Zootaxa 4175 (6): 521–538
http://www.mapress.com/j/zt/

Article

ISSN 1175-5326 (print edition)
ZOOTAXA
ISSN 1175-5334 (online edition)

http://doi.org/10.11646/zootaxa.4175.6.2
http://zoobank.org/urn:lsid:zoobank.org:pub:8676D18F-E27A-4255-BF1F-BBD72496844D

The cladorhizid fauna (Porifera, Poecilosclerida) of the Caribbean and adjacent waters

JON T. HESTETUN[1,3], SHIRLEY A. POMPONI[2] & HANS TORE RAPP[1]

[1]*Department of Biology and Centre for Geobiology, University of Bergen, Norway*
[2]*Harbor Branch Oceanographic Institute, Florida Atlantic University, Fort Pierce, Florida, USA*
[3]*Corresponding author. E-mail: Jon.hestetun@uib.no*

Abstract

The carnivorous sponge family Cladorhizidae has been subject to several recent studies, yet the cladorhizid fauna of the Caribbean and adjacent areas remain comparatively poorly known. In this article we provide a description of the novel species *Abyssocladia polycephalus* **sp. nov.** from the Muir Seamount NE of Bermuda, belonging to the mainly Pacific genus *Abyssocladia*, and *Asbestopluma (Asbestopluma) caribica* **sp. nov.** from the Beata Ridge. Additionally, we provide a re-description of the poorly known species *Chondrocladia (Chondrocladia) verticillata* Topsent, 1920, and compare this species with the closely related species *C. (C.) concrescens* Schmidt, 1880. Finally, we provide a brief overview of the carnivorous sponges known from the Gulf of Mexico, Caribbean Sea and adjacent Atlantic Ocean.

Key words: Carnivorous sponges, *Abyssocladia*, *Chondrocladia*, *Asbestopluma*, taxonomy, deep-sea, Porifera

Introduction

Cladorhizidae is a family of mostly deep-sea demosponges with a worldwide distribution. They are known mainly for their highly unusual carnivorous feeding strategy, considered an evolutionary adaptation to the nutrient-poor deep sea. They display morphological features such as erect bodies, reduction or lack of the sponge aquiferous system, and the ability to capture prey such as small crustaceans with the use of adhesive surfaces, filaments or inflatable spheres (e.g. Vacelet, 2007).

Compared to the NE Atlantic and Arctic, the cladorhizid fauna of the Western Atlantic and Caribbean is little known. In this paper, we describe a new Atlantic species from the mainly Pacific genus *Abyssocladia* with a unique morphology, collected by the *Alvin* submersible on the Muir Seamount off Bermuda, and a new species from genus *Asbestopluma*, collected at the Beata Ridge in the Caribbean Sea. Based on material from the National Museum of Natural History, the Bergen University Museum and a specimen collected by the Harbor Branch Oceanographic Institute (Florida), we provide a re-description of the little known Caribbean cladorhizid *Chondrocladia (Chondrocladia) verticillata* Topsent, 1920 and compare this species to the closely related *C. (C.) concrescens* Schmidt, 1880 from the same area. Finally, we provide a short overview of cladorhizids from off the coast of the Southeast United States and the Caribbean (Fig. 1).

Material and methods

The holotype specimen of *Abyssocladia polycephalus* **sp. nov.** is deposited at the Yale Peabody Museum (YPM IZ 053327). The holotype and paratype specimens of *Asbestopluma (A.) caribica* are deposited at the National Museum of Natural History (USNM 30433; USNM 1417730). Specimens of *Chondrocladia (C.) verticillata* were borrowed from the collections of the National Museum of Natural History (USNM 975; 31180) and the Bergen University Museum (ZMBN 39), as well as a recent specimen (HBOM 003:01095) collected by the *Kraken 2* ROV

Accepted by E. Hajdu: 29 Aug. 2016; published: 19 Oct. 2016

south of Pulley Ridge (Florida). Specimens were examined and studied using standard methods (Boury-Esnault & Rützler, 1997), with 30 measurements of each spicule type. Partial 28S rDNA and COI molecular markers were successfully sequenced for specimen HBOM 003:01095 in order to show its phylogenetic relationship to other species of *Chondrocladia* present in GenBank. Maximum likelihood and Bayesian inference analyses were performed on a concatenated dataset of 28S rDNA, COI and ALG11 using the method described in Hestetun *et al.* (2016b).

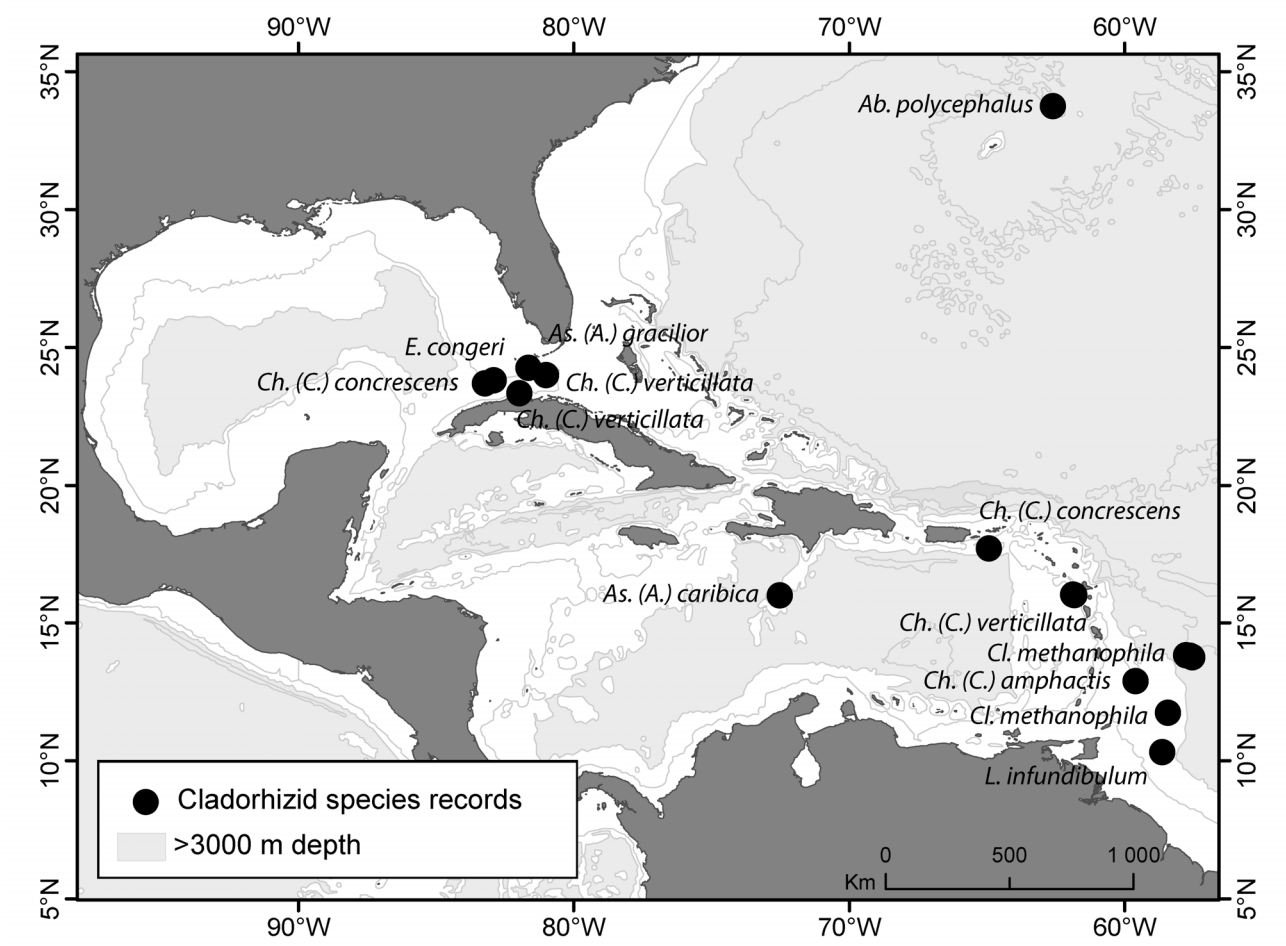

FIGURE 1. A map of the of the Atlantic off the SE United States and the Caribbean Sea and Gulf of Mexico, showing cladorhizid records from the area. Species record sources are given in Table 3. Ab = *Abyssocladia*, As = *Asbestopluma*, Ch = *Chondrocladia*, Cl = *Cladorhiza*, E = *Eucheliplum*a, L = *Lycopodina*.

Results

SYSTEMATICS

Phylum PORIFERA Grant, 1836

Class DEMOSPONGIAE Sollas, 1885

Subclass HETEROSCLEROMORPHA Cárdenas, Perez & Boury-Esnault, 2012

Order POECILOSCLERIDA Topsent, 1928

Family CLADORHIZIDAE Dendy, 1922

Genus *Abyssocladia* Lévi, 1964

Diagnosis. Cladorhizidae most often pedunculate, carrying a disciform or flabelliform body with a radial architecture, in other cases pinnate or branching. Microscleres are a combination of abyssochelae, cleistochelae, arcuate chelae and/or sigmancistras, but not placochelae (from Hestetun *et al.*, 2016b).

