Morphological and cytological descriptions of a new *Polymastia* species (Hadromerida, Demospongiae) from the North-West Mediterranean Sea

Nicole Boury-Esnault[(1*)], Chantal Bézac[(2)]

[(1)] Aix-Marseille Université, CNRS UMR-6540 DIMAR, Centre d'Océanologie de Marseille. Station Marine d'Endoume. Rue Batterie des Lions, 13007. Marseille, France. nicole.boury_esnault@univmed.fr
[(2)] Aix-Marseille Université, CNRS UMS-2196, Centre d'Océanologie de Marseille. Station Marine d'Endoume. Rue Batterie des Lions, 13007. Marseille, France

Abstract: A new species of *Polymastia* (Hadromerida, Polymastiidae), *P. harmelini* is described from the coast of Provence (NW Mediterranean). Although this region has been intensively studied, new species are regularly found there. Its description includes morphological, anatomical and cytological features and the species is compared to the *Polymastia* species from the Atlanto-Mediterranean area.

Keywords: Hadromerida, *Polymastia*, skeleton, anatomy, cytology, taxonomy

Introduction

Even in the new era of "bar-coding" precise morphological and anatomical descriptions of organisms are still necessary for an unassailable systematics. As Jenner (2006) stressed "The study of morphology needs no excuse. It is the uncontested and irreplaceable documentation of life's diversity". This is particularly essential in animals such as sponges. The framework of the existing classification for Porifera has been recently revisited in a collective book "Systema Porifera" (Hooper and van Soest 2002). In the last 20 years the taxonomy of the genus *Polymastia* Bowerbank, 1864 (Demospongiae, Hadromerida, Polymastiidae) has been improved by taking into account the precise organisation of the skeleton in the main body and in the papilla (Boury-Esnault 1987, Kelly-Borges and Bergquist 1997, Morrow and Boury-Esnault 2000, Boury-Esnault 2002). It has been shown also the importance of cytological criteria as discriminating characters (Boury-Esnault 1974, Boury-Esnault *et al.* 1994). In a survey of the sponge fauna from the caves of the NW Mediterranean coast, Jean-Georges Harmelin has discovered at the entrance of the 3PP cave a new species belonging to the genus *Polymastia* (Fig. 1).

Materials and methods

The specimens were collected by SCUBA diving during a survey of "La Ciotat 3PP cave" (43°09'N, 5°36'E). The 3PP cave (Vacelet *et al*. 1994) is a long term biodiversity research focal site of the NW Mediterranean (Warwick *et al.* 2003). The specimens were collected in 1999, 2002 and 2004 fixed in buffered formalin 4% and then transferred to alcohol 70%. To study the shape and size of spicules, dissociation of siliceous skeleton in HNO_3 was done using routine procedures (Boury-Esnault and Rützler 1997), and then mounted on a slide in a drop of epoxy resin.

For the skeleton thin sections were made after inclusion in epoxy resin of small pieces of the specimen following Boury-Esnault *et al.* (2002). Sections of about 1 mm were made with an 11-1180 Isomet low speed saw (Buehler). The sections were then adhered to a slide, ground and polished with a polisher (ESCIL 200 GTL) to a thickness of 15 µm. The finishing touches were done by hand with abrasive papers n° 600 and n° 1200, and 8 and 3 µm alumina powder. The thin section was then coloured with toluidine blue under heat for several seconds. A coverslip with a small drop of resin was placed on the thin slides for observation.

For cytology in light and transmission electron microscopy (TEM), the specimens were fixed in glutaraldehyde 2.5% in a mixture of 0.4 M cacodylate buffer and seawater (4 vol: 5 vol) (Boury-Esnault *et al.* 1984). They were postfixed during 1h in 2% osmium tetroxide in seawater, dehydrated through an alcohol series, and embedded in Araldite. Semi-thin sections were stained with toluidine blue. Thin sections, contrasted with uranyl acetate and lead citrate, were observed under a ZEISS EM912 transmission electron microscope.

Results

Polymastia Bowerbank, 1864

Polymastia Bowerbank, 1864: p. 177; type species *Halichondria (Spongia) mamillaris* by original designation.

Pencillaria Gray, 1867: p. 527; type species *Spongia mamillaris* by original designation

