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Geographic range extensions of stalked, flabelliform sponges (Porifera) from eastern Canada with a new combination of a species of *Plicatellopsis* in the North Atlantic

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Abstract

Three new species records, *Axinella arctica* (Vosmaer, 1885), *Semisuberites cribrosa* (Miklucho-Maclay, 1870), and *Cladocroce spatula* (Lundbeck, 1902), and one new combination, *Plicatellopsis bowerbanki* (Vosmaer, 1885) **comb. nov.** from eastern Canada are described. The four species have similar growth forms which are either fan or cup-shaped with obvious stalks. This is the first description of a member of the genus *Plicatellopsis* in the North Atlantic, and the second record of the genus in the northern hemisphere. The four species described here have a history of misidentification in eastern Canada and this work aims to guide future identifications in the region.

Key words: Porifera, Gulf of St. Lawrence, Canadian Arctic, Geographic Range Extensions, Taxonomy, Northwest Atlantic Ocean

Introduction

Sponges in the class Demospongiae have growth forms that range from very simple crusts to elaborate branches and even human-sized barrels (Lee *et al.* 2012; McMurray *et al.* 2008). Although the growth form of a sponge—whether massive, encrusting, tubular, or branched—can be a useful taxonomic character, shape is not always definitively diagnostic of a particular taxonomic group. Instead it is often essential to study microscopic characters to accurately identify species (Ackers *et al.* 1992; Hooper & Van Soest 2002). It is common for sponge species within a genus to have vastly different growth forms despite having similar skeletal arrangements and even molecular sequence identities. As filter feeders, the growth form of a particular sponge can be influenced by the external environment, especially the flow regime of the surrounding water (Bidder 1923; Palumbi 1984, Vogel 1977). The sponge body form is optimized to efficiently remove as much suspended food as possible to maintain a balanced metabolic energy budget (Leys *et al.* 2011). This is evident in the North Atlantic where several species across sponge orders have convergent external morphologies (Ackers *et al.* 1992; Picton & Goodwin 2017; Van Soest *et al.* 2000). Some of the most striking, but often unrelated, sponges in the North Atlantic form large fans and vases, creating complex three-dimensional underwater seascapes.

A variety of sponge assemblages can be found throughout the world (Maldonado *et al*. 2017). Sponge grounds are dense aggregations of sponges that form structurally complex habitats that enhance local benthic biodiversity (Hogg *et al.* 2010). In Canadian waters, sponge grounds formed by large, dense, often boulder-shaped sponges are common in the North Atlantic (Hogg *et al.* 2010; Klitgaard & Tendal 2004), and elaborate glass sponge reefs occur near British Columbia (Conway *et al.* 1991; Krautter *et al.* 2001; Maldonado *et al.* 2017) which form habitat for diverse communities of invertebrates and fish (Chu & Leys 2010; Dunham *et al.* 2018). Less elaborate sponge aggregations described as sponge gardens have also been identified in Canada, including dense patches of bush-like *Iophon* sponges in Frobisher Bay (Dinn *et al.* 2019). Conversely, flabelliform sponges (including leaf-like and vase shaped forms) are often solitary, though some species may aggregate in particular habitats (Ginn *et al.* 2000) . These fan-shaped sponges are conspicuous in underwater surveys and are associated with increased biodiversity (Beazley

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et al. 2013). Flabelliform sponges can constitute a large proportion of the benthic fauna and the three dimensional structure of a given benthic area, but do not necessarily form the majority of the benthic fauna as in the case of massive *Geodia* sp. sponge grounds in the boreal Atlantic (ICES 2009; Maldonado *et al.* 2017).

Recent efforts to identify sponge fauna of the western Atlantic have focused primarily on characterizing large charismatic sponges that could fit the criteria for vulnerable marine ecosystem designation (Kenchington *et al.* 2015). However, cryptic or less obvious species are often misidentified, and in many cases, specimens are placed in broadly defined taxa, which generates confusion. For example, fan-shaped sponges found in photo and video surveys in the Flemish Pass and fan-shaped and stalked sponges in a guide to sponges of the North Atlantic Fisheries region were identified as Family Axinellidae (Beazley *et al.* 2013, Kenchington *et al.* 2015). However, the same authors later questioned these classifications, recognizing that not all fan-shaped and lamellate sponges in the region may belong to the family Axinellidae (Beazley & Kenchington 2015). Grouping sponges that are similar in appearance could lead to the mischaracterization of faunal associations with some sponge species over others, or incorrect species distribution data.

The aim of this study is to provide a useful taxonomic guide for four species from eastern Canada that span different sponge orders, but whose identities are often confused due to similar external morphology and overlapping geographic distribution. Three of the species discussed have not been formally described from Eastern Canada, and one species is discussed as a new combination of a little-known genus in the northern hemisphere.

Methods

Study area and collections

Species were collected during several research surveys in eastern Canada (Figure 1). Arctic specimens were collected during two research cruises on the *CCGS Amundsen* (July 14–27, 2016; July 13–August 17, 2017) using an Agassiz trawl (1.5 m opening, 40 mm net mesh size, with a 5 mm cod end liner) towed for 3 minutes at 1.5 knots (2.8 km km h^{-1}), a box core (BX 650 MK III 50 cm x 50 cm, maximum penetration depth 60 cm) or a Sub-Atlantic SuperMohawk remotely operated vehicle (ROV), and a cruise on the *AQVIQ* (July 21–Sept. 4, 2018) using a Campelen or modified Campelen trawl (with a 12.7 mm cod end liner) towed for 15 minutes at 2 knots (3.7 km h^{-1}). Gulf of St. Lawrence specimens were collected during three surveys: the 2018 snow crab survey aboard the *Jean Mathieu* (July 19 –September 16, 2018) using a modified *Nephrops* trawl with a 40 mm cod-end liner towed for 5 minutes at 2 knots; the 2018 research vessel bottom-trawl survey of the southern Gulf of St. Lawrence aboard the *CCGS Teleost* (September 4–October 5, 2018) using a Western IIA trawl towed for 30 minutes at 3.5 knots (6.5 km h^{-1}); and the 2018 ground fish and shrimp multidisciplinary survey in the estuary and northern Gulf of St. Lawrence aboard the *CCGS Teleost* (August 4–September 1, 2018) using a Campelen 1800 trawl towed for 15 minutes at 3 knots (5.6 km h^{-1}). Specimens were also collected during a cruise in the Gulf of St. Lawrence (August 23–30, 2017) using the ROV ROPOS (www.ropos.com) aboard the *CCGS Martha L. Black.*

Sponge specimens were photographed on board with a scale for size reference and then either preserved in 95% ethanol or frozen. Arctic specimens collected aboard the *CCGS Amundsen* were analyzed at the University of Alberta, Edmonton, Alberta and the Gulf of St. Lawrence specimens and Arctic specimens collected aboard the *AQVIQ* were analyzed at the Gulf Fisheries Centre, Moncton, New Brunswick.

Taxonomy and Systematics

Sponge spicules were isolated from both outer (ectosomal) and inner (choanosomal) regions of the sponge body. Pieces of sponge were placed in undiluted household bleach overnight to remove tissue, then rinsed 4 times in distilled water allowing spicules to settle for 15 minutes between rinses, and cleaned in two washes of 95% ethanol. Cleaned spicules were dried on glass slides, mounted in DPX mounting medium (Sigma-Aldrich, St. Louis, MO) and imaged on a compound or stereomicroscope. Thick sections were made using a razor blade, cleared in clove oil, and mounted in Canada Balsam (Sigma-Aldrich, St. Louis, MO). For scanning electron microscopy (SEM), cleaned spicules were placed on metal stubs, coated with gold and viewed with a Hitachi SU3500 SEM. Spicule measurements (n = 30, unless otherwise noted) were made with ImageJ 1.52 and are reported as mean and range. Specimens were deposited at the Canadian Museum of Nature (CMN), Ottawa, Ontario, the Institut Maurice-Lamontagne (IML), Mont-Joli, Quebec, and the Atlantic Reference Centre (ARC), St. Andrews, New Brunswick. The World Porifera Database, which implements the classification system for Demospongiae proposed by Morrow and Cárdenas (2015), was used as the taxonomic authority (Van Soest *et al.* 2019).

