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New records, taxonomic notes, descriptions and redescriptions of some uncommon thecate hydroids (Cnidaria: Hydrozoa: Leptothecata)

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Abstract: The present report provides new records, taxonomic notes, descriptions and redescriptions of several species of lesser-known thecate hydroids. Five species belong to the family Sertularellidae Maronna *et al*., 2016, one to the Syntheciidae Marktanner-Turneretscher, 1890, and one to the Aglaopheniidae Marktanner-Turneretscher, 1890. Type material of *Sertularella conica* Allman, 1877 was re-examined, and a modern redescription is provided, together with notes on its problematic synonymy that now includes *S. gayi unituba* Calder, 1991. Fertile specimens of *S. inconstans* Billard, 1919 are rediscovered, and its synonymy is broadened through the inclusion of *S. natalensis* Millard, 1968. A new species, *S. malagasiensis* sp. nov., is described from the south of Madagascar. *Sertularia exigua/laxa* Allman, 1888, a hydroid assignable to the genus *Sertularella* Gray, 1848, is found to have both primary and secondary homonyms; its taxonomy is discussed, and the replacement name *S. mutatnomen* nom. nov. is introduced for it. *Sertularella pellucida* Jäderholm, 1907 is recorded for the first time from the Mid-Atlantic Ridge, outside its previously-known main area of occurrence, in the Arctic Ocean. The sexually-dimorphic gonothecae of *Synthecium brucei* Vervoort & Watson, 2003 are described for the first time. *Halicornaria setosa* Armstrong, 1879 is rediscovered in material from the Red Sea, and the binomen is removed from the synonymy of *Taxella eximia* Allman, 1874, while transferring it to the genus *Taxella* Allman, 1874, as *T. setosa* comb. nov., on the account of its gonothecae not protected by phylactocarps.

Keywords: Systematics - taxonomy - Sertularellidae - Syntheciidae - Aglaopheniidae.

INTRODUCTION

Seven hydroids, mostly belonging to poorly-known or undescribed species, were found scattered among various collections entrusted to me for study. Type material of *Serturella conica* Allman, 1877, a hydroid originally described from off Florida, USA, was never reexamined so far to provide an up-to-date account on it, although a considerable number of records attributable to it exist in the literature, and are in need of a reevaluation. *Sertularella inconstans* Billard, 1919, with a type from the Halmahera Sea, Indonesia, is rediscovered as fertile specimens in a collection from the Gulf of Guinea. A congener that appears to belong to an undescribed species occurs in material from southern Madagascar. Fertile specimens belonging to another collection are assignable to *S. laxa* (Allman, 1888), making it possible to check the pertinence of its inclusion in the synonymy of *S. unituba* Calder, 1991 (Medel & Vervoort, 1998). *Sertularella pellucida* Jäderholm, 1907, essentially known from the Arctic Ocean (Naumov, 1969) is now found in material from the Mid-Atlantic Ridge. Fertile specimens of *Synthecium brucei* Vervoort & Watson, 2003 occur in a collection from off southern New Caledonia. Finally, several specimens of an aglaopheniid hydroid from the Red Sea fit the original account of *Halicornaria setosa* Armstrong, 1879. All these hydroids are in need of a better knowledge, and modern descriptions and/or taxonomic revisions are now provided.

MATERIAL AND METHODS

Samples were collected by hand (*CALYPSO* Cruise 1951-1952), scuba diving [*CALYPSO* Cruise 1956; *ATIMO VATAE* Cruise (Bouchet *et al*., 2010)], dredging [1869 Cruise of the Steamer *Bibb*; *BATHUS 3* (De Forges, 1993)] or using a remotely-operated vehicle [*TRANSECT* Cruise (Le Bris 2018)]. Study methods are as given in Galea (2007). The material examined is housed in

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the Museum of Comparative Zoology (Harvard, MA, USA – MCZ:IZ:number), Muséum National d'Histoire Naturelle (Paris, France – MNHN-IK-numbers), and the private collection of the author (HRG-number).

TAXONOMIC PART

Class Hydrozoa Owen, 1843
Order Leptothecata Cornelius, 1992
Family Sertularellidae Maronna *et al.*, 2016
Genus *Sertularella* Gray, 1848

Sertularella conica Allman, 1877

Fig. 1; Tables 1, 2

Sertularella conica Allman, 1877: 21, pl. 15 figs 6-7. – ? Clarke, 1879: 246. – Hartlaub, 1901a: 66, fig. 39. – Nutting, 1904 (*pro parte*): 79, pl. 15 figs 1-2. – Bedot, 1912: 352. – Bedot, 1916: 202. – Billard, 1925: 143. – Leloup, 1935: 44. – ? Fraser, 1947: 10. – Deevey, 1954 (*pro parte*): 270. – Van Gemerden-Hoogeveen, 1965: 32, fig. 7. – Vervoort, 1968 (*pro parte*): 104.

Sertularella gayi unituba Calder, 1991: 103, fig. 54 (**syn. nov.**).

Sertularella unituba. – Medel & Vervoort, 1998 (*pro parte*): 58, fig. 17. – Calder, 2013: 30, fig. 9A-B. – Calder, 2019: 90, fig. 21J.

non *Sertularella conica*. – Calkins, 1899: 359, pl. 4 fig. 22.– Hartlaub, 1901b: 354. – Fraser, 1911: 68, pl. 5 figs 2-4. – Fraser, 1912: 373, fig. 37. – Fraser, 1913a: 154. – Fraser, 1913b: 174. – Fraser, 1914: 190, pl. 29 fig. 110. – Bedot, 1918: 236. – Fraser, 1918: 357. – Stechow, 1920: 28. – Fraser, 1921: 172, fig. 85. – Stechow, 1921b: 230. – Jarvis, 1922: 341, fig. 9. – Stechow, 1925: 473, 524, fig. 33. – Fraser, 1932: 52. – Fraser, 1935: 145. – Fraser, 1936: 126. – Fraser, 1937: 151, pl. 34 fig. 179. – Leloup, 1937: 92, 104. – Fraser, 1938a: 51. – Fraser, 1938b: 134. – Fraser, 1939: 160. – Fraser, 1944: 258, pl. 54 fig. 243. – Fraser, 1947: 78, 290. – Fraser, 1948: 187, 241. – Deevey, 1954 (*pro parte*): 270. – Vervoort, 1968 (*pro parte*): 104. – Vervoort, 1972: 123, fig. 38. – Defenbaugh & Hopkins, 1973: 102, fig. 49. – Wedler, 1975: 332. – Stepanjants, 1979: 86, pl. 16 fig. 3A-B. – Blanco, 1982: 154, figs 2-5. – Calder, 1983: 11, fig. 4. – Calder, 1991: 99, fig. 52. – Blanco, 1994: 198. – Migotto, 1996: 67, fig. 12J-K. – Genzano & Zamponi, 1997: 291. – Grohmann *et al.*, 1997: 230. – Zamponi *et al.*, 1998: 9. – Calder *et al.*, 2003: 1211. – Genzano & Zamponi, 2003: 308. – Grohmann, 2006: 103. – Calder & Cairns, 2009: 393. – Castellanos Iglesias *et al.*, 2009: 99. – Genzano *et al.*, 2009: 38. – Da Silveira & Morandini, 2011: 450. – Miranda *et al.*, 2011: 343, fig. 18. – Calder, 2013: 29, fig. 8I.

non *Sertularella unituba*. – Medel & Vervoort,1998 (*pro parte*): 51, figs 14-16 (= *S. robusta* Allman, 1874a). – Vervoort, 2006: 269.

Material examined: MCZ:IZ:147890; holotype of *Sertularella conica* Allman, 1877, now coming as many small colony fragments (of generally 1, 2 or 3 hydrothecate internodes, not exceeding 9 of these) belonging to at least 3 stems (Allman's pl. 15 fig. 6 depicts a colony composed of 3 simple stems, although his description states that there were stems with "an occasional short branch"); U.S. Coast Survey, Gulf Stream Exploration 1868-1869, SW of Dry Tortugas, Florida, USA; 24.49583, -83.28333; 110 m, Steamer *Bibb*, coll. Louis F. Pourtalès; 18.01.1869.

Description: Holotype colony very fragmentary; one or two pieces comprise basal portions of stems still attached to remains of hydrorhizae; stems monosiphonic, proximal part (above origin from stolon) of varied length, with a few transverse, break lines; distal part regularly divided into internodes by faint, slightly oblique constrictions of the perisarc; internodes smooth-walled, slightly geniculate, moderately long, bearing distally a laterally-placed hydrotheca; perisarc of stem, and even that of the hydrothecae, quite thick

Table 1. Comparative measurements of *S. conica* Allman, 1877, in µm.

	Present study, type, MCZ:IZ:147890	Van Gemerden-Hoogeveen, 1965	Calder (1991), as *S. gayi unituba*	Medel & Vervoort (1998), holotype of *S. gayi unituba*
Internodes				
- length	865-1145	840-970	1042-1319	1195-1520
- diameter at node	175-255	125-250	242-317	175-215
Hydrothecae				
- free adaxial wall	335-430	420-470	336-438	430-435
- adnate adaxial wall	375-520	420-500	419-466	475-520
- abaxial wall	500-575	575-625	531-615	520-650
- maximum width	315-390	370-410	unavailable	unavailable
- diameter at aperture	240-275	250-315	228-261	260-280
Gonotheca				
- total length	absent	absent	*ca.* 1500	1520-1630
- maximum width	absent	absent	*ca.* 750	800-825

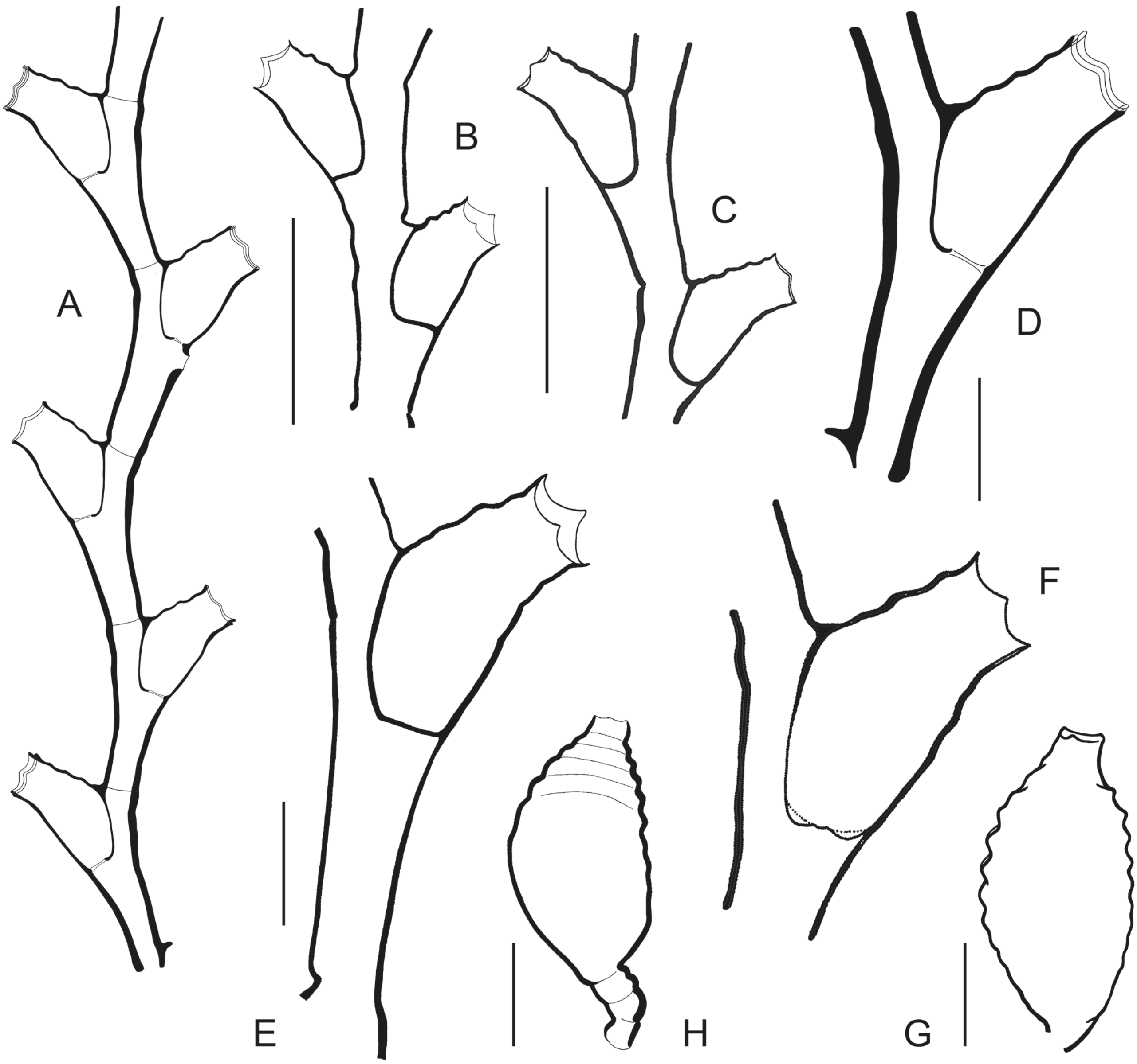

Fig. 1. *Sertularella conica* Allman, 1877. Colony portion from the holotype (A) compared to counterparts of *S. gayi unituba* Calder, 1991 [B, C – modified after Calder (2013: fig. 9A) and Calder (2019: fig. 21J), respectively]. Hydrotheca from holotype (D) compared to hydrothecae of *S. gayi unituba* from the type [E, F – modified after Calder (1991: fig. 54A) and Medel & Vervoort (1998: fig. 17C), respectively]. Two gonothecae, one from the type of *S. gayi unituba* [G – modified after Calder (1991: fig. 54B)], the other from additional material [H – modified after Calder (2013: fig. 9B)]. Scale bars: 300 µm (D-F), 500 µm (G, H), 1 mm (A-C).

and brown-colored, gradually thinning out distally and becoming more transparent; no stem fragments bearing side branches or stumps of side branches were seen. Hydrothecae biseriate, alternate along the stem, flask-shaped, adnate for slightly less than half their adaxial length to their corresponding internodes; free adaxial wall with 3 distinct undulations fading away rapidly and not reaching the opposite wall; adnate adaxial wall slightly concave to almost straight, ending at the base of hydrotheca in perisarc plug, leaving a quite large foramen for the passage of the hydranth into the theca; abaxial wall straight in its basal 2/3rd, curving away from the internode below the hydrothecal aperture; the latter composed of 4 blunted triangular cusps separated by shallow embayments; closing apparatus lost; renovations frequent, up to 4; intrathecal cusps absent; no remains of hydranths. Below some hydrothecae, there are scars that evidently correspond to the insertion of gonothecae (their foramina are comparatively smaller compared to putative insertion points of side branches); gonothecae likely shed in this material.

