Zootaxa 4689 (1): 001–141
https://www.mapress.com/j/zt/

Monograph

ISSN 1175-5326 (print edition)
ZOOTAXA
ISSN 1175-5334 (online edition)

https://doi.org/10.11646/zootaxa.4689.1.1
http://zoobank.org/urn:lsid:zoobank.org:act:4C926BE2-D75D-449A-9EAD-14CADACFFADD

ZOOTAXA

4689

On a collection of hydroids (Cnidaria, Hydrozoa) from the southwest coast of Florida, USA

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Magnolia Press
Auckland, New Zealand

Accepted by B. Bentlage: 9 Sept.. 2019; published: 25 Oct. 2019

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(*Zootaxa* 4689)

141 pp.; 30 cm.

25 Oct. 2019

ISBN 978-1-77670-799-7 (paperback)

ISBN 978-1-77670-800-0 (Online edition)

FIRST PUBLISHED IN 2019 BY

Magnolia Press

P.O. Box 41-383

Auckland 1346

New Zealand

e-mail: magnolia@mapress.com

https://www.mapress.com/j/zt

ISSN 1175-5326 (Print edition)

ISSN 1175-5334 (Online edition)

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Abstract

Sixty species of hydroids, assigned to 24 families and 39 genera, are recognized and discussed in a collection of material from the southwest coast of Florida. One new species (*Clytia joycei*) is described from turtlegrass (*Thalassia testudinum*) and reported as well from the Caribbean coast of Panama. Under provisions of the First Reviser Principle in the *International Code of Zoological Nomenclature*, *Antennopsis nigra* Nutting, 1900 is assigned precedence over its simultaneous synonym *A. longicorna* Nutting, 1900. Also included as a synonym of *A. nigra* is *A. sinuosa* Fraser, 1947b. The species is now assigned to *Nemertesia* Lamouroux, 1816, as *N. nigra*. Following Reversal of Precedence provisions in the code, the well-known name *Halecium nanum* Alder, 1859 is designated as valid and conserved as a nomen protectum, while *Hydra articulata* Bosc, 1797 is relegated to a nomen oblitum. The genus *Monotheca* Nutting, 1900 is upheld as valid on the basis of both morphological and molecular evidence. *Sertularia pourtalesi* Nutting, 1904, a seldom-reported species, is assigned to *Dynamena* Lamouroux, 1812 and recognized as distinct from *D. disticha* (Bosc, 1802). *Calyptospadix cerulea* Clarke, 1882 and *Bimeria franciscana* Torrey, 1902 (also known as *Garveia franciscana*) are taken to be conspecific, with *Calyptospadix* Clarke, 1882 treated as a valid genus. Confusion over the identity of *Lovenella gracilis* Clarke, 1882 in literature on North American hydroids is addressed, and topotypic specimens from the Chesapeake Bay region are illustrated to document characters that distinguish the species. *Campanularia colombiana* (Wedler, 1976) is reported for the first time outside the Caribbean coast of Colombia. The fauna studied here consists largely of species known to occur in the tropical and subtropical western Atlantic. [Zoobank URL: urn:lsid:zoobank.org:act:4C926BE2-D75D-449A-9EAD-14CADACFFADD]

Key words: Anthoathecata, Hydroidolina, Leptothecata, marine invertebrates, Medusozoa, Gulf of Mexico, taxonomy, zoological nomenclature

Introduction

Louis Agassiz (1807–1873) of Harvard College commenced a survey of the navigationally hazardous “Florida Reefs” for the United States Coast Survey in 1851. It led to subsequent studies of that region by Prof. Agassiz, his students, and his associates. In terms of hydroids, the first account of a species from southwest Florida was of *Pennaria gibbosa* L. Agassiz, 1860 (=*Pennaria disticha*) from Key West (L. Agassiz 1860, 1862). Colonies were said to be common on pilings in the harbour. Additional records of hydroids collected in the Florida Reef region by the Harvard group exist in a catalogue of the Museum of Comparative Zoology by A. Agassiz (1865). Included along with *P. gibbosa* were *Aglaophenia pelasgica* (=*A. latecarinata*), *A. trifida*, *Parypha cristata* (=*Ectopleura cristata*), *Plumularia quadridens* (=*Monostaechas quadridens*), *Velella mutica* (=*V. velella*), *Porpita linnaeana* (=*P. porpita*), and *Millepora alcicornis*.

The most significant contributions to knowledge of the hydroid fauna of southwest Florida were based on extensive dredge collections obtained during 1867–1869 in the Straits of Florida by Count Louis François de Pourtalès

(1824–1880) of the United States Coast Survey. An initial report (Pourtalès 1867) on benthic biota included accounts of several new species of hydroids (*Antennularia triseriata*, *Thoa pulchella*, *T. capillaris*, *T. siphonata*, *Tubularia crinis*, and the stylasterids *Crypthelia peircei*, *Stylaster complanatus*, *Errina cochleata*, *E. glabra*, *Distichopora sulcata*, *Heliopora tubulata*, and *H. carinata*. In the same report, Pourtalès proposed the binomen *Stylaster duchassaingii* as a replacement name for a junior homonym). Descriptions of other stylasterids from the region exist in subsequent works (Pourtalès 1868, 1871, 1878; Cairns 1986; Reed *et al*. 2005). Pourtalès deposited his collection of benthic organisms from the straits, including a substantial and diverse assemblage of hydroids, in the Museum of Comparative Zoology at Harvard. The hydroids, most of them species from relatively deep water, were sent by Alexander Agassiz (1835–1910) to George James Allman (1812–1898) for identification. After several years of work, Allman (1877) published a landmark report on the collection, with descriptions of 64 new species, seven new genera, and one new family. Many of the new species are now known to be of widespread distribution and of ecological importance in the tropical and subtropical western Atlantic.

In 1893, Charles Cleveland Nutting (1858–1927) of the University of Iowa led an expedition to the Bahamas, Cuba, the Florida Keys, and the Dry Tortugas aboard the schooner *Emily E. Johnson*. A narrative of the expedition (Nutting 1895), as well as his monographs on Plumulariidae (Nutting 1900), Sertulariidae (Nutting 1904), and Campanulariidae (Nutting 1915), provide records of hydroids collected in southwest Florida.

The Tortugas Marine Laboratory of the Carnegie Institution of Washington, established in 1903, provided a base for several studies on hydroids in southwest Florida. Alfred Goldsborough Mayer (1868–1922), founding director of the laboratory, had undertaken extensive investigations on hydrozoans in the Dry Tortugas earlier as a student of Alexander Agassiz. While his work focused on hydromedusae, observations on certain hydroid species were provided as well (Mayer 1900b, 1910a, b). Meanwhile, two new species of hydrozoans were described by Perkins (1908) during a stay at the Tortugas Laboratory in 1905. His account provided details on the complete life cycle and general biology of *Cladonema mayeri* (=*Cladonema radiatum*) and on the hydroid and developing medusa stages of *Campanularia macrotheca* (=*Clytia macrotheca*). In 1908, a three-month study on hydroids of the Dry Tortugas was undertaken at the Tortugas Laboratory by Wallace (1909). An estimated 50 or more species were discovered by him in the area. His preliminary report provided identifications of more than three dozen of them, although numerous misspellings of taxon names and a number of unreliable identifications detract from the account.

Finally, scattered records of hydroid species from southwest Florida appear in reports such as those of Clarke (1879), Ritchie (1910), Fraser (1925, 1943, 1944), Leloup (1935a, 1937), Deevey (1954), Van Gemerden-Hoogeveen (1965), Vervoort (1968), Bogle (1975, 1990), Peña Cantero *et al*. (2007), Calder & Cairns (2009), Tolley *et al*. (2010), and Vervoort *et al*. (2011). Also relevant are records of hydroids from the northern Gulf coast of Florida in the unpublished theses of Joyce (1961) and Shier (1965).

This paper provides an account of hydroids from the southwest coast of Florida in collections at the Royal Ontario Museum (ROM). Biogeographically, the study area encompasses both sides of a boundary between the West Atlantic Tropical Province and the warm-temperate Carolinian Province, with Cape Romano (25°50’25.79”N, 81°40’25.79”W), Florida, an approximate border between the two (Briggs 1974; Neigel 2009). Most collections examined here, especially those from inshore areas, were made at Sanibel Island and Fort Myers Beach, both a short distance to the north of Cape Romano and thus within the Carolinian Province. A few collections of predominantly tropical species came from neritic waters of the middle and outer Southwest Florida Shelf. The present report addresses only those species represented in collections at the ROM, and it does not constitute an exhaustive overview of hydroid diversity in the region.

Materials and methods

Hydroids reported herein from offshore waters of southwest Florida were collected during surveys by the consulting firm Continental Shelf Associates in 1980 and 1981. The specimens were shipped to the Royal Ontario Museum (ROM) for identification. Vouchers of each species, held in collections of the Invertebrate Zoology Section of the Department of Natural History, ROM, were re-examined here. These collections, from the continental shelf, were supplemented with new material collected during this project from nearshore and estuarine areas of the study area in 2012–2014 and 2017–2018. Primary inshore collection sites were at Sanibel Island and at Fort Myers Beach on Estero and San Carlos islands.

Geographic limits of the study area extend northwards to latitude 27°N, westwards to the edge of the southwest Florida continental shelf, southwards to the edge of the continental shelf in the Straits of Florida, and eastwards to the coastline and then over water to a line between Key Largo, Florida, and Punta Hicacos, Cuba (23°12'N, 81°08'W). That line was taken by Felder *et al.* (2009) to mark the eastern limits of the Gulf of Mexico.

The classification system adopted here generally follows that of Schuchert (2012) for Anthoathecata, and Maronna *et al*. (2016) for Leptothecata. With the phylogeny of Zygophylacidae Quelch, 1885 currently unsettled, the family is included here, as in traditional classifications, within the suborder Lafoeida Bouillon, 1984. Synonymy lists are restricted to original accounts of species, together with works providing primary records of species from the Gulf Coast of Florida. All citations have been examined and verified. References dated in square brackets (e.g., Hincks 1868 [1869]) follow the Harvard-citation *referens* for a work in which the original stated date ("1868") has been found to be otherwise ("1869"). Nematocyst classification generally follows Weill (1934) and Östman (1979a, b, 1982, 1999). Illustrations of nematocysts herein, from photomicrographs taken at 1000x, are all to the same magnification.

A "Reported Distribution" section for each species includes original published records of hydroids from the entire Gulf of Mexico coast of Florida, followed by those from localities elsewhere in the western North Atlantic (west of the Mid-Atlantic Ridge). Records in these sections, mostly from the taxonomic literature, are meant to be comprehensive but not necessarily complete. In particular, references were generally excluded if actual collection sites were unclear, particularly in the case of frequently reported species (e.g., *Obelia geniculata*; *Pennaria disticha*). Also excluded were *de facto* non-records (such as certain kinds of species lists) based solely on accounts from other published works.

The following abbreviations used in this work refer to the following:

ICZN	*International Code of Zoological Nomenclature. Fourth Edition* (International Commission on Zoological Nomenclature 1999)
ROM	Royal Ontario Museum, Toronto, Ontario, Canada
ROMIZ	Invertebrate Zoology collections, Royal Ontario Museum, Toronto, Ontario, Canada
SMF	Senckenberg Forschungsinstitut und Naturmuseum, Frankfurt am Main, Germany
WoRMS	World Register of Marine Species (http://www.marinespecies.org, last consulted 15 August 2019), with content on Hydrozoa from the World Hydrozoa Database by Peter Schuchert (http:// www.marinespecies.org/hydrozoa).

Systematic Account

Phylum Cnidaria Verrill, 1865

Subphylum Medusozoa Petersen, 1979

Class Hydrozoa Owen, 1843

Subclass Hydroidolina Collins, 2000

Order Anthoathecata Cornelius, 1992

Suborder Capitata Kühn, 1913

Family Pennariidae McCrady, 1859

Genus *Pennaria* Goldfuss, 1820

Pennaria disticha Goldfuss, 1820

Fig. 1a

Pennaria disticha Goldfuss, 1820: 89.
Pennaria gibbosa L. Agassiz, 1860: pl. 15, figs. 1, 2.—L. Agassiz, 1862: 278.—A. Agassiz, 1865: 186.
Pennaria symmetrica.—Jäderholm, 1896: 5.
Pennaria tiarella.—Mayer, 1910a: 25, text-fig. 2, pl. 1, fig. 5.—Fraser, 1943: 87; 1944: 84.—Menzel, 1956: 2.—Joyce, 1961: 45, pl. 7, figs. 3, 4.—Shier, 1965: 28, pl. 14.
Pennaria.—Wallace, 1909: 137.
Pennaria sp.—Joyce, 1961: 44, pl. 7, figs. 1, 2.—Shier, 1965: 30, pls. 15, 16.

Type locality. Italy: Gulf of Naples (see Calder 2013: 7).

Material examined. Naples (FL), Doctors Pass, north jetty, channel side, on boulder, 26°10'29.14"N, 81°48'53.45"W, ELWS, 06 December 2017, two colony fragments, up to 3.7 cm high, without gonophores, coll. D. Calder, ROMIZ B4345.—Sanibel Island, beach at Lighthouse Point, on tube of the polychaete *Diopatra cuprea*, ELWS, 02 January 2018, two colony fragments, up to 1.7 cm high, without gonophores, coll. D. Calder, ROMIZ B4346.—Fort Myers Beach, 26°27'21"N, 81°57'45"W, detached at water's edge, 16 March 2018, 18° C, 34‰, two colonies, up to 12 cm high, without gonophores, coll. D. Calder, ROMIZ B4347.—Sanibel Island, beach at Lighthouse Point, 26°26'38"N, 82°01'36"W, on stranded *Thalassia*, 28 March 2018, 21° C, 35‰, one colony, 1.1 cm high, with gonophores, coll. D. Calder, ROMIZ B4348.—Fort Myers Beach, Salty Sam's Marina, 26°27'21.7"N, 81°56'34.6"W, on floating dock, <0.1 m, 29° C, 25‰, 27 August 2018, several colony fragments, up to 14 cm high, with gonophores, coll. D. Calder, ROMIZ B4418.

Remarks. Hydroids identified as *Pennaria disticha* Goldfuss, 1820 are widespread, conspicuous, distinctive, often abundant, and easily collected in shallow, warm waters along the Atlantic coast of North America. This relatively large species was one of the earliest hydroids to be reported from the region, having been discovered in the eastern United States as early as the 1850s by Ayres (1852, as *Globiceps tiarella*), Leidy (1855, as *Eucoryne elegans*), and McCrady (1859, **as** *Pennaria tiarella*). As noted in introductory remarks above, it was also the first hydroid to have been reported from the southwest coast of Florida (by L. Agassiz 1860, 1862, as *P. gibbosa*). A frequent component of shallow fouling communities in tropical and temperate regions, *P. disticha* is held to be an invasive species with a particularly wide geographic distribution. Barcoding techniques have recently provided evidence of a complex of cryptic species within hydroids identified as *P. disticha* (Miglietta *et al.* 2015, 2018a), but the taxonomy and nomenclature of the various lineages presently remain unresolved. While a name change may be necessary in the future, current usage of the binomen *P. disticha* is maintained for the species here.

The hydroid stage of this species, often identified in the western North Atlantic region as *P. tiarella* (Ayres, 1852), has been widely utilized in morphological, experimental, and ecological studies. Many of the distribution records listed below are based on specimens utilized in such work. If that hydroid proves to be a species distinct from the European *P. disticha*, and morphological differences in colonies from the two regions have indeed been noted (Wallace 1909; Mayer 1910a; Brinckmann-Voss 1970), the name *P. tiarella* will be upheld as valid for at least one population here. The possible existence of cryptic species in *Pennaria* Goldfuss, 1820 on the east coast of the United States is suggested from the molecular work of Miglietta *et al***.** (2015, 2018a) and from earlier morphological accounts such as those of Hargitt (1900) and Mayer (1910a).

More detailed accounts of this species are given elsewhere (Calder 1988, 2010, 2013; Schuchert 2006).

Reported distribution. *Gulf coast of Florida.* Key West (L. Agassiz 1860: pl. 15, figs. 1, 2, as *Pennaria gibbosa*; L. Agassiz 1862: 280, as *Pennaria gibbosa*; A. Agassiz 1865: 186, as *Pennaria gibbosa*; Jäderholm 1896: 5, as *Pennaria symmetrica*; Fraser 1943: 87, as *Pennaria tiarella*).—Dry Tortugas (Wallace 1909: 137, as *Pennaria*; Mayer 1910a: pl. 1, fig. 5, text-fig. 2, as *Pennaria tiarella*; Fraser 1944: 86**, as** *Pennaria tiarella*).—Florida Reefs (Mayer 1910a: 27, as *Pennaria tiarella***)**.—St. George Sound—Apalachee Bay region (Menzel 1956: 2, as *Pennaria tiarella*).—Seahorse Key (Joyce 1961: 44, 45, as *Pennaria* sp. A and *Pennaria tiarella*).—Cape San Blas area (Shier 1965: 28, 30, as *Pennaria tiarella* and *Pennaria* sp.).

Elsewhere in western North Atlantic. USA: New York, Long Island, Sag Harbor (Ayres 1852: 195, as *Globiceps tiarella*).—USA: Rhode Island, Point Judith (Leidy 1855: 136, as *Eucoryne elegans*).—USA: New Jersey, Great Egg Harbor (Leidy 1855: 138, as *Eucoryne elegans*).—USA: South Carolina, Charleston Harbor (McCrady 1859: 153, as *Pennaria tiarella*).—Haiti: Jérémie (A. Agassiz 1865: 186, as *Pennaria gibbosa*; Fraser 1944: 86, as *Pennaria tiarella*).—USA: Massachusetts, Massachusetts Bay (medusa) + Suisconset (=Siasconset) (medusa) + Naushon (medusa) + Beverly (hydroid) + West Yarmouth (hydroid) + Nahant (hydroid) (A. Agassiz 1865: 189, as *Pennaria tiarella*).—USA: Rhode Island, Newport (medusa) (A. Agassiz 1865: 189, as *Pennaria tiarella*).—USA: Massachusetts: Woods Hole (Verrill 1874d: 520, as *Pennaria tiarella*; Bumpus 1898: 857, as *Pennaria tiarella*; Smallwood 1899: 861, as *Pennaria tiarella*; Hargitt 1900: 388, as *Pennaria tiarella*; Hargitt 1901a: 311, as *Pennaria tiarella*; Nutting 1901: 337, as *Pennaria tiarella*; Weill 1934: 376, as *Pennaria tiarella*; Puckett 1936: 393, as *Pennaria tiarella*; Weill 1937: 1750, as *Pennaria tiarella*; Petersen 1964: 18, as *Pennaria tiarella*; Wyttenbach *et al*. 1973: 364, as *Pennaria tiarella*).—USA: New Jersey, Great Egg Harbor (Verrill 1874d: 735, as *Pennaria tiarella*).—USA: Connecticut, near New Haven (Verrill 1874d: 735, as *Pennaria tiarella*).—USA: Massachusetts, Vineyard Sound, low water to 10 ftm (18 m), and floating algae (Verrill 1874d: 735, as *Pennaria tiarella*).—Cuba: Bahía Honda (Clarke 1879: 240, as *Pennaria symmetrica*).—USA: Massachusetts, Vineyard Sound (Verrill & Rathbun 1880: 230, as *Globiceps tiarella*).—USA: North Carolina, Beaufort (Brooks 1882: 136, as *Pennaria tiarella*).—USA: North Carolina, outside Fort Macon (Brooks 1882: 144, as *Pennaria inornata*).—Saint-Barthélemy (Jäderholm 1903: 264, as *Pennaria symmetrica*).—Bermuda (Congdon 1907: 464, as *Pennaria tiarella*; Weill 1937: 1750, as *Pennaria tiarella*; Calder 1986: 132, as *Halocordyle disticha*).—USA: Rhode Island, Newport (Mayer 1910a: 25, pl. 1, figs. 2–4, as *Pennaria tiarella*).—USA: North Carolina, Beaufort area (Wilson 1911: 282, as *Pennaria tiarella*).—USA: North Carolina, Morehead City + Beaufort (Fraser 1912b: 355, as *Pennaria tiarella*).—USA: Massachusetts, Woods Hole and vicinity + Vineyard Sound + Buzzards Bay (Sumner *et al*. 1913: 561, as *Pennaria tiarella*).—Virgin Islands of the United States: St. Thomas, Charlotte Amalie (Stechow 1919: 7, as *Pennaria tiarella*).—Bermuda: Hamilton Harbour + Great Sound + flats outside (Bennitt 1922: 243, as *Pennaria tiarella*).—USA: Massachusetts, Woods Hole region, on eelgrass, rocks and rockweed, pilings (Allee 1923: 175, as *Pennaria tiarella*).—USA: Florida, "Tablot" Island (=Talbot Island) (Fraser 1933: 262, as *Pennaria tiarella*).—USA: New York, Great South Bay (Conard 1935: 449, as *Pennaria tiarella*).—USA: Massachusetts, Woods Hole (Baker 1936: 251, as *Pennaria tiarella*; Ballard 1942: 329, as *Pennaria tiarella*; Kepner 1943: 310, as *Pennaria tiarella*).—Venezuela: Puerto Cabello (Leloup 1937: 92, footnote, as *Pennaria disticha*).—USA: North Carolina, Beaufort (McDougall 1943: 336, as *Pennaria tiarella*; Kepner 1943: 299, as *Pennaria tiarella*; Maturo 1959: 123, as *Pennaria tiarella*; Sutherland 1974: 861, as *Pennaria tiarella*; Sutherland & Karlson 1977: 427, as *Pennaria tiarella*; Martin & Thomas 1977: 198, as *Pennaria tiarella*; Karlson 1978: 230, as *Pennaria tiarella*; Sutherland 1978: 258, as *Pennaria tiarella*; Sutherland 1981: 503, as *Pennaria tiarella*; Walch *et al*. 1986: 353, as *Pennaria tiarella*; Martin & Archer 1986a: 486, as *Pennaria tiarella*; Holm *et al*. 1997: 192, as *Pennaria tiarella*).—USA: Massachusetts, Buzzards Bay off Parkers Island, 11 ftm (20 m) + Vineyard Sound near West Chop Light, 14 ftm (26 m) (Fraser 1944: 86, as *Pennaria tiarella*).—USA: Rhode Island, Narragansett Bay off Prudence Light, 14.5 ftm (27 m) (Fraser 1944: 86, as *Pennaria tiarella*).—USA: North Carolina, off Cape Hatteras, 35°25'30"N, 75°20'30"W, 15 ftm (27 m) + 35°20'40"N, 75°18'40"W, 16 ftm (29 m) + Ocracoke (Fraser 1944: 86, as *Pennaria tiarella*).—USA: Florida, Biscayne Bay (Weiss 1947: 57, as *Pennaria tiarella*; Weiss 1948: 158, as *Pennaria tiarella*; Jones 2002: 218, as *Halocordyle disticha*).—Unstated location (Woods Hole Oceanographic Institution 1952: 187, as *Pennaria tiarella*).—Bermuda: vicinity of the Bermuda Biological Station (Cowden 1965: 870, as *Pennaria tiarella*; Martin & Thomas 1977: 198, as *Pennaria tiarella*).—USA: Virginia, Hampton Roads, Norfolk, Norfolk Naval Base Pier 12, on fouling panels, 5 m (Calder & Brehmer 1967: 153, as *Pennaria tiarella*).—Jamaica: Kingston (Vervoort 1968: 4, as *Halocordyle disticha*).—Virgin Islands of the United States: St. Thomas, sound (Vervoort 1968: 4, as *Halocordyle disticha*).—Barbados (Vervoort 1968: 4, as *Halocordyle disticha*).—Venezuela: La Guaira + Puerto Cabello (Vervoort 1968: 4, as *Halocordyle disticha*).—Panama: Colón (Vervoort 1968: 4, as *Halocordyle disticha*).—Costa Rica: Limón (Vervoort 1968: 4, as *Halocordyle disticha*).—Curaçao: Piscadera Bay (Vervoort 1968: 5, as *Halocordyle disticha*).—Bermuda: Flatts Inlet (Summers & Haynes 1969: 82, as *Pennaria tiarella*; Summers 1970: 117, as *Pennaria tiarella*; 1972: 229, as *Pennaria tiarella*; Keough & Summers 1976: 507, as *Pennaria tiarella*; Lesh-Laurie 1976: 366, as *Pennaria tiarella*).—USA: Virginia, Perrin + Gloucester Point + Norfolk Naval Base + Cape Charles (Calder 1971: 25, as *Halocordyle disticha*).—USA: Virginia, York River, Big Mumford Island, 37°16'N, 76°31'W, on *Zostera* (Marsh 1973: 93, as *Halocordyle tiarella*).—USA: Gulf Stream off South Carolina, 32°00'N, 79°00'W, on *Sargassum pteropleuron* (Rackley 1974: 14).—Colombia: Santa Marta area (Wedler 1975: 340, as *Halocordyle disticha*; Bandel & Wedler 1987: 39, as *Halocordyle disticha*).—Jamaica (Mergner 1977: 122, as *Halocordyle disticha*; 1987: 187, as *Halocordyle disticha*).—Colombia (Mergner 1977:

122, as *Halocordyle disticha*; 1987: 187, as *Halocordyle disticha*).—Costa Rica: east coast (Mergner 1977: 122, as *Halocordyle disticha*; 1987: 187, as *Halocordyle disticha*).—USA: Florida, southeast coast (Mergner 1977: 122, as *Halocordyle disticha*; 1987: 187, as *Halocordyle disticha*).—USA: Massachusetts, Nonamesset Island (41°31'N, 70°40'4"W) (Osman 1978: 398, as *Pennaria tiarella*).—USA: South Carolina, Murrells Inlet + Beaufort River + Calibogue Sound (Calder & Hester 1978: 88, as *Halocordyle disticha*).—USA: North Carolina, Wrightsville (Bynum 1980: 228, as *Pennaria tiarella*).—USA: North Carolina, Morehead City (Martin & Thomas 1980: 27, as *Pennaria tiarella*; Martin & Thomas 1981a: 303, as *Pennaria tiarella*; Martin & Thomas 1981b: 304, as *Pennaria tiarella*; Martin & Thomas 1983: 18, as *Pennaria tiarella*; Martin & Archer 1986b: 116, as *Pennaria tiarella*; Clark & Cook 1986: 406, as *Halocordyle disticha* and *Pennaria tiarella*; Martin 1987: 325, as *Halocordyl* (sic) *disticha*; Kolberg & Martin 1988: 250, as *Halocordyle disticha*; Martin 1988a: 321, as *Halocordyle disticha*; Martin 1988b: 67, as *Halocordyle disticha*; Martin 1990: 11, as *Pennaria tiarella*; Martin 1991: 76, as *Pennaria tiarella*; Martin 1992: 432, as *Pennaria tiarella*; Brumwell & Martin 1996: 14, as *Pennaria tiarella*; Martin & Archer 1997: 42, as *Pennaria tiarella*; Martin 2000: 243, as *Pennaria tiarella*).—Belize: Carrie Bow Cay region (medusa) (Larson 1983: 254, as *Halocordyle disticha*).—USA: North Carolina, Wrightsville Beach, floating docks (Hotchkiss *et al*. 1984: 718, as *Pennaria tiarella*).—USA: Florida, Sebastian Inlet (Winston 1982: 164, as *Pennaria tiarella*).—Belize: Carrie Bow Cay (Spracklin 1982: 240, as *Halocordyle disticha*).—Colombia: Bahía de Cartagena (Flórez González 1983: 123, as *Halocordyle disticha*).—Dominican Republic: south coast (Williams *et al*. 1983: 43, as *Halocordyle disticha*).—USA: South Carolina, Murrells Inlet, jetties + Murrells Inlet, Capt. Dick's marina, floating docks (Fox & Ruppert 1985: 93, 104, as *Halocordyle disticha*).—Puerto Rico: Isabela + La Parguera (Wedler & Larson 1986: 73, as *Halocordyle disticha*).—Bermuda: Coney Island (Clark & Cook 1986: 406, as *Halocordyle disticha* and *Pennaria tiarella*).—USA: North Carolina, coast (Edwards *et al*. 1987: 381, as *Halocordyle disticha*).—USA: North Carolina, Wrightsville Beach (Thomas *et al*. 1987: 92, as *Halocordyle disticha*).—USA: North Carolina coast (Edwards *et al*. 1987: 381, as *Halocordyle disticha*).—Puerto Rico: Mona Island + Desecheo Island (Larson 1987: 514, as *Halocordyle disticha*).—British Virgin Islands: Virgin Gorda (Larson 1987: 514, as *Halocordyle disticha*).—Bermuda: Castle Harbour near Tuckers Town, 7 m + Flatts Inlet, 3 m + Whalebone Bay, 1 m (Calder 1988, as *Halocordyle disticha*).—USA: South Carolina, continental shelf, fouling plates (Van Dolah *et al*. 1988: 684, as *Halocordyle disticha*).—USA: South Carolina, coastal areas, in stomachs of Atlantic spadefish (Hayse 1990: 81, as *Halocordyle disticha*).—Belize: Twin Cays, on *Rhizophora* (Ellison & Farnsworth 1990: 96, as *Halocordyle disticha*).—Belize: Big Creek, on *Rhizophora* + Lark Cay, on *Rhizophora* + Northeast Cay, on *Rhizophora* + Twin Cays, on *Rhizophora* (Ellison & Farnsworth 1992: 90, as *Halocordyle disticha*).—Colombia: Bahía de Chengue, on *Rhizophora* (Reyes & Campos 1992: 108, as *Halocordyle disticha*).—USA: Florida, Boca Raton, on nearshore artificial reef (Cummings 1994: 1208, as *Pennaria* sp.).—USA: North Carolina, Wilmington (Martin & Archer 1997: 42, as *Pennaria tiarella*).—Cuba: Ciudad de La Habana province (Ortiz 2001b: 68, as *Halocordyle disticha*).—Costa Rica: Limón (Kelmo & Vargas 2002: 603).—Panama: Colón, Fort Sherman dock + Colón, Isla Margareta + Galeta + Bocas del Toro area (Calder & Kirkendale 2005: 480).—French Lesser Antilles: Guadeloupe, Basse-Terre, N of Malendure, 16°10´25.00"N, 61°46´58.00"W + Basse-Terre, Petite Anse, 16°05´47.00"N, 61°46´17.00"W + Basse-Terre, Anse à la Barque, 16°05´21"N, 61°46´00"W (Galea 2008: 13).—French Lesser Antilles: Les Saintes, Terre-de-Haut, Pompierre Bay, 15°52´25"N, 61°34´15"W + Terre-de-Haut, Pain de Sucre, 15°51´45"N, 61°35´60"W (Galea 2008: 13).—Cuba: Golfo de Batabanó (Castellanos-Iglesias *et al*. 2011: 14, as *Halochordyle* (sic) *disticha*).—Cuba: Golfo de Ana María (Rodríguez-Viera *et al*. 2012: 33).—USA: Florida, Fort Pierce Inlet, north jetty, 0.1 m (Calder 2013: 7).—French Lesser Antilles: Martinique (Galea 2013: 49).—Panama: Bocas del Toro (Miglietta *et al*. 2015: 5).—Honduras (Miglietta *et al*. 2015: 5).—USA: Florida, Fort Pierce (Miglietta *et al*. 2015: 5).—USA: North Carolina, Beaufort (Miglietta *et al*. 2015: 5).—Caribbean Sea (Wedler 2017b: 69, figs. 50—54).—Mexico: Alacranes Reef, on sponges, corals, molluscs, ascidians, rocks, artificial reefs (Mendoza-Becerril *et al*. 2018b: 129).—Cuba: Havana, coral reef system west of the city (Castellanos *et al*. 2018: Supplementary Table S2).—USA: Florida, Fort Pierce (Miglietta *et al*. 2018a: published online, no assigned pages).—USA: North Carolina, Beaufort (Miglietta *et al*. 2018a: published online, no assigned pages).—Sint Eustatius (Miglietta *et al*. 2018a: published online, no assigned pages).—Honduras: Caribbean coast (Miglietta *et al*. 2018a: published online, no assigned pages).—USA(?): Gulf of Mexico (Miglietta *et al*. 2018a: published online, no assigned pages).—Panama: Bocas del Toro area (Miglietta *et al*. 2018a: published online, no assigned pages).—Panama: Bocas del Toro area, Crawl Cay + Swan's Cay (Miglietta *et al*. 2018b: 108).

Suborder Filifera Kühn, 1913

Family Oceaniidae Eschscholtz, 1829

Genus *Corydendrium* Van Beneden, 1844a

Corydendrium parasiticum (Linnaeus, 1767)

Fig. 1b

Sertularia parasitica Linnaeus, 1767: 1315.

Type locality. "Habitat in Oceano, sæpe in *Corallina rubente*" (Mediterranean Sea) (Linnaeus 1767: 1315).

Material examined. Southwest Florida Shelf, outer shelf NW of the Dry Tortugas, 25°16.83'N, 83°57.35'W, 127 m, 03 August 1981, triangle dredge, two colony fragments, 13 mm and 6 mm high, without gonophores, coll. Continental Shelf Associates, ROMIZ B449.

Remarks. Although not reported before from southwest Florida, *Corydendrium parasiticum* is widely distributed in tropical and subtropical waters of the western Atlantic Ocean (Calder & Kirkendale 2005; Galea 2013; Oliveira *et al*. 2016). Specimens examined here were collected at the deep end of its known bathymetric range (1–127 m). An overview of the species is given in Schuchert (2004).

Reported distribution. ***Gulf coast of Florida***. First record.

Elsewhere in western North Atlantic. Colombia (Wedler 1975: 333; Flórez González 1983: 118; Bandel & Wedler 1987: 39).—Belize (Spracklin 1982: 240).—Puerto Rico (Wedler & Larson 1986: 82).—USA: Louisiana, on coastal petroleum platforms, 12–18 m (Lewbel *et al*. 1987: 219).—Bermuda: Flatts Inlet, 3 m, under flat rock + 2 km SE of Castle Roads, 60-90 m, on rubble + Harrington Sound, near Flatts Inlet bridge, 1.5 m, on ledge (Calder 1988: 6).—USA: North Carolina, Wrightsville Beach (Lindquist & Hay 1996: 448; Stachowicz & Lindquist 2000: 282; Lindquist *et al*. 2000: 1291).—Panama: Colón + Bocas del Toro (Calder & Kirkendale 2005: 477).—Cuba: Ciudad de La Habana, Miramar, 12 m (Varela *et al*. 2005: 177).—French Lesser Antilles: Martinique (Galea 2013: 6).—French Lesser Antilles: Guadeloupe (Galea 2013: 6).—Caribbean Sea (Wedler 2017b: 41, figs. 33–35).—Mexico: Alacranes Reef, on sponges, corals, molluscs, ascidians, artificial reefs (Mendoza-Becerril *et al*. 2018b: 129).—Cuba: Havana, coral reef system west of the city (Castellanos *et al*. 2018: Supplementary Table S2).

Genus *Rhizogeton* L. Agassiz, 1862

Rhizogeton sterreri (Calder, 1988)

Figs. 1c, d

Rhizogeton fusiformis.—Joyce, 1961: 26, pl. 1, figs. 1, 2.—Shier, 1965: 8, pl. 1 [not *Rhizogeton fusiformis* L. Agassiz, 1862].
Rhizodendrium sterreri Calder, 1988: 10, figs. 7, 8.

Type locality. Bermuda: Whalebone Bay, on pelagic *Sargassum* (Calder 1988: 10, as *Rhizodendrium sterreri*).

Material examined. Sanibel Island, beach at Lighthouse Point, 26°26'57"N, 82°01'06"W, on detached *Thalassia* at water's edge, 13 March 2018, 20° C, 33.5‰, two colonies or colony fragments, up to 2 mm high, with male gonophores, coll. D. Calder, ROMIZ B4323.—Sanibel Island, beach at Lighthouse Point, 26°26'57"N, 82°01'06"W, on detached *Thalassia* at water's edge, 13 March 2018, 20° C, 33.5‰, coll. D. Calder, ROMIZ B4324 [initially preserved in 70% ethanol (never in formalin)].—Sanibel Island, beach at Lighthouse Point, 26°27'00"N, 82°01'01"W, on detached *Thalassia* at water's edge, 15 March 2018, 18° C, 34‰, two colonies, up to 2 mm high, without gonophores, coll. D. Calder, ROMIZ B4325.—Fort Myers Beach, 26°27'27"N, 81°57'51"W, on detached *Thalassia* at water's edge, 22 March 2018, 21° C, 33.5‰, one colony, 2 mm high, with male gonophores, coll. D. Calder, ROMIZ B4326.

Remarks. This small and inconspicuous hydroid has been reported twice before from the Gulf coast of Florida, as *Rhizogeton fusiformis* L. Agassiz, 1862, in the unpublished theses of Joyce (1961) and Shier (1965). With *R. fusiformis* being a species from cold waters in the boreal western North Atlantic (L. Agassiz 1862; Fraser 1944; Calder

2017), the binomen *R. sterreri* (Calder, 1988) has been adopted here for the Florida population. The name *R. sterreri* was applied originally to a species found on pelagic *Sargassum* in warm waters of Bermuda (Calder 1988, as *Rhizodendrium sterreri*). Similar hydroids from the tropical islands of Guadeloupe, Les Saintes, and Martinique in the French Lesser Antilles, Caribbean Sea, have likewise been identified as *R. sterreri* (Galea 2008, 2013). Moreover, records of *Rhizodendrium* sp. from the Caribbean coast of Panama by Calder & Kirkendale (2005) are considered here to have been based on the same species. As noted earlier (Calder 2017), however, the various species of *Rhizogeton* L. Agassiz, 1862 have yet to be clearly differentiated on the basis of morphology, and all need to be compared by molecular methods to resolve relationships.

The reported geographic range of *R. sterreri* extends from Bermuda (Calder 1988, as *Rhizodendrium sterreri*) and Florida (this study) to the southern Caribbean Sea (Bandel & Wedler 1987, as *Rhizogeton fusiformis*), and from there to northern Bahía, Brazil (Kelmo & Santa-Isabel 1998). *Rhizogeton sterreri*, like other species of the genus, is normally found in shallow to relatively shallow water (for the bathymetric range of *R. nudus* Broch, 1909 [1910], most frequently reported of the species, see Schuchert 2004). It is nevertheless an inhabitant also of the high seas, occurring as part of the epibenthos on pelagic *Sargassum* in the Gulf Stream and Sargasso Sea (see the Reported Distribution section below for records).

While originally described from pelagic *Sargassum* (Calder, 1998, as *Rhizodendrium sterreri*), the hydroid appears to be a substrate generalist. Joyce (1961) reported it on Cuban shoal weed (*Halodule wrightii*), Shier (1965) on a chiton, and Galea (2008) on algae, sponges, mineral concretions, and in crevices on both scleractinians and hydrocorals. It was found here on the seagrass *Thalassia testudinum*.

Hydroids observed in this study were brownish to rusty red in colour when alive. As described by Galea (2008), the gastrodermis at the bases of the tentacles was bright white.

More details on the widespread but relatively obscure and inadequately known genus *Rhizogeton* and its putative species are given in works by Schuchert (2004, 2012), Galea (2008), and Calder (2010, 2017).

Reported distribution. ***Gulf coast of Florida.*** Seahorse Key (Joyce 1961: 26, as *Rhizogeton fusiformis*).—Cape San Blas area (Shier 1965: 8, as *Rhizogeton fusiformis*).