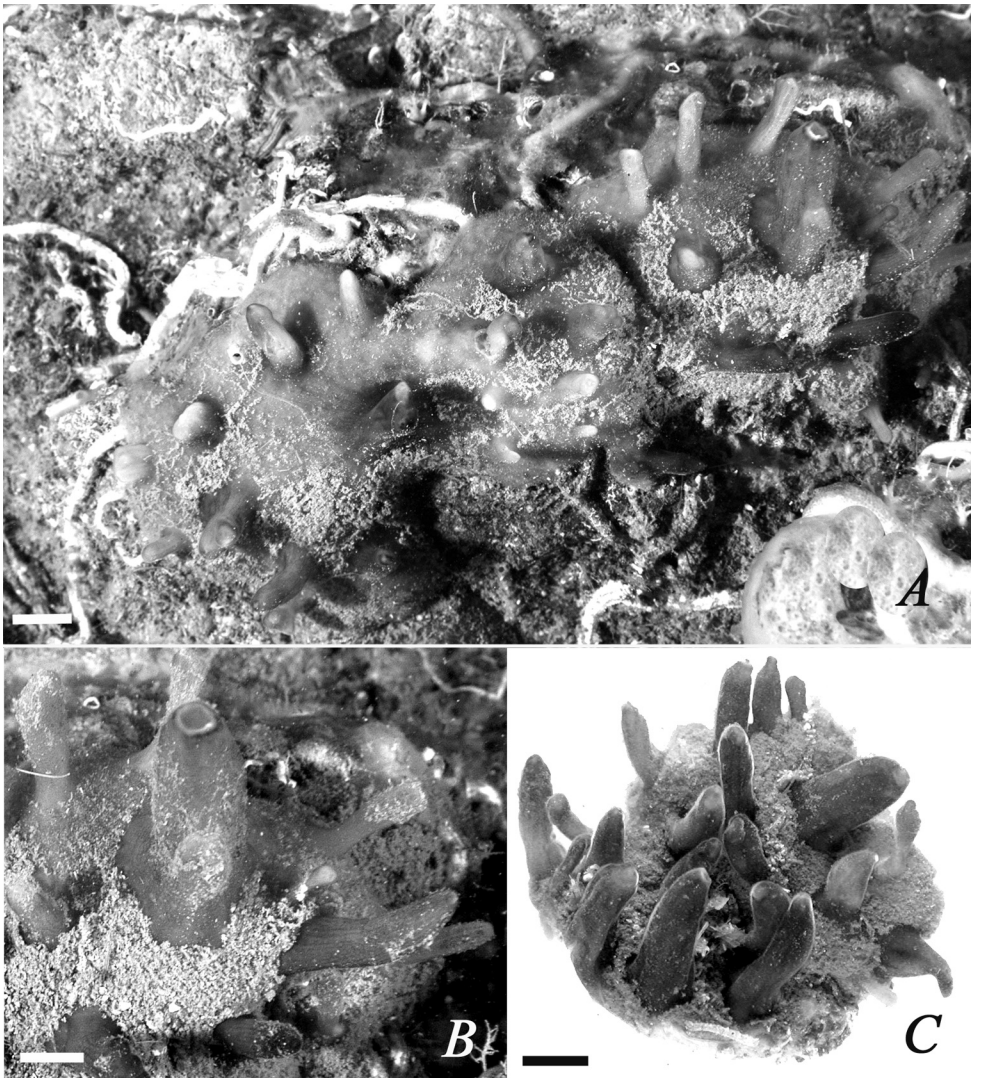

Fig. 1: A. *Polymastia harmelini* sp. nov. Living specimen photographed *in situ*. The specimen was covered by sediments, scale bar: 0.8 cm. **B.** Detail of an exhalant papilla of *P. harmelini* sp. nov. Note the dark ring below the oscule, scale bar: 0.4 cm. (photos Roland Graille). **C.** Type specimen in alcohol, scale bar: 0.5 cm.

Rinalda Schmidt, 1870: p. 51; type species *Rinalda uberrima* by original designation.

Diagnosis: Polymastiidae, thickly encrusting, spherical or cushion-shaped, always with papillae. Skeleton composed of radial tracts of principal spicules with free spicules scattered in between. Cortex composed of at least two layers, the superficial layer is a palisade of small tylostyles, the lower layer is made of intermediary spicules, tangential, semi-tangential or perpendicular to the surface. Exotyles echinating the surface may be present. The principal spicules can be tylostyles, subtylostyles, styles, or strongyloxeas, intermediary spicules are most often tylostyles, and ectosomal spicules are always tylostyles.

Polymastia harmelini sp. nov.

Material examined: 5.08.1999 type specimen (Fig. 1C); 13.09.1999; 6.11.2002; threshold of the 3PP cave in La Ciotat (Provence coast). Type specimen deposited in the "Museum national d'Histoire naturelle de Paris" (MNHN-DNBE.1562).

Type locality: on the threshold of the 3PP cave (43°09'N/5°36'E) at the basis of the west wall of the entrance at about 18 m deep.

Description

External characters (Fig. 1): The specimens are cushion shaped and cover a surface of about 100 cm^2. The thickness is about 3-5 mm. *In situ* (Fig. 1A) the papillae only are visible. The body is covered by sediments and particles trapped by the hispid surface. The colour of the papillae is brown, as well as the surface. The choanosome has a deep yellow colour in life. The cortex is difficult to tear but it is easily detachable from the choanosome. There are about 28 inhalant papillae and 1 exhalant papilla bearing an oscule per specimen. A dark ring followed by a white one surrounds the oscule (Fig. 1B). The length of the inhalant papilla is 4-10 x 1.5-3 mm and that of the exhalant ones is 8-12 x 4 mm.

