

Polymastiidae (Porifera: Demospongiae) of the Nordic and Siberian Seas

ALEXANDER PLOTKIN¹, ELENA GERASIMOVA² AND HANS TORE RAPP^{1,3,4}

¹Department of Biology, University of Bergen, Postbox 7803, 5020 Bergen, Norway, ²Rådgivende Biologer AS, Bredsgården, Bryggen, 5003 Bergen, Norway, ³Centre for Geobiology, University of Bergen, Postbox 7803, 5020 Bergen, Norway, ⁴Uni Environment, Uni Research AS, Postbox 7810, 5020 Bergen, Norway

Polymastiidae (Porifera: Demospongiae) of the Nordic and Siberian Seas are revised and compared with the related species of the North Atlantic based on the morphological data from the type and comparative material and the molecular data from fresh samples. Twenty species from six polymastiid genera are recorded. Two species, Polymastia svenseni from Western Norway and Spinularia njordi from the Norwegian Sea, are new to science. One species, Polymastia andrica, is new to the Nordic Seas and two species, Polymastia cf. bartletti and P. penicillus, are new to the Scandinavian Coast. Distribution of the polymastiids in the North Atlantic and Arctic is discussed and the allegedly wide distribution of Spinularia sarsii and S. spinularia is questioned.

Keywords: sponges, Demospongiae, Polymastiidae, North Atlantic, Nordic and Siberian Seas, new species

Submitted 16 July 2016; accepted 16 February 2017; first published online 3 April 2017

INTRODUCTION

The Nordic Seas, a collective geographic name usually referring to the Greenland, Iceland and Norwegian Seas (Drange *et al.*, 2005; Koralev *et al.*, 2014), but here extended to also include the Barents Sea, constitute the main gateway where the relatively warm and saline North Atlantic Current enters the cold and subsaline waters of the Arctic Ocean (Hansen & Østerhus, 2000; Blindheim & Østerhus, 2005) and, consequently, the Atlantic and Arctic biotas interchange (Loeng & Drinkwater, 2007). Hence the biodiversity studies of the Nordic Seas are of great significance, especially in regard to a possible shutdown of thermohaline circulation. Furthermore, this region is characterized by a quite variable geomorphology with steep slopes and deep fjords along the coastline and seamounts, ridges and trenches in the offshore areas (Blindheim & Østerhus, 2005). Due to such varying environments, the Nordic Seas host a highly diverse sessile invertebrate fauna (Shields & Hughes, 2009; Anisimova *et al.*, 2010; Schander *et al.*, 2010; Kędra *et al.*, 2013). One of the most prominent groups is the phylum Porifera, the sponges, which, in some areas, form dense aggregations known as ‘sponge grounds’ and play a crucial role in the functioning of bottom ecosystems (Klitgaard *et al.*, 1997; Klitgaard & Tendal, 2004; Cárdenas *et al.*, 2013; Maldonado *et al.*, 2016). The Nordic sponge fauna was extensively studied during more than 200 years, starting with the classical survey by Müller (1806) and followed by Schmidt (1870, 1875), Sars (1872), von Marenzeller (1878), Solles (1882), Vosmaer (1882, 1885), Hansen (1885), Fristedt (1887), Arnesen (1900, 1903, 1920), Lundbeck (1902, 1905, 1907, 1909, 1910), Breitfuss

(1911, 1912, 1930), Topsent (1913), Rezvoj (1924, 1928), Brøndsted (1914, 1932, 1933), Hentschel (1916, 1929), Burton (1930a, 1959a), Arndt (1935), Koltun (1964, 1966) and Ereskovsky (1993a, 1994a, b, 1995a, b, c). Although these studies have provided us with thorough descriptions of species and a comprehensive knowledge on their distribution, their data are nowadays seriously re-considered based on the novel material from poorly studied areas (e.g. Rapp, 2006, 2015 on calcareous sponges) and the molecular approaches in sponge taxonomy (e.g. Cárdenas *et al.*, 2013 on geodiid sponges).

Vast marine areas north of Russia, known as the Siberian Seas, are characterized by an inhospitable environment, with, for the most part, shallow depths, a strong influx of fresh water from the great Siberian rivers and considerable temperature fluctuations between winter, when the sea surface is covered with ice and the water temperature sinks below zero, and the warm season, when the surface water layers may be heated (Coachman & Aagaard, 1974). The impact of the freshwater inflow, the ice movements and the summer heating is especially severe in the large shallow-water areas along the coast. The bottom here comprises spacious plains covered with mud and clay (Herman, 1974; Weber, 1989). Due to the unstable environment, both in the water body and on the seabed, the biodiversity, especially the diversity of sessile macrobenthos, of these areas is considerably poorer than along the coasts of the Nordic Seas (Golikov & Scarlato, 1989). On the contrary, in the offshore areas of the Siberian Seas the salinity is more stable, a branch of the Atlantic current brings warm water to the deep (Coachman & Aagaard, 1974), and the northern coast of large offshore archipelagos, e.g. Severnaya Zemlya and New Siberian Islands, is characterized by the rock cliffs and steep slopes running to great depths (Herman, 1974; Weber, 1989). These areas are oases hosting a relatively rich bottom fauna, particularly some diverse sponge communities (Golikov

Corresponding author:

A. Plotkin

Email: alexander.s.plotkin@gmail.com

et al., 1990). The studies of the sponge fauna in the Siberian Seas were started by Fristedt (1887) and Levinsen (1887) and continued by Rezvoj (1924, 1928), Gorbunov (1946) and Koltun (1966). The latter study until now remains the most comprehensive description of the Arctic sponge species, although some data presented there are obviously out of date and need a serious revision based on the modern taxonomic concepts. Among the northern seas of Russia, the White Sea, a large semi-isolated, brackish gulf of the Barents Sea, stands out for its peculiar hydrological conditions affecting the biodiversity. The deep waters of the White Sea, where the temperature is below zero all the year round, are inhabited predominantly by Arctic species. Conversely, the shallow depths, where seasonal fluctuations of the water temperature are considerable, host opportunistic Atlantic species (Babkov & Golikov, 1984). The exploration of the White Sea sponge communities begun by Merejkowsky (1878) was continued by Swarczewsky (1906), Koltun (1966) and Ereskovsky (1993a, b, 1994a, b, 1995a, b, c). However, these unique communities still need further studies based on up-to-date approaches.

Among all diverse sponge taxa inhabiting the Nordic and Siberian Seas the family Polymastiidae Gray, 1867 is one of the most common. Despite the polymastiids never reaching such large sizes as, for example, the astrophorid species do (Cárdenas *et al.*, 2013), they are subdominants of shallow-water hard bottom communities in some Norwegian fjords (Svensen, personal communication), in the White Sea (Plotkin *et al.*, 2005) and Laptev Sea (Golikov *et al.*, 1990). In the deep waters common polymastiids such as *Tentorium semisuberites* (Schmidt, 1870) and *Radiella* spp. are often the most frequently recorded macrobenthic species (Barthel & Tendal, 1993; Witte, 1996). Polymastiidae were described in all studies on the Nordic and Russian sponge faunas (see the references above) and these records were summarized by Koltun (1966), who listed eight polymastiid species for the Greenland Sea, 12 species for the Norwegian and Barents Sea, four species for the White Sea and eight species for the Siberian Seas and the Arctic Ocean. The White Sea list was appended by one more polymastiid by Ereskovsky (1993b), while Plotkin (2004) provided the re-descriptions of all these species and proposed some changes in their taxonomy.

Meanwhile, the records of most species presented by Koltun (1966) and Plotkin (2004) were based on non-type material that may question their identification. Furthermore, the polymastiids of the Scandinavian Coast and Svalbard have been never properly revised. Additionally, rich sponge samples recently taken from the poorly studied underwater mountains and vents in the Greenland and Norwegian Sea must be examined. Finally, recently recovered sponge phylogenies based on molecular data (e.g. Cárdenas *et al.*, 2012; Morrow *et al.*, 2012, 2013; Redmond *et al.*, 2013; Morrow & Cárdenas, 2015) challenge the traditional taxonomy based on morphology. Particularly they question the generally accepted concept of the relationships between the polymastiid genera (Boury-Esnault, 2002) as well as between the Polymastiidae and other families (Hooper & Van Soest, 2002). A monotypic order, Polymastiida Morrow & Cárdenas, 2015, is established for the polymastiids, and a homoplasy of most morphological characters traditionally used in the taxonomy of this family and a non-monophly of four genera from 15 polymastiid genera altogether known (Van Soest *et al.*, 2016) are revealed (Plotkin *et al.*, 2016b).

The aim of the present study is to revise the polymastiid fauna of the Nordic and Siberian Seas based on morphological examination of the type material and other historical collections as well as on both morphological and molecular data from fresh material. We also provide a key for identification of the polymastiid species in the area of study (Appendix 1). The area covered by the study comprises the Scandinavian Coast from the Swedish Western Coast and Southern Norway to the Norwegian-Russian border, Russian Coasts (including the White Sea) from the border to the easternmost point, Icelandic Coast, Southern and Eastern Coasts of Greenland, offshore archipelagos Svalbard, Franz Josef Land, Novaya Zemlya, Nordenskjold and Severnaya Zemlya, offshore areas of the Greenland, Norwegian, Barents, Kara, Laptev, East-Siberian and Chukchi Seas and adjacent areas of the Arctic Ocean. We also compare the Nordic and Siberian sponges with individuals from the British Isles, Canadian Atlantic Coast and some other regions in order to explore the dispersal of the species.

MATERIALS AND METHODS

The study was based on historical and fresh material stored in 14 museums (Table 1). Altogether more than 1700 sponge individuals were studied (Online resource 1). The architecture of their skeletons was examined under light microscope on histological sections prepared on a precise saw with a diamond wafering blade after embedding of sponge fragments in epoxy resin as described by Boury-Esnault *et al.* (2002), Vacelet (2006) and Boury-Esnault & Bézac (2007). Spicules were examined under light microscope and SEM after their isolation from organic matter in nitric acid following standard procedures. The number of specimens used for spicule measurements is given in the corresponding section of the description of each species. The number of spicules of each category measured in one specimen is indicated as N. Measurements are presented as minimum–mean–maximum, unless otherwise indicated.

Table 1. List of museums whose collections were used in the present study.

Museum acronym	Museum title and affiliation
BELUM	Ulster Museum, National Museums of Northern Ireland, Belfast
BMNH	Natural History Museum, London
CMNI	Canadian Museum of Nature, Ottawa
GNM	Göteborgs Naturhistoriska Museum
MNHN	Muséum National d'Histoire Naturelle, Paris
MOM	Musée Océanographique de Monaco
NHMUO	Naturhistorisk museum, Universitetet i Oslo
NTNU-VM	Vitenskapsmuseet, Norges teknisk-naturvitenskapelige universitet, Trondheim
RMNH	Naturalis Biodiversity center, Leiden
UPSZTY	Evolutionsmuseet, Uppsala Universitet
ZIN RAS	Zoological Institute of Russian Academy of Sciences, Saint-Petersburg
ZMB	Museum für Naturkunde, Berlin
ZMBN	Universitetsmuseet i Bergen
ZMUC	Statens Naturhistoriske Museum, Københavns Universitet

Genetic synapomorphies and autapomorphies of the species were defined in the 5'-end barcoding region of cytochrome oxidase subunit I (CO1) and the region coding the RNA of the large ribosomal subunit (28S rDNA) from helix B10 to helix E19. The sequences, the alignments and the respective phylogenies were presented by Plotkin *et al.* (2016b). GenBank accessions are indicated in Online resource 1, this study. Alignments and the respective phylogenetic trees are deposited in TreeBase and available at <http://purl.org/phylo/treebase/phylows/study/TB2:S18487> (see Matrix M34248 and Tree Tr91844 for CO1, Matrix M34250 and Trees Tr91846–Tr91847 for 28S rDNA, complete dataset, and Matrix M34256 and Tree Tr91856 for 28S rDNA fragment D1–D19 demonstrating intragenomic polymorphism). Generalized phylogeny reconstructed from the concatenated dataset is presented in Figure 1, while the main apomorphies are indicated in Online resources 2 (for CO1) and 3 (for 28S rDNA), this study. Apomorphies in 28S rDNA were defined only within the unambiguously aligned parts of the matrix (positions 1–449, 492–577, 585–667, 685–940 and 949–2155 in the alignment). Based on the phylogenies recovered by Plotkin *et al.* (2016b) we accept the abandonment of *Radiella* Schmidt, 1870. However, we stick to the traditional taxonomy of other genera (Boury-Esnault, 2002; Van Soest *et al.*, 2016) even, if they are not monophyletic in these phylogenies, until a new classification of Polymastiidae is built.

SYSTEMATICS

Systematic index

Class DEMOSPOONGIAE Sollias, 1885
Suborder HETEROSCLEROMORPHA Cárdenas, Perez & Boury-Esnault, 2012

Order POLYMASTIIDAE Morrow & Cárdenas, 2015

Family POLYMASTIIDAE Gray, 1867

Genus *Polymastia* Bowerbank, 1862

P. andrica de Laubenfels, 1949

P. arctica (Merejkowsky, 1878)

P. cf. bartletti de Laubenfels, 1942

P. boletiformis (Lamarck, 1815)

P. grimaldii (Topsent, 1913)

P. hemisphaerica (Sars, 1872)

P. mamillaris (Müller, 1806)

P. nivea (Hansen, 1885)

P. penicillus (Montagu, 1814)

P. senseni sp. nov.

P. thielei Koltun, 1964

P. uberrima (Schmidt, 1870)

Polymastia sp.

Genus *Quasillina* Norman, 1869

Q. brevis Bowerbank, 1866

Genus *Sphaerotylus* Topsent, 1898

S. borealis (Swarczewsky, 1906)

S. capitatus (Vosmaer, 1885)

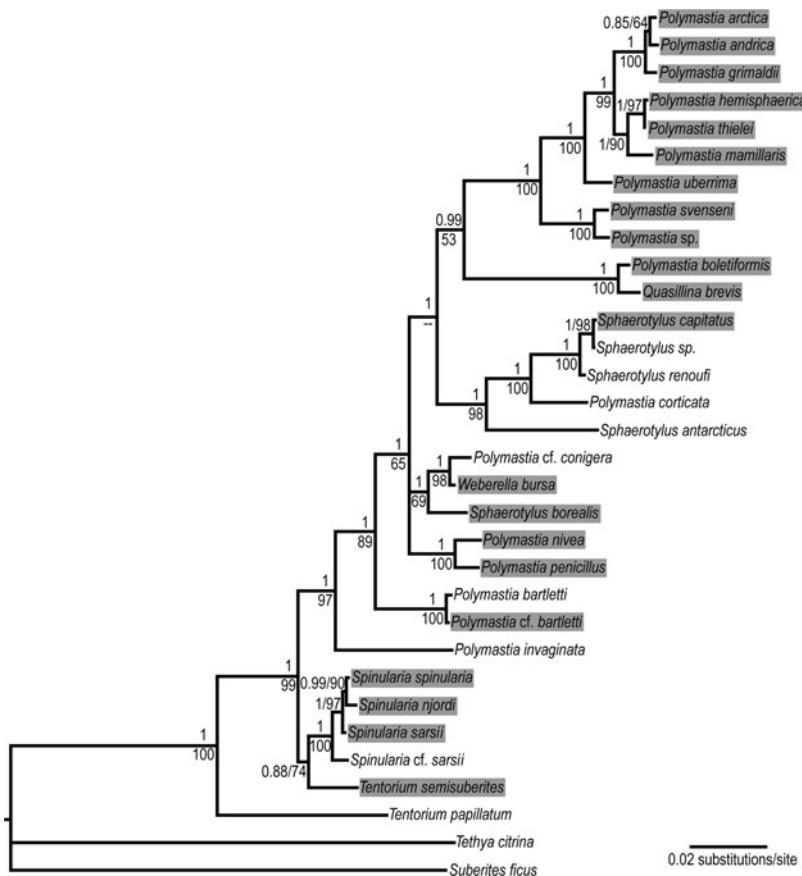


Fig. 1. Bayesian consensus tree reconstructed from the concatenated dataset CO1 + 28S rDNA of 30 polymastiid species. Nodal supports: upper values – Bayesian posterior probabilities, lower values – ML bootstrap supports in percentages. Data are taken from Plotkin *et al.* (2016b). Complete 28S rDNA alignment is used. The original trees are available at <http://purl.org/phylo/treebase/phylows/study/TB2:S18487>. Branches corresponding to different individuals of the same species are collapsed. The species from the Nordic and Siberian Seas are highlighted. The following species from Plotkin *et al.* (2016b) are renamed according to the classification accepted in the present study: *Polymastia* sp. 1 as *Polymastia senseni*, *Radiella hemisphaerica* as *Polymastia hemisphaerica*, *Radiella sarsi* as *Spinularia sarsi*, *Radiella* sp. as *Spinularia njordi* and *Sphaerotylus* sp. 2 as *Sphaerotylus renoufi*.

- Genus *Spinularia* Gray, 1867
S. njordi sp. nov.
S. sarsii (Ridley & Dendy, 1886) comb. nov.
S. spinularia (Bowerbank, 1866)
Genus *Tentorium* Vosmaer, 1887
T. semisuberites (Schmidt, 1870)
Genus *Weberella* Vosmaer, 1885
W. bursa (Müller, 1806)

Description of taxa

Family POLYMASTIIDAE Gray, 1867

DIAGNOSIS

Sponges of encrusting, massive, globular, hemispherical, discoid, columnar or pedunculate body shape. Oscula are often located at the summits of papillae or, sometimes, directly on the surface of the main body. Assortment of spicules comprises at least two size categories of smooth monactines. Tracts of principal monactines radiating from the sponge base or forming a reticulation constitute the main choanosomal skeleton or the innermost layer of the cortex. Auxiliary choanosomal skeleton comprises smaller spicules, free-scattered or grouped in little bundles, which may be smooth monactines, smooth or acanthose oxeas, raphides in trichodragmata or astrotylostyles. A complex specialized cortical skeleton is developed to a greater or lesser degree, composed of at least a palisade of smooth tylostyles, subtylostyles, or oxeas and/or exotyles. A fringe of extra-long monactines may be present at the edge of the body where it is in contact with the substrate.

Genus *Polymastia* Bowerbank, 1862

Original description: *Polymastia* Bowerbank, 1862, p. 1104.

SYNONYMS

- Pencillaria* Gray, 1867, p. 527.
Polymastica Gray, 1867, p. 527.
Rinalda Schmidt, 1870, p. 51.
Trichostemma Sars, 1872, p. 62.

TYPE SPECIES

Halichondria mamillaris Johnston, 1842 (= *Spongia mamillaris* Müller, 1806) (by original designation).

DIAGNOSIS

Polymastiidae of encrusting, massive, globular, hemispherical or discoid body shape, always bearing papillae with oscula at the summits. Main choanosomal skeleton composed of tracts of principal monactines radiating from the sponge base or forming a reticulation. Auxiliary choanosomal skeleton comprises smaller monactines, free-scattered or grouped in little bundles. Cortical skeleton constituted at least by a superficial palisade of small smooth tylostyles or subtylostyles and an internal layer of larger monactines lying obliquely to the surface and may include middle layers. A fringe of extra-long monactines may be present at the edge of the body.

DISCUSSION

Polymastia Bowerbank, 1862, with its currently accepted assortment of species (Boury-Esnault, 2002; Van Soest et al., 2016), is not monophyletic as was suggested by Plotkin et al. (2012) based on morphological data and confirmed by

Plotkin et al. (2016b) based on the CO1 and 28S rDNA phylogenies (see also Figure 1, this study). In both phylogenies the type species of *Polymastia*, *P. mamillaris* (Müller, 1806), formed a strongly supported clade with only five other species of this genus, *P. andrica* de Laubenfels, 1949, *P. arctica* (Merejkowsky, 1878), *P. grimaldii* (Topsent, 1913), *P. uberrima* (Schmidt, 1870) and *P. thielei* Koltun, 1964, along with *Trichostemma hemisphaericum* Sars, 1872, which was in fact the type species of *Trichostemma* Sars, 1872 accepted as *Radiella hemisphaerica* at the time of the study by Plotkin et al. (2016b). However, no morphological synapomorphies of this clade could be defined. In the 28S rDNA tree a pair of unidentified species *Polymastia* sp. 1 and *Polymastia* sp. 2 was the sister to the *Polymastia*-clade with a strong Bayesian support. In the CO1 tree a trio of unidentified species *Polymastia* sp. 1, *Polymastia* sp. 2 and *Polymastia* sp. 3 was the sister to the *Polymastia*-clade, although with a weak support. All other *Polymastia* spp. including four species described in the present study, *P. boletiformis* (Lamarck, 1815), *P. bartletti* de Laubenfels, 1942, *P. nivea* (Hansen, 1885) and *P. penicillus* (Montagu, 1814), fell in the clades with the species of other genera in both molecular trees.

In the present study based on these phylogenies *Trichostemma* is regarded as a junior synonym of *Polymastia*. *Polymastia* sp. 1 is described as *P. svenseni* sp. nov., *Polymastia* sp. 2 is described as an unidentified species and *Polymastia* sp. 3 is not considered because it occurs outside the area covered by the study. Meanwhile, for the sake of taxonomic stability until a new classification of Polymastiidae is built, we retain the allocation of *P. boletiformis*, *P. bartletti*, *P. nivea* and *P. penicillus* to *Polymastia*, though it contradicts the molecular phylogenies. Consequently, the diagnosis of *Polymastia* (see above) is emended accordingly.

Polymastia andrica de Laubenfels, 1949
(Figure 2)

Original description: *Polymastia andrica* de Laubenfels, 1949, p. 22, figures 19 & 20.

SYNONYMS AND CITATIONS

Polymastia mamillaris (Whiteaves, 1874, p. 184; Lambe, 1896, p. 196, pl. III figure 1; Whiteaves, 1901, p. 13).

TYPE MATERIAL

Holotype (lost?): Gulf of St. Lawrence, Canada, coll. Whiteaves.

Several individuals sampled by Whiteaves from various localities in the Gulf of St. Lawrence in 1871–1872 were identified by him (Whiteaves, 1874, 1901) as *Polymastia mamillaris*. Lambe (1896) studied four of these individuals and confirmed the identification. De Laubenfels (1949) designated one of these sponges, with field number 8, as the holotype of his new species *Polymastia andrica*. Only three individuals of the four described by Lambe (1896) are now available in the Canadian Museum of Nature (Online resource 1), but none of them bear field number 8. We have examined histological sections and spicules from these sponges and found that they fit with the descriptions by Lambe (1896) and de Laubenfels (1949).

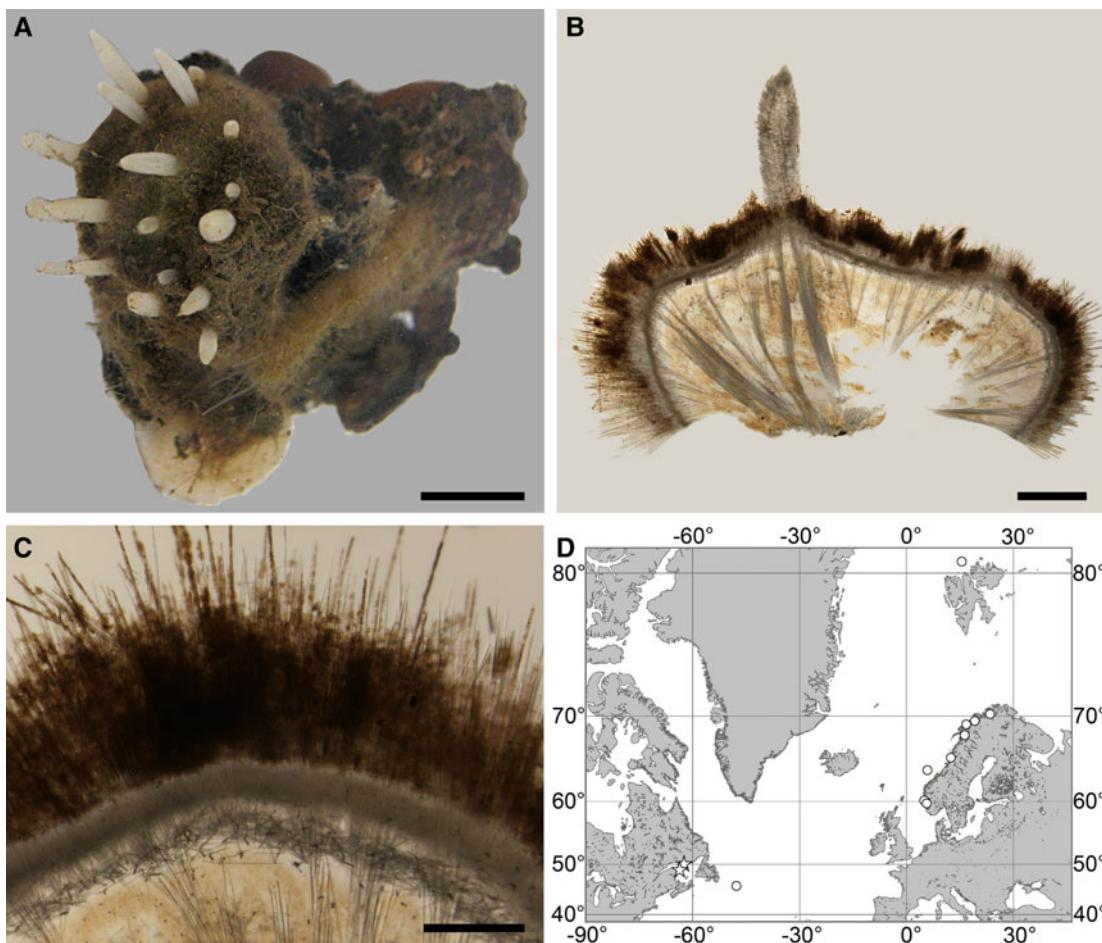


Fig. 2. *Polymastia andrica*: (A) ZMBN 098057, habitus; (B) the same individual, longitudinal section through the body, general view; (C) the same section, detail of cortex; (D) distribution: white stars, type localities; white circles, our data. Scale bars: A, 1 cm; B, 2 mm; C, 0.5 mm.

MATERIAL EXAMINED

(see Online resource 1 for details)

Canada: Quebec, Gulf of St. Lawrence: CMNI 1980-0436 (spicule slide from one specimen), CMNI 1980-0437/0440/0441 (histological sections and spicule slides from one specimen), CMNI 1980-0438 (spicule slide from one specimen), Newfoundland: ZMBN 098102 (one specimen).

Norway: Hordaland: ZMBN 098057 and ZMBN 107572 (two specimens), Nordland: NTNU-VM-54990, NTNU-VM-55034 and NTNU-VM-72533 (three specimens), Troms: NTNU-VM-55603 and ZMBN 098074 (two specimens), Finnmark: NTNU-VM-54850 (one specimen), Svalbard: ZMBN 098055 (one specimen).

Norwegian Sea, offshore: ZMBN 098108 (one specimen).

DESCRIPTION

External morphology

Cushion-shaped sponges covering the substrate and occupying up to 6 cm² (Figure 2A). Surface strongly hispid, covered with sediment, with up to several tens of cylindrical or flattened, greyish or whitish papillae which are 1–12 mm long and 1–5 mm wide. In preserved sponges exhalant and inhalant papillae do not differ in size or shape.

Anatomy

Choanosome in alcohol yellowish or greyish, dense. Main choanosomal skeleton composed of radiating tracts (88–

417 µm thick) of principal spicules crossing the cortex and forming a surface hispidation reinforced with exotyles (Figure 2B). Ascending tracts also form a framework of the papilla skeleton. Auxiliary choanosomal skeleton comprises free-scattered small spicules, being especially abundant in the subcortical area. Cortex in alcohol light-coloured, firm, not detachable. Cortical skeleton constituted by a superficial palisade (116–232 µm thick) of small spicules, a middle layer (40–272 µm thick) of collagen fibres with low density of spicules and an internal layer (56–170 µm thick) of tangentially arranged intermediary spicules (Figure 2C). Skeleton of the papilla walls composed of two layers only, the superficial palisade and the internal tangential layer. Single small and intermediary spicules reinforce the bulkheads separating aquiferous canals and vestibules in the papillae.

Spicules

(Measurements based on seven specimens, individual variation presented in Table 2)

Principal spicules – styles (in the Canadian sponges) or subtylostyles to styles (Norwegian sponges), usually straight, fusiform, with tyles (if present) slightly displaced along the shafts, occasionally polytylote. Length 613–1248–2132 µm, diameter of tyle (if present) 5.1–11.1–14.3 µm, proximal diameter of shaft 3.8–11.1–18.2 µm, maximum diameter of shaft 8.9–23.9–33.8 µm, N = 230.

Table 2. Individual variation of spicule dimensions of *Polymastia andrica* (given in µm as minimum–mean–maximum). Parameters: length, diameter of tyle, proximal diameter of shaft, maximum diameter of shaft, number of spicules measured (N).

Specimen	Principal spicules	Intermediary spicules	Small spicules	Exotyles
CMNI 1980-0436 (Canada, Gulf of St. Lawrence)	969–1226–1474 Tyles absent 5.2–11.3–14.3 13–25.8–33.8 N = 30	427–538–857 6.5–9.9–11.7 5.2–9.5–13 9.1–12.8–18.2 N = 30	100–149–286 2.1–4–7.8 1.8–3.1–7.8 2.1–3.7–7.8 N = 40	1632–1908–2145 Tyles absent 5.2–7.5–11.7 13–19.7–31.2 N = 5
CMNI 1980-0438 (Canada, Gulf of St. Lawrence)	1013–1360–1605 Tyles absent 5.2–12.1–18.2 15.6–26.3–33.8 N = 30	403–586–898 7.8–9.6–11.7 6.5–9–13 13–15.2–20.8 N = 19	145–178–247 4.7–7.1–10.4 3.9–4.8–6.5 5.2–7.8–10.4 N = 30	1895–2689–3763 Tyles absent 5.2–7.3–10.4 13–16.6–20.8 N = 5
CMNI 1980-0440/0441 (Canada, Gulf of St. Lawrence)	1118–1464–2132 tyles absent 9.1–11.9–15.6 20.8–26.1–31.2 N = 50	316–575–837 9.1–11.4–15.6 6.5–10.2–14.3 10.4–14.2–26 N = 60	153–192–280 3.9–7.3–13 2.6–5.2–10.4 3.9–8.7–15.6 N = 90	2395–3553–5500 tyles absent 5.2–8.9–13 14.3–16.9–18.2 N = 6
ZMBN 98055 (Norway, Svalbard)	905–1226–1624 11.4–12.4–14 8.9–10.8–12.7 16.5–18.8–20.3 N = 30	417–510–784 7.6–9.5–12.7 6.4–7.5–8.9 7.6–11.1–14 N = 30	140–177–229 7.6–8.4–10.2 4.6–5.2–6.4 7.6–8.4–10.2 N = 30	2058–2598–3125 2.5–7.8–12.7 7.6–10–15.2 N = 11
ZMBN 98057 (Norwegian Coast, Hordaland)	992–1208–1637 5.1–10.3–12.7 3.8–9.1–11.4 12.7–19.4–25.4 N = 30	362–485–563 7.6–8.5–10.2 6.4–7.6–10.2 10.2–12.1–14 N = 30	140–177–231 3.8–5.3–6.4 2.5–3.6–5.1 5.1–5.8–8.9 N = 30	2604 6.4 5.1 12.7 N = 1
ZMBN 98074 (Norwegian Coast, Troms)	613–783–1045 7.1–10.3–14 5.1–8.4–12.7 8.9–12–16.5 N = 30	372–420–523 7.6–8.4–10.7 5.6–7.2–7.6 7.6–9.3–11.4 N = 30	132–169–216 5.1–5.8–7.6 2.5–3.8–5.1 3–4.8–6.4 N = 30	1314–1493–1736 tyles absent 2.5–3.5–5.1 5.1–8.3–10.2 N = 16
ZMBN 98102 (Canada, Newfoundland)	1017–1322–1637 8.1–10.9–12.7 7.6–9.3–10.2 20.3–22.7–26.7 N = 30	362–472–704 6.4–8.9–11.4 5.1–7.5–10.2 10.2–12.7–14 N = 30	138–167–241 5.1–6.9–8.1 2.5–4–5.1 3.8–6.2–7.6 N = 30	1786–2671–3497 tyles absent 3.8–5–7.6 11.4–13.5–15.2 N = 14

Intermediary spicules – subtylostyles to styles, straight or gently bent, fusiform, occasionally with tylos slightly displaced along the shafts. Length 316–517–898 µm, diameter of tyle (if present) 6.4–9.9–15.6 µm, proximal diameter of shaft 5.1–9.1–14.3 µm, maximum diameter of shaft 7.6–13.2–26.0 µm, N = 229.

Small spicules – tylostyles, often gently bent in the proximal part, usually slender, occasionally stout. Length 100–176–286 µm, diameter of tyle 2.1–6.5–13 µm, proximal diameter of shaft 1.8–4.5–10.4 µm, maximum diameter of shaft 2.1–7.1–15.6 µm, N = 280.

Exotyles – filiform styles (Canadian sponges and individual ZMBN 98074 from Troms) or filiform subtylostyles with weakly developed, often slightly displaced tylos (other Norwegian sponges). Length 1314–2358–5500 µm, diameter of tyle (if present) 2.5–6.7–12.7 µm, proximal diameter of shaft 2.0–5.6–13 µm, maximum diameter of shaft 5.1–12.6–31.2 µm, N = 58.

Strongyles (registered only in individual CMNI1980-0436 from the Gulf of St. Lawrence) – straight, fusiform or slender, occasionally with one or two weakly developed tylos. Length 26–47–156 µm, proximal diameter of shaft

9.1–15.3–18.2 µm, maximal diameter of shaft 9.1–21–41.6 µm, N = 30.

Genetic data

CO1 sequences obtained from five individuals of *Polymastia andrica* are identical, but an intragenomic polymorphism was observed in 28S rDNA of one individual (Matrix M34256 in TreeBase). *Polymastia andrica* is closely related to *P. arctica* and *P. grimaldii*, sharing with them five synapomorphies in CO1 (Online resource 2, p. 1) and four synapomorphies in 28S rDNA (Online resource 3, p. 1), which distinguish these three species from all other polymastiids. 28S rDNA of *P. andrica*, *P. arctica* and *P. grimaldii* displays a high level of intraspecific and intragenomic polymorphism with some identical gene versions found in the individuals from different species (Plotkin *et al.*, 2016b; Matrices M34250 and M34256 in TreeBase). On the contrary, the CO1 data are consistent. In this gene *P. andrica* and *P. arctica* share one synapomorphy distinguishing them from all other polymastiids, and, additionally *P. andrica* has one autapomorphy (Online resource 2, p. 1). Apart from this autapomorphy, *P. andrica* differs from *P. arctica* by eight base pairs (bps), from *P. grimaldii* by 12 bps and from the type species of *Polymastia*, *P. mammillaris*, by 32 bps in CO1 (Matrix M34248 in TreeBase).

OCCURRENCE (Figure 2D)

Canadian Atlantic Coast: Gulf of St. Lawrence (218–382 m according to Lambe, 1896), Newfoundland (619–699 m). Norwegian Coast: Hordaland (28–300 m), Nordland (120–721 m), Troms (25–220 m), Finnmark (30–80 m). Norwegian Sea, offshore areas (626–628 m). Svalbard (215 m).

DISCUSSION

Before our study, *Polymastia andrica* was recorded only from the type locality, the Gulf of St. Lawrence (de Laubenfels, 1949). We have identified as *P. andrica* a sponge from Newfoundland and 10 Norwegian individuals based on their morphological similarities with the material from the type locality (although the exyles in the Norwegian specimens are shorter than those in the Canadian sponges) and the identity of CO1 from the Newfoundland specimen and the Norwegian specimens. *Polymastia andrica* is morphologically very similar to *P. arctica* and *P. mammillaris*, but differs from these two by the presence of exyles. Additionally *P. andrica* differs from *P. arctica* by the absence of threads with buds at the summits of the inhalant papillae and by the absence of size difference between the inhalant and exhalant papillae. All genetic data obtained support the discrimination between *P. andrica* and *P. mammillaris* based on morphology. The morphological differences between *P. andrica* and *P. arctica* are only confirmed by the CO1 data, but not by 28S rDNA.

Polymastia arctica (Merejkowsky, 1878)

(Figure 3)

Original description: *Rinalda arctica* Merejkowsky, 1878, p. 4, pl. I figures 7–12, pl. II figures 6–8, pl. III figures 1–3, 6–10, 20–22, 30–39.

SYNONYMS AND CITATIONS

Polymastia arctica (Plotkin, 2004, p. 541, figures 1a & 2a; Plotkin & Boury-Esnault, 2004, p. 15, figures 1–3).

Polymastia mammillaris (Arnesen, 1918, p. 8, pl. 1 figures 1–4, pl. 2 figures 1–5, pl. 3 figures 6–9, pl. 4 figures 1–2; pl. 5 figures 1–2, pl. 6 figures 1–4; Ereskovsky, 1993a, p. 22, 1995c, p. 724; Plotkin & Ereskovsky, 1997, p. 127).

Polymastia mammillaris mammillaris (Koltun, 1966, p. 69, text-figure 38, pl. XX figure 6 pars.).

Polymastia penicillus (Swarczewsky, 1906, p. 313, pl. 13 figure 1).

Rinalda arctica (Merejkowsky, 1880, p. 421).

TYPE MATERIAL

Lectotype (designated by Plotkin & Boury-Esnault, 2004): ZIN RAS 10610 (specimen and slide 5526a), Archipelago of Solovki, Onega Bay, White Sea, 64°57.0'N 35°29.4'E – 65°10.8'N 35°51.6'E, 9–22 m, summer 1877, coll. Merejkowsky.

Paralectotypes: ZIN RAS 10611 (specimen and slide 5526b) and ZIN RAS 10612 (four specimens), from the same sample as the lectotype.

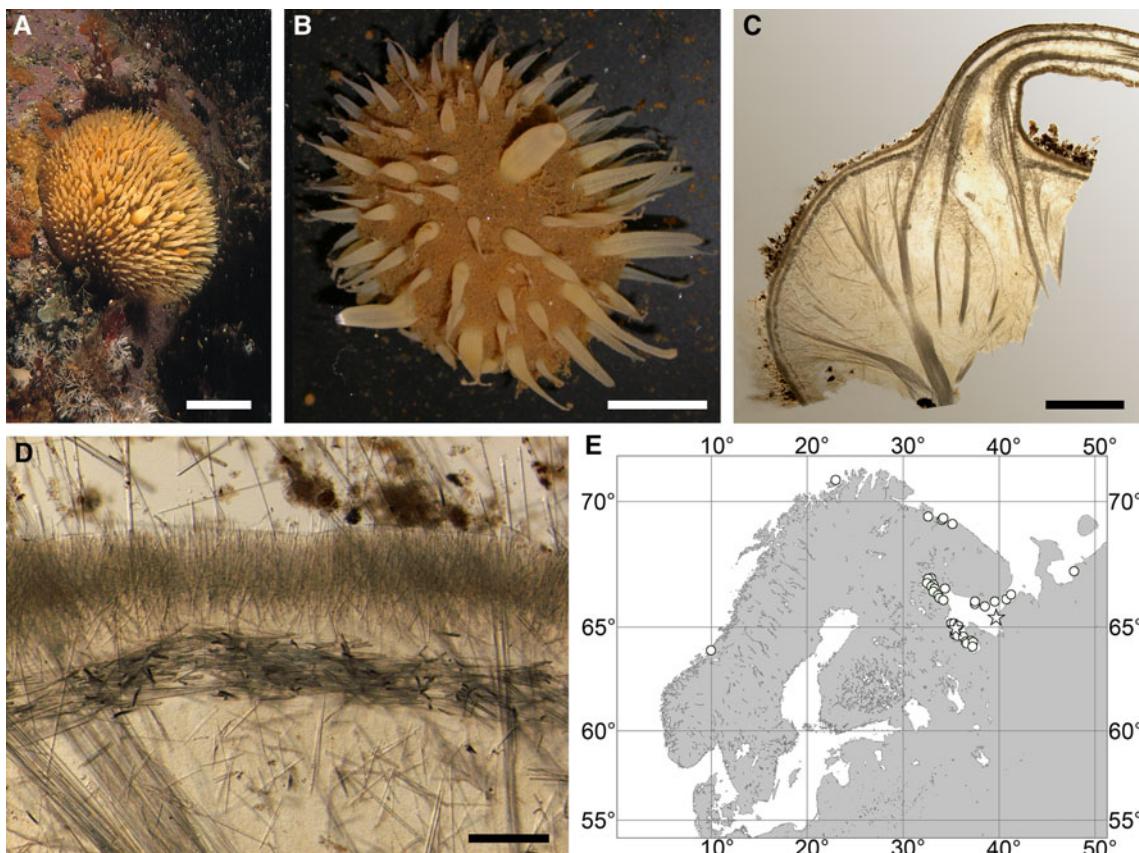


Fig. 3. *Polymastia arctica*: (A) an individual *in situ*, Kandalaksha Bay, White Sea (courtesy of M. Fedyuk, St. Petersburg State University); (B) an individual in aquarium; (C) ZMBN 098068, longitudinal section through the body, general view; (D) the same section, detail of cortex; (E) distribution: white stars, type localities; white circles, our data. Scale bars: A, 2 cm; B, 1 cm; C, 3 mm; D, 0.2 mm.

Paralectotypes: ZIN RAS 10613 (two specimens and slide 9112), Cape Kerets, Dvina Bay, White Sea, $65^{\circ}25'N$ $39^{\circ}38'E$, 11 m, 22.06.1876, coll. Merejkowsky.

Detailed description of the type material was presented by Plotkin & Boury-Esnault (2004).

COMPARATIVE MATERIAL

(see Online resource 1 for details)

Norway: Sør-Trøndelag: NTN-VM-55865 (two specimens), Finnmark: ZMBN 098065 and ZMBN 098068 (two specimens).

Russia: Murman Coast: ZIN RAS ocpm078, ZIN RAS ocpm079, ZIN RAS ocpm131, ZIN RAS ocpm132, ZIN RAS ocpm148 (five specimens), Chyosha Bay of the Barents Sea: ZIN RAS ocpm145 (one specimen), White Sea: ZMBN 098060, ZMBN 098062, ZMBN 098063 (three specimens) and 114 specimens deposited in ZIN RAS.

DESCRIPTION

External morphology

Cushion-shaped sponges covering the substrate and occupying up to 100 cm^2 (Figure 3A, B). Surface thickly or thinly hispid, usually covered with sediment, with up to several hundred papillae. In living sponges the colour of papillae and the areas of the surface free of sediment cream to yellowish. Most papillae inhalant, cylindrical in shape, 2–18 mm in length and 1–6 mm in diameter. Average density of the inhalant papillae 13 per 1 cm^2 of the surface. The inhalant papillae may bear at the summits threads with up to six buds arranged in line (Figure 3B). Exhalant papillae usually conical, 3–12 mm long, 3–7 mm wide at base and 1–5 mm wide at summit, with oscula about 0.5 mm in diameter. One sponge may have up to 19 exhalant papillae.

Anatomy

Choanosome in life orange, dense. Main choanosomal skeleton composed of radial, or longitudinal tracts (170–460 μm thick) of principal spicules branching in the subcortical area, crossing the cortex and forming a surface hispitation (Figure 3C). Ascending tracts also form a framework of the papilla skeleton. Auxiliary choanosomal skeleton comprises free-scattered bundles, each of two to five small spicules, being especially abundant in the subcortical area. Cortex in life cream-coloured, firm, not detachable. Cortical skeleton constituted by a superficial palisade (180–310 μm thick) of small spicules, a middle layer (90–180 μm thick) of collagen fibres with low density of spicules and an internal layer (160–250 μm thick) of tangentially arranged intermediary spicules (Figure 3D). Skeleton of the papilla walls composed of two layers only, the superficial palisade and the internal tangential layer. Single intermediary spicules reinforce the bulkheads separating aquiferous canals and vestibules in the papillae.

Spicules

(measurements based on 43 specimens)

Principal spicules – subtylostyles, straight, fusiform. Length 620–868–1100 μm , maximal diameter of shaft 8.8–14.3–20.0 μm , N = 500.

Intermediary spicules – subtylostyles, straight or gently bent, slender. Length 270–414–550 μm , diameter of shaft 5.0–9.5–17.5 μm , N = 500.

Small spicules – tylostyles, gently bent, fusiform. Length 120–161–215 μm , diameter of tyle 3.8–5.5–7.5 μm , maximal diameter of shaft 3.8–4.8–6.3 μm , N = 500.

Genetic data

CO1 sequences obtained from five individuals of *Polymastia arctica* are identical, but these individuals differ in 28S rDNA (Matrix M34250 in TreeBase) and, moreover, three of them exhibit a polymorphism in this gene (Matrix M34256 in TreeBase). By both genes *P. arctica* is closely related to *P. andrica* and *P. grimaldii* (see the synapomorphies in the Genetic data section for *P. andrica* above). 28S rDNA of these three species displays a high level of intraspecific and intragenomic polymorphism, while the CO1 data are consistent (Plotkin et al., 2016b). In this gene *P. arctica* has two autapomorphies (Online resource 2, p. 1). Apart from them, *P. arctica* differs from *P. andrica* by 7 bps, from *P. grimaldii* by 11 bps and from the type species of *Polymastia*, *P. mamillaris*, by 28 bps in CO1 (Matrix M34248 in TreeBase).

OCCURRENCE

(Figure 3E)

Literature data: Norwegian Coast: Troms and Finnmark (73–182 m) (as *Polymastia mammilaris* – Arnesen, 1918). Norwegian and Barents Sea (as *P. mammilaris* – Koltun, 1966). White Sea (as *Rinalda arctica* – Merejkowsky, 1878, 1880; as *P. penicillus* – Swarczewsky, 1906; as *P. mammilaris* – Koltun, 1966).

Our data: Norwegian Coast: Sør-Trøndelag (27–50 m), Finnmark (127 m). Barents Sea: Murman Coast (60–108 m), Chyosha Bay (7 m). White Sea (4–109 m).

DISCUSSION

Polymastia arctica is morphologically very similar to *P. andrica* and *P. mammilaris*. The main feature distinguishing *P. arctica* from the latter two is the presence of threads with buds at the summits of some inhalant papillae (Arnesen, 1918; Plotkin & Ereskovsky, 1997), although the budding intensity in the populations displays a considerable seasonal fluctuation with some individuals stopping bud formation in the warmest period (Plotkin & Ereskovsky, 1997). Additionally *P. arctica* differs from *P. andrica* by the absence of exostyles and from *P. mammilaris* by the relatively thicker middle cortical layer and the presence of spicules in the bulkheads separating aquiferous canals in the papillae. Some minute differences between these three species in the shape of spicules were also reported, e.g. principal spicules usually being fusiform subtylostyles in *P. arctica* and strongly-loxeas in *P. mammilaris* (Plotkin & Boury-Esnault, 2004), but our study has revealed instability of this character. All genetic data obtained support the discrimination between *P. arctica* and *P. mammilaris* based on morphology. The morphological differences between *P. arctica* and *P. andrica* are only confirmed by the CO1 data, but not by 28S rDNA.

Polymastia cf. bartletti de Laubenfels, 1942

(Figure 4)

Original description: *Polymastia bartletti* de Laubenfels, 1942, p. 265.

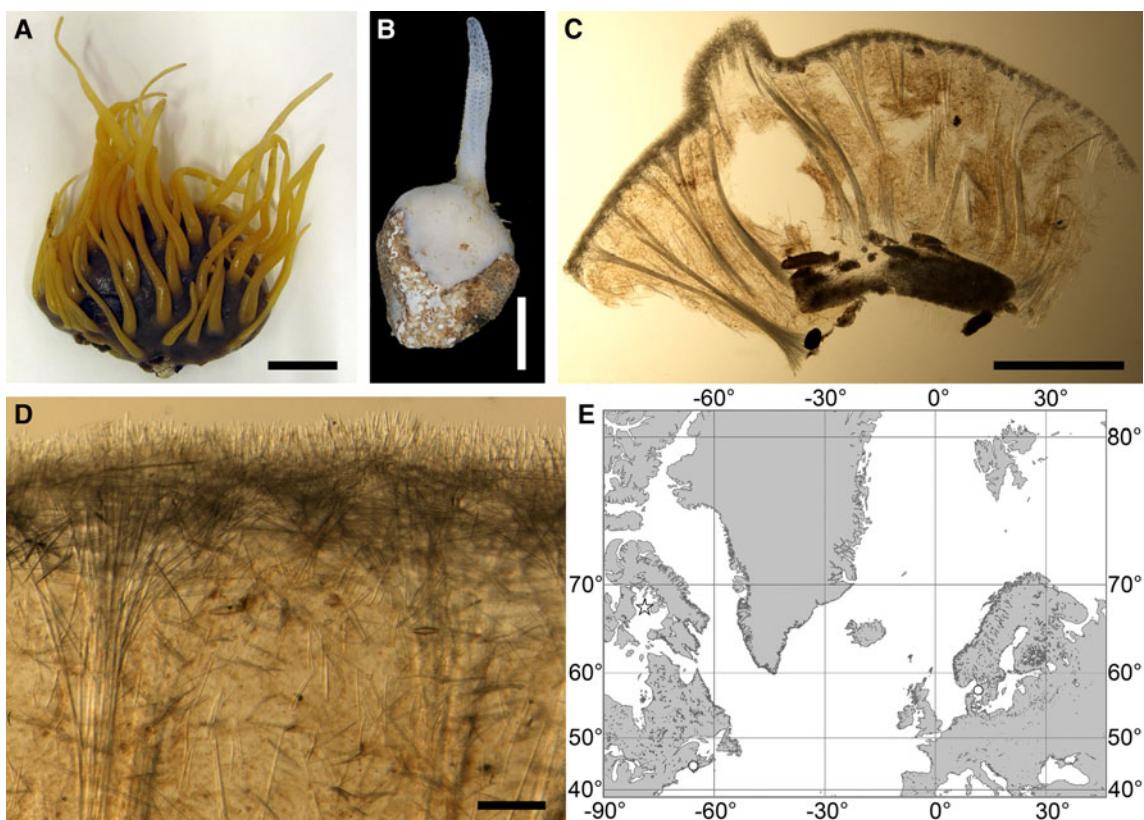


Fig. 4. *Polymastia bartletti*: (A) ZMBN 098111, habitus; (B) GNM 904:1, habitus; (C) ZMBN 098111, longitudinal section through the body, general view; (D) the same section, detail of cortex; (E) distribution: white stars, type localities; white circles, our data. Scale bars: A, 2 cm; B, 0.5 cm; C, 3 mm; D, 0.2 mm.

