

Two large structure-forming sponges from opposite North American coasts: a taxonomic review of Arctic–Pacific *Mycale* (*Mycale*) *loveni* and the description of a new Arctic–Atlantic *Mycale*

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Abstract

Mycale (*Mycale*) *loveni* (Fristedt, 1887) is a very large structure-forming sponge that has previously been reported in the North Pacific, North Atlantic, and Arctic oceans. Through morphological and molecular examination, North Atlantic and Eastern Canadian Arctic specimens are now described as a new species, *Mycale* (*Mycale*) *lorea* sp. nov. The two species have similar external morphology; however, the spicules that make up their skeletons differ in size and shape, and the species are also separated phylogenetically by multiple genetic markers.

Key words: Porifera, Atlantic, Pacific, Arctic, *Mycale*, new species

Introduction

The genus *Mycale* is a large group of sponges (phylum Porifera) with a global distribution, containing 12 subgenera and more than 255 species (van Soest et al. 2021; de Voogd et al. 2023). The synapomorphic features that distinguish the group are the presence of palmate anisochelae and mycalostyle spicules (van Soest et al. 2021). Members of the genus usually have a plumose or plumoreticulate skeleton of styles or oxeas with palmate chelae, sigmas, toxas, and spined microxeas or raphides as possible microscleres (van Soest and Hajdu 2002). The subgenus *Mycale* (*Mycale*) is a likely non-monophyletic group (Loh et al. 2012) with an ectosomal skeleton that consists of confused single, intercrossing spicules (van Soest et al. 2021). Members of the subgenus are common in North American waters (Stone et al. 2011; Murillo et al. 2012, 2016a, 2018; Neves et al. 2014; Kenchington et al. 2016; Goodwin 2017; Dinn et al. 2019, 2020b; Dinn 2020; Nozères et al. 2020). In the Atlantic, the wide-ranging species *Mycale* (*Mycale*) *lingua* (Bowerbank, 1866) is considered a vulnerable marine ecosystem (VME) indicator species by the Northwest Atlantic Fisheries Organization (NAFO 2017) due to its size and the habitat-forming function it provides.

Mycale (*Mycale*) *loveni* (Fristedt, 1887) is a very large, structure-forming sponge with a North Pacific distribution ranging from the collection location of the original type specimen near Cape Yakan in the Chukchi Sea (Fristedt 1887 as *Clathria loveni*) to Monterey Bay on the Northern California coast (de Laubenfels 1932, as *Mycale bellabellensis* (Lambe, 1905)). The species has been reported from the Atlantic, particularly in the Newfoundland and Labrador region (Fuller 2011; Murillo et al. 2016b). The species has also been recorded in collections from the eastern Canadian Arctic (Murillo et al. 2018); however, those specimens were reanalyzed along with others from the North Atlantic and were subsequently reported as *M. (M.)* cf. *loveni* due to spicule size differences between those specimens and published records from the Pacific (Bouchard Marmen et al. 2021).

Here we examine *M. (M.) loveni* specimens loaned from the Royal British Columbia Museum (RBCM), a syntype of *M. bellabellensis* provided by the Canadian Museum of Nature (CMN), and additional Pacific specimens. We also describe a new species of *Mycale* from the North Atlantic based on morphologic and molecular evidence from several collected specimens.

Materials and methods

Specimens were collected from multiple sources and locations under the auspices of Fisheries and Oceans Canada (DFO) and the National Oceanic and Atmospheric Administration (NOAA). Fisheries and Oceans Canada collects sponge specimens as part of bottom trawl fisheries surveys in the eastern Canadian Arctic, Atlantic, and Pacific. Gulf of St. Lawrence specimens were collected during the ecosystemic survey in the Lower Estuary and northern Gulf of St. Lawrence aboard the CCGS *Teleost* from 2005 to 2020 using a Campelen 1800 trawl towed for 15 min at 3 knots (Bourdages et al. 2020). Northern Gulf of St. Lawrence sponge specimens have been photo-catalogued since 2005, with systematic physical sampling since 2011 (Nozères et al. 2020). Newfoundland and Labrador specimens were collected during the Autumn Multi-Species RV Bottom Trawl Surveys aboard the CCGS *Teleost* or the CCGS *Alfred Needler* using a Campelen 1800 trawl towed for 30 min at 3.5 knots. Additional specimens were collected from the Flemish Cap and Tail of the Grand Bank aboard European Union groundfish surveys, and morphological measurements for these specimens were made previously (Murillo et al. 2016b). Arctic specimens were collected during multispecies trawl surveys (2010–2012) aboard the Greenland Institute of Natural Resources research vessel *Paamiut* using an Alfredo trawl towed for 30 min at 3 knots. Specimens were also collected by NOAA from within and adjacent to the Olympic Coast National Marine Sanctuary (OCNMS) off the Olympic Peninsula in Washington, USA, during a research cruise aboard the *EV Nautilus* in August 2017 and September–October 2020. Samples were collected from Juan de Fuca, Quinault, and Grays Canyons with the remotely operated vehicle (ROV) *Hercules* and are part of a collection held by the OCNMS and on loan through the courtesy of NOAA. Three specimens were collected off the Oregon and California coasts in 2018 using an ROV during a cruise on the NOAA Ship *Bell M. Shimada* and one during a 2019 cruise on the NOAA Ship *Reuben Lasker*. Sponge specimens were preserved in 95% ethanol, frozen, or dried. Images of specimens were taken *in situ*, onboard, or in the lab after preservation. Type material was examined from the collections of the CMN, and additional specimens were obtained from the RBCM. Specimen collection was conducted in accordance with applicable laws, guidelines, and regulations.

Tissue sections were prepared by sectioning very thin portions of tissue previously dehydrated in ethanol. Sections were clarified in clove oil for several minutes, and then mounted on a microscope slide in Canada balsam. Tissue sections were imaged using a stereo or compound microscope. To isolate spicules, pieces of sponge were placed in undiluted household bleach overnight to remove tissue, then rinsed four times in distilled water and cleaned in two washes of 95% ethanol. Spicules were allowed to settle for at least 10 min between rinses, and then the upper layer of liquid was pipetted off, leaving the spicules undisturbed. Cleaned spicules were dried on glass slides, mounted in DPX mounting medium (Sigma–Aldrich, St. Louis, MO) or Canada balsam and imaged using a compound microscope. For scanning electron microscopy (SEM), spicules were cleaned with nitric acid and

treated with albumen (Reiswig and Browman 1987) before being placed on metal stubs, coated with gold, and viewed with a Hitachi SU3500 SEM (Mount Allison University, Sackville, NB). Spicule measurements ($n = 30$ unless otherwise stated) were made with ImageJ 1.53. Analysis methods for eastern Canadian Arctic specimens are presented in Bouchard Marmen et al. (2021). Measurements are reported as minimum–mean–maximum.

Voucher specimens are deposited at the CMN, Ottawa, Canada. NOAA specimens (NA) were deposited at the Olympic Coast National Marine Sanctuary and the Museum of Comparative Zoology, Massachusetts, USA. RBCM specimens were loaned from Victoria, BC. Eastern Canadian Arctic specimens (PAA) were previously assessed in Bouchard Marmen et al. (2021). Pacific specimens (RL and SH) are held at the Northwest Fisheries Science Center, Seattle, WA. The World Porifera Database, which implements the classification system for Demospongiae proposed by Morrow and Cárdenas (2015), was used as the taxonomic authority (de Voogd et al. 2023).

