Systema Porifera: A Guide to the Classification of Sponges, Edited by John N.A. Hooper and Rob W.M. Van Soest

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Family Cladorhizidae Dendy, 1922

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Cladorhizidae Dendy (Demospongiae, Poecilosclerida, Mycalina) are predominantly deep water taxa, encompassing fifteen nominal genera of which only three genera are considered to be valid. Sponges usually small, symmetrical, possessing diagonal, radiating supporting processes and basal root adaptations for living in soft sediments, with the axial skeleton composed of monactinal or diactinal megascleres from which radiating extra-axial tracts diverge to the ectosome. Microscleres include (an)isochelae, sigmas, forceps or micro(subtylo)styles (microspined, spear-shaped in a few cases). However, the family lacks any remarkable synapomorphy, with characters such as the presence of forceps, unguiferate chelae, sigmancistras, stipitate growth form, deep-water habitat, carnivorous habit and/or lack of an aquiferous system not universal amongst all genera (or at least not yet demonstrated to be so), nor are these features unique to the family. These genera are retained within this family as understood by previous authors.

Keywords: Porifera; Demospongiae; Poecilosclerida; Mycalina; Cladorhizidae; *Asbestopluma*; *Chondrocladia*; *Cladorhiza*.

DEFINITION, DIAGNOSIS, SCOPE

Synonymy

Cladorhizeae Dendy, 1922: 58. Cladorhizidae de Laubenfels, 1936a: 122.

Diagnosis

Sponges usually small, symmetrical, mostly in deep water, with diagonal, radiating supporting processes and basal root adaptations for living in soft sediments. Axial skeleton composed of monactinal or diactinal megascleres, from which radiating extra-axial tracts diverge to the ectosome. Microscleres include (an)isochelae, sigmas, forceps or micro(subtylo)styles (microspined, spear-shaped in a few cases). Considerable reduction to complete loss of the choanocyte layer is known for some species, being associated with an adaptation to carnivory, preying on relatively large food items.

Remarks

A strong synapomorphy is missing for the Cladorhizidae. Characters such as the presence of forceps, unguiferate chelae, sigmancistras, stipitate growth form, deep-water habitat, carnivorous habit and/or lack of an aquiferous system, are not shared by all members, or at least have not yet been demonstrated to be so; nor are these characters confined to the family. On the basis of morphological evidence alone we prefer to keep the family intact, as understood by previous authors (e.g., Lévi, 1973; Hooper, 1997) who assigned it to the vicinity of the Mycalidae and allied families. The decision to keep *Asbestopluma, Chondrocladia* and *Cladorhiza* within a single family appears to be the most parsimonious at present, although their affinities to sponges such as *Esperiopsis desmophora* Hooper & Lévi, 1989 (Esperiopsidae) and *Euchelipluma pristina* Topsent, 1909 (Guitarridae) remain unclear. These sponges share some of the characters referred to above, but additional features strongly point to distinct assignments (palmate isochelae and mycalostyles in *E. desmophora*, typical of the Esperiopsdae – but see alternative interpretation in Hajdu (Guitarridae, Esperiopsdae, this volume), and complex placochelae in *E. pristina*, typical of the Guitarridae).

There is still doubt concerning authorship of family Cladorhizidae. Dendy (1922) erected Cladorhizeae assigning only *Amphilectus (?) unguiculatus* to it, with the only reference to inclusion of *Cladorhiza* being the proposed family name. He made no other comments on the taxon. De Laubenfels (1936a) was much more thorough, which is probably why some contemporary authors have attributed the authorship to him. Nevertheless, ICZN Article 11.7 (Anon., 1999) supports recognition of Dendy's authorship with the inclusion of *Cladorhiza* in the family 'inferred from the stem'.

Scope

A great deal of attention has been focused on cladorhizids over the past decade due to the observation of some remarkable biological traits in this mostly deep-water group (Vacelet & Boury-Esnault, 1995a,b, 1996; Vacelet *et al*., 1995, 1996). In part, these discoveries were made possible as a consequence of the discovery of a thriving shallow-water population of the carnivorous *Asbestopluma hypogea* Vacelet & Boury-Esnault, 1996. The most interesting aspect of this discovery is the total absence of choanocyte chambers associated with a carnivorous existence (presumed secondary loss), with choanocytes being amongst the strongest synapomorphy for the entire Porifera.

