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A reassessment of *Halopteris polymorpha* (Billard, 1913) (Cnidaria: Hydrozoa), with descriptions of three new species

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Abstract: Several hydroids, corresponding to various morphotypes included earlier in the synonymy of *Halopteris polymorpha* (Billard, 1913), occur in materials obtained recently from Indonesia and the Maldives, or are housed in the collection of the Muséum d'histoire naturelle of Geneva, Switzerland. Among them, new specimens, indistinguishable morphologically from the lectotype, are fully redescribed, together with the so-called variety *sibogae* Billard, 1913. While the latter displays in life an original, not yet documented coloration (bright yellow cauline polyps contrasting with their pure white cladial counterparts), the former is uniformly yellow throughout. This feature, combined with a series of morphological differences, demonstrates that we are dealing with a well-characterized species, whose name should be *H. sibogae* (Billard, 1913). The so far unknown gonothecae of the latter are described for the first time, together with the males of the nominal species. The taxonomy of *H. polymorpha* is analyzed in-depth and reassessed, where available also using 16S DNA sequences. Morphological traits can be used to split the species complex and allow the separation of three as yet undescribed species, *H. australis* from New Caledonia and French Polynesia, *H. millardae* from the Maldives and the Seychelles, and *H. brasiliensis* from Brazil. Additionally, new records of *H. vervoorti* Galea, 2008 extend its known geographical distribution to Madagascar, the Maldives and Indonesia, while some literature records suggest that it could spread as far as Australia, Japan and Fiji. All species are fully described and illustrated, and their morphology is compared to that of their related congeners.

Keywords: Halopterididae - taxonomy - Indo-Pacific - western Atlantic - 16S DNA barcoding.

INTRODUCTION

Hydroids belonging to the Family Halopterididae Millard, 1962 are easily distinguished from other members of the Superfamily Plumularioidea McCrady, 1859 through the presence of cauline hydrothecae (Bouillon *et al.*, 2006). However, according to Schuchert (1997), their identification to species is made occasionally difficult due to the lack of reliable morphological features, or succinct original descriptions, sometimes complicated by the loss of type material.

Among the hydroids collected in the frame of the *Siboga* Expedition, Billard (1913) described a new species, *Halopteris polymorpha*, as well as a variety of it, *H. polymorpha* var. *sibogae*. The latter differs from

the nominal species on the account of its long lateral nematothecae, greatly surpassing the hydrothecal rim. Despite this noteworthy difference, it was constantly regarded by many authors (Millard & Bouillon, 1973; Hirohito, 1983, 1995; Schuchert, 1997) as a mere variety, its taxonomic status remaining uncertain until today.

Halopteris polymorpha, as understood by Billard (1913), was based on cormoids originating, sometimes as single specimens, from three different stations of the *Siboga* Expedition, viz. Stn. 77, 80 and 299. Other nominal species co-occurred at these localities, namely *H. platygonotheca* Schuchert, 1997 and *H. plagiocampa* (Pictet, 1893) at Stn. 77 (Schuchert, 1997), as well as *H. campanula* (Busk, 1852), *H. nuttingi* (Billard, 1911)

(Billard, 1913), and *H. diaphragmata* (Billard, 1913) (Schuchert, 1997) at Stn. 80. Among these, Billard (1913) was able to select “une série de formes” or, in other words, different morphotypes displaying a panoply of intergrading, though supposedly convergent characters, so as to form his *H. polymorpha*.

Syntype material of *H. polymorpha* was re-examined, redescribed and better illustrated by Schuchert (1997), who also selected as a lectotype the cormoid from *Siboga* Stn. 80. This material is characterized by its notably longer cladial ahydrothecate internodes, shallower hydrothecae, and shorter apophyses supporting the lateral nematothecae, compared to the materials from Stn. 77 and 299. In addition, its hydrocladia are heteromerously segmented, and their ahydrothecate internodes bear commonly two nematothecae. Conversely, in the cormoid from Stn. 77, the hydrocladia are often divided homomerously, and their ahydrothecate internodes are comparatively shorter and bear generally but a single nematotheca. Finally, the cormoid from Stn. 299 is reportedly said to be similar to the lectotype (Billard, 1913; Schuchert, 1997).

Although these morphotypes were pooled together, their morphological and morphometrical features indicate evident differences (Billard, 1913; Schuchert, 1997) that may reflect the involvement of more than one species. However, during over a century, many hydroids with various geographical origins, and exhibiting more or less discrete morphological differences, were included in the synonymy of this taxon, e.g. Cape Verde (Ansín Agís *et al.*, 2001), South Africa (Vervoort, 1966; Millard, 1975), Seychelles (Millard & Bouillon, 1973), Indonesia (Di Camillo *et al.*, 2008), Australia (Watson, 2000; Preker & Lawn, 2010, 2012), Coral Sea (Ansín Agís *et al.*, 2009), Fiji (Ryland & Gibbons, 1991), Philippines (Vervoort, 1941, as *Antennella polymorpha*), Guam (Kirkendale & Calder, 2003), and Japan (Hirohito, 1983).

In addition, a series of records of hydroids assigned to *H. buskii* (Bale, 1884) were also included in the synonymy of *H. polymorpha* (see Schuchert, 1997; Ansín Agís *et al.*, 2009), viz. Zanzibar (Rees & Vervoort, 1987), India (Thornely, 1916), Sri Lanka (Thornely, 1904), Christmas I. (Ritchie, 1910), Australia (Preker, 2001, 2005), New Caledonia (Redier, 1966), Fiji (Ryland & Gibbons, 1991), French Polynesia (Vervoort & Vasseur, 1977), Philippines (Nutting, 1927), Japan (Hirohito, 1974, 1983, 1995), Hawai'i (Hartlaub, 1901), and Brazil (Migotto, 1996).

Rare, further assignments, such as *Antennella secundaria* (Gmelin, 1791) (Vervoort, 1967, Red Sea) and *Plumularia nuttingi* Billard, 1911 (original account, Indonesia), were also considered as belonging to *H. polymorpha* [Ansín Agís *et al.* (2009) and Schuchert (1997), respectively].

Recent surveys of the hydrozoan fauna of Bali, Ambon and Siladen in Indonesia, and of the Faafu Atoll in the Republic of Maldives, revealed the presence of a number of morphotypes dealt with in some of the literature

records mentioned above. Some others (originating from Madagascar, the Seychelles, New Caledonia, and Brazil) are housed in the collection of *Muséum d'histoire naturelle* of Geneva, Switzerland, and were examined for the purpose of the present study, with the aim of reassessing their morphological characters in order to establish their true relationships.

Since DNA extracts could only be obtained for a subset of the described species (Appendix 2), a genetic study was not intended as the primary goal of the present work. However, even if partly incomplete, the available 16S data represent nevertheless crucial, independent evidence for the validity of the concerned taxa and their relationship to other congeners.

MATERIAL AND METHODS

Sampling was done by scuba diving (0–50 m) or snorkeling (0–1 m). Hydroid colonies were carefully removed from their substrate using haemostatic forceps so as to preserve the integrity of the adjacent fauna. The collected specimens were fixed in 4% borax-buffered formalin in seawater and, sometimes, in 90% ethanol for molecular studies. Although the coloration was documented in living material, most observations were done on formalin-preserved specimens, using the methods described in Galea (2007, 2008). Representative samples were deposited in collections of *Muséum d'histoire naturelle* of Geneva, Switzerland, and registration codes are indicated by MHNG-INVE- followed by five-digit numbers. Additional samples dealt with herein are housed in the Naturalis Biodiversity Center (NBC), Leiden, The Netherlands, the *Muséum national d'Histoire naturelle*, Paris, France (MNHN), the *Musée Royal de l'Afrique Centrale*, Tervuren, Belgium (MRAC), as well as in the private collections of the authors (the registration codes are indicated by HRG-, CDC-, and DM&SM-, respectively, followed by numbers, or combinations of letters and numbers).

Genomic DNA was extracted from ethanol-fixed samples following either the protocols described in Zietara *et al.* (2000) or Coffroth *et al.* (1992). A fragment of the 16S *rRNA* gene was amplified using hydrozoan-specific primers and protocol described in Cunningham & Buss (1993). PCR products were purified and then sequenced using an ABI 3730xl DNA Analyzer (Applied Biosystem, CA, USA). Sequences were examined manually from chromatogram files using Sequencher v. 4.1.4 (Gene Codes Corporation) and were submitted to the NCBI GenBank database (for accession numbers see Appendix 2). Sequences from this study were aligned with sequences downloaded from GenBank belonging to other representatives of Halopterididae and outgroups using the EINS-i option of MAFFT v. 7.110 (Katoh & Standley, 2013). Sequence alignments were run through Gblocks (Castresana, 2000) using the default ‘less

stringent' settings. jModelTest v.2 (Darriba *et al.*, 2012) was used to determine the best-fitting molecular model (Akaike information criterion: GTR+I+ Γ). Phylogenetic analyses were performed using RAxML v. 8.2.10 (Stamatakis, 2014) and MrBayes v. 3.2 (Ronquist *et al.*, 2012) for maximum likelihood (ML) and Bayesian inference (BI) analyses, respectively. For the maximum likelihood analysis, clade stability was assessed by bootstrap analysis (1000 replicates) and for the Bayesian analysis, four parallel MCMC runs were run for 5×10^6 generations, sampling every 100 steps, and burn-in was set to 25%.

In addition to the material described in the next section, specimens of the following *Halopteris* species were examined and compared. See also Appendices 1 and 2 for more examined material and data.

H. alternata (Nutting, 1900):

HRG-0890; France, Martinique, Sainte Anne, 14.44095° -60.89626, 10-15 m, coll. H.R. Galea; 11.02.2012; several stems, up to 2.3 cm high, mostly fertile and bearing gonothecae of both sexes. – HRG-1341; France, Martinique, Case-Pilote, 14.64337° -61.14199°, 1-2.5 m, coll. R. Ferry; 24.07.2017; several sterile cormoids, 0.5-1.6 cm high; 16S sequence MF773748.

H. concava (Billard, 1911):

HRG-0990; Indonesia, Tukangbesi Archipelago, Hoga I., -5.44633° 123.76417°, 20 m, coll. G. Allard; 27.09.2011; a few fragmented stems, up to 2.5 cm high, some cladia bearing female gonothecae.

H. liechtensternii (Marktanner-Turneretscher, 1890):

HRG-0120; France, La Ciotat, Mugel creek, 43.16404° 5.60770°, 0.5 m, coll. H.R. Galea; 20.08.2002; numerous plumes, up to 2.5 cm high, some bearing female gonothecae. – HRG-0162; France, La Ciotat, Mugel creek, 43.16404° 5.60770°, 1 m, coll. H.R. Galea; 13.08.2009; numerous plumes, up to 2.6 cm high, with gonothecae of both sexes present.

H. platygonotheca Schuchert, 1997:

MHNG-INVE-97928; Indonesia, Bali, Tulamben, Liberty shipwreck, -8.274168° 115.59264°, 22 m, coll. H.R. Galea; 29.09.2016; 6 cormoids, 25-35 mm high, of which 5 bear female gonothecae; 16S sequence MF784527. – MHNG-INVE-97943; Indonesia, Bali, Tulamben, Drop-off, -8.27841° 115.59599°, 10-15 m, coll. H.R. Galea; 31.01.2017; 7 cormoids, 13-34 mm high, of which 2 are fertile and bear gonothecae of both sexes. – MHNG-INVE-97944; Indonesia, Bali, Tulamben, Drop-off, -8.27841° 115.59599°, 10-15 m, coll. H.R. Galea; 31.01.2017; 19 cormoids, 17-35 mm high, nearly all fertile, bearing either male or female gonothecae, or both; 16S sequence MF784532. – MHNG-INVE-97935; Indonesia, Bali, Banyuning, Japanese shipwreck, -8.3560° 115.6925°, 0-20 m, coll. H.R. Galea; 04.10.2016; one 1.5 cm high cormoid in alcohol, one cormoid on microslide (after DNA extraction); 16S sequence MF784529. – DM&SM-MA0416141; Republic of Maldives, Faafu Atoll, 3.09008° 72.96792°,

12 m, coll. D. Maggioni & S. Montano; 18.04.2016; 5 sterile stems, 6-11 mm high; 16S sequence MF773744. – DM&SM-MA0416149; Republic of Maldives, Faafu Atoll, 3.09383° 72.96650°, 13 m, coll. D. Maggioni & S. Montano; 18.04.2016; 5 sterile stems, 7-13 mm high; 16S sequence MF773745. – DM&SM-MA0416168; Republic of Maldives, Faafu Atoll, 3.09008° 72.96792°, 20 m, coll. D. Maggioni & S. Montano; 20.04.2016; 5 sterile stems, 4-16 mm high; 16S sequence MF773746.

H. tenella (Verrill, 1874):

HRG-0893; France, Martinique, Le Prêcheur, Pointe Lamare, 14.780460° -61.21193°, 10-17 m, coll. H.R. Galea; 14.02.2012; two colonies with stems up to 0.9 cm high, many bearing male gonothecae. – HRG-0894; France, Martinique, Le Prêcheur, Pointe Lamare, 14.780460° -61.21193°, 4-10 m, coll. H.R. Galea; 28.01.2012; a colony with stems up to 0.7 cm high, some bearing female gonothecae.

TAXONOMY AND RESULTS

Order Leptothecata Cornelius, 1992

Family Halopterididae Millard, 1962

Genus *Halopteris* Allman, 1888

Halopteris polymorpha (Billard, 1913)

Figs 1A, 2A, 3A-K; Tables 1, 2; Appendix 1

Plumularia polymorpha Billard, 1913 (*pro parte*): 24, figs 14A, 15. – Van Soest, 1976: 89.

non *Plumularia polymorpha* Billard, 1913 (*pro parte*): 24, fig. 14B, C.

Thecocarpus polymorphus – Bedot, 1921: 9. – Von Schenck, 1965: 928.

Heterotheca polymorpha – Stechow, 1923: 15.

Halopteris polymorpha – (?) Pennycuik, 1959: 178. – Schuchert, 1997 (*pro parte*): 64, fig. 20A, C-F. – Ryland & Gibbons, 1991: 530, fig. 4. – Di Camillo *et al.*, 2008: 1592.

non *Halopteris polymorpha* – Vervoort, 1966: 132, fig. 35. – Millard & Bouillon (*pro parte*), 1973: 83, fig. 10F-H, J; 1974: 9. – Millard, 1975: 354, fig. 112G-L; 1977: 107; 1978: 193; 1980: 132. – Hirohito, 1983: 62, fig. 31. – Bouillon *et al.*, 1995: 49. – Schuchert, 1997 (*pro parte*): 64, figs 20B, 21-23. – Watson, 2000: 46, fig. 35. – Ansin Agis *et al.*, 2001: 167, fig. 70. – Preker, 2001: 154. – Kirkendale & Calder, 2003: 169. – Preker, 2005: 49. – Preker & Lawn, 2005: 342. – Ansin Agis *et al.*, 2009: 53. – Preker & Lawn, 2010: 120; 2012: 45, fig. 7.

non *Antennella polymorpha* – Vervoort, 1941: 218.

non *Antennella secundaria* – Vervoort, 1967: 42, fig. 12 [not *Antennella secundaria* (Gmelin, 1791)].

non *Plumularia nuttingi* Billard, 1911: 66, fig. 8 – Van Soest, 1976: 89.

non *Plumularia buskii* – Thornely, 1904: 120. – Ritchie, 1910: 832. – Thornely, 1916: 150. – Nutting, 1927: 221.

non *Plumularia buski* – Hartlaub, 1901: 374, pl. 22 figs 22, 32, 36. – Billard, 1913: 21, fig. 11, pl. 1 fig. 15. – Redier, 1966: 90, pl. 2 figs 1 & 3, pl. 3 fig. 1 (incorrect subsequent spelling).

non *Heterotheca buski* – Hirohito, 1974: 30, fig. 14 (incorrect subsequent spelling).

non *Halopteris buskii* – Vervoort & Vasseur, 1977: 72, fig. 31. – Rees & Vervoort, 1987 (*pro parte*): 119, fig. 25A-B. – Ryland & Gibbons, 1991: 527, fig. 2. – Bouillon *et al.*, 1995: 49. – Migotto, 1996: 48, fig. 9F-H. – Preker, 2001: 154; 2005: 48.

non *Halopteris buski* – Rees & Thursfield, 1965: 160. – Hirohito, 1983: 61; 1995: 244, fig. 82 (incorrect subsequent spelling).

Material examined: MHNG-INVE-97937; Indonesia, Bali, Padangbai, Jepun shipwreck, -8.52819° 115.51478°, 20 m, coll. H. R. Galea; 06.10.2016; several sterile plumes, up to 3.7 cm high; 16S sequence MF784530. – MNHG-INVE-97951; Indonesia, Bunaken National Marine Park, Manado Tua I., Negeri, 1.61684° 124.70140°, 10 m, coll. G. Allard; 22.11.2010; several plumes, up to 3.7 cm high, some bearing female gonothecae. – HRG-0421; Indonesia, Bunaken National Marine Park, off Bunaken I., Leukan 2, 1.59989° 124.76697°, 10 m, coll. G. Allard; 21.11.2010; 6 stems up to 3 cm high, one of which bears female gonothecae, and three others carrying male gonothecae. – CDC002; Indonesia, Bali, Tulamben, Liberty shipwreck, -8.27417° 115.59265°, 18 m, coll. C. G. Di Camillo; 21.10.2008; two sterile cormoids, 14 and 21 mm high. – CDC003; Indonesia, Ambon, Laha I., -3.69221° 128.12310°, 10-15 m, coll. C. G. Di Camillo; 14.10.2008; a 17 mm high cormoid and a 12 mm high fragment, both infertile. – CDC004; Indonesia, Bunaken National Marine Park, Raymond's Point, 1.62713° 124.73363°, 40-50 m, coll. C. G. Di Camillo; 01.09.2003; two sterile fragments, 7 and 16 mm high, likely from different cormoids. – CDC005; Indonesia, Bunaken National Marine Park, Mandolin's Point, 1.61095° 124.73257°, 20 m, coll. C. G. Di Camillo; 12.02.2005; a 27 mm high cormoid bearing a gonotheca, probably male.

Additional material: MNHN H.L.1309; Indonesia, Rote Island, Buka Bay, -10.87333 123.01833, 34 m, *Siboga* Stn. 299; a 1.1 cm high sterile cormoid belonging to the syntype of *Plumularia polymorpha* Billard, 1913.

Diagnosis: *Halopteris* with cormoids reaching heights of up to 3.7 cm, with monosiphonic, unbranched stems, divided homomerously into rather long internodes bearing a hydrotheca, a lateral apophysis, and up to 9 nematothecae [1 mesial, a pair of laterals, an axillar one, and generally 2-3 (though up to 5 possibly present) above hydrotheca]. Cladia alternately arranged along stem, heteromerously divided into internodes; hydrothecate internodes slightly shorter than their ahydrothecate counterparts, carrying a hydrotheca and its up to 4 associated nematothecae (1 mesial, a pair of laterals, and occasionally an axillar one); ahydrothecate internodes with 1-2 nematothecae. Hydrothecae conical and shallow; lateral nematothecae with either lowered, emarginated or sinuated margin adaxially, not

surpassing hydrothecal rim, borne on inconspicuous apophyses. Female gonotheca broadly ovoid, with apical, large, rounded aperture perpendicular to long axis of the theca, and closed by glass-watch-shaped operculum; 2-3 basal nematothecae. Male gonotheca smaller than female, ovoid, without noticeable aperture, with 2 basal nematothecae. Cormoids yellow throughout in life.

