded at Cabo Verde (Schmidt, 1870), the Gulf of Cadiz (Sitjà et al., 2019) and the Strait of Gibraltar (Topsent, 1895). This is the first record of the species in the Mediterranean Sea, increasing its already wide distribution. However, a revision of the species is needed, and it is likely that such a cosmopolitan distribution may indicate that *L. pupa* represents a species complex. However, deep-sea species tend to be more widely distributed than shallow ones, probably because of the uniformity of in the environmental conditions (McClain & Hardy, 2010). A detailed examination of worldwide specimens, combined with molecular methods, may shed more light on it.

DISCUSSION

Biogeography and seamount singularity

The present study increases the knowledge of the sponge diversity of the Mediterranean seamounts. We describe a new genus, three new species, and 15 new geographical reports, including two new reports for the Mediterranean Sea. This study also highlights *Foraminospongia balearica* sp. nov. as one of the most common sponges at AM and EB, being large and easily distinguishable. This species was never recorded at other previously explored Mediterranean seamounts or ridges of a similar depth range, such as the Seco de los Olivos or the Alboran Ridge, whose sponge fauna has been already studied (Sitjà & Maldonado, 2014; Würtz & Rovere, 2015; De la Torre et al., 2018). Therefore, the Mallorca Channel seamounts may be considered unique faunal refuges, appealing to what is called the “Seamount endemism hypothesis” (De Forges, Koslow & Poore, 2000), which suggests that geographical separation of seamounts is reflected by genetic isolation of their fauna, which promotes speciation by vicariance. This hypothesis has been questioned, as some works have shown that benthic fauna (including sponges) is well connected among isolated seamounts (Samadi et al., 2006; Ekins et al., 2016).

However, others have shown structured populations between seamounts (*Castelin et al., 2010*), or between seamounts and the continental shore populations (*Crochelet et al., 2020*). Other authors suggest that there is a mixture of panmictic and structured populations, largely dependent on the characteristics of the single species nature (*Rogers, 2018*). If we consider that the dispersal of sponges tend to be very limited (*Maldonado, 2006; Riesgo et al., 2019; Shaffer et al., 2020; Griffiths et al., 2021*), it is plausible that certain seamount sponge populations are highly structured. This limitation in the dispersal may be enhanced in isolated seamounts or in those with peculiar or unique ecological characteristics. In this sense, both AM and EB have very shallow summits and are placed in an area of special oligotrophy (e.g., *Bosc, Bricaud & Antoine, 2004; Uitz et al., 2012*). The nearest habitat with similar features is the continental shelf of the Balearic promontory, although these areas tend to be under the impact of bottom-trawling (*Farriols et al., 2017; Ordines et al., 2017*), with the consequent impoverishment of benthic communities (*Jennings & Kaiser, 1998*). In fact, most of the species of SO, AM and the EB had not been found at the continental shelf of the Balearic Islands (*Bibiloni, 1990; 1993; Grinyó et al., 2018; Santín et al., 2018*), except for *Phakellia robusta*, *P. hirondellei* (*Santín et al., 2018*), *Petrosia* (*Petrosia*) *raphida*, and *Hemiasterella elongata* (this work).

The particular conditions of the Balearic Islands, extreme oligotrophy, geographical isolation, low fishing pressure and heterogeneity of habitats (*Quetglas et al., 2012; Massutí et al., 2014*) suggest this area is a hotspot of sponge diversity, with much of its fauna still unknown, especially at depth below 90 m (*Bibiloni, 1990; Santín et al., 2018; Díaz et al., 2020*). In recent years, this high diversity has been evidenced by the presence of rich benthic assemblages (*Ordines & Massutí, 2009; Barberá et al., 2012; Ordines et al., 2011*), as well as by a high number of new species and new geographical reports (e.g., *Kovačić, Ordines & Schliewen, 2017; Kovacic et al., 2019; Guzzetti et al., 2019; Ordines et al., 2019; Díaz et al., 2020*). Thus, there is a need to find out which sponge species inhabit those waters and how much do they contribute to the benthic biomass. Sponges are key components of the benthic ecosystems, playing important biogeochemical roles (*De Goeij et al., 2013*) and serving as food or refuge to many other animals (*Maldonado et al., 2016*). Future works should characterize those benthic habitats of the continental shelf and slope around the Balearic Islands that are potentially similar to those of the Mallorca Channel seamounts (e.g., non-impacted sedimentary and rocky bottoms with rhodoliths and gravels located between 90 and 150 m deep and rocky slopes down to 400–500 m deep). Then, both biocenosis should be compared to confirm the singularity of the habitats of the Mallorca Channel seamounts.

Integrative taxonomy

The generalized lack of distinctive characters has caused sponges to be one of the most difficult groups to classify. This difficulty is also reflected by sponge phylogenetic relationships, with polyphyletic taxa present in all the levels of the Linnean classification (e.g., *Cárdenas, Perez & Boury-Esnault, 2012; Díaz et al., 2020*). Thus, the use of both morphology and molecular markers is central to the improvement of the knowledge of this group of organisms. Following this approach, here we have proposed the new genus

Foraminospongia to be erected in the family Hymerhabdiidae, supported by the two new species *Foraminospongia balearica* sp. nov. and *Foraminospongia minuta* sp. nov., confirmed by morphological traits and both COI and 28S markers. On the other hand, the species *Heteroxya* cf. *beauforti* has shown no variability in its COI sequence relative to its North Atlantic congeners, which highlights the importance of morphology and the need to combine both approaches. The COI is known to be a low-resolution marker to discriminate species of sponges (Wörheide 2006), so we also sequenced the more variable 28S marker. However, no 28S sequences are currently available in any database for comparison with the other *Heteroxya* spp.: this issue should thus be addressed in the future.

A key subject in sponge taxonomy is the robustness of the skeletal characters as a species diagnostic tool, and how reliable they are for discriminating species and populations. Reliable discrimination is further complicated by the fact that skeletal elements may change depending on environmental conditions such as temperature, depth, or nutrient concentration; skeletal elements may also change due to intraspecific plasticity, overall modifying length, width, morphology, and even their presence or absence (Cárdenas, Perez & Boury-Esnault, 2012; Abdul Wahab et al., 2020). No consensus has ever been reached to consider a given morphological deviation as enough evidence to erect a new species, a fact that remains arbitrary. We have found differences in the spicular morphometry between the specimens of the Balearic Islands and specimens of other areas of the Mediterranean and the North Atlantic Ocean; these differences have been described here for most of the species to some extent. Since the dispersive potential, long-distance connectivity, and speciation of sponges are poorly understood, most of the diagnosis in the present work were performed under a conservative approach, only proposing new species when we found solid morphological evidence. Taking this into account, factors like vast geographical distances, presence of oceanographic barriers or minor morphometric differences were not considered enough evidence for species delimitation. In the case of *Calyx* cf. *tufa*, its potential conspecificity with the North Atlantic species *C. tufa* cannot be discarded. We did not get access to any material of *C. tufa*, and no sequences are available for comparison; moreover, the original description is too vague and general. However, as stated above, the absence of any intermediate records of such a big, conspicuous, and easily recognizable sponge is noteworthy. Also, the recorded depths of *C. tufa* for the Atlantic are much deeper than those for *C. cf. tufa* (219 and 300 m vs. 105–114 m). Future work is needed to clarify if both species are synonyms, or if *C. cf. tufa* is a new species for science.