De Laubenfels (1936a) emphasised the symmetrical, mostly stalked habit, and deep-water habitat as diagnostic features of the Cladorhizidae, although already recognising convergent evolution of similar traits on other deep-water sponges. Microscleres, especially the chelae, were considered diagnostic at the genus level, of which he considered nine genera to be valid. Fifteen nominal genera were considered here, of which only three are considered valid. One is transferred to the Crambeidae. Taxonomic decisions made here follow the rationale proposed by Van Soest & Hajdu (Mycalina, this volume).

KEY TO GENERA

(1)	Anisochelae	2
	Unguiferate isochelae	***Chondrocladia***
(2)	Palmate anisochelae	***Asbestopluma***
	Anchorate or unguiferate anisochelae	***Cladorhiza***

ASBESTOPLUMA TOPSENT, 1901

Synonymy

[*Cometella*] Schmidt, 1870: 49 (*nomen oblitum*). [*Asbestopluma*] Lankester, 1882: 478 [*nomen nudum*]. *Asbestopluma* Topsent, 1901d: 23. *Lycopodina* Lundbeck, 1905: 58. *Cotylina* Lundbeck, 1905: 68. *Helophloeina* Topsent, 1928d: 8.

Type species

Cladorhiza pennatula Schmidt, 1875 (by subsequent designation; Topsent, 1901d).

Diagnosis

Cladorhizidae with palmate anisochelae.

Description of type species

Asbestopluma pennatula (Schmidt, 1875) (Fig. 1).

Synonymy. *Cladorhiza pennatula* Schmidt, 1875: 119, pl. I figs 14–16. *Cladorhiza bihamatifera* Vosmaer, 1882a: 47, pl. I figs 105–112. *Esperia bihamatifera*; Hansen, 1885: 15, pl. III fig. 7, pl. IV, fig. 2, pl. VII figs 5, 14. *Cladorhiza nordenskiöldii* Fristedt, 1887: 455, pl. 25 figs 56–59, pl. 31, fig. 25. *Asbestopluma pennatula*; Topsent, 1901d: 24, 28, pl. III figs 9a–d. *Esperella plumosa* Arnesen, 1903: 11, pl. II fig. 1, pl. IV fig. 3, pl. VI fig. 7 (Not *Esperia plumosa* Carter, 1882a). Taxonomic decision for synonymy: Lundbeck (1905).

Material examined. Holotype: Not seen. Other material. MNRJ 1236 – don. O.S. Tendal, 'Ingolf' Stn. 67, 61°30′N, 22°30′W (sample from ZMK). MNRJ 1237 – don. O.S. Tendal, 'Ingolf' Stn. 68, 62°06′N, 22°30′W (sample from ZMK). MNRJ 1238 – don. O.S. Tendal, 'Ingolf' Stn. 78, 60°37′N–27°52′W (sample from ZMK).

Description (adapted from Lundbeck, 1905). Slender, penniform, reaching over 18 cm high; axis slightly compressed and the variably long lateral branches inserted in the sides (Fig. 1A). Oscula and pores apparently lacking. Axial skeleton with a relatively powerful, densely spiculated exterior layer. Microscleres abound in the layer coating the branches. Megascleres: styles in the central portion of the main axis, 680–1000 μm long, 15–32 μm thick (Fig. 1B); subtylostyles in the branches and in the outer layer of the axis, 520–750 μm long, 9–17 μm thick (Fig. 1C). Microscleres: subtylostrongyles, irregularly sinuous, microspined, in the coating of the stalk, 50–137 μm long, 1–2.8 μm thick (Fig. 1D); large palmate anisochelae, with the lower end polylobate, 48–63 μm in total height (Fig. 1G); small palmate anisochelae, fusiform, 10–11.4 μm in total height (Fig. 1F); sigmancistras, 21–24 μm long (Fig. 1E).