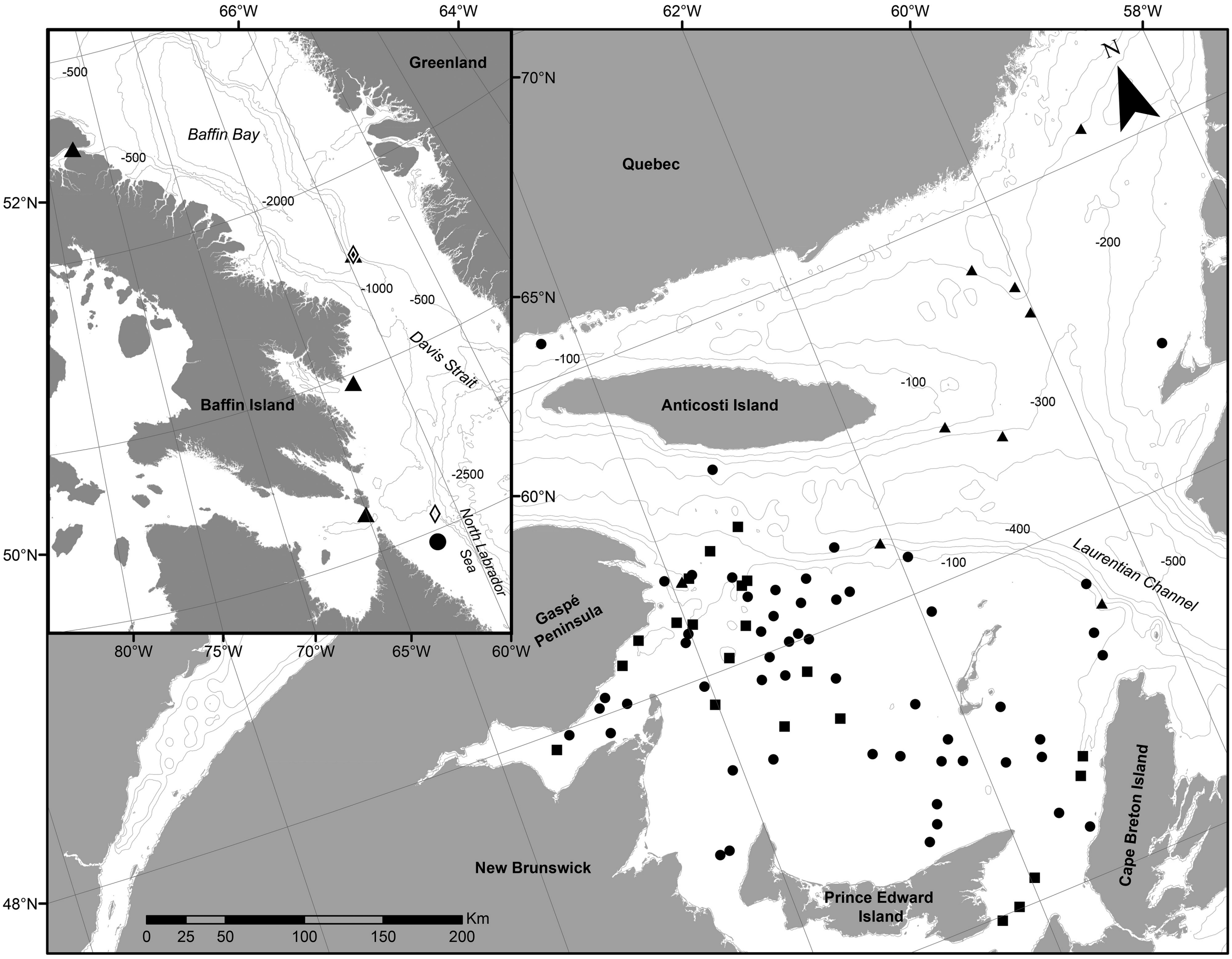

FIGURE 1. Map of the collection sites in Baffin Bay/ Davis Strait (inset) and collections in the Gulf of St. Lawrence. Hollow diamonds, *Axinella arctica*; filled circles, *Cladocroce spatula*; filled squares, *Semisuberites cribrosa*; filled triangles, *Plicatellopsis bowerbanki* comb. nov.

Barcoding of 28S rDNA and COI mtDNA

Total DNA was extracted using the DNeasy Blood and Tissue kit (Qiagen, Valencia, CA) following the manufacturer's instructions, using approximately 0.2 cm^2 of sponge tissue to account for spicule weight. Spicules were allowed to settle in the post-lysis mixture for 10 minutes before the mixture was applied to the spin column to prevent the transfer of spicules which would clog the column. DNA purity was assessed on a NanoDrop ND-1000 or ND-2000 (Thermo Scientific, Waltham, MA).

The 5' end region of COI was amplified using dgLCO1490 and dgHCO2198 degenerate Folmer fragment primers (Folmer et al. 1994; Meyer 2003). Sometimes M13F/M13R tails were added to the Folmer primers to improve sequencing results. Amplification of 28S rDNA was performed using Por28S-830F/1520R for region D3-D5 (Morrow *et al.* 2012). For COI and 28S amplifications, reactions used Platinum High-Fidelity Taq Polymerase (Invitrogen, Carlsbad, CA) and were run using a standard protocol of 94.0°C for 5 min; (95.0°C for 30 s; 48.0°C for 30 s; 72.0°C for 30 s) × 40 cycles; 72.0°C for 10 min. The sequencing reaction was run on an Applied Biosystems 3730 Genetic Analyzer at the Molecular Biology Service Unit (MSBU) at the University of Alberta. Contigs were assembled in BioEdit version 7.2 and manually checked for sequencing errors. The consensus sequences of the contigs were trimmed to remove primer residuals. Consensus sequences were aligned in MEGA (v.7.02) and species affinities were confirmed by BLAST nucleotide search (Altschul *et al.* 1990). Sequences were submitted to GenBank and accession numbers are provided with each description.

Results

Taxonomy

Phylum Porifera

Class Demospongiae

Subclass Heteroscleromorpha Cárdenas, Pérez & Boury-Esnault, 2012

Order Axinellida Lévi, 1953

Family Axinellidae Carter, 1875

Genus *Axinella* Schmidt, 1862

***Axinella arctica* (Vosmaer, 1885)**
(Figure 2, Table 1)

Original description: *Phakellia arctica* Vosmaer, 1885. 25, Pl. V, fig. 25-26
Synonyms: *Axinella calyciformis* (Lamarck, 1814), *Spongia calyciformis* Lamarck, 1814, *Spongia pocillum* Lamouroux, 1816, *Tragosia arctica* (Vosmaer, 1885), *Tragosia calyciformis* (Lamarck, 1814).

Material examined

North Labrador Sea: CMNI 2018-0094, 60.468 N, 61.287 W, 412 m depth; CMNI 2018-0099, 60.466 N, 61.278 W, 452 m depth. Western Greenland Shelf: CMNI 2018-0146 67.967 N, 59.484 W, 877 m depth. Larne, Antrim, Northern Ireland: *Axinella infundibuliformis* BELUM.Mc38, 54.93 N, 5.742 W, 23 m depth. Near Lundy, Bristol Channel, England: *Axinella infundibuliformis* BELUM.Mc41, 51.178 N, 4.683 W, 23 m depth.

External appearance (Figure 2A-D)

Axinella arctica (Vosmaer, 1885) is a cup-like or flabellate shaped sponge. The species often forms an inverted, hollow cone that ranges 5–25 cm in diameter, and has a solid stalk. The sponge is pale yellow or buff to white in colour. The surface of the inner portions has many pin-hole sized openings; smaller openings are present on the outside surface. Dense longitudinal ribs extend from the stalk to the distal portions on the outside surface. The consistency is firm, and pieces will break off when bent more than 45°. The walls of the specimens are up to 0.5 cm thick. The distal lip is hispid from protruding spicules.

Spicules and skeleton (Figure 2E–F)

Megascleres are styles 401–**467**–561 x 13–**17**–25 µm, and oxeas 329–**386**–443 x 13–**18**–24 µm. No microscleres are present. The skeleton consists of dense axial tracts of oxeas with loose extra-axial fibres consisting of styles which form long spicule brushes at the surface. Oxeas connect the extra-axial fibres.

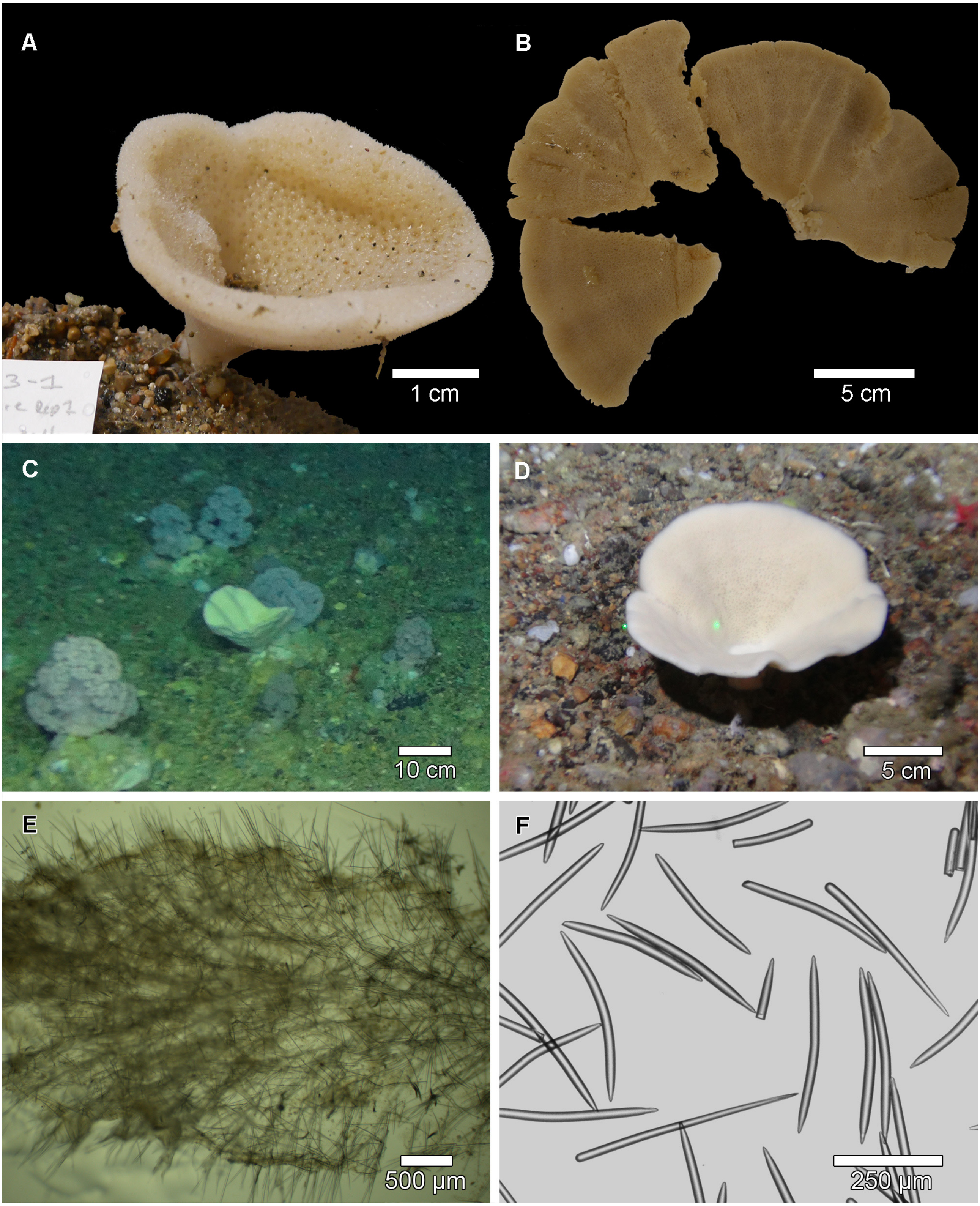

FIGURE 2. *Axinella arctica* (Vosmaer, 1885): A. small specimen attached to pebble, thick stalk visible; B. underside of collected fragments; C. specimen amongst *Duva* sp. soft corals; D. specimen from B *in situ*; E. skeleton; F. spicules, oxeas and styles. *In situ* photo credit: DFO/CSSF/ArcticNet.

Genetic data

COI for CMNI 2018–0099 (GenBank MK570860) was sequenced. The species is a perfect match to GenBank sequence for *Axinella infundibuliformis* BELUM:Mc4438 (GenBank HQ379410.1) based on 539 of 584 nucleotides. Although no apparent genetic difference in the COI mtDNA region exists between the two specimens, the lack of trichodragmata spicules and skeleton are characteristic of *Axinella arctica*; therefore until more comprehensive DNA–based distinctions in a less-conserved gene region can be made, the specimens collected from eastern Canada are considered here to be *Axinella arctica* based on morphology.