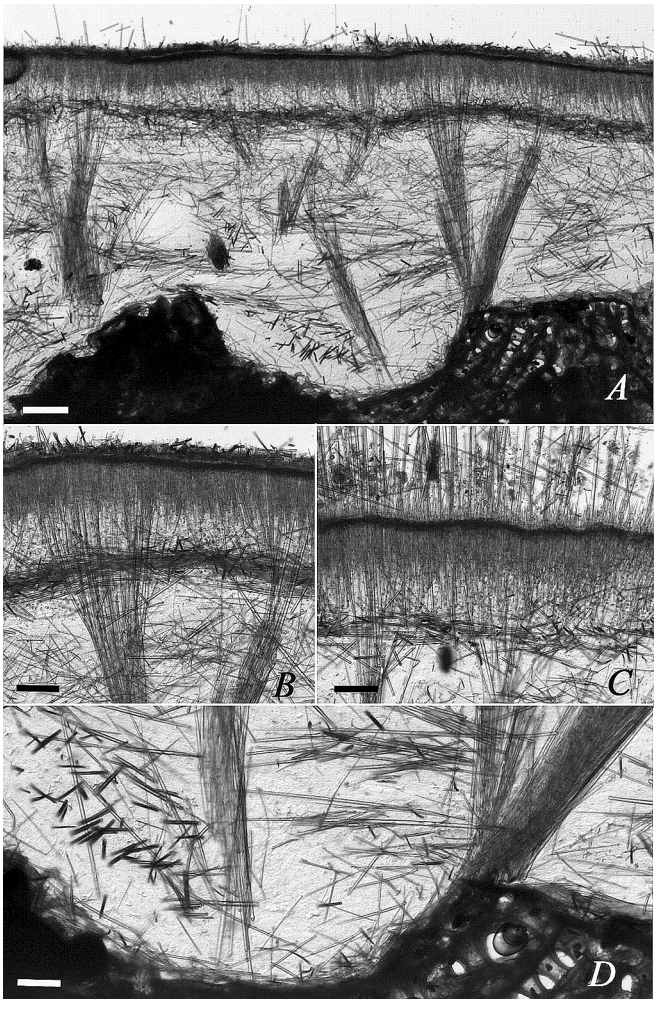

Fig. 2: *Polymastia harmelini* sp. nov. Organisation of the main body skeleton. **A.** General view, scale bar: 175 µm. **B.** Detail of the cortex, scale bar: 115 µm. **C.** Detail of the cortex, scale bar 115 µm. **D.** detail of the base, scale bar: 115 µm.

Skeleton (Fig. 2-3): The ectosomal skeleton is about 320-370 µm thick and composed of three layers: the upper one is a dense palisade (150-170 µm) of tylostyles which lie on a layer of collagen (90-120 µm) (Fig. 2A). The basal layer of the cortex is a tangential layer (50-80 µm) made of intermediary spicules (Figs 2A-C). Right below the surface is a layer of cells with granular inclusions (25 µm) which is responsible for the brown colour of the ectosome (Fig. 2B-C). The basal part in contact with the substratum is constituted by the tangential layer of intermediary spicules (Figs 2A and 2D). The palisade is absent and the sponge is fixed to the substratum by a collagen layer (Fig. 2D).

Choanosomal tracts of principal spicules can reach 340 µm in thickness at the basis. These tracts are divided into two or three smaller ones (170 µm) below the ectosome (Fig. 2A). They cross the ectosome and echinate the surface at distances of approximately 400-500 µm (Fig. 2C). Ectosomal and intermediary spicules are scattered between the choanosomal tracts (Fig. 2).

The skeleton of the papilla consists of ascending multispicular tracts running through the length of the papillae (Fig. 3). About 25 to 35 tracts are present in a papilla and each tract has a diameter of 50-100 µm. The central exhalant canal is about 160 µm in diameter. It is surrounded in the exhalant papilla by about 10 inhalant canals 80 to 150 µm in diameter. The septa between the canals are strengthened by intermediary spicules (Fig. 3). The ectosomal skeleton of the papilla is about 260-300 µm thick and composed of two layers (Fig. 3). Towards the periphery there is a layer of tangentially arranged intermediary spicules (50 µm) and followed by a palisade of ectosomal spicules (180-290 µm). Towards the surface, the extremities of the ectosomal spicules form a regular hispidation of about 100 µm in height. Below the cell surface there is a layer of spherulous cells of about 50 µm thick.

Spicules (Fig. 4): Ectosomal spicules are tylostyles with a well-marked head 122-239 x 1.7-5.2 µm (mean = 193 x 2.8 µm) straight or slightly bent (Fig. 4C). Intermediary spicules

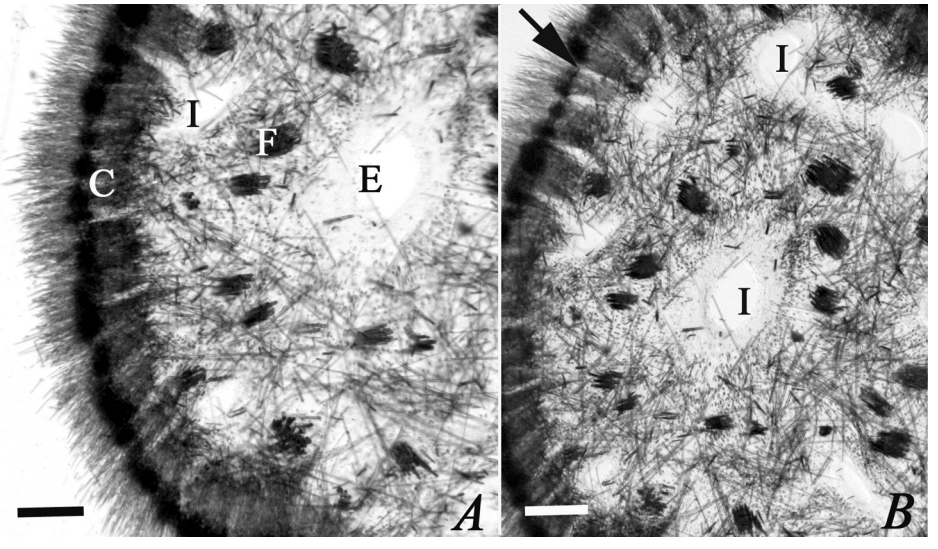

Fig. 3: *Polymastia harmelini* sp. nov. Organisation of the papilla skeleton. **A.** Exhalant papilla, scale bar: 100 µm. **B.** Detail of the inhalant part of a papilla. The arrow indicates inhalant opening, scale bar: 100 µm. Abbreviations: C: cortex; E: exhalant canal; F: transversal section of fascicle of principal spicules. I: inhalant canal.

Fig. 4: *Polymastia harmelini* sp. nov. SEM views of spicules. **A.** Principal spicules, scale bar: 48 µm. **B.** Intermediary spicules, scale bar: 38 µm. **C.** Ectosomal spicules, scale bar: 15 µm. Abbreviations: i: intermediary spicules; e: ectosomal spicules.

