

Description of new chiactine-bearing sponges provides insights into the higher classification of Calcaronea (Porifera: Calcarea)

ADRIANA ALVIZU^{1,4}, JOANA R. XAVIER^{1,2} & HANS TORE RAPP^{1,3}

¹Department of Biological Sciences and K.G. Jebsen Centre for Deep-sea Research, University of Bergen, P.O. Box 7803, N-5020 Bergen, Norway

²CIIMAR—Interdisciplinary Centre of Marine and Environmental Research, University of Porto, Avenida General Norton de Matos, 4450-208 Matosinhos, Portugal

³NORCE—Norwegian Research Centre AS, NORCE Environment, Nygårdsgaten 112, 5008 Bergen, Norway

⁴Corresponding author. E-mail: adriana.alvizu@uib.no; adriana.alvizu@gmail.com

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Abstract

A recent phylogenetic study revealed a close relationship between chiactine-bearing (family Achramorphidae, order Leucosolenida) and pugiole-bearing (order Baerida) calcaronean sponges as well as new putative taxa within Achramorphidae. In this study, we present a revision of chiactine-bearing sponges based on morphological re-examination of type material and recently collected specimens, in addition to new molecular data for the ribosomal 18S and C-region of the 28S. We provide re-descriptions for all known chiactine-bearing species, and further describe two new species from the Antarctic (*Achramorpha antarctica* sp. nov. and *Megapogon schiaparellii* sp. nov.) and two new species and

a new genus from the Nordic Seas (*Achramorpha ingolfi* sp. nov. and *Sarsinella karasikensis* gen. nov. sp. nov.). The new phylogenetic reconstruction based on ribosomal 18S and C-region of the 28S confirms previous findings about the close relationship of some members of Baerida and the family Achramorphidae of the order Leucosolenida. However, new material and the addition of molecular data from the type species of both taxa would be required to formally propose changes at (sub-)ordinal levels within the classification of Calcaronean sponges.

key words: *Achramorpha*, Antarctic, Baerida, C-region, *Megapogon*, Nordic Seas, Petrobionidae, *Sarsinella*, Taxonomy

Introduction

It is well known that the classification of the subclass Calcaronea Bidder, 1898 is largely artificial, and characterized by frequent secondary loss, high levels of homoplasy and convergent evolution (Manuel *et al.* 2004; Dohrmann *et al.* 2006; Manuel 2006; Voigt *et al.* 2012; Voigt & Wörheide 2016; Alvizu *et al.* 2018). In recent years, major efforts have been made to better understand the diversity and evolutionary history of calcaronean sponges, and as result, numerous new species have been described (Azevedo & Klautau 2007; Rapp 2015; Cóndor-Luján *et al.* 2018; van Soest & de Voogd 2018), revealing new and unexpected phylogenetic relationships (Dohrmann *et al.* 2006; Voigt *et al.* 2012; Voigt & Wörheide 2016; Alvizu *et al.* 2018). This is the case of the nested position of the order Baerida Borojević, Boury-Esnault & Vacelet, 2000 within the order Leucosolenida Hartman, 1958 (Dohrmann *et al.* 2006; Voigt *et al.* 2012; Voigt & Wörheide 2016; Alvizu *et al.* 2018). In a recent phylogenetic study, Alvizu *et al.* (2018) showed that an undescribed species of *Achramorpha* collected from deep waters in the Nordic Seas, is closely related to the order Baerida, and postulated that this relationship can be associated with the similarity found between the pugioles (small harpoon-shaped tetractines) characteristic for the order Baerida, and the “cruciform” spicules present in the family Achramorphidae Borojević, Boury-Esnault, Manuel & Vacelet, 2002.

Achramorphidae is a family of the order Leucosolenida, that was originally proposed by Jenkin (1908) under the name Staurorrhaphidae, to include sponges characterized by the presence of “cruciform” spicules, called chiactines (tetractines with the apical actine bent in the same alignment as the unpaired actine, but in the opposite direction). However, because the family name Staurorrhaphidae was a *nomem nudum*, the name Achramorphidae was erected by Borojević *et al.* (2002b) to replace it. Another unique feature of members in this family is the absence of a tangential atrial skeleton, which is reduced only to the area adjacent to the osculum where the tetractines are laying in the ordinary position (Jenkin 1908; Borojević *et al.* 2000). These modifications in the skeletal arrangement together with the presence of chiactines represent the main characteristics of the family. The Achramorphidae currently includes 11 species in the two genera *Achramorpha* Jenkin, 1908 and *Megapogon* Jenkin, 1908, comprising six and five species, respectively. Eight of the species known at present occur in shallow Antarctic waters, and is considered one of the most species-rich families in Antarctic waters (Downey *et al.* 2012; Rapp *et al.* 2013).

However, in a recent phylogenetic study, the family Achramorphidae was retrieved as non-monophyletic, with *Megapogon raripilus* Jenkin, 1908 and *Achramorpha* sp. forming a non-supported clade with members of the order Baerida (Alvizu *et al.* 2018). In addition, new specimens collected from the Nordic Seas formed a clade of uncertain relationship with this family. This prompted us to undertake a revision of chiactine-bearing calcareous sponges, based on the examination of type material and newly collected material, in order to provide a re-description of this group and a re-assessment of its phylogenetic status in regard to the classification of Calcaronea.

Material and methods

Sample collection. The samples used in the present study were collected over the most recent years through expeditions in the Nordic Seas and the Antarctic, organized by the University of Bergen and the Italian National Antarctic Research Program, respectively. This recent material has been deposited in the Italian National Antarctic Museum (MNA) and in the University Museum of Bergen (ZMBN). Specimens of the new genus were collected at two different localities along the Arctic Mid-Ocean Ridge (AMOR; Table 1). Samples were fixed in ethanol 96%. All material available of *Achramorpha* spp. and *Megapogon* spp. in the collections of the Natural History Museum of London (BMNH), the Muséum National d’Histoire Naturelle of Paris (MNHN) and the Zoological Museum of

Copenhagen (SNM), was included to ensure a good as possible taxonomic coverage of the family Achramorphidae (Table 1).

Identification and histological sections. The identification of the specimens was based on the skeletal organization, including type of spicules present on each body section (cortex, choanosome, sub-atrial skeleton and oscular region). Spicules measurements were made using spicule preparations and histological sections available in the collections, and for this reason there are some cases where we could not measure the standard 30 spicules of each type. Spicule measurements are presented in tables and reported as minimum, average, maximum, standard deviation (SD) and number of spicules measured (n). For recently collected specimens, permanent spicule preparations were made following standard procedures used in previous studies (Rapp *et al.* 2001; Rapp 2006), and histological sections were also included to investigate the arrangement of spicules. This procedure consists of passing the sponge tissue through a dehydration series, then cleared in acetone, embedded in Agar low viscosity epoxy resin (Agar Scientific Ltd, UK) and stained with toluidine blue. In addition, scanning electron microscopy (SEM) images of spicules and tissue were taken using a ZEISS Supra 55VP microscope.

Molecular sequencing. DNA extractions of seven specimens (two *Sarsinella karasikensis* gen. nov. sp. nov., one *Leuconia* cf. *nivea*, two *Leucosolenia complicata*, and one *Sycon ciliatum*) were made using QIAGEN DNeasy Blood and Tissue Kit, following the manufacturer's (spin-column) protocol. Amplification of a fragment of 18S rRNA gene (1100–1200 bp) was performed using the reversed primer 329R (5'-TAAT GATCCTCCGCAGGTT-3'), -A-F (5 i- CAGCMGCCGCGGTAAATWC-3'). The PCR conditions used for this gene were: 1x [94 °C: 5 min]; 34x [94 °C: 1 min, 50 °C: 1 min, and 72 °C: 2 min], 72 °C: 7 min (Alvizu *et al.* 2018). The C-region (441 bp) of the 28S rRNA gene was made using the standard LSU primers proposed by Chombard *et al.* (1998), 28S-C2F: 5'-GAAAAGAACTTGRARAGAGAGT-3' and 28S-D2R: 5'-TCCGTGTTCAAGACGGG-3', and the forward modified primer LSU for calcareous sponges (5'-GAAAAGCACTTGAAAAGAGA-3'; Voigt & Wörheide 2016). The PCR conditions used for this gene fragment were: 1x [94 °C: 4 min, 57 °C: 2 min and 72 °C: 2 min]; 30x [94 °C: 1 min, 57 °C: 1 min, and 72 °C: 1 min], 72 °C: 4 min (Chombard *et al.* 1998). Polymerase chain reactions (PCR) were performed in reactions of 25 µL and purified using ExoSAP reactions of 10 µL (Exonuclease 1: 10 U µL⁻¹, and shrimp alkaline phosphatase: 10 U µL⁻¹, USB®). Purified PCR products were sequenced using Big Dye Terminator 3.1, on a capillary-based Applied Biosystem 3730XL Analyzer. Consensus sequences were generated using Geneious R10 (<http://www.geneious.com>, Kearse *et al.* 2012). Additional sequences of the C-region of 28S from Calcaronea were downloaded from GenBank (<https://www.ncbi.nlm.nih.gov/genbank/>; Table 1).

Alignment and phylogenetic analyses. The sequences were initially aligned using Geneious R10 (<http://www.geneious.com>, Kearse *et al.* 2012), and manually refined according to secondary structure models using SeaView 4.6.1 (Gouy *et al.* 2010). For the 18S gene, we used models proposed for some calcaronean species, available at <http://www.palaeontologie.geo.lmu.de/molpal/RRNA/index.htm> (Voigt *et al.* 2008). In the case of the C-region, the LSU rRNA secondary model proposed by Voigt & Wörheide (2016) was used. The dataset was concatenated using SequenceMatrix (Vaidya *et al.* 2011). The final dataset comprises 32 sequences, of which eight sequences (four for each gene) are new (see Table 1). The length of the final alignment was 2219 bp. The PERL scripts 2analysis.pl created by Voigt *et al.* (2012) was used to convert the alignment files with secondary structure information to a nexus file to be used in MrBayes 3.2.6 (Ronquist *et al.* 2012). The dataset was partitioned into stems and loops, and the partitioned Doublet + GTR model, which is intended for stem regions of ribosomal sequences, was used. This model has been shown to provide less biased phylogenies (for example Dohrmann *et al.* 2006; Erpenbeck *et al.* 2007). For the loops partition, we used the AIC implemented in PartitionFinder 2 (Guindon & Gascuel 2003; Lanfear *et al.* 2012; Lanfear *et al.* 2017) to select the best-fitting model, which was GTR+I+G. Phylogenetic reconstructions were made using Bayesian Inference (BI) implemented in MrBayes 3.2.6 (Ronquist *et al.* 2012) by running three independent chains of five million generations each. The final phylogenetic tree was produced using FigTree available at <http://tree.bio.ed.ac.uk/software/figtree/>. In addition, Maximum likelihood (ML) phylogenetic analysis was performed in RAxML (Stamatakis 2014) under the configuration of rapid bootstrapping analyses of 1000 bootstrap replicates. The model used for the looped sites was GTR+I+G, and 16 state model A for the paired sites.

TABLE 1. List of specimens analysed in this study. Taxonomy, voucher numbers, locality and accession numbers of species included in the phylogenetic analysis. Holotype (H); Lectotype (L); Paralectotype (PL); Paratype (P). Species in bold are new species described in this study. (*) Material previously identified under this name but that needs to be assigned to groups without chiaictines.

Species name	Voucher number	Locality and depth	GenBank accession number	
			18S	C-region
<i>Achramorpha nivalis</i> (P)	BMNH-1907.8.6.111	Winter Quarters Bay, Antarctic	--	--
<i>Achramorpha nivalis</i>	BMNH 1907.8.6.119	Winter Quarters Bay, Antarctic	--	--
<i>Achramorpha nivalis</i> (H)	BMNH 1907.8.6.122–124	Winter Quarters Bay, Antarctic	--	--
<i>Achramorpha nivalis</i>	BMNH 1907.8.6.125	Winter Quarters Bay, Antarctic	--	--
<i>Achramorpha nivalis</i>	BMNH 1907.8.6.128	Winter Quarters Bay, Antarctic	--	--
<i>Achramorpha nivalis</i>	BMNH 1907.8.6.129	Winter Quarters Bay, Antarctic	--	--
<i>Achramorpha nivalis</i>	BMNH 1926.10.26.49	Antarctic	--	--
<i>Achramorpha truncata</i> (H)	MNHN C1968–810	Booth-Wandel Island, Antarctic, 40 m	--	--
<i>Achramorpha antarctica</i> sp. nov. (H)	NHMD-611894	Weddell Sea (73°22'36.0"S 21°10'36.0"W), 333–338 m.	--	--
<i>Achramorpha glacialis</i> (L)	BMNH 1926.10.26.250	Antarctic	--	--
<i>Achramorpha glacialis</i> (PL)	BMNH 1907.8.6.101	Winter Quarters, Antarctic	--	--
<i>Achramorpha grandinis</i> (H)	BMNH 1907.8.6.103–104	Winter Quarters, Antarctic	--	--
<i>Achramorpha diomediae*</i>	BMNH 1938.7.4.108	Winter Quarters, Antarctic	--	--
<i>Achramorpha diomediae*</i>	BMNH-1938.7.4.72	Swedish Bank	--	--
<i>Achramorpha diomediae*</i>	BMNH-1938.7.4.73	Sea of Okhotsk	--	--
<i>Achramorpha ingolfi</i> sp. nov. (P)	ZMBN-127208	Norwegian Sea (73°42'07.7"N 7°23'51.2"E), 2651 m.	MH385157	MH385224
<i>Achramorpha ingolfi</i> sp. nov. (H)	ZMBN-127207	Norwegian Sea (73°35'19.2"N 7°45'07.1"E), 2425–2463 m.	MH385158	MH385225
<i>Achramorpha ingolfi</i> sp. nov. (P)	NHMD-611895	Norwegian Sea (69°31'00.0"N 7°06'00.0"W), 2465 m.	--	--
<i>Megapogon crucifer</i> (H)	BMNH 1884.4.22.46	Azores (38°37'00.0"N 28°30'00.0"W), 822 m depth	--	--
<i>Megapogon crucifer</i> *	BMNH 1948.3.8.2	West Africa (13°43'00.0"N 17°23'00.0"W), 65–89 m.	--	--
<i>Megapogon raripilus</i> (L)	BMNH 1907.8.6.139	Winter Quarters Bay, Antarctic	--	--
<i>Megapogon raripilus</i> (PL)	BMNH 1907.8.6.140	Flagon point, Winter Quarters Bay, Antarctic, 18–36 m.	--	--
<i>Megapogon raripilus</i> (PL)	BMNH 1907.8.6.145	Winter Quarters Bay, Antarctic	--	--
<i>Megapogon schiparellii</i> sp. nov. (P)	MNA 02762	Tethys Bay, Antarctic (74°41'25.0"S 164°06'09.2"E), 23 m.	MK696125	MH385273
<i>Megapogon schiparellii</i> sp. nov. (P)	MNA07813	Caletta, Antarctic (74°45'43.5"S 164°05'46.4"E), 146 m.	--	MH385275
<i>Megapogon schiparellii</i> sp. nov. (H)	MNA08193	Northwest Basin, Antarctic (72°51'41.4"S 171°05'13.8"E), 530 m.	--	MH385274
<i>Megapogon villosus</i> (L)	BMNH-1907.8.6.146	Winter Quarters Bay, Antarctic	--	--
<i>Megapogon villosus</i> (PL)	BMNH-1907.8.6.151	Winter Quarters Bay, Antarctic	--	--

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TABLE 1. (Continued)

Species name	Voucher number	Locality and depth	GenBank accession number	
			18S	C-region
<i>Megapagon pollicaris</i> (H)	BMNH-1907.8.6.135	Winter Quarters Bay, Antarctic	--	--
<i>Megapagon crispatus</i> (H)	BMNH-1907.8.6.131	Winter Quarters Bay, Antarctic	--	--
<i>Sarsinella karasikensis</i> sp. nov. (P)	ZMBN-127210	Karasik Seamount, Gakkel Ridge (86°51'29.4"N 61°35'45.6"E), 684 m.	--	--
<i>Sarsinella karasikensis</i> sp. nov. (P)	ZMBN-127211	Arctic Mid Ocean Ridge (73°48'42.3"N 7°30'50.3"E), 773 m.	MH385159	MH385223
<i>Sarsinella karasikensis</i> sp. nov. (H)	ZMBN-127212	Arctic Mid Ocean Ridge (73°47'16.8"N 7°35'06.6"E), 652–1314 m.	MH385160	MH385222
<i>Sarsinella karasikensis</i> sp. nov. (P)	ZMBN-127213	Karasik Seamount, Gakkel Ridge (86°51'29.4"N 61°35'45.6"E), 684 m.	--	MK696119
<i>Sarsinella karasikensis</i> sp. nov. (P)	ZMBN-127214	Karasik Seamount, Gakkel Ridge (86°51'29.4"N 61°35'45.6"E), 684 m.	--	MK696120
<i>Eilhardia schulzei</i>	QM G316071	Pacific, GBR, Mac's reef	--	JQ272256
<i>Leuconia</i> cf. <i>nivea</i> (Ski03)	ZMBN-127215	Askøy, Norway	MK696122	MK696116
<i>Leuconia nivea</i>	--	--	--	AY563534
<i>Leuconia nivea</i>	MC3329	--	HE591470	--
<i>Petrobiona massiliiana</i>	GW1729	Mediterranean Sea, Marseille	--	JQ272307
<i>Petrobiona massiliiana</i>	--	--	--	AF452026
<i>Grania arctica</i> FB23	ZMBN-127231	West Greenland	MH385167	AY563533
<i>Leucandra penicillata</i> (FB40)	ZMBN-127232	West Greenland	MH385168	MH385236
<i>Leucandra penicillata</i> (FB49)	ZMBN-127216	West Greenland	MH385180	MH385237
<i>Leucandra penicillata</i> (FB77)	ZMBN-127217	West Greenland	MH385181	MH385253
<i>Leucandra penicillata</i> (FB35)	ZMBN-127218	West Greenland	MH385182	MH385254
<i>Leucascandra cayeolata</i>	ZMBN-127219	West Greenland	MH385179	MH385255
<i>Leucosolenia complicata</i> (SK101)	QM G316057	Pacific, GBR, Hardline	AM180973	JQ272259
<i>Leucosolenia complicata</i> (SK102)	ZBMMN-127254	Askøy, Norway	MK696123	MK696117
<i>Sycon abyssale</i> (GIN06)	ZBMMN-127255	Norwegian Sea	MK696124	MK696118
<i>Sycon ciliatum</i> (SA126)	ZBMMN- 127220	Norway, 2600 m.	MH385201	MH385293
<i>Sycon ciliatum</i> (SA41)	ZBMMN- 127221	Bergen, Norway	MH385204	MH385299
<i>Sycon ciliatum</i> (SA42)	ZBMMN- 127228	Bergen, Norway	MK696121	MH385208
<i>Ute ampullacea</i>	QM G313669	Pacific, GBR, Wistari Reef	MH385303	MH385206
			AM180972	JQ272266

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Results

Systematics

Class Calcarea Bowerbank, 1862

Subclass Calcaronea Bidder, 1898

Order Leucosolenida Hartman, 1958

Family Achramorphidae Borojević, Boury-Esnault, Manuel & Vacelet, 2002

For family definition see comments in the discussion section.

Genus *Achramorpha* Jenkin, 1907

Diagnosis. Achramorphidae with syconoid organization (Borojević *et al.* 2002b).

Scope. Five species of *Achramorpha* are currently accepted: *A. diomediae* Hôzawa, 1918; *A. glacialis* Jenkin, 1908; *A. grandinis* Jenkin, 1908; *A. nivalis* Jenkin, 1908 and *A. truncata* (Topsent, 1907). Two new species are described in this study; *A. ingolfi* sp. nov. and *A. antarctica* sp. nov.

Type species: *Achramorpha nivalis* Jenkin, 1908 (by subsequent designation by Dendy & Row 1913).

Achramorpha nivalis Jenkin, 1908

(Figs 1A–H; Table 2)

Original description. Jenkin 1908, p. 33, pl. XXVII, figs 7–8, pl. XXXV and XXXVI, figs 105–112.

Type locality. Winter Quarters Bay, Antarctic.

Synonyms and citations. *Achramorpha nivalis* Dendy & Row 1913, p. 765; *A. nivalis* Hôzawa 1918, p. 542; *A. nivalis*, Brønsted 1931, p. 32; *A. nivalis* Burton 1963, p. 93, 526 (fig 332).

Material examined. **Holotype:** BMNH-1907.8.6.122 (one section slide), Winter Quarters Bay, Antarctic, collection date 11.11.1902. **Paratype:** BMNH-1907.8.6.111 (one complete specimen and four slides; see Table 1), Winter Quarters Bay, Antarctic, collection date 29.08.1903. **Additional material:** BMNH-1907.8.6.119: one slide, National Antarctic Expedition (HMS Discovery), collection date 08.09.1903. BMNH-1907.8.6.122–124: three slides, National Antarctic Expedition (HMS Discovery). BMNH-1907.8.6.125: one slide, National Antarctic Expedition (HMS Discovery), collection date 08.09.1903. BMNH-1907.8.6.128: one slide, National Antarctic Expedition (HMS Discovery), collection date 24.10.1902. BMNH-1907.8.6.129: one slide, National Antarctic Expedition (HMS Discovery), collection date 24.10.1902. BMNH-1926.10.26.49: one slide, British Antarctic Expedition 1910–1913 (Terra Nova).

Morphology. Sponge cylindrical, wider at the base and with well-developed oscular fringe at the narrow end (Fig 1A). Surface hispid due to long diactines projecting from the choanosome. Colour light brown in ethanol. Aquiferous skeleton syconoid with elongated choanocyte chambers (Fig 1B). The cotype is 12.95 mm high, 1.87–2.94 mm wide and 0.61–0.86 mm thick (Fig 1A).

Skeleton. The cortical skeleton is made up by triactines positioned tangentially, diactines and microdiactines (Fig 1C). Diactines are very long and protruding, unevenly scattered and can cross through the body wall to the atrial cavity (Fig 1D). Microdiactines are spined and organized around the ostia (Figs 1C, 1F). Choanoskeleton inarticulated and mainly composed of the unpaired actines of the atrial chiactines and by the large diactines (Figs 1B, 1D). Some cortical triactines can be observed in the middle of the choanosome (Fig 1D). The chiactines are oriented perpendicularly to the atrium, with the long paired actines adjacent to the atrial wall and the apical actines projecting into the atrial cavity (Fig 1B). The oscular region is composed of long trichoxes which form the oscular fringe, and also by thin but large tetractines, which are positioned longitudinally with the unpaired actines pointing towards the base of the sponge (Fig 1E).

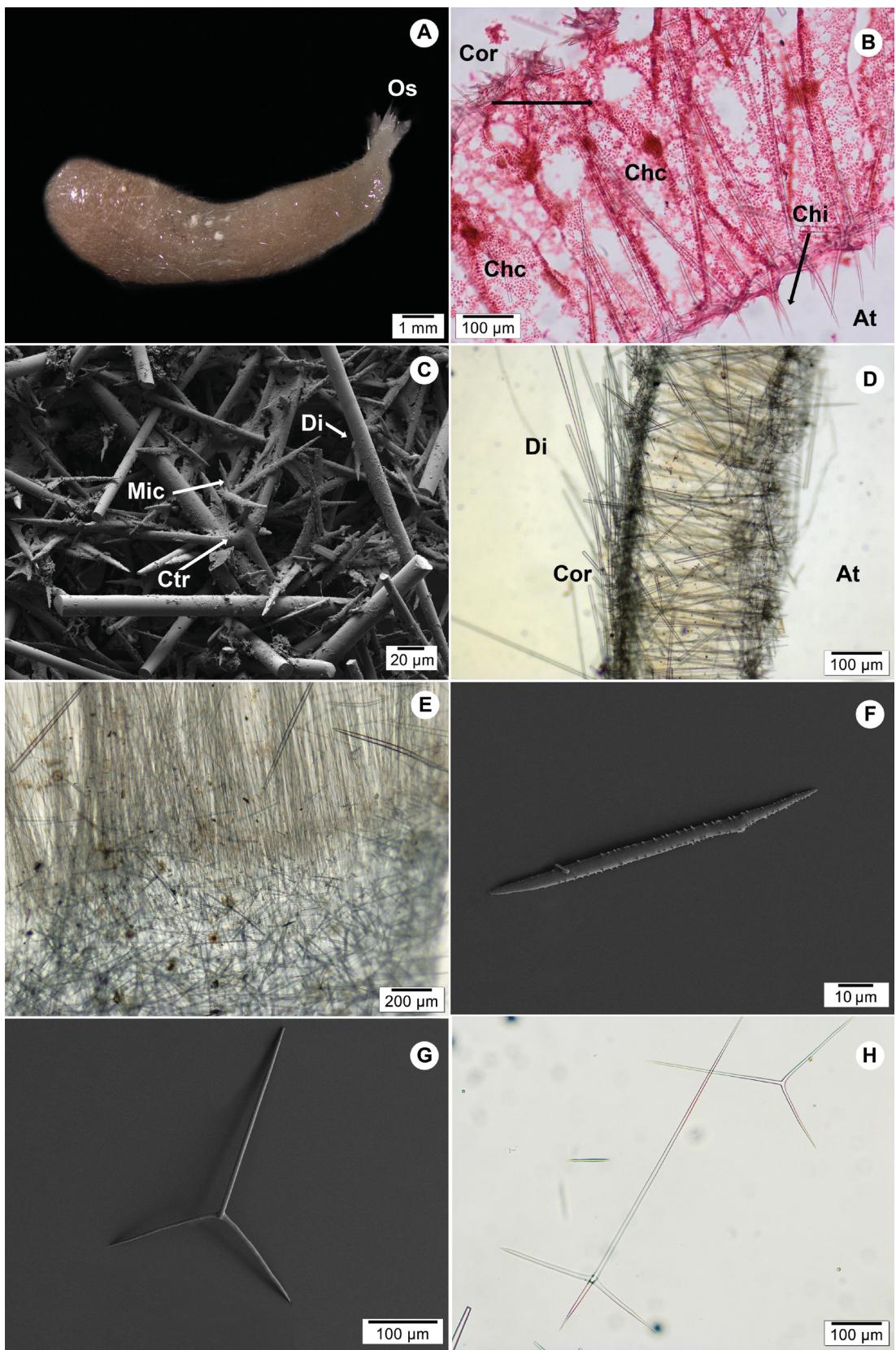


FIGURE 1A–H. *Achramorpha nivalis*. **A:** preserved paratype BMNH-1907.8.6.111. **B:** histological section including cortical layer, choanosome and atrial cavity. **C:** SEM image of the cortical layer. **D:** cross-section showing cortical layer, choanosome and atrial cavity. **E:** oscular region. **F–G:** SEM images of microdiactine (**F**) and triactine (**G**). **H:** atrial chiactine. Abbreviations: At = atrial cavity; Chc = choanocyte chamber; Chi = chiactines; Cor = cortical layer/cortex; Ctr = cortical triactines; Di = diactines; Mic = microdiactines; Os = osculum.