Table 2. Non-exhaustive list of records incorrectly or doubtfully assigned to *Sertularella conica* Allman, 1877.

Source of record(s)	**Locality**	**Correct identification**	**Remarks and/or references**
Calkins (1899: 359, pl. 4 fig. 22)	Puget Sound, WA, USA	*S. conella* Stechow, 1920	Stechow (1920: 29); Choong (2015: 392)
Hartlaub (1901b: 354)	Puget Sound, WA, USA	*S. conella* Stechow, 1920	Hartlaub makes reference to the material studied by Calkins (1899), whose synonymy is given above
Nutting (1904: 79, *pro parte*)	Sta Cruz Province, Argentina	*S. cruzensis* El Beshbeeshy, 2011	Galea *et al*. (2017: 271-272)
Fraser (1911: 68, pl. 5 figs 2-4)	San Juan Is, USA; Vancouver I., BC, Canada	*S. conella* Stechow, 1920	Stechow (1920: 29); Fraser (1937: 151). Synonymy of Fraser's (1937) material is given in Choong (2015: 392)
Fraser (1912: 373, fig. 37)	Beaufort, NC, USA	Unidentifiable	Needs reexamination
Fraser (1913a: 154)	Vancouver I., BC, Canada	*S. conella* Stechow, 1920	Possibly the same species as in Fraser (1914), see remarks under that record below
Fraser (1913b: 174)	Canso Banks, NS, Canada	Unidentifiable	No formal description, illustration
Fraser (1914: 190, pl. 29 fig. 110)	Vancouver I. region, BC, Canada	*S. conella* Stechow, 1920	Fraser's (1914) pl. 29 fig. 110B, reproduced in Fraser (1937) pl. 34 fig. 179B, likely accounts on the same hydroid. Synonymy of Fraser's (1937) material is given in Choong (2015: 392)
Bedot (1918: 236)	Puget Sound, WA, USA	*S. conella* Stechow, 1920	Bedot (1918) makes reference to the record by Calkins (1899), see above
Fraser (1918: 357)	Canso Banks, NS, Canada	Unidentifiable	No formal description, illustration. Appears to be the same record as that in Fraser (1913b)
Stechow (1920: 28)	Cape Verde Is	*S. robusta* Allman, 1874	Same species as in Stechow (1925), see below
Fraser (1921: 172, fig. 85)	Eastern Canada	Unidentifiable	Needs reexamination
Stechow (1921: 230)	Cape Verde Is	*S. robusta* Allman, 1874	Redescribed and illustrated in Stechow (1925), see below
Jarvis (1922: 341, fig. 9)	Zanzibar	Unidentifiable	Needs reexamination
Stechow (1925: 473, fig. 33)	Cape Verde Is	*S. robusta* Allman, 1874	Present study
Fraser (1932: 52)	San Juan Is, USA; Vancouver I., BC, Canada	*S. conella* Stechow, 1920	Geographical distribution. Synonymy as for Fraser's (1911, 1914) records, see above
Fraser (1935: 145)	Vancouver I., BC, Canada	*S. conella* Stechow, 1920	Likely same species as that dealt with in Fraser (1911, 1914, 1937). Synonymy of Fraser's (1937) material is given in Choong (2015: 392)
Fraser (1936: 126)	Haida Gwaii Is, BC, Canada	*S. conella* Stechow, 1920	Conspecific with Fraser's (1937) material (Fraser 1937: 152), whose synonymy is dealt with in Choong (2015: 392)
Fraser (1937: 151, pl. 34 fig. 179)	Geographical distribution	*S. conella* Stechow, 1920	Choong (2015: 392)
Leloup (1937: 92, 104)	Tampa Bay, FL, USA	Unidentifiable	No formal description, illustration
Fraser (1938a: 51)	Mexico: Revillagigedo Is (Col.), Petatlán Bay (Gro.), Tenacatita Bay (Jal.), Cedros I. (B.C.); Galápagos Is, Ecuador;	Unidentifiable	No formal description, illustration
Fraser (1938b: 134)	Chacahua Bay (Oax.), Mexico; Galápagos Is, Ecuador; Peru: Chincha Is and San Juan Bay	Unidentifiable	No formal description, illustration
Fraser (1939: 160)	Geographical distribution	Unidentifiable	No formal description, illustration

Source of record(s)	Locality	Correct identification	Remarks and/or references
Fraser (1944: 258, pl. 54 fig. 243)	Geographical distribution	*S. conella* Stechow, 1920	Illustration similar to that in Fraser (1914, pl. 29 fig. 110B; 1937, pl. 34 fig. 179). Synonymy of Fraser's (1937) material is given in Choong (2015: 392)
Fraser (1947: 78, 290)	Geographical distribution	Unidentifiable	Not illustrated, possibly based on a mix of species
Fraser (1948: 187, 241)	Mexico: Tenacatita Bay (Jal.), Chacahua Bay (Oax.); Secas Is, Panama; Rocas Octavia, Colombia; Galápagos Is, Ecuador	Unidentifiable	No formal description, illustration
Deevey (1954: 270, *pro parte*)	Geographical distribution	Mix of species	Distribution
Vervoort (1968: 104, *pro parte*)	Geographical distribution	Mix of species	Summarized records
Vervoort (1972: 123, fig. 38)	Argentina; Falkland Is	*S. cruzensis* El Beshbeeshy, 2011	Galea *et al*. (2017: 271)
Defenbaugh & Hopkins (1973: 102, fig. 49)	Galveston Bay area, TX, USA	*S. conella* Stechow, 1920	Illustration reproduced from Fraser (1944) depicting Stechow's (1920) species
Wedler (1975: 332)	Santa Marta, Colombia	Unidentifiable	No formal description, illustration
Stepanjants (1979: 86, pl. 16 fig. 3A-B)	Argentinean coast; South Georgia	Unidentifiable	Needs reexamination
Blanco (1982: 154, figs 2-5)	Argentina: Off Chubut and Tierra del Fuego, Antártida e Islas des Atlántico Sur	*S. blanconae* El Beshbeeshy, 2011	Galea *et al*. (2017: 264)
Calder (1983: 11, fig. 4)	South Carolina, USA	*S. calderi* Galea, 2013	Galea (2013: 21)
Calder (1991: 99, fig. 52)	Bermuda	*S. calderi* Galea, 2013	Present study
Blanco (1994: 198)	Geographical distribution	*S. blanconae* El Beshbeeshy, 2011	Galea *et al*. (2017: 264)
Migotto (1996: 67, fig. 12J-K)	São Sebastião Channel, SP, Brazil	*S. peculiaris* (Leloup, 1935)	Galea (2008: 32, 2013: 22)
Genzano & Zamponi (1997: 291)	Argentina	Unidentifiable	No formal description, illustration
Grohmann *et al*. (1997: 230)	Vitória, ES, Brazil	Unidentifiable	No formal description, illustration
Zamponi *et al*. (1998: 9)	Mar del Plata, Argentina	Unidentifiable	No formal description, illustration
Calder *et al*. (2003: 1211)	Galápagos Is, Ecuador	Unidentifiable	List of records
Genzano & Zamponi (2003: 308)	Mar del Plata, Argentina	Unidentifiable	Galea *et al*. (2017: 318)
Grohmann (2006: 103)	Vitória, ES, Brazil	Unidentifiable	No formal description, illustration
Calder & Cairns (2009: 393)	Gulf of Mexico, extended distribution	Unidentifiable	List of records
Castellanos Iglesias *et al*. (2009: 99)	Geographical distributions	Unidentifiable	No formal description, illustration
Genzano *et al*. (2009: 38)	Mar del Plata, Argentina	Unidentifiable	No formal description, illustration
Da Silveira & Morandini (2011: 450)	São Paulo State, Brazil	? *S. peculiaris* (Leloup, 1935)	Possibly based on Migotto's (1996) account, see above
Miranda *et al*. (2011: 343, fig. 18)	Bombinhas, SC, Brazil	*S. peculiaris* (Leloup, 1935)	Material conspecific with that of Migotto (1996); see under that record

Remarks: Based on the accounts by Calder (1991: 103, fig. 54) and Medel & Vervoort (1998: 58, fig. 17), there is little doubt that *S. gayi unituba* Calder, 1991 belongs to the present species (compare Fig. 1A and 1D to Fig. 1B, C and 1E, F, respectively; see also Table 1), a finding that confirms my earlier assumptions regarding its identity (Galea, 2008: 34, 2013: 24). The holotype of *S. conica* originally comprised ca. 2.5 cm high stems, either "simple or with an occasional short branch, not fascicled" (Allman, 1877: 21). In *S. gayi unituba*, the stems reached as much as 3.7 cm in height, and were "monosiphonic […] unbranched or with [a] branch arising just below a hydrotheca" (Calder, 1991: 103). Medel & Vervoort's (1998: 58) assumption that the holotype of Calder's subspecies was "probably a branch or a top part" of a larger, fascicled colony is purely speculative; indeed, the paratypes were undamaged colonies of comparable size possessing a "creeping hydrorhiza" (Calder, 1991: 103).

The gonothecae of this species (Fig. 1G, H) are "elongate-oval in lateral view, nearly round in cross section, with about 10 to 12 transverse ridges distinct distally, becoming almost imperceptible proximally", apically "with about three low spines" (Calder, 1991: 103).

There has been much confusion over the taxonomy of *S. conica* due to its perfunctory original description and rather sketchy illustrations. Consequently, many records attributable to it are actually assignable to other nominal species, while some others are unreliable due to the absence of formal descriptions and/or illustrations (see synonymy above and Table 2). In brief, many records from the Pacific coast of Canada and USA (e.g. Fraser, 1911, 1914, 1937) are likely attributable to *S. conella* Stechow, 1920 (Choong, 2015: 392). However, it is unclear whether the hydroid occurring on the Atlantic coast of North America is the same (e.g. Calkins, 1899; Fraser, 1912, 1921). Additional records from Mexico (Fraser, 1938a, b, 1948), Panama (Fraser, 1948), Colombia (Fraser, 1948), Peru (Fraser, 1938b) and the Galapagos (Fraser, 1938a, b, 1948) are also highly questionable, due to the absence of formal descriptions and illustrations. Moreover, the eastern Atlantic records, notably from the Cape Verde region (e.g. Stechow, 1920, 1921b, 1925) are better assignable to *S. robusta* Allman, 1874a.

Gil *et al*. (2020: 431) have introduced the specific name *porcupine* for *S. gayi* var. *robusta* Allman, 1874a, arguing that it "is an invalid junior homonym of *Sertularella robusta* Coughtrey, 1879 (*sic*)". Their interpretation is evidently unfounded, as Coughtrey's species was created in 1876, and cannot be the senior homonym of a hydroid described in 1874. In this sense, Calder & Faucci (2021: 25) highlighted that Coughtrey's nominal species "is a permanently invalid junior homonym of *S. gayi* var. *robusta* Allman, 1874a (ICZN 1999, Art. 57.2)", and introduced into use the replacement binomen *S. quasiplana* Trebilcock, 1928 for the former. Moreover, it should be noted that Gil *et al*. (2020: 430), Calder & Vervoort (1998: 39) and Medel & Vervoort (1998: 45), following the observations made earlier by Ramil & Vervoort (1992: 223), did not dissociate the so-called varieties *robusta* Allman, 1874a and *elongata* Billard, 1906a of *S. gayi*. For the time being, only the former was regarded as (specifically) distinct, and is easily recognizable in the illustrations by Billard (1906b: fig. 9B), Ramil & Vervoort (1992: fig. 62A), Calder & Vervoort (1998: fig. 19A), Medel & Vervoort (1998: fig. 12B) and Gil *et al*. (2020: fig. 3E). On the other hand, the "variety" *elongata* has comparatively longer and slenderer internodes, as well as smaller, more tubular and distinctly-ringed hydrothecae, as depicted by Billard (1906b: fig. 9C), Ramil & Vervoort (1992: fig. 62C), Calder & Vervoort (1998: fig. 19B) and Medel & Vervoort (1998: fig. 12A). Consequently, it would be germane to have the specific identity of the latter clarified through a more comprehensive study.