TYPE MATERIAL

Holotype (not studied): USNM 22692 (in the Smithsonian National Museum of Natural History, Washington), Foxe Basin, Nunavut, Canada, $67^{\circ}45'N$ $79^{\circ}09'W$, 69 m, 24.08.1927, coll. Bartlett.

MATERIAL EXAMINED

(see Online resource 1 for details)

Canada: Nova Scotia: ZMBN 098111 (one specimen).

Sweden: Västra Götaland, Kattegat: GNM 904:1 (one specimen, identification under doubt).

DESCRIPTION

External morphology

Cushion-shaped sponges covering the substrate. Surface smooth, free of sediment, with long papillae lacking visible oscula. Canadian sponge $\sim 51 \times 42 \times 4$ mm in size, with 45 cylindrical papillae, which are 14–44 mm long and 1–4 mm wide. In life the surface is brown and the papillae are yellowish (Figure 4A). In alcohol both the surface and the papillae have become whitish. Swedish sponge $12 \times 9 \times 0.7$ mm in size, with one cylindrical papilla which is 12 mm long and 1.8 mm wide (Figure 4B). Surface and papilla are whitish in alcohol.

Anatomy

Choanosome in alcohol whitish, dense. In both sponges studied main choanosomal skeleton composed of tracts of principal spicules (Figure 4C). The tracts, 71–135 μm thick in the middle of the body, radiate towards the base and the cortex. Ascending tracts also form a framework of the

papilla skeleton. Examination of the auxiliary choanosomal skeleton and the cortex in the Swedish individual was not possible because of its small size. In the Canadian sponge the auxiliary choanosomal skeleton comprises small and intermediary spicules, most free-scattered, some in bundles of three to seven. Cortex dense, but friable, not detachable. Cortical skeleton constituted by a superficial palisade (106–166 μm thick) of small spicules, which is overlapped with an inner layer (203–286 μm thick) of criss-cross intermediary spicules (Figure 4D).

Spicules

GNM 904:1 (Sweden):

Principal spicules – mainly styles, occasionally subtylostyles with weakly developed tyles, usually straight, fusiform. Length 568–752–905 μm , proximal diameter of shaft 2.5–10.2–12.7 μm , maximum diameter of shaft 6.4–14.1–16.5 μm , N = 30.

Intermediary spicules – subtylostyles to styles, usually gently curved, slightly fusiform. Length 246–391–503 μm , diameter of tyle (if present) 6.4–9.2–12.7 μm , proximal diameter of shaft 5.1–8.0–10.2 μm , maximum diameter of shaft 7.6–10.1–12.7 μm , N = 30.

Small spicules – tylostyles, usually gently curved, slender. Length 94–134–165 μm , diameter of tyle 3.8–5.2–7.6 μm , proximal diameter of shaft 2.0–3.6–5.1 μm , maximum diameter of shaft 2.5–4.0–5.1 μm , N = 30.

ZMBN 098111 (Canada):

Principal spicules – styles, usually straight, fusiform. Length 930–1162–1327 μm , proximal diameter of shaft 10.2–

12.1–15.2 µm, maximum diameter of shaft 14.0–17.1–20.3 µm, N = 30.

Intermediary spicules – subtylostyles to styles, usually gently curved, slightly fusiform. Length 467–565–648 µm, diameter of tyle (if present) 8.9–10.2–12.7 µm, proximal diameter of shaft 7.6–8.4–10.2 µm, maximum diameter of shaft 10.2–11.8–15.2 µm, N = 30.

Small spicules – tylostyles, usually gently curved, slender. Length 127–161–192 µm, diameter of tyle 4.6–5.3–6.4 µm, proximal diameter of shaft 2.5–3.5–5.1 µm, maximum diameter of shaft 3.8–5–6.4 µm, N = 30.

Holotype USNM 22692 (according to de Laubenfels, 1942): Principal choanosomal spicules – tylostyles. Length 540–600 µm, diameter of shaft 9–12 µm.

Small choanosomal spicules – length 200 µm, diameter of shaft 4 µm.

Cortical spicules (de Laubenfels did not distinguish between small and intermediary cortical spicules) – tylostyles. Length 350–400 µm, diameter of shaft 6 µm.

Genetic data

The Canadian *Polymastia bartletti* and the Swedish *Polymastia cf. bartletti* are distinguished by two bps in CO1 (Matrix M34248 in TreeBase) and four bps in 28S rDNA (Matrix M34250 in TreeBase). At the same time these sponges share nine synapomorphies in CO1 (Online resource 2, p. 3) and two synapomorphies in 28S rDNA (Online resource 3, p. 3) distinguishing them from other polymastiids. Apart from these synapomorphies, both *P. bartletti* and *P. cf. bartletti* differ from morphologically similar *P. nivea* by 27 bps in CO1 (Matrix M34248 in TreeBase) and 60 bps in 28S rDNA (Matrix M34250 in TreeBase) and from the type species of *Polymastia*, *P. mamillaris*, by 61 bps in CO1 (Matrix M34248 in TreeBase) and 84 bps in 28S rDNA (Matrix M34250 in TreeBase).

OCCURRENCE

(Figure 4E)

Literature data: Canadian Atlantic Coast: Foxe Basin (69 m) (de Laubenfels, 1942).

Our data: Canadian Atlantic Coast: Nova Scotia (depth unknown). Swedish Western Coast: Kattegat (19–31 m).

DISCUSSION

Before our study *Polymastia bartletti* was known only from the type locality, the Foxe Basin (de Laubenfels, 1942). We have identified as *P. bartletti* a specimen from Newfoundland based on its external and anatomical similarities with the original description, and a specimen from Sweden based on the similarities of its external features and DNA with the Newfoundland sponge. But we cannot exclude that the Swedish individual may in fact represent another species since its spicules in all categories are slightly shorter than those in the Canadian individual, and the sequences of the phylogenetic markers from these sponges are not completely identical. More careful morphological examination and genetic studies of larger material are required to check this assumption.

Polymastia bartletti is morphologically very similar to the NE Atlantic species, *P. nivea*. Discrimination between these two species is based mainly on their large genetic difference. In its turn *P. nivea* was often confused with *P. robusta*

Bowerbank, 1862 and *P. boletiformis* (e.g. Koltun, 1966). *Polymastia nivea* and *P. boletiformis* in fact differ considerably both in morphology (Plotkin, 2004; Plotkin et al., 2012; present study) and genetics (Plotkin et al., 2016; present study), while the status of *P. robusta* is questionable (Plotkin et al., 2012; present study). The records of *P. robusta* from the Canadian Atlantic (e.g. Lambe, 1896; Whiteaves, 1901) may indicate *P. bartletti*, but the respective material should be re-examined to test this assumption.

Polymastia boletiformis (Lamarck, 1815) (Figure 5)

Original description: *Alcyonium boletiforme* Lamarck, 1815, p. 332.

SYNONYMS AND CITATIONS

Polymastia boletiformis (Burton, 1959a, 11 pars.; Van Soest et al., 2000, 2016; Van Soest, 2001, p. 74; Morrow et al., 2012, p. 177; Plotkin et al., 2012, p. 25, figure 1i).

Polymastia robusta (Topsent, 1900, p. 147, pl. IV figures 3–7, 14; Arndt, 1928, p. 31, figure 29a; 1933, p. 45; Burton, 1930a, p. 496; Arndt, 1935, p. 34, figure 51; Alander, 1942, p. 75; Borojevic, 1967, p. 1, pls I–II; Cabioch, 1968, p. 215; Boury-Esnault, 1987, p. 44, figure 8).

TYPE MATERIAL

Lamarck (1815) reported neither the museum number, nor the type locality in the original description. Topsent (1933) examined a sponge with Lamarck's original label '*Alcyonium boletiforme*' considered as the holotype of this species and stored in MNHN. Since then nobody has re-examined this individual and it is regarded as lost by MNHN.

MATERIAL EXAMINED

(see Online resource 1 for details)

Sweden: Västra Götaland: GNM 901:1, GNM 903:1 and GNM 903:2 (three specimens).

Norway: Vest-Agder: ZMBN 098088 and ZMBN 098089 (two specimens), Rogaland: ZMBN 107584 and ZMBN 107585 (three specimens), Hordaland: ZMBN 098047, ZMBN 098048, ZMBN 098081, ZMBN 107559, ZMBN 107560, ZMBN 107562, ZMBN 107563, ZMBN 107564, ZMBN 107565, ZMBN 107566, ZMBN 107567, ZMBN 107568, ZMBN 107569, ZMBN 107571 (14 specimens), Møre and Romsdal: ZMBN 107493, ZMBN 107570 (two specimens).

DESCRIPTION

External morphology

Sponges cushion-shaped, covering the substrate or massive (Figure 5A). The largest individuals may occupy up to 100 cm². Surface smooth, sometimes covered with sediment, with cylindrical or conical papillae. In living sponges both the surface and the papillae bright orange or yellow. Inhalant papillae 6–18 mm long and 2–5 mm wide. About 2–3 inhalant papillae per 1 cm² of the surface. Exhalant papillae 16–36 mm long and 3–6 mm wide, with well visible oscula at the summits. A sponge may bear 1–6 exhalant papillae.

Anatomy

Choanosome in life slightly darker than cortex, crumbly. Main choanosomal skeleton composed of tracts of principal spicules

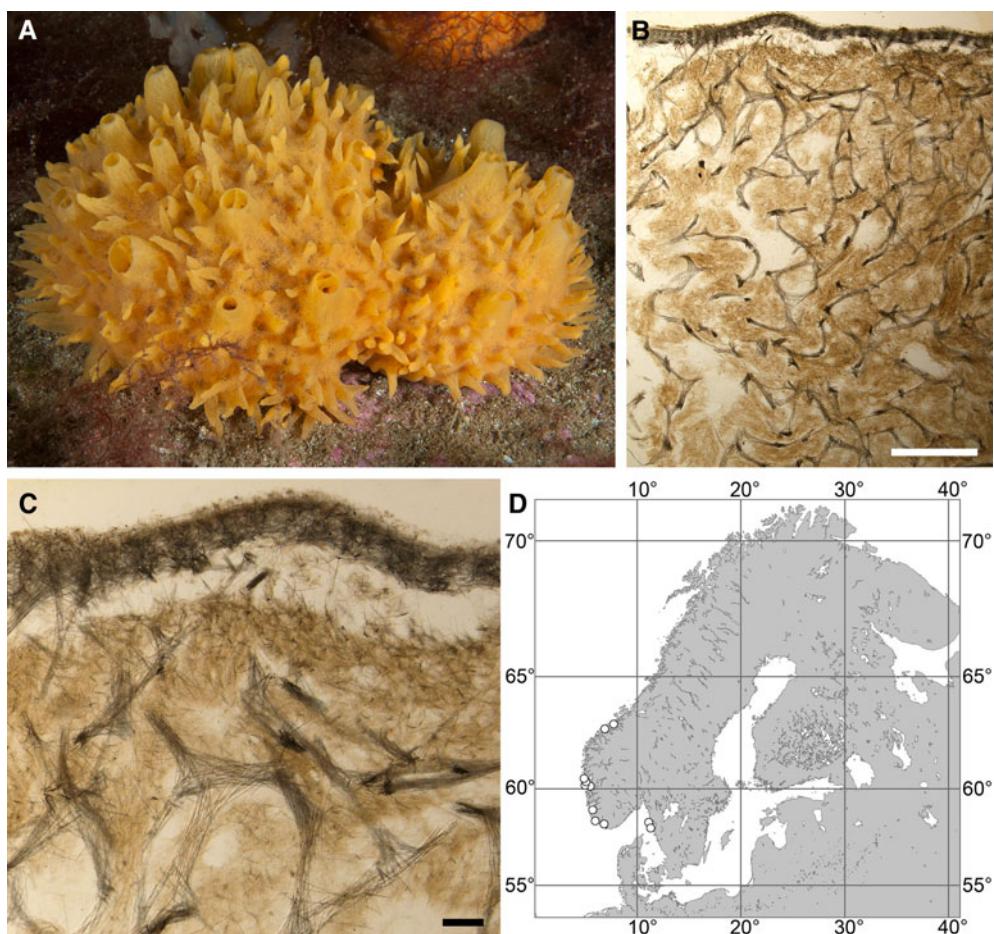


Fig. 5. *Polymastia boletiformis*: (A) an individual *in situ*, Tingelsædet, Egersund, Norway (courtesy of E. Svensen, OceanPhoto/Dalane Tidende AS, Egersund); (B) ZMBN 107563, longitudinal section through the body, general view; (C) the same section, detail of cortex and subcortical area; (D) distribution along the Scandinavian Coast: white circles, our data; for distribution in other regions see Boury-Esnault (1987; as *Polymastia robusta*). Scale bars: B, 2 mm; C, 0.5 mm.

forming a reticulation or meanders (Figure 5B, C). Ascending tracts form a framework of the papilla skeleton. Auxiliary choanosomal skeleton comprises free-scattered principal spicules. Cortex leather-like, easily detachable. Cortical skeleton constituted by a superficial palisade (80–250 µm thick) of small spicules and an internal layer (169–420 µm thick) of criss-cross principal spicules (Figure 5C). Aquiferous cavities connected with ostia in the surface and separated by bundles of intermediary spicules lie in a space (125–400 µm thick) between the cortex and the choanosome. Both cortical layers extend to the walls of papillae. Each papilla bears several inhalant canals, and in exhalant papilla there are also one to three exhalant canals located midmost. Bulkheads separating the canals are reinforced with free-scattered principal spicules.

Spicules

(Measurements based on four specimens)

Principal spicules – subtylostyles, straight or gently curved, slender or slightly fusiform. Length 261–540–735 µm, proximal diameter of shaft 5.1–6.7–9.0 µm, maximum diameter of shaft 7.5–10.4–12.7 µm, N = 120.

Small spicules – subtylostyles with weakly developed tylos, usually gently bent in the proximal part, slender. Length 91–153–232 µm, proximal diameter 2.0–3.1–3.9 µm, maximum diameter of shaft 2.0–3.2–3.9 µm, N = 124.

Genetic data

In both CO1 and 28S rDNA phylogenies *Polymastia boletiformis* is the sister to morphologically quite distinct *Quasillina brevis* (Bowerbank, 1866) (Plotkin *et al.*, 2016b). These species share three synapomorphies in CO1 (Online resource 2, p. 4) and 24 synapomorphies in 28S rDNA (Online resource 3, p. 4). CO1 data were obtained from two specimens of *P. boletiformis*, of which one differs from *Q. brevis* just by one bp in this gene, while the other differs from *Q. brevis* by six bps (Matrix M34248 in TreeBase). 28S rDNA sequences obtained from six Scandinavian *P. boletiformis* are identical to the sequences of a British *P. boletiformis* (GenBank accessions HQ379232, HQ379306 and HQ379372, Morrow *et al.*, 2012) and display six synapomorphies distinguishing them from all other polymastiids (Online resource 3, p. 4). Apart from these synapomorphies, *P. boletiformis* differs from *Q. brevis* by 17 bps in 28S rDNA (Matrix M34250 in TreeBase) and from the type species of *Polymastia*, *P. mamillaris* by 64–67 bps in CO1 (considering the intraspecific polymorphism, Matrix M34248) and 89 bps in 28S rDNA (Matrix M34250).

OCCURRENCE

Literature data: Portuguese, Spanish and French Atlantic Coast (as *Polymastia robusta* – Topsent, 1900; Borojevic, 1967; Cabioch, 1968; Boury-Esnault, 1987). Mediterranean

Sea, English Channel (as *Polymastia robusta* – Boury-Esnault, 1987). British Isles (as *P. robusta* – Boury-Esnault, 1987; as *P. boletiformis* – Van Soest et al., 2000, 2016). Sweden (as *P. robusta* – Alander, 1942). Depths – from 10 m and deeper down the shelf (Boury-Esnault, 1987). Records from the continental slope, 2354 m by Burton (1959a) and 1267 m by Boury-Esnault (1987), cause doubt. Our data (Figure 5D): Skagerrak: Swedish Western Coast (22–60 m). Norwegian Coast: Vest-Agder (30–40 m), Rogaland (18–31 m), Hordaland (18–40 m), Møre and Romsdal (20–130 m).

DISCUSSION

Polymastia boletiformis has a confused taxonomic history. Since the description of *Alcyonium boletiforme* from an unknown locality by Lamarck (1815) this name had not been in use until Topsent (1933) reported that Lamarck's type material and *Polymastia robusta* Bowerbank, 1862 from the British Isles were the same species. Although *A. boletiforme* was an older name than *P. robusta* Topsent (1933) relegated the former to a synonym of the latter, and this was followed by most of the later authors (e.g. Arndt, 1935; Alander, 1942; Koltun, 1966; Cabioch, 1968; Boury-Esnault, 1987) except for Burton (1959a) who retained the name *P. boletiformis*. In the recent literature (Van Soest et al., 2000; Van Soest, 2001, 2016; Morrow et al., 2012; Plotkin et al., 2012) the name *P. boletiformis* was, however, prioritized instead of *P. robusta* following the principle of priority (Article 23.1 in Anonymous, 1999).

Polymastia robusta/P. boletiformis was recorded from a large geographic area from the Canadian Atlantic Coast (Lambe, 1896; Whiteaves, 1901) and Iceland (Burton, 1959a) to the European Atlantic Coast (Topsent, 1900; Arndt, 1935; Borojevic, 1967; Cabioch, 1968; Boury-Esnault, 1987), British Isles (Boury-Esnault, 1987; Van Soest et al., 2000), Swedish Coast (Alander, 1942), Norwegian Coast (Burton, 1930a), Barents Sea (Topsent, 1913) and Arctic Ocean (Koltun, 1966). The depth range recorded for *P. robusta/P. boletiformis* was also very large with the extreme deep-sea records by Burton (1959a) and Boury-Esnault (1987). Furthermore, four species were relegated to synonyms of *P. robusta*: *P. bulbosa* Bowerbank, 1866 and *P. ornata* Bowerbank, 1866 from the British Isles by Topsent (1900), *Reniera nivea* Hansen, 1885 from the Norwegian Sea by Burton (1930a) and *P. euplectella* Rezvoj, 1927 from the Barents and White Sea by Koltun (1966).

However, Plotkin (2004) demonstrated clear morphological distinctions between *P. euplectella* and *P. robusta*, a radial choanosomal skeleton and three size categories of spicules in the former against a reticulate skeleton and two spicule categories in the latter. The present study has confirmed these differences by genetic data. Meanwhile, we have revealed the strong similarities between *P. euplectella* and *Reniera nivea*, relegating the former to a synonym of the latter (see Description of *Polymastia nivea* below). We can now assume that all records of *P. robusta/P. boletiformis* to the North and North-East from Nordmøre Coast in Norway very probably indicate *P. nivea*. Moreover, the present study has shown that *P. bartletti*, a Canadian species morphologically very similar to the Arctic-Scandinavian *P. nivea*, differs greatly from the latter as well as from the European *P. boletiformis* by genetics. We can therefore assume that the records of *P. robusta/P. boletiformis* from

Canada may indicate *P. bartletti* (see the description of this species above). Finally, we have examined one of the dry syntypes of *P. robusta* BMNH 1930.7.3.20 and found that its choanosomal skeleton is radial as distinct from the commonly accepted definition of *P. boletiformis* (Boury-Esnault, 1987; Van Soest et al., 2000; Plotkin et al., 2012), but the condition of the syntypes prevents us from more detailed study. Unfortunately we have not examined *P. bulbosa* and *P. ornata*, and therefore we cannot conclude whether these two are separate species or conspecific with *P. boletiformis*, *P. robusta* or some other species.

Thus, for the moment, we gather under the name *P. boletiformis* South European, British and South Scandinavian *Polymastia* with intensive orange or yellow colour, a smooth surface with differentiated exhalant and inhalant papillae, a reticulate choanosomal skeleton and two spicule categories. These morphological similarities are confirmed by the genetic identity of the British and South Scandinavian individuals.

Polymastia grimaldii (Topsent, 1913) (Figure 6)

Original description: *Trichostemma grimaldii* Topsent, 1913, p. 21, pl. I figure 4.

SYNOMYMS AND CITATIONS

Polymastia grimaldii (Topsent, 1927a, p. 257; Boury-Esnault, 1987, p. 42, figure 7; Plotkin, 2004, p. 542, figures 1e & 2e; Plotkin et al., 2012, p. 25, figure 2l).

Polymastia mamillaris (Vosmaer, 1885, p. 14, text-figure 5, pl. I figure 5, pl. III figures 10, 11–14, 21).

Polymastia mamillaris grimaldii (Koltun, 1966, p. 70, text-figures 39–40, pl. XX figures 1–5).

Polymastia mamillaris var. *hyperborea* Hentschel, 1916, p. 8 (Hentschel, 1929, pp. 868 and 923).

Polymastia penicillus (Vosmaer, 1882, p. 26, pl. I figures 12 & 13, pl. IV figures 127–132; Hansen, 1885, p. 9; Fristedt, 1887, p. 434; Levinsen, 1887, p. 346).

Radiella grimaldii (Burton, 1959a: 13; Koltun, 1964, p. 149).

TYPE MATERIAL

Lectotype of *Trichostemma grimaldii* (designated herein, Figure 6A–C): MOM 04-0840e, East off Iceland, 65°21'N 10°42'W, 650 m, Campagnes scientifiques accomplies par le Prince Albert I de Monaco, RV 'Princesse-Alice', station 1040, 07.09.1898.

Paralectotypes of *Trichostemma grimaldii*: MOM 04-0840a–d, f–l (11 specimens), from the same sample as the lectotype.

Holotype of *Polymastia mamillaris* var. *hyperborea* Hentschel, 1916 (Figure 6D–F; herein considered as a synonym of *Polymastia grimaldii*): UPSZTY 2103, mouth of Nordfjorden, Svalbard, ~78°27.5'N 15°03.0'E, 197–190 m, Swedish expedition to Spitzbergen, station 99, 27.08.1908.

COMPARATIVE MATERIAL

(see Online resource 1 for details)

Canada: Newfoundland: ZIN RAS ocpgo59, ZIN RAS ocpgo60, ZIN RAS ocpgo61, ZIN RAS ocpgo83, ZIN RAS ocpgo96 and ZMBN 098110 (six specimens).

Greenland: Kangerdlugssuaqfjord: ZMBN 107579 (one specimen).

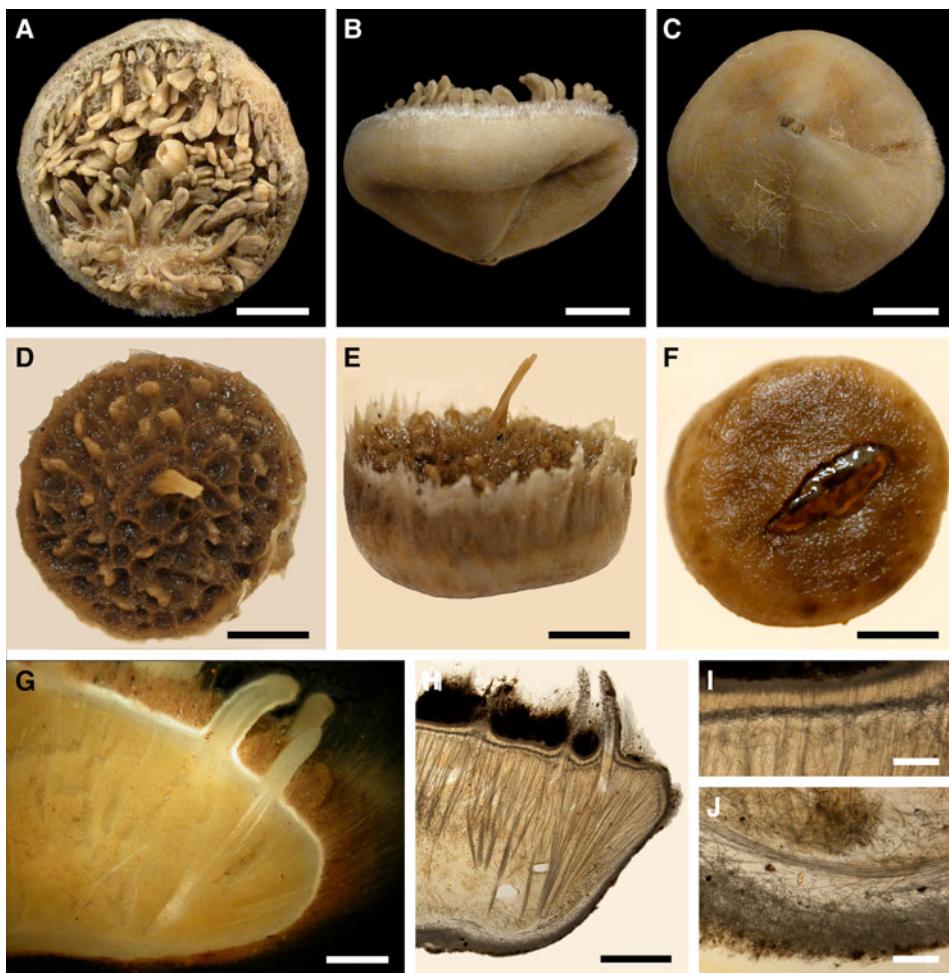


Fig. 6. *Polymastia grimaldii*: (A) lectotype of *Trichostemma grimaldii*, MOM 04-0840e, habitus, view from above; (B) the same, side view; (C) the same, bottom view; (D) holotype of *Polymastia mammilaris* var. *hyperborea* (synonym of *P. grimaldii*), UPSZTY 2103, habitus, view from above; (E) the same, side view; (F) the same, bottom view; (G) a fresh dissected individual from the Kandalaksha Bay, White Sea, (H) ZMBN 107576, longitudinal section through the body, general view; (I) the same section, detail of upper cortex; (J) the same section, detail of basal cortex. D–F: courtesy of P. Cárdenas, BioMedical Centre, University of Uppsala. Scale bars: A–F, 1 cm; G–H, 3 mm; I–J, 0.5 mm.

Denmark Strait: ZIN RAS ocpg133 (one specimen).
Norwegian Sea, offshore: ZIN RAS ocpgo29, ZIN RAS ocpgo30, ZIN RAS ocpgo82 and ZIN RAS ocpg116 (five specimens).
Barents Sea, offshore: ZMBN 098112, ZMBN 107576 (two specimens) and 156 specimens deposited in ZIN RAS.
Norway: Troms: ZIN RAS ocpgo75 (one specimen), Finnmark: ZMBN 098064 (one specimen).
Russia: Murman Coast: ZIN RAS ocpgo51 (one specimen), White Sea: ZIN RAS ocpgo01, ZIN RAS ocpgo02, ZIN RAS ocpgo03, ZIN RAS ocpgo04, ZIN RAS ocpg147, ZIN RAS ocpg165, ZIN RAS ocpg166 and ZIN RAS ocpg167 (10 specimens), Kanin Peninsula: ZIN RAS ocpgo88 (one specimen), Novaya Zemlya: ZIN RAS ocpg10, ZIN RAS ocpgo20 and ZIN RAS ocpgo97 (seven specimens), Taymyr Peninsula: ZIN RAS ocpgo79, ZIN RAS ocpg126, ZIN RAS ocpg135, ZIN RAS ocpg143 and ZIN RAS ocpg158 (five specimens), Severnaya Zemlya: ZIN RAS ocpg160 (one specimen).
Kara Sea: ZIN RAS ocpgo15, ZIN RAS ocpgo64, ZIN RAS ocpgo69, ZIN RAS ocpgo95, ZIN RAS ocpgo98, ZIN RAS ocpg100, ZIN RAS ocpg105, ZIN RAS ocpg113, ZIN RAS ocpg125 and ZIN RAS ocpg131 (10 specimens).
Laptev Sea: ZIN RAS ocpg146 (one specimen).

East Siberian Sea: ZIN RAS ocpg163 (seven specimens).
Arctic Ocean: ZIN RAS ocpg164 (four specimens).

DESCRIPTION

External morphology

Lectotype with almost circular, flat upper surface, 40–41 mm in diameter, and convex basal surface with a central point 22 mm distant from the upper surface (Figure 6A–C). Upper surface strongly hispid, greyish, with a single central exhalant papilla, cylindrical in shape, 9 mm long and 4 mm in diameter, and 118 inhalant papillae, most flattened, slightly widened towards the top, 1–6 mm in length and 0.7–2 mm in diameter at base (Figure 6A). Basal surface sleek, beige to grey, damaged in a central point indicating that the sponge was attached to a tiny substrate (Figure 6C). A fringe of extra-long spicules, 1.5 mm wide, developed at the sponge edge between the upper and basal surface (Figure 6B). Other sponges discoid, hemispherical with either the upper or the basal surface being convex, or sometimes lenticular. Upper surface up to 200 cm², strongly hispid, usually covered with sediment, with up to 300 papillae, of which most are inhalant and one to six are exhalant, with well-visible oscula. The exhalant papillae cylindrical or conical, up to 16 mm in length. The inhalant

papillae flattened, leaf-shaped, or sometimes cylindrical, up to 9 mm in length. Basal surface smooth, sometimes even sleek, attached to a small substrate only by a central point. Marginal fringe of extra-long spicules preventing sinking of the sponge into the sediment may be reduced in some individuals.

Anatomy

Choanosome in life pale orange or beige, firm (Figure 6G). Main choanosomal skeleton composed of tracts (65–655 µm thick) of principal spicules radiating from sponge base and dividing into two to four thinner tracts, which cross the upper cortex and form a surface hispidation (Figure 6G, H). Ascending tracts also form a framework of the papilla skeleton. Auxiliary choanosomal skeleton comprises free-scattered small spicules, especially concentrating below the upper cortex. Cortex in life whitish, firm, not detachable (Figure 6G). Skeleton of the upper cortex constituted by a superficial palisade (170–210 µm thick) of small spicules, a middle layer (100–180 µm thick) of collagen fibres with low density of spicules and an internal layer (100–140 µm thick) of tangentially arranged intermediary spicules (Figure 6I). Skeleton of the basal cortex (520–700 µm thick) formed by the peripheral tracts of principal spicules running parallel to the surface overlapped by a superficial palisade of small spicules and an inner confused mass of intermediary spicules (Figure 6J). Marginal fringe composed of bundles of extra-long spicules (exotypes) embedded into the cortex. Skeleton of the papilla walls composed of the superficial palisade and the internal tangential layer. Both inhalant and exhalant papillae with single central canals.

Spicules

(measurements based on 15 specimens)

Principal spicules – strongyloxeas, straight or gently curved. Length 1450–2358–3235, maximum diameter of shaft 21.0–24.8–29.2 µm, N = 450.

Intermediary spicules – tylostyles, straight or gently bent, fusiform. Length 212–445–671 µm, maximum diameter of shaft 15.8–18.4–24.0 µm, N = 450.

Small spicules – tylostyles to subtylostyles, straight or gently bent, usually slender. Length 147–228–287 µm, maximum diameter of shaft 3.8–6.4–7.8 µm, N = 450.

Exotypes (spicules of the marginal fringe) – flexuous styles, occasionally subtylostyles. Length 2020–4527–7000 µm, maximum diameter 8.0–9.4–10.6 µm, N = 150.

Genetic data

CO1 sequences obtained from three individuals of *Polymastia grimaldii* are identical. 28S rDNA available only from one of these individuals is polymorphic (Matrix M34256 in TreeBase). By both genes *P. grimaldii* is closely related to *P. andrica* and *P. arctica* (see the synapomorphies in the Genetic data section for *P. andrica* above). 28S rDNA of these three species displays intraspecific and intragenomic polymorphism, while the CO1 data are consistent (Plotkin et al., 2016b). In CO1 *P. grimaldii* has one autapomorphy (Online resource 2, p. 1). Apart from the latter, this species differs from *P. andrica* by 12 bps, from *P. arctica* by 12 bps and from the type species of *Polymastia*, *P. mammillaris*, by 31 bps in CO1 (Matrix M34248 in TreeBase).

OCCURRENCE

(Figure 7)

Our data (agree with the literature data): Canadian Atlantic Coast: Newfoundland (315–440 m). Greenland Sea: (640–680 m). Denmark Strait: (511 m). Norwegian Sea, offshore areas (120–420 m). Norwegian Coast: Troms (320 m), Finnmark (211 m). Barents Sea: Murman Coast (190 m), Kanin Peninsula (62 m), offshore areas (53–460 m). White Sea (18–100 m). Svalbard (190–197 m). Novaya Zemlya (93–459 m). Taymyr Peninsula (23–58 m). Severnaya Zemlya (237 m). Kara Sea (49–305 m). Laptev Sea (51 m). East Siberian Sea (73 m). Arctic Ocean (1900–1630 m).

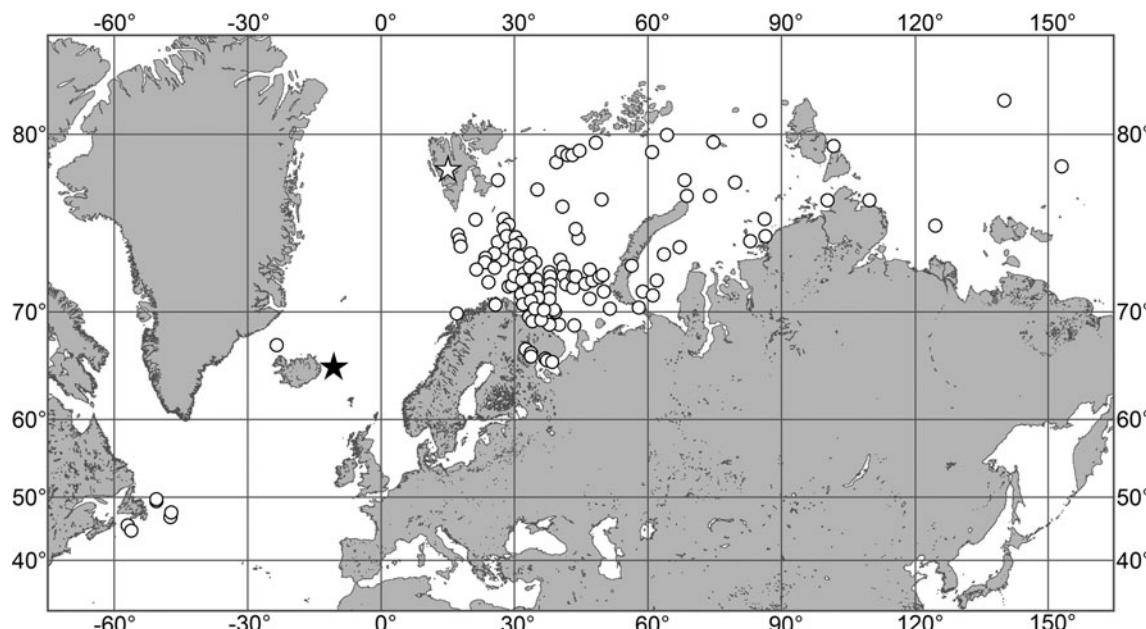


Fig. 7. *Polymastia grimaldii*, distribution: black star, type locality of *Trichostemma grimaldii*; white star, type locality of *Polymastia mammillaris* var. *hyperborea* (synonym of *P. grimaldii*); white circles, our data.

DISCUSSION

Polymastia grimaldii was a key species in a long discussion on the relationships between a broadly acknowledged genus *Polymastia* and two genera with uncertain status, *Radiella* Schmidt, 1870 and *Trichostemma* Sars, 1872. The latter two names were since Schmidt (1880) often regarded as the synonyms for the same genus, but there were some debates about which of them should be considered as the senior name (see Discussion on *Polymastia hemisphaerica* (Sars, 1872) below) until Boury-Esnault (2002) relegated *Trichostemma* to a synonym of *Radiella* following the principle of priority (Article 23.1 in Anonymous, 1999).

Radiella/Trichostemma was usually distinguished from *Polymastia* by a radial growth pattern (a sponge attached to the substrate by a small point of the basal surface), the presence of a basal cortex distinct from the upper cortex and the presence of a fringe of extra-long monactines at the boundary between the upper and basal surface (Boury-Esnault, 2002; Plotkin *et al.*, 2012). All these features are displayed by *Polymastia grimaldii*, but at the same time this species possesses numerous papillae and a three-layered cortex including a middle layer of collagen fibres that rather resemble the type species of *Polymastia*, *P. mamillaris*, than *Radiella* spp. or *Trichostemma* spp. (Boury-Esnault, 1987; Plotkin, 2004; Plotkin *et al.*, 2012). Based on the similarities between *P. grimaldii*, *P. mamillaris* and other *Polymastia* spp. several early authors identified some sponges with evident distinctive features of *Radiella/Trichostemma* as *P. penicillus* (Vosmaer, 1882; Hansen, 1885; Fristedt, 1887; Levinsen, 1887) or *P. mamillaris* (Vosmaer, 1885). It was Topsent (1913) who established a new species, *Trichostemma grimaldii*, for the

sponges combining the features of *Radiella/Trichostemma* and *Polymastia*. But, after a time, he re-considered the generic allocation of this species transferring it to *Polymastia* (Topsent, 1927a). In the same manner Koltun (1964) initially placed *grimaldii* in *Radiella*, but two years later (Koltun, 1966) relegated it to a subspecies of *Polymastia mamillaris*. The uncertainty about the taxonomic affinities of *P. grimaldii* was perfectly expressed by Boury-Esnault (1987, p. 44): '*P. grimaldii* may be considered as a step on the evolutionary line which starts at *Polymastia* advancing to *Trichostemma*'.

This uncertainty was recently resolved by the phylogenies reconstructed from CO1 and 28S rDNA datasets (Plotkin *et al.*, 2016b), where *P. grimaldii* formed a clade with *Radiella hemisphaerica* (formerly *Trichostemma hemisphaericum*, the type species of *Trichostemma*), *P. mamillaris* (the type species of *Polymastia*) and four other *Polymastia* spp. At the same time two species of *Radiella* grouped with the type species of *Spinularia* Gray, 1867, *S. spinularia* (Bowerbank, 1866), outside the *Polymastia*-clade (see Discussion on the genus *Spinularia* below). Consequently, *grimaldii* and *hemisphaerica* are now affiliated with *Polymastia*.

Polymastia hemisphaerica (Sars, 1872) (Figure 8)

Original description: *Trichostemma hemisphaericum* Sars, 1872, p. 62, pl. VI figures 1–15.

SYNONYMS AND CITATIONS

Halicnemria hemisphaerica (von Marenzeller, 1878, p. 371).

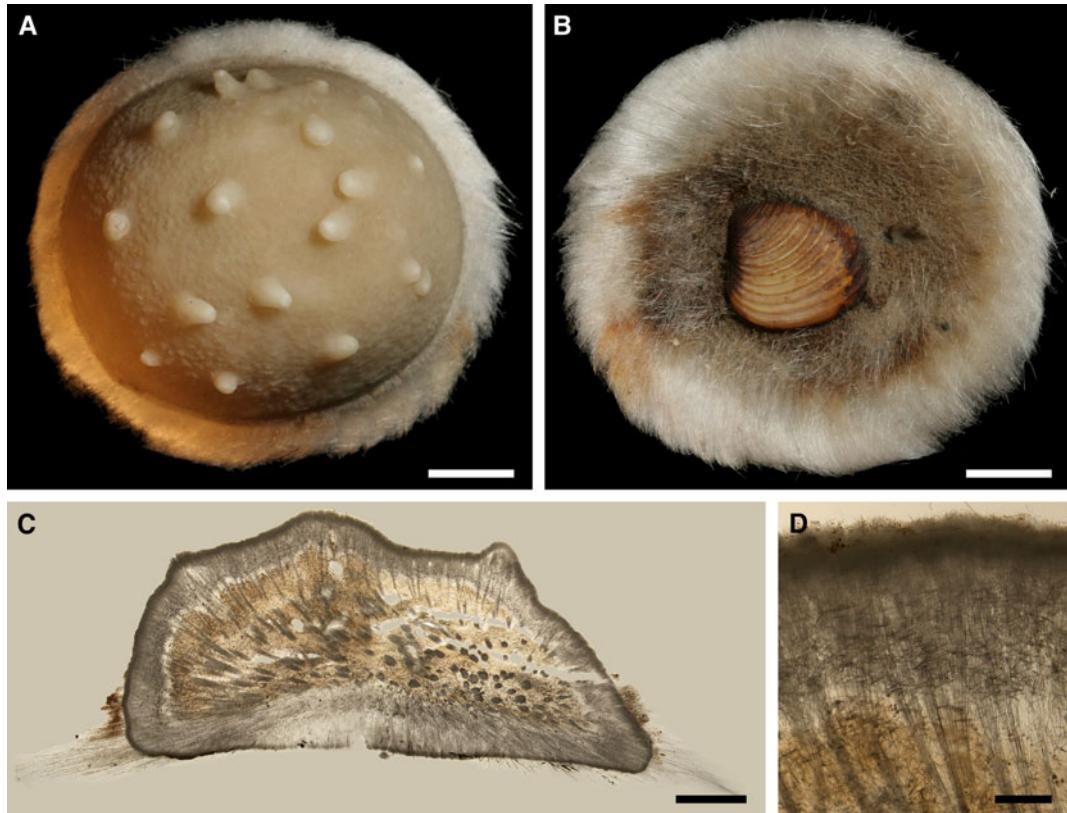


Fig. 8. *Polymastia hemisphaerica*: (A) holotype, NHM B862, habitus, view from above; (B) the same, bottom view; (C) ZMBN 098043, longitudinal section through the body, general view; (D) the same section, detail of upper cortex. Scale bars: A–B, 1 cm; C, 3 mm; D, 0.5 mm.

Polymastia hemisphaerica (Vosmaer, 1885, p. 12; Topsent, 1892, p. 132; Rezvoj, 1924, p. 242).

Polymastia hemisphaericum (Koltun, 1966, p. 78, text-figure 51, pl. XXIX figures 1–5).

Radiella hemisphaerica (Plotkin, 2004, p. 542, figures 1f & 2f; Plotkin et al., 2012, p. 27, figure 2k).

Radiella sol (Hansen, 1885, p. 7; Burton, 1930a: 510 pars., 1959a: 12 pars.).

Suberites radians Hansen, 1885, p. 10, pl. II figure 7.

Trichostemma hemisphaericum (Sars, 1869, p. 250, 265, 268 nomen nudum; Whiteaves, 1874, p. 184, 1901, p. 14; Lambe, 1896, p. 197, pl. II figures 7 & 7a–e; Lundbeck, 1909, p. 451; Topsent, 1913, p. 20, pl. I figure 2, pl. II figures 1 & 2).

TYPE MATERIAL

Holotype (specimen in alcohol): NHMUO B862, Lofoten, Nordland, Norway, 218–546 m.

Paralectotypes (three dry specimens): NHMUO B863, Brattesnes, Lofoten, Nordland, Norway, 182–218 m.

Paralectotype (specimen in alcohol): ZMBN 000136, Lofoten, Nordland, Norway, 218 m.

COMPARATIVE MATERIAL

(see Online resource 1 for details)

Canada: Nova Scotia: ZIN RAS ocp002 (one specimen), Labrador and Newfoundland: ZIN RAS ocp004, ZIN RAS ocp024, ZIN RAS ocp025 and ZIN RAS ocp032 (four specimens), offshore areas of NW Atlantic: ZIN RAS ocp022, ZIN RAS ocp023, ZIN RAS ocp026, ZIN RAS ocp031 and ZIN RAS ocp038 (five specimens).

Greenland, SE Coast: ZIN RAS ocp037 and ZIN RAS ocp043 (two specimens).

Iceland: ZIN RAS ocp007, ZIN RAS ocp042 and ZMBN 098069 (three specimens).

Norwegian Sea, offshore: ZIN RAS ocp029, ZIN RAS ocp034, ZIN RAS ocp036 and ZIN RAS ocp041 (four specimens).

Barents Sea, offshore: ZIN RAS ocp008, ZIN RAS ocp011, ZIN RAS ocp012, ZIN RAS ocp013, ZIN RAS ocp014, ZIN RAS ocp015, ZIN RAS ocp016, ZIN RAS ocp017, ZIN RAS ocp018, ZIN RAS ocp019, ZIN RAS ocp020, ZIN RAS ocp027, ZIN RAS ocp028, ZIN RAS ocp030, ZIN RAS ocp035, ZIN RAS ocp040, ZIN RAS ocp044, ZMBN 098071 and ZMBN 107577 (19 specimens).

Norway: Hordaland: ZMBN 098043, ZMBN 098056, ZMBN 098058, ZMBN 098077 and ZMBN 107561 (five specimens), Møre and Romsdal: ZMBN 107486 (one specimen); Nord-Trøndelag: NTNU-VM-72542 (21 specimens), Nordland: NTNU-VM-66581 and NTNU-VM-72513 (two specimens).

Russia: Novaya Zemlya: ZIN RAS ocp001 and ZIN RAS ocp021 (two specimens).

Kara Sea: ZIN RAS ocp006 (one specimen).

DESCRIPTION

External morphology

Holotype hemispherical, 80–86 mm in diameter. Upper surface convex, knobbly, cream-coloured, with 18 papillae (Figure 8A). Papillae conical, 1–5 mm long and 1.5–3.5 mm wide at base, with considerably contracted oscula at the summits. Basal surface shaggy, pale grey in colour, attached to a bivalve shell by the central point (Figure 8B).

A fringe of extra-long spicules, 4–9 mm wide, developed at the sponge edge separating the upper and basal surface. Other sponges hemispherical or discoid, up to 65 mm in diameter, with the marginal spicule fringe up to 13 mm in width. Upper surface whitish or cream-coloured in life, knobbly, with up to 30 conical papillae. In living sponges the papillae with well visible oscula. Under sampling and preservation the papillae stretch and the oscula contract. Basal surface shaggy or hispid, attached to a small substrate.

Anatomy

Choanosome in life yellowish or pale orange, firm. Main choanosomal skeleton composed of tracts (190–416 µm thick) of principal spicules radiating from the basal area and entering the cortex (Figure 8C). In the upper cortex the tracts run perpendicular to the surface and do not protrude. Some tracts ascend to the papillae. In the basal cortex the tracts run obliquely to the surface and stick out forming a thick hispitation. Auxiliary choanosomal skeleton comprises free-scattered small spicules and bundles of intermediary spicules concentrated in the subcortical area. Cortex in life whitish, firm, not detachable. Cortical skeleton constituted by a notched superficial palisade (366–522 µm thick) of small spicules and an internal layer (663–930 µm thick in the upper cortex and up to 1280 µm thick at the basal central point) of criss-cross intermediary spicules (Figure 8C, D). Marginal fringe composed of bundles of extra-long spicules (exotyles) embedded into the cortex. In the upper part of the body the cortex and the choanosome separated by an area with low concentration of spicules (127–206 µm thick). Papilla walls reinforced with the cortical palisade. Each papilla with a central exhalant canal and several peripheral inhalant canals.

Spicules

(Measurements based on 10 specimens)

Principal spicules – styles to subtylostyles, straight or gently curved, slightly fusiform. Length 1920–3125–5400, maximum diameter of shaft 10.9–20.2–32.3 µm, N = 200. Intermediary spicules – tylostyles, straight, fusiform. Length 390–512–618 µm, maximum diameter of shaft 17.2–19.9–26.2 µm, N = 300.

Small spicules – tylostyles, usually gently bent in the distal part, slender. Length 160–229–305 µm, maximum diameter of shaft 4.2–5.8–8.4 µm, N = 300.

Exotyles (spicules of the marginal fringe) – styles, straight, slightly fusiform. Length 4990–6511–8015 µm, maximum diameter 45.8–47.5–50.1 µm, N = 100.