Spicules. *Diactines*: long and straight with both ends sharp. Size: $688.4 \pm 328.6 \mu\text{m}$ length, $14.2 \pm 8.2 \mu\text{m}$ width (Figs 1C–D; Table 2).

TABLE 2. Spicule measurements of *Achramorpha nivalis* (cotype BMNH 07.8.6.111). Measurements from the original description by Jenkin (1908) are included below.

BMNH 07.8.6.111									
Spicules	Length (μm)				Width (μm)				n
	Min	Mean	Max	SD	Min	Mean	Max	SD	
Diactines*	170.0	688.4	1412	328.6	5.1	14.2	34.3	8.2	23
Microdiactines	53.3	80.4	81.1	11.5	1.7	3.4	4.2	0.9	30
Cortical triactines									
Unpaired actines	76.5	230.9	332.7	73.1	2.0	6.7	9.0	2	14
Paired actines	49.9	136.6	188.8	43.8	1.8	6.4	9.6	2	
Chiactines									
Unpaired actines	304.4	426.1	600.6	113.1	8.1	9.4	11.6	1.1	12
Paired actines	142.0	175.2	201.7	18.9	6.2	8.8	12.3	1.8	
Apical actines	67.0	102.5	123.3	15.9	5.7	7.7	8.9	1.0	
Oscular tetractines									
Unpaired actines**	197.4	259.7	382.1	65.7	8.5	9.4	10.5	0.6	5
Paired actines	158.9	167.0	172.7	6.1	12.2	12.7	13.7	0.5	
Apical actines	45.0	49.9	56.9	5.0	6.4	7.7	9.2	1.1	3
Measurements from the original description (Jenkin 1908)									
Spicules	Length (μm)				Width (μm)				
Diactines I	2700				14				
Diactines II***	75–85				5–6				
Diactines III†	120–140				4				
Oscular diactines	2500				6				
Cortical triactines									
Unpaired actines	200–380				8–10				
Paired actines	140–210				8				
Chiactines									
Unpaired actines	400–600				8–10				
Paired actines	160–200				8				
Apical actines	110–130				8–12				
Oscular tetractines (large)									
Unpaired actines	850				12				
Paired actines	450				6–16				
Apical actines	100				10				
Oscular tetractines (small)									
Unpaired actines	150				12				
Paired actines	120				10				
Apical actines	20				16				

(*) Most of the diactines were broken.

(**) Unpaired actines broken or not completely visible in the slides.

(***) Diactines II = Microdiactines.

(†) Similar to diactines II but longer.

Microdiactines: small with hastate points and minute spines towards the hastate tip, which is slender than the other one. Some of these diactines are slightly curved. Size: $80.4 \pm 11.5 \mu\text{m}$ length, $3.4 \pm 0.9 \mu\text{m}$ width (Figs 1C, 1F; Table 2).

Cortical triactines: sagittal with the unpaired actines straight and longer than the paired actines, which are slightly curved upwards forming a round bend. Paired actines of similar length. Size: unpaired actines 230.9 ± 73.1 μm length, 6.7 ± 2 μm width; paired actines 136.6 ± 43.8 μm length, 6.4 ± 2 μm width (Fig 1G; Table 2). There are a few triactines with the paired angle almost straight, which probably are from the oscular region.

Chiactines: unpaired actines straight and longer than the paired actines. Apical actine straight and tapering to a sharp tip. Size: unpaired actines 462.1 ± 113.1 μm length, 9.4 ± 1.1 μm width; paired actines 175.2 ± 18.9 μm length, 8.8 ± 1.2 μm width; apical actine 102.5 ± 15.9 μm length, 7.7 ± 1 μm width (Figs 1B–H; Table 2).

Oscular tetractines: the unpaired actines are longer and thinner than the paired actines. The apical actine is curved and pointing towards the osculum. Size: unpaired actines 259.7 ± 65.7 μm length, 9.4 ± 0.6 μm width; paired actines 167 ± 6.1 μm length, 12.7 ± 0.5 μm width; apical actines 49.9 ± 5 μm length, 7.7 ± 1.1 μm width (Table 2).

Oscular trichoxeas: it was difficult to measure them in the spicule preparations, but according to Jenkin (1908) they are around 2.5 mm length and 6.0 μm width and minutely hastate at the distal end (Fig 1E).

Molecular identification. Not available.

Distribution and depth. *A. nivalis* has been reported from two localities around the Antarctic: Winter Quarters Bay (Jenkin 1908), and Winterstation in Wilkes Land in the East-Antarctic, at 350–385 m depth (Brønsted 1931).

Remarks. Jenkin (1908) mentioned that there were 14 specimens of *A. nivalis* in the collection at the BMNH. However, the material available in the museum collection was only one slide from the holotype, one specimen labelled as cotype and several spicules preparations and histological sections, probably from those specimens mentioned by Jenkin (1908).

Following the 4th edition of the International Code of Zoological Nomenclature (ICZN) the term cotype is not recognized by the Code and should not be used in zoological nomenclature, especially e.g. in the sense of syntype or paratype (recommendation 73E). Therefore, the specimen BMNH-1907.8.6.111 which was labelled as cotype, is now erected as paratype.

All the examined slides from different specimens present the same long projecting diactines in the cortical skeleton, but these are shorter than what was reported in the original description (see Table 2), probably due to the fact that most of them were broken. Jenkin (1908) divided the tetractines in two categories according to the size (see Table 2). This may be associated to the position of the spicules in the oscular area, since it has been observed in other *Achramorpha* spp. that they are smaller the closer they are to the oscular fringe. However, as most tetractines were broken or not easily visible in the sections, we were only able to measure five complete ones.

A third type of diactines was mentioned by Jenkin (1908), who described them as “rather longer, small, straight hastate oxea” and of size 120–140 μm long, and 4 μm thick. However, we could not find this type of diactines in the material examined, but according to the figure presented by Jenkin (1908) they look similar to microdiactines, but slightly longer (Table 2).

Achramorpha truncata (Topsent, 1907)

(Figs 2A–F; Table 3)

Original description. *Grantia truncata* Topsent 1907, p. 540 (Topsent 1908, p. 6, pl. V, fig 4).

Type locality. Booth-Wandel Island, Antarctic (Topsent 1907).

Synonyms and citations. *Grantia truncata*, Topsent 1907, p. 540; Topsent 1908, p. 6, pl. V, figure 4; *Achramorpha truncata* Dendy & Row 1913, p. 765; *A. truncata* Hôzawa 1918, p. 542; *A. truncata*, Downey *et al.* 2012.

Material examined. Holotype: MNHN C1968-810 (one complete specimen), Booth-Wandel Island, Antarctic, 40 m depth. **Additional material:** BMNH-1926.10.26.250: dry material, British Antarctic Expedition 1910–1913 (Terra Nova), st. nr. 339.

Morphology. Tubular sponge with one apical osculum. Surface slightly hispid due to diactines protruding the surface. Colour is yellowish in ethanol (Fig 2A). Consistency fragile. Aquiferous system syconoid with radial chambers straight and from 0.10 to 0.13 mm wide (Topsent 1907). The holotype is 20.7 mm long and 2.5–2.8 mm wide.

Skeleton. Inarticulated, composed of diactines, chiactines and two types of triactines. Cortical skeleton is made up of sagittal triactines placed tangentially and perpendicular diactines (Fig 2B) which present a fairly distinctive shape at their distal ends (Figs 2C–D). The choanosomal skeleton is composed of the unpaired actines of atrial tri-

actines and chiactines, which are placed with the paired actines adjacent to the atrial wall, and apical actines straight and projecting towards the atrial cavity.

Spicules. *Cortical diactines*: slightly curved, with proximal ends sharper and thinner than the distal ends which present two oblique discs that form a kind of fissure at the tip (Figs 2C–D). Size: $226.5 \pm 32.2 \mu\text{m}$ length, $17.3 \pm 2.6 \mu\text{m}$ width (Table 3).

TABLE 3. Spicule measurements of *Achramorpha truncata* (holotype MNHN C1968-810). Measurements from the original description by Jenkin (1908) are included below.

MNHN C1968-810									
Spicules	Length (μm)				Width (μm)				n
	Min	Mean	Max	SD	Min	Mean	Max	SD	
Diactines	138.6	226.5	302.0	32.2	11.6	17.3	21.6	2.6	22
Cortical triactines									
Unpaired actines	118.5	171.5	223.7	26.9	8.6	11.2	14.1	1.3	25
Paired actines	85.7	123.1	157.9	19.4	8.6	11.1	14.2	1.8	
Atrial triactines									
Unpaired actines	359.1	446.7	554.9	59.2	9.7	12.4	16.8	2.4	10
Paired actines	122.7	158.4	202.8	29.0	9.6	11.8	14.3	1.5	
Chiactines									
Unpaired actines	399.1	464.4	513.7	31.7	12.3	13.8	15.1	0.9	10
Paired actines	130.0	153.3	192.0	18.0	11.4	13.5	17.0	1.6	
Apical actines	42.4	63.8	75.2	10.1	6.6	8.0	9.5	1.0	
Measurements from the original description (Topsent 1907; 1908)									
Spicules	Length (μm)				Width (μm)				
Diactines	400				25				
Triactines									
Unpaired actines	--				--				
Paired actines	160-170				13				
Chiactines									
Unpaired actines	--				15				
Paired actines	--				--				
Apical actines	--				10				

(--) Measurements not available.

Cortical triactines: unpaired actines straight and longer than the paired actines which are slightly irregular. Size: unpaired actines $171.5 \pm 26.9 \mu\text{m}$ length, $11.2 \pm 1.3 \mu\text{m}$ width; paired actines $123.1 \pm 19.4 \mu\text{m}$ length, $11.1 \pm 1.8 \mu\text{m}$ width (Fig 2E; Table 3).

Atrial triactines: T-shaped triactines with unpaired actines straight and longer than the paired actines. Size: unpaired actines $446.7 \pm 59.2 \mu\text{m}$ length, $12.4 \pm 2.4 \mu\text{m}$ width; paired actines $158.4 \pm 29.0 \mu\text{m}$ length, $11.8 \pm 1.5 \mu\text{m}$ width (Fig 2F; Table 3).

Chiactines: unpaired actines longer than the paired actines. Apical actines straight, slender, and sharply pointed (Fig 2E). Size: unpaired actines $464.7 \pm 31.7 \mu\text{m}$ length, $13.8 \pm 0.9 \mu\text{m}$ width; paired actines $153.3 \pm 18.0 \mu\text{m}$ length, $13.5 \pm 1.6 \mu\text{m}$ width; apical actines $63.8 \pm 10.1 \mu\text{m}$ length, $8.0 \pm 1.0 \mu\text{m}$ width (Table 3).

Distribution and depth. *A. truncata* is considered an endemic species from Antarctic waters. The species presents a wide depth range from shallow waters to a maximum depth record of 1500 m (Downey *et al.* 2012).

Molecular identification. Not available.

Remarks. Topsent (1907;1908) mentioned that “a remarkable characteristic” of this species was the lance-shape of the diactines, which present a conspicuous form at the distal end. After checking the holotype, we confirm that this characteristic is unique for the species and it was not found in the additional material examined and previously identified as *A. truncata*. Because of this and other differences mentioned below, we considered that the record by Barthel *et al.* (1997) is not conspecific with *A. truncata* and this material is here described as *A. antarctica* sp. nov. (see below).

Another characteristic of *A. truncata* is the absence of the minute and spined diactines that are found around the ostia and choanocyte chambers in other *Achramorpha* spp. It was not possible to analyse the oscular region because the sub-sample was taken at the base of the sponge to avoid altering the shape of the holotype.

In the information available for *A. truncata* in the World Porifera Database (van Soest *et al.* 2019) two voucher numbers, MNHN DT1647 and MNHN C1968810, are mentioned. Both codes identify the same specimen, the second number being the right one (information provided by Isabelle Domart-Coulon, curator in charge of the collection in the MNHN).

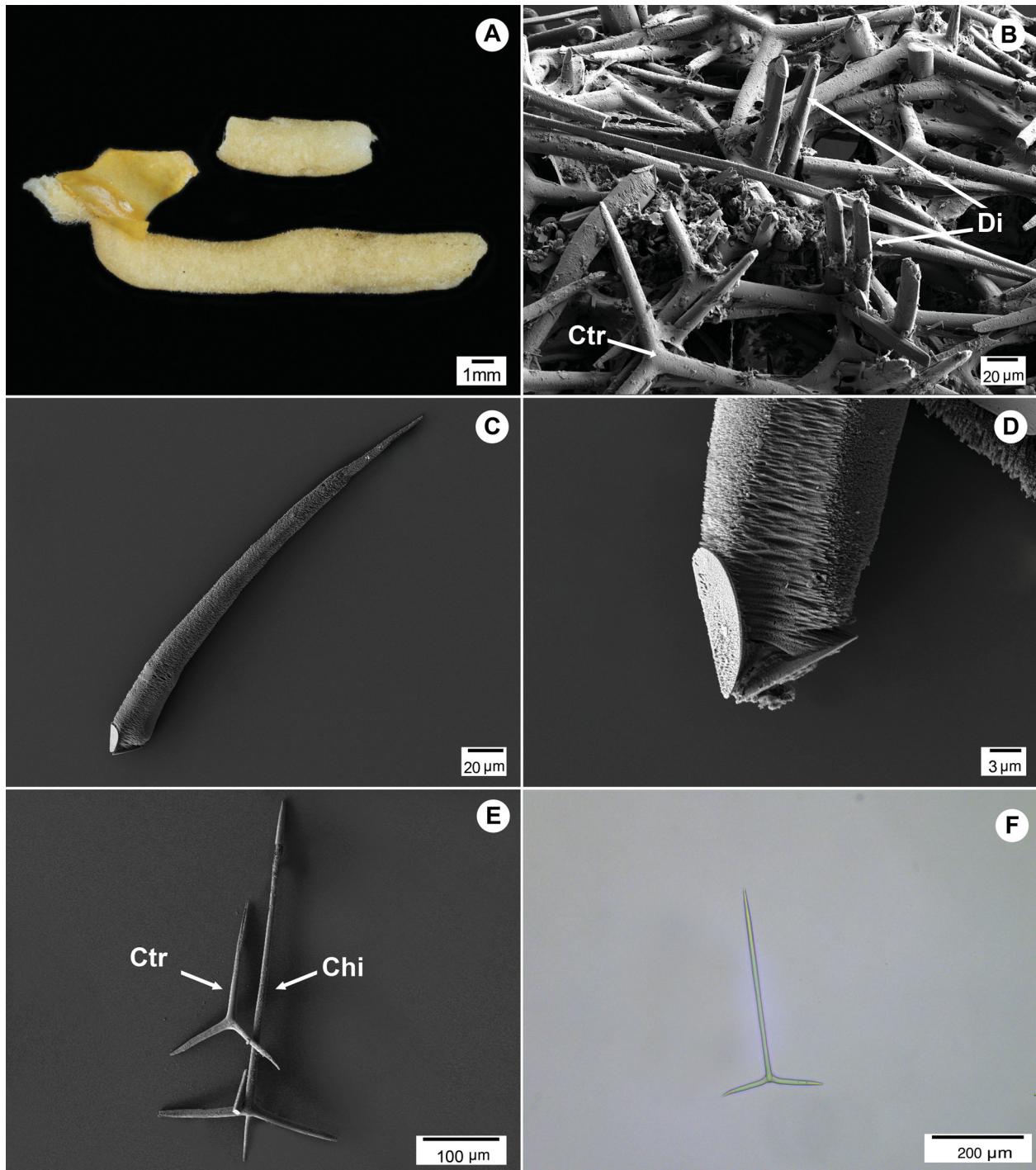


FIGURE 2A–F. *Achramorpha truncata*. **A:** preserved holotype MNHN C1968-810. **B:** SEM image of the cortical layer. **C–D:** SEM images of the cortical diactines and details of the distal end. **E:** SEM images of chiactines and cortical triactines. **F:** atrial triactine. **Abbreviations:** Chi = chiactines; Ctr = cortical triactines; Di = diactines.

Achramorpha antarctica sp. nov.

(Figs 3A–F, 4A–E; Table 4)

Diagnosis. *Achramorpha* with a cortical skeleton composed of triactines and long bundles of diactines/trichoxeas which penetrate the choanosome and may reach the atrium. There is only one type of diactines present in this species, which are long, nearly straight, with smooth surface and with both tips sharpened.

Type locality. Weddell Sea, Antarctic.

Synonyms and citations. *Achramorpha truncata*, Burton 1929, p. 402; *A. truncata*, Barthel *et al.* 1997, p. 47.

Material examined. Holotype: NHMD-611894 (one complete specimen), Weddell Sea, between the stations Vestkapp and Halley, 333–338 m depth ($73^{\circ}22.60' S$, $21^{\circ}10.60' W$) (Barthel *et al.* 1997). **Paratype:** BMNH-1926.10.26.250 (dry material), British Antarctic Expedition 1910–1913, st. nr. 339.

Etymology. Named after the type locality.

Morphology. Tubular sponge with surface hispid due to long diactines and long trichoxeas protruding the surface (Fig 3A). Colour is whitish in ethanol. Consistency fragile. Aquiferous system syconoid with elongated choanocyte chambers with sizes ranging from 429.8 to 599.6 μm length and from 103.0 to 156.7 μm width. The size of the holotype is 24.6 mm long, 8.7 mm wide and 0.46–1.03 mm thick; and the paratype (BMNH-1926.10.26.250) 11.9 mm large, 7.9 mm wide and around 0.8 mm thick.

Skeleton. Inarticulated skeleton composed of diactines, trichoxeas, chiactines and triactines. Sagittal tetractines can be found only in the oscular region (Fig 3B). Cortical skeleton is formed by triactines tangentially positioned, and by long diactines and trichoxeas arranged in bundles (Figs 3C–3E), which penetrate the choanosome and may reach the atrium. Smaller diactines are arranged radially penetrating the choanosome and protruding the surface (Fig 3D). The choanosomal skeleton is composed of the bundles of diactines/trichoxeas (Fig 3E), and of unpaired actines of atrial triactines and chiactines (Fig 3F). Few triactines can also be found in the atrial skeleton (Fig 3F). The atrial skeleton consists mainly of chiactines which are placed in the atrial wall with unpaired actines pointing towards the cortex, paired actines adjacent to the atrial wall, and apical actines straight and projecting towards the atrial cavity (Figs 3B, 3F). The oscular region is the only part of the skeleton with a proper atrial skeleton composed of triactines and tetractines with the unpaired actines pointing downwards. The apical actines from the tetractines are short and slightly bent pointing to the osculum (Fig 3B).

Spicules. *Cortical diactines:* highly variable in length and thickness. All diactines present smooth surface and are nearly straight with sharp tips (Figs 4A–B). Size: $845.6 \pm 322.9 \mu\text{m}$ length, $17.6 \pm 5.5 \mu\text{m}$ width (Table 4).

TABLE 4. Spicule measurements of *Achramorpha antarctica* sp. nov. (holotype NHMD-611894).

Spicules	Length (μm)				Width (μm)				n
	Min	Mean	Max	SD	Min	Mean	Max	SD	
Trichoxeas	280.4	1106.7	2455.1	612.1	1.1	5.1	11.8	2.6	21
Diactines	229.2	845.6	1989.3	322.9	7.4	17.6	33.1	5.5	30
Cortical triactines									
Unpaired actines	222.5	318.3	417.5	50.6	7.7	10.0	13.2	1.5	20
Paired actines	147.8	220.0	273.8	30.2	7.4	10.2	13.6	1.6	
Atrial triactines									
Unpaired actines	525.1	756.8	923.2	138	9.8	12.7	18.4	3.1	10
Paired actines	204.1	282.3	460.7	90.1	11.2	13.1	20.0	3.4	
Chiactines									
Unpaired actines	299.8	599.1	945.2	176.3	9.3	12.9	17.8	2.3	23
Paired actines	166.0	230.8	292.3	44.5	9.4	13.1	16.8	1.9	
Apical actines	32.2	84.9	133.2	29.2	6.6	9.2	13.0	1.7	
Oscular tetractines									
Unpaired actines	189.1	257.1	325.2	96.2	15.0	16.9	18.8	2.6	3
Paired actines	143.9	168.1	192.4	34.2	15.8	17.4	19.0	21.0	
Apical actines	87.6	102.5	117.4	21.0	17.4	18.1	18.8	0.9	

Trichoxeas: long and straight, with sharp tips. Most of them were broken. Size: $1106.7 \pm 612.1 \mu\text{m}$ length, $5.1 \pm 2.6 \mu\text{m}$ width (Fig 3C; Table 4).

Cortical triactines: sagittal with unpaired actines longer than the paired actines. Some triactines present one of the paired actines slightly bent. Actines conical and sharply pointed. Size: unpaired actine $318.3 \pm 50.6 \mu\text{m}$ length, $10 \pm 1.5 \mu\text{m}$ width; paired actines $220 \pm 30.2 \mu\text{m}$ length, $10.2 \pm 1.6 \mu\text{m}$ width (Fig 4C; Table 4).

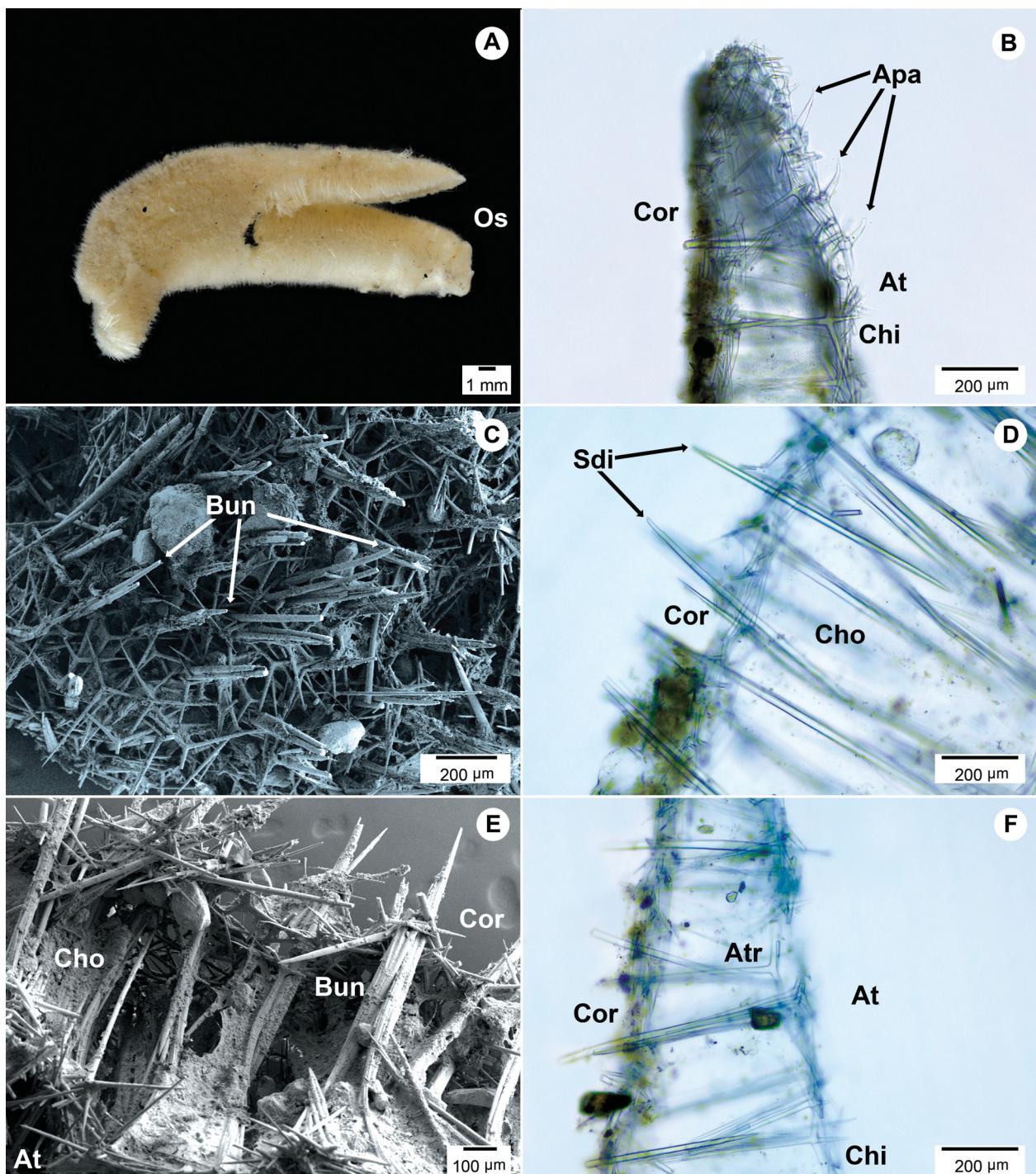


FIGURE 3A–F. *Achramorpha antarctica* sp. nov. **A:** preserved holotype. **B:** longitudinal section of the oscular region, including cortical layer, choanosome and atrial cavity. **C:** SEM image of the cortical layer. **D:** cross-section showing details of the cortical layer and the choanosome. **E:** SEM image of the choanosome. **F:** longitudinal section including cortical layer, choanosome and atrial cavity. **Abbreviations:** Apa = apical actines of tetractines; At = atrial cavity; Atr = atrial triactines; Bun = bundles of diactines and trichoxeas; Chi = chiactines; Cho = choanosome; Cor = cortical layer/cortex; Sdi = small diactines; Os = osculum.

