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

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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
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 = *Euchelipluma*, 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.

**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* Kolton, 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)


**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.

![Asbestopluma caribica sp. nov.](image)

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

**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.

**Synonyms 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.) roberthallardi* 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*.

<table>
<thead>
<tr>
<th>Spicule Type</th>
<th><em>C. (C.) verticillata</em></th>
<th><em>C. (C.) concrescens</em></th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Mycalostyles 1</strong></td>
<td>No measurements given</td>
<td>No measurements given</td>
</tr>
<tr>
<td><strong>Mycalostyles 2</strong></td>
<td>370–450 x 3–5</td>
<td>73–80 / 60–74, 6 (7) teeth</td>
</tr>
<tr>
<td><strong>Acanthostyles</strong></td>
<td>73–80 / 60–74, 6 (7) teeth</td>
<td></td>
</tr>
<tr>
<td><strong>Anchorate isochelae 1</strong></td>
<td>21–25, 5–6 teeth</td>
<td>17–30, sparse</td>
</tr>
<tr>
<td><strong>Anchorate isochelae 2</strong></td>
<td>13–(15)–18</td>
<td>17–(19)–23 (and 47–(58)–68)</td>
</tr>
<tr>
<td><strong>Sigmas</strong></td>
<td>17–(19)–23 (and 47–(58)–68)</td>
<td></td>
</tr>
</tbody>
</table>

**Table Note**: Measurements are given for each type of spicule in the respective specimens.

<table>
<thead>
<tr>
<th>Specimen</th>
<th>Mycalostyles 1</th>
<th>Mycalostyles 2</th>
<th>Acanthostyles</th>
<th>Anchorate isochelae 1</th>
<th>Anchorate isochelae 2</th>
<th>Sigmas</th>
</tr>
</thead>
<tbody>
<tr>
<td>ZMBN 39</td>
<td>728–(1269)–2258 x 16–(25)–36</td>
<td>449–(543)–674 x 10–(16)–18</td>
<td>192–(236)–296</td>
<td>55–(62)–68</td>
<td>13–(15)–18</td>
<td>17–(19)–23 (and 47–(58)–68)</td>
</tr>
<tr>
<td>USNM 975</td>
<td>1407–(2107)–2815 x 27–(33)–38</td>
<td>440–(786)–1259 x 9–(17)–31</td>
<td>260–(376)–500</td>
<td>58–(61)–66</td>
<td>13–(14)–17</td>
<td>16–(20)–25</td>
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<tr>
<td>USNM 31180</td>
<td>1432–(2022)–2346 x 20–(27)–34</td>
<td>420–(635)–1240 x 12–(17)–27</td>
<td>234–(308)–355</td>
<td>66–(70)–75</td>
<td>16–(18)–20</td>
<td>16–(18)–22</td>
</tr>
<tr>
<td>HBOM 003:01095</td>
<td>1374–(1680)–1900 x 25–(29)–33</td>
<td>447–(664)–1044 x 10–(16)–23</td>
<td>256–(313)–383</td>
<td>41–(68)–78</td>
<td>16–(26)–34</td>
<td>18–(22)–27</td>
</tr>
<tr>
<td><strong>Total</strong></td>
<td>728–1606–2815 x 13–(27)–38</td>
<td>420–(589)–1240 x 9–(15)–27</td>
<td>192–(310)–500</td>
<td>41–(65)–78, 6 (7) teeth</td>
<td>13–(18)–34, 6 (5) teeth</td>
<td>16–(20)–27</td>
</tr>
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</table>

**Chondrocladia (C.) concrescens**

<table>
<thead>
<tr>
<th>Spicule Type</th>
<th>No measurements given</th>
<th>No measurements given</th>
<th>Not mentioned</th>
<th>71–120, 6 teeth</th>
<th>29–31 long teeth</th>
<th>Not mentioned</th>
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<tbody>
<tr>
<td><strong>Acanthostyles</strong></td>
<td>Not mentioned</td>
<td>71–120, 6 teeth</td>
<td>29–31 long teeth</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><strong>Anchorate isochelae 1</strong></td>
<td>No cover layer in examined specimen</td>
<td>110–130, 6 teeth</td>
<td>27–40, 4–6 long teeth</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><strong>Anchorate isochelae 2</strong></td>
<td>No cover layer in examined specimen</td>
<td>110–130, 6 teeth</td>
<td>27–40, 4–6 long teeth</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><strong>Sigmas</strong></td>
<td>69–97</td>
<td>69–97</td>
<td>69–97</td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