Distribution and ecology

Axinella arctica (Vosmaer, 1885) is found on rocky bottoms attached to hard substrates. In the North Labrador Sea and Baffin Bay the species was collected in deep water > 412 m. The species was also collected in the North Labrador Sea by Murillo *et al.* (2018), and reported from the Barents Sea, Nordic Seas, and European Waters (Stephens 1921; Van Soest *et al.* 2000, 2019). This species has a more northern distribution and was not collected in the Gulf of St. Lawrence.

TABLE 1. Comparison of individual variation of spicule dimensions of *Axinella arctica* (Vosmaer, 1885) given in micrometers as minimum-**mean**-maximum of length x width. n = 30 measurements of individual spicules, except from literature sources and where otherwise specified.

Specimen	Lat., Long.	Depth (m)	Styles (µm)	Oxeas (µm)
Phakellia arctica Vosmaer, 1885 from Stephens (1921) (Northern Norway)	72.6083N, 24.9583E	256	300–700 x 20	300–460 x 14
Tragosia arctica (Vosmaer, 1885) from Stephens (1921) (near Achill Head, Ireland)	53.9666N, 10.15W	699	300–750 x 20	375–600 x 20
CMNI 2018-0094 (Saglek Bank, North Labrador Sea)	60.4697N, 61.2894W	412	401–**467**–561 x 13–**17**–25	329–**386**–443 x 13–**18**–24
CMNI 2018-0099 (Saglek Bank, North Labrador Sea)	60.4526N, 61.2686W	452	390–**553**–704 x 12.5–**21**–29	303–**414**–530 x 13–**19**–25
CMNI 2018-0146 (Base portion only. Western Greenland Shelf)	67.9783N, 59.4845W	877	305–**381**–422 x 19–**22**–26 N=14	411–**462**–527 x 17–**22**–26

Remarks

The specimens considered here were previously described briefly by Dinn & Leys (2018), which was the first georeferenced record of the species in the North Labrador Sea and Baffin Bay.

The feature of this species that distinguishes it from other cup-shaped specimens in the region is the presence of oxeas and styles. The growth form and shape *in situ* is similar to *Plicatellopsis bowerbanki* (Vosmaer, 1885) **comb. nov.**, but *A. arctica* can be differentiated by its dense stalk and thicker tissue.

A. infundibuliformis was apparently collected by Whiteaves (1874) from the Gulf of St. Lawrence, but no spicule measurements or description were given. It is probable that the specimen collected by Whiteaves was another flabelliform species because *A. infundibuliformis* is not otherwise recorded from the western Atlantic (Van Soest *et al.* 2019). By contrast *A. infundibuliformis* has styles 260–360 µm and oxeas 210–280 µm, considerably smaller than the specimens collected in the North Labrador Sea. *A. infundibuliformis* also has trichodragmata microscleres, though these may be scarce (Ackers *et al.* 1992). The skeleton of *A. infundibuliformis* is also much more dense than *A. arctica*, with oxeas forming thick axial tracts and styles in multiple, tightly arranged extra-axial fibres. Interconnecting oxeas form a more noticeable reticulation in *A. infundibuliformis* and extra-axial fibres of styles ramify closer to the choanosome than in *A. arctica*, forming less obvious spicule brushes. Although *A. arctica* and *A. infundibuliformis* are difficult to distinguish from outer morphology, the size of the megascleres and skeletal arrangement are distinct. The genetic variation between the two species is, however, not discernable using the COI Folmer fragment gene region.

The spicule measurements from the North Labrador Sea specimens are only slightly shorter than those of the type specimens of *Phakellia arctica* (Vosmaer, 1885) measured by Stephens (1921) where the styles are 300–700 x 20 µm, and the oxeas are 300–460 x 14 µm. Stephens (1921) also collected specimens from Ireland, which have styles 300–750 x 20 µm and oxeas 375–600 x 20 µm. According to Stephens (1921), the Irish specimens agree more with Norwegian specimens collected by Topsent (1913) than the original description by Vosmaer (1885). Stephens (1921) reassigned *P. arctica* to the genus *Tragosia* rather than *Phakellia* or *Axinella* based on the arrangement of spicules in the skeleton. This placement was later refuted by Dendy (1922) because trichodragmata spicules were suggested to be a unique character of *Tragosia*. However, the presence of trichodragmata does not appear to be unique to any one genus of the Axinellidae and thus this species, as well as other members of *Tragosia*, were transferred to the genus *Axinella* (Alvarez & Hooper 2002).

Order Haplosclerida Topsent, 1928

Family Chalinidae Gray, 1867

Genus *Cladocroce* Topsent, 1892

Cladocroce spatula (Lundbeck, 1902)

(Figure 3, Table 2)

Original description: *Chalina spatula* Lundbeck, 1902: 11, Pl. II, Fig. 3, Pl. VIII, Fig. 8–9.
Synonyms: *Haliclona spatula* (Lundbeck, 1902)

Material Examined

Gulf of St. Lawrence: IML 11893, 49.1467N, 63.2727W, 241 m depth. Additional collected specimens are noted in Table 2.

External appearance (Figure 3A–C)

Cladocroce spatula (Lundbeck, 1902) is stalked and spatulate with one or more flat, leaf-shaped lobes extending out from a central stalk. Specimens can reach 35 cm in height and more than 20 cm in width at the widest breadth of the fan. The sponge is light brown in colour, though the sponge holds a substantial amount of water which may drain after collection causing the sponge to appear lighter in colour. Many large, round, raised oscula up to 0.3 cm in diameter run along the fan and stalk. There is sometimes a large visible osculum on the distal portion of a lobe *in situ*, but this collapses after collection. The consistency is elastic and soft. The axial skeleton beneath the ectosome forms dense, stringy fibres which result in a sponge that is difficult to tear. The stalk is more or less cylindrical and flares out at the base to form roots. The periphery of the lobes appear slightly hispid, but remains soft to the touch. The interior of the fan or lobes is hollow, though the sponge is always flattened. Epibionts and mud are common on the lower stalk.

Spicules and skeleton (Figure 3 D–E)

The spicules are oxeas 245–**228**–326 x 15–**18**–20 µm that are slightly bent. Some spicules may be thin, but these are less common and may represent developmental forms. The ends of the oxeas are sharply pointed near the distal portion, though in thinner spicules the point begins to taper closer to the centre. Stylote modifications and blunt ends are common. The skeleton is chalinid, a mostly anisotropic reticulation of multiple primary axial tracts of 2–3 spicules that run towards the surface in a slightly recurved, rib-like manner. The primary tracts are joined by single spicules forming a mostly square mesh. Primary tracts and nodes where single spicules join the primary skeleton are joined by spongin. There is no obvious ectosomal skeleton.

TABLE 2. Comparison of individual variation of spicule dimensions of *Cladocroce spatula* (Lundbeck, 1902) given in micrometers as minimum-**mean**-maximum of length x width. n = 30 measurements of individual spicules, except from literature sources.

Specimen	Lat., Long.	Depth (m)	Oxeas (µm)
Chalina spatula Lundbeck, 1902 (Western Greenland Shelf)	65.2833N, 54.2833W	101	190–**208**–220 x 10–12
IML 11893 (Near Anticosti Island)	49.1467N, 63.2727W	241	245–**228**–326 x 15–**18**–20
ARC 81418 (Baie des Chaleurs)	47.9046N, 65.4910W	55	192–**220**–250 x 13–**16**–18.5
ARC 81419 (Baie des Chaleurs)	47.9620N, 65.3404W	25	197–**227**–261 x 8–**16**–20
ARC 81420 (Baie des Chaleurs)	47.8873N, 64.9849W	26	189–**204**–221 x 12–**17**–20
ARC 81421 (Gulf of St. Lawrence)	48.1355N, 63.4003W	49	162–**208**–229 x 11–**17**–21

Distribution and ecology

Few specimens of *Cladocroce spatula* (Lundbeck, 1902) have been reported in the literature. The species is very common in the Gulf of St. Lawrence from 20–365 m while most specimens were collected above 100 m on shallow shelves in the southern Gulf of St. Lawrence. The species was observed during an ROV dive in the northern Laurentian Channel south of Anticosti Island. It was on soft sediment bottom attached to a rock. A single specimen was collected in the North Labrador Sea. A further record was identified from a preserved specimen ZMA.POR.20373 from Scotland (56.8066N, 7.4317W) by R.W.M. Van Soest in 2006. The species was also reported from Korshavn, Norway (NHMUK 1938.8.18.7). The type specimen (Lundbeck, 1902) was collected on the west Greenland Shelf, east of Cumberland Sound (65.2833N, 54.2833W).

Remarks

This is the first record of this species from the Gulf of St. Lawrence. Although the species is not often reported, it was the most common sponge collected during the 2018 *CCGS Teleost* survey in the southern Gulf of St. Lawrence. The specimens fit the description by Lundbeck (1902), except that spicules are slightly thicker. This species is most easily distinguished by the flabellate form with large oscula. The form described by Lundbeck was similar to some specimens collected in the Gulf of St. Lawrence (Fig. 3B), but other collected individuals grew into much larger elaborate fans or lobes (Fig. 3A,C). *Cladocroce ventilabrum* (Fristedt, 1887) was apparently collected along the Scotian Shelf near Muscongus Bay, but no museum specimens exist from those collections (OBIS, 2019). *C. ventilabrum* has slightly longer spicules that are 250 µm in length and the sponge itself is described as being ventilabriform. The specimens collected in the Gulf of St. Lawrence resemble the congeneric *Cladocroce kiska* Lehnert & Stone 2013 from the Aleutian Islands, but *C. kiska* has sigmas and longer oxeas. The consistency and arrangement of oscula in *C. spatula* is reminiscent of *Haliclona (Haliclona) oculata* (Linnaeus, 1759), although *H. (H.) oculata* forms many long finger-like extensions rather than the spatulate form of this species, and *H. (H.) oculata* has smaller spicules. *Cladocroce spatula* is often confused with *Isodictya palmata* (Ellis & Solander, 1786) in the Gulf of St. Lawrence due to the similar shape and presence of many large oscula, although *I. palmata* may grow much more pronounced, digitate branches. *C. spatula* differs from *I. palmata* in lacking chelae, but the oxeas of the two species overlap in size. It should be noted that the skeletal architecture of *C. spatula* is similar to that of *I. palmata* (Hajdu *et al.* 1994), even though the sponges are classified in different sponge orders. *I. palmata* was not identified from specimens collected from the Gulf of St. Lawrence in the survey year 2017–2018, but the species was collected in the North Labrador sea during the *AQVIQ* cruise. *I. palmata* specimens were much thicker than the predominantly flat *C. spatula* specimens, and the chelae are very distinct in spicule preparations. *I. deichmannae* (de Laubenfels 1949) was also collected from the Bay of Fundy, but that species has styles and chelae.

