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## Monograph

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

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**Abstract.** Thirty-six species of various thecate hydroids occur in two recent, deep-water collections from off New Caledonia. Of these, nine are new, namely *Solenoscyphus subtilis* Galea, sp. nov., *Hincksella immersa* Galea, sp. nov., *Synthecium rectangulatum* Galea, sp. nov., *Diphasia alternata* Galea, sp. nov., *Dynamena opposita* Galea, sp. nov., *Hydrallmania clavaformis* Galea, sp. nov., *Symplectoscyphus acutistriatus* Galea, sp. nov., *Symplectoscyphus elongatulus* Galea, sp. nov. and *Zygophylax niger* Galea, sp. nov. The male and female gonothecae of *Caledoniana decussata* Galea, 2015, the female gonothecae of *Caledoniana microgona* Galea, 2015, as well as the gonothecae of both sexes of *Solenoscyphus striatus* Galea, 2015 are described for the first time. The systematic position of the genera *Solenoscyphus* Galea, 2015 and *Caledoniana* Galea, 2015 is discussed on both morphological and molecular grounds, and both are confidently placed within the family Staurothecidae Maronna *et al.*, 2016. In light of the molecular data, the genera *Billardia* Totton, 1930 and *Dictyocladium* Allman, 1888 are assigned to the families Syntheciidae Marktanner-Turneretscher, 1890 and Symplectoscyphidae Maronna *et al.*, 2016, respectively. The previously undescribed gonothecae of *Hincksella neocaledonica* Galea, 2015, and the male gonothecae of *Sertularella tronconica* Galea, 2016, were found. *Thyroscyphus scorpioides* Vervoort, 1993, a peculiar hydroid with putative stem nematothecae, is redescribed and assigned to the new genus *Tuberocaulus* Galea, gen. nov. Noteworthy new records from the study area are: *Tasmanaria edentula* (Bale, 1924), *Hincksella sibogae* Billard, 1918, *Dictyocladium reticulatum* (Kirchenpauer, 1884), *Salacia sinuosa* (Bale, 1888) and *Billardia hyalina* Vervoort & Watson, 2003. Most species are illustrated to facilitate their identification, and the morphology of the new ones is compared to that of their related congeners.

**Keywords.** Deep water, Leptothecata, taxonomy, new species, 16S DNA barcoding.

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## Introduction

The hydroid fauna of New Caledonia has received increasing attention over the last three decades, owing greatly to the rich materials collected in the frame of the French Tropical Deep-Sea Benthos Program (Bouchet *et al.* 2008). Several resulting studies, occasionally including specimens from additional areas of the tropical western Pacific, have been published to date, namely Vervoort (1993), Ansin Agis *et al.* (2009, 2014, 2016), Peña Cantero & Vervoort (2010) and Galea (2015a, 2016).

Two recent expeditions have also provided hydroid material: KANACONO took place between 8–31 August 2016 around the Isle of Pines, southeast of Grande Terre, while KANADEEP was conducted between 31 August–27 September 2017 in the Coral Sea. Only a part of the hydroids gathered during these expeditions is treated here, and concerns various families of Leptothecata Cornelius, 1992, among which the Staurothecidae Maronna *et al.*, 2016, Syntheciidae Marktanner-Turneretscher, 1890, Sertulariidae Lamouroux, 1812, Sertularellidae Maronna *et al.*, 2016, Symplectoscyphidae Maronna *et al.*, 2016 and, only superficially, Zygophylacidae Quelch, 1885. Although a number of species from the area has been dealt with by Vervoort (1993) and Galea (2015a, 2016), additional records (including new species) are provided, along with supplementing data on morphology.

## 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 the Muséum national d'histoire naturelle (MNHN) of Paris, France, and catalogue numbers are indicated as MNHN-IK-2015- followed by 3-digit numbers. Fragments, cut off from a number of specimens with sufficient coenosarc, were used to extract DNA. The residual perisarc, mounted as permanent microscopic slides, is deposited as voucher specimens in the collections of the Muséum d'histoire naturelle of Geneva (MHNG), Switzerland; catalogue numbers, in this case, are indicated as MHNG-INVE- followed by 6-digit numbers, while the DNA isolates are identified by the prefix DNA followed by 4-digit numbers.

Molecular biological methods, as well as maximum likelihood analyses with Phyml ver. 2.4.4. (Guindon & Gascuel 2003), were performed as described in Schuchert (2014, 2016). About 600 bp of the large mitochondrial ribosomal RNA (16S) was amplified using the primers SHA (ACGGAATGAACTCAAATCATGT) and SHB (TCGACTGTTTACCAAAAACATA) (Cunningham & Buss 1993) (35 cycles, profile: 20 sec at 94°C, 45 sec at 50°C, and 120 sec at 68°C). Not all extractions gave positive PCR results. All resulting 16S sequences were deposited in the GenBank database under the accession numbers MK073078 to MK073115. The deposited set comprises also some new sequences of samples originating from outside New Caledonia that proved useful in the context of the present study. Their collection data and voucher numbers can be obtained via their accession numbers given in Fig. 20, and a search in the GenBank database. Additional 16S sequences of related taxa were retrieved from GenBank. Also, their meta-data can be obtained via the accession numbers. Two species names were not used as given in GenBank, namely: *Symplectoscyphus turgidus* (FJFJ550462) is referred to as *Xingyurella turgida* (Trask, 1857) (Song *et al.* 2018), while *Sertularella sanmatiasensis* El Beshbeeshy, 2011 (FN424141) is reidentified as *S. antarctica* Hartlaub, 1901 (Galea *et al.* 2017: 263).

Comprehensive synonymies are given only for uncommon and/or lesser known taxa, while – for most species – only a few references, including good descriptions and illustrations, are provided. To facilitate comparisons between the species belonging to the same genera, all colony fragments, hydro- and gonothecae are drawn to the same scales, respectively.

## Results

### *Systematic account*

Class Hydrozoa Owen, 1843  
Subclass Hydroidolina Collins, 2000  
Order Leptothecata Cornelius, 1992  
Family Staurothecidae Maronna *et al.*, 2016

*Caledoniana decussata* Galea, 2015

Fig. 1A–B

*Caledoniana decussata* Galea, 2015a: 4, figs 1B, 2C–D.

### Material examined

PACIFIC OCEAN • originally a 5.8 cm high colony; off New Caledonia, stn DW4744; 22°55' S, 167°37' E; 310–290 m; 23 Aug. 2016; KANACONO leg.; a 3.0 cm long, basal, fascicled portion was cut off for DNA extraction, DNA1342; voucher MHNG-INVE-120777; MNHN-IK-2015-359 • a 3.8 cm high colony fragment with single, basal, immature gonotheca; off New Caledonia, stn DW4775; 23°03' S, 168°17' E; 140–277 m; 28 Aug. 2016; KANACONO leg.; used as a whole for DNA extraction, DNA1343; voucher MHNG-INVE-120778 • originally a 4.5 cm high colony fragment with a short basal branch, carrying 3 female gonothecae; off New Caledonia, stn DW4697; 22°48' S, 167°15' E; 465–449 m; 16 Aug. 2016; KANACONO leg.; a 1.2 cm long, distal portion was cut off for DNA extraction, DNA1344; voucher MHNG-INVE-120779; barcode identifier MK073078; MNHN-IK-2015-36 • a 2.5 cm high, unbranched colony without gonothecae; off New Caledonia, stn DW4726; 22°40' S, 167°03' E; 240–181 m; 20 Aug. 2016; KANACONO leg.; MNHN-IK-2015-362 • a colony without gonothecae, 6.0 × 3.5 cm (height × width; the same applies to all subsequent materials and species), with one side branch; same collecting data as for preceding; MNHN-IK-2015-362 • a colony, 2.3 × 3.7 cm, with 2 side branches, carrying an immature female gonotheca; same collecting data as for preceding; MNHN-IK-2015-362 • a ca 9 × 7 cm, branched (up to 2<sup>nd</sup> order branches), fully fertile male colony; same collecting data as for preceding; a short, distal fragment was cut off for DNA extraction, DNA1345; MNHN-IK-2015-362 • originally a 4.5 cm high colony with one side branch, the latter bearing an immature, likely female, gonotheca; same collecting data as for preceding; a 1 cm long fragment from the branch was cut off for DNA extraction, DNA1346; voucher MHNG-INVE-120780; MNHN-IK-2015-362 • a ca 11 × 12 cm, fan-shaped, fully fertile male colony; off New Caledonia, stn DW4728; 22°43' S, 167°02' E; 150 m; 20 Aug. 2016; KANACONO leg.; a short, distal fragment was cut off for DNA extraction, DNA1347; voucher MHNG-INVE-120781; barcode identifier MK073079; MNHN-IK-2015-365.

### Remarks

The decussate arrangement of the hydrothecae, although quite irregular within a given colony, occurs in all the material examined, a condition never met within the two other species of the genus, *C. alata* Galea, 2015 and *C. microgona* Galea, 2015. The species is monoecious and sexually dimorphic. The gonothecae arise laterally from below the hydrothecal bases. The male ones are club-shaped, ca 3200 µm long and 1170 µm wide (one gonotheca measured), tapering below into an indistinct pedicel; there is no noticeable aperture distally. The female gonothecae are large, ca 3890 µm high and 2630 µm wide in lateral view (one gonotheca measured), recalling a closed hand wearing a mitten; they are bilaterally symmetrical and contain a large, globular, inner cavity protecting at least a large, ovoid oocyte, the latter ca 925 × 590 µm; the aperture is half-moon-shaped, faces downwards, and does not appear to possess an opercular apparatus.

Although the morphology of the fully-formed gonotheca of *C. alata*, the type species of the genus, is as yet unknown, it is assumed that the specimen depicted by Galea (2015a, Fig. 2A) is likely to adopt a similar shape to that of its counterparts produced by both *C. decussata* and *C. microgona* (see below), thus further justifying their assignment to the same genus.

The three species of *Caledoniana* Galea, 2015 were included provisionally in the family Sertulariidae Lamouroux, 1812 (Galea 2015a), but it is now demonstrated that, at least *C. decussata* and *C. microgona*, belong instead to the Staurothecidae Maronna *et al.*, 2016 (see ‘Molecular study’ section).

As noted earlier by Galea (2015a), *C. decussata* shows affinities with *Staurotheca megalotheca* Vervoort & Watson, 2003, especially regarding the size and the decussate arrangement of their hydrothecae. However, the gonothecae of the latter differ much from those of both *C. decussata* and *C. microgona*, in having a small, rounded, eccentric, sub-terminal aperture borne on a short neck region, unless it is proved that its gonothecae are sexually dimorphic, thus strongly resembling to the males of “*Solenoscyphus*” *striatus* Galea, 2015a (see below). Anyway, it could be reasonably assumed that *S. megalotheca* is a true staurothecid hydroid, although its assignment to a given genus is impossible in the absence of evidence from molecular data.

In addition, *Giganthotheca maxima* Vervoort & Watson, 2003 (Vervoort & Watson 2003: fig. 26E–F) has female gonothecae approaching the morphology of those met with in both *C. decussata* and *C. microgona*, suggesting not only a reasonable assignment of this species to the Staurothecidae, but also a possible genus transfer to *Caledoniana*. But, again, only molecular data are expected to solve the intricacies of this species group.

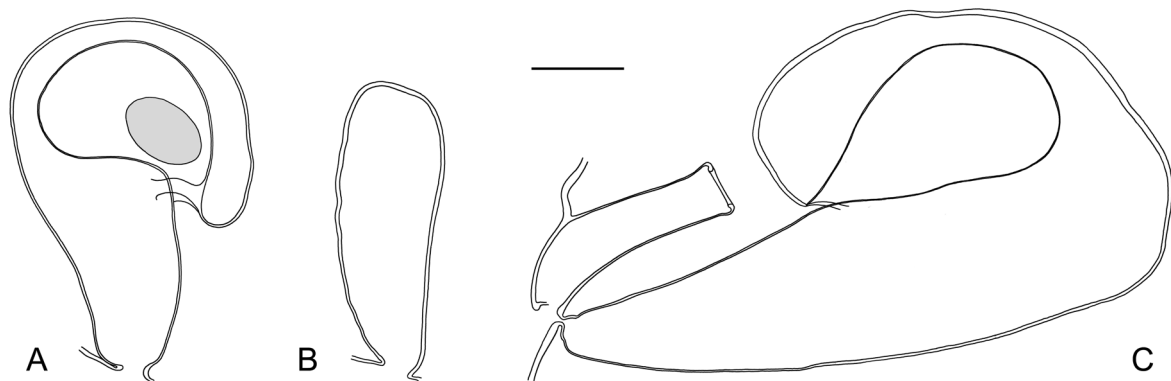
### Distribution

Only known from off New Caledonia (Galea 2015a; present study).

### *Caledoniana microgona* Galea, 2015

Fig. 1C

*Caledoniana microgona* Galea, 2015a: 6, figs 1C, 2E–G.



**Fig. 1.** A–B. *Caledoniana decussata* Galea, 2015, female (MNHN-IK-2015-361) and male (MNHN-IK-2015-362), gonothecae. — C. *Caledoniana microgona* Galea, 2015, female gonotheca arising from below base of hydrotheca (MNHN-IK-2015-363). Scale bar: 1 mm.



**Material examined**

PACIFIC OCEAN • a 2.4 cm high colony fragment with 3 male gonothecae in middle part, with only the perisarc left; off New Caledonia, stn DW4672; 22°47' S, 167°26' E; 310–290 m; 13 Aug. 2016; KANACONO leg.; MNHN-IK-2015-360 • originally a 1.8 cm high colony fragment bearing a 2.2 cm long side branch, the latter carrying 2 female gonothecae; off New Caledonia, stn DW4670; 22°58' S, 167°24' E; 680–612 m; 12 Aug. 2016; KANACONO leg.; a 0.8 cm long fragment of the main axis was cut off for DNA extraction, DNA1348; voucher MHNG-INVE-120782; barcode identifier MK073080; MNHN-IK-2015-363.

**Remarks**

The hydrothecae are closer to one another in this species than in *C. decussata* and, as stated by Galea (2015a), their adaxial wall is comparatively shorter, these two characters readily distinguishing them. Like the previous species, *C. microgona* also appears sexually dimorphic and forming monoecious colonies. Its specific name is obviously inappropriate, as the hydroid was originally described based on specimens provided with 'small', saccular gonothecae that were not recognized then as being male. The female gonothecae are similar to those described in *C. decussata* (see above), but are of comparatively larger proportions (ca 6890 µm long and 3715 µm wide, when seen laterally; one gonotheca measured).

**Distribution**

Only known from off New Caledonia (Galea 2015a; present study).

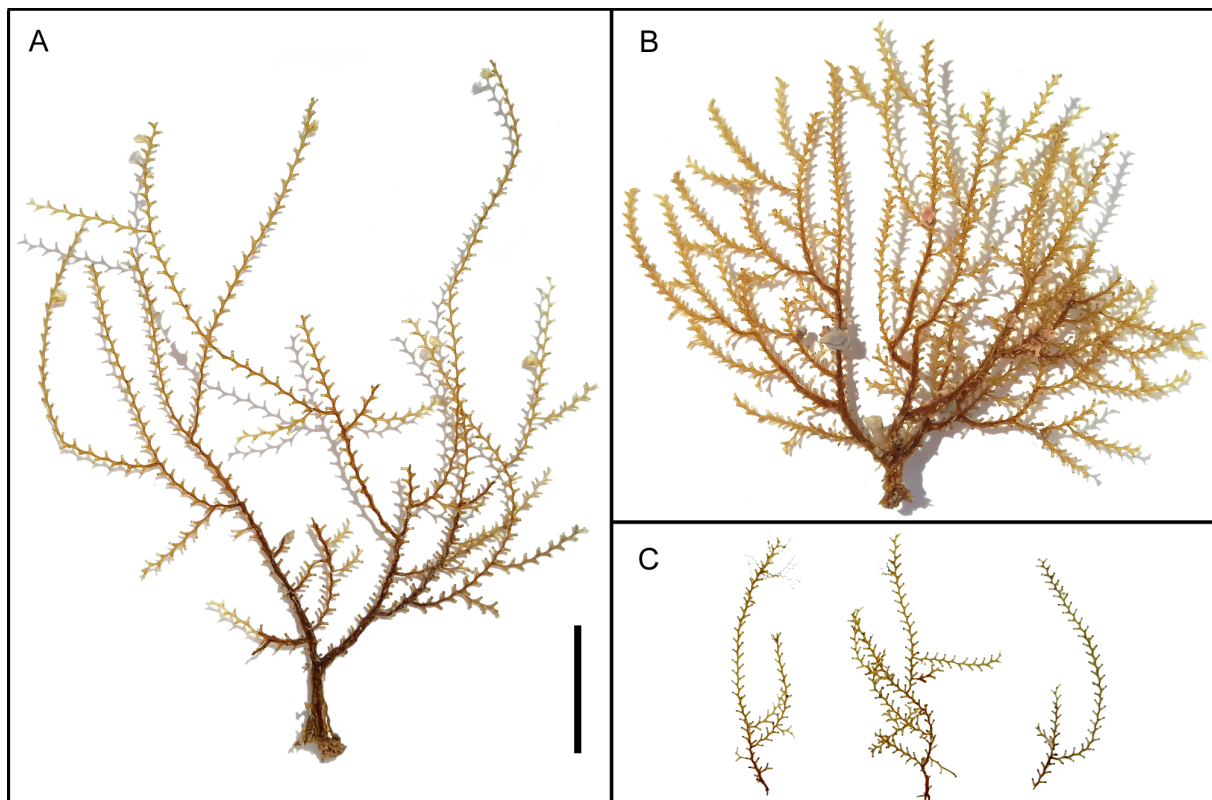
? *Solenoscyphus striatus* Galea, 2015  
Figs 2A–B, 3A–K; Table 1

*Solenoscyphus striatus* Galea, 2015a: 10, figs 3C, 4E–G.

**Material examined**

PACIFIC OCEAN • two colonies, one of which is 10×8 cm and has a few female gonothecae, the other is 5.5×4.5 cm and devoid of gonothecae, as well as a number of fragments resulting from the breakage of both; off New Caledonia, stn DW4700; 22°43' S, 167°16' E; 245–295 m; 16 Aug. 2016; KANACONO leg.; three fragments from the largest colony were cut off for DNA extraction, DNA1349; voucher MHNG-INVE-120783; barcode identifier MK073081; MNHN-IK-2015-364 • two colonies without gonothecae, 6.5×6.5 cm and 6.5×2.5 cm, respectively; off New Caledonia, stn DW4758; 23°12' S, 168°04' E; 330 m; 26 Aug. 2016; KANACONO leg.; two small fragments from the largest colony were removed for DNA extraction, DNA1350; voucher MHNG-INVE-120784; barcode identifier MK073082; MNHN-IK-2015-366 • a colony without gonothecae, 5×5.5 cm; off New Caledonia, stn DW4697; 22°48' S, 167°15' E; 465–449 m; 16 Aug. 2016; KANACONO leg.; MNHN-IK-2015-367 • a 6.5×2.7 cm colony with several male gonothecae; off New Caledonia, stn DW4705; 22°46' S, 167°19' E; 290–317 m; 17 Aug. 2016; KANACONO leg.; two small fragments were cut off for DNA extraction, DNA1351; voucher MHNG-INVE-120785; MNHN-IK-2015-368 • two colonies, 8×3.5 cm and 3.5×3.5 cm, respectively, as well as a colony fragment 4.5×4.5 cm, all without gonothecae; off New Caledonia, stn CP4658; 22°42' S, 167°13' E; 303–315 m; 10 Aug. 2016; KANACONO leg.; MNHN-IK-2015-369 • a 6 cm high colony with two short basal side branches, without gonothecae; off New Caledonia, stn DW4762; 23°16' S, 168°06' E; 810–805 m; 26 Aug. 2016; KANACONO leg.; MNHN-IK-2015-370 • a colony without gonothecae, 3×3 cm; off New Caledonia, stn DW4737; 22°45' S, 167°42' E; 387–456 m; 22 Aug. 2016; KANACONO leg.; used as a whole for DNA extraction, DNA1352; voucher MHNG-INVE-120786; MNHN-IK-2015-371 • three colonies without gonothecae, 4×1 cm, 2.2×1.8 cm, and 3×2 cm; same collecting data as for preceding; MNHN-IK-2015-371 • a colony without gonothecae, 3.2×0.8 cm, with two short side branches; off New Caledonia, stn DR4773;

23°02' S, 168°20' E; 400–230 m; 28 Aug. 2016; KANACONO leg.; MNHN-IK-2015-372 • a colony without gonothecae, 5.5 × 4 cm, with only the perisarc left; off New Caledonia, stn DW4770; 22°58' S, 168°21' E; 455–470 m; 28 Aug. 2016; KANACONO leg.; MNHN-IK-2015-373 • two colonies without gonothecae, 9.5 × 8 cm and 9.5 × 6 cm, respectively, as well as a few smaller fragments resulting from their breakage; off New Caledonia, stn DW4768; 23°25' S, 168°01' E; 180–210 m; 27 Aug. 2016; KANACONO leg.; a fragment from the smallest colony used for DNA extraction, DNA1353; voucher MHNG-INVE-120787; barcode identifier MK073083; MNHN-IK-2015-374 • a colony without gonothecae, 5 × 1.8 cm; off New Caledonia, stn DW4678; 22°51' S, 167°34' E; 308–303 m; 13 Aug. 2016; KANACONO leg.; MNHN-IK-2015-465 • a 4.7 × 4.5 cm colony (distinct morphotype) with a couple of fully formed female gonothecae, and a few others immature; off New Caledonia, stn DW4682; 22°22' S, 167°24' E; 465–495 m; 14 Aug. 2016; KANACONO leg.; a fragment was used for DNA extraction, DNA1359; voucher MHNG-INVE-120793; MNHN-IK-2015-380 • a 7.3 × 9.2 cm colony (distinct morphotype) with numerous male gonothecae, of which only a few are fully formed; off New Caledonia, stn DW4681; 22°23' S, 167°23' E; 490–480 m; 14 Aug. 2016; KANACONO leg.; a fragment was used for DNA extraction, DNA1356; voucher MHNG-INVE-120790; MNHN-IK-2015-377 • a colony, 6.2 × 5.5 cm, with distinct morphotype; off New Caledonia, stn DW4741; 22°52' S, 167°41' E; 210 m; 23 Aug. 2016; KANACONO leg.; a fragment was used for DNA extraction, DNA1357; voucher MHNG-INVE-120791; barcode identifier MK073086; MNHN-IK-2015-378 • two colonies without gonothecae, 5.5 × 3 cm and 4.5 × 3.4 cm, respectively; same collecting data as for preceding; MNHN-IK-2015-378 • a 3.8 × 5.5 cm colony (distinct morphotype) with a few immature male gonothecae; off



**Fig. 2.** A. ? *Solenoscyphus striatus* Galea, 2015, fertile colony from sample MNHN-IK-2015-364. — B. ? *S. striatus*, morphotype with approximated hydrothecae, sample MNHN-IK-2015-377. — C. ? *Solenoscyphus subtilis* Galea, sp. nov., paratype colony (left), MNHN-IK-2015-487; holotype colony (middle), MNHN-IK-2015-382; one colony from sample MNHN-IK-2015-488 (right). Scale bar: 2 cm.

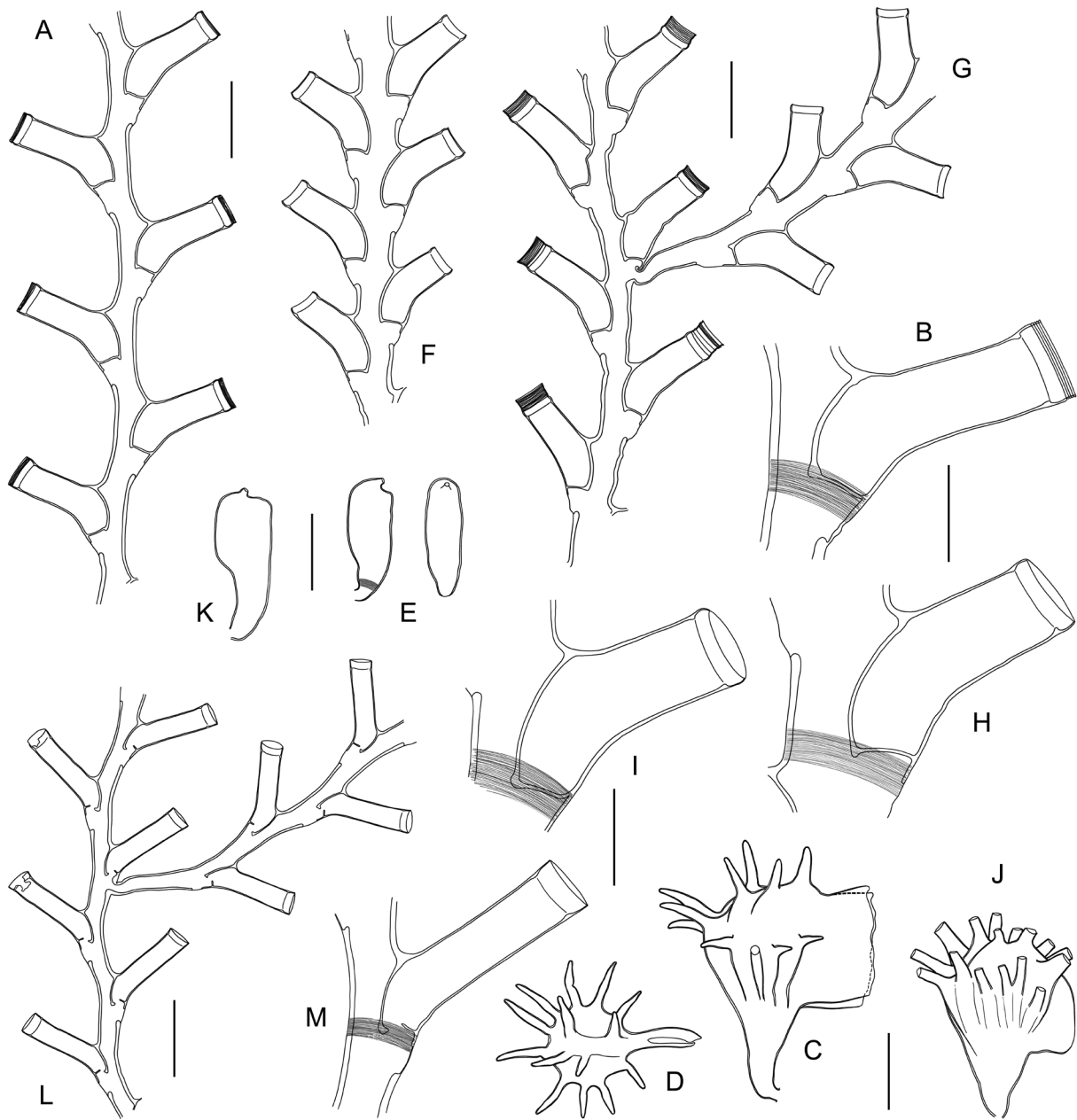
**Table 1.** Measurements of ? *Solenoscyphus* spp., in µm.

	? <i>S. striatus</i> Galea, 2015a Galea (2015a); present study *	? <i>S. striatus</i> (morphotype) Present study	? <i>S. subtilis</i> Galea, sp. nov. Present study
<b>Internodes</b>			
- length, ordinary	1170–1445	895–1225	835–1040
- length, 1 <sup>st</sup> internode	ca 2435 *	2100–2295	1535–1670
- diameter at node	360–430	245–525	245–295
<b>Hydrotheca</b>			
- free adaxial wall	950–1075	615–870	835–920
- adnate adaxial wall	590–655	640–860	405–440
- abaxial wall	1335–1420	1165–1225	980–1080
- maximum width	420–445	465–505	280–305
- diameter at rim	430–450	380–405	280–305
<b>Female gonotheca</b>			
- length w/o spines	ca 2840 *	ca 2625	–
- length w. spines	ca 3450 *	ca 2280	–
- width w/o spines	ca 1050 *	ca 2085	–
- width w. spines	ca 2080 *	ca 1535	–
<b>Male gonotheca</b>			
- length w/o tube	ca 1495 *	ca 1900	–
- maximum width	ca 590 *	ca 735	–
- tube-length	ca 85 *	ca 75	–
- tube, diameter at aperture	ca 70 *	ca 75	–

New Caledonia, stn DW4679; 22°49' S, 167°33' E; 245–249 m; 13 Aug. 2016; KANACONO leg.; a fragment was used for DNA extraction, DNA1358; voucher MHNG-INVE-120792; barcode identifier MK073087; MNHN-IK-2015-379 • a colony without gonothecae, 2.4 × 1.9 cm (distinct morphotype); off New Caledonia, stn DW4685; 22°28' S, 167°29' E; 405–404 m; 14 Aug. 2016; KANACONO leg.; MNHN-IK-2015-381.

