

# Alleged cosmopolitanism in sponges: the example of a common Arctic *Polymastia* (Porifera, Demospongiae, Hadromerida)

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## ABSTRACT

For several years the cosmopolitanism in sponges has been questioned. We studied populations of a very abundant *Polymastia* from the Arctic (White Sea and Barents Sea) commonly referred to *P. mamillaris* (Müller, 1806). The redescription of the type material of *P. arctica* (Merejkowsky, 1878) which was synonymized with *P. mamillaris* and its comparison with types of *P. mamillaris* and other common Arctic and NE Atlantic species shows that *P. arctica* is a valid species. It differs from *P. mamillaris* and *P. penicillus* by the presence of a thick (90-180 µm) collagenous layer in the cortex, the presence of spicules in the papilla internal laminae and the formation of buds at the top of the papillae. This result demonstrates that the often-cited “cosmopolitanism” in sponges is the result of over-conservative systematics rather than true genetic homogeneity.

## KEY WORDS

Porifera,  
Demospongiae,  
*Polymastia arctica*,  
biogeography,  
White Sea,  
Barents Sea,  
buds.

## RÉSUMÉ

*Le prétendu cosmopolitisme chez les éponges : l'exemple d'une Polymastia (Porifera, Demospongiae, Hadromerida) commune de l'Arctique.*

Depuis plusieurs années le cosmopolitisme chez les espèces d'éponges a été remis en question. Nous avons étudié des populations d'une *Polymastia* arctique très abondante communément identifiée à *P. mamillaris* (Müller, 1806). La redescription du matériel type de *P. arctica* (Merejkowsky, 1878) mis en synonymie avec *P. mamillaris* et sa comparaison avec les types de *P. mamillaris* et d'autres espèces communes de l'Arctique et de l'Atlantique du nord-est a montré que *P. arctica* est une espèce valide. Elle diffère de *P. mamillaris* et *P. penicillus* (Montagu, 1818) par la présence d'une couche épaisse de collagène (90-180 µm) dans l'ectosome et de spicules dans les lames cellulaires des papilles, et par la formation de bourgeon au sommet des papilles. Ce résultat montre une fois de plus que le prétendu cosmopolitisme chez les éponges est du à une systématique trop conservatoire plutôt qu'à une véritable homogénéité génétique.

## MOTS CLÉS

Porifera,  
Demospongiae,  
*Polymastia arctica*,  
biogéographie,  
mer Blanche,  
mer de Barents,  
bourgeons.

## INTRODUCTION

The presumed cosmopolitanism among invertebrates species has been recently questioned, especially among species with limited means of dispersal. This type of problem is particularly well illustrated in sponges where traditional taxonomy is based on few morphological characters (Klautau *et al.* 1999). It led at the end of the 19th century to an era of "lumping" of many morphologically similar species described by the earlier taxonomists into single, artificially cosmopolitan morphospecies. These "lumpers" have been followed until recently. *Polymastia mamillaris* (Müller, 1806) is an example of a species with such a cosmopolitan distribution (Topsent 1900). Many early described species of *Polymastia* Bowerbank, 1864 have been synonymized with *Polymastia mamillaris* (see Topsent 1900). But recent redescriptions of the NE Atlantic *Polymastia* species from the type specimens have made it possible to demonstrate that some of these synonymies are erroneous. In particular, the confusion between *P. mamillaris* and *P. penicillus* (Montagu, 1818) has recently been clarified (Morrow & Boury-Esnault 2000), but all the synonymies with *P. mamillaris* have to be reevaluated.

