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Monograph

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Swedish marine demosponge fauna (Porifera: Demospongiae) sampled 80 years after Jägerskiöld's inventory

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Abstract. It has been 80 years since Leonard Axel Jägerskiöld's thorough marine faunistic inventory of the Swedish west coast (1921–1938), which represents the latest update of the Swedish sponge marine fauna. In this study, we present an update of the demosponge fauna with new specimens collected by the Swedish Taxonomic Initiative expeditions (2007–2008), new dredges (2012–2020), and SCUBA (2018–2020). Identifications were based on morphology and a molecular tree-based approach using the Folmer fragment of coxI, and the D3-D5 region of the 28S rRNA-encoding gene. From the 417 specimens examined, 57 different species were identified, of which five were identified to the genus/family level, eight were new reports for Sweden and one was new to science (*Halisarca hansghanssoni* sp. nov.). Furthermore, we reinstated the name *Hymedesmia dujardinii* (Bowerbank, 1866). The Swedish Taxonomic Initiative campaigns aimed to replicate the collecting efforts of the Jägerskiöld's campaigns, thus making them easily comparable. Using the identified sponges of the Jägerskiöld's inventory possibly changes in the Swedish sponge fauna over the last 80 years are discussed.

Keywords. Swedish sponge fauna, Demospongiae, CoxI, 28S D3-D5, barcode.

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Introduction

The Swedish west coast includes the eastern part of Kattegat and Skagerrak. This area is one of the best-studied marine regions in the world, and it was the site of one of the first systematic benthic fauna inventories, between 1921 and 1938, led by Leonard Axel Jägerskiöld (Jägerskiöld 1971). The survey comprises 440 stations, logging a total of 1400 species and 33661 specimens, of which sponges (Porifera) constitute a substantial part. Prior to the Jägerskiöld survey, the sponge fauna of this area had already been studied by Fristedt (1885), Levinsen (1893) (from Danish waters), and Alander (1935). The Jägerskiöld survey was, nevertheless, an opportunity for Alander to acquire samples for his thesis (Alander 1942) which is the most comprehensive study of the Swedish marine sponge fauna to date. After Jägerskiöld's campaigns, the Swedish benthic fauna waited nearly 80 years for another similar survey, undertaken by the Swedish Taxonomy Initiative (STI) between 2004 and 2009 (Karlsson *et al.* 2014). The STI campaigns conducted in 2007–2008 (Karlsson *et al.* 2014) aimed to replicate Jägerskiöld's campaigns (1921–1938) in both methods and station location, which allows for a comparative analysis of the fauna over time.

In spite of the area being rather well studied, this recent effort has already resulted in one newly described sponge species (Cárdenas & Thollesson 2016). Between the two faunistic inventories, there have been significant changes in the environment, with an increase in eutrophication (Pearson *et al.* 1985) and trawling/fishing (Olsgard *et al.* 2008). Even though it was initially thought that the environmental changes were producing a shift of dominant species in favour of suspension-feeders and predators (Pearson *et al.* 1985; Rosenberg & Nilsson 2005), recent studies indicate a loss of rare species as well as a dominance shift for the Kattegat and Skagerrak region (Göransson 2010; Obst *et al.* 2018). However, these studies have not explicitly looked into sponge diversity. In this study, we describe the demosponge (class Demospongiae) fauna and its distribution on the Swedish west coast using specimens from the STI marine inventory, in addition to specimens collected in this region by the authors using dredging and SCUBA.

Material and methods

Sampling

In this study, we examined specimens collected on the Swedish west coast by the STI campaigns of 2007–2008 (Karlsson *et al.* 2014), and several SCUBA dive surveys (2018–2020) (Fig. 1). The STI campaigns consist of 92 stations (Fig. 1) and 224 specimens, ranging in size from 11 to 20 cm (with the exception of large specimens of *Phakellia* Bowerbank, 1862), while the SCUBA surveys cover nine sites (Fig. 1) and 129 specimens ranging from 1 to 10 cm in size. Additionally, 64 specimens varying in size from 1 to 20 cm, were dredged from localities around Gullmaren fjord with R/V Belone, within the framework of Uppsala University courses (2006-2019).

The majority of the specimens were preserved in ethanol but some older STI specimens were first fixed in formaldehyde. All the specimens, except for the paratype of *Halisarca* sp. nov., are deposited in Göteborg Natural History Museum (GNM), Sweden. See Supp. file. 1.

Morphology: slide preparation and identification

For all samples, we performed a cross and a tangential section by hand, except for thinly encrusting or very small specimens. For spicule preparations we used a solution of 7% sodium hypochlorite (NaOCl), followed by subsequent washes with distilled water, 70% ethanol and 90% ethanol. For all slides (spicules, cuts or tissues), we used Canada balsam (Sigma-Aldrich) as an embedding medium, hardened at 50°C. Slides were photographed using an Olympus BX50 light microscope (Olympus, Tokyo, Japan) and a Nikon DS-Vi1 camera (Nikon, Tokyo, Japan) operated with NIS-Element F3.0 (Olympus, Tokyo, Japan) software package. In case of sections or long spicules, we have several photos to encompass the entirety of the spicule or the feature of interest in the section. Additionally, for some thick sections we performed manual stacking on feature details that required a wide focus depth. The photos were then stitched using Affinity

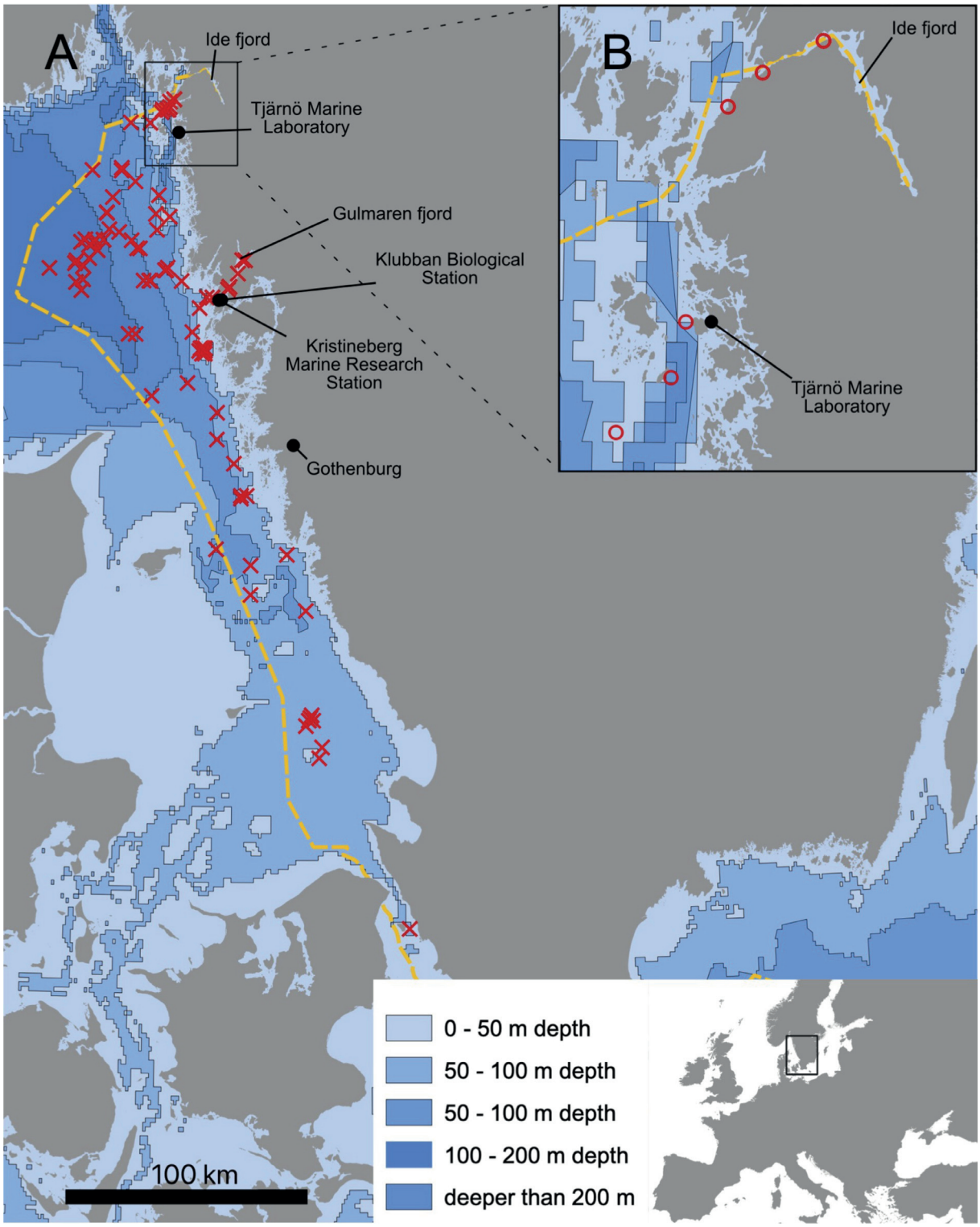

Fig. 1. Map with sampling sites. **A**. Sampling done with dredging (X). **B**. Sampling done with dredging SCUBA diving (O). Bathymetry from ETOPO1 Arc-Minute Global Relief Model (https://doi.org/10.7289/V5C8276M) and, EEZ (yellow dashed line) from Havs- och vattenmyndigheten (https://www.havochvatten.se/). Projected coordinates system: SWEREF99 TM.

Photo ver. 1.10 'focus merge' and/or 'panorama' algorithm. We refer to all images produced this way as 'stitched'. For the measurements, we used a Leitz light microscope (Leitz, Wetzlar, Germany) with a Canon 1100D DSLR camera (Canon, Tokyo, Japan) operated with µMicromager ver. 2.0.0 Gamma1, (Stuurman *et al.* 2007) and ImageJ (ver. 1.51, (Schneider *et al.* 2012)). Throughout this work we present the measurement per species as follows: minimum–**average**–maximum length ± standard deviation × minimum–**average**–maximum width ± standard deviation (N = number measured), or average length × average width when the number of spicules measured is reduced. In our measurements, both length and width correspond to the longest or widest point of each spicule.

For identifications we used Systema Porifera (Hooper & van Soest 2002), as well as Alander's Ph.D. thesis (Alander 1942) and the Marine Species Identification Portal (van Soest *et al.* 2000). However, for the hierarchical classification to the family level and higher, we followed Morrow & Cárdenas (2015). Furthermore, we used the World Porifera Database (de Voogd *et al.* 2021) as a taxonomic authority in order to assess the validity of species and genus names.

DNA extraction and amplification

DNA was extracted using chloroform isoamyl alcohol followed by proteinase K digestion for up to 8 hours at 60°C (Winnepenninckx *et al.* 1993). DNA concentration was quantified a QUBIT® 3.0 Fluorometer (Thermo Scientific). We amplified the coxI Folmer region and 28S D3-D5 region, using the universal Folmer primer pair LCO1490 - HCO2198 (Folmer *et al.* 1994) or the Folmer degenerated primers (Meyer 2003), and the demosponge primers Por28S-830F - Por28S-1520R (Morrow *et al.* 2011), respectively. We used the same master mix for all the PCR reactions with a total volume of 25 µl per reaction, 0.4 µm of each primer, 1.2 mM of DNTPs, and 1X DreamTaq Master Mix (Thermo Scientific), which included 2 mM of MgCl2. We followed the standard amplification protocol in Morrow *et al.* (2011) for the 28S fragment amplification: 94°C, 5 min; (94°C, 30 s; 53°C, 30 s; 72°C, 30 s) × 30 cycles; 72°C, 5 min. For the amplification of the coxI Folmer region, we used the following protocol: 94°C, 3 min; (94°C 1 min; 45°C, 90 s; 72°C, 1 min) × 34 cycles; 72°C, 5 min. We also amplified the 28S D1-D2 of the undescribed species using the primers Por28S-15F - Por28S-878R, with the standard amplification protocol (Morrow *et al.* 2011). We purified the amplicons with Illustra ExoProStarTM (GE Healthcare) according to manufacturer instructions and sent them for sequencing to Macrogen Standard sequencing services (Amsterdam, Netherlands). The generated sequences together with the associated specimen information were deposited in the Barcode of Life Data (BOLD; www.barcodinglife.org) (Ratnasingham & Hebert 2007) aggregated into dataset DS-2020SSF (DOI after made public) and with GenBank accession numbers: a) OM436217 - OM628824, ON113815, OR269461 and PP415521 for coxI, b) OM415572 - OM628826, ON129357, ON129358 for 28S D3-D5, and c) PP763168 for 28S D1-D2 (Table 1).

Phylogenetic analysis and taxon comparison

In order to discard possible contaminations, we verified the sponge nature of the sequences by BLAST (Altschul *et al.* 1990) against the full NCBI database (https://www.ncbi.nlm.nih.gov/BLAST/) before assembling the contigs. We used Lasergene SeqMan Pro™ versions 12 to 14 (DNASTAR Inc.) to assemble contigs and remove primer sequences. In order to select sequences from reliably identified and closely related specimens from the ones sequenced in this study, we used BLAST against the full NCBI database after assembling the contigs (Altschul *et al.* 1990) and selected a maximum of three sequences per taxon/species with a tractable specimen. Furthermore, we qualitatively characterised the sequences according to their reliability and usefulness (for this study). In order to do so, we compiled the following priority list: sequences coming from a) specimens identified by experts in published peer-reviewed journals and collected in the northeast Atlantic, b) specimens identified by experts in published peer-reviewed journals, but collected in other areas, c) specimens identified by experts but not published

in peer-reviewed journals, and d) specimens published in peer-reviewed papers that are not identified by experts and originating from anywhere in the world. For category d) we considered the sequence taxon assignments as dubious and were therefore only selected when the other categories were not available. This manual selection allowed us to obtain sequences closely related to ours from specimens with reliable identifications and tractable to museum or private collection specimens. As for the outgroup, we selected GenBank sequences from specimens identified as belonging to the class Homoscleromorpha. The full list of sequences used for the phylogenetic inference can be found in Supp. file 2.

We used MAFFT (Katoh *et al.* 2002) to produce the multiple sequence alignments of both regions (https://doi.org/10.6084/m9.figshare.18129482). For model selections and maximum likelihood phylogenetic inference, we choose IQ-tree version 2 (Nguyen *et al.* 2015), using ModelFinder (Kalyaanamoorthy *et al.* 2017) to select the best fitting model under Akaike Information Criteria (AIC) and 1000 bootstrap replicates to produce a majority consensus tree. Branches with bootstrap inferior or equal to 80% were collapsed (Hillis & Bull 1993; Simmons & Norton 2014).

Species delimitation analysis

We analysed a smaller coxI alignment, using Assemble Species by Automatic Partitioning (ASAP) (Puillandre *et al.* 2021) to determine whether certain specimens might belong to undescribed species. This is a pairwise distance-based method that uses a hierarchical clustering algorithm. For the distances matrix we used the Jukes-Cantor model (JC69).

Results

We examined a total of 417 specimens resulting in 411 specimens being identified to the species level. A total of 52 species of demosponges were found encompassing 22 families and 11 orders (Table 1). Eight of these species are new reports for Sweden: *Aplysilla glacialis* (Merejkowsky, 1878), *Crambe stellifera* (Goodwin & Picton, 2009) comb. nov., *Hymeraphia elongata* Picton & Goodwin, 2007, *Hymedesmia jecusculum* Bowerbank, 1866, *Hymedesmia hibernica* Stephens, 1916, *Phorbas dives* (Topsent, 1891), *Mycale macilenta* (Bowerbank, 1866), and *Raspaciona aculeata* (Johnston, 1842). We identified one undescribed species, herein described as *Halisarca hansghanssoni* sp. nov.

The number of specimens per species was low, with 32 species represented by three or less specimens and 12 species that were found only once. This suggests that the species richness of demosponge species in the region is still largely underestimated.

Regarding species diversity, the family Hymedesmiidae Topsent, 1928 (order Poecilosclerida Topsent, 1928) was the most represented with 12 species, followed by families Suberitidae Schmidt, 1870 (order Suberitida Nardo, 1833) and Raspailiidae Nardo, 1833 (order Axinellida Lévi, 1953), with five species each. However, Hymedesmiidae represented only 11% of the specimens, while Bubaridae and Suberitidae accounted for 16.5% and 16% of all specimens, respectively.

Phylogenetic analyses

We obtained 72 sequences for coxI (Folmer fragment) of which 66 were specimens identified to the species level, as well as 82 sequences for 28S D3-D5 of which 77 were from specimens identified to the species level. While the 28S D3-D5 marker was easily amplified in many different demosponge groups (but exceptions were *Aplysilla, Spongionella, Phakellia Axinella*, etc), that was less the case for the coxI region. Most *Hymedesmia* specimens were difficult to amplify and sequence with the Folmer primers (Folmer *et al.* 1994) or the Folmer degenerated primers (Meyer 2003). Furthermore, PCR amplification was less successful for STI specimens (61% success rate) than for the specimens

Table 1 (continued on the next 5 pages). Classification for the specimens identified to the genus level and non-dubious identification status. Including number of specimens and accession numbers for Cox*I* Folmer regions and DNA encoding for 28S (D3-D5). Accession numbers aligned in the same row are originated from a single specimen. Full list i.e., with dubious identification can be found in Supp. file 1. (N) being number of specimens.

Classification Order Family Genus	Species	N	CoxI	28S (D3-D5)
Chondrillida Redmond *et al.*, 2013				
Halisarcidae Schmidt, 1862				
Halisarca Johnston, 1842	*Halisarca dujardinii* (Johnston 1842)	7	OM436267	OM415634
			OM436238	
			OM436274	
			OM436253	OM415611
			OM436243	OM415604
	Halisarca hansghanssoni sp. nov.	2	OM436239	
			OR269461	
	Halisarca cf. *hansghanssoni*	1	PP415521	
Dendroceratida Minchin, 1900				
Darwinellidae Merejkowsky, 1879				
Aplysilla Schulze, 1878	*Aplysilla sulfurea* Schulze, 1878	3		
	Aplysilla glacialis (Merejkowsky, 1879)	1		
Dictyodendrillidae Bergquist, 1980				
Spongionella Bowerbank, 1686	*Spongionella pulchella* (Sowerby, 1804)	3		
Dictyoceratida Minchin, 1900				
Dysideidae Gray, 1867				
Dysidea Johnston, 1842	*Dysidea fragilis* (Montagu, 1814)	18		OM415602
				OM415583
Pleraplysilla Topsent, 1905	*Pleraplysilla spinifera* (Schulze, 1879)	4	OM436221	
				OM415592
			OM436226	OM415572
				OM415621
Haplosclerida Topsent, 1928				
Chalinidae Gray, 1867				
Chalinula Schmidt, 1868	*Chalinula limbata* (Montagu, 1814)	1		

Table 1 (continued). Classification for the specimens identified to the genus level and non-dubious identification status. Including number of specimens and accession numbers for CoxI Folmer regions and DNA encoding for 28S (D3-D5). Accession numbers aligned in the same row are originated from a single specimen. Full list i.e. with dubious identification can be found in Supp. file 1. (N) being number of specimens.

Classification Order Family Genus	Species	N	CoxI	28S (D3-D5)
Haliclona Grant, 1841	*Haliclona* urceolus (Rathke & Vahl, 1806)	24	OM436259	
			OM436218	
			OM436270	
			OM436227	
			OM436240	
			OM436225	
			OM436231	OM415596
			OM436229	
				OM415626
	Haliclona oculata (Linnaeus, 1759)	2	OM436232	OM415598
				OM415642
	Haliclona sp.1	1	OM436271	OM415636
Niphatidae van Soest, 1980	*Niphatidae* sp. 1	1	OM436284	OM415650
Axinellida Lévi, 1953 Axinellidae Carter, 1875 *Axinella* Schmidt, 1862	*Axinella infundibuliformis* (Linnaeus, 1759)	25		
	Axinella rugosa (Bowerbank, 1866)	41		
Stelligeridae Lendenfeld, 1898		3	OM436247	
Paratimea Hallmann, 1917	*Paratimea loennbergi* (Alander, 1942)		OM436262	OM415629
			OM628823	
Raspailiidae Nardo, 1833 *Eurypon* Gray, 1867	*Eurypon coronula* (Bowerbank, 1874)	1	OM436224	OM415590
Hymeraphia Bowerbank, 1864	*Hymeraphia stellifera* Bowerbank, 1864	4	OM436255	OM415615
			OM436237	
	Hymeraphia elongata Picton & Goodwin, 2007	3	OM436273	
			OM436250	
			OM436254	
Raspailia Nardo, 1833	*Raspailia aculeata* (Johnston, 1842)	3		OM415584
				OM415589

Table 1 (continued). Classification for the specimens identified to the genus level and non-dubious identification status. Including number of specimens and accession numbers for CoxI Folmer regions and DNA encoding for 28S (D3-D5). Accession numbers aligned in the same row are originated from a single specimen. Full list i.e. with dubious identification can be found in Supp. file 1. (N) being number of specimens.

Classification Order Family Genus	Species	N	CoxI	28S (D3-D5)
Bubarida Morrow & Cárdenas, 2015 Bubaridae Topsent, 1894 *Phakellia* Bowerbank, 1862	*Phakellia robusta* Bowerbank, 1866	3		
	Phakellia ventilabrum (Linnaeus, 1767)	25		
Biemnida Morrow *et. al.*, 2013 Biemnidae Hentschel, 1923 *Biemna* Gray, 1862	*Biemna variantia* (Bowerbank, 1858)	3		OM415582
Polymastiida Morrow & Cárdenas, 2015 Polymastiidae Gray, 1867 *Polymastia* Bowerbank, 1862	*Polymastia boletiformis* (Lamarck, 1815)	7		OM415588
Spinularia Gray, 1867	*Spinularia spinularia* (Bowerbank, 1866)	42		
Poecilosclerida Topsent, 1928 Acarnidae Dendy, 1922 *Iophon* Gray, 1867	*Iophon hyndmani* (Bowerbank, 1858)	1		
	Iophon nigricans (Bowerbank, 1858)	3		
Esperiopsidea Hentschel, 1923 *Amphilectus* Vosmaer, 1880	*Amphilectus fucorum* (Esper, 1794)	3		
	Amphilectus ovulum (Schmidt, 1870)	14	OM436236	OM415579 OM415580 OM415578 OM415621 OM415610 OM415573 OM415614 OM415591 OM415609 OM415612 OM415589
Hymedesmiidae Topsent, 1928 *Hymedesmia* Bowerbank, 1864	*Hymedesmia jecusculum* (Bowerbank, 1866)	5	OM436251 OM436265	
	Hymedesmia paupertas (Bowerbank, 1866)	1		

Table 1 (continued). Classification for the specimens identified to the genus level and non-dubious identification status. Including number of specimens and accession numbers for CoxI Folmer regions and DNA encoding for 28S (D3-D5). Accession numbers aligned in the same row are originated from a single specimen. Full list i.e. with dubious identification can be found in Supp. file 1. (N) being number of specimens.

Classification Order Family Genus	Species	N	CoxI	28S (D3-D5)
	Hymedesmia stellifera Goodwin & Picton, 2009	1		OM415624
	Hymedesmia dujardinii (Bowerbank, 1866)	8		OM415574
				OM415575
				OM415619
				OM415622
				OM415641
	Hymdesmia aequata Lundbeck, 1910	2		
	Hymedesmia hibernica Stephens, 1916	11	OM436264	
			OM436279	OM415648
				OM415586
				OM415581
				OM415613
				OM415616
				OM415623
				OM415627
				OM415639
				OM415640
				OM415643
	Hymedesmia primitiva Lundbeck, 1910	6	OM436256	OM415617
			OM436245	
			OM436275	
	Hymedesmia stylifera (Alander, 1942)	1		
	Hymedesmia sp. 1	1		OM415620
	Hymedesmia sp. 2	1	OM436219	
	Hymedesmia sp. 3	1	OM436233	
	Hymedesmia sp. 4	1		OM415632
Plocamionida Topsent, 1927	*Plocamionida ambigua* (Bowerbank, 1866)	3		
	Plocamionida tylotata Brøndsted, 1932	1		

Table 1 (continued). Classification for the specimens identified to the genus level and non-dubious identification status. Including number of specimens and accession numbers for CoxI Folmer regions and DNA encoding for 28S (D3-D5). Accession numbers aligned in the same row are originated from a single specimen. Full list i.e. with dubious identification can be found in Supp. file 1. (N) being number of specimens.

Classification Order Family Genus	Species	N	CoxI	28S (D3-D5)
Phorbas Duchassaing & Michelotti, 1864	*Phorbas dives* (Topsent, 1891)	2	OM436258	
	Phorbas fictitius (Bowerbank, 1866)	2	OM436280	
			OM436220	OM415577
Mycalidae Lundbeck, 1905				
Mycale Gray, 1867	*Mycale lingua* (Bowerbank, 1866)	7		
	Mycale macilenta (Bowerbank, 1866)	1		OM415625
Microcionidae Carter, 1875	*Clathria barleei* (Bowerbank, 1866)	3	OM436235	
Clathria Schmidt, 1862				
Myxillidae Dendy, 1922		9	OM436222	OM415587
Myxilla Schmidt, 1862	*Myxilla incrustans* (Johnston, 1842)		OM436244	OM415605
				OM415593
				OM415576
				OM628825
	Myxilla fimbriata (Bowerbank, 1866)	5	OM436266	OM415633
Plocamiancora Topsent, 1927	*Plocamiancora arndti* Alander, 1942	2		
Clionaida Morrow & Cárdenas, 2015	*Cliona celata* Grant, 1826	3		
Clionaidae d'Orbigny, 1851				
Cliona Grant, 1826				
	Cliona lobata Hancock, 1849	2		
Suberitida Chombard & Boury-Esnault, 1999		3	OM436223	
			OM628824	OM415645
Suberitidae Schmidt, 1870	*Protosuberites* sp.			
Protosuberites Swartschewsky, 1905				
Suberites Nardo, 1833	*Suberites ficus* (Johnston, 1842)	7	OM436283	
			OM436268	
			OM436277	
			OM436234	OM415599
			OM436278	OM415644
			OM436282	
			OM436246	

Table 1 (continued). Classification for the specimens identified to the genus level and non-dubious identification status. Including number of specimens and accession numbers for CoxI Folmer regions and DNA encoding for 28S (D3-D5). Accession numbers aligned in the same row are originated from a single specimen. Full list i.e. with dubious identification can be found in Supp. file 1. (N) being number of specimens.