Distribution: Dry Tortugas, Florida (Allman, 1877; ? Clarke, 1879; Leloup, 1935; Van Gemerden-Hoogeveen, 1965); Atlantic coast of Florida (Calder, 2013, as *S. unituba*); SW Florida Shelf (Calder, 2019, as *S. unituba*); Gulf of Mexico (Nutting, 1904, *pro parte*); Castle Roads, Bermuda (Calder, 1991, as *S. gayi unituba*); ? Aruba Island (Fraser, 1947). The bathymetric range is from 8 m (Leloup, 1935) to 110 m (Allman, 1877).

Sertularella inconstans Billard, 1919

Fig. 2; Table 3

Sertularella inconstans Billard, 1919: 19, fig. 1C. – Billard, 1925: 142, fig. 12. – Van Soest, 1976: 83. – Vervoort & Vasseur, 1977: 48, fig. 18D, E.

Sertularella natalensis Millard, 1968: 271, fig. 4E-G (**syn. nov.**). – Millard, 1975: 297, fig. 96D-F. – Millard, 1978: 198. – Millard, 1979: 144.

non *Sertularella inconstans* – Vannucci Mendes, 1946: 569, pl. 4 fig. 38 [= *S. peculiaris* (Leloup, 1935)]. – Vannucci, 1949: 243, pl. 2 figs 35-36 [= *S. peculiaris* (Leloup, 1935)]. – Vannucci, 1950: 88. – Vannucci, 1951: 107, 110, 111, 113, 115, 117. – Wedler, 1975: 333, 334, 340, 353. – Calder & Hester, 1978: 91 (= *S. calderi* Galea, 2013).

non *Sertularella natalensis* – Mergner & Wedler, 1977: 20, pl. 3 fig. 21. – Park, 1993: 271.

Material examined: MNHN-IK-2019-2146; a quite profuse, fully fertile colony composed of many stems, up to 3 cm high, detached from their original substrate; *Calypso* Cruise to the Gulf of Guinea, Stn. 59 (bottom dredge), Gabon, off Libreville; -0.63889°, 8.80556°; 35 m; 16.06.1956.

Description: Colony comprising many up to 3 cm high, erect stems arising from creeping hydrorhiza; stems flaccid, unable to support themselves when out of liquid; monosiphonic, composed of a quite long, athecate, proximal part with an occasional slight bulge immediately above its origin from stolon (from which it is separated by a constriction), and a much longer, distal part, regularly divided into internodes by oblique constrictions of the perisarc slanting alternately in opposite directions; internodes relatively short, smooth-walled, slightly geniculate, gradually widening towards their distal end where they accommodate a laterally-placed hydrotheca; branching of the stem

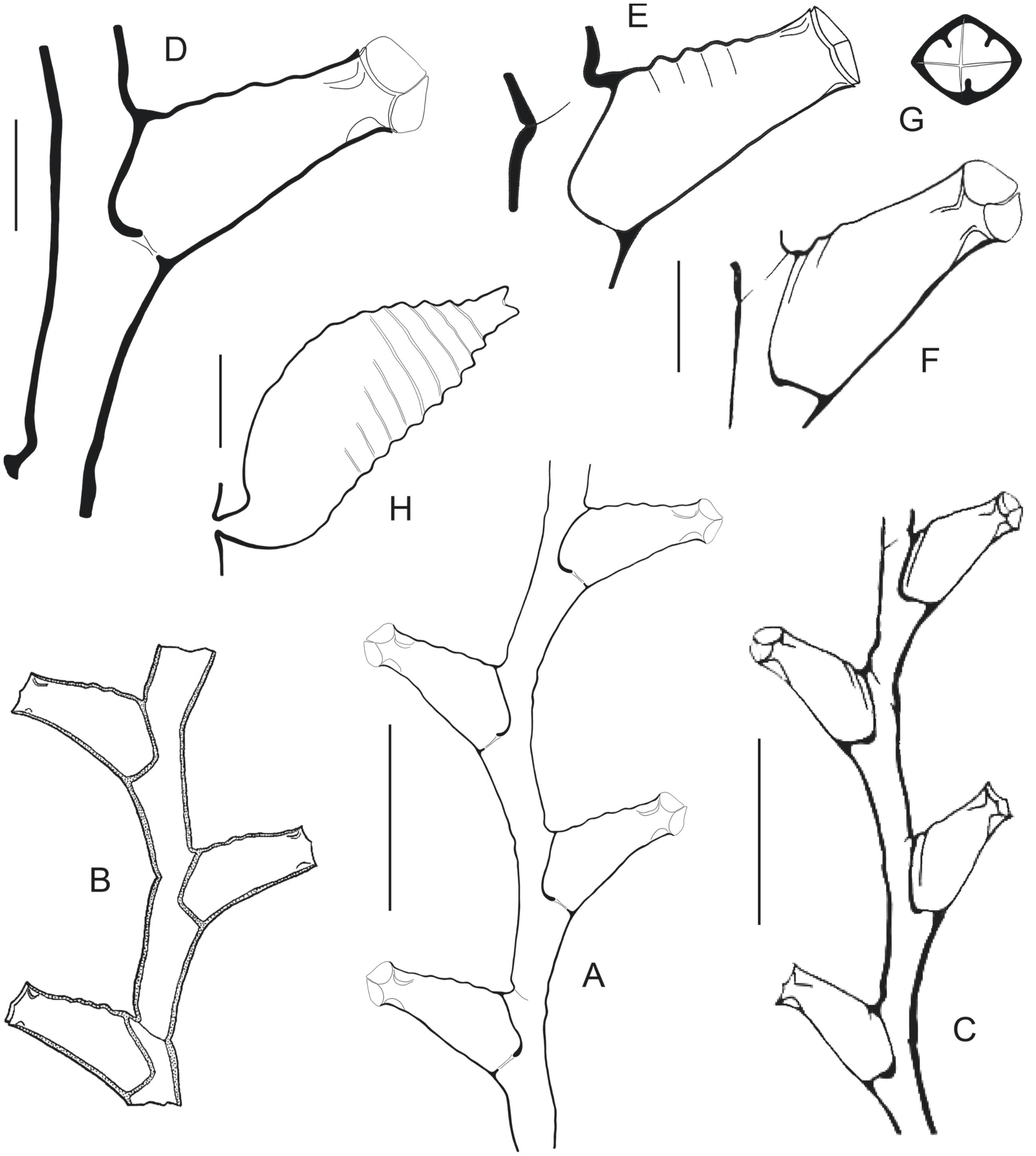

Fig. 2. *Sertularella inconstans* Billard, 1919. Colony portion (A) compared to counterparts from the type material [B – modified after Billard (1925: fig. 12G)] and the type of *S. natalensis* Millard, 1968 (C – modified after her fig. 4G). Hydrotheca (D) compared to hydrothecae from the type material [E – modified after Vervoort & Vasseur (1977: fig. 18E)] and the type of *S. natalensis* [F – modified after Millard (1958: fig. 4E)]. Hydrothecal aperture in frontal view (G). Gonotheca (H). Scale bars: 300 µm (D-G), 500 µm (H), 1 mm (A-C).

scant, irregular, with up to 3 side branches given off laterally and in the same plane with it; up to 2nd order branches observed; branches usually long, sometimes longer than the main stem itself; structure identical to that of the caulus, with the exception of the proximal most internode that is usually twice or more of the length of its subsequent counterparts; occasionally, stems with terminal stolonization. Hydrothecae flask-shaped, 1/3 adnate to their corresponding internodes, slightly tumid in their proximal halves, conical distally, slightly constricted below the aperture; free adaxial wall with 4 distinct, transverse, rounded ridges prolonged abaxially as mere undulations; aperture quadrangular, set transversely to the long axis of the theca, margin with 4 low, triangular cusps separated by 4 broad, shallow embayments; 1-2 occasional renovations; closing apparatus composed of 4 triangular valves with concentric growing striae, meeting centrally to form a low, pyramidal roof; 3 prominent, submarginal, intrathecal, lamellar projection of the perisarc: 2 latero-adaxial and 1 abaxial. Gonothecae arising singly from both the stem and branches, below a given hydrotheca, either frontally or laterally; broadly ovoid, proximal half flattened to concave through (their occasionally strong) compression against the internodes behind, distal half diverging from the stem/branch; transversely-ridged almost throughout, with 9-11 strong, angular folds of the walls; proximal end tapering abruptly and forming an indistinct pedicel, distal end strongly constricted, forming a short neck region bearing apically generally 2, rarely 3 or 4, conical projections flanking a central, small, circular aperture; lumen of some thecae containing what appears to be a structurally homogenous, fusiform, tissular mass, possibly a male gonophore, encircling a simple, slender blastostyle. Perisarc of the colony straw-colored.

Remarks: The present material fits the description and illustrations of *S. inconstans* given by Billard (1925) (compare Fig. 2A and 2B) and Vervoort & Vasseur (1977) (compare Fig. 2D and 2E), except for the monosiphonic condition of its stems.

There is little doubt that *S. natalensis* Millard, 1958 is a junior synonym of the present species (compare Fig. 2A to 2C, and 2D to 2F). The number of submarginal, intrahydrothecal, lamellar projections of perisarc is variable, and ranges from 3 (Millard, 1975; present study) to 5 (Millard, 1968), similarly to the situation met with in other species, in which 5 cusps may occur in some hydrothecae of a colony whose other thecae already possess 3 of these [e.g. *Sertularella* sp. in Galea (2010a: fig. 4M); *S. fraseri* Galea, 2010b in Galea (2010b: fig. 4D); *Sertularella* sp. in Galea & Schories (2012: fig. 5P); *S.* aff. *sinensis* Jäderholm, 1896 in Galea (2016: fig. 8R)].

The southern African records (Millard, 1975) mark the transition between the type locality, in the Halmahera Sea, and the present record from the Gulf of Guinea. Those by Vannucci Mendes (1946) and Vannucci (1949, 1950), in contrast, are better assignable to the tropical western Atlantic *S. peculiaris* (Leloup, 1935). They are conspecific with Migotto's (1996: 67, as *S. conica*) material that was reassigned by Galea (2008: 32, 2013: 22) to the synonymy of Leloup's hydroid.

Of note, Leloup (1935: 33, figs 15-17) incorrectly ascribed to *Thyroscyphus intermedius* Congdon, 1907 [now known as *Symmetroscyphus intermedius* (Congdon, 1907) (Calder, 1986)] a new "form", *peculiaris*, characterized by the presence of 5 lamellar, submarginal,

Table 3. Measurements of *Sertularella* spp., in µm.

	S. inconstans **Billard, 1919**	***S. malagasiensis*** **sp. nov.**	***S. mutatnomen*** **nom. nov.**	***S. pellucida*** **Jäderholm, 1907**
Internodes				
- length	700-990	645-1180	765-910	1685-2245
- diameter at node	170-205	265-480	165-230	150-170
Hydrothecae				
- abaxial wall	685-720	610-640	500-515	1040-1145
- free adaxial wall	585-630	390-545	315-335	975-1025
- adnate adaxial wall	325-340	410-470	360-405	315-335
- base	180-200	190-250	140-155	205-230
- maximum width	380-390	335-435	325-335	475-490
- aperture diameter	240-250	260-280	210-215	390-415
Gonotheca				
- total length	1935-2080	2465-2795	1645-1795	*ca.* 1735
- maximum width	740-790	985-1165	685-740	*ca.* 915

intrahydrothecal cusps. Later (Leloup, 1974: 34, footnote 1), he acknowledged his error, and assigned a new binomen, *Sertularella peculiaris*, to that hydroid. In doing so, he created an unwanted imbroglio: indeed, if f. *peculiaris* Leloup, 1935 is raised to species, and the hydroid is transferred to *Sertularella*, as *S. peculiaris* (Leloup, 1935), then it becomes a senior secondary homonym of *S. peculiaris* Leloup, 1974. I myself treated the same species two different ways (Galea, 2008: 31, Galea, 2013: 22, respectively), but the correct authority and date are Leloup (1935).

Distribution: Halmahera Sea, Indonesia (Billard, 1925); South Africa (Millard, 1968, 1975, both as *S. natalensis*); Mozambique (Millard, 1975, as *S. natalensis*); Gulf of Guinea (present study). Occurs between 1 m (Millard, 1975, as *S. natalensis*) and 1089 m (Billard, 1925).

Sertularella malagasiensis sp. nov.

Figs 3A-D, 4A, 5A, C, D, F; Table 3

Holotype: MNHN-IK-2019-2; a profuse, fully fertile colony with stems to 7.5 cm high, and likely male gonothecae; *ATIMO VATAE* Cruise, Stn. TA54, Madagascar, Mananivo Bay, Choumare islet -24.865°, 47.151667°; 15-25 m; 13.06.2010.

Comparison material: HRG-1447; colony of *Sertularella polyzonias* (Linnaeus, 1758) with stems up to 8 cm high, bearing female gonothecae; France, Brittany, Pléneuf-Val-André, Verdelet islet; 48.60218°, -2.55716°; low tide; 11.09.2018.