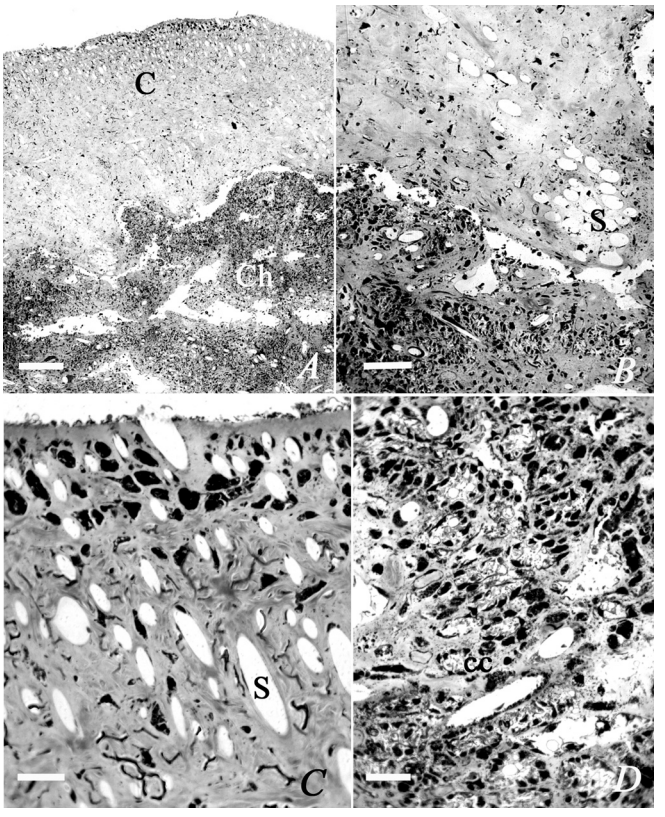

Fig. 5: A *Polymastia harmelini* sp. nov. anatomy of the main body, semithin sections. **A.** General view, scale bar: 100 µm. **B.** Detail of the limit between ectosome and choanosome, scale bar: 50 µm. **C.** Detail of the upper part of the ectosome, scale bar: 25 µm. **D.** Detail of the choanosome, scale bar: 25 µm. Abbreviations: C: cortex; Ch: choanosome; cc: choanocyte chamber; S: location of spicules.

are styles, subtylostyles or tylostyles straight 370-583 x 5.3-11 µm (mean = 456 x 6.5 µm) (Fig. 4B). Principal spicules are styles, subtylostyles or tylostyles straight 646-837 x 8-16 µm (mean = 745 x 11 µm) (Fig. 4A).

Anatomy (Fig. 5-6): The cortex, 430-600 µm thick, is collagenous with few cells present except close to the surface (Fig. 5). The choanosome has a higher density of cells. On semi-thin sections, choanocyte chambers have a diameter of about 15-25 µm which correspond to an estimated volume of 1750-8120 μm^3. The number of choanocytes is 8-18 on a section of a choanocyte chamber. Using the indirect method of Rasmont and Rozenfeld (1981) the estimated number of choanocytes is 75-120 per chamber. The choanocytes have a periflagellar sleeve between the flagellum and the collar of microvillies.

Oocytes are visible in the semithin sections in the specimen collected in August 1999. The oocytes are ovoid or spherical in shape. The size is about 32 x 12 µm and the nucleus 8.5 x 5 µm. They have a homogeneous content.

The papillae have a higher cell density than the cortex especially close to the surface where cells with inclusions constitute a layer of about 30 µm (Fig. 6A-B). The exhalant canal is surrounded by a sphincter of contractile cells, absent around the inhalant canals (Fig. 6A and 6C).

Cytology (Figs. 7-9): The most abundant cells are the cells with granular inclusions, which constitute a layer close to the surface (Figs. 2, 5A, 6A, 7) and which confer a brown colour to the cortex. These cells are dispersed in the mesohyl. They have an ovoid to spherical shape (Fig. 7A-B) and the size is about 6.3-11.6 x 2.8-7.9 µm. The cytoplasm is reduced to small strands and the nucleus is distorted by the abundance of granular inclusions the diameter of which varies from 0.8 to 4.9 µm (Fig. 7A-B). In some cells the inclusions seem to have completely fused and the cell has a granular appearance (Fig. 7B). The distorted nucleus has a diameter from 1.6 to 2.6 µm and is often smaller than the inclusions.

Cells with a cytoplasmic paracrystalline inclusion are present in the mesohyl (Fig. 8). The cells are ovoid in shape and are 5.6-6.9 µm in length and 3.2-5.9 µm in thickness. The cytoplasm is reduced to thin strands due to the presence of vacuoles (0.9-1.7 µm in diameter) with a heterogenous content and a paracrystalline rod of 2.4-5.6 µm in length to 1.6-2.4 µm in thickness (Fig. 8A). The crystalline structure