Elsewhere in western North Atlantic. Atlantic Ocean: Gulf Stream, on pelagic *Sargassum* + Sargasso Sea, on pelagic *Sargassum* (Burkenroad, in Parr 1939: 23, as "…resembles *Clava*").—USA: Gulf Stream off New Jersey, 40°09'N, 70°56'W, on *Sargassum* nr. *ramifolium* (Rackley 1974: 19, as *Rhizogeton fusiformis*).—USA: Gulf Stream off North Carolina, 34°21'N, 75°36'W, on *Sargassum* nr. *ramifolium* (Rackley 1974: 19, as *Rhizogeton fusiformis*).—Sargasso Sea, E of North Carolina, 33°26'N, 71°56'W, on *Sargassum* nr. *ramifolium* (Rackley 1974: 19, as *Rhizogeton fusiformis*).—Colombia: Santa Marta area (Bandel & Wedler 1987: 39, as *Rhizogeton fusiformis*).—Bermuda: Whalebone Bay, on pelagic *Sargassum* (Calder 1988: 10, as *Rhizodendrium sterreri*).—Panama: Bocas del Toro area, Bastimentos (north), 09°20.898'N, 82°09.959'W, 1-4 m + Bocas del Toro area, Drago 2, 2-4 m (Calder & Kirkendale 2005: 477, as *Rhizodendrium* sp.).—French Lesser Antilles: Guadeloupe, Basse-Terre, Petite Anse, 16°05'47.00"N, 61°46'17.00"W, on algae, concretions + Basse-Terre, Anse à la Barque, 16°05'21"N, 61°46'00"W, on coral + Grande-Terre, Anse des Salines, 16°14'58.80"N, 61°10'50.45"W, on hydrocoral (Galea 2008: 8).—French Lesser Antilles: Les Saintes, Terre-de-Haut, Pain de Sucre, 15°51'45"N, 61°35'60"W, on algae, concretions, sponge (Galea 2008: 8).—French Lesser Antilles: Martinique (Galea 2013: 49).—Caribbean Sea (Wedler 2017b: 42, figs. 36A–D, as *Rhizogeton fusiformis*).—Panama: Bocas del Toro area, Bocas del Drago (Miglietta *et al*. 2018b: 108).

Genus *Turritopsis* McCrady, 1857

Turritopsis nutricula McCrady, 1857

Fig. 1e

Oceania (*Turritopsis*) *nutricula* McCrady, 1857: 55, pl. 4, figs. 1–10, 12–15, 28a, pl. 5, figs. 11, 16 18, 28b [medusa stage].

Turritopsis nutricula McCrady, 1857: 58 [medusa stage].—Mayer, 1900b: 39 [medusa stage]; 1910a: 143, text-figs. 75, 76, pl. 15, figs. 12, 13 [hydroid & medusa stages].

Turritopsis nutricola.—Vanhöffen, 1916: 418 [medusa stage] [incorrect subsequent spelling].

Type locality. USA: South Carolina, Charleston Harbor area (McCrady 1857: 55).

Material examined. Fort Myers Beach, 26°27’27”N, 81°57’51”W, on detached barnacle cluster at water’s edge, 22 March 2018, 21° C, 33.5‰, one colony, 2 mm high, without gonophores, coll. D. Calder, ROMIZ B4327.

Remarks. The original account of *Turritopsis nutricula* by McCrady (1857) was based solely on the medusa stage. A previously unknown hydroid was linked to it in life cycle studies by Brooks (1883). While he provided no illustration of either hydroid or medusa of the species in that work, an excellent one appeared in another publication three years later (Brooks 1886: pl. 37). The same drawing was included later in the monograph of Mayer (1910a: fig. 76).

McCrady’s (1857) description of *T. nutricula* made no direct mention of the collection locale. However, his pioneering research on hydrozoans of the southeastern United States was carried out in Charleston Harbor and vicinity, South Carolina (Stephens & Calder 1992). The type locality can therefore be taken to be the Charleston Harbor area. The species was described again in a classic paper on Hydrozoa of Charleston Harbor (McCrady 1859), and specimens collected from Charleston, by McCrady, were included in a catalogue of the Museum of Comparative Zoology by A. Agassiz (1865).

In a report on anthoathecate hydroids of Bermuda (Calder 1988), I wrote that the generic name *Turritopsis* McCrady was threatened by a virtually unused subjective synonym (*Clavula* Wright, 1859). McCrady’s paper, in which *Turritopsis* was first established, is now known to have been published in 1857 (Calder *et al.* 1992) and not in 1859 as generally believed at the time. *Turritopsis* therefore has priority over *Clavula*, a name proposed by Wright (1959) in the July 1859 issue of *Edinburgh New Philosophical Journal*. For the same reason, the binomen *Clavula gossii* Wright, 1859 is not a nomenclatural threat to *Turritopsis nutricula*. Indeed, the two species names are no longer held to be synonyms (Schuchert 2004).

An account of the medusa of *T. nutricula* by A. Agassiz (1865) from Naushon, Massachusetts, was based on a misidentification (Brooks 1882; Mayer 1910a). Reports of the species (misspelled as *T. nutricola*) by L. Agassiz (1862) from the same location, in collections by A. Agassiz, are likewise excluded from distribution records below as likely misidentifications. So too is a report of it from Massachusetts, based on the records of L. and A. Agassiz, by Verrill (1874d: 454, 734). Recent fanciful accounts of the species as “the immortal jellyfish” have largely been based on misidentifications of the European *T. dohrnii* (Weismann, 1883).

By the mid- and late 20th century, both hydroid and medusa stages of *T. nutricula* were widely thought to be almost circumglobal in distribution (Kramp 1961; Calder 1988). Evidence from recent reproductive and molecular studies (Schuchert 2004; Miglietta *et al*. 2007; Miglietta & Lessios 2009; Miglietta 2016; Kubota & Nagai 2018) indicate that the species is far more restricted in distribution, occurring largely or exclusively in the warm-temperate western Atlantic. As noted by Schuchert (2016), however, 16S sequences of specimens attributed to *T. nutricula* thus far are inconclusive in having been based on specimens collected at considerable distances from the type locality in South Carolina. Analyses of topotypic material are needed to confirm results of those sequences.

Medusae of *T. nutricula* are dioecious and oviparous (Schuchert 2004), thereby differing from those of the European *T. polycirrha* (Keferstein, 1862). Morphological characters distinguishing *T. nutricula* from *T. polycirrha*, the Mediterranean *T. dohrnii*, and the Pacific *T. rubra* (Farquhar, 1895) are outlined in Schuchert (2004), with differences being most apparent in medusae of the species. The hydroid colony examined here from Fort Myers Beach lacked medusa buds, with identification of it as *T. nutricula* being based largely on its occurrence within a biogeographic region related to that of the type locality of the species elsewhere in the southern United States. Moreover, medusae of *T. nutricula* have been reported nearby from the Dry Tortugas in southwest Florida (Mayer 1900b, 1910a; Vanhöffen 1916). Hydroids identified as the relatively deep water *T. fascicularis* Fraser, 1943 also occur in the region (Fraser 1944; Calder 2013; Miglietta 2016), but they differ in having much larger, polysiphonic colonies. As for *T. fascicularis*, it has now been linked through DNA sequence data to *Oceania armata* Kölliker, 1853 (Schuchert 2016).

Turritopsis nutricula has been reported infrequently in the Gulf of Mexico. As noted above, medusae of the species have been recorded at the Tortugas. Medusae were also collected in the Bahía de Campeche, Mexico, by Martell-Hernández *et al*. (2014). Earlier, Segura-Puertas (1992) reported the medusa stage from the Yucatan Shelf and the Mexican Caribbean, but it is unclear whether the species was collected in the Gulf of Mexico. The hydroid stage has been identified from coastal petroleum platforms in Texas (Fotheringham 1981) and Louisiana (Lewbel *et al*. 1987). Its reported range elsewhere in the western North Atlantic extends from southern Massachusetts to the southern Caribbean Sea (see records below). Records of *T. nutricula* from South America are summarized in Oliveira *et al*. (2016).

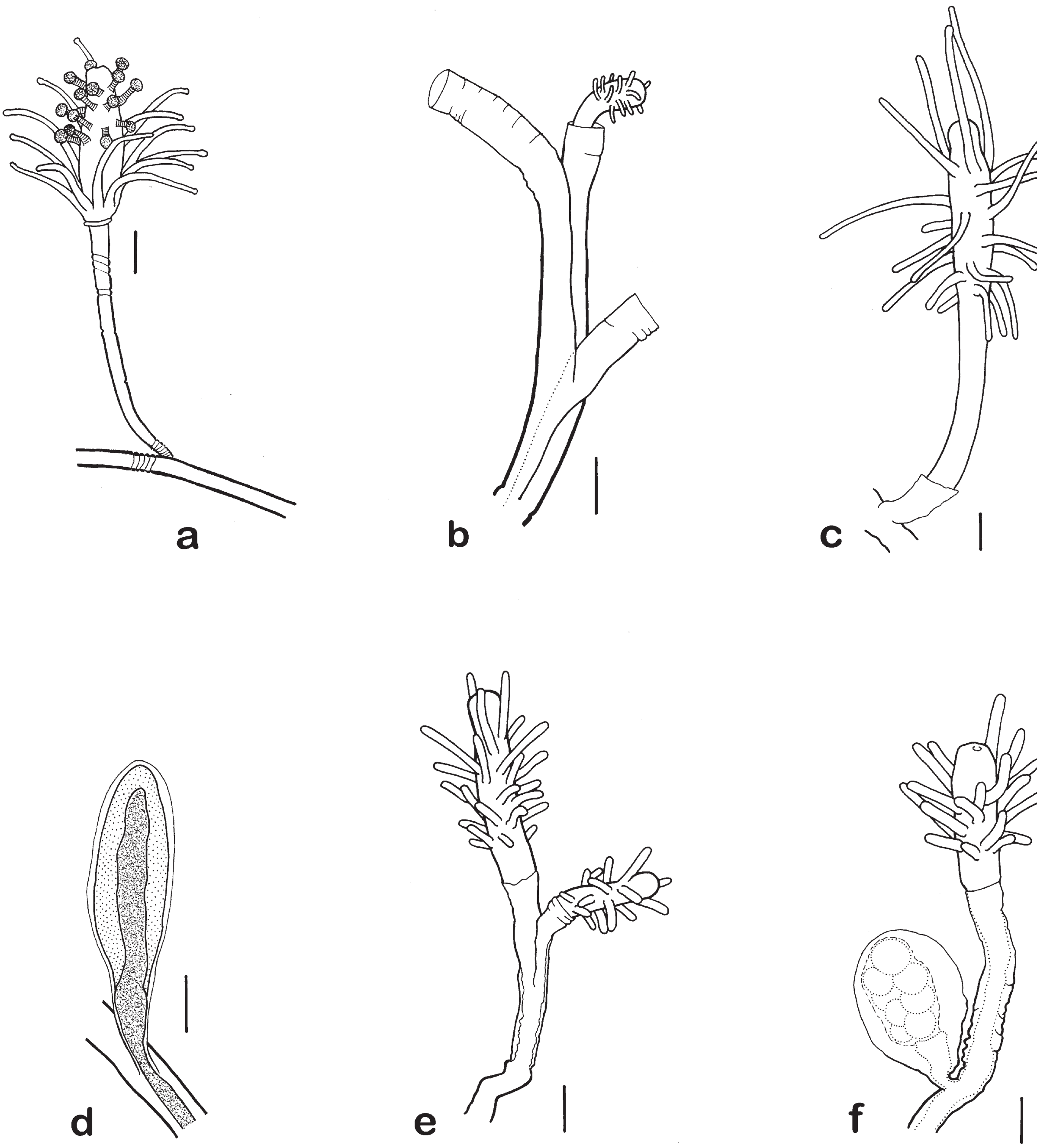

FIGURE 1. a, *Pennaria disticha*: part of branch, with pedicel and hydranth, Fort Myers Beach, ROMIZ B4347. Scale equals 0.5 mm. **b, *Corydendrium parasiticum*:** part of colony with a reduced hydranth, Southwest Florida Shelf, ROMIZ B449. Scale equals 0.5 mm. **c, *Rhizogeton sterreri*:** hydranth and stolon, Fort Myers Beach, ROMIZ B4326. Scale equals 0.2 mm. **d, *Rhizogeton sterreri*:** male gonophore and stolon, Fort Myers Beach, ROMIZ B4326. Scale equals 0.2 mm. **e, *Turritopsis nutricula*:** colony with two hydranths, Fort Myers Beach, ROMIZ B4327. Scale equals 0.2 mm. **f, *Cordylophora caspia*:** part of colony with hydranth and female gonophore, Caloosahatchee River at Fort Myers, ROMIZ B4329. Scale equals 0.2 mm.

Reported distribution. ***Gulf coast of Florida.*** Tortugas (medusa) (Mayer 1900b: 39; 1910a: 144, captions to pl. 15, figs. 12, 13).—Tortugas (medusa) (Vanhöffen 1916: 418, as *Turritopsis nutricola*).

Elsewhere in western North Atlantic. USA: South Carolina, Charleston Harbor (medusa) (McCrady 1857: 58; 1859: 128).—USA: Massachusetts, Buzzards Bay, Naushon (medusa) (Fewkes 1881b: 149, as *Modeeria multitentaculata*).—USA: North Carolina, Beaufort, the most common medusa (medusa) (Brooks 1882: 143).—USA: North Carolina, Beaufort (medusa) + Morehead City (hydroid) (Brooks 1883: 465; 1886: 390).—Bermuda: Castle

Harbor (Fewkes 1883: 79, 80, as *Modeeria multitentaculata* and *Modeeria* (*Turritopsis*) *nutricula*).—USA: Virginia, Hampton Roads (medusa) (Brooks 1886: 389).—USA: Rhode Island, Newport (medusa) (Mayer 1900b: 39; 1910a: figure caption to plate 15).—Cuba: (medusa) (Mayer 1900b: 39; 1910a: 144).—USA: South Carolina, Charleston Harbor (medusa) (Mayer 1900b: 39; 1910a: 144).—USA: Massachusetts, Woods Hole (medusa) (Nutting, 1901: 375).—Bahamas: (medusa) (Mayer 1904: 10; 1910a: 144).—USA: Massachusetts, Woods Hole (medusa) (Hargitt 1904: 37).—USA: North Carolina, Beaufort (medusa, juvenile hydroid reared from medusa) (Brooks & Rittenhouse 1907: 433, 437).—USA: North Carolina, on pilings of bridge between Beaufort and Morehead City, low water + Bogue Sound, 10 feet (3 m) + Cape Lookout, on boathouse pilings (Fraser 1912b: 345).—Virgin Islands of the United States: St. Thomas, Charlotte Amalie, surface, on algae on an old barge (Stechow 1919: 12, as *Turritopsis nutricola*).—USA: Massachusetts, Woods Hole region (medusa) (Fish 1925: 124).—Virgin Islands of the United States: St. Thomas, Charlotte Amalie, surface, on algae (Fraser 1944: 38).—Northwest Atlantic Ocean: 26°56’N, 53°09’W, 1000 m (medusa, identification uncertain) (Kramp 1959: 9).—USA: North Carolina, Beaufort region, inshore waters (medusa) (Allwein 1967: 122).—Curaçao: Port + Schottegat, on algae (Vervoort 1968: 6).—Panama: Colón, on algae on experimental plates (Vervoort 1968: 6).—USA: Virginia, York River (Tue Marsh Light + Gloucester Point + Page’s Rock) + James River (Hampton Roads Middle Ground) + southern Chesapeake Bay (Calder 1971: 30).—Colombia: Santa Marta area (Wedler 1975: 333).—USA: South Carolina, estuaries (Calder 1976: 169).—USA: South Carolina, Price Creek + Charleston Harbor + North Edisto River + St. Helena Sound + Colleton River (Calder & Hester 1978: 89).—USA: South Carolina, Bull Bay + Price Creek + Inlet Creek + Charleston Harbor + North Edisto River (medusa) (Calder & Hester 1978: 89).—USA: Texas, Buccaneer oil field, on oil platform (Fotheringham 1981: 194).—Belize: Carrie Bow Cay, on reefs, mangroves, sand troughs (Spracklin 1982: 248).—Colombia: Bahía de Cartagena (Flórez González 1983: 123).—USA: South Carolina and Georgia, inner, middle and outer continental shelf (Wenner *et al*. 1984: 20, 39).—USA: South Carolina, North Inlet area, Town Creek and tributaries + Murrells Inlet, Capt. Dick’s Marina, floating docks + Charleston area + Folly River area, Oak Island, oyster reefs + Isle of Palms, marina, floating docks (Fox & Ruppert 1985: 61, 104, 141, 152, 177).—Bermuda: common inshore and on offshore buoy chains (Calder 1986: 134).—Puerto Rico, La Parguera, on mangrove roots and sponges, 1–5 m (Wedler & Larson 1986: 86).—USA: Louisiana, on coastal petroleum platforms (Lewbel *et al*. 1987: 214).—Colombia: Santa Marta area (Bandel & Wedler 1987: 39).—Bermuda: Whalebone Bay + Flatts Inlet (Calder 1988: 8).—USA: South Carolina, continental shelf, fouling plates (Van Dolah *et al*. 1988: 684).—USA: South Carolina, inner continental shelf, on artificial reef (Wendt *et al*. 1989: 1116).—Belize: Twin Cays (Calder 1991b: 223).—Mexico: Campeche Bank + Mexican Caribbean (medusa) (Segura-Puertas & Ordóñez-López 1994: 108).—Bermuda: Argus (=Plantagenet) Bank (Calder 2000: 1134).—USA: North Carolina, Beaufort Inlet (medusa) (Schuchert 2004: 323).—Panama: Mole Buoy, Atlantic entrance to canal + Colón, Fort Sherman dock, wood, 09°22’12”N, 79°56’59”W, 0-2 m + Colón, bridge near Fort Sherman, 09°17’33”N, 79°55’22”W, 0-1 m + Colón, Fort Sherman dock, marina, 09°20’57”N, 79°54’10”W, 0-2 m + Colón, Club Nautico, steel pilings, 09°21’51”N, 79°53’39”W, 0-1 m + Colón, Isla Margareta, Fort Randolph, shore, 09°23’15”N, 79°53’11”W, 0-1 m + Bocas del Toro area, Hospital Point, 09°20’00.7”N, 82°13’06.8”W, 0-2 m + Bocas del Toro area, Mangrove Inn, 09°19.52.6”N, 82°15’17.7’W, 2-3 m + Bocas del Toro area, Almirante pilings, 09°16.218’N, 82°23.382’W, 1-10 m + Bocas del Toro area, Hospital Point, 09°20’01.9”N, 82°13’07.7”W, 2-13 m + Bocas del Toro area, Crawl Cay, 09°15.261’N, 82°07.787’W, 2-4 m + Bocas del Toro area, Boca del Drago, no coordinates, 0-3 m (Calder & Kirkendale 2005: 479).—USA: Massachusetts, Woods Hole (Miglietta *et al*. 2007: 13).—USA: South Carolina, North Inlet estuary (medusa) (Marshalonis & Pinckney 2007: 1032).—French Lesser Antilles: Guadeloupe, Basse-Terre, Petite Anse, 16°05’47.00”N, 61°46’17.00”W, rocky shore (Galea 2008: 9, identification provisional, as *Turritopsis* cf. *nutricula*).—USA: Massachusetts, Woods Hole (Miglietta & Lessios 2009: 833).—Cuba: Bahía de Cochinos, 0.5 m, on *Pecten* sp. (Varela *et al*. 2010: 30, as *Turritopsis nutricola*).—French Lesser Antilles: Martinique, Le Prêcheur, Les Jardins des Abîmes, 14.809044, -61.228853, 10–15 m, on sponge and worm tubes + Le Prêcheur, Pointe Lamare, 14.780461°, -61.211935°, 15–18 m, on *Pennaria disticha* (Galea 2013: 6).—Mexico: southern Gulf of Mexico (medusa) (Martell-Hernández *et al*. 2014: 23).—USA: Massachusetts, Woods Hole (Devarapalli *et al*. 2014: 590).—USA: east coast (Miglietta 2016: 431).—Caribbean Sea (Wedler 2017b: 43, figs. 38, 39A, B).—USA: Massachusetts, Woods Hole (Kubota & Nagai 2018: 3).—USA: New Jersey, Barnegat Bay (medusa) (Bologna *et al*. 2018: 222).—Cuba: Havana, coral reef system west of the city (Castellanos *et al*. 2018: Supplementary Table S2).

Family Cordylophoridae von Lendenfeld, 1885

Genus *Cordylophora* Allman, 1843

Cordylophora caspia (Pallas, 1771)

Fig. 1f

Tubularia caspia Pallas, 1771: 479.
Cordylophora lacustris Wurtz & Roback, 1955: 178.—Mason *et al*., 1994: 152.

Type locality. "In Mari Caspio…" (Pallas 1771: 479).

Material examined. Caloosahatchee River at Fort Myers, on floating dock, <1 m, 22° C, 0.17‰, 02 November 2017, one colony, 0.9 cm high, without gonophores, coll. D. Calder, ROMIZ B4328.—Caloosahatchee River at Fort Myers, on floating dock, <1 m, 20° C, 6‰, 06 February 2018, several colonies, up to 9 mm high, with gonophores, coll. D. Calder, ROMIZ B4329.

Remarks. *Cordylophora caspia* is reported here for the first time from the southwest coast of Florida. The species has been recorded previously from the Escambia River (Wurtz & Roback 1955) and from the Suwannee River system (Mason *et al*. 1994), both in northern parts of the state. Somewhat inland from the Gulf coast of Florida, colonies of *C. caspia* were found by Streever (1992) in a flooded cave system at Little River Spring, Suwannee County.

When first collected during this study, from the Caloosahatchee River estuary at Fort Myers, Florida (ROMIZ B4328), specimens of *C. caspia* were dormant. Within 24 hours, however, a hydranth appeared on one of the hydrocauli held in a fingerbowl of brackish water. Colonies are believed to have been inactive at the time due to environmental stresses introduced after passage of Hurricane Irma through south Florida on 11 September 2017. As a result of the storm, heavy freshwater discharge into the river from nearby Lake Okeechobee had been authorized by the United States Army Corps of Engineers to prevent catastrophic flooding in the vicinity. Normal salinities at the location are in the oligohaline (0.5–5‰) to mesohaline (5–18‰) range, but river waters at Fort Myers were still fresh (0.17‰) when the dormant stems and stolons were collected. At the same site a few months later, active colonies with gonophores (ROMIZ B4329) were collected (06 February 2018) in salinities that were somewhat higher (6‰). With still higher salinities (15‰) the following month (29 March 2018), however, neither active nor inactive colonies were found.

Remarks on this well-known invasive hydroid, and on the likely existence of cryptic species under the name *C. caspia*, have been given previously (Folino 2000; Schuchert 2004; Folino-Rorem *et al*. 2009; Calder 2010).

Reported distribution. ***Gulf coast of Florida.*** Escambia River, 1.2 miles (1.9 km) from mouth (Wurtz & Roback 1955: 178, as *Cordylophora lacustris*).—Suwannee River and Estuary (Mason *et al*. 1994: 152, as *Cordylophora lacustris*).

Elsewhere in western North Atlantic. Atlantic and Gulf coasts of North America: widespread in areas of low salinity (see Folino 2000; Folino-Rorem *et al*. 2009; National Exotic Marine and Estuarine Species Information System: http://invasions.si.edu/nemesis/CH-INV.jsp?Species_name=Cordylophora+caspia).

Family Bougainvilliidae Lütken, 1850

Genus *Bimeria* Wright, 1859

Bimeria humilis Allman, 1877

Fig. 2a

Bimeria humilis Allman, 1877: 8, pl. 5, figs. 3, 4.
Bimeria franciscana.—Joyce, 1961: 36, pl. 5, figs 3, 4 [not *Bimeria franciscana* Torrey, 1902].

Type locality. USA: Florida, Dry Tortugas, shallow water (Allman 1877: 9).

Material examined. Fort Myers Beach, stranded intertidally on detached octocoral, 16 February 2013, one colony, 4 mm high, without gonophores, coll. D. Calder, ROMIZ B4330.—Sanibel Island, beach at Lighthouse Point, on a detached and stranded colony of *Thyroscyphus*, 13 December 2017, one colony, 6 mm high, without gonophores, coll. D. Calder, ROMIZ B4331.

Remarks. *Bimeria humilis* Allman, 1877 from the southwest coast of Florida (Allman 1877), and other locations in the warm western Atlantic (Vervoort 1968), has frequently been considered a junior synonym of *B. vestita* Wright, 1859 from Scotland and elsewhere in northwest Europe (Schuchert 2007). This hypothesis needs confirmation given the very different environmental conditions extant at these locations. Allman's (1877) species is provisionally upheld as valid here.

Hydroids misidentified as *Bimeria franciscana* by Joyce (1961) from Seahorse Key, on the Gulf Coast of Florida, were based on specimens of *Bimeria humilis* Allman, 1877.

Reported distribution. ***Gulf coast of Florida.*** Dry Tortugas, shallow water (Allman 1877: 9).—Seahorse Key (Joyce 1961: 36, misidentified as *Bimeria franciscana*).

Elsewhere in western North Atlantic. Bermuda (Congdon 1907: 467; Bennitt 1922: 243).—Bahamas: off Orange Key (Fraser 1943: 86).—Trinidad: Maguaripe Bay (=Macqueripe Bay) (Fraser 1943: 86).—USA: Texas, Palacios (Deevey 1950: 335).—USA: Louisiana, Grand Isle (Deevey 1950: 335).—Virgin Islands of the United States: St. Thomas (Vervoort 1968: 7, as *Garveia humilis*).—Panama: Colón (Vervoort 1968: 7, as *Garveia humilis*).—Venezuela: La Guaira + Puerto Cabello (Vervoort 1968: 7, as *Garveia humilis*).—USA: Texas, Galveston Bay area (Defenbaugh & Hopkins 1973: 50).—USA: Gulf Stream E of Florida, 29°30'N, 78°29'W, on *Sargassum polyceratium* (Rackley 1974: 20, as *Garveia humilis*).—USA: Gulf Stream E of Florida, 30°30'N, 79°30'W, on *Sargassum hystrix* (Rackley 1974: 20, as *Garveia humilis*).—Colombia (Wedler 1975: 340, as *Garveia humilis*; Flórez González 1983: 123, as *Garveia humilis*).—USA: South Carolina, inshore waters (Calder & Hester 1978: 89, as *Garveia humilis*).—Belize (Spracklin 1982: 40, as *Garveia humilis*).—USA: South Carolina and Georgia shelf (Wenner *et al*. 1984: 20, 39).—Puerto Rico: La Parguera, 1–3 m (Wedler & Larson 1986: 89, as *Bimeria* (?*Garveia*) *humilis*).—Bermuda: Flatts Inlet, 3 m, undersides of flat rocks + Green Bay Cave, on *Eudendrium carneum* + Harrington Sound at Flatts Bridge, on algae (Calder 1988: 21, as *Bimeria vestita*).—Panama: Bocas del Toro area, Swan's Key, 09°27'12.2"N, 82°18'01.8"W, 1-4 m (Calder & Kirkendale 2005: 479, as *Bimeria vestita*).—USA: Florida, Fort Pierce (Calder 2013: 12, as *Bimeria vestita*).—French Lesser Antilles: Martinique, Case-Pilote, 14.637536, -61.139743, 12–15 m, on *Hincksella formosa* (Galea 2013: 5, as *Bimeria vestita*).—Caribbean Sea (Wedler 2017b: 21, figs. 4, 5A–C, as *Bimeria vestita*).

Genus *Bougainvillia* Lesson, 1830

Bougainvillia Lesson, 1830: 118.

Type species. *Bougainvillia macloviana* Lesson, 1830, by monotypy.

Remarks. The genus *Bougainvillia* Lesson, 1830, with life cycles including both hydroid and medusa stages, is well-represented in the western North Atlantic. The guidebook on hydroids of the Atlantic coast of North America by Fraser (1944) includes five species under the genus, namely *B. superciliaris* L. Agassiz, 1849, *B. carolinensis* (McCrady, 1859), *B. rugosa* Clarke, 1882, *B. longicirra* Stechow, 1914, and *B. inaequalis* Fraser, 1944. In studies on medusae, Kramp (1959, 1961) reported nine species of *Bougainvillia* from the same region, including *B. britannica* (Forbes, 1841), *B. ramosa* (Van Beneden, 1844b) (=*B. muscus* Allman, 1863), *B. superciliaris* L. Agassiz, 1849, *B. principis* (Steenstrup, in Lütken, 1850), *B. carolinensis* (McCrady, 1859), *B. platygaster* (Haeckel, 1879), *B. rugosa* Clarke, 1882, *B. niobe* Mayer, 1894, and *B. frondosa* Mayer, 1900b. *Bougainvillia aberrans* Calder, 1993a, a deep-water species differing from the others in having a reduced medusa stage, is added here to these lists.

Significant knowledge gaps exist about the hydroid and medusa stages of several species assigned to *Bougainvillia* in the western North Atlantic. Both *B. longicirra and B. inaequalis* are poorly known and based to date solely on their hydroid stages.The validity of the former has been questioned by Fraser (1944), and that of the latter by Deevey (1950). The taxonomic status of each one needs to be explored, although the validity of *B. inaequalis* was upheld by Calder & Choong (2018). The medusa *B. frondosa* seems well-founded taxonomically, but its hydroid stage is unknown (Vannucci & Rees 1961). Meanwhile, attempts at linking the two stages of a given species have sometimes resulted in error or uncertainty. In the original account of *B. superciliaris* by L. Agassiz (1849), only the medusa stage was described. Later, a hydroid forming a rather large (ca. 5 cm high), erect, irregularly branched, monosiphonic colony was taken to be its polypoid stage (L. Agassiz 1862). That concept of the species, adopted in subsequent publications on hydroids of eastern North America (see synonymy list in Fraser 1944), is amost certainly mistaken, as discussed elsewhere (Vannucci & Rees 1961; Schuchert 2007; Calder 2017). Life cycle studies by Werner (1961) and others indicate that the hydroid of *B. superciliaris* is stolonal. The identity of the erect and branched colony described by Agassiz is thus uncertain. In the case of *B. carolinensis*, McCrady (1859) provided a satisfactory account of the medusa, but the hydroid somewhat tenuously linked to it by him was described simply as having about 12 tentacles and measuring "…about an inch (2.5 cm) or slightly more in height." That description has been insufficient to distinguish the species. Detailed descriptions of a hydroid thought to be *B. carolinensis* by Mayer (1910a), Fraser (1944), and others, following an account by A. Agassiz (1865, as *Margelis carolinensis*),may well have been based on a different species. The very large hydroid (up to 30 cm high) described by Agassiz was found growing in abundance on *Fucus vesiculosus*, a boreal algal species that does not occur in warm-temperate Charleston Harbor, South Carolina, where McCrady's medusa was found. The identity of McCrady's hydroid thus remains uncertain, as does the one of A. Agassiz. The life cycle of *B. carolinensis* has yet to be carefully followed in the laboratory, and genetic studies on hydroids and medusae of the species are lacking.

Of the species listed above, reliable characterizations of both hydroid and medusa stages have been described for *B. rugosa* (Clarke 1881; Calder 1971), *B. muscus* (Russell 1953, as *B. ramosa*; Calder 1988, 2010; Schuchert 2007), and *B. aberrans* (Calder 1993a), all of which have erect colonies. Complete life cycles are also known for *Bougainvillia britannica*, with mostly stolonal colonies having unusually long pedicels (Edwards 1964, 1966), and *B. principis*, with stolonal colonies (Edwards 1966). Hydroids of those two species have yet to be identified from the east coast of North America. As for *B. platygaster*, polyp and medusa buds arise from the manubrium of the medusa (Kramp 1957, 1959; Schuchert 2007). No polypoid stage is known in *B. niobe* (Vannucci & Rees 1961), another species in which medusa buds are produced on the manubrium.

Given the unsatisfactory state of knowledge of hydroids of *Bougainvillia* in the western North Atlantic, a description is provided below of a species assigned here to *B. rugosa*. Meanwhile, genetic evidence does not support monophyly of *Bougainvillia*, nor of the family Bougainvilliidae as currently constituted (Mendoza-Becerril *et al*. 2018a).

***Bougainvillia rugosa* Clarke, 1882**

Figs. 2b–d, 3

Bougainvillia rugosa Clarke, 1882: 135.
Bougainvillea rugosa Clarke, 1882: 140, pl. 8, figs. 21–24 [incorrect subsequent spelling of *Bougainvillia*].

Type locality. USA: Virginia, Hampton Roads and lower Chesapeake Bay (Clarke 1882: 141).

Material examined. Fort Myers Beach, on stranded *Idiellana pristis*, 01 March 2013, one colony, 9 mm high, with gonophores, coll. D. Calder, ROMIZ B4332.—Sanibel Island, beach at Lighthouse Point, on stem of *Eudendrium carneum* stranded on shore, 13 December 2017, one colony, 6 mm high, with medusa buds, medusae liberated and cultured five days, coll. D. Calder, ROMIZ B4333.—Sanibel Island, beach at Lighthouse Point, on stem of *Eudendrium carneum* stranded on shore, 13 December 2017, one colony, 1.1 mm high, with medusa buds, coll. D. Calder, ROMIZ B4334 [preserved in 70% ethanol (never in formalin)].—Sanibel Island, beach at Lighthouse Point, detached and stranded on shore, 29 January 2018, one colony, 6 cm high, with medusa buds, medusae liberated, coll. D. Calder, ROMIZ B4335.—Fort Myers Beach, Salty Sam's Marina, 26°27'21.7"N, 81°56'34.6"W, on floating dock, <0.1 m, 19° C, 05 February 2018, four colonies or colony fragments, up to 3.5 cm high, with gonophores, medusae liberated, coll. D. Calder, ROMIZ B4336.

Description. Colonies with some stolonal hydranths but most with erect hydrocauli, up to 6 cm high, growth monopodial with terminal hydranths. Hydrocaulus slender, monosiphonic, not robust, often crooked and most slender at base, arising from a creeping hydrorhiza, giving rise to more-or-less alternate pedicels; pedicels unbranched or with an occasional secondary pedicel. Each pedicel slender basally, gradually increasing in diameter distally, supporting a terminal hydranth. Perisarc thin, irregularly smooth, without annulations everywhere, encrusted with particles of silt, extending over base of hydranth as a pseudohydrotheca, not investing bases of tentacles or hypostome. Pseudohydrothecae cup-shaped around retracted hydranths, sheath-like over extended ones, slightly striated horizontally. Hydranths fusiform when contracted, nearly cylindrical when extended, with a distal whorl of tentacles, hypostome prominent, typically dome-shaped. Tentacles filiform, highly contractile, about 11–13 in number on fully developed hydranths, amphicoronate in extended polyps, arranged in two very close whorls. Perisarc light-tan; hydranths white, with endoderm faintly ochre-coloured.

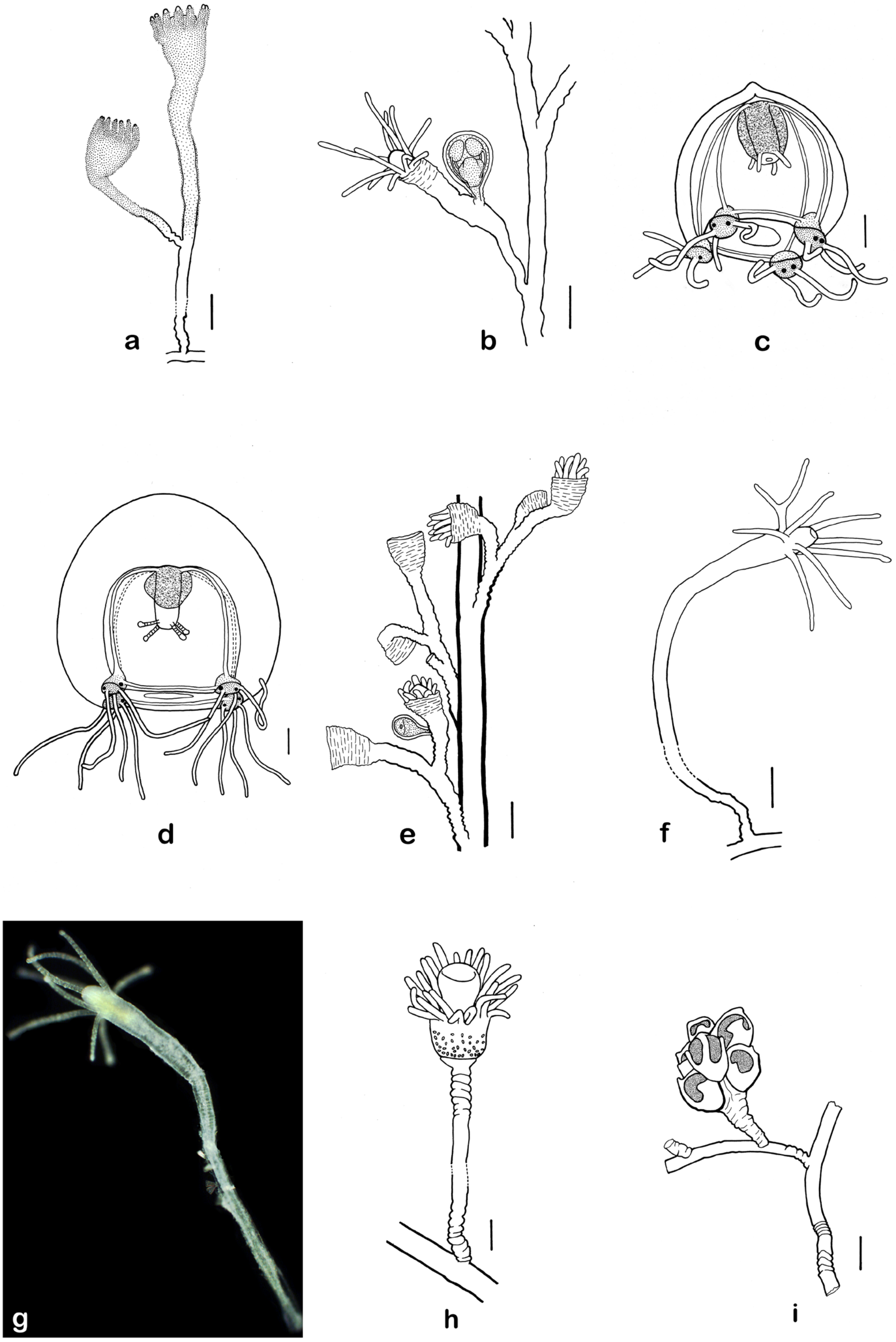

FIGURE 2. a, ***Bimeria humilis*****:** colony with two hydranths, Fort Myers Beach, ROMIZ B4330. Scale equals 0.2 mm. **b,** ***Bougainvillia rugosa*****:** part of colony with hydranth and medusa bud, Sanibel Island, ROMIZ B4333. Scale equals 0.2 mm. **c,** ***Bougainvillia rugosa*****:** newly liberated medusa from same hydroid, ROMIZ B4333. Scale equals 0.1 mm. **d,** ***Bougainvillia rugosa*****:** 3-day-old laboratory-raised medusa from same hydroid, ROMIZ B4333. Scale equals 0.1 mm. **e,** ***Calyptospadix cerulea*****:** part of hydrocaulus with branches, pedicels, hydranths, and a female gonophore, Caloosahatchee River at Fort Myers, ROMIZ B4340. Scale equals 0.3 mm. **f,** ***Amphinema*** **sp.:** hydranth and pedicel, Captiva Island, ROMIZ B4338. Scale equals 0.2 mm. **g,** ***Amphinema*** **sp.:** hydranth and pedicel, Captiva Island, ROMIZ B4338. **h,** ***Eudendrium carneum*****:** hydranth and pedicel, Sanibel Island, ROMIZ B4343. Scale equals 0.2 mm. **i,** ***Eudendrium carneum*****:** part of female colony with encapsulated embryos, Sanibel Island, ROMIZ B4344. Scale equals 0.4 mm.

