Polar Biology (2020) 43:523–533
https://doi.org/10.1007/s00300-020-02654-x

ORIGINAL PAPER

A new species of *Isodictya* (Porifera: Poecilosclerida) from the Southern Ocean

Pilar Ríos[1,2] · Ana Riesgo[3] · Sergio Taboada[3,4] · Javier Cristobo[1,2]

Received: 23 July 2019 / Revised: 17 March 2020 / Accepted: 19 March 2020 / Published online: 31 March 2020

Abstract
We discovered a new species of Porifera belonging to the genus *Isodictya* Bowerbank, 1864 during cruises aboard R/V Hesperides in Antarctica. Collected samples are mostly part of the surveys of the Spanish project BENTART whose main objective has been to study the benthic communities inhabiting sea bottoms of Livingston and Deception Island in the South Shetlands archipelago and the Antarctic Peninsula. *Isodictya filiformis* sp. nov., described here, is characterized by its fragile and thin morphology (very different from other known species in the area) and by having microxeas as additional microscleres. Three specimens were collected from Marguerite Bay, Low Island and Deception Island (Antarctic Peninsula) and one specimen at Peter I Island (Bellingshausen Sea). Its presence in Peter Island is quite relevant as this location is 390 km away from the nearest coast in the Bellingshausen Sea, an area that has scarcely been investigated in the past. However, results from the Bentart 03 Expedition seem to indicate that Peter I Island has a wide variety of benthic organisms, in contrast to the deep adjacent areas of Bellingshausen Sea. Apart from the morphological analyses, we place the new *Isodictya* species within its phylogenetic context using two nuclear markers (*18S* rDNA and *28S* rDNA) and provide some information about the ecological preferences of the new species.

Keywords Taxonomy · Biodiversity · Phylogeny · Bellingshausen Sea · Peter I island · Antarctica

Introduction

Peter I is a very remote island in the middle of the Bellingshausen Sea in the Southern Ocean. Inaccessible nearly all year-round due to the heavy surrounding pack ice, Peter I covers 158 km^2 and is 95% glaciated. It was discovered on January 21, 1821 by the Russian Fabian von Bellingshausen. Several expeditions, as The “Belgica” Expedition (1897–1899) collected the first few specimens, then “Old I” (1927), and later “Bahía Aguirre” (1954–1955) carried out geographic and geologic studies at the island, but it was not until 1965 (and 1969–1971) when the icebreaker “General San Martín” made the first biological expedition in which 21 species of marine invertebrates were identified, with no reports on the sponge fauna.

Even though information about the benthic macrofauna of the Bellingshausen Sea and Peter I Island is scarce, in the last decade, there has been a growing effort in studying several aspects of it, particularly the soft-bottom molluscs (Troncoso et al. 2007; Troncoso and Aldea 2008; Aldea and Troncoso 2008, 2010; Aldea et al. 2008, 2011; Garcia-Alvarez et al. 2010), suprabenthic mysids (San Vicente 2007; San Vicente and Sorbe 2008; San Vicente et al. 2009), cumaceans (Corbera and Ramos 2005; Corbera et al. 2009), nemerteans (Fernández-Álvarez and Anadón, 2012, 2013), other crustaceans (Klages et al. 1995; Arana and Retamal 1999; García-Raso et al. 2005), pycnogonids (Munilla and

Electronic supplementary material The online version of this article (https://doi.org/10.1007/s00300-020-02654-x) contains supplementary material, which is available to authorized users.

✉ Pilar Ríos
pilar.rios@ieo.es; pilar.rios.lopez@gmail.com

1 Instituto Español de Oceanografía, Centro Oceanográfico de Gijón, C/Príncipe de Asturias 70 Bis, 33212 Gijón, Asturias, Spain

2 Dpto. Ciencias de la Vida, EU-US Marine Biodiversity Group, Universidad de Alcalá, 28871 Alcalá de Henares, Spain

3 Department of Life Sciences, The Natural History Museum of London, Cromwell Road, London SW7 5BD, UK

4 Departamento de Biología (Zoología), Facultad de Ciencias, Universidad Autónoma de Madrid, Cantoblanco, 28049 Madrid, Spain

Soler-Membrives 2009, 2015), fishes (Matallanas and Olaso 2007; Eakin et al. 2008, 2009; Matallanas 2009a, b, 2010; Matallanas et al. 2012), annelids (López 2011; Moreira and Parapar 2011; Parapar et al. 2011, 2013), bryozoans (López-Fé 2005), echinoderms (Moya et al. 2012; O'Loughlin et al. 2009), ascidians (Varela and Ramos-Esplá 2008), invertebrate larvae (Ameneiro et al. 2012) and also the community structure and spatial distribution of benthic fauna (Saiz et al. 2008). But in any case, the Bellingshausen Sea is still understudied and we know almost nothing about its sponge fauna.

The family Isodictyidae Dendy (1924) currently has two genera: *Coelocarteria* Burton (1934) and *Isodictya* Bowerbank (1864) (Hajdu and Lôbo-Hajdu 2002). The genus *Coelocarteria*, with three valid species, is known from the Indian and Pacific Ocean. On the other hand, the genus *Isodictya* consists of 39 species (Van Soest et al. 2020). Interestingly, this genus is particularly rich in the Southern Ocean with 17 valid species (Janussen and Downey 2014; Goodwin et al. 2016). Here, we describe a new Antarctic member of the genus *Isodictya* using a combined morphological and molecular approach.

Material and methods

Sampling and preservation

The material examined was collected from Peter I Island (Bellingshausen Sea, Antarctica, 68°49′ 37″ S; 90°48′ 47″ W), at a depth of 208–210 m in February 2003 on muddy substrate with sand using a box corer (Fig. 1). Additional material from Low Island (Antarctic Peninsula, 63° 26′ 13″ S; 62° 14′ 42″ W) and Marguerite Bay (Antarctic Peninsula, 68° 07′ 43″ S; 69° 35′ 28″ W) was also collected at a depth of 97 m and 159 m, respectively, in February 2006. We collected one additional sample from Deception Island (62° 59.022′ S; 60° 35.847′ W) at 113 m depth in January 2006 using a modified Agassiz Trawl (Fig. 1). All materials were collected during the Bentart 03, Bentart 06, ECOQUIM and ACTIQUIM projects. Once on board, samples were photographed and subsequently preserved in 70% ethanol.

Morphological analysis

For the study of dissociated spicules, the organic matter was digested with nitric acid taken to boiling point following the methods of Rützler (1978) and Cristobo et al. (1993). The skeleton sections were made following protocols as outlined in Ríos (2006). Spicules of the holotype were examined with a Leica S440 Scanning Electron Microscope, previously metalized with gold–palladium in a sputtering Polarun SC 7640. The data for spicule sizes are based on 25 measurements for each spicule category, comprising minimum, average and maximum lengths in micrometers (µm). General classification and the names of class, subclass, order and suborders follow the classification proposed by Morrow and Cárdenas (2015) and highlighted in the World Porifera Database (Van Soest et al. 2020).

The type material was deposited at the Museo Nacional de Ciencias Naturales, Madrid, Spain (MNCN), Natural History Museum, London, United Kingdom (NHM) and Museum National d'Histoire Naturelle, Paris, France (MNHN).