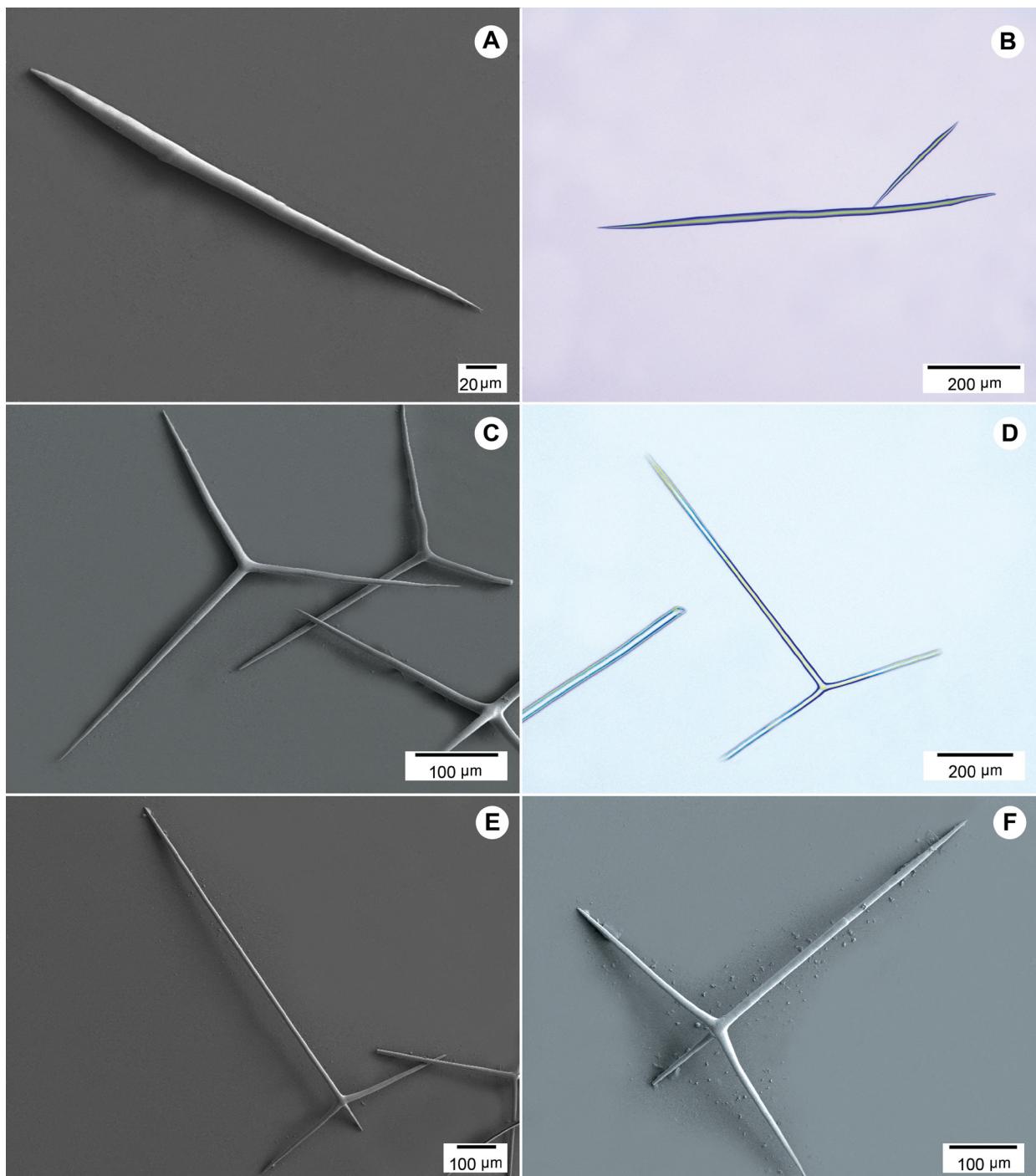


FIGURE 4A–F. Spicules of *Achramorpha antarctica* sp. nov. **A:** long cortical diactines. **B:** long and short cortical diactines. **C:** cortical triactines. **D:** atrial triactines. **E–F:** chiactines.

Atrial/oscular triactines: sagittal. T-shaped triactines with unpaired actines longer than the paired ones, and slender sharp tips. Size: unpaired actine 756.8 ± 138 μm length, 12.7 ± 3.1 μm width; paired actines 282.3 ± 90.1 μm length, 13.1 ± 3.4 μm width (Fig 4D; Table 4).

Chiactines: unpaired actines longer than the paired ones, with similar width. The apical actine is strait and slender with sharp tip. Size: unpaired actine 599.1 ± 176.3 μm length, 12.9 ± 2.3 μm width; paired actines 230.8 ± 44.5 μm length, 13.1 ± 1.9 μm width; apical actine 84.9 ± 29.2 μm length, 9.2 ± 1.7 μm width (Figs 4E–F; Table 4).

Oscular tetractines: measures not available because they were difficult to find intact in the spicule preparations and sections (Fig 3B; Table 4).

Distribution and depth. This species has been registered off McMurdo Sound at 256 m depth (Burton 1929), and in the Weddell Sea, 333–338 m (Barthel *et al.* 1997).

Molecular identification. Not available.

Remarks. As it was mentioned above, the specimens analysed here were previously identified as *A. truncata*, probably because they present external morphology similar to *A. truncata*. However, after re-examining the holotype of *A. truncata* and comparing it with the most recently collected specimens, we found morphological differences that confirm that these species are not conspecific. The long bundles of diactines/trichoxeas are fairly noticeable and represent a distinctive character of the species and makes it easy to separate from the most closely related species, *A. truncata*. Additional morphological differences are: 1) presence of long trichoxeas in *A. antarctica* sp. nov.; 2) different form and size of the cortical diactines, significantly longer in *A. antarctica* sp. nov. ($845.6 \pm 322.9 \mu\text{m}$ length in *A. antarctica* sp. nov. vs. $226.5 \pm 32.2 \mu\text{m}$ length in *A. truncata*); 3) chiactines, cortical and atrial triactines longer in *A. antarctica* sp. nov. than in *A. truncata*.

Achramorpha glacialis Jenkin, 1908

(Figs 5A–H; Table 5)

Original description. Jenkin 1908, p. 31, pl. XXIV, figs 98–102.

Type locality. Winter Quarters Bay, Antarctic.

Synonyms and citations. *Achramorpha glacialis*, Dendy & Row 1913, p. 765; *A. glacialis* Hôzawa 1918, p. 542; *A. glacialis*, Brønsted 1931, p. 31; *A. glacialis*, Burton 1963, p. 93, 524, fig 330.

Material examined. **Lectotype:** BMNH-1907.8.6.101 (one complete specimen and one slide), National Antarctic Expedition (HMS Discovery), collection date 05.09.1902. **Paralectotype:** BMNH-1907.8.6.103-104 (three fragments of a specimen and three slides), National Antarctic Expedition (HMS Discovery), collection date 23.01.1903.

Morphology. Cylindrical sponge, slender at the base and towards the apical osculum. Surface slightly hispid due to cortical diactines that cross the surface. Colour is white-beige in ethanol (Fig 5A). Aquiferous system sycnoid with long choanocyte chambers that taper at their distal ends, forming large inhalant cavities (Fig 5B). The lectotype is 5.6 mm long, 0.4–0.7 mm wide and 0.2–0.3 mm thick.

Skeleton. Cortical skeleton made up by triactines arranged tangentially, and by protruding diactines and trichoxeas (Figs 5B–C). Neither the diactines nor trichoxeas are arranged in tufts or bundles, but rather irregularly scattered. Minute and spined microdiactines are found also in the cortical skeleton (Fig 5D). The atrial skeleton is composed of chiactines which are placed radially with the unpaired actine pointed towards the choanosome, the paired actines adjacent to the atrial wall, and the apical actine projected towards the atrial cavity (Fig 5B). Tetractines are found only in the oscular region with the unpaired actines pointing downwards, the paired actines tangentially lined up with the atrial wall, and the apical actines pointing towards the atrium (Fig 5E). The oscular fringe is not well-developed and is composed mainly of short trichoxeas, and some scattered diactines (Fig 5C).

Spicules. *Cortical diactines:* bent, with sharp tip at the proximal end, while distal end is wider and has a blunt tip. Size: $338.4 \pm 73.8 \mu\text{m}$ length, $14.8 \pm 4.2 \mu\text{m}$ width (Fig 5F; Table 5).

Microdiactines: minute and slightly bent with scattered spines. Size: $63.1 \pm 36.7 \mu\text{m}$ length, $2.8 \pm 0.4 \mu\text{m}$ width (Fig 5D; Table 5).

Trichoxeas: straight and hastate, smaller than diactines. Size: $147.6 \pm 5.9 \mu\text{m}$ length, $2.6 \pm 0.4 \mu\text{m}$ width (Fig 5C; Table 5).

Cortical triactines: sagittal alate with acerate tips. The unpaired actines are longer but slightly slender than paired actines. Size: unpaired actines $235.3 \pm 42.7 \mu\text{m}$ length, $10.5 \pm 1.6 \mu\text{m}$ width; paired actines $146.9 \pm 23.4 \mu\text{m}$ length, $10.9 \pm 1.9 \mu\text{m}$ width (Figs 5G; Table 5).

Chiactines: unpaired actines straight, sharply pointed, and longer than paired actines, which bent irregularly. The apical actines taper to an acerate end and can be straight or slightly bent as the paired actines. Size: unpaired actines $334.2 \pm 38.0 \mu\text{m}$ length, $13.4 \pm 2.2 \mu\text{m}$ width; paired actines $160.4 \pm 18.3 \mu\text{m}$ length, $12.5 \pm 1.6 \mu\text{m}$ width; apical actine $85.0 \pm 7.5 \mu\text{m}$ length, $9.9 \pm 1.7 \mu\text{m}$ width (Fig 5H; Table 5).

Distribution and depth. *A. glacialis* has been reported in two different expeditions in Antarctic waters. The first one is the National Antarctic Expedition from where Jenkin obtained the samples used for the species description (Jenkin 1908). The second expedition was the “Deutschen Süd-polar Expedition”, where *A. glacialis* was recorded in the station called “Winterstation” and in the nearby area, at 350–385 m depth (Brønsted 1931).

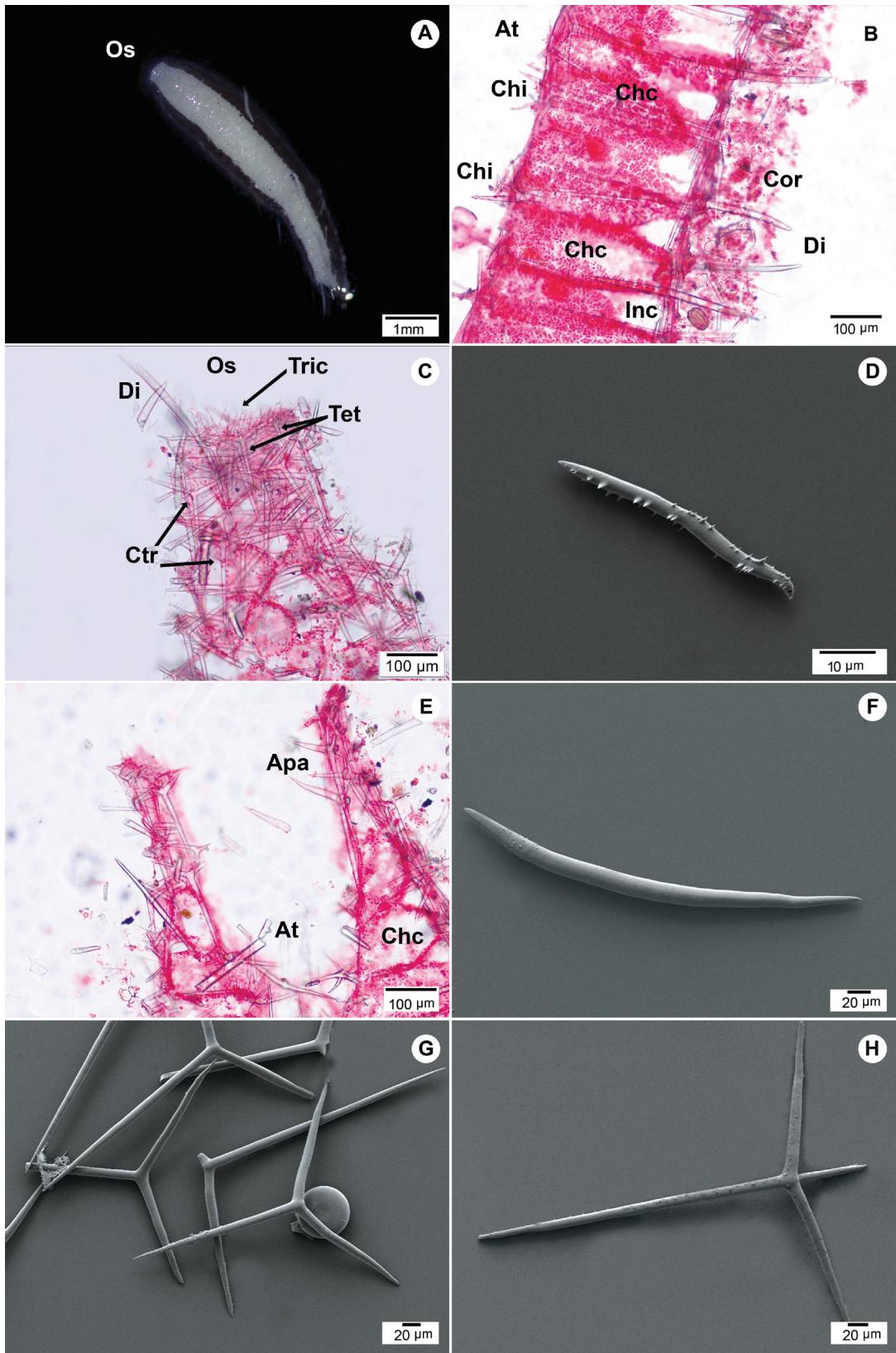


FIGURE 5A–H. *Achramorpha glacialis*. **A:** preserved lectotype BMNH-1907.8.6.101. **B:** histological section including cortical layer, choanosome and atrial cavity. **C:** histological section of the cortical layer. **D:** SEM image of microdiactine. **E:** histological sections of the oscular region. **F–H:** SEM images of spicules; cortical diactine (F), cortical triactines (G) and chiaictines (H). **Abbreviations:** Apa = apical actines of tetractines; At = atrial cavity; Chc = choanocyte chamber; Chi = chiaictines; Cor = cortical layer/cortex; Ctr = cortical triactines; Di = diactines; Inc = inhalant cavity; Os = osculum; Tet = tetractines; Tric = trichoxeas.

TABLE 5. Spicule measurements from specimens of *Achramorpha glacialis* (lectotype BMNH1907.8.6.101; cotype BMNH1907.8.6.103-104). Measurements from the original description by Jenkin (1908) are included below.

Spicules	Length (μm)				Width (μm)				n
	Min	Mean	Max	SD	Min	Mean	Max	SD	
Diactines	120.8	338.4	395.1	73.8	6.3	14.8	20.1	4.2	15
Microdiactines	48.5	63.1	65.7	36.7	2.0	2.8	3.3	0.4	10
Trichoxeas*	143.2	147.6	156.3	5.9	2.0	2.6	3.1	0.4	4
Cortical triactines									
Unpaired actines	174.9	235.3	317.0	42.7	7.7	10.5	13.5	1.6	20
Paired actines	107.3	146.9	187.2	23.4	7.3	10.9	15.1	1.9	
Chiactines									
Unpaired actines	282.4	334.2	402.0	38.0	9.5	13.4	15.7	2.2	10
Paired actines	133.2	160.4	188.4	18.3	9.8	12.5	14.4	1.6	
Apical actines	68.8	85.0	98.5	7.5	7.5	9.9	13.0	1.7	
Ocular tetractines									
Unpaired actines	105.3	174.1	244.6	49.0	8.8	11.6	15.3	2.3	7
Paired actines**	--	--	--	--	--	--	--	--	--
Apical actines	24.6	68.2	135.6	38.8	5.7	9.8	13.5	2.4	12
Measurements from the original description (Jenkin 1908)									
Spicules	Length (μm)				Width (μm)				
Diactines I	280-440				12-24				
Diactines II***	35-40				2-3				
Trichoxeas	>400				--				
Cortical triactines									
Unpaired actines	200-380				12				
Paired actines	130-180				10-14				
Chiactines									
Unpaired actines	340-400				15				
Paired actines	130-180				16				
Apical actines	70-100				12				
Ocular tetractines (small)									
Unpaired actines	100-120				9-10				
Paired actines	50-100				7-8				
Apical actines	--				--				
Ocular tetractines									
Unpaired actines	>220				--				
Paired actines	>200				--				
Apical actines	120				--				

(*) Most of them broken.

(**) Paired actines not completely visible in the slides.

(***) Diactines II = Microdiactines.

(--) Measurements not available.

Molecular identification. Not available.

Remarks. Six specimens were reported in the original description by Jenkin (1908). However only two specimens were found in the collection of the BMNH, and none were marked as being the holotype. Because one of the specimens was selected as lectotype, and the remaining specimen is now erected as paralectotype according to recommendation 74F of the ICZN .

According to Jenkin (1908), the trichoxeas in *A. glacialis* are 400 μm length or more. The discrepancy in the

size of the trichoxeas reported by Jenkin (1908) and ours (147.6 ± 5.9 μm length) is because these spicules were difficult to find intact in the slides. Despite this, we found that the trichoxeas present in *A. glacialis* are not as long as in *Achramorpha antarctica* sp. nov. (1106.7 ± 612.1 μm length), and they are not organized in bundles with the cortical diactines as in the new species *A. antarctica*.

Achramorpha grandinis Jenkin, 1908

(Figs 6A–H; Table 6)

Original description. Jenkin 1908, p. 32, pl. XXVII, figs 4, pl. XXXIV and XXXV, figs 103–104.

Type locality. Winter Quarters, Antarctic.

Synonyms and citations. *Achramorpha grandinis*, Dendy & Row 1913, p. 765; *A. grandinis* Hôzawa 1918, p. 542; *A. grandinis*, Brønsted 1931, p. 32; *A. grandinis*, Burton 1963, p. 93, 525, fig 331.

Material examined. Holotype: BMNH-1907.8.6.108 (one fragment of the specimen and two slides).

Morphology. Based on the fragment examined, the specimen seems to be cylindrical and slender towards one end, which probably is where the osculum was (Fig 6A). Surface hispid due to very long and scattered diactines that protrude the surface. The size of the holotype fragment is 6.0 mm in length and 2.5 mm wide. It was not possible to determine the type of aquiferous system of the species.

Skeleton. Cortical skeleton made up of tangential triactines, long protruding diactines, and microdiactines irregularly scattered (Figs 6B–C). The long diactines can cross the atrial wall. Chiactines compose the atrial skeleton, and they are placed with the unpaired actines pointing and projecting the cortical skeleton. The apical actines project towards the atrial cavity (Fig 6D). The oscular region is built up by tri- and tetractines placed with the unpaired actines pointing towards the base of the sponge. The short apical actines of the tetractines are bent upwards and crosses the atrial wall (Figs 6E, 6H). There is no oscular fringe (Fig 6E).

Spicules. *Cortical diactines*: long and straight diactines that taper in sharp points. Size: 879.1 ± 408.0 μm length, 15.4 ± 4.3 μm width (Figs 6B–C; Table 6).

Microdiactines: small and nearly straight. One blunt tip and the other hastate. Surface with small scattered spines. Size: 93.6 ± 20.3 μm length, 4.0 ± 0.8 μm width (Figs 6C, 6F; Table 6).

Cortical triactines: large, alate with straight unpaired actines, and shorter paired actines. All actines are tapering uniformly to sharp points. Size: unpaired actines 424.8 ± 91.9 μm length, 10.1 ± 1.0 μm width; paired actines 247.1 ± 26.6 μm length, 10.6 ± 1.5 μm width (Fig 6G; Table 6).

Chiactines: large and straight unpaired actines, and slightly slender than the paired actines which are shorter and form a wide angle (around 160°). Apical actine sharply pointed. Size: unpaired actines 410.1 ± 46 μm length, 11.1 ± 1.6 μm width; paired actines 231.4 ± 34.4 μm length, 11.9 ± 1.8 μm width; apical actine 120.3 ± 22.8 μm length, 10.1 ± 1.8 μm width (Fig 6H; Table 6).

Oscular tetractines: alate and straight tetractines, with all actines tapering into sharp tips. Apical actine conical and shorter than the unpaired and paired actines. The length of the unpaired actines is most likely underestimated as they were often broken or not clearly visible in the slides (Fig 6H; Table 6).

Distribution and depth. The species has been reported in two localities in Antarctic waters; Winter Quarters (Jenkin 1908) and between “Winterstation” and the coast of Kaiser Wilhelm II Land, at 350–385 m depth (Brønsted 1931).

Molecular identification. Not available.

Remarks. Because the original description was based on one fragment of the specimen (Jenkin 1908), some characters, such as aquiferous system and the arrangement of the choanoskeleton, are not mentioned. However, according to our observations the atrial skeleton seems to be made up only by chiactines with long unpaired actines that project the cortical surface. This skeletal organization suggests that *A. grandinis* has an inarticulated skeleton as in the rest of the *Achramorpha* spp. However, it will be necessary to include new material and additional histological sections to properly show the skeletal organization and aquiferous system of this species.

Jenkin (1908) mentioned that the osculum of *A. grandinis* differs considerably from the other species, because it does not have an oscular fringe nor special oscular ring/collar of tetractines at the edge of the sponge. According to Jenkin (1908) observations, it seems that *A. grandinis* presents a naked osculum, which could represent a distinctive characteristic of the species. Moreover, the absence of protruding trichoxeas in the cortical skeleton can also be considered as another difference of *A. grandinis*. However, we have to examine more specimens to conclude whether the absence of these morphological characters is consistent.

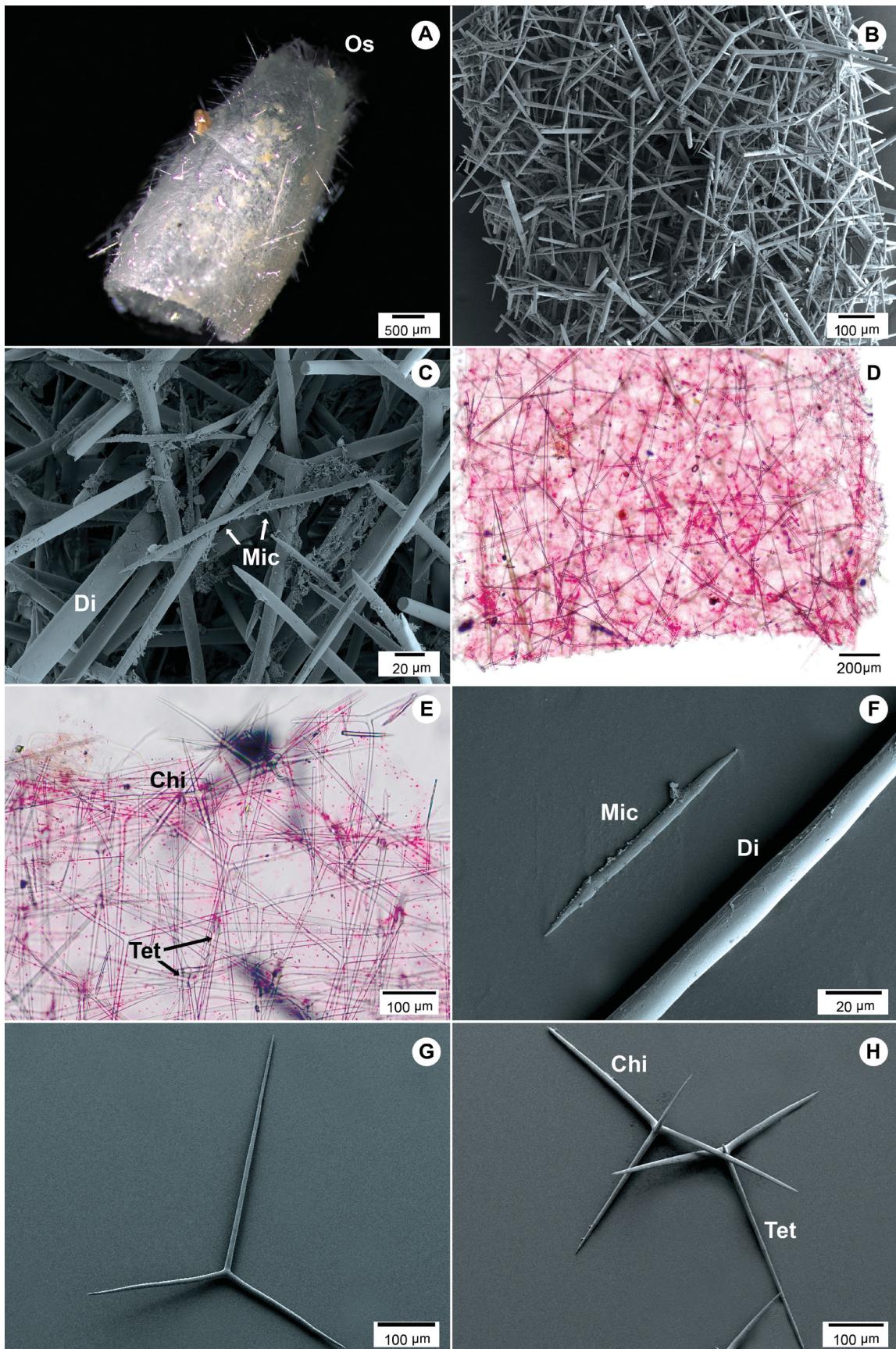


FIGURE 6A–H. *Achramorpha grandinis*. **A:** preserved holotype BMNH-1907.8.6.108. **B–C:** SEM of the cortical layer. **D–E:** histological section of the cortical layer and oscular region. **F–H:** SEM images of spicules; microdiactine (**F**), cortical triactine (**G**) and chiactines and tetractine (**H**). **Abbreviations:** Chi = chiactines; Di = diactines; Mic = microdiactines; Os = osculum; Tet = tetractines.