Classification Order Family Genus	Species	N	CoxI	28S (D3-D5)
	Suberites montalbidus Carter, 1880	23	OM436272	OM415638
				OM415606
				OM415635
	Suberites virgultosus (Johnston, 1842)	29	OM436269	
			OM436241	OM415601
			OM436230	
			OM436261	OM415628
			OM436276	
			OM436263	OM415631
				OM415647
				OM415637
				OM415597
				OM628826
	Suberites spermatozoon (Schmidt, 1875)	5	OM436260	
			OM436257	OM415618
Halichondriidae Gray, 1867	*Halichondria panicea* (Pallas 1766)	20	OM436248	
Halichondria Fleming, 1828			OM436242	OM415603
			OM436228	OM415594
			OM436249	OM415607
			OM436281	OM415649
			OM436217	
				OM415600
Vosmaeria Fristedt, 1885	*Vosmaeria crustacea* Fristedt, 1885	2		
Total number of specimens		416		

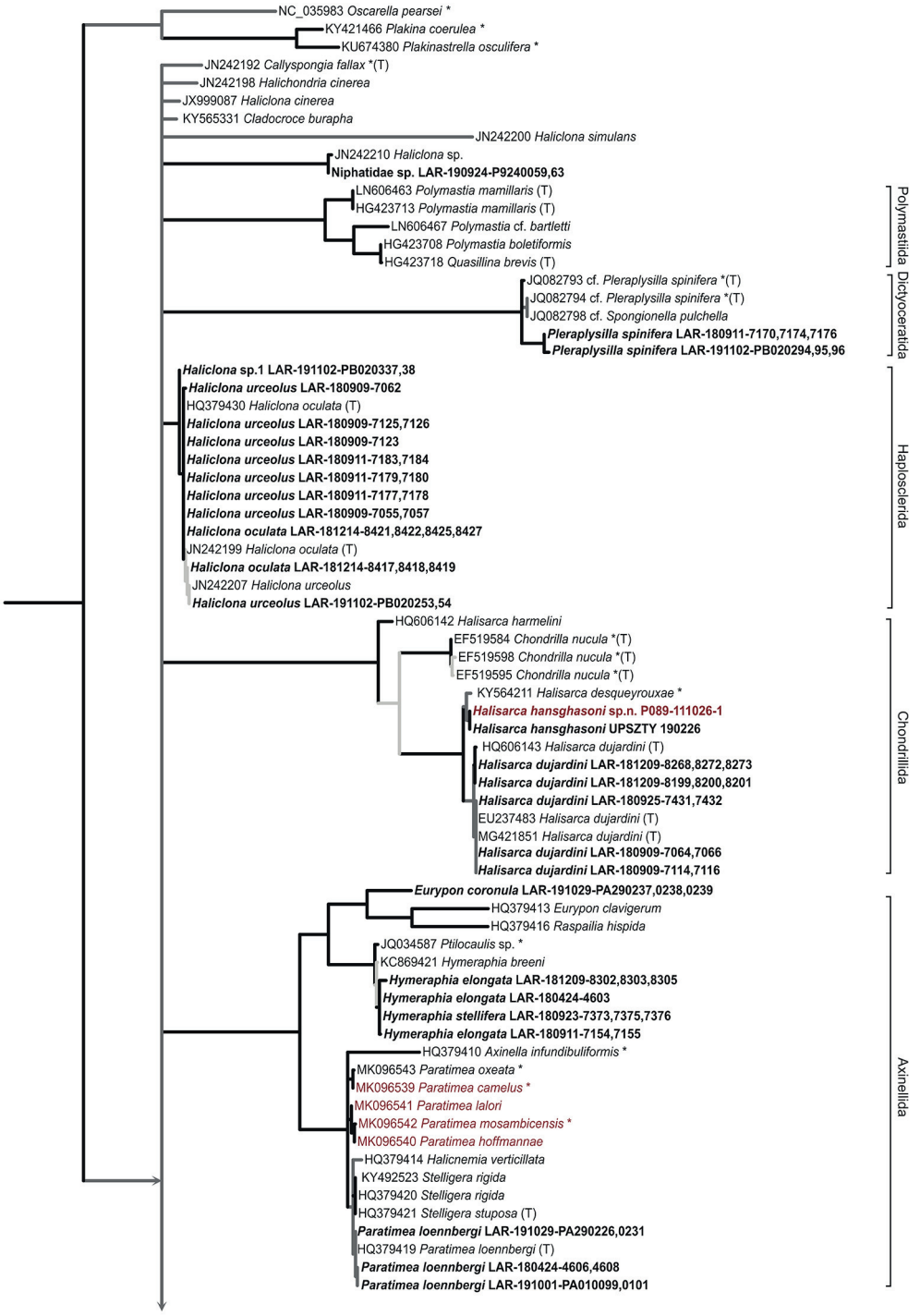

Fig. 2. Maximum Likelihood tree based on coxI gene (Folmer fragment) by IQTREE under the model TIM2+F+I+G4. The node support in bootstrap (bt) is shown in grayscale: light gray - 80 < bt < 90%; bark gray - 90% ≤ bt < 95%; black - bt ≥ 95%. The tips show the taxon and accession number (sequences retrieved from GenBank) or specimens sequenced in this study (in bold). All sequences in red are associated to type specimens. Sequences retrieved from GenBank are coded: (T) type taxon; * specimens that are not collected in the North East Atlantic.

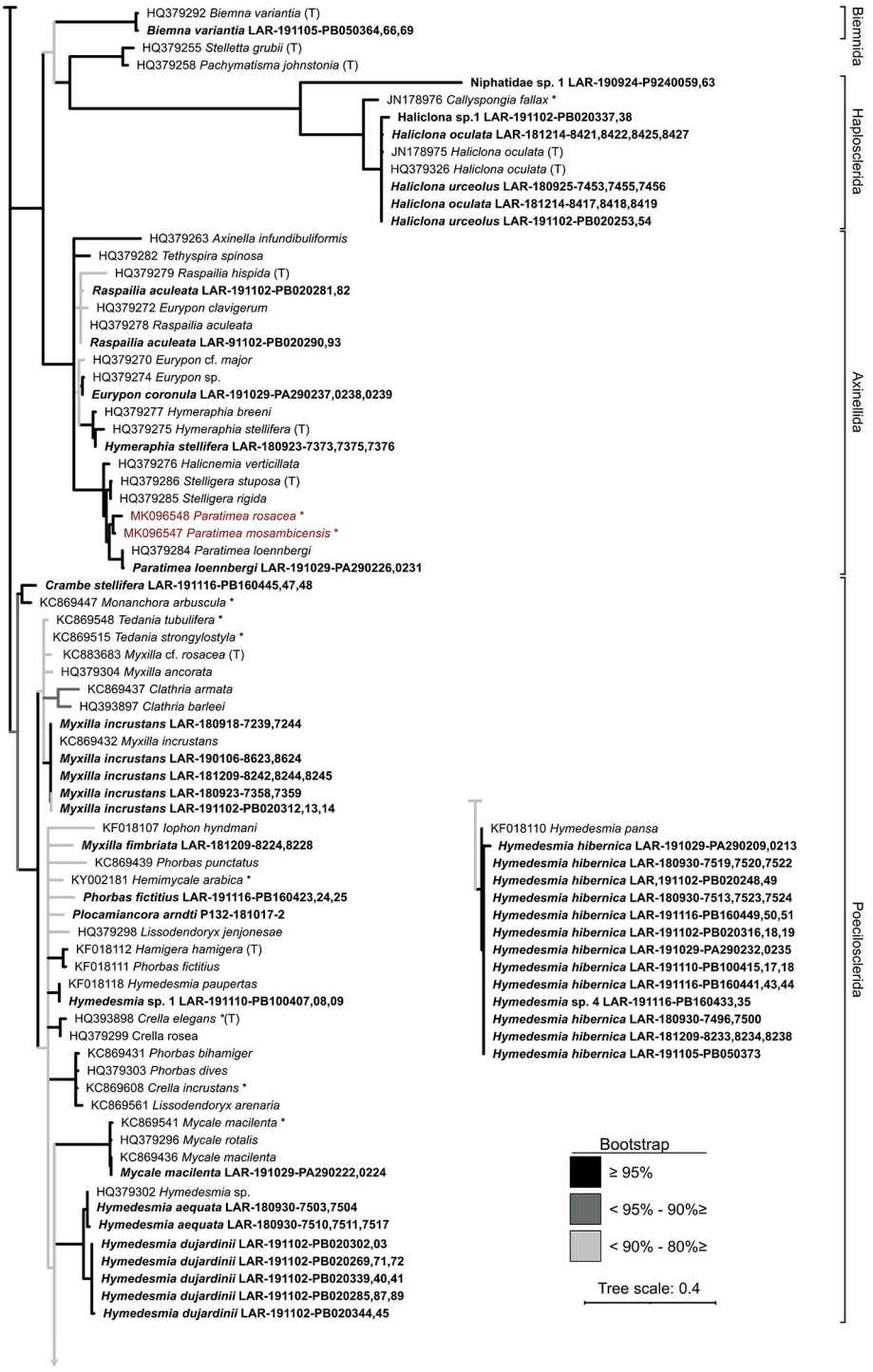

Fig. 3. Maximum Likelihood tree based on DNA region encoding for 28S (D3D5) by IQTREE under the model TIM2+F+I+G4. The node support in bootstrap (bt) is shown in grayscale: light gray - 80 < bt < 90%; bark gray - 90% ≤ bt < 95%; black - bt ≥ 95%. The tips show the taxon and accession number (sequences retrieved from GenBank) or specimens sequenced in this study (in bold). All sequences in red are associated to type specimens. Sequences retrieved from GenBank are coded: (T) type taxon; * specimens that are not collected in the North East Atlantic.

collected by SCUBA (80% success rate), which was to be expected since the STI specimens were generally fixed in ethanol 70% instead of ethanol 96%.

The multiple sequence alignments comprised 151 sequences and 670 base pair positions for coxI and 168 sequences and 774 positions for 28S D3-D5. The modelfinder selection through IAC criteria favoured the substitution model TIM2+F+I+G4 for coxI (Folmer fragment) and GTR+F+I+G4 for 28S D3-D5.

The coxI (Fig. 2) and 28S D3-D5 (Fig. 3) phylogenies are congruent at species level. Furthermore, the phylogenetic analyses are overall compatible with our morphological identifications, with a few exceptions:

a) Specimen P089-111026-1, was initially morphologically identified as *Halisarca dujardinii* Johnston, 1842, but groups as a sister-species of *Halisarca desqueyrouxae* Willenz, Ereskovsky & Lavrov, 2016 (KY564211, coxI sequence of type) and not with *H. dujardinii* in the coxI maximum likelihood tree (Fig. 2). This prompted a re-examination and it is now described as a species new to science, *H. hansghanssoni* sp. nov. We use molecular species delimitation techniques to support this assignment (see Material and methods – Species delimitation section);

b) Specimen P088-111101-1 identified as *Amphilectus ovulum* (Schmidt, 1870) was found in a clade with sequences of *Clathria barleei* (Bowerbank, 1866), which may due to DNA cross-contamination, as misidentification seems less likely (Fig. 2);

c) A specimen of *Hymeraphia stellifera*, is found within poecilosclerids even after two independent DNA extractions thus indicating a persistent environmental contamination, possibly from an associated species;

d), *Phorbas dives* (Topsent, 1891) and *Myxilla incrustans* (Johnston, 1842) group closely together in coxI consensus tree (Fig. 2), suggesting they could be the same species. This contrasts with the 28S D3-D5 phylogeny using a *P. dives* GenBank sequence (Fig. 3);

e) Other species not discriminated by one or both molecular markers include *Haliclona urceolus* vs *Haliclona oculata* (coxI and 28S) and *Hymeraphia stellifera* vs. *Hymeraphia elongata* (coxI).

In the following section, we describe species previously unreported for Sweden or species for which knowledge on their distribution or morphology is lacking. The synonymy list we provide is limited, encompassing the original combination, synonyms used in the literature discussed within this study, and the currently accepted name.

Taxonomy

Class Demospongiae Sollas, 1885
Order Chondrillida Redmond *et al.*, 2013
Family Halisarcidae Schmidt, 1862
Genus *Halisarca* Johnston, 1842

Halisarca hansghanssoni sp. nov.
urn:lsid:zoobank.org:act:E7E4A2DA-CA9E-4583-A7E9-49B667220BA6
Fig. 4–5

Etymology

The species is named in memory of Hans G. Hansson (1945–2011), a marine invertebrate specialist at the University of Gothenburg's field station at Tjärnö. He shared his knowledge and fascination for

marine fauna with cohorts of students and was instrumental in the Skagerrak inventory undertaken by the Swedish Taxonomy Initiative.

Material examined

Holotype

SWEDEN • 1 spec.; 58.1345° N, 10.8012° E; 248–206 m depth; 25 Aug. 2006; Artprojektets Skagerrak-inventering leg. [SK58 (SK37 återbesök)]; dredge; P089-111026-1; GenBank no.: OM436239 (coxI); GNM Porifera 594.

Paratype

NORWAY • 1 spec.; BIOSKAG 2006, STN6 (off Grimstad); 58.2129° N, 9.3447° E; 664–663 m depth; muddy bottom; 25 Jun. 2006; Paco Cárdenas leg.; Sneli sledge; PC1387; GenBank nos: OR269461 (coxI), PP763168 (28S D1-D2); UPSZTY 190226.

Confer status specimen

NORWAY • 1 spec.; Skorpeodden-Korsfjord; 60.1608° N, 5.1691° E; 10 Mar. 2006; Paco Cardenas leg.; GenBank no.: PP415521 (coxI); UPSZMC 191711.

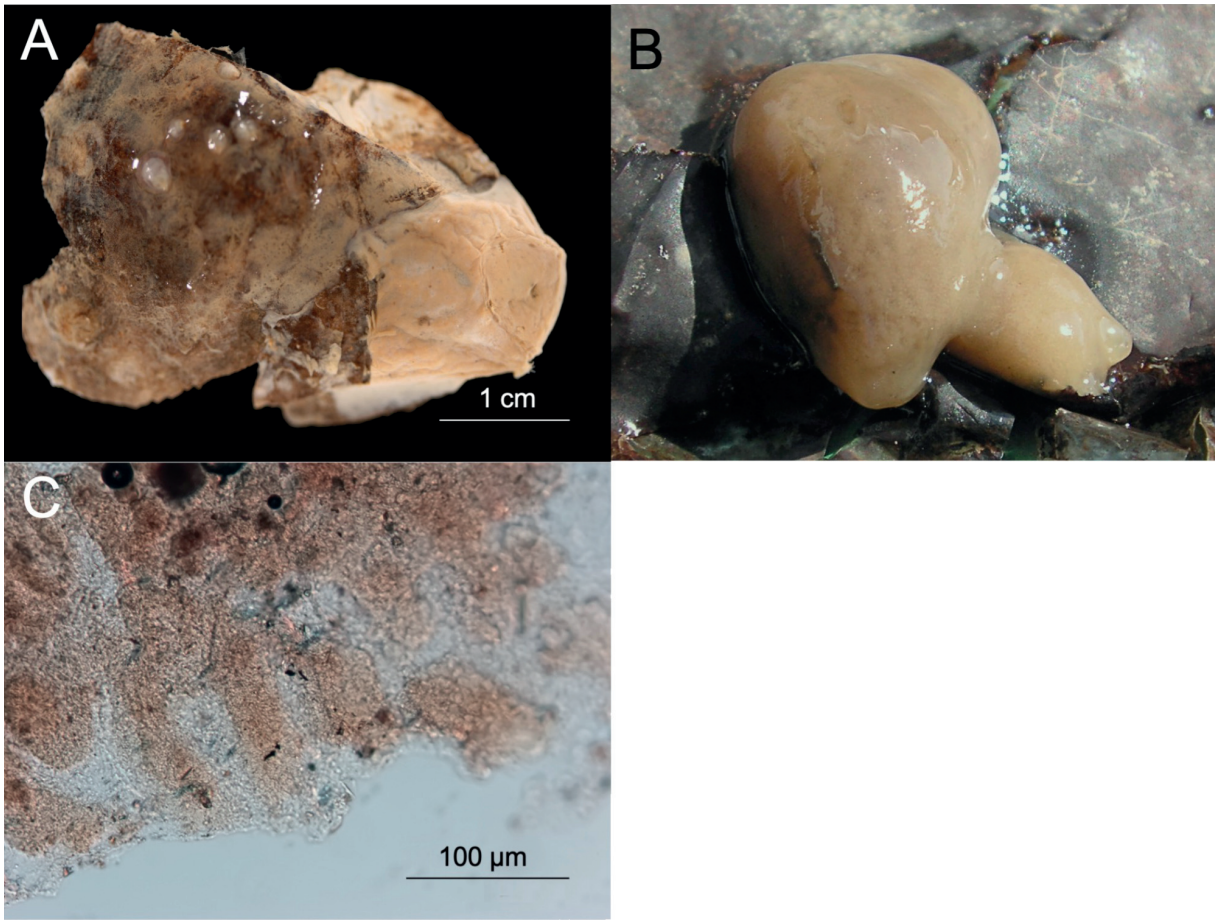

Fig. 4. *Halisarca hansghanssoni* sp. nov. **A**. GNM Porifera 594 (P089-111026-1) (holotype), preserved specimen growing on dead shell. **B**. UPSZTY 190226 (paratype), specimens fresh/in vivo growing on plastic. Notice one oscule on top surface. **C**. GNM Porifera 594 (P089-111026-1), thick section showing choanocyte chambers.

Description

The holotype is a small encrusting specimen, growing on a dead bivalve shell, with a maximum diameter of 1.70 cm and a maximum thickness of 3 mm. Surface is smooth but with the canals of the aquiferous system visible as depressions.(Fig. 4A). Consistency firm but compressible and non-friable. Preserved in ethanol, and unknown color when alive. The other two specimens examined, including the paratype, presented a natural colour of creamy pale brown when alive (Fig. 4B).

For the holotype only one osculum is visible, in the thicker area of the specimen. Its shape was slightly oval and without a visible rim, measuring 1 mm maximum diameter. The ostia were visible and uniformly scattered on the surface, measuring 554.2–**763.2**–991.4 ± 139 µm (N = 17) in diameter (Fig. 4A). The paratype was growing on a piece of plastic while the west Norwegian specimen (UPSZMC 191711) was growing on the sponge *Stelletta normani* Sollas, 1880.

Micro-anatomy

The choanocyte chambers are elongated (Fig. 4C), measuring 107–133 × 23–32 µm (N = 3). Embryos were not found in the sections of the holotype.

Remarks

The specimens were all preserved in ethanol upon collection, which prevented rigorous histological work. However, when comparing its choanocyte chamber sizes with the species described for *Halisarca* (Ereskovsky *et al.* 2011; Alvizu *et al.* 2013; Willenz *et al.* 2016), only five species are compatible with the present specimens, of which none have been reported from the northeast Atlantic (NEA) or the Mediterranean. Furthermore, all of those species have a distribution restricted to shallow waters.

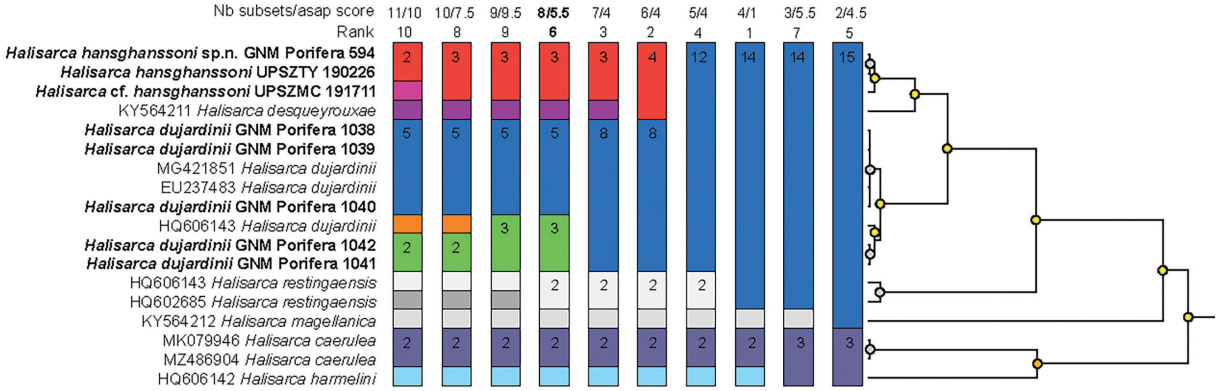

Fig. 5. Species delimitation results by Assemble Species by Automatic Partitioning (ASAP) (Puillandre *et al.* 2020) using coxI (Folmer fragment) multiple sequence alignment to calculate pairwise genetic distances according to the Jukes-Cantor model. On the left the columns (partitions) represents a possible way to group the genetic data into distinct clusters (subsets/putative species), which are distinguished by colour and with the numbers inside representing the number of tips/sequences grouped within it. Nb subsets – number of subsets/putative species. asap score – support for species delineation for each partition. Rank – ranked scores based on distance matrix. On the right a distance matrix cladogram with nodes coloured according to the probability of merging with known distances within each subset (from dark to light), where an unlikely group is indicated by a dark colour and grey representing uncalculated nodes.

The species with a similar size range of choanocyte chambers are: a) *Halisarca cerebrum* (Bergquist & Kelly 2010) described from Palau (West-central Pacific ocean) characterised by a convoluted surface, b) *Halisarca melana* de Laubenfels, 1954, also from Palau, presenting a jet-black colour alive or purple-brown when preserved in ethanol, c) *Halisarca magellanica* (Topsent 1901) described from southern Chilean fjords, exhibits high polymorphism, including pink or ivory colouration, encrusting morphology with 'dripping' outgrowths or massive encrusting, and surfaces that are smooth, slimy, or velvety, d) *Halisarca sacra* de Laubenfels, 1930 from Northeast Pacific (California) with a very soft consistency and elongated choanocyte chambers (140–200 µm × 40 µm), and e) *Halisarca laxus* (Lendenfeld 1885) from Southwest Indian ocean, with a soft consistency, lobate or digitate habitus. Our specimens deviate from the abovementioned species in terms of colour (*H. melana* and one morphotype of *H. magellanica*), surface and consistency (*H. magellanica* - ivory white, *H. sacra*), and habitus (*H. laxus*), by presenting yellowish-grey or brown-beige coloration, a firm but compressible and non-friable consistency, and an encrusting morphology, respectively.

In the NEA and Mediterranean there are three other species, which have been reported at a similar depth range as our specimens (Arndt 1935; Lévi 1956): a) *Halisarca dujardinii* (Johnston 1842) is the closest in morphology but is usually found in shallow waters and has larger choanocyte chambers (120–600 × 24–90 µm for *H. dujardinii*) (Ereskovsky *et al.* 2011), b) *Halisarca metschnikovi* (Lévi 1953) from Brittany, France, which is described with the same choanocyte chambers than what is reported for *H. dujardinii*, thus possessing larger choanocyte chambers than our specimen, c) *Halisarca harmelini* (Willenz *et al.* 2016), from the Mediterranean, has choanocyte chambers that are very narrow and the specimens are thin encrusting, with natural colour either translucent or slightly opaque and with very small chimney-like osculum measuring 100–500 height × 500 diameter µm (Ereskovsky *et al.* 2011), a description not fitting with our specimen.

Apart from the morphology indicating the specimen examined is an undescribed species, the phylogenetic analysis of coxI (Folmer fragment) (Fig. 2) shows that our specimens are more closely related to *Halisarca desqueyrouxae* (Willenz *et al.* 2016) presenting 1.42% of sequence divergence between them (KY564211) while the dissimilarity with *Halisarca dujardinii* sequences is of 2.63% (five specimens from Sweden were sequenced in this study). Furthermore, the overall sequence dissimilarity within *H. dujardinii* is 0.70% .Given this, we conclude that the specimen P089-111026-1 is not *H. dujardinii,* but rather more closely related to *Halisarca desqueyrouxae* (Willenz *et al.* 2016), described from Patagonia. The ASAP (Puillandre *et al.* 2021) results (Fig. 5) show that these specimens belong to the same partition apart from *H. desqueyrouxae* with a p-value of 0.5 (see Supp. file. 3), suggesting it to be a sister species to *H. desqueyrouxae*. The molecular evidence is further supported by morphology. While our specimens has an incrusting habitus*, H. desqueyrouxae* has a wrinkled surface, up to 2 cm thick with digitation and ridges or tubular overgrowths. Furthermore, both morphotypes of *H. desqueyrouxae* have elongated and convoluted choanocyte chambers that are 50–260 × 20–60 µm which is marginally larger than our measurements. After identification of this new species, two additional specimens were discovered in the private collection of co-author P. Cárdenas. The paratype (Fig. 4B) was collected deeper in the Skagerrak, off Grimstad in southern Norway, and had the exact same cox1 as the holotype. The second specimen, collected in the Korsfjord south of Bergen in western Norway, has a cox1 with 1 bp difference so we prefer to identify it as *H.* cf. *hansghanssoni* for now.

Subclass Keratosa Grant, 1861
Order Dendroceratida Minchin, 1900
Family Darwinellidae Merejkowsky, 1879
Genus *Aplysilla* Schulze, 1878

Aplysilla sulfurea Schulze, 1878
Fig. 6

Aplysilla sulfurea Schulze, 1878: 405–416, pl. XXIII– XXIV figs 15, 19–30.

Aplysilla sulphurea – Alander 1942: 18.

Material examined (3 specimens)

SWEDEN • 1 spec.; Saltbacken; 59.0832° N, 11.2242° E; 30 m depth; 24 Apr. 2018; Mats Larsson leg. [MM-180424-1]; SCUBA; LAR-180424-4596; voucher: GNM Porifera 991 • 1 spec.; Lunneviken; 59.0546° N, 11.1690° E; 30 m depth; 18 Sep. 2018; Mats Larsson leg. [MM-180916-1]; SCUBA; LAR-180918-7202, 7205; voucher: GNM Porifera 992 • 1 spec.; Yttre Vattenholmen; 58.8754° N, 11.1056° E; 30 m depth; 16 Nov. 2019; Mats Larsson leg. [MM-191116-1]; SCUBA; LAR-191116-PB160463–64, 66; voucher: GNM Porifera 993.

Description

The specimens have a thick encrusting morphology. The living specimens had a yellow sulphur colour, turning to dark purple when fixed in ethanol. The surface is conulose (Fig. 6A). In some specimens (in situ and while expanded) it is possible to observe a network of membranous polygonal areas heavily pierced by multiple ostia, enabling to see the inside of the sponge. The oscula are spread, often on oscular chimneys, and with translucent membranous rims.

Skeleton

The skeleton is composed of dendritic fibres (i.e., the fibres might ramify but never coalesce) attached to a spongin basal plate, clear of debris (Fig. 6B). The fibres have a distinct core, darker, that occupies 80–90% of the total thickness of the fibre. Fibres are thicker at the base becoming thinner toward the tip.

Ecology and distribution

Specimens of this species have been reported worldwide. However, most reports are in the Atlantic, North Sea and Mediterranean (GBIF.org 2021) from the littoral zone (under rocks or in crevices) to 230 m (Ackers *et al.* 2007). The type locality is in the Adriatic Sea.