***Abyssocladia polycephalus* sp. nov.**
(Figure 2–3)

Type material. Holotype: YPM IZ 053327, R/V "Atlantis" cruise AT07-35 (2003–06–05, Muir Seamount, *Alvin* St. 1, 33°45.42'N, 062°36.06'W, 2829 m). The holotype was recovered during the 2003 R/V "Atlantis" cruise AT07-35 to the Muir, Manning and Gregg seamounts off Bermuda, collected using the *Alvin* submersible.

Etymology. From Greek *poly*, meaning many and *cephalus*, latinized form of the Greek *kephalos*, meaning head. The name is derived from the multiple disc-shaped bodies of the species.

FIGURE 2. Habit of *Abyssocladia polycephalus* **sp. nov.** holotype YPM IZ 053327. A) The whole specimen, stuck to a *Geodia* directly after retrieval (courtesy of Eric Lazo-Wasem), B) disc-shaped body, C) skeletal structure of body with D) detail and E) filament.

Diagnosis. Erect, slender *Abyssocladia* consisting of a central stem with side branches each ending in a disc-like body bearing filamentous projections. Megascleres are mycalostyles, subtylostyles and substrongyles; microscleres are arcuate isochelae and sigmancistras.

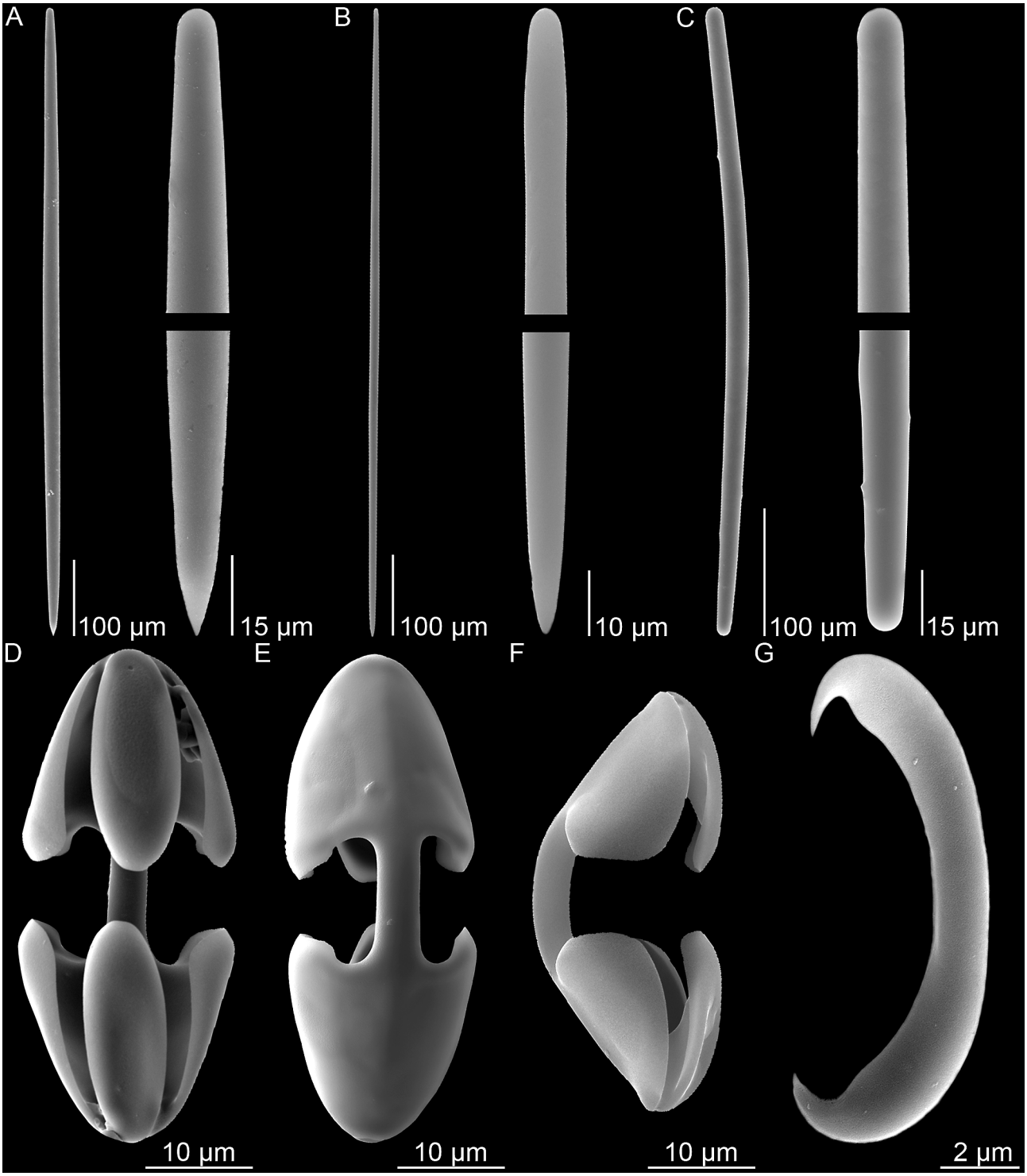

FIGURE 3. Spicules of *Abyssocladia polycephalus* **sp. nov.** holotype YPM IZ 053327. A) Mycalostyle, B) subtylostyle, C) strongyle, D) arcuate isochelae, E) sigmancistra.

Description. A single specimen consisting of a 35 mm long smooth, curving and flexible stem, with 3–4 up to 10 mm long slightly thinner side branches broken off during collection and preservation. The basal part of the sponge is missing. The branches and main stem each end with a slightly swollen, elongated, disc-like body with radiating filaments. Color is white in ethanol, with a slight yellow tint. No aquiferous system was observed (Fig.

2A–B). The specimen was recovered on the surface of an unknown *Geodia* (aff. *megastrella*, possibly undescribed) using the *Alvin* submersible, but it is unknown whether it was originally attached to this sponge.

Skeleton. The central stem and branches consist of densely packed bundles of mycalostyles. Each disc-shaped body is composed of a slightly expanded continuation of the connecting stem or branch with the addition of a network of less well organized subtylostyles as well as radiating bundles of mycalostyles projecting from the body and constituting the skeleton of the filaments. Arcuate isochelae and sigmancistras are found throughout the body tissue, but their exact placement was not determined (Fig. 2C–E).

Spicules. Mycalostyles, straight and fusiform, 720–(933)–1070 µm long, 14–(17)–22 µm wide (Fig. 3A).

Subtylostyles to **mycalostyles**, thin, straight and fusiform, with faint, slightly elongated tyle, 430–(686)–960 µm long, 5–(10)–13 µm wide (Fig. 3B).

Strongyles, stout and slightly bent, 380–(568)–780 µm long, 15–(18)–22 µm wide (Fig. 3C).

Arcuate isochelae, tridentate, with strongly arched shafts, in the body tissue and covering the filaments, 28–(43)–50 µm (Fig. 3D–F).

Sigmancistras, thick, straight or contorted, with the concave side clearly flattened into fimbria-like structures towards each end, 9.4–(9.8)–11.0 µm (Fig. 3G).

Remarks. The majority of known species within the genus *Abyssocladia* are small, pedunculate, with a single disc-shaped body and radiating filaments. This body is commonly elongated to a certain degree, and in some species has been modified into a long, flattened central axis with opposite rows of filaments along the sides (e.g. Hestetun *et al.*, 2015; Vacelet, 2006). The habit of *A. polycephalus* **sp. nov.**, consisting of a branching central stem with several disc-shaped bodies, is highly unusual and has not been recorded in the genus before.

Genus *Abyssocladia* is mostly known from the Pacific, and only three species have been described from the Atlantic: *A. faranauti* Hestetun *et al.*, 2015, *A. tecta* Hestetun *et al.*, 2015 and *A. atlantica* Lopes & Hajdu, 2014. These can be distinguished from *A. polycephalus* based on their elongated habit as well as differences in spicule complement. The unique habit and lack of cleistochelae or abyssochelae in *A. polycephalus* make it difficult to distinguish any closely related species. Among other *Abyssocladia* species, *A. claviformis* Koltun, 1970 (NW Pacific) lacks cleistochelae and abyssochelae, and has arcuate chelae and sigmancistras of approximately the same size, but can easily be distinguished from *A. polycephalus* based on morphology and geographical distance.

Genus *Asbestopluma* Topsent, 1901

[*Cometella*] Schmidt, 1870:49 (*nomen oblitum*); [*Asbestopluma*] Lankester, 1882:478 (*nomen nudum*); *Asbestopluma* Topsent, 1901:23; *Helophloeina* Topsent, 1929:8; not *Lycopodina* Lundbeck, 1905:58; *Cotylina* Lundbeck, 1905:68.

Diagnosis. Cladorhizidae with at least one small category of palmate, in a few species modified to anchorate unguiferate, anisochela. Usually with a second larger type of palmate to arcuate anisochela that may be modified to isochela, anisoplacochela, tridentate anchorate chela or anisocercichela. Sigmancistras and basal acanthotylostyles are also present with a few exceptions. Never forceps spicules (modified from Hestetun et al., 2016b).

Type species. *Cladorhiza pennatula* Schmidt, 1875 (by subsequent designation; Topsent, 1901).