Total DNA was extracted using the DNeasy Blood and Tissue Kit (Qiagen, Valencia, CA) following the spin-column protocol for animal tissues. The 5' end region of cytochrome *c* oxidase I (COI) was amplified using M13F-tailed dgLCO1490 and M13R-tailed dgHCO2198 degenerate Folmer fragment primers (Folmer et al. 1994; Meyer 2003). The D13–E13 domains of the 28S rDNA fragment were amplified using M13F-tailed NL4F and M13R-tailed NL4R primers (Nichols 2005). The internal transcribed spacer (ITS) region, consisting of the two spacers (ITS1 and ITS2) and the 5.8S ribosomal DNA, was amplified using M13F-tailed 18S and M13R-tailed 28S primers (Lôbo-Hajdu et al. 2003; Klautau et al. 2013). PCR reactions used Platinum Taq Polymerase (Invitrogen, Carlsbad, CA) and were run on a mini16 thermal cycler (miniPCR, Cambridge, MA, USA). COI and ITS reactions used a protocol consisting of 95.0 °C for 5 min, (95.0 °C for 30 s; 50.0 °C for 30 s; 72.0 °C for 45 s) × 35 cycles, and 72.0 °C for 2 min. D13–E13 28S rDNA reactions used an annealing temperature of 56 °C. Clean-up and bidirectional sequencing of PCR products using M13R/F sequencing primers were performed by Génome Québec (Montréal, QC) using an Applied Biosystem's 3730xl DNA Analyzer. NOAA-provided samples were amplified and sequenced using nontailed NL4F and NL4R primers (Nichols 2005). PCR reactions for NOAA specimens were prepared using GoTaq reagents (Promega, Madison, WI) and were run using a protocol of 94.0 °C for 2 min, (94.0 °C for 1 min; 55.0 °C for 1 min; 72.0 °C for 1 min) × 35 cycles, and 72.0 °C for 5 min. PCR products were cleaned using Millipore (Burlington, MA) PCR clean-up plates and Sanger-sequenced using BigDye (ThermoFisher) chemistry and NL4F/NL4R primers on an ABI 3500 at NOAA-NWFSC. Geneious R 9.1.8 or BioEdit 7.2 was used to trim low-quality regions and pair forward and reverse chromatograms of the same sample. Primer sequences and low-quality bases were trimmed from the ends and aligned with the MAFFT algorithm, and a few manual adjustments were made. The resulting nucleotide sequences were submitted to GenBank (COI: OP419492–OP419495, ITS: OP620772–OP620776, and D13–E13 28S: OP458345–OP458353). Additional *Mycale* ITS and D13–E13 28S accessions were down-

loaded from GenBank and aligned with our *Mycale* sequences using ClustalW. Maximum likelihood gene trees were estimated in MEGA X (Kumar et al. 2018) using the Jukes–Cantor substitution model, and bootstrap support was evaluated with 1000 replicates.

Results

Phylum Porifera Grant, 1836
 Class Demospongiae Sollas, 1885
 Subclass Heteroscleromorpha Cárdenas, Pérez, and Boury-Esnault, 2012
 Order Poecilosclerida Topsent, 1928
 Family Mycalidae Lundbeck, 1905
 Genus *Mycale* Gray, 1867
 Subgenus *Mycale (Mycale)* Gray, 1867

Mycale (Mycale) loveni (Fristedt, 1887)
 (Figs. 2 and 3 and Table 1)

SYNONYMS: *Clathria loveni* Fristedt, 1887, *Esperella bellabellensis* Lambe, 1905, *Esperella fisheri* de Laubenfels, 1926, *Esperia loveni* (Fristedt, 1887), *Myclae (Carmia) bellabellensis* (Lambe, 1905), *Mycale bellabellensis* (Lambe, 1905), *Mycale fisheri* (de Laubenfels, 1926), and *Mycale loveni* (Fristedt, 1887).

DIAGNOSIS: Stalked sponge with a cavernous funnel- or tube-shaped body, though specimens may be highly polymorphic and attain massive forms. Sponge body varies in size from a few centimetres in length to over one metre in funnel-shaped specimens. Generally found in deep water (>200 m), though the holotype (22 m) and other specimens have been collected in shallow water (Fristedt 1887). The sponge body varies in size from a few centimetres in length to over one metre in funnel-shaped specimens.

MATERIALS EXAMINED:

Mycale cf. *bellabellensis* (Lambe, 1905), RBCM 978-00084-002, Edge of Clayoquot Canyon, British Columbia, Canada, 48.955°N, 126.415°W, 201 m depth, collected by PBS/JAT, 26 May 1962.

Mycale (Mycale) loveni (Fristedt, 1887), RBCM 003-00036-002, off southern Alaska, USA, 55.883°N, 153.75°W, 228 m depth, collected by PBS, 1963.

Mycale (Mycale) loveni (Fristedt, 1887), RBCM 009-00134-005, Dixon Entrance, British Columbia, Canada, 54.45°N, 131.7°W, collected by Pacific Biological Station (PBS), 12 August 1965.

Mycale (Mycale) loveni (Fristedt, 1887), NA086-086-03, West of Olympic Peninsula, Washington, USA, 48.2503°N, 125.0129°W, 257 m depth, collected by NOAA, 26 August 2017.

Mycale (Mycale) loveni (Fristedt, 1887), NA086-102, West of Olympic Peninsula, Washington, USA, 48.129°N, 125.084°W, 276 m depth, collected by NOAA, 28 August 2017.

Mycale (Mycale) loveni (Fristedt, 1887), NA086-103-01, West of Olympic Peninsula, Washington, USA, 48.129°N, 125.084°W, 276 m depth, collected by NOAA, 28 August 2017.

Mycale (Mycale) loveni (Fristedt, 1887), SH1812-039, Daisy Bank, off Salem Oregon USA, 44.665°N, 124.809°W, 342 m depth, collected by NOAA, 15 October 2018.

Mycale (Mycale) loveni (Fristedt, 1887), SH1812-091, Mendocino Ridge, northern California, USA, 40.2873°N, 124.6901°W, 364 m depth, collected by NOAA, 20 October 2018.

Mycale (Mycale) loveni (Fristedt, 1887), SH1812-190, Santa Lucia Bank, central California, USA, 34.679°N, 121.172°W, 549 m depth, collected by NOAA, 1 November 2018.

Mycale (Mycale) loveni (Fristedt, 1887), SH1812-245, Sverdrup Bank, southern California, USA, 33.140°N, 120.356°W, 263 m depth, collected by NOAA, 6 November 2018.

Mycale (Mycale) loveni (Fristedt, 1887), RL1905-069B, Wind Farm West, central California, USA, 35.062°N, 121.532°W, 706 m depth, collected by NOAA, 30 October 2019.

Mycale (Mycale) loveni (Fristedt, 1887), NA121-057B, Quinault Canyon, WA, USA, 47.2179°N, 124.9047°W, 325 m depth, collected by NOAA, 27 September 2020.

Mycale (Mycale) loveni (Fristedt, 1887), NA121-145B, Grays Canyon, Washington, USA, 46.9137°N, 124.8914°W, 294 m depth, collected by NOAA, 1 October 2020.

COMPARATIVE MATERIAL EXAMINED: Syntype: *Esperella bellabellensis* Lambe, 1905, CMNI 1994-0038/CMNI 1994-0039, off Bella Bella, Campbell Island, British Columbia, Canada, 52.17°N, 128.17°W, 549 m, collected by F. Landsberg, 1904.

EXTERNAL APPEARANCE (Figs. 2A, 2B, 2D, 3A, 3B, and 3C): The external morphology of *Mycale (Mycale) loveni* is variable. Most authors report *M. (M.) loveni* as being stalked, though some Gulf of Alaska specimens were reported as massive (Stone et al. 2011). Fristedt's (1887) original description from the Chukchi Sea depicts branching, thickly stalked specimens where lateral branches form subquadrangular cells filled with softer macerated tissue. Koltun (1959) reported Russian specimens (Chukchi, Bering, and Okhotsk Seas) with broad funnel-shaped stalks, though some specimens lack the large funnel. The surface is rough and may be grooved or micro-hispid. The colour while alive is greenish yellow to light yellow to brown. Consistency is somewhat compressible; it is not easily torn across spicule tracts, but smaller spicule tracts can be teased apart. Sponge tissue is easily removed from between the thick skeletal fibres and may be absent upon collection. Table 1 lists the outer morphologies that were examined and those from literature sources.

SKELETON (Fig. 2C): The choanosome is composed of branching and anastomosing thick, multispicular tracts composed of styles echinated at varying intervals by loose styles. Between these thick tracts, secondary tracts form polygonal reticulations 1200–1600 µm across, often partly infilled with style brushes. Anisochelae are concentrated on the surface of spicule tracts and scattered throughout. Spicule tracts expand into plumes at the surface, and spicules protrude 100–200 µm beyond the surface singly or in groups. At the surface, tangential tracts of styles cross-connect these plumes, forming a polygonal reticulation with meshes highly variable in shape and dimension, from 300 to 1200 µm in diameter. Large anisochelae form rosettes that occur sparingly in the ectosome and choanosome. Single large and small anisochelae are scattered throughout the sponge and are concentrated in the outer tissue layer that covers living specimens.

Table 1. Comparison of individual variation of spicule dimensions of *Mycale (Mycale) loveni* (Fristedt, 1887) given in micrometres as minimum–mean–maximum of length × width.