### Remarks

Colonies larger (up to 10 cm high and 8 cm wide) than those described originally by Galea (2015a) occur in the present collection, as exemplified by material MNHN-IK-2015-364. The hydrorhiza is a rooted mass of stolonal fibers firmly anchoring the colonies to their substrates. The colonies are flaccid, unable to support themselves when out of liquid; flabellate, with indistinct main stems, except for a short, proximal portion (ca 1 cm long) above the origin from hydrorhiza, then irregularly branching, forming up to 5<sup>th</sup> order branchlets. Stem and main branches are strongly fascicled. The branches are almost straight, except proximally, where they curve upwards immediately after their origin. The largest colony is fertile and carries female gonothecae; they originate laterally from below the hydrothecal bases at sites conspicuously marked by comparatively thinner perisarc than in the rest of the colony, forming rounded, filmy patches. The gonotheca is bilaterally symmetrical; broadly piriform, gradually tapering in its lower half into an indistinct pedicel; upper half globular, provided with a number of hollow spines arranged into two whorls (4–5 in the upper one, 8–9 in the lower one); one side of the gonotheca (that facing its corresponding hydrotheca) is provided with a pair of quadrangular crests forming two closely-set ‘lips’, leaving a slit-like passage for a few, large oocytes (badly preserved in present material); the spines, occasionally with truncated tips, have their bases prolonged downwards over the gonothecal wall as broad, prominent, rounded ridges, those from the lower whorl reaching almost the gonothecal base.



**Fig. 3.** A–E. ? *Solenoscyphus striatus* Galea, 2015, branch fragment (A), hydrotheca (B), female gonotheca in lateral (C) and apical (D) views, all from sample MNHN-IK-2015-364; male gonotheca (E) in lateral (left) and frontal (right) aspects, from sample MNHN-IK-2015-368. — F–K. ? *S. striatus*, morphotype with approximated hydrothecae: colony fragments (E–F, from samples MNHN-IK-2015-376 and MNHN-IK-2015-377, respectively), hydrothecae (H–I, from samples MNHN-IK-2015-378 and MNHN-IK-2015-377, respectively), male gonotheca (K, from sample MNHN-IK-2015-377). — L–M. ? *Solenoscyphus subtilis* Galea, sp. nov., colony fragment (L), hydrotheca (M), both from sample MNHN-IK-2015-382. Scale bars: B, H–I, M = 500  $\mu$ m; A, C–G, J–L = 1 mm.



The colonies are monoecious and there is a notable sexual dimorphism of the gonothecae. Indeed, material MNHN-IK-2015-368 bears male gonothecae. Similarly to the females, they arise laterally from below the hydrothecal bases, and are bilaterally symmetrical; broadly amphora-shaped, base appressed to its corresponding hydrotheca and tapering abruptly into indistinct pedicel, perisarc finely and densely-striated basally; slightly flattened laterally, distally a short neck region bearing apically a small, rounded aperture; neck inclined to one side.

Opercula are well discernible in many hydrothecae from sample MNHN-IK-2015-370. Terminal stolonization may occasionally occur, as exemplified by samples MNHN-IK-2015-371 and -374; in addition, a tendril may be continued distally by a short sequence of thecate internodes. Multiple, closely-set renovations of the hydrothecal margin occur in MNHN-IK-2015-372.

A peculiar morphotype of this species (Figs 2B, 32F–K) occurs in several samples, viz. MNHN-IK-2015-377 to MNHN-IK-2015-381. Its main distinguishing features rely in its more compact appearance of the colonies (compare Fig. 2B and 2A, respectively), the hydrothecae closer to one another (compare Fig. 3F and 3A), adnate for about half their length to their corresponding internodes. In material MNHN-IK-2015-380, the female gonothecae are provided with a number of hollow, distally truncated, occasionally twin spines arranged into two whorls.

As stated earlier by Galea (2015a), this species does not resemble either *S. candelabrum* Galea, 2015 (type species of the genus) or *S. decidualis* Galea, 2015, especially in colony form, although all possess rounded, filmy, deciduous hydrothecal opercula. Unlike *S. striatus*, the last two species form regularly-pinnate colonies, their perisarc is entirely smooth, and there is no conspicuous raised collar of thickened perisarc just below their hydrothecal aperture. In addition, the cladia of *S. candelabrum* are spirally twisted proximally, and its hydrothecae possess a conspicuous pattern of internal perisarc thickenings. Gonothecae are only known in *S. striatus*, and the females – notably – resemble those of some species of *Staurotheca*, e.g., *S. echinocarpa* (Allman, 1888) (Peña Cantero & Vervoort 2003), suggesting that the present species belongs to the family Staurothecidae.

Similar female gonothecae were also described in *Giganthotheca raukumarai* Vervoort & Watson, 2003 (Vervoort & Watson 2003: figs 27B–C, 28B), suggesting that this species could be confidently removed from the Sertulariidae and reasonably assigned to the Staurothecidae, as noted above for *G. maxima*. In addition, the gonothecae illustrated by these authors (Vervoort & Watson 2003: fig. 29B, D) are undoubtedly male, and come morphologically close to those of *S. striatus*. However, the relationships between *G. raukumarai* and *S. striatus* are far from fully understood, and only a molecular evidence is expected to clarify the case.

As it will be shown in the ‘Molecular study’ section at the end of this report, *S. decidualis* does not cluster with either *S. striatus* or *S. subtilis* sp. nov. (for description, see below), suggesting that they are not congeneric. Given the morphological peculiarities of *S. candelabrum*, it could be justifiably assumed that it forms a so-far monotypic genus, while *S. decidualis*, on one hand, and both *S. striatus* and *S. subtilis* sp. nov., on the other hand, could well belong to two undescribed genera. For this reason, when combining the genus *Solenoscyphus* to one of these three species, it is preceded by a question mark, pending additional data to clarify their taxonomic statuses. For additional comments, see the ‘Molecular study’ section.

### **Distribution**

Only known from off New Caledonia (Galea 2015a; present study).



? *Solenoscyphus subtilis* Galea, sp. nov.

[urn:lsid:zoobank.org:act:B6AF627E-5000-401E-A02D-F5301FECB368](https://doi.org/10.3897/ejt.562.14611)

Figs 2C, 3L–M; Table 1

### Diagnosis

Colonies flabellate, arising from root-like hydrorhiza. Stems lightly fascicled, irregularly branched several times; division into internodes indistinct. Hydrothecae alternate, rather distant; long, tubular, adnate for  $\frac{1}{4}$  their length, with an apical raised collar of distinctly thickened perisarc. Whole colony covered by finely and densely-striated perisarc. Gonothecae unknown.

### Etymology

From the Latin ‘*subtilis*’, meaning ‘slender’, to describe the shape of its hydrothecae.

### Material examined

#### Holotype

PACIFIC OCEAN • a colony without gonothecae, 4.1×2.3 cm; off New Caledonia, stn DW4759; 23°12′ S, 168°03′ E; 317–343 m; 26 Aug. 2016; KANACONO leg.; a fragment was used for DNA extraction, DNA1360; voucher MHNG-INVE-120794; barcode identifier MK073088; MNHN-IK-2015-382.

#### Paratype

PACIFIC OCEAN • a colony without gonothecae 3.8×0.8 cm; off New Caledonia, stn DW4759; 23°12′ S, 168°03′ E; 317–343 m; 26 Aug. 2016; KANACONO leg.; MNHN-IK-2015-487.

#### Additional material

PACIFIC OCEAN • two colonies without gonothecae, 3×0.5 cm and 3.3×0.8 cm, respectively; off New Caledonia, stn DW4759; 23°12′ S, 168°03′ E; 317–343 m; 26 Aug. 2016; KANACONO leg.; MNHN-IK-2015-488 • originally a 2.3 cm high colony without gonothecae; off New Caledonia, stn DW4760; 23°15′ S, 168°03′ E; 319–304 m; 26 Aug. 2016; KANACONO leg.; a 0.7 cm long distal fragment was cut off for DNA extraction, DNA1361; voucher MHNG-INVE-120795; barcode identifier MK073089; MNHN-IK-2015-383.

### Description

Colonies flabellate, up to 4.1 cm high and 2.3 cm wide, arising from root-like hydrorhiza firmly anchoring the colony to its substrate. Main stem indistinct, except for its basal 1–3 mm above origin from hydrorhiza, then branching irregularly and forming up to 2<sup>nd</sup> order branchlets; lightly fascicled basally, grading to monosiphonic distally; division into internodes indistinct; stem and branches with similar structure: each equivalent of internode moderately-long, slightly geniculate, bearing a hydrotheca distally; 1<sup>st</sup> internode of a side branch comparatively longer than subsequent ones; branches given off nearly perpendicularly to axis of higher order branches, but rapidly pointing upwards at geniculation introduced by 1<sup>st</sup> hydrotheca. Hydrothecae alternate, in two parallel, coplanar rows; exceedingly long, cylindrical, adnate for ca  $\frac{1}{4}$  their length to the corresponding internodes; free adaxial and abaxial walls parallel and straight; adnate adaxial wall curved, ending in basal perisarc plug; there is no complete base for the hydrotheca, but only a short lamellar projection of the perisarc on abaxial side; a conspicuous raised collar of thickened perisarc immediately below the rounded aperture; opercula not observed. Perisarc straw colored to lightly dark in older parts, finely and densely-striated throughout the colony. Gonothecae unknown.

### Remarks

The present species comes close to *S. striatus* through the appearance of its colonies and their hydrothecae with striated walls and thickened apertures. Evidence from molecular data confirms the fact that they are, indeed, congeneric (see ‘Molecular study’ section below). As a specific difference, *S. subtilis* sp. nov. has comparatively slenderer (hence its specific name) and less adnate hydrothecae (compare Fig. 3M and 3B).

### Distribution

Only known from off New Caledonia (present study).

? *Solenoscyphus decidualis* Galea, 2015

*Solenoscyphus decidualis* Galea, 2015a: 9, figs 3B, 4C–D.

### Material examined

PACIFIC OCEAN • a 5.7 cm high colony and the 1.1 cm long tip of a second colony, both without gonothecae; off New Caledonia, stn DW4715; 22°50' S, 167°27' E; 424 m; 18 Aug. 2016; KANACONO leg.; one cladium from the largest colony was used for DNA extraction, DNA1354; voucher MHNG-INVE-120788; barcode identifier MK073084; MNHN-IK-2015-375 • a colony without gonothecae, 6.8 cm high; off New Caledonia, stn CP4676; 22°51' S, 167°30' E, 383 m; 13 Aug. 2016; KANACONO leg.; a basal cladium was cut off and used for DNA extraction, DNA1355; voucher MHNG-INVE-120789; barcode identifier MK073085; MNHN-IK-2015-376.

### Remarks

The present material, forming pinnate colonies with lightly fascicled stems and long, tubular, weakly adnate hydrothecae, is in full agreement with the holotype described earlier by Galea (2015a). The perisarc of the colony (including that of the hydrothecae) is uniformly smooth, and the hydrothecal rim is thickened distally for only a very short distance (ca 40 µm) just below the aperture.

Despite forming regularly-pinnate colonies provided with tubular hydrothecae possessing rounded, deciduous opercula, the present species and *S. candelabrum* may prove to not be congeneric. The available 16S sequences place this species clearly outside the clades of *Solenoscyphus* and Staurothecidae (Fig. 20 and ‘Molecular study’ section), but without any supported relationships to other taxa. This makes it likely that this species does not belong to the genus *Solenoscyphus*. However, the available 16S data do not resolve sufficiently well the family relationships, and additional markers are needed for this purpose. Therefore, and also because no diagnostic traits are evident, we decided to leave it in the genus *Solenoscyphus* until a more detailed study allows firmer conclusions.

### Distribution

Only known from off New Caledonia (Galea 2015a; present study).

Genus *Tasmanaria* Watson & Vervoort, 2001

*Tasmanaria edentula* (Bale, 1924)

Fig. 4

*Tasmanaria edentula* – Vervoort & Watson 2003: 238, fig. 57A– E.

### Material examined

PACIFIC OCEAN • a 6.8 cm high, unbranched colony fragment, with only the perisarc left; off New Caledonia, stn DW4932; 25°05' S, 160°00' E; 287–290 m; 3 Sep. 2017; KANADEEP leg.; MNHN-IK-2015-472.

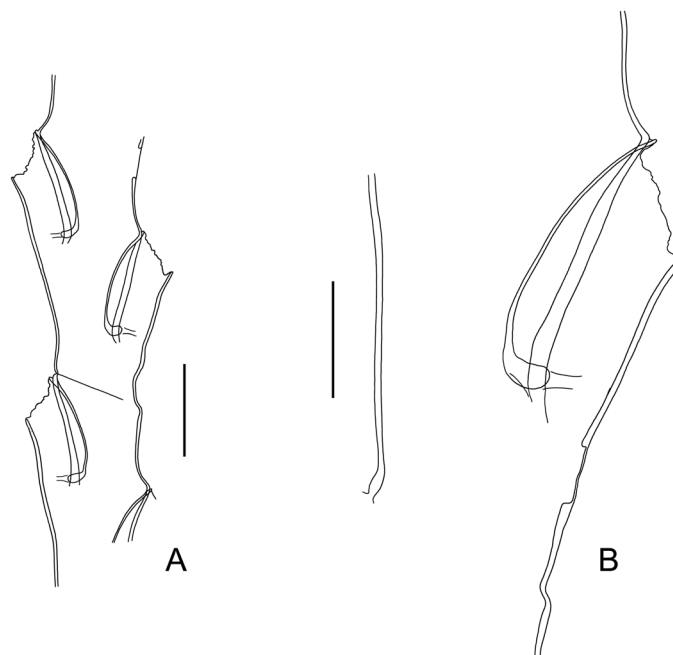
### Remarks

The present material likely represents a branch fragment, since no (remains of) apophyses could be seen as in a portion of stem. It was likely fertile, but all gonothecae are now lost; their attachment points are clearly visible in its proximal part, while future foramina could be noted distally as rounded, flimsy perisarc patches below the hydrothecal bases. The hydrothecae are partly damaged (especially their margins) due to the collecting technique, and some are filled in with sand particles. Their morphology, combined to their dimensions (adnate wall = 1215–1290 µm long, diameter at aperture = 480–505 µm, maximum width = 515–540 µm) point, with little doubt, towards *T. edentula*, as described by Vervoort & Watson (2003).

Owing to the distinctive morphology of its hydrothecae, this species may prove to belong to the Staurothecidae, instead of the Sertulariidae. Vervoort & Watson (2003: 238) observed in some hydrothecae “remnants of hyaline opercular material, usually attached inside [the] hydrothecal rim”. Antsulevich & Vervoort (1993: 439) cite Bale (1924: 238), who described the operculum as “trivalvate”, hence their provisional assignment of this species to their new genus, *Papilionella* Antsulevich & Vervoort, 1993.

On the other hand, “a low operculum of one saucer-shaped valve, much torn and usually collapsed inward” was noted in *T. aegis* Watson & Vervoort, 2001, the type species of the genus (Watson & Vervoort 2001: 172).

Its gonotheca shows morphological affinities with those of species of *Staurotheca*, e.g., *S. amphorophora* Naumov & Stepanjants, 1962 (Stepanjants 1979). In addition, the hydrothecal shape and the gonothecae



**Fig. 4.** *Tasmanaria edentula* (Bale, 1924). **A–B.** Portion of branch (A), hydrotheca (B), both from sample MNHN-IK-2015-472. Scale bars: A : 1 mm; B = 500 µm.

provided with apical spines in *T. pacifica* Vervoort & Watson, 2003 (see original account), suggest possible affinities with the Staurothecidae, as well. New molecular evidence is expected to shed light on the systematic position of the genus.

### Distribution

Off northern New Zealand (Vervoort & Watson 2003) and off New Caledonia (present study).

Family Syntheciidae Marktanner-Turneretscher, 1890  
Genus *Billardia* Totton, 1930

*Billardia hyalina* Vervoort & Watson, 2003  
Fig. 5; Table 2

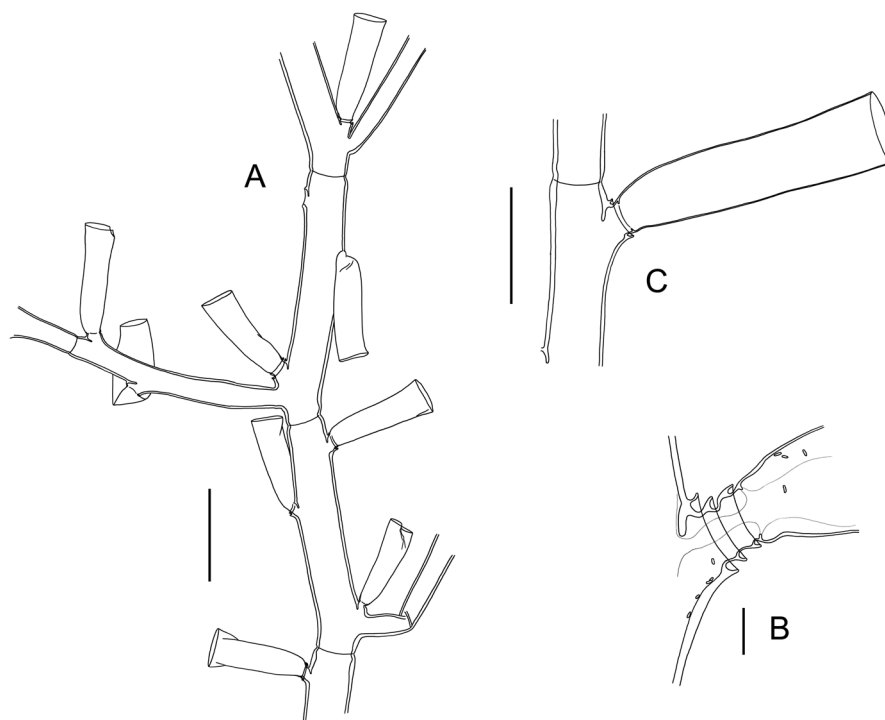
*Billardia hyalina* Vervoort & Watson, 2003: 413, fig. 102A–C.

### Material examined

PACIFIC OCEAN • a colony without gonothecae, 4.5 cm high; off New Caledonia, stn DW5041; 20°05' S, 158°53' E; 410–380 m; 23 Sep. 2017; KANADEEP leg.; a portion of stolon was removed for DNA extraction, DNA 1394; barcode identifier MK073106; MNHN-IK-2015-474.

### Description

Colony erect, up to 4.5 cm high, arising from creeping, branching, tortuous stolon. Stem simple, monosiphonic, composed of a short (ca 1 cm long), proximal, smooth part, and a distal, comparatively longer hydrothecate and hydrocladiate part, the latter divided almost regularly into internodes by



**Fig. 5.** *Billardia hyalina* Vervoort & Watson, 2003. A–C. Portion of stem with proximal parts of three consecutive cladia (A), detail of stem apophysis for insertion of hydrotheca (B, note regenerations), hydrotheca (C), all from sample MNHN-IK-2015-474. Scale bars: A = 1 mm; B = 100 µm; C = 500 µm.

**Table 2.** Measurements of *Billardia hyalina* Vervoort & Watson, 2003, in  $\mu\text{m}$ .

	Present study	Vervoort & Watson (2003)
<b>Stem</b>		
- internode length	2370–2695	2870–3200
- diameter at node	240–590	215–375 (basally 490)
<b>Cladia</b>		
- length of 1 <sup>st</sup> internode	1340–1830	–
- distance between successive hydrothecae	605–1170	–
- diameter at node	155–210	–
<b>Hydrotheca</b>		
- total depth	945–1190	1230–1395
- diameter at rim	315–355	325–345

means of transverse nodes; each internode slightly geniculate, composed of an indistinct apophysis supporting a cladium, an axillary hydrotheca associated to it, and two alternate hydrothecae above. Cladia generally alternate, coplanar, usually unbranched, divided into internodes by means of transverse nodes; up to 1.1 cm long and composed of up to ten hydrothecae internodes; first internode with a long, athecate, proximal part and two alternate hydrothecae distally; remainder of hydrocladium composed of internodes with three successive, alternate hydrothecae. Hydrothecae with the same shape and size on both stem and cladia; borne on short apophyses, often renovated several times; exceedingly long, tapering imperceptibly from aperture to base, slightly asymmetrical, proximal adaxial wall slightly more convex than abaxial wall, elsewhere both straight; base with annular constriction to which the base of the hydranth attaches; rim circular, not everted; perisarc thin, smooth, transparent and easily collapsible; hydranths without caecum, with 20–22 long, filiform tentacles. Gonothecae not observed.

### Remarks

The exceedingly long, almost tubular hydrothecae, with easily collapsible perisarc, are diagnostic (Vervoort & Watson 2003).

Occasionally, the stem internodes bear three alternate hydrothecae (instead of only two) above the axillar hydrotheca; consequently, the cladia flanking them are given off on the same side of the stem. Similarly, two cladia separated by an axillary stem hydrotheca were found. Aberrant, additional, ‘twin’ cladia are given off at the same level from the lower half of the stem, and point towards either the frontal or dorsal sides of the colony. Moreover, one distal cladium shows the beginning of secondary branching below one of its hydrothecae.

### Distribution

Norfolk Ridge (Vervoort & Watson 2003), off New Caledonia (present study).



Genus *Hincksella* Billard, 1918

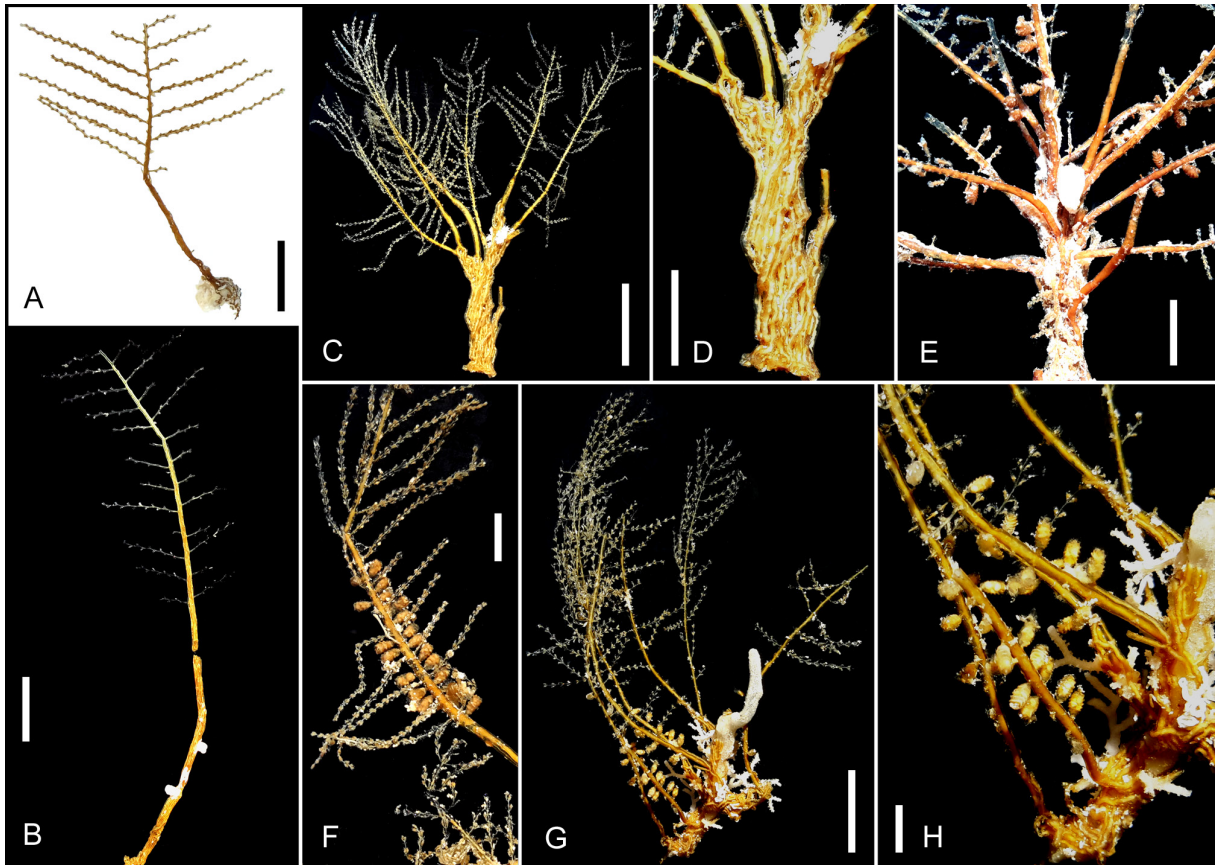
*Hincksella immersa* Galea, sp. nov.

[urn:lsid:zoobank.org:act:20EE4072-852E-492F-869A-80E120C82AE5](https://zoobank.org/urn:lsid:zoobank.org:act:20EE4072-852E-492F-869A-80E120C82AE5)

Figs 6A, 7A–F; Table 3

### Diagnosis

Colonies erect, regularly-pinnate; stems lightly fascicled, divided by indistinct transverse nodes; each equivalent of internode with a proximal apophysis and its axillary hydrotheca, two alternate hydrothecae above, and a second, distal apophysis together with its axillar hydrotheca. Cladia alternate, coplanar, separated from corresponding apophyses by transverse nodes; division into internodes indistinct; each equivalent of internode relatively short, provided with a hydrotheca distally. Hydrothecae cup-shaped, relatively shallow, almost completely adnate. Gonothecae given off from below the bases of cladial hydrothecae; ovoid, laterally flattened, tapering below, apically rounded.



**Fig. 6.** A. *Hincksella immersa* Galea, sp. nov., holotype colony, MNHN-IK-2015-390. — B. *Hincksella sibogae* Billard, 1918, one colony from sample MNHN-IL-2015-391. — C–F. *Syntheceium hians* Millard, 1957, one colony from sample MNHN-IK-2015-494 (C) and detail of its fascicled base (D); individual stems diverging from common base (E) and fertile stem (F), both from sample MNHN-IK-2015-486. — G–H. *Syntheceium rectangulatum* Galea, sp. nov., holotype colony (G) and gonothecae on proximal parts of the stems (H), both from sample MNHN-IK-2015-485. Scale bars: A–B, D–E = 1 cm; C, G = 2 cm; F, H = 5 mm.

**Table 3.** Measurements of *Hincksella* spp., in  $\mu\text{m}$ .

	<i>H. immersa</i> Galea, sp. nov. MNHN-IK-2015-390	<i>H. sibogae</i> Billard, 1918 MNHN-IK-2015-391
<b>Stem</b>		
- internode length	730–950	900–1060
- internode diameter	340–425	295–335
- apophysis length	185–260	160–210
<b>Cladium</b>		
- 1 <sup>st</sup> internode length	1125–1260	1260–1555
- ordinary internode length	680–1035	800–1100
- internode diameter	310–345	210–235
<b>Cauline hydrothecae</b>		
- free adaxial wall	15–125	–
- adnate adaxial wall	330–460	–
- abaxial wall	315–340	–
- diameter at rim	315–345	–
<b>Cladial hydrothecae</b>		
- free adaxial wall	0–75	240–290
- adnate adaxial wall	380–475	300–325
- abaxial wall	290–350	385–405
- diameter at rim	300–340	335–365
<b>Gonotheca</b>		
- total length	1090–1120	–
- maximum width	510–565	–
- diameter at aperture	ca 300	–

### Etymology

From the Latin ‘*immergo*, -si, -sum, -ēre’, meaning ‘immersed’, to depict the condition of its hydrothecae.

