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## Research article

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# Aglaopheniid hydroids (Cnidaria: Hydrozoa: Aglaopheniidae) from off New Caledonia collected during KANACONO and KANADEEP expeditions of the French Tropical Deep-Sea Benthos Program

Horia R. GALEA

Hydrozoan Research Laboratory, 405 Chemin Les Gatiers, 83170 Tourves, France.  
Email: [horia.galea@gmail.com](mailto:horia.galea@gmail.com)

[urn:lsid:zoobank.org:author:DE5AC672-0243-46F2-A910-AFF4E91A4C5D](https://zoobank.org/author:DE5AC672-0243-46F2-A910-AFF4E91A4C5D)

**Abstract.** Sixteen aglaopheniid hydroids occurring in two recent, deep water collections from off New Caledonia are reported upon, of which 8 species are new, namely *Cladocarpus asymmetricus* sp. nov., *C. partitus* sp. nov., *C. pennatus* sp. nov., *Lytocarpia fragilis* sp. nov., *L. pilosa* sp. nov., *L. pseudoctenata* sp. nov., *L. subtilis* sp. nov. and *Macrorhynchia spiralis* sp. nov., the latter producing medusoid gonophores. Although not occurring in the present collections, brief notes on *M. disjuncta* (Pictet, 1893), including the first description of its gonosome, are provided to support its specific separation from *M. phoenicea* (Busk, 1852).

**Keywords.** Deep water, Leptothecata, taxonomy, new species.

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## Introduction

This is the second report of a developing series dealing with the hydroids collected during the KANACONO (2016) and KANADEEP (2017) expeditions of the French Tropical Deep-Sea Benthos Program.

The first report (Galea & Schuchert 2019) dealt with hydroids belonging to various families, viz. Staurothecidae Maronna *et al.*, 2016, Syntheciidae Marktanner-Turneretscher, 1890, Sertulariidae Lamouroux, 1812, Sertularellidae Maronna *et al.*, 2016, Symplectoscyphidae Maronna *et al.*, 2016, Thyrosocyphidae Stechow, 1920 and Zygophylacidae Quelch, 1885.

The present report focuses on the family Aglaopheniidae Marktanner-Turneretscher, 1890, which provided 16 species assignable to the genera *Aglaophenia* Lamouroux, 1812 (two species), *Cladocarpus* Allman, 1874 (four species, of which one is new), *Gymnangium* Hincks, 1874 (one species), *Lytocarpia* Kirchenpauer, 1872 (seven species, of which four are new) and *Macrorhynchia* Kirchenpauer, 1872 (two species, one of which is new). Brief notes on the hydroid *Macrorhynchia disjuncta* (Pictet, 1893),

not occurring in the present material, are provided in order to support its specific separation from *M. phoenicea* (Busk, 1852), a species present in both collections.

## Material and methods

Study methods were described in Galea (2007, 2008). Station numbers, as indicated in the text, are preceded by a two-letter prefix referring to the sampling gear used to secure the material, either a beam trawl (CP), a rocky bottom dredge (DR) or a Warrén dredge (DW). The material, fixed and preserved in ethanol, is deposited in the collections of Muséum national d'histoire naturelle (MNHN) of Paris, France, and catalogue numbers are indicated as MNHN-IK-2015- followed by 3-digit numbers.

## Results

### *Systematic account*

Class Hydrozoa Owen, 1843  
Subclass Hydroidolina Collins, 2000  
Order Leptothecata Cornelius, 1992  
Family Aglaopheniidae Marktanner-Turneretscher, 1890  
Genus *Aglaophenia* Lamouroux, 1812

*Aglaophenia howensis* Briggs, 1918  
Figs 1A–B, 2

*Halicornaria* sp. nov. Whitelegge, 1899a: 41.

*Aglaophenia howensis* Briggs, 1918: 27, pl. 5 figs 1–2, pl. 6 fig. 1.

*Lytocarpia howensis* – Vervoort & Watson 2003: 311, fig. 75a–d.

### Material examined

PACIFIC OCEAN • 3 plumes without hydrorhizae, 5 cm, 10 cm and 10 cm, respectively, the latter bearing gonothecae; off New Caledonia, stn CP4786; 22°46' S, 167°42' E; 350–469 m; 29 Aug. 2016; KANACONO leg.; MNHN-IK-2015-544.

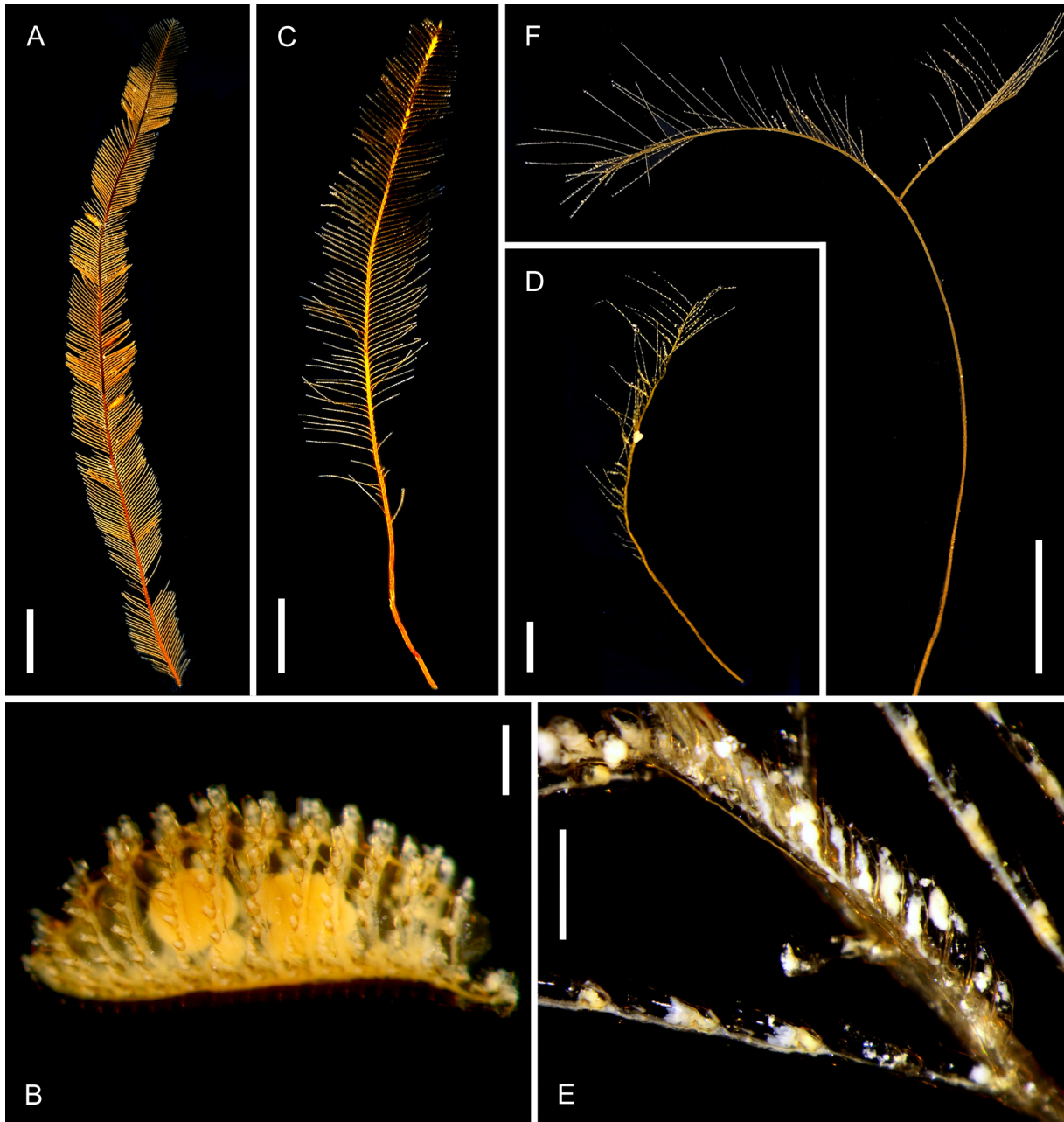
### Remarks

For a thorough description of this species, refer to Briggs (1918). Vervoort & Watson (2003) removed it from *Aglaophenia* Lamouroux, 1816 and placed it in *Lytocarpia* Kirchenpauer, 1872, on the account of peculiarities of its hydrothecae, not taking into account the morphology of its gonosome, otherwise well documented in the original account. The species was then transferred back to *Aglaophenia* after the examination of the present material with corbulae, whose structure does not include hydrothecae at the base of the costae (Fig. 1B).

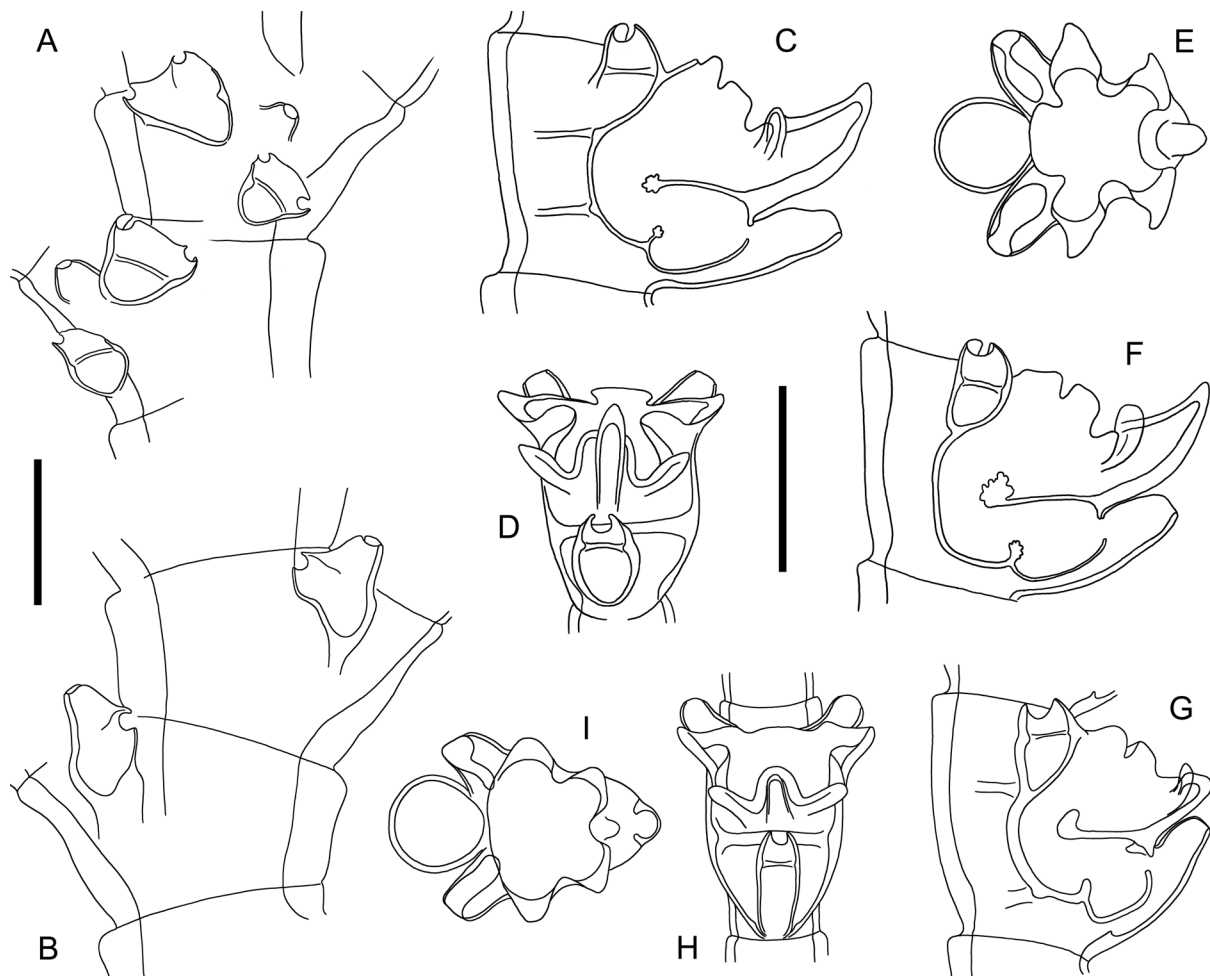
As noted by Briggs (1918), a reversal of the orientation of cladia, whose hydrothecae face either the frontal (F) or dorsal (D) aspect of the cormoid, could be noted. In the fertile plume available, this change occurs 12 times, as follows (from proximal to distal end): 15 (F), 10 (D), 7 (F), 12 (D), 19 (F), 10 (D), 8 (F), 13 (D), 34 (F), 26 (D), 29 (F), 32 (D), and 13 (F), the numbers representing the number of consecutive cladia per side of cormoid and per group of orientation. Implicitly, when corbulae are present within a given group, their orientation with respect to the side of the plume changes as well.

**Distribution**

Scattered records from the Tasman Sea area, up to Norfolk Island in the North (Vervoort & Watson 2003); New Caledonia (present report).



**Fig. 1.** A–B. *Aglaophenia howensis* Briggs, 1918, fertile cormoid (A) and corbula (B), both from sample MNHN-IK-2015-544. — C. *Aglaophenia sinuosa* Bale, 1888, cormoid from sample MNHN-IK-2015-545. — D–E. *Cladocarpus asymmetricus* sp. nov., fertile cormoid (D) and phylactocarp (E) from sample MNHN-IK-2015-530 (holotype). — F. *Cladocarpus keiensis* Schuchert, 2003, colony from sample MNHN-IK-2015-534. Scale bars: F = 2 cm; A, C–D = 1 cm; E = 1 mm; B = 500  $\mu$ m.



**Fig. 2.** *Aglaophenia howensis* Briggs, 1918, from sample MNHN-IK-2015-544. **A–B.** Portion of a stem in frontal aspect (A) and of another stem in dorsal aspect (B). **C–F.** Two hydrothecae from one colony in lateral (C, F), frontal (D) and apical (E) views. **G–I.** A hydrotheca from another colony in lateral (G), frontal (H) and apical (I) aspects. Scale bars: A–H = 200  $\mu$ m.

*Aglaophenia sinuosa* Bale, 1888

Figs 1C, 3

*Aglaophenia sinuosa* Bale, 1888: 790, pl. 21 figs 1–2.

*Aglaophenia bakeri* Bale, 1919: 353, pl. 17 figs 7–8.

*Aglaophenia sinuosa* – Whitelegge 1889b: 194. — Jäderholm 1917: 19, pl. 2 fig. 9. — Bale 1919: 352. — Watson 1994: 67; 2002: 347, fig. 6e–h; 2018: 19, fig. 8b–f. — Vervoort & Watson 2003: 278, figs 65e–f, 66a–e.

*Aglaophenia bakeri* – Watson 1994: 67; 2018: 19.

**Material examined**

PACIFIC OCEAN • 1 plume, ca 8.5 cm high, hydrorhiza and gonothecae missing; off New Caledonia, stn DW4970; 21°01' S, 158°31' E; 750 m; 8 Sep. 2017; KANADEEP leg.; MNHN-IK-2015-545.

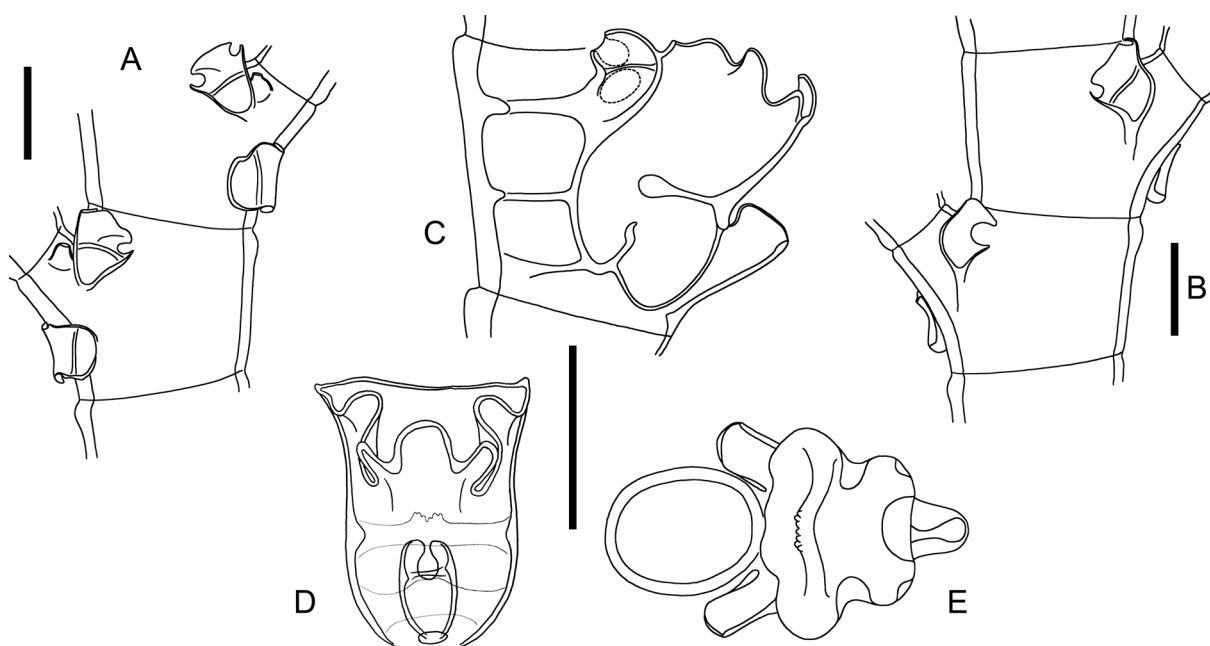
**Remarks**

For modern descriptions of this species, refer to Watson (2002, 2018) and Vervoort & Watson (2003).

As noted by Watson (2002), *A. sinuosa* is easily recognizable through the sinuous bends at intervals along the stem that mark a reversal of the orientation of cladia. Although a reversal is present in sample MNHN-IK-2015-545, the condition of the stem is little affected.

**Distribution**

South and SE Australia, Tasman Sea (Watson 2018), New Caledonia (present study).



**Fig. 3.** *Aglaophenia sinuosa* Bale, 1888, from sample MNHN-IK-2015-545. A–B. Same portion of a stem in frontal (A) and dorsal (B) aspects. C–E. Same hydrotheca in lateral (C), frontal (D) and apical (E) views. Scale bars: A–E = 200  $\mu$ m.

Genus *Cladocarpus* Allman, 1874

*Cladocarpus asymmetricus* sp. nov.

[urn:lsid:zoobank.org:act:765A957F-FEF6-47A6-B09A-314F31F0440E](https://zoobank.org/act:765A957F-FEF6-47A6-B09A-314F31F0440E)

Figs 1D–E, 4; Table 1

**Diagnosis**

*Cladocarpus* with lightly fascicled, unbranched stems divided into fairly long internodes, each with 2–3 frontal nematothecae, a mamelon and an axillar nematotheca. Cladia close to one another. Cormidia with up to 7 intranodal, adaxial septa. Hydrothecae elongated, asymmetrical in frontal view, with two lateral transverse ridges projecting into the lumen, rim with 9 rounded cusps. Phylactocarps given off from first cormidium, gonothecae concrescent with the rachis basally, crescent-shaped, with three types of nematothecae on both body and apex.

### **Etymology**

From the Latin ‘*āsymmetēr, -tra, -trum*’, meaning ‘asymmetrical’, with reference to the shape of the hydrotheca in frontal view.

### **Material examined**

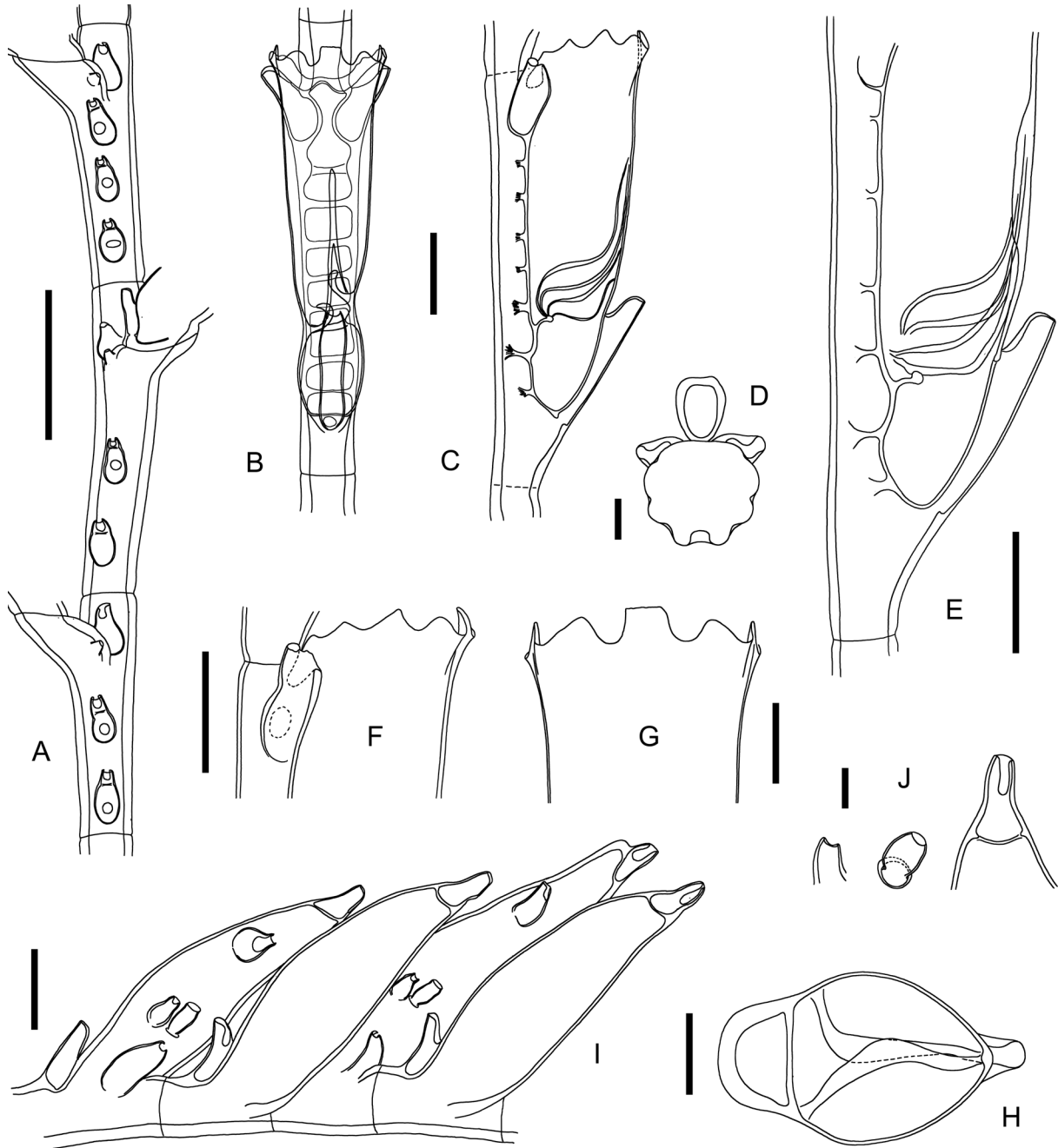
#### **Holotype**

PACIFIC OCEAN • 1 single plume, ca 8.5 cm high, hydrorhiza missing; off New Caledonia, stn DW4979; 19°42' S, 158°37' E; 315–295 m; 9 Sep. 2017; KANADEEP leg.; MNHN-IK-2015-530.