TABLE 6. Spicule measurements of *Achramorpha grandinis* (holotype BMNH-1907.8.6.108). Measurements from the original description by Jenkin (1908) are included below.

BMNH-1907.8.6.108									
Spicules	Length (μm)				Width (μm)				n
	Min	Mean	Max	SD	Min	Mean	Max	SD	
Diactines*	337.8	879.1	1787.3	408.0	5.6	15.4	23.8	4.3	16
Microdiactines	61.6	93.6	139.2	20.3	2.1	4.0	5.7	0.8	19
Cortical triactines									
Unpaired actines	250.1	424.8	534.9	91.9	7.9	10.1	12.7	1.0	20
Paired actines	193.8	247.1	291.2	26.6	8.2	10.6	13.5	1.5	
Chiactines									
Unpaired actines	337.4	410.1	478.9	46.0	7.3	11.1	15.4	1.6	20
Paired actines	137.6	231.4	275.9	34.4	8.1	11.9	14.6	1.8	
Apical actines	49.4	120.3	150.9	22.8	6.0	10.1	14.1	1.8	
Oscular tetractines									
Unpaired actines**	122.6	157.2	212.9	33.9	7.1	9.8	14.7	3.0	5
Paired actines**	179.0	242.0	306.3	59.8	6.5	8.8	11.4	2.0	
Apical actines	77.7	14.6	116.8	14.6	8.1	9.3	11.5	1.3	
Measurements from the original description (Jenkin 1908)									
Spicules	Length (μm)				Width (μm)				
Diactines I	3500				23				
Diactines II***	65-120				3-6				
Cortical triactines									
Unpaired actines	420-500				12-15				
Paired actines	200-260				12-14				
Chiactines									
Unpaired actines	450-550				12-16				
Paired actines	240-270				12-14				
Apical actines	160				14-16				
Oscular tetractines									
Unpaired actines	650				12				
Paired actines	560				14				
Apical actines	120				9				

(*) Most of them broken.

(**) Unpaired actines broken or not completely visible in the slides.

(***) Diactines II = Microdiactines.

Achramorpha ingolfi sp. nov.

(Figs 7A–H, 8A–D; Table 7)

Diagnosis. *Achramorpha* with cortical skeleton composed of big triactines and thin diactines. Aquiferous system syconoid with rounded choanocyte chambers.

Type locality. Norwegian Sea.

Synonyms and citations. *Leucosolenia* sp. Borojević & Graat-Kleeton 1965, p. 84; *Clathrina* sp. Barthel *et al.* 1993, p. 85.

Material examined. **Holotype:** ZMBN-127207, Norwegian Sea, G.O. Sars 2008-SL1, collection date 03.07.2008, 2425 m depth (73°35.32'N 07°45.119'E). **Paratype:** ZMBN-127208, Norwegian Sea, GS14-AGT04-N24, collection date 30.7.2014, 2651 m depth (73°42.129'N 07°23.854'E). **Paratype:** NHMD-611895, Norwegian Sea, Ingolf expedition st. 113, collection date 21-22.07.1896, 2465 m depth (69°31'N 07°06'W).

Etymology. Named after the Danish Ingolf Expedition where the first specimens were collected in 1896.

Morphology. Tubular sponge with single osculum and thin-walls ($140 \pm 28.6 \mu\text{m}$). Surface smooth. Colour in ethanol light beige (Figs 7A–B). Aquiferous system syconoid with spherical choanocyte chambers of about 50–75 μm in diameter (Fig. 7C). The holotype size is up to 2 cm in length and 1–3 mm wide.

Skeleton. Cortical skeleton composed of big tangential triactines to which scattered thin diactines are added (Figs 7D–E). Characteristic but very scarce chiactines are found in the atrial skeleton, with their paired actines adjacent to the atrial wall, and the apical actines straight and projecting towards the atrial cavity (Fig 7F). Oscular collar composed of the same type of diactines found in the cortical skeleton (Figs 7B, 7E). All spicules are slender and sharply pointed.

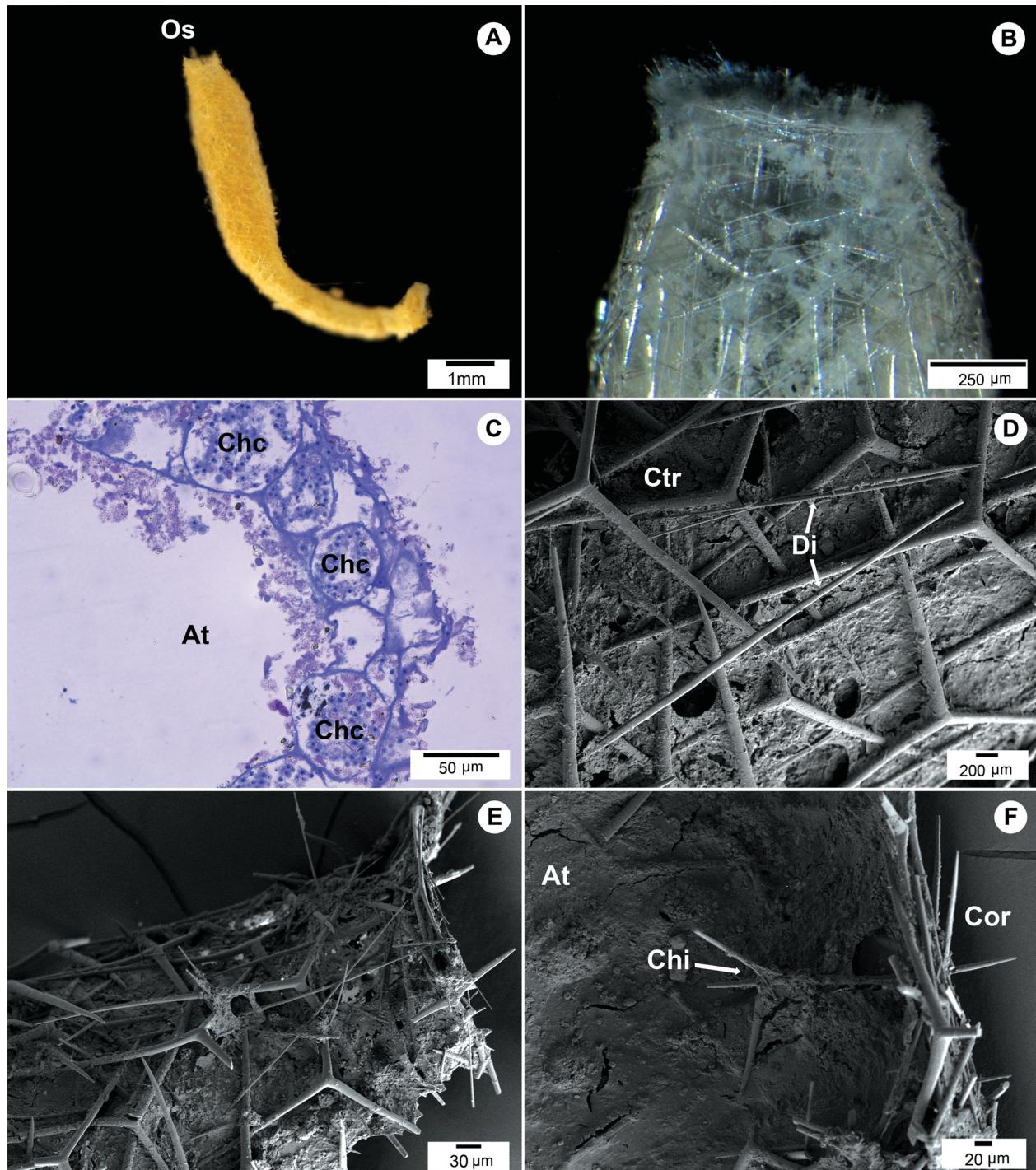


FIGURE 7A–H. *Achramorpha ingolfi* sp. nov. **A:** preserved holotype. **B:** LM image of the oscular region. **C:** cross section including cortical layer, choanosome and atrial cavity. **D–E:** SEM images of the cortical layer. **F:** SEM image of the atrial cavity. **Abbreviations:** At = atrial cavity; Chi = chiactines; Chc = choanocyte chamber; Cor = cortical layer/cortex; Ctr = cortical triactines; Di = cortical diactines; Os = osculum; Tri = triactines.

Spicules. *Diactines*: thin and straight with sharply pointed ends. One of the ends can be lanceolate asymmetrically (Figs 7D, 8A–B). Some diactines are also thin but curved (Fig 8B). Both group of diactines are found in the oscular region and in the cortical skeleton. Size: $135.5 \pm 31.6 \mu\text{m}$ length, $3.0 \pm 0.9 \mu\text{m}$ width (Table 7).

TABLE 7. Spicule measurements from specimens of *Achramorpha ingolfi* sp. nov. (holotype ZMBN-127207, paratype ZMBN-127208).

ZMBN-127207									
Spicules	Length (μm)				Width (μm)				n
	Min	Mean	Max	SD	Min	Mean	Max	SD	
Diactines	96.2	135.5	205.0	31.6	1.8	3.0	5.0	0.9	15
Cortical triactines									
Unpaired actines	255.0	368.6	428.4	42.7	9.1	12.0	14.3	1.3	30
Paired actines	137.8	235.6	304.2	35.9	9.1	12.3	16.9	1.8	
Chiactines									
Unpaired actines	244.8	297.7	397.8	50.7	7.8	9.5	13.0	1.2	16
Paired actines	101.4	138.5	239.2	23.7	5.2	7.9	13.0	1.5	30
Apical actines	20.8	64.2	91.0	16.0	3.9	6.0	9.1	1.3	30
ZMBN-127208									
Spicules	Length (μm)				Width (μm)				n
	Min	Mean	Max	SD	Min	Mean	Max	SD	
Diactines	76.4	136.2	184.6	39.0	2.4	3.3	5.0	0.8	15
Cortical triactines									
Unpaired actines	153.0	514.8	652.8	105.2	9.1	17.3	20.8	2.0	30
Paired actines	112.2	347.1	408.0	60.6	11.7	18.2	20.8	1.9	
Chiactines									
Unpaired actines	234.6	283.1	316.2	34.7	10.4	11.7	13.0	1.1	4
Paired actines	80.6	140.5	174.2	27.3	9.1	13.6	15.6	1.7	24
Apical actines	70.2	87.1	111.8	9.9	6.5	8.7	10.4	0.8	22

Cortical triactines: sagittal with slightly bent paired actines, and straight and longer unpaired actines. Size: unpaired actines $368.6 \pm 42.7 \mu\text{m}$ length, $12.0 \pm 1.3 \mu\text{m}$ width; paired actines $235.6 \pm 35.9 \mu\text{m}$ length, $12.3 \pm 1.8 \mu\text{m}$ width (Fig 8C; Table 7).

Chiactines: paired and unpaired actines straight, forming a tripod, while the apical actine is sharply bent, with the shape of a blade. Size: unpaired actines $297.7 \pm 50.7 \mu\text{m}$ length, $9.5 \pm 1.2 \mu\text{m}$ width; paired actines $138.5 \pm 23.7 \mu\text{m}$ length, $7.9 \pm 1.5 \mu\text{m}$ width; apical actines $64.2 \pm 16.0 \mu\text{m}$ length, $6.0 \pm 1.3 \mu\text{m}$ width (Fig 8D; Table 7).

Distribution and depth. This is a deep-sea species which has been found in the Norwegian Sea and Greenland Basin, at 2425–2651 m depth.

Molecular identification. Sequences available in GenBank under the following accession numbers: for 28S rRNA MH385224 (ZMBN-127208, GIN05), MH385157 (ZMBN-127207, SA127); and for 18S rRNA MH385225 (ZMBN-127208, GIN05), MH385158 (ZMBN-127207, SA127) (Alvizu *et al.* 2018).

Remarks. The shape of the diactines and the absence of tetractines, represent distinctive characters of this new species from the deep-sea. Some of the diactines present a similar shape than the typical minute diactines reported in most species of the family Achramorphidae, but instead of presenting minute spines, the diactines of *A. ingolfi* sp. nov. are lanceolate with smooth surface and slightly longer. The spicule sizes are very variable, both within each sponge, and between different specimens. The triactines are the most variable in size (unpaired actines 153.0–652.8 μm length, 12.0–17.3 μm width; paired actines 112.2–408.0 μm length, 12.3–18.2 μm width), but also the chiactines show differences, especially the width (unpaired actines 9.5–11.7 μm width; paired actines 7.9–13.6 μm width; apical actines 6.0–8.7 μm width).

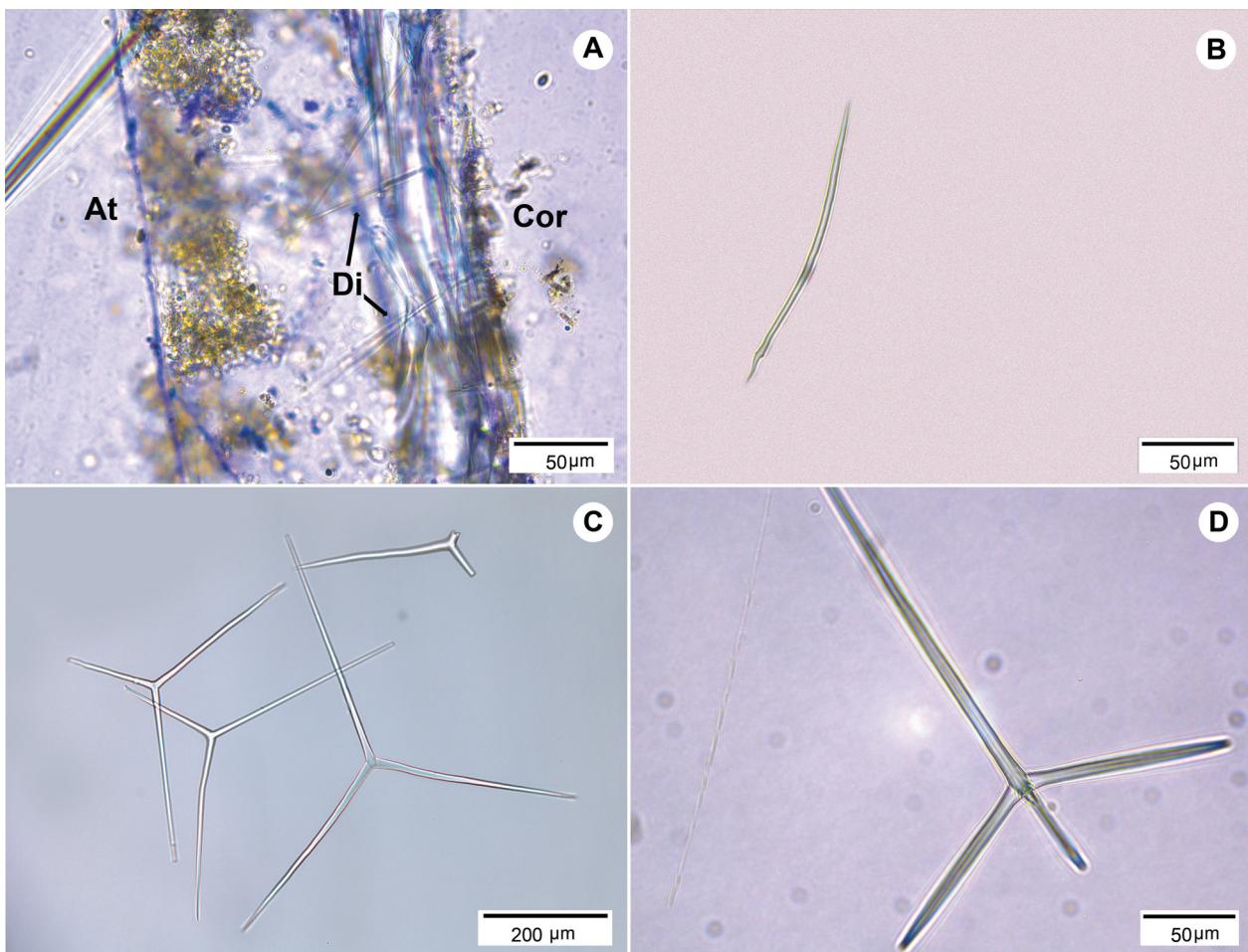


FIGURE 8A–D. *Achramorpha ingolfi* sp. nov. **A:** histological section including cortical layer, choanosome and atrial cavity. **B:** diactine. **C:** triactines. **D:** chiactine. **Abbreviations:** At = atrial cavity; Cor = cortical layer/cortex; Di = cortical diactines.

Achramorpha diomediae Hôzawa, 1918

Original description. Hôzawa 1918, p. 540, pl. 85, fig 10.

Type locality. Off Cape Rollin, Simushir Island, Kuriles. St. 4803, 418 m depth.

Synonym and citations. *Achramorpha diomediae*, Burton 1963, p. 93.

Type material. [Cat. No. 1971, U.S.N.M.: one specimen].

Material examined. BMNH-1938.7.4.72: one specimen and one slide, Swedish Bank, Zool. Inst. Acad. Sci. Leningrad. BMNH-1938.7.4.73: three specimens of different species, and one slide, Sea of Okhotsk, St. 214, Zool. Inst. Acad. Sci. Leningrad.

Remarks. Based on the original description, *Achramorpha diomediae* mainly differs from all other *Achramorpha* species due to the presence of an atrial skeleton composed of tetractines with their unpaired actines directed toward the base of the sponge (Hôzawa 1918). Another difference is the absence of chiactines, which are not mentioned by Hôzawa (1918), and based on the spicule figures presented in the original description, this type of tetractines is not present in *A. diomediae*. In line with these characteristics, *A. diomediae* does not fit into the definition of the genus *Achramorpha* and should be excluded. However, the formal reallocation of this species to another genus requires an examination of the holotype.

The material analysed from the BMNH collection identified as *A. diomediae* also presents some incongruences. First, the material available in the collection is in two jars, the first one with one specimen (BMNH-1938.7.4.72) and the second (BMNH-1938.7.4.73) contains three different specimens with fairly distinctive morphology. Secondly, the slide from the specimen BMNH-1938.7.4.72 does not have chiactines in the atrial skeleton, presenting instead an atrial skeleton built up by tetractines with very long apical actines, similar to *Breitfussia*. Third, the slide of the

specimen BMNH-1938.7.4.73, does not specify to which of the three specimens it belongs. Fourth, after examination of this second slide, we noticed that the skeletal arrangement is completely different than that in the slide of the specimen BMNH-1938.7.4.72. In summary, the samples available in the BMNH collection under the name *A. diomediae* are not *Achramorpha*, and should not be considered within this group of chiactines-bearing sponges.

Genus *Megapogon* Jenkin, 1908

Diagnosis. Achramorphidae with sylleibid or leuconoid organization (Borojević *et al.* 2002b).

Scope: Five species have been allocated by Jenkin (1908) to this genus: *Megapogon crucifer* (Poléjaeff 1883), *M. raripilus* Jenkin 1908, *M. villosus* Jenkin 1908, *M. pollicaris* Jenkin 1908 and *M. crispatus* Jenkin 1908. One new species from the Antarctic is described in this study; *Megapogon schiaparellii* sp. nov.

Type species. *Leuconia crucifera* Poléjaeff 1883, accepted as *Megapogon crucifer* (Poléjaeff 1883; type by subsequent designation by Jenkin 1908).

Megapogon crucifer (Poléjaeff, 1883)

(Figs 9A–B; Table 8)

Original description. Poléjaeff 1883, p. 60, pl. VII, figs 5a–5d.

Type locality. Azores.

Synonyms and citations. *Leuconia crucifera*, Poléjaeff 1883, p. 60 (pl. VII, figs 5a–5d); *Megapogon cruciferus* Jenkin 1908, p. 36 (pl. XXXVI, figs 114); *M. cruciferus* Dendy & Row 1913, p. 768; not *M. cruciferus* Burton 1956, p. 117; *Leuconia crucifera* Burton 1963, p. 117.

Material examined. **Holotype:** BMNH-1884.4.22.46a (one section slide), Challenger collection, St. 75, collection date: 02.07.1873, at 822 m depth (450 fathoms), off the Azores (38°37'N, 28°30'W) (Poléjaeff 1883). **Additional material:** BMNH-1948.3.8.2: wet material (three pieces), Atlantide—Danish Expedition to the Coasts of Tropical West Africa.

Morphology. It was not possible to present a proper morphological description for this species because the only material available is one slide of the holotype. The only morphological character visible from this slide is the presence of big diactines protruding the surface and crossing the entire choanosome (Fig 9A).

Skeleton. Based on the material examined, we could record that the cortical skeleton seems to be composed of triactines and long and thick diactines (Fig 9A). Microdiactines were observed in the atrial skeleton (Fig 9B; Table 8).

Spicules. Few spicules were measured from the slide (see Table 8). The type of spicules distinguished from the slide were long diactines, microdiactines and triactines (Figs 9A–B).

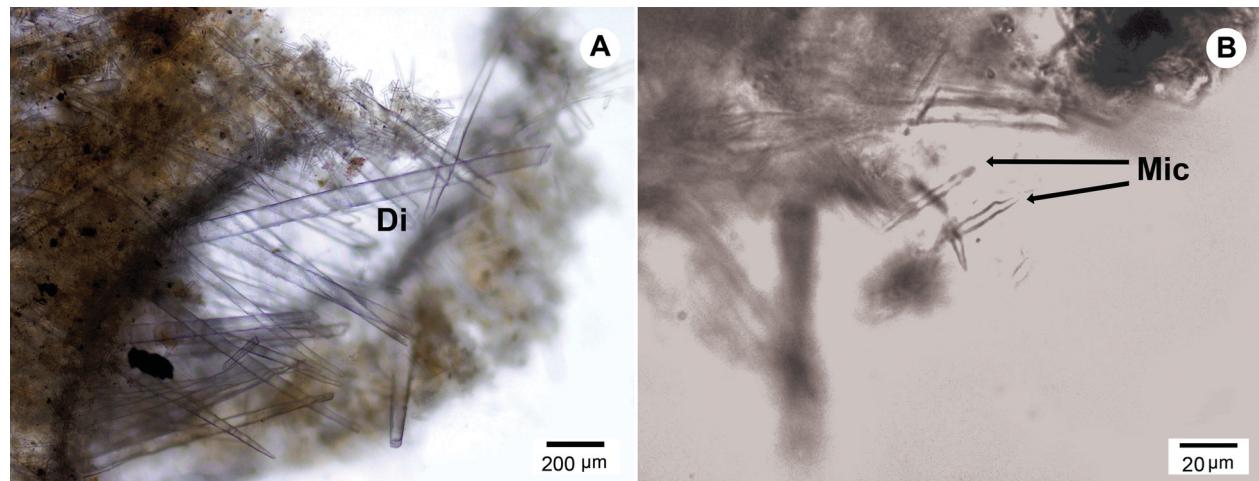


FIGURE 9A–B. *Megapogon crucifer*. A–B: sections of the holotype BMNH-1884.4.22.46a. **Abbreviations:** Di = diactines; Mic = microdiactines.

TABLE 8. Spicule measurements from specimens of *Megapogon crucifer* (holotype BMNH 1884.4.22.46; additional material BMNH 1948.3.8.2). Measurements from the original description by Poléjaeff (1883) are included below.

BMNH 1884.4.22.46									
Spicules	Length (μm)				Width (μm)				n
	Min	Mean	Max	SD	Min	Mean	Max	SD	
Diactines*	at least	1442.7	--	--	55.2–85.4		--	--	1
Microdiactines	37.3	40.0	42.7	3.8	2.4	3.0	3.6	0.8	2
Triactines									
Unpaired actines	276.7		--	--	14.7		--	--	1
Paired actines	187.8		--	--	16.2		--	--	
BMNH 1948.3.8.2									
Spicules	Min	Mean	Max	SD	Min	Mean	Max	SD	n
Diactines	906.53	678.4*	1483.6	104	28.1	26.6	45.4	3.7	11
Microdiactines	--	57.9	--	--	--	3.2	--	--	1
Triactines I									
Unpaired actines	90.8	158.9	239.4	46.2	6.0	8.2	10.8	1.9	6
Paired actines	108.7	139.1	167.7	18.1	4.4	7.5	12.0	2.4	
Triactines II									
Unpaired actines	71.8	90.6	116.9	17.6	4.2	6.1	7.4	1.1	4
Paired actines	140.6	207.9	308.4	61.6	6.7	6.9	7.2	0.1	
Chiactines									
Unpaired actines	173.2	186.4	199.6	13.2	7.6	7.8	7.9	0.1	2
Paired actines	173.7	212	313.8	47.3	6.3	7.9	10.3	1.3	6
Apical actines	51.7	70.6	80.0	11.2	5.8	7.7	9.2	1.2	5
Measurements from the original description (Poléjaeff 1883)									
Spicules	Length (μm)				Width (μm)				
Diactines I: stout acerate, spindle-shaped, either straight or slightly curved	3000				100 (30:1)				
Diactines II: slender acerate, spindle-shaped or more or less cylindrical, straight.	800				2.5				
Cortical triactines									
Unpaired actine: straight, tapering from the base to sharp points.	200–300				18				
Paired actines: curved forwards	200				18				
Chiactines									
Unpaired actine	250				15				
Paired actines	200				15				
Apical actine: same length as the paired actines, often rather shorter and thinner									

(*) Most of the diactines were broken.

(--) Measurements not available.

Distribution and depth. The first record of this species is from Azores, at 822 m depth (450 fathoms) (Poléjaeff 1883), and a second record was found in the tropical coast of West Africa (Senegal), at 65–89 m depth (Burton 1956). However, this second record does not correspond to *M. crucifer* (see remarks section).

Molecular identification. Not available.

Remarks. According to the original descriptions presented by Poléjaeff (1883), the skeleton of *M. crucifer* consists of: atrial chiactines, tubar triactines, cortical triactines, stout acerate diactines, which are piercing the choanosome obliquely and projecting their distal ends, and slender acerate diactines, scattered on the “outer surface” (cortex) in small bundles. The presence of minute spined diactines (microdiactines) was reported by Jenkin (1908) after the re-examination of the original material.

The original description of *M. crucifer* is based on a single fragment “belonging to the interior part” of the sponge (Poléjaeff 1883), and for this reason there are some morphological characters, such as the type of aquiferous system, that are not mentioned by the author. New material is urgently needed to present a better description of this species which is the type species of the genus *Megapogon*.