In the recent redescriptions of *Polymastia* species from the NE Atlantic (Boury-Esnault 1987; Boury-Esnault *et al.* 1994) the populations from the Arctic area have not been reassessed and are commonly considered as belonging to *P. mamillaris* (Ereskovsky 1993; Plotkin & Ereskovsky 1997; Plotkin *et al.* 1999). However, Merejkowsky (1878) described under the name *Rinalda arctica* a polymastid species from the White Sea. The genus *Rinalda* was described by Schmidt (1870) for the species *R. uberrima* from the Norwegian coast. Vosmaer (1882, 1885) synonymized *Rinalda* with *Polymastia* and he was followed by all subsequent authors (Topsent 1900; Kelly-Borges & Bergquist 1997; Morrow & Boury-Esnault 2000; Boury-Esnault 2002). The species *P. uberrima* was considered as a valid species, but *R. arctica* was put in synonymy with the type species of the genus *Polymastia*, *P. mamillaris*. "Dr. C. de Merejkowsky was kind enough to send me a fragment of his *Rinalda arctica*, and I am now sure that it is identical with *P. mamillaris* Bowerbank" (Vosmaer 1885: 14). This has been accepted since that time (Koltun 1966) and the taxonomic status of *Rinalda arctica* has never been reassessed.

In this paper we redescribe the type series of *Polymastia arctica* and compare it with other

material from Arctic stored in the Zoological Institute of the Russian Academy of Sciences (ZIRAS). The NE Atlantic *P. penicillus* (Montagu 1818: 93) and *P. mamillaris* (Müller 1806: 44) are also compared with the Arctic species.

## SYSTEMATICS

Family POLYMASTIIDAE Gray, 1867

Genus *Polymastia* Bowerbank, 1864

*Polymastia* Bowerbank, 1864: 177.

*Penicillaria* Gray, 1867: 527.

*Rinalda* Schmidt, 1870: 51.

TYPE SPECIES. — *Spongia mamillaris* Müller, 1806: 44 (by monotypy).

DIAGNOSIS (from Boury-Esnault 2002). — Polymastiidae, thickly encrusting, spherical or cushion-shaped, always with papillae. Choanosomal skeleton composed of radial tracts of principal spicules between which free spicules are scattered. Ectosomal skeleton composed of at least two layers, the superficial one is a palisade of small tylostyles, the lower layer is made of intermediary spicules, tangential to the surface. The principal spicules can be tylostyles, subtylostyles, styles or stronglyloxeas, intermediary spicules are most often tylostyles, and ectosomal spicules are always tylostyles.

*Polymastia arctica* (Merejkowsky, 1878)

*Rinalda arctica* Merejkowsky, 1878: 4; 1880: 421.

*Polymastia arctica* – Vosmaer 1885: 14.

*Polymastia penicillus* – Swarczewsky 1906: 7.

*Polymastia mamillaris* – Arnesen 1918: 8. — Ereskovsky 1993: 22; 1995: 724. — Plotkin & Ereskovsky 1997: 127. — Plotkin *et al.* 1999: 18.

*Polymastia mamillaris mamillaris* – Koltun 1966 (partly): 69.

TYPE MATERIAL. — **White Sea.** Dvina and Onega bays, 1876-1877, Merejkowsky coll., 8 syntypes (ZIRAS). Merejkowsky (1878: 15) had not designated a holotype. Lectotype (present designation): Archipelago of Solovki, Onega Bay, 64°57'0"-65°10'8"N, 35°29'4"-35°51'6"E, 9-22 m, summer 1877 (ZIRAS catalogue n° 84a, spicule slide n° 5526a, section slide n° 1);

paralectotypes: Archipelago of Solovki, Onega Bay, 64°57'0"-65°10'8"N, 35°29'4"-35°51'6"E, 9-22 m, summer 1877, 5 specimens (ZIRAS catalogue n° 83, 84b; spicule slides n° 103/02a-d, 5526b); Dvina Bay, off Cape Kerets, 65°25'N, 39°38'E, 11 m, 22.VI.1876, 2 specimens (ZIRAS catalogue n° 85, spicule slides N 9112a-b).

OTHER MATERIAL EXAMINED. — Specimens from ZIRAS collections.