DNA extraction, marker amplification and phylogeny

DNA was extracted from a specimen of *Isodictya filiformis* sp. nov. (*28S* MT032134 and *18S* MT032130) and a sample identified as *Isodictya kerguelenensis* (Ridley and Dendy 1886) (*28S* MT032133 and *18S* MT032129) using a Qiagen DNeasy Blood and Tissue Kit (QIAgen) following an adapted version of the protocol provided by the manufacturer (overnight incubation in lysis buffer and proteinase K). We selected two molecular markers to amplify *18S rDNA* (*18S*) and *28S rDNA* (*28S*). The complete *18S* (1766 bp) was amplified in three legs using the primers 1F-5R, 4F-7R, and a.20-9R (Giribet and Wheeler 2001), and a fragment of 589 bp of *28S* (D6–D8 region) was amplified using the primers CMPOR1490F and CMPOR2170R (Morrow et al. 2012). D6–D8 region was selected because these were the most successful PCRs regarding *28S*. All *18S* fragments were amplified using the PCR protocol 94 °C, 5 min; (94 °C, 1 min, 52 °C, 1 min, 72 °C, 1 min) × 38 cycles; 72 °C, 10 min. We used a different protocol for *28S* of 94 °C, 5 min; (94 °C, 1 min, 55 °C, 1 min, 72 °C, 1 min) × 38 cycles; 72 °C, 10 min. All DNA markers were amplified in 12.5 µL reactions using 10.5 µL of VWR Red Taq DNA Polymerase 1.1 × Master Mix (VWR International bvba/sprl, Belgium), 0.5 µL of the forward and reverse primers, and 1 µL of DNA template. PCR products, stained with GelRed® (Biotium, USA), were visualized in a 2.5% agarose gel electrophoresis and run at 90 V for 30 min. Sequencing was conducted on an ABI 3730XL DNA Analyser (Applied Biosystems, USA) at the Molecular Core Labs (Sequencing Facility) of the NHMUK, using the forward and reverse primers mentioned above. Sequences were deposited in GenBank under accession numbers (See Online Resource 1).

Sequences were checked and cleaned using Geneious Prime 2019.1.1 (https://www.geneious.com). Forward and reverse reads were assembled into contigs and primers were trimmed out. Alignments were built with MAFTT v.5 (Katoh and Standley 2013) and phylogenetic trees were built using a GTR + G + I model in RAxML (Stamatakis 2006) with 10 runs and 100 bootstrap replicates. Sequences for

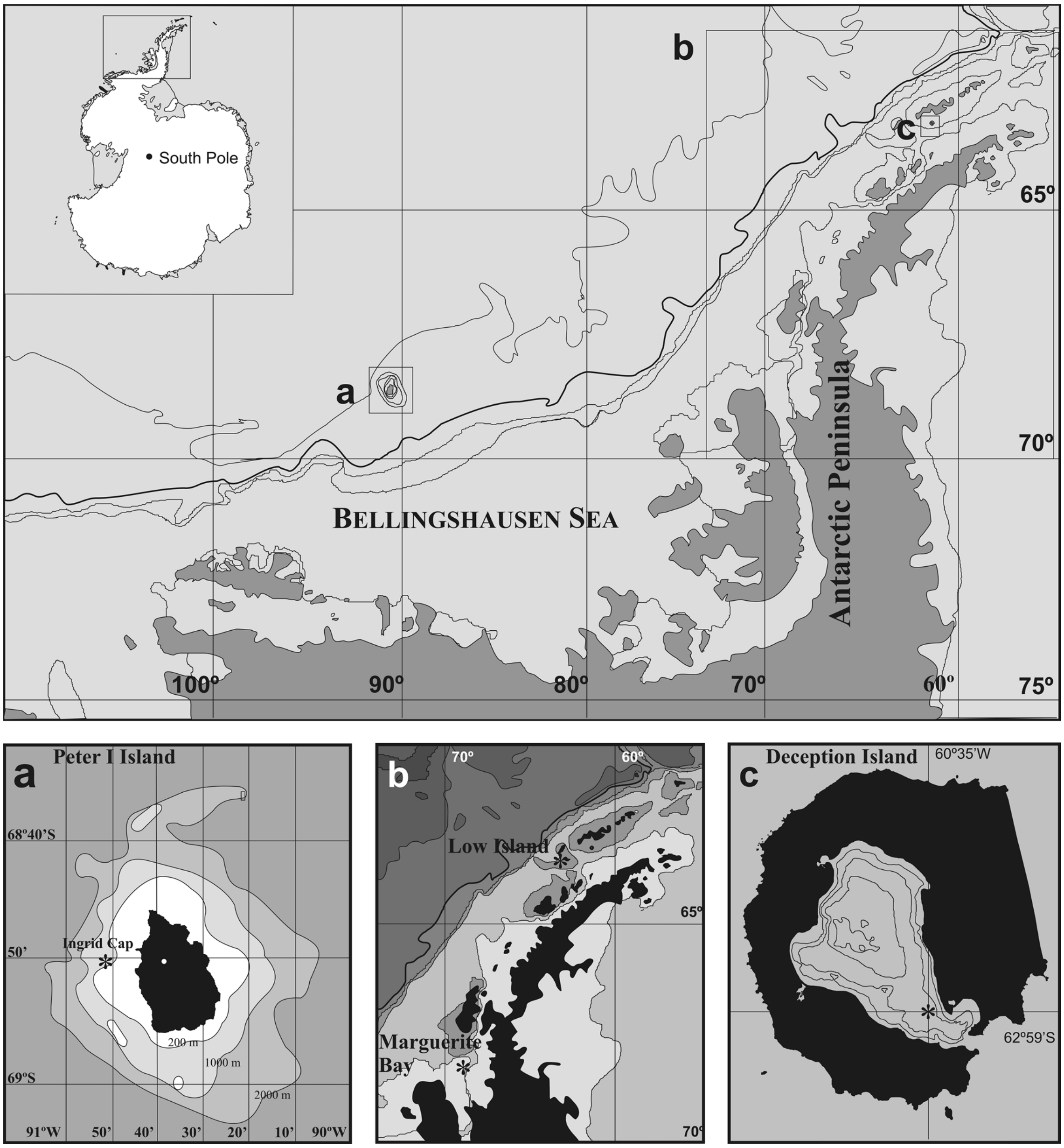

Fig. 1 Location of the collection sites of *Isodictya filiformis* sp. nov. in the Antarctic Peninsula and Bellingshausen Sea. The asterisks indicate the exact collecting sites. 1, Peter I Island. 2, Marguerite Bay and Low Island. 3. Deception Island

18S and *28S* from other sponge species were sourced from NCBI (Online Resource 1).

Results and discussion

Systematics

Class DEMOSPONGIAE Sollas (1885).

Subclass HETEROSCLEROMORPHA Cárdenas et al. (2012).

Order POECILOSCLERIDA Topsent (1928).

Family ISODICTYIDAE Dendy (1924).

Genus *Isodictya* Bowerbank (1864).

Isodictya filiformis sp. nov.

(Figures 2, 3, 4 and 5).

Type material

Holotype MNCN (MNCN 1.01/6 130 39), Museo Nacional de Ciencias Naturales de Madrid. Peter I Island (Antarctic), 68° 49′ 37″ S; 90° 48′ 47″ W, 208–210 m depth, Coll. R/V “Hespérides”, 05.02.2003. One specimen. Muddy substrate with sand. In 70% ethanol.