After re-examining specimens and slides (BMNH-1948.3.8.2) of *M. crucifer* collected in the tropical coast of West Africa and identified by Burton (1956), we consider the specimen from West Africa as non-conspecific with *M. crucifer*. The West Africa sample consists of three fragments with tubular shape, and a slightly hispid surface. These fragments present two different types of triactines, the first one has longer unpaired actines and the paired actines are bent upwards forming a round angle. The second type of triactines are “T” shaped but with paired actines much longer than the unpaired actines. Similar to the first type of triactines, some tetractines have the paired actines bent upwards forming a round angle. Some of these tetractines look like chiaactines but we could not confirm their presence in this sample. The diactines were difficult to measure because all of them were broken, but they are slender and shorter than the stout diactines reported by Topsent (1907) in the original description of *M. crucifer*. All these characteristics differ from the holotype of *M. crucifer* and its original description, suggesting that the specimen from the tropical West Africa is not conspecific with *M. crucifer* from the Azores Island. However, further analyses of the holotype and additional material (if available) is necessary to make a better re-description of this species.

***Megapogon raripilus* Jenkin, 1908**

(Figs 10A–F, 11A–D; Table 9)

Original description. Jenkin 1908, p. 38, pl. XXXVI, figs 120–124.

Type locality. Winter Quarters Bay, Antarctic.

Synonyms and citations. *Megapogon raripilus*, Brøndsted 1931, p. 32; *M. raripilus*, Burton 1963, p. 93; not *M. raripilus* Alvizu *et al.* 2018, p. 282; not *M. raripilus* Ghiglione *et al.* 2018, p. 149.

Material examined. **Lectotype:** BMNH-1907.8.6.139 (one slide and one specimen), National Antarctic Expedition (HMS Discovery), collection date 28.11.1902. **Paralectotype:** BMNH-1907.8.6.145: one slide, National Antarctic Expedition (HMS Discovery), collection date 13.9.1902. **Paralectotype:** BMNH-1907.8.6.140: four slides and one specimen, National Antarctic Expedition (HMS Discovery), collection date 17.01.1903, Flagon point, Winter Quarters Bay.

Morphology. Tubular sponge, slightly thicker at the base, with an apical osculum without a well-developed fringe (Figs 10A–B). Colour in alcohol is beige-yellowish. Surface hispid due to projecting diactines and trichoxeas. Aquiferous system leuconoid with rounded inhalant cavities and choanocyte chambers, and larger exhalant cavities (Fig 10C). The thickness of the sponge wall is 1.7–1.8 mm. The size of the lectotype (BMNH-1907.8.6.139) is 11.43 mm long and 1.1–2.2 mm wide. The size of the paralectotype examined is 9.6 mm long and 1.5 mm wide (BMNH-1907.8.6.140).

Skeleton. Cortical skeleton composed of sagittal tangential triactines, trichoxeas, diactines and microdiactines. Bundles of trichoxeas are arranged radially, penetrating the choanosome but do not reach the atrium (Figs 10C–10E). The choanoskeleton is semi-articulated (see remarks), made up by the same type of triactines found in the cortex (Figs 10C–E). Small and spined microdiactines are found around the choanocyte chambers and scattered in the atrial skeleton. The atrial skeleton is mainly supported by the paired actines of chiaactines with the unpaired actines pointing towards the cortex, and the apical actines crossing through the atrial wall into the atrium (Fig 10F). Sagittal triactines are irregularly scattered in the atrial skeleton, and the unpaired actines from those closer to the cortex, can project into the surface (Figs 10E–F). The oscular margin is composed of the same cortical diactines and long trichoxeas.

Spicules. *Diactines:* large, curved towards the distal end and with blunt tip. The proximal end is thinner and sharply pointed (Fig 11A). Size: $596.4 \pm 92.1 \mu\text{m}$ length, $20.6 \pm 3.6 \mu\text{m}$ width (Table 9).

Microdiactines: minute, slightly bent, strongly spined and sharply pointed (Fig 11B). Size: $60.4 \pm 14.8 \mu\text{m}$ length, $3.4 \pm 1.1 \mu\text{m}$ width (Table 9).

Trichoxeas: long and straight. It was not possible to measure the trichoxeas because they were broken or not clearly visible in the slides.

Cortical triactines: sagittal, with the unpaired actines longer than the paired ones. Cortical triactines size: unpaired actines $381.7 \pm 98.9 \mu\text{m}$ length, $13.4 \pm 3.5 \mu\text{m}$ width; paired actines $157.6 \pm 21.7 \mu\text{m}$ length, $10.1 \pm 2.4 \mu\text{m}$ width (Fig 11C).

Atrial triactines: “T” shaped with unpaired actines longer than the paired ones. These triactines are longer than the cortical triactines. Size: unpaired actines $556.7 \pm 58.5 \mu\text{m}$ length, $13.4 \pm 3.5 \mu\text{m}$ width; paired actines $221.7 \pm 25.2 \mu\text{m}$ length, $11.2 \pm 2.7 \mu\text{m}$ width (Fig 10F, Table 9).

Chiactines: unpaired actines straight and longer than the paired actines, which are slightly bent. Apical actines short, straight, slender, and sharply pointed. Size: unpaired actines 555 ± 172.3 µm length, 13.4 ± 1.7 µm width; paired actines 226.3 ± 27.4 µm length, 15 ± 1.4 µm width; apical actines 79.1 ± 12.2 µm length, 10.2 ± 2.9 µm width (Fig 11D, Table 9).

Oscular tetractines: not measured because they were difficult to find in the spicule preparations and in the sections.

TABLE 9. Spicule measurements from specimens of *Megapogon rariplius* (BMNH 1907.8.6.140). Measurements from the original description by Jenkin (1908) are included below.

Spicules	Length (µm)				Width (µm)				n
	Min	Mean	Max	SD	Min	Mean	Max	SD	
Trichoxeas	--	--	--	--	--	--	--	--	--
Diactines	300.3	596.4	708	92.1	10.8	20.6	27.7	3.6	30
Microdiactines	29.8	60.4	78.4	14.8	1.0	3.4	5.6	1.1	15
Cortical triactines									
Unpaired actine	250.0	381.7	541.8	98.9	8.7	13.4	16.3	3.5	15
Paired actines	173.6	221.7	272	25.2	5.6	11.2	18.2	2.7	
Atrial triactines									
Unpaired actine	496.3	556.7	646	58.5	8.0	13.4	16.4	3.5	10
Paired actines	184.9	217.0	249.2	26.4	8.7	13.2	20.1	3.3	
Chiactines									
Unpaired actine	104.4	555	822.7	172.3	9.8	13.4	16.5	1.7	15
Paired actines	187.3	226.3	281.8	27.4	13.0	15.0	16.8	1.4	
Apical actine	56.9	79.1	97.0	12.2	5.9	10.2	17.5	2.9	
Oscular tetractines	--	--	--	--	--	--	--	--	--
Measurements from the original description (Jenkin 1908)									
Spicules	Length (µm)			Width (µm)					
Trichoxeas	>500			1					
Diactines I	About 700			30–65					
Diactines II**	60–150			4–5					
Diactines III	350			20					
Cortical triactines									
Unpaired actine	170–700			10–18					
Paired actines	120–270			10–16					
Atrial triactines									
Unpaired actine	700			16					
Paired actines	200–320			20					
Chiactines									
Unpaired actine	600–750			14					
Paired actines	200–280			16–20					
Apical actine	80			12					
Oscular diactines*	380–480			18					
Oscular tetractines									
Unpaired actine	140			8					
Paired actines	70			10					
Apical actine	20			8					

(--) Measurements not available.

(*) This kind of spicules is found forming the external fringe (Jenkin 1908).

(**) Diactines II = Microdiactines.

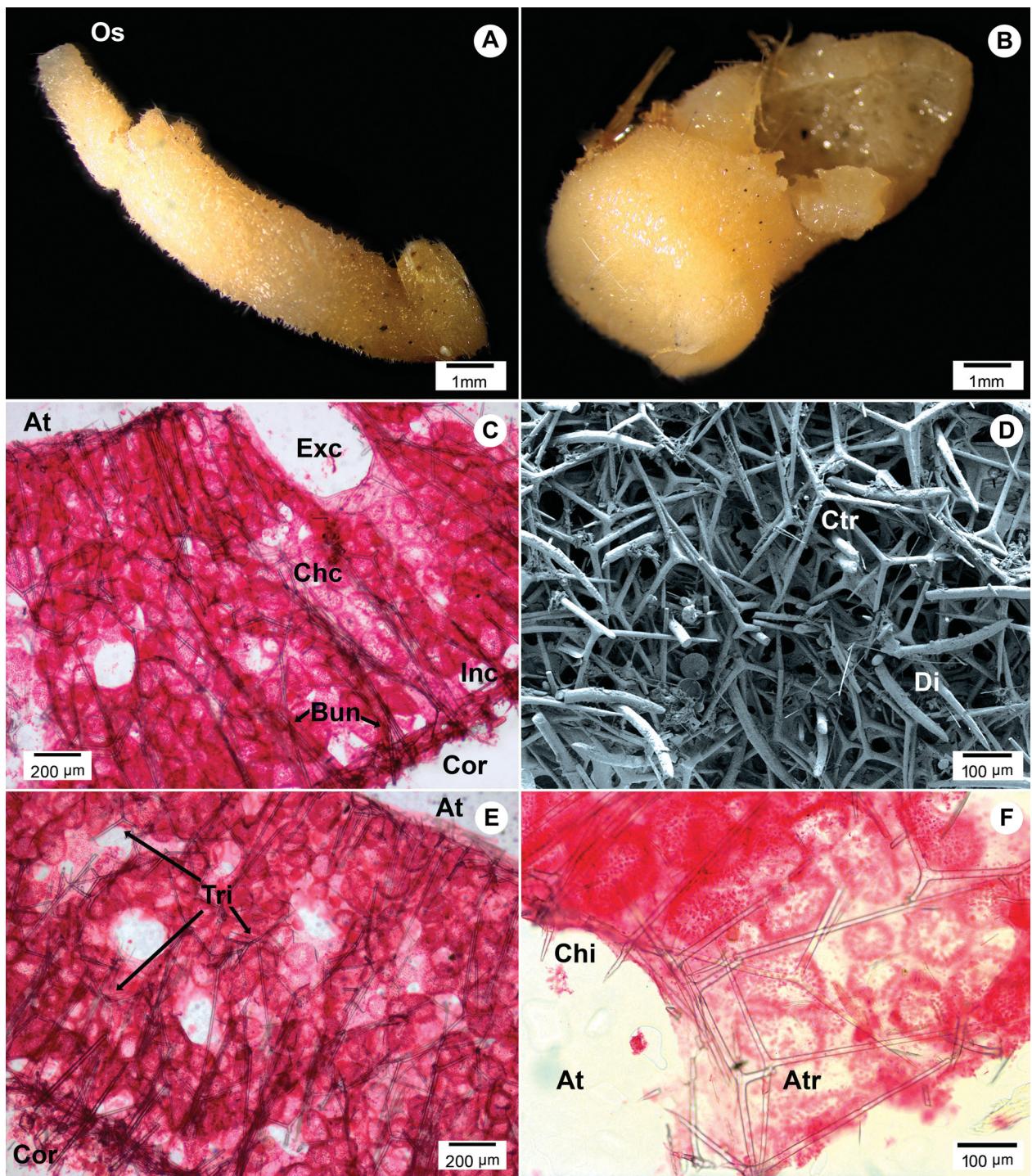


FIGURE 10A–H. *Megapogon rariplius*. **A:** preserved lectotype BMNH-1907.8.6.139. **B:** preserved of additional material BMNH-1907.8.6.140. **C:** histological section including cortical layer, choanosome and atrial cavity. **D:** SEM image of cortical layer. **E–F:** histological sections including cortical layer, choanosome and atrial cavity. **Abbreviations:** At = atrial cavity; Atr = atrial triactines; Bun = bundles of trichoxeas; Di = diactines; Chc = choanocyte chambers; Chi = chiactines; Cor = cortical layer/cortex; Ctr = cortical triactines; Exc = exhalant cavity; Inc = inhalant cavity; Os = osculum; Tric = trichoxeas.

Distribution and depth. *M. rariplius* was found around Winter Quarters Bay, in shallow waters (Jenkin 1908).

Molecular identification. Not available.

Remarks. The three specimens examined here were the same used by Jenkin (1908) to describe the species, and those labelled as cotype should now be considered as paralectotype (recommendation 74F of the ICZN).

After re-examining the material of *M. rariplius*, we found that the choanosomal organization can be unambigu-

ously diagnosed, because in these specimens the choanoskeleton looks like “articulate” due to the layer of triactines present in the choanosome. According to Jenkin (1908), the “dermal cortex” is formed of a thick layer of irregularly scattered triactines. However, an articulated skeleton is defined as “choanoskeleton composed of several rows of similar spicules”, while inarticulate is “choanoskeleton composed only of the unpaired rays of subatrial spicules... without specific spicules of the choanoskeleton” (Boury-Esnault & Rützler 1997). Based on these descriptions, the choanoskeleton of *M. raripilus* should not be considered articulated, because the triactines present in the choanosome are not well-organized in rows, and they are the same type of triactines found in the cortical skeleton. However, the skeleton is not completely inarticulated neither, and thus we define it as “semi-articulated”. The differences observed in the skeleton organization can be associated with the body wall thickness and the volume of the sponges, as it has been observed by Lanna *et al.* (2017) in the species *Paraleucilla magna* where they found that variability in the skeleton organization is mainly influenced by these two morphological traits.

According to Jenkin (1908), *M. raripilus* present a third type of diactines from the body wall, which he described as small and irregular diactines with a “set-over” often in the middle of their length, and the size is about 350 µm x 20 µm. However, we considered that this kind of spicules is the same as diactines found in the cortical skeleton, because there is not distinction between sizes, and based on the figure presented by Jenkin, they look similar.

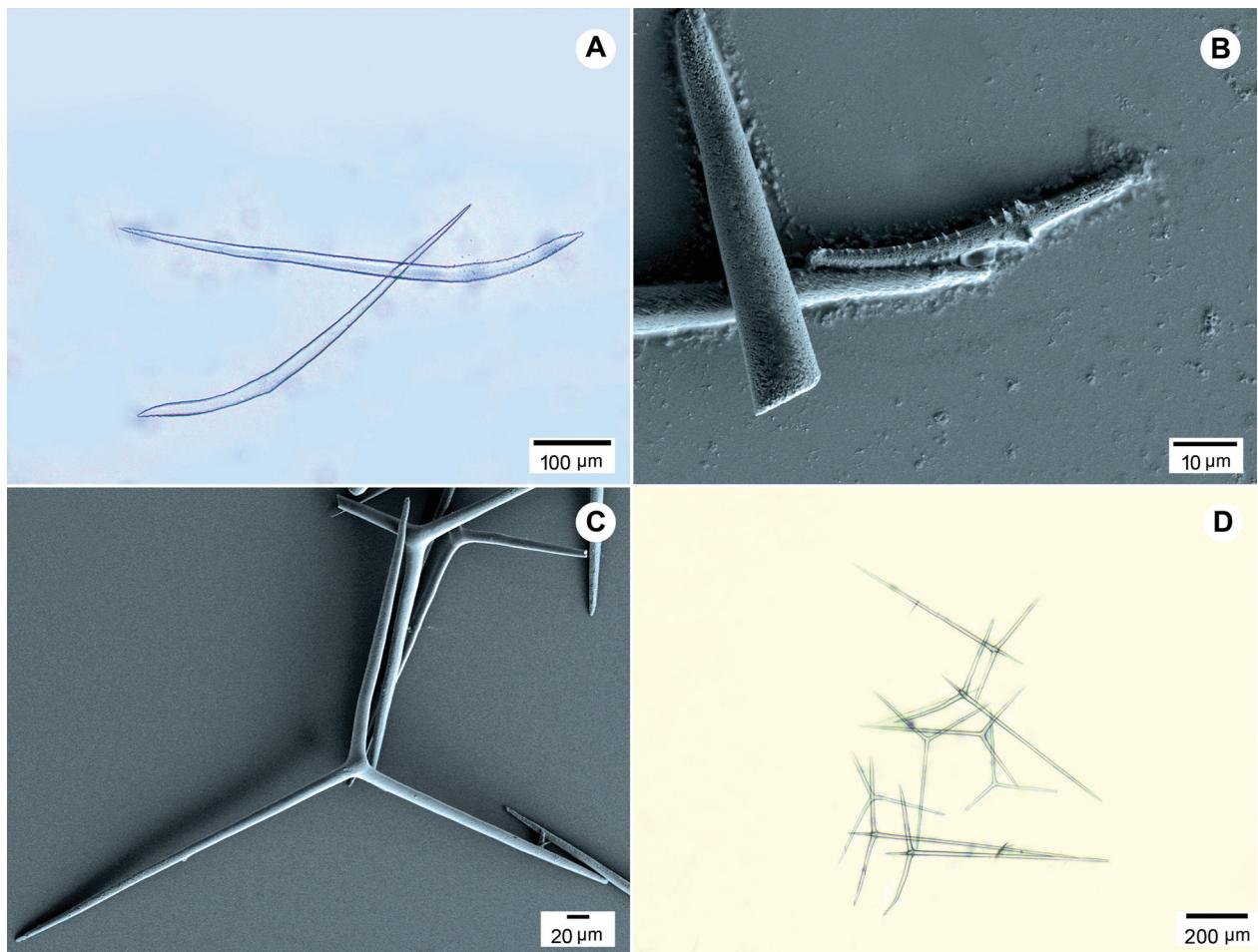


FIGURE 11A–D: Spicules of *Megapogon raripilus*. **A:** diactines. **B:** microdiactine. **C:** cortical triactines. **D:** chiaxines.

Megapogon schiaparellii sp. nov.

(Figs 12A–F, 13A–D; Table 10)

Diagnosis. *Megapogon* with sylleibid aquiferous system. Cortical skeleton is composed of sagittal triactines, trichoxeas and two types of diactines positioned perpendicularly. Spined microdiactines present scattered in the choanoskeleton and atrial skeleton.

Type locality. Tethys Bay, Antarctic.

Synonym and citations. *M. raripilus*, Alvizu et al. 2018, p. 282; *M. raripilus*, Ghiglione et al. 2018, p. 149.

Material examined. **Holotype:** MNA-08193 (complete specimen), PNRA XVII Exp 01/02, Grab 18, 11.01.2002, Northwest Basin, 530 m depth ($72^{\circ}51'41.4''S$ $171^{\circ}05'13.8''E$), Leg. Remia Alessandro & Oliverio Marco. **Paratype:** MNA-07813 (complete specimen), PNRA XXVIII Expedition 12/13, Dredge 6, collection date 15.01.2013, Caletta, 146 m depth ($74^{\circ}45'43.5''S$ $64^{\circ}05'46.4''E$), Leg. Stefano Schiaparelli. **Paratype:** MNA-02762 (complete specimen), PNRA XXV Expedition 09/10, Dive 5, collection date 13.12.2009. Tethys Bay “zecca”, 23 m depth ($74^{\circ}41'25.0''S$ $164^{\circ}06'09.2''E$), Leg. Stefano Schiaparelli.

Etymology. Named after the Dr. Stefano Schiaparelli from Italian National Antarctic Museum, in Genoa Italy, who organized the collection of the material.

Morphology. Cylindrical sponge, with an apical osculum without a well-developed fringe. Surface minutely hispid due to projecting diactines and trichoxeas (Fig 12A). Aquiferous system sylleibid formed by choanocyte chambers more or less rounded (Fig 12B). The holotype size (MNA-08193) is 17.5 mm long and 9 mm wide. The paratypes size are 25.3 mm long and 5.3 mm wide (MNA-02762) and 13.1 mm long and 3.3 mm wide (MNA-07813) is 13.1 mm long and 3.3 mm wide.

Skeleton. Cortical skeleton composed of sagittal tangential triactines, trichoxeas and two types of diactines positioned perpendicularly (Figs 12C–D). The trichoxeas are arranged in bundles which penetrate the choanosome but do not reach the atrium (Fig 12D). The choanoskeleton is inarticulated. Small and spined microdiactines are found around the choanocyte chambers and scattered in the atrial skeleton (Figs 12E–F). The atrial skeleton is mainly supported by the paired actines of chiactines with the unpaired actines pointing towards the cortex, and the apical actines crossing through the atrial wall into the atrium. Sagittal triactines are irregularly scattered in the atrial skeleton (Fig 12D). The oscular margin is composed of the same cortical diactines I and long trichoxeas.

Spicules. *Diactines I:* large projecting, curved towards the distal end and with blunt tip. The proximal end is thinner and sharply pointed (Fig 13A). Size: $494 \pm 101.2 \mu\text{m}$ length, $16.4 \pm 4.2 \mu\text{m}$ width (Table 10).

Diactines II: cortical diactines smaller than diactines I, and slightly spined. The ring on the “set-over” can be less pronounced (Fig 13B). This type of diactines is also found in the trichoxeas bundles that cross the choanosome. Size: $151.1 \pm 15.1 \mu\text{m}$ length, $5.6 \pm 0.8 \mu\text{m}$ width (Table 10).

Microdiactines: minute, slightly bent, strongly spined and sharply pointed (Fig 12F). Size: $71.1 \pm 8.7 \mu\text{m}$ length, $3.9 \pm 0.9 \mu\text{m}$ width (Table 10).

TABLE 10. Spicule measurements of *Megapogon schiaparellii* sp. nov. (holotype MNA08193).

Spicules	Length (μm)				Width (μm)				n
	Min	Mean	Max	SD	Min	Mean	Max	SD	
Trichoxeas	629.6	742.4	856.7	74.2	3.0	3.8	4.4	0.6	15
Diactines I	269.1	494	640	101.2	8.0	16.4	24.5	4.21	30
Diactines II	114.0	151.0	182.0	15.1	4.3	5.65	6.7	0.81	30
Microdiactines	58.8	71.1	92.0	8.7	2.4	3.94	6.3	0.9	30
Cortical triactines									
Unpaired actine	157.7	205.7	279.3	42.6	7.3	10.5	14.0	1.9	15
Paired actines	128.6	157.6	190.5	21.7	7.0	10.1	13.6	2.4	
Atrial triactines									
Unpaired actine	174.2	335	460.6	84.8	8.3	10.8	13.5	1.3	25
Paired actines	133.7	187.6	232.2	28.6	7.2	10.0	12.7	1.6	
Chiactines									
Unpaired actine	167.5	411.3	655.1	135.6	8.0	12.0	14.6	1.7	25
Paired actines	80.9	195.7	265.4	48.3	8.3	11.9	14.5	1.6	
Apical actine	53.3	78.3	102.6	17.0	7.2	10.2	13.8	1.9	
Oscular tetractines	--	--	--	--	--	--	--	--	--

(--) Measurements not available.

Trichoxeas: long and straight (Fig 12D). Size: $742.4 \pm 74.2 \mu\text{m}$ length, $3.8 \pm 0.6 \mu\text{m}$ width (Table 10).

Cortical triactines: sagittal with unpaired actines longer than the paired ones. The paired actines are bent up-

wards making the unpaired angle rounded (Fig 13C). Size: unpaired actines 205.7 ± 42.6 μm length, 10.5 ± 1.9 μm width; paired actines 157.6 ± 21.7 μm length, 10.1 ± 2.4 μm width (Table 10).

Atrial triactines: “T” shaped with unpaired actines longer than the paired ones. Some atrial triactines have the unpaired angle rounded similar to cortical triactines (Fig 13D). Size: unpaired actines 335 ± 84.8 μm length, 10.8 ± 1.3 μm width; paired actines 187.6 ± 28.6 μm length, 10 ± 1.6 μm width (Table 10).

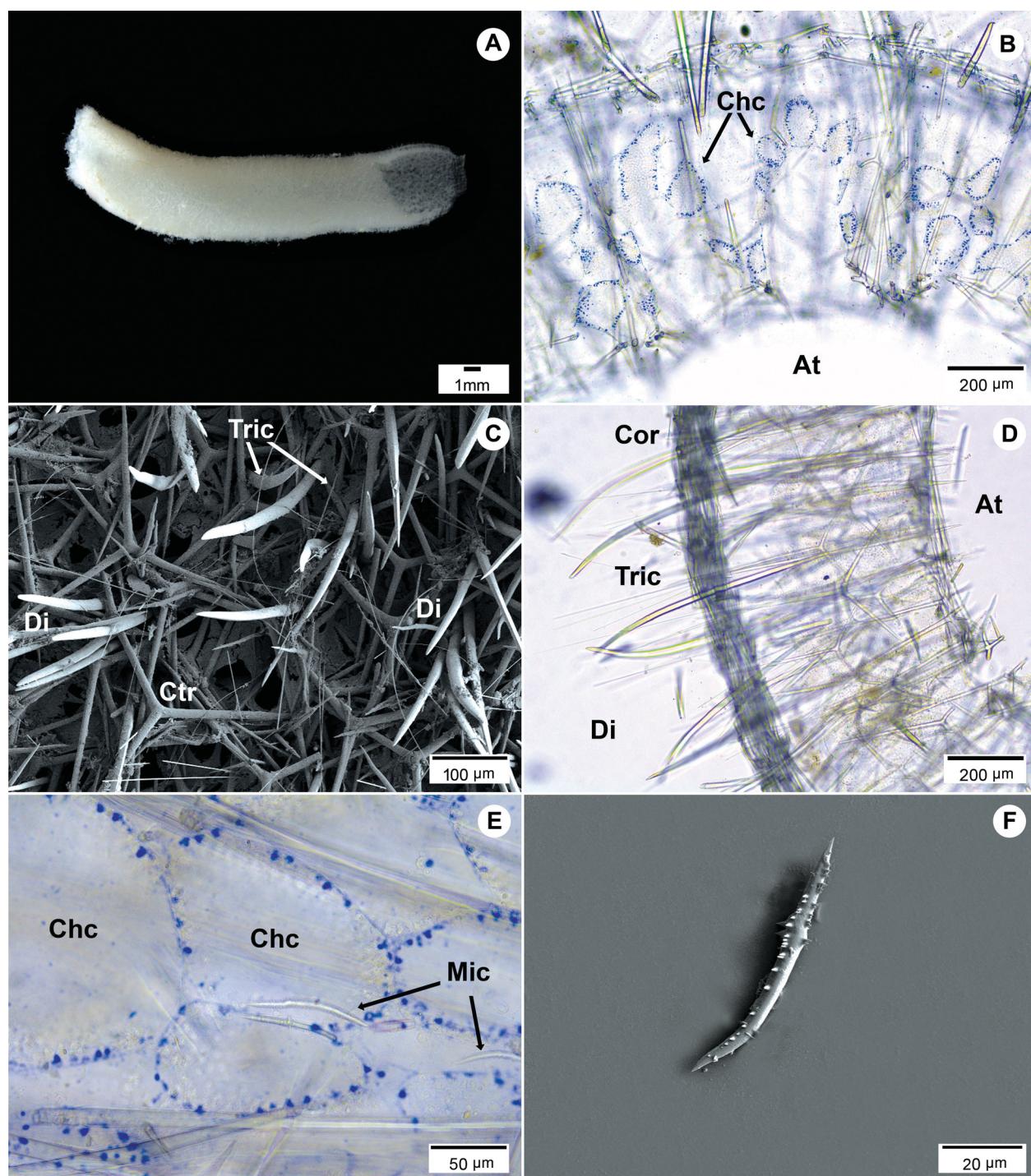


FIGURE 12A–F: *Megapogon schiaparelli* sp. nov. **A:** preserved holotype MNA-02762. **B:** histological section including cortical layer, choanosome and atrial cavity. **C:** SEM image of cortical layer. **D:** histological section including cortical layer, choanosome and atrial cavity. **E:** histological section showing choanocyte chambers. **F:** SEM image of microdiactine. **Abbreviations:** At = atrial cavity; Chc = choanocyte chambers; Cor = cortical layer/cortex; Ctr = cortical triactines; Di = diactines; Mic = microdiactines; Tric = trichoxeas.