Etymology: Named after its presently-known area of occurrence, Madagascar.

Description: Colony profuse, composed of numerous erect, stiff stems, to 7.5 cm high, arising independently from a branched, tortuous network of stolonal fibers anchoring it in sediment. Stems exclusively monosiphonic, with thick, straw-colored perisarc, composed of a proximal, ahydrothecate part of varied length (3-18 mm) and a much longer, distal part divided regularly into internodes by means of faint constrictions of the perisarc slanting in alternate directions; branching of the stem usually profuse and irregular; sometimes most branches are given off on the same side of the stem, sometimes there is almost the same number of branches per side, although not establishing a true, regularly pinnate pattern; when the branches are too long or too ramified, and are caused to cross distally, they simply overlap, but do not adopt another orientation than that of the general plane of the colony; branches are given off nearly perpendicular to the stem at their origin, then rapidly curve upwards at a superior angle of 30-50° with the stem; 1 to 11 hydrothecae between successive side branches, regardless of their position on one side or the other of the stem; primary branches of varied length, reaching as much as 4 cm long, occasionally branching again,

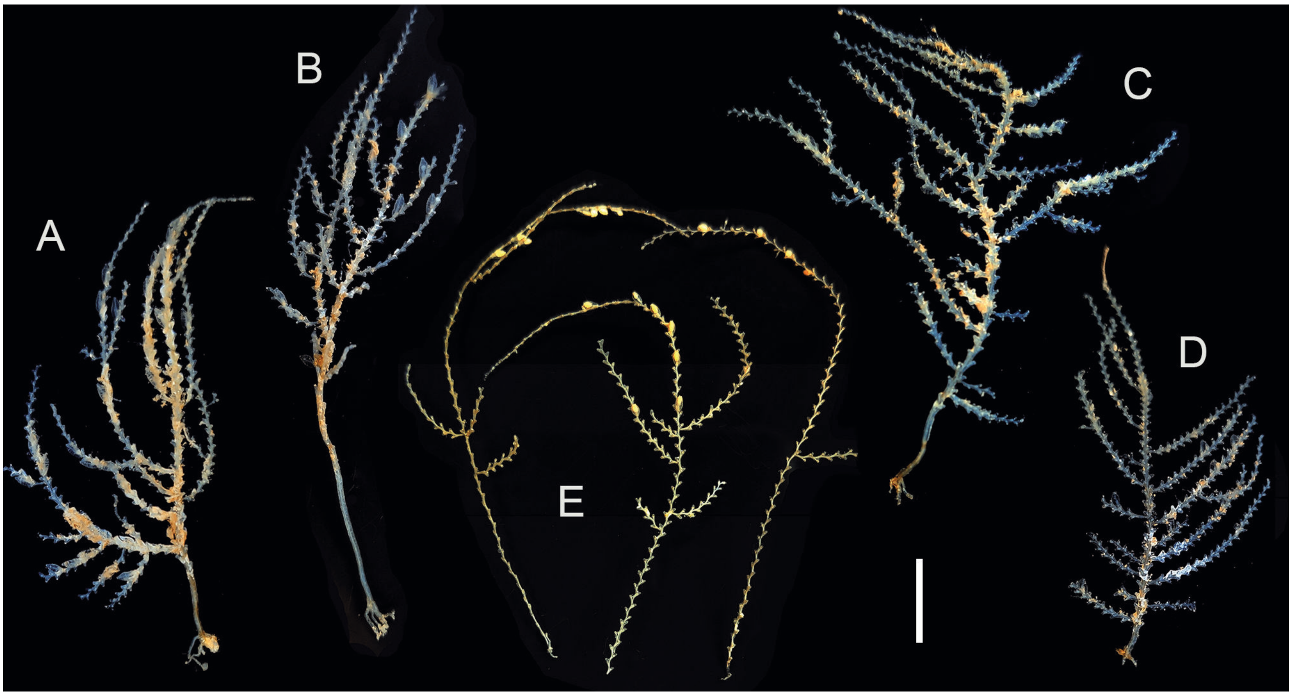

Fig. 3. *Sertularella malagasiensis* sp. nov. Four colonies (A-D) compared to three colonies of *S. polyzonias* (Linnaeus, 1958) (E), to show differences. Scale bar: 1 cm (A-E).

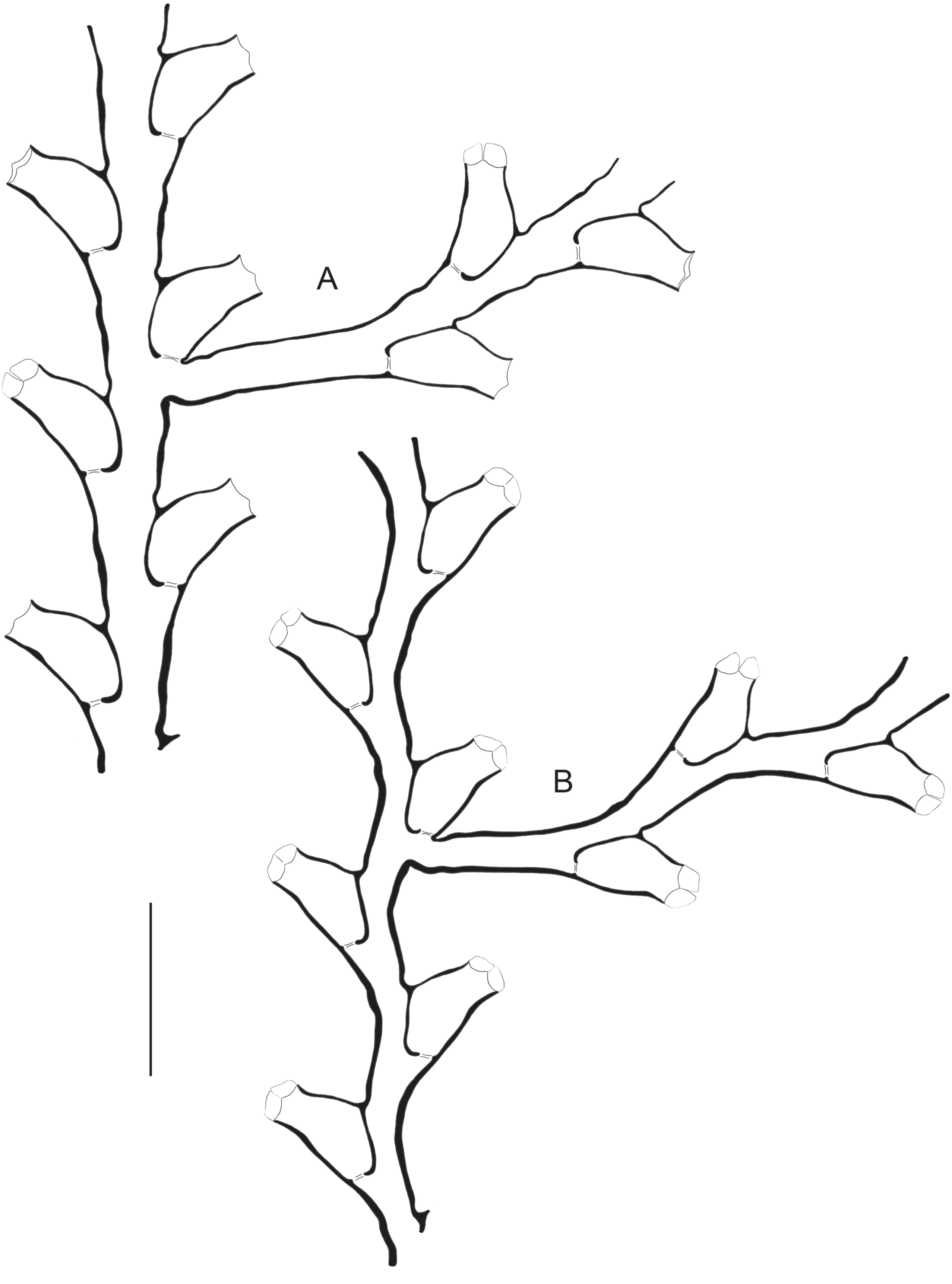

Fig. 4. *Sertularella malagasiensis* sp. nov. Portion of colony (A) compared to counterpart from *S. polyzonias* (Linnaeus, 1958) (B), to show differences. Scale bar: 1 cm (A, B).

giving rise to comparatively shorter, 2nd order branches. Internodes of stem and branches alike, collinear, very short, barely accommodating a hydrotheca; only the proximal most internode of the branches is slightly longer than its subsequent counterparts. Hydrothecae flask-shaped, adnate for less than half their adaxial length to the corresponding internode; perisarc quite thick; abaxial wall broadly convex, with a broad, though inconspicuous bulge in middle part; free adaxial wall sigmoid, the hydrotheca becoming narrower below the aperture; adnate adaxial wall concave, ending basally in a perisarc plug delimiting the hydrothecal base; hydrothecal aperture transverse, four-cusped, cusps blunted-triangular, separated by shallow embayments; occasional renovations; opercular apparatus composed of 4 triangular flaps meeting centrally. Gonothecae borne on both the stem and its branches, always on the same side of the colony; they are given off from slightly below the hydrothecal bases, on side of the internode opposite to that of the hydrotheca; gonothecae dorsally flattened for 1/3-2/3 of their length through compression against the internodes behind; broadly ovoid in frontal view, spanning the length of about 4 hydrothecate internodes; transversely ringed in upper part, where 3-5 rings are always well developed, most basal, additional ones fading away gradually; aperture apical, small, circular, delimited by 2 horns; occasionally, a 3rd cusp could be observed, in some cases one of the cusps of the pair being bifid; gonothecae clearly at maturity, either spent or containing a compact, elongated mass of cells surrounding a central blastostyle, suggesting that their sex is likely male.

Remarks: The microscopic features of the trophosome, notably its hydrothecae, recall those of *S. polyzonias*

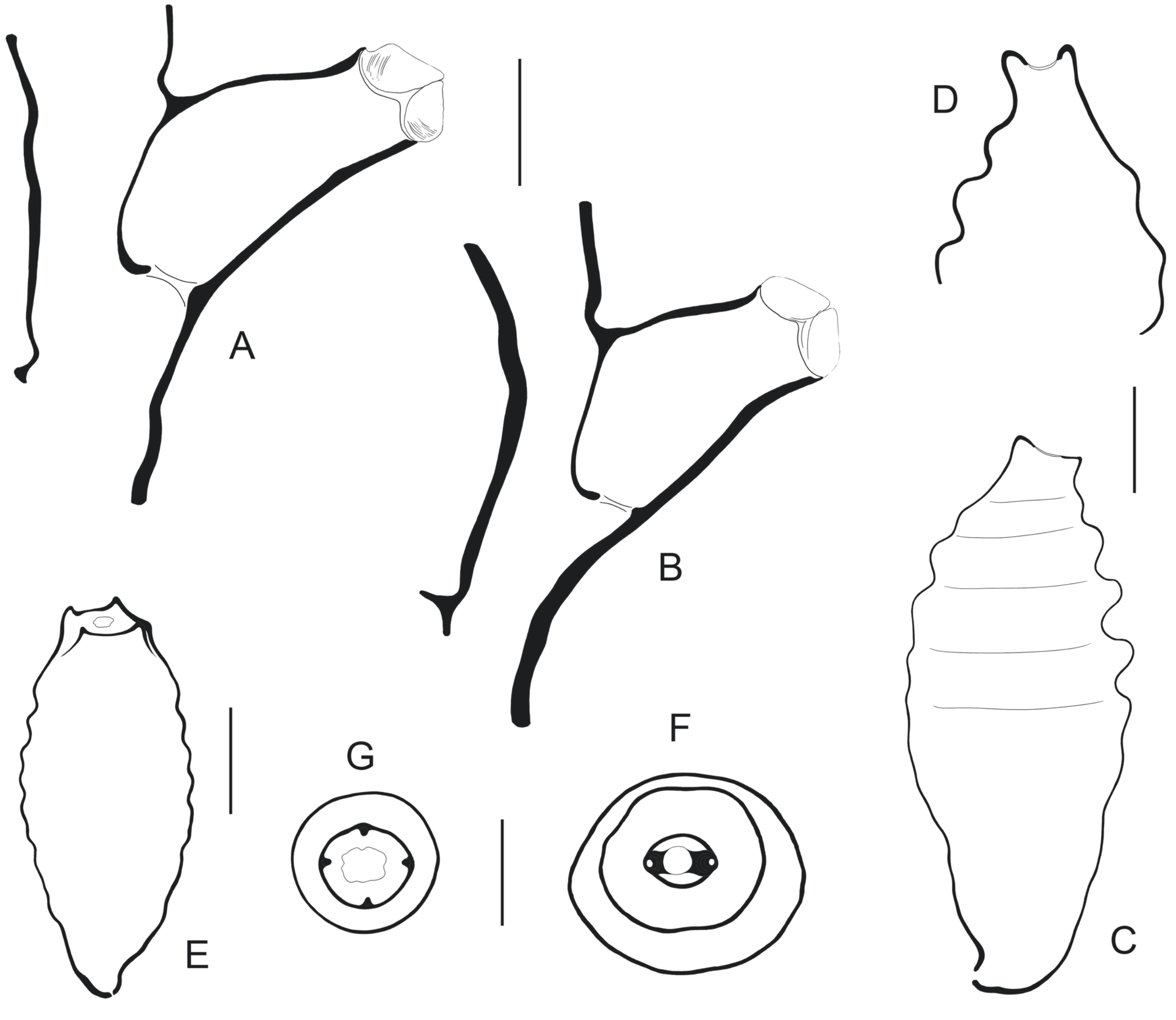

Fig. 5. *Sertularella malagasiensis* sp. nov. (concluded). Hydrotheca (A) compared to counterpart from *S. polyzonias* (Linnaeus, 1958) (B). Whole gonotheca (C) and distal part of a second gonotheca (D), compared to counterpart from *S. polyzonias* (E). Gonothecal aperture in apical view (F) compared to the same from *S. polyzonias* (G). Scale bars: 300 µm (A, B), 500 µm (C-G).