### Material examined

#### Holotype

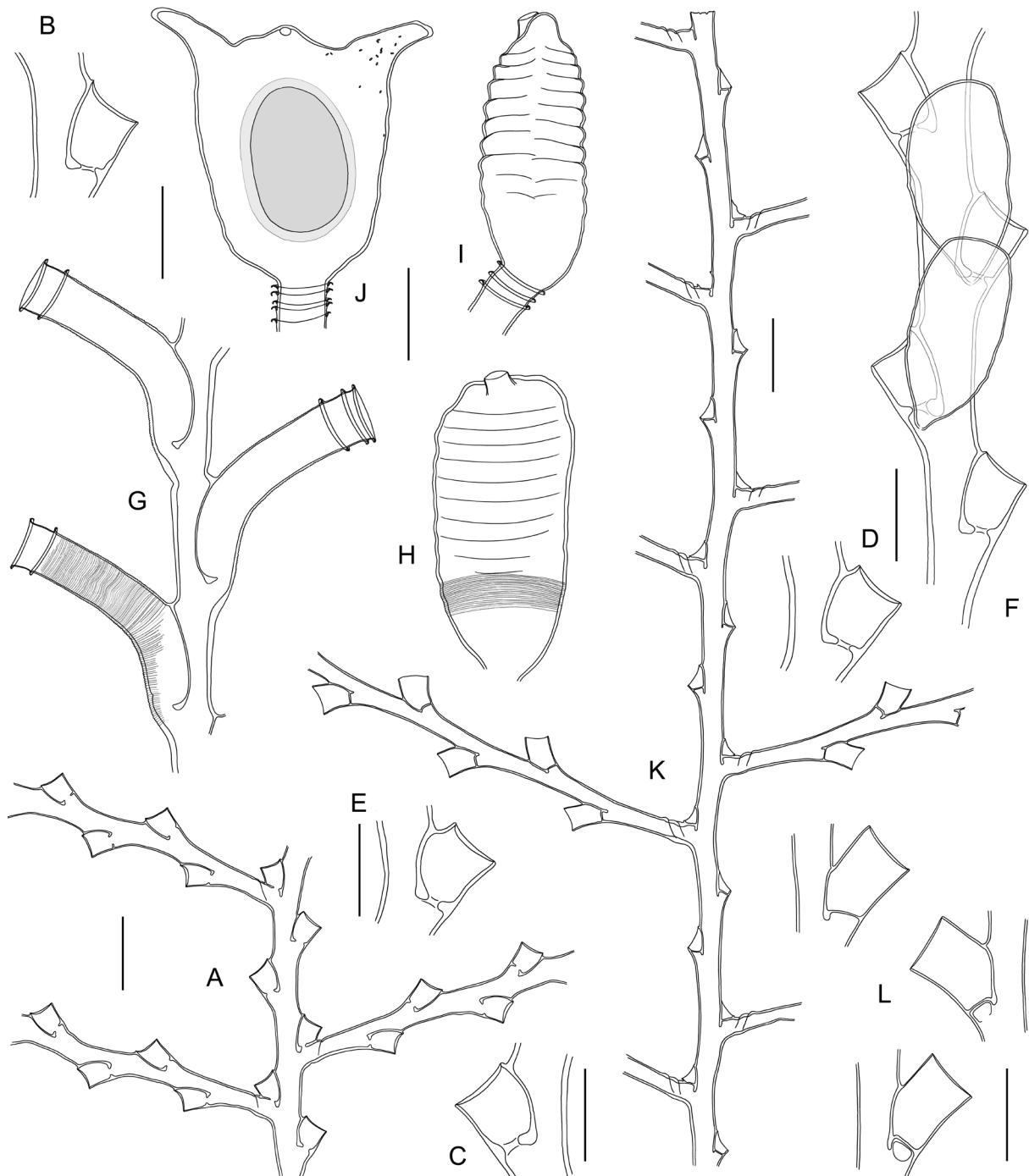
PACIFIC OCEAN • a 3.8 cm high broken in middle, bearing numerous gonothecae on cladia; off New Caledonia, stn DW4768; 23°25' S, 168°01' E; 180–210 m; 27 Aug. 2016; KANACONO leg.; a portion of cladium was used for DNA extraction, DNA1367; voucher MHNG-INVE-120801; barcode identifier MK073091; MNHN-IK-2015-390.

#### Paratype

PACIFIC OCEAN • a colony without gonothecae, 4.3 cm high; off New Caledonia, stn DW1712; 23°22' S, 168°03' E; 180–250 m; 26 Jun. 2001; NORFOLK 1 leg.; MNHN-IK-2015-392.

### Description

Colonies erect, up to 4.3 cm high, arising from root-like hydrorhiza strongly anchoring the colony to its substrate. Stems simple, fascicled for most of their length, grading to monosiphonic distally; perisarc thick, brownish; division into internodes indistinct; equivalents of internodes with quite regular structure, composed of a proximal apophysis supporting a cladium and its associated axillar hydrotheca, two alternate hydrothecae above, and a second, distal cladial apophysis given off on opposite side, together with its associated axillar hydrotheca; occasionally three instead of only two alternate hydrothecae



**Fig. 7.** A–F. *Hincksella immersa* Galea, sp. nov., portion of stem with three cladia (A), four hydrothecae (B–E) showing varied degree of immersion, portion of cladium with gonothecae (F), all from sample MNHN-IK-2015-390. — G–J. ?*Hincksella neocaledonica* Galea, 2015, portion of stem with three hydrothecae (G), immature gonotheca in frontal (H) and lateral (I) views, all from sample MNHN-IK-2015-384; fully-formed gonotheca (J) from sample MNHN-IK-2015-385. — K–L. *Hincksella sibogae* Billard, 1918, portion of colony showing branching pattern (K), three hydrothecae (L), all from sample MNHN-IK-2015-391. Scale bars: A, K = 1 mm; B–J, L = 500  $\mu$ m.

intervene between the proximal and distal cladial apophyses. Cladia alternate, coplanar, borne on short stem apophyses separated from their 1<sup>st</sup> internodes by distinct oblique nodes; cladia distant of 2.5–3 mm on each side; division by nodes indistinct, but each equivalent of internode relatively short, widening abruptly distally to accommodate a hydrotheca; internodes collinear. Hydrothecae alternate, in two parallel, coplanar rows; cup-shaped, deeply immersed into their corresponding internodes, leaving only a short portion of their adaxial wall free; abaxial wall straight to slightly convex, adnate adaxial wall distinctly curved, forming large perisarc plug basally; there is no complete base for the hydrotheca, as the abaxial wall invaginates basally for only a limited extent at junction between the hydrothecal lumen and internode; aperture circular, rim smooth. Gonothecae inserted slightly laterally under the bases of cladial hydrothecae; saccular, flattened ‘dorso-ventrally’, tapering basally into indistinct pedicel, distally rounded; no distinct aperture.

### Remarks

This species, through its colony structure and origin of gonothecae, comes close to the type species of the genus, *H. sibogae* Billard, 1918. It is distinguished from it through its comparatively shorter internodes, and much immersed hydrothecae (compare Fig. 7A–E and 7K–L).

According to the present concept (Bouillon *et al.* 2006), the genus *Hincksella* Billard, 1918 includes not only species forming pinnate colonies, but also congeners with simple, unbranched stems. Among the former category, *H. alternans* (Allman, 1888) gives rise to gonothecae from within the hydrothecal lumina, while *H. formosa* (Fewkes, 1881), the present new species, as well as *H. sibogae* produce external gonothecae. As for *H. indiana* Millard, 1967, a species with so-far undescribed gonothecae, it could instead belong to *Staurotheca* Allman, 1888.

Conversely, among the species with simple stems, *H. cornuta* Galea, 2015 (Galea 2015a), *H. cylindrica* (Bale, 1888) (Preker & Lawn 2010), *H. neocaledonica* Galea, 2015 (see below) and *H. pusilla* (Ritchie, 1910) (Galea 2015b) give rise to their gonothecae from within their hydrothecae. The latter also produces stolonial gonothecae (Hirohito 1969, as *Cyclonia pusilla*). As for the remaining four species, viz. *H. corrugata* Millard, 1958, *H. projecta* (Fraser, 1938), *H. rigida* (Fraser, 1938) and *H. similis* Galea, 2015, their gonothecae have not yet been described.

Owing to the above-mentioned features, it is likely that the genus *Hincksella* is polyphyletic. The 16S tree, indeed, shows that the four included species of *Hincksella* do not group into a common clade (see Fig. 20 and the ‘Molecular study’ section) and are rather scattered.

### Distribution

Only known from off New Caledonia (present study).

? *Hincksella neocaledonica* Galea, 2015  
Fig. 7G–J

*Hincksella neocaledonica* Galea, 2015a: 15, fig. 5E–F.

### Material examined

PACIFIC OCEAN • a colony composed of 6 stems 0.7–2.3 cm high, one of which bears a gonotheca; off New Caledonia, stn DW4768; 23°25' S, 168°01' E; 180–210 m; 27 Aug. 2016; KANACONO leg.; one stem was used for DNA extraction, DNA1362; voucher MHNG-INVE-120796; barcode identifier MK073090; MNHN-IK-2015-384 • a colony composed of 12 stems 0.4–2.3 cm high, one of which bears a gonotheca; same collecting data as for preceding; one stem was used for DNA extraction, DNA1363;

voucher MHNG-INVE-120797; 16S sequence identical to MK073090; MNHN-IK-2015-384 • a profuse colony with 0.5–2.3 cm high stems, some bearing gonothecae; off New Caledonia, stn DW4781; 22°57' S, 167°47' E; 295–255 m; 29 Aug. 2016; KANACONO leg.; one stem was used for DNA extraction, DNA1364; voucher MHNG-INVE-120798; MNHN-IK-2015-385 • a colony composed of 8 stems 2–2.3 cm high, three of which bear gonothecae; off New Caledonia, stn DW4742; 22°53' S, 137°37' E; 290–345 m; 23 Aug. 2016; KANACONO leg.; one stem was used for DNA extraction, DNA1365; voucher MHNG-INVE-120799; MNHN-IK-2015-386 • a profuse colony on fascicled axis of unidentified hydroid, with stems up to 2.2 cm high, many of them bearing gonothecae; same collecting data as for preceding; one stem was used for DNA extraction, DNA1366; voucher MHNG-INVE-120800; MNHN-IK-2015-386 • a profuse colony with stems up to 2 cm high, some bearing gonothecae; off New Caledonia, stn DW4782; 23°00' S, 167°55' E; 856–845 m; 29 Aug. 2016; KANACONO leg.; MNHN-IK-2015-387 • a colony composed of ca 10 stems without gonothecae, 0.5–2 cm high; off New Caledonia, stn DW4741; 22°52' S, 167°41' E; 210 m; 23 Aug. 2016; KANACONO leg.; MNHN-IK-2015-388 • a colony composed of ca 10 stems without gonothecae, 1–2 cm high; off New Caledonia, stn DW4743; 22°52' S, 167°34' E; 380–340 m; 23 Aug. 2016; KANACONO leg.; MNHN-IK-2015-389.

### Remarks

Unlike the holotype, some colonies in the present material are fertile. The gonothecae, of undetermined sex, are given off from within the hydrothecal lumina; broadly ovoid, ca 1420 µm long (and ca 1505 µm long including the spines, only one measured), laterally flattened (ca 1080 µm wide on widest side, only one measured), with 9–12 transverse ridges on both flattened sides, not meeting laterally, where two longitudinal, rounded, smooth ‘ridges’ are present. The small (ca 55 µm wide), rounded aperture is placed sub-apically, on a short, conical neck region, sometimes projecting outwards. The pair of apical ‘horns’ (distant of ca 1545 µm at their tips) is variably developed among colonies; in material MNHN-IK-2015-386, for example, they are almost indistinct, while an unequal development could be observed in sample MNHN-IK-2015-387.

In the light of the present findings, it could be noted that the fully-formed gonothecae of *H. neocaledonica* are similar to those of *H. cornuta* Galea, 2015 through both their size and shape (compare Fig. 7J to Galea 2015a: fig. 5D). However, these species can be readily distinguished on characters displayed by their trophosomes (compare Galea 2015a: figs 5E and 5A, respectively).

Unlike the type species of the genus, *H. sibogae* Billard, 1918 (see below), the present hydroid does not form rather tall colonies with fascicled stems, and its hydrothecae protrude for a long distance from the internodes. It comes close instead to *Cyclonia gracilis* Stechow, 1921 (now included in the synonymy of *H. pusilla* (Ritchie, 1910), see Galea (2010: 20) and Galea & Ferry (2015: 236)), suggesting a possible future resurrection of the genus *Cyclonia* Stechow, 1921 to accommodate a group of species with short, simple, monosiphonic stems, long, tubular hydrothecae, and gonothecae arising from within the hydrothecae (occasionally also from the stolon, as in *H. pusilla*).

### Distribution

Only known from off New Caledonia (Galea 2015a; present study).

### *Hincksella sibogae* Billard, 1918

Figs 6B, 7K–L; Table 3

*Hincksella sibogae* – Vervoort & Watson 2003: 245, fig. 58D–E.



### Material examined

PACIFIC OCEAN • two colonies without gonothecae, ca 9 cm high; one of them was cut into two pieces for convenient microscopical examination; off New Caledonia, stn DW4736; 22°42' S, 167°41' E; 303–308 m; 22 Aug. 2016; KANAONO leg.; a cladium from the same colony, containing remains of coenosarc, was removed for DNA extraction, DNA1368; voucher MHNG-INVE-120802; barcode identifier MK073092; MNHN-IK-2015-391.

### Remarks

The present material agrees well with the descriptions given by Billard (1925) and Vervoort & Watson (2003), and it is characterized by the following: a) the unbranched hydrocaulus is fascicled for most of its length; b) its main tube is undivided and has a regular structure, with equivalents of internodes composed of a basal cladial apophysis and its associated axillary hydrotheca, two alternate hydrothecae above, and a second cladial apophysis (on side opposite to preceding one) with its associated axillary hydrotheca; c) hydrocladia are simple and undivided into internodes, up to 1.3 cm long, and bear up to 13 alternate hydrothecae; the first internode is comparatively longer than subsequent ones and provided with a couple of proximal twists; ordinary internodes are moderately-long; d) the hydrothecae are immersed for about half their adaxial length into their corresponding internodes, and they narrow basally; their base is convex, entire, with occasional fenestrae below (as sites for the origin of gonothecae); e) the hydranth is attached to the lower third of the inner hydrothecal wall; f) the perisarc of the colonies is rather thin and easily collapsible, especially on hydrothecae.

### Distribution

Indonesia, the Great Barrier Reef, Tasman Sea near Lord Howe Island (Vervoort & Watson 2003), New Caledonia (present study).

Genus *Synthecium* Allman, 1872

*Synthecium hians* Millard, 1957  
Figs 6C–F, 8A–F; Table 4

*Synthecium hians* Millard, 1957: 204, fig. 9A–C.

*Synthecium hians* – Millard 1964: 25; 1975: 238, fig. 77C–D; 1980: 144, fig. 5A–B.

### Material examined

PACIFIC OCEAN • several colonies, some fertile, with stems up to 13.5 cm high, with strongly fascicled bases; off New Caledonia, stn DW4726; 22°40' S, 167°03' E; 240–181 m; 20 Aug. 2016; KANAONO leg.; a fully fertile colony was used for DNA extraction, DNA 1400; voucher MHNG-INVE-120860; MNHN-IK-2015-486 • three colonies without gonothecae, with strongly fascicled bases: a profuse one, 8 × 7 cm, a less profuse one, with only four stems, 6 × 8 cm, and one with only a single intact stem and many stumps, 7 × 5 cm; off New Caledonia, stn DW4718; 22°47' S, 167°09' E; 350 m; 19 Aug. 2016; KANAONO leg.; MNHN-IK-2015-494 • many stems without gonothecae, up to 11 cm high, most of them independent, a few ones aggregated basally through their intertwined hydrorhizae; off New Caledonia, stn DW4784; 22°51' S, 167°44' E; 310–322 m; 29 Aug. 2016; KANAONO leg.; one stem was used for DNA extraction, DNA 1398; voucher MHNG-INVE-120858; MNHN-IK-2015-484 • many colonies with strongly fascicled bases, up to 11 cm high, some bearing gonothecae; off New Caledonia, stn DW4724; 22°40' S, 167°07' E; 260–255 m; 20 Aug. 2016; KANAONO leg.; a fragment of stem from one colony was used for DNA extraction, DNA 1397; voucher MHNG-INVE-120857; MNHN-IK-2015-483 • several colonies with fascicled stems and fragments resulting from their breakage, largest

18 cm high, all without gonothecae; off New Caledonia, stn DW4735; 22°40' S, 167°40' E; 233–195 m; 22 Aug. 2016; KANACONO leg.; MNHN-IK-2015-501.

### Description

Colonies erect, bushy, up to 18 cm high, arising from root-like hydrorhiza composed of tortuous, branching and anastomosing fibers firmly adhering to the substrate; usually, profuse colonies with strongly fascicled base, up to 1 cm wide, of varied length, although smaller colonies composed of many independent stems exist. Stems diverging at varied angles from their common base; composed of a smooth, basal athecate and ahydrocladate part of varied length, and a much longer, distal part bearing both hydrothecae and hydrocladia; division into internodes not always distinct but, when present (nodes transverse), each internode composed of a pair of opposite hydrothecae proximally, followed by a pair of opposite apophyses supporting cladia and their associated axillary hydrothecae, as well as a second pair of opposite hydrothecae above; often, the hydrothecae are damaged, leaving scars in the stem, and not regenerating subsequently. Stem apophyses short, delimited from corresponding cladia by transverse constrictions of the perisarc, obvious mainly on upper parts of the colonies. Cladia given off laterally and slightly upwards in opposite, coplanar pairs; cladia distant of 3–4 mm, up to 1.8 cm long and bearing up to 18 thecate ‘internodes’; division by nodes indistinct, occasionally a transverse constriction of the perisarc intervenes between successive pairs of hydrothecae; the first ‘internode’ bears an unpaired hydrotheca facing downwards, while the 2–4 subsequent internodes display subalternate pairs of hydrothecae, changing gradually to strictly opposite distally. Often, the cladia show signs of breakage and subsequent regeneration at level of the proximal most internode; in this case, the first internode, similarly to the subsequent ones, bears invariably a pair of strictly opposite hydrothecae. Hydrothecae deep, cylindrical, curved outwards, adnate to the corresponding internode for most of their length; free adaxial wall short, slightly concave, perisarc thin, gently flaring distally; adnate adaxial wall distinctly curved, perisarc moderately thick, ending downwards into perisarc plug; abaxial wall more or less straight, distal  $\frac{2}{3}$  with distinctly thickened perisarc, often forming an internal swelling in middle, distal end slightly everted; aperture circular, rim relatively scooped in lateral view; up to three closely-set renovation could be note occasionally. Gonothecae, generally occurring in pairs, replace the (strongly) damaged stem hydrothecae in the lower halves of the colonies, arising from a hole in their adnate adaxial wall; urn-shaped, laterally flattened and thus bilaterally symmetrical; in a frontal view of the colonies, the gonothecae show their narrowest side; flattened sides are provided with 6–7 broad, convexly-arched ridges, the distalmost being the most prominent, grading proximally to the less conspicuous; viewed from their narrowest sides, the gonothecal ridges adopt a concave shape. Male and female gonothecae (sexes not always discernible), similar in shape. Female gonothecae with ca ten large, ovoid eggs.

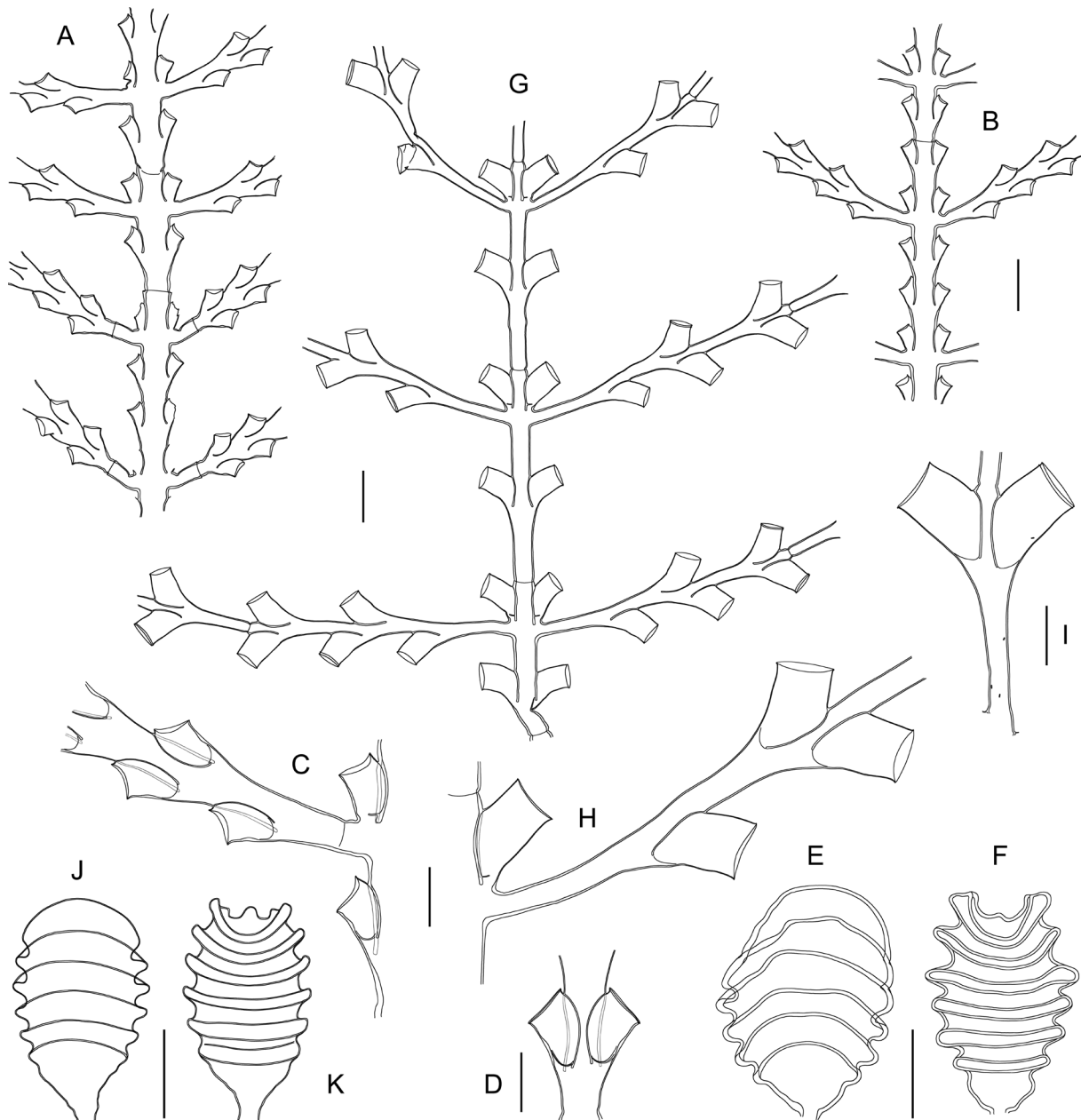
### Remarks

In rare instances, there can be no additional pair of hydrothecae between two successive pairs of cladia other than the axillar hydrothecae associated to the lower pair of cladia. In other cases, besides the axillary hydrothecae, only one pair (instead of two) of hydrothecae above separate two successive pairs of cladia. In one instance, a gonotheca replaced one cladium of a pair.

There is little doubt that the present material belongs to the species of Millard (1957), especially giving the following features: 1) the presence of a thick, tangled hydrorhiza, “with diameter of stolons equal to that of stem” (Millard 1957); as noted by Millard (1975), in “rich colonies the hydrorhizal tubes may rise up from the surface in a tangled bundle simulating a fascicled stem, the individual tubes anastomosing with one another and with the bases of the stems”; 2) the distinctive segmentation of the stem; 3) the presence of an unpaired proximal hydrotheca, followed by a few subopposite pairs; 4) the shape and size of hydrothecae, especially their narrow base, “widening strongly to margin, adnate for most of its length, only very slightly bent outwards [...]. Margin smooth, everted [...]. Diaphragm oblique, with outer edge

reaching sometimes as far as half-way up the abcauline wall. Perisarc thin, sometimes thickened below margin on abcauline wall” (Millard 1957: 204).

The gonothecae, were described subsequently by Millard (1980) and, in her material, they arose directly from the hydrorhiza or “from with the ends of short tubes which are probably damaged stems or hydrorhizal fibers” (Millard 1980: 144).



**Fig. 8.** A–F. *Syntheceum hians* Millard, 1957, distal portions of two stems (A–B), fragment of stem with insertion of cladium (C), all from sample MNHN-IK-2015-486; pair of hydrothecae from distal part of cladium (D) from sample MNHN-IK-2015-494; gonotheca in frontal (E) and lateral (F) aspects, from sample MNHN-IK-2015-486. — G–K. *Syntheceum rectangulatum* Galea, sp. nov., distal portion of a stem (G), fragment of stem with insertion of cladium (H), pair of hydrothecae from distal part of cladium (I), gonotheca in frontal (J) and lateral (K) aspects, all from sample MNHN-IK-2015-485. Scale bars: A–B, G = 1 mm; C–F, H–K = 500 µm.

**Table 4.** Measurements of *Synthecium* spp., in µm.

	<i>Synthecium hians</i> Millard, 1957		<i>Synthecium rectangulatum</i> Galea, sp. nov.
	MNHN-IK-2015-486	Millard (1967, 1980*)	MNHN-IK-2015-485
<b>Stem</b>			
- internode length	ca 2500	–	3800–4000
<b>Cladia</b>			
- diameter at node	ca 205	–	170–230
- length of 1 <sup>st</sup> thecate segment	1200–1410	–	1900–2305
- distance between consecutive pairs of hydrothecae	780–975	510–740	1715–1950
<b>Hydrotheca (cladial)</b>			
- free adaxial wall	30–70	30–50	315–400
- adnate adaxial wall	520–585	300–370	635–685
- maximum width	285–310	–	500–520
- diameter at rim	290–325	230–270	420–435
<b>Gonotheca</b>			
- length	ca 2665	2100–3000 *	ca 2525
- width (wide side)	ca 1850	2000–2400 *	ca 1560
- width (narrow side)	ca 1605	–	ca 1445

A closely related congener (or, possibly, a mix of two species) to both *S. hians* and *S. rectangulatum* sp. nov. (see below) is the one likely erroneously assigned by Vervoort & Watson (2003) to *S. protectum* Jäderholm, 1903. Indeed, these authors mention a basally fascicled colony with stems up to 12 cm high (NZOI Stn I85), and the gonotheca described and illustrated in their fig. 60F shows obvious similarities to those of the two species discussed herein. However, since there is no formal description provided by these authors, their material could not be assigned with certainty to one of the species dealt with herein. In addition, it should be stressed that *S. protectum* has comparatively smaller hydrothecae, and its gonothecae are radically different (Galea 2007: 77, fig. 18E–J, table 31, as *S. robustum* Nutting, 1904).

### Distribution

South Africa (Millard 1957) and New Caledonia (present study).

### *Synthecium rectangulatum* Galea, sp. nov.

[urn:lsid:zoobank.org:act:6791A674-EFEB-4666-A21A-C83247D402F3](https://zoobank.org/act:6791A674-EFEB-4666-A21A-C83247D402F3)

Figs 6G–H, 8G–K; Table 4

### Diagnosis

Profuse colonies comprising multiple, possibly auto-epizoic stems, forming a common, fascicled base. Above, stems monosiphonic, divided into long internodes, composed of a proximal pair of hydrothecae and a distal pair of cladial apophyses together with their associated axillary hydrothecae. Cladia with proximal, unpaired hydrotheca facing downwards, followed by additional pairs of hydrothecae adopting gradually a strictly opposite arrangement towards the distal end. Hydrothecae large, tubular, adnate for about half their adaxial length; free adaxial and abaxial walls straight and imperceptibly convergent

distally. Gonothecae of varied origins, urn-shaped, laterally flattened, with 6–7 convex ridges on their broadest sides, these becoming concave on their narrowest sides; aperture on top of an apical dome.

### **Etymology**

The specific name results from the fusion of two Latin words, ‘*rectus*, -a, -um’, meaning ‘straight’, and ‘*angulātus*, -a, -um’, meaning ‘provided with angles’, to illustrate the approximate shape of the hydrothecae in lateral view.

### **Material examined**

#### **Holotype**

PACIFIC OCEAN • a fertile colony with stems up to 10 cm high; off New Caledonia, stn CP4984; 20°47' S, 160°57' E; 410–430 m; 10 Sep. 2017; KANADEEP leg.; one fragment was used for DNA extraction, DNA1399; voucher MHNG-INVE-120859; barcode identifier MK073109; MNHN-IK-2015-485.

#### **Paratypes**

PACIFIC OCEAN • one colony with four large stems, up to 8 cm high, some fertile, on coral; off New Caledonia, stn CP4984; 20°47' S, 160°57' E; 410–430 m; 10 Sep. 2017; KANADEEP leg.; MNHN-IK-2015-475 • at least two neighboring colonies, possibly united originally through their stolons, each composed of several stems up to 9.5 cm high, some with gonothecae; off New Caledonia, stn CP4984; 20°47' S, 160°57' E; 410–430 m; 10 Sep. 2017; KANADEEP leg.; MNHN-IK-2015-503.

#### **Additional material**

PACIFIC OCEAN • two colonies, one comprising five stems fused basally, up to 11 cm high, some bearing gonothecae on both cauli and hydrorhiza, and the other composed of two independent stems without gonothecae, arising from the same substrate, and attaining ca 7 cm in height; off New Caledonia, stn CP4985; 20°49' S, 160°57' E; 480–540 m; 10 Sep. 2017; KANADEEP leg.; MNHN-IK-2015-500.