Specimen	Morphotype	Location	Depth (m)	Styles	Large anisochelae	Medium anisochelae	Small anisochelae
<i>Esperella bellabellensis</i> Lambe, 1905 CMNI 1994-0038	Funnel	Near Campbell Island, BC 52.170°N, 128.170°W	549	425–456–496 × 11–13–15.5	83–88–94	43–54–67	19–22–25, n = 13
<i>Mycale cf. bellabellensis</i> (Lambe, 1905) RBCM 978-00084-002	Tube	Near Vancouver Island, BC 48.955°N, 126.415°W	201	418–450–486 × 11–13–15	81–88–97	40–45–49	21–32–37
<i>Mycale (Mycale) loveni</i> (Fristedt, 1887) RBCM 003-00036-002	Funnel	South of Kodiak Island, AK 55.883°N, 153.75°W	228	389–431–485 × 12–14–16	81–91–102	51–58–70	30–36–40
NA086-086-03	Tube	West of the Olympic Peninsula, WA 48.250°N, 125.013°W	257	399–476–515 × 10–13–16, n = 50	70–91–101, n = 50	47–56–73, n = 50	29–39–52, n = 50
NA086-102	Tube	West of the Olympic Peninsula, WA 48.129°N, 125.084°W	276	420–474–525 × 10–12–13, n = 50	78–84–91, n = 50	55–61–73, n = 50	34–46–52, n = 50
NA086-103-01	Tube	West of the Olympic Peninsula, WA 48.129°N, 125.084°W	276	336–463–546 × 10–12–13, n = 50	78–90–101, n = 50	57–65–75, n = 50	34–49–55, n = 50
RL1905-069B	Fragment	W of Santa Maria, CA 35.062°N, 121.532°W	706	452–552–609 × 10.4–11.6–13.3, n = 50	75.4–84.2–93.6, n = 50	52.0–56.3–65.0, n = 3	23.4–33.7–41.6, n = 50
SH1812-039	Stalked club	Daisy Bank, W of Newport, OR 44.665°N, 124.809°W	342	375–492–642 × 10.4–11.9–14.0, n = 50	75.4–84.8–96.2, n = 50	49.4–59.3–70.2, n = 50	20.8–34.8–46.8, n = 50
SH1812-190	Fan	Santa Lucia Bank, SW of Santa Maria, CA 34.679°N, 121.172°W	549	483–548–599 × 10.1–11.1–13.0, n = 50	72.8–79.3–85.8, n = 50	49.4–57.8–70.2, n = 50	23.4–39.1–49.4, n = 50
SH1812-245	Immature funnel	Sverdrup Bank, W of San Nicolas Island, CA 33.140°N, 120.356°W	263	462–527–557 × 10.4–12.4–14.3, n = 50	75.4–91.6–101.4, n = 50	41.6–53.5–70.2, n = 50	18.2–28.8–41.6, n = 49
SN1812-091	Massive	Mendocino Ridge NE Pacific off N Baja, CA 40.2873°N, 124.6901°W	364	452–525–588 × 10.4–13.3–15.9, n = 50	80.6–85.0–93.6, n = 13	46.8–59.2–72.8, n = 35	23.4–40.1–44.2, n = 99

Table 1. (concluded).

Specimen	Morphotype	Location	Depth (m)	Styles	Large anisochelae	Medium anisochelae	Small anisochelae
<i>Clathria loveni</i> Fristedt, 1887*	Fan/funnel	Chukchi Sea 69.533°N, 177.683°E	22	350–450	100	35	–
<i>Clathria loveni</i> (Fristedt, 1887) from Lambe (1895)*	Tube	Aleutians, Chika Island, Akutan Pass, Unalaska Island	–	383–465 × 13	72	–	–
<i>Esperella fisheri</i> de Laubenfels, 1926*	Funnel	Monterey Bay, CA	110	390–400–425 × 12	75	Not mentioned	–
<i>Mycale (Mycale) loveni</i> (Fristedt, 1887) from Stone et al. (2011)*	Polymorphic	Chukchi Sea, Bering Sea, Aleutian Islands, Gulf of Alaska, Sea of Okhotsk, Pacific Coast of the Kuril Islands, Chukchi Sea (Russia), Arctic Ocean (East Siberian Sea), and British Columbia	56–744 (mas- sive form), 171–191 (stalked form)	370–495 × 10–15	80–110	30–42	–
<i>Mycale (Mycale) loveni</i> (Fristedt, 1887) from Koltun (1959)*	Funnel	Chukchi, Bering and Okhotsk Seas, near the Pacific shore of the Kuril Islands	87–400	350–509 × 13–16	72–111	31–54	–
<i>Mycale (Mycale) loveni</i> (Fristedt, 1887) from Hentschel (1929)*	Funnel	Bering Strait, Eastern Aleutians	–	350–465	72–100	35	–

Note: $n = 30$ measurements of individual spicules unless otherwise noted.

*From literature sources.

SPICULES (Figs. 2E–2L and 3D–3K and Table 1): From examined specimens, the spicule complement consists of styles as megascleres and anisochelae microscleres, usually clearly divisible into three size classes, each with somewhat different morphologies.

Measurements from CMNI 1994-0038:

Styles: 425–456–496 × 11–13–15.5 μm. Straight, sharp points may be lanceolate or mucronate. Styles either lack the constriction in the shaft just below the head found in most *Mycale* species (mycalostyles) or the constriction is slight.

Large anisochelae: 83–88–94 μm. Frontal alae are narrow, and slightly rounded. The free portion of the shaft is approximately 1/4 of the total spicule length. Rosettes are variably present and scattered throughout the sponge.

Medium anisochelae: 43–54–67 μm. Slight variations in shape are noted between a likely fan-shaped fragment (RBCM 003-00036-002, Figs. 2I and 2J) and a club-shaped specimen (RBCM 978-00084-002; Figs. 3H and 3I), where the alae are stouter in the club-shaped specimen. However, this variation is only visible at high magnification and may not be consistent between the two morphotypes.

Small anisochelae: 19–22–25 μm. Elongated. In some spicules, there is a miniscule median tooth-like extension arising from the lower alae along the upper rim, but most often this upper rim is flat.

GENETIC DATA: D13–E13 domains of 28S and ITS gene fragments were obtained from Pacific *Mycale* (*Mycale*) *loveni* specimens. Only about 40 bp overlapped in *M. (M.) loveni* ITS sequences due to low sequence quality from stutter artifacts following three successive homopolymer repeats greater than 9 bp in length (Fazekas et al. 2010). Maximum likelihood trees comparing available *Mycale* ITS and D13–E13 28S sequences resulted in a monophyletic clade for *M. (M.) loveni* (Figs. 4 and 5). COI sequences for *M. (M.) loveni* were only obtained in one direction, so consensus sequences were not created; however, most of the top nucleotide BLAST search results for the single direction reads were members of the genus *Mycale*.

DISTRIBUTION AND ECOLOGY: *Mycale* (*Mycale*) *loveni* has a very wide distribution range that spans the Arctic and North Pacific oceans. The holotype originates from the Chukchi Sea (Fig. 1A), with records also identified from the Bering Sea, Aleutian Islands, Gulf of Alaska, and British Columbia, between 22 and 800 m depth. Records from NOAA's national database for deep-sea corals and sponges (Hourigan et al. 2015) show *M. (M.) loveni* to be particularly common around the Aleutian Islands and the Gulf of Alaska, which reflects the historical sampling intensity in this region. There are also sparse records as far south as California, within the Monterey Bay National Marine Sanctuary (Hourigan et al. 2015). From ROV observations off British Columbia, Canada, *in situ* sponges were commonly attached to hard substratum ranging in size from small cobbles to exposed bedrock. The usual stalked morphology of *M. (M.) loveni* may allow this species to inhabit areas inimical to sponge growth once the larvae successfully settle. *Mycale* (*Mycale*) *loveni* was observed to be a common, large, habitat-forming demosponge at Learmonth

Bank, Dixon Entrance in sites that were dominated by the abundance of several large glass sponge species, notably *Farella* sp., *Aphrocallistes vastus* (Schulze, 1886) and *Heterochone calyx* (Schulze, 1886) (Chu 2010). Other fauna co-occurring with *M. (M.) loveni* include *Sebastes* spp. rockfish, alcyonacean corals such as *Primnoa pacifica* Kinoshita, 1907, cup corals, other small corals, crinoids, anemones, holothurians, brachiopods, and sponges (Chu 2010).

REMARKS: The specimens analyzed here are consistent with Fristedt's (1887) original description of *C. loveni*. Fristedt described an erect and irregularly ramous specimen with several slender branches issuing from a firm stalk, and the branches form a mesh that is filled with softer tissue. The styles of this species were described to be thickest near the pointed end, and this holds true for most of the examined specimens; however, the more hastate spicules as described by Koltun (1959) are not present in all specimens. Here we also suggest that the species has three size categories of anisochelae rather than two. This is contrary to Fristedt's original description, which does not mention a small size category, while de Laubenfels (1932) reported four size categories for large specimens that he considered as *Mycale bellabellensis*. In most specimens, the separation of anisochelae size categories by length alone is possible using a light microscope, but the spicule shape between the medium- and small-size categories is noticeably different when viewing spicules using SEM. The syntype of *Esperella bellabellensis* was initially described by Lambe (1905) as having only large anisochelae with many immature anisochelae, and small sigmas. After examination of the syntype, it is clear that there are three size categories of anisochelae (Table 1), and the sigmas drawn by Lambe were seen in the prepared slides, though they are unlikely to be spicules but rather contamination of the slide.