(Linnaeus, 1758) (compare Fig. 5A to 5B). A comparison with specimens of that species from the French coast of the Channel [Ellis' (1755: 5, pl. I figs a, A) "Great tooth coralline" (N° 3), on which Linnaeus (1758: 813) based his *S. polyzonias*, originates from Queenborough, Sheppey I., Kent, UK (Ellis, 1755: 6), at the junction between the Channel and the North Sea] reveal that the Malagasy hydroid is a more robust, much densely-branched congener (compare Figs 3A-D to 3E). In addition, its gonothecae are comparatively larger, and are provided apically with only a pair of horns (compare Fig. 5C to 5E, and 5D, F to 5G); only occasionally, a 3rd cusp could be noted (in 16% of the gonothecae examined, n=88), but never 4, as those met with in *S. polyzonias*. Although the microscopical morphological traits of these hydroids are reduced in number and extent (compare Fig. 4A and 4B), their general macroscopic appearance is very distinctive, indicating that the Malagasy hydroid belongs to a species that is different from *S. polyzonias*.

Distribution: Only known from southern Madagascar (present study).

Sertularella mutatnomen nom. nov.

Fig. 6; Table 3

Sertularia exigua Allman, 1888: 55, pl. 26 figs 2, 2a. – Bedot, 1916: 204. – Medel & Vervoort, 1998: 60, 62, figs 18, 19. – Calder, 2013: 30. – Calder, 2019: 90.

Sertularia laxa Allman, 1888: legend of pl. 26 (replacement name for *S. exigua*). – Pictet & Bedot, 1900: 22. – Bedot, 1916: 204. – Medel & Vervoort, 1998: 60, 62, figs 18-19. – Calder, 2013: 30. – Calder, 2019: 90.

Sertularella laxa – Hartlaub, 1901a: 53, 59, 85, pl. 5 fig. 20. – Billard, 1908: 1357. – Billard, 1909a: 1065. – Billard, 1909b: 313. – Billard, 1910: 12. – Billard, 1922: 111, fig. 5 (redescription). – Stechow, 1925: 524.

Sertularella unituba – Medel & Vervoort, 1998 (*pro parte*): 58, fig. 17 (non *S. gayi unituba* Calder, 1991 = *S. unituba* Calder, 1991 = *S. conica* Allman, 1877).

non *Sertularia exigua* Allman, 1877: 24, pl. 16 figs 7, 8 [= *Dynamena disticha* (Bosc, 1802)]. – Billard, 1906b: 186 [= *Dynamena disticha* (Bosc, 1802)].

non *Sertularella exigua* Thompson, 1879: 101, pl. 16 fig. 3.

non *Sertularia laxa* Lamarck, 1816: 116 [= *Thyroscyphus fruticosus* (Esper, 1797)].

Material examined: MNHN-IK-2019-2157; three colony fragments, 0.7-1.2 cm high, the two largest bearing 2 and 3 gonothecae; hydrothecae smooth-walled; unknown origin; J. Picard's sample #190. – MNHN-IK-2019-2158; five colonies or colonies fragments, 0.8-2.4 cm high, all sterile; one stem was attached to a slender, dichotomously-branched bryozoan; hydrothecae from smooth-walled to distinctly ridged; unknown origin; J. Picard's sample #105.

Description: Stems to 2.4 cm high arising from tortuous, creeping, branching hydrorhiza; monosiphonic, proximal part short (though of varied length among different stems), athecate, with perisarc either smooth or forming a few faint annuli above the origin from stolon; distal and much longer part of caulus regularly divided into internodes; the latter short, slightly geniculate, smooth-walled, gradually widening distally (and there accommodating a hydrotheca), separated by oblique constrictions of the perisarc slanting in alternate directions, more markedly-incised above a hydrotheca. Branching irregular, scant, coplanar; side branches given off laterally from below a given stem hydrotheca, and unbranched subsequently; length varied, comprising a few to many internodes; an unusual side branch arises from within a damaged hydrotheca; side branches morphologically identical to the stem, except the proximal most internode that is comparatively longer than the subsequent ones. Hydrothecae flask-shaped, half adnate to their corresponding internodes, swollen in proximal half, diverging from the internode (at about 50°) in distal half, and there distinctly constricted and adopting a slightly conical appearance; abaxial wall broadly sigmoid, perisarc smooth; free adaxial wall slightly convex, with smooth to wrinkled to distinctly transversely ridged perisarc (2-3 ridges fading out abaxially); adnate adaxial wall spoon-shaped, ending basally in a slightly swollen perisarc plug; three conspicuous, lamellar, internal, submarginal cusps (2 latero-adaxial, one abaxial) variably present among the hydrothecae; margin, occasionally renovated once or twice, with 4 pointed triangular cusps separated by moderately-deep embayments; closing apparatus composed of 4 triangular flaps meeting apically to form a pyramidal roof; hydranths badly-preserved, tentacle number could not be counted. Gonothecae arising from both the stems and branches, a short distance below the base of a given hydrotheca, perpendicular to the plane of the colony; broadly ovoid in frontal view, dorsally-flattened in lateral aspect, as they are half compressed against the stem/branch behind; proximally tapering abruptly, and devoid of a proper pedicel, summit rather flattened, and there bearing a distinct, slender neck region ending in four pointed cusps surrounding a circular aperture; wall with 6-7 faint transverse annuli; all gonothecae spent, their sex could not be ascertained. Perisarc of the colony straw-colored.

Remarks: Originally named by Allman (1888) *Sertularia exigua*, the specific epithet was replaced by *laxa* in the legend of plate 26, with the laconic explanation "It has been found necessary to change the name since the Plate was printed off". Indeed, the original basionym is a primary homonym of *Sertularia exigua* Allman, 1877 [now recognized as a junior synonym of *Dynamena disticha* (Bosc, 1802), see Medel & Vervoort (1998: 26)] and a secondary homonym of *Sertularella exigua* Thompson, 1879.

Unfortunately, the replacement name *Sertularia laxa* introduced by Allman is also threatened by *Sertularia laxa* Lamarck, 1816 [now recognized as a junior synonym of *Thyroscyphus fruticosus* (Esper, 1797) (Bedot, 1901: 471)]. According to Art. 57.2 of the ICZN (1999 edition), the junior primary homonyms are permanently invalid. So are the junior secondary homonyms under the rule of Art. 57.3. Consequently, another replacement name, *Sertularella mutatnomen* **nom. nov.**, is proposed for this species, while satirizing its nomenclatural history.

The taxonomic history of this species is marked by multiple trial and error. Billard (1908: 1357), upon the examination of the type, noted the presence of

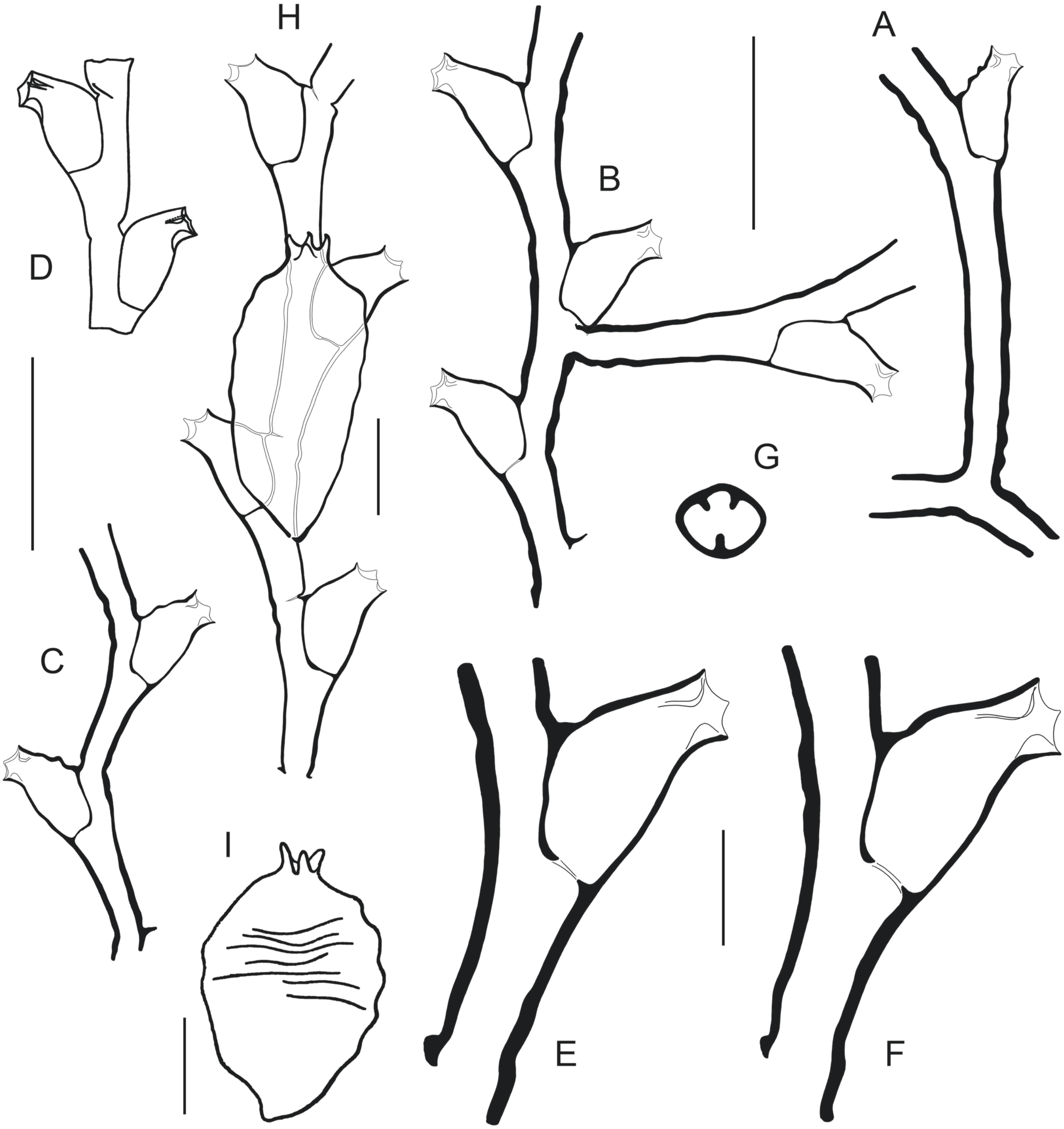

Fig. 6. *Sertularella mutatnomen* nom. nov. Portions of colony (A-C) compared to the same from the type material [D – modified after Billard (1922: fig. 5A)]. Two hydrothecae (E, F), and apical view of a theca (G). Portion of colony with gonotheca (H), and gonotheca from type material [I – modified after Billard (1922: fig. 5B)]. Scale bars: 300 µm (E-G), 500 µm (H, I), 1 mm (A-D).

submarginal, intrathecal cusps, similar to those met with in *S. mediterranea* Hartlaub, 1901a, and he concluded that the latter should be assigned to the synonymy of the former. Later on (Billard, 1910: 12), after a reinspection of the type, he concluded that it is specifically indistinguishable from *S. gaudichaudi* (Lamouroux, 1824), an opinion followed by Bedot (1916: 204, 1918: 238) [Incidentally, Bedot (1916) incorrectly interpreted the substitution of the specific epithet, and considered *exigua* as the replacement name of *laxa*. Vervoort (2006: 269) did the same]. However, a further re-examination eventually convinced Billard (1922: 111) about its validity, while also holding *S. mediterranea* distinct (Billard, 1922: 107). Finally, type material of *S. laxa* was re-examined by Medel & Vervoort (1998: 60, figs 18, 19) [apparently unaware of the account by Billard (1922)], who found it "quite dirty and […] covered by many sedimentary Foraminifera, that obscure the exact structure of the hydrothecae", thus misleading them and prompting them to assign it to the synonymy of *S. unituba* Calder, 1991. As demonstrated above, the latter is now regarded as a junior synonym of *S. conica* Allman, 1877. Conversely, *S. mutatnomen* nom. nov. is, in my opinion, a morphologically-distinctive hydroid, and a well-defined species.

Unlike the present specimens, the syntype series originally consisted of comparatively larger, "much and irregularly branched" colonies (Allman, 1888: 55; Medel & Vervoort, 1998: 61). According to pl. 26 in Allman (1888), there were up to 4th order side branches, yet the species displaying a "very slender" appearance.

Distribution: Azores region (Allman, 1888; Pictet & Bedot, 1900; Hartlaub, 1901a). The origin of the present material is unknown. Depth range: 120 m (Pictet & Bedot, 1900) to 853 m (Hartlaub, 1901a).