Subgenus *Asbestopluma* Topsent, 1901

Diagnosis. *Asbestopluma* without spear-shaped microtylostyles (from Lopes, Bravo, & Hajdu, 2011).

Type species. *Cladorhiza pennatula* Schmidt, 1875 (by subsequent designation; Topsent, 1901).

Asbestopluma caribica sp. nov.

(Figure 4; Table 1)

Type material. Holotype: USNM 30433; paratype USNM 1417730, R/V “Bartlett” (1981–10–28, Beata Ridge, Caribbean Sea, st. 40, 15°08'N, 069°13'W, 4007 m).

Etymology. The species is named after the Caribbean Sea, where it was collected.

Diagnosis. Erect, very fine single-stem *Asbestopluma* with an upper stem carrying two oppositely arranged rows of filamentous projections. Megascleres are mycalostyles and subtylostyles; microscleres are anisocercichelae, palmate anisochelae and sigmancistras.

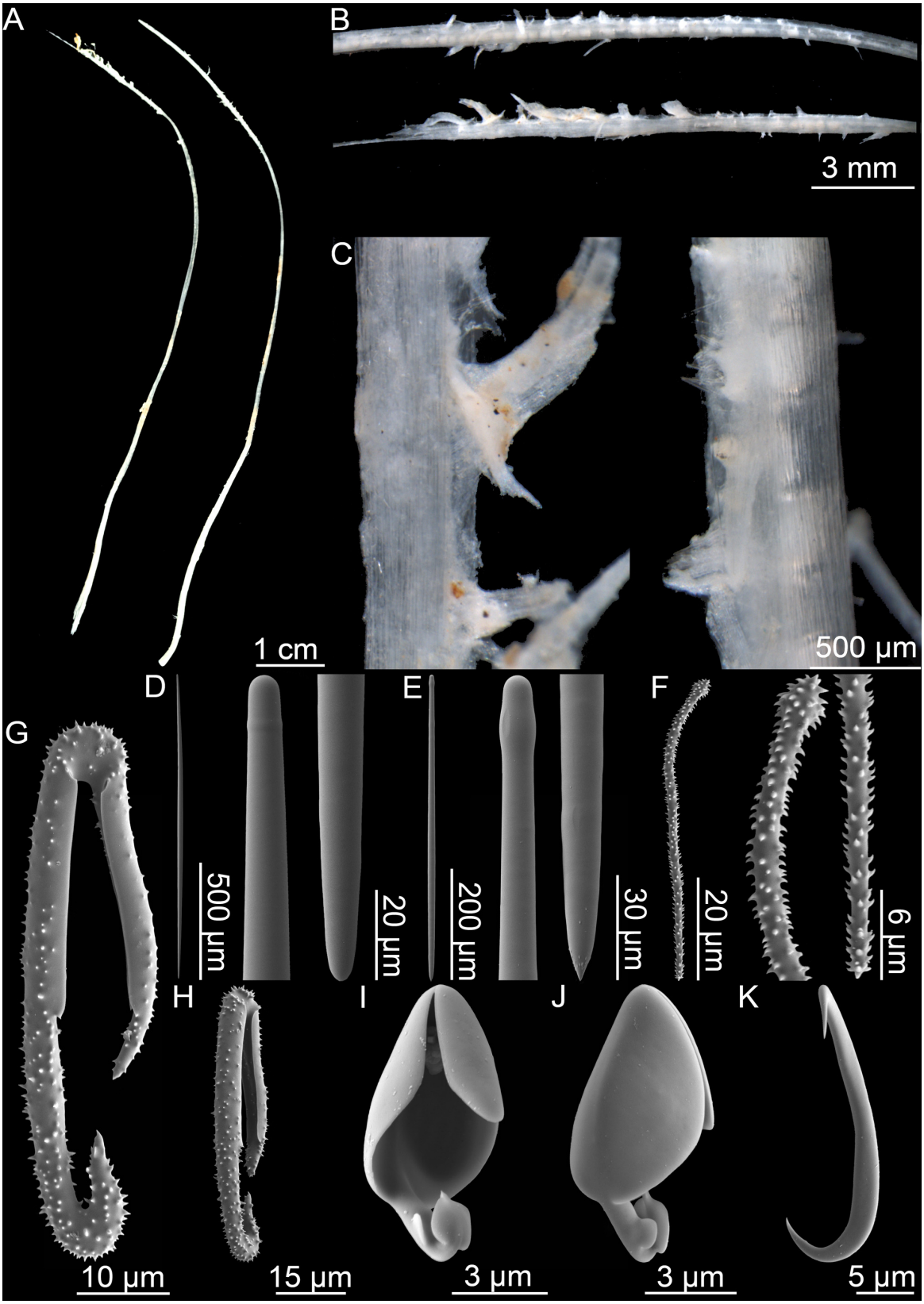

FIGURE 4. *Asbestopluma caribica* **sp. nov.** A) The holotype (left) and paratype (right), B) detail of the filament-bearing upper stem, C) filaments and stem detail, D) mycalostyle, E) subtylostyle, F) acanthotylostyle, G–H) anisocercichela side and back views, I–J) palmate anisochela front and back views, K) sigmancistra.

Description. There are two specimens of this sponge, designated here as the holotype and paratype. Both are fine, single stems with some abrasive damage from collection. The holotype is 83 mm tall, and the paratype is 109 mm tall. Both stems are divided into a bare lower part and filament-bearing upper part. The filament-bearing part is 21 mm and 27 mm in the holotype and paratype respectively. The stems are around 1 mm in diameter at the basal end, gradually diminishing to 0.5 mm in diameter before expanding back to around 1 mm in diameter at the filament-bearing portion. The upper parts of both stems are translucent to white, while the lower stems, due to a very thin cover of fine sediment, are partly light brown. The lower ends of both stems are broken. Filaments are found in two opposite rows spaced approximately every 1 mm. They are in almost all cases reduced to stumps <1 mm long and are probably damaged (Fig. 4A–B).

TABLE 1. Individual spicule measurements from the *Asbestopluma (A.) caribica* **sp. nov.** holotype and paratype.

Specimen	Holotype USNM 30433	Paratype USNM 1417730
Mycalostyles	990–(1162)–1290 x 20–(26)–33	1066–(1227)–1426 x 18–(21)–24
Subtylostyles	320–(571)–660 x 8–(12)–14	327–(528)–645 x 9–(12)–14
Acanthotylostyles	86–(115)–194	74–(114)–171
Anisocercichelae	52–(60)–68	60–(67)–74
Palmate anisochelae	9–(10)–11	8–(10)–12
Sigmancistras	24–(25)–28	19–(27)–34

Skeleton. The stem is made up of longitudinally arranged mycalostyles with apical tips. The skeleton of the filaments is anchored perpendicularly into the stem, pointing slightly upwards, and is made up of subtylostyles (Fig. 4C). Microscleres are found at the stem surface, with anisocercichelae confined to the filament-bearing part. The acanthotylostyles are found at the surface of the basal part of the stem.

Spicules. Mycalostyles, straight and fusiform, 990–(1194)–1426 µm long and 18–(23)–33 µm wide (Fig. 4D).

Subtylostyles, straight and slightly fusiform, with faint, slightly elongated tyle, 320–(550)–660 µm long, 8–(12)–14 µm wide (Fig. 4E).

Acanthotylostyles, curved, in the basal stem sheath, 74–(114)–194 µm long (Fig. 4F)

Anisocercichelae, with weakly arched shafts and one central extension tooth or extension in each end, with rudimentary alae or fimbria-like structures in the upper end and covered with minute spines. The spines are not clearly visible using a light microscope. The upper edge is about two thirds of the total length and the lower edge is about 20% of total length. In the upper stem and filaments, 52–(64)–74 µm (Fig. 4G–H).

Palmate chelae, with strongly arched shafts and alae 80% of the total length of the spicule, 8–(10)–12 µm (Fig. 4I–J).

Sigmancistras, straight or contorted, with the concave edge flattened, 19–(26)–34 µm (Fig. 4K).

Remarks. The spicule complement is mostly typical for *Asbestopluma*, with one category each of mycalostyle and subtylostyle, basal stem acanthotylostyles, palmate anisochelae and sigmancistras. The major diagnostic character feature of *A. (A.) caribica* **sp. nov.** is that the alae of the larger type of palmate anisochela common in the genus have been reduced, accentuating a long projection at either end, and featuring minute spines. Our interpretation is that this spicule represents a transformation of a palmate anisochela in a probably separate, but analogous event to the transformation from isochela or abyssochela to cercichela in *Cercicladia australis* Ríos, Kelly & Vacelet, 2011. Thus, we have chosen to use the term anisocercichela here.

The only other *Asbestopluma* known from the area is *Asbestopluma (A.) gracilior* (Schmidt, 1870), which has a stalked, ovoid body, lacks the large category of anisochela, and was collected at ~600 m rather than 4000 m as is the case with *A. (A.) caribica*. The pennate morphology of *A. (A.) caribica* is common in the genus, as is the general features of its spicule complement, but the unique presence of anisocercichelae makes it difficult to identify particular close relatives.

Genus *Chondrocladia* Thomson, 1873

Diagnosis. Cladorhizidae with anchorate isochelae (from Lee, Reiswig, Austin, & Lundsten, 2012).