Stone et al. (2011) synonymized *M. (M.) loveni* and *M. bellabellensis* and suggested that different morphotypes of the species are geographically isolated, with club-shaped specimens occurring in the Gulf of Alaska and vase/funnel-shaped specimens occurring in the Aleutians. However, the various morphotypes examined herein are present throughout the range of the species (Table 1). Several morphotypes were observed during an ROV dive at Learmonth Bank (Figs. 2B–2D and 3C) (Chu 2010). Despite some variation in spicule shape between specimens seen using SEM, we maintain that the species is simply highly polymorphic.

Mycale (*Mycale*) *lorea* sp. nov.

(Fig. 6 and Table 2)

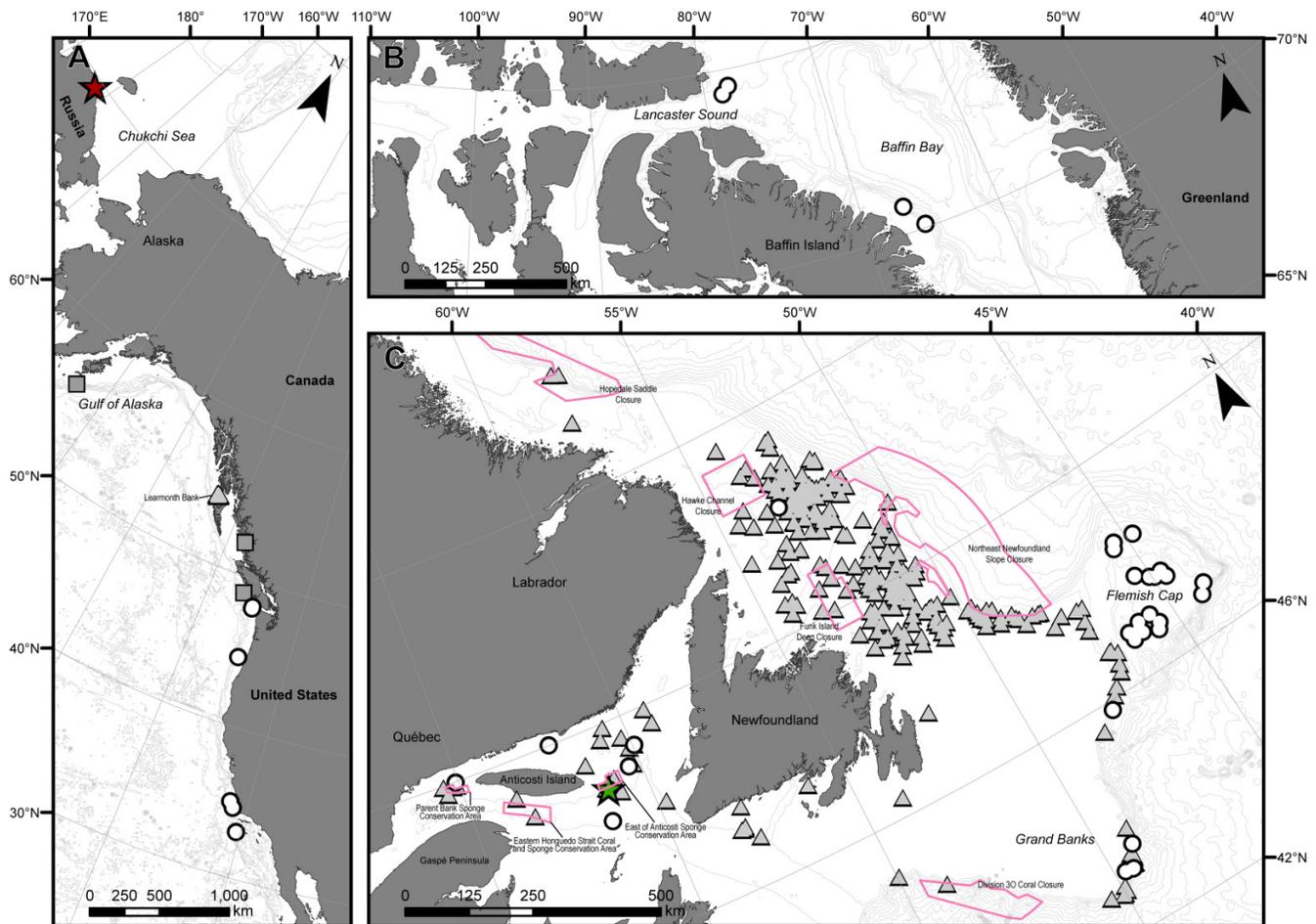
ZOOBANK LSID: urn:lsid:zoobank.org:act:0C67A722-A22B-4F48-8AE5-68CD2571D47A.

DIAGNOSIS: Large vase-shaped sponge with dense, protruding, light yellow veining spicule tracts and a firm, thick stalk. Often collected as large fragments in trawl samples.

MATERIALS EXAMINED:

Holotype: CMNI 2022-0001, Gulf of St. Lawrence, SE of Anticosti Island, 48.829°N, 61.106°W, 211 m, collected by Fisheries and Oceans Canada, 17 August 2018.

Fig. 1. Map of collection locations. (A) Pacific (*Mycale (Mycale) loveni*, holotype = star). (B, C) Atlantic (*Mycale (Mycale) lorea* sp. nov., holotype = star), museum specimens = squares, spicule measured specimens = circles, additional specimens identified visually = triangles. Other effective area-based conservation measures (OECMs) where sponges were collected or observed are outlined in pink. The figure was created using ArcMap version 10.8 (Esri, Inc., Redlands, CA, USA) and assembled from the following data sources: collection data sourced from Fisheries and Oceans Canada and NOAA; base map from GSHHG (Wessel and Smith 1996); contour lines from ETOPO1 (NOAA 2009).



Paratypes:

CMNI 2022-0002, southern Tail of the Bank, Newfoundland, 43.09°N, 49.518°W, 589 m, collected by Fisheries and Oceans Canada, 23 October 2012.

CMNI 2022-0003, NL Shelf, west of southern Labrador, 52.167°N, 53.135°W, 220 m, collected by Fisheries and Oceans Canada, 4 December 2020.

CMNI 2022-0004, west of the Flemish Cap, Newfoundland, 46.37°N, 47.0983°W, 770 m, collected by Fisheries and Oceans Canada, 16 January 2015.

CMNI 2022-0005, Gulf of St. Lawrence, SW of Anticosti Island, 48.855°N, 61.162°W, 181 m, collected by Fisheries and Oceans Canada, 16 August 2018.

CMNI 2022-0006, Gulf of St. Lawrence, NW of Anticosti Island, 49.926°N, 65.074°W, 160 m, collected by Fisheries and Oceans Canada, 25 August 2017.

ADDITIONAL SPECIMENS EXAMINED:

QC_2020_215, Gulf of St. Lawrence, W of Anticosti Island, 49.401°N, 59.948°W, 206 m, collected by Fisheries and Oceans Canada, 24 August 2020.

Specimens from Bouchard Marmen et al. (2021):

PAA2010009061246, Davis Strait, northeast of Clyde River Nunavut, 70.677°N, 66.811°W, 677 m, collected by Fisheries and Oceans Canada, 25 October 2010.

PAA2010009067237, Davis Strait, southeast of Clyde River Nunavut, 70.090°N, 65.692°W, 467 m, collected by Fisheries and Oceans Canada, 26 October 2010.