Sertularella pellucida Jäderholm, 1907

Fig. 7; Table 3

Sertularella pellucida Jäderholm, 1907: 374. – Jäderholm, 1909: 99, pl. 11 figs 8-11. – Kudelin, 1914a: 118. – Kudelin, 1914b: 505, fig. 173. – Gorbunov, 1946: 37. – Naumov, 1960: 336, fig. 225. – Naumov, 1969: 363, fig. 225. – Antsulevich, 1987: 68. – Stepanjants, 1994: 124. – Antsulevich, 2015: 485, fig. 239.

Material examined: MNHN-IK-2015-2992; a colony composed of a dozen stems to 2.5 cm high, one bearing an empty gonotheca; *TRANSECT* Cruise, Stn. PL686 (collected with a ROV), Mid Atlantic Ridge; 36.229583°, -33.904859°; 2358 m; 13.07.2018.

Description: Colony composed of many erect, to 2.5 cm high, stems arising from branched, tortuous stolon creeping over mineral particles; monosiphonic, composed of a proximal, smooth-walled, athecate portion of varied length (reaching as much as 7 mm long) and a much longer, distal portion comprising a regular succession of up to 11 thecate internodes separated by oblique constrictions of the perisarc; the latter strongly geniculate, exceedingly long and slender, though widening gradually and imperceptibly distally to accommodate laterally a hydrotheca; perisarc smooth; apical stolonization occurs in a stem. Branching infrequent, irregular, only met with in a couple of stems, each of which giving rise to a side branch bearing no more than 6 hydrothecate internodes; branches arising from below the bases of stem hydrothecae, slightly in front/back of the colony; structure similar to that of the stem, though first internode slightly longer than subsequent ones. Hydrothecae adnate for ca. 1/4 of their length to the corresponding internodes; long, slightly conical, longitudinal axis straight or imperceptibly bent away from the stem, ab- and adaxial walls slightly converging apically, walls thin, with 6-8 transverse rings, more marked on adaxial side; adnate adaxial wall slightly sigmoid in lateral view; aperture distally-placed, set transversely, rhomboidal to quadrate in frontal view, margin with 4 little raised, pointed, triangular cusps separated by wide, shallow embayments; intrathecal, submarginal, perisarcal cusps missing; closing apparatus composed of 4 triangular flaps meeting centrally to form a low roof; hydranths strongly contracted near the hydrothecal bottom, bearing apparently ca. 16 short, filiform tentacles. The single gonotheca occurring on one stem arise frontally, from below the base of a cauline hydrotheca; broadly ovoid, thin-walled, transversely-ringed (8-9 rings), apically provided with 5 prominent, rounded projections around the aperture; lumen empty, sex could not be ascertained. Perisarc of the colony thin and straw-colored.

Remarks: Larger (5-6 cm high) and more ramified colonies than those dealt with herein were occasionally reported (*e.g.* Kudelin, 1914b). The gonothecae described and depicted by Jäderholm (1909) were "broadly truncated at the top, and provided with a small, though well-defined, smooth-edged, muzzle-shaped tube with a narrow aperture". Other authors, described and/or depicted (in this unmistakable species) gonothecae provided with 4 (Kudelin, 1914b), 5-6 (Naumov, 1969), or as much as 9 (Antsulevich, 2015) apical projections, and I concur with Naumov that the gonothecae occurring in the type were, most probably, not fully developed.

Broch (1918: 105) had incorrectly assigned this species to the synonymy of *S. fusiformis* (Hincks, 1861), a nominal species with decidedly spindle-shaped, instead of conical, hydrothecae.

Distribution: Spitzbergen (Jäderholm, 1907, 1909), East Siberian Sea (Gorbunov, 1946; Stepanjants, 1994), Tartar Strait in the Sea of Japan (Kudelin, 1914b), Mid-Atlantic Ridge (present study). The previous known depth range was 45-54 m (Naumov, 1969), but the present material extends it down to 2358 m.

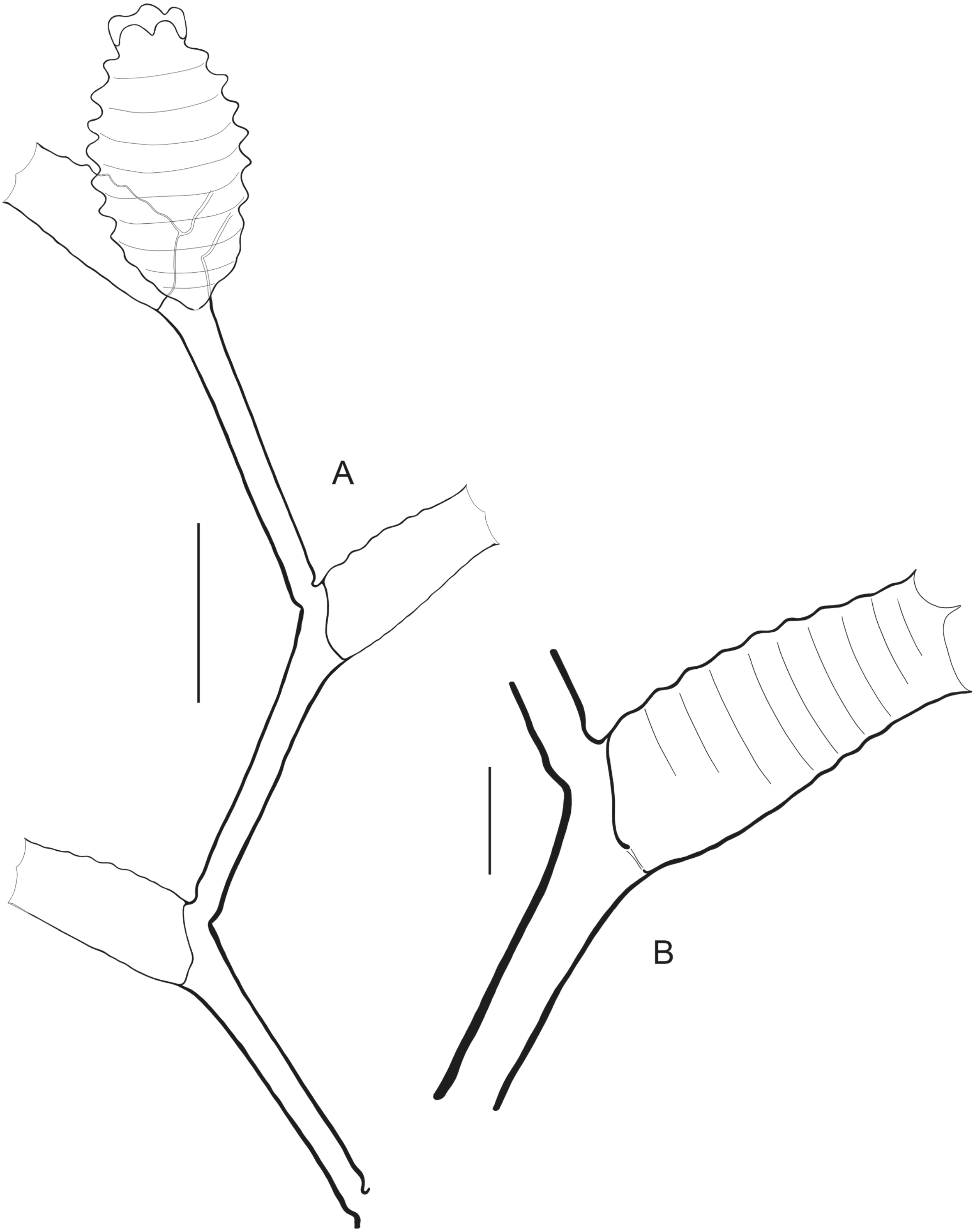

Fig. 7. *Sertularella pellucida* Jäderholm, 1907. Portion of colony with gonotheca (A). A hydrotheca, enlarged (B). Scale bars: 300 µm (B), 1 mm (A).

Family Syntheciidae Marktanner-Turneretscher, 1890

Synthecium brucei Vervoort & Watson, 2003

Fig. 8; Table 4

Synthecium brucei Vervoort & Watson, 2003: 247, fig. 58F-H.

Material examined: MNHN-IK-2019-2159; colony composed of many stems up to 5 cm high, some bearing short gonothecae; *BATHUS 3*, Stn. CP814, Norfolk Ridge; -23.800°, 168.283°; 444-530 m; 28.11.1993. – MNHN-IK-2019-2160; colony originally composed of several stems, of which only four remained intact, attaining 3.6 cm high, two of them bearing elongate gonothecae; *BATHUS 3*, Stn. CP821, Norfolk Ridge; -23.316°, 167.983°; 864-880 m; 29.11.1993. – MNHN-IK-2019-2161; one stem 2.8 cm high, bearing a couple of elongate gonothecae; *BATHUS 3*, Stn. CP804, Norfolk Ridge; -23.683°, 168.000°; 244-278 m; 27.11.1993.

Description: Colonies arising from tortuous, branching, anastomosing stolons creeping on calcareous bryozoans; composed of erect, rather stiff, monosiphonic,

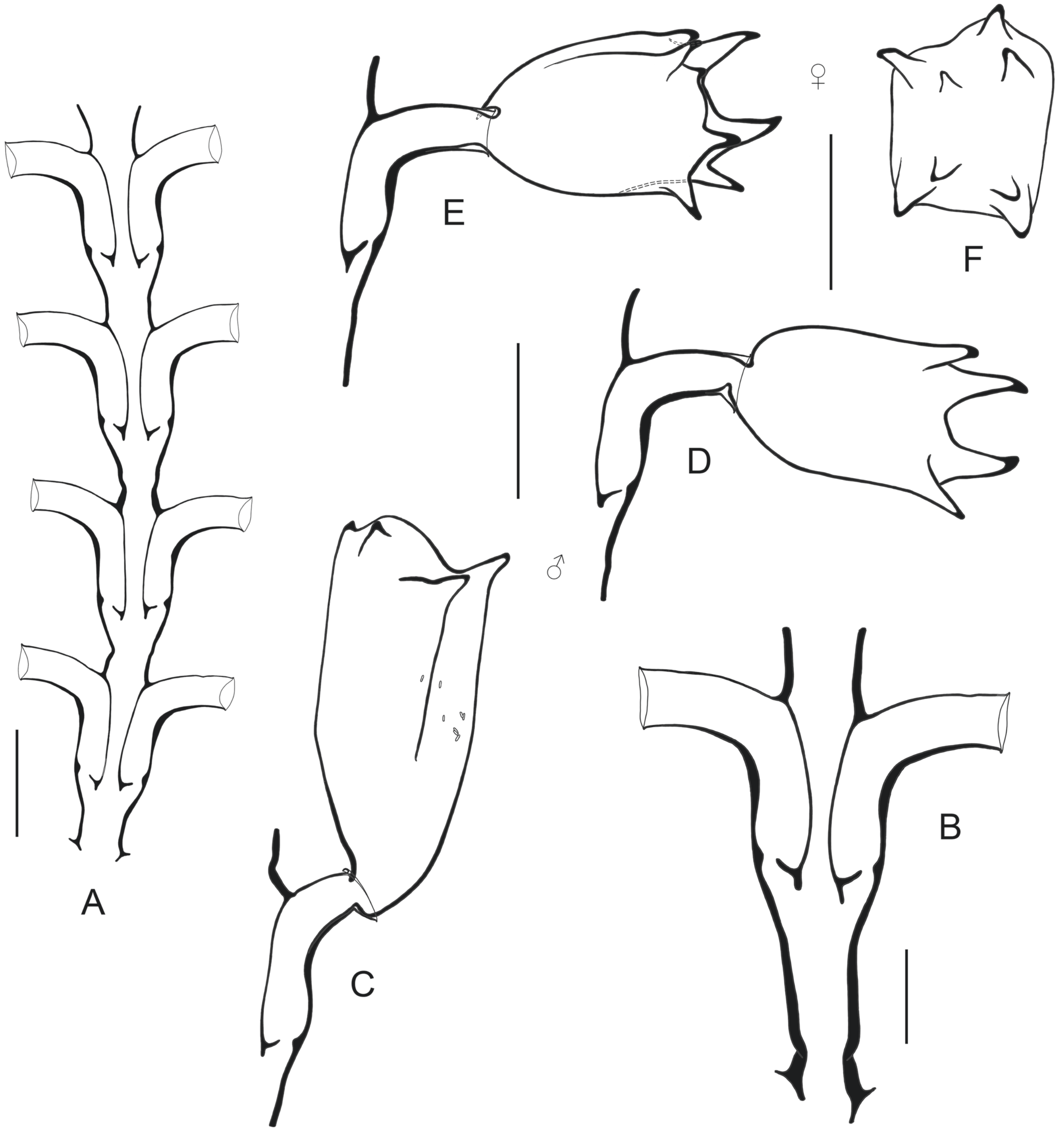

Fig. 8. *Synthecium brucei* Vervoort & Watson, 2003. Portion of colony (A). Hydrothecal pair, enlarged (B). Various gonothecae seen laterally (C-E), the latter also in apical view (F). Scale bars: 500 µm (B), 1 mm (A, C-F).

unbranched shoots attaining a height of 5 cm; proximal part of stems athecate and of a varied length, up to 2 cm long, often bearing transverse marks of breakage and subsequent regeneration; above, stem regularly divided into up to 20 internodes delimited by weak transverse constrictions of the perisarc, occasionally more deeply incised here and there; internodes short, collinear, bearing a pair of strictly opposite hydrothecae. Hydrothecae projecting slightly obliquely in front of the stem, half adnate to their corresponding internodes; opposite hydrothecae laterally distant from one another on the internode; tubular, free half arching away at 90° with respect to the proximal half; free adaxial wall slightly but distinctly convex, adnate counterpart similar in shape, ending in perisarc plug at junction with the base; the latter set obliquely, not reaching abaxial wall; abaxial wall strongly curved outwards, convex in shape, with comparatively thicker perisarc than its opposite counterpart; aperture slightly but distinctly everted, broadly ovoid in frontal view (adaxial side relatively flattened, abaxial side decidedly concave), slightly but distinctly scooped in lateral view. Hydranths with 14-16 filiform tentacles. Colonies dioecious; gonothecae arising from within the proximal most hydrothecal pairs; sexually dimorphic; female short, urn-shaped, with 4-5 longitudinal ridges, each of which ending distally in commonly 2 (occasionally 1) spines, top of gonotheca dome-shaped, with thinner perisarc in central part (aperture not distinctly formed), gonophore a single, large oocyte attached dorsally to the blastostyle; male gonothecae comparatively longer, vasiform, 3 to 4-sided, each longitudinal ridge ending in single spine, gonophore a homogenous, spindle-shaped mass of sperm cells encircling the blastostyle. Perisarc of colonies transparent, grading to straw colored in older parts; coenosarc (including the hydranths) white in these alcohol-preserved specimens; oocytes dark yellow; sperm mass pale yellow.