**White Sea.** Kandalaksha Bay, 66°31'5"N, 33°18'5"E, 109 m, 22.VIII.1964, 1 specimen (as *P. mamillaris mamillaris* (Koltun 1966)) (catalogue n° 10, spicule slide n° 104/02). — Onega Bay, 64°40'2"N, 35°24'4"E, 35 m, 22.X.1964, 1 specimen (as *P. mamillaris mamillaris* (Koltun 1966)) (catalogue n° 73a, spicule slide n° 2/02a, section slide n° 2a). — Onega Bay, Archipelago of Solovki, 18 m, summer 1905, 1 specimen (as *P. penicillus* (Swarzewsky 1906)) (catalogue n° 144, spicule slide n° 9114, section slide n° 3).

**Barents Sea.** Murman Coast, Kildin Straight, 69°18'0"N, 34°10'8"E, 100 m; 25.VII.1884, 2 specimens (as *P. mamillaris mamillaris* (Koltun 1966)) (catalogue n° 78-79, spicule slides n° 9107 and 5603). — Chesha Bay, off Cape Veliky Nos, 67°21'5"N, 47°46'5"E, 7 m, 13.X.1964, 1 specimen (as *P. mamillaris mamillaris* (Koltun 1966)) (catalogue n° 145, spicule slide n° 13732). — Murman Coast, Bay of Teriberka, 69°09'0"N, 35°09'0"E, depth unknown, summer 1880, 4 specimens (as *P. robusta* (Koltun 1966)) (catalogue n° 148, spicule slides n° 5602a-d, section slide n° 41). Personal collection of the authors:

**White Sea.** Kandalaksha Bay, the Keret' Straight, 66°17'4"N, 33°43'8"E, 15 m, 11.VII.1998, 6 specimens. — Sredny Island, Yushkovka Harbour, 66°17'4"N, 33°45'0"E, 10 m, 3.VII.2000, 1 specimen. — Sredny Island, Nagovitsa Harbour, 66°17'4"N, 33°38'4"E, 4 m, 19.VI.1998, 1 specimen; 8-10 m, 8.VIII.1998, 12 specimens; 10 m, 28.VI.2001, 1 specimen. — Chupa Inlet, Levaya Harbour, 66°20'4"N, 33°39'6"E, 25.X.2000, 6 m, 2 specimens; 25 m, 9.VII.2001, 1 specimen.

**Barents Sea.** Murman Coast, Bay of Dal'nie Zelentsy, Nemetsky Island, 69°07'2"N, 36°06'0"E, 15 m, 14.VIII.2001, 1 specimen.

## DESCRIPTION

### *External characters*

The lectotype is a cushion-shaped sponge measuring approximately 32 × 30 × 10 mm attached to a bivalve shell (Fig. 1A). The upper surface is hispid and partly covered with silt. The colour of the surface areas without silt and the papillae is cream in alcohol. Among other specimens of the collection, the largest ones may occupy more than 100 cm<sup>2</sup>. The colour of the living specimens

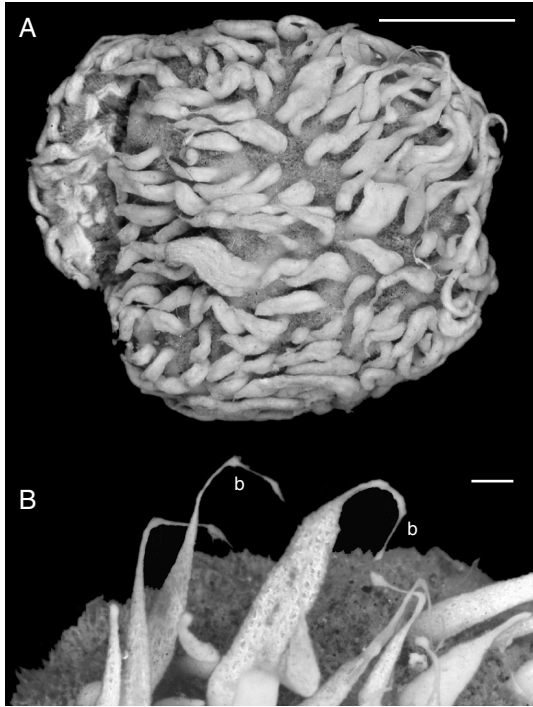


FIG. 1. — Lectotype of *Polymastia arctica* (Merejkowsky, 1878); **A**, whole sponge; **B**, fragment with budding papillae. Abbreviation: **b**, buds. Scale bars: **A**, 1 cm; **B**, 1 mm.

is yellow for the papillae and the surface free from silt and orange for the choanosome.