ACKNOWLEDGEMENTS

The authors wish to thank the captain and crew of R/Vs *Ángeles Alvariño*, *Sarmiento de Gamboa* and *Miguel Oliver*, as well as the participants in the INTEMARES surveys at the Mallorca Channel seamounts and the MEDITS 2017, 2019 and 2020 surveys. Special thanks to Dr. Ferran Hierro (University of the Balearic Islands) for the technical assistance at the scanning electron microscope, to Dr. Paco Cárdenas, for taxonomic advice, to Maria Teresa Farriols and Helena Marco for the logistic work during the development of the INTEMARES surveys. Lastly, we would like to thank Professor Maurizio Pansini and the

two anonymous reviewers for their constructive comments and corrections to the original manuscript.

ADDITIONAL INFORMATION AND DECLARATIONS

Funding

This research has been performed within the scope of the LIFE IP INTEMARES project, coordinated by the Biodiversity Foundation of the Ministry for the Ecological Transition and the Demographic Challenge. It receives financial support from the European Union's LIFE programme (LIFE15 IPE ES 012). The MEDITS surveys are co-funded by the European Union through the European Maritime and Fisheries Fund (EMFF) within the National Program of collection, management and use of data in the fisheries sector and support for scientific advice regarding the Common Fisheries Policy. Julio A. Diaz is supported by FPI contract co-funded by the Regional Government of the Balearic Islands and the European Social Fund. Sergio Ramírez-Amaro is funded by a post-doctoral contract from the regional government of the Balearic Islands, co-funded by the Regional Government of the Balearic Islands European Social Fund. The funders had no role in study design, data collection and analysis, decision to publish, or preparation of the manuscript.

Grant Disclosures

The following grant information was disclosed by the authors:

LIFE IP INTEMARES.

Biodiversity Foundation of the Ministry for the Ecological Transition and the Demographic Challenge.

European Union's LIFE Programme: LIFE15 IPE ES 012.

MEDITS.

European Union through the European Maritime and Fisheries Fund (EMFF).
National Program.

Common Fisheries Policy.

FPI.

Regional Government of the Balearic Islands and the European Social Fund.
Government of the Balearic Islands.

Competing Interests

The authors declare that they have no competing interests.

Author Contributions

- Julio A. Díaz conceived and designed the experiments, performed the experiments, analyzed the data, prepared figures and/or tables, authored or reviewed drafts of the paper, and approved the final draft.
- Sergio Ramírez-Amaro conceived and designed the experiments, performed the experiments, analyzed the data, authored or reviewed drafts of the paper, and approved the final draft.

- Francesc Ordines conceived and designed the experiments, performed the experiments, analyzed the data, authored or reviewed drafts of the paper, and approved the final draft.

Data Availability

The following information was supplied regarding data availability:

The COI (MW858346–MW858351 and MZ570433) and 28S (MW881149–MW881153) sequences are available at GenBank.

All the specimens were deposited in the Marine Fauna Collection (<http://www.ma.ieo.es/cfm/>) based at the Centro Oceanográfico de Málaga (Instituto Español de Oceanografía), with the numbers from CFM7356 to CFM7417 (Table S1).

New Species Registration

The following information was supplied regarding the registration of a newly described species:

Publication:

urn:lsid:zoobank.org:pub:47EC2384-A88C-4654-8425-A7A46BC47AC5

Foraminospongia new **gen. nov.**:

urn:lsid:zoobank.org:act:5CC3710C-0749-47BD-B2BA-92158E5B0758

Foraminospongia balearica **sp. nov.**:

urn:lsid:zoobank.org:act:A1582919-710A-4E64-BBB5-0908B81F5206

Foraminospongia minuta **sp. nov.**:

urn:lsid:zoobank.org:act:8EE74D72-BFF2-4FC4-8E43-354FCC35F11F

Heteroxya cf beauforti

urn:lsid:zoobank.org:act:BF907E49-598F-4348-87F5-AEA11F0D3944

Paratimea massutii **sp. nov.**:

urn:lsid:zoobank.org:act:5A9B89F8-2777-4AB7-845F-9EC4BB91D518.

Supplemental Information

Supplemental information for this article can be found online at <http://dx.doi.org/10.7717/peerj.11879#supplemental-information>.

REFERENCES

- Abdul Wahab MA, Wilson NG, Prada D, Gomez O, Fromont J. 2020. Molecular and morphological assessment of tropical sponges in the subfamily Phyllospongiinae, with the descriptions of two new species. *Zoological Journal of the Linnean Society* 33:381 DOI 10.1093/zoolinnean/zlaa133.
- Acosta J, Ancochea E, Canals M, Huertas MJ, Uchupi E. 2004. Early Pleistocene volcanism in the Emile Baudot Seamount, Balearic Promontory western Mediterranean Sea. *Marine Geology* 207(1–4):247–257 DOI 10.1016/j.margeo.2004.04.003.
- Aguilar R, López -Correa M, Calcinai B, Pastor X, De la Torriente A, García S. 2011. First records of Asbestopluma hypogea Vacelet and Boury-Esnault, 1996 Porifera, Demospongiae Cladorhizidae on seamounts and in bathyal settings of the Mediterranean Sea. *Zootaxa* 2925(1):33–40 DOI 10.11646/zootaxa.2925.1.3.
- Alander H. 1942. Sponges from the Swedish west-coast and adjacent waters. Ph.D. Thesis. (University of Lund, H. Struves: Göteborg), 1–95.