### **Description**

Colony erect, at least 8.5 cm high, hydrorhiza missing. Stem unbranched, fairly fascicled, accessory tubes forming a beam around the main tube; no deeply-cut, proximal, oblique nodes; elsewhere division into internodes indistinct, except for distalmost, monosiphonic part, with thinner perisarc, where transverse nodes (165–180 µm wide) delimit rather long (820–1030 µm) internodes composed of 2–3 (occasionally 4) proximal nematothecae in a row, a lateral cladial apophysis with its associated conical nematotheca (with rounded, apical aperture), and an axillar nematotheca rather lateral to the apophysis; dorsal axillar nematotheca absent; all stem nematothecae sac-shaped, adnate for  $\frac{2}{3}$  of their length, with apical, gutter-shaped aperture facing adaxially; each accessory tube of the stem with a row of saccate, deeply immersed nematothecae, with only their ovoid apertures slightly protruding from the perisarc. Cladial apophyses alternate along the stem, ending distally in a deeply oblique node; cladia close to one another, up to 1.9 cm long, divided into rather long internodes (1025–1090 µm) by means of slight, transverse (115–120 µm wide) constrictions of the perisarc, each accommodating a hydrotheca and its 3 nematothecae: one mesial and a pair of laterals flanking the aperture. Hydrotheca elongated, 895–950 µm deep, slightly compressed laterally below the rim, with straight adaxial and slightly curved abaxial walls, with an intrathecal septum given off from the lower  $\frac{1}{4}$  of the adaxial wall, and projecting for a short distance into the lumen; in frontal view, lower part of hydrotheca asymmetrical, due to the presence of two conspicuous, semicircular, intrathecal plates given off at two different levels from the lateral walls; free edges slightly overlapping in the middle of the lumen; in a lateral view of the hydrotheca, the attachment sites of these septa are distinctly sigmoid. Mesial nematotheca long, tubular, adnate for about  $\frac{3}{4}$  its length, leaving distally a short (90–95 µm), gutter-shaped aperture; lateral nematothecae short (195–200 µm), tubular, tapering towards the distal aperture, the latter with deeply scooped margin on adaxial side. Hydrothecal aperture 300–305 µm wide, rim with 9 cusps: one median, abaxial with squared outline, and 4 pairs of laterals, the latter triangular in shape, with rounded tips, becoming gradually lower and wider towards the adaxial side of the theca; up to 7 intranodal septa, all given off from the adaxial wall of the hydrothecae and projecting for a relatively short distance into the lumen of the internode; of these, 2 cusps are given off from the adaxial thecal wall below the intrahydrothecal septum, while up to 5 others from above it. Phylactocarp given off laterally from first cormidium, borne on distinct, athecate apophysis with distal, oblique node; phylactocarp up to 6 mm long, composed of a slightly geniculate rachis divided into up to 20 short (250–305 µm) internodes by means of slightly-marked, transverse nodes; each internode with a proximal nematotheca, a basally concrescent gonotheca, and a second nematotheca lateral to its insertion (both nematothecae elongated, with scooped rims adaxially); the proximalmost internode has an extra proximal nematotheca. Gonothecae crescent-shaped in lateral view, ca 850 × 250 µm, those with curvature on one side alternating with those curved oppositely from the other side; circular in transverse section, tapering gently below and gradually above to form a pointed apex bearing a nematotheca with scooped rim; two dissimilar nematothecae, placed at nearly the same level on the adaxial side of the thecal wall, at about  $\frac{1}{3}$  of the length above from the insertion of the gonotheca on the rachis: one nematotheca is conical, with thick walls and has a small, slightly scooped aperture, while the other is barrel-shaped, with thin walls and has a broad, circular aperture with entire

margin; upper third of the adaxial gonothecal wall with 1 (occasionally 2) sac-shaped nematotheca(e) with scooped rim on adaxial side.



**Fig. 4.** *Cladocarpus asymmetricus* sp. nov., from sample MNHN-IK-2015-530. A. Portion of stem. B–H. Hydrotheca in frontal (B), lateral (C) and apical (D) views; details of its proximal (E) and distal (F) parts seen laterally, and of the rim in frontal view (G); intrathecal septum in an apical view of the hydrotheca (H). I–J. Portion of phylactocarp with gonothecae (I) and details of the nematothecae borne by the gonothecae (J). Scale bars: A = 500  $\mu$ m; B–C, E–F, I = 200  $\mu$ m; D, G–H = 100  $\mu$ m; J = 50  $\mu$ m.

**Table 1.** Nominal species of *Cladocarpus* Allman, 1874 with (occasionally asymmetrical) hydrothecae provided with sigmoid (or nearly so) lateral ridges, similar to those of *C. asymmetricus* sp. nov., and their morphological differences with the new species.

Nominal species	Brief description, with emphasis on the distinctive features, and geographical distribution
<i>Cladocarpus elongatus</i> Bedot, 1921	Colonies rather tall (up to 15 cm high), occasionally branched, fascicled; stem internodes with one frontal and a pair of axillar nematothecae, flanking the cladial apophyses, mamelon <i>absent</i> ; cormidia with 7–8 intranodal septa, of which 2 are abaxial on proximal part; hydrothecae elongated, aperture <i>slightly tilted</i> forwards, margin with <i>11 rounded cusps</i> , of which the median, abaxial one is the most developed; mesial nematotheca adnate for a <i>very short</i> portion of the basal abaxial wall of hydrotheca, laterals not overtopping the hydrothecal aperture; internal septum <i>oblique</i> rather than decidedly sigmoid, insertions on lateral walls of hydrotheca at different levels; phylactocarp borne on first cormidium, <i>pinnate</i> , branchlets with successive pairs of opposite to subopposite nematothecae; gonothecae <i>ovoid</i> , borne on <i>apophyses</i> of branchlets, male with apical, rounded, operculate aperture <i>inclined</i> to one side, female bigger, with broad, ovoid, <i>lateral, subterminal</i> aperture. Distribution: off the Atlantic coast of Morocco (Bedot 1921; Ramil <i>et al.</i> 1998).
<i>Carpocladus fertilis</i> Vervoort & Watson, 2003	Colonies rather tall (ca 12 cm high), with unbranched, fascicled stems; internodes with 1 <i>frontal</i> and a fronto-axillar nematotheca, apophyses alternate, <i>without</i> mamelons; cormidia with ca 7 intranodal septa, of which 3 are abaxial, below the hydrotheca, the remaining 4 on adaxial side of the hydrotheca; abaxial wall with <i>median carina</i> , forming a conspicuous <i>dagger-shaped projection</i> on front of median marginal cusp; aperture <i>slightly tilted</i> forwards, rim with 4 pairs of lateral cusps; a strong adaxial ledge projecting into hydrothecal lumen, prolonged upwards sigmoidally on lateral walls; mesial nematotheca covering basal third of abaxial hydrothecal wall, laterals just over-reaching margin; phylactocarps borne on first cormidia, each internode with a gonotheca and a <i>forked</i> costa comprising a <i>hydrotheca</i> . Distribution: Tasman Sea (Vervoort & Watson 2003).
<i>Cladocarpus sigma</i> (Allman, 1877)	Stems <i>tall</i> (ca 15 cm high), unbranched, fascicled (Allman 1877); internodes with 1 frontal nematotheca and 2 axillar nematothecae, conical nematotheca <i>absent</i> ; cormidia with 5–7 intranodal septa; hydrotheca <i>cup-shaped</i> , with two lateral, intrathecal, sigmoidal ridges arising at different levels; margin with median abaxial cusps and <i>5 pairs</i> of lateral cusps; mesial nematotheca <i>short, barely surpassing</i> hydrothecal base; lateral nematothecae <i>short</i> , not always reaching hydrothecal rim; phylactocarps <i>pinnate</i> , an <i>ovate gonotheca</i> at base of each costa (Bogle 1975). Distribution: tropical and subtropical western Atlantic (Vervoort 1972).
<i>Cladocarpus unilateralis</i> Schuchert, 2015	Colony <i>tall</i> (ca 40 cm high), stem <i>loosely branched</i> , fascicled, axis <i>helical</i> ; cladia <i>spirally arranged</i> ; hydrotheca longitudinally asymmetrical, with two “loop-shaped ridges” on its lateral walls, <i>not connecting</i> ab- and adaxial walls; mesial nematotheca short, <i>below</i> the hydrothecal base; a lateral <i>nematotheca</i> on the cormidial internode; hydrothecal rim <i>smooth</i> , except for the median, abaxial cusp; lateral nematothecae <i>exceedingly elongated</i> , projecting <i>frontally, almost reaching</i> abaxial cusp. Distribution: Japan (Schuchert 2015).



**Remarks**

The relationships between several related aglaopheniid genera, viz. *Cladocarpus* Allman, 1874, *Aglaophenopsis* Fewkes, 1881, *Streptocaulus* Allman, 1883 and *Nematophorus* Broch, 1918, have been discussed and interpreted by a number of authors (e.g., Ramil & Vervoort 1992a; Ansin Agís *et al.* 2001; Altuna *et al.* 2013) on the account of morphological characters alone. To these should be added other genera, such as *Carpocladus* Vervoort & Watson, 2003, *Cladocarpoides* Bogle, 1984 and *Wanglaophenia* Vervoort & Watson, 2003, that make the case even more complex and, taken globally, it becomes evident that only a genetic study can be expected to clarify their relationships objectively.

The present hydroid, as well as *Cladocarpus partitus* sp. nov. and *C. pennatus* sp. nov. (see below), have gonosomes that do not conform accurately to any diagnosis of the abovementioned genera, displaying only some of their characters, as well as additional, distinctive ones. For this reason, these three new species are provisionally accommodated in the genus *Cladocarpus*, the oldest available name, pending a future phylogenetic study based on molecular markers.

A few congeners have hydrothecae resembling those of *C. asymmetricus* sp. nov., notably with respect to their elongated appearance and the presence of two lateral, oblique, intrathecal ridges. Their distinctive features are summarized in Table 1.

The new species is also highly distinctive in that its gonothecae are provided with nematothecae, a situation unknown in any of the *Cladocarpus*-like species described so far. Moreover, these nematothecae have three different morphologies and are present at different positions on the gonotheca.

**Distribution**

Known only from its type locality, off New Caledonia (present study).

*Cladocarpus keiensis* Schuchert, 2003

Figs 1F, 5

*Cladocarpus keiensis* Schuchert, 2003: 231, fig. 74.

**Material examined**

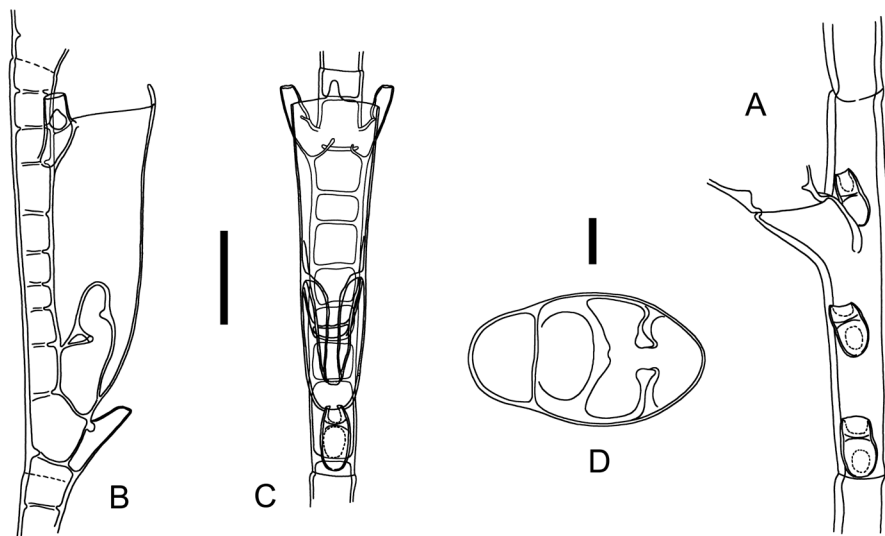
PACIFIC OCEAN • 1 colony, ca 15 cm high with a 2.3 cm-long side branch, hydrorhiza and gonosome missing; off New Caledonia, stn DW4763; 23°17' S, 168°15' E; 192–260 m; 27 Aug. 2016; KANACONO leg.; MNHN-IK-2015-543.

**Remarks**

For a description of this species, refer to Schuchert (2003), who documented gonocladia bearing incipient gonothecae only, while the mature ones are still to be described. According to the present material, the plate-like intrahydrothecal septum is pierced in its center by a large, rounded foramen. The passage of the hydranth takes place in front of the septum and its body passes between the two lateral, arched perisarcal ridges.

**Distribution**

Kei Islands, Indonesia (Schuchert 2003), New Caledonia (present study).



**Fig. 5.** *Cladocarpus keiensis* Schuchert, 2003, portion of stem (A), hydrotheca in lateral (B), frontal (C) and apical (D) aspects; all from sample MNHN-IK-2015-543. Scale bars: A–C = 50  $\mu$ m; D = 200  $\mu$ m.

*Cladocarpus partitus* sp. nov.

[urn:lsid:zoobank.org:act:498492D3-3B64-485D-9414-2BD05CF55103](https://zoobank.org/act:498492D3-3B64-485D-9414-2BD05CF55103)

Figs 6A–B, 7

**Diagnosis**

*Cladocarpus* with lightly fascicled, unbranched stems, whose rather long internodes bear a frontal row of 2–3 nematothecae, a lateral apophysis with a basal mamelon, as well as an anterior axillar nematotheca. Cladia relatively spaced from one another. Cormidia elongated, with up to 8 internal septa, 2 abaxial up to 6 adaxial. Hydrotheca deep, mesial nematotheca short, rim with median abaxial cusp, nearly smooth elsewhere; an internal ridge projecting forwards and slightly upwards from the lower fourth of the adaxial wall of hydrotheca, as well as an arched, two-winged septum above, leaving a slit-like, median passage for the hydranth. Phylactocarp borne on stem internode by means of a short apophysis; segmented into moderately-long internodes, each with one frontal, triangular nematotheca; gonothecae on distalmost internodes; tubular, with a main, lateral, subterminal, slit-like aperture, and an inconspicuous, secondary gutter-shaped aperture above.

**Etymology**

From the Latin ‘*partior, -itus sum, -iri*’, meaning ‘partitioned’, with reference to its hydrothecae that are divided by a transverse, bilobate septum.

**Material examined**

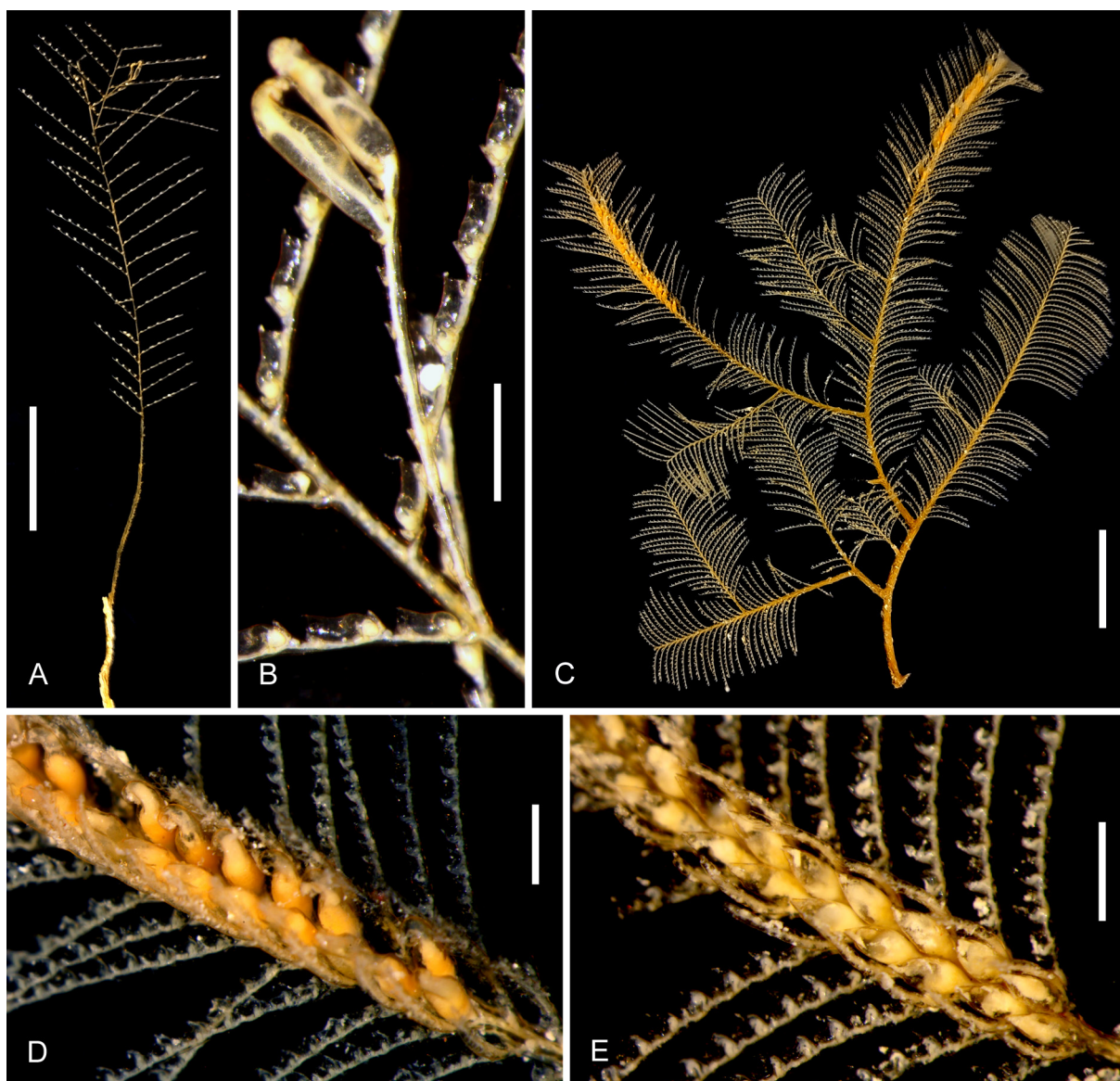
**Holotype**

PACIFIC OCEAN • 1 colony, ca 6.5 cm high, hydrorhiza missing; off New Caledonia, stn DW4770; 22°58' S, 168°21' E; 455–470 m; 28 Aug. 2016; KANACONO leg.; MNHN-IK-2015-529.

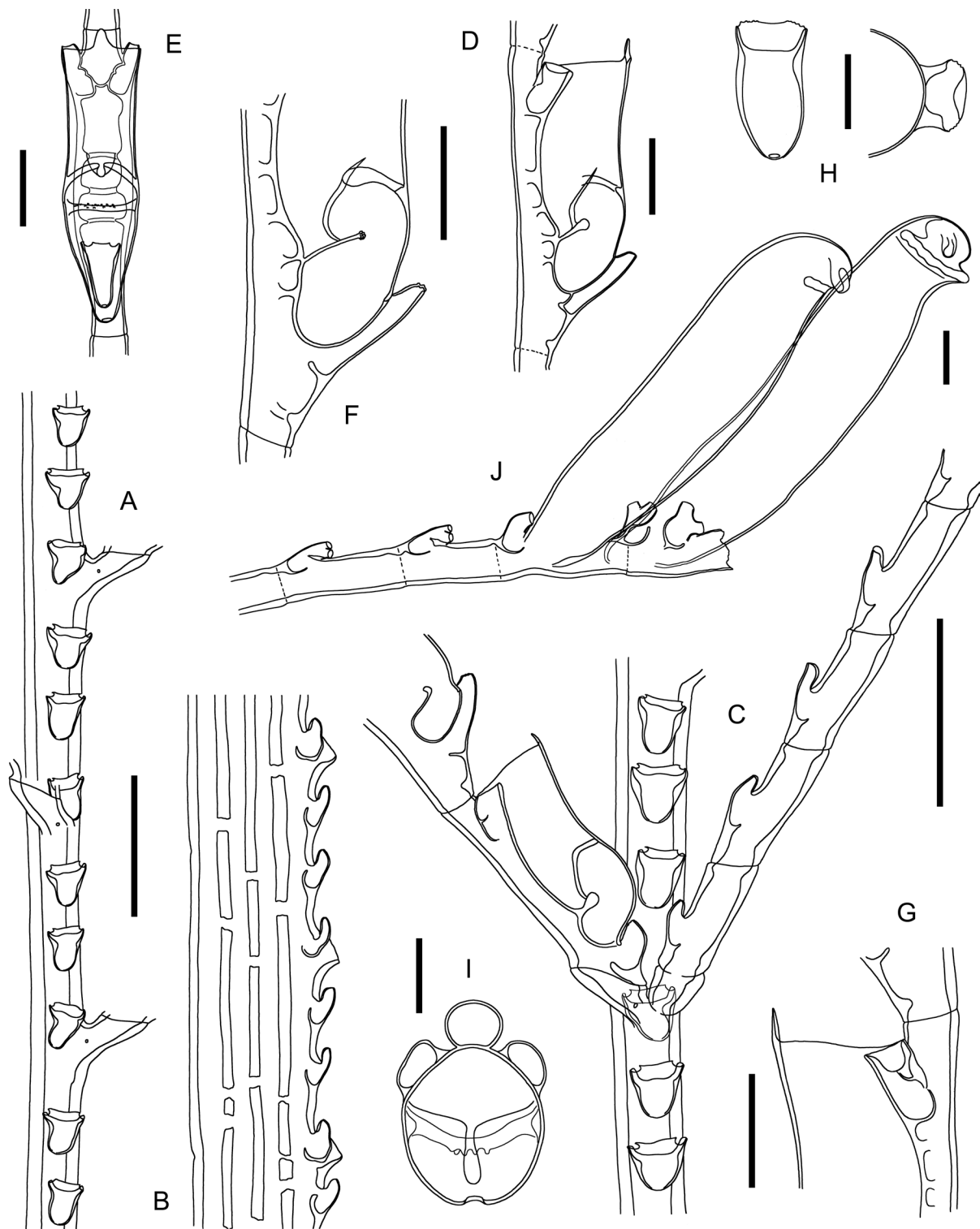
**Description**

Colony erect, feather shaped, delicate, ca 6.5 cm high, hydrorhiza not observed. Stem unbranched although, in the present specimen, the distal part had been partly broken off, but still remained attached,

and was consequently displaced laterally by a new, regenerative colony tip that has grown up vertically, giving the impression that the old apex is merely a lateral branch; stem fascicled proximally, grading to monosiphonic distally; every additional auxiliary tube adhering to the dorsal side of the preceding one, not forming a beam around the main tube, but resulting in a laterally-flattened structure (Fig. 7B); division into internodes indistinct, except for 3–4 oblique, deeply-cut nodes towards the proximal part of hydrocaulus, passing through all cauline tubes at a time. Equivalent internodes 700–1050  $\mu\text{m}$  long, 200–225  $\mu\text{m}$  wide, composed of 2–3 frontal nematothecae in a row, a short lateral cladial apophysis, a reduced nematotheca (with small, rounded aperture) on an inconspicuous mamelon at its base, as well as an axillar, anterior nematotheca rather lateral to it; there is no dorsal axillar nematotheca. Stem nematothecae large, inverted-triangular, with thick perisarc, apertures distal, wide, with inwardly-



**Fig. 6.** A–B. *Cladocarpus partitus* sp. nov., fertile cormoid (A) and phylactocarp (B) from sample MNHN-IK-2015-529 (holotype). — C–E. *Cladocarpus pennatus* sp. nov., fertile colony (C) and phylactocarp with male gonothecae (D) from sample MNHN-IK-2015-534 (holotype); phylactocarp with female gonothecae from sample MNHN-IK-2015-537 (one paratype). Scale bars: A, C–E = 1 cm; B = 1 mm.