Subgenus *Chondrocladia* Thomson, 1873

Diagnosis. *Chondrocladia* without a layer of special spicules (spear-like tylostyles or trochirhabds), lacking special rostriform (snoutlike) subtylostyles in filaments or terminal balls, and without planar vanes formed of evenly spaced upright branches (from Lee *et al.*, 2012).

***Chondrocladia (Chondrocladia) verticillata* Topsent, 1920**
(Figure 5–7; Table 2)

Original description. *Chondrocladia verticillata* Topsent, 1920:12.

Synonoms and citations. *Cladorhiza concrescens* in part (Schmidt, 1880:83); *Chondrocladia verticillata* (Topsent, 1930:430)

Material examined. U.S. Coast Survey, str. "Blake", st. 162 Ag, ZMBN 39 (Guadeloupe, 1879–01–19, 16°02.67'N, 061°50.47'W, 1342 m). This specimen, probably sent to the Bergen Museum by Schmidt, is most likely part of the material given as "Grenada, 533 bis 734 Faden" in the original description of *Chondrocladia (C.) concrescens* (Schmidt, 1880). The closest matches to this information in the Blake station list are the stations 161 Ag and 162 Ag, given as off Guadeloupe, at 583 and 734 fathoms respectively (Smith & Rathbun, 1888), and presumably there has been a misattribution to Grenada as well as a transcription error in the depth of station 161. This is corroborated by the label of specimen ZMBN 39, which states the collection locality as Guadeloupe. U.S. Coast Survey, str. "Blake", st. 163 Ag, USNM 975 (Guadeloupe, 1879–01–20, 16°03'10"N, 061°52'20"W, 1406 m). R/V "Alaminos" 65A, st. 65A9–2, USNM 31180 (Between Florida and Cuba, 1965–07–02, 24°00'N, 081°00'W, 1000 m). *Kraken 2* ROV, specimen HBOM 003:01095 (Florida, south of Pulley Ridge, 2011–09–19, 24°39.71'N, 083°55.08'W, 779 m).

Comparative material examined. *Chondrocladia (C.) gigantea* (Hansen, 1885); *C. (C.) grandis* (Verrill, 1879); *C. (C.) michaelsarsi* Arnesen, 1920; *C. (C.) robertballardi* Cristobo, Rios, Pomponi & Xavier, 2015; *C. (C.) virgata* Thomson, 1873.

Diagnosis. Erect *Chondrocladia* consisting of a single straight stem. The upper part of the stem contains node-like enlargements at regular intervals from which branches issue in each direction from the stem, typically in groups of four per node. Branches have terminal swellings. Megascleres are two categories of mycalostyles and acanthostyles; microscleres are larger anchorate anisochelae in the range of 41–(65)–78 μm, smaller anchorate anisochelae in the range of 13–(18)–34 μm and sigmas in the range of 16–(20)–27 μm.

Description. The examined specimens all have a similar morphology consisting of an erect, single, and straight cylindrical stem carrying lateral projections except for a short lower portion at the base. Specimens are all fragments, lacking either the basal or top part. The largest and best preserved specimen (HBOM 003:01095) is 19.5 cm long (25 cm at time of collection before removal of part of the specimen for subsampling). The smallest fragment is 4 cm long. The lower part of the stem, up to 6 cm long in fragment USNM 975, is 2–4 mm in diameter and without projections. The main part of the stem is slightly wider, 3–6 mm in diameter, and has numerous nodular swellings at regular intervals spaced 5–10 mm apart serving as attachment for the projections. The projections are up to 40 mm long, but more typically 20 to 25 mm in length, and are 1 mm in diameter. There are four projections per node equally distributed every 90° around the stem, with the projections of adjacent nodes offset about 45°. The projections terminate in swellings that are inflated *in situ*, but are deflated in preserved specimens. The main stem is mostly covered in a soft outer layer coated with fine sediment particles also present at the base of the processes, creating a sleeve-like transition. Specimen USNM 31180 retains a partial base, showing that the sponge is connected to the substrate by splitting off the basal stem into several root-like processes. Color in ethanol ranges from white to light brown (Fig. 5A–H).

Skeleton. The core skeleton of the main stem is made up of easily visible fibers of mycalostyles in a slightly spiraling pattern reminiscent of a rope, though this torsion is less pronounced than in other *Chondrocladia* species such as *C. (C.) gigantea*. The outer layer of the lower stem is soft, easily detaches from the central stem, and contains subtly spined acanthostyles. The outer layer of the upper stem is firmer. Between the core stem and the outer layer there is a less dense lacunose layer containing only small amounts of megascleres and containing longitudinal canals, parts of the modified aquiferous system present in the sponge. The skeleton of the branch

processes is made up of tightly packed mycalostyles and originates in the central part of the main stem (Fig. 6A–D). Microscleres are found throughout the outer layer of the stem and branches.

Spicules. Mycalostyles 1, straight, fusiform, 728–(1606)–2815 µm long, 13–(27)–38 µm wide. Most common in the branch processes rather than the central stem, but present in both locations (Fig. 6E).

Mycalostyles 2, straight or curved, making up the main part of the central stem, 420–(589)–1240 µm long, 9–(15)–27 µm wide (Fig. 6F).

TABLE 2. Spicule size comparison between *Chondrocladia* (*C.*) *verticillata* and *C.* (*C.*) *concrescens*.

	Mycalostyles 1	Mycalostyles 2	Acanthostyles	Anchorate isochelae 1	Anchorate isochelae 2	Sigmas
Chondrocladia (C.) verticillata						
Topsent, 1920/1930	No measurements given	No measurements given	370–450 x 3–5	73–80 / 60–74, 6 (7) teeth	21–25, 5–6 teeth	17–30, sparse
This article						
ZMBN 39	728–(1269)–2258 x 16–(25)–36	449–(543)–674 x 10–(16)–18	192–(236)–296	55–(62)–68	13–(15)–18	17–(19)–23 (and 47–(58)–68)
USNM 975	1407–(2107)–2815 x 27–(33)–38	440–(786)–1259 x 9–(17)–31	260–(376)–500	58–(61)–66	13–(14)–17	16–(20)–25
USNM 31180	1432–(2022)–2346 x 20–(27)–34	420–(635)–1240 x 12–(17)–27	234–(308)–355	66–(70)–75	16–(18)–20	16–(18)–22
HBOM 003:01095	1374–(1680)–1900 x 25–(29)–33	447–(664)–1044 x 10–(16)–23	256–(313)–383	41–(68)–78	16–(26)–34	18–(22)–27
Total	728–1606–2815 x 13–(27)–38	420–(589)–1240 x 9–(15)–27	192–(310)–500	41–(65)–78, 6 (7) teeth	13–(18)–34, 6 (5) teeth	16–(20)–27
Chondrocladia (C.) concrescens						
Schmidt, 1880	No measurements given	No measurements given	Not mentioned	71–120, 6 teeth	29–31 long teeth	Not mentioned
Topsent, 1920/1930	No measurements given	No measurements given	No cover layer in examined specimen	110–130, 6 teeth	27–40, 4–6 long teeth	69–97

Acanthostyles, curved, with very fine knobs or spines that might be difficult to see properly in some specimens, 192–(310)–500 µm. Associated with the soft outer layer of the lower stem and basal part of branches (Fig. 6G).

Anchorate isochelae 1, numerous, with a curved shaft, usually six, sometimes seven teeth in each end and fimbriae. Teeth less than 20% of total spicule length, fimbriae around twice the length of the teeth, 41–(65)–78 µm (Fig. 6H).

Anchorate isochelae 2, less numerous than the larger kind, but not uncommon, with a strongly curved shaft, usually six, sometimes five teeth in each end. The points of the teeth are modified into claw-like structures. Fimbriae are rudimentary. Teeth around 25% of total spicule length, 13–(18)–34 µm (Fig. 6I).

Sigmas, common, stout, with a somewhat uneven curvature and terminal points bent slightly inwards, 16–(20)–27 µm (Fig. 6J). In specimen ZMBN 39 a small number of a second type of sigma was also encountered: 47–(58)–68 µm, possibly contamination.

Molecular sequence. A COI extended barcode (1215 bp) and partial 28S rDNA (C1–D2, 771 bp) of specimen HBOM 003:01095 has been uploaded to GenBank with accession numbers KU950333 (COI) and KU950334 (28S rDNA).