The lectotype has about 150 cylindrical inhalant and two conical exhalant papillae. The inhalant papillae are 4–9 mm in length and 1–3 mm in diameter. The exhalant papillae are 5 and 7 mm long. The diameter decreases approximately from 5 mm at the base to 3 mm at the top. The diameter of the osculum is about 0.5 mm. The number of papillae for the different studied specimens depends on body size (Plotkin *et al.* 1999) and may exceed 400 inhalant and 19 exhalant papillae per specimen (mean 13 inhalant papillae per cm<sup>2</sup>). They are respectively 2–18/1–6 mm and 3–12/3–7 mm in length. The osculum diameter is 0.2–1.0 mm. Young small sponges bear a single papilla with both exhalant and inhalant canals.

In the lectotype, about 60 inhalant papillae bear short threads with spherical buds at the top (one to three buds per papillae) (Fig. 1B). Of the other

42 examined specimens, 35 also possess buds at the top of the inhalant papillae. Buds are usually spherical (0.2–1.5 mm in diameter), slightly hispid and attached to a papilla by a thread formed by spicules and organic material. During the growing of buds, the thread becomes thinner. One thread may bear up to six buds arranged in line.

#### *Skeleton*

The ectosomal skeleton of the lectotype (Fig. 2A) is about 580  $\mu$ m thick and consists of three layers: an external dense palisade layer of small tylostyles (270  $\mu$ m), a middle layer of collagen (90  $\mu$ m) and an internal layer of tangential intermediary spicules (220  $\mu$ m). The ectosomal skeleton of the other specimens varies from 480 to 680  $\mu$ m thick (mean 562  $\pm$  47,  $n = 11$ ) and the thickness of the three layers is respectively 180–310  $\mu$ m (234  $\pm$  32  $\mu$ m), 90–180  $\mu$ m (129  $\pm$  19  $\mu$ m) and 160–250  $\mu$ m (198  $\pm$  18  $\mu$ m).

In the lectotype the choanosomal skeleton (Fig. 2A) is composed of tracts of principal spicules (250–300  $\mu$ m thick), which run perpendicular to the surface. They may divide below the cortex into two or three thinner ones (85–135  $\mu$ m). Groups from two to five free spicules corresponding to the ectosomal tylostyles are scattered between the choanosomal tracts. They are especially abundant below the tangential layer of intermediary spicules forming a layer of about 720  $\mu$ m thick. In other studied specimens the tracts of principal spicules are 170–460  $\mu$ m (mean 281  $\pm$  60  $\mu$ m,  $n = 70$  tracts) thick at the base, and after several divisions they are 70–140  $\mu$ m (mean 110  $\pm$  12  $\mu$ m,  $n = 73$  tracts) below the cortex. They cross the ectosome and echinate the surface by approximately 390–1600  $\mu$ m (mean 800  $\pm$  254  $\mu$ m,  $n = 11$ ). Groups of from two to five free ectosomal spicules are scattered between the spicule tracts. They are especially abundant below the cortex forming a layer of 320–780  $\mu$ m thick (mean 558  $\pm$  104  $\mu$ m).