**Fig. 7.** *Cladocarpus partitus* sp. nov., from sample MNHN-IK-2015-529. Portions from proximal (A, seen frontally; B, seen laterally) and distal (C, with insertion of phylactocarp) parts of stem. Hydrotheca seen laterally (D) and frontally (E), and details of its basal (F) and distal (G) parts; mesial nematotheca (H) seen frontally (left) and apically (right); internal septa in an apical view of the hydrotheca (I). Distal end of phylactocarp with two gonothecae (J). Scale bars: A–C = 500  $\mu$ m; D–G, J = 200  $\mu$ m; H, I = 100  $\mu$ m.

rolled abaxial wall, giving the impression that two circular apertures are present laterally; apophyses slightly shifted onto the anterior side of the colony, the two rows of hydrocladia forming an obtuse angle. Cladia relatively spaced from one another, up to 1 cm long, unbranched, divided into up to 12 cormidia by means of transverse, though not clearly demarcated nodes (75–95 µm wide), each internode 775–865 µm long, accommodating a hydrotheca and its 3 associated nematothecae: one mesial and a pair of laterals; up to 8 intranodal projections of the perisarc, of which 2 are given off from the abaxial side below the hydrothecal base, and up to 6 arise from the dorsal wall of the hydrotheca and project for a short distance into the lumen of the internode. Hydrotheca elongated, 600–635 µm deep, laterally-flattened, ad- and abaxial walls with slight basal bulges; a septum projecting slightly upwards from the lower portion of the adaxial wall reaches up to the middle of the thecal lumen, and is provided anteriorly with a distal swelling scattered with granular projections; a second, lamellar, two-winged septum is given off upwardly from the lateral sides of the hydrotheca at a rather acute angle, then changes its orientation and slightly plunges downwards, attaching its anterior border to the abaxial wall of the theca, leaving a slit-like, median passage between its two lateral ‘wings’; hydrothecal aperture 225–230 µm wide, rim with a prominent, central, well-developed, abaxial cusp, nearly smooth elsewhere. Mesial nematothecae elongated, rather broad in frontal view, adnate for most of their length, leaving a short (40–50 µm) portion free from the base of the corresponding hydrotheca; aperture broad, abaxial wall inwardly-rolled, rim crenelate at corners; mesial nematotheca of first cormidium short, gutter-shaped and not coalescent with the hydrothecal base. Lateral nematothecae 145–155 µm long, broadly cylindrical, reaching the level of the hydrothecal rim; adaxial wall deeply scooped out, abaxial wall crenelate to wavy. Phylactocarp mounted on a short stem apophysis arising laterally, next to a cladial apophysis, on opposite side; divided into several moderately-long (360–485 µm) internodes by means of transverse to slightly oblique nodes, each bearing a frontal nematotheca similar to those of stem, with large apical apertures and inwardly-rolled abaxial walls, giving the impression that the nematothecae are bifid; last couple of internodes additionally provided with a basally concrescent gonotheca; the latter long, tubular (ca 1630 × 400 µm), tapering below, distally with a main, broad, subterminal, slit-like aperture with flimsy, wavy rim, above which a second, short, slender, gutter-shaped aperture is to be found. Sex undeterminable.

### Remarks

Although not comprehensively described and/or illustrated, especially upon an apical examination of the hydrothecae, the internal septa of *Cladocarpus bicuspis* (G.O. Sars, 1874) possibly share morphological affinities with those of the present species. Indeed, a transverse septum, originating from the latero-abaxial hydrothecal walls, projects nearly horizontally midway into the lumen, then plunges down so as to meet the distal, swollen border of the adaxial hydrothecal ridge (G.O. Sars 1874: pl. 2 fig. 9; Kramp 1935: fig. 71b; Cornelius 1995: fig. 47c). Frontal views of the hydrotheca illustrated in the literature (Broch 1918: fig. 48c; Schuchert 2001: fig. 114b) do not provide sufficient information on the global aspect of the abaxial projection. Besides this possible common feature, the hydrothecae of *C. bicuspis* are distinctive through the presence of a median, abaxial pair of marginal cusps, separated from a squared to V-shaped gap prolonged downwards, till the level of abaxial ridge, as a perisarcal thickening; additional features related to its gonosome allow a rapid separation from the present new species (Cornelius 1995).

Also similar seems to be the abaxial septum of *Wanglaophenia longicarpa* Vervoort & Watson, 2003, as observed from the illustration in Vervoort & Watson (2003: fig. 81g). This species, however, possesses hydrothecae with a distinct, abaxial, thorn-shaped crest prolonged downwards as a longitudinal ridge, and its phylactocarp has forked costae provided with hydrothecae (Vervoort & Watson 2003).

### Distribution

Known only from its type locality, off New Caledonia (present study).

*Cladocarpus pennatus* sp. nov.

[urn:lsid:zoobank.org:act:7E29B1BC-C12D-43BE-8D91-0BB238C6CDBA](https://doi.org/10.21203/rs.3.rs-441111/v1)

Figs 6C–E, 8–9; Table 2

**Diagnosis**

*Cladocarpus* with large, fan-shaped colonies, with strongly fascicled stems and side branches. Nodes rather indistinct, internodes with a proximal, frontal nematotheca, a cladial apophysis with its cone-shaped nematotheca, as well as a fronto-axillar nematotheca. Cladia close to one another, divided into short internodes; first internode short, with a nematotheca, but no hydrotheca; remainder of cladium with normal cormidia. Hydrothecae facing backwards with respect to the antero-posterior plane of the colony; sigmoid, variously bulging abaxially from their lower halves; mesial nematotheca conspicuous, half adnate, projecting obliquely forward and upward (shorter and strongly pointing laterally on first cormidium); hydrothecal aperture with a median, triangular cusp and 1–2 pairs of laterals, decreasing in size adaxially; an internal, adaxial septum plunging down into the hydrothecal lumen for half its width. Gonosome composed of gonothecae arising from the cladial apophyses and phylactocarps borne on the first cormidium of a cladium that has lost its proximalmost, nematothecate internode. Phylactocarps elongated, set with consecutive pairs of lateral nematothecae, an additional, median, distal row occasionally present. Gonothecae dimorphic, male tubular, with recurved distal end bearing large aperture flanked by two lobes, female comparatively smaller and fusiform.

**Etymology**

From the Latin ‘*pennātus*, -a, -um’, meaning ‘bearing plumes’, with reference to the plumose appearance of its colonies.

**Material examined**

**Holotype**

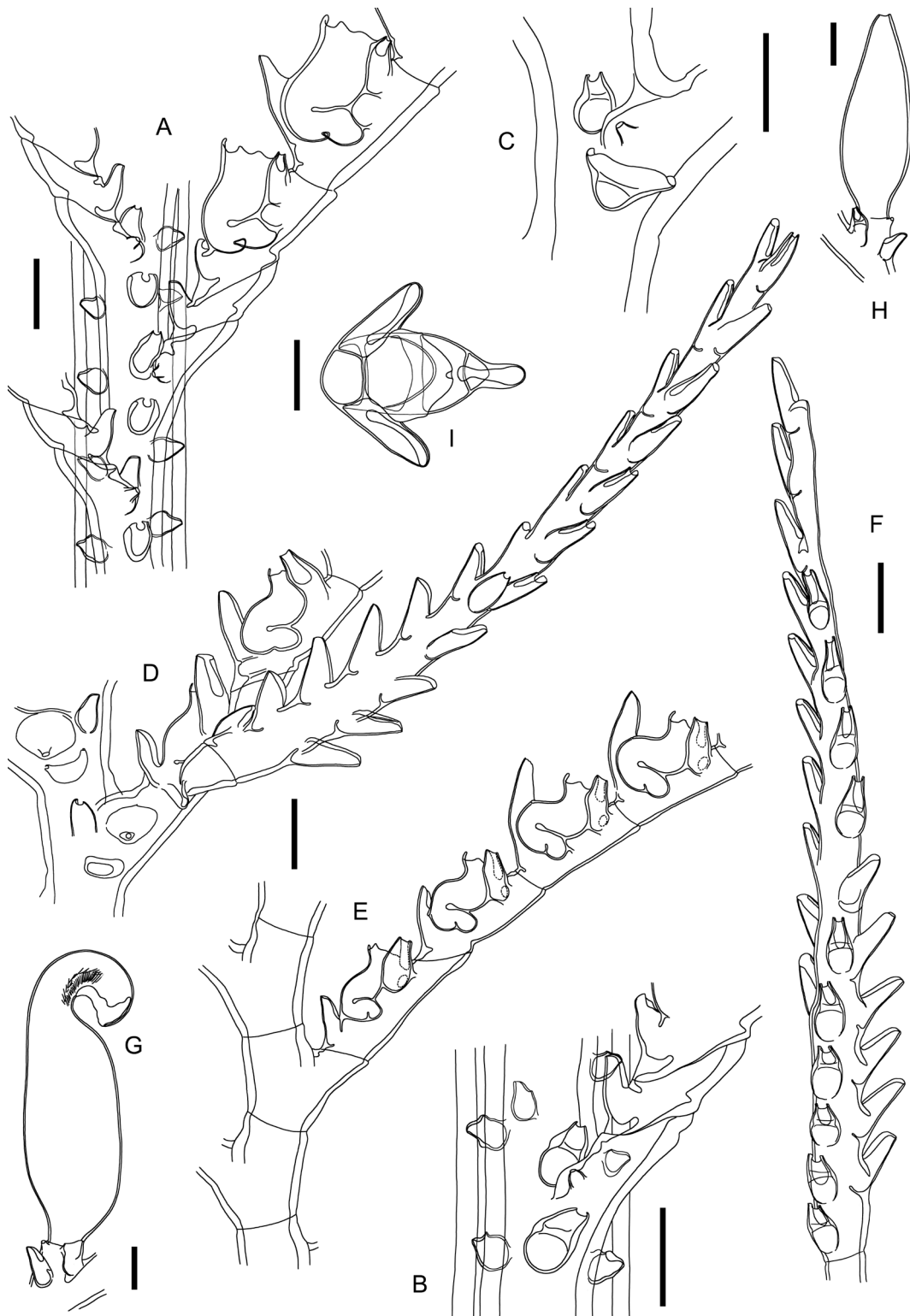
PACIFIC OCEAN • 1 colony, ca 6 × 6 cm, hydrorhiza missing, bearing male gonothecae; off New Caledonia, stn DW4720; 22°50' S, 167°11' E; 374–400 m; 19 Aug. 2016; KANACONO leg.; MNHN-IK-2015-534.

**Paratypes**

PACIFIC OCEAN • 1 colony, ca 4.5 × 6.5 cm, hydrorhiza missing, bearing female gonothecae with well-discerned oocytes; off New Caledonia, stn DW4720; 22°50' S, 167°11' E; 374–400 m; 19 Aug. 2016; KANACONO leg.; MNHN-IK-2015-535 • two colonies, ca 8 × 4.5 cm and 5 × 4.5 cm, both without hydrorhizae, but bearing female gonothecae; off New Caledonia, stn DW4707; 22°46' S, 167°23' E; 291–259 m; 17 Aug. 2016; KANACONO leg.; MNHN-IK-2015-537.

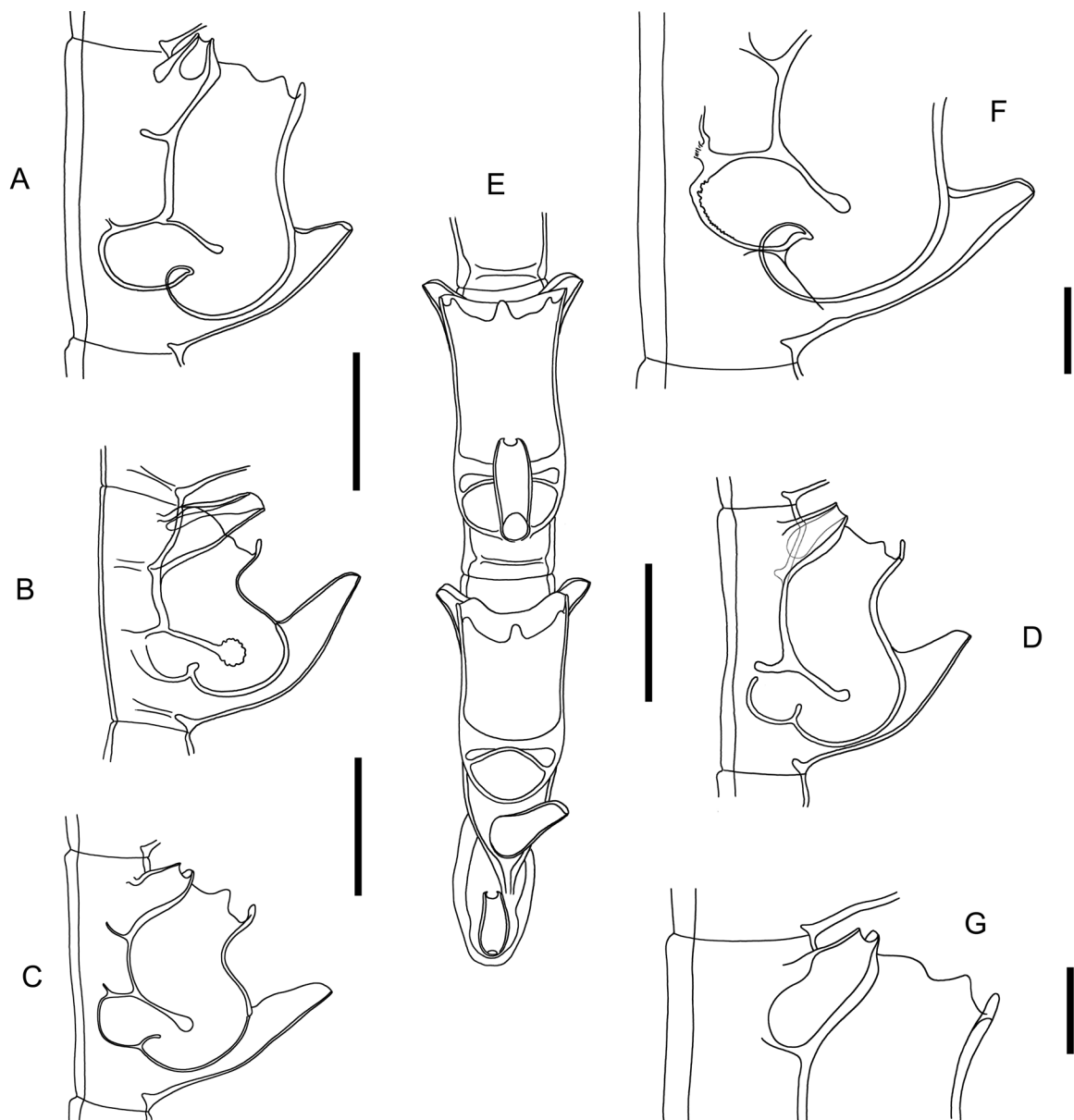
**Additional material**

PACIFIC OCEAN • 1 colony, ca 11 × 8.5 cm, bearing female gonothecae; off New Caledonia, stn CP4704; 22°46' S, 167°19' E; 365–356 m; 17 Aug. 2016; KANACONO leg.; MNHN-IK-2015-531 • 1 young, unbranched, sterile colony, 7 cm high, hydrorhiza missing; off New Caledonia, stn DW4762; 23°16' S, 168°06' E; 810–805 m; 26 Aug. 2016; KANACONO leg.; MNHN-IK-2015-532 • 1 colony fragment, ca 3.8 × 2 cm, bearing female gonothecae; off New Caledonia, stn DW4713; 22°47' S, 167°47' E; 356–380 m; 18 Aug. 2016; KANACONO leg.; MNHN-IK-2015-533 • 3 colonies, ca 10 × 7 cm, 8 × 5.5 cm and 10 × 7 cm, with female gonothecae, 1 colony, 12 × 4 cm, without gonothecae; off New Caledonia, stn CP4675; 22°50' S, 167°30' E; 350–366 m; 13 Aug. 2016; KANACONO leg.; MNHN-IK-2015-536 • 3 colonies with or without hydrorhizae and no gonothecae, ca 7.5 × 4.5 cm, 5.5 × 2 cm, and 5.5 × 7.5 cm, respectively, 1 colony, ca 5 × 6.5, without hydrorhiza and starting to reproduce (only phylactocarps but no gonothecae are present), 1 male colony, 5 × 3 cm, hydrorhiza missing,



**Fig. 8.** *Cladocarpus pennatus* sp. nov. (part). Portion of stem showing insertions of successive cladia (A) and details of apophysis with its associated nematothecae (B–C). Proximal portions of fertile cladia in frontal (D, with phylactocarp) and dorsal (E, phylactocarp on first cormidium not shown) aspects. Phylactocarp (F). Male (G) and female (H) gonothecae. Hydrotheca seen apically (I). From samples MNHN-IK-2015-532 (A–C), MNHN-IK-2015-533 (E, I), MNHN-IK-2015-537 (G) and MNHN-IK-2015-540 (D, F, H). Scale bars: G = 100  $\mu$ m; A–F, H, I = 200  $\mu$ m.

upper part of 1 large colony, ca  $4.2 \times 6$  cm, with male gonothecae; off New Caledonia, stn DW4717;  $22^{\circ}44'$  S,  $167^{\circ}11'$  E; 336–361 m; 19 Aug. 2016; KANACONO leg.; MNHN-IK-2015-538 • 1 long fragment, 2.7 cm, without gonothecae, with strongly bent hydrothecae and hypertrophied nematothecae; off New Caledonia, stn CP4676;  $22^{\circ}51'$  S,  $167^{\circ}30'$  E; 383 m; 13 Aug. 2016; KANACONO leg.; MNHN-IK-2015-539 • 2 colony fragments, ca  $4 \times 2$  cm and 2.4 cm, respectively, both with male gonothecae, 1 unbranched colony, 6 cm high, without gonothecae; off New Caledonia, stn DW4679;  $22^{\circ}49'$  S,  $167^{\circ}33'$  E; 245–249 m; 13 Aug. 2016; KANACONO leg.; MNHN-IK-2015-540 • 1 colony, ca  $7 \times 5$  cm, with female gonothecae, 1 colony, ca  $6.5 \times 4.5$  cm, hydrothiza and gonothecae missing; off New



**Fig. 9.** *Cladocarpus pennatus* sp. nov. (continued). A–E. Hydrothecae from different colonies seen in lateral view (A–D), to show variation in abaxial curvature, and proximalmost part of a hydrocladium seen frontally (E). F–G. Details of the basal (F) and distal (G) parts of a hydrotheca seen laterally. From samples MNHN-IK-2015-531 (C), MNHN-IK-2015-532 (A, E–G), MNHN-IK-2015-536 (D) and MNHN-IK-2015-539 (B). Scale bars: A–E = 200  $\mu$ m; F–G = 100  $\mu$ m.



Caledonia, stn DW4706; 22°47' S, 167°24' E; 355–343 m; 17 Aug. 2016; KANACONO leg.; MNHN-IK-2015-541 • 1 colony, ca 8 × 4 cm, without hydrorhiza, bearing male gonothecae; off New Caledonia, stn DW4708; 22°44' S, 167°21' E; 71–68 m; 17 Aug. 2016; KANACONO leg.; MNHN-IK-2015-542 • 1 unbranched colony, ca 5 cm high, without hydrorhiza and gonothecae; off New Caledonia, stn DW4745; 22°57' S, 167°39' E; 310–403 m; 23 Aug. 2016; KANACONO leg.; MNHN-IK-2014-2594.

### Description

Colonies erect, fan-shaped, up to 11 cm high and 8.5 cm wide, arising from rhizoid stolon composed of numerous branching, anastomosing, contiguous fibers firmly anchoring the whole structure on its substrate. Stems strongly fascicled, branched irregularly with a tendency to alternate, main stem supported dorsally by beam of auxiliary tubes, each provided with a longitudinal row of deeply-immersed, saccate nematothecae, having only their distal parts, bearing the apertures, protruding from the perisarc. There are no proximal oblique nodes passing through the fascicled stem; main tube with indistinct division into internodes, except for the distalmost parts of a colony, where the perisarc is thinner, and where weak transverse node delimit very short internodes; the latter composed of a proximal, frontal nematotheca, a laterally-directed cladial apophysis with its reduced conical nematotheca (with small, rounded aperture), and a second, frontal (axillar) nematotheca rather lateral to the apophysis; stem nematothecae elongated, with gutter-shaped apertures, occasionally inverted-triangular, with wide distal apertures and backwardly-rolled abaxial walls. Apophyses alternate along the stem, well-developed, delimited from the corresponding cladium by a deeply-cut, very oblique node; cladia close to one another, up to 7 mm long, slightly convex, proximally pointing upwards and distally downwards, the two rows coplanar; first cladial internode very short, ahydrothecate, but provided with a frontal, gutter-shaped nematotheca, ending in oblique node, separating it from the remainder of cladium, the latter comprising a regular succession of short internodes delimited by means of transverse nodes (100–115 µm wide); each internode 350–365 µm long, with a hydrotheca and its 3 associated nematothecae: one mesial and a pair of laterals; through a torsion of the cladium at its insertion on the corresponding apophysis, all hydrothecae face backwards with respect to the antero-posterior plane of the colony. Hydrothecae 260–270 µm deep, S-shaped, with thick abaxial wall, with an internal septum given off from the lower ¼ of the cavity and projecting slightly downwards so as to reach about the middle of the thecal lumen, ending distally in a perisarc plug; aperture ca 160 µm wide, rim with a central, prominent, triangular, abaxial cusp, continued laterally with 1–2 additional cusps decreasing in size adaxially. Mesial nematotheca adnate for ¾ to ½ of its length to the hydrothecal base, free part 115–125 µm long, aperture adaxial and gutter-shaped over entire length of free part; lateral nematothecae long (ca 145 µm), tubular, pointing out- and upwards, adaxial wall deeply scooped out. First cladial hydrotheca with comparatively shorter mesial nematotheca, given off from below its base, and distinctly pointing towards the dorsal side of the colony. Gonosome composed of phylactocarps, each associated with one gonotheca; gonothecae given off from the cladial apophyses just above the conical nematotheca and lateral to the distalmost internodal stem nematotheca; phylactocarps given off from cladia modified proximally as follows: the proximalmost ahydrothecate internode carrying the single, frontal nematotheca is replaced by a complete cormidium delimited by very oblique nodes; its mesial nematotheca is comparatively shorter than the subsequent ones, is given off from below the hydrothecal base, and is distinctly shifted on to the dorsal side of the colony; the second cormidium, also complete, is delimited proximally by an oblique node and distally by the first transverse node of the cladium; its mesial nematotheca is more elongated than that of the first cormidium and surpasses, for a certain distance, the hydrothecal base, but is still slightly shifted laterally; the third and subsequent cormidia are similar to those of a normal hydrocladium, with well-defined, straight mesial nematothecae. The phylactocarps are given off from the first cormidium, lateral to and above the mesial nematotheca, towards the front of the colony, by means of a short, conical apophysis delimited distally by transverse node, and having a long, gutter-shaped nematotheca at its base; phylactocarp composed of a double row of nematothecae, 6–10 in female colonies and up to 30 in males; in the latter, the double row is often supplemented distally

**Table 2.** *Cladocarpus*-like hydroids with S-shaped hydrothecae provided with an adaxial septum, and their distinctive features with respect to *Cladocarpus pennatus* sp. nov.