FIGURE 3. *Cladocroce spatula* (Lundbeck, 1902). A–C, collected specimens; D. skeleton showing anisotrophic reticulation and axial fibres; E. spicules. Thin oxeas are uncommon and may represent a developmental form.

Order Poecilosclerida Topsent, 1928

Family Esperiopsidae Hentschel, 1923

Genus *Semisuberites* Carter, 1877

***Semisuberites cribrosa* (Miklucho-Maclay, 1870)**
(Figure 4, Table 3)

Original description: *Veluspa polymorpha* var. *cribrosa* Miklucho-Maclay, 1870. 6–7, Fig. 12, 13.

Synonyms: *Auletta elegans* Vosmaer, 1882, *Axinella variabilis* (Vosmaer, 1882), *Cribrochalina sluiteri* Vosmaer, 1882, *Cribrochalina variabilis* Vosmaer, 1882, *Cribrochalina variabilis* var. *crassa Vosmaer*, 1882, *Cribrochalina variabilis* var. *salpingoides* Vosmaer, 1882, *Reniera infundibuliformis* Hansen, 1885, *Semisuberites arctica* Carter, 1877, *Siphonocalypta elegans* (Vosmaer, 1882), *Stylissa stipitata* de Laubenfels, 1961, *Veluspa cribrosa* Miklucho-Maclay, 1870, *Veluspa flabelliformis* Miklucho-Maclay, 1870, *Veluspa polymorpha* var. *cribrosa* Miklucho-Maclay, 1870, *Veluspa polymorpha* var. *flabelliformis* Miklucho-Maclay, 1870, *Veluspa polymorpha* var. *infundibuliformis* Miklucho-Maclay, 1870.

Material Examined

Gulf of St. Lawrence: IML 3004, 48.350N, 64.460W; IML 3005 collected in Baie des Chaleurs; IML 11897, 48.5891N, 63.8339W, 163 m depth. Additional collected specimens are noted in Table 3.

External appearance (Figure 4A–C)

Semisuberites cribrosa (Miklucho-Maclay, 1870) is variable in size, but is often a trumpet shaped sponge with a long stalk that forms a holdfast, sometimes with visible roots. The diameter of the cup can approach 35 cm and the sponge can extend up to 25 cm in height. The surface is velvety with a very soft consistency. Larger specimens may have more elaborate forms where more than one stalk may intertwine and give rise to two vases. The distal lip of the sponge is often frayed after collection. Specimens are white to brown or grey in colour. The stalk may have epibionts growing down its length, giving a dark brown or muddy appearance.

Spicules and skeleton (Figure 4D–E)

The spicules are exclusively styles that are highly variable in size 186–**390**–540 x 6–**10**–14 µm. Some authors separate the spicules into two categories (Van Soest 2016; Van Soest & Hajdu 2002), but it is unclear whether this is consistent across all specimens. Styles from the Gulf of St. Lawrence specimens did not have obvious swollen heads, nor did they appear mycalostyle-like, although this is reported to be common (Van Soest & Hajdu 2002). The chonaosomal skeleton is formed by loose longitudinal tracts aligned parallel to the surface. The ectosomal skeleton consists of dense spicule brushes forming a loose palisade near the surface. Single spicules are loosely placed throughout the skeleton, mostly perpendicular to the surface.

Distribution and ecology

Semisuberites cribrosa (Miklucho-Maclay, 1870) was mostly collected in the southern Gulf of St. Lawrence from 34–289 m. It has also been reported from Arctic and northern boreal waters (Van Soest *et al.* 2019). It appears to grow mainly in soft sediment environments where the stalk is somewhat submerged beneath the substrate.

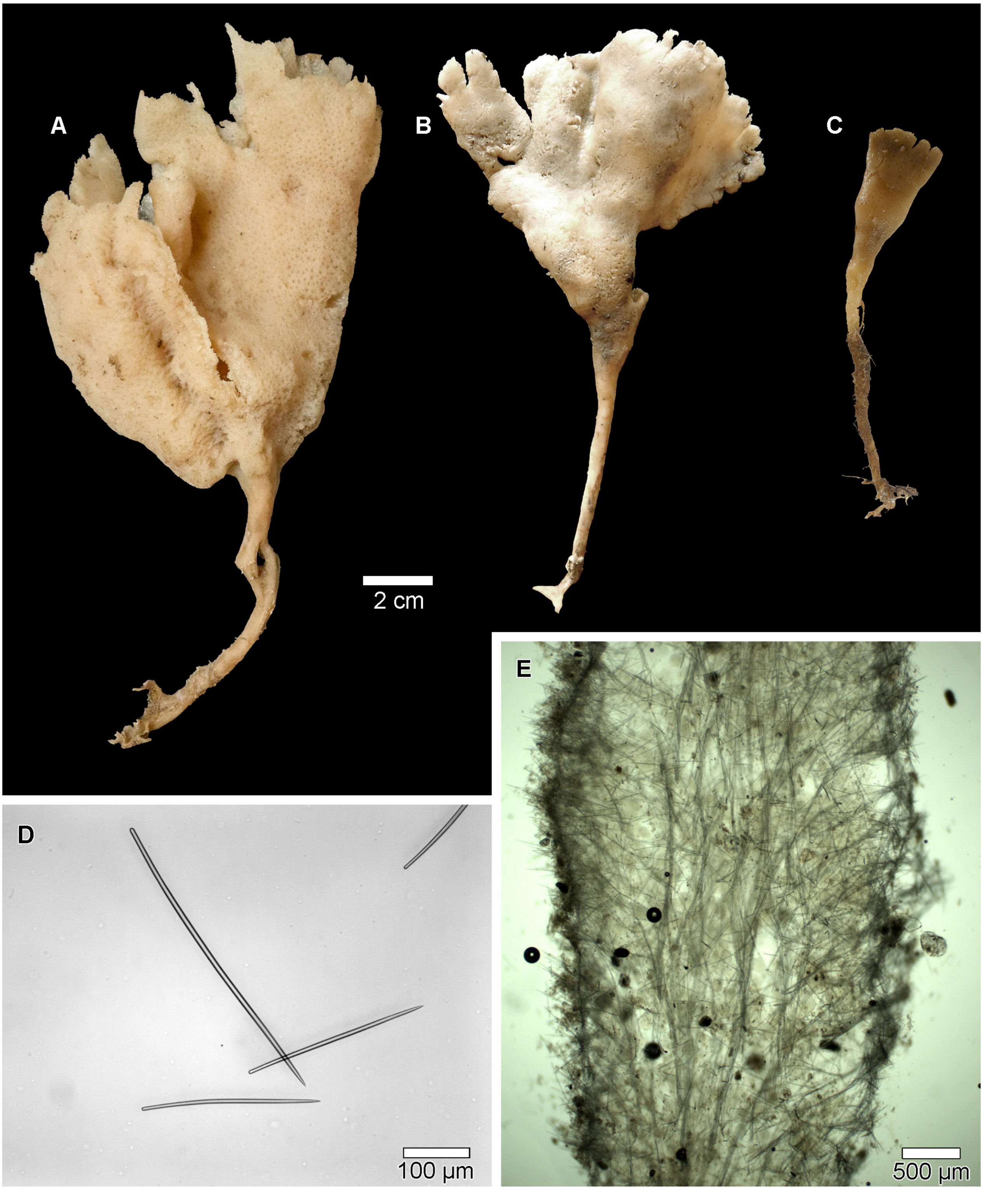

FIGURE 4. *Semisuberites cribrosa* (Miklucho-Maclay 1870). A–C. collected specimens showing long stalks; D. spicules, styles of various sizes; E. skeleton.

Remarks

This is the first record of the species from the Gulf of St. Lawrence and it represents the southernmost extent of its known distribution in the North Atlantic. The species is often confused with, and sometimes reported as, *Phakellia ventilabrum* (Linnaeus, 1767) in eastern Canada. Specimen IML 3004 was originally labelled as *P. ventilabrum* in the museum's collection. The description of *P. ventilabrum* from the Gulf of St. Lawrence by Lambe (1896) does not include strongyle spicules, but rather flexuous styles. It is therefore probable that the specimens collected by Lambe (1896) do not belong to the genus *Phakellia* due to the lack of strongyles, but instead could be *S. cribrosa*; however Lambe's specimens were not reviewed for this present work.

TABLE 3. Comparison of individual variation of spicule dimensions of *Semisuberites cribrosa* (Miklucho-Maclay 1870) given in micrometers as minimum-**mean**-maximum of length x width. n = 30 measurements of individual spicules, except from literature sources.

Specimen	Lat., Long.	Depth (m)	Styles (µm)
Semisuberites cribrosa from Van Soest 2016 (Multiple localities)	-	75–170	215–260 x 5–7 and 500–565 x 9–11
Semisuberites cribrosa from Van Soest & Hajdu 2002 (Multiple localities)	-	100	200–300 and 400–500
Phakettia cribrosa (Miklucho-Maclay, 1870) from Koltun, 1959 (Multiple localities)	-	14–325	60–600
IML 3004	48.35N, 64.46W	Unknown	186–**390**–540 x 6–**10**–14
IML 3005 (Baie des Chaleurs)	Position unknown	Unknown	198–**374**–496 x 8–**11**–15
IML 11897	48.5891N, 63.8339W	163	241–**382**–534 x 7–**10**–14
ARC 81422	48.2009N, 63.5084W	53	203–**323**–512 x 8–**12**–14
ARC 81423	47.5510N, 63.5138W	31	184–**317**–465 x 7–**11**–16

Order Suberitida Chombard & Boury-Esnault, 1999

Family Suberitidae Schmidt, 1870

Genus *Plicatellopsis* Burton, 1932

Plicatellopsis bowerbanki (Vosmaer, 1885) comb. nov.

(Figure 5–6, Table 4)
urn:lsid:zoobank.org:act:2DEB1044-86E4-4281-B597-BAD49B4C6353

Original description: *Phakellia bowerbanki* Vosmaer, 1885: 24, Pl. I, Fig. 18, Pl. IV, Fig. 7–8, Pl. V, Fig. 45–47.
Synonyms: *Cribrochalina ambigua* Marenzeller, 1886, 9, Fig. 1., *Isodictya dicksonii* Fristedt, 1887, 427–428, Pl. 24, Fig. 14.