Description: Colonies composed of a varied number of cormoids arising from creeping, branching stolon, not carrying nematothecae. Cormoids erect (though flaccid when out of liquid), up to 3.7 cm high. Cauli simple, monosiphonic (Figs 1A, 2A), composed of an up to 1 cm long, ahydrothecate, proximal part above origin from stolon, and a much longer, distal part carrying both hydrothecae and hydrocladia. Basal part usually divided by up to 4 transverse nodes into segments of varied length, bearing a number of nematothecae (up to 34 observed) arranged into two parallel, closely-set rows; distalmost segment delimited from the remainder of caulus through a deeply-cut, oblique node. Stem above basal part longer, homomerously segmented into up to 37 internodes through oblique constrictions of the perisarc (Fig. 3A); internodes long, bearing one hydrotheca in their lower third, a number of nematothecae, and an apophysis lateral to the hydrotheca supporting a cladium (two apophyses are usually present in the proximal most internode, and these support a pair of cladia) (Fig. 3B); nematothecae: one mesial, a pair of laterals, one axillar, as well as usually 2-3 (though occasionally 1-5 possibly present) above the hydrotheca, arranged in two closely-set rows. Cladia, except for the proximal most that can be paired, alternately-arranged along caulus; up to 5 mm long, usually less so; each composed of a short, proximal, athecate, quadrangular segment, followed by a succession of ahydrothecate and hydrothecate internodes, delimited through a heteromerous segmentation; ahydrothecate internodes with proximal node transverse and distal node oblique; the reverse in hydrothecate internodes. First ahydrothecate internode quite long, and longer than its subsequent counterparts, bearing constantly two superior nematothecae in a single row; remaining ahydrothecate internodes provided with commonly 1, or rarely 2, nematothecae. Hydrothecate internodes, up to 7 (usually 4-6) per cladium, relatively short, with a hydrotheca confined to most of their length (Fig. 3B), and up to four nematothecae: one mesial, a pair of laterals and, occasionally, an axillar one (Fig. 3E). Hydrothecae cup-shaped and shallow, walls slightly divergent, rim circular, entire (Fig. 3D, F). All nematothecae of the colony bithalamic and movable; mesial ones short, triangular in frontal view, rim of upper chamber with deep, adaxial emargination (Fig. 3G^{3, 4}); laterals short, not surpassing the hydrothecal rim (Fig. 3D, F), and mounted on very short apophyses, conical in

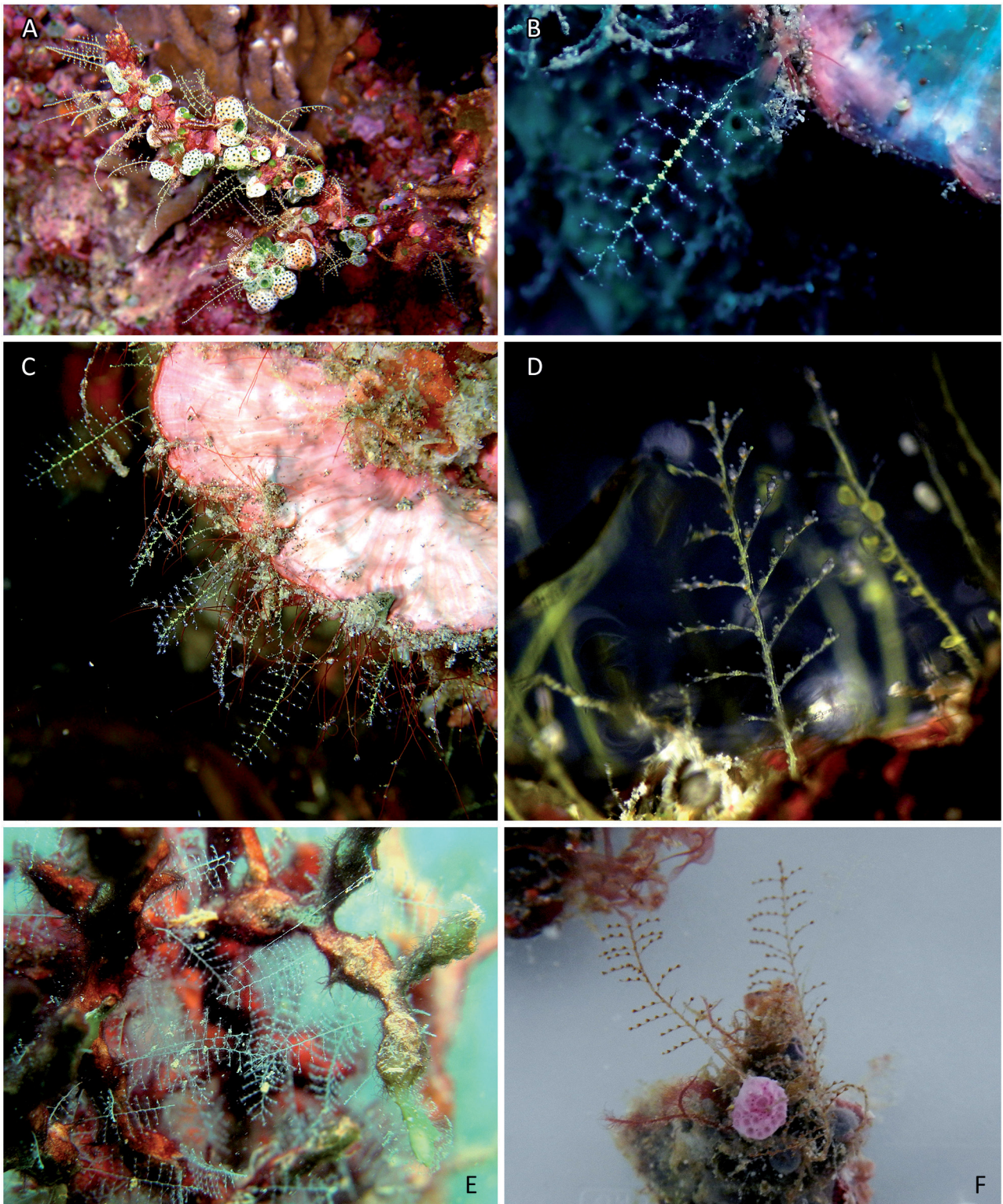


Fig. 1. Living colonies of *Halopteris* spp. showing their natural coloration. (A) *H. polymorpha* (Billard, 1913) from Bunaken, *in situ* (photo CGDC). (B, C) *H. sibogae* (Billard, 1913) from Bali, *in situ*. (D) *H. vervoorti* Galea, 2008 from the Maldives, *ex situ* (photo DM & SM). (E) *H. australis* sp. nov. from New Caledonia, *in situ*. (F) *H. millardae* sp. nov. from the Maldives, *ex situ* (photo DM & SM). Photos courtesy: N. & J-M. Bertot (B, C), E. Tardy (E).

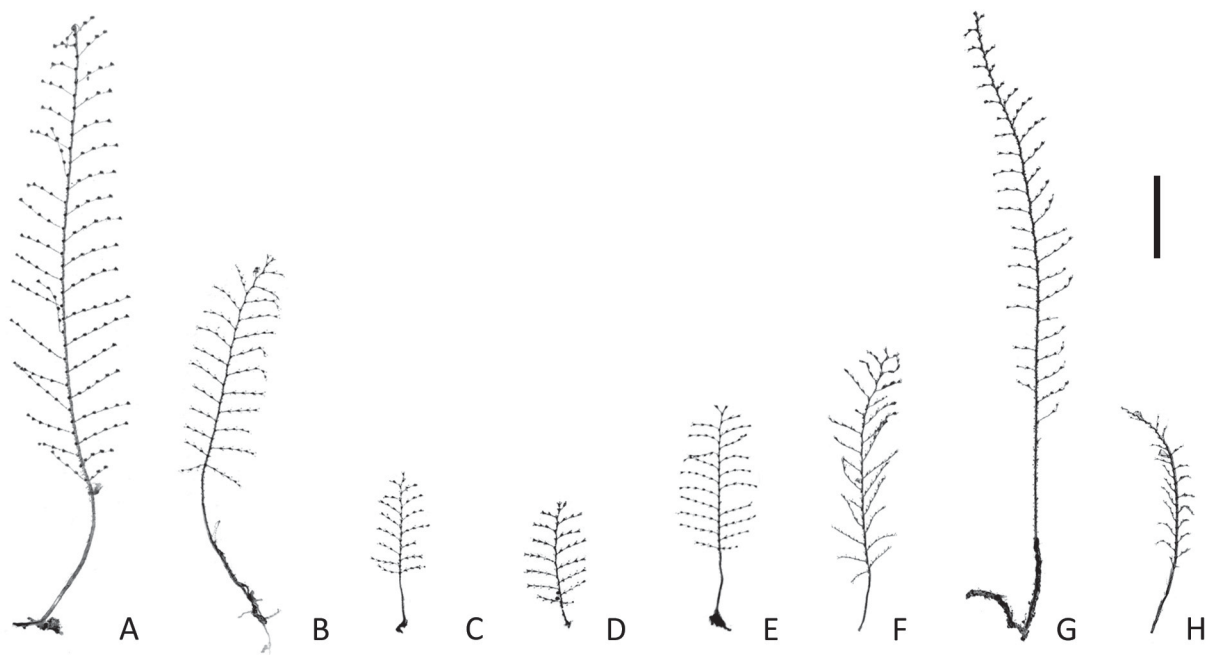


Fig. 2. Preserved cormoids of *Halopteris* spp. showing differences in their appearance. (A): *H. polymorpha* (Billard, 1913), MHNG-INVE-97937. (B): *H. sibogae* (Billard, 1913), MHNG-INVE-97938. (C-E): *H. vervoorti* Galea, 2008 from Bali (MHNG-INVE-97952), Toliara (MHNG-INVE-98633) and Martinique (HRG-0897), respectively. (F): *H. australis* sp. nov. (MHNG-INVE-82742). (G): *H. millardae* sp. nov., MHNG-INVE-98634. (H): *H. brasiliensis* sp. nov., MHNG-INVE-37495, slide H12/37. Scale bar: 5 mm.

shape, aperture wide, margin of upper chamber of variable shape: variously lowered to emarginated to sigmoid adaxially (Fig. 3G⁵⁻⁹); cauline (Fig. 3G¹) and cladial (Fig. 3G²) nematothecae long, with tall basal and shallow upper chambers, rim scooped adaxially; axillar nematothecae conical to broadly ovoid, rather inconspicuous due to their comparatively smaller size and thinner perisarc (Fig. 3G^{10, 11}). Hydranths with 15-16 filiform tentacles; in life, whole colony of a distinctive yellow tinge (Fig. 1A). Colonies dioecious. Gonothecae borne on both stems and cladia, inserted singly beside the base of a hydrotheca through a short, lateral apophysis, and mounted on single quadrangular pedicel; female large, broadly ovoid, tapering below, and there provided with 2-3 basal nematothecae; aperture distal, perpendicular to long axis of the theca, large and circular, with conspicuously thickened rim, closed by a watch-glass-shaped operculum (Fig. 3H, I); male comparatively smaller than female, ovoid, tapering below, without distinct aperture, provided basally with

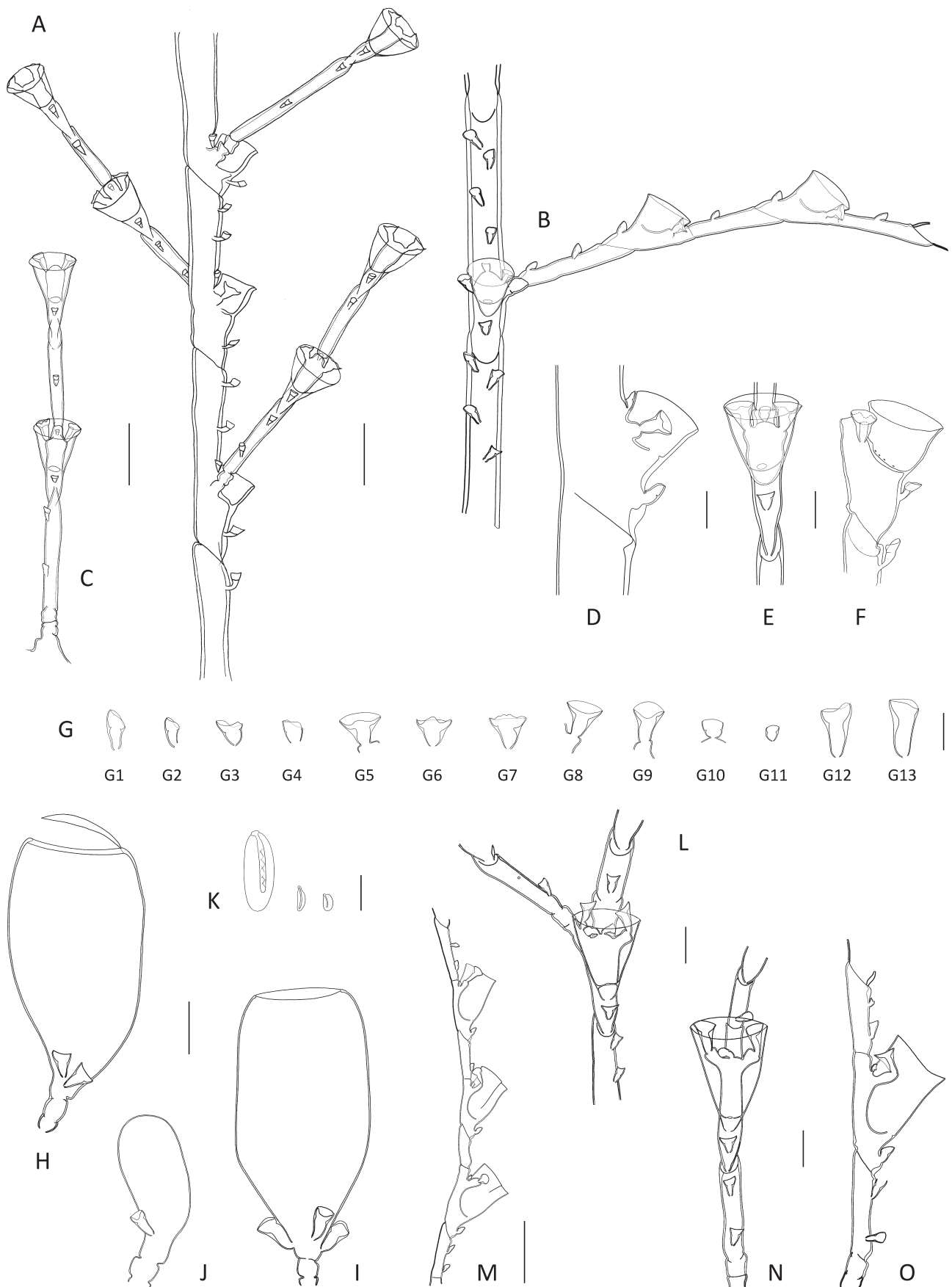
a couple of nematothecae (Fig. 3J). Cnidome (Fig. 3K) composed of 3 types of microbasic mastigophores: large, elongated-ovoid [(21.9-22.6) × (8.2-8.5) μm, in nematophores, as well as scattered in the coenosarc]; small, banana-shaped [(6.9-7.5) × ca. 2.4 μm, in tentacles]; small, ovoid capsules [(4.5-5.1) × (2.8-2.9) μm, scattered in the coenosarc].

Dimensions: See Table 1.

Remarks: The ordinary cauline internodes bear usually 2-3 nematothecae above their corresponding hydrothecae (60.8% and 34.8%, respectively, n=115), though exceptionally as few as 1, or as much as 4 or even 5, may occur (1%, 1.7% and 1.7%, respectively, n=115). The basalmost cauline internodes, supporting pairs of cladia, bear an increased number of nematothecae, usually 4-5. The ordinary cladial ahydrothecate internodes bear generally 1 and, less frequently, 2 nematothecae (92% and 8%, respectively, n=110).

Fig. 3. (A-K) *Halopteris polymorpha* (Billard, 1913). Portions of stems (A, B) and proximal part of a cladium (C). Stem (D) and cladial (E, F) hydrothecae, the latter in frontal and lateral views, respectively. Nematothecae (G) cauline (G¹), cladial (G²), mesial from cauline (G³) and cladial (G⁴) hydrothecae, laterals from cladial hydrothecae (G⁵⁻⁹), axillar from caulus (G¹⁰) and cladium (G¹¹), and associated to the female gonotheca (G^{12, 13}). Female (H, I) and male (J) gonothecae. Cnidome (K). (L-O) *Halopteris* sp. from Siboga Stn. 299, belonging to the syntype series of *Plumularia polymorpha* Billard, 1913. Cauline internode (L). Portion of a cladium (M), and the same much enlarged in frontal (N) and lateral (O) views. Specimens CDC004 (A, C, F), MHNG-INVE-97937 (B, D, E, G^{1-7, 10, 11}, H, K), HRG-0421 (G^{8, 9, 12, 13}, I, J), H.L. 1309 (L-O). Scale bars: 10 μm (K), 100 μm (D-G, L, N, O), 200 μm (H-J), 300 μm (A-C, M).





Behind each cauline hydrotheca, there is large foramen for the passage of a nematophore, itself protected by a bithalamic nematotheca; the latter is occasionally lost, but the constant presence of the foramen in all internodes indicates the pre-existence of an axillar nematotheca. Conversely, the cladial hydrothecae bear only occasionally single axillar nematothecae, but their basal foramina are inconspicuous.

Terminal stolonization is quite common in the available samples, but no branched cladia have been observed.

The bulk of the syntype material of *H. polymorpha* (Billard, 1913) is housed in the collection of NBC but, due to important ongoing renovation works, could not be re-examined for the purpose of the present study (Koos van Egmond, *pers. comm.*).

However, the lectotype (from *Siboga* Stn. 80) – designated and well-illustrated by Schuchert (1997) – is distinctive through its long cauline and cladial ahydrothecate internodes, and its rather shallow hydrothecae, provided with short, conical lateral nematothecae borne on inconspicuous apophyses. The present material fully agrees with these, allowing an updated and more comprehensive account on *H. polymorpha* to be done.

A microslide (H.L.1309), stored in MNHN and containing a sterile cormoid from *Siboga* Stn. 299, was re-examined. The caulus is homomerously segmented, with the exception of its distalmost part, where transverse nodes intervene; each internode is moderately long and comprises a hydrotheca in its lower half, a lateral apophysis and up to 7 nematothecae (1 mesial, a pair of laterals, a pair of axillar, as well as 1-2 superior ones, a certain distance one above the other, and slightly displaced laterally to one another) (Fig. 3L). The hydrocladia are heteromerously segmented; the 1st ahydrothecate internode is longer than its subsequent counterparts, and bears generally 2 nematothecae (although 3 were noted in one instance); the ordinary ahydrothecate internodes are of a rather varied length and carry 1-2 nematothecae (Fig. 3M); the hydrothecate internodes bear a hydrotheca and its 4 associated nematothecae (1 mesial, a pair of laterals, and an axillar one) (Fig. 3N). All nematothecae, including the axillar ones, are bithalamic. The hydrothecae are deep and almost cylindrical, and their lateral nematothecae are mounted on well-developed apophyses, and scarcely reach the hydrothecal rim (Fig. 3O). Its gonothecae remain to be discovered.

Accordingly, it results that the material from *Siboga* Stn. 299 is morphologically different from the lectotype of *H. polymorpha* (compare Fig. 3A-F and 3L-O; see also Table 1), a finding that contrasts with earlier views expressed by both Billard (1913) and Schuchert (1997). The former material obviously belongs to a different, possibly an as yet unnamed species, whose comprehensive description requires additional, fertile material.

The 3rd morphotype belonging to the syntype of *H. polymorpha*, from *Siboga* Stn. 77, is presently the less documented (the available data are summarized in

Table 4 herein). According to Billard (1913), its cladia, besides the proximal most, quadrangular segment, begin with an ahydrothecate internode provided with only one nematotheca, followed by a succession of “mostly” homomerously-segmented internodes bearing “most often” a single nematotheca. The rather deep hydrothecae, provided with lateral nematothecae borne on well-developed apophyses, combined with the structure of the hydrocladia, suggest – with little doubt – that the material from *Siboga* Stn. 77 is specifically different from both the lectotype of *H. polymorpha* and the material in hand described above, thus contradicting – again – the opinions expressed by both Billard (1913) and Schuchert (1997).

Halopteris nuttingi (Billard, 1911) was synonymized with *H. polymorpha* by Schuchert (1997), an opinion not shared here. However, we agree with him that its inclusion in the synonymy of *H. buskii* (Bale, 1884), proposed by Billard (1913), is not justified as they have morphologically different gonothecae. According to Billard (1913), *H. nuttingi* [as *Plumularia buski* (*sic!*)] and *H. polymorpha* could be confidently distinguished through the shape of the upper chamber of their lateral nematothecae: globular with distinctly emarginated ad- and abaxial walls in the former, and conical with slight adaxial emargination in the latter (it was stated above that the complete panoply of shapes displayed by the latter also include a sinuated rim or an adaxial emargination). In Schuchert’s (1997) view, this character is unreliable, arguing that in other halopteridids, *e.g.* *Antennella quadriaurita* Ritchie, 1909, “it is notoriously variable”. However, since then, it has been suggested that the former concept of *A. quadriaurita* likely includes a complex of species (Galea, 2013: 29), and it has been demonstrated, for instance, that at least one “morphotype” represents a distinct, well-characterized species (Galea & Ferry, 2015: 237). Moreover, besides the distinctive shape of the lateral nematothecae, the number and position of their counterparts confined to the cauline internodes distal to hydrotheca is different in *H. nuttingi* (see Billard, 1913). Last but not least, according to both Billard (1911, fig. 8; 1913, fig. 11) and Schuchert (1997, fig. 21C), this nominal species has shorter cladial ahydrothecate internodes and deeper hydrothecae compared to *H. polymorpha*.

Additionally, it should be stressed that *H. nuttingi* was created based on a syntype, as it results from Billard’s [1913, as *Plumularia buski* (*sic!*) Bale, 1884] work, but not from his original account (Billard, 1911). Moreover, according to the former publication, it is very likely that the syntype contains a mix of species, as Billard mentions (p. 22) ahydrothecate cladial internodes either short or long, and provided with one or two nematothecae. However, a neotype (*sic!*) for *H. nuttingi* has been designated (Coel. 5241) by Schuchert (1997: 64), who also provided reliable illustrations of it (N.B.: This material should be best referred to as the lectotype). Besides Billard’s (1911, 1913) record of *H. nuttingi*,

at least two others seem to occur in the literature, viz. Redier [1966: 90, pl. 2 figs 1 & 3, pl. 3 fig. 1; as *P. buskii* (sic!)] and Watson (2000: 46, fig. 35C, E; *pro parte* as *H. polymorpha*).

Literature records of *H. polymorpha* are a matter of debate, due to several main factors: 1) the lack of formal descriptions, or descriptions too succinct, sometimes not accompanied by illustrations, a situation mainly occurring in older literature; 2) only sterile material was available, thus generating confusion with *H. buskii* (Bale, 1884); 3) the artificial inclusion in the synonymy of Billard's (1913) species of a variety of hydroids displaying a large panoply of morphological features, the specific name "*polymorpha*" being obviously misleading. Schuchert (1997) and Ansín Agis *et al.* (2001, 2009) provided extensive lists of synonyms for this taxon (a compilation is given in the synonymy above), though only a few prove reliable in light of the present observations.