Nominal species	Brief description, with emphasis on the distinctive features, and geographical distribution
<i>Cladocarpus cartieri</i> Bedot, 1921	Stem internodes with 1 frontal nematotheca and 2 <i>axillar</i> , flanking each cladial apophysis on both sides of the stem; <i>no mamelon</i> ; cormidia <i>long, slender</i> , with <i>up to 9</i> intranodal septa, one of which is proximal and abaxial; hydrothecae <i>elongated</i> , adaxial septum <i>short</i> , aperture rounded, rim <i>entirely smooth</i> ; mesial nematotheca a short distance <i>below</i> hydrothecal base, laterals elongate, <i>overtopping</i> aperture (Ramil & Vervoort 1992b). Distribution: Azores, Mid Atlantic Ridge (Calder & Vervoort 1998).
<i>Streptocaulus dollfusi</i> (Billard, 1924)	Stem internodes with 2–5 <i>frontal</i> nematothecae, a fronto-axillar one, but <i>no conical nematotheca</i> on cladial apophysis; cormidia with 6–8 <i>intranodal ridges</i> ; hydrothecae <i>elongated</i> , adaxial septum set <i>upwards</i> , rim with 1 median abaxial cusp variably developed, elsewhere <i>smooth to weakly undulated</i> ; mesial nematotheca below hydrothecal base, laterals facing upwards and forwards, <i>overtopping</i> hydrothecal rim; phylactocarps borne laterally on 1 <sup>st</sup> hydrotheca, composed of a succession of short internodes with distal pairs of nematothecae (Ansin Agís <i>et al.</i> 2001); gonothecae on phylactocarps: female <i>elongated</i> , aperture <i>lateral, subterminal</i> , male fusiform, <i>distally truncate</i> (Billard 1934). Distribution: eastern Atlantic from the Bay of Biscay to Morocco (Ansin Agís <i>et al.</i> 2001).
<i>Cladocarpus millardae</i> Vervoort, 1966	Stem with 2–4 <i>frontal</i> nematothecae (each with 4 <i>apertures</i> ) between successive cladial apophyses, <i>single axillar</i> nematotheca, and <i>no conical nematotheca</i> on apophysis; cormidia <i>long, S-shaped</i> , with <i>centrally-placed</i> hydrotheca; mesial nematotheca with 4 <i>apertures</i> , seated <i>below</i> the hydrothecal base; lateral nematothecae <i>antler-shaped</i> , with 5–7 apertures; hydrothecal <i>rim without cusps</i> ; internodes of phylactocarp with 2 lateral nematothecae, each with 2–3 <i>apertures</i> ; gonotheca <i>globular</i> , distally truncate. Distribution: Mozambique, NE coast of South Africa (Millard 1975).
<i>Cladocarpus paraventricosus</i> Ramil & Vervoort, 1992	Stem internodes with 1 frontal nematotheca, <i>single axillar nematotheca</i> , and <i>no conical nematotheca</i> on apophysis; cormidia <i>long, slightly sigmoid</i> , with centrally-placed hydrotheca; mesial nematotheca <i>below</i> the hydrothecal base, laterals <i>long, tubular</i> , surpassing the rim; margin with median, conspicuous cusp and 5 <i>pairs of laterals</i> , slightly marked; intrathecal septum <i>short, projecting upwards</i> ; phylactocarps borne on first cormidium, <i>branched pseudodichotomously</i> , a gonotheca after each ramification; gonotheca <i>ovoid</i> , aperture lateral, subapical. Distribution: Strait of Gibraltar (Ramil & Vervoort 1992b).
<i>Cladocarpus sinuosus</i> Vervoort, 1966	Stem with 1–5 <i>frontal</i> nematothecae between successive cladial apophyses, with <i>single axillar</i> nematotheca, and <i>no conical nematotheca</i> on apophysis; cormidia <i>long, slightly sinusoid</i> , hydrotheca placed <i>in middle portion, elongated</i> , mesial nematotheca <i>below</i> the hydrothecal base; rim of hydrotheca, besides the median abaxial cusps, with <i>faintly sinuous</i> lateral edges; internodes of phylactocarp with <i>two very long, curved nematothecae</i> ; gonothecae <i>ovoid</i> with <i>truncate distal end</i> (Vervoort 1966; Millard 1975). Distribution: Alboran Sea, Guinea Bissau, South Africa (Ansin Agís <i>et al.</i> 2001).
<i>Cladocarpus unicornus</i> Millard, 1975	Main tube of the stem with <i>intranodal septa</i> , 1–3 frontal nematothecae between successive cladial apophyses, <i>single axillar</i> nematotheca, and <i>no conical nematotheca</i> on apophysis; hydrotheca with basal <i>abaxial bulge capped by short solid horn of perisarc</i> ; mesial nematotheca <i>free</i> from hydrotheca, lateral nematothecae <i>elongated, with 3 apertures</i> , margin with median, abaxial, inturned cusp, elsewhere <i>smooth</i> . Distribution: endemic to South Africa (Millard 1975).
<i>Cladocarpus ventricosus</i> Allman, 1877	Stem internodes with 3–8 <i>frontal nematothecae</i> , 2 axillar nematothecae, and a mamelon on each hydrocladial apophysis; cormidia <i>fairly long</i> , with up to 9 <i>intranodal septa</i> ; hydrotheca <i>ventricose</i> , adaxial ridge directed <i>upwards</i> ; mesial nematotheca <i>below</i> the hydrothecal base <i>or slightly surpassing it</i> ; lateral nematothecae <i>overtopping</i> hydrothecal rim; rim with median abaxial cusp and <i>slightly crenate</i> edges; gonothecae borne <i>on stem, oval</i> , aperture <i>lateral, subterminal</i> ; phylactocarp borne on first cormidium, <i>antler-shaped</i> , with 3–4 <i>branchlets</i> (Bogle 1975; Ramil & Vervoort 1992b). Distribution: Florida and Straits of Florida (Bogle 1975).
<i>Cladocarpoides yucatanicus</i> Bogle, 1984	Stem with at least one frontal nematotheca, a pair of axillar nematothecae, and a mamelon; internodes as long as to accommodate a hydrotheca and its 3 nematothecae; hydrotheca <i>fairly long</i> , adaxial septum projecting <i>upwards</i> , mesial nematotheca <i>adnate</i> to lower abaxial thecal wall, laterals <i>overtopping</i> margin; rim <i>sinuous</i> , except for the median, abaxial cusp; gonothecae <i>obovate</i> , borne on base of stem apophyses; phylactocarp borne on first cormidium, <i>corbula-like</i> , costae <i>antler-shaped</i> , with associated <i>hydrotheca</i> and terminated in <i>nematophorous spike</i> . Distribution: Yucatan Channel (Bogle 1984).

by a number of additional nematothecae situated dorsally in a median row. Colonies dioecious; the gonothecae occur in groups towards the distal parts of the colonies, and are given off simultaneously from numerous consecutive apophyses of the branches; male gonothecae large (ca  $1395 \times 460 \mu\text{m}$ ), tapering below, distally narrowing to a downwardly-curved neck, with broad aperture flanked by a pair of lobes; female comparatively smaller (ca  $955 \times 330 \mu\text{m}$ ), fusiform, with minute (ca  $35 \mu\text{m}$  wide), apical aperture, despite the much larger size of the oocytes.

### Remarks

Several *Cladocarpus*-like hydroids possess S-shaped hydrothecae provided with an adaxial septum, similar to those of *C. pennatus* sp. nov. However, there are morphological features enabling their specific separation, and these are summarized in Table 2.

The male gonothecae of the new species recall those of *Wanglaophenia longicarpa* Vervoort & Watson, 2003 (see Vervoort & Watson: fig. 81h), but the carinate hydrothecae and the forked phylactocarps bearing hydrothecae (Vervoort & Watson 2003) of the latter readily distinguishes these hydroids.

### Distribution

Known only from off New Caledonia (present study).

Genus *Gymnangium* Hincks, 1874

*Gymnangium expansum* (Jäderholm, 1903)

Fig. 10

*Gymnangium expansum* – Vervoort 1966: 165, figs 65–66. — Rees & Vervoort 1987: 163, fig. 38a–b. — Vervoort & Watson 2003: 289, figs 68g, 69a.

### Material examined

PACIFIC OCEAN • 1 colony, ca 10 cm high, lightly fascicled, fertile; off New Caledonia, stn DW5007; 22°12' S, 159°02' E; 290–750 m; 19 Sep. 2017; KANADEEP leg.; MNHN-IK-2015-515 • 1 colony, ca 10.5 cm high, lightly fascicled, sterile; off New Caledonia, stn DW4777; 23°03' S, 168°16' E; 330–353 m; 28 Aug. 2016; KANAACONO leg.; MNHN-IK-2015-516 • two sterile stems, the first ca 16 cm high and monosiphonic, the second ca 20 cm high and lightly fascicled; off New Caledonia, stn DW4711; 22°47' S, 167°24' E; 335–338 m; 18 Aug. 2016; KANAACONO leg.; MNHN-IK-2015-517 • 1 colony, ca 16 cm high, lightly fascicled, sterile; off New Caledonia, stn CP4674; 22°48' S, 167°29' E; 311–302 m; 13 Aug. 2016; KANAACONO leg.; MNHN-IK-2015-518 • 1 colony, ca 12 cm high, lightly fascicled, sterile; off New Caledonia, stn DW4672; 22°47' S, 167°26' E; 310–290 m; 13 Aug. 2016; KANAACONO leg.; MNHN-IK-2015-521.

### Remarks

For a description of this species, refer to Vervoort (1966) and Rees & Vervoort (1987); a quite recent synonymy is given in Vervoort & Watson (2003). In these accounts, only slightly bent hydrothecae, whose nematothecae have single apical apertures, were documented, not reaching the extreme degree of curvature (aperture parallel to long axis of the internode) met with in material MNHN-IK-2015-516, in which, additionally, the mesial nematothecae display 4–6 frontal apertures, while the pairs of laterals have bifid apertures. In contrast, the material MNHN-IK-2015-515 has less curved hydrothecae (their apertures form an angle of 45° with the long axis of the internode), but their mesial nematothecae still display 2–3 frontal apertures, while the laterals possess only one. An intermediate situation is met with in sample MNHN-IK-2015-518, in which the hydrothecal apertures form an angle of ca 70° with the

internode and the mesial nematothecae possess 1–2 frontal apertures, while the laterals have only one. Bifid mesial nematothecae were observed so far in specimens from Japan studied by Schuchert (2015).

In all samples examined the branching pattern is ‘trifid’, with either mono- (the 16 cm-high colony from sample MNHN-IK-2015-517) or lightly polysiphonic (all remaining material) stems; in addition, their hydrothecae are free from their corresponding internodes for ca  $\frac{1}{3}$  of their adaxial length, fitting the original account by Jäderholm (1903).

There is no thorough description available of the mode of branching in this species, especially at microscopic level. The original account is quite evasive (“*Die Verästelung ist sehr regelmässig und charakteristisch. Die nach allen Seiten gerichteten Äste sitzen fast immer zu zweien zusammen, sind sehr deutlich spiralförmig angeordnet und nach aussen gebogen*” [The branching is very regular and characteristic. The branches are directed to all sides, almost always they are given off in pairs, are arranged in an obvious spiral, and are bent outwards]). However, Jäderholm (1903: pl. 14 fig. 5) provides a comprehensive illustration of the macroscopic appearance of a typical colony. According to his figure, a pair of plumes is given off at each geniculation of the stem, the successive pairs facing outwards with respect to the spiral built up by the stem.

Subsequent accounts seem to provide rather divergent data. Indeed, the material studied by Stechow (1909: 103, fig. 8) was devoid of the characteristic spiral growth pattern, the main stem giving rise, here and there, to secondary branches that further divide trichotomously. The colony studied by Billard (1918: 25, as *Halicornaria sibogae*) formed a helicoid sympodium (“*Colonie [...] ramifiée en sympode hélicoïde*”), thus partly agreeing with the type, although nothing is said about its branching pattern. The account given by Vervoort (1966: 165) (“The structure of the colony is sympodially [*sic*]: the main axis is formed by the basal parts of successive plumes, arranged in spiral fashion, each succeeding plume rising about 8 mm from the base of the preceding plume”) does not conform with the structure of the type either since, at each geniculation, only one plume, instead of two, is given off. Rees & Vervoort (1987) observed a “Sympodially built stem with helically arranged, unbranched plumes ...” in their material, resembling those examined earlier by Vervoort (1966).

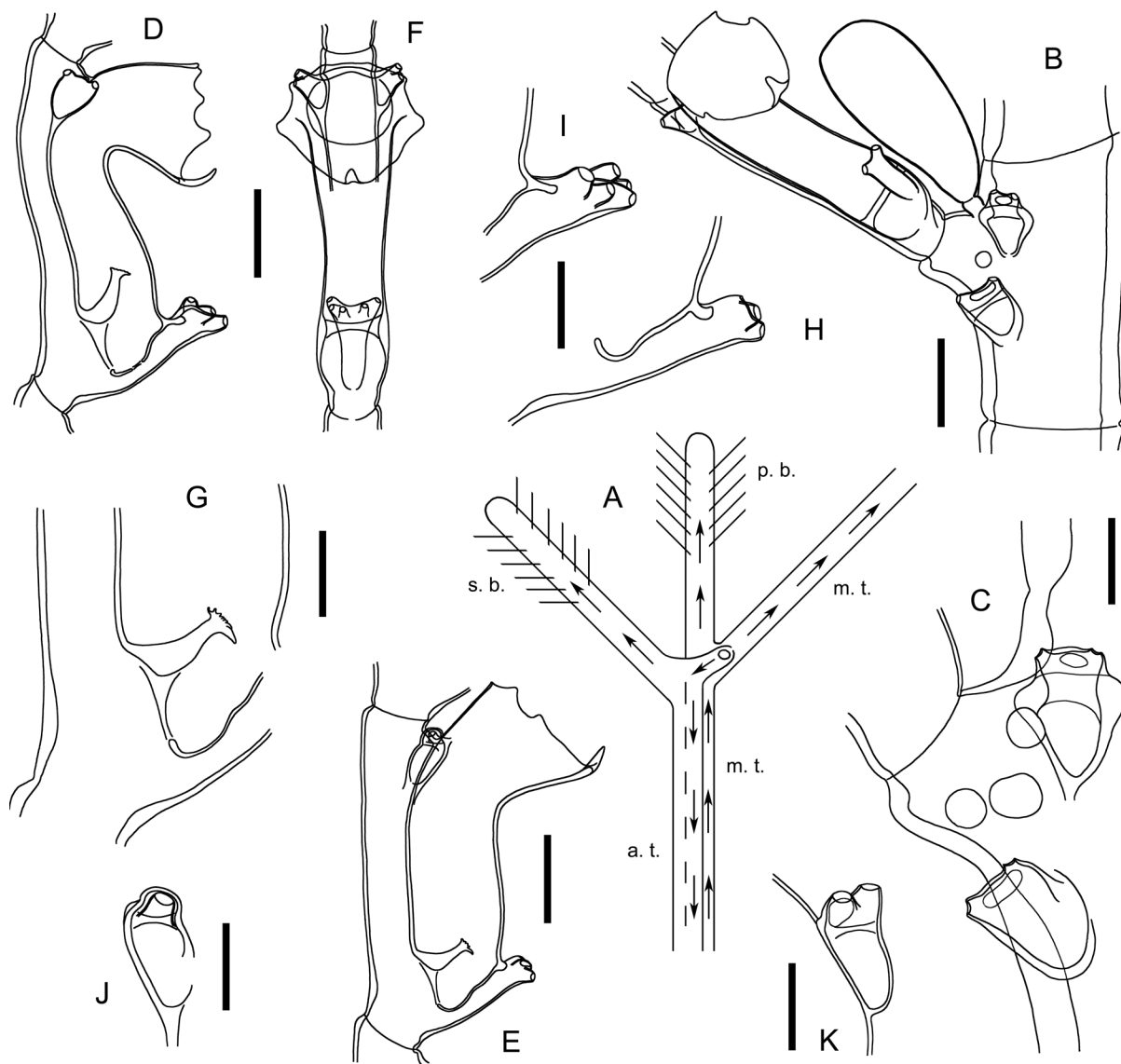
On the other hand, the colony illustrated by Rho & Park (1980: pl. 9 fig. 1) is undoubtedly similar to that of the type, despite their description (Rho & Park 1980: 27) providing only limited details: “Colonies large, not fascicled, spirally branched. The hydrocaulus [*is*] divided into regular internodes, zigzag-shaped”.

Finally, Vervoort & Watson (2003: 289) claim that they “have little to add to the descriptions of this characteristic species given by previous authors”.

As noted above, the branching pattern met with in the present material from New Caledonia is superficially trifid, as follows: the stem is geniculate and describes a spiral; at more or less regular intervals, the main tube bifurcates at each geniculation: in the exact continuation of the long axis of the original portion before the geniculation, it is prolonged as a plume (bearing hydrocladia), while the divergent part continues, slightly inclined (with respect to the preceding longitudinal axis), as the main stem proper; from the base of the divergent portion of the stem, two (originally twin) tubes are given off: one runs downwards along the preceding portion of the stem below the geniculation (bringing polysiphony to the colony), while the other is given away upwards, forming a second plume (bearing hydrocladia) (Fig. 10A).

In this context, the specific separation between *G. expansum* and its closest congener, *Gymnangium tubulifer* (Bale, 1914), seems to rely exclusively on the appearance of the colonies resulting from their mode of branching. When describing his species, Bale (1914) referred to the structure of the colony of

*G. vegae* (Jäderholm, 1903), as did Vervoort & Watson (2003), who stated that the stem of *G. tubulifer* "... is geniculate and more or less spiral, composed of the proximal parts of stem elements that at each geniculation turn aside to form a branch. At the same place the proximal element splits off to form 3 ramifications of which [one] continues as the "stem", [one] as a branch pointing away from the original element, and [one] as a downwardly directed tube, covering the more proximal parts of the "stem"". This results in a colony whose distinctive appearance is depicted by Jäderholm (1903: pl. 15 fig. 1).



**Fig. 10.** *Gymnangium expansum* (Jäderholm, 1903). A. Diagrammatic illustration of the mode of branching of the stem: main (m. t.) and accessory (a. t.) tubes, primary (p. b.) and secondary (s. b.) branches with cladia. B–C. Stem internode with gonotheca (B) and detail (C), showing the nematotheca associated to the hydrocladial apophysis. Hydrothecae in lateral (D–E) and frontal (F) views, and detail of their base (G). H–K. Nematothecae: mesial with bifid (H) and quintuple (I) aperture; lateral with simple (J) and bifid (K) apertures. From samples MNHN-IK-2015-515 (B, C, E, G, H, J) and MNHN-IK-2015-516 (D, F, I, K). Scale bars: B, D–F = 200  $\mu$ m; C, G–K = 100  $\mu$ m.

In a molecular study by Ronowicz *et al.* (2017), *G. expansum* is shown to cluster with members of the genus *Gymnangium* Hincks, 1874 instead of with *Taxella* Allman, 1874, in spite of the colony structure showing obvious affinities with the latter. As noted by these authors, Stechow (1921) proposed a new genus, *Halicetta*, to accommodate *G. expansum*, with the following diagnosis: “hydrothecae elongated, curved but not bent, with no abaxial septum”. This, however, does not differ much from characters of *Taxella*, even though emphasis was placed on characters of the gonosome in particular. A more comprehensive analysis is necessary to elucidate the generic affinities of Jäderholm’s (1903) hydroid.

### Distribution

Scattered records from the tropical and subtropical Indian and Pacific Oceans, from Zanzibar to Japan (Vervoort & Watson 2003).

Genus *Lytocarpia* Kirchenpauer, 1872

*Lytocarpia brevis* (Busk, 1852)

Fig. 11A

*Lytocarpia brevis* – Di Camillo *et al.* 2011: 525, figs 2c, 3b, f, 6d, 7–8.

### Material examined

PACIFIC OCEAN • several plumes branched or unbranched, 1.8–4.5 cm high, of which one bears a young corbula; off New Caledonia, stn DW4774; 23°01' S, 168°19' E; 100–90 m; 28 Aug. 2016; KANACONO leg.; MNHN-IK-2015-514.

### Remarks

For a recent description of this well-known species, refer to Di Camillo *et al.* (2011), who also provided an extensive synonymy.

### Distribution

Widespread in tropical parts of the Indian Ocean, from Africa to Indonesia, and the northeastern South Pacific (Di Camillo *et al.* 2001).

*Lytocarpia fragilis* sp. nov.

[urn:lsid:zoobank.org:act:92370DAB-142D-4322-8CA0-DE8B96EA9CD4](https://zoobank.org/act:92370DAB-142D-4322-8CA0-DE8B96EA9CD4)

Figs 11B–K, 12A–C

### Diagnosis

*Lytocarpia* with moderately tall, delicate colonies, with lightly fascicled, unbranched stems, divided into rather long internodes, each comprising 2–3 frontal nematothecae in a row, a lateral apophysis supporting a cladium with its conical nematotheca, and a couple of axillar nematothecae flanking the apophysis on each side of the stem. Cladia fairly close to one another, cormidia moderately long, with 6 intranodal septa, hydrotheca occupying distal ¾. Hydrotheca distinctly S-shaped, swollen basally, mesial nematotheca adnate for most of its length, free part projecting nearly upwards, and provided with large aperture behind an inwardly-rolled abaxial wall; lateral nematothecae tubular, with adaxially scooped walls, overtopping hydrothecal aperture. Rim with rounded-triangular median cusp, edges with two low, triangular cusps prolonged adaxially by a mere undulation. Gonosome an open corbula, distally on cladia, each internode with a costa and an axillar nematotheca; costae with a basal hydrotheca and a short appendage comprising 3–4 pairs of laterally-placed nematothecae; gonothecae lenticular.

**Etymology**

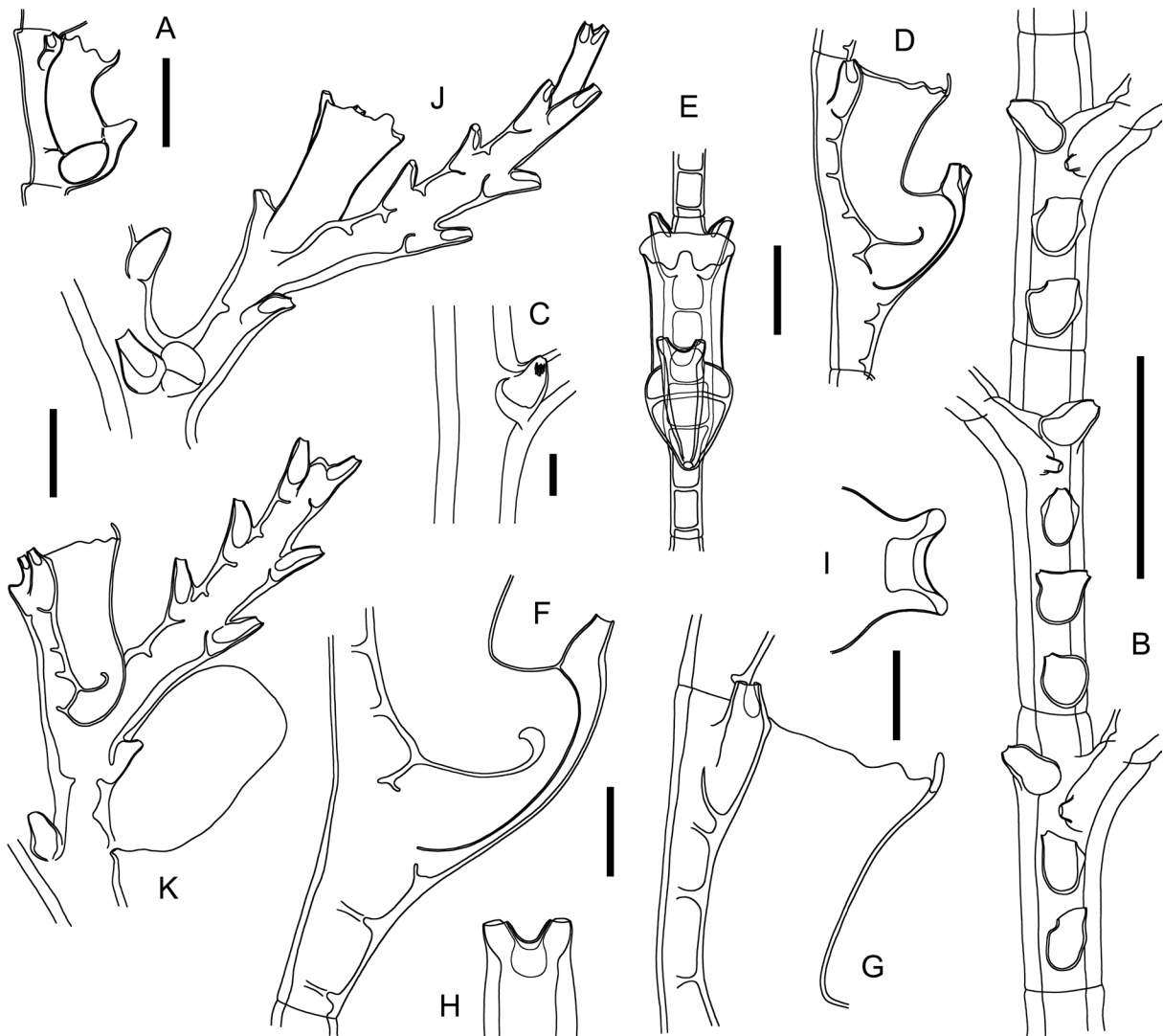
From the Latin '*frāgīlis*', meaning 'frail', with reference to the delicate appearance of its colonies.

**Material examined****Holotype**

PACIFIC OCEAN • 1 colony, devoid of its distal part, ca 7.5 cm high, fertile; off New Caledonia, stn DW4770; 22°58' S, 168°21' E; 455–470 m; 28 Aug. 2016; KANACONO leg.; MNHN-IK-2015-523.