### **Description**

Colonies erect, up to 11 cm high, composed of either independent or basally-fused stems arising from tortuous, creeping, branching, anastomosing hydrorhizae. Stems unbranched, either monosiphonic or lightly fascicled basally; in the latter case, auxiliary tubes run up and down the stems, forming additional hydrorhizal fibers. In profuse colonies, there seems to be a tendency to auto-epizoism, with new stems settling down on older ones, and forming bunches arising from a common, fascicled base. Basal parts of individual stems, above their common base, of varied length, monosiphonic, ahydrothecate and acladiate, with smooth perisarc; remainder of stem, comparatively longer, divided into regular internodes by means of transverse constrictions of the perisarc, more obvious in the upper parts; each internode long, composed of a pair of opposite hydrothecae proximally and a pair of opposite apophyses above, together with their associated axillary hydrothecae; pairs of hydrothecae widely-spaced; stem apophyses supporting the cladia distant of 4–4.5 mm; there is no very distinct node at junction between apophysis and cladium, although a slight notch in the perisarc of upper side could sometimes be noted. Most stem hydrothecae, especially those situated proximally, damaged and not regenerated subsequently. Cladia up to 17 mm long, given off at wide angle with the stem; pairs of opposite cladia coplanar; divided into irregular internodes by means of transverse nodes; proximal most internode with a long, smooth, athecate base, an unpaired hydrotheca facing downwards, followed by a distinctly subopposite pair of hydrothecae, and a distal pair of nearly opposite hydrothecae; occasionally, this internode is devoid of the second, and hence distalmost, pair of hydrothecae, the latter being confined to the next internode; subsequent internodes with either two or three strictly opposite pairs of hydrothecae; a fully-formed cladium comprises, besides the unpaired proximal hydrotheca, up to nine pairs of thecae. In most



colonies, many cladia, especially the basal ones, show signs of breakage and subsequent regeneration (a distinctive, transverse breakage line could be noted); in this case, the cladia comprise exclusively pairs of strictly opposite hydrothecae, the proximal most, unpaired one being replaced. Hydrothecae on both stems and cladia form two parallel, coplanar rows; almost tubular, adnate for slightly more than half their adaxial length to the corresponding internodes; free adaxial and abaxial walls slightly and gradually convergent towards distal end; aperture circular, rim slightly everted; hydranths with ca 18 filiform tentacles. The gonothecae arise often in pairs from scars of damaged hydrothecae on proximal parts of the stems; occasionally, they can replace a cladium of a pair, arise from auxiliary tubes of the stem, and are also profusely given off from the hydrorhiza. Gonothecae similar in both sexes (although sexes not always recognizable with certainty), urn-shaped, bilaterally symmetrical, laterally flattened; they show their narrowest side when the colonies are seen frontally; on their broadest sides, they are provided with 6–7 convex, rounded crests, more curved distally, and comparatively less arched basally; the narrowest sides show the same crests, but they are concave therein; distally, a dome-shaped protuberance bearing apically the aperture; ca six large, ovoid oocytes per gonotheca.

### Remarks

Through its fascicled stems and distinctive gonothecae, this species comes close to *S. hians* (see above) and the material incorrectly assigned by Vervoort & Watson (2003) to *S. protectum* (see above). No other nominal species, besides *S. hians* and *S. rectangulatum* sp. nov., are known to possess fascicled stems. The differences between these two hydroids could be noted in Fig. 8. It should be noted that, as stated above, Vervoort & Watson's material possibly comprises a mix of species, of which one (NZOI P34, slide 2225) has proportionally longer hydrothecae than *S. rectangulatum* sp. nov., and seems therefore specifically different, while the other (NMNZ BS904, slides 4285) has shorter hydrothecae, and could also belong to another species.

Family Sertulariidae Lamouroux, 1812

Genus *Diphasia* L. Agassiz, 1862

*Diphasia alternata* Galea, sp. nov.

[urn:lsid:zoobank.org:act:EF062F46-F580-4DA9-9EFD-E822F8D7393B](https://zoobank.org/urn:lsid:zoobank.org:act:EF062F46-F580-4DA9-9EFD-E822F8D7393B)

Fig. 9; Table 5

### Diagnosis

Colony with short, monosiphonic, sparingly-branched stems arising from creeping hydrorhiza; stem and branches divided into moderately-long internodes, each accommodating a hydrotheca distally; hydrothecae alternate, tubular, adnate for  $\frac{1}{3}$  or less, strongly curved outwards, aperture gutter-shaped. Gonothecae unknown.

### Etymology

From the Latin '*alternus*, *-āvi*, *-ātum*, *-ārei*', meaning 'to alternate/alternating', to characterize the condition of its hydrothecae.

### Material examined

#### Holotype

PACIFIC OCEAN • a colony without gonothecae, with stems up to 1 cm high, on antipatharian; off New Caledonia, stn DW4977; 19°46' S, 158°30' E; 280–304 m; 9 Sep. 2017; KANADEEP leg.; MNHN-IK-2015-471.

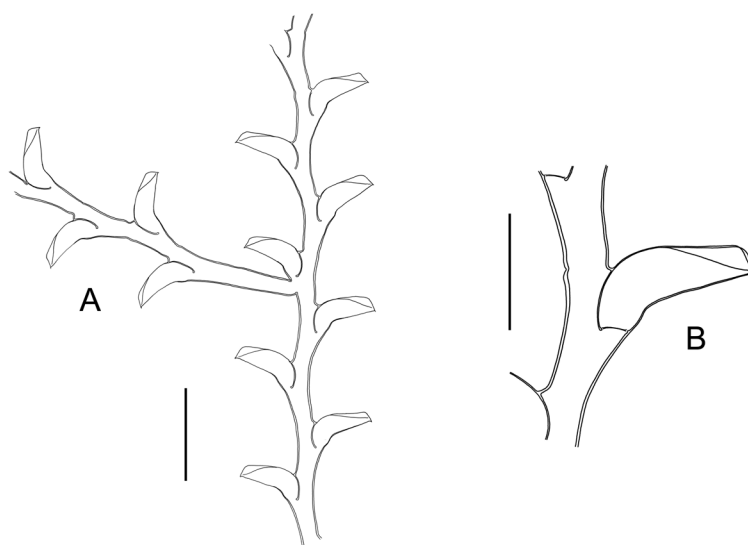
## Description

Colony arising from tortuous, branching, anastomosing hydrorhiza creeping on antipatharian host. Stems erect, up to 1 cm high, monosiphonic, unbranched or with, at most, single side branches; proximal part of varied length, though short, ahydrothecate, with smooth perisarc, and basal constriction above origin from stolon; above, remainder of stem hydrothecate, divided into a regular succession of moderately-long internodes through oblique constrictions of the perisarc slanting in alternate directions, more conspicuous distally; each internode relatively short, widening distally, where it bears a hydrotheca. Side branches, when present, of varied length, given off laterally from below the base of a stem hydrotheca through indistinct apophysis; structure similar to that of stem, except for the first internode that is comparatively longer than subsequent ones. Hydrothecae in two coplanar rows on both stems and branches, alternate, immersed for  $\frac{1}{3}$  or less into their corresponding internodes; tubular, strongly curved outwards from internode (at nearly right angle), perisarc smooth throughout; proximal abaxial wall distinctly swollen, then straight to slightly concave in middle; free adaxial wall convex, collapsed on distal half over abaxial wall, leaving two broad, lateral ‘wings’ forming a gutter-shaped aperture; the latter, slightly everted distally on abaxial side, rim occasionally bearing 1–2 renovations; adnate adaxial wall convex, ending basally in perisarc plug; there is no hydrothecal base; opercular apparatus not clearly discernible, but likely composed of one adaxial flap. Hydranths badly-preserved, though there is no evidence of an abaxial caecum; tentacle number could not be ascertained. Gonothecae not observed.

## Remarks

This is a very delicate, small species, with sparingly-branched stems and strictly alternate hydrothecae, distinctly curved outwards, adnate for (at most)  $\frac{1}{3}$  of their adaxial length. There are only three congeners displaying an alternate arrangement of their hydrothecae, namely: *D. inornata* Nutting, 1927, *D. nuttingi* Stechow, 1913, and *D. paarmani* Nutting, 1904.

However, *D. inornata* from the Philippine region forms rather tall (7.5 cm high), pinnate colonies, and its hydrothecae are deeply immersed, leaving only about  $\frac{1}{4}$  of their adaxial wall free from the internode (Nutting 1927). In the Japanese *D. nuttingi*, the hydrothecae are adnate for less than half their length, and their free parts point “obliquely upwards, not bending”; in addition, their wall is provided with five longitudinal ridges: two latero-adaxial, two lateral and one abaxial (Hirohito 1995). The western



**Fig. 9.** *Diphasia alternata* Galea, sp. nov. **A–B.** Portion of stem with proximal part of side branch (A), hydrotheca (B), both from sample MNHN-IK-2015-471. Scale bars: A = 1 mm; B = 500  $\mu\text{m}$ .

**Table 5.** Measurements of *Diphasia alternata* Galea, sp. nov., in  $\mu\text{m}$ .

<b>Internodes</b>	
- length	550–750
- 1 <sup>st</sup> cladial, length	ca 1450
- diameter at node	165–215
<b>Hydrotheca</b>	
- free adaxial wall	550–560
- adnate adaxial wall	290–300
- abaxial wall	610–635
- maximum width	220–230

Atlantic *D. paarmani* forms large (7.6 cm high), pinnate colonies (Nutting 1904); stem hydrothecae “are arranged in pairs basally but gradually, towards the top part of the colony, they become sub-alternate”, although the cladial ones are always alternate (Vervoort 1972). The thecae are free for only  $\frac{1}{3}$  from their corresponding internodes, and curve only gently outwards (Nutting 1904).

### Distribution

Only known from off New Caledonia (present study).

### *Diphasia cristata* Billard, 1920

*Diphasia cristata* – Galea 2016: 4, fig. 1C–J.

### Material examined

PACIFIC OCEAN • four colonies 2.5–4.5 cm high, two of which bearing female gonothecae; off New Caledonia, stn DW4775; 23°03' S, 168°17' E; 140–277 m; 28 Aug. 2016; KANACONO leg.; one colony was used for DNA extraction, DNA 1372; voucher MHNG-INVE-120833; barcode identifier MK073095; MNHN-IK-2015-401 • a 4 cm high colony bearing a male gonotheca; off New Caledonia, stn DW4726; 22°40' S, 167°03' E; 240–181 m; 20 Aug. 2016; KANACONO leg.; MNHN-IK-2015-402.

### Remarks

The mode of branching is characteristically trifid: each stem gives rise basally to two opposite side branches that become secondary stems; each of these gives rise again, from below their basalmost pair of hydrothecae, to an opposite pair of 2<sup>nd</sup> order branches, and the process is repeated again until 4<sup>th</sup> order branches are obtained, as observed in material MNHN-IK-2015-401.

### Distribution

Philippines, Japan, New Caledonia, Vanuatu, Fiji and Tonga (Galea 2016).

Genus *Dynamena* Lamouroux, 1812

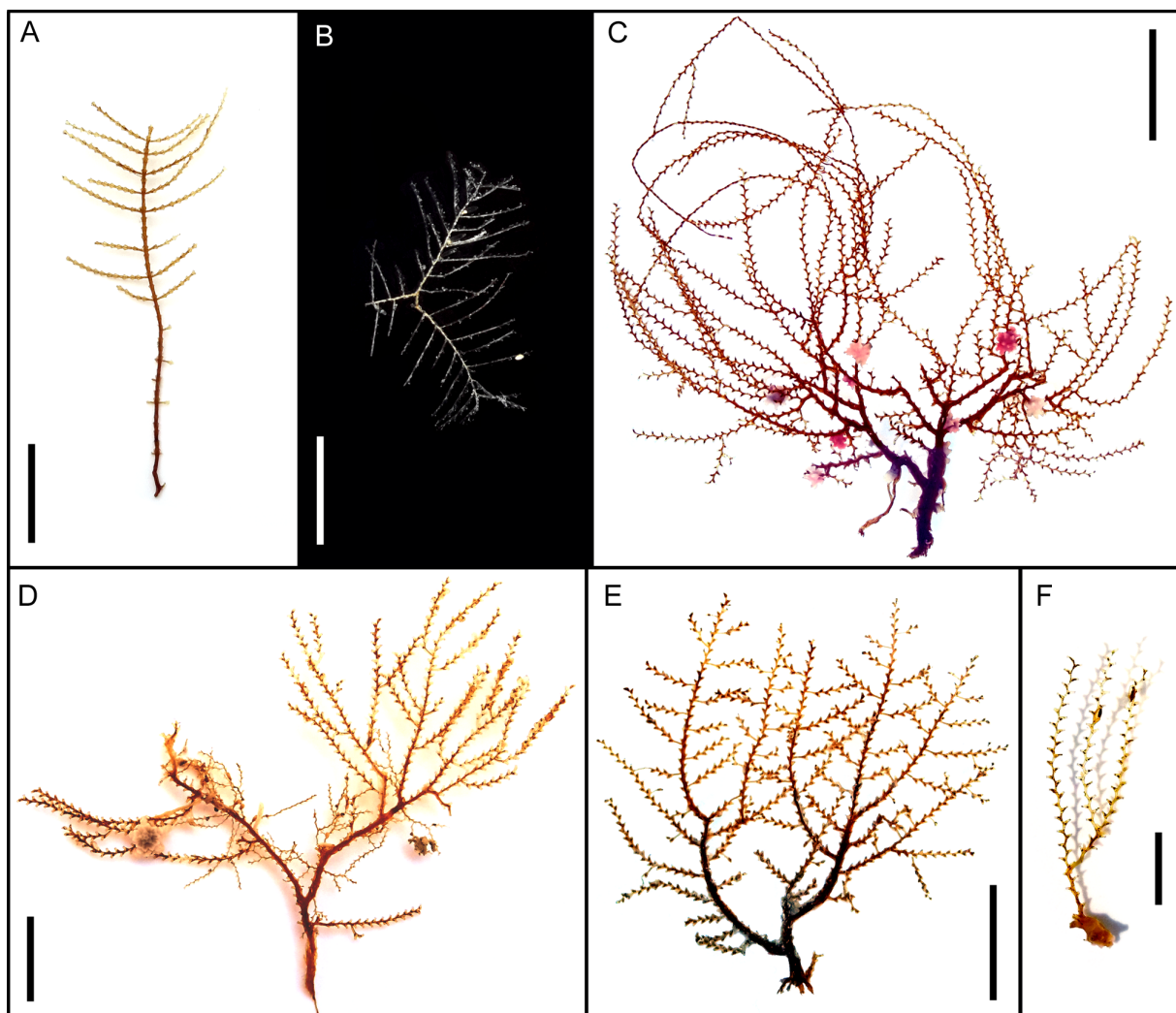
*Dynamena opposita* Galea, sp. nov.

[urn:lsid:zoobank.org:act:375154A7-28FA-4897-A522-362AA994DDA1](https://zoobank.org/urn:lsid:zoobank.org:act:375154A7-28FA-4897-A522-362AA994DDA1)

Figs 10A, 11; Table 6

### Diagnosis

Stems simple, monosiphonic, bearing pinnately-arranged hydrocladia in opposite pairs. Division into internodes irregular; each internode with a pair of indistinct apophyses supporting cladia and their associated axillary hydrothecae, as well as 0–3 pairs of hydrothecae below. Cladia divided into more or less regular internodes comprising 0–3 pairs of opposite hydrothecae. Hydrothecae tubular, deeply immersed into internode, not contiguous, aperture facing outwards, provided with two lateral, triangular cusps. Gonothecae unknown.



**Fig. 10.** A. *Dynamena opposita* Galea, sp. nov., holotype colony, MNHN-IK-2015-470. — B. *Hydrallmania clavaformis* Galea, sp. nov., holotype colony, MNHN-IK-2015-404. — C. *Sertularella leiocarpoides* Vervoort, 1993, one colony from sample MNHN-IK-2015-420. — D. *Sertularella novaecaledoniae* Vervoort, 1993, colony from sample MNHN-IK-2015-424. — E. *Sertularella* aff. *sinensis* Jäderholm, 1896, one colony from sample MNHN-IK-2015-418. — F. *Sertularella tronconica* Galea, 2016, colony from sample MNHN-IK-2015-419. Scale bars: A–B, D–E = 1 cm; C = 2 cm; F = 5 mm.

**Etymology**

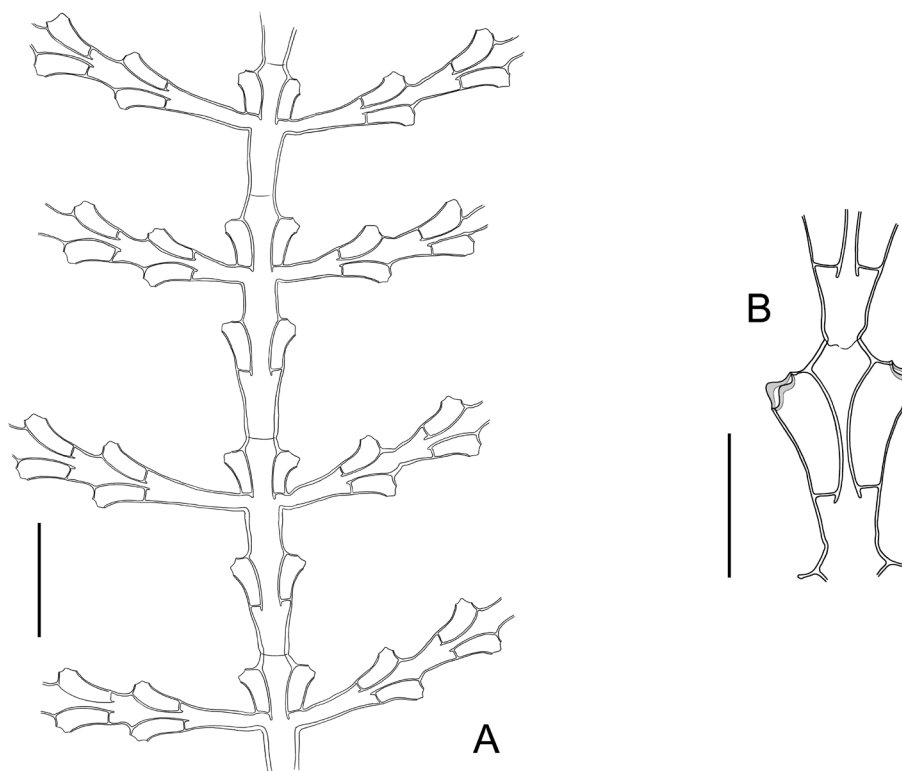
From the Latin ‘*oppositus*, -a, -um’, meaning ‘opposite’, to illustrate the relative position of the two rows of stem apophyses supporting the cladia.

**Material examined****Holotype**

PACIFIC OCEAN • a 3.8 cm high colony without gonothecae, detached from substrate, with mostly only the perisarc left; off New Caledonia, stn DW4735; 22°40' S, 167°40' E; 233–195 m; 22 Aug. 2016; KANACONO leg.; MNHN-IK-2015-470.

**Description**

Colony erect, 3.8 cm high, stiff when out of liquid, arising from creeping, branching hydrorhiza; stem monosiphonic, unbranched, composed of a short (3.5 mm long), athecate, basal part above the origin from stolon, and a much longer, distal thecate and cladiate part; the latter divided into irregular internodes by means of transverse constrictions of the perisarc; each internode long, composed distally of a pair of axillar hydrothecae above the insertion of two opposite cladia, as well as 0–3 pairs of hydrothecae below; hydrothecae opposite and distant from each one within a pair. No distinct stem apophyses supporting the cladia; successive pairs of cladia distant of 1.5–4 mm, depending of the number of intervening pairs of hydrothecae; cladia up to 1.3 cm long and comprising up to 16 pairs of successive hydrothecae; divided by transverse nodes, occasionally indistinct, into rather irregular internodes, generally comprising a single pair of hydrothecae distally, although 2–3 of these may occur elsewhere; first, proximal most internode comparatively longer than subsequent ones. Hydrothecae in strictly opposite pairs, not contiguous,



**Fig. 11.** *Dynamena opposita* Galea, sp. nov. **A–B.** Distal part of colony showing branching pattern (A), cladial internode with pair of hydrothecae (B). Scale bars: A = 1 mm; B = 500  $\mu$ m.



**Table 6.** Measurements of *Dynamena opposita* Galea, sp. nov., in  $\mu\text{m}$ .

<b>Internodes</b>	
- cauline, diameter at node	210–405
- 1 <sup>st</sup> cladial, length	860–1310
- ordinary cladial, length	590–870
- cladia, diameter at node	100–195
<b>Hydrotheca</b>	
- free adaxial wall	75–100
- adnate adaxial wall	435–465
- abaxial wall	325–340
- diameter at rim	135–140

though much closer to one another compared with their cauline counterparts; almost tubular, gently curving outwards, deeply immersed into the corresponding internode, leaving  $\frac{1}{6}$ – $\frac{1}{7}$  of their adaxial wall free; the latter consequently short and distinctly concave; adnate adaxial wall concave; abaxial wall slightly curved outwards, especially distally; margin thickened, provided with two conspicuous, lateral, triangular cusps with rounded tips; opercular apparatus lost. Hydranths badly-preserved, presence of an abaxial gastric diverticulum could not be ascertained. Gonothecae absent. Perisarc of the colony thick and brown.

#### Remarks

According to Galea & Ferry (2015: 230–231, table 2), only two nominal species of *Dynamena* described so far form pinnate colonies with opposite cladia, namely *D. anceps* (Fraser, 1938) and *D. japonica* Stechow, 1920.

Through the courtesy of D. Geiger of the Santa Barbara Museum of Natural History (SBMNH), CA, USA, one of us (H.R.G.) was able to see several macrophotographs of the lecto- and one of the paralectotypes of *D. anceps*, demonstrating that it is a much slenderer species, with hydrothecae free from their corresponding internodes for a much longer portion than in *D. opposita* sp. nov.

Unlike the new species, *D. japonica* is a large hydroid (colonies reaching as much as 20 cm in height), with thick and brown perisarc (Hirohito 1995), with cladia separated by 2–8 pairs of hydrothecae, the latter being closely approximated on both stems and cladia (Hirohito 1995; Stechow 1913, as *Thuiaria articulata* (Pallas, 1766); Park & Rho 1986, as *T. articulate*). In addition, its hydrothecae are bigger, having notably a wider rim (Hirohito 1995).

#### Distribution

Only known from off New Caledonia (present study).

Genus *Geminella* Billard, 1925

*Geminella ceramensis* (Billard, 1925)

*Geminella ceramensis* – Schuchert 2003: 174, fig. 31. — Galea 2016: 7, fig. 1P.

#### Material examined

PACIFIC OCEAN • a small colony with stems up to 0.5 cm high, without gonothecae, on axis of dead antipatharian; off New Caledonia, stn DW4726; 22°40' S, 167°03' E; 240–181 m; 20 Aug. 2016;

KANACONO leg.; three stems were used for DNA extraction, DNA 1373; barcode identifier MK073096; MNHN-IK-2015-403.

### Distribution

Indonesia, Philippines, New Caledonia and Vanuatu (Galea 2016).

Genus *Hydrallmania* Hincks, 1868

*Hydrallmania clavaformis* Galea, sp. nov.

[urn:lsid:zoobank.org:act:9C4EF457-3442-4007-9159-B6F710471D3C](https://zoobank.org/act:9C4EF457-3442-4007-9159-B6F710471D3C)

Fig. 10B, 12; Table 7

### Diagnosis

Stems helicoidal, giving rise laterally to secondary branches with pinnate arrangement of cladia. Nodes mostly indistinct, but equivalents of internodes comprising a proximal apophysis (supporting a cladium) and its associated axillar hydrotheca, two alternate hydrothecae above, and a second, distal apophysis together with its axillar hydrotheca. Stem hydrothecae relatively distant, shifted on to the anterior side, small, deeply-immersed into internodes; cladial hydrothecae closely-set, large, adnate for less than half their adaxial length, strongly projecting outwards in opposite directions. Gonothecae borne below the bases of axillar stem hydrothecae; exceedingly long, club-shaped, aperture distal, rounded, borne on recurved (at right angle) apex of gonotheca.

### Etymology

From the Latin ‘*clāva*’, meaning ‘mace’, and ‘*forma*’, meaning ‘shape’, to characterize the morphology of its gonotheca.

### Material examined

#### Holotype

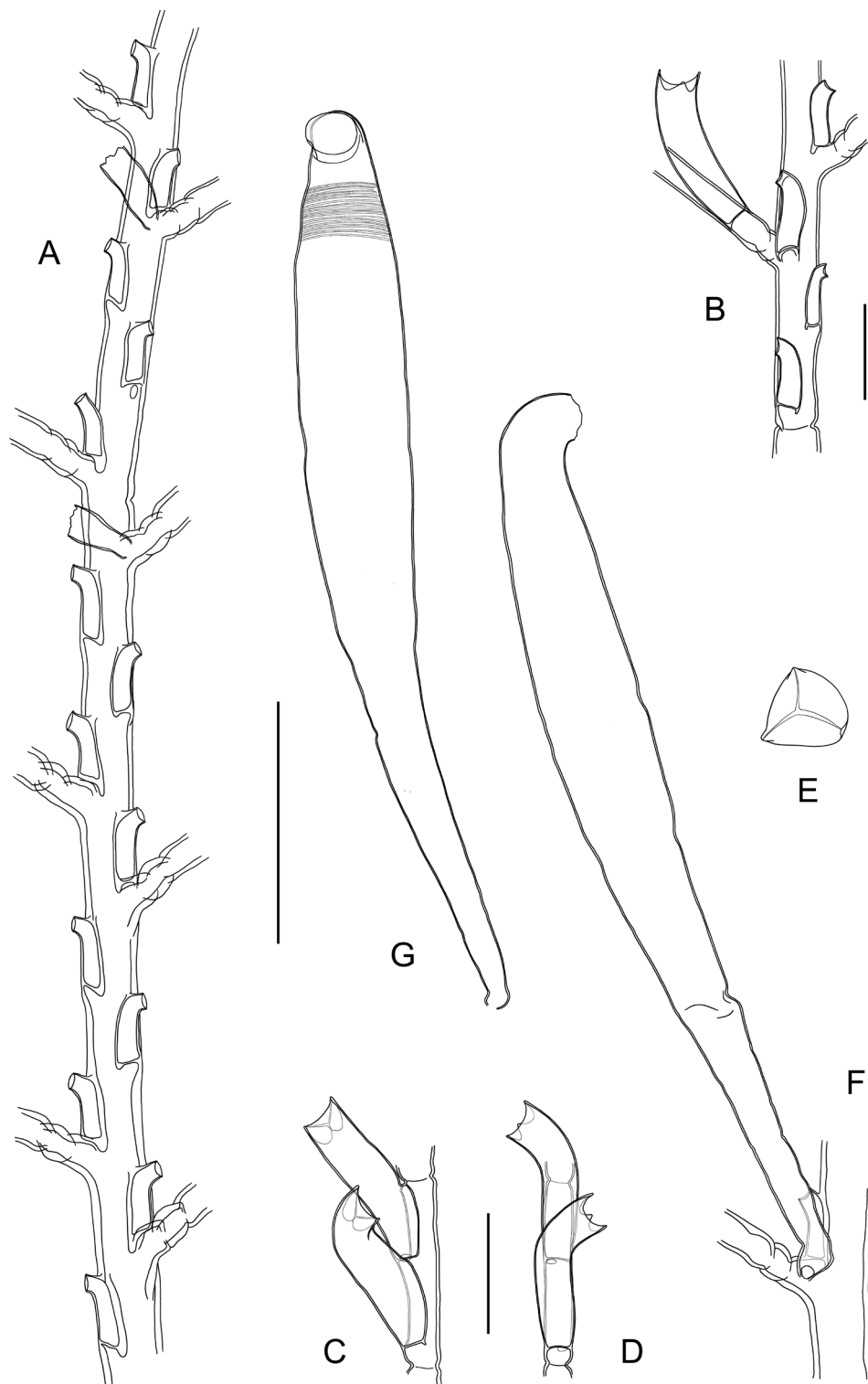
PACIFIC OCEAN • a 1.5 cm high, apical part of a fertile colony, with three side branches, with almost no traces of coenosarc; off New Caledonia, stn DW4744; 22°55' S, 167°37' E; 310–290 m; 23 Aug. 2016; KANACONO leg.; MNHN-IK-2015-404.

#### Paratype

PACIFIC OCEAN • upper (1.7 cm long) part of a colony with four side branches, with fairly-preserved coenosarc, without gonothecae; off New Caledonia, stn DW4678; 22°51' S, 167°3' E; 308–303 m; 13 Aug. 2016; KANACONO leg.; MNHN-IK-2015-502.

### Description

The holotype comprises the apical part of a fertile colony; its lightly fascicled stem was obviously branched in open spiral throughout the colony, but only the three distalmost secondary branches subsist, each of which displays a pinnate arrangement of its hydrocladia. The paratype is equally devoid of its very proximal part comprising the hydrorhiza, but possesses a much longer (9 mm) proximal portion of its stem above the origin from stolon; the main tube, accompanied by a couple of accessory counterparts, is repeatedly divided (by transverse nodes) into short segments, each of which bears a hydrotheca and, occasionally, a lateral apophysis immediately below (its associated hydrotheca thus becoming axillar), carrying the stump of a branch. Remainder of stem gives rise to four side branches arranged helicoidally and having pinnately-inserted hydrocladia. Branches, given off in either anti-clockwise (holotype) or clockwise (paratype) manner, composed of a short, quadrangular segment, a succession of 3–4 alternate hydrothecae, and a much longer, regular, hydrocladiate part. The latter, displaying a mostly indistinct



**Fig. 12.** *Hydrallmania clavaformis* Galea, sp. nov. A–G. Portions of branch with insertion of cladia (A–B), cladial internode in lateral (C) and apical (D) aspects, opercular apparatus (E), gonotheca in lateral (F) and frontal (G) aspects, all from sample MNHN-IK-2015-404. Scale bars: A–B = 1 mm; C–D = 500  $\mu$ m; E = 100  $\mu$ m.

**Table 7.** Measurements of *Hydrallmania clavaformis* Galea, sp. nov., in  $\mu\text{m}$ . \* When this comprises only two successive hydrothecae.