Genetic data

CO1 was obtained from six individuals of *Polymastia hemisphaerica*, while 28S rDNA were sequenced only from three of them. By both genes *P. hemisphaerica* is closely related to morphologically quite different *P. thielei* (Plotkin et al., 2016b). These species share two synapomorphies in CO1 (Online resource 2, p. 2) and two synapomorphies in 28S rDNA (Online resource 3, p. 2) and, apart from them, differ from the type species of *Polymastia*, *P. mamillaris*, by 18 bps in CO1 (Matrix M34248 in TreeBase) and six bps in 28S rDNA (Matrix M34250 in TreeBase). At the same time *P. hemisphaerica* demonstrates an intraspecific polymorphism. In CO1 five individuals of this species differ from *P. thielei* just by one bp, while one individual, ZMBN 098056, differs from *P. thielei* by two bps (Matrix M34248

in TreeBase). On the contrary, by 28S rDNA ZMBN 098056 is identical to two other conspecific sponges differing from *P. thielei* just by one insertion in this gene, while another individual of *P. hemisphaerica*, ZMBN 098043 possessing the same insertion, is distinguished from both the conspecific individuals and *P. thielei* by three bps in 28S rDNA (Matrix M34250 in TreeBase).

OCCURRENCE (Figure 9)

Literature data: Canadian Atlantic Coast: Gulf of St. Lawrence (204 m) (Whiteaves, 1874, 1901; Lambe, 1896).

Our data: Canadian Atlantic Coast: Nova Scotia (355–480 m), Newfoundland (our data: 383–415 m, Topsent, 1892: 1267 m), Labrador (225–485 m), offshore areas (230–450 m). Greenland, SE Coast (212–405 m). Iceland (214–650 m). Norwegian Sea, offshore (250–480 m). Norwegian Coast: Hordaland (300–312 m), Møre and Romsdal (100 m), Nord-Trøndelag (200 m), Nordland (182–850 m). Barents Sea, offshore (180–369 m). Russia: Novaya Zemlya (153–270 m). Kara Sea (our data: 368 m, Rezvoj, 1924: 91–200 m).

DISCUSSION

Polymastia hemisphaerica was originally described as *Trichostemma hemisphaericum* Sars, 1872 designated as the type species of *Trichostemma* Sars, 1872. In fact, this genus and this species were first mentioned in a list of the Norwegian sponges three years earlier (Sars, 1869), although without any description. Von Marenzeller (1878) regarded *Trichostemma* as a synonym of *Halicnemia* Bowerbank, 1864, while Schmidt (1880) put *T. hemisphaericum* in synonymy with *Radiella sol* Schmidt, 1870, one of the two species for which he had earlier established *Radiella* Schmidt, 1870 (for more details on the taxonomic history of *Radiella* see Discussion on the genus *Spinularia* below). Consequently, *Trichostemma* was regarded as a synonym of *Radiella* (Schmidt, 1880). This was encouraged by Hansen (1885) and Burton (1930a, b, 1959a). However, all other

authors recognized *Trichostemma hemisphaericum* and *T. sol* as two different species, although they agreed that *Trichostemma* and *Radiella* were synonyms. Most authors encouraged the precedence of the former over the latter, referring to its first record in Sars (1869) (Whiteaves, 1874, 1901; Ridley & Dendy, 1886, 1887; von Lendenfeld, 1887; Lambe, 1896; Topsent, 1904, 1913, 1928; Lundbeck, 1909; Wilson, 1925; Boury-Esnault, 1987; Uriz & Rosell, 1990; Boury-Esnault et al., 1994). Conversely, Vacelet (1961) and Koltun (1964) considered *Radiella* as the senior synonym, while Vosmaer (1885), Levinsen (1887) and Rezvoj (1924) relegated *Trichostemma* to a synonym of *Polymastia* and Vosmaer (1887) and Koltun (1966) relegated both *Radiella* and *Trichostemma* to synonyms of *Polymastia*. Boury-Esnault (2002) recognized *Radiella* as a valid genus and the record of *Trichostemma* by Sars (1869) as *nomen nudum*, and hence acknowledged the synonymization of *Trichostemma* with *Radiella* based on the principle of priority (Article 23.1 in Anonymous, 1999). This decision was further encouraged by Plotkin (2004) and Plotkin et al. (2012).

However, very recently, Plotkin et al. (2016b) reconsidered the relationships between *Trichostemma*, *Radiella* and *Polymastia* based on genetic data. In the CO1 and 28S rDNA phylogenies *Trichostemma hemisphaericum* (referred to as *Radiella hemisphaerica* by Plotkin et al., 2016b) appeared in a strongly supported clade including the type species of *Polymastia*, *P. mamillaris*, and five other *Polymastia* spp. At the same time two species of *Radiella*, *R. sarsi* (Ridley & Dendy, 1886) and *Radiella* sp., fell in a remote clade (for details on the current status of *Radiella* see Discussion on the genus *Spinularia* below). Since *Polynastia* was an older name than *Trichostemma*, the latter was relegated to a synonym of the former (Plotkin et al., 2016b). This is followed in the present study.

Polymastia mamillaris (Müller, 1806) (Figure 10)

Original description: *Spongia mamillaris* Müller, 1806, p. 44.

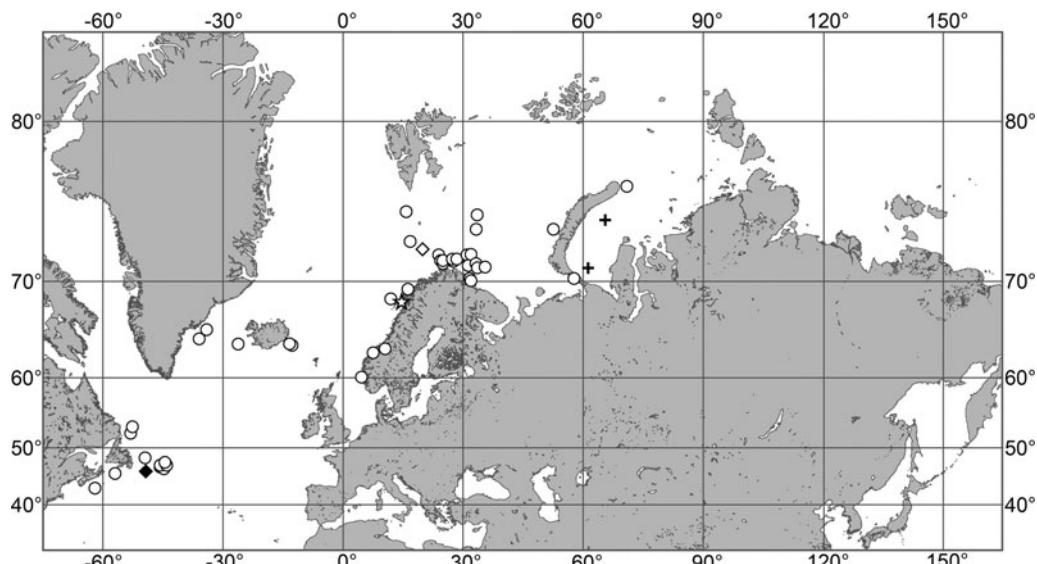


Fig. 9. *Polymastia hemisphaerica*, distribution: white star, type locality; black crosses, data from Rezvoj (1924); black diamond, data from Topsent (1892); white diamond, data from Topsent (1913); white circles, our data.

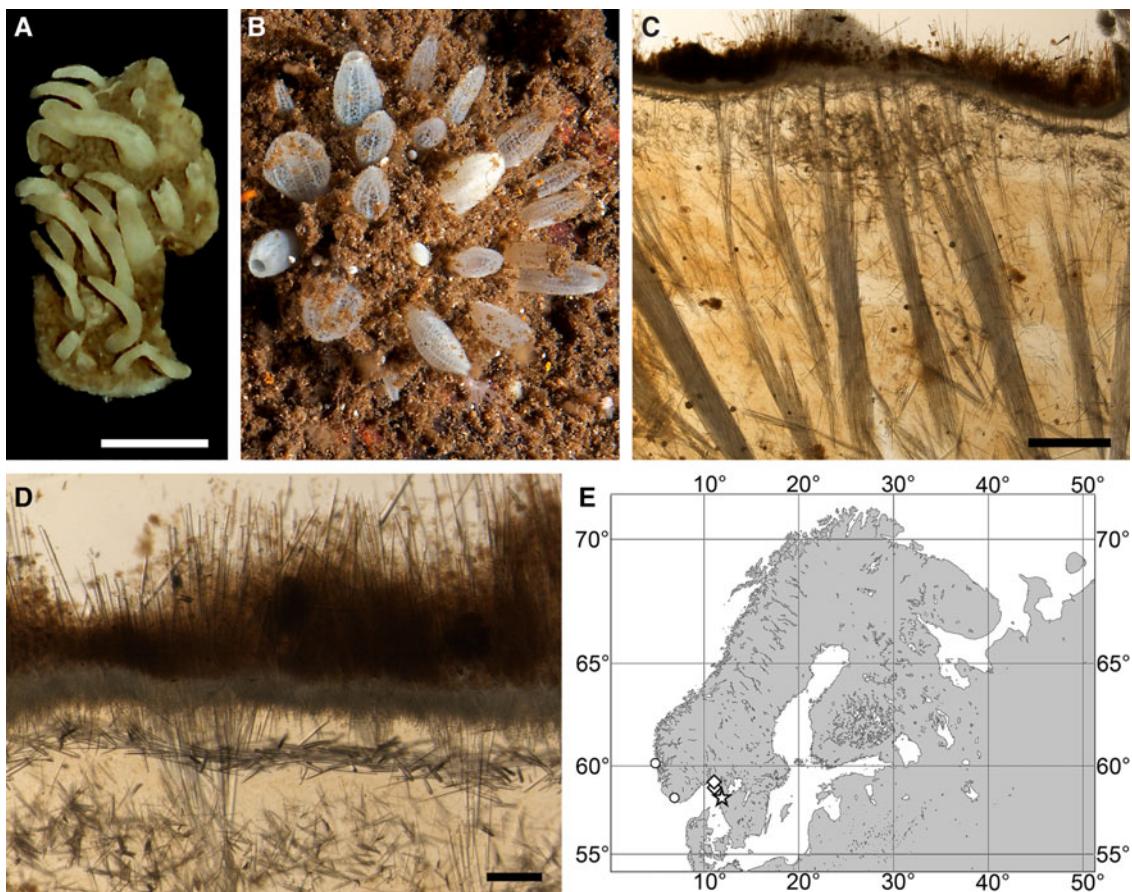


Fig. 10. *Polymastia mamillaris*: (A) holotype, ZMUC-DEM-394, habitus; (B) ZMBN 098083 *in situ*, Fedafjorden, Norway (courtesy of E. Svensen, OceanPhoto/Dalane Tidende AS, Egersund); (C) holotype, ZMUC-DEM-394, longitudinal section through the body, general view; (D) the same section, detail of upper cortex; (E) distribution: white star, type locality; white diamonds, data from Morrow & Boury-Esnault (2000); white circles, our data. Scale bars: A, 1 cm; C, 1 mm; D, 0.2 mm.

SYNONYMS AND CITATIONS

Pencillaria penicillus (Gray, 1867, p. 527 pars.).

Polymastia mamillaris (Fristedt, 1885, p. 15; Alander, 1942, p. 75; Morrow & Boury-Esnault, 2000, p. 329, figures 1 & 2D–F; Boury-Esnault, 2002, p. 203, figure 2; Plotkin *et al.*, 2012, p. 25, figure 11).

Non *Polymastia mamillaris* (Bowerbank, 1862, p. 1104, 1864, p. 178, 1866, p. 71; Vosmaer, 1885, p. 14, text-figure 5, pl. I figure 5, pl. III figures 10, 11–14, 21; Verrill, 1874, p. 505; Whiteaves, 1874, p. 184; Lambe, 1896, p. 196, pl. III figure 1; Whiteaves, 1901, p. 13; Arnesen, 1918, p. 8, pl. 1 figures 1–4, pl. 2 figures 1–5, pl. 3 figures 6–9, pl. 4 figures 1–2; pl. 5 figures 1–2, pl. 6 figures 1–4; Koltun, 1966, p. 69; Boury-Esnault, 1987, p. 32, figure 1; Ereskovsky, 1993a, p. 22; Plotkin & Ereskovsky, 1997, p. 127).

TYPE MATERIAL

Holotype (Figure 10A): ZMUC-DEM-394, East of Aspholmen in Byfjorden, Orust, Västra Götaland, Sweden, 58°15'N 11°50'E, depth unknown.

Detailed description of the holotype was presented by Morrow & Boury-Esnault (2000).

COMPARATIVE MATERIAL (see Online resource 1 for details)

Norway: Vest-Agder: ZMBN 098083 (one specimen), Hordaland: ZMBN 098078 (one specimen).

DESCRIPTION

External morphology

Cushion-shaped sponges covering the substrate and occupying up to 9 cm². Surface hispid, usually covered with sediment, with up to 30 papillae, 5–12 mm long and 2–5 mm wide at base (Figure 10A, B). In living sponges the papillae tapering towards the summits, some with visible oscula (Figure 10B). Colour of papillae whitish in life and cream-coloured in alcohol.

Anatomy

Choanosome in life cream-coloured, firm. Main choanosomal skeleton of radiating tracts (240–370 µm thick) of principal spicules dividing into two to three thinner tracts, which cross the cortex and form a surface hispidation (Figure 10C). Ascending tracts also form a framework of the papilla skeleton. Auxiliary choanosomal skeleton comprises free-scattered bundles, each of two to five small spicules, being especially abundant in the subcortical area. Cortex in life whitish, firm, not detachable. Cortical skeleton constituted by a superficial palisade (120–150 µm thick) of small spicules, a middle layer (65–105 µm thick) of collagen fibres with low density of spicules and an internal layer (85–155 µm thick) of

tangentially arranged intermediary spicules (Figure 10D). Skeleton of the papilla walls composed of two layers only, the superficial palisade and the internal tangential layer.

Spicules

(Measurements based on three specimens, individual variation presented in Table 3)

Principal spicules – straight strongyloxeas or straight, fusiform styles to subtylostyles. Length 603–1075–1761 µm, diameter of tyle (if present) 5.6–9.8–15.2 µm, proximal diameter of shaft 2.5–8.3–12.7 µm, maximum diameter of shaft 7.6–18.0–29.2 µm, N = 90.

Intermediary spicules – styles, occasionally subtylostyles, usually straight, slightly fusiform. Length 241–422–538 µm, diameter of tyle (if present) 5.1–7.4–10.2 µm, proximal diameter of shaft 2.5–6.1–8.9 µm, maximum diameter of shaft 6.4–8.9–14.0 µm, N = 90.

Small spicules – tylostyles, gently curved or straight, stout. Length 94–148–206 µm, diameter of tyle 3.8–6.0–10.2 µm, proximal diameter of shaft 1.3–3.8–8.9 µm, maximum diameter of shaft 2.5–6.3–11.4 µm, N = 90.

Genetic data

CO₁ sequences obtained from two individuals of *Polymastia mamillaris* are identical (Matrix M34248 in TreeBase), but these sponges are distinguished by one bp in 28S rDNA (Matrix M34250 in TreeBase). *Polymastia mamillaris* differs from all other polymastiids by five autapomorphies in CO₁ (Online resource 2, p. 1) and one autapomorphy in 28S rDNA (Online resource 3, p. 1). More details on the differences between *P. mamillaris* and other *Polymastia* spp. are presented in the Genetic data sections for these species.

OCCURRENCE

(Figure 10E)

Literature data: Swedish Western Coast: Skagerrak (76–225 m) (Morrow & Boury-Esnault, 2000).

Our data: Norwegian Coast: Vest-Agder (40–45 m), Hordaland (300–310 m).

DISCUSSION

Polymastia mamillaris has a very confused taxonomic history. This species was originally described from the Swedish Western Coast as *Spongia mamillaris* (Müller, 1806). Johnston, 1842 transferred it to *Halichondria* Fleming, 1828 and simultaneously relegated a British species *Spongia penicillus* Montagu, 1814 to a synonym of *H. mamillaris*. Bowerbank (1862) erected a new genus, *Polymastia*, for *H. mamillaris*. For unclear reason Gray (1867) erected another new genus, *Pencillaria*, for *Polymastia mamillaris*, but this was not acknowledged by the later authors. Vosmaer (1882) admitted that *Spongia mamillaris* and *S. penicillus* were the same species of *Polymastia*, but considered *penicillus* as the senior synonym for this species despite it having been described earlier than *mamillaris*. Moreover, in the same paper Vosmaer synonymized a White Sea species *Rinalda arctica* Merejkowsky, 1878 with *P. penicillus* and also placed in this species some Barents Sea sponges which were in fact distinguished from the original descriptions of *Spongia mamillaris*, *S. penicillus* and *R. arctica* by a radial growth type and a marginal spicule fringe (i.e. the evident features of the species now recognized as *P. grimaldii*, see the respective Description and Discussion above). Three years later (Vosmaer, 1885) he re-considered the synonymy by declaring *Polymastia mamillaris* the senior synonym. Fristedt (1885) recorded *P. mamillaris* along the Swedish Western Coast. Later (Fristedt, 1887) he identified as *P. penicillus* some sponges with the radial growth type and the marginal spicule fringe from Greenland, Svalbard and the Siberian Seas referring to Vosmaer (1882) and noted that *P. penicillus* (Montagu, 1814) *sensu* Vosmaer (1882) from the Arctic region and *Polymastia mamillaris* (Müller, 1806) from Sweden were different species. Levinsen (1887) recorded *P. penicillus* from the Kara Sea and agreed with Vosmaer (1882), although with some doubt, that *P. mamillaris* and *Rinalda arctica* were the synonyms of *P. penicillus*. Whiteaves (1874, 1901) and Lambe (1896) recorded *P. mamillaris* in the Canadian Atlantic. But de Laubenfels (1949) established a new species *P. andrica* for these Canadian sponges, although without good argumentation. Topsent (1913) erected a new species, *Trichostemma grimaldii*, for the Nordic *Polymastia*-looking

Table 3. Individual variation of spicule dimensions of *Polymastia mamillaris* (given in µm as minimum–mean–maximum). Parameters: length, diameter of tyle, proximal diameter of shaft, maximum diameter of shaft, number of spicules measured (N).

Specimen	Principal spicules	Intermediary spicules	Small spicules
Holotype ZMUC 2-1-93 (Swedish Coast, Skagerrak)	794–1097–1426 Tyles absent 6.4–9.5–12.7 22.9–26.0–29.2 N = 30	241–411–462 Tyles absent or weakly developed 3.8–7.0–8.9 6.4–9.9–14.0 N = 30	94–163–206 3.8–7.2–10.2 2.5–5.1–8.9 6.4–8.7–11.4 N = 30
ZMBN 98078 (Norwegian Coast, Vest-Agder)	1005–1309–1761 8.9–11.8–15.2 6.4–10.0–12.7 14–17.5–20.3 N = 30	377–445–503 6.4–7.9–10.2 5.1–6.6–8.9 7.6–9.5–12.7 N = 30	127–147–178 5.1–5.8–6.4 2.5–3.7–5.1 3.8–5.7–7.6 N = 30
ZMBN 98078 (Norwegian Coast, Hordaland)	603–820–1045 5.6–7.9–10.2 2.5–5.1–7.6 7.6–10.4–12.7 N = 30	251–411–538 5.1–6.9–8.9 2.5–4.6–6.4 6.4–7.2–10.2 N = 30	102–133–179 3.8–5–5.1 1.3–2.6–3.8 2.5–4.5–5.1 N = 30

sponges with the radial growth type and the marginal spicule fringe. But later (Topsent, 1927a) he transferred *grimaldii* to *Polymastia*. Hentschel (1916) described a new variety, *P. mamillaris* var. *hyperborea* from Svalbard, which in fact resembled *P. grimaldii*. Koltun (1966) relegated *grimaldii* to a subspecies of *P. mamillaris*. According to his extended definition *P. mamillaris* included three subspecies, *P. mamillaris mamillaris* comprising all sponges similar to *Spongia mamillaris* Müller, 1806 and *Rinalda arctica* Merejkowsky, 1878 from the North Atlantic, Nordic Seas and Arctic, *P. mamillaris grimaldii* comprising all sponges from the same regions, resembling *P. mamillaris mamillaris* by numerous papillae and architecture of the upper cortex, but differing by the radial growth type and the marginal spicule fringe, and *P. mamillaris rara* Koltun, 1966, a NW Pacific subspecies differing from *P. mamillaris mamillaris* by longer principal spicules.

Since Boury-Esnault (1987) *P. mamillaris* and *P. grimaldii* are, however, recognized as two separate species. Later, based on a careful comparison between the holotypes of *Spongia mamillaris* and *S. penicillus* and additional material Morrow & Boury-Esnault (2000) demonstrated that *P. mamillaris* and *P. penicillus* were different species too. According to this study most of the previous records of *P. mamillaris* from the British Isles, French, Spanish and Portuguese Coasts in fact represent *P. penicillus* characterized by a two-layered cortex and spicules in all size categories being tylostyles. *Polymastia mamillaris* distributed only along the

Swedish Coast is distinguished by a three-layered cortex (with a middle layer of collagen fibres), principal spicules being strongyloxeas and intermediary spicules being styles. Furthermore, Plotkin & Boury-Esnault (2004) proved that *Polymastia arctica* (originally placed in *Rinalda*) commonly synonymized either with *P. mamillaris* or with *P. penicillus* was actually a valid species distributed in the White and Barents Sea and distinguished by the bud formation on the papillae, relatively thick middle and intermediate layers in the cortex and the presence of spicules in the bulkheads separating canals in the papillae. Now we can finally confirm the morphological differences between *P. arctica*, *P. grimaldii*, *P. mamillaris* and *P. penicillus* by genetic evidence (Plotkin et al., 2016b; present study). Moreover, we have revealed that *P. andrica* erected by de Laubenfels (1949) for the Canadian records of *P. mamillaris* is a valid species distributed from Canada to the Norwegian Coast and Svalbard, differing from the similar *Polymastia* spp. by genetics and morphologically distinguished by the presence of extra-long cortical spicules (exotyles) (see the respective description above).

Polymastia nivea (Hansen, 1885)
(Figure 11)

Original description: *Reniera nivea* Hansen, 1885, p. 5, pl. I figure 6.

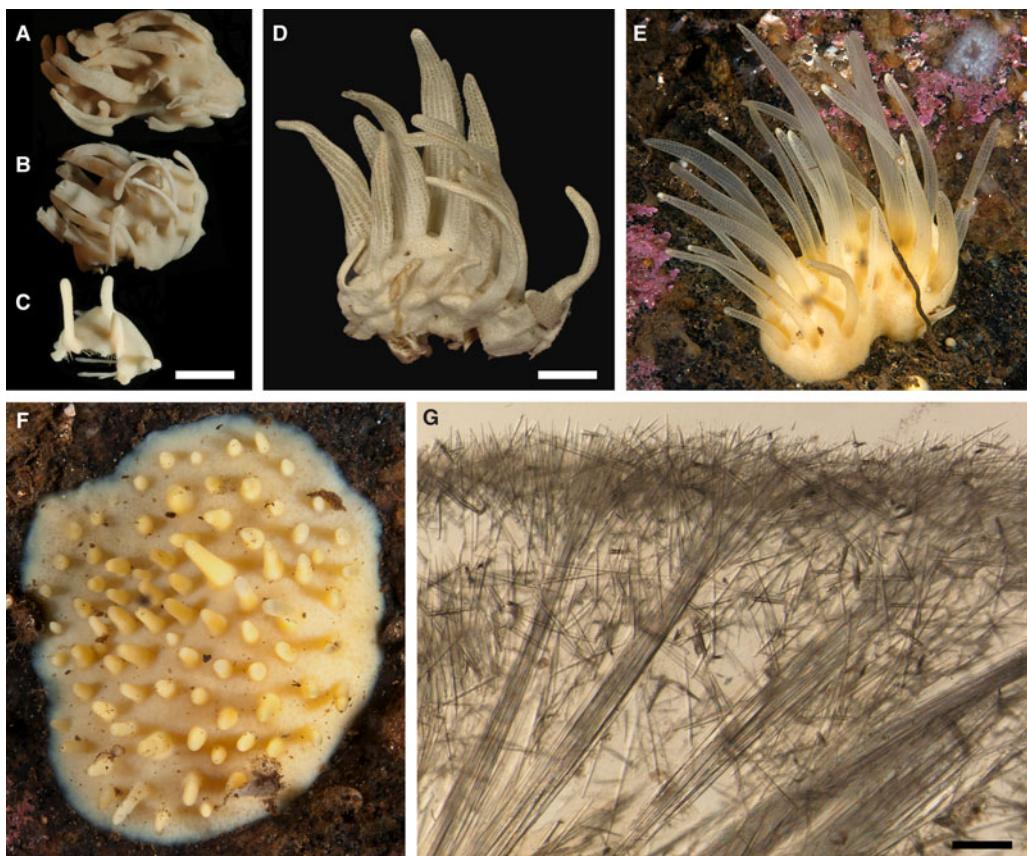


Fig. 11. *Polymastia nivea*: (A) lectotype of *Reniera nivea*, ZMBN 000055, habitus; (B) and (C) paralectotypes of *Reniera nivea*, ZMBN 000055, habitus; (D) holotype of *Polymastia euplectella* (synonym of *P. nivea*), ZIN RAS 7102/7103, habitus; (E) an individual *in situ*, Sor-Trøndelag, Norway (courtesy of E. Svensen, OceanPhoto/Dalane Tidende AS, Egersund); (F) an individual *in situ*, Fedafjorden, Norway (courtesy of E. Svensen); (G) lectotype of *Reniera nivea*, ZMBN 000055, longitudinal section through the body. Scale bars: A–D, 1 cm; G, 0.2 mm.

SYNONYMS AND CITATIONS

Polymastia euplectella Rezvoj, 1927, p. 301, figure a, b (Plotkin, 2004, p. 541, figures 1b & 2b; Plotkin et al., 2012, p. 25, figure 1k).

Polymastia robusta robusta (Koltun, 1966, p. 74, text-figure 44, pl. XXI figures 1–4).

TYPE MATERIAL

Lectotype (designated herein, Figure 11A) and two paralectotypes of *Reniera nivea* Hansen, 1885: ZMBN 000055, Norwegian Sea, precise locality and depth unknown, Norwegian North Atlantic Expedition, 1876–1878.

Holotype of *Polymastia euplectella* Rezvoj, 1927: ZIN RAS 7102/7103 (slide 125), Three Sisters Rocks, Kildin Strait, Murman Coast of the Barents Sea, Russia, 69°18.31'N 34°18.82'E, depth unknown, 31.07.1924. Herein *P. euplectella* is relegated to a synonym of *P. nivea*.

COMPARATIVE MATERIAL

(see Online resource 1 for details)

Norway: Vest-Agder: ZMBN 098085, ZMBN 098086 and ZMBN 098087 (three specimens), Hordaland: ZMBN 009667 (one specimen), Møre and Romsdal: ZMBN 107484 (one specimen), Sør-Trøndelag: NTNU-VM-54701 (one specimen), Nordland: NTNU-VM-55006, NTNU-VM-58254, NTNU-VM-72508, NTNU-VM-72514 (18 specimens), Finnmark: NTNU-VM-54880 and ZMBN 098044 (three specimens).

Barents Sea, offshore: ZIN RAS ocpeo14 (one specimen).

Russia: Murman coast: ZIN RAS ocpeo01, ZIN RAS ocpeo09, ZIN RAS ocpeo10, ZIN RAS ocpeo11, ZIN RAS ocpeo12, ZIN RAS ocpe12 and ZIN RAS ocpe15 (seven specimens), White Sea: ZIN RAS ocpeo02, ZIN RAS ocpeo04, ZIN RAS ocpeo05, ZIN RAS ocpeo06 and ZIN RAS ocpeo08 (12 specimens).

DESCRIPTION

External morphology

All type specimens of *Reniera nivea* cream-coloured in alcohol, with smooth surface bearing damaged cylindrical papillae (Figure 11A–C). Lectotype ~30 × 17 × 6 mm, with 19 papillae (Figure 11A). Larger paralectotype 24 × 18 × 5 mm, with 20 papillae (Figure 11B). Smaller lectotype is a small sponge fragment with five papillae (Figure 11C). Holotype of *Polymastia euplectella* ~30 × 12 × 5 mm (Figure 11D). Surface smooth, with 18 papillae, 10–40 mm long and 3–7 mm wide at base, gently pointed at the summits. Colour of both the surface and papillae whitish in alcohol. Papilla walls display a conspicuous tracery network of spicules.

Other sponges cushion-shaped, covering the substrate and occupying up to 20 cm². Surface smooth, free of sediment, with up to 30 papillae (Figure 11E, F). Colour of the surface in life pale orange or pale yellow, sometimes whitish, in alcohol always becoming whitish. Papillae of most living individuals cylindrical, 8–60 mm in length and 2–8 mm in diameter, semitransparent with well-visible spicule network, oscula not visible (Figure 11E). Some sponges with much smaller (2–6 mm in length and 1–4 mm in diameter) papillae of the same colouration as the surface (Figure 11F).

Anatomy

Choanosome dense. Main choanosomal skeleton composed of longitudinal or radial tracts (110–310 µm thick) of principal spicules (Figure 11G). Auxiliary choanosomal skeleton comprises small and intermediary spicules, most free-scattered, some in bundles of three to seven. Cortex 275–460 µm thick, dense, but friable, not detachable, with small aquiferous cavities connected with ostia in the surface. Cortical skeleton constituted by a superficial palisade of small spicules, which is overlapped with an inner layer of criss-cross intermediary spicules (Figure 11G). Papilla with a single central canal enveloped by a network made of the tracts of principal spicules

Table 4. Individual variation of spicule dimensions of *Polymastia nivea* (given in µm as minimum–mean–maximum). Parameters: length, diameter of style, proximal diameter of shaft, maximum diameter of shaft, number of spicules measured (N).

Specimen	Principal spicules	Intermediary spicules	Small spicules
Lectotype of <i>Reniera nivea</i> , ZMBN 00055 (Norwegian Sea)	967–1355–1686 Tyles absent or weakly developed 7.6–11.2–15.2 16.5–20.8–25.4 N = 30	342–484–719 5.1–12–17.8 3.8–8.6–11.4 10.2–17.5–21.6 N = 30	132–161–198 Tyles weakly developed 2.5–3.8–4.6 3.8–4.7–5.1 N = 30
Holotype of <i>Polymastia euplectella</i> , ZIN RAS 07102/07103 (Barents Sea, Murman Coast)	1087–1197–1370 Tyles absent 7.6–10.9–14.8 17.3–19.9–21.8 N = 30	498–634–771 4.5–11.6–18.2 4.0–9.2–12.0 9.4–14.8–18.4 N = 30	138–173–210 Tyles weakly developed 2.5–3.9–4.7 4.0–4.5–5.5 N = 30
ZMBN 98085 (Norwegian Coast, Vest-Agder)	573–916–1141 8.9–10.2–11.4 2.5–7–8.9 8.9–11.6–15.2 N = 30	271–408–598 7.6–9.7–12.7 5.1–6.6–8.9 7.6–9.9–15.2 N = 30	127–170–197 3.8–4.4–5.1 2.5–3.1–4.6 2.5–4.6–5.1 N = 30
ZMBN 98044 (Norwegian Coast, Finnmark)	930–1309–1513 Tyles absent 7.6–10.7–14 17.8–19.7–21.6 N = 30	296–410–563 11.4–14.2–16.5 7.6–10.3–12.7 12.7–17.3–20.3 N = 30	114–161–231 5.1–6.1–7.6 2–3.6–5.1 3–5–7.6 N = 30

ascending from the choanosome crossed by bundles of intermediary spicules from the outside. Superficial layer of small spicules covers this network.

Spicules

(Measurements based on four specimens, individual variation presented in Table 4)

Principal spicules – strongyloxeas (ZMBN 000055), slender styles to subtylostyles (ZIN RAS 07102/07103, ZMBN 098044), or fusiform subtylostyles with displaced tyles (ZMBN 098085), usually straight, occasionally gently curved. Length 573–1194–1686 µm, diameter of tyle (if present) 8.9–10.2–11.4 µm, proximal diameter of shaft 2.5–9.6–15.2 µm, maximum diameter of shaft 8.9–17.4–25.4 µm, N = 120.

Intermediary spicules – gently curved tylostyles, usually stout or slightly fusiform (most sponges), occasionally slenderer (ZMBN 098085). Length 271–434–771 µm, diameter of tyle (if present) 5.1–11.9–18.2 µm, proximal diameter of shaft 3.8–8.4–12.7 µm, maximum diameter of shaft 7.6–14.7–21.6 µm, N = 120.

Small spicules – subtylostyles with weakly developed tyles, usually curved and slender. Length 114–164–231 µm, diameter of tyle 3.8–5.2–7.6 µm, proximal diameter of shaft 2.0–3.5–5.1 µm, maximum diameter of shaft 2.5–4.8–7.6 µm, N = 120.

Genetic data

CO1 was obtained from four individuals of *Polymastia nivea*, 28S rDNA was sequenced from three of them and no intraspecific polymorphism was revealed. In the phylogenies based on these genes *P. nivea* is closely related to *P. penicillus* (Plotkin et al., 2016b), although these species share just two synapomorphies in 28S rDNA distinguishing them from other polymastiids (Online resource 3, p. 3) and no such synapomorphies in CO1. At the same time *P. nivea* possesses one autapomorphy in CO1 (Online resource 2, p. 3) and four autapomorphies in 28S rDNA (Online resource 3, p. 3). Apart from these autapomorphies, *P. nivea* differs from *P. penicillus* by 6 bps in CO1 (Matrix M34248 in TreeBase) and 19 bps in 28S rDNA (Matrix M34250 in TreeBase) and from the type species of *Polymastia*, *P. mamillaris*, by 56 bps in CO1 (Matrix M34248 in TreeBase) and 85 bps in 28S rDNA (Matrix M34250 in TreeBase).

OCCURRENCE

(Figure 12)

Our data: Norwegian Coast: Vest-Agder (40–45 m), Hordaland (75 m), Møre and Romsdal (70–130 m), Sør-Trøndelag (100–300 m), Nordland (80–360 m), Finnmark (250–284 m). Barents Sea: Murman Coast (9–127 m), offshore areas (122 m). White Sea (10–78 m).

DISCUSSION

Describing his new species, *Reniera nivea* from the Norwegian Sea, Hansen (1885, p. 5) apparently confused individuals with quite different morphology, pyriform sponges ('isolated individuals' in his interpretation, depicted in pl. I figure 6a in his paper) and encrusting sponges with papillae ('collections of individuals on plates' depicted in pl. I figure 6b). Burton (1930a) synonymized Hansen's sponges bearing papillae with *Polymastia robusta* and pyriform sponges with *Quasillina brevis*. Later *P. robusta* was synonymized with

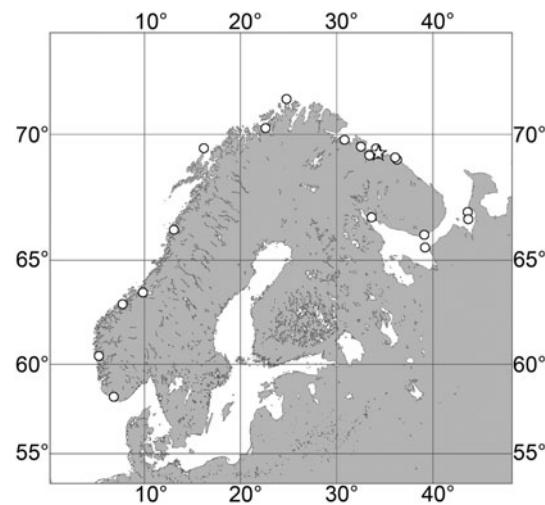


Fig. 12. *Polymastia nivea*, distribution: white star, type locality of *Polymastia euplectella* (synonym of *P. nivea*); white circles, our data. Precise type locality of *Reniera nivea* is unknown.

P. boletiformis (Topsent, 1933; see also Discussion on the latter species above in the present paper). Meanwhile, a new species *P. euplectella* strongly resembling Hansen's sponges with papillae was described from the Barents Sea by Rezvoj (1927). Koltun (1966) relegated *P. euplectella* to a synonym of *P. robusta*, but Plotkin (2004) resurrected the status of *P. euplectella*. Based on the re-examination of the type material of both *P. euplectella* and *R. nivea* (except for Hansen's pyriform sponges which are considered as lost) we can conclude that they belong to the same species, which gets the name *Polymastia nivea* in accordance with the principle of priority (Anonymous, 1999). This species is distinguished from *P. boletiformis* by its pale colouration, longer papillae, all without visible oscula, longitudinal choanosomal skeleton, overlapping spicule layers in the cortex and the presence of three spicule categories. Meanwhile, *P. nivea* is morphologically very similar to *P. bartletti* (see the description of the latter above). Genetic data clearly indicate that *P. bartletti*, *P. boletiformis* and *P. nivea* are three separate species (Plotkin et al., 2016b).

Polymastia penicillus (Montagu, 1814) (Figure 13)

Original description: *Spongia penicillus* Montagu, 1814, p. 93, pl. XIII figure 7.

SYNONYMS AND CITATIONS

Halichondria mamillaris (Jonhston, 1942, p. 142, pl. XVI figure 2).

Pencillaria mamillaris (Gray, 1867, p. 527).

Polymastia mamillaris (Bowerbank, 1862, p. 1104, 1864, p. 178, 1866, p. 71; Boury-Esnault, 1987, p. 32, figure 1).

Polymastia penicillus (Morrow & Boury-Esnault, 2000, p. 330, figures 2A–C & 3).

Non *Polymastia penicillus* (Vosmaer, 1882, p. 26, pl. I figures 12 & 13, pl. IV figure 127–132; Hansen, 1885, p. 9; Fristedt, 1887, p. 434; Levinson, 1887, p. 346; Swarczewsky, 1906, p. 313, pl. 13 figure 1).

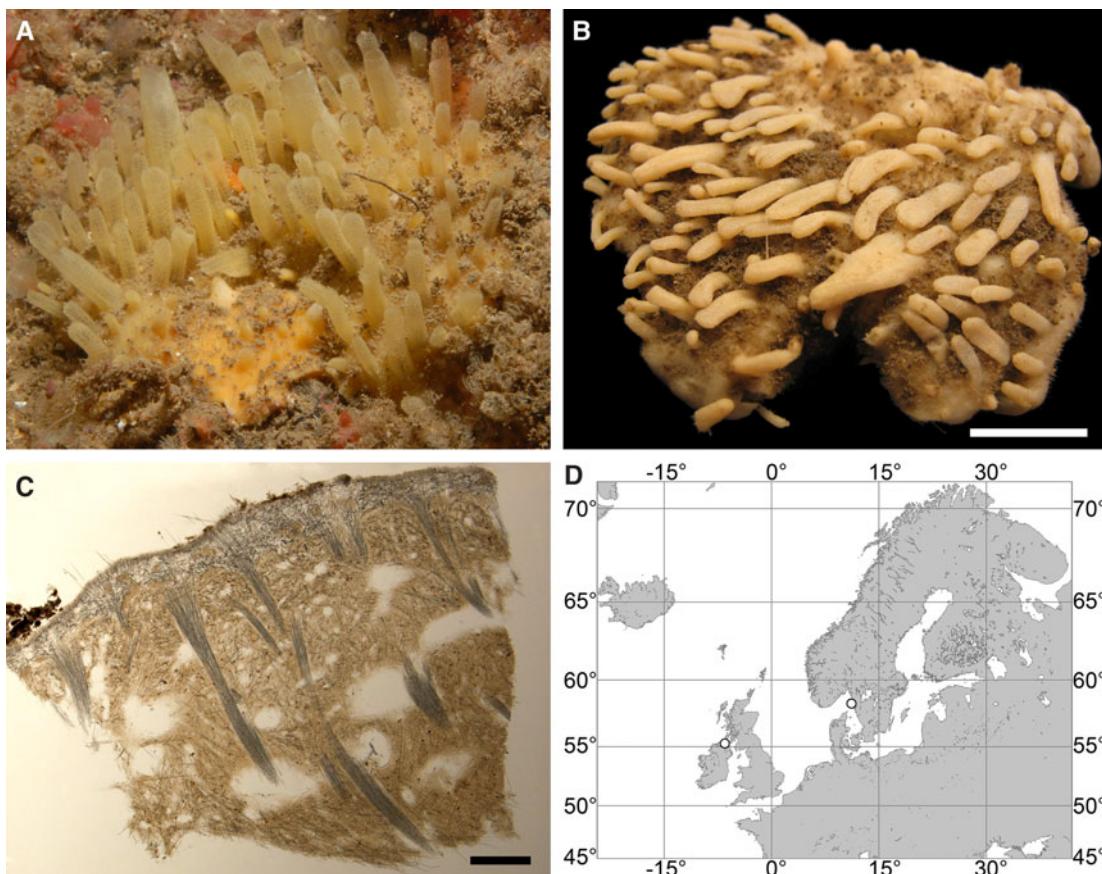


Fig. 13. *Polymastia penicilllus*: (A) BELUM MC6505 *in situ*, North Channel, Irish Coast (courtesy of B.E. Picton, Ulster Museum, Belfast); (B) the same individual in preserved state; (C), the same individual, longitudinal section through the body; (D) distribution of the individuals studied; for other documented localities see Boury-Esnault (1987; as *P. mamillaris*). Scale bars: B, 1 cm; C, 1 mm.

TYPE MATERIAL

Holotype: BMNH 1930.7.3.26, Devon Coast, England, precise locality and depth unknown.

Detailed description of the holotype was presented by Morrow & Boury-Esnault (2000).

COMPARATIVE MATERIAL

(see Online resource 1 for details)

Northern Ireland, Co Antrim, North Channel: BELUM MC6505 (one specimen).

Sweden: Västra Götaland, Skagerrak: GNM 460:1 and GNM 460:2 (two specimens).

DESCRIPTION

External morphology

Cushion-shaped sponges up to 10 mm thick, covering the substrate and occupying up to 300 cm² (Figure 13A, B). Surface velvety rather than hispid, with up to 200 papillae, of which several (one to five depending on sponge size) with visible oscula at the summits. In life the surface dirty grey to yellow or pale orange. The papillae cream-coloured to pale yellow, up to 12 mm in length and 5 mm in diameter, cylindrical or gently tapering towards the summits (Figure 13A). Under sampling the papillae contract and the oscula close (Figure 13B). Sponges usually buried in sediment with only the papillae protruding outwards.

Anatomy

Choanosome in alcohol firm, cream-coloured. Main choanosomal skeleton composed of longitudinal or radial tracts (125–360 µm thick) of principal spicules fanning under the cortex, crossing the cortex and forming a fine surface hispitation (Figure 13C). Auxiliary choanosomal skeleton comprises free-scattered intermediary spicules. Cortex in alcohol whitish, firm, not detachable. Cortical skeleton constituted by a superficial palisade (110–140 µm thick) of small spicules and an internal layer (350–500 µm thick) of tangentially arranged intermediary spicules (Figure 13C). Skeleton of the papilla walls is a framework of the tracts ascending from the choanosome and covered with the cortical layers.

Spicules

(Measurements based on four specimens)

Principal spicules – tylostyles (holotype and the Irish individual) or styles to subtylostyles with weakly developed, displaced tyles (Swedish sponges), usually straight and fusiform. Length 603–959–1490 µm, proximal diameter of shaft 2.5–8.3–12.7 µm, maximum diameter of shaft 7.6–12.3–20.3 µm, N = 120.

Intermediary spicules – tylostyles, occasionally subtylostyles with weakly developed tyles, gently curved or straight, usually slender, occasionally fusiform. Length 300–478–710 µm, diameter of tyle 5.1–8.0–10.2 µm, proximal diameter of shaft 2.5–6.4–8.9 µm, maximum diameter of shaft 5.1–10.0–15.2 µm, N = 120.

Small spicules – tylostyles, gently curved, slender or slightly fusiform. Length 79–155–201 µm, diameter of tyle 3.8–4.7–6.4 µm, proximal diameter of shaft 1.5–3.0–5.1 µm, maximum diameter of shaft 1.5–3.3–6.4 µm, N = 120.

Genetic data

28S rDNA sequences obtained from three individuals of *Polymastia penicillus*, two from Sweden and one from Northern Ireland, are identical. CO1 was obtained only from the Irish sponge, and this sequence is identical to the CO1 sequence from a Portuguese *P. penicillus* (GenBank accessions KF225486 and KF225487, Plotkin et al., 2013). In both 28S rDNA and CO1 phylogenies *P. penicillus* is related to *P. nivea* (Plotkin et al., 2016b), although these species share just two synapomorphies and display many differences (for details see the Genetic data section for *P. nivea* above). *Polymastia penicillus* is distinguished from all other polymastiids by two autapomorphies in 28S rDNA (Online resource 3, p. 3). Apart from them, *P. penicillus* differs from the type species of *Polymastia*, *P. mamillaris*, by 51 bps in CO1 (Matrix M34248 in TreeBase) and 82 bps in 28S rDNA (Matrix M34250 in TreeBase).

OCCURRENCE

Literature data: Portuguese, Spanish and French Atlantic Coast, Mediterranean Sea, English Channel, British Isles (as *Polymastia mamillaris* – Boury-Esnault, 1987; as *P. penicillus* – Van Soest et al., 2000, 2016). Depth – 0–600 m (Boury-Esnault, 1987). Records of *Polymastia penicillus* from the deep-sea, 2500 m near Jan Mayen and 1267 m near Newfoundland (Boury-Esnault, 1987) most likely represent other species.

Our data (Figure 13D): North Channel between Ireland and Great Britain: Irish Coast (depth unknown). Skagerrak: Swedish Western Coast (23–44 m).

DISCUSSION

Polymastia penicillus was for a long time confused with the sympatric species *P. mamillaris* (Johnston, 1842; Bowerbank, 1862; Gray, 1867; Vosmaer, 1885; Boury-Esnault, 1987) and *P. grimaldii* (Vosmaer, 1882; Fristedt, 1887; Levinsen, 1887) until Morrow & Boury-Esnault (2000) demonstrated that these three were separate species (see the detailed taxonomic history in Discussion on *P. mamillaris* above), that is now confirmed by genetic data (Plotkin et al., 2016b; present study). Morphologically *P. penicillus* is distinguished by a surface smoother than in *P. mamillaris* and *P. grimaldii* and by a two-layered cortex against the three-layered cortex in the latter two species. At the same time *P. penicillus* and *P. mamillaris* share the encrusting growth pattern and the presence of just three spicule categories that differentiate them from *P. grimaldii*. Minor differences between *P. penicillus* and *P. mamillaris* in spicule shape emphasized by Morrow & Boury-Esnault (2000) appear to be unstable.

Polymastia svenseni sp. nov.
(Figure 14)

TYPE MATERIAL

Holotype: ZMBN 098092, Ramsvik in Stavanger, Rogaland, Norway, 58°57.404'N 05°45.796'E, 25–18 m, coll. Plotkin and Svensen, 02.09.2012.

Paratype: ZMBN 098091, from the same sample as the holotype.

COMPARATIVE MATERIAL

ZMBN 107558, from the same sample as the holotype.

ETYMOLOGY

Named after Erling Svensen, a Norwegian underwater photographer, who has discovered a large population of this species in Stavanger.

DESCRIPTION

External morphology

Both holotype and paratype cushion-shaped, removed from a rock cliff. Surface, for the most part, smooth, cream-coloured in alcohol, with sparse rests of sediment and papillae, which may be conical tapering towards the summits, cylindrical or leaf-shaped expanding towards the summits. Holotype 105 × 52 × 13 mm, with 157 papillae 2–13 mm long and 1.5–5.5 mm (Figure 14A). Paratype 67 × 44 × 12 mm, with 76 papillae 2–15 mm long and 1.4–6.7 mm wide. Other sponges cushion-shaped, occupying up to 250 cm² of the substrate (Figure 14B). Surface cream-coloured or whitish in life, smooth, partly covered with sediment, with up to 400 papillae tapering towards the summits. Few papillae with visible oscula at the summits.

Anatomy

Choanosome in life pale orange or yellowish, firm. Main choanosomal skeleton composed of tracts (112–321 µm thick) of large spicules radiating from the base and ending in the cortex (Figure 14C). Ascending tracts also form a framework of the papilla skeleton. Auxiliary choanosomal skeleton comprises free-scattered large and small spicules. Cortex in life whitish, firm, not detachable. Cortical skeleton constituted by a superficial palisade (220–240 µm thick) of small spicules, a middle layer (130–150 µm thick) and an internal layer (100–125 µm thick), both composed of criss-cross large spicules lying loosely in the middle layer and much more condensed in the internal layer (Figure 14C). Skeleton of the papilla walls composed of two cortical layers, the superficial palisade and the internal layer.

Spicules

(Measurements based on three specimens, individual variation presented in Table 5)

Large spicules – mainly styles (Figure 14D–F), occasionally subtylostyles with weakly developed and displaced tyles (Figure 14G–I), usually straight, sometimes gently curved, fusiform to a greater or lesser extent. Length 312–658–1364 µm, diameter of tyle (if present) 3.0–7.8–14.0 µm, proximal diameter of shaft 2.5–6.8–11.4 µm, maximum diameter of shaft 3.8–10.9–16.5 µm, N = 187. The large spicules vary greatly in size, both in the cortex and choanosome, but the frequency distribution of their dimensions exhibits just one peak and hence they cannot be divided into two size categories.

Small spicules – tylostyles, usually gently curved, slender (Figure 14J–O). Length 132–175–225 µm, diameter of tyle 3.6–4.7–5.1 µm, proximal diameter of shaft 2.0–2.8–3.8 µm, maximum diameter of shaft 2.5–3.7–5.1 µm, N = 90.