Material examined

Norway: BMNH 1910.1.1.1477 "*Phakellia bowerbanki*, Willem Barents Expedition, Dr. Vosmaer, portion of Type" [var. b] (Portion of lectotype. ZMA.POR.1781) 72.2347N, 22.5E; BMNH 1910.1.1.609.a "*Phakellia bowerbanki*, Type, 12B" [var. b] (Also portion of lectotype. ZMA.POR.1781); BMNH 10.1.1.610.a "*Phakellia bowerbanki*, Type, 12A" [var. α] 72.6013N, 24.95138E. Baffin Bay: CMNI 2018-0135 (Western Greenland Shelf) 67.9674N, 59.4847W, 878 m depth; CMNI 2018-0136 (Western Greenland Shelf) 67.9673, 59.4838W, 877 m depth; CMNI 2018-0145 (Western Greenland Shelf) 67.9673N, 59.4840W 877 m depth; CMNI 2018-0202 (Near Pond Inlet, Northern Baffin Island) 72.8289N, 77.6090W 856 m depth. Additional collected specimens are noted in Table 4.

TABLE 4. Comparison of individual variation of spicule dimensions of *Plicatellopsis bowerbanki* (Vosmaer, 1885) comb. nov. given in micrometers as minimum-**mean**-maximum of length x width. n = 30 measurements of individual spicules, except from literature sources.

Specimen	Lat., Long.	Depth (m)	Tylostyles I (µm)	Tylostyles II (µm)
BMNH 1910.1.1.1477 "*Phakellia bowerbanki*, Willem Barents Expedition, Dr. Vosmaer, portion of Type" [var. b] (Portion of lectotype. ZMA.POR.1781)	72.2347N, 22.5E	283	213–**273**–326 x 8–**13**–16.5	Few thin spicules present.
BMNH 1910.1.1.609.a "*Phakellia bowerbanki*, Type, 12B" [var. b] (Portion of lectotype. ZMA.POR.1781)	72.2347N, 22.5E	283	215–**266**–319 x 10.5–**14**–17	-
BMNH 10.1.1.610.a "Phakellia bowerbanki, Type, 12A" [var. α]	72.6013N, 24.95138E	256	275–**316**–370 x 11–**16**–20	-
Isodictya dicksonii Fristedt, 1887 (Greenland, Baffin Bay)	75.4333N, 65.45W	475	300	-
Cribrochalina ambigua Marenzeller, 1886 (Near Jan Mayen Island)	-	230	230–340	-
Phakellia bowerbanki from Koltun, 1959 (Multiple localities)	-	73–320	218–374 x 8–16	Not given
CMNI 2018-0135 (Western Greenland Shelf)	67.9674N, 59.4847W	878	266–**320**–364 x 19–**22**–27	-
CMNI 2018-0136 (Western Greenland Shelf)	67.9673N, 59.4838W	877	265–**317**–346 x 11–**17**–21	Thinner category probable.
CMNI 2018-0145 (Western Greenland Shelf)	67.9673N, 59.4840W	877	284–**334**–389 x 15–**20**–26	-
CMNI 2018-0202 (Near Pond Inlet, Northern Baffin Island)	72.8289N, 77.6090W	856	258–**316**–359 x 14–**18**–21	-
IML 11902 (Northern Gulf of St. Lawrence)	48.5825N, 63.9085W	95	266–**306**–340 x 17.5–**20**–22	240–**282**–330 x 11–**14**–16
IML 11900 (Northern Gulf of St. Lawrence)	48.5876N, 63.9039W	84	289–**332**–397 x 15–**18**–23	251–**294**–333 x 7.5–**9**–12
IML 11909 (Northern Gulf of St. Lawrence)	49.2865N, 60.029W	222	205–**298**–352 x 16–**19**–22	230–**270**–326 x 11.5–**14**–16
IML 11910 (Northern Gulf of St. Lawrence)	49.46317N, 60.0667W	136	252–**291**–332 x 16–**19**–22	213–**262**–295 x 11–**14**–16
IML 11911 (Northern Gulf of St. Lawrence)	50.1685N, 58.9112W	203	313–**340**–382 x 15–**22**–26	234–**308**–361 x 6–**11**–14.5
IML 11912 (Northern Gulf of St. Lawrence)	49.65917N, 60.3698W	179	243–**308**–386 x 16–**19**–23	203–**265**–319 x 8–**13**–16
ARC 81425 (Southern Gulf of St. Lawrence)	47.5104N, 60.4842W	77	235–**310**–348 x 14–**18**–21	-
ARC 81424 (Southern Gulf of St. Lawrence)	48.3619N, 62.1095W	153	198–**258**–344 x 13–**19**–24	-

External appearance (Figure 5)

Plicatellopsis bowerbanki (Vosmaer, 1885) **comb. nov**. is generally a large, vase shaped sponge that forms a funnel at the base (Fig. 5 A–E). However, the sponge is somewhat polymorphic, and a more fan shape form has been observed that grew to 30 cm wide (Fig. 5 F). In some individuals, secondary vases may extend from the distal portions of the primary vase (Fig. 5 C). The primary stalk attaches to a hard substrate, usually rock walls, but can grow on dead coral skeletons and pebbles. The inner and outer surfaces have irregularly spaced pores <1 mm in diameter. In larger specimens, the outer surface is rippled, with ridges and depressions. In larger specimens the raised portions appear to form concentric rings or lateral ribs on the underside of the cup (Fig. 5 C), but when viewed from above the ridges appear as depressions (Fig. 5 D, F). The distal lip of the fan is smoothly curved but in an irregular scalloped manner, and is often frayed both *in situ* and after collection. Most specimens have large circular holes irregularly placed throughout the sponge body which can include the stem (Fig. 5 B, D–F, Vosmaer 1885, Pl. 1 Fig. 18). It is unknown if these holes form naturally or are caused by spongivorous predators. However, since no specimens appeared to have predators on or near the sponge body *in situ*, or after collection, and because the holes are present on specimens throughout the large geographic area in which the sponge was collected, it is suggested that the apertures occur naturally and are thus considered diagnostic of the species.

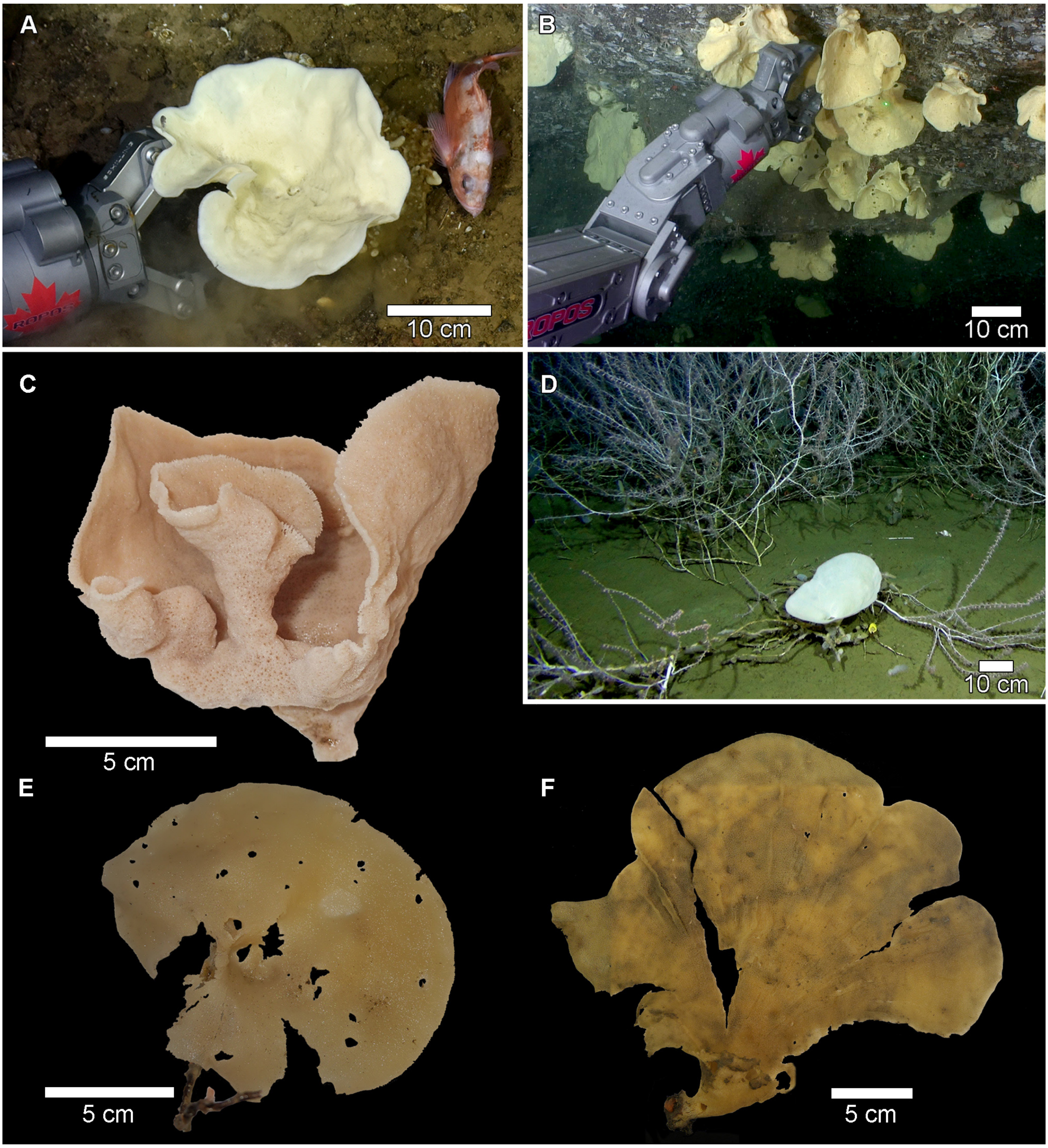

FIGURE 5. *Plicatellopsis bowerbanki* (Vosmaer, 1885) **comb. nov**. from eastern Canada. A. specimen *in situ*; B. specimens growing on rock wall in Northern Gulf of St. Lawrence; C. IML 11900 showing secondary vase extending from single base; D. specimen living amongst *Keratoisis* sp. coral on the western Greenland Shelf; E. CMNI 2018-0136, growing on dead *Keratoisis* sp. coral fragment. F. CMNI 2018-0202 from Pond Inlet, Baffin Island. *In situ* photo credit: DFO/CSSF/Oceana Canada (A,B); DFO/CSSF/ArcticNet (D).