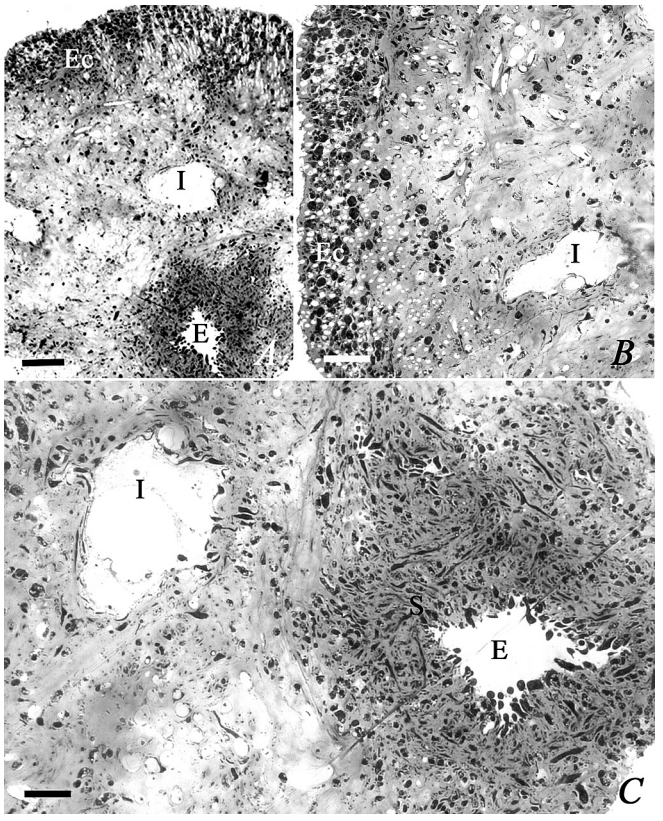

Fig. 6: *Polymastia harmelini* sp. nov. Anatomy of the papillae, semithin section. **A.** General view, scale bar: 70 µm. **B.** Detail of the external part of the ectosome, scale bar: 25 µm. **C.** Detail of the internal part and of the sphincter of contractile cells around the exhalant canal, scale bar: 25 µm. Abbreviations: E: exhalant canal; Ec: ectosome; I: inhalant canal.

has a mesh of 0.03 µm in diameter (Fig. 8B). The nucleus is 1.7-1.9 µm in diameter.

Spiculocytes are present in the mesohyl of the choanosome. They are elongated cells which contain a vacuole with a triangular axial filament around which a spicule is secreted. The nucleus is often nucleolated and numerous mitochondria are present in the cytoplasm.

The contractile cells present around the exhalant canals and the oscule have a length which can reach more than 20 µm for a thickness of about 3 µm at the level of the nucleus (Fig. 9A). The nucleus is ovoid (3 x 1.6 µm). All along the length of the cell, contractile filaments of about 0.025 µm thick are aligned (Fig. 9B).

Archaeocytes are present in the mesohyl (Fig. 9C). They are ovoid cells about 6 x 3.5 µm and a nucleus of 3.2 x 2.6 µm. The nucleus is nucleolated and the diameter of the nucleolus is about 0.5 µm. A very active Golgi apparatus is always present. A variable number of phagosomes (about 1 µm in diameter) is observed in the cytoplasm.

Rare glycocytes which possess small osmiophilic inclusions and rosettes α of glycogen are also present in the mesohyl (Fig. 9D). They measure 5.4-8.6 x 2-4.6 µm; the nucleus is about 2 µm in diameter and the osmiophilic inclusions about 0.2-0.3 µm.

Discussion

In the Atlanto-Mediterranean area three *Polymastia* species have a cortex made of three layers: an external palisade of tylostyles, an intermediary layer of collagen, and an internal layer of tangential intermediary spicules: *P. mamillaris* (Müller, 1806), *P. arctica* (Merejkowsky, 1878) and *P. grimaldi* (Topsent, 1913) and these species have been often mixed up

Table 1: Comparison of *P. harmelini* sp. nov. with the three species of the Atlantic area sharing a cortex of three layers as recently redescribed in Boury-Esnault (1987) for *P. grimaldi*, Morrow and Boury-Esnault (2000) for *P. mamillaris* and Plotkin and Boury-Esnault (2004) for *P. arctica* (measures in µm).

Characters		***P. harmelini* sp. nov**	***P. mamillaris***	***P. arctica***	***P. grimaldi***
Cortex	Thickness	350	400	560	650
	Number of layers	3	3	3	3
	Palisade layer	170	300	235	250
	Collagenous layer	100	20	130	150
	Tangential layer	80	80	200	250
Choanosome	Subcortical layer of free spicules	absent	500	560	absent
	Free spicule type	ectosomal and intermediary	ectosomal	ectosomal	ectosomal
Papillae	Number/specimen	>10	>10	>100	>100
	Budding	absent	absent	present	absent
Spicules	Ectosomal	tylostyles	fusiform tylostyles	fusiform tylostyles	tylostyle
	Size	190 x 3	170 x 12	170 x 5	220 x 7
	Intermediary	tylostyles	subtylostyles	styles	fusiform tylostyles
	Size	456 x 6.5	445 x 13	410 x 10	440 x 14
	Principal	tylostyles	fusiform strongyloxea	fusiform tylostyles	fusiform strongyloxea
	Size	745 x 11	1052 x 24	800 x 14	1800 x 23
	Exotyles	absent	absent	absent	present
	Size	-	-	-	4000 x 10
Distribution		NW Mediterranean	Swedish west coast	White and Barrents Sea	Boreal Atlantic
Depth range		18 m	76-225 m	4-109 m	70-650 m

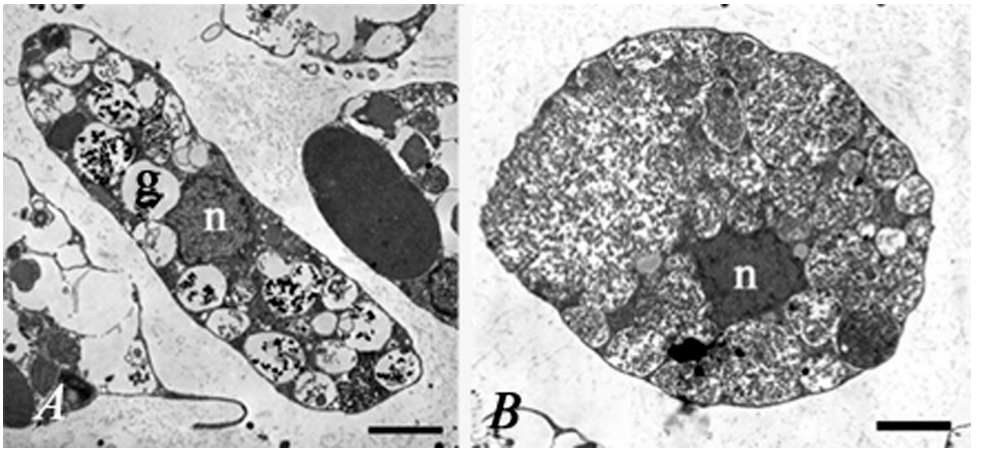

Fig. 7: *Polymastia harmelini* sp. nov. TEM micrographs of cells with inclusions. **A.** Cell with individualized granular inclusions, scale bar: 1.5 µm. **B.** Cell with fused granular inclusions, scale bar: 1.5 µm. Abbreviations: n: nucleus; g: granular inclusion.