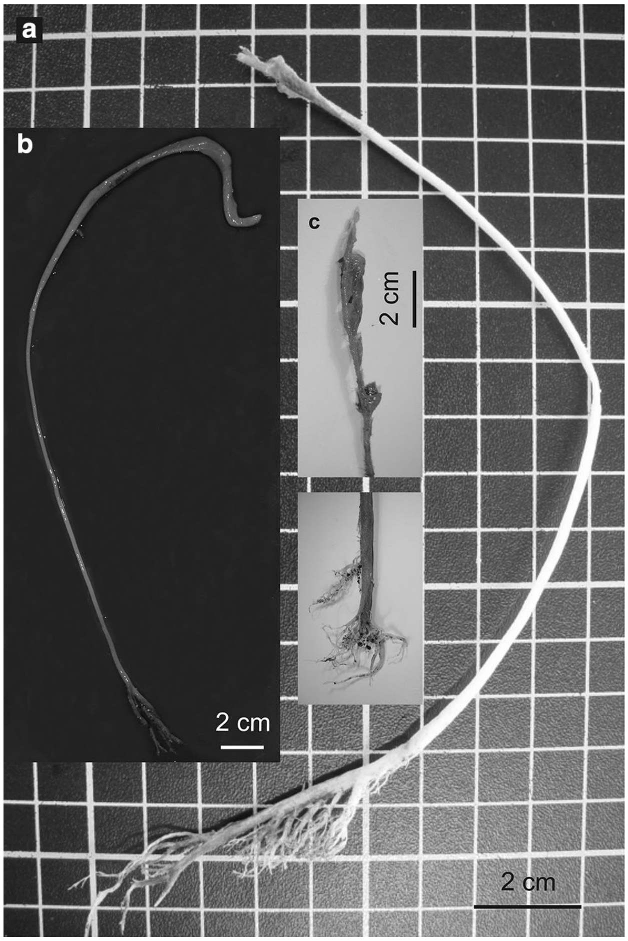

Fig. 2 *Isodictya filiformis* sp. nov. Habitus. **a**, Holotype, Peter I Island. **b**, Paratype 1, Low Island. c, Paratype 2, Deception Island

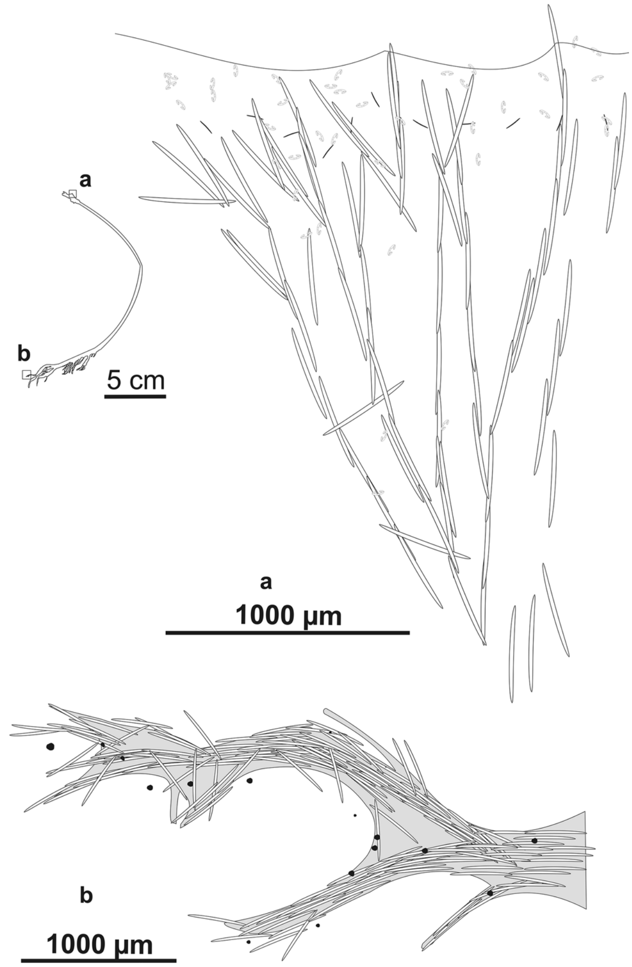

Fig. 3 *Isodictya filiformis* sp. nov. Skeleton. **a**, Section through the distal area. **b**, Base of the sponge showing anchoring roots

Paratype 1 (NHMUK 2020.3.26.5), Natural History Museum of London. Low Island (Antarctic Peninsula). 63° 26′ 13″ S; 62° 14′ 42″ W. 97 m depth. Coll. R/V "Hespérides", 12.02.2006. One specimen. In 70% ethanol.

Paratype 2 (MNHN-IP-2019–13), Museum National d'Histoire Naturelle, Paris. Deception Island (South Shetlands). 62° 59.022′ S; 60° 35.847′ W. 113 m depth. Coll. R/V "Hespérides", 07.01.2006. One specimen. In 70% ethanol.

Collection information of collected specimens was archived in the PANGAEA data repository https://doi.pangaea.de/10.1594/PANGAEA.913490.

Comparative material examined

Isodictya delicata var. *megachela* Burton (1934). Paratype Natural History Museum of London: NHMUK 1933.3.17.7 (wet specimen) and NHMUK 1933.3.17.7a (slide); we took a small fragment of the wet specimen to take the SEM pictures. Type locality Seymour Island, Graham Land (Antarctic).

Description

External morphology (Fig. 2a, b). Filiform specimens, fixed to the substratum by means of small roots. Dimensions of holotype, 24 cm long and 3 mm diameter in its middle part and 1 cm at the top of the apex. Smooth and hard texture. Flexible but consistent shaft. At first sight neither oscula nor perforations observed. In its upper part, an apical multispicular axis can be made out, with secondary fibres in perpendicular arrangement to this axis. Beige colour in vivo and white in alcohol, except for its basal area and in its apical area, which were brown.

One specimen (collected during the 2006 expedition) has the same external morphology with more organic material in the apical area (Fig. 2c).

Skeleton (Fig. 3). Choanosomal skeleton made up of bundles of oxeas along the stalk of the sponge. Ectosomal skeleton made up of oxeas with few spicules, with scattered isochelae not forming a defined layer, among which we may

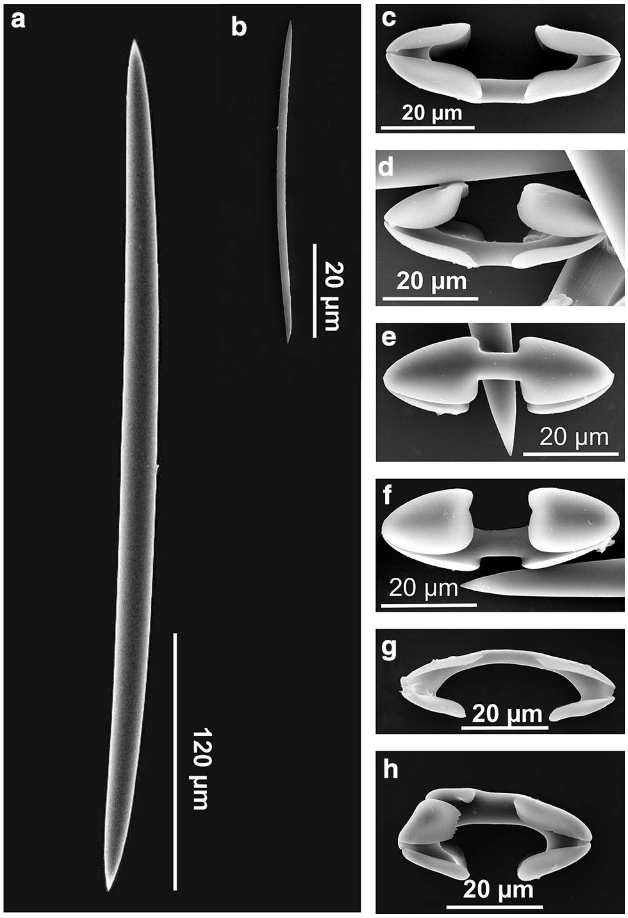

Fig. 4 *Isodictya filiformis* sp. nov. Spicules (SEM): **a**, Oxea. **b**, Microxea. **c**–**g**, Palmate isochelae. **h**, Isochela malformation

also find microxeas. On the base of the sponge, there are formations that work as anchoring roots, also made up of spicular bundles, but in some specimens no isochelae noticed. Roots normally accumulate sand grains.