Gonophores free medusae. Medusa buds pyriform to bulbous, arising singly on relatively short stalks, most arising from hydranth pedicels but a few from hydrocaulus, invested in perisarc prior to release; developing gonads apparent in advanced buds. Newly liberated medusae dome-shaped, umbrella about 0.55 mm high and wide; mesoglea fairly thick, umbilical canal present in some but absent in most, with vestige of attachment to hydroid sometimes forming an apical cone; gastric peduncle lacking; manubrium tubular, quite short, extending less than half-way to velar opening; mouth simple; oral tentacles four, unbranched, inserted just above mouth, appearing slightly capitate in having a distal cluster of nematocysts; radial canals four; ring canal present; tentacle bulbs four, conical, with rounded bases; marginal tentacles filiform, highly contractile, nearly always 12 in number, with three per tentacle bulb, ocelli eight, conspicuous, dark red, with one at base of each of first two tentacles in each bulb, in clockwise order around oral end of medusa; tentacles having ocelli somewhat more developed than those lacking that structure; velum broad. Gonads developed, or obviously developing, in newly liberated medusae. Endoderm brownish orange, colour intensity varying from one specimen to another but typically quite faint, gonad sometimes appearing slightly green. Medusae active swimmers. Three-day-old medusae larger (ca. 0.8–1 mm in diameter), with much thicker mesoglea and with more advanced gonadal development, but otherwise little changed, having a short manubrium, four unbranched oral tentacles, no gastric peduncle, and four marginal tentacle bulbs, each with three marginal tentacles and usually with two ocelli, less frequently with three. After five days, with little morphological change but with signs of declining vigour, all remaining medusae were preserved.

Remarks. *Bougainvillia rugosa* Clarke, 1882 is an infrequently reported and insufficiently known species, and its validity has even been questioned (Kramp 1959). For those reasons, both polypoid and medusoid stages have been described here. The hydroid of *B. rugosa*, which can attain a significant size, has been reported more often than its small and relatively short-lived medusa. Much smaller, monosiphonic colonies assigned here to *B. rugosa* (ROMIZ B4333) were at first thought to be a different species. However, a continuum appears to exist from these tiny colonies to those that are large and polysiphonic (ROMIZ B4335, ROMIZ B4336), as is considered typical of *B. rugosa*.

In support of the identification made here, medusae liberated from hydroids collected during December 2017 (ROMIZ B4333) were cultured at ambient temperatures (ca. 19–23° C) and in polyhaline salinities for five days. Specimens were fed fragments of yolk from hardboiled eggs twice each day. Other than an increase in size, a thickening of the mesoglea, and increasing development of the gonads (all males), no significant morphological changes were observed. Marginal tentacle numbers remained at 12, oral tentacles did not become branched, and ocelli were eight in number (Figs. 2c, d). In this, the development corresponded with that of *B. rugosa*, as described earlier (Clarke 1882; Calder 1971).

While fully developed hydroids of *B. rugosa* are large (up to 25 cm high), robust, and polysiphonic, some of those examined here (ROMIZ B4333) were small (ca. 6 mm high), slender, and monosiphonic, as noted above. Larger (6 cm high), more robust, and strongly polysiphonic specimens (ROMIZ B4335, ROMIZ B4336), like those described from Chesapeake Bay (Clarke 1882; Calder 1971), were also collected. Most of the medusae liberated from those colonies had the usual 12 marginal tentacles and eight ocelli, but a few had 1–2 additional but miniscule ocelli, with one at the base of the somewhat less-developed third tentacle on each marginal bulb. Cnidomes of the two morphotypes (Fig. 3) comprised desmonemes (3.2–3.8 long x 1.9–2.3 µm wide, undischarged, n=10, ROMIZ B4333; 3.8–4.2 long x 2.3–2.7 µm wide, undischarged, n=10, ROMIZ B4335) and heterotrichous microbasic euryteles (5.1–5.7 long x 2.2–2.9 µm wide, undischarged, n=10, ROMIZ B4333; 5.2–5.8 long x 2.3–2.8 µm wide, undischarged, n=10, ROMIZ B4335).

In colony size and form, small hydroids of *B. rugosa* somewhat resemble those of *B. muscus*. However, their newly liberated medusae had 12 marginal tentacles (three per tentacle bulb) instead of eight (two per tentacle bulb) as in *B. muscus*, and their gonads were partially developed. Indeed, gonads were apparent even on medusa buds still attached to the hydroid. With growth, medusae of the two species become much more alike, at least initially, typically having 12 marginal tentacles, eight ocelli, and unbranched (or minimally branched) oral tentacles. Those of the two species appear to be relatively short-lived, and their eggs are armed with an outer envelope bearing numerous heterotrichous microbasic euryteles. Another species having a medusa with 12 marginal tentacles at liberation is the boreal *B. principis* (Steenstrup, in Lütken, 1850). However, it has 12 ocelli instead of eight, its gonads are undeveloped, its oral tentacles are branched, its exumbrella bears numerous nematocysts, and its hydroid is stolonal (Schuchert 2007). Newly liberated medusae of *B. macloviana* Lesson, 1830 have 2–5 marginal tentacles and 2–3 ocelli per tentacle bulb, and branched or slightly branched oral tentacles. Unlike *B. rugosa*, its hydroid is stolonal and the species is autochthonous to high latitudes (Schuchert 2007).

The hydroid of *B. rugosa* is eurytopic, having been found at salinities between 18‰–34‰ (Calder 1976) and at water temperatures between 6–32° C (Calder 1990). Colonies with medusa buds were collected during autumn and winter in southwest Florida during this study. The species was found on a variety of substrates in tributaries of southern Chesapeake Bay (Calder 1971), including submerged ropes, wooden pier pilings and fouling panel frames, test panels of acrylic plastic and asbestos fibre, sponges (*Lissodendoryx isodictyalis*), bryozoans (*Alcyonidium verrilli*), tubicolous polychaetes (*Hydroides hexagona*), shells of oysters (*Crassostrea virginica*), a crab carapace (*Libinia* sp.), and ascidians (*Molgula manhattensis*).

Bougainvillia rugosa has been reported from Chesapeake Bay (Clarke 1882; Calder 1971) to the Gulf of Mexico (Calder & Cairns 2009), and with question to the Caribbean Sea (Stechow 1919). It has also been reported from Brazil (Migotto 1996). Stechow's record of the species, from the U.S. Virgin Islands, is somewhat uncertain in having been based on sterile material. Also of uncertain identity is a medusa identified as *B. rugosa* by Mayer (1910a) from Charleston Harbor, South Carolina. Unlike *B. rugosa*, 12 ocelli instead of eight were present adjacent to the 12 marginal tentacles in his specimen.

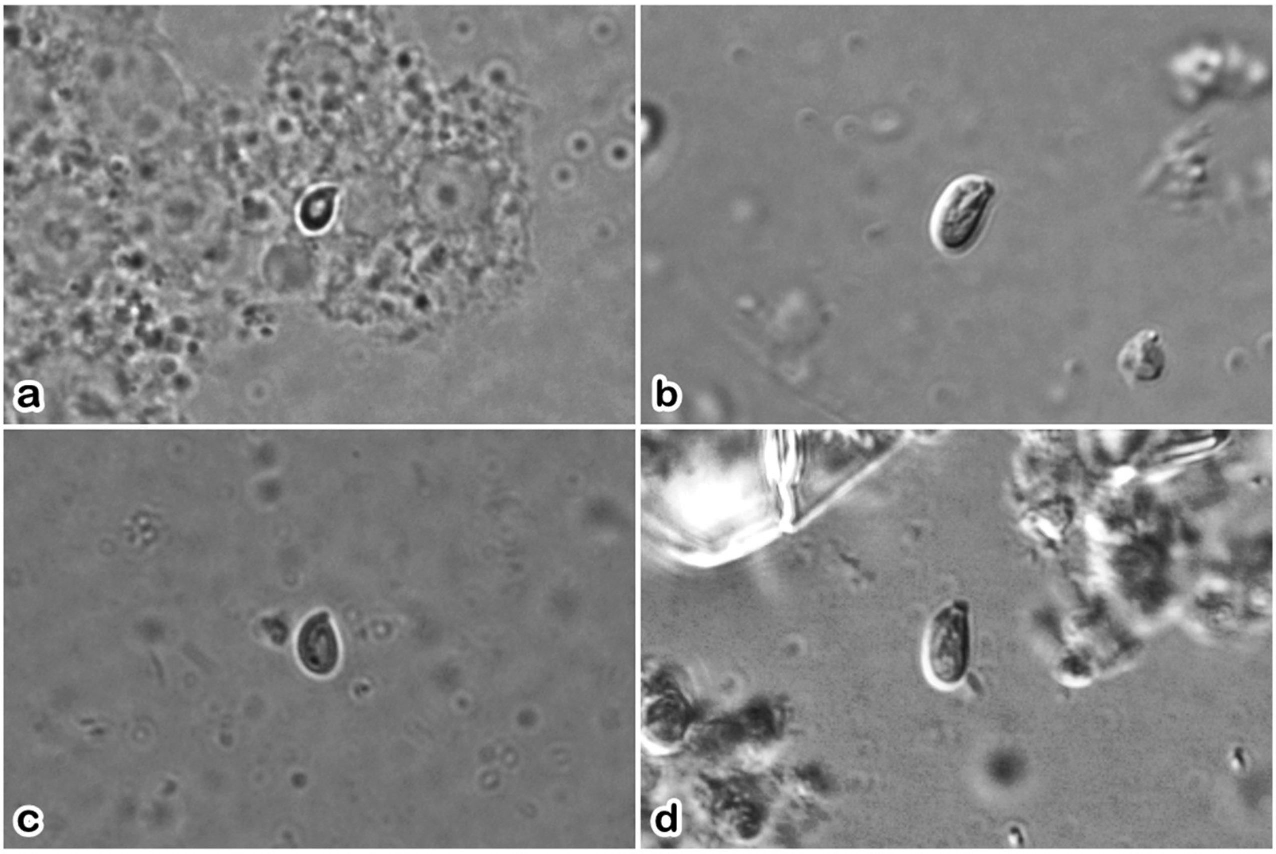

FIGURE 3. ***Bougainvillia rugosa***: nematocysts of hydroid stage. **a,** desmoneme, ROMIZ B4333. **b,** heterotrichous microbasic eurytele, ROMIZ B4333. **c,** desmoneme, ROMIZ B4335. **d,** heterotrichous microbasic eurytele, ROMIZ B4335.

Based on current knowledge, *B. rugosa* is an inhabitant of shallow inshore waters in warm-temperate regions of the western Atlantic, and especially the southeastern United States. The morphologically similar *B. inaequalis* Fraser, 1944 occurs under similar ecological conditions. Clarification of relationships between the two is warranted, although hydroids of *B. inaequalis* appear to have perisarc on stems and branches that is much more deeply wrinkled than in *B. rugosa*. That species has been thought to intergrade with *B. carolinensis* McCrady, 1859 as well (Deevey 1950).

Reported distribution. ***Gulf coast of Florida.*** First record.

Elsewhere in western North Atlantic. USA: Virginia, Hampton Roads and areas in lower Chesapeake Bay, "Laminarian zone", on *Alcyonidium* (Clarke 1882: 141, as *Bougainvillea rugosa*).—?USA: South Carolina, Charleston Harbor, medusa (Mayer 1910a: 171, pl. 17, fig. 2).—USA: North Carolina, Bogue Sound, 10 or 12 feet (3 or 4 m) + Marshallberg, near low water (Fraser 1912b: 347).—?Virgin Islands of the United States: St. Thomas, Charlotte Amalie, surface (Stechow 1919: 27).—USA: Louisiana, Bayou Mussel + Pass Sortie (Fraser 1944: 53).—USA: Virginia, Norfolk, Norfolk Naval Base Pier 12, on fouling panels, 5 m (Calder & Brehmer 1967: 153).—USA: North Carolina, Beaufort (medusa) (Allwein 1967: 122).—USA: Virginia, York River (Ellen Island; Gloucester Point) + James River (Hampton Bar; Norfolk Naval Base Pier 12; Hampton Roads Middle Ground) (Calder 1971: 36).—USA: Virginia, entrances of the Rappahannock, York, and James river estuaries (Andrews 1973: 231).—USA: South Carolina, coastal zone, many areas (Calder 1976; 1990; Calder & Hester 1978: 89).—USA: South Carolina, Folly River area, Oak Island, oyster reef + Folly river area, pilings + Isle of Palms, marina, floating docks + Beaufort River, channel + Hunting Island, seawall and rubble + Beaufort River area, floating docks (Fox & Ruppert 1985: 152, 160, 177, 204, 226, 232).—USA: South Carolina, Beaufort, floating dock, 32°26’16”N, 80°40’29”W (Caine 1987: 84; 1989: 425; 1998: 317).—USA: Georgia: St. Catherines Island, docks (Prezant *et al*. 2002: 22).—USA: Georgia, Sea Islands, on loggerhead turtles (Frick *et al*. 2002: 954).—Caribbean Sea (Wedler 2017b: 22, figs. 6A–C, in caption as *Bougainvillia ramosa*).

Genus *Calyptospadix* Clarke, 1882

Calyptospadix cerulea Clarke, 1882

Fig. 2e

Calyptospadix cerulea Clarke, 1882: 136, pl. 7, figs. 1–9.
Bimeria franciscana Torrey, 1902: 28, pl. 1, fig. 4.
not *Bimeria franciscana*.—Joyce, 1961: 36, pl. 5, figs 3, 4 [=*Bimeria humilis* Allman, 1877].
Garveia franciscana.—Garman *et al.* 2011: 71.

Type locality. USA: Virginia, Hampton Roads, Fort Wool (Clarke, 1882: 136).

Material examined. Caloosahatchee River at Fort Myers, 26°38.790’N, 81°52.354’W, on floating dock, less than 1 m, 18 July 2012, 7‰, one colony, 7.5 cm high, with a few developing female gonophores, coll. D. Calder, ROMIZ B4340.—Caloosahatchee River at Fort Myers, 26°38.790’N, 81°52.354’W, on floating dock, less than 1 m, 18 July 2012, 7‰, one colony, 2.5 cm high, without gonophores, coll. D. Calder, ROMIZ B4341.—Fort Myers Beach, Salty Sam’s Marina, 26°27’21.7”N, 81°56’34.6”W, on floating dock on oyster shells, <0.1 m, 24° C, 22 February 2018, five colony fragments, up to 5 cm high, with male gonophores, coll. D. Calder, ROMIZ B4342.—Fort Myers Beach, Salty Sam’s Marina, 26°27’21.7”N, 81°56’34.6”W, on floating dock, <0.1 m, 29° C, 27 August 2018, three colony fragments, up to 13 cm high, with female gonophores, coll. D. Calder, ROMIZ B4417.

Remarks. *Calyptospadix cerulea* Clarke, 1882 was originally described from Hampton Roads, Virginia, at the mouth of the James River estuary. The species has been reported relatively few times under that name, mostly from areas of reduced salinity along the Atlantic coast of North America (Fraser 1944). Much resembling it is the more widely reported *Bimeria franciscana* Torrey, 1902, first discovered in the San Francisco Bay estuary on the Pacific coast of the United States. That hydroid is commonly believed to be an invasive estuarine endemic with a disjunct but widespread geographic distribution in temperate and tropical regions. The only apparent morphological difference between the two putative species is the supposed number of planulae generated per female sporosac, with several originally reported in *C. cerulea* and one in *B. franciscana*. On examining specimens of the common morphotype from Virginia during this study, some colonies had gonophores with a single egg cell, corresponding to *B. franciscana*, while others had several cells or possibly zygotes, corresponding to *C. cerulea*. The latter were interpreted as cell aggregations resulting from cleavage of the single egg. Hydroids of the two were otherwise indistinguishable. Meanwhile, specimens examined here from Fort Myers Beach (ROMIZ B4417) had, on the same colony, some female gonophores with a single egg and others containing a varying number of cells. The latter were again taken to have been the result of cell division. While gonosomes of the two supposed species may differ, the apparent difference is believed to simply reflect different stages of embryological development. Thus, *C. cerulea* and *B. franciscana* are treated here as conspecific. Molecular analyses of populations from the two type localities, and ones supposedly differing in their gonosomes, are nevertheless needed to better resolve the synonymy of the two. Of the two subjective synonyms, the junior name (*B. franciscana*) is the more familiar. However, nomenclatural stability is not greatly threatened by application of the Principle of Priority, and *C. cerulea* is adopted here as the name of the species.

A change in the binomen *Bimeria franciscana* is necessary in any case because the species has been assigned to the wrong genus. These hydroids have been referred in most recent works to *Garveia* Wright, 1859, as *G. franciscana* or *G. cerulea*. However, specimens do not match the diagnosis of that genus, as outlined by Schuchert (2007). Instead, *Calyptospadix* Clarke, 1882 is recognized here as valid, referable to family Bougainvilliidae Lütken, 1850, and the original binomen of the species (*Calyptospadix cerulea*) is restored. Meanwhile, *Garveia* was recently removed from Bougainvilliidae to Pandeidae Haeckel, 1879 in having vasiform hydranths surrounded by pseudohydrothecae, and notably robust hypostomes (see Calder 2017). Molecular data in Prudkovsky et al. (2016) provide additional support for assignment of *Garveia* to Pandeidae. As noted earlier, Bougainvilliidae as presently constituted is taken to be polyphyletic (Mendoza-Becerril 2018a).

Hydroids identified here as *C. cerulea* were abundant on a floating dock at 26°38.790'N, 81°52.354'W in the Caloosahatchee River estuary at Fort Myers, Florida, during July 2012 (ROMIZ B4340, ROMIZ B4341). In the aftermath of Hurricane Irma passing through south Florida in September 2017, a massive discharge of fresh water passed through the estuary from Lake Okeechobee upstream. Colonies of *C. cerulea* disappeared at that location under salinities of less than 1‰ and were replaced by the more fresh-water tolerant *Cordylophora caspia*. Instead, hydroids of the species appeared down-estuary in Estero Bay on floating docks at Salty Sam's Marina (26°27'21.7"N, 81°56'34.6"W), San Carlos Island, in winter 2018 (ROMIZ B4342). Colonies with abundant female gonophores were found at the same location in late summer 2018 (ROMIZ B4418).

Calyptospadix cerulea has been reported elsewhere on the Gulf coast of Florida from Crystal Beach Spring (Garman *et al.* 2011, as *Garveia franciscana*). The report of *Bimeria franciscana* by Joyce (1961) from Seahorse Key, on the Florida Gulf coast, is based on a misidentification of *B. humilis* Allman, 1877, as noted elsewhere. Also likely misidentified are reports of the species by Fox & Ruppert (1985), as *Garveia franciscana*, from typically high salinity areas in coastal South Carolina. The species is regarded as an estuarine endemic, with a reported bathymetric range of 0–5 m (Calder & Cairns 2009).

Reported distribution. ***Gulf coast of Florida.*** Crystal Beach, Crystal Beach Spring (Garman *et al.* 2011: 71, as *Garveia franciscana*).

Elsewhere in western North Atlantic. USA: Virginia, Hampton Roads, Fort Wool (Clarke, 1882: 136).—USA: Massachusetts, Woods Hole + Buzzard's Bay (Hargitt 1909: 371, 372; Fraser 1912a: 41).—Canada: New Brunswick, Miramichi Bay (Fraser 1926: 212).—USA: Louisiana coast (Fraser 1943: 86, as *Bimeria tunicata*).—USA: tributaries of Chesapeake Bay (Fraser 1944: 55; 1945: 21, as *Bimeria tunicata*; Cory 1967: 79, as *Bimeria franciscana*; Calder & Brehmer 1967: 153, as *Calyptospadix cerulea*; Cory & Nauman 1969: 215, as *Bimeria franciscana*; Calder 1971: 39, as *Garveia cerulea*; 1971: 40, as *Garveia franciscana*; McLean 1972: 229, as *Bimeria franciscana*; Andrews 1973: 231, as *Garveia franciscana* (=*Bimeria*).—USA: coast of Louisiana and Texas (Deevey 1950: 335; 1954: 269; both as *Bimeria franciscana*).—USA: Louisiana, Lake Pontchartrain (Crowell & Darnell 1955: 516, as *Bimeria franciscana*; Poirrier & Mulino 1977: 15, as *Garveia franciscana*).—USA: Mississippi, Mississippi Sound, most abundant hydroid observed (Fincher 1955: 91, as *Bimeria tunicata*).—USA: Delaware Bay (Watling & Maurer 1972: 646, as *Garveia franciscana*; Smedes & Hurd 1981: 1568, as *Garveia franciscana*).—USA: Texas, Galveston Bay (Defenbaugh 1972: 387, as *Bimeria franciscana*; Defenbaugh & Hopkins 1973: 49, as *Bimeria franciscana*).—Colombia: Ciénaga Grande de Santa Marta (Wedler 1973: 32; Palacios 1979: 114; Bandel & Wedler 1987: 39, as *Garveia cerula*).—USA: North Carolina, Pamlico River estuary (Dean & Bellis 1975: 6, as *Garveia cerulea*).—USA: South Carolina, estuaries (Calder & Hester 1978: 89, as *Garveia franciscana*).—?USA: South Carolina, Folly River + Breach Inlet, jetties + Beaufort area, pilings and jetties (Fox & Ruppert 1985: 162, 167, 219, as *Garveia franciscana*).—USA: Virginia, James River, oyster reefs (Larsen 1985: 800, as *Garveia franciscana*).—Venezuela: Lake Maracaibo (de Rincon & Morris 2003: 17, as *Garveia franciscana*).—Caribbean Sea (Wedler 2017b: 23, figs. 7, 8, as *Garveia franciscana*).

Family Pandeidae Haeckel, 1879

Genus *Amphinema* Haeckel, 1879

Amphinema sp.

Fig. 2f, g, 4

Material examined. Naples (FL), Doctors Pass, north jetty, channel side, on stolonal bryozoan on boulder, 26°10’29.14”N, 81°48’53.45”W, ELWS, 06 December 2017, one stolonal colony, 2 mm high, without gonophores, coll. D. Calder, ROMIZ B4337.—Captiva Island, Turner Beach, on jetty, 26°28’57.3”N, 82°11’02.8”W, on rocks at low tide, 01 March 2018, several colony fragments, up to 4 mm high, without gonophores, coll. D. Calder, ROMIZ B4338.

Remarks. While these hydroids have been assigned to *Amphinema* Haeckel, 1879 (family Pandeidae Haeckel, 1879), no gonophores were present in the examined specimens. Their trophosomes resemble those of species such as *A. dinema* (Péron & Lesueur, 1810) and *A. rugosum* (Mayer, 1900a), whose medusa stages have been reported from the southeastern Gulf of Mexico (Mayer 1910a; Segura-Puertas *et al*. 2009), but these sterile specimens cannot be confirmed as conspecific with either one from current evidence. The cnidome comprised the usual categories of nematocysts found in pandeids and bougainvilliids, namely desmonemes (3.2–3.8 long x 1.7–2.2 µm wide, undischarged, n=10, ROMIZ B4338) and microbasic euryteles (6.2–7.1 long x 1.9–2.2 µm wide, undischarged, n=10, ROMIZ B4338). In size and shape, the euryteles approached those of *A. dinema* (Péron & Lesueur, 1810) as described by Russell (1938), and those of both *A. dinema* and *A. rugosum* as described by Schuchert (1996). Most notably, they were longer and much more slender than those of the bougainvilliid *Bougainvillia rugosa* from the study area. Nevertheless, life cycle or molecular studies of conspecifics from the study area are needed to resolve the specific identity of this hydrozoan.

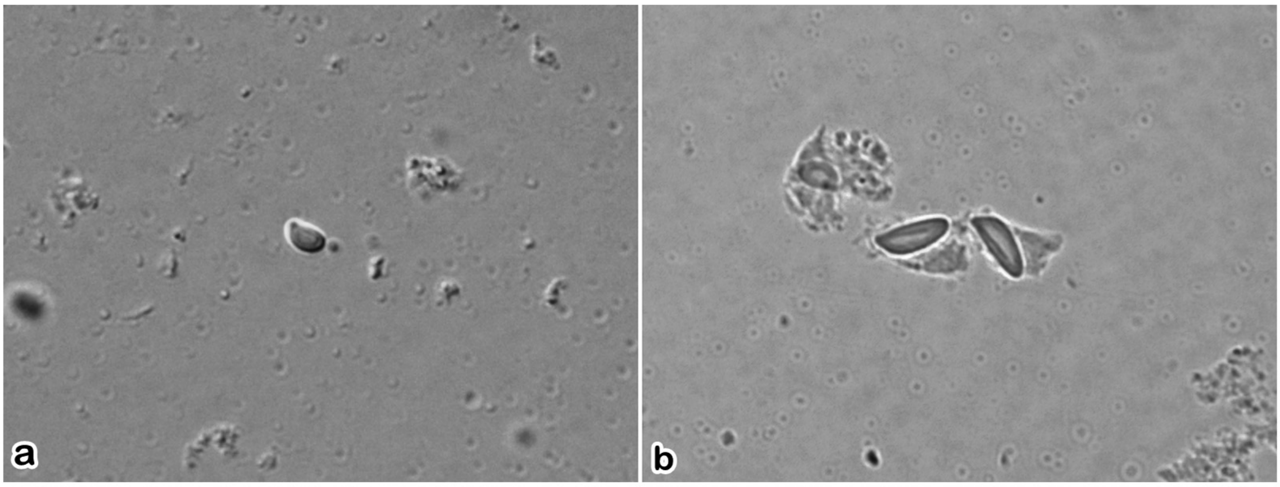

FIGURE 4. ***Amphinema* sp.:** nematocysts of hydroid stage, ROMIZ B4338. **a,** desmoneme. **b,** heterotrichous microbasic euryteles.

Family Eudendriidae L. Agassiz, 1862

Genus *Eudendrium* Ehrenberg, 1834

Eudendrium carneum Clarke, 1882

Figs. 2h, i, 5

Eudendrium carneum Clarke, 1882: 137, pl. 7, figs. 10–17.—Wallace, 1909: 137.—Menzel, 1956: 2.—Joyce, 1961: 33, pl. 4, figs. 1–4.—Shier, 1965: 18, pl. 7.—Philp *et al*., 2003: 222.

Type locality. USA: Virginia, Hampton Roads, Fort Wool (Clarke 1882: 137).

Material examined. Sanibel Island, beach at Lighthouse Point, detached and stranded on shore, 13 December 2017, one colony, 15 cm high, without gonophores, coll. D. Calder, ROMIZ B4343.—**Sanibel Island,** beach at Lighthouse Point, detached and stranded on shore, 29 January 2018, one colony fragment, 5 cm high, with female gonophores, coll. D. Calder, ROMIZ B4344.

Remarks. *Eudendrium carneum* was first described by Clarke (1882) from Hampton Roads, Virginia, USA, an important naval and commercial port within Chesapeake Bay. A common component of the fouling community (e.g. McDougall 1943; Sutherland 1974, 1978, 1981; Sutherland & Karlson 1977; Karlson & Osman 2012; Oliveira *et al*. 2016) and a hydroid having a wide geographic distribution, the species has likely been dispersed, at least in part, by shipping (Watson 1985). In the western North Atlantic, it has been reported from southern Massachusetts to the southern Caribbean Sea (see records below). Previous reports of *E. carneum* to the north of Cape Cod on this coast, such as that by Fraser (1944) from Nova Scotia (Misaine Bank E of Cape Canso, 45°22'N, 58°43'45"W, 137 m), are believed here to have been based on misidentifications given temperature tolerances of the species (Calder 1990). *Eudendrium carneum* is essentially a warm-temperate to tropical species, unlikely to occur in boreal waters.

A combination of morphological characters distinguish *E. carneum* from its numerous congeners. Hydroids of the species are typically robust and extensively branched, with polysiphonic hydrocauli and polysiphonic or monosiphonic branches. The nematocyst complement comprises small microbasic euryteles (7.9–9.0 μm long x 3.3–3.9 μm wide, undischarged, n=10, ROMIZ B4343) and large heterotrichous anisorhizas (26.3–29.5 μm long x 10.5–12.7 μm wide, undischarged, n=10, ROMIZ B4343), the latter arranged in a band around the base of each hydranth as well as occurring on the hypostome and male gonophores. Both male and female gonophores are borne on reduced or aborted hydranths. Those of the male occur on several peduncles, each of which comprises a linear series of up to five chambers; the distalmost chamber is armed with heterotrichous anisorhizas. Most importantly, female gonophores are distinguished in having a bifid spadix that curves over the egg; with development, embryos surrounded by capsules of perisarc appear in clusters along ultimate branchlets. Hydranths and gonophores are reddish to orange in colour.

A species much like *E. carneum* is *E. tayronensis*, recently described by Wedler (2017a) from a coastal lagoon (Bahía de Chengue) in Colombia. That species differs from *E. carneum* in having branched gonophore peduncles in the male and embryos that are completely rather than partially enclosed in the female.

Additional details on the hydroid of *E. carneum* are given elsewhere (Calder 1988, 2010, 2013; Schuchert 2008).

Reported distribution. ***Gulf coast of Florida.*** Dry Tortugas (Wallace 1909: 137).—St. George Sound—Apalachee Bay region (Menzel 1956: 2).—Seahorse Key (Joyce 1961: 33).—Cape San Blas area (Shier 1965).—Dickerson Bay (Philp *et al*. 2003: 222).

Elsewhere in western North Atlantic. USA: South Carolina, Sullivan's Island (McCrady 1859: 167, as *Eudendrium ramosum*).—USA: South Carolina, Charleston (A. Agassiz 1865: 160, as *Eudendrium ramosum*).—USA: Virginia, Hampton Roads, Fort Wool (Clarke 1882: 137).—USA: no location given, but in collections of the U.S. Fish Commission at Woods Hole, Massachusetts (Nutting 1901: 333).—Bermuda: location unspecified (Congdon 1906: 27, 1907: 464, as *Eudendrium ramosum*).—USA: Massachusetts, Martha's Vineyard, Vineyard Haven + off Naushon Island + Gay Head (Hargitt 1908: 97).—USA: Massachusetts, Woods Hole (Fraser 1912a: 42; Weill 1934: 388, as *Eudendrium ramosum*).—USA: North Carolina, Beaufort area (Wilson 1911: 282).—USA: North Carolina, Morehead City + Beaufort + Shackleford Banks, 12 ft (4 m) (Fraser 1912b: 349).—Bermuda: Hamilton Harbour (Bennitt 1922: 245, as *Eudendrium ramosum*).—USA: North Carolina, Beaufort (Wilson 1923: 40; Pearse 1936: 178; McDougall 1943: 337).—USA: Massachusetts, off Chatham, 41°38'N, 69°53'W, 7.5 ftm (14 m) + 5.75 miles (12 km) off Chatham Light, 14 ftm (26 m) + SE of Nantucket, 46 ftm (84 m) + between Nantucket and High Duck Islands, 4 ftm (7 m) + Nantucket Sound, 18 ftm (33 m) + off Martha's Vineyard, 396 ftm (724 m) + Vineyard Sound, near West Chop Light, 14 ftm (26 m) + off West Falmouth, 7 ftm (13 m) + off Naushon Island + Buzzards Bay (Fraser 1944: 65).—USA: Rhode Island, Tiverton + Narragansett Bay, off Fort Dumpling, 20 ftm (37 m) (Fraser 1944: 65).—USA: New York, Long Island, Greenport (Fraser 1944: 65).—Puerto Rico: N of Culebra Island, 18°19'10"N, 65°19'40"W, 10 ftm (18 m) (Fraser 1944: 65).—USA: North and South Carolina, reefs on the continental shelf (Pearse & Willams 1951: 136).—USA: North Carolina, Beaufort area (Maturo 1959: 123; Wells 1961: 246; Sutherland 1974: 861; 1978: 258; 1981: 503; Sutherland & Karlson 1977: 427; Karlson 1978: 231; Lindquist & Hay 1996: 448; Schmitt *et al*. 1998: 126; Stachowicz & Hay 1999: 2086).—USA: North Carolina, Core Banks, on *Aequipecten gibbus*, 17–20 ftm (31–37 m) (Wells *et al*. 1964: 566).—USA: Massachusetts: Woods Hole region (Petersen 1964: 18; Wyttenbach *et al*. 1973: 364).—Venezuela: Puerto Cabello (Vervoort 1968: 8).—Costa Rica, Limón (Vervoort 1968: 8).—Bermuda: Flatts Bridge (Summers 1972: 149, as *Eudendrium ramosum*).—Colombia (Wedler 1975: 340; Flórez González 1983: 123; Criales 1984: 309; Bandel & Wedler 1987: 35).—USA: South Carolina, estuaries across the state (Calder & Hester 1978: 89).—USA: North Carolina, Bogue Sound (Bynum 1980: 227).—USA: Florida, Indian River region (Winston 1982: 164; 2009: 232).—USA: South Carolina and Georgia, inner, middle and outer continental shelf (Wenner *et al*. 1984: 20, 39).—USA: South Carolina, North Inlet, pilings + Murrells Inlet, jetties + Charleston area + Folly River + Breach Inlet, jetties + Isle of Palms, marina, floating docks + Beaufort area, marinas, floating docks (Fox & Ruppert 1985: 84, 92, 140, 162, 167, 177, 232).—USA: Louisiana, shelf hard bottoms (Putt *et al*. 1986: 56).—Bermuda: shallow inshore waters (Calder 1986).—Puerto Rico: La Parguera, 1–2 m (Wedler & Larson 1986: 84).—USA: Louisiana, on coastal petroleum platforms, 12–18 m (Lewbel *et al*. 1987:

214).—Bermuda: Hamilton Harbour, 2.5 m + Flatts Inlet, 0.5–2 m + Castle Harbour, Castle Grotto, 1 m + Ferry Reach, 0.5–2 m + Somerset Bridge, 2 m (Calder 1988: 43).—USA: South Carolina and Georgia, inner continental shelf, on artificial reefs (Wendt *et al*. 1989: 1119).—USA: North Carolina, Beaufort (Walters 1992: 1102).—USA: North Carolina (Lindquist 1996: 435).—USA: North Carolina, Beaufort (Holm *et al*. 1997: 192).—USA: North Carolina, Wrightsville Beach (Henrikson & Pawlik 1998: 252).—Bermuda: "Hamilton Sound" (=Great Sound?) + Gibbons Bay (Marques *et al*. 2000: 90).—USA: Florida, Miami, Ragged Keys, 25°47'N, 80°11'W + Guard Bridge, 25°47'N 80°11'W (Marques *et al*. 2000: 91).—USA: Georgia: St. Catherines Island, main dock (Prezant *et al*. 2002: 22).—Costa Rica: Limón (Kelmo & Vargas 2002: 602).—USA: Florida, Biscayne Bay (Jones 2002: 216.—Panama: Colón, Fort Sherman dock, 0–2 m + Colón, bridge near Fort Sherman, 0–1 m + Bocas del Toro, Swan's Key, 1–4 m + Bocas del Toro, Bastimentos, 1–4 m + Bocas del Toro, Drago, 2–4 m (Calder & Kirkendale 2005: 479).—Honduras: Utila, 16.0687°N, 86.9555°W, 20 m (Schuchert 2008: 700).—USA: Massachusetts, (Martha's Vineyard), Lagoon Pond Bridge (Schuchert 2008: 700).—USA: Florida, Fort Pierce Inlet, north jetty, intertidal (Calder 2013: 13).—Caribbean Sea (Wedler 2017b: 31, figs. 14A, B, 15–17, 18A, B).—Mexico: Alacranes Reef, on algae, buoys, chains, shipwreck (Mendoza-Becerril *et al*. 2018b: 129).—Cuba: Havana, coral reef system west of the city (Castellanos *et al*. 2018: Supplementary Table S2).—Panama: Bocas del Toro area, Punta Hospital + Swan's Cay (Miglietta *et al*. 2018b: 108).

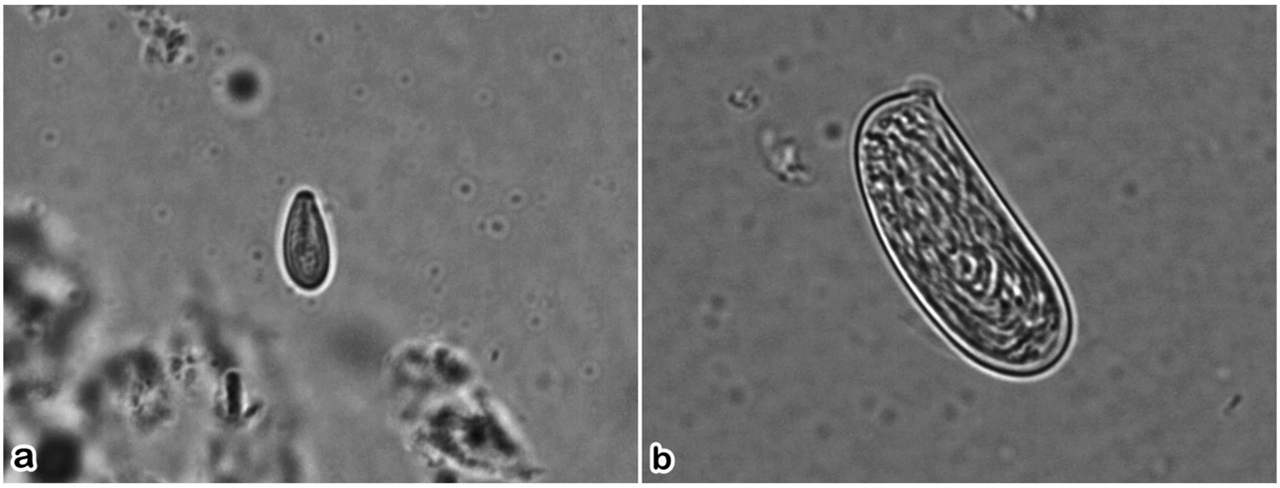

FIGURE 5. ***Eudendrium carneum*:** nematocysts of hydranth, ROMIZ B4343. **a,** microbasic heterotrichous eurytele. **b,** heterotrichous anisorhiza.

Order Leptothecata Cornelius, 1992

Suborder Lafoeida Bouillon, 1984

Family Lafoeidae A. Agassiz, 1865

Genus *Acryptolaria* Norman, 1875

Acryptolaria longitheca (Allman, 1877)

Figs. 6a, b, 7a

Cryptolaria longitheca Allman, 1877: 19, pl. 13, figs. 4–5.—Clarke, 1879: 244, pl. 2, figs. 7–10.
Acryptolaria longitheca.—Fraser 1943: 90.

Type locality. Bahamas: Cay Sal Bank, Double-Headed Shot Key, 315 ftm (576 m) (Allman 1877: 19, as *Cryptolaria longitheca*).

Material examined. Southwest Florida Shelf, middle shelf west of North Naples, 26°16'30"N, 83°42'30"W, 80.5 m, 03 November 1980, three colony fragments, up to 7 cm high, without gonophores, coll. Continental Shelf Associates, ROMIZ B1907.—Southwest Florida Shelf, middle shelf west of North Naples, 26°16.72′N, 83°46.82′W, 83 m, 24 July 1981, otter trawl, one colony, 8.3 cm high, without gonophores, coll. Continental Shelf Associates, ROMIZ B1905.—Southwest Florida Shelf, outer shelf west of North Naples, 26°16.67′N, 84°04.08′W, 137 m, 25 July 1981, triangle dredge, five colony fragments, up to 9.3 cm high, some with coppiniae, coll. Continental Shelf Associates, ROMIZ B1902.

Remarks. Allman's (1877) original description of *Acryptolaria longitheca* (as *Cryptolaria longitheca*) was brief and in some respects inaccurate. In particular, hydrothecae were said to be "…cylindrical throughout, presenting no diminution of their diameter towards the base…" That characterization was followed by Fraser (1943, 1944) in his accounts of the species. However, Clarke (1879: 244) found that hydrothecae in Allman's type indeed tapered towards the base. His observation was confirmed by Peña Cantero *et al*. (2007), who examined, illustrated, and redescribed the holotype colony. A combination of hydrothecal characters was used by them to distinguish the species from others of the genus *Acryptolaria* Norman, 1875: (1) abcauline wall homogeneously curved; (2) diameter of hydrothecal cavity distinctly wider in free part than in adnate part; (3) hydrothecal base gradually tapered rather than abruptly bottle-necked; (4) hydrothecal aperture diameter <300 µm rather than >300 µm; (5) adcauline wall adnate for half rather than 2/3 of its length; (6) free part of adcauline wall nearly straight (Peña Cantero *et al*. 2007: 273). Material examined here from the Southwest Florida Shelf conformed with all of these characters. The species has been taken to be valid in major recent works on *Acryptolaria* by Peña Cantero *et al*. (2007) and Peña Cantero & Vervoort (2010).