- Altschul SF, Gish W, Miller W, Myers EW, Lipman DJ. 1990.** Basic local alignment search tool. *Journal of Molecular Biology* **215**(3):403–410 DOI [10.1016/S0022-2836\(05\)80360-2](https://doi.org/10.1016/S0022-2836(05)80360-2).
- Alvarez B, Hooper JNA. 2002.** Family Axinellidae Carter, 1875—pp. 724–747. In: Hooper JNA, Van Soest RWM, eds. *Systema Porifera: A guide to the Classification of Sponges*. New York, Boston, Dordrecht, London, Moscow: 1 Kluwer Academic/ Plenum Publishers, 724–747.
- Barberá C, Moranta J, Ordines F, Ramón M, De Mesa A, Díaz-Valdés M, Grau AM, Massutí E. 2012.** Biodiversity and habitat mapping of Menorca Channel (western Mediterranean): implications for conservation. *Biodiversity and Conservation* **21**:701–728.
- Bergquist PR. 1961.** A collection of Porifera from Northern New Zealand, with Descriptions of Seventeen New Species. *Pacific Science* **15**(1):33–48.
- Bertolino M, Bo M, Canese S, Bavestrello G, Pansini M. 2015.** Deep sponge communities of the Gulf of St Eufemia (Calabria, southern Tyrrhenian Sea), with description of two new species. *Journal of the Marine Biological Association of the United Kingdom* **95**(7):1371–1387 DOI [10.1017/S0025315413001380](https://doi.org/10.1017/S0025315413001380).
- Bertolino M, Cerrano C, Bavestrello G, Carella M, Pansini M, Calcinai B. 2013.** Diversity of Porifera in the Mediterranean coralligenous accretions, with description of a new species. *ZooKeys* **336**(2):1–37 DOI [10.3897/zookeys.336.5139](https://doi.org/10.3897/zookeys.336.5139).
- Bertrand JA, De Sola LG, Papaconstantinou C, Relini G, Souplet A. 2002.** The general specifications of the MEDITS surveys. *Scientia Marina* **66**:9–17.
- Bibiloni MA. 1990.** Fauna de Esponjas de las Islas Baleares—Variación cualitativa y cuantitativa de la población de esponjas en un gradiente batimétrico: Comparación Baleares-Costa Catalana. PhD Thesis. Universitat de Barcelona, Barcelona, Spain.
- Bibiloni MA. 1993.** Some new or poorly known sponges of the Balearic Islands western Mediterranean. *Scientia Marina* **57**:307–318.
- Bo M, Bertolino M, Borghini M, Castellano M, Harriague AC, Di Camillo CG, Gasparini G, Gasparini C, Paolo M, Povero P, Pusceddu A, Schroeder K, Bavestrello G. 2011.** Characteristics of the mesophotic megabenthic assemblages of the Vercelli seamount North Tyrrhenian Sea. *PLOS ONE* **6**2:e16357.
- Bo M, Coppari M, Betti F, Enrichetti F, Bertolino M, Massa F, Bava S, Gay G, Cattaneo-Vietti R, Bavestrello G. 2020.** The high biodiversity and vulnerability of two Mediterranean bathyal seamounts support the need for creating offshore protected areas. *Aquatic Conservation: Marine and Freshwater Ecosystems* **31**(3):543–566.
- Born IVon. 1778.** Index rerum naturalium Musei Cæsarei Vindobonensis. Pars I.ma. Testacea. Verzeichniß der natürlichen Seltenheiten des k. k. Naturalien Cabinets zu Wien. In: *Erster Theil. Schalthiere. [1-40], 1-458, [1-82]. Vindobonae [Vienna]; (Kraus).* .
- Bosc E, Bricaud A, Antoine D. 2004.** Seasonal and interannual variability in algal biomass and primary production in the Mediterranean Sea, as derived from 4 years of SeaWiFS observations. *Global Biogeochemical Cycles* **18**:GB1005.
- Boury-Esnault N. 1987.** The Polymastia species (Demosponges, Hadromerida) of the Atlantic area. In: Vacelet J, Boury-Esnault N, eds. *Taxonomy of Porifera from the N.E. Atlantic and the Mediterranean Sea. NATO Advanced Science Institutes Series G, Ecological Sciences*. Vol. 13. Heidelberg: Springer, 29–66.
- Boury-Esnault N, Pansini M, Uriz MJ. 1994.** Spongiaires bathyaux de la mer d'Alboran et du golfe ibéro-marocain. *Mémoires du Muséum national d'Histoire naturelle* **160**:174.
- Bowerbank JS. 1858.** On the Anatomy and Physiology of the Spongiadae. *Part I. On the Spicula. Philosophical Transactions of the Royal Society* **148**(2):279–332.
- Bowerbank JS. 1866.** *A Monograph of the British Spongiadae*. Vol. 2. London: Ray Society, 1–388.

- Burton M. 1931.** On a collection of marine sponges mostly from the Natal Coast. *Annals of the Natal Museum* **6(3)**:337–358.
- Calcinai B, Moratti V, Martinelli M, Bavestrello G, Taviani M. 2013.** Uncommon sponges associated with deep coral bank and maerl habitats in the Strait of Sicily Mediterranean Sea. *Italian Journal of Zoology* **80**:412–423.
- Carvalho FC, Cárdenas P, Ríos P, Cristobo J, Rapp HT, Xavier JR. 2020.** Rock sponges (lithistid demospongiae) of the northeast atlantic seamounts, with description of ten new species. *PeerJ* **8**:e8703.
- Carter HJ. 1873.** On the Hexactinellidae and Lithistidae generally, and particularly on the Aphrocallistidae, Aulodictyon, and Farreae, together with Facts elicited from their Deciduous Structures and Descriptions respectively of Three New Species. *Annals and Magazine of Natural History* **12(71)**:349–373.
- Carter HJ. 1887.** Report on the marine sponges, chiefly from King Island, in the Mergui Archipelago, collected for the Trustees of the Indian Museum, Calcutta, by Dr. John Anderson, F.R.S., Superintendent of the Museum. *Journal of the Linnean Society, Zoology* **21(127-128)**:61–84.
- Castelin M, Lambourdiere J, Boisselier MC, Lozouet P, Couloux A, Cruaud C, Samadi S. 2010.** Hidden diversity and endemism on seamounts: focus on poorly dispersive neogastropods. *Biological Journal of the Linnean Society* **1002**:420–438.
- Cedro VR, Hajdu E, Correia MD. 2013.** Three new intertidal sponges Porifera: Demospongiae from Brazil's fringing urban reefs Maceió, Alagoas, Brazil, and support for Rhabderemia's exclusion from Poecilosclerida. *Journal of Natural History* **4733–4734**:2151–2174.
- Chombard C, Boury-Esnault N, Tillier S. 1998.** Reassessment of homology of morphological characters in Tetractinellid sponges based on molecular data. *Systematic Biology* **47**:351–366.
- Clark MR, Schlacher TA, Rowden AA, Stocks KI, Consalvey M. 2012.** Science priorities for seamounts: research links to conservation and management. *PLOS ONE* **71**:e29232.
- Corbera G, Iacono CL, Gràcia E, Grinyó J, Pierdomenico M, Huvenne VA, Aguilar R, Gili JM. 2019.** Ecological characterisation of a Mediterranean cold-water coral reef: cabliers Coral Mound Province Alboran Sea, western Mediterranean. *Progress in Oceanography* **175(12)**:245–262 DOI [10.1016/j.pocean.2019.04.010](https://doi.org/10.1016/j.pocean.2019.04.010).
- Costa G, Bavestrello G, Micaroni V, Pansini M, Strano F, Bertolino M. 2019.** Sponge community variation along the Apulian coasts Otranto Strait over a pluri-decennial time span—does water warming drive a sponge diversity increasing in the Mediterranean Sea? *Journal of the Marine Biological Association of the United Kingdom* **99(7)**:1519–1534 DOI [10.1017/S0025315419000651](https://doi.org/10.1017/S0025315419000651).
- Crochelet E, Barrier N, Andrello M, Marsac F, Spadone A, Lett C. 2020.** Connectivity between seamounts and coastal ecosystems in the Southwestern Indian Ocean. *Deep Sea Research Part II: Topical Studies in Oceanography* **176**:104774.
- Cárdenas P, Perez T, Boury-Esnault N. 2012.** Sponge systematics facing new challenges. In: *Advances in Marine Biology*. Vol. 61. London: Academic Press, 79–209.
- Danovaro R, Fanelli E, Canals M, Ciuffardi T, Fabri MC, Taviani M, Argyrou M, Azurro E, Bianchelli S, Cantafaro A, Carugati L, Corinaldesi C, P.De Haan W, Dell'Anno A, Evans J, Fogliani F, Galil B, Gianni M, Goren M, Greco S, Grimalt J, Güell-Bujons Q, Jadaud A, Knittweis L, Lopez JL, Sanchez-Vidal A, Schembri PJ, Snelgrove P, Vaz S, Angeletti L, Barsanti M, Borg JA, Bosso M, Brind'Amour A, Castellan G, Conte F, Delbono I, Galgani F, Morgana G, Prato S, Schirone A, Soldevilla E. 2020.** Towards a marine strategy for the deep