**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.)
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>
<thead>
<tr>
<th>Area</th>
<th>Depth</th>
<th>Morphology</th>
<th>Spicules</th>
<th>Mycalostyles / subtlystoyles</th>
<th>Strongyles</th>
<th>Arcuate isochelae</th>
<th>Sigmancistras</th>
<th>Source(s)</th>
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</thead>
<tbody>
<tr>
<td>Abyssocladiina</td>
<td></td>
<td></td>
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<tr>
<td>Abyssocladiina polycephalus sp. nov.</td>
<td>2829 m</td>
<td>Central stem and branches each with a disc-shaped body.</td>
<td>Mycalo</td>
<td>720–(933)–1070 x 14–(17)–22</td>
<td>380–(568)–780 x 15–(18)–22</td>
<td>28–(43)–50</td>
<td>9–(10)–11</td>
<td>This article</td>
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<tr>
<td><em>Abyssocladiina</em></td>
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<td>Asbestoplasma</td>
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<tr>
<td>Asbestoplasma (A.) caribica sp. nov.</td>
<td>4007 m</td>
<td>Erect single stem with two opposite rows of filaments. Pedunculate with ovate main body.</td>
<td>Mycalostyles</td>
<td>990–(1194)–1426 x 18–(23)–33</td>
<td>320–(550)–660 x 8–(12)–14</td>
<td>74–(114)–194</td>
<td>52–(64)–74</td>
<td>This article</td>
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<tr>
<td>Asbestoplasma (A.) gracilior (Schmidt, 1870)</td>
<td>585–640 m</td>
<td></td>
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<td></td>
<td></td>
<td></td>
<td></td>
<td>(Hajdu &amp; Vacelet, 2002; Schmidt, 1870)</td>
</tr>
<tr>
<td>Chondrocladia</td>
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</tr>
<tr>
<td>Chondrocladia (C.) amphactis Schmidt, 1880</td>
<td>527 m</td>
<td>Pedunculate spherical body with lateral branches.</td>
<td>Mycalostyles</td>
<td>665–1075 x 6–25</td>
<td>Present</td>
<td>Unknown</td>
<td>50–55, 3 teeth</td>
<td>46 (Schmidt, 1880; Topsent, 1930)</td>
</tr>
<tr>
<td>Chondrocladia (C.) concrescens Schmidt, 1880</td>
<td>825–1573 m?</td>
<td>Erect single stem with branches.</td>
<td>Mycalostyles</td>
<td>728–(1606)–2815 x 13–(27)–38</td>
<td>420–(589)–1240 x 9–(15)–27</td>
<td>192–(315)–680</td>
<td>41–(65)–78, 6 (7) teeth</td>
<td>(Schmidt, 1880; Topsent, 1920, 1930)</td>
</tr>
<tr>
<td>Chondrocladia (C.) verticillata Topsent, 1920</td>
<td>1000–1472 m</td>
<td>Erect single stem with branches.</td>
<td>Mycalostyles</td>
<td>728–(1606)–2815 x 13–(27)–38</td>
<td>420–(589)–1240 x 9–(15)–27</td>
<td>192–(315)–680</td>
<td>41–(65)–78, 6 (7) teeth</td>
<td>(Topsent, 1920, 1930; this article)</td>
</tr>
</tbody>
</table>

......continued on the next page
### TABLE 3. (Continued)

<table>
<thead>
<tr>
<th>Area</th>
<th>Depth</th>
<th>Morphology</th>
<th>Spicules</th>
<th>Anchorate anisochelae</th>
<th>Sigma</th>
<th>Sigmancistras</th>
<th>Source(s)</th>
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<tbody>
<tr>
<td><strong>Cladorhiza</strong></td>
<td></td>
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<td></td>
<td></td>
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<tr>
<td>Euchelipluma</td>
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</tr>
<tr>
<td>Euchelipluma congeri de Laubenfels, 1936</td>
<td>1047 m</td>
<td>Stem expanding into conical apex with filaments.</td>
<td>Subtylostyles 553–1004 x 9–13</td>
<td>Placochele 13–15</td>
<td>18–21</td>
<td></td>
<td>(de Laubenfels, 1936)</td>
</tr>
<tr>
<td>Lycopodina</td>
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<tr>
<td>Lycopodina infundibulum</td>
<td>South of Barbados. 1947 m</td>
<td>Pedunculated cup.</td>
<td>Styles / subtylostyles 280–570 x 5–8</td>
<td>Subtylostyles 132–274 x 3–6</td>
<td>Tapering subtylostyles 450–910 x 3–6</td>
<td>Arcuate anisochelae 16–(18.5)–20</td>
<td>Forceps spicules Present in species, not present in specimen (Hestetun et al., 2015)</td>
</tr>
</tbody>
</table>

*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. 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).

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References


CLADORHIZIDS OF THE CARIBBEAN AND ADJACENT WATERS

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