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SHALLOW-WATER HYDROIDS OF BERMUDA: SUPERFAMILY PLUMULARIOIDEA

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Cover: Colony of *Macrorhynchia allmani* (Nutting, 1900) dredged from a station 2.5 km SE of Castle Roads, Bermuda, on limestone rubble, -82 m, 5 September 1992, ROMIZ B408.

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Contents

Shallow-Water Hydroids of Bermuda: Superfamily Plumularioidea

Abstract

The taxonomy of 16 species, eight genera, and four families of hydroids referable to the superfamily Plumularioidea McCrady, 1859, from Bermuda is here reviewed and revised. The study was limited to species collected over a depth range from the intertidal zone to 100 m. Diagnoses are provided of all the genera and family-group taxa represented, and each of the 16 species is described and illustrated.

Taxa recognized as new include Gymnangiinae, subf. nov., and Cladocarpini, tribe nov. *Cladacanthella* is proposed as a replacement name for *Acanthella* Allman, 1883, an invalid junior homonym of *Acanthella* Schmidt, 1862. Type species are designated for seven nominal genera: *Lowenia* Meneghini, 1843, *Pachyrhynchia* Kirchenpauer, 1872, *Isocola* Kirchenpauer, 1876, *Anisocola* Kirchenpauer, 1876, *Apostasis* von Lendenfeld, 1885b, *Haptotheca* von Lendenfeld, 1885b, and *Polysiphonia* von Lendenfeld, 1885b [not *Polysiphonia* Hertwig, 1882]. A lectotype is designated of *Gymnangium variabilis* (Nutting, 1900). Under the First Reviser Principle (ICZN, 1985, Art. 24), precedence is assigned to the name *Aglaophenia latecarinata* Allman, 1877, over *A. perpusilla* Allman, 1877, and to *Macrorhynchia savignyana* Kirchenpauer, 1872, over *M. pennaria* Kirchenpauer, 1872. *Nuditheca*, *Astrolabia*, *Pentatheca*, and *Anarthroclada* are transferred from the family Aglaopheniidae Marktanner-Turneretscher, 1890, to the Halopterididae Millard, 1962, based on the morphology of their nematothecae and gonothecae, and the presence, in some cases obscured, of cauline hydrothecae.

Introduction

The first two parts of this series on the shallow-water hydroids of Bermuda dealt respectively with the families, genera, and species of athecates (Calder, 1988), and with those of thecates exclusive of the superfamily Plumularioidea McCrady, 1859 (Calder, 1991a). This report on the plumularioid taxa completes my taxonomic study of the thecates of the Bermuda Platform, and concludes the series. Literature on the taxonomy of the hydroids of Bermuda is discussed in the two previously published parts and in an investigation of the ecology and zoogeography of the hydrozoans of the study area (Calder, 1993).

Of 93 species of hydroids reported from depths of 0–100 m on the Bermuda Platform (Calder, 1993), 17 were plumularioids. Hydroids of this superfamily are much more speciose in lower than in higher latitudes (see Nutting, 1900; Fraser, 1944). Given the affinities of Bermuda hydrozoans with those of the West Indies (Calder, 1992), and the richness of the West Indian plumularioid fauna (Allman, 1877; Nutting, 1900; Fraser, 1944; Van Gemerden-Hoogeveen, 1965; Vervoort, 1968; Bogle, 1975), it is zoogeographically noteworthy that only 16 species are represented in this study.

Following objectives similar to those in the first two publications in the series, this report reviews and in some cases revises the taxonomy of the various families, genera, and species of Plumularioidea currently known from depths of 0–100 m on the Bermuda Platform. Particular attention has been given to nomenclatural matters, following the *International Code of Zoological Nomenclature* (International Commission on Zoological Nomenclature [ICZN], 1985).

Materials and Methods

The plumularioid hydroid species dealt with here were collected during nine field trips to Bermuda (1–22 September 1977, 26 February–10 March 1982, 17 July–6 August 1982, 15 June–13 July 1983, 20 September–11 October 1984, 24 September–8 October 1986, 22 November–9 December 1989, 10–31 May 1991, and 1–22 April 1992). Much of the study material was obtained around the northeastern end of Bermuda, especially from Whalebone Bay, Flatts Inlet, Harrington Sound, Castle Harbour, and the fore-reef slope southeast of Castle Roads (see Calder, 1993, fig. 1). Only those species obtained at depths of 100 m or less are included in this report. Collecting was undertaken inshore in bays, sounds, inlets, caves, ponds, and shallow reefs by snorkelling, SCUBA diving, and manual collecting. Offshore, dredging was done south of Castle Harbour (aboard M/V *Northstar*, 3 September 1977; R/V *Culver*, 1 July 1983; R/V *Weatherbird*, 27 September 1984; M/V *Polaris*, 13–14, 19, 22–23, 26 May 1991, 8–9, 19 April 1992; R/V *BBS II*, 27 May 1991), north of North Lagoon (R/V *BBS II*, 28 May 1991), and on Challenger Bank (R/V *BBS II*, 3 October 1984, 17 May 1991) (Calder, 1993, figs. 1–2). Specimens were also collected 2 km southeast of Castle Roads during a mollusc-trapping cruise aboard M/V *Polaris* (24 July 1982). Hydroids formerly in the collections stored at the Bermuda Biological Station for Research and now housed at the Bermuda Natural History Museum were also examined.

Anatomical terminology employed here is largely as defined and applied by Millard (1975), Svoboda and Cornelius (1991), and Cornelius (1995). Descriptions and illustrations in this report are based exclusively on material from Bermuda in collections of the Invertebrate Section of the Centre for Biodiversity and Conservation Biology, Royal Ontario Museum (ROMIZ), unless otherwise stated. Comparative material was obtained on loan from the Agassiz Museum of Comparative Zoology, Harvard University, Cambridge (MCZ); Allan Hancock Foundation, University of Southern California, Los Angeles (AHF); the Natural History Museum, London (BMNH); California Academy of Sciences, San Francisco (CAS); Muséum National d'Histoire Naturelle, Paris (MNHN); National Museum of Natural History, Smithsonian Institution, Washington (USNM); Royal British Columbia Museum, Victoria (RBCM); and the Zoological Institute, Russian Academy of Sciences, St. Petersburg (ZISP).

All names and citations contained in this report, including those in the synonymy lists, were traced and checked in the original sources. However, the synonymies are not purported to be complete. The *International Code of Zoological Nomenclature* (ICZN, 1985) was consulted in dealing with problems on scientific names. The "Reported Range" sections herein comprise (1) a complete or virtually complete summary of previous taxonomic records of each plumularioid species reported from Bermuda, and (2) broad ranges of each species, including occurrences (if any) in the western and eastern Atlantic, the Indian Ocean, and the western and eastern Pacific. In the interests of brevity, only one reference is given to document the occurrence of each species in each of these major regions.

Systematic Account

Superfamily Plumularioidea McCrady, 1859

DIAGNOSIS

Colonies erect, with a creeping, encrusting, or rootlike hydrorhiza. Hydrocladia given off from hydrocaulus, or directly from hydrorhiza. Hydrothecae on hydrocladia only, or on both hydrocladia and hydrocauli; uniseriate in almost all species; more or less bilaterally symmetrical; sessile, with adcauline wall partly to entirely adnate to internode; hydrothecal base with distinct floor perforated by hydropore. Hydrothecal margin entire or cusped; operculum absent. Hydranth typically retractable into hydrotheca; hypostome conical, surrounded by a single whorl of filiform tentacles. Nematophores invariably present, typically protected by nematothecae.

Gonophores fixed sporosacs or in a few species released as medusoids; solitary or aggregated; corbulae or other phylactocarps present or absent.

REMARKS

The classification of the Plumularioidea McCrady, 1859, has been revised repeatedly as knowledge of the diversity of and relationships within the group has advanced. Allman (1883) divided a broadly defined family Plumulariidae McCrady, 1859, into two subfamilies based on the type of nematotheca present. However, the names he proposed for them (Eleutheroplea for those with "moveable" nematothecae, and Statoplea for those with "fixed" nematothecae) were not formed in accordance with rules of zoological nomenclature and are invalid (ICZN, 1985, Art. 11f). Nevertheless, these two family-group names or modifications of them persisted in various publications well into the 20th century (e.g., Billard, 1913; Bedot, 1923; Fraser, 1944; Naumov, 1960; von Schenck, 1966).

Bedot (1923) distinguished four subfamilies in the group on the basis of nematophore type and arrangement, namely, Eleutheroplea; Statoplea; "Kirchenpauerina" Stechow, 1921a (established for species lacking lateral nematothecae); and "Nudithecata" (a new subfamily comprising only the type genus *Nuditheca* Nutting, 1900). This classification, nomenclaturally less advanced than another published the same year by Stechow (1923a), was never widely adopted. Stechow divided the Plumulariidae sensu lato into four subfamilies based largely on nematophore type, recognizing the Plumulariinae McCrady, 1859 (essentially equivalent to Eleutheroplea); Aglaopheniinae Marktanner-Turneretscher, 1890 (replacing Statoplea); Kirchenpaueriinae Stechow, 1921a; and a new subfamily, Acladiinae Stechow, 1923a (encompassing species considered intermediate between Eleutheroplea and Statoplea). The subfamily Acladiinae was subsequently abandoned by Stechow (1925b), however, and its taxa were included in the Plumulariinae. Bedot's (1923) "Nudithecata" (emended to Nudithecinae by Stechow, 1923a:236) never gained acceptance as a family name, and its only genus, *Nuditheca*, has usually been referred to the Plumulariidae sensu lato or to the Aglaopheniinae (or Aglaopheniidae). The genus is assigned here to the family Halopterididae Millard, 1962, instead (see Subfamily Gymnangiinae, Remarks). Reasons for employing the junior name Halopterididae in place of the senior name Nudithecidae Bedot, 1923, are discussed elsewhere (see Family Halopterididae, Remarks).

Millard (1962) correctly emphasized the limitations of using nematophore characteristics alone in defining subgroups within plumulariids, and employed additional characters, such as presence or absence of cauline hydrothecae and the type of branching, in delimitation of taxa. She retained and redefined Plumulariinae, Kirchenpaueriinae, and Aglaopheniinae, and distinguished a new subfamily, Halopterinae, within the group.

Some or all of the four subfamilies as defined by Millard (1962) have been elevated to the rank of family in a number of recent works (e.g., see Bouillon, 1985; Cornelius, 1995). I concur with Bouillon (1984, 1985) in recognizing all four of these as distinct families within the Plumularioidea. However, a revision of plumularioid classification seems much needed.

The hydroid is overwhelmingly the dominant stage in the life cycle of plumularioids. No species currently assigned to the superfamily is known to have a "well-developed," long-lived medusa stage. Only five species, *Nemertesia antennina* (Linnaeus, 1758); *Monotheca obliqua* (Johnston, 1847); *Gymnangium ferlusi* (Billard, 1901a); *Macrorhynchia philippina* Kirchenpauer, 1872; and *Aglaophenia* sp. (see Allman, 1871; Motz-Kossowska, 1907; Gravier, 1970a; Gravier-Bonnet, *in* Bouillon, 1985; Boero and Bouillon, 1989; Cornelius, 1995) have been reported to liberate medusoids. For a basic review of the diversity of hydroid-colony form within the Plumularioidea, see Nutting (1900) and Millard (1975). Plumularioid homologies were analysed by von Schenck (1966).

Representatives of all four families currently recognized within the Plumularioidea occur in Bermuda. Among 103 species of plumularioids currently recognized from the western North Atlantic (Calder, unpublished data), 16 are known from depths of 100 m or less around Bermuda and are discussed here.

Family Kirchenpaueriidae Stechow, 1921a

Kirchenpaueriinae Stechow, 1921a:259.

DIAGNOSIS

Colonies with hydrocaulus erect, branched or unbranched, monosiphonic or polysiphonic, with a creeping hydrorhiza. Hydrocladia alternate, arising in polysiphonic hydrocauli from a single axial tube. Hydrothecae small, with or without marginal cusps, with or without an abcauline intrathecal septum, occurring only on hydrocladia. Nematophores with nematothecae, or occurring as naked sarcostyles. When present, nematothecae simple, typically monothalamic although bithalamic in some; not fused to hydrothecae; paired lateral nematothecae absent.

Gonophores fixed sporosacs. Gonothecae solitary, lacking nematothecae, not protected by phylactocarps.

REMARKS

Stechow (1921a) proposed the Kirchenpaueriinae as one of four subfamilies within the Plumulariidae McCrady, 1859, but gave neither diagnosis nor indication of its scope. Later, he defined the taxon (Stechow, 1923a) much as it is currently understood (Millard, 1975; Bouillon, 1985). Kirchenpaueriids are immediately distinguishable morphologically from other plumularioids in lacking paired lateral nematothecae.

The status of *Kirchenpaueria* Jickeli, 1883, type genus of the family Kirchenpaueriidae, was reviewed by Bedot (1916b) and Broch (1918). The name *Kirchenpaueria* first appeared as a junior synonym ("*Kirchenpaueria elegans* Graeffe in litt.") of *Retihornera graeffei*, a new nominal genus and species of Bryozoa (Kirchenpauer, 1869:XXX). However, the name has not been employed as a senior synonym within the Bryozoa and does not threaten the way in which the name is used in the nomenclature of Hydrozoa (ICZN, 1985, Art. 11e).

Stechow (1923a) held that hydroids referred to the Kirchenpaueriinae were "primitive" plumulariids, in part because nematothecae in the group were morphologically simple. Millard (1962) maintained that the Halopterinae Millard, 1962, the only plumularioids with cauline hydrothecae, were closest to the ancestral state. Bouillon's (1984) diagram of relationships within the thecates does not clarify the matter. To date, a cladistic analysis of the group has not been undertaken and the phylogeny of the Plumularioidea is unresolved. For the present I concur with the view of Stechow (1923a) that kirchenpaueriids are closest to the ancestor of the group, given the similarity of taxa in this family to nematophorate haleciids, which may have given rise to plumularioids. Differences of kirchenpaueriids from haleciids, and from lafoeids, are especially small in genera such as *Hydrodendron* Hincks, 1874 (Millard, 1975; Rees and Vervoort, 1987; Calder, 1991a). Cauline hydrothecae characteristic of Halopterididae, as well as paired lateral nematothecae present in all plumularioids except kirchenpaueriids, are considered here to have arisen later in the phylogeny of the Plumularioidea.

Genera referred to this family by Bouillon (1985) comprised *Halicornopsis* Bale, 1882; *Kirchenpaueria* Jickeli, 1883; *Ophinella* Stechow, 1919a; *Oswaldella* Stechow, 1919b; and *Pycnotheca* Stechow, 1919a [replacement name for *Diplocheilus* Allman, 1883, an invalid junior homonym of *Diplocheilus* van Hasselt and Temminck, 1823 (Pisces)]. *Ventromma* Stechow, 1923a, regarded as congeneric with *Kirchenpaueria* by Bouillon (1985), is now frequently recognized as a valid genus (e.g., Mammen, 1965; Hirohito, 1974; Cornelius and Garfath, 1980; Cornelius, 1995) and is represented in Bermuda by the widely distributed species *Ventromma halecioides* (Alder, 1859).

Genus *Ventromma* Stechow, 1923a

Ventromma Stechow, 1923a:219.
Ventroma da Cunha, 1944:26 [incorrect subsequent spelling].

DIAGNOSIS

Colonies erect, with branched or unbranched hydrocauli arising from creeping hydrorhizae. Hydrocladia alternate, typically unbranched. Hydrothecae occurring only on hydrocladia, cup-shaped, margin entire, without an abcauline intrathecal septum. Nematophores with small nematothecae; lateral nematophores and nematothecae absent.

Gonophores and gonothecae as described for family.

TYPE SPECIES

Plumularia halecioides Alder, 1859, by subsequent designation by Rees and Thursfield (1965).

REMARKS

Stechow (1923a) established *Ventromma* for *Plumularia halecioides* Alder, 1859, and four other nominal species. The genus was clearly founded on characters observed in *P. halecioides*, but Stechow did not explicitly designate it as the type species. Rees and Thursfield (1965) are credited here with having first designated *P. halecioides* as the type species of *Ventromma*.

Ventromma resembles *Kirchenpaueria* Jickeli, 1883, and the two are sometimes regarded as congeneric (e.g., Millard, 1975; Bouillon, 1985). *Ventromma*, possessing nematophores with nematothecae, differs from *Kirchenpaueria*, which has naked sarcostyles (Stechow, 1923a).

Ventromma halecioides (Alder, 1859)

Fig. 1

Plumularia halecioides Alder, 1859:353, pl. 12, figs. 1–5.
Anisocalyx bifrons Heller, 1868:43, pl. 2, fig. 6.
Anisocalyx pinnatifrons Heller, 1868:43, pl. 2, figs. 7–8.
Plumularia helecioides—Norman, 1869:321 [incorrect subsequent spelling].
Plumularia bifrons—Kirchenpauer, 1876:28, pl. 1, fig. 16.
Plumularia halecioides var. *adriatica* Kirchenpauer, 1876:28.
?*Plumularia oligopyxis* Kirchenpauer, 1876:48, pl. 6, figs. 9, 9a–b.
?*Plumularia (Anisocola) oligopyxis* var *monopyxis* Kirchenpauer, 1876:49.
?*Plumularia (Anisocola) oligopyxis* v. *bipyxis* Kirchenpauer, 1876:49.
?*Plumularia (Anisocola) oligopyxis* v. *tripyxis* Kirchenpauer, 1876:49.
?*Monopyxis tenella* Kirchenpauer, 1876:49.
Anisocola halecioides—Jickeli, 1883:636, pl. 28, figs. 10–23.
Anisocola bifrons—Jickeli, 1883:646.
?*Plumularia alleni* Nutting, 1896:153.
Plumularia tenuis Schneider, 1898:485.
Plumularia inermis Nutting, 1900:62, pl. 5, figs. 1–2, 2A.
Plumularia haloecioides—Billard, 1901b:523 [incorrect subsequent spelling].
Plumularia halecioides variété A Billard, 1903:58.
Plumularia halecioides variété V Billard, 1903:58.

Plumularia halecioides adriatica Billard, 1904a:189.
Plumularia mermis—Wallace, 1909:136 [incorrect subsequent spelling].
Plumularia pinnatifrons—Bedot, 1912:343.
Plumella halecioides—Stechow, 1920:45.
?*Plumella oligopyxis*—Stechow, 1921a:259.
Plumella tenuis—Stechow, 1921a:259.
Antennularia pinnata—Bennitt, 1922:252, fig. 2 [not *Antennularia pinnata* Nutting, 1900].
Kirchenpaueria inermis—Bedot, 1923:233.
Ventromma halecioides—Stechow, 1923a:220.
?*Ventromma oligopyxis*—Stechow, 1923a:220.
Ventromma tenuis—Stechow, 1923a:221.
Kirchenpaueria halecioides—Bedot, 1925:253.
?*Diplocyathus gracilis*—Leloup, 1935:11, fig. 2 [not *Ophiodes gracilis* Fraser, 1914].
Antenella halecioides—Leloup, 1935:51 [incorrect subsequent spelling].
?not *Plumularia inermis*—Fraser, 1938a:64, pl. 15, figs. 74a–b.
Ventroma halecioides—da Cunha, 1944:26 [incorrect subsequent spelling].
?*Ophiodissa gracilis*—Fraser, 1944:204 [not *Ophiodes gracilis* Fraser, 1914].
Plumularia irregularis Millard, 1958:210, Figs. 13A–C [not *Plumularia irregularis* Fraser, 1948].
Ventromma adriatica—Picard, 1958:192.
Ventromma halecoides—Bruce, Colman and Jones, 1963:54 [incorrect subsequent spelling].
Ventromma halecioides var. *minutus* Mammen, 1965:295, fig. 92.
Ventromma inermis—Hirohito, 1974:47.
Kirchenpaueria irregularis—Millard, 1975:370, figs. 118D–G.
Plumularia halecoides—Wedler, 1975:332 [incorrect subsequent spelling].
Plumularia bifroms—Gili, 1982:85 [incorrect subsequent spelling].
Plumularia haleciodes—Spracklin, 1982:246 [incorrect subsequent spelling].
Plumularia helecoides—Bandel and Wedler, 1987:88 [incorrect subsequent spelling].

TYPE LOCALITY

Northeast England (Cullercoats [Northumberland] and Roker [Durham]).

MATERIAL EXAMINED

Ferry Reach, on submerged rope, –0.5 m, 2 September 1977, four colonies, up to 20 mm high, two colonies with gonophores and two without, ROMIZ B117. Whalebone Bay, on *Thalassia*, –1 m, 22 July 1982, one colony, 2.5 mm high, without gonophores, coll. A., E., and N. Calder, ROMIZ B286. Castle Harbour adjacent to Tucker's Town, on patch reef, –5 m, 3 August 1982, one colony, 5.5 mm high, without gonophores, ROMIZ B289. Green Bay, on algae on concrete wall, –1 m, 21 September 1984, one colony, up to 3 mm high, without gonophores, ROMIZ B382. Walsingham Bay, on *Rhizophora*, –0.5 m, 1 December 1989, several colonies, up to 7 mm high, without gonophores, ROMIZ B383. Pilchard Bay, on *Rhizophora*, –0.5 m, 28 November 1989, several colonies, up to 20 mm high, without gonophores, ROMIZ B384.

DESCRIPTION

Colonies up to 2 cm high, with creeping hydrorhizae. Hydrocaulus branched or unbranched, monosiphonic or polysiphonic, hydrocaulus if polysiphonic with one or more secondary, unsegmented peripheral tubes adhering to a primary axial tube bearing alternate hydrocladia; peripheral tubes sometimes giving rise to secondary hydrocauli. Primary tube of hydrocaulus straight to zigzag, divided at regular intervals into internodes by distinct transverse nodes; internodes 280–494 μm long, 39–75 μm wide at nodes, each with a distal axillary nematotheca and a hydrocladial apophysis having an axillary mamelon on its upper surface. Apophyses alternate, bearing hydrocladia with one to 11 hydrothecae each. Hydrocladia typically unbranched, up to 5.5 mm long but typically much shorter, nodes slightly oblique; with one or more thecate internodes and occasionally with a short athecate internode proximally. Thecate internodes 363–727 μm long, 33–47 μm wide at nodes, each with a distal hydrotheca, a median inferior nematotheca, and a median superior nematotheca; distalmost internode of a hydrocladium with a distal hydrotheca and a median inferior nematotheca, but often without a median superior nematotheca; occasional hydrocladia with one or more internodes having neither hydrothecae nor nematothecae. Internodal septa absent; lateral nematothecae absent. Nematothecae small with thin perisarc, bithalamic, movable, more or less cone-shaped; axillary nematothecae 42–51 μm long, 15–21 μm wide at aperture; internodal nematothecae 38–42 μm long, 13–18 μm wide at aperture; nematophores often elongate and extending well beyond end of nematothecae. Hydrotheca small, shallow, cup-shaped, main axis oblique to that of hydrocladium, abcauline wall 65–75 μm long, length adcauline wall free 37–58 μm; margin entire; aperture diameter 90–112 μm; base of hydrotheca with ring of desmocytes. Hydranth larger than hydrotheca, with about 18 filiform tentacles surrounding a dome-shaped hypostome; no basal tentacular web.

Gonophores fixed sporosacs. Gonotheca elongate-oval with distinct transverse ridges, truncate at distal end, approximately 500 μm wide, 1100 μm long from base to orifice, arising by a short pedicel from primary axial tube of hydrocaulus; orifice about 380 μm in diameter, essentially round in cross-section.

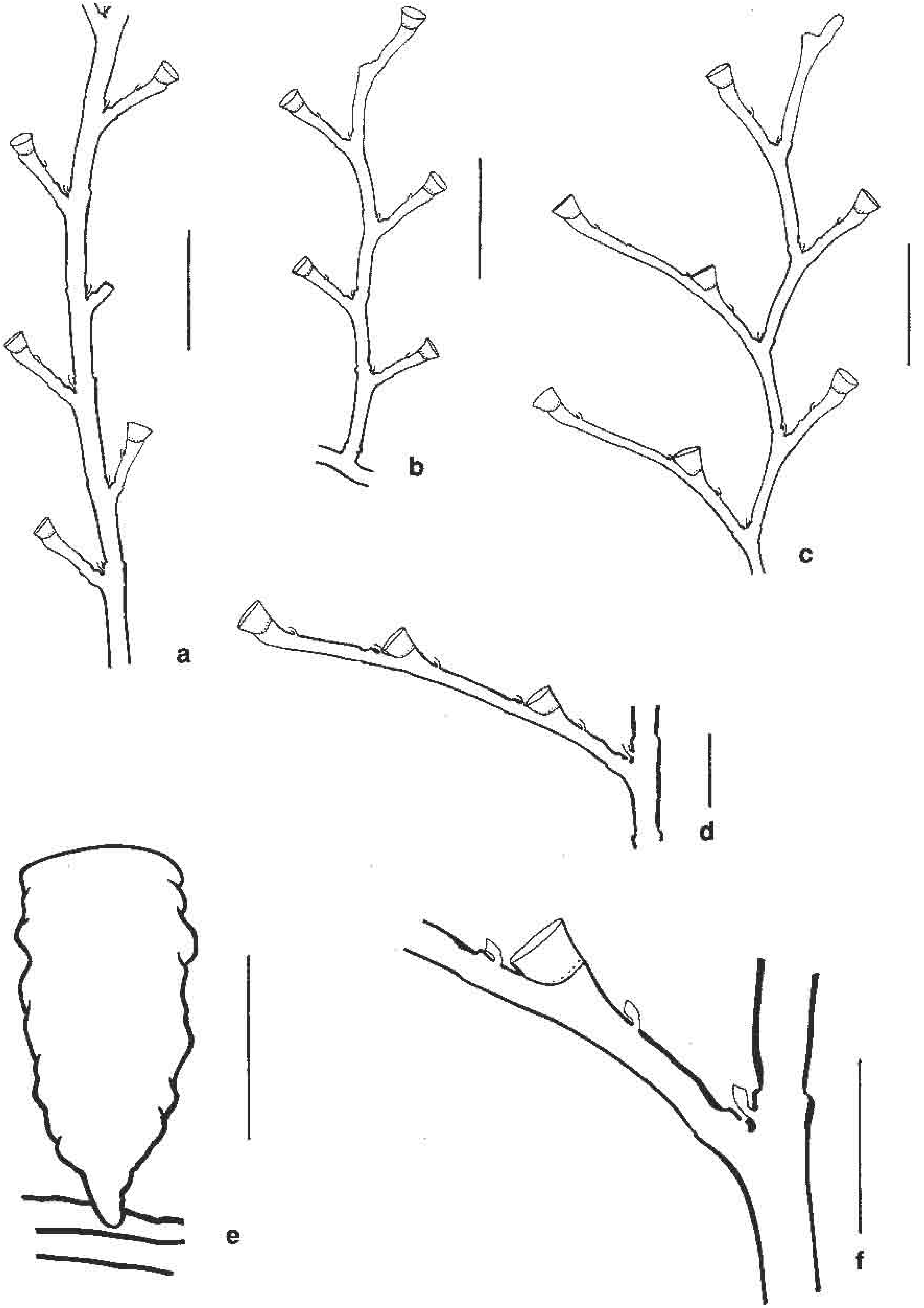

FIG. 1. *Ventromma halecioides: a,* part of hydrocaulus, with monothecate hydrocladia, ROMIZ B117; *b,* small colony with hydrocaulus and monothecate hydrocladia, ROMIZ B382; *c,* part of hydrocaulus with both monothecate and bithecate hydrocladia, ROMIZ B383; *d,* hydrocaulus and hydrocladium, ROMIZ B117; *e,* gonotheca, ROMIZ B117; *f,* hydrocaulus and basal part of hydrocladium, ROMIZ B117. Scales for *a, b, c,* and *e* qual 0.5 mm; scales for *d* and *f* equal 0.25 mm.

REMARKS

The synonymy compiled here is based on the conclusions of a number of earlier taxonomists. *Anisocalyx pinnatifrons* Heller, 1868, was referred to the synonymy of *Ventromma halecioides* (Alder, 1859) following Jickeli (1883) and Bedot (1912). *Anisocalyx bifrons* Heller, 1868, was regarded as conspecific by Gili (1982), whereas Bedot (1921a) had earlier regarded the two as questionably conspecific. The binomena *Plumularia oligopyxis* Kirchenpauer, 1876; *Plumularia adriatica* Kirchenpauer, 1876; and *Plumularia tenuis* Schneider, 1898 (not *Plumularia tenuis* Warren, 1908, renamed *P. warreni* by Stechow, 1919a) were regarded as coterminous with *V. halecioides* by Picard (1958). However, *Plumularia oligopyxis* is listed as questionably conspecific here because the gonotheca of that species was illustrated and described by Kirchenpauer (1876) as "cyathiform" rather than barrel-shaped with distinct ribs as in *V. halecioides*. Bedot (1912) referred the name *Monopyxis tenella* Kirchenpauer, 1876, to the synonymy of *Plumularia oligopyxis*. Cornelius (1995) discussed the status of *Plumularia alleni* Nutting, 1896, and assigned it with some doubt to *V. halecioides*. Although he noted that it might have been based on *P. setacea* (Linnaeus, 1758), its gonotheca as described and illustrated by Nutting (1898) seemed to indicate otherwise. In spite of Fraser's (1944) arguments to the contrary, I concur with authors such as Bedot (1921a, 1923, 1925), Leloup (1935), Van Gemerden-Hoogeveen (1965), and Vervoort (1968) that *Plumularia inermis* Nutting, 1900, is identical to *V. halecioides*. However, hydroids from the eastern Pacific identified as *Plumularia inermis* by Fraser (1938a) do not seem to correspond in gonothecal shape with that species and may have been misidentified (Van Gemerden-Hoogeveen, 1965; Hirohito, 1974). As noted by Hirohito, Fraser's (1944) description of the gonotheca of *P. inermis* in his book on Atlantic hydroids appears to have been based on the material of questionable identity from the Pacific. I concur with Leloup (1935) and Hirohito (1974) that Bennitt's (1922) record of *Antennularia pinnata* Nutting, 1900, from Bermuda is based on misidentified specimens of *V. halecioides*. *Plumularia irregularis* Millard, 1958, seems inseparable from *V. halecioides* on the basis of existing descriptions, and the two were regarded as conspecific by García, Aguirre, and Gonzalez (1978). Whether or not this is so, the name *P. irregularis* Millard, 1958, is an invalid junior primary homonym of *P. irregularis* Fraser, 1948.

According to Cornelius and Garfath (1980), it is unclear whether specimens of *Ventromma halecioides* in the Alder Collection of hydroids at the Hancock Museum, University of Newcastle upon Tyne, are syntypes or subsequent material.

Ventromma halecioides has long been known as a morphologically varied species (Billard, 1903). In particular, small colonies (Fig. 1b), such as those collected during this study on *Thalassia* in Whalebone Bay (ROMIZ B286) and on algae in Green Bay (ROMIZ B382), were difficult to distinguish from certain species referred to the haleciid genus *Hydrodendron* Hincks, 1874, and especially from *Hydrodendron gracilis* (Fraser, 1914). Hydrocladia of these minute specimens were short, and each hydrocladium supported a single, terminal hydrotheca. Nevertheless, they were also similar morphologically to small branches of otherwise unmistakable colonies (Fig. 1a) of *V. halecioides* from Ferry Reach (ROMIZ B117), and to an unnumbered illustration of that species from the British Isles by Hincks (1868, frontispiece). In addition, colonies of *V. halecioides* from Walsingham Bay (ROMIZ B383) had monothecate hydrocladia as well as more typical bithecate hydrocladia on the same colony (Fig. 1c). Moreover, small colonies with exclusively monothecate hydrocladia arose from the same stolon system as larger colonies with polythecate hydrocladia in the specimens from Walsingham Bay.

In light of the variations noted above, hydroids identified from Bonaire and Aruba by Leloup (1935) as *Diplocyathus gracilis* (Fraser, 1914) are provisionally referred here to *Ventromma halecioides*. Some uncertainty remains about the identity of Leloup's specimens because they were infertile. As for *Ophiodes gracilis* Fraser, 1914, its identity is unclear. It appears that no holotype of the species, originally described from Rose Spit, British Columbia, was ever designated (see Arai, 1977:25), and no other material from the type locality is represented in the Fraser hydroid collection housed at the Royal British Columbia Museum (RBCM). A hydroid subsequently identified by Fraser (1936) as *O. gracilis* from Houston Stewart Channel, British Columbia (RBCM 976-510-1), and reexamined here, has lateral nematothecae and is a plumulariid rather than a haleciid or a kirchenpaueriid. If this slide-mounted material is conspecific with *O. gracilis*, then Fraser's (1914) original description and illustrations of the species are misleading. More likely, Fraser (1936) may have misidentified the hydroid in the RBCM collection as *O. gracilis*.

REPORTED RANGE

Bermuda: Hamilton Harbour, on a floating buoy (Bennitt, 1922, as *Antennularia pinnata*); Fairyland Creek, on turtle grass (Bennitt, 1922, as *Plumularia inermis*); inlets, sheltered bays, sounds, reefs (Calder, 1993).

Circumglobal distribution: western Atlantic (Van Gemerden-Hoogeveen, 1965); eastern Atlantic (Cornelius and Garfath, 1980); Indian Ocean (Mammen, 1965); western Pacific (Hirohito, 1974); ?eastern Pacific (Fraser, 1937).

Family Plumulariidae McCrady, 1859

Plumularidae McCrady, 1859:198 [emended to Plumulariidae by Hincks, 1868:279].

DIAGNOSIS

Colonies with hydrocauli erect, branched or unbranched, monosiphonic or polysiphonic, arising from creeping, rootlike, or disc-shaped hydrorhizae. Hydrocladia alternate, opposite, or in verticils, arising in polysiphonic hydrocauli from a single axial tube. Hydrothecae typically small, with or without marginal cusps, occurring only on hydrocladia. Nematophores with nematothecae, not as naked sarcostyles. Nematothecae well developed, typically bithalamic and movable, not fused to hydrothecae; a minimum of three (one median inferior nematotheca and a pair of lateral nematothecae) adjacent to each hydrotheca.

Gonophores fixed sporosacs, or in a few species released as free but short-lived medusoids. Gonothecae solitary, without nematothecae, with or without phylactocarps.

REMARKS

Authorship of the name Plumulariidae is usually attributed to L. Agassiz (1862:358), who was first to unequivocally recognize the family as valid under that name. However, there is nothing in an earlier conditional use of the name by McCrady (1859:198), in reference to the same taxon, that either precludes its availability from McCrady's publication or otherwise invalidates his authorship of it (ICZN, 1985, Arts. 11d [i], 11e, 15, 50). McCrady (1859) used the name Plumularidae (*sic*) conditionally when he observed that a group of genera with nematophores, including *Plumularia* Lamarck, 1816; *Antennularia* Lamarck, 1816 (=*Nemertesia* Lamouroux, 1812); and *Aglaophenia* Lamouroux, 1812, might warrant separation from sertulariids such as *Sertularia* Linnaeus, 1758; *Thuiaria* Fleming, 1828; and *Dynamena* Lamouroux, 1812, which lacked such structures. Under the Principle of Coordination in zoological nomenclature (ICZN, 1985, Art. 36), McCrady (1859) must also be credited with authorship of the superfamily name Plumularioidea, and of other names derived from the stem of the type genus *Plumularia* within the same family group.

Although the Plumulariidae appears to be a rather clearly defined family, classification of the group at the generic level remains unsettled and in need of revision. In Bouillon's (1985) synopsis, six recent genera of plumulariids were recognized: *Nemertesia*; *Plumularia*; *Polyplumaria* G. O. Sars, 1874; *Hippurella* Allman, 1877; *Callicarpa* Fewkes, 1881; and *Dentitheca* Stechow, 1920. In contrast, 11 of the genera recognized by Stechow (1923a) (*Nemertesia*; *Plumularia*; *Polyplumaria*; *Callicarpa*; *Dentitheca*; *Antennopsis* Allman, 1877; *Sciurella* Allman, 1883; *Acanthella* Allman, 1883 [not *Acanthella* Schmidt, 1862]; *Monotheca* Nutting, 1900; *Antomma* Stechow, 1919b; and *Nemertella* Stechow, 1923c) are referable to the Plumulariidae as defined by Bouillon.

Of the 12 plumulariid genera above recognized by Stechow (1923a) or Bouillon (1985), or both, the following are considered valid or probably valid taxa here: *Nemertesia*, *Plumularia*, *Polyplumaria*, *Hippurella*, *Callicarpa*, *Acanthella* (but see nomenclatural problem discussed two paragraphs below), *Monotheca*, and *Dentitheca*. Like Hirohito (1969, 1983), and Rho and Park (1986), I also consider *Sibogella* Billard, 1911a, characterized by peculiar monothecate hydrocladia, to be valid. In addition, *Monothecella* Stechow, 1923b, also with monothecate hydrocladia but with distinctive nematothecae (see Genus *Monotheca*, Remarks), is recognized as valid here. The status and taxonomic affinities of *Plumella* Stechow, 1920, remain unresolved, although it is referred with question in this study to the synonymy of *Plumularia* (see Genus *Plumularia*, Remarks). *Stechowia* Nutting, 1927 [not *Stechowia* Poche, 1914], is considered congeneric with *Sibogella*, as noted by Billard (1929). Of questionable validity is *Sciurella*, differing from *Nemertesia* in its unusual gonophores. Bedot (1921a) is followed here in recognizing *Sciurella* as distinct. *Sphaerocystis* Fraser, 1943, referred to *Plumularia* by Bouillon (1985), is assigned here to *Dentitheca* instead because of the characteristic structure of its hydrothecal margin. According to Fraser (1943), the genus *Sphaerocystis* is marked by the presence of both globular and clavate nematophores on the hydroid colony. Although type material of *Sphaerocystis heteronema* Fraser, 1943, type species of the genus (MCZ 9002), is now dry and the nematophores are no longer intact, the specimen appears indistinguishable from *Dentitheca dendritica* (Nutting, 1900), and I regard the two as conspecific. The name *Sphaerocystis* Fraser, 1943, is an invalid junior homonym of *Sphaerocystis* Léger, 1892 (Protozoa). Bouillon's (1985:170) spelling of the name, as *Sphaerocystys*, is incorrect.

I concur with Bouillon (1985) that *Antennularia*, *Antennopsis*, and *Nemertella* should be regarded as congeneric with *Nemertesia*, although *Antennopsis* has sometimes been distinguished from *Nemertesia* in having a non-canaliculated coenosarc in the hydrocaulus (Nutting, 1900:73). Stechow (1923c:116) held that *Nemertella*, with secondarily branched hydrocladia, should be distinguished from *Nemertesia*, typically with unbranched hydrocladia, just as differences in colony branching have been used to distinguish *Polyplumaria* from *Plumularia*. However, secondary hydrocladial branching does not seem to set *Nemertella* apart from *Nemertesia* as much as opposite pinnate branching distinguishes *Polyplumaria* from *Plumularia*. Although presence or absence of hydrocladial branching has been widely used as a generic character in plumularioids and especially in halopteridids (see Millard, 1962:269–270), it remains open to question in my opinion whether or not it is an appropriate criterion for such purposes.

The name *Acanthella* Allman, 1883, is an invalid junior homonym of *Acanthella* Schmidt, 1862 (a sponge), and a replacement name, *Cladacanthella* nom. nov. (derived from the Greek words *cladus* [branch] and *acanthella* [diminutive of thorn]; gender: feminine), is established for the genus here. The margin of the hydrotheca of *Cladacanthella effusa* (Busk, 1852), type species of the genus, is cusped as in *Dentitheca*, but *Cladacanthella* is immediately distinguishable from that genus in having hydrocladia reduced to spines at the ends of the branches.

Much confusion exists in the literature over the status of *Hippurella*. The genus was established for *Hippurella annulata* Allman, 1877, a species originally described as having proximal hydrocladia of the branches pinnately arranged, and distal hydrocladia essentially in verticils. Examination of the type (MCZ, no catalogue number) of *H. annulata* confirms the general accuracy of Allman's (1877) description of the hydrocaulus, primary branches, and hydrothecae of the species. Unfortunately, hydrocladia are now missing in the type except for one stub given off from the hydrocaulus. According to Allman, gonophores were lacking in material of *H. annulata*. Fewkes (1881) subsequently described the gonophores of a hydroid that he misidentified as *H. annulata* (see Nutting, 1900:84). Nutting retained Fewkes's hydroid in *Hippurella* but provided it with a new species name, *H. longicarpa*. After studying the types of both *H. annulata* and *H. longicarpa* (MCZ, no catalogue numbers) during this study, I agree with the conclusion of Nutting that they are different species. Meanwhile, Nutting (1900:75) referred *H. annulata* to *Antennopsis*, expressing the view that *Hippurella* as defined by Allman (1877) was congeneric with that genus. Yet Nutting (1900:84) retained and redefined *Hippurella*, inexplicably basing its diagnosis on the trophosome of a species (*Hippurella annulata* Allman, 1877) that he referred to *Antennopsis* and on the gonosome of a species (*H. longicarpa*) that he retained in *Hippurella*. Nutting's mistake in referring the type species of *Hippurella* to *Antennopsis*, while retaining *Hippurella* as valid without it, was followed by Fraser (1944). Stechow (1919b) referred *H. longicarpa* to a new genus, *Antomma*, introduced as a replacement name for what he supposed was a junior homonym (*Hippurella* sensu Nutting, 1900) of *Hippurella* Allman, 1877. He later erred (Stechow, 1923a:217) in following Nutting's composite definition of the genus *Hippurella* for *Antomma*, and in referring *Hippurella* sensu Allman (1877) to *Antennopsis*. Although Bouillon (1985) regarded *Hippurella* and *Antomma* as congeneric, their gonosomes appear to differ according to some accounts in the literature. As described by Nutting (1900:75), those of *Hippurella annulata*, type species of *Hippurella*, are axillary and by inference unprotected (in being assigned to *Antennopsis*), while those of *H. longicarpa*, type species of *Antomma*, are protected by phylactocarps at the ends of the branches. However, evidence exists that the two nominal genera do not differ in this regard at all, and I agree with the view of Bouillon that they are identical. Gonophores in *Antennopsis ramosa* Fewkes, 1881, regarded as conspecific with *Hippurella annulata* by Nutting (1900:75), are protected by phylactocarps at the distal ends of the branches. After examining type specimens (MCZ, no catalogue numbers) of *H. annulata* and *A. ramosa*, I concur with the opinion of Nutting that they are conspecific. Moreover, phylactocarps in specimens labelled *A. ramosa* give the distal ends of the primary branches the appearance of having hydrocladia scattered or in irregular verticils, as originally described in *H. annulata* by Allman (1877). From this, it seems probable that Allman's (1877) material of *H. annulata* had phylactocarps after all. Although phylactocarps also occur in *Callicarpa*, they are unlike those of *Hippurella* in that each occurs on a specially modified branch.

Ramil and Vervoort (1992c) concluded, in founding *Pseudoplumaria*, that it was intermediate between the families Plumulariidae and Halopterididae. They assigned it to the Plumulariidae, but it is regarded as a halopteridid here (see Family Halopterididae, Remarks). Also referred here to the Halopterididae is *Polyplumaria*, with characters much like those of *Pseudoplumaria*. The two differ from each other principally in their hydrocladia, which are branched in *Polyplumaria* and unbranched in *Pseudoplumaria* (Ramil and Vervoort, 1992c).

The distinction between plumulariids and halopteridids, often combined in earlier work despite their differences in colony form, has been emphasized by Millard (1962). In fact, she commented that halopteridids tend to resemble *Aglaophenia* more than *Plumularia* in their overall appearance.

Two genera of plumulariids, *Plumularia* and *Monotheca*, are currently known from the Bermuda Platform.

Genus *Monotheca* Nutting, 1900

Monotheca Nutting, 1900:72.

Monoteca Vannucci, 1951:89 [incorrect subsequent spelling].

DIAGNOSIS

Colonies small, with erect, unbranched or sparingly branched hydrocauli arising from either creeping or flat and digitate hydrorhizae. Hydrocladia alternate, unbranched, short, not extending beyond hydrotheca, each with two internodes and a single terminal hydrotheca. Hydrothecae occurring only on hydrocladia, cup-shaped, margin more or less entire. Hydrothecate internode of hydrocladium with a single median inferior nematotheca and a terminal pair of lateral nematothecae.

Gonophores eumedusoid, reportedly released in at least one species (*Monotheca obliqua*). Gonothecae solitary, arising from hydrocladial apophyses, lacking nematothecae, not protected by corbulae or other phylactocarps.

TYPE SPECIES

Monotheca margaretta Nutting, 1900, by monotypy.

REMARKS

Nutting (1900) proposed *Monotheca* as a new scientific name for *Monopyxis* sensu Kirchenpauer (1876) [not *Monopyxis* Ehrenberg, 1834]. He stated that Kirchenpauer had established *Monopyxis* as a new genus-group name, and noted that it was preoccupied by *Monopyxis* Ehrenberg, 1834. In fact, Kirchenpauer (1876:15, 17, 29) was aware of Ehrenberg's earlier use of the name and recognized his predecessor's authorship of it. Instead of establishing the name as new, Kirchenpauer erroneously employed *Monopyxis* in reference to a different taxon from Ehrenberg, including it as one of three subgenera of *Plumularia* Lamarck, 1816. *Monopyxis* Ehrenberg, 1834 (type species *Sertularia geniculata* Linnaeus, 1758, by monotypy), has long been regarded as congeneric with *Obelia* Péron and Lesueur, 1810 (Hincks, 1868; Cornelius, 1982; Calder, 1991a), and it was a mistake to use the name for a group of plumulariids. Meneghini (1845:193, pl. 13, fig. 3) had made a similar error earlier in assigning the plumulariid *Plumularia obliqua* Johnston, 1847, to *Monopyxis*, misidentifying it as the campanulariid species *M. dichotoma*. The latter hydroid is known today as *Obelia dichotoma* (Linnaeus, 1758). Thus, the name *Monotheca* is recognized as valid here.

If *Monopyxis* had been founded as a nominal taxon by Kirchenpauer (1876), one of the two taxa he included (*Plumularia obliqua* and *Plumularia obliqua* var. *australis* Kirchenpauer, 1876 [=*Plumularia australis* Kirchenpauer, 1876]) would have to have been designated as the type species of *Monotheca* (ICZN, 1985, Art. 67h [1]). However, *Monopyxis* was not so established by Kirchenpauer, and the type species of *Monotheca* is *M. margaretta* Nutting, 1900, by monotypy.

Many authors (e.g., Vanhöffen, 1910; Bedot, 1921a, 1925; Totton, 1930; Broch, 1933; Leloup, 1935, 1960; da Cunha, 1944; Fraser, 1944; Pennycuik, 1959; Ralph, 1961; Van Gemerden-Hoogeveen, 1965; Vervoort, 1968; Watson, 1973; Millard, 1975; García, Aguirre, and Gonzalez, 1978; Boero, 1981; Gili, 1982; Hirohito, 1983; Bouillon, 1985; Izquierdo, García-Corrales, and Bacallado, 1986; Gili, Vervoort, and Pagès, 1989) have explicitly or implicitly regarded *Monotheca* as congeneric with *Plumularia*. Others have recognized it as a distinct genus (e.g., Vannucci Mendes, 1946; Picard, 1958; Yamada, 1959; Rho, 1969; Castric-Fey, 1970; Patriti, 1970; Hirohito, 1974; Rho and Park, 1986; Cornelius and Ryland, 1990; Ryland and Gibbons, 1991; Park, 1993; Cornelius, 1995). Some, including Stechow (1925a, 1925b), have treated *Monotheca* as a subgenus of *Plumularia*. Totton (1930) argued that the habit of hydroids assigned to *Monotheca*, with their monothecate hydrocladia, may be attributable to environmental factors. He based this conclusion on observations by Motz-Kossowska (1903), who studied *Monotheca obliqua* (Johnston, 1847) growing in rough water conditions at Banyuls-sur-Mer, France. However, monothecate hydrocladia also occur in colonies of this species from relatively sheltered seagrass beds in the Mediterranean (e.g., Boero, 1981; Bouillon et al., 1987). The characters of *Monotheca* are viewed here as genotypic and as an indication of close relationship among similar species. They seem to depart enough in hydrocladial morphology, gonophore type, and gonotheca shape from those of the genus *Plumularia* for *Monotheca* to be recognized as a valid genus.

Monotheca and *Monothecella* Stechow, 1923b, are much alike in colony form, each having hydrocladia with a single hydrotheca located at the distal end. Bouillon (1985) considered the two to be congeneric with *Plumularia*. However, Stechow (1923b) reported that the nematothecae of *Plumularia compressa* Bale, 1882, type species of *Monothecella*, and related species were monothalamic and "immovable", and as such unlike those of either *Monotheca* or *Plumularia*. Gonothecae of *M. compressa* are also quite unlike those of *Monotheca* in being cowl-shaped. *Monothecella*, established as a subgenus of *Monotheca* by Stechow (1923b), is recognized here as a valid genus (see also Stechow, 1925a), differing from *Monotheca* and *Plumularia* in the morphological characters of its nematothecae and gonothecae. The resemblance of *Monothecella* to *Monotheca* in colony form seems more likely due to convergence than to immediate relationship.

Motz-Kossowska (1907) found that mature gonophores of *Monotheca obliqua* from Banyuls are released as free but reduced and short-lived medusoids. It is not known whether those of *Monotheca margaretta* are liberated as well.

Monotheca margaretta **Nutting, 1900**

Fig. 2

Plumularia obliqua—Tizard et al., 1885:136. —Adams, 1960:81 [not *Plumularia obliqua* Johnston, 1847].
Monotheca margaretta Nutting, 1900:72, pl. 11, figs. 1–3.
Plumularia margaretta—Vanhöffen, 1910:333.
Plumuralia obliqua—Hentschel, 1922:4 [incorrect subsequent spelling] [not *Plumularia obliqua* Johnston, 1847].
Monotheca margaritta—Winge, 1923:13 [incorrect subsequent spelling].
Monotheca margaretta f. *typica* Vannucci Mendes, 1946:578, pl. 5, fig. 48; pl. 6, fig. 54.
Monotheca margaretta f. *curta* Vannucci Mendes, 1946:578, pl. 5, figs. 49–50; pl. 6, fig. 55.
Monoteca margaretta f. *typica*—Vannucci, 1951:89 [incorrect subsequent spelling].
?*Monotheca*—Weis, 1968:556.
Monotheca oblica—Patriti, 1970:58, fig. 83b [not *Plumularia obliqua* Johnston, 1847] [incorrect subsequent spelling].
Monotheca margareta—Wedler, 1975:332 [incorrect subsequent spelling].
not *Plumularia margaretta*—Cooke, 1977:100, fig. 27.
Plumularia femina García, Aguirre, and Gonzalez, 1978:57.
Plumalaria femina García, Aguirre, and Gonzalez, 1978:58, figs. 26A–E [incorrect subsequent spelling].
Plumularia femenia García, Aguirre, and Gonzalez, 1978:61 [incorrect original spelling].
Plumularia pulchella—Izquierdo, García-Corrales, and Bacallado, 1986:54, figs. 5A–D [not *Plumularia pulchella* Bale, 1882].
Monotheca (*Plumularia*) *margaretta*—Bandel and Wedler, 1987:42.
Monotheca (*Plumularia*) *margareta*—Bandel and Wedler, 1987:67 [incorrect subsequent spelling].

TYPE LOCALITY

"Shallow water, near Little Cat Island, Bahamas . . . attached to algae" (Nutting, 1900:72).

MATERIAL EXAMINED

Natural Arches Beach, on stranded *Sargassum fluitans*, 8 March 1982, two colonies, up to 7 mm high, without gonophores, ROMIZ B122. Castle Harbour, W of Castle Roads, on *Thalassia testudinum*, –2 to –3 m, 30 July 1982, three colonies, up to 11 mm high, with gonophores, ROMIZ B275. Natural Arches Beach, on stranded *Sargassum fluitans*, 4 August 1982, one colony, 5 mm high, without gonophores, ROMIZ B288. Whalebone Bay, on pelagic *Sargassum fluitans*, 2 September 1977, two colonies, up to 3 mm high, without gonophores, ROMIZ B391. St. Catherine's Beach, on stranded *Sargassum fluitans*, 15 June 1983, one colony, 6 mm high, without gonophores, ROMIZ B392. Atlantic Ocean, 2 km off Castle Roads, on calcareous rubble, –73 m, 1 July 1983, three colonies, up to 14 mm high, without gonophores, ROMIZ B393. Burchall's Cove, on pelagic *Sargassum fluitans*, 23 November 1989, one colony, 4 mm high, without gonophores, ROMIZ B394. Atlantic Ocean, 2 km off Natural Arches Beach, on a rhodolith, –70 m, 13 May 1991, three colonies, up to 13 mm high, without gonophores, ROMIZ B395.

DESCRIPTION

Colonies up to 14 mm high, with creeping hydrorhizae having internal perisarcal projections and occasional nematothecae. Hydrocaulus monosiphonic, more or less geniculate, unbranched in specimens from shallow water but often irregularly branched in those from deeper water, divided at regular intervals into internodes by distinct transverse nodes; internodes 252–401 μm long, 23–56 μm wide at nodes, without septa, each typically with two to three nematothecae in the axil of a distal apophysis and one on proximal half of internode on side opposite apophysis. Apophyses given off alternately from opposite sides of hydrocaulus, bearing hydrocladia each with a single hydrotheca. Branches, when present, one to three in number, irregularly arranged, given off at a wide angle from hydrocaulus, each supported by an apophysis inserting into a hydrocladial apophysis; branches giving off hydrocladia and resembling primary hydrocaulus. Hydrocladia unbranched, 196–326 μm long, with one or rarely two short athecate internodes proximal to a longer thecate internode; nodes nearly straight; athecate internodes with proximal and distal septa internally, lacking nematothecae; thecate internodes saddle-shaped in lateral view, each with a hydrotheca, a median inferior nematotheca, and two lateral nematothecae each borne on a short apophysis; thecate internode curved around adcauline wall of hydrotheca, terminating bluntly between apophyses of lateral nematothecae, narrow and Y-shaped beneath hydrotheca. Nematothecae bithalamic, movable, cone-shaped; median nematothecae 65–75 μm long, typically reaching less than halfway along abcauline wall of hydrotheca; lateral nematothecae 56–89 μm long, extending well beyond hydrothecal margin. Hydrothecae 130–186 μm deep, almost completely adnate to internode, cup-shaped with a convex adcauline wall and a concave abcauline wall; perisarc of abcauline wall sometimes quite thick; margin nearly perpendicular to hydrocladium, rim entire except for a median adcauline notch, aperture diameter 130–140 μm; base of hydrotheca with a ring of desmocytes; intrathecal septum lacking.