Spicules (Fig. 4). *Megascleres*. Erect or slightly curved oxeas, ending in a very short tip. Its axial channel can be noticed. Some spicules present deformations such as central enlargements, junction of one of the ends, in which one of them is atrophied and even some of the spicules have become styles. Spicules of the shaft shorter than apical or root areas. Size: 215 – 400.43 – 580 × 5 – 14.37 – 22.5 μm. *Microscleres*. Palmate isochelae with side alae slightly longer than its front palms. These have a triangular aspect with slightly rounded edges. In the centre of the palm, a small fold that points at the outer part of the spicule can be clearly noticed. The shaft is straight. Size: 35 – 52.35 – 75 × 12.5 – 19.55 – 27.5 µm. Microxeas are mostly frequent in the lower part of the sponge with similar appearance to the root of a plant. Spicules are straight, with slightly erect pointed ends, not found in the sample from Marguerite Bay. Size: 47.5 – 131.87 – 257.5 µm long.

Etymology

The specific name is given because of the filiform morphology of the sponge.

Remarks

To date, 20 valid species of *Isodictya* are present in the Southern Ocean and South Atlantic (Goodwin et al. 2016). The peculiar morphology of the collected specimens is similar to the design of *Isodictya delicata* var. *megachela* described by Koltun (1964). The spicular dimensions of the specimen of Bentart 03 and paratypes 1 and 2 are slightly shorter than the ones given by Burton (1934), Koltun (1964) and Desqueyroux (1975) in their descriptions of *I. delicata* var. *megachela*, who, in any case, did not report the presence of microxeas (Table 1). In the current specimens studied, an additional spicular category was also observed, the microxeas, which were never described in the other *Isodictya* species from the Southern Ocean.

Most *Isodictya* species present in the Southern Ocean have oxeas as main spicules and its microscleres are isochelae and canonochelae (genus *Cercidochela* Kirkpatrick (1907), synonymised by Hajdu and Lobo-Hajdu 2002 with *Isodictya*). To our knowledge, the presence of additional microscleres has only been recorded in *Isodictya erinacea* (Topsent 1916) and *Isodictya toxophila* Burton (1932). For *I. erinacea*, the presence of raphides was common in the preparation of the type, but in other specimens studied, their presence could not be confirmed. In the case of *I. toxophila*, the presence of toxas could be corroborated in all the specimens that were preserved in good condition (Ríos 2006).

The original description of *Isodictya delicata* var. *megachela* was carried out using two specimens; the holotype (887A) is flabellate and stipitate with even but coarsely hispid surface, and oscules arranged in linear series along the margin of the sponge. The other specimen (889) was very similar in shape as the one determined by Stephens (1915) as *Homoeodictya compressa* (Esper 1794) from South Africa, but it had the same skeleton and the spicular dimensions matched those of the *I. delicata* var. *megachela* holotype. *I. delicata* (Thiele 1905) differs in the dimensions of the size of isochelae (Burton 1934).

As Burton (1934) never made any illustration of *I. delicata* var. *megachela* and the picture drawn by Koltun (1964) was similar to what has been observed in our specimens, we proceeded to the study the type of this species. Some photographs of the preparations of the paratype sent from the NHM of London were taken and the spicules were observed using SEM (Fig. 5). These did not match with the new species; in the case of the preparations of the paratype, it can be seen a skeletal arrangement and isochelae are similar to those in *Isodictya bentarti* Ríos et al. (2004). However, it

Table 1 Comparison of spicule sizes between *Isodictya delicata* var. *megachela* Burton (1934) and *Isodictya filiformis* sp. nov

References	Morphology	Megascleres (μm) Oxea	Microscleres (μm) Isochela	Microxea	Locality	Depth (m)
Burton (1934) (*I. delicata* var. *megachela*)	Flabellate and stipitate	400–520	70		Seymour Island, Graham Land	150
Koltun (1964) (*I. delicata* var. *megachela*)	Fan-shaped, borne on a stalk	400–520 × 17–20	54–63		Costa Knox and George V	920
Desqueyroux (1975) (*I. delicata* var. *megachela*)	Flabellate and stipitate	390 × 14	57		Deception Island	45
Bentart 03 (*Isodictya filiformis* sp. nov.) Holotype	Filiform	265–380.8–460 × 7.5–12.15–15	35–47.37–52.5 × 12.5–15.99–20	47.5–70.45–92.5	Peter I Island	208–210
Bentart 06 (*I. filiformis* sp. nov.) Paratype 1	Filiform	270–380.6–430 × 10–15–18.75	37.5–46.2–57.5 × 12.5–18.5–22.5	157.5–212.75–257.5	Low Island	97
Ecoquim 06 (*I. filiformis* sp. nov.) Paratype 2	Filiform	215–334.16–430 × 7.5–12.66–17.5	40–50.43–57.5 × 15–20.75–25	47.5–50.83–55	Deception Island	113
Bentart 06 (*I. filiformis* sp. nov.)	Filiform	430–519.4–580 × 5–18–22.5	57.5–65–75 × 20–23.2–27.5	No found	Marguerite Bay	159

also possesses sigmas, spicules that are not present in *I. bentarti* and *I. filiformis* sp. nov. The spicules observed in the fragment from the paratype, the same isochelae as those of *I. kerguelenensis* were observed as prevailing, therefore they seem to be two different species and, in any case, they are different from *I. filiformis* sp. nov.

I. filiformis sp. nov. is characterized by its fragile and thin morphology and by the fact that it has microxeas as additional microscleres. Its presence in Pedro I Island is quite significant as this is 390 km away from the nearest coast in Bellingshausen Sea and very few taxonomical results have been published in this area (Klages et al. 1995; Eakin et al. 2009), as it has been seldom visited by scientific expeditions. However, the Bentart 03 Expedition seems to indicate that it has a wide variety of benthic organisms, in contrast to the deep adjacent areas of Bellingshausen Sea.