For instance, the material studied by Di Camillo *et al.* (2008) and re-examined herein, belongs to the present species. In addition, the Fijian record by Ryland & Gibbons (1991: 530) is also in agreement with it, since it displays the distinctively long cladial ahydrothecate internodes, relatively shallow hydrothecae, lateral nematothecae (with flared upper chamber) borne on inconspicuous apophyses, as well as the occasional presence of axillar nematothecae behind the cladial hydrothecae (it is assumed that their cauline counterparts were overlooked by the authors). Although neither formally described, nor illustrated, the Queensland record by Pennycuik (1959) is reportedly said similar with Billard's fig. 14A, presently known as representing the lectotype of *H. polymorpha*. Besides these few records, many others clearly deviate morphologically from the lectotype. Among them, there are morphotypes characteristically forming either tall (> 4 cm high) or small-sized (< 2 cm high) cormoids. Specimens with tall stems were described, for instance, in materials from South Africa (Millard, 1975), Zanzibar (Rees & Vervoort, 1987; as *H. buskii*), and the Seychelles (Millard & Bouillon, 1973). Millard's (1975) material is, obviously, a mix of species: one with very deep, almost tubular hydrothecae (her fig. 112K), while the other (her fig. 112L) corresponds morphologically to the redescription of the lectotype of *H. buskii* provided by Schuchert (1997). Conversely, the specimens from Zanzibar and the Seychelles (part of the latter re-examined herein) belong to an as yet undescribed species, *Halopteris millardae* (see below).

On the other hand, among the materials with small-sized cormoids, several morphological groups could be distinguished. First, there are specimens whose hydrothecae distinctly display sinuated margins (Vervoort & Vasseur, 1977), and these belong to the new species, *Halopteris australis*, described below. Second, there are materials whose hydrothecae possess an even rim, but further divide into a subgroup with homomerously-segmented cladia (e.g. Vervoort, 1966; Hirohito, 1983) and another one displaying a heteromerous division

into internodes [e.g. Vervoort (1967), as *Antennella secundaria*; Hirohito (1974), as *Heterotheca buskii* (sic!); Ryland & Gibbons (1991), as *H. buskii*; Hirohito (1995), as *H. buskii* (sic!); Preker & Lawn (2010, 2012)]. Some specimens, among the materials with heteromerous cladia, are thought to belong to *H. vervoorti* Galea, 2008 (see below under this species), while the taxonomic status of the remaining ones is uncertain in light of the available data (see Tables 2 and 4). The reexamination of extant specimens, the availability of newly-collected materials, as well as modern, molecular approaches are expected to gradually solve the intricacies of this species group.

A sample provisionally identified as *H. polymorpha*, originating from the Mediterranean, was first used in a molecular phylogeny by Leclère *et al.* (2007). The voucher specimen used in that work (MHNG-INVE-30117, data in Appendix 2) was re-examined for the purpose this study. The single cormoid is sterile and thus not reliably identifiable. It resembles *H. vervoorti*, notably in having pairs of axillar nematothecae associated to the cauline hydrothecae. More and especially fertile material is needed for a correct identification, as it likely belongs to an as yet undescribed species, according to the 16S data (Fig. 9; DQ855922).

Halopteris polymorpha, as presently understood, can be separated from its congeners [see list in Schuchert (2015)] through a series of morphological features. The following hydroids can be excluded *a priori* from the comparison, on the account of a series of diagnostic traits which separate them easily from the species discussed here:

- 1) the fascicled habit of their stems [occasional in *H. campanula* (Busk, 1852), common in *H. valdiviae* (Stechow, 1923)];
- 2) their cladia arranged in opposite pairs [*H. catharina* (Johnston, 1833), *H. clarkei* (Nutting, 1900), *H. enersis* Galea, 2006, *H. gemellipara* Millard, 1962, *H. geminata* (Allman, 1877), *H. opposita* (Mulder & Trebilcock, 1911), *H. plagiocampa* (Pictet, 1893), *H. prominens* Vervoort & Watson, 2003];
- 3) their gutter-shaped hydrothecae [*H. everta* (Mulder & Trebilcock, 1909)], or 4) their hydrothecae divided by internal septa [*H. diaphragmata* (Billard, 1911), *H. jedani* (Billard, 1913)], or
- 5) provided with either an abaxial cusp (*H. rostrata* Millard, 1975) or
- 6) a longitudinal carina (*H. carinata* Allman, 1877);
- 7) the presence of two pairs of lateral nematothecae (*H. infundibulum* Vervoort, 1966).

As to the remaining species, their differences to *H. polymorpha* are summarized in Appendix 1.

Among them, according to the phylogenetic tree shown in Fig. 9, *H. polymorpha* comes close to *H. platygonotheca* Schuchert, 1997. Besides notable differences in their respective female gonothecae (pear-shaped in the former, and conspicuously laterally-flattened in the latter), their trophosomes display several common characters: 1) their stem internodes are long and provided with several

nematothecae distal to the hydrothecae [commonly 2-3 (but up to 5 possible) in *H. polymorpha*, and from 1 (sample MHNG-INVE-97943) to 1-3 (sample HRG-1288) in *H. platygonotheca*]; 2) the occurrence (regular in the former and occasional in the latter) of an axillar nematotheca behind the cauline hydrothecae; 3) their cladial ahydrothecate internodes are long; 4) the apophyses supporting their lateral nematothecae are inconspicuous, and the thecae themselves do not reach the hydrothecal rim.

Taken together, the previous supposed morphological variability of, and the implicit difficulty in establishing a specific limitation in *H. polymorpha*, are now solved through the discovery of additional records in perfect agreement with the lectotype designated by Schuchert (1997). It is concluded that Billard's (1913) species is well-characterized and morphologically homogenous, as illustrated with the present material belonging to various geographically-distant Indonesian populations.

Distribution: Scattered records from Indonesia, viz. off Kalimantan (Billard, 1913, *Siboga* Stn. 80), Bali and Ambon (present study), Bunaken National Park (Di Camillo *et al.*, 2008; present study). Also occurring in Fiji (Ryland & Gibbons, 1991). A doubtful record from Queensland, Australia (Pennycuik, 1959).

Halopteris sibogae (Billard, 1913)

Figs 1B-C, 2B, 4; Table 1; Appendix 1

Plumularia polymorpha var. *sibogae* Billard, 1913: 25, fig. 16.
– Van Soest, 1976: 89.

Thecocalculus polymorphus var. *sibogae* – Bedot, 1921: 9. –
Stechow, 1925: 497.

Halopteris polymorpha var. *sibogae* – Millard & Bouillon,
1973: 84, fig. 10K. – (?) Hirohito, 1983: 62; 1995: 244.

Halopteris polymorpha – Schuchert, 1997 (*pro parte*): 66, 69,
fig. 22E [non *Halopteris polymorpha* (Billard, 1913)].

Material examined: MHNG-INVE-97926; Indonesia, Bali, Tulamben, Liberty shipwreck, -8.27417° 115.59265°, 22 m, coll. H. R. Galea; 29.09.2016; numerous plumes up to 23 mm high, of which many bear male gonothecae; 16S sequence MF784526. – MHNG-INVE-97938; Indonesia, Bali, Padangbai, Jepun shipwreck, -8.52812° 115.51478°, 20 m, coll. H. R. Galea; 06.10.2016; numerous plumes up to 25 mm high, of which 2 bear female gonothecae; 16S sequence MF784531. – HRG-0991; Indonesia, Tukang Besi Archipelago, reef north off Hoga I., -5.44633° 123.76417°, 20 m, coll. G. Allard; 27.09.2011; several infertile plumes up to 20 mm high.

Diagnosis: *Halopteris* with cormoids reaching heights of up to 2.5 cm, with monosiphonic, unbranched stems, divided homomerously into short internodes bearing a hydrotheca, a lateral apophysis, and up to 8 nematothecae (1 mesial, a pair of laterals, 1-2 axillary ones, and commonly 2-3 above hydrotheca). Cladia

alternately arranged along stem, heteromerously divided into internodes; hydrothecate internodes longer than their ahydrothecate counterparts, carrying a hydrotheca and its up to 5 associated nematothecae (1 mesial, a pair of laterals, and 1-2 axillary ones); ahydrothecate internodes short, provided with 1-2 nematothecae. Hydrothecae deep, almost tubular. Lateral nematothecae borne on well-developed apophyses; basal chamber tall, whole nematotheca greatly surpassing hydrothecal margin; rim of upper chamber with adaxial emargination. Female gonotheca broadly ovoid, with large, rounded, apical aperture perpendicular to long axis of the theca, and closed by glass-watch-shaped operculum; 3 basal nematothecae. Male gonotheca smaller than female, ovoid, without noticeable aperture, with 2 basal nematothecae. In life, cauline polyps yellow, contrasting with their purely white cladial counterparts.

Description: Colonies composed of numerous cormoids arising from tubular, creeping, branching hydrorhiza lacking nematothecae. Cormoids erect (though flaccid when out of liquid), up to 2.5 cm high. Cauli simple, monosiphonic (Figs 1B-C, 2B), from straight in their lower halves to distinctly geniculate in their upper halves; basal parts of varied length (1-11 mm long), rarely entire, generally subdivided into segments by a number of transverse nodes (up to 4 observed); segments ahydrothecate, but carrying a total of 0-43 nematothecae arranged in two distinct, longitudinal, closely-set rows; distal end of last segment marked by deeply-cut, oblique node. Remainder of stem longer, with strict homomerous segmentation; each cauline internode (Fig. 4A) moderately-long, bearing a hydrotheca in its lower half, a number of nematothecae, as well as at least a short, lateral apophysis supporting a cladium; up to 33 successive internodes observed. The proximal most internode bears always two opposite apophyses supporting a pair of cladia, but there may be up to 3 consecutive segments displaying this feature; all are demarcated by deeply-incised, oblique nodes, both proximally and distally. Above, the segments are separated by less-marked, oblique constrictions of the perisarc, and each bears but a single apophysis originating laterally next to the hydrotheca; apophyses alternate along the stem. There are 6-9 nematothecae per internode, of which 4-5 are associated to the hydrotheca: 1 mesial, a pair of laterals, 1-2 axillar, as well as 2-4 superior ones arranged in two parallel rows (Fig. 4A); all cauline nematothecae, exclusive of those associated to the hydrothecae, tightly and backwardly appressed against stem (turned posteriad), at least in preserved material. Cladia up to 3 mm long; composed of a very short, proximal, quadrangular, athecate segment, followed by a succession of alternating ahydrothecate and hydrothecate internodes (Fig. 4A, C); ahydrothecate internodes with proximal transverse node and oblique distal node; the reverse in hydrothecate internodes. First ahydrothecate internode

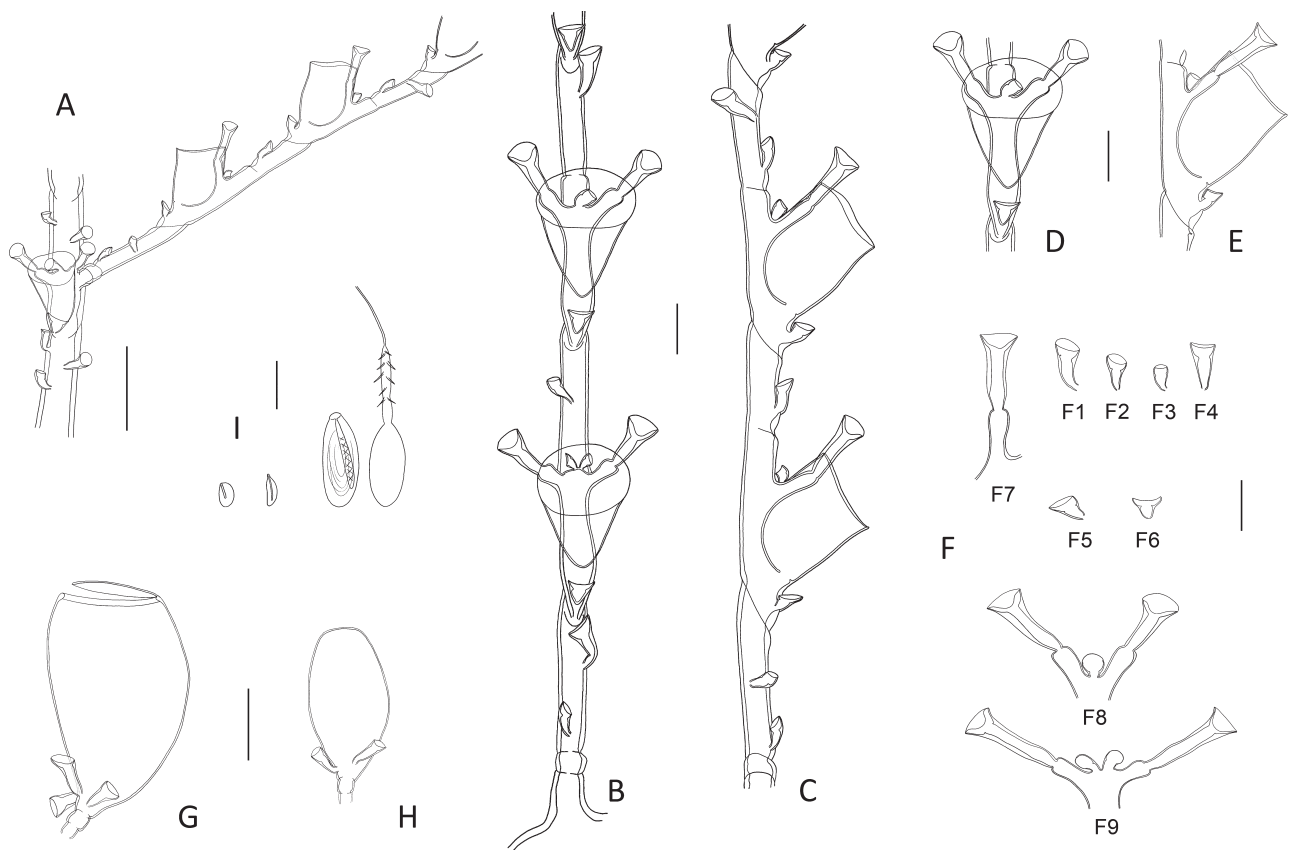


Fig. 4. *Halopteris sibogae* (Billard, 1913). Portion of stem and proximal part of a cladium in frontal (B) and lateral (C) aspects. Hydrotheca in frontal (D) and lateral (E) views. Cladial nematothecae (F): from ahydrothecate internodes (F¹⁻⁴), mesial (F^{5,6}), lateral (F⁷), single (F⁸) and paired (F⁹) axillar ones. Female (G) and male (H) gonothecae. Cnidome (I). Specimens MHNG-INVE-97938 (A-G, I), MHNG-INVE-97926 (H). Scale bars: 10 μ m (F), 100 μ m (D, E, I), 200 μ m (G, H), 300 μ m (A-C).

comparatively longer than following counterparts, and always carrying 2 nematothecae in a row; remaining internodes with either 1 or 2 nematothecae in a row. Hydrothecate internodes, up to 8 per cladium, relatively short, accommodating a hydrotheca in their lower 3/4th and its 4-5 associated nematothecae: 1 mesial, a pair of laterals, and 1-2 axillar (Fig. 4B, D). Hydrothecae cup-shaped and relatively deep, adnate for half their length to corresponding internode, free adaxial and abaxial walls parallel, flaring slightly to margin; the latter circular in apical view, and slightly sigmoid laterally, with imperceptible scoop between side facing the lateral nematothecae and abaxial wall (Fig. 4C, E). All nematothecae, including the axillar ones, bithalamic and movable. Mesial ones triangular in frontal view, upper chamber with conspicuously lowered margin on adaxial side (Fig. 4F^{5,6}). Lateral nematothecae mounted on well-developed apophyses (Fig. 4F⁷); long, greatly surpassing the hydrothecal rim (Fig. 4C, E), lower chamber high, upper one relatively shallow, and with adaxial emargination. Axillar nematothecae cornucopia-shaped, adaxial wall of upper chamber with significant emargination (Fig. 4F^{8,9}). Remaining nematothecae

from both caulus (not shown) and cladia (Fig. 4F¹⁻⁴) similar to the lateral ones, though comparatively shorter. Hydranths with 13-15 filiform tentacles; in life, all belonging to the stem characteristically yellow, contrasting with those from the cladia that are uniformly white (Fig. 1C). Colonies dioecious. Gonothecae arising laterally from below the stem hydrothecae through a short, lateral apophysis; mounted on short, quadrangular pedicel, broadly ovoid, though sexually dimorphic, with the males comparatively smaller than females; the latter provided basally with 3 nematothecae similar to the laterals of the hydrotheca, and a large, watch-glass-shaped apical lid closing a rounded aperture with conspicuously thickened perisarc at margin (Fig. 4G); male gonothecae bearing two basal nematothecae and no noticeable aperture; a globular mass of sperm cells encircles a central, digitiform blastostyle (Fig. 4H); all female gonothecae observed ripe and empty, with the exception of basal remains of the blastostyle. Cnidome (Fig. 4I) composed of 3 types of microbasic mastigophores: large, elongated-ovoid [(18.1-19.8) $\times$ (6.6-7.3) μ m, in nematophores, as well as scattered in the coenosarc]; small, banana-shaped [(6.1-6.6) $\times$ (2.1-

2.3) μm , in tentacles]; small, ovoid capsules [(5.1-5.4) $\times$ (2.9-3.1) μm , scattered in the coenosarc].

Dimensions: See Table 1.

Remarks: In most stems, the proximal most hydrothecate internode gives rise to a pair of cladia; occasionally, two successive internodes are involved; in one instance, three proximal pairs occurred, followed by an internode provided with a single apophysis, and by another one giving rise to a pair of cladia. In such internodes, there are always 3 or even 4 nematothecae above the hydrotheca. The remaining stem internodes are randomly provided with either 2 or 3 nematothecae in two parallel rows. Both cauline and cladial hydrothecae bear either one (70% and 80% of cases, respectively, $n=50$ examined hydrothecae) or two (30% and 20% of cases, respectively) axillar nematothecae.

Terminal stolonization occurs occasionally from the distal ends of both stems and cladia. Rarely, aberrant branching of cladia occurs: a short apophysis is given off laterally from either one or both apophyses supporting the lateral nematothecae; the structure of these 2nd order branchlets (not exceeding two hydrothecate internodes) is similar to that of a normal cladia, and begins with a short, quadrangular, athecate segment, followed by the first ahydrothecate intersegment carrying but a single nematotheca, instead of two as in the 1st order cladia.

Sterile cormoids, similar to the present ones, with hydrothecae provided with exceedingly long lateral nematothecae were already reported notably from Indonesia by Billard (1913) and the Seychelles by Millard & Bouillon (1973) (both as *Halopteris polymorpha* var. *sibogae*). According to the former author, this character mainly distinguishes his so-called variety from the nominal species.

Similarly to the present observations, Millard & Bouillon indicate that “Intermediate athecate internodes [are] absent on stem but invariably present on hydrocladia”, although Billard observed that, on cladia, the ahydrothecate internodes may be occasionally fused to their preceding hydrothecate counterparts. Among the quite rich material studied here, only one case of fusion (Fig. 4B, after the proximal most hydrotheca) was noted upon the careful examination of 10 cormoids from sample MHNG-INVE-97938.

As noted above, the most prominent morphological difference between *H. polymorpha* and its so-called variety *sibogae* is to be found in the shape and size of their lateral nematothecae, including their corresponding apophyses (compare Fig. 3D-F and 4B-E). Another noteworthy difference relies in the comparatively shallower hydrothecae (compare Fig. 3D & E and 4C & E), and shorter cauline (compare Fig. 4A and 3A-B) and cladial ahydrothecate (compare Fig. 4C and 3B) internodes in the former. Moreover, only noticeable in living material, the bicolor aspect of the cormoids of the latter is striking (Fig. 1B, C), compared to the wholly yellow tinge observed in the former (Fig. 1A),

especially when both species occur in sympatry. Other morphological and morphometrical differences observed in the material studied herein are listed in Table 1. In light of these differences, we advocate here that the so-called variety *sibogae* must be recognized as a full species, different from *H. polymorpha*. The 16S data clearly corroborated this (Fig. 9).

Raising *Plumularia polymorpha* var. *sibogae* Billard, 1913 to full species is not threatened by *Plumularia sibogae* Billard, 1911, because the former is to be correctly placed in the genus *Halopteris* Allman, 1877 [as *H. sibogae* (Billard, 1913)], while the latter is accommodated in *Antennella* Allman, 1877.

Halopteris sibogae differs from its congeners through a series of characters. A number of species with “peculiarities” (see under *H. polymorpha*) should be excluded from the comparison, while the remaining ones are compared in Appendix 1.

Among them, and in accordance with the phylogenetic tree, *H. sibogae* comes close to *H. vervoorti* Galea, 2008 (see below an account on the latter). Besides its exceedingly long, and thus very distinctive, lateral nematothecae, *H. sibogae* shares the following features with *H. vervoorti*: 1) their cauline internodes are rather short and bear 1-2 nematothecae distal to each hydrotheca; 2) there are 1-2 axillar nematothecae associated to both cauline and cladial hydrothecae; 3) their cladia are heteromerously-segmented, their ahydrothecate internodes are short compared to their hydrothecate counterparts, and bear single nematothecae; 4) their female gonothecae are indistinguishable morphologically (compare Fig. 4G and 5H, I, P).

Distribution: Indonesia [between Misool I. and West Papua (Billard, 1913), Bali (present study), Tukang Besi Archipelago (present study)], Seychelles (Millard & Bouillon, 1973), and questionably Japan (Hirohito, 1983).

Halopteris vervoorti Galea, 2008

Figs 1D, 2C-E, 5; Tables 3, 4; Appendix 1

Halopteris vervoorti Galea, 2008: 42, fig. 9; 2010: 3, 4; 2013: 50.

Halopteris polymorpha – Ansin Agis *et al.*, 2001: 167, fig. 70. – (?) Preker & Lawn, 2010: 120 [non *Plumularia polymorpha* Billard, 1913 (*pro parte*): 24, fig. 14B, C].

Heterotheca buskii – (?) Hirohito, 1974: 30, fig. 14 (incorrect subsequent spelling).