Gonophores presumed to be fixed sporosacs. Gonothecae one per hydrocaulus, barrel-shaped, with

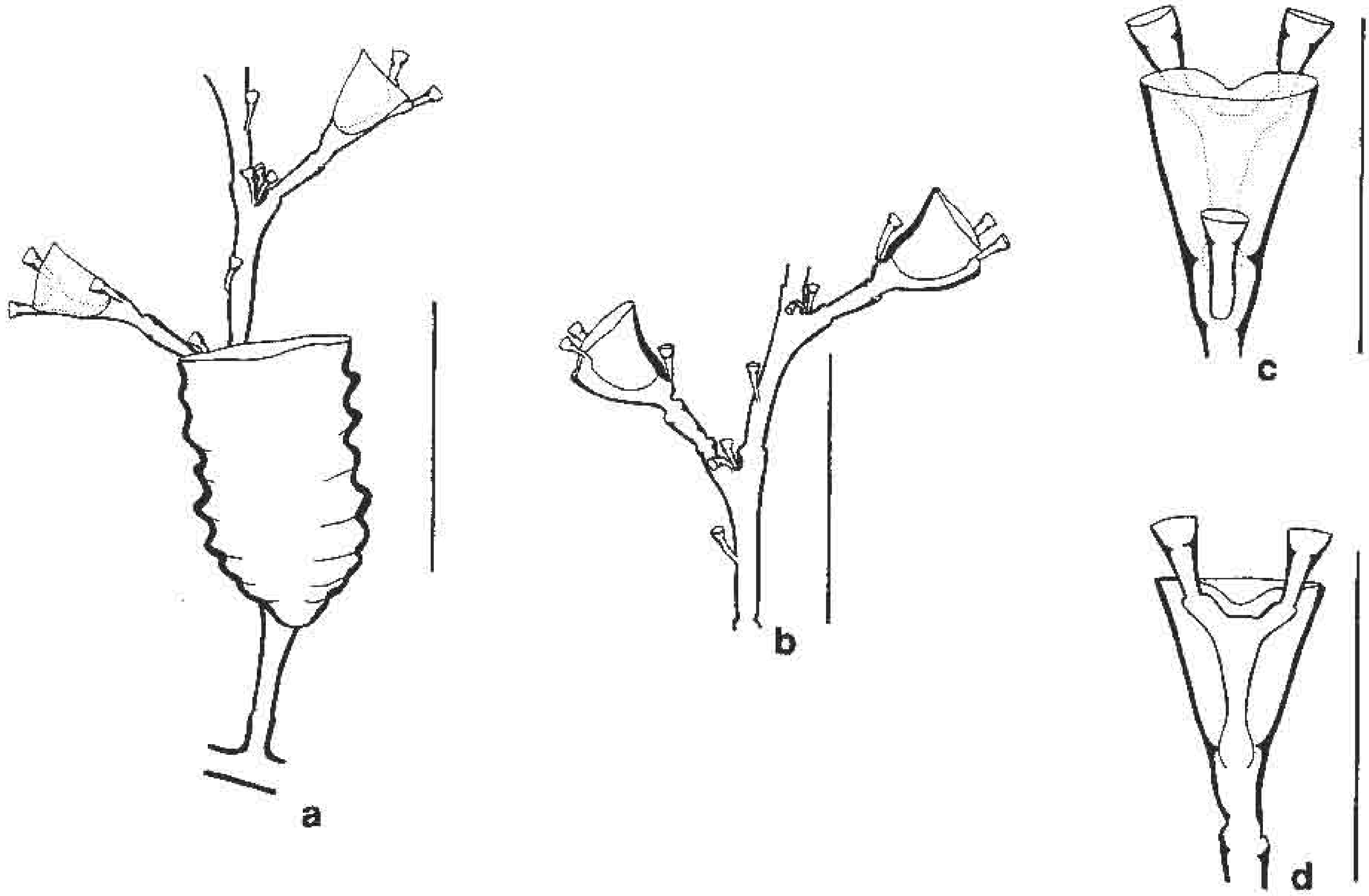

FIG. 2. *Monotheca margaretta: a,* part of colony with two hydrocladia and gonotheca, ROMIZ B275; *b,* part of hydrocaulus with two hydrocladia, ROMIZ B122; *c,* front view of hydrotheca, ROMIZ B122; *d,* back view of hydrotheca, ROMIZ B288. Scales for *a* and *b* equal 0.5 mm; scales for *c* and *d* equal 0.25 mm.

prominent transverse ridges, each arising by a short and curved pedicel from first hydrocladial apophysis at base of hydrocaulus, oval to deltoid in lateral outline, truncate distally with a wide terminal aperture, spherical to subspherical in cross-section, approximately 500–600 μm long, 300–320 μm wide at orifice; perisarc moderately thick.

REMARKS

Nutting (1900) described *Monotheca margaretta* from material collected during the Bahama Expedition of the State University of Iowa in 1893. He had mentioned the species in an earlier account (Nutting, 1895:225), noting that it was "allied to" *Plumularia obliqua* Johnston, 1847. Records of *P. obliqua* on *Sargassum* in the western Atlantic by Tizard et al. (1885) and Adams (1960) are considered here as misidentifications of this species.

Monotheca margaretta is quite distinctive from other species of plumulariids in the western North Atlantic, and its synonymy is relatively uncomplicated. In some works it has been referred to *Plumularia* Lamarck, 1816, dating from Vanhöffen (1910), instead of *Monotheca* Nutting, 1900. Reasons for recognizing *Monotheca* as distinct from *Plumularia* are discussed above (see Genus *Monotheca*, Remarks).

Vannucci Mendes (1946) recognized two forms of this species in waters of Brazil, *Monotheca margaretta* f. *typica* and *M. margaretta* f. *curta*. The latter had shorter and wider internodes with thicker perisarc than the former. I agree with the view of Van Gemerden-Hoogeveen (1965) that the characters used to separate the two are variable and do not provide sufficient basis to recognize them as taxonomically distinct.

Patriti's (1970) account of *Monotheca oblica* (lapsus for *obliqua*) from Morocco accords instead with *M. margaretta*. Only the figure of the gonotheca in Patriti's work, copied from Hincks (1868), resembles *M. obliqua*.

The hydroid identified as *Plumularia margaretta* from Hawaii by Cooke (1977) is certainly referable to another species. In particular, the shape of the hydrotheca in Cooke's material is quite different from that of *Monotheca margaretta*.

The hydroid described as *Plumularia femina* by García, Aguirre, and Gonzalez (1978) from the Mediterranean coast of Spain is considered here to be identical with *Monotheca margaretta*. The notch on the margin of the adcauline wall of the hydrotheca seems less distinct than in *M. margaretta* from Bermuda, but otherwise the hydroids are much alike in colony form and size. The spelling *Plumularia femenia* by García, Aguirre, and Gonzalez (1978:61) was an error: the specific name was formed that way only once, whereas it was spelled *femina* in all other parts of their paper (pp. 7, 57–58, 60).

Hydroids of *Monotheca margaretta* generally resemble those of *M. obliqua*, a related species from the eastern Atlantic Ocean and elsewhere, but differ in (1) having straight or concave rather than decidedly convex abcauline hydrothecal walls, (2) lacking septa in internodes of the hydrocaulus as well as in thecate internodes of hydrocladia, (3) having two to three nematothecae in each hydrocladial axil instead of one or two, (4) having a distinct median adcauline notch on the hydrothecal margin, (5) lacking an intrathecal septum even in older parts of colonies, and (6) having gonothecae with prominent transverse ridges rather than with smooth or wrinkled walls. Of other species referable to *Monotheca*, *M. margaretta* is most like *M. pulchella* (Bale, 1882) and *M. flexuosa* (Bale, 1894). Its trophosome differs from that of both species in having a median adcauline notch on the hydrothecal margin. Moreover, its gonothecae are unlike those of *M. pulchella* in lacking an obliquely truncate margin and internal submarginal cusps (Bale, 1882, 1884; Watson, 1973), and differ from those of *M. flexuosa* in having distinctly ribbed walls and a wider terminal aperture.

Hydroid material from the Canary Islands was assigned by Izquierdo, García-Corrales, and Bacallado (1986) to *Plumularia pulchella*. However, the description and illustrations of the species in their work correspond more closely with *Monotheca margaretta*. Moreover, their conclusion that *P. femina* is conspecific with *P. pulchella* seems mistaken, unless *M. margaretta* is eventually shown to be identical with *P. pulchella*.

Hydrocauli were unbranched in all of the shallow-water material of *M. margaretta* examined from Bermuda, while those of hydroids from deeper collections (ROMIZ B393, ROMIZ B395) in the study area were mostly branched. No taxonomic significance is ascribed to that difference here.

Monotheca margaretta is common in warm waters of the western Atlantic, particularly on pelagic *Sargassum* and *Turbinaria* (e.g., Vanhöffen, 1910; Fraser, 1912, 1944; Winge, 1923; Burkenroad, *in* Parr, 1939; Van Gemerden-Hoogeveen, 1965; Weis, 1968; Morris and Mogelberg, 1973; Defenbaugh, 1974; Calder, 1991b, 1993, 1995). Van Gemerden-Hoogeveen (1965) summarized information on the geographical distribution of *M. margaretta*, including records of the species from the eastern Atlantic and eastern Pacific.

REPORTED RANGE

Bermuda: Challenger Station 36 (Challenger Bank) (Stechow, 1912); on floating *Sargassum* (Bennitt, 1922); sounds, deeper coastal waters, floating *Sargassum* (Calder, 1993, 1995).

Circumglobal distribution: western Atlantic (Van Gemerden-Hoogeveen, 1965); eastern Atlantic (Picard, 1951a); ?eastern Pacific (Fraser, 1948).

Genus *Plumularia* Lamarck, 1816

Plumularia Lamarck, 1816:123.
Lowenia Meneghini, 1843:404.
Plumaria Irvine, 1854:245 [incorrect subsequent spelling].
Heteropyxis Heller, 1868:44.
Plumalaria Kirchenpauer, 1876:9 [incorrect subsequent spelling].
Isocola Kirchenpauer, 1876:26.
Anisocola Kirchenpauer, 1876:27.
Apostasis von Lendenfeld, 1885b:640.
Haptotheca von Lendenfeld, 1885b:640.
Plumutaria Bedot, 1905:98 [incorrect subsequent spelling].
Plumulularia Kühn, 1913:232 [incorrect subsequent spelling].
Aposthasis Bedot, 1918:152 [incorrect subsequent spelling].
?*Plumella* Stechow, 1920:45.
Plumuralia Hentschel, 1922:4 [incorrect subsequent spelling].

DIAGNOSIS

Colonies normally erect (hydrocladia may arise from hydrorhiza when epizootic); hydrocauli mostly monosiphonic, branched or unbranched, giving off alternate apophyses, arising from a creeping hydrorhiza or from anchoring filaments. Hydrocladia typically unbranched, pinnately arranged or sometimes occurring in a gradual spiral but not in verticils, divided into internodes, not modified into spine-shaped appendages at distal ends of hydrocaulus and branches; typically two or more hydrothecae per hydrocladium. Hydrothecae occurring only on hydrocladia, small, typically cup-shaped, margin entire. Nematothecae ordinarily bithalamic, movable; lateral nematothecae flanking each hydrotheca.

Gonophores fixed sporosacs. Gonothecae solitary, generally arising from hydrocladial apophyses, neither armed with nematothecae nor protected by corbulae or other phylactocarps.

TYPE SPECIES

Plumularia cristata Lamarck, 1816, by subsequent designation by Busk (1851). Nomenclatural problems associated with this type designation were discussed by Calder and Cornelius (1996). Their submission to the International Commission on Zoological Nomenclature, proposing that Broch's (1918) designation of *Sertularia setacea* Linnaeus, 1758, as the type species of *Plumularia* Lamarck, 1816, be confirmed, is pending.

REMARKS

The genus name *Plumularia* was introduced by Lamarck (1816), who assigned 17 nominal species to it. Included were some of the same ones referred, at about the same time, to *Aglaophenia* Lamouroux, 1812 (see Lamouroux, 1812, 1816). The taxonomic distinction recognized between *Plumularia* and *Aglaophenia* was not well established until McCrady (1859) redefined the two (see Genus *Aglaophenia*, Remarks).

The concept of *Plumularia* as a genus has long differed from that defined by reference to its current type species. Nomenclatural problems arising from the subsequent designation by Apstein (1915) of *Sertularia pinnata* Linnaeus, 1758, as type species of *Plumularia* were discussed by Broch (1918), Cornelius (1995), and Calder and Cornelius (1996). As noted elsewhere (see *Plumularia setacea*, Remarks), *S. pinnata* is now referred to *Kirchenpaueria* Jickeli, 1883, and was designated by Broch (1918:195) as the type species of that genus. However, Apstein's designation is invalidated by an earlier, widely overlooked, and yet potentially more nomenclaturally disruptive type species designation by Busk (1851). As noted by Calder and Cornelius (1996), *Plumularia cristata* Lamarck, 1816, was designated in Busk's work as the type species of *Plumularia*. The binomen *P. cristata* is a junior subjective synonym of *Sertularia pluma* Linnaeus, 1758, the type species of *Aglaophenia*. To regard the extensively used names *Plumularia* and *Aglaophenia* as synonyms again, or to significantly alter their identities, would be counter to the interests of nomenclatural stability. A case to the ICZN seeking validation of current usage was submitted by Calder and Cornelius (1996), who proposed that the designation by Broch (1918) of *Sertularia setacea* Linnaeus, 1758, as the type species of *Plumularia* be confirmed. *Plumularia setacea* has been widely treated as though it were the type species of *Plumularia* (e.g., see Broch, 1918; Millard, 1975; Cornelius, 1995), and that general concept of the genus is likewise adopted here. Earlier, Busk (1851) had recognized that *Plumularia* as he conceived it (encompassing both *Aglaophenia* and *Plumularia*) was "an artificially constructed genus" and noted that *P. setacea* might be taken as the type of a second genus if *Plumularia* should be subdivided. Busk thus came close to modern ideas about the taxon, although his nomenclature was confused.

Plumularia has been restricted in scope repeatedly since its initial redefinition by McCrady (1859). Various nominal species have been reassigned from it to other plumularioid genera including *Kirchenpaueria*, *Polyplumaria* G. O. Sars, 1874; *Antennella* Allman, 1877; *Halopteris* Allman, 1877; *Monostaechas* Allman, 1877; *Schizotricha* Allman, 1883; *Gattya* Allman, 1885; *Monotheca* Nutting, 1900; *Pycnotheca* Stechow, 1919a; *Oswaldella* Stechow, 1919b; *Dentitheca* Stechow, 1920; *Ventromma* Stechow, 1923a; *Monothecella* Stechow, 1923b; and *Pseudoplumaria* Ramil and Vervoort, 1992c. Nevertheless, opinions continue to differ on the overall limits of the taxon (e.g., Bouillon, 1985; this work).

Kirchenpauer (1876) recognized a broadly defined genus, *Plumularia*, which he subdivided into three subgenera, *Monopyxis* Ehrenberg, 1834, and two new subgenera, *Isocola* and *Anisocola*. The name *Monopyxis*, a subjective synonym of *Obelia* Péron and Lesueur, 1810, should not have been applied to a plumularioid taxon (see Genus *Monotheca*, Remarks). Moreover, both *Isocola* and *Anisocola* as used by Kirchenpauer were polyphyletic and included species now referred to several genera. Jickeli (1883) recognized both as valid, but the names fell into disuse thereafter. Bedot (1912, 1916a) and Stechow (1923a) regarded *Isocola* and *Anisocola* as congeneric with *Plumularia*, but I have found no previous type designation for either. To retain their synonymy with *Plumularia*, *P. setacea* (Linnaeus, 1758) is here designated as the type species of *Anisocola*, and *P. gaimardi* (Lamouroux, 1824) (as *P. gaymardi* in Kirchenpauer, 1876) is designated as the type species of *Isocola*.

Originally assigned to the nominal genus *Lowenia* Meneghini, 1843, were *Sertularia setacea*, *S. pinnata*, and a nomen nudum, *Lowenia tetrasticha*. Criteria of availability of *L. tetrasticha* were not met until later (Meneghini, 1845). The subsequent designation of *L. tetrasticha* as type species of the genus by Stechow (1923a) is therefore invalid (A. Gentry, ICZN, pers. comm.), and only *S. setacea* and *S. pinnata* are eligible for such designation. If *S. pinnata* were to be designated as the type species of the nominal genus, *Lowenia* would become a senior objective synonym of the more familiar name *Kirchenpaueria* Jickeli, 1883 (the type genus of the plumularioid family Kirchenpaueriidae Stechow, 1921a). In the interests of nomenclatural stability, *Sertularia setacea* Linnaeus, 1758, is designated here as the type species of *Lowenia*. Thereby, *Lowenia* and its replacement name, *Heteropyxis* Heller, 1868, both seldom used in the nomenclature of the Hydrozoa, become junior synonyms of the familiar name *Plumularia*.

Von Lendenfeld (1885b) founded *Apostasis*, *Haptotheca*, and *Polysiphonia* [not *Polysiphonia* Hertwig, 1882] as new nominal subgenera of *Plumularia*. All were included without comment as congeners of *Plumularia* by Stechow (1923a). However, several nominal species of Australian hydroids were included in each nominal subgenus by von Lendenfeld, including halopteridids, and no type species seems ever to have been designated for any of them. Thus, *Plumularia badia* Kirchenpauer, 1876, is designated here as the type species of *Apostasis*, and *Plumularia ramsayi* Bale, 1884, the name of which is a junior subjective synonym of *P. badia* (e.g., see Bale, 1913; Bedot, 1918; Vervoort, 1941; Pennycuik, 1959), is designated as the type species of *Haptotheca*. The names *Apostasis* and *Haptotheca* may thereby be regarded as junior subjective synonyms of *Plumularia*. *Plumularia campanula* Busk, 1852, a species now generally referred to *Halopteris* (e.g., see Totton, 1930; Leloup, 1938b; Pennycuik, 1959; Ralph, 1961; Schmidt, 1972; Watson, 1973, 1975; Hirohito, 1983; Rees and Vervoort, 1987), is designated in this work as the type species of *Polysiphonia* von Lendenfeld, 1885b. Accordingly, *Polysiphonia* von Lendenfeld, 1885b, an invalid junior homonym of *Polysiphonia* Hertwig, 1882 (an actinian), is included here in the synonymy of *Halopteris* instead of *Plumularia*.

Stechow (1920:45) founded *Plumella* to accommodate *Plumularia goodei* Nutting, 1900, from California. Although the nematophores of *P. goodei* are monothalamic rather than bithalamic, *Plumella* was implicitly or explicitly regarded as congeneric with *Plumularia* by Bedot (1921a), Fraser (1937, 1946, 1948), Leloup (1938a), Bouillon (1985), and Cairns et al. (1991). Stechow (1920, 1923a) regarded it as closer to *Kirchenpaueria* than to *Plumularia*, although paired lateral nematothecae are reportedly present (Nutting, 1900). More information is needed about the status and relationships of *Plumella*, which may prove to be a valid genus.

Bouillon (1985) referred five genus-group names to the synonymy of *Plumularia*, namely, *Acanthella* Allman, 1883, *Monotheca*, *Plumella*, *Monothecella* Stechow, 1923b, and *Sphaerocystys* (*sic;* lapsus for *Sphaerocystis* Fraser, 1943). Of these, only *Plumella* is regarded here as congeneric or possibly so with *Plumularia*. The taxon assigned the name *Acanthella* Allman, 1883 (an invalid junior homonym of *Acanthella* Schmidt, 1862) is considered valid, and the replacement name *Cladacanthella* has been proposed for it above (see Family Plumulariidae, Remarks). Likewise, *Monotheca* and *Monothecella* are considered valid genera (see Family Plumulariidae, Remarks; Genus *Monotheca*, Remarks). The generic name *Sphaerocystis* is transferred herein to the synonymy of *Dentitheca* (see Family Plumulariidae, Remarks).

Plumularia, even as currently restricted, comprises a large and diverse assemblage of hydroids. Indeed, among the three species from Bermuda assigned here to *Plumularia*, *P. floridana* Nutting, 1900, seems to differ considerably in hydrothecal and gonothecal characters from *P. setacea* and *P. strictocarpa* Pictet, 1893. Taxonomic reappraisal of the genus is needed, and further subdivision seems likely.

Plumularia floridana **Nutting, 1900**

Fig. 3

Plumularia floridana Nutting, 1900:59, pl. 2, figs. 4–5.
?*Plumularia alicia* Torrey, 1902:75, pl. 10, figs. 96–97.
Plumularia florida—Wallace, 1909:137 [incorrect subsequent spelling].
?*Plumularia alicia* var. *minuta* Billard, 1927:472.
Plumularia sinuosa Fraser, 1938a:67, pl. 15, fig. 77.
Plumularia floridina—Pennycuik, 1959:183 [incorrect subsequent spelling].
Plumularia sp.—Pennycuik, 1959:183, pl. 3, fig. 7. —Spracklin, 1982:246, fig. 117g. —Florez Gonzalez, 1983:121, photo 46.
?*Plumularia indica* Mammen, 1965:300, fig. 96.
Plumularia pennycuikae Millard and Bouillon, 1973:85, figs. 10N, 10P.
Plumularia pennycuikai—Rho and Park, 1986:12 [incorrect subsequent spelling].

TYPE LOCALITY

"Two miles west of Cape Romano, Florida" (Nutting, 1900:59).

MATERIAL EXAMINED

Hungry Bay, on barnacle on underside of rock, –1 m, 6 September 1977, one colony with several hydrocauli, 9 mm high, with gonophores, ROMIZ B120. Whalebone Bay, on *Thalassia*, –1 m, 6 March 1982, two colonies with several hydrocauli, 8 mm high, without gonophores, ROMIZ B124. Atlantic Ocean, 2 km SE of Castle Roads, on a rhodolith, –73 m, 1 July 1983, two colonies, up to 15 mm high, with gonophores, ROMIZ B428. Atlantic Ocean, 2 km off Natural Arches Beach, on a rhodolith, –70 m, 13 May 1991, seven separate hydrocladia, up to 11 mm high, with gonophores, ROMIZ B429.

DESCRIPTION

Colonies up to 15 mm high, with a creeping hydrorhiza. Hydrocaulus monosiphonic, branched or unbranched, more or less straight basally, geniculate elsewhere, divided at regular intervals beyond basal region into internodes by distinct transverse nodes; internodes 298–606 μm long, 47–93 μm wide at nodes, with distinct to indistinct septa adjacent to nodes; each internode with a distal apophysis and typically with two or three nematothecae, one or two axillary and one (infrequently two) part way along internode on side opposite apophysis; cauline nematothecae bithalamic, movable, cone-shaped to scoop-shaped. Apophyses short, alternate, each bearing a mamelon on dorsal side near node and supporting a hydrocladium. Branches, when present, one or two in number, irregularly arranged, inserted at an angle of about 50° to the hydrocaulus, each replacing a hydrocladium and arising from an apophysis; branches giving off hydrocladia and resembling primary hydrocaulus. Hydrocladia unbranched, up to 3.2 mm long, directed outward at an angle of about 60° from axis of hydrocaulus, divided into alternating athecate and thecate internodes each with two variably developed internal septa, one at each end; most proximal internode 93–336 μm long, with a straight node proximally and an

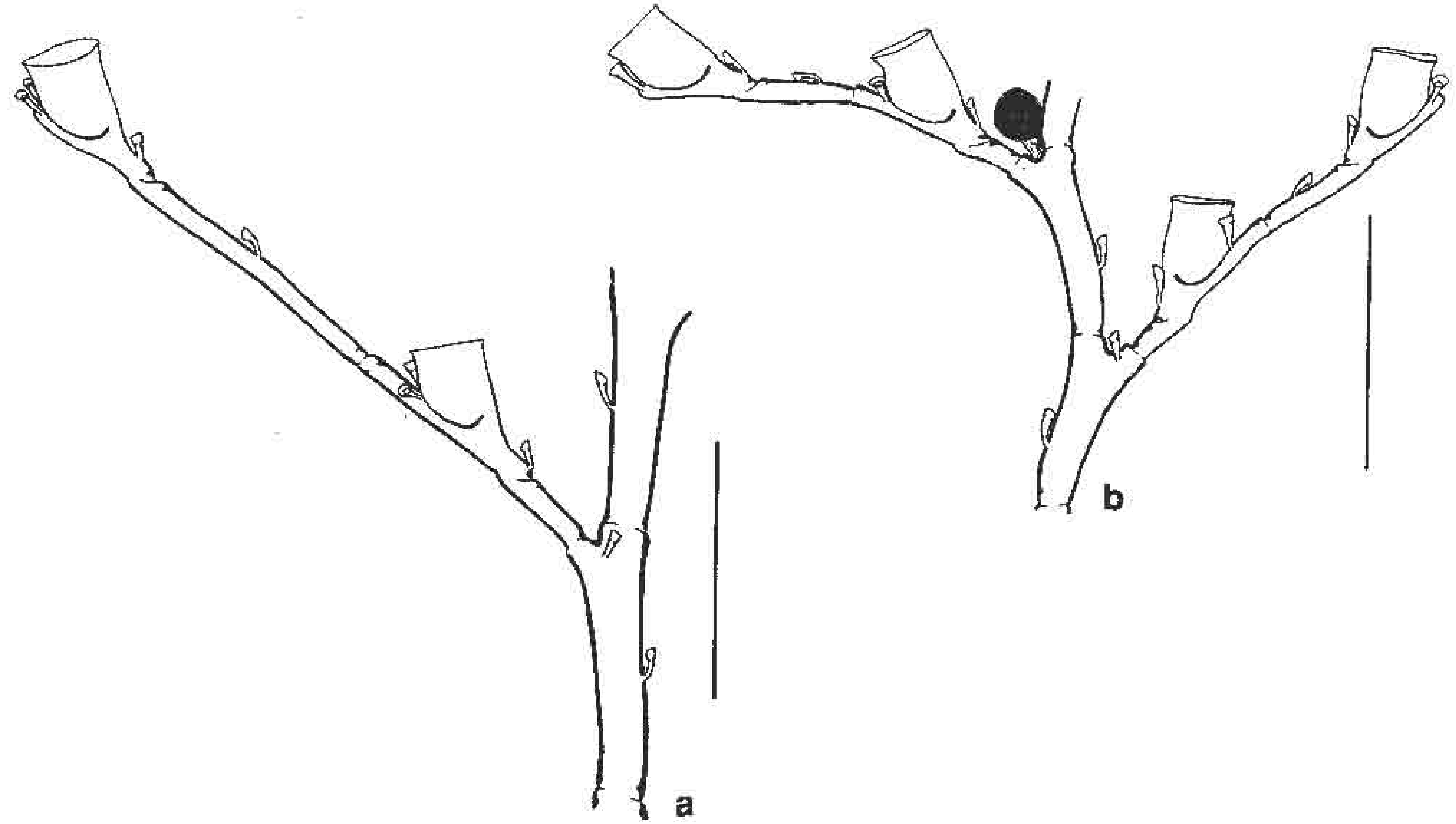

FIG. 3. *Plumularia floridana: a,* part of hydrocaulus with hydrocladium, ROMIZ B429; *b,* part of hydrocaulus with two hydrocladia and female gonotheca, ROMIZ B120. Scales equal 0.5 mm.

oblique node distally, lacking hydrothecae and nematothecae, this internode followed by one to five pairs of alternating thecate and athecate internodes; thecate internodes 242–410 µm long, each with an oblique node proximally, a straight node distally, a median inferior nematotheca, a relatively large hydrotheca, and two lateral nematothecae; athecate internodes beyond the most proximal one 196–596 µm long, with a straight node proximally, an oblique node distally, and typically with one intermediate nematotheca. Nematothecae of hydrocladia bithalamic, movable, cone-shaped to scoop-shaped; median nematothecae 42–56 µm long, typically ending proximal to or just reaching base of hydrotheca; lateral nematothecae 56–65 µm long, not reaching to margin of hydrotheca. Hydrothecae 149–177 µm deep, cup-shaped, distal third or more of adcauline wall free from internode, axis oblique to that of internode; abcauline wall slightly convex basally and slightly concave distally; adcauline wall convex basally, concave distally; margin entire, perpendicular or nearly so to axis of hydrotheca, aperture oval in outline, diameter 117–144 µm; without intrathecal septum.

Gonophores fixed sporosacs. Developing ova visible as amoeboidlike cells in coenosarc of hydrocaulus. Gonothecae each arising via a T-shaped pedicel from apophysis, perisarc thin and filmy, ovoid to nearly spherical, perisarcal walls collapsing after liberation of gonothecal contents; length of pedicel and gonotheca combined 140–172 µm, maximum diameter 84–103 µm.

REMARKS

The original description and illustrations of *Plumularia floridana* by Nutting (1900) were misleading in some respects since they implied that the hydrocladial nodes were all straight (p. 55; pl. 2, figs. 4–5). Although the type material of this species (USNM 22016) is now in rather poor condition, the hydrocladial nodes are alternately straight and oblique as in the hydroids described above from Bermuda. In other respects as well, particularly in shape and orientation of the hydrothecae, type material corresponded with the specimens from Bermuda.

The unusual gonotheca of this species was not known to Nutting (1900). Described later (Calder, 1983), it is small and constitutes little more than a filmy envelope of perisarc enclosing a nearly spherical cell mass. In the mature female, each gonotheca encloses a single ovum or developing planula. Additional large ova are sometimes clearly visible at low magnification as amoeboid-shaped cells in the coenosarc of the hydrocaulus. The perisarc of the gonotheca is so thin that the structure shrivels after release of its contents.

Gonothecae of *Plumularia floridana* are quite different in shape and size from those of *P. setacea* (Linnaeus, 1758), proposed as the type species of *Plumularia* Lamarck, 1816 (Calder and Cornelius, 1996). As currently defined, *Plumularia* comprises a large and diverse assemblage of species and is probably polyphyletic (see Genus *Plumularia*, Remarks). Based on present knowledge, however, it seems best to retain *P. floridana* in *Plumularia*.

Hydroids of *Plumularia alicia* Torrey, 1902, from southern California appear similar to those of *P. floridana* in trophosome and gonosome character states. Torrey's (1902) hydroids were much larger (about 8–13 cm versus 2-3 cm high) and had stems that were more robust and brown instead of slender and whitish. Because such differences could be due to environmental factors, and because the two so closely correspond in form otherwise, they may prove conspecific. Also possibly conspecific with *P. floridana* is *P. alicia* var. *minuta* Billard, 1927, from Cameroon, Africa.

Fraser's (1938a) brief original description and sketchy illustration of *Plumularia sinuosa*, from the Galápagos and from the Islas Revillagigedos in the eastern Pacific, depict a hydroid considered here to have been conspecific with *P. floridana*. Gonophores of *P. sinuosa*, described in other material later (Fraser, 1948), also correspond with those of *P. floridana*. Fraser (1948:188–189) reported *P. sinuosa* and *P. floridana*, as well as *P. alicia*, from some of the same general areas in warm waters of the eastern Pacific.

Plumularia indica Mammen, 1965, from waters between India and Sri Lanka, appears much like *P. floridana*, although nematothecae were reportedly lacking on the cauline internodes. Unfortunately, Mammen's (1965) material also lacked gonothecae. *Plumularia indica* may be conspecific with *P. floridana* but it is too poorly known at present to be certain.

The description and illustrations of *Plumularia pennycuikae* from the Seychelles by Millard and Bouillon (1973) correspond with *P. floridana* in all respects, and their hydroids are considered the same species here. Millard and Bouillon regarded the Seychelles material as identical to hydroids identified from Australia as *Plumularia* sp. by Pennycuik (1959).

Hydroids reported as *Plumularia* sp. from Belize by Spracklin (1982) and from Colombia by Florez Gonzalez (1983) are considered to have been based on specimens of *P. floridana*. Gonothecae and hydrothecae typical of *P. floridana* were apparent in the illustrations of their material.

Colonies of *Plumularia floridana* from Bermuda varied considerably in form. Those from offshore waters (Fig. 3a) were much more gracile than those from shallow bays (Fig. 3b). This is a eurytopic species, tolerating both reduced salinities (from full seawater to 25‰) and a considerable range of water temperature (at least 10°–32° C) (Calder, 1976, 1990).

REPORTED RANGE

Bermuda: location unspecified (Calder, 1983); sheltered bays, deeper coastal waters (Calder, 1993).

Circumglobal distribution: western Atlantic (Calder, 1983); ?eastern Atlantic (Billard, 1927, as *Plumularia alicia* var. *minuta*); Indian Ocean (Millard, 1975, as *P. pennycuikae*); western Pacific (Hirohito, 1974, as *P. pennycuikae*); eastern Pacific (Fraser, 1948).

Plumularia setacea **(Linnaeus, 1758)**

Fig. 4

Sertularia setacea Linnaeus, 1758:813.

Sertularia pinnata β—Linnaeus, 1767:1312 [not *Kirchenpaueria pinnata* (Linnaeus, 1758)].

La Sertolara pennata—Cavolini, 1785:228 [incorrect subsequent spelling] [not *Kirchenpaueria pinnata* (Linnaeus, 1758)] [unavailable name, ICZN, 1985, Art. 11c].

Sertularia pinnata—Berkenhout, 1789:219. —Stewart, 1802:430; 1817:446. —Bertolonii, 1819:270. —Cuvier, 1830:301. —Denotaris, 1846:79 [not *Kirchenpaueria pinnata* (Linnaeus, 1758)].

Sertularia pennata—Sprengel, 1813:106 [not *Kirchenpaueria pinnata* (Linnaeus, 1758)].

Pennaria setacea—Oken, 1815:94.

Plumularia setacea—Lamarck, 1816:129.

Aglaophenia setacea—Lamouroux, 1816:172.

Sertularia templetoni Fleming, 1828:543.

Anisocalyx pinnatum—Costa, 1842:17 [not *Kirchenpaueria pinnata* (Linnaeus, 1758)].

Lowenia setacea—Meneghini, 1843:404.

Sertularia (*Plumularia*) *setacea*—Maitland, 1851:53.

Plumaria setaecea—Irvine, 1854:245 [incorrect subsequent spelling].

Halicorneria setacea—Parfitt, 1866:11 [incorrect subsequent spelling].

not *Anisocalyx setaceus*—Heller, 1868:41 [=*Kirchenpaueria pinnata* (Linnaeus, 1758)].

Anisocola setacea—Jickeli, 1883:641, pl. 28, fig. 9.

Plumularia tripartita von Lendenfeld, 1885a:477, pl. 12, figs. 8–10.

Plumularia multinoda Allman, 1885:157, pl. 26, figs. 4–6.

?*Plumularia turgida* Bale, 1888:779, pl. 20, figs. 12–13.

not *Plumularia setacea*—Nutting, 1900:57 [part]. —Ritchie, 1909a:89. —Stechow, 1912:362 [part]. —Bennitt, 1922:256. —Fraser, 1944:352 [part]. —Deevey, 1950:347; 1954:271 [part]. —Rees and Thursfield, 1965:162 [part]. —Defenbaugh and Hopkins, 1973:113. —Spracklin, 1982:246, fig. 117f [=*Plumularia strictocarpa* Pictet, 1893].

Plumularia corrugata Nutting, 1900:64, pl. 6, figs. 1–3.

?*Plumularia palmeri* Nutting, 1900:65, pl. 6, figs. 4–5.

Pennaria (Sertularia) setacea—Bedot, 1901a:461.

Plumularia milleri Nutting, 1905:951, pl. 5, fig. 1; pl. 12, figs. 6–7.

Plumularia cetacea—Wallace, 1909:137 [incorrect subsequent spelling].

Plumularia setacea forma *typica* Broch, 1914:25, pl. 1, fig. 1.

Plumularia setacea forma *microtheca* Broch, 1914:26.

Plumularia setacea var. *elongata* Bedot, 1921b:10, pl. 1, fig. 1.

?*Plumularia palmira*—Vervoort, 1946:176 [incorrect subsequent spelling].

Plumaria setacea—Vannucci, 1950:89 [incorrect subsequent spelling].

Plumularia setacea var. *setacea*—Ralph, 1961:33, figs. 3e, 4a, 4c–d.

Plumularia seteca—Schmidt, 1972:43 [incorrect subsequent spelling].

Plumularia setaca—Rho and Park, 1986:11 [incorrect subsequent spelling].

TYPE LOCALITY

"Habitat in Oceano" (Linnaeus, 1758:813). The name is based on *Corallina setacea*, described from Brighthelmstone (Brighton) and Whitstable, England, by Ellis (1755).

MATERIAL EXAMINED

Atlantic Ocean, 2 km off Castle Roads, on polypropylene buoy line, –60 m, 3 September 1977, 24 fragments, up to 11 cm high, with gonophores, ROMIZ B129. Atlantic Ocean, 2.5 km SE of Castle Roads, on an octocoral, –75 m, 27 September 1984, one colony, 5.4 cm high, with gonophores, ROMIZ B430. Atlantic Ocean, 2 km off Natural Arches Beach, on octocoral stems, –70 m, 13 May 1991, three colonies, up to 9 cm high, with gonophores, ROMIZ B431. Atlantic Ocean, 2.5 km SE of Castle Roads, on a rhodolith and an octocoral, –70 m, 22 May 1991, two colonies, up to 6 cm high, with gonophores, ROMIZ B432. Atlantic Ocean, 2.5 km SE of Castle Roads, on a rhodolith and an octocoral, –70 m, 22 May 1991, two colonies, up to 3.4 cm high, without gonophores, ROMIZ B433. Challenger Bank, on rhodoliths, –60 m, 17 May 1991, three colonies, up to 3.3 cm high, with empty gonothecae, ROMIZ B434.

DESCRIPTION

Colonies up to 11 cm high, with a creeping hydrorhiza. Hydrocaulus monosiphonic, unbranched, sometimes zigzag distally but otherwise more or less straight, divided at regular intervals beyond basal region into internodes by distinct transverse nodes; perisarc thick basally, thinner distally. Cauline internodes 438–895 µm long, 91–228 µm wide, 89–224 µm wide at nodes, without septa; each internode with a distal apophysis and commonly with three nematothecae, two axillary and one part way along internode on side opposite apophysis, occasionally with as many as six nematothecae arising from a single apophysis and two others on shaft of internode; cauline nematothecae bithalamic, movable, cone-shaped, 112–130 µm long. Apophyses fairly long, most given off alternately from opposite sides of hydrocaulus, those at distal ends of some hydrocauli given off in a spiral; each apophysis bearing a mamelon on dorso-lateral side near node, a prominent internal septum distally, and a hydrocladium. Hydrocladia typically unbranched, up to 6.5 mm long, directed outward at an angle of about 70° from axis of hydrocaulus, typically divided into alternating athecate and thecate internodes, occasionally with two or more athecate internodes together. Most proximal internode 72–103 µm long, with a straight node proximally, an oblique node distally, and a prominent internodal septum; hydrothecae and nematothecae lacking; this basal internode followed by one to eight pairs of alternating thecate and athecate internodes, each hydrocladial internode having two distinct internal septa, one at each end; thecate internodes 382–587 µm long, those of a given hydrocladium tending to be progressively shorter distally, each with an oblique node proximally, a nearly straight node distally, a median inferior nematotheca, a small hydrotheca, and two lateral nematothecae; athecate internodes beyond the most proximal one 252–410 µm long, those of a given hydrocladium tending to be progressively longer distally, each with an almost straight node proximally, an oblique node distally, and generally with one intermediate nematotheca. Nematothecae of hydrocladia bithalamic, movable, cone-shaped; median nematothecae ending proximal to base of hydrotheca; lateral nematothecae reaching well beyond margin of hydrotheca. Hydrothecae small, 65–79 µm deep, cup-shaped, axis nearly parallel with that of internode; adcauline wall convex, adnate to internode; abcauline wall straight, or slightly concave, or slightly convex; margin entire or slightly ragged, perpendicular to axis of hydrotheca or nearly so, aperture circular, diameter 89–98 µm; intrathecal septum lacking.

Gonophores fixed sporosacs; colonies dioecious. Gonothecae each arising from apophysis via a short pedicel, sometimes two or three gonothecae together, perisarc fairly thin. Female gonothecae fusiform, 615–932 µm long, maximum diameter 168–298 µm, aperture diameter 66–121 µm. Male gonothecae fusiform, 466–531 µm long, maximum diameter 126–140 µm, aperture diameter 37–46 µm.

REMARKS

The binomen *Sertularia setacea* was applied by Linnaeus (1758) to a hydroid that Ellis (1755) had earlier named *Corallina setacea*. Later, Linnaeus (1767) referred the

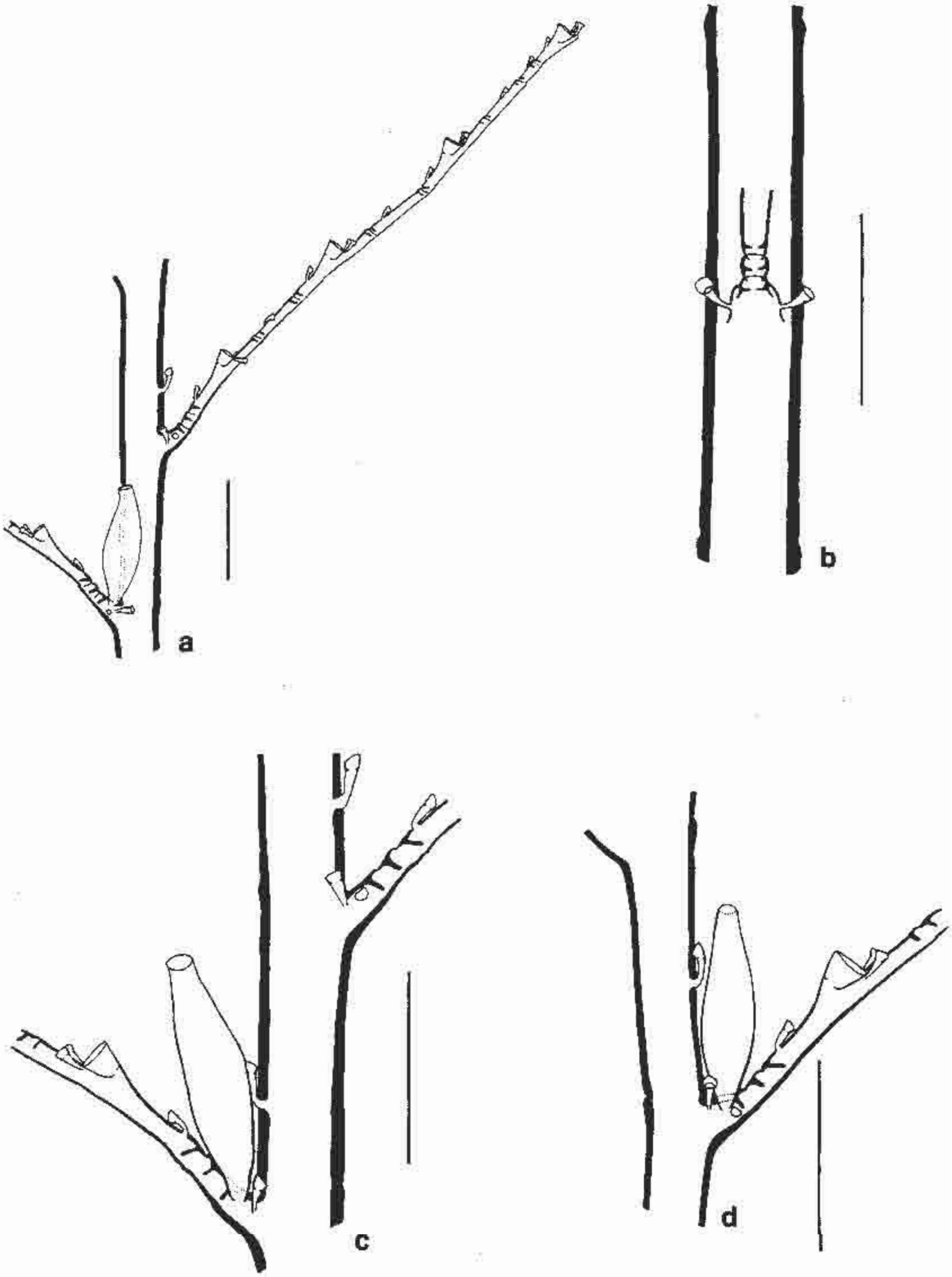

FIG. 4. *Plumularia setacea: a*, part of hydrocaulus with two hydrocladia and female gonotheca, ROMIZ B129; *b*, lateral view of hydrocaulus, hydrocladial apophysis, and proximal end of hydrocladium, with two axillary nematothecae, ROMIZ B129; *c*, part of hydrocaulus, with two hydrocladia and female gonotheca, ROMIZ B129; *d*, part of hydrocaulus, with hydrocladium and male gonotheca, ROMIZ B431. Scales equal 0.5 mm.

name to the synonymy of *Sertularia pinnata* Linnaeus, 1758, as *S. pinnata* ß. The species was subsequently referred to as *Sertularia pinnata*, with variation in spelling, by several authors (see synonymy). However, *S. setacea* and *S. pinnata* have long been recognized as separate species (e.g., see Ellis and Solander, 1786; Bosc, 1802; Lamarck, 1816; Lamouroux, 1816; Johnston, 1833, 1847; Couch, 1844; L. Agassiz, 1862; Hincks, 1868; Bedot, 1901a). Indeed, they are now assigned to different genera, *S. setacea* to *Plumularia* Lamarck, 1816, and *S. pinnata* to *Kirchenpaueria* Jickeli, 1883 (e.g., see Bedot, 1916b; Broch, 1918; Vervoort, 1946; Rees and Thursfield, 1965; Millard, 1975; Hirohito, 1983; Rho and Park, 1986; Cornelius and Ryland, 1990; Ramil and Vervoort, 1992a; Cornelius, 1995). Both species names continue in use for these respective taxa.

Lamouroux (1824) described as *Aglaophenia gaimardi* a hydroid from the Cape of Good Hope. Billard (1909), in a revision of Lamouroux's types, concluded that *A. gaimardi* was conspecific with *Plumularia setacea*, although he recognized it as a distinct variety (*P. setacea* var. *gaimardi*). Millard (1975) held that *A. gaimardi* was questionably conspecific with *P. lagenifera* Allman, 1885, instead of *P. setacea*. *Plumularia lagenifera* and *P. setacea* are currently regarded as similar but likely different species (Millard, 1957, 1975; Rees and Thursfield, 1965; Vervoort, 1966).

The virtually forgotten name *Sertularia templetoni* was applied by Fleming (1828) to a hydroid from Britain. The name was not listed by either Johnston (1847) or Hincks (1868). Bedot's (1905) conclusion that it is referable to *P. setacea* is accepted here.

The hydroid identified as *Anisocalyx setaceus* by Heller (1868) was referred to *Kirchenpaueria pinnata* (see Bedot, 1918). Earlier, Hincks (1872a) recognized that it was different from *Plumularia setacea* and had renamed it *P. helleri*.

Von Lendenfeld (1885a) established the name *Plumularia tripartita* for a hydroid from Port Phillip, Australia, and Timaru, New Zealand. Bale (1888) reexamined the types of *P. tripartita* and found them indistinguishable from *P. setacea*. His conclusion regarding this synonymy was accepted by Stechow (1909) and Bedot (1914). Also referred to the synonymy of *P. setacea* by Bale (1924) were *Plumularia multinoda* Allman, 1885, from Tauranga, New Zealand, and *P. turgida* Bale, 1888, from Lyttleton, New Zealand. Bale's (1924) *P. setacea* var. *opima* is distinguished by wide internodes separated by deep constrictions. Although Ralph (1961) and Leloup (1974) retained it as a variety of *P. setacea*, *P. setacea opima* is excluded from the synonymy list above until more is known about its specific affinities.

The name *Plumularia corrugata* was established by Nutting (1900) for hydroid specimens from the coast of Brazil and from the Bahamas. I follow authors such as Bedot (1914), Bale (1924), Vannucci Mendes (1946), and Vervoort (1966) in regarding the name *P. corrugata* as a synonym of *P. setacea*. Opinions differ concerning the identity of *Plumularia palmeri* Nutting, 1900, from San Diego, California. Fraser (1914) concluded that it was conspecific with *P. lagenifera*, while Torrey (1902, 1904), Stechow (1909), Billard (1913), Bedot (1914, 1918, 1921a), Bale (1924), and Vervoort (1946, 1966) included it in the synonymy of *P. setacea*.

Plumularia milleri from Hawaii was established by Nutting (1905) for a species resembling *P. setacea* but having slender and horizontally projecting gonothecae and a pair of axillary nematothecae. Billard (1913) and Bedot (1921a) are followed in regarding it as conspecific with *P. setacea*, although Stechow (1919a) recognized it as valid.

A previous record of *Plumularia setacea* from Bermuda by Bennitt (1922:256), repeated in Fraser (1944), is regarded here as a misidentification of *P. strictocarpa* Pictet, 1893. Also referred here to *P. strictocarpa* are several reports of hydroids from pelagic *Sargassum* that were identified as *P. setacea* (Nutting, 1900; Ritchie, 1909a; Stechow, 1912; Deevey, 1950, 1954; Rees and Thursfield, 1965; Defenbaugh and Hopkins, 1973; Spracklin, 1982) (see *Plumularia strictocarpa*, Remarks).

Plumularia filicula Allman, 1877, *P. attenuata* Allman, 1877, and *P. megalocephala* Allman, 1877, all originally described from the Straits of Florida region, superficially resemble hydroids of *P. setacea*. Unlike the Bermuda material, however, hydrocladial apophyses of each of Allman's (1877) hydroids have a prominent cylindrical extension distal to the mamelon, and the small athecate internodes at the proximal end of the hydrocladia are elongate and bear nematothecae. Gonothecae of *P. filicula* are truncate distally with a wide oblique aperture, instead of tubular distally with a narrow circular aperture as in *P. setacea*. The gonotheca ascribed to *P. megalocephala* by Fraser (1944) is pyriform instead of fusiform, and its aperture appears to be lateral (see MCZ, "Atlantis" Sta. 3781) instead of terminal. Colonies of *P. megalocephala* also appear to be irregularly branched instead of unbranched. Examination of the type of *Plumularia attenuata* (MCZ, no catalogue number) confirmed that internodes of the hydrocladia beyond the most proximal athecate internode typically all have hydrothecae (as depicted by Allman, 1877, pl. 18, fig. 6), whereas those of *P. setacea* are alternately athecate and thecate. Unfortunately, the type of *P. filicula* is missing from the Museum of Comparative Zoology, Harvard University, while that attributed to *P. megalocephala* is questionable (Ardis Johnston, MCZ, pers. comm.).

Plumularia antonbruuni Millard, 1967, from the Indian Ocean off Africa (Millard, 1967; Rees and Vervoort, 1987) resembles *P. setacea*. However, *P. antonbruuni* is different in several respects: (1) the hydrorhiza is filamentous instead of creeping; (2) internodes of the hydrocaulus are apparent only at the distal end, instead of throughout; (3) hydrocladia may or may not have athecate internodes beyond the proximal short one, instead of having alternating athecate and thecate internodes; (4) all nodes of the hydrocladium are slightly oblique, instead of being alternately straight and oblique; (5) gonothecae are elongate oval, instead of fusiform.

Specimens from Bermuda examined here share most of the morphological characters typical of hydroids assigned to *Plumularia setacea* (Linnaeus, 1758), a widespread and morphologically varied species (e.g., see Broch, 1918; Ralph, 1961; Vervoort, 1966; Millard, 1973, 1975; Hughes, 1986; Ramil and Vervoort, 1992a; Cornelius, 1995). They differ from "typical" colonies of this species in their larger size (up to 11 cm high as opposed to about 4 cm), in numbers of axillary nematothecae per internode (two to six as opposed to one), and in hydrocladial arrangement (arising from opposite sides of the hydrocaulus instead of from the frontal side). Yet these characters overlap the range of variability ascribed previously to *P. setacea*. Colonies of *P. setacea* may grow to a height of six inches (15 cm) (e.g., Johnston, 1847), have more than one axillary nematotheca (e.g., Mergner and Wedler, 1977), and have hydrocladia that arise obliquely or in one plane (e.g., Ramil and Vervoort, 1992a). Thus, the Bermuda population is considered conspecific with *P. setacea* (Calder, 1986, 1993).

In some respects, hydroids described here are intermediate between *Plumularia setacea* and *P. diploptera* Totton, 1930, from New Zealand. Like the New Zealand species, they have two or more nematothecae on each hydrocladial apophysis and hydrocladia that are inserted laterally instead of frontally on the hydrocaulus. Like *P. setacea*, however, they differ from *P. diploptera* (see Totton, 1930; Ralph, 1961; Rees and Vervoort, 1987) in having shorter internodal apophyses, less strongly septate internodes, and thecate internodes with septa at proximal and distal ends only, instead of proximally, distally, and adjacent to the hydrothecae.

Plumularia setacea has been reported several times previously from the warm western Atlantic (Nutting, 1900, in part; Wallace, 1909, as *P. cetacea*; Vervoort, 1968; Wedler, 1975; Florez Gonzalez, 1983). Vervoort's (1968) well-described material from the U.S. Virgin Islands, unlike *P. setacea* from Bermuda, is small (1.5–2.0 cm high) and has a single nematotheca in the axil of each hydrocladial apophysis.

As noted above, *Plumularia setacea* is recognized as a morphologically varied species. Extremely modified epizootic forms were described by Millard (1973) from the hydroid *Nemertesia cymodocea* (Busk, 1851). These included stunted colonies in which the hydrocladia were short and sometimes bore single hydrothecae with tiny lateral nematothecae, or even solitary hydrocladia arising from the hydrorhiza. Comparable stunting was described among plumularioids by Millard (1973) in species of *Gymnangium* Hincks, 1874 (see Genus *Gymnangium*, Remarks).

Hughes (1986) noted that *Plumularia setacea* was an opportunistic species, as indicated by its small size, rapid growth, early maturity, high recruitment, and high mortality. The species has been reported as a fouling organism on ships' hulls, buoys, and test surfaces (e.g., Woods Hole Oceanographic Institution, 1952:188).

Plumularia setacea was common on octocorals and rhodoliths in offshore waters of the Bermuda Platform. They were also abundant at times on polypropylene buoy lines of crab traps set on the upper slope of the Bermuda Pedestal. Based on the relatively short immersion periods of these buoy lines, growth appeared to be rapid.

REPORTED RANGE

Bermuda: on crab trap lines offshore (Calder, 1986); shallow coastal waters, deeper coastal waters, banks, upper slope (>100 m) of Bermuda Pedestal (Calder, 1993).

Circumglobal distribution: western Atlantic (Vervoort, 1968); eastern Atlantic (Ramil and Vervoort, 1992a); Indian Ocean (Millard, 1975); western Pacific (Rho and Park, 1986); eastern Pacific (Leloup, 1974).

Plumularia strictocarpa Pictet, 1893

Fig. 5

Plumularia strictocarpa Pictet, 1893:55, pl. 3, figs. 47–49.

Plumularia compacta Thornely, 1900:457, pl. 44, fig. 3.

Plumularia setacea—Nutting, 1900:57 [part]. —Ritchie, 1909a:89. —Stechow, 1912:362 [part]. —Bennitt, 1922:256. —Deevey, 1950:347; 1954:271 [part]. —Rees and Thursfield, 1965:162 [part]. —Defenbaugh and Hopkins, 1973:113. —Spracklin, 1982:246, fig. 117f [not *Plumularia setacea* (Linnaeus, 1758)].

Plumularia sargassi Vanhöffen, 1910:333, fig. 46.

Plumularia setaceoides—Fraser, 1912:382, figs. 51A–B; 1918:362; 1921:179; 1943:96; 1944:353, pl. 76, figs. 343a–c; 1946:92, 364; 1947:14. —Burkenroad, *in* Parr, 1939:24. —Deevey, 1954:271. —Vervoort, 1968:110. —Morris and Mogelberg, 1973:22, figs. 32a–c. —Butler et al., 1983:42 [not *Plumularia setaceoides* Bale, 1882].

Plumularia corrugata—Bennitt, 1922:255. —Fraser, 1944:341; 1946:91, 353 [part]. —Morris and Mogelberg, 1973:19. —Defenbaugh, 1974:101, fig. 14. —Butler et al., 1983:42 [not *Plumularia corrugata* Nutting, 1900 =*Plumularia setacea* (Linnaeus, 1758)].

Plumularia strictocarpa var. *japonica* Stechow and

Uchida, 1931:565, fig. 12; pl. 15, fig. 6.

Plumularia strictocarpa var. *compacta*—Stechow and Uchida, 1931:566.

Plumularia strictocarpa var. *sargassi*—Stechow and Uchida, 1931:566.

Plumularia japonica Stechow and Uchida, 1931:568.

?*Plumularia* spec.—Timmermann, 1932:297–303 [?part].