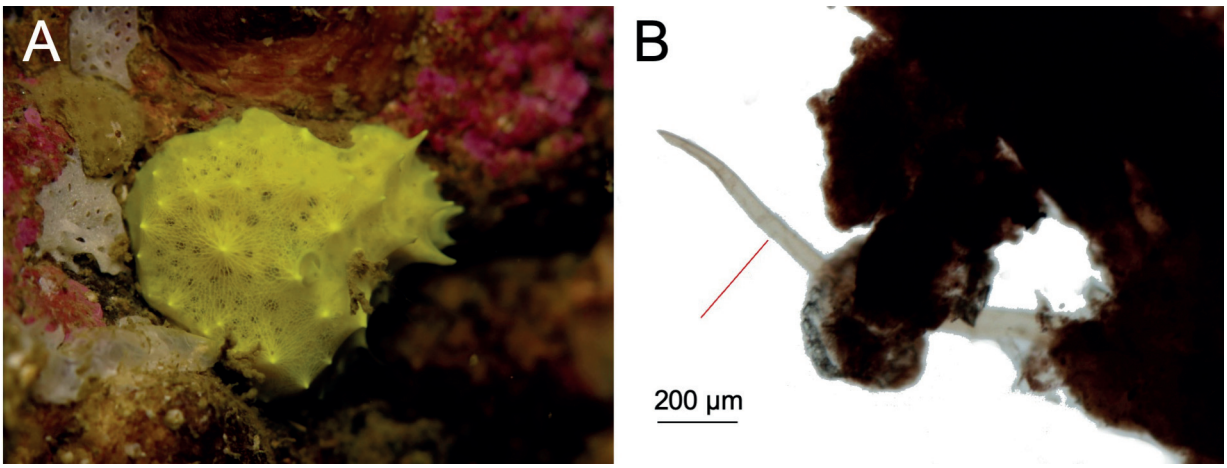

Fig. 6. *Aplysilla sulfurea* Schulze, 1878. **A**. Live specimen, GNM Porifera 992 (LAR-180918- 7202, 7205). **B**. Fibers from specimen, GNM Porifera 991 (LAR-180424-4596).

Remarks

The species of the genus *Aplysilla* can be discriminated by the colour as it seems to be a stable feature in the genus (Bergquist 1980). However, a few specimens identified as *A. sulfurea* have been reported with a pale yellow colour as opposed to the typical bright/sulphurous yellow. All specimens we examined had a bright yellow colour.

The distinction between species relies primarily on external features, such as colour and conule size. These features are difficult to observe in preserved, or damaged specimens, which could explain the low number of described species. The microscopic features that distinguish the species are: the fibre pigmentation, and fibre ramifications, which can be easily overlooked, or dependent on the size of the sponge.

Aplysilla glacialis (Merejkowsky, 1878)
Fig. 7

Simplicella glacialis Merejkowsky, 1878: 264–265.

Aplysilla glacialis – de Laubenfels 1948: 164–165, fig. 24.

Material examined

SWEDEN • 1 spec.; Saltbacken; 59.0832° N, 11.2242° E; 24 Apr. 2018; Mats Larsson leg. [MM-180424-1]; SCUBA; LAR-180424-4587–4588; voucher: GNM Porifera 990.

Description

An encrusting sponge of which we collected a fragment measuring 7 mm long by 6 mm. Colour in vivo is dirty white, turning snow white in ethanol. The surface is conulose (Fig. 7A) with smaller/shorter conules than *A. sulfurea*. The surface presents a network composed of polygonal areas of translucent membrane with multiple ostia. The osculum has a high translucent rim almost papillae-like.

Skeleton

The skeleton of the specimen of *Aplysilla glacialis* closely resembles that of *Aplysilla sulfurea* (Fig. 7B).

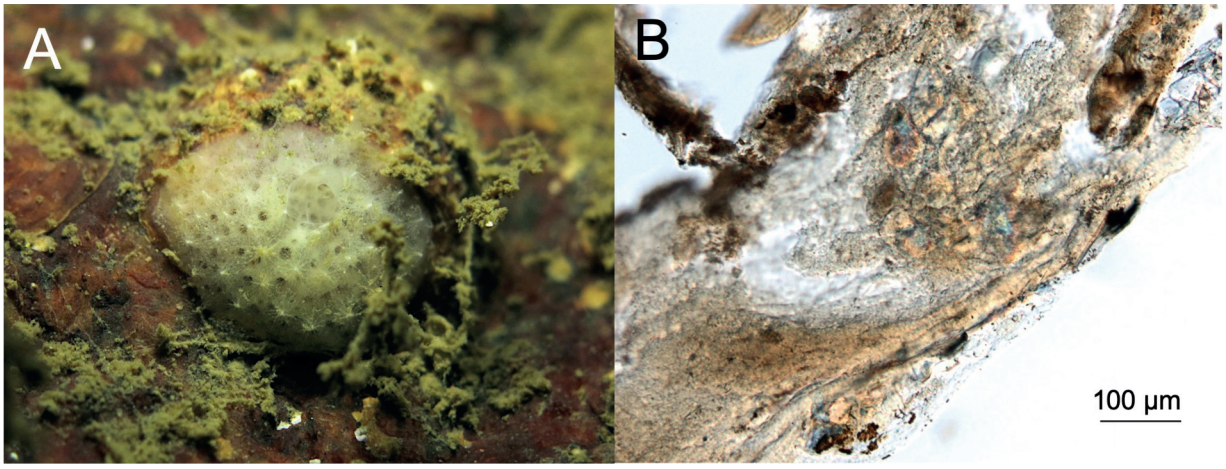

Fig. 7. *Aplysilla glacialis* (Merejkowsky, 1878). **A**. Live specimen with thin encrusting morphology, GNM Porifera 990 (LAR-180424-4587–4588). **B**. Cross section.

Ecology and distribution

The original distribution is the White Sea, next to the Barents Sea (Merejkowsky 1878a). In synonymy, the species has records from the east South Pacific up to California and within the west South Pacific, specifically in Australia. However, this is likely incorrect, see Remarks below.

Remarks

Our specimen conforms to the description of *Aplysilla glacialis* (Merejkowsky 1878b) which has its type locality in the White Sea. De Laubenfels (1948) synonymised several other names with *A. glacialis*, namely: a) *Aplysilla arenosa* Hentschel, 1929, from the North Atlantic a preoccupied name later substituted with *Aplysilla arctica* by de Laubenfels (1948), b) *Aplysilla palida* Lendenfeld, 1889, from Australia, and c) *Aplysilla lendenfeldi* Thiele, 1905, from southern Chile. The latter two synonymies are dubious since they would imply a cosmopolitan distribution for *A. glacialis*. The species *A. arctica* is reported from northern Norway (Hentschel 1929), and Hentschel (1929) considers its main distinguishing feature to be strong content of organic foreign material. However, the descriptions for *A glacialis* do not mention the inclusion of the foreign particles. It is a possible that *A. arctica* constitutes a junior synonym of *A. glacialis*, but further studies are warranted to support this hypothesis.

Order Haplosclerida Topsent, 1928
Family Chalinidae Gray, 1867
Genus *Haliclona* Grant, 1841

Haliclona sp. 1
Fig. 8

Material examined

SWEDEN • 1 spec.; Lunneviken; 59.0546° N, 11.169° E; 25 m depth; 2 Nov. 2019; Mats Larsson leg. [MM-191102-1]; SCUBA; LAR-191102-PB020337–38; GenBank nos: OM436271 (coxI), OM415636 (28S D3-D5); voucher: GNM Porifera 1021.

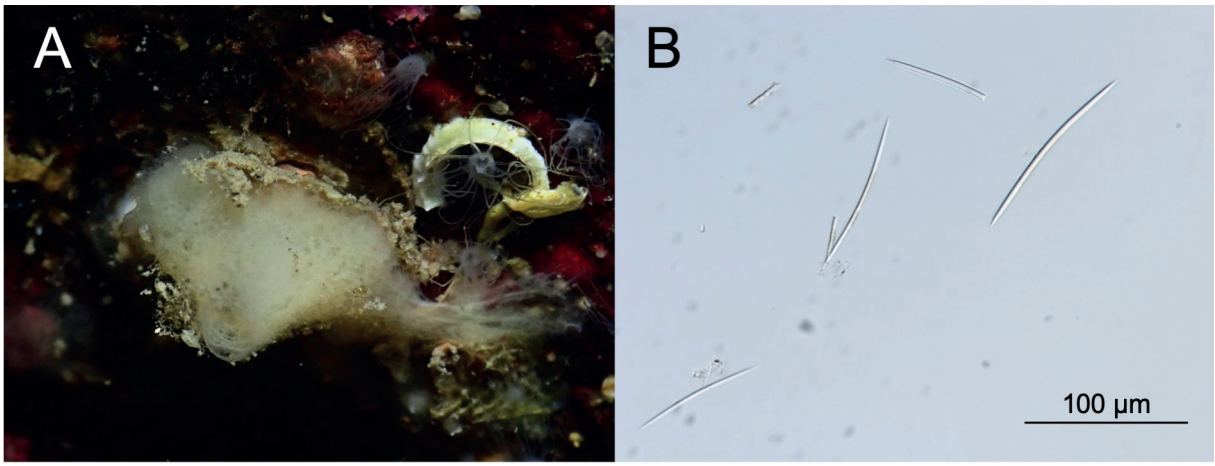

Fig. 8. *Haliclona* sp. 1. specimen GNM Porifera 1021, (LAR-191102-PB020337–38). **A**. Live specimen. **B**. Oxeas.

Description

A massive encrusting specimen, of which only a fragment was collected ca 3 mm long by 2 mm wide. The sponge was roughly cone-shaped, with an osculum on top of the 'chimney'. The surface is velvety. The specimen was creamy white when alive, but turned yellowish beige when preserved in ethanol (Fig. 8A).

Skeleton

Due to the dimensions of the collected fragment it was not possible to produce a thick section. Spicules are thin oxeas, with a wide range of sizes (Fig. 8B), measuring: 71.4–**103.8**–136.1 ± 10.26 × 0.1–**3.1** – 6.1 ± 1.27 µm (N = 61).

Family Niphatidae van Soest 1990

Niphatidae sp. 1
Fig. 9

Material examined

SWEDEN • 1 spec.; Svartejan; 59.1102° N, 11.3219° E; 24 Sep. 2019; Mats Larsson leg. [MM-190924-1]; SCUBA; LAR-190924-P9240059, 63; GenBank no.: OM436284 (coxI), OM415650 (28S D3-D5); voucher: GNM Porifera 1090.

Description

A massive encrusting specimen, from which we collected a fragment ca 4 mm long. The specimen was growing on a vertical rock. Its pores are visible as well as a single simple osculum, which was on the top of a cone; in situ, some of the aquiferous canals were visible in the thinnest areas of the sponge. The surface is hispid. The natural colour is whitish-grey (Fig. 9A), transitioning to snow white in ethanol.

Skeleton

The small dimensions of the collected fragment did not allow us to produce a thick section. The spicules are thick, slightly curved oxeas with sharp points (Fig. 9B), measuring: 100.0–**183.4**–210.0 ± 20.18 × 5–**7.4**–10 ± 1.25 µm (N = 29) (Fig. 8B). We did no find microscleres.

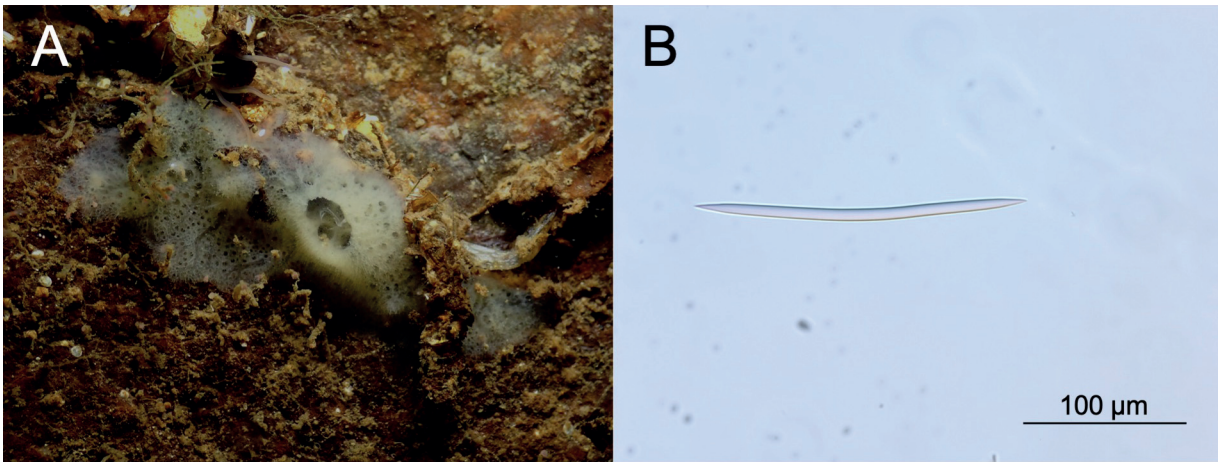

Fig. 9. Niphatidae sp. 1. specimen, GNM Porifera 1090 (LAR-190924-P2940059, 63). **A**. Live specimen. **B**. Oxea.

Order Axinellida Lévi, 1953
Family Raspailiidae Nardo, 1833
Genus *Hymeraphia* Bowerbank, 1864

Hymeraphia elongata Picton & Goodwin, 2007
Fig. 10

Hymeraphia elongata Picton & Goodwin 2007: 1448, fig. 5.

Material examined (3 specimens)

SWEDEN • 1 spec.; Svartejan; 59.1102° N, 11.3219° E; 30 m depth; 11 Aug. 2018; Mats Larsson leg. [MM-180911-1]; SCUBA; LAR-180911-7154–7155; GenBank no.: OM436254 (coxI); voucher: GNM Porifera 1077 • 1 spec.; same collection data as for preceding; 22 Dec. 2018; Mats Larsson leg. [MM-181222-1]; SCUBA; LAR-181222-8561, 8563, 8569; voucher: GNM Porifera 1078 • 1 spec.; Bergylteskär; 58.8289° N, 11.0831° E; 30 m depth; 9 Dec. 2018; Mats Larsson leg. [MM-181209-1]; SCUBA; LAR-181209-8302–8303, 8305; GenBank no.: OM436250 (coxI); voucher: GNM Porifera 1076.

Description

The three specimens have a thin incrusting morphology and were partially covered in silt. The surface is microhispid, and with visible pores and oscula. The oscula are elevated in a translucent chimney (Fig. 10A). The aquiferous system is partially visible at the surface. The colour in live specimens ranges from greyish-yellow (Fig. 10B) to orange-yellow (Fig. 10A) and changes to white when specimens are preserved in ethanol.

Skeleton

Megascleres are long tylostyles with an inflated head similar to the ones of acanthostyles (Fig. 10C), measuring 394.3–**850.3–**1275.7 ± 311.5 × 3–**7.1**–12.5 ± 2.6 µm (N = 16). Additionally, there are long hair-like styles (common) or oxeas (rare) (Fig. 10D) with 184.7–**258.0–**321.5 ± 42.9 × 0.6–**1.5–**2.2 ± 0.4 µm (N = 32) in size, and short acanthostyles with an inflated triangular head and shorts spines only at the tip (Fig. 10E), measuring 49.3–**89.9**–118.4 ± 21.3 × 7–**13.5–**16 ± 2.3 µm (N = 32).

Remarks

The major differences between *H. elongata* and *H. stellifera* are: the size of the spines in the acanthostyles, length of the anisoxeas, the colouration, and surface texture. The specimens of *H. elongata* present shorter spines in the acanthostyles and longer anisoxeas than what is reported for *H. stellifera*. Moreover, *H. elongata* presents a beige colour when alive and a smooth surface whereas *H. stellifera*'s life colour is deep orange and a microshipid or vilose surface. In comparison, the acanthostyles in *Hymeraphia breeni* Picton & Goodwin, 2007 have few but longer spines at the tip, than what is reported for *H. elongata* or *H. stellifera*.

This species is a new record for Sweden, which is not surprising since the species was described in 2007. The specimens collected in Sweden present slightly shorter styles than what is reported for the type specimens (Picton & Goodwin 2007), which might indicate the presence of regional differences or cryptic species. However, further studies are warranted to understand the order of inter- and intra-specific diversity, as well as micro-morphological diversity or plasticity within this genus. In fact, this is the first time that specimens of *H. elongata* are sequenced. In spite of morphological differences, the coxI sequences reveal at least two haplotypes with 1–2 bp differences, which show no clear distinction between *H. elongata* and *H. stellifera* (Fig. 2). However, the lack of resolution using coxI is perhaps

expected as this marker is known for having a substitution rate that is too low for adequate species discriminations (e.g., Erpenbeck *et al.* 2006). Therefore, future research is required to assess the validity of *H. elongata*. This could involve utilizing 28S D1-D2, known for its ability to distinguish between *Hymeraphia* species (Morrow *et al.* 2018), and incorporating sequences from the type specimen or specimens from the type locality.

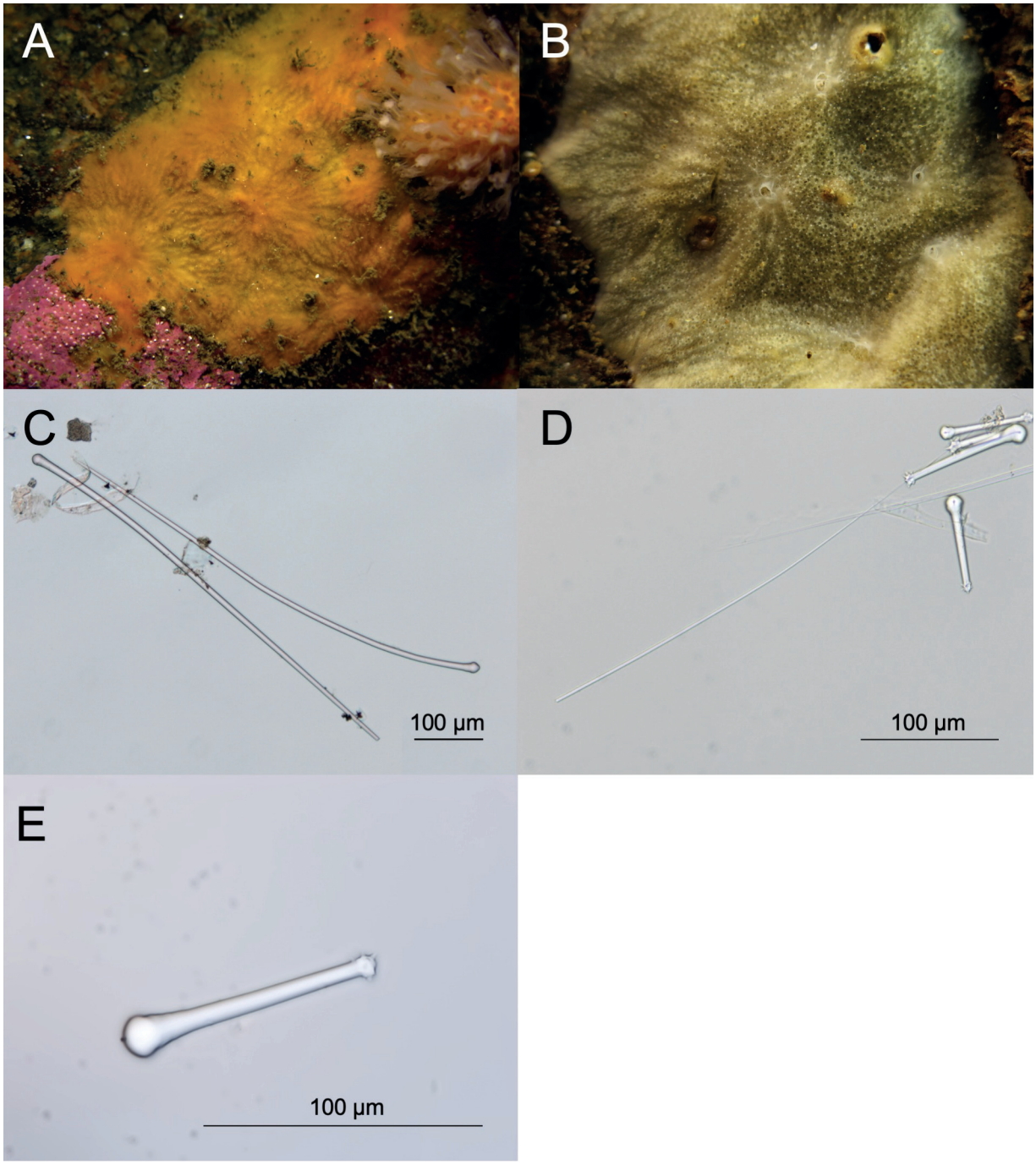

Fig. 10. *Hymeraphia elongata* Picton & Goodwin, 2007. **A**. Live specimen with thin encrusting morphology (LAR-180930-7526–7528), orange colour. **B**. Living specimen, GNM Porifera 1078 (LAR-181222-8561, 8563, 8569), yellow pale colour. **C**. Tylostyles (LAR-180424-4603). **D**. Long and thin style (LAR-180424-4603). **E**. Acanthostyle (LAR-180424-4603).

Genus *Raspailia* Nardo, 1833

Raspailia aculeata (Johnston, 1842)
Fig. 11

Halichondria aculeata Johnston 1842: 131, pl. XIII figs 1–3.

Dictyocylindrus aculeatus Bowerbank, 1866: 109. – Bowerbank 1874: 48, pl. XIX figs 5–12.
Raspailia aculeata – Hanitsch 1894: 196. — Arndt 1935: 82–83, fig. 72.

Not *Raspailia aculeata* – Topsent, 1925: 682–685, pl. VIII, fig. 14. — Uriz 1978: 149–161, figs 88–94.
Not *Raspaciona aculeata* –Topsent 1936: 49–50.

Material examined (2 specimens)

SWEDEN • 1 spec.; Saltbacken; 59.0832° N, 11.2242° E; 51–25 m depth; 1 Oct. 2019; Mats Larsson leg. [MM-191001-1]; SCUBA; LAR-191001-PA010107–0108, voucher: GNM Porifera 1118 • 1 spec.; Lunneviken; 59.0546° N, 11.1690° E; 51–25 m depth; 12 Nov. 2019; Mats Larsson leg. [MM-191102-1]; SCUBA; LAR-191102-PB020290, 93; GenBank no.: OM415584 (28S D3-D5); voucher: GNM Porifera 1119.

Description

The specimens have an encrusting morphology with digitiform projections. The colour, while alive, was dirty white or wax yellow turning white in ethanol. The surface is hispid and covered with sediment (Fig. 11A). Neither oscula nor pores were visible (Fig. 11A).

Skeleton

The skeleton is reticulated and formed by dense plurispicular fibres, with slightly curved styles, which can protrude the surface, especially at the very end of the digitiform projections. Moreover, the protruding styles often have a tyle at their end, i.e., they are often styloids. Acanthostyles are rare and present in the choanosome. The ectosome is composed by a membrane containing parallel oxeas or anisoxeas. At the base of the specimen, these oxeas/anisoxeas have a confused arrangement.

There are three types of megascleres: slightly curved styles that are often modified in styloids (Fig. 11D), measuring 619.3–**949.9**–1325.9 ± 267.97 × 3.4–**6.1**–12.1 ± 2.85 µm (N = 8), curved anisoxeas, which can have blunt tips (rare) (Fig. 11E), measuring 253.9–**357. 2**–475.7 ± 62.5 × 0.8–**2.5**–4.5 ± 0.93 µm (N = 36), and curved, fully spined acanthostyles (Fig. 10F), of 98.6–**154.1**–294.3 ± 65.37 × 4.0–**6.5**–10.1 ± 1.57 µm in size (N = 16).

Ecology and distribution

This species is reported in the northeast Atlantic (NEA), from North Ireland to the Azores and with a depth range from the subtidal to 15 m depth. Furthermore, there are reports of this species in the Mediterranean Sea. However, given that the morphology of the Mediterranean specimens most likely conforms to the description by Topsent (1936), which differs significantly from the descriptions of *R. aculeata* in (Ackers *et al.* 1985, according to the WPD), we doubt the Mediterranean reports to be referring to the same species.

Remarks

In the re-examination of Mr Beans' collection, Bowerbank (1866) reported aspiculate gemmulae. However, this was never mentioned by subsequent authors. Therefore, we cannot assert that gemmulae occur in *R. aculeata*, nor how common they are.

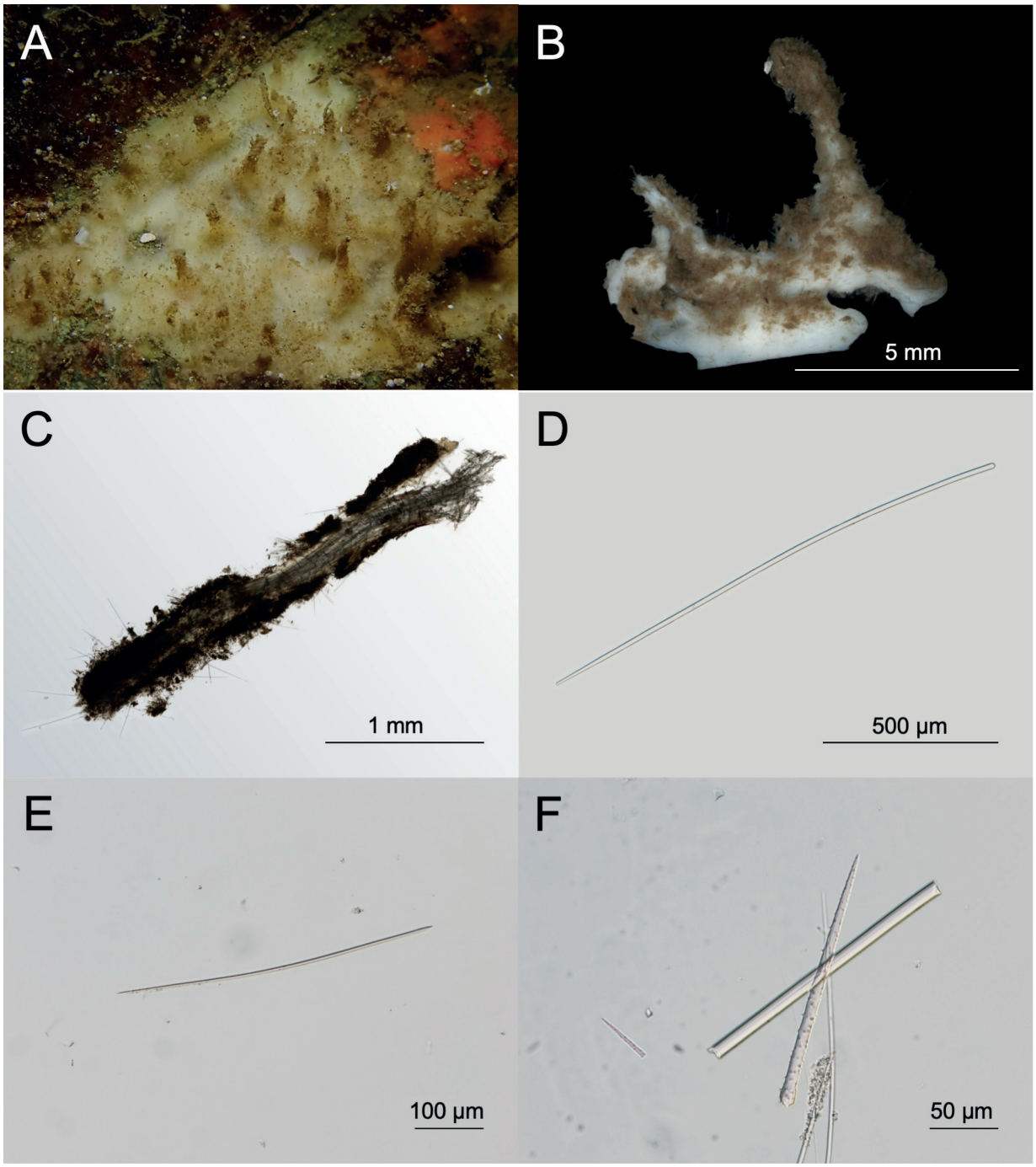

Fig. 11. *Raspailia aculeata* (Johnston, 1842). **A**. Specimen in situ, GNM Porifera 1119 (LAR-191102-PB20290, 93). **B**. Specimen preserved. **C**. Hand-section of LAR-191001-PA0107, 0109–0110. **D**. Style. **E**. Oxea. **F**. Acanthostyle.