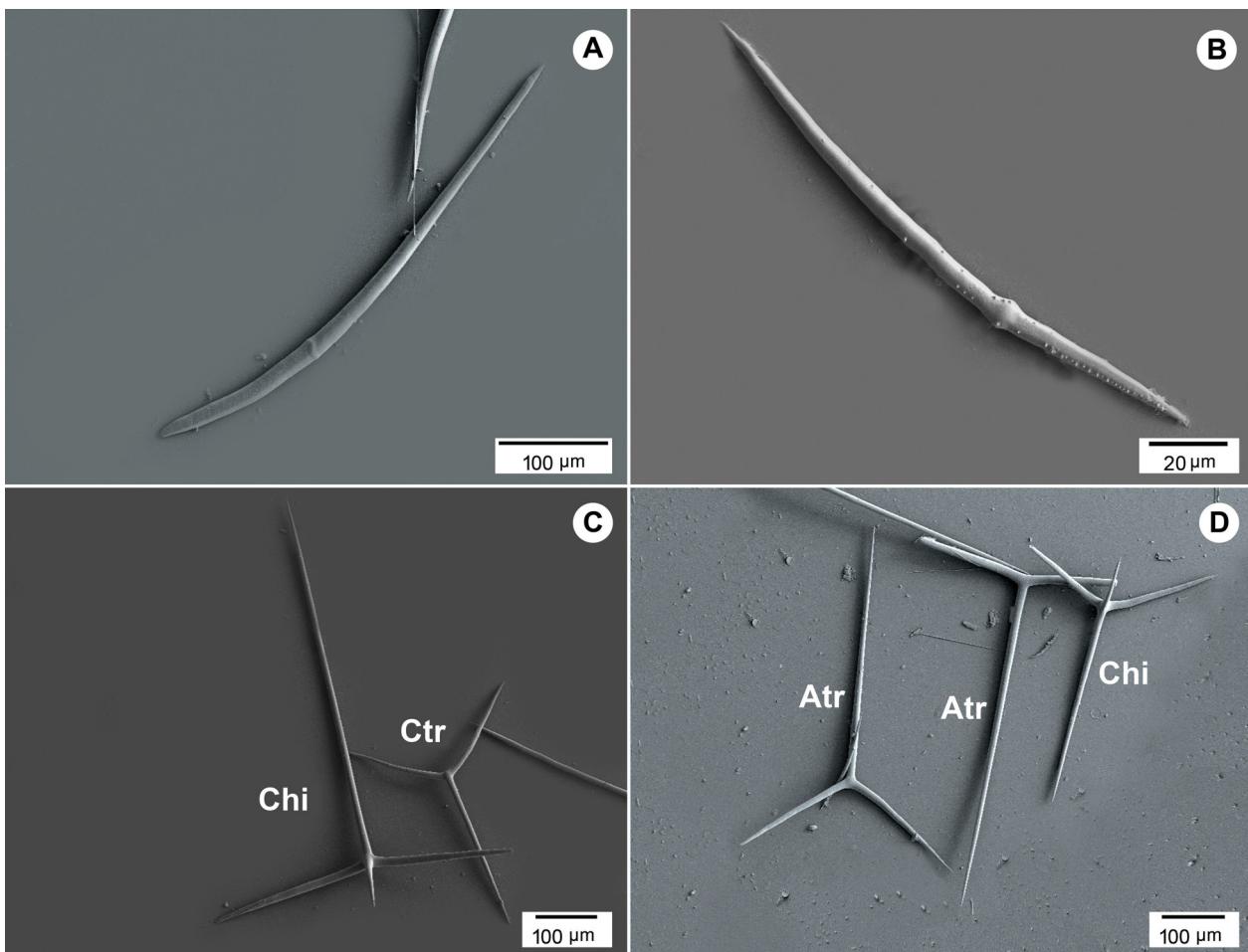


FIGURE 13A–D. SEM images of spicules of *Megapogon schiaparelli* sp. nov. **A:** diactine I. **B:** diactine II. **C–D:** cortical triactines, atrial triactines and chiactines. **Abbreviations:** Atr = atrial triactines; Chi = chiactines; Ctr = cortical triactines.

Chiactines: longer and straight unpaired actines and the paired actines can be straight with the unpaired angle around 180° (Fig. 13C), or slightly bent forming a rounded bend (Fig 13D). Both types can be found in the atrial skeleton and in the oscular region. Size: unpaired actines $411.3 \pm 135.6 \mu\text{m}$ length, $12 \pm 1.7 \mu\text{m}$ width; paired actines $195.7 \pm 48.3 \mu\text{m}$ length, $11.9 \pm 1.6 \mu\text{m}$ width; apical actines $78.3 \pm 17 \mu\text{m}$ length, $10.2 \pm 1.9 \mu\text{m}$ width (Table 10).

Oscular tetractines: not measured because they were difficult to find in the spicule preparations and in the sections.

Distribution and depth. This new species of *Megapogon* has been reported in different localities around the Antarctic, including the ecoregions Ross Sea and East Antarctic Wilkes Land. *Megapogon schiaparelli* sp. nov. also presents a wide depth distribution, from 18 m to 530 m.

Molecular identification. The 28S sequences available in GenBank with the accession numbers MH385273, MH385274 and MH385275, that previously were assigned to *M. raripilus* (Alvizu *et al.* 2018) are now reallocated to the new species *M. schiaparelli*. An additional sequence of 18S rRNA for *M. schiaparelli* sp. nov. was added in GenBank under the accession number MK696125.

Remarks. After re-examination of the type material of *M. raripilus* we found consistent morphological differences between this species and the specimens identified as *M. raripilus* in previous studies (Ghiglione *et al.* 2018, Alvizu *et al.* 2018). The most remarkable difference is the sylleibid aquiferous system found in *M. schiaparelli* sp. nov., while in *M. raripilus* it is leuconoid. The spiculation is also dissimilar, for example the new species presents a type of diactines (type II) that is absent in *M. raripilus*. Based on these morphological characteristics the two species can be easily separated. Therefore, the specimens identified as *M. raripilus* in Alvizu *et al.* (2018) and Ghiglione *et al.* (2018) are reallocated to the new species *M. schiaparelli*.

Megapogon villosus (Jenkin, 1908)

(Figs 14A–F, 15A–D; Table 11)

Original description. Jenkin 1908, p. 37, pl. XXXVI, figs 115–119.

Type locality. Winter Quarters Bay, Antarctic.

Synonym and citations. *Megapogon villosus*, Burton 1929, p. 403; *M. villosus*, Burton 1963, p. 93, 527 (figs 333–334).

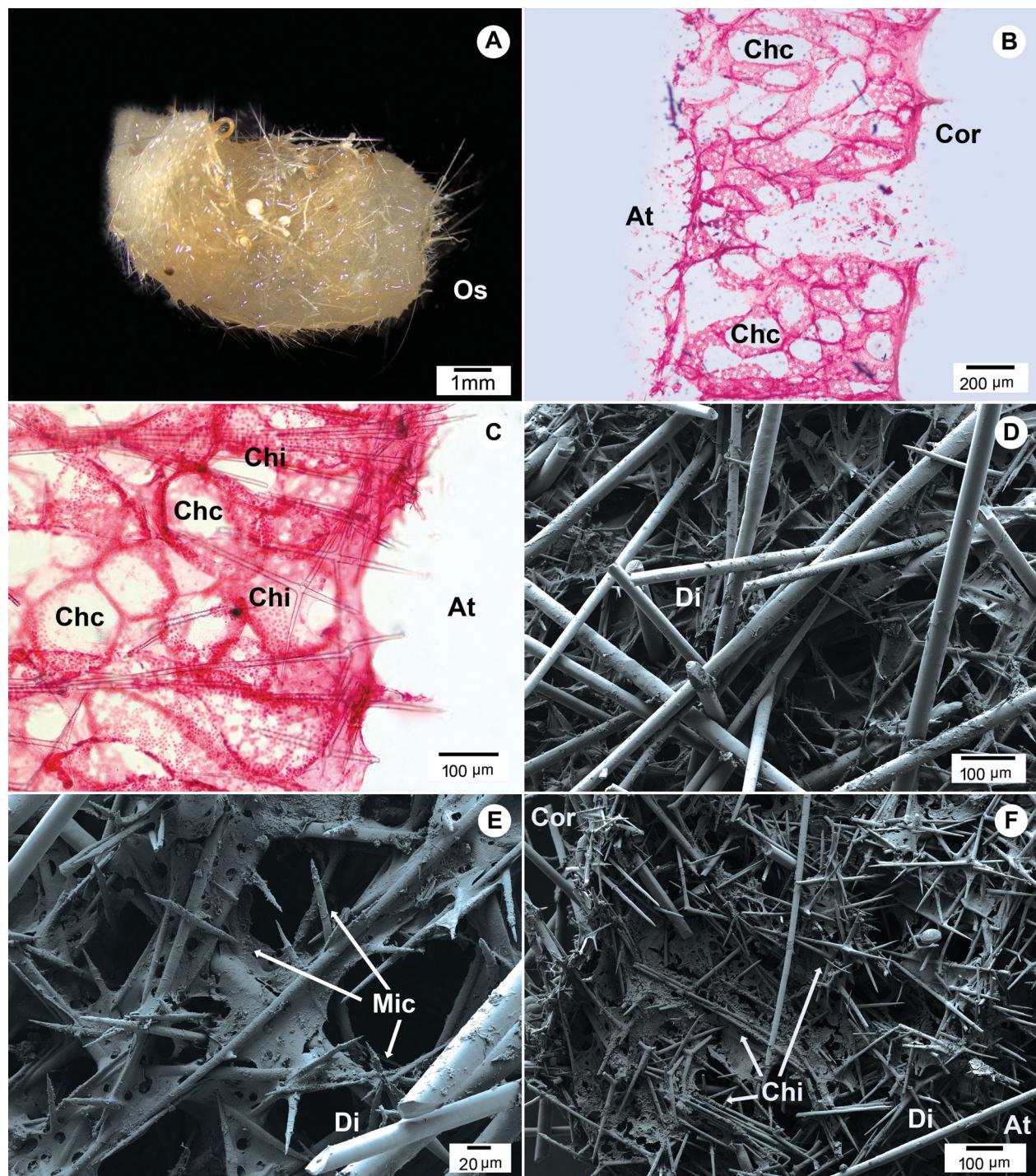


FIGURE 14A–F. *Megapogon villosus*. **A:** preserved cotype BMNH-1907.8.6.151. **B–C:** histological section including cortical layer, choanosome and atrial cavity. **D–E:** SEM images of cortical layer. **F:** SEM image of choanosome section, including cortical layer, choanosome and atrial cavity. **Abbreviations:** At = atrial cavity; Chc = choanocyte chambers; Chi = chiactines; Cor = cortical layer/cortex; Di = diactines; Mic = microdiactines; Os = osculum.

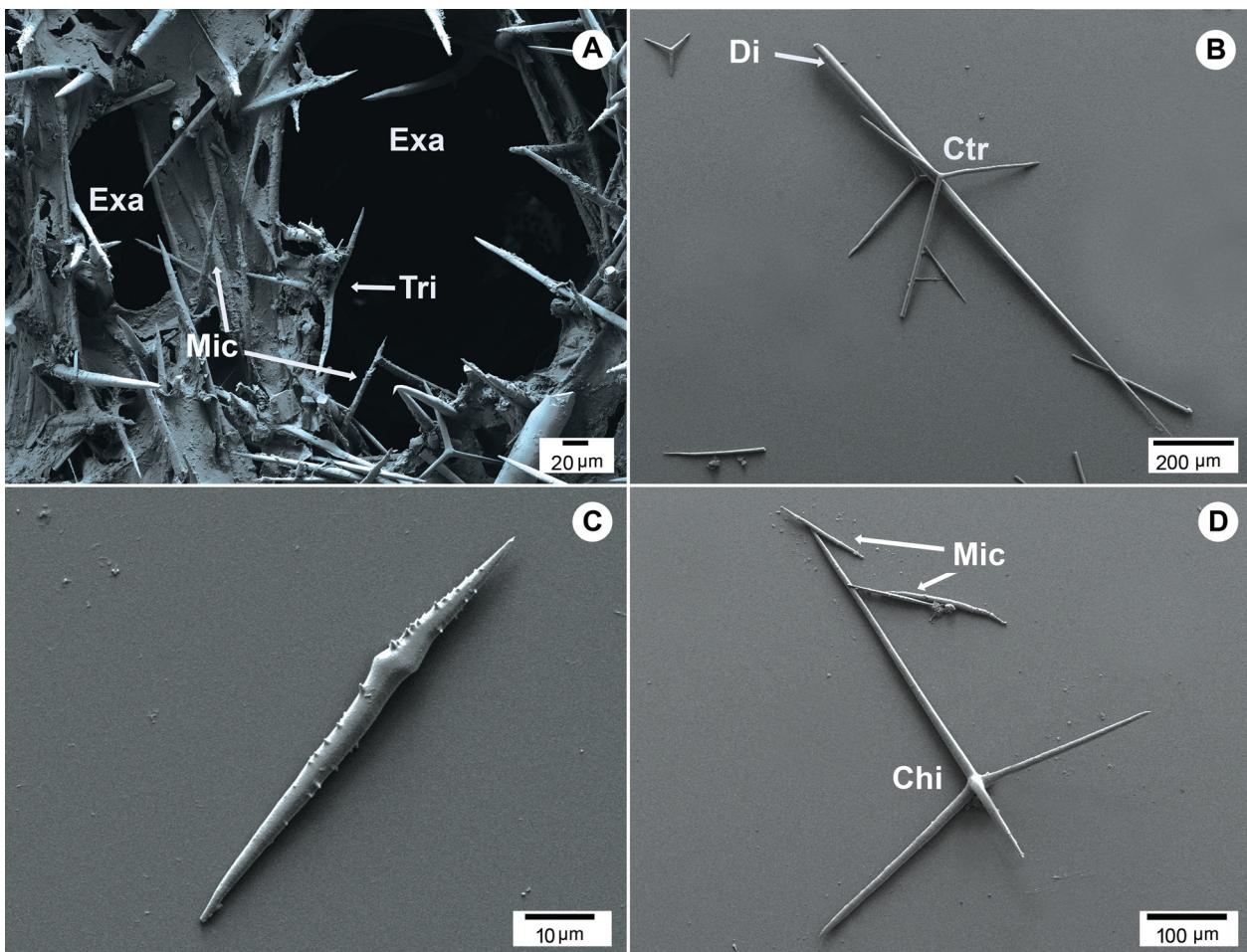


FIGURE 15A–D: *Megapogon villosus*. **A:** SEM image of atrial layer. **B–D:** SEM images of spicules; fragmented diactine and cortical triactines (B), microdiactine (C), chiactine (D). **Abbreviations:** Chi = chiactines; Ctr = cortical triactines; Di= diactines; Mic = microdiactines; Exa = exhalant aperture; Tri = triactines.

Material examined. **Lectotype:** BMNH-1907.8.6.146 (fragments of one specimen and four slides), National Antarctic Expedition (HMS Discovery). **Paralectotype:** BMNH-1907.8.6.151 (one fragmented specimen and one slide), National Antarctic Expedition (HMS Discovery). **Paralectotype:** BMNH-1907.8.6.153 (one fragmented specimen and one slide), Winter Quarters Bay, National Antarctic Expedition (HMS Discovery). **Paralectotype:** BMNH-1907.8.6.152: one slide, National Antarctic Expedition (HMS Discovery).

Morphology. Vase-shaped sponge, without a well-developed oscular fringe. Surface strongly hispid due to a dense mat of very long diactines, which point down towards the base of the sponge (Fig 14A). The lectotype is 14.6 mm long, 3.6–7.8 mm wide, and 0.8–1.1 mm thick. Colour beige in ethanol. Aquiferous system seems to be leucocnoid with rounded choanocyte chambers scattered in the mesohyl (Figs 14B–C).

Skeleton. Cortical skeleton composed of tangentially arranged triactines, and a dense mat of long diactines that cross the surface (Fig 14D). Smaller and spiny microdiactines are placed around the inhalant pores (Fig 14E). In the choanoskeleton there are chiactines and triactines with their unpaired actines that can project through the surface (Figs 14C–F). The atrial skeleton comprises chiactines with their long unpaired actines pointing towards, and often projecting through the cortex (Figs 14C–F). The atrial wall is supported by the paired actines of the chiactines, and among them some triactines and microdiactines can be found (Fig 15A).

Spicules. Diactines: very long and straight with sharp points. Most of them were broken (Fig 15B, Table 11).

Microdiactines: small and slightly bent diactines. Some smooth, and some with spines. One end lanceolate, and the other hastate (Figs 14E, 15C–D). Size: $105.3 \pm 15.9 \mu\text{m}$ length; $4.5 \pm 1.1 \mu\text{m}$ width (Table 11).

Cortical triactines: alate triactines with straight unpaired actines longer than the paired actines. Paired actines nearly straight (Fig 15B). Size: unpaired actines $289.6 \pm 188.5 \mu\text{m}$ length, $8.5 \pm 2.2 \mu\text{m}$ width; paired actines $158.5 \pm 82.2 \mu\text{m}$ length, $8.4 \pm 2.4 \mu\text{m}$ width (Table 11).

Chiactines: unpaired actines straight and longer than the paired actines. Apical actine straight, slightly slender, and sharply pointed (Fig 15D). Size: unpaired actines $466.8 \pm 80.4 \mu\text{m}$ length, $11.9 \pm 2.9 \mu\text{m}$ width; paired actines $199.0 \pm 69.1 \mu\text{m}$ length, $10.7 \pm 1.8 \mu\text{m}$ width; apical actines $121.3 \pm 33.0 \mu\text{m}$ length, $10.4 \pm 2.0 \mu\text{m}$ width (Table 11).

Distribution and depth. All the specimens included in Jenkin (1908), were taken around Winter Quarters Bay, and most of them from shallow waters.

Molecular identification. Not available.

Remarks. Among the species of *Megapogon* described from the Antarctic, *M. villosus* is the only one that presents a strongly hispid surface due to the presence of very long diactines. These diactines were difficult to measure because they were broken but based on the original description (Jenkin 1908), they can reach up to $1500 \mu\text{m}$ length, which is as long as in *M. crucifer* from the Azores.

The four specimens examined here were the same used by Jenkin (1908) to describe the species, and those specimens labelled as cotype are now erected as paralectotype (recommendation 74F of the ICZN).

The oscular region could not be examined, but according to Jenkin (1908), the osculum is at the end of a collar built up by tetractines laying tangentially on the inside, with their unpaired actines pointing downwards and the apical actines projecting into the atrium. On the outside there are also tangentially arranged triactines and a few special diactines placed horizontally (Jenkin 1908). These horizontal diactines have not been mentioned before in any of the *Megapogon* species. However, we would need more material where the oscular area is included, to examine this character in greater detail.

TABLE 11. Spicule measurements of *Megapogon villosus* (lectotype BMNH-1907.8.6.146). Measurements from the original description by Jenkin (1908) are included below.

Spicules	BMNH-1907.8.6.146									
	Length (μm)				Width (μm)				SD	n
	Min	Mean	Max	SD	Min	Mean	Max	SD		
Diactines*	986.0	--	--	--	25.4	--	--	--	1	
Microdiactines	74.5	105.3	143.0	15.9	2.5	4.5	7.1	1.1	25	
Cortical triactines										
Unpaired actines	54.7	289.6	547.3	188.5	4.9	8.5	12.5	2.2	15	
Paired actines	38.4	158.5	261.6	82.2	5.0	8.4	12.3	2.4		
Chiactines										
Unpaired actines**	336.9	466.8	541.8	80.4	8.7	11.9	15.8	2.9	6	
Paired actines	124.8	199.0	312.3	69.1	8.8	10.7	12.6	1.8		
Apical actines	83.9	121.3	153.4	33.0	7.7	10.4	12.1	2.0		

Measurements from the original description (Jenkin 1908)

	Length (μm)	Width (μm)
Diactines I	1500	36-43
Diactines II***	80-160	6
Cortical triactines		
Unpaired actines	220-700	10-16
Paired actines	170-300	12-14
Chiactines		
Unpaired actines	600-1120	10-16
Paired actines	240	13
Apical actines	140-220	8-16

(*) Most of the diactines were broken.

(**) Unpaired actines broken or not completely visible in the slides.

(***) Diactines II = Microdiactines.

***Megapogon pollicaris* (Jenkin, 1908)**

(Figs 16A–H; Table 12)

Original description. Jenkin 1908, p. 40, pl. XXXVII and XXXVIII, figs. 125–130.

Type locality. Winter Quarters Bay, Antarctic.

Synonym and citations. *Megapogon pollicaris*, Burton 1963, p. 93.

Material examined. Holotype: BMNH-1907.8.6.135 (one fragment and three slides), Winter Quarters Bay, Antarctic, National Antarctic Expedition (HMS Discovery).

Morphology. There is only one fragment of the holotype. Dark brown coloration because it was fixed in osmic acid (Jenkin 1908). Surface slightly hispid. Oscular region absent in the fragment. Size of the fragment 3.5 mm large, 2.3 mm wide and 0.6 mm thick (Fig 16A). The aquiferous system is leuconoid composed of rounded inhalant cavities under the cortex, and round choanocyte chambers which are scattered in the choanosome (Fig 16B).

Skeleton. Cortical skeleton formed by triactines tangentially placed and large projecting diactines (Fig 16C). Choanoskeleton composed of the unpaired actines of the atrial chiactines, which can project outside the surface (Figs 16D–E). A few triactines can also be present in the choanosome, with the unpaired actines pointing towards the cortical skeleton (Fig 16E). Abundant spined microdiactines are irregularly scattered in the choanosome (Fig 16F). Atrial skeleton made up by chiactines with the paired actines placed tangentially, and the apical actines projecting into the atrial cavity (Fig 16B).

Spicules. Diactines: large and bent towards the distal end which is blunt and thicker than the proximal end (Fig 16G). Size: $506.8 \pm 43.1 \mu\text{m}$ length, $20.0 \pm 3.4 \mu\text{m}$ width (Table 12).

Microdiactines: small, curved and spined. One hastate end and the other sharply pointed (Figs 16F, 16H). Size: $60.1 \pm 4.0 \mu\text{m}$ length, $2.8 \pm 0.5 \mu\text{m}$ width (Table 12).

TABLE 12. Spicule measurements from the holotype of *Megapogon pollicaris* (holotype BMNH-1907.8.6.135). Measurements from the original description by Jenkin (1908) are included below.

Spicule	BMNH-1907.8.6.135								
	Length (μm)				Width (μm)				n
	Min	Mean	Max	SD	Min	Mean	Max	SD	
Diactines	415.3	506.8	555.0	43.1	13.3	20.0	25.0	3.4	8
Microdiactines	53.4	60.1	64.7	4.0	2.1	2.8	3.6	0.5	8
Cortical triactines									
Unpaired actines	207.4	289.5	464.4	64.0	7.5	11.5	15.5	2.1	20
Paired actines	139.6	182.2	227.0	22.7	6.5	10.8	18.1	2.7	
Chiactines									
Unpaired actines	220.7	338.9	620.4	106.8	10.2	12.9	16.4	2.1	12
Paired actines	175.0	204.5	244.0	22.6	9.5	12.7	16.8	2.3	
Apical actines	63.1	81.2	98.7	13.8	8.1	10.0	12.9	1.4	

Measurements from the original description (Jenkin 1908)

	Length (μm)	Width (μm)
Diactines I	460–640	24–25
Diactines II*	50–60	2–3.1
Cortical triactines		
Unpaired actines	130–330	8–15
Paired actines	90–320	8–14
Chiactines		
Unpaired actines	460–580	14–18
Paired actines	160–280	14–16
Apical actines	100	12

(*) Diactines II = Microdiactines.