Plumularia strictocarpa japonica—Yamada, 1959:79.

?*Plumularia*—Weis, 1968:556 [?part].

TYPE LOCALITY

"Baie d'Amboine" (Pictet, 1893:56), Moluccas, Indonesia.

MATERIAL EXAMINED

Natural Arches Beach, on stranded pelagic *Sargassum*, 8 March 1982, two colonies each with several hydrocauli, up to 9 mm high, without gonophores, ROMIZ B111. Whalebone Bay, on pelagic *Sargassum*, 27 February 1982, one colony with several hydrocauli, 8 mm high, with gonophores, ROMIZ B113. Whalebone Bay, on pelagic *Sargassum*, 2 September 1977, two colonies each with several hydrocauli, up to 6 mm high, without gonophores, ROMIZ B116. Whalebone Bay, on benthic algae, –4 m, 4 March 1982, four colonies each with several hydrocauli, up to 13 mm high, without gonophores, ROMIZ B123. Whalebone Bay, on benthic algae, –3 m, 28 July 1982, one colony with several hydrocauli, 8 mm high, without gonophores, ROMIZ B273. Castle Harbour, south shore near Castle Roads, on underside of rocks, –2 m, 30 July 1982, two colonies, up to 10 mm high, without gonophores, ROMIZ B274. Stream Passage Cave, on limestone rock, –1 m, 27 July 1982, two colonies, up to 23 mm high, without gonophores, ROMIZ B279. Castle Grotto, Castle Harbour, on polychaete tube, –1 m, 20 July 1982, one colony, with several hydrocauli, up to 11 mm high, without gonophores, ROMIZ B281. Natural Arches Beach, on stranded pelagic *Sargassum*, 4 August 1982, one colony with several hydrocauli, up to 6 mm high, with gonophores, ROMIZ B283. Atlantic Ocean, 2 km off Castle Roads, on pelagic *Sargassum*, 24 July 1982, one colony, 6 mm high, without gonophores, ROMIZ B285. Burchall's Cove, on pelagic *Sargassum*, 23 November 1989, one colony with several hydrocauli, 9 mm high, without gonophores, ROMIZ B435. John Smith's Bay, on tar ball washed ashore on beach, 8 September 1992, one colony with several hydrocauli, 6 mm high, without gonophores, ROMIZ B436.

DESCRIPTION

Colonies up to 23 mm high, with a creeping, wrinkled hydrorhiza bearing occasional nematothecae; hydrorhiza of colonies on *Sargassum* and tubular benthic algae with internal septa. Hydrocaulus monosiphonic, unbranched, more or less straight basally, zigzag distally, divided at regular intervals beyond base into internodes by distinct transverse nodes; perisarc thick basally, becoming thinner distally. Cauline internodes 252–391 µm long, 47–84 µm wide in mid-region, 37–84 µm wide at nodes, with distinct to indistinct septa at each end; each internode with a distal apophysis and commonly with two nematothecae, one axillary and one part way along internode on side opposite apophysis; cauline nematothecae bithalamic, movable, cone-shaped, 61–75 µm long. Apophyses fairly long, given off alternately from opposite sides of hydrocaulus; each apophysis bearing a mamelon on dorso-lateral side near node, a prominent internal septum, and a hydrocladium. Hydrocladia almost always unbranched, up to 5 mm long but typically less than half of that, directed outward at an angle of about 60°–70° from axis of hydrocaulus, generally divided into alternating athecate and thecate internodes. Most proximal internode 65–93 µm long, with a straight node proximally, an oblique node distally, and a prominent internodal septum, hydrothecae and nematothecae lacking; this basal internode followed by one to nine pairs of alternating thecate and athecate internodes. Thecate internodes 275–401 µm long, those of a given hydrocladium tending to be progressively shorter distally, each with an oblique node proximally, a nearly straight node distally, a median inferior nematotheca, a hydrotheca, two lateral nematothecae, a distinct internal septum at each end, and typically with a distinct to indistinct septum beneath base of hydrotheca. Athecate internodes beyond the most proximal one 140–261 µm long, those of a given hydrocladium sometimes longer distally than proximally, each with a septum and an almost straight node proximally, another septum and an oblique node distally, and typically with one intermediate nematotheca. Nematothecae of hydrocladia bithalamic, movable, cone-shaped; median nematothecae not reaching as far as base of hydrotheca; lateral nematothecae extending beyond margin of hydrotheca. Hydrothecae small, 65–84 µm deep, cup-shaped, axis slightly oblique to that of internode, a ring of small desmocytes visible basally in cleared material; adcauline wall convex, adnate to internode; abcauline wall nearly straight, or tending to be slightly convex basally and concave distally; margin entire, oblique to axis of hydrotheca, aperture circular, diameter 84–98 µm; intrathecal septum lacking.

Gonophores fixed sporosacs. Gonothecae barrel-shaped to coccoon-shaped, typically one but infrequently two per hydrocaulus, each arising via a short pedicel from a basal apophysis, length about 1 mm, maximum diameter 0.5 mm; walls with seven to 11 distinct spiral annulations, perisarc thick; aperture nearly round, at end of short collar, diameter 0.2 mm; gonothecae of hydroids on *Sargassum* sometimes compressed vertically, with one wall partially appressed to algal substrate.

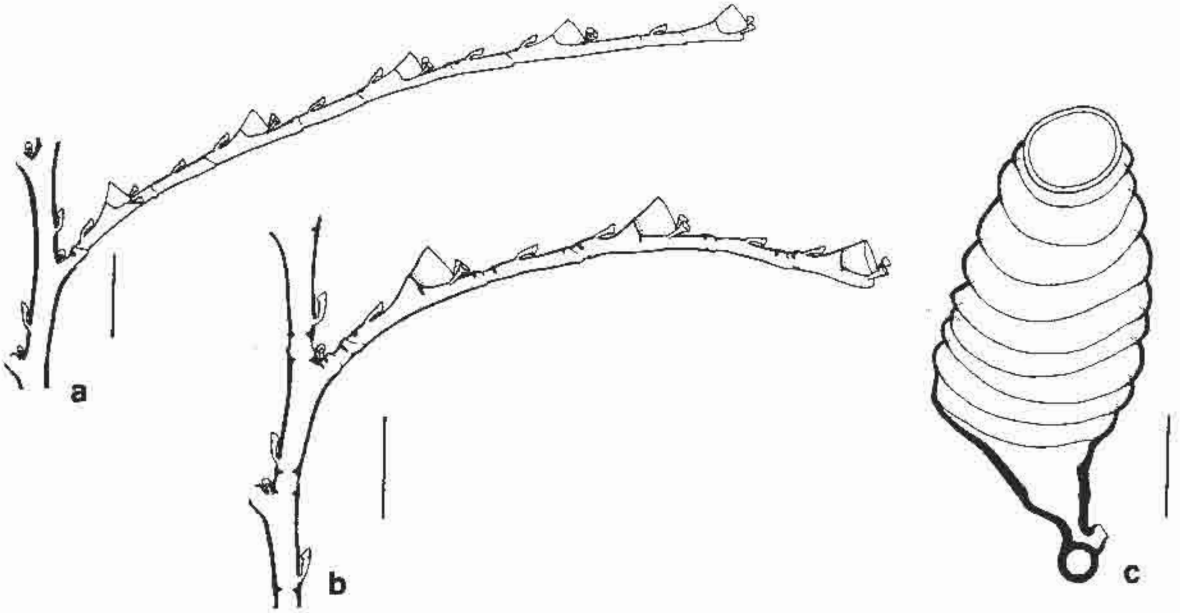

FIG. 5. *Plumularia strictocarpa: a*, part of hydrocaulus with hydrocladium, ROMIZ B279; *b*, part of hydrocaulus with hydrocladium, ROMIZ B436; *c*, gonotheca, ROMIZ B283. Scales equal 0.25 mm.

REMARKS

Pictet (1893) first recognized this species as distinct from *Plumularia setacea* (Linnaeus, 1758), and instituted the name *P. strictocarpa* for it. The two were differentiated on characters of the gonotheca, those of *P. setacea* being fusiform with a tubular neck, and those of *P. strictocarpa* being barrel-shaped without a neck but with spiral annulations. Pictet recognized that it would be difficult to distinguish these species in the absence of gonothecae. He suggested that the athecate internodes of the hydrocladia were a little longer in relation to the thecate internodes in *P. strictocarpa* than in *P. setacea*, but this is not a reliable character.

Stechow and Uchida (1931) regarded *Plumularia compacta* Thornely, 1900, and *P. sargassi* Vanhöffen, 1910, as varieties of *P. strictocarpa*. Their material of the species, from Japan, was established as a new variety (*P. strictocarpa* var. *japonica*; also referred to in the same paper as *P. japonica*). Differences in the number of annulations on the gonothecae were reported among these forms by Stechow and Uchida. Hirohito (1974) discounted the taxonomic significance of this character and united all of these purported varieties under the name *P. strictocarpa*.

Several reports of *Plumularia setacea* appear to have been based instead on hydroids of *P. strictocarpa*. Vanhöffen (1910) referred records of *P. setacea* by Pictet and Bedot (1900), Billard (1906), and Ritchie (1909a), as well as part of Nutting's (1900:57) material (that described as a "distinct variety" from "gulf weed"), to his *P. sargassi*. I agree that those of Nutting (1900) and Ritchie (1909a), both found on *Sargassum* in the North Atlantic, were almost certainly referable to *P. strictocarpa*. There seems less likelihood that the specimens of Pictet and Bedot (1900) and Billard (1906), all from deeper waters, were this species (see also Billard, 1913:33). Other records of *P. setacea* at least partly from *Sargassum* (Stechow, 1912; Bennitt, 1922; Deevey, 1950, 1954; Rees and Thursfield, 1965; Defenbaugh and Hopkins, 1973; Spracklin, 1982), are considered here to have been based on *P. strictocarpa*.

Reports of *Plumularia setaceoides* Bale, 1882, from *Sargassum* in the western North Atlantic by Fraser (1912) and others (see synonymy list above), are regarded here as based on misidentified hydroids of *P. strictocarpa*. Where illustrated, none of these hydroids resembles the true *P. setaceoides*, with its (1) partially free and thickened abcauline hydrothecal wall, (2) extremely oblique hydrothecal margin, (3) relatively short lateral nematothecae (not reaching the hydrothecal margin), (4) cylindrical to ovate gonothecae, and (5) larger colony size (e.g., see Bale, 1882; Ralph, 1961).

Bennitt (1922) identified a hydroid found on floating *Sargassum* at Bermuda as *Plumularia corrugata* Nutting, 1900. Having seen numerous colonies of *P. strictocarpa* on that substrate in the area (Calder, 1993, 1995, this report), but none corresponding with descriptions of *P. corrugata* (=*P. setacea*), I consider Bennitt's record to be in error. Fraser (1944) incorporated the misidentification in his account of *P. corrugata*. Morris and Mogelberg (1973), following Fraser, listed the species among those occurring on *Sargassum*. From Defenbaugh's (1974) description and illustration of a hydroid identified as *P. corrugata*, found on floating *Sargassum* off the coast of

Texas, it is apparent that his material too was probably *P. strictocarpa.*

Timmermann (1932) and Weis (1968) reported hydroids identified simply as *Plumularia* spec. and as *Plumularia*, respectively, from pelagic *Sargassum* in the Sargasso Sea. It is likely that these were based on colonies of *P. strictocarpa*, although the plumularioid *Halopteris diaphana* (Heller, 1868) is also relatively frequent on that substrate in the same area (e.g., see Calder, 1995; see also *Halopteris diaphana,* Remarks).

Vannucci (1949:254) regarded *Plumularia palmeri* Nutting, 1900, from San Diego, California, as probably conspecific with *P. strictocarpa.* Hirohito (1974) excluded the name *P. palmeri* from the synonymy of *P. strictocarpa*, and I agree that there is insufficient evidence to regard them as identical. Hydroids assigned to *P. palmeri* by Nutting (1900) were large (height 4 inches [10 cm]) and appear more like *P. lagenifera* Allman, 1885 (e.g., Fraser, 1914) or *P. setacea* (see *Plumularia setacea,* Remarks) than *P. strictocarpa.*

Plumularia strictocarpa is one of the most frequently encountered hydroid species on pelagic *Sargassum* in the Sargasso Sea (Burkenroad, *in* Parr, 1939; Butler et al., 1983; Calder, 1995). In an earlier study (Calder, 1995), hydroids of this species were observed on 40 of 60 thalli of *S. natans*, and on 57 of 60 thalli of *S. fluitans* examined over four seasons at Bermuda. They also occur on pelagic tar balls (ROMIZ B436).

Hydroids of *Plumularia strictocarpa* varied considerably in morphology from one environment to another. Specimens from pelagic substrates (*Sargassum,* floating tar balls) examined here (Fig. 5b) were uniformly minute (6–9 mm high), and had distinct internodal septa. Those from benthic substrates (Fig. 5a) tended to be larger (8–23 mm high) and more gracile, and had less distinct internodal septa.

REPORTED RANGE

Bermuda: on pelagic *Sargassum* (Bennitt, 1922, as *Plumularia corrugata* and *P. setacea*; Butler et al., 1983, as *Plumularia setaceoides*, *P. corrugata*, and *P. strictocarpa*; Calder, 1993, 1995).

Circumglobal distribution: western Atlantic (Van Gemerden-Hoogeveen, 1965, as *Plumularia sargassi*); eastern Atlantic (Ritchie, 1909a, as *Plumularia setacea*); Indian Ocean (Millard and Bouillon, 1973), western Pacific (Hirohito, 1974).

Family Halopterididae Millard, 1962

Nudithecata Bedot, 1923:235 [emended to Nudithecinae by Stechow, 1923a:236].

Acladiinae Stechow, 1923a:214.

Halopterinae Millard, 1962:268 [emended to Halopterididae by Cairns et al., 1991:27].

DIAGNOSIS

Colonies with erect hydrocauli, or with hydrocladia arising directly from hydrorhiza. Hydrocaulus, when present, branched or unbranched, monosiphonic or polysiphonic, arising from a creeping or rootlike hydrorhiza, giving rise to alternate, opposite, or irregularly arranged hydrocladia. Hydrocladia branched or unbranched; when arising from polysiphonic hydrocauli and branches, given off from either a single axial tube or from superficial tubes. Hydrothecae on hydrocladia typically large, with or without marginal cusps. Cauline hydrothecae typically present, well developed, less frequently atrophied; lacking on polysiphonic hydrocladia and branches when component tubes give rise to hydrocladia. Nematophores with nematothecae, not as naked sarcostyles. Nematothecae typically well developed, bithalamic or monothalamic, movable or immovable, not fused to hydrothecae; a minimum of three (one median inferior and a pair of lateral nematothecae) adjacent to each hydrotheca.

Gonophores fixed sporosacs. Gonothecae solitary, frequently sexually dimorphic, with or without nematothecae, without phylactocarps.

REMARKS

Bedot (1923) founded the Nudithecata as one of four subfamilies that he recognized within a broadly defined family Plumulariidae McCrady, 1859. To it, he assigned only the type genus *Nuditheca* Nutting, 1900. The name Nudithecata, emended to Nudithecinae by Stechow (1923a), has not subsequently been employed as the name of a taxon in hydrozoan nomenclature. Instead, its type genus has been assigned either to the Aglaopheniinae/Aglaopheniidae (e.g., Stechow, 1923a; Bouillon, 1985) or to the Plumulariidae sensu lato (e.g., Fraser, 1937; Naumov, 1960; Antsulevich, 1987). As noted elsewhere (see Superfamily Plumularioidea, Remarks; Subfamily Gymnangiinae, Remarks), however, its characters place it instead in a group of genera assigned here to the Halopterididae Millard, 1962. The latter family-group name, now well established in hydrozoan classifications since being founded by Millard (1962), is thereby threatened by a virtually unused senior synonym, Nudithecidae.

Stechow (1923a) established the Acladiinae for plumularioids having fixed mesial nematothecae separated from proximate hydrothecae, and fixed or movable lateral nematothecae. To this subfamily he assigned seven nominal genera: *Halopteris* Allman, 1877; *Heteroplon* Allman, 1883; *Gattya* Allman, 1885; *Acladia* Marktanner-Turneretscher, 1890; *Antennellopsis* Jäderholm, 1896; *Paragattya* Warren, 1908; and *Heterotheca* Stechow, 1921a. Two years later, Stechow (1925b) abandoned the name Acladiinae, concluding that it was coterminous with Plumulariinae McCrady, 1859. He regarded *Acladia* (type genus of the Acladiinae) as congeneric with *Heteroplon*, but erroneously included the latter as a subgenus of *Plumularia* Lamarck, 1816 (type species of the Plumulariinae). Instead, *Heteroplon* and *Acladia* are both currently taken to be congeneric with *Halopteris* (see Genus *Halopteris*, Remarks).

In a review of the classification of the Plumulariidae sensu lato, Millard (1962) argued that nematotheca characters alone provided insufficient basis for recognition of higher taxa. She proposed instead that a group of genera sharing a character of fundamental importance, namely, the possession of cauline hydrothecae, constituted a new subfamily, the Halopterinae. Assigned to this group by Millard, in addition to *Halopteris* and *Gattya*, were *Antennella* Allman, 1877; *Monostaechas* Allman, 1877; *Schizotricha* Allman, 1883; and *Corhiza* Millard, 1962. Millard maintained that the name Acladiinae could not be retained for the taxon because *Acladia*, the type genus of Stechow's nominal family, was a junior subjective synonym of *Halopteris*. Although this conclusion was nomenclaturally unjustified (ICZN, 1985, Art. 40), the name Halopterinae has now been widely adopted. Stability of nomenclature would not be served by replacing the familiar name Halopterinae with the senior but seldom-used name Acladiinae. Also for reasons of nomenclatural stability, the name Halopterinae, emended to Halopterininae (ICZN, 1985, Art. 29b), is adopted here rather than the oldest name for the group, Nudithecinae. Under the current rules of nomenclature, the case should be referred to the ICZN, requesting validation of the junior synonym Halopterininae. As for the rank of the group, I concur with authors such as Bouillon (1985), Gili, Vervoort, and Pagès (1989), Cairns et al. (1991), and Ramil and Vervoort (1992a) in recognizing it as a distinct family, the Halopterididae.

Genera assigned to the Halopterididae by Bouillon (1985) included *Calvinia* Nutting, 1900, as well as the six (*Antennella, Corhiza, Gattya, Halopteris, Monostaechas*, and *Schizotricha*) referred to the group initially by Millard (1962). *Nuditheca, Anarthroclada* Naumov, 1955, *Astrolabia* Naumov, 1955, and *Pentatheca* Naumov, 1955, are also transferred to the family here for reasons discussed elsewhere (see Family Aglaopheniidae, Remarks; Subfamily Gymnangiinae, Remarks). *Antennellopsis* Jäderholm, 1896, is also recognized as valid here, rather than as a congener of *Antennella*, because of its immovable median and lateral nematothecae (see Genus *Antennella*, Remarks). Differences in characters such as nematotheca morphology among halopteridids may eventually lead to recognition of subfamilies within the group.

Pseudoplumaria Ramil and Vervoort, 1992c, was regarded by its authors as a plumulariid, but they noted that it exhibited some characters typical of the family Halopterididae. These included gonothecae with adherent nematothecae, and "large mamelons" (regarded by Ramil and Vervoort as atrophied hydrothecae) on the hydrocladia. In a colony of *P. sabinae* Ramil and Vervoort, 1992c, type species of the genus, they described the "gradual transformation of the 'mamelon' on the hydrocladial apophysis into a hydrotheca" (Ramil and Vervoort, 1992c:488). Possibly the ontogeny is the reverse of this description, with hydrothecae becoming reduced to mamelonlike structures on all but the youngest parts of the hydrocaulus and the branches. The shape of the nematothecae in species assigned to *Pseudoplumaria* by Ramil and Vervoort (1992c), and especially those in *P. marocana* (Billard, 1930), also indicates a greater affinity with the Halopterididae than with the Plumulariidae. Accordingly, *Pseudoplumaria* is here referred to the Halopterididae.

Also regarded as a halopteridid rather than a plumulariid here is *Polyplumaria* G. O. Sars, 1874. The structure of the nematothecae and gonothecae in *P. flabellata* G. O. Sars, 1874, type species of the genus, is much like those in *Pseudoplumaria sabinae*, *P. marocana*, and other species of halopteridids. Moreover, the "large mamelon" or "pseudonematotheca" (e.g., see Bedot, 1921b; Vervoort, 1966) present in the axil between an apophysis and the hydrocaulus or branch is interpreted here as homologous with the vestigial hydrotheca of *Pseudoplumaria*. The genus *Polyplumaria* had earlier been classified under the Halopterididae by Vervoort (1966).

Millard (1962) regarded the family Halopterididae as the most primitive group in the Plumularioidea McCrady, 1859. For reasons given earlier (see Family Kirchenpaueriidae, Remarks), the family Kirchenpaueriidae is regarded here as likely closest to the ancestor of the group, while the halopteridids are regarded as intermediate between the families Plumulariidae and Aglaopheniidae Marktanner-Turneretscher, 1890 (see Genus *Halopteris*, Remarks).

Halopteridids are most diverse in lower latitudes, although they occur from Arctic and Antarctic waters to the tropics. They seem largely restricted bathymetrically to neritic and bathyal bottoms (e.g., Fraser, 1944; Millard, 1975), although *Schizotricha gracilis* Naumov, 1960, has been reported as deep as 2300 m off the Russian Pacific coast (Naumov, 1960; Vervoort, 1966).

Of the 13 genera assigned above to the family Halopterididae, two (*Antennella* and *Halopteris*) are known from shallow-water habitats in the vicinity of Bermuda.

Genus *Antennella* Allman, 1877

Listera Meneghini, 1843:404 [invalid junior homonym of *Listera* Turton, 1822 (Mollusca)].

Antennella Allman, 1877:38.

Antenella Allman, 1877:38 [incorrect original spelling].

Antenel a Bedot, 1914:84 [incorrect subsequent spelling].

Antennela Pennycuik, 1959:176 [incorrect subsequent spelling].

DIAGNOSIS

Colonies small, with hydrocladia arising directly from a creeping hydrorhiza; hydrocladia typically unbranched, less frequently with a few dichotomous branches. Hydrothecae cup-shaped to vase-shaped, margin entire. Nematothecae bithalamic, movable; lateral nematothecae flanking each hydrotheca, borne on prominent peduncles adhering to hydrothecal wall.

Gonophores fixed sporosacs. Gonothecae solitary, sexually dimorphic, borne on hydrocladia; nematothecae present basally; not protected by corbulae or other phylactocarps.

TYPE SPECIES

Antennella gracilis Allman, 1877, a junior subjective synonym of *A. secundaria* (Gmelin, 1791), by monotypy.

REMARKS

In founding this genus, Allman (1877) spelled its name two ways, *Antenella* and *Antennella*. Both spellings have been used frequently in 20th-century literature on hydroids. *Antennella* was chosen as the correct original spelling by Bedot (1912), acting as First Reviser (ICZN, 1985, Art. 24c). Bedot (1917) referred 19 nominal species to *Antennella* but suggested that some of them would likely prove conspecific.

Earlier, the generic name *Listera* had been established by Meneghini (1843) for *Sertularia secundaria* Gmelin, 1791. That species is now generally assigned to *Antennella* (e.g., see Millard, 1975; Vervoort and Vasseur, 1977; Rees and Vervoort, 1987; Cornelius, 1995). However, the name *Listera* Meneghini, 1843, is an invalid junior homonym of *Listera* Turton, 1822, an appellation applied to a mollusc, and it does not threaten the familiar name *Antennella*.

The genus *Monostaechas* Allman, 1877, is closely related to *Antennella* but is distinguished by having colonies with dichotomously or helically branched hydrocladia (Allman, 1877; Millard, 1975). Millard (1962) noted that unbranched hydrocladia arise directly from the hydrorhiza in some colonies of *Monostaechas natalensis* Millard, 1958, which thereby resemble species assigned to *Antennella*. Conversely, she observed that some colonies of *Antennella secundaria* (Gmelin, 1791) are dichotomously branched, as is *Monostaechas*. Branching of a similar form was prevalent also in colonies of *A. quadriaurita* Ritchie, 1909a, from Bermuda, discussed below. Nevertheless, Millard (1962) argued for recognition of both genera, as well as of *Halopteris* Allman, 1877, a similar halopteridid genus with typically pinnate hydroid colonies. She suggested that the three represented different phylogenetic lines within the same family. That concept has been followed in this report, although the validity of distinguishing these genera essentially on the mode of branching they exhibit has been questioned (e.g., Nutting, 1900).

Antennellopsis Jäderholm, 1896, has been regarded as a valid genus name (e.g., Stechow, 1909, 1923a; Bedot, 1918; Jäderholm, 1919; Yamada, 1959; Rees and Thursfield, 1965) and as a junior synonym of *Antennella* (e.g., Bedot, 1921a; Millard, 1975; Hirohito, 1983; Bouillon, 1985; Rho and Park, 1986; Park, 1992, 1993). Although the colony form of *Antennellopsis integerrima* Jäderholm, 1896, type species of the genus by monotypy, resembles that of *Antennella*, all of its nematothecae are rigid and cowl-shaped rather than movable and cone- to scoop-shaped. Totton (1930) held that *Antennella* as then constituted was a polyphyletic group, based on differences in the "minute structure" of the included species, though he did not specifically mention *A. integerrima*. Until more is known about their relationships, *Antennellopsis* and *Antennella* are held to be distinct here because of their decidedly different kinds of nematothecae.

Corhiza Millard, 1962, a genus characterized by having strongly polysiphonic hydrocauli, seems closely allied to *Antennella* and *Monostaechas* (see Millard, 1962). However, hydrocladia of *Antennella* arise from a creeping hydrorhiza rather than from a polysiphonic bundle of similar stolons as in *Corhiza*, while the characteristic branching of the hydrocladia in *Monostaechas* generally distinguishes it from the other two.

Among synonyms of *Antennella* listed by Stechow (1923a) was the name *Anisocalyx*, attributed by him to Meneghini (1845). Stechow regarded this name as preoccupied (by *Anisocalyx* Costa, 1842, a junior objective synonym of *Aglaophenia* Lamouroux, 1812). Meneghini (1845) used the name in the combination *Anisocalyx secundarius* (Gmelin, 1791), assigning the specific name to a genus he knew had been founded earlier by Costa (1842). Stechow's inclusion of the name in the synonymy of *Antennella* may therefore be disregarded. The nomenclatural status of *Anisocalyx* Costa, 1842, is discussed elsewhere (see Genus *Aglaophenia,* Remarks).

Gonophores in *Antennella*, where known, are sexually dimorphic. Female gonothecae tend to be larger than male, and are typically pear-shaped rather than spindle-shaped. Gonothecae of both sexes may be produced on the same colony, on occasion even on the same hydrocladium (Totton, 1930; Millard, 1975).

Antennella quadriaurita Ritchie, 1909a

Fig. 6

Antennella gracilis—Nutting, 1900:77 [part] [not *Antennella gracilis* Allman, 1877 =*A. secundaria* (Gmelin, 1791)].

Antenella quadriaurita Ritchie, 1909a:92, figs. 9a–c [incorrect subsequent spelling].

Antennella quadriaurita—Billard, 1913:10.

Antenella quadriaurita f. *africana* Broch, 1914:26 [incorrect subsequent spelling].

Antenella quadriaurita forma *typica* Broch, 1914:44 [incorrect subsequent spelling].

Antennella quadriaurita forma *africana*—Bedot, 1917:116.

Antenella africana—Stechow, 1923b:13 [incorrect subsequent spelling].

Antennella serrata Totton, 1930:212, fig. 53.

Antenella quadriaurata—Leloup, 1932b:162, pl. 16, fig. 2 [incorrect subsequent spelling].

Antenella quadriaurata africana—Leloup, 1932b:163 [incorrect subsequent spelling].

Antenella serrata—Leloup, 1932b:163 [incorrect subsequent spelling].

Antennella africana—Millard, 1957:226.

Halopteris quadriaurita—Stepanjants, 1979:124, pl. 23, figs. 2A–C.

Antennella serreta—Stepanjants, 1979:124 [incorrect subsequent spelling].

[*Halopteris*] *africana*—Stepanjants, 1979:124.

Antennella sp.—Calder, 1993:68 [part].

TYPE LOCALITY

"Gough Island. Trawled at a depth of 100 fathoms [183 m]. Bottom deposit, Bryozoa and rock" (Ritchie, 1909a).

MATERIAL EXAMINED

Atlantic Ocean, 4 km NW of North Rock, on *Sertularella diaphana*, 73 m, 28 May 1991, one colony, 6 mm high, with gonophores, ROMIZ B440. Atlantic Ocean, 5 km SSE of Castle Roads, on *Macrorhynchia allmani*, 85 m, 26 May 1991, one colony, 7 mm high, without gonophores, ROMIZ B441. Atlantic Ocean, 2 km off Natural Arches Beach, on rhodolith, –70 m, 13 May 1991, two colonies, up to 10 mm high, without gonophores, ROMIZ B442.

DESCRIPTION

Colonies up to 10 mm high, arising as hydrocladia directly from a creeping hydrorhiza. Basal part of hydrocladium with one or more athecate internodes of varied length, often long and tubular, about 55–105 µm in diameter, some specimens with several short internodes and with distal part clearly regenerated; nodes transverse; nematothecae few and irregularly placed, or absent. Distal part of hydrocladium typically divided into four to 13 alternating athecate and thecate internodes; less frequently with two or more athecate internodes in sequence. Hydrocladia sometimes unbranched but typically branched up to three times; branches with first internode athecate and with alternating thecate and athecate internodes distal to it, resembling main hydrocladium, each originating from a small apophysis inserting at distal end of an athecate internode, given off from back or sides of internode, colony thus appearing dichotomously branched. Apophyses short, stump-shaped; nematothecae and mamelon absent. Thecate internodes 294–820 µm long, tending to become shorter distally; each with an oblique node proximally, a nearly straight node distally, a median inferior nematotheca, a pair of large lateral nematothecae each borne on a prominent peduncle, and a pair of smaller lateral nematothecae arising from base of peduncles and oriented towards distal end of hydrocladium. Athecate internodes beyond base 168–503 µm long, each with an almost straight node proximally, an oblique node distally, and typically with two or three median nematothecae. All nematothecae relatively large, bithalamic, considered movable, scoop- to cone-shaped; larger lateral ones typically reaching beyond hydrothecal rim. Hydrothecae 163–256 µm deep, cup-shaped, axis oblique to that of internode; adcauline wall adnate to internode for about two-thirds of length, convex proximally, free distal part concave, relatively close to internode; abcauline wall convex basally, nearly straight distally; margin entire, slightly flaring, perpendicular or nearly so to axis of hydrotheca; aperture circular, diameter from abcauline to adcauline wall 140–168 µm; intrathecal septum lacking.

Gonophores presumably fixed sporosacs. Female gonotheca pear-shaped, about 515 µm long, 195 µm wide, aperture 80 µm; each gonotheca arising via a two-segmented pedicel from proximal end of thecate internode, pedicel inserted near base of hydrotheca and to one side of median; perisarc of moderate thickness; basal region bearing two large bithalamic nematothecae. Male gonotheca not seen.

REMARKS

This hydroid was first recognized as an undescribed species by Ritchie (1909a), who applied the binomen *Antenella* (*sic*) *quadriaurita* to it. According to Stechow (1919a), part of the material assigned earlier by Nutting (1900) to *Antennella gracilis* Allman, 1877 [=*A. secundaria* (Gmelin, 1791)], namely, that from the coast of Cuba off Havana, should be referred to *A. quadriaurita*. The reported range of the species was thereby extended from Gough Island, in the antiboreal South Atlantic, to warm water in the Caribbean.

Broch (1914) referred specimens from the coast of tropical west Africa to a newly recognized form, *Antenella*

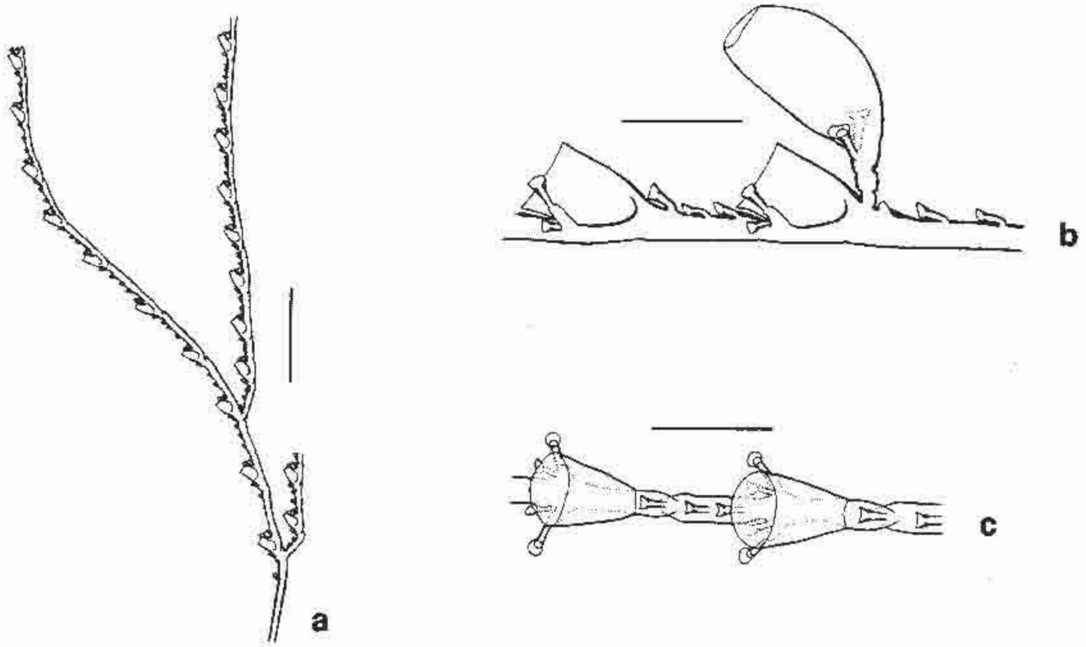

FIG. 6. *Antennella quadriaurita: a,* colony with branched hydrocladium, ROMIZ B441; *b,* part of hydrocladium, lateral view, with two hydrothecae and gonotheca, ROMIZ B440; *c,* part of hydrocladium, front view, with two hydrothecae, ROMIZ B440. Scale for *a* equals 1 mm; scales for *b* and *c* equal 0.25 mm.

[*sic*] *quadriaurita* f. *africana*, because of the presence of a single nematotheca on each athecate internode instead of two to four of them. Stechow (1923b) discovered the same form in Valdivia collections from the coast of South Africa and elevated the name to specific rank as *Antenella* [*sic*] *africana*. Leloup (1932b), noting considerable variation in the length of the athecate internodes and in the number of nematothecae on them in material from south India, regarded *A. africana* as conspecific with *A. quadriaurita*. The same conclusion was reached later by Millard (1977), who examined extensive material from South Africa and from several oceanic islands in the South Atlantic Ocean. She found no justification either on length of athecate internode or in number of nematothecae per internode for separating the two. Stepanjants (1979) also regarded the two as conspecific, and this conclusion has been followed here.

Totton (1930) described *Antennella serrata* as a new species from New Zealand. Like Broch's (1914) hydroids of *A. quadriaurita* forma *africana*, the athecate internodes of the hydrocladia typically bore a single nematotheca. Totton separated the species on the basis of (1) the meagre information provided by Broch about his hydroid, (2) the close approximation of hydrothecae in New Zealand material, and (3) their different provenances—Pacific and Atlantic. Ralph (1961) compared New Zealand specimens with others from South Africa, provided by N. A. H. Millard, and concluded that *A. serrata* and *A. africana* (=*A. quadriaurita*) were conspecific. The opinion that the two are identical was also held by Millard (1975) and Stepanjants (1979).

Like *Antennella quadriaurita*, three nominal species discussed by Billard (1913) from collections of the Siboga Expedition to southeast Asia, *Antennella sibogae* (Billard, 1911b), *A. varians* (Billard, 1911b), and *A. balei* (Billard, 1911b) (an invalid junior primary homonym of *Plumularia balei* Bartlett, 1907), have two lateral nematothecae of unequal size on each side of the hydrotheca. However, each of these three differs from *A. quadriaurita* in having more robust internodes, and one or more pairs of laterally inserted nematothecae situated distal to each hydrotheca. *Antennella biarmata* Nutting, 1927, from the Philippines resembles *A. quadriaurita* but differs in its elongated and closely placed hydrothecae and in the apparent separation of the two lateral nematothecae on a given side of a proximate hydrotheca. *Antennella ritchiei* Totton, 1930, from New Zealand also resembles *A. quadriaurita* in its arrangement of nematothecae, and the two were regarded as conspecific by Stepanjants (1979). Totton (1930) and Ralph (1961) distinguished *A. ritchiei* from *A. quadriaurita* by its much more divergent hydrothecae and indistinctly demarcated hydrocladial internodes. Several species currently assigned to other halopteridid genera (e.g., *Monostaechas* Allman, 1877; *Halopteris* Allman, 1877; *Corhiza* Millard, 1962) have two pairs of lateral nematothecae as well (see Vervoort, 1966; Millard, 1975), but they differ from *A. quadriaurita* in colony form.

Whereas unbranched hydrocladia were observed in a specimen of *Antennella quadriaurita* from Bermuda (ROMIZ B441), as is typical of the genus *Antennella* Allman, 1877, others on the same colony and in other material (ROMIZ B440, ROMIZ B442) were sparingly branched and thus resembled species assigned to *Monostaechas* Allman, 1877. Comparably branched hydrocladia have been reported previously in hydroids of *A. quadriaurita* from the Vema Seamount (Millard, 1966). As noted above, however (see Genus *Antennella*, Remarks), sympodially branched hydrocladia have been observed on occasion in colonies of species assigned to *Antennella*, just as unbranched hydrocladia sometimes occur in hydroids assigned to *Monostaechas* (Millard, 1962:270). In having sparsely branched or unbranched hydrocladia, this hydroid seems justifiably assigned to *Antennella*.

Stechow (1919a) noted that the smaller of the two pairs of lateral nematothecae flanking each hydrotheca in *Antennella quadriaurita* were somewhat difficult to see, especially in lateral view. Moreover, Ritchie (1909a) remarked earlier that they were fragile and easily detached. Their presence, most easily discerned in anterior aspect, immediately distinguishes this species from its more common congener, *A. secundaria* (Gmelin, 1791).

Although *Antennella quadriaurita* has been reported from shallow waters and even from the intertidal zone (Broch, 1914; Millard, 1962), most records of the species are from neritic and upper bathyal depths to 825 m (Millard, 1977). Off Bermuda, it has been collected at depths of 70–85 m.

Hydroids identified earlier from Bermuda as *Antennella* sp. (Calder, 1993) are referable to two different species. Part of the material is based on specimens assigned here to *A. quadriaurita*, and part on material referred to *A. secundaria*, discussed elsewhere in this report.

REPORTED RANGE

Bermuda: deeper coastal waters (Calder, 1993, as *Antennella* sp. [part]).

Circumglobal distribution: western Atlantic (Stechow, 1919a); eastern Atlantic (Millard, 1966); Indian Ocean (Millard, 1975, as *Antennella africana*); western Pacific (Ralph, 1961, as *Antennella africana*).

Antennella secundaria (Gmelin, 1791)

Fig. 7

La Sertolara secondaria—Cavolini, 1785:226, pl. 8, figs. 15–16 [unavailable name].

Sertularia secundaria Gmelin, 1791:3854.

Aglaophenia secundaria—Lamouroux, 1816:172.

Plumularia secundaria—de Blainville, 1830:442.

Aglatophenia secundaria—Costa, 1839:185 [incorrect subsequent spelling].

Anisocalyx secundarius—Costa, 1842:12, pl. 2, fig. 2.

Listera secondaria—Meneghini, 1843:404 [incorrect subsequent spelling].

Plumularia catharina—Hincks, 1868:299 [part]. —Crawshay, 1912:330 [part] [not *Plumularia catharina* Johnston, 1833].

Antennella gracilis Allman, 1877:38, pl. 22, figs. 6–7.

Antenella gracilis—Fewkes, 1881:127 [incorrect subsequent spelling].

Plumularia (Sertularia) secundaria—Bedot, 1901a:499.

Listera (Aglaophenia) secundaria—Bedot, 1905:101.

Antennella secundaria—Stechow, 1907:199.

Antennella natalensis Warren, 1908:318, figs. 14A–C.

Antenella secundaria—Ritchie, 1910a:14 [incorrect subsequent spelling].

Plumularia dubiaformis Mulder and Trebilcock, 1911:119, pl. 2, fig. 7.

Antenella natalensis—Bedot, 1914:82 [incorrect subsequent spelling].

Antennella dubiaformis—Bedot, 1917:116.

Antennella scundaria—Bedot, 1917:125 [incorrect subsequent spelling].

Antennella secondaria—Neppi, 1918:54 [incorrect subsequent spelling].

Plumularia secondaria—Hargitt, 1924:500 [incorrect subsequent spelling].

Antennella paucinoda Fraser, 1935:110, pl. 2, figs. 10a–b.

Schizotricha secundaria—Blackburn, 1942:108.

Polyplumaria secundaria—Picard, 1951b:261.

Anisocalyx secundarium—Riedl, 1959:653 [incorrect subsequent spelling].

Antennela secundaria—Pennycuik, 1959:176 [incorrect subsequent spelling].

Antenella paucinoda—Yamada, 1959:77 [incorrect subsequent spelling].

Antenella secunda—Yamada, 1959:96 [incorrect subsequent spelling].

Antenella sp.—Riedl, 1963:131, pl. 38 [incorrect subsequent spelling].

Sertularia secunda—Mammen, 1965:296 [incorrect subsequent spelling].

Plumularia catharina v. *acaule* Redier, 1967:402 [not *Plumularia catharina* Johnston, 1833].

Antenella secondaria—Patriti, 1970:57, fig. 81 [incorrect subsequent spelling].

Antennella secundaria dubiaformis—Watson, 1973:183, figs. 45–46.

Antennella secundaria secundaria—Zoological Record, 1980:61.

Anisocalix secundaria—Gili, 1982:79 [incorrect subsequent spelling].

Halopteris secundaris—Antsulevich, 1983:1145, fig. 1b [incorrect subsequent spelling].

Halopteris (*Antennella*) *secundaris*—Antsulevich, 1987:46 [incorrect subsequent spelling].

Antennella sp. Calder, 1993:68 [part].

TYPE LOCALITY

"Habitat in mari mediterraneo" (Gmelin, 1791:3854).

MATERIAL EXAMINED

Whalebone Bay, on rock, –3 m, 4 March 1982, one colony, 13 mm high, without gonophores, ROMIZ B114. Atlantic Ocean, 2 km off Castle Roads, on calcareous rubble, 60–90 m, 3 September 1977, one colony, 6 mm high, without gonophores, ROMIZ B115. Atlantic Ocean, 2 km SE of Castle Roads, on calcareous rubble, –73 m, 1 July 1983, two colonies, up to 7 mm high, without gonophores, ROMIZ B443. Atlantic Ocean, 2.5 km SSE of Castle Roads, on a bryozoan, –91 m, 9 April 1992, one colony, 11 mm high, with gonophores, ROMIZ B444. Atlantic Ocean, 2 km SE of Castle Roads, on a hydroid stem, –91 m, 8 April 1992, one colony, 8 mm high, without gonophores, ROMIZ B445. Challenger Bank, on calcareous rubble, –70 m, 3 October 1984, two colonies, up to 8 mm high, without gonophores, ROMIZ B446.

DESCRIPTION

Colonies up to 13 mm high, with hydrocladia arising directly from a creeping hydrorhiza. Basal part of hydrocladium stalklike, with one or more athecate internodes of varied length, typically long and tubular, 53–128 μm in diameter, occasionally with one or two short internodes and with distal part clearly regenerated; distalmost node oblique, all others transverse; nematothecae typically scarce or absent basally, more frequent and regularly placed distally. Distal part of hydrocladium divided into as many as 16 alternating thecate and athecate internodes by distinct oblique and less distinct transverse nodes; sometimes with two or more athecate internodes in sequence. Hydrocladia unbranched, or branched up to three times; branches with first internode long, stalklike, athecate; remainder of branch with alternating thecate and athecate internodes, resembling main hydrocladium, originating from a small apophysis inserted at distal end of an athecate internode, given off from back of internode, colony thus appearing dichotomously branched. Apophyses short, stump-shaped; nematothecae and mamelon absent. Thecate internodes 298–531 μm long, each with an oblique node at proximal end, a nearly transverse node at distal end, a median inferior nematotheca, a pair of lateral nematothecae each borne on a prominent peduncle, and a median superior nematotheca arising in axil between adcauline hydrothecal wall and internode. Athecate internodes beyond base 336–997 μm long, each with an almost straight node proximally, an oblique node distally, and typically with two or three median nematothecae. All nematothecae bithalamic, considered movable, scoop- to cone-shaped; large except for smaller median superior nematothecae; lateral nematothecae typically reaching to or nearly to hydrothecal rim. Hydrothecae 149–298 μm deep, cup-shaped, axis decidedly oblique to that of internode; adcauline wall adnate to internode for about half to two-thirds of length, free part concave and diverging from internode; abcauline wall convex basally, nearly straight distally, typically with thickened perisarc; margin entire, slightly flaring, perpendicular or nearly so to axis of hydrotheca, aperture circular, diameter from adcauline to abcauline wall 168–252 μm; intrathecal septum lacking. Hydranth with about 16 filiform tentacles.

Gonophores fixed sporosacs. Female gonothecae pear-shaped, about 500 μm long, 280 μm wide, aperture diameter 158 μm; each gonotheca arising via a two-segmented pedicel from proximal end of thecate internode, pedicel inserting near base of hydrotheca, and to one side of median; perisarc of moderate thickness; basal region bearing two large bithalamic nematothecae. Male gonothecae not seen.

REMARKS

The appellation *Sertularia secundaria* Gmelin, 1791, has long been recognized as the earliest available name of this hydroid. According to Cornelius (1995), Cavolini's (1785) prior name for the species, "La Sertolara secondaria," was not binominal and therefore nomenclaturally unavailable (ICZN, 1985, Art. 11c). Although the specific name has subsequently been combined with various nominal genera, it is now most often assigned to *Antennella* Allman, 1877 (e.g., Millard, 1975; Mergner and Wedler, 1977; Vervoort and Vasseur, 1977; Gravier-Bonnet, 1979; Boero, 1981; Hirohito, 1983; Altuna et al., 1983; Rho and Park, 1986; Yamada and Kubota, 1987; Rees and Vervoort, 1987; Gili, Vervoort, and Pagès, 1989; Ryland and Gibbons, 1991; Ramil and Vervoort, 1992a; Cornelius, 1995).

Hincks (1868) assigned a "stemless" hydroid resembling *Sertularia secundaria* to *Plumularia catharina* Johnston, 1833, and concluded that their names were synonymous. These are now regarded as separate species, and Hincks's stemless form is considered to have been referable to *Antennella secundaria* (e.g., Stechow, 1923a, 1925b; Rees, 1957; Redier, 1967; Fey, 1969; Cornelius, 1995).

Allman (1877) founded the genus *Antennella* for *A. gracilis*, a hydroid from Carysfort Reef, Florida, having "simple stems." He recognized that several hydroids, including *Sertularia secundaria*, *Antennularia cyathifera* Dana, 1846, and the stemless form assigned by Hincks (1868) to *Plumularia catharina*, were almost certainly referable to the genus as well. *Antennella gracilis* was

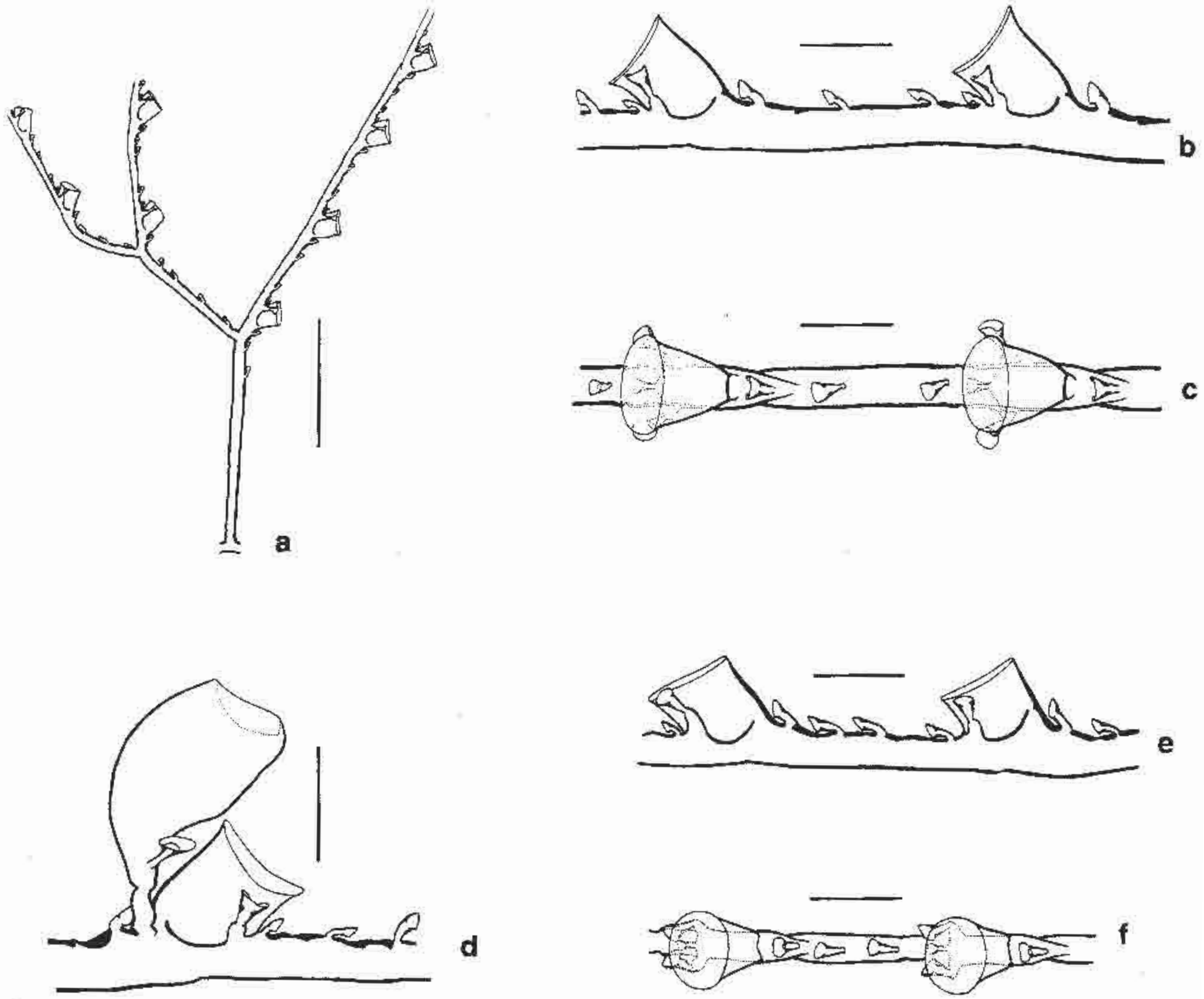

FIG. 7. *Antennella secundaria: a,* colony with branched hydrocladium, ROMIZ B443; *b,* part of hydrocladium, lateral view, with two hydrothecae, ROMIZ B444; *c,* part of hydrocladium, front view, with two hydrothecae, ROMIZ B444; *d,* part of hydrocladium, lateral view, with hydrotheca and gonotheca, ROMIZ B444; *e,* part of hydrocladium, lateral view, with two hydrothecae, ROMIZ B114; *f,* part of hydrocladium, front view, with two hydrothecae, ROMIZ B114. Scale for *a* equals 1 mm; scales for *b–f* equal 0.25 mm.

regarded as conspecific with *A. secundaria* by Neppi (1918), although Bedot (1914) maintained earlier that there was insufficient knowledge to judge whether they were conspecific. Fraser (1944:315) indicated that *A. gracilis* differed from *A. secundaria* in having a fully developed superior nematotheca, located some distance from the hydrotheca, instead of a small axillary one. Examination of the type of *A. gracilis* (MCZ, no catalogue number) revealed that Fraser's interpretation, and Allman's (1877) original illustration, were incorrect in the matter. Although now difficult to see in material that appears to have at some time been dry, small axillary nematothecae were found in a cleared and stained preparation. *Antennella gracilis* and *A. secundaria* seem otherwise alike, and I concur with Neppi (1918), and with Cornelius (1995), that they are conspecific. Together in the same bottle with type material of *A. gracilis* were hydroids labelled "*Monostachas* [*sic*] *dichotoma* Allm." *Monostaechas dichotoma* Allman, 1877, was reported from a different location and depth than *A. gracilis*, and the samples in which they were found appear to have been accidentally combined.

Antsulevich (1983) included *Antennella avalonia* Torrey, 1902, from Catalina Island, California, in the synonymy of *A. secundaria* (as *Halopteris secundaris*). Fraser (1946) recognized that the two were similar, but distinguished *A. avalonia* based on supposed differences in colony size, length of nodes, location of hydrothecae on thecate internodes, nematophore arrangement, and gonophore shape. Earlier, Bedot (1917) had suggested that *A. avalonia* was conspecific with *A. siliquosa* Hincks, 1877. The status of *A. avalonia* remains unclear.

Antennella natalensis Warren, 1908, from South Africa was regarded as conspecific with *A. secundaria* by Ritchie (1910a, 1910b). His conclusion, widely accepted (e.g., Billard, 1913; Bedot, 1914, 1917, 1921a; Stechow, 1919a, 1925b; Millard, 1958, 1975; Pennycuik, 1959; Van Gemerden-Hoogeveen, 1965; Mammen, 1965; Rees and Thursfield, 1965; Millard and Bouillon, 1973; Gili, 1982; Rees and Vervoort, 1987), is followed in the synonymy above.

Watson (1973) relegated *Plumularia dubiaformis* Mulder and Trebilcock, 1911, from Australia to a subspecies of *Antennella secundaria*. Stechow and Müller (1923) and Hirohito (1974) considered the two to be identical. Vervoort and Vasseur (1977) also held that there was no reason to recognize a distinct subspecies for the Australian hydroid. Earlier, Billard (1913), Bedot (1917), and Blackburn (1938) had implied that *P. dubiaformis* and *A. secundaria* were probably coterminous.

Leloup (1938b) has been followed here in considering *Antennella paucinoda* Fraser, 1935, from Sagami Bay, Japan, as conspecific with *A. secundaria*. The indistinctness of the nodes in Fraser's material was attributed by Leloup to the age of the colonies. Nevertheless, *A. paucinoda* was treated as a valid species by Yamada (1959).

Cornelius (1995) regarded *Halopteris diaphana* (Heller, 1868), *H. cornucopiae* (Hincks, 1872b), and *H. alternata* (Nutting, 1900) as conspecific, and I agree (see *Halopteris diaphana*, Remarks). However, he assigned all three to the synonymy of *Antennella secundaria*, regarded here as a different species. *Halopteris diaphana* differs from *A. secundaria* in lacking a reduced median superior nematotheca in the axil between adcauline hydrothecal wall and internode (e.g., Van Gemerden-Hoogeveen, 1965; Ramil and Vervoort, 1992a). The two usually differ as well in colony form, with hydrocladia typically arising from a hydrocaulus in *H. diaphana* and directly from the hydrorhiza in *A. secundaria*. Cornelius (1995) also included *Plumularia siliquosa* Hincks, 1877, in the synonymy of *A. secundaria*. *Antennella siliquosa* is regarded here as a valid species, differing from *A. secundaria* in having all or nearly all of its hydrocladial internodes thecate (see *Halopteris diaphana*, Remarks).