In addition to hydrothecal characters, the cnidome was also found by Peña Cantero *et al*. (2007) to be useful in distinguishing species of *Acryptolaria*. Large nematocysts in material examined here (Fig. 7a) appeared to be macrobasic mastigophores (19.4–23.0 µm long x 5.9–6.5 µm wide, undischarged, n=10, ROMIZ B1902). These were somewhat more slender than ones described in type material of *A. longitheca* (21–23 µm long × 6.5–8 µm wide) by Peña Cantero *et al*. (2007) and Peña Cantero & Vervoort (2010), but the difference was small and considered taxonomically inconsequential.

Gonothecae in material identified as *A. longitheca* by Clarke (1879) from the western edge of the Southwest Florida Shelf (25°33'N, 84°21'W), and considered correctly identified by Peña Cantero *et al*. (2007) and Peña Cantero & Vervoort (2010), also correspond in morphology with those examined here (Fig. 6b). Clarke described them as "…polygonal in form, largest at the distal end, tapering to the base, crowded so closely together that the walls of adjoining bodies are in contact throughout their length, and are provided with a small tubular orifice arising from the centre of the distal end…" Gonothecae of specimens identified as *A. longitheca* by Calder & Vervoort (1998) from the Mid-Atlantic Ridge differ in being much more slender, and that deep water material may be referable to a different species.

Distribution records of this species were listed by Peña Cantero *et al*. (2007: 289). Most of them were considered questionable, and with justification. Considered valid, in addition to Allman's (1877) account from the Bahamas, was that of Clarke (1879) from the Southwest Florida Shelf. Material examined here came from the same general locality. Elsewhere, Peña Cantero & Vervoort (2010) reported *Acryptolaria longitheca* from the western Pacific Ocean (Loyalty Islands and Norfolk Ridge). If only on zoogeographic grounds, those records need confirmation. Said by them to be similar to *A. longitheca* is *A. gemini* Peña Cantero & Vervoort, 2010 from Gemini Seamount, Vanuatu.

Reported distribution. ***Gulf coast of Florida.*** Southwest Florida Shelf, NW of the Dry Tortugas, 25°33′N, 84°21′W, 101 ftm (185 m) (Clarke 1879: 244, as *Cryptolaria longitheca*).—?S of Florida Keys, 24°18'N, 80°58'30"W, 324 ftm (593 m) (Fraser 1943: 90).

Elsewhere in western North Atlantic. Bahamas: Cay Sal Bank, Double-Headed Shot Key, 315 ftm (576 m) (Allman 1877: 19, as *Cryptolaria longitheca*).—?Dominica: 76 ftm (139 m) (Fewkes 1881a: 128, as *Cryptolaria longitheca*).—?French Lesser Antilles: Martinique, 334 ftm (611 m) (Fewkes 1881a: 128, as *Cryptolaria longitheca*).—?Barbados: 103 ftm (188 m) (Fewkes 1881a: 128, as *Cryptolaria longitheca*).—Barbados: 13°11'54"N, 59°38'45"W, 73 ftm (134 m) (Fraser 1943: 90).—?North Atlantic Ocean: abyss E of South Carolina, USA, 32°34'N, 74°21.5'W, 4681 m (Vervoort 1972: 45).—?Bermuda: Bermuda Pedestal, on stalks of hexactinellid sponges, 3550 m + 3011 m (Calder 1996: 1723).—Bahamas: Cay Sal Bank, Double-Headed Shot Key, 315 ftm (576 m) (Calder & Vervoort 1998: 24; re-examination of holotype).—?USA: Louisiana, continental slope, 540–560 m, from vestimentiferan aggregrations on water cold seeps (Bergquist *et al*. 2003: 205).—Bahamas: Cay Sal Bank, Double-Headed Shot Key, 315 ftm (576 m) (Peña Cantero *et al*. 2007: 252; re-examination of holotype).

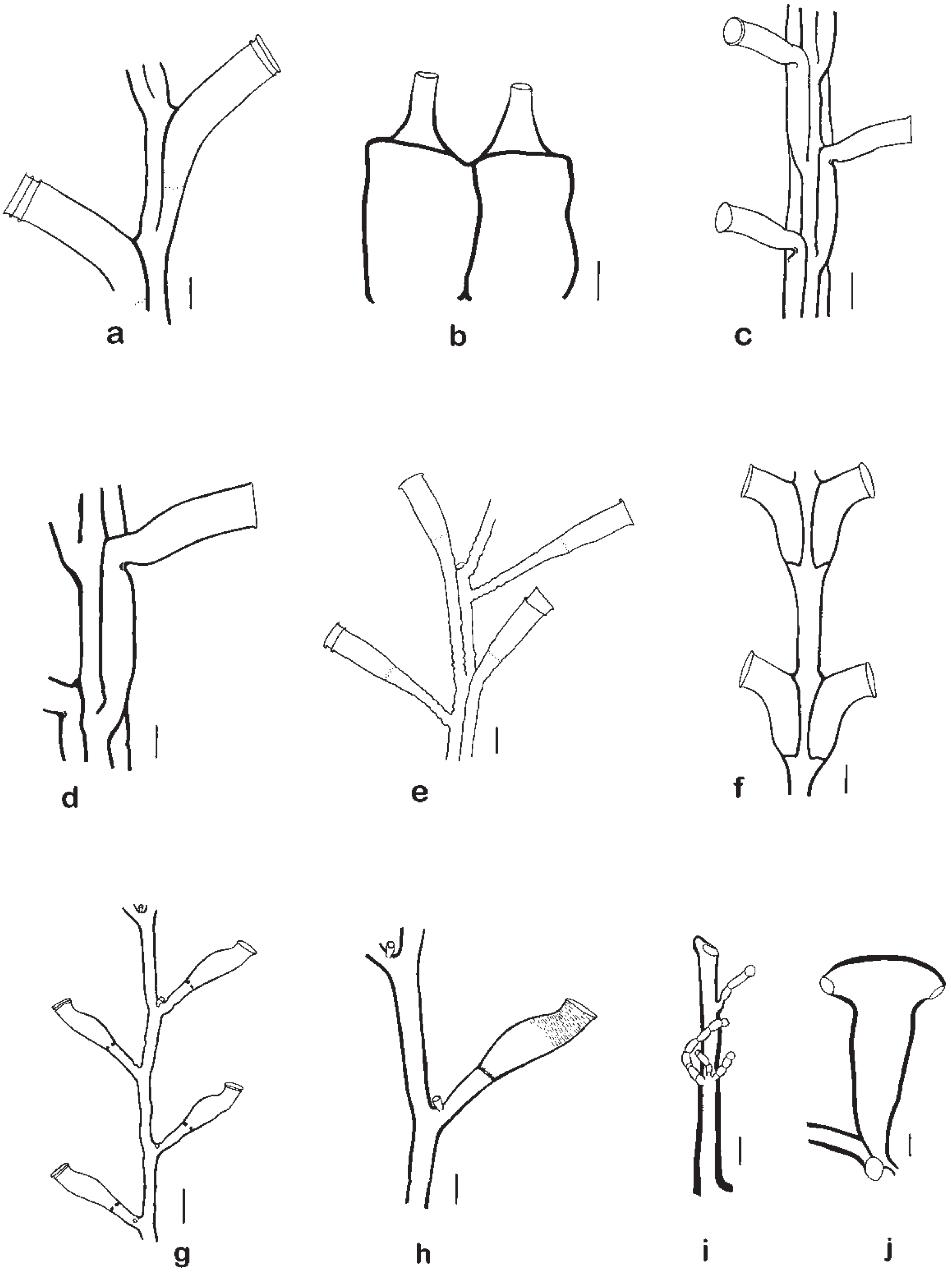

FIGURE 6. a, ***Acryptolaria longitheca*****:** part of colony with two hydrothecae, Southwest Florida Shelf, ROMIZ B1902. Scale equals 0.2 mm. **b,** ***Acryptolaria longitheca*****:** two gonothecae from a coppinia, Southwest Florida Shelf, ROMIZ B1902. Scale equals 0.1 mm. **c,** ***Acryptolaria tortugasensis*****:** part of colony with three hydrothecae, Southwest Florida Shelf, ROMIZ B1906. Scale equals 0.2 mm. **d,** ***Acryptolaria tortugasensis*****:** part of colony with a hydrotheca, Southwest Florida Shelf, ROMIZ B1906. Scale equals 0.1 mm. **e,** ***Lafoea coalescens*****:** part of colony with four hydrothecae, Southwest Florida Shelf, ROMIZ B1915. Scale equals 0.2 mm. **f,** ***Synthecium tubithecum*****:** part of colony with two hydrothecal pairs, Southwest Florida Shelf, ROMIZ B1929. Scale equals 0.2 mm. **g,** ***Zygophylax convallaria*****:** part of colony with four hydrothecae, Southwest Florida Shelf, ROMIZ B1921. Scale equals 0.2 mm. **h,** ***Zygophylax convallaria*****:** part of colony with a hydrotheca, Southwest Florida Shelf, ROMIZ B1921. Scale equals 0.1 mm. **i,** ***Zygophylax convallaria*****:** nematophorous ramule, Southwest Florida Shelf, ROMIZ B1921. Scale equals 0.1 mm. **j,** ***Zygophylax convallaria*****:** gonotheca, Southwest Florida Shelf, ROMIZ B1921. Scale equals 0.1 mm.

Acryptolaria tortugasensis Leloup, 1935a

Figs. 6c, d, 7b

Acryptolaria tortugasensis Leloup, 1935a: 13, figs. 3, 4.—Peña Cantero *et al*., 2007: 265, figs. 14A–F, 16F, 18F, 19G.—Peña Cantero & Vervoort, 2010: 325.

Acryptolaria rectangularis.—Rezak *et al.*, 1985: 224.—Calder & Cairns, 2009: 392 [not *Cryptolaria rectangularis* Jarvis, 1922: 335, pl. 24, fig. 3].

Type locality. USA: Florida, Dry Tortugas, 27 ft (8 m) (Leloup 1935a: 15).

Material examined. Southwest Florida Shelf, middle shelf west of North Naples, 26°16.72′N, 83°46.82′W, 83 m, 24 July 1981, two colonies, up to 6.5 cm high, without gonophores, coll. Continental Shelf Associates, ROMIZ B1906.

Remarks. *Acryptolaria tortugasensis* is known previously only from the Dry Tortugas, Florida. Originally described by Leloup (1935a), the holotype was later included in a collection catalogue by Bouillon *et al*. (1995) and then re-examined and described by Peña Cantero *et al*. (2007). Although the species is reported as such for only the second time here, hydroids from shelf waters off Texas identified by me in the early 1980s as *Acryptolaria rectangularis* (Jarvis, 1922), and mentioned in Rezak *et al*. (1985), are referable instead to *A. tortugasensis*. The same error in identification is repeated in a species list of hydroids from the Gulf of Mexico (Calder & Cairns 2009), based on the same specimens examined here. The binomen *A. tortugasensis* had been included in the synonymy of *A. conferta* until being recognized as valid in a revision of the genus *Acryptolaria* Norman, 1875 by Peña Cantero *et al*. (2007), and later by Peña Cantero & Vervoort (2010). It is clearly distinct from *A. conferta* in having hydrothecae with an abcauline intrathecal cusp and a pronounced outward bend, much as in *A. rectangularis*. Hydroids of *A. tortugasensis* and *A. rectangularis*, a poorly known species from the Indian Ocean, are similar in morphology, but are held to be distinct in the revisionary works cited immediately above.

Large nematocysts in material examined here (Fig. 7b), exceptionally large for species of the genus, appear to be macrobasic mastigophores (30.5–32.5 μm long x 9.0–10.6 μm wide, undischarged, n=10, ROMIZ B1906). They were slightly longer than those described in type material of *A. tortugasensis* (28–30 μm long x 9–10.5 μm wide) by Peña Cantero *et al*. (2007) and Peña Cantero & Vervoort (2010), but the identity of specimens from the SW Florida Shelf nevertheless seems certain.

Line drawings, photographs, and a redescription of the holotype colony of *A. tortugasensis* are given by Peña Cantero *et al*. (2007). The coppinia of this little-known species has yet to be described.

Reported distribution. ***Gulf coast of Florida.*** Tortugas (Leloup 1935a; Peña Cantero *et al*. 2007).—Middle continental shelf west of North Naples (Calder & Cairns 2009, as *Acryptolaria rectangularis*).

Elsewhere in western North Atlantic. USA: Texas, middle continental shelf (Rezak *et al.* 1985, as *Acryptolaria rectangularis*).

Genus *Lafoea* Lamouroux, 1821

Lafoea coalescens Allman, 1877

Fig. 6e

Lafoea coalescens Allman, 1877: 13, pl. 10, figs. 1, 2.—Fraser, 1943: 90.

Type locality. USA: Florida, south of the Marquesas Keys, 140 ftm (256 m) (Allman 1877: 13).

Material examined. Southwest Florida Shelf, inner shelf west of North Naples, 26°16.82’N, 82°44.02’W, 32.3 m, 19 July 1981, triangle dredge, one colony fragment, 2.7 cm high, without gonophores, coll. Continental Shelf Associates, ROMIZ B1914.—Southwest Florida Shelf, outer shelf northwest of the Dry Tortugas, 25°16.83’N, 83°57.35’W, 127 m, 03 August 1981, triangle dredge, several colony fragments, up to 3 cm high, without gonophores, coll. Continental Shelf Associates, ROMIZ B1915.

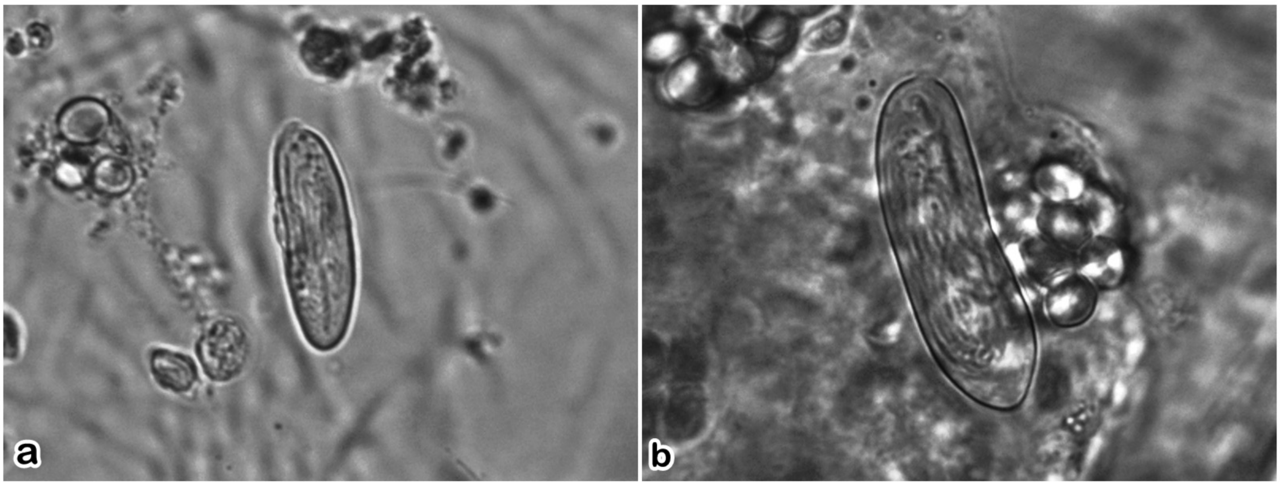

FIGURE 7. ***Acryptolaria* spp.:** large nematocysts (macrobasic mastigophores?). **a,** ***A. longitheca*:** ROMIZ B1902. **b,** ***A. tortugasensis*:** ROMIZ B1906.

Remarks. *Lafoea coalescens* Allman, 1877 is morphologically distinctive amongst its congeners. Its hydrothecae are quite unusual in having flared margins and symmetrical or nearly symmetrical walls, and its pedicels exist in two forms. They may be either straight, long, free from hydrocaulus and branches, and annulated basally, or curved, relatively short, partly adnate to hydrocaulus and branches, and smooth throughout. An infrequently reported species, records nevertheless suggest that it is widely distributed. After being originally described from the Marquesas Keys, Florida, hydroids of the species have been reported from Bermuda (Calder 1990 [1991a]), Bowditch Seamount near Bermuda (Calder 2000), the Blake Plateau (Henry *et al.* 2008), and the Almirante Saldanha Seamount (22.38°S, 37.58°W) off Brazil (Miranda *et al*. 2015). *Lafoea coalescens* also appears to have a wide bathymetric range, having been reported at depths from 32 m (this study) to 1285–1381 m (Calder 2000). It may be a predominantly bathyal species that penetrates into neritic waters.

A more detailed account of the species is given elsewhere (Calder 1990 [1991a]). The gonosome has yet to be described.

Reported distribution. ***Gulf coast of Florida.*** South of the Marquesas (Allman 1877: 13; Fraser 1943: 90; 1944: 221).

Elsewhere in western North Atlantic. Bermuda: 2 km SE of Castle Roads, 60–90 m, on calcareous rubble (Calder 1990 [1991a]: 37).—Bowditch Seamount, NNE of Bermuda, 32°44'N, 64°32.8'W, 1285–1381 m, on coral rubble (Calder 2000: 1134).—USA: Blake Plateau off Cape Canaveral, Florida, 28.7931, -79.6214, 737 m, 6.7° C, on dead corals (Henry *et al.* 2008: 791).

Family Syntheciidae Marktanner-Turneretscher, 1890

Genus *Synthecium* Allman, 1872

Synthecium tubithecum (Allman, 1877)

Fig. 6f

Sertularia tubitheca Allman, 1877: 24, pl. 16, figs. 5, 6.
Synthecium tubithecum.—Nutting, 1904: 134.—Leloup, 1935a: 33.—Fraser, 1943: 91.
Synthecium nanum Fraser, 1943: 80, 91, pl. 18, fig. 10.

Type locality. USA: Florida, Dry Tortugas, 16 ftm (29 m) (Allman 1877: 24).

Material examined. Southwest Florida Shelf, middle shelf west of North Naples, 26°16.83'N, 83°23.81'W, 59.5 m, 19 July 1981, triangle dredge, one colony fragment, 6 mm high, without gonophores, coll. Continental Shelf Associates, ROMIZ B1929.

Remarks. Originally described by Allman (1877) from material collected near the Dry Tortugas, Florida, *Synthecium tubithecum* has been reported several times since then from the Southwest Florida Shelf (Nutting 1904; Leloup 1935a, Fraser 1943; this study). An essentially tropical species with a wide distribution in the Caribbean Sea, its known geographic range extends as far north as the Carolinas (Wenner *et al*. 1984) and Bermuda (Calder 1990 [1991a]), and as far south as Brazil (Oliveira *et al*. 2016). While the reported bathymetric range of *S. tubithecum* is wide (1–505 m; see below), it is regarded here as a typically neritic species found most often at depths of less than 100 m (Fraser 1944; Vervoort 1968; Reported Distribution section below).

A taxonomic and nomenclatural account of this hydroid has been provided elsewhere (Calder 1990 [1991a]). Its cnidome, comprising small microbasic mastigophores (6.3–6.6 long × 1.8–2.0 μm wide) and large (?) macrobasic mastigophores (40.0–42.5 long × 10.7–11.5 μm wide), has been described by Galea (2010).

Reported distribution. ***Gulf coast of Florida.*** Dry Tortugas, 16 ftm (29 m) (Allman 1877: 24, as *Sertularia tubitheca*).—W of Gasparilla Island, 26°47'30"N, 83°25'15"W, 28 ftm (48 m) (Nutting 1904: 135).—SW Florida Shelf, 26°N, 82°57'30"W, 24 ftm (44 m) (Nutting 1904: 135).—N of the Dry Tortugas, 25°04'30"N, 82°59'15"W, 26 ftm (48 m) (Nutting 1904: 135).—Dry Tortugas (Leloup 1935a: 33).—West of Florida, 20 ftm (37 m) (Fraser 1943: 91).—W of the Dry Tortugas, 24°36'40"N, 83°02'20"W, 16 ftm (29 m) (Fraser 1943: 91, as *Synthecium nanum*).

Elsewhere in western North Atlantic. Barbados: 76 ftm (139 m) (Fewkes 1881a: 128, as *Sertularia tubitheca*).—Cuba: off Morro Castle, 100–250 ftm (183–457 m) (Nutting 1895: 88, as *Sertularia tubitheca*).—Anguilla: 70–200 ftm (128–366 m) (Jäderholm 1903: 291).—USA: South Carolina, E of Bulls Bay, 32°55'N, 77°54'W, 79 ftm (144 m) (Nutting 1904: 135).—Cuba: off Havana, 23°10'31"N, 82°19'55"W, 114 ftm (208 m) (Nutting 1904: 135).—Cuba, near Havana, (Nutting 1904: 135, as *Synthecium rectum*).—USA: Georgia, continental slope, 31°26'N, 77°07'W, 276 ftm (505 m) (Nutting 1904: 135, as *Synthecium rectum*).—Barbados (Nutting 1919: 115, as *Synthecium tubulifera*).—Puerto Rico: off north coast, 18°31'N, 66°10'15"W, 38 ftm (69 m) + 18°30'N, 66°12'20"W, 46–56 ftm (84–102 m) + 18°30'30"N, 66°23'05"W, 40 ftm (73 m) + off west coast, 18°14'30"N, 67°25'30"W, 20–40 ftm (37–73 m) (Fraser 1944: 237).—USA: Georgia, mid-continental shelf E of Savannah, 32°03'N, 79°49'30"W, 14 ftm (26 m) (Fraser 1945: 21).—Colombia: 2 miles (3 km) SW of Cabo de la Vela, 21–22 ftm (38–40 m) (Fraser 1947b: 10, as *Synthecium* (?) *nanum*).—Virgin Islands of the United States: St. Thomas, Sound + Savannah Passage (Vervoort 1968: 30, as *Synthecium tubitheca*).—Colombia: off Santa Marta (Wedler 1975: 332).—USA: South Carolina and Georgia, inner to outer continental shelf (Wenner *et al*. 1983: 181; 1984: 21, 40, as *Synthecium tubitheca*).—Colombia: vicinity of Bahía de Cartagena (Flórez González 1983: 123).—Bermuda: 2 km SE of Castle Roads, 60–90 m + Castle Grotto, Castle Harbour, 1 m (Calder 1990 [1991a]: 84).—Cuba: north coast (Ortiz Rosado 2000: 88).—Bermuda: Challenger Bank + Argus (=Plantagenet) Bank (Calder 2000:1133).—Panama: Bocas del Toro area, Cayos Zapotilla, 09°15.564'N, 82°02.750'W, 7-8 m (Calder & Kirkendale 2005: 484).—French Lesser Antilles: Guadeloupe, Grande-Terre, Grotte aux Barracudas, 16°27.343'N, 61°32.244'W, 21 m + Pointe Plate, 16°27.220'N, 61°32.128'W + Les Ancres, 16°27.002'N, 61°32.320'W, 15–18 m (Galea 2010: 23, 24).—Cuba: Golfo de Batabanó, Punta Francés, reef, 10 m (Castellanos-Iglesias *et al*. 2011: 23).—USA: Florida, east coast, 1.2 km off Palm Beach, 29 m (Calder 2013: 34).—French Lesser Antilles: Martinique (Galea 2013: 50).—Caribbean Sea (Wedler 2017b: 141, figs. 159–161).—Mexico: Alacranes Reef, on stony corals (Mendoza-Becerril *et al*. 2018b: 130).

Family Zygophylacidae Quelch, 1885

Genus *Zygophylax* Quelch, 1885

Zygophylax convallaria (Allman, 1877)

Figs. 6g–j

Lafoea convallaria Allman, 1877: 12, pl. 9, figs. 1, 2.—Clarke, 1879: 243, pl. 4, fig. 23.

Type locality. USA: Florida, off Florida Reef, 152 ftm (278 m) (Allman 1877: 12).

Material examined. Southwest Florida Shelf, outer shelf northwest of the Dry Tortugas, 25°44.84'N, 84°21.03'W, 159 m, 26 July 1981, triangle dredge, one colony fragment, 2.8 cm high, without gonophores, coll. Continental Shelf Associates, ROMIZ B1920.—Southwest Florida Shelf, outer shelf northwest of the Dry Tortugas, 25°16.50'N, 84°14.77'W, 159 m, 02 August 1981, triangle dredge, three colony fragments, up to 3.1 cm high, one fragment with gonophores, coll. Continental Shelf Associates, ROMIZ B1921.

Remarks. Both the trophosome and gonosome of *Zygophylax convallaria* (Allman, 1877) have been thoroughly described by Vervoort (1972) based on specimens from the continental slope off Georgia, USA. He correctly noted that Fraser's (1944) account of the species, in a book on hydroids of the Atlantic coast, was based on specimens of *Z. cervicornis* (Nutting, 1905) from Hawaii. The two, considered conspecific by Fraser, are now considered distinct (Rees & Vervoort 1987; Vervoort & Watson 2003; Schuchert 2015). Most notably, differences exist in the morphology of their gonosomes, with gonothecae of *Z. convallaria* having long horizontal necks and being protected by few tubules, and those of *Z. cervicornis* usually lacking gonothecal necks but having numerous protective tubules (Schuchert 2015).

Zygophylax convallaria is a deep-sea species, having been reported largely from bathyal bottoms. As apparent from present material, however, it also ranges upwards into the lower neritic zone. The known bathymetric range on this coast is from 139 m (Fewkes, 1881a) to 748 m (Henry *et al*. 2008). Geographically, it has been reported in the western Atlantic from North Carolina (Henry *et al*. 2008) to the southern Caribbean Sea (Fewkes 1881a). Although recorded from the Pacific Ocean as well (e.g., Hirohito 1995; Stepanjants 2013), confirmation of its occurrence there seems warranted.

Henry *et al*. (2008) considered *Z. convallaria* to be a "characteristic species" of deep-water coral habitats off the southeastern United States. The species was collected at more than half of the stations they occupied, all located in slope waters between Cape Lookout, North Carolina, and Cape Canaveral, Florida. Colonies were found on live and dead coral, as well as other invertebrates. Fertile specimens were observed in that area during October and November.

Nomenclaturally, the specific name *convallaria* is a noun in apposition, and its ending need not be changed to agree in gender with any generic name with which it is combined.

Classification of the family Zygophylacidae Quelch, 1885 is unsettled (Maronna *et al*. 2016), with few species having been included in molecular analyses to date. The taxon has therefore been included here in the suborder Lafoeida Bouillon, 1984, following many traditional taxonomic accounts.

Reported distribution. *Gulf coast of Florida.* Off the Florida Reef, 152 ftm (278 m) (Allman 1877: 12, as *Lafoea convallaria*).—SW Florida shelf, outer shelf NW of Dry Tortugas, 25°33'N, 84°21'W, 101 ftm (185 m) (Clarke 1879: 243, as *Lafoea convallaria*).

Elsewhere in western North Atlantic. Cuba: off Havana, 160–177 ftm (293–324 m) (Clarke 1879: 243, as *Lafoea convallaria*); 23°09'N, 81°27'30"W, off Matanzas, 190 ftm (347 m) Fraser 1943: 91, as *Lictorella convallaria*).—Barbados: 76 ftm (139 m) + 94 ftm (172 m) (Fewkes 1881a: 128, as *Lafoea convallaria*); 13°03'50"N, 59°37'05"W, 94 fathoms (172 m) (Fraser 1943: 91, as *Lictorella convallaria*).—French Lesser Antilles: Martinique, 76 ftm (139 m) (Fewkes 1881a: 128, as *Lafoea convallaria*).—French Lesser Antilles: Guadeloupe, 150 ftm (274 m) (Fewkes 1881a: 128, as *Lafoea convallaria*).—USA: continental slope east of Georgia, 31°54'N, 79°05'W, 413 m (Vervoort 1972: 74).—USA: Texas, banks on the continental shelf (Rezak *et al*. 1985: 224).—Cuba: north coast (Ortiz Rosado 2000: 88, as *Lictorella convallaria*).—USA: North Carolina, continental slope SE of Cape Lookout, 34.1876, -75.8966, 389 m + 34.3232, -75.7923, 369 m (Henry *et al.* 2008: 790, as *Zygophylax convallarius*).—USA: South Carolina, Stetson Banks on continental slope E of Hilton Head Island, 32.2689, -77.4746, 582 m (Henry *et al.* 2008: 790, as *Zygophylax convallarius*).—USA: Georgia, Savannah Banks on continental slope E of St. Catherines Sound, 31.7042, -79.1233, 551 m (Henry *et al.* 2008: 790, as *Zygophylax convallarius*).—USA: Florida, Jacksonville lithoherms on continental slope E of Jacksonville, 30.5168, -79.6618, 548 m + 30.5016, -79.6531, 593 m + 30.8008, -79.6420, 538 m + 30.5191, -79.6597, 585 m + 30.5186, -79.6603, 590 m (Henry *et al.* 2008: 791, as *Zygophylax convallarius*).—USA: Florida, off Cape Canaveral, 28.7771, -79.6161, 748 m + 28.0393, -79.6130, 686 m (Henry *et al.* 2008: 791, as *Zygophylax convallarius*).

Family Hebellidae Fraser, 1912b

Genus *Hebella* Allman, 1888

Hebella venusta (Allman, 1877)

Fig. 8a

Lafoea venusta Allman, 1877: 11, pl. 6, figs. 2, 3.—Ritchie, 1910: 816.—Fraser, 1943: 91.
Hebella venusta.—Leloup, 1935a: 15, fig. 5.

Type locality. USA: Florida, Loggerhead Key, 9 ftm (16 m) (Allman 1877: 12).

Material examined. Southwest Florida Shelf, middle shelf west of North Naples, 26°16.83"N, 83°23.81"W, 59.5 m, 19 July 1981, triangle dredge, on *Synthecium tubithecum*, one colony with two hydrothecae, 0.6 mm high, without gonophores, coll. Continental Shelf Associates, ROMIZ B1929.

Remarks. *Hebella venusta*, originally described by Allman (1877) from Loggerhead Key in the Dry Tortugas, southwest Florida, is widely distributed in tropical and subtropical regions of the western Atlantic. It ranges there from North Carolina (Cain 1972) to the southern Caribbean Sea (Leloup 1937) and has also been reported from Brazil (Oliveira *et al*. 2016). Although the validity of *H. venusta* was questioned by Boero *et al*. (1997), it has otherwise been recognized in multiple recent works (Ortiz Rosado 2000; Cairns *et al*. 2002; Calder & Cairns 2009; Galea 2010; Calder 2013, 2015; Oliveira *et al*. 2016; Wedler 2017b; Mendoza-Becerril *et al*. 2018b; Castellanos *et al*. 2018; WoRMS). Characters distinguishing it from several related species worldwide were summarized by Galea (2010). Hydrothecae of the species are distinctive, and striking, in being deep and transversely annulated.

The life cycle of *H. venusta* remains unknown. A free medusa seems likely, but gonophores have yet to be described. Empty gonothecae of the species were discovered and illustrated by Galea (2010) in specimens from Guadeloupe, in the Caribbean Sea.

Reported distribution. ***Gulf coast of Florida.*** Off Loggerhead Key, 9 ftm (16 m) (Allman 1877: 12, as *Lafoea venusta*).—West Florida, 20 ftm (37 m) (Ritchie 1910: 816, as *Lafoea venusta*).—Dry Tortugas (Leloup 1935a: 16).—West coast of Florida off North Naples, 26°16'10"N, 82°25'40"W, 20 ftm (37 m) (Fraser 1943: 91, as *Lafoea venusta*).

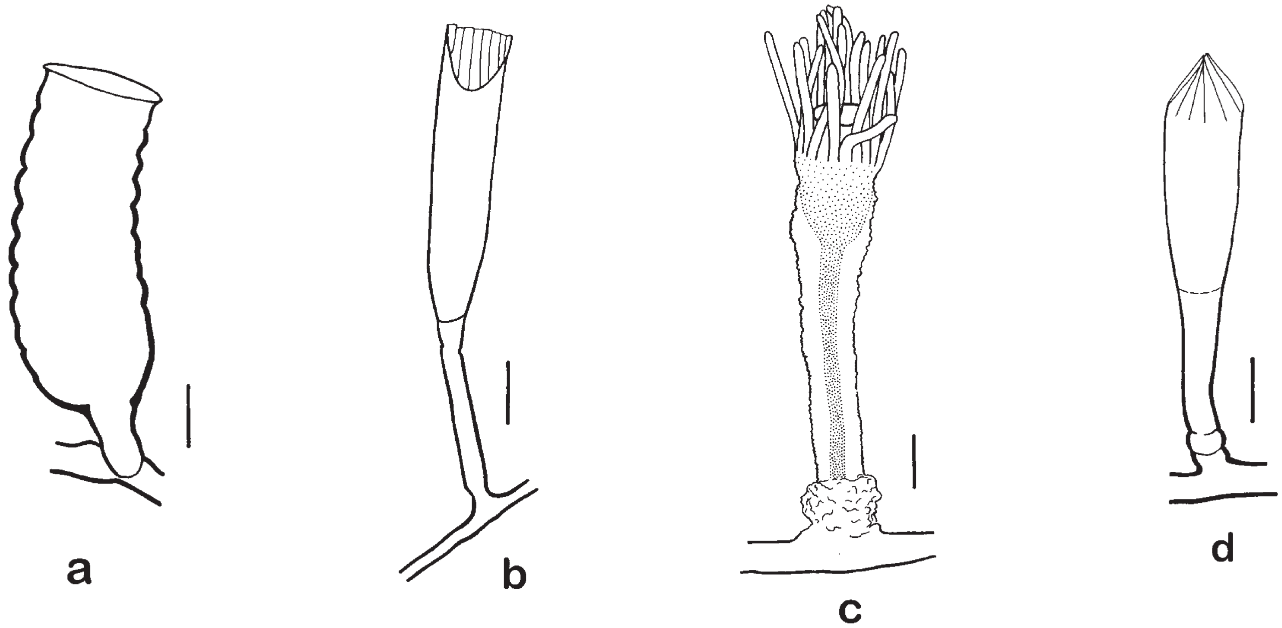

FIGURE 8. a, *Hebella venusta*: hydrotheca, pedicel, and stolon, Southwest Florida Shelf, ROMIZ B1929. Scale equals 0.1 mm. **b, *Modeeria rotunda***: hydrotheca, pedicel, and stolon, Southwest Florida Shelf, ROMIZ B4350. Scale equals 0.2 mm. **c, *Eutima* sp.:** hydranth and stolon, Sanibel Island, ROMIZ B4349. Scale equals 0.1 mm. **d,** Genus and species indeterminate: hydrotheca, pedicel, and stolon, Southwest Florida Shelf, ROMIZ B4355. Scale equals 0.1 mm.

Elsewhere in western North Atlantic. Mexico: off Zoblos Island (=Isla Holbox) (Clarke 1879: 243, as *Lafoea venusta*).—Cuba: off Morro Castle, 100–250 ftm (183–457 m) (Nutting 1895: 88, as *Lafoea venusta*).—Anguilla: 100–150 ftm (183–274 m) (Jäderholm 1903: 274, as *Lafoea venusta*).—Bermuda: Challenger Bank, 30 ftm (55 m) (Ritchie 1909: 261; Calder 1990 [1991a]: 41; Boero *et al*. 1997: 39).—West Indies, unspecified location (Stechow 1921b: 227, as *Hebella westindica*).—Venezuela: off Isla Tortugilla, 8–12 ftm (15–22 m) (Leloup 1937: 97).—Bahamas: Orange Key, 9 ftm (16 m) (Fraser 1943: 91, as *Lafoea venusta*).—Trinidad: Maguaripe Bay (=Macqueripe Bay) (Fraser 1943: 91, as *Lafoea venusta*).—Unstated location: on buoys (Woods Hole Oceanographic Institution 1952: 187, as *Lafoea venusta*).—Virgin Islands of the United States: St. Thomas, Sound, on *Thyroscyphus ramosus* (Vervoort 1968: 26; Boero *et al*. 1997: 40).—USA: North Carolina, *Lithothamnion* reef S of Cape Lookout (Cain 1972: 80).—Belize: Carrie Bow Cay, 23 m (Spracklin 1982: 246).—Colombia: Isla de Tierra Bomba <5 m (Flórez González 1983: 123).—USA: South Carolina, inner (17–18 m), middle (32–36 m), and outer (46–69 m) continental shelf + Georgia, inner (17–22 m), middle (23–29 m) and outer (59–67 m) continental shelf (Wenner *et al*. 1983: 151; 1984: 21, 40).—Cuba: north coast (Ortiz Rosado 2000: 88).—French Lesser Antilles: Guadeloupe (Galea 2010: 13).—French Lesser Antilles: Martinique (Galea 2010: 49).—Cuba: Golfo de Batabanó (Castellanos-Iglesias *et al*. 2011: 20).—USA: Florida, Bethel Shoal off Vero Beach, 27°42.6'N, 80°06.8'W, 24 m (Calder 2013: 17).—Caribbean Sea (Wedler 2017b: 115, fig. 112).—Mexico: Alacranes Reef, on seagrass (Mendoza-Becerril *et al*. 2018b: 129, as *Hebella* cf. *venusta*).—Cuba: Havana, coral reef system west of the city (Castellanos *et al*. 2018: Supplementary Table S2).

Suborder Laodiceida Maronna, Miranda, Peña Cantero, Barbeitos & Marques, 2016

Family Tiarannidae Russell, 1940

Genus *Modeeria* Forbes, 1848

Modeeria rotunda (Quoy & Gaimard, 1827)

Fig. 8b

Dianaea rotunda Quoy & Gaimard, 1827: 181, pl. 6A, figs. 1, 2 [medusa stage].
Stegopoma fastigiatum.—Leloup, 1935a: 12.
Stegopoma fastigiata.—Fraser, 1944: 178.

Type locality. Mediterranean Sea, at the Strait of Gibraltar (Quoy & Gaimard 1827: 182).

Material examined. Southwest Florida Shelf, middle shelf west of North Naples, 26°16.72'N, 83°46.82'W, 83 m, 24 July 1981, otter trawl, on *Acryptolaria longitheca*, three colony fragments, up to 3 mm high, without gonophores, coll. Continental Shelf Associates, ROMIZ B4350.

Remarks. The hydroid *Stegopoma fastigiatum* (Alder, 1860), reported earlier from southwest Florida by Leloup (1935a) and Fraser (1944), has been linked to the medusa *Modeeria rotunda* (Quoy & Gaimard, 1827) in life cycle studies (Edwards 1973). The latter name has nomenclatural priority. Hydrothecae of the species resemble those of *Stegopoma plicatile* in having a gable-shaped operculum (Cornelius 1995b), but colonies of *M. rotunda* are stolonal rather than erect with polysiphonic hydrocauli.

Both polyp and medusa stages of this species have been widely reported, mainly in deep waters, with a bathymetric range extending from the neritic zone to a depth of at least 677 ftm (1238 m) (Fraser 1944, as *Stegopoma fastigiata*; Kramp 1959, as *Tiaranna rotunda*; Cornelius 1995b).

Reported distribution. ***Gulf coast of Florida.*** S of the Dry Tortugas, 92–94 ftm (168–172 m), on a large spider crab (Leloup 1935a: 13, as *Stegopoma fastigiatum*; Fraser 1944: 179, as *Stegopoma fastigiata*).