Remarks. A canal system is lacking in *Asbestopluma hypogea* Vacelet & Boury-Esnault, 1996 (Vacelet & Boury-Esnault, 1995a; Figs 1H–J), and it is likely that this feature may be widespread in the genus. The subgenera of Lundbeck (1905), viz., *Asbestopluma*, *Cotylina* [type species established here as being *Esperella infundibulum* Levinsen, 1887 (=*Asbestopluma infundibulum*), no material reexamined] and *Lycopodina* [type species *Esperella cupressiformis var. lycopodium* Levinsen, 1886 (=*Asbestopluma lycopodia*); by subsequent designation; de Laubenfels, 1936a), no material re-examined] were defined mostly on the basis of habit, which has subsequently been shown to be an unstable character (Hentschel, 1914; Vacelet & Boury-Esnault, 1996). The use of these subgenera should thus be avoided. De Laubenfels' (1936a) suggestion of raising *Lycopodina* to full generic rank is not accepted. Conversely, *Helophloeina* (type species *H. stylivarians* Topsent, 1928d; by monotypy, no material re-examined), was erected by Topsent (1928d) on the basis of a unique combination of spicules. Hooper & Lévi (1989) and Hooper (1997) suggested it may be synonymous to *Meliiderma* Ridley & Dendy, 1887, which is not accepted here. *Meliiderma* (syntypes re-examined, see below) is a likely synonym of *Chondrocladia* Thomson, 1873, well distinguished from *Asbestopluma*. *Chondrocladia* and *Helophloeina* share small fusiform anisochelae which is here considered as strong evidence for their close relationship. Despite the fact that the short/stout micro(tylost)(strong)yles found in both *Helophloeina* and *Meliiderma* are indeed similar in overall shape, their distinct dimensions (11–12 μm vs. 60–100 μm, respectively), coupled with the presence of tylost(rong)yles in the ectosome of *Asbestopluma* and *Chondrocladia*, suggest the plausibility of the alternative interpretation given above. As argued elsewhere (Hajdu, 1999), the use of derived monotypic genera (e.g., *Helophloeina* with desmas) clearly pertaining to more universal plesiomorphic genera (e.g., *Asbestopluma* without desmas) is undesirable for it highlights the amount of apomorphy in a single species, at the cost of making paraphyletic an assemblage where many species are classified. In parallel with decisions taken for the Mycalidae (Hajdu, 1999 and this volume), *Asbestopluma* and *Helophloeina* could be given subgeneric rank within a larger, supposedly monophyletic genus *Asbestopluma*. It should be made clear though that for phylogenetic purposes genus *Asbestopluma* would mean absolutely the same as subgenus *Asbestopluma*, the latter being thus redundant and useless. The same reasoning applies to *Helophloeina*, be it a genus or a subgenus, and species *H. stylivarians* Topsent, 1928d.

The genus *Cometella* Schmidt, 1870: 49 was erected for type species *Cometella gracilior* Schmidt, 1870: 49 pl. IV fig. 9 (by subsequent designation; De Laubenfels, 1936a: 151). Schmidt's drawing shows a pedunculate sponge with a small ovate main body. A slide of the lectotype BMNH 70.5.3.97 was reexamined. This contains sections and many dissociated spicules. The spicule complement conforms to *Asbestopluma*, with megascleres styles with blunt endings, 900–1400 × 20–25 μm, smooth echinating