Billard (1910) and Ritchie (1910a) considered Bale's (1884) *Plumularia campanula* var. *B*, an unbranched halopteridid described earlier by Bale (1882) as *Plumularia indivisa*, to be indistinguishable from *Antennella secundaria*. Bale (1913) emphasized that both the branched and unbranched varieties of *Plumularia campanula* Busk, 1852, now commonly assigned to *Halopteris* Allman, 1877, differ from *A. secundaria* in nematotheca shape and arrangement. The two have been widely recognized as different species in recent literature (for extensive references on both, see Rees and Vervoort, 1987).

Colonies of *Antennella secundaria* from Bermuda were quite varied in morphology, particularly in length and diameter of hydrocladial pedicels, length of athecate internodes, size and depth of hydrothecae, and thickness of hydrothecal and internodal perisarc (see also Pennycuik, 1959; Millard, 1975; Gravier-Bonnet, 1979). Moreover, previous accounts and illustrations indicate that numbers of nematothecae on athecate internodes vary in the species (e.g., Pennycuik, 1959; Hirohito, 1974; Millard, 1975; Vervoort and Vasseur, 1977; Rho and Park, 1986). A morphotype from the Indo-west-Pacific having exceedingly long lateral nematothecae was assigned to *A. secundaria* by authors including Billard (1913), Millard (1975), and Rees and Vervoort (1987). However, Mammen (1965) considered Billard's (1913) hydroid to be more like *Antennella allmani* Armstrong, 1879.

Antennella secundaria was found around Bermuda during this study over a depth range extending from 3 to 91 m, and from depths exceeding 100 m down the Bermuda slope (Calder, 1993). Occasional colonies from offshore waters (ROMIZ B443, ROMIZ B444, ROMIZ B446) were dichotomously branched (Fig. 7a), as in some hydroids of *A. quadriaurita* Ritchie, 1909a, thus resembling species assigned to *Monostaechas* Allman, 1877. Similarly branched colonies have been described previously in this species (e.g., Billard, 1913; Van Gemerden-Hoogeveen, 1965; Millard and Bouillon, 1973; Millard, 1975; Vervoort and Vasseur, 1977).

REPORTED RANGE

Bermuda: off Castle Roads (Calder, 1991a, as *Antennella gracilis*); exposed bays, reefs, deeper coastal waters, banks, and upper slope (>100 m) of Bermuda Pedestal (Calder, 1993, as both *Antennella secundaria* and *Antennella* sp. [part]).

Circumglobal distribution: western Atlantic (Van Gemerden-Hoogeveen, 1965); eastern Atlantic (Gili, Vervoort, and Pagès, 1989); Indian Ocean (Rees and Vervoort, 1987); western Pacific (Rho and Park, 1986); eastern Pacific (Fraser, 1948, as *Antennella gracilis*).

Genus *Halopteris* Allman, 1877

Halicornaria Hincks, 1865:409.
Halicorneria Parfitt, 1866:11 [incorrect subsequent spelling].
Halopteris Allman, 1877:32.
Heteroplon Allman, 1883:31.

Polysiphonia von Lendenfeld, 1885b:641 [not *Polysiphonia* Hertwig, 1882 (Anthozoa)].

Acladia Marktanner-Turneretscher, 1890:261.

Halopetris Wallace, 1909:137 [incorrect subsequent spelling].

Heterophon Billard, 1913:22 [incorrect subsequent spelling].

Thecocaulus Bale, 1915:294.

Heterotheca Stechow, 1921a:260.

Tecocaulus Riedl, 1959:684 [incorrect subsequent spelling].

Heteropolon Mammen, 1965:304 [incorrect subsequent spelling].

Theocaulus Schmidt, 1972:43 [incorrect subsequent spelling].

Halicornis Van Praët, 1979:934 [incorrect subsequent spelling].

DIAGNOSIS

Colonies typically erect; hydrocauli monosiphonic or less frequently polysiphonic with an axial tube, unbranched or sparsely branched, arising from a creeping or rootlike hydrorhiza, often with a hinge-joint near base. Hydrocladia alternate, or in opposite pairs, or opposite basally and alternate distally, in one plane; almost always unbranched. Hydrothecae cup-shaped, on hydrocaulus and hydrocladia; margin with a median abcauline cusp, or entire. Nematothecae polymorphic, with fixed and movable ones on a given colony; either all bithalamic, or both bithalamic and monothalamic; lateral nematothecae flanking each hydrotheca, typically borne on prominent peduncles adhering to hydrothecal wall.

Gonophores fixed sporosacs. Gonothecae solitary, arising from hydrocaulus or hydrocladia, with or without nematothecae; not protected by corbulae or other phylactocarps.

TYPE SPECIES

Halopteris carinata Allman, 1877, by monotypy.

REMARKS

In founding the genus *Halopteris*, Allman (1877) remarked that it was intermediate in form between *Aglaophenia* Lamouroux, 1812, and *Plumularia* Lamarck, 1816. He noted that the general appearance of the paired lateral nematothecae, and the fixed median inferior nematothecae, approached that of species assigned to *Aglaophenia*. In contrast, the presence of azygous hydrocladial nematothecae, more widely separated hydrothecae, and essentially entire hydrothecal margins were more like those in *Plumularia*. Allman's conclusions are basically upheld here, with the family Halopterididae Millard, 1962, regarded as intermediate between the Plumulariidae McCrady, 1859, and the Aglaopheniidae Marktanner-Turneretscher, 1890.

The scope of the genus *Halopteris* adopted in this report is essentially that put forward by Totton (1930), refined by Millard (1962, 1975), and followed by Bouillon (1985) and others. It may be too broad. In particular, the question arises whether species with entire hydrothecal margins (e.g., *Plumularia catharina* Johnston, 1833; *Anisocalyx diaphanus* Heller, 1868) should be included in the same genus with those having a median abcauline cusp (e.g., *Halopteris carinata* Allman, 1877). More focus on characters of the type species, *H. carinata*, and especially on its cusped hydrothecal margin, seems necessary in diagnoses of the genus.

The now widely familiar generic name *Halopteris* of Allman (1877) is predated by *Halicornaria*, used by Hincks (1865) in the combination *Halicornaria* (*Plumularia*) *catherina* (lapsus for *catharina*). The name *Halicornaria* was ascribed to G. Busk by Hincks (1868) and later by Allman (1874a), who used the name in reference to a different taxon (see Genus *Gymnangium*, Remarks). However, Busk's use of *Halicornaria* was limited to an unpublished manuscript, and the name was first made available in Hincks's (1865) work. *Plumularia catharina* and *Halopteris carinata*, type genera of *Halicornaria* and *Halopteris* respectively, are now usually regarded as congeneric (e.g., Totton, 1930; Millard, 1962; Vervoort, 1968). Assuming this view to be correct, the familiar name *Halopteris* is threatened by *Halicornaria*, a name most often used in the invalid meaning of Allman (1874a) for an aglaopheniid genus. To avoid nomenclatural confusion, current useage is maintained here pending resolution of the problem.

Allman (1883) established *Heteroplon* to accommodate *H. pluma* Allman, 1883, from Bass Strait, Australia. *Heteroplon pluma* has been considered conspecific with *Halopteris glutinosa* (Lamouroux, 1816) (e.g., see Billard, 1909, 1910; Stechow, 1925b; Schmidt, 1972; Millard, 1975). *Heteroplon* was regarded as a subgenus of *Plumularia* by Stechow (1925b) and as a valid genus by Mammen (1965), but I follow authors including Millard (1975) and Bouillon (1985) in regarding *Heteroplon* as a junior subjective synonym of *Halopteris*.

Polysiphonia was proposed by von Lendenfeld (1885b) as the name of a subgenus of *Plumularia*. One of the four nominal species originally assigned to it, *Plumularia campanula* Busk, 1852, was designated above as its type species (see Genus *Plumularia*, Remarks). As noted there, *Plumularia campanula* is now generally referred to *Halopteris*. *Polysiphonia* von Lendenfeld, 1885b, an invalid junior homonym of *Polysiphonia* Hertwig, 1882, is therefore included here as a synonym of *Halopteris*.

The binomen *Acladia africana* Marktanner-Turneretscher, 1890, was erected for a supposed new nominal genus and species of hydroid from Algoa Bay, South

Africa. Millard (1962) presented evidence that *A. africana* was conspecific with *Plumularia tuba* Kirchenpauer, 1876, a species currently assigned to *Halopteris* (e.g., Millard, 1962, 1975). *Acladia* Marktanner-Turneretscher, 1890, was included in the synonymy of *Heteroplon* by Stechow (1925b), and in that of *Halopteris* by Millard (1962, 1975) and Bouillon (1985).

Bale (1915) applied the name *Thecocaulus* to a so-called section of the genus *Plumularia* within which *P. catharina* and *P. campanula* were considered "typical." Stechow (1923a) regarded *Thecocaulus* as a valid genus, but concluded later (Stechow, 1926) that it was congeneric with *Halopteris*. Totton (1930) subsequently designated *P. catharina* as the type species of *Thecocaulus*, and also relegated it to the synonymy of *Halopteris*. That conclusion was followed by Millard (1962, 1975), Bouillon (1985), and others, and is accepted here, although the type species of the two nominal genera differ in the morphology of their hydrothecae and nematothecae.

Heterotheca was introduced as a genus name by Stechow (1921a) for *Plumularia sulcata* Lamarck, 1816. Three other nominal species, *P. campanula*, *P. buskii* Bale, 1884, and *P. zygocladia* Bale, 1914, were also originally assigned to it. Vervoort and Vasseur (1977) argued that *Heterotheca* was congeneric with *Halopteris*, an opinion upheld by Hirohito (1983). Earlier, the type species of *Heterotheca*, *P. sulcata*, had been assigned to *Halopteris* by Millard (1962:269) and Rees and Thursfield (1965:161).

Gattya Allman, 1885, seems closely related to *Halopteris*, if not congeneric with it. The two are usually differentiated on the nature of the hydrothecal margin, the rim of *Gattya* being clearly dentate and that of *Halopteris* purportedly being entire (e.g., see Millard, 1975; Bouillon, 1985). However, a median abcauline cusp is present on the hydrothecal margin in hydroids of *H. carinata*, the type species of *Halopteris*. Millard (1962) acknowledged that it was a matter of opinion whether the difference was sufficient basis for separating the two nominal genera. She retained *Gattya* as valid, however, and her position is adopted for the present. As for *Paragattya* Warren, 1908, its type species (*P. intermedia* Warren, 1908) was shown by Millard (1962) to be conspecific with the type species of *Gattya* (*G. humilis* Allman, 1885).

Certain species assigned to *Halopteris* are known to vary considerably in morphology. Examples of morphologically varied characters, discussed by Millard (1975) and Vervoort and Vasseur (1977), included length and thickness of the hydrocaulus, prominence and position of cauline nodes, arrangement of hydrocladia, numbers of nematothecae on athecate internodes, and size and shape of hydrothecae.

Halopteris carinata Allman, 1877

Fig. 8

Halopteris carinata Allman, 1877:33, pl. 19, figs. 3–7.

Halopetris carinata—Wallace, 1909:137 [incorrect subsequent spelling].

Halopteris (*Plumularia*) *carinata*—Bedot, 1923:216, figs. 3A–C.

Plumularia carinata—Bedot, 1921a:26.

Halopteris carinatus—Fraser, 1944:24 [incorrect subsequent spelling].

TYPE LOCALITY

Florida, "off Carysfort Reef, from a depth of 35 fathoms [64 m]" (Allman, 1877:33).

MATERIAL EXAMINED

Off St. George's Island, 1 km NE of Town Cut, on vertical rock wall, –20 m, 30 July 1982, one colony with two hydrocauli, 4 cm high, without gonophores, coll. E. Ruppert, ROMIZ B284.

DESCRIPTION

Colony 4 cm high, with a rootlike hydrorhiza. Hydrocaulus monosiphonic, unbranched, straight; perisarc thick basally, thinner distally. Proximal end of hydrocaulus with several internodes of varied length, up to 0.5 mm in diameter, marked by straight to slightly oblique nodes, each internode with an annulus at each end and with three to 14 median to fronto-laterally placed, bithalamic, movable, scoop-shaped nematothecae; hydrothecae and hydrocladial apophyses lacking. Hydrocaulus beyond proximal end divided at more or less regular intervals into internodes by slightly oblique nodes; these internodes 0.73–1.20 mm long, up to 0.47 mm wide, each with a proximal median nematotheca, a hydrotheca, two lateral nematothecae, four to six distal nematothecae arranged in two or three fronto-lateral pairs, no median superior nematothecae or a single one, one or infrequently two apophyses given off laterally to hydrotheca, and an annulus at each end. Apophyses short, stump-shaped, typically given off from alternate sides, arranged in one plane, each apophysis supporting a hydrocladium (except where broken off); nematothecae absent, mamelon absent. Hydrocladia typically unbranched, up to 2.8 mm long, each with as many as seven hydrothecae; most proximal internode of hydrocladium athecate, about 310 µm long, with a straight node proximally, an oblique node distally, and one bithalamic, movable nematotheca; remaining internodes of hydrocladium typically thecate; sometimes with thecate and athecate internodes alternating. Thecate internodes 391–485 µm long, each with a large median inferior nematotheca, a hydrotheca, two lateral nematothecae each borne on a long peduncle adhering to hydrothe-

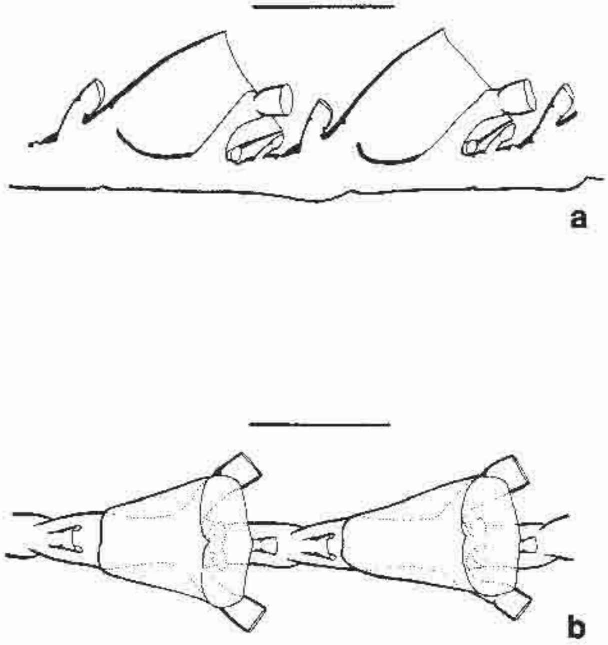

FIG. 8. *Halopteris carinata*, ROMIZ B284: *a*, part of hydrocladium, lateral view, with two hydrothecae; *b*, part of hydrocladium, front view, with two hydrothecae. Scales equal 0.25 mm.

cal wall, a pair of reduced axillary nematothecae between internode and free adcauline wall of hydrotheca, a small median superior nematotheca, and decidedly oblique nodes at proximal and distal ends; sometimes an indistinct straight node just distal to hydrotheca marking off an athecate internode bearing a median nematotheca, such athecate internodes 200–312 µm long, each with an almost straight node proximally and a decidedly oblique node distally. Median inferior nematothecae bithalamic, margin scoop-shaped, considered immovable; lateral nematothecae cup-shaped with circular rim, bithalamic, immovable, reaching beyond margin of hydrotheca; reduced axillary nematothecae monothalamic, immovable; median superior nematothecae bithalamic, margin scoop-shaped, movable. Hydro-thecae large, 233–256 µm deep, cup-shaped to bell-shaped, axis oblique to that of internode; adcauline wall adnate to internode for about half to two-thirds of length, convex proximally, straight to slightly concave distally; abcauline wall convex, with a slight carina; margin perpendicular or nearly so to axis of hydrotheca, entire except for a small median abcauline cusp; aperture irregularly oval in outline, diameter from abcauline to adcauline wall 186–224 µm; intrathecal septum lacking.

Gonophores not seen.

REMARKS

Halopteris carinata Allman, 1877, was originally described from material collected in the Straits of Florida by L. F. de Pourtalès of the United States Coast Survey. Allman's (1877) type material lacked gonothecae, but the species is readily distinguished by its cup-shaped lateral nematothecae, each of which occurs at the end of a long peduncle; by the small median abcauline cusp on the otherwise entire hydrothecal margin; and by the weakly developed hydrothecal carina. Gonothecae were subsequently described by Nutting (1900), and first illustrated by Vervoort (1968). In being both morphologically distinct and relatively restricted in range, and in being the type species of a widely recognized genus, *H. carinata* has had an uncomplicated taxonomic and nomenclatural history.

Illustrations of *Halopteris carinata* by Allman (1877) depict hydrothecae that are more flattened in frontal aspect than in material examined here from Bermuda. Hydrothecae of hydroids studied by Vervoort (1968) from Tortugas, Florida, and from St. Thomas, West Indies, were also less flattened than indicated in Allman's original description of *H. carinata*. No taxonomic significance was accorded this apparent difference by Vervoort, who concluded that Allman's drawings were likely made from specimens distorted by cover slips. Hydroids from the northeast rim of the Bermuda Platform resembled those of Allman (1877) and were especially similar to those of Vervoort (1968); they have thus been assigned to *H. carinata*.

Hydroids of *Halopteris carinata* have been reported only from the warm western Atlantic. The species is quite widespread in the Caribbean region (Fraser, 1943; 1944; 1947; Vervoort, 1968; Wedler, 1975; Spracklin, 1982; Florez Gonzalez, 1983; Bandel and Wedler, 1987). It has also been recorded from Bermuda (Calder, 1993), south Florida (Allman, 1877; Wallace, 1909; Stechow, 1926), the Bahamas (Nutting, 1895, 1900), and Brazil (Calder and Maÿal, unpublished data).

Spracklin (1982) found *Halopteris carinata* to be frequent on the barrier reef of Belize. Hydroids were common in the low-relief spur and groove zone, on the outer ridge, in sand troughs, and on the fore-reef slope, as well as on patch reefs. Wedler (1975) reported the species on sponges and gorgonians from hard bottoms in Colombia. The known bathymetric distribution of *H. carinata* extends from shallow subtidal waters to 161 m (Fraser, 1944; Vervoort, 1968).

REPORTED RANGE

Bermuda: deeper coastal substrates (Calder, 1993).

Circumglobal distribution: western Atlantic (Vervoort, 1968).

Halopteris diaphana **(Heller, 1868)**

Fig. 9

Anisocalyx diaphanus Heller, 1868:42, pl. 2, fig. 5.

Plumularia cornu-copiae Hincks, 1872b:389, pl. 21, figs. 1–3 [incorrect original spelling].

Plumularia cornucopiae—Verrill, 1874:732 [justified emendation].

Plumularia diaphana—Kirchenpauer, 1876:27, pl. 1, fig. 13.

Plumularia catharina var. *alternans* Driesch, 1890:661. —Kühn, 1909:445 [not *Plumularia catharina* Johnston, 1833].

Plumularia cornu copiae—Marktanner-Turneretscher, 1890:257 [incorrect subsequent spelling].

Plumularia alternata Nutting, 1900:62, pl. 4, figs. 1–2.

?*Plumularia buski*—Hartlaub, 1901:374, pl. 22, figs. 22, 32, 36 [?not *Plumularia buskii* Bale, 1884].

Plumularia catharina—Broch, 1913:4, fig. 1. —Timmermann, 1932:296. —Burkenroad, *in* Parr, 1939:24. —Friedrich, 1969:199. —Morris and Mogelberg, 1973:19. —Butler et al., 1983:42 [not *Plumularia catharina* Johnston, 1833].

Anisocalyx (*Plumularia*) *diaphanus*—Bedot, 1914:93.

Schizotricha diaphana—Bedot, 1921a:12.

not *Plumularia alternata*—Jarvis, 1922:345, pl. 25, figs. 16A–B [part] [=*Halopteris glutinosa* (Lamouroux, 1816)].

Thecocaulus diaphanus—Stechow, 1923a:224.

Plumularia sp. nr. *alternata*—Gravely, 1927:16, pl. 3, figs. 19–20.

Antenella diaphana forma *typica* Broch, 1933:24 [incorrect subsequent spelling].

Plumularia cornucopia—Broch, 1933:24 [incorrect subsequent spelling].

?*Antenella diaphana* forma *siliquosa*—Broch, 1933:26 [not *Antennella siliquosa* (Hincks, 1877)] [incorrect subsequent spelling].

Antenella diaphana—Leloup, 1934:15 [incorrect subsequent spelling].

?not *Antenella diaphana* forme *siliquosa*—Leloup, 1935:53 [=?*Antennella* sp.] [incorrect subsequent spelling].

Anisocalyx diaphana—Fraser, 1944:342.

?*Schizotricha billardi* Vannucci, 1951:88.

Polyplumaria diaphana—Picard, 1951b:261.

Tecocaulus diaphanus—Riedl, 1959:684 [incorrect subsequent spelling].

Antennella diaphana—Vervoort, 1959:289.

not *Antennella diaphana* f. *siliquosa*—Vervoort, 1959:286, figs. 43a–b [=?*Antennella siliquosa* (Hincks, 1877)].

Antennella diaphana f. *typica*—Vervoort, 1959:289.

Halopteris diaphana—Pennycuik, 1959:177.

Antennella diaphana diaphana—Van Gemerden-Hoogeveen, 1965:49, figs. 23–28.

Thecocarpus diaphanus—Mammen, 1965:304.

Halopteris diaphana diaphana—Vervoort, 1968:58, fig. 27.

not *Halopteris diaphana siliquosa*—Vervoort, 1968:61 [=*Antennella siliquosa* (Hincks, 1877)].

Antenella diaphana diaphana—Leloup, 1974:47, fig. 42 [incorrect subsequent spelling].

not *Halopteris diaphana* f. *siliquosa*—García, Aguirre, and Gonzalez, 1978:45, fig. 19. —Ramil and Vervoort, 1992a:148, fig. 38a [=?*Antennella siliquosa* (Hincks, 1877)].

Anisocalix diaphana—Izquierdo, García-Corrales, and Bacallado, 1986:51 [incorrect subsequent spelling].

Thecocaulos diaphanus—Pires et al., 1992:6 [incorrect subsequent spelling].

TYPE LOCALITY

Capocesto, Adriatic Sea (Heller, 1868:42).

MATERIAL EXAMINED

Whalebone Bay, on pelagic *Sargassum*, 5 September 1977, one colony with several hydrocauli, up to 6 mm high, without gonophores, ROMIZ B119. Whalebone Bay, on *Cnidoscyphus marginatus*, –1 m, 7 September 1977, one colony, 13 mm high, without gonophores, ROMIZ B121. Castle Harbour, just W of Castle Roads, on benthic algae, –1 to –2 m, 30 July 1982, one colony, 10 mm high, without gonophores, ROMIZ B272. Stream Passage Cave (Harrington Sound), on rock, –1 m, 27 July 1982, one colony, 16 mm high, with developing gonophores, ROMIZ B276. Whalebone Bay, on *Pennaria disticha*, –1.5 m, 28 July 1982, one colony with several hydrocauli, up to 8 mm high, without gonophores, ROMIZ B278. Atlantic Ocean, 2 km SE of Castle Roads, on coral rubble, –73 m, 1 July 1983, one colony, 22 mm high, without gonophores, ROMIZ B437. Flatts Inlet, on pelagic *Sargassum natans*, 1 December 1989, one colony, with several hydrocauli, up to 9 mm high, without gonophores, ROMIZ B438. Atlantic Ocean, 2 km off Castle Roads, on algae on rhodoliths, –70 m, 13 May 1991, five colonies, up to 19 mm high, without gonophores, ROMIZ B439. Atlantic Ocean, 2.5 km SSE of Castle Roads, on rhodoliths, –60 m, two colonies, up to 29 mm high, without gonophores, ROMIZ B440.

DESCRIPTION

Colonies up to 29 mm high, with a creeping hydrorhiza. Hydrocaulus monosiphonic, unbranched, straight basally, geniculate distally, divided at regular intervals beyond basal region into internodes by distinct oblique nodes; most cauline internodes hydrothecate but shorter athecate ones also frequent, all cauline internodes with perisarc

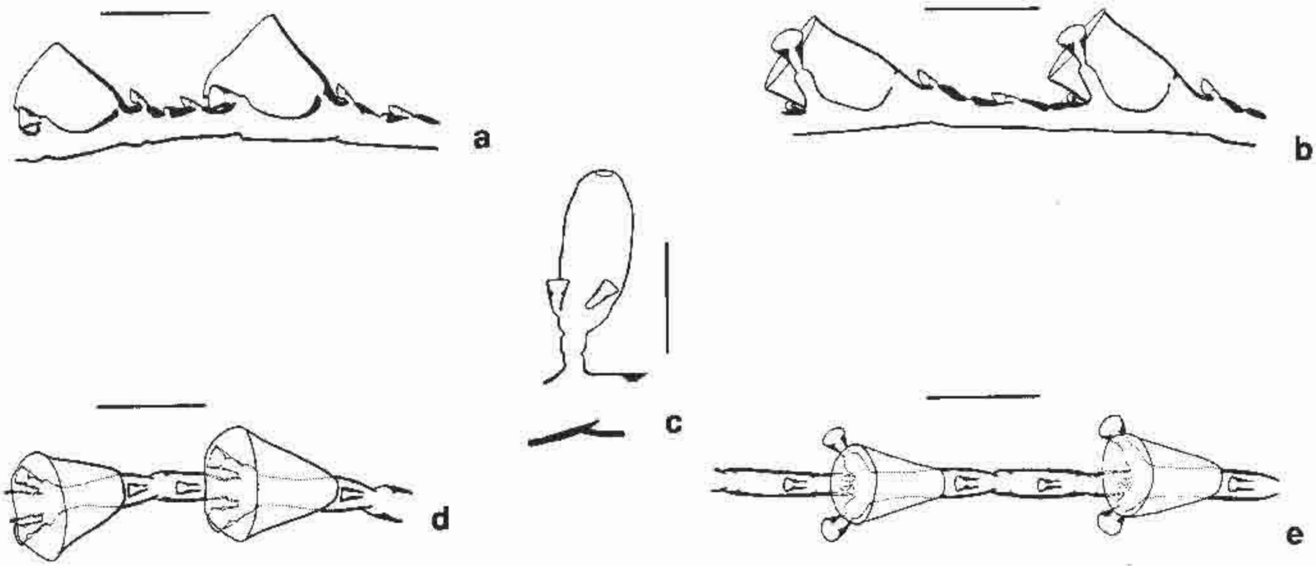

FIG. 9. *Halopteris diaphana: a,* part of hydrocladium, lateral view, with two hydrothecae, ROMIZ B438; *b,* part of hydrocladium, lateral view, with two hydrothecae, ROMIZ B439; *c,* gonotheca, ROMIZ B276; *d,* part of hydrocladium, front view, with two hydrothecae, ROMIZ B438; *e,* part of hydrocladium, front view, with two hydrothecae, ROMIZ B439. Scales equal 0.25 mm.

thickened near proximal and distal ends; hydrothecate cauline internodes 363–885 µm long, 93–186 µm wide, 70–177 µm wide at nodes, each with a proximal nematotheca, a hydrotheca, two lateral nematothecae, one to three distal nematothecae, and one or two apophyses given off laterally to hydrotheca; proximalmost hydrothecate internode of hydrocaulus typically with two opposite apophyses, second hydrothecate internode with one apophysis or less frequently with two opposite ones, remaining hydrothecate internodes typically with a single apophysis each, these apophyses given off alternately from each side. Apophyses short, stump-shaped, each supporting a hydrocladium; nematothecae typically absent, mamelon absent. Hydrocladia almost always unbranched, up to 5 mm long, directed outward at an angle of about 70° from axis of hydrocaulus, frontal side convex; most proximal internode short, 47–79 µm in length, demarcated by a straight node proximally and a slightly oblique node distally, hydrothecae and nematothecae lacking; remainder of hydrocladium typically divided into one to 10 alternating athecate and thecate internodes; sometimes with two or more thecate internodes or with two or more athecate internodes in sequence. Thecate internodes 280–671 µm long, each with a decidedly oblique node proximally, a nearly straight node distally, a median inferior nematotheca, a large hydrotheca, two lateral nematothecae each borne on a variably developed peduncle, and with or without a tiny median superior nematotheca in axil between internode and adcauline wall of hydrotheca; athecate internodes beyond most proximal one 149–359 µm long, each with an almost straight node proximally, a decidedly oblique node distally, and with one or less frequently two nematothecae. All nematothecae bithalamic, scoop-shaped to cone-shaped; median nematothecae considered immovable; lateral nematothecae movable, variably developed, sometimes reaching beyond margin of hydrotheca and sometimes not. Hydrothecae large, 186–242 µm deep, cup-shaped to bell-shaped, axis oblique to that of internode; adcauline wall adnate to internode for about two-thirds of length, convex proximally, straight to concave distally; abcauline wall nearly straight, or convex basally and concave distally; margin entire, flaring, perpendicular or nearly so to axis of hydrotheca, aperture circular, diameter 186–238 µm; intrathecal septum lacking. Hydranths with about 14 to 18 filiform tentacles.

Gonophores fixed sporosacs. Gonothecae clavate, about 375 µm long, 295 µm wide, aperture diameter 30 µm; each gonotheca arising via short pedicel from hydrocladial apophysis; perisarc thin; basal region bearing two nematothecae.

REMARKS

Anisocalyx diaphanus was originally described by Heller (1868) from a single hydroid specimen collected on the Dalmatian coast of the Adriatic Sea. Heller provided a sketch of the species, but no satisfactory figure of it under that specific name appeared until Stechow (1912) illustrated fertile material from Villefranche, France. The specific name has subsequently been combined with various plumularioid generic names, including *Plumularia* Lamarck, 1816; *Polyplumaria* G. O. Sars, 1874; *Halopteris* Allman, 1877; *Antennella* Allman, 1877; *Schizotricha* Allman, 1883; *Thecocarpus* Nutting, 1900; and *Thecocaulus* Bale, 1915. Most recent authors (e.g., Vervoort, 1968; Millard and Bouillon, 1973; García, Aguirre, and Gonzalez, 1978; Ryland and Gibbons, 1991; Cairns et al., 1991; Pires et al., 1992; Calder, 1993) have applied the binomen *Halopteris diaphana* to the species.

Driesch (1890) described a hydroid from the Adriatic Sea as *Plumularia catharina* var. *alternans*. Stechow (1919a) is followed here in assigning that record to the synonymy of *Halopteris diaphana*.

Stechow (1912) compared this species with *Plumularia alternata* Nutting, 1900, from the West Indies, and concluded that the two were likely conspecific. Later that same year, Billard (1912) assigned material from Roscoff, France, to *P. alternata*. Differences used to distinguish *Plumularia alternata*, as well as *P. cornucopiae* Hincks, 1872b, from *Halopteris diaphana* were reviewed in detail by Bedot (1914). Bedot discounted the taxonomic significance of variable characters purportedly separating these species, such as cauline internode length, general hydrothecal size, prominence of the peduncles supporting lateral nematothecae, and number of nematothecae on cauline athecate internodes. He concluded that the three were coterminous, an opinion upheld by authors including Stechow (1919a), Hamond (1957), and Cornelius (1995). The warm western Atlantic *P. alternata* was also referred to *P. diaphana* by Fraser (1944).

Hartlaub (1901) assigned hydroids from Laysan Island, Pacific Ocean, to *Plumularia buskii* Bale, 1884. Billard (1913:31, footnote) concluded that Hartlaub's material was probably referable instead to *Plumularia alternata* (=*Halopteris diaphana*). I follow Billard, and Vannucci Mendes (1946), in regarding Hartlaub's record of *P. buskii* as a possible misidentification of the present species.

Broch (1913) identified hydroids on floating seaweed from the Sargasso Sea as *Plumularia catharina* Johnston, 1833. The description and illustration of this material indicate that Broch's material was almost certainly the same species herein identified as *Halopteris diaphana*. Broch's suggestion that *P. alternata* should be referred to *P. catharina* was refuted, with justification, by Stechow (1919a). Other reports of *Halopteris catharina* from pelagic *Sargassum* in the North Atlantic (e.g., Timmermann, 1932; Burkenroad, *in* Parr, 1939; Friedrich, 1969; Morris and Mogelberg, 1973; Butler et al., 1983) are likewise regarded here as misidentifications of *H. diaphana*. At Bermuda in the Sargasso Sea area, *Halopteris diaphana* has been reported on both *Sargassum fluitans* and *S. natans* (Calder, 1995); by contrast, *H. catharina* was not found there on either species.

Jarvis (1922) identified hydroids from several locations in the western Indian Ocean as *Plumularia alternata*. Millard (1962) reexamined the material and concluded that part of it was referable to *Halopteris glutinosa* (Lamouroux, 1816). Although Jarvis' record was questionably included in the synonymy of *H. diaphana* by Millard and Bouillon (1973), it was reassigned again to *H. glutinosa* by Millard (1975).

Broch (1933) regarded *Plumularia siliquosa* Hincks, 1877, from the coast of Guernsey as a form of the species that he called *Antenella* [*sic*] *diaphana*. The species described by Hincks (1877) lacked an erect hydrocaulus, typically present in *Halopteris diaphana*, and its hydrocladial internodes were all thecate instead of alternately athecate and thecate. In spite of its decidedly different colony construction, several authors have followed Broch in regarding *P. siliquosa* as a form of *H. diaphana* (e.g., Leloup, 1935; Vervoort, 1959, 1968; García, Aguirre, and Gonzalez, 1978; Ramil and Vervoort, 1992a). Cornelius (1995) regarded *P. siliquosa*, as well as *H. diaphana*, as conspecific with *Antennella secundaria* (Gmelin, 1791). I follow authors such as Stechow (1923a), Riedl (1959), Rees and Thursfield (1965), and Patriti (1970) in recognizing *Antennella siliquosa* as a valid species, distinct from *H. diaphana* and *A. secundaria*.

Stechow (1919a), Bedot (1921a, 1925), Bennitt (1922), and Vannucci (1949) regarded *Schizotricha tenella* (Verrill, 1874) as conspecific with *Halopteris diaphana*. *Schizotricha tenella* can be distinguished from *H. diaphana* in having (1) branched instead of unbranched hydrocladia, (2) hydrocladial internodes of three alternating types (short athecate, long athecate, and thecate) instead of two (athecate and thecate), and (3) larger colonies (Calder, 1983).

Fraser (1944), without explanation, referred Leloup's (1935) record of *Antenella* [*sic*] *diaphana* from the Caribbean to *Schizotricha tenella*. However, Van Gemerden-Hoogeveen (1965) reexamined Leloup's material and assigned it to *Antennella diaphana diaphana*. As for *S. tenella*, there now appear to be no valid records of it from the Caribbean region. The species is common to abundant in temperate coastal waters and estuaries of the east coast of the United States (Fraser, 1944; Calder, 1983), and has been collected from a coastal river system in Pernambuco state, Brazil (Calder and Maÿal, unpublished data).

Vannucci (1951) established *Schizotricha billardi* as a new name for material from Obock, Red Sea, that Billard (1904b) had identified as *Plumularia alternata*. The identity of Billard's hydroid had been questioned earlier by Bedot (1914), who suggested that it might represent a distinct variety or even a different species. However, Stechow (1919a) and Bedot (1925) assigned Billard's report of *P. alternata* to *P. diaphana*, and Vannucci's records of *S. billardi* from Brazil were considered referable to *Halopteris diaphana* by Pires et al. (1992).

Hydroids assigned to this species from Bermuda varied considerably in colony form. Those growing on pelagic *Sargassum* and on substrates exposed to wave action were small (6–13 mm high), internodes were short (Fig. 9a), lateral nematothecae barely if at all reached the hydrothecal margin, and a small median superior nematotheca was absent in the hydrothecal axil. Those collected in deeper waters offshore were taller (19–29 mm high), internodes were longer (Figs. 9b, 9d), lateral nematothecae often reached beyond the hydrothecal margin, and a small median superior nematotheca was often present in the hydrothecal axil. Such variations generally accord with differences in Caribbean material ascribed to *Halopteris diaphana* by Van Gemerden-Hoogeveen (1965) and Vervoort (1968). Although hydrocladia sometimes arise directly from the hydrorhiza in hydroids of this species (e.g., Van Gemerden-Hoogeveen, 1965), colonies from Bermuda were all plumose in form.

Reduction in size of hydroids on pelagic *Sargassum*, noted here for *Halopteris diaphana*, is frequent among invertebrate species associated with this substrate in the open North Atlantic (Ekman, 1953; Adams, 1960).

REPORTED RANGE

Bermuda: floating *Sargassum* and shallow inshore waters (Congdon, 1907, as *Plumularia alternata*; Bennitt, 1922, as *Plumularia diaphana*; Calder, 1986, 1993, 1995).

Circumglobal distribution: western Atlantic (Vervoort, 1968); eastern Atlantic (Izquierdo, García-Corrales, and Bacallado, 1986); Indian Ocean (Mammen, 1965, as *Schizotricha diaphana*); western Pacific (Pennycuik, 1959); eastern Pacific (Fraser, 1948, as *Plumularia diaphana*).

Family Aglaopheniidae Marktanner-Turneretscher, 1890

Aglaopheniidae Marktanner-Turneretscher, 1890:262.

Halicornariidae Marktanner-Turneretscher, 1890:277 [invalid name, type genus *Halicornaria* Allman, 1874a, a junior homonym of *Halicornaria* Hincks, 1865].

DIAGNOSIS

Colonies with hydrocauli erect, branched or unbranched, monosiphonic or polysiphonic, arising from a creeping hydrorhiza or from anchoring filaments. Hydrocladia alternate or opposite in one plane, or arranged spirally. Hydrothecae with or without marginal cusps, with or without an intrathecal septum, occurring only on hydrocladia. Nematophores with nematothecae, not as naked sarcostyles. Nematothecae well developed, monothalamic, immovable, those of cormidia typically at least partly fused to hydrothecae; each cormidium (part of a hydrocladium comprising an internode, a hydrotheca, and nematothecae) with one or more pairs of lateral nematothecae flanking a hydrotheca, and typically with an unpaired median inferior nematotheca that may be doubled or have two terminal apertures.

Gonophores fixed sporosacs or rarely liberated as medusoids; gonothecae solitary or aggregated, lacking nematothecae, either unprotected or protected by corbulae or other phylactocarps.

REMARKS

Allman (1883) subdivided the Plumulariidae McCrady, 1859, as broadly understood at the time, by recognizing the subfamily Eleutheroplea for species with "movable" nematothecae, and the subfamily Statoplea for those with "fixed" nematothecae (see Superfamily Plumularioidea, Remarks). As noted earlier, neither of these names, nor subsequent modifications of them, are available under the code (ICZN, 1985, Art. 11f).

Marktanner-Turneretscher (1890) acknowledged Allman's (1883) two major subdivisions of Plumulariidae sensu lato. In his classification, however, he included a more restricted family Plumulariidae under the Eleutheroplea, and founded two new family-group names (Aglaopheniidae and Halicornariidae) under the Statoplea. Although either Stechow (1911) or Broch (1918) has usually been credited as author of the name Aglaopheniidae, Marktanner-Turneretscher made the name available earlier. Broch contributed by providing a diagnosis of the Aglaopheniidae, and by strongly justifying its recognition as a family separate from the Plumulariidae. As discussed below (Subfamily Gymnangiinae, Remarks), the name Halicornariidae is invalid because its type genus is a junior homonym (ICZN, 1985, Art. 39).

The number of genera admitted to the Aglaopheniidae is still unsettled. Stechow (1923a), who recognized the group as a subfamily (Aglaopheniinae), assigned 15 nominal genera to it (*Aglaophenia* Lamouroux, 1812; *Lytocarpia* Kirchenpauer, 1872; *Macrorhynchia* Kirchenpauer, 1872; *Gymnangium* Hincks, 1874; *Cladocarpus* Allman, 1874a; *Nematophorus* Clarke, 1879; *Halicornopsis* Bale, 1882; *Acanthocladium* Allman, 1883; *Streptocaulus* Allman, 1883; *Monoserius* Marktanner-Turneretscher, 1890; *Nuditheca* Nutting, 1900; *Dinotheca* Stechow, 1911; *Haliaria* Stechow, 1921b; *Halicetta* Stechow, 1921b; and *Aglaria* Stechow, 1923b). Leloup (1932a) referred 12 nominal genera to the family (*Aglaophenia*, *Cladocarpus*, *Streptocaulus*, *Monoserius*, *Dinotheca*, and *Aglaria*, as well as *Aglaophenopsis* Fewkes, 1881; *Lytocarpus* Allman, 1883; *Pentandra* von Lendenfeld, 1884; *Thecocarpus* Nutting, 1900;

Nematocarpus Broch, 1918; and *Halicornaria* auct.). Bouillon (1985) also included 12 nominal genera in the Aglaopheniidae (*Aglaophenia*, *Gymnangium*, *Cladocarpus*, *Lytocarpus*, *Streptocaulus*, *Monoserius*, *Thecocarpus*, and *Nuditheca*, plus *Tetranema* Fraser, 1937 [not *Tetranema* Haeckel, 1879]; *Anarthroclada* Naumov, 1955; *Pentatheca* Naumov, 1955; and *Cladocarpoides* Bogle, 1984). The status of each of several nominal genera related to *Cladocarpus* was considered by Vervoort (1966) and Ramil and Vervoort (1992b). Besides *Cladocarpus*, Ramil and Vervoort recognized *Nematocarpus*, *Aglaophenopsis*, *Streptocaulus*, and *Cladocarpoides* as valid or provisionally so.

Of the 25 nominal genera referred to the taxon by these authors, 11 are assigned to the Aglaopheniidae here (*Aglaophenia*, *Macrorhynchia*, *Lytocarpia*, *Gymnangium*, *Cladocarpus*, *Aglaophenopsis*, *Acanthocladium*, *Streptocaulus*, *Pentandra*, *Monoserius*, and *Cladocarpoides*). Three are regarded as congeneric with *Gymnangium* (*Haliaria*, *Halicetta*, *Halicornaria* auct.), two with *Lytocarpia* (*Lytocarpus*, *Thecocarpus*), and one each with *Aglaophenia* (*Aglaria*), *Macrorhynchia* (*Nematophorus*), and *Aglaophenopsis* (*Nematocarpus*). Synonymies are discussed in more detail elsewhere in this report (see Subfamily Aglaopheniinae, Remarks; see also Genus *Gymnangium*, Remarks; Genus *Aglaophenia*, Remarks; and Genus *Macrorhynchia*, Remarks). *Halicornopsis* resembles some aglaopheniid genera, but seems to share more characters with kirchenpaueriids. It was included in the subfamily Kirchenpaueriinae by Millard (1975) and in the family Kirchenpaueriidae by Bouillon (1985), and is treated here as a kirchenpaueriid. *Dinotheca* was recognized as valid by Leloup (1932a) and Vervoort (1966), although they considered it close to *Cladocarpus*. Millard (1975), Bouillon (1985), and Rees and Vervoort (1987) regarded *Dinotheca* as congeneric with *Cladocarpus*. Ramil and Vervoort (1992a) implied that *Dinotheca* should be referred to *Streptocaulus* instead, based on the morphology of the phylactocarp. The name *Tetranema* Fraser, 1937, is an invalid junior homonym of *Tetranema* Haeckel, 1879 (ICZN, 1985, Art. 52), and is replaced by *Astrolabia* Naumov, 1955. *Nuditheca*, *Astrolabia*, *Pentatheca*, and *Anarthroclada* are referred here to the Halopterididae Millard, 1962, instead of the Aglaopheniidae (see Family Halopterididae, Remarks; Subfamily Gymnangiinae, Remarks).

Aglaopheniids range from high latitudes to the tropics, and from intertidal habitats to ocean trenches. As with plumularioids generally, however, they are predominantly warm-water hydroids. Off the Atlantic coast of North America, for example, only five species have been reported north of Cape Cod (Fraser, 1944) compared with 41 for the tropical western Atlantic (Bogle, 1975). Yet aglaopheniids are also represented overall by more species at depths of 200–1000 m in the western North Atlantic than any other hydroid family (Calder, unpublished data). The Aglaopheniidae was also the most diverse hydroid family in collections from depths of 200–6000 m by the Galathea Expedition (Vervoort, 1966).

The family Aglaopheniidae is represented by three genera in Bermuda, *Gymnangium* Hincks, 1874; *Aglaophenia* Lamouroux, 1812; and *Macrorhynchia* Kirchenpauer, 1872.

Subfamily Gymnangiinae, subf. nov.

DIAGNOSIS

Aglaopheniid hydroids with gonophores unprotected by phylactocarps.

REMARKS

For more than a century it has been recognized that aglaopheniids (or "statopleans") are divisible into two distinct groups based on presence or absence of phylactocarps associated with gonophores. Those taxa with protected gonophores have been named "Statoplea Phylactocarpa" (e.g., Allman, 1883:4) or "Aglaopheniidae phylactocarpa" (Leloup, 1932a:13). Their counterparts, with unprotected gonophores, have been called "Statoplea Gymnocarpa" or "Aglaopheniidae gymnocarpa." None of these names has standing in zoological nomenclature (ICZN, 1985, Art. 4). Biological differences between the two groups are such that separate subfamilies are recognized for them here. In addition to the subfamily Aglaopheniinae Marktanner-Turneretscher, 1890, which includes all aglaopheniids with protected gonophores, a new subfamily, Gymnangiinae, is founded here for those in which the gonophores are unprotected.

The nominal family Halicornariidae Marktanner-Turneretscher, 1890, though intended to be similar in scope to Gymnangiinae as defined here, is invalid (ICZN, 1985, Art. 39). Its type genus, *Halicornaria* Allman, 1874a, is a junior homonym of *Halicornaria* Hincks, 1865 (see Genus *Gymnangium*, Remarks; see also Genus *Halopteris*, Remarks). It is clear from the taxa included by Marktanner-Turneretscher that his Halicornariidae was based on the usage of the name *Halicornaria* auct. (=*Gymnangium* Hincks, 1874), and not on *Halicornaria* Hincks, 1865.

The subfamily Gymnangiinae currently includes only its type genus, *Gymnangium* Hincks, 1874. The genus *Nematocarpus* Broch, 1918, reputedly has unprotected gonophores (Broch, 1918), but hydrocladial appendages resembling phylactocarps of Aglaopheniinae are present. *Nematocarpus* is referred here to the subfamily Aglaopheniinae, although as a congener of *Aglaophenopsis* Fewkes, 1881.

Gonophores are unprotected by corbulae or by phylactogonia in four other genera frequently assigned to the Aglaopheniidae (i.e., *Nuditheca* Nutting, 1900; *Anarthroclada* Naumov, 1955; *Astrolabia* Naumov, 1955 (=*Tetranema* Fraser, 1937, an invalid junior homonym of *Tetranema* Haeckel, 1879); and *Pentatheca* Naumov, 1955). In these four, however, gonothecae are morphologically like those of halopteridids and decidedly unlike those of aglaopheniids. In establishing *Nuditheca*, Nutting (1900) remarked on its resemblance to the "eleutheroplea" in characters such as nematophore shape, hydrocladial branching, and gonophore morphology. Moreover, axillary hydrothecae are present on the hydrocaulus in the type (USNM 4424) of *Nuditheca dallii* (Clark, 1876), type species of *Nuditheca*, as well as in *Astrolabia* (Fraser, 1937; Naumov, 1955, 1960). The presence of cauline hydrothecae is diagnostic of the family Halopterididae Millard, 1962. Axillary hydrothecae are also present in material (Zoological Institute, Russian Academy of Sciences [ZISP], no catalogue number) of *Anarthroclada parmata* Naumov, 1955, type species of *Anarthroclada*. The hydrocaulus in a specimen (ZISP, no catalogue number) of *Pentatheca angulifera* Naumov, 1955, type species of *Pentatheca*, was strongly polysiphonic, even at the distal end of the colony, and axillary hydrothecae were hidden. However, they were apparent when a fragment of the specimen was treated with a sodium hypochlorite solution, the outer tubes of the stem removed with fine forceps, and the primary axial tube stained with chlorazol black. The morphology of nematothecae and gonothecae and the presence of cauline hydrothecae set these four genera apart from aglaopheniids (and from plumularioids other than halopteridids). They are referred here to the family Halopterididae.

Genus *Gymnangium* Hincks, 1874

Gymnangium Hincks, 1874:128.

Halicornaria auct. [not *Halicornaria* Allman, 1874a:476; invalid junior homonym of *Halicornaria* Hincks, 1865 (Hydrozoa)].

Taxella Allman, 1874b:179.

Gonangium Bedot, 1916a:109 [incorrect subsequent spelling].

Haliaria Stechow, 1921b:897.

Halicetta Stechow, 1921b:897.

Gymnagium Wedler, 1975:333 [incorrect subsequent spelling].

Gymnanguim Van Praët, 1979:934 [incorrect subsequent spelling].

Gymnnangium Rees and Vervoort, 1987:166 [incorrect subsequent spelling].

DIAGNOSIS

Colonies with hydrocauli erect, often stout, monosiphonic or polysiphonic, branched or unbranched, arising from a creeping hydrorhiza or from anchoring filaments. Hydrocladia unbranched, alternate or opposite, given off from opposite sides of hydrocaulus. Hydrothecae occurring only on hydrocladia; typically more or less cone- to sac-shaped; margin with or without cusps; abcauline intrathecal septum present or absent. Each hydrotheca with a pair of lateral nematothecae and a single adnate median inferior nematotheca.

Gonophores fixed sporosacs or released as medusoids. Gonothecae solitary, lacking nematothecae, not protected by corbulae or other phylactocarps, typically borne on hydrocladia or on hydrocladial apophyses.

TYPE SPECIES

Halicornaria montagui Billard, 1912 [replacement name for *Aglaophenia pennatula* sensu Hincks (1868) (not Ellis and Solander, 1786)], by subsequent designation by Stechow (1923a).

REMARKS

Gymnangium Hincks, 1874, *Halicornaria* Allman, 1874a, and *Taxella* Allman, 1874b, have long been treated as coterminous generic names. Stechow (1921c) clarified the relative priority of the three, noting that Hincks's (1874) published account of *Gymnangium* in February predated Allman's (1874a) establishment of *Halicornaria* in April and Allman's (1874b) founding of *Taxella* in December of the same year. Although extensive usage of *Halicornaria* in reference to this taxon continued for some time after Stechow's (1921c) account, the name *Gymnangium* is now widely recognized as the valid name of the genus (e.g., Rees and Thursfield, 1965; Mammen, 1965; Vervoort, 1966; Bogle, 1975; Millard, 1975; Bouillon, 1985; Rees and Vervoort, 1987; Cornelius, 1995).

In fact, *Halicornaria* Allman, 1874a, is an invalid junior homonym of *Halicornaria* Hincks, 1865. The name *Halicornaria* was attributed to G. Busk by both Hincks (1868) and Allman (1874a), and later by Nutting (1900), Fraser (1944), Ralph (1961), and many others. However, Busk used the name only in an unpublished manuscript (Bedot, 1910; Stechow, 1919a). *Halicornaria* was first made available by Hincks (1865), as discussed elsewhere in this report (see Genus *Halopteris*, Remarks), and later by Allman (1874a) to denote a different taxon.

Moreover, as defined by their type species, it appears doubtful that *Halicornaria* Allman, 1874a, and

Gymnangium are actually congeneric. *Halicornaria* was inadequately founded taxonomically and nomenclaturally by Allman (1874a), and it remained so for nearly a century because of the lack of a valid type-species designation. Allman (1874a:277) originally included "*Plumularia pennatula* of Lamarck" from Britain [=*Aglaophenia pennatula* sensu Hincks (1868) (not Ellis and Solander, 1786)] and *Halicornaria ramulifera* Allman, 1874a, in *Halicornaria*, but did not specify either as its type species. Broch's (1918:195) subsequent designation of *Halicornaria bipinnata* Allman, 1876, as type species is invalid because the species was not one of the two originally included in the genus (ICZN, 1985, Art. 69). Vervoort (1966) incorrectly considered *H. ramulifera* to be the type by monotypy, but that designation is nevertheless valid under current ICZN rules (ICZN, 1985, Art. 69a [iv]). With that established, I doubt that *Halicornaria ramulifera*, type species of *Halicornaria*, and *Halicornaria montagui* Billard, 1912, type species of *Gymnangium*, should be assigned to the same genus, considering the significant character differences between them.

Earlier, Broch (1918) removed *H. ramulifera* from *Halicornaria* to a monotypic new genus, *Nematocarpus*, characterized by its peculiarly branched hydrocladia. *Nematocarpus*, a junior objective synonym of the invalid name *Halicornaria* Allman, 1874a, was subsequently referred to the synonymy of *Cladocarpus* Allman, 1874a, by authors such as Stechow (1923a), Millard (1975), and Bouillon (1985). This seems inconsistent because gonophores of *Cladocarpus*, where known, are protected by phylactocarpial appendages of hydrocladia while those of *N. ramuliferus* are described as unprotected (Broch, 1918). Vervoort (1966) observed that the differences between *Cladocarpus* and *Nematocarpus* were unclear. I agree with the view of Bogle (1975), however, that gonophores are afforded protection by hydrocladial appendages in hydroids of the genus, and that these appendages are morphologically different from those of *Cladocarpus*. *Nematocarpus* is regarded here as congeneric with *Aglaophenopsis* Fewkes, 1881 (see Subfamily Aglaopheniinae, Remarks).

Stechow (1921b) established *Haliaria* and *Halicetta* as nominal genera distinguished from *Gymnangium* on the basis of hydrothecal characters. Leloup (1932a) regarded them as no more than subgenera of *Halicornaria* auct. (=*Gymnangium*). I concur with recent authors such as Bouillon (1985) and Rees and Vervoort (1987) that *Haliaria* and *Halicetta* are best included within *Gymnangium*, at least until more is known about relations among species within the genus. In particular, additional information is needed on the nature of the gonophores in these hydroids (Rees and Vervoort, 1987).

Bouillon (1985) included *Aglaophenoides* Fraser, 1943, in the synonymy of *Gymnangium*. *Aglaophenoides* was established by Fraser (1943) for fertile material of a hydroid that he considered to be conspecific with *Aglaophenia mammillata* Nutting, 1900. Gonothecae in Fraser's material, reportedly unprotected and arising from the cavities of hydrothecae at the proximal ends of hydrocladia, were considered by him to be diagnostic of the nominal genus. Bogle (1975) reserved judgment about the nature of these putative gonophores, but she suspected that Fraser's hydroids may have been identical with *Aglaophenia latecarinata* Allman, 1877. I agree, after comparing hydroids studied by Fraser (1943) in establishing *Aglaophenoides* (MCZ, no catalogue number) with specimens of *A. latecarinata* from Bermuda having corbulae. Gonophores in the MCZ material are indeed much as Fraser described them (see Fig. 17e), but the hydroids are otherwise indistinguishable morphologically from *A. latecarinata*. These peculiar gonophores, the only basis for recognition of *Aglaophenoides*, are interpreted as possibly teratological here. Accordingly, Fraser's nominal genus is removed from the synonymy of *Gymnangium* to that of *Aglaophenia* Lamouroux, 1812. Even if *Aglaophenoides* is not congeneric with *Aglaophenia*, it should be excluded from *Gymnangium* because reproductive structures characterizing the two are different in their location and morphology.

Gymnangium is immediately distinguishable from other genera of aglaopheniids in having neither corbulae nor other phylactogonia.

Recognition and separation of species in *Gymnangium* is problematic because morphological variability within some taxa of the genus is reported to be considerable. There is evidence, particularly from studies on *Gymnangium hians* (Busk, 1852), that the dentition of the hydrothecal margin and the length of the median inferior nematotheca are quite variable intraspecifically in hydroids of the genus (e.g., see Billard, 1913; Millard, 1975; Vervoort and Vasseur, 1977).