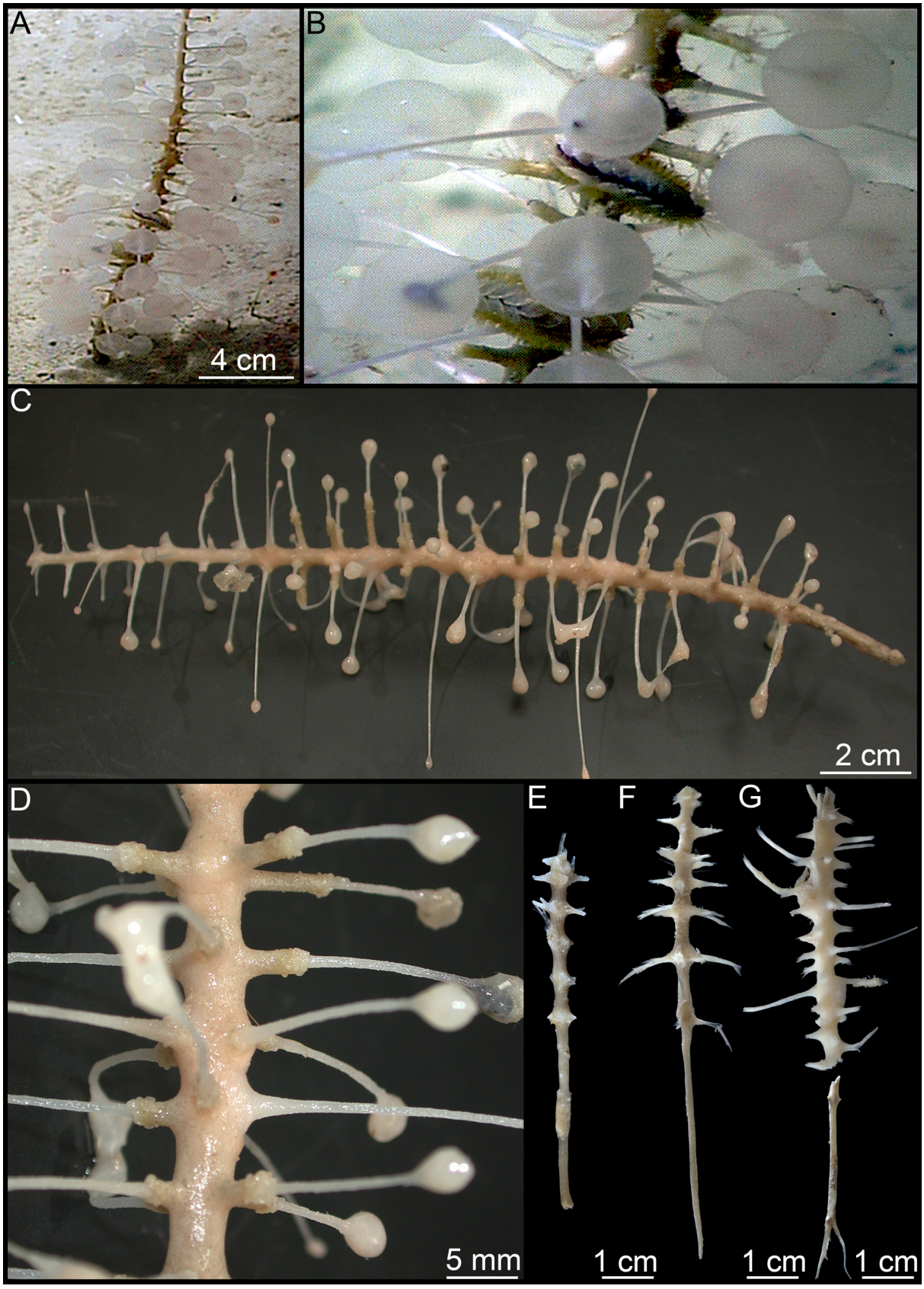

FIGURE 5. *Chondrocladia* (*Chondrocladia*) *verticillata*. A–B) In situ pictures of specimen HBOM 003:01095, C) specimen HBOM 003:01095, D) stem detail with branches from specimen HBOM 003:01095, E) specimen ZMBN 39 ("Blake" st. 161 Ag, Guadeloupe), F) specimen USNM 975 "Blake" st. 163 Ag, Guadeloupe), G) specimen USNM 31180 ("Alaminos" st 65A9–2, Between Florida and Cuba).

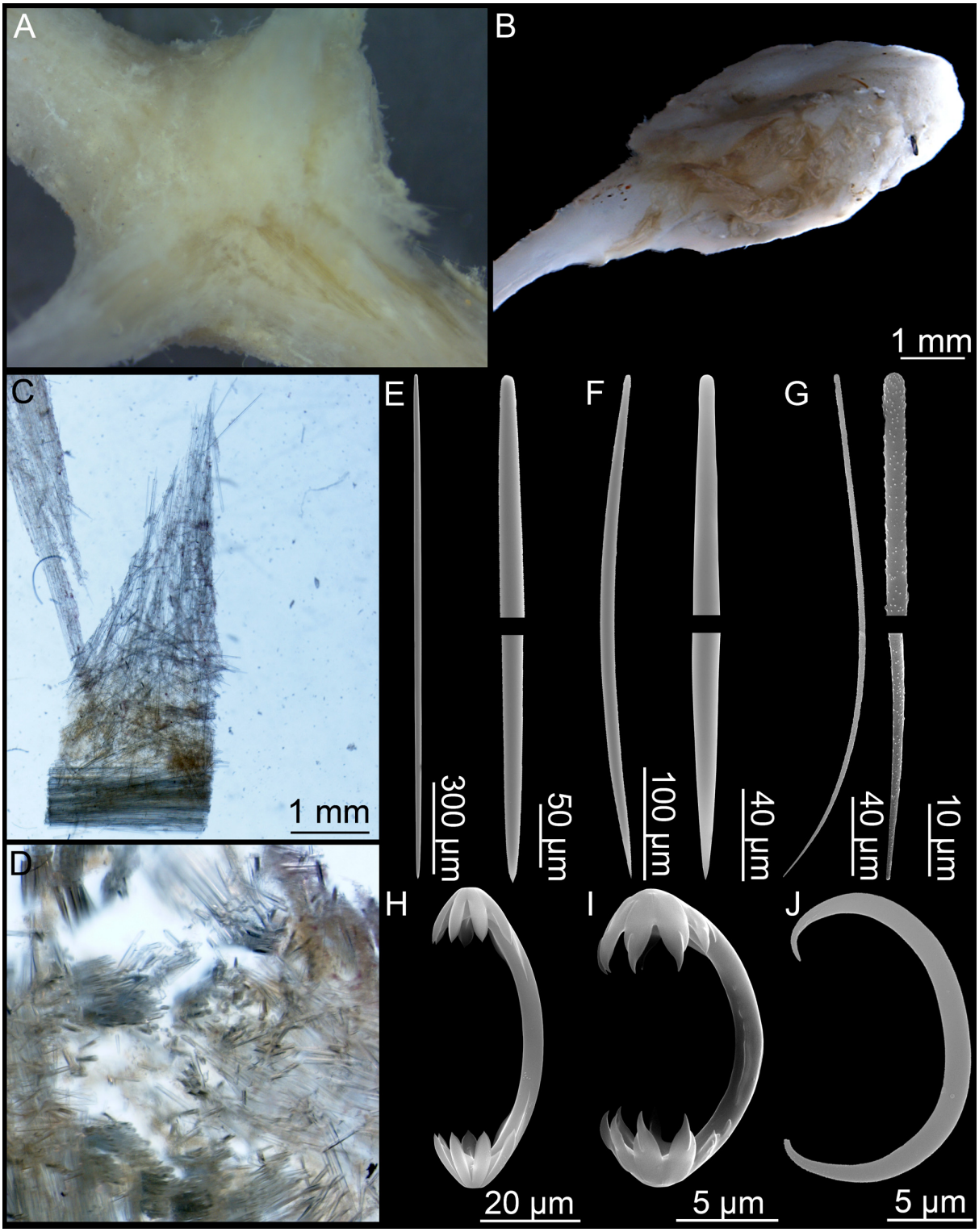

FIGURE 6. *Chondrocladia* (*Chondrocladia*) *verticillata*. A) Node detail from USNM 975, B) terminal branch swelling from HBOM 003:01095, C) longitudinal section of stem and base of branch from USNM 31180, D) cross section of stem from USNM 31180, E) mycalostyle 1, F) mycalostyle 2, G) acanthostyles, H) anchorate isochela 1, I) anchorate isochela 2, J) sigma. Spicule SEM images from specimen ZMBN 39.

Remarks. From its general morphology, *Chondrocladia (C.) verticillata* is a close relative to *C. (C.) concrescens* Schmidt, 1880, also originally described from the Caribbean. As they are mentioned specifically by Schmidt, specimens from "Blake" stations 41, 130, 161 and 162 Ag should be considered syntypes of *C. (C.) concrescens*, however, the specimen from station 162 Ag examined here (as well as a specimen from 163 Ag not

mentioned by Schmidt) is *C. (C.) verticillata*. As it is, the only specimen certain to be *C. (C.) concrescens* is the specimen or specimens actually used by Schmidt for his spicule measurements (clearly not including all listed syntypes) and the subsample examined by Topsent (1920), which lacks collection information. The status of the remaining three syntype locations is unknown, and the specific distributions of *C. (C.) concrescens* and *C. (C.) verticillata* are thus not known, though it can be established that the material mentioned by Schmidt contains both species. The identification of "*concrescens*-type" *Chondrocladia* is difficult owing to the uncertainties in the amount of variation of the spicules of this species (Vacelet, 2006), and several Pacific specimens have been attributed to *C. (C.) concrescens* (Koltun, 1970; Lévi, 1993; Ridley & Dendy, 1886, 1887), probably incorrectly (*cf.* Topsent, 1930; Vacelet, 2006).