Spicules (Figure 6A–F)

The spicules of *Plicatellopsis bowerbanki* (Vosmaer, 1885) **comb. nov.** are stout, slightly bent tylostyles with very slight tyles. Most spicules look like styles at lower magnifications (Fig. 6 A), but the tyles are evident upon closer inspection (Fig. 6 B–F). The tylostyles can sometimes be separated into two thickness categories, but the thick and thin spicules are consistently similar lengths, and in some specimens the thickness categories are indistinguishable as the widths may overlap. Thinner tylostyles, if present, are not as common and are sometimes difficult to find in spicule preparations due to their inconsistent distribution throughout the sponge tissue. For this reason, thin spicule placement in the skeleton does not appear to be a useful taxonomic character of the species. The skeleton of the lectotype (BMNH 10.1.1.1477 *Phakellia bowerbanki* Vosmaer, 1885 var. β) was examined here and tylostyles with slight tyles were present, measuring 213–**273**–326 x 8–**13**–16.5 µm. Only two spicules that were less than 10 µm in thickness were measured from the lectotype. This suggests that the less common thin tylostyles are also present in the specimens from the original description by Vosmaer (1885), but a sufficient number could not be measured as they were not visible in the slide preparation. A specimen from Baffin Bay, CMNI 2018-0202 has tylostyles that are 258–**317**–359 x 14–**18**–21µm, and thinner spicules were not seen. A comparison of spicule sizes for specimens collected is presented in Table 4.

Skeleton (Figure 6 G, H)

The skeletal architecture of the species consists of dense spicule tracts forming an axial skeleton, which branch out into extra-axial bundles towards the surface, terminating in spicule brushes (Fig. 6G, H). The axial and extra-axial spicule tracts consist of between 2–6 spicules. The axial skeleton of tight spicule bundles causes the sponge to have a fibrous texture when cut. When present, the thinner tylostyles are not localized in the skeleton, but rather appear to be loosely placed throughout the sponge tissues (Fig. 6 G). The skeleton matches the definition of the genus given by Van Soest (2002) and Burton (1932), except in the surface skeleton where no palisade of smaller spicules is present in the lectotype or in specimens from eastern Canada. In individuals that have a second category of thinner tylostyles, those spicules are not concentrated at the surface like the smaller spicules in other species of the genus, but rather they occur scattered in the choanosomal skeleton without a consistent distribution. The spicules outside of the axial and extra-axial skeletons form a loose, irregularly aligned reticulation of bundles and single spicules.

Genetic data

COI mtDNA sequences were obtained for CMNI 2018-0136 (GenBank MK570857), CMNI 2018-0145 (GenBank-MK570858), CMNI 2018-0202 (Genbank: MK561021), and ARC 81425 (GenBank MK570859). There is no genetic difference in the COI Folmer fragment between specimens from the Gulf of St. Lawrence, Western Greenland Shelf, or Pond Inlet despite differing external morphologies. The 28S gene was sequenced for CMNI 2018-0202 and confirms placement of the species within the Suberitidae, but sequence quality was not sufficiently high to submit to Genbank.

Distribution and ecology

Plicatellopsis bowerbanki (Vosmaer, 1885) **comb. nov.** appears to be ubiquitous on the east coast of Canada, extending from the northern tip of Baffin Bay to the northern portions of the Gulf of St. Lawrence. In Canadian waters it is found at depths ranging between 73 and 878 m. *Plicatellopsis bowerbanki* (Vosmaer, 1885) **comb. nov.** is abundant in the Banc-des-Américains Marine Protected Area and the Disko Fan Conservation Area which were recently closed to bottom contact fishing by the Department of Fisheries and Oceans, Canada. *Plicatellopsis bowerbanki* (Vosmaer, 1885) **comb. nov.** has been seen growing on varied substrates, but often attached to harder objects such as dead coral, pebbles and rock walls in otherwise soft sediment environments. The species has also been collected in the waters off Norway, The Faroe Islands, Iceland, Greenland, and in the Barents Sea. (Burton 1930; Fristedt 1887; Hentschel 1929; Lundbeck 1909; Marenzeller 1886).

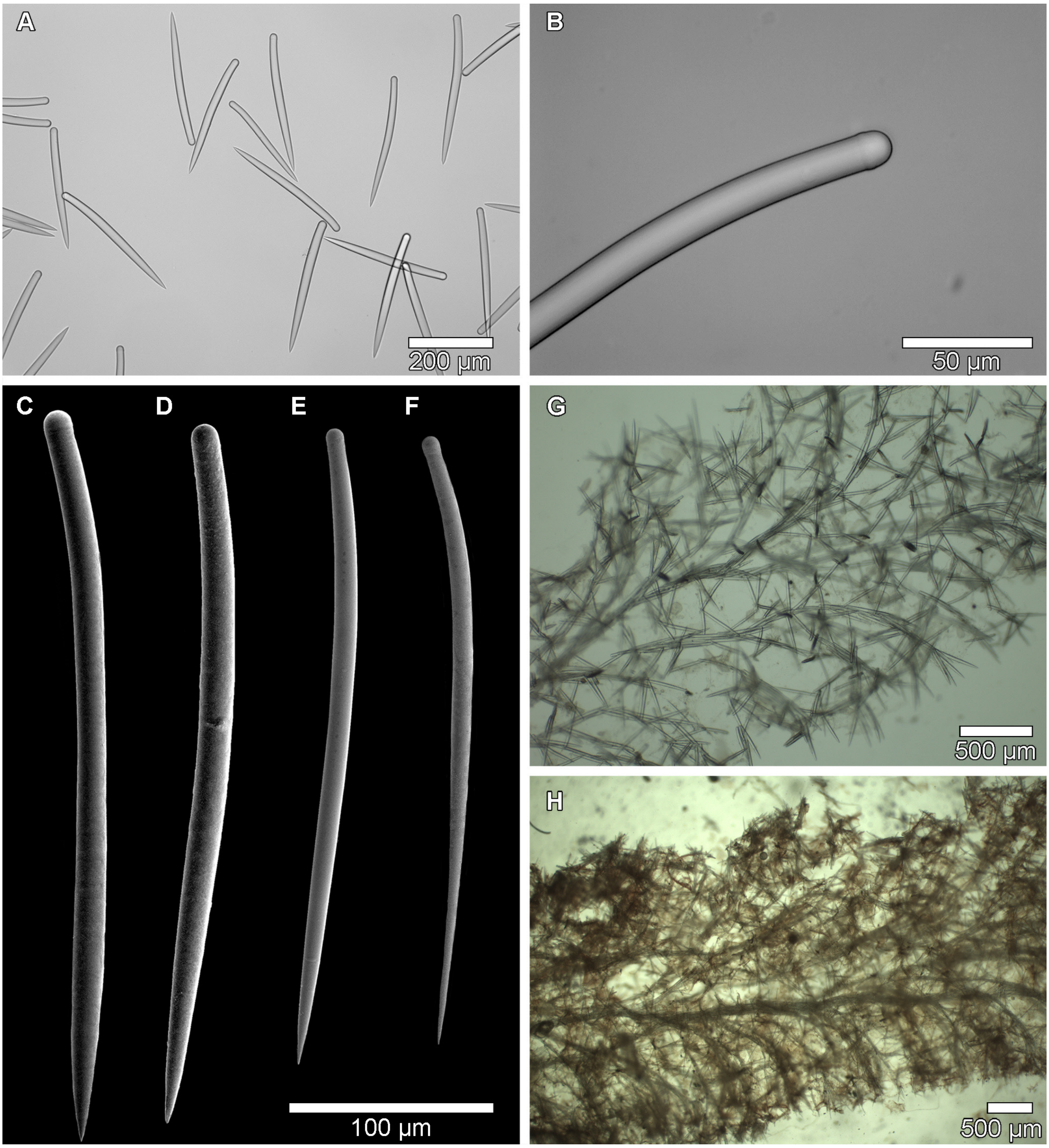

FIGURE 6. *Plicatellopsis bowerbanki* (Vosmaer, 1885) **comb. nov**. spicules and skeleton. A. spicules; B. detail of slight tyle; C,D. SEM of tylostyle I; E,F. SEM of tylostyle II; G. skeleton of Baffin Bay specimen, ectosomal skeleton of spicule brushes are visible at the surface; H. skeleton of BMNH 1910.1.1.1477 (from lectotype).

Remarks

The original description of *Phakellia bowerbanki* (Vosmaer, 1885) stated that placement of the species in the genus was "dubious" as the sponge was lacking "flexible spicules", likely in reference to vermiform strongyles. Vosmaer argues that Schmidt, Carter, Ridley and others have placed other flabelliform species which lack sinuous spicules in the genus and thus follows this precedent by placing *Phakellia bowerbanki* var. α and var. β, as well as *Phakellia arctica* in the genus *Phakellia*. *P. arctica* has subsequently been transferred to the genus *Axinella* (originally *Spongia calyciformis* (Lamarck 1814)), due to the presence of oxeas and styles in the skeleton of that species.

Vosmaer (1885) describes the species as "Great, thin, or funnelshaped [sic]" with strong skeletal fibres. It was also noted that most specimens were torn. Plate I, Fig. 18 (Vosmaer, 1885) shows a large, red coloured fan-shaped sponge with the characteristic circular aperture, which was also noted in material collected throughout eastern Canada. The deep red or purple colour was not seen in our specimens, although several had a light pink hue after preservation in 95% ethanol. The colour may depend on the method of collection, exposure to air, or the means of preservation, but this remains to be tested.

The original description lists the spicules as acuate (*tr. ac.*), and stout. Plate V, Figs. 45–47 (Vosmaer 1885) clearly show that the spicules for both varieties contain styles, each with a slight bend towards the rounded end. Koltun (1959) describes the spicules as styles, also figured with a slight bend, measuring 218–374 µm. Vosmaer and Koltun both suggest that thinner styles were also present, but were of a length similar to the thicker variety. The original description for the synonymous *Cribrochalina ambigua* Marenzeller, 1886 shows styles with very slight apical swellings measuring 230–340 µm. *Isodictya dicksonii* (Fristedt 1887) from Baffin Bay is also described as a large fan-shaped sponge with smooth styles 300 µm in length. *I. dicksonii* was listed as a synonym of *P. bowerbanki* by Hentschel (1929). A sponge listed as "*Phakellia dicksoni* (Fristedt)" by Breitfuss (1912) from the Barents Sea likely represented the same species, although no description was given.

The skeleton of *P. bowerbanki* (Vosmaer, 1885) **comb. nov.** was not described in great detail previously. Vosmaer stated only that the skeletal fibres were strong (var. α) or not much developed (var. β). Koltun described a skeleton consisting of "thick fibres extending along the body and parallel to it", with "transverse bundles of spicules, as well as individual spicules" (from an English translation of the original Russian manuscript, Koltun 1959). The skeleton of the lectotype (Fig. 6 H) shows clearly that the tylostyles form a dense axial skeleton, and the extra-axial skeleton fans outwards towards the surface forming spicule brushes. The section of the lectotype does indeed show a well-developed axial skeleton, contrary to Vosmaer's original description of var. β. There does not seem to be sufficient difference between the type specimens of varieties α and β for the specimens to be considered separate species.