Auto-epizoism, in which some hydroids grow as epizoites on the same or on related species (Millard, 1973, 1975), is known to occur in several species of *Gymnangium*. Auto-epizoites are commonly stunted and usually abnormal in appearance, adding another complication to the recognition of species in this genus.

Although gonothecae have been presumed to be fixed in species of this genus, medusoids are liberated in *Gymnangium ferlusi* (Billard, 1901a) according to N. Gravier-Bonnet (*in* Bouillon, 1985).

Species of *Gymnangium* occur in lower latitudes on both sides of the Atlantic, in the Indian Ocean, and from the western Pacific eastward to Hawaii. As noted by Fraser (1946), none has apparently been discovered to date in the eastern Pacific.

***Gymnangium sinuosum* (Fraser, 1925)**

Fig. 10

Halicornaria speciosa—Nutting, 1900:127 [part] [not *Gymnangium speciosum* (Allman, 1877)].
Halicornaria sinuosa Fraser, 1925:171, figs. 7a–c.
Aglaophenia allmani—Leloup, 1935:57 [part] [not *Aglaophenia allmani* Nutting, 1900].
not *Halicornaria sinuosa*—Leloup, 1937a:110, fig. 13 [=*Gymnangium speciosum* (Allman, 1877)].
Halicornaria hians var. *balei*—Van Gemerden-Hoogeveen, 1965:70, figs. 39–41 [?not *Gymnangium hians balei* (Marktanner-Turneretscher, 1890)].
Gymnangium hians var. *balei*—Vervoort, 1968:114 [?not *Gymnangium hians balei* (Marktanner-Turneretscher, 1890)].
Gymnangium sinuosum—Vervoort, 1968:114.

TYPE LOCALITY

"Fishhawk Station 7511, 2-1/8 miles SSE of Fowey Rock Light, Gulf Stream off Cape Florida, 45 fathoms [82 m]" (Fraser, 1925).

MATERIAL EXAMINED

Atlantic Ocean, 2.5 km E of St. David's Lighthouse, on an aglaopheniid hydrocaulus on calcareous rubble, –85 m, 27 May 1991, one colony, 3.3 cm high, without gonophores, ROMIZ B385.

DESCRIPTION

Colony 3.3 cm high, arising from apophysis of an 8.5-cm-long aglaopheniid hydrocaulus that lacked intact hydrocladia. Hydrocaulus 470 μm wide basally, unbranched, monosiphonic, relatively straight, divided into internodes by distinct to indistinct transverse nodes; each internode with one or two fronto-laterally situated hydrocladial apophyses. These apophyses short, given off alternately from each side of hydrocaulus, quite closely spaced, directed upward at an angle of about 60° or more with vertical; each apophysis with two axillary nematothecae and one inferior nematotheca and supporting a hydrocladium (except where broken off); cauline nematothecae sac-shaped, aperture single, large, oval. Hydrocladia reaching 10 mm long, unbranched; top and frontal sides slightly convex; each hydrocladium arising directly from an apophysis and divided into short internodes by nearly transverse nodes. Hydrocladial internodes 503–624 μm long, 93–186 μm wide at nodes, each with one frontally placed hydrotheca, one median inferior nematotheca, and one pair of lateral nematothecae; internodal septa absent; adjacent hydrothecae quite close to one another. Hydrothecae 308–336 μm deep from tip of marginal cusp to base, curved outward, mitten-shaped; adcauline wall convex, adnate to hydrocladial internode except for a small free part distally; abcauline wall convex basally, concave medially, nearly straight distally; abcauline intrathecal septum prominent, curved inward and away from hydrocaulus, extending more than halfway across intrathecal cavity; perisarc of moderate thickness. Hydrothecal aperture 200–214 μm in diameter from adcauline to abcauline wall, irregularly oval, plane of orifice oblique to axis of internode and to that of hydrotheca; margin with a pair of shallow lateral concavities located towards adcauline wall and a single shallow concavity medially on adcauline wall. Median inferior nematotheca anvil-shaped, adnate to abcauline wall of hydrotheca but becoming free distally; apex reaching to or just beyond margin of hydrotheca; aperture scoop-shaped, open from apex to abcauline wall of hydrotheca; without an aperture into hydrothecal cavity. Lateral nematothecae resembling cauline nematothecae.

Gonophores not seen.

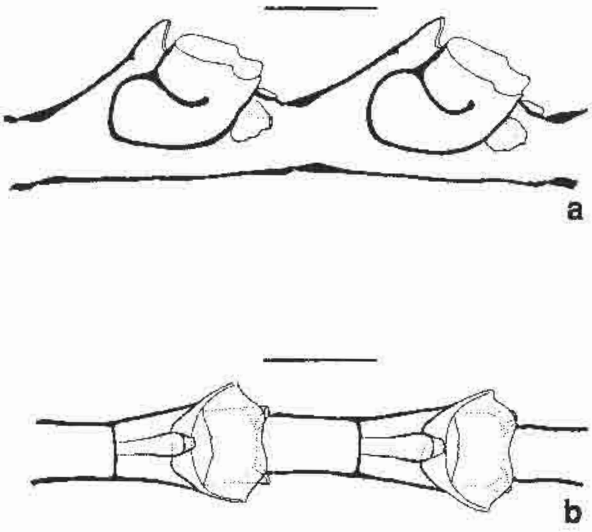

FIG. 10. *Gymnangium sinuosum*, ROMIZ B385: *a*, part of hydrocladium, lateral view, with two hydrothecae; *b*, part of hydrocladium, front view, with two hydrothecae. Scales equal 025 mm.

REMARKS

Gymnangium sinuosum is scarcely recognizable from the inadequate original description and illustrations provided by Fraser (1925). Somewhat better drawings of this hydroid, and a key to western North Atlantic species assigned to *Halicornaria* auct. (=*Gymnangium* Hincks, 1874), were provided later by Fraser (1944). The best characterization of the species to date was given by Bogle (1975). She located syntype material at the California Academy of Sciences (CAS 021804, reexamined here), studied other specimens of *G. sinuosum* from waters off south Florida, and provided excellent illustrations and a sound description of this hydroid. Bogle also reported that part of the material identified by Nutting (1900) as *Halicornaria speciosa* Allman, 1877 (specifically that from Albatross Station 2640, Straits of Florida south of Carysfort Reef, 25°05'N, 80°15'W, depth 56 fathoms), was referable to *G. sinuosum* as well. I agree with her conclusion, after reexamining slides of these hydroids (USNM 18703–18704) during this study.

Inadequate initial characterization of *Gymnangium sinuosum* by Fraser (1925) led to a number of subsequent errors in identification of this species. Part of the material identified as *Aglaophenia* (?) *allmani* by Leloup (1935) was reexamined by Van Gemerden-Hoogeveen (1965) and referred, along with additional specimens, to *Halicornaria hians* (Busk, 1852) var. *balei* (Marktanner-Turneretscher, 1890). These hydroids in turn were considered identical with *Gymnangium sinuosum* by Bogle (1975), based on the description and clear illustrations of them provided by Van Gemerden-Hoogeveen (1965), and I concur. Bogle also noted that hydroids assigned to *Halicornaria sinuosa* by Leloup (1937a) from Tampa Bay, Florida, appear to be referable to *Gymnangium speciosum* (Allman, 1877) instead. A pair of lateral indentations, rather than a single pair as in *G. sinuosum*, were depicted on the hydrothecal margin by Leloup in an illustration of his specimen.

Gymnangium sinuosum and *G. speciosum*, both originally described from the vicinity of the Straits of Florida, have been distinguished largely on the basis of differences in dentition on the hydrothecal margin. However, studies such as those on *Gymnangium hians* (Busk, 1852), a related species from the Pacific and Indian oceans, indicate that this character is inconstant (see Genus *Gymnangium*, Remarks). These observations raise the question whether *G. speciosum* and *G. sinuosum* are separate species, and whether in fact they are distinct from *G. hians*. The two are treated as separate and distinct here because of differences in hydrothecal shape (compare Figs. 10 and 11). Bogle (1975) expressed little doubt that they were different after examining material from Florida, the Bahama Islands, and the Gulf of Mexico.

Gymnangium sinuosum also resembles *Gymnangium balei* (Marktanner-Turneretscher, 1890), originally described from the Red Sea. The latter was regarded by Billard (1913) as no more than a variety of the reportedly widespread Indo-Pacific species *Gymnangium hians*, an opinion adopted as well by a number of subsequent authors including Van Gemerden-Hoogeveen (1965), Vervoort and Vasseur (1977), and Rees and Vervoort (1987). As noted above, hydroids from the tropical western Atlantic, considered conspecific with those identified as *G. sinuosum* here, were referred to "*Halicornaria hians* var. *balei*" by Van Gemerden-Hoogeveen (1965). The names *G. sinuosum* and *G. balei* (as well as *G. hians*) may eventually prove to be synonyms, given the apparent similarity between Atlantic and Indo-Pacific populations of these hydroids. However, the taxonomy of and relationship between *G. balei* and *G. hians* still seem somewhat confused and unsettled, from a brief survey of some relevant literature (e.g., Ritchie, 1910a; Billard, 1913; Stechow, 1919a, 1923a; Rees and Thursfield, 1965; Van Gemerden-Hoogeveen, 1965; Millard, 1975; Vervoort and Vasseur, 1977; Rees and Vervoort, 1987), and a careful revision is warranted. Removal of the name *G. sinuosum* to the synonymy of either one seems premature at present.

The single hydroid colony assigned here to *Gymnangium sinuosum* was found growing on an old stem of an aglaopheniid, presumably of the same species. Its hydrocaulus appeared to have arisen from a hydrocladial apophysis on the original colony.

REPORTED RANGE

Bermuda: deeper coastal waters (Calder, 1993).
Circumglobal distribution: western Atlantic (Bogle, 1975).

Gymnangium speciosum (Allman, 1877)

Fig. 11

Halicornaria speciosa Allman, 1877:54, pl. 34, figs. 1–5.
Halicornaria variabilis Nutting, 1900:127, pl. 33, figs. 6–11.
Gymnangium speciosum—Stechow, 1923a:237.
?not *Halicornaria speciosa*—Hargitt, 1927:516 [=?*Gymnangium hians* (Busk, 1852)].
Halicornaria sinuosa—Leloup, 1937a:110, fig. 13 [not *Gymnangium sinuosum* (Fraser, 1925)].
Gymnangium speciosa—Yamada, 1959:84.
Gymnagium speciosum—Wedler, 1975:333 [incorrect subsequent spelling].

TYPE LOCALITY

"Double-Headed Shot Key (Bahamas), from a depth of from 4 to 5 fathoms [7–9 m]" (Allman, 1877:55).

MATERIAL EXAMINED

Atlantic Ocean, 5 km SSE of Castle Roads, on *Macrorhynchia allmani*, –73 m, 26 May 1991, four colonies, up to 7 cm high, without gonophores, ROMIZ B386. Atlantic Ocean, 5 km SSE of Castle Roads, on *Macrorhynchia allmani*, –65 m, 26 May 1991, 11 colonies, up to 10.5 cm high, three colonies with gonophores, ROMIZ B387. Atlantic Ocean, 2.5 km E of St. David's Lighthouse, on *Macrorhynchia allmani*, –73 m, 27 May 1991, five colonies, up to 5.5 cm high, with gonophores, ROMIZ B388. Atlantic Ocean, 4 km NW of North Rock, on limestone rubble, –73 m, 28 May 1991, one colony, 7 cm high, without gonophores, ROMIZ B389. Atlantic Ocean, 4 km NW of North Rock, on limestone rubble, –69 m, 28 May 1991, one colony, 14 cm high, without gonophores, ROMIZ B390.

DESCRIPTION

Colonies up to 14 cm high; each hydrocaulus arising from a stolon system creeping over limestone rubble or other hydroids. Hydrocauli reaching up to 800 µm or more in width basally, unbranched, monosiphonic, relatively straight, divided into internodes by distinct to indistinct transverse nodes; each internode typically with one or two fronto-laterally situated hydrocladial apophyses. These apophyses short, given off alternately from each side of hydrocaulus, quite closely spaced, directed upward at an angle of about 60° or more with vertical; each apophysis with two axillary nematothecae and one inferior nematotheca and supporting a hydrocladium (except where broken off); cauline nematothecae varying in size, typically sac-shaped with a single, large, oval to elongate-oval aperture. Hydrocladia reaching 17 mm long, unbranched; top and frontal sides slightly convex; each hydrocladium arising directly from an apophysis and separated from it by a distinct to almost imperceptible oblique node, divided into short internodes by oblique nodes. Hydrocladial internodes 363–471 µm long, 140–214 µm wide at nodes, each with one frontally placed hydrotheca, one median inferior nematotheca, and one pair of lateral nematothecae; internodal septa absent; adjacent hydrothecae relatively close to one another. Hydrothecae 284–345 µm deep from tip of marginal cusp to base, curved outward, sac-shaped; adcauline wall convex, adnate to hydrocladial internode except for a small free part distally; abcauline wall convex basally, concave medially, nearly straight distally; abcauline intrathecal septum prominent, curved inward and away from hydrocaulus, extending about halfway across intrathecal cavity; perisarc of moderate thickness. Hydrothecal aperture 186–214 µm in diameter from adcauline to abcauline wall, irregularly oval, plane of aperture oblique to axis of internode and to that of hydrotheca; margin with two pairs of shallow lateral concavities and a single shallow concavity medially on abcauline wall. Median inferior nematotheca typically curved and somewhat beak-shaped, adnate to abcauline wall of hydrotheca but becoming free distally; length quite varied, apex typically extending some distance beyond margin of hydrotheca; aperture scoop-shaped, open from apex to abcauline wall of hydrotheca; without an aperture into hydrothecal cavity. Lateral nematothecae resembling cauline nematothecae, extending beyond margin of hydrotheca.

Gonophores apparently fixed sporosacs. Gonothecae essentially cylindrical, each approximately 700 µm high, truncate at distal end, arising by a short baso-lateral pedicel given off from hydrocladial apophysis; orifice oval to almost round in cross-section, about 530 µm in diameter.

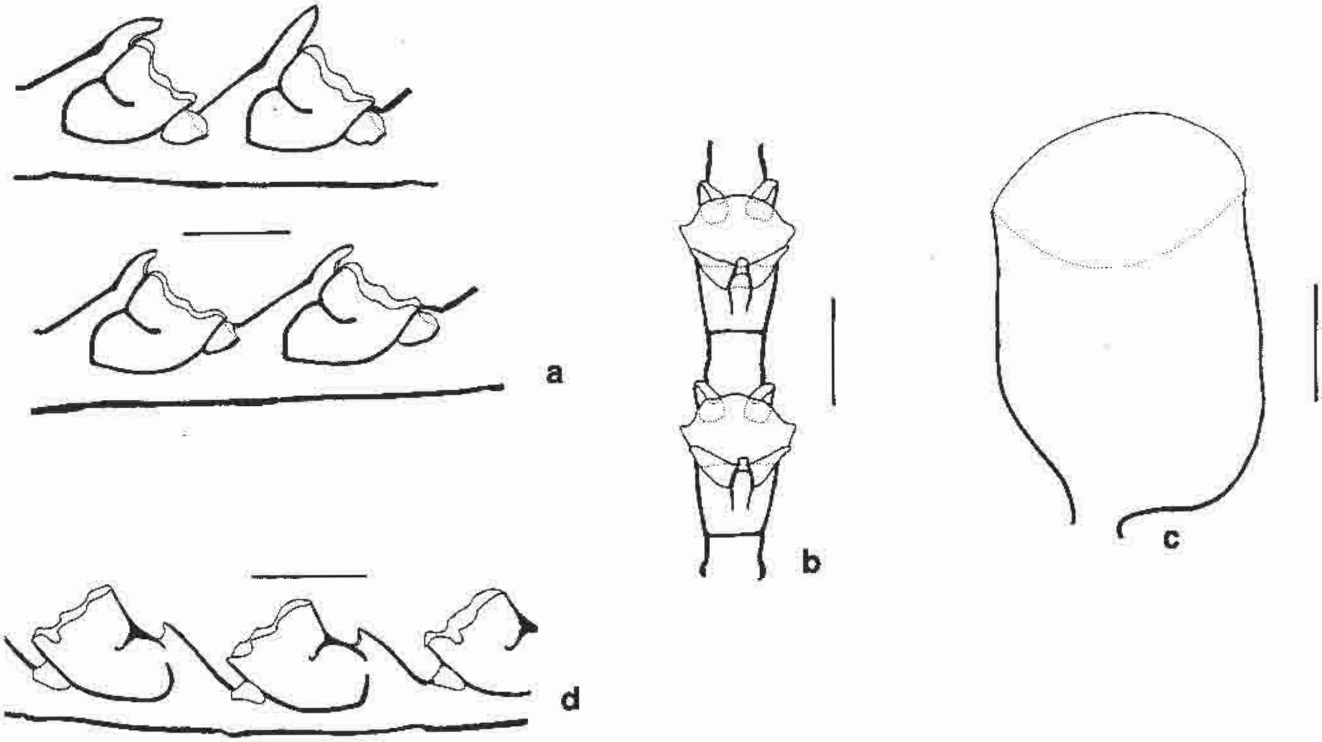

FIG. 11. *Gymnangium speciosum: a,* parts of two hydrocladia, lateral view, each with two hydrothecae, ROMIZ B387; *b,* part of hydrocladium, front view, with two hydrothecae, ROMIZ B387; *c,* gonotheca, ROMIZ B387; *d,* part of hydrocladium of paralectotype colony of *Halicornaria variabilis* Nutting, 1900, between Eleuthera and Little Cat Island, Bahamas, lateral view, with three hydrothecae, USNM 18706. Scales equal 0.25 mm.

REMARKS

Bogle (1975) recognized three species of *Gymnangium* in the tropical western North Atlantic as valid: *G. speciosum* (Allman, 1877), *G. sinuosum* (Fraser, 1925), and with some reservation *G. longicauda* (Nutting, 1900). To this should apparently be added *G. arcuatum* (Lamouroux, 1816), the type locality of which is reportedly "Mer des Antilles." This species has not subsequently been reported from the tropical western Atlantic, although it has been recorded from South Africa and the Indian Ocean (Millard, 1975). It is distinctive in being dichotomously branched (Lamouroux, 1816) and in lacking a true intrathecal septum (Billard, 1907; Van Praët, 1979). *Halicornaria plumosa* Allman, 1883 (an invalid junior homonym of *Halicornaria plumosa* Armstrong, 1879) from Brazil is much like and possibly conspecific with *G. longicauda*. As for the invalid name *H. plumosa* Allman, 1883, Marktanner-Turneretscher (1890) established the name *Halicornaria allmanii* for material from South Africa that he considered conspecific with Allman's species, but accounts of the two appear to be different.

Halicornaria variabilis was described by Nutting (1900) from material collected at three stations (69, 72, 76) during the Bahama Expedition of the State University of Iowa. Nutting (1900:128) recognized the similarity of this species to *Gymnangium speciosum*, but distinguished it largely on the size and shape of its cauline nematothecae. Syntypes from Station 72 (USNM 18707, and two of three slides catalogued USNM 18705) are certainly much like *G. speciosum*. Other syntype specimens from Station 69 (two of three slides catalogued USNM 18706) and Station 76 (one slide catalogued USNM 18705, another as USNM 18706) appear different in having decidedly reduced median inferior nematothecae (Fig. 11d). In spite of such seeming differences Bogle (1975) referred all of these syntypes (USNM 18705, 18706, 18707) to *G. speciosum*, discounting supposed dissimilarities in nematotheca development or in size of cauline nematothecae alluded to by Nutting (1900). She reported finding the same characters in type material of *G. speciosum* that Nutting considered diagnostic of *G. variabilis*.

I accept Bogle's (1975) conclusion that *Gymnangium variabilis* and *G. speciosum* are conspecific, given the variations noted by Millard (1973, 1975) in South African species of this genus and especially in the characters of epizootic specimens of *G. arcuatum*, *G. africanum* (Millard, 1958), and *G. exsertum* (Millard, 1962). Notably, data on slides of material from Station 76 indicate that at least some syntypes of *G. variabilis* were "parasitic" (i.e., epizootic), and their development was described by Nutting (1900) as follows. Young colonies, growing on *Macrorhynchia allmani* (Nutting, 1900), consisted of single hydrocladia given off from a creeping hydrorhiza. Erect colonies on the same hydrorhiza were presumably formed from the conversion of a hydrocladium to a hydrocaulus, which in turn gave off hydrocladia. This account is similar in some respects to that outlined by Millard (1973) for modified epizootic forms of *G. arcuatum*, although a hydrocaulus in that species appears to develop directly and not from the transformation of a hydrocladium. Millard found that hydrothecae on erect parts of epizootic colonies were more like those of the "normal form" in their development, making it possible to establish the identity of the species. It therefore seems possible that all of Nutting's material of *G. variabilis* is conspecific, in spite of its variability, and paralectotype colonies from Station 72 support Bogle's conclusion that the species is identical to *G. speciosum*.

Two syntype colonies of *Gymnangium variabilis* from Station 72, one unstained and the other stained, are mounted on slide USNM 18707. The unstained colony is chosen here as the lectotype of *G. variabilis*. The stained colony and those on slides USNM 18705 and USNM 18706 are hereby designated as paralectotypes of the same species. The lectotype is an 8-mm-high fragment of a colony, with hydrocladia but without gonothecae. The slide label includes the following information about the specimen: "*Halicornaria variabilis* Nutting, Station 72, Bahama Exped. 1893." The hydroid was collected in July 1893 in "shallow water between Eleuthera and Little Cat Island, Bahamas" (Nutting, 1895, 1900).

Bogle (1975) noted that there was considerable variation in her material of *Gymnangium speciosum*, including the length of the median inferior nematotheca. She ques-

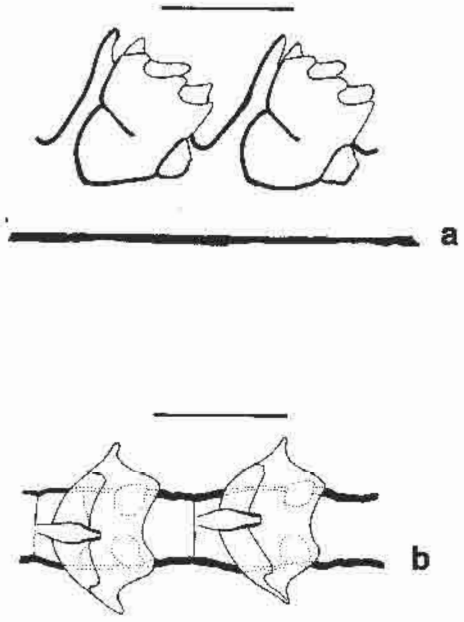

FIG. 12. *Gymnangium hians*, Torres Strait, BMNH 99.7.1.6250: *a*, part of hydrocladium, lateral view, with two hydrothecae; *b*, part of hydrocladium, front view, with two hydrothecae. Scales equal 0.25 mm.

tioned whether *G. longicauda*, largely distinguished by its long median inferior nematothecae, might not be identical to *G. speciosum*. The status of *G. longicauda* is still unclear, although it was not recognized as valid in Cairns et al. (1991). No specimens approaching the form of *G. longicauda* were observed among hydroids collected from Bermuda.

Gymnangium speciosum is similar to hydroids from tropical and subtropical regions of the Pacific and Indian oceans that have been assigned to *G. hians* (Busk, 1852). This is apparent when specimens referable to the two are compared (Figs. 11–12). Busk's (1852) material of *G. hians* from Torres Strait, northern Australia (BMNH No. 99.7.1.6250, labelled "type?"), differs from *G. speciosum* in having (1) hydrothecae inserted with their main axis at a much wider angle to the internode, (2) more sharply pointed marginal cusps, (3) shorter internodes, (4) a longer free distal wall, (5) a straighter intrathecal septum, (6) lateral nematothecae that appear smaller and are hidden beneath the margin of the hydrotheca when viewed from the top, (7) a wider orifice, and (8) a concave distal wall. Many of these characters are known to vary in species of the genus, but the differences between Atlantic and western Pacific hydroids are such that separate species are recognized for them here.

Hydroids from Amoy (Xiamen), southern China, were referred to this species by Hargitt (1927). His specimens may have been referable to *Gymnangium hians* instead.

REPORTED RANGE

Bermuda: deeper coastal waters (Calder, 1993).
Circumglobal distribution: western Atlantic (Bogle, 1975).

Subfamily Aglaopheniinae Marktanner-Turneretscher, 1890

DIAGNOSIS

Aglaopheniid hydroids with gonophores protected by phylactocarps; these phylactocarps either occur in place of hydrocladia, or arise as appendages of normal or reduced hydrocladia.

REMARKS

Aglaopheniids are divided here into two subfamilies, one in which the gonothecae are protected by phylactocarps (subfamily Aglaopheniinae Marktanner-Turneretscher, 1890), and another in which the gonothecae are not so protected (Gymnangiinae, subf. nov.). All known genera of the family Aglaopheniidae Marktanner-Turneretscher, 1890, except *Gymnangium* Hincks, 1874, are referable to the Aglaopheniinae. This nominotypical subfamily, as defined above, is a large and rather diverse assemblage. Further study may show that it should be divided, and that additional aglaopheniid subfamilies should be recognized.

Genera referred to the Aglaopheniinae are distinguished in part on characters of the accessory structures (phylactocarps) protecting the gonothecae. These phylactocarps are elements of highly modified hydrocladia in one group of genera, while in a second group they arise as appendages of hydrocladia that may or may not be reduced. Based on these differences, two tribes are recognized here within the subfamily Aglaopheniinae. The nominotypical tribe Aglaopheniini Marktanner-Turneretscher, 1890, includes those genera, like the type genus *Aglaophenia* Lamouroux, 1812, with phylactocarps formed from highly modified hydrocladia. The Cladocarpini, tribe nov., is defined as a group of aglaopheniid genera with phylactocarps arising as hydrocladial appendages, as in its type genus, *Cladocarpus* Allman, 1874a.

Phylactocarps, representing modified hydrocladia, form pod-shaped corbulae in *Aglaophenia; Lytocarpia* Kirchenpauer, 1872; *Acanthocladium* Allman, 1883; and *Pentandra* von Lendenfeld, 1884. Gonothecae are protected within corbulae by overarching ribs bearing nematothecae. Corbula ribs each bear a hydrotheca basally in *Lytocarpia* and *Acanthocladium* (genera sometimes considered coterminous, e.g., Bogle, 1975; Bouillon, 1985), while those of *Aglaophenia* and *Pentandra* do not. Corbula morphology is rather complex, as is the terminology applied to parts of this structure (see von Schenck, 1966; Svoboda and Cornelius, 1991; Svoboda, 1992).

The phylactocarps of *Macrorhynchia* Kirchenpauer, 1872, and *Monoserius* Marktanner-Turneretscher, 1890, are also formed from modified hydrocladia, but they constitute open gonotheca-bearing phylactogonia rather than true corbulae. Phylactogonia of *Macrorhynchia* may occur singly, or may be aggregated to form a pseudocorbula. In *Monoserius*, phylactogonia are in the form of a "demicorbula" or "semicorbula." Nematocladia arch part way over the gonothecae in this genus, but they arise from only one side of the phylactogonium.

Several different kinds of phylactocarps are also apparent in genera assigned here to the Cladocarpini, aglaopheniids in which phylactogonia arise as appendages of modified or unmodified hydrocladia. Several distinct types occur in species commonly assigned to *Cladocarpus* Allman, 1874a. In one group, including the type species of the genus (*Cladocarpus formosus* Allman, 1874a), phylactocarps are dichotomously or alternately branched structures resembling stag antlers. In a second group of species (e.g., *Aglaophenia lignosa* Kirchenpauer, 1872; *Cladocarpus pectiniferus* Allman, 1883; *Cladocarpus distomus* Clarke, 1907; *Dinotheca dofleini* Stechow, 1911), phylactocarps are unbranched or irregularly branched. Along its length, the rachis of such a phylactocarp bears one or more gonothecae and several pairs of more or less opposite lateral nematothecae of varied length. When the rachis and nematothecae are long, such phylactocarps are centipede-shaped. Other morphological forms of phylactocarps exist as well (e.g., see those of *Cladocarpus paradiseus* Allman, 1877). Given such morphologically different types of phylactocarps in species assigned to the genus, several authors have suggested that *Cladocarpus* should be subdivided (e.g., see Bogle, 1975; Calder, 1984; Rees and Vervoort, 1987; Ramil and Vervoort, 1992b). With justification, Ramil and Vervoort restricted the genus *Cladocarpus* to species of the first group. Those of the second group were assigned by them to *Streptocaulus* Allman, 1883, based on the similarities of the phylactocarps to those of *S. pulcherrimus* Allman, 1883 (type species of *Streptocaulus* by monotypy). The spiral arrangement of hydrocladia in hydroids of *S. pulcherrimus*, usually deemed diagnostic of *Streptocaulus*, was discounted by Ramil and Vervoort as a generic character because young colonies are reportedly pinnate (Quelch, 1885). Ongoing refinement of the scope of these two genera seems highly likely. In particular, *Streptocaulus* still seems polyphyletic based on phylactocarp morphology.

Other genera referable to the Cladocarpini, as understood here, include *Aglaophenopsis* Fewkes, 1881, and *Cladocarpoides* Bogle, 1984. In *A. hirsuta* Fewkes, 1881, type species of *Aglaophenopsis*, putative phylactocarps arise lateral to the median inferior nematotheca of the first cormidium on unmodified hydrocladia. These phylactocarps are usually unbranched structures that are divided into strongly septate internodes (Fewkes, 1881; Nutting, 1900; Fraser, 1944; Vervoort, 1972; Bogle, 1975). They possess a linear series of unpaired median nematothecae, and one or more hydrothecae may be present. I agree with Bogle (1975) that characters of the phylactocarps set *Aglaophenopsis* apart from *Cladocarpus*.

Appendages similar in morphology to the phylactocarps of *Aglaophenopsis hirsuta* occur in *Halicornaria ramulifera* Allman, 1874a, type species of *Nematocarpus* Broch, 1918 (Allman, 1874a; Broch, 1918). This nominal genus was founded by Broch (1918) based on the occurrence of secondary branches on the hydrocladia, and especially on grounds that these branches were not necessarily associated with gonothecae. Hydrocladial branches arise in *H. ramulifera* from several cormidia of a given hydrocladium, are typically rebranched and strongly septate, and bear a single row of nematothecae. Hydrothecae are also frequently present. These secondary branches are regarded here as homologous to those appendages considered to be phylactocarps in *A. hirsuta*. Opinions differ among recent authors regarding the status of *Aglaophenopsis* and *Nematocarpus*. Bogle (1975) was uncertain whether the two should be considered identical, or whether *Nematocarpus* should be recognized as a distinct subgenus of *Aglaophenopsis*. Millard (1975) and Bouillon (1985) lumped them, together with *Dinotheca* Stechow, 1911, and *Cladocarpella* Bale, 1915, in a broadly defined genus, *Cladocarpus*. Somewhat tentatively, Ramil and Vervoort (1992b) treated both *Aglaophenopsis* and *Nematocarpus* as valid. *Aglaophenopsis* is regarded here as valid, and *Nematocarpus* as congeneric with it.

In *Cladocarpoides*, the phylactocarp arises from the proximal internode of an unmodified hydrocladium but it resembles an open corbula in shape. This structure consists of a long rachis supporting alternate and dichotomously branched phylactogonia, each of which bears a single hydrotheca on the basal branch.

The subfamily Aglaopheniinae is represented in shallow waters of the Bermuda Platform by species referable to the genera *Aglaophenia* and *Macrorhynchia*.

Genus *Aglaophenia* Lamouroux, 1812

Aglaophenia Lamouroux, 1812:184.

Aglaophena Oken, 1817:1164 [incorrect subsequent spelling].

Aglatophenia Costa, 1839:185 [incorrect subsequent spelling].

Anisocalyx Costa, 1842:1.

Aglaophaenia Costa, 1842:2 [incorrect subsequent spelling].

Aglaophnia Costa, 1842:12 [incorrect subsequent spelling].

Agalophenia Costa, 1842:18 [incorrect subsequent spelling].

Aglaofenia Meneghini, 1843:402 [incorrect subsequent spelling].

Aglaofenie Meneghini, 1843:404 [incorrect subsequent spelling].

Aglaophana L. Agassiz, 1848:31 [incorrect subsequent spelling].

Anisoscalyx Heller, 1868:41 [incorrect subsequent spelling].

Aglaphenia Allman, 1872:447 [incorrect subsequent spelling].

Calathophora Kirchenpauer, 1872:20.

?*Pachyrhynchia* Kirchenpauer, 1872:20.

Aglaophemia Kirchenpauer, 1876:12 [incorrect subsequent spelling].

Calatophora Kirchenpauer, 1876:33 [incorrect subsequent spelling].

Aglaiophenia Whiteaves, 1878:465 [incorrect subsequent spelling].

Anisocalix Pieper, 1884:187 [incorrect subsequent spelling].

Anisicalyx Nutting, 1900:59 [incorrect subsequent spelling].

Aglaoplenia Billard, 1904a:81 [incorrect subsequent spelling].

Anysocalyx Bedot, 1905:101 [incorrect subsequent spelling].

Agalaophenia Cary and Spaulding, 1909:6 [incorrect subsequent spelling].

Aglaaphenia Bedot, 1918:54 [incorrect subsequent spelling].

Aglaria Stechow, 1923b:16.

Agloaphenia Leloup, 1937b:72 [incorrect subsequent spelling].

Aglaophenoides Fraser, 1943:82.

?*Corbulifera* Naumov, 1960:489.

Aglaophenie Patriti, 1970:145 [incorrect subsequent spelling].

Aglaeophenia Morris and Mogelberg, 1973:17 [incorrect subsequent spelling].

Aglaeophenoides Morris and Mogelberg, 1973:19 [incorrect subsequent spelling].

Aqlaophenia Venugopalan and Wagh, 1986:277 [incorrect subsequent spelling].

DIAGNOSIS

Colonies erect; hydrocauli branched or unbranched, monosiphonic or polysiphonic, arising from a creeping hydrorhiza or from anchoring filaments. Hydrocladia unbranched, pinnately arranged, arising from alternate apophyses on hydrocaulus and branches. Hydrothecae occurring only on hydrocladia, typically more or less cone- to sac-shaped, margin dentate; intrathecal septum variably developed. Each hydrotheca flanked by a pair of lateral nematothecae and one partly adnate median inferior nematotheca.

Gonophores fixed sporosacs (reportedly released as medusoids in one species). Gonothecae aggregated, enclosed within a corbula developed in place of a hydrocladium; corbula pod-shaped, composed of ribs arising as alternate appendages from two sides of axis of corbula, ribs fused or unfused, bearing nematothecae but lacking hydrothecae. Corbulae sometimes sexually dimorphic.

TYPE SPECIES

Sertularia pluma Linnaeus, 1758, by subsequent designation by Apstein (1915:126).

REMARKS

The genus *Aglaophenia* was founded by Lamouroux (1812) to accommodate five species, namely, *Sertularia pluma* Linnaeus, 1758; *S. pennatula* Ellis and Solander, 1786; *S. pennaria* Linnaeus, 1758; *S. myriophyllum* Linnaeus, 1758; and *S. echinata* Linnaeus, 1761. Of these five, only *S. pluma* is currently assigned to the genus, and is its type species.

Aglaophenia was expanded to encompass an even more heterogeneous assemblage of some 22 nominal species by Lamouroux (1816). Within its scope he included plumularioids (other than species referred to *Nemertesia* Lamouroux, 1812), two sertulariids (*Sertularia echinata* and *S. falcata* Linnaeus, 1758; see Cornelius, 1979, for synonymies), and several nominal species of uncertain identity (Bedot, 1901a). The same year, Lamarck (1816) established the genus *Plumularia* for 17 nominal species, including several of the same ones referred to *Aglaophenia* by Lamouroux (1812, 1816). *Aglaophenia* remained poorly defined, and largely treated as a congener of *Plumularia*, until the mid 19th century. Forbes (1844:390), Johnston (1847:118), and Busk (1851:118) recognized that *Plumularia*, including *Aglaophenia* as then constituted, was probably "artificial" based on the varied morphology of accessory reproductive structures apparent within the group. However, none of these three authors attempted a revision of the genus.

McCrady (1859) redefined *Aglaophenia*, recognizing it as distinct from *Plumularia* and restricting it to species now assigned to *Aglaophenia* or to other genera of the family Aglaopheniidae Marktanner-Turneretscher, 1890. His concept of the genus was largely adopted by major contemporary authors including L. Agassiz (1862) and A. Agassiz (1865) in North America, and Hincks (1868) and Allman (1871, 1872) in Europe. In redefining *Aglaophenia*, McCrady (1859:201) took *Plumularia cristata* Lamarck, 1816 (generally considered a junior synonym of *Sertularia pluma* Linnaeus, 1758) as "the nucleus of this group." However, McCrady's work does not meet ICZN criteria for valid designation of a type species of *Aglaophenia* (ICZN, 1985, Art. 69). *Plumularia cristata* was not one of the nominal species originally included in *Aglaophenia* by Lamouroux (1812) (ICZN, 1985, Art. 69a). Neither did McCrady specifically include *P. cristata* in the synonymy of any of these nominal species (including *Sertularia pluma* Linnaeus, 1758, with which it is considered conspecific) (ICZN, 1985, Art. 69a [v]). I regard the later designation of *Sertularia pluma* by Apstein (1915) as the first unequivocal and valid designation of a type species of *Aglaophenia*. Earlier, Kirchenpauer (1872:15) had designated *S. pluma* as the type species of the subgenus *Calathophora*, which is therefore a junior objective synonym of *Aglaophenia*.

In addition to *Calathophora*, Kirchenpauer (1872) recognized three other subgenera within a broadly defined genus *Aglaophenia*, namely, *Pachyrhynchia*, *Lytocarpia*, and *Macrorhynchia*. Of these, *Calathophora* and *Pachyrhynchia* came to be regarded as congeners of *Aglaophenia*, while *Lytocarpia* and *Macrorhynchia* were eventually elevated to the rank of genus (see Allman, 1883; Nutting, 1900; Bedot, 1912; Stechow, 1919a, 1923a; Rees and Vervoort, 1987; see also Genus *Macrorhynchia*, Remarks). The scope of *Aglaophenia* was thereby narrowed to exclude species with open mature corbulae having hydrothecae at the bases of the costae (*Lytocarpia*) and those with phylactocarps formed from modified hydrocladia (*Macrorhynchia*). This more restricted concept of *Aglaophenia* has changed little through the 20th century. Diagnoses of the genus by Nutting (1900) and Broch (1918) differ relatively little from those by authors such as Millard (1975), Bouillon (1985), and Svoboda and Cornelius (1991).

Although Kirchenpauer's (1872) subgenus *Pachyrhynchia* has implicitly or explicitly (e.g., see Allman, 1883; Bedot, 1912; Stechow, 1923a; Bogle, 1975) been included in the synonymy of *Aglaophenia*, a type species has never been designated for it to my knowledge. Of the four nominal species originally referred to the subgenus (*Aglaophenia cupressina* Lamouroux, 1816; *A. spicata* Lamouroux, 1816; *A. tricuspis* McCrady, 1859; and *Plumularia macgillivrayi* Busk, 1852), only *A. cupressina* is currently recognized as valid. Accordingly, *A. cupressina* is designated here as type species of *Pachyrhynchia*. Although it is an extensively branched and unusually robust species, *A. cupressina* has usually been assigned to *Aglaophenia* (e.g., Bedot, 1901a; Billard, 1913; Jarvis, 1922; Leloup, 1937b; Vervoort, 1941; Pennycuik, 1959; Redier, 1964; von Schenck, 1966; Millard, 1975). *Pachyrhynchia* is included here, with some question concerning its taxonomic rank, as a subgenus of *Aglaophenia*.

Stechow (1923b) founded *Aglaria* to accommodate *Aglaophenia septata* Ritchie, 1909b, a deep-water species with an unusual corbula. *Aglaria* has been recognized as valid by some authors (e.g., Leloup, 1932a; Pennycuik, 1959; Ralph, 1961; Mammen, 1965; Rees and Thursfield, 1965), as congeneric with *Aglaophenia* by Vervoort (1966), and as congeneric with *Lytocarpus* sensu Allman, 1883 (=*Macrorhynchia* Kirchenpauer, 1872) by Bouillon (1985). Vervoort's (1966) evidence that the corbula of *A. septata* is fundamentally of the type seen in *Aglaophenia* seems strong, and his conclusion regarding the status of *Aglaria* is adopted here (see Genus *Macrorhynchia*, Remarks).

Stechow (1923a) listed the name *Anisocalyx* Costa, 1842, as a synonym of *Aglaophenia*. Costa (1842) had included in *Anisocalyx* several nominal species previously referred to *Aglaophenia* by Lamouroux (1812) and to *Plumularia* by Lamarck (1816). Bedot (1901a) remarked that the name *Anisocalyx* had not been adopted, and recommended that it be abandoned. No type species had apparently been designated for the nominal genus until Cornelius (1995) selected *Sertularia pluma* Linnaeus, 1758. The generic name *Anisocalyx* thus became a junior objective synonym of *Aglaophenia*.

Aglaophenoides Fraser, 1943, regarded as congeneric with *Gymnangium* Hincks, 1874, by Bouillon (1985), has been reassigned here to *Aglaophenia* (see Genus *Gymnangium*, Remarks; *Aglaophenia latecarinata*, Remarks). Its type species, *Aglaophenia mammillata* Nutting, 1900, is regarded as identical to *A. latecarinata* Allman, 1877. The unusual gonophores in Fraser's (1943) material, and the character upon which *Aglaophenoides* was based, are considered here as abnormal.

Naumov (1960) established the nominal genus *Corbulifera* for *Plumularia macgillivrayi* Busk, 1852, a nominal species assigned earlier to the subgenus *Pachyrhynchia* by Kirchenpauer (1872). *Plumularia macgillivrayi* is generally considered (e.g., Billard, 1909; Bedot, 1910; Vervoort, 1941; Pennycuik, 1959; Millard, 1975) to be conspecific with *Aglaophenia cupressina*, the type species of *Pachyrhynchia*. Therefore, the name *Corbulifera* is regarded as a junior subjective synonym of *Pachyrhynchia*, as noted earlier by Bogle (1975) and Bouillon (1985), and both nominal genera are included provisionally here in *Aglaophenia*.

Pentandra von Lendenfeld, 1884, has been regarded congeneric with *Aglaophenia* by authors including Stechow (1923a) and Bouillon (1985, as *Petandra*). Others (e.g., Bale 1887; Marktanner-Turneretscher, 1890; Nutting 1900; Bedot, 1916a; Leloup, 1932a; Pennycuik, 1959; Naumov, 1960; Ralph, 1961; von Schenck, 1966) have treated it as valid. The characters upon which *Pentandra* was based seem to set it apart from *Aglaophenia* (see Bale, 1887:89), although it is poorly known. Leloup (1932a) concluded that it seemed best to maintain *Pentandra* as valid, given our current state of knowledge, and I agree.

Bogle (1975) noted that *Aglaophenia* has served to some extent as a catchall genus for aglaopheniids of uncertain generic identity, particularly for species whose gonosomes are unknown. Moreover, she noted that some authors (e.g., Nutting, 1900) failed to recognize the degree of variation possible within some species of the genus. The result was the founding or continued recognition of many nominal species that she considered either invalid or of doubtful validity. Of some 29 nominal species from the tropical or subtropical waters of the North American Atlantic coast assigned to *Aglaophenia* by Fraser (1944), Bogle recognized only 14. Many of her ideas concerning taxonomy of aglaopheniids were incorporated in the species list of American and Canadian hydroids by Cairns et al. (1991).

Where known, gonophores in species of *Aglaophenia* are almost always fixed sporosacs. To date, the only reported exception is that of an ephemeral medusa from a hydroid identified as *Aglaophenia* sp. from Papua New Guinea (Boero and Bouillon, 1989).

Sexual dimorphism exists in the corbulae of several species assigned to *Aglaophenia*. Svoboda (1992) reviewed the literature on the subject and provided an account of differences between male and female corbulae in *Aglaophenia tubulifera* (Hincks, 1861) and *A. lophocarpa* Allman, 1877 (=*A. apocarpa* Allman, 1877). In such species, the nematocladia (upper ribs) in corbulae of female colonies of a given species are typically more completely fused than in those of the male. Svoboda (1992) also reviewed the complex morphology of corbulae in *Aglaophenia*, and the terminology applied to them.

Species assigned to *Aglaophenia* range bathymetrically from the intertidal zone (e.g., *A. struthionides* (Murray, 1860)) to the deep sea (e.g., *A. septata* Ritchie, 1909b). Most are known from the upper 500 m (e.g., see Nutting, 1900; Fraser, 1944; Millard, 1975; Svoboda and Cornelius, 1991). Kramp (1956) referred two sterile hydroid colonies from depths exceeding 6000 m to *Aglaophenia tenuissima* Bale, 1914, and *A. galatheae* Kramp, 1956, but the generic affinities of both seem unclear at present.

Algal symbionts are known to occur in three species currently referred to *Aglaophenia*, namely, *A. tubiformis* Marktanner-Turneretscher, 1890; *A. harpago* von Schenck, 1965; and *A. cupressina* (see Svoboda and Cornelius, 1991). *Aglaophenia cupressina* is also venomous to humans (e.g., Allman, 1883; Vervoort, 1941; Halstead, 1988; Millard, 1975).

Aglaophenia dubia Nutting, 1900

Fig. 13

Aglaophenia gracilis Allman, 1877:42, pl. 25, figs. 1–4 [not *Aglaophenia gracilis* Lamouroux, 1816 =?*Nemertesia ramosa* (Lamarck, 1816)].

Aglaophenia dubia Nutting, 1900:92, pl. 18, fig. 5.

Aglaophenia flowersi Nutting, 1900:93, pl. 19, figs. 1–2.

Aglaophenia lophocarpa—Bennitt, 1922:252 [not *Aglaophenia lophocarpa* Allman, 1877 =*Aglaophenia apocarpa* Allman, 1877].

Aglaophenia (?) *allmani*—Leloup, 1935:57 [part] [not *Macrorhynchia allmani* (Nutting, 1900)].

Aglaophenia elongata—Leloup, 1937a:112. —Deevey, 1954:271. —Van Gemerden-Hoogeveen, 1965:79, fig. 44. —Vervoort, 1968:112. —Defenbaugh, 1974:101, figs. 11a–c [not *Aglaophenia elongata* Meneghini, 1845].

?*Aglaophenia dubia*—Fraser, 1938b:135.

Aglaophenia acacia—Svoboda, 1979:79 [part]. —Svoboda and Cornelius, 1991:14 [part] [not *Aglaophenia acacia* Allman, 1883].

Aglaophenia apocarpa—Calder, 1993:68 [not *Aglaophenia apocarpa* Allman, 1877].

Aglaophenia sp.—Calder, 1993:68.

TYPE LOCALITY

Florida, "off Carysfort Reef, from a depth of 52 fathoms [95 m]" (Allman, 1877).

MATERIAL EXAMINED

Atlantic Ocean, 2 km SE of Castle Roads, substrate unknown, –50 to –80 m, 27 August 1977, one colony, about 20 cm high, with male gonophores, coll. J. Markham, ROMIZ B126. Atlantic Ocean, 2.5 km SE of Castle Roads, on calcareous rubble, –82 m, 5 September 1992, two colonies, up to 17 cm high, with female gonophores, ROMIZ B410. Atlantic Ocean, 2 km SE of Castle Roads, on calcareous rubble, –91 m, 8 April 1992, five colonies, up to 10 cm high, without gonophores, ROMIZ B411. Atlantic Ocean, 2.5 km E of St. David's Lighthouse, on calcareous rubble, –85 m, 27 May 1991, five colonies, up to 9 cm high, without gonophores, ROMIZ B412. Atlantic Ocean, 4 km NW of North Rock, on calcareous rubble and rhodoliths, –62 m, 28 May 1991, five colonies, up to 7.5 cm high, without gonophores, ROMIZ B413. Atlantic Ocean, 2.5 km SSE of Castle Roads, on rhodoliths, –60 m, 23 May 1991, five colonies, up to 13 cm high, without gonophores, ROMIZ B414. Atlantic Ocean, 4 km NW of North Rock, on rhodolith and central axis of an octocoral, –70 m, 28 May 1991, three colonies, up to 9 cm high, without gonophores, ROMIZ B415. Atlantic Ocean, 2 km SSE of Castle Roads, on calcareous rubble, –91 m, 9 April 1992, three colonies, up to 3.6 cm high, without gonophores, ROMIZ B416. Atlantic Ocean, 2.5 km SSE of Castle Roads, on rhodolith, –70 m, 22 May 1991, one colony, 3.5 cm high, without gonophores, ROMIZ B417. Atlantic Ocean, 2.5 km SE of Castle Roads, on rhodoliths, –70 m, 22 May 1991, three colonies, up to 5.7 cm high, without gonophores, ROMIZ B418. Atlantic Ocean, 5 km SSE of Castle Roads, on *Macrorhynchia allmani*, –85 m, 26 May 1991, three colonies, up to 4.9 cm high, without gonophores, ROMIZ B419.

DESCRIPTION

Colonies up to about 20 cm high, with a creeping hydrorhiza. Hydrocaulus monosiphonic, wiry and slender, reaching 0.7 mm wide basally; relatively straight and unbranched in small colonies, gradually curved and branched in larger ones; basal part of hydrocaulus in large colonies sometimes devoid of apophyses, hydrocladia, nematophores, and regular nodes, merging imperceptibly and without an oblique hinge-joint with hydrocladium and nematophore-bearing part above; perisarc thick except at distal ends; nodes obliterated or mostly so except in young colonies or on distalmost parts of older colonies; cauline internodes when apparent marked by distinct to indistinct transverse nodes; each internode with a fronto-laterally situated hydrocladial apophysis, a pair of axillary nematothecae, and one or two inferior nematothecae.

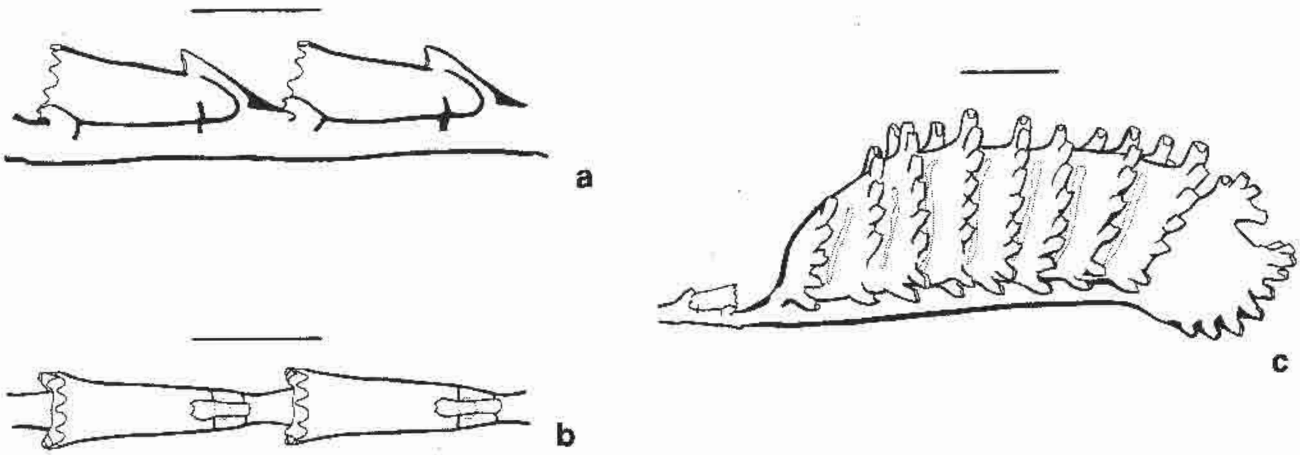

FIG. 13. *Aglaophenia dubia*, ROMIZ B410: *a*, part of hydrocladium, lateral view, with two hydrothecae; *b*, part of hydrocladium, front view, with two hydrothecae; *c*, female corbula. Scales for *a* and *b* equal 0.25; scale for *c* equals 0.5 mm.

Apophyses short, given off alternately from two sides of hydrocaulus, adjacent pair on a given side generally 1 mm or more apart; each apophysis with a cone-shaped mamelon and supporting a hydrocladium (except where broken off); mamelon with a round orifice. Cauline nematothecae scoop- to sac-shaped; aperture single, keyhole-shaped. Branching sparse and appearing dichotomous; branches originating from front of hydrocaulus, sometimes arising in pairs but typically given off singly, either unbranched or rebranched like hydrocaulus, anterior surfaces of branches generally facing hydrocaulus or branch from which they originate. Hydrocladia unbranched, reaching 17 mm long, directed outward at an angle of about 50°–60° from axis of hydrocaulus; top and frontal sides slightly convex; each hydrocladium arising directly from an apophysis and divided by nearly transverse nodes into internodes; nodes distinct to indistinct. Hydrocladial internodes 336–494 μm long, 75–130 μm wide at nodes, each with one frontally placed hydrotheca, one median inferior nematotheca, and one pair of lateral nematothecae; internodal septa two, with one at base of intrathecal septum and a less prominent one at bases of lateral nematothecae. Hydrothecae relatively distant from one another for this genus, 252–410 μm deep from tip of median abcauline cusp to base, deeply cone-shaped, axis just slightly oblique to that of internode; adcauline wall slightly convex, adnate to hydrocladial internode; abcauline wall convex basally, slightly concave distally from median inferior nematotheca to margin; intrathecal septum short, extending no more than halfway across intrathecal cavity; perisarc quite thin; abcauline wall lacking a carina. Hydrothecal aperture 126–205 μm in diameter, outline nearly round except for flattened part adnate to internode, plane of orifice slightly oblique to that of hydrotheca; margin with nine cusps, one median and four pairs of laterals, median abcauline cusp slightly larger than others, laterals nearly equal in size, all cusps acute, separated by U-shaped incisions. Median inferior nematotheca anvil-shaped, adnate to abcauline wall of hydrotheca basally, small part free distally; reaching one-third of the way along abcauline wall of hydrotheca; distal aperture scoop-shaped; a small circular aperture providing connection with hydrothecal cavity, perisarc thickened at proximal end. Lateral nematothecae duct-shaped, distal end bent forward and somewhat outward, terminal orifice scoop-shaped, reaching to or just beyond hydrothecal margin; base of each lateral nematotheca with an aperture into internode.

Gonophores fixed sporosacs. Corbulae pod-shaped, sexually dimorphic, each occurring in place of a hydrocladium on branches. Mature female corbula closed, up to 3.9 mm long, 0.9 mm wide, borne on peduncles with from one to three cormidia; rachis straight to slightly curved, bearing alternate nematocladia indistinctly separated from metabasal cladia; either side of rachis with six to 13 fused nematocladia each with a row of hoof-shaped nematothecae; free proximal, lateral, and distal ribs occasionally present. Mature male corbula open, up to 3.5 mm long, 0.8 mm wide, borne on peduncles with one or two cormidia; rachis curved, bearing alternate nematocladia indistinctly separated from metabasal cladia; either side of rachis with nine to 14 partially fused or unfused nematocladia with hoof-shaped nematothecae; no free proximal, lateral, or distal ribs like those of female. Interior of male and female corbulae with oval gonothecae arising from rachis.

REMARKS

The binomen *Aglaophenia gracilis*, originally established for this species by Allman (1877), is a permanently invalid junior primary homonym (ICZN, 1985, Art. 52b) of *Aglaophenia gracilis* Lamouroux, 1816. *Aglaophenia dubia*, proposed as a replacement name for Allman's *A. gracilis* by Nutting (1900), is here adopted for the species.