- Mediterranean Sea: analysis of current ecological status. *Marine Policy* **112(8)**:103781 DOI [10.1016/j.marpol.2019.103781](https://doi.org/10.1016/j.marpol.2019.103781).
- De Forges BR, Koslow JA, Poore GCB. 2000.** Diversity and endemism of the benthic seamount fauna in the southwest Pacific. *Nature* **4056789(6789)**:944–947 DOI [10.1038/35016066](https://doi.org/10.1038/35016066).
- De Goeij JM, Van Oevelen D, Vermeij MJ, Osinga R, Middelburg JJ, De Goeij AF, Admiraal W. 2013.** Surviving in a marine desert: the sponge loop retains resources within coral reefs. *Science* **3426154(6154)**:108–110 DOI [10.1126/science.1241981](https://doi.org/10.1126/science.1241981).
- De la Torriente A, Serrano A, Fernández-Salas LM, García M, Aguilar R. 2018.** Identifying epibenthic habitats on the Seco de los Olivos Seamount: species assemblages and environmental characteristics. *Deep Sea Research Part I: Oceanographic Research Papers* **135(3)**:9–22 DOI [10.1016/j.dsr.2018.03.015](https://doi.org/10.1016/j.dsr.2018.03.015).
- de Laubenfels MW. 1934.** New sponges from the Puerto Rican deep. *Smithsonian Miscellaneous Collections* **91(17)**:1–28.
- Delle Chiaje S. 1828.** Memorie sulla storia e notomia degli animali senza vertebre del regno di Napoli/di Stefano delle Chiaje. *Stamperia della societa tipografica, Napoli* **3(xx + 232)**:32–49.
- Dendy A. 1889.** Report on a second collection of sponges from the gulf of manaar. *Annals and Magazine of Natural History* **6(3)**:73–99.
- Dendy A. 1924.** Porifera. Part I. Non-Antarctic sponges. *Natural History Report. British Antarctic (Terra Nova) Expedition* **6(3)**:269–392.
- Díaz JA, Ramírez-Amaro S, Ordines F, Cárdenas P, Ferriol P, Terrasa B, Massutí E. 2020.** Poorly known sponges in the Mediterranean with the detection of some taxonomic inconsistencies. *Journal of the Marine Biological Association of the United Kingdom* **100(8)**:1247–1260.
- D’Onghia G, Capezzuto F, Cardone F, Carlucci R, Carluccio A, Chimienti G, Corriero G, Longo C, Maiorano P, Mastrototaro F, Panetta P, Rosso A, Sanfilippo R, Sion L, Tursi A. 2015.** Macro-and megafauna recorded in the submarine Bari Canyon southern Adriatic, Mediterranean Sea using different tools. *Mediterranean Marine Science* **161**:180–196.
- Ekins M, Erpenbeck D, Wörheide G, Hooper JN. 2016.** Staying well connected-Lithistid sponges on seamounts. *Journal of the Marine Biological Association of the United Kingdom* **2(2)**:437–451 DOI [10.1017/S0025315415000831](https://doi.org/10.1017/S0025315415000831).
- Enrichetti F, Bavestrello G, Betti F, Coppari M, Toma M, Pronzato R, Canese S, Bertolino M, Costa G, Pansini M, Bo M. 2020.** Keratose-dominated sponge grounds from temperate mesophotic ecosystems (NW Mediterranean Sea). *Marine Ecology* **41(6)**:e12620.
- Esper EJC. 1794.** Die Pflanzthiere in Abbildungen nach der Natur mit Farben erleuchtet, nebst Beschreibungen. *Zweyter Theil. (Raspe: Nürnberg)* 1–303.
- Estrada M. 1996.** Primary production in the northwestern Mediterranean. *Scientia Marina* **60**:355–364.
- Evcen A, Çinar ME. 2012.** Sponge Porifera species from the Mediterranean coast of Turkey Levantine Sea, eastern Mediterranean, with a checklist of sponges from the coasts of Turkey. *Turkish Journal of Zoology* **36**:460–464.
- Farriols MT, Ordines F, Somerfield PJ, Pasqual C, Hidalgo M, Guijarro B, Massutí E. 2017.** Bottom trawl impacts on Mediterranean demersal fish diversity: not so obvious or are we too late? *Continental Shelf Research* **137**:84–102.
- Ferrer Hernández F. 1914.** Esponjas del Cantábrico: parte 2—III: Myxospongida—IV: Tetraxonida—V: Triaxonida. *Trabajos del Museo Nacional de Ciencias Naturales Zoológica* **17**:1–46.