Raspailia cf. ***aculeata*** (Johnston, 1842)
Fig. 12

Material examined

Sweden • 1 spec.; 58.1352° N, 11.2512° E; 46–51 m depth; 20 Aug. 2007; Artprojektets Skagerrak-inventering leg. [SK67]; dredge; P053-111101-2; voucher: GNM Porifera 763.

Description

This specimen was collected through dredging and consists only of fragments that are interpreted as the digitiform projections (Fig. 12A). However, due to the poor condition of the specimen, we cannot be certain. For the same reason, the external morphology of these specimens cannot be assessed. The surface appears to be hispid. The natural colour is unknown and the colour in ethanol is dark beige (Fig. 12A).

Skeleton

The skeleton is as described previously for *Raspailia aculeata* (see above) but presenting differences in the spicules, which warrant the confer status: slightly curved styles (Fig. 12B) (rarely modified into styloids), measuring 840.0–**1135.3**–1300.0 ± 134.84 × 7.5–**9.9**–15.0 ± 1.41 µm (N = 29), curved anisoxeas, majority of which have one tip blunt and the other tip mucronate or stepped, measuring 310.0–**428.6**–530.0 ± 48.99 (N = 29) × 2.5–3.6–5 ± 1.09 µm (N = 29), and curved and fully acanthostyles (Fig. 12D), with 105.0–**185.8**–320 ± 53.88 × 10.0–**12.7**–17.5 ± 2.07 µm in size (N = 30).

Remarks

The specimen P053-111101-2 was collected by dredging at ca 50 m depth, which is deeper than reported for the species *R. aculeata*. Coincidentally, P053-111101-2 presents some differences in its spicules when compared with the two previous specimens of *R. aculeata*, namely the oxeas being slightly larger and with different tips. Unfortunately, given the poor preservation condition of P053-111101-2, we have not succeeded in obtaining any amplicon to confirm the specimen assignment. This specimen could also be *Raspailia virgultosa* (Bowerbank, 1866). However, in the absence of a revision of these species, we have decided to maintain this specimen assigned to *Raspailia* cf. *aculeata*.

Order Bubarida Morrow & Cárdenas, 2015
Family Bubaridae Topsent, 1894
Genus *Phakellia* Bowerbank, 1862

Phakellia rugosa (Bowerbank, 1866)

Dictyocylindrus rugosus Bowerbank 1866: 119–120.

Axinella rugosa – Fristedt 1885: 47–48; 1887: 461. — Arndt 1935: 89, fig. 188. — Alander 1942: 70–71.
Pseudaxinella sulcata Schmidt, 1865 – Alander 1942: 69–70 (key), 70 (description).

Material examined (41 specimens)

SWEDEN • 1 spec.; Kosterhavet; 58.8833° N, 11.0833° E; 1 Nov 2001; Fredrik Pleijel leg. [TML-01]; P006-011116-1; voucher: GNM Porifera 1096 • 1 spec.; 58.7439° N, 10.7336° E; 102–76 m depth; 31 May 2006; Artprojektets Skagerrak-inventering leg. [SK 15]; dredge; P006-111006-1; voucher: GNM Porifera 949; P006-111006-1 • 1 spec.; same collection data as for preceding; voucher: GNM Porifera 950 • 1 spec.; same collection data as for preceding; P006-111124-6–7; voucher:

GNM Porifera 502 • 1 spec.; 57.6451° N, 11.6114° E; 74–39 m depth; 24 Aug. 2006; Artprojektets Skagerrak-inventering leg. [SK51]; dredge; P006-111006-3; voucher: GNM Porifera 536 • 1 spec.; 58.7014° N, 11.0372° E; 172–140 m depth; 1 Jun. 2006; Artprojektets Skagerrak-inventering leg. [SK 17]; dredge; P006-111007-1; voucher: GNM Porifera 503 • 7 specs; same collection data as for preceding; P006-111007-2–8; voucher: GNM Porifera 503 • 1 spec.; 58.3888° N, 10.4314° E; 353–335 m depth; 29 May 2006; Artprojektets Skagerrak-inventering leg. [SK 2]; dredge; P006-111010-1; voucher: GNM Porifera 500 • 1 spec.; 58.3566° N, 10.4727° E; 353–331 m depth; 5 Jun. 2006; Artprojektets Skagerrak-inventering leg. [SK 22]; dredge; P006-111010-2; voucher: GNM Porifera 951 • 1 spec.; 58.6828° N, 10.8174° E; 163 m depth; 1 Jun. 2006; Artprojektets Skagerrak-inventering leg. [SK 18]; dredge; P006-111010-3; voucher: GNM Porifera 504 • 1 spec.; 58.9628° N, 11.0229° E; 49–14 m depth; 24 Aug. 2007; Artprojektets Skagerrak-inventering leg. [SK96]; dredge; P006-111013-1; voucher: GNM Porifera 895 • 1 spec.; 58.6453° N, 11.0148° E; 118–44 m depth; 22 Aug. 2007; Artprojektets Skagerrak-inventering leg. [SK74]; dredge; P006-111013-2; voucher: GNM Porifera 513 • 1 spec.; 58.4356° N, 10.8732° E; 100–93 m depth; 30 Aug. 2007; Artprojektets Skagerrak-inventering leg. [SK125]; dredge; P006-111013-3; voucher: GNM Porifera 519 • 1 spec.; 57.5164° N, 11.6549° E; 44–28 m depth; 21 Aug. 2007; Artprojektets Skagerrak-inventering leg. [KA126]; dredge; P006-111107-1; voucher: GNM Porifera 537 • 1 spec.; Svaberget; 58.3626° N, 11.062° E; 67–40 m depth; 16 Sep. 2010; Artprojektets Skagerrak-inventering leg. [SK265]; dredge; P006-111110-1; voucher: GNM Porifera 1097 • 1 spec.; 58.7399° N, 10.7403° E; 151–102 m depth; 22 Aug. 2007; Artprojektets Skagerrak-inventering leg. [SK79]; dredge; P006-111124-1; voucher: GNM Porifera 669

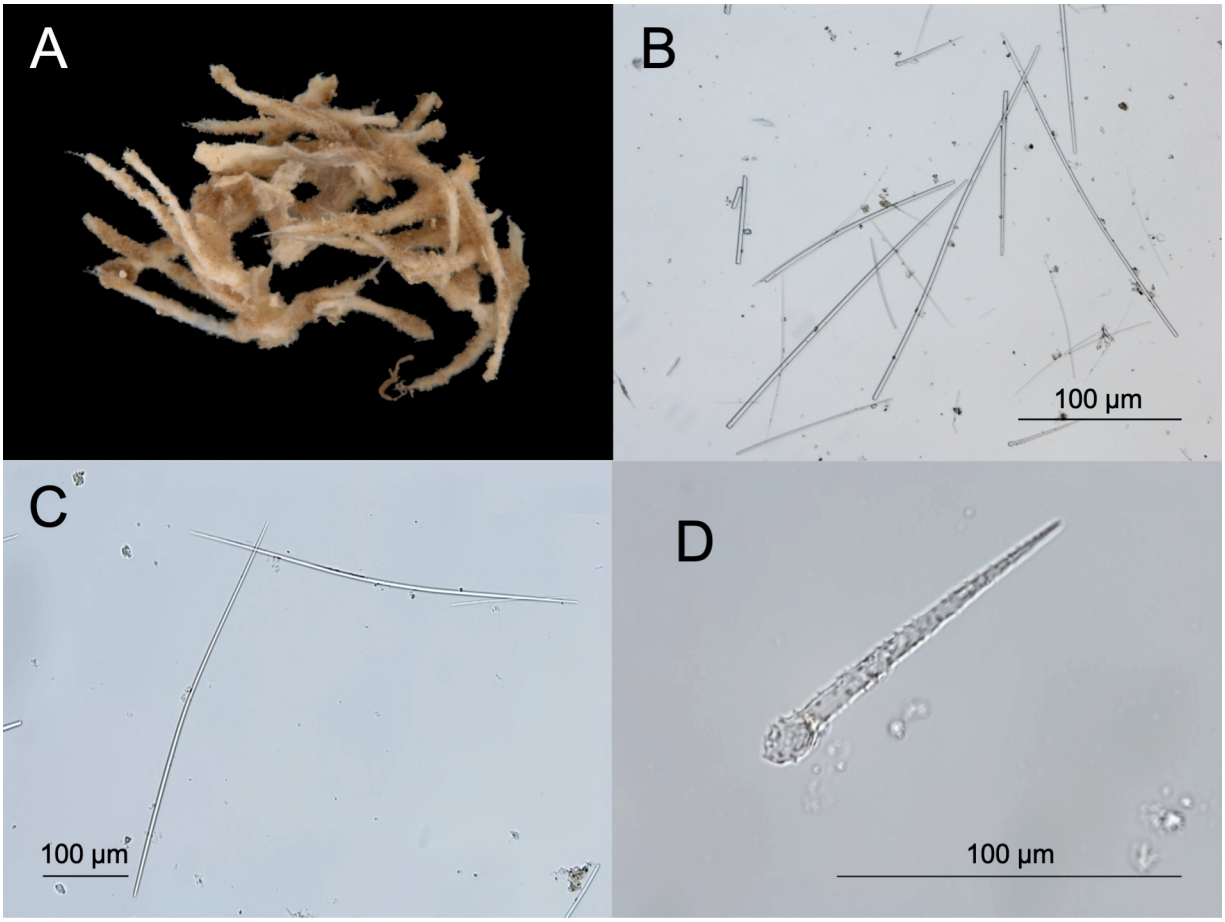

Fig. 12. *Raspailia* cf. *aculeata* (Johnston, 1842) specimen, GNM Porifera 763 (P053-111101-2). **A**. Specimen preserved in ethanol. **B**. Thin styles. **C**. Oxeas. **D**. Acanthostyle.

• 3 specs; 58.1352° N, 11.2512° E; 51–46 m depth; 20 Aug. 2007; Artprojektets Skagerrak-inventering leg. [SK67]; dredge; P006-111124-2–4; voucher: GNM Porifera 511 • 1 spec.; 58.487° N,′10.4228° E; 348–326 m depth; 30 Aug. 2007; Artprojektets Skagerrak-inventering leg. [SK128]; dredge; P006-111124-5; voucher: GNM Porifera 521 • 2 specs; 58.3888° N, 10.4314° E; 353–335 m depth; 29 May 2006; Artprojektets Skagerrak-inventering leg. [SK 2]; dredge; P006-111125-1 and 2; voucher: GNM Porifera 505 • 2 specs; 58.5696° N, 10.9829° E; 60–46 m depth; 21 Aug. 2007; Artprojektets Skagerrak-inventering leg. [SK71]; dredge; P006-111125-3–4; voucher: GNM Porifera 512 • 4 specs; 58.487° N, 10.4228° E; 348–326 m depth; 21 Aug 2007; Artprojektets Skagerrak-inventering leg. [SK128]; dredge; P006-111125-5 to 8; voucher: GNM Porifera 520 • 1 spec.; 58.4754° N, 10.5578° E; 260–222 m depth; 11 Oct. 2012; leg. [PM9-546]; dredge; P006-161123-1; voucher: GNM Porifera 1098 • 1 spec.; 58.2858° N, 10.4646° E; 394–345 m depth; 6 Feb. 2013; leg. [PM15-559]; dredge; P006-161123-2; voucher: GNM Porifera 1099 • 1 spec.; 58.6954° N, 10.8392° E; 64–42 m depth; 22 Aug. 2007; Artprojektets Skagerrak-inventering leg. [SK75]; dredge; P009-111013-1; voucher: GNM Porifera 668 • 1 specs; same collection data as for preceding; PA242-110404-1; voucher: GNM Porifera 668 • 1 spec.; 58.5032° N, 10.7195° E; 136–132 m depth; 28 Aug. 2007; Artprojektets Skagerrak-inventering leg. [SK115]; dredge; P065-110629-1; voucher: GNM Porifera 518 • 1 spec.; 57.5336° N, 11.6488° E; 38–24 m depth; 20 Aug. 2009; Artprojektets Skagerrak-inventering leg. [KA117]; dredge; PA413-110404-1; voucher: GNM Porifera 976.

Description

The specimens presented various morphotypes ranging from branching erect with distinct branches/projections to fuse branches, i.e., lamellated morphology. When preserved in ethanol, the colour is pale yellow. Given that the specimens were not observed in situ, the natural colour is unknown. However, the specimens of this species have been reported with a live colour ranging from white-grey to pale yellow. The surface is uneven rugose, varying in different specimens from almost conulose to smooth.

Skeleton

The skeleton is composed by a thick mesh of strongyles and oxeas, and with styles protruding the surface. Megascleres are: flexuous strongyles and oxeas measuring 570–1200 µm × 14–20 µm (N = 4), and styles measuring 975–1175 × 10–15 µm (N = 4).

Genus *Phakellia* Bowerbank, 1862

Phakellia robusta Bowerbank, 1866

Phakellia robusta Bowerbank 1866: 120–122.

Phakellia robusta – Fristedt 1885: 45 (key), 46–47. – Alander 1942: 70 (key), 71 (description).

Material examined (3 specimens)

SWEDEN • 1 spec.; Kosterhavet; 58.8833° N, 11.0833° E; 1 Nov. 2002; Fredrik Pleijel leg. [TML-02]; dredge; P009-021111-1; voucher: GNM Porifera 1094 • 1 spec.; 58.9537° N, 11.0189° E; 24 Aug. 2007; Artprojektets Skagerrak-inventering leg. [SK94]; dredge; P009-111010-1; voucher: GNM Porifera 706 • 1 spec.; 58.459° N, 10.548° E; 296–250 m depth; 12 Oct. 2012; leg. [PM14-556]; dredge; P009-130125-1; voucher: GNM Porifera 1095.

Description

The specimens have a thinly lamellated morphology. The colour is yellow when preserved in ethanol and unknown live. Furthermore, the specimens were covered in sediment, most likely due to collection method. The consistency is stiff.

Skeleton

The skeleton is composed of: curved styles measuring 1925–580 × 23–30 μm (N = 2) straight oxeas and strongyles 460–630 × 20–30 μm (N = 4), and flexuous/"vermiform" oxeas 975–1250 × 28–38 μm (N = 4).

Order Polymastiida Morrow & Cárdenas, 2015
Family Polymastiidae Gray, 1867
Genus *Spinularia* Gray, 1867

Spinularia spinularia (Bowerbank, 1866)
Fig. 13

Tethea spinularia Bowerbank 1866: 83, 94–96.

Radiella spinularia – Fristedt 1885: 16–17.
Spinularia spinularia – Stephens 1915: 31–32. – Alander 1942: 76.

Material examined (42 specimens)

SWEDEN • 2 specs; 57.6451° N, 11.6114° E; 71–39 m depth; 24 Aug. 2006; Artprojektets Skagerrak-inventering leg. [SK51]; dredge; P069-111011-1 and P069-111122-5; voucher: GNM Porifera 781 • 1 spec.; 58.1345° N, 10.8012° E; 248–206 m depth; 25 Aug. 2006; Artprojektets Skagerrak-inventering leg. [SK58 (SK37 återbesök)]; dredge; P069-111011-2; voucher: GNM Porifera 782 • 3 specs; 58.7274° N, 10.5400° E; 134–126 m depth; 30 May 2006; Artprojektets Skagerrak-inventering leg. [SK 7]; dredge; P069-111011-3 to 5; voucher: GNM Porifera 780 • 1 spec.; 58.9628° N, 11.0229° E; 49–14 m depth; 24 Aug. 2007; Artprojektets Skagerrak-inventering leg. [SK96]; dredge; P069-111013-1; voucher: GNM Porifera 788 • 1 spec.; 58.9537° N, 11.0189° E; 47–13 m depth; 24 Aug. 2007; Artprojektets Skagerrak-inventering leg. [SK94]; dredge; P069-111031-1; voucher: GNM Porifera 787 • 1 spec.; 58.3191° N, 10.9575° E; 111–91 m depth; 13 Jun. 2008; Artprojektets Skagerrak-inventering leg. [SK156]; dredge; P069-111107-1; voucher: GNM Porifera 796 • 1 spec.; 58.4728° N, 10.6203° E; 210–178 m depth; 16 Jun. 2008; Artprojektets Skagerrak-inventering leg. [SK181]; dredge; P069-111122-1; voucher: GNM Porifera 966 • 3 specs; 58.5058° N, 10.6734° E; 179–147 m depth; 28 Aug. 2007; Artprojektets Skagerrak-inventering leg. [SK114]; dredge; P069-111122-9–11; voucher: GNM Porifera 789 • 3 specs; 58.9308° N, 10.9894° E; 34–18 m depth; 23 Aug. 2007; Artprojektets Skagerrak-inventering leg. [SK92]; dredge; P069-111122-12 to 14; voucher: GNM Porifera 786 • 7 specs; 58.4870° N, 10.4228° E; 348–326 m depth; 30 Aug. 2007; Artprojektets Skagerrak-inventering leg. [SK128]; dredge; P069-111122-15 to 21; voucher: GNM Porifera 792 • 2 specs; 58.1352° N, 11.2512° E; 51–46 m depth; 20 Aug. 2007; Artprojektets Skagerrak-inventering leg. [SK67]; dredge; P069-111122-2 and 3; voucher: GNM Porifera 964 • 1 spec.; 58.3772° N, 10.4784° E; 373–317 m depth; 30 Aug. 2007; Artprojektets Skagerrak-inventering leg. [SK129]; dredge; P069-111122-4; voucher: GNM Porifera 793 • 1 spec.; 57.9272° N, 11.2378° E; 102–100 m depth; 21 May 2007; Artprojektets Skagerrak-inventering leg. [SK65]; dredge; P069-111122-6; voucher: GNM Porifera 783 • 1 spec.; 58.6954° N, 10.8392° E; 64–42 m depth; 22 Aug. 2007; Artprojektets Skagerrak-inventering leg. [SK75]; dredge; P069-111122-7; voucher: GNM Porifera 785 • 1 spec.; 58.5068° N, 10.996° E; 70–38 m depth; 29 Aug. 2007; Artprojektets Skagerrak-inventering leg. [SK118]; dredge; P069-

111122-8; voucher: GNM Porifera 791 • 11 specs; 58.7295° N, 10.7331° E; 112–77 depth; 15 Jun. 2008; Artprojektets Skagerrak-inventering leg. [SK172]; dredge; P069-111128-1 to 10; voucher: GNM Porifera 965; same collection data as for preceding; P069-111128-13; voucher: GNM Porifera 967 • 1 spec.; 57.8331° N, 11.448° E; 66–42 m depth; 9 Jun. 2008; Artprojektets Skagerrak-inventering leg. [SK141]; dredge; P069-111128-11; voucher: GNM Porifera 794 • 1 spec.; 58.1151° N, 10.8574° E; 228–171 m depth; 12 Jun. 2008; Artprojektets Skagerrak-inventering leg. [SK144]; dredge; P069-111128-12; voucher: GNM Porifera 795.

Description

The specimens have cushion or globular morphology. The colour pale brown when preserved in ethanol. Given the fact that the specimens were not observed, in situ, their natural colour is unknown. The oscula are visible on papillae. The surface is hispid (Fig. 13A).

Skeleton

The skeleton is clearly divided between the cortex (ectosome) and the choanosome (Fig. 13B). Its conformation is radial with a denser mass of tylostyles at the surface, creating the hispidation. Megascleres are: tylostyles with 170–1300 μm × 7.5 × 15 μm in size (N = 7), and very thin oxeas/trichodragmas, measuring 50.1–**71.5**–132.9 ± 17.37 μm (N = 34) (Fig. 12C).

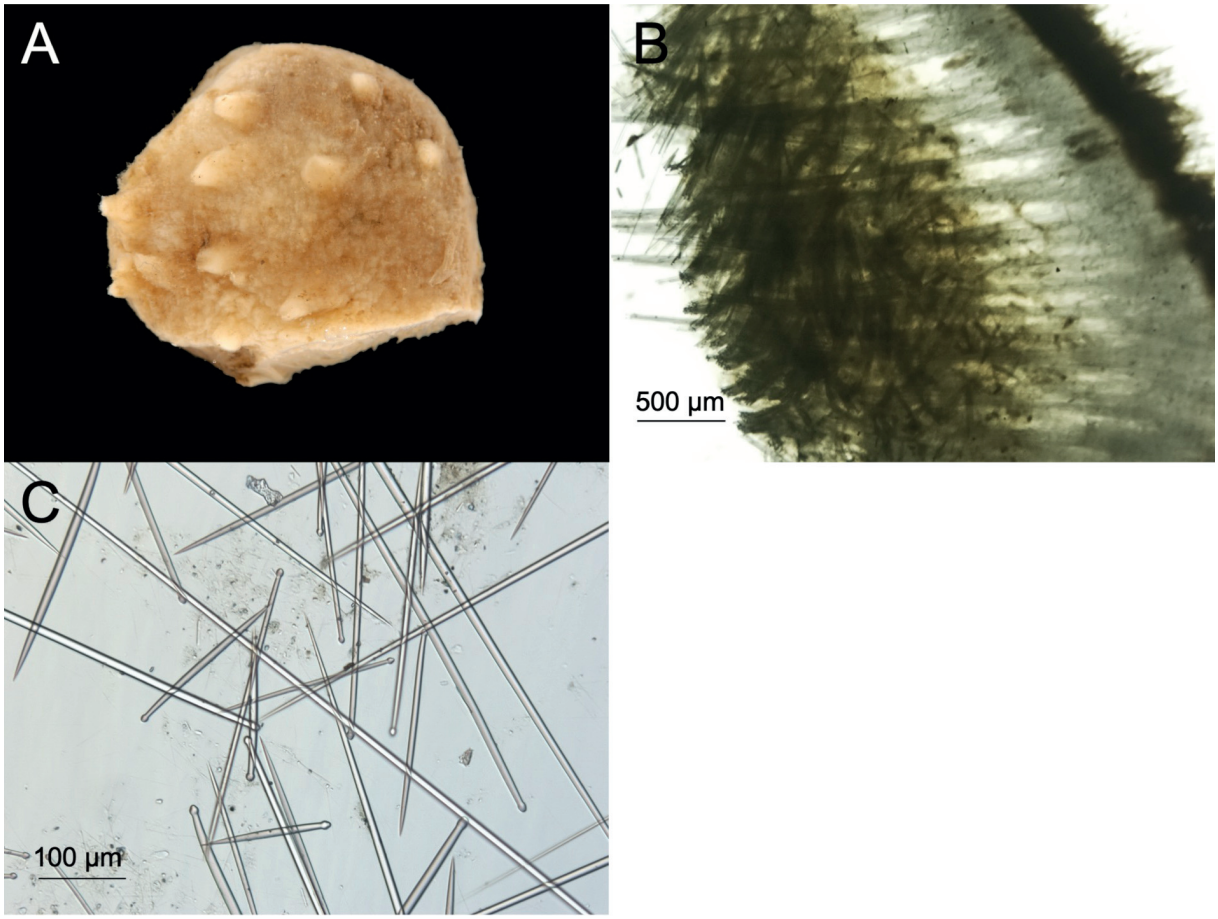

Fig. 13. *Spinularia spinularia* (Bowerbank, 1866). **A**. Full specimen preserved in ethanol, GNM Porifera 781 (P069-111011-1). **B**. Tangential section, GNM Porifera 788 (P069-111031-1). **C**. Tylostyles and oxeas, GNM Porifera 789 (P069-111013-1).

Order Poecilosclerida Topsent, 1928
Family Acarnidae Dendy, 1922
Genus *Iophon* Gray, 1867

Iophon nigricans (Bowerbank, 1858)
Fig. 14

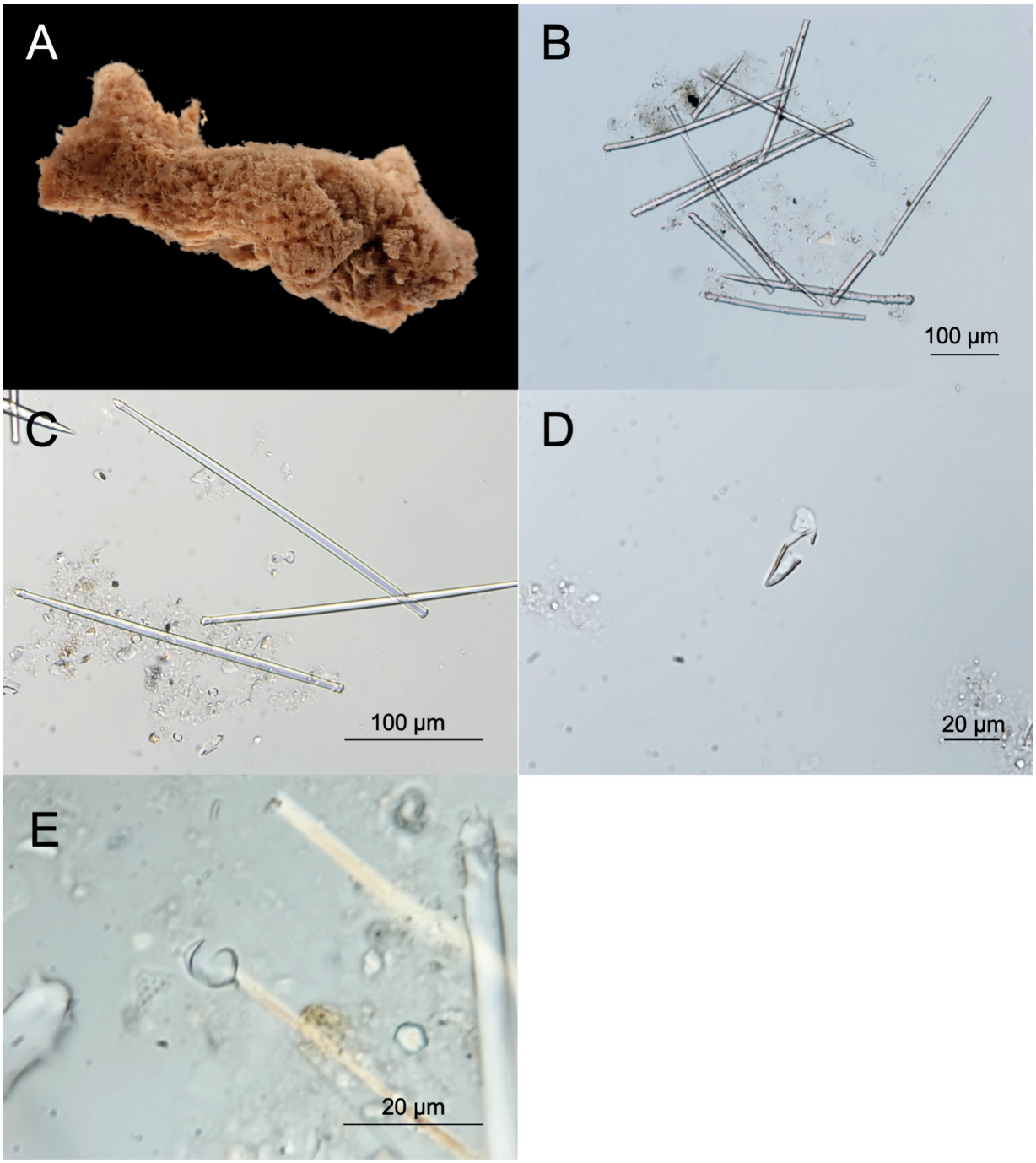

Fig. 14. *Iophon nigricans* (Bowerbank, 1858) specimen, GNM Porifera 890 (P067-111006-1). **A**. Full specimen preserved in alcohol. **B**. Acantostyles. **C**. Acanthostyles with swollen tips. **D**. Chelae. **E**. Bipocilles.