Phylogenetic analyses

In our analyses, 18S showed more resolution for family level relationships than 28S within Poecilosclerida (Thacker et al. 2013). The Maximum Likelihood analysis of *18S* place *I. filiformis* sp. nov. in a well-supported clade with four other species of *Isodictya*: *I. kerguelenensis*, *I. frondosa* (Pallas 1766), and *I. compressa* (Esper 1794), and the type species *I. palmata* (Ellis and Solander 1786). In addition, the species *Amphilectus fucorum* (Esper 1794), which belongs to the family Esperiopsidae, Hentschel (1923), also clustered with *Isodictya* species (Fig. 6a). Similarly, the phylogenetic hypothesis for *28S* place *I. filiformis* sp. nov. and *I. kerguelenensis* closely related to *A. fucorum* and all the rest of *Isodictya* species forming a monophyletic group (Fig. 6b). Previously, a close relationship of the families Isodictyidae and Esperiopsidae was obtained using 18S and 28S (Redmond et al. 2013; Thacker et al. 2013). Morphologically, the choanosomal skeleton of Esperiopsidae consists of a reticulation of tracts of styles, without a special ectosomal skeleton. Microscleres, if present, are palmate isochelae and/or sigmas (Van Soest and Hajdu 2002). In turn, the Isodictyidae have (plumo)reticulate skeletal architecture, formed by thick tracts of oxeas, and rarely styles. The ectosomal skeleton is a dense tangential reticulation of strongyles or tufts of oxeas or styles. (Hajdu and Lôbo-Hajdu 2002). In light of our and previous results (Redmond et al. 2013; Thacker et al. 2013), it seems necessary to undertake a revision of Esperiopsiidae & Isodictyidae, and to obtain sequences of type species of the genera of both families to understand clearly their relationships.

Interestingly, in the *18S* topology, the species *Isodictya ectofibrosa* (Lévi 1963) was not recovered within the Isodictyidae clade, but as sister group of the families Coelosphaeridae Dendy (1922) and Hymedesmiidae Topsent

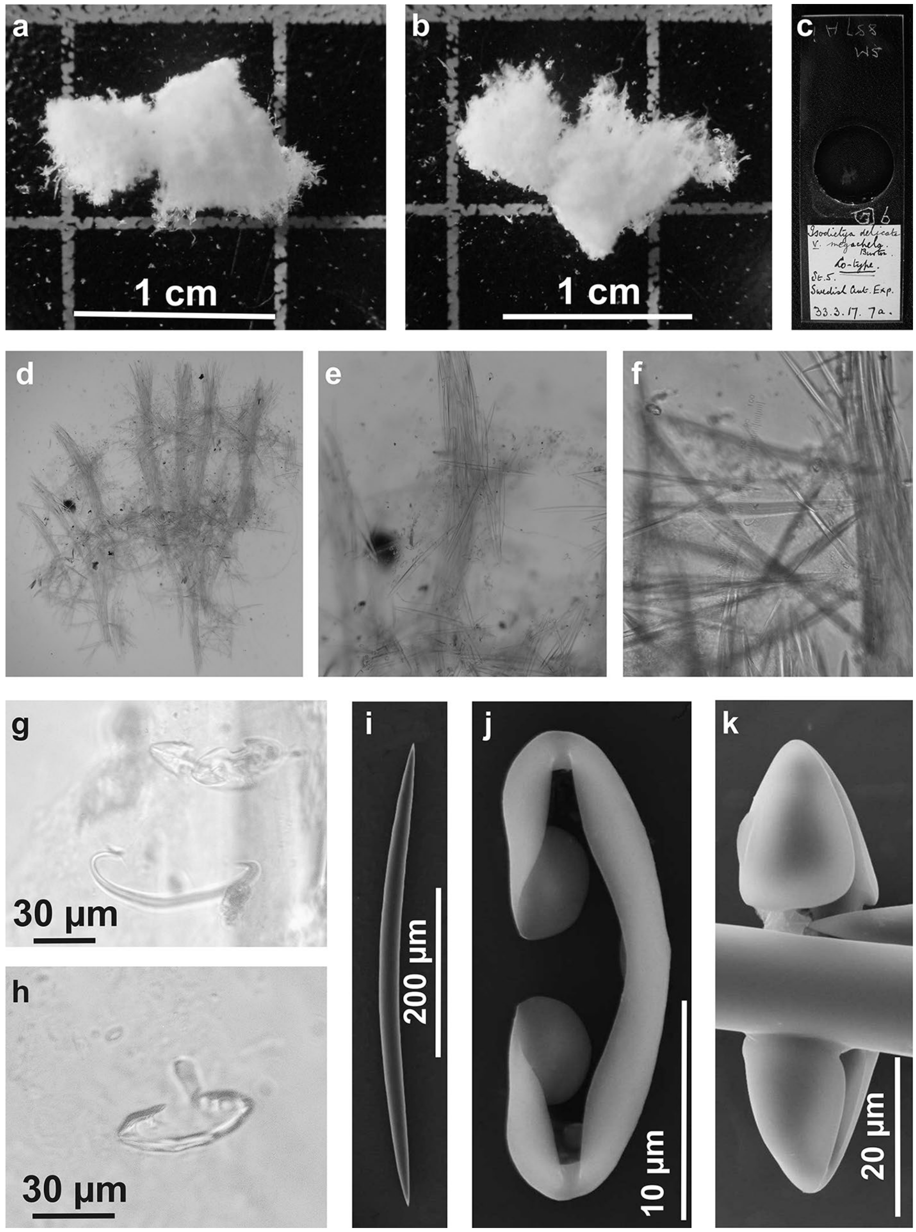

Fig. 5 *Isodictya delicata* var. *megachela* Burton (1934). Natural History Museum of London (NHM): 33.3.17.7a. **a**, **b**, Paratype, fragment of the NHMUK 1933.3.17.7 specimen to take the photographs with the Scanning Electron Microscope. **c**, Slide of the Paratype. **d**–**f**, Skeleton. **g**, Isochelae and sigma. **h**, Isochela. **i**, Oxea. **j**, **k**, Isochelae

(1928), as in Redmond et al. (2013). In fact, the spicules in *I. ectofibrosa* make it more similar to known Hymedesmiidae, and therefore a review of its status might be necessary. Neither in the phylogenetic hypothesis for *18S* or 28S the relationship of the clade formed by family Isodictyidae (and Esperiopsidae) could be resolved (Fig. 6a). While in the topology of the *18S* seemed to be a sister clade to the rest of families of Poecilosclerida except for Lévi (1963) (Fig. 6a), in that of *28S* (Fig. 6b), they appeared to be closely related to a clade formed by the families Myxillidae Dendy (1922), Coelosphaeridae Dendy (1922), and Tedaniidae (Ridley and Dendy 1886).