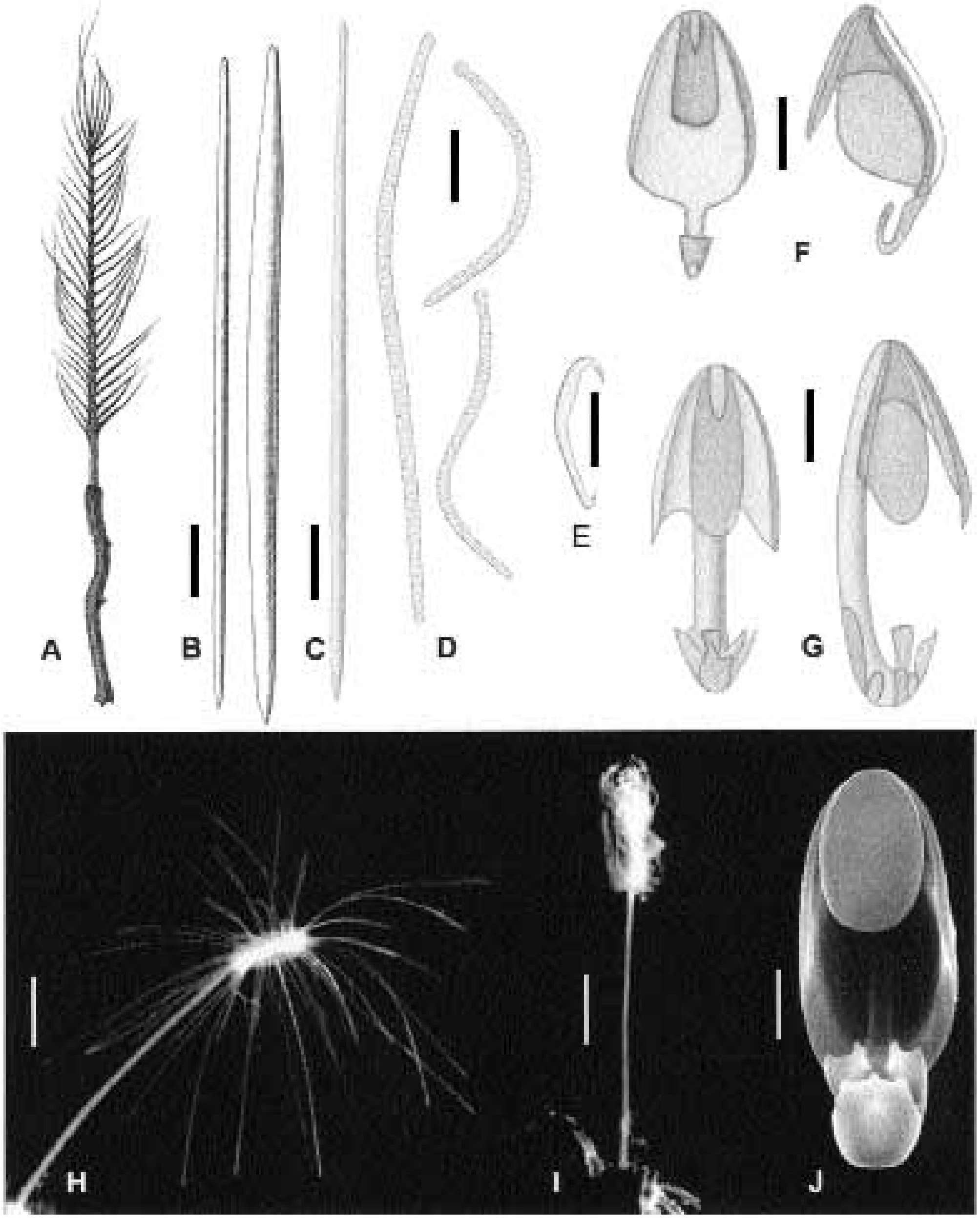

Fig. 1. A, *Asbestopluma pennatula* Schmidt (as *Cladorhiza*) (reproduced from Schmidt, 1875, pl. 1, fig. 14). B–F, *Asbestopluma pennatula*, drawings of spicules (reproduced from Lundbeck 1905, pl. 10, fig. 4). B, styles from the axis (scale 80 μm). C, subtylostyle from the lateral branches (scale 75 μm). D, microspined subtylostrongyles from the stalk-coating (scale 17.5 μm). E, sigmancistra (scale 10 μm). F, small palmate anisochelae (scale 3.2 μm). G, large palmate anisochelae (scale 12 μm). H–J, *Asbestopluma hypogea* Vacelet & Boury-Esnault, 1996. H, living specimen (scale 2.5 mm). I, holotype preserved in formalin (scale 3.1 mm). J, SEM photo of a palmate anisochelae (scale 2 μm).

subtylostyles, 300–600 × 2–4 μm, irregularly sinuous microspined subtylostrongyles, 90–120 × 1–3 μm, sigmancistras 20–25 μm, and palmate anisochelae10–12 μm. The genus *Cometella* was not recognized so far as a genus in Cladorhizidae, as Schmidt himself used it for sponges from a variety of families, *Cometella stellata* Schmidt, 1870 (= *Halicometes* in Tethyidae) and *Cometella spermatozoon* Schmidt, 1875 (=*Suberites* in Suberitidae), whereas Carter used it for sponges of yet another series of families: *Cometella simplex* Carter, 1876 (=*Stylocordyla* in Stylocordylidae), and *Cometella pyrula* Carter, 1876 (=*Crella* in Crellidae). More importantly, the name has not been used after 1876 and the junior name *Asbestopluma* has prevailing usage in the sense of ICZN article 23.9. [*Cometella*] is a nomen oblitum in favour of *Asbestopluma*.