<b>Caulus</b>	
- apophysis length	100–125
<b>Cladia</b>	
- length of quadrangular segment	100–120
- internode length*	680–850
- diameter at node	100–125
<b>Cauline hydrothecae</b>	
- free adaxial wall	50–65
- adnate adaxial wall	250–315
- abaxial wall	245–270
- diameter at rim	55–65
<b>Cladial hydrothecae</b>	
- free adaxial wall	330–485
- adnate adaxial wall	315–450
- abaxial wall	680–705
- diameter at rim	150–175
<b>Gonotheca</b>	
- total length	3820–3880
- maximum width	425–445
- diameter at aperture	190–200

division into internodes, is composed of a short, lateral apophysis, an axillar hydrotheca associated to it, two alternate hydrothecae above, and a second lateral cladial apophysis on opposite side, together with its corresponding axillary hydrotheca; cladia alternate along the branch. Apophyses short, each supporting a cladium, from which they are separated through straight nodes; the two rows of apophyses not coplanar, but shifted upwards; cladia divided into thecate internodes through transverse constrictions of the perisarc; there is a short, quadrangular segment proximally; each internode with generally two, occasionally three, hydrothecae, although 1<sup>st</sup> internode bearing usually an increased number of hydrothecae, reaching as many as six. Two types of hydrothecae occur within the colony: cauline and cladial, differing much in their morphology. Cauline hydrothecae relatively distant from each other, small, slender, deeply immersed into internodes, with only a short free adaxial part left; tubular, with thick perisarc, free part curved outwards, rim rounded, slightly everted, occasionally renovated once, with no trace of opercular apparatus. Cauline hydrothecae and cauline apophyses distinctly shifted on to the ‘anterior’ side of the stem. Cladial hydrothecae large, tubular, adnate for less than half their length to their corresponding internodes; successive hydrothecae closely-set, free parts strongly projecting outwards in opposite directions; perisarc thin, finely and densely striated; aperture tricuspidate, with an adaxial and two latero-abaxial cusps; abaxial cusps separated by a shallow embayment, while deep, rounded embayments occur between the adaxial and latero-abaxial cusps; opercular apparatus composed of three triangular valves: two latero-adaxial, and a much wider abaxial one; hydranths with 10–12 filiform tentacles; no caecum. Gonothecae given off from below the hydrothecal bases of cauline axillar hydrothecae; club-shaped, exceedingly long, perisarc finely and densely-striated especially on upper half, becoming smooth basally, apex of gonotheca curved abruptly outwards and there carrying a large, rounded aperture; sex could not be ascertained.

### Remarks

According to Vervoort (1993), four valid nominal species belonging to the genus could be recognized, namely *H. distans* Nutting, 1899, *H. falcata* (Linnaeus, 1758), *H. franciscana* (Trask, 1857), and *H. plumulifera* (Allman, 1877). Should the assumption of Broch (1918: 137) be confirmed, *H. distans* becomes a junior synonym of *H. falcata*. Anyhow, a critical revision of the genus is necessary, as both *H. franciscana* and *H. plumulifera* need modern redescriptions.

None of the nominal species mentioned above displays such strongly bimorphic hydrothecae and forms such exceedingly elongate, club-shaped gonothecae as *H. clavaformis* sp. nov. Indeed, the gonothecae of the poorly-known *H. distans* and *H. plumulifera* were described by Nutting (1904) and Jäderholm (1896), respectively, while those of the well-known *H. falcata* are dealt with, among others, by Cornelius (1995). All are short, broadly ovoid, tapering basally, with a round, distal aperture on top of a short neck region. Only specimens of *H. franciscana* without gonothecae are known to date.

Unlike its congeners, the new species possesses an opercular apparatus composed of three triangular flaps meeting centrally to form a low pyramidal roof. Vervoort (1993: 185) debated on the composition of this structure (presence of either a single adaxial flap, or of a larger adaxial and a smaller abaxial one, according to the statements of different authors), and concluded that two flaps occurred in the Atlantic material at his disposal.

Despite these morphological peculiarities, the present species is provisionally accommodated within the genus *Hydrallmania* Hincks, 1868, on the account of its mode of branching and the unilateral arrangement of the side branches and hydrothecae, pending the availability of additional material suitable for molecular analyses expected to confidently clarify its correct systematic position.

### Distribution

Only known from off New Caledonia (present study).

Genus *Salacia* Lamouroux, 1816

*Salacia sibogae* Billard, 1924

*Salacia sibogae* – Schuchert 2003: 177, fig. 34. — Galea 2016: 23, fig. 7H.

### Material examined

PACIFIC OCEAN • a colony composed of a dozen stems up to 11 cm high, without gonothecae; off New Caledonia, stn DW4746; 22°59' S, 167°43' E; 508–494 m; 23 Aug. 2016; KANACONO leg.; a fragment from one colony was used for DNA extraction, DNA 1374; voucher MHNG-INVE-120835; MNHN-IK-2015-473.

### Distribution

Indonesia, Japan, Philippines (Galea 2016) and New Caledonia (present study).

*Salacia sinuosa* (Bale, 1888)

Fig. 13

*Salacia sinuosa* – Schuchert 2003: 180, fig. 36.



**Material examined**

PACIFIC OCEAN • a 20.5 cm high, sparingly-branched colony, and the upper part of a colony, 14 × 11 cm, both without gonothecae; off New Caledonia, stn DW4741; 22°52' S, 167°41' E; 210 m; 23 Aug. 2016; KANACONO leg.; MNHN-IK-2015-476 • a fertile colony, 25 × 17 cm; same collecting data as for preceding; a fragment was removed for DNA extraction, DNA 1375; voucher MHNG-INVE-120836; MNHN-IK-2015-476 • upper part of a large colony, 25 × 14 cm, without gonothecae; off New Caledonia, stn DW4776; 23°02' S, 168°16' E; 180–311 m; 28 Aug. 2016; KANACONO leg.; MNHN-IK-2015-477.

**Remarks**

Unlike stated by Watson (2000), the gonothecae in the present material are provided with a short, tubular pedicel.

**Distribution**

Australia, Tasmania, Indonesia (Watson 2000), off New Caledonia (present study).

Family Sertularellidae Maronna *et al.*, 2016

Genus *Sertularella* Gray, 1848

*Sertularella acutidentata* Billard, 1919

*Sertularella acutidentata acutidentata* – Vervoort 1993: figs 38C–E, 39B.

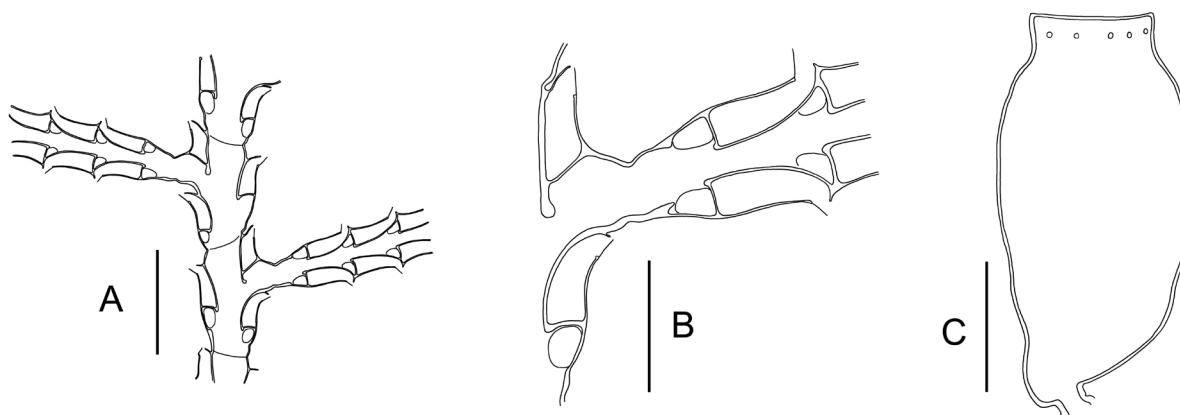
*Sertularella acutidentata* – Galea 2016: 23, fig. 7I.

**Material examined**

PACIFIC OCEAN • a 4.5 cm high colony, without gonothecae; off New Caledonia, stn DW4945; 25°22' S, 159°43' E; 130–108 m; 4 Sep. 2017; KANADEEP leg.; MNHN-IK-2015-462.

**Distribution**

Indonesia, Japan, Philippines, New Caledonia, and north of New Zealand (Vervoort & Watson 2003).



**Fig. 13.** *Salacia sinuosa* (Bale, 1888). A–C. Portion of stem with insertion of two consecutive cladia (A), axillar stem hydrotheca and basal portion of cladium (B), gonotheca (C), all from sample MNHN-IK-2015-476. Scale bars: A = 1 mm; B–C = 500 µm.

*Sertularella areyi* Nutting, 1904

*Sertularella areyi* – Vervoort & Watson 2003: 156, fig. 35F–L. — Galea 2016: 24, fig. 7J.

**Material examined**

PACIFIC OCEAN • a colony composed of two stems, 1 and 1.1 cm high, respectively, each bearing a gonotheca; off New Caledonia, stn DW4768; 23°25' S, 168°01' E; 180–210 m; 27 Aug. 2016; KANACONO leg.; the whole sample was used for DNA extraction, DNA 1376; MHNG-INVE-120837 • a profuse, fertile colony with stems up to 2 cm high; off New Caledonia, stn CP4739; 22°41' S, 167°41' E; 393–358 m; 22 Aug. 2016; KANACONO leg.; MNHN-IK-2015-408.

**Distribution**

Tropical and subtropical parts of the Atlantic and Indo-Pacific (Vervoort & Watson 2003).

*Sertularella helenae* Vervoort, 1993

*Sertularella helenae* Vervoort, 1993: 218, fig. 47B–E.

*Sertularella helenae* – Galea 2016: 27, fig. 8H.

**Material examined**

PACIFIC OCEAN • three colonies, 1.8×2.5 cm, 3.4×2.5 cm, and 2.8×2.4 cm, respectively, all without gonothecae; off New Caledonia, stn DW4764; 23°20' S, 168°15' E; 350–356 m; 27 Aug. 2016; KANACONO leg.; one colony fragment was used for DNA extraction, DNA 1377; voucher MHNG-INVE-120838; MNHN-IK-2015-409 • four colonies, 1.5×0.9 cm, 2.1×1.2 cm, 2.5×2.2 cm, and 3.8×1.7 cm, respectively, without gonothecae; off New Caledonia, stn DW4744; 22°55' S, 167°37' E; 310–290 m; 23 Aug. 2016; KANACONO leg.; MNHN-IK-2015-410 • a colony, 3×4 cm, composed of three stems whose branches anastomose so as to form a single flabellate colony, without gonothecae; off New Caledonia, stn DW4720; 22°50' S, 167°11' E; 374–400 m; 19 Aug. 2016; KANACONO leg.; MNHN-IK-2015-411 • three colonies, 1.3×1.5 cm, 2.1×1.7 cm, and 2.5×2.2 cm, respectively, without gonothecae; off New Caledonia, stn DW4783; 22°56' S, 167°48' E; 385–395 m; 29 Aug. 2016; KANACONO leg.; MNHN-IK-2015-412 • two colonies, 2.5×2 cm and 1.8×1.5 cm, respectively, without gonothecae; off New Caledonia, stn DW4725; 22°41' S, 167°05' E; 240–256 m; 20 Aug. 2016; KANACONO leg.; MNHN-IK-2015-413 • a colony, 3×2.8 cm, without gonothecae; off New Caledonia, stn DW4731; 22°31' S, 167°35' E; 460–457 m; 22 Aug. 2016; KANACONO leg.; MNHN-IK-2015-414 • nine colonies without gonothecae, largest 3×3.2 cm; off New Caledonia, stn CP4658; 22°42' S, 167°13' E; 303–315 m; 10 Aug. 2016; KANACONO leg.; MNHN-IK-2015-415 • three colonies without gonothecae, 1.3×1.5 cm, 1.5×1.6 cm, and 2.5×2.5 cm, respectively; off New Caledonia, stn DW4743; 22°52' S, 167°34' E; 380–340 m; 23 Aug. 2016; KANACONO leg.; MNHN-IK-2015-416 • numerous colonies and fragments, all without gonothecae, largest 3×3 cm; off New Caledonia, stn DW4651; 22°42' S, 167°14' E; 295–300 m; 09 Aug. 2016; KANACONO leg.; one colony was used for DNA extraction, DNA 1378; voucher MHNG-INVE-120839; barcode identification MK073097; MNHN-IK-2015-417 • a 2.5×2.5 cm, colony without gonothecae; off New Caledonia, stn CP4675; 22°50' S, 167°30' E; 350–366 m; 13 Aug. 2016; KANACONO leg.; whole colony used for DNA extraction, DNA1379; barcode identification MK073098; MHNG-INVE-120840 • two colonies without gonothecae, 3.5×4 cm and 4.5×4 cm, respectively; off New Caledonia, stn DW4744; 22°55' S, 167°37' E; 310–290 m; 23 Aug. 2016; KANACONO leg.; MNHN-IK-2015-440 • two colonies without gonothecae, both 2.5×3 cm; off New Caledonia, stn DW4782; 23°00' S, 167°55' E; 856–845 m; 29 Aug. 2016; KANACONO leg.; MNHN-IK-2015-441 • four colonies without gonothecae, 3.2×3 cm, 3.5×3 cm, 3.5×3.5 cm, and 4.2×4.5 cm, respectively; off New Caledonia, stn DW4741; 22°52' S,

167°41' E; 210 m; 23 Aug. 2016; KANACONO leg.; MNHN-IK-2015-442 • a 3.5×3 cm colony without gonothecae; off New Caledonia, stn DW4745; 22°57' S, 167°39' E; 310–403 m; 23 Aug. 2016; KANACONO leg.; MNHN-IK-2015-443 • two colonies without gonothecae, 4×4 cm and 4.5×4.5 cm, respectively; off New Caledonia, stn DW4781; 22°57' S, 167°47' E; 295–255 m; 29 Aug. 2016; KANACONO leg.; MNHN-IK-2015-444 • twenty colonies without gonothecae, largest 6×6 cm; off New Caledonia, stn DW4743; 22°52' S, 167°34' E; 380–340 m; 23 Aug. 2016; KANACONO leg.; MNHN-IK-2015-445.

### Remarks

Colonies of reticulate appearance, formed through anastomoses of terminal tendrils on neighboring branchlets, are met with in material MNHN-IK-2015-440. Tendrils may also settle down on main stems, forming accessory tubes. Abortive branchlets, given off from below the hydrothecal bases, may never develop hydrothecate internodes, transforming directly into tendrils that reach other hydrothecal bases, uniting laterally neighboring side branches, as illustrated by material MNHN-IK-2015-409. Despite the abundance of the material available both earlier (Vervoort 1993) and in the present collections, the gonothecae of this species have yet to be discovered.

### Distribution

New Caledonia, Norfolk Ridge and Solomon Islands (Galea 2016).

### *Sertularella leiocarpoides* Vervoort, 1993

Fig. 10C

*Sertularella leiocarpoides* Vervoort, 1993: 223, fig. 49.

*Sertularella leiocarpoides* – Galea 2016: 33, figs 9D–G, 10A.

### Material examined

PACIFIC OCEAN • a fertile colony, 7.5×8 cm; off New Caledonia, stn DW4718; 22°47' S, 167°09' E; 350 m; 19 Aug. 2016; KANACONO leg.; a fragment was used for DNA extraction, DNA 1380; voucher MHNG-INVE-120841; barcode identification MK073099; MNHN-IK-2015-420 • a colony, 13×10.5 cm, without gonothecae; same collecting data as for preceding; MNHN-IK-2015-420 • a colony, 6×6.5 cm, bearing two gonothecae; off New Caledonia, stn DW4720; 22°50' S, 167°11' E; 374–400 m; 19 Aug. 2016; KANACONO leg.; two fragments, of which one carrying a gonotheca, were used for DNA extraction, DNA 1381; voucher MHNG-INVE-120842; barcode identification MK073100; MNHN-IK-2015-421 • six colonies, 7×3.5 cm (without gonothecae), 8×2.5 cm (without gonothecae), 7.7×4 cm (without gonothecae), 7×4.5 cm (without gonothecae), 7×6.5 cm (fertile), and 11×8 cm (fertile); same collecting data as for preceding; MNHN-IK-2015-421 • a fertile colony 4×6 cm, as well as a 3.1×3.1 cm colony fragment without gonothecae; off New Caledonia, stn DW4764; 23°20' S, 168°15' E; 350–356 m; 27 Aug. 2016; KANACONO leg.; MNHN-IK-2015-422 • a sparingly-branched, 9 cm high colony, as well as the basal part of another colony, 3.5 cm high, both without gonothecae; off New Caledonia, stn DW4784; 22°51' S, 167°44' E; 310–322 m; 29 Aug. 2016; KANACONO leg.; MNHN-IK-2015-423 • two colonies without gonothecae, 6×4.3 cm and 4.6×3 cm, respectively; off New Caledonia, stn CP4675; 22°50' S, 167°30' E; 350–366 m; 13 Aug. 2016; KANACONO leg.; MNHN-IK-2015-425 • two colonies without gonothecae, 3×2.1 cm and 4×2.3 cm, respectively; off New Caledonia, stn DW4711; 22°47' S, 167°24' E; 335–338 m; 18 Aug. 2016; KANACONO leg.; MNHN-IK-2015-427 • a ca 6 cm high, sparingly-branched, fertile colony; off New Caledonia, stn DW4695; 22°47' S, 167°27' E; 200–290 m; 15 Aug. 2016; KANACONO leg.; MNHN-IK-2015-428 • a sparingly-branched, 4.5 cm high colony, with only the perisarc left and no gonothecae; off New Caledonia, stn Stn.

DW4672; 22°47' S, 167°26' E; 310–290 m; 13 Aug. 2016; KANACONO leg.; MNHN-IK-2015-429 • a colony, 4.5 × 3.5 cm, without gonothecae; off New Caledonia, stn DW4758; 23°12' S, 168°04' E; 330 m; 26 Aug. 2016; KANACONO leg.; MNHN-IK-2015-430 • numerous colonies, largest 8 × 9.5 cm, some bearing rare gonothecae; off New Caledonia, stn DW4741; 22°52' S, 167°41' E; 210 m; 23 Aug. 2016; KANACONO leg.; MNHN-IK-2015-431 • a fertile colony, 5 × 5.5 cm; off New Caledonia, stn DW4759; 23°12' S, 168°03' E; 317–343 m; 26 Aug. 2016; KANACONO leg.; MNHN-IK-2015-433 • several colonies and fragments, some bearing rare gonothecae, largest 5 × 5.5 cm; off New Caledonia, stn DW4714; 22°49' S, 167°25' E; 394–443 m; 18 Aug. 2016; KANACONO leg.; MNHN-IK-2015-435 • numerous well-developed colonies, highest 7.5 cm high, widest 8 cm wide, some bearing gonothecae; off New Caledonia, stn DW4745; 22°57' S, 167°39' E; 310–403 m; 23 Aug. 2016; KANACONO leg.; a fragment from a fertile colony was used for DNA extraction, DNA 1382; voucher MHNG-INVE-120843; barcode identification MK073101; MNHN-IK-2015-436 • four colonies, 4.3 × 3 cm (without gonothecae), 7 × 1.5 cm (without gonothecae), 4 × 3 cm (with two gonothecae), and 2.8 × 2.5 cm (with one gonotheca); off New Caledonia, stn DW4711; 22°47' S, 167°24' E; 335–338 m; 18 Aug. 2016; KANACONO leg.; MNHN-IK-2015-437 • several sparingly-branched colonies and fragments, highest 8 cm, two of them bearing one gonotheca each; off New Caledonia, stn CP4674; 22°48' S, 167°29' E; 13 Aug. 2016; KANACONO leg.; MNHN-IK-2015-438 • a fertile colony, 5 × 4.5 cm; off New Caledonia, stn CP4676; 22°51' S, 167°30' E; 383 m; 13 Aug. 2016; KANACONO leg.; MNHN-IK-2015-439 • two colonies highly overgrown by other organisms, 7.3 × 9 cm and 7 × 10 cm, respectively, without gonothecae; off New Caledonia, stn CP4786; 22°46' S, 167°42' E; 350–469 m; 29 Aug. 2016; KANACONO leg.; MNHN-IK-2015-447 • a colony without gonothecae, 4 × 2.5 cm; off New Caledonia, stn DW4760; 23°15' S, 168°03' E; 319–304 m; 26 Aug. 2016; KANACONO leg.; MNHN-IK-2015-448 • two colonies, 4.4 × 5.5 cm (with one gonotheca) and 4.5 × 5 cm (without gonothecae), respectively; off New Caledonia, stn DW4755; 23°12' S, 168°02' E; 360–340 m; 26 Aug. 2016; KANACONO leg.; MNHN-IK-2015-449 • two fertile colonies, 5.2 × 6 cm and 5.5 × 7.5 cm, respectively; off New Caledonia, stn DW4746; 22°59' S, 167°43' E; 508–494 m; 23 Aug. 2016; KANACONO leg.; MNHN-IK-2015-450 • a colony without gonothecae, 7.5 × 5.5 cm; off New Caledonia, stn DW4742; 22°53' S, 167°37' E; 290–345 m; 23 Aug. 2016; KANACONO leg.; MNHN-IK-2015-451 • four colony fragments, largest 6.5 × 3.5 cm, two of which bear gonothecae; off New Caledonia, stn DW4651; 22°42' S, 167°14' E; 295–300 m; 9 Aug. 2016; KANACONO leg.; MNHN-IK-2015-452 • a colony without gonothecae, 3.3 × 4.5 cm; off New Caledonia, stn DW4717; 22°44' S, 167°11' E; 336–361 m; 19 Aug. 2016; KANACONO leg.; MNHN-IK-2015-453 • five colonies, 3.2 × 4.5 cm (without gonothecae), 4 × 3.5 cm (without gonothecae), 4 × 5.5 cm (without gonothecae), 4.5 × 3 cm (without gonothecae) and 6 × 6.5 cm (fertile); off New Caledonia, stn DW4677; 22°53' S, 167°35' E; 390–376 m; 13 Aug. 2016; KANACONO leg.; MNHN-IK-2015-454 • two colonies, 3.3 × 3 cm and 3.5 × 5 cm, respectively, each bearing one gonotheca; off New Caledonia, stn DW4713; 22°47' S, 167°24' E; 356–380 m; 18 Aug. 2016; KANACONO leg.; MNHN-IK-2015-458.

### Distribution

New Caledonia, Solomon Islands (Galea 2016).

*Sertularella novaecaledoniae* Vervoort, 1993

Fig. 10D

*Sertularella novaecaledoniae* Vervoort, 1993: 225, figs 50, 51A, 52A.

*Sertularella novaecaledoniae* – Galea 2016: 25, fig. 7N–Q.

**Material examined**

PACIFIC OCEAN • a fertile colony 4.8 × 6.4 cm; off New Caledonia, stn DW4748; 23°05' S, 167°44' E; 700–740 m; 23 Aug. 2016; KANACONO leg.; a small fragment bearing a gonotheca was used for DNA extraction, DNA 1383; voucher MHNG-INVE-12084; MNHN-IK-2015-424 • a fertile colony, 5 × 4 cm; off New Caledonia, stn DW4747; 23°02' S, 167°44' E; 550–590 m; 23 Aug. 2016; KANACONO leg.; a small fragment was used for DNA extraction, DNA 1384; voucher MHNG-INVE-120845; MNHN-IK-2015-432 • two fertile colonies, 5 × 5 cm and 7 × 3.3 cm, respectively; same collecting data as for preceding; MNHN-IK-2015-432 • two colonies without gonothecae, 8.5 × 8.5 cm and 8 × 7.5 cm, respectively; off New Caledonia, stn DW4670; 22°58' S, 167°24' E; 680–612 m; 12 Aug. 2016; KANACONO leg.; a fragment from one colony was used for DNA extraction, DNA 1385; voucher MHNG-INVE-120846; MNHN-IK-2015-455 • two colony fragments without gonothecae, 4.5 × 3.5 cm and 5 × 3.5 cm, respectively; off New Caledonia, stn DW4686; 22°29' S, 167°31' E; 249–255 m; 14 Aug. 2016; KANACONO leg.; MNHN-IK-2015-456 • a colony without gonothecae, 8.5 × 9 cm; off New Caledonia, stn DW4677; 22°53' S, 167°35' E; 390–376 m; 13 Aug. 2016; KANACONO leg.; MNHN-IK-2015-457 • three colonies without gonothecae, 10.7 × 7.2 cm, 6.5 × 6.5 cm, and 5.8 × 4.2 cm, respectively; off New Caledonia, stn DW4672; 22°47' S, 167°26' E; 310–290 m; 13 Aug. 2016; KANACONO leg.; MNHN-IK-2015-467.

**Distribution**

New Caledonia, Norfolk Ridge (Galea 2016).

*Sertularella* aff. *sinensis* Jäderholm, 1896

Figs 10E, 14A–B

*Sertularella sinensis* – Vervoort & Watson, 2003: 177, fig. 41D–H.

*Sertularella* aff. *sinensis* – Galea 2016: 30, fig. 8P–S.

**Material examined**

PACIFIC OCEAN • a 4.7 × 3.8 cm colony, now broken into two pieces, bearing one gonotheca; off New Caledonia, stn DW4741; 22°52' S, 167°41' E; 210 m; 23 Aug. 2016; KANACONO leg.; MNHN-IK-2015-418 • a colony without gonothecae, 3.5 × 3.3 cm; same collecting data as for preceding; a small fragment was used for DNA extraction, DNA 1386; voucher MHNG-INVE-120847; MNHN-IK-2015-418 • a 2.2 × 1.7 cm colony fragment bearing three gonothecae; same collecting data as for preceding; MNHN-IK-2015-418 • a 4 × 1.6 cm colony with one gonotheca; same collecting data as for preceding; MNHN-IK-2015-418 • a fertile colony, with stems up to 4 cm high; off New Caledonia, stn DW4720; 22°50' S, 167°11' E; 374–400 m; 19 Aug. 2016; KANACONO leg.; MNHN-IK-2015-466.

**Remarks**

The colonies are flabellate, with no definite main stem, as this branches many times, first branching occurring a short distance after its origin from stolon. The stem and side branches are strongly fascicled, tending gradually to monosiphonic distally. The hydrothecae are provided with 14–16 transverse ridges, while Galea (2016) reported hydrothecae with 19–21 ridges in material from New Caledonia examined so far. The gonothecae, ca 2790 µm long and 1570 µm wide (only one measured), display 6–8 broad transverse ridges; in one colony with three gonothecae, there are 4–6 apical spines surrounding the aperture; in two other colonies, each with but one gonotheca, seven and eight spines could be found, respectively, demonstrating that in the New Caledonian population, at least, their number is inconstant, and ranges from four to eight.

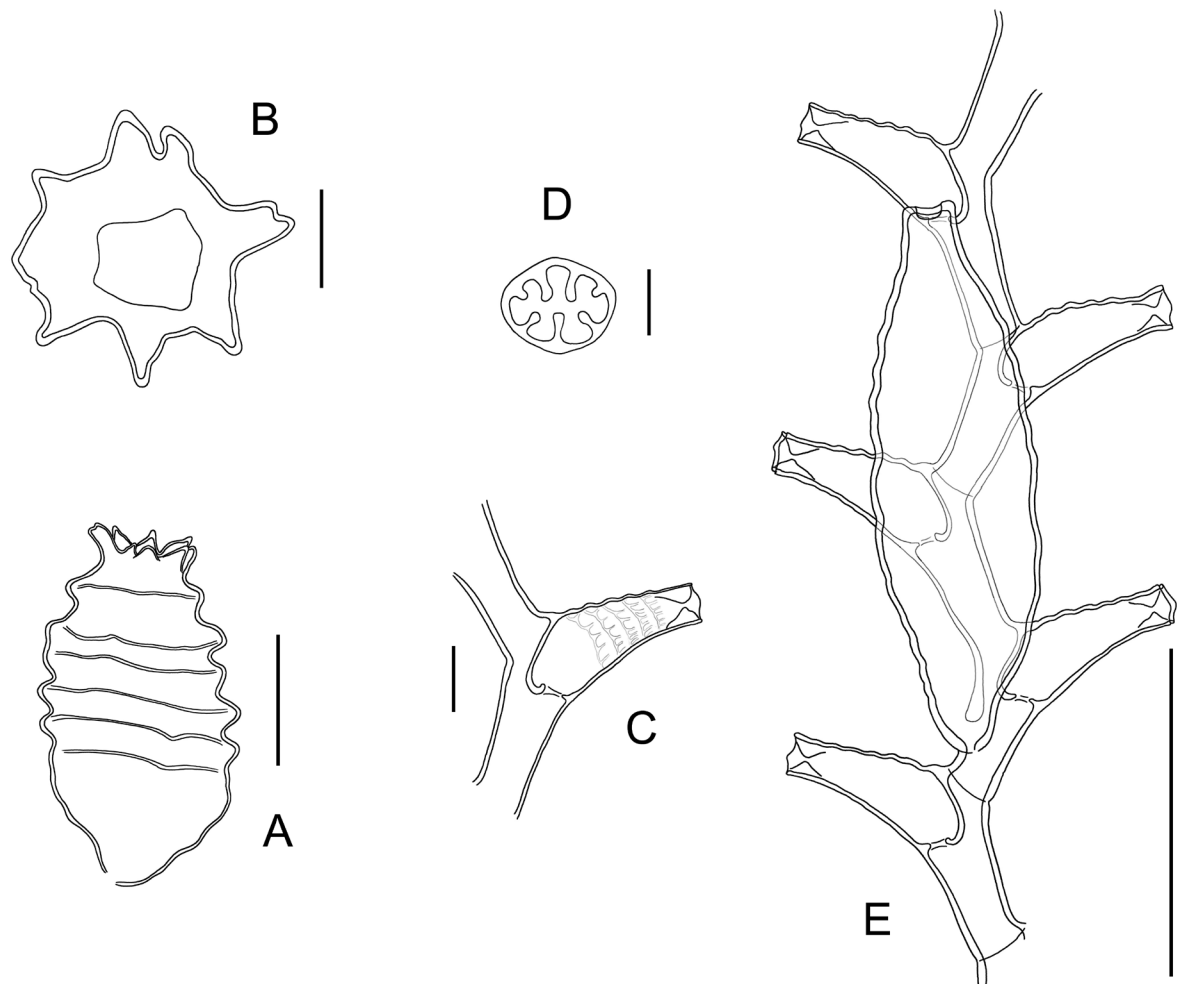


Galea (2016) pointed out morphological and morphometrical differences in materials studied by various authors, notably the condition of the stem, the number of hydrothecal ridges, and the size of gonothecae. The latter, in the present material, are the largest ever reported in this species, while Vervoort & Watson (2003) found 1720–1935  $\mu\text{m}$  long and 1230–1280  $\mu\text{m}$  wide gonothecae, although even smaller ones occurred in material studied by Hirohito (1995) (750–800  $\times$  550–700  $\mu\text{m}$ ).