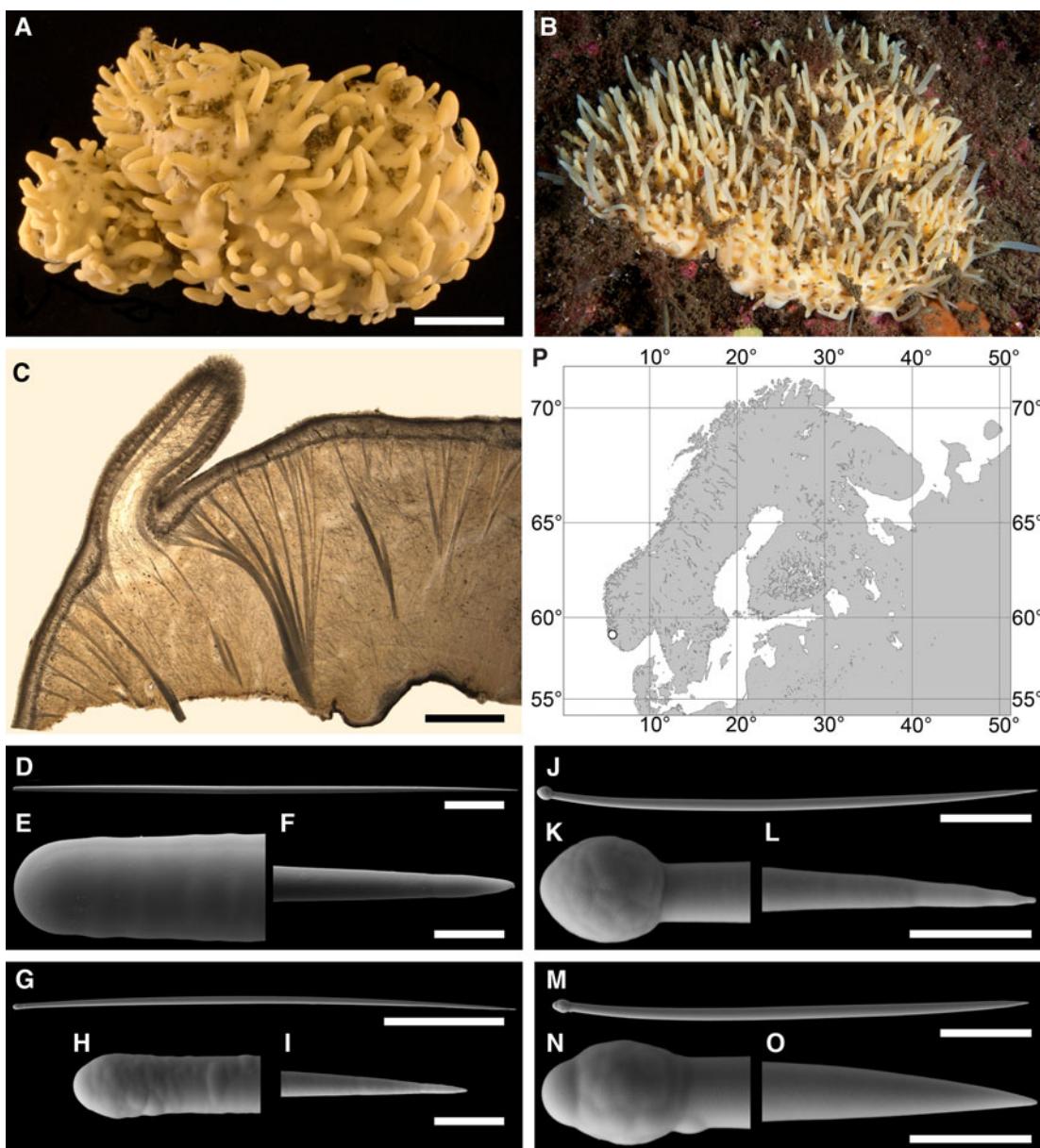


Fig. 14. *Polymastia svenseni*: (A) holotype ZMBN 098092, habitus; (B) an individual *in situ*, Ramsvik, Stavanger, Norway (courtesy of E. Svensen, OceanPhoto/Dalane Tidende AS, Egersund); (C) holotype ZMBN 098092, longitudinal section through the body; (D) – (O) spicules of the holotype: (D) large style, general view; (E) the same style, detailed view of the proximal tip; (F) the same style, detailed view of the distal tip; (G) large subtylostyle, general view; (H) the same subtylostyle, detailed view of the proximal tip; (I) the same subtylostyle, detailed view of the distal tip; (J) small tylostyle with terminal tyle, general view; (K) the same tylostyle, detailed view of the tyle; (L) the same tylostyle, detailed view of the distal tip; (M) small tylostyle with displaced tyle, general view; (N) the same tylostyle, detailed view of the distal tip; (P), type locality (white circle). Scale bars: A, 2 cm; C, 2 mm; D, 0.1 mm; E and F, 0.005 mm; G, 0.1 mm; H and I, 0.005 mm; J, 0.03 mm; K and L, 0.005 mm; M, 0.03 mm; N and O, 0.005 mm.

Genetic data

CO1 and 28S rDNA obtained from two individuals of *Polymastia svenseni* display no intraspecific polymorphism. B10–C1 region of 28S rDNA sequenced by Morrow *et al.* (2012) from an unidentified Irish *Polymastia* sp. (GenBank accession KF017187) is identical to the corresponding gene fragment of *P. svenseni* (about 1/3 length of our sequences). By both CO1 and 28S rDNA *P. svenseni* is closely related to a Norwegian *Polymastia* sp. described below, and by CO1 alone these two are closely related to an unidentified Canadian *Polymastia* (Plotkin *et al.*, 2016b), for which no 28S rDNA is available and which is not covered by the present study. These sponges share nine synapomorphies in

CO1 (Online resource 2, p. 3, Matrix M34248 in TreeBase). *Polymastia svenseni* and the Norwegian *Polymastia* sp. also share two synapomorphies in 28S rDNA distinguishing these taxa from all other polymastiids (Online resource 3, p. 3). At the same time *P. svenseni* is distinguished by two autapomorphies in 28S rDNA (Online resource 3, p. 3). Apart from these autapomorphies, it differs from the Norwegian *Polymastia* sp. by 21 bps in CO1 (Matrix M34248 in TreeBase), from the Canadian *Polymastia* sp. by 17 bps in CO1 (Matrix M34248 in TreeBase), and from the type species of *Polymastia*, *P. mamillaris*, by 65 bps in CO1 (Matrix M34248 in TreeBase) and 21 bps in 28S rDNA (Matrix M34250 in TreeBase). In the CO1 phylogeny the

Table 5. Individual variation of spicule dimensions of *Polymastia svenseni* (given in μm as minimum–mean–maximum). Parameters: length, diameter of tyle, proximal diameter of shaft, maximum diameter of shaft, number of spicules measured (N).

Specimen	Principal spicules	Small spicules
Holotype ZMBN 98092	312–632–965 3.8–7.4–12.7 2.5–6.6–10.2 5.1–10.5–16.5 N = 63	135–177–224 3.8–4.7–5.1 2.5–3.0–3.8 2.5–3.7–4.6 N = 30
Paratype ZMBN 98091	322–694–1364 3.0–7.7–11.4 2.5–6.9–10.7 3.8–11.3–15.2 N = 64	137–174–225 3.6–4.5–5.1 2.0–2.7–3.8 2.5–3.3–4.6 N = 30
ZMBN 107558	372–645–930 6.4–8.3–14 3.8–6.8–11.4 6.4–10.3–15.2 N = 60	132–175–203 3.8–5–5.1 2.5–2.8–3.8 3.8–4.1–5.1 N = 30

trio *Polymastia svenseni* + Norwegian *Polymastia* sp. + Canadian *Polymastia* sp. is the sister to the clade of seven other *Polymastia* spp. including *P. mamillaris*, although with a weak Bayesian support (Plotkin et al., 2016b). In the 28S rDNA phylogeny the pair *Polymastia svenseni* + Norwegian

Polymastia sp. is the sister to the same clade with a high support (the same study).

OCCURRENCE

Literature data: Ireland (Morrow et al., 2012: the record based only on the genetic data).

Our data (Figure 14P): Norwegian Coast: Rogaland (18–25 m).

DISCUSSION

Polymastia svenseni is established as a new species of *Polymastia* primarily based on the CO1 and 28S rDNA phylogenies and on its autapomorphies in the latter gene. However, no morphological autapomorphies distinguishing this species from other *Polymastia* spp. are revealed. *Polymastia svenseni* resembles *P. boletiformis* by the smooth surface and the presence of only two categories of spicules. On the contrary, by its radial main choanosomal skeleton and three-layered cortex *P. svenseni* resembles *P. andrica*, *P. arctica*, *P. grimaldii* and *P. mamillaris*.

Polymastia thielei Koltun, 1964 (Figure 15)

Original description: *Polymastia thielei* Koltun, 1964, p. 149, figure 4.

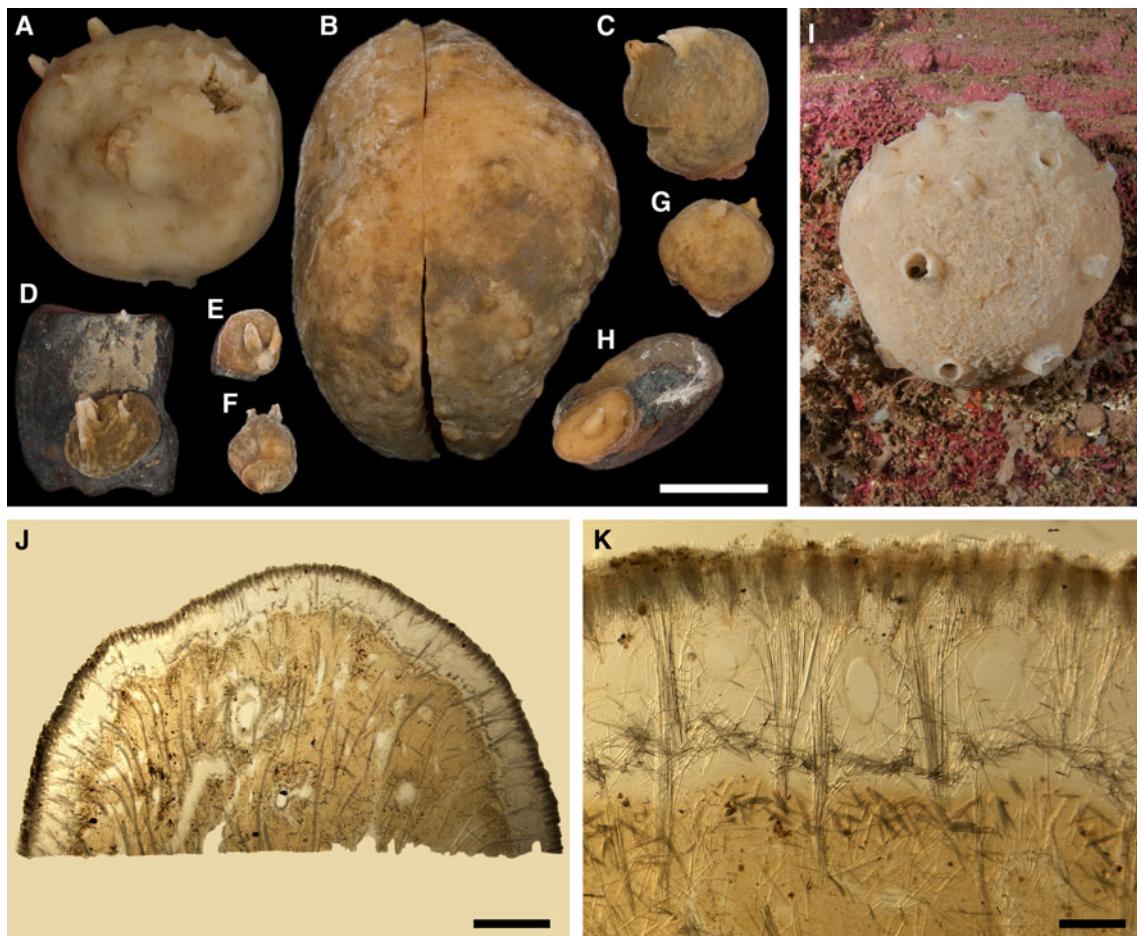


Fig. 15. *Polymastia thielei*: (A) lectotype ZIN RAS 10640, habitus; (B) paralectotype ZIN RAS 10638, habitus; (C)–(H) paralectotypes ZIN RAS 10639, habitus; (I) an individual *in situ*, Hinlopenstretet, Svalbard, Norway (courtesy P. Leopold, University of Tromsø); (J) ZMBN 98070, longitudinal section through the body, general view; (K) the same section, detail of cortex and subcortical area. Scale bars: A–H, 2 cm; J, 3 mm, K, 0.5 mm.

SYNONYMS AND CITATIONS

Polymastia thielei (Koltun, 1966, p. 76, text-figures 47–48, pl. XXVII figures 1–5; Plotkin, 2004, p. 541, figures 1c & 2c).
Polymastia uberrima (Lundbeck, 1909, p. 450, pl. XIV figure 4; Topsent, 1913, p. 18, pl. II figure 5; Burton, 1959a: 12 pars.; Boury-Esnault, 1987, p. 48, figure 10).
Rinalda uberrima (Hansen, 1885, p. 8, pl. VI figure 18; Thiele, 1903, p. 376, figure 2).

TYPE MATERIAL

Lectotype (designated herein, see figure 1c in Plotkin, 2004 and Figure 15A in the present study): ZIN RAS 10640 (slide 6153), Greenland Sea, 80°31'N 06°59'W, 259 m, RV 'Ob', station 33 28.08.1956, coll. Koltun.
Paralectotype: ZIN RAS 10638 (slide 6024), North-East off Franz Josef Land, Arctic Ocean, 81°52.5'N 60°32'E, 230–246 m, RV 'Litke', station 14, 15.09.1955, coll. Koltun.
Six paralectotypes: ZIN RAS 10639 (slide 6085), North-West off Franz Josef Land, Arctic Ocean, 82°00'N 42°00'E, 418–415 m, RV 'Litke', station 26, 18.09.1955, coll. Koltun.

COMPARATIVE MATERIAL

(see Online resource 1 for details)

Canada, Newfoundland: ZIN RAS ocpto17 (one specimen).
Denmark Strait: ZIN RAS ocpto30 and ZMBN 098107 (two specimens).
Iceland: ZIN RAS ocpto04 and ZMBN 098070 (two specimens).
Iceland Sea: ZIN RAS ocpto26 (one specimen).
Faroes: ZIN RAS ocpto13 (one specimen).
Norwegian Sea, offshore: MOM 04-0851 (identified as *Polymastia uberrima* by Topsent, 1913), NTNU-VM-54993, NTNU-VM-72524, ZMBN 098109, ZMBN 107580 and ZMBN 107581 (six specimens).
Barents Sea, offshore: ZIN RAS ocpto07, ZIN RAS ocpto09, ZIN RAS ocpto11, ZIN RAS ocpto14, ZIN RAS ocpto27 and ZIN RAS ocpto29 (six specimens).
Norway: Møre and Romsdal: NTNU-VM-54960, ZMBN 107495 and ZMBN 107496 (three specimens), Nord-Trøndelag: NTNU-VM-54884, NTNU-VM-54887, NTNU-VM-54888 and NTNU-VM-72537 (five specimens), Nordland: NTNU-VM-72519 and NTNU-VM-72540 (two specimens), Troms: ZIN RAS ocpto05 (one specimen), Finnmark: ZIN RAS ocpto01 (one specimen), Svalbard: ZIN RAS ocpto02, ZIN RAS ocpto28, ZMBN 098052 and ZMBN 098053 (four specimens).
Russia: Murman Coast: ZIN RAS ocpto06 (one specimen), Franz Josef Land: ZIN RAS ocpto22 (one specimen), Novaya Zemlya: ZIN RAS ocpto16 (one specimen), Taymyr Peninsula: ZIN RAS ocpto03, ZIN RAS ocpto21 and ZIN RAS ocpto25 (three specimens), Nordenskjold Archipelago: ZIN RAS ocpto20 (one specimen).
Kara Sea: ZIN RAS ocpto08, ZIN RAS ocpto12, ZIN RAS ocpto15, ZIN RAS ocpto18, ZIN RAS ocpto19, ZIN RAS ocpto23 and ZIN RAS ocpto24 (seven specimens).

DESCRIPTION

External morphology

Lectotype globular, about 50 mm in diameter, attached to small stones (Figure 15A). Surface velvety, pale beige with sparsely scattered small brown stains, bearing 18 papillae. The papillae crater-shaped (very short and wide) or conical,

1.5–5.5 mm long and 1.7–9.2 mm wide at base, most with well-visible oscula at the summits. Paratype ZIN RAS 10638 irregularly ovoid, 81 × 60 mm in diameter, split across, removed from the substrate (Figure 15B). Surface velvety, pale brown with darker stains, bearing 23 wart-like small papillae, the largest with oscula at the summits. Paratypes ZIN RAS 10639 are small, massive sponges on stones or removed from the substrates (Figure 15C–H). Surface, for the most part, velvety or knobby, porous in some individuals, brownish, with one or few conical or crater-shaped papillae, all with oscula at the summits. Some paratypes with minute hispidation around the base. Other sponges massive, fist-shaped, globular or ovoid, up to 250 mm in diameter (Figure 15I). Surface knobby, velvety or smooth, with well-visible ostia. Colour in life whitish, cream-coloured or beige, occasionally with large dark brown spots. In alcohol the colouration darkens and the ostia contract. Up to 30 papillae, all with oscula at the summits, crater-shaped in life and often stretching under sampling.

Anatomy

Choanosome pale brown to dark brown, both in life and in alcohol, somewhat loose, porous, with prominent meandering and anastomosing exhalant canals (up to 8 mm in diameter) running to the papillae. Main choanosomal skeleton composed of tracts (90–360 µm thick) of principal spicules radiating from the sponge base (Figure 15J). In the central part of the choanosome the tracts often meander and ramify, sometimes anastomose and form a network. Auxiliary choanosomal skeleton comprises small spicules, free-scattered or grouped in little bundles, especially abundant in a subcortical area (200–350 µm thick). Within the choanosome the walls of the exhalant canals paved with criss-cross small and intermediary spicules. Cortex in life cream-coloured, dense, but detachable. Cortical skeleton includes a superficial layer (340–650 µm thick) formed by bouquets of small spicules and an internal layer (150–250 µm thick) of criss-cross intermediary spicules (Figure 15K). A space (650–880 µm thick) between the spicule layers is occupied by oval aquiferous cavities (190–480 × 70–240 µm in diameter) connected with ostia which are located between the superficial spicule bouquets. Bulkheads between the aquiferous cavities reinforced with the ascending choanosomal tracts and criss-cross intermediary spicules. The papillae walls reinforced with the ascending choanosomal tracts and covered with the spicule cortical layers.

Spicules

(Measurements based on 10 specimens)

Principal spicules – styles to subtylostyles, usually straight and fusiform. Length 693–1277–1705 µm, proximal diameter of shaft 5.0–9.8–14.2 µm, maximum diameter of shaft 12.5–18.4–25.1 µm, N = 300.
Intermediary spicules – subtylostyles to tylostyles, straight or gently curved, fusiform. Length 445–539–648 µm, diameter of tyle 4.2–7.0–8.2 µm, proximal diameter of shaft 3.2–5.8–7.1 µm, maximum diameter of shaft 10.5–11.2–12.3 µm, N = 300.

Small spicules – tylostyles, gently curved, slender or slightly fusiform. Length 219–297–363 µm, diameter of tyle 3.8–5.5–7.4 µm, proximal diameter of shaft 1.7–3.8–5.7 µm, maximum diameter of shaft 4.1–6.8–9.3 µm, N = 300.

Genetic data

CO₁ sequences obtained from five individuals of *Polymastia thielei* are identical. 28S rDNA was obtained only from one of these sponges. By both genes *P. thielei* is closely related to morphologically quite different *P. hemisphaerica* (Plotkin et al., 2016b). The synapomorphies and differences between these species are described above in the Genetic data section for *P. hemisphaerica*.

OCCURRENCE

(Figure 16)

Our data (agree with the literature data): Canadian Atlantic Coast: Newfoundland (340–375 m). Denmark Strait (317–650 m). Iceland (165–318 m). Iceland Sea (1280 m). Faroes (350 m). Greenland Sea (259 m). Norwegian Coast: Møre and Romsdal: (120–200 m), Nord-Trøndelag: (28–400 m), Nordland: (200–800 m), Troms (280 m), Finnmark (275 m). Norwegian Sea, offshore areas (440–1580 m). Barents Sea: Murman Coast: (272 m), offshore areas: (165–365 m). Svalbard (40–820 m). Franz Josef Land: (122–246 m). Novaya Zemlya (293 m). Taymyr Peninsula (49–60 m). Nordenskjold Archipelago (75 m). Kara Sea (85–446 m). Arctic Ocean (415–418 m).

DISCUSSION

Before Koltun (1964) established *Polymastia thielei* the sponges with the characteristic features of this species had usually been identified as *P. uberrima* because of some external similarity between these species (e.g. Hansen, 1885; Thiele, 1903; Lundbeck, 1909; Topsent, 1913). *Polymastia thielei* also displays some similarities in body shape and architecture of the cortex with *Weberella bursa* (Müller, 1806). The main distinctive features of *P. thielei* are much smaller number of papillae and their conspicuous crater-like shape. *Weberella bursa* differs from both *P. thielei* and *P. uberrima* by the pale colouration of both the cortex and the choanosome, much thinner cortex, the reticulate choanosomal skeleton and the presence of just two size categories of spicules. *Polymastia uberrima* is distinguished by the presence of a

marginal hispid collar absent in both *P. thielei* and *W. bursa* and the regular radial choanosomal skeleton, while in *P. thielei* the choanosomal skeleton is less regular, with a tendency to meandering and anastomosing. The morphological differences between *P. thielei*, *P. uberrima* and *W. bursa* are clearly confirmed by the genetic data.

Polymastia uberrima (Schmidt, 1870) (Figure 17)

Original description: *Rinalda uberrima* Schmidt, 1870, p. 51, pl. VI figure 3.

SYNONYMS AND CITATIONS

Polymastia infrapilosa Topsent, 1927b, p. 4 (Topsent, 1928, p. 147, pl. II figures 25–26, pl. VI figure 3; Boury-Esnault, 1987, p. 40, figure 6).

Polymastia uberrima (Hentschel, 1929, p. 868 and 923; Arndt, 1935, p. 35 pars.; Gorbunov, 1946, p. 37; Burton, 1959a, p. 12 pars.; Koltun, 1966, p. 75, text-figure 46, pl. XXV figures 1–3; Plotkin, 2004, p. 542, figures 1d & 2d; Plotkin et al., 2012, p. 25, figure 1f).

Rinalda uberrima (? von Marenzeller, 1878, p. 369, pl. II figure 2).

Non *Polymastia uberrima* (Lundbeck, 1909, p. 450, pl. XIV figure 4; Topsent, 1913, p. 18, pl. II figure 5; Boury-Esnault, 1987, p. 48, figure 10).

Non *Rinalda uberrima* (Hansen, 1885, p. 8, pl. VI figure 18; Thiele, 1903, p. 376, figure 2).

TYPE MATERIAL

Holotype of *Polymastia uberrima* (Figure 17A): ZMUC-DEM-395, Iceland, precise locality unknown.

Lectotype (designated herein, Figure 17B, C) and two paralectotypes of *Polymastia infrapilosa* Topsent, 1927: MOM 04-1449, SE of Halifax, Nova Scotia, Canada, 44°10'N 62°27.5'W, 75 m, Scientific campaigns by Albert the 1st of Monaco, station 3425, 13.08.1913. Herein *P. infrapilosa* is

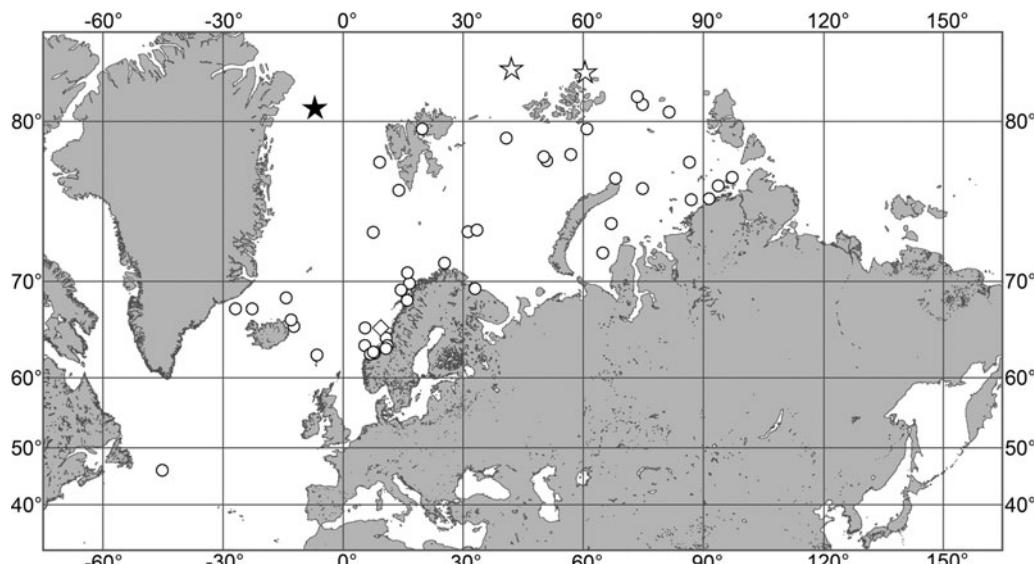


Fig. 16. *Polymastia thielei*, distribution: black star, locality of lectotype; white stars, localities of paralectotypes; white diamond, locality of MOM 04-0851 identified as *P. uberrima* by Topsent (1913) and re-identified as *P. thielei* herein; white circles, our data.

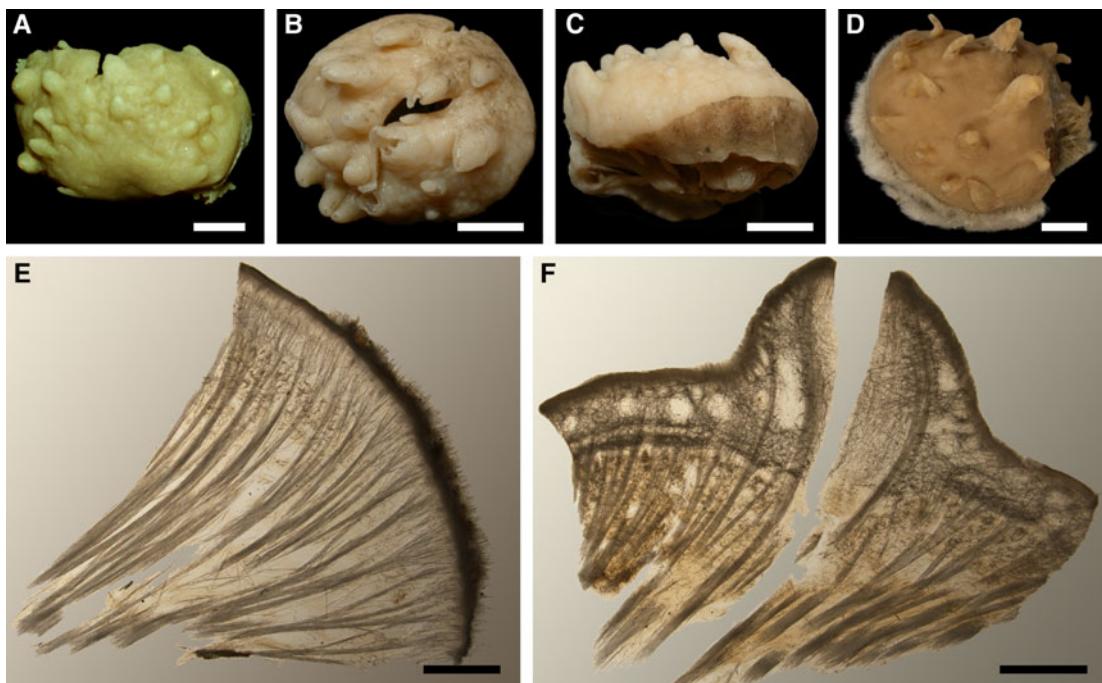


Fig. 17. *Polymastia uberrima*: (A) holotype of *Rinalda uberrima*, ZMUC-DEM-395, habitus; (B) lectotype of *Polymastia infrapilosa* (a synonym of *P. uberrima*), MOM 04-1449, habitus, view from above; (C) the same, side view; (D) ZIN RAS ocpuo05, habitus; (E) holotype of *Rinalda uberrima*, ZMUC-DEM-395, longitudinal section through the body, peripheral area; (F) the same individual, longitudinal section through a papilla and adjacent area. Scale bars: A–D, 1 cm; E, 3 mm; F, 2 mm.

relegated to a synonym of *P. uberrima* (see Discussion on this species below).

COMPARATIVE MATERIAL

(see Online resource 1 for details)

Canada: Nova Scotia: ZIN RAS ocpuo04, ZIN RAS ocpuo05 and ZIN RAS ocpuo94 (three specimens), Newfoundland: ZIN RAS ocpuo02, ZIN RAS ocpuo15, ZIN RAS ocpuo20, ZIN RAS ocpuo22, ZIN RAS ocpuo23, ZIN RAS ocpuo24, ZIN RAS ocpuo26, ZIN RAS ocpuo27, ZIN RAS ocpuo31, ZIN RAS ocpuo33, ZIN RAS ocpuo34, ZIN RAS ocpuo43, ZIN RAS ocpuo44 and ZIN RAS ocpuo45 (17 specimens), Labrador: ZIN RAS ocpuo03, ZIN RAS ocpuo16, ZIN RAS ocpuo17, ZIN RAS ocpuo21, ZIN RAS ocpuo25 and ZIN RAS ocpuo28 (six specimens), offshore areas of the NW Atlantic: ZIN RAS ocpuo46 (one specimen).

Greenland: SW Coast/Davis Strait: ZIN RAS ocpuo18, ZIN RAS ocpuo19, ZIN RAS ocpuo29 and ZIN RAS ocpuo32 (four specimens), SE Coast: ZIN RAS ocpuo42, ZIN RAS ocpuo49, ZIN RAS ocpuo97 and ZIN RAS ocpuo102 (four specimens).

Iceland: ZIN RAS ocpuo35, ZIN RAS ocpuo39, ZIN RAS ocpuo41, ZIN RAS ocpuo48 and ZIN RAS ocpuo50 (11 specimens).

North-East Atlantic, offshore: ZIN RAS ocpuo36, ZIN RAS ocpuo40, ZIN RAS ocpuo38 and ZIN RAS ocpuo96 (four specimens).

Norwegian Sea, offshore: ZIN RAS ocpuo06, ZIN RAS ocpuo07, ZIN RAS ocpuo08, ZIN RAS ocpuo09, ZIN RAS ocpuo10, ZIN RAS ocpuo13, ZIN RAS ocpuo99 and ZMBN 098066 (10 specimens).

Barents Sea, offshore: ZIN RAS ocpuo11, ZIN RAS ocpuo53, ZIN RAS ocpuo57, ZIN RAS ocpuo61, ZIN RAS ocpuo63, ZIN RAS ocpuo66, ZIN RAS ocpuo67, ZIN RAS ocpuo70,

ZIN RAS ocpuo73, ZIN RAS ocpuo80, ZIN RAS ocpuo81, ZIN RAS ocpuo82, ZIN RAS ocpuo85, ZIN RAS ocpuo100, ZIN RAS ocpuo101 and ZIN RAS ocpuo104 (21 specimens).

Norway: Nordland: NTNU-VM-55002, NTNU-VM-72520 and NTNU-VM-72534 (three specimens), Troms: NTNU-

VM-72530, ZMBN 098073, ZMBN 107574 and ZMBN

107575 (four specimens), Finnmark: NTNU-VM-72503,

NTNU-VM-72528, ZIN RAS ocpuo95 and ZMBN 107578 (five specimens), Svalbard: ZIN RAS ocpuo12 and ZIN RAS

ocpuo14 (three specimens).

Russia: Murman Coast: ZIN RAS ocpuo51, ZIN RAS ocpuo56,

ZIN RAS ocpuo62, ZIN RAS ocpuo64, ZIN RAS ocpuo71,

ZIN RAS ocpuo74, ZIN RAS ocpuo75, ZIN RAS ocpuo76,

ZIN RAS ocpuo77, ZIN RAS ocpuo83, ZIN RAS ocpuo84,

ZIN RAS ocpuo88, ZIN RAS ocpuo89, ZIN RAS ocpuo90,

ZIN RAS ocpuo91, ZIN RAS ocpuo92 and ZIN RAS

ocpuo103 (21 specimens), White Sea: ZIN RAS ocpuo72 (one

specimen), Franz Josef Land: ZIN RAS ocpuo107 (one speci-

men), Severnaya Zemlya: ZIN RAS ocpuo105 and ZIN RAS

ocpuo106 (two specimens).

Arctic Ocean, offshore: ZIN RAS ocpuo60 and ZIN RAS ocpuo98 (three specimens).

DESCRIPTION

External morphology

Holotype of *Rinalda uberrima* massive, ~46 × 27 × 29 mm, removed from the substrate (Figure 17A). Surface, for the most part, smooth, cream-coloured, with about 20 papillae and a minutely hispid greyish edging, 5–6 mm wide, on the undamaged side. Most papillae wart-like, weakly developed, but some conical, up to 5 mm long and 7 mm wide at base, with visible oscula at the summits. Lectotype and paralectotypes of *Polymastia infrapilosa* massive, removed from the substrates. Surface, for the most part, smooth, cream-

coloured, with a minute hispitation, 6–7 mm wide, along the undamaged edge and conical, occasionally cylindrical, papillae bearing oscula at the summits. Lectotype $\sim 42 \times 38 \times 21$ mm, split across, with 49 papillae, which are 2–12 mm long, 2–8 mm wide at base and 1–2 mm wide at summit (Figure 17B, C). Paralectotypes $\sim 36 \times 30 \times 16$ mm, with 23 papillae, and $37 \times 29.5 \times 10$ mm, with 30 papillae. The latter with several surface protuberances, each bearing one to three buds, 2–3 mm in diameter. Other sponges massive or globular, occupying up to 100 mm² of the substrate. Except for a marginal collar, the surface smooth or velvety, whitish in life, but often darkening in alcohol, with up to 150 conical or cylindrical papillae, in life all with visible oscula. The marginal collar is a rough, hispid or even shaggy area of various widths (Figure 17D).

Anatomy

Choanosome yellowish in life, but may become dark brown in alcohol, dense. Main choanosomal skeleton composed of tracts (207–571 µm thick) of principal spicules radiating from the sponge base and occasionally ramifying under the cortex (Figure 17E, F). Most tracts end in the cortex except for the marginal area where they protrude above the surface. Some tracts ascend to the papillae (Figure 17F). Auxiliary

choanosomal skeleton comprises small bundles of intermediary spicules, especially abundant in a subcortical area (423–1484 µm thick). Cortex in life cream-coloured, firm, not detachable. Cortical skeleton includes a superficial palisade (201–257 µm thick) of small spicules, a middle layer of loosely and confusedly lying bundles of intermediary spicules (672–1437 µm thick) and an internal layer (181–326 µm thick) with a high concentration of criss-cross intermediary spicules. In the areas under the papillae the middle layer contains aquiferous cavities connected with the surface ostia (Figure 17F). The papillae walls reinforced with the ascending choanosomal tracts and covered with the superficial palisade and internal cortical layer. Several exhalant and inhalant canals running into the papillae are separated by bulkheads reinforced with the ascending tracts and free-scattered intermediary spicules.

Spicules

(Measurements based on nine specimens, individual variation presented in Table 6)

Principal spicules – styles to subtylostyles, straight, fusiform. Length 715–1409–1889 µm, proximal diameter of shaft 7.9–13.1–17.2 µm, maximum diameter of shaft 10.7–23.1–30.4 µm, N = 270.

Table 6. Individual variation of spicule dimensions of *Polymastia uberrima* (given in µm as minimum–mean–maximum). Parameters: length, proximal diameter of shaft, maximum diameter of shaft, number of spicules measured (N).

Specimen	Principal spicules	Intermediary spicules	Small spicules
Holotype of <i>Rinalda uberrima</i> , ZMUC	1228–1415–1649 10.2–13.7–15.2 20.3–24.6–29.2 N = 30	422–549–633 6.4–7.6–11.4 10.2–12.6–16.5 N = 30	175–202–239 2.5–2.8–3.8 5.1–6.9–8.9 N = 30
Lectotype of <i>Polymastia infrapilosa</i> , MOM 04-1449a	1174–1609–1873 9.8–13.8–16.4 20.2–25.2–29.2 N = 30	441–552–690 6.4–8.9–12.2 8.2–11.4–15.1 N = 30	153–212–316 2.2–3.3–4.5 6.4–6.9–8.2 N = 30
Paralectotype of <i>Polymastia infrapilosa</i> , MOM 04-1449b	1219–1685–1889 10.1–14.1–17.2 20.2–25.4–30.2 N = 30	453–581–699 6.6–9.6–12.3 8.4–12.2–15.8 N = 30	157–225–298 2.3–3.3–4.2 6.1–7.0–7.9 N = 30
Paralectotype of <i>Polymastia infrapilosa</i> , MOM 04-1449c	1406–1630–1845 12.9–14.7–16.6 20.3–24.5–29.5 N = 30	438–563–706 6.4–9.3–12.5 8.2–11.8–16 N = 30	161–224–304 2.4–2.9–4.2 6.5–7.0–8.0 N = 30
ZIN RAS pu020 (Canada, Newfoundland)	1215–1607–1851 10.1–14.1–16.7 20.1–25.2–30.4 N = 30	381–538–686 5.8–8.7–11.9 7.2–11.4–15.4 N = 30	169–212–257 2.4–3–3.8 5.7–6.4–7.3 N = 30
ZIN RAS pu096 (Faroes)	1102–1414–1670 9.5–13–15.9 19.4–22.2–24.8 N = 30	458–582–654 6.5–9.4–11.6 8.4–11.7–14.4 N = 30	263–276–307 2.8–3.3–4.2 3.3–4.6–6.5 N = 30
ZMBN 098066 (Norwegian Sea)	973–1173–1611 9.4–12–15 17.7–20.3–23.4 N = 30	448–529–629 6.4–8.7–11.3 8.0–10.8–13.9 N = 30	167–225–293 2.5–3.2–4.0 3.7–4.7–6.0 N = 30
ZMBN 107578 (Norway, Finnmark)	792–1176–1581 8.2–11.2–14.7 11.7–17.2–23.7 N = 30	487–567–612 6.5–8.8–10.8 9.0–11.4–13.5 N = 30	208–270–311 2.4–3.5–4.3 3.8–5.1–6.2 N = 30
ZIN RAS pu051 (Barents Sea, Murman Coast)	715–1053–1446 7.9–10.4–13.8 10.7–16.4–22.5 N = 30	450–549–607 6.2–8.5–10.5 8.2–10.9–13.2 N = 30	282–307–327 2.8–3.7–4.4 4.4–5.3–6.7 N = 30

Intermediary spicules – styles to subtylostyles, occasionally tylostyles, straight or occasionally gently curved, fusiform. Length 381–550–706 µm, proximal diameter of shaft 5.8–8.5–12.5 µm, maximum diameter of shaft 7.2–11.8–16.5 µm, N = 270.

Small spicules – subtylostyles to tylostyles, gently curved or straight, fusiform. Length 153–218–327 µm, proximal diameter of shaft 2.2–3.1–4.5 µm, maximum diameter of shaft 3.3–6.4–8.9 µm, N = 270.

Genetic data

CO₁ sequences obtained from two individuals of *Polymastia uberrima* are identical, but these sponges differ by one bp in 28S rDNA (Matrix M34250 in TreeBase). In both CO₁ and 28S rDNA phylogenies *P. uberrima* falls in the clade with six other *Polymastia* spp. including the type species of this genus, *P. mamillaris* (Plotkin *et al.*, 2016b). However, *P. uberrima* does not have sister relation to any of these species. It is distinguished by two autapomorphies in CO₁ (Online resource 2, p. 2) and three autapomorphies in 28S rDNA (Online resource 3, p. 2) from all other polymastiids. Apart from these autapomorphies, *P. uberrima* differs from *P. mamillaris* by 31 bps in CO₁ (Matrix M34248 in TreeBase) and 15 bps in 28S rDNA (Matrix M34250 in TreeBase).

OCCURRENCE

(Figure 18)

Our data (agree with the literature data): Canadian Atlantic Coast: Nova Scotia (75–480 m), Newfoundland and Labrador (135–700 m), offshore areas (2070 m). Davis Strait (110–350 m). South-East Greenland (245–450 m). Denmark Strait (132–345 m). Iceland (165–475 m). North-East Atlantic, offshore areas (430–485 m). Norwegian Sea, offshore areas (220–500 m). Norwegian Coast: Nordland (120–1100 m), Troms (35–220 m), Finnmark (130–286 m). Barents Sea: Murman Coast (31–270 m), offshore areas (80–350 m). Svalbard (100–230 m). Franz Josef Land (317 m). White Sea (depth unknown). Laptev Sea/Severnaya Zemlya (108–139 m). Arctic Ocean (360–477 m).

DISCUSSION

Polymastia uberrima exhibits some similarity with *P. thielei* in external morphology, but is well-distinguished by the presence of a marginal more or less hispid collar. This collar may be destroyed during sampling, and that might be the reason why some early authors did not distinguish between *P. uberrima* and *P. thielei* (von Marenzeller, 1878; Hansen, 1885; Thiele, 1903; Lundbeck, 1909; Topsent, 1913; Boury-Esnault, 1987). Furthermore, *P. uberrima* differs greatly from *P. thielei* by the architecture of the cortex and choanosomal skeleton (see Discussion on *P. thielei* above) and these morphological distinctions between the two species are confirmed by genetic data. At the same time *P. infrapilosa* established by Topsent (1927b) for *Polymastia* possessing the marginal collar in fact has no differences from *P. uberrima* and hence is regarded as a junior synonym of *P. uberrima*.

Polymastia sp.
(Figure 19)

MATERIAL EXAMINED

ZMBN 098080 (one specimen), West off Marstein, Hordaland, Norway, 60°07.9'–60°07.8'N 04°50.5'–04°51.4'E, 312 m, RV 'Hans Brattstrøm', station 2, coll. Plotkin, 03.07.2012.

DESCRIPTION

External morphology

Encrusting sponge, about 12 mm in diameter and 5 mm thick, removed from the substrate (Figure 19A). Surface strongly hispid, covered with sediment, bearing a conical papilla, 16.5 mm long and 4.6 mm wide at base, with a small osculum at the summit.

Anatomy

Choanosome in alcohol pale orange, firm. Main choanosomal skeleton composed of radiating tracts (92–106 µm thick) of principal spicules crossing the cortex and forming a surface hispidation reinforced with exotyles (Figure 19B). Auxiliary

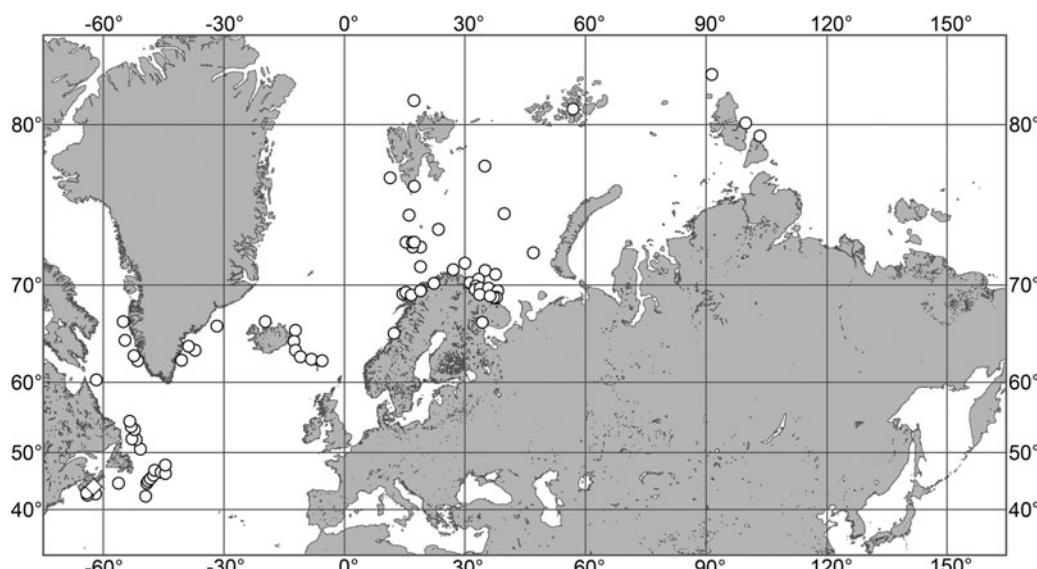


Fig. 18. *Polymastia uberrima*, distribution: white diamond, type locality of *Polymastia infrapilosa* (a synonym of *P. uberrima*); white circles, our data. Precise type locality of *Rinalda uberrima* is unknown.

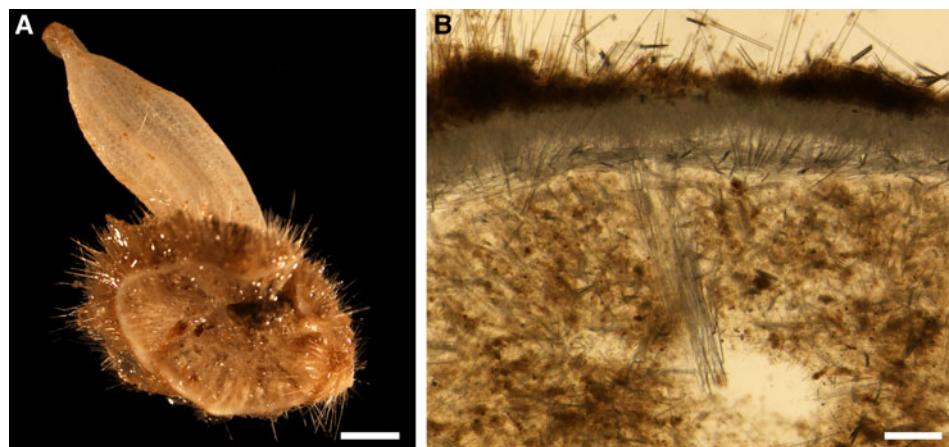


Fig. 19. *Polymastia* sp., ZMBN 098080: (A) habitus; (B) longitudinal section through the body. Scale bars: A, 3 mm; B, 0.2 mm.

choanosomal skeleton comprises bundles of free-scattered small spicules. Cortex in alcohol light-coloured, firm, not detachable. Cortical skeleton constituted by a superficial palisade (170–200 µm thick) of small spicules and an internal layer (139–184 µm thick) of criss-cross intermediary spicules (Figure 19B).

Spicules

Principal spicules – subtylostyles with slightly displaced tyles, occasionally polytylote, straight, fusiform. Length 880–1257–2034 µm, diameter of tyle 8.1–12.2–17.8 µm, proximal diameter of shaft 6.4–9.7–11.4 µm, maximum diameter 12.7–16.8–20.3 µm, N = 30.

Intermediary spicules – subtylostyles, straight, slender. Length 442–557–693 µm, diameter of tyle 7.6–8.7–10.2 µm, proximal diameter of shaft 5.1–6.7–8.9 µm, maximum diameter 7.6–10.0–11.4 µm, N = 30.

Small spicules – tylostyles, often bent in the proximal part, stout. Length 132–162–183 µm, diameter of tyle 3.8–5.6–7.6 µm, proximal diameter of shaft 2.5–3.7–5.1 µm, maximum diameter of shaft 2.5–5.0–6.4 µm, N = 30.

Exostyles – filiform subtylostyles. Length 1860–2590–3770 µm, diameter of tyle 12.7–14.1–16.5 µm, proximal diameter of shaft 7.6–10.9–14.0 µm, maximum diameter of shaft 10.2–13.8–17.8 µm, N = 10.

Genetic data

The Norwegian *Polymastia* sp. described above is genetically very close to *P. svenseni* and an unidentified Canadian *Polymastia* (Plotkin et al., 2016b). The relationships of this trio with other polymastiids and the synapomorphies between the Norwegian *Polymastia* sp. and *P. svenseni* are described in the Genetic data section for the latter species above. Three synapomorphies in CO1 distinguish the Norwegian *Polymastia* sp. and the Canadian *Polymastia* sp. from all other polymastiids (Online resource 2, p. 3, Matrix M34248 in TreeBase). At the same time the Norwegian *Polymastia* sp. is distinguished by two autapomorphies in this gene (Online resource 2, p. 3). Apart from them, it differs from the Canadian *Polymastia* sp. by four bps in CO1 (Matrix M34248 in TreeBase), from *P. svenseni* by 19 bps in CO1 (Matrix M34248 in TreeBase) and two bps in 28S rDNA (Matrix M34250 in TreeBase) and from the type species of *Polymastia*, *P. mamillaris*, by 68 bps in CO1

(Matrix M34248 in TreeBase) and 21 bps in 28S rDNA (Matrix M34250 in TreeBase).