CHONDROCLADIA THOMSON, 1873

Synonymy

Chondrocladia Thomson, 1873: 188. *Crinorhiza* Schmidt, 1880b: 83. *Meliiderma* Ridley & Dendy, 1887: 102, text-fig. 6, pl. XX fig. 11, pl. XXI figs 6a–c, 14. *Neocladia* Koltun, 1970: 193, text-figs 18.1–6, pl. VI fig. 6.

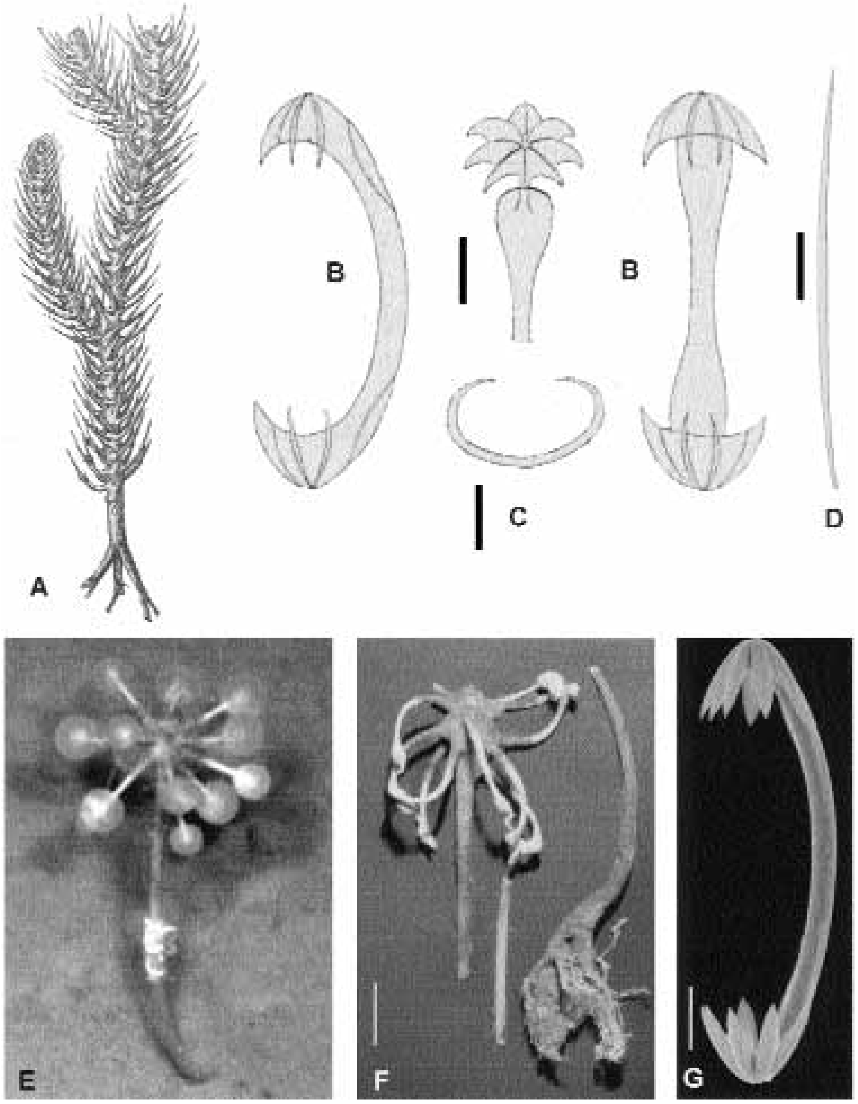

Fig. 2. A, *Chondrocladia virgata* Thomson (reproduced from Thomson, 1873: 188, 20–40 cm high). B–D, *Chondrocladia virgata*, drawings of spicules (reproduced from Carter, 1874a, pl. 14 fig. 20–21 and pl. 15 fig. 38). B, anchorate isochelae (scale 10.6 μm). C, sigma (scale 10 μm). D, style (scale 230 μm). E, a living specimen of *Chondrocladia* sp. photographed in situ in the North Pacific, 5320 m depth (from Tendal *et al*., 1993, photo Volodin). F, same specimen after collection, preserved in alcohol (scale 3.5 mm). G, SEM photo of an anchorate isochelae of an unidentified *Chondrocladia* from the deep North Pacific (scale 30 μm).

Type species

Chondrocladia virgata Thomson, 1873 (by monotypy).

Diagnosis

Cladorhizidae with isochelae.

Description of type species

Chondrocladia virgata Thomson, 1873 (Fig. 2).