- Fiorentini L, Dremière P-Y, Leonori I, Sala A, Palumbo V. 1999.** Efficiency of the bottom trawl used for the Mediterranean international trawl survey (MEDITS). *Aquatic Living Resources* **12**(3):187–205 DOI [10.1016/S0990-7440\(00\)88470-3](https://doi.org/10.1016/S0990-7440(00)88470-3).
- Folmer O, Black M, Hoeh W, Lutz R, Vrijenhoek R. 1994.** DNA Primers for amplification of mitochondrial cytochrome c oxidase subunit I from diverse metazoan invertebrates. *Molecular Marine Biology and Biotechnology* **3**:294–299.
- Fourt M, Goujard A, Pérez T, Chevaldonné P. 2017.** Guide de la faune profonde de la mer Méditerranée: explorations des roches et des canyons sous-marins des côtes françaises. *Patrimoines Naturels* **75**:1–184.
- Galil B, Zibrowius H. 1998.** First benthos samples from Eratosthenes Seamount, eastern Mediterranean. *Senckenbergiana Maritima* **284-6**:111.
- George WC, Wilson HV. 1919.** Sponges of Beaufort (N.C.) Harbor and Vicinity. *Bulletin of the Bureau of Fisheries, Washington* **36**:129–179.
- Gerovasileiou V, Voultziadou E. 2012.** Marine caves of the mediterranean sea: a sponge biodiversity reservoir within a biodiversity hotspot. *PLOS ONE* **77**:e39873.
- Griffiths SM, Butler MJ, Behringer DC, Pérez T, Preziosi RF. 2021.** Oceanographic features and limited dispersal shape the population genetic structure of the vase sponge *Ircinia campana* in the Greater Caribbean. *Heredity* **126**:63–76.
- Grinyó J, Gori A, Greenacre M, Requena S, Canepa A, Ambroso S, Purroy A, Gili JM. 2018.** Megabenthic assemblages in the continental shelf edge and upper slope of the Menorca Channel, Western Mediterranean Sea. *Progress in Oceanography* **162**:40–51.
- Guzzetti E, Salabery E, Ferriol P, Díaz JA, Tejada S, Faggio C, Sureda A. 2019.** Oxidative stress induction by the invasive sponge *Paraleucilla magna* growing on *Peyssonnelia squamaria* algae. *Marine Environmental Research* **150(Suppl. 2)**:104763 DOI [10.1016/j.marenvres.2019.104763](https://doi.org/10.1016/j.marenvres.2019.104763).
- Hall T. 1999.** Bioedit: a user-friendly biological sequence alignment editor and analysis program for Windows 95/98/NT. *Nucleic Acids Symposium Series* **41**:95–98.
- Hentschel E. 1929.** Die Kiesel- und Hornschwämme des Nördlichen Eismees—pp. 857–1042, pls XII–XIV. In: Römer F, Schaudinn F, Brauer A, Arndt W, eds. *Fauna Arctica—Eine Zusammenstellung der arktischen Tierformen mit besonderer Berücksichtigung des Spitzbergen-Gebietes auf Grund der Ergebnisse der Deutschen Expedition in das Nördliche Eismeer im Jahre 1898*, 5 4 G. Jena: Fischer.
- Hooper JNA. 2003.** *Spongguide: guide to sponge collection and identification version 2003*. Australia: John N. A. Hooper Qld. Museum.
- Hooper JNA, Van Soest RW. 2002.** *Systema porifera: a guide to the classification of sponges*. New York: Kluwer Academic/Plenum Publishers.
- Ijima I. 1904.** Studies on the Hexactinellida. Contribution IV. Rossellidae. *Journal of the College of Sciences, Imperial University of Tokyo* **18**(7):1–307.
- Jennings S, Kaiser MJ. 1998.** The effects of fishing on marine ecosystems. *Advances in Marine Biology* **34(41)**:201–352 DOI [10.1016/S0065-2881\(08\)60212-6](https://doi.org/10.1016/S0065-2881(08)60212-6).
- Katoh K, Misawa K, Kuma K, Miyata T. 2002.** MAFFT: a novel method for rapid multiple sequence alignment based on fast Fourier transform. *Nucleic Acids Research* **30(14)**:3059–3066 DOI [10.1093/nar/gkf436](https://doi.org/10.1093/nar/gkf436).
- Kovačić M, Ordines F, Schliewen UK. 2017.** A new species of *Buenia* Teleostei: gobiidae from the western Mediterranean Sea, with the description of this genus. *Zootaxa* **4250(5)**:447–460 DOI [10.11646/zootaxa.4250.5.3](https://doi.org/10.11646/zootaxa.4250.5.3).