OCCURRENCE

(Figure 20)

Norwegian Coast: Hordaland (312 m).

DISCUSSION

The sponge described above is placed in *Polymastia* based on the CO1 and 28S rDNA phylogenies. Meanwhile, it cannot be identified as any known *Polymastia* spp. It strongly resembles *Polymastia andrica* by the presence of four categories of spicules and a surface hispidation formed by the tracts of principal spicules crossing the cortex and reinforced with exostyles. However, in the molecular phylogenies *Polymastia* sp. is closely related to the morphologically quite distinct *P. svenseni*, while *P. andrica* falls in another subclade. We assume that *Polymastia* sp. may be a species new to science, but postpone the formal erection of this species until more material in addition to the single tiny individual becomes available.

Genus *Quasillina* Norman, 1869

Original description: *Quasillina* Norman, 1869, p. 329.

SYNONYMS

Bursalina Schmidt, 1875, p. 116.

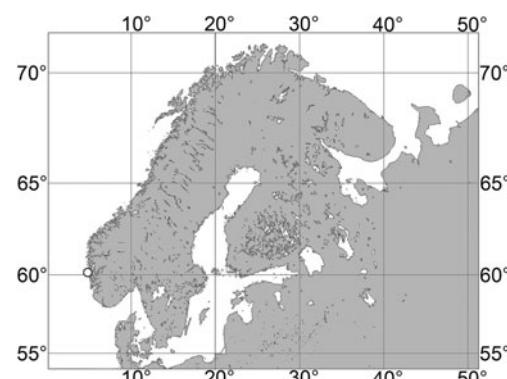


Fig. 20. *Polymastia* sp., ZMBN 098080: locality (white circle).

TYPE SPECIES

Polymastia brevis Bowerbank, 1866 (by original designation).

DIAGNOSIS

Polymastiidae of pedunculate or columnar body shape with a smooth surface and a single osculum located either directly at the summit of the main body or at the summit of a short papilla. Choanosomal skeleton is a mass of small monactines. Cortex comprises a superficial palisade of small monactines, a middle layer of criss-cross large or intermediary monactines and an inner layer of longitudinal tracts of large monactines lying parallel to the surface.

DISCUSSION

Quasillina Norman, 1869 is very similar to *Ridleia* Dendy, 1888. Both genera lack one of the main morphological synapomorphies usually defined for Polymastiidae (Boury-Esnault, 2002), the presence of main choanosomal skeleton composed of tracts of principal spicules. In *Ridleia* the choanosomal skeleton is restricted to a subcortical layer of criss-cross small spicules, whereas in *Quasillina* it is an unordered mass of small spicules scattered over the choanosome that corresponds to the auxiliary choanosomal skeleton in other polymastiids. At the same time in both *Quasillina* and *Ridleia* longitudinal tracts of principal spicules are located in the inner part of the cortex making it very similar to the papilla wall in other polymastiids. Of the alternative phylogenies of Polymastiidae based on 25 morphological characters, one, suggesting the absence of papillae in *Quasillina* and *Ridleia*, displayed the position of these genera outside the clade of

other polymastiids, whereas the other, interpreting their body as a single hyper-developed papilla with reduced choanosome, testified for the monophyly of Polymastiidae including *Quasillina* and *Ridleia* (Plotkin et al., 2012). Phylogenies based on CO1 and 28S rDNA confirmed that *Quasillina* is a polymastiid (Plotkin et al., 2016b; Figure 1 in this study), but no molecular data on *Ridleia* are available so far.

Quasillina brevis (Bowerbank, 1866)
(Figure 21)

Original description: *Polymastia brevis* Bowerbank, 1866, p. 64.

SYNONYMS AND CITATIONS

Bursalina muta (Schmidt, 1875, p. 116, pl. I figures 3 & 4).
Euplectella brevis (Bowerbank, 1861, p. 236 *nomen nudum*; 1861, p. 71 *nomen nudum*).
Polymastia brevis (Bowerbank & Norman, 1882, p. 16 and 31; Fristedt, 1887, p. 433; Topsent, 1888, p. 140).
Quasillina brevis (Norman, 1869, p. 329; Vosmaer, 1885, p. 20, 1887, p. 330, pl. XXVI, figure 12; Ridley & Dendy, 1886, p. 490, 1887, p. 226, figure 10; Dendy, 1888, p. 520, figures 8–12; Topsent, 1892, p. 132, 1900, p. 158; Hanitsch, 1894, p. 175 and 203; Whiteaves, 1901, p. 14; Lundbeck, 1909, p. 452; Brøndsted, 1914, p. 522; 1932, p. 6, 1933, p. 14; Stephens, 1915, p. 30; Rezvoj, 1928, p. 81; Hentschel, 1929, p. 869; Burton, 1930a, p. 496; 1959a, p. 13; Alander, 1942, p. 76; Lévi, 1950, p. 9; Koltun, 1966, p. 89, text-figure 89, pl. XIX figures 9 & 10, pl. XXVI figures 3–5); Boury-Esnault et al.,

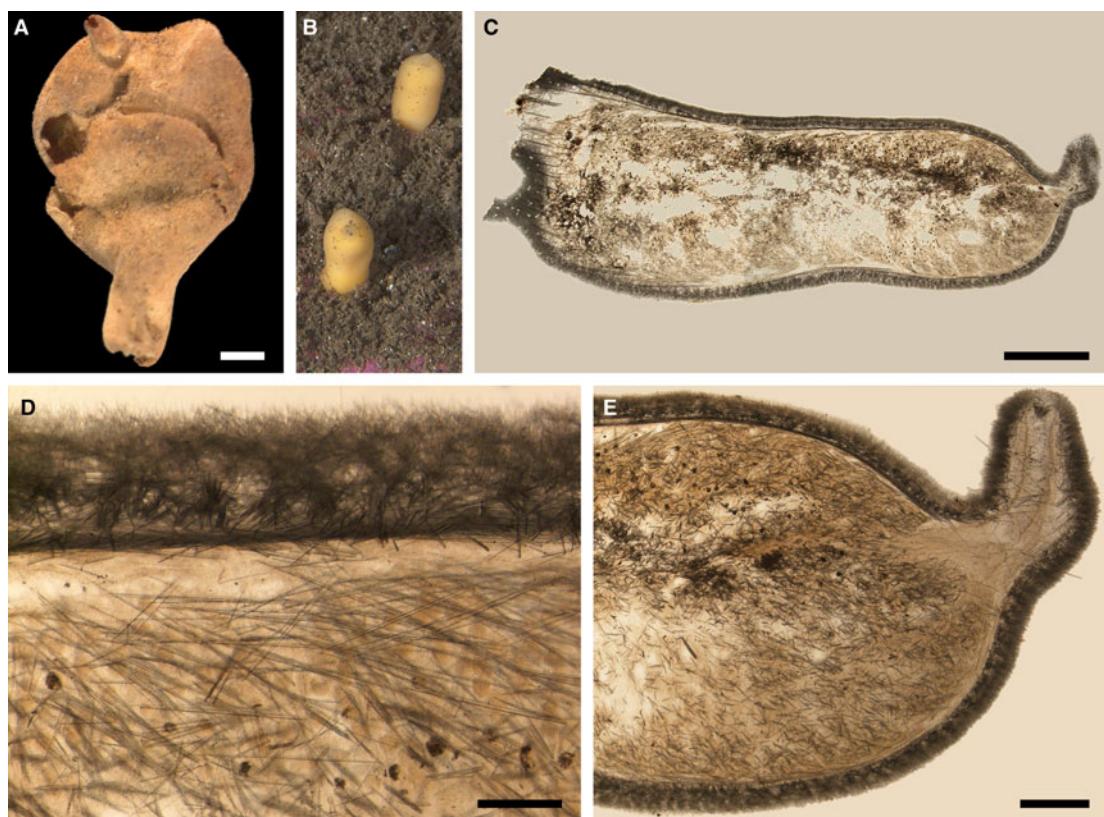


Fig. 21. *Quasillina brevis*: (A) lectotype BMNH 1910.1.1.5-6, habitus; (B) individuals *in situ*, Tingelsædet, Egersund, Norway (courtesy of E. Svensen, OceanPhoto/Dalane Tidende AS, Egersund); (C) ZMBN 098084, longitudinal section through the body, general view; (D) the same section, detail of cortex; (E) ZMBN 098084, longitudinal section through a papilla and adjacent area. Scale bars: A, 0.5 cm; C, 3 mm; D, 0.3 mm; E, 1 mm.

1994, p. 71, figure 46; Boury-Esnault, 2002, p. 211, figure 8; Plotkin, 2004, p. 545, figures 1l & 2l; Plotkin *et al.*, 2012, p. 25, figure 1h).

Quasillina richardi Topsent, 1913, p. 19, pl. III figure 7 and pl. V figure 14 (Alander, 1942, p. 76; Gorbunov, 1946, p. 37; Burton, 1959a, p. 13).

TYPE MATERIAL

Lectotype of *Polymastia brevis* (designated herein, Figure 21A): BMNH 1910.1.1.5–6 (dry specimen), Shetland, UK, precise locality unknown, 109–164 m.

Paralectotypes of *Polymastia brevis*: BMNH 1910.1.1.5–6 (six intact specimens and several fragments, all dry), BMNH 1898.5.7.59 (two specimens in alcohol) and BMNH 1910.1.1.597A (two specimens in alcohol), from the same sample as the lectotype.

Syntypes of *Quasillina richardi* Topsent, 1913: MOM 04-0817 (two specimens in alcohol), between Bear Island and Norwegian Coast, 72°37'N 20°00'E, 394 m, Campagnes scientifiques accomplies par le Prince Albert I de Monaco, RV 'Princesse-Alice', station 960, 29.07.1898. Herein *Q. richardi* is regarded as a synonym of *Q. brevis*.

COMPARATIVE MATERIAL

(see Online resource 1 for details)

Canada: offshore areas of NW Atlantic: ZIN RAS ocqbo07 (one specimen).

Iceland/Denmark Strait: ZMBN 098067 (one specimen).

North-East Atlantic, offshore: ZIN RAS ocqbo06 (one specimen).

Norwegian Sea, offshore: ZIN RAS ocqbo10 (one specimen). Barents Sea, offshore: ZIN RAS ocqbo01, ZIN RAS ocqbo02, ZIN RAS ocqbo04, ZIN RAS ocqbo09, ZIN RAS ocqbo12, ZIN RAS ocqbo13, ZIN RAS ocqbo14, ZIN RAS ocqbo15, ZIN RAS ocqbo16, ZIN RAS ocqbo17, ZIN RAS ocqbo18, ZIN RAS ocqbo19 and ZIN RAS ocqbo20 (13 specimens).

Norway: Vest-Agder: ZMBN 098084, ZMBN 098090 and ZMBN 107573 (three specimens), Rogaland: ZMBN 098082 (one specimen), Sogn and Fjordane: ZMBN 098049 (one specimen), Møre and Romsdal: ZMBN 107489 and ZMBN 107491 (two specimens), Nord-Trøndelag: NTNU-VM-54600, NTNU-VM-54747, NTNU-VM-54751, NTNU-VM-54754, NTNU-VM-54755 and NTNU-VM-72545 (15 specimens), Nordland: NTNU-VM-72516 (two specimens), Finnmark: NTNU-VM-72501 (two specimens). Svalbard: ZIN RAS ocqbo08 (one specimen).

Russia: Murman Coast: ZIN RAS ocqbo11 (one specimen), Novaya Zemlya: ZIN RAS ocqbo05 (one specimen).

Arctic Ocean, offshore: ZIN RAS ocqbo03 (one specimen).

DESCRIPTION

External morphology

Lectotype of *Polymastia brevis* has an irregularly ovoid main body, ~25 mm in diameter and 28 mm high, sitting on a stalk, ~11 mm high and 7 mm in diameter and bearing a well developed cylindrical papilla, ~5 mm long and 3 mm in diameter, with an osculum at the summit (Figure 21A). Paralectotypes smaller, some with weakly developed papillae, others lacking papillae and bearing oscula directly on the body summits. Most other sponges columnar, up to 35 mm high and up to 8 mm in diameter, with no segregation between main body and stalk (Figure 21B). Few sponges with ovoid or pyriform main bodies sitting on stalks. Papillae, if

present, are weakly developed. Colour in life pale orange or yellowish. Syntypes of *Quasillina richardi* are small fragments, one on a stalk lacking the major part of the main body, the other being a residual of the main body.

Anatomy

In life choanosome is an intensive yellow or orange, unstructured, semi-fluid mass without any spicule tracts. This mass is often washed away under preservation. Choanosomal skeleton comprises free-scattered bundles of small spicules (Figure 21C). Cortex in life pale orange or pale yellow, leather-like. Cortical skeleton comprises a superficial palisade (150–200 µm thick) of bouquets of small spicules and two inner overlapping layers, a layer of criss-cross large spicules (270–300 µm thick) located midst in the cortex and an internal layer (35–80 µm thick) of longitudinal tracts of large spicules (Figure 21D). Skeleton of the papilla wall is the same as the cortical skeleton (Figure 21E).

Spicules

(Measurements based on 15 specimens)

Principal spicules – subtylostyles to styles, straight, or occasionally gently curved, fusiform. Length 570–862–1098 µm, maximum diameter 11.2–17.8–25.5 µm, N = 450.

Small spicules – styles to subtylostyles, often bent in the distal part, slender. Length 140–227–306 µm, maximum diameter of shaft 1.9–4.0–5.8 µm, N = 450.

Genetic data

Data obtained from five individuals of *Quasillina brevis* are identical in both genes studied. *Quasillina brevis* is closely related, especially in the CO1 phylogeny, to morphologically distinct *Polymastia boletiformis* (see the synapomorphies in the Genetic data section for the latter species above). At the same time *Q. brevis* possesses six autapomorphies in 28S rDNA distinguishing it from all other polymastiids (Online resource 3, p. 4) and, apart from them, differs from *P. boletiformis* by 18 bps in this gene (Matrix M34250 in TreeBase).

OCCURRENCE

(Figure 22)

Literature data:

Canadian Atlantic Coast: Nova Scotia (155 m) (Ridley & Dendy, 1886, 1887). Azores (318 m) (Topsent, 1892). West of Gibraltar (218–524 m) (Boury-Esnault *et al.*, 1994). Mediterranean Sea: Moroccan Coast (144–145 m) (Boury-Esnault *et al.*, 1994). Northern French Coast (Lévi, 1950). British Isles: Ireland (706 m) (Stephens, 1915), Shetland (73–309 m) (Bowerbank, 1866; Norman, 1869). Iceland (83–557 m) (as *Q. brevis* and *Q. richardi* – Burton, 1959a). South Greenland (120 m) (Brøndsted, 1933). East Greenland (231 m) (Lundbeck, 1909). Faroes (160 m) (Brøndsted, 1932). Swedish Western Coast (85–360 m) (as *Q. brevis* and *Q. richardi* – Alander, 1842). Norwegian Coast: Rogaland (193 m) (as *Bursalina muta* – Schmidt, 1875; as *Q. brevis* – Burton, 1930a), Hordaland (Burton, 1930a), Sør-Trøndelag (Burton, 1930a), Troms (Burton, 1930a), Finnmark (273 m) (Fristedt, 1887). Norwegian Sea (67–500 m) (as *Q. brevis* – Vosmaer, 1885; Hentschel, 1929; Koltun, 1966; as *Q. richardi* – Topsent, 1913). Barents Sea (67–500 m) (Vosmaer, 1885; Rezvoj, 1928; Koltun, 1966). Kara and Laptev Sea (67–500 m) (Gorbunov, 1946; Koltun, 1966).

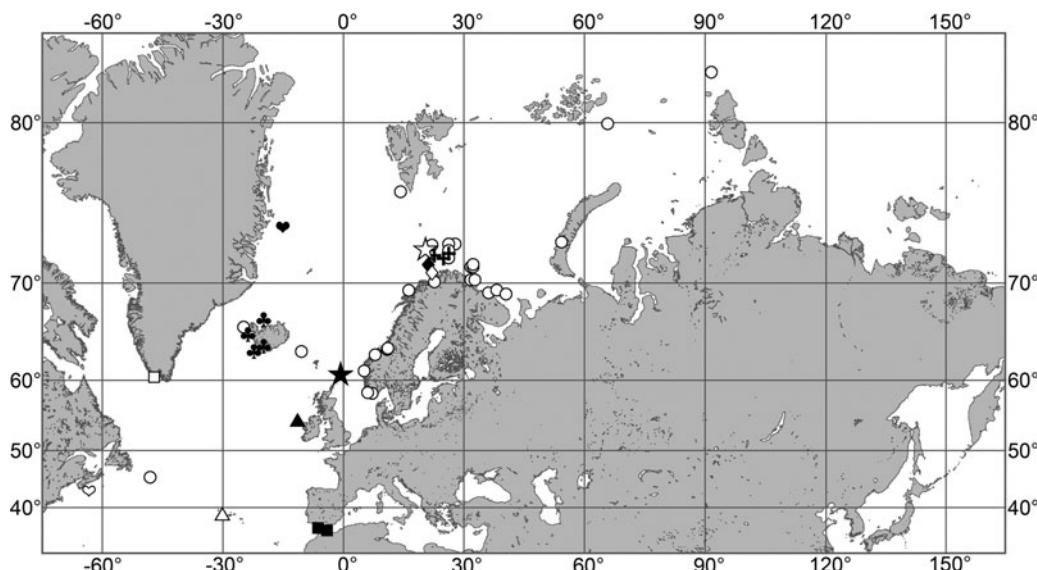


Fig. 22. *Quasillina brevis*, distribution: black star, type locality of *Polymastia brevis*; white star, type locality of *Quasillina richardi* (synonym of *Q. brevis*); black squares, data from Boury-Esnault *et al.* (1994); white square, data from Brøndsted (1933); black trefoils, data from Burton (1959a); black diamond, data from Hentschel (1929); white diamond, data from Fristedt (1887); black heart, data from Lundbeck (1909); white heart, data from Ridley & Dendy (1886); black triangle, data from Stephens (1915); white triangle, data from Topsent (1892); white circles, our data.

Our data: Canadian Atlantic Coast: offshore areas (380–415 m). Iceland/Denmark Strait (118 m). North-East Atlantic (400 m). Norwegian Sea, offshore (394–500 m). Norwegian Coast: Vest-Agder (30–45 m), Rogaland (25–31), Sogn and Fjordane (241–254 m), Møre and Romsdal (100–120 m), Nord-Trøndelag (15–110 m), Nordland (360 m), Finnmark (250 m). Barents Sea: Murman Coast (110–146 m), offshore areas (90–442 m). Svalbard (759 m). Novaya Zemlya (8 m). Arctic Ocean, offshore (360 m).

DISCUSSION

Quasillina brevis is recorded in a wide geographic area, but there is some doubt whether all these records indicate the same species. Topsent (1913) established a new species of *Quasillina*, *Q. richardi*, for the sponges from the Northern Norwegian Sea based on their difference from *Q. brevis* from more southern areas (British Isles, French Coast, Azores). In the former species small spicules were bent in the distal part, while in the latter they were straight. However, the correlation of the spicule shape in *Quasillina* to geography was questioned by several records of both *Q. brevis* and *Q. richardi* from the same localities, e.g. from Iceland (Burton, 1959a) and the Swedish Western Coast (Alander, 1942). In our material from the Nordic Seas we have found both individuals with bent and straight small spicules, without any correlation to geography. Therefore, until molecular data on the British, South European and Azorean *Quasillina* become available and comparable with our data on the Nordic sponges, we follow Koltun (1966) and Plotkin (2004) and conclude that *Q. richardi* should be regarded as a junior synonym of *Q. brevis*.

Genus *Sphaerotylus* Topsent, 1898
Original description:
Sphaerotylus Topsent, 1898, p. 244.

TYPE SPECIES

Polymastia capitata Vosmaer, 1885 (by original designation).

DIAGNOSIS

Polymastiidae of hemispherical, dome, cushion-like or button-like body shape, always with papillae. Spicule assortment comprises smooth monactines in at least two size categories and exotyles with ornamented distal extremities, which may be rough, spined, granulated, tuberculated or wrinkled, often with knobs varying from spherical to hemispherical, fungiform, umbrelliform or lobate. Main choanosomal skeleton composed of radial or longitudinal tracts of principal monactines. Auxiliary choanosomal skeleton comprises free-scattered, small and/or intermediary monactines, and, occasionally exotyles. A superficial cortical palisade composed of either exotyles with sparse small monactines or small monactines reinforced with sparse exotyles. An inner layer of criss-cross intermediary monactines may also be present.

DISCUSSION

According to the CO₁ and 28S rDNA phylogenies *Sphaerotylus* Topsent, 1898 is not monophyletic (Plotkin *et al.*, 2016b; Figure 1 in this study). The two species described below, the type species, *S. capitatus* (Vosmaer, 1885), and *S. borealis* (Swarczewsky, 1906) fall in remote clades. However, here we follow the traditional taxonomy of *Sphaerotylus* spp. (Boury-Esnault, 2002; Plotkin *et al.*, 2016a), since no alternative classification is proposed for Polymastiidae so far (Plotkin *et al.*, 2016b).

Sphaerotylus borealis (Swarczewsky, 1906)
(Figure 23)

Original description: *Proteleia borealis* Swarczewsky, 1906, p. 315, pl. X figure 1, pl. XIII figure 2.

SYNONYMS AND CITATIONS

Proteleia borealis (Boury-Esnault, 2002, p. 204).

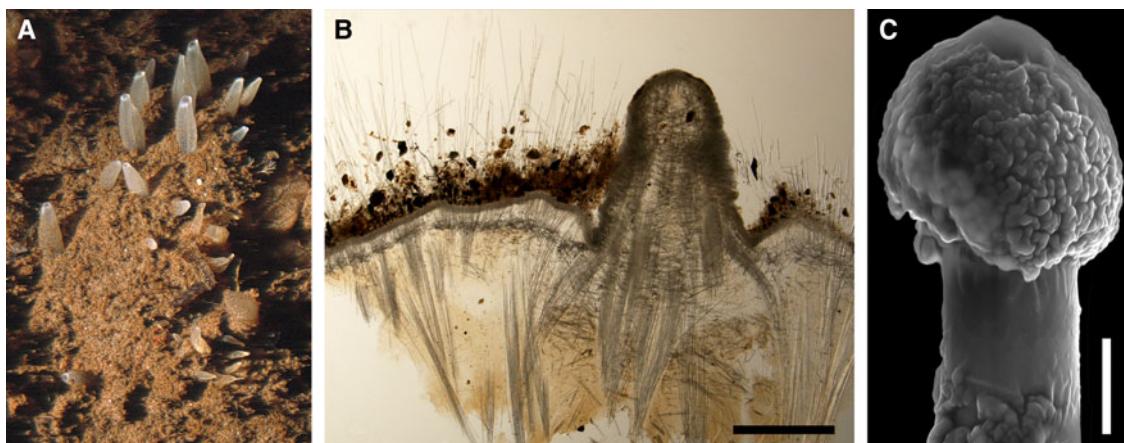


Fig. 23. *Sphaerotylus borealis*: (A) an individual *in situ*, Kandalaksha Bay, White Sea (courtesy of M. Fedyuk, St. Petersburg State University); (B) ZMBN 098059, longitudinal section through the body; (C) ZMBN 098036, proximal tip of exotyle. Scale bars: B, 2 mm; C, 0.005 mm.

Sphaerotylus borealis (Rezvoj, 1928, p. 78, figures 4 & 5; Koltun, 1966, p. 83, pl. XXX figures 1–5, text-figure 55; Plotkin, 2004, p. 543, figures 1i, 2i & 4b).

Sphaerotylus schoenus var. *borealis* (Hentschel, 1929, p. 925).

TYPE MATERIAL

Neotype: ZIN RAS 11194, Sredny Island, Keret' Inlet, Kandalaksha Bay, White Sea, $66^{\circ}17.391'N$ $33^{\circ}38.025'E$, 10–13 m, 12.07.2000, coll. Plotkin.

Designation and detailed description of the neotype was done by Plotkin *et al.* (2016a).

COMPARATIVE MATERIAL

(see Online resource 1 for details)

Iceland: ZIN RAS 11169 and ZIN RAS 11184 (two specimens).

Norwegian Sea, offshore: ZIN RAS 11145 (one specimen).

Barents Sea, offshore: ZIN RAS 11146, ZIN RAS 11156, ZIN RAS 11157, ZIN RAS 11158, ZIN RAS 11159, ZIN RAS 11160, ZIN RAS 11163, ZIN RAS 11165, ZIN RAS 11166, ZIN RAS 11167, ZIN RAS 11170, ZIN RAS 11171, ZIN RAS 11176, ZIN RAS 11177 and ZIN RAS 11181 (15 specimens).

Russia: Murman Coast: ZIN RAS 11164, ZIN RAS 11168, ZIN RAS 11174 and ZIN RAS 11183 (four specimens), White Sea: ZIN RAS 11144, ZIN RAS 11147, ZIN RAS 11148, ZIN RAS 11149, ZIN RAS 11150, ZIN RAS 11151, ZIN RAS 11155, ZIN RAS 11161, ZIN RAS 11162, ZIN RAS 11175, ZIN RAS 11180, ZIN RAS 11182, ZIN RAS 11195, ZMBN 098036, ZMBN 098059 and ZMBN 098061 (31 specimens), Severnaya Zemlya: ZIN RAS 11179 (one specimen).

Arctic Ocean, offshore: ZIN RAS 11178 (one specimen).

DESCRIPTION

(according to Plotkin *et al.*, 2016a)

External morphology

Sponges thickly encrusting or cushion-shaped, the largest up to 100 cm². Surface shaggy, silted with sediment making it dirty greyish or brownish in colour. Up to 50 cylindrical or conical papillae, whitish in life, but usually becoming pale yellow, brownish or pinkish in alcohol. On soft bottoms living sponges are often completely covered by sediment with only erect papillae protruding above (Figure 23A). On

hard bottoms the sponges may contract the papillae. After sampling and fixation the papillae always considerably contract and invaginate into the surface hispidation. Oscula not visible in preserved sponges.

Skeleton

Choanosome in life orange, dense. Main choanosomal skeleton composed of longitudinal tracts of principal spicules which cross the cortex and make up a dense and thick surface hispidation (Figure 23B). Auxiliary choanosomal skeleton comprises small, occasionally intermediary, spicules often arranged in bundles, 3–7 spicules each. Cortex in life whitish, dense, not detachable. Cortical skeleton composed of a 115–120 µm thick superficial palisade of small spicules and an internal layer (~210 µm thick) of tangentially arranged intermediary spicules (Figure 23B). In areas around papillae these layers are separated by an intermediate, aspicular zone (about 100 µm thick). Exotyles cross the cortex and join the surface hispidation. Walls of papillae lack the tangential cortical layer. Single intermediary spicules scattered both in the walls and in the bulkheads between canals.

Spicules

(Measurements based on 10 specimens)

Principal spicules – styles to subtylostyles, often polytylote straight, slender. Length 1100–2423–5000 µm, diameter of shaft 12.0–16.2–19.0 µm, N = 100.

Intermediary spicules – tylostyles, usually straight, occasionally curved, slightly fusiform. Length 200–502–796 µm, diameter of tyle 6.9–9.2–11.1 µm, proximal diameter of shaft 5.0–7.1–9.0 µm, maximum diameter of shaft 6.9–10.8–14.3 µm, N = 100.

Small spicules – tylostyles, straight or curved, usually slender. Length 94–125–160 µm, diameter of tyle 3.9–4.6–5.1 µm, diameter of shaft 3.0–3.5–4.0 µm, N = 100.

Exotyles slender, 5100–6117–7520 µm long, usually with weakly developed or completely reduced proximal tyles. Shafts 13.8–17.2–20 µm in maximum diameter. Distal knobs (14.1–19.9–27.0 µm in diameter) usually irregularly fungiform or umbrelliform (Figure 23C), more rarely hemispherical or spherical, occasionally with short protuberances on the edges, sometimes slightly displaced along the shaft or comprising several swellings. Surface of the knobs and the

adjacent portions of the shafts rough, wrinkled, granulated or tuberculated.

Genetic data

Of the three individuals of *Sphaerotylus borealis*, from which genetic data were obtained, two sponges differ neither by CO1, nor by 28S rDNA. The third individual is distinguished by two bps in 28S rDNA (Matrix M34250 in TreeBase), but no CO1 was obtained from it. In both CO1 and 28S rDNA phylogenies *S. borealis* does not group with any of the congeners (Plotkin *et al.*, 2016b). The difference between *S. borealis* and the type species of *Sphaerotylus*, *S. capitatus*, is 26 bps in CO1 (Matrix M34248 in TreeBase) and 86 bps in 28S rDNA, excluding the intraspecific polymorphism in both species (Matrix M34250 in TreeBase). At the same time *S. borealis* possessing just one autapomorphy in 28S rDNA (Online resource 3, p. 3) forms a clade with two morphologically quite distinct species, *Polymastia* cf. *conigera* Bowerbank, 1874 (a British species not covered by the present study) and *Weberella bursa* (the type species of *Weberella* Vosmaer, 1885 described below) in both CO1 and 28S rDNA phylogenies (Plotkin *et al.*, 2016b). However, the Bayesian support for this clade is weak (Plotkin *et al.*, 2016b). These three species share just two synapomorphies in 28S rDNA distinguishing them from all other polymastiids (Online resource 3, p. 3, Matrix M34250 in TreeBase), while the differences between them are large. *Sphaerotylus borealis* differs from *P. cf. conigera* by 17 bps in CO1 (Matrix M34248 in TreeBase) and 35 bps in 28S rDNA (Matrix M34250 in TreeBase) and from *W. bursa* by 7 bps in CO1 (Matrix M34248 in TreeBase) and 33 bps in 28S rDNA (Matrix M34250 in TreeBase).

OCCURRENCE

(Figure 24)

Our data (agree with the literature data): Iceland (157–240 m). Norwegian Sea, offshore areas (342 m). Barents Sea: Murman Coast (91–130 m), offshore areas (124–420 m). White Sea (10–57 m). Severnaya Zemlya (43 m). Arctic Ocean, offshore areas (415 m).

DISCUSSION

Sphaerotylus borealis (Swarczewsky, 1906) was originally assigned to *Proteleia* Dendy & Ridley, 1886, but later (Koltun, 1966) transferred to *Sphaerotylus*. The large morphological differences between *S. borealis* and the type species of *Proteleia*, *P. sollasi* Dendy & Ridley, 1886, were described by Plotkin *et al.* (2016a). At the same time *S. borealis* shares many features, e.g. the shaggy surface and the giant exotyles with umbrelliform or fungiform distal ornaments, with *S. antarcticus* Kirkpatrick, 1907. By these features both *S. borealis* and *S. antarcticus* are distinguished from the type species of *Sphaerotylus*, *S. capitatus*. Meanwhile, in CO1 and 28S rDNA phylogenies *S. borealis* and *S. capitatus* fall in remote clades, while the relationships between *S. antarcticus* and *S. capitatus* are ambiguous (Plotkin *et al.*, 2016b). Grouping of *S. borealis* with *Polymastia* cf. *conigera* and *Weberella bursa* in the molecular phylogenies has a weak Bayesian support, and no morphological synapomorphies can, for the moment, be defined for this grouping (Plotkin *et al.*, 2016b). Thus, the taxonomic position of *S. borealis* remains unclear.

Sphaerotylus capitatus (Vosmaer, 1885) (Figure 25)

Original description: *Polymastia capitata* Vosmaer, 1885, p. 16, pl. IV figures 25–29.

SYNONYMS AND CITATIONS

Polymastia capitata (Breitfuss, 1911, p. 218).

Polymastia schoenus (Dendy & Ridley, 1886, p. 155, text-figure).

Radiella schoenus (Sollas, 1882, p. 162, considered as *nomen nudum* by Kirkpatrick, 1908, p. 18).

Sphaerotylus capitatus (Topsent, 1898, p. 244; Boury-Esnault, 2002, p. 206, figure 4; Plotkin, 2004, p. 543, figures 1H, 2H & 4A; Plotkin *et al.*, 2012, p. 27, figure 2d).

Sphaerotylus schoenus (Topsent, 1913, p. 23, pl. II figure 6, 1928, p. 154; Koltun, 1966, p. 85, pl. XXX figures 6 & 7, text-figure 56; Desqueyroux-Faúndez & Van Soest, 1997, p. 421).

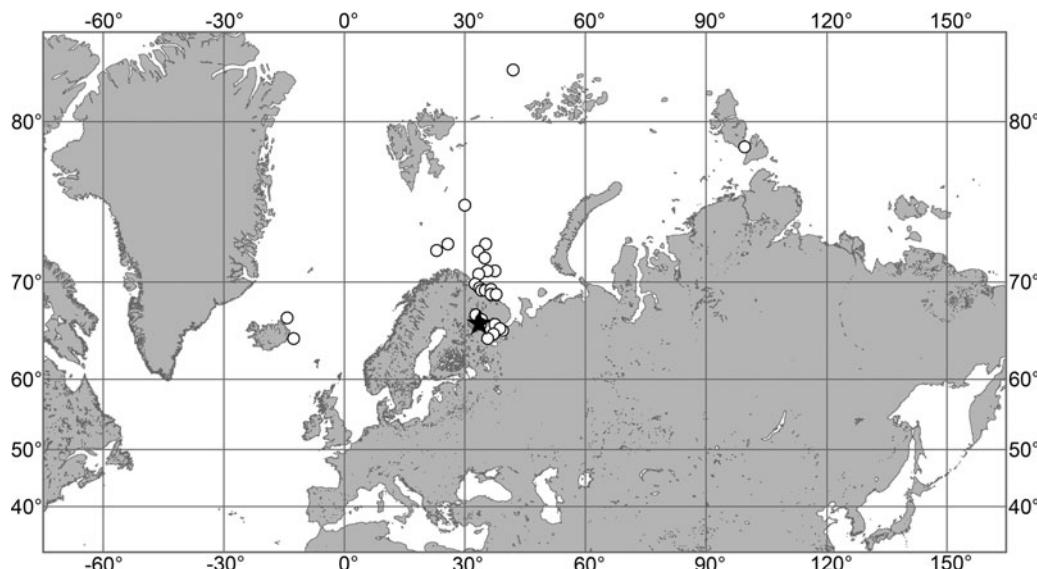


Fig. 24. *Sphaerotylus borealis*, distribution: black star, type locality; white circles, our data.

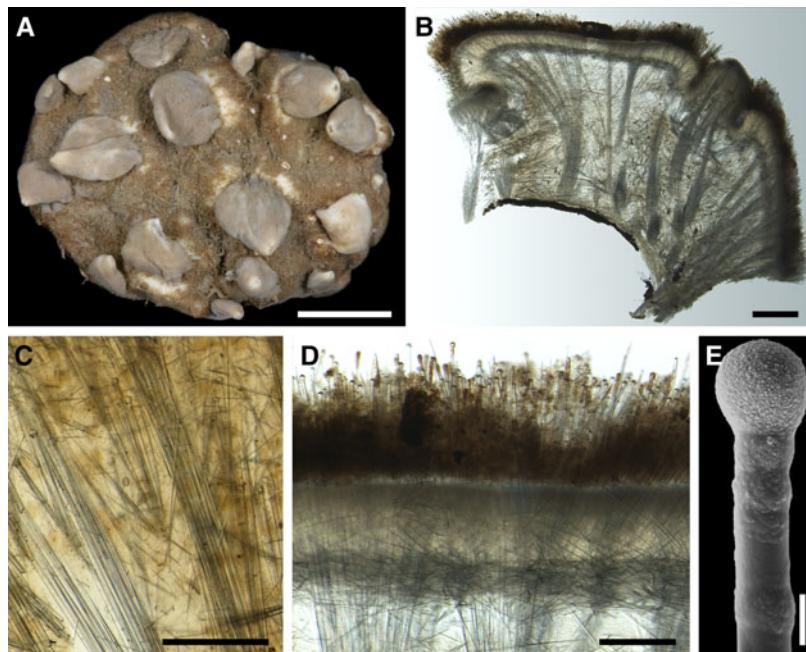


Fig. 25. *Sphaerotylus capitatus*: (A) GNM 899, habitus; (B) ZMBN 107485, longitudinal section through the body, general view; (C) paralectotype BMNH 1910.1.1.1199, detail of choanosome with exotyles; (D) ZMBN 107485, longitudinal section through the body, detail of cortex; (E) ZMB 10855, proximal tip of exotype. Scale bars: A, 1 cm; B, 1 mm; C–D, 0.3 mm; E, 0.02 mm.

TYPE MATERIAL

Lectotype and one paralectotype: RMNH 704, Norwegian Sea, $72^{\circ}14.8'N$ $22^{\circ}30.9'E$, about 300 m, ‘Willem Barentz’ Expedition, station 28, 30.06.1881.

Paralectotype: BMNH 1910.1.1.612 (specimen in alcohol) and BMNH 1910.1.1.1196–1200 (slides), from the same sample as the lectotype.

Paralectotype: ZMA 1841 (specimen, not studied), from the same sample as the lectotype.

Detailed description of the type material was presented by Plotkin *et al.* (2016a).

COMPARATIVE MATERIAL

(see Online resource 1 for details)

Greenland: ZIN RAS 1193 (one specimen).

Sweden: Västra Götaland: GNM 899, GNM 900:1–2 and GNM 902 (four specimens).

Norway: Hordaland: ZMB 10855 and ZMBN 098042 (two specimens), Møre and Romsdal: NTNU-VM-69133, ZMBN 107485, ZMBN 107487 and ZMBN 107490 (four specimens), Sør-Trøndelag: NTNU-VM-54686 and NTNU-VM-57267 (two specimens), Nord-Trøndelag: NTNU-VM-54629 and NTNU-VM-66578 (two specimens), Nordland: NTNU-VM-55862 and NTNU-VM-72521 (three specimens), Troms: ZMBN 098075 (one specimen), Finnmark: ZIN RAS 1190 (one specimen), Svalbard: ZIN RAS 1185 and ZIN RAS 1192 (two specimens).

Russia: Murman Coast: ZIN RAS 1186, ZIN RAS 1187 and ZIN RAS 1188 (three specimens).

Barents Sea, offshore: ZIN RAS 1189 and ZIN RAS 1191 (two specimens).

DESCRIPTION

External morphology

Sponges thickly encrusting, cushion-shaped or massive, fist- or dome-shaped, occupying up to 50 cm^2 of the substrate.

Surface velvety, knobby, dark brown in colour, with up to 30 papillae (Figure 25A). Papillae of living sponges whitish or pale yellow in colour, conical, with small, scarcely visible oscula at the summits. In alcohol-preserved specimens the papillae may be considerably contracted looking like tubercles, while their colour does not change much.

Skeleton

Choanosome in life yellowish or pale orange, dense. Main choanosomal skeleton composed of radial or longitudinal tracts of principal spicules which enter the cortex (Figure 25B). Auxiliary choanosomal skeleton comprises small and intermediary spicules usually scattered singly or sometimes arranged in small groups. Besides these spicules some individuals possess exotyles between the choanosomal tracts (Figure 25C). Cortex in life whitish, firm, not detachable. Cortical skeleton composed of a superficial palisade ($\sim 110\text{ }\mu\text{m}$ thick) of small spicules, an internal layer (about $170\text{ }\mu\text{m}$ thick) of tangentially arranged intermediary spicules and a middle layer (180 – $190\text{ }\mu\text{m}$ thick) with a low concentration of spicules (Figure 25D). Exotyles cross the cortex forming a dense superficial layer with their distal knobs rising above the palisade. Papillae walls without internal cortical layer. Single intermediary spicules scattered both in the papillae walls and in the bulkheads between the canals.

Spicules

(Measurements based on five specimens)

Principal spicules – subtylostyles to styles, often polytylote, straight, slightly fusiform or slender. Length 650 – 998 – $1505\text{ }\mu\text{m}$, diameter of tyle, if present, 10.0 – 12.8 – $16.0\text{ }\mu\text{m}$, proximal diameter of shaft 8.9 – 11.5 – $15.1\text{ }\mu\text{m}$, maximum diameter of shaft 14.0 – 19.5 – $26.0\text{ }\mu\text{m}$, N = 50.

Intermediary spicules – tylostyles, straight or gently curved, slender or slightly fusiform. Length 314 – 484 – $650\text{ }\mu\text{m}$,

diameter of tyle 9.1–11.4–14.0 µm, proximal diameter of shaft 6.9–8.8–11.0 µm, maximum diameter of shaft 9.0–13.0–16.5 µm, N = 50.

Small spicules – tylostyles, straight or curved, usually slender. Length 96–155–221 µm, diameter of tyle 2.9–4.6–6.1 µm, proximal diameter of shaft 1.1–2.3–3.2 µm, maximum diameter of shaft 2.0–5.0–7.0 µm, N = 50.

Exotyles straight or gently curved, slender, 650–974–1250 µm long. Proximal tyles varying from well-developed (6.8–11.0–14.0 µm in diameter) to reduced. Distal knobs usually regularly spherical (Figure 25E), occasionally hemispherical or elongated, 18.0–22.8–30.0 µm in diameter. Surface of the knobs and the adjacent portions of the shafts usually rough, spined or granulated. Shafts gradually expanding towards the distal knobs, N = 50.

Genetic data

CO₁ sequences obtained from three individuals of *Sphaerotylus capitatus* are identical (Matrix M34248 in TreeBase). 28S rDNA sequences obtained only from two of these sponges differ by two bps (Matrix M34250 in TreeBase) and exhibit one synapomorphy distinguishing *S. capitatus* from other polymastiids (Online resource 3, p. 4). In the CO₁ and 28S rDNA phylogenies *S. capitatus* forms a clade with two British unidentified species, *Sphaerotylus* sp. 1 and *Sphaerotylus* sp. 2, not covered by the present study (Plotkin *et al.*, 2016b). These three species share three synapomorphies in CO₁ (Online resource 2, p. 4, Matrix M34248 in TreeBase) and three synapomorphies in 28S rDNA (Online resource 3, p. 4, Matrix M34250 in TreeBase) distinguishing them from all other polymastiids. One more synapomorphy in 28S rDNA is shared only by *S. capitatus* and *Sphaerotylus* sp. 1 (Online resource 3, p. 4, Matrix M34250 in TreeBase). Meanwhile, *S. borealis*, a Nordic species described above, does not fall in this clade (see the differences between *S. borealis* and *S. capitatus* in the Genetic data section for the former species).

OCCURRENCE

(Figure 26)

Literature data (only the locality distinct from our data is given): Canadian Atlantic Coast: Nova Scotia (75 m) (as *Sphaerotylus schoenus* – Topsent, 1928).

Our data (agree with most literature data): Greenland (420–450 m). Norwegian Sea, offshore areas (300 m), Skagerrak: Swedish Western Coast (239–317 m). Norwegian Coast: Hordaland (200–500 m), Møre and Romsdal (130–250 m), Sør-Trøndelag (45–100 m), Nord-Trøndelag (20–130 m), Nordland (150–800 m), Troms (25 m), Finnmark (275 m). Barents Sea: Murman Coast (31–235 m), offshore areas (142–309 m). Svalbard (819 m).

DISCUSSION

Sphaerotylus capitatus is a well-defined species and identification of it usually causes no difficulties. Meanwhile, molecular data on a larger set of species are required for reconstruction of the relationships between *S. capitatus* and its congeners.

Genus *Spinularia* Gray, 1867

Original description: *Spinularia* Gray, 1867, p. 524.

SYNONYMS

Radiella Schmidt, 1870, p. 48 pars.

Raphidorus Topsent, 1898, p. 244.

TYPE SPECIES

Tethya spinularia Bowerbank, 1866 (by original designation).

DIAGNOSIS

Polymastiidae of discoid, hemispherical, lenticular or cushion-like body shape with a shaggy or minutely hispid surface and one to 15 weakly developed exhalant papillae. Main choanosomal skeleton composed of longitudinal or radial tracts of principal monactines crossing the cortex. Auxiliary choanosomal skeleton comprises free-scattered small and/or intermediary

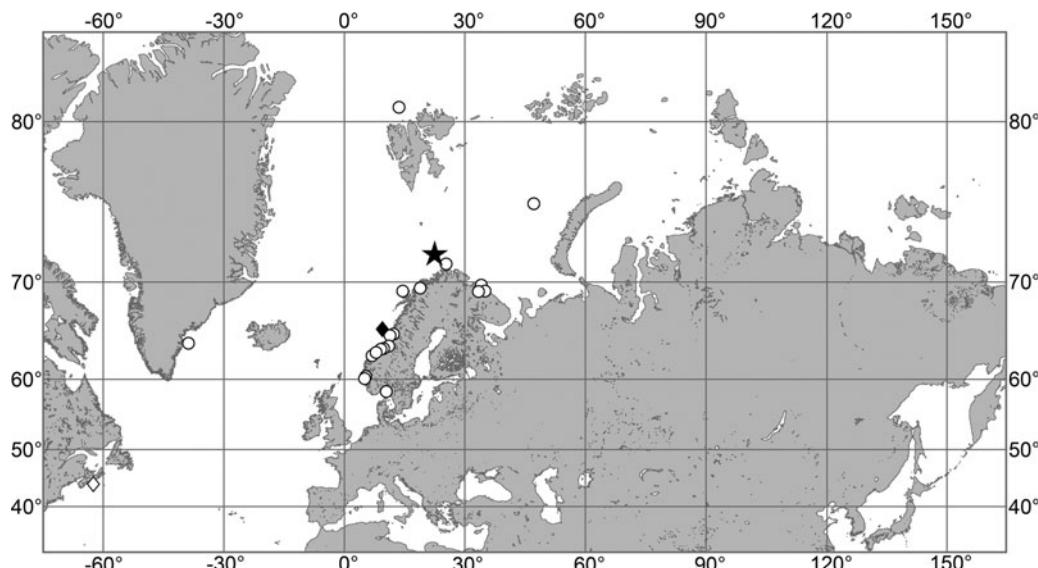


Fig. 26. *Sphaerotylus capitatus*, distribution: black star, type locality; black diamond, data from Topsent (1913); white diamond, data from Topsent (1928); white circles, our data.

(sub)tylostyles and may also include raphides in trichodragmata. Cortical skeleton may, in addition to the superficial palisade of small tylostyles, include extra spicule layers. Basal cortex, if present, reinforced with the peripheral tracts of principal spicules lying parallel to the surface. A spicule fringe is always present at the edge of the body.

GENETIC SYNAPOMORPHIES

Spinularia spp. are distinguished from other polymastiids by two synapomorphies in CO₁ (Online resource 2, p. 5) and one synapomorphy in 28S rDNA (Online resource 3, p. 5).

DISCUSSION

Taxonomic history of *Spinularia* is closely related to *Radiella* and *Trichostemma*. *Spinularia* was established by Gray (1867) for a new species name *Spinularia tetheoides* Gray, 1867 for unknown reasons proposed as a replacement for *Tethea spinularia* Bowerbank, 1866. This replacement was, however, not acknowledged by the subsequent authors. *Radiella* was established by Schmidt (1870) for two species, his new species *Radiella sol* Schmidt, 1870 and *Tethea spinularia*, without designation of the type species. In that way *Spinularia* was consequently regarded as a synonym of *Radiella*, although the former had precedence over the latter. But three years later Schmidt (1880) reconsidered the status of *Radiella spinularia* (ex *Tethea spinularia*) acknowledging that it was conspecific with *Halicnemia patera* Bowerbank, 1864. Moreover, he admitted that *Radiella* might be a synonym of *Halicnemia* Bowerbank, 1864. However, Fristedt (1885, 1887) preferred to retain *Tethea spinularia* in *Radiella* as *R. spinularia*, while Hanitsch (1894) transferred it to *Polymastia* Bowerbank, 1862, although with some doubt. *Spinularia* was resurrected by Stephens (1915) who defined the main feature distinguishing this genus from *Polymastia*, *Halicnemia* and *Radiella*, the presence of raphides (filiform oxea-like spicules) packed in trichodragmata. In the same paper Stephens stated that the type species of *Rhaphidorus* Topsent, 1898, *R. setosus* Topsent, 1898, which also possessed raphides in trichodramata, is synonymous with *S. spinularia*, and, consequently, *Rhaphidorus* was synonymized with *Spinularia*. The actions performed by Stephens were acknowledged by most subsequent authors (Topsent, 1928; Burton, 1930a; Alander, 1942; Lévi, 1993; Boury-Esnault, 2002; Plotkin et al., 2012). Since *Tethea spinularia* was the type species of *Spinularia*, *Radiella sol* was designated as the type species of *Radiella* (Boury-Esnault, 2002).

Trichostemma was established by Sars (1872) for his new species *T. hemisphaericum* Sars, 1872, although these names first appeared in a faunistic list three years earlier (Sars, 1869). Schmidt (1880) considered *T. hemisphaericum* to be a synonym of *Radiella sol* and, consequently, *Trichostemma* to be a synonym of *Radiella*. However, most subsequent authors recognized *T. hemisphaericum* and *R. sol* as different species, although they agreed that *Trichostemma* and *Radiella* were synonymous, and there were debates on which of these names preceded until Boury-Esnault (2002) acknowledged the synonymization of *Trichostemma* with *Radiella* based on the principle of priority (for references and other details see Discussion on *Polymastia hemisphaerica* above).