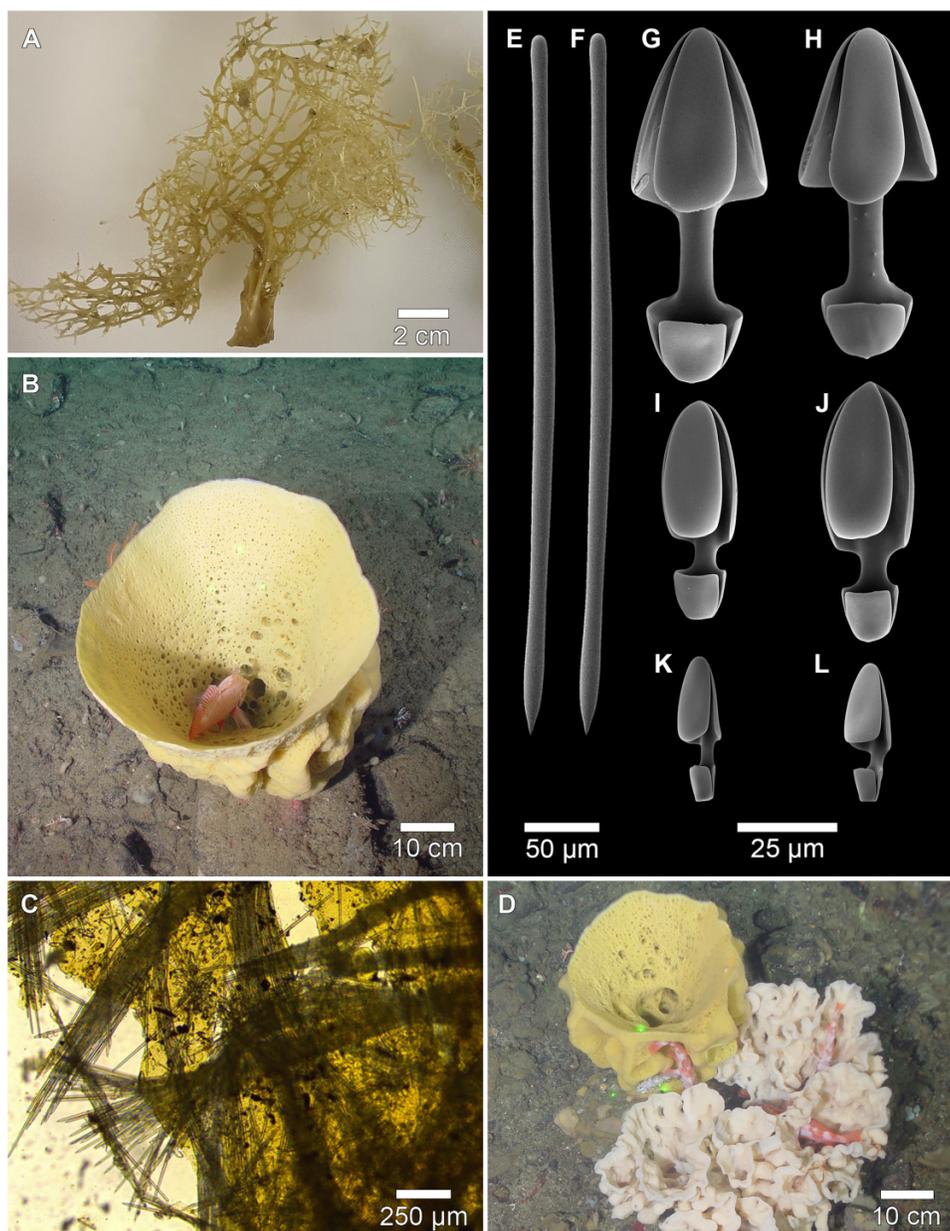
PAA2012007038033, Baffin Bay, eastern entrance to Lancaster Sound, 74.446°N, 78.432°W, 663 m, collected by Fisheries and Oceans Canada, 5 October 2012.

PAA2012007037332, Baffin Bay, eastern entrance to Lancaster Sound, 74.612°N, 77.832°W, 442 m, collected by Fisheries and Oceans Canada, 5 October 2012.

COMPARATIVE MATERIAL EXAMINED: Syntype: *Esperella bellabelensis* Lambe, 1905 CMNI 1994-0038/CMNI 1994-0039, off Bella Bella, Campbell Island, British Columbia, 52.17°N 128.17°W, 549 m, collected by F. Landsberg, 1904.

ETYMOLOGY: From the Latin *lorea* meaning a laurel branch, crown, or wreath. The distinctive light-coloured veining

Fig. 2. *Mycale (Mycale) loveni* fan- and vase-shaped specimens. (A) RBCM 003-00036-002, (B) specimen from Learmonth Bank BC, (C) skeleton from CMNI 1994-0038, and (D) specimen growing among *Heterochone calyx* sponges from Learmonth Bank, BC. (E–L) Spicules from RBCM 003-00036: (E, F) styles; (G, H) large anisochelae; (I, J) medium anisochelae; and (K, L) small anisochelae (underwater photos: Leys, Tunnicliffe, CSSF).



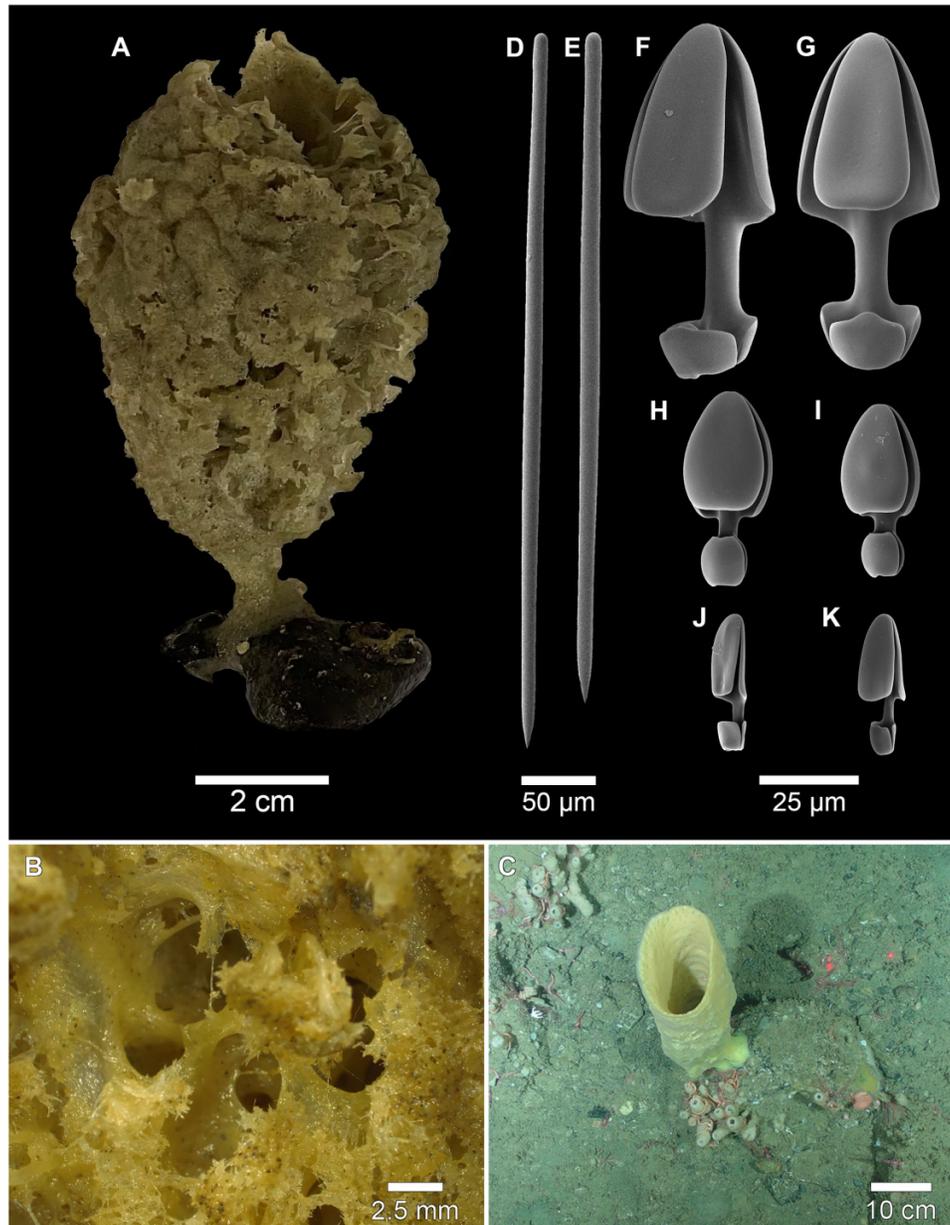
spicule tracts are diagnostic of the species and resemble the roots and branches of a bay laurel tree.

EXTERNAL APPEARANCE (Figs. 6A and 6B): Large vase-shaped sponge with a thick stalk. The vase is bolstered by thick, protruding spicule tracts, which are lightly coloured and thickest on the outer surface of the vase. The interconnecting spicule tracts form an irregular lattice filled with softer tissue. Specimens are firm and difficult to tear; however, choanosomal tissue may be removed easily while spicule tracts stay intact. A presumed specimen was seen *in situ* during a benthic video survey in the Eastern Houguedo Strait Coral and

Sponge Conservation Area in July 2022, with a distinct vase shape and visible light-coloured veining spicule bundles (Fig. 6B).