**Description**

Colony erect, of a delicate appearance, comprising a single plume, originally taller than the 7.5 cm-high fragment left after the breakage and subsequent loss of its distal part; arising from a rhizoid stolon firmly attached to hard substrate. Stem unbranched, lightly fascicled, grading to monosiphonic distally;



**Fig. 11.** A. *Lytocarpia brevirostris* (Busk, 1852), hydrotheca from sample MNHN-IK-2015-514. — B–K. *Lytocarpia fragilis* sp. nov., from sample MNHN-IK-2015-523. A–B. Portions of stems in frontal (B) and dorsal (C) aspects. D–G. Hydrotheca seen laterally (D) and frontally (E), and details of its basal (F) and distal (G) parts, both in lateral view. H–I. Distal part of mesial nematotheca seen frontally (H) and apically (I). J–K. Two corbulacostae. Scale bars: B = 500  $\mu$ m; A, D–E, J–K = 200  $\mu$ m; C, F–I = 100  $\mu$ m.

main tube composed of a long (3.5 cm) proximal part devoid of hydrocladia but bearing large, saccate nematothecae in a single, frontal row, and a shorter part bearing cladia; both parts are separated by a short intervening prosegment with one frontal nematotheca, delimited at both ends by very oblique, deeply-cut nodes. Upper part divided, sporadically, into long segments by means of a few oblique nodes; segments further divided into regular, moderately long (680–840  $\mu\text{m}$ ) internodes delimited by transverse nodes (150–170  $\mu\text{m}$  wide), inconspicuous wherever the perisarc is thick, but becoming obvious in youngest parts; each internode with 2–3 frontal nematothecae in a single row, a short cladial apophysis with its basal, simple nematotheca mounted on an inconspicuous mamelon, a nematotheca lateral to the apophysis (axillar, in front of stem), as well as an axillar nematotheca on dorsal side of the stem. Frontal nematothecae large, saccate, with wide aperture behind, sometimes giving the impression that one or two lateral apertures are present, due to their inwardly-rolled abaxial walls. Cladia alternate, fairly close to one another on each row, up to 1.3 cm long, composed of up to 18 cormidia. The latter moderately long (705–715  $\mu\text{m}$  long, 65–70  $\mu\text{m}$  wide at node), accommodating a hydrotheca in their distal  $\frac{3}{4}$ , and its 3 associated nematothecae: one mesial and a pair of laterals; 6 intranodal projections of the perisarc: 4 given off from the adaxial wall of the hydrotheca, while the remaining 2 from the abaxial perisarc of the internode. Hydrotheca 475–485  $\mu\text{m}$  deep, S-shaped in lateral view, lower half distinctly swollen when seen frontally; mesial nematotheca adnate for most of its length, leaving a short, free, bifid portion reaching the middle of the theca; aperture wide, abaxial wall inwardly-rolled; lateral nematothecae conical, with gutter-shaped apertures in their adaxial wall; hydrothecal aperture 230–240  $\mu\text{m}$  wide, rim with a prominent, rounded, abaxial cusp, lateral edges with two pairs of low, triangular cusps, prolonged adaxially by a mere undulation of the margin. Gonosome an open corbula on the modified distal portion of a cladium, after a sequence of 3–6 normal cormidia proximally; rachis divided into short internodes by means of transverse nodes; each internode with a costa (there is no distinct apophysis supporting it; costae alternate) and a large, saccate nematotheca (with gutter-shaped aperture) lateral to it; unlike the subsequent ones, the first internode of the corbula possesses an axillar nematotheca at junction between the insertion of costa and the internode; costae composed of a modified hydrotheca that retains its lateral nematothecae at their normal place, while the mesial one (with single, gutter-shaped aperture in this case) is placed a certain distance below the hydrothecal base, so as to allow the formation of a rib composed of about 3–4 pairs of nematothecae arranged along its length; except for hydrothecae of the 1<sup>st</sup> or 2<sup>nd</sup> rib, those placed more distally in the corbula possess an extra, gutter-shaped nematotheca on their dorsal side (compare Fig. 11J and 11K). The gonothecae, lenticular in shape, are inserted at the bases of costae, close to the large internodal nematotheca; perisarc flimsy.

## Remarks

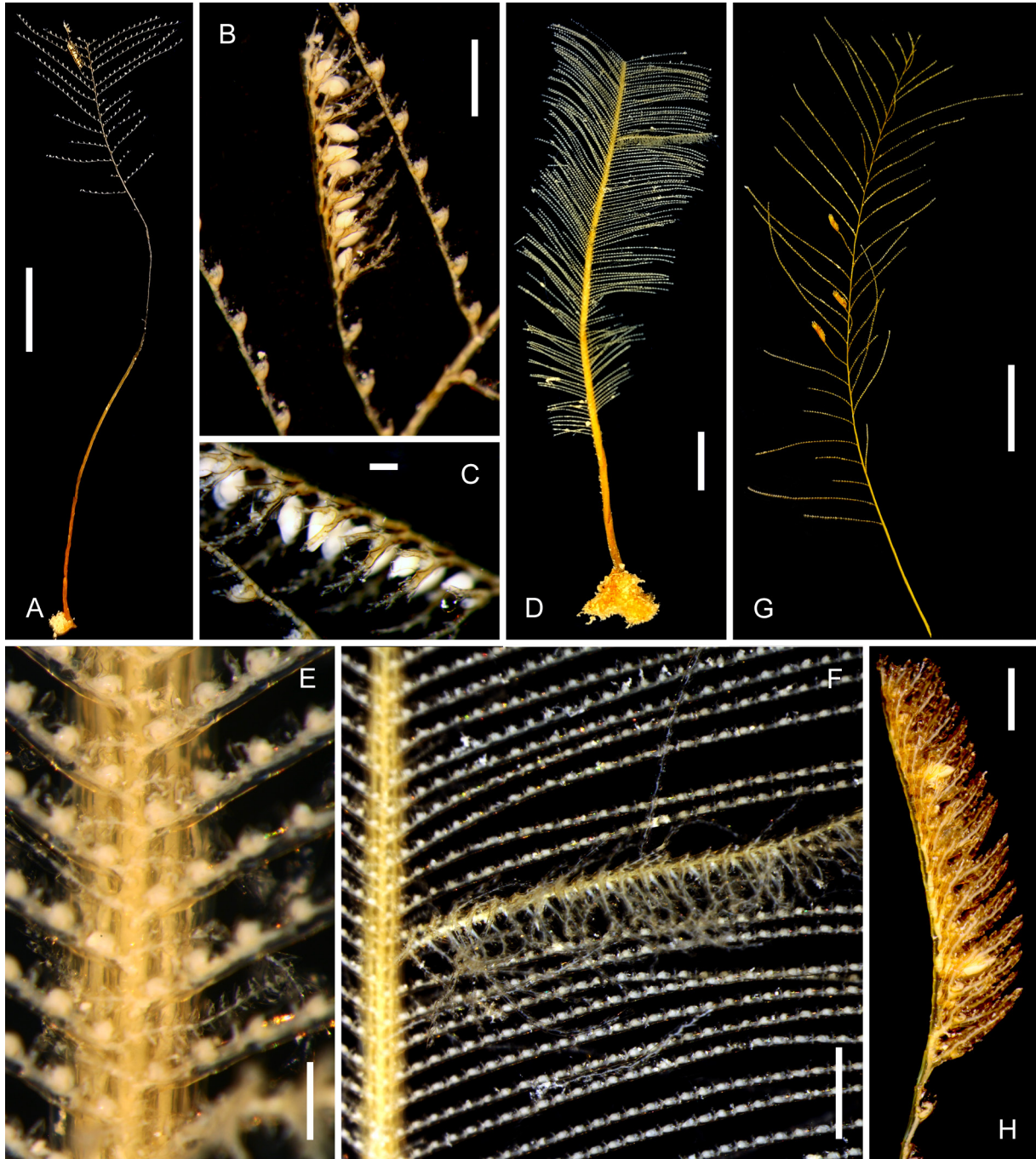
The hydrothecae of *L. fragilis* sp. nov. are mainly characterized by the notable bulging (both abaxially and laterally) of their lower halves, recalling the thecae of *L. brevirostris* (Busk, 1852) and *L. tridentata* (Versluys, 1899). The former is equally present in the material dealt with herein (Fig. 11A) and is readily distinguished from the new species through its hydrothecae occupying the entire length of the cormidium, the lack of lateral swelling in their lower half, a mesial nematotheca provided with a single, gutter-shaped aperture as well as a hydrothecal rim bearing three pairs of large, triangular cusps, in addition to the median, abaxial one. Hydrothecae of *L. tridentata* share the same distinctive characters as those listed in *L. brevirostris*, but their rim is set with a pair of low, broad, triangular, lateral cusps, in addition to the median one (Migotto 1996).

As noted above in the description, the mesial nematotheca of *L. fragilis* sp. nov. has a wide apical aperture, partly camouflaged by a backwardly-rolled abaxial wall (Fig. 11I) that creates laterally two circular passages, giving the impression – upon a frontal view of the hydrotheca – that the nematotheca is bifid (Fig. 11H). Nematothecae having a similar aperture have been described in *L. bathyalis* Ryland & Gibbons, 1991 (original account, Ryland & Gibbons 1991: fig. 14d–e) but, in this species, the nematotheca is adnate to the entire length of the abaxial wall of the hydrotheca, leaving only a short portion free that surpasses the rim. Conversely, a true bifid mesial nematotheca is to be found in *L. furcata* (Vervoort, 1941) (original account Vervoort 1941).



**Distribution**

Known only from its type locality, off New Caledonia (present study).



**Fig. 12.** A–C. *Lytocarpia fragilis* sp. nov, fertile colony (A) and details of a corbula (B–C), all from sample MNHN-IK-2015-523 (holotype). — D–F. *Lytocarpia pilosa* sp. nov., fertile colony (D), portion of stem, showing proximal parts of pseudophylactocarps (E), and corbula (F), all from sample MNHN-IK-2015-524 (holotype). — G–H. *Lytocarpia pseudoctenata* sp. nov., fertile colony (G) and corbula (H), all from sample MNHN-IK-2015-527 (holotype). Scale bars: A, D = 1 cm; B, H = 1 mm; C, E = 500  $\mu$ m; F = 2 mm; G = 2 cm.

*Lytocarpia nigra* (Nutting, 1905)

Fig. 13

*Thecocarpus niger* Nutting, 1905: 953, pl. 5 fig. 5, pl. 13 figs 1–6.

*Thecocarpus niger* – Stechow 1913: 96, figs 65–67. — Park 2010: 166, fig. 93.

*Lytocarpia niger* – Rho 1967: 346, fig. 7, pl. 1 fig. 1. — Xu *et al.* 2014: 493, fig. 365.

*Lytocarpia nigra* – Hirohito 1983: 77, fig. 40; 1995: 295, fig. 104c–e. — Schuchert 2015: 360, fig. 32.

*Aglaophenia* sp. – Inaba 1891: 307 (nr. 28), figs 82–85.

**Material examined**

PACIFIC OCEAN • 1 colony, 8.5 cm high, fertile; off New Caledonia, stn CP4786; 22°46' S, 167°42' E; 350–469 m; 29 Aug. 2016; KANACONO leg.; MNHN-IK-2015-509.

**Description**

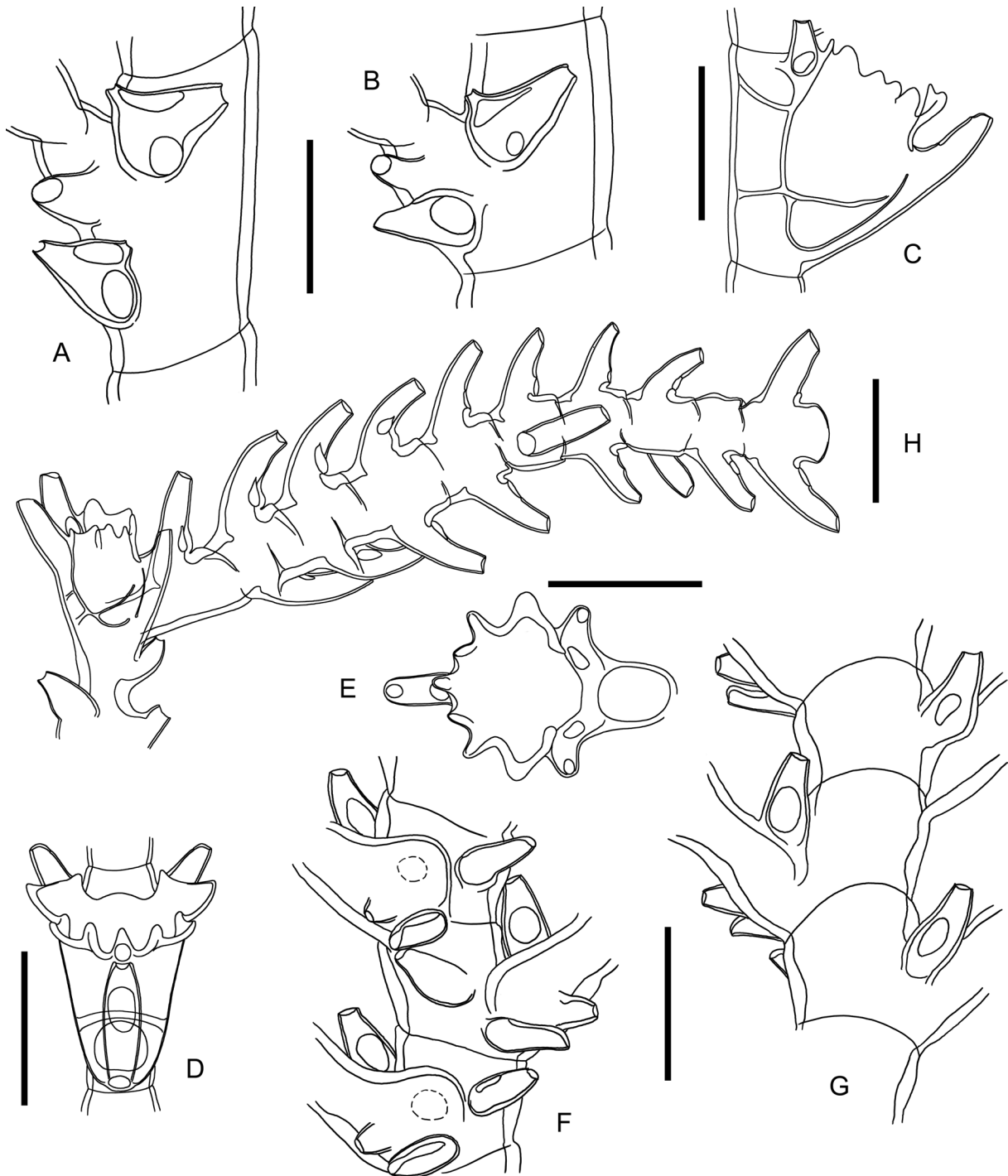
Colony erect, with lightly fascicled stem irregularly branched, up to the 4<sup>th</sup> order, so as to form an arborescent structure. Stem and branches divided into short internodes by means of transverse nodes. Proximal portion of branches devoid of cladia, but with a frontally-placed nematotheca on each internode. Subsequent internodes bearing alternate cladia, each accommodating a short apophysis and 3 nematothecae: one proximal, below the apophysis, one lateral next to it (axillar), and one conical at the base of the apophysis. Nematothecae on proximal internodes of side branches, as well as the inferior and axillar ones, inverted-triangular in general outline, basally adnate and rounded, distally free and there with a broad aperture with inwardly-curved adaxial wall, giving the impression that two lateral apertures are present. Conical nematotheca fairly developed, with rounded, apical aperture. Cladia close to one another, divided into short cormidia by means of transverse nodes, each cormidium comprising a hydrotheca and its 3 associated nematothecae: one mesial and a pair of laterals. Two intranodal septa are present: one basal, prolonged on opposite side into the hydrothecal lumen as a transverse to slightly upwardly-directed intrathecal septum, and one distal, at base of the lateral nematothecae. Mesial nematotheca arched, long, tubular, adnate for  $\frac{2}{3}$  of its length, free part almost reaching the hydrothecal rim; a short, spout-like apical aperture, as well as an ovoid one near junction with abaxial hydrothecal wall. Lateral nematothecae rather short, merely surpassing the hydrothecal rim, with circular aperture apically, and large, ovoid foramen adaxially. Hydrothecal rim with 7 cusps: median, abaxial one with thickened perisarc forming a small triangular anterior projection, and 3 pairs of laterals. First cusp narrow and triangular, second (middle) cusp often split in middle, and third (posterior) wide and broadly rectangular. Terminal stolonization often present on tips of branches. Corbula open, up to 9 mm long, replacing normal cladium, composed proximally of a normal cormidium, followed by a short internode bearing a mesial nematotheca, and a succession of up to 70 internodes bearing alternate costae; nodes oblique. Costal internodes short, bearing an arched costa and 4 nematothecae: 3 on ventral (internal) side, and one dorsally (external). Ventral nematothecae: one at base of the costa, another one lateral to it (both elongated and with gutter-shaped apertures), as well as a short, conical nematotheca at the base of the insertion of costa. Dorsal nematotheca conical, with rounded apical aperture and a large, rounded, adaxial foramen. Gonothecae lenticular, with flimsy, transparent perisarc, borne on base of costa by means of short, indistinct pedicel. Gonophores not seen.

**Remarks**

As indicated by the specific name, living colonies of this species are characteristically dark colored, due to a black pigment found in the coenosarc. This, however, has been lost in the present alcohol-preserved specimen, but its morphological features match those described earlier (see synonymy).

**Distribution**

Hawai'i, Japan, Korea (Schuchert 2015), China (Xu *et al.* 2014), New Caledonia (present study).



**Fig. 13.** *Lytocarpia nigra* (Nutting, 1905), from sample MNHN-IK-2015-509. **A–B.** Two stem internodes, to show variation in the shape of the frontal nematocystae. **C–E.** Hydrotheca in lateral (**C**), frontal (**D**) and apical (**E**) views. **F–H.** Rachis of corbula in frontal (**F**) and dorsal (**G**) aspects, and costa (**H**). Scale bars: A–H = 200  $\mu$ m.

*Lytocarpia pilosa* sp. nov.

urn:lsid:zoobank.org:act:D976AA1A-85C8-4F35-A03C-44118BDAF3B3

Figs 12D–F, 14

**Diagnosis**

*Lytocarpia* forming robust, rigid, unbranched colonies with strongly fascicled stems. Division into internodes indistinct, but each module with a proximal, frontal nematotheca, a cladial apophysis with its conical nematotheca and a pseudophylactocarp, as well as a fronto-axillar nematotheca. Pseudophylactocarps composed of a long succession of internodes bearing a mesial and two lateral nematothecae. Cladia close to one another, composed of short internodes, each accommodating a strongly S-shaped hydrotheca and its 3 gutter-shaped nematothecae; mesial one half adnate, projecting obliquely upwards, overtopping hydrothecal rim; the latter with strong median triangular cusp and 3 lateral pairs of wider and lower cusps. Corbulae on modified cladia, after a sequence of two normal cormidia; rachis geniculate, repetitive units with a costa and a spout-like nematotheca lateral to it; each costa with a proximal nematotheca, a hydrotheca with a posterior nematotheca and a downwardly-displaced mesial nematotheca, so as to give rise to a sequence of internodes, each with a complement of 3 nematothecae. Gonothecae lenticular, flimsy, inserted at the base of costae.

**Etymology**

From the Latin '*pīlōsus*, -a, -um', meaning 'hairy', with reference to the hirsute aspect of its colonies, due to the profuse occurrence of pseudophylactocarps.

**Material examined**

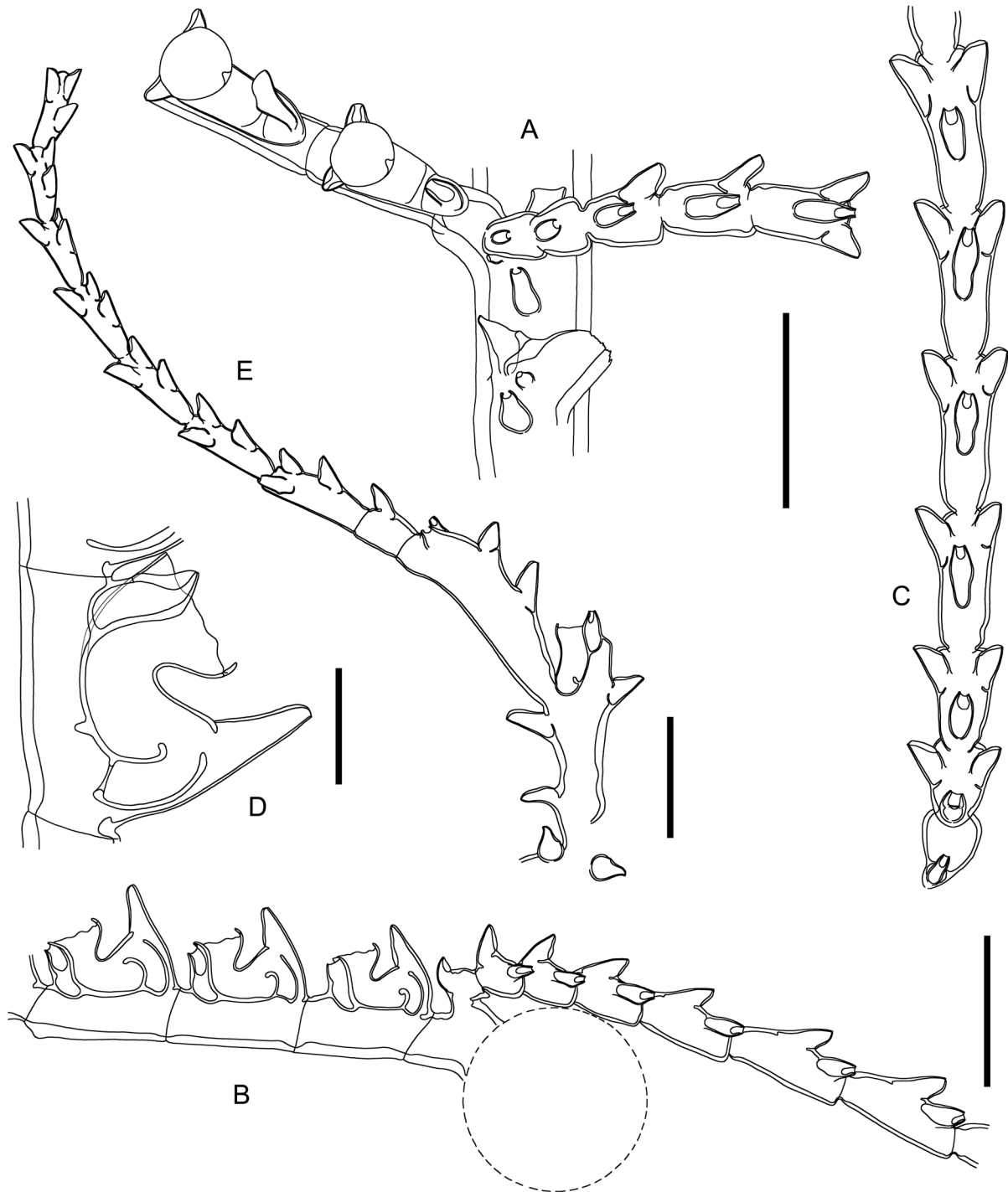
**Holotype**

PACIFIC OCEAN • 1 colony devoid of its distal part, 9 cm high, fertile; off New Caledonia, stn CP4675; 22°50' S, 167°30' E; 350–366 m; 13 Aug. 2016; KANACONO leg.; MNHN-IK-2015-524.

**Description**

Colony erect, of strongly-built appearance, comprising a single plume arising from a well-developed, much branched hydrorhizal mass. Stem unbranched, strongly fascicled, proximal part (2.5 cm long) devoid of hydrocladia, and provided with two deeply-incised, oblique nodes passing through all (main and accessory) tubes at a time. Main tube with thick perisarc, without evident division into internodes, but comprising a regular succession of modules composed of a proximal, frontal nematotheca, a lateral apophysis supporting a cladium, bearing a conical nematotheca (with small, rounded, apical aperture) near its base, as well as a fronto-axillar nematotheca; stem nematothecae large, saccate, adnate for more than half their length, adaxial wall strongly emarginated. Exceedingly long and lax pseudophylactocarps are regularly given off from the cladial apophyses, projecting onto the side opposite to corresponding cladium, freely rippling with the water currents; pseudophylactocarps composed of a succession of elongated (390–405 µm long) internodes comprising triplets of nematothecae, one proximal and mesial in position, and two other distal and laterally-displaced; proximalmost internode comparatively shorter, retaining only its mesial nematotheca. Cladia close to one another, arched backwards, up to 1.8 cm long, divided into relatively short (385–435 µm) internodes by means of transverse nodes, each internode accommodating a hydrotheca with its three associated nematothecae (all gutter-shaped): one mesial and a pair of laterals. Hydrotheca strongly S-shaped, with an internal septum given off from the proximal portion of its adaxial wall, the end of which reaches almost the middle of the lumen; mesial nematotheca about half adnate, projecting out- and upwards, and overtopping the hydrothecal margin; aperture 180–185 µm wide, rim provided with a prominent, rounded, central, abaxial cusp, followed laterally by 3 pairs of low, wide, rather inconspicuous, triangular cusps; lateral nematothecae almost tubular, strongly projecting forwards and slightly upwards. Corbulae on highly modified hydrocladia, arising after a couple of normal cormidia; corbula up to 17 mm long, open, tubular, rachis decidedly geniculate, not divided into distinct internodes; each equivalent of internode with a costa and a spout-shaped nematotheca lateral

to it; up to 34 costae per side of gonotheca; costa composed of a proximal, short, tubular part provided with a nematotheca, followed by a hydrotheca whose mesial nematotheca was displaced far below its base, so as to accommodate the insertion of a succession of highly modified hydrothecae not retaining their cavities, but represented only by their respective nematothecae; basal hydrotheca provided with an additional, posterior nematotheca; first modified hydrotheca in the row comparatively longer than the



**Fig. 14.** *Lytocarpia pilosa* sp. nov., from sample MNHN-IK-2015-524. **A–C.** Portion of stem seen frontally (**A**) and basally (**B**), and detached pseudophylactocarp (**C**). **D.** Hydrotheca. **E.** Costa of corbula. Scale bars: **A–C, E** = 500 µm; **D** = 200 µm.

subsequent ones, and provided with two mesial nematothecae; all nematothecae on costa spout-shaped. Gonothecae lenticular, with flimsy perisarc, insert near the base of each costa.