The relationships between *Polymastia*, *Spinularia*, *Radiella* and *Trichostemma* were re-considered by Plotkin et al. (2016b). Based on the CO₁ and 28S rDNA phylogenies *Radiella sarsii* and *Radiella* sp. (here described as *Spinularia njordi* sp. nov., see below) forming a strongly supported

clade with *Spinularia spinularia* (Figure 1) were transferred to *Spinularia*. Conversely, *Trichostemma hemisphaericum*, falling into a clade with the type species of *Polymastia* (*P. mamillaris*), was transferred to *Polymastia*. Consequently, *Trichostemma* Sars, 1872 was regarded as a junior synonym of *Polymastia* Bowerbank, 1862 (Plotkin et al., 2016b). These actions are followed in the present study, and the definition of *Spinularia* is extended to cover the species lacking raphides in trichodragmata (see Diagnosis above). *Spinularia australis* Lévi, 1993, a species from New Caledonia originally placed in *Spinularia*, perfectly fits with this diagnosis. It possesses raphides like *S. spinularia* and, at the same time, resembles *S. sarsii* by body shape and the presence of basal cortex. We also agree that *Rhaphidorus* is a synonym of *Spinularia*, although we question the synonymization of *R. setosus* with *S. spinularia* (for details see Discussion on *S. spinularia* below).

Meanwhile, the status of the type species of *Radiella*, *R. sol*, remains uncertain. Its type material is lost (Plotkin et al., 2012) and no fresh material is available. The age-old non-type specimen identified as *R. sol* by Schmidt (1880) and re-described by Boury-Esnault (2002) resembles *Polymastia hemisphaerica* by its relatively narrow marginal spicule fringe (Plotkin & Janussen, 2008; Plotkin et al., 2012). But it does not match the drawing in the original description of *R. sol* (Schmidt, 1870: pl. 4, figure 6), which displays a wider marginal fringe rather resembling *Spinularia sarsii* (Plotkin & Janussen, 2008; Plotkin et al., 2012). However, regardless of the relationships of *R. sol* with *P. hemisphaerica* and *S. sarsii*, *Radiella* is abandoned since both *Polymastia* and *Spinularia* are older names (Plotkin et al., 2016b).

Spinularia njordi sp. nov. (Figure 27)

TYPE MATERIAL

Holotype: ZMBN 098040 (specimen), Low-angle fault to the west of Loki's Castle, North Norwegian Sea, 73°34.738'–73°35.005'N 08°03.034'–08°01.085'E, 2457–1997 m, RV 'G.O. Sars', expedition H2DEEP, station 09-40-DR 03, 09.08.2009.

Paratype: ZMBN 098041 (specimen), from the same sample as the holotype.

Paratype: ZMBN 098038 (sections and spicule slides; the specimen was completely used for the preparations), Schultz Massive, North Norwegian Sea, 73°47.385'N 07°40.413'E, 1997 m, RV 'G.O. Sars', expedition BIODEEP, 07-90-ROV 10 rock 2, 14.07.2007, coll. Augustin.

COMPARATIVE MATERIAL

(see Online resource 1 for details)

Norwegian Sea: Southern part, Storegga: ZMBN 107497, ZMBN 107498 and ZMBN 107499 (three specimens), Eastern part, ~160 km North from Andenes: NTNU-VM-72525 (10 specimens), Northern part, Schultz Massive – Loki's Castle: 58 specimens deposited in ZMBN.

ETYMOLOGY

Named after Njord, the god of ocean, seafaring and fishing in Norse mythology. Referring to the occurrence of this species in the offshore areas of the Norwegian Sea.

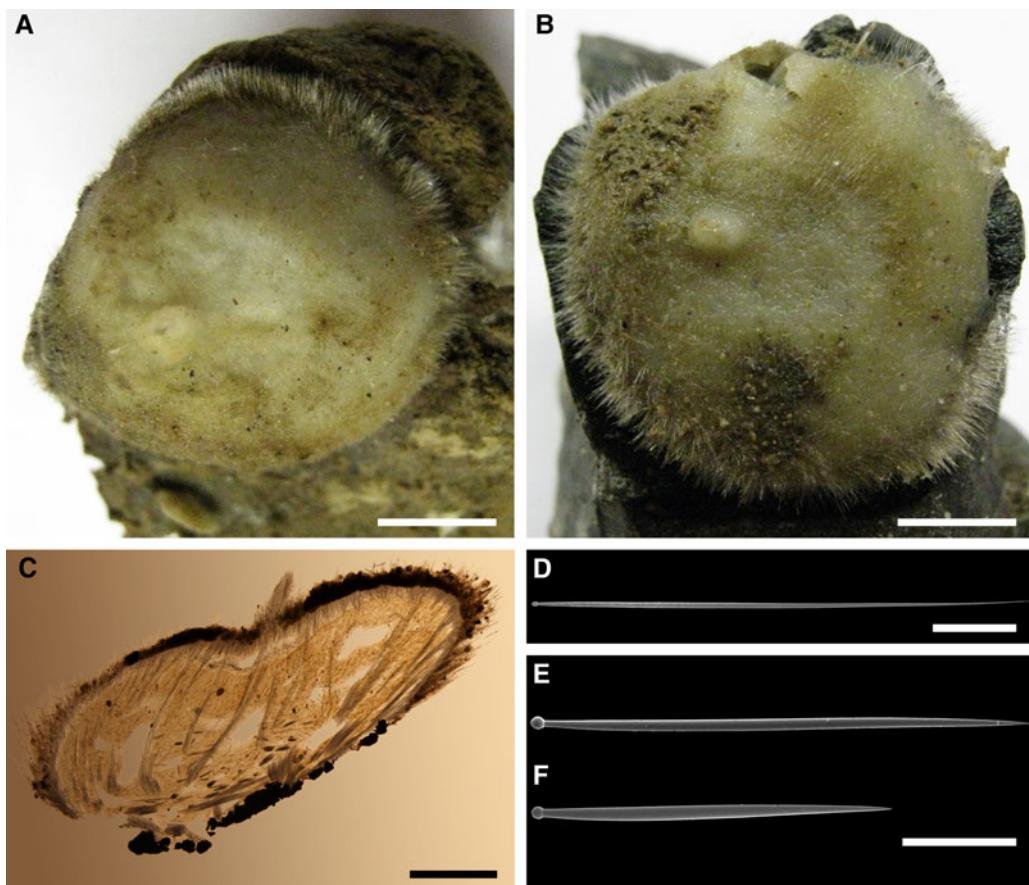


Fig. 27. *Spinularia njordi*: (A) holotype ZMBN 098040, habitus; (B) paratype ZMBN 098041, habitus; (C) paratype ZMBN 098038, longitudinal section through the body; (D) the same individual, principal subtylostyle; (E) the same individual, intermediary tylostyle; (F) the same individual, small tylostyle. Scale bars: A–B, 0.5 cm; C, 2 mm; D, 0.2 mm; E–F, 0.1 mm.

DESCRIPTION

External morphology

Holotype and both paratypes hemispherical, with a minutely and unevenly hispid surface edged with a narrow spicule fringe and bearing a single weakly developed papilla with an osculum at the summit. Holotype 16–17 mm in diameter and ~9 mm in height, attached to a volcanic porous concretion (Figure 27A). Surface dirty grey, with a whitish papilla. Paralectotype ZMBN 098041 17–18 mm in diameter and ~6 mm in height, attached to a basalt piece (Figure 27B). Surface dirty grey, with a whitish papilla. Paratype ZMBN 098038 was, before dissection, 11 mm in diameter and 4 mm in height, attached to small gravels. Surface was brownish, with a yellowish papilla located in a small depression. Other sponges hemispherical, lenticular or irregular, up to 24 mm in diameter. Surface, for the most part, hispid, occasionally shaggy, dark brown or dark grey because of the covering sediment. A single papilla and the surrounding area on the body top, which may be gently depressed, are smooth and pale in colour. Marginal spicule fringe up to 3 mm wide in the largest individuals.

Anatomy

Choanosome in alcohol light or dark brown, dense. Main choanosomal skeleton composed of tracts (96–310 µm thick) of principal spicules radiating from the basal area, where the sponge is attached to the substrate, occasionally

ramifying, crossing the cortex and protruding above the surface (Figure 27C). At the body edge the protruding tracts form a prominent fringe. Some tracts ascend to the papilla walls. Auxiliary choanosomal skeleton comprises free-scattered small and intermediary spicules, the latter occasionally gathered in small bundles. Cortex in alcohol whitish or pale brown, firm, not detachable. Cortical skeleton comprises a superficial palisade (217–300 µm thick) of small spicules. In the central area of the upper cortex there is also an internal layer (116–494 µm thick) of criss-cross intermediary spicules. Under the papilla the palisade and the internal layer are separated by an aquiferous cavity (~268–810 µm in diameter).

Spicules

(Measurements based on seven specimens, individual variation presented in Table 7)

Principal spicules (Figure 27D) – subtylostyles to tylostyles, usually straight and slender. Length 1116–1492–2579 µm, diameter of tyle (if present) 8.9–13.3–16.5 µm, proximal diameter of shaft 6.4–9.1–14.0 µm, maximum diameter of shaft 8.9–14.9–21.6 µm, N = 284.

Intermediary spicules (Figure 27E) – tylostyles to subtylostyles, usually straight, occasionally gently curved, slender. Length 422–685–1128 µm, diameter of tyle (if present) 8.9–13.0–16.5 µm, proximal diameter of shaft 5.1–7.9–11.4 µm, maximum diameter of shaft 8.9–13.3–17.8 µm, N = 254.

Table 7. Individual variation of spicule dimensions of *Spinularia njordi* (given in µm as minimum–mean–maximum). Parameters: length, diameter of tyle, proximal diameter of shaft, maximum diameter of shaft, number of spicules measured (N).

Specimen	Principal spicules	Intermediary spicules	Small spicules
Holotype ZMBN 98038	1166–1460–1823 10.2–13.2–16.5 7.6–9–12.7 12.7–15–20.3 N = 104	422–713–1128 10.2–12.2–14 5.1–7.4–8.9 8.9–12.3–15.2 N = 91	251–328–402 10.2–12.3–15.2 5.1–7.6–10.2 10.2–12.9–16.5 N = 73
Paratype ZMBN 98040	1141–1628–2108 8.9–14–15.2 7.6–9.8–11.4 10.2–17–20.3 N = 35	422–572–942 12.7–13.6–15.2 7.6–8–8.9 12.7–14.6–17.8 N = 19	231–338–422 12.7–13.3–15.2 7.6–8.3–10.2 12.7–14.5–17.8 N = 30
ZMBN 107498	1116–1754–2579 8.9–12.3–16.5 7.6–10.2–14 8.9–14.2–21.6 N = 41	422–547–1116 8.9–12.8–15.2 7.6–8.8–11.4 10.2–14.4–16.5 N = 30	286–327–392 10.2–12.2–14 5.1–7.4–8.9 10.2–13.7–17.8 N = 30
ZMBN 107499	1166–1267–1364 10.2–13.1–15.2 6.4–8.1–10.2 10.2–14.9–17.8 N = 12	427–775–1116 10.2–12.5–14 6.4–7.5–7.6 11.4–13.7–15.2 N = 24	201–292–382 8.9–11.8–14 3.8–6.8–8.9 8.9–12.6–14 N = 30
ZMBN 107500	1166–1607–2058 12.7–13.5–15.2 7.6–8.8–10.2 12.7–14.6–16.5 N = 32	422–581–1005 10.2–12.7–15.2 5.1–6.7–7.6 10.2–11.9–12.7 N = 30	261–331–412 12.7–12.8–14 6.4–7–7.6 11.4–12.8–15.2 N = 30
ZMBN 107504	1141–1266–1488 11.4–13.6–15.2 7.6–8.9–10.2 12.7–13.8–15.2 N = 30	422–730–1128 12.7–14.2–16.5 7.6–9–10.2 12.7–13.7–15.2 N = 30	221–342–412 12.7–14–16.5 7.6–9.1–12.7 12.7–14.4–20.3 N = 30
ZMBN 107505	1141–1282–1401 11.4–13.8–15.2 7.6–9.1–10.2 12.7–14–15.2 N = 30	437–794–1116 10.2–13.2–15.2 6.4–7.9–8.9 8.9–12.7–15.2 N = 30	251–336–412 12.7–13.8–15.2 7.6–9.4–10.2 12.7–14.4–16.5 N = 30

Small spicules (Figure 27F) – tylostyles, often gently bent at the proximal part, occasionally straight, usually slightly fusiform. Length 201–328–422 µm, diameter of tyle 8.9–12.6–16.5 µm, proximal diameter of shaft 3.8–7.8–12.7 µm, maximum diameter of shaft 8.9–13.3–20.3 µm, N = 253.

Genetic data

Data obtained from three individuals of *Spinularia njordi* are identical in both genes studied. Moreover, the CO1 sequences from *S. njordi* are identical to those from the type species of *Spinularia*, *S. spinularia*, and the Norwegian individuals of *S. sarsii*, but not the Mozambican *S. cf. sarsii* (Online resource 2, p. 5). At the same time *S. njordi* displays seven autapomorphies in 28S rDNA distinguishing it from the congeners (Matrix M34250 in TreeBase). Of these autapomorphies one is unique among all polymastiid species from which 28S rDNA has ever been obtained (Online resource 3, p. 5).

OCCURRENCE

(Figure 28)

Norwegian Sea, offshore: southern areas (733–790 m), eastern areas (1580 m), northern areas (1262–2457 m).

DISCUSSION

Spinularia njordi resembles the type species of *Spinularia*, *S. spinularia*, by the encrusting growth pattern, the consequent absence of the basal cortex and the relatively small marginal fringe composed of the spicules of the same category as those forming the main choanosomal tracts. These features distinguish *S. njordi* and *S. spinularia* from other *Spinularia* spp. At the same time *S. njordi* differs from *S. spinularia* by the shaggy surface, the presence of an additional cortical layer made of intermediary monactines and the absence of raphides in trichodragmata in the choanosome. These features rather resemble *S. sarsii*. Based on the absence of raphides *S. njordi* and *S. sarsii* were provisionally allocated to *Radiella*, as *Radiella* sp. and *R. sarsii* respectively (Plotkin *et al.*, 2016b). However, based on the 28S rDNA phylogeny and the identity of the CO1 5'-end barcodes from these species and *S. spinularia*, they were transferred to *Spinularia* (Plotkin *et al.*, 2016b). *Spinularia njordi* is established as a new species primarily based on its autapomorphies in 28S rDNA (see the Genetic data above).

Spinularia sarsii (Ridley & Dendy, 1886)
(Figure 29)

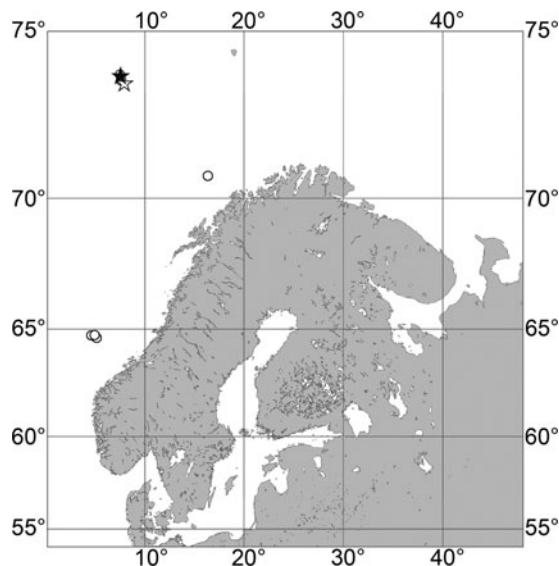


Fig. 28. *Spinularia njordi*, distribution: black star, locality of holotype and paratype ZMBN 098041; white star, locality of paratype ZMBN 098038; white circles, other data.

Original description: *Trichostemma sarsii* Ridley & Dendy, 1886, p. 488.

SYNONYMS AND CITATIONS

Radiella sarsii (Gorbunov, 1946, p. 37; Plotkin, 2004, p. 543, figures 1g & 2g; Plotkin *et al.*, 2012, p. 27, figure 2j).
Radiella sol (Koltun, 1964, p. 149, figure 3).

Polyamia sol sol (Koltun, 1966, p. 81, text-figure 52, pl. XXX figures 8 & 9, pl. XXXI figures 10 & 11).

Trichostemma sarsii (Ridley & Dendy, 1887, p. 218, pl. XLIII figures 1, la, 2, 2a, 3 & 3a; Topsent, 1892, p. 132, 1904, p. 120, 1928, p. 154; Uriz & Rosell, 1990, p. 380, figures 3, 5e & 6; Boury-Esnault *et al.*, 1994, p. 73, figure 49).

Trichostemma sol (Barthel & Tendal, 1993, p. 88, figure 5).

Non *Radiella sarsii* (Burton, 1959b, p. 208).

Non *Trichostemma sarsii* (Dendy, 1922, p. 151).

TYPE MATERIAL

Lectotype (designated herein, Figure 29A, B): BMNH 1887.5.2.38.1, off Azores, 38°30'N 31°14'W, RV 'Challenger', 1820 m, station 73, 30.06.1873.

Paralectotypes: BMNH 1887.5.2.38.2 (small fragment), BMNH 1887.5.2.61 (two specimens) and BMNH 1887.5.2.66 (one specimen, Figure 29C, D), from the same sample as the lectotype.

Paralectotype: BMNH 1887.5.2.40 (one specimen, Figure 29E, F), SE off Cape York, Australia, 12°08'S 145°10'E, 2548 m, RV 'Challenger', station 184, 29.08.1874.

COMPARATIVE MATERIAL

(see Online resource 1 for details)

Greenland: East Coast: ZIN RAS ocrsoo2 (one specimen), NE Coast: ZIN RAS ocrsoo3 (one specimen).

Greenland Sea: ZIN RAS ocrsoo1 and ZIN RAS ocrsoo4 (two specimens).

Norwegian Sea, offshore: NTNU-VM-72506, ZMBN 098039, ZMBN 098098, ZMBN 107582 and ZMBN 107583 (five specimens).

Indian Ocean: Mozambican Coast: ZMBN 098103 (one specimen identified as *Radiella cf. sarsii* by Plotkin *et al.*, 2016b).

DESCRIPTION

External morphology

Lectotype discoid, flattened, with hispid, grey upper and basal surfaces and a marginal spicule fringe (Figure 29A, B). Body ~9 mm in diameter (excluding the fringe) and ~6 mm thick. Upper surface bears four tiny papillae with oscula at the summits (Figure 29A). Basal surface without any trace of the substrate (Figure 29B). Fringe 1.5–4 mm wide. All paralectotypes externally resemble the lectotype. Paralectotype BMNH 1887.5.2.38.2 is a body sector with a 3.0–3.5 mm wide fringe and without papillae. Paralectotype BMNH 1887.5.2.40 discoid, ~9 mm in diameter, with a convex, smooth basal surface and a flattened, hispid upper surface bearing a single papilla damaged at the summit (Figure 29E, F). Fringe 1.5–2.5 mm wide. One of the paralectotypes BMNH 1887.5.2.61 flattened, irregular, ~6 × 8 mm, with hispid upper and basal surfaces and without visible papillae. Fringe 1–2 mm wide. The other paralectotype BMNH 1887.5.2.61 discoid, flattened, ~4 mm in diameter, with an almost smooth basal surface and a hispid upper surface bearing a single papilla. Fringe 0.7–3.0 mm wide. Paralectotype BMNH 1887.5.2.66 discoid, ~5.0–5.5 mm in diameter, with a convex, almost smooth basal surface and a flattened, strongly hispid upper surface lacking visible papillae (Figure 29C, D). Fringe 1.3–2.6 mm wide. Other sponges discoid, lenticular, hemispherical, occasionally irregular, up to 13 mm in diameter (Figure 29G, H). Upper surface flattened, hispid or shaggy, covered with sediment, bearing a single papilla, more rarely few, small papillae with oscula at the summits (Figure 29G). Basal surface often convex, smooth, attached to the substrate with a central point (Figure 29H). A small substrate may be plunged into the basal cortex. Some individuals are free of any substrates. Width of the marginal fringe may reach half of body diameter.

Anatomy

Choanosome in alcohol light or dark brown, dense. Main choanosomal skeleton composed of tracts (119–283 µm thick) of principal spicules radiating from the central basal point, crossing the upper cortex and protruding above the surface (Figure 29I). Some tracts ascend to the papilla walls. Auxiliary choanosomal skeleton comprises free-scattered bundles of intermediary spicules. Cortex in alcohol whitish, firm, not detachable. Skeleton of the upper cortex comprises a superficial palisade (about 300 µm thick) of small spicules, a middle space (340–405 µm thick) with low concentration of spicules except for ascending choanosomal tracts and an internal layer (100–110 µm thick) of criss-cross intermediary spicules. Skeleton of the basal cortex formed of peripheral tracts of principal spicules running parallel to the surface and free-scattered single small spicules. Extra-long spicules (exotyles) composing the marginal fringe are embedded in the tracts.

Spicules

(Measurements based on 13 specimens)

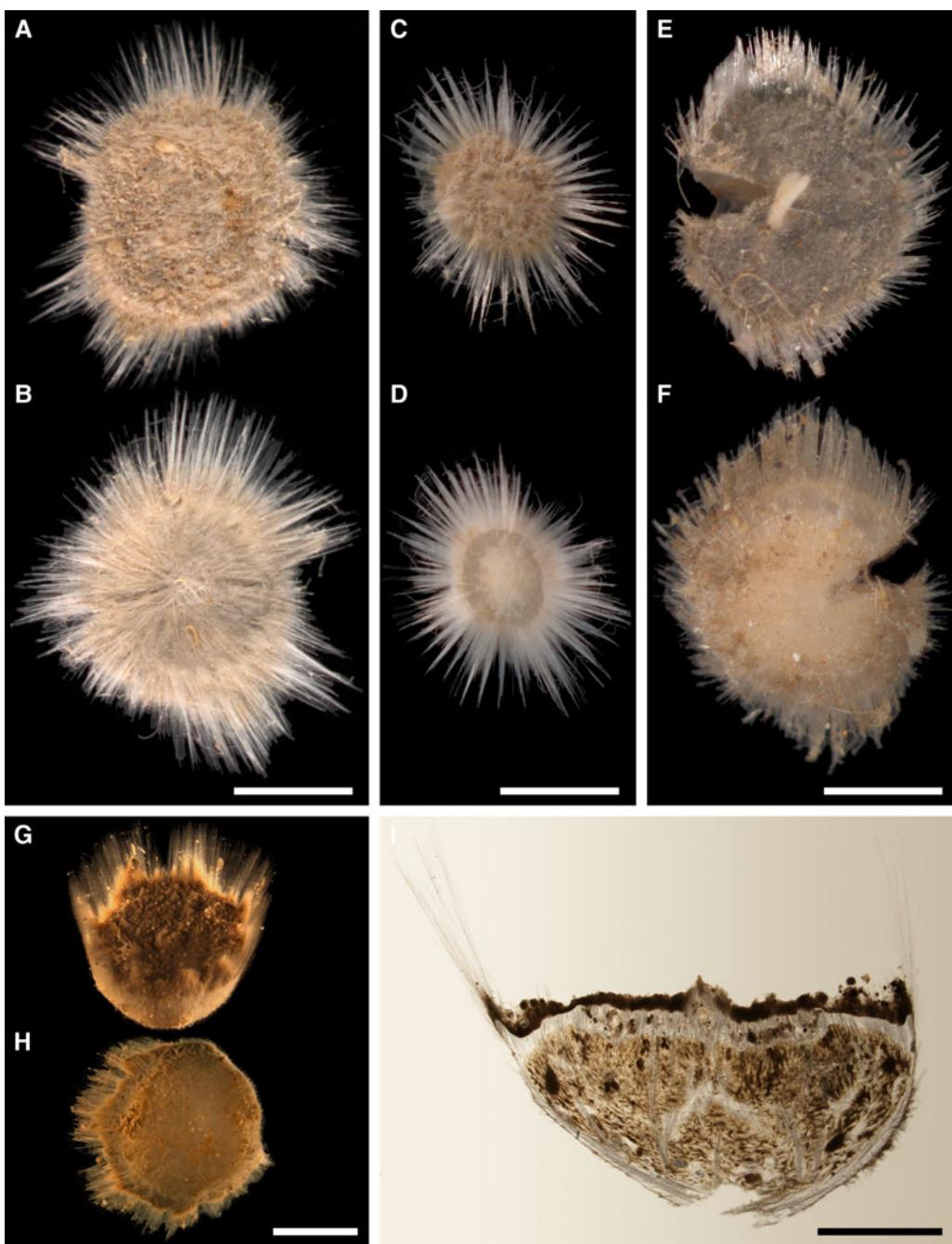


Fig. 29. *Spinularia sarsii*, type series, habitus: (A) lectotype BMNH 1887.5.2.38.1, view from above; (B) the same, bottom view; (C) paralectotype BMNH 1887.5.2.66, view from above; (D) the same, bottom view; (E) paralectotype BMNH 1887.5.2.40, view from above; (F) the same, bottom view; (G) ZMBN 107582, habitus, side view; (H) the same, bottom view; (I) the same individual, longitudinal section through the body. Scale bars: A–H, 5 mm; I, 3 mm.

Principal spicules – styles, occasionally subtylostyles, usually straight and fusiform. Length 871–1787–2900 µm, maximum diameter of shaft 13.0–19.3–26.6 µm, N = 130. Intermediary spicules – subtylostyles to tylostyles, usually straight, slightly fusiform. Length 250–471–632 µm, maximum diameter of shaft 6.1–7.6–8.7 µm, N = 390. Small spicules – tylostyles, often gently bent at the proximal part, fusiform. Length 152–232–298 µm, maximum diameter of shaft 8.1–9.8–10.4, N = 390. Exostyles (spicules of the marginal fringe) – styles, occasionally subtylostyles, straight or slightly curved, fusiform. Length 3890–5010–6030 µm, maximum diameter of shaft 24.5–27.3–29.8 µm, N = 70.

Genetic data

Certain genetic differences are revealed between the morphologically very similar *Spinularia sarsii* from Norway and *Spinularia cf. sarsii* from Mozambique. Data obtained from two Norwegian individuals are identical in both genes studied. Moreover, the CO1 sequences from these individuals are identical to those from the type species of *Spinularia*, *S. spinularia*, and *S. njordi* and display one synapomorphy distinguishing them from other polymastiids including the Mozambican *S. cf. sarsii* (Online resource 2, p. 5). In 28S rDNA the Norwegian *S. sarsii* differs from *S. spinularia* by 6 bps and from *S. njordi* by 12 bps (Matrix M34250 in TreeBase) and shares with them two synapomorphies

(Online resource 3, p. 5). At the same time the Mozambican *S. cf. sarsi* is distinguished from all polymastiids by three autapomorphies in CO1 (Online resource 2, p. 5). Apart from these autapomorphies, it differs from the congeners by five bps in CO1 (Matrix M34248 in TreeBase). In 28S rDNA the Mozambican *S. cf. sarsi* differs from the Norwegian *S. sarsi* by 13 bps, from *S. njordi* by 18 bps and from *S. spinularia* by 14 bps (Matrix M34250 in TreeBase).

OCCURRENCE

(Figure 30)

Type locality: North-East Atlantic: Azores (1820 m). The other type locality (Coral Sea near Australia, 2548 m) probably represents another species (see Discussion below).

Other literature data: Canadian Atlantic Coast: off Newfoundland (1267 m) (Topsent, 1892). North-East Atlantic: Azores (861–2102 m) (Topsent, 1892, 1904), Cape Verde (1209–1417 m) (Topsent, 1928), Madeira (2380–3118) (Topsent, 1928), Moroccan Coast/Saharan Upwelling (851–2142 m) (Topsent, 1928; Boury-Esnault *et al.*, 1994). Mediterranean Sea: Iberian Sea (1020–1580 m) (Uriz & Rosell, 1990). Arctic Ocean, Greenland Sea and Norwegian Sea (800–2892 m) (Gorbunov, 1946; Koltun, 1964, 1966; Plotkin, 2004). Barents Sea, Kara Sea and Laptev Sea (from 145 m and deeper) (Koltun, 1966).

Our data: Greenland, East and NE Coast (368–2581 m). Greenland Sea, offshore (1447–2754 m). Norwegian Sea, offshore (2387–2463 m).

DISCUSSION

Spinularia sarsi was originally described as *Trichostemma sarsi* Ridley & Dendy, 1886, despite *Trichostemma* having been synonymized earlier with *Radiella* (Schmidt, 1880). After long debates on which of the names, *Trichostemma* or *Radiella*, preceded, Boury-Esnault (2002) finally proved the action by Schmidt (1880) (for details see Discussion on the genus *Spinularia* above). *Radiella* was defined as sponges with the upper and basal cortex of different architecture and a spicule fringe developed at the boundary between the upper and basal surface (Boury-Esnault, 2002). *Radiella sarsi* perfectly fitted with this definition (Plotkin, 2004; Plotkin *et al.*, 2012). The marginal spicule fringe was also typical of another genus, *Spinularia*, but the latter was distinguished from *Radiella* by the presence of raphides in trichodragmata (Boury-Esnault, 2002). However, based on the CO1 and 28S rDNA phylogenies, Plotkin *et al.* (2016b) transferred *R. sarsi* to *Spinularia* (for details see Discussion on the genus *Spinularia* and *S. njordi* above).

The other problem with *Spinularia sarsi* is the allegedly cosmopolitan distribution reported for this species. Its type localities are such remote regions as Azores and Australia (Ridley & Dendy, 1886). Besides these *S. sarsi* is recorded from quite remote localities in the North Atlantic (Newfoundland (Topsent, 1892), Azores (Topsent, 1892, 1904), Cape Verdi (Topsent, 1928), Madeira (Topsent, 1928), Moroccan Coast (Topsent, 1928; Boury-Esnault *et al.*, 1994), West Mediterranean Sea (Uriz & Rosell, 1990)),

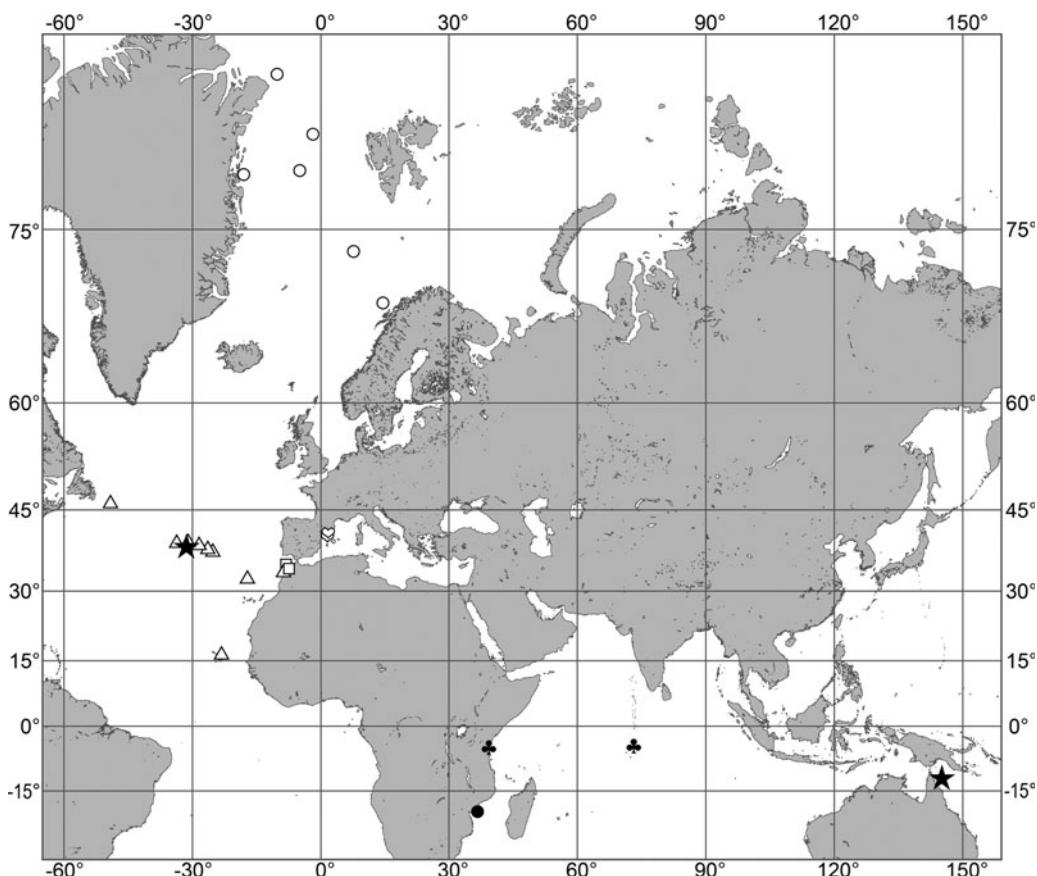


Fig. 30. *Spinularia sarsi*, distribution: black stars, type localities; white squares, data from Boury-Esnault *et al.* (1994); black trefoils, data from Burton (1959b); white triangles, data from Topsent (1892, 1904, 1928); white hearts, data from Uriz & Rosell (1990); white circles, our data from the Nordic Seas; black circle, our data from Mozambique.

Arctic Ocean, Greenland and Norwegian Sea (Gorbunov, 1946; Plotkin, 2004) and Indian Ocean (Mozambique (Plotkin et al., 2016b), Zanzibar (Burton, 1959b), Saya de Malha (Dendy, 1922), South off Maldives (Burton, 1959b)). This list may also be appended with the records of *Radiella sol* from the Barents, Kara and Laptev Sea by Koltun (1964, 1966) and *Trichostemma sol* from the Norwegian–Greenland Sea by Barthel & Tendal (1993), who at that time regarded *Radiella sarsii* to be a synonym of *Radiella sol*, which was in fact originally described from the Mexican Gulf (Schmidt, 1870). Furthermore, Van Soest et al. (2016) assumed that *Suberites alveus* Hansen, 1885 and *Suberites conica* Hansen, 1885 from the Norwegian Sea were very probably conspecific with *Spinularia sarsii*, just displaying variation of the body shape resembling a hive-like cone in *S. alveus* and a flattened cone in *S. conica*.

The cosmopolitan distribution of *Spinularia sarsii* is questioned by Plotkin et al. (2016b) and the present study based on genetic data. In the 28S rDNA phylogeny morphologically very similar *S. sarsii* (former *Radiella sarsii*) from the Norwegian Sea and *S. cf. sarsii* from the Mozambican Coast (former *Radiella cf. sarsii*) do not group together, although they fall in the same clade (Plotkin et al., 2016b). Furthermore, the Mozambican sponge is distinguished from the congeners in CO1, whereas the sequences of this phylogenetic marker obtained from the Norwegian *S. sarsii*, *S. spinularia* and *S. njordi* are identical. Based on these data the records of *S. sarsii* from the northern and southern hemisphere are assumed to represent two different species. However, herein we do not formally establish a new species for the Mozambican individual because the locality is outside our study area and more material is required for a careful morphological description. At the same time there are no genetic data on *S. sarsii* from North Atlantic regions other than the Norwegian Sea, while the comparison of the Norwegian *S. sarsii* with the type material from Azores reveals no morphological differences. Neither can we check

whether *Suberites alveus* and *Suberites conica* from the Norwegian Sea are indeed conspecific with *Spinularia sarsii* because the type material of the first two species is unfortunately lost. Therefore, for the moment we consider all records of *Spinularia sarsii* from the northern hemisphere as one species.

Spinularia spinularia (Bowerbank, 1866) (Figures 31 & 32)

Original description: *Tethea spinularia* Bowerbank, 1866, p. 94.

SYNOMYMS AND CITATIONS

Polymastia spinularia (Hanitsch, 1894, p. 202).

Radiella spinularia (Schmidt, 1870, p. 48, pl. IV figures 7 & 8; Fristedt, 1885, p. 16, 1887, p. 435).

Spinularia spinularia (Stephens, 1915, p. 31, pl. III figure 5, pl. V figure 3; Burton, 1930a, p. 496; Alander, 1942, p. 76; Boury-Esnault, 2002, p. 216, figure 13; Plotkin et al., 2012, p. 27, figure 2i).

Spinularia tethaeoides (Gray, 1867, p. 524).

Tethea spinularia (Bowerbank, 1874: pl. XV figures 23–30).

Non *Spinularia spinularia* (Topsent, 1928, p. 150).

TYPE MATERIAL

Lectotype of *Tethea spinularia* (designated herein, dry specimen (Figure 31A) and seven slides labelled BR 393): BMNH 1910.1.1.34A, Shetland, UK, precise locality unknown, coll. Alfred M. Norman.

Paralectotypes of *Tethea spinularia*: BMNH 1910.1.1.34B (one dry specimen and three fragments): from the same sample as the lectotype.

Slides from the paralectotypes of *Tethea spinularia*: BMNH 10.1.1.1820, BMNH 10.1.1.1821 and 10.1.1.1822.

Holotype of *Rhaphidorus setosus* Topsent, 1898 (in alcohol): MOM 04-0303, East off Sao Miguel, Azores, 38°09'N 23°15.75'W – 38°08'N 23°18.75'W, 4020 m, Campagnes

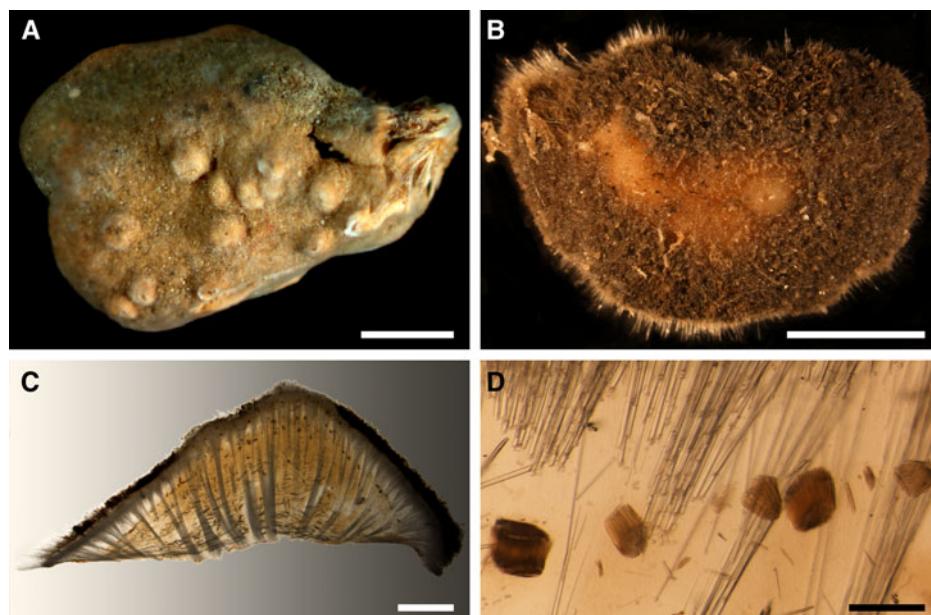


Fig. 31. *Spinularia spinularia*: (A) lectotype BMNH 1910.1.1.34A, habitus; (B) an individual from Hardangerfjorden, Norway, habitus; (C) the same individual, longitudinal section through the body, general view; (D) the same section, detail of subcortical area with trichodragmata. Scale bars: A–B, 0.5 cm; C, 2 mm; D, 0.2 mm.

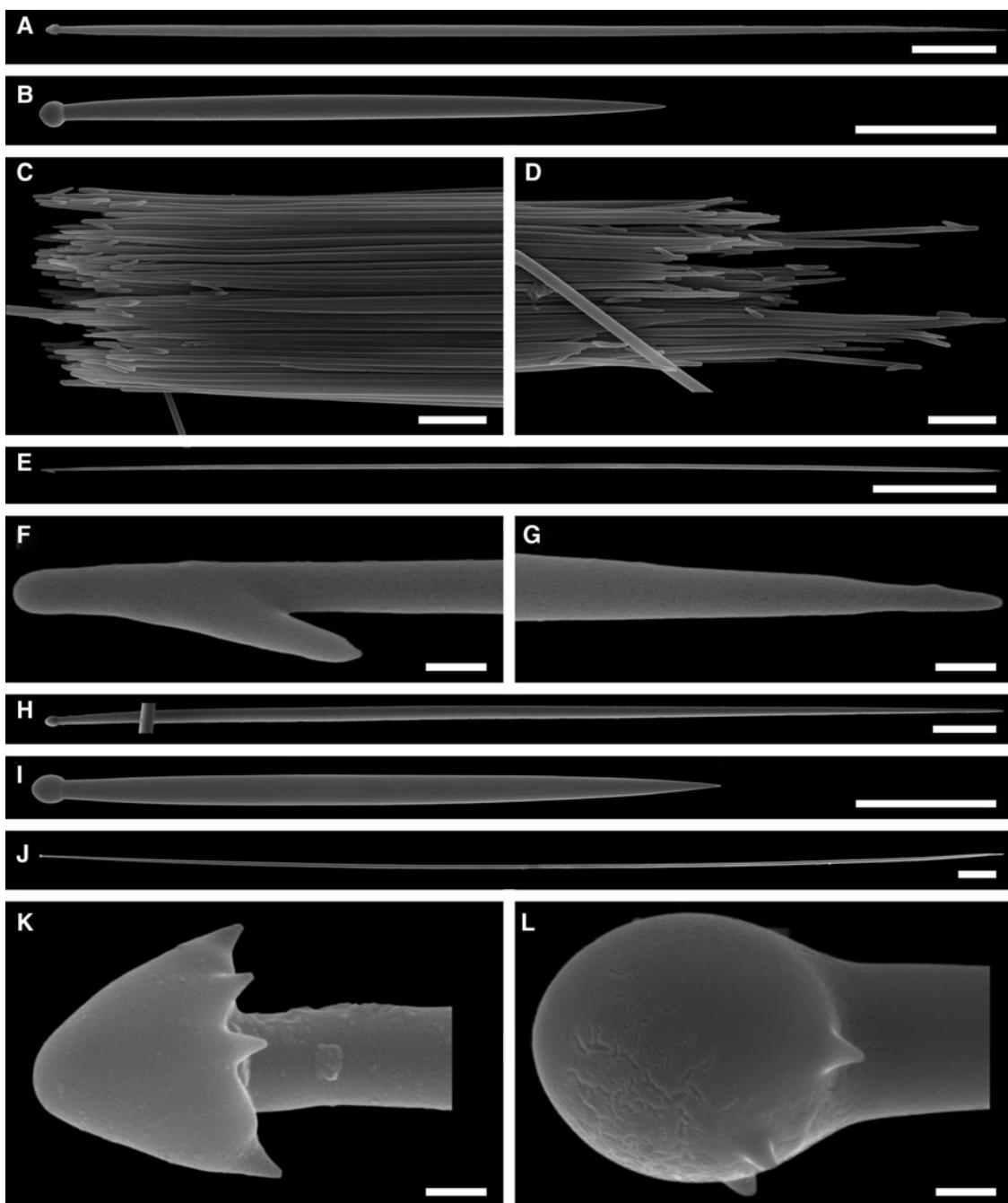


Fig. 32. *Spinularia spinularia* and *S. setosa*, spicules: (A) *S. spinularia*, principal tylostyle; (B) *S. spinularia*, small tylostyle; (C) and (D) *S. spinularia*, details of a trichodragma of raphides, (E) *S. spinularia*, raphide, general view; (F) the same spicule, detail of harpoon-shaped tip; (G) the same spicule, detail of the opposite tip; (H) *S. setosa*, principal tylostyle; (I) *S. setosa*, small tylostyle; (J) *S. setosa*, raphide, general view; (K) the same spicule, detail of umbrelliform tip; (L) another raphide of the same sponge, detail of subspherical tip. Scale bars: A, 0.1 mm; B, 0.05 mm; C and D, 0.002 mm; E, 0.01 mm; F and G, 0.2 µm; H, 0.1 mm; I, 0.05 mm; J, 0.01 mm; K and L, 0.2 µm.

scientifiques accomplies par le Prince Albert I de Monaco, RV 'Princesse-Alice', station 527, 25.06.1895. *Rhaphidorus setosus* was relegated to a synonym of *Spinularia spinularia* by Stephens (1915), but herein it is assumed to be a separate species *Spinularia setosa* (see Discussion below).

COMPARATIVE MATERIAL (see Online resource 1 for details)

Sweden: Västra Götaland: GNM 792:1 (one specimen).

Norway: Aust-Agder: ZMBN 107587 (one specimen), Hordaland: ZMBN 098037, ZMBN 098076 and ZMBN 098079 (three specimens), Sogn and Fjordane: ZMBN 098050 (one specimen), Møre and Romsdal: ZMBN 107488 and ZMBN 107494 (two specimens), Sør-Trøndelag: NTNU-VM-54615 (one specimen), Nord-Trøndelag: NTNU-VM-54669, NTNU-VM-56952, NTNU-VM-72538 and NTNU-VM-72546 (seven specimens). Norwegian Sea, offshore: ZMBN 107586 (one specimen).

DESCRIPTION

External morphology

Lectotype of *Tethea spinularia* cushion-shaped, $\sim 23 \times 15 \times 12$ mm, removed from the substrate (Figure 31A). Surface rough, beige in the central area and grey in the periphery, bearing 11 wart-like papillae, most with oscula at the summits. The most intact paralectotype cushion-shaped, $\sim 9 \times 8 \times 5$ mm, removed from the substrate. Surface minutely hispid, covered with grey sediment in the periphery and clean, pale orange in the central area around a single wart-like papilla. Two paralectotypes are fragments of cushion-shaped sponges with minutely hispid surface, without papillae, removed from the substrates. The smallest paralectotype is a tiny encrust on a stone. Holotype of *Rhaphidorus setosus* cushion-shaped, about 12 mm in diameter, considerably damaged, attached to a stone. Scandinavian sponges cushion-shaped, occupying up to 9 cm² of the substrate (Figure 31B). Surface minutely hispid, occasionally smooth and free of sediment in the central area and more hispid and covered with sediment in the periphery, bearing up to 15 papillae. Many individuals with tiny spicule fringes at the body edges. Papillae small, usually wart-like, with oscula at the summits.

Anatomy

Description is based on the lectotype of *Tethea spinularia* and Scandinavian individuals. Anatomy of the holotype of *Rhaphidorus setosus* is not studied because of its considerable damage. Choanosome in life pale orange, dense. Main choanosomal skeleton composed of tracts (72–380 µm thick) of principal spicules radiating from the base, crossing the cortex and protruding above the surface (Figure 31C). Some tracts ascend to the papilla walls. Auxiliary choanosomal skeleton comprises free-scattered bundles of small spicules spread all over the body, bundles of principal spicules concentrated in the basal area and lying perpendicular to the main tracts, and trichodragmata (dense packs, 69–391 long and 56–453 µm wide) of raphides concentrated in the subcortical area (Figures 31D & 32C–D). Cortex in life whitish, cream-coloured or pale brown, firm, not detachable. Cortical skeleton comprises a superficial palisade (368–643 µm thick) of small spicules and an inner space (256–1128 µm thick) with low concentration of spicules, both reinforced with the ascending choanosomal tracts. Papilla wall covered with a superficial palisade.

Spicules

Lectotype of *Tethea spinularia*, two Swedish individuals and seven Norwegian individuals:

Principal spicules (Figure 32A) – tylostyles with roundish, occasionally oval, tyles, usually straight and slender. Length 404–758–1355 µm, diameter of tyle 6.8–9.3–14.4 µm, proximal diameter of shaft 3.2–6.0–10.0 µm, maximum diameter of shaft 5.8–10.0–14.6 µm, N = 300.

Small spicules (Figure 32B) – tylostyles, straight or occasionally gently bent, slightly fusiform. Length 161–290–373 µm, diameter of tyle 6.6–8.8–11.5 µm, proximal diameter of shaft 2.8–5.6–7.8 µm, maximum diameter of shaft 5.4–8.8–13.4 µm, N = 300.

Raphides (Figure 32C–G) – thin monactines with one tip acerated (Figure 32G) and the other harpoon-shaped, with a blunt point and a lateral barb (Figure 32F). Length 65–79–

85 µm, maximum diameter of shaft 0.3–0.4–0.4 µm, N = 200.

Holotype of *Rhaphidorus setosus*:

Principal spicules (Figure 32H) – tylostyles with roundish, occasionally oval, tyles, usually straight and slightly fusiform. Length 548–1458–2185 µm, diameter of tyle 10.5–16.2–20.2 µm, proximal diameter of shaft 7.4–14.1–19.5 µm, maximum diameter of shaft 11.9–17.5–22.8 µm, N = 30.

Small spicules (Figure 32I) – tylostyles, usually straight and slender. Length 216–252–330 µm, diameter of tyle 11.1–11.7–12.5 µm, proximal diameter of shaft 7.2–7.7–8.4 µm, maximum diameter of shaft 10.9–12.0–12.7 µm, N = 30.

Raphides (Figure 32J) – thin monactines with one tip acerated and the other bearing an umbrelliform (Figure 32K) or sub-spherical ornamentation (Figure 32L) with tiny jags along the edge. Length 233–245–260 µm, maximum diameter of shaft 1.0–1.2–1.3 µm, N = 20.

Genetic data

28S rDNA was obtained from five individuals of *Spinularia spinularia*, while CO1 was sequenced only from four of them. The CO1 sequences are identical, but a polymorphism is revealed in 28S rDNA. Two subspecies groups, one comprising three individuals and the other two individuals, differ by two bps in this gene (Matrix M34250 in TreeBase). The synapomorphies and distinctions of *S. spinularia* from the congeners are described in the Genetic data sections for *S. njordii* and *S. sarsii*.