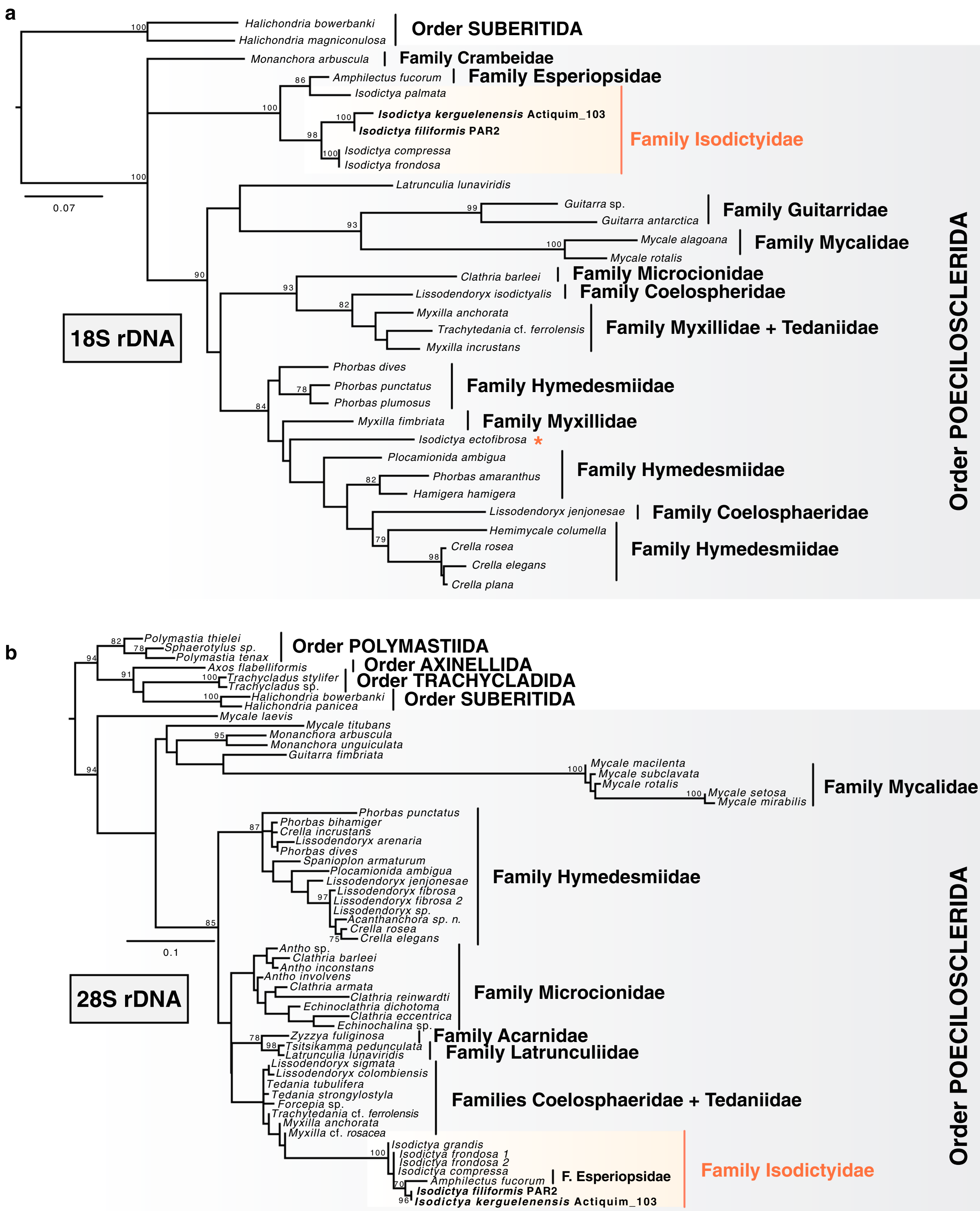

Fig. 6 Phylogenetic hypotheses for the relationships of *Isodictya filiformis* sp. nov. within the order Poecilosclerida using 18S rDNA (**a**) and 28S rDNA (**b**). The phylogeny was obtained with Maximum Likelihood (bootstrap values over branches, only > 60 shown)

Acknowledgements We are grateful to Clare Valentine of the Natural History Museum of London (NHM) who kindly provided the material of material *Isodictya delicata* var. *megachela* NHMUK 1933.3.17.7 (wet specimen) and NHMUK 1933.3.17.7a (slide) for examination. We would like to thank the crew and UTM technicians of R/V 'Hespérides', who helped in the collection of samples, Ana Ramos and the colleagues of BENTART team and to Manuel Ballesteros, Conxita Avila and Laura Núñez-Pons, colleagues of ECOQUIM and ACTIQUIM, who helped in several parts of this work. We also thank the reviewers for their constructive comments to a previous version of this manuscript.

Funding This study was funded by the BENTART projects: Spanish Ministry of Science and Technology REN2001-1074ANT, REN2003-01881/ANT, REN2003-00545/ANT and MEC CGL2004-21066-E and a contribution to the ECOQUIM-2 (CGL2004-03356/ANT) and ACTIQUIM (CGL2007-65453/ANT) projects. The 'BENTART-06′ cruise was funded by the Antarctic Programme GLC2004-01856/ANT of the Spanish Government. Sequencing was performed using internal funds to AR at the Natural History Museum of London (DIF: SDF14029).

Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

References

Aldea C, Troncoso JS (2008) Systematics and distribution of shelled molluscs (Gastropoda, Bivalvia and Scaphopoda) from the South Shetland Islands to the Bellingshausen Sea West Antarctica. Iberus 26(2):43–117

Aldea C, Olabarria C, Troncoso J (2008) Bathymetric zonation and diversity gradient of gastropods and bivalves in West Antarctica from the South Shetland Islands to the Bellingshausen Sea. Deep Sea Res I 55(3):350–368. https://doi.org/10.1016/j.dsr.2007.12.002

Aldea C, Troncoso JS (2010) Moluscos del mar de Bellingshausen (Antartica). Observaciones y distribución de los gasterópodos con concha, bivalvos y scafópodos del oeste de la península Antartica recolectados en las campañas antarticas españolas BENTART 2003 y 2006. Edición propia, Vigo

Aldea C, Zelaya DG, Troncoso JS (2011) A new gigantic species of *Zeidora* Adams, 1860 from Antarctic waters (Gastropoda: Fissurellidae). Nautilus-Sanibel 125(2):79

Ameneiro J, Mouriño-Carballido B, Parapar J, Vázquez E (2012) Abundance and distribution of invertebrate larvae in the Bellingshausen Sea (West Antarctica). Polar Biol 35:1359–1373. https://doi.org/10.1007/s00300-012-1177-4

Arana PM, Retamal MA (1999) Nueva distribución de Paralomis birsteini Macpherson, 1988 en aguas antarticas (Anomura, Lithodidae, Lithodinae). Investig Mar 27:101–110. https://doi.org/10.4067/S0717-71781999002700011

Bowerbank JS (1864) A Monograph of the British Spongiadae, vol. 1, Ray Society, London, pp i–xx, 1–290

Burton M (1932) Sponges. Discov Rep 6:237–392

Burton M (1934) Sponges. Further zoological results of the swedish antarctic expedition 1901–1903 under the direction of Dr. Otto Nordenskjöld. 3(2). Norstedt & Söner, Stockholm, pp 1–58

Cárdenas P, Pérez T, Boury-Esnault N (2012) Sponge systematics facing new challenges. In: Becerro MA, Uriz MJ, Maldonado M, Turon X (eds) Advances in sponge science: phylogeny, systematics, ecology. Adv Mar Biol 61:79–209. https://doi.org/10.1016/b978-0-12-387787-1.00010-6

Corbera J, Ramos A (2005) Cumaceans from the Bellingshausen Sea and neighbouring waters. In: Thatje S, Calcagno JA, Arntz WE (eds) Evolution of Antarctic Fauna. Extended abstracts of the IBMANT/ANDEEP International Symposium and Workshop in 2003. Berichte zur Polar- und Meeresforschung 507:125–128

Corbera J, San Vicente C, Sorbe JC (2009) Cumaceans (Crustacea) from the Bellingshausen Sea and oV the western Antarctic Peninsula: a deep-water link with fauna of the surrounding oceans. Polar Biol 32:611–622. https://doi.org/10.1007/s00300-008-0561-6

Cristobo FJ, Urgorri V, Solórzano MR, Ríos P (1993) Métodos de recogida, estudio y conservación de las colecciones de poríferos. Int Symp First World Congr Preserv Conserv Nat Hist Collect 2:277–287

Dendy A (1922) Report on the Sigmatotetraxonida collected by H.M.S. 'Sealark' in the Indian Ocean. In: Gardiner JS (ed) Reports of the Percy Sladen trust expedition to the Indian Ocean in 1905. Transactions of the Linnean Society of London, London, pp 1–164