In the lectotype the skeleton of the papillae (Fig. 2A) consists of ascending tracts of principal spicules that run the length of the papillae. They are the continuation of the tracts of the choanosome. Each tract contains seven to 14 spicules. From the outside to the inside the papilla wall is

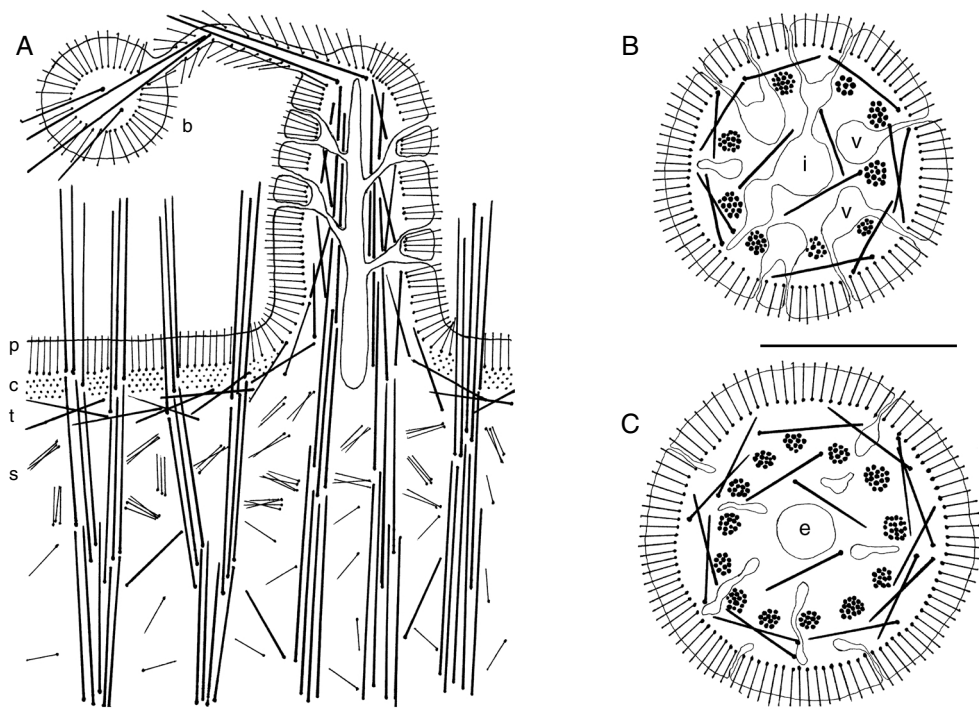


FIG. 2. — *Polymastia arctica* (Merejkowsky, 1878); **A**, longitudinal section of the body and inhalant papilla; **B**, transversal section of the inhalant papilla; **C**, transversal section of the exhalant papilla. Abbreviations: **b**, bud; **c**, collagenous layer; **e**, exhalant canal; **i**, inhalant canal; **p**, palisade layer; **s**, subcortical layer of diffuse choanosomal spicules; **t**, tangential layer; **v**, vestibule. Scale bars: 1 mm.

composed of a palisade of ectosomal tylostyles (170–200  $\mu\text{m}$ ), and a tangential layer of intermediary spicules (40–60  $\mu\text{m}$ ). The collagenous layer presented in the main body cortex is absent in the papillae. Inhalant papillae usually possess nine tracts and a single central inhalant canal (Fig. 2B). The canal is connected with lateral vestibules, which open by ostioles in the wall. The internal laminae separating vestibules and the central canal contain intermediary spicules. Exhalant papillae possess 15 tracts and the central exhalant canal surrounded by several inhalant canals connected with vestibules and ostioles (Fig. 2C). Intermediary spicules are present in the laminae between exhalant and inhalant canals.

The number of spicules in each tract varies from six to 47 in the other studied specimens (mean 21 spicules/tract). Inhalant and exhalant papillae possess respectively seven to 11 and 11–15 tracts/

papillae. All cavities of the papillae are separated by internal laminae with intermediary spicules. Several principal spicule tracts of an inhalant papilla may fuse at the top forming an extension, which is the central axis of a bud thread (Fig. 2A). The thread is echinated by ectosomal tylostyles. The bud skeleton consists of an external dense palisade of ectosomal tylostyles, a few free intermediary spicules inside and some principal spicules of the thread which cross the bud.

#### *Spicules (Fig. 3)*

All spicule measurements were made on 43 specimens and 10 spicules of each type were measured for each sponge.