OCCURRENCE

(Figure 33)

Literature data: East Greenland (237 m) (Fristedt, 1887), Ireland (1001 m) (Stephens, 1915). Shetland (Bowerbank, 1866, 1874). Swedish Western Coast (50 m) (Fristedt, 1885; Alander, 1942). Norwegian Coast: Rogaland, Hordaland (70 m and deeper) (Burton, 1930a; Alander, 1942).

Our data: Skagerrak: Swedish Western Coast (45–60 m), Southern Norwegian Coast (Aust-Agder) (137–149 m). Norwegian Coast: Hordaland (30–310 m), Sogn and Fjordane (240–243 m), Møre and Romsdal (depth unknown), Sør-Trøndelag (14–35 m), Nord-Trøndelag (25–400 m). Norwegian Sea, offshore areas (272–311 m).

DISCUSSION

Since Bowerbank (1866) established *Tethea spinularia* for several sponges from Shetland the validity of this species was not disputed except for the proposal by Schmidt (1880) to synonymize it with *Halicnemia patera* not supported by the subsequent authors. Meanwhile, there was some disagreement on what genus it should be placed in. Gray (1867) established for *T. spinularia* a new genus *Spinularia*. However, Schmidt (1870) and Fristedt (1885, 1887) proposed to place *T. spinularia* in *Radiella*, while Hanitsch (1894) allocated it to *Polymastia*. *Spinularia* was resurrected by Stephens (1915) defining the main distinguishing feature of its type species, the presence of raphides in trichodragmata. Based on this feature she also synonymized an Azorean species *Rhaphidorus setosus* Topsent, 1898 with *S. spinularia*. Both actions were encouraged by most subsequent authors (Topsent, 1928; Burton, 1930a; Alander, 1942; Boury-Esnault, 2002; Plotkin et al., 2012). However, examination of the type and comparative material of *S. spinularia* and the holotype of *R. setosus* has revealed that in the latter both the

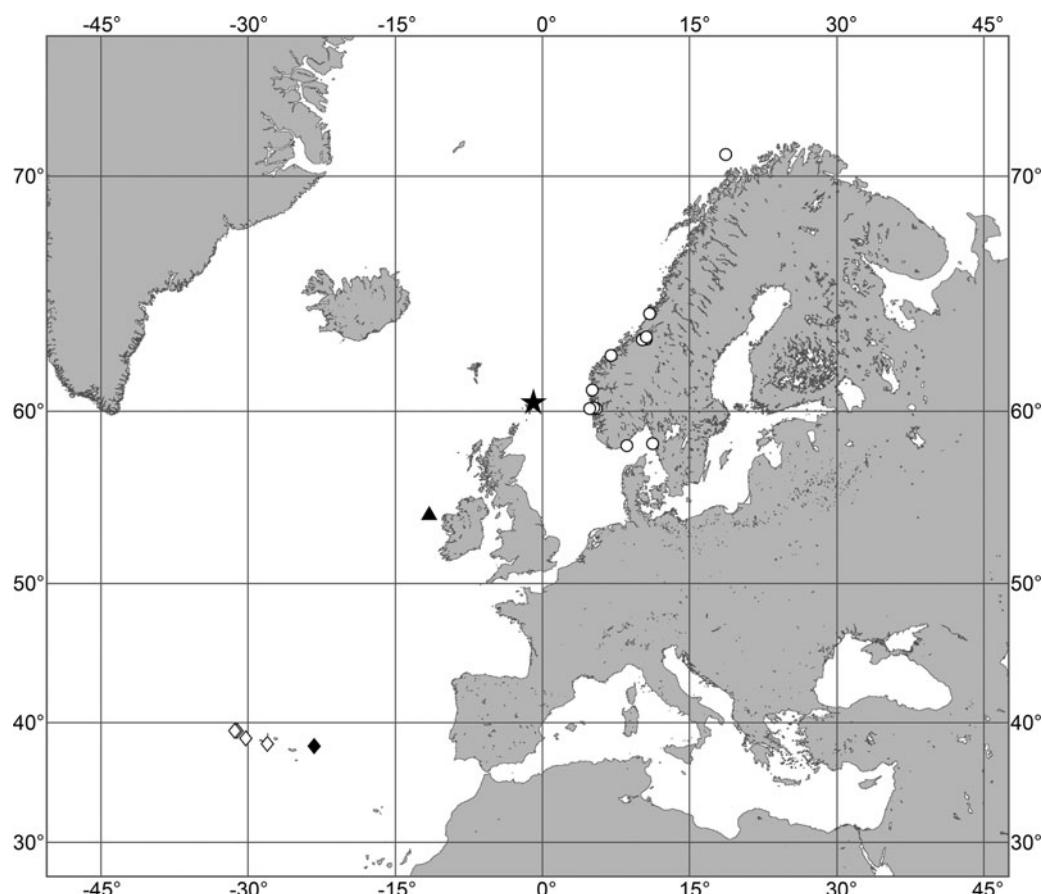


Fig. 33. *Spinularia spinularia* and *S. setosa*, distribution: black star, type locality of *S. spinularia*; black triangle, data on *S. spinularia* from Stephens (1915); white circles, our data on *S. spinularia*; black diamond, type locality of *S. setosa*, white diamonds, other records of *S. setosa* (Topsent, 1904, 1928).

principal spicules and the raphides are longer than in *S. spinularia*. Moreover, the raphides in *R. setosus* bear umbrelliform or subspherical distal ornaments, whereas in *S. spinularia* they are harpoon-shaped. Based on these differences we assume that *R. setosus* may be accepted as a separate species of *Spinularia*, *S. setosa*, although this should preferably be tested further with molecular data.

Genus *Tentorium* Vosmaer, 1887

Original description: *Tentorium* Vosmaer, 1887, p. 329, pl. II figure 4, pl. 21 figure 19.

SYNONYMS

Thecophora Schmidt, 1870, p. 50 (preoccupied by *Thecophora* Rondani, 1845, a genus of flies).

TYPE SPECIES

Thecophora semisuberites Schmidt, 1870 (by original designation).

DIAGNOSIS

Polymastiidae of columnar or globular body shape, always with papillae. Main choanosomal skeleton constituted by longitudinal or radial tracts of principal monactines. Skeleton of the upper cortex comprises a palisade of small monactines. Skeleton of the lateral cortex may be either the same palisade or a dense layer of criss-cross principal or intermediary spicules.

DISCUSSION

In the CO1 and 28S rDNA phylogenies *Tentorium* Vosmaer, 1887 is not monophyletic (Plotkin *et al.*, 2016b; Figure 1 in this study). The type species, *T. semisuberites* and *T. papillatum* Kirkpatrick, 1908 do not group together and, moreover, in the 28S rDNA tree the Arctic *T. semisuberites* and the Antarctic *T. cf. semisuberites* are not sisters. At the same time these phylogenies are unable to reconstruct the relationships between *Tentorium* spp. and other polymastiids, and therefore no alternative classification is proposed. Until more molecular data on a larger set of species become available, we recognize *Tentorium* as a valid genus, but emend its diagnosis proposed by Boury-Esnault (2002) so that all species currently allocated to *Tentorium* (Van Soest *et al.*, 2016) fit with it.

Tentorium semisuberites (Schmidt, 1870) (Figure 34)

Original description: *Thecophora semisuberites* Schmidt, 1870, p. 50, pl. VI figure 2.

SYNONYMS AND CITATIONS

Tecophora semisuberites (Fristedt, 1885, p. 17, 1887, p. 433). *Thecophora elongata* von Marenzeller, 1878, p. 368, pl. II figure 4. *Thecophora ibla* Thompson, 1873, p. 147, figure 24 (Verrill, 1874, p. 500, 505, pl. VIII figure 8; Whiteaves, 1874, p. 184).

Thecophora semisuberites (Thompson, 1873, p. 147, figure 23; Whiteaves, 1874, p. 184; von Marenzeller, 1878, p. 368; Vosmaer, 1882, p. 30, 1885, p. 18, text-figure 9, pl. I figures 23 & 24 and pl. III figures 22–26; Hansen, 1885, p. 8).

Tentorium semisuberites (Vosmaer, 1887, p. 329, pl. II figure 4 and pl. XXI figure 19; Ridley & Dendy, 1887, p. 221; Lambe, 1896, p. 198, pl. III figures 2, 2a–c; Topsent, 1892, p. 132; Lambe, 1900, p. 25; Whiteaves, 1901, p. 14; Topsent, 1904, p. 124, 252–253; 1913, p. 25, 1928, p. 151, pl. VI, figure 10; Lundbeck, 1909, p. 452; Gorbunov, 1946, p. 37; Koltun, 1966, p. 85, text-figure 57, pl. XIX figures 4–8, pl. XXXI figure 12; Barthel & Tendal, 1993, p. 88, figure 8; Boury-Esnault, 2002, p. 215, figure 12; Plotkin, 2004, p. 544, figures 1j & 2j; Plotkin *et al.*, 2012, p. 25, figure 1g).

TYPE MATERIAL

Holotype: ZMUC-DEM-396, Greenland, precise locality unknown.

COMPARATIVE MATERIAL

(see Online resource 1 for details)

Canada: Newfoundland and Labrador: ZIN RAS octs140, ZIN RAS octs142, ZIN RAS octs143 and ZIN RAS octs150 (four specimens).

Greenland: South-East Coast: ZIN RAS octs101, ZIN RAS octs138, ZIN RAS octs197, ZIN RAS octs199 and ZIN RAS octs201 (six specimens), East Coast: ZIN RAS octs092, ZIN RAS octs173 and ZIN RAS octs176 (six specimens), North-East Coast: ZIN RAS octs174 (one specimen).

Icelandic Coast and Iceland Sea: ZIN RAS octs088, ZIN RAS octs132, ZIN RAS octs141, ZIN RAS octs151 and ZIN RAS octs193 (27 specimens).

Denmark Strait: ZIN RAS octs139 (four specimens).

North-East Atlantic, offshore: ZIN RAS octs146, ZIN RAS octs147, ZIN RAS octs148 and ZIN RAS octs200 (four specimens).

Greenland Sea, offshore: ZIN RAS octs090, ZIN RAS octs091, ZIN RAS octs093, ZIN RAS octs094, ZIN RAS octs095, ZIN RAS octs096, ZIN RAS octs175, ZIN RAS octs178, ZIN RAS octs179, ZIN RAS octs180, ZIN RAS octs181, ZIN RAS octs182, ZIN RAS octs204, ZIN RAS octs209 and ZIN RAS octs216 (26 specimens).

Norwegian Sea, offshore: NTNU-VM-72502, NTNU-VM-72512, NTNU-VM-72526, ZIN RAS octs023, ZIN RAS

octs034, ZIN RAS octs067, ZIN RAS octs068, ZIN RAS octs087, ZIN RAS octs104, ZIN RAS octs105, ZIN RAS octs126, ZIN RAS octs152, ZIN RAS octs161 and ZIN RAS octs203 (69 specimens).

Barents Sea, offshore: 141 specimens deposited in ZIN RAS. Norway: Hordaland: ZMBN 098099 (one specimen), Møre and Romsdal: ZMBN 107492 (one specimen), Nord-Trøndelag: NTNU-VM-72539 and NTNU-VM-72547 (two specimens), Nordland: NTNU-VM-72517 (one specimen), Troms: NTNU-VM-72531 (one specimen), Svalbard: ZIN RAS octs084, ZIN RAS octs099, ZIN RAS octs106 and ZMBN 098054 (17 specimens).

Russia: Murman Coast: ZIN RAS octs054, ZIN RAS octs058, ZIN RAS octs100, ZIN RAS octs130, ZIN RAS octs135, ZIN RAS octs156, ZIN RAS octs157, ZIN RAS octs158, ZIN RAS octs159, ZIN RAS octs191, ZIN RAS octs194 and ZIN RAS octs211 (51 specimens), Kanin Peninsula: ZIN RAS octs053 (six specimens), Pechora Sea: ZIN RAS octs028 (five specimens), Franz Josef Land: ZIN RAS octs014, ZIN RAS octs113, ZIN RAS octs122, ZIN RAS octs145, ZIN RAS octs153, ZIN RAS octs188 and ZIN RAS octs189 (21 specimens), Novaya Zemlya: ZIN RAS octs001, ZIN RAS octs006 and ZIN RAS octs206 (four specimens), Taymyr Peninsula: ZIN RAS octs079 and ZIN RAS octs215 (four specimens), Nordenskjold Archipelago: ZIN RAS octs089, ZIN RAS octs123, ZIN RAS octs124 and ZIN RAS octs214 (92 specimens), Severnaya Zemlya: ZIN RAS octs011, ZIN RAS octs013, ZIN RAS octs015, ZIN RAS octs016, ZIN RAS octs082, ZIN RAS octs108, ZIN RAS octs109, ZIN RAS octs115, ZIN RAS octs116 and ZIN RAS octs117 (144 specimens).

Kara Sea: ZIN RAS octs002, ZIN RAS octs003, ZIN RAS octs004, ZIN RAS octs008, ZIN RAS octs009, ZIN RAS octs085, ZIN RAS octs102, ZIN RAS octs103, ZIN RAS octs154, ZIN RAS octs198, ZIN RAS octs205, ZIN RAS octs207, ZIN RAS octs208, ZIN RAS octs210, ZIN RAS octs213 and ZIN RAS octs219 (43 specimens).

Laptev Sea: ZIN RAS octs007 and ZIN RAS octs110 (three specimens).

East Siberian Sea: ZIN RAS octs086, ZIN RAS octs098, ZIN RAS octs171 and ZIN RAS octs172 (27 specimens).

Arctic Ocean, offshore: ZIN RAS octs081, ZIN RAS octs097, ZIN RAS octs107, ZIN RAS octs111, ZIN RAS octs112, ZIN RAS octs128, ZIN RAS octs149, ZIN RAS octs177, ZIN RAS

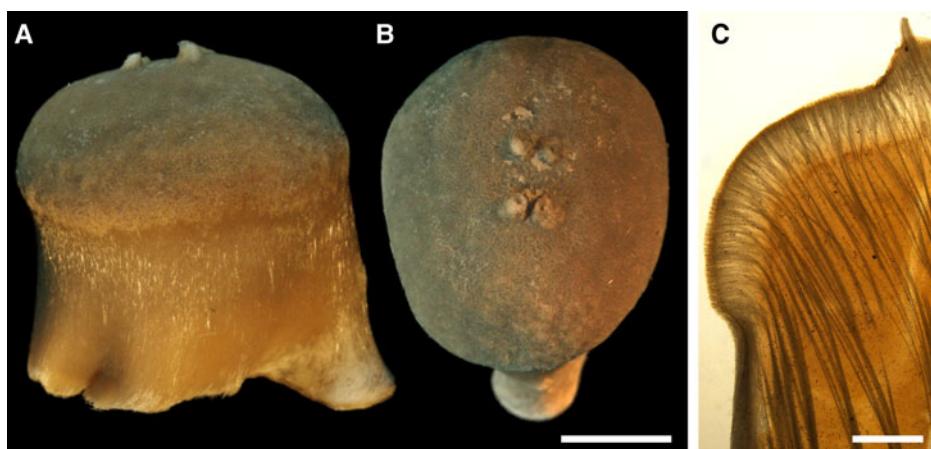


Fig. 34. *Tentorium semisuberites*: (A) holotype ZMUC-DEM-396, habitus, side view; (B) the same, view from above; (C) ZIN RAS octs059, longitudinal section through the body. Scale bars: A–B, 0.5 cm; C, 2 mm.

octs184, ZIN RAS octs185, ZIN RAS octs186, ZIN RAS octs187 and ZIN RAS octs190 (69 specimens).

DESCRIPTION

External morphology

Holotype fungiform, ~16 mm high and 13–15 mm in diameter, removed from the substrate (Figure 34A, B). Lateral surface smooth, pale beige (Figure 34A). Upper surface minutely hispid, beige, with four small exhalant papillae at the summit (Figure 34B). Other sponges columnar, fungiform, occasionally drum-shaped, up to 35 mm high and 30 mm in diameter, with distinct difference between the smooth, palely coloured lateral surface and the more or less hispid, phaeochrous upper surface bearing one to 20 exhalant papillae. In some individuals the papillae considerably stretched, thread like, with the length exceeding the height of the main body by several times. When growing on soft sediments, the sponges often form long root-like structures made of spicule bundles.

Anatomy

Choanosome in life pale orange, pale yellow or light brown, dense. Main choanosomal skeleton composed of longitudinal tracts (430–1000 µm thick) of principal spicules running from the base, branching and entering the cortex (Figure 34C). Some tracts ascend to the papilla walls. No auxiliary choanosomal skeleton observed. Cortex in life whitish or light beige, firm, not detachable. Skeleton of the lateral cortex (500–780 µm thick) is a dense layer of criss-crossed intermediary spicules. Skeleton of the upper cortex (1000–1600 µm thick) comprises radiating tracts of principal spicules ascending from the choanosome perpendicular to the surface and a superficial palisade (450–650 µm thick) of small spicules.

Spicules

(Measurements based on 15 individuals)

Principal spicules – subtylostyles to tylostyles, usually straight and slender. Length 956–1642–2400 µm, maximum diameter of shaft 13.2–20.8–25.2 µm, N = 450.

Intermediary spicules – tylostyles, straight, fusiform. Length 810–955–1138 µm, maximum diameter of shaft 20.5–24.7–31.2 µm, N = 450.

Small spicules – tylostyles, straight, fusiform. Length 274–467–670 µm, maximum diameter of shaft 12.8–16.8–19.8 µm, N = 450.

Genetic data

In the CO1 phylogeny *Tentorium semisuberites* is the sister to the clade of *Spinularia* spp., but in the 28S rDNA it has no close relations (Plotkin *et al.*, 2016b). At the same time *T. semisuberites* possesses just one autapomorphy in CO1 distinguishing it from all other polymastiids (Online resource 2, p. 5). Moreover, an intraspecific polymorphism in both genes is observed in this species. The two individuals, from which the data were obtained, differ by two bps in CO1 (Matrix M34248 in TreeBase) and four bps in 28S rDNA (Matrix M34250 in TreeBase).

OCCURRENCE

(Figure 35)

Literature data (only the localities distinct from our data are given): US Atlantic Coast: Gulf of Maine (Verrill, 1874). Canadian Atlantic Coast: Nova Scotia (1458 m) (Topsent, 1928), Gulf of St. Lawrence (91–175 m) (as *Thecophora semisuberites* and *T. ibla* – Whiteaves, 1874; as *Tentorium semisuberites* – Lambe, 1896; Whiteaves, 1901). Davis Strait (273 m) (Lambe, 1900; Whiteaves, 1901). West Greenland: Uummannaq Fjord (211–746 m) (Fristedt, 1887). North Atlantic: Azores (200–3018 m) (Topsent, 1892, 1904, 1928), Bay of Biscay (248 m) (Topsent, 1892).

Our data (agree with most literature data): Canadian Atlantic Coast: Newfoundland and Labrador (208–375 m). Greenland: South-East Coast (180–400 m), East Coast (56–165 m), North-East Coast (83 m). Icelandic Coast and Iceland Sea

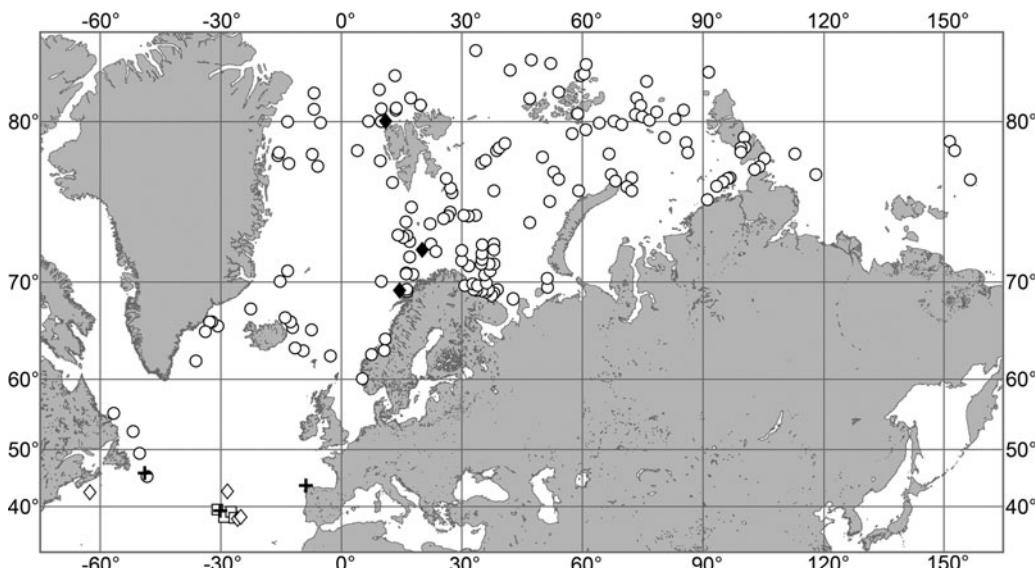


Fig. 35. *Tentorium semisuberites*, distribution: black crosses, data from Topsent (1892); white squares, data from Topsent (1904); black diamonds, data from Topsent (1913); white diamonds, data from Topsent (1928); white circles, our data. Precise type locality is unknown.

(165–1075 m). Denmark Strait (650 m). North-East Atlantic, offshore areas (385–485 m). Greenland Sea, offshore areas (136–2800 m). Norwegian Sea, offshore areas (180–1820 m). Norwegian Coast: Hordaland (100–500 m), Møre and Romsdal (108–109 m), Nord-Trøndelag (40–400 m), Nordland (360 m), Troms (200–220 m). Barents Sea: Murman Coast (75–271 m), Kanin Peninsula (228 m), Pechora Sea (64 m), offshore areas (66–395 m). Svalbard (81–550 m). Franz Josef Land (124–285 m), Novaya Zemlya (307–368 m), Taymyr Peninsula (53 m), Nordenskjold Archipelago (53–82 m), Severnaya Zemlya (43–257 m). Kara Sea (41–580 m). Laptev Sea (86–459 m). East Siberian Sea (65–81 m). Arctic Ocean, offshore areas (165–2899 m).

DISCUSSION

Taxonomic identification of *Tentorium semisuberites* usually causes no difficulties. *Thecophora ibla* Thomson, 1873 and *Thecophora elongata* von Marenzeller, 1878 represent in fact just varieties of body shapes in *T. semisuberites*. Meanwhile, the phylogenetic relationships of *T. semisuberites* are unresolved (see Genetic data for this species and Discussion on the genus *Tentorium* above).

Genus *Weberella* Vosmaer, 1885

Original description: *Weberella* Vosmaer, 1885, p. 16, text-figures 6 & 8, pl. III figures 16–19.

TYPE SPECIES

Alcyonium bursa Müller, 1806 (by original designation).

DIAGNOSIS

Polymastiidae of massive or globular body shape, with a smooth surface always bearing papillae. Spicule assortment restricted to two size categories of smooth monactines. Main choanosomal skeleton is a reticulation formed by tracts of principal monactines. Auxiliary choanosomal skeleton comprises free-scattered small monactines. Cortical skeleton composed of a palisade of small tylostyles or subtylostyles and an internal layer of criss-cross principal monactines separated by a middle layer with aquiferous cavities.

DISCUSSION

Weberella is morphologically well-defined, but the relationships between *Weberella* spp. are unclear because for the moment the genetic data are only available from the type species, *W. bursa*.

Weberella bursa (Müller, 1806) (Figure 36)

Original description: *Alcyonium bursa* Müller, 1806, p. 43, pl. CLVIII figures 1 & 2.

SYNONYMS AND CITATIONS

Polymastia bursa (Koltun, 1964, p. 149, 1966, p. 76, text-figure 49, pl. IX figure 2; pl. XXIII figure 1–2, pl. XXIV figures 1 & 2).

Polymastia uberrima (Burton, 1959a: 12 pars.).

Weberella bursa (Vosmaer, 1885, p. 16, text-figures 6 & 8, pl. III figures 16–19, 1887, p. 329 pl. XXVI figure 10; Topsent, 1928, p. 149, pl. II, figure 19; Boury-Esnault et al., 1994, p.

76, figure 51, 2002, p. 214, figure 11; Plotkin, 2004, p. 544, figures 1k & 2k; Plotkin et al., 2012, p. 25, figure 1j). Non *Polymastia bursa* (von Lendenfeld, 1898, p. 117, pl. VI figure 79).

TYPE MATERIAL

Unknown.

COMPARATIVE MATERIAL

(see Online resource 1 for details)

Canada: Newfoundland: ZIN RAS ocwbo04 (one specimen), offshore areas of the NW Atlantic: ZIN RAS ocwbo10 (one specimen).

Greenland: SW Coast/Davis Strait: ZIN RAS ocwbo33 and ZIN RAS ocwbo35 (two specimens), SE Coast: ZIN RAS ocwbo03 and ZIN RAS ocwbo31 (two specimens).

Denmark Strait: ZIN RAS ocwbo25 (one specimen).

Iceland: ZIN RAS ocwbo05, ZIN RAS ocwbo15, ZIN RAS ocwbo18 and ZIN RAS ocwbo36 (four specimens).

Faroës: ZIN RAS ocwbo11 (one specimen).

Norwegian Sea, offshore: ZIN RAS ocwbo12 and ZIN RAS ocwbo20 (two specimens).

Barents Sea, offshore: ZIN RAS ocwbo01, ZIN RAS ocwbo02, ZIN RAS ocwbo06, ZIN RAS ocwbo07, ZIN RAS ocwbo08, ZIN RAS ocwbo09, ZIN RAS ocwbo13, ZIN RAS ocwbo16, ZIN RAS ocwbo19, ZIN RAS ocwbo21, ZIN RAS ocwbo23, ZIN RAS ocwbo26, ZIN RAS ocwbo27, ZIN RAS ocwbo28, ZIN RAS ocwbo29, ZIN RAS ocwbo30 and ZIN RAS ocwbo32 (17 specimens).

Norway: Sør-Trøndelag: NTNU-VM-56951 (one specimen), Nord-Trøndelag: NTNU-VM-54951 (one specimen), Nordland: NTNU-VM-72522 (one specimen), Troms: NTNU-VM-72532 and ZMBN 098072 (two specimens), Finnmark: NTNU-VM-72504 and ZIN RAS ocwbo24 (two specimens), Svalbard: ZIN RAS ocwbo22 and ZMBN 098051 (two specimens).

Russia: Franz Josef Land: ZIN RAS ocwbo17 (one specimen), Novaya Zemlya: ZIN RAS ocwbo14 and ZIN RAS ocwbo34 (two specimens).

DESCRIPTION

External morphology

Massive, fist-shape, or occasionally globular sponges occupying up to 100 cm² of the substrate (Figure 36A, B). Surface smooth, white or pale cream both in life and alcohol, with up to 200 papillae, all with oscula at the summits. The papillae conical, 2–8 mm long, up to 8 mm wide at base and 2 mm wide at summit.

Anatomy

Choanosome crumbly, pale yellow in life, but becoming slightly darker in alcohol. Main choanosomal skeleton composed of reticulating tracts (47–254 µm thick) of principal spicules (Figure 36C). Some tracts ascend to the cortex and the papillae. Auxiliary choanosomal skeleton comprises free-scattered small spicules. Cortex both in life and alcohol whitish, firm, but detachable. Cortical skeleton includes a superficial palisade (246–337 µm thick) composed of tufts of small spicules, a middle layer (513–1011 µm thick) with aquiferous cavities separated by the ascending and radiating choanosomal tracts and an internal layer (100–233 µm thick) of obliquely lying small spicules (Figure 36D). The cortical palisade and the internal layer stretch to the papillae

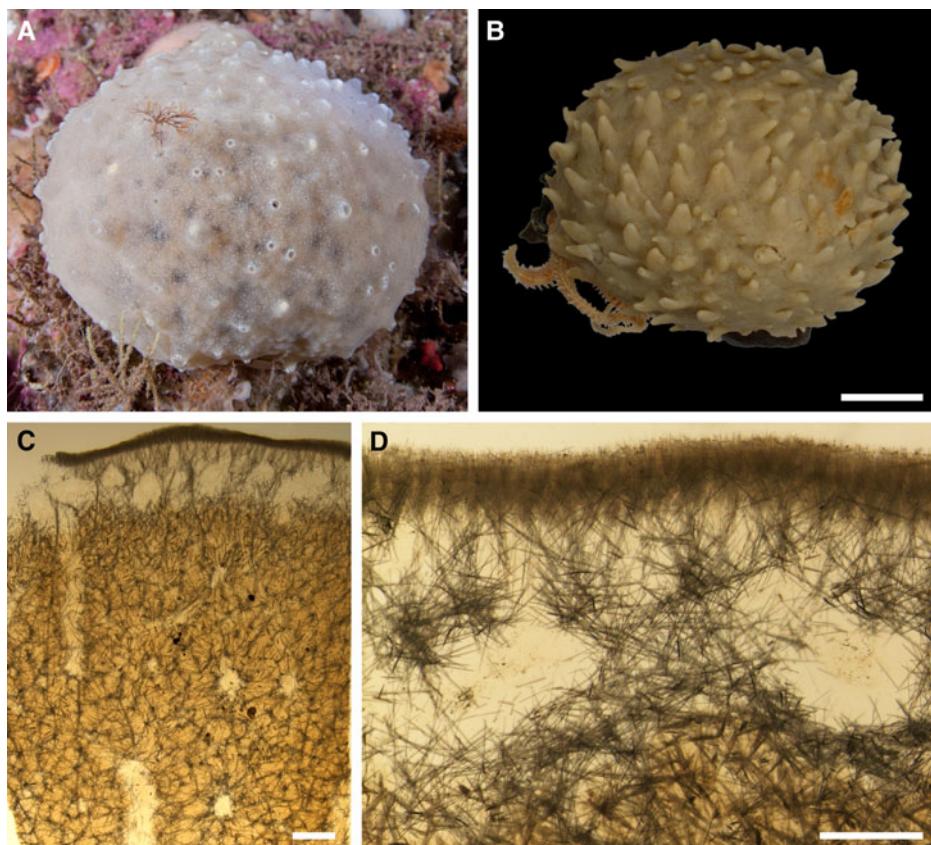


Fig. 36. *Weberella bursa*: (A) ZMBN 098051 *in situ*, Hinlopenstretet, Svalbard, Norway (courtesy P. Leopold, University of Tromsø); (B) ZIN RAS ocwb016, habitus; (C) the same, longitudinal section through the body, general view; (D) the same section, detail of cortex. Scale bars: B, 2 cm; C, 1 mm; D, 0.5 mm.

walls. Each papilla has a large central exhalant canal and numerous small inhalant canals in the periphery. Bulkheads separating the canals reinforced with the ascending tracts of principal spicules and free-scattered small spicules.

Spicules

(Measurements based on 12 individuals)

Principal spicules – subtylostyles, occasionally styles, usually straight and slender. Length 407–538–700 µm, diameter of tyle 8.8–11.0–13.0 µm, proximal diameter of shaft 7.4–9.6–12.5 µm, maximum diameter of shaft 8.8–11.0–12.6, N = 360.

Small spicules – tylostyles, occasionally subtylostyles, usually straight and slender. Length 90–201–273 µm, diameter of tyle 2.5–4.8–7.7 µm, proximal diameter of shaft 1.9–3.3–5.0 µm, maximum diameter of shaft 1.9–3.6–5.3, N = 360.

Genetic data

Two individuals of *Weberella bursa*, from which the genetic data were obtained, differ neither by CO1, nor by 28S rDNA. In the phylogenies based on these genes *W. bursa* is the sister to morphologically quite distinct *Polymastia cf. conigera* (a British species not covered by the present study), although the Bayesian support for this relationship is weak (Plotkin *et al.*, 2016b). These species share two unique synapomorphies in CO1 (Online resource 2, p. 3, Matrix M34248 in TreeBase) and three synapomorphies in 28S rDNA, of which one is unique and two are also shared by *Sphaerostylus borealis* (Online resource 3, p. 3, Matrix M34250 in TreeBase). The difference between *W. bursa* and *P. cf. conigera* is 13 bps in CO1

(Matrix M34248 in TreeBase) and five bps in 28S rDNA (Matrix M34250 in TreeBase). The distinctions between *W. bursa* and *S. borealis* are described in the Genetic data section for the latter species.

OCCURRENCE

(Figure 37)

Literature data: North-East Atlantic: North off Azores (150–932 m) (Topsent, 1928), West off Strait of Gibraltar (133–137 m) (Boury-Esnault *et al.*, 1994). Norwegian and Barents Sea: off Finnmark Coast in Norway (255–282 m) (Vosmaer, 1885). Norwegian and Barents Sea (elsewhere), Svalbard (62–485 m) (Koltun, 1964, 1966).

Our data: Canadian Atlantic Coast: Newfoundland (415 m), offshore areas (410–430 m). Davis Strait (75–195 m). South Greenland (184–300 m). Denmark Strait (348 m). Iceland (125–490 m). Faroes (525 m). Norwegian Sea, offshore areas (500–525 m). Barents Sea, offshore areas (130–250 m). Norwegian Coast: Sør-Trøndelag (50–200 m), Nord-Trøndelag (30–100 m), Nordland (750–800 m), Troms: (16–220 m), Finnmark: (200–260 m). Svalbard (40–215 m). Franz Josef Land (246 m). Novaya Zemlya (110–133 m).

DISCUSSION

Weberella bursa exhibits some external similarities with *Polymastia thielei* and *P. uberrima*, but is distinguished from these two by the reticulate choanosomal skeleton, the presence of only two size categories of spicules and some other features (see more in Discussions on *P. thielei* and *P. uberrima*). These

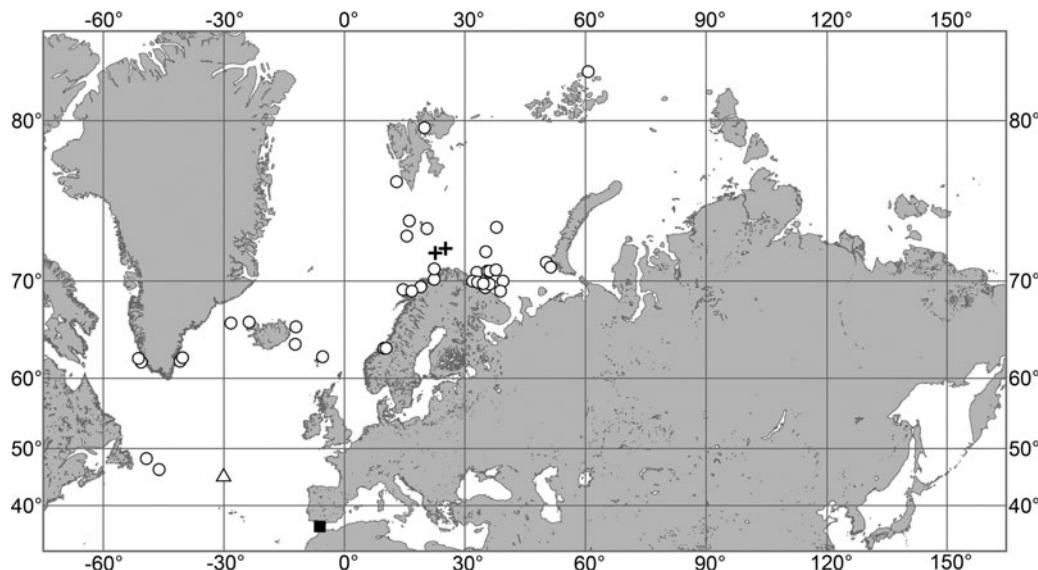


Fig. 37. *Weberella bursa*, distribution: black square, data from Boury-Esnault *et al.* (1994); white triangle, data from Topsent (1928); black crosses, data from Vosmaer (1885); white circles, our data. Type locality is unknown.

morphological differences are confirmed by the molecular phylogenies. At the same time the sister relationships between *W. bursa* and *Polymastia cf. conigera* as well as the sister relationships between this pair and *S. borealis* revealed in the molecular phylogenies, but insufficiently supported, need more studies on a larger set of species.

Koltun (1964, 1966) put *Weberella* in synonymy with *Polymastia*, that was not accepted further (Boury-Esnault, 2002). *Polymastia bursa* (Müller, 1806) *sensu* Koltun should not be mixed with *Polymastia bursa* (Schmidt, 1862) *sensu* von Lendenfeld (1898). The latter is *taxon inquirendum* originally described as *Suberites bursa* Schmidt, 1862 from the Adriatic Sea (see Van Soest *et al.*, 2016).

CONCLUDING REMARKS

Diversity of species

Altogether 20 species from six polymastiid genera were recorded in the Nordic and Siberian Seas (Table 8). Of these two species, *Polymastia Svenseni* and *Spinularia njordi*, are new to science, one species, *Polymastia andrica*, is new to the Nordic Seas and two species, *P. cf. bartletti* and *P. penicilllus*, are new to the Scandinavian Coast. The sponge from Western Norway herein identified as *Polymastia* sp. may potentially be another new species, but more material is required to check this. The new findings listed above were mainly done based on molecular data. *Polymastia Svenseni* and *S. njordi* are distinguished by genetic autapomorphies, but exhibit no clear morphological autapomorphies. *Polymastia cf. bartletti* is morphologically very similar to *P. nivea* and therefore these species can be separated only based on their considerable genetic distinctions. *Polymastia andrica* exhibits just one clear morphological distinction, the presence of exotyles, and several distinctions in CO1 from the sibling species *P. arctica*, although the relationship between these two needs more studies taking into account the intragenomic polymorphism of their 28S rDNA, which

probably may indicate a gene flow through hybridization between these species (Plotkin *et al.*, 2016b). *Polymastia penicilllus* was identified based on its both morphological and genetic distinctions from the congeners. *Polymastia* sp. is morphologically very similar to *P. andrica*, but considerably differs from the latter by both CO1 and 28S rDNA. Moreover, based on the 28S rDNA phylogeny *Polymastia* sp. is a sibling of morphologically distinct *P. Svenseni*.

In addition to the species described in our study, one more polymastiid was recorded in the Nordic Seas – *Polymastia paupera* Fristedt, 1887 found east off South Greenland. However, Boury-Esnault (1987) suggested that this was a suberitid. We agree with her opinion after examining the holotype of this species (Swedish Museum of Natural History, Stockholm, Type-1207). It is a sponge piece without papillae. The skeleton is made of tylostyles with lobate tylos (one size category) located obliquely to the surface. Cortex is not differentiated. None of these traits are found in the polymastiids.

PATTERNS OF DISTRIBUTION

Of all the species studied, 10 species, *Polymastia andrica*, *P. grimaldii*, *P. hemisphaerica*, *P. thielei*, *P. uberrima*, *Quasillina brevis*, *Sphaerotylus capitatus*, *Spinularia sarsii*, *Tentorium semisuberites* and *W. bursa*, have an amphi-Atlantic boreoarctic distribution ranging from Nova Scotia, Newfoundland and Labrador at the Canadian Atlantic Coast and north-eastwards over the Nordic Seas and along the coasts of Greenland, Iceland, Scandinavia and Russia up to the Arctic Ocean and the Siberian Seas (Table 8). In the south-western parts of this area the occurrence of these species is usually limited to the depths below 100–200 m, while in the north-east most of them spread to shallow waters (Figure 38). The distribution of two species, *P. hemisphaerica* and *S. sarsii*, is limited to the deep-sea (to 150 m for the former species and to 300 m for the latter) in all regions. The prevalence of the amphi-Atlantic boreoarctic species in the Nordic and Arctic faunas was earlier demonstrated on several demosponge genera, e.g. *Geodia* Lamarck, 1815 from the family Geodiidae Gray, 1867 (Cárdenas *et al.*,

Table 8. Geographic distribution of Polymastiidae in the Nordic and Siberian Seas. + our and literature data, x only literature data. Numeration of species: 1 – *Polymastia andrica*, 2 – *Polymastia arctica*, 3 – *Polymastia cf. bartletti*, 4 – *Polymastia boletiformis*, 5 – *Polymastia grimaldii*, 6 – *Polymastia hemisphaerica*, 7 – *Polymastia mamillaris*, 8 – *Polymastia nivea*, 9 – *Polymastia penicillus*, 10 – *Polymastia svenseni*, 11 – *Polymastia thielei*, 12 – *Polymastia uberrima*, 13 – *Polymastia* sp., 14 – *Quasillina brevis*, 15 – *Sphaerotylus borealis*, 16 – *Sphaerotylus capitatus*, 17 – *Spinularia njordi*, 18 – *Spinularia sarsii*, 19 – *Spinularia spinularia*, 20 – *Tentorium semisuberites*, 21 – *Weberella bursa*.

Region	Species																				
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21
Greenland Sea, offshore										+								+	+	+	
Greenland				+	+					+		x		+			+	x	+	+	+
Denmark Strait			+						+			+								+	+
Icelandic Coast and Iceland Sea			+	+					+	+	x	+							+	+	
Faroës											x										+
NE Atlantic, offshore											+										+
Norwegian Sea, offshore	+									+	+			+	+	+	+	+	+	+	+
Barents Sea, offshore								+			+	+		+	+	+	x		+	+	+
Swedish Western Coast		+	+				+	+					x		+						+
Norwegian Coast and offshore islands																					
Aust-Agder																					+
Vest-Agder																					
Rogaland																					x
Hordaland	+																				
Sogn og Fjordane																					
Møre og Romsdal																					
Sør-Trøndelag		+																			
Nord-Trøndelag																					
Nordland																					
Troms		+	x																		
Finnmark		+	+																		
Svalbard		+																			
Russian coasts and offshore islands																					
Murman Coast		+																			
White Sea		+																			
Kanin Peninsula																					
Chyosha Bay																					
Pechora Sea																					
Franz Josef Land																					
Novaya Zemlya					+	+															
Taymyr Peninsula																					
Norden-skjold																					
Severnaya Zemlya																					
Kara Sea																		x			
Laptev Sea																		x			
East-Siberian Sea																					
Arctic Ocean, offshore																					

2013) and *Thenea* Gray, 1867 (Cárdenas & Rapp, 2012) from Theneidae Carter, 1883, and on hexactinellids, e.g. *Asconema* Kent, 1870 from Rossellidae Schulze, 1885 (Tabachnick & Menshenina, 2007).

Meanwhile, it is still unclear how far southwards in the central North Atlantic and along the European and African coasts the amphi-Atlantic boreoarctic polymastiids may be found. The records of *Q. brevis* and *W. bursa* from Azores (Topsent, 1892, 1928), the entrance to the Gibraltar Strait and the Mediterranean Sea (Uriz & Rosell, 1990; Boury-Esnault *et al.*, 1994) as well as the records of *T. semisuberites* from Azores (Topsent, 1892, 1904, 1928) and the Bay of Biscay (Topsent, 1892) need verification with molecular data. The allegedly cosmopolitan distribution of *S. sarsii* is already questioned based on the observed genetic differences between the Norwegian and Mozambican sponges, but a thorough comparison between the Norwegian, Azorean and NW African individuals is still required.

The distribution of other polymastiid species studied is narrower (Table 8). Four species, *Polymastia arctica*, *P. nivea*, *Sphaerotylus borealis* and *Spinularia spinularia* may be regarded as NE Atlantic high-boreoarctic. The known occurrence of *Sphaerotylus borealis* is limited to Iceland in the south-west and the eastern Kara Sea in the north-east. The distribution of *Polymastia arctica* and *P. nivea* is limited to the Norwegian Coast and Russian Coast of the Barents and White Sea. The former species has never been recorded to the south-west from Central Norway (Sør-Trøndelag), while the latter has been found up to Southern Norway (Vest-Agder). *Spinularia spinularia* is widely distributed along the Scandinavian Coast, East Greenland Coast and around the British Isles, while its records from Azores (Topsent, 1898, 1904, 1928) are considered as a separate species, *S. setosa*, based on distinct differences in morphology. Atlantic high-boreoarctic species were earlier recorded among other demosponge families, e.g.

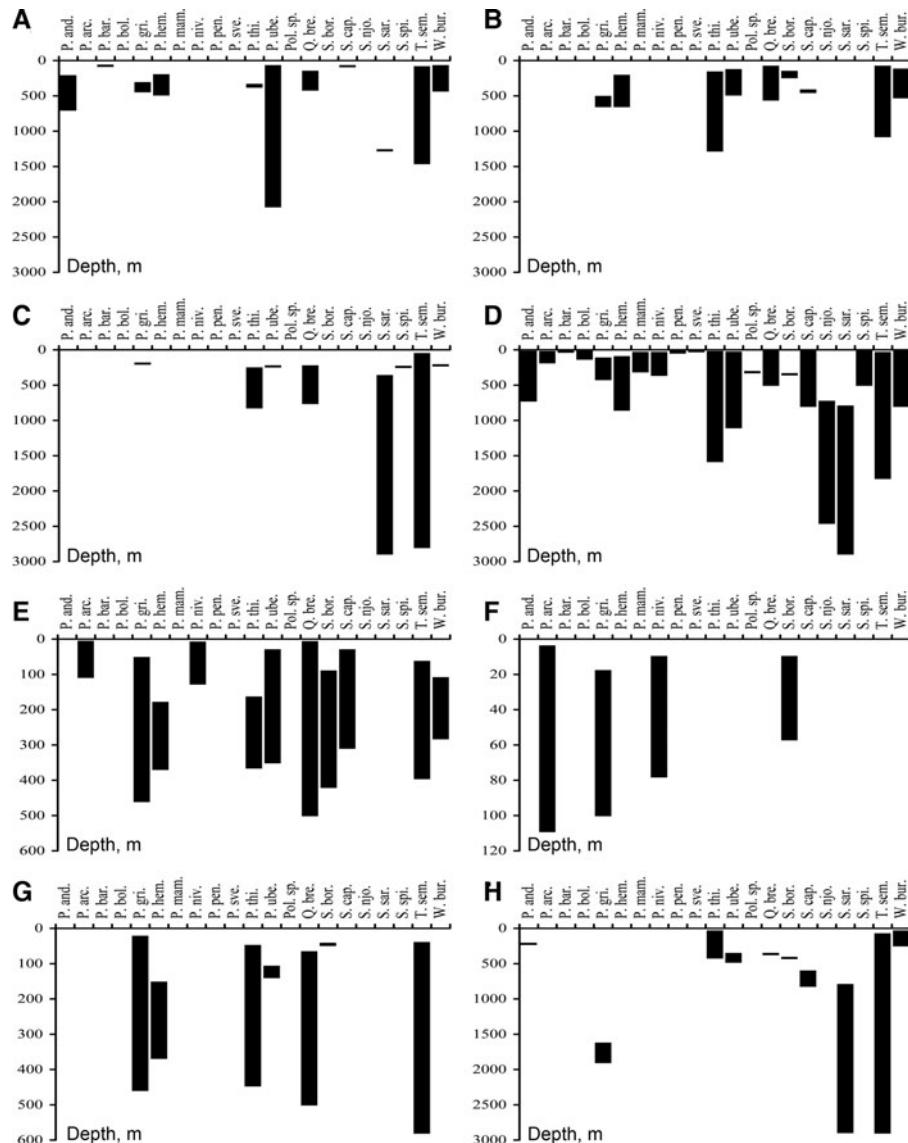


Fig. 38. Vertical distribution of Polymastiidae in the Nordic and Siberian Seas (our and literature data): (A) NW Atlantic (offshore areas, Canadian Coast and Davis Strait); (B) NE Atlantic (offshore areas), Southern Greenland Coast, Denmark Strait, Iceland Sea, Icelandic Coast and Faroes; (C) Greenland Sea (offshore areas and Eastern Greenland Coast); (D) Norwegian Sea (offshore areas) and Scandinavian Coast from Western Sweden to Northern Norway; (E) Barents Sea (offshore areas, archipelagos and Russian Coast); (F) White Sea; (G) Siberian Seas (offshore areas, archipelagos and Russian Coast); (H) Arctic Ocean. Labelling species: P. and., *Polymastia andrica*, P. arc., *Polymastia arctica*, P. bar., *Polymastia bartletti* and P. cf. *bartletti*, P. bol., *Polymastia boletiformis*, P. gri., *Polymastia grimaldii*, P. hem., *Polymastia hemisphaerica*, P. mam., *Polymastia mamillaris*, P. niv., *Polymastia nivea*, P. pen., *Polymastia penicillus*, P. sve., *Polymastia svenseni*, P. thi., *Polymastia thielei*, P. ube., *Polymastia uberrima*, Pol. sp., *Polymastia* sp., Q. bre., *Quassilina brevis*, S. bor., *Sphaerotylus borealis*, S. cap., *Sphaerotylus capitatus*, S. njo., *Spinularia njordi*, S. sar., *Spinularia sarsi*, S. spi., *Spinularia spinularia*, T. sem., *Tentorium semisuberites*, W. bur., *Weberella bursa*.

Geodia hentscheli Cárdenas *et al.*, 2010 and *G. parva* Hansen, 1885 from Geodiidae (Cárdenas *et al.*, 2013), *Tetilla sibirica* (Fristedt, 1887) from Tetillidae Sollas, 1886 (Koltun, 1966), and *Thenea abyssorum* Koltun, 1964 from Theneidae (Cárdenas & Rapp, 2012). A few records of the sponge species distribution limited to the Arctic Ocean and Siberian Seas, e.g. demosponges *Hemimycale rhodus* (Hentschel, 1929), *Cladorhiza arctica* Koltun, 1959 and *Pseudosuberites sadko* Koltun, 1966, should be verified on the additional material. It seems that the Arctic sponge fauna is predominantly composed of the species dispersed from the Atlantic.