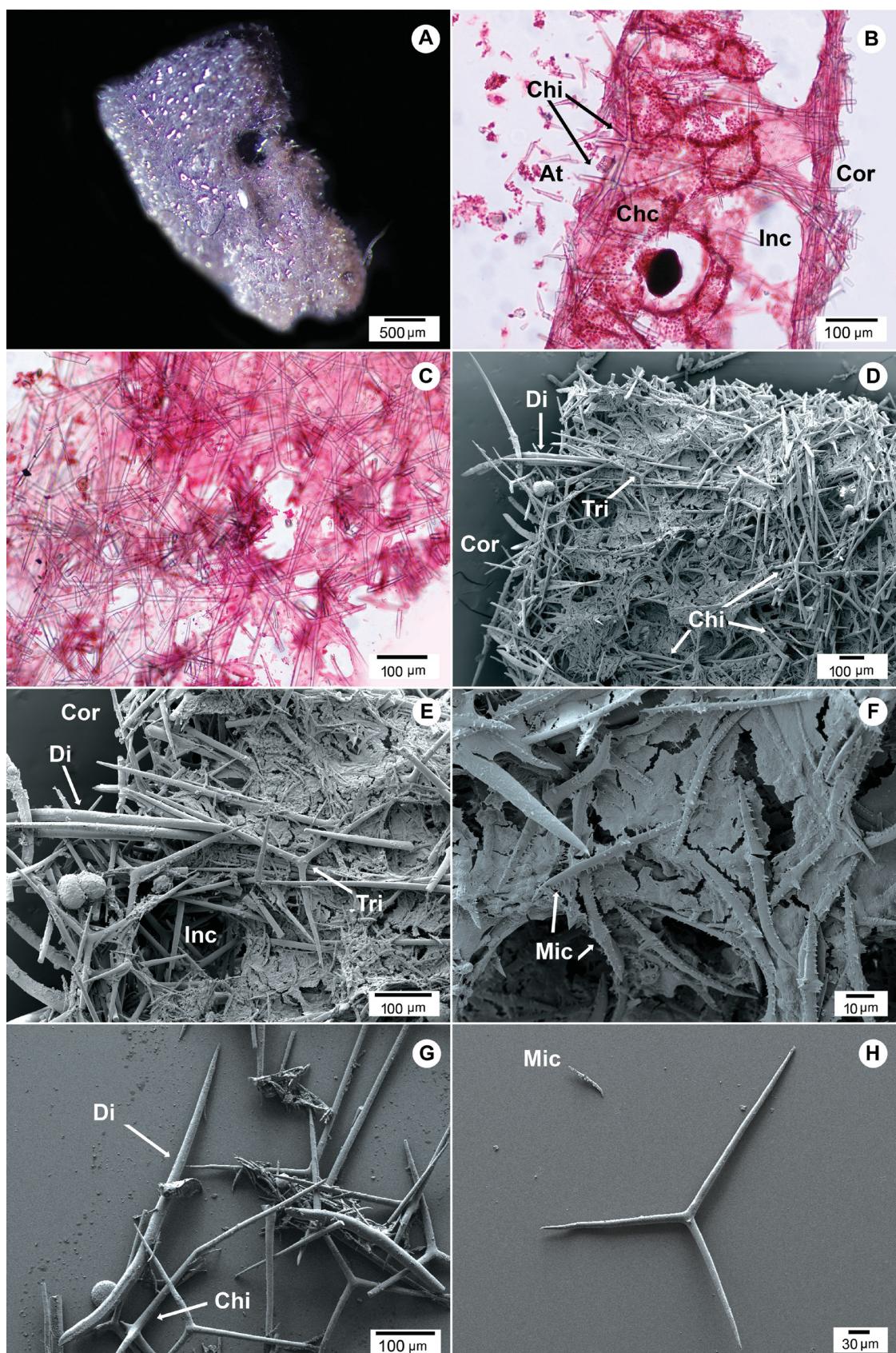


FIGURE 16A–H. *Megapogon pollicaris*. **A:** preserved holotype BMNH-1907.8.6.135. **B:** histological section including cortical layer, choanosome and atrial cavity. **C:** LM image of cortical layer. **D–F:** SEM images of the choanosome including cortical layer, choanosome and atrial cavity. **G–H:** SEM images of spicules: diactines, triactines and chiactines (**G**), microdiactines and triactine (**H**). **Abbreviations:** At = atrial cavity; Chc = choanocyte chambers; Chi = chiactines; Cor = cortical layer/cortex; Ctr = cortical triactines; Di = diactines; Mic = microdiactines; Inc = inhalant cavity; Tri = triactines.

Cortical triactines: sagittal with straight and long unpaired actines. Paired actines shorter, nearly straight or slightly irregular (Fig 16H). Size: unpaired actines 289.5 ± 64.0 µm length, 11.5 ± 2.1 µm width; paired actines 182.2 ± 22.7 µm length, 10.8 ± 2.7 µm width (Table 12).

Chiactines: unpaired actines straight and longer than the paired ones. Apical actines short and acerate (Figs 16B, 16G). Size: unpaired actines 338.9 ± 106.8 µm length, 12.9 ± 2.1 µm width; paired actines 204.5 ± 22.6 µm length, 12.7 ± 2.3 µm width; apical actines 81.2 ± 13.8 µm length, 10.0 ± 1.4 µm width (Table 12).

Distribution and depth. Specimens taken around Winter Quarters Bay, Antarctic shallow waters (Jenkin 1908).

Molecular identification. Not available.

Remarks. After re-examining the holotype of *M. pollicaris* (BMNH-1907.8.6.135), we found that this species presents similarities with *M. raripilus*, for example, shape of the diactines and microdiactines, presence of triactines in the atrial skeleton, and size of the spicules. Also, according to Jenkin (1908), *M. pollicaris* has an oscular collar built up in a similar way as in other species of *Megapogon* and *Achramorpha*, i.e. with tetractines and triactines with the unpaired actines pointing downwards, but without an oscular fringe as in *M. raripilus*. However, these two species show some differences; microdiactines are more abundant in *M. pollicaris*, diactines are slightly longer in *M. raripilus* (300–800 µm), and absence of trichoxeas in the cortical skeleton of *M. pollicaris*. However, it has been suggested that trichoxeas are not very reliable in differentiating species, e.g. in the genera *Leucandra* (Rapp 2015) and *Clathrina* (Azevedo *et al.* 2017). The aquiferous system in both species is leuconoid with rounded choanocyte chambers, which are bigger in *M. raripilus* (131.2 ± 31.7 µm diameter) µm than in *M. pollicaris* (109.2 ± 12.5 µm diameter). Also, the rounded inhalant cavities are also slightly bigger in *M. raripilus* (146.8 ± 36.4 µm diameter) µm than in *M. pollicaris* (141.9 ± 33.8 µm diameter), but these are more marked and numerous in *M. pollicaris*.

Based on our observations, we suspect that *M. raripilus* and *M. pollicaris* are different but closely related species, however, to be able to have a confident decision, it is necessary to have new and larger specimens of *M. pollicaris*, for a better examination and for molecular evidence.

Megapogon crispatus Jenkin, 1908

(Figs 17A–H; Table 13)

Original description. Jenkin 1908, p. 41, pl. XXVII and XXXVIII, figs 131–136.

Type locality. Winter Quarters Bay, Antarctic.

Synonym and citations. *Megapogon crispatus*, Brønsted 1931, p. 32; *M. crispatus*, Burton 1963, p. 93.

Material examined. Holotype: BMNH-1907.8.6.131, (two specimens and slides). Winter Quarters, Antarctic, National Antarctic Expedition (HMS Discovery).

Morphology. Vase-shaped without fringe but with a well-developed oscular collar. Colour whitish in ethanol. Surface villose due to long diactines that cross the surface (Fig 17A–B). Size of the fragment 2.4–3.1 mm long, 1.5–1.8 mm wide and 0.1 mm thick. Aquiferous system is leuconoid with spherical choanocyte chambers of similar size than inhalant cavities (Fig 17C).

Skeleton. Skeleton inarticulated and composed of diactines, microdiactines, triactines and chiactines. Tetractines are found only in the oscular area (Figs 17B, 17D). Cortical skeleton composed of tangential triactines (Fig 17E) and of large projecting diactines which are bent towards the proximal end (Figs 17B–E, 17G). Two types of microdiactines with spines are placed irregularly on the surface (Fig 17E). These microdiactines are also present amongst the atrial spicules, and around the choanocyte chambers (Figs 17F). Chiactines and few triactines form the atrial skeleton, with their unpaired actines pointing to the surface, and the paired actines giving support to the atrial wall. Tri- and tetractines of the same size, laid tangentially with the unpaired actines pointing downwards, are forming the oscular collar (Fig 17D). The oscular fringe is mainly composed of slightly shorter diactines, and by diactines similar to those found in the cortical skeleton but longer and thinner. It was not possible to measure the spicules from the oscular region, because they were broken or not easily visible in the sections.

Spicules. Diactines: large and curved towards the distal end which has a knob. Proximal end hastate (Figs 17A–B, 17G). Size: 513.8 ± 168.2 µm length, 15 ± 4 µm width (Table 13).

Microdiactines I: small, straight and with spines. Size: 23.2 ± 4.0 µm length, 1.1 ± 0.2 µm width (Fig 17F; Table 13).

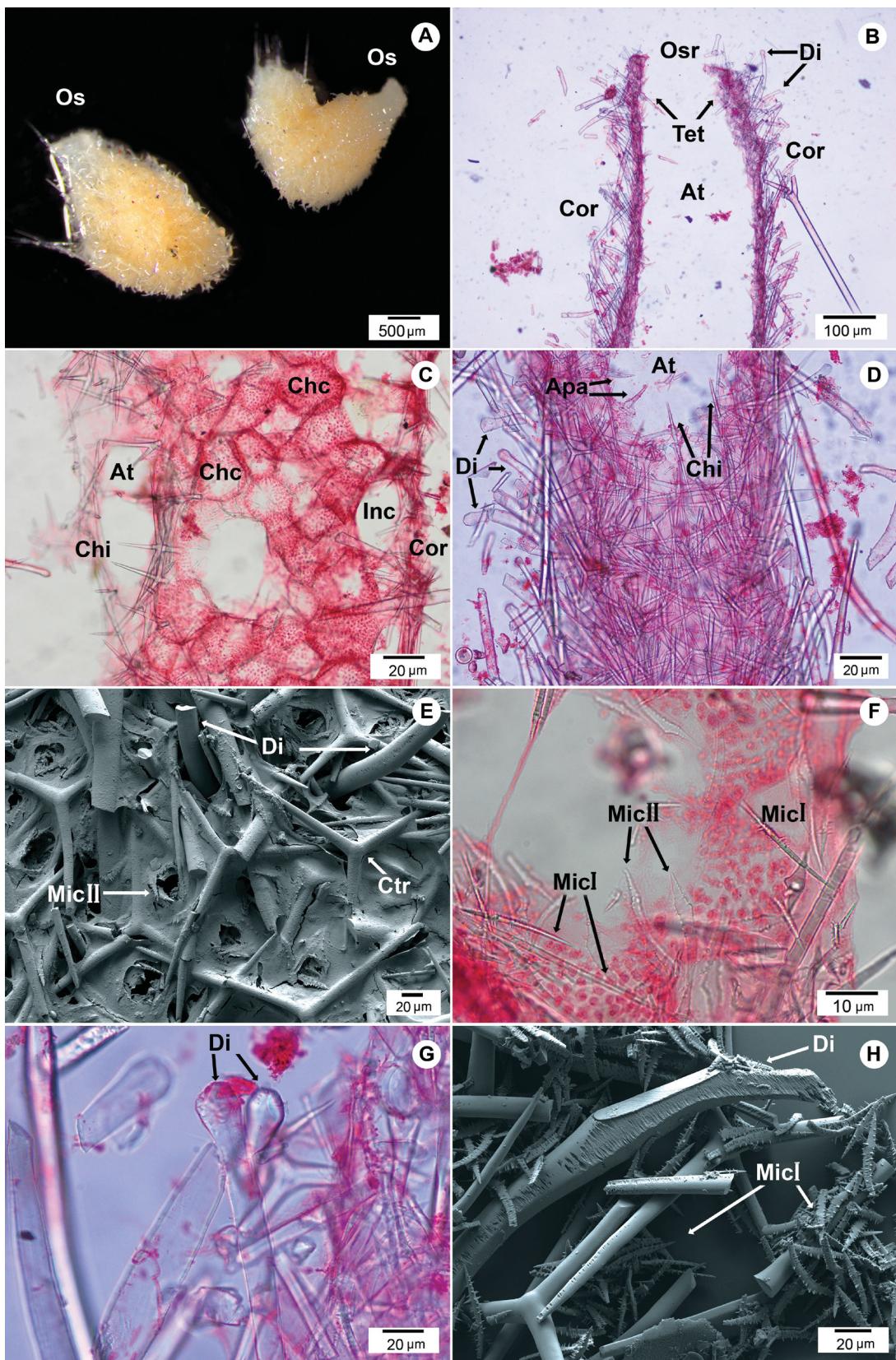


FIGURE 17A–H. *Megapogon crispatus*. **A:** preserved holotype BMNH-1907.8.6.131. **B:** histological section including the oscular region. **C:** histological section including cortical layer, choanosome and atrial cavity. **D:** histological section including cortical layer and oscular region. **E:** SEM image of cortical layer. **F:** histological section of a choanosome chamber. **G–H:** LM and SEM images of diactines, showing details of the distal ends. **Abbreviations:** Apa = apical actines of tetractines; At = atrial cavity; Chc = choanocyte chambers; Chi = chiactines; Cor = cortical layer/cortex; Ctr = cortical triactines; Di = diactines; MicI = microdiactines I; MicII = microdiactines II; Inc = inhalant cavity; Tet = tetractines.

TABLE 13. Spicule measurements from the holotype of *Megapogon crispatus* (holotype BMNH-1907.8.6.131). Measurements from the original description by Jenkin (1908) are included below.

Spicule	BMNH-1907.8.6.131								
	Length (μm)				Width (μm)				
	Min	Mean	Max	SD	Min	Mean	Max	SD	n
Diactines	231.7	513.8	979.4	168.2	7.5	15.0	25.8	4.0	30
Microdiactines I*	18.6	23.2	26.1	4.0	0.9	1.1	1.2	0.2	3
Microdiactines II**	18.7	33.6	54.2	9.4	1.2	3.1	6.7	1.3	20
Cortical triactines									
Unpaired actines	69.2	149.4	308.8	42.7	4.7	9.4	13.6	2.2	30
Paired actines	83.3	149.1	263.8	40.8	4.7	9.0	13.6	2.0	
Chiactines									
Unpaired actines	199.0	289.0	414.9	74.5	6.6	9.7	13.1	2.1	15
Paired actines	108.3	142.4	214.2	28.7	8.6	11.1	14.5	1.6	
Apical actines	39.5	69.4	84.3	13.3	6.4	8.0	9.8	1.0	
Measurements from the original description (Jenkin 1908)									
	Length (μm)				Width (μm)				
Diactines I	550-950				20-28				
Diactines II*	50				1.2				
Diactines III**	55				4-5				
Cortical triactines									
Unpaired actines	110-220				8-12				
Paired actines									
Atrial triactines									
Unpaired actines	400-500				12				
Paired actines									
Chiactines									
Unpaired actines	300-500				11-12				
Paired actines	120-160				10-12				
Apical actines	100				8				
Oscular diactines I***	330				20				
Oscular diactines II†	100-200				1-3				
Oscular small tetractines									
Unpaired actines	50-90				6				
Paired actines	30-60				5				
Apical actines	20				5				
Oscular large tetractines									
Unpaired actines	200				7-9				
Paired actines	110-130				9				
Apical actines	50-70				10-13				

(*) Diactines II = Microdiactines I. Straight, refringent and thin.

(**) Diactines III = Microdiactines II. Curved, hastate and thicker.

(***) Same as diactines I but smaller.

(†) Similar to microdiactines I but longer and thinner.

Microdiactines II: small, curved, hastate and strongly spined diactines. Size: $33.6 \pm 9.4 \mu\text{m}$ length, $3.1 \pm 1.3 \mu\text{m}$ width (Figs 17E–17F, 17H; Table 13).

Cortical triactines: almost regular with straight and sharply pointed actines. Size: unpaired actines $149.4 \pm 42.7 \mu\text{m}$ length, $9.4 \pm 2.2 \mu\text{m}$ width; paired actines $149.1 \pm 40.8 \mu\text{m}$ length, $9.0 \pm 2.0 \mu\text{m}$ width (Fig 17E; Table 13).

Atrial triactines: alate with straight and sharply pointed actines. Measurements not available (see Table 13).

Chiactines: Size: unpaired actines 289.0 ± 74.5 μm length, 9.7 ± 2.1 μm width; paired actines 142.4 ± 28.7 μm length, 11.1 ± 1.6 μm width; apical actines 69.4 ± 13.3 μm length, 8.0 ± 1.0 μm width (Fig 17C; Table 13).

Distribution and depth. The species has been found in shallow waters, in two different localities around the Antarctic; stations Winter Quarters (Jenkin 1908) and Gauss-station (Brønsted 1931).

Molecular identification. Not available.

Remarks. *M. crispatus* has a characteristic surface due to the curved diactines, which also present a distinctive shape with a knob on the distal end. This character seems to be constant because both specimens examined present the same type of diactines in the cortex. Also, the presence of a second type of microdiactines with spines is also characteristic of the species and has not been reported in other *Megapogon* spp. Jenkin (1908) also described the spicules found in the oscular region: two categories of diactines which are similar to the cortical diactines I and II; and two size categories of tetractines. However, we could not measure the spicules of the oscular region because they were difficult to find in the slides and sections.

Genus *Sarsinella* gen. nov.

Diagnosis. Achramorphidae with syconoid aquiferous system and articulated skeleton composed of several rows of sagittal tetractines with short and conical apical actines, which are pointing to the atrium.

Etymology. Named after the father and son Michael Sars and Georg Ossian Sars for their pioneering work exploring the deep Norwegian Sea.

Type species. *Sarsinella karasikensis* sp. nov.

Sarsinella karasikensis sp. nov.

(Figs 18A–H, 19A–H, 20A–F; Table 14)

Diagnosis. *Sarsinella* with strongly villous surface due to very long protruding diactines and trichoxeas, which are organized in tufts. Well-developed oscular fringe, which is formed by long and straight trichoxeas. Articulated skeleton composed of several rows of tetractines.

Type locality. Arctic Mid Ocean Ridge.

Material examined. Holotype: ZMBN-127212, Arctic Mid Ocean Ridge, G.O. Sars 2016, St. GS16-ROV4, Protocol 18, 652–1314 m depth ($73^{\circ}47.28'N$, $07^{\circ}35.11'E$). **Paratype:** ZMBN-127210, Karasik Seamount, Gakkel Ridge, Polarstern 2016, ps101/200#3, 684 m depth ($86^{\circ}51.49'N$, $061^{\circ}35.76'E$). **Paratype:** ZMBN-127211, Arctic Mid Ocean Ridge, St no. GS16-BC1, Protocol #3, 773 m depth ($73^{\circ}48.705'N$, $07^{\circ}30.838'E$). **Paratype:** ZMBN-127213, Karasik Seamount, Gakkel Ridge, Polarstern 2016, ps101/200 #2, 684 m depth, ($86^{\circ}51.49'N$, $061^{\circ}35.76'E$). **Paratype:** ZMBN-127214, Karasik Seamount, Gakkel Ridge, Polarstern 2016, ps101/200 #1, 684 m depth, ($86^{\circ}51.49'N$, $061^{\circ}35.76'E$).

Etymology. Named after the locality Karasik Seamount on the Gakkel Ridge where most of the paratypes were found.

Morphology. Sponge vase-shaped, broadest at mid-height, and with one apical osculum with well-developed fringe. Surface strongly villous due to very long diactines and trichoxeas that are protruding the surface (Fig 18A). The size of the sponge is 2–4 cm height, and 0.5–2 cm width. The thickness of the sponge wall is 607.1–1256.2 μm . Colour in life and in ethanol is similar, white-brownish due to sediment trapped on the surface. Aquiferous system syconoid with elongated choanocyte chambers that are completely free, with sizes ranging from 724.3 to 1238.1 μm length and from 133.5 to 227.4 μm width (Fig 18B).

Skeleton. Cortical skeleton composed of two types of triactines placed tangentially, and diactines with small spines which are scattered around the inhalant pores (Fig 18C). Fairly long diactines and trichoxeas organized in tufts are also part of the cortical skeleton (Figs 18D–E). Choanoskeleton articulated with several rows of tetractines (Fig 18F). These tubar tetractines are placed with the unpaired actines towards the cortex, paired actines adjacent to the atrial wall, and apical actines straight and projecting into the atrial cavity (Figs 18G–H). Atrial skeleton built by two kinds of chiactines, which are placed as the tubar tetractines (Figs 18F, 18H). Oscular collar composed of tetractines and triactines, and the oscular fringe is well-developed, and is formed by long and straight trichoxeas (Fig 19A).

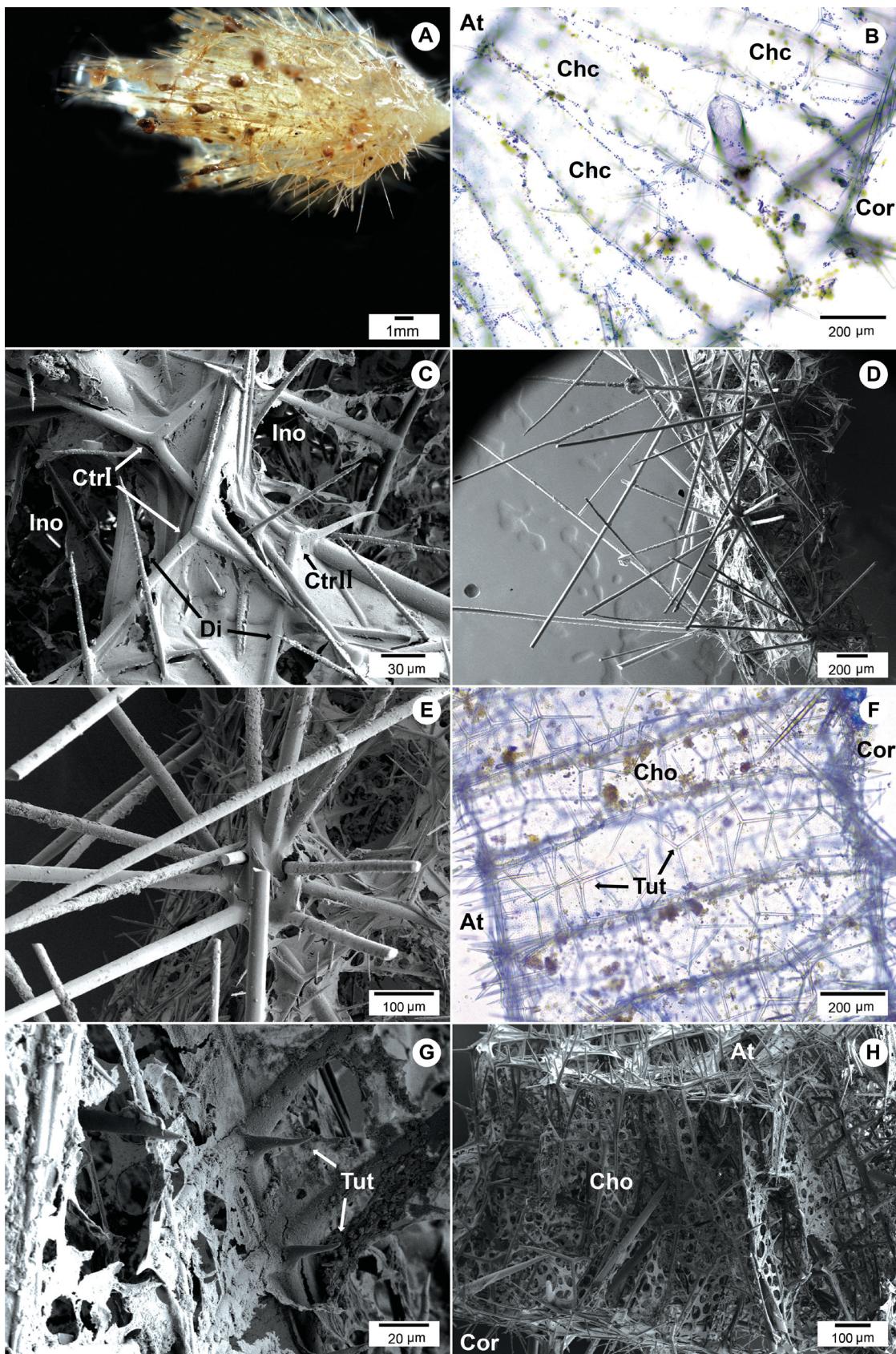


FIGURE 18A–H. *Sarsinella karasikensis* sp. nov. **A:** preserved holotype. **B:** histological section including cortical layer, choanosome and atrial cavity. **C–E:** SEM images of the cortical layer. **F:** histological section of the choanosome. **G–H:** SEM images of the choanosome. **Abbreviations:** At = atrial cavity; Chc = choanocyte chambers; Cho = choanosome; Cor = cortical layer/cortex; Ctrl = cortical triactines I; CtrlI = cortical triactines II; DiI = diactines I; Ino = inhalant openings; Tut = tubar tetractines.