### Remarks

Hydrothecae of *L. pilosa* sp. nov. are morphologically similar to those of *L. brevirostris* (Busk, 1852) and *L. tridentata* with respect to their sigmoid shape in lateral view. However, in none of these the hydrothecae are produced abaxially (in their lower halves) to a similar extent, and their apertures are less tilted frontally. In addition, the new species is a much more robust hydroid, with a thick and strongly fascicled stem, with longer and densely-set cladia, and with profuse, defensive structures, the pseudophylactocarps.

Among its congeners, pseudophylactocarps were documented so far in *L. angulosa* (Lamarck, 1816) but, in this species, they replace normal hydrocladia (Billard 1913: fig. 73). Such structures also occur in the genus *Taxella* Allman, 1874 but, there, the 2–3 proximalmost internodes are represented by normal cormidia, while the remainder of the hydrocladium is modified so as to include only nematothecate internodes (e.g., *T. longicornis* (Busk, 1852) [Watson 2000: fig. 48e; Ronowicz *et al.* 2017: fig. 11d], *T. hornelli* (Thornely, 1904) [Thornely 1904: pl. 3 fig. 1a; Ronowicz *et al.* 2017: fig. 10c–d]). The new species *Macrorhynchia spiralis* sp. nov., described below, equally bears pseudophylactocarps, although their number per colony is far from significant.

### Distribution

Known only from the type locality, off New Caledonia (present study).

#### *Lytocarpia pseudoctenata* sp. nov.

[urn:lsid:zoobank.org:act:F9BD38C7-AFF6-4703-B6E4-3C11BB0EFE16](https://zoobank.org/act:F9BD38C7-AFF6-4703-B6E4-3C11BB0EFE16)

Figs 12G–H, 15

### Diagnosis

Species of *Lytocarpia* with tall, slender, pinnate colonies of delicate appearance. Stems unbranched, slightly fascicled, with long internodes provided with a frontal row of 4–10 nematothecae, a lateral apophysis supporting a cladium and its conical nematotheca, as well as with a fronto-axillar nematotheca. Cladia fairly distant from one another, shifted on to the anterior side of the colony. Cormidia short, with up to 7 intranodal ridges; hydrothecae strongly S-shaped, with ad- and abaxial ridges projecting far into their lumina; mesial nematotheca adnate for  $\frac{3}{4}$  its length, free part projecting upwards, not reaching hydrothecal margin; the latter with strong, median, abaxial cusps and edges with 3 pairs of additional cusps, the 2<sup>nd</sup> being comparatively more developed. Corbula on distal end of a hydrocladium, after a sequence of 5–18 normal cormidia; rachis geniculate, segments with a costal apophysis and a nematotheca lateral to it; costae forked, with a hydrotheca (devoid of its lateral nematothecae) in middle and appendages with successive pairs of opposite to subopposite nematothecae; gonothecae lenticular, flimsy, arising from the base of costal apophyses.

### Etymology

The specific name indicates obvious resemblances with *Aglaophenia ctenata* (Totton, 1930).

### Material examined

#### Holotype

PACIFIC OCEAN • 1 colony, ca 14 cm high, hydrorhiza missing, bearing 3 corbulae; off New Caledonia, stn CP4739; 22°41' S, 167°41' E; 393–358 m; 22 Aug. 2016; KANACONO leg.; MNHN-IK-2015-527.

**Paratype**

PACIFIC OCEAN • 1 colony fragment, 2.2 cm long, with one gonotheca in middle part; off New Caledonia, stn DR4772; 23°02' S, 168°21' E; 795–230 m; 28 Aug. 2016; KANACONO leg.; MNHN-IK-2015-528.

**Description**

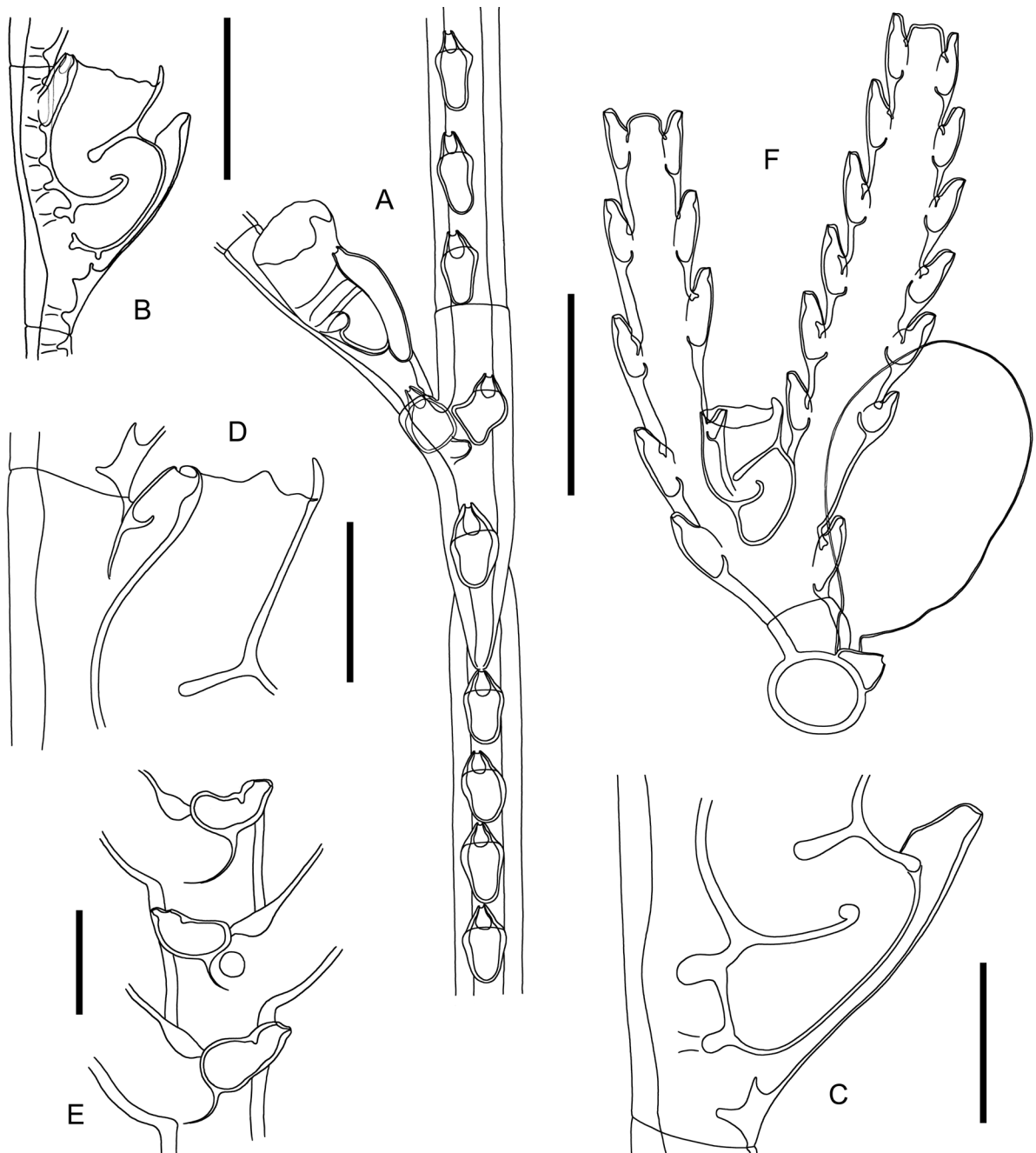
Undamaged colonies reaching more than 14 cm high; erect, slender and of delicate appearance, unable to support themselves when out of liquid, though perisarc rather thick throughout the colony; hydrorhiza not seen; stems lightly fascicled, composed of several superimposed auxiliary tubes, each adhering to the dorsal side of the preceding one, not forming a beam around the main tube, but rather resulting in a laterally-flattened structure; a notable deeply-cut, oblique node some distance above the origin from hydrorhiza, passing through all cauline tubes at a time; occasional oblique nodes sporadically along the remainder of stem; division into additional internodes not always distinct, though transverse nodes (170–180 µm wide) are more noticeable in the younger parts of the stem, where the perisarc is thinner; each internode 2–4 mm long, comprising a frontal row of 4–10 saccate nematothecae (with gutter-shaped, adaxial apertures), a short (ca 60 µm) cladial apophysis above carrying basally a conical nematotheca (with small, rounded, apical aperture), as well as an elbow nematotheca (also with gutter-shaped aperture) lateral to the insertion of apophysis on the internode (fronto-axillar). Basalmost cladia broken off, but arrangement alternate along the longest portion of the stem; up to 3.7 cm long, the two rows shifted on to the anterior side of the colony so as to form an acute angle; cladia fairly distant from one another in each row; divided into rather short (585–600 µm) internodes by means of transverse nodes (145–150 µm wide), each comprising a hydrotheca and its three associated nematothecae: one mesial and a pair of laterals; hydrotheca 525–540 µm deep, strongly S-shaped, with 2 internal septa, one adaxial arising a short distance above the base, and one abaxial given off a certain distance below the aperture from the abaxial wall, both septa protruding at least into the middle of the hydrothecal lumen; internodes with a number of incomplete internal septa: 2 abaxial and up to 5 on their adaxial side; mesial nematotheca long, tubular, adnate for more than  $\frac{3}{4}$  its length, leaving only a short (100–115 µm) portion free, provided with a gutter-shaped aperture along its whole free length; lateral nematothecae tubular, 215–220 µm long, aperture with rim deeply-scooped adaxially; hydrothecal margin with a prominent, rounded, abaxial cusp, continued on each side by three broad, triangular cusps, the second being the most developed. Gonosome an open corbula borne on a hydrocladium after a sequence of 5–18 normal cormidia; rachis slightly geniculate, divided into very short internodes (by means of transverse nodes), each bearing a costal apophysis and an elbow nematotheca lateral to it; costa separated from apophysis by transverse node; costa forked, with a basal hydrotheca (lateral nematothecae lost) in middle; mesial nematotheca situated far below the hydrothecal base, so as to accommodate the insertion of the ‘anterior’ arm, comprising 5–6 pairs of opposite to subopposite nematothecae; a nematotheca on the back of the hydrotheca, above which is inserted the ‘posterior’ arm, comprising 7–8 opposite to subopposite nematothecae; proximalmost costa of a corbula with the mesial nematotheca immediately below the hydrothecal base, not giving rise to the “anterior” arm set with nematothecae; all nematothecae elongated, with deeply-scooped adaxial margins. Gonothecae lenticular, with flimsy perisarc, arising from the base of the costal apophyses.

**Remarks**

None of the nominal species of *Lytocarpia* described so far (Schuchert 2019) possesses simultaneously two (ab- and adaxial) strongly-developed internal septa, creating such a distinctive, S-shaped appearance of their hydrothecae, as *L. pseudoctenata* sp. nov.

The new species shows striking resemblances with *Aglaophenia ctenata* (Totton, 1930) with respect to the morphology of both hydrothecae and some components of the gonosome. Indeed, hydrothecae of both are borne on short internodes, are strongly S-shaped and possess two intrathecal ridges, one

abaxial, the other adaxial, projecting halfway across their lumina (compare Fig. 15B with Totton (1930: fig. 69a)). However, the hydrothecal apertures of *A. ctenata* appear more tilted forward (Totton 1930: fig. 69a; Ralph 1961: fig. 9b; Vervoort & Watson 2003: fig. 62e, g–i). Although both species possess similarly long cladia, those of *A. ctenata* are ‘tightly packed’ (compare image ‘a’ from the frontispiece of Vervoort & Watson (2003) with Fig. 12G herein). Its stem internodes possess “one terminal apophysis with a pair of opposite nematothecae at their base and one or two nematothecae on the proximal part



**Fig. 15.** *Lytocarpia pseudoctenata* sp. nov. **A.** Portion of stem. **B–D.** Hydrotheca (**B**) and details of its basal (**C**) and distal (**D**) parts, all seen laterally. **E–F.** Portion of the rachis of corbula, and costa with gonotheca (**F**). From samples MNHN-IK-2015-527 (**C–D**) and MNHN-IK-2015-528 (**A–B, E–F**). Scale bars: **A, F** = 500 µm; **B–E** = 200 µm.



[...]. No mamelon has been observed [...]" (Vervoort & Watson 2003). As with the gonohydrocladium of *L. pseudectenata* sp. nov., that of *A. ctenata* also appears bifid (Vervoort & Watson 2003: fig. 62j), but there is no hydrotheca associated with it, and the number and position of the nematothecae are also slightly different.

### Distribution

Known only from off New Caledonia (present study).

### *Lytocarpia cf. spiralis* (Totton, 1930)

Figs 16A, 17A–B

*Thecocarpus spiralis* Totton, 1930: 238, fig. 69c–d.

*Thecocarpus spiralis* – Ralph 1961: 59, figs 8i–j, 10d.

*Lytocarpia spiralis* – Vervoort & Watson 2003: 321, figs 77d–h, 78a–e.

### Material examined

PACIFIC OCEAN • 1 colony, ca 46 cm high, bearing 11 plumose side branches, without gonothecae, hydrothecae with mostly damaged rims; off New Caledonia, stn DW5038; 19°55' S, 158°35' E; 340 m; 22 Sep. 2017; KANADEEP leg.; MNHN-IK-2015-546.

### Remarks

The present material agrees well with descriptions of *Lytocarpia spiralis* (Totton, 1930) by Ralph (1961) and Vervoort & Watson (2003) but, since it is devoid of its gonosome and the condition of the hydrothecal rim could not be assessed properly, it is assigned with a query to it.

### Distribution

Previously known from waters around New Zealand (Vervoort & Watson 2003); New Caledonia (present study).

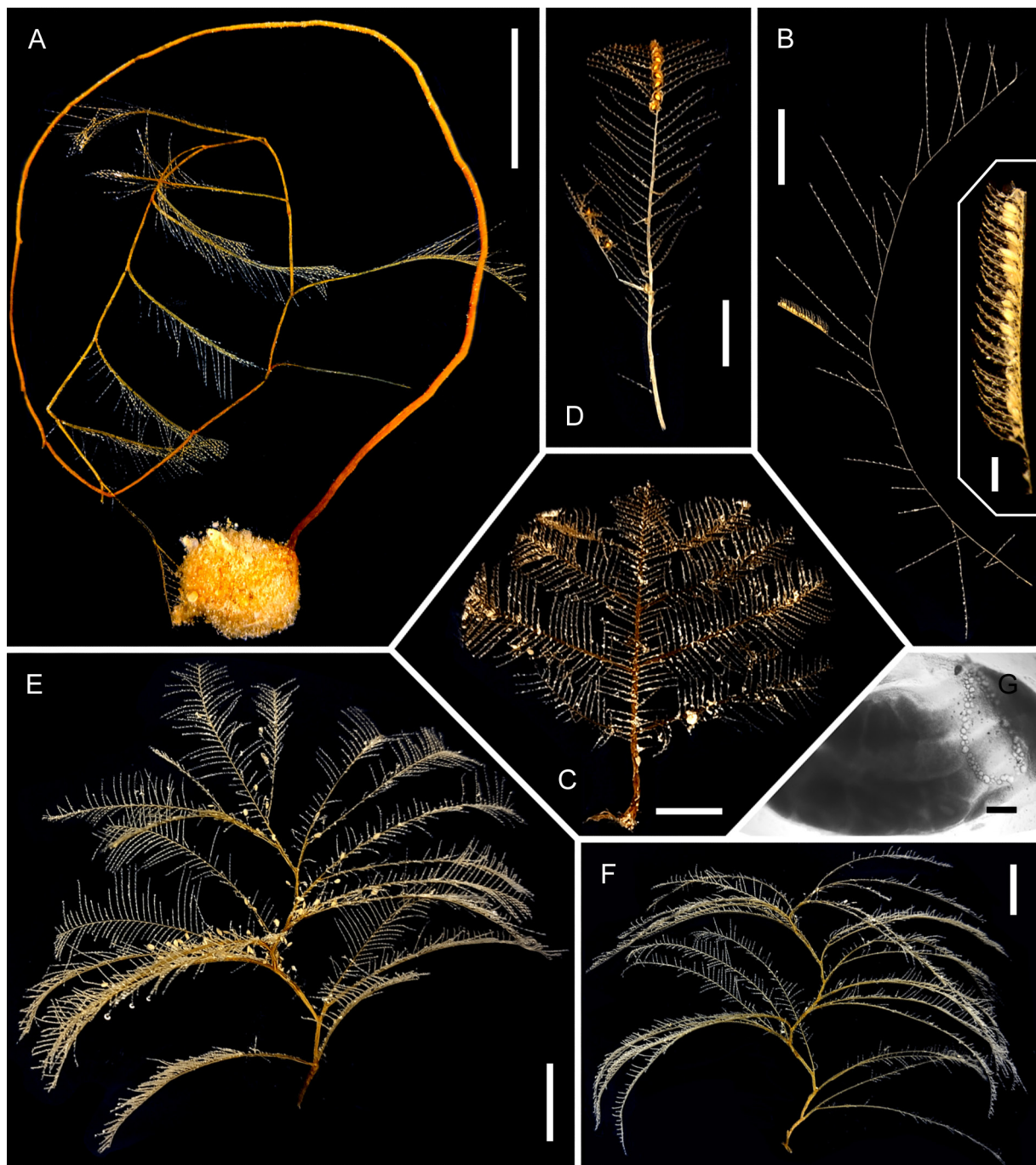
### *Lytocarpia subtilis* sp. nov.

[urn:lsid:zoobank.org:act:F077EEF0-D13A-499A-AA86-6F8D82062D42](https://zoobank.org/urn:lsid:zoobank.org:act:F077EEF0-D13A-499A-AA86-6F8D82062D42)

Figs 16B, 17C–J

### Diagnosis

Species of *Lytocarpia* with tall, exceedingly slender, pinnate colonies of a very delicate appearance, with lightly fascicled, unbranched stems. Division into internodes indistinct; a row of 8–17 frontal nematothecae between two successive cladial apophyses, the latter with a basal, simple, conical nematotheca, and a fronto-axillar nematotheca. Cladia widely-spaced from one another; cormidia quite long, with up to 11 intranodal septa, accommodating an elongate hydrotheca and its 3 associated nematothecae; free part of mesial nematotheca gutter shaped, borne on a prominent, basal, abaxial bulge of the hydrotheca; an adaxial, intrathecal septum projecting slightly upwards and over halfway into the hydrothecal lumen; rim with prominent, median, abaxial cusps, edges wavy. Corbula on distal end of cladium; rachis indistinctly divided; each segment with a lateral costa and a nematotheca near to its insertion point; costae with a hydrotheca with its full complement of nematothecae, as well as an additional one on dorsal side of internode; mesial nematotheca far below hydrothecal base, so as to give rise to an appendage set with lateral nematothecae.



**Fig. 16.** A. *Lytocarpia cf. spiralis* (Totton, 1930), colony from sample MNHN-IK-2015-546. — B. *Lytocarpia subtilis* sp. nov., colony and corbula (insert) from sample MNHN-IK-2015-525 (holotype). — C–D. *Macrorhynchia phoenicea* (Busk, 1852) (C), from sample MNHN-IK-2015-512, compared to *M. disjuncta* (Pictet, 1893) (D), from sample MNHN-IK-2015-513. — E–G. *Macrorhynchia spiralis* sp. nov., colonies from samples MNHN-IK-2015-519 (E, holotype) and MNHN-IK-2015-520 (F, one paratype), and medusoid gonophore (G) from former sample. Scale bars: A = 3 cm; B–F = 1 cm; B (insert) = 1 mm; G = 100 μm.

**Etymology**

From the Latin '*subtilis*', meaning 'slender', to describe the appearance of its hydrothecae.

**Material examined****Holotype**

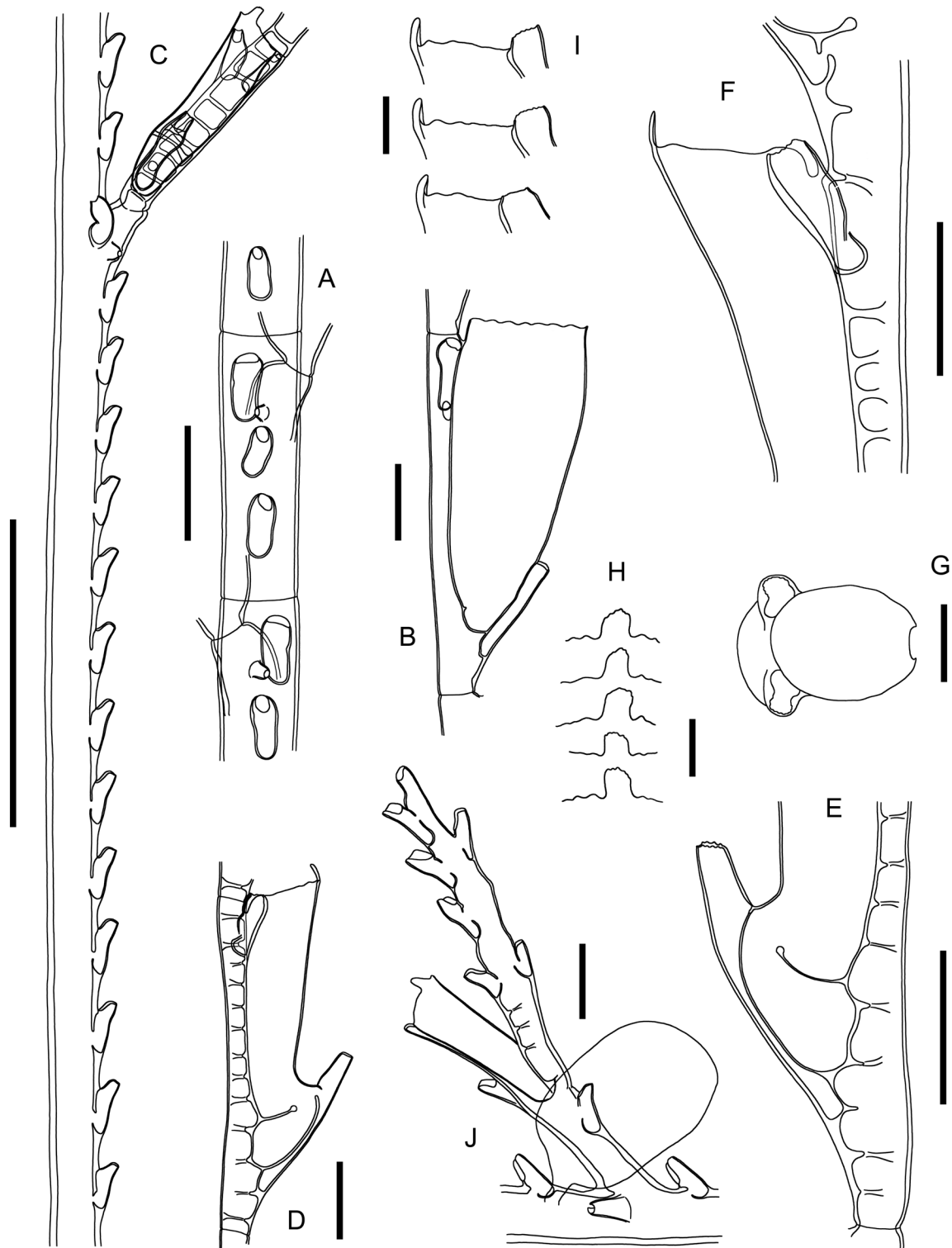
PACIFIC OCEAN • 1 upper part of colony, ca 8.5 cm long, bearing a corbula; off New Caledonia, stn DW4711; 22°47' S, 167°24' E; 335–338 m; 18 Aug. 2016; KANACONO leg.; MNHN-IK-2015-525.