Dendy A (1924) Porifera. Part I. Non-Antarctic sponges. Natural History Report. British Antarctic (Terra Nova) Expedition, 1910 (Zoology). 6 (3): 269–392

Desqueyroux R (1975) Esponjas (Porifera) de la region antartica chilena. Cah Biol Mar 16(1):47–82

Eakin RR, Eastman JT, Near TJ (2009) A new species and a molecular phylogenetic analysis of the Antarctic fish genus *Pogonophryne* (Notothenioidei: Artedidraconidae). Copeia 4:705–713. https://doi.org/10.1643/CI-09-024

Eakin RR, Eastman JT, Matallanas J (2008) New species of *Pogonophryne* (Pisces, Artedidraconidae) from the Bellingshausen Sea. Antarct Polar Biol 31:1175–1179. https://doi.org/10.1007/s00300-008-0455-7

Ellis J, Solander D (1786) The natural history of many curious and uncommon zoophytes collected from various parts of the globe. Systematically arranged and described by the late Daniel Solander. Benjamin White & Son, London, pp 1–206

Esper ECJ (1794) Die Pflanzenthiere in Abbildungen nach der Natur mit Farben erleuchtet nebst Beschreibungen Zweyter Theil. Raspe, Nürnberg, pp 1–303

Fernández-Álvarez FA, Anadón N (2012) Oligodendrorhynchus hesperides gen. et sp. N. (Heteronemertea) from the Bellingshausen Sea. Pol Polar Res 33(1):81–98. https://doi.org/10.2478/v10183-012-0006-3

Fernández-Álvarez FA, Anadón N (2013) Redescription of Tubulanus mawsoni (Wheeler 1940) comb nov (Palaeonemertea: Tubulanidae) from the Bellingshausen Sea (Antarctica). N Z J Zool 40(4):263–279. https://doi.org/10.1080/03014223.2013.778302

Garcia-Alvarez O, Zamarro M, Urgorri V (2010) New species of Mollusca Solenogastres from the Bellingshausen Sea and the Antarctic Peninsula (Bentart2006 Expedition). Iberus 28(2):23–38

García-Raso JE, Manjón-Cabeza ME, Ramos A, Olaso I (2005) New record of Lithodidae (Crustacea Decapoda, Anomura) from the Antarctic (Bellingshausen Sea). Polar Biol 28:642–646. https://doi.org/10.1007/s00300-005-0722-9

Giribet G, Wheeler WC (2001) Some unusual small-subunit ribosomal RNA sequences of metazoans. Am Mus Novit 3337:1–16. https://doi.org/10.1206/0003-0082(2001)337%3c0001:SUSSRR%3e2.0.CO;2

Goodwin C, Jones J, Neely K, Brickle P (2016) Sponge biodiversity of Beauchêne and the Sea Lion Islands and south-east East Falkland, Falkland Islands, with a description of nine new species. In Schönberg CHL, Fromont J, Hooper NA, Sorokin S, Zhang W, de Voogd N (eds) New Frontiers in Sponge Science. J Mar