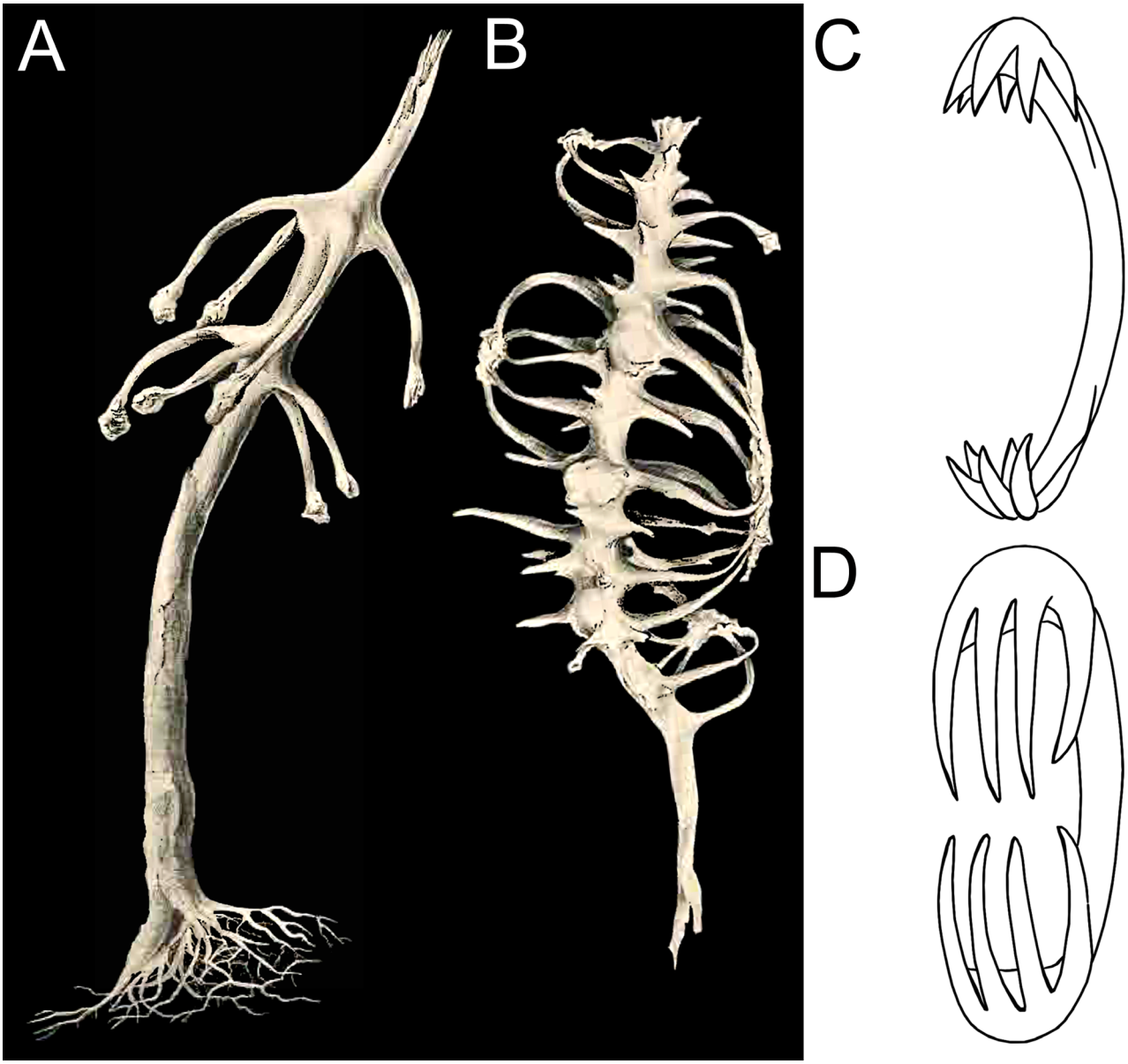

FIGURE 7. *Chondrocladia* (*Chondrocladia*) *concrescens*. (A–B) Facsimile from Schmidt (1880) Pl. X, Fig. 8–9 showing two specimens identified as *C.* (*C.*) *concrescens*. Possibly (B) is *C.* (*C.*) *verticillata*. (C–D) Re-drawing of spicule morphology of *C.* (*C.*) *concrescens* from Topsent (1920) Fig. 3 showing the long teeth of the smaller type of chela (D).

While all specimens examined here proved to be *C. (C.) verticillata*, there are clear differences between the characters across these specimens and *C. (C.) concrescens* as described by both Schmidt (1880) and Topsent (1920), and there is no reason to doubt that Topsent did a thorough investigation on the differences between *C. (C.) concrescens* and *C. (C.) verticillata* when erecting the latter species: In both the original description by Schmidt and the following re-examination by Topsent, the larger category of isochela is significantly larger in *C. (C.)*

concrescens compared to *C. (C.) verticillata*, as are the sigmas. Another clear difference regards the morphology of the smaller type of isochela: Both Schmidt and Topsent emphasize long, fine teeth, where the upper teeth almost touch the lower in *C. (C.) concrescens* (Fig. 7), while this character is not present at all in the specimens identified as *C. (C.) verticillata*. Thus *C. (C.) verticillata* is by all appearances a valid species distinct from *C. (C.) concrescens*. It should be noted that of the two specimens illustrated by Schmidt (1880) (reproduced here, Fig. 7), the spacing of the projections is quite different, which could indicate that one of them (Fig. 7A) is *C. (C.) concrescens* while the other (Fig. 7B) is *C. (C.) verticillata*.

The results of the phylogenetic analysis of specimen HBOM 003:01095 shows that *C. (C.) verticillata* is most closely related to two as of yet undescribed species of *Chondrocladia* from Patagonia (species "A", SW Atlantic) and the New Zealand EEZ (species "C") (Fig. 8). More distant relatives within the same clade include the Northern Atlantic and Arctic species *C. (C.) gigantea* (Hansen, 1885) and *C. (C.) robertballardi* Cristobo, Rios, Pomponi & Xavier, 2015. These results are in general agreement with morphological characters, as all the related species have a roughly similar habit consisting of a single or branching stem with numerous branches along the upper part of the axis, as opposed to other members of subgenus *Chondrocladia* which typically have a pedunculate, spherical morphology.

Related species. *Chondrocladia (Chondrocladia) concrescens* Schmidt, 1880; *C. (C.) concrescens sensu* Ridley & Dendy, 1886 (= *C (C.)* "*challengeri*", *cf.* Topsent, 1920; 1930); *C. (C.) gigantea* Hansen, 1885; *C. (C.) grandis* (Verrill, 1879); *C. (C.) michaelsarsi* Arnesen, 1920; *C. (C.) robertballardi* Cristobo, Rios, Pomponi & Xavier, 2015; *C. (C.) virgata* Thomson, 1873; *C. (C.) yatsui* Topsent, 1930.