**Paratype**

PACIFIC OCEAN • 3 specimens (1 colony, nearly complete, ca 14.5 cm high, with hydrorhiza but missing its distalmost part, without gonosome, 1 colony fragment, ca 14.5 cm long, missing both hydrorhiza and distal part, without gonosome, and 1 colony fragment, ca 5.5 cm long, missing both its hydrorhiza and distal part, bearing a corbula); off New Caledonia, stn CP4674; 22°48' S, 167°29' E; 311–302; 13 Aug. 2016; KANACONO leg.; MNHN-IK-2015-526.

**Description**

Colony erect, unable to support itself outside liquid, exceedingly slender and delicate; arising from branched, rhizoid stolon anchoring it in sandy bottom. Stem unbranched, lightly fascicled proximally, monosiphonic for most of its length; a deeply-cut, oblique node a certain distance above its origin from hydrorhiza; below the node, a succession of large, saccate nematothecae in a row along the main tube; above the node, the stem bears widely-spaced (2.5–3 mm apart), alternate cladia, the latter borne on short (ca 70  $\mu$ m) apophyses given off laterally and towards the 'front' of the colony, the two rows of cladia forming an acute angle; division into internodes (nodes transverse, 160–170  $\mu$ m wide) inconspicuous on stem, but equivalents of internodes comprising a row of 8–17 frontal, saccate nematothecae, a lateral apophysis above them, a simple, conical nematotheca (with small, rounded, apical aperture) on the basal part of the apophysis, as well as fronto-axillar nematotheca, rather lateral to the apophysis, having the distal part shifted on to the opposite direction; all stem nematothecae, except that borne on the mamelon, with large, adaxial, gutter-shaped apertures. Cladia up to 1.8 cm long, composed of up to 21 cormidia, not distinctly demarcated by transverse nodes; each cormidium 810–860  $\mu$ m long, 100–105  $\mu$ m wide at node, with a hydrotheca placed some distance after its proximal node, and three associated nematothecae: one mesial and a pair of laterals; 10–11 internodal projections of the perisarc, all but two given off from the adaxial wall of the hydrotheca; hydrothecae exceedingly long (680–705  $\mu$ m), slightly conical, with a basal abaxial bulge, on the top of which is mounted the free portion of the mesial nematotheca; the latter long, cylindrical, slightly concave in general outline, adnate for about  $\frac{2}{3}$  of its length, free part 120–130  $\mu$ m long, with gutter-shaped aperture all the way down to the junction with the lower abaxial wall of hydrotheca, apical rim distinctly crenulated; lateral nematothecae moderately long (170–175  $\mu$ m), broadly tubular, reaching the hydrothecal margin, aperture scooped out on adaxial side, abaxial rim distinctly crenulated; hydrothecal aperture 225–235  $\mu$ m wide, rim with a prominent abaxial cusp with crenulated apex, ridges rather wavy, without distinct cusps; an internal septum is given off from the lower part of the adaxial wall of the theca and projects for  $\frac{2}{3}$  into the lumen. Gonosome an open corbula borne on distal ends of cladia, after a succession of 6–10 normal cormidia; corbula up to 8 mm long, tubular, with straight rachis, not distinctly divided into internodes; segments short, with an indistinct lateral apophysis bearing a costa and a saccate nematotheca (with gutter-shaped aperture) lateral to it; gonothecae lenticular, with flimsy perisarc, borne near the insertion of the costa on the rachis; costae up to 20–21 per side of the gonotheca, comprising a hydrotheca with a complete set of nematothecae, in addition to which there is an extra nematotheca on the dorsal side of the internode; mesial nematotheca far below the hydrothecal base, leaving room for the insertion of a long appendage carrying 7–11 variously arranged nematothecae on both sides.



**Fig. 17.** A–B. *Lytocarpia* cf. *spiralis* (Totton, 1930), portion of stem (A) and hydrotheca (B), from sample MNHN-IK-2015-546. — C–J. *Lytocarpia subtilis* sp. nov. C. Portion of stem. D–I. Lateral view of a hydrotheca (D), with details of its basal (E) and distal (F) parts; hydrotheca seen apically (G), and variation in the shape of its margin seen frontally (H) and laterally (I). J. Portion of corbula rachis with costa and gonotheca. From samples MNHN-IK-2015-525 (C, E–G) and MNHN-IK-2015-526 (D, H–J). Scale bars: A = 300  $\mu$ m; B, D–F, J = 200  $\mu$ m; C = 1 mm; G–I = 100  $\mu$ m.

**Remarks**

None of the nominal species of *Lytocarpia* Kirchenpauer, 1872 described so far (Schuchert 2019) possesses such exceedingly long and slender hydrothecae. Elongate, but not slender, hydrothecae are met with in *L. alata* Vervoort & Watson, 2003 (original account), *L. distans* Allman, 1877 (Ramil & Vervoort 1992b), *M. myriophyllum* (Linnaeus, 1758) (Ramil *et al.* 1998), and *L. spiralis* (Totton, 1930) (dealt with in the present study, Fig. 17B).

**Distribution**

Known only from off New Caledonia (present study).

Genus *Macrorhynchia* Kirchenpauer, 1872

*Macrorhynchia phoenicea* (Busk, 1852)

Figs 16C–D, 18A

*Macrorhynchia phoenicea* – Di Camillo *et al.* 2009: 218, figs 2h–i, 6, 9.

**Material examined**

PACIFIC OCEAN • 1 profuse colony on gorgonian, with stems up to 10 cm high, some bearing phylactocarps; off New Caledonia, stn DW4945; 25°22' S, 159°43' E; 130–108 m; 4 Sep. 2017; KANADEEP leg.; MNHN-IK-2015-510 • 1 colony, composed of a couple of stems, 2.5 and 4 cm high; off New Caledonia, stn DW4775; 23°03' S, 168°17' E; 140–277 m; 28 Aug. 2016; KANACONO leg.; MNHN-IK-2015-511 • 5 colonies, 2.5–3.5 cm high, of which 4 bear incipient phylactocarps; off New Caledonia, stn DW4774; 23°01' S, 168°19' E; 100–90 m; 28 Aug. 2016; KANACONO leg.; MNHN-IK-2015-512.

**Comparative material**

PACIFIC OCEAN • 1 complete colony, 6.5 cm high, as well as 3 fragments (1.5, 2.5 and 3.5 cm long) of *Macrorhynchia disjuncta* (Pictet, 1893), all fertile; off Vanuatu, stn CP1104; 15°04' S, 167°07' E; 125–129 m; 7 Oct 1994; MUSORSTOM 8 leg.; MNHN-IK-2015-513.

**Remarks**

For a recent description of this well-known species, refer to Di Camillo *et al.* (2009), who also provide an extensive synonymy.

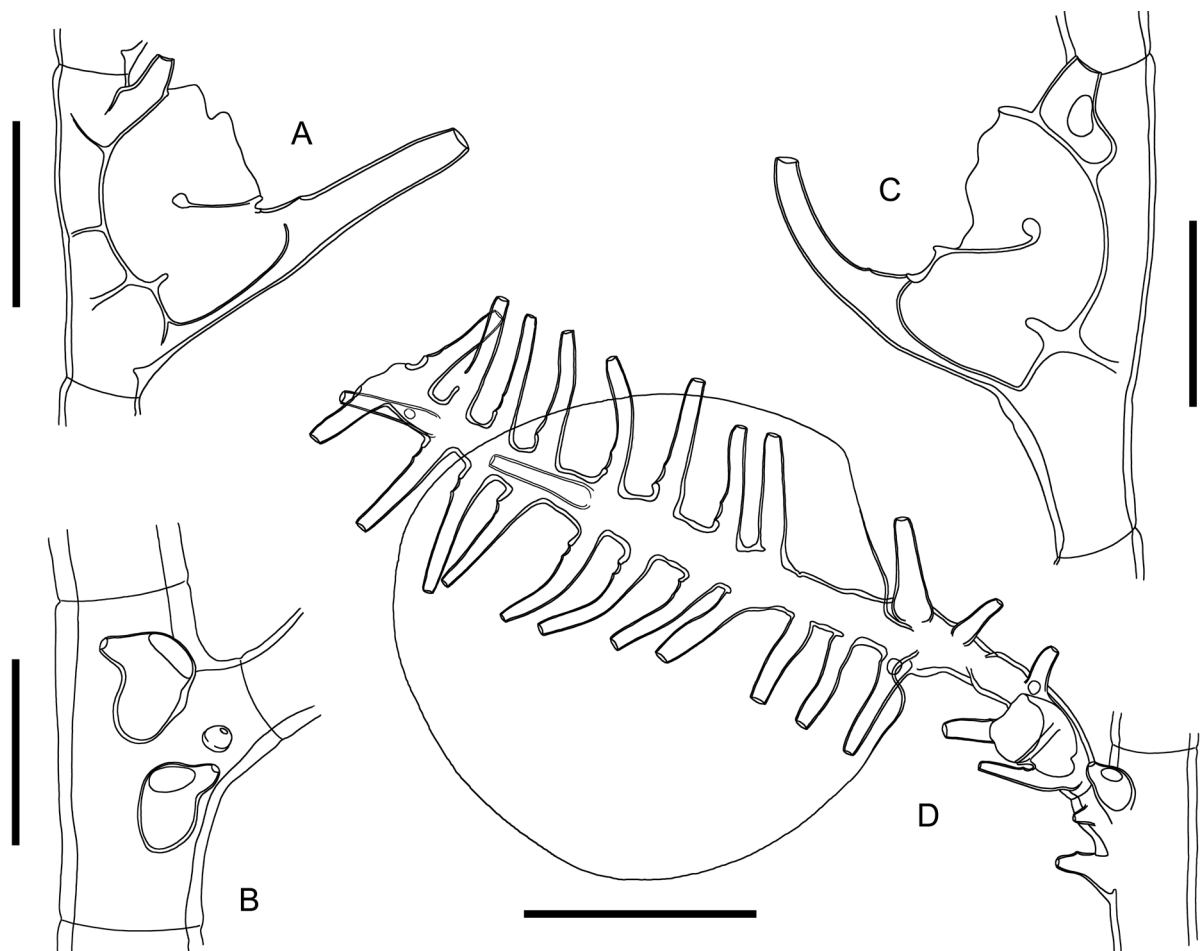
Schuchert (2003) noted striking resemblances between the hydrothecae of *Aglaophenia disjuncta* Pictet, 1893, a hydroid with a so far unknown gonosome, and those of the present species, and questioned their possible conspecificity. A few well-preserved, fertile specimens, undoubtedly assignable to Pictet's species, occur in material from off Vanuatu gathered during the MUSORSTOM 8 Expedition. Their appearance (Fig. 16D) immediately distinguishes them from typical colonies of *M. phoenicea* (Fig. 16C), in being more delicate, with a less rigid and straw-colored perisarc, with more distant and comparatively longer cladia, with longer cormidia and slightly larger hydrothecae.

Stems of the species described by Pictet (1893) are lightly fascicled and scarcely branched, as for instance with one branch occurring in the tallest (6.5 cm high) specimen available. The stem and side branches are transversely divided into moderately long internodes, each bearing a cladial apophysis and 3 nematothecae, two large and one reduced: one at the base of the apophysis, a second axillar, and a short, conical theca on a mamelon (Fig. 18B). The large nematothecae are half adnate to the internode and possess a small, rounded aperture projecting laterally, as well as a large, broadly ovoid

aperture behind. The proximal parts of the stem and branches are devoid of cladia, bear a row of large nematothecae with a conical distal half and have one of their apertures pointing upwards, while the other is comparatively larger and situated behind. The characteristic shape of the hydrothecae is depicted in Fig. 18C. The gonosome is typical of *Macrorhynchia*, and replaces a normal cladium, not forming pseudo-corbulae, but isolated phylactocarps; the proximalmost internode is a normal cormidium, on the distal part of which is inserted a long appendage with pinnate appearance resulting from the presence of (often) opposite pairs of exceedingly long nematothecae with two apertures: one small, apical, the other ovoid, at the base of the nematotheca. Occasionally, a few additional nematothecae in a row are to be found on the outer side of the phylactocarp. The gonothecae are large and lenticular, with flimsy perisarc, and are borne near the base of the appendage, amongst the proximalmost nematothecae.

### Distribution

Widespread in the tropical parts of the Indian and southern Pacific oceans (Di Camillo *et al.* 2009).



**Fig. 18.** A. *Macrorhynchia phoenicea* (Busk, 1852), hydrotheca from sample MNHN-IK-2015-510. — B–D. *Macrorhynchia disjuncta* (Pictet, 1893), portion of stem (B), hydrotheca (C) and phylactocarp with gonotheca (D) from sample MNHN-IK-2015-513. Scale bars: A–C = 200  $\mu$ m; D = 500  $\mu$ m.

*Macrorhynchia spiralis* sp. nov.

[urn:lsid:zoobank.org:act:DA1E42B9-C682-4639-B3B1-4A9A7E2C7143](https://doi.org/10.21203/rs.3.rs-1414143/v1)

Figs 16E–G, 19; Table 3

**Diagnosis**

Species of *Macrorhynchia* with a distinctly spirally-twisted stem, giving rise at each bend to a side branch that branches soon again, forming a bifid ramification. Stem and side branches strongly fascicled. Internodes short, with a proximal frontal nematotheca, a cladial apophysis above with its simple, conical nematotheca and a fronto-axillar nematotheca; cauline nematothecae saccate, with deeply scooped adaxial walls. Cladia alternate, fairly close to one another; cormidia moderately long, hydrotheca cup-shaped, rather deep, aperture slightly sloping frontally, rim with 9 triangular cusps with rounded tips, of which the median, abaxial one is the most prominent; a slightly sigmoid, adaxial, intrathecal septum given off softly obliquely, reaching almost to abaxial wall; mesial nematotheca with short, spout-like aperture, not reaching middle level of hydrotheca; lateral nematothecae barrel-shaped, with rim scooped out adaxially. Pseudophylactocarps, composed of chains of atrophied hydrothecae, borne on proximal parts of branches. Phylactocarp borne on a modified cladium, after 1–2 normal cormidia; first (occasionally second) segment, an atrophied hydrotheca, with its mesial nematotheca displaced more distally, and a short, lateral projection (on one side) bearing a couple of nematothecae similar to the laterals; gonotheca lenticular, flimsy, on top of atrophied hydrotheca, between the lateral nematothecae; gonophore, a medusoid.

**Etymology**

From the Latin ‘*spīra*’, meaning ‘spiral’, with reference to the distinctive shape of the stem.

**Material examined**

**Holotype**

PACIFIC OCEAN • upper part of 1 colony, ca 6.5 cm high, with female gonophores; off New Caledonia, stn DW4954; 24°12' S, 159°41' E; 300 m; 5 Sep. 2017; KANADEEP leg.; MNHN-IK-2015-519.

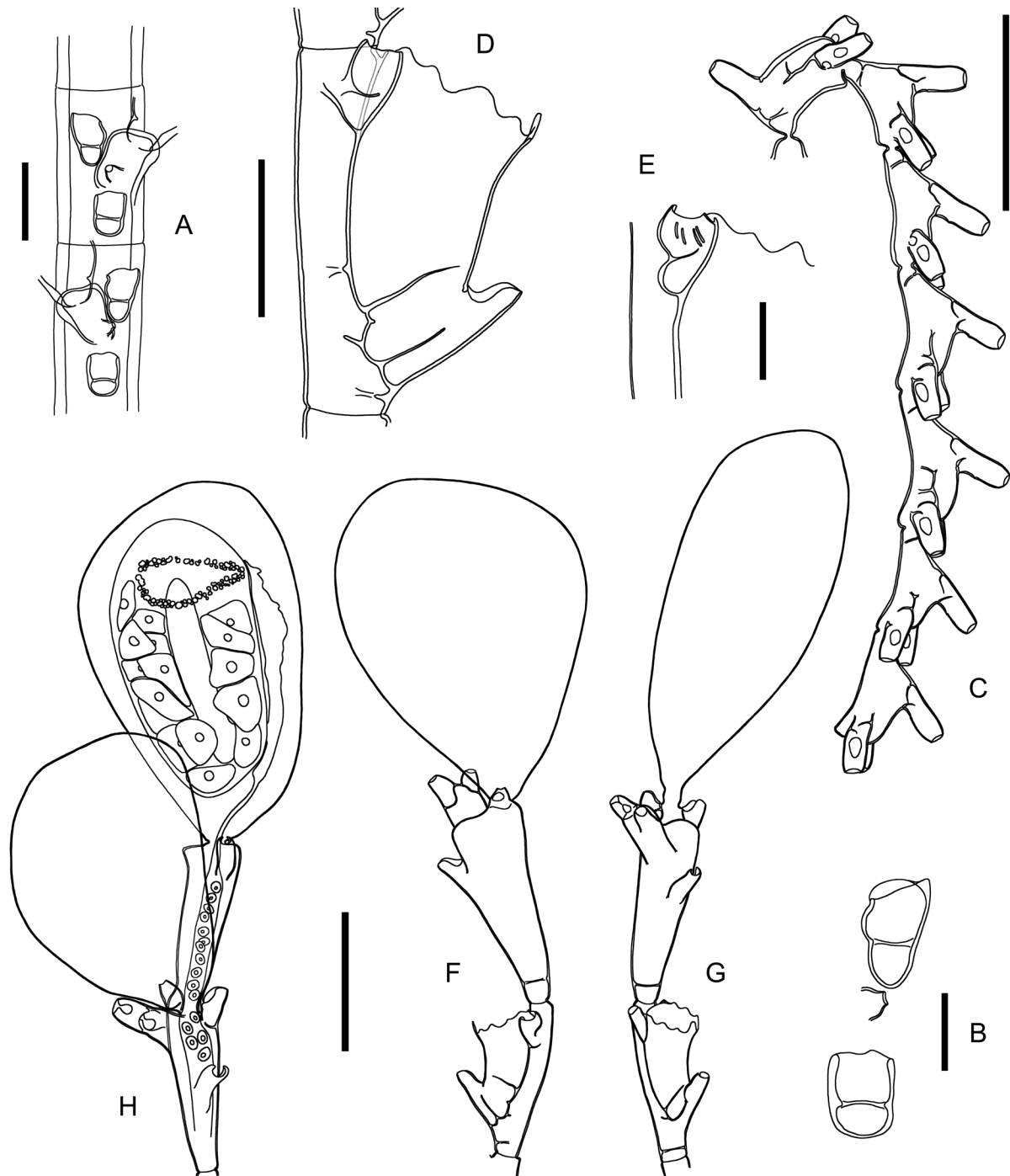
**Paratypes**

PACIFIC OCEAN • upper part of 1 colony, ca 8 cm high, with gonophores; off New Caledonia, stn DW5007; 22°12' S, 159°02' E; 290–750 m; 19 Sep. 2017; KANADEEP leg.; MNHN-IK-2015-520 • 1 entire sterile colony, ca 10.5 cm high; off New Caledonia, stn DW5008; 22°12' S, 159°02' E; 300–750 m; 19 Sep. 2017; KANADEEP leg.; MNHN-IK-2015-522.

**Description**

Colonies erect, sympodially built, with fascicled stems and side branches, grading to monosiphonic distally. Stem straight basally for a varied length, then bends at irregular intervals adopting a spiral arrangement. At each bend, a side branch arises as a rectilinear prolongation of the preceding portion of the stem, and usually ramifies once a short distance from its origin, both branches bearing hydrocladia for most of their length; proximally, a linear succession of saccate nematothecae with large apical foramina. Division into internodes indistinct wherever the perisarc is thick, but becomes evident towards the distal parts of the branches; internodes relatively short (400–420 µm long, 245–250 µm wide at node), with a large, proximal nematotheca, a cladial apophysis above, a fronto-axillar nematotheca, and a simple, conical nematotheca (with small, rounded, apical aperture) on the basal part of apophysis; nematothecae saccate, adnate for most of their length, having apically a large aperture whose rim is lowered adaxially. Cladia alternate, up to 14 mm long, composed of short cormidia (475–490 µm long, 95–100 µm wide at node), each accommodating a hydrotheca and its three nematothecae: one mesial and a pair of laterals. Hydrotheca cup-shaped, rather deep (390–400 µm), abaxial wall 215–240 µm long, straight for most of

its length, gently expanding towards aperture; the latter 205–215  $\mu\text{m}$  wide, slightly sloping frontally; rim with 9 rounded cusps, the uneven, abaxial one being the most prominent, and slightly inwardly-curved, the 4 pairs on the edges being comparatively broader and of varied development; an internal



**Fig. 19.** *Macrorhynchia spiralis* sp. nov., from sample MNHN-IK-2015-519. **A– B.** Portion of stem (A) and detail of the nematothecae from the vicinity of a cladial apophysis (B). **C.** Pseudophylactocarp. **D–E.** Hydrotheca (D) and one of its lateral nematothecae (E), both in lateral view. **F–H.** Same phylactocarp with empty gonotheca in two different views (F–G), and phylactocarp with two gonothecae, one of which bears a female medusoid gonophore (H). Scale bars: A, D = 200  $\mu\text{m}$ ; B, E = 100  $\mu\text{m}$ , C, F–H = 500  $\mu\text{m}$ .



**Table 3.** Nominal species of *Macrorhynchia* Kirchenpauer, 1872 with saccate hydrothecae and adaxial but no abaxial, intrathecal septa, similar to those of *Macrorhynchia spiralis* sp. nov., and their morphological differences to the new species.