- Kovacic M, Ordines F, Ramirez-Amaro S, Schliewen UK. 2019.** Gymnesigobius medits (Teleostei: Gobiidae), a new gobiid genus and species from the western Mediterranean slope bottoms. *Zootaxa* **4651**:513–530.
- Kumar S, Stecher G, Li M, Knyaz C, Tamura K. 2018.** MEGA X: molecular evolutionary genetics analysis across computing platforms. *Molecular Biology and Evolution* **35(6)**:1547.
- Lambe LM. 1900.** Sponges from the coasts of north-eastern Canada and Greenland. *Transactions of the royal Society of Canada* **6**:19–49.
- Linnaeus C. 1767.** Systema naturae per regna tria naturae: secundum classes, ordines, genera, species, cum characteribus, differentiis, synonymis, locis. Ed. 12. 1., Regnum Animale. 1 & 2. Holmiae [Stockholm], Laurentii Salvii, 533–1327.
- Longo C, Cardone F, Pierri C, Mercurio M, Mucciolo S, Marzano CN, Corriero G. 2018.** Sponges associated with coralligenous formations along the Apulian coasts. *Marine Biodiversity* **484(4)**:2151–2163 DOI [10.1007/s12526-017-0744-x](https://doi.org/10.1007/s12526-017-0744-x).
- Lundbeck W. 1905.** Porifera—part II: Desmacidonidae. *The Danish Ingolf-Expedition* **62**:1–219.
- Lundbeck W. 1909.** The Porifera of East Greenland. *Meddelelser om Grønland* **29**:423–464.
- Maldonado M. 1992.** Demosponges of the red coral bottoms from the Alboran Sea. *Journal of Natural History* **26(6)**:1131–1161 DOI [10.1080/00222939200770661](https://doi.org/10.1080/00222939200770661).
- Maldonado M. 2006.** The ecology of the sponge larva. *Canadian Journal of Zoology* **842**:175–194.
- Maldonado M, Aguilar R, Bannister RJ, Bell JJ, Conway KW, Dayton PK, Díaz C, Gutt J, Kelly M, Kenchington RELR, Leys SP, Pomponi SA, Rapp HT, Rützler K, Tendal OS, Vacelet J, Young CM. 2016.** Sponge grounds as key marine habitats: a synthetic review of types, structure, functional roles, and conservation concerns. In: Rossi S, ed. *Marine animal forests*. Switzerland: Springer International Publishing, 1–39.
- Maldonado M, Aguilar R, Blanco J, Garcia S, Serrano A, Punzon A. 2015.** Aggregated clumps of lithistid sponges: a singular, reef-like bathyal habitat with relevant paleontological connections. *PLOS ONE* **105**:e0125378.
- Maldonado M, Carmona MC, Uriz MJ, Cruzado A. 1999.** Decline in Mesozoic reef-building sponges explained by silicon limitation. *Nature* **401**:785–788.
- Manconi R, Padiglia A, Cubeddu T, Pronzato R. 2019.** Long-term sponge stranding along the shores of Sardinia Island (Western Mediterranean Sea). *Marine Ecology* **40(6)**:e12567.
- Massutí E, Olivar MP, Monserrat S, Rueda L, Oliver P. 2014.** Towards understanding the influence of environmental conditions on demersal resources and ecosystems in the western Mediterranean: motivations, aims and methods of the IDEADOS project. *Journal of Marine Systems* **138**:3–19.
- McClain CR, Hardy SM. 2010.** The dynamics of biogeographic ranges in the deep sea. *Proceedings of the Royal Society B: Biological Sciences* **277(1700)**:3533–3546 DOI [10.1098/rspb.2010.1057](https://doi.org/10.1098/rspb.2010.1057).
- Miller MA, Pfeiffer W, Schwartz T. 2010.** Creating the CIPRES science gateway for inference of large phylogenetic trees. In: *Proceedings of the Gateway Computing Environments Workshop GCE*. 1–8.
- Monserrat S, López-Jurado JL, Marcos M. 2008.** A mesoscale index to describe the regional circulation around the Balearic Islands. *Journal of Marine Systems* **713–714(3–4)**:413–420 DOI [10.1016/j.jmarsys.2006.11.012](https://doi.org/10.1016/j.jmarsys.2006.11.012).
- Morato T, Kvile KØ, Taranto GH, Tempera F, Narayanaswamy BE, Hebbeln D, Menezes GM, Wienberg C, Santos RS, Pitcher TJ. 2013.** Seamount physiography and biology in the north-east Atlantic and Mediterranean Sea. *Biogeosciences* **105(5)**:3039–3054 DOI [10.5194/bg-10-3039-2013](https://doi.org/10.5194/bg-10-3039-2013).

- Morrow C, Picton B, Erpenbeck D, Boury-Esnault N, Maggs C, Allcock A. 2012.** Congruence between nuclear and mitochondrial genes in Demospongiae: A new hypothesis for relationships within the G4 clade (Porifera: Demospongiae). *Molecular Phylogenetics and Evolution* **62**(1):174–190.
- Morrow C, Cárdenas P, Boury-Esnault N, Picton B, McCormack G, Van Soest R, Collins A, Redmond N, Maggs C, Sigwart J, Allcock LA. 2019.** Integrating morphological and molecular taxonomy with the revised concept of Stelligeridae (Porifera: Demospongiae). *Zoological Journal of the Linnean Society* **187**(1):31–81 DOI [10.1093/zoolinnean/zlz017](https://doi.org/10.1093/zoolinnean/zlz017).
- OCEANA. 2011.** *Montañas submarinas de las Islas Baleares: canal de Mallorca—propuesta de protección para Ausias March, Emile Baudot y Ses Olives*. Washington, D.C.: OCEANA, 64.
- Okada Y. 1932.** Report on the hexactinellid sponges collected by the United States Fisheries steamer ‘Albatros’ in the northwestern Pacific during the summer of 1906. *Proceedings of the United States National Museum* **81**(2935):1–118.
- Ordines F, Jordà G, Quetglas A, Flexas M, Moranta J, Massutí E. 2011.** Connections between hydrodynamics, benthic landscape and associated fauna in the Balearic Islands, western Mediterranean. *Continental Shelf Research* **31**(17):1835–1844 DOI [10.1016/j.csr.2011.08.007](https://doi.org/10.1016/j.csr.2011.08.007).
- Ordines F, Massutí E. 2009.** Relationships between macro-epibenthic communities and fish on the shelf grounds of the western Mediterranean. *Aquatic Conservation: Marine and Freshwater Ecosystems* **19**(4):370–383 DOI [10.1002/aqc.969](https://doi.org/10.1002/aqc.969).
- Ordines F, Ramón M, Rivera J, Rodríguez-Prieto C, Farriols MT, Guijarro B, Pascual C, Massutí E. 2017.** Why long term trawled red algae bedsoff Balearic Islands (western Mediterranean) still persist? *Regional Studies in Marine Science* **15**:39–49.
- Ordines F, Ramírez-Amaro S, Fernandez-Arcaya U, Marco-Herrero E, Massutí E. 2019.** First occurrence of an Ophiohelidae species in the Mediterranean: the high abundances of *Ophiomyces grandis* from the Mallorca Channel seamounts. *Journal of the Marine Biological Association of the United Kingdom* **99**(8):1817–1823 DOI [10.1017/S0025315419000808](https://doi.org/10.1017/S0025315419000808).
- Pansini M. 1984.** Notes on some Mediterranean Axinella with description of two new species. *Bollettino dei Musei e degli Istituti Biologici dell’Università di Genova* **50–51**:79–98.
- Pansini M, Manconi R, Pronzato R. 2011.** Porifera I—calcareo, demospongiae (partim), hexactinellida, homoscleromorpha. In: *Fauna d’Italia*. Vol. 46. Bologna: Calderini-Il Sole 24 Ore, 554.
- Pardo E, Rubio RA, García S, Ubero J. 2011.** Documentación de arrecifes de corales de agua fría en el Mediterráneo occidental Mar de Alborán. *Chronica Naturae* **1**:20–34.
- Pinot JM, López-Jurado JL, Riera M. 2002.** The CANALES experiment 1996–1998: interannual, seasonal, and mesoscale variability of the circulation in the Balearic Channels. *Progress in Oceanography* **55**–554(3–4):335–370 DOI [10.1016/S0079-6611\(02\)00139-8](https://doi.org/10.1016/S0079-6611(02)00139-8).
- Plotkin A, Gerasimova E, Rapp HT. 2012.** Phylogenetic reconstruction of polymastiidae (Demospongiae: Hadromerida) based on morphology. *Hydrobiologia* **687**:21–41.
- Pulitzer-Finali G. 1983.** A collection of Mediterranean Demospongiae Porifera with, in appendix, a list of the Demospongiae hitherto recorded from the Mediterranean Sea. *Annali del Museo civico di storia naturale Giacomo Doria* **84**:445–621.
- Pulitzer-Finali G, Hadromerida A, Poecilosclerida H. 1978.** Report on a collection of sponges from the bay of Naples—III Hadromerida, Axinellida, Poecilosclerida, Halichondrida, Haplosclerida. *Bollettino dei Musei e degli Istituti Biologici dell’Università di Genova* **45**:7–89.
- Quetglas A, Guijarro B, Ordines F, Massutí E. 2012.** Stock boundaries for fisheries assessment and management in the Mediterranean: the Balearic Islands as a case study. *Scientia Marina* **76**(1):17–28.