SKELETON (Figs. 6C and 6D): The skeleton consists of a dense mesh of spicule tracts formed by densely packed styles. On the outer surface of the sponge, these tracts are especially thick and prominently lightly coloured, reaching from the stem to the outer fringe. Thin tissue is spread between the dense tracts, with a mostly confused arrangement of loose tracts of styles, with palmate anisochelae variably occurring in rosettes (Fig. 6D). Styles flare out into soft tissue as spicule

Fig. 3. *Mycale (Mycale) loveni* tube- and club-shaped specimens. (A) RBCM 978-00084-002. (B) Detail of dense fibres throughout the sponge. (C) Specimen from Learmonth Bank, BC. (D–K) Spicules from RBCM 978-00084-002: (D, E) styles; (F, G) large anisochelae; (H, I) medium anisochelae; and (J, K) small anisochelae (underwater photo: Leys, Tunnicliffe, CSSF).



brushes at the ends of the dense tracts (Figs. 6C and 6D). In heavily damaged and trawl-worn specimens, tissue containing chelae may not be abundant.

SPICULES (Figs. 6E–6L and Table 2):

From the holotype CMNI 2022-0001:

Styles: 354–397–428 × 14–17–19 µm, generally straight, but some are slightly curved. The head of the spicule near the rounded end is thin, and the spicule thickens at about a quarter of its length, with the thickest portion near the midpoint. From the middle, styles gradually taper to a sharply pointed tip. In some specimens, thinner styles show a slightly pronounced rounded head, somewhat reminiscent of a sub-

tylostyle. Some specimens may have styles with multiple swellings down the shaft, but this is uncommon.

Large anisochelae: 56–61–64 µm, with well-developed and broad upper alae. The free portion of the shaft is short, at less than 1/5 of the total spicule length. The upper alae have a considerable width, which may be wider than half the length of the whole spicule. The lower alae have a straight upper rim. A rounded, tooth-like extension protrudes above the upper rim of the lower alae, arising from the centre.

Medium anisochelae: 27–34–39 µm, have an overall elongated shape with the free part of the shaft variable in size, less than 1/5 of the length of the spicule. Lower alae also have a straight upper rim but no noticeable protrusions.

Fig. 4. Maximum likelihood phylogenetic tree of ITS1, 5.8S, and ITS2 rDNA constructed with the Jukes–Cantor model in MEGA X. This gene tree shows a monophyletic Atlantic *Mycale (Mycale) lorea* sp. nov. as a sister species of the Pacific *Mycale (Mycale) loveni*. Values at each node indicate bootstrap support generated from 1000 replicates.

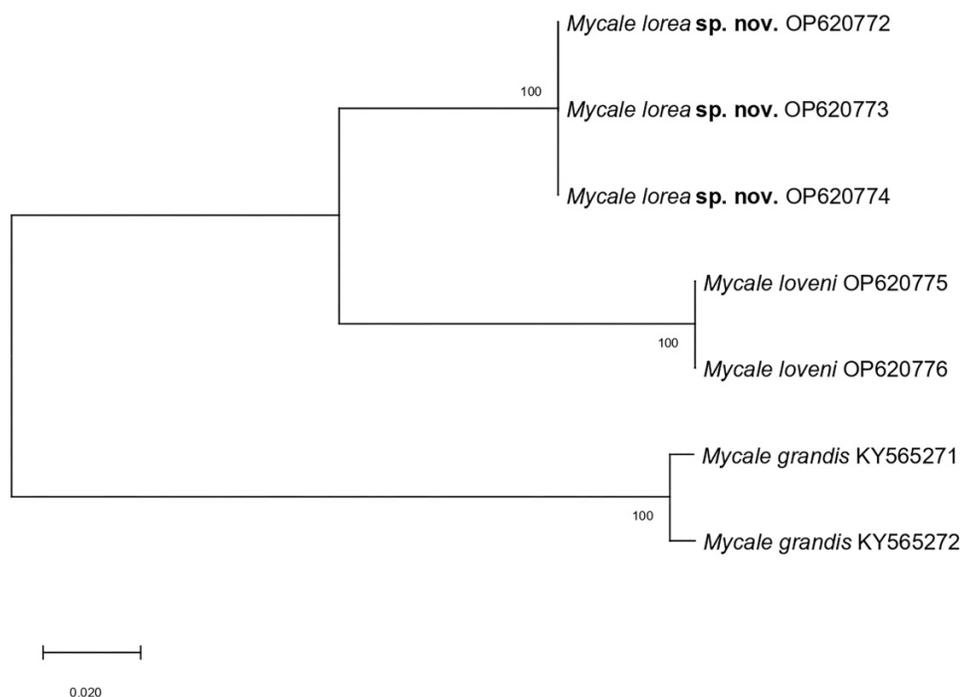
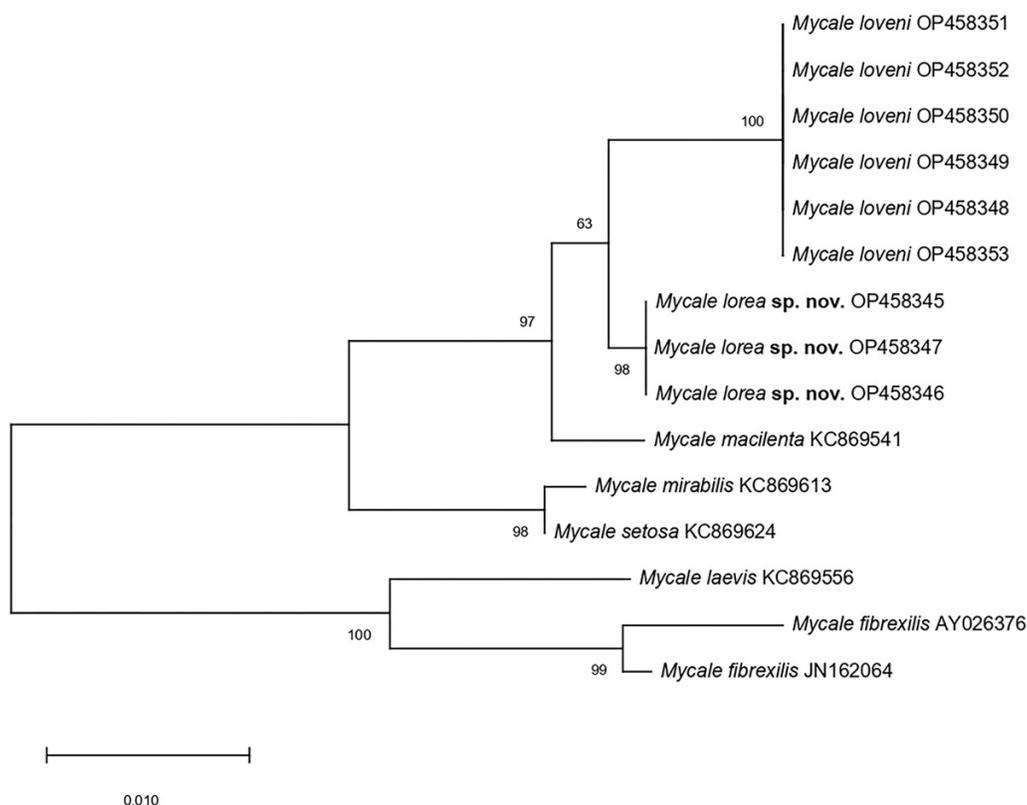
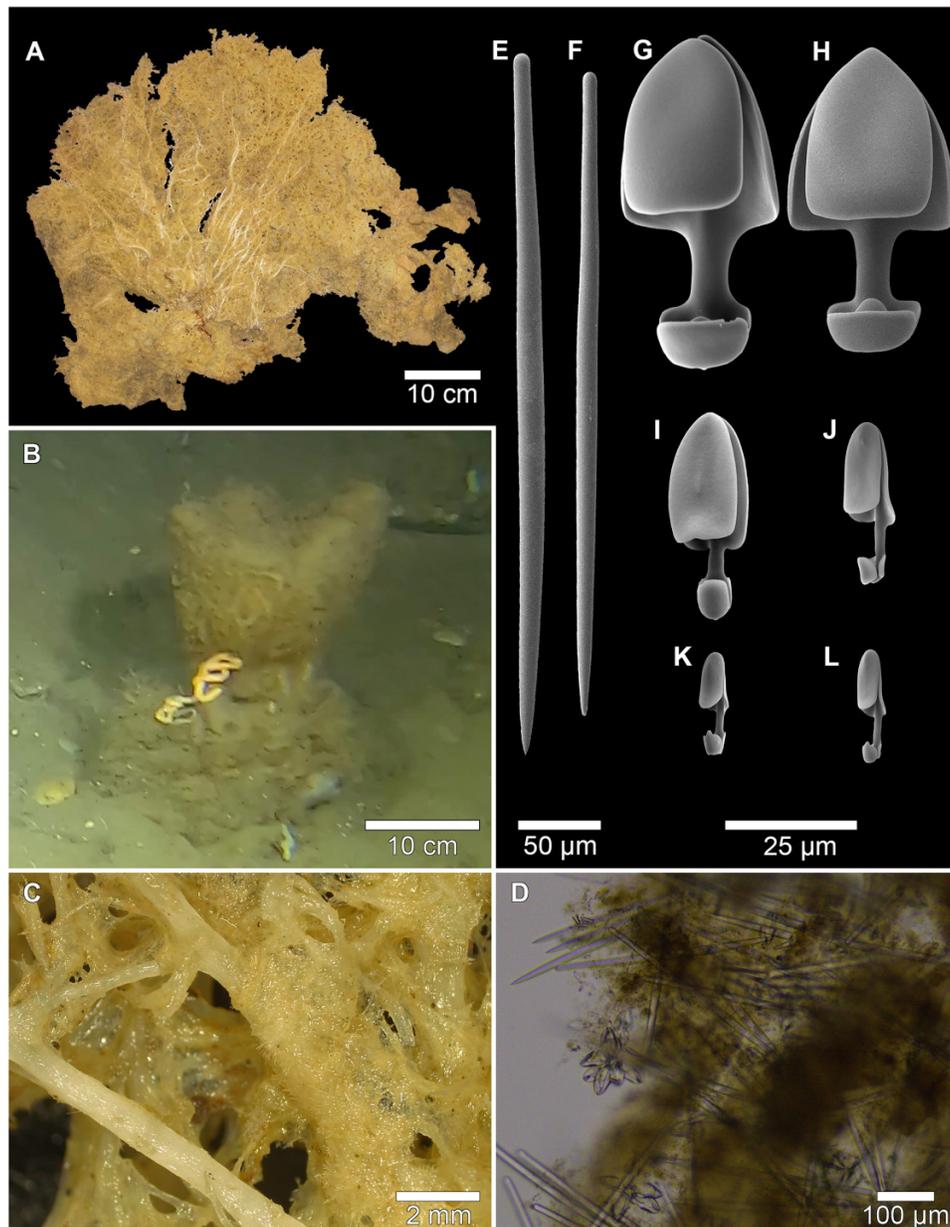