Nominal species	Brief description, with emphasis on the distinctive features, and geographical distribution
<i>M. allmani</i> (Nutting, 1900)	Mesial nematotheca adnate for most of its length to the abaxial wall of hydrotheca, distal tip <i>reaching</i> the hydrothecal aperture. Gonosome described by Galea (2013). Distribution: tropical western Atlantic (Calder 1997).
<i>M. clarkei</i> (Nutting, 1900)	Mesial nematotheca adnate for most of its length to the abaxial wall of hydrotheca, distal tip <i>reaching</i> the hydrothecal aperture. Gonosome described by Ansín Agís <i>et al.</i> (2001). Distribution: tropical western Atlantic, Cape Verde Islands (Calder 2013).
<i>M. curta</i> (Nutting, 1900)	Poorly known species, with mesial nematotheca reaching <i>middle part</i> of the abaxial wall of hydrotheca. Gonosome unknown. Distribution: Bahamas (Nutting 1900).
<i>M. furcata</i> (Nutting, 1900)	Poorly known species, with mesial nematotheca reaching <i>middle part</i> of the abaxial wall of hydrotheca. Gonosome unknown. Distribution: Bahamas (Nutting 1900).
<i>M. grandis</i> (Clarke, 1879)	Poorly known species, with mesial nematotheca adnate for most of its length to the abaxial wall of hydrotheca, distal tip <i>reaching or surpassing</i> the hydrothecal aperture. Gonosome described by Nutting (1900) Distribution: tropical western Atlantic (Calder 1997).
<i>M. hawaiiensis</i> (Nutting, 1905)	Poorly known species, with mesial nematotheca <i>becoming free in middle</i> of hydrotheca, tip not reaching aperture; one median abaxial cusp and <i>2 pairs of 2 small, uneven lateral cusps</i> . Gonophore described by Nutting (1905). Distribution: Hawai'i (Nutting 1905).
<i>M. longiramosa</i> (Fraser, 1945)	Poorly known species, with mesial nematothecae <i>almost as long</i> as the abaxial side of the hydrotheca, becoming free <i>just below</i> the thecal aperture. Gonosome unknown. Distribution: Dorsey Canyon, Gulf of Mexico (Fraser 1945).
<i>M. mercatoris</i> (Leloup, 1937)	Poorly known species, with mesial nematotheca adnate for most of its length to the abaxial wall of hydrotheca, tip <i>almost reaching</i> the rim; first cormidium with <i>asymmetrical</i> lateral nematothecae. Distribution: Florida, USA (Leloup 1937).
<i>M. mulderi</i> (Bartlett, 1907)	Small hydroid. Hydrotheca <i>constricted</i> above the site where the mesial nematotheca becomes free; with <i>abaxial carina</i> ending distally in <i>rounded crest</i> ; mesial nematotheca partly adnate to lower abaxial wall of hydrotheca; lateral nematothecae reaching the rim; margin with 1 median, abaxial cusp narrow and incurved, as well as 4 pairs of laterals: 1 <sup>st</sup> <i>rounded triangular, slightly projecting outwards</i> , 2 <sup>nd</sup> long, roughly <i>rectangular</i> , strongly <i>incurved over</i> hydrothecal aperture, 3 <sup>rd</sup> broad, rounded at apex and <i>projecting outwards</i> , 4 <sup>th</sup> long, <i>narrow, slightly incurved over</i> hydrothecal aperture (Mulder & Trebilcock 1916). Gonosome described by Watson (1973). Distribution: southern Australia (Mulder & Trebilcock 1916, Watson 1973).
<i>M. racemifera</i> (Allman, 1883)	Poorly known species, with mesial nematotheca adnate for most of its length to the abaxial wall of hydrotheca, distal tip <i>overtopping</i> the hydrothecal aperture. Gonosome described in the original account. Distribution: off Bahia, Brazil (Allman 1883).
<i>M. ramosa</i> (Fewkes, 1881)	Poorly known species, with mesial nematotheca adnate for most of its length to the abaxial wall of hydrotheca, distal tip <i>overtopping</i> the hydrothecal aperture. Distribution: tropical western Atlantic (Calder 1997).
<i>M. robusta</i> (Fewkes, 1881)	Poorly known species, with mesial nematotheca adnate for <i>almost the whole length</i> of the abaxial wall of hydrotheca. Gonosome unknown. Distribution: Montserrat (Fewkes 1881).
<i>M. similis</i> (Nutting, 1905)	Poorly known species, with <i>rather deep</i> hydrothecae, with <i>nearly horizontal</i> aperture; rim with median, abaxial cusps and <i>3 pairs</i> of laterals; mesial nematotheca becoming <i>free in middle</i> of hydrotheca, laterals <i>tubular and narrow, distinctly overtopping</i> the hydrothecal rim; phylactocarps with normal cormidium proximally, followed by a few <i>short</i> internodes carrying abortive (closed) hydrothecae that retain only their <i>normal</i> complement of nematothecae; <i>no pseudophylactocarps</i> . Distribution: Hawai'i (Nutting 1905).

septum, of a slightly sigmoid appearance, is given off softly obliquely from the lower part of the adaxial thecal wall, penetrating deep into the lumen, almost reaching the abaxial wall; mesial nematotheca fused to the abaxial wall of hydrotheca for most of its length, leaving distally a short (45–60 µm long), spout-shaped aperture, not reaching the middle of the hydrotheca; lateral nematothecae broadly barrel-shaped, 110–120 µm long and ca 50 µm wide at aperture, rim scooped out on adaxial side. Fertile colonies produce two distinct structures: one not associated to the gonosome, the other being part of it. The former are pseudophylactocarps, composed of a chain of modified hydrothecae devoid of lumina, but retaining their complement of nematothecae (the latter are all tubular, with a rounded distal aperture and an ovoid, proximal, adaxial one); they are abundantly borne on small, alternate apophyses arising regularly and slightly laterally to the nematothecae of the proximal (acladiate) portion of branches, and encircle their long axis; no gonothecae have been observed associated with the pseudophylactocarps. The gonosome proper is borne on the distal parts of distally-modified cladia that retain proximally 1 (occasionally up to 4) normal cormidia, followed by 1–2 elongated internodes representing atrophied hydrothecae (devoid of lumina) that retain their normal complement of nematothecae, in addition to which a pair of nematothecae (similar to the laterals) is mounted on a conspicuous lateral, subterminal projection. There is some variation in the structure of the proximal part of the fertile cladium: the proximalmost hydrotheca (when only one is present) may be suppressed and replaced by one or two short internodes, the proximalmost bearing one nematotheca, the second three (one mesial and a pair of laterals). Gonothecae lenticular, 1150–1380 µm long and 750–795 µm wide, with flimsy perisarc, inserted between the pair of lateral nematothecae of the distalmost, atrophied hydrotheca; the gonophore is a medusoid, composed of a central spadix encircled by a single layer of large oocytes (the holotype is a female colony), and bearing apically a belt of refringent corpuscles.

### Remarks

Hydrothecae with similar shape as those of *M. spiralis* sp. nov., i.e., cup-shaped, with intrathecal adaxial but not abaxial ridge, are found in a number of congeners. Their distinguishing features with respect to the new species are emphasized in Table 3.

As noted above, this species produces a medusoid gonophore. At least three other nominal species reproduce in a similar way, namely *M. filamentosa* (De Lamarck, 1816), *M. philippina* Kirchenpauer, 1872 and *M. racemifera* (Allman, 1883) (Galea 2018), suggesting that this mode of dispersal could be the rule within the genus, as it probably is in the plumulariid genus *Dentitheca* Stechow, 1920 (Galea *et al.* 2012).

### Distribution

Known only from off New Caledonia (present study).

### Discussion

No account published so far dealt expressly with the aglaopheniid hydroids of New Caledonia. However, other families have been studied quite accurately (e.g., Sertularellidae Maronna *et al.*, 2016, Sertulariidae Lamouroux, 1812, Lafoeidae Hincks, 1868, Halopterididae Millard, 1962, Kirchenpaueriidae Stechow, 1921 and Plumulariidae McCrady, 1859), while some others have received lesser attention due to a limited number of collected specimens (e.g., Staurothecidae Maronna *et al.*, 2016, Symplectoscyphidae Maronna *et al.*, 2016, Syntheciidae Marktanner-Turneretscher, 1890, Thyroscyphidae Stechow, 1920 and Zygophylacidae Quelch, 1885) (all reviewed and/or dealt with in Galea (2016) and Galea & Schuchert (2019)). The aglaopheniid hydroids belong to the latter category, with only 16 species occurring in collections from the KANACONO and KANADEEP expeditions. Of these, eight hydroids represent new species: three belong to the genus *Cladocarpus* Allman, 1874, four to *Lytocarpia* Kirchenpauer, 1872 and one to *Macrorhynchia* Kirchenpauer, 1872, thus advancing our knowledge on the hydroid fauna of the region.

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## References

- Allman G.J. 1877. Report on the Hydroida collected during the exploration of the Gulf Stream by L. F. de Pourtalès, Assistant United States Coast Survey. *Memoirs of the Museum of Comparative Zoölogy at Harvard College* 5 (2): 1–66. <https://doi.org/10.5962/bhl.title.10420>
- Allman G.J. 1883. Report on the Hydroida dredged by H.M.S. *Challenger* during the years 1873–76. Part I. – Plumularidae. *Report on the Scientific Results of the Voyage of H.M.S. Challenger during the Years 1873–76, Zoology* 7 (20): 1–55. <https://doi.org/10.5962/bhl.title.11299>
- Altuna A., Murillo F.J. & Calder D.R. 2013. Aglaopheniid hydroids (Cnidaria: Hydrozoa: Aglaopheniidae) from bathyal waters of the Flemish Cap, Flemish Pass, and Grand Banks of Newfoundland (NW Atlantic). *Zootaxa* 3757 (5): 501–537. <https://doi.org/10.11646/zootaxa.3737.5.1>
- Ansín Agís J., Ramil F. & Vervoort W. 2001. Atlantic Leptolida (Hydrozoa, Cnidaria) of the families Aglaopheniidae, Halopterididae, Kirchenpaueriidae and Plumulariidae collected during the CANCAP and Mauritania-II expeditions of the National Museum of Natural History, Leiden, the Netherlands. *Zoologische Verhandelingen, Leiden* 333: 1–268.  
Available from <https://repository.naturalis.nl/document/46286> [accessed 6 Mar. 2020].
- Bale W.M. 1888. On some new and rare Hydroida in the Australian Museum collection. *Proceedings of the Linnean Society of New South Wales* 2 (3) 2: 745–799. <https://doi.org/10.5962/bhl.title.26267>
- Bale W.M. 1914. Report on the Hydroida collected in the Great Australian Bright and other localities, II. Fisheries. *Zoological (and Biological) Results of the Fishing Experiments carried out by F.I.S. “Endeavour”, 1909–1910* 2 (4): 164–188.
- Bale W.M. 1919. Further notes on Australian hydroids. IV. *Proceedings of the Royal Society of Victoria* 31 (2): 327–362.
- Bedot M. 1921. Hydroïdes provenant des campagnes des Yachts *Hirondelle* et *Princesse-Alice* (1887–1912). *Résultats des Campagnes scientifiques accomplies sur son Yacht par Albert I<sup>er</sup> Prince souverain de Monaco* 60: 1–74.
- Billard A. 1913. Les hydroïdes de l’expédition du Siboga. I. Plumulariidae. *Siboga-Expeditie Monographie* 7a: 1–115.
- Billard A. 1918. Notes sur quelques espèces d’hydroïdes de l’Expédition du Siboga. *Archives de Zoologie expérimentale et générale* 57: 21–27.
- Billard A. 1934. Note sur quelques hydroïdes du Maroc. *Bulletin de la Société zoologique de France* 59: 227–231.
- Bogle M.A. 1975. *A Review and Preliminary Revision of the Aglaopheniinae (Hydroida: Plumulariidae) of the Tropical Western Atlantic*. MSc Thesis, University of Miami, Coral Gables, USA.

- Bogle M.A. 1984. *Cladocarpoides yucatanicus*, a new genus and species of Aglaopheniinae (Coelenterata: Hydrozoa: Plumulariidae) from Arrowsmith Bank, Yucatan Channel. *Bulletin of Marine Science* 34 (1): 135–140.
- Briggs E.A. 1918. Descriptions of two new hydroids, and a revision of the hydroid-fauna of Lord Howe Island. *Records of the Australian Museum* 12 (3): 27–47. <https://doi.org/10.3853/j.0067-1975.12.1918.878>
- Broch H. 1918. Hydrozoa (Part II). *Danish Ingolf-Expedition* 5 (7): 1–206.
- Calder D.R. 1997. Shallow-water hydroids of Bermuda: superfamily Plumularioidea. *Royal Ontario Museum Life Sciences Contributions* 161: 1–84.
- Calder D.R. 2013. Some shallow-water hydroids (Cnidaria: Hydrozoa) from the central east coast of Florida, USA. *Zootaxa* 3648 (1): 1–72. <https://doi.org/10.11646/zootaxa.3648.1.1>
- Calder D.R. & Vervoort W. 1998. Some hydroids (Cnidaria: Hydrozoa) from the Mid-Atlantic Ridge, in the North Atlantic Ocean. *Zoologische Verhandelingen, Leiden* 319: 1–65.  
Available from <https://www.repository.naturalis.nl/document/149104> [accessed 6 Mar. 2020].
- Cornelius P.F.S. 1995. North-west European thecate hydroids and their medusae. Part 2. Sertulariidae to Campanulariidae. *Synopses of the British Fauna* 50: 1–386.
- Di Camillo C.G., Puce S. & Bavestrello G. 2009. *Macrorhynchia* species (Cnidaria: Hydrozoa) from the Bunaken Marine Park (North Sulawesi, Indonesia) with a description of two new species. *Italian Journal of Zoology* 76 (2): 208–228. <https://doi.org/10.1080/11250000802182018>
- Di Camillo C.G., Puce S. & Bavestrello G. 2011. *Lytocarpia* and *Cladocarpus* (Cnidaria: Hydrozoa, Aglaopheniidae) from the Bunaken National Marine Park (North Sulawesi, Indonesia). *Marine Biology* 41 (4): 517–536. <https://doi.org/10.1007/s12526-011-0081-4>
- Fewkes J.W. 1881. Report on the Acalephae. In: Reports on the results of dredging, under the supervision of Alexander Agassiz, in the Caribbean Sea, in 1878, 1879, and along the Atlantic coast of the United States, during the summer of 1880, by the U.S. Coast Survey Steamer Blake. *Bulletin of the Museum of Comparative Zoölogy, at Harvard College* 8 (7): 127–140.  
Available from <https://www.biodiversitylibrary.org/page/28870347> [accessed 6 Mar. 2020].
- Fraser C.M. 1945. Notes on some recently collected hydroids in the United States National Museum, with descriptions of three new species. *Journal of the Washington Academy of Sciences* 35 (1): 21–23.
- Galea H.R. 2007. Hydroids and hydromedusae (Cnidaria: Hydrozoa) from the fjords region of southern Chile. *Zootaxa* 1597: 1–116.
- Galea H.R. 2008. On a collection of shallow-water hydroids (Cnidaria: Hydrozoa) from Guadeloupe and Les Saintes, French Lesser Antilles. *Zootaxa* 1878: 1–54.
- Galea H. R. 2013. New additions to the shallow-water hydroids (Cnidaria: Hydrozoa) from the French Lesser Antilles: Martinique. *Zootaxa* 3686 (1): 1–50. <https://doi.org/10.11646/zootaxa.3686.1.1>
- Galea H.R. 2016. Notes on some sertulariid hydroids (Cnidaria: Hydrozoa) from the tropical western Pacific, with descriptions of nine new species. *European Journal of Taxonomy* 218: 1–52. <https://doi.org/10.5852/ejt.2016.218>
- Galea H.R. 2018. A swimming medusoid gonophore in the life cycle of *Ventromma halecioides* (Alder, 1859) (Hydrozoa: Leptothecata: Kirchenpaueriidae). *Revue suisse de Zoologie* 125 (1): 137–147. <https://doi.org/10.5281/zenodo.1196038>
- Galea H.R. & Schuchert P. 2019. Some thecate hydroids (Cnidaria: Hydrozoa) from off New Caledonia collected during KANACONO and KANADEEP expeditions of the French Tropical Deep-Sea Benthos Program. *European Journal of Taxonomy* 562: 1–70. <https://doi.org/10.5852/ejt.2019.562>

- Galea H.R., Ferry R. & Bertot J.M. 2012. Medusoids in the life cycle of *Dentitheca dendritica* (Nutting, 1900) and *Nemalecium gracile* sp. nov. (Cnidaria: Hydrozoa). *Zootaxa* 3527: 43–54.  
<https://doi.org/10.11646/zootaxa.3527.1.3>
- Hirohito, Emperor of Japan. 1983. *Hydroids from Izu Ōshima and Niijima*. Publications of the Biological Laboratory, Imperial Household, Tokyo.
- Hirohito, Emperor of Japan. 1995. *The hydroids of Sagami Bay. II. Thecata*. Publications of the Biological Laboratory, Imperial Household, Tokyo.
- Inaba M. 1891. Hydroids obtained at Misaki, Miura, Sôshû. *Dobutsugaku Zasshi (Zoological Magazine, Tokyo)* 3 (34): 301–309.
- Jäderholm E. 1903. Aussereuropäische Hydroiden im schwedischen Reichsmuseum. *Arkiv för Zoologi* 1: 259–312.
- Jäderholm E. 1917. Hydroids from the South Seas. *Redogörelse för Norrköpings Högre Allmänna Läsvverk Läsaret 1916–1917*: 1–25.
- Kramp P.L. 1935. Polypdyr (Coelenterata). I. Ferskvardspolypper og Goplepolypper. *Danmarks Fauna* 41: 1–207.
- Leloup E. 1937. Hydropolypes et Scyphopolypes recueillis par C. Dawydoff sur les côtes de l’Indochine française. *Mémoires du Musée royal d’Histoire naturelle de Belgique* 2 (12): 1–73.
- Migotto A.E. 1996. Benthic shallow-water hydroids (Cnidaria, Hydrozoa) of the coast of São Sebastião, Brazil, including a checklist of Brazilian hydroids. *Zoologische Verhandelingen, Leiden* 306: 1–125. Available from <https://www.repository.naturalis.nl/document/148871> [accessed 6 Mar. 2020].
- Millard N.A.H. 1975. Monograph on the Hydroida of southern Africa. *Annals of the South African Museum* 68: 1–513.
- Mulder J.F. & Trebilcock R.E. 1916. Notes on Victorian Hydroida. Part VI. *Geelong Naturalist* 6 (4): 73–84.
- Nutting C.C. 1900. American hydroids. Part I. The Plumularidae. *Special Bulletin of the United States National Museum* 4 (1): 1–285. <https://doi.org/10.5962/bhl.title.1327>
- Nutting C.C. 1905. Hydroids of the Hawaiian islands collected by the Steamer Albatross in 1902. *Bulletin of the United States Fish Commission* 23 (3): 931–959.
- Park J.H. 2010. Invertebrate fauna of Korea. Cnidaria: Hydrozoa: Thecatae. Thecates. *Flora and Fauna of Korea* 4 (1): 1–183.
- Ralph P.M. 1961. New Zealand thecate hydroids. Part III. Family Sertulariidae. *Transactions of the Royal Society of New Zealand* 88 (4): 749–838.
- Ramil F. & Vervoort W. 1992a. Some consideration concerning the genus *Cladocarpus* (Cnidaria: Hydrozoa). *Scientia Marina* 56 (2–3): 171–176. Available from <http://scimar.icm.csic.es/scimar/pdf/56/sm56n2171.pdf> [accessed 6 Mar. 2020].
- Ramil F. & Vervoort W. 1992b. Report on the Hydroida collected by the “BALGIM” expedition in and around the Strait of Gibraltar. *Zoologische Verhandelingen, Leiden* 277: 1–262. Available from <https://www.repository.naturalis.nl/document/149146> [accessed 6 Mar. 2020].
- Ramil F., Vervoort W. & Ansín Agís J. 1998. Report on the Haleciidae and Plumularioidea (Cnidaria, Hydrozoa) collected by the French Seamount 1 Expedition. *Zoologische Verhandelingen, Leiden* 322: 1–42. Available from <https://www.repository.naturalis.nl/document/149163> [accessed 6 Mar. 2020].

- Rees W.J. & Vervoort W. 1987. Hydroids from the John Murray expedition to the Indian Ocean, with revisory notes on *Hydrodendron*, *Abietinella*, *Cryptolaria* and *Zygophylax* (Cnidaria: Hydrozoa). *Zoologische Verhandelingen, Leiden* 237: 1–209. Available from <https://www.repository.naturalis.nl/document/148867> [accessed 6 Mar. 2020].
- Rho B.J. 1967. Marine hydroids from the West and the South Sea of Korea. *Korean Cultural Research Institute, Ehwa Womans University* 10: 341–360.
- Rho B.J. & Park J.H. 1980. A systematic study on the marine hydroids in Korea 6. Thecata. *Journal of Korean Research Institute for Better Living* 25: 15–43.
- Ronowicz M., Boissin E., Postaire B., Bourmaud C. A.-F., Gravier-Bonnet N. & Schuchert P. 2017. Modern alongside traditional taxonomy – Integrative systematics of the genera *Gymnangium* Hincks, 1874 and *Taxella* Allman, 1874 (Hydrozoa, Aglaopheniidae). *PLOS ONE* 12 (4): 1–43. <https://doi.org/10.1371/journal.pone.0174244>
- Ryland J.S. & Gibbons M.J. 1991. Intertidal and shallow water hydroids from Fiji. II. Plumulariidae and Aglaopheniidae. *Memoirs of the Queensland Museum* 30 (3): 525–560.
- Sars G.O. 1874. Bidrag til Kundskaben om Norges Hydroider. *Forhandlinger i Videnskabs-Selskabet i Kristiania* 1873: 91–150.
- Schuchert P. 2001. Hydroids of Greenland and Iceland. *Meddelelser om Grønland, Bioscience* 53: 1–184.
- Schuchert P. 2003. Hydroids (Cnidaria, Hydrozoa) of the Danish expedition to the Kei Islands. *Steenstrupia* 27 (2): 137–256.
- Schuchert P. 2015. On some hydroids (Cnidaria, Hydrozoa) from the Okinawa Islands, Japan. *Revue suisse de Zoologie* 122 (2): 325–370. <https://doi.org/10.5281/zenodo.30004>
- Schuchert P. 2019. World Hydrozoa Database. *Lytocarpia* Kirchenpauer, 1872. Available from <http://www.marinespecies.org/hydrozoa/aphia.php?p=taxdetails&id=117002> [accessed 8 Oct. 2019].
- Stechow E. 1913. Hydroidpolypen der japanischen Ostküste. II. Teil: Campanularidae, Halecidae, Lafoeidae, Campanulinidae und Sertularidae, nebst Ergänzungen zu den Athecata und Plumularidae. In: Dofflein F. (ed.) Beiträge zur Naturgeschichte Ostasiens. *Abhandlungen der Königlich Bayerischen Akademie der Wissenschaften, Supplementband zu den Abhandlungen der Mathematisch-naturwissenschaftlichen Klasse* 3 (2): 1–162. <https://doi.org/10.5962/bhl.title.11621>
- Stechow E. 1921. Über Hydroiden der Deutschen Tiefsee-Expedition, nebst Bemerkungen über einige andre Formen. *Zoologischer Anzeiger* 53: 223–236.
- Thornely L.R. 1904. Report on the Hydroida collected by Professor Herdman, at Ceylon, in 1902. *Ceylon Pearl Oyster Fisheries, Supplemental Report* 8: 107–126.
- Totton A.K. 1930. Coelenterata. Part V. Hydroida. *Natural History Report of the British Antarctic ("Terra Nova") Expedition, 1910. Zoology* 5 (5): 131–252.
- Vervoort W. 1941. The Hydroida of the Snellius Expedition (Milleporidae and Stylasteridae excluded). *Temminckia* 6: 186–240.
- Vervoort W. 1966. Bathyal and abyssal hydroids. *Scientific Results of the Danish Deep-Sea Expedition 1950–1952. Galathea Report* 8: 97–174.
- Vervoort W. 1972. Hydroids from the Theta, Vema and Yelcho cruises of the Lamont-Doherty Geological Observatory. *Zoologische Verhandelingen, Leiden* 120: 1–247. Available from <https://www.repository.naturalis.nl/document/149147> [accessed 6 Mar. 2020].

Vervoort W. & Watson J.E. 2003. The marine fauna of New Zealand: Leptothecata (Cnidaria: Hydrozoa) (thecate hydroids). *NIWA Biodiversity Memoir* 119: 1–538.

Available from <https://archive.org/details/niwabiodiversitymemoir01192003> [accessed 6 Mar. 2020].

Watson J.E. 1973. Pearson Island Expedition 1969. – 9. Hydroids. *Transactions of the Royal Society of South Australia* 97 (3): 153–200.

Watson J.E. 1994. Shallow water hydroids from eastern Bass Strait. *Victoria Naturalist* 111 (2): 65–70.

Watson J.E. 2000. Hydroids (Hydrozoa: Leptothecata) from the Beagle Gulf and Darwin Harbour, northern Australia. *The Beagle, Records of the Museum and Art Galleries of the Northern Territory* 16: 1–82. Available from <https://www.biodiversitylibrary.org/page/55260920#page/5/mode/1up> [accessed 6 Mar. 2020].

Watson J.E. 2002. Hydroids (Cnidaria: Hydrozoa) from southern Queensland. *Memoirs of the Museum of Victoria* 59 (2): 337–354. <https://doi.org/10.24199/j.mmv.2002.59.6>

Watson J.E. 2018. Some hydroids (Cnidaria, Hydrozoa) from the Great Australian Bight in the collection of the South Australian Museum. *Zootaxa* 4410 (1): 1–34. <https://doi.org/10.11646/zootaxa.4410.1.1>

Whitelegge T. 1899a. Hydrozoa. In: Etheridge, Jr. R. (ed.) *The General Zoology of Lord Howe Islands; Containing also an Account of the Collections Made by the Australian Museum Collecting Party, Aug.–Sep. 1887. Memoirs of the Australian Museum* 2: 41.

Whitelegge T. 1899b. List of the marine and fresh-water invertebrate fauna of Port Jackson. *Proceedings of the Royal Society of New South Wales* 23: 163–323.

Xu Z.Z., Huang J.Q., Lin M., Guo D.H. & Wang C.G. 2014. *Study of Marine Biodiversity. The Superclass Hydrozoa of the Phylum Cnidaria in China. Vol. II.* China Ocean Press, Beijing.

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