- Reiss H, Kröncke I, Ehrich S. 2006.** Estimating the catching efficiency of a 2-m beam trawl for sampling epifauna by removal experiments. *ICES Journal of Marine Science* **63(8)**:1453–1464 DOI [10.1016/j.icesjms.2006.06.001](https://doi.org/10.1016/j.icesjms.2006.06.001).
- Ridley SO, Dendy A. 1886.** XXXIV.—Preliminary Report on the Monaxonida collected by H.M.S. 'Challenger'. *Annals and Magazine of Natural History* **18(107)**:325–351 DOI [10.1080/00222938609459982](https://doi.org/10.1080/00222938609459982).
- Riesgo A, Taboada S, Pérez-Portela R, Melis P, Xavier JR, Blasco G, López-Legentil S. 2019.** Genetic diversity, connectivity and gene flow along the distribution of the emblematic Atlanto-Mediterranean sponge *Petrosia ficiformis* (Haplosclerida, Demospongiae). *BMC Evolutionary Biology* **19(1)**:24 DOI [10.1186/s12862-018-1343-6](https://doi.org/10.1186/s12862-018-1343-6).
- Rogers AD. 2018.** The biology of seamounts: 25 years on. In: *Advances in Marine Biology*. Vol. 79. London: Academic Press, 137–224.
- Ronquist F, Teslenko M, Van Der Mark P, Ayres DL, Darling A, Höhna S, Larget B, Liu L, Suchard MA, Huelsenbeck JP. 2012.** MrBayes 3.2: efficient Bayesian phylogenetic inference and model choice across a large model space. *Systematic Biology* **61(3)**:539–542 DOI [10.1093/sysbio/sys029](https://doi.org/10.1093/sysbio/sys029).
- Rützler K. 1990.** Association between Caribbean sponges and photosynthetic organisms. In: *New Perspective in Sponge Biology: 3D International Sponge Conference, 1985* Smithsonian Institution Press.
- Samadi S, Bottan L, Macpherson E, De Forges BR, Boisselier M-C. 2006.** Seamount endemism questioned by the geographic distribution and population genetic structure of marine invertebrates. *Marine Biology* **149**:1463–1475.
- Samadi S, Schlacher T, De Forges BR. 2007.** Seamount benthos. In: *Seamounts: Ecology, Fisheries and Conservation*. Oxford: Blackwell, 119–140.
- Santín A, Grinyó J, Ambroso S, Uriz MJ, Gori A, Dominguez-Carrió C, Gili JM. 2018.** Sponge assemblages on the deep Mediterranean continental shelf and slope (Menorca Channel, Western Mediterranean Sea). *Deep Sea Research Part I: Oceanographic Research Papers* **131**:75–86.
- Santinelli C. 2015.** DOC in the Mediterranean Sea. In: *Biogeochemistry of marine dissolved organic matter*. London: Academic Press, 579–608.
- Sarà M. 1958a.** Contributo all consoscenza dei Poriferi del Mar Ligure. *Annali di Museo Civico di Storia Naturale Genova* **70**:207–244.
- Sarà M. 1958b.** Studio sui Poriferi di una grotta di marea del Golfo di Napoli. *Archivio Zoologico Italiano* **43**:203–281.
- Sarà M. 1959.** *Pseudotrachya oxystyla* sp.n. (Demospongiae) e suo rinvenimento nella zona litorale dell'isola d'Ischia. *Annuario dell'Istituto e Museo de Zoologia dell'Università di Napoli* **11(5)**:1–5.
- Schulze FE. 1897.** Revision des Systemes der Asconematiden und Rosselliden. *Sitzungsberichte der Preussischen Akademie der Wissenschaften zu Berlin* **1**:520–558.
- Schindelin J, Arganda-Carreras I, Frise E, Kaynig V, Longair M, Pietzsch T, Preibisch S, Rueden C, Saalfeld S, Schmid B, Tinevez J-Y, White DJ, Hartenstein V, Eliceiri K, Tomancak P, Cardona A. 2012.** Fiji: an open-source platform for biological image analysis. *Nature Methods* **9(7)**:676–682 DOI [10.1038/nmeth.2019](https://doi.org/10.1038/nmeth.2019).
- Schmidt O. 1870.** *Grundzüge einer Spongien-Fauna des atlantischen Gebietes*. Leipzig: Wilhelm Engelmann. iii-iv, 1-88, pls I-VI.
- Schmidt O. 1875.** Spongien. Die Expedition zur physikalisch-chemischen und biologischen Untersuchung der Nordsee im Sommer 1872. *Jahresbericht der Commission zur Wissenschaftlichen Untersuchung der Deutschen Meere in Kiel* **2–3**:115–120.