Synonymy. *Chondrocladia virgata* Thomson, 1873: 188. Carter, 1874a: 217, pl. XIV figs 20–21, pl. XV fig. 38.

Material examined. Holotype: Not seen. Other material. *Chondrocladia alaskensis* Lambe, 1894: CMNI1900–2828 – Chika Island, Alaska, U.S.A. CMNI1900–2869 (fragments from syntypes) – Kyska Harbour, 'Unalashka', U.S.A. *Chondrocladia gigantea* (Hansen, 1885): MNRJ 1243 – don. O.S. Tendal, 'Michael Sars', 62°53′N, 04°14′E, det. W. Lundbeck (sample from ZMK). MNRJ 1244 – don. O.S. Tendal, 'Godthåb', stn. 162, 62°48′N, 60°46′W (sample from ZMK). MNRJ 1245 – don. O.S. Tendal, 'Bioice', stn. 2085, 67°15.67′N, 17°26.41′W, det. O.S. Tendal (sample from ZMK). *Chondrocladia pulchra* Lambe, 1894: CMNI19002824 (fragment from syntype) – Chika Island, Alaska, U.S.A. Syntypes of *Meliiderma stipitata* (Ridley & Dendy, 1886): BMNH 1887.5.2.191 and BMNH 1891.10.3.52a.

Description (adapted from Carter, 1874a; Thomson, 1875). Erect, branching scantily and dichotomously, 20–40 cm high. With divergent rooting processes, short straight stalk (ca. 6 mm wide), long axis bearing abundant conical processes (ca. 25 mm long, 4 mm across at the base) arranged around it in a confused spiral manner (Fig. 2A). Choanosomal skeleton a central axis formed by long subtylostyles, from which transverse bundles built by the same spicules radiate to form the conical processes. Ectosomal skeleton with large amounts of microscleres, and smaller megascleres piercing the sponge surface. Axis and spicules diminishing in size upwards from the base. Megascleres: (subtylo)styles, smooth, slightly curved, fusiform, head narrower than the shaft, ca. 1530 μm long (average largest size) and 28 μm across (greatest diameter, Fig. 2D). Microscleres: anchorate isochelae, with seven teeth at each end, curved shaft, ca. 67 μm long (average largest size) and 21 μm across (breadth of head, Fig. 2B). Sigmas, smooth, ca. 25 μm long (average largest size, Fig. 2C).

Remarks. In some preserved specimens of *Chondrocladia* the conical processes bear irregular swellings which appear to be inflated, translucent spheres in the living state (Tendal *et al*., 1993; Kübler & Barthel, 1999; Fig. 2E–G). The aquiferous system consists of rows of large choanocyte chambers running along the main axis of the sponge. *Crinorhiza* (no material re-examined here) was erected for cladorhizids with branches condensed around a flattened stalked body (cf. Topsent, 1930), the branches without terminal swellings, and a special category of ectosomal microsubtylostyles missing. Ridley & Dendy (1887) did not attach much confidence to these diagnostic characters, and used the name '*Crinorhiza*' to denote a special habit only. Topsent's (1930) subgeneric arrangement for *Chondrocladia* should be abandoned. For instance, forms of '*Crinorhiza*' were described for *Cladorhiza* too, thus rendering any group of species recognized on the basis of the diagnostic characters for *Crinorhiza* very suspect in phylogenetic terms. The type species of *Crinorhiza, C. amphactis* Schmidt, 1880b, possesses the characteristic spicule complement of a *Chondrocladia*, and our opinion is that both genera are synonyms. This contrasts with opinions implicit in the recent literature (e.g., Lévi, 1973; Hooper, 1997). *Chondrocladia (Amorphocladia)* Topsent, 1930, was erected for *Chondrocladia alaskensis* Lambe, 1894 and *C. pulchra* Lambe, 1894, but these species are best referred to *Crambe* Vosmaer, 1880b/*Monanchora* Carter, 1883c (see Crambeidae, this volume). The above explanation leaves only *Chondrocladia (Chondrocladia)* as a potentially valid, but certainly superfluous subgeneric assemblage. *Meliiderma* (type species *Chondrocladia stipitata* Ridley & Dendy, 1886; type specimen re-examined) is considered a synonym of *Chondrocladia* in view of its possession of typical anchorate isochelae, this being the original interpretation by Ridley & Dendy too (Ridley & Dendy, 1886). The possession of micro(tylost)(strong)yles in the ectosome of *Meliiderma* sets the species apart, but does not warrant the erection of a monotypic higher taxon. *Neocladia* (no material examined), on the contrary, is set apart by the peculiar shape of its forceps/birotule-like isochelae, but again it is considered here that the erection of a monotypic taxon is unwarranted (refer to the discussion of *Asbestopluma/ Helophloeina* above).