A more comprehensive study, based on materials of different origins, is needed to understand the variations reported so far in the literature.

### Distribution

*Sertularella sinensis*, sensu stricto, occurs from China (Jäderholm 1896) and Korea (Park 2010) to the Sea of Okhotsk (Naumov 1969). Additional material, possibly not conspecific, was recorded from New Caledonia (Vervoort 1993; Galea 2016; present study), Tonga (Galea 2016) and New Zealand (Vervoort & Watson 2003).



**Fig. 14.** A–B. *Sertularella* aff. *sinensis* Jäderholm, 1896, gonotheca in lateral view (A), apical view of gonotheca showing spines and central aperture (B), both from sample MNHN-IK-2015-418. — C–E. *Sertularella tronconica* Galea, 2015, hydrotheca (C), apical view of aperture showing internal, submarginal cusps (D), portion of colony with male gonotheca (E). Scale bars: A, E = 1 mm; B = 300  $\mu\text{m}$ ; C = 200  $\mu\text{m}$ ; D = 100  $\mu\text{m}$ .

*Sertularella tronconica* Galea, 2016

Figs 10F, 14C–E

*Sertularella tronconica* Galea, 2016: 38, figs 9Q–T, 10D.

**Material examined**

PACIFIC OCEAN • a 1.8 cm high colony with two (likely male) gonothecae, with almost only the perisarc left; off New Caledonia, stn CP4687; 22°29' S, 167°30' E; 256–268 m; 14 Aug. 2016; KANACONO leg.; MNHN-IK-2015-419 • a 1.7 cm high colony bearing an immature female gonotheca; off New Caledonia, stn DW4743; 22°52' S, 167°34' E; 380–340 m; 23 Aug. 2016; KANACONO leg.; MNHN-IK-2015-426 • a 1.5 cm high colony with two female gonothecae; off New Caledonia, stn DW4744; 22°55' S, 167°37' E; 310–290 m; 23 Aug. 2016; KANACONO leg., MHNG-INVE-120848 • a 1.5 cm high colony bearing one male gonotheca; off New Caledonia, stn DW4678; 22°51' S, 167°34' E; 308–303 m; 13 Aug. 2016; KANACONO leg.; MNHN-IK-2015-464.

**Remarks**

In material MNHN-IK-2015-426, the perisarc of the colony may be wavy to wrinkled in places, and the corrugations of the hydrothecae are more conspicuous, encompassing also their abaxial wall.

The hydrothecae in sample MNHN-IK-2015-419 display seven internal projections of the perisarc: four latero-adaxial, of which the two adaxial-most are the most prominent, one large abaxial, and two smaller latero-abaxial (Fig. 14D). Its gonothecae are believed to be male, owing their shape and size (ca 1680 µm long and 505 µm wide, only one measured), compared to those from the holotype (see Galea 2016); they are given off laterally from the middle of the internode on side opposite to hydrotheca but, soon after, they are shifted on to the anterior/posterior side of the colony; club-shaped, with slightly undulated walls, aperture distal, rounded, small (ca 100 µm wide), borne on rather short and narrow neck region.

**Distribution**

New Caledonia, Norfolk Ridge (Galea 2016).

*Sertularella tubulosa* Galea, 2016

*Sertularella tubulosa* Galea, 2016: 40, fig. 9U–X.

**Material examined**

PACIFIC OCEAN • a 3.5×2.7 cm colony without gonothecae; off New Caledonia, stn DW4747; 23°02' S, 167°44' E; 550–590 m; 23 Aug. 2016; KANACONO leg.; MNHN-IK-2015-434 • two colonies without gonothecae, 4×3.8 cm and 4×3.3 cm, respectively; off New Caledonia, stn DW4782; 23°00' S, 167°55' E; 856–845 m; 29 Aug. 2016; KANACONO leg.; MNHN-IK-2015-459.

**Remarks**

The gonothecae of this distinctive species are still to be discovered.

**Distribution**

New Caledonia (Galea 2016).

Family Symplectoscyphidae Maronna *et al.*, 2016  
Genus *Dictyocladium* Allman, 1888

*Dictyocladium reticulatum* (Kirchenpauer, 1884)

Fig. 15

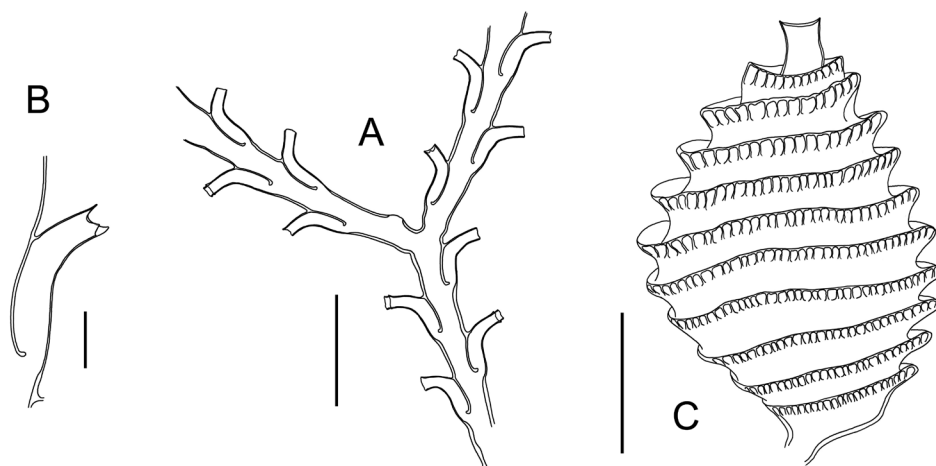
*Dictyocladium reticulatum* – Vervoort & Watson 2003: 124, figs 24E–G, 25A–C.

#### Material examined

PACIFIC OCEAN • a colony, 3.5 × 3.5 cm, with female gonothecae; off New Caledonia, stn DW4725; 22°41' S, 167°05' E; 240–256 m; 20 Aug. 2016; KANA CONO leg.; a fragment was used for DNA extraction, DNA 1402; voucher MHNG-INVE-120831; MNHN-IK-2015-405 • four colonies, 2.7 × 1.6 cm (without gonothecae), 2.7 × 3.8 cm (with female gonothecae), 3 × 2.9 cm (with female gonothecae) and 4 × 2.6 cm (with female gonothecae); same collecting data as for preceding; MNHN-IK-2015-405 • a colony, 2.5 × 1.7 cm, without gonothecae; off New Caledonia, stn DW4741; 22°52' S, 167°41' E; 210 m; 23 Aug. 2016; KANA CONO leg.; used as a whole for DNA extraction, DNA 1371; voucher MHNG-INVE-120832; barcode identifier MK073094; MNHN-IK-2015-406 • three colonies, 4.3 × 1.7 cm (without gonothecae), 4 × 3.5 cm (with female gonothecae), and 3 × 3.3 cm (with female gonothecae, and carrying epizoic *Synthecium* colony); same collecting data as for preceding; MNHN-IK-2015-406 • four colonies without gonothecae, 4.5 × 4 cm, 1.5 × 1 cm, 1.5 × 2 cm, and 2.5 × 1 cm, respectively; off New Caledonia, stn CP4674; 22°48' S, 167°29' E; 311–302 m; 13 Aug. 2016; KANA CONO leg.; MNHN-IK-2015-407 • a fertile colony, 5.2 × 5.5 cm; off New Caledonia, stn DW4743; 22°52' S, 167°34' E; 380–340 m; 23 Aug. 2016; KANA CONO leg.; MNHN-IK-2015-468.

#### Remarks

The present material agrees in nearly all details with the description given by Vervoort & Watson (2003) of this species. However, some colonies have their stems and the basal part of their lower branches lightly but distinctly fascicled. In addition, examination of many gonothecae (from different colonies) seen in apical view showed that the external ridges are not always spirally arranged, as stated by Vervoort & Watson (2003), but they also form concentric ridges that are perfectly transverse in lateral view. All gonothecae agreed with the supposedly female ones described by these authors, but had up to 14 ridges in material MNHN-IK-2015-405 and up to 20 in material MNHN-IK-2015-406, although any



**Fig. 15.** *Dictyocladium reticulatum* (Kirchenpauer, 1884). A–C. Colony fragment (A), hydrotheca (B), gonotheca (C), all from sample MNHN-IK-2015-405. Scale bars: A = 1 mm; B = 200  $\mu$ m; C = 500  $\mu$ m.

other morphological difference could be noted (e.g., a slenderer appearance, as in the supposedly males described by these authors).

The 16S data (see Fig 20 and the ‘Molecular study’ section) strongly suggest that this species belongs to the Symplectoscyphidae, and not the Sertularidae in the sense of Maronna *et al.* (2016).

### Distribution

Bass Strait, Tasmania (Vervoort & Watson 2003), New Caledonia (present study).

Genus *Symplectoscyphus* Marktanner-Turneretscher, 1890

? *Symplectoscyphus acutustriatus* Galea, sp. nov.

[urn:lsid:zoobank.org:act:DDBE1A82-BE69-405E-A1AD-E5093423E389](https://zoobank.org/act:DDBE1A82-BE69-405E-A1AD-E5093423E389)

Figs 16A, 17A–E; Tables 8–10

### Diagnosis

Colonies erect, with up to 2.5 cm high, monosiphonic, sparingly-branched stems, divided into moderately-long, geniculate, regular internodes by oblique nodes slanting in alternate directions. Branches with similar structure to that of the stems. Hydrothecae biseriate, alternate, coplanar, conical, adnate for  $\frac{1}{3}$  or less to the internode, surface distinctly ridged; ridges projecting apically as almost free frills; 7–8 ridges on free axial wall, 8–10 on abaxial wall; up to seven submarginal, internal projections of the perisarc, present in basalmost hydrothecae, but missing elsewhere and, sometimes, in a whole colony. Gonothecae borne laterally on the stem internodes; elongated-ovoid, transversely ringed, aperture on top of short neck region.

### Etymology

The specific name combines two Latin words ‘*ācūtus*, -a, -um’, meaning ‘sharp’, and ‘*striātus*, -a, -um’, meaning ‘provided with striae’, to describe the particulars of the transverse ridges of the outer hydrothecal wall.

### Material examined

#### Holotype

PACIFIC OCEAN • a small, fertile colony on limestone, composed of five stems up to 2 cm high, four of which bear one gonotheca each; off New Caledonia, stn DW4977; 19°46' S, 158°30' E; 280–304 m; 9 Sep. 2017; KANADEEP leg.; MNHN-IK-2015-460.

#### Paratype

PACIFIC OCEAN • a rather profuse, colony on dead gorgonian with stems up to 2.5 cm high, without gonothecae; off New Caledonia, stn DW4945; 25°22' S, 159°43' E; 130–108 m; 4 Sep. 2017; KANADEEP leg.; two small stems were used for DNA extraction, DNA1388; voucher MHNG-INVE-120849; barcode identifier MK073102; MNHN-IK-2015-461.

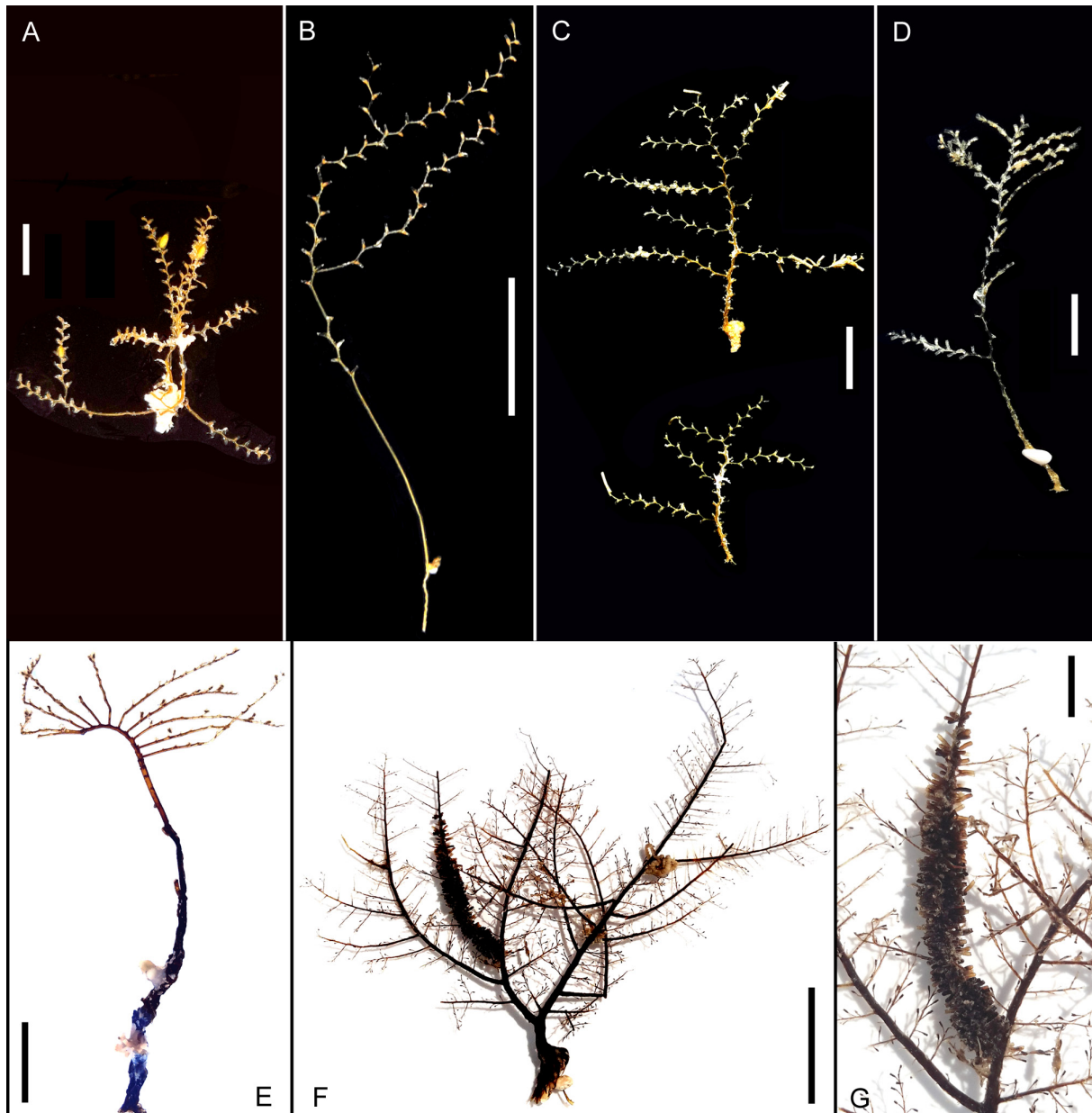
#### Additional material

PACIFIC OCEAN • a colony composed of several stems, up to 2 cm high, without gonothecae; off New Caledonia, stn DW5026; 20°22' S, 158°40' E; 360–410 m; 21 Sep. 2016; KANADEEP leg.; MNHN-IK-2015-446.

### Description

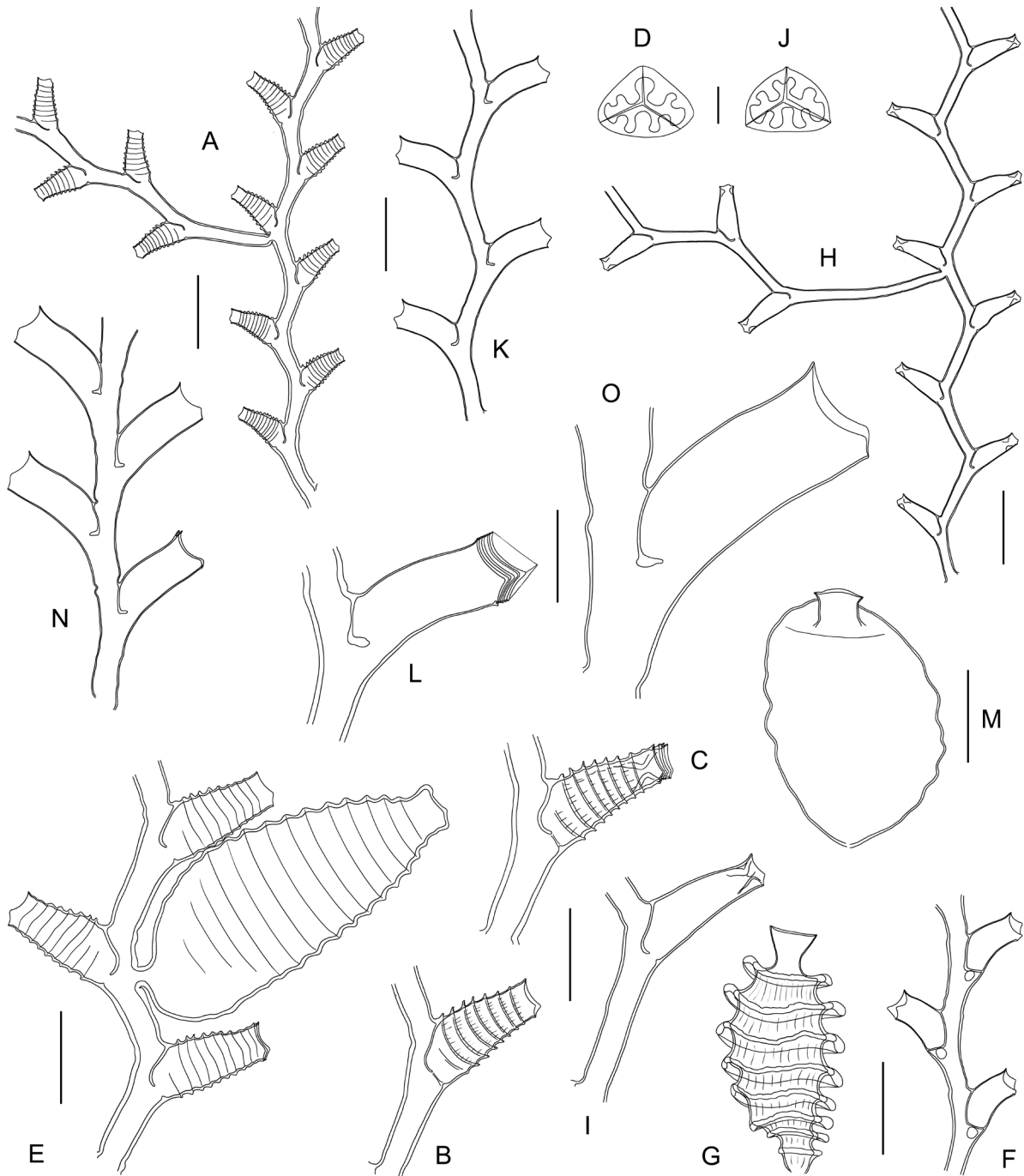
Colonies arising from creeping, branching, anastomosing hydrorhiza. Stems erect, monosiphonic, up to 2.5 cm high, composed of a basal, smooth, ahydrothecate part, 3–7 mm long above origin from

stolon, and a much longer, distal, hydrothecate part above; the latter divided into regular internodes by means of almost indistinct oblique nodes slanting in alternate directions; branching sparse, with up to three coplanar side branches given off laterally and irregularly from below the bases of some stem hydrothecae, on one or both sides of the stem; branches with similar structure to that of the stem. Internodes relatively short, distinctly geniculate, each bearing distally a hydrotheca; the latter alternate



**Fig. 16.** A. ? *Symplectoscyphus acutustriatus* Galea, sp. nov., holotype colony, MNHN-IK-2015-460. — B. ? *Symplectoscyphus elongatulus* Galea, sp. nov., holotype colony, MNHN-IK-2015-463. — C. *Symplectoscyphus paulensis* Stechow, 1923, colonies from sample MNHN-IK-2015-393. — D. *Symplectoscyphus* cf. *tropicus* (Hartlaub, 1901), colony from sample MNHN-IK-2015-394. — E. *Tuberocaulus scorpioides* (Vervoort, 1993) gen. et comb. nov., colony from sample MNHN-IK-2015-400. — F–G. *Zygophylax niger* Galea, sp. nov., holotype colony (F) and detail of its coppinia (G) from sample MNHN-IK-2015-478. Scale bars: A, G = 5 mm; B–E = 1 cm; F = 2 cm.





**Fig. 17.** A–E. ? *Symplectoscyphus acutistriatus* Galea, sp. nov., portion of stem with side branch (A, from sample MNHN-IK-2015-460); hydrothecae without (B) and with (C) internal, submarginal cusps, aperture in apical view (D), portion of colony with gonotheca (E), all from sample MNHN-IK-2015-461. — F–G. *Symplectoscyphus commensalis* Vervoort, 1993, portion of colony with internodes and hydrothecae (F), gonotheca (G), both from sample MNHN-IK-2015-399. — H–J. ? *Symplectoscyphus elongatulus* Galea, sp. nov., portion of stem with proximal part of cladium (H), hydrotheca (I), apical view of aperture showing submarginal, intrathecal cusps (J), all from sample MNHN-IK-2015-463. — K–M. *Symplectoscyphus paulensis* Stechow, 1923, colony fragment (K), hydrotheca (L), gonotheca (M), all from sample MNHN-IK-2015-393. — N–O. *Symplectoscyphus* cf. *tropicus* (Hartlaub, 1901), portion of colony (N), hydrotheca (O), both from sample MNHN-IK-2015-394. Scale bars: A, H, K, N = 1 mm; B–C, E–G, I, L–M, O = 500  $\mu$ m; D, J = 100  $\mu$ m.

**Table 8.** Measurements of *Symplectoscyphus* spp., in  $\mu\text{m}$ .

	<i>S. acutistriatus</i> Galea, sp. nov. MNHN-IK-2015-460	<i>S. elongatulus</i> Galea, sp. nov. MNHN-IK-2015-463
<b>Internodes</b>		
- ordinary internodes	600–775	955–1140
- 1 <sup>st</sup> internode of a side branch	1165–1470	2370–3310
- diameter at node	145–210	145–245
<b>Hydrotheca</b>		
- free adaxial wall	465–560	525–600
- adnate adaxial wall	220–245	280–300
- abaxial wall	585–680	690–700
- maximum width	310–330	280–300
- diameter at aperture	190–210	190–215
<b>Gonotheca</b>		
- total length	1705–1900	–
- maximum width	825–895	–
- diameter at aperture	ca 35	–

in position, the two rows being coplanar. Hydrothecae moderately-long, conical, adnate for  $\frac{1}{3}$  or less to the corresponding internodes; surface conspicuously ridged; ridges well-developed, projecting apically almost as free frills; there are 7–8 complete ridges encircling the hydrotheca distally, and up to 8–10 on the abaxial wall, the basalmost ones incomplete; there are seven intrathecal, submarginal projections of the perisarc, visible in the lower stem hydrothecae, but disappearing towards distal parts of the colony: two latero-adaxial, one abaxial, and two latero-abaxial. Gonotheca borne on stems and/or branches, given off laterally in middle of internode on side opposite to hydrotheca; large, piriform, transversely-ridged (12–14 ridges), tapering abruptly basally into indistinct pedicel, distally walls merging progressively; aperture apical, small, rounded, on short neck region with broadly polygonal perimeter, occasionally forming 3 indistinct projections of perisarc.

### Remarks

The prominent ridges on the outer walls of the hydrothecae are distinctive. Only a few congeners are provided with transverse undulations or ridges (see Table 9 for comparison), but in none their development reaches the extent met with in *S. acutistriatus* sp. nov.

The internal, submarginal cusps are variably present among the hydrothecae belonging to the same stem (e.g., MNHN-IK-2015-460), and are even absent in stems of some colonies (e.g., MNHN-IK-2015-446). Only a few congeners have been shown to possess such structures, and their main distinguishing features are summarized in Table 10.

The systematic position of this species is discussed in the ‘Molecular study’ section.

### Distribution

Only known from off New Caledonia (present study).

**Table 9.** Species of *Symplectoscyphus* with transversely-ridged hydrothecae and their differences to *S. acutistriatus* Galea, sp. nov.

Species name	Specific differences
<i>S. howensis</i> Vervoort & Watson, 2003	Colonies with unbranched or irregularly-branched stems; internodes weakly geniculate towards tips of stems and branches; hydrothecae “basally fairly wide, narrowing gradually apically, slightly tumid. <b>Free adcauline wall about 1.5 times as long as adnate part</b> [...] with <b>5 or 6 transverse undulations fading distally towards abcauline hydrothecal wall</b> ”; no submarginal intrathecal cusps; gonothecae with an apical “circular platform with rounded depression”. Tasman Sea, near Lord Howe Island (Vervoort & Watson 2003)
<i>S. indivisus</i> (Bale, 1882)	Stems unbranched, internodes relatively short, geniculate; <b>hydrothecae adnate for about half their length</b> , “ <b>walls with 3 or 4 annulations</b> starting at adcauline side and running downwards, gradually fading out, in many hydrothecae <b>annulations mere undulations of hydrothecal wall</b> ”; “3 small submarginal intrathecal cusps in embayments between marginal cusps”; gonothecae broadly ovoid, walls with “5-7 indistinct, low ribs [...]. Apex [...] narrowing rather sharply, provided with 3 thick, rounded prominences”. Southeast Australia, Tasmania, Kermadec Islands (Vervoort & Watson 2003)
<i>S. macrothecus</i> (Bale, 1882)	Stems short, unbranched, <b>internodes very short, twisted, inflated behind hydrotheca</b> ; hydrothecae “ <b>directed towards front of stem</b> [...] <b>barrel-shaped</b> , narrowing to margin, with 2-3 shallow annular ridges passing completely around mid-region of thecal wall [...]. Margin contracted, small, <b>rim heavily thickened</b> ”, adaxial cusp “forming a raised beak-shaped crest”; 4 internal, submarginal cusps (1 adaxial, 2 latero-adaxial, 1 abaxial); gonothecae ovoid, with “5 strong, crumpled annular ridges, and 3 low, fairly sharp apertural teeth”. Australia [Watson 1973, as <i>S. rostratus</i> sp. nov. N.B.: There are no reliable arguments supporting the separation between <i>S. macrothecus</i> and <i>S. rostratus</i> , according to the accounts of on the one hand Bale (1882) and Bartlett (1907) and on the other hand Watson (1973), respectively]
<i>S. multinodus</i> (Fraser, 1948)	<b>Colonies rigid</b> , stems sparingly-branched, branches irregularly alternate; <b>internodes very short; hydrothecae nearly cylindrical</b> though slightly swollen basally and tapered distally, <b>surface with 3–5 broad, rounded, transverse corrugations</b> ; gonothecae elongated-ovoid, tapering at both ends, surface with <b>10–11 rounded, transverse corrugations</b> , aperture distal, on short, slender neck region. Cedros Island, Baja California, Mexico (Fraser 1948; Calder <i>et al.</i> 2009)
<i>S. neglectus</i> (Thompson, 1879)	<b>Stems pinnately-branched</b> , hydrocladia alternate; hydrothecae adnate for $\frac{2}{3}$ their adaxial length, “ <b>facing frontally</b> and obliquely upwards [...] <b>walls moderately to distinctly rugose</b> , typically with <b>five more or less transverse ridges</b> meeting at an obtuse angle on abcauline sector of wall”; margin with “ <b>three equidistant tall cusps with thickened perisarc</b> , embayments between deep”, 3 internal submarginal cusps; gonothecae sexually dimorphic, elongate, transversely corrugated. Southern and western Australia (Watson 2005)
<i>S. similis</i> (Fraser, 1948)	<b>Colonies rigid</b> , stems unbranched or with, at most, two side branches. Photographs of the lectotype show that this species has <b>very short and nearly collinear internodes</b> [exactly as illustrated by Fraser (1948: pl. 28, fig. 19B–C)], <b>large hydrothecae</b> (“nearly 1.0 mm in length”), <b>surface with 7–8 rounded, transverse ridges</b> . Partida Island, Baja California, Mexico (Fraser 1948; Calder <i>et al.</i> 2009)

**Table 10.** Species of *Symplectoscyphus* with submarginal, intra-hydrothecal cusps, and their differences to *S. acutistriatus* Galea, sp. nov. and *S. elongatulus* Galea, sp. nov. N.B.: To these should be added *S. indivisus* (Bale, 1882), *S. macrothecus* (Bale, 1882) and *S. neglectus* (Thompson, 1879) dealt with in Table 9.