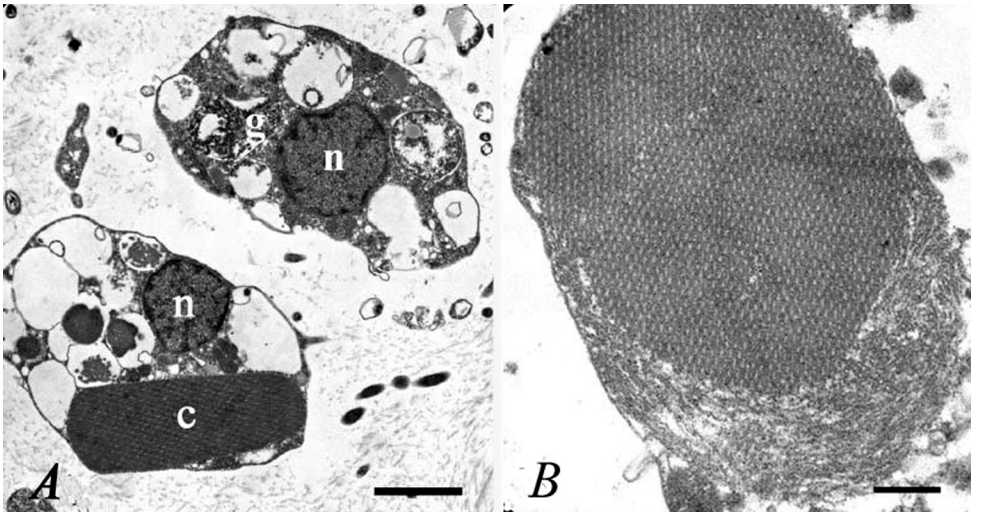

Fig. 8: *Polymastia harmelini* sp. nov. TEM micrographs. **A.** Cell with a paracrystalline inclusion, cell with granular inclusion, scale bar: 1.6 µm **B.** Detail of a paracrystalline inclusion, scale bar: 0.3 µm. Abbreviations: c: paracrystalline inclusion; g: granular inclusion; n: nucleus.

Table 2: Comparison of the cytology of *P. harmelini* sp. n with the three species of *Polymastia* for which we have cytological data.

Cell types	***P. harmelini* sp. nov**	***P. penicillus***	***P. robusta***	***P. janeirensis***
Exopinacocytes	T-shaped	T-shaped	T-shaped	T-shaped
Cells with intranuclear paracrystalline inclusions	-	endopinacocyte	-	collencytes, glycocytes
Cells with paracrystalline inclusions in the cytoplasm	+	+	-	-
Spherulous cells	-	+	-	-
Vacuolar cells	-	-	several vacuoles	1 vacuole
Bacteriocyte	-	-	+	-
Glycocytes	+	+	+	+
Contractile cells around exhalant canals and oscule	+	+	+	and at the limit ectosome/ choanosome
Periflagellar sleeve	+	+	+	+

until the recent redescription of their type specimens (Table 1) (Boury-Esnault 1987, Morrow and Boury-Esnault 2000, Plotkin and Boury-Esnault 2004). *Polymastia harmelini* sp. nov. shares with these three species a cortex constituted by three layers. *Polymastia grimaldi* differs from the three other species by the presence of a fringe of exotyles at the limit between the upper and the lower surface. *Polymastia mamillaris* (type species of the genus) differs from the other species by the shape and size of ectosomal spicules, and the thinness of the collagenous layer. *Polymastia mamillaris* and *P. arctica* share the presence of a layer of groups of ectosomal spicules at the limit of the choanosome (Morrow and Boury-