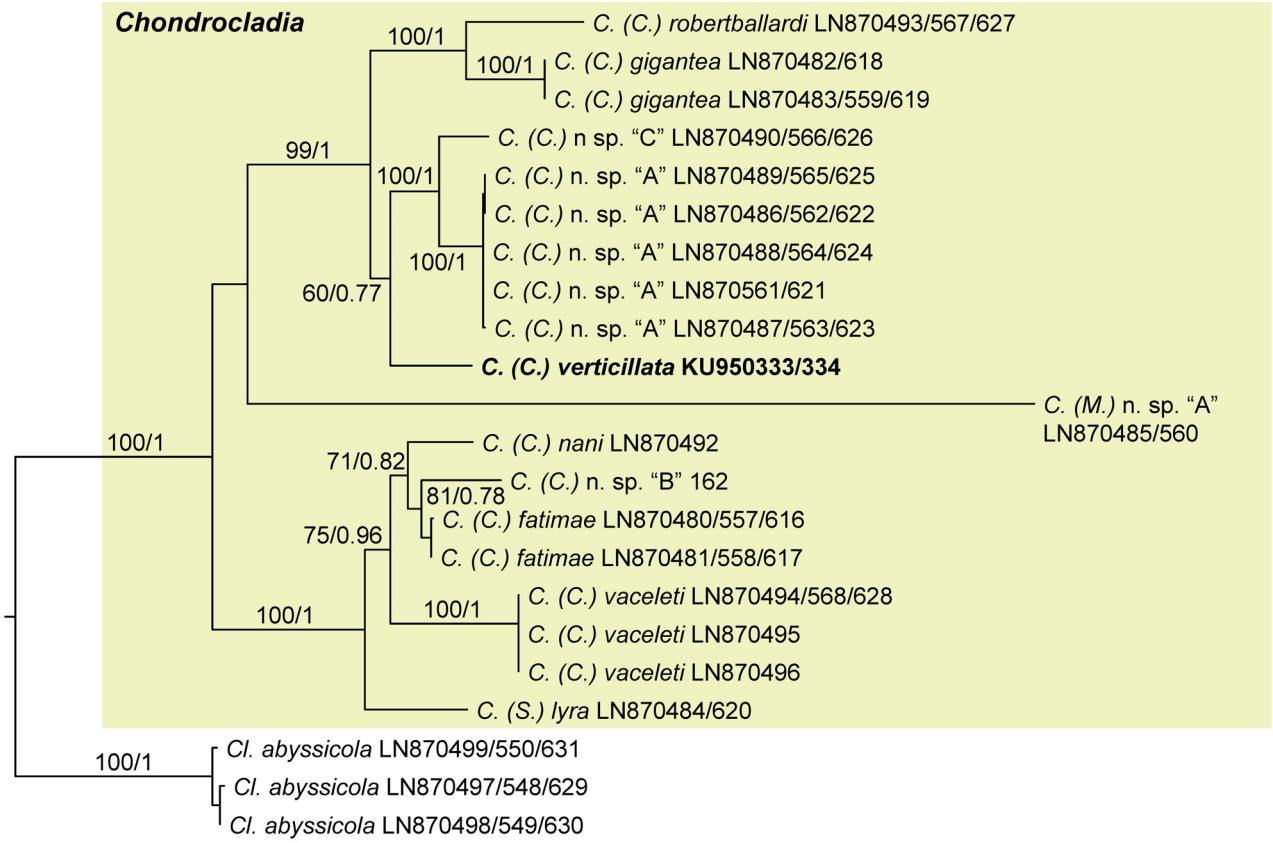

FIGURE 8. Maximum likelihood (ML) consensus tree from the phylogenetic analysis of a concatenated dataset of partial 28S rDNA, COI and ALG11 for *Chondrocladia* spp. from GenBank and *C. (C.) verticillata* specimen HBOM 003:01095 (bold). Accession numbers are given after species names. ML bootstrap support values and Bayesian posterior probabilities are indicated for clades > 50/0.5 for both analyses.

TABLE 3. List of records of Cladorhizidae from the Caribbean Sea and adjacent Atlantic Ocean. Spicule measurements are an aggregation of those reported by the listed sources.

	Area	Depth	Morphology	Spicules						Source(s)
Abyssocladia				**Mycalostyles**	**Mycalostyles / subtylostyles**	**Strongyles**	**Arcuate isochelae**	**Sigmancistras**		
Abyssocladia polycephalus sp. nov.	Muir Seamount, NE of Bermuda.	2829 m	Central stem and branches each with a disc–shaped body.	720–(933)–1070 x 14–(17)–22	430–(686)–960 x 5–(10)–13	380–(568)–780 x 15–(18)–22	28–(43)–50	9–(10)–11		This article
Asbestopluma				**Mycalostyles**	**Subtylostyles**	**Acantho–tylostyles**	**Anisocercichelae**	**Palmate anisochelae**	**Sigmancistras**	
Asbestopluma (A.) caribica sp. nov.	Beata Ridge, Caribbean Sea.	4007 m	Erect single stem with two opposite rows of filaments.	990–(1194)–1426 x 18–(23)–33	320–(550)–660 x 8–(12)–14	74–(114)–194	52–(64)–74	8–(10)–12	19–(26)–34	This article
Asbestopluma (A.) gracilior (Schmidt, 1870)	Probably between Florida and Cuba.	585–640 m	Pedunculate with ovate main body.	900–1400 x 20–25	300–600 x 2–4	90–120 x 1–3		10–12	20–25	(Hajdu & Vacelet, 2002; Schmidt, 1870)
Chondrocladia				**Mycalostyles**	**Mycalostyles**	**Acanthostyles**	**Anchorate isochelae**	**Anchorate isochelae**	**Sigmas**	
Chondrocladia (C.) amphactis Schmidt, 1880	East of Barbados.	527 m	Pedunculate spherical boy with lateral branches	665–1075 x 6–25			50–55, 3 teeth		46	(Schmidt, 1880; Topsent, 1930)
Chondrocladia (C.) concrescens Schmidt, 1880	Guadeloupe? St. Croix? Between Florida and Cuba?	825–1573 m?	Erect single stem with branches.	Present		Unknown	71–130, 6 teeth	27–40, 4–6 long teeth	69–97	(Schmidt, 1880; Topsent, 1920, 1930)
Chondrocladia (C.) verticillata Topsent, 1920	Guadeloupe, between Florida and Cuba.	1000–1472 m	Erect single stem with branches.	728–(1606)–2815 x 13–(27)–38	420–(589)–1240 x 9–(15)–27	192–(315)–680	41–(65)–78, 6 (7) teeth	13–(18)–34, 6 (5) teeth	16–(20)–27	(Topsent, 1920, 1930); this article

……*continued on the next page*

TABLE 3. (Continued)

	Area	Depth	Morphology	Spicules						Source(s)
Cladorhiza				**Mycalostyles**			**Anchorate anisochelae**	**Sigmas**	**Sigman–cistras**	
Cladorhiza methanophila Vacelet & Boury-Esnault, 2002	East of Barbados.	1447–4943 m	Arbuscular.	310–680 x 5–20			20–25, 5 teeth	100–140	35–48	(Vacelet & Boury-Esnault, 2002), unpublished material
Eucheliplum				**Subtylostyles**			**Placochelae**	**Sigmancistras**		
Eucheliplum congeri de Laubenfels, 1936	Between Dry Tortugas and Cuba.	1047 m	Stem expanding into conical apex with filaments.	553–1004 x 9–13			13–15	18–21		(de Laubenfels, 1936)
Lycopodina				**Styles / subtylostyles**	**Subtylostyles**	**Tapering subtylostyles**	**Arcuate anisochelae**	**Forceps spicules**		
Lycopodina infundibulum (Levinsen, 1887)*	South of Barbados.	1947 m	Pedunculated cup.	280–570 x 5–8	132–274 x 3–6	450–910 x 3–6	16–(18.5)–20	Present in species, not present in specimen		(Hestetun *et al.*, 2015)

*This species is also found in the North Atlantic and Arctic. Data given is for the Barbados specimen only.

Discussion

Abyssocladia polycephalus **sp. nov.** described here was collected at approximately 3000 m depth on one of a series of isolated seamounts NE off Bermuda. Two other *Abyssocladia* spp. from the Atlantic have been found at lower bathyal to abyssal depths on the Mid-Atlantic Ridge (Hestetun *et al.*, 2015), while the third known *Abyssocladia* species from the Atlantic was collected in shallower waters (~1130 m) off the Southern coast of Brazil (Lopes & Hajdu, 2014). This shows that while the majority of described species in the genus are still from the Pacific, the genus is present in the Atlantic as well at both upper bathyal and lower bathyal and abyssal depths.

Asbestopluma (Asbestopluma) caribica **sp. nov.**, *Chondrocladia (Chondrocladia) verticillata* Topsent, 1920, and *C. (C.) concrescens* Schmidt, 1880 have been reported from the Caribbean only, and no species have been reported on the United States coastal shelf in the area between New England to Florida. While this could be because of lack of sampling, the species described from the Caribbean are clearly different than species reported from Eastern Canada and New England. This mirrors the situation in the Eastern Atlantic where, with a couple of exceptions such as *Cladorhiza abyssicola* Sars, 1872 and *Lycopodina infundibulum* (Levinsen, 1887), the species reported to the south of Great Britain are also different than the North Atlantic and Arctic fauna.

Given the lack of species overlap to other regions it is clear that the Caribbean contains an endemic cladorhizid fauna (Table 3). Several recent publications (e.g. Hestetun *et al.*, 2016a; Kelly & Vacelet, 2011; Lopes & Hajdu, 2014; Vacelet, 2006; Vacelet, Kelly, & Schlacher-Hoenlinger, 2009) have shown that examination of material from previously poorly known areas reveal a high diversity of cladorhizid species. Thus it is probable that further examination of the Caribbean sponge fauna will yield additional species.

Acknowledgements

We would like to thank Eric Lazo-Wasem and Lourdes Rojas from the Yale Peabody Museum as well as Klaus Rützler, William Moser and Paul Greenhall from the National Museum of Natural History for allowing us to examine cladorhizid specimens from the YPM and USNM museum collections. We would like to thank Rob van Soest for valuable input regarding the naming of the anisocercichela type spicule. We would also like to thank Paco Cárdenas for input regarding the unidentified *Geodia* from which *Abyssocladia polycephalus* was retrieved. *Chondrocladia (C.) verticillata* was collected during an expedition conducted by the Cooperative Institute for Ocean Exploration, Research, and Technology (HBOI-FAU), aboard the NOAA ship Nancy Foster and with the ROV *Kraken 2* (University of Connecticut).

Funding. JTH and HTR were the supported by the Research Council of Norway (through contract number 179560) and the Norwegian Academy of Science and Letters. Funding for collection of *Chondrocladia (C.) verticillata* from Florida was provided by the National Oceanic and Atmospheric Administration (NOAA), Office of Ocean Exploration and Research (grant #NA09OAR4320073), the Deep Sea Coral Research and Technology Program, and the Office of Marine and Aviation Operations.

References

Arnesen, E. (1920) Spongia. *In: Report on the Scientific Results of the "Michael Sars" North Atlantic Deep-Sea Expedition, 1910*. John Grieg, Bergen, pp. 1–29.

Boury-Esnault, N. & Rützler, K. (1997) *Thesaurus of Sponge Morphology. Smithsonian Contributions to Zoology No 596*. Smithsonian Institution Press, Washington, D.C., 55 pp.