Ectosomal spicules are small fusiform slightly bent tylostyles with well marked heads. In the lectotype they measure 150–215/5.0–6.3  $\mu\text{m}$  (mean 171/5.1  $\mu\text{m}$ ,  $n = 10$ ), the head is 5.0–7.5  $\mu\text{m}$

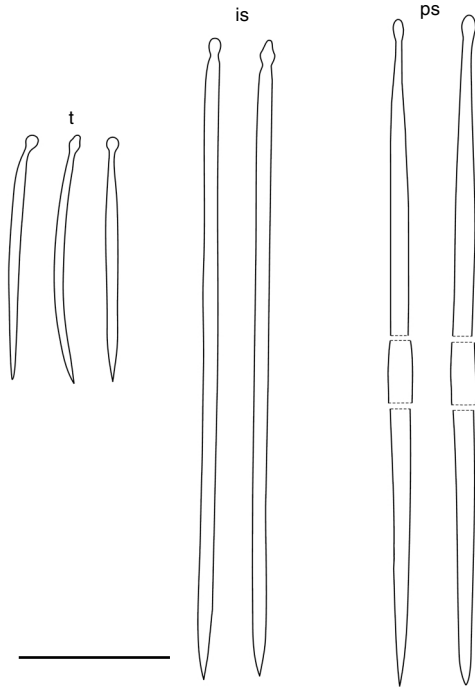


FIG. 3. — *Polymastia arctica* (Merejkowsky, 1878), spicules. Abbreviations: **is**, intermediate subtylostyles; **ps**, principal subtylostyles; **t**, small palisade tylostyles. Scale bar: 100  $\mu$ m.

(mean 5.6  $\mu$ m,  $n = 10$ ) in diameter. In the other specimens 120-215/3.8-6.3  $\mu$ m (mean 161  $\pm$  7/4.8  $\pm$  0.2  $\mu$ m). The diameter of the head is 3.8-7.5  $\mu$ m (mean 5.5  $\pm$  0.3).

Intermediary spicules are straight or slightly bent subtylostyles 380-470/10.0-12.5  $\mu$ m (mean 429/10.7  $\mu$ m,  $n = 10$ ) in the lectotype; 270-550/5.0-17.5  $\mu$ m (mean 414  $\pm$  22/9.5  $\pm$  0.8  $\mu$ m) in the other specimens.

Principal spicules are fusiform straight subtylostyles: 620-960/10.0-16.3  $\mu$ m (mean 803/13.8  $\mu$ m,  $n = 10$ ) in the lectotype; 620-1100/8.8-20.0  $\mu$ m (mean 868  $\pm$  40/14.3  $\pm$  0.8  $\mu$ m) in the other specimens.

## DISCUSSION

*Polymastia arctica* is characterized by: 1) formation of buds at the tops of the papillae; 2) presence of a thick (90-180  $\mu$ m) intermediary

collagenous layer in the cortex; 3) presence of spicules in internal laminae of the papillae; 4) principal spicules are fusiform subtylostyles; and 5) intermediary spicules are subtylostyles.

*Polymastia mamillaris* and *P. penicillus* are characterized by: 1) absence of budding; 2) presence of thin (about 20  $\mu$ m) collagenous layer in *P. mamillaris* versus its absence in *P. penicillus*; 3) absence of spicules in internal laminae; 4) principal spicules are fusiform strongyloxea in *P. mamillaris* or tylostyles in *P. penicillus*; and 5) intermediary spicules are styles in *P. mamillaris* or tylostyles in *P. penicillus*. Thus, *P. arctica*, *P. penicillus* and *P. mamillaris* considered as synonymous since Vosmaer (1885) are in fact different species (Table 1).