Elsewhere in western North Atlantic. Canada: off NE tip of Georges Bank, 41°25'N, 65°42.3'W, 430 ftm (786 m) (Verrill 1873: 9, as *Calycella fastigiata*).—Greenland: Davis Strait (Levinsen 1893: 180, as *Stegopoma fastigiatum*).—USA: off Martha's Vineyard, 40°03'N, 70°31'W, 100 ftm (183 m), on *Halecium* (Fraser 1940: 578, 1944: 179, as *Stegopoma fastigiata*).—Canada: off Brown's Bank, 41°47'N, 65°37'30"W, 677 ftm (1238 m) (Fraser 1944: 179, as *Stegopoma fastigiata*).—USA: off Marthas Vineyard, 40°01'N, 68°54'W, 640 ftm (1170 m) + 39°58'N, 70°37'W, 115 ftm (210 m) + 39°54'N, 69°51'30"W, 134 ftm (245 m) + 39°34'N, 71°56'W, 374 ftm (584 m) (Fraser 1944: 179, as *Stegopoma fastigiata*).—USA: off North Carolina (Fraser 1944: 179, as *Stegopoma fastigiata*).—USA: South Carolina, middle shelf (32–36 m) (Wenner *et al*. 1984: 21).—USA: Georgia, outer continental shelf (59–67 m) (Wenner *et al*. 1984: 21, 40).—Greenland: west coast, 66.15°N, 56.12°W, 160-200 m (Schuchert 2001: 51).—USA: Louisiana, continental slope, 540–560 m, from vestimentiferan aggregrations on water cold seeps, on *Halecium* sp. (Bergquist *et al*. 2003: 205).—USA: Virginia, outer continental shelf, on shipwreck (Meyer *et al*. 2017: 20).

Suborder Statocysta Leclère, Schuchert, Cruaud, Couloux & Manuel, 2009

Infraorder Campanulinida Bouillon, 1984

Family Campanulinidae Hincks, 1868 [1869]

Genus *Eutima* McCrady, 1859

? *Eutima* sp.

Fig. 8c

Material examined. Sanibel Island, beach at Lighthouse Point, 26°26’57”N, 82°01’06”W, on detached *Thalassia* at water’s edge, 13 March 2018, 20° C, 33.5‰, one colony, 1 mm high, without gonophores, coll. D. Calder, ROMIZ B4349.

Remarks. The identity of this tiny hydroid is obscure. Gonophores were lacking in the colony observed here. A species closely matching its trophosome in morphology has been identified elsewhere (Calder 1971; Calder & Hester 1978) as “*Campanopsis*” sp. The generic name *Campanopsis*, applied by Claus (1881) to a hydroid subjectively linked to the medusa *Octorchis gegenbauri* Haeckel, 1864 (now *Eutima gegenbauri*), is a junior subjective synonym of both *Eutima* McCrady, 1859 and its junior synonym *Octorchis* Haeckel, 1864. The present hydroid, resembling that described by Claus, is provisionally assigned here to the genus *Eutima*.

Several species of medusae have been assigned to *Eutima* on the east coast of the United States (Kramp 1959, 1961), and the hydroid examined here may be the polyp stage of one of them. *Eutima mira* McCrady, 1859, originally described from Charleston Harbor, South Carolina, ranges from Massachusetts to Florida. *Eutima variabilis* McCrady, 1859, also first described from Charleston, has been reported from North Carolina to Florida. *Eutima coerulea* (L. Agassiz, 1862), with a type locality at Key West, is known from the Bahamas and Florida. *Eutima cuculata* Brooks, 1882, from Beaufort, North Carolina, is a *species inquirenda*. Meanwhile, hydroids identified as *Campanopsis* sp. have been reported in the western North Atlantic from southern Chesapeake Bay (Calder 1971) and South Carolina (Calder & Hester 1978). One of the medusa species listed above (*E. mira*) co-occurs with the hydroid *Campanopsis* sp. (=*Eutima* sp.) in the Chesapeake estuary (Calder 1971), but such evidence is insufficient to link the two. The taxonomy of this hydroid thus remains unresolved. The higher classification adopted above for it generally follows that outlined in a previous work (Calder 1990 [1991a]: 5, 6).

The hydroids reported here, from southwest Florida, were found on turtle grass (*Thalassia testudinum*). Specimens believed to be the same species, but reported as *Campanopsis* sp. by me (Calder 1971), were found on sponges (*Halichondria bowerbanki*), tubes of a polychaete (*Hydroides hexagona*), and oyster shells (*Crassostrea virginica*) in the southern Chesapeake Bay region, Virginia. In South Carolina, hydroids identified as *Campanopsis* sp. were reported from sponges (Calder & Hester 1978).

Reported distribution. ***Gulf coast of Florida.*** First record.

Elsewhere in western North Atlantic. USA: Virginia, Gloucester Point (Calder 1971: 67, as ?*Campanopsis* sp.).—USA: South Carolina, North Edisto River (Calder & Hester 1978: 91, as *Campanopsis* sp.).

Family Incertae Sedis

Genus and species indeterminate

Fig. 8d

Material examined. Southwest Florida Shelf, outer shelf northwest of the Dry Tortugas, 25°16.83'N, 83°57.35'W, 127 m, on *Lafoea coalescens*, 03 August 1981, triangle dredge, one pedicel and hydranth, 0.5 mm high, without gonophores, coll. Continental Shelf Associates, ROMIZ B4355.

Remarks. This material has been treated as unidentifiable in having a somewhat damaged hydrotheca, a single pedicel, a short length of stolon, and few distinguishing characters. *Eucuspidella pedunculata* Allman, 1877, originally described from a depth of 260 fathoms (475 m) off Tortugas, was considered but ruled out as a possibility. Hydrothecae of that species are fusiform rather than tapered towards the base, as in this hydroid, and hydranth pedicels are shown in the original account by Allman (1877) to be smooth throughout rather than being annulated at the base. While also resembling certain species of *Egmundella* Stechow, 1921b, no nematophores were observed as in that genus.

The operculum of this miniscule hydroid (0.5 mm high) was indistinctly demarcated from the hydrothecal rim. Crease lines at the intersection of the two structures were invisible in lateral view, although they were seen in apical view. Meanwhile, a thin line observed at the base of a hydranth remnant may have marked the location of a thin diaphragm. The specimen is illustrated (Fig. 8d) for possible future reference.

Family Lovenellidae Russell, 1953

Genus *Lovenella* Hincks, 1868 [1869]

Lovenella gracilis Clarke, 1882

Figs. 9a–g

Lovenella gracilis Clarke, 1882: 139, pl. 9, figs. 25–39.—Shier, 1965: 42 (in part).

not *Lovenella gracilis*.—Joyce, 1961: 61, pl. 14, figs. 2, 3.—Shier, 1965: 42 (in part), pl. 23 [=*Lovenella grandis* Nutting, 1901].

Type locality. USA: Chesapeake Bay, 3–10 ftm (5–18 m) (Clarke 1882: 135).

Material examined. Sanibel Island, beach at Lighthouse Point, on detached *Thalassia* in water along shore, 13 December 2017, one colony, 4 mm high, with gonothecae, coll. D. Calder, ROMIZ B4351.—Fort Myers Beach, on dead sand dollars (*Mellita quinquiesperforata*) near low water, 19 January 2018, several colony fragments, up to 5 mm high, without gonothecae, coll. D. Calder, ROMIZ B4352.—Sanibel Island, beach at Lighthouse Point, 26°26'55"N, 82°01'08"W, on detached *Syringodium* in water along shore, 21° C, 34.5‰, 19 March 2018, one colony, 3 mm high, without gonothecae, coll. D. Calder, ROMIZ B4353.

Non-Florida material examined. USA: Virginia, York River entrance off Ellen Island, 37°15'N, 76°25'W, 06 August 1966, several colonies, with gonophores, coll. D. Calder, ROMIZ B1548.—USA: South Carolina, Folly Beach, 18 November 1973, intertidal, on *Mulinia lateralis* and adhering barnacles, coll. D. Calder, ROMIZ B1551.—USA: New Jersey, Avalon, 01 September 2001, on *Donax*, coll. J. Dougherty, ROMIZ B3504.—USA: South Carolina, Bulls Bay, 32°55.9'N, 79°36.2'W, 5 m, 06 January 1976, coll. D. Calder, ROMIZ B1546 (*Lovenella* sp.).

Remarks. Clarke (1882) described both hydroid and young medusa stages of this species from the Chesapeake Bay region, USA. While assigning the binomen *Lovenella gracilis* to it, he expressed uncertainty about its relationships and systematic position. Such questions still need attention. Given its resemblance to *L. clausa* (Lovén, 1836) from northwest Europe, including habit of growth, turbinate hydrothecae, proboscis morphology, and number of tentacles and opercular facets, Clarke decided to refer his new species to *Lovenella* Hincks, 1868 [1869] rather than create a new genus for it. While recognizing certain similarities between it and *L. clausa*, he regarded the two as distinct. Clarke's illustrations show that his hydroids differ in having: (1) a hydrocaulus that is segmented beyond the base by single nodes into a series of cylindrical internodes rather than being annulated or wrinkled; (2) hydrothecae that are relatively shallow and funnel-shaped rather than deep and nearly cylindrical; (3) an operculum that is not distinctly demarcated from the hydrotheca. From accounts of the medusa stage of *L. clausa* by Hincks (1871) and Russell (1936a, as *Eucheilota hartlaubi*; 1936b, as *E. clausa*; 1953, as *L. clausa*), several differences are also immediately apparent between the planktonic stages of the two species: (1) gonads are developed at liberation in *L. gracilis*, but they do not appear until several days after release in *L. clausa*; (2)

interradial marginal cirri occur in *L. clausa* but not in *L. gracilis*; (3) the umbrella is oval in cross-section in *L. gracilis* but circular in *L. clausa*. The two species are clearly different.

In his original description of *L. gracilis*, Clarke (1882) did not specify in detail where his specimens were collected. Although his work was done in Chesapeake Bay, Clarke spent research time there at both Crisfield, Maryland, and Fort Wool, Virginia. The type locality is therefore listed here simply as Chesapeake Bay.

Fraser (1912a, b) erroneously reported the European *L. clausa* from the east coast of the United States, and included *L. gracilis* as its synonym. In examining specimens from Bogue Sound, North Carolina, parts of his description and two of his figures (Fraser 1912b, fig. 26B, 26C) were taken from accounts of *L. clausa* by Hincks (1868 [1869], 1871) and Hartlaub (1897). He later recognized that the two species were distinct (Fraser 1944: 174), acknowledged that his report of *L. clausa* from eastern North America was wrong, and stated that the European species had not been observed in the western Atlantic. Regrettably, descriptions and illustrations actually based on those Carolinian hydroids by Fraser (1912b: 364, fig. 26A, 1944: 174, pl. 31, fig. 147b) conform more closely with characters of *L. grandis* Nutting, 1901 rather than *L. gracilis*. Hydrothecae of his specimens were much deeper than those of *L. gracilis*, and his drawings show distinct crease lines separating the opercular facets from the hydrothecal margin. Fraser's record of the species from North Carolina is therefore assigned to *L. grandis* here. Specimens referred by Fraser (1912b) to *L. clausa* from Woods Hole, Massachusetts, were not illustrated and are of uncertain identity. Errors in characterization of *L. gracilis* in Fraser's publications lead to confusion about the species in subsequent works on hydroids of this coast. For example, Defenbaugh & Hopkins (1973) considered specimens much like and probably conspecific with *L. gracilis* from Texas to be a new species, while a clearly different one resembling *L. grandis* was misassigned to it. Specimens referred to *L. gracilis* from Seahorse Key, Florida, by Joyce (1961), and part of those from the Cape San Blas area, Florida, by Shier (1965), also appear to have been misidentified. From descriptions of the operculum by Shier ("There are eight opercular sections; the basal hinge of these sections is often indistinct"), however, both species may have been present in her collections. Ones with "indistinct hinges" were likely assigned correctly to *L. gracilis*. Identifications of the hydroid of *L. gracilis* should be based on the original description of Clarke (1882), or on later accounts of specimens from the same general locality (Calder 1971, this work), rather than on information in the guidebook of Fraser (1944). To further document the distinguishing characters of *L. gracilis*, topotypic specimens from southern Chesapeake Bay region (ROMIZ B1548) were examined during this study and are illustrated here (Figs. 9e, f).

Huvé (1952) compared the medusa stages of *L. gracilis* and *Dipleuron parvum* Brooks, 1882 from Beaufort, North Carolina, and concluded that they were identical. He thereupon applied the binomen *Dipleuron gracilis* to the species. His opinion that they were conspecific was shared by me (Calder 1971), although I retained the name *L. gracilis* for it. The specific name *gracilis* of Clarke (1882), published in January of that year, has priority over *parvum* of Brooks (1882), published in March. In two later works (Calder 1990 [1991a]: 3; Calder & Stephens 1997: 31), *Dipleuron* Brooks, 1882 was accepted as distinct from *Lovenella* based on characters such as the unusual morphology of the stems of the hydroid, being segmented by variably spaced nodes rather than annulated, and the lack of a crease at the base of the operculum. Pires-Miranda *et al*. (2013), in a study of specimens identified as *L. gracilis* from Brazil, upheld the synonymy of the two genera. Although unresolved issues remain in the taxonomy and nomenclature of this and other lovenellids, current usage of the binomen *L. gracilis* for the species has been maintained here, following Cairns *et al*. (1991, 2002).

A long-held belief that *Lovenella* is closely related to *Eucheilota* McCrady, 1859 (e.g., Russell 1953; Kramp 1961) is supported, at least in part, by preliminary molecular studies (Maronna *et al*. 2016). However, such results also suggest that both *Lovenella* and *Eucheilota* as presently constituted may be polyphyletic, and diagnoses of these genera likely need revision. Morphological and molecular studies of their type species (*L. clausa* and *Eucheilota ventricularis* McCrady, 1859), based on topotypic material, are needed. Critically, no hydroid has yet been linked to *E. ventricularis*, a major limitation in definitive characterization of *Eucheilota* and in overall understanding of both genera. Another taxonomic question needing resolution is whether populations of hydroids assigned to *L. gracilis* from the open coast, especially those attached to shells of the bivalve *Donax* and other substrates along sandy ocean shores, are conspecific with those from estuarine areas such as the tributaries of Chesapeake Bay.

The medusa known as *Dipleuron parvum* (=*L. gracilis*) has been assigned by some authors to the genus *Eucheilota*, and to the synonymy of *E. duodecimalis* L. Agassiz, 1862 (Mayer, 1910b, as *E. duodecimalis* var. *par-*

vum; Allwein 1967, as *E. duodecimalis*). However, life cycle studies (Calder 1971) have shown that the number of marginal vesicles in medusae of *L. gracilis* is indefinite, as currently stated in diagnoses of *Lovenella*, rather than fixed, as in *Eucheilota* (Russell 1953; Kramp 1961; Bouillon *et al.* 2006). For that reason, conclusions that the species is fully conspecific with or constitutes only a variety of *E. duodecimalis* has not been adopted here. Allwein (1967: 127) reported finding both *E. duodecimalis* and *E. duodecimalis* var. *parvum* (=*L. gracilis*) in the plankton at Beaufort, North Carolina.

A number of hydroids from other geographic regions resemble *L. gracilis*, particularly in the peculiar segmentation of the hydrocaulus. One of these, *Clytia bakeri* Torrey, 1904, was found on bivalves in the surf zone at Pacific Beach near San Diego, California. Its medusa stage, described by Torrey (1909) as *Phialium bakeri*, is much like that of *L. gracilis*. No operculum was noted in the original description of the hydroid by Torrey (1904), but the species cannot be assigned to *Clytia* Lamouroux, 1812 or any other campanularioid genus given the characters of its medusa stage. Hydrothecal margins were said to have been damaged, and Huvé (1952) and Calder (1971) speculated that opercula may have been lost in Torrey's material. The species was assigned to *Eucheilota* by Cairns *et al.* (1991), but returned to *Lovenella* by Cairns *et al.* (2002). It was discussed as *Eucheilota bakeri* in Mills *et al.* (2007). Molecular studies reveal a particularly close genetic relationship of the species to hydroids identified as *L. gracilis* (Maronna *et al.* 2016), and the two are almost certainly congeneric. Another hydroid resembling *L. gracilis* was described as *Gonothyraea (?) nodosa* by Stechow (1914) from Rio de Janeiro, Brazil. Pires-Miranda *et al.* (2013) were uncertain of its taxonomic status, but Oliveira *et al.* (2016) included it in the synonymy of *L. gracilis*. Meanwhile, *L. nodosa* Fraser, 1938a, originally described from Ecuador (Santa Elena Bay) and the Pacific coast of Mexico (off Morro de Petatlan, Tenacatita Point; Isabel Island; off Thurloe Point), differs from *L. gracilis* in having hydrocauli with fewer nodes and much deeper hydrothecae. *Lovenella corrugata* Thornely, 1908, from 20 fathoms (37 m) off Khor Shin'ab, along the Red Sea coast of Sudan, has a hydrocaulus with neither annulations nor nodes. Its hydrothecae are distinct in being relatively deep and cylindrical, with corrugated walls.

Several other species with hydroid stages currently or recently assigned to *Lovenella* differ from *L. gracilis* in having hydrocauli with annulations or sinuous constrictions rather than cylindrical internodes [*L. clausa* (Lovén, 1836) from NW Europe; *L. briggsi* Mulder & Trebilcock, 1915 from Australia; *L. rugosa* Fraser 1938b from the Pacific coast of Mexico; *L. chiquitita* Millard, 1957 from South Africa] or much deeper hydrothecae (*L. grandis* Nutting, 1901). Two species of hydroids until recently included in *Lovenella* by some authors are now assigned to other genera after their polyp and medusa stages were linked in DNA barcoding studies by Schuchert *et al.* (2017). Firstly, the hydroid *L. panicula* (G.O. Sars, 1874) and the medusa *Foersteria quadrata* Hosia & Pagès, 2007 were found to be stages of the same species. The name *Earleria quadrata* (Hosia & Pagès, 2007) was applied to the species by Schuchert *et al.*, but the binomen *Earleria panicula* (G.O. Sars, 1874) has nomenclatural priority. Secondly, the hydroid *Lovenella producta* (G.O. Sars, 1874) and the medusa *Cyclocanna welshi* Bigelow, 1918 were shown to be conspecific, with *Cyclocanna producta* becoming the valid name of the species. Hydroids of both species differ significantly from those of *L. gracilis* in the morphology of their hydrothecae and hydrocauli. The taxonomy of hydroid and medusa species that have been assigned to *Lovenella* has been updated in WoRMS, and the characters of most have been summarized in Pires-Miranda *et al.* (2013).

The reported range of *L. gracilis* in the western North Atlantic extends from southern New England (Calder 1975) to the southern Caribbean Sea (Wedler 1975; Bandel & Wedler 1987), and includes the Gulf of Mexico (Calder & Cairns 2009). It has also been identified as far south as Brazil in the western South Atlantic (Oliveira *et al.* 2016). Hydroids identified as *Lovenella gracilis* from the Caribbean Sea by Wedler (2017b) are shown with distinct crease lines at the base of the opercula, and his specimens appear more like *L. grandis* in that character. Their identity is regarded here as doubtful, bringing those reported by Wedler (1975) and Bandel & Wedler (1987) into question as well.

Fewkes (1891) included *L. gracilis* in a guide to invertebrates of New England. No collection data were provided on the species in that work, and it is unclear whether specimens were ever collected by him in the New England region or elsewhere. The account has been excluded from the distribution records below. *Lovenella gracilis* was reported from a depth of 16 fathoms (29 m) off Cape Hatteras by Fraser (1944), but the identification is considered questionable. To the south in South Carolina (Calder, unpublished), hydroids largely indistinguishable from *L. gracilis* were found in the lower intertidal zone of sandy beaches on bivalve molluscs (*Mulinia lateralis*) and adhering barnacles (ROMIZ B1551). Farther north, specimens of the species were found on coquina clams

(*Donax variabilis*) at Avalon, New Jersey (Fig. 9g). Other specimens (ROMIZ B1546) generally resembling the species, from Bulls Bay, South Carolina (32°55.9'N, 79°36.2'W), were unusual in being exceptionally large (up to 11 cm high) and profusely branched (Fig. 9h). The identity of the latter hydroids as a possible new species needs to be established. During studies of hydroids from the Chesapeake Bay region, the type locality of *L. gracilis*, colonies of the species were reported in shallow waters (1-6 m) from a variety of substrates including algae (*Agardhiella tenera*), eelgrass (*Zostera marina*), other hydroids (*Sertularia argentea*), oyster shells (*Crassostrea virginica*), and slipper shells (*Crepidula fornicata*) (Calder 1971). In southwest Florida during this investigation, specimens were found on turtle grass (*Thalassia testudinum*), manatee grass (*Syringodium filiforme*) and dead sand dollars (*Mellita quinquiesperforata*). Hydroids of the species were found active in the Chesapeake region from late April through late October over a temperature range of 15-27° C, and medusa production was observed from July through October. Interactions between hydroids identified as *L. gracilis* and bivalve molluscs, and especially coquina clams (*Donax*) on sandy beaches, have been explored in studies such as those of Manning and Lindquist (2003) and Dougherty & Russell (2005).

Reported distribution. *Gulf coast of Florida.* Cape San Blas area (Shier 1965: 42 (part)).

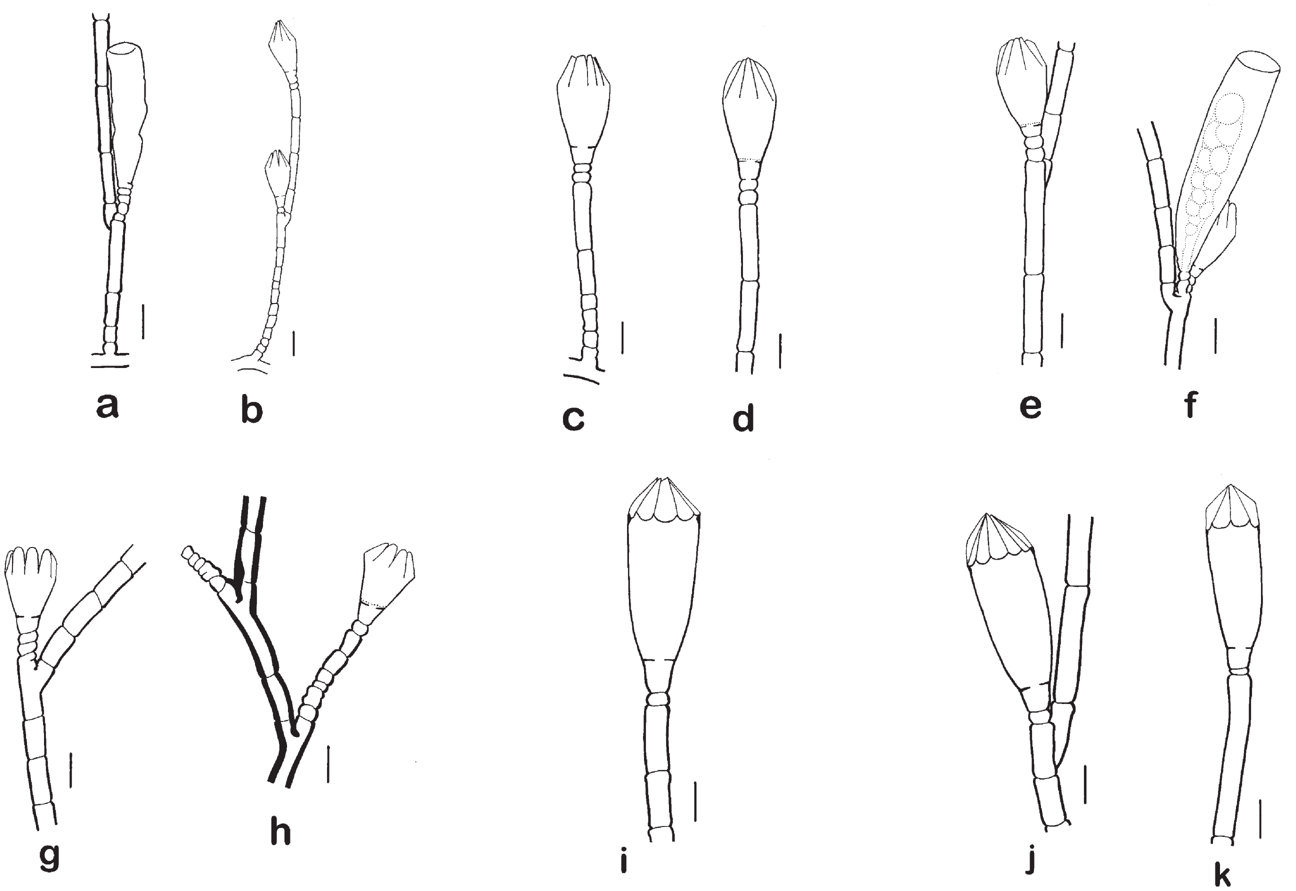

FIGURE 9. a, ***Lovenella gracilis*****:** part of colony with a gonotheca, Sanibel Island, ROMIZ B4351. Scale equals 0.2 mm. **b,** ***Lovenella gracilis*****:** colony with two hydrothecae, Sanibel Island, ROMIZ B4353. Scale equals 0.3 mm. **c,** ***Lovenella gracilis*****:** pedicel and hydrotheca, Sanibel Island, ROMIZ B4351. Scale equals 0.2 mm. **d,** ***Lovenella gracilis*****:** hydrotheca and part of pedicel, Fort Myers Beach, ROMIZ B4352. Scale equals 0.2 mm. **e,** ***Lovenella gracilis*****:** part of colony with a hydrotheca, York River, Virginia, USA, ROMIZ B1548. Scale equals 0.2 mm. **f,** ***Lovenella gracilis*****:** part of colony with a gonotheca, York River, Virginia, USA, ROMIZ B1548. Scale equals 0.2 mm. **g,** ***Lovenella gracilis*****:** part of colony with a hydrotheca, on *Donax,* New Jersey, USA, ROMIZ B3504. Scale equals 0.2 mm. **h,** ***Lovenella*** **sp.:** part of colony with a hydrotheca, Bulls Bay, South Carolina, USA, ROMIZ B1546. Scale equals 0.2 mm. **i,** ***Lovenella grandis*****:** hydrotheca and distal end of pedicel, Fort Myers Beach, ROMIZ B4354. Scale equals 0.2 mm. **j,** ***Lovenella grandis*****:** part of colony with a hydrotheca, Murrells Inlet, South Carolina, USA, ROMIZ B1549. Scale equals 0.2 mm. **k,** ***Lovenella grandis*****:** hydrotheca and distal end of pedicel, Nantucket Sound, Massachusetts, USA, ROMIZ B3500. Scale equals 0.2 mm.

Elsewhere in western North Atlantic. USA: Chesapeake Bay, 3–10 ftm (5–18 m) (Clarke 1882).—USA: North Carolina, Beaufort (medusa) (Brooks 1882: 140, as *Dipleuron parvum*).—USA: North Carolina, off Cape Fear (medusa) (Mayer 1910b: 284, as *Eucheilota duodecimalis* var. *parvum*).—?USA: Massachusetts, Woods Hole, surface tow (Fraser 1912a: 45, as *Lovenella clausa*).—USA: Mississippi, off Horn Island, on clam shell (Fincher 1955: 92).—USA: North Carolina, Beaufort area (medusa) (Allwein 1967: 127, as *Eucheilota duodecimalis* (part)).—USA: Virginia, York River (Ellen Island, Perrin, Gloucester Point, Page's Rock, Bell Rock) + James River (Hampton Flats) (Calder 1971: 62).—USA: Delaware, Indian River Bay (Watling & Maurer 1972: 648).—USA: Texas, off Galveston, 3–6 ftm (5–11 m) (Defenbaugh & Hopkins 1973: 92, as *Lovenella* new species).—USA: Massachusetts, Cape Cod Bay, off Provincetown + Jeremy Point, Wellfleet (Calder 1975: 298).—?Colombia: Santa Marta area, on gastropod shells, sandy substrates (Wedler 1975: 336; Bandel & Wedler 1987: 41).—USA: Delaware, Indian River (Maurer 1977: 597).—USA: South Carolina, exposed beaches (on shells of *Donax* and *Mulinia*) + higher salinity regions of estuaries (on shells of *Crassostrea*) (Calder & Hester 1978: 90, as (?) *Lovenella gracilis*).—USA: South Carolina, sandy beaches near Murrells Inlet, on *Donax* (Knott *et al*. 1983: 585).—USA: South Carolina, Huntington Beach (Fox & Ruppert 1985: 38).—USA: Georgia: St. Catherines Island, Engineer Point + Middle Beach + North Beach + Picnic Point + Seaside Delta (Prezant *et al*. 2002: 8).—USA: New Jersey, Seaside Park, sandy beach, on *Donax* (Manning & Lindquist 2003: 416).—USA: North Carolina, Pine Knoll Shores, sandy beaches, on *Donax* (Manning & Lindquist 2003: 416).—USA: New Jersey, sandy beaches, on *Donax*, Sea Isle City, 39°12.9'N, 74°70.7'W + Avalon, 39°07.3'N, 74°74.0'W + museum specimens: Atlantic City (from ~1886) + Wildwood (from 1900) + Sea Isle City (from 1901) + Avalon (from 1962) (Dougherty & Russell 2005: 35, 37).—USA: Delaware, on *Donax*, museum specimens Indian River Inlet (from 1965) (Dougherty & Russell 2005: 35, 37).—USA: New Jersey, Wildwood Crest (Govindarajan *et al*. 2006: 824).—?Caribbean Sea (Wedler 2017b: 119, figs. 114A–D).

Lovenella grandis Nutting, 1901

Figs. 9i–k

Lovenella grandis.—Nutting, 1901: 354, fig. 45.—Joyce, 1961: 59, pl. 13, figs 3, 4, pl. 14, fig. 1.—Shier, 1965: 44, pl. 24.
Lovenella gracilis.—Joyce, 1961: 59, pl. 14, figs. 2, 3.—Shier, 1965: 42, pl. 23 [not *Lovenella gracilis* Clarke, 1882].

Type locality. USA: Rhode Island, Newport Harbor, off Castle Hill (Nutting 1901: 354).

Material examined. Fort Myers Beach, on tests of dead sand dollars (*Mellita quinquiesperforata*), near low water, 19 January 2018, several colony fragments, up to 3 mm high, without gonothecae, coll. D. Calder, ROMIZ B4354.

Non-Florida material examined. USA: South Carolina, Murrells Inlet, inner channel, 22 May 1975, coll. D. Calder, ROMIZ B1549.—USA: Massachusetts, Nantucket Sound, E of Chop Light, 41°27.425'N, 70°31.591'W. 12 m, 15 October 2001, on shell, coll. D. Calder, ROMIZ B3500.

Remarks. *Lovenella grandis* Nutting, 1901, collected infrequently, is poorly known. Originally described from Rhode Island, the species has been reported thus far only from a few locations along the Atlantic and Gulf coasts of the United States. Its known geographic range extends from the Woods Hole region, Massachusetts (Hargitt 1908; Sumner *et al*. 2013), to central Florida (Calder 2013) along the east coast, and from southwest Florida (this study) to Texas (Defenbaugh & Hopkins 1973, as *Lovenella gracilis*) in the Gulf of Mexico. The hydroid has been found earlier on the Gulf coast of Florida (Joyce 1961; Shier 1965). If *Calycella gabriellae* Vannucci, 1951 is conspecific, the species extends into the Caribbean Sea (Wedler 2017b) and southwards to Brazil (Oliveira *et al*. 2016).

The distribution of *L. grandis* partly overlaps that of the related *L. gracilis* Clarke, 1882. As noted in the Remarks section on *L. gracilis* immediately above, trophosomes of the two are easy to distinguish. In *L. grandis*, hydrothecae are much deeper than those of its supposed congener, and a clearly-defined sinuous crease separates its operculum from the hydrothecal margin. Nevertheless, misidentifications in the influential publications of Fraser (1912b, 1944) have lead to confusion over characters of the two species. Details are summarized in remarks on *L. gracilis* and need not be repeated here.

Hydroids of *L. grandis* also resemble those of *L. clausa* (Lovén, 1836) from the eastern North Atlantic, but differ most obviously in having a hydrocaulus comprised of internodes that are divided into a series of cylindrical segments instead of being annulated to sinuous. Neither Nutting (1901a) nor Fraser (1941, 1944) mentioned or illustrated the segmented hydrocaulus of this species, much like that of *L. gracilis*. However, specimens examined during this study from South Carolina (Fig. 9j), Massachusetts (Fig. 9k), and the Atlantic coast of Florida, as well as those from southwest Florida reported here, all believed identical with *L. grandis*, exhibited this unusual character.

The life cycle of *L. grandis* has yet to be described in detail. Blastostyles of the gonosome produce medusa buds (Fraser 1941), but the hydroid has not yet been linked to a known medusa. In my report on hydroids from the Atlantic coast of Florida (Calder 2013), I stated in error that Nutting (1901) had described the gonosome, but he observed only the trophosome. The comments I quoted from Nutting were taken from his diagnosis of the genus *Lovenella* Hincks, 1868 [1869] and not from his description of the species.

Hydroids of *L. grandis* have been reported from various substrates including shells (Joyce 1961: 60; Shier 1965: 121; Calder 2013: 14), the tracheophyte *Syringodium* (Shier 1965: 119), tests of the sand dollar *Mellita quinquiesperforata* (Joyce 1961: 60; this study), and exoskeletons of the horseshoe crab *Limulus* (Shier 1965: 121). Joyce (1961) reported that almost every dead test of *M. quinquiesperforata* examined by him from the Seahorse Key area of Florida had colonies of the species. Hydroids identified as *L. gracilis* by Defenbaugh & Hopkins (1973), but believed here to have been *L. grandis*, were reported from shells of gastropods and bivalves, and from shell fragments. Specimens of *L. grandis* have been found on the Florida Gulf coast during summer (Joyce 1961: July, August), autumn (Shier 1965: September–December), winter (this study: January), and spring (Shier 1961: April, May).

Reported distribution. *Gulf coast of Florida.* Seahorse Key (Joyce 1961: 59).—Seahorse Key (Joyce 1961: 61, as *Lovenella gracilis*).—Cape San Blas area (Shier 1965: 42 (part), as *Lovenella gracilis*).—Cape San Blas area (Shier 1965: 44).

Elsewhere in western North Atlantic. USA: Rhode Island, Newport Harbor, off Castle Hill (Nutting 1901: 354).—USA: Massachusetts, Woods Hole (Hargitt 1908: 112).—USA: North Carolina, Bogue Sound, 10 feet (3 m) (Fraser 1912b: 364, as *Lovenella clausa*).—USA: Massachusetts, Marthas Vineyard, Kopeecon Point, 6-7.5 ftm (11–14 m) (Sumner *et al.* 2013: 571).—USA: Rhode Island, Sakonnet River, near mouth, 10.5 ftm (19 m) (Fraser 1941: 83).—?USA: Rhode Island, off Newport (Fraser 1944: 174, as *Lovenella gracilis*).—?USA: North Carolina, off Cape Hatteras, 35°20'40"N, 75°18'40"W, 16 ftm (29 m) (Fraser 1944: 174, as *Lovenella gracilis*).—USA: Texas, Galveston Bay area (Defenbaugh 1972: 387).—?USA: Texas, off Galveston (Defenbaugh & Hopkins 1973: 94, as *Lovenella gracilis*).—USA: Texas, Galveston Island, off West Beach, 30 feet (9 m) (Defenbaugh & Hopkins 1973: 95).—USA: South Carolina, Murrells Inlet (Calder & Hester 1978: 90, as *Lovenella* sp.).—USA: Florida, off St. Lucie Inlet, 27°08.5'N, 80°01.6'W, 32 m (Calder 2013: 14).—USA: South Carolina, Murrells Inlet, Main Creek, 33°32'51"N, 79°01'27"W + 33°33'14"N, 79°01'20"W (Calder 2013: 14).—USA: Massachusetts, Nantucket Sound off Martha's Vineyard, east of East Chop Lighthouse, 41°27.425'N, 70°31.591'W, 12 m (Calder 2013: 14).—?Caribbean Sea: on *Thalassia*, 3–10 m (Wedler 2017b: 101, figs. 92A, B, as *Calycella gabriellae*).

Infraorder Proboscoida Broch, 1909 [1910]

Family Campanulariidae Johnston, 1837

Genus *Campanularia* Lamarck, 1816

Campanularia colombiana (Wedler, 1976)

Figs. 10a, b

Clytia sp. A.—Joyce, 1961: 51, pl. 9, figs. 3, 4, pl. 10, fig. 1.
Clytia species Joyce.—Shier, 1965: 37, pls. 19, 20.
Clytia colombiana Wedler, 1975: 332, 340, 352 (*nomen nudum*).
Clytia colombiana Wedler, 1976: 41, figs. 1a–c, 2a, b, pl. 1, a–d.

Type locality. Colombia: Santa Marta area (Wedler, 1976: 41, as *Clytia colombiana*).

Material examined. Sanibel Island, beach at Lighthouse Point, 26°26'57"N, 82°01'06"W, on detached *Thalassia* at water's edge, 13 March 2018, 20° C, 33.5‰, one colony, 1 mm high, with gonophores, coll. D. Calder, ROMIZ B4356.—Sanibel Island, beach at Lighthouse Point, 26°27'00"N, 82°01'01"W, on detached *Thalassia* at water's edge, 15 March 2018, two colonies or colony fragments, up to 3 mm high, with gonophores, coll. D. Calder, ROMIZ B4422 [initially preserved in 70% ethanol; later transferred to the same preservative].

Non-Florida material examined. SYNTYPE. Colombia: Santa Marta, Rodadero, 3-5 m, on seagrass, 24 February 1972, one colony, 2 mm high, without gonophores, coll. E. Wedler, SMF 3606 [slide].

Remarks. This hydroid was first recognized as an undescribed species in a master's thesis by Joyce (1961, as *Clytia* sp. A). His specimens, in collections from the Seahorse Key area on the Gulf coast of Florida, USA, were found on floating seagrass in April and August of 1960. Fertile colonies were present in both collections. Four years later the species was reported again, from the Cape San Blas area on the Florida Gulf coast, in a master's thesis by Shier (1965, as *Clytia* species Joyce). She found it on all three species of seagrasses in the region (*Thalassia testudinum*, *Halodule wrightii*, *Syringodium filiforme*). Specimens were collected by her every month of the year, with peaks of abundance in April and October. Hydroids with gonothecae were observed every month except June. Joyce and Shier neither published accounts of the species nor proposed a specific name for it.

The hydroid was subsequently described and named by Wedler (1976), as *Clytia colombiana*, based on material from the Santa Marta area on the Caribbean coast of Colombia. The binomen *C. colombiana* had been mentioned a year earlier in an ecological work by Wedler (1975), but as a *nomen nudum* (see ICZN Art. 13). No name-bearing types of the species were designated in the original description by Wedler (1976). One of his specimens (SMF 3606), examined here, is currently listed as the holotype in collections at the Senckenberg Forschungsinstitut und Naturmuseum. Under the code (ICZN Art. 72), however, it merely constitutes part of the syntype series. In not having examined the entire collection of the species at Senckenberg, no lectotype is designated here.

The generic identity of this hydroid is somewhat obscure, although its assignment to *Clytia* Lamouroux, 1812 is certain to be incorrect. In having thickened perisarc at the base of the hydrotheca instead of a true diaphragm, a subhydrothecal spherule at the distal end of the hydrothecal pedicel instead of a typical annulation, and fixed sporosacs rather than free and well-developed medusae, it conforms instead with genera such as *Campanularia* Lamarck, 1816 and *Orthopyxis* L. Agassiz, 1862. The latter two are morphologically close and sometimes considered identical (e.g., Millard 1975; Schuchert 2001), although molecular studies thus far uphold the distinction between them (Cunha *et al*. 2015, 2017; Maronna *et al*. 2016). While resembling *Orthopyxis* in having somewhat thickened hydrothecal walls, this hydroid appears closer to *Campanularia* in having fixed sporosacs rather than medusoids, and stolons that do not appear to anastomose. The binomen *Campanularia colombiana* is adopted for the species here. Bandel & Wedler (1987) had used the combination earlier, although with the specific name misspelled as *columbiana*. Morphological distinctions between *Campanularia* and *Orthopyxis* have been reviewed in works such as those of Calder (1991a), Cornelius (1995b), and Bouillon *et al*. (2006).