Halopteris buskii – (?) Ryland & Gibbons, 1991: 527, fig. 2.

Halopteris buskii – (?) Hirohito, 1995: 244 fig. 82 (incorrect subsequent spelling).

non *Plumularia buskii* Bale, 1884: 125, pl. 10 fig. 3, pl. 19 figs 34-35.

Antennella secundaria – (?) Vervoort, 1967: 42, fig. 12 [non *Antennella secundaria* (Gmelin, 1791)].

Material examined: MHNG-INVE-98635; Republic of Maldives, Faafu Atoll, Magoodhoo Island, 3.07606°

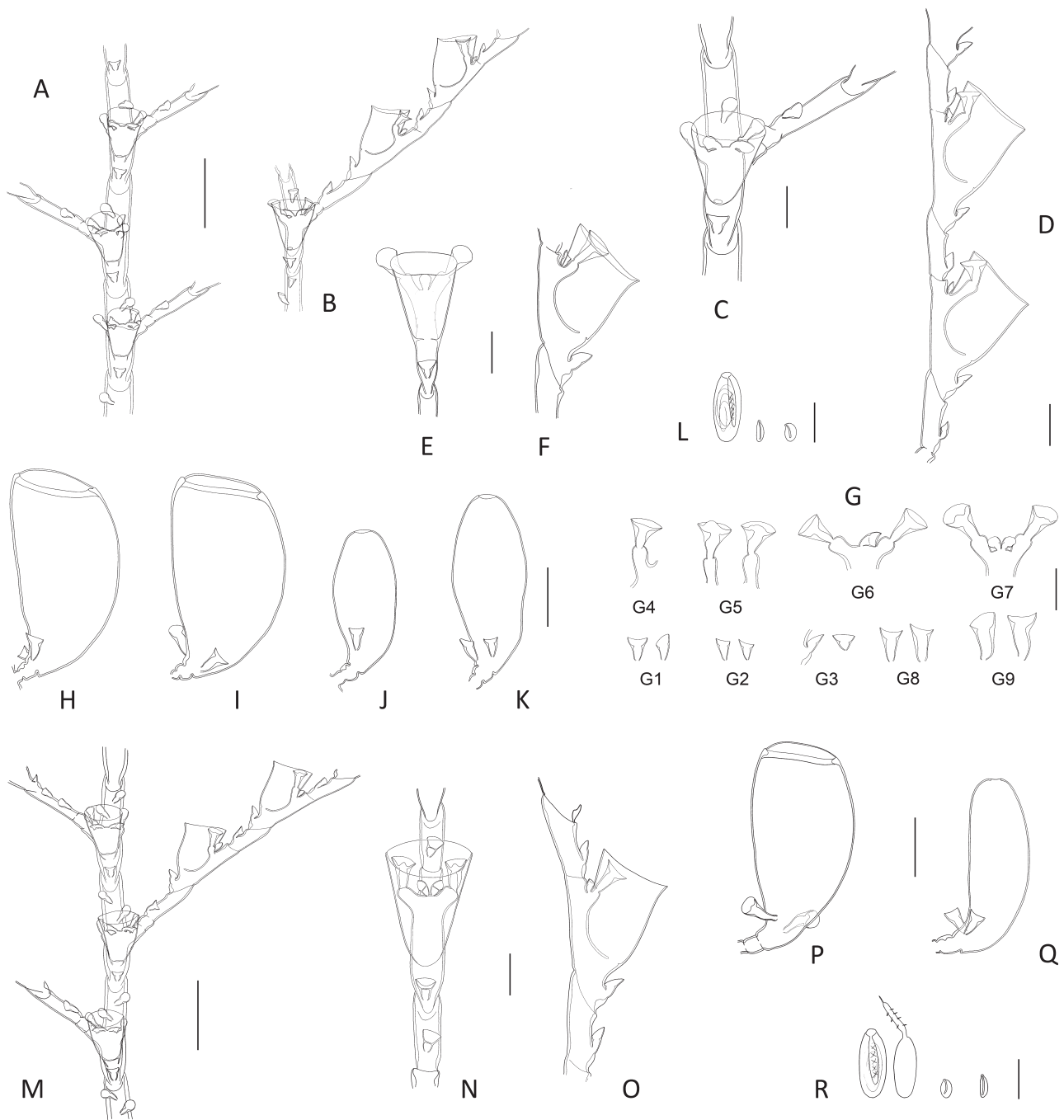


Fig. 5. *Halopteris vervoorti* Galea, 2008 from the Indian Ocean (A-K) and the Caribbean (M-R). Portions of stems with cladia (A, B, M). Cauline internode (C). Portion of cladium, enlarged (D). Hydrothecate internodes in frontal (E, N) and lateral (F, O) aspects. Nematothecae (G): from caulus (G¹) and cladia (G²), mesial (G³) and laterals (G^{4,5}) from cladial hydrothecae, single (G⁶) and paired (G⁷) axillar associated to cladial hydrothecae. Female (H, I, P) and male (J, K, Q) gonothecae. Cnidomes (L, R). Specimens MHNG-INVE-98635 (A, C, G⁷), MHNG-INVE-97952 (B, F, G^{4,6}, L), MHNG-INVE-98633 (D, E, G^{1-3,5,8,9}, H-K), HRG-1339 (M, P), HRG-0897 (O), HRG-0337 (Q, R). Figure in N is reproduced after Galea (2008). Scale bars: 10 μ m (L, R), 100 μ m (C-G, N, O), 200 μ m (H-K, P, Q), 300 μ m (A, B, M).

72.96159°, 3 m, coll. D. Maggioni and S. Montano; 29.01.2016; many stems, up to 1.3 cm high, some of them bearing female gonothecae; 16S sequence MF773743. – MHNG-INVE-98636; Republic of Maldives, Faafu Atoll, 3.07478° 72.96628°, 10 m, coll. D. Maggioni and S. Montano; 13.04.2016; 4 stems, 5–7 mm high, of which one bears two young female gonothecae; 16S sequence MF773742. – MHNG-INVE-97952; Indonesia, Bali, Pemuteran, -8.14338° 114.65805°, 0.5 m, coll. H.R. Galea; 04.10.2015; several sterile cormoids, up to 1.2 cm high. – MHNG-INVE-98633; Madagascar, Bay of Toliara, Dimadimatsy reef, -23.48234° 43.73285°, 1–2 m, coll. N. Gravier-Bonnet; 13.09.1969; fertile (monoecious) colony on alga, stems up to 0.8 cm high. – HRG-0337; France, Guadeloupe, Basse-Terre, Petite Anse, 16.09639° -61.77139°, 0–1 m, coll. H.R. Galea; 22.01.2008; numerous cormoids, up to 1.2 cm high, some bearing male gonothecae. – HRG-0897; France, Martinique, Case-Pilote, 14.64311° -61.14171°, 5–7 m, coll. H.R. Galea; 27.02.2014; several infertile plumes, up to 1.3 cm high. – HRG-1339; France, Martinique, Case-Pilote, 14.64337° -61.14199°, 1–2.5 m, coll. R. Ferry; 24.07.2017; numerous cormoids, up to 1.9 cm high, many bearing male gonothecae, and one their female counterpart; 16S sequence MF773741. – DM&SM-CU005; Dutch Caribbean, Curaçao I., Piscadera Bay, 12.12139° -68.96917°, 11 m, coll. S. Montano; 09.06.2017; two sterile stems, *ca.* 15 mm high; 16S sequence MF773740.

Diagnosis: Small-sized (up to 2.0 cm high) *Halopteris* with homomerously-divided stems; internodes rather short, comprising a hydrotheca in their lower 2/3rd part, a well-developed lateral apophysis, and up to 7 nematothecae (1 mesial, a pair of laterals, 2 axillar, and 1–2 superior ones in a median row). Cladia alternate, divided heteromerously; hydrothecate internodes comparatively longer than their ahydrothecate counterparts, bearing a centrally-placed hydrotheca and up to 5 nematothecae (1 mesial, a pair of laterals and generally 1, exceptionally 2, axillar nematothecae); ahydrothecate internodes very short, carrying single nematotheca in their lower halves. Hydrotheca deep, tubular, slightly flaring below aperture, rim circular, slightly scooped in lateral view. Lateral nematothecae barely surpassing hydrothecal rim, borne on well-developed apophyses; conical, walls of lower chamber gradually thickening distally, apical chamber shallow, rim from lowered to sinuated adaxially. Male gonothecae elongated-ovoid, borne on short, quadrangular pedicel; 2 basal nematothecae; distally a narrow, circular aperture. Female gonothecae comparatively larger, borne on short, quadrangular pedicel; broadly ovoid, tapering below, with large apical aperture with thickened rim, closed by glass-watch-shaped operculum; basally 2–3 nematothecae.

Description: Colonies composed of varied number of cormoids arising from tubular, creeping, branching

hydrorhiza, devoid of nematothecae. Stems simple, erect (up to 13 mm high in present material), monosiphonic (Figs 1D, 2C–E), composed of a basal, ahydrothecate part, and a much longer, distal part bearing hydrothecae and cladia. Basal part of varied length, almost straight, irregularly divided into successive segments of unequal length through up to 6 transverse nodes, bearing a total of up to 18 nematothecae arranged in two parallel, closely-set, longitudinal rows; distalmost segment separated from hydrothecate part of caulus through deeply-incised, oblique node. Upper part of caulus almost collinear proximally, becoming decidedly geniculate distally, divided into up to 15 regular internodes by means of oblique nodes (Fig. 5A, M); distally, the segmentation may occasionally change to heteromerous through the insertion of transverse nodes. Each stem internode composed of a hydrotheca situated in its proximal half, a lateral apophysis (or a pair in the proximal most internode), and up to 7 nematothecae (a mesial, a pair of laterals, a pair of axillar, as well as 1 or, occasionally, 2 superior ones in a median row (Fig. 5C); superior nematothecae confined to a separate, ahydrothecate internode, where caulus segmentation becomes heteromerous; often a pair of laterally-displaced superior nematothecae, inserted at same level, on proximal most stem internode bearing the pair of cladia); internodes slightly bent above hydrotheca in opposite direction to corresponding cladium. Apophyses, exclusive of those of proximal most internode (that are paired), alternate along stem, each supporting a cladium. Cladia composed of a proximal, short, athecate, quadrangular internode, followed by a succession of a- and hydrothecate internodes resulting through a heteromerous segmentation (Fig. 5B). Ahydrothecate internodes with transverse proximal node and oblique distal node, carrying proximally a single nematotheca; internodes very short, though proximal most one slightly longer than subsequent counterparts (Fig. 5D). Hydrothecate internodes, up to 4 per cladium, with oblique proximal node and transverse distal node, rather short, accommodating a centrally-placed hydrotheca and its up to 5 associated nematothecae (1 mesial, a pair of laterals, as well as 1, or exceptionally 2, axillar nematothecae) (Fig. 5E, N). All hydrothecae deep, conical, adnate for about half their adaxial length; free adaxial wall straight, abaxial wall slightly sigmoid (basally imperceptibly concave, distally slightly everted below rim); aperture wide, circular, rim slightly scooped in lateral view (Fig. 5F, O); hydranths with *ca.* 14 filiform tentacles. Gonothecae borne on both caulus and cladia through short, lateral apophyses arising midway between hydrothecal bases and mesial nematothecae. Female gonothecae large, piriform, borne on short quadrangular pedicels; basally a couple of nematothecae; distally a large, ovoid, transverse aperture, with conspicuously thickened rim, closed by

a glass-watch-shaped operculum (Fig. 5H, I, P). Male gonothecae borne on single, quadrangular pedicels; fusiform to elongated-ovoid, with couple of basal nematothecae, and a distal, narrow, circular, transverse aperture, closed by thin perisarc sheet (Fig. 5J, K, Q). All nematothecae bithalamic, including the axillar ones; mesial triangular in frontal view, upper chamber slightly shallower than basal one, with conspicuously lowered rim on adaxial side (Fig. 5G³); laterals borne on well-developed apophyses, conical, moderately-long (Fig. 5G^{4, 5}), not always reaching the hydrothecal rim (Fig. 5D, F, O); basal chamber narrow, tubular, rather tall; upper chamber shallow, wide, margin either lowered or sigmoid on adaxial side; cauline (Fig. 5G¹) and cladial (Fig. 5G²) nematothecae, other than those associated to the hydrothecae, as well as those borne by the gonothecae (Fig. 5G^{8, 9}), long conical, with tall basal chamber and comparatively shallow upper chamber, with rim slightly lowered adaxially; axillar nematothecae (Fig. 5G^{6, 7}) with much thinner perisarc than their exposed counterparts, short, with chambers of nearly the same depth, wall of upper chamber facing adaxial hydrothecal wall distinctly lowered. Cnidome (Fig. 5L, R) composed of 3 types of microbasic mastigophores: large, elongated-ovoid [(16.8-18.2) × (6.5-6.8) μm, in nematophores, as well as scattered in the coenosarc]; small, banana-shaped [(5.6-5.8) × (1.9-2.1) μm, in tentacles]; small, ovoid capsules [(4.5-4.9) × (2.8-2.9) μm, scattered in the coenosarc]. Color in life from pale yellow to brownish.

Remarks: The segmentation of cauli is generally homonomous, although the insertion of transverse node towards their distal parts introduces a heteronomous segmentation. The cladia are generally divided heteronomously, though an occasional absence of transverse nodes could be noted in material MHNG-INVE-98635, this not supposing a homonomous segmentation throughout the involved cladium. The cauline hydrothecae generally display a pair of axillar nematothecae, though only one, placed medially, may occasionally occur in distalmost hydrothecae. In contrast, generally a single axillar nematotheca is associated to each cladial hydrotheca though, exceptionally, a couple may occur. The stems internodes bear generally 1, occasionally 2, median superior nematothecae (*ca.* 95% and 5%, respectively, *n*=150); these are arranged in a single row in ordinary internodes, while they are shifted laterally and occur at the same level in the basalmost internodes giving rise to pairs of cladia. The first cladial internodes bear generally but a single nematotheca; rarely, two nematothecae were observed in some cormoids from MHNG-INVE-98635. The material MHNG-INVE-9833 comprises monoecious stems, while only female gonothecae seem to occur in former.

The trophosomes of the present materials from the Indian Ocean were compared with those of specimens from the

Lesser Antilles, and all appear indistinguishable, both morphologically and morphometrically (compare Fig. 5A, B, D and 5M, O). In addition, the as yet unknown female gonothecae of the Caribbean population, were found only recently (sample HRG-1339), and do not differ from those of the Indian Ocean counterparts (compare Fig. 5P and 5H & I; Table 3). Moreover, the molecular study supports the conclusions based on the morphological observations (Fig. 9).

Several literature records of hydroids conform, through the segmentation of both the stem and cladia, and the number and position of the nematothecae they carry, to the morphology of the present species. However, minor discrepancies could be occasionally noted, although they are thought to reflect rather overlooked details. Thus, Vervoort's (1967) material from the Red Sea, obviously erroneously assigned to *Antennella secundaria* (Gmelin, 1791), is reportedly said to carry single axillar nematothecae behind the cauline hydrothecae, a situation – indeed – met with only distally in the stems of the present species. Moreover, it should be stated that one nematotheca belonging to a pair, namely that given off on the same side as the corresponding cladium, may be difficult to notice as it is hidden (in frontal view) by the apophysis supporting the lateral nematotheca originating on the same side (see Fig. 5C – lateral nematotheca on same side as the cladium expressly shown).

The “second pair of lateral nematothecae [...] mesial to and much smaller than normal pair”, observed by Ryland & Gibbons (1991) in their Fijian specimens assigned to *H. buskii*, is nothing else than the couple of cauline axillar nematothecae. Similarly so, besides the commonly seen single cladial axillar nematotheca, “two medio-superior nematothecae are often present behind the free adcauline wall of the hydrotheca”. These, combined to the heteronomous segmentation of cladia, the shape and size of both hydro- and lateral nematothecae, and the morphology of the female gonotheca, suggest that their specimens are, most probably, conspecific with *H. vervoorti*.

The Japanese materials assigned to both *Heterotheca* and *Halopteris buski* (*sic!*) by Hirohito (1974, 1995, respectively) are morphologically close to the present species, as their cauli and cladia display the same segmentation, the same number and position of nematothecae, and the monoecious condition of their cormoids. However, a pending genetic study is expected to clarify their relationships undoubtedly.

The presence of *H. vervoorti*, originally described from the Caribbean (Galea, 2008), in the Indian Ocean is not entirely surprising. The reverse situation is, indeed, more common at present, with many examples of hydroids, primarily known to occur in the Indo-Pacific that were subsequently recorded from the Caribbean, *viz.* *Sertularia rugosissima* Thornely, 1904 (Galea, 2008), *S. tongensis* (Stechow, 1919) (Galea, 2010), *S. hattorii* Leloup, 1940 (Galea & Ferry, 2015), *Aglaophenia postdentata* Billard,

1913 (Galea, 2013), and *Clytia edentula* Gibbons & Ryland, 1989 (Galea & Ferry, 2015). Whether these species primarily occurred in one geographical area and spread afterwards elsewhere, could not be established at this stage, but it is obvious that only the frequency of the collecting efforts first revealed their presence in one area but not in the other.

Halopteris vervoorti comes close to a number of nominal species through the occurrence of paired axillar nematothecae behind the cauline hydrothecae and the heteromorous segmentation of its cladia, viz. *H. australis* sp. nov. (see below), *H. brasiliensis* (see below), *H. liechtensternii* (Marktanner-Turneretscher, 1890), and *H. sibogae* (Billard, 1913). However, unlike *H. australis*, it does not possess hydrothecae with distinctly sinuated margins or exceedingly-long lateral nematothecae, respectively. On the other hand, *H. brasiliensis* is a species forming taller cormoids, with thicker stems and cladia, broader hydrothecae, and cauline superior nematothecae distinctly arranged into two longitudinal rows; unlike in *H. vervoorti*, its cauline hydrothecae occupy nearly the whole length of the internode. *Halopteris liechtensternii* is a species with comparatively longer stem internodes (and, implicitly, more widely-spaced cladia), provided regularly with 2-3 superior nematothecae arranged in two distinct rows, its female gonothecae are much longer and almost cylindrical, while its males appear dwarfed compared to those of the present species. *Halopteris sibogae*, besides many common features shared with *H. vervoorti* (see under the former), is immediately distinguishable through its exceedingly long lateral nematothecae. Additional differences to other congeners are summarized in Appendix 1.

Distribution: Lesser Antilles (Galea, 2008, 2010, 2013), Cape Verde (Ansín Agís *et al.*, 2001, as *H. polymorpha*), (?) Red Sea (Vervoort, 1967; as *Antennella secundaria*), Madagascar, the Maldives, Indonesia (present study), (?) Australia (Preker & Lawn, 2010, as *H. polymorpha*), (?) Japan [Hirohito (1974), as *Heterotheca buskii* (sic!); Hirohito (1995), as *Halopteris buskii* (sic!)], (?) Fiji (Ryland & Gibbons, 1991, as *Halopteris buskii*).

***Halopteris australis* Galea, sp. nov.**

Figs 1E, 2F, 6; Table 5; Appendix 1

Halopteris buskii – Vervoort & Vasseur, 1977: 72, fig. 31 [non *Halopteris buskii* (Bale, 1884)].

Halopteris polymorpha – Schuchert, 1997 (*pro parte*): 64, fig. 23 [non *Halopteris polymorpha* (Billard, 1913)].

Type material: MHNG-INVE-82742; France, New Caledonia, Nouméa, south of N'Géa islet, -22.296° 166.489°, 9 m, coll. E. Tardy; 06.10.2012; fertile (female) colony in alcohol and two microslides (H20/37-38), with stems up to 1.8 cm high, growing on algae.

Diagnosis: Small-sized *Halopteris*, with cormoids not exceeding 2.5 cm high. Stems monosiphonic, homomously-segmented, internodes rather long, bearing a hydrotheca in their proximal half, a lateral apophysis, and up to 8 nematothecae (1 mesial, a pair of laterals, a pair of axillar, as well as up to 3 superiors in two parallel rows). Cladia alternate, heteromously-segmented; 1st ahydrothecate internode with 1, exceptionally 2, nematothecae in a row; ordinary ahydrothecate internodes with 1 nematotheca; hydrothecate internodes with a hydrotheca and its up to 5 associated nematothecae (1 mesial, a pair of laterals, and 1, or rarely 2, axillar); hydrotheca cup-shaped, deep, adnate for 2/3rd its adaxial wall, swollen basally, rim distinctly sinuated in lateral view, aperture circular, lateral nematothecae long, borne on well-developed apophyses, surpassing hydrothecal rim. Female gonothecae given off from caulus; piriform, borne on quadrangular pedicel, 2 basal nematothecae, aperture large, circular, perpendicular to long axis of theca, rim thickened, a watch-glass-shaped operculum.

Etymology: From the Latin *austrālis*, meaning “of the south” with reference to its occurrence in the South Pacific.