Phakellia generally has a thick primary skeleton composed of sinuous strongyle or strongyoxea tracts, echinated or connected by styles, strongyles, or strongyloxeas (Alvarez & Hooper 2002). The genus also has no specialized ectosomal skeleton. The specimens reviewed here do not fit this description as they lack strongyles and strongyoxeas. The skeleton formed of axial and extra-axial tracts, tylostyles and the presence of brushes of spicules in the ectosome fit the description of *Plicatellopsis*, except that there is no palisade of tylostyles at the surface (Van Soest 2002). This is not the first species identified as *Phakellia* that has been subsequently transferred to the Suberitidae. *Phakellia lobata* (Wilson 1902), described as having tylostyles has been identified as belonging to the genus *Suberites* (Alvarez *et al.* 1998).

Phakellia ventilabrum (Linnaeus, 1767) was reportedly collected from the Gulf of St. Lawrence by Whiteaves (1874) and Lambe (1896), but is described by Lambe (1896) as only having sinuous styles (440 x 13 µm and 274 x 3 µm); strongyles were not mentioned. Lambe also described a specimen collected from Davis Strait as *P. ventilabrum* (Lambe 1900) but did not give spicule measurements for the specimen. It is likely that, based on the presence of styles only, the specimens identified by Lambe were actually *S. cribrosa*, but these specimens were not reviewed here.

The World Porifera Database lists six species of *Plicatellopsis.* Five of the six species occur only in the southern hemisphere. A single species, *Plicatellopsis borealis* Lehnert & Stone (2017), was recently described from the Bering Sea. Apart from biogeographic considerations, the North Atlantic species described here is clearly distinct from all others due to the consistently short spicules which are smaller than the tylostyles in other members of the genus (Table 4). Thinner tylostyles are of a similar length to the thicker tylostyles. Thin tylostyles are therefore not considered to be a distinguishing feature of the species. Thin tylostyles occur in some specimens and are rare in others. As tissue from different body regions was routinely dissolved for spicule preparations, thin tylostyles do not appear to have a taxonomic significance. There is no variation between COI Folmer fragment mtDNA in specimens from Davis Strait and the Gulf of St. Lawrence, though this DNA region is conserved in sponges and may not resolve species-level differences (Erpenbeck *et al.* 2006). The presence of stout tylostyles and the skeletal arrangement lacking a dense ectosomal palisade of small spicules are unique to the species. A review of spicule sizes and for other members of the genus were presented by Lehnert & Stone (2017). *Plicatellopsis borealis* Lehnert & Stone (2017) has large subtylostyles, which exceed the maximum length of spicules found in *Plicatellopsis bowerbanki* (Vosmaer, 1885) **comb. nov.**, and the small tylostyles are smaller than the minimum length of spicules in eastern Canadian specimens. The external appearance of *P. borealis* is similar to *Plicatellopsis bowerbanki* (Vosmaer, 1885) **comb. nov.**, where the distal edge of the cup is frayed and irregular, and the pores along the body appear to be distributed similarly in both species. However, *Plicatellopsis bowerbanki* (Vosmaer, 1885) **comb. nov.** often has large, rounded holes along the body of the sponge which are not seen in *P. borealis.*

Concluding Remarks

Although this is far from a complete review of all species in eastern Canada that may form a cup or vase shape, the four species described here exemplify the difficulties associated with identifying sponge specimens *in situ* or from gross morphology alone. Because the four species are similar in colour, size and general shape, in the past they have been often confused and given different species names. As a result, it is presently difficult to determine the correct distribution of flabelliform sponge species in eastern Canada. Efforts to monitor the health of marine sponge assemblages, particularly in newly established marine refuges in eastern Canada, will benefit from species-level identifications to better understand the potential differences in ecosystem services and habitat functioning provided by similar-shaped, yet unrelated species. Considering the number of synonyms and the history of incorrect taxonomic placement of the species discussed here, it is apparent that close review of morphology, spicules, and molecular data are required for accurate species-level identification.

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References

Ackers, R.G., Moss, D. & Picton, B.E. (1992) *Sponges of the British Isles ('Sponges V'). A Colour Guide and Working Document*. Marine Conservation Society, Ross-on-Wye, 175 pp.

Altschul, S.F., Gish, W., Miller, W., Myers, E.W. & Lipman, D.J. (1990) Basic local alignment search tool. *Journal of Molecular Biology*, 215, 403–410.
https://doi.org/10.1016/S0022-2836(05)80360-2

Alvarez, B. & Hooper, J.N.A. (2002) Family Axinellidae Carter, 1875. *In*: Hooper, J.N.A. & Van Soest, R.W.M. (Eds.), *Systema Porifera. A guide to the classification of sponges*. Kluwer Academic/Plenum Publishers, New York, Boston, Dordrecht, London and Moscow, pp. 724–747.
https://doi.org/10.1007/978-1-4615-0747-5_80

Alvarez, B., Van Soest, R.W.M. & Rützler, K. (1998) A Revision of the Axinellidae (Porifera: Demospongiae) of the Central-West Atlantic Region. *Smithsonian Contributions to Zoology*, 1998, 1–47.
https://doi.org/10.5479/si.00810282.598

Beazley, L.I. & Kenchington, E.L. (2015) Epibenthic Megafauna of the Flemish Pass and Sackville Spur (Northwest Atlantic) Identified from in Situ Benthic Image Transects. *Canadian Technical Report of Fisheries and Aquatic Sciences*, 3127, 1–72.

Beazley, L.I., Kenchington, E.L., Murillo, F.J. & Sacau, M.D. (2013) Deep-sea sponge grounds enhance diversity and abundance of epibenthic megafauna in the Northwest Atlantic. *ICES Journal of Marine Science*, 70, 1471–1490.
https://doi.org/10.1093/icesjms/fst124

Bidder, G.P. (1923) The relation of the form of a sponge to its currents. *Journal of Cell Science*, 1923, 293–324.

Breitfuss, L.L. (1912) Zur Kenntniss der Spongio-Fauna des Kola Fjords. *Travaux de la Société Impériale des Naturalistes de St. Petersbourg*, Section Zoologie, 1912, 61–80.

Burton, M. (1930) Norwegian Sponges from the Norman Collection. *Proceedings of the Zoological Society of London*, 1930, 487–546.
https://doi.org/10.1111/j.1096-3642.1930.tb00989.x

Burton, M. (1932) Sponges. *Discovery Reports*, 6, 237–392.
https://doi.org/10.5962/bhl.part.24379

Chu, J.W.F. & Leys, S.P. (2010) High resolution mapping of community structure in three glass sponge reefs (Porifera, Hexactinellida). *Marine Ecology Progress Series*, 417, 97–113.
https://doi.org/10.3354/meps08794

Conway, K.W., Barrie, J.V., Austin, W.C. & Luternauer, J.L. (1991) Holocene sponge bioherms on the western Canadian continental shelf. *Continental Shelf Research*, 11, 771–790.
https://doi.org/10.1016/0278-4343(91)90079-L

de Laubenfels, M.W. (1949) The sponges of Woods Hole and adjacent waters. *Bulletin of the Museum of Comparative Zoology at Harvard College*, 103, 1–55.

Dendy, A. (1922) Note on the Genus *Tragosia*, Gray. *Annals and Magazine of Natural History*, Series 9, 9 (50), 169–174.
https://doi.org/10.1080/00222932208632652

Dinn, C., Edinger, E. & Leys, S.P. (2019) Sponge (Porifera) fauna of Frobisher Bay, Baffin Island, Canada with the description of an *Iophon* rich sponge garden. *Zootaxa*, 4576 (2), 301–325.
https://doi.org/10.11646/zootaxa.4576.2.5

Dinn, C. & Leys, S.P. (2018) *Field Guide to Sponges of the Eastern Canadian Arctic*. Department of Biological Sciences, Education and Resource Archive, University of Alberta, Edmonton AB, 102 pp.
https://doi.org/10.7939/R3DF6KJ4G

Dunham, A., Archer, S.K., Davies, S.C., Burke, L.A., Mossman, J., Pegg, J.R. & Archer, E. (2018) Assessing condition and ecological role of deep-water biogenic habitats: Glass sponge reefs in the Salish Sea. *Marine Environmental Research*, 141, 88–99. https://doi.org/10.1016/j.marenvres.2018.08.002

Erpenbeck, D., Hooper, J.N.A. & Worheide, G. (2006) CO1 phylogenies in diploblasts and the "Barcoding of Life" - are we sequencing a suboptimal partition? Molecular Ecology Notes 6, 550–553.
https://doi.org/10.1111/j.1471-8286.2005.01259.x

Folmer, O., Black, M., Wr, H., Lutz, R. & Vrijenhoek, R. (1994) DNA primers for amplification of mitochondrial Cytochrome C oxidase subunit I from diverse metazoan invertebrates. *Molecular Marine Biology and Biotechnology*, 3, 294–299.

Fristedt, K. (1887) Sponges from the Atlantic and Arctic Oceans and the Behring Sea. *Vega-Expeditionens Vetenskap. Iakttagelser, Nordenskiöld*, 4, 401–471.

Ginn, B.K., Logan, A. & Thomas, M.L.H. (2000) Sponge ecology on sublittoral hard substrates in a high current velocity area. *Estuarine, Coastal and Shelf Science*, 50, 403–414.
https://doi.org/10.1006/ecss.1999.0563

Hajdu, E., De Weerdt, W.H. & Van Soest, R.W.M. (1994) Affinities of the "Mermaid's Glove" sponge *Isodictya palmata*, with a discussion on the synapomorphic value of chelae microscleres. *In*: Van Soest, R.W.M., van Kempen T.M.G., Braekman J.C. (Eds.), *Sponges in Time and Space. Biology, Chemistry, Paleontology.* Balkema, Rotterdam, pp. 141–150.

Hentschel, E. (1929) Die Kiesel- und Hornschwämme des Nördlichen Eismeers. *In*: Römer, F., Schaudinn, F., Brauer, A. & Arndt, W. (Eds.), *Fauna Arctica. Eine Zusammenstellung der arktischen Tierformen mit besonderer Berücksichtigung des Spitzbergen-Gebietes auf Grund der Ergebnisse der Deutschen Expedition in das Nördliche Eismeer im Jahre 1898*, 5 (4), pp. 857–1042.

Hogg, M.M., Tendal, O.S., Conway, K.W., Pomponi, S.A., Van Soest, R.W., Gutt, J., Krautter, M. & Roberts, J.M. (2010) *Deep-sea Sponge Grounds: Reservoirs of Biodiversity. UNEP-WCMC Biodiversity Series No. 32*. UNEP-WCMC, Cambridge, 84 pp.