- Shaffer MR, Luter HM, Webster NS, Abdul Wahab MA, Bell JJ. 2020.** Evidence for genetic structuring and limited dispersal ability in the Great Barrier Reef sponge *Carteriospongia foliascens*. *Coral Reefs* **39**(1):39–46 DOI [10.1007/s00338-019-01876-8](https://doi.org/10.1007/s00338-019-01876-8).
- Simpson TL. 1978.** The biology of the marine sponge *Microciona prolifera* Ellis and Sollander—III: spicule secretion and the effect of temperature on spicule size. *Journal of Experimental Marine Biology and Ecology* **35**(1):31–42 DOI [10.1016/0022-0981\(78\)90088-6](https://doi.org/10.1016/0022-0981(78)90088-6).
- Sitjà C, Maldonado M. 2014.** New and rare sponges from the deep shelf of the Alboran Island Alboran Sea, Western Mediterranean. *Zootaxa* **3760**(2):141–179 DOI [10.11646/zootaxa.3760.2.2](https://doi.org/10.11646/zootaxa.3760.2.2).
- Sitjà C, Maldonado M, Farias C, Rueda JL. 2019.** Deep-water sponge fauna from the mud volcanoes of the Gulf of Cadiz North Atlantic, Spain. *Journal of the Marine Biological Association of the United Kingdom* **99**(4):807–831 DOI [10.1017/S0025315418000589](https://doi.org/10.1017/S0025315418000589).
- Solórzano MR. 1990.** Poríferos del litoral gallego: estudio faunístico, distribución e inventario. Phd Thesis Universidad de Santiago de Compostela 1036.
- Spedicato MT, Massutí E, Mérigot B, Tserpes G, Jadaud A, Relini G. 2019.** The MEDITS trawl survey specifications in an ecosystem approach to fishery management. *Scientia Marina* **83**(S1):9–20 DOI [10.3989/scimar.04915.11X](https://doi.org/10.3989/scimar.04915.11X).
- Stamatakis A. 2014.** RAxML version 8: a tool for phylogenetic analysis and post-analysis of large phylogenies. *Bioinformatics* **30**(9):1312–1313 DOI [10.1093/bioinformatics/btu033](https://doi.org/10.1093/bioinformatics/btu033).
- Tabachnick KP. 2002.** Family Rossellidae Schulze, 1885. In: Hooper JNA, Van Soest RWM, eds. *Systema Porifera: A Guide to the Classification of Sponges*. Vol. 2. New York, NY: Kluwer Academic/Plenum, 1441–1505.
- Topsent E. 1890.** Notice préliminaire sur les spongiaires recueillis durant les campagnes de l'Hirondelle. *Bulletin de la Société Zoologique de France* **15**:26–32 DOI [10.5962/bhl.part.18721](https://doi.org/10.5962/bhl.part.18721).
- Topsent E. 1892.** Contribution à l'étude des Spongiaires de l'Atlantique Nord Golfe de Gascogne, Terre-Neuve, Açores: résultats des campagnes scientifiques accomplies par le Prince Albert I. *Monaco* **2**:1–165 pls I–XI.
- Topsent E. 1898.** Eponges nouvelles des Açores. (Première serie). *Mémoires de la Société zoologique de France* **11**:225–255.
- Topsent E. 1895.** Campagnes du yacht Princess Alice: notice sur les spongiaires recueillis en 1894 et 1895. *Bulletin de la Société Zoologique de France* **20**:213–216.
- Topsent E. 1904.** Spongiaires des Açores: résultats des campagnes Scientifiques accomplies par le Prince Albert I. *Monaco* **25**:1–280.
- Topsent E. 1925.** Etude des Spongiaires du Golfe de Naples. *Archives de Zoologie expérimentale et générale* **635**:623–725.
- Topsent E. 1927.** Diagnoses d'Éponges nouvelles recueillies par le Prince Albert Ier de Monaco. *Bulletin de l'Institut océanographique Monaco* **502**:1–19.
- Topsent E. 1928.** Spongiaires de l'Atlantique et de la Méditerranée provenant des croisières du Prince Albert Ier de Monaco: résultats des campagnes scientifiques accomplies par le Prince Albert I. *Monaco* **74**:1–376 pls I–XI.
- Trainito E, Baldacconi R, Mačić V. 2020.** All-around rare and generalist: countercurrent signals from the updated distribution of *Calyx nicaensis* Risso, 1826 Porifera. *Demospongiae Studia Marina* **33**:1.
- Uitz J, Stramski D, Gentili B, D'Ortenzio F, Claustre H. 2012.** Estimates of phytoplankton class-specific and total primary production in the Mediterranean Sea from satellite ocean color observations. *Global Biogeochemical Cycles* **26**(2):GB2024 DOI [10.1029/2011GB004055](https://doi.org/10.1029/2011GB004055).

- Uriz MJ. 1984.** Material para la fauna de esponjas ibéricas: nuevas senalizaciones de Demosponjas en nuestras costas. *Actas do IV Simposio ibérico de estudos do benthos marinho* 3:131–140.
- Vacelet J. 1961.** Spongiaires Démosponges de la région de Bonifacio Corse. *Recueil des Travaux de la Station marine d'Endoume* 22(36):21–45.
- Vacelet J. 1969.** Eponges de la Roche du Large et de l'étage bathyal de Méditerranée récoltes de la soucoupe plongeante Cousteau et dragages. *Mémoires du Muséum National d'Histoire Naturelle* 59:145–219.
- Vacelet J, Boury-Esnault N. 1996.** A new species of carnivorous sponge (Demospongiae: Cladorhizidae) from a mediterranean cave, recent advances in sponge biodiversity inventory and documentation. In: Willenz Ph, ed. *Bulletin de l'Institut royal des Sciences naturelles de Belgique. Biologie*. Vol. 66. 109–115.
- Valisano L, Pozzolini M, Giovine M, Cerrano C. 2012.** Biosilica deposition in the marine sponge *Petrosia ficiformis* Poiret, 1789: the model of primmorphs reveals time dependence of spiculogenesis. In: Maldonado M, Becerro MA, Turon X, Uriz MJ, eds. *Ancient Animals, New Challenges*. Dordrecht: Springer, 259–273.
- Vân Le HL, Lecointre G, Perasso R. 1993.** A 28S rRNA-based phylogeny of the gnathostomes: first steps in the analysis of conflict and congruence with morphologically based cladograms. *Molecular Phylogenetics and Evolution* 21:31–51.
- Van Soest RWM, Hooper JNA. 1993.** Taxonomy, phylogeny and biogeography of the marine sponge genus *Rhabdermia* Topsent, 1890 (Demospongiae, Poecilosclerida). *Scientia Marina* 57(4):319–351.
- Van Soest RWM, Boury-Esnault N, Hooper JNA, Rützler K, de Voogd NJ, Alvarez B, Hajdu E, Pisera AB, Manconi R, Schönberg C, Klautau M, Kelly M, Vacelet J, Dohrmann M, Díaz M-C, Cárdenas P, Carballo JL, Ríos P, Downey R, Morrow CC. 2021.** World porifera database. Available at <http://www.marinespecies.org/porifera> on 2021-08-11.
- White M, Mohn C. 2004.** Seamounts: a review of physical processes and their influence on the seamount ecosystem. OASIS EU Project Report 37. Available at https://epic.awi.de/id/eprint/37314/17/OASIS_Oceanography.pdf.
- Wörheide G. 2006.** Low variation in partial cytochrome oxidase subunit I (COI) mitochondrial sequences in the coralline demosponge *Astrosclera willeyana* across the Indo-Pacific. *Marine Biology* 148(5):907–912 DOI 10.1007/s00227-005-0134-y.
- Würtz M, Rovere M. 2015.** *Atlas of the Mediterranean seamounts and seamount-like structures*. Gland, Switzerland: IUCN.