Species name	Specific differences
<i>S. fuscus</i> (Trebilcock, 1928)	<b>Colonies pinnate</b> , branches alternate, each <i>given off from below every stem hydrotheca</i> ; <b>branches shifted on to the “anterior” side of the colony</b> , forming an angle of 45° or less; <b>hydrothecae unilaterally arranged</b> , forming an angle of 90° or less, adnate for ca 1/3, surface smooth, free adaxial wall swollen proximally, abaxial wall nearly straight; margin thickened and everted, especially on adaxial side; “three small and often inconspicuous submarginal” cusps (Trebilcock 1928). Gonothecae possibly sexually dimorphic; broadly ovoid, ringed throughout, distally with 3 obtuse cusps. Eastern coasts of New Zealand (Vervoort & Watson 2003)
<i>S. johnstoni</i> (Gray, 1843)	<b>Stems pinnately-branched</b> , cladia alternate; hydrothecae smooth-walled, “ <b>approximately half the adcauline side free of the stem and branch</b> [...]”, conical, considerably narrower at the aperture than in the middle which is generally the region of maximum diameter; free dcauline side a low convex curve, abcauline side, slightly bulged at base, narrowing towards the margin or frequently with a submarginal convexity; margin with three well developed pointed teeth [...] the median adcauline tooth may be slightly recurved” (Ralph 1961); 3 internal, submarginal cusps (2 latero-adaxial, 1 abaxial) in hydrothecae of the syntype (Totton 1930); gonothecae elongated-ovoid, proximal adaxial side flattened, walls with 8–14 evenly spaced transverse ridges, aperture on top of a short apical neck region. New Zealand (Vervoort & Watson 2003)
<i>S. odontiferus</i> Vervoort & Watson, 2003	Stems mono- or <b>basally weakly fascicled</b> ; <b>side branches pinnately-arranged, alternate</b> , coplanar; <b>internodes almost collinear</b> , rather short, nodes indistinct; “ <b>two-thirds or slightly less of adcauline [hydrothecal] wall adnate</b> ”; “3 big, rounded submarginal intrathecal cusps present below deepest point of embayments [= 2 latero-adaxial, 1 abaxial]”. Off Norfolk Island, SW Pacific (Vervoort & Watson 2003).
<i>S. sibogae</i> (Billard, 1924)	Stem unbranched, nodes indistinct, <b>internodes collinear</b> , rather short; hydrothecate smooth-walled, saccate, swollen basally, narrowing basally below mouth, <b>adnate for more than half their length</b> , margin everted; 3 internal cusps (2 latero-adaxial, 1 abaxial). Indonesia, southern Queensland (Billard 1925; Watson 2002)

*Symplectoscyphus commensalis* Vervoort, 1993

Fig. 17F–G

*Symplectoscyphus commensalis* Vervoort, 1993: 247, figs 56C–F, 57, 58A–E.

**Material examined**

PACIFIC OCEAN • female colony with stems up to 1 cm high on stem of sertulariid hydroid; off New Caledonia, stn DW4670; 22°58' S, 167°24' E; 680–612 m; 12 Aug. 2016; KANACONO leg.; one stem was used for DNA extraction, DNA 1389; voucher MHNG-INVE-120850; barcode identifier MK073103; MNHN-IK-2015-399.

**Remarks**

A small species, with minute hydrothecae resembling those of *S. ralphae* Vervoort, 1993 through their shape and size (compare Fig. 17F with Galea 2016: fig 10Q–T). Unlike *S. commensalis* that forms irregularly-branched colonies (up to 2<sup>nd</sup> order branches observed), the latter builds regularly-pinnate colonies. In addition, their respective gonothecae are different [compare Fig. 17G with Galea 2016: fig. 10U–V).

**Distribution**

Only known from off New Caledonia (Vervoort 1993; present study).

? *Symplectoscyphus elongatulus* Galea, sp. nov.

[urn:lsid:zoobank.org:act:E30569B6-8BC4-4B3C-8E84-8EC1A2300839](https://doi.org/10.21203/rs.3.rs-1234567/v1)

Figs 16B, 17H–J; Tables 8, 10

### Diagnosis

Sparingly-branched symplectoscyphid forming delicate, coplanar colonies, with erect, monosiphonic stems. Internodes long, slender, distinctly geniculate, each carrying distally a hydrotheca; the latter long, slightly conical, smooth-walled, adnate for  $\frac{1}{3}$ , abaxial wall straight or nearly so, free adaxial wall imperceptibly convex proximally, and distinctly concave below aperture; adaxial cusp produced, slightly everted; eight internal, submarginal projections of perisarc. Gonothecae unknown.

### Etymology

From the Latin ‘*ēlongo*, -*āvi*, -*āre*’, meaning ‘to lengthen’, with the apposition of the suffix ‘-*ulus*, -*ula*, *ulum*’, as a diminutive, to characterize the shape of the internodes of this delicate, straggling species.

### Material examined

#### Holotype

PACIFIC OCEAN • a 5.1 cm high colony without gonothecae; off New Caledonia, stn DW5010; 22°10' S, 159°03' E; 290–820 m; 19 Sep. 2017; KANADEEP leg.; MNHN-IK-2015-463.

### Description

Colony erect, 5.1 cm high, arising from creeping hydrorhiza. Stem monosiphonic, flaccid, unable to support itself when out of liquid; basal 1.6 cm ahydrothecate, with smooth perisarc; remainder of stem divided into regular internodes by means of indistinct oblique nodes slanting in alternate directions; internodes distinctly geniculate, long, each bearing distally a hydrotheca; branching sparse, irregular: only two side branches, neither branching further, occur in the present specimen; they are given off laterally and in opposite directions, from below the bases of two distant stem hydrothecae, and are coplanar. Hydrothecae long, slightly conical, adnate for  $\frac{1}{3}$  or less to their corresponding internodes; abaxial wall straight for most of its length, imperceptibly convex distally; free adaxial wall slightly sigmoid, convex for most of its length, then concave towards aperture; aperture three-cusped, adaxial cusp slightly produced, latero-abaxial cusps less prominent, with rounded tips, separated by wide, shallow embayments; operculum composed of three triangular flaps meeting centrally to form a pyramidal roof; 8 internal, submarginal projections of the perisarc: one minute adaxial, two pairs of latero-adaxial, one large abaxial, and two latero-abaxial. Gonothecae not observed.

### Remarks

Only a restricted number of congeners display a combination of long, slender, geniculate internodes and weakly-adnate hydrothecae, namely: *S. amphoriferus* Allman, 1877 (Millard 1977; Schuchert 2001), *S. bathyalis* Vervoort, 1972 (original account, Calder & Vervoort 1998), *S. dentiferus* (Torrey, 1902) (Nutting 1904), *S. effusus* Vervoort, 1993 (original account, Galea 2016), *S. macrocarpus* (Billard, 1918) (original account, Billard 1925), *S. minutus* (Nutting, 1904) (original account), *S. naumovi* Blanco, 1969 (Peña Cantero *et al.* 2002), *S. nesioticus* Blanco, 1977 (original account, Peña Cantero *et al.* 2002), *S. paucicatillus* Galea, 2016 (original account), *S. paulensis* Stechow, 1923 (Vervoort 1993; present report), *S. pedunculatus* (Billard, 1919) (Billard 1925; Vervoort 1993) and *S. plectilis* (Hickson & Gravely, 1907) (Millard 1977). However, in any of these the hydrothecae do not adopt the distinctive shape met with in *S. elongatulus* sp. nov., and none displays submarginal, intrathecal cusps.



Through its *Sertularella*-like hydrothecae, provided with only three marginal cusps, the present species comes close to ? *Symplectoscyphus acutistriatus* sp. nov. (see above), whose systematic position is discussed in the ‘Molecular study’ section.

### Distribution

Only known from off New Caledonia (present study).

### *Symplectoscyphus paulensis* Stechow, 1923

Figs 16C, 17K–M; Table 11

*Symplectoscyphus paulensis* Stechow, 1923: 8.

*Symplectoscyphus vervoorti* El Beshbeeshy, 2011: 184, fig. 61.

*Symplectoscyphus paulensis* – Stechow 1925: 467, fig. 28. — Millard 1967: 183, fig. 4G–H; 1975: 317, fig. 102A–C; 1977: 107; 1978: 199; 1979: 142; 1980: 144, fig. 5A–B. — Vervoort 1972: 180, figs 60B, 61; 1993: 263, figs 63, 65A. — Hirohito 1983: 51, fig. 24. — Vervoort & Watson 2003: 222, fig. 53A–B. — Watson 2003: 170, fig. 20. — Soto Àngel & Peña Cantero 2019: 37, fig. 11I.

*Sertularella paulensis* – Stepanjants 1979: 71, pl. 17 fig. 2.

### Material examined

PACIFIC OCEAN • a colony, 3 × 3.2 cm, without gonothecae; off New Caledonia, stn DW4759; 23°12' S, 168°03' E; 317–343 m; 26 Aug. 2016; KANACONO leg.; one fragment was used for DNA extraction, DNA 1390; voucher MHNG-INVE-120851; barcode identifier MK073104; MNHN-IK-2015-393 • a fertile colony, 4.5 × 5 cm; same collecting data as for preceding; MNHN-IK-2015-393.

### Remarks

The present material fits the description and illustrations given by Vervoort (1993) of *S. paulensis*. It is mainly characterized by 1) its rootlike hydrorhiza, firmly adhering the colony to a hard substrate; 2) the stem is unbranched but fascicled, tending to monosiphonic distally; 3) the internodes are weakly indicated, and composed of a minute apophysis (supporting a cladium) together with its associated axillar hydrotheca, as well as two alternate hydrothecae above; 4) the cladia are given off regularly in an alternate manner; unbranched, up to 3 cm long, composed of up to 26 hydrothecate internodes separated by weak oblique nodes; 5) the gonothecae are laterally flattened, with undulated walls; aperture rounded atop of a neck region borne on a terminal, slightly depressed plateau; likely female, containing 1–2 large, ovoid bodies.

El Beshbeeshy (2011) created *S. vervoorti* for material studied earlier by both Vervoort (1972, as *S. paulensis*) and Stepanjants (1979, as *Sertularella paulensis*), on the account of 1) wider internodes and nodes; 2) hydrothecae circular in cross section and isodiametric throughout; 3) hydrothecal aperture everted, rim provided with pointed cusps. However, in light of the reexamination of the lectotype of *S. paulensis* by Vervoort (1993: fig. 43A–D) and the comparative measurements given in Table 11, this doesn't seem justified. Indeed, Vervoort (1993: 263) clearly stated that the “Valdivia material is in perfect agreement with specimens described by Vervoort (1972: 180–183, figs 60b, 61)”.

### Distribution

Off St. Paul (Stechow 1923), off Mozambique (Millard 1967), Vema Seamount (Vervoort 1972), South Africa (Millard 1975), Patagonian Shelf (Stepanjants 1979; El Beshbeeshy 2011, as *S. vervoorti* sp. nov.), New Caledonia (Vervoort 1993, present study), New Zealand (Vervoort & Watson 2003),

**Table 11.** Measurements of *Symplectoscyphus paulensis* Stechow, 1923 from various sources, in  $\mu\text{m}$ .

	Present study	Vervoort (1993), lectotype	Vervoort (1993); material from Millard (1967)	Vervoort (1972)	Stepanjants (1979) as <i>Sertularella paulensis</i>	EI Beshbeeshy (2011) as <i>Symplectoscyphus vervoorti</i> sp. nov.	Vervoort & Watson (2003)	Watson (2003)
<b>Internodes</b>								
- ordinary internodes	1005–1425	1410–1845	865–1300	1285–1430	1260–1400	1067–1531	–	1000–1440
- diameter at node	–	195–370	130–215	340–405		290–406	195–260	120–176
<b>Hydrotheca</b>								
- free adaxial wall	725–785	865–935	910–935	595–835	790–910	603–951	1015–1145	792–840
- adnate adaxial wall	280–310	540–585	370–390	500–580	460–600	464–556	345–395	328–392
- abaxial wall	665–710	670–870	760–825	675–755	950–1060	672–759	1065–1130	880–960
- total length	–	1105–1260	1100–1130	920–1055			1310–1345	
- maximum width	–	455–500	410–435	460–485			460–510	–
- diameter at aperture	370–390	410–435	390–415	365–475	500–550	440–487	425–440	400–480
<b>Gonotheca</b>								
- total length	1435–1485	–	1520	–	–	1800–1856	1720	–
- maximum width	930–970	–	1065	–	–	928–997	1195	–
- length of funnel	170–205	–	–	–	–	127–139	164	–
- diameter at aperture	220–270	–	–	–	–	232–243	130	–

Japan (Hirohito 1983), Macquarie Island (Watson 2003) and Antarctica (Peña Cantero 2012; Soto Ángel & Peña Cantero 2019).

*Symplectoscyphus ralphae* Vervoort, 1993

*Symplectoscyphus ralphae* Vervoort, 1993: 270, figs 65E–F, 66A–C.

*Symplectoscyphus ralphae* – Galea 2016: 45, fig. 10M–V.

**Material examined**

PACIFIC OCEAN • male colony with stems up to 1.4 cm high, on axis of antipatharian; off New Caledonia, stn DW4714; 22°49' S, 167°25' E; 394–443 m; 18 Aug. 2016; KANACONO leg.; MNHN-IK-2015-395 • two female colonies, 2.6 and 3.7 cm high, respectively; off New Caledonia, stn DW4784; 22°51' S, 167°44' E; 310–322 m; 29 Aug. 2016; KANACONO leg.; MNHN-IK-2015-396 • a colony composed of several stems up to 1.4 cm high, one of them with a female gonotheca; off New Caledonia, stn DW4715; 22°50' S, 167°27' E; 424 m; 18 Aug. 2016; KANACONO leg.; MNHN-IK-2015-397 • a stem 2.5 cm high with male gonothecae; off New Caledonia, stn CP4675; 22°50' S, 167°30' E; 350–

366 m; 13 Aug. 2016; KANAONO leg.; used as a whole for DNA extraction, DNA 1392; MHNG-INVE-120853 • male and female colonies with stems up to 4 cm high, on different substrates; off New Caledonia, stn CP4674; 22°48' S, 167°29' E; 311–302 m; 13 Aug. 2016; KANAONO leg.; MNHN-IK-2015-398 • a profuse male colony, with stems up to 1.8 cm high; off New Caledonia, stn DW4720; 22°50' S, 167°11' E; 374–400 m; 19 Aug. 2016; KANAONO leg.; a fertile stem was used for DNA extraction, DNA 1391; voucher MHNG-INVE-120852; barcode identifier MK073105; MNHN-IK-2015-469.

### Remarks

In view of the present material, always fertile, it can be now stated that the gonothecae are sexually dimorphic, as suspected earlier by Galea (2016). Female gonothecae are longer and larger, and possess a larger number of transverse ridges, and a comparatively wider terminal funnel.

### Distribution

New Caledonia (Vervoort 1993; present study), Norfolk Ridge (Galea 2016).

### *Symplectoscyphus* cf. *tropicus* (Hartlaub, 1901)

Figs 16D, 17N–O; Table 12

*Sertularia variabilis* Clarke, 1894: 75, pls 4–5 figs 17–22 [non *Sertularella variabilis* Bale, 1888 = *Symplectoscyphus indivisus* (Bale, 1882)].

*Sertularella tropica* – Hartlaub 1901: 41, fig. 19 (new name for *S. variabilis* Clarke, 1894). — Nutting 1904: 102, pl. 26 figs 3–4. — Clarke 1907: 14, pl. 10 figs 1–3, 3B. — Billard 1925: 165, fig. 26. — Redier 1971: 142.

### Material examined

PACIFIC OCEAN • a 6.5 cm high colony, bearing an incompletely-formed gonotheca on the proximal part of a cladium; off New Caledonia, stn DW4672; 22°47' S, 167°26' E; 310–290 m; 13 Aug. 2016; KANAONO leg.; MNHN-IK-2015-394.

### Description

Colony arising from a root-like, ramified hydrorhiza firmly anchoring it to its substrate. Stem simple, 6.5 cm high, fascicled over its proximal 2 cm; divided by weakly-indicated transverse nodes, each internode composed of an indistinct apophysis (supporting a cladium) with its associated axillary hydrotheca, and two alternate hydrothecae above. Cladia generally alternate, but there can be exceptions especially when one, three or four hydrothecae (instead of only two) occur above an axillar hydrotheca. Cladia given off slightly laterally from below the bases of stem hydrothecae, and distinctly shifted on to the ‘anterior’ side of the colony; up to 1.8 cm long and carrying up to 15 hydrothecate internodes separated by distinct oblique nodes; generally unbranched, though one cladium bears three short, secondary branchlets of up to six hydrothecate internodes. Hydrothecae alternate, large, tubular, adnate for about  $\frac{2}{3}$  to the corresponding internodes; free adaxial wall long, convex proximally, concave distally; adnate adaxial wall slightly curved, ending basally in conspicuous perisarc plug; there is no hydrothecal base, the abaxial wall being a continuation of the internode; aperture circular in frontal view, rim everted on adaxial side, provided with three broad, low, triangular cusps separated by shallow embayments; opercular apparatus composed of three triangular flaps meeting centrally to form a pyramidal roof. A single gonotheca arises from below the base of a cladial hydrotheca, but it is incomplete, having only its basal, vasiform part already formed.

**Table 12.** Measurements of *Symplectoscyphus* cf. *tropicus* (Hartlaub, 1901), in  $\mu\text{m}$ .

	Present study	Billard (1925)
<b>Internodes</b>		
- ordinary internodes	–	–
- 1 <sup>st</sup> internode of a side branch	–	–
- diameter at node	–	–
<b>Hydrotheca</b>		
- free adaxial wall	1115–1165	–
- adnate adaxial wall	405–440	–
- abaxial wall	1130–1165	–
- total depth	1310–1375	890–960
- maximum width	545–555	–
- diameter at aperture	600–615	420–440
<b>Gonotheca</b>		
- total length	–	2320
- maximum width	–	1040
- length of funnel	–	–
- diameter at aperture	–	–

**Remarks**

The present material comes close to that assigned by Billard (1925) to *Symplectoscyphus tropicus* (Hartlaub, 1901), although it is of slightly bigger proportions, and doesn't have fully-formed gonothecae so as to facilitate their comparison. In addition, it is not clear whether this record and that of Billard belong to the same species as the material of Clarke (1894), especially since there are no available measurements for the latter. However, the gonothecae illustrated by both Billard and Clarke appear very similar in shape, supporting a possible conspecificity.

Hartlaub (1901) noted the secondary homonymy between *Sertularia variabilis* (Clarke, 1894) and *Sertularella variabilis* Bale, 1888, and renamed the former *Sertularella tropica*. Both Clarke's and Bale's hydroids should be correctly assigned to the tricuspidate genus *Symplectoscyphus*. In addition, the latter is now considered as a junior synonym of *Symplectoscyphus indivisus* (Bale, 1882) (Vervoort & Watson 2003).

**Distribution**

Off Panama (Clarke 1894), off Ecuador (Clarke 1907), Indonesia (Billard 1925), French Polynesia (Redier 1971) and New Caledonia (present study).

Family Thyroscyphidae Stechow, 1920

Genus *Tuberocaulus* Galea, gen. nov.

[urn:lsid:zoobank.org:act:317807A0-E2BB-4EBF-9305-9917A818E1E9](https://zoobank.org/act:317807A0-E2BB-4EBF-9305-9917A818E1E9)

**Diagnosis**

Stems unbranched, strongly fascicled basally, arched downwards distally, and there giving rise to a row of cladia arranged unilaterally; division into internodes indistinct; each equivalent of internode with short, lateral apophysis supporting a cladium, an axillar nematotheca and second nematotheca on opposite side and slightly above; cladia divided into moderately-long internodes, each bearing a hydrotheca distally; the two rows of hydrothecae forming a sharp angle; hydrothecae long, tubular,

tapering in lower halves, adnate for a minute portion of their adaxial wall to the internode, aperture with three pointed cusps (one abaxial, two latero-adaxial) separated by deep, rounded embayments, rim thickened. Gonothecae given off laterally from below the hydrothecae; short, club-shaped, aperture subterminal, semi-circular. Perisarc filmy and easily collapsible on both hydro- and gonothecae.

### Type species

*Thyroscyphus scorpioides* Vervoort, 1993, as *Tuberocaulus scorpioides* (Vervoort, 1993) gen. et comb. nov. The genus is currently monotypic.

### Etymology

From the Latin ‘*tūbĕr*’, meaning ‘protuberance’, and ‘*caulis*’, meaning ‘stem’, to illustrate the presence of putative nematothecae on stems.

### Remarks

The genus *Tuberocaulus* gen. nov. is monotypic so far and comprises *Tuberocaulus scorpioides* (Vervoort, 1993) gen. et comb. nov. This species was originally placed in *Thyroscyphus* Allman, 1877 on account of the attachment of the hydranth to the inner hydrothecal wall (whose surface is lined by “a sheath of tissue” = mantle) “by means of a circular fold”. However, unlike *Thyroscyphus*, the hydrotheca of this species is given off from the internode, and it is not borne on a distinct apophysis; additionally, it has a well-defined (though short) adnate adaxial wall, as well as a base (see description above).

The fascicled condition of the stem and its peculiar appearance, the presence of what appears to be stem nematothecae, as well as the unilateral arrangement of cladia and their hydrothecae, are not features shared by the genus of Allman (1877).

The systematic position of *T. scorpioides* could not be ascertained on morphological grounds alone. Indeed, its long, tubular, tricuspidate hydrothecae superficially recall those of *Parascyphus simplex* (Lamouroux, 1816), but in that species, the thecae are borne on distinct stem apophyses, their ‘bases’ are represented by an internal annular thickening of the perisarc, and the marginal cusps adopt a different position (one adaxial and two latero-abaxial cusps, see Galea *et al.* 2014).

Being fused to the corresponding internodes, the hydrothecae of *T. scorpioides* are reminiscent of those met with in members of the Sertulariida Maronna *et al.*, 2016 (with only *Gonaxia* Vervoort, 1993 showing the same position of the marginal cusps), although nematothecae have never been reported in any genus belonging to it.

The relationship of *Tuberoscyphus* gen. nov. to the other Leptothecata families remains to be investigated by molecular phylogenies. In the absence of such studies for the time being, the genus is left provisionally in the Thyroscyphidae.

*Tuberocaulus scorpioides* (Vervoort, 1993) gen. et comb. nov.

Figs 16E, 18

*Thyroscyphus scorpioides* Vervoort, 1993: 276, figs 66F, 67E–F.

### Material examined

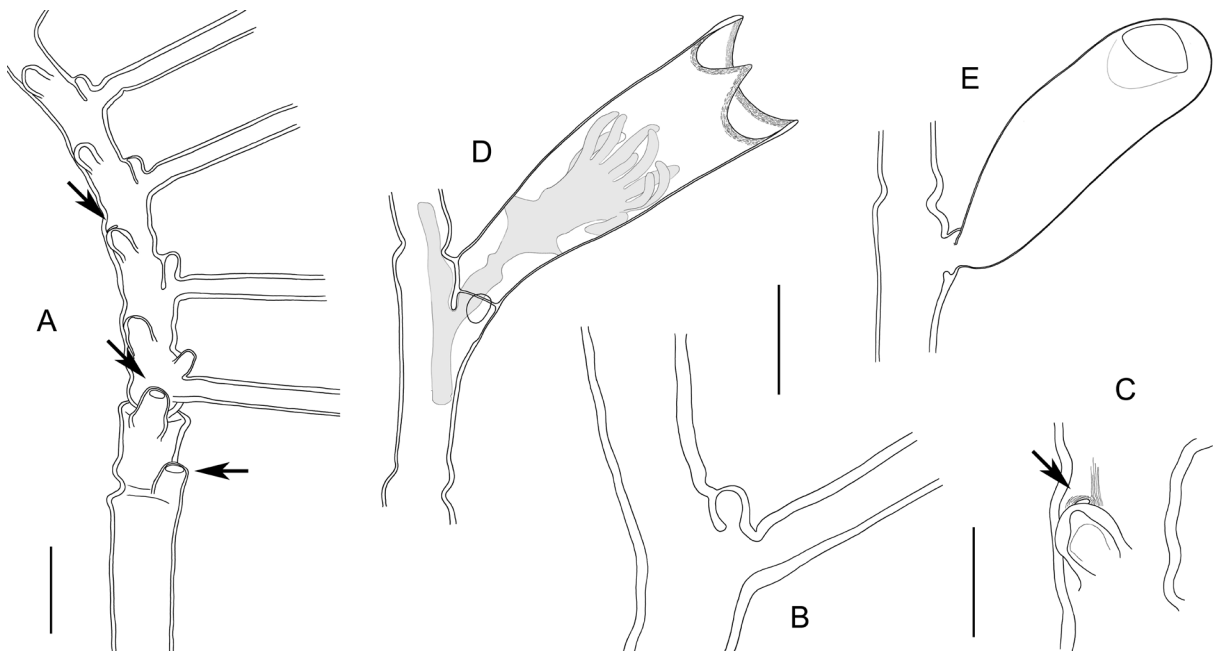
PACIFIC OCEAN • a fertile colony 6.5 cm high, in relatively bad condition, with most of its hydro- and gonothecae damaged; off New Caledonia, stn DW4697; 22°48' S, 167°15' E; 465–449 m; 16 Aug.



2016; KANAONO leg.; a shed cladium was used for DNA extraction, DNA 1393; voucher MHNG-INVE-120854; MNHN-IK-2015-400.

### Description

Colony erect, 6.5 cm high, relatively stiff when out of liquid, arising from much branched, rhizoid hydrorhiza firmly attached to the substrate. Stem simple, strongly fascicled proximally, grading to monosiphonic 4 cm after its origin from stolon. Main tube composed of a long, straight, proximal part devoid of cladia and having irregularly wrinkled to smooth perisarc, and a comparatively shorter, distal part bearing hydrocladia, distinctively curved downwards. Proximal part undivided, except for a distal, short, quadrangular segment separating it from the distal hydrocladiate part through two broad, conspicuous transverse nodes; basal and quadrangular segments provided distally with large, prominent nematothecae with distinct, apical, rounded aperture (Fig. 18A, arrowheads). Hydrocladiate part divided into internodes through transverse constrictions of the perisarc, distinct basally, becoming obsolete distally. Each internode comprises a short, lateral apophysis (supporting a cladium), an axillar nematotheca, as well as a second, lateral nematotheca in middle of opposite site; all apophyses given off on same side of the stem. The two rows of stem nematothecae distinctly shifted on to the ‘anterior’ side of the colony in the lower portion of the hydrocladiate part of the stem, becoming gradually almost coplanar distally; similarly, the cladia adopt a more lateral arrangement along the stem towards its distal end. Axillar nematothecae tubular on proximal portion of the hydrocladiate part of the stem, becoming mere mamelons distally; no distinct aperture could be noted on any of them. Nematothecae in opposite row comparatively less prominent, resembling mamelons in shape, provided occasionally with slit-like aperture in axil formed with the corresponding stem internode (Fig. 18A, C, arrowheads). Cladia distant of 1–1.5 mm, up to 2 cm long, divided into up to 18 thecate internodes by means of transverse nodes; proximal most internode comparatively longer than subsequent ones; internodes moderately long, each provided with a hydrotheca distally. Hydrothecae alternate but conspicuously shifted on to the upper side of cladia, the two rows forming a very acute angle; long, tubular, lower halves gradually tapering



**Fig. 18.** *Tubero-caulus scorpioides* (Vervoort, 1993) gen. et comb. nov. A–E. Junction between proximal and distal parts of stem (A), showing apically- or axillary-opened nematothecae (arrowheads), detail of insertion of cladium (B), upper stem nematotheca with aperture in axil (C, arrowhead), hydrotheca (D), gonotheca (E), all from sample MNHN-IK-2015-400. Scale bars: A = 1 mm; B–E = 500 µm.

basally, adnate to the internode for a minute portion of their adaxial wall; distally, a large, circular aperture surrounded by three prominent, pointed, triangular cusps (one abaxial, two latero-adaxial) separated by large, deep, rounded embayments; rim thickened; a perisarc plug extending downwards the adnate adaxial wall of hydrotheca at junction with its base; a rounded fenestra below the base, as attachment site for the gonotheca. Hydranths large, attached to lower  $\frac{1}{4}$  of inner hydrothecal wall, provided with ca 16–20 filiform tentacles. Gonothecae club-shaped, with large, semi-circular, subterminal aperture, in a rounded depression in the gonothecal wall on side facing the hydrotheca. Perisarc of both hydro- and gonothecae almost filmy and easily collapsible, explaining why so many of those are partially or totally broken.