Table 4. Measurements of *Synthecium brucei* Vervoort & Watson, 2003, in µm.

Internodes	
- length	1510-1970
- diameter at nodes	290-425
Hydrothecae	
- free adaxial wall	820-865
- adnate adaxial wall	945-1040
- abaxial wall	1100-1275
- diameter at aperture	320-330
Gonothecae	
- total length	2480-2760 (♂), 1810-1930 (♀)
- width below the spine region	835-1060 (♂), 930-1120 (♀)

Remarks: Taller, though invariably unbranched stems, reaching as much as 7 cm high, were reported upon earlier (Vervoort & Watson, 2003: 247). Gonothecae of both sexes, not documented so far, occur in the present material, allowing a comprehensive knowledge of the species.

Distribution: Norfolk Ridge (Vervoort & Watson, 2003; present report). Occurs between 113 m (Vervoort & Watson, 2003) and 880 m (present study).

Family Aglaopheniidae Marktanner-Turneretscher, 1890

Taxella setosa (Armstrong, 1879) comb. nov.

Figs 9A-C, 10, 11A

Halicornaria setosa Armstrong, 1879: 99, pl. 10. – Bale, 1884: 153. – Thornely, 1904: 122. – Bedot, 1912: 301. – Bedot, 1916: 121. – Bedot, 1918: 150. – Bedot, 1921: 347. – Rees & Vervoort, 1987: 156. – Ronowicz *et al*., 2017: 15.

Gymnangium setosum – Stechow, 1923: 236. – Mammen, 1965: 311.

Gymnangium eximium – Rees & Vervoort, 1987 (*pro parte*): 156, fig. 37A-C (non *Taxella eximia* Allman, 1874b).

non *Halicornaria setosa* – Thornely, 1904: 122.

Material examined: MNHN-IK-2019-2162; a 5 × 5.5 cm, fertile colony; 1951-1952 *Calypso* South Red Sea Expedition, Saudi Arabia, off Al Lith, Shab Suleim reef; 19.916°, 40.000°; 0.5-1.5 m; 22 Jan 1952. – MNHN-IK-2019-2165; a colony composed of two stems, 4.5 × 2.7 cm, and smaller fragments, all sterile; same data as above. – MNHN-IK-2019-2163; a 3.8 × 3 cm, fertile colony; same data as above. – MNHN-IK-2019-2164; a 4 × 3 cm fertile colony; same data as above.

Comparison material: HRG-1707; a 8.5 cm high, fertile colony of *Taxella eximia* Allman, 1874b; 1951-1952 *Calypso* South Red Sea Expedition, locality name illegible on label, the latter with no additional collecting data.

Description: Light brown-colored, relatively stiff, flabellate colonies, up to 5 cm high and 5.5 cm wide, arising from quite large masses of hydrorhizae composed of tortuous, irregularly branched, anastomosed fibers firmly attached to presumably hard substrates (all colonies were removed from them). Colonies composed of one or multiple stems; the latter strongly fascicled, up to 2 mm wide basally, giving off regularly to alternate side branches about 1 cm long; branches arising at about 70° with the long axis of the stem, those belonging to the same side distant of about 2 mm from one another; some branches elongate further, giving rise to up to 4th order branches, occasionally bearing tendrils apically; stem

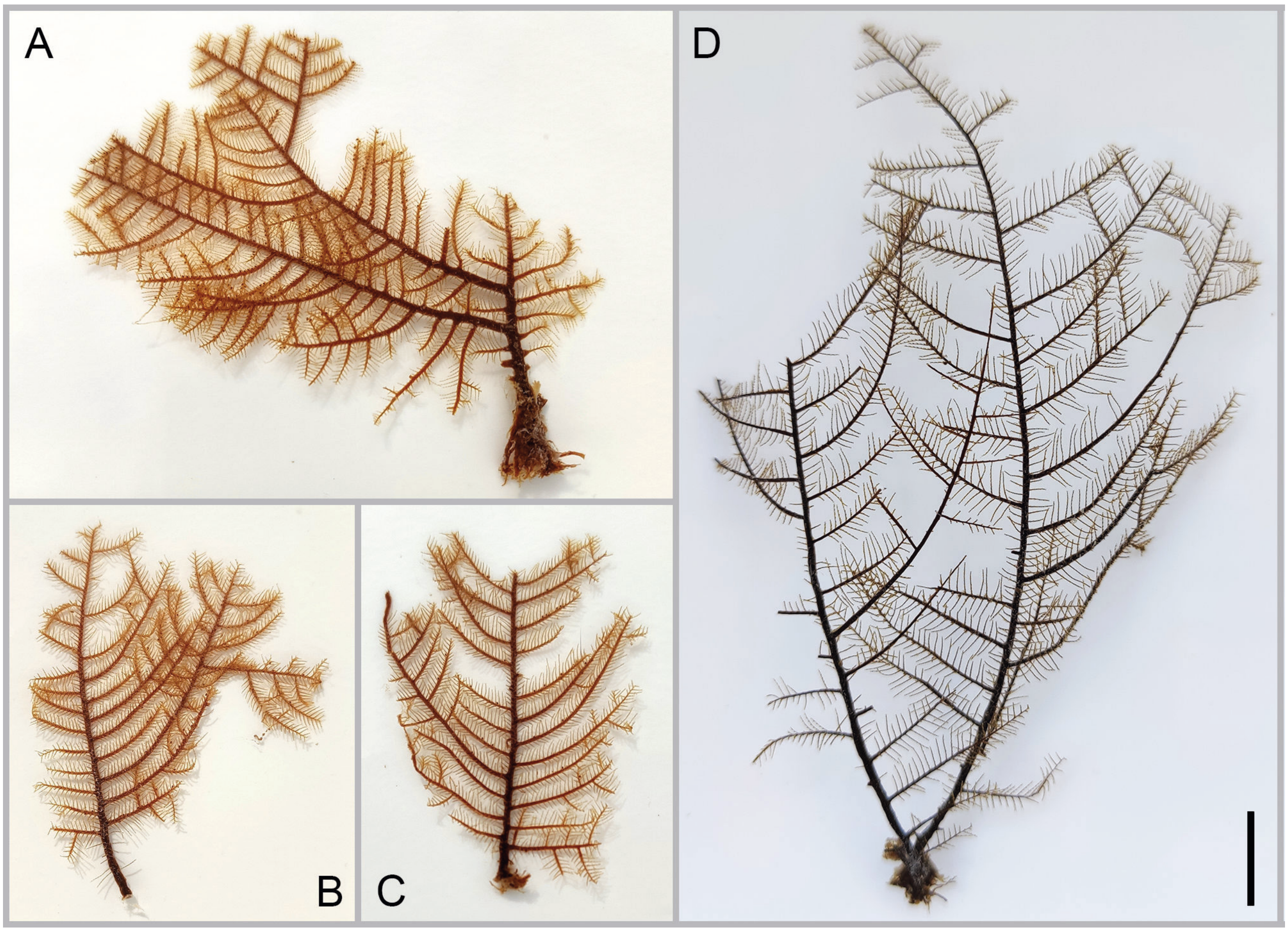

Fig. 9. *Taxella setosa* (Armstrong, 1879), comb. nov. Three colonies (A-C) compared to a colony of *T. eximia* Allman, 1874b (D), to show differences. Scale bar: 1 mm (A-D).

and branches thinning out gradually towards their very tips, where they are monosiphonic; main tubes of the side branches not given off from the branching of the main cauline tube, but derived from various accessory tubes of the stem; main tubes of both stem and branches regularly divided into short internodes by inconspicuous, transverse constrictions of the perisarc; each internode bears, close to its proximal end, a short, fronto-lateral apophysis supporting a cladium; apophyses alternate, each with two associated nematothecae: one globular to conical, with gutter-shaped aperture, borne frontally near the origin of the apophysis, while the second is set laterally and slightly above the apophysis itself, sac-shaped, with inwardly-rolled margin of the abaxial wall; accessory tubes of the stem and branches running parallel to the corresponding main tubes, and only restricted to their backsides; from straight to tortuous in outline, bearing two parallel rows of regularly-spaced nematothecae, set at the same level on both sides, and along the junctions with the adjacent tubes; nematothecae with elongated apertures whose long diameters are parallel to the axes of the tubes; large, ovoid holes in the perisarc allow the communication between the coenosarcs of adjacent tubes. Cladia up to 2.5 mm long, regularly divided (by means of transverse nodes) into up to 11 cormidia; commonly there are only 5-7 cormidia per cladium, not exceeding 1.5 mm in length; cormidia short, barely accommodating a hydrotheca and its three associated nematothecae (a mesial and a pair of laterals). Hydrothecae adnate for most of their length, leaving but a very short free portion distally; distinctly curved outwards, aperture flared, set obliquely, margin with a pair of broad, lateral, triangular lobes, notably scooped posteriorly between the two lateral nematothecae, forming two cusps; adnate adaxial wall slightly concave, ending proximally in perisarc plug forming an incomplete septum in the internode behind; abaxial wall short, distinctly concave, often projecting a short, crescent-shaped ridge into the hydrothecal lumen at the level of its extreme curvature. Mesial nematotheca adjacent for about 3/4 to the hydrotheca, leaving only a short portion free; aperture either gutter-shaped, or with two orifices, one apical and circular, the other

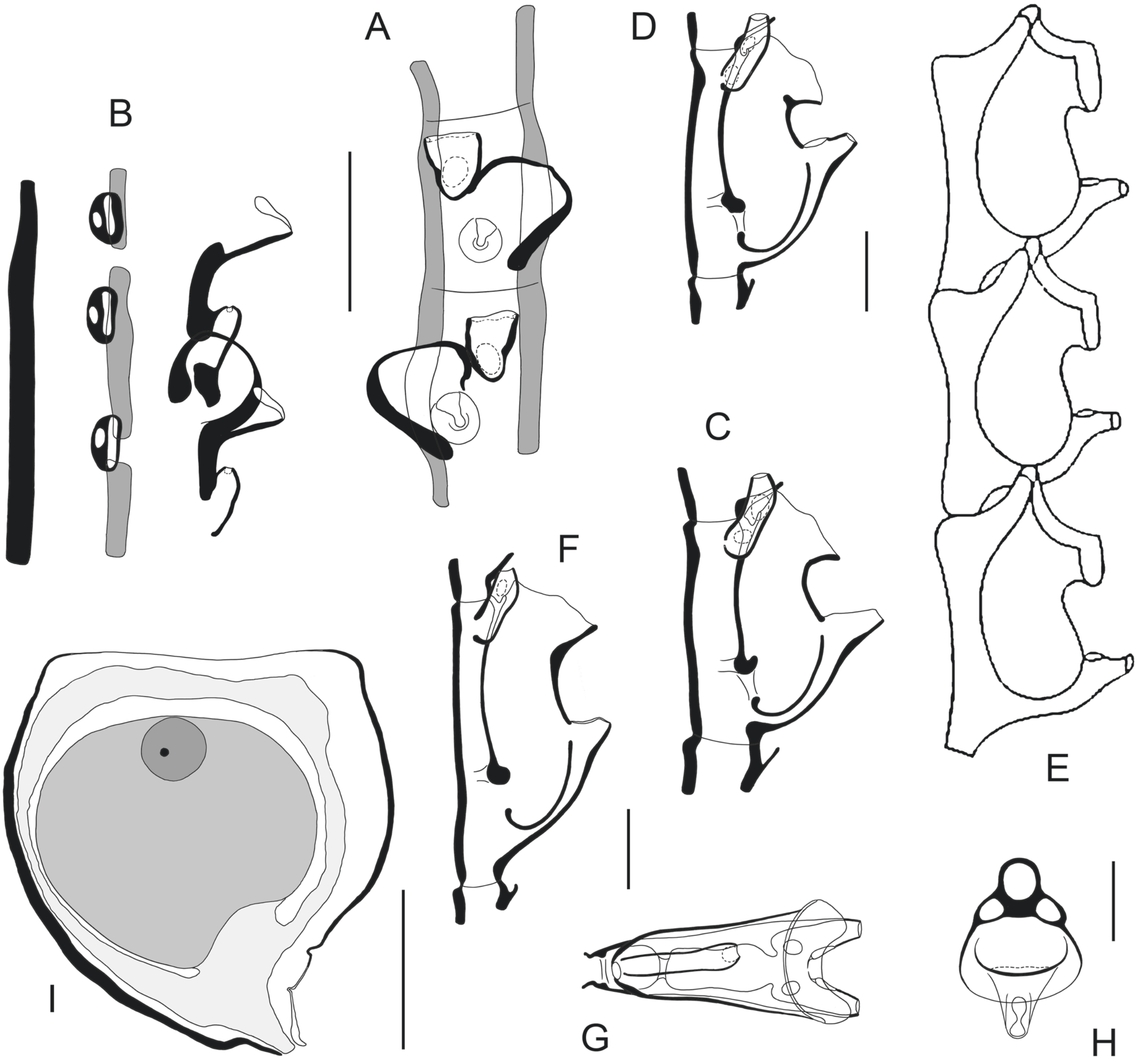

Fig. 10. *Taxella setosa* (Armstrong, 1879), comb. nov. Portion of stem in frontal (A) and lateral (B) aspects, to show the cladial apophyses and their associated nematothecae. Two hydrothecae seen laterally (C, D), compared to those originally drawn by Armstrong (1879) (E – modified after his pl. 10) and a theca of *T. eximia* Allman, 1874b (F). Two other hydrothecae, one seen frontally (G), the other apically (H). Gonotheca, showing lumen with large oocyte (I). Scale bars: 100 µm (C-H), 200 µm (A, B, I).