Two species studied, *Polymastia boletiformis* and *P. penicillus*, represent the southern boreal component in the Scandinavian sponge fauna. They are quite common in the shallow depths along the European coasts (Figure 38), with their northernmost records from Møre and Romsdal in Norway for *P. boletiformis*

and the British Isles and the Swedish Western Coast for *P. penicillus*. The occurrence of the southern boreal species along the Scandinavian Coast was earlier recorded for other sponge families, e.g. a calcarean *Clathrina coriacea* (Montagu, 1814) from Clathrinidae Minchin, 1900 (Rapp, 2006), demosponges *Characella pachastrelloides* (Carter, 1876) and *Poecillastra compressa* (Bowerbank, 1866) from Pachastrellidae Carter, 1875 and *Thenea muricata* (Bowerbank, 1858) from Theneidae (Cárdenas & Rapp, 2012).

Even though we have got numerous and well-documented records for most species studied, our knowledge of the distribution of other species is still poor. Particularly, more data on the rare species *Polymastia bartletti* and two new species, *P. svenseni* and *Spinularia njordi*, are required. The observed distribution patterns of the polymastiids in the area of study should therefore be considered as preliminary until more

comprehensive material from adjacent waters can be included. It is recommended that further research on the biogeography of polymastiids should be based on an integrative approach including detailed morphological studies and analyses of a larger set of phylogenetic markers.

SUPPLEMENTARY MATERIAL

The supplementary material for this article can be found at <https://doi.org/10.1017/S0025315417000285>

ACKNOWLEDGEMENTS

We would like to express our gratitude to all colleagues, who kindly provided the access to the sponge collections of their institutions: Jean-Marc Gagnon (Canadian Museum of Nature, Ottawa), Erica Mejlon (Museum of Evolution, University of Uppsala), Kennet Lundin and Carola Azurduy Högström (Gothenburg Natural History Museum), Michèle Bruni (Musée Océanographique de Monaco), Carsten Lüter (Museum für Naturkunde, Berlin), Isabelle Domart-Coulon (Muséum National d'Histoire Naturelle, Paris), Clare Valentine, Andrew Cabrinovic and Emma Sherlock (Natural History Museum, London), Nicole de Voogd and J. Koos van Egmond (Naturalis Biodiversity center, Leiden), Lutz Bachmann and Åse Ingvild Wilhelmsen (Natural History Museum, University of Oslo), Ole Secher Tendal (Natural History Museum of Denmark, University of Copenhagen), Bernard E. Picton (Ulster Museum, National Museums of Northern Ireland, Belfast), Jon Anders Kongsrød (University Museum of Bergen, Natural History Collections), Torkild Bakken (University Museum of the Norwegian University of Science and Technology, Trondheim), Olga Bozhenova (Zoological Institute of Russian Academy of Sciences, Saint-Petersburg). We are also thankful to Bjørn Gulliksen (University of Tromsø), Bjørn Tore Dragnes (OMNIMAR Dragnes, Tromsø), Peter Leopold (University Centre in Svalbard) and Erling Svensen (OceanPhoto/Dalane Tidende AS, Egersund), who arranged the sampling of fresh material along the Norwegian Coast and on Svalbard and provided us with high-quality underwater images. The colleagues, who granted us fresh samples from other regions, are also greatly acknowledged: Christine Morrow (Department of Zoology, Ryan Institute, National University of Ireland, Galway) and Bernard E. Picton (Ulster Museum, National Museums of Northern Ireland, Belfast) for the samples and photos of sponges from the British Isles, Javier Cristobal and Pilar Rios (Spanish Institute of Oceanography, Madrid) for the samples from Mozambique, and Natalia Chervyakova (Moscow State University) for the material from the White Sea. Paco Cárdenas (BioMedical Centre, Uppsala) is acknowledged for the photos of sponges from Museum of Evolution, University of Uppsala. Thanks also come to Egil Severin Erichsen and Irene Heggstad (University of Bergen, Laboratory for Electron Microscopy) for their careful assistance at SEM, to Kenneth Meland, Solveig Thorkildsen and Louise Lindblom (University of Bergen, BioDiversity Laboratories at the Department of Biology) for their great assistance under the obtaining and treatment of molecular data and to Endre Willassen (University Museum of Bergen, Natural History Collections) and Oliver Voigt

(Ludwig-Maximilians-Universität München, Palaeontology and Geobiology) for their inestimable help with the phylogenetic computing. Last but not least, we would like to thank the two reviewers for the great work they have done when reading our manuscript.

FINANCIAL SUPPORT

This study was supported by the Norwegian Biodiversity Information Centre, Artsdatabanken (project No. 70184219), the Norwegian Academy of Science and Letters (grant to HTR), the Research Council of Norway (through contract No. 179560) and the European Union's Horizon 2020 research and innovation programme under grant agreement No. 679849 (the SponGES project). The visit of AP to the Natural History Museum (London) in 2010 received funding from the SYNTHESYS Project (<http://www.synthesys.info/>) financed by European Community Research Infrastructure Action under the FP7 Integrating Activities Programme.

REFERENCES

- Alander H. (1942) *Sponges from the Swedish west-coast and adjacent waters*. PhD thesis. Lund University. Göteborg: Henrik Struvés.
- Alex A., Silva V., Vasconcelos V. and Antunes A. (2013) Evidence of unique and generalist microbes in distantly related sympatric intertidal marine sponges (Porifera: Demospongiae). *PLoS ONE* 8, e80653. doi: 10.1371/journal.pone.0080653.
- Anisimova N.A., Jørgensen L.L., Lyubin P.A. and Manushin I.E. (2010) *Mapping and monitoring of benthos in the Barents Sea and Svalbard waters: results from the joint Russian–Norwegian benthic programme 2006–2008*. IMR–PINRO Joint Report Series, 1.
- Anonymous (1999) *International code of zoological nomenclature*, 4th edition. International Trust for Zoological Nomenclature. London: The Natural History Museum.
- Arndt W. (1928) Porifera, Schwämme, Spongien. In Arndt W., Broch H., Krumbach T., Pax F. and Lieberkind I. (eds) *Porifera, Hydrozoa, Coelenterata, Echinodermata. Die Tierwelt Deutschlands und der angrenzenden Meeresteile nach ihren Merkmalen und nach ihrer Lebensweise*, Volume 4. pp. 1–94.
- Arndt W. (1935) Porifera. In Gruppe G. and Wagler E. (eds) *Die Tierwelt der Nord- und Ostsee, Teil IIIa*. Leipzig: Academische Verlagsgesellschaft m.b.H., pp. 1–140.
- Arnesen E. (1900) Spongier fra den norske kyst. I. Calcarea. *Bergens Museums Aarbog* 5, 1–46.
- Arnesen E. (1903) Spongien von der norwegischen Küste. ii, Monaxonida: Halichondrina. *Bergens Museums Aarbog* 1, 1–30.
- Arnesen E. (1918) Brutknospenbildung bei *Polymastia mammilaris* (O.F. Müller). Bow. (*Rinalda arctica* Merej.). *Det Kongelige Norske Videnskabers selskabs skrifter* 1, 1–24.
- Arnesen E. (1920) Spongia. *Report on the Scientific Results of the ‘Michael Sars’ North Atlantic Deep-Sea Expedition in 1910* 3, 1–29.
- Babkov A.I. and Golikov A.N. (1984) *Hydrobiocomplexes of the White Sea*. Leningrad: Publications of the Zoological Institute, Academy of Sciences of USSR. [In Russian]
- Barthel D. and Tendal O.S. (1993) The sponge association of the abyssal Norwegian-Greenland Sea – species composition, substrate relationships and distribution. *Sarsia* 78, 83–96.

- Blindheim J. and Østerhus S.** (2005) The Nordic Seas, main oceanographic features. In Drange H., Dokken T., Furevik T., Gerdes R. and Berger W. (eds) *The Nordic Seas, main oceanographic features, in the Nordic Seas: an integrated perspective*. AGU Monograph 158, Washington, DC: American Geophysical Union, pp. 11–37.
- Borojevic R.** (1967) La ponte et le développement de *Polymastia robusta* (Demosponges). *Cahiers de Biologie Marine* 8, 1–6.
- Boury-Esnault N.** (1987) The *Polymastia* species (Demosponges, Hadromerida) of the Atlantic area. In Vacelet J. and Boury-Esnault N. (eds) *Taxonomy of Porifera from the N.E. Atlantic and Mediterranean Sea*. NATO ASI Series, G 13. Berlin–Heidelberg: Springer, pp. 29–66.
- Boury-Esnault N.** (2002) Family Polymastiidae Gray, 1867. In Hooper J.N.A. and Van Soest R.W.M. (eds) *Systema Porifera. a guide to the classification of sponges*, Volume 1. New York, NY: Kluwer Academic/Plenum Publishers, pp. 201–219.
- Boury-Esnault N. and Bézac C.** (2007) Morphological and cytological descriptions of a new *Polymastia* species (Hadromerida, Demospongiae) from the North-West Mediterranean Sea. In Custódio M.R., Lobo-Hajdu G., Hajdu E. and Muricy G. (eds) *Porifera research: biodiversity, innovation and sustainability*. Rio de Janeiro: Museu Nacional, Série Livros 28, pp. 23–30.
- Boury-Esnault N., Marschal C., Kornprobst J.-M. and Barnathan G.** (2002) A new species of *Axinyssa* Lendenfeld, 1897 (Porifera, Demospongiae, Halichondrida) from the Senegalese coast. *Zootaxa* 117, 1–8.
- Boury-Esnault N., Pansini M. and Uriz M.-J.** (1994) Spongiaires bathyaux de la mer d'Alboran et du golfe ibéro-marocain. *Mémoires du Muséum national d'Histoire naturelle* 160, 1–174.
- Bowerbank J.S.** (1858) On the anatomy and physiology of the Spongiidae. Part I. On the spicula. *Philosophical Transactions of the Royal Society* 148, 279–332.
- Bowerbank J.S.** (1861) List of British sponges. In McAndrew R. (ed.) *List of the British marine invertebrate fauna. Report of the British Association for the advancement of science*, Volume 30. London: Taylor & Francis, pp. 235–236, 830–836.
- Bowerbank J.S.** (1862) On the anatomy and physiology of the Spongiidae. Part III. On the generic characters, the specific characters, and on the method of examination. *Philosophical Transactions of the Royal Society* 152, 1087–1135.
- Bowerbank J.S.** (1864) *A monograph of the British Spongiidae*, Volume 1. London: The Ray Society.
- Bowerbank J.S.** (1866) *A monograph of the British Spongiidae*, Volume 2. London: The Ray Society.
- Bowerbank J.S.** (1874) *A monograph of the British Spongiidae*, Volume 3. London: The Ray Society.
- Bowerbank J.S. and Norman A.M.** (1882) *A monograph of the British Spongiidae*, Volume 4 (Supplement). London: The Ray Society.
- Breitfuss L.L.** (1911) Zur Kenntnis der Spongio-Fauna des Kola-Fjords. *Travaux de la Société Impériale des Naturalistes de St. -Pétersbourg* Section Zoologie, 42, 209–226.
- Breitfuss L.L.** (1912) Zur Kenntnis der Spongio-Fauna des Kola Fjords. II. *Travaux de la Société Impériale des Naturalistes de St. Petersburg* Section Zoologie, 41, 61–80.
- Breitfuss L.L.** (1930) Biogeographischer Beitrag zur Kenntniss der Spongiifauna der Arktis. *Sitzungsberichte der Gesellschaft Naturforschender Freunde zu Berlin* 1929, 274–282.
- Brøndsted H.V.** (1914) Conspectus faunæ groenlandicæ. Porifera. *Meddelelser om Grönland* 23, 457–544.
- Brøndsted H.V.** (1932) Marine Spongia. III. In Jensen A.S., Lundbeck W. and Ragnar Spärck M.T. (eds) *The zoology of the Faroes*. Copenhagen: A.F. Høst & Son, pp. 1–34.
- Brøndsted H.V.** (1933) Porifera. *Meddelelser om Grönland* 104, 1–10.
- Burton M.** (1930a) Norwegian sponges from the Norman collection. *Proceedings of the Zoological Society of London* 1930, 487–546.
- Burton M.** (1930b) Additions to the Sponge fauna of the Gulf of Manaar. *Annals and Magazine of Natural History* 5, 665–676.
- Burton M.** (1959a) Spongia. In Fridriksson A. and Tuxen S.L. (eds) *The zoology of Iceland*. Copenhagen: Ejnar Munksgaard, pp. 1–71.
- Burton M.** (1959b) Sponges. In *Scientific Reports. John Murray Expedition 1933–34*, Volume 10, issue 5. London: British Museum (Natural History), pp. 151–281.
- Cabioch L.** (1968) Contribution à la connaissance de la faune des Spongiaires de la Manche Occidentale. Démospanges de la région de Roscoff. *Cahiers de Biologie Marine* 9, 211–246.
- Cárdenas P., Perez T. and Boury-Esnault N.** (2012) Sponge systematics facing new challenges. *Advances in Marine Biology* 61, 79–209.
- Cárdenas P. and Rapp H.T.** (2012) A review of Norwegian streptaster-bearing Astrophorida (Porifera: Demospongiae: Tetractinellida), new records and a new species. *Zootaxa* 3253, 1–52.
- Cárdenas P., Rapp H.T., Klitgaard A.B., Best M., Thollesson M. and Tendal O.S.** (2013) Taxonomy, biogeography and DNA barcodes of *Geodia* species (Porifera, Demospongiae, Tetractinellida) in the Atlantic boreo-arctic region. *Zoological Journal of the Linnean Society* 169, 251–311.
- Cárdenas P., Rapp H.T., Schander C. and Tendal O.S.** (2010) Molecular taxonomy and phylogeny of the Geodiidae (Porifera, Demospongiae, Astrophorida) – combining phylogenetic and Linnaean classification. *Zoologica Scripta* 39, 89–106.
- Carter H.J.** (1875) Notes introductory to the study and classification of the Spongida. Part II. Proposed classification of the Spongida. *Annals and Magazine of Natural History* 4, 126–145.
- Carter H.J.** (1876) Descriptions and figures of deep-sea sponges and their spicules, from the Atlantic Ocean, dredged up on board H.M.S. ‘Porcupine’, chiefly in 1869 (concluded). *Annals and Magazine of Natural History* 18, 388–410.
- Carter H.J.** (1883) Contributions to our knowledge of the Spongida. *Annals and Magazine of Natural History* 12, 308–329.
- Coachman L.K. and Aagaard K.** (1974) Physical oceanography of Arctic and Subarctic waters. In Herman Y. (ed.) *Marine geology and oceanography of the Arctic Seas*. New York, NY: Springer-Verlag, pp. 1–72.
- de Laubenfels M.W.** (1942) Porifera from Greenland and Baffinland collected by Capt. Robert A. Bartlett. *Journal of the Washington Academy of Sciences* 32, 263–269.
- de Laubenfels M.W.** (1949) The sponges of Woods Hole and adjacent waters. *Bulletin of the Museum of Comparative Zoology at Harvard College* 103, 1–55.
- Dendy A.** (1888) Studies on the comparative anatomy of sponges. I. On the genera *Ridlea*, n. gen., and *Quasillina*, Norman. *Quarterly Journal of Microscopical Science* 282, 513–529.
- Dendy A.** (1922) Report on the Sigmatotetradonida collected by H.M.S. ‘Sealark’ in the Indian Ocean. *Reports of the Percy Sladen Trust Expedition to the Indian Ocean in 1905*, Volume 7. *Transactions of the Linnean Society of London* 18, 1–164.
- Dendy A. and Ridley S.O.** (1886) On *Proteleia sollasi*, a new genus and species of monaxonid sponges allied to *Polymastia*. *Annals and Magazine of Natural History* 18, 152–159.

- Desqueyroux-Faúndez R. and Van Soest R.W.M.** (1997) Shallow water Demosponges of the Galápagos Islands. *Revue Suisse de Zoologie* 104, 379–467.
- Drange H., Dokken T., Furevik T., Gerdes R., Berger W., Nesje A., Orvik K.A., Skagseth Ø., Skjelvan I. and Østerhus S.** (2005) The Nordic Seas: an overview. In Drange H., Dokken T., Furevik T., Gerdes R. and Berger W. (eds) *The Nordic Seas, main oceanographic features, in the Nordic Seas: an integrated perspective*. AGU Monograph 158. Washington, DC: American Geophysical Union, pp. 1–10.
- Ereskovsky A.V.** (1993a) Materials to the faunistic study of the White and Barents Seas sponges. 1. Taxonomic composition. *Bulletin of St. Petersburg State University Series 3* 3, 19–28. [In Russian]
- Ereskovsky A.V.** (1993b) Addition to the fauna of sponges (Porifera) of the White Sea. *Bulletin of St. Petersburg State University Series 3* 2, 3–12. [In Russian]
- Ereskovsky A.V.** (1994a) Materials to the faunistic study of the White Sea and Barents Sea sponges. 2. Biogeographical and comparative-faunistic analysis. *Bulletin of St. Petersburg State University Series 3* 1, 13–26. [In Russian]
- Ereskovsky A.V.** (1994b) Materials to the faunistic study of the White Sea and Barents Sea sponges. 3. Dependence of sponge distribution on the temperature and salinity. *Bulletin of St. Petersburg State University Series 3* 3, 3–10. [In Russian]
- Ereskovsky A.V.** (1995a) Materials to the faunistic study of the White Sea and Barents Sea sponges. 4. Vertical distribution. *Bulletin of St. Petersburg State University Series 3* 1, 3–17. [In Russian]
- Ereskovsky A.V.** (1995b) Materials to the faunistic study of the White Sea and Barents Sea sponges 5. Quantitative distribution. *Berliner Geowissenschaftliche Abhandlungen Reihe E: Paleobiologie* 16, 709–714.
- Ereskovsky A.V.** (1995c) Materials to the faunistic study of the White Sea and Barents Sea sponges 6. The origin of the White and Barents seas sponge faunas. *Berliner Geowissenschaftliche Abhandlungen Reihe E: Paleobiologie* 16, 715–730.
- Fleming J.** (1828) *A history of British animals, exhibiting the descriptive characters and systematical arrangement of the genera and species of quadrupeds, birds, reptiles, fishes, Mollusca, and Radiata of the United Kingdom; including the indigenous, extirpated, and extinct kinds, together with periodical and occasional visitants*. Edinburgh: Bell and Bradfute.
- Fristedt K.** (1885) Bidrag till Kannedomen om de vid Sveriges vestra Kust lefvande Spongiae. *Kungliga Svenska vetenskapsakademiens handlingsar* 21, 1–56.
- Fristedt K.** (1887) Sponges from the Atlantic and Arctic Oceans and the Behring Sea. *Vega-Expeditionens Vetenskapelige Iakttagelser (Nordenskiöld)* 4, 401–471.
- Golikov A.N. and Scarlato O.A.** (1989) Evolution of Arctic ecosystems during the Neogene period. In Herman Y. (ed.) *The Arctic Seas. Climatology, oceanography, geology, and biology*. New York, NY: Springer, pp. 257–279.
- Golikov A.N., Scarlato O.A., Averincev V.G., Menshutkina T.V., Novikov O.K. and Sheremetevsky A.M.** (1990) Ecosystems of the New Siberian shoals, their distribution and functioning. In Golikov A.N. (ed.) *Ecosystems of the New Siberian shoal and the fauna of the Laptev Sea and adjacent waters, Explorations of the fauna of the seas*, Volume 37. Leningrad: Nauka, pp. 4–79. [In Russian]
- Gorbunov G.P.** (1946) Bottom life of the Novosiberian shoalwaters and central part of the Arctic Ocean. *Transactions of the Glavsevmorput' drifting expedition onboard ice-breaker "G. Sedov" in 1937–1940* III, 30–136. [In Russian]
- Gray J.E.** (1867) Notes on the arrangement of sponges, with the descriptions of some new genera. *Proceedings of the Zoological Society of London* 1867, 492–558.
- Hanitsch R.** (1894) Revision of the generic nomenclature and classification in Bowerbank's 'British Spongiidae'. *Proceedings and Transactions of the Liverpool Biological Society* 8, 173–206.
- Hansen B. and Østerhus S.** (2000) North Atlantic–Nordic Seas exchanges. *Progress in Oceanography* 45, 109–208.
- Hansen G.A.** (1885) Spongiidae. *The Norwegian North-Atlantic Expedition 1876–1878. Zoologi* 13, 1–26.
- Hentschel E.** (1916) Die Spongien des Eisfjords. In Théel H.J. and Lönnberg E. (eds) *Zoologische Ergebnisse der Schwedischen Expedition nach Spitzbergen, 1908*, Volume 54(3). Stockholm: Kungliga Svenska vetenskapsakademiens Handlingar, pp. 1–18.
- Hentschel E.** (1929) Die Kiesel- und Hornschwämme des Nördlichen Eismeers. In Römer F., Schaudinn F., Brauer A. and 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*, Volume 5(4). Jena: G. Fischer, pp. 857–1042.
- Herman Y.** (1974) Topography of the Arctic Ocean. In Herman Y. (ed.) *Marine geology and oceanography of the Arctic Seas*. New York, NY: Springer-Verlag, pp. 73–81.
- Hooper J.N.A. and Van Soest R.W.M.** (eds) (2002) Order Hadromerida Topsent, 1894. In *Systema Porifera. A guide to the classification of Sponges*, Volume 1. New York, NY: Kluwer Academic/Plenum Publishers, pp. 169–172.
- Johnston G.** (1842) *A history of British Sponges and Lithophytes*. Edinburgh: W.H. Lizars.
- Kędra M., Renaud P.E., Andrade H., Goszczko I. and Ambrose W.G.** (2013) Benthic community structure, diversity, and productivity in the shallow Barents Sea bank (Svalbard Bank). *Marine Biology* 160, 805–819.
- Kent W.S.** (1870) On the 'Hexactinellidae' or hexradiate spiculed silicious sponges taken in the 'Norna' Expedition off the coast of Spain and Portugal. With description of new species, and revision of the order. *Monthly Microscopical Journal* 4, 241–252.
- Kirkpatrick R.** (1907) Preliminary report on the Monaxonellida of the National Antarctic Expedition. *Annals and Magazine of Natural History* 20, 271–291.
- Kirkpatrick R.** (1908) Porifera (Sponges). II. Tetraxonida, Dendy. *National Antarctic Expedition, 1901–1904. Natural History, series 4, Zoology*, pp. 1–56.
- Kitgaard A.B. and Tendal O.S.** (2004) Distribution and species composition of mass occurrences of large-sized sponges in the northeast Atlantic. *Progress in Oceanography* 61, 57–98.
- Kitgaard A.B., Tendal O.S. and Westerberg H.** (1997) Mass occurrences of large sized sponges (Porifera) in Faroe Island (NE-Atlantic) shelf and slope areas: characteristics, distribution and possible causes. In Hawkins L.E., Hutchinson S., Jensen A.C., Shearer M. and Williams J.A. (eds) *The responses of marine organisms to their environments. Proceedings of the 30th European Marine Biology Symposium*. Southampton: University of Southampton, pp. 129–142.
- Koltun V.M.** (1959) *Siliceous horny sponges of the Northern and Far Eastern Seas of the USSR*. Identifiers of the USSR fauna issued by the Zoological Institute of the Academy of Sciences of the USSR. Moscow–Leningrad: Nauka, Academy of Sciences of the USSR, p. 67. [In Russian]
- Koltun V.M.** (1964) Sponges (Porifera) collected in the Greenland Sea and in the North area off Spitzbergen and Frantz Josef Land by the ice-breaker "F. Litke" in 1955, the steamer "Ob" in 1956 and the steamer

- "Lena" in 1957–1958. *Proceeding of the Arctic and Antarctic Research Institute* 259, 143–166. [In Russian]
- Koltun V.M.** (1966) *Four-rayed sponges (order Tetraxonida) of the Northern and Far Eastern Seas of the USSR*. Identifiers of the USSR fauna issued by the Zoological Institute of the Academy of Sciences of the USSR. Moscow–Leningrad: Nauka, Academy of Sciences of the USSR, p. 90. [In Russian]
- Koralev A., Smirnov A. and Baranova O.K.** (2014) Climatological atlas of the Nordic Seas and Northern North Atlantic. In Seidov D. and Parsons A.R. (eds) *NOAA Atlas NESDIS*, Volume 77. Silver Spring, MD: NESDIS. doi: 10.7289/V54B2Z78.
- Lamarck J.B.P.** (1815) Suite des polypiers empâtés. *Mémoires du Muséum d'Histoire naturelle* 1, Paris, 69–80, 162–168, 331–340.
- Lambe L.M.** (1896) Sponges from the Atlantic coast of Canada. *Transactions of the Royal Society of Canada* 2, 181–211.
- Lambe L.M.** (1900) Sponges from the coasts of north-eastern Canada and Greenland. *Transactions of the Royal Society of Canada* 6, 19–49.
- Lévi C.** (1950) Spongaires. *Travaux de la Station biologique de Roscoff* Supplement 2, 1–28.
- Lévi C.** (1993) Porifera Demospongiae: Spongaires bathyaux de Nouvelle-Calédonie, récoltés par le 'Jean Charcot'. Campagne BIOCAL, 1985. In Crosnier A. (ed.) *Résultats des campagnes MUSORSTOM*, Volume 11. *Mémoires du Muséum national d'Histoire naturelle (A, Zoologie)* 158, 9–87.
- Levinseñ G.M.R.** (1887) Kara-Havets Svampe (Porifera). In Lütken C.F. (ed.) *Dijmphna-Togtets zoologisk-botaniske Udbytte*. København: Komission hos H. Hagerup, pp. 339–372.
- Loeng H. and Drinkwater K.** (2007) An overview of the ecosystems of the Barents and Norwegian Seas and their response to climate variability. *Deep Sea Research Part II: Topical Studies in Oceanography* 54, 2478–2500.
- Lundbeck W.** (1902) Porifera. Part I. Homorrhaphidae and Heterorrhaphidae. In *The Danish Ingolf-Expedition*, Volume 6(1). Copenhagen: Bianco Luno, pp. 1–108.
- Lundbeck W.** (1905) Porifera. Part II. Desmacidonidae (pars.). In *The Danish Ingolf-Expedition*, Volume 6(2). Copenhagen: Bianco Luno, pp. 1–219.
- Lundbeck W.** (1907) Porifères. In Gerlache de Gomery A.V.J. baron de and Orléans L.P.R. duc Duc d' (eds) *Croisière Océanographique accompagnée à bord de la 'Belgica' dans la Mer du Grönland en 1905. Résultats scientifiques*. Bruxelles: Charles Bulens, pp. 558–559.
- Lundbeck W.** (1909) The Porifera of East-Greenland. *Meddelelser om Grönland* 29, 423–464.
- Lundbeck W.** (1910) Porifera. Part III. Desmacidonidae (pars.). In *The Danish Ingolf-Expedition*, Volume 6(3). Copenhagen: Bianco Luno, pp. 1–124.
- Maldonado M., Aguilar R., Bannister R.J., Bell J., Conway K.W., Dayton P.K., Diaz C., Gutt J., Kelly M., Kenchington E.L.R., Leys S.P., Pomponi S.A., Rapp H.T., Rützler K., Tendal O.S., Vacelet J. and Young C.M.** (2016) Sponge grounds as key marine habitats: a synthetic review of types, structure, functional roles and conservation concerns. In Rossi S., Bramanti L., Gori A. and Orejas C. (eds) *Marine animal forests – the ecology of benthic biodiversity hotspots*. New York, NY: Springer, pp. 1–39. On-line first view. Available at http://dx.doi.org/10.1007/978-3-319-17001-5_24-1.
- Merejkowsky C.S.** (1878) Etudes sur les éponges de la Mer Blanche. *Mémoires de l'Académie Impériale des Sciences de St.-Petersbourg Serie 7* 26, 1–51.
- Merejkowsky C.S.** (1880) Reproduction des éponges par bourgeonnement extérieur. *Archives de Zoologie expérimentale et générale* 8, 417–432.
- Minchin E.A.** (1900) Chapter III. Sponges. In Lankester E.R. (ed.) *A Treatise on Zoology. Part II. The Porifera and Coelenterata*. 2. London: Adam & Charles Black, pp. 1–178.
- Montagu G.** (1814) An essay on sponges, with descriptions of all the species that have been discovered on the coast of Great Britain. *Memoirs of the Wernerian Natural History Society* 2, 67–122.
- Morrow C.C. and Boury-Esnault N.** (2000) Redescription of the type species of the genus *Polymastia* Bowerbank, 1864 (Porifera, Demospongiae, Hadromerida). *Zoosystema* 22, 327–335.
- Morrow C.C. and Cárdenas P.** (2015) Proposal for a revised classification of the Demospongiae (Porifera). *Frontiers in Zoology* 12, 1–27.
- Morrow C.C., Picton B.E., Erpenbeck D., Boury-Esnault N., Maggs C.A. and Allcock A.L.** (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, 174–190.
- Morrow C.C., Redmond N.E., Picton B.E., Thacker R.W., Collins A.G., Maggs C.A., Sigwart J.D. and Allcock A.L.** (2013) Molecular phylogenies support homoplasy of multiple morphological characters used in the taxonomy of Heteroscleromorpha (Porifera: Demospongiae). *Integrative and Comparative Biology* 53, 428–446.
- Müller O.F.** (1806) *Zoologia danica seu animalium Daniae et Norvegiae rariorum ac minus notorum descriptiones et historia*, Volume 4. Havniae: N. Christensen.
- Norman A.M.** (1869) Notes on a few Hebridean Sponges, and on a new Desmacidon from Jersey. *Annals and Magazine of Natural History* 3, 296–299.
- Plotkin A.** (2004) Biodiversity and distribution of Polymastiidae (Demospongiae, Hadromerida) in the Arctic area. In Pansini M., Pronzato R., Bavestrello G. and Manconi R. (eds) *Sponge sciences in new millennium*. Bollettino dei Musei e degli Istituti Biologici dell'Università di Genova 68, Rapallo (Genoa). Genoa: Officine Grafiche Canessa, pp. 535–547.
- Plotkin A. and Boury-Esnault N.** (2004) Alleged cosmopolitanism in sponges: the example of a common Arctic *Polymastia* (Porifera, Demospongiae, Hadromerida). *Zoosystema* 26, 13–20.
- Plotkin A. and Ereskovsky A.V.** (1997) Ecological aspects of asexual reproduction of the White Sea sponge *Polymastia mammillaris* (Demospongiae, Tetractinomorpha) in the Kandalaksha Bay. *Berliner Geowissenschaftliche Abhandlungen Reihe E: Paleobiologie* 20, 127–132.
- Plotkin A., Gerasimova E. and Rapp H.T.** (2012) Phylogenetic reconstruction of Polymastiidae (Demospongiae: Hadromerida) based on morphology. *Hydrobiologia* 687, 21–41.
- Plotkin A. and Janussen D.** (2008) Polymastiidae and Suberitidae (Porifera: Demospongiae: Hadromerida) of the deep Weddell Sea, Antarctic. In Martínez Arbizu P. and Brix S. (eds) *Bringing light into deep-sea biodiversity*. Zootaxa 1866, 95–135.
- Plotkin A., Morrow C.C., Gerasimova E. and Rapp H.T.** (2016a) Polymastiidae (Demospongiae: Hadromerida) with ornamented exo-styles: a review of morphological affinities and description of a new genus and three new species. *Journal of the Marine Biological Association of the United Kingdom* 1–56. On-line first view. Available at <http://dx.doi.org/10.1017/S0025315416000655>.
- Plotkin A., Railkin A., Gerasimova E., Pimenov A. and Sipenкова T.** (2005) Subtidal underwater rock communities of the White Sea: structure and interaction with bottom flow. *Russian Journal of Marine Biology* 31, 335–343.
- Plotkin A., Voigt O., Willassen E. and Rapp H.T.** (2016b) Molecular phylogenies challenge the classification of Polymastiidae (Porifera, Demospongiae) based on morphology. *Organisms Diversity and Evolution*

- Evolution* 1–22. On-line first view, Available at <http://dx.doi.org/10.1007/s13127-016-0301-7>.
- Rapp H.T.** (2006) Calcareous sponges of the genera *Clathrina* and *Guancha* (Calcinea, Calcarea, Porifera) of Norway (NE Atlantic) with the description of five new species. *Zoological Journal of the Linnean Society* 147, 331–365.
- Rapp H.T.** (2015) A monograph of the calcareous sponges (Porifera, Calcarea) of Greenland. *Journal of the Marine Biological Association of the United Kingdom* 95, 1395–1459.
- Redmond N.E., Morrow C.C., Thacker R.W., Diaz M.C., Boury-Esnault N., Cárdenas P., Hajdu E., Lôbo-Hajdu G., Picton B.E., Pomponi S.A., Kayal E. and Collins A.G.** (2013) Phylogeny and systematics of Demospongiae in light of new small subunit ribosomal DNA (18S) sequences. *Integrative and Comparative Biology* 53, 388–415.
- Rezvoj P.D.** (1924) Contribution towards the sponge fauna of the Kara and Barents Seas. *Bulletin de l'Institut Lesshaft* 8, 241–250. [In Russian with English summary]
- Rezvoj P.D.** (1927) A new species of sponges, *Polymastia euplectella*, from the Murman Coast. *Comptes Rendus de l'Académie des Sciences URSS* 18, 301–302.
- Rezvoj P.D.** (1928) Sponges of the Barents Sea from the samples of the cruises along the Kola meridian. *Proceedings of the Institute of the Research of the North, USSR* 37, 67–95.
- Ridley S.O. and Dendy A.** (1886) Preliminary report on the Monaxonida collected by H.M.S. 'Challenger'. Part 1 and 2. *Annals and Magazine of Natural History* 18, 325–351, 470–493.
- Ridley S.O. and Dendy A.** (1887) Report on the Monaxonida collected by H.M.S. 'Challenger' during the years 1873–1876. *Report on the Scientific Results of the Voyage of H.M.S. 'Challenger', 1873–1876. Zoology* 20, 1–275.
- Rondani C.** (1845) Sulle differenze sessuali delle Conopinae e Myopinae negli insetti ditteri. Memoria undecima per servire alla ditterologia italiana. *Nuovi Annali delle Scienze Naturali, Bologna* 3, 5–16.
- Sars G.O.** (1869) Fortsatte bemærkninger over det dyriske livs utbredning i havets dybder. *Forhandlinger i Videnskabsselskabet i Christiania* 1868, 246–275.
- Sars G.O.** (1872) *On some remarkable forms of animal life from the great deeps off the Norwegian coast. Part 1, partly from posthumous manuscripts of the late Prof. Michael Sars.* University Program for the 1st half-year 1869. Christiania: Brøgger & Christie.
- Schander C., Rapp H.T., Kongsrød J.A., Bakken T., Berge J., Cochrane S., Oug E., Byrkjedal I., Cedhagen T., Fosshagen A., Gebruk A., Larsen K., Nygren A., Obst M., Plejel F., Stöhr S., Todt C., Warén A., Handler-Jacobsen S., Kuening R., Levin L., Mikkelsen N.T., Petersen K.K., Thorseth I.H. and Pedersen R.B.** (2010) The fauna of hydrothermal vents on the Mohn Ridge (North Atlantic). *Marine Biology Research* 6, 155–171.
- Schmidt O.** (1862) *Die Spongien des adriatischen Meeres.* Leipzig: Wilhelm Engelmann.
- Schmidt O.** (1870) *Grundzüge einer spongien-fauna des Atlantischen gebietes.* Leipzig: Wilhelm Engelmann.
- Schmidt O.** (1875) Spongien. In Die Expedition zur physikalisch-chemischen und biologischen Untersuchung der Nordsee im Sommer 1872. *Jahresbericht der Commission zur Wissenschaftlichen Untersuchung der Deutschen Meere in Kiel*, Volume 2–3. Berlin: Wiegandt, Hempel & Parey, pp. 115–120.
- Schmidt O.** (1880) Die Spongien des Meerbusen von Mexico (und des caraibischen Meeres). Heft II. Abtheilung II. Hexactinelliden. Abtheilung III. Tetractinelliden. Monactinelliden und Anhang. Nachträge zu Abtheilung I (Lithistiden). In *Reports on the dredging under the supervision of Alexander Agassiz, in the Gulf of Mexico, by the USCSS 'Blake'*. Jena: Gustav Fischer, pp. 33–90.
- Schulze F.E.** (1885) The Hexactinellida. In Tizard T.H., Moseley H.M., Buchanan J.Y. and Murray J. (eds) *Report on the Scientific Results of the Voyage of H.M.S. 'Challenger', 1873–1876*, Volume 1. Narrative, pp. 437–451.
- Shields M.A. and Hughes D.J.** (2009) Large-scale variation in macrofaunal communities along the eastern Nordic Seas continental margin: a comparison of four stations with contrasting food supply. *Progress in Oceanography* 82, 125–136.
- Sollas W.J.** (1882) The sponge-fauna of Norway; a report on the Rev. A.M. Norman's collection of sponges from the Norwegian Coast. *Annals and Magazine of Natural History* 9, 141–165, 426–453.
- Sollas W.J.** (1885) A classification of the Sponges. *Scientific Proceedings of the Royal Dublin Society (new series)* 5, 112.
- Sollas W.J.** (1886) Preliminary account of the Tetractinellid sponges dredged by H.M.S. 'Challenger' 1872–76. Part I. The Choristida. *Scientific Proceedings of the Royal Dublin Society (new series)* 5, 177–199.
- Stephens J.** (1915) Sponges of the coasts of Ireland. I. The Triaxonida and part of the Tetraxonida. *Fisheries, Ireland Scientific Investigations* 1914, 1–43.
- Swarczewsky B.A.** (1906) Beiträge zur Spongieng-Fauna des Weissen Meeres. *Mémoires de la Société des Naturalistes de Kiew* 20, 307–371.
- Tabachnick K.R. and Menshenina L.L.** (2007) Revision of the genus *Asconema* (Porifera: Hexactinellida: Rossellidae). *Journal of the Marine Biological Association of the United Kingdom* 87, 1403–1429.
- Thiele J.** (1903) Beschreibung einiger unzureichend bekannten monaxonen Spongien. *Archiv für Naturgeschichte* 69, 375–398.
- Thomson C.W.** (1873) *The depths of the sea.* London: Macmillan and Co.
- Topsent E.** (1888) Contribution à l'étude des Clionides. *Archives de Zoologie expérimentale et générale* 2, 1–165.
- 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 de Monaco* 2, 1–165.
- Topsent E.** (1898) Eponges nouvelles des Açores. Première série. *Mémoires de la Société zoologique de France* 11, 225–255.
- Topsent E.** (1900) Etude monographique des spongiaires de France. III. Monaxonida (Hadromerina). *Archives de Zoologie expérimentale et générale* 3, 1–331.
- Topsent E.** (1904) Spongiaires des Açores. *Résultats des campagnes scientifiques accomplies par le Prince Albert I de Monaco* 25, 1–280.
- Topsent E.** (1913) Spongiaires provenant des campagnes scientifiques de la 'Princesse Alice' dans les Mers du Nord (1898–1899, 1906–1907). *Résultats des Campagnes Scientifiques Accomplies par le Prince Albert I de Monaco* 45, 1–67.
- Topsent E.** (1927a) Croisière du 'Pourquoi-Pas?' en 1926. Eponges du Scoresby Sund (Groenland oriental). *Annales de l'Institut Océanographique* 4, 253–260.
- Topsent E.** (1927b) Diagnoses d'éponges nouvelles recueillies par le Prince Albert 1er 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 1er de Monaco. *Résultats des campagnes scientifiques accomplies par le Prince Albert I de Monaco* 74, 1–376.
- Topsent E.** (1933) Eponges de Lamarck conservées au Muséum de Paris. Fin. *Archives du Muséum national d'histoire naturelle Paris* 6, 1–60.

- Uriz M.-J. and Rosell D.** (1990) Sponges from bathyal depths (1000–1750 m) in the Western Mediterranean Sea. *Journal of Natural History* 24, 373–391.
- Vacelet J.** (1961) Quelques Eponges remarquables de Méditerranée. *Revue des Travaux de l'Institut des Pêches maritimes* 25, 351–354.
- Vacelet J.** (2006) New carnivorous sponges (Porifera, Poecilosclerida) collected from manned submersibles in the deep Pacific. *Zoological Journal of the Linnean Society* 148, 553–584.
- Van Soest R.W.M.** (2001) Porifera. In Costello M.J., Embley C. and White R. (eds) *European register of marine species: a check-list of the marine species in Europe and a bibliography of guides to their identification*. Collection Patrimoines Naturels, 50, 70–86, pp. 362–363.
- Van Soest R.W.M., Boury-Esnault N., Hooper J.N.A., Rützler K., de Voogd N.J., Alvarez de Glasby B., Hajdu E., Pisera A.B., Manconi R., Schoenberg C., Janussen D., Tabachnick K.R., Klautau M., Picton B.E., Kelly M., Vacelet J., Dohrmann M., Diaz M.-C. and Cárdenas P.** (2016) *World Porifera database*. Available at <http://www.marinespecies.org/porifera> (accessed 5 November 2016).
- Van Soest R.W.M., Picton B.E. and Morrow C.C.** (2000) Sponges of the North East Atlantic. In *World Biodiversity Database CD-ROM Series, Windows/Mac version 1.0*. Amsterdam: ETI, University of Amsterdam. Available at http://species-identification.org/species.php?species_group=sponges&id=104&menuentry=soorten (accessed 5 November 2016).
- Verrill A.E.** (1874) Results of recent dredging expeditions on the coast of New England. *American Journal of Science and Arts Series* 3 7, 498–505.
- von Marenzeller E.** (1878) Die Coelenteraten, Echinodermen und Würmer der K.K.Österreichisch-Ungarischen Nordpol-Expedition. *Denkschriften der Kaiserlichen Akademie der Wissenschaften, Mathematisch-naturwissenschaftliche Classe Wien* 35, 357–398.
- von Lendenfeld R.** (1887) On the systematic position and classification of sponges. *Proceedings of the Zoological Society of London* 1886, 558–662.
- von Lendenfeld R.** (1898) Die Clavulina der Adria. *Nova acta Academiae Caesareae Leopoldino Carolinae germanicae naturae curiosorum* 69, 1–251.
- Vosmaer G.C.J.** (1882) Report on the sponges dredged up in the Arctic Sea by the 'Willem Barents' in the years 1878 and 1879. *Niederländisches Archiv für Zoologie* Supplement 1, 1–58.
- Vosmaer G.C.J.** (1885) The sponges of the 'Willem Barents' expedition 1880 and 1881. *Bijdragen tot de Dierkunde* 12, 1–47.
- Vosmaer G.C.J.** (1887) Klassen und Ordnungen der Spongien (Porifera). In Bronn H.G. (ed.) *Die Klassen und Ordnungen des Thierreichs*, Volume 2. Leipzig–Heidelberg: C.F. Winter'sche Verlagshandlung, pp. 1–496.
- Weber J.** (1989) Physiography and bathymetry of the Arctic Ocean sea-floor. In Herman Y. (ed.) *The Arctic Seas. Climatology, oceanography, geology, and biology*. New York, NY: Springer, pp. 797–828.
- Whiteaves J.F.** (1874) Report on deep-sea dredging operations in the Gulf of St. Lawrence with notes on the present condition of the marine fisheries and oyster beds of part of the region. In *Annual Report of the Department of Marine and Fisheries, Canada, for 1873 Appendix U*. Ottawa: I.B. Taylor, pp. 178–204.
- Whiteaves J.F.** (1901) *Catalogue of the marine invertebrates of eastern Canada*. Geological Survey of Canada, Publication No. 772. Ottawa: S.W. Dawson.
- Wilson H.V.** (1925) Siliceous and horny sponges collected by the U.S. Fisheries Steamer 'Albatross' during the Philippine Expedition, 1907–10. *Contributions to the biology of the Philippine Archipelago and adjacent regions*. *Bulletin of the United States National Museum* 100, 273–532.
- and
- Witte U.** (1996) Seasonal reproduction in deep-sea sponges – triggered by vertical particle flux? *Marine Biology* 124, 571–581.
- Correspondence should be addressed to:**
- A. Plotkin
Department of Biology, University of Bergen, Postbox 7803,
5020 Bergen, Norway.
email: alexander.s.plotkin@gmail.com

APPENDIX 1

KEY FOR THE NORDIC AND ARCTIC SPECIES OF THE FAMILY POLYMASTIIDAE

1. Pedunculate, columnar, fungiform or drum-shaped body.....2
– Other body shape3
2. Body pedunculate or columnar, but never fungiform or drum-shape. Choanosome is a semi-fluid, amorphous mass with free-scattered bundles of small spicules. Tracts of principal spicules stretch in the cortex parallel to the surface.*Quasillina brevis*
– Body columnar, pedunculate, fungiform or drum-shaped. Choanosome dense, with longitudinal tracts of principal spicules crossing the upper surface.....*Tentorium semisuberites*
3. Raphids in trichodragmata present (in the subcortical area)*Spinularia spinularia*
– Raphids in trichodragmata absent4
4. Exotyles with ornamented distal knobs present.5
– Exotyles absent or, if present, without any distal ornaments.6
5. Exotyles 5–7.5 mm long, with distal knobs of irregular shape varying from fungiform and umbrelliform to hemispherical or subspherical*Sphaerotylus borealis*
– Exotyles not exceeding 1.5 mm in length, with regular, spherical distal knobs*Sphaerotylus capitatus*
6. Body discoid, hemispherical or lenticular, attached to the substrate only by the central basal point. A prominent spicule fringe present at the boundary between the upper and basal surface7
– Body globular, massive, cushion-shaped or encrusting. Basal surface completely attached to the substrate. Marginal spicule fringe tiny or absent.9
7. Upper surface smooth*Polymastia hemisphaerica*
– Upper surface hispid8
8. Papillae well-developed. Body may reach 80 mm in diameter and possess up to 300 papillae, of which most are inhalant (blind) and few are exhalant (with oscula at the summits). Exhalant papillae larger than the inhalant ones*Polymastia grimaldii*
– One to five weakly developed papillae, of which all are exhalant. Body not larger than 13 mm in diameter.*Spinularia sarsii*
9. Surface completely, or at least for the most part smooth or velvety10
– Surface completely hispid or shaggy16
10. Main choanosomal skeleton is a reticulation of spicule tracts11

- Main choanosomal skeleton composed of radial or longitudinal spicule tracts, occasionally meandering or anastomosing 12
11. Colour in life intensively orange or yellow. Exhalant papillae larger than the inhalant ones. *Polymastia boletiformis*
 - Colour in life pale cream or whitish. All papillae are exhalant and do not differ in size or shape *Weberella bursa*
12. Body massive or globular 13
 - Body cushion-shaped or encrusting 14
13. Surface uniformly smooth or velvety, with not more than 30 papillae, crater-shaped (very short and wide) in life. Aquiferous cavities all over the cortex. Choanosomal spicule tracts may meander or anastomose *Polymastia thielei*
 - Surface smooth or velvety, but with a marginal hispid collar. Up to 150 conical or cylindrical papillae. Aquiferous cavities concentrated in the cortical areas around the papillae. Choanosomal skeleton spicule tracts never meander or anastomose *Polymastia uberrima*
14. Although the spicules considerably vary in length, only two size categories can be distinguished. Large spicules present both in cortex and choanosome. Cortex comprises three prominent layers, a superficial palisade of small spicules, a middle layer of loosely lying criss-cross large spicules and an internal layer of densely packed criss-cross large spicules *Polymastia svenseni*
 - Three size categories of spicules clearly distinguished. Large spicules comprise choanosomal tracts. Cortex of two layers, a superficial palisade of small spicules and an internal layer of densely packed criss-cross intermediary spicules 15
15. Oscula at the summits of papillae not visible. In the cortex superficial spicule palisade and internal layer of criss-cross spicules intermingle *Polymastia bartletti* or *Polymastia nivea* (discrimination possible only based on molecular data)
 - In life some papillae with visible oscula at the summits. In the cortex superficial spicule palisade and internal layer of criss-cross spicules clearly segregated *Polymastia penicillus*
16. Body not exceeding 24 mm in diameter, with a single weakly developed papilla and a tiny marginal spicule fringe. Cortex comprises a superficial palisade of small spicules and an internal layer of criss-cross spicules in the central area and only the palisade in the periphery *Spinularia njordi*
 - Body with numerous well-developed papillae, usually exceeds 30 mm in diameter, often reaching up to 100 mm. Marginal spicule fringe absent. Cortex uniform, comprising a superficial palisade of small spicules, a middle layer of collagen fibres with low density of spicules and an internal layer of criss-cross spicules 17
17. Four size categories of spicules including filiform monactines averaging 2.5 mm in length and reinforcing the surface hispidation. *Polymastia andrica* or *Polymastia* sp. (discrimination possible only based on molecular data)
 - Three size categories of spicules with the largest not exceeding 1.8 mm in length. Filiform monactines absent 18
18. Inhalant papillae often bear at the summits threads with buds. Middle cortical layer up to 180 µm thick *Polymastia arctica*
 - Inhalant papillae without buds. Middle cortical layer thinner than 110 µm *Polymastia mamillaris*