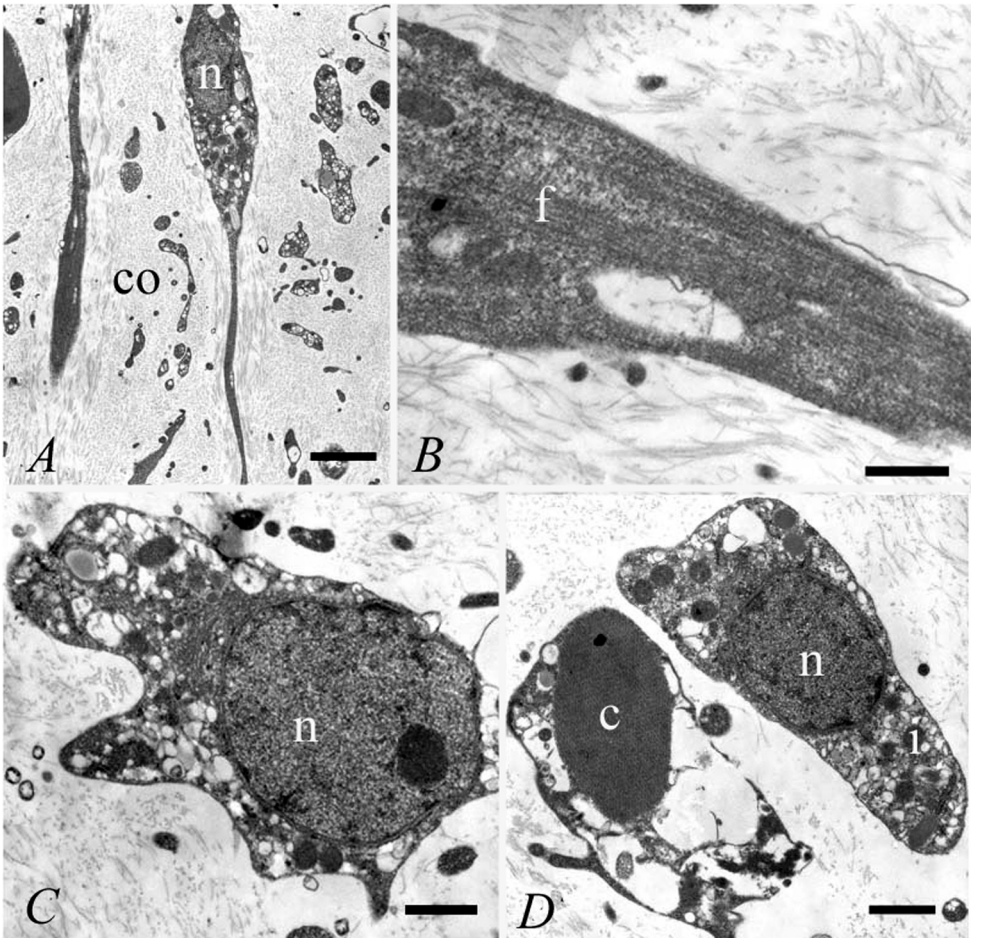

Fig. 9: *Polymastia harmelini* sp. nov. TEM micrographs. **A.** Elongated contractile cells in the sphincter around the exhalant canal, scale bar: 3 µm. **B.** Detail of the contractile filaments of a contractile cell, scale bar: 0.3 µm. **C.** Archaeocyte with a large nucleolated nucleus, scale bar: 0.7 µm. **D.** Glycocyte with small osmiophilic inclusions and cell with a paracrystalline inclusion, scale bar: 1 µm. Abbreviations: c: paracrystalline inclusion; co: collagen; f: contractile filaments; i: osmiophilic inclusion; n: nucleus.

Esnault 2000, Plotkin and Boury-Esnault 2004) absent in *P. harmelini* sp. nov. and *P. grimaldi*. *Polymastia arctica* is the only species of *Polymastia* known so far which show buds at the extremity of the papillae.

The cytology is known only in three species: *P. penicillus* (Montagu, 1818) [under the name *P. mamillaris*], *P. robusta* (Bowerbank, 1861) [Boury-Esnault 1974, Boury-Esnault 1976] and *P. janeirensis* (Boury-Esnault, 1973) [Boury-Esnault *et al*. 1994]. The four species show identical cytological characters such as T-shaped exopinacocytes as it is general in Demospongiae, the presence of contractile cells around exhalant canals and oscules and, at the limit of ectosome and choanosome in *P. janeirensis*, of a periflagellar sleeve around the flagella, a character of Hadromerida. The volume of the choanocyte chamber is in the same range as that known for *P. janeirensis* (3400-7800 µm^3) and more generally in Hadromerida (Boury-Esnault 2006). Glycocytes are present in the four species even if they are less abundant in *P. harmelini* sp. nov. The cells with inclusions are the most characteristic features of the four species. Spherulous cells are present in *P. penicillus*, cells with paracrystalline inclusions in the cytoplasm and cells with granular inclusions in *P. harmelini* sp. nov., endopinacocytes with intranuclear paracrystalline inclusion in *P. penicillus* and collencytes with intranuclear paracrystalline inclusion in *P. janeirensis* and vacuolar cells in *P. robusta* and *P. janeirensis.*

Biogeography

In the Mediterranean Sea six *Polymastia* species have been recorded: *P. mamillaris*, *P. robusta*, *P. inflata* Cabioch, 1968*, P. polytylota* Vacelet, 1969, *P. tissieri* (Vacelet, 1961) [Uriz and Rosell 1990], and *P. sola* Pulitzer-Finali, 1983. The specimens under the name *P. mamillaris* are probably *P. penicillus* (Morrow and Boury-Esnault 2000). Thanks to the precise drawing it is possible to reassign the specimens collected by Uriz (1983) to *P. penicillus* but such a reassignment is difficult in many other cases (Sarà 1958, Carballo and Gómez 1994).

The *Polymastia* species collected in the Mediterranean Sea so far are bathyal or circalittoral species and are also present in the nearby Atlantic (Boury-Esnault *et al.* 1994). *Polymastia harmelini* sp. nov. has been collected on the threshold of a cave at 18 m. Sarà (1958) has collected a "*P. mamillaris"* from littoral cave of the Italian coast. However the description of Sarà is not sufficiently precise to understand to which species the specimens collected belong. Carballo and Garcia-Gómez (1994) have also collected specimens of *Polymastia* in a littoral cave of the Gibraltar strait. There is

no description in the paper and it is impossible to understand to which species the specimens belong. *Polymastia sola* is insufficiently described and the type specimen is not available. In conclusion with this new species six species have been found in NW Mediterranean: *P. penicillus* [under the name *P. mammillaris*], *P. robusta*, *P. inflata*, *P. tissieri*, *P. polytylota* and this new species *P. harmelini* sp. nov. which is for the time being the only Mediterranean endemic species.