ovoid and set in the axil formed by the free part of the nematotheca with the abaxial wall of the hydrotheca. Lateral nematothecae elongated, overtopping the hydrothecal margin, provided with a small, circular, apical aperture, as well as with a large, ovoid, adaxial aperture. Gonothecae in two parallel, neat, continuous lines along the stems and branches; each gonotheca arising from the upper axil of the cladial apophyses; lenticular in shape, tapering abruptly below into a short, indistinct pedicel, distally with two lateral, angular projections, at maturity apex splitting up longitudinally along a portion of their perimeter, allowing the release of gametes (zygotes, embryos ?); female gonophores observed herein, composed of a large, rounded oocyte with very visible nucleus and nucleolus, surrounded by a ramified blastostyle.

Remarks: The material examined here, forming medium-sized, brown-colored, flabellate colonies (Fig. 9A-C), essentially fits the original account of *Halicornaria setosa* Armstrong, 1879 [no exact type locality stated, but collected between Kanyakumari (Cape Comorin), India and Nagaye Angu (Cape Negrais), Myanmar] (the colony drawn by Armstrong is reproduced here, for comparison, in Fig. 11A). The

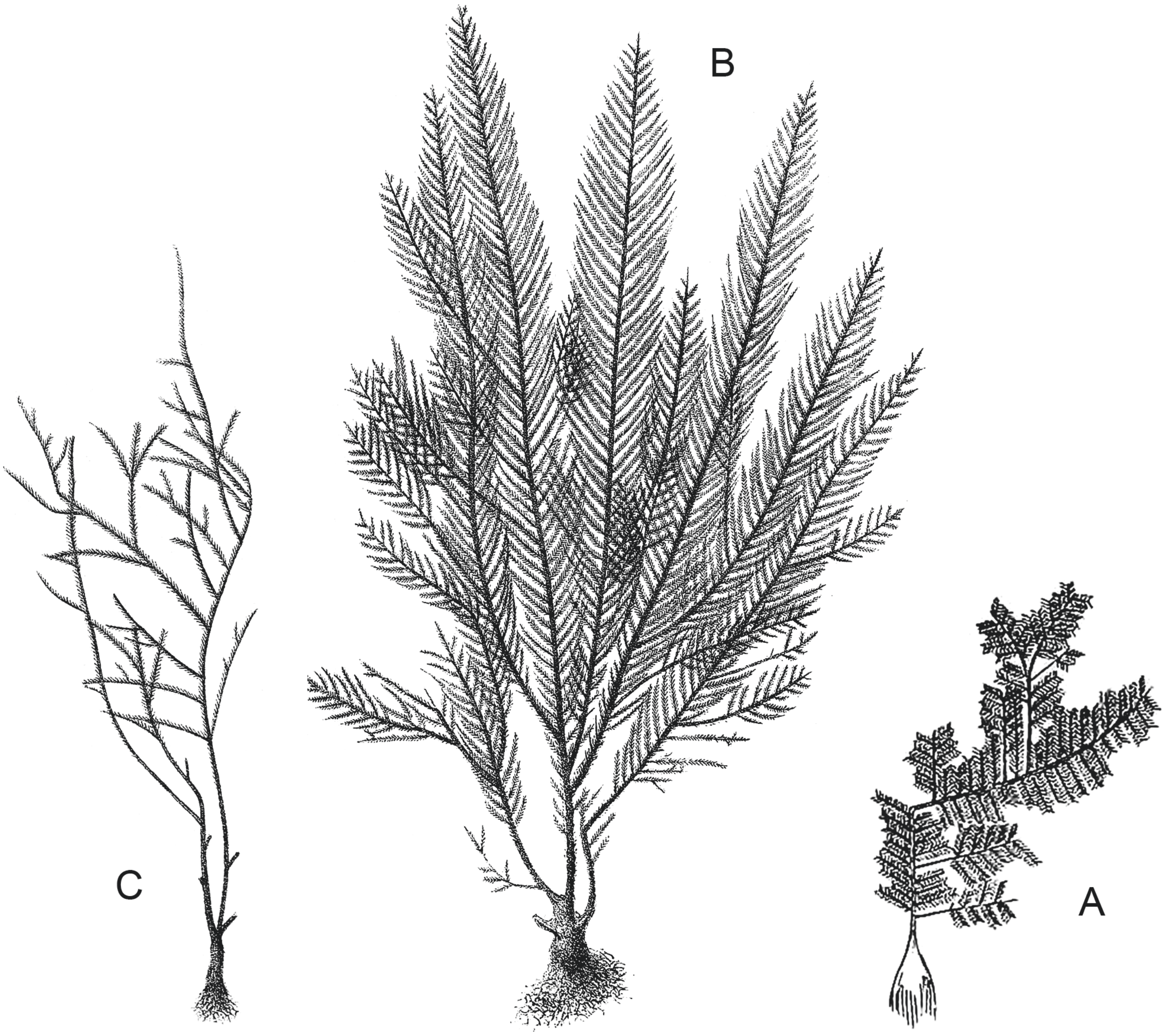

Fig. 11. Historical illustrations of the colonies of three nominal species previously assigned to the synonymy of *T. eximia* Allman, 1874b: *Halicornaria setosa* Armstrong, 1879 [A – modified after his pl. 10)], *H. bipinnata* Allman, 1876 [B – modified after his pl. 23 fig. 2)], and *H. saccaria* Allman, 1876 [C – modified after his pl. 15 fig. 4)]. All are half the natural size.

general microscopic structure, depicted in the other figures included by that author in the same plate, further support their identity (compare, for example, Fig. 10C, D to 10E).

Its repeatedly-branched, strongly fascicled colonies recall those met with in *Macrorhynchia* Kirchenpauer, 1872, but the absence of phylactocarps protecting the gonothecae exclude it from that genus. It is also excluded from *Gymnangium* Hincks, 1874 on the account of the branched condition of its colonies and their polysiphony. It could not belong to *Lytocarpia* Kirchenpauer, 1872, either, due to the absence of corbulae, but it is tentatively assigned here to *Taxella* Allman, 1874b, as *T. setosa* (Armstrong, 1879), comb. nov., pending a molecular analysis.

For instance, only five species are confidently placed in the genus *Taxella*, namely *T. elfica* Ronowicz *et al*., 2017, *T. eximia* Allman, 1874b, *T. gracilicaulis* (Jäderholm, 1903), *T. hornelli* (Thornely, 1904), and *T. longicorne* (Busk, 1852) (Schuchert, 2021). Additional species are morphologically-related and could also belong here, *e.g. Halicornaria expansa* Jäderholm, 1903 (type species of the genus *Halicetta* Stechow, 1921a), *Halicornaria tubulifera* Bale, 1914, and *Halicornaria vegae* Jäderholm, 1903 (type species of the genus *Haliaria* Stechow, 1921a).

Of these, *T. setosa* comes closest to *T. eximia*, according to the present concept on this species (Ronowicz *et al*., 2017: 15, figs 7A, 8). By a fortuitous coincidence, a fertile colony (sample HRG-1707), assignable to

T. eximia occurs in the same material from the Red Sea gathered by the *Calypso* during her 1951-1952 cruise. That colony (Fig. 9D) is comparatively larger, darker-colored, slenderer in appearance, decidedly less fasciculate, with longer cladia (bearing up to 12 cormidia) and deeper hydrothecae (compare Fig. 10F to 10C, D); unlike in *T. setosa*, the main tube of the cladia-bearing branches begins with a long, proximal portion bearing a row of several conical nematothecae with gutter-shaped apertures, similar to those borne at the base of the hydrocladial apophyses in *T. setosa*; the complement of nematothecae associated to the apophyses is pretty much the same in both species.

In my opinion, *T. setosa* was unjustifiably included by Rees & Vervoort (1987: 156) and Ronowicz *et al*. (2017: 15) in the synonymy of *T. eximia*, a species with a complicated, still unresolved taxonomic history. Indeed, Allman (1874b: 179) gave only insignificant indications on the specific identity of his hydroid, and a formal description and illustrations of the holotype are wanting. In his note, he mentioned another species, *Makrorhynchia* (sic) *insignis*, belonging to the same collection from Sri Lanka made by Holdsworth, and only this one was subsequently dealt with in detail in Allman (1876), as *Halicornaria insignis*. However, in the same paper, two other congeners, also from Sri Lanka, were additionally described, namely *H. bipinnata* and *H. saccaria*, but there was no further mention of *T. eximia*, whose specific name was possibly dropped, for an obscure reason, in favor of one of the two most recent ones.

Of note, several nominal species, namely *H. bipinnata*, *H. saccaria*, *H. flabellata* Marktanner-Turneretscher, 1890, *Lytocarpia* (?) *multiplicatopinnata* Stechow, 1919 and *H. copiosa* Jarvis, 1922 were variously assigned to the synonymy of Allman's (1874b) hydroid by a number of authors (e.g. Schmidt, 1971: 39; Rees & Vervoort, 1987: 156-157; Vervoort, 1993: 549). In doing so, they likely focused their attention on microscopic features alone, mainly on the shape of their hydrothecae. It should be stated that, except for *H. flabellata*, *H. copiosa* and *L.* (?) *multiplicatopinnata*, for which there are no available illustrations of their whole colonies, the three other species (i.e. *H. bipinnata*, *H. saccaria* and *H. setosa*) build colonies that are highly dissimilar (Fig. 11). Additional differences in their microscopic anatomy, possibly sufficient to separate them specifically, seem also to exist, in spite of the perfunctory original accounts and the rather sketchy illustrations accompanying them.

My colony of *T. eximia* is similar to that depicted by Ronowicz *et al*. (2017) in their fig. 8A, and both appear to differ from both the very regular branching pattern displayed by *H. bipinnata* [Allman's (1876) pl. 23 fig. 2, reproduced here in Fig. 11B] and the slender appearance of the colonies of *H. saccaria* [Allman's (1876) pl. 15 fig. 4, reproduced here in Fig. 11C], suggesting the existence of distinct species.

Rees & Vervoort (1987: 159, as *Gymnangium eximium*) acknowledged that their "various colonies referred to this species differ considerably", and there is no doubt that they had several taxa. Among these, the colonies from Stn. 24 (Gulf of Aden, fig. 37A-C) match with *T. setosa*. Those from other stations exhibit either a conspicuous abaxial projection (Stn. 10, figs 36A = *T. longicorne* ?), a longer abaxial hydrothecal wall (Stn. 118, fig. 37F = *T. eximia* ?) or a broadly-cusped, distinctly-flared hydrothecal aperture (Stn. 27, fig. 37D).

Given the current situation, it is realized that a broader, thorough study of *T. eximia* and its allies, including the reexamination of the existing types and the study of recently-collected material, by combining mandatorily morphological and genetic approaches, would be germane, in order to avoid spreading controversy on this already difficult species group. Of note, type material (ZMH C 3657) of *Aglaophenia (Macrorhynchia) multiplicato pinnata* was destroyed by fire in 1943, during World War II, as indicated on an old file card at the *Centrum für Naturkunde*, Hamburg, Germany (Helma Roggenbuck, *pers. comm.*). That material probably included also the single, mounted, sterile fragment that remained from the holotype by the time when Stechow (1919: 131) provided an account of it.

Distribution: Red Sea (present study), and from the south coast of India to those of Rakhine (Arakan) and Bago (Pegu) in Myanmar (Armstrong, 1879). Occurs from below the surface (present study) down to 146 m (Armstrong, 1879).

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