Wedler (1976) observed and described two morphotypes of *C. colombiana* in his original account of this species. Specimens of "Type I", from shallow waters (3–5 m) at Ensenada de Concha and Banco Pobea, Bahía de Santa Marta, differed from those of "Type II", from deeper depths (20 m) at Bahía de Gaira, in having hydrothecae that were much smaller and more shallow. Hydroids from southwest Florida examined here (ROMIZ B4356, ROMIZ B4422) corresponded in both shape and size with the "Type II" form. Those found and illustrated by Joyce (1961, as *Clytia* sp. A) and Shier (1965, as *Clytia* species Joyce) from other locations on the Gulf coast of Florida appear to resemble "Type I".

Fertile colonies of this little-known hydroid were collected during March 2018 from *Thalassia* at Sanibel Island, Florida. Gonophores were fixed sporosacs, with well-developed eggs observed inside the gonothecae.

Thus far, *C. colombiana* is known only from the Caribbean coast of Colombia and the Gulf coast of Florida, USA. With colonies that are tiny (<5 mm high) and superficially similar to certain other campanulariids and clytiids, the species is easy to overlook. Its distribution in the warm western North Atlantic is almost certainly much wider than currently reported.

Reported distribution. ***Gulf coast of Florida.*** Seahorse Key (Joyce 1961: 51, as *Clytia* sp. A).—Cape San Blas area (Shier 1965: 37, as *Clytia* species Joyce).

Elsewhere in western North Atlantic. Colombia: Santa Marta area (Wedler 1976: 42, as *Clytia colombiana*; Bandel & Wedler 1987: 41, as *Campanularia columbiana* (sic); Wedler 2017b: 88, figs. 77–79, as *Clytia colombiana*).

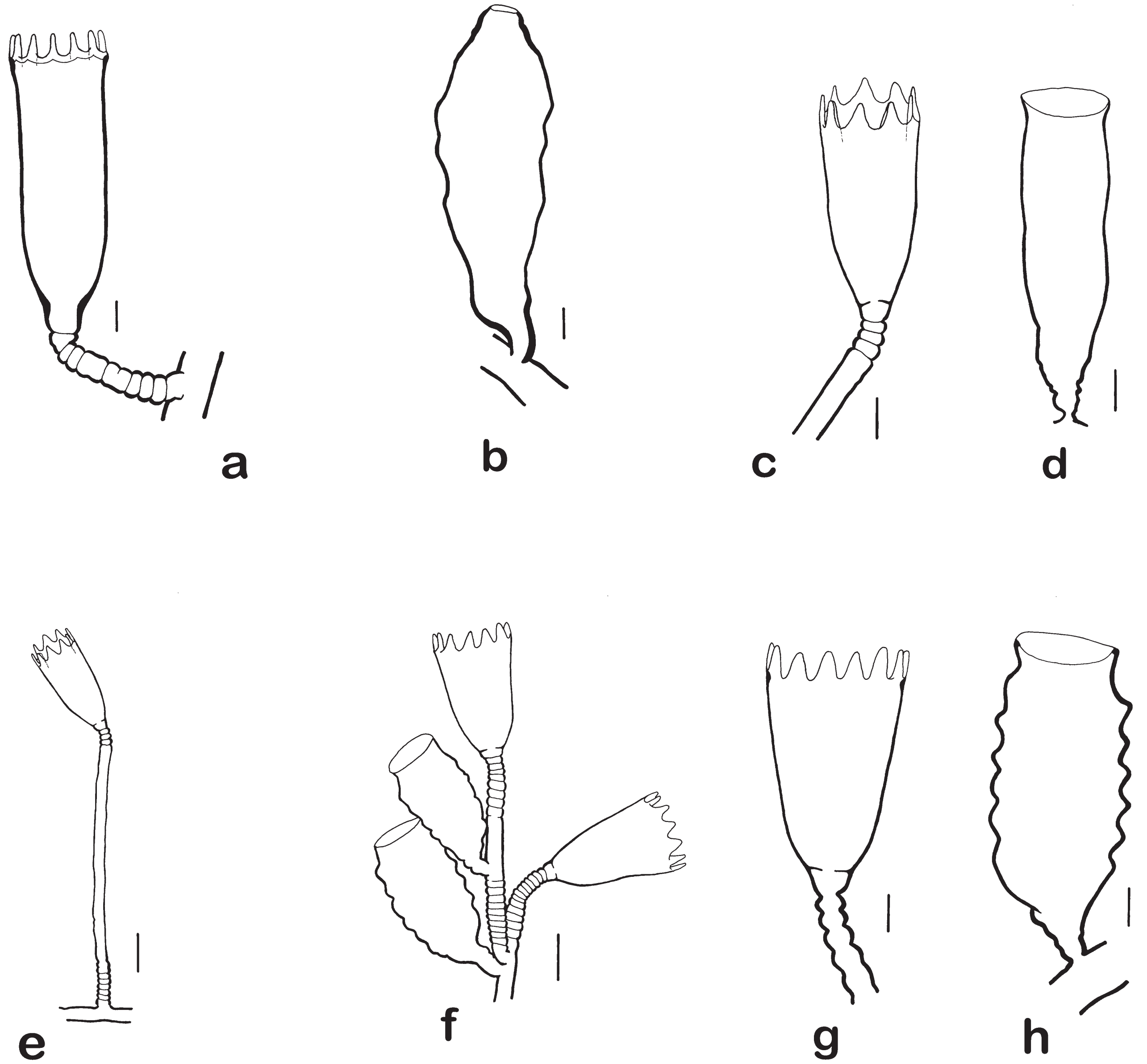

FIGURE 10. a, ***Campanularia colombiana*****:** hydrotheca, pedicel and stolon, Sanibel Island, ROMIZ B4356. Scale equals 0.1 mm. **b,** ***Campanularia colombiana*****:** gonotheca and stolon, Sanibel Island, ROMIZ B4356. Scale equals 0.1 mm. **c,** ***Clytia elsaeoswaldae*****:** hydrotheca and part of pedicel, Sanibel Island, ROMIZ B4369. Scale equals 0.1 mm. **d,** ***Clytia elsaeoswaldae*****:** gonotheca, Sanibel Island, ROMIZ B4369. Scale equals 0.1 mm. **e,** ***Clytia elsaeoswaldae*****:** pedicel and hydrotheca, Sanibel Island, ROMIZ B4369. Scale equals 0.2 mm. **f,** ***Clytia hemisphaerica*****:** part of colony with hydrothecae and gonothecae, Sanibel Island, ROMIZ B4371. Scale equals 0.2 mm. **g,** ***Clytia hemisphaerica*****:** hydrotheca and part of pedicel, Sanibel Island, ROMIZ B4372. Scale equals 0.1 mm. **h,** ***Clytia hemisphaerica*****:** gonotheca, Sanibel Island, ROMIZ B4372. Scale equals 0.1 mm.

Family Clytiidae Cockerell, 1911

Genus *Clytia* Lamouroux, 1812

Clytia elsaeoswaldae Stechow, 1914
Figs. 10c–e, 11

Clytia elsae-oswaldae Stechow, 1914: 125, fig. 4.

?*Clytia coronata*.—Nutting, 1915: 51 [part].
?*Clytia coronata*.—Fraser, 1944: 134 [part].
Gonothyraea gracilis.—Fraser, 1944: 148 [part] [not *Laomedea gracilis* M. Sars, 1850].
Clytia cylindrica.—Joyce, 1961: 53, pl. 10, fig. 4, pl. 11, figs. 1, 2.—Shier, 1965: 34, pls. 17, 20 [not *Clytia* (*Platypyxis*) *cylindrica* L. Agassiz, 1862].

Type locality. Virgin Islands of the United States: St. Thomas, port of Charlotte Amalie (Stechow 1914: 125, as *Clytia elsae-oswaldae*).

Material examined. Sanibel Island, beach at Lighthouse Point, 26°26'57"N, 82°01'07"W, on a detached alga, in intertidal pool, 03 August 2014, two colonies or colony fragments, to 4 mm high, with gonothecae, coll. D. Calder, ROMIZ B4369.—Sanibel Island, beach at Lighthouse Point, 26°26'55"N, 82°01'08"W, on detached *Syringodium* in water along shore, 21° C, 34.5‰, 19 March 2018, several young colonies, 1 cm high, without gonothecae, coll. D. Calder, ROMIZ B4370.—Fort Myers Beach, 26°27'55"N, 81°58'04"W, on stranded *Sargassum filipendula*, 05 February 2018, two colonies, up to 6 mm high, with gonophores, coll. D. Calder, ROMIZ B4409.

Remarks. Hydroids of the genus *Clytia* Lamouroux, 1812, as currently defined, are distinctive in overall colony form. However, identification of the various species is frequently a challenge. Given a preponderance of perfunctory original descriptions, a limited number of taxonomically useful morphological characters, and the likelihood of considerable intraspecific morphological variability, uncertainty and confusion exist about the identity and scope of several species. In view of the difficulties encountered by traditional taxonomists in dealing with this group, more molecular analyses are required to resolve the diversity, identities and relationships of clytiid species. Indeed, *Clytia* as presently constituted appears to be polyphyletic given the ambiguous placement of *C. hummelincki* (Leloup, 1935) and *C. paulensis* (Vanhöffen, 1910) in phylograms of Proboscoida Broch, 1909 [1910] (Cunha *et al*. 2017). Significant contributions to knowledge of *C. hemisphaerica* (Linnaeus, 1767), *C. gracilis* (M. Sars, 1850), *C. noliformis* (McCrady, 1859), and *C. elsaeoswaldae* Stechow, 1914, all of which occur along the east coast of the United States, have recently been made in papers such as those of Lindner and Migotto (2001, 2002), Lindner *et al*. (2011), and Cunha *et al*. (2017).

Hydroids of *C. elsaeoswaldae* are much like those of the boreal *C. gracilis* in morphology, and the two were considered conspecific for much of the 20th century. In some works (e.g., Cornelius 1982), both were included in the synonymy of *C. hemisphaerica*, but recent molecular studies reveal that the three are distinct genetically (Lindner *et al*. 2011; Cunha *et al.* 2017). According to Lindner *et al*., characters distinguishing *C. elsaeoswaldae* from *C. gracilis* include: (1) colonies are stolonal or mostly so rather than being branched, and (2) gonothecae arise from the hydrorhiza rather than from the branches. Morphological differences said to exist between *C. elsaeoswaldae* and *C. hemisphaerica* are summarized under the latter species below. Meanwhile, phylogenetic analyses by Lindner *et al*. and Cunha *et al*. indicate that the *C. gracilis* morphotype comprises several cryptic species.

Establishing the identities of several morphologically similar species of *Clytia* reported in 19th and 20th century literature of the Americas remains nearly unfathomable. Particular difficulties were encountered during this study in sorting out records that apply to *C. elsaeoswaldae* and *C. hemisphaerica*, both of which are reported here, and those that were based on specimens of the cool-temperate *C. gracilis*. Records in the Reported Distribution section below have been based for the most part on current ideas concerning synonymies of species, with consideration given also to probable biogeographic affinities of the species. Reports most likely to be sound are those in which gonothecae of specimens were described and illustrated. While most accounts of the cool-temperate *C. gracilis* (also reported as *C. cylindrica* and *Gonothyraea gracilis*) from the tropical and warm-temperate western North Atlantic are likely based on the warm water *C. elsaeoswaldae*, those from pelagic *Sargassum* are here included under *C. hemisphaerica* unless gonothecae with smooth walls were described. The latter species is frequent on gulfweed in the western North Atlantic (Rackley 1974; Calder 1995) while *C. elsaeoswaldae* is much less so. Records of *C. gracilis* to the north of Cape Hatteras are taken to have been correctly assigned to that species (or that species complex), and have been excluded from the list below on *C. elsaeoswaldae*. A few records of *C. coronata* Clark, 1879 from the warm western Atlantic have been included under *C. hemisphaerica*, following synonymy adopted in earlier work (Calder 1990 [1991a]: 60). However, Fraser's (1912b, 1944, 1946 [1947a]) concept of *C. coronata* more closely corresponds with that of *C. elsaeoswaldae*, especially in having gonothecae with smooth walls. His records of *C. coronata*, and those of several North American authors (e.g., Deevey 1950; Fincher 1955; Defenbaugh & Hopkins 1973) following him, remain highly uncertain. As records are interpreted here, *C. elsaeoswaldae* is believed to have a range in coastal waters from North Carolina to the southern Caribbean Sea, including Bermuda and the Gulf of Mexico, and southwards to Brazil in the western South Atlantic (Lindner *et al*. 2011).

The name of this species was originally founded by Stechow (1914) as *Clytia elsae-oswaldae*. Following the code (ICZN Art. 32.5.2.3), the specific name has been corrected in earlier work (Vervoort 1968: 15) to *elsaeoswaldae*. As noted below under *C. hemisphaerica*, *Thaumantias elsaeoswaldae* Stechow, 1914 was described as a different species, although it too is now assigned to *Clytia*. Of the two homonymous names, *C. elsaeoswaldae* Stechow, 1914 and *C. elsaeoswaldae* (Stechow, 1914), precedence was assigned to the former under the Principle of the First Reviser (ICZN Art. 24.2) because gonothecae were present in its type material, and the species has been recognized as valid a number of times (Calder 1990 [1991a]).

Two distinctly different categories of nematocysts were observed in hydroids of this species, with the larger of the two appearing to occur in two somewhat different forms (Fig. 11). They appear to correspond with A-type b-mastigophores (5.5–6.4 µm long x 1.2–1.5 µm wide, undischarged, n=10, ROMIZ B4369) and B-type b-mastigophores (7.0–8.0 long x 1.6–2.2 µm wide, undischarged, n=10, ROMIZ B4369).

The medusa stage of *C. elsaeoswaldae* has been described in life cycle studies by Lindner & Migotto (2011).

Reported distribution. *Gulf coast of Florida.* ?Cape Romano (as Cape Romanos) (Nutting 1915: 52, as *Campanularia coronata*).—?Cape Romano (Fraser 1944: 134, as *Clytia coronata*).—?West of Cape Romano, 2 miles (3 km) (Fraser 1944: 149, as *Gonothyraea gracilis*).—Seahorse Key area; gonothecae smooth (Joyce 1961: 53, as *Clytia cylindrica*).—Cape San Blas area, on ascidians, sponges, shells, the octocoral *Leptogorgia virgulata*, and the seagrasses *Syringodium* and *Thalassia*; gonothecae smooth (Shier 1965: 34, as *Clytia cylindrica*).

Elsewhere in western North Atlantic. USA: North Carolina, Beaufort Harbor, on floating seaweed; gonothecae smooth (Fraser 1912b: 358, as ? *Clytia coronata*).—?USA: North Carolina, near Beaufort, on *Pennaria* from piles of railroad bridge + seaward side of Bogue Bank, on gulfweed; gonothecae smooth (Fraser 1912b: 361, as *Gonothyraea gracilis*).—Virgin Islands of the United States: St. Thomas, Charlotte Amalie, on algae from an old wooden boat, surface (Stechow 1914: 125, as *Clytia elsae-oswaldae*).—Venezuela: near Islas Los Tortuguillos, 8–12 feet (2–4 m) (Leloup 1937: 100, as *Laomedea cylindrica*).—?USA: Louisiana, Grand Isle + Pass Christian, on floating seaweed (Fraser 1944: 134, as *Clytia coronata*).—?USA: Louisiana, East Bay (Fraser 1944: 135, as *Clytia cylindrica*).—?USA: Texas, Gulf coast (Fraser 1944: 135, as *Clytia cylindrica*).—?USA: North Carolina, off Cape Hatteras, 35°20’55”N, 75°20’55”W, 16 ftm (29 m) (Fraser 1944: 149, as *Gonothyraea gracilis*).—?USA: Louisiana, Bayou Pass + Grand Isle + East Bay (Fraser 1944: 149, as *Gonothyraea gracilis*).—Colombia: 1 mile (2 km) SW of Cabo de la Vela, 10–13 ftm (18–24 m) (Fraser 1947b: 7, as *Gonothyraea gracilis*).—Venezuela: 3 miles (5 km) N of Isla de Coche, 21–22 ftm (38–40 m) (Fraser 1947b: 7, as *Gonothyraea gracilis*).—USA: Texas, Buoy I-24, Sabine Pass (Deevey 1950: 343, as *Gonothyraea gracilis*).—?USA: Texas, Port Aransas, jetties, on rocks, shells, and occasionally stranded on beach (Hedgpeth 1950: 73, as *Gonothyraea gracilis*).—?USA: Louisiana, Grand Isle (Deevey 1950: 339, as *Clytia coronata*).—?USA: Louisiana, Grand Isle (Deevey 1950: 341, as *Clytia cylindrica*).—?USA: Louisiana, Grand Isle, on floating log (Behre 1950: 7, as *Clytia coronata*).—?USA: Mississippi, Mississippi Sound (Fincher 1955: 92, as *Clytia coronata*).—?Panama: Colón, on an alga on an experimental plate (Vervoort 1968: 13, as *Campanularia* (*Clytia*) *cylindrica*).—?Guatemala: Puerto Barríos, on a hydroid on jetty (Vervoort 1968: 13, as *Campanularia* (*Clytia*) *cylindrica*).—Virgin Islands of the United States: St. Thomas, sound; gonothecae smooth, on hydrorhiza (Vervoort 1968: 15, as *Laomedea* (*Phialidium*) *pelagica*).—USA: Texas, West Flower Garden Bank, on a float cable, 24 feet (7 m); gonothecae smooth (Defenbaugh 1974: 97, as *Clytia cylindrica*).—USA: Texas, West Flower Garden Bank, on a floating sea bean; gonothecae smooth (Defenbaugh 1974: 99, as *Gonothyraea gracilis*).—Gulf Stream, several stations between Florida and North Carolina, on *Sargassum natans* I, *S. fluitans* III, *S. polyceratium*, *S. pteropleuron*; scarce; gonothecae smooth (Rackley 1974: 24, as *Clytia cylindrica*).—?USA: South Carolina, Charleston, in mariculture tanks (Sandifer *et al*. 1974: 56, as *Clytia gracilis*; Calder & Hester 1978: 90, as *Clytia gracilis*).—?Colombia: Santa Marta area, on seagrasses, rocky littoral (Wedler 1975: 332, 333, as *Clytia pelagica*).—?Colombia: Santa Marta area, on algae, *Thalassia*, other hydroids (Wedler 1975: 340, as *Clytia cylindrica*).—Colombia: Bahía de Cartagena (Flórez González 1983: 119, as *Clytia cylindrica*).—USA: South Carolina, inner (17–18 m), middle (32–36 m), and outer (46–69 m) continental shelf + Georgia, inner (17–22 m), middle (23–29 m) and outer (59–67 m) continental shelf (Wenner *et al*. 1984: 20, 39, as *Clytia cylindrica*).—Bermuda:

shallow inshore waters, common; gonothecae smooth (Calder 1986: 136, as *Clytia cylindrica*).—?USA: Louisiana, on a coastal petroleum platform (Lewbel *et al*. 1987, as *Clytia cylindrica*).—Bermuda: Whalebone Bay, on algae from ledge at entrance, 1 m + Flatts Inlet, on algae, 0.5–1.5 m + Castle Harbour, midway along causeway, on algae, 1.5 m (Calder 1990 [1991a]: 55, as *Clytia gracilis*).—Colombia: Bahía de Chengue, on *Rhizophora* (Reyes & Campos 1992: 108, as *Clytia cylindrica*).—Bermuda: Argus (=Plantagenet) Bank + Challenger Bank (Calder 2000: 1133, as *Clytia gracilis*).—Panama: Mole Buoy, Atlantic entrance to canal + US Army Harbor Craft Ops. Pier #1, Atlantic side + Colón, Isla Margareta, Fort Randolph, shore, 09°23'15"N, 79°53'11"W, 0–1 m + Portobelo Harbor, dock, 09°33'14"N, 79°39'34"W, 0-1 m + Bocas del Toro area, Almirante pilings, 09°16.218'N, 82°23.382'W, 1–10 m + Bocas del Toro area, Hospital Point, 09°20'01.9"N, 82°13'07.7"W, 2–13 m + Bocas del Toro area, Cayo Solarte Sud, 09°18'45.3"N, 82°12'46.6"W, 2–3 m (Calder & Kirkendale 2005: 486, as *Clytia gracilis*).—Virgin Islands of the United States: St. Thomas, Charlotte Amalie, on algae from an old wooden boat (see Stechow 1914), surface (Ruthensteiner *et al*. 2008: 13, as *Clytia elsae-oswaldae*).—French Lesser Antilles: Guadeloupe, Grande-Terre, E of Saint François, 16°15'18.00"N, 61°14'37.00"W, on *Thalassia* + Basse-Terre, Petite Anse, 16°05'47.00"N, 61°46'17.00"W, on algae and concretions (Galea 2008: 17, as *Clytia gracilis*).—French Lesser Antilles: Les Saintes, Terre-de-Haut, Pompierre Bay, 15°52'25"N, 61°34'15"W, on *Thalassia* + Terre-de-Haut, Pain de Sucre, 15°51'45"N, 61°35'60"W, on *Halimeda* (Galea 2008: 17, as *Clytia gracilis*).—French Lesser Antilles: Guadeloupe, Grande-Terre, Pointe Plate, 16°27.220'N, 61°32.128'W, 15–20 m + Grande-Terre, Passe à Colas, 16°21.269'N, 61°34.193'W, 10–15 m (Galea 2010: 3, 4, as *Clytia gracilis*).—French Lesser Antilles: Les Saintes, Terre-de-Haut, Pointe Morel, 15°53.050'N, 61°34.410'W, 6–11 m (Galea 2010: 3, 4, as *Clytia gracilis*).—Cuba: Villa Clara, Marina Periquillo, 2 m, on marine phanerogams (Varela *et al*. 2010: 30, as *Clytia gracilis*).—Virgin Islands of the United States: St. Thomas, Charlotte Amalie, on algae from an old wooden boat (see Stechow 1914) (Lindner *et al*. 2011: 27).—USA: Florida, off St. Lucie Inlet, 27°10.7'N, 80°02.7'W, on *Eudendrium carneum*, 23 m (Calder 2013: 54).—French Lesser Antilles: Martinique, Le Prêcheur, 14.780461, -61.211935, 15–18 m (Galea 2013: 13, figs. 80A–C, as *Clytia gracilis*).—Caribbean Sea (Wedler 2017b: 89, figs. 80A–C, as *Clytia gracilis*).—Mexico: Alacranes Reef, on seagrass, sponges (Mendoza-Becerril *et al*. 2018b: 131, as *Clytia* cf. *gracilis*).—Panama: Bocas del Toro area, San Cristóbal (Miglietta *et al*. 2018b: 108, as *Clytia gracilis*).

Clytia cf. *hemisphaerica* (Linnaeus, 1767)

Figs. 10f–h

Medusa hemisphaerica Linnaeus, 1767: 1098 [medusa stage].
Clytia bicophora.—Wallace, 1909: 37.
?*Campanularia minuta*.—Wallace, 1909: 37.
?*Campanularia* (*edwardsii?*).—Wallace, 1909: 37 [incorrect subsequent spelling].
Clytia edwardsi.—Joyce, 1961: 50, pl. 9, fig. 2.
Clytia johnstoni.—Fraser, 1943: 88.—Joyce, 1961: 55, pl. 11, figs. 3, 4.—Shier, 1965: 36, pls. 18, 20.

Type locality. "Habitat in Oceano Belgico" (Linnaeus 1767: 1098, as *Medusa hemisphaerica*).

Material examined. Sanibel Island, beach at Lighthouse Point, on a detached and stranded colony of *Eudendrium carneum*, 13 December 2017, two colonies or colony fragments, to 4 mm high, with gonothecae, coll. D. Calder, ROMIZ B4371.—Sanibel Island, beach at Lighthouse Point, 26°26'58"N, 82°01'04.5"W, on stranded *Sargassum pteropleuron*, 21 March 2018, 22° C, 34.5‰, several colonies, up to 3 mm high, with gonophores, coll. D. Calder, ROMIZ B4372.

Remarks. Trophosomes of *Clytia hemisphaerica* (Linnaeus, 1767), *C. gracilis* (M. Sars, 1850), and *C. elsaeoswaldae* Stechow, 1914 are all much alike, and their geographic distributions overlap in the western North Atlantic. Identification of sterile colonies is therefore difficult. According to Cornelius (1995b), hydroids of *C. hemisphaerica* differ from those of *C. gracilis* in having (1) colonies that tend to be shorter and less frequently branched, (2) hydrothecae that are shallower and less delicate, (3) hydrothecal cusps that are upright rather than oblique when viewed laterally, (4) a hydrothecal diaphragm that is thicker, (5) hydranths with typically 24–26 tentacles rather than 18–20. Differences in nematocyst morphology also have also been noted in the two species (Östman 1979a, b, 1987, 1999; Östman *et al*. 1987; Lindner & Migotto 2001). Most notably, fertile colonies of *C. hemisphaerica* differ from those of *C. gracilis* and *C. elsaeoswaldae* in having gonothecae with walls that are spirally ribbed rather than being predominantly smooth (but see Cunha *et al*. 2017). Besides differences in gonothecal morphology, characters said to distinguish hydroids of *C. hemisphaerica* from those of *C. elsaeoswaldae* include (1) hydrothecal cusps that are rounded and usually upright rather than pointed and inclined to the right when viewed laterally, (2) gonothecae that commonly arise from both stolons and hydrothecal pedicels rather than predominantly or exclusively from the hydrorhiza (Hincks 1868 [1869]; Cornelius 1982, 1995b; Lindner & Migotto 2011). In a multigene phylogenetic analysis by Lindner & Migotto (2011), *C. elsaeoswaldae* was found to be closely related to, but distinct from, a clade including *C. hemisphaerica* and two species of the *C. gracilis* morphotype.

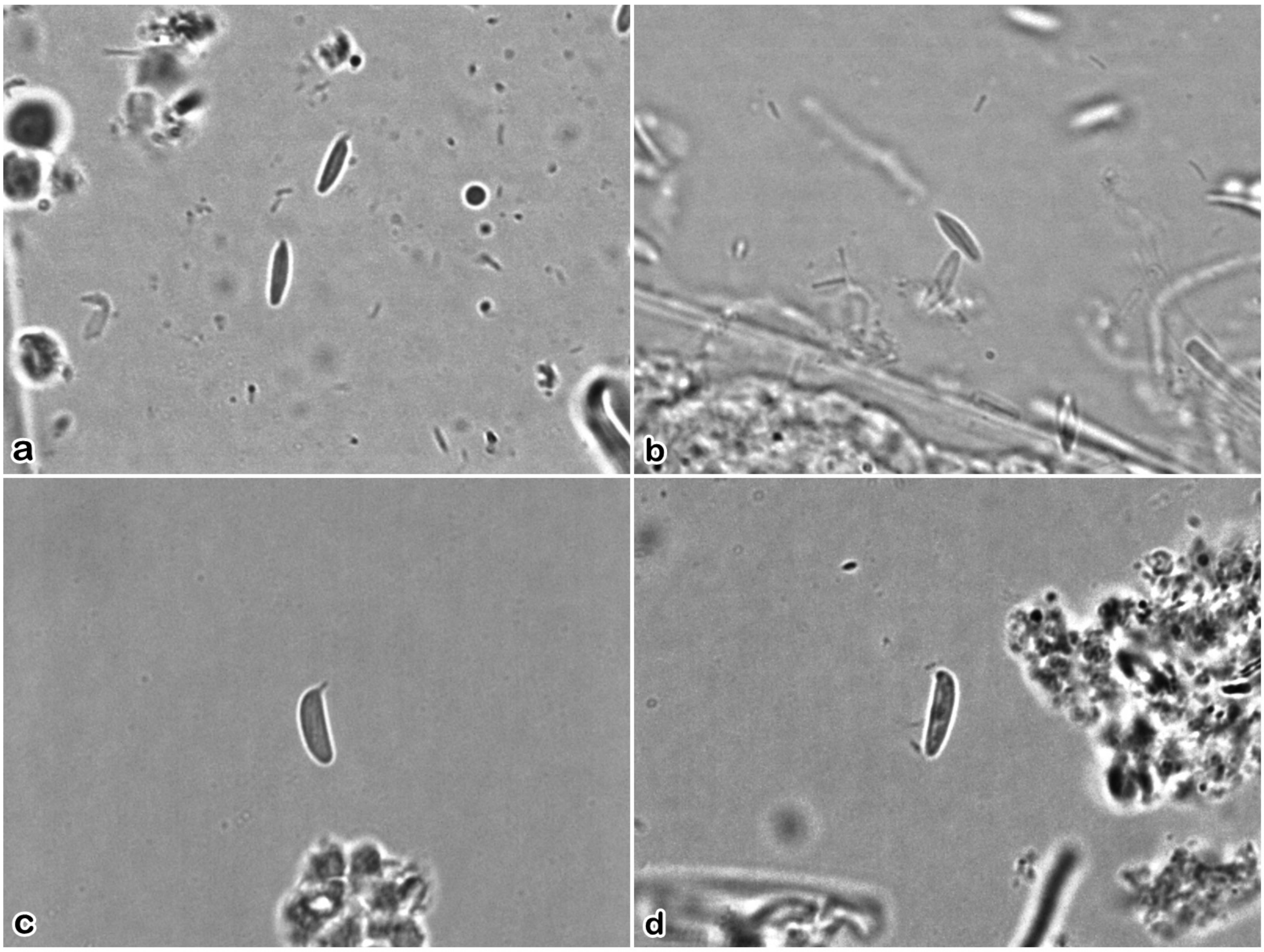

FIGURE 11. ***Clytia elsaeoswaldae*:** nematocysts, ROMIZ B4369. **a,** A-type b-mastigophores. **b,** A-type b-mastigophore. **c,** B-type b-mastigophore. **d,** B-type b-mastigophore.

At present, *C. hemisphaerica* (Linnaeus, 1767) is widely taken to be a species with a nearly cosmopolitan distribution in coastal waters (Cornelius 1995b). Commonly included among its synonyms in literature on hydroids reported from eastern North America are *C. johnstoni* (Alder 1856), *C. bicophora* L. Agassiz, 1862, *C. coronata* (Clarke, 1879), *C. grayi* Nutting, 1901, *C. minuta* (Nutting, 1901), and *C. edwardsi* (Nutting, 1901). The question whether *C. hemisphaerica* truly occurs from boreal waters of Atlantic Canada to the tropical Caribbean Sea in the western North Atlantic, as reported, has yet to be settled. While suspecting that cryptic species exist under the binomen, it was decided, based on current assumptions, to include records of the nominal species and its subjective synonyms across that entire latitudinal range in the Reported Distribution below. If the warm water hydroid population from lower latitudes and from pelagic *Sargassum* assigned here to *C. hemisphaerica* eventually proves to be a distinct species, the name *C. coronata* may need to be resurrected for it. Reports summarized below refer largely to the hydroid stage of this species, with only a few accounts of the medusa stage having been listed.

Clytia intermedia L. Agassiz, 1862 from New England, included as a synonym of *C. hemisphaerica* by Fraser (1944), appears from the original description and illustrations to have been based on a species of *Campanularia*

Lamarck, 1816 or *Orthopyxis* L. Agassiz, 1862. Rather than having a true diaphragm as in *Clytia* Lamouroux, 1812, an annular perisarcal thickening was present at the base of the hydrotheca, and a subhydrothecal spherule was present. Records of *C. intermedia* have therefore been excluded from distribution records below. Likewise excluded are records of *C. johnstoni* by Leloup (1937) from the Bahamas and the Sargasso Sea. From illustrations provided by Leloup, those specimens were likely referable to *C. noliformis* (McCrady, 1859) rather than *C. hemisphaerica*.

Thaumantias (?) *elsaeoswaldae* Stechow, 1914 (not *Clytia elsaeoswaldae* Stechow, 1914), mentioned below in the Reported Distribution records, is a *species inquirenda* assigned with doubts to the synonymy of *C. hemisphaerica*. No gonothecae were present in type material of the species, but it is clearly referable to *Clytia* Lamouroux, 1812. As briefly discussed above under *C. elsaeoswaldae* Stechow, 1914, *T. elsaeoswaldae* was founded as a different species and its current binomen (*C. elsaeoswaldae*) constitutes a secondary homonym.

The taxonomy and nomenclature of *C. hemisphaerica* has been discussed in greater detail elsewhere (Calder 1990 [1991a]; Cornelius 1995b). Medel & Vervoort (2000) provided an extensive bibliography and a review of worldwide distribution records. The identity of *Clytia noliformis*, unclear from the original description (McCrady, 1859) but appearing similar to *C. hemisphaerica*, was conserved as a distinct species through designation of a neotype (Lindner & Calder 2000; Opinion 1986, International Commission on Zoological Nomenclature 2002).

Clytia hemisphaerica has recently become a model organism for the study of various biological processes (Cook *et al*. 2016). Even a draft genome of the species has been assembled (Leclere *et al*. 2019), with distinct transcriptome signatures in polyp, medusa, and planula larva stages.

Reported distribution. ***Gulf coast of Florida.*** Dry Tortugas (Wallace 1909: 137, as *Clytia bicophora*).—?Dry Tortugas (Wallace 1909: 137, as *Campanularia minuta*).—?Dry Tortugas (Wallace 1909: 137, as *Campanularia* (*edwardsii?*)).—Dry Tortugas (Fraser 1943: 88, as *Clytia johnstoni*).—Seahorse Key area, on *Syringodium filiforme*; gonothecae ribbed (Joyce 1961: 50, as *Clytia edwardsi*).—Seahorse Key area, on floating grasses; gonothecae ribbed (Joyce 1961: 55, as *Clytia johnstoni*).—Cape San Blas area; gonothecae ribbed (Shier 1965: 36, as *Clytia johnstoni*).

Elsewhere in western North Atlantic. Canada: New Brunswick, Grand Manan (L. Agassiz 1862: 304–306, as *Clytia* (*Trochopyxis*) *bicophoba* [sic], and *Clytia bicophora*).—USA: Massachusetts, Vineyard Sound (L. Agassiz 1862: 304–306, as *Clytia* (*Trochopyxis*) *bicophoba* [sic], and *Clytia bicophora*).— USA: Maine, Eastport, hydroid & medusa (A. Agassiz 1865: 79, as *Clytia bicophora*).—USA: Massachusetts, Massachusetts Bay + Vineyard Sound + Naushon + Beverly, hydroid + Nahant, medusa (A. Agassiz 1865: 79, as *Clytia bicophora*).—Canada: New Brunswick, Grand Manan, medusa (A. Agassiz 1865: 79, as *Clytia bicophora*).—Canada: Gulf of St. Lawrence, Orphan Bank (Whiteaves 1874: 185, as *Clytia johnstoni*).—USA: Maine, Casco Bay, among the islands, 8–30 ftm (15–55 m) (Verrill 1874a: 44, as *Clytia johnstoni*).—USA: Maine, Casco Bay, 8–34 ftm (15–62 m) (Verrill 1874c: 364).—USA: Vineyard Sound and vicinity, bays and sounds, rocky shores + rocky bottoms + gravelly and shelly bottoms (Verrill 1874d: 334, 408, 411, 424, as *Clytia johnstoni*).—USA: Connecticut, Long Island Sound + New Haven area and Thimble Islands, 2–6 ftm (4–11 m) and in tidepools (Verrill 1874d: 725, as *Clytia johnstoni*).—USA: Rhode Island, Watch Hill, 3–5 ftm (5–9 m) + off Block Island, 29 ftm (53 m) (Verrill 1874d: 725, 726, as *Clytia johnstoni*).—USA: Massachusetts, Buzzards Bay + Vineyard Sound, 1–14 ftm (2–26 m) (Verrill 1874d: 726, as *Clytia johnstoni*).—USA: Maine, Casco Bay (Verrill 1874d: 726, as *Clytia johnstoni*).—Canada/USA: Bay of Fundy (Verrill 1874d: 726, as *Clytia johnstoni*).—USA: Massachusetts, Georges Bank (Verrill 1874d: 726, as *Clytia johnstoni*).—Canada: Nova Scotia, LaHave Bank (actually Baccaro Bank), 42°56.5’N, 64°51.3’W, 45 ftm (82 m), gravelly and stony bottom (Smith & Harger 1875: 13, as *Clytia johnstoni*).—USA: Massachusetts, Cashes Ledge, 27–73 ftm (49–134 m) (Verrill 1875a: 414, as *Clytia johnstoni*).—USA: New Hampshire, Jeffreys Ledge (Verrill 1875a: 414, as *Clytia johnstoni*).—USA: Maine, Gulf of Maine, 43°11’N, 69°35’W, 32 ftm (59 m) (Verrill 1875a: 414, as *Clytia johnstoni*).—Mexico: 10 miles (16 km) N of Zoblos Island (=Isla Holbox) (Clarke 1879: 242, as *Clytia coronata*).—USA: Massachusetts, Provincetown, Long Point beach, inner shore, on stranded *Fucus* (Rathbun 1880: 132, as *Clytia johnstoni*).—USA: Massachusetts, Woods Hole, on *Mytilus* (Bumpus 1898: 857, as *Clytia bicophora*).—USA: Massachusetts, Woods Hole region, shallow water, on shells, algae, and other hydroids including *Ectopleura crocea* on U.S. Fish Commission dock (Nutting 1901: 343, as *Clytia bicophora*).—USA: Massachusetts, S of Martha’s Vineyard, 40°46’30”N, 70°40’W, 31 ftm (57 m), on worm tubes of sand (Nutting 1901: 343, as *Clytia grayi*).—USA: Massachusetts, New Bedford, on *Obelia* stems from wharf piles (Nutting 1901: 345, as *Campanularia minuta*).—USA: Massachusetts, Woods Hole, on U.S. Fish Commission dock (Nutting 1901: 346, as *Campanularia edwardsi*).—USA: northeast coast, on *Fucus*, shells, other hydroids (Hargitt 1901b: 381, as *Clytia* *bicophora*).—USA: Massachusetts, on *Sargassum* (Hargitt 1909: 373, as *Clytia volubilis*).—USA: Louisiana, seasonally abundant on stranded gulfweed (Cary & Spaulding 1909: 6, as *Clytia cylindrica*).—USA: New England coast, in shallow tidepools, on seaweeds and other hydroids; gonothecae ribbed (Mayer 1910b: 263, as *Clytia volubilis*).—USA: Massachusetts, Woods Hole area, Fays Wharf + Penzance (Fraser 1912a: 44, as *Clytia edwardsi*).—USA: Massachusetts, Martha's Vineyard, Vineyard Haven, bridge at entrance to Lagoon Pond, on stems of *Eudendrium* + Woods Hole, Fay's Wharf, on a tubulariid (Fraser 1912a: 44, as *Clytia minuta*).—USA: Rhode Island, Newport, on eelgrass (Fraser 1912a: 44, as *Clytia minuta*).—USA: Massachusetts, Vineyard Sound (Fraser 1912a: 44, as *Clytia minuta*).—USA: North Carolina, Beaufort area, seaward side of Bogue Bank, on floating *Sargassum*; gonothecae ribbed (Fraser 1912b: 359, as *Clytia johnstoni*).—Canada: New Brunswick, St. Andrews (Stafford 1912b: 73, as *Clytia johnstoni*).—Canada: Nova Scotia, Barrington Passage, shallow water + Canso, on mussel shells and *Obelia commissuralis* (=*O. longissima*) under wharves and in harbour near low water (Fraser 1913: 165, as *Clytia johnstoni*).—USA: Massachusetts, Woods Hole area, on *Fucus*, other hydroids, shells (Sumner *et al*. 2013: 568, as *Clytia bicophora*).—USA: Massachusetts, Crab Ledge (Sumner *et al*. 2013: 568, as *Clytia grayi*).—?Virgin Islands of the United States: St. Thomas, Charlotte Amalie, port, surface, on a bryozoan (Stechow 1914: 122, as *Thaumantias (?) elsae-oswaldae*).—?Bahamas: Great Bahama Bank, on seaweed (Nutting 1915: 52, as *Clytia coronata*).—Canada: New Brunswick, from Grand Manan to the head of Passamaquoddy Bay (Fraser 1918: 345, as *Clytia johnstoni*).—Canada: Nova Scotia, Brier Island, 22 ftm (40 m) (Fraser 1918: 345, as *Clytia johnstoni*).—Canada: New Brunswick, St. Andrews Point (Fraser 1918: 345, as *Clytia edwardsi*).—Bermuda: unspecified location, on *Sargassum* (Bennitt 1922: 246, as *Campanularia raridentata*).—Bermuda: Cow Ground Flat, on *Pennaria* (Bennitt 1922: 247, as *Clytia bicophora*).—Bermuda: Agar's Island, on *Sargassum* + off north shore, on floating *Sargassum* (Bennitt 1922: 247, as *Clytia cylindrica*).—Bermuda: unspecified location, one of commonest species on floating *Sargassum*; gonothecae ribbed (Bennitt 1922: 248, as *Clytia johnstoni*).—Sargasso Sea, on *Sargassum* (Hentschel 1922: 4, as *Clytia johnstoni*).—USA: Massachusetts, Woods Hole region, on rocks and rockweed (Allee 1923: 175, as *Clytia grayi*).—USA: Massachusetts, Woods Hole region, on eelgrass, rocks and rockweed, pilings (Allee 1923: 175, as *Clytia bicophora*).—Canada: New Brunswick, Miramichi River estuary, inside Portage and Fox islands, >15 m (Fraser 1926: 210, as *Clytia edwardsi*).—Canada: New Brunswick, Miramichi River estuary, outside Portage and Fox islands, >15 m (Fraser 1926: 210, as *Clytia johnstoni*).—?Sargasso Sea: 34°25'N, 40°05'W, on *Sargassum* (Timmermann 1932: 298, as *Clytia cylindrica*).—Klein Bonaire: west coast, 0.3 m, on algae (Leloup 1935: 19, as *Clytia coronata*).—Bonaire: Kralendijk, Pasanggrahan, 0.2–0.3 m, on algae + De Hoop, 0.7 m, on algae + Plaja Oranje Pan, on stranded octocoral (Leloup 1935: 19, as *Clytia coronata*).—Aruba: Rif Boekoetie, 0.2 m, on a brachyuran crab (Leloup 1935: 19, as *Clytia coronata*).—USA: Maine, Mount Desert region, shore to 239 feet (73 m) (Procter 1933: 120, as *Clytia bicophora*).—Gulf Stream, on pelagic *Sargassum* + Sargasso Sea, on pelagic *Sargassum* (Burkenroad, in Parr 1939: 24, as *Clytia bicophora*).—?USA: North Carolina, 100 miles (161 km) E of Cape Hatteras, on *Sargassum* (Fraser 1943: 88, as *Clytia cylindrica*).—USA: Maine, Casco Bay (Fraser 1944: 136, as *Clytia edwardsi*).—USA: Massachusetts, Gloucester Harbor, 7 ftm (13 m) (Fraser 1944: 136, as *Clytia edwardsi*).—USA: Massachusetts, Cape Cod, off Nasett Light (Nauset Light, Eastham, MA), 61.5 ftm (112 m) (Fraser 1944: 136, as *Clytia edwardsi*).—USA: Rhode Island, Narragansett Bay, near Fort Dumpling, 20 ftm (37 m) (Fraser 1944: 136, as *Clytia edwardsi*).—Canada: Newfoundland and Labrador, Labrador (Fraser 1944: 140, as *Clytia johnstoni*).—USA: Maine, off Portsmouth, 43°11'N, 69°35'W, 32 ftm (59 m) (Fraser 1944: 140, as *Clytia johnstoni*).—Canada: Nova Scotia, continental slope S of Halifax, 42°44'N, 62°43'W, 620 ftm (1134 m) (Fraser 1944: 140, as *Clytia johnstoni*).—USA: Massachusetts, off Gloucester, 42°30'15"N, 70°38'W, 45 ftm (82 m) + SE of Salem, 42°30'N, 70°45'W, 22 ftm (40 m) + off Cape Cod, 42°07'N, 69°59'W + Cape Cod Bay, 41°48'30"N, 70°12'W, 7 ftm (13 m) + off Chatham Light, 5.75 miles (9 km), 14 ftm (26 m) + Gloucester, on piles + Provincetown, Long Point, on floating *Sargassum* + Georges Bank, 45 ftm (72 m) + Between Nantucket and High Duck islands, 4 ftm (7 m) (Fraser 1944: 140, as *Clytia johnstoni*).—USA: New York, S of Fishers Island (Fraser 1944: 140, as *Clytia johnstoni*).—USA: Rhode Island, Block Island, off North Light, 13 ftm (24 m) (Fraser 1944: 140, as *Clytia johnstoni*).—USA: Connecticut, off Stonington (Fraser 1944: 140, as *Clytia johnstoni*).—Bahamas: Cay Sal Bank (Fraser 1944: 140, as *Clytia johnstoni*).—Venezuela: 3 miles (5 km) N of Isla de Coche, 19–33 ftm (35–60 m) + Isla Cubagua, shallow water, on algae (Fraser 1947b: 6, as *Clytia similis*).—USA: Maine, Boothbay Harbor (Berrill 1950: 1, as *Clytia johnstoni*).—?USA: Texas, Buoy I-3 off Sabine Pass + Port Aransas, on driftwood, *Sargassum*, tar + Palacios (Deevey 1950: 339, as *Clytia coronata*).—?USA: Texas, Port Aransas, on *Sargassum*, tar + Palacios (Deevey 1950: 341, as *Clytia cylindrica*).—USA: Louisiana, Grand Isle area, open Gulf of Mexico, on *Sargassum*