Halichondria nigricans Bowerbank 1866: 266–268.

Esperia nigricans – Fristedt 1885: 34–35, pl. III fig. 5.
Dendoryx (*Iophon*) *nigricans* – Topsent 1891: 528.
Iophon nigricans – Stephens 1916: 233; 1920: 29.
Iophon pattersoni – Alander 1942: 55.

Material examined (3 specimens)

SWEDEN • 1 spec.; 57.6451° N, 11.6114° E; 74–39 m depth; 24 Aug. 2006; Artprojektets Skagerrak-inventering leg. [SK51]; dredge; P067-111006-1; voucher: GNM Porifera 890 • 1 spec.; 57.1492° N, 11.6842° E; 30–27 m depth; 31 Aug. 2006; Artprojektets Skagerrak-inventering leg. [KA19]; dredge; P067-111104-1; voucher: GNM Porifera 618 • 1 spec.; 57.5213° N, 11.6144° E; 30–25 m depth; 20 Aug. 2009; Artprojektets Skagerrak-inventering leg. [KA111]; dredge; P067-111107-1; voucher: GNM Porifera 960.

Description

The three specimens have a cushion or arborescent morphology. The colour is dark brown when preserved in ethanol and the natural colour is unknown. The surface is irregular with visible ridges that correspond to the aquiferous system (Fig. 13A). However, the transparent membrane at the surface, typical for specimens of *I. nigricans*, is not visible. This membrane was possibly lost during collecting as all specimens were collected by dredging. The surface is hispid (Fig. 13A). The consistency is friable and very compressible.

Skeleton

Megascleres are: acanthostyles (Fig. 13B). measuring 198–**267.9**–293.9 ± 26.6 × 4–**7.4**–10.6 ± 2.39 µm (N = 11), and tylotyles with spined crowns at the ends (Fig. 13C), measuring 220–**252.1**–278.9 ± 21.73 × 3.9–**5.8**–7.5 ± 1.24 µm (N = 8). Microscleres are: palmate anisochelae in two size categories (Fig. 13C–D), 10 µm and 30 µm, and very small bipocilles (Fig. 13E), ca 7.5 µm.

Distribution and ecology

The type locality is off Cornwall, England. Furthermore, this species has been reported from the North Atlantic (both eastern and western parts), from the Bering Sea to southern Portugal. There are also some reports from the Mediterranean Sea. This wide distribution might indicate that *Iophon nigricans* is a species complex.

Remarks

Unfortunately, we were not successful in generating sequences for these specimens. The amplicons obtained resulted in sequences of bacterial contamination from the phylum Pseudomonadota.

Family Hymedesmiidae Topsent, 1928
Genus *Hymedesmia* Bowerbank, 1864

Hymedesmia jecusculum Bowerbank, 1866
Fig. 15

Hymeniacidon jecusculum Bowerbank 1866: 198–200.

Hymedesmia jecusculum – Ackers 2007: 100.

Material examined (4 specimens)

SWEDEN • 1 spec.; Lunneviken; 59.0546° N, 11.1690° E; 30 m depth; 18 Sep. 2018; Mats Larsson leg. [MM-180916-1]; SCUBA; LAR-180918-7215, 7217; GenBank no.: OM436251 (coxI); voucher: GNM Porifera 1071 • 1 spec.; same collection data as for preceding; LAR-180918-7254, 7256; voucher: GNM Porifera 1072; 23 Sep. 2018; Mats Larsson leg. [MM-180923-1]; SCUBA; LAR-180923-7367–7368, 7372; voucher: GNM Porifera 1073 • 1 spec.; Bergylteskär; 58.8290° N, 11.0831° E; 30 m depth; 9 Dec. 2018; Mats Larsson leg. [MM-181209-1]; SCUBA; LAR-181209-8217, 8219, 8222; GenBank no.: OM436265 (coxI); voucher: GNM Porifera 1074 • 1 spec.; Yttre Vattenholmen; 58.8754° N, 11.1056° E; 30 m depth; 16 Nov. 2019; Mats Larsson leg. [MM-191116-1]; SCUBA; LAR-191116-PB160453–55; voucher: GNM Porifera 1075.

Description

The specimens have a thin incrusting morphology, with a micro-velvety to smooth surface. Oscula are not visible, and pores are concentrated in elevated pore sieves (Fig. 15A). The natural colour ranges from dark orange and red to pale reddish-white, turning beige in ethanol.

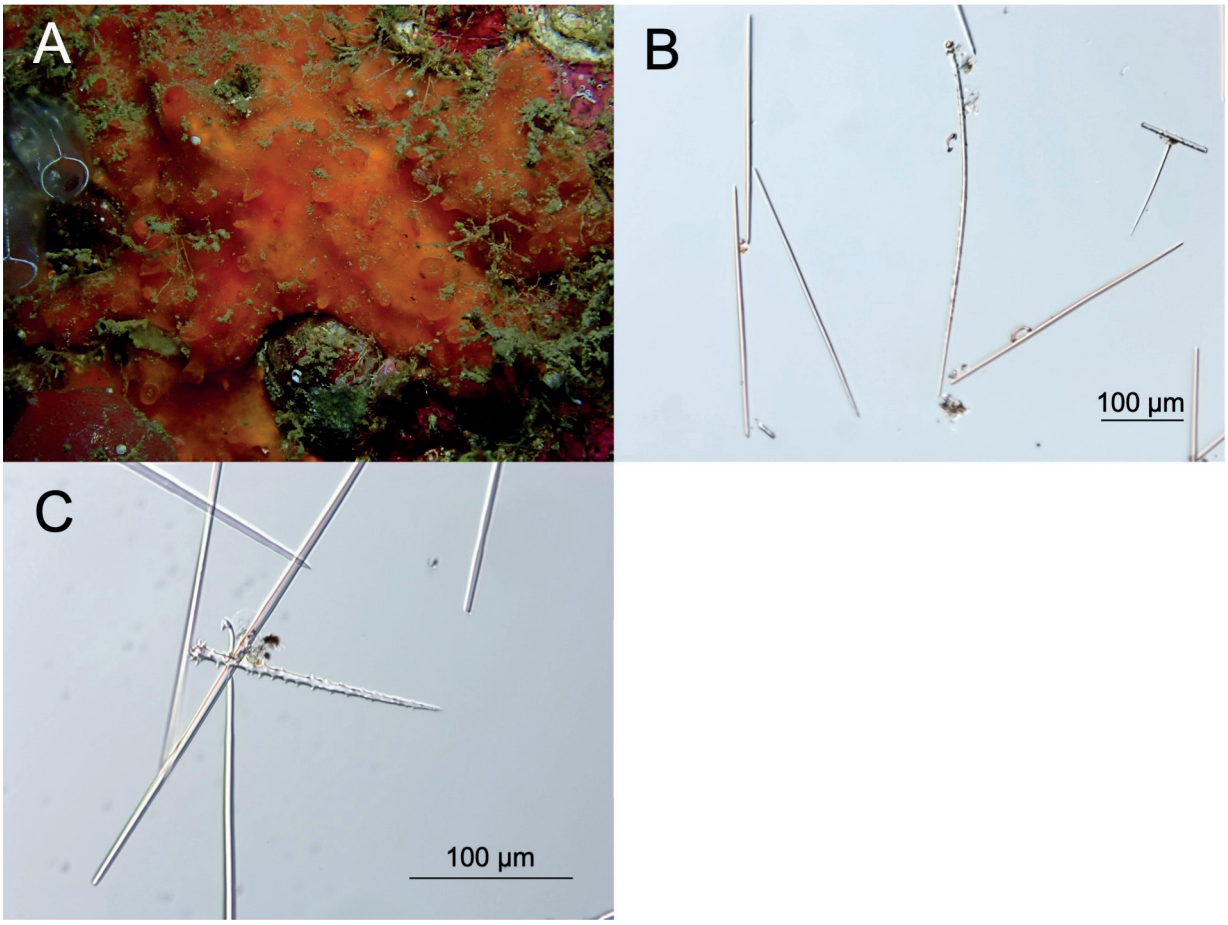

Fig. 15. *Hymedesmia jecusculum* Bowerbank, 1866. **A**. Specimen, GNM Porifera 1075 (LAR-191116-PB160453–55). **B**. Spicule preparation showing one long acanthostyle, tornotes and arcuate chelae, GNM Porifera 1072 (LAR-180918-7254, 7256). **C**. Detail of a small acanthostyle GNM Porifera, 1072 (LAR-180918-7254, 7256).

Skeleton

Megascleres are acanthostyles curved near the base and symmetrical tornotes. The acanthostyles present two size classes: spined at the base up to ⅔ of the shaft measuring 360 × 7.5 μm (N = 4), and fully spined with 120 × 5 μm (N = 3) in size. The tornotes are symmetrical, measuring 277.0–**314.6**–350.4 ± 22.38 × 3.1–**4.6–**6.0 ± 0.92 μm (N = 8). Microscleres, are arcuate 20 μm long isochelae (Fig. 15B–C).

Remarks

The species *Hymedesmia jecusculum* is a new report for Sweden. However, there is significant morphological similarity between *H. jecusculum* and *Phorbas fictitius* (Bowerbank, 1866). The latter has been previously reported for Sweden by Alander (1942), under the name *Hymedesmia fictitia*. However, we believe this identification to be correct given that Alander's description is closely resembling what has previously been reported for *P. fictitius*. Furthermore, Alander (1942) reported for the Norwegian parts of Skagerrak a single specimen of *Hymedesmia proteidea* (Schmidt, 1868) (spelled as *Hymedesmia proteida*), which is now synonymised with *P. fictitius*. We argue that this indicates that Alander considered *H. proteidea* and *H. fictitia* to be different species, which could indicate that the specimen identified as *H. proteidea* could be *H. jecusculum*. However, Alander's description of *H. proteidea* is insufficient to test this hypothesis.

There are some consistent morphological differences between specimens of *H. jescusculum* and *P. fictitius*: type of tornotes, the arrangement of spines on acanthostyles, and slight differences in external morphology features. While *H. jecusculum* possesses symmetrical tornotes and primary acanthostyles with spines almost entirely on the shaft, *P. fictitius* possesses anisotornotes and primary acanthostyles with spines only at the base. Regarding the external morphology, *P. fictitius* specimens are usually thick encrusting or cushions and a surface densely covered with areolae (depressions of pore sieves). This contrasts with the thin encrusting sheet-like morphology and the elevated pore sieves typical for *H. jecusculum*. In spite of these morphological differences, the coxI sequences of the specimens identified as *P. fictitius* and *H. jecusculum* are identical or 1 bp difference (Fig. 3), thus it is possible that these two names refer to different growth stages of the same species. A similar remark was made for *Phorbas dives* (Topsent 1891). Specimens could present skeletal architecture ranging from hymedesmoid architecture, i.e., single subtylostyles erected from the basal plate, to the typical *Phorbas* architecture, i.e., plumose tracts of subtylostyles (Soest 2002; Topsent 1891). This leads us to question the validity and circumscriptions of the genera *Hymedesmia* Bowerbank, 1864 and *Phorbas* Duchassaing & Michelotti, 1864. However, both the assessment of the validity of these two genera, and whether *P. fictitius* and *H. jecusculum* are different species or synonyms are beyond the scope of this study.

Hymedesmia stellifera Goodwin & Picton, 2009
Fig. 16

Hymedesmia stellifera Goodwin & Picton, 2009: 905–906, fig. 8a–b.

Material examined

SWEDEN • 1 spec.; Yttre Vattenholmen; 58.8754° N, 11.1056° E; 27 m depth; 16 Nov. 2019; Mats Larsson leg. [MM-191116-1]; SCUBA; LAR-191116-PB160445, 47–48; GenBank no.: OM415624 (28S D3-D5); voucher: GNM Porifera 1122.

Description

The specimen is an orange-yellow crust growing on a nearly vertical rock (Fig. 16A). The colour in ethanol is beige with some dark spots. Pores are visible and oscula are very conspicuous, surrounded by excurrent channels and possessing small translucent rims (Fig. 16B). The oscula are regularly distributed giving the surface a star-like pattern (Fig. 16A). Pore sieves are absent.

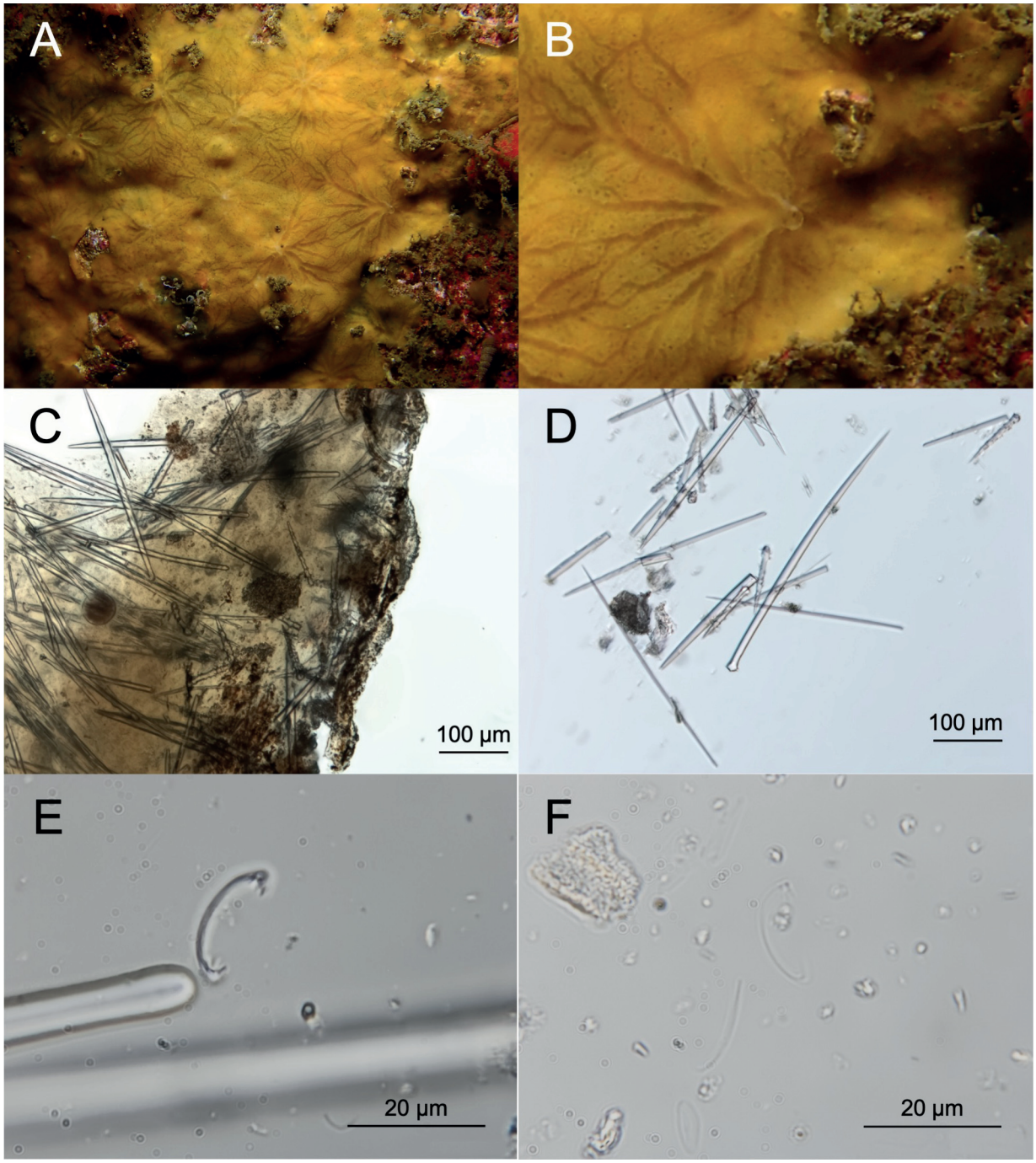

Fig. 16. *Hymedesmia stellifera* Goodwin & Picton, 2009. **A**. Live specimen, GNM Porifera 1122 (LAR-191116-PB160445, 47–48). **B**. Detail of an osculum. **C**. 'Stitched' thick section. **D**. Spicule preparation with the two size classes of acanthostyles and the ectosomal styles. **E**. Chelae. **F**. Sigma.

Skeleton

The skeleton is composed of two size classes of acanthostyles erected with their heads in the basal layer and ectosomal styles raised in columns (Fig. 16C–D). Megascleres are acanthostyles of two size classes: a) The large acanthostyles (Fig. 14D) are sparsely spined at their base and smooth in the shaft, measuring 277.7–**352.3–**459.8 ± 52.58 × 6.8–**9.4–**13.0 ± 1.97 μm (N = 14), and b) small acanthostyles are fully spined (Fig. 16D), with a small head, measuring 39.3–**95.1**–124.6 ± 16.34 × 3.4–**7.6**–12.8 ± 2.5 μm (N = 38), c) ectosomal styles, with a poorly developed tyloted head, measuring 206–**282.2**–322.5 ± 24.27 × 1.6–**5.6**–9.6 ± 1.7 μm (N = 36). The acanthostyles present forms that are constituted by two acanthostyles fused by the heads; however, this form is rare for the larger acanthostyles. The microscleres are: chelae (Fig. 16E), rare, measuring 12.8–**17.0**–21.5 ± 2.82 μm (N = 15), and sigmas (Fig. 16F) measuring 10.9–**16.5**–21.2 ± 2.51 μm (N = 32).

Ecology and distribution

This species was first described between Northern Ireland and western Scotland from 25 to 32 m depth. However, there has been a recent report from southern Norway (community iNaturalist 2020; GBIF.org 2023), and given that this species has been only recently described, it is natural that its real bathymetric and geographical distribution could be much larger than what is currently known. Our specimen represents a new report for Sweden.

Remarks

The specimen examined has an external morphology conforming to the original description (Goodwin & Picton 2009). Furthermore, the shape of the megascleres are overall concordant with the original description, with the exception of the small acanthostyles which present fused forms, and are slightly larger (39.3–**95.1**–124.6 × 3.4–**7.6**–12.8) than what has been previously reported (65–**79**–95 × 8–10) (Goodwin & Picton 2009). However, the size range of the microscleres seems to be different than what was originally reported: here, both chelae and sigmas had the same size range while there was an obvious size class difference between sigmas and chelae in the type material (sigmas: 10–12 μm and, chelae: 15–18 μm) (Goodwin & Picton 2009). These differences might be associated with different environments, populations or simply the number of spicules measured. Since only one specimen was collected it is difficult to generalize these observations.

This species was originally described within the genus *Hymedesmia*. However, the 28S D3-D5 sequence of our specimen does not group with sequences of *Hymedesmia* species (Fig. 3) but with *Monanchora arbuscula* (Duchassaing & Michelotti, 1864) belonging to the Crambeidae Lévi, 1969 (see Supp. file. 2 for more information in this sequence). This grouping is very well supported (bt ≥95%) and there is a sequence similarity of 97.22%. *H. stellifera* furthermore presents acanthostyles similar to what is reported for *Hymedesmia zetlandica* (Bowerbank, 1864), which is the type species of the genus, thus suggesting that the genus *Hymedesmia* could also belong to the Crambeidae. Alander (1937) described *Hymoxenia inflata* Alander, 1937 (now *Hymesdesmia inflata*), which also possesses acanthostyles similar to the *H. zetlandica* thus likely belonging to the same group. For now, it can be concluded that the genus *Hymedesmia* is polyphyletic but we cannot revise the classification based on our limitated sampling, with no sequences from the type species.

Hymedesmia dujardinii (Bowerbank, 1866)
Fig. 17

Hymeniacidon dujardinii Bowerbank 1866: 224–225.
Stylopus coriaceus Fristedt, 1885: 28–29, pl. II fig. 8a–g.

Stylopus dujardini (Bowerbank, 1866) — Levinsen 1893: 419. — Arndt 1935: 64.
Stylopus dujardini var. *coriaceus* – Topsent 1928: 283.
Hymedesmia dujardini – Lundbeck 1910: 101–104, pl. X fig. 5. — Stephens 1917: 11; 1921: 40. — Hentschel 1929: 962.
Hymedesmia brondstedi Burton, 1930 – Ackers 2007: 99.

Material examined (7 specimens)

SWEDEN • 1 spec.; Saltbacken; 59.0832° N, 11.2242° E; 40–25m depth; 1 Oct. 2019; Mats Larsson leg. [MM-191001-1]; SCUBA; LAR-191001-PA010087, 0089; voucher: GNM Porifera 1068 • 1 spec.; Lunneviken; 59.0546° N, 11.1690 °E; 40–25 m depth; 2 Nov. 2019; Mats Larsson leg. [MM-191102-2]; SCUBA; LAR-191102-PB020269, 71–72; GenBank no.: OM415619 (28S D3-D5); voucher: GNM Porifera 1046 • 1 spec.; same collection data as for preceding; LAR-191102-PB020285, 87, 89; GenBank no.: OM415622 (28S D3-D5); voucher: GNM Porifera 1069 • 1 spec.; same collection data as for preceding; LAR-191102-PB020302–03; GenBank no.: OM415641 (28S D3-D5) • 1 spec.; same collection data as for preceding; LAR-191102-PB020339–41; GenBank no.: OM415575 (28S D3-D5); voucher: GNM Porifera 1120 • 1 spec.; same collection data as for preceding; LAR-191102-PB020344–45; GenBank no.: OM415574 (28S D3-D5); voucher: GNM Porifera 1121 • 1 spec.; Gåseklovan; 58.3099° N, 11.5389° E; 40–25m depth; 10 Oct. 2015; leg. [Gåseklovan, 151010]; ROV; P110-151015-1; voucher: GNM Porifera 1070.

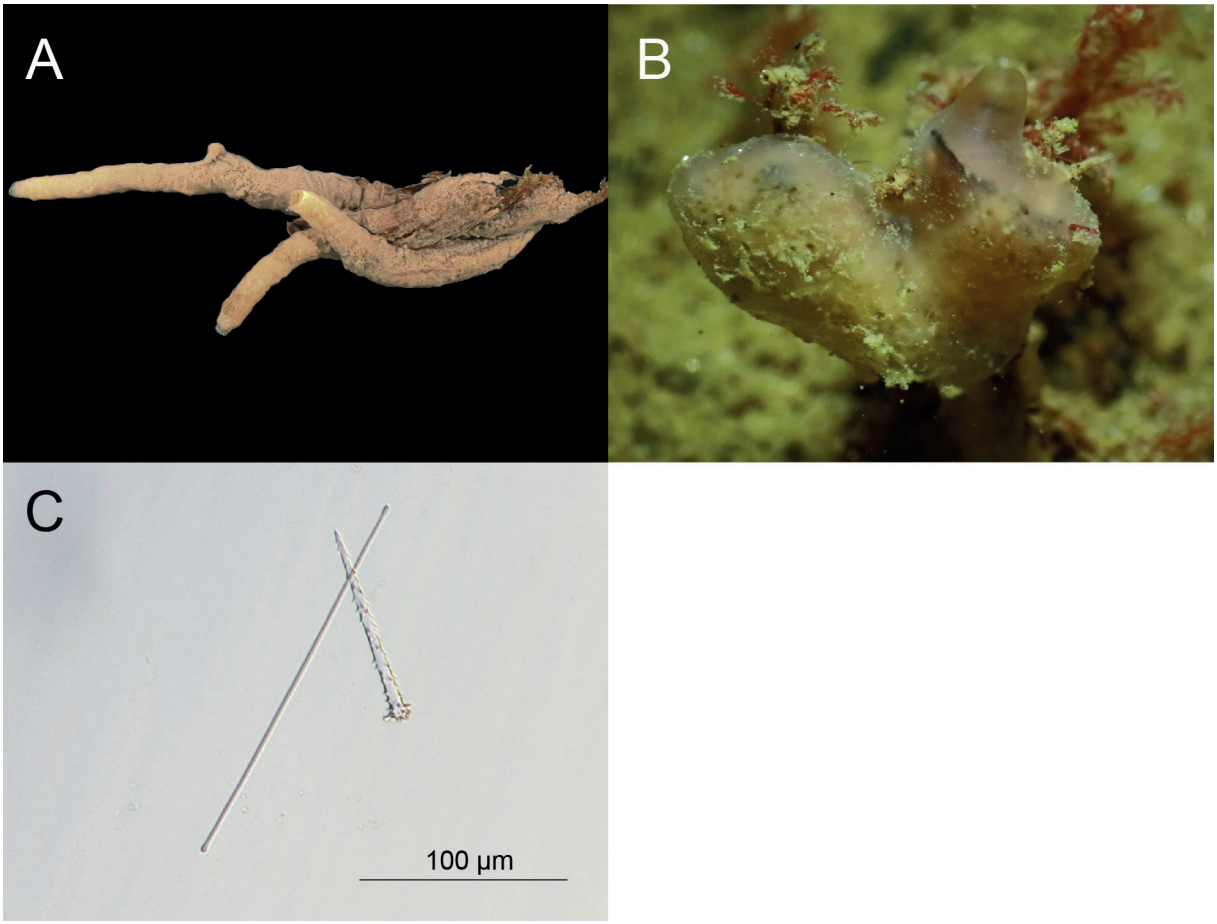

Fig. 17. *Hymedesmia dujardinii* (Bowerbank, 1866). **A**. Full specimen, GNM Porifera 1070 (P110-151015-1). **B**. Full specimen, GNM Porifera 1121 (LAR-191102-PB020344–45). **C**. Acanthostyles and tornotes.