Description: Colonies composed of a varied number of upright cormoids, up to 2 cm high in present material, arising from creeping, branching, anastomosing hydrorhiza. Stems erect, simple, monosiphonic (Figs 1E, 2F), composed of a basal, ahydrothecate part, irregularly divided into a few segments (up to 5) by means of transverse constrictions of the perisarc, and carrying a varied number of nematothecae arranged in two parallel rows; above, remainder of stem comprising a much longer, hydrothecate part, homomously-segmented into regular internodes by means of oblique nodes (Fig. 6A), slightly marked proximally to more conspicuous distally; occasionally, transverse nodes can be inserted towards the distal end of cauli, creating a heteromorous segmentation; a hinge joint between the two parts of the stem. Up to 26 relatively long cauline internodes, almost collinear proximally, gradually becoming geniculate towards distal end; each provided with a hydrotheca in its proximal half, a well-developed, lateral apophysis, as well as up to 8 nematothecae: 1 mesial, a pair of laterals, a pair of axillar (only one of these subsisting distally on stem) (Fig. 6B), as well as 1-3 superior ones in two parallel, closely-set rows (when only two of these are present, they may occur at the same level, or one above the other; they are confined to a separate ahydrothecate segment when transverse nodes intervene towards distal end of caulus). Cladia up to 2.5 mm long, alternate, except in the proximal most cauline internodes, where they are opposite; composed of a short, quadrangular segment proximally, followed by a heteromorous division into alternating ahydrothecate and hydrothecate internodes; the former

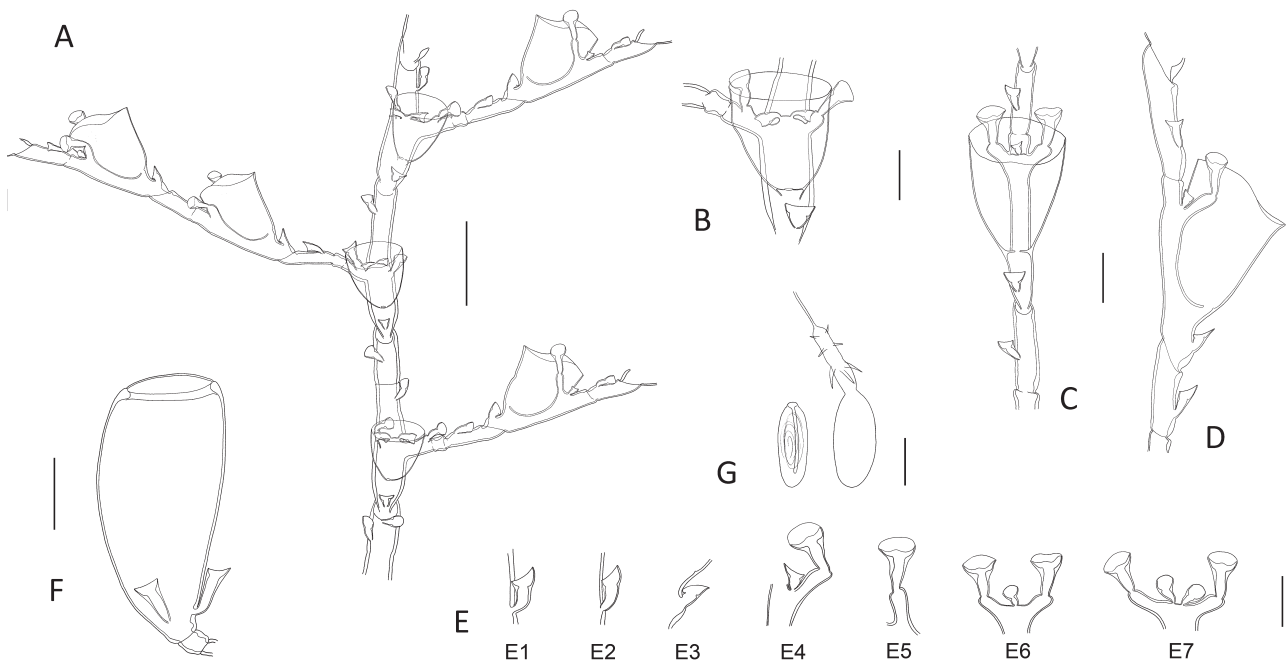


Fig. 6. *Halopteris australis* sp. nov. Portion of stem and basal parts of three cladia (A). Stem internode with hydrotheca (B). Portions of cladia enlarged in frontal (C) and lateral (D) aspects. Nematothecae (E): from caulus (E¹) and cladia (E²), mesial from cladial hydrotheca (E³), lateral from cauline (E⁴) and cladial (E⁵) hydrothecae, single (E⁶) and paired (E⁷) axillar associated to cladial hydrothecae. All from sample MHNG-INVE-82742. Scale bars: 10 μ m (G), 100 μ m (B-E), 200 μ m (F), 300 μ m (A).

with proximal node transverse and distal node oblique; the reverse in hydrothecate internodes (Fig. 6D); 1st ahydrothecate internode comparatively longer than subsequent ones, and carrying single nematotheca (exceptionally 2); ordinary ahydrothecate internodes short, and provided with one nematotheca; hydrothecate internodes up to 5 per cladium, comparatively longer than their ahydrothecate counterparts, and carrying a centrally-placed hydrotheca and its up to 5 associated nematothecae: a mesial, a pair of laterals, and generally one axillar, although a pair could be occasionally noted (Fig. 6C). Hydrothecae cup-shaped, rather deep, about 1/3rd adnate; abaxial wall slightly sigmoid, rounded proximally and slightly flaring below the rim; aperture circular in apical view, but distinctly sigmoid when seen laterally, due to broad (though shallow) abaxial emargination, giving the impression that an abaxial cusp occurs (Fig. 6A, D). All nematothecae, including the axillar ones, bithalamic and movable; mesial nematothecae triangular in frontal view, with deep adaxial emargination (Fig. 6E³); laterals relatively long, surpassing the hydrothecal rim (Fig. 6D), and borne on well-developed apophyses; basal chamber high and narrow, upper chamber shallow, with sigmoid adaxial wall (Fig. 6E⁴⁻⁷); axillar nematothecae (Fig. 6E^{6,7}) small, with wall of upper chamber lowered on side facing adaxial wall of hydrotheca; both cladial (Fig. 6E²) and cauline (Fig. 6E¹) nematothecae characteristically turned posteriad, tall, conical, with rim of apical

chamber lowered adaxially. Female gonothecae borne on cauli by means of short, lateral apophyses given off from below the hydrothecae, followed by a pedicel composed of a quadrangular segment; large, piriform, with 2 basal nematothecae, and a large, apical aperture with thickened rim, perpendicular to long axis of the theca, and closed by a watch-glass-shaped operculum (Fig. 6F). Male gonothecae elongated-ovoid, curved proximally and provided there with single nematotheca; aperture distal, small, circular. Hydranths badly preserved, tentacle number could not be ascertained. Cnidome (Fig. 6G): only large capsules (*ca.* 17.5 $\times$ 6.3 μ m), likely pseudostenoteles, observed in the material in hand. Color in life: milky white (Fig. 1E).

Dimensions: See Table 5.

Remarks: There is little doubt that the present material from New Caledonia is conspecific with the specimens with distinctly sinuated hydrothecal margins from French Polynesia examined by Vervoort & Vasseur (1977, as *H. buskii*) and, subsequently, by Schuchert (1997, provisionally assigned to *H. polymorpha*). Their main morphological and morphometrical features are compared in Table 5. Unfortunately, it was not possible to obtain the material of Vervoort & Vasseur for a re-examination, due to ongoing renovation of NBC.

The cauline internodes bear commonly 1 (52%) or 2 (44%) superior nematothecae, although up to 3 may occasionally (4%, *n* = 75 internodes belonging to 5

different stems) be present in the material in hand. Schuchert (1997), however, reports up to 5 of these. The number of axillar nematothecae was apparently overlooked by Vervoort & Vasseur (1977):

- 1) Schuchert (1997) stated that, occasionally, these may occur in pairs behind the hydrocladial hydrothecae, a conclusion confirmed by our observations;
- 2) it was noted that, on cauli, one nematotheca of a pair, namely that bent towards the cladium, is hidden by the apophysis supporting its lateral counterpart, and requires a careful examination to be noticed; alternatively, it should be stated that only one nematotheca of a pair subsists on the distalmost cauline internodes.

Only female gonothecae occur in the present material (Fig. 6F), although those of both sexes were illustrated by Schuchert (1997, fig. 23B, right).

Halopteris australis, through the presence of pairs of axillar nematothecae especially on the stem, and the heteromerous segmentation of its cladia, resembles *H. brasiliensis* sp. nov., *H. liechtensternii*, and *H. vervoorti*. However, any of these is provided with the distinctively sinuated hydrothecal margin displayed by it. In addition, *H. brasiliensis* has thicker stems and cladia, its lateral nematothecae are relatively short and conical, and do not surpass the hydrothecal rim. *Halopteris liechtensternii* is readily distinguished through the shape and size of its gonothecae, the females being long and almost tubular, while the males are dwarfed. *Halopteris vervoorti* forms comparatively shorter cormoids, with shorter stem internodes (and, consequently, more approximated cladia) provided with 1-2 superior nematothecae characteristically arranged in a row, and its hydrothecae are slightly shorter and narrower. Additional differences to other congeners are summarized in Appendix 1.

Distribution: New Caledonia (present study), French Polynesia (Vervoort & Vasseur, 1977; as *H. buskii*).

***Halopteris millardae* Galea, sp. nov.**

Figs 1F, 2G, 7; Table 5; Appendix 1

Halopteris polymorpha – Millard & Bouillon, 1973 (*pro parte*): 83, fig. 10F, G, H, J. – Bouillon *et al.*, 1995: 49. – Schuchert, 1997 (*pro parte*): 66, 72, fig. 22A-D [non *Halopteris polymorpha* (Billard, 1913)].

non *Halopteris polymorpha* – Millard & Bouillon, 1973 (*pro parte*): 83 (= *H. platygonotheca* Schuchert, 1997).

Halopteris buskii – Rees & Vervoort, 1987 (*pro parte*): 119, fig. 25A-B [non *Halopteris buskii* (Bale, 1884)].

Holotype material: MACT2700; Seychelles, Mahé I., coll. J. Bouillon (MRAC Expedition); 1966; numerous cormoids, 1.5-7 cm high, with both female and male gonothecae [material studied by Millard & Bouillon (1973), as *H. polymorpha* (Billard, 1913); not studied here due to ongoing renovation of MRAC; however,

4 microslides (MHNG-INVE-37494, H12/32-35) prepared from the holotype, were examined for the purpose of the present study; according to Schuchert (1997: 55), cormoids of *H. platygonotheca* Schuchert, 1997 co-occur in the original sample].

Paratype: MHNG-INVE-98634; Republic of Maldives, Faafu Atoll, 3.06497° 72.9212°, 35 m, coll. D. Maggioni and S. Montano; 14.04.2016; colony composed of 6 sterile stems, 1.7-3.9 cm high; 16S sequence MF773747.

Diagnosis: *Halopteris* with tall cormoids, reportedly reaching 7 cm high; stems homomerously-segmented, each internode moderately-long, carrying a hydrotheca, a lateral apophysis, and up to 7 nematothecae: 1 mesial, a pair of laterals, a scale-shaped axillar one, as well as 2-3 superior ones arranged in two parallel rows; cladia alternate, heteromerously-segmented; ahydrothecate internodes with 2 laterally-displaced nematothecae (distally, only 1 of these subsists); hydrothecate internodes with a hydrotheca and its 4 associated nematothecae: 1 mesial, a pair of laterals, and a small, scale-shaped axillar one. Colonies monoecious. Female gonotheca borne on stems, large, ovoid, laterally flattened, with 2 basal nematothecae, and a distal, transverse aperture closed by glass-watch-shaped operculum. Male gonothecae borne on both stems and cladia, small, fusiform, with narrow distal aperture, and one basal nematotheca.

Etymology: This species honors the late N.A.H. Millard (1914-1997) for her outstanding contribution to the hydrozoan research.

Description: Colonies composed of a varied number of tall stems (reportedly up to 7 cm in height) arising from tortuous, creeping, branching, anastomosing hydrorhiza, devoid of nematothecae. Stems erect, simple, monosiphonic (Figs 1F, 2G), composed of a basal, ahydrothecate part of varied length, and a much longer, distal part bearing hydrothecae and hydrocladia; basal part arising directly from hydrorhiza without constriction above origin, usually not segmented by transverse nodes, and carrying a varied number of nematothecae in two parallel rows; distalmost node deeply-cut and oblique; remainder of stem homomerously-segmented into regular internodes by means of oblique nodes; each internode moderately long, with a hydrotheca in its basal half, a short lateral apophysis supporting a cladium, and up to 8 nematothecae: 1 mesial, a pair of laterals, a small, scale-shaped axillar one, as well as generally 2, occasionally 3, or exceptionally 4, superior nematothecae arranged in two parallel rows (Fig. 7A, B); proximal most internode carries 2 opposite apophyses supporting a pair of cladia, and usually bears 3-4 superior nematothecae. Cladia borne on corresponding stem apophyses, alternate, composed of a proximal, short, quadrangular segment, followed by a succession

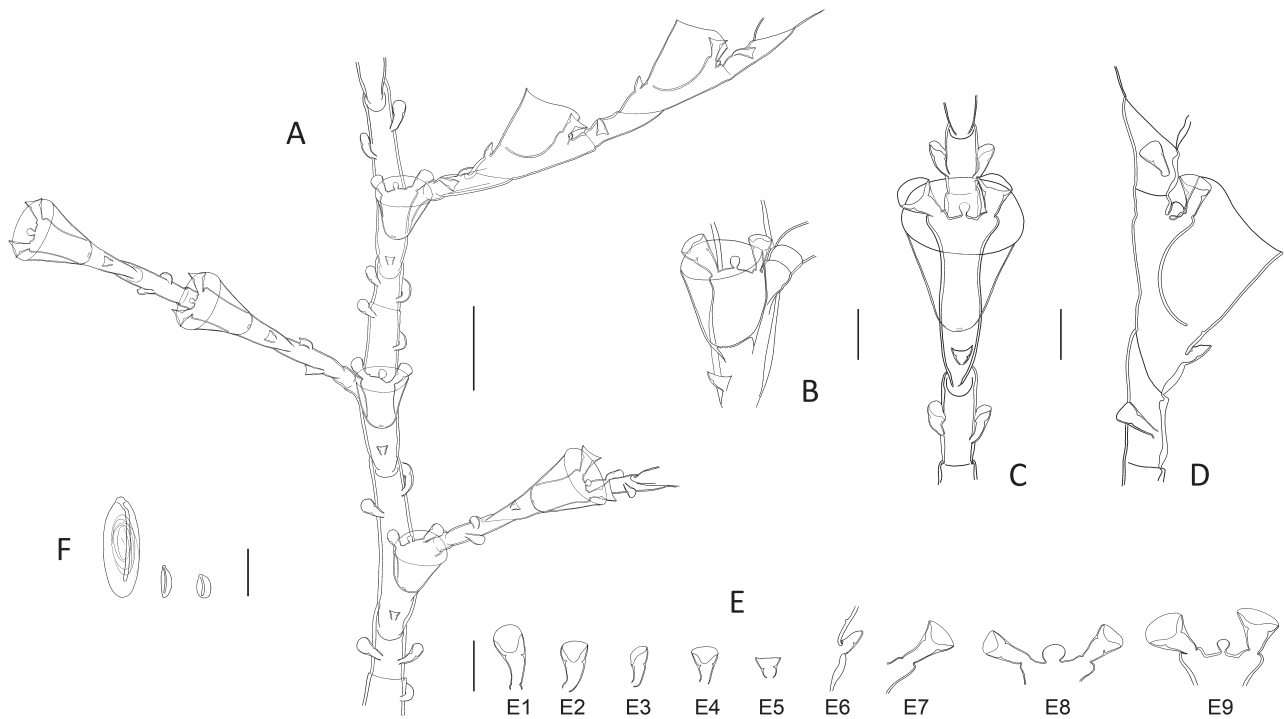


Fig. 7. *Halopteris millardae* sp. nov. Portion of stem with basal parts of three cladia (A). Hydrothecae from stem (B) and cladia (C, D), the latter in frontal and lateral aspects, respectively. Nematothecae (E): from caulus ($E^{1,2}$) and ahydrothecate cladial internodes ($E^{3,4}$), mesial ($E^{5,6}$) and lateral (E^7) from cauline hydrotheca, and axillar associated to both cauline (E^8) and cladial (E^9) hydrothecae. All from sample MHNG-INVE-98634. Scale bars: 10 μm (F), 100 μm (B-E), 300 μm (A).

of athecate and thecate internodes resulting from a heteromerous segmentation (Fig. 7A); ahydrothecate internodes with straight node proximally and oblique node distally; the reverse in hydrothecate internodes; the latter, up to 5 per cladium in the material in hand, comprising a centrally-placed hydrotheca, and its 4 associated nematothecae: 1 mesial, a pair of laterals, as well as a minute, scale-shaped axillar one (Fig. 7C, D); ahydrothecate internodes shorter than their hydrothecate counterparts, with generally 2 laterally-displaced nematothecae, either opposite or subopposite, more often found in proximal most internodes, whereas only one of these is retained by the distalmost internodes. Hydrothecae cup-shaped, moderately-deep, fused for about 1/3rd their adaxial length; abaxial wall straight for most of its length, slightly everted below aperture; the latter perfectly circular in apical view, slightly flaring and showing a sinuated rim in lateral view, though not producing an abaxial cusp (Fig. 7D). All nematothecae, except the axillar ones, bithalamic and movable; mesial ones triangular in frontal view, with deeply-scooped rim on adaxial side (Fig. 7E^{5,6}); laterals borne on rather short apophyses, conical, with thickened walls (Fig. 7E⁷), not surpassing the hydrothecal rim (Fig. 7D); cauline (Fig. 7E^{1,2}) and cladial (Fig. 7E^{3,4}) nematothecae characteristically turned posteriad (Fig. 7A, C), long, conical, with tall basal chambers and

comparatively shallow apical chambers, with adaxially-scooped rims; axillar nematothecae associated to the hydrothecae of both caulus (Fig. 7E⁸) and cladia (Fig. 7E⁹), monothalamic. Stems monoecious. Female gonothecae borne below the stem hydrothecae through short lateral apophyses and a single-segmented, quadrangular pedicel; large, ovoid, laterally-flattened, with two nematothecae on base, and a distal, transverse, conspicuously thickened aperture closed by a glass-watch-shaped operculum. Male gonothecae borne on both stems and cladia, through short, lateral apophyses and a single-segmented, quadrangular pedicel; comparatively smaller than female, fusiform, with distal, narrow, circular aperture, and a basal nematotheca. Color in life: brownish (Fig. 1F). Cnidome (Fig. 7F) composed of 3 types of microbasic mastigophores: large, elongated-ovoid [(19.9-21.3) $\times$ (7.3-8.0) μm , in nematophores, as well as scattered in the coenosarc]; small, banana-shaped [(5.8-6.5) $\times$ (2.1-2.3) μm , in tentacles]; small, ovoid capsules [(5.1-5.8) $\times$ (2.9-3.1) μm , scattered in the coenosarc].

Dimensions: See Table 5.

Remarks: Upon comparison of the newly-collected Maldivian specimens with the slide material MHNG-INVE-37494 (H12/32-35) prepared from the holotype designated herein [sample MACT2700 studied by

Millard & Bouillon (1973), as *H. polymorpha* (Billard, 1913)], it appears that both are conspecific.

The description of the gonothecae, often distorted in the slide material available (H12/32: ♂; H12/33: ♂ & ♀; H12/35: ♂), was taken after Millard & Bouillon (1973: 84, fig. 10H & J) and Schuchert (1997: 22, fig. 22D, as *H. polymorpha*).

The tallest cormoid examined here (3.9 cm high) bears 54 cauline hydrothecate internodes. Not only the proximal most internode gives rise to a pair of cladia, but this situation is also repeated in several subsequent, consecutive, more distal internodes. In one cormoid, a secondary stem arises from one of the paired, basalmost hydrocladia.

The first cladial ahydrothecate internodes do not differ much in length compared to their subsequent counterparts; they generally bear 2 nematothecae, though exceptionally 3 were noted. The remaining internodes equally bear 2 nematothecae (although, exceptionally, two pairs could be found) when they are found in the proximal parts of the cladia, while only one nematotheca occurs in those internodes confined to the distalmost parts of the cladia. Rees & Vervoort's (1987) record from Zanzibar (Stn. 112) assigned to *H. buskii* likely belongs to the present species. Indeed, the occurrence of pairs of suprahydrothecal nematothecae, and of a single axillar nematotheca on the cauline internodes, are distinctive. However, the authors mention only one nematotheca per ahydrothecate cladial internode; as stated above, this situation is, quite often, met with in the distalmost internodes of the material MHNG-INVE-37494. It should also be stressed that only one nematotheca of a couple is visible when the cladia are seen laterally, especially in material mounted between slide and coverslip. Strangely, Rees & Vervoort do not mention a sinuated hydrothecal rim, though it should be underlined that this peculiarity is only noticeable towards the adaxial thecal wall, where the presence of lateral nematothecae could make it less obvious upon a routine examination.

Halopteris millardae comes close to a few congeners with homomerously-segmented cauli and a heteromerous division of their cladia, and whose both cauline and cladial hydrothecae are provided with an axillar nematotheca, namely *H. nuttingi* (Billard, 1911) and *H. polymorpha*. *Halopteris nuttingi* has proportionally shorter cauline internodes [compare fig. 21B in Schuchert (1997) with Fig. 7A herein], provided with up to three pairs of superior nematothecae in two parallel rows, and the upper chamber of its lateral nematothecae is globular, with the rim scooped on both ad- and abaxial walls [Billard (1913), as *H. buski* (*sic!*); Schuchert (1997, fig. 21C, H), as *H. polymorpha*]. *Halopteris polymorpha* has comparatively longer stem and cladial ahydrothecate internodes (Fig. 3A, B), its hydrothecae are shallower (Fig. 3D, F) and are provided with an even rim. Additional differences to other congeners are summarized in Appendix 1.

Distribution: Seychelles [Millard & Bouillon (1973), as *H. polymorpha* (Billard, 1913)], Maldives (present study), Zanzibar [Rees & Vervoort (1987), as *H. buskii* (Bale, 1884)].

Halopteris brasiliensis Galea, sp. nov.