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References

Boury-Esnault N (1973) Campagnes de la Calypso au large des côtes atlantiques de l'Amérique du Sud (1961-1962). 29. Spongiaires. *Rés Sci Camp Calypso 10: 263-295*

Boury-Esnault N (1974) Structure et ultrastructure des papilles d'éponges du genre *Polymastia* Bowerbank. *Arch Zool exp gén* 115: 141-165

Boury-Esnault N (1976) Morphogénèse expérimentale des papilles inhalantes de l'éponge *Polymastia mamillaris* (Müller). *Arch Zool exp gén* 117 : 181-196

Boury-Esnault N (1987) The *Polymastia* species (Demosponges, Hadromerida) of the Atlantic area. *In:* Vacelet J, Boury-Esnault N (eds). *Taxonomy of Porifera from the N.E. Atlantic and Mediterranean Sea*, vol. 13. Springer-Verlag, Berlin Heidelberg. pp. 29-66

Boury-Esnault N (2002) Family Polymastiidae Gray, 1867. *In:* Hooper JNA, van Soest RWM (eds). *Systema Porifera: a guide to the classification of sponges*, vol. 1. Kluwer Academic/Plenum Publishers, New York. pp. 201-219

Boury-Esnault N (2006) Systematics and evolution of Demospongiae. *Can J Zool* 84: 205-224

Boury-Esnault N, Rützler K (1997) *Thesaurus of sponge morphology*. Smithsonian Press, Washington

Boury-Esnault N, De Vos L, Donadey C, Vacelet J (1984) Comparative study of the choanosome of Porifera: I. The Homoscleromorpha. *J Morphol* 180: 3-17

Boury-Esnault N, Hajdu E, Klautau M, Custódio M, Borojevic R (1994) The value of cytological criteria in distinguishing sponges at the species level: the example of the genus *Polymastia*. *Can J Zool* 72: 795-804

Boury-Esnault N, Marschal C, Kornprobst J-M, Barnathan G (2002) A new species of *Axinyssa* Lendenfeld, 1897 (Porifera, Demospongiae, Halichondrida) from the Senegalese coast. *Zootaxa* 117: 1-8

Bowerbank JS (1861) List of British sponges. *In:* McAndrew R (ed). List of the British marine invertebrate fauna. *Rep Br Ass Advmt Sci* 30: 235-236

Bowerbank JS (1864) *A monograph of the British Spongiadae*. Robert Hardwicke, London

Cabioch L (1968) Contribution à la connaissance de la faune des Spongiaires de la Manche occidentale. Démosponges de la région de Roscoff. *Cah Biol mar* 9: 211-246

Carballo JL, García-Gómez JC (1994) Esponjas del Estrecho de Gibraltar y áreas próximas, con nuevas aportaciones para la fauna iberica. *Cah Biol mar* 35: 192-211

Gray JE (1867) Notes on the arrangement of sponges, with the description of some new genera. *Proc Zool Soc London* 1867(2): 492-558

Hooper JNA, van Soest RWM (2002) *Systema Porifera: a guide to the classification of sponges*, vol. 1. Kluwer Academic/Plenum Publishers, New York

Jenner RA (2006) Challenging received wisdoms: Some contributions of the new microscopy to the new animal phylogeny. *Integr Comp Biol* 46: 93-103

Kelly-Borges M, Bergquist PR (1997) Revision of Southwest Pacific Polymastiidae (Porifera: Demospongiae: Hadromerida) with descriptions of new species of *Polymastia* Bowerbank, *Tylexocladus* Topsent, and *Acanthopolymastia* gen. nov. from New Zealand and the Norfolk Ridge, New Caledonia. *N Z J Mar Freshwat Res* 31: 367-402

Merejkowsky C de (1878) Les éponges de la mer Blanche. *Mém Acad imp Sci, St Petersburg* 26: 1-51

Montagu G (1818) An essay on sponges, with descriptions of all the species that have been discovered on the Coast of Great Britain. *Mem Werner Nat Hist Soc* 2: 67-121

Morrow CC, Boury-Esnault N (2000) Redescription of the type species of the genus *Polymastia* Bowerbank, 1864 (Porifera, Demospongiae, Hadromerida). *Zoosystema* 22: 327-335

Müller OF (1806) *Zoologia danica*. Havniae, Copenhagen

Plotkin AS, Boury-Esnault N (2004) Alleged cosmopolitanism in sponges: the example of a common Arctic *Polymastia* (Porifera, Demospongiae, Hadromerida). *Zoosystema* 26: 13-20

Pulitzer-Finali G (1983) A collection of Mediterranean Demospongiae (Porifera) with, in appendix, a list of the Demospongiae hitherto recorded from the Mediterranean Sea. *Ann Mus Civ Stor Nat Genova* 84: 445-621

Rasmont R, Rozenfeld F (1981) Etude micro-cinématographique de la formation des chambres choanocytaires chez une éponge d'eau douce. *Ann Soc R Zool Belg* 111: 33-44

Sarà M (1958) Studio sui Poriferi di una grotta di marea del Golfo di Napoli. *Arch Zool Ital* 43: 203-280

Schmidt O (1870) *Grundzüge einer Spongien Fauna des Atlantischen Gebietes*. Wilhelm Engelmann, Leipzig

Topsent E (1913) *Spongiaires provenant des campagnes scientifiques de la «Princesse Alice» dans les mers du Nord (1898-1899 - 1906-1907)*. Imprimerie de Monaco, Monaco

Uriz MJ (1983) Contribución a la fauna de esponjas (Demospongia) de Catalunya. *An Sec Cienc Col Univ Gerona* 7: 1-220

Uriz MJ, Rosell D (1990) Sponges from bathyal depths (1000-1750m) in the western Mediterranean Sea. *J Nat Hist* 24: 373-391

Vacelet J (1961) Quelques éponges remarquables de Méditerranée. *Rec Trav Inst Pêches maritimes* 25: 351-354

Vacelet J (1969) Eponges de la Roche du Large et de l'étage bathyal de Méditerranée (récoltes de la Soucoupe plongeante Cousteau et dragages). *Mém Mus natl Hist nat* 59: 145-219

Vacelet J, Boury-Esnault N, Harmelin J-G (1994) Hexactinellid cave, a unique deep-sea habitat in the scuba zone. *Deep-Sea Res* 41: 965-973

Warwick RM, Emblow C, Féral J-P, Hummel H, Avesaath P van, Heip C (2003) European marine biodiversity research sites. NIOO-CEME, Yerseke, the Netherlands