Cristobo, F.J., Ríos, P., Pomponi, S.A. & Xavier, J.R. (2015) A new carnivorous sponge, *Chondrocladia robertballardi* sp. nov. (Porifera: Cladorhizidae) from two north–east Atlantic seamounts. *Journal of the Marine Biological Association of the United Kingdom*, 95, 1345–1352.
http://dx.doi.org/10.1017/S0025315414001325

de Laubenfels, M.W. (1936) *A Discussion of the Sponge Fauna of the Dry Tortugas in Particular and the West Indies in General, with Material for a Revision of the Families and Orders of the Porifera. Vol. 30. Carnegie Institute of Washington Publication 467*. Carnegie institution of Washington, Washington, 225 pp.

Hajdu, E. & Vacelet, J. (2002) Family Cladorhizidae Dendy, 1922. *In:* Hooper, J.N. & van Soest, R.W. (Eds.), *Systema Porifera. A guide to the classification of sponges*. Kluwer Academic/Plenum, New York, Boston, Dordrecht, London,

Moscow, pp. 636–641.
http://dx.doi.org/10.1007/978-1-4615-0747-5_68
Hansen, G.A. (1885) Spongiadæ. *The Norwegian North-Atlantic Expedition 1876–1878*, 1885, 1–26, pls. I–VII.
Hestetun, J., Fourt, M., Vacelet, J., Boury-Esnault, N. & Rapp, H. (2015) Cladorhizidae (Porifera, Demospongiae, Poecilosclerida) of the deep Atlantic collected during Ifremer cruises, with a biogeographic overview of the Atlantic species. *Journal of the Marine Biological Association of the United Kingdom*, 95, 1311–1342.
http://dx.doi.org/10.1017/S0025315413001100
Hestetun, J.T., Rapp, H.T. & Xavier, J. (2016a) Carnivorous sponges (Porifera, Cladorhizidae) from the Southwest Indian Ocean Ridge seamounts. *Deep Sea Research Part II: Topical Studies in Oceanography*. [in press]
http://dx.doi.org/10.1016/j.dsr2.2016.03.004
Hestetun, J.T., Vacelet, J., Boury-Esnault, N., Borchiellini, C., Kelly, M., Ríos, P., Cristobo, J. & Rapp, H.T. (2016b) The systematics of carnivorous sponges. *Molecular phylogenetics and evolution*, 94, 327–345.
http://dx.doi.org/10.1016/j.ympev.2015.08.022
Kelly, M. & Vacelet, J. (2011) Three new remarkable carnivorous sponges (Porifera, Cladorhizidae) from deep New Zealand and Australian (Macquarie Island) waters. *Zootaxa*, 1976, 55–68.
Koltun, V.M. (1970) Sponge fauna of the northwestern Pacific from the shallows to the hadal depths. *In:* Bogorov, V. (Ed.), *Fauna of the Kurile–Kamchatka Trench and its environment. Institute of Oceanology of the Academy of Sciences of the U.S.S.R. [English translation, 1972]*. Israel Program for Scientific Translations Ltd., Jerusalem, pp. 1–372, pls. I–VIII.
Lankester, E.R. (1882) Dredging in the Norwegian Fjords. *Nature*, 1882, 478–479.
http://dx.doi.org/10.1038/026478a0
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.
http://dx.doi.org/10.1111/Ivb.12001
Lévi, C. (1993) Porifera Demospongiae: Spongiaires bathyaux de Nouvelle-Calédonie, récoltés par le «Jean Charcot» Campagne BIOCAL, 1985. *Mémoires du Muséum national d'histoire naturelle*, 158, 9–87.
Levinsen, G.M.R. (1887) Kara-Havets Svampe (Porifera). *In: Dijmphna-Togtets zoologisk-botaniske Udbytte*, pp. 339–372, pls XXIX–XXXI.
Lopes, D.A., Bravo, A. & Hajdu, E. (2011) New carnivorous sponges (Cladorhizidae: Poecilosclerida: Demospongiae) from off Diego Ramírez Archipelago (south Chile), with comments on taxonomy and biogeography of the family. *Invertebrate Systematics*, 25, 407–443.
http://dx.doi.org/10.1071/is11015
Lopes, D.A. & Hajdu, E. (2014) Carnivorous sponges from deep–sea coral mounds in the Campos Basin (SW Atlantic), with the description of six new species (Cladorhizidae, Poecilosclerida, Demospongiae). *Marine Biology Research*, 10, 329–356.
http://dx.doi.org/10.1080/17451000.2013.797587
Lundbeck, W. (1905) Porifera. (Part II.) Desmacidonidae (pars.). *In: The Danish Ingolf-Expedition. 6 (2)*. BiancoLuno, Copenhagen, pp. 1–219, pls. I–XX.
Ridley, S.O. & Dendy, A. (1886) Preliminary Report on the Monaxonida collected by HMS 'Challenger'. *Annals and Magazine of Natural History*, 5, 325–351, 470–493.
http://dx.doi.org/10.1080/00222938609459998
Ridley, S.O. & Dendy, A. (1887) Report on the Monaxonida collected by H.M.S. 'Challenger' during the years 1873–1876. *Report on the Scientific Results of the Voyage of H.M.S. 'Challenger', 1873–1876*, Zoology 20 (59), pp. i–lxviii + 1–275, pls. I–LI.
Ríos, P., Kelly, M. & Vacelet, J. (2011) *Cercicladia australis*, a new carnivorous sponge with novel chelae from the Tasman Basin and the Argentine Patagonian Margin (Porifera, Cladorhizidae). *Zootaxa*, 3131 (1), 52–62.
http://dx.doi.org/10.11646/zootaxa.3131.1.3
Sars, G.O. (1872) *On Some Remarkable Forms of Animal Life from the Great Deeps Off the Norwegian Coast. Part 1, partly from posthumous manuscripts of the late professor Dr. Michael Sars. University Program for the 1st half–year 1869*. Brøgger & Christie, Christiania, 244 pp.
Schmidt, O. (1870) *Grundzüge einer Spongien-Fauna des atlantischen Gebietes*. Wilhelm Engelmann, Leipzig, 2 + (iii–iv) + 88 pp., VI pls.
Schmidt, O. (1875) Spongien. *Die Expedition zur physikalisch-chemischen und biologischen Untersuchung der Nordsee im Sommer 1872. Jahresbericht der Commission zur Wissenschaftlichen Untersuchung der Deutschen Meere in Kiel*, 1875, 115–120, pl. I.
Schmidt, O. (1880) Die Spongien des Meerbusen von Mexico (Und des caraibischen Meeres). Heft II. Abtheilung II. Hexactinelliden. Abtheilung III. Tetractinelliden. Monactinelliden und Anhang. Nachträge zu Abtheilung I (Lithistiden). *In: Reports on the dredging under the supervision of Alexander Agassiz, in the Gulf of Mexico, by the USCSS 'Blake'*. Gustav Fischer, Jena, pp. 33–90, pls. V–X.
Smith, S. & Rathbun, R. (1888) *Lists of Dredging Stations in North American Waters from 1867 to 1887 [Extracted from the Annual Report of the Commissioner of Fish and Fisheries for 1886]*. Government Printing Office, Washington, 144 pp.

http://dx.doi.org/10.5962/bhl.title.52030
Thomson, W.C. (1873) *The Depths of the Sea*. Macmillan and Co., London, 686 pp.
Topsent, E. (1901) Spongiaires. *In: Résultats du voyage du S.Y. 'Belgica'en 1897–99 sous le commandement de A. de Gerlache de Gomery. Expédition antarctique belge*, 1901, 1–54, pls. I–VI.
Topsent, E. (1920) Spongiaires du Musée Zoologique de Strasbourg. Monaxonides. *Bulletin de l'Institut océanographique,* 1920, 1–36.
Topsent, E. (1929) Notes sur *Helophloeina stylivarians*, n. g., n. sp., Mycaline à desmes des Canaries. *Bulletin de l'Institut océanographique de Monaco*, 1929, 1–8.
Topsent, E. (1930) *Chondrocladia yatsui* n. sp., de la Baie de Sagami. *Annotationes zoologicae japonenses*, 1930, 421–432.
Vacelet, J. (2006) New carnivorous sponges (Porifera, Poecilosclerida) collected from manned submersibles in the deep Pacific. *Zoological Journal of the Linnean Society*, 148, 553–584.
http://dx.doi.org/10.1111/j.1096-3642.2006.00234.x
Vacelet, J. (2007) Diversity and evolution of deep–sea carnivorous sponges. *Porifera research: biodiversity, innovation and sustainability. Série Livros*, 28, 107–115.
Vacelet, J. & Boury-Esnault, N. (2002) A new species of carnivorous deep–sea sponge (Demospongiae : Cladorhizidae) associated with methanotrophic bacteria. *Cahiers De Biologie Marine*, 43, 141–148.
Vacelet, J., Kelly, M. & Schlacher-Hoenlinger, M. (2009) Two new species of *Chondrocladia* (Demospongiae: Cladorhizidae) with a new spicule type from the deep south Pacific, and a discussion of the genus *Meliiderma*. *Zootaxa*, 2073, 57–68.
Verrill, A.E. (1879) Notice of recent additions to the marine invertebrates of the northeastern coast of America, with descriptions of new genera and species, and critical remarks. *Proceedings of the United States National Museum*, 2, 165–205.
http://dx.doi.org/10.5479/si.00963801.76.165