As for *A. gracilis* Lamouroux, 1816, Billard (1909) concluded that it was founded on a fragment of a species referable to *Nemertesia* Lamouroux, 1812, and probably to *N. ramosa* (Lamarck, 1816). Lamouroux (1816) is sometimes cited as the author of *N. ramosa*, but publication of the name by Lamarck (March, 1816) predates that applied to the same species by Lamouroux (October, 1816) (see Sherborn, 1922).

Allman (1877) held that hydroids assigned to *Aglaophenia rigida* Allman, 1877, were similar to and might represent a variety of *A. gracilis* (=*A. dubia*). Fewkes (1881) also suggested that the two might be conspecific, but Nutting (1900) and subsequent authors considered them to be distinct species. Although the mode of branching is similar in these species, colonies of *A. rigida* attain a much larger size than those of *A. dubia* (Nutting, 1900; Fraser, 1944). Furthermore, hydrothecae of *A. rigida* are proportionately much shallower than those of *A. dubia*, and the median inferior nematotheca extends further (about halfway) along the abcauline wall. Calder (1983) examined type material of *A. rigida* (MCZ 2109) from Cape Fear, North Carolina, and concluded that it was conspecific to *A. trifida* L. Agassiz, 1862, from Charleston and Sullivan's Island, South Carolina.

Bedot (1921b:48) regarded *Aglaophenia dubia* as conspecific with *A. elongata* Meneghini, 1845, a species common in the Mediterranean. Likewise regarded as probably identical to *A. elongata* by Bedot was *A. flowersi* Nutting, 1900, also from the warm western Atlantic. In discussing material from Tampa Bay, Florida, Leloup (1937a) concluded that *A. dubia* and *A. flowersi* were both conspecific with *A. elongata*. Also referred to *A. elongata* by Van Gemerden-Hoogeveen (1965) was part of the hydroid material from Tortugas, Florida, identified by Leloup (1935) as *Aglaophenia* (?) *allmani* Nutting, 1900.

Bogle (1975) accepted Leloup's (1937a) conclusion that *Aglaophenia dubia* and *A. flowersi* were identical, but expressed uncertainty that they were conspecific with *A. elongata*. She noted that hydroids from the eastern Atlantic, identified as *A. elongata*, differed somewhat from western Atlantic material corresponding with *A. dubia* and *A. flowersi*. In particular, Bogle noted that Meneghini's (1845: pl. 13, fig. 2) original illustration of *A. elongata* differed from her material in having deeper and more widely separated hydrothecae, and wider hydrocladial internodes. In addition, Bogle remarked that more costae (nematocladia) were present in corbulae of western Atlantic hydroids than in eastern Atlantic *A. elongata*. Nevertheless she retained western Atlantic material in *A. elongata*, concluding that such differences might be due to intraspecific variability.

I follow Leloup (1937a) and Bogle (1975) in regarding *Aglaophenia dubia* and *A. flowersi* as conspecific, and as First Reviser (ICZN, 1985, Art. 24) assign precedence to the name *A. dubia* for the species. However, Bermudian specimens referred here to *A. dubia* differ from hydroids assigned to *A. elongata* from the Mediterranean (ROMIZ B1231) by Svoboda and Cornelius (1991) in having (1) elongate instead of egg-shaped corbulae, with six to 14 instead of only four to six pairs of nematocladia, (2) corbula peduncles with one to three hydrothecae instead of a single one, (3) corbulae with frequent free ribs instead of no free ribs, and (4) cormidia with smaller lateral nematothecae that do not project as far beyond the margins of the hydrothecae (Figs. 13–14). Although less conclusive taxonomically, Bermuda material also differed from specimens of *A. elongata* collected at Elba, Italy (ROMIZ B1231), in having (1) longer (up to 14 mm versus about 5 mm) and less curved hydrocladia, (2) much thicker hydrocauli (0.7 mm versus 0.4 mm), and (3) indistinct rather than distinct nodes on hydrocauli. Based on all these differences, and on zoogeographic grounds, *A. dubia* is regarded as a valid species here. In fact, Svoboda and Cornelius (1991) regarded as erroneous all records of *A. elongata* outside the Mediterranean.

Material from Tortugas, Florida, assigned by Van Gemerden-Hoogeveen (1965) to *Aglaophenia elongata* (but here ascribed to *A. dubia*), was referred by Svoboda (1979) and Svoboda and Cornelius (1991) to *A. acacia* Allman, 1883. Van Gemerden-Hoogeveen's hydroids, and materials assigned herein to *A. dubia*, appear to differ from *A. acacia* (Figs. 13, 15) in having (1) relatively deeper and decidedly more slender hydrothecae, (2) much smaller lateral nematothecae that project to or just beyond, instead of well beyond, the hydrothecal margin, (3) median inferior nematothecae that extend one-third of the distance instead of halfway along the abcauline hydrothecal wall, and (4) branches that arise singly rather than typically in pairs. Earlier reports of *A. acacia* from the western North Atlantic (Fraser, 1912, 1944) are also regarded here as questionable. Fraser's records of *A. acacia*, both from North Carolina, were likely based on specimens of *A. trifida*. The latter species, somewhat resembling *A. acacia*, is common along the coast of the United States between North Carolina and Florida (Calder, unpublished data). Vervoort (1972) regarded *A. rigida* (=*A. trifida*) and *A. acacia* as different species, and I agree.

Fraser (1938b) reported *Aglaophenia dubia* from a depth of 70–80 fathoms (128–146 m) off Daphne Minor Island, Galápagos. The colony he studied (Allan Hancock Collections, Velero Station 792–38), reexamined here, was sterile and unbranched. Both the cormidia (Fig. 16) and the hydrocaulus of this hydroid were decidedly more robust than those in specimens of *A. dubia* from Bermuda. The Galápagos material is here regarded as questionably conspecific with *A. dubia* because of the apparent differences. Fraser's report is the only record of this species

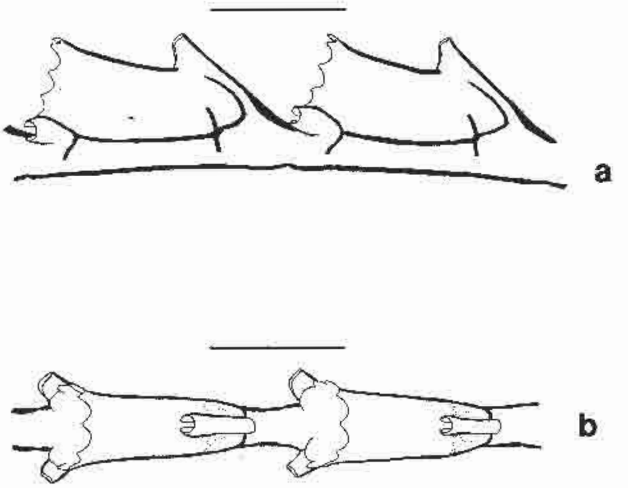

FIG. 14. *Aglaophenia elongata*, Capo d'Enfola, Elba, Italy, ROMIZ B1231: *a*, part of hydrocladium, lateral view, with two hydrothecae; *b*, part of hydrocladium, front view, with two hydrothecae. Scales equal 0.25 mm.

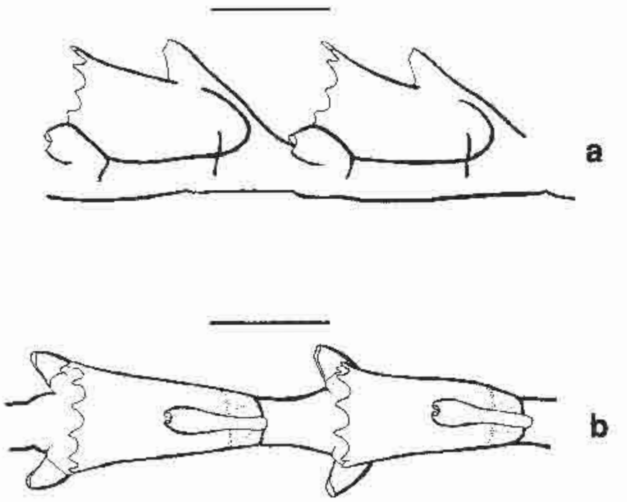

FIG. 15. *Aglaophenia acacia*, Tarragona, Spain, ROMIZ B1230: *a*, part of hydrocladium, lateral view, with two hydrothecae; *b*, part of hydrocladium, front view, with two hydrothecae. Scales equal 0.25 mm.

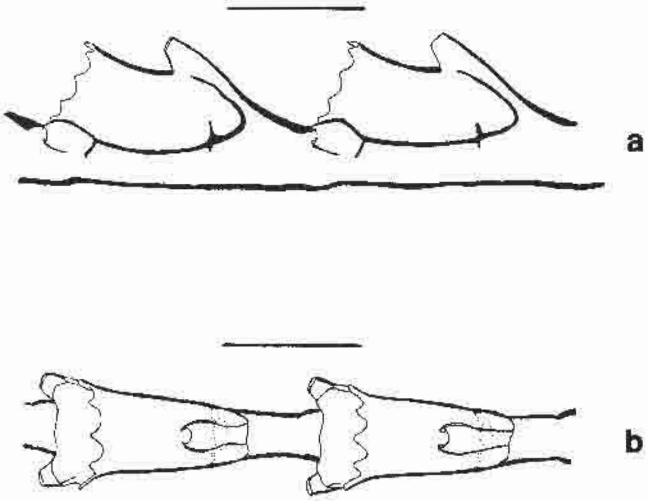

FIG. 16. *Aglaophenia* sp. (*A. dubia?*), Daphne Minor Island, Galápagos, AHF Velero Station 792–38: *a*, part of hydrocladium, lateral view, with two hydrothecae; *b*, part of hydrocladium, front view, with two hydrothecae. Scales equal 0.25 mm.

outside warm waters of the western Atlantic.

Hydroids of *Aglaophenia dubia* resemble those of another warm western Atlantic species, *A. apocarpa* Allman, 1877. However, colonies of *A. dubia* are branched (except when small) and distinguishable from those of *A. apocarpa*, which are unbranched. Small, unbranched colonies of *A. dubia* can be distinguished from those of *A. apocarpa* by the shape of their cormidia (a term defined by von Schenck, 1966, and Svoboda and Cornelius, 1991:6). In *A. dubia*, hydrothecae are more elongate than in *A. apocarpa* and median inferior nematothecae are smaller and less protuberant distally. Corbulae of *A. apocarpa* are typically short with five to 13 pairs of costae, whereas those of *A. dubia* are longer, with up to 25 pairs of costae (Bogle, 1975).

Bennitt's (1922) record of *Aglaophenia lophocarpa* Allman, 1877, from Challenger Bank (southwest of Bermuda) was based on several young hydroid colonies growing on a larger aglaopheniid. Young specimens of *A. dubia* could easily be mistaken for *A. lophocarpa*, not otherwise reported from the Bermuda area. I consider Bennitt's record of *A. lophocarpa* to have been based on material of *A. dubia*, the most common species of the genus in deeper waters of the Bermuda Platform. The record of *A. apocarpa* Allman, 1877, from the Bermuda area by Calder (1993) was based on Bennitt's (1922) earlier and likely mistaken report of *A. lophocarpa*. As for *A. apocarpa* and *A. lophocarpa*, there is confusion over which name is valid when they are regarded as conspecific (see Bedot, 1921b; Stechow, 1923a; Vervoort, 1968; Bogle, 1975; Svoboda, 1979; Gili, Vervoort, and Pagès, 1989; Svoboda and Cornelius, 1991; Svoboda, 1992). Bedot (1921b), acting as First Reviser (ICZN, 1985, Art. 24), assigned precedence to the name *A. apocarpa*. Stechow's (1923a) assertion that the name *A. lophocarpa* should have priority because it appeared before *A. apocarpa* in Allman's (1877) publication is contrary to the International Code of Zoological Nomenclature.

Hydroids from Bermuda assigned here to *Aglaophenia dubia* include colonies identified earlier by Calder (1993) as *Aglaophenia* sp.

REPORTED RANGE

Bermuda: Challenger Bank (Bennitt, 1922, as *Aglaophenia lophocarpa*); deeper coastal waters (Calder, 1993, as *Aglaophenia apocarpa* and *Aglaophenia* sp.).

Circumglobal distribution: western Atlantic (Rees and Thursfield, 1965; (?) eastern Pacific (Fraser, 1938b).

Aglaophenia latecarinata Allman, 1877

Fig. 17

?*Sertularia pluma*—Bosc, 1802:95, pl. 29, fig. 1 [not *Aglaophenia pluma* (Linnaeus, 1758)].

?*Aglaophenia pelagica* Lamouroux, 1816:170 [nomen dubium].

?*Plumularia pelagica*—H. Milne Edwards, *in* Lamarck, 1836:167.

?*Plumularia simplex* d'Orbigny, 1846:27, pl. 13 (Polypiers), figs. 1–2 [nomen dubium].

?*Aglaophenia pelasgica*—McCrady, 1859:202 [incorrect subsequent spelling] [not *Hydra pelagica* Bosc, 1797].

?*Aglaophenia simplex*—Kirchenpauer, 1872:25, pl. 1, fig. 1.

not *Aglaophenia perforata* Kirchenpauer, 1876:25 [nomen nudum] [=*Macrorhynchia philippina* Kirchenpauer, 1872].

Aglaophenia perpusilla Allman, 1877:48, pl. 29, figs. 5–7.

Aglaophenia late-carinata Allman, 1877:56 [incorrect original spelling].

Aglaophenia minuta Fewkes, 1881:132, pl. 3, fig. 7.

Aglaophenia perforata Allman, 1885:150, pl. 21, figs. 5–8.

Aglaophenia latecarinata—Tizard et al., 1885:136 [justified emendation].

Aglaophenia mammillata Nutting, 1900:98, pl. 21, figs. 6–10.

Aglaophenia minima Nutting, 1900:98, pl. 21, figs. 11–13.

?*Anisocalyx* (*Aglaophenia*) *pelagica*—Bedot, 1905:48.

Aglaophenia latecarinata madagascariensis Billard, 1907:387.

Agalaophenia minuta—Cary and Spaulding, 1909:6 [incorrect subsequent spelling].

not *Aglaophenia* (*Macrorhynchia*) *perforata* Stechow, 1919a:132 [unavailable name, published as a junior synonym] [=*Macrorhynchia philippina* Kirchenpauer, 1872].

Aglaophenia mamillata—Bedot, 1921b:42 [incorrect subsequent spelling].

Aglaophenoides mammillata—Fraser, 1943:83, pl. 19, figs. 14a–b [incorrect original spelling].

not *Aglaophenia latecarinata*—Vervoort, 1959:309, fig. 54b [part] [=*Aglaophenia rhynchocarpa* Allman, 1877].

Aglaophenia latecerinata—Adams, 1960:81 [incorrect subsequent spelling].

?*Aglaophenia*—Weis, 1968:556.

Aglaeophenia latecarinata—Morris and Mogelberg, 1973:17, figs. 21a–d [incorrect subsequent spelling].

Aglaeophenia perpusilla—Morris and Mogelberg, 1973:17, figs. 22a–b [incorrect subsequent spelling].

Aglaeophenoides mammillata—Morris and Mogelberg, 1973:19, figs. 24a–b [incorrect subsequent spelling].

not *Aglaophenia latecarinata*—García, Aguirre, and Gonzalez, 1978:65, figs. 31A–B [?=*Aglaophenia picardi* Svoboda, 1979].

Aglaophenia latercarinata—Florez Gonzalez, 1983:138 [incorrect subsequent spelling].

Aglaophenia mammilata—Mayal, 1983:8 [incorrect subsequent spelling].

Aglaophenia latecanaria—Butler et al., 1983:229 [incorrect subsequent spelling].

not *Aglaophemia latecarinata*—Izquierdo, García-Corrales, and Bacallado, 1986:62 [=*Aglaophenia* sp.] [incorrect subsequent spelling].

Aglaophenoides mammillatus—Cairns et al., 1991:29 [justified emendation].

TYPE LOCALITY

"Gulf of Mexico . . . attached to Gulf Weed" (Allman, 1877:56).

MATERIAL EXAMINED

Whalebone Bay, on stranded *Sargassum fluitans*, 27 February 1982, two colonies, up to 8 mm high, without gonophores, ROMIZ B125. Town Cut, on limestone wall, –2 m, 5 July 1983, four colonies, up to 17 mm high, without gonophores, ROMIZ B420. Shelly Bay Beach, on stranded *Sargassum fluitans*, 5 December 1989, one (?) colony, up to 10 mm high, with gonophores, ROMIZ B421. Atlantic Ocean, 2 km off Natural Arches Beach, on rhodoliths, –70 m, 13 May 1991, four colonies, up to 27 mm high, without gonophores, ROMIZ B422. Challenger Bank, on calcareous rubble, –70 m, 3 October 1984, one colony, 15 mm high, without gonophores, ROMIZ B423. Shelly Bay beach, on stranded plastic, 4 December 1989, one (?) colony, up to 16 mm high, with gonophores, ROMIZ B424. Flatts Inlet, on pelagic *Sargassum fluitans*, at surface, 4 December 1992, one (?) colony, up to 10 mm high, with gonophores, ROMIZ B425. Flatts Inlet, on pelagic *Sargassum natans*, at surface, 1 December 1989, one colony, up to 10 mm high, without gonophores, ROMIZ B426. Fort St. Catherine's Beach, on stranded *Sargassum fluitans*, 25 September 1984, three colonies, up to 7 mm high, with gonophores, ROMIZ B427.

DESCRIPTION

Colonies up to 27 mm high (to 10 mm on *Sargassum*), with a creeping, wrinkled hydrorhiza; lumen of hydrorhiza of colonies on *Sargassum* with septa. Hydrocaulus monosiphonic, slender, unbranched, 0.1–0.2 mm wide basally, slightly to distinctly convex frontally; perisarc relatively thick basally, thinning progressively towards distal end. Basal part of hydrocaulus varying in length, with several irregular annulations/nodes just above juncture with hydrorhiza; devoid of apophyses and hydrocladia; reinforced by irregularly placed internal septa in colonies on *Sargassum*; one or more large cauline nematothecae present; separated from hydrocladium-bearing part above by a short internode having a single nematotheca and oblique hinge-joints proximally and distally. Distal part of hydrocaulus divided into internodes by distinct to indistinct

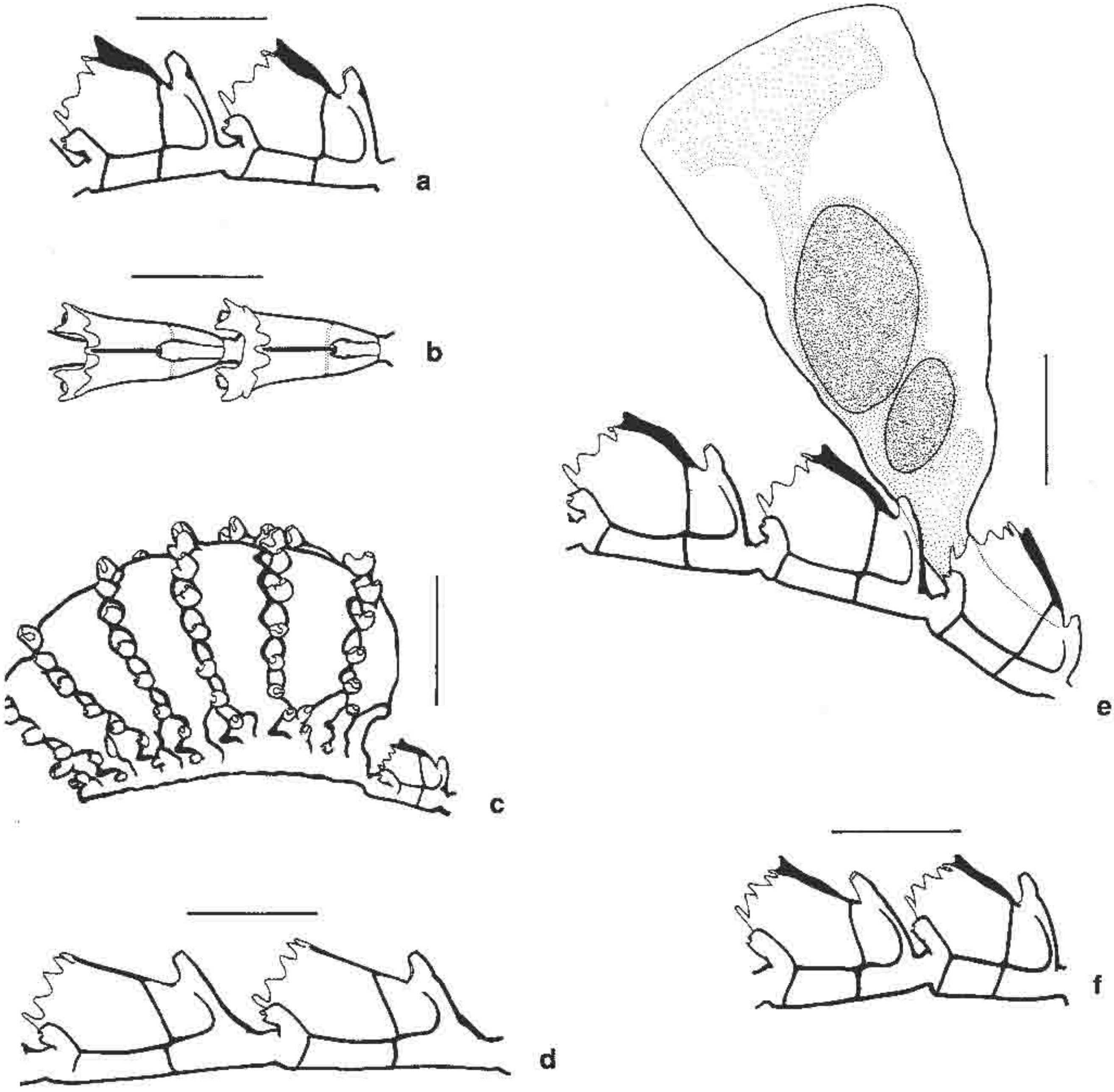

FIG. 17. *Aglaophenia latecarinata: a,* part of hydrocladium, lateral view, with two hydrothecae, ROMIZ B421; *b,* part of hydrocladium, front view, with two hydrothecae, ROMIZ B421; *c,* corbula, ROMIZ B421; *d,* part of hydrocladium, lateral view, with two hydrothecae, ROMIZ B422; *e, Aglaophenoides mammillata* of Fraser (1943), part of hydrocladium, lateral view, with three hydrothecae and gonotheca, MCZ, no catalogue number; *f,* part of hydrocladium of type colony of *Aglaophenia perforata* Allman, 1885, St. Vincent, Windward Islands, lateral view, with two hydrothecae, BMNH 1956.10.23.2. Scales for *a, b, d, e,* and *f* equal 0.25 mm; scale for *c* equals 0.5 mm.

transverse nodes; each internode of hydrocaulus typically with a large, cowl-shaped, inferior nematotheca, a frontolaterally situated hydrocladial apophysis, and a pair of small, sac-shaped, axillary nematothecae; internodes in colonies on *Sargassum* each with a proximal and a distal internal septum. Apophyses short, given off alternately from each side of hydrocaulus, adjacent pair on a given side about 0.5–1.0 mm apart; each apophysis with a cone-shaped mamelon basally and supporting a hydrocladium distally (except where broken off); mamelon prominent, with a round to oval orifice. Hydrocladia reaching about 4 mm long (typically less than half that in colonies on *Sargassum*), unbranched, directed outward at an angle of about 65° or more from axis of hydrocaulus; frontal sides convex; top sides convex to nearly straight; each hydrocladium arising directly from an apophysis and divided into short internodes by nearly transverse nodes. Hydrocladial internodes 214–419 μm long, 51–61 μm wide at nodes, each with one frontally placed hydrotheca, one median inferior nematotheca, and one pair of lateral nematothecae; internodal septa typically two, with one at base of intrathecal septum and another at bases of lateral nematothecae, both well developed and reaching across internode, occasionally with an additional more weakly developed septum between these two. Hydrothecae close together, 242–317 μm deep from tip of median abcauline cusp to base, cone-shaped, axis oblique to that of internode; adcauline wall convex, occasionally with a slight concavity at proximal end, notched at intrathecal septum, adnate to hydrocladial internode except for small free part at distalmost end; abcauline wall convex basally, nearly straight to slightly concave from juncture of intrathecal septum to margin; intrathecal septum prominent, slightly oblique, extending from adcauline to abcauline wall of hydrotheca, appearing in lateral view to divide cavity into two sections; abcauline wall with a carina of varying thickness, from thin and almost imperceptible to thick and keel-shaped, extending forward to median abcauline cusp, distal end of carina prow-shaped; perisarc elsewhere of moderate thickness. Hydrothecal aperture 140–168 μm in diameter from adcauline wall to base of median abcauline cusp, irregularly oval in outline, plane of orifice nearly perpendicular to long axis of hydrotheca; margin with nine rounded cusps, one median and four pairs of laterals, all cusps prominent, separated by U-shaped incisions; cusps sometimes more or less equal in size but when unequal, third pair of laterals largest. Median inferior nematotheca anvil-shaped, adnate to abcauline wall of hydrotheca basally, small part free distally; apex reaching from one-third to one-half distance along abcauline wall of hydrotheca; distal aperture scoop-shaped, or keyhole-shaped, or round to oval with an additional oval aperture at juncture with abcauline wall of hydrotheca; nematothecal and hydrothecal cavities connected by a small circular aperture. Lateral nematothecae horn-shaped, directed outward, terminal orifice scoop-shaped, reaching to or just beyond hydrothecal margin; base of each lateral nematotheca with an aperture into internode.

Gonophores fixed sporosacs. Corbulae bean-shaped, each occurring in place of a proximal hydrocladium. Mature corbula up to 1.6 mm long, 1 mm wide, borne on peduncle having a single cormidium; rachis wrinkled, slightly curved to almost straight, bearing alternate nematocladia arising from metabasal cladia; either side of rachis with four to seven partially fused nematocladia each with a row of hoof-shaped nematothecae; base of nematocladium with a prominent anterior spur; gaps between adjacent metabasal cladia large, irregular in shape, and continuing upward between proximal parts of adjoining nematocladia; smaller oval gaps laterally and distally on corbula between adjacent nematothecae. Interior of corbulae with several oval gonothecae, each arising from rachis.

REMARKS

Lamouroux (1816) described, as *Aglaophenia pelagica*, a small plumularioid found growing on the pelagic seaweed "*Fucus natans*." Based on the substrate, it seems likely that it was conspecific with the hydroid now known as *A. latecarinata* Allman, 1877. Billard (1909), too, maintained that Lamouroux's type material of *A. pelagica* was probably identical to *A. latecarinata*, although it was not well-enough preserved to be certain. The two specimens on the type slide of *A. pelagica* (MNHN L 889) indeed resemble *A. latecarinata*, but their hydrothecae are damaged beyond positive identification. With the lingering uncertainty about the identity of *A. pelagica*, and its nomenclatural threat to a better-known junior name, Billard (1909) proposed that the binomen employed by Lamouroux be suppressed. Fraser (1944) treated *A. pelagica* and *A. latecarinata* as separate species to avoid the nomenclatural problem, although he likewise suspected that the two were conspecific. Lamouroux's nominal species is dealt with here as a nomen dubium instead (see also Bogle, 1975), but a case should be submitted to the ICZN requesting suppression of the now virtually abandoned specific name *pelagica* of Lamouroux (1816).

As for hydroids identified by McCrady (1859) and A. Agassiz (1865) as *A. "pelasgica,"* they are likely to have been identical to the species currently known as *A. latecarinata*. However, McCrady and Agassiz mistakenly thought that Bosc's (1802) *Sertularia pelasgica* was the same species, and adopted that spelling of the specific name. The binomen *Sertularia pelasgica*, used by Bosc (1802), is an incorrect subsequent spelling of *Hydra pelagica* Bosc, 1797. Rather than an aglaopheniid, *H. pelagica* is likely referable to the genus *Obelia* Péron and Lesueur, 1810, and probably to *O. dichotoma* (Linnaeus, 1758). Meanwhile, Bosc's (1802) record of *Sertularia* *pluma* Linnaeus, 1758, from hydroids attached to *Sargassum* ("*Fucus natans*") may have been based on misidentified material of *A. latecarinata*.

Nutting (1900) recognized a "*minuta* group" of six nominal species within the genus *Aglaophenia* Lamouroux, 1812, in American waters, namely, *A. simplex* (d'Orbigny, 1846); *A. perpusilla* Allman, 1877; *A. minuta* Fewkes, 1881; *A. perforata* Allman, 1885; *A. mammillata* Nutting, 1900; and *A. minima* Nutting, 1900. He regarded the name *Aglaophenia latecarinata* as a junior synonym of *A. minuta*, mistakenly thinking that the former was founded by Allman (1885) instead of Allman (1877). The name *A. latecarinata* was established (as *A. late-carinata*) in an addendum at the end of Allman's (1877) publication, together with a definition distinguishing the species from a similar form (*A. perpusilla*). Criteria of availability are met for *A. latecarinata* in that publication, although it was later described as new by Allman (1885).

Bedot (1918, 1921b) commented that *Aglaophenia simplex* was indeterminable and suggested that the name should be suppressed. Based on its substrate (pelagic *Sargassum*), its small size, and its general morphology (as described by d'Orbigny, 1846), it may have been identical to hydroids assigned today to *A. latecarinata*. Kirchenpauer (1872) provided additional records and an illustration, redrawn in Nutting (1900, pl. 22, fig. 1), but it is questionable whether Kirchenpauer's hydroids were referable to the species described by d'Orbigny. Given the uncertainty about the identity of *A. simplex*, the name is regarded here as a nomen dubium.

The name *Aglaophenia perpusilla* was applied by Allman (1877) to a minute species collected during the Pourtalès explorations of the Straits of Florida. Although reportedly collected at a depth of 34 fathoms (62 m), the hydroid was found on "seaweed." This suggests that the material may have originated in shallower water, and Bogle (1975) questioned whether the substrate may have been *Sargassum*. Bedot (1921b) regarded *A. perpusilla* as similar to and possibly conspecific with *A. latecarinata*. Vervoort (1972) recognized *A. perpusilla* as valid and provisionally compared it with material recovered from 5159 m on the Hatteras Abyssal Plain. Hydrothecae of Vervoort's material were filled with dirt, and he suspected, with justification, that it originated in shallow waters. Bogle (1975) concluded that *A. perpusilla* and *A. latecarinata* were conspecific, based on the variability of the characters used by Allman (1877, 1885) to distinguish *A. perpusilla* and *A. latecarinata* (width of the hydrothecal carina, hydrothecal depth, and thickness of the intrathecal ridge). She adopted the more commonly used of the two names, *A. latecarinata*, for the species in her Master's thesis. I agree with Bogle that the two are coterminous. Applying the Principle of the First Reviser (ICZN, 1985, Art. 24), *A. latecarinata* is assigned precedence here over *A. perpusilla*. According to Bogle, the type of *A. perpusilla* is missing from its bottle at the Museum of Comparative Zoology, Harvard University.

Fewkes (1881) described *Aglaophenia minuta* from material collected at 233 fathoms (426 m) on the continental slope off Charleston, South Carolina. Hydroids occurred on the thallus of an alga, indicating a shallower origin of the material. The substrate was probably sinking *Sargassum* (see Johnson and Richardson, 1977), common in certain deep-sea areas of the western North Atlantic (Grassle and Morse-Porteous, 1987). *Aglaophenia minuta* and *A. latecarinata* have been regarded as conspecific throughout the 20th century (e.g., see Nutting, 1900; Billard, 1907; Ritchie, 1909a; Stechow, 1912; Bedot, 1912, 1916a; Leloup, 1932b; Fraser, 1944; Vannucci Mendes, 1946; Millard, 1958; Rees and Thursfield, 1965; Van Gemerden-Hoogeveen, 1965; Vervoort, 1968; Bogle, 1975; Mergner and Wedler, 1977; Calder, 1995), although there has been confusion over the relative priority of the two names. As noted above, this stems from the mistaken impression that *A. latecarinata* dates from Allman (1885), whereas the name was actually made available earlier by Allman (1877). The binomen *A. minuta* has been abandoned as a valid name over the past 50 years.

The binomen *Aglaophenia perforata* was established by Allman (1885) for a "minute" species of *Aglaophenia* on gulf-weed (*Sargassum* sp.) from St. Vincent, Windward Islands (not Florida, as reported by Vervoort (1968) and Bogle (1975)). Nutting (1900) noted the resemblance of *A. perforata* to others in his *minuta* group, but concluded that it differed from all of them in lacking a hydrothecal keel (carina). In fact, a well-developed carina is present on the hydrotheca in type material (BMNH 1956.10.23.2) of *A. perforata* (Fig. 17f). Purported differences distinguishing *A. perforata* from the related *A. minima*, according to Nutting (1900), were its obconic hydrothecal shape and its corbula morphology. Bogle (1975) discounted the taxonomic utility of such characters within this group, noting their variability in material she assigned to *A. latecarinata*. Another attribute used to distinguish *A. perforata* from related species in the western North Atlantic is the number of cusps on the hydrothecal margin. Based on Allman's (1885) original description, Fraser (1944) reported 11 cusps in *A. perforata* as opposed to nine (or eight) in other species of Nutting's (1900) *minuta* group. In fact, hydrothecae in Allman's type material, reexamined here, have nine cusps on the margin. *Aglaophenia perforata* and *A. latecarinata* are regarded here as identical, with the latter name having priority. The names *Aglaophenia perforata* and *Aglaophenia* (*Macrorhynchia*) *perforata* were used by Kirchenpauer (1876) and Stechow (1919a), respectively, for a hydroid here considered identical to *Macrorhynchia philippina* Kirchenpauer, 1872, but neither meets ICZN criteria of availability (see *M. philippina*, Remarks).

Therefore, they do not constitute homonyms of *Aglaophenia perforata* Allman, 1885.

Aglaophenia mammillata was established by Nutting (1900) for a small species (<4 cm high) collected at a depth of 15 fathoms (27 m) off Cape Fear, North Carolina. Its resemblance to *A. perpusilla*, or to others regarded here as identical to *A. latecarinata*, has been noted several times (Bedot, 1921b; Fraser, 1946; Bogle, 1975). Characters used by Nutting (1900) to distinguish *A. mammillata* from others of his *minuta* group (greater colony height, narrower hydrothecal carina, smooth hydrorhiza, and smaller processes at the base of each hydrocladium) were found to vary in material assigned to *A. latecarinata* from Brazil (Vannucci Mendes, 1946). Bogle (1975) noted that the larger colony size and lack of hydrorhizal "annulations" of Nutting's material might be attributed to its occurrence on a substrate other than *Sargassum*. Moreover, she found that hydrothecae of type material were virtually identical to those identified by Nutting (1900) as *A. minuta* (*A. latecarinata*). As for the development of the hydrothecal carina, it is now known to be decidedly variable (e.g., see Van Gemerden-Hoogeveen, 1965; Vervoort, 1968). The presence or absence of "annulations" on the hydrorhiza depends upon whether or not internal septa are present (see Leloup, 1932b), and is likely a function of substrate. I follow Vannucci Mendes (1946) and Mayal (1983) in considering *A. mammillata* to be conspecific with *A. latecarinata*. Specimens from coastal waters of Bermuda (ROMIZ B422) and from Challenger Bank (ROMIZ B423) corresponding with Nutting's original description of *A. mammillata* (Fig. 17d) are included here in *A. latecarinata*. Apparent deviations from typical *A. latecarinata* (larger colonies, more widely separated hydrocladia, deeper and more widely separated hydrothecae, thinner perisarc, weakly developed carinae, and absence of septa in hydrorhizae and hydrocauli) are attributed to the influence of different environmental conditions on morphologically variable characters.

Fraser (1943) removed *Aglaophenia mammillata* to a new genus, *Aglaophenoides*, as discussed elsewhere in this report (see Genus *Gymnangium*, Remarks). Fraser's material, illustrated in Fig. 17e, is assigned here to *A. latecarinata*.

The final member of Nutting's (1900) *minuta* group, *Aglaophenia minima* from the Bahamas, was reportedly the smallest and most delicate of the six. It was distinguished from others of the group by (1) its complete lack of a hydrothecal carina, (2) its nearly cylindrical hydrotheca, and (3) its short and stout corbula. Bogle (1975) discounted the taxonomic significance of these differences and regarded *A. minima* as conspecific with *A. perforata*. Earlier, Vervoort (1959) regarded *A. minima* as identical to *A. latecarinata*, an opinion also held here.

The records of *Aglaophenia latecarinata* from west Africa by Vervoort (1959) appear to have been based on material of two species, *A. latecarinata* and *A. rhynchocarpa* Allman, 1877 (see *Aglaophenia rhynchocarpa*, Remarks). Vervoort speculated that colonies resembling *A. rathbuni* Nutting, 1900 (=*A. rhynchocarpa*) might represent male colonies of *A. latecarinata*, but there has been no additional evidence to support that view.

Material identified as *Aglaophenia latecarinata* from the Mediterranean coast of Spain by García, Aguirre, and Gonzalez (1978) is considered here to be a different species. In contrast to *A. latecarinata*, the specimens had weakly developed intrathecal septa, no hydrothecal carinae, and regularly rounded marginal cusps. Their hydroids resemble *A. picardi* Svoboda, 1979, a species known throughout the Mediterranean (Svoboda and Cornelius, 1991). In addition, hydroids from the Canary Islands, identified as *A. latecarinata* by Izquierdo, García-Corrales, and Bacallado (1986), are considered here to be referable to another species.

According to Allman (1885:152), *Aglaophenia latecarinata* "appears indeed to be quite a characteristic form of the hydroid fauna of the floating Sargasso field of the North Atlantic." Around Bermuda, it is one of the principal hydroid dominants on the holopelagic alga *Sargassum fluitans* (Burkenroad, *in* Parr, 1939; Calder, 1995).

REPORTED RANGE

Bermuda: on pelagic *Sargassum* (Congdon, 1907; Smallwood, 1910; Bennitt, 1922; Burkenroad, *in* Parr, 1939: as *Aglaophenia minuta*. Morris and Mogelberg, 1973; Butler et al., 1983; Calder, 1986, 1993, 1995: as *A. latecarinata*); Challenger Bank, Agar's Island (Bennitt, 1922, as *A. minuta*).

Circumglobal distribution: western Atlantic (Vervoort, 1968); eastern Atlantic (Vervoort, 1968, as *A. latecarinata*, in part), Indian Ocean (Millard, 1975); western Pacific (Hirohito, 1983).

Aglaophenia rhynchocarpa Allman, 1877

Fig. 18

Aglaophenia rhynchocarpa Allman, 1877:40, pl. 23, figs. 5–8.

Aglaophenia rhyncocarpa—Fewkes, 1881:131 [incorrect subsequent spelling].

Aglaophenia cylindrata Versluys, 1899:49, figs. 19–21.

Aglaophenia rathbuni Nutting, 1900:101, pl. 22, figs. 4–6.

Aglaophenia rynchocarpa—Bedot, 1918:64 [incorrect subsequent spelling].

Aglaophenia insolens Fraser, 1943:81, pl. 19, figs. 13a–c.

Aglaophenia latecarinata—Vervoort, 1959:309, fig. 54b [part] [not *Aglaophenia latecarinata* Allman, 1877].

Aglaophenia rhynchocarpha—Florez Gonzalez, 1983:

123,125 [incorrect subsequent spelling].

Aglaophenia rynchocarpha—Florez Gonzalez, 1983:124 [incorrect subsequent spelling].

TYPE LOCALITY

Triangle Shoal, Key West, Florida (Allman, 1877).

MATERIAL EXAMINED

Challenger Bank, on *Sertularella diaphana*, –32 fathoms (–59 m), 23 April 1873, one colony with two hydrocauli, 2.5 cm high, without gonophores, Challenger Expedition Station 36, fragment from BMNH 1888.11.13.12A, ROMIZ B409.

DESCRIPTION

Colony 2.5 cm high, with a hydrorhiza originally growing on stem of a thecate hydroid. Hydrocaulus 215 μm wide basally, unbranched, monosiphonic, relatively straight; divisible into two distinct parts. Basal part of hydrocaulus with nematothecae but lacking apophyses and hydrocladia, varying in length, articulating with distal hydrocladium-bearing part of hydrocaulus by an oblique hinge-joint; perisarc thick, internodes obliterated or mostly so. Rest of hydrocaulus divided into internodes by distinct to indistinct transverse nodes, these nodes more distinct distally than proximally; each internode with a fronto-laterally situated hydrocladial apophysis, a pair of axillary nematothecae, and an inferior nematotheca; perisarc relatively thick basally, thinner distally. Apophyses short, given off alternately from each side of hydrocaulus, quite closely spaced; each apophysis with a cone-shaped mamelon and supporting a hydrocladium (except where broken off); mamelon with a round orifice. Cauline nematothecae sac-shaped; aperture single, quite small. Hydrocladia reaching 5 mm long, unbranched, directed outward at an angle of about 70° or more from axis of hydrocaulus; top and frontal sides slightly convex; each hydrocladium arising directly from an apophysis and divided into short internodes by nearly transverse nodes. Hydrocladial internodes 270–322 μm long, 56–89 μm wide at nodes, each with one frontally-placed hydrotheca, one median inferior nematotheca, and one pair of lateral nematothecae; internodal septa variably developed, typically four in number, with one at base of hydrotheca, one at base of intrathecal septum, one mid-way along hydrothecal wall, and one at bases of lateral nematothecae, most prominent septum typically being the one at base of intrathecal septum. Hydrothecae close to one another, 252–308 μm deep from tip of median abcauline marginal cusp and tips of adcauline cusps to base, deeply cone-shaped to nearly cylindrical, axis slightly oblique to that of internode; adcauline wall convex proximally and distally, notched at intrathecal septum, adnate to hydrocladial internode except for a small free part distally; abcauline wall convex basally, concave medially, nearly straight distally; intrathecal septum prominent, oblique, slightly sigmoid in lateral view, extending from adcauline to abcauline wall of hydrotheca; perisarc quite thin. Hydrothecal aperture 112–130 μm in diameter from adcauline wall to base of median abcauline cusp, irregularly oval in outline, plane of

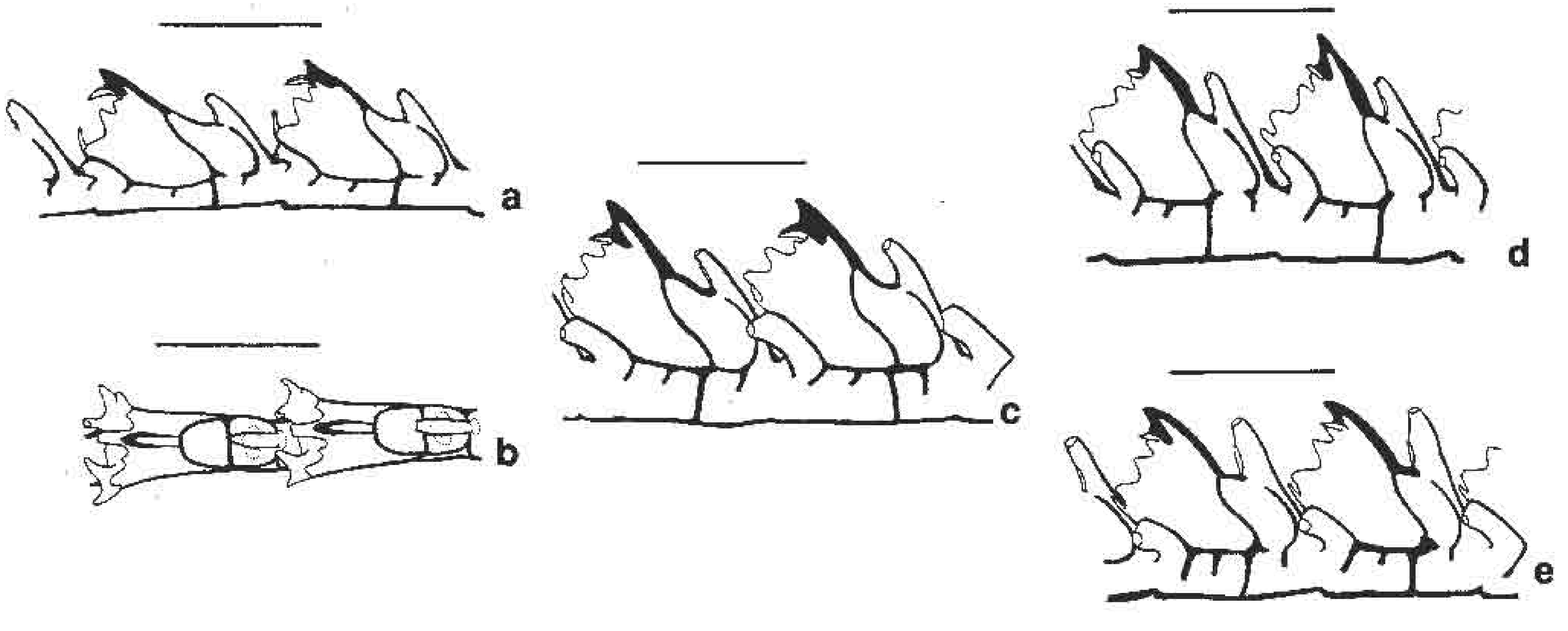

FIG. 18. *Aglaophenia rhynchocarpa: a,* part of hydrocladium, lateral view, with two hydrothecae, BMNH 1888.11.13.12A; *b,* part of hydrocladium, front view, with two hydrothecae, BMNH 1888.11.13.12A; *c,* part of hydrocladium of type material of *Aglaophenia rhynchocarpa* Allman, 1877, Key West, Florida, lateral view, with two hydrothecae, MCZ, no catalogue number; *d,* part of hydrocladium of type material of *Aglaophenia rathbuni* Nutting, 1900, Caravellas, Brazil, lateral view, with two hydrothecae, USNM 18657; *e,* part of hydrocladium of type material of *Aglaophenia insolens* Fraser, 1943, Maguaripe Bay, Trinidad, lateral view, with two hydrothecae, MCZ 9001. Scales equal 0.25 mm.

orifice nearly perpendicular to that of hydrotheca; margin with nine cusps, one median and four pairs of lateral; median abcauline cusp long, linguiform in top view, convex and visor-shaped in lateral view, curved towards pair of cusps on adcauline wall, concave along median axis; pair of cusps lateral to median abcauline cusp typically quite low, with acute tips; next pair of cusps larger, with blunt tips; next pair larger still, with blunt tips; pair flanking adcauline median wall long, fang-shaped, curved upwards towards median abcauline cusp, tips acute. Abcauline wall of hydrotheca with a well but variably developed carina extending forward to median abcauline cusp, distal end of carina prow-shaped. Median inferior nematotheca anvil-shaped, adnate to abcauline wall of hydrotheca basally, approximately one-third free distally, apex reaching less than halfway along abcauline wall of hydrotheca; distal aperture circular; basal aperture present anteriorly; a small circular aperture providing connection with hydrothecal cavity. Lateral nematothecae horn-shaped to somewhat tubular, distal end bent forward and slightly to the side, terminal orifice round, reaching to or just beyond hydrothecal margin; base of each lateral nematotheca with an aperture into internode.

Gonophores not seen.

REMARKS

Aglaophenia rhynchocarpa was originally described by Allman (1877) from the important collection of hydroids obtained in the Straits of Florida by L. F. de Pourtalès. It shares with *A. gracillima* Fewkes, 1881, an oblique and slightly sigmoid intrathecal septum but it lacks the exceedingly long median abcauline spine extending forward from the margin of the hydrotheca (Fig. 18c). As well, the corbula peduncle of *A. rhynchocarpa* is comprised of a single cormidium whereas that of *A. gracillima* includes three or four cormidia (Fraser, 1944).

Aglaophenia cylindrata Versluys, 1899, with a similar intrathecal septum, was described from infertile material dredged near the Testigos Islands, West Indies. Later, a fertile hydroid from Anguilla with an elongate and cigar-shaped corbula was referred to *A. cylindrata* by Jäderholm (1903). This structure appeared unlike the shorter, pod-shaped corbula of *A. rhynchocarpa* described by Allman (1877). However, Vervoort (1968) attributed the differences in shape to sexual dimorphism and concluded that *A. cylindrata* was conspecific with *A. rhynchocarpa*. Bogle (1975) reported corbulae of both shapes in material assigned by her to *A. rhynchocarpa*, and on close examination found them to be structurally similar. She agreed with Vervoort that *A. cylindrata* and *A. rhynchocarpa* were coterminous. Trophosomes of the two appear much alike from original descriptions and illustrations (Allman, 1977; Versluys, 1899), and I follow Vervoort (1968) and Bogle (1975), and Bedot (1925) earlier, in regarding them as conspecific.

Aglaophenia rathbuni Nutting, 1900, from Brazil and *A. insolens* Fraser, 1943, from Trinidad appear much alike morphologically. Each possesses a sigmoid intrathecal septum and resembles type material of *A. rhynchocarpa* (MCZ, no catalogue number), although both seem to diverge slightly in hydrothecal shape and orientation (Figs. 18d–e). Bogle (1975) compared types of both *A. rathbuni* and *A. insolens* and concluded that they were conspecific. I support her conclusion after reexamining the same type material (USNM 18657, 18658; MCZ 9001). Neither of these two names was included by Bogle in the synonymy of *A. rhynchocarpa*, although she inferred that *A. rathbuni* (including *A. insolens*) was merely a variant of that species. Hydroids with hydrothecae intermediate in form between typical *A. rhynchocarpa* and *A. rathbuni* were reportedly present in her material. Moreover, she found corbulae of the two morphotypes to be similar. Based on her observations, on the morphological resemblance of type specimens of all three, and on the considerable variations in hydrothecal morphology known to occur in aglaopheniids, I conclude that *A. rathbuni* and *A. insolens* are conspecific with *A. rhynchocarpa*. The Challenger material examined here from Bermuda corresponds closely to the type of *A. rhynchocarpa* (Figs. 18a–c), but differs principally in having (1) more widely spaced hydrocladia, resulting in a more open colony form, (2) hydrothecae with their axes more nearly parallel with that of the hydrocladium, and (3) linguiform instead of acute median abcauline cusps.

Vervoort (1959) identified as *Aglaophenia latecarinata* Allman, 1877, two tufts of hydroids collected off Freetown, Sierra Leone, Africa (Atlantide Station 141). Vervoort's illustrations suggest that one of these colonies was indeed *A. latecarinata* (fig. 54a), while the other (figs. 54b–c) was not. The latter seems indistinguishable in the figures from *A. rathbuni* (=*A. rhynchocarpa*). It is taken here to be the only record of *A. rhynchocarpa* outside warm waters of the western Atlantic. Bogle (1975) came to the same conclusion earlier.

The hydroid colony assigned here to *Aglaophenia rhynchocarpa* was collected at the north end of Challenger Bank during the Challenger Expedition. The same specimen had been examined earlier and identified as *Aglaophenia cylindrata* by Ritchie (1909c). Allman (1883) did not include the species in his report on Challenger plumularioids, perhaps because the hydroid was preserved together with material of *Campanularia insignis* Allman, 1888 [=*Cnidoscyphus marginatus* (Allman, 1877)] (BMNH 1888.11.13.12A) that was described later. Also present in the same bottle with these species were the thecate hydroids *Hebella venusta* (Allman, 1877) and *Sertularella diaphana* (Allman, 1885) (see Calder, 1991a).

REPORTED RANGE

Bermuda: Challenger Bank (Ritchie, 1909c; Bennitt, 1922; Rees and Thursfield, 1965: as *Aglaophenia cylindrata*); banks (Calder, 1993).

Circumglobal distribution: western Atlantic (Vervoort, 1968); eastern Atlantic (Vervoort, 1959, as *Aglaophenia latecarinata*, in part).

Genus *Macrorhynchia* Kirchenpauer, 1872

Macrorhynchia Kirchenpauer, 1872:20.

Makrorhynchia Kirchenpauer, 1872: pls. 1, 8 [incorrect original spelling].

Makrorynchia Allman, 1874b:179 [incorrect subsequent spelling].

Macrorhynihia Kirchenpauer, 1876:25 [incorrect subsequent spelling].

Macrorynchia Kirchenpauer, 1876:26 [incorrect subsequent spelling].

Nematophorus Clarke, 1879:248.

Pleurocarpa Fewkes, 1881:136.

Macrorhyncha Hincks, 1889:134 [incorrect subsequent spelling].

Macrorhinchia Naumov, 1960:478 [incorrect subsequent spelling].

DIAGNOSIS

Colonies erect; hydrocauli branched, polysiphonic, often stout, arising from a creeping hydrorhiza or from anchoring filaments. Cauline internodes with triangular nematothecae. Hydrocladia unbranched, arranged pinnately, arising alternately from apophyses on axial tube of hydrocaulus and branches. Hydrothecae occurring only on hydrocladia, typically more or less cone- to sac-shaped; margin dentate; abcauline or adcauline intrathecal septum typically present. Each hydrotheca with a pair of lateral nematothecae and one partly adnate median inferior nematotheca.

Gonophores fixed sporosacs, or released as medusoids. Gonothecae on phylactocarps that are unbranched phylactogonia, these occurring singly or aggregated to form a pseudocorbula; each phylactogonium a modified hydrocladium with a proximal hydrothecate internode.

TYPE SPECIES

Macrorhynchia savignyana Kirchenpauer, 1872, replacement name for *Aglaophenia pennaria* sensu Audouin (1826) [not *Aglaophenia pennaria* (Linnaeus, 1758)], by original designation.

REMARKS

Macrorhynchia, *Calathophora*, *Pachyrhynchia*, and *Lytocarpia*, were established as subgenera of *Aglaophenia* Lamouroux, 1812, by Kirchenpauer (1872). Later, *Macrorhynchia* and *Lytocarpia* were elevated to generic rank (see Bedot, 1912:259; Stechow, 1923a:239, 244). Both are now frequently employed as names of genera (e.g., Yamada, 1959; Rho, 1967; Hirohito, 1969, 1983; Bogle, 1975; Rees and Vervoort, 1987; Ryland and Gibbons, 1991). Millard (1975), and Bouillon (1985) apparently following Millard, included the names *Macrorhynchia* and *Lytocarpia* in the synonymy of *Lytocarpus* Allman, 1883, but that is contrary to the Principle of Priority in zoological nomenclature (ICZN, 1985, Art. 23). Both Millard and Bouillon mistakenly credited Stechow (1919a) instead of Kirchenpauer (1872) as author of the first two of these three generic names (see ICZN, 1985, Art. 43). As for *Calathophora* and *Pachyrhynchia*, both have been referred back to the synonymy of *Aglaophenia* (see Stechow, 1919a:130; 1923a:218) and neither name is in current use (see Genus *Aglaophenia*, Remarks).

Kirchenpauer (1872:39) designated *Aglaophenia pennaria* sensu Audouin (1826) as type species of *Macrorhynchia* (for authorship and date of Audouin's report, see Sherborn, 1898). Kirchenpauer recognized that Audouin's species was different from *A. pennaria* (Linnaeus, 1758), and established the new name *M. savignyana* for it. Under provisions of the International Code of Zoological Nomenclature (ICZN, 1985, Arts. 11i, 70c), Kirchenpauer is also deemed in the same work to have established the name *M. pennaria* for this species. To remove potential confusion over the name of the type species, *M. savignyana* is here assigned precedence over its heretofore unused objective synonym *M. pennaria* under the Principle of the First Reviser (ICZN, 1985, Art. 24). Stechow's (1923a:240–241) subsequent rejection of *M. savignyana* (=*A. pennaria* sensu Audouin) as the type species of *Macrorhynchia* is invalid (ICZN, 1985, Art. 61). Likewise, his selection of *M. filamentosa* (Lamarck, 1816) (=*M. patula* Kirchenpauer, 1872) as the type species of the genus is invalid.