CLADORHIZA SARS, 1872

Synonymy

Cladorhiza Sars, 1872: 65, pl. VI figs 16–34. [*Trochoderma*] Ridley & Dendy, 1886: 344 (preocc. by *Trochoderma* Théel, 1877, Echinodermata). *Axoniderma* Ridley & Dendy, 1887: 96, text-fig. 5, pl. XX fig. 5, pl. XXI figs 8–10 (replacement name for *Trochoderma* Ridley & Dendy). *Exaxinata* de Laubenfels, 1936a: 122. *Raoa* de Laubenfels, 1936a: 123.

Type species

Cladorhiza abyssicola Sars, 1872 (by monotypy).

Diagnosis

Cladorhizidae with anchorate/unguiferate anisochelae (Fig. 3f).

Description of type species

Cladorhiza abyssicola Sars, 1872 (Fig. 3).

Synonymy. *Cladorhiza abyssicola* Sars, 1872: 65, pl. VI, figs 16–34; Lundbeck, 1905: 79, pl. XII, fig. 2.

Material examined. Holotype: Not seen. Other material. Syntype of *Axoniderma mirabile* (Ridley & Dendy, 1886): BMNH 1887.5.2.141. *Cladorhiza corticocancellata* Carter, 1876: MNRJ 1246 – don. O.S. Tendal, 'Ingolf', stn. 143, 62°58′N, 07°09′W, det. W. Lundbeck (sample from ZMK). *Cladorhiza gelida* Lundbeck, 1905: MNRJ 1240 (syntype) – don. O.S. Tendal, 'Ingolf', stn. 113, 69°31′N, 07°06′W (sample from ZMK, syntype); MNRJ 1241 – don. O.S. Tendal, 'Michael Sars', 60°19′N, 05°39′E (sample from ZMK). *Cladorhiza tenuisigma* Lundbeck, 1905: MNRJ 1242 (syntype) – don. O.S. Tendal, 'Ingolf', stn. 105, 65°34′N, 07°31′W (sample from ZMK).

Description (adapted from Sars, 1872; Lundbeck, 1905). Slender, unbranched (young specimens), or with relatively long branches issuing from a central axis; below a richly branched root. Total length may exceed 7 cm. Secondary processes, thin conical pointed and slightly curved, strongly compressed laterally, issue circularly from the stem and the side branches. A variably long section of the stem, just above the roots, may be devoid of secondary processes (Fig. 3A). Live-colour yellowish transparent to reddish-yellow. The skeleton is closely dependent on the form; it consists in axes and branches of a powerful, polyspicular fibre, often of great thickness, where the fibres supporting the branchlets are inserted. In the axial fibres spongin is found. Spicules: megascleres – styles, slightly fusiform or not, slightly bent or straight, 390–730 μm (Fig. 3B). Microscleres – anchorate/unguiferate anisochelae with five teeth on each termination, 21–25 μm (Fig. 3E); sigmata, large, typical, 78–100 μm (Fig. 3C); sigmancistras, 40–42 μm (Fig. 3D).

Remarks. The smaller sigmas of *C. abyssicola* are treated here as sigmancistras – Lundbeck (1905) leaves no doubt in this respect. Nevertheless, a definitive decision can only be made after Sars' (1872) specimens have been re-examined. *Trochoderma* Ridley & Dendy (1886) is a junior homonym of *Trochoderma* Théel (1877, Echinodermata), and was replaced by *Axoniderma* Ridley & Dendy. The latter genus (type species *Trochoderma mirabile* Ridley & Dendy, 1886), comprises a single species, distinguished by the peculiar shape of its 'pseudoamphiasters', which are indeed birotule-like, modified anchorate isochelae. In spite of arguing for this character's possible low classificatory/phylogenetic significance, Ridley & Dendy (1887) erected the genus *Axoniderma*, which differs from *Cladorhiza* mainly by the possession of these 'pseudoamphiasters'. *Exaxinata* (no material re-examined; type species *C. oxeata* Lundbeck, 1905), is another monotypic genus, erected on account of its possession of oxeas instead of the typical styles in most cladorhizids. *Raoa* (no material re-examined; type species *C. tridentata* Ridley & Dendy, 1886), is yet another monotypical genus, set apart by its anchorate anisochelae with only three teeth and hollow cup-shaped sponge habit. It is postulated here that *A. mirabile*, *C. oxeata* and *C. tridentata* belong to a clade together