### Remarks

Vervoort (1993) noted “perisarcal protuberance[s]” in the axil formed by the cladia with the stem, but not on the opposite side of the stem internodes, and did not comment on their significance. These structures, occasionally showing distinct apical apertures, or apertures in the axil formed with the stem internodes, are thought to be nematothecae, although an accumulation of nematocysts could not be confirmed in this material with badly-preserved coenosarc.

### Distribution

Only known from off New Caledonia (Vervoort 1993; present study).

Family Zygophylacidae Quelch, 1885

Genus *Zygophylax* Quelch, 1885

*Zygophylax niger* Galea, sp. nov.

[urn:lsid:zoobank.org:act:5ED994EF-6147-4508-9C5B-7DDF69E72D8C](https://doi.org/10.5281/zenodo.3244444)

Figs 16F–G, 19; Tables 13–14

### Diagnosis

Colonies flabellate, with much branched, heavily-fascicled stems. Division into internodes indistinct, but equivalents of internodes with a proximal cladial apophysis and its associated axillary hydrotheca, two alternate hydrothecae above, and a second cladial apophysis, given off on side opposite to the preceding one; hydrothecae long, tubular, with slightly everted, circular margin, tapering in lower third into long, proximally annulated pedicel. No nematothecae on the hydrothecal apophyses. Gonothecae aggregated into long masses of coppinia around the side branches, but neither fused, nor appressed against each other; long, tubular, walls slightly wrinkled, basally tapering into minute pedicel, distally truncate.

### Etymology

From the Latin ‘*nigĕr*’, meaning ‘black’ or ‘dark’, to emphasize the color of its colonies.

### Material examined

#### Holotype

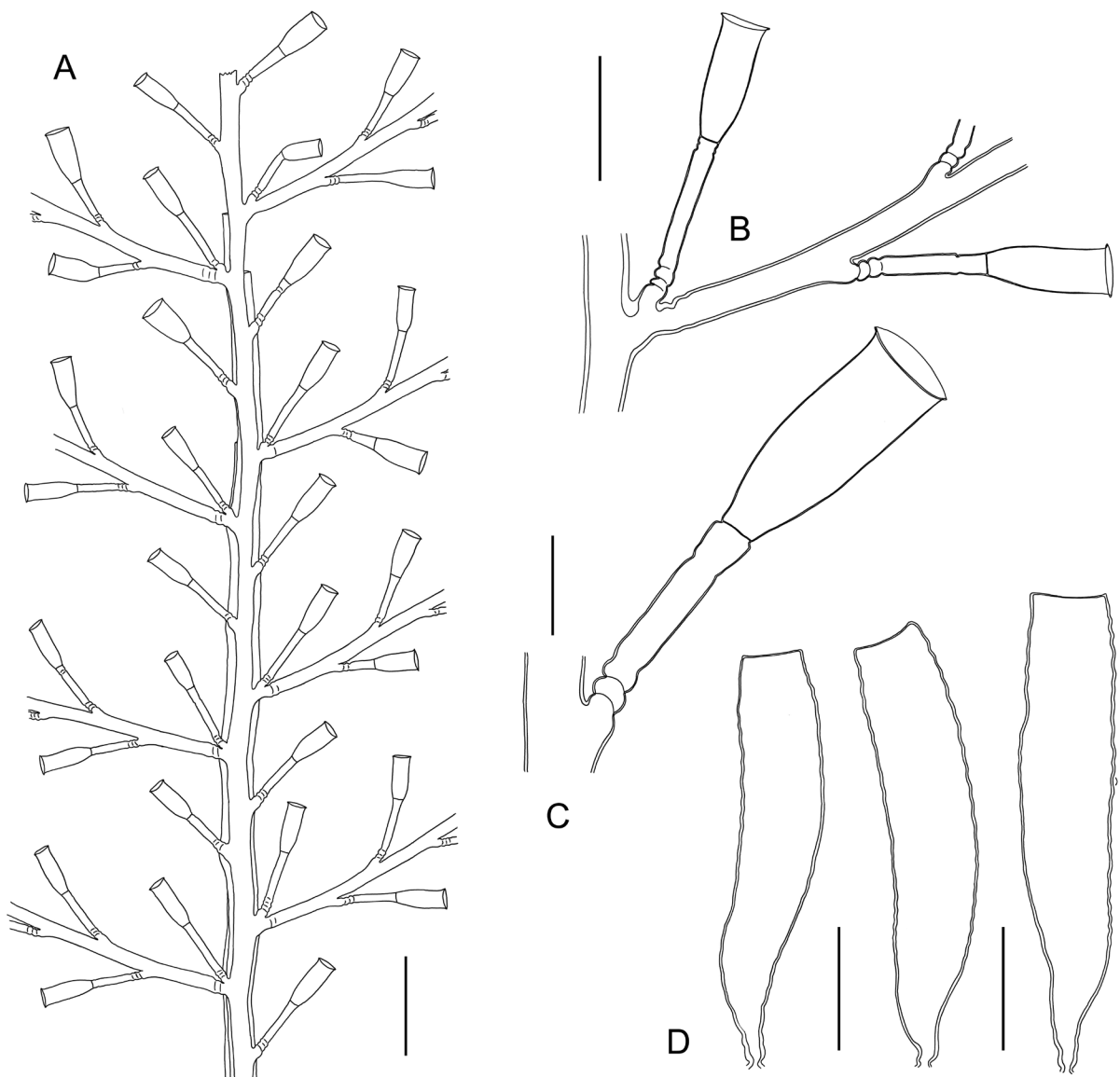
PACIFIC OCEAN • a fertile colony, 7.5 × 7.5 cm; off New Caledonia, stn DW4742; 22°53' S, 167°37' E; 290–345 m; 23 Aug. 2016; KANACONO leg.; MNHN-IK-2015-478.

#### Paratype

PACIFIC OCEAN • a fertile colony, 6.5 × 5 cm; off New Caledonia, stn DW4742; 22°53' S, 167°37' E; 290–345 m; 23 Aug. 2016; KANACONO leg.; MNHN-IK-2015-480.

**Additional material**

PACIFIC OCEAN • four colonies (of which the largest is 8 × 8.5 cm), as well as a few smaller fragments, all without gonothecae; off New Caledonia, stn DW4742; 22°53' S, 167°37' E; 290–345 m; 23 Aug. 2016; KANAONO leg.; a fragment from one colony was used for DNA extraction, DNA 1396; voucher MHNG-INVE-120856; barcode identifier MK073108; MNHN-IK-2015-481 • three colonies, 10.5 × 6 cm (now broken into three pieces, without gonothecae), 6.5 × 5 cm (fertile, now broken into two pieces) and 10.5 × 5.5 cm (now broken into three pieces, without gonothecae); off New Caledonia, stn CP4779; 23°02' S, 168°17' E; 270–293 m; 28 Aug. 2016; KANAONO leg.; a small fragment detached from one of these colonies was used for DNA extraction, DNA 1395; voucher MHNG-INVE-120855; barcode identifier MK073107; MNHN-IK-2015-479 • a colony fragment, 6.5 × 4.5 cm,



**Fig. 19.** *Zygophylax niger* Galea, sp. nov. **A–D.** Tip of colony showing mode of branching (A), portion of stem with axillar hydrotheca and proximal part of cladium (B), hydrotheca atop its pedicel (C), three gonothecae (D), all from sample MNHN-IK-2015-479. Scale bars: A = 1 mm; B, D = 500  $\mu$ m; C = 200  $\mu$ m.

**Table 13.** Measurements of *Zygophylax niger* Galea, sp. nov., in  $\mu\text{m}$ .

<b>Caulus</b>	
- internode length	2500–2700
- apophysis length	75–90
<b>Cladium</b>	
- distance between two successive hydrothecae	510–560
- diameter	120–145
- apophysis length	25–35
<b>Hydrotheca</b>	
- depth	470–560
- width in middle	160–185
- diameter at rim	195–210
- pedicel length	470–625
- pedicel width	70–85
<b>Gonotheca</b>	
- length	1605–1935
- maximum width	340–380
- width at top	290–330

without gonothecae; off New Caledonia, stn CP4786; 22°46' S, 167°42' E; 350–469 m; 29 Aug. 2016; KANACONO leg.; MNHN-IK-2015-482.

### Description

Colonies flabellate, up to 10.5 cm high, arising from root-like hydrorhiza, firmly attached to the substrate. Main stem branched irregularly, with up to 5<sup>th</sup> order side branches; stem and branches heavily fascicled for most of their length, grading to monosiphonic distally; stems up to 3 mm thick basally. Perisarc dark in fascicled parts, brownish in monosiphonic ones. Stem divided into indistinct internodes with the following sequence: a prominent, proximal apophysis (supporting a cladium) and its associated axillary hydrotheca (itself borne on a short, distinct apophysis), followed by two alternate hydrothecae above (each borne on a short stem apophysis), and a second, distal, apophysis (supporting following cladium), together with its associated hydrotheca (itself borne on a stem apophysis). Cladia alternate, monosiphonic, divided through generally indistinct, slightly oblique nodes into moderately-long internodes bearing distally a short apophysis supporting a hydrotheca; apophyses alternate, coplanar; cladia with up to 13 hydrothecate internodes; first internode with a couple of spiral twists basally. Hydrothecae borne on relatively long pedicels, invariably annulated basally (usually two, but up to four annuli observed), but also distally (0–4 annuli), occasionally in middle. Hydrotheca cup-shaped, elongated, proximal  $\frac{1}{3}$  tapering gradually below, distal  $\frac{2}{3}$  tubular; aperture circular, rim slightly but distinctly everted, margin smooth; perisarc thin and smooth; hydrotheca delimited basally from pedicel by thin diaphragm. Hydranths with ca 16 filiform tentacles, with no caecum. Nematothecae absent throughout. Gonothecae grouped in certain parts of the colonies, but independent from each other (neither contiguous, nor fused), arising from accessory tubes of the side branches; long, tubular, slightly curved in middle part, tapering below, distally truncate, walls undulated, perisarc rather thick and dark brown. No nematophorous ramuli amongst the gonothecae.

### Remarks

The gonosome of the new species shows striking resemblances to that of *Z. polycarpa* Vervoort & Watson, 2003, a species discovered from off Three Kings Island, New Zealand. Indeed, coppinia of

**Table 14** (continued on next page). Species of *Zygophylax* with long hydrothecal pedicels and non-fused gonothecae, and their differences to *Z. niger* Galea, sp. nov.

Species name	Main distinguishing morphological features
<i>Z. abyssicola</i> (Stechow, 1926)	Species not illustrated (Rees & Vervoort 1987). Hydrothecae biseriate, alternate, <b>shifted on unilaterally</b> , borne on long pedicels; very elongated, ca 2.5 times as long as wide. Gonothecae individualized, borne on short, smooth pedicels; with 2–3 broad rings, distally truncated and provided with <b>2 opposite apertures, each borne on a short, wide lateral tube; a network of mesh-like, branched, nematophorous tubes</b> amongst gonothecae (Stechow 1926)
<i>Z. bifurcata</i> Billard, 1942	“apophyses and their hydrothecae [...] <b>directed obliquely forward</b> . Hydrothecal pedicels long, with wrinkled to indistinctly ringed portions [...]”. Hydrothecae moderately-long, tapering in lower half, occasionally asymmetrical. “ <b>Nematothecae</b> , where present, invariably found <b>on hydrothecal apophyses</b> ”. Gonothecae “contiguous but not fused [...] elongate-ovate, constricted basally, with short pedicel, <b>apical portion with two diverging funnels pointing in opposite directions</b> , each with rather wide, slit-shaped opening”. <b>Nematophorous tubules</b> , dichotomously-branched, curving over the gonothecae (Rees & Vervoort 1987)
<i>Z. concinna</i> (Ritchie, 1911)	“The hydrothecae [...] lie in one plane [...]. Each hydrotheca rests on a well-marked projection from stem or branch. On this is perched a long, cylindrical stalk [...] half or a little more than half the length of the hydrotheca. The hydrothecae are deep, tubular, and <b>cyathiform</b> , the abcauline profile forming a simple convex curve, the adcauline a compound curve, first convex, then concave”. Nematothecae absent (Ritchie 1911). “The gonangia are <b>ovate with undulated edges, truncated at the distal end</b> , and tapering towards the proximal extremity. [...] In frontal aspect each gonangium is a little narrowed in near the distal end and then widens outwards forming a conspicuous round projection or <b>shoulder at each side of the top</b> where the gonangium reaches its maximum width. These <b>shoulders are produced slightly downwards into truncated processes, each of which ends in a small circular aperture directly facing towards the proximal extremity of the gonangium</b> ” (Briggs 1922)
<i>Z. convallaria</i> (Allman, 1877)	“Hydrothecae usually borne <b>on one side of hydrocaulus</b> , facing a plane perpendicular to the plane of the branches [...] “ <b>bending near distal end to varied extent</b> , occasionally at a right angle [...]. <b>Nematothecae</b> present on tubes of stem and branches, on apophysis or on rare occasions on the internodes” (Hirohito 1995). Gonothecae independent from each other, “anchor-shaped, <b>apex with two downwardly directed flukes, at the of which is an opening</b> . <i>Protective ramules</i> with some nematothecae occasionally present” (Rees & Vervoort 1987)
<i>Z. elongata</i> Ramil & Vervoort, 1992	“Hydrothecae [...] <b>directed frontally</b> , tubular, placed on pedicel of considerable length [...]. Adcauline hydrothecal wall distinctly convex and abcauline wall concave, giving <b>hydrotheca a characteristic, curved appearance</b> . [...] <b>Nematothecae</b> inserting on apophyses, one on each side of hydrothecae, on base of side-branches (hydrocladia) and dispersed on axis and secondary tubules. [...] Gonothecae separate, without adnate walls, ovoid, <b>apically with bifurcate process</b> , bifurcations ending in gonothecal apertures, two for each gonotheca” (Ramil & Vervoort 1992)
<i>Z. infundibulum</i> Millard, 1958	“The two rows of hydrothecae on stem and branches not in the same plane, but <b>shifted on to the anterior surface and forming a sharp angle</b> (about 15-40°) between them”. Hydrotheca “elongated, <b>curving upwards in the distal part</b> , with abcauline wall convex, and adcauline wall convex in proximal two-thirds and concave in distal third. [...] One <b>nematotheca</b> on the apophysis next to each hydrothecal pedicel” (Millard 1958). “Gonothecae not adpressed, <b>narrow at base and widening distally, then divided into two outwardly curved necks bearing the terminal apertures</b> . <i>Protective tubular structures numerous, arising amongst the gonothecae and rising above them</i> , completely obscuring them and forming a bristly coat to the coppinia; each branching irregularly and bearing many nematothecae similar to those of the trophosome” (Millard 1980).



**Table 14** (continued). Species of *Zygophylax* with long hydrothecal pedicels and non-fused gonothecae, and their differences to *Z. niger* Galea, sp. nov.

<i>Z. leloupi</i> Ramil & Vervoort, 1992	“Front of axis of hydrocladia with series of apophyses [...]. Hydrothecae [...] <b>directed frontally</b> , with tubular, with <b>fairly long pedicels</b> [...]. Adcauline wall [...] convex over greater part of its length but just under rim with <b>slight concavity</b> giving hydrotheca characteristic appearance [...]; abcauline wall <b>convex</b> and slightly longer than adcauline wall. [...] <b>Nematothecae</b> inserting on apophyses, one on each side of the hydrothecal pedicel. [...] Gonothecae ovoid, aggregated though not adnate, at <b>distal extremity with two or three short, tubular processes, pointing obliquely upwards</b> , each with one terminal aperture” (Ramil & Vervoort 1992)
<i>Z. levinseni</i> (Saemundsson, 1911)	“apophyses alternately directed obliquely left and right and frontally, on which insert the hydrothecae that consequently are also <b>frontally directed and are not placed in the same plane</b> [...]. Hydrotheca on fairly long pedicel [...] tubular, <b>slightly asymmetric</b> as adcauline wall is slightly convex and abcauline wall slightly concave. [...] <b>Nematothecae</b> inserting on apophyses, usually one on each side of hydrothecal pedicel [...]. Coppiniae [...] composed of dense aggregations of individual, non-adnate gonothecae. Each gonotheca ovoid, <b>slightly laterally compressed, distally produced into a pair of laterally curved tubes</b> ” (Ramil & Vervoort 1992)
<i>Z. pinnata</i> (G.O. Sars, 1874)	Hydrothecae “bell-shaped to tubular, rather deep, tapering in lower third, often <b>with slight asymmetric bulge imparting pseudo-bilateral symmetry</b> ; always roughly straight on outer side [...]; pedicel continuing tapered outline of hydrotheca, varied in length, sometimes with annulus, and many with rather deep fold on adjacent side just above axil. No nematophores or nematothecae” (Cornelius 1995). Coppinia “composed of closely packed, but not coalesced, gonothecae without protective nematophorous ramuli. Gonothecae <b>elongate, sac-shaped bodies, apically with 2-4 circular openings at end of short funnel</b> ” (Rees & Vervoort 1987)
<i>Z. sibogae</i> Billard, 1919	Hydrothecae <b>shifted on frontally, distinctively curved in middle</b> , “with deep constriction on <b>adcauline side</b> ”; “ <b>nematothecae</b> present on peripheral tubes, singly on each lateral side of each apophysis, on rare occasions on hydrothecal pedicel”; gonothecae “pouch-like, bearing one or two long tubes at the distal end; tubes facing to various directions” (Hirohito 1995). “Gonothecae loosely aggregated in coppinia on stem, gonothecae not adnate, shape very irregular sac-shaped [...], with <b>1–3 openings on tubular extensions</b> . Coppinia comprise also <b>protective branches</b> , branched, forming canopy over gonothecae, with nematothecae” (Schuchert 2015)
<i>Z. stechowi</i> (Jäderholm, 1919)	Trophosome poorly described by Jäderholm (1919). Hydrothecae alternate, coplanar, borne on moderately-long, wrinkled to occasionally ringed pedicels; hydrothecae long, almost tubular, tapering basally. Gonothecae not contiguous to each other, without nematophorous tubules, <b>slender, T-shaped, distally with two opposite apertures</b> (Hirohito 1995)
<i>Z. unilateralis</i> Totton, 1930	“Hydrothecae <b>more or less unilateral</b> [...] relatively longer than pedicels”; <b>curved</b> , apertures “facing both upwards and outwards, so that those of one side are at right angles to those of the other “; <b>nematothecae</b> “one on the outer side of each stem or branch apophysis at base of hydrothecal pedicel” (Totton 1930). “Though the gonothecae touch they are not compressed but have open spaces in between, from which abundant <b>nematophorous ramules</b> project. Each gonotheca <b>sac-shaped, swollen and more or less oval to round in outline. Apex with 3 laterally projecting, short funnels</b> , slightly flared at the rim, openings directed variously” (Rees & Vervoort 1987)

both species are composed of loosely-packed, separate, elongated, tubular gonothecae, and are devoid of nematophorous structures. However, *Z. polycarpa* possesses sessile, and comparatively shorter and broader hydrothecae, not perfectly symmetrical, but rather convex, especially on adaxial side (Vervoort & Watson 2003).

The differences to *Z. niger* sp. nov. of the congeners displaying both hydrothecae borne on long pedicels and separate, loosely-aggregated gonothecae, are summarized in Table 14.

The trophosome of *Z. tottoni* Rees & Vervoort, 1987, a species from off Oman with a so far unknown gonosome, shows a few similarities to that of *Z. niger* sp. nov., notably the mode of branching of its stems, the shape of its hydrothecae, and the presence of rather long hydrothecal pedicels. However, the latter does not possess proximally the distinctive basal annuli, its hydrothecae are comparatively shorter and narrower, and there is one nematotheca on frontal side of each apophysis supporting a hydrotheca (Rees & Vervoort 1987).

### **Distribution**

Only known from off New Caledonia (present study).

### ***Molecular study***

For 30 samples described in this study it was possible to obtain about 600 bp of the mitochondrial 16S gene sequence that could be compared in a maximum likelihood tree (Fig. 20). All sequences were initially compared to all GenBank sequences using BlastN (Johnson *et al.* 2008). This allowed to control whether each new sequence was, indeed, of hydrozoan origin, and concomitantly identified closely-related sequences that proved important for subsequent comparisons. A total of 90 sequences were thus aligned and used to determine the optimal probabilistic model of sequence evolution, as well as to make the phylogenetic analyses. The optimal substitution model suggested was GTR+I+G. There was no need to remove regions with uncertain alignments, as there were few such regions, and their exclusion did not alter the results significantly. The resulting maximum likelihood tree has numerous unresolved basal nodes, but several families appear in well supported clades (> 70% bootstrap support: Syntheciidae, Symplectoscyphidae, Lafoeidae, Sertularellidae, Staurothecidae, and Zygophylacidae). The family Sertulariidae sensu Maronna *et al.* (2016) appears also as clade, but with insufficient bootstrap support (58%).

Taxonomically noteworthy results are as follows:

- two species of *Caledoniana* and two of *Solenoscyphus* are more closely-related to the Staurothecidae than to Sertulariidae. Only *Solenoscyphus decidialis* mapped outside the *Solenoscyphus* and Staurothecidae clades, but without any supported relationship to other taxa;
- *Billardia hyalina* and *B. subrufa* (Jäderholm, 1904) (FN424117) are deeply embedded in the well supported Syntheciidae clade;
- the four *Hincksella* species dealt with herein do not group into a common clade, but are scattered over the whole tree. The type species of the genus (*H. sibogae*; see Totton 1930) associates with *Zygophylax*, but the node support is not significant;
- *Dictyocladium reticulatum* clusters with the Symplectoscyphidae;
- *Symplectoscyphus acutustriatus* sp. nov. is deeply embedded in the clade Sertularellidae and not in Symplectoscyphidae, the parent taxon of the genus *Symplectoscyphus*.

### **Discussion**

The principal utility of DNA barcodes (Hebert *et al.* 2003; Hebert & Gregory 2005), as produced in this study, is to permit a more objective discussion of species identifications and also to provide the essential database for future species community analyses via metabarcoding (e.g., Ji *et al.* 2013; McInnes *et al.* 2017). Additionally, and if sufficiently long, they often also permit to obtain phylogenetic trees and to study the evolutionary relationships between clades (Fig. 20). While standard animal barcode sequences are based on COI sequences, this marker proved to be difficult or impossible to amplify for some hydrozoan families (Schuchert 2014). The 16S gene has thus gained much more acceptance as a barcode marker for Hydrozoa (Schuchert 2016, and references therein). The 16S marker is a rapidly evolving marker and, as such, not so well suitable for phylogenies at or above the family level. However, well supported clades in a 16S based phylogeny (i.e., bootstrap support > 70%) have so far been confirmed



when additional markers, like 18S or 28S, were included (e.g., Leclère *et al.* 2009; Maronna *et al.* 2016). Therefore, the well supported family clades in the present analysis (Fig. 20) are most likely robust enough to be confirmed by a deeper analysis (study in progress).

The genera *Caledoniana* and two *Solenoscyphus* species clearly belong to the Staurothecidae, a family recently separated from the Sertulariidae by Maronna *et al.* (2016). Morphological features also suggest this reclassification (see above the Taxonomy section). However, some uncertainty remains, as the type species of both genera were not included in the analysis. Moreover, *Solenoscyphus decidualis* mapped outside the Staurothecidae clade (Fig. 20), but without any supported relationship to other taxa. This does not necessarily mean that *S. decidualis* is not a member of the Staurothecidae, and more likely reflects the lack of resolving power of the 16S marker at this taxonomic level. Additional markers are needed to settle down the question. However, considering the long distances of *S. decidualis* with respect to its congeners, it is almost certain that the former must be classified in a separate, new genus. Until a more comprehensive study becomes available, we prefer to keep the combination *Solenoscyphus decidualis* for the sake of nomenclatural stability.

According to Maronna *et al.* (2016), the genus *Billardia* cannot be placed with certainty within the Leptothecata and it was classified as a “rogue taxon”. However, we suspect that this was due to either a misidentification or a sequencing error of one of their samples (KT266603, *Billardia subrufa*). This sequence clusters with the Symplectoscyphidae (own unpublished results, not shown). Another 16S sequence of the same species available in GenBank (FN424117) has about 13% divergence from KT266603, a value which is clearly too high for intraspecific variation. Moreover, the former sample maps within the family Syntheciidae in our analysis. Due to this ambiguity, the sequence KT266603 was not used in the analysis shown in Fig. 20.

Our sequence of *Billardia hyalina* and that of *B. subrufa* (FN424117) are deeply embedded in the well supported Syntheciidae clade (Fig. 20). This confirms the opinion of Cornelius (1982), that *Billardia* is part of the Syntheciidae.

The four species of *Hincksella* dealt with herein do not group into a common clade, but are scattered over the whole tree. The type species of the genus (*H. sibogae*; see Totton, 1930) associates with *Zygophylax*, but the node support is not significant. An analysis with additional markers is thus needed to resolve accurately their relationships. The genus *Hincksella* is nevertheless almost certainly polyphyletic. At the species level, however, the data prove that the three species treated here are obviously distinct. In addition, it will be likely necessary in the future to split *Hincksella* again, and re-validate one of its actual synonyms, *Cyclonia* Stechow, 1921. The latter was proposed for hydroids recalling *Hincksella* possessing tubular, largely protruding hydrothecae, similar to those present in *H. neocaledonica*. The type species of *Cyclonia* is *Cyclonia gracilis* Stechow, 1921 (by monotypy), a West-Indian species, now considered as conspecific with the Indo-Pacific *Hincksella pusilla* (Ritchie, 1910) (Galea 2010: 20; Galea & Ferry 2015: 236). However, before *Cyclonia* is resurrected, the type material of its type species must be re-examined and illustrated. Ideally, also 16S sequences from new Caribbean specimens should be obtained and compared to the sequences of *Hincksella* given herein.

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**Fig. 20** (opposite page). 16S maximum likelihood phylogenetic tree of selected Leptothecata species obtained with PhyML (GTR+G+I model) and based on 622 aligned basepair positions of the mitochondrial 16S gene. Node-support values are bootstrap values of 100 pseudoreplicates (shown only if > 70%). Species treated in this study are in bold. Some family clades with sufficient bootstrap support discussed in the present study are highlighted in blue boxes. N.B.: Two species names were not used as given in GenBank (FJFJ550462 and FN424141), and the reasons are given in the Material and methods section.



*Dictyocladium* is a rare genus that has not been included in any molecular phylogeny so far. After the splitting of the Sertulariidae in several separate families by Maronna *et al.* (2016), it was unclear to which family it should belong. Currently, the WoRMS database (Schuchert, 2018) includes it in the family Sertulariidae. In the present dataset, *Dictyocladium reticulatum* shows a well-supported relationship with the Symplectoscyphidae. The type species of the genus *Dictyocladium* is *Dictyocladium dichotomum* Allman, 1888, a junior synonym of *D. reticulatum* (Kirchenpauer, 1884) (Vervoort & Watson 2003). Our sample is thus representative for the genus. *Dictyocladium* and *Symplectoscyphus* have both hydrothecal margins with three cusps at the same position (one adaxial, two latero-abaxial). It seems therefore justified to transfer the genus *Dictyocladium* from the family Sertulariidae to the Symplectoscyphidae.

The traditional scope and the relationships of the genus *Symplectoscyphus*, and its parent taxon Symplectoscyphidae, seem to be more intricate than given in Maronna *et al.* (2016). Recently, Song *et al.* (2018), using DNA data, showed that some species of *Symplectoscyphus*, characterized by gonothecae with spiny processes instead of transverse ridges, do not belong to the Symplectoscyphidae, but to the Sertularellidae, this despite their hydrothecae having three instead of four marginal cusps. For those species, the genus *Xingyurella* Song *et al.*, 2018 has been created.

We confirmed the same for an additional species usually attributable morphologically to *Symplectoscyphus*. While three *Symplectoscyphus* for which we have new sequence information (*S. commensalis*, *S. ralphae* and *S. paulensis*) unambiguously map within the Symplectoscyphidae (Fig. 20), a fourth, *Symplectoscyphus acutustriatus* sp. nov., is deeply embedded in the family Sertularellidae. As the species shows no affinities with the *Xingyurella* clade, it cannot be simply reclassified as a congener. This apparent conflict of morphological classification and molecular relationships cannot be confidently resolved for the time being, and needs a more detailed analysis. It can also not be excluded that some error in the molecular work has occurred, e.g., amplification of a nuclear copy of the 16S gene. However, morphologically speaking, a noteworthy observation is that the hydrothecae of both *Xingyurella* and *S. acutustriatus* sp. nov. are *Sertularella*-like, i.e., conical in shape, not tubular as in most species confidently assigned to *Symplectoscyphus*. This character, even taken alone, demonstrates obvious morphological affinities with the Sertularellidae, instead of the Symplectoscyphidae. It is also interesting to note that the species to which *S. acutustriatus* sp. nov. is compared in Table 9 display similar conical hydrothecae; in addition, they possess barrel-shaped, transversely-ringed gonothecae, with no distinct apical funnel bearing the aperture, the latter being occasionally surrounded by a few projections of the perisarc, also recalling hydroids of the genus *Sertularella*. Pending a corroboration of the results with additional markers, we prefer to use the combination *Symplectoscyphus acutustriatus* sp. nov.

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