Description

All specimens presented a thin encrusting habitus and were growing on clean rock, algae or *Chaetopterus norvegicus* polychaete tubes. The surface is smooth. The colour alive was translucent white-cream; white-pink (Fig. 17A–B) or light-brown colour changing to pale beige when preserved in ethanol. Pores were visible and regularly distributed and without pore-sieve. Oscula were present on a slightly elevated 'chimney' (Fig. 17B).

Skeleton

The skeleton conformation was hymedesmoid, with acanthostyles erected with base attached in the substrate, and surface smooth tornotes. Megascleres are one class size of acanthostyles spined mostly at the base but somewhat extending along the shaft, measuring 50.0–**124.5–**207.5 ± 47.69 × 1.3–**5.1**–8.8 ± 1.80 μm (N = 65), and smooth spicules that can be tylotes, anisotornotes or strongyles, measuring 72.5–**196.6**–242.5 ± 35.5 × 1.3–**2.8–**3.8 ± 0.80 μm (N = 31) (Fig. 17C).

Ecology and distribution

This species presents ample geographical and bathymetrical distributions, with reports from the Arctic to northern Africa and the Mediterranean, and from shallow waters to 1200 m depth. Additionally, specimens of this species have been observed on various substrates, including rock, brachiopod shells, and *Chaetopterus* tubes. Given the wide distribution, lack of substrate preference, and spicules variability, it is likely that *H. dujardinii* represents a species complex. The type locality for *H. dujardinii* is North Yorkshire, UK, and the specimen was growing on brachiopod shells. In spite of that, it is worth noting that this species is currently considered in the WPD a synonym of *H. coriacea* (Fristedt, 1885) (see Remark below), which was firstly described in Bohuslän, Sweden, by Fristedt (1885) growing on *Chaetopterus* tubes (as in present study).

Remarks

Bowerbank (1866) introduced the name *Hymeniacidon dujardinii* for this species; however, under the mistaken assumption that it was the same as *Halisarca dujardinii* (Johnston, 1842). This led Burton (1930) to dismiss Bowerbank's name as unavailable and also introduce the replacement name *Hymedesmia brondstedi*. This rejection of Bowerbank's name was maintained by Alander (1942), who also identified *Stylopus coriaceus* Fristedt, 1885 as an available senior synonym to *Hymedesmia brondstedi*. We find, however, that Burton's conclusion was not justified according to the current International Code of Zoological Nomenclature (henceforth, the Code) (ICZN 1999), even though, it is certainly not a clear-cut case. Our argument is the following: a) Bowerbank (1866) provided a detailed description (by his contemporary standards) of the species and listed the specimen on which this was based, b) he used a new binomial for this sponge (not opening problems of homonymy), c) he headed his description '*Hymeniacidon Dujardinii*, *Bowerbank*', stating that he was the first to use this binomial for this species d) although he did not claim to describe a new species, he explicitly differentiated his sponge from Johnston's *Halisarca dujardinii* and, e) the Code (ICZN 1999) prescribes in Art. 16 'intention of authors to establish new nominal taxa to be explicit' only for names proposed after 1999. This leads us to conclude that *Hymeniacidon dujardinii* Bowerbank, 1866 is an available name for nomenclatorial purposes. This does not necessarily imply that it should be used as the valid name, for example if Art. 23.9 of the Code could be applied. However, the name has been used by several authors after 1899; some are listed under synonyms, see above, and, e.g., as *Leptosia dujardini* by Topsent (1901; 1904) or as *Stylopus dujardini* by Topsent (1925, 1928), thus disqualifying application of Art. 23.9 (ICZN 1999).

We conclude that the name *Hymedesmia* (*Stylopus*) *dujardinii* (Bowerbank, 1866) is the valid name for this species hypothesis and hence that it should be reinstated. Consequently, *H.* (*S.*) *coriaceus* (Fristedt, 1885) becomes a junior synonym of *H.* (*S.*) *dujardinii*.

Hymedesmia stylifera (Alander, 1942)

Stylopus stylifera Alander 1942: 45–46.

Material examined

SWEDEN • 1 spec.; 58.5609° N, 11.0891° E; 83 m depth; 28 Aug. 2007; Artprojektets Skagerrak-inventering leg. [SK116]; dredge; P093-111031-1; voucher: GNM Porifera 975.

Description

The specimen is thin encrusting. The surface presents small papillae. Due the collection method, the colour in situ is unknown; the preserved specimen has a pale brown colour.

Skeleton

We have not observed the skeleton conformation. The skeleton consists of straight acanthostyles, which come in two distinct sizes: a) small acanthostyles are fully spined, with pronounced spines measuring 95–107 × 7 μm (N = 4), and b) larger fully spined acanthostyles but with smaller spines along the shaft, measuring 205–420 × 7–10 μm (N = 6). In addition to acanthostyles, thin and straight styles are common, measuring 217–430 × 5–7 μm. The microscleres are absent.

Ecology and distribution

The type locality is Säcken (Bohuslän, Sweden) at 85 m depth associated with a *Desmophyllum pertusum* (Linnaeus, 1758) coral garden. The species was also reported in the Norwegian part of Skagerrak (15 miles south-east of Jomfruland, Norway) at 400 m depth (Alander 1942) and Outer Hebrides, Mingulay (Scotland, UK) in an area now known for harbouring a vast cold-water coral reef (Banana reef). Although we do not know if the Norwegian specimens were collected in a cold-water coral reef, the fact that the types (Alander 1942) and the specimens from Scotland were, leads us to suspect that this species might be associated with cold-water water corals.

Remark

Due to the limited number of collected specimens of this species, our understanding of the ecology and distribution of *H. stylifera* is limited. However, the species might be associated with cold-water coral reefs, particularly the coral species *D. pertusum.* This implies a larger suitable habitat than what is currently known. Consequently, the potential association of this species with cold-water coral species and deep-sea coral reefs makes the collection of new specimens challenging. These areas are often protected, rendering destructive collection methods unavailable.

Hymedesmia sp. 1

Fig. 18

Material examined

SWEDEN • 1 spec.; Slatbacken; 59.0832° N, 11.2242° E; 19 m depth; 10 Nov. 2019; Mats Larsson leg. [MM-191110-1]; LAR-191110-PB100407–09; SCUBA; GenBank no.: OM415620 (28S D3-D5).

Description

The specimen, of which a 5 mm fragment was collected, is thick encrusting and was found growing on a rock. The colour alive is saffron-yellow turning light greyish-white in ethanol. The surface presents high pore-sieves while oscules were not visible (Fig. 18A). The consistency of this specimen is extremely friable.

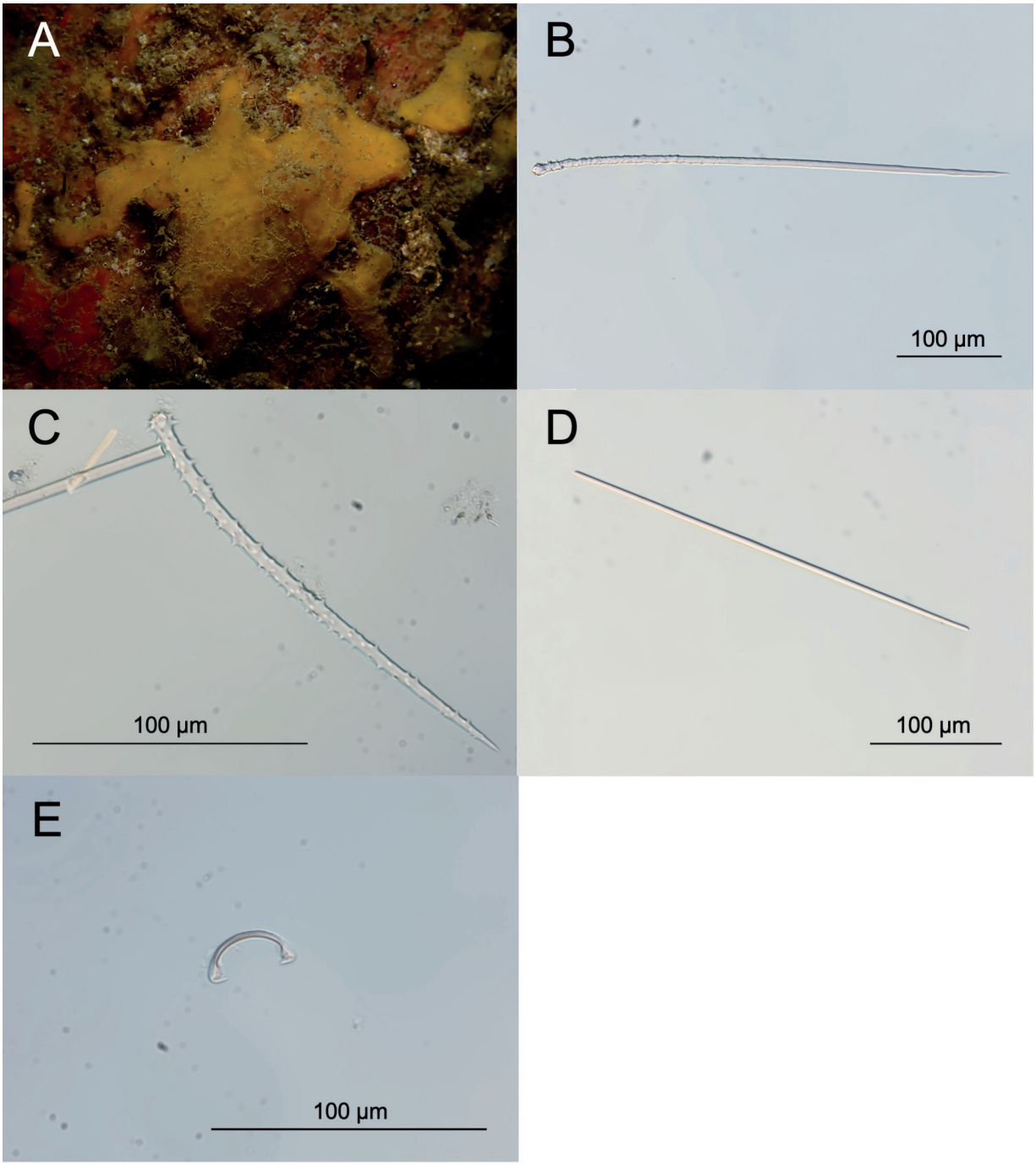

Fig. 18. *Hymedesmia* sp. 1. GNM Porifera 1048 (LAR–191110-PB100407–09). **A**. Live specimen. **B**. Large acanthostyles 'stitched'. **C**. Small acanthostyles. **D**. Tornotes/strongyles. **E**. Chelae.

Skeleton

Unfortunately, due to the size and consistency of the fragment, it was not possible to do a section. The skeleton is composed of two size classes of acanthostyles both curved near the base: a) large acanthostyles with a poorly developed tyle and spines reach ⅔ of the shaft (Fig. 18B) measuring 354.9–**409.6**–437.6±47.43×4–**4.8**–6.0±1.10 µm (N=30), and b) small acanthostyles that are fully spined with spines more defined than for the large acanthostyles (Fig. 18C), measuring 134.7–**156.3**–291.6±3.16×3.2–**4.8**–9.6±1.41 µm (N=28). The ectosomal spicules are strongyles (Fig. 18D) measuring 179–**307.7**–362.1±37.11×1.4–**2.9**–4.3±0.71 (N=32). The microscleres are arcuated chelae, with a very wide and curved shaft and short alae (Fig. 18E): 20.6–**33.2**–64.2±12.99 µm (N=15).

Remarks

This specimen somewhat resembles *Hymedesmia rathlinia* Goodwin & Picton, 2009. However, several characters distinguish it from this species: our specimen a) is light greyish white in ethanol rather than black or brown, b) it has no visible oscular papillae and c) it has chelae with a more curved shaft and shorter alae than what is presented for *H. rathlinia*. Therefore, we are inclined to conclude that our specimen is not conspecific with *H. rathlinia*. Also, our specimen lacks the polytyloted ectosomal spicules and the well-developed spines at the base of its large acanthostyles reported for *Hymedesmia gustafsoni* Alander, 1942. Hence, we are disinclined to assign this specimen to that species.

Hymedesmia sp. 2
Fig. 19

Material examined

SWEDEN • 1 spec.; Lunneviken; 59.0546 ° N, 11.169 ° E; 27 m depth; 23 Sep. 2018; Mats Larsson leg. [MM-180923-1]; SCUBA; LAR-180923-7380, 7383–7384; GenBank no.: OM436219 (coxI); voucher: GNM Porifera 1045.

Description

The specimen, of which a 3–4 mm fragment was collected, is encrusting an algae stalk. The colour of the live specimen was yellow but turned greyish white in ethanol. The surface is smooth, and we did not observe any pores or oscula, neither in situ nor in the preserved fragment (Fig. 19A).

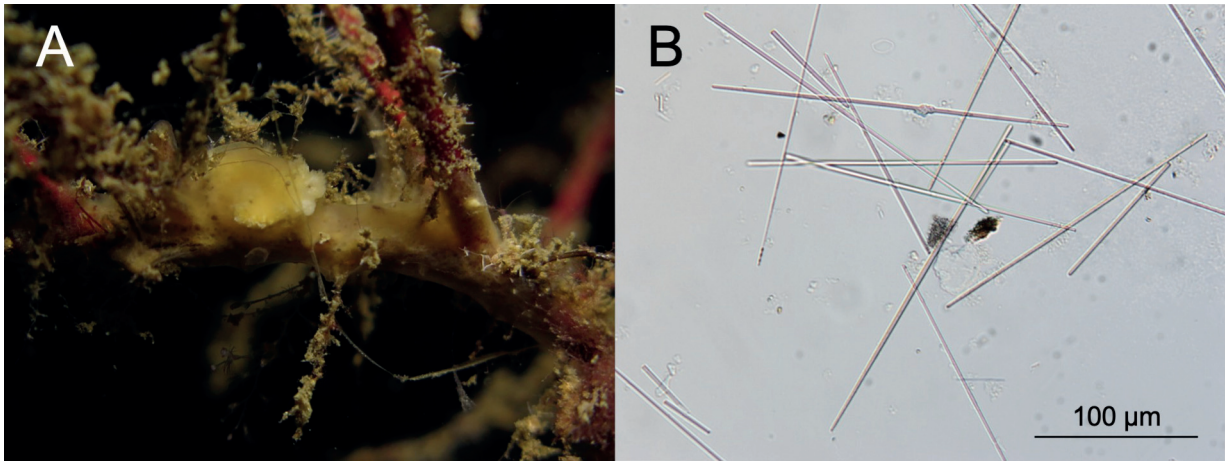

Fig. 19. *Hymedesmia* sp. 2. GNM Porifera 1045 (LAR-180923-7380, 7383–7384). **A**. Live specimen. **B**. Tornotes.

Skeleton

Due to the size and consistency of the fragment, we could not do a section. The skeleton is composed of tornotes strongyloides (Fig. 19B) measuring 139.2–**201.8**–239.1 ± 27.42 × 1.3–**1.9**–2.9 ± 0.54 µm (N = 10), which sometimes present irregular tyles along the shaft as wide as 6 µm. In this case, the width was not measured at maximum width (in the irregular tyles) because that measure would not be representative of the spicule shape.

Remarks

The size of the tornotes and the coxI sequences are similar to those for *Hymedesmia primitiva*. However, the specimen lacks acanthostyles and the surface does not present any pore sieves, perhaps due the small size of the specimen. Therefore, we have not assigned the specimens to any species. Conversely, the allocation of this specimen to the genus *Hymedesmia* is exclusively due to the presence of the tornotes and the coxI sequence placement.

Hymedesmia sp. 3
Fig. 20

Material examined

SWEDEN • 1 spec.; Lunneviken; 59.0546° N, 11.169° E; 30 m depth; 16 Sep. 2018; Mats Larsson leg. [MM-180916-1]; SCUBA; LAR-180918-7197–7198; GenBank no.: OM436233 (coxI); voucher: GNM Porifera 998.

Description

The specimen has a thin encrusting morphology. The colour alive was saffron yellow and slightly translucent, i.e., the substrate colour and structure can be seen through (Fig. 20A). The colour in ethanol is dark brown. The surface does not have obvious oscula and the canals of the aquiferous system are partially visible and slightly raised from the surface (Fig. 20B). The pores are visible, scattered regularly and not in pore-sieves.

Skeleton

Due to the size and consistency of the fragment, we could not do a section. The skeleton is composed of one single size class of acanthostyles (Fig. 20C) measuring 66.1–**122.9**–171.8 ± 27.44 × 2.5–**7.0**–12.4 ± 2.59 µm (N = 31), and anisotylotes (Fig. 20D), measuring 126.4–**196.8**–251.4 ± 29.74 × 0.4–**1.4**–3.0 ± 0.54 µm (N = 39).

Remarks

The placement of this specimen within the genus *Hymedesmia* was primarily based on the presence of tylotes (Fig. 20C) and the coxI sequence. This specimen appears as sister species to specimens identified as *H. primitiva* (Fig. 2). There are 31 accepted species of *Hymedesmia* (*Stylopus*), a subgenus characterised by the lack of chelae. However, there are only 15 species for the NEA and Mediterranean, none of which is described to only have small acanthostyles or the very small anisotylotes, as observed in this specimen. Among the species reported for the South Atlantic, Pacific or Indian oceans, only two seem to resemble what we observe in our specimen: *Hymedemia parvispicula* (Burton & Rao, 1932) from the Mergui Archipelago (Andaman Sea, Indian Ocean), and b) *Hymedesmia alcoladoi* van Soest, 2017 from the Guyana Shelf. Our specimen seems to resemble *H. parvispicula* more closely, with the smooth surface, without visible pores or oscula, and the presence of small acanthostyles and anisotylotes. However, the holotype of *H. parvispicula* is yellow in 'spirit' contrasting with the dark brown colour of our specimen.

Furthermore, the spicules of *H. parvispicula* are considerably smaller (acanthostyles: 130–105 × 4 µm and anisotylotes 21 × 3 µm) (Burton & Rao 1932) than what we measure in our specimen. As for the species *H. alcoladoi*, the skeleton is composed of acanthostyles and ectosomal spicules with sizes similar to what we observe in our specimen, 213–62 × 17–6.5 µm and, 151–222 × 2–4 µm, respectively (van Soest 2017). However, the ectosomal spicules for *H. alcoladoi* are tornotes with mucronate ends whereas our specimen presents tylotes. Additionally, *H. alcoladoi* presents two size classes of acanthostyles while we could only observe one in our specimen. Therefore, we are hesitant to assign this specimen to either *H. alcoladoi* or *H. parvispicula*, two species furthermore described from geographically remote areas and in habitats different from the shallow west coast waters of Sweden. However, we refrain from describing this specimen as a new species and prefer to wait for additional specimens and/or *Hymedesmia* sequences.

Hymedesmia sp. 4
Fig. 21

Material examined

SWEDEN • 1 spec.; Yttre Vattenholmen; 58.8754° N, 11.1056° E; 27 m depth; 16 Nov. 2019; Mats Larsson leg. [MM-191116-2]; SCUBA; LAR-191116-PB160433, 35; GenBank no.: OM415632 (28S D3-D5); voucher: GNM Porifera 1049.

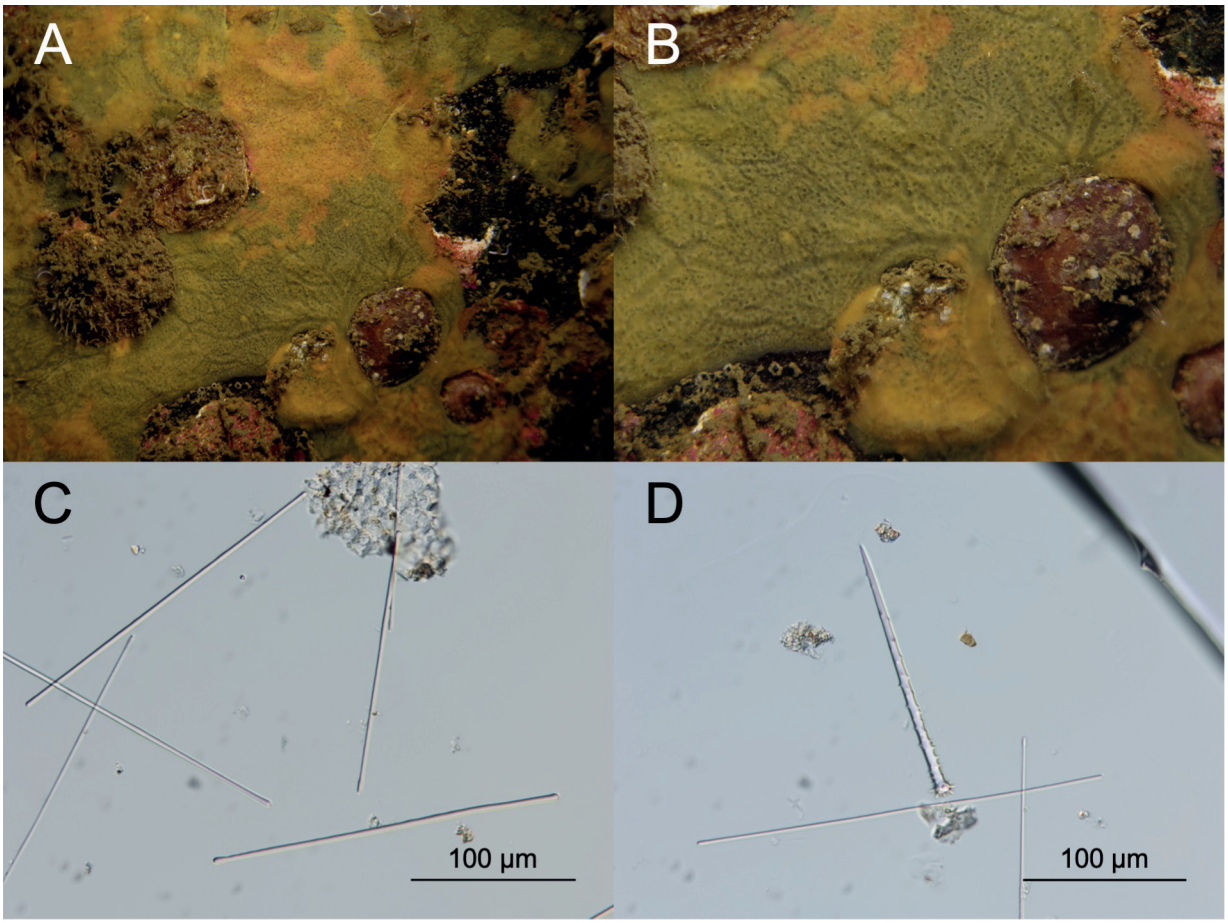

Fig. 20. *Hymedesmia* sp. 3. GNM Porifera 998 (LAR-180918-7197–7198). **A**. Live specimen. **B**. Detailed of the surface. **C**. Tornotes. **D**. Acanthostyle.

Description

The specimen, of which a 5 mm fragment was collected, presents an encrusting morphology, growing on rock covered with coralline algae. The colour alive of the specimen is orangish-yellow presenting white dots that are possibly embryos (Fig. 21A). Its colour in ethanol is beige. The specimen does not present evident osculum, pore-sieves nor pores. The consistency is very fragile after being preserved in ethanol.

Skeleton

Skeleton composed of two size classes of acanthostyles: a) large acanthostyles with a small base, spines covering ⅓ of the length, some spines seem poorly formed by being extremely thin in the shaft, measuring 212.5–**239. 1**–270.4 ± 23.37 × 4.1–**6.7**–10.1 ± 2.7 µm (N = 5), b) small acanthostyles are fully spined (Fig. 21B) and have a well-developed tyle at base, measuring: 104.–**116.3**–138.2 ± 9.32 × 3.4–**5.3**–7.8 ± 1.60 µm (N = 11) (Fig. 20B). Additionally, the skeleton also presents a single class size of anisostrongyles measuring 124.2–**220.9**–287.5 ± 26.32 × 0.8–**1.8**–4.6 ± 0.66 µm (N = 46) (Fig. 21C).

Remarks

The specimen examined presents a peculiar external morphology by lacking apparent structure on its surface. However, given the presence of several 'white dots', it is possible that the specimen is

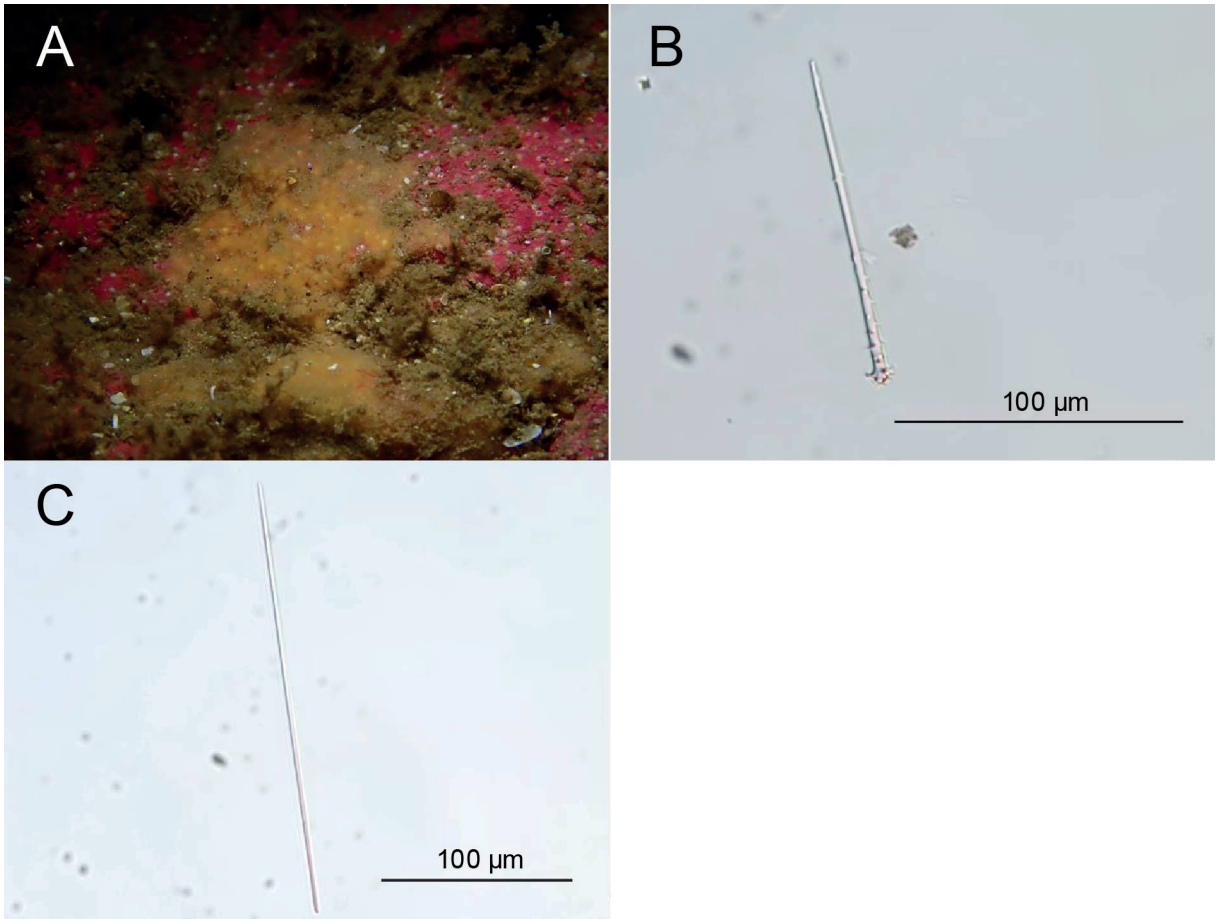

Fig. 21. *Hymedesmia* sp. 4. GNM Porifera 1049 (LAR-191116-PB160433, 35). **A**. Live specimen. **B**. Small acanthostyle. **C**. Anisostrongyle.

riddled with embryos and has lost its usual external morphology. The specimen does not present any nucleotide difference in the 28S D3-D5 sequences, when compared with other specimens identified as *H. hibernica* (Fig. 2). However, the lack of pore-sieves and the presence of small acanthostyles, thinner than what is reported for *H. hibernica* leads us to keep this specimen as *Hymedesmia* sp.