Fig. 5. Maximum likelihood phylogenetic tree D13–E13 28S rDNA constructed with the Jukes–Cantor model in MEGA X. This gene tree shows a monophyletic Atlantic *Mycale (Mycale) lorea* sp. nov. as a sister species of the Pacific *Mycale (Mycale) loveni*. Values at each node indicate bootstrap support generated from 1000 replicates.



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Fig. 6. *Mycale (Mycale) lorea* sp. nov. (A) External appearance of collected specimen. (B) *In situ* image of presumed specimen. (C) Detail of thick, light-coloured fibres within the sponge body. (D) Skeleton, showing large anisochelae rosettes. (E–L) Spicules: (E, F) styles; (G, H) large anisochelae; (I, J) medium anisochelae; and (K, L) small anisochelae.



Small anisochelae: 15–19–23 μm , also elongated and similar in overall shape to the medium size category; however, there is a median tooth-like extension arising from the lower alae along the upper rim.

Medium and small anisochelae measurements from eastern Canadian Arctic specimens are combined into a single size category (Table 2) as these measurements were taken prior to SEM imagery confirmation of the three size categories of anisochelae (Bouchard Marmen et al. 2021).

GENETIC DATA: COI, D13–E13 28S, and ITS sequences were obtained for *Mycale (Mycale) lorea* sp. nov. The sequences of the three gene regions appear most similar to species from the

genus *Mycale* based on a BLAST search. Maximum likelihood trees comparing available *Mycale* ITS and D13–E13 28S sequences were constructed, which resulted in separate monophyletic clades for *Mycale (Mycale) loveni* and *M. (M.) lorea* sp. nov. (Figs. 4 and 5). As assembled COI sequences for *M. (M.) loveni* were not obtained, *M. (M.) lorea* sp. nov. could not be positively differentiated using this gene fragment.

DISTRIBUTION AND ECOLOGY: *Mycale (Mycale) lorea* sp. nov. has a wide range in the western North Atlantic. Specimens from DFO catch databases have been collected from 114 to 1336 m depth. The species has been collected in the eastern Canadian Arctic, along the Newfoundland and Labrador Shelf, and

Table 2. Comparison of individual variation of spicule dimensions of *Mycale (Mycale) lorea* sp. nov. given in micrometres as minimum–mean–maximum of length × width.

Specimen	Lat., long.	Depth (m)	Styles	Large anisochelae	Medium anisochelae	Small anisochelae
CMNI 2022-0001 (holotype)	48.829°N, 61.106°W	211	354–397–428 × 14–17–19	56–61–64	27–34–39	15–19–23
CMNI 2022-0002 (paratype)	43.090°N, 49.518°W	589	383–422–452 × 12–15–17	52–57–63	27–30–37	15–16–22
CMNI 2022-0003 (paratype)	52.167°N, 53.135°W	220	372–419–447 × 12–15–17	56–63–69	25–32–39	17–20–23
CMNI 2022-0005 (paratype)	48.855°N, 61.162°W	181	342–408–446 × 13–17–19 and 295–366–428 × 4–7–10 (likely immature)	53–63–73	27–32–41	18–21–24
QC_2020_215	49.401°N, 59.948°W	206	388–413–446 × 14–17–19	54–60–66	33–37–46	19–22–29
PAA2010009061246	70.677°N, 66.811°W	677	415–454–480 × 13–16–18	61–66–74		23–33–37
PAA2012007038033	74.446°N, 78.432°W	663	394–448–473 × 14–15–17, n = 10	63–67–73, n = 10		21–29–44, n = 10
PAA2010009067237	70.090°N, 65.692°W	677	404–441–472 × 14–16–17, n = 10	59–66–71, n = 10		24–32–36, n = 10
PAA2012007037332	74.612°N, 77.832°W	442	404–452–483 × 12–15–16, n = 11	58–69–86, n = 10		24–33–44, n = 10

Note: n = 30 measurements of individual spicules unless otherwise noted.

in the northern Gulf of St. Lawrence (Figs. 1B and 1C). The species is also present on the Grand Banks of Newfoundland. This area includes both the southern extremity known as the Tail of the Bank and the Flemish Cap, areas outside of Canada's exclusive economic zone (Fig. 1C). A presumed specimen was seen *in situ* at 334 m depth during a video survey of sea pen (*Pennatula aculeata* Danielssen, 1860; *Balticina finmarchica* (Sars, 1851)) fields in the Eastern Hanguedo Coral and Sponge Conservation Area (DFO 2023) aboard the *Coriolis II*, living in a mud/silt bottom habitat attached to a rock showing the diagnostic vase shape and light-coloured veining formed by style bundles (Fig. 6B). From underwater video, the surrounding habitat in the conservation area was home to redfish (*Sebastes* spp.), Marlin-spike grenadier (*Nezumia bairdii* (Goode & Bean, 1877)), Norway king crab (*Lithodes maja* (Linnaeus, 1758)), and several sponge species, including *Polymastia* spp. From survey trawls in the northern Gulf of St. Lawrence, *M. (M.) lorea* sp. nov. was collected along with large catches of Atlantic Cod (*Gadus morhua* Linnaeus, 1758), Redfish (*Sebastes* spp.), Greenland halibut (*Reinhardtius hippoglossoides* (Walbaum, 1792)), white hake (*Urophycis tenuis* (Mitchill, 1814)), and northern shrimp (*Pandalus borealis* Krøyer, 1838). In shallower habitats (100–200 m depth), the sponge was collected alongside American plaice (*Hippoglossoides platessoides* (Fabricius, 1780)) and striped shrimp (*Pandalus montagui* Leach, 1814). The direct association of fish and invertebrate species with sponges cannot be inferred from these occurrences, and sponge catchability in trawls is low (Kenchington et al. 2011); therefore, the distribution of this species may be more widespread than is currently known. Both Atlantic and striped wolffish (*Anarhichas lupus* Linnaeus, 1758; *A. minor* Olafsen, 1772) also occurred in some captures of the sponge southeast of Anticosti Island, which is of particular interest as the former is listed under Canada's Species at Risk Act as a species of special concern and the latter as a threatened species (Government of Canada 2002). *Mycale (Mycale) lorea* sp. nov. also co-occurs in trawl catches with other sponge species, notably *Polymastia* spp., *Crella (Crella) cutis* Goodwin, Dinn, Nefedova, Nijhof, Murillo, and Nozeres, 2021, and *Plicatellopsis bowerbanki* (Vosmaer, 1885) (Dinn et al. 2020a; Goodwin et al. 2021).