(Behre 1950: 6, as *Gonothyraea gracilis*).—USA: North Carolina and South Carolina, reefs on continental shelf (Pearse & Willams 1951: 136, as *Clytia johnstoni*).—USA: Massachusetts, Woods Hole area (Brock & Strehler 1963: 23, as *Clytia johnstoni*).—USA: Massachusetts, Woods Hole region (Petersen 1964: 17, as *Clytia edwardsi* and *C. johnstoni*).—USA: Virginia, Norfolk, Naval Station Norfolk, Pier 12, on test panels, 5 m (Calder & Brehmer 1967: 153, as *Clytia edwardsi*).—USA: Virginia, York River (Gloucester Point; Bell Rock) + James River (Hampton Roads Middle Ground; Norfolk, Naval Station Norfolk, Pier 12, on test panels, 5 m) + Chesapeake Bay (Willoughby Bank; Thimble Shoal; Chesapeake Bay Bridge-Tunnel, Virginia Beach span) (Calder 1971: 49, as *Clytia edwardsi*).—?USA: Virginia, Pamunkey River + James River (Hampton Roads Middle Ground; Deep Water Shoal; Hog Island), on the hydroids “*Garveia* sp.” (*Calyptospadix cerulea*) and *Sertularia argentea* (Calder 1971: 50).—USA: Massachusetts, Woods Hole area, studies on bioluminescence (Morin & Cooke 1971b: 718, as *Clytia edwardsi*; Morin & Hastings 1971: 307, as *Clytia edwardsi*).—USA: Texas, Galveston Island near San Luis Pass, on *Sargassum*; gonothecae ribbed (Defenbaugh & Hopkins 1973: 78, as *Clytia johnstoni*).—Sargasso Sea + Gulf Stream, several stations between Florida and New Jersey, on *Sargassum natans* I, *S. natans* IX, *S. fluitans* III, *S. fluitans* X, *S. ramifolium*, *S. filipendula, S. polyceratium*, *S. pteropleuron, S. hystrix, Sargassum* sp.; frequent; gonothecae ribbed (Rackley 1974: 28).—USA: North Carolina, Pamlico River estuary (Dean & Bellis 1975: 5).—USA: Massachusetts, Cape Cod Bay, 8–10 m; gonothecae ribbed (Calder 1975: 300).—USA: Massachusetts, Nonamesset Island, Sheep Pen Harbor, 41°31’N, 70°40’40”W, on slate settling panels (Osman 1977: 48, as *Clytia johnstoni* and *C. edwardsi*).—USA: Gulf of Maine, 25–33 m (Kuzirian 1979: 242, as *Clytia johnstoni*).—Belize: Carrie Bow Cay, on algae, *Thalassia*, mangrove roots, *Sargassum*, hydroids, and dead corals and gorgonians; gonothecae ribbed (Spracklin 1982: 246, as *Clytia hemisphaerica*).—Sargasso Sea: Hydrostation “S” off Bermuda, *31*°45’N, 64°10’W, on pelagic *Sargassum* (Butler *et al*. 1983: 230, as *Clytia johnstoni*).—USA: South Carolina, middle (32–36 m) continental shelf + Georgia, inner (17–22 m) and outer (59–67 m) continental shelf (Wenner *et al*. 1984: 39, as *Clytia johnstoni*).—USA: New York, off Fire Island, 3 km S of Altair Lighthouse, on artificial reef, 20 m (Woodhead & Jacobson 1985: 366).—USA: New Jersey, Delaware Bay, on oyster grounds (Ismail 1985: 385, as *Clytia edwardsi*).—?USA: South Carolina, North Inlet area, Town Creek and tributaries (Fox & Ruppert 1985: 61, as *Clytia coronata*).—?USA: South Carolina, North Inlet area, Baruch Plantation, oyster landing + Murrells Inlet, jetties + Folly River + Breach Inlet, jetties + Isle of Palms, marina, floating docks + Beaufort area, pilings and seawalls + Hunting Island, seawall and rubble (Fox & Ruppert 1985: 76, 92, 162, 167, 177, 219, 226).—USA: Virginia, James River, Wreck Shoal, oyster bed, 3–4 m (Rheinhardt & Mann 1990: 20).—Bermuda: Flatts Inlet, near bridge, 2 m, on *Eudendrium* sp. + Whalebone Bay, on pelagic *Sargassum* + Whalebone Bay, 1–3 m, on benthic algae and *Thalassia* + Harrington Sound, in shaft connecting to Flatts Inlet, 1 m, on rock + Harrington Sound, Stream Passage Cave, 6 m from entrance, 1 m, on rock (Calder 1990 [1991a]: 58).—Belize: Twin Cays, common (Calder 1991b: 223).—Belize: Twin Cays, on *Rhizophora*, *Thalassia*, benthic algae, sponges, other hydroids, mollusc shells, wooden test panels (Calder 1991c: 2068).—Canada: Quebec, Gulf of St. Lawrence, north shore, on navigation buoys (Ardisson & Bourget 1992: 22).—Belize: South Water Cay, South Water Cut, ca. 4 m, on *Thalassia* (Kaehler & Hughes 1992: 331).—Bermuda: various locations, on *Sargassum natans* and *S. fluitans*; gonothecae ribbed (Calder 1995: 540).—Bermuda: Argus (=Plantagenet) + Challenger Bank (Calder 2000: 1133).—Canada: Nova Scotia, Bay of Fundy (Henry & Kenchington 2004: 127).—Canada: New Brunswick, Passamaquoddy Bay, Sherrod’s Beach (Henry & Kenchington 2004: 131).—Canada: New Brunswick and Prince Edward Island, Northumberland Strait (Calder 2004a: 559).—USA: Maine, Cobscook Bay (Trott 2004: 272).—Panama: Bocas del Toro area, Cayo Solarte Sud, 09°18’45.3”N, 82°12’46.6”W, 2–3 m + Bocas del Toro area, near Laguna Bocatorito, 2–4 m (Calder & Kirkendale 2005: 486).—Cuba: Miramar, playa, 12 m (Varela *et al*. 2005: 178).—?Cuba: Golfo de Batabanó, wreck of *La Patana*, 83°13’41.5”N, 21°40’59.5”W, 9–11 m (Castellanos *et al*. 2011: 14).—French Lesser Antilles: Martinique, Le Diamant, 14.442310, -61.039697, on *Thyroscyphus marginatus* (Galea 2013: 11).—USA: Connecticut, Westport (Cunha *et al*. 2017: 120).—USA: Massachusetts, Salem + Bourne (Cunha *et al*. 2017: 120).—USA: Rhode Island, Point Judith (Cunha *et al*. 2017: 120).—Belize: Carrie Bow Cay + Twin Cays, Fisheries dock + Twin Cays, Cuda Cut (Cunha *et al*. 2017: 120).—Canada: Nova Scotia, Petit Passage, S of East Ferry, extreme low tide (Calder 2017: 79).—Canada: New Brunswick, Deer Island, Richardson, 44°59’42”N, 66°56’47”W, on *Ascophyllum nodosum* on pontoon slip of public wharf, <1 m (Calder 2017: 80).—?Caribbean Sea (Wedler 2017b: 90, figs. 81, 82A, B).—Mexico: Alacranes Reef, on *Sargassum* sp., *Thalassia*, shipwreck (Mendoza-Becerril *et al*. 2018b: 131).—Cuba: Havana, coral reef system west of the city (Castellanos *et al*. 2018: Supplementary Table S2).—Panama: Bocas del Toro area, Crawl Cay + near Bocatorito Bay (Miglietta *et al*. 2018b: 108).

Clytia joycei, sp. nov.

Figs. 12, 13, 14a–e

Clytia sp. C. Calder & Kirkendale, 2005: 487.

Type locality. USA: Florida, Sanibel Island, beach at Lighthouse Point, 26°26’57”N, 82°01’06”W, on stranded *Thalassia*.

Material examined. Holotype: Sanibel Island, beach at Lighthouse Point, 26°26’57”N, 82°01’06”W, on detached *Thalassia* in water along shore, 24° C, 35‰, 03 April 2018, one colony, 3 mm high, without gonothecae, coll. D. Calder, ROMIZ B4373.—Paratype: Sanibel Island, beach at Lighthouse Point, 26°26’57”N, 82°01’06”W, on detached *Thalassia* in water along shore, 24° C, 35‰, 03 April 2018, one colony, 2 mm high, without gonothecae, coll. D. Calder, ROMIZ B4374.—Non-type: Sanibel Island, beach at Lighthouse Point, 26°26’57”N, 82°01’06”W, on detached *Thalassia* in water along shore, 24° C, 35‰, 03 April 2018, one colony, 2 mm high, without gonothecae, coll. D. Calder, ROMIZ B4421.

Non-Florida material examined. Panama: Bocas del Toro area, Almirante pilings, 09°16.218’N, 82°23.38’W, 03 August 2004, 1–10 m, on *Thalassia*, three colonies or colony fragments, up to 1.5 mm high, without gonothecae, coll. L. Kirkendale, ROMIZ B4375.

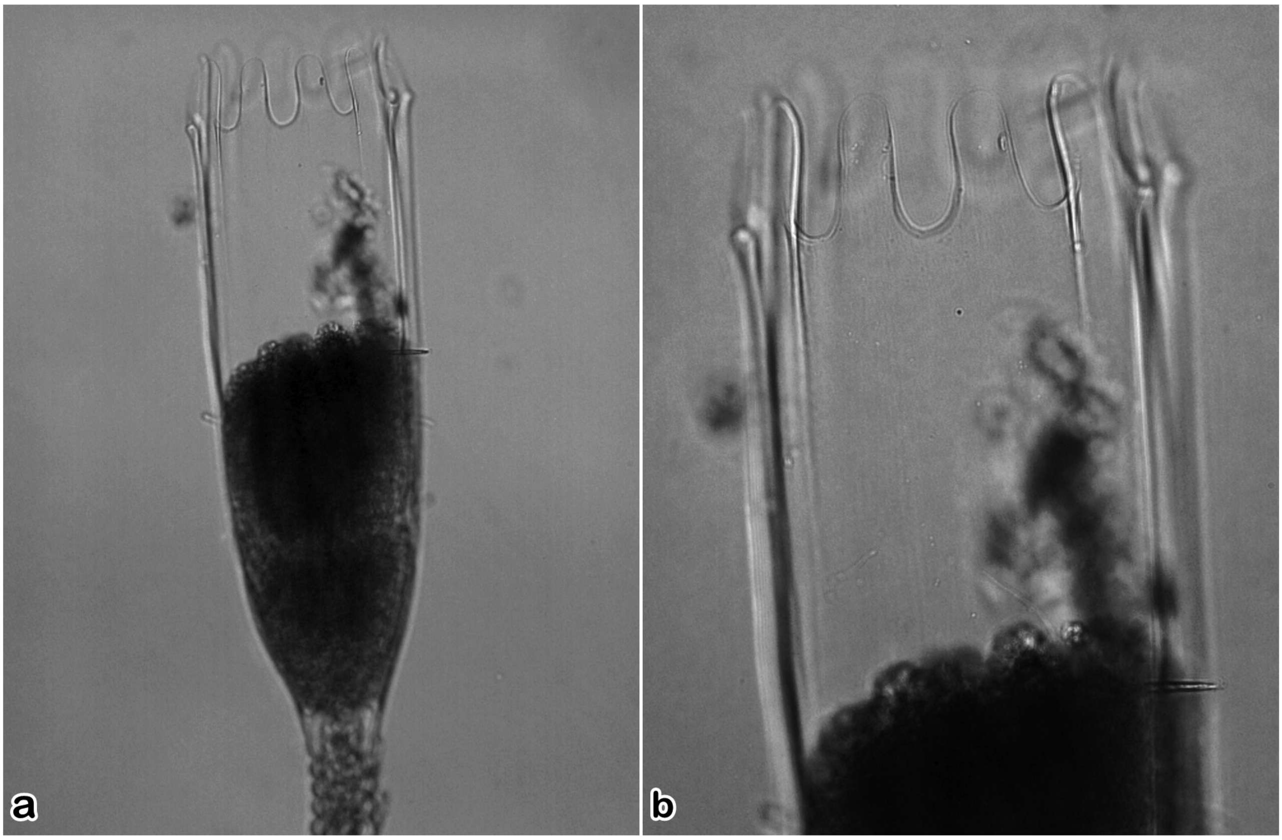

FIGURE 12. ***Clytia joycei***: holotype colony, ROMIZ B 4373. **a,** hydrotheca. **b,** distal end of hydrotheca, showing marginal cusps.

Description of holotype. Hydroid colonies minute, stolonal, arising from a reptant hydrorhiza adhering to blades of the seagrass *Thalassia testudinum*. Stolons of hydrorhiza smooth, tubular, 70–100 µm in diameter, mostly simple, little branched, not anastomosing, with moderately slender perisarc; internal septa absent. Hydranth pedicels erect, mostly straight, unbranched, arising at relatively close intervals, short to moderately short in length, 0.2–2.7 mm high, 58–90 µm in diameter, each supporting a hydrotheca at distal end, annulated proximally, smooth medially, then annulated again distally below base of hydrotheca, occasionally with one or more nodes or with a few annulations medially as well, infrequently annulated throughout; annulations somewhat compressed, their numbers at both proximal and distal ends varied; subhydrothecal spherule absent; pedicel perisarc of moderate thickness. Hydrothecae deep, slender, circular in cross-section, 630–880 µm high, 215–295 µm in diameter at rim, 80–115 µm in diameter at diaphragm, tapering only slightly from distal to proximal end and appearing nearly cylindrical, becoming constricted at base; hydrothecal walls smooth, perisarc fairly thin, out-turned a little and appearing thickened somewhat at base of marginal cusps; basal chamber usually large to quite large, cup-shaped, set apart by a true diaphragm with a small hydropore, diaphragm thin, horizontal to slightly oblique; hydrothecal rim with about 8–11 cusps separated by deep U-shaped embayments reaching 55–95 µm into rim of hydrotheca, each cusp linguiform, with blunt, rounded tip; viewed in cross-section, abaxial side of cusp strongly concave and U-shaped, adaxial side convex; base of each embayment expanded outwards, contributing to undulated appearance of hydrothecal rim in cross-section; in lateral view, resulting folds may appear as faint longitudinal lines extending a short distance down hydrothecal wall. Hydranths highly contractile, fully retractable into hydrothecal cavity, each with a distal whorl of filiform tentacles; tentacle number appearing to be about 16–20 from preserved material; hypostome globose to dome-shaped.

Gonophores and gonothecae not seen.

Nematocysts (Fig. 13): A-type b-mastigophores (7.3–7.8 µm long x 1.8–2.2 µm wide); B-type b-mastigophores (15.5–18 µm long x 3.2–4.5 µm wide). Identifications of nematocyst categories are tentative; few discharged threads were observed in formalin-preserved material and their morphology was indistinct.

Remarks. These hydroids, collected on *Thalassia* from the beach at Lighthouse Point, Sanibel Island, Florida, were at first thought to be simply a variant morphotype of *Clytia macrotheca* (Perkins, 1908). While resembling that species in colony form and hydrothecal shape, marginal cusps are linguiform rather than truncate to castellate, and embayments separating the cusps are considerably deeper. Such differences are now taken to be beyond the expected limits of intraspecific variation, and the specimens are hereby assigned to a new species under the binomen *C. joycei*. In addition, hydrothecae of *C. joycei* are consistently larger than those of *C. macrotheca* as measured by Calder (1990 [1991a]) (hydrothecal height 438–569 µm; diameter at rim 168–205 µm; diameter at diaphragm 47–75 µm) and Galea (2008) (hydrothecal height 435–610 µm; diameter at rim 150–235 µm; diameter at diaphragm 40–75 µm). The nematocyst complement of the two species appears to be the same, but differences exist in the size of their B-type b-rhabdoids. Those of *C. joycei* (see above) are larger than those of *C. macrotheca* (13.5–14.8 µm x 2.8–4.0 µm).

Among other described species of *Clytia* Lamouroux, 1812, *C. joycei* resembles *C. gigantea* (Hincks, 1866), originally described from Lamlash Bay, Scotland. Unlike the boreal *C. gigantea*, hydroids of the apparently warm-temperate/tropical *C. joycei* are stolonal rather than erect and branched in colony form, and their hydrothecae are much smaller (<1 mm vs. 1–3 mm in hydrothecal height) and cylindrical rather than gradually tapered. Also similar is the hydroid of *C. fascicularis* Fraser 1938a from the Pacific coast of the Americas (southern California to Peru). In *C. fascicularis*, however, cusps at the margin of the hydrotheca are not as deeply cut, colonies are sometimes erect rather than stolonal, and stems may be slightly polysiphonic.

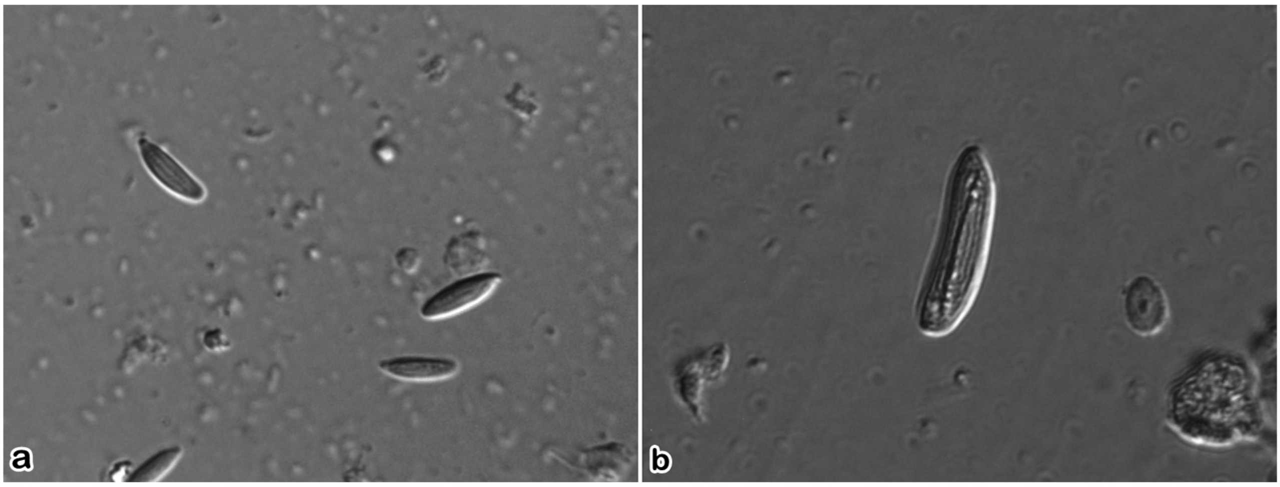

FIGURE 13. ***Clytia joycei***: nematocysts, holotype colony, ROMIZ B4373. **a,** A-type b-mastigophores. **b,** B-type b-mastigophore.

Although gonophores and gonothecae were lacking in the present material, there is little doubt that this species is referable to *Clytia*. The following combination of characters accord with current diagnoses of the genus (Calder

1990 [1991a]; Cornelius 1995; Bouillon *et al*. 2006): (1) colonies were minute and stolonal; (2) hydrothecae were deeply campanulate and radially symmetrical, with marginal cusps, unthickened perisarc, a true diaphragm, and no operculum; (3) a subhydrothecal spherule was absent. From existing diagnoses of *Clytia*, it is likely that gonothecae of the species will prove to be conical to clavate in shape, and that a free medusa stage will be liberated.

Several species of medusae, referable to *Clytia*, have been reported from the southeastern Gulf of Mexico region (Kramp 1961; Segura-Puertas *et al*. 2009). Of these, hydroids have yet to be reliably described for *C. folleata* (McCrady, 1859), *C. discoida* (Mayer, 1900b), *C. gelatinosa* (Mayer, 1900b), and *C. globosa* (Mayer, 1900b). It remains to be determined whether one of these is conspecific with the hydroid *C. joycei*.

Following the nematocyst classification and nomenclature of Östman (1979a, 1999), two types of nematocysts were observed in polyp stages of *C. joycei*, A-type b-rhabdoids (also known as microbasic b-mastigophores) and much larger but less common B-type b-rhabdoids (Fig. 13). Capsules of the larger nematocysts somewhat resemble merotrichous isorhizas, as described by Lindner & Migotto (2001) in *Clytia noliformis*, although they were smaller than in that morphologically distinct species. For information on the cnidomes of certain species of *Clytia*, and on the utility of nematocyst categories and sizes as useful taxonomic characters in the genus, see works such as those by Östman (1979a, b, 1999), Lindner & Migotto (2001, 2002), and Lindner *et al*. (2011).

In addition to its occurrence in southwest Florida, *C. joycei* has been collected from the Caribbean coast of Panama. Hydroids from the Bocas del Toro area (ROMIZ B4375), re-examined and illustrated here (Fig. 14e), were reported as *Clytia* sp. C by Calder & Kirkendale (2005). They too were sterile. Specimens from Panama are smaller but otherwise morphologically indistinguishable from those collected in Florida.

Etymology. The specific name honours Edwin Anthony Joyce, Jr. (1937–2014), who studied hydroids of the Florida Gulf Coast while a graduate student at the University of Florida, Gainesville. His M.S. thesis (Joyce 1961) has been cited frequently in this report.

Reported distribution. ***Gulf coast of Florida.*** First record.

Elsewhere in western North Atlantic. Panama: Bocas del Toro area, Almirante pilings, 09°16.218’N, 82°23.382’W, 1–10 m (Calder & Kirkendale, 2005: 487, as *Clytia* sp. C).

Clytia macrotheca **(Perkins, 1908)**

Figs. 14f, g, 15

Campanularia macrotheca Perkins, 1908: 146, pl. 3, figs. 12, 13.
not *Campanularia macrotheca* Leloup, 1930: 101, figs. 1–3 [invalid junior primary homonym of *Campanularia macrotheca* Perkins, 1908].
Laomedea macrotheca.—Leloup, 1935a: 21, fig. 8.

Type locality. USA: Florida, Dry Tortugas, Fort Jefferson, in the moat (Perkins 1908: 147).

Material examined. Sanibel Island, beach at Lighthouse Point, on stranded *Thalassia*, 31 August 2018, 29° C, 34‰, two colony fragments, up to 1.5 mm high, without gonothecae, coll. D. Calder, ROMIZ B4420.

Remarks. This species was originally described from the southwest coast of Florida, as *Campanularia macrotheca*, by Perkins (1908). The binomen *Campanularia macrotheca* Leloup, 1930, applied to a different species from Monaco, is an invalid junior primary homonym. Leloup’s hydroid has been taken to be conspecific with *Campanularia hincksii* Alder, 1856 by authors including Patriti (1970) and Cornelius (1982), and that synonymy has been adopted in WoRMS.

Perkins (1908) fully described and illustrated this hydroid, found on filamentous algae in the moat at Fort Jefferson on Garden Key in the Dry Tortugas. Amongst the material examined by him were two fertile colonies, each having a gonotheca with two well-developed medusa buds. Based on the morphology of those medusa buds, the species was justifiably reassigned to *Clytia* Lamouroux, 1812 by Stechow (1923b: 109). From the account of Perkins there is little doubt that a free medusa exists in *Clytia macrotheca*, but that stage currently remains unknown.

The hydroid of *Clytia joycei* sp. nov., described immediately above, is much like that of *C. macrotheca* in morphology and habitat. It differs in having somewhat larger hydrothecae than those of *C. macrotheca*, and hydrothecal cusps that are much more deeply incised and more linguiform. Differences also exist in the size of their B-type b-rhabdoid nematocysts, with those of *C. joycei* (15.5–18 µm long x 3.2–4.5 µm wide) being larger than those of *C. macrotheca* (13.5–14.8 µm long x 2.8–4.0 µm wide).

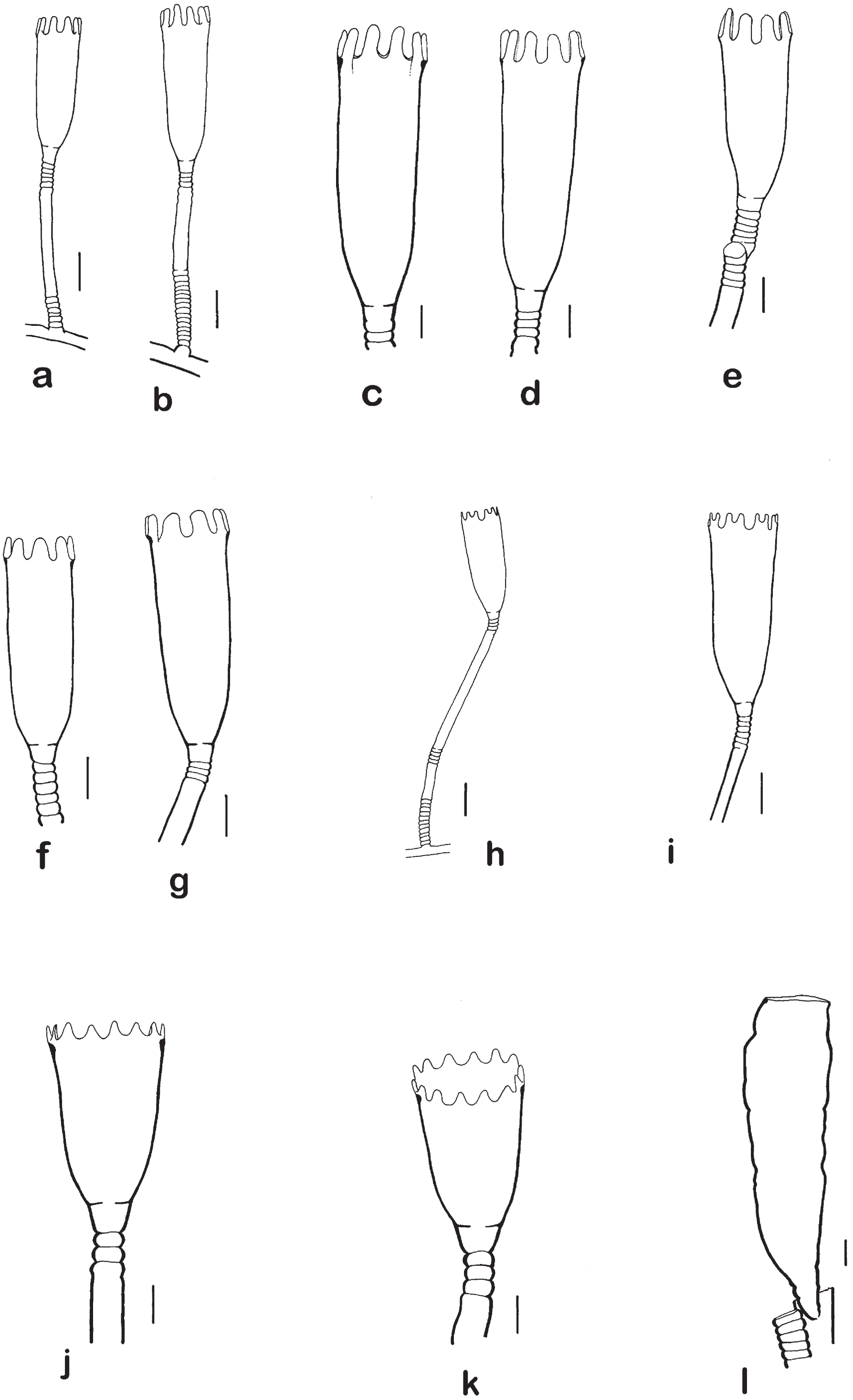

FIGURE 14. a, *Clytia joycei*, sp. nov., holotype: hydrotheca, pedicel and part of stolon, Sanibel Island, ROMIZ B4373. Scale equals 0.2 mm. **b, *Clytia joycei*, sp. nov., holotype:** hydrotheca, pedicel and part of stolon, Sanibel Island, ROMIZ B4373. Scale equals 0.2 mm. **c, *Clytia joycei*, sp. nov., holotype:** hydrotheca, Sanibel Island, ROMIZ B4373. Scale equals 0.1 mm. **d, *Clytia joycei*, sp. nov., holotype:** hydrotheca, Sanibel Island, ROMIZ B4373. Scale equals 0.1 mm. **e, *Clytia joycei*, sp. nov.:** part of colony with a hydrotheca, Bocas del Toro, Panama, ROMIZ B4375. Scale equals 0.1 mm. **f, *Clytia macrotheca*:** hydrotheca, Sanibel Island, ROMIZ B4420. Scale equals 0.1 mm. **g, *Clytia macrotheca*:** hydrotheca, Sanibel Island, ROMIZ B4420. Scale equals 0.1 mm. **h, *Clytia paulensis*:** pedicel and hydrotheca, Southwest Florida Shelf, ROMIZ B1742. Scale equals 0.1 mm. **i, *Clytia paulensis*:** hydrotheca and part of pedicel, Southwest Florida Shelf, ROMIZ B1742. Scale equals 0.1 mm. **j, *Clytia* sp.:** hydrotheca, Caloosahatchee River at Fort Myers, 18 July 2012, ROMIZ B4376. Scale equals 0.1 mm. **k, *Clytia* sp.:** hydrotheca, Caloosahatchee River at Fort Myers, ROMIZ B4376. Scale equals 0.1 mm. **l, *Clytia* sp.:** gonotheca, Caloosahatchee River at Fort Myers, ROMIZ B4376. Scale equals 0.1 mm.

A species of very shallow waters, *C. macrotheca* has been recorded from various substrates including algae, other hydroids, rocks, corals, *Halimeda*, *Rhizophora*, and miscellaneous invertebrates (Perkins 1908; Leloup 1935a; Calder 1990 [1991a], 1991c; Galea 2008, 2010; Oliveira *et al*. 2016). Although reported infrequently, the species is now known to occur in the warm western Atlantic from Bermuda (Calder 1990 [1991a]) to the Caribbean Sea (Galea 2008, 2010), and southwards to Brazil (Oliveira *et al*. 2016).

Nematocysts of two categories were observed in this hydroid (Fig. 15). They were identified as A-type b-mastigophores (7.1–8.0 long x 2.0–2.3 µm wide, undischarged, n=10, ROMIZ B4420) and B-type b-mastigophores (13.5–14.8 long x 2.8–4.0 µm wide, undischarged, n=10, ROMIZ B4420).

Reported distribution. ***Gulf coast of Florida.*** Dry Tortugas, Garden Key, Fort Jefferson, on an alga (Perkins 1908: 147, as *Campanularia macrotheca*).—Dry Tortugas (Leloup 1935a: 21, as *Laomedea macrotheca*).

Elsewhere in western North Atlantic. Bonaire: Lac, Soerebon, 0.2 m, on *Halecium bermudense* (Leloup 1935a: 21, as *Laomedea macrotheca*).—Bermuda: Whalebone Bay, ledges at entrance, on algae, 1 m + Walsingham Pond, entrance of underground passage, on rock, 1 m (Calder 1990 [1991a]: 64).—Belize: Twin Cays (Calder 1991b: 223).—French Lesser Antilles: Les Saintes, Terre-de-Haut, Pompierre Bay, 15°52'25"N, 61°34'15"W, on *Halimeda* in seagrass meadows + Terre-de-Haut, Pain de Sucre, 15°51'45"N, 61°35'60"W, on *Halimeda* from rocky shore (Galea 2008: 20).—French Lesser Antilles: Guadeloupe, Grande-Terre, mangrove of Petit Canal, 16°21.891'N, 61°30.137'W, 0.5 m (Galea 2010: 4).—Cuba: Havana, coral reef system west of the city (Castellanos *et al*. 2018: Supplementary Table S2, as *Clytia macroteca*).

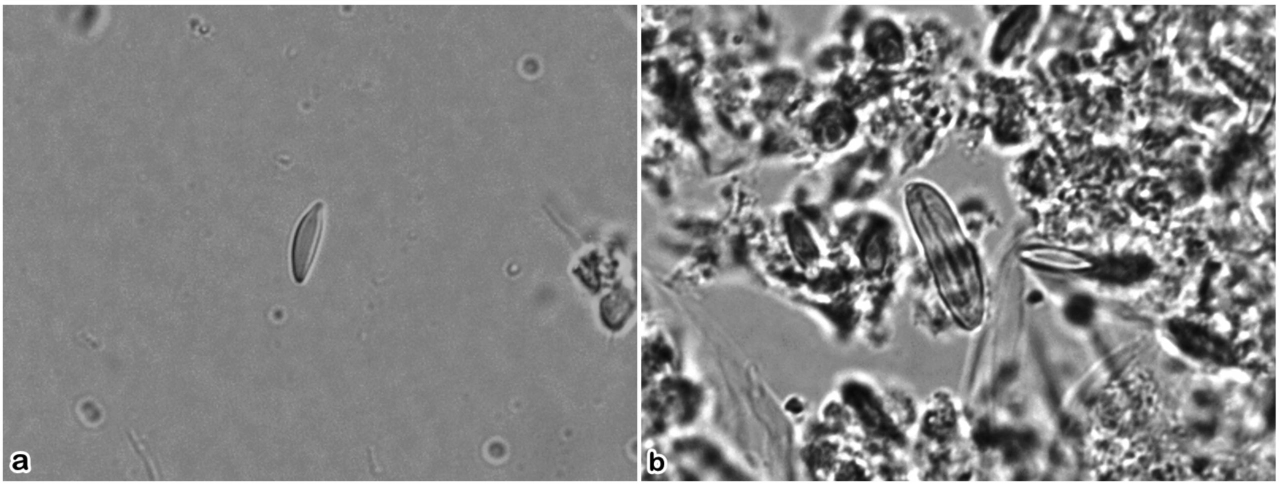

FIGURE 15. ***Clytia macrotheca*:** nematocysts, ROMIZ B4420. **a,** A-type b-mastigophore. **b,** B-type b-mastigophore.

Clytia paulensis (Vanhöffen, 1910)

Figs. 14h, i

Campanularia paulensis Vanhöffen, 1910: 298, figs. 19a, b.

Type locality. Île Saint-Paul, in the crater basin, shallow water (Vanhöffen 1910: 298).

Material examined. Southwest Florida Shelf, outer shelf northwest of the Dry Tortugas, 25°16.83'N, 83°57.35'W, 127 m, on *Lafoea coalescens*, 03 August 1981, triangle dredge, several colony fragments, up to 2.5 cm high, without gonophores, coll. Continental Shelf Associates, ROMIZ B1742.