Figs 2H, 8; Table 5; Appendix 1

Halopteris buskii. – Migotto, 1996: 48, fig. 9F-H [non *Halopteris buskii* (Bale, 1884)].

Halopteris polymorpha. – Schuchert, 1997 (*pro parte*): 72, fig. 22F-H [non *Halopteris polymorpha* (Billard, 1913)].

Holotype material: MHNG-INVE-37495; Brazil, São Sebastião Channel, 6–8 m, coll. A.E. Migotto; 06.10.1987; two slides, H12/36 & 37, each containing a ca. 1.6 cm high cormoid provided with a female gonotheca.

Diagnosis: *Halopteris* with medium-sized plumes, reaching 3 cm high; stems simple, monosiphonic, homomerously-segmented; internodes rather short, with a lateral apophysis, a hydrotheca, and its up to 7 associated nematothecae (1 mesial, a pair of laterals, a pair of axillar, and generally 2 superiors, the latter either opposite or subopposite). Hydrocladia alternate, heteromerously-segmented; ahydrothecate internodes very short, with 1 nematotheca; hydrothecate internodes comparatively longer, with one hydrotheca and up to 5 nematothecae (1 mesial, a pair of laterals, and commonly 1, rarely 2, axillar). Female gonothecae borne on stems; large, piriform, with 2–3 long, basal nematothecae, aperture distal, wide, circular, perpendicular to long axis of theca, closed by glass-watch-shaped operculum.

Etymology: Named after the country of occurrence.

Description: Colonies composed of reportedly up to 3 cm high cormoids arising from creeping, branching hydrorhiza. Stems erect, simple, monosiphonic (Fig. 2H), composed of a basal, ahydrothecate portion, and a much longer, distal part bearing both hydrothecae and hydrocladia. The former of varied length, irregularly divided into a number of segments by means of transverse nodes, bearing nematothecae arranged in two longitudinal rows; last node deeply-cut and oblique. Remainder of caulus homomerously-segmented into rather short internodes by means of oblique nodes (Fig. 8A); each internode with a hydrotheca in its proximal half, a cladial apophysis lateral to it (two opposite in proximal most internode), and up to 7 nematothecae, of which 5 are associated to the hydrotheca (1 mesial, a pair of laterals, and a pair of axillar) (Fig. 8B), and 2 (slightly displaced laterally and, thus, forming an opposite or a subopposite pair) occur distally on the internode (occasionally, only one of these is present; however, in the basalmost internodes bearing pairs of cladia, 2–3 of these occur). Hydrocladia

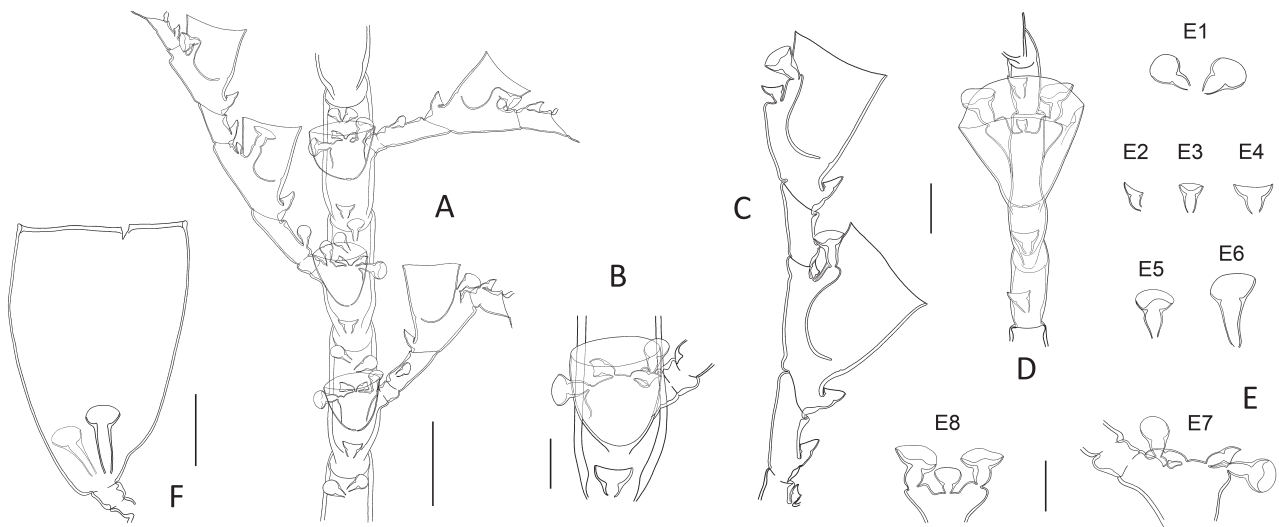


Fig. 8. *Halopteris brasiliensis* sp. nov. Portion of stem with basal parts of three cladia (A). Stem hydrotheca (B). Portions of cladia in lateral (C) and frontal (D) aspects. Nematothecae (E): from caulus (E¹) and ahydrothecate cladial internodes (E^{2,3}), mesial from cauline hydrotheca (E⁴), lateral from cladial hydrotheca (E⁵), from female gonotheca (E⁶), pair of axillar from cauline hydrotheca (E⁷) and single axillar from cladial hydrotheca (E⁸). All from sample MHNG-INVE-37495. Scale bars: 100 μ m (B-E), 200 μ m (F), 300 μ m (A).

alternate, borne on corresponding cauline apophyses; composed of a short, athecate, quadrangular segment, followed by an alternation of ahydrothecate and hydrothecate internodes resulting from a heteromerous segmentation (Fig. 8C); ahydrothecate internodes with proximal node transverse and distal node oblique; the reverse in hydrothecate internodes; first ahydrothecate internode comparatively longer than subsequent ones, and carrying a single nematotheca; ordinary ahydrothecate internodes very short and provided with single nematotheca; hydrothecate internodes, reportedly up to 7 per hydrocladium, accommodating a hydrotheca and its up to 5 associated nematothecae (1 mesial, a pair of laterals, and commonly one – rarely a pair – of axillar nematothecae) (Fig. 8D). Hydrothecae cup-shaped, rather deep, adnate for about half their height, walls slightly divergent, abaxial one imperceptibly sigmoid (concave proximally, convex below aperture), free part of adaxial one straight; aperture wide, circular, rim even (Fig. 8C). Hydranths with conical hypostome and 16-17 filiform tentacles. All nematothecae, including the axillar ones, bithalamic and movable; mesial ones short, with lower and upper chambers of nearly same depth (Fig. 8E⁴), and rim of upper chamber lowered on adaxial side; lateral nematothecae borne on well-developed apophyses, with tall basal chamber and shallow upper chamber with sigmoid rim on adaxial side (Fig. 8E⁵); whole nematotheca barely reaching hydrothecal rim (Fig. 8C); cauline (Fig. 8E¹) and cladial (Fig. 8E^{2,3}) nematothecae similar in shape to the laterals, but with lowered rim on the adaxial side of upper chamber; cauline axillar nematothecae displaced laterally and facing outwards in opposite directions

(Fig. 8E⁷); cladial axillar nematothecae commonly occurring singly (Fig. 8E⁸), reportedly in pairs in rare instances. Gonothecae (only female known) borne on both cauli and cladia, given off laterally from below the hydrothecal bases; large, piriform, with 2-3 long, basal nematothecae, and a broad, circular aperture with thickened rim, perpendicular to long axis of the theca (Fig. 8F), and closed by glass-watch-shaped operculum. In life, coenosarc yellowish, hydranths white. Cnidome: at least pseudostenoteles [(18.0-21.5) $\times$ (7.5-9.0) μ m] and microbasic mastigophores [(6.0-7.0) $\times$ ca. 2.0 μ m] reported to date.

Dimensions: See Table 5.

Remarks: The description given above is based on the holotype, although some additional data, such as the cnidome composition, are taken from Migotto (1996, as *H. buskii*).

Through the presence of pairs of cauline axillar nematothecae and the heteromerous segmentation of its cladia, *H. brasiliensis* comes close to a number of congeners, viz. *H. australis* sp. nov., *H. liechtensternii*, *H. sibogae*, and *H. vervoorti*. *Halopteris australis* is immediately distinguished through its distinctly sinuated hydrothecal margin. *Halopteris liechtensternii*, when fertile, has comparatively longer and more tubular female gonothecae. *Halopteris sibogae* has distinctive, exceedingly long nematothecae (Fig. 2C). *Halopteris vervoorti* forms comparatively shorter stems (compare Fig. 2C-E and 2H), their cauli and cladia are thinner (compare Fig. 5A, B, M and 8A), and their cauline hydrothecae are placed in the lower halves of the corresponding internodes, leaving enough place for

Table 1. Comparative morphological and morphometrical features of *H. polymorpha* (Billard, 1913) (present study and syntype materials from *Siboga* Stn. 80 and 299) and *H. sibogae* (Billard, 1913) (Ho stands for homonomous, and He for heteronomous).

	<i>Halopteris polymorpha</i> (Billard, 1913)				<i>Halopteris</i> sp.		<i>Halopteris sibogae</i> (Billard, 1913)	
	Present study, MHNG- INVE-97937	Billard (1913), <i>Siboga</i> Stn. 80	Schuchert (1997), <i>Siboga</i> Stn. 80		Present study, MNHN H.L. 1309, <i>Siboga</i> Stn. 299		Present study, MHNG- INVE-97926	Billard (1913), as <i>H. polymorpha</i> var. <i>sibogae</i>
Caulus (seen frontally)								
- segmentation	Ho	-	Ho		Ho (distally He)		Ho	-
- superior nematothecae / internode with opposite cladia	4-5	-	-		-		3-4	-
- nematothecae above hydrotheca in ordinary internodes	Commonly 2-3 (range 1-5)	-	2 (rarely 1 or 3)		2		2-3	-
- number of axillar nematothecae	1	1	1		2		1-2	-
- internode length	695-955	-	-		515-570		450-605	-
- diameter at node	145-230	-	-		115-130		90-125	-
- length of apophysis	70-80	-	-		-		70-80	-
- length of nematothecae	80-100	-	-		65-70		100-125	-
- diameter of nematothecae at rim	55-65	-	-		35-45		45-50	-
Cladia (seen laterally)								
- segmentation	He	He	He		He		He	He
- nematothecae on 1st ahydrothecate internode	2	2	2		2 (occ. 3)		2	
- nematothecae on ordinary ahydrothecate internodes	1-2	Commonly 2	2		1-2		1-2	1
- number of axillar nematothecae	0-1	1	1		1		1-2	-
- length of quadrangular segment	65-80	-	-		45-60		40-45	-
- length of 1st ahydrothecate internode	475-730	580-700	-		220-310		270-365	200-240
- length of ordinary ahydrothecate internodes	315-460	380-470	340-400		160-300		180-270	135-190
- length of hydrothecate internodes	350-395	340-380	320		255-330		285-350	270-380
- diameter at transverse node	65-80	-	-		35-45		40-50	55-60
- length of nematothecae	55-80	-	-		40-60		55-110	-
- diameter at rim of nematotheca	35-50	-	-		35-40		35-50	-
Hydrotheca (cladial)								
- length abaxial wall	145-165	135-160	150-160		200-235		200-215	190-215
- length free adaxial wall	90-110	-	80-90		110-125		100-110	-
- diameter at rim	220-245	200-215	200-210		160-200		160-180	190-200

	<i>Halopteris polymorpha</i> (Billard, 1913)		<i>Halopteris</i> sp.		<i>Halopteris sibogae</i> (Billard, 1913)	
	Present study, MHNG-INVE-97937	Billard (1913), <i>Siboga</i> Stn. 80	Schuchert (1907), <i>Siboga</i> Stn. 80	Present study, MNHN H.L. 1309, <i>Siboga</i> Stn. 299	Present study, MHNG-INVE-97926	Billard (1913), as <i>H. polymorpha</i> var. <i>sibogae</i>
- length apophyses of lateral nematothecae	40-55	-	-	50-60	95-105	-
- length lateral nematotheca	70-80	-	-	80-90	125-145	-
- diameter of lateral nematotheca at rim	65-80	-	-	50-60	55-65	-
- length of mesial nematotheca	60-65	-	-	45-55	55-60	-
- diameter at rim of mesial nematotheca	45-50	-	-	40-45	45-50	-
- length of axillar nematotheca	ca. 40	-	-	30-35	40-55	-
- diameter of axillar nematotheca at rim	ca. 35	-	-	ca. 20	30-40	-
Gonothea						
- length of pedicel	70-80 (♂); ca. 80 (♀)	-; -	-; -	-; -	30-45 (♂); ca. 45 (♀)	-; -
- length (excluding pedicel)	490-560 (♂); 1015-1040 (♀)	-; -	- (♂); ca. 650 (♀)	-; -	330-440 (♂); 620-685 (♀)	-; -
- maximum width	210-240 (♂); 480-510 (♀)	-; -	-; -	-; -	165-220 (♂); 310-365 (♀)	-; -
- diameter at aperture (♀)	330-350	-	-	-	180-215	-
- number of basal nematothecae	2 (♂); 2-3 (♀)	- (♂); 3 (♀)	- (♂); 2-3 (♀)	-; -	2 (♂); 3 (♀)	-; -

Table 2. Literature records included earlier in the synonymy of *Halopteris polymorpha* (Billard, 1913), but deviating from the present concept of this species (*H.* stands for *Halopteris*).
N.B.: Italics are used to emphasize the distinguishing characters.

Original assignment	Reference	Geographical origin	Morphological features not agreeing with <i>H. polymorpha</i>	Possible correct taxonomical status
<i>Plumularia nuttingi</i> Billard, 1911	Billard (1911)	Indonesia	Cauline internodes with 1 axillar and 1-2 pairs of superior nematothecae; cladia homotomously-segmented; hydrothecate internodes with 1 axillar nematotheca; ahydrothecate internodes with 1-2 nematothecae; upper chamber of lateral nematothecae globular, with distinctly emarginated ad- and abaxial walls	<i>H. nuttingi</i> (Billard, 1911)
<i>Plumularia buskii</i> Bale, 1884	Thornely (1904) Ritchie (1910)	Sri Lanka Christmas I.	Neither described, nor illustrated	Unidentifiable
	Thornely (1916) Nutting (1927)	India Philippines	Description incomplete, partly illustrated subsequently by Vervoort & Vasseur (1977, fig. 30C)	Unidentifiable
			Neither described, nor illustrated	Unidentifiable
			No formal description, no illustration	Unidentifiable

Original assignation	Reference	Geographical origin	Morphological features not agreeing with <i>H. polymorpha</i>	Possible correct taxonomical status
<i>Plumularia buskii</i> (sic.) Bale, 1884	Hartlaub (1901) Billard (1913)	Hawai'i Indonesia	No formal description, illustrations insufficient Cauline internodes with 1 axillar and 1-3 pairs of superior nematothecae; cladia homotomomerously-segmented; hydrothecate internodes with 1 axillar nematotheca; ahydrothecate internodes with 1-2 nematothecae; upper chamber of lateral nematothecae globular; with distinctly emarginated ad- and abaxial walls	Unidentifiable <i>H. nuttingi</i> (Billard, 1911)
<i>Halopteris buskii</i> (Bale, 1884)	Redier (1966) Vervoort & Vasseur (1977) Rees & Vervoort (1987) Ryland & Gibbons (1991) Migotto (1996) Preker (2001, 2005) Hirohito (1974) Hirohito (1995)	New Caledonia Fr. Polynesia Zanzibar Fiji Brazil Australia Japan Japan	No formal description, but homomerous segmentation of the cladia, and lateral nematothecae with globular upper chamber Hydrotheca with distinctly sinuated margin, tall lateral nematothecae Relatively tall stems; cauline internodes with unpaired axillar nematotheca and 2 laterally-displaced nematothecae above hydrotheca Cauline internodes with 2 axillar nematothecae and 1-3 superiors; cladia heteromerously-segmented, ahydrothecate internodes shorter than hydrothecate counterparts and with 1 nematotheca, hydrothecate internodes with 1-2 axillar nematothecae Cauline internodes with 2 axillar nematothecae and 1-2 superiors displaced laterally; cladia heteromerously-segmented, ahydrothecate internodes with 1 nematotheca, hydrothecate internodes with 1-2 axillar nematothecae Neither described, nor illustrated Neither described, nor illustrated Cauline internodes with 2 axillar and 1-2 superior nematothecae; cladia heteromerously-segmented, ahydrothecate internodes shorter than hydrothecate counterparts and with 1 nematotheca, hydrothecate internodes with 1-2 axillar nematothecae	<i>H. nuttingi</i> (Billard, 1911) <i>H. australis</i> sp. nov. <i>H. millardae</i> sp. nov. Presumably <i>H. vervoortii</i> Galea, 2008 <i>H. brasiliensis</i> sp. nov. Unidentifiable Unidentifiable Presumably <i>H. vervoortii</i> Galea, 2008
<i>Heterotheca buskii</i> (Bale, 1884) (sic.)	Hirohito (1974)	Japan	Cauline internodes with 2 axillar nematothecae and 1, exceptionally 2, superiors; cladia heteromerously-segmented; ahydrothecate internodes shorter than hydrothecate counterparts and with 1 axillar nematotheca	Presumably <i>H. vervoortii</i> Galea, 2008
<i>Antennella polymorpha</i> (Billard, 1913)	Vervoort (1941)	Philippines	No formal description, no illustration, possibly a mix of species	Unidentifiable in the absence of a reexamination
<i>Halopteris polymorpha</i> (Billard, 1913)	Pennycuik (1959) Vervoort (1966)	Australia South Africa	Material reportedly agreeing "closely with Billard's figure XIVa", though neither described, nor illustrated Stems internodes with single axillar nematotheca and 1 median superior nematotheca, cladia homomerously-segmented, internodes with single axillar and median superior nematotheca	Questionably <i>H. polymorpha</i> (Billard, 1913) Related to <i>H. vervoortii</i> Galea, 2008, but of larger proportions; unidentifiable
	Millard & Bouillon (1973)	Seychelles	Mix of species (Schuchert, 1997)	<i>H. millardae</i> sp. nov. + <i>H. platygonotheca</i> Schuchert, 1997
	Millard & Bouillon (1974)	Mozambique	Small-sized cormoids, neither described, nor illustrated	Uncertain in the absence of a reexamination
	Millard (1975)	South Africa	Likely a mix of species: one with deep, cylindrical hydrothecae (fig. 112K), the other with shallow and conical hydrothecae (fig. 112L)	Unidentifiable species + (?) <i>H. buskii</i> (Bale, 1884), respectively
	Millard (1977)	South Africa	Neither described, nor illustrated	Uncertain in the absence of a reexamination
	Millard (1980)	South Africa	Neither described, nor illustrated	Uncertain in the absence of a reexamination

Original assignment	Reference	Geographical origin	Morphological features not agreeing with <i>H. polymorpha</i>	Possible correct taxonomical status
<i>Plumularia polymorpha</i> Billard, 1913	Hirohito (1983)	Japan	Stem internodes with 2 axillar and 1-2 laterally-displaced superior nematothecae; cladia homomerously-segmented, internodes with 1-2 axillar and 1 median superior nematothecae; hydrothecae large	Unidentifiable
	Ryland & Gibbons (1991)	Fiji	Long cauline and cladial hydrothecate internodes, shallow hydrothecae, short apophyses supporting the lateral nematothecae, single axillar nematothecae	<i>H. polymorpha</i> (Billard, 1913)
	Bouillon <i>et al.</i> (1995)	Seychelles	No description or illustrations available	Presumably <i>H. millardae</i> sp. nov.
	Schuchert (1997)	Various localities	Mix of species	<i>H.</i> sp. (fig. 20B), <i>H. nuttingi</i> (Billard, 1911) (fig. 21), <i>H. millardae</i> sp. nov. (fig. 22A-D), <i>H. sibogae</i> (Billard, 1913) (fig. 22E), <i>H. brasiliensis</i> sp. nov. (fig. 22F-H), <i>H. australis</i> sp. nov. (fig. 23).
	Watson (2000)	Australia	Likely 2 species involved, one with comparatively deeper hydrothecae and flared lateral nematothecae (35D), the other shallow hydrothecae and lateral nematothecae with globular upper chamber (fig. 35C); description incomplete, some illustrations either misleading (e.g. fig. 35B, number of axillar and superior nematothecae unclear) or providing insufficient details (e.g. fig. 35A, number of cauline nematothecae impossible to ascertain)	Possibly <i>H. vervoorti</i> Galea, 2008 + unidentifiable species, respectively
	Ansín Agis <i>et al.</i> (2001)	Cape Verde	See Galea (2008)	Presumably <i>H. vervoorti</i> Galea, 2008
	Preker (2001, 2005)	Australia	Neither described, nor illustrated	Unidentifiable
	Kirkendale & Calder (2003)	Guam	Neither described, nor illustrated, but cormoids reportedly said “translucent-white”, thus different from the distinctive yellow ones of <i>H. polymorpha</i>	Unidentifiable
	Preker & Lawn (2005)	Australia	Neither described, nor illustrated	Unidentifiable
	Ansín Agis <i>et al.</i> (2009)	Coral Sea	Neither formally described, nor illustrated	Unidentifiable
<i>Antennella secundaria</i> (Gmelin, 1791)	Preker & Lawn (2010)	Australia	Stem internodes with 1 axillar nematotheca and 2 superiors; cladia heteromerously-segmented, ahydrothecate internodes shorter than hydrothecate counterparts, and bearing 1 (rarely 2) nematothecae; hydrothecate internodes with 1 axillar nematotheca	Presumably <i>H. vervoorti</i> Galea, 2008
	Preker & Lawn (2012)	Australia	Single cauline axillar nematothecae, and 1-2 superiors; cladia heteromerously-segmented, ahydrothecate internodes longer than hydrothecate counterparts and bearing 1-2 nematothecae; hydrothecate internodes with single axillar nematotheca	Unidentifiable
	Billard (1913)	Indonesia	According to the description, illustrations, and measurements, likely three species are involved	<i>H. polymorpha</i> (Siboga Stn. 80), <i>H.</i> sp. (Stn. 77), and <i>H.</i> sp. (Stn. 299)
	Vervoort (1967)	Red Sea	Stem internodes with 1 axillar nematotheca and “(usually) a distal” nematotheca. Cladia heteromerously-segmented, ahydrothecate internodes comparatively shorter than hydrothecate counterparts and with 1 nematotheca, hydrothecate internodes with single axillar nematotheca	Presumably <i>H. vervoorti</i> Galea, 2008

Table 3. Comparative measurements (in μm) and main morphological features of *H. vervoorri* Galea, 2008 from various localities. Ho stands for homonomous and He for heteronomous.