The identity of *Macrorhynchia savignyana*, originally reported from the Red Sea by Audouin (1826, as *Aglaophenia pennaria*), remains uncertain. Subsequent records of it, such as those from the Adriatic Sea by Kirchenpauer (1872) and from Haiti by Marktanner-Turneretscher (1890), have been recognized as more or less questionable. Stechow (1923a) discussed the identity of *M. savignyana* and remarked on its resemblance to the familiar *M. philippina* Kirchenpauer, 1872. Fraser (1944, 1946) assigned the species to *Cladocarpus* Allman, 1874a, based on accounts of it by Marktanner-Turneretscher (1890) and Nutting (1900). Vervoort (1966) referred the species with doubt to *Cladocarpus*, as *C. savignyanus*, noting that its gonophores had not been described. The illustrations of the species by Savigny (1826) support

Stechow's contention, although its gonophores were not portrayed. For purposes of this report, *M. savignyana* is taken to be a hydroid much like and possibly conspecific with that known as *M. philippina*.

Macrorhynchia is distinct from *Lytocarpia*, as defined by its type species *L. myriophyllum* (Linnaeus, 1758), principally in the characters of the phylactocarps. Although phylactocarps of both are modified hydrocladia (gonocladia), those of *Macrorhynchia* lack costae and are phylactogonia, while those of *Lytocarpia* as currently defined have costae (each with a basal hydrotheca) and form corbulae.

Confusion over the name and identity of *Lytocarpia* has persisted for more than a century. The nomenclature of this aglaopheniid genus was confounded by Allman (1883:40), who intentionally changed its spelling from *Lytocarpia* to *Lytocarpus*. More critically, Allman provided a revised definition that significantly altered the concept of the genus. *Lytocarpus*, although nomenclaturally a junior objective synonym of *Lytocarpia* (ICZN, 1985, Art. 33b [iii]), corresponded in Allman's diagnosis with *Macrorhynchia*. Allman's unjustified emendation of *Lytocarpia* to *Lytocarpus* (ICZN, 1985, Art. 33) and his misdiagnosis of the genus were widely followed by hydroid taxonomists for many years. Stechow's (1919a, 1923a) subsequent corrections of these errors were largely ignored. The familiar name *Lytocarpus* is now being replaced by *Macrorhynchia* for the genus, and *Lytocarpia* is again being used in the original sense of Kirchenpauer (1872). *Thecocarpus* Nutting, 1900, another familiar but invalid name in aglaopheniid taxonomy, is also finally being recognized as a junior synonym of *Lytocarpia* in recent literature (see Bogle, 1975; Rees and Vervoort, 1987:177; Gili, Vervoort, and Pagès, 1989; Cornelius and Ryland, 1990:158; Ryland and Gibbons, 1991:544; Cornelius, 1995; and others). In fact, *Lytocarpia* and *Thecocarpus* are objective synonyms because *L. myriophyllum* is the type species by original designation of both nominal genera (see Kirchenpauer, 1872:28; Nutting, 1900:106; Stechow, 1923a:244).

The nominal genus *Nematophorus* Clarke, 1879, has been referred, explicitly or implicitly, to the synonymy of *Lytocarpus* sensu Allman (1883) (=*Macrorhynchia*) by authors such as Versluys (1899), Nutting (1900), Fraser (1944), and Bouillon (1985), and to *Macrorhynchia* by Bogle (1975). Clarke (1879:248) established *Nematophorus* as a new genus based on the presence of "peculiar processes borne on the bases of the pinnae." Versluys and Nutting discounted the generic significance of this character, noting that such protuberances occur in several other genera of aglaopheniids. Clarke's (1879) material of *N. grandis*, type species of *Nematophorus* by monotypy, was sterile. Phylactocarps in material assigned to *N. grandis* by Versluys (1899) were modified hydrocladia resembling those present in species of *Macrorhynchia*. Stechow (1923a) indicated that phylactocarps appeared to form pseudocorbulae in *N. grandis* and several related species, instead of occurring singly, and recognized *Nematophorus* as distinct from *Macrorhynchia*. I follow the arguments of Versluys (1899), Nutting (1900), and Bogle (1975) that the two are coterminous.

Fewkes (1881) established *Pleurocarpa*, type species *P. ramosa* Fewkes, 1881, by monotypy, for an aglaopheniid hydroid from the Caribbean having an "open corbula." This structure, in fact a pseudocorbula, was formed at the proximal end of an otherwise normal branch by modified hydrocladia. Versluys (1899) and Nutting (1900) demonstrated that the pseudocorbula of *Nematophorus* was essentially like that of *Pleurocarpa*. They and subsequent authors regarded *Pleurocarpa* and *Nematophorus* as congeneric, with the latter name having priority. That conclusion is upheld here following examination of type material of *Nematophorus grandis* (MCZ 2160, 2244, 2255) and *Pleurocarpa ramosa* (MCZ 2159), type species of these two nominal genera. Except for Stechow (1923a), who recognized *Nematophorus* as valid, both names in turn have been regarded as junior synonyms of *Lytocarpus* sensu Allman (=*Macrorhynchia*).

Opinions vary on the status of *Aglaria* Stechow, 1923b, established on the basis of an unusual phylactocarp in its type species, *Aglaophenia septata* Ritchie, 1909b. *Aglaria* was regarded as congeneric with *Lytocarpus* sensu Allman, 1883 (=*Macrorhynchia*) by Bouillon (1985), and with *Aglaophenia* by Vervoort (1966). Others (e.g., Leloup, 1932a; Pennycuik, 1959; Ralph, 1961; Mammen, 1965; Rees and Thursfield, 1965) retained *Aglaria* as a distinct genus. The phylactocarp presumed to be that of *A. septata* by Ritchie (1909b, 1910a) was described as a peculiar cigar-shaped corbula with upper and lower tiers of phylactocarpial appendages that lacked hydrothecae. Gonophores were present within the lumen of the corbula. Vervoort (1966) subsequently discovered fertile hydroids of *A. septata* in collections of the Galathea Expedition. He concluded that the phylactocarp of the species was a true corbula that seemed unusual because of basal and apical spurs on the costae. Based on Vervoort's observations and conclusions, *Aglaria* is regarded here as congeneric with *Aglaophenia* and not with *Macrorhynchia* (see Genus *Aglaophenia*, Remarks).

Gravier (1970a) described gonophores in *Macrorhynchia philippina* from Madagascar that were liberated as medusoids, each having a ring of concretions around the umbrella margin. Tentacles, tentacle bulbs, radial canals, and a ring canal were lacking in these short-lived swimming gonophores. By contrast, hydroids of *M. philippina* from Venezuela bore either a single large egg or a mass of spermatocytes in each gonotheca (Vervoort, 1968:90). Hirohito (1983:80) reported that gonothecae of

M. philippina from Sagami Bay, Japan, contained one to three eggs or planulae. Gonophores in *M. phoenicea* (Busk, 1852) are evidently fixed (see Gravier-Bonnet and Fontaine, 1981:114).

As noted by Gravely (1927), Halstead (1988), and others, certain species of this genus (e.g., *Macrorhynchia philippina*) are noted for being venomous to humans.

***Macrorhynchia allmani* (Nutting, 1900)**

Fig. 19

Aglaophenia ramosa Allman, 1877:39, pl. 23, figs. 1–4 [invalid junior secondary homonym of *Aglaophenia ramosa* (Busk, 1852), and replaced before 1961].
Aglaophenia allmani Nutting, 1900:100, pl. 22, figs. 2–3 [replacement name for *Aglaophenia ramosa* Allman, 1877, not *A. ramosa* (Busk, 1852)].
Lytocarpus philippinus—Congdon, 1907:484, fig. 37. — Smallwood, 1910:137 [not *Macrorhynchia philippina* Kirchenpauer, 1872].
Macrorhynchia bermudensis Stechow, 1920:44.
Lytocarpus clarkei—Bennitt, 1922:254 [not *Macrorhynchia clarkei* (Nutting, 1900) =?*Macrorhynchia grandis* (Clarke, 1879)].
not *Aglaophenia* (?) *allmani*—Leloup, 1935:57 [part] [=*Aglaophenia dubia* Nutting, 1900].
?*Aglaophenia* (?) *mercatoris* Leloup, 1937a:113, figs. 15A–D.
Aglaophenia longiramosa Fraser, 1945:22, figs. 2a–c.
Macrorhynchia clarkei—Calder, 1986:139, pl. 39 [not *Macrorhynchia clarkei* (Nutting, 1900) =?*Macrorhynchia grandis* (Clarke, 1879)].
Lytocarpus (*Aglaophenia*) *allmani*—Bandel and Wedler, 1987:117.
Macrorhynchia allmani—Cairns et al., 1991:29.

TYPE LOCALITY

"Florida Reef, from a depth of from 2 to 3 fathoms [3.7–5.5 m]" (Allman, 1877:40).

MATERIAL EXAMINED

Atlantic Ocean, 2.5 km SE of Castle Roads, on limestone rubble, –60 to –90 m, 3 September 1977, one colony, ~20 cm high, without gonophores, ROMIZ B127. Atlantic Ocean, 1 km NE of Town Cut, on vertical limestone rock wall, –20 m, 30 July 1982, one colony, 14 cm high, without gonophores, coll. E. Ruppert, ROMIZ B287. Challenger Bank, on limestone rubble, –60 m, 17 May 1991, one colony, 16 cm high, without gonophores, ROMIZ B403. Challenger Bank, on limestone rubble, –70 m, 3 October 1984, three colonies, up to 18 cm high, without gonophores, ROMIZ B404. Atlantic Ocean, 2 km S of St. David's Lighthouse, on limestone rubble, –90 m, two colonies, up to 8 cm high, without gonophores, ROMIZ B405. Atlantic Ocean, 2.5 km SE of Castle Roads, on limestone rubble, –73 m, one fragmentary colony, 6 cm high, without gonophores, ROMIZ B406. Atlantic Ocean, 2.5 km SSE of Castle Roads, on limestone rubble, –60 m, 23 May 1991, two colonies, up to 27 cm high, without gonophores, ROMIZ B407. Atlantic Ocean, 2.5 km SE of Castle Roads, on limestone rubble, –82 m, 5 September 1992, seven colonies, up to 28 cm high, without gonophores, ROMIZ B408.

DESCRIPTION

Colonies up to 28 cm high; each hydrocaulus arising from a rootlike system of stolons adhering to limestone rock. Hydrocauli alternately to irregularly branched, branches simple or branched in like manner, polysiphonic except at ends of hydrocaulus and branches; base reaching up to 3 mm or more in diameter; hydrocauli and branches gradually curved backward; primary axial tube divided into internodes by indistinct nodes, each internode typically with a fronto-disto-laterally situated hydrocladial apophysis and two triangular nematothecae, one scoop-shaped inferior and one two-spined or scoop-shaped axillary; apophyses short and bearing a distinct mamelon, given off alternately from each side of axial tube, adjacent pair on same side typically about 1.5 mm apart, directed upward at an angle of about 45° with vertical. Hydrocladia up to about 1 cm long, unbranched; top and frontal sides slightly convex; each hydrocladium arising directly from an apophysis and separated from it by a distinct to almost imperceptible oblique node, divided into short internodes

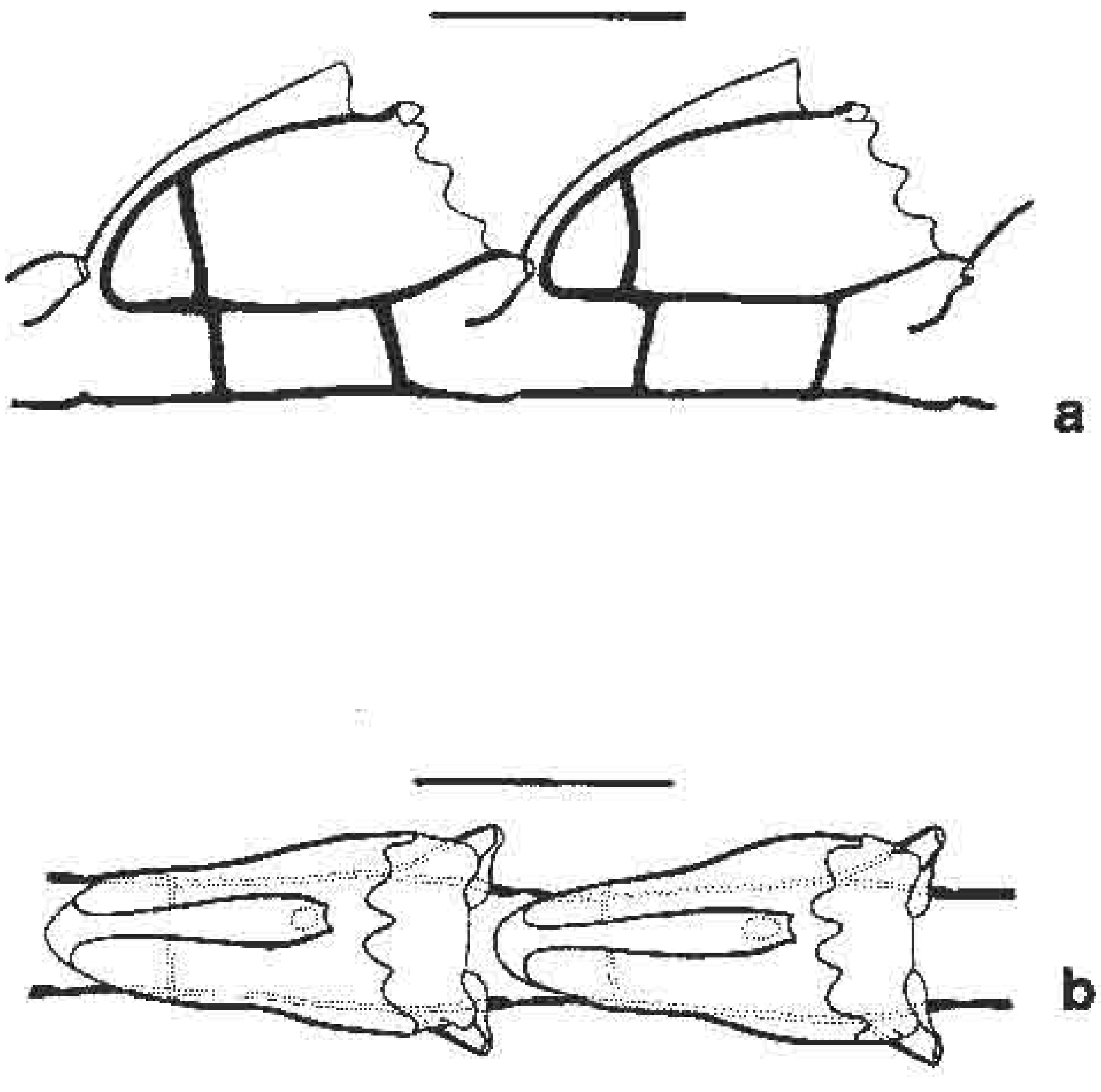

FIG. 19. *Macrorhynchia allmani*, ROMIZ B127: *a*, part of hydrocladium, lateral view, with two hydrothecae; *b*, part of hydrocladium, front view, with two hydrothecae. Scales equal 0.25 mm.

by nearly transverse nodes. Hydrocladial internodes 394–450 μm long, 75–150 μm wide at nodes, each with one frontally placed hydrotheca, one median inferior nematotheca, one pair of lateral nematothecae, one internodal septum adjacent to intrathecal septum, and typically with another internodal septum beneath lateral nematothecae; adjacent hydrothecae relatively close to one another. Hydrothecae 319–375 μm deep from tips of marginal cusps to base, more or less cone-shaped; adcauline wall nearly straight, adnate to hydrocladial internode; abcauline wall convex except for a small concavity just below margin; intrathecal septum prominent, nearly straight, extending across intrathecal cavity; perisarc of moderate thickness. Hydrothecal aperture 150–188 μm in diameter from adcauline to abcauline wall, irregularly oval, plane of aperture oblique to axis of internode and to that of hydrotheca; margin with seven rounded cusps, pair adjacent to lateral nematothecae bilobed. Median inferior nematotheca curved and adnate for much of its length to abcauline wall of hydrotheca, distal part free, horn-shaped, length somewhat variable, apex seldom extending beyond margin of hydrotheca; aperture either open from apex to abcauline wall of hydrotheca or closed in the middle and open at apex and at juncture with hydrothecal wall; with an aperture into hydrothecal cavity. Lateral nematothecae horn-shaped, extending beyond margin of hydrotheca, each with a distal orifice and another at margin of hydrotheca, or scoop-shaped and open from apex to base.

Gonophores not seen.

REMARKS

These specimens from Bermuda were compared with type material of *Aglaophenia ramosa* Allman, 1877 (MCZ, no catalogue number) from Florida Reef; *Nematophorus grandis* Clarke, 1879 (MCZ 2160, 2244, 2255) from Zoblos Island (eastern Gulf of Mexico); *Pleurocarpa ramosa* Fewkes, 1881 (MCZ 2159) from St. Vincent (Windward Islands, West Indies); and *Lytocarpus clarkei* Nutting, 1900 (USNM 18698) from the Bahamas. Materials from Bermuda were most like the type of *A. ramosa* morphologically, and in this report they are assigned to that species.

Nutting (1900:100) considered the name *Aglaophenia ramosa* to be an invalid junior secondary homonym of *Plumularia ramosa* Busk, 1852, the binomen of an Australian species subsequently referred to *Aglaophenia* Lamouroux, 1812, by Kirchenpauer (1872, 1876), Bale (1882), Stechow (1923a), and others. A new name, *A. allmani*, was established by Nutting for the American hydroid of Allman. That species is now assigned to *Macrorhynchia* Kirchenpauer, 1872, instead of *Aglaophenia*, and secondary homonymy no longer exists. However, the correct species name is *M. allmani* because the specific name *ramosa* for this hydroid is invalid under the code (ICZN, 1985, Art. 59b).

Bogle, in her thesis (1975), provisionally assigned *Aglaophenia allmani* to *Macrorhynchia*, but that paper does not meet criteria of publication in nomenclature (ICZN, 1985, Arts. 7–8). Some uncertainty remains about the generic classification of this species because its gonophores and phylactocarps have never been described. Nevertheless, the hydroid colony form resembles that of other species assigned to *Macrorhynchia*. Bogle (1975) suggested that such species typically have one or more of the following characters: (1) a polysiphonic hydrocaulus, (2) a much branched hydrocaulus, (3) large and triangular cauline nematothecae, (4) lateral nematothecae of asymmetrical length, (5) quite shallow hydrothecae, and (6) median inferior nematothecae that are largely adnate to the abcauline hydrothecal wall. Asymmetry in the length of the lateral nematothecae was not especially noticeable in hydroids assigned to *M. allmani* from Bermuda (Fig. 19b), but the other characters were generally applicable to these specimens.

Types of *Aglaophenia ramosa* (=*Macrorhynchia allmani*) and the hydroids from Bermuda resemble *Nematophorus grandis*, *Pleurocarpa ramosa*, and *Lytocarpus clarkei*, but differ from them in having more widely spaced hydrocladia, longer hydrocladial internodes, deeper hydrothecae, and shorter median inferior nematothecae that do not extend beyond the hydrothecal margin (Figs. 19–20). Based on these differences, *A. allmani* is considered here to be a species distinct from the others. As for *N. grandis*, *P. ramosa*, and *L. clarkei*, they are much alike, and I concur with Bogle (1975) that they are likely all conspecific and referable to *Macrorhynchia*. The binomen *M. grandis* has priority over these three names. Bogle (1975) likewise provisionally regarded *M. grandis* and *M. allmani* as separate species.

Vervoort (1968:68) remarked on the seeming resemblance between *Macrorhynchia allmani* and *Aglaophenia mercatoris* Leloup, 1937a, from Tampa Bay, Florida. He suggested that study of more material might show that the two are conspecific. Bogle (1975) also held that they were likely identical. Yet Leloup's (1937a) description provided no indication of the size of his fragmentary specimen, and no mention was made as to the presence of branches. Because *A. mercatoris* is so poorly known, it appears open to question whether it is conspecific with *M. allmani*.

Part of the hydroid material from Tortugas, Florida, that Leloup (1935) assigned to *Aglaophenia* (?) *allmani* was referred instead to *A. elongata* Meneghini, 1845, by Van Gemerden-Hoogeveen (1965). The species is referred here to *A. dubia* Nutting, 1900 (see *Aglaophenia dubia*, Remarks).

Aglaophenia longiramosa Fraser, 1945, was regarded by Bogle (1975) as probably conspecific with *M. allmani*, and I agree. As to the collection locale of *A. longiramosa*, reports by Fraser (1945, 1946) are contradictory.

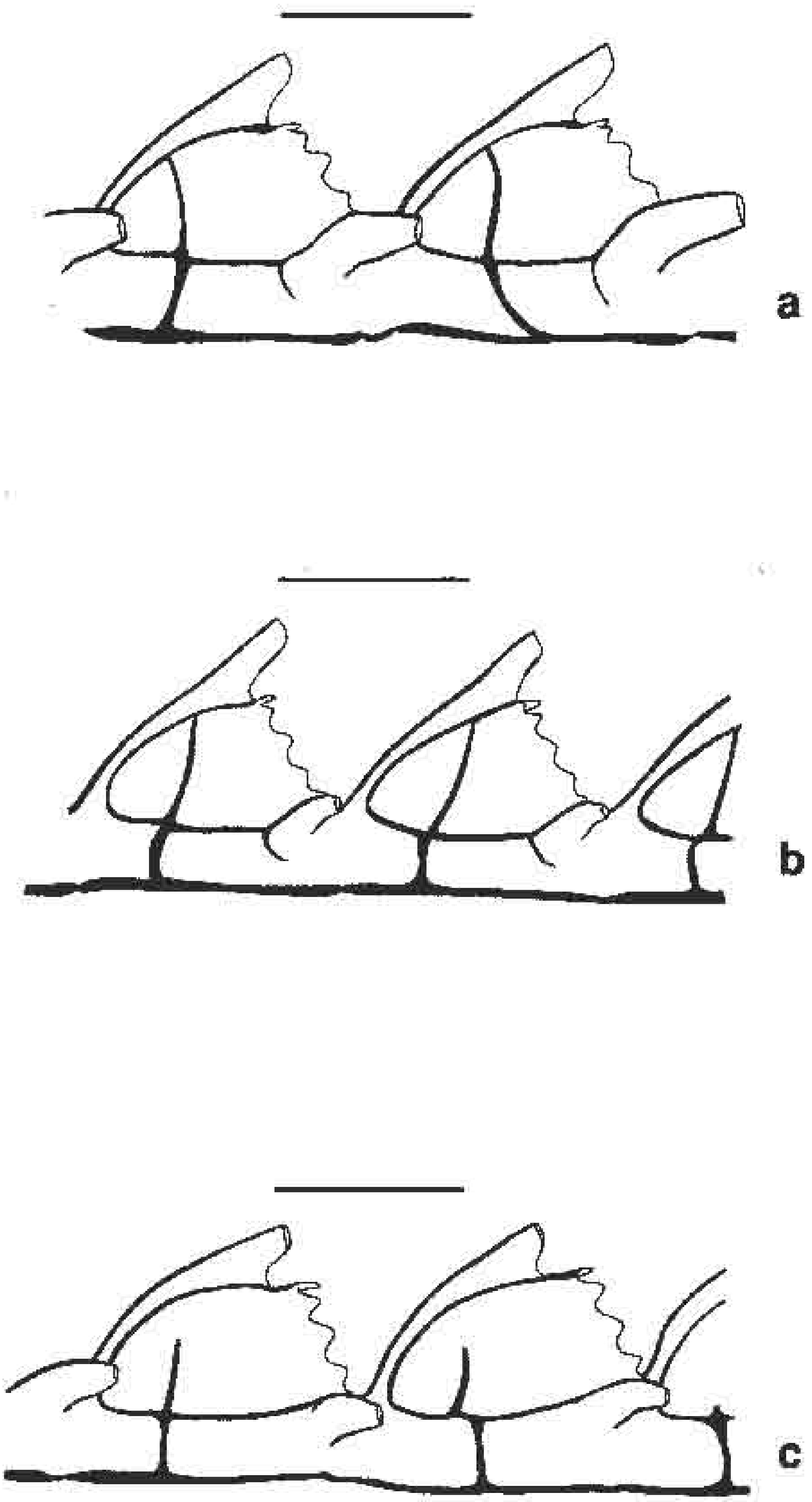

FIG. 20. *Macrorhynchia grandis: a*, part of hydrocladium of type material of *Nematophorus grandis* Clarke, 1879, Zoblos Island, Gulf of Mexico, lateral view, with two hydrothecae, MCZ 2160; *b*, part of hydrocladium of type material of *Pleurocarpa ramosa* Fewkes, 1881, St. Vincent, West Indies, lateral view, with two hydrothecae, MCZ 2159; *c*, part of hydrocladium of type material of *Lytocarpus clarkei* Nutting, 1900, Little Cat Island, Bahamas, lateral view, with two hydrothecae, USNM 18698. Scales equal 0.25 mm.

Coordinates of the collection station published with the original description (Fraser, 1945) were given as 29°58'N, 88°03'W (a location in the Gulf of Mexico off the coast of Alabama). Fraser's (1946) statement that the species was obtained off northern Georgia is assumed to be in error.

Macrorhynchia allmani was common on limestone rubble in dredge tows from the fore-reef slope off Bermuda, and was also collected during this study from Challenger Bank. The record of *Macrorhynchia clarkei* from Bermuda by Calder (1986) is a misidentification of hydroids of this species. Congdon (1907) identified hydroids from Bermuda and Challenger Bank as *Lytocarpus philippinus* Kirchenpauer, 1872, but his illustration of the species indicates that it was almost certainly *M. allmani* instead. Stechow (1920) had recognized that Congdon's species was different from *M. philippina* and founded a new name for it, *M. bermudensis*. The name *Macrorhynchia bermudensis* is included in the synonymy of the present species. Hydroids reported by Bennitt (1922) from Bermuda, as *Lytocarpus clarkei*, were also likely specimens of *M. allmani*. So, too, were specimens identified as *Lytocarpus philippinus* by Smallwood (1910). Allman's (1883:2) record of the species from the Bermuda region, as *Aglaophenia ramosa*, was probably based on specimens collected from Challenger Bank.

Curiously, no phylactocarps have yet been observed in specimens of *Macrorhynchia allmani* from Bermuda or elsewhere.

REPORTED RANGE

Bermuda: shores of Bermuda, and Challenger Bank (Congdon, 1907, as *Lytocarpus philippinus*; Smallwood, 1910, as *L. philippinus*; Stechow, 1920, as *Macrorhynchia bermudensis*); Challenger Bank (Bennitt, 1922, as *Lytocarpus clarkei*); location unspecified (Allman, 1883, as *Aglaophenia ramosa*; Calder, 1986, as *Macrorhynchia clarkei*); banks, deeper coastal waters, upper slope (>100 m) of Bermuda Pedestal (Calder, 1993).

Circumglobal distribution: western Atlantic (Vervoort, 1968).

Macrorhynchia philippina Kirchenpauer, 1872

Fig. 21

Macrorhynchia philippina Kirchenpauer, 1872:19.

Aglaophenia philippina Kirchenpauer, 1872:45, text-fig. p. 17; pl. 1, fig. 26; pl. 2, figs. 26a–b; pl. 7, fig. 26.

Aglaophenia urens Kirchenpauer, 1872:46, pl. 1, fig. 27; pl. 2, fig. 27; pl. 7, fig. 27.

Aglaophenia perforata Kirchenpauer, 1876:25 [nomen nudum] [not *Aglaophenia perforata* Allman, 1885].

Lytocarpus phillipinus—Bale, 1888:786, pl. 21, figs. 5–7 [incorrect subsequent spelling].

Aglaophenia phillipina—Bale, 1888:788 [incorrect subsequent spelling].

Lytocarpus urens—Bale, 1888:789.

Aglaophenia (Lytocarpus) phillipina—Bale, 1888:789 [incorrect subsequent spelling].

Lytocarpus philippinus—Marktanner-Turneretscher, 1890:274, pl. 6, figs. 15–16.

not *Lytocarpus philippinus*—Congdon, 1907:484, fig. 37

[=*Macrorhynchia allmani* Nutting, 1900].
Lytocarpus crosslandi Ritchie, 1908:511, pl. 24, fig. 11; pl. 26, figs. 2–4.
Lytocarpus philippinnus—Wallace, 1909:137 [incorrect subsequent spelling].
Lytocarpus philippinus atlanticus Billard, 1913:78.
Lytocarpia philippina—Stechow, 1919a:132, fig. Z^{1}.
Aglaophenia (*Macrorhynchia*) *perforata* Stechow, 1919a:132 [unavailable name, published as a junior synonym].
Aglaophenia (*Macrorhynchia*) *philippina*—Stechow, 1919a:132.
Aglaophenia perforata Stechow, 1919a:132, fig. Z^{1} [unavailable name, published as a junior synonym].
Macrorhynchia crosslandi—Stechow, 1923a:241.
Macrorhynchia urens—Stechow, 1923a:241.
Aglaophenia philippinus—Vervoort, 1941:225 [incorrect subsequent spelling].
Macrorhynchia crosslandica—Mammen, 1965:316 [incorrect subsequent spelling].
Lytocarnus philippinus—Gravier, 1970b:125 [incorrect subsequent spelling].
Lytocarpus (*Macrorhynchia*) *philippinus*—Boero and Bouillon, 1987:242.
?not *Macrorhynchia philippina*—Rees and Vervoort, 1987:177, fig. 43.
Lytocarpus phillippinus—Bandel and Wedler, 1987:49 [incorrect subsequent spelling].
Lithocarpus philippinus—Bandel and Wedler, 1987:63 [incorrect subsequent spelling].

TYPE LOCALITY

Manila, Philippines.

MATERIAL EXAMINED

Flatts Inlet, on rock, –2 m, 21 September 1977, one colony, 6.0 cm high, without gonophores, ROMIZ B128. Harrington Sound, entrance of Cripplegate Cave, on rock, –1 m, 6 October 1986, two colonies, 4.2 and 5.8 cm high, without gonophores, ROMIZ B366. Harrington Sound, in aquaduct to Flatts Inlet, –1 m, 29 October 1986, three colonies, 8.0, 4.5, and 6.5 cm high, without gonophores, ROMIZ B368.

DESCRIPTION

Colonies up to 8 cm high; each hydrocaulus arising from a network of stolons attached to substrate. Hydrocauli pinnately, twice-pinnately, or thrice-pinnately branched, reaching up to 1 mm or more in width basally. Hydrocauli and branches polysiphonic except at distal ends, curved gradually backward; nodes indistinct. Cauline internodes each with a hydrocladial apophysis and two nematothecae, one distal axillary and one proximal; nematothecae sac-shaped, tapering to a slender cone distally, orifice small,

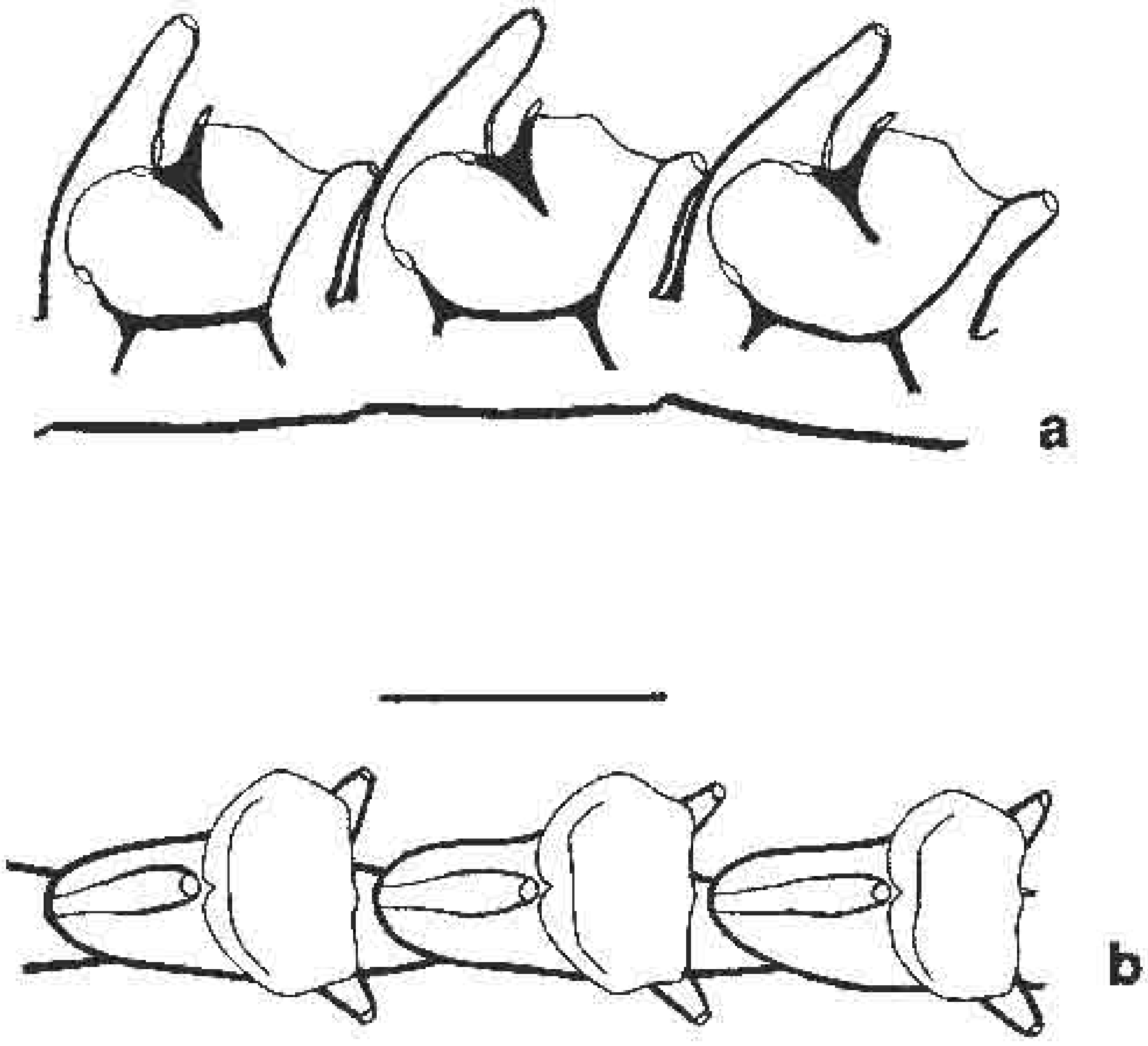

FIG. 21. *Macrorhynchia philippina*, ROMIZ B368: *a*, part of hydrocladium, lateral view, with three hydrothecae; *b*, part of hydrocladium, front view, with three hydrothecae. Scales equal 0.25 mm.

spherical to oval. Hydrocladial apophyses short, each bearing a cone-shaped mamelon on anterior surface; given off alternately from frontal surface of axial tubes of hydrocaulus and branches, quite closely spaced, directed outward at an angle of about 40° from axis of adjacent hydrocaulus or branch, supporting a hydrocladium (except where broken off). Hydrocladia up to 5 mm long, unbranched; top and frontal sides convex; each hydrocladium arising directly from apophysis and separated from it by an oblique node; divided into short internodes by nearly straight nodes. Hydrocladial internodes 242–308 µm long, 75–112 µm wide at nodes, each with one frontally placed hydrotheca, one median inferior nematotheca, one pair of lateral nematothecae, and two internodal septa; adjacent hydrothecae close to one another. Hydrothecae slipper-shaped, 252–270 µm deep from adcauline wall at margin to base, curving abruptly outward distally; adcauline wall convex, adnate to hydrocladial internode except for distal quarter; abcauline wall convex except for pronounced concavity just below margin; abcauline intrathecal septum prominent, cusp-shaped, curved away from hydrocaulus, extending about halfway across intrathecal cavity; perisarc of moderate thickness. Hydrothecal aperture 130–158 µm in diameter from adcauline to abcauline wall, irregularly oval, plane of aperture oblique to axis of internode and to that of hydrotheca; margin with an acute median abcauline cusp, a pair of low and rounded lateral cusps, a low and indistinct median adcauline cusp, and a flange on either side where rim meets lateral nematothecae; aperture distinctly flaring in top view. Median inferior nematotheca long, anvil-shaped, reaching beyond margin of hydrotheca distally, slightly curved, adnate to abcauline wall of hydrotheca as far as intrathecal septum, distal third free, conch-shaped, length free 117–140 μm; external apertures two, both nearly round, one at distal end and one at insertion of nematotheca with hydrotheca; aperture between nematotheca and hydrothecal cavity located just proximal to abcauline intrathecal septum. Lateral nematothecae tubular, largely adnate to hydrothecal wall, distal end tapered and curved forward, extending a varying distance beyond margin of hydrothecae; terminal aperture small, spherical; internal aperture oval to irregular in shape.

Gonophores not seen.

REMARKS

Kirchenpauer (1872) founded the name *Aglaophenia philippina* for this species and included it in *Macrorhynchia*, a new subgenus of *Aglaophenia* Lamouroux, 1812. Stechow (1923a) elevated the rank of *Macrorhynchia* to genus and assigned to it several species, including *A. philippina*. Originally described from the western Pacific, the range of the species is regarded as essentially circumglobal in tropical and subtropical waters (Van Gemerden-Hoogeveen, 1965; Millard, 1975; Calder, 1983).

Pictet (1893) observed that *Aglaophenia urens* Kirchenpauer, 1872, and *Macrorhynchia philippina* were similar. Bale (1919) concluded that they were coterminous, and as First Reviser assigned priority to the latter name. The opinion that *A. urens* and *M. philippina* are conspecific was upheld by Stechow (1923a:241).

The binomen *Aglaophenia perforata*, cited in the synonymy list above, was first employed by Kirchenpauer (1876) as nomen nudum (ICZN, 1985, Art. 12). Stechow (1919a) provided a description and illustration of the hydroid upon which the name was based, and included *A. perforata* as a junior synonym of *Macrorhynchia philippina*. The name *A. perforata* has not been made available nomenclaturally for this hydroid, by either Kirchenpauer (1876) or Stechow (1923a) (ICZN, 1985, Art. 11e), and it does not enter into homonymy with *Aglaophenia perforata* Allman, 1885 [=*Aglaophenia latecarinata* Allman, 1877].

Billard (1907) suggested that *Lytocarpus balei* Nutting, 1905, from Hawaii was conspecific with *Macrorhynchia philippina*. Nutting's species was recognized as valid by Stechow (1909), who examined material from Sagami Bay, Japan. Billard (1913) found additional hydroids of *M. balei* in collections from the Siboga Expedition, and considered it to be a valid species.

Macrorhynchia philippina was reported from Bermuda by Congdon (1907) as *Lytocarpus philippinus*. Several authors, including Bale (1919) and Stechow (1920), recognized that Congdon's record was based on misidentified material. The illustration provided by Congdon indicates that his hydroid was likely referable to *Macrorhynchia allmani* (Nutting, 1900) instead (see *Macrorhynchia allmani*, Remarks).

Lytocarpus crosslandi Ritchie, 1908, from Cape Verde Islands was regarded as no more than a local variety of *Macrorhynchia philippina* by Billard (1913). Rees and Thursfield (1965) commented that *M. crosslandi* might prove to be a form of *M. philippina*. I follow Van Gemerden-Hoogeveen (1965) in considering *M. crosslandi* and *M. philippina* to be conspecific. The affinities of several related nominal species from the Pacific, and the distinctness of their hydroids from *M. philippina*, remain unresolved.

The name *Lytocarpus philippinus atlanticus* Billard, 1913, was established for Atlantic populations of this species. Hydroid morphology of *Macrorhynchia philippina* is quite varied (e.g., see Vervoort, 1968; Millard, 1975), and Vervoort (1968) discounted the taxonomic importance of purported differences between Atlantic and Pacific material.

A hydroid collected in the Gulf of Aden and assigned to *Macrorhynchia philippina* by Rees and Vervoort (1987) belongs to another species, in my opinion. All hydrothecae of their specimen lacked the median abcauline cusp on the hydrothecal margin as well as the distinctive triangular intrathecal septum found in *M. philippina*. Moreover, as noted by Rees and Vervoort, the number of septa in hydrocladial internodes was higher and their development greater than in hydroids of the present species.

Aglaophenia tricuspis McCrady, 1859, from the coast of South Carolina is a hydroid of doubtful identity (Bedot, 1925; Fraser, 1944). From parts of McCrady's (1859) description, and from the limited number of plumularioid species known to occur in the type locality (Calder, 1983), the hydroid may have been identical to *Macrorhynchia philippina*. Yet, unlike fully developed colonies of *M. philippina*, the species reportedly grew "in solitary plumes" (McCrady, 1859:203). Unfortunately, none of McCrady's types, including *A. tricuspis*, is known to exist (Stephens and Calder, 1992). Given the uncertainty surrounding application of the name, *A. tricuspis* is regarded here as a nomen dubium. As such, it does not nomenclaturally threaten the well-known name *M. philippina*.

As mentioned above (see Genus *Macrorhynchia*, Remarks), the hydroid of this species is known to be venomous to humans (e.g., see Gravely, 1927; Halstead, 1988; Rifkin, Fenner, and Williamson, 1993). Moreover, its gonophores sometimes appear to be liberated as medusoids (Gravier, 1970a).

Macrorhynchia philippina was regarded as moderately photophilous and rheophilous in coral-reef environments by Mergner (1987). In Bermuda it was found at three locations, all characterized by strong water currents.

One of these areas (Flatts Inlet) was exposed to direct light for much of the day while the other two (the entrance of Cripplegate Cave, and an underground aquaduct between Harrington Sound and Flatts Inlet) were in deep shade. Earlier, Bennitt (1922) reported *M. philippina* from Bermuda at Somerset Bridge, an area also swept by strong tidal currents.

REPORTED RANGE

Bermuda: Somerset Bridge (Bennitt, 1922); inlets, caves (Calder, 1983, 1986, 1993).

Circumglobal distribution: western Atlantic (Vervoort, 1968); eastern Atlantic (Ritchie, 1908, as *Lytocarpus crosslandi*); Indian Ocean (Millard, 1975); western Pacific (Hirohito, 1983); eastern Pacific (Fraser, 1948).

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Literature Cited

ADAMS, J.

1960 A contribution to the biology and postlarval development of the Sargassum fish, *Histrio histrio* (Linnaeus), with a discussion of the *Sargassum* complex. Bulletin of Marine Science of the Gulf and Caribbean 10:55–82.

AGASSIZ, A.

1865 Illustrated catalogue of the Museum of Comparative Zoölogy, at Harvard College. No. II, North American Acalephae. Cambridge. 234 pp.

AGASSIZ, L.

1848 Nomenclatoris zoologici, index universalis. Soloduri, Gassmann. 1133 pp.

1862 Contributions to the natural history of the United States of America. Vol. IV. Boston, Little, Brown. 380 pp.

ALDER, J.

1859 Descriptions of three new species of sertularian zoophytes. Annals and Magazine of Natural History, 3rd ser., 3:353–356.

ALLMAN, G. J.

1871 A monograph of the gymnoblastic or tubularian hydroids. In two parts. I. The Hydroida in general. London, Ray Society, pp. 1–154.

1872 A monograph of the gymnoblastic or tubularian hydroids. Conclusion of Part I, and Part II, containing descriptions of the genera and species of the Gymnoblastea. London, Ray Society, pp. 155–450.

1874a Report on the Hydroida collected during the expeditions of H.M.S. "Porcupine." Transactions of the Zoological Society of London 8:469–481.

1874b On the diagnosis of new genera and species of hydroids. Nature 11:179.

1876 Diagnoses of new genera and species of Hydroida. Journal of the Linnean Society, Zoology 12:251–284.

1877 Report on the Hydroida collected during the exploration of the Gulf Stream by L. F. de Pourtalès, assistant, United States Coast Survey. Memoirs of the Museum of Comparative Zoölogy at Harvard College 5(2): 1–66.

1883 Report on the Hydroida dredged by H.M.S. Challenger during the years 1873–76. Part I.—Plumularidae. Report on the Scientific Results of the Voyage of H.M.S. Challenger during the Years 1873–76. Zoology 7(20): 1–54.

1885 Description of Australian, Cape, and other Hydroida, mostly new, from the collection of Miss H. Gatty. Journal of the Linnean Society, Zoology, 19:132–160.

1888 Report on the Hydroida dredged by H.M.S. Challenger during the years 1873–76. Part II—The Tubularinae, Corymorphinae, Campanularinae, Sertularinae, and Thalamophora. Report on the Scientific Results of the Voyage of H.M.S. Challenger during the Years 1873–76. Zoology 7(23): 1–90.

ALTUNA, A., A. ROMERO, A. SANZ, J. A. TORRES, and M. IBAÑEZ

1983 Contribución al conocimiento de la fauna marina de la Costa de Guipuzcoa I. Lurralde 6:127–155.

ANTSULEVICH, A. E.

1983 Novye dlya fauny SSSR gidroidy iz pribrezhnykh vod Yaponskogo Morya. Akademiya Nauk SSSR, Zoologicheskii Zhurnal 62:1141–1147.

1987 Gidroidy shelfa Kurilskikh Ostrovov. Leningrad, Akademiya Nauk SSSR, Zoologicheskii Institut. 163 pp.

APSTEIN, C.

1915 Nomina conservanda. Sitzungsberichte der Gesellschaft Naturforschender Freunde zu Berlin 1915, pp. 119–202.

ARAI, M. N.

1977 Specimens of new hydroid species described by C. M. Fraser in the collections of the British Columbia Provincial Museum. Syesis 10:25–30.

ARMSTRONG, J.

1879 A description of some new species of hydroid zoophytes from the Indian coasts and seas. Journal of the Asiatic Society of Bengal, Part 2, 48:98–103.

AUDOUIN, V.

1826 Explication sommaire des planches de polypes de l'Égypte et de la Syrie, publiées par Jules-César Savigny, Membre de l'Institut; offrant un exposé des caractères naturels des genres avec la distinction des espèces. Description de l'Égypte, Histoire Naturelle. Vol. 1. Paris, Imprimerie Imperiale, pp. 225–244.

BALE, W. M.

1882 On the Hydroida of south-eastern Australia, with descriptions of supposed new species, and notes on the genus *Aglaophenia*. Journal of the Microscopical Society of Victoria 2:15–48.

1884 Catalogue of the Australian hydroid zoophytes. Sydney, Australian Museum, catalogue no. 8. 198 pp.

1887 The genera of the Plumulariidae, with observations on various Australian hydroids. Transactions and Proceedings of the Royal Society of Victoria 23:73–110.

1888 On some new and rare Hydroida in the Australian Museum collection. Proceedings of the Linnean Society of New South Wales, 2nd ser., 3:745–799.

1894 Further notes on Australian hydroids, with descriptions of some new species. Proceedings of the Royal Society of Victoria, n.s., 6:93–117.

1913 Further notes on Australian hydroids.—II. Proceedings of the Royal Society of Victoria, n.s., 26:114–147.

1914 Report on the Hydroida collected in the Great Australian Bight and other localities. Part II. Biological Results of the Fishing Experiments

Carried on by the F.I.S. "Endeavour," 1909–1914 2(4): 164–188.

1915 Report on the Hydroida collected in the Great Australian Bight and other localities. Part III. Biological Results of the Fishing Experiments Carried on by the F.I.S. "Endeavour," 1909–14, 3(5): 241–336.

1919 Further notes on Australian hydroids—IV. Proceedings of the Royal Society of Victoria, n.s., 31:327–361.

1924 Report on some hydroids from the New Zealand coast, with notes on New Zealand Hydroida generally, supplementing Farquhar's list. Transactions and Proceedings of the New Zealand Institute 55:225–268.

BANDEL, K., and E. WEDLER

1987 Hydroid, amphineuran and gastropod zonation in the littoral of the Caribbean Sea, Colombia. Senckenbergiana Maritima 19:1–129.

BARTLETT, G. C.

1907 Notes on hydroid zoophytes. Geelong Naturalist, 2nd ser., 3:60–66.

BEDOT, M.

1901a Matériaux pour servir à l'histoire des hydroïdes. 1re période. Revue Suisse de Zoologie 9:379–515.

1901b De la stolonisation chez les hydroïdes. Comptes Rendus Hebdomadaires des Séances de l'Académie des Sciences 133:521–524.

1905 Matériaux pour servir à l'histoire des hydroïdes. 2me période (1821 à 1850). Revue Suisse de Zoologie 13:1–183.

1910 Matériaux pour servir à l'histoire des hydroïdes. 3me période (1851 à 1871). Revue Suisse de Zoologie 18:189–490.

1912 Matériaux pour servir à l'histoire des hydroïdes. 4me période (1872 à 1880). Revue Suisse de Zoologie 20:213–469.

1914 Nouvelles notes sur les hydroïdes de Roscoff. Archives de Zoologie Expérimentale et Générale 54:79–98.

1916a Matériaux pour servir à l'histoire des hydroïdes. 5e période (1881 à 1890). Revue Suisse de Zoologie 24:1–349.

1916b Sur le genre *Kirchenpaueria*. Revue Suisse de Zoologie 24:637–648.

1917 Le genre *Antennella*. Revue Suisse de Zoologie 25:111–129.

1918 Matériaux pour servir à l'histoire des hydroïdes. 6e période (1891 à 1900). Revue Suisse de Zoologie 26, fascicule supplémentaire:1–376.

1921a Notes systématiques sur les plumularides. 2me partie. Revue Suisse de Zoologie 29:1–40.

1921b Hydroïdes provenant des campagnes des yachts Hirondelle et Princesse-Alice (1887 à 1912). I. Plumularidae. Résultats des Campagnes Scientifiques Accomplies sur son Yacht par Albert Ier, Prince Souverain de Monaco 60:1–70.

1923 Notes systématiques sur les plumularides. Revue Suisse de Zoologie 30:213–243.

1925 Matériaux pour servir à l'histoire des hydroïdes. 7e période (1901 à 1910). Revue Suisse de Zoologie 32, fascicule supplémentaire, pp. 1–657.

BENNITT, R.

1922 Additions to the hydroid fauna of the Bermudas. Proceedings of the American Academy of Arts and Sciences 57:241–259.

BERKENHOUT, J.

1789 Synopsis of the natural history of Great-Britain and Ireland. Containing a systematic arrangement and concise description of all the animals, vegetables, and fossils, which have hitherto been discovered in these kingdoms. Vol. 1. London, T. Cadell. 334 pp.

BERTOLONII, A.

1819 Specimen zoophytorum Portus Lunae. *In* Bertolonii, A., Amoenitates italicae. Bononiae, pp. 246–280.

BILLARD, A.

1901a Note sur la *Polyplumularia flabella* G. O. Sars, et sur l'*Halicornaria Ferlusi* n.sp. Bulletin du Muséum d'Histoire Naturelle, Paris 7:117–121.

1901b De la stolonisation chez les hydroïdes. Comptes Rendus Hebdomadaires des Séances de l'Académie des Sciences 133:521–524.

1903 Note sur les variations du *Plumularia halecioides* Alder. Bulletin du Muséum d'Histoire Naturelle de Paris 9:57–62.

1904a Contribution à l'étude des hydroïdes (multiplication, régénération, greffes, variations). Annales des Sciences Naturelles, Zoologie et Paléontologie, 8me sér., 20:1–251.

1904b Hydroïdes récoltés par M. Ch. Gravier dans le Golfe de Tadjourah. Bulletin du Muséum d'Histoire Naturelle 10:480–485.

1906 Hydroïdes. Expéditions Scientifiques du "Travailleur" et du "Talisman" 1906, pp. 153–243.

1907 Hydroïdes de Madagascar et du sud-est de l'Afrique. Archives de Zoologie Expérimentale et Générale, 4me sér., 7:335–396.

1909 Revision des espèces types d'hydroïdes de la collection Lamouroux conservée à l'Institut Botanique de Caen. Annales des Sciences Naturelles, Zoologie, 9e sér., 9:307–337.

1910 Revision d'une partie de la collection des hydroïdes du British Museum. Annales des Sciences Naturelles, Zoologie, 9e sér., 11:1–67.

1911a Note sur un nouveau genre et nouvelle espèce d'hydroïde: *Sibogella erecta*. Archives de Zoologie Expérimentale et Générale, Notes et Revue, 5e sér., 6:108–109.

1911b Note préliminaire sur les espèces nouvelles de Plumulariidae de l'Expédition du "Siboga." Archives de Zoologie Expérimentale et Générale, Notes et Revue, 5e sér., 8:67–71.

1912 Hydroïdes de Roscoff. Archives de Zoologie Expérimentale et Générale 51:459–478.

1913 Les hydroïdes de l'expédition du Siboga. I. Plumulariidae. Siboga-Expeditie, Monographie 7a:1–115.

1927 Hydrozoa I. Hydrozoa benthonica (excl. Hydrocorallidae). Faune des Colonies Françaises, Contribution à l'Étude de la Faune du Cameroun 1:467–474.

1929 Sur l'identité des genres *Sibogella* et *Stechowia* (Plumularidae). Bulletin de la Société Zoologique de France 54:72–73.

1930 Note sur deux espèces d'hydroïdes de la côte Atlantique du Maroc. Bulletin de la Société des Sciences Naturelles du Maroc 10:79–80.

BLACKBURN, M.

1938 The Sir Joseph Banks Islands. Reports of the Expedition of the McCoy Society for Field Investigation and Research. Part One. 3. Hydrozoa. Proceedings of the Royal Society of Victoria, n.s., 50:312–328.

1942 A systematic list of the Hydroida of South Australia with a summary of their distribution in other seas. Transactions of the Royal Society of South Australia 66:104–118.

BLAINVILLE, H. M. D. de

1830 Zoophytes, Zoophyta. *In* Levrault, F. G., ed., Dictionnaire des sciences naturelles . . . par plusieurs professeurs du Jardin du Roi, et des principales écoles de Paris. Tome 60. Paris, Le Normant, pp. 1–548.

BOERO, F.

1981 Systematics and ecology of the hydroid population of two *Posidonia oceanica* meadows. Pubblicazioni della Stazione Zoologica di Napoli I: Marine Ecology 2:181–197.

BOERO, F., and J. BOUILLON

1987 Inconsistent evolution and paedomorphosis among the hydroids and medusae of the Athecatae/Anthomedusae and the Thecatae/Leptomedusae (Cnidaria, Hydrozoa). *In* Bouillon, J., F. Boero, F. Cicogna, and P. F. S. Cornelius, eds., Modern trends in the systematics, ecology, and evolution of hydroids and hydromedusae. Oxford, Clarendon Press, pp. 229–250.

1989 An evolutionary interpretation of anomalous medusoid stages in the life cycles of some Leptomedusae (Cnidaria). *In* Ryland, J. S., and P. A. Tyler, eds., Reproduction, genetics and distributions of marine organisms. Fredensborg (Denmark), Olsen and Olsen, pp. 37–41.

BOGLE, M. A.

1975 A review and preliminary revision of the Aglaopheniinae (Hydroida: Plumulariidae) of the tropical western Atlantic. Master's thesis, University of Miami, Coral Gables. 307 pp.

1984 *Cladocarpoides yucatanicus*, a new genus and species of Aglaopheniinae (Coelenterata: Hydroida: Plumulariidae) from Arrowsmith Bank, Yucatan Channel. Bulletin of Marine Science 34:135–140.

BOSC, L. A. G.

1797 Description des objets nouveaux d'histoire naturelle, trouvés dans une traversée de Bordeaux à Charles-Town. Bulletin des Sciences, par la Société Philomathique de Paris 1(2): 9–10.

1802 Histoire naturelle des vers, contenant leur description et leurs moeurs; avec figures dessinées d'après nature. Tome 3. Paris, Guilleminet. 270 pp.

BOUILLON, J.