Hooper, J.N.A. & Van Soest, R.W.M. (Eds.) (2002) *Systema Porifera: a guide to the classification of sponges. Vol. 1.* Kluwer Academic/Plenum Publishers, New York, Boston, Dordrecht, London and Moscow, XLVIII + 1101 pp.

ICES (2009) Report of the ICES-NAFO. Working Group on Deep-water Ecology (WGDEC). 9–13 March 2009. Available from: http://vme.ices.dk/download/WGDEC_2009.pdf (accessed 7 February 2020)

Kenchington, E., Beazley, L., Murillo, F.J., Tompkins MacDonald, G. & Baker, E. (2015) Coral, Sponge, and Other Vulnerable Marine Ecosystem Indicator Identification Guide, NAFO Area. *NAFO Scientific Council Studies*, 47, 1–101.
https://doi.org/10.2960/S.v47.m1

Klitgaard, A.B. & Tendal, O.S. (2004) Distribution and species composition of mass occurrences of large-sized sponges in the northeast Atlantic. *Progress in Oceanography*, 61, 57–98.
https://doi.org/10.1016/j.pocean.2004.06.002

Koltun, V.M. (1959) Siliceous horny sponges of the northern and fareastern seas of the U.S.S.R. *Opredeliteli po faune SSR, izdavaemye Zoologicheskim muzeem Akademii nauk*, 67, 1–236. [in Russian]

Krautter, M., Conway, K.W., Barrie, J.V. & Neuweiler, M. (2001) Discovery of a "Living Dinosaur": Globally unique modern hexactinellid sponge reefs off British Columbia, Canada. *Facies*, 44, 265–282.

https://doi.org/10.1007/BF02668178
Lamarck, J.B.P. & De Monet, C. (1814) Sur les polypiers empâtés. *Annales du Museum national d'Histoire naturelle*, 1814, 294–458.
Lambe, L.M. (1896) Sponges from the Atlantic coast of Canada. *Transactions of the Royal Society of Canada*, 1896, 181–211.
Lambe, L.M. (1900) Sponges from the Coasts of Northeastern Canada and Greenland. *Transactions of the royal Society of Canada*, 1900, 19–49.
Lee, W.L., Reiswig, H.M., Austin, W.C. & Lundsten, L. (2012) An extraordinary new carnivorous sponge, Chondrocladia lyra, in the new subgenus Symmetrocladia (Demospongiae, Cladorhizidae), from off of northern California, USA. *Invertebrate Biology*, 131, 259–284.
https://doi.org/10.1111/ivb.12001
Lehnert, H. & Stone, R.P. (2013) Four new species of Haplosclerida (Porifera, Demospongiae) from the Aleutian Islands, Alaska. *Zootaxa*, 3700 (4), 573–582.
https://doi.org/10.11646/zootaxa.3700.4.5
Lehnert, H. & Stone, R.P. (2017) Two new species of Suberitida (Porifera, Heteroscleromorpha) from the Bering Sea. *Zootaxa*, 4338 (3), 546–556.
https://doi.org/10.11646/zootaxa.4338.3.9
Leys, S.P., Yahel, G., Reidenbach, M.A., Tunnicliffe, V., Shavit, U. & Reiswig, H.M. (2011) The sponge pump: the role of current induced flow in the design of the sponge body plan. *PLoS One* 6, e27787.
https://doi.org/10.1371/journal.pone.0027787
Lundbeck, W. (1902) Porifera. (Part I.) Homorrhaphidae and Heterorrhaphidae. *The Danish Ingolf-Expedition*, 6 (1), 1–108.
Lundbeck, W. (1909) The Porifera of East Greenland. *Meddelelser om Grønland*, 29, 423–464.
Maldonado, M., Aguilar, R., Bannister, R.J., Bell, J.J., Conway, K.W., Dayton, P.K., Díaz, C., Gutt, J., Kelly, M., Kenchington, E.L.R., Leys, S.P., Pomponi, S.A., Rapp, H.T., Rützler, K., Tendal, O.S., Vacelet, J. & Young, C.M. (2017) Sponge grounds as key marine habitats: A synthetic review of types, structure, functional roles, and conservation concerns. *In*: Rossi, S. (Ed.), *Marine Animal Forests: The Ecology of Benthic Biodiversity Hotspots*. Springer International Publishing, Cham, pp. 1–39.
https://doi.org/10.1007/978-3-319-21012-4_24
Marenzeller, E. von (1886) Poriferen, Anthozoen, Ctenophoren und Würmer von Jan Mayen. *Die Österreichische Polarstation Jan Mayen Beobachtungs-Ergebnisse, Kaiserlichen Akademie der Wissenschaften*, 3, 9–23.
McMurray, S.E., Blum, J.E. & Pawlik, J.R. (2008) Redwood of the reef: Growth and age of the giant barrel sponge Xestospongia muta in the Florida Keys. *Marine Biology*, 155, 159–171.
https://doi.org/10.1007/s00227-008-1014-z
Meyer, C.P. (2003) Molecular systematics of cowries (Gastropoda : Cypraeidae) and diversification patterns in the tropics. *Biological Journal of the Linnean Society*, 79, 401–459.
https://doi.org/10.1046/j.1095-8312.2003.00197.x
Miklucho-Maclay, N.N. (1870) Uber einige Schwämme des nördlichen Stillen Oceans und des Eismeeres, welche im Zoologischen Museum der Kaiserlichen Akademie der Wissenschaften in St. Petersburg aufgestellt sind. Ein Beitrag zur Morphologie und Verbreitung der Spongien. *Mémoires de l'Académie Impériale des Sciences de St. Petersbourg,* 15 (3), 1-24.
https://doi.org/10.5962/bhl.title.6306
Morrow, C.C., Picton, B.E., Erpenbeck, D., Boury-Esnault, N., Maggs, C.A. & Allcock, A.L. (2012) Congruence between nuclear and mitochondrial genes in Demospongiae: A new hypothesis for relationships within the G4 clade (Porifera: Demospongiae). *Molecular Phylogenetics and Evolution*, 62, 174–190.
https://doi.org/10.1016/j.ympev.2011.09.016
Murillo, F., Kenchington, E., Tompkins, G., Beazley, L., Baker, E., Knudby, A. & Walkusz, W. (2018) Sponge assemblages and predicted archetypes in the eastern Canadian Arctic. *Marine Ecology Progress Series*, 597, 115–135.
https://doi.org/10.3354/meps12589
OBIS (2019) Ocean Biogeographic Information System. Intergovernmental Oceanographic Commission of UNESCO. Available from: http://www.iobis.org. (accessed 18 April 2019)
Palumbi, S.R. (1984) Tactics of acclimation: Morphological changes of sponges in an unpredictable environment. *Science*, 225, 1478–1480.
https://doi.org/10.1126/science.225.4669.1478
Picton, B.E. & Goodwin, C.E. (2007) Sponge biodiversity of Rathlin Island , Northern Ireland. *Journal of the Marine Biological Association of the UK*, 87, 1441–1458.
https://doi.org/10.1017/S0025315407058122
Stephens, J. (1921) Sponges of the Coasts of Ireland. II. The Tetraxonida (concluded). *Scientific Investigations of the Fisheries Branch. Department of Agriculture for Ireland*, 2, 1–75.
Topsent, E. (1913) Spongiaires provenant des campagnes scientifiques de la "Princesse Alice" dans les Mers du Nord (1898–1899–1906–1907). *Résultats des campagnes scientifiques accomplies par le Prince Albert I de Monaco*, 45, 1–16.
Van Soest, R.W.M. (2016) Sponge-collecting from a drifting ice floe: the Porifera obtained in the Kara Sea by the Dutch Polar Expedition 1882-83. *Contributions to Zoology*, 85, 311–336.
https://doi.org/10.1163/18759866-08503004

Van Soest, R.W.M. & Hajdu, E. (2002) Family Esperiopsidae Hentschel, 1923. *In*: Hooper, J.N.A. & Van Soest, R.W.M. (Eds.), *Systema Porifera. A guide to the classification of sponges. Vol. 1.* Kluwer Academic Plenum Publishers, New York, Boston, Dordrecht, London and Moscow, pp. 656–664.
https://doi.org/10.1007/978-1-4615-0747-5_71

Van Soest, R.W.M. (2002) Family Suberitidae Schmidt, 1870. *In*: Hooper, J.N.A. & Van Soest, R.W.M. (Eds.), *Systema Porifera. A guide to the classification of sponges. Vol. 1.* Kluwer Academic Plenum Publishers, New York, Boston, Dordrecht, London and Moscow, pp. 227–244.
https://doi.org/10.1007/978-1-4615-0747-5_25

Van Soest, R.W.M., Boury-Esnault, N., Hooper, J.N., Rützler, K., De Voogd, N.J., Alvarez, B., Hajdu, E., Piscera, A.B., Manconi, R., Schoenberg, C., Janussen, D., Tabachnick, K.R., Klautau, M., Picton, B.E., Kelly, M., Vacelet, J., Dohrmann, M., Díaz, C. & Cárdenas, P. (2019) World Porifera Database. Available from: http://www.marinespecies.org/porifera. (accessed 18 April 2019)

Van Soest, R.W.M., Picton, B.E. & Morrow, C. (2000) Sponges of the North East Atlantic. *In*: World Biodiversity Database CD-ROM Series, Windows/Mac Version 1.0. ETI, University of Amsterdam, Amsterdam. Available from: https://sponges-ne-atlantic.linnaeus.naturalis.nl/linnaeus_ng/app/views/introduction/topic.php?id=3392&epi=168 (accessed 20 January 2020)

Vogel, S. (1977) Current-induced flow through living sponges in nature. *Proceedings of the National Academy of Sciences*, 74, 2069–2071.
https://doi.org/10.1073/pnas.74.5.2069

Vosmaer, G.C.J. (1885) The Sponges of the "Willem Barents" Expedition 1880 and 1881. *Bijdragen tot de Dierkunde*, 12, 1–47.
https://doi.org/10.1163/26660644-01201001

Whiteaves, J.F. (1874) *Report on deep-sea dredging operations in the Gulf of St. Lawrence: with notes on the present condition of the marine fisheries and oyster beds of part of the region*. S.N., Ottawa, 29 pp.
https://doi.org/10.5962/bhl.title.50697

Wilson, H.V. (1902) The sponges collected in Porto Rico in 1899 by the U.S. Fish Commission Steamer Fish Hawk. *Bulletin of the United States Fish Commission*, 2, 375–411.