Geographical origin		Bali	Madagascar	Maldives	Guadeloupe, Martinique (*)
Reference(s)	Present study	Present study	Present study	Present study	Galea (2008); present study (*)
Caulus (seen frontally)					
- maximum height (cm)	1.2	0.8		1.3	2
- segmentation	Ho (dist. He)	Ho (dist. He)		Ho (dist. He)	Ho (dist. He)
- superior nematothecae / internode with opposite cladia	2	1-2		1-2	1-2 (*)
- nematothecae above hydrotheca in ordinary internodes	1-2, in a median row	1-2, in a median row		1-2, in a median row	1-2, in a median row
- number of axillar nematothecae	2 (distally 1)	2 (distally 1)		2 (distally 1)	2 (distally 1) (*)
- internode length	380-445	410-490		360-500	330-465
- diameter at node	55-110	45-105		60-115	-
- length of apophysis	65-80	85-95		60-75	60-70
- length of nematothecae	55-75	65-70		65-80	-
- diameter of nematothecae at rim	45-50	35-45		40-45	-
Cladia (seen laterally)					
- segmentation	He	He		He (occ. Ho)	He
- number of nematothecae on 1st ahydrothecate internode	1	1		1 (occ. 2)	1 (occ. 2) (*)
- nematothecae on ordinary ahydrothecate internodes	1	1		1	1
- number of axillar nematothecae	1 (rarely 2)	1 (rarely 2)		1 (rarely 2)	1 (rarely 2)
- length of quadrangular segment	45-50	50-60		40-55	70-90
- length of 1st ahydrothecate internode	190-270	160-240		175-255	155-215
- length of ordinary ahydrothecate internodes	125-160	160-205		140-190	115-170
- length of hydrothecate internodes	245-330	255-315		270-315	251-300
- diameter at transverse node	35-40	40-45		40-45	-
- length of nematothecae	50-70	55-65		55-70	-
- diameter at rim of nematotheca	35-40	35-40		30-45	-
Hydrotheca (cladial)					
- shape of the rim (lateral view)	Even	Even		Even	Even
- length abaxial wall	180-215	180-205		180-215	220-245
- length free adaxial wall	110-115	110-120		110-120	115-135
- diameter at rim	155-175	180-190		165-175	170-195
- length apophyses of lateral nematothecae	55-50	70-80		50-60	74-86
- length lateral nematothecae	75-85	80-95		75-95	74-88
- diameter of apical chamber of lateral nematotheca at rim	65-70	60-70		60-70	63-72

Geographical origin		Bali	Madagascar	Maldives	Guadeloupe, Martinique (*)
Reference(s)	Present study	Present study	Present study	Present study	Galea (2008); present study (*)
- length of mesial nematotheca	50-55	50-60	60-65	-	-
- diameter at rim of mesial nematotheca	45-50	45-55	50-55	-	-
- length of axillar nematotheca	40-55	35-40	35-40	-	-
- diameter of axillar nematotheca at rim	30-40	ca. 30	30-35	-	-
Gonothecca					
- length of pedicel	- (♂); - (♀)	45-60 (♂); 45-50 (♀)	- (♂); 50-60 (♀)	ca. 45 (♂); ca. 50 (♀) (*)	
- length (excluding pedicel)	- (♂); - (♀)	430-625 (♂); 660-705 (♀)	- (♂); 585-670 (♀)	500-630 (♂); 695-730 (♀) (*)	
- maximum width	- (♂); - (♀)	180-260 (♂); 390-425 (♀)	- (♂); 315-350 (♀)	195-275 (♂); ca. 330 (♀) (*)	
- diameter at aperture	- (♂); - (♀)	55-70 (♂); 245-290 (♀)	- (♂); 205-240 (♀)	ca. 30 (♂) (*); ca. 225 (♀) (*)	
- number of basal nematothecae	- (♂); - (♀)	2 (♂); 2 (♀)	- (♂); 2 (♀)	2 (♂); 2-3 (♀) (*)	

Table 4. Various records approaching the phenotype of *Halopteris vervoorti* Galea, 2008, and their possible taxonomic status (L stands for length, Φ for diameter, Ho and He for homo- and heteromorous, respectively, and *Ha.*, *He.* and *A.* for *Halopteris*, *Heterothecca* and *Antennella*, respectively).

Possible taxonomic status		Unsettled	Unsettled	(?) <i>Ha. vervoorti</i>	Unsettled	(?) <i>Ha. vervoorti</i>	(?) <i>Ha. vervoorti</i>	Unsettled
Cormoids								
- geographical distribution	Indonesia	S Africa	Red Sea	Japan	Japan	Fiji	Australia	Australia
- max. height (mm)	8	23	15	10	18	9	9	21
Caulus								
- segmentation	Ho	Ho	Ho	Ho	Ho	Ho	Ho	Ho
- axillar nematothecae	1	1	1	2	2	2	1	1
- nematothecae above hydroth.	?	1	Usually 1	1-2	1-2	< 3	2	2
Cladia								
- segmentation	He/Ho	Ho/He	He	He	Ho	He	He	He

	Billard (1913), <i>Siboga</i> Stn. 77, as <i>Ha.</i> <i>polymorpha</i>	Vervoort (1966), as <i>Ha.</i> <i>polymorpha</i>	Vervoort (1967), as <i>A. secundaria</i>	Hirohito (1974), as <i>He. buski</i> (sic!)	Hirohito (1983), as <i>Ha.</i> <i>polymorpha</i>	Ryland & Gibbons (1991), as <i>Ha. buskii</i> (BM1988.11.10.6- 7)	Ryland & Gibbons (1991), as <i>Ha. buskii</i> (QM GL10293)	Hirohito (1995), as <i>Ha. buski</i> (sic.)	Preker & Lawn (2010), as <i>Ha. polymorpha</i>	Preker & Lawn (2012), as <i>Ha. polymorpha</i>
- nematoth. on 1st ahydroth. internode	1	1	1	1	1-2	1	1	1	-	-
- nematoth. on ordinary ahy- droth. inter- nodes	1 (occ. 2)	1 (on fused part)	1	1	1 (on fused part)	1	1	1 (rarely 2)	1-2	1-2
- axillar nematoth.	1	1	1	1 (exc. 2)	1-2	1 (occ. 2)	1 (occ. 2)	1	1	1
Measurements (µm)										
Caulus, L inter- node	-	-	270-325	-	-	360-380	265-325	-	320-420	498-1494
Cladia, L 1st ahydroth. intern.	245-270	-	-	-	-	-	-	-	-	66-100
Cladia, L ordi- nary ahydroth. intern.	190-255	Fused	130-140	-	Fused	130-140	100-150	-	150-260	282-415
Cladia, L hy- droth. intern.	310-365	675-1080 (fused)	245-250	-	-	190-240	175-230	-	260-340	249-315
Hydrotheca, L abaxial wall or Depth	215-230	240-255	190-215	ca. 270	260-270 (fused)	175-210	150-180	180-220	112-180	183-249
Hydrotheca, L free adaxial wall	-	54-68	130-135	-	-	100-130	100-120	-	80-88	100-116
Hydrotheca, Φ aperture	175-190	245-270	150-165	ca. 160	260-270	160-180	160-185	180-200	152-160	149-189
Lateral nemato., L	-	55-60	-	-	-	-	-	-	-	50-100
Lateral nemato., Φ rim	-	45-55	-	-	-	-	-	-	-	42-83
Gonothecae, L	- (♂)	- (♂)	- (♂)	- (♂)	- (♂)	450-612 (♂)	- (♂)	- (♂)	- (♂)	- (♂)
	- (♀)	- (♀)	400-460 (♀)	- (♀)	- (♀)	- (♀)	558-738 (♀)	- (♀)	- (♀)	830-913 (♀)

	Billard (1913), <i>Siboga</i> Stn. 77, as <i>Ha.</i> <i>polymorpha</i>	Vervoort (1966), as <i>Ha.</i> <i>polymorpha</i>	Vervoort (1967), as <i>A. secundaria</i>	Hirohito (1983), as <i>Ha.</i> <i>polymorpha</i>	Ryland & Gibbons (1991), as <i>Ha. buskii</i> (BM1988.11.10.6- 7)	Ryland & Gibbons (1991), as <i>Ha. buskii</i> (QM GL10293)	Hirohito (1995), as <i>Ha. buskii</i> (sic.)	Preker & Lawn (2010), as <i>Ha. polymorpha</i>	Preker & Lawn (2012), as <i>Ha. polymorpha</i>
Gonothecae, max. width	- (♂)	- (♂)	- (♂)	- (♂)	216-234 (♂)	- (♂)	- (♂)	- (♂)	- (♂)
	- (♀)	- (♀)	250-300 (♀)	- (♀)	- (♀)	252-360 (♀)	- (♀)	- (♀)	265-598 (♀)
Gonothecae, Φ aperture	- (♂)	- (♂)	- (♂)	- (♂)	45-54 (♂)	- (♂)	- (♂)	- (♂)	- (♂)
	- (♀)	- (♀)	- (♀)	- (♀)	- (♀)	162-234 (♀)	- (♀)	- (♀)	249-282 (♀)
Gonothecae, number of basal nematothecae	- (♂)	- (♂)	- (♂)	- (♂)	- (♂)	- (♂)	1 (♂)	- (♂)	- (♂)
	- (♀)	2 (♀)	2 (♀)	- (♀)	- (♀)	2 (♀)	2-3 (♀)	- (♀)	2 (♀)

Table 5. Measurements (in μm) and main morphological features of *Halopteris australis* sp. nov., *H. millardae* sp. nov., and *H. brasiliensis* sp. nov.

	<i>Halopteris australis</i> sp. nov.			<i>Halopteris millardae</i> sp. nov.			<i>Halopteris brasiliensis</i> sp. nov.
Geographical origin	New Caledonia	French Polynesia	Seychelles (*); Maldives	Zanzibar	Brazil		
Reference(s)	Present study	Vervoort & Vasseur (1977), as <i>H. buskii</i>	Millard & Bouillon (1973) (*); Present study	Rees & Vervoort (1987), as <i>H. buskii</i> (Stn. 112)	Migotto (1996); present study (*)		
Caulus (seen frontally)							
- maximum height (cm)	1.8	2.5	7 (*); 3.9	4.0	3.0		
- segmentation	Ho (dist. He)	Ho	Ho	Ho	Ho		
- superior nematothecae / internode with opposite cladia	2-3	-	3-4	-	2-3 (*)		
- nematothecae above hydrotheca in ordinary inter- nodes	1-2 (exc. 3), in two parallel rows	2, in two parallel rows	2-3 (exc. 4), in two parallel rows	2, in two rows	2 (occ. 1), in two parallel rows (*)		
- number of axillar nematothecae	2 (rarely 1 distally)	1	1	1	2 (*)		
- internode length	465-680	475-550	490-845	460-520	325-600		
- diameter at node	45-105	100-125	110-220	270-320	110-180		
- length of apophysis	100-115	-	85-110	-	75-85 (*)		
- length of nematothecae	90-100	-	100-170	-	65-95 (*)		
- diameter of nematothecae at rim	45-50	-	55-85	-	50-60 (*)		

	<i>Halopteris australis</i> sp. nov.		<i>Halopteris millardae</i> sp. nov.		<i>Halopteris brasiliensis</i> sp. nov.
Cladia (seen laterally)					
- segmentation	He	He	He	He/Ho	He
- number of nematothecae on 1st ahydrothecate internode	1 (exc. 2)	1	2 (exc. 3), in two parallel rows	-	1
- nematothecae on ordinary ahydrothecate internodes	1	1	2 (exc. 4), in two parallel rows; distally 1	1	1
- number of axillar nematothecae	1 (rarely 2)	1	1	1	1 (rarely 2) (*)
- length of quadrangular segment	45-50	45-55	45-65	-	40-50 (*)
- length of 1st ahydrothecate internode	210-280	-	170-245	-	137-320
- length of ordinary ahydrothecate internodes	150-195	210-250	180-230	Fused 495-580	150-200
- length of hydrothecate internodes	290-390	320-335	340-370	-	240-440
- diameter at transverse node	35-40	-	60-65	115-120	50-70
- length of nematothecae	60-75	-	75-95	-	50-70 (*)
- diameter at rim of nematotheca	30-40	-	35-50	-	40-50 (*)
Hydrotheca (cladial)					
- shape of the rim (lateral view)	Distinctly sinuated	Distinctly sinuated	Slightly sinuated	Reportedly even	Even
- length abaxial wall	205-240	200-220	170-220	175-200	162-237
- length free adaxial wall	105-115	40-55	75-80	-	120-135 (*)
- diameter at rim	175-190	-	210-220	220-235	180-205
- length apophyses of lateral nematothecae	65-80	-	30-35	-	50-65 (*)
- length lateral nematothecae	90-100	85-95	85-110	95-140	75-125
- diameter of apical chamber of lateral nematotheca at rim	55-70	45-50	70-75	65-80	50-82
- length of mesial nematotheca	55-60	-	45-50	-	50-87
- diameter at rim of mesial nematotheca	45-50	-	35-40	-	35-60
- length of axillar nematotheca	45-50	-	20-30	-	40-50 (*)
- diameter of axillar nematotheca at rim	ca. 35	-	20-25	-	40-45 (*)
Gonothea					
- length of pedicel	- (♂); ca. 70 (♀)	- (♂); - (♀)	- (♂); - (♀)	- (♂); - (♀)	- (♂); 75-80 (♀) (*)
- length (excluding pedicel)	- (♂); ca. 730 (♀)	- (♂); 400-420 (♀)	< 470 (♂) (*), < 1150 (♀) (*)	- (♂); - (♀)	- (♂); 800-910 (♀)
- maximum width	- (♂); ca. 340 (♀)	- (♂); 230-250 (♀)	< 210 (♂) (*), < 730 (♀) (*)	- (♂); - (♀)	- (♂); 310-450 (♀)
- diameter at aperture	- (♂); ca. 225 (♀)	- (♂); - (♀)	- (♂); - (♀)	- (♂); - (♀)	- (♂); - (♀)
- number of basal nematothecae	- (♂); 2 (♀)	- (♂); 1 (♀)	1 (♂) (*); 2 (♀) (*)	- (♂); - (♀)	- (♂); 1-3 (♀)

1-2 superior nematothecae, arranged in one row, to be confined to their distal halves (Fig. 5C). Additional differences to other congeners are summarized in Appendix 1.

Distribution: Only known from Brazil (Migotto, 1996).

DNA SEQUENCE RESULTS AND DISCUSSION

The phylogenetic trees obtained with the Bayesian and the ML methods were largely identical and, therefore, only the ML is shown here (Fig. 9). The tree was rooted with the outgroup *Schizotricha frutescens* (comp. Peña Cantero *et al.*, 2010). The 16S gene is relatively rapidly evolving and, for Hydrozoa, it is only suitable for phylogenetic analyses at the specific and generic levels (comp. Leclère *et al.*, 2009). The genus *Antennella* appears clearly polyphyletic, as it has already been suggested by Schuchert (1997). Also, *Halopteris* appears to be polyphyletic and splits into at least two prominent

clades. More detailed conclusions are not possible, mainly because samples of other important Halopterididae genera – *e.g.* *Corhiza* Millard, 1962 and *Gattyia* Allman, 1885 – could not be obtained for the present analysis. Moreover, our study focuses on species delimitations.

Halopteris sibogae, raised to species level in the taxonomy section above, is clearly a distinct species and is not related to *H. polymorpha* (of which it was considered to be a mere variant). Likewise, *H. millardae* sp. nov. is also distinct from *H. polymorpha*, as was argued above. A Mediterranean sample (DG855922) formerly identified as *H. polymorpha* in Leclère *et al.* (2007) does not belong to this species, and is likely an as yet unnamed taxon. Despite coming from two different oceans, the samples of *H. vervoorti* clustered closely together. The two samples from the Atlantic and their two counterparts from the Indian Ocean map into two different subclades, but their divergences appear low, comparable to intraspecific divergences

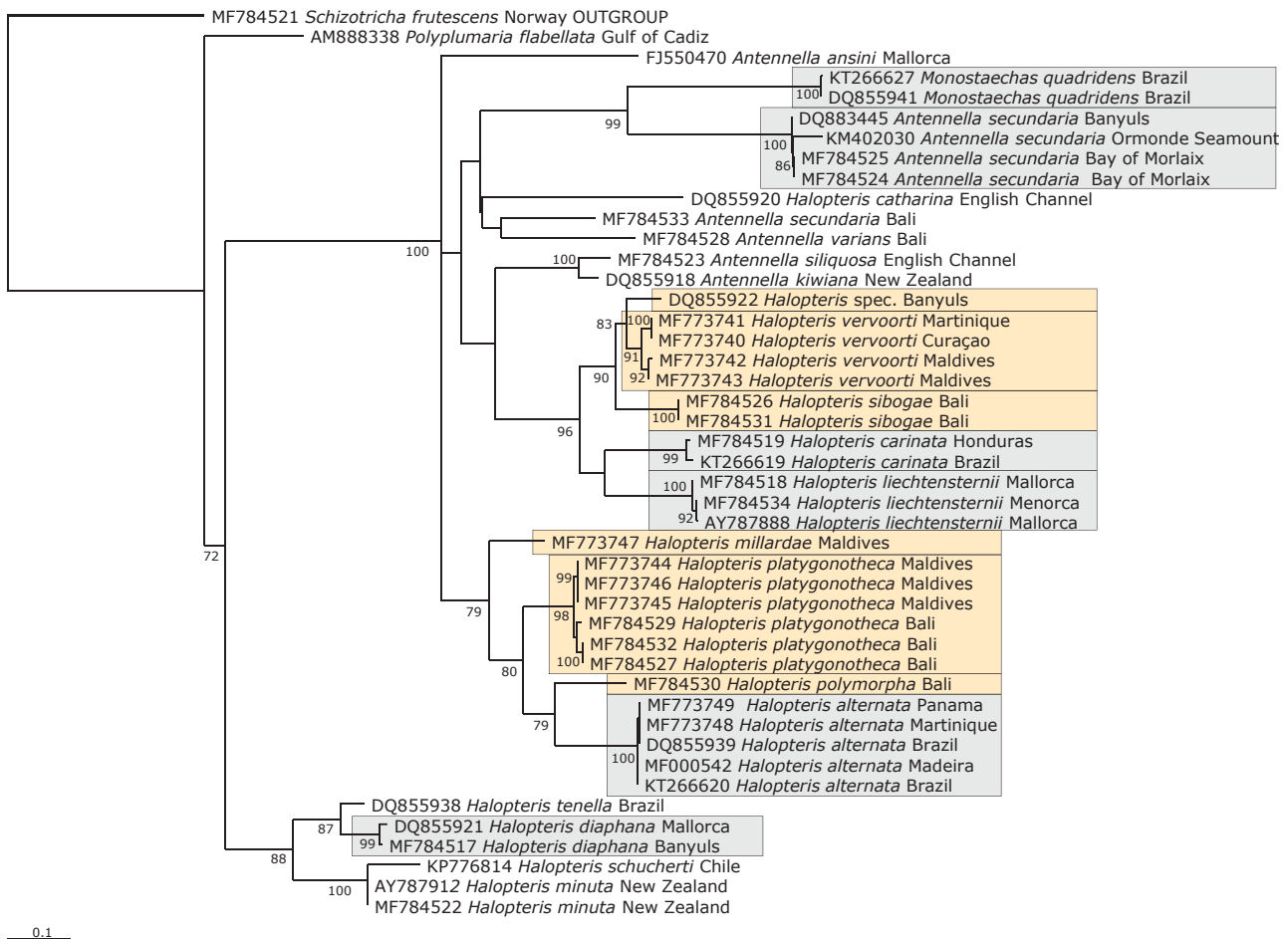


Fig 9. Maximum likelihood phylogenetic tree of Halopterididae species obtained with RAXML (GTR + G + I model) based on 547 bp positions (after Gblock treatment) of the mitochondrial 16S gene. Node-support values are bootstrap values of 100 pseudoreplicates (shown only if > 70%). For more details, see text and Appendix 2. Highlighted in yellow boxes are species discussed in the text, boxed in grey are other species clades with more than one sample, which permit to assess the intraspecific divergences observed in this family.

seen in other species clades (e. g. *H. platygonotheca* or *H. carinata* Allman, 1877). However, a more detailed analysis with more samples and markers is needed. *Halopteris platygonotheca* resembles morphologically *H. diaphana* (Heller, 1868), *H. tenella* (Verrill, 1874), and *H. alternata* (Nutting, 1900). Some of them have been considered conspecific, but they can be distinguished by the shape of the female gonothecae (Schuchert, 1997). The 16S data confirmed that all four species are distinct and well separated. *Antennella secundaria* (Gmelin, 1791), as currently accepted, has a circumglobal distribution, but Schuchert (1997) suspected that it is a species complex. This was also observed with the 16S data, where the Indonesian sample of *A. secundaria* (MF784533) appears unrelated to its Atlantic counterparts.