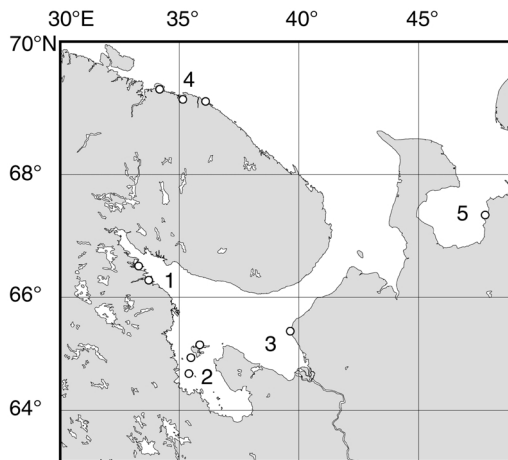
*Polymastia arctica* shares several traits with other North Atlantic *Polymastia*. With *P. grimaldi* (Topsent, 1913) it shares the large number of papillae, pronounced hispidation, thick collagenous layer in the cortex and spicules embedded in internal laminae of the papillae. Based on this similarity, Koltun (1966) considered *P. arctica* and *P. grimaldi* to be two subspecies of the same species. On the other hand, and similarly to many other *Polymastia*, *P. arctica* possesses no fringe made of accessory spicules and no smooth basal cortex in contrast to *P. grimaldi*.

The most important character of *P. arctica* is the budding (Merejkowsky 1880), the ecological aspects of which were recently studied by Plotkin & Ereskovsky (1997). No other Arctic or North Atlantic Polymastiidae are known to produce buds, with the exception of an insufficient description of budding in the Norwegian shallow water *Polymastia* (Arnesen 1918). Arnesen's specimens have yet to be revised in order to verify that they belong to *P. arctica*. However the phenomenon of papilla budding is well known for several *Polymastia* from the Southern Hemisphere (Bergquist *et al.* 1970; Ayling 1980; Battershill & Bergquist 1990).

From a biogeographical point of view, the range occupied by *P. arctica* includes the White Sea and the south coast of the Barents Sea from 47°46'5E in the East to 34°10'8E in the West (Fig. 4). These sponges are found mainly in shallow waters (4-40 m) where hard substrata are avail-

TABLE 1. — Discriminating characters and distribution of *Polymastia arctica* (Merejkowsky, 1878), *P. mamillaris* (Müller, 1806) and *P. penicillus* (Montagu, 1818). All measurements are given in µm.

Characters		<i>P. arctica</i>	<i>P. mamillaris</i>	<i>P. penicillus</i>
Cortex	Thickness	560	400	500
	Number of layers	3	3	2
	Palisade layer	235	300	170
	Collagenous layer	130	20	absent
	Tangential layer	200	80	330
Choanosome	Subcortical layer of free spicules	560	500	absent
	Free spicule type	ectosomal	ectosomal	intermediary
Papillae	Number/specimen	> 100	> 10	> 10
	Budding	present	absent	absent
Spicules	In internal lamina	present	unknown	absent
	Type of ectosomal	fusiform tylostyles	fusiform tylostyles	tylostyles
	Type of intermediary	subtylostyles	styles	tylostyles
	Type of principal	fusiform subtylostyles	fusiform strongyloxea	tylostyles
Distribution		White Sea, Barents Sea	Swedish west coast	NE Atlantic
Depth range		4-109 m	76-225 m	0-600 m

FIG. 4. — Distribution of *Polymastia arctica* (Merejkowsky, 1878), White Sea: 1, Kandalaksha Bay; 2, Onega Bay; 3, Dvina Bay; Barents Sea: 4, Murman Coast; 5, Chesha Bay.

able; rarely they inhabit deeper sites (down to 100 m). *Polymastia penicillus* is found in the North Atlantic to depths of 600 m (Boury-Esnault 1987). The known range of *P. mamillaris*

is currently restricted to the Swedish west coast and at the depth range of 76-225 m (Morrow & Boury-Esnault 2000). The presumed extensive geographical distribution of *P. mamillaris* across the entire North Atlantic and Arctic and as far as the Pacific coast suggested by Koltun (1966) appears to be the result of over-conservative taxonomy (lumping of species) as has been demonstrated for many other complex sponge species (Boury-Esnault *et al.* 1999; Klautau *et al.* 1999).

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