Biol Assoc U K 96:263–290. https://doi.org/10.1017/S0025315414001775
Hajdu E, Lôbo-Hajdu G (2002) Family Isodictyidae Dendy, 1924. In: Hooper JNA, Van Soest RWM (eds) Systema Porifera A guide to the classification of sponges. Kluwer Academic/Plenum Publishers, New York, pp 703–706
Hentschel E (1923) Erste Unterabteilung der Metazoa: Parazoa, Porifera-Schwämme. In: Kükenthal W, Krumbach T (eds) Handbuch der Zoologie Eine Naturgeschichteder Stämme des Tierreiches. Protozoa, Porifera, Coelenterata, Mesozoa Walter de Gruyter und Co, Berlin
Janussen D, Downey RV (2014) Porifera. In: De Broyer C, Koubbi P, Griffiths HJ, Raymond B, d'Udekem d'Acoz C, Van de Putte A, Danis B, David D, Grant S, Gutt J, Held C, Hosie G, Huettmann F, Post A, Ropert-Coudert Y (eds) Biogeographic Atlas of the Southern Ocean. Scientific Committee on Antarctic Research, Cambridge, pp 94–102
Katoh K, Standley DM (2013) MAFFT multiple sequence alignment software version 7: improvements in performance and usability. Mol Biol Evol 30(4):772–780. https://doi.org/10.1093/molbev/mst010
Kirkpatrick R (1907) Preliminary Report on the Monaxonellida of the National Antarctic Expedition. Ann Mag Nat Hist 7(20):271–291
Klages M, Gutt J, Starmans A, Bruns T (1995) Stone crabs close to the Antarctic continent: *Lithodes murrayi* Henderson, 1888 (Crustacea, Decapoda; Anomura) off Peter I Island (68°51'S,90°51'W). Polar Biol 15:73–75. https://doi.org/10.1007/BF00236128
Koltun VM (1964) Sponges of the Antarctic. 1 Tetraxonida and Cornacuspongida. In: Pavlovskii EP, Andriyashev AP and Ushakov PV (eds), Biological Reports of the Soviet Antarctic Expedition (1955–1958), Akademya Nauk SSSR [English translation,1966, Israel Program for Scientific Translation] pp. 6–133, 443–448
Lévi C (1963) Spongiaires d'Afrique du Sud (1) Poecilosclérides. Trans R Soc South Afr. 37(1):1–72
López E (2011) A new species of *Laonice* (Spionidae, Polychaeta, Annelida) from Bellingshausen Sea (West Antarctica). Helgol Mar Res 65(2):257–261. https://doi.org/10.1007/s10152-011-0248-1
López-Fé CM (2005) Cheilostomate Bryozoa of the Bellingshausen Sea (Western Antarctica): a preliminary report of the results of the 'Bentart 2003' Spanish Expedition. In: Moyano M, Cacho C, Wyse J (eds) Bryozoan studies 2004. Taylor and Francis, London, pp 173–179
Matallanas J, Olaso I (2007) Fishes of the Bellingshausen Sea and Peter I Island. Polar Biol 30:333–341
Matallanas J (2009a) Description of *Gosztonyia antarctica*, a new genus and species of Zoarcidae (Teleostei: Perciformes) from the Antarctic Ocean. Polar Biol 32(1):15–19. https://doi.org/10.1007/s00300-008-0496-y
Matallanas J (2009b) Description of a new genus and species of zoarcid fish, *Bellingshausenia olasoi*, from the Bellingshausen Sea (Southern Ocean). Polar Biol 32(6):873–878. https://doi.org/10.1007/s00300-009-0588-3
Matallanas J (2010) Description of two new genera, *Santelmoa* and *Bentartia* and two new species of Zoarcidae (Teleostei, Perciformes) from the Southern Ocean. Polar Biol 33(5):659–672. https://doi.org/10.1007/s00300-009-0742-y
Matallanas J, Corbella C, Møller PR (2012) Description of two new species of *Santelmoa* (Teleostei, Zoarcidae) from the Southern Ocean. Polar Biol 35:1395–1405. https://doi.org/10.1007/s00300-012-1179-2
Moreira J, Parapar J (2011) Sphaerodoridae (Annelida: Polychaeta) from the Bellingshausen Sea (Antarctica) with the description of two new species. Polar Biol 34:193–204. https://doi.org/10.1007/s00300-010-0869-x
Morrow C, Cárdenas P (2015) Proposal for a revised classification of the Demospongiae (Porifera). Front Zool 12:7. https://doi.org/10.1186/s12983-015-0099-8
Morrow CC, Picton BE, Erpenbeck D, Boury-Esnault N, Maggs CA, Allcock AL (2012) Congruence between nuclear and mitochondrial genes in Demospongiae: a new hypothesis for relationships within the G4 clade (Porifera: Demospongiae). Mol Phyl Evolut 62:174–190. https://doi.org/10.1016/j.ympev.2011.09.016
Moya F, Saucède T, Manjón-Cabeza ME (2012) Environmental control on the structure of echinoid assemblages in the Bellingshausen Sea (Antarctica). Polar Biol 35(9):1343–1357. https://doi.org/10.1007/s00300-012-1176-5
Munilla T, Soler-Membrives A (2009) Check-list of the pycnogonids from Antarctic and sub-Antarctic waters: zoogeographic implications. Antarct Sci 21(2):99–111. https://doi.org/10.1017/S095410200800151X
Munilla T, Soler-Membrives A (2015) Pycnogonida from the Bellingshausen and Amundsen seas: taxonomy and biodiversity. Polar Biology 38(3): 413–430 https://doi.org/10.1007/s00300-014-1585-8, https://doi.org/10.1007/s00300-014-1603-x (Erratum)
O'Loughlin PM, Manjón-Cabeza ME, Moya Ruiz F (2009) Antarctic Holothuroids from The Bellingshausen Sea, with descriptions of new species (Echinodermata: Holothuroidea). Zootaxa 2016:1–16. https://doi.org/10.5281/zenodo.185959
Pallas PS (1766) Elenchus zoophytorum sistens generum adumbrationes generaliores et specierum cognitarum succintas descriptiones, cum selectis auctorum synonymis. Fransiscum Varrentrapp, Hagae, p 451
Parapar J, López E, Gambi MC, Núñez J, Ramos A (2011) Quantitative analysis of soft-bottom polychaetes of the Bellingshausen Sea and Gerlache Strait (Antarctica). Polar Biol 34:715–730. https://doi.org/10.1007/s00300-010-0927-4
Parapar J, Moreira J, Gambi MC, Caramelo C (2013) Morphology and biology of *Laetmonice producta producta* Grube (Polychaeta: Aphroditidae) in the Bellingshausen Sea and Antarctic Peninsula (Southern Ocean, Antarctica). Ital J Zool 80(2):255–272. https://doi.org/10.1080/11250003.2012.758783
Redmond NE, Morrow CC, Thacker RW, Diaz MC, Boury-Esnault N, Cárdenas P, Hajdu E, Lôbo-Hajdu G, Picton BE, Pomponi SA, Kayal E (2013) Phylogeny and systematics of Demospongiae in light of new small-subunit ribosomal DNA (18S) sequences. Integr Comp Biol 53(3):388–415. https://doi.org/10.1093/icb/ict078
Ridley SO, Dendy A (1886) Preliminary report on the Monaxonida collected by H.M.S. Challenger Part I. Ann Mag Nat Hist 18:325–351
Ríos P (2006) Esponjas del orden Poecilosclerida de las campañas españolas de bentos Antártico. PhD Thesis, University of Santiago de Compostela, Santiago de Compostela
Ríos P, Cristobo FJ, Urgorri V (2004) Poecilosclerida (Porifera, Demospongiae) collected by the spanish antarctic expedition BENTART–94. Cah Biol Mar 45:97–119
Rützler K (1978) Sponges on coral reef. In: Stoddart DR, Johanness RE (eds) Coral reefs: research methods. UNESCO, Paris, pp 81–120
Saiz JI, García F, Manjón-Cabeza ME, Parapar J, Peña-Cantero A, Saucede T, Troncoso JS, Ramos A (2008) Community structure and spatial distribution of benthic fauna in the Bellingshausen Sea (West Antarctica). Polar Biol 31:735–743. https://doi.org/10.1007/s00300-008-0414-3
San Vicente C (2007) A new species of *Marumomysis* (Mysidacea: Mysidae: Erythropini) from the benthos of the Bellingshausen Sea (Southern Ocean). Sci Mar 71(4):683–690
San Vicente C, Sorbe JC (2008) *Hansenomysis anaramosae* n. sp., a new suprabenthic mysid (Crustacea: Mysidacea: Petalophthalmidae) from the Bellingshausen Sea (Southern Ocean). Org Divers Evolut 8:21–22. https://doi.org/10.1016/j.ode.2006.08.005

San Vicente C, Munilla T, Corbera J, Sorbe JC, Ramos A (2009) Suprabenthic fauna from Bellingshausen Sea and West Antarctic Peninsula: spatial distribution and community structure. Sci Mar 73(2):357–368. https://doi.org/10.3989/scimar.2009.73n2357

Sollas WJ (1885) A classification of the Sponges. Ann Mag Nat Hist 16(95):395

Stamatakis A (2006) Raxml-vi-hpc: maximum likelihood-based phylogenetic ana-lyses with thousands of taxa and mixed models. Bioinformatics 22:2688–2690. https://doi.org/10.1093/bioinformatics/btl446

Stephens J (1915) Atlantic sponges collected by the scottish national antarctic expedition. Trans R Soc Edinb 50(2):423–467

Thacker RW, Hill AL, Hill MS, Redmond NE, Collins AG, Morrow CC, Spicer L, Carmack CA, Zappe ME, Pohlmann D, Hall C (2013) Nearly complete 28S rRNA gene sequences confirm new hypotheses of sponge evolution. Integr Comp Biol 53:373–387. https://doi.org/10.1093/icb/ict071

Thiele J (1905) Die Kiesel- und Hornschwämme der Sammlung Plate. Zoologische Jahrbücher Supplement 6 (Fauna Chiliensis III): 407–496

Topsent E (1916) Diagnoses d'éponges recueillies dans l'Antarctique par le Pourquoi-Pas? Bull Mus Nat Hist Nat 22(3):163–172

Topsent E (1928) Spongiaires de l'Atlantique et de la Méditerranée provenant des croisières du Prince Albert ler de Monaco. Résultats des campagnes scientifiques accomplies par le Prince Albert I. Monaco 74:1–376

Troncoso JS, Aldea C (2008) Macrobenthic mollusc assemblages and diversity in the West Antarctica from the South Shetland Islands to the Bellingshausen Sea. Polar Biol 31:1253–1265. https://doi.org/10.1007/s00300-008-0464-6

Troncoso JS, Aldea C, Arnaud P, Ramos A, García F (2007) Quantitative analysis of soft-bottom molluscs in the Bellingshausen Sea and around Peter I Island. Polar Res 26(2):126–134. https://doi.org/10.3402/polar.v26i2.6226

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 MC, Cárdenas P, Carballo JL, Ríos P, Downey R, Morrow CC (2020) World Porifera Database. 10.14284/359. https://www.marinespecies.org/porifera. Accessed 12 Mar 2020

Van Soest RWM, Hajdu E (2002) Family Esperiopsidae Hentschel, 1923. In: Hooper JNA, Van Soest RWM (eds) Systema Porifera A guide to the classification of sponges. Kluwer Academic/Plenum Publishers, New York

Varela MM, Ramos-Esplá A (2008) *Didemnum bentarti* (Chordata: Tunicata) a new species from the Bellingshausen Sea. Antarct Polar Biol 31(2):209–213. https://doi.org/10.1007/s00300-007-0348-1