Genus *Phorbas* Duchassaing & Michelotti, 1864

Phorbas dives (Topsent, 1891)
Fig. 22

Microciona dives Topsent, 1891: 543–544, pl. XXII figs 2–3.

Material examined (2 specimens)

SWEDEN • 1 spec.; Saltbacken; 59.0832° N, 11.2242° E; 26 m depth; 28 Aug. 2018; Mats Larsson leg. [MM-180828-1]; SCUBA; LAR-180828-7014–7016; GenBank no.: OM436258 (coxI); voucher: GNM Porifera 1104 • 1 spec.; Bergylteskär; 58.8290° N, 11.0831° E; 26 m depth; 9 Dec. 2018; Mats Larsson leg. [MM-181209-1]; SCUBA; LAR-181209-8253, 8255, 8257; voucher: GNM Porifera 110.

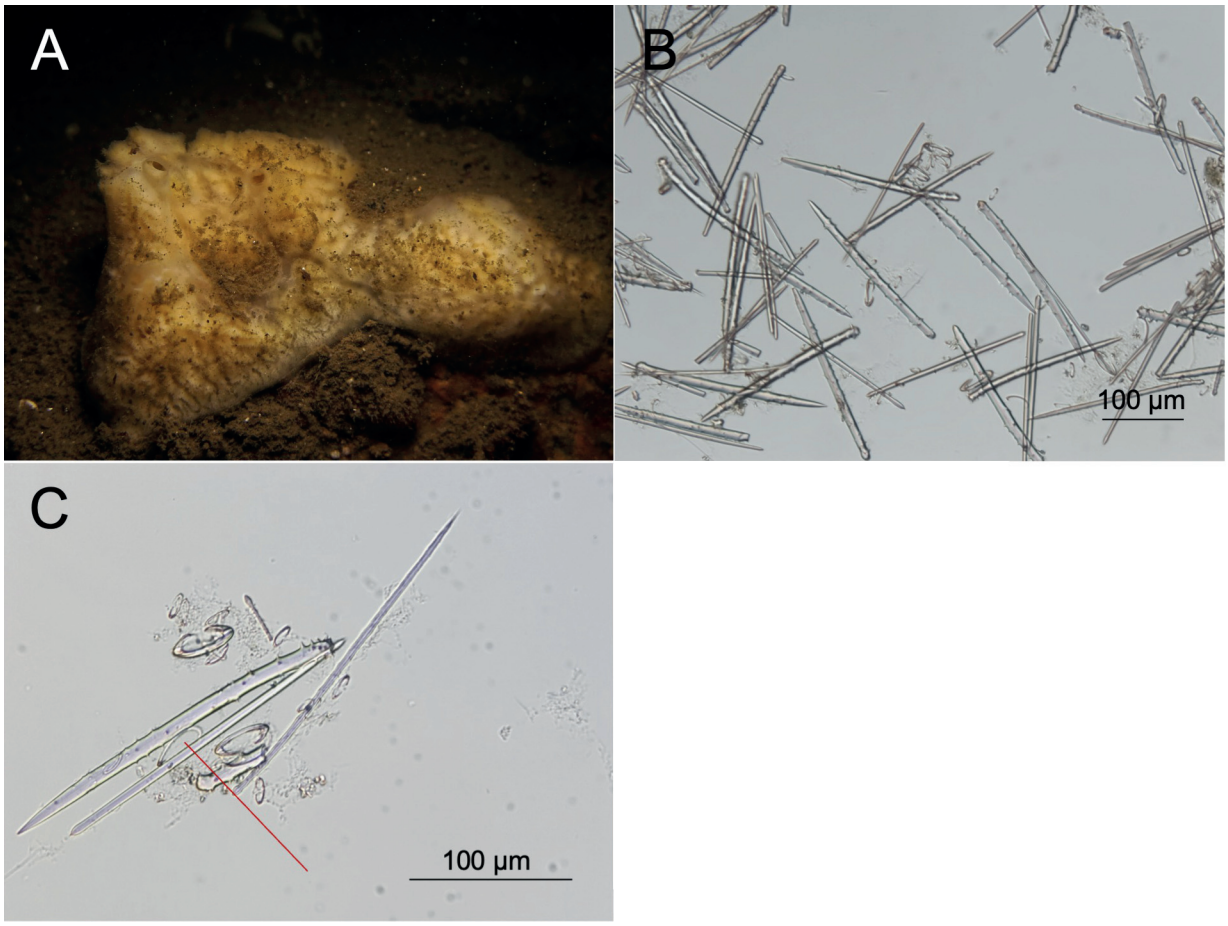

Fig. 22. *Phorbas dives* (Topsent, 1891). **A**. Live specimen, GNM Porifera 1104 (LAR-180828-7014, 7016). **B**. Spicule slide showing the size range of the acanthostyles. **C**. Spicule slide showing, 2 sizes of isochelae; one tornote and one sigma (red line).

Description

All the specimens examined presented a thick encrusting or cushion morphology. The surface is smooth with wide, clearly observable, subsurface channels terminating in the oscula (Fig. 22A). The colour of the specimens alive was light-beige turning to whitish-beige when preserved in ethanol.

Skeleton

The skeleton presents a plumose conformation with multispicular tracts of acanthostyles and tornotes disposed perpendicularly to the surface while sigmas and arcuated isochelae are mostly found near the surface. The acanthostyles (Fig. 22B–C) are divided in two categories with overlapping sizes but with different spinations: a) slightly curved and sparsely spined throughout the shaft to the tip, measuring 167.5–**200.1–**327.2 ± 37.80 × 2.9–**7.0**–12.1 ± 2.4 µm (N = 25), and b) heavily spined, measuring 160.5–**194.6–**318.8 ± 30.70 × 2.7–**5.9–**9.6 ± 1.60 µm (N = 31). The tornotes measure 108.5–**164.3**–187.5 ± 12.55 × 1.8–**3.7**–5.2 ± 0.68 µm (N = 34). The arcuate isochelae (Fig. 22C) occur in two size classes: a) 11.4–**16.3–**21.2 ± 2.4 µm (N = 36), and b) 26.2–**32.9–**1 ± 3.7 µm (N = 17). Finally, the sigmas (Fig. 22C) measure 12.1–**26.9–**39.9 ± 8.1 µm (N = 25).

Ecology and distribution

The type locality for this species is Roscoff in Brittany, France (Topsent 1891). However, *P. dives* has been previously reported from Wales (UK), Ireland to northern Spain (Descatoire 1969), the Canary Islands and the Azores (Simó 2002), as well as from the Mediterranean, in Italy (Sarà & Siribelli 1960) and Tunisia (Mustapha *et al.* 2003). In spite of this large geographical range, this species had not been previously reported for Sweden or Norway. Our specimens were collected by SCUBA in Idefjorden and the Koster area, between 15 and 25 m depth, thereby extending the geographical range of this species.

Phorbas dives seems to prefer a hard substrate and vertical or overhanging sites, possibly to avoid sediment deposition (Ackers *et al.* 2007). This combined with its encrusting morphology makes this species difficult to detect and collect.

Remarks

Two other species are similar to *P. dives*: *Phorbas bihamigera* (Waller, 1878) from Torbay near Plymouth, southern England, and *Phorbas microchelifer* (Cabioch 1968) from Brittany, France. None of these species have been reported in Sweden or Norway. *Phorbas bihamigera* differs from *P. dives* by having a higher abundance of chelae and more prominent aquiferous channels while *P. microchelifer* has smaller chelae (20 µm vs 36 µm in *P. dives*) (Cabioch 1968). Cabioch (1968) has seen many specimens from the type locality of which only the holotype (MNHN-IP-2015-649) was deposited. Cabioch (1968) compared *P. microchelifer* with specimens of *P. dives* from Roscoff, identified by Topsent himself (according to Cabioch 1968), thus we can reasonably consider this species as valid even if awaiting confirmation from molecular data.

Our coxI phylogeny (Fig. 2) places our specimens of *P. dives* within a *Myxilla incrustans* clade. This contradicts current classifications, as *Phorbas* belongs to Hymedesmiidae, while *Myxilla* belongs to Myxillidae. We are confident in our identifications since the spiculation of our specimens matches better *P. dives*, and differs from *M. incrustans* in its tornotes: our specimens' tornotes are completely smooth (as reported for *P. dives*), while *M. incrustans* has typical spines at the terminations of the tornotes. Additionally, the family Hymedesmiidae is often regarded as a taxonomic waste basket, and shown to be polyphyletic (e.g., Morrow *et al.* 2013; Redmond *et al.* 2013: this study) thus the presence of species from other clades, still classified as hymedesmids is unsurprising. A full revision of Hymedesmiidae and Myxillidae with molecular data is required to revise the precise allocation of *P. dives*.

Family Mycalidae Lundbeck, 1905
Genus *Mycale* Gray, 1867

Mycale macilenta (Bowerbank, 1866)
Fig. 23

Hymeniacidon macilenta Bowerbank, 1866: 176.

Hymeniacidon macilenta – Bowerbank 1874, pl. XXXIII fig. 7–13.
Mycale macilenta – Arndt 1935: 48, fig. 82. – Ackers 2007: 112–113.

Material examined

SWEDEN • 1 spec.; Saltbacken; 59.0832° N, 11.2242° E; 28m depth; 28 Oct. 2019; Mats Larsson leg. [MM-191029-2]; SCUBA; LAR-191029-PA290222, 0224; GenBank no.:OM415625 (28S D3-D5); voucher: GNM Porifera 1082.

Description

The specimen was 5 cm in diameter but we only collected a 4 mm fragment. Its morphology is thin, encrusting with a single osculum at the centre in a small erect tube. The surface presented several pores regularly scattered and the aquiferous canals were partially visible. The specimen alive presented a translucent pale pinkish colour. However, given that the substrate was partially visible under the sponge, its true colour is difficult to ascertain (Fig. 23A). The specimen is white when preserved in ethanol.

Skeleton

Unfortunately, the fragment was too small to section, thus we have not observed the skeleton conformation. The megascleres are straight subtylostyles/tylostyles (Fig. 23B) measuring 193.6–**272**–308.7 ± 23.28 × 2.2–**3.5**–5.7 ± 0.98 µm (N = 33). The microscleres are palmate anisochelae (Fig. 23C) with three size classes: a) 8.9–**12.2**–16.8 ± 1.31 µm (N = 107), b) 17.4–**22.4**–24.4 ± 1.78 µm (N = 25), and c) 27.1–**32.9**–40.6 ± 3.39 (N=22). Sigmas (Fig. 23D) came in two size classes: a) 18–**23.7**–33.4 ± 4.18 × 0.3–**0.8–**1.4 ± 0.33 µm (N = 14) , and b) 67.5–**84.5**–110.0 ± 11.36 × 3.2–**4.6**–6.7 ± 1.02 µm (N=25). Finally, there are smooth toxas (Fig. 23E) in a single size class, measuring 56.2–**75.5**–103.4 ± 13.13 (N= 11).

Remarks

This is a common temperate species found in the northeast Atlantic (NEA) and the Mediterranean Sea, the type locality being the Guernsey Islands in the English Channel. This is the first published report from Sweden, but an unpublished specimen from Sweden has previously been identified by Ole Tendal, it was found in the collections at Naturalis Biodiversity Centre, Leiden. Recording *M. macilenta* in Swedish waters means it can withstand colder waters than those of the English Channel. On the Swedish west coast, the average sea surface temperature (SST) varies between 2°C and 8°C in winter and spring, reaching 23°C in the summer, but with an overall average of 10°C (SMHI data). In contrast, the English Channel in the winter and spring has a SST present temperature between 9°C and 11°C reaching up to 22°C, and with an overall average of 13°C (Morris *et al.* 2016).

There are reports of *Mycale macilenta* in the NEA and Mediterranean Sea, from the Canary Islands up to the Celtic Sea. However, the spicules in this species seem to vary, especially when it comes to the chelae and sigma size classes (e.g., Pestana 2018; van Soest 2014). Nonetheless, when comparing

our specimen with the description based on the re-examination of the type (van Soest 2002), we note that our specimen presents the same three size classes of chelae (sizes reported for the type: 11–15 µm, 17–24 µm, and 33–59 µm). Furthermore, we observe that the smallest size of chelae is far more common than the other two size classes. This was also a general pattern noted both in the original description (Bowerbank 1866) and later re-examination of the type (van Soest 2002).

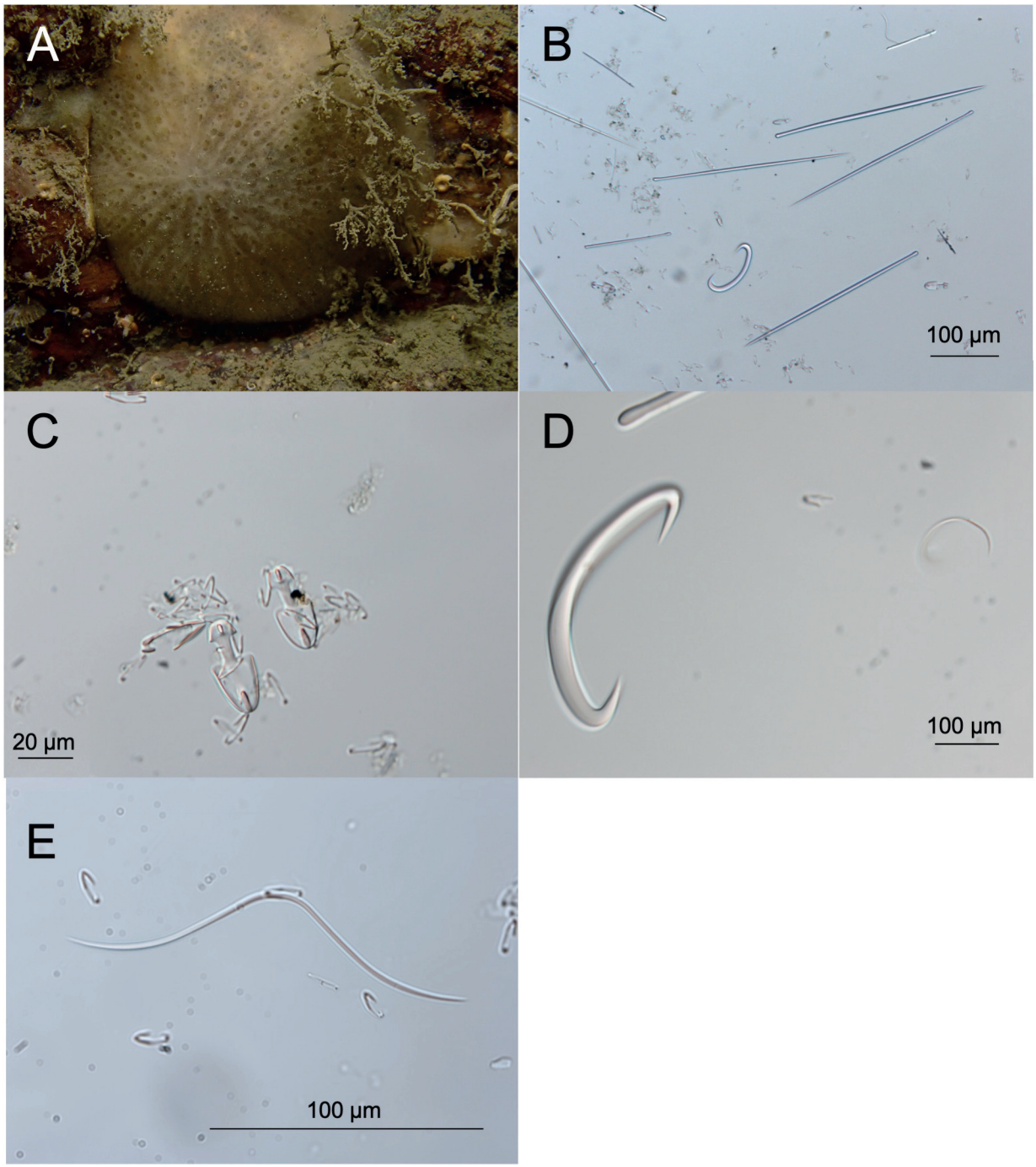

Fig. 23. *Mycale macilenta* (Bowerbank, 1866). **A**. Live specimen, GNM Porifera 1082 (LAR-191029-PA290222, 0224). **B**. Spicule slide showing the subtylostyles. **C**. Three class sizes of chelae. **D**. Large sigma. **E**. Toxa.

Regarding sigmas, our specimen presents the same two size classes as the holotype (65–115 µm and 21–28 µm) (van Soest 2002). Our specimen presents a variable size of toxas but we do not find toxas longer than 103 µm while those in the holotype are 60–250 µm long. Finally, our specimen does not seem to present the same colour alive than what was reported in the original description (bright red) (Bowerbank 1866). Despite slight differences between our specimen and the holotype description, namely pale colouration and slightly smaller toxas, we consider our specimen to be conspecific with the holotype of *M. macilenta*.

Order Clionaida Morrow & Cárdenas, 2015
Family Clionaidae d'Orbigny, 1851
Genus *Cliona* Grant, 1826

Cliona lobata Hancock, 1849

Cliona lobata Hancock 1849: 341–342, pl. XII fig. 4, 8.

Cliona lobata – Alander 1942: 80.
?*Cliona howsei* Hancock, 1849 – Levinsen 1893: 415 fig. 27.

Material examined (2 specimens)

SWEDEN • 1 spec.; 57.3042° N, 11.9321° E; 51–49 m depth; 31 May 2007; Artprojektets Skagerrak-inventering leg. [KA68]; dredge; P082-111026-1; voucher: GNM Porifera 554 • 1 spec.; 58.1352° N, 11.2512° E; 51–49 m depth; 27 Aug. 2007; Artprojektets Skagerrak-inventering leg. [SK67]; dredge; P082-111026-2; voucher: GNM Porifera 555.

Description

The specimens had a boring morphology growing in shells, but papillae protruding from them. The colour in situ is unknown and light yellow when preserved in ethanol.

Skeleton

The skeleton is composed of megascleres, which are tylostyles measuring 230–350 × 7.5 µm (N=4), and spirasters as microscleres, which may be rare in some individuals, measuring 12.5–17.5 µm (N=2) in length.

Ecology and distribution

The type locality is in the English Channel. However, there are reports from Denmark to South Africa, as well as from the Mediterranean and the Black Sea.

Remark

The species *C. lobata* differs from *C. celata* by several external morphological features, namely smaller and more abundant papillae, and thinner boring galleries. Additionally, *C. lobata* consistently possesses spirasters, while their presence in *C. celata* is only documented by Topsent (1900). However, given that *C. celata* is a species complex (Xavier *et al*., 2010) in dire need of taxonomic studies, and as spirasters can be rare in specimens of *C. lobata*, especially in massive morphotypes, it is possible that many specimens identified as *C. celata* in the past might actually belong to *C. lobata*.

Order Suberitida
Family Suberitidae Schmidt, 1870

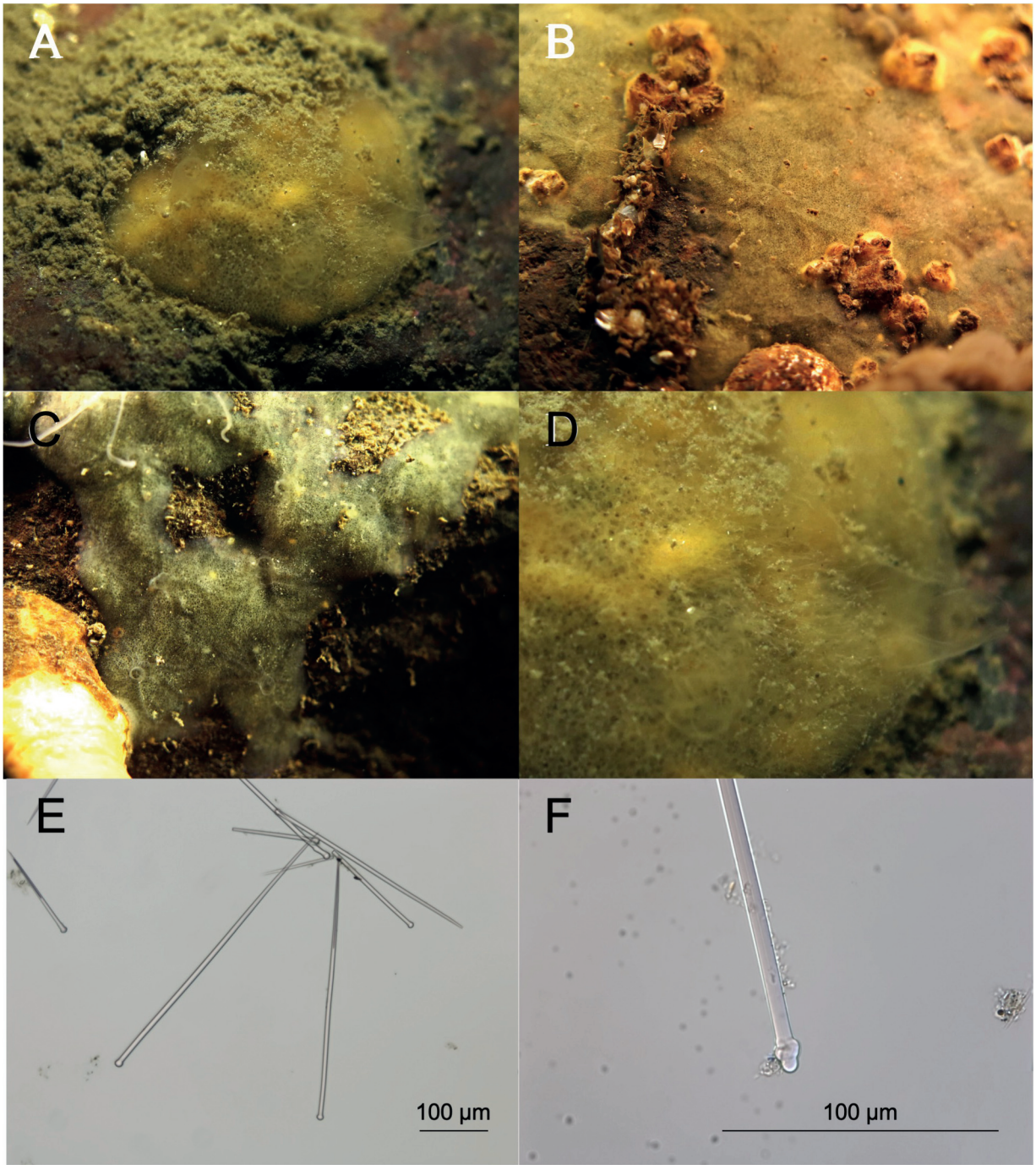

Fig. 24. *Protosuberites* sp. **A**. Live specimen in situ, GNM Porifera 1114 (LAR-180424-4583–4584). **B**. Live specimen in situ, GNM Porifera 1115 (LAR-181204-8156, 8159–8160). **C**. Live specimen in situ, GNM Porifera 1116 (LAR-181218-8476, 8478, 8481). **D**. Detail of A showing bundles of spicules at the surface (LAR-180424-4583–4584). **E**. Tylostyles in specimen GNM Porifera 1114 (LAR-180424-4583–4584). **F**. Subtylostyle (rare).

Protosuberites sp.
Fig. 24

Material examined (3 specimens)

SWEDEN • 1 spec.; Saltbacken; 59.0832° N, 11.2242° E; 24 Apr. 2018; Mats Larsson leg. [MM-180424-1]; SCUBA; LAR-180424-4583–4584; GenBank no.: OM436223 (coxI); voucher: GNM Porifera 1114 • 1 spec.; Svartejan; 59.1102° N, 11.3219° E; 4 Dec. 2018; Mats Larsson leg. [MM-181204-1]; SCUBA; LAR-181204-8156, 8159–8160; GenBank nos: OM628824 (coxI), OM415645 (28S D3-D5); voucher: GNM Porifera 1115 • 1 spec.; same collection data as for preceding; LAR-181218-8476, 8478, 8481; voucher: GNM Porifera 1116.

Description

The specimens were all thin encrusting, 6 mm of maximum diameter (Fig. 24A–C). The alive colour was pale yellow or greenish yellow turning beige when preserved in ethanol. The surface is microhispid, with visible spicules in bouquets/bundles (Fig. 24D). The pores as well as the oscula are visible. Oscules are elevated in translucid chimneys (Fig. 24A–B).

Skeleton

Skeleton is confused apart from the bouquets/bundles of tylostyles on the surface. Megascleres are tylostyles (Fig. 24E), usually straight and with a very defined head, rarely displaced in the shaft (Fig. 24F) or in ring shape. They are in a wide size range, but not separated in discrete size classes (Fig. 24C), measuring 74.4–**187.9**–449.9 ± 101.8 × 2.3–**3.6**–3.4 ± 1.4 µm (N = 13). Some tylostyles are slightly curved near the tyle. No microscleres were found.

Remarks

There are currently nine valid species of *Protosuberites* reported in the Mediterranean and the NEA. The external morphology in colour and in habitus is similar to what is described for the common European *P. denhartogi* van Soest & de Kluijver, 2003, and this includes the subsurface patterns. However, our specimens present tylostyles smaller than what is reported for *P. denhartogi*, which presents the smallest size of tylostyles (74 µm in length) in one occurrence whereas the remaining spicules are all bigger than 100 µm, averaging 248 µm in size. In contrast, our specimens have an average spicule size of 189 µm. We were inclined to call these specimens *P. denhartogi*, but coxI does not group with a sequence of *P. denhartogi* (Fig. 2). Therefore, we prefer to call these specimens *Protosuberites* sp. for now. More specimens of *Protosuberites* need to be barcoded to begin to understand this group.