1984 Révision de la famille des Phialuciidae (Kramp, 1955) (Leptomedusae, Hydrozoa, Cnidaria), avec un essai de classification des Thecatae-Leptomedusae. Indo-Malayan Zoology 1 (1984): 1–24.

1985 Essai de classification des hydropolypes-hydroméduses (Hydrozoa-Cnidaria). Indo-Malayan Zoology 1 (1985): 29–243.

BOUILLON, J., F. BOERO, F. CICOGNA, and P. F. S. CORNELIUS, eds.

1987 Modern trends in the systematics, ecology, and evolution of hydroids and hydromedusae. Oxford, Clarendon Press. 328 pp.

BROCH, H.

1913 Hydroida from the "Michael Sars" North Atlantic Deep-Sea Expedition 1910. Report on the Scientific Results of the "Michael Sars" North Atlantic Deep Sea Expedition 1910. Vol. 3, Part 1, Zoology, pp. 1–18.

1914 Hydrozoa benthonica. Beiträge zur Kenntnis der Meeresfauna Westafrikas 1:19–50.

1918 Hydroida (Part II). Danish Ingolf-Expedition 5(7). 205 pp.

1933 Zur Kenntnis der Adriatischen Hydroidenfauna von Split, Arten und Variationen. Skrifter Utgitt av det Norske Videnskaps-Akademi i Oslo I, Matematisk-Naturvidenskapelig Klasse, 1933(4): 1–115.

BRUCE, J. R., J. S. COLMAN, and N. S. JONES

1963 Marine fauna of the Isle of Man and its surrounding seas. Liverpool Marine Biology Committee Memoirs on Typical British Marine Plants and Animals, Memoir 36. Liverpool, Liverpool University Press. 307 pp.

BUSK, G.

1851 A list of sertularian zoophytes and Polyzoa from Port Natal, Algoa Bay, and Table Bay, in South Africa; with remarks on their geographical distribution, and observations on the genera *Plumularia* and *Catenicella*. British Association for the Advancement of Science 20:118–120.

1852 An account of the Polyzoa, and sertularian zoophytes, collected in the voyage of the "Rattlesnake," on the coasts of Australia and the Louisiade Archipelago, etc. *In* J. MacGillivray, Narrative of the voyage of H.M.S. Rattlesnake, commanded by the late Captain Owen Stanley, R.N., F.R.S., etc., during the years 1846–1850. Vol. 1, Appendix 4. London, T. and W. Boone, pp. 343–402.

BUTLER, J. N., B. F. MORRIS, J. CADWALLADER, and A. W. STONER

1983 Studies of *Sargassum* and the *Sargassum* community. Bermuda Biological Station Special Publication No. 22, pp. 1–306.

CAIRNS, S. D., D. R. CALDER, A. BRINCKMANN-VOSS,
C. B. CASTRO, P. R. PUGH, C. E. CUTRESS, W. C. JAAP,
D. G. FAUTIN, R. J. LARSON, G. R. HARBISON, M. N. ARAI, and
D. M. OPRESKO

1991 Common and scientific names of aquatic invertebrates from the United States and Canada: Cnidaria and Ctenophora. American Fisheries Society Special Publication 22. 75 pp.

CALDER, D. R.

1976 The zonation of hydroids along salinity gradients in South Carolina estuaries. *In* Mackie, G. O., ed., Coelenterate ecology and behavior. New York, Plenum Press, pp. 165–174.

1983 Hydroida from estuaries of South Carolina, USA: families Sertulariidae and Plumulariidae. Proceedings of the Biological Society of Washington 96:7–28.

1984 New observations on *Cladocarpus flexuosus* Nutting, 1900 (Hydrozoa: Plumulariidae), a bathyal hydroid from the Gulf of Mexico. Proceedings of the Biological Society of Washington 97:408–412.

1986 Class Hydrozoa. *In* Sterrer, W., ed., Marine fauna and flora of Bermuda: a systematic guide to the identification of marine organisms. New York, Wiley-Interscience, pp. 127–155.

1988 Shallow-water hydroids of Bermuda: the Athecatae. Royal Ontario Museum, Life Sciences Contributions 148. 107 pp.

1990 Seasonal cycles of activity and inactivity in some hydroids from Virginia and South Carolina, U.S.A. Canadian Journal of Zoology 68:442–450.

1991a Shallow-water hydroids of Bermuda: the Thecatae, exclusive of Plumularioidea. Royal Ontario Museum, Life Sciences Contributions 154. 140 pp.

1991b Associations between hydroid species assemblages and substrate types in the mangal at Twin Cays, Belize. Canadian Journal of Zoology 69:2067–2074.

1992 Similarity analysis of hydroid assemblages along a latitudinal gradient in the western North Atlantic. Canadian Journal of Zoology 70:1078–1085.

1993 Local distribution and biogeography of the hydroids (Cnidaria) of Bermuda. Caribbean Journal of Science 29:61–74.

1995 Hydroid assemblages on holopelagic *Sargassum* from the Sargasso Sea at Bermuda. Bulletin of Marine Science 56:509–518.

CALDER, D. R., and P. F. S. CORNELIUS

1996 *Plumularia* Lamarck, 1816 (Cnidaria, Hydrozoa): proposed conservation by designation of *Sertularia setacea* Linnaeus, 1758 as the type species. Bulletin of Zoological Nomenclature 53:167–170.

CARY, L. R., and H. M. SPAULDING

1909 Further contributions to the marine fauna of the Louisiana coast. Gulf Biologic Station Bulletin 12:1–21.

CASTRIC-FEY, A.

1970 Sur quelques hydraires de l'Archipel de Glénan (Sud-Finistère). Vie et Milieu, sér. A: Biologie Marine, 21:1–23.

CAVOLINI, F.

1785 Memorie per servire alla storia de' polipi marini. Napoli. 279 pp.

CLARK, S. F.

1876 Report on the hydroids collected on the coast of Alaska and the Aleutian Islands, by W. H. Dall, U.S. Coast Survey, and party, from 1871 to 1874 inclusive. Proceedings of the Academy of Natural Sciences of Philadelphia 1876:209–235.

CLARKE, S. F.

1879 Report on the Hydroida collected during the exploration of the Gulf Stream and Gulf of Mexico by Alexander Agassiz, 1877–78. Bulletin of the Museum of Comparative Zoölogy at Harvard College 5:239–252.

1907 Reports on the scientific results of the expedition to the eastern tropical Pacific, in charge of Alexander Agassiz, by the U.S. Fish Commission steamer "Albatross," from October, 1904, to March, 1905, Lieut.-Commander L. M. Garrett, U.S.N., commanding. VIII. The hydroids. Memoirs of the Museum of Comparative Zoölogy at Harvard College 35(1): 1–18.

CONGDON, E. D.

1907 The hydroids of Bermuda. Proceedings of the American Academy of Arts and Sciences 42:463–485.

COOKE, W. J.

1977 Order Hydroida. *In* Devaney, D. M., and L. G. Eldredge, eds., Reef and shore fauna of Hawaii. Section 1: Protozoa through Ctenophora. Bernice P. Bishop Museum Special Publication 64:71–104.

CORNELIUS, P. F. S.

1979 A revision of the species of Sertulariidae (Coelenterata: Hydroida) recorded from Britain and nearby seas. Bulletin of the British Museum (Natural History), Zoology 34:243–321.

1982 Hydroids and medusae of the family Campanulariidae recorded from the eastern North Atlantic, with a world synopsis of genera. Bulletin of the British Museum (Natural History), Zoology 42:37–148.

1995 North-west European thecate hydroids and their medusae (Cnidaria, Leptolida, Leptothecatae). Part 2. Synopses of the British Fauna, n.s., 50. 396 pp.

CORNELIUS, P. F. S., and J. B. GARFATH

1980 The coelenterate taxa of Joshua Alder. Bulletin of the British Museum (Natural History), Zoology 39:273–291.

CORNELIUS, P. F. S., and J. S. RYLAND

1990 Class Hydrozoa. *In* Hayward, P. J., and J. S. Ryland, eds., The marine fauna of the British Isles and north-west Europe. Oxford, Clarendon Press, pp. 107–158.

COSTA, O.-G.

1839 Corrispondenza zoologica destinata a diffondere nel regno delle due Sicilie. Napoli, Azzolino e Compagno. 194 pp.

1842 Fauna del regno di Napoli. Zoofiti. Genere

Anisocalice; *Anisocalyx*. Don. Napoli, Azzolino e Compagno. 24 pp.

COUCH, R. Q.

1844 A Cornish fauna; being a compendium of the natural history of the county. Part III. Containing the zoophytes and calcareous corallines. Truro, L. E. Gillet. 164 pp.

CRAWSHAY, L. R.

1912 On the fauna of the outer western area of the English Channel. Journal of the Marine Biological Association of the United Kingdom, n.s., 9:292–393.

CUNHA, A. X. da

1944 Hidropólipos das costas de Portugal. Memórias e Estudos do Museu Zoológico da Universidade de Coimbra 161:1–101.

CUVIER, G.

1830 Le règne animal distribué d'après son organization. Édition 2. Vol. 3. Paris, Déterville. 504 pp.

DANA, J. D.

1846 United States Exploring Expedition. During the years 1838, 1839, 1840, 1841, 1842. Under the command of Charles Wilkes, U.S.N. Zoophytes. Philadelphia, Lea and Blanchard. 740 pp.

DEEVEY, E. S., Jr.

1950 Hydroids from Louisiana and Texas, with remarks on the Pleistocene biogeography of the western Gulf of Mexico. Ecology 31:334–367.

1954 Hydroids of the Gulf of Mexico. Fishery Bulletin of the United States Fish and Wildlife Service 55:267–272.

DEFENBAUGH, R.

1974 Hydroids. *In* Bright, T. J., and L. H. Pequegnat, eds., Biota of the West Flower Garden Bank. Houston, Gulf Publishing Company, pp. 94–112.

DEFENBAUGH, R. E., and S. H. HOPKINS

1973 The occurrence and distribution of the hydroids of the Galveston Bay, Texas, area. Texas A & M University TAMU-SG-73-210. 202 pp.

DENOTARIS, G.

1846 Zoofiti. Descrizione di Genova e del Genovesato. Vol. 1, Part 2. Genova, Ferrando, pp. 75–80.

DRIESCH, H.

1890 Die Tektonik von *Plumularia Catharina* Johnston. Zoologischer Anzeiger 13:660–662.

EHRENBERG, C. G.

1834 Beiträge zur physiologischen Kenntniss der Corallenthiere im allgemeinen, und besonders des rothen Meeres, nebst einem Versuche zur physiologischen Systematik derselben. Abhandlung der Königlichen Akademie der Wissenschaften, Berlin 1:225–380.

EKMAN, S.

1953 Zoogeography of the sea. London, Sidgwick and Jackson. 417 pp.

ELLIS, J.

1755 An essay towards a natural history of the corallines, and other marine productions of the like kind, commonly found on the coasts of Great Britain and Ireland. To which is added the description of a large marine polype taken near the North Pole, by the whale-fishers, in the summer 1753. London. 103 pp.

ELLIS, J., and D. SOLANDER

1786 The natural history of many curious and uncommon zoophytes, collected from various parts of the globe by the late J. Ellis . . . Systematically arranged and described by the late Daniel Solander . . . London. 206 pp.

FEWKES, J. W.

1881 Reports on the results of dredging, under the supervision of Alexander Agassiz, in the Caribbean Sea, in 1878, 1879, and along the Atlantic coast of the United States, during the summer of 1880, by the U.S. Coast Survey Steamer "Blake," Commander J. R. Bartlett, U.S.N., commanding. XI. Report on the Acalephae. Bulletin of the Museum of Comparative Zoölogy at Harvard College 8:127–140.

FEY, A.

1969 Peuplements sessiles de l'archipel de Glénan 1.—Inventaire: Hydraires. Vie et Milieu, sér. B: Océanographie, 20:387–413.

FLEMING, J.

1828 A history of British animals, exhibiting the descriptive characters and systematical arrangement of the genera and species of quadrupeds, birds, reptiles, fishes, Mollusca, and Radiata of the United Kingdom. Edinburgh, Bell and Bradfute. 565 pp.

FLOREZ GONZALEZ, L.

1983 Inventario preliminar de la fauna hydroide de la Bahía de Cartagena y áreas adyacentes. Boletin Museo del Mar, Bogotá 11:112–140.

FORBES, E.

1844 On the morphology of the reproductive system of the sertularian zoophyte, and its analogy with the reproductive system of the flowering plant. Annals and Magazine of Natural History 14:385–391.

FRASER, C. M.

1912 Some hydroids of Beaufort, North Carolina. Bulletin of the United States Bureau of Fisheries 30:339–387.

1914 Some hydroids of the Vancouver Island region. Transactions of the Royal Society of Canada, 3rd ser., Section 4, 8:99–216.

1918 Hydroids of eastern Canada. Contributions to Canadian Biology 1917–1918, pp. 329–367.

1921 Key to the hydroids of eastern Canada. Contributions to Canadian Biology 1918–1920, pp. 137–180.

1925 Some new and some previously unreported hydroids, mainly from the Californian coast. University of California Publications in Zoology 28:167–172.

1935 Some Japanese hydroids, mostly new. Transactions of the Royal Society of Canada, 3rd ser., Section 5, 29:105–112.

1936 Hydroid distribution in the vicinity of the Queen Charlotte Islands. Canadian Field-Naturalist 50:122–126.

1937 Hydroids of the Pacific coast of Canada and the United States. Toronto, University of Toronto Press. 207 pp.

1938a Hydroids of the 1934 Allan Hancock Pacific Expedition. Allan Hancock Pacific Expeditions 4:1–105.

1938b Hydroids of the 1932, 1933, 1935, and 1938 Allan Hancock Pacific Expeditions. Allan Hancock Pacific Expeditions 4:129–153.

1943 Distribution records of some hydroids in the collection of the Museum of Comparative Zoölogy at Harvard College, with description of new genera and new species. Proceedings of the New England Zoölogical Club 22:75–98.

1944 Hydroids of the Atlantic coast of North America. Toronto, University of Toronto Press. 451 pp.

1945 Notes on some recently collected hydroids in the United States National Museum, with descriptions of three new species. Journal of the Washington Academy of Sciences 35:21–23.

1946 Distribution and relationship in American hydroids. Toronto, University of Toronto Press. 464 pp.

1947 Hydroids of the 1939 Allan Hancock Caribbean Sea Expedition. Allan Hancock Atlantic Expedition 4:1–24.

1948 Hydroids of the Allan Hancock Pacific Expeditions since March, 1938. Allan Hancock Pacific Expeditions 4:179–335.

FRIEDRICH, H.

1969 Marine biology. An introduction to its problems and results. Seattle, University of Washington Press. 474 pp.

GARCÍA, P., A. AGUIRRE, and D. GONZALEZ

1978 Contribución al conocimiento de los hidrozoos de las costas Españolas. Parte I: halecidos, campanularidos y plumularidos. Boletin del Instituto Español de Oceanografía 4:3–73.

GEMERDEN-HOOGEVEEN, G. C. H. VAN

1965 Hydroids of the Caribbean: Sertulariidae, Plumulariidae and Aglaopheniidae. Studies on the Fauna of Curaçao 22:1–87.

GILI, J.-M.

1982 Fauna de cnidaris de les illes Medes. Treballs de la Institució Catalana d'História Natural 10. 175 pp.

GILI, J.-M., W. VERVOORT, and F. PAGÈS

1989 Hydroids from the west African coast: Guinea Bissau, Namibia and South Africa. Scientia Marina 53:67–111.

GMELIN, J. F.

1791 Caroli a Linné, systema naturae per regna tria naturae, secundum classes, ordines, genera, species, cum characteribus, differentiis, synonymis, locis. Editio decima tertia, aucta reformata. Tomus 1, Pars 6. Lipsiae, G. E. Beer, pp. 3021–4120.

GRASSLE, J. F., and L. S. MORSE-PORTEOUS

1987 Macrofaunal colonization of disturbed deep-sea environments and the structure of deep-sea benthic communities. Deep-Sea Research 34A:1911–1950.

GRAVELY, F. H.

1927 The littoral fauna of Krusadai Island in the Gulf of Manaar. Coelenterata. Class Hydrozoa. Orders Gymnoblastea and Calyptoblastea. Bulletin of the Madras Government Museum, n.s., Natural History, 1:7–20.

GRAVIER, N.

1970a Libération de médusoides par *Macrorhynchia philippina* Kirchenpauer, 1872 (Hydroida, Plumulariidae). Recueil des Travaux de la Station Marine d'Endoume, Fascicule Hors Série Supplément 10:253–257.

1970b Étude des hydraires epiphytes des phanérogames marines de la région de Tulear (sud-ouest de Madagascar). Recueil des Travaux de la Station Marine d'Endoume, Fascicule Hors Série Supplément 10:111–161.

GRAVIER-BONNET, N.

1979 Hydraires semi-profonds de Madagascar (Coelenterata Hydrozoa), étude systématique et écologique. Zoologische Verhandelingen 169:1–76.

GRAVIER-BONNET, N., and M.-F. FONTAINE

1981 *Lytocarpus sibogae* Billard, 1913, espèce nouvelle pour l'Océan Indien (Coelenterata, Hydrozoa, Plumulariidae). Tethys 10:103–115.

HAECKEL, E.

1879 Das System der Medusen. Erster Theil einer Monographie der Medusen. Denkschriften der Medizinisch- Naturwissenschaftlichen Gesellschaft zu Jena 1. 360 pp.

HALSTEAD, B. W.

1988 Poisonous and venomous marine animals of the world. 2nd rev. ed. Princeton, Darwin Press. 1168 pp.

HAMOND, R.

1957 Notes on the Hydrozoa of the Norfolk coast. Journal of the Linnean Society of London, Zoology, 43:294–324.

HARGITT, C. W.

1924 Hydroids of the Philippine Islands. Philippine Journal of Science 24:467–507.

1927 Some hydroids of South China. Bulletin of the Museum of Comparative Zoölogy at Harvard College 67:491–520.

HARTLAUB, C.

1901 Hydroiden aus dem Stillen Ocean. Ergebnisse einer Reise nach dem Pacific (Schauinsland 1896–97). Zoologische Jahrbücher, Abtheilung für Systematik, Geographie und Biologie der Thiere 14:349–379.

HASSELT, J. C. van, and C. J. TEMMINCK

1823 Uittreksel uit een' brief van den Heer J. C. van Hasselt, aan den Heer C. J. Temminck. Algemeene Konst- en Letter-Bode 1823:130–133.

HELLER, C.

1868 Die Zoophyten und Echinodermen des Adriatischen Meeres. Verhandlungen der Kaiserlich-Königlichen Zoologisch-Botanischen Gesellschaft in Wien 18:1–88.

HENTSCHEL, E.

1922 Über den Bewuchs auf den treibenden Tangen der Sargassosee. Mitteilungen aus dem Zoologischen Staatsinstitut und Zoologischen Museum in Hamburg 38:1–26.

HERTWIG, R.

1882 Report on the Actiniaria dredged by H.M.S. Challenger during the years 1873–1876. Report on the Scientific Results of the Voyage of H.M.S. Challenger during the Years 1873–76, Zoology, 6(15): 1–136.

HINCKS, T.

1861 A catalogue of the zoophytes of south Devon and south Cornwall. Annals and Magazine of Natural History, 3rd ser., 8:251–262.

1865 Zoophytes: the history of their development. Quarterly Journal of Science, London, 2:401–418.

1868 A history of the British hydroid zoophytes. London, John van Voorst. 338 pp.

1872a Note on Prof. Heller's Catalogue of the Hydroida of the Adriatic. Annals and Magazine of Natural History, 4th ser., 9:116–121.

1872b Contributions to the history of the Hydroida. Annals and Magazine of Natural History, 4th ser., 10:385–395.

1874 Notes on Norwegian Hydroida from deep water. Annals and Magazine of Natural History, 4th ser., 13:125–137.

1877 Contributions to the history of the Hydroida. Annals and Magazine of Natural History, 4th ser., 19:148–152.

1889 On the Polyzoa and Hydroida of the Mergui Archipelago collected for the Trustees of the Indian Museum, Calcutta, by Dr. J. Anderson, F.R.S., superintendent of the museum. Journal of the Linnean Society, Zoology, 21:121–135.

HIROHITO, HIS MAJESTY THE SHOWA EMPEROR

1969 Some hydroids of the Amakusa Islands. Tokyo, Biological Laboratory, Imperial Household. 32 pp.

1974 Some hydrozoans of the Bonin Islands. Tokyo, Biological Laboratory, Imperial Household. 55 pp.

1983 Hydroids from Izu Ôshima and Niijima. Tokyo, Biological Laboratory, Imperial Household. 83 pp.

HUGHES, R. G.

1986 Differences in the growth, form and life history of *Plumularia setacea* (Ellis and Solander)(Hydrozoa: Plumulariidae) in two contrasting habitats. Proceedings of the Royal Society of London, ser. B, 228:113–125.

ICZN (INTERNATIONAL COMMISSION ON ZOOLOGICAL NOMENCLATURE)

1985 International code of zoological nomenclature. 3rd ed. Adopted by the XX General Assembly of the International Union of Biological Sciences. Berkeley, University of California Press. 338 pp.

IRVINE, A.

1854 Catalogue of zoophytes found in Dublin Bay and in its vicinity. Natural History Review 1:244–247.

IZQUIERDO, S., P. GARCÍA-CORRALES, and J. J. BACALLADO

1986 Contribución al conocimiento de los hidrozoos caliptoblástidos del Archipiélago Canario. Parte II: Plumulariidae. Boletín del Instituto Español de Oceanografía 3(2): 49–66.

JÄDERHOLM, E.

1896 Ueber aussereuropäische Hydroiden des zoologischen Museums der Universität Upsala. Bihang till Kongliga Svenska Vetenskaps-Akademiens Handlingar 21, Afd. 4, 6:1–20.

1903 Aussereuropäische Hydroiden im schwedischen Reichsmuseum. Arkiv för Zoologi 1:259–312.

1919 Zur Kenntnis der Hydroidenfauna Japans. Arkiv för Zoologi 12(9): 1–34.

JARVIS, F. E.

1922 The hydroids from the Chagos, Seychelles and other islands and from the coasts of British East Africa and Zanzibar. Transactions of the Linnean Society of London (Zoology) 18:331–360.

JICKELI, C. F.

1883 Der Bau der Hydroidpolypen. II. Über den histiologischen Bau von *Tubularia* L., *Cordylophora* Allm., *Cladonema* Duj., *Coryne* Gärtn., *Gemmaria* M'Crady, *Perigonimus* Sars, *Podocoryne* Sars, *Camponopsis* Claus, *Lafoëa* Lam., *Campanularia* Lam., *Obelia* Pér., *Anisocola* Kirchenp., *Isocola* Kirchenp., *Kirchenpaueria* Jick. Morphologisches Jahrbuch 8:580–680.

JOHNSON, D. L., and P. L. RICHARDSON

1977 On the wind-induced sinking of *Sargassum*. Journal of Experimental Marine Biology and Ecology 28:255–267.

JOHNSTON, G.

1833 Illustrations in British zoology. Magazine of Natural History 6:497–499.

1847 A history of the British zoophytes. 2nd ed. London, John van Voorst. 488 pp.

KIRCHENPAUER, G. H.

1869 Neue Bryozoen. Catalog IV des Museum Godeffroy, Hamburg. Pp. xxxv-xxxiv.

1872 Ueber die Hydroidenfamilie Plumularidae, einzelne Gruppen derselben und ihre Fruchtbehälter. I. *Aglaophenia* Lx. Abhandlungen aus dem Gebiete der Naturwissenschaften herausgegeben von dem Naturwissenschaftlichen Verein in Hamburg 5(3): 1–52.

1876 Ueber die Hydroidenfamilie Plumularidae, einzelne Gruppen derselben und ihre Fruchtbehälter. II. *Plumularia* und *Nemertesia*. Abhandlungen aus dem Gebiete der Naturwissenschaften herausgegeben vom Naturwissenschaftlichen Verein zu Hamburg-Altona 6:1–59.

KRAMP, P. L.

1956 Hydroids from depths exceeding 6000 meters. Galathea Report 2:17–20.

KÜHN, A.

1909 Sprosswachstum und Polypenknospung bei den Thecaphoren. Studien zur Ontogenese und Phylogenese der Hydroiden. Zoologische Jahrbücher, Abteilung für Anatomie und Ontogenie der Tiere 28:387–476.

1913 Entwicklungsgeschichte und Verwandtschaftsbeziehungen der Hydroiden. I. Teil: Die Hydroiden. Ergebnisse und Fortschritte der Zoologie 4:1–284.

LAMARCK, J. B. P. A. de

1816 Histoire naturelle des animaux sans vertèbres. Tome 2. Paris, Verdière. 568 pp.

1836 Histoire naturelle des animaux sans vertèbres. Edition 2. Tome 2. Paris, J. B. Baillière. 683 pp.

LAMOUROUX, J. V. F.

1812 Extrait d'un mémoire sur la classification des polypiers coralligènes non entièrement pierreux. Nouveau Bulletin des Sciences, par la Société Philomatique de Paris 3:181–188.

1816 Histoire des polypiers coralligènes flexibles, vulgairement nommés zoophytes. Caen, F. Poisson. 559 pp.

1824 Description des polypiers flexibles. *In* Quoy, J. R. C., and J. P. Gaimard, Voyage autour du monde, entrepris par ordre du Roi, exécuté sur les corvettes de S. M. l'Uranie et la Physicienne, pendant les années 1817, 1818, 1819 et 1820. Zoologie. Paris, Pillet Aîné, pp. 603–643.

LÉGER, L.

1892 Recherches sur les grégarines. Tablettes Zoologiques 3:1–182.

LELOUP, E.

1932a L'homologie des parties constituantes du gonosome chez *Thecocarpus* et *Aglaophenia* et la classification des Aglaopheniidae. Bulletin du Musée Royal d'Histoire Naturelle de Belgique 8(1): 1–26.

1932b Une collection d'hydropolypes appartenant l'Indian Museum de Calcutta. Records of the Indian Museum 34:131–170.

1934 Note sur les hydropolypes de la rade de Villefranche-sur-Mer (France). Bulletin du Musée Royal d'Histoire Naturelle de Belgique 10(31): 1–18.

1935 Hydraires calyptoblastiques des Indes Occidentales. Mémoires du Musée Royal d'Histoire Naturelle de Belgique 2(2): 1–73.

1937a Résultats scientifiques des croisières du navire-école belge "Mercator." VI. Hydroidea, Siphonophora, Ceriantharia. Mémoires du Musée Royal d'Histoire Naturelle de Belgique, 2^{me} sér., 9:91–121.

1937b Hydropolypes et scyphopolypes recueillis par C. Dawydoff sur les côtes de l'Indochine Française. Mémoires du Musée Royal d'Histoire Naturelle de Belgique, 2^{me} sér., 12:1–73.

1938a Quelques hydraires des côtes orientale et occidentale des États-Unis. Bulletin du Musée Royal d'Histoire Naturelle de Belgique 14(3): 1–9.

1938b Quelques hydropolypes de la Baie de Sagami, Japon. Bulletin du Musée Royal d'Histoire Naturelle de Belgique 14(28): 1–22.

1960 Hydropolypes du Muséum National d'Histoire Naturelle de Paris. Mémoires du Muséum National d'Histoire Naturelle, n.s., sér. A, Zoologie, 17:217–241.

1974 Hydropolypes calyptoblastiques du Chili. Report No. 48 of the Lund University Chile Expedition 1948–1949. Sarsia 55:1–61.

LENDENFELD, R. von

1884 Die australischen Plumulariden. Zoologischer Anzeiger 7: 548–550.

1885a The Australian Hydromedusae. Part IV. The Graptolithidae, Plumularidae and Dicorynidae. Proceedings of the Linnean Society of New South Wales 9:467–492.

1885b Über Coelenteraten der Südsee. V. Mittheilung. Die Hydromedusen des australischen Gebietes. Zeitschrift für Wissenschaftliche Zoologie 41:616–682.

LINNAEUS, C.

1758 Systema naturae per regna tria naturae, secundum classes, ordines, genera, species cum characteribus, differentiis, synonymis, locis. Editio decima, reformata. Holmiae, Laurentii Salvii. 823 pp.

1761 Fauna Suecica, sistens animalia Sueciae regni: Mammalia, Aves, Amphibia, Pisces, Insecta, Vermes. Distributa per classes & ordines, genera & species, cum differentiis specierum, synonymis auctorum, nominibus incolarum, locis natalium, descriptionibus insectorum. Editio altera, auctior. Stockholmiae, Laurentii Salvii. 544 pp.

1767 Systema naturae per regna tria naturae, secundum classes, ordines, genera, species, cum characteribus, differentiis, synonymis, locis. Tomus 1. Pars II. Editio duodecima, reformata. Holmiae, Laurentii Salvii, pp. 533–1317.

McCRADY, J.

1859 Gymnopthalmata of Charleston Harbor. Proceedings of the Elliott Society of Natural History 1:103–221.

MAITLAND, R. T.

1851 Descriptio systematica animalium, Belgii septentrionalis adjectis synonymis nec non locis in quibus reperiuntur, secundum classificationem Professoris J. van der Hoeven disposita. Editio 2. Leiden, C. C. van der Hoek. 234 pp.

MAMMEN, T. A.

1965 On a collection of hydroids from south India. III. Family Plumulariidae. Journal of the Marine Biological Association of India 7:291–324.

MARKTANNER-TURNERETSCHER, G.

1890 Die Hydroiden des K. K. Naturhistorischen Hofmuseums. Annalen des K. K. Naturhistorischen Hofmuseums 5:195–286.

MAYAL, E. M.

1983 Distribuição de hidróides (Hydrozoa, Thecata) na costa do estado de Pernambuco, Brasil. Boletim de Zoologia, Universidade de São Paulo 6:1–13.

MENEGHINI, G.

1843 Osservazioni sull' ordine delle sertulariee della classe dei polipi. Atti delle Adunanze dell' Imperiale Reale Istituto Veneto di Scienze, Lettere ed Arti 1(2): 402–404.

1845 Osservazioni sull' ordine delle sertulariee della classe de' polipi. Memorie dell' Imperiale Reale Istituto Veneto di Scienze, Lettere ed Arti 2:183–199.

MERGNER, H.

1987 Hydroids as indicator species of environmental factors on coral reefs. *In* Bouillon, J., F. Boero, F. Cicogna, and P. F. S. Cornelius, eds., Modern trends in the systematics, ecology, and evolution of hydroids and hydromedusae. Oxford, Clarendon Press, pp. 185–195.

MERGNER, H., and E. WEDLER

1977 Über die Hydroidpolypenfauna des Roten Meeres und seiner Ausgänge. "Meteor" Forschungs-Ergebnisse D, 24:1–32.

MILLARD, N. A. H.

1957 The Hydrozoa of False Bay, South Africa. Annals of the South African Museum 43:173–243.

1958 Hydrozoa from the coasts of Natal and Portuguese East Africa. Part I. Calyptoblastea. Annals of the South African Museum 44:165–226.

1962 The Hydrozoa of the south and west coasts of South Africa. Part I. The Plumulariidae. Annals of the South African Museum 46:261–319.

1966 Hydroids of the Vema Seamount. Annals of the South African Museum 48:489–496.

1967 Hydroids from the south-west Indian Ocean. Annals of the South African Museum 50:169–194.

1973 Auto-epizoism in South African hydroids. Publications of the Seto Marine Biological Laboratory 20:23–34.

1975 Monograph on the Hydroida of southern Africa. Annals of the South African Museum 68:1–513.

1977 The South African Museum's *Meiring Naude* cruises. Part 3. Hydroida. Annals of the South African Museum 73:105–131.

MILLARD, N. A. H., and J. BOUILLON

1973 Hydroids from the Seychelles (Coelenterata). Annales du Musée Royal de l'Afrique Centrale, sér. In-8°, Sciences Zoologiques, 206:1–106.

MORRIS, B. F., and D. D. MOGELBERG

1973 Identification manual to the pelagic *Sargassum* fauna. Bermuda Biological Station for Research Special Publication No. 11, pp. 1–63.

MOTZ-KOSSOWSKA, S.

1903 Sur l'action morphogène de l'eau en mouvement sur les hydraires. Comptes Rendus Hebdomadaires des Séances de l'Académie des Sciences 137:863–865.

1907 Sur les gonophores de *Plumularia obliqua* Saunders et *Sertularia operculata* L. Archives de Zoologie Expérimentale et Générale, Notes et Revue, 4^e sér., 7:114–118.

MULDER, J. F., and R. E. TREBILCOCK

1911 Notes on Victorian Hydroida, with description of new species. Geelong Naturalist, 2nd ser., 4:115–124.

MURRAY, A.

1860 Description of new Sertulariadae from the Californian coast. Annals and Magazine of Natural History, 3rd ser., 5:250–252.

NAUMOV, D. V.

1955 Novye rody i vidy gidroidov (Hydroidea) iz morei Dal'nego Vostoka. Trudy Zoologicheskogo Instituta Akademiya Nauk SSSR 18:19–25.

1960 Gidroidy i gidromeduzy morskikh, solonovatovodnykh i presnovodnykh basseinov SSSR. Akademiya Nauk SSSR, Opredeliteli po Faune SSSR 70:1–626.

NEPPI, V.

1918 Osservazioni sui polipi idroidi del Golfo di Napoli. Pubblicazioni della Stazione Zoologica di Napoli 2:29–65.

NORMAN, A. M.

1869 Shetland final dredging report.—Part II. On the Crustacea, Tunicata, Polyzoa, Echinodermata, Actinozoa, Hydrozoa, and Porifera. Report of the 38th Meeting of the British Association for the Advancement of Science, 1869:247–336.

NUTTING, C. C.

1895 Narrative and preliminary report of Bahama Expedition. Bulletin from the Laboratories of Natural History of the State University of Iowa 3:1–251.

1896 Notes on Plymouth hydroids. Journal of the Marine Biological Association of the United Kingdom, n.s., 4:146–154.

1898 On three new species of hydroids and one new to Britain. Annals and Magazine of Natural History, ser. 7, 1:362–366.

1900 American hydroids. Part 1. The Plumularidae. Smithsonian Institution, United States National Museum Special Bulletin 4(1): 1–285.

1905 Hydroids of the Hawaiian Islands collected by the steamer Albatross in 1902. Bulletin of the United States Fish Commission for 1903, pp. 931–959.

1927 Report on the Hydroida collected by the United States Fisheries Steamer "Albatross" in the Philippine region, 1907–1910. Smithsonian Institution, United States National Museum Bulletin 100(6): 196–242.

OKEN, L.

1815 Okens Lehrbuch der Naturgeschichte. III. Theil. Zoologie. Vol. 1. Jena, Oken. 842 pp.

1817 Isis oder encyclopädische Zeitung von Oken. No. 146. Jena, 1161–1168.

ORBIGNY, A. d'

1846 Voyage dans l'Amerique Méridionale (le Brésil, la République Orientale de l'Uruguay, la République Argentine, la Patagonie, la République du Chili, la

République de Bolivia, la République du Pérou), exécuté pendant les années 1826, 1827, 1828, 1829, 1830, 1831, 1832 et 1833. Tome 5, 4e Partie: Zoophytes. Paris, Levrault. 28 pp.

PARFITT, E.

1866 A catalogue of the fauna of Devon, with notes and observations. Zoophytes. Exeter, William Pollard. 40 pp.

PARK, J. H.

1992 Zoogeographical distribution of marine hydroids (Cnidaria: Hydrozoa: Hydroida) in Korea. Korean Journal of Systematic Zoology 8:279–299.

1993 Marine hydroids (Cnidaria: Hydrozoa: Hydroida) from Cheju Island, Korea. Korean Journal of Systematic Zoology 9:261–280.

PARR, A. E.

1939 Quantitative observations on the pelagic *Sargassum* vegetation of the western North Atlantic. Bulletin of the Bingham Oceanographic Collection 6(7): 1–94.

PATRITI, G.

1970 Catalogue des cnidaires et cténaires des côtes atlantiques marocaines. Travaux de l'Institut Scientifique Chérifien et de la Faculté des Sciences, Série Zoologie 35:1–149.

PENNYCUIK, P. R.

1959 Faunistic records from Queensland. Part V.—Marine and brackish water hydroids. Papers from the Department of Zoology, University of Queensland 1:141–210.

PÉRON, F., and C. A. LESUEUR

1810 Tableau des caractères génériques et spécifiques de toutes les espèces de méduses connues jusqu'à ce jour. Annales du Muséum d'Histoire Naturelle 14:325–366.

PICARD, J.

1951a Hydraires littoraux du Sénégal récoltés par H. Sourie aux environs de Dakar. Bulletin de l'Institut Fondamental d'Afrique Noire 13:109–115.

1951b Les hydraires des formations coralligènes des côtes Françaises de la Méditerranée. Vie et Milieu 2:255–261.

1958 Origines et affinités de la faune d'hydropolypes (gymnoblastes et calyptoblastes) et d'hydroméduses (anthoméduses et leptoméduses) de la Méditerranée. Rapport et Procès-Verbaux des Réunions, Commission Internationale pour l'Exploration Scientifique de la Mer Méditerranée 14:187–199.

PICTET, C.

1893 Étude sur les hydraires de la Baie d'Amboine. Revue Suisse de Zoologie et Annales du Musée d'Histoire Naturelle de Genève 1:1–64.

PICTET, C., and M. BEDOT

1900 Hydraires provenant des campagnes de l'Hirondelle (1886–1888). Résultats des Campagnes Scientifiques Accomplies sur son Yacht par Albert Ier, Prince Souverain de Monaco 18:1–59.

PIEPER, F. W.

1884 Ergänzungen zu "Heller's Zoophyten etc. des adriatischen Meeres." Zoologischer Anzeiger 7:185–188.

PIRES, D., C. B. CASTRO, Á. E. MIGOTTO, and A. C. MARQUES

1992 Cnidários bentônicos do arquipélago de Fernando de Noronha, Brasil. Boletim do Museu Nacional, Rio de Janeiro, n.s., Zoologia 354:1–21.

POCHE, F.

1914 Das System der Coelenterata. Archiv für Naturgeschichte 80, Abteilung A, Heft 5, pp. 47–128.

QUELCH, J. J.

1885 On some deep-sea and shallow-water Hydrozoa. Annals and Magazine of Natural History, 5th ser., 16:1–20.

RALPH, P. M.

1961 New Zealand thecate hydroids Part IV.—The family Plumulariidae. Transactions of the Royal Society of New Zealand, Zoology, 88:19–74.

RAMIL, F., and W. VERVOORT

1992a Report on the Hydroida collected by the "BALGIM" expedition in and around the Strait of Gibraltar. Zoologische Verhandelingen 277:1–262.

1992b Some consideration concerning the genus *Cladocarpus* (Cnidaria: Hydrozoa). Scientia Marina 56:171–176.

1992c *Pseudoplumaria* gen. nov. a new Atlantic genus of the family Plumulariidae (Cnidaria: Hydrozoa). Zoologische Mededelingen 66:485–492.

REDIER, L.

1964 Révision des hydraires de la collection Lamarck (Muséum National d'Histoire Naturelle). Bulletin du Muséum National d'Histoire Naturelle, 2e sér., 36:122–156.

1967 Révision de la collection du muséum des hydraires de Lamouroux. Bulletin du Muséum National d'Histoire Naturelle, 2e sér., 39:381–410.

REES, W. J.

1957 Order Hydroida. *In* Marine Biological Association, Plymouth Marine Fauna. 3rd ed. Plymouth, Marine Biological Association of the United Kingdom, pp. 37–51.

REES, W. J., and S. THURSFIELD

1965 The hydroid collections of James Ritchie. Proceedings of the Royal Society of Edinburgh, Section B (Biology) 69:34–220.

REES, W. J., and W. VERVOORT

1987 Hydroids from the John Murray Expedition to the Indian Ocean, with revisory notes on *Hydrodendron*, *Abietinella*, *Cryptolaria* and *Zygophylax* (Cnidaria: Hydrozoa). Zoologische Verhandelingen 237:1–209.

RHO, B. J.

1967 Marine hydroids from the west and south sea of Korea. Papers of the Korean Cultural Institute 10:341–360.

1969 Studies on the marine hydroids in Korea. Journal of

Korean Research Institute for Better Living, Ewha Womans University 2:161–174.

RHO, B. J., and J. H. PARK

1986 A systematic study on the marine hydroids in Korea. 10. The family Plumulariidae. Journal of Korean Research Institute for Better Living, Ewha Womans University 37:87–112.

RIEDL, R.

1959 Die Hydroiden des Golfes von Neapel und ihr Anteil an der Fauna unterseeischer Höhlen. Pubblicazioni della Stazione Zoologica di Napoli 30 (supplemento): 591–755.

1963 Hydroidea-Polypengeneration (Hydropolypen). *In* Riedl, R., ed., Fauna und Flora der Adria. Hamburg and Berlin, Paul Parey, pp. 124–133.

RIFKIN, J. F., P. J. FENNER, and J. A. H. WILLIAMSON

1993 First aid treatment of the sting from the hydroid *Lytocarpus philippinus*: the structure of, and *in vitro* discharge experiments with its nematocysts. Journal of Wilderness Medicine 4:252–260.

RITCHIE, J.

1908 On collections of the Cape Verde Islands marine fauna, made by Cyril Crossland, M.A. (Cantab.), B.Sc. (Lond.), F.Z.S., of St. Andrews University, July to September, 1904.—The hydroids. Proceedings of the Zoological Society of London 1907:488–514.

1909a Supplementary report on the hydroids of the Scottish National Antarctic Expedition. Transactions of the Royal Society of Edinburgh 47:65–101.

1909b New species and varieties of Hydroida Thecata from the Andaman Islands. Annals and Magazine of Natural History, 8th ser., 3:524–528.

1909c Two unrecorded "Challenger" hydroids from the Bermudas, with a note on the synonymy of *Campanularia insignis*. The Zoologist, 4th ser., 13:260–263.

1910a The hydroids of the Indian Museum. I.—The deep-sea collection. Records of the Indian Museum 5:1–30.

1910b The marine fauna of the Mergui Archipelago, Lower Burma, collected by Jas. J. Simpson, M.A., B.Sc., and R. N. Rudmose-Brown, D.Sc., University of Aberdeen, February to May 1907.—The hydroids. Proceedings of the Zoological Society of London 1910:799–825.

RYLAND, J. S., and M. J. GIBBONS

1991 Intertidal and shallow water hydroids from Fiji. II. Plumulariidae and Aglaopheniidae. Memoirs of the Queensland Museum 30:525–560.

SARS, G. O.

1874 Bidrag til kundskaben om norges Hydroider. Forhandlinger i Videnskabs-Selskabet i Christiania 1873:91–150.

SAVIGNY, J.-C.

1826 Description de l'Égypte ou recueil des observations et des recherches qui ont été faites en Égypte pendant l'expédition de l'armée française. Édition 2. Atlas, Histoire Naturelle. Vol. 2. Paris, Panckoucke.

SCHENCK, D. A. von

1965 *Aglaophenia harpago*, a new species of the Plumulariidae (Hydroidea). Pubblicazioni della Stazione Zoologica di Napoli 34:211–215.

1966 Die Kormentektonik der Plumulariiden (Coelenterata, Hydrozoa). Revue Suisse de Zoologie 72:885–1021.

SCHMIDT, H.-E.

1972 Some new records of hydroids from the Gulf of Aqaba with zoogeographical remarks on the Red Sea area. Journal of the Marine Biological Association of India 13:27–51.

SCHMIDT, O.

1862 Die Spongien des adriatischen Meeres. Leipzig, W. Engelmann. 88 pp.

SCHNEIDER, K. C.

1898 Hydropolypen von Rovigno, nebst Uebersicht über das System der Hydropolypen im Allgemeinen. Zoologische Jahrbücher, Abtheilung für Systematik, Geographie und Biologie der Thiere 10:472–555.

SHERBORN, C. D.

1898 On the dates of the natural history portion of Savigny's "Description de l'Égypte." Proceedings of the Zoological Society of London 1897:285–288.

1922 Index animalium. Part I. Introduction, bibliography and index A-Aff. London, British Museum (Natural History). i–cxxxi + 128 pp.

SMALLWOOD, W. M.

1910 Notes on the hydroids and nudibranchs of Bermuda. Proceedings of the Zoological Society of London, 1910, pp. 137–145.

SPRACKLIN, B. W.

1982 Hydroidea (Cnidaria: Hydrozoa) from Carrie Bow Cay, Belize. *In* Rützler, K., and I. G. Macintyre, eds., The Atlantic barrier reef ecosystem at Carrie Bow Cay, Belize, I. Structure and communities. Smithsonian Contributions to the Marine Sciences 12:239–251.

SPRENGEL, W.

1813 Philipp Cavolini's Abhandlungen über Pflanzen-Thiere des Mittelmeers. Nürnburg, J. Leonhard. 131 pp.

STECHOW, E.

1907 Neue japanische Athecata und Plumularidae aus der Sammlung Dr. Doflein. Zoologischer Anzeiger 32:192–200.

1909 Beiträge zur Naturgeschichte Ostasiens. Herausgegeben von Dr. F. Doflein. Hydroidpolypen der japanischen Ostküste. I. Teil: Athecata und Plumularidae. Abhandlungen der Mathematisch-Physikalischen Klasse der Königlichen Bayerischen Akademie der Wissenschaften, Supplement-Band 1(6): 1–111.

1911 Über Hydroiden der Deutschen Tiefsee-Expedition. Ein neues Genus thecater Hydroiden. Zoologischer Anzeiger 37:193–197.

1912 Hydroiden der Münchener Zoologischen Staatssammlung. Zoologische Jahrbücher, Abteilung für Systematik, Geographie und Biologie der Tiere 32:333–378.

1919a Zur Kenntnis der Hydroidenfauna des Mittelmeeres, Amerikas und anderer Gebiete, nebst Angaben über einige Kirchenpauer'sche Typen von Plumulariden. Zoologische Jahrbücher, Abteilung für Systematik, Geographie und Biologie der Tiere 42:1–172.

1919b Neue Ergebnisse auf dem Gebiete der Hydroidenforschung. Münchener Medizinische Wochenschrift 66:852–853.

1920 Neue Ergebnisse auf dem Gebiete der Hydroidenforschung. Sitzungsberichte der Gesellschaft für Morphologie und Physiologie in München 31:9–45.

1921a Neue Genera und Species von Hydrozoen und anderen Evertebraten. Archiv für Naturgeschichte, Abteilung A. 3. Heft, 87:248–265.

1921b Neue Ergebnisse auf dem Gebiete der Hydroidenforschung III. Münchener Medizinische Wochenschrift 68:897.

1921c Über Hydroiden der Deutschen Tiefsee-Expedition, nebst Bemerkungen über einige andre Formen. Zoologischer Anzeiger 53:223–236.

1923a Zur Kenntnis der Hydroidenfauna des Mittelmeeres, Amerikas und anderer Gebiete. II. Teil. Zoologische Jahrbücher, Abteilung für Systematik, Ökologie und Geographie der Tiere 47:29–270.

1923b Neue Hydroiden der Deutschen Tiefsee-Expedition, nebst Bemerkungen über einige andre Formen. Zoologischer Anzeiger 56:1–20.

1923c Über Hydroiden der Deutschen Tiefsee-Expedition, nebst Bemerkungen über einige andre Formen. Zoologischer Anzeiger 56:97–119.

1925a Hydroiden von West- und Südwestaustralien nach den Sammlungen von Prof. Dr. Michaelsen und Prof. Dr. Hartmeyer. Zoologische Jahrbücher, Abteilung für Systematik, Geographie und Biologie der Tiere 50:191–270.

1925b Hydroiden der Deutschen Tiefsee-Expedition. Wissenschaftliche Ergebnisse der Deutschen Tiefsee-Expedition auf dem Dampfer "Valdivia" 1898–1899, 17:383–546.

1926 Einige neue Hydroiden aus verschiedenen Meeresgebieten. Zoologischer Anzeiger 68:96–108.

STECHOW, E., and H. C. MÜLLER

1923 Hydroiden von den Aru-Inseln. Abhandlungen herausgegeben von der Senckenbergischen Naturforschenden Gesellschaft 35:459–478.

STECHOW, E., and T. UCHIDA

1931 Report of the Biological Survey of Mutsu Bay. 21. Hydroiden von Mutsu-Bai, Nord-Japan. Science Reports of the Tôhoku Imperial University, 4th ser. (Biology), 6:545–571.

STEPANJANTS, S. D.

1979 Gidroidy vod Antarktikh i Subantarktikh. Rezultaty Biologieskikh Issledovaniy Sovetskikh Antarkticheskikh Ekspedtsiy. Akademiya Nauk SSSR, Leningrad 22(30): 1–200.

STEPHENS, L. D., and D. R. CALDER

1992 John McCrady of South Carolina: pioneer student of North American Hydrozoa. Archives of Natural History 19:39–54.

STEWART, C.

1802 Elements of natural history; being an introduction to the Systema Naturae of Linnaeus. Vol. 2. London, Cadell and Davies. 491 pp.

1817 Elements of the natural history of the animal kingdom. Vol. 2. Edinburgh, Bell and Bradfute. 511 pp.

SVOBODA, A.

1979 Beitrag zur Ökologie, Biometrie und Systematik der mediterranen *Aglaophenia* Arten (Hydroidea). Zoologische Verhandelingen 167:1–114.

1992 Sexual dimorphism in *Aglaophenia tubulifera* and *Aglaophenia lophocarpa* (Cnidaria, Hydrozoa). Scientia Marina 56:177–183.

SVOBODA, A., and P. F. S. CORNELIUS

1991 The European and Mediterranean species of *Aglaophenia* (Cnidaria: Hydrozoa). Zoologische Verhandelingen 274:1–72.

THORNELY, L. R.

1900 The hydroid zoophytes collected by Dr. Willey in the southern seas. *In* Willey, A., Zoological results based on material from New Britain, New Guinea, Loyalty Islands and elsewhere, collected during the years 1895, 1896 and 1897. Part IV. Cambridge, Cambridge University Press, pp. 451–457.

TIMMERMANN, G.

1932 Biogeographische Untersuchungen über die Lebensgemeinschaft des Treibenden Golfkrautes. Zeitschrift für Morphologie und Ökologie der Tiere 25:288–335.

TIZARD, T. H., H. N. MOSELEY, J. Y. BUCHANAN, and J. MURRAY

1885 Narrative of the cruise of H.M.S. Challenger with a general account of the scientific results of the expedition. Report on the Scientific Results of the Voyage of H.M.S. Challenger during the Years 1873–76. Narrative. Vol. I, Part 1. 509 pp.

TORREY, H. B.

1902 The Hydroida of the Pacific coast of North America, with especial reference to the species in the collection of the University of California. University of California Publications, Zoology 1:1–104.

1904 The hydroids of the San Diego region. University of California Publications, Zoology 2:1–43.

TOTTON, A. K.

1930 Coelenterata. Part V.—Hydroida. British Antarctic ("Terra Nova") Expedition, 1910, Natural History Report, Zoology 5(5): 131–252.

TURTON, W.

1822 Conchylia insularum Britannicarum. The shells of the British Islands, systematically arranged. Exeter, R. Cullum. 279 pp.

VAN PRAËT, M.

1979 Les types de polypes d'hydraires conservés au Muséum National d'Histoire Naturelle de Paris. Bulletin du Muséum National d'Histoire Naturelle de Paris, 4^{me} sér., Section A, 1:871–940.

VANHÖFFEN, E.

1910 Die Hydroiden der Deutschen Südpolar-Expedition 1901–1903. Deutsche Südpolar-Expedition 1901–1903, 11, Zoologie 3(4): 269–340.

VANNUCCI, M.

1949 Hydrozoa do Brasil. Boletim da Faculdade de Filosofia, Ciências e Letras, Universidade de São Paulo, Zoologia 14:219–265.

1950 Resultados cientificos do cruzeiro do "Baependi" e do "Vega" à Ilha da Trindade. Boletim do Instituto Paulista de Oceanografia 1:81–96.

1951 Hydrozoa e Scyphozoa existentes no Instituto Paulista de Oceanografia. Boletim do Instituto Paulista de Oceanografia 2(1): 69–100.

VANNUCCI MENDES, M.

1946 Hydroida Thecaphora do Brasil. Arquivos de Zoologia do Estado de São Paulo 4:535–597.

VENUGOPALAN, V. P., and A. B. WAGH

1986 A note on the fouling hydroids from the offshore waters of Bombay. Mahasagar—Bulletin of the National Institute of Oceanography 19:275–277.

VERRILL, A. E.

1874 Report upon the invertebrate animals of Vineyard Sound and the adjacent waters, with an account of the physical features of the region. Report of the Commissioner of Fisheries for 1871-1872, pp. 295–747.

VERSLUYS, J.

1899 Hydraires calyptoblastes recueillis dans la mer des Antilles pendant l'une des croisières accomplies par le Comte R. de Dalmas sur son yacht CHAZALIE. Mémoires de la Société Zoologique de France 12:29–58.

VERVOORT, W.

1941 Biological results of the Snellius Expedition. XI. The Hydroida of the Snellius Expedition (Milleporidae and Stylasteridae excluded). Temminckia 6:186–240.

1946 Hydrozoa (C 1). A. Hydropolypen. Fauna van Nederland, Aflevering 14. 336 pp.

1959 The Hydroida of the tropical west coast of Africa. Atlantide Report 5:211–325.

1966 Bathyal and abyssal hydroids. Galathea Report 8:97–174.

1968 Report on a collection of Hydroida from the Caribbean region, including an annotated checklist of Caribbean hydroids. Zoologische Verhandelingen 92:1–124.

1972 Hydroids from the Theta, Vema and Yelcho cruises of the Lamont-Doherty Geological Observatory. Zoologische Verhandelingen 120:1–247.

VERVOORT, W., and P. VASSEUR

1977 Hydroids from French Polynesia with notes on distribution and ecology. Zoologische Verhandelingen 159:1–98.

WALLACE, W. S.

1909 A collection of hydroids made at the Tortugas, during May, June, and July, 1908. Carnegie Institution of Washington, Year Book 7:136–138.

WARREN, E.

1908 On a collection of hydroids, mostly from the Natal coast. Annals of the Natal Government Museum 1:269–355.

WATSON, J. E.

1973 Pearson Island Expedition 1969—9. Hydroids. Transactions of the Royal Society of South Australia 97:153–200.

1975 Hydroids of Bruny Island, southern Tasmania. Transactions of the Royal Society of South Australia 99:157–176.

WEDLER, E.

1975 Ökologische Untersuchungen an Hydroiden des Felslitorals von Santa Marta (Kolumbien). Helgoländer Wissenschaftliche Meeresuntersuchungen 27:324–363.

WEIS, J. S.

1968 Fauna associated with pelagic *Sargassum* in the Gulf Stream. American Midland Naturalist 80:554–558.

WHITEAVES, J. F.

1878 On some marine Invertebrata from the west coast of North America. Canadian Naturalist 8:464–471.

WINGE, Ö.

1923 The Sargasso Sea, its boundaries and vegetation. Report on the Danish Oceanographical Expeditions 1908–1910 to the Mediterranean and Adjacent Seas. Vol. III. Miscellaneous Papers 2:1–34.

WOODS HOLE OCEANOGRAPHIC INSTITUTION

1952 Marine fouling and its prevention. Annapolis, Maryland, United States Naval Institute. 388 pp.

YAMADA, M.

1959 Hydroid fauna of Japanese and its adjacent waters. Publications from the Akkeshi Marine Biological Station 9:1–101.

YAMADA, M., and S. KUBOTA

1987 Preliminary report on the marine hydroid fauna in Okinawa Islands. Galaxea 6:35–42.

ZOOLOGICAL RECORD

1980 Coelenterata together with Ctenophora. Zoological Record 114, Section 4 (1977). 88 pp.

Index

Bold numbers indicate page number of illustration