REMARKS: It has been suggested that megasclere size is a solid taxonomic character to distinguish closely related species (van Soest et al. 2021), and in the case of *Mycale (Mycale) loveni* and *M. (M.) lorea* sp. nov., the megascleres are not only different in size, but in shape as well. The styles are often longer than 450 µm and thickest near the point in *M. (M.) loveni*, and the styles in *M. (M.) lorea* sp. nov. are generally less than 450 µm in length and are thickest near the middle. A single specimen from the Gulf of St. Lawrence had many thinner styles, which were measured here as a second size category (Table 2); however, silica concentration in ambient water has also been suggested to affect spicule width (Stone 1970; Mercurio et al. 2000; Austin et al. 2014). Further, van Soest et al. (2021) state that differences in width are strongly influenced by the growth stage of the individual spicules and are not likely diagnostic. Although both species have three size categories of anisochelae, the size difference and shape

difference between the species are obvious in light micrographs for most specimens.

Four specimens collected in the eastern Canadian Arctic were previously documented as *M. (M.) loveni* (Murillo et al. 2018) and subsequently as *M. (M.) cf. loveni* (Bouchard Marmen et al. 2021). Here those specimens were reassessed and are now considered as *M. (M.) lorea* sp. nov. It is possible that other records of *M. (M.) loveni* from the Atlantic are misidentified *M. (M.) lorea* sp. nov. specimens, such as records of *M. (M.) loveni* occurrence in Newfoundland (Fuller 2011; Murillo et al. 2016b) and Greenland waters (Blicher and Hammeken Arboe 2021); however, the northern extent of the two species is not yet known, and overlapping species ranges in the Arctic are possible.

Discussion

Mycale is a species-rich genus that includes at least 255 described species that are generally distinguished by measuring megascleres and microscleres in distinct size categories (van Soest et al. 2021). Descriptions of *Mycale* species from the 19th and early 20th centuries relied on light micrographs, which may have led to lumping of similarly sized spicules, especially small microscleres (van Soest et al. 2021). Now with access to higher magnification objectives and SEM tools, we can better separate spicule categories based on the micromorphology of microsclere spicules and not rely solely on length/width measurements. Access to many internationally collected specimens over a wide geographic range also contributes to the ability to separate similar, though geographically distinct, species. This is also the first instance that DNA barcodes have been obtained for *M. (M.) loveni* and *M. (M.) lorea* sp. nov. These data will potentially aid in the detection of additional cryptic species within the genus, and may also help with eDNA metabarcoding projects throughout the three oceans surrounding North America.

Members of the genus *Mycale* are generally opportunistic in their growth form, and their overall shape likely depends on the surrounding habitat (van Soest et al. 2021). The large, stalked funnel shape of *M. (M.) loveni* and *M. (M.) lorea* sp. nov. is seemingly unique for the genus. Coupled with a basic spicule complement consisting of only styles and anisochelae, these species are easily distinguished from other *Mycale* sponges in their respective regions. *Mycale (Carmia) carlilei* Lehnert, Stone & Heimler, 2006 is a Pacific species that is also stalked but has a cylindrical habit and has sigma spicules. Pacific reef sponges such as *Rhabdocalyptus dawsoni* (Lambe, 1892), *H. calyx* (Schulze, 1886), and *A. vastus* Schulze, 1886 may also be confused with *M. (M.) loveni* due to their generous size and possible funnel-shaped habit (Stone et al. 2011); however, the skeleton of these hexactinellid sponges differs markedly from the demosponges described here. In the Atlantic and eastern Canadian Arctic, *M. (M.) lorea* sp. nov. is often confused with *Mycale (Mycale) lingua* (Bowerbank, 1866), especially when specimens are damaged (Nozères et al. 2020; Bouchard Marmen et al. 2021). *Mycale (Mycale) lingua* attains a more massive growth form with dense, soft tissue; however, the skeleton thickens near the base and forms a dense bundle of spicule tracts that attach to a substrate.

When only the base portion of *M. (M.) lingua* is collected, the yellow colour and dense fibres can be easily confused with *M. (M.) lorea* sp. nov., though spicule analysis would reveal sigma and raphide spicules in the former species (Dinn 2020). The Atlantic *M. (M.) lorea* sp. nov. is also likely to be confused with another large species, *Hemigellius arcofer* (Vosmaer, 1885), which grows in thick sheets with a lattice-like structure (Dinn 2020; Nozères et al. 2020); however, that species is very dense with thin spicule tracts and circular canal openings (de Weerd and van Soest 1987; Dinn 2020), rather than the thinner body, thicker spicule tracts, and more quadrilateral mesh of *M. (M.) lorea* sp. nov.

Koltun (1959) stated that very few sponge species appear to penetrate the Arctic from the Pacific and the Bering Sea, but *M. (M.) loveni* is one of the few boreal exceptions to cross into the Chukchi Sea. Several theories about the spread of species from Pacific and Atlantic boreal regions into the Arctic exist (Morozov et al. 2021), with evidence of species migrations into the Arctic from each ocean. Interestingly, there are several species endemic to the Arctic that are genetically similar to species in both the North Atlantic and North Pacific, suggesting allopatric speciation of these species pairs has occurred over time (Morozov et al. 2021). Since sponges have limited dispersal capabilities (Maldonado 2006; Uriz et al. 2008; Lanna and Riesgo 2020), it is more likely that similar cryptic and reproductively isolated species may occur across large geographic distances. For example, the three species of iconic giant barrel sponges in the genus *Xestospongia*, while genetically and morphologically similar, are geographically and reproductively separate species found in three separate oceans with no known steppingstones between the Pacific and Atlantic (Setiawan et al. 2016). However, there is potential for sponge species to spread due to human influence including larval settlement on human-made structures such as buoys (Lim et al. 2009) and marine debris (Santín et al. 2020), and introduced accidentally with intentional species imports (Harbo et al. 2021). Recently, two non-native sponge species were found growing on the hull of a boat in the Atlantic (Ribeiro et al. 2022), suggesting that mobile human-made structures can be vectors of species dispersal across oceans, though human-mediated dispersal is less likely for deep-water species.

The subgenus *Mycale* is likely nonmonophyletic (Loh et al. 2012), and based on 28S sequencing results, *M. (M.) loveni* and *M. (M.) lorea* sp. nov. appear to be most closely related to *Mycale (Carmia) macilenta* (Bowerbank, 1866) (Fig. 5). Clades within the genus *Mycale* are groupings of convenience based on skeleton morphology (Hooper and van Soest 2002) and may not necessarily reflect true genetic relatedness; however, further molecular analysis may help to resolve differences within and between these clades.

Sponges such as these large *Mycale* species contribute important habitat and ecosystem services throughout their respective distributions (Buhl-Mortensen et al. 2010; Miller et al. 2015; Guillas et al. 2019; Pham et al. 2019). Sponge grounds are increasingly being afforded special protections because of their role in identifying essential fish habitats, ecologically and biologically significant areas, and VMEs (Hourigan 2009;

Vad et al. 2018; Chu et al. 2019). As such, marine protected areas (MPAs) and OECMs that encompass areas with high coral and sponge biomass were created by Fisheries and Oceans Canada (Government of Canada 2017; DFO 2021, 2023). Some *M. (M.) lorea* sp. nov. specimens were collected within OECMs with conservation objectives to protect corals, sponges, and sensitive benthic habitats (Fig. 1). Some specimens from the Gulf of St. Lawrence were collected within the Parent Bank Sponge Conservation Area and the East of Anticosti Island Sponge Conservation Area. A suspected specimen was seen *in situ* using underwater video in the Eastern Honguedo Strait Coral and Sponge Conservation Area (DFO 2017; Fig. 6B). Specimens were also collected in the Northeast Newfoundland Slope Closure, Hawke Channel Closure, Hopedale Saddle Closure, Division 30 Coral Closure, and Funk Island Deep Closure along the Newfoundland and Labrador Shelf (DFO 2023). Additional coral and sponge conservation areas are present in the Canadian Atlantic; however, *M. (M.) lorea* sp. nov. has not yet been collected or identified from those closures. This large habitat-forming sponge does, however, occur mostly outside of conservation areas and is thus prone to fishing pressure and other human activities (Fig. 1). The identification of large sponges such as *M. (M.) lorea* sp. nov. will facilitate monitoring efforts within OECMs and MPAs, particularly for projects using non-destructive sampling methods such as video surveys and targeted research to better understand sponges and their habitats.

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Data availability

Data generated or analyzed during this study are provided in full within the published article.

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Competing interests

The authors declare there are no competing interests.

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