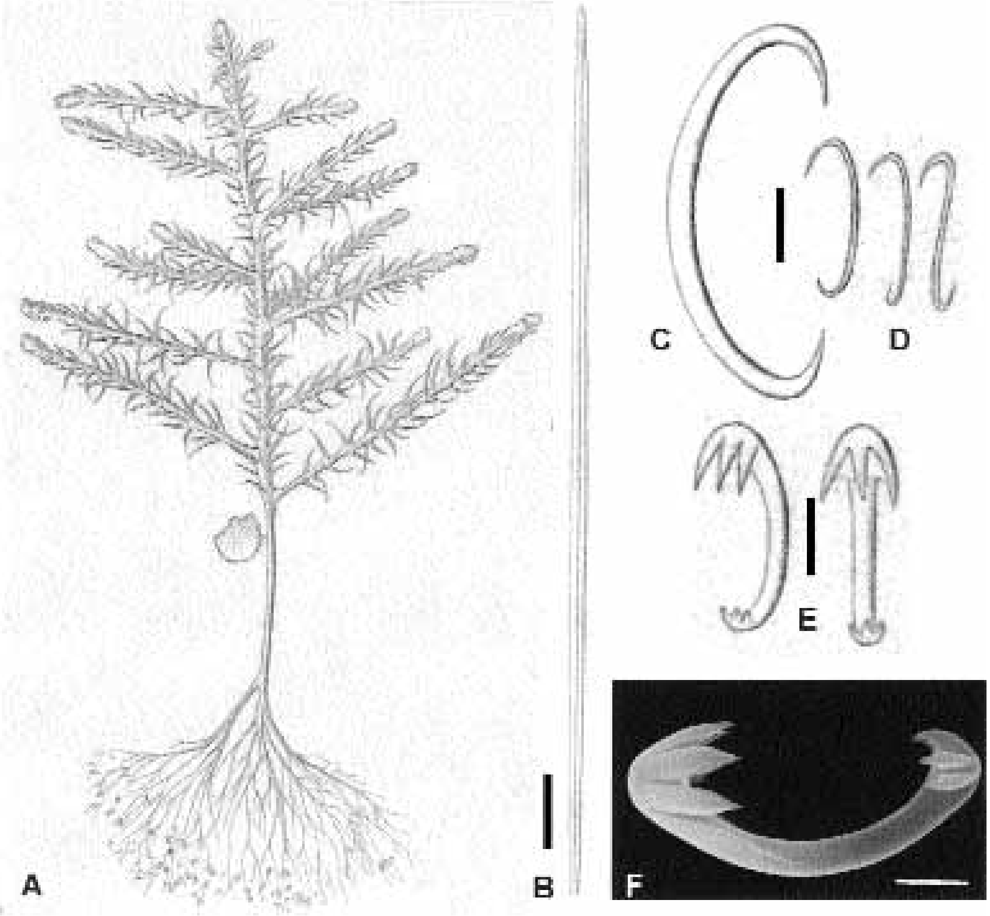

Fig. 3. A, *Cladorhiza abyssicola* Sars 1872, a ramified specimen (from Sars, 1872: fig. 17). B–E, *C. abyssicola*, drawings of spicules (reproduced from Sars, 1872). B, style from the axis (scale 50 μm). C, sigma (scale 20 μm). D, sigmancistras (scale 20 μm). E, anchorate anisochelae (scale 6.5 μm). F, SEM view of an anisochelae from an undescribed species from Barbados (scale 4.4 μm).

with *C. abyssicola*, to which neither species of *Asbestopluma* or *Chondrocladia* belong. In the absence of a phylogeny for the species of *Cladorhiza, Axoniderma, Exaxinata* and *Raoa* are considered here subjective synonyms of *Cladorhiza*. Otherwise, *Cladorhiza* may quite possibly be made paraphyletic. A canal system is apparently lacking, as verified in *Cladorhiza Metanophila* by Vacelet & Boury-Esnault, 2002.

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