Genus ***Suberites*** Nardo, 1930

Remarks on the genus

The genus *Suberites* Nardo, 1930 is characterised by a confused skeleton constituted by (sub)tylostyles and/or microscleres that are microspined centrotylote oxeas, strongyles or even styles, with all of these microscleres possibly in the same specimen. The species of this genus do not have clear ectosomal differentiation. The habitus is thin encrusting to massive, has a compact consistency, velvety surface, and the colour is from beige to tawny. This description together with other similar descriptions of other genera within the family Suberitidae makes the assignment of a specimen to the correct genus difficult. For the genus itself, many of the species were described more than a century ago and many of the names have been synonymised (e.g., Burton 1953) or forgotten, and many of the species have a very short and cryptic description. There are currently 83 accepted species for the genus and about

102 unaccepted names. For the NEA there are currently 76 accepted species. Here, we present very preliminary names for the *Suberites* species, pending a thorough taxonomic revision.

Suberites spermatozoon (Schmidt, 1875)

Cometella spermatozoon Schmidt, 1875: 116 pl. I fig. 2.

Suberites spermatozoon – Fristedt 1885: 18–19; 1887: 429–430.
?Ficulina spermatozoon – Burton 1930: 496.
Choanites spermatozoon – Alander 1942: 79.

Material examined (5 specimens)

SWEDEN • 1 spec.; Gullmaren, Skåreskär; 58.2973° N, 11.5150° E; 105–100 m depth; 24 May 2014; Erica Mejlon leg. [Skåreskär 140424]; dredge; P062-140504-1; GenBank no.: OM436260 (coxI); voucher: GNM Porifera 1154 • 1 spec.; same collection data as for preceding; P062-140504-2; voucher: GNM Porifera 1155 • 1 spec.; same collection data as for preceding; P062-140504-3; GenBank nos: OM436257 (coxI), OM415618 (28S D3-D5); voucher: GNM Porifera 1156 • 1 spec.; same collection data as for preceding; P062-140504-4; voucher: GNM Porifera 1157 • 1 spec.; Gullmaren, Skåreskär; 58.2942° N, 11.5138° E; 105–100 m depth; 5 May 2014; Erica Mejlon leg. [Skåreskär, 140505]; dredge; P062-140513-1; voucher: GNM Porifera 1158.

Description

The specimens are small, only a couple of centimeters long, pyriform with a hollow body and a long peduncle. The same pedicle can be connected to several bodies. Our specimens were not attached to hard substrate when dredged in the muddy bottoms. A simple osculum is present on the top of each specimen. Colour yellowish-grey, both alive and preserved in ethanol.

Skeleton

The skeleton was composed by (sub)tylostyles, either straight or flexuous, with a bimodal size distribution, i.e., there is too much overlap to be two bona fide size classes, measuring: a) 320–**430.3** - 840±78.1×2.5 - **6.6** - 10±1.8 μm (N=80), and b)–135 - **247.7** - 317.5±38.7×2.5 - **5.3** -10±1.6 (N=54). These megascleres sometimes present abnormal forms, such as styles or strongyles. Microscleres are microspined centrotyloted slightly curved strongyles or oxeas. The tyle is less evident than in other *Suberites* species and could present a displacement from the centre of the spicule. These microscleres measure 11.3–**32.5**–72±10.3×2–**2.6** – 4 +/ 0.5 (N=130). Finally, all specimens have modified microrhabds that are spherical and smooth. These spheres are found in the peduncles of the specimens but in very low numbers making them difficult to find in spicules preparations. The diameter is the same as for the length of the microscleres.

Ecology and distribution

The type locality of *Suberites spermatozoon* is near Mandal (southern Norway), but it has been reported in the Kara Sea (Fristedt 1887), Bering Sea (Hentschel 1929) and Sweden (Fristedt 1885; Alander 1942). In Sweden, this species was common in Gullmaren fjord, between 65 and 90 m depth (Alander, 1942), which is where we collected our specimens.

Remarks

The distribution of this species is poorly known, as its small size and fragile bodies combined with its habitat (muddy bottoms) makes it difficult to detect. Furthermore, it has been reported from great

depths varying from 38 m (Fristedt 1887) to 400 m depth (Alander 1935), which makes sampling and observation nearly impossible by any other means than dredging. The specimens here examined come from Gullmaren fjord, ca 100 m depth.

Family Halichondriidae Gray, 1867
Genus *Halichondria* Fleming, 1828

Halichondria panicea (Pallas, 1776)
Fig. 25

Spongia panicea Pallas, 1766: 388.

Amorphina panicea – Fristedt 1885: 26.
Halichondria panicea – Levinsen, 1893: 415–416. — Alander 1942: 28, pl. 6.

Material examined (21 specimens)

SWEDEN • 1 spec.; Svartejan; 59.1102° N, 11.3219° E; 30 m depth; 11 Oct. 2018; Mats Larsson leg. [MM-180911-1]; SCUBA; LAR-180911-7191, 7194; GenBank no.: OM436248 (coxI); voucher: GNM Porifera 1003 • 1 spec.; same collection data as for preceding; 25 Oct. 2018; Mats Larsson leg. [MM-180925-1]; SCUBA; LAR-180925-7457, 7460, 7463; GenBank nos: OM436249 (coxI), OM415607 (28S D3-D5); voucher: GNM Porifera 1009 • 1 spec.; same collection data as for preceding; 4 Dec. 2018; Mats Larsson leg. [MM-181204-1]; SCUBA; LAR-181204-8186–8188; GenBank nos: OM436281 (coxI), OM415649 (28S D3-D5); voucher: GNM Porifera 1010 • 1 spec.; same collection data as for preceding; LAR-181204-8189–8191; GenBank nos: OM436228 (coxI), OM415594 (28S D3-D5); voucher: GNM Porifera 1011 • 1 spec.; Gullmaren; 58.2550° N, 11.4446° E; 1 Apr. 2012; dredge; P016-230414-7; GNM Porifera 1007; • 1 spec.; same collection data as for preceding; P088-120403-1; GNM Porifera 1016; • 1 spec.; Gullmaren; 58.2667° N, 3.5812° E; 28 Apr. 2018; P088-180425-2; GNM Porifera 1018; • 1 spec.; Gullmaren; 58.2667° N, 3.58125° E; 24 Apr. 2018; dredge; P088-180425-2; GNM Porifera 1018; • 1 spec.; same collection data as for preceding; P088-180425-3; GNM Porifera 1019 • 1 spec.; Lunneviken; 59.0546° N, 11.1690° E; 30 m depth; 18 Sep. 2018; LAR-180918-7245–7246; GNM Porifera 1004 • 1 spec.; Bergylteskär; 58.8210 °N, 11.0831° E; 9 Dec. 2018; Mats Larsson leg. [MM-181209-1]; SCUBA; LAR-181209-8193, 8197–8198; GenBank no.: OM415600 (28S D3-D5); voucher: GNM Porifera 1012 • 1 spec.; same collection data as for preceding; LAR-181209-8205, 8207–8208; GenBank nos: OM436242 (coxI), OM415603 (28S D3-D5); voucher: GNM Porifera 1013 • 1 spec.; Trindeknubben; 58.7829° N, 10.9962° E; 24 Jun. 2019; Mats Larsson leg. [MM-190624-1]; SCUBA; LAR-190624-9497; voucher: GNM Porifera 1005 • 1 spec.; Yttre Vattenholmen; 58.8754° N, 11.1056° E; 16 Nov. 2019; Mats Larsson leg. [MM-191116-1]; SCUBA; LAR-191116-PB160514–16; voucher: GNM Porifera 1006 • 1 spec.; Kosterhavet; 58.8833° N, 11.0833° E; 1 Nov, 2001; Fredrik Pleijel leg. [TML-01]; dredge; P002-011112-1; voucher: GNM Porifera 1014 • 2 specs; 58.0723° N, 11.3267° E; 11-30 m depth; 23 Sep. 2009; Artprojektets Skagerrak-inventering leg. [201]; dredge; P088-111026-1; GNM Porifera 585; Skagerrak; 58.0651° N, 11.3234° E; 2326 m depth; 24 Sep. 2009; Artprojektets Skagerrak-inventering leg. [212]; dredge; P088-111026-2; GNM Porifera 586 • 1 spec.; Gullmarens inlopp; 8 May 2012; staff and students of courses 1BG217 and 1BG394 cohort 2012 leg. [Gullmarens inlopp, 120508]; dredge; P088-120410-1; GNM Porifera 1017 • 1 spec.; Gullmaren, Långgap, 58.2577° N, 11.4262° E; 18 m depth; 20 Apr. 2016; students and staff of course 1BG217, cohort 2015 leg. [1BG217-2015-25]; dredge; P088-160505-1; GNM Porifera 1008 • 1 spec.; Gullmaren, Långgap; 58.2550° N, 11.4447° E; 12 m depth; 21 Apr. 2016; staff and students of course 1BG217 cohort 2016 leg. [1BG217-2016-5]; dredge; P002-160504-1; GNM Porifera 1015 • 1 spec.;

Gullmaren, Flatholmen; 14 m depth; 23 Apr. 2019; staff and students of course BG393 cohort 2019 leg. [Flatholmen, 190423 [34]] P088-190424-1; GNM Porifera 1021.

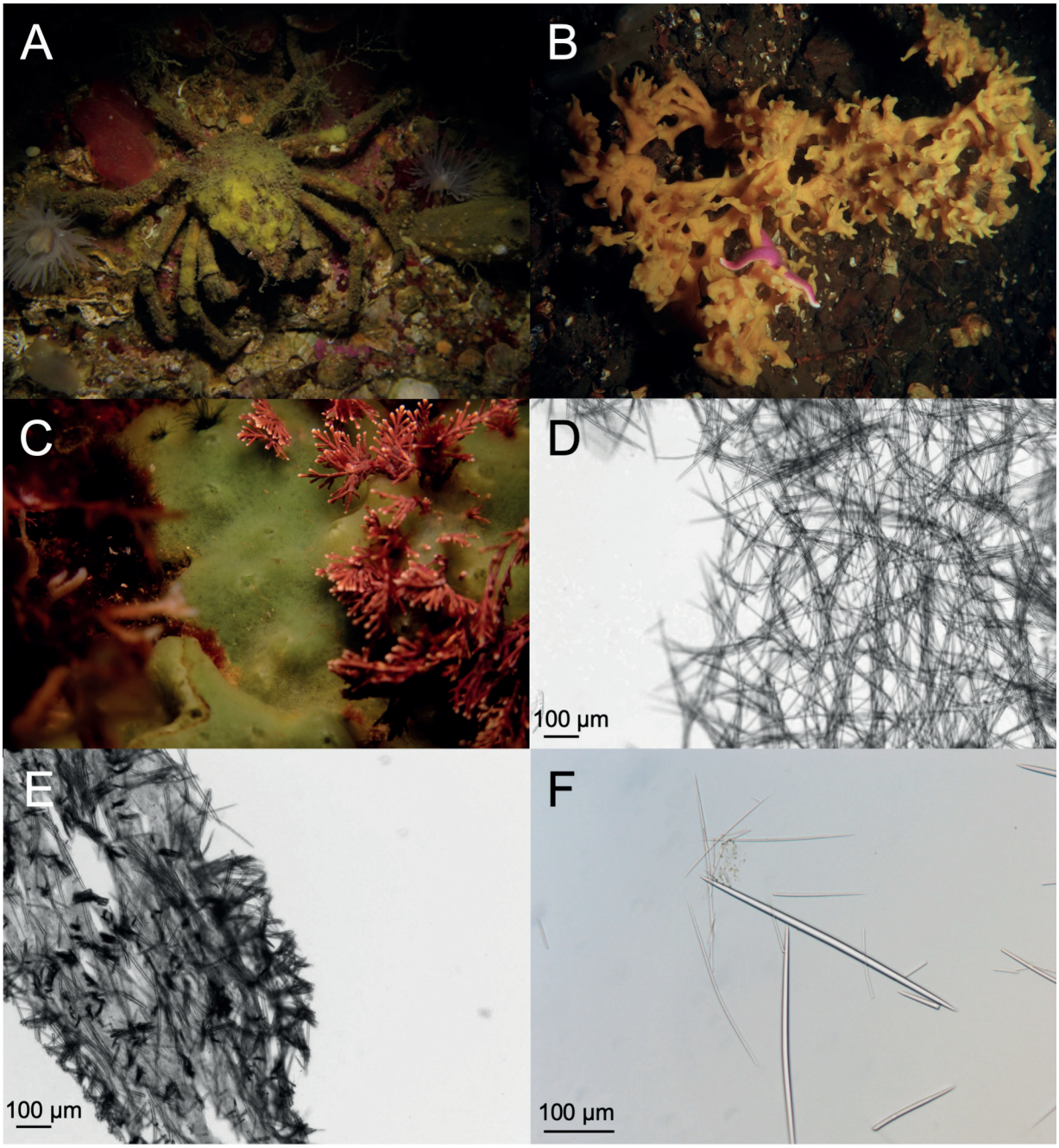

Fig. 25. *Halichondria panicea* (Pallas, 1776). **A**. Live specimen with thin encrusting morphology, GNM Porifera 1004 (LAR-180918-7245–7246). **B**. Live specimens with branching morphology, GNM Porifera 1003 (LAR-180911-7191, 7194). **C**. Live specimens with thick encrusting morphology (LAR-190624-9497). **D.** Tangential section showing ectosomal structure, GNM Porifera 1005 (LAR-180911-7191, 7194). **E**. Cross section of specimen GNM Porifera 1003 (LAR-180911- 7191, 7194). **F**. Oxeas in specimen GNM Porifera 1004 (LAR-180918-7245–7246).

Description

Specimens presented morphologies from thin sheets to thick encrusting or even branching (Fig. 25A–C). However, the most common form is thick encrusting (Fig. 25C). The oscula are elevated on chimneys, scattered evenly across the surface. The colour alive varied from green to dark yellow turning to beige/cream in ethanol. The surface is smooth, easy to peel off and with tracts of the aquiferous system observable even in living specimens.

Skeleton

The skeleton has a confused skeleton arrangement except for the ectosome (i.e., halichondrioid skeleton). The ectosome is reticulated (Fig. 25D–E). The specimens presented only curved oxeas as megascleres, measuring 391.2–**256.4–**128.2 ± 47.26 × 12.3.4–**4.7–**2.3 ± 2.17 μm (N =167).

Ecology and distribution

Halichondria panicea is a common species, found from the intertidal/subtidal down to 500 m. In shallow waters it often grows on boulders and brown algae. In Sweden it can be found from the intertidal to 569 m depth (Alander 1942).

Remarks

The different morphotypes that this species can present are attributed to different water regimes (Palumbi 1986; Barthel 1991). This species is sympatric with *Halichondria bowerbanki* Burton, 1930 and the two species can be easily confused. However, specimens of *H. panicea* have a peelable 'skin-like' surface, and can have a green colour, which *H. bowerbanki* never has. Additionally, the specimens of *H. bowerbanki* rarely yield an amplicon when using the standard coxI primers. The *H. panicea* presents a very wide distribution ranging from the northeast Pacific (Bering Sea) to the southwest Atlantic but the Pacific reports of *H. panicea* probably refer to a distinct species (Erpenbeck *et al.* 2004).). Six coxI sequences were obtained, corresponding to three haplotypes (1–2 bp differences). Still more studies need to be done to test if the NEA *H. panicea* is a species complex.

Discussion

Reported demosponge fauna largely different between studies

In this work, we examined morphologically 417 demosponge specimens. Of these, we were able to identify 411 to the species level totalling 57 different species, and an additional five specimens identified to the genus level, overall encompassing 22 families and 10 orders (Table 1). Eight species were new to Sweden and one new to science. Interestingly, the species identified in this study show little overlap with those reported in previous major faunal surveys of marine sponges in Sweden (Fristedt 1885; Levinsen 1893; Alander 1942). Notably, these earlier surveys also exhibit limited overlap among themselves (Fig. 26, Supp. file. 4). Only 13 species are present in all surveys (including the present). Moreover, Alander (1942) stands out since of the 149 species he reported, a surprising 90 (60%) were not found in any other survey, including the present study. This might be due to the lack of sampling in the sensitive *Desmophyllum pertusum* coral reef in Sweden by the STI campaigns, given that Alander (1942) reported many sponges species from that habitat. The results of Jägerskiöld's and STI campaigns are directly comparable. This is possible because both campaigns targeted the same locations (apart from the deep-sea coral reefs), using similar or comparable methods, hence both survey results can be compared. This comparison was partially done by Mathias Obst and collaborators to assess biotic shifts through time (Obst *et al.* 2018). However, their study does not account for the demosponge fauna, as most of the sponge specimens from Jägerskiöld's campaigns still remain unidentified (ca 300 lots at Gothenburg Natural History Museum). In the present study, we examined the sponge specimens from the STI campaigns. However, until the processing of the sponge collection from Jägerskiöld's

campaigns is done, it is not possible to analyze the demosponge fauna shift for Sweden. In spite of this fact, we noticed that, for example, *S. spermatozoon* previously reported as common in Gullmaren fjord (Fristedt 1885; Alander 1935) was encountered only twice (four specimens), even with extensive yearly sampling efforts. Anthropogenic pressure such as bottom altering fishing methods, like trawling (Rosenberg & Nilsson 2005; Eigaard *et al.* 2016), and eutrophication (Pearson *et al.* 1985; Rosenberg *et al.* 1996), or acidification change (Göransson 2017), leads us to raise conservation concerns over some species of demosponges.

Sampling bias

Dredging and SCUBA diving yielded a limited overlap in species. Only 19% of the 57 species identified were collected using both methods. This difference can be explained by the sampling methods. Dredging on hard/rocky bottoms which present crevices and fissures is difficult and often results in the loss or damage of the gear. However, this type of environment is not an issue when sampling with SCUBA gear. Thus, many of the small encrusting sponges can only be collected by SCUBA. Admittedly, SCUBA has been important to achieve a better overview of sponge fauna in other cold-water regions in the world, e.g., Ireland (Ackers *et al.* 2007; Picton & Goodwin 2007; Goodwin & Picton 2009), the Falkland Islands (Goodwin *et al.* 2010 2016) and Chile (Hajdu *et al.* 2013). Less than 9% of demosponge specimens from the STI campaign exhibited an encrusting or boring

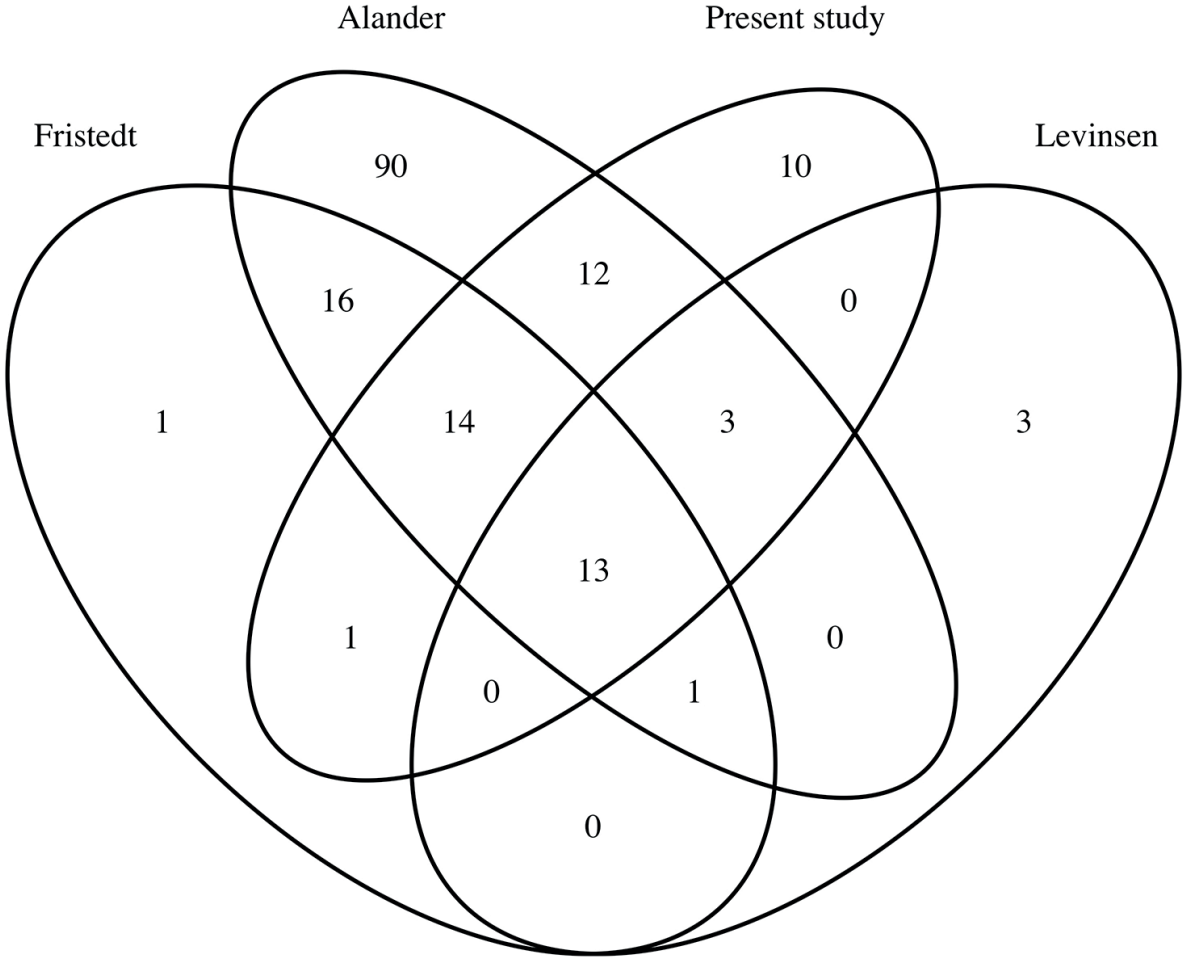

Fig. 26. Venn diagram showing (shared) number of species treated in the present inventory of Swedish marine Demospongiae, and by Fristedt (1885, 1987), Levinsen (1893) and Alander (1942).

habitus, contrasting with over 73% of those collected by SCUBA. Our own dredging efforts yielded a higher proportion (over 16%) of boring or encrusting specimens compared to the STI campaigns. This suggests that inconspicuous sponges might have been overlooked during sorting onboard STI vessels, rather than simply not being retrieved by the dredging method itself. Even though dredging can sample deeper than SCUBA, more than 49% of all dredging stations have a minimum depth that is accessible by SCUBA, i.e., not exceeding 40 m. This way, parsing the possible bathymetrical ranges of species treated from the sampling bias is impossible when only looking at this study's sampling.

From the 417 specimens, we successfully sequenced 66 and 77 of fully identified specimens for coxI (Folmer fragment) and 28S D3-D5, respectively. While sequencing of 28S D3-D5 was successful across all the different sponge groups encountered (using primers Por28S-830F and Por28S-1520R), we noticed a strong bias against amplifying coxI (using the Folmer and degenerated primers) in poecilosclerids, particularly *Hymedesmia* species. This seems to be a general problem given that for 188 species currently accepted in *Hymedesmia*, there are only two coxI sequence available in GenBank (KU659137 and OM729626). The present study brings an additional nine *Hymedesmia* coxI sequences from five species. In the future, this group of sponges will require either a new primer pair for coxI, or a new marker, in order to start building a barcoding database. In the same way, we failed to sequence coxI for *Phakellia robusta,* which is perhaps unsurprising given that shallow populations in the NEA of this species seem to have a mitochondrial intron in the coxI gene (Cranston *et al.* 2021), which renders amplification with standard PCR protocols impossible.

Barcoding effort mismatch described diversity

Our integrated approach for species identification, i.e., the use of morphology and phylogenetics, allows us to assess possible erroneous identifications impossible to detect in larger surveys or when some of the material is limited. Yet, given that our independent analyses both largely agree, we can now be confident of our identifications. This approach has also shown good results in other faunistic surveys for demosponges before (e.g., Vargas *et al.* 2015; Erpenbeck *et al.* 2016, 2020; Pons *et al.* 2017; Ngwakum *et al.* 2021). The NEA region harbours most of the demosponge species' type localities (van Soest *et al.* 2012). However, the majority of the recent demosponge faunistic surveys with both molecular and morphological data are from other regions, resulting in a mismatch between morphologically described diversity and available molecular data. In fact, there is a substantial number of species without molecular data available, or for which the only molecular data available is from specimens collected far from the type locality. The missing data seems to be true even for what is referred to as common shallow water species, and an in-depth study would be required to identify all taxa that are in need of coxI data and are easy to collect in their type locality. The missing data also means that many of the systematic revisions, up until now, are likely to change when type material is added to the systematic studies. In this regard, our study presents one of the few recent demosponge fauna studies for shallow water of the NEA, although important contributions to fill up the gaps had already been done in Ireland (Picton & Goodwin 2007; Goodwin & Picton 2009; Morrow *et al.* 2012, 2013).

In the present study, 16% and 23% fully identified specimens are assigned to orders Poecilosclerida and Suberitida, respectively. It is important to note, however, that the systematics of Poecilosclerida and Suberitida (species delimitation, as well as phylogenetic relationships) is still largely unresolved. Given the fraction of the specimens from these orders, it is likely that we underestimate the species richness, both regarding the sampling so far, but also the real diversity.

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Supplementary files

Supp. file 1. Collection sites and species assignments for the specimens examined in this study. vouchers GNM Porifera are deposited in Göteborg Natural History Museum's Porifera collection. https://doi.org/10.5852/ejt.2025.2835.12913

Supp. file 2. List of sequences used for the phylogenetic inference, using: coxI gene (Folmer region) in Fig. 2 and; DNA encoding region for 28S rRNA (fragment D3-D5) in Fig. 3. The (T) in specimens from sequences retrieved from GenBank, represents types i.e., the sequences belong to type specimens. In BOLD the accession numbers produced in this study. https://doi.org/10.5852/ejt.2025.2835.12921

Supp. file 3. Species of demosponges treated in the studies of Fristedt (1885, 1887), Levinsen (1893) and Alander (1942) as well as the present study. Taxonomic equivalence has not been directly assessed (with the exception of Alander's reevaluation of Fristedt), only nomenclatorial equivalence is used. Author strings are verbatim and names introduced as new species are in bold. Valid names are the current preferred names from World Porifera Database, WPD (de Voogd *et al.* n.d.). https://doi.org/10.5852/ejt.2025.2835.12923

Supp. file 4. Species of demosponges treated in the studies of Fristedt (1885, 1887), Levinsen (1893) and Alander (1942) as well as the present study. Taxonomic equivalence has not been directly assessed (with the exception of Alander's reevaluation of Fristedt), only nomenclatorial equivalence is used. Author strings are verbatim and names introduced as new species are in bold. Valid names are the current preferred names from World Porifera Database, WPD (de Voogd *et al.* n.d.). https://doi.org/10.5852/ejt.2025.2835.12929