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Appendix 1. Comparative morphological features of several nominal *Halopteris* species.

Species name / color in life / geographical distribution / main references	Caulus		Cladia		Hydrotheca	Lateral nematothecae	Female gonotheca
	Maximum height / Segmentation / Number and position of nematothecae above hydrotheca	Axillar nematothecae	Segmentation / Relative length of ahydrothecate internodes / Number of nematothecae distal to hydrotheca	Axillar nematothecae			
<i>H. alternata</i> (Nutting, 1900) / white / eastern and western Atlantic / Schuchert (1997); Galea (2008); present study	20 mm / Homomerous (occasionally heteromerous distally) / 1 median	1, displaced laterally	Heteromerous / Slightly longer than hydrothecate counterparts / 1	0	Conical, rim even, slightly flaring	Short / Not surpassing hydrothecal rim / Conical; adaxial wall uneven, either variably lowered or sinuated	Elongated-ovoid, lid perpendicular to longitudinal axis / up to 800 $\times$ 320 μ m / 2
<i>H. australis</i> sp. nov. / white / French Polynesia, New Caledonia / Vervoort & Vasseur (1977); Schuchert (1997); present study	25 mm / Homomerous (occasionally heteromerous distally) / 1-3 (5), displaced laterally	2, median	Heteromerous / Shorter than hydrothecate counterparts / 1	1-2	Conical, rim conspicuously sinuated	Long / Surpassing hydrothecal rim / Conical, adaxial wall sigmoid	Elongated-ovoid, tapering basally, lid perpendicular to longitudinal axis / ca. 730 $\times$ 340 μ m / 2
<i>H. brasiliensis</i> sp. nov. / yellowish / Migotto (1996); Schuchert (1997); present study	30 mm / Homomerous / 2 (occasionally 1) displaced laterally	2, median	Heteromerous / Shorter than hydrothecate counterparts / 1	1-2	Conical, rim even	Rather short / Not surpassing hydrothecal rim / Conical; adaxial wall sinuated	Broadly-ovoid, tapering basally, lid perpendicular to longitudinal axis / (800-910) $\times$ (310-450) μ m / 1-3
<i>H. concava</i> (Billard, 1911) / - / Indonesia, Philippines / Billard (1913); Ansin Agis <i>et al.</i> (2009); present study	60 mm / Homomerous / 6-7 displaced laterally	1, median	Homomerous / - / 2-3	1	Tubular, adaxial wall with distinct concavity; in frontal view distinctly swollen in middle	Relatively short / Barely surpassing hydrothecal rim / Globular; adaxial wall distinctly emarginated	Elongated-ovoid, lid oblique to longitudinal axis / (400-410) $\times$ (155-160) μ m / 2
<i>H. crassa</i> (Billard, 1911) / - / Indonesia, New Zealand / Billard (1913); Schuchert (1997)	150 mm / Homomerous / 2-4 displaced laterally	1, median	Homomerous / - / 0	1	Tubular on stem, conical on cladia; rim even	Relatively short / Reaching hydrothecal rim / Conical; adaxial wall emarginated	Elongated-ovoid, lid perpendicular to longitudinal axis / (1980-2150) $\times$ (840-910) μ m / 2-5
<i>H. diaphana</i> (Heller, 1868) / white / circumglobal in tropical and temperate seas / Schuchert (1997)	14 mm / Heteromerous / Generally 2 (occasionally 1 or 3) on ahydrothecate segments	0	Heteromerous / Longer than hydrothecate counterparts / 1	0	Conical, rim even	Very short / Not surpassing hydrothecal rim / Conical; adaxial wall occasionally emarginated	Cornucopia-shaped, lid perpendicular to distal end of longitudinal axis / up to 700 μ m long / 2-4
<i>H. glutinosa</i> (Lamouroux, 1816) / brilliant scarlet / Australia, Tasman Sea, Indonesia, Japan / Schuchert (1997), as <i>H. buskii</i> ; Watson (2005)	50 mm / Unsegmented (homomerous distally) / 1-4	1 (2 ?)	Homomerous (occasionally heteromerous) / 1 (rarely 2)	1	Conical, rim even	Well-developed / Reaching hydrothecal rim / Conical; deep adaxial emargination	Broadly ovoid, lid perpendicular to longitudinal axis, up to 12 nematothecae in 2 parallel rows / up to 1200 μ m
<i>H. liechtensterinii</i> (Marktanner-Turneretscher, 1890) / pale straw to greenish / Mediterranean / Schuchert (1997); present study	27 mm / Homomerous (occasionally heteromerous distally) / 2-3 displaced laterally	2, median	Heteromerous / Shorter than, or as long as, hydrothecate counterparts / 1-2	1-2	Conical, rim even, slightly flaring	Well-developed / Reaching hydrothecal rim / Conical; rim either emarginated adaxially or sinuated	Elongated, nearly tubular, lid perpendicular to longitudinal axis / up to 1000 μ m long / 2-3

Species name / color in life / geographical distribution / main references	Caulus		Cladia		Hydrotheca	Lateral nematothecae	Female gonotheca
	Maximum height / Segmentation / Number and position of nematothecae above hydrotheca	Axillar nematothecae	Segmentation / Relative length of ahydrothecate internodes / Number of nematothecae distal to hydrotheca	Axillar nematothecae	Shape	Length of apophyses / Relative length of theca / Shape of its upper chamber	Shape / Measurements / Number of basal nematothecae
<i>H. millardae</i> sp. nov. / brownish / Seychelles, Maldives / Millard & Bouillon (1973); Schuchert (1997); present study	70 mm / Homomerous / 2-3 (4) displaced laterally	1, median	Heteromerous / Shorter than hydrothecate counterparts / 2 (occasionally 1 distally)	1	Conical, rim slightly sinuated	Rather short / scarcely reaching hydrothecal rim / Conical; sinuated adaxially	Broadly ovoid, lid perpendicular to longitudinal axis / up to 1150 × 730 µm / 2
<i>H. minuta</i> (Treblecock, 1928) / - / New Zealand, French Polynesia / Schuchert (1997); Ralph (1961, as <i>H. constricta</i>)	9 mm / Heteromerous / 1 median, supra-axillar on hydrothecate internode + 1-2 median on ahydrothecate internode	0	Heteromerous / Shorter than hydrothecate counterparts / 1	0	Conical, rim even, slight adaxial concavity	Relatively short / Reaching hydrothecal rim / Conical; rim lowered on adaxial side	Strongly S-shaped, lid perpendicular to distal end of longitudinal axis, basal septum / (910-1000) × ca. 420 µm / 2
<i>H. nuttingi</i> (Billard, 1911) / - / Indonesia, Australia, New Caledonia / Billard (1911, 1913); Schuchert (1997)	25 mm / Homomerous / 2-5 displaced laterally	1	Homo- and heteromerous / Of nearly the same length as their hydrothecate counterparts / 1-2	1	Conical, rim even	Relatively short / Not reaching hydrothecal rim / Globular, deeply scooped adaxially	Broadly ovoid, lid perpendicular to longitudinal axis / (740-810) × (310-365) µm / 2
<i>H. peculiaris</i> (Billard, 1913) / - / Zanzibar, South Africa, Borneo / Billard (1913); Schuchert (1997)	90 mm / Homomerous / 2-3 displaced laterally	1	Homo- et heteromerous / When present, much shorter than hydrothecate counterpart / 0-1	1	Conical, rim even	Relatively short / Reaching hydrothecal rim / Conical, variably scooped adaxially, sometimes abaxially	Broadly ovoid, lid perpendicular to longitudinal axis / (2000-2100) × (1040-1135) µm / 3
<i>H. platygonotheca</i> Schuchert, 1996 / pale-green / Comoros, Madagascar, Seychelles, Red Sea, Indonesia / Schuchert (1996); present study	40 mm / Homomerous (occasionally heteromerous distally) / 1-3 in a median row	0-1, median	Heteromerous / Slightly longer than hydrothecate counterparts / 1	0	Conical, rim even	Short / Not reaching hydrothecal rim / Conical; rim sinuated	Broadly ovoid, strongly flattened laterally, lid perpendicular to longitudinal axis / up to 1100 µm long / 2
<i>H. plumosa</i> Galea & Schories, 2012 / white / Chile, Argentina / Galea & Schories (2012); Galea <i>et al.</i> (2014)	34 mm / Homomerous (occasionally heteromerous distally) / 1-2 (rarely 3) displaced laterally	0	Homomerous in adult colonies, heteromerous in young ones / Much shorter than hydrothecate counterparts / 1 (exceptionally 2)	0	Tubular, curved adaxially, rim even	Rather short / Reaching hydrothecal rim / Conical; rim scooped adaxially	Strongly S-shaped, lid perpendicular to distal end of longitudinal axis, basal septum / ca. 860 × 455 µm / 2
<i>H. polymorpha</i> (Billard, 1913) / yellow throughout / Indonesia, Fiji / present study	37 mm / Homomerous / commonly 2-3 (range 1-5)	1, median	Heteromerous / Of nearly the same length / 1-2	0-1	Conical, shallow, rim even	Very short / Barely reaching hydrothecal rim / Conical; rim sinuated or emarginated adaxially	Broadly ovoid, lid perpendicular to longitudinal axis / (1015-1040) × (480-510) µm / 2-3
<i>H. pseudoconstricta</i> Millard, 1975 / - / South Africa, Angola, Verna Seamount, Three King Is. / Millard (1975); Schuchert (1997)	9 mm / Heteromerous / 1 median supra-axillar on hydrothecate internode + 1-2 median on ahydrothecate internodes	0	Heteromerous / Shorter than hydrothecate counterparts / 1-2 on ahydrothecate internode	0	Tubular, with distinct adaxial concavity, rim even; occasionally an internal adaxial projection of perisarc	Inconspicuous / Not reaching hydrothecal rim / Conical; rim even	Cornucopia-shaped, lid perpendicular to distal end of longitudinal axis / up to 660 × 400 µm / 2
<i>H. regressa</i> (Billard, 1918) / - / Indonesia / Billard (1918)	> 5 mm / Homomerous (heteromerous distally) / 1	0	Heteromerous / - / 1	0	Conical, rim supposedly even	Short / - / Globular; deeply scooped adaxially	Unknown

Species name / color in life / geographical distribution / main references	Caulus		Cladia		Hydrotheca	Lateral nematothecae	Female gonotheca
	Maximum height / Segmentation / Number and position of nematothecae above hydrotheca	Axillar nematothecae	Segmentation / Relative length of ahydrothecate internodes / Number of nematothecae distal to hydrotheca	Axillar nematothecae			
<i>H. schucherti</i> Galea, 2006 / white / Chile / Galea (2006)	75 mm / Homomerous / 1 median, supra-axillar + 6-8 displaced laterally	0	Homo- and heteromerous / When present, longer than hydrothecate counterparts / 1 median proximal + 4-5 above	0	Conical, rim even	Very short / Not surpassing hydrothecal rim / Conical; variably scooped adaxially	Broadly ovoid, with S-shaped longitudinal axis, lid oblique, basal septum / (730-790) × (333-394) µm / 2
<i>H. sibogae</i> (Billard, 1913) / yellow & white / Indonesia, Seychelles, Japan / present study	25 mm / Homomerous / 2-3 displaced laterally	1-2, median	Heteromerous / Shorter than hydrothecate counterparts / 1-2	1-2	Tubular, rim imperceptibly sigmoid in lateral view	Well-developed / Greatly surpassing hydrothecal rim / Conical; rim scooped adaxially	Broadly ovoid, lid perpendicular to longitudinal axis / (620-685) × (310-365) µm / 3
<i>H. simplex</i> (Warren, 1914) / - / South Africa / Warren (1914); Millard (1975)	14 mm / Homomerous / 0	0	Heteromerous / Much shorter than hydrothecate counterparts / 1	0	Conical, rim even	Well-developed / Barely overtopping hydrothecal rim / Globular; emarginated on both ad- and abaxial sides	Piriform, flattened laterally, lid perpendicular to longitudinal axis / ca. 810 × 510 µm / 2
<i>H. tenella</i> (Verrill, 1874) / white / southern California to Panama, Massachusetts to Caribbean, Brazil / Galea (2013); present study	50 mm / Heteromerous / 0-2 on hydrothecate internodes + 1-4 on ahydrothecate internodes, in almost a median row	0	Heteromerous / Much longer than hydrothecate counterparts / 1-2	0	Conical, rim even	Inconspicuous / Reaching hydrothecal rim / Conical; rim even	Cornucopia-shaped, lid perpendicular to distal end of longitudinal axis / ca. 1335 × 370 µm / 3
<i>H. tuba</i> (Kirichenpauer, 1876) / - / South Africa / Millard (1962); Schuchert (1997)	220 mm / Unsegmented for most of their length (homomerous distally) / 0	2, median	Homomerous / 0	1, naked	Forming two longitudinal rows along stem; conical, rim even	Well-developed / Greatly surpassing hydrothecal rim / Conical; rim even	Broadly ovoid, flattened laterally / (2950-3360) × (1510-1940) µm / 3
<i>H. urceolata</i> Watson, 2015 / white / Australia / Watson (2015)	15 mm / Heteromerous / 1 on ahydrothecate internodes	0	Heteromerous / - / 1 on ahydrothecate internode	0	Tubular, rim even, adaxial wall distinctly concave	Inconspicuous / Not reaching hydrothecal rim / Conical; rim even	Unknown
<i>H. vervoortii</i> Galea, 2008 / pale yellow to brownish / Lesser Antilles, Cape Verde, (?) Red Sea, Madagascar, Indonesia, Maldives, (?) Australia, (?) Japan, (?) Fiji / present study	20 mm / Homomerous (heteromerous distally) / 1-2 in a row	2 (distally 1), median	Heteromerous / Much shorter than hydrothecate counterparts / 1	1-2	Conical, rim even, slightly flaring, imperceptibly scooped laterally	Well-developed / Reaching hydrothecal rim / Conical; rim sinuated adaxially	Broadly ovoid, tapering below, lid perpendicular to longitudinal axis / (660-705) × (390-425) µm / 2
<i>H. violae</i> Calder <i>et al.</i> , 2003 / - / Galapagos / Calder <i>et al.</i> (2003)	23 mm / Homomerous (occasionally heteromerous distally) / 1 median + 2-4 displaced laterally	0	Heteromerous / Of same or slightly surpassing length / 1-2	0	Conical, rim even	Inconspicuous / Reaching hydrothecal rim / Conical; rim even	Elongated-ovoid, lid almost perpendicular to longitudinal axis / (600-700) × ca. 200 µm / 2

Appendix 2. Sample data used for the molecular analyses. GenBank numbers in bold are new sequences. nd = no data.

Species	GenBank accession number	Voucher	Locality	Latitude (+ N; - S)	Longitude (+ E; - W)	Collection date	Depth (m)
<i>Antennella ansini</i>	FJ50470	MHNG-INVE-32157	Mallorca, Spain	39.4518	3.2785	31.07.2001	3
<i>Antennella kiiviana</i>	DQ855918	MHNG-INVE-33623	Hauraki Gulf, New Zealand	-36.8123	174.8025	28.7.2002	0-1
<i>Antennella secundaria</i>	DQ883445	MHNG-INVE-32969	Banyuls-sur-Mer, France	42.5060	3.177	15.05.2002	62
<i>Antennella secundaria</i>	KM402030	DBUA1504.02	Ormonde seamount, Portugal	36.7143	-11.1661	10.06.2008	37-42
<i>Antennella secundaria</i>	MF784524	MHNG-INVE-79493	Baie de Morlaix, France	48.6763	-3.8842	30.08.2011	24-28
<i>Antennella secundaria</i>	MF784525	MHNG-INVE-89886	Baie de Morlaix, France	48.6768	-3.8861	10.09.2014	5-30
<i>Antennella secundaria</i>	MF784533	MHNG-INVE-97947	Bali, Indonesia	-8.3077	115.6208	02.02.2017	20
<i>Antennella siliquosa</i>	MF784523	MHNG-INVE-79490	Roscoff, France	48.7972	-3.9682	30.08.2011	70-75
<i>Antennella varians</i>	MF784528	MHNG-INVE-97931	Bali, Indonesia	-8.3560	115.6925	04.10.2016	0-20
<i>Halopteris alternata</i>	DQ855939	-	São Sebastião, Brazil	nd	nd	Sep. 2001	nd
<i>Halopteris alternata</i>	KT266620	MZUSP:1662	Barra de São Miguel, Brazil	-9.8333	-35.8847	22.10.2006	nd
<i>Halopteris alternata</i>	MF000542	MHNG-INVE-89422	Madeira, Portugal	32.8661	-17.1656	04.08.2014	0-2
<i>Halopteris alternata</i>	MF773748	HRG-1341	Martinique, France	14.6434	-61.1419	24.07.2017	1-2.5
<i>Halopteris alternata</i>	MF773749	DM&SM-BT014	Bocas del Toro, Panama	9.35	-82.23	30.07.2015	5
<i>Halopteris carinata</i>	KT266619	MZUSP:1681	Barra de São Miguel, Brazil	-9.7703	-35.8395	23.10.2006	nd
<i>Halopteris carinata</i>	MF784519	MHNG-INVE-35473	Honduras	16.0687	-86.9555	11.02.2004	20
<i>Halopteris catharina</i>	DQ855920	-	Roscoff, France	48.7300	-4.0000	April 1998	nd
<i>Hal. aff. polymorpha</i>	DQ855922	MHNG-INVE-30117	Banyuls-sur-Mer, France	42.5024	3.1273	23.06.1997	0-2
<i>Halopteris diaphana</i>	DQ855921	MHNG-INVE-30116	Mallorca, Spain	39.452	3.279	15.07.1997	nd
<i>Halopteris diaphana</i>	MF784517	MHNG-INVE-30118	Banyuls-sur-Mer, France	42.4803	3.1441	14.09.1995	2
<i>Halopteris liechtesternii</i>	AY787888	MHNG-INVE-29751	Mallorca, Spain	nd	nd	nd	nd
<i>Halopteris liechtesternii</i>	MF784518	-	Mallorca, Spain	-36.8123	174.8025	13.06.1997	1-3
<i>Halopteris liechtesternii</i>	MF784534	MHNG-INVE-97954	Menorca, Spain	40.0246	4.1936	26.05.2017	0-1
<i>Halopteris millardae</i>	MF773747	MHNG-INVE-98634	Faafu Atoll, Maldives	3.0649	72.9212	14.04.2016	35
<i>Halopteris minuta</i>	AY787912	MHNG-INVE-25073	Auckland, New Zealand	-36.8192	174.8068	14.10.1998	/
<i>Halopteris minuta</i>	MF784522	MHNG-INVE-88252	Auckland, New Zealand	-36.8192	174.8068	14.10.1998	/
<i>Hal. platygonotheca</i>	MF773744	DM&SM-MA0416141	Faafu Atoll, Maldives	3.0901	72.9679	18.04.2017	12
<i>Hal. platygonotheca</i>	MF773745	DM&SM-MA0416149	Faafu Atoll, Maldives	3.0938	72.9665	18.04.2017	13
<i>Hal. platygonotheca</i>	MF773746	DM&SM-MA0416168	Faafu Atoll, Maldives	3.0901	72.9679	20.04.2017	20
<i>Hal. platygonotheca</i>	MF784527	MHNG-INVE-97928	Bali, Indonesia	-8.2742	115.5926	29.09.2016	22

Species	GenBank accession number	Voucher	Locality	Latitude (+ N; - S)	Longitude (+ E; - W)	Collection date	Depth (m)
<i>Hal. platygonotheca</i>	MF784529	MHNG-INVE-97935	Bali, Indonesia	-8.3559	115.6925	04.10.2016	0-20
<i>Hal. platygonotheca</i>	MF784532	MHNG-INVE-97944	Bali, Indonesia	-8.2784	115.5970	31.01.2017	10-15
<i>Halopteris polymorpha</i>	MF784530	MHNG-INVE-97937	Bali, Indonesia	-8.5281	115.5148	06.10.2016	0-20
<i>Halopteris schucherti</i>	KP776814	MHNG-INVE-35930	Chile, Punta Huinay	-42.3745	-72.4281	09.03.2004	26.5
<i>Halopteris sibogae</i>	MF784526	MHNG-INVE-97926	Bali, Indonesia	-8.2742	115.5926	29.09.2016	22
<i>Halopteris sibogae</i>	MF784531	MHNG-INVE-97938	Bali, Indonesia	-8.5281	115.5148	06.10.2016	0-20
<i>Halopteris tenella</i>	DQ855938	-	São Sebastião, Brazil	-	-	-	-
<i>Halopteris vervoortii</i>	MF773740	DM&SM-CU005	Curaçao, The Netherlands	12.1214	-68.9692	09.06.2017	11
<i>Halopteris vervoortii</i>	MF773741	HRG-1339	Martinique, France	14.6434	-61.1419	24.07.2017	1-2.5
<i>Halopteris vervoortii</i>	MF773743	MHNG-INVE-98635	Faafu Atoll, Maldives	3.0761	72.9616	29.01.2016	3
<i>Halopteris vervoortii</i>	MF773742	MHNG-INVE-98636	Faafu Atoll, Maldives	3.0748	72.9663	13.04.2016	10
<i>Monost. quadridens</i>	DQ855941	-	Ilhabela, Brazil	-	-	Feb. 2002	nd
<i>Monost. quadridens</i>	KT266627	MZUSP.4632	Florianopolis, Brazil	-27.2280	-48.433	17.04.2008	nd
<i>Polyplumaria flabellata</i>	AM888338	-	Gulf of Cadiz, Morocco	35.17	-6.46	07.10.2006	451
<i>Schizotricha frutescens</i>	MF784521	MHNG-INVE-91725	Raunefjord, Norway	60.3382	5.1867	20.04.2015	30