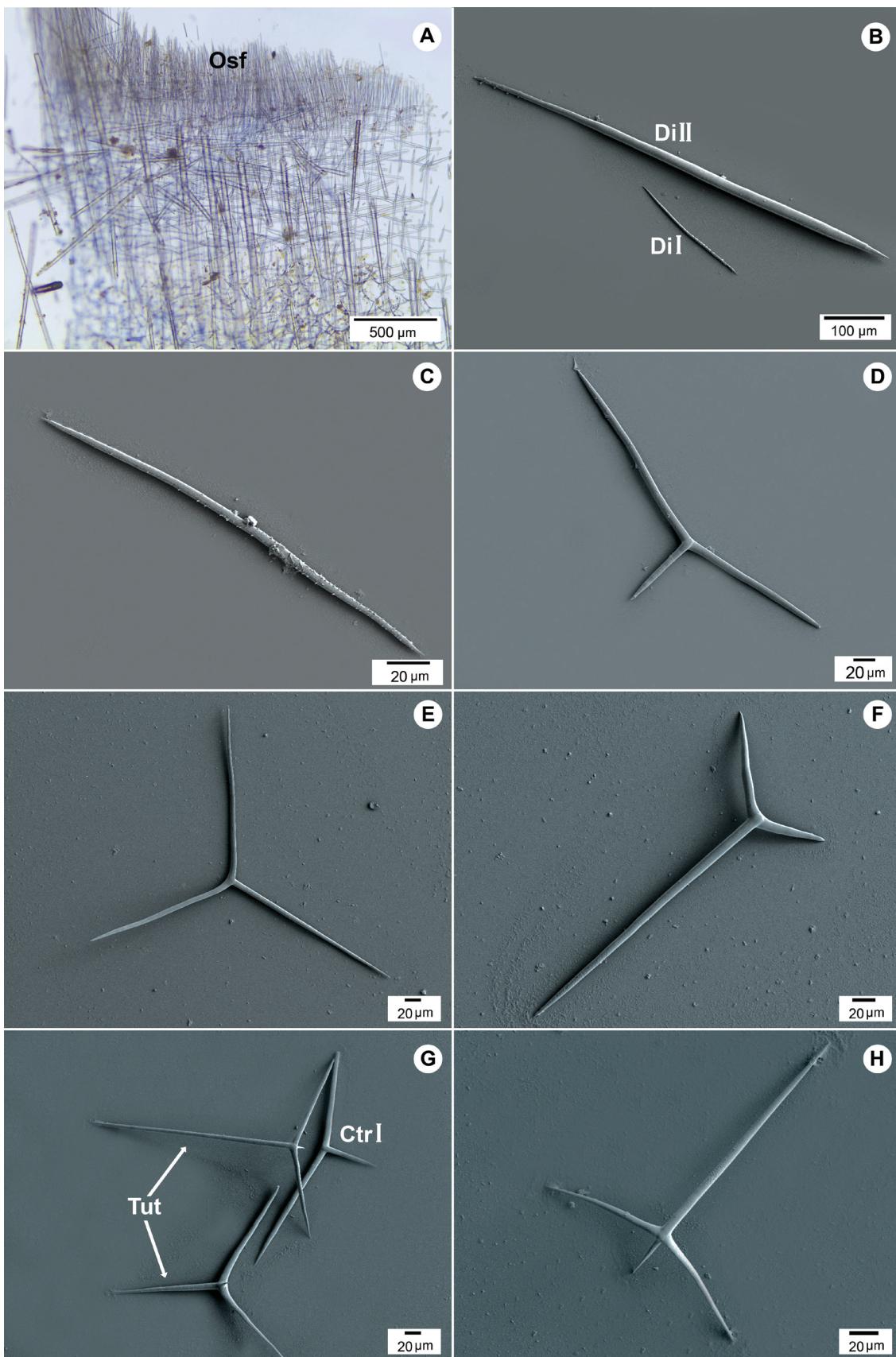


FIGURE 19A–H. *Sarsinella karasikensis* sp. nov. **A:** histological section of the oscular region. **B–C:** SEM images of diactines I and II. **D:** SEM image of cortical triactines I. **E–F:** SEM images of cortical triactines II. **G:** SEM image of tubar tetractines. **H:** chiactines. **Abbreviations:** Ctrl = cortical triactines I; DiI = diactines I; DiII = diactines II; Tut = tubar tetractines; Osf = oscular frame.

Spicules. *Cortical diactines I*: very long diactines with hastate points. Size: $1417.2 \pm 509.3 \mu\text{m}$ length, $18.6 \pm 5.1 \mu\text{m}$ width (Fig 19B; Table 14).

Cortical diactines II: small, straight and spined with sharp tips. This type of diactines are also found in the tufts of diactines II and trichoxeas (Figs 19B–C). Size: $169.6 \pm 30.1 \mu\text{m}$ length, $3.7 \pm 0.7 \mu\text{m}$ width (Table 14).

TABLE 14. Spicule measurements of *Sarsinella karasikensis* gen. nov. sp. nov. (holotype ZMBN-127212; paratype ZMBN-127211)

ZMBN-127212									
Spicules	Length (μm)					Width (μm)			
	Min	Mean	Max	SD	Min	Mean	Max	SD	n
Cortical diactines I	684.2	1417.2	2750.5	509.3	9.0	18.6	29.2	5.1	30
Cortical diactines II	127.4	169.6	248.1	30.1	2.0	3.7	4.9	0.7	30
Cortical triactines I									
Unpaired actine	42.3	101.5	175.0	34.3	5.9	8.9	11.8	1.7	20
Paired actines	86.9	154.5	235.0	36.2	6.0	9.0	11.7	1.5	
Cortical triactines II									
Unpaired actine	118.9	266.1	373.5	81.7	4.5	6.1	8.4	0.8	20
Paired actines	83.6	178.2	226.7	38.6	4.3	5.7	7.9	0.8	
Tubar tetractines									
Unpaired actine	136.0	229.8	310.2	56.6	7.5	9.4	11.0	0.9	30
Paired actines	85.7	137.3	162.8	18.5	8.1	9.8	11.5	1.0	
Apical actine	14.4	34.5	56.1	10.1	3.1	6.4	8.4	1.6	
Chiactines									
Unpaired actine	61.3	215.1	366.8	79.2	4.4	7.3	10.8	1.2	30
Paired actines	74.6	131.8	182.5	25.8	4.9	7.4	10.1	1.4	
Apical actine	43.6	81.6	105.2	16.2	4.5	6.2	8.3	1.0	
Trichoxeas	140.3	1043.5	1789.2	396.9	1.3	3.7	8.5	1.8	30
Oscular chiactines									
Unpaired actine	301.5	481.2	675.1	160.0	5.4	7.8	10.0	1.5	10
Paired actines	59.4	171.1	324.7	90.8	5.5	8.3	13.0	2.7	
Apical actine	58.3	86.2	99.4	13.9	5.5	6.6	8.5	1.0	
Oscular triactines									
Unpaired actine	259.3	461.9	746.1	123.1	3.6	6.1	9.6	2.0	20
Paired actines	102.6	139.8	192.7	34.3	5.1	7.7	11.1	1.6	
ZMBN-127211									
Spicules	Length (μm)					Width (μm)			
	Min	Mean	Max	SD	Min	Mean	Max	SD	n
Cortical diactines I	143.5	1431.0	2251.7	533.9	5.5	10.6	15.7	2.6	30
Cortical diactines II	104.5	158.3	320.8	51.5	2.3	4.6	15.0	2.7	30
Cortical triactines I									
Unpaired actine	52.4	87.3	206.4	37.8	5.4	7.0	10.3	1.2	20
Paired actines	86.7	140.5	178.7	26.0	5.0	6.9	9.8	1.0	
Cortical triactines II									
Unpaired actine	88.4	225.5	326.1	70.8	3.2	8.2	13.5	2.3	25
Paired actines	71.0	154.0	210.1	43.2	3.9	8.2	12.1	3.9	
Tubar tetractines									
Unpaired actine	116.0	236.0	458.0	94.6	5.0	7.6	11.0	1.6	25
Paired actines	58.8	130.6	208.0	58.8	5.0	7.6	10.7	1.5	
Apical actine	8.0	23.2	44.8	8.0	2.0	4.0	6.0	1.2	

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TABLE 14. (Continued)

Chiactines	Length (μm)				Width (μm)				n
	Min	Mean	Max	SD	Min	Mean	Max	SD	
Unpaired actine	45.4	228.7	456.9	82.2	2.1	8.7	14.2	2.5	30
Paired actines	34.3	135.6	208.6	40.0	1.7	8.5	13.5	2.7	
Apical actine	20.4	81.0	162.3	38.6	1.4	6.0	10.9	2.0	
Trichoxeas	251.0	1124.1	1987.1	459.5	1.6	4.8	7.0	1.4	30
Oscular chiactines									
Unpaired actine	251.8	424.6	704.6	153.9	4.7	7.3	9.5	1.3	20
Paired actines	92.4	143.1	295.7	56.9	6.4	8.5	13.0	1.9	
Apical actine	42.6	86.0	101.7	18.7	4.5	6.4	9.2	1.3	
Oscular triactines									
Unpaired actine	36.3	305.7	448.0	95.4	2.2	9.1	14.4	2.5	30
Paired actines	34.5	159.1	268.3	49.0	2.1	9.1	14.1	2.5	

Cortical triactines I: sagittal, alate with unpaired actines shorter than the paired ones (Figs 18C, 19D). Size: unpaired actines 101.5 ± 34.3 μm length, 8.9 ± 1.7 μm width; paired actines 154.5 ± 36.2 μm length, 9.0 ± 1.5 μm width (Table 14).

Cortical triactines II: unpaired actines longer than the paired actines, which are slightly bent upwards forming a round bend (Figs 18C, 19E). Some of this triactines present paired actines with different length (Fig 19F). Both types of triactines are scattered unevenly on the cortical skeleton (Fig 18C). Size: unpaired actines 266.1 ± 81.7 μm length, 6.1 ± 8.4 μm width; paired actines 178.2 ± 38.6 μm length, 5.7 ± 0.8 μm width (Table 14).

Tubar tetractines: unpaired actines longer than the paired ones. Apical actines very short with conical shape and slightly bent upwards (Fig 19G). The tetractines placed closer to the cortex have the paired actines slightly bent upwards forming a round angle, while those tetractines closer to the atrium have an unpaired angle almost straight (Fig 19G). Size: unpaired actines 229.8 ± 56.6 μm length, 9.4 ± 0.9 μm width; paired actines 137.3 ± 18.5 μm length, 9.8 ± 1.0 μm width; apical actines 34.5 ± 10.1 μm length, 6.4 ± 1.6 μm width (Table 14).

Chiactines: most have straight and longer unpaired actines, and the paired ones are bent forwards and can present different length (Figs 19H, 20A). The chiactines found around the apertures of the choanocyte chambers to the exhalant cavities present unpaired actines shorter than the paired actines, and even shorter than the apical actine (Figs 20B–C). Apical actines are conical and with hastate tip. Size: unpaired actines 215.1 ± 79.2 μm length, 7.3 ± 1.2 μm width; paired actines 131.8 ± 25.8 μm length, 7.4 ± 1.4 μm width; apical actines 81.6 ± 16.2 μm length, 6.2 ± 1.0 μm width (Table 14).

Trichoxeas: very long and straight which form the well-developed oscular fringe and the tufts of diactines and trichoxeas in the cortical skeleton. Size: 1043.5 ± 396.9 μm length, 3.7 ± 1.8 μm width (Fig 20D; Table 14).

Oscular chiactines: chiactines with unpaired and paired actines longer than those found in the atrial skeleton. The oscular chiactines together with the oscular triactines support the oscular frame. Size: unpaired actines 481.2 ± 160.0 μm length, 7.8 ± 1.5 μm width; paired actines 171.1 ± 90.8 μm length, 8.3 ± 2.3 μm width; apical actines 86.2 ± 13.9 μm length, 6.6 ± 1.0 μm width (Fig 20E; Table 14).

Oscular triactines: long and alate triactines. Size: unpaired actines 461.9 ± 123.1 μm length, 6.1 ± 2.0 μm width; paired actines 139.8 ± 34.3 μm length; 7.7 ± 1.6 μm width (Fig 20F, Table 14).

Molecular identification. Sequences of 18S and 28S rRNA genes are available on GenBank with the following accession number: 18S: MH385159, MH385160; 28S: MH385223, MH385222 (Alvizu *et al.* 2018), MK696119 and MK696120.

Remarks. The distinctive characteristics of this new chiactines-bearing species is the presence of a real articulated skeleton composed only of tetractines, and also the absence of the typical minute spined diactines which are present in almost all species within this family. There was no intraspecific variation registered between the sequences of the four specimens examined.

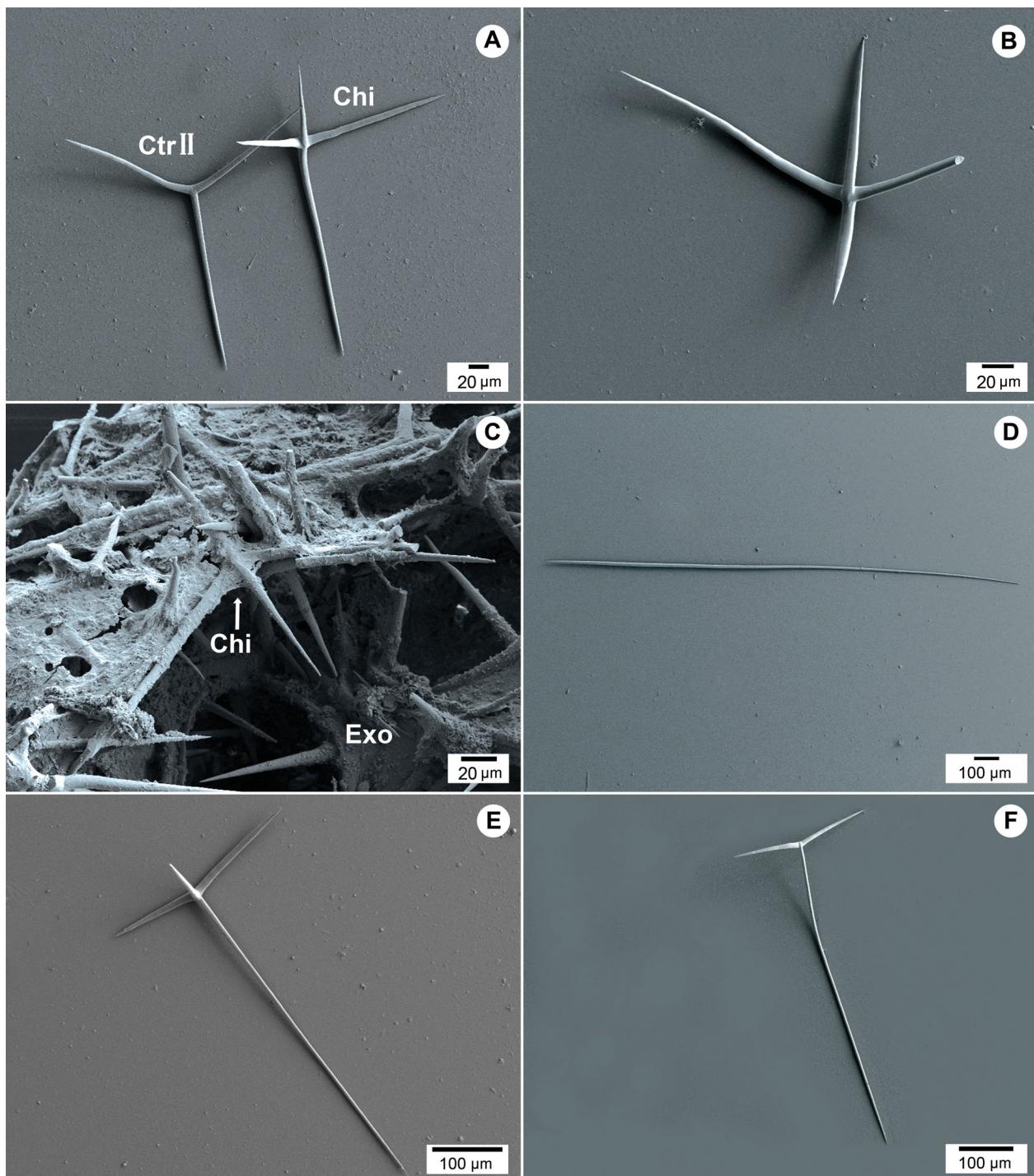


FIGURE 20A–F. *Sarsinella karasikensis* sp. nov. **A:** SEM image of atrial chiaactine and cortical triactine type II. **B:** SEM image of a chiaactine found around the exhalant opening. **C:** SEM images of the atrial layer including an exhalant opening. **D:** SEM image of trichoxea. **E:** SEM images of oscular chiaactine. **F:** SEM images of oscular triactine. **Abbreviations:** Chi = chiaactines; CtrII = cortical triactines II; Exo = exhalant opening.

Molecular results

Based on our phylogeny, members of the order Baerida were recovered in a well-supported clade (PP = 0.99; BS = 61) formed by chiaactine-bearing taxa (*i.e.* *Sarsinella*, *Megapogon* and *Achramorpha*) within the order Leucosolenida (Fig 21). The sequences from four specimens of *Sarsinella karasikensis* gen. nov. sp. nov. were identical and formed a well-supported clade (PP = 1; BS = 100), with a sister-group relationship of a moderately supported clade

(PP = 0.92; BS = 56) constituted by Petrobionidae Borojević, 1979, Baeriidae Borojević, Boury-Esnault & Vacelet, 2000 and two species of Achramorphidae (Fig 21). The clade consisting of sequences of *Megapogon schiaparelli* sp. nov. was well-supported (PP = 1; BS = 100) and according to our phylogeny is closely related to a clade comprising *Achramorpha ingolfi* sp. nov. and the Baerida members: *Petrobiona massiliiana*, *Leuconia nivea* and *Eilhardia schulzei*.

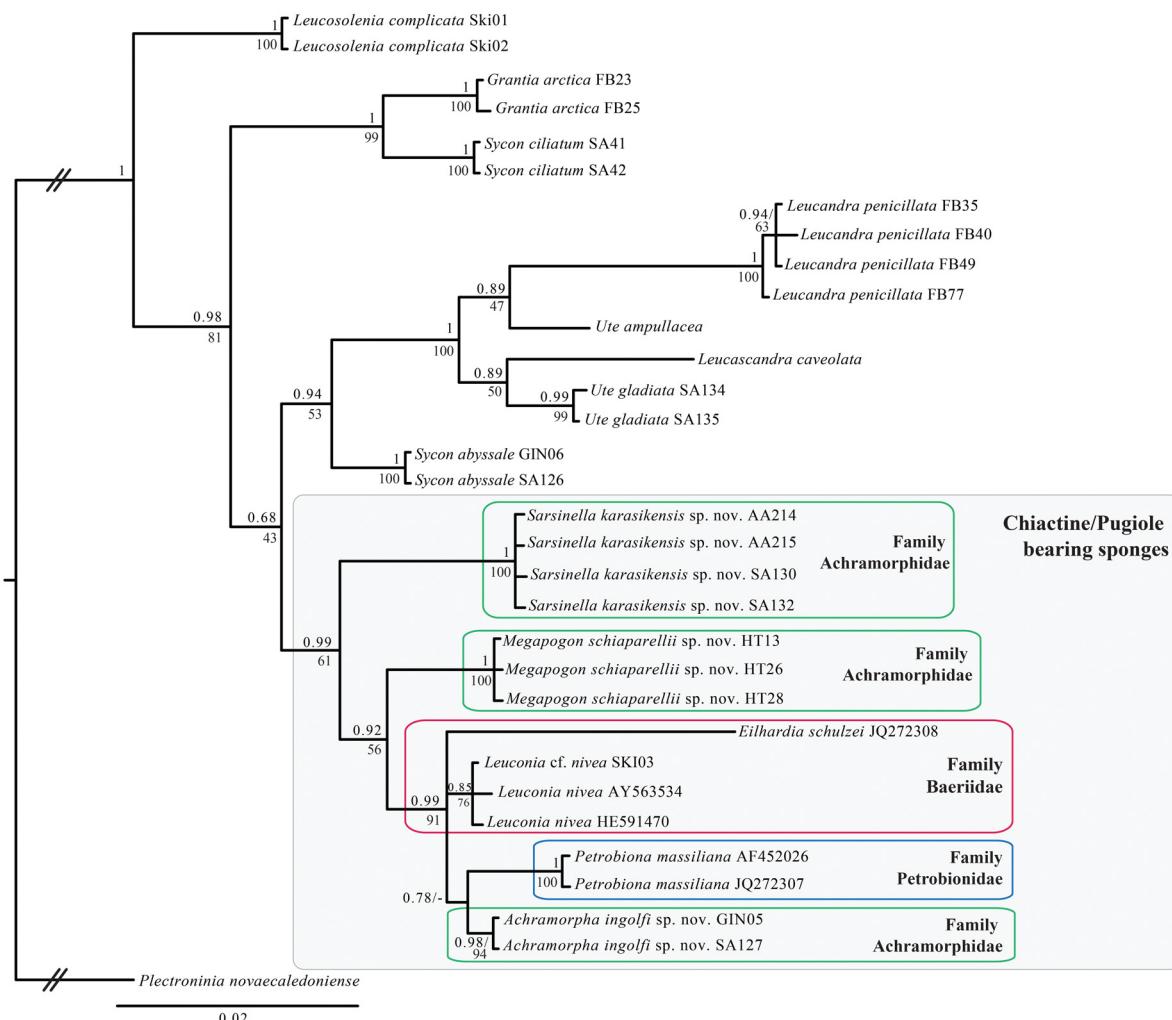


FIGURE 21. Phylogenetic reconstruction using Bayesian inference (MrBayes, Doublet+GTR/GTR+I+G) of 18S + C-region rDNA for the chiactine/pugiole-bearing sponges. Posterior probability and bootstrap values are given at the nodes, respectively.

Discussion and conclusions

New chiactines-bearing taxa. In this study we describe four new species and one new genus and provide re-descriptions with more detailed information of most of the known chiactine-bearing species. Two of these new species are from the Antarctic, *Achramorpha antarctica* sp. nov. and *Megapogon schiaparelli* sp. nov. The other two species, *Achramorpha ingolfi* sp. nov. and *Sarsinella karasikensis* gen. nov. sp. nov. are from the Nordic Seas. Except for the species *A. diomediae*, all species examined in this study, matched the diagnoses previously proposed to the family Achramorphidae (Jenkin 1908; Borojević *et al.* 2002b), establishing that the presence of chiactines and a radial atrial skeleton are its main distinctive characters. An additional characteristic is the presence of spined microdiactines, which are present in all *Megapogon* spp. and in three species of *Achramorpha* (*A. nivalis*, *A. glacialis* and *A. grandinis*). The presence of those morphological characters reveals that *Sarsinella karasikensis* gen. nov. sp. nov. is closely related with the other chiactine-bearing sponges, and is further supported by its position in the phylogenetic tree (Fig 21).

New insights into the classification of Calcaronea. The nested position of some members of the order Baerida within the order Leucosolenida has been obtained in several previous phylogenetic studies (Manuel *et al.* 2004; Dohrmann *et al.* 2006; Manuel 2006; Voigt *et al.* 2012; Voigt & Wörheide 2016). However, it was only recently revealed to which taxa these Baerida members are closely related (Alvizu *et al.* 2018). In Alvizu *et al.* (2018), *Achramorpha ingolfi* sp. nov. and two species of the family Baeriidae and the monotypic family Petrobionidae were recovered in a well-supported clade. However, the association between these members of Baerida and the family Achramorphidae was unresolved because this last family was recovered as non-monophyletic. In the present study, the combination of the 18S rRNA and the C-region of 28S datasets resulted in a better resolution of the deeper phylogenetic nodes supporting a monophyletic status of the chiaquine- and pugiole-bearing sponges (order Baerida).

In agreement with our molecular results, there are some morphological characters that support the nested position of Petrobionidae and members of Baeriidae within Leucosolenida. For instance, Alvizu *et al.* (2018) mentioned that the chiaquines and the pugioles (small harpoon-shaped tetractines) present in some Baerida, may be homologous and could explain the close relationship between these taxa. In agreement with this idea, the arrangement of the atrial skeleton in Achramorphidae and in some Baerida, can also give support to this relationship. The organization of the atrial skeleton in most taxa of Leucosolenida is characterized by rows of triactines and tetractines placed tangentially, however, in the case of chiaquine/pugiole-bearing sponges, the atrial wall is supported by these derived tetractines, which are organized radially. Therefore, the presence of a radial atrial skeleton supported by tetractines with their unpaired actines in the same arrangement as the apical actines (pugioles/chiaquines), may represent a synapomorphy for this well-supported clade. However, in some Baerida these morphological characters can be absent, such as in the case of the monospecific genera *Eilhardia* and *Leucopsila* which do not present pugioles in their atrial skeleton. Interestingly, the species *Eilhardia schulzei* is recovered in a well-supported clade composed of chiaquine/pugiole-bearing sponges. This result suggests that the absence of this type of spicule in *Eilhardia* and *Leucopsila* may be consequence of secondary loss, which seems to be a common evolutionary event in Calcaronea (Manuel 2006; Voigt *et al.* 2012). This could also explain the absence of an atrial skeleton in the monotypic family Petrobionidae, that is characterized by the presence of a massive basal skeleton of calcite, which has not been recognized in any other calcaronean taxa.

The other two families of the order Baerida, Lepidoleuconidae Vacelet, 1967 and Trichogypsiidae Borojević, Boury-Esnault & Vacelet, 2000, also present unique morphological characteristics. For instance, Lepidoleuconidae is a monotypic family represented by the species *Lepidoleucon inflatum* Vacelet, 1967 (Borojević *et al.* 2002a). This species presents a leuconoid organization with an irregular outer layer of scales derived from triactines, which are not found in any other group. The choanoskeleton is exclusively composed of scattered microdiactines, and the osculum presents a circlet of modified tetractines (Vacelet 1967; Borojević *et al.* 2002a). The oscular tetractines and the “microtetractines” present the unpaired actines and the apical actines in the same alignment, as in pugioles and chiaquines (see illustrations in Vacelet 1967). These morphological characteristics could indicate affinities with the well-supported clade of chiaquine/pugiole-bearing sponges. However, due to lack of molecular data in our study of this taxa, this hypothesis remains to be tested.

In the case of the family Trichogypsiidae, its relationship with the chiaquine/pugiole-bearing sponges is also unclear, especially because this taxon presents a skeleton entirely formed by diactines of unusual shape (see Borojević *et al.* 2000). These morphological characteristics make this taxon unique within the sub-class Calcaronea. As such, the relationship of this family with the chiaquine/pugiole-bearing sponges, and even within Calcaronea, remains uncertain until the analyses of additional material and the inclusion of molecular data.

Our results together with previous studies (Dohrmann *et al.* 2006; Voigt *et al.* 2012; Alvizu *et al.* 2018) reject the ordinal classification of Calcaronea, and suggest changes into the classification of Leucosolenida. However, the addition of molecular data from additional taxa and particularly of the type species of Baerida [*i.e.* *Lamontia zona* Kirk, 1895 and *Leucopsila stylifera* (Schmidt, 1870) for Baeriidae; and the type species for the families Lepidoleuconidae and Trichogypsiidae] and Achramorphidae (*i.e.* *Achramorpha nivalis* and *Megapogon crucifer*), would be required to verify this hypothesis beyond doubt. If the patterns found in our study would hold after the inclusion of such taxa, then major changes to the higher classification of Calcaronean sponges would be warranted, including: 1) the re-assignment of all (or part) of the families currently in Baerida to Leucosolenida; 2) the redefinition of the family Petrobionidae to include some genera previously assigned to Baerida; 3) synonymization of the families Achramorphidae and Baeriidae with Petrobionidae (following the priority principle); and 4) redefinition of the order Leucosolenida following the previous changes. However, in the absence of such material and data, we refrain from formally proposing these changes at this time.

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