Remarks. If they all belong to the same species, hydroid colonies reported under the binomen *Clytia paulensis* Vanhöffen, 1910 have a remarkable geographic distribution. Undescribed until its discovery just over a century ago in the crater basin of remote Île Saint-Paul in the southern Indian Ocean, the species was reported from Europe in 1919 (Stechow 1919: 45), from South Africa in 1923 (Stechow 1923a: 111), from Australia in 1924 (Stechow 1924: 69), from California in 1925 (Stechow 1925: 211), from eastern North America in 1971 (Calder 1971: 51), from Japan in 1995 (Hirohito 1995: 68), from eastern South America in 1997 (Grohmann *et al*. 1997: 231; Genzano & Zamponi 1997: 291; but not *C. paulensis* in Blanco 1968), and from western South America in 2007 (Galea 2007:

90). A report of the hydroid from the Antarctic (Naumov & Stepanjants 1972, as *Obelia paulensis*) is likely to have been based on a different species. Of particular interest, however, was the discovery of specimens in collections at the Natural History Museum, London, collected in 1899 by E.T. Browne from Devon, England (Cornelius 1982: 90; 1995b: 260). Those hydroids were not recognized as *C. paulensis* until 1978.

Given initial misgivings about the identity of hydroids from Chesapeake Bay as *C. paulensis*, specimens were compared with colonies of the species from South Africa provided by N.A.H. Millard (Calder 1971). Overlap was found in length and width measurements of pedicels, hydrothecae, and gonothecae in materials from the two regions. American specimens tended to have about one less marginal cusp, but that apparent difference was considered unimportant taxonomically and the two populations were taken to be conspecific. While hydrothecae of *C. paulensis* somewhat resemble those of *Obelia bidentata* Clark, 1875 and *O. oxydentata* Stechow, 1914 in having bimucronate marginal cusps, the colony form of the species differs in being mostly stolonal rather than erect with a distinct and regularly sympodial hydrocaulus. Measurements of hydrothecae and pedicels of specimens from southwest Florida, examined here, fell within or close to the range of specimens from Virginia and South Africa.

Clytia paulensis as generally conceived is a species of warm-temperate to tropical regions (Cornelius 1982, 1995b; Medel & Vervoort 2000; Peña Cantero & García Carrascosa 2002). Its reported distribution in the western North Atlantic, from the mid-Atlantic states of the USA (Calder 1971) to the Caribbean Sea (Calder 1991b; Calder & Kirkendale 2005), coincides with that concept. In Chesapeake Bay, at the northern end of its range on this coast, the species is active only during the warmer months of the year (May to November) (Calder 1990). Previous records from the Gulf of Mexico include those of Defenbaugh & Hopkins (1973) from Texas, Mendoza-Becerril *et al*. (2018b) from Mexico, and Castellanos *et al*. (2018) from the north coast of Cuba. This is the first account of it from the Gulf coast of Florida. *Clytia paulensis* has been reported from Brazil and Argentina in the western South Atlantic (Oliveira *et al*. 2016). *Clytia longitheca* Fraser, 1914, reported from British Columbia, Canada, to Oaxaca, Mexico (Fraser 1946 [1947a]), appears to be essentially indistinguishable from *C. paulensis* (Calder 1971; Peña Cantero & García Carrascosa 2002; Calder & Choong 2018).

Specimens examined here were found, as epizoites on the hydroid *Lafoea coalescens*, at a depth of 127 m. Hydrothecae were quite varied in size, as apparent from Figs. 14h and i. *Clytia paulensis* appears to be eurybathic, with a reported depth range from the intertidal zone to 4751 m (Cornelius 1995b; Fernandez & Marques 2018). Other hydroids are a frequent substrate of the species (Peña Cantero & García Carrascosa 2002), although those authors also mentioned reports of it from polychaete tubes, bryozoans, ascidians, mollusc shells, algae, sea grasses, stones, and anthozoans. Stechow (1923b) included a record of the species from spines of an echinoid, and specimens from Chesapeake Bay were found on sponges, hydroids, polychaete tubes, and mollusc shells (Calder 1971).

The medusa stage of *C. paulensis* is as yet unknown (Cornelius 1982, 1995b).

Reported distribution. ***Gulf coast of Florida.*** First record.

Elsewhere in western North Atlantic. USA: Virginia, York River (Tue Marsh Light; Ellen Island; off VEPCO power plant at Yorktown; Gloucester Point; Pages Rock) + James River (Old Point Comfort; Hampton Flats; Newport News Bar; Hampton Roads Middle Ground) + Chesapeake Bay (Chesapeake Bay Bridge-Tunnel, mid-span) (Calder 1971: 51).—USA: Texas, off Galveston (Defenbaugh & Hopkins 1973: 80, as *Clytia longitheca*).—USA: Georgia, outer continental shelf, 59–67 m (Wenner *et al*. 1983: 39).—Belize: Twin Cays (Calder 1991b: 223).—USA: South Carolina estuaries, Bulls Bay + Prices Creek + St. Helena Sound + Port Royal Sound (Calder & Hester 1978: 90).—Bermuda: Challenger Bank (Calder 2000: 1134).—Panama: Colón, Fort Sherman dock, wood, 09°22’12”N, 79°56’59”W, 0-2 m (Calder & Kirkendale 2005: 486).—USA: Florida, Off St. Lucie Inlet, 27°10.8’N, 80°00.8’W, 44 m (Calder 2013: 57).—Mexico: Alacranes Reef, on sponges, soft corals (Mendoza-Becerril *et al*. 2018b: 131).—Cuba: Havana, coral reef system west of the city (Castellanos *et al*. 2018: Supplementary Table S2).

Clytia sp.

Figs. 14j–l, 16

Material examined. Caloosahatchee River at Fort Myers, 26°38.790’N, 81°52.354’W, on floating dock, less than 1 m, 18 July 2012, 7‰, several colonies, up to 2.1 cm high, with gonophores, coll. D. Calder, ROMIZ B4376.

Remarks. Colonies of this species were found in abundance at a low-salinity site (7‰) in the estuary of the

Caloosahatchee River at Fort Myers, Florida. For a species of the genus *Clytia* Lamouroux, 1812, the hydroids were notably robust, mostly erect and branched, and large in size (to 2 cm or more). Although colonies with mostly smooth gonothecae were collected, they could not be assigned with confidence to *Clytia elsaeoswaldae* Stechow, 1914, or *C. gracilis* (M. Sars, 1850), or any other species of the genus *Clytia* discussed above.

Two types of nematocysts were observed in this hydroid (Fig. 16). They appear to correspond with A-type b-mastigophores (6.1–6.8 long x 1.6–2.0 µm wide, undischarged, n=10, ROMIZ B4376) and B-type b-mastigophores (9.0–10.3 long x 3.0–3.6 µm wide, undischarged, n=10, ROMIZ B4376). Those of the latter type (Fig. 16b) differ in size and shape from those of hydroids identified here as *C. elsaeoswaldae* (Figs. 11c, d), providing additional evidence that the two are specifically distinct.

Certain species of *Clytia* are known to inhabit brackish waters, but their identities remain obscure. One ecological equivalent is a hydroid identified by me (Calder 1971) as *Clytia hemisphaerica* (Linnaeus, 1767), found to be abundant in oligohaline waters (0.5–5‰) of both the Pamunkey River and the upper James River, Virginia, USA. I now regard that identification as questionable, even though *C. hemisphaerica* appears to be a euryhaline species (Cornelius 1995b: 254). Wedler (1973) identified hydroids from salinities above 20‰ in the brackish Ciénaga Grande of Santa Marta, Colombia, as *Laomedea tottoni* Leloup, 1935. That species, taken to be identical with *C. linearis* (Thornely, 1900), is different from material examined here.

I consider this species unidentifiable from presently known characters, and include it here simply as *Clytia* sp.

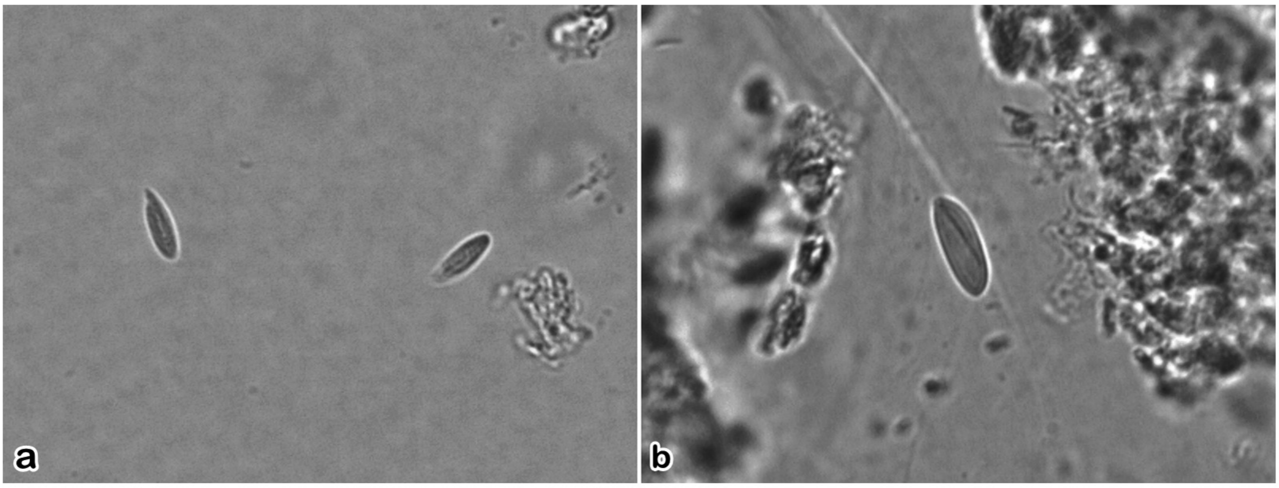

FIGURE 16. ***Clytia* sp.:** nematocysts, ROMIZ B4376. **a,** A-type b-mastigophores. **b,** B-type b-mastigophore.

Family Obeliidae Haeckel, 1879

Genus *Obelia* Péron & Lesueur, 1810

Obelia geniculata (Linnaeus, 1758)

Fig. 17a

Sertularia geniculata Linnaeus, 1758: 812.
Obelia geniculata.—Joyce, 1961: 57, pl. 12, figs. 3, 4.—Bros, 1987: 503.

Type locality. UK: Dover (see Cornelius 1975a: 273).

Material examined. Sanibel Island, beach at Lighthouse Point, 26°26’58”N, 82°01’04.5”W, on stranded *Sargassum pteropleuron*, 21 March 2018, 22° C, 34.5‰, two colonies, up to 4.5 mm high, without gonophores, coll. D. Calder, ROMIZ B4357.

Remarks. Of all the hydroids known to science, *Obelia geniculata* (Linnaeus, 1758) is likely one of the most familiar. Along with species of *Hydra* Linnaeus, 1758, it is often mentioned in science textbooks, studied in laboratories of introductory biology and invertebrate zoology, and used in experimental research. In being widespread in distribution, abundant over many parts of its range, easy to collect because of its occurrence in shallow waters, recognizable from its distinctive morphology, and addressed in many classic and influential early taxonomic works on hydroids (e.g., Johnston 1838, 1847; Hincks 1868 [1869], Nutting 1915; Fraser 1937, 1944), it has long been well-known. Long lists of references in publications such as those by Nutting (1915) and especially Medel & Vervoort (2000) attest to the volume of research undertaken on the species. While named early on by Linnaeus (1758: 812), as *Sertularia geniculata*, the synonymy of the species in that publication referred back even further in time to the "Knotted-thread Coralline" ("*Corallina minor repens caule nodoſo, articulato & veſiculis alternis inſtructo*") of Ellis (1755: 22, pl. 12, fig. b, B). Cornelius (1975a: 273) offered evidence that the account of this hydroid by Linnaeus was based solely on the illustration by Ellis, and that the type locality is likely to have been Dover, UK.

Distribution records of *O. geniculata* below suggest an essentially continuous range of the species on this coast from northern Hudson Bay and Hudson Strait (Fraser 1944; Calder 1970), and the west coast of Greenland (Kramp 1932: 66), to the southern Caribbean Sea (Versluys 1899; Wedler 1975; Flórez González 1983; Bandel & Wedler 1987). The hydroid has also been reported in the western South Atlantic from Brazil, Argentina, the Falkland Islands, and South Georgia (Oliveira *et al*. 2016). Hydroids identified as *O. geniculata* occur in the Pacific and Indian oceans (Fraser 1938a, b; Millard 1975; Hirohito 1995) as well as in the Atlantic.

While *O. geniculata* has generally been regarded as essentially cosmopolitan in shallow neritic waters, misgivings have existed whether this can be so based on the exceptionally wide reported distribution of the species, morphological variations in populations from one location to another, and more recently on differences in DNA. Latitudinally, the hydroid is believed to occur from subpolar to tropical waters, exceptional for a marine species. In New Zealand, Ralph (1956) found that hydroids assigned to *O. geniculata* from the subantarctic were eight times taller than those from subtropical locations. She also documented a poleward increase in the extent of branching and in the size of both internodes and gonothecae. Observed differences were attributed by her to latitudinal and water temperature effects, and she assigned no taxonomic significance to them. Ralph nevertheless recognized three forms of *O. geniculata*: forma *subtropica*, forma *intermedia*, and forma *subantarctica*. In their monograph on New Zealand leptothecates, Vervoort & Watson (2003) considered these forms to be unwarranted. In the western North Atlantic, morphological differences between populations from boreal (Passamaquoddy Bay, New Brunswick, Atlantic Canada) and temperate (Chesapeake Bay, Virginia, USA) regions have been documented (Calder 1971: 56, 57). While there was overlap in most characters considered, the cauline internodal perisarc of specimens from Virginia was always uniformly thin rather than being much thickened internally on the side beneath the hydrotheca, as in specimens from New Brunswick. Again, however, observed differences were interpreted as taxonomically unimportant. More significantly, and on a global scale, Govindarajan *et al*. (2005) detected considerable genetic differentiation and the possible existence of cryptic species in a study of hydroids assigned to *O. geniculata* from Canada (St. Andrews, New Brunswick), USA (Woods Hole, Massachusetts), France (Roscoff), Iceland (Garour/Sandgerdi), Japan (Misaki, Sagami Bay), and New Zealand (Wellington) based on comparisons of two mitochondrial markers in the populations. Three reciprocally monophyletic clades were detected, one from New Zealand, another from Japan, and a third from the North Atlantic (St. Andrews + Woods Hole + Garour/Sandgerdi + Roscoff). Govindarajan *et al*. suggested that these three clades may well represent different species. If the nominal species is eventually subdivided, the Atlantic population will retain the binomen *O. geniculata*, with that name having been applied originally to hydroids from northwest Europe. Low haplotype diversity within examined Atlantic populations was taken to be consistent with a more recent origin, perhaps by invasion from the North Pacific after the Bering Strait opened some 3.1–4.1 million years ago (Govindarajan *et al*. 2005).

In spite of their stunted colony form compared with hydroids of the boreal Atlantic, and their existence under warmer water temperatures, specimens from southwest Florida are retained here in *O. geniculata*. Comparisons are nevertheless warranted between populations from the cold-temperate North Atlantic (especially from the type locality in the UK) and those considered in this work from tropical and subtropical regions of the Americas.

For more on the taxonomy and nomenclature of this species, see Cornelius (1975a, 1995b) and Medel & Vervoort (2000).

Reported distribution. ***Gulf coast of Florida.*** Seahorse Key, on *Halodule* (Joyce 1961: 57).—Tampa Bay, ca. 1.5 km W of Ben T. Davis beach, on glass settlement plates, 1.8 m (Bros 1987: 503).

Elsewhere in western North Atlantic. Canada: Quebec, Gulf of St. Lawrence, on seaweeds (Dawson 1858: 408, as *Laomedea geniculata*).—USA: Massachusetts, Nahant + Naushon, shallow water, on *Laminaria* and other seaweeds (L. Agassiz 1862: 322, 352, as *Eucope diaphana*).—USA: Massachusetts, Nahant + Naushon, near low water, on *Fucus vesiculosus* (A. Agassiz 1865: 85, as *Eucope diaphana*).—USA: Massachusetts, Nahant + Nantasket (A. Agassiz 1865: 86, as *Eucope alternata*).—USA: Massachusetts, Nahant (A. Agassiz 1865: 87, as *Eucope polygena*).—USA: Massachusetts, Nahant (A. Agassiz 1865: 87, as *Eucope parasitica*).—USA: Massachusetts, Nahant (A. Agassiz 1865: 90, as *Eucope fusiformis*).—USA: Maine, Casco Bay, off Cape Elizabeth, near East and West Cod ledges + Casco Bay, among the islands, 8–30 ftm (15–55 m) (Verrill 1874a: 41, 44).—USA: Maine, Casco Bay, lower intertidal and tidepools + Casco Bay, Quahog Bay, low water (Verrill 1874b: 133, 136).—USA: Maine, Casco Bay off Cape Elizabeth, near East and West Cod ledges (Verrill 1874c: 359).—USA: Maine, Casco Bay, 8–30 ftm (15–55 m) + Casco Bay, rocky shores, intertidal + Casco Bay, Quahog Bay (Verrill 1874c: 364, 370, 374).—USA: Vineyard Sound and vicinity, rocky shores + sandy bottoms + outer rocky shores (Verrill 1874d: 327, 429, 489, as *Obelia diaphana*).—USA: Vineyard Sound and vicinity, rocky shores + rocky bottoms + gravelly and shelly bottoms + outer rocky shores (Verrill 1874d: 334, 411, 424, 489).—USA: Long Island Sound (Verrill 1874d: 727, as *Obelia diaphana* and *O. geniculata*).—USA: Massachusetts, Massachusetts Bay (Verrill 1874d: 727, as *Obelia diaphana*).—Canada: Labrador (Verrill 1874d: 727).—USA: Connecticut, near New Haven, common + Thimble Islands (Verrill 1874d: 727).—USA: Rhode Island, Watch Hill (Verrill 1874d: 727).—USA: Massachusetts, Vineyard Sound, 4–15 ftm (7–27 m) + Massachusetts Bay (Verrill 1874d: 727).—USA: Maine, Casco Bay (Verrill 1874d: 727).—Canada/USA: Bay of Fundy (Verrill 1874d: 727).—Canada: Gulf of St. Lawrence (Whiteaves 1874: 185).—USA: Massachusetts, Vineyard Sound (Verrill & Rathbun 1880: 229).—USA: Massachusetts, Provincetown, Long Point beach, inner shore, on floating *Fucus* (Rathbun 1880: 132).—USA: Massachusetts, Boston (Marktanner-Turneretscher 1890: 207).—USA: New England (Fewkes 1891: 87, as *Obelia diaphana*, *O. geniculata* and *O. fusiformis*).—Colombia: Bahía Honda, 5 m, on algae (Versluys 1899: 30).—USA: Massachusetts and north Atlantic coast, common, on *Fucus* and *Laminaria* (Hargitt 1901b: 382).—USA: Massachusetts, Woods Hole region, on docks, floating seaweed, etc., one of commonest species (Nutting 1901: 351).—USA: North Carolina, Beaufort, U.S. Bureau of Fisheries wharf (Fraser 1912: 362).—Canada: Quebec, Gaspé (Stafford 1912a: 59; 1912b: 72).—Canada: New Brunswick, St. Andrews (Stafford 1912b: 72).—Canada: Nova Scotia, Canso (Stafford 1912b: 72).—Canada: Quebec, Seven Islands (Sept-Îles) (Stafford 1912b: 72).—USA: Massachusetts, Vineyard Sound + Buzzards Bay, 1–16 ftm (2–29 m), on *Laminaria*, other seaweeds, pilings, floating timbers (Sumner *et al*. 2013: 569, as *Obelia geniculata*, in part).—Canada: Nova Scotia, Canso, low water, on *Laminaria*, seaweeds, pilings + Barrington Passage, 3 ftm (5 m) (Fraser 1913: 167).—USA: Massachusetts, Woods Hole (Nutting 1915: 76).—USA: Massachusetts, Georges Bank, on floating *Zostera* (Fraser 1915: 311).—Canada: New Brunswick, Bay of Fundy, Grand Manan Island (High Duck Island; Horse Island; Whale Cove off Swallowtail light) + The Wolves + north of Green Island + Bliss Island + Deer Island + St. Andrews, off Joe's Point (Fraser 1918: 350).—USA: Massachusetts, Woods Hole (Root 1922: 77; Hyman & Bellamy 1922: 330).—USA: Massachusetts, Woods Hole region, on eelgrass, rocks and rockweed, pilings (Allee 1923: 175).—Canada: New Brunswick, Miramichi River estuary, outside Portage and Fox islands, >15 m (Fraser 1926: 210).—Canada: Nova Scotia, Cape Breton, Eastern Harbour, along shore (Fraser 1927: 326).—Canada: Nova Scotia, Cape Breton, Aspy Bay, 20 m (Fraser 1927: 326).—Canada: Quebec, Magdalen Islands, Pleasant Bay (Baie de Plaisance), 15 m (Fraser 1927: 326).—Canada: Nova Scotia, Gulf of St. Lawrence, Cape Breton, Pleasant Bay (Grand Anse), 20-25 m (Fraser 1927: 326).—Canada: Quebec, St. Lawrence River near Trois Pistoles, on laminarians (Préfontaine 1932: 214).—Greenland: Fylla Bank (=Fyllas Bank, off Nuuk), abt. 64°N, 50 m, on *Laminaria* (Kramp 1932: 66, as *Laomedea geniculata*).—USA: Maine, Mount Desert region, attached to algae, shore to 60 feet (18 m) (Procter 1933: 120).—USA: New York, Montauk Point, on *Laminaria* (Conard 1935: 446).—USA: Connecticut, between Milford and New Haven (Leloup 1938: 1, 2, as *Laomedea geniculata*).—USA: Massachusetts, Nahant (Fraser 1943: 88).—USA: South Carolina, Charleston (Fraser 1943: 88).—Trinidad and Tobago, Trinidad, Maguaripe Bay (=Macqueripe Bay) (Fraser 1943: 88).—Canada: Nunavut, Hudson Strait, 3 miles (5 km) from Southhampton light (Fraser 1944: 160).—Canada: Nova Scotia, Minas Basin + Scots Bay + Cobequid Bay (Fraser 1944: 160).—Canada: Quebec, Matamek + Trois Pistoles, laminarian zone (Fraser 1944: 160).—Canada: Nova Scotia, near Halifax, Outer Halibut Island + White Island (Fraser 1944: 160).—USA: Maine, Eastport (Fraser 1944: 160).—USA: Maine, Casco Bay, 8–30 ftm (15–55 m) (Fraser 1944: 160).—USA: Maine, Quahog Bay, low water (Fraser 1944: 160).—USA: Massachusetts, Monomoy Point, from bird's stomach (Fraser 1944: 160).—USA: Massachusetts, Gloucester, near Eastern Point light, 45 ftm (82 m) (Fraser 1944: 160).—USA: Massachusetts, Little Stellwagen Basin N of Provincetown, 42°09'N, 70°13'W, 30 ftm (55 m) + Stellwagen Bank + Provincetown, Long Point + Provincetown, on stranded *Fucus* (Fraser 1944: 160).—USA:

Maine, Casco Bay, East and West Cod ledges (Fraser 1944: 160).—USA: Massachusetts, Nantucket Shoal, 15 ftm (27 m) (Fraser 1944: 160).—Atlantic Ocean: E of New Jersey, 40°00’45”N, 70°54’15”W, surface (Fraser 1944: 160).—USA: Massachusetts, Vineyard Sound, 10 ftm (18) (Fraser 1944: 160).—USA: Rhode Island, Narragansett Bay, near Fort Dumpling + off Newport, 11.25 ftm (21 m) + Block Island, off North light, 13 ftm (24 m) (Fraser 1944: 160).—USA: Connecticut, Long Island Sound, Noank (Fraser 1944: 160).—USA: New York, Long Island, Greenport, piles + Gardners Bay (Fraser 1944: 160).—USA: Delaware, offshore waters, surface, 38°29’N, 73°21’W (Fraser 1944: 160).—Antilles (Fraser 1944: 160).—USA: Maine, Boothbay Harbor, on *Laminaria*, producing gonangial buds (Berrill 1948: 94).—USA: Maine, Boothbay Harbor (Berrill 1950: 2).—USA: Texas, Sabine Pass, on buoy (Deevey 1950: 345).—Location unspecified: on buoys (Woods Hole Oceanographic Institution 1952: 187).—Canada: Nova Scotia, Minas Basin + Bass River, intertidal + Scots Bay, intertidal (Bousfield & Leim 1960: 14).—Canada: Quebec, Baie de Trois-Pistoles, on rocks and algae (Préfontaine & Brunel 1962: 246).—USA: Massachusetts, Woods Hole area, on floats, piles, *Laminaria* (Petersen 1964: 18).—USA: Massachusetts, Woods Hole area, studies on bioluminescence (Morin *et al*. 1968: 429; Morin & Reynolds 1969: 410; 1970: 430; 1974: 398; Morin & Cooke 1971a: 690; 1971b: 708; 1971c: 723; Morin & Hastings 1971: 305).—Canada: Nunavut, Hudson Bay, Coats Island, 62°57.5’N, 82°43’W, 18 m (Calder 1970: 1522).—USA: Virginia, York River (Tue Marsh Light; Guinea Neck; Perrin; Gloucester Point), on *Zostera* + Chesapeake Bay (New Point Comfort; Cape Charles), on *Zostera* (Calder 1971: 55).—Canada: New Brunswick, Passamaquoddy Bay (Calder 1971: 57).—USA: Texas, Galveston, on detached *Sargassum* (Defenbaugh & Hopkins 1973: 88).—USA: Texas, West Flower Garden Bank, on floating *Sargassum* (Defenbaugh 1974: 100).—USA: Connecticut, Noank, on *Laminaria* and *Zostera* (Clark 1975: 34, 40).—USA: Massachusetts, Cape Cod Bay, 2–33 m, 1.5° C–17° C, 30.16‰–32.49‰ (Calder 1975: 303).—Colombia: Santa Marta area, rocky littoral, on algae, *Zostera*, other hydroids (Wedler 1975: 340, as *Laomedea geniculata*).—USA: Rhode Island, Newport, on wood, 25 m (Cornelius 1975a: 276).—USA: Maine, South Harpswell, Potts Point, on *Fucus* (Cornelius 1975a: 276).—USA: Massachusetts, Vineyard Sound, on *Laminaria* (Cornelius 1975a: 276).—USA: Massachusetts, Nonamesset Island, Sheep Pen Harbor, 41°31’N, 70°40’40”W, on slate settling panels (Osman 1977: 48; 1978: 398).—Canada: New Brunswick, Bay of Fundy (Linkletter *et al*. 1977: 7; Henry 2003: 129; Henry & Kenchington 2004: 127).—USA: Massachusetts, Woods Hole (Harrigan & Alkon 1978: 433).—Canada: Nova Scotia, Minas Basin (Bromley 1979: 520; Bromley & Bleakney 1985: 22; both as *Laomedea geniculata*).—Canada: Quebec, Gulf of St. Lawrence, north shore and lower north shore, on navigation buoys (Fradette & Bourget 1980: 985; 1981: 139).—Colombia: Bahía de Cartagena region, 0.2–2.5 m, on the coast, some areas exposed to the sea (Flórez González 1983: 123).—USA: South Carolina, Murrells Inlet, jetties (Fox & Ruppert 1985: 93).—Colombia: Santa Marta area, rocky littoral, surf zone, on *Sargassum vulgare*, rocks (Bandel & Wedler 1987: 41).—USA: South Carolina, coastal areas, in stomachs of Atlantic spadefish (Hayse 1990: 81).—USA: Maine, York, Cape Neddick, ca. 43°10’N, 70°36’W, on *Laminaria*, with nudibranch predators (Lambert 1991: 36; 1993: 116; Berman *et al*. 1992: 437; Lambert *et al*. 1992: 304).—Canada: Quebec, St. Lawrence River estuary + Gaspé + Anticosti Island (Île d’Anticosti) + Gulf of St. Lawrence, north shore, all on navigation buoys (Ardisson & Bourget 1992: 24).—USA: Georgia, St. Catherines Island, Northwest Marsh (Prezant *et al*. 2002: 8).—USA: New Hampshire, Portsmouth, Coast Guard Station pilings (Frick 2003: 369).—USA: Massachusetts, Woods Hole (Naranjo *et al*. 1994: 1300).—Canada: Northumberland Strait, 5–32 m, 6.2° to 16.2° C (Calder 2004a: 559).—USA: Maine, Cobscook Bay (Trott 2004: 272).—USA: Maine, Eastport (Sisson 2005: 1725).—Canada: New Brunswick, St. Andrews (Govindarajan *et al*. 2005: 214).—USA: Massachusetts, Woods Hole (Govindarajan *et al*. 2005: 214).—Canada: Nova Scotia, Western Bank (Henry *et al*. 2006: 68).—USA: Rhode Island, Point Judith Pond, 41°23’N, 71°31’W (Maranda *et al*. 2007: 627).—USA: Virginia, Yorktown, on experimental substrates (Bullard *et al*. 2010: 589).—Cuba: “Oriente”, but without precise location, on *Emerita talpoida* (Varela 2012: 6).—USA: Florida, off Fort Pierce, between Capron Shoal and the beach, on *Thyroscyphus ramosus* + Hutchinson Island, Walton Rocks area, 27°20’19”N, 80°13’59”W, on algae + Fort Pierce Inlet, north jetty, 27°28’24.2”N, 80°17’20.3”W, on *Thyroscyphus ramosus*, 0.1 m + Sebastian Inlet, 27°51’43”N, 80°26’47”W, on stranded *Sargassum* (Calder 2013: 57, 58).—USA: Maine, South Freeport (Cunha *et al*. 2017: 121).—USA: New Hampshire, New Castle (Cunha *et al*. 2017: 121).—Canada: New Brunswick, Deer Island, Fairhaven, <1 m, on kelp (Calder 2017: 81).—Canada: Nova Scotia, Digby Neck, Sandy Cove, intertidal (Calder 2017: 81).—Canada: Nova Scotia, Black Rock, Canada Creek, in tidepool, on algae (Calder 2017: 81).—Canada: Nova Scotia, Petit Passage, south of East Ferry, extreme low tide (Calder 2017: 81).—Canada: New Brunswick, St. Andrews, on pontoon slip of wharf at Atlantic Biological Station, <1 m (Calder 2017: 81).—Canada: Nova Scotia, Brier Island, Westport, on kelp on floating dock, <1 m (Calder 2017: 81).—Canada: New Brunswick, Deer Island, Richardson, on pontoon slip of wharf, <1 m, on *Agarum cribrosum* (Calder 2017: 81).—USA: Maine, Eastport, Harris Point, on *Ascophyllum nodosum* and *Laminaria* sp., <1 m (Calder 2017: 81).—Caribbean Sea (Wedler 2017b: 98, figs. 90, 90A–C).

Obelia hyalina Clarke, 1879

Fig. 17b, 18

Obelia hyalina Clarke, 1879: 241, pl. 4, fig. 21.—Fraser, 1943: 89; 1944: 160.—Shier, 1965: 40, pl. 22.
Obelia dichotoma.—Wallace, 1909: 137 [not *Obelia dichotoma* (Linnaeus, 1758)].

Type locality. Mexico: "Ten miles (16 km) north of Zoblos Island" (= Isla Holbox) (Clarke 1879: 242).

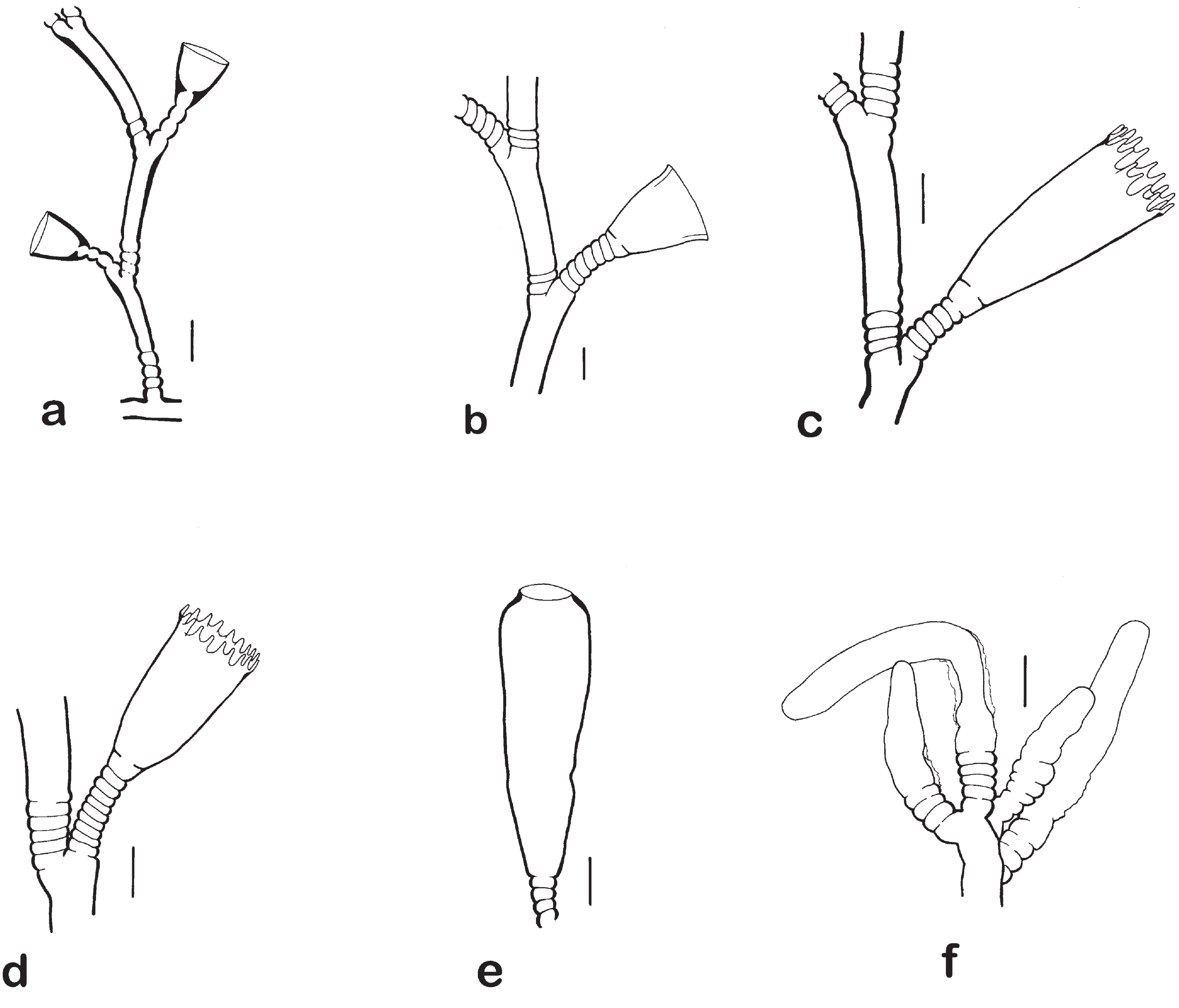

FIGURE 17. a, *Obelia geniculata*: basal part of hydrocaulus with two hydrothecae, Sanibel Island, ROMIZ B4357. Scale equals 0.2 mm. **b, *Obelia hyalina*:** part of hydrocaulus with a hydrotheca, Fort Myers Beach, ROMIZ B4358. Scale equals 0.1 mm. **c, *Obelia oxydentata*:** part of hydrocaulus with a hydrotheca, Sanibel Island, ROMIZ B4364. Scale equals 0.1 mm. **d, *Obelia oxydentata*:** part of hydrocaulus with a hydrotheca, Caloosahatchee River at Fort Myers, ROMIZ B4362. Scale equals 0.1 mm. **e, *Obelia oxydentata*:** gonotheca, Caloosahatchee River at Fort Myers, ROMIZ B4362. Scale equals 0.1 mm. **f, *Obelia oxydentata*:** colony undergoing stolonization from the hydrocaulus, Caloosahatchee River at Fort Myers, ROMIZ B4362. Scale equals 0.1 mm.

Material examined. Fort Myers Beach, on stranded shell with *Idiellana pristis*, 01 March 2013, one colony, 7 mm high, without gonophores, coll. D. Calder, ROMIZ B4358.—Fort Myers Beach, on dead sand dollars (*Mellita quinquiesperforata*) near low water, 19 January 2018, several colony fragments, up to 1.4 mm high, without gonothecae, coll. D. Calder, ROMIZ B4359.—Captiva Island, Turner Beach, 26°28'57.3"N, 82°11'02.8"W, on jetty, rocks at low tide, 01 March 2018, several colony fragments, up to 9 mm high, without gonothecae, coll. D. Calder, ROMIZ B4360.—Sanibel Island, beach at Lighthouse Point, 26°26'57"N, 82°01'06"W, on detached *Thalassia* at water's edge, 13 March 2018, 20° C, 33.5‰, one colony, 6 mm high, without gonophores, coll. D. Calder, ROMIZ B4361.

Remarks. *Obelia hyalina* was generally recognized as a valid species over the first half of the 20th century. Thereafter, it was treated in most works as conspecific with the supposedly cosmopolitan *O. dichotoma* (Linnaeus, 1758). Once again, for reasons outlined in a previous study (Calder 2013), *O. hyalina* is recognized as valid here. Separating records of the two species in accounts by authors who had combined them under one binomen is problematic. Reports of the boreal *O. dichotoma* from the Gulf of Mexico and Caribbean regions are taken here, and in distribution records below, to have been based on specimens of the tropical and warm-temperate *O. hyalina*. Morphologically, *O. hyalina* differs from *O. dichotoma* in a number of characters: (1) colonies are small (<2.5 cm high); (2) hydrocauli are little if at all branched, and are almost always monosiphonic; (3) hydrothecae lack distal longitudinal folds; (4) hydrothecal rims are entire rather than crenulate or slightly so.

Differences in cnidome have been found to exist in polyps of certain species of *Obelia* Péron & Lesueur, 1810 from Europe (Östman 1982, 1987, 1999). In *O. dichotoma*, the nematocyst complement consists of so-called A-type b-rhabdoids (microbasic b-mastigophores), as well as curved and exceedingly slender I_d-type isorhizas and curved but somewhat thicker I_D-type isorhizas. The cnidome of specimens from southwest Florida identified as *O. hyalina* (Fig. 18) comprises nematocysts like the first two types, with the third resembling I_g-type isorhizas found in *O. geniculata* (Linnaeus, 1758) (Östman 1982, 1999). Most abundant in material examined here were A-type b-mastigophores (5.3–5.8 long x 1.5–1.8 µm wide, undischarged, n=10, ROMIZ B4361), although I_g-type isorhizas (7.1–8.2 long x 0.8–1.3 µm wide, n=10, undischarged, ROMIZ B4361) and I_d-type isorhizas (6.2–7.3 long x 0.4–0.7 µm wide, undischarged, n=10, ROMIZ B4361) were also well-represented. The presence of isorhizas more closely resembling the I_g-type rather than the I_D-type in these specimens is taken as additional evidence that *O. hyalina* is distinct from *O. dichotoma*.

As with other species of the genus *Obelia*, *O. hyalina* is known to have a metagenetic life cycle. Its newly liberated medusa stage was described by Vannucci (1955), based on specimens from Brazil. Medusae of *Obelia*, including those of *O. hyalina*, are reduced and morphologically unique. Unusual characters of note include: (1) presence of an umbrella that is flattened and disc-shaped, with thin and flexible mesoglea; (2) marginal tentacles that are solid, short, stiff, essentially inextensible, and with endodermal bases projecting into the mesoglea of the umbrella margin; (3) a velum that is rudimentary or absent. While *Obelia* medusae are thereby highly distinctive, those liberated by the various hydroid species of the genus are so alike in morphology that they have long been considered essentially indistinguishable (Russell 1953: 297; Kramp 1959: 146). An overview of the medusoid characters of *Obelia* has been given by Cornelius (1975a, 1990, 1995b, 1999), and others.

In being a component of the biota associated with pelagic *Sargassum*, *O. hyalina* is transported wherever floating gulfweed is carried by ocean currents. Thus, it has been reported to the east of Nova Scotia in the Gulf Stream (Fraser 1918), from mid-ocean (43.4°N, 31°W) in the North Atlantic Drift (Leloup 1935), and from across the Sargasso Sea (Timmermann 1932), as well as from tropical and warm-temperate inshore waters. However, its normal range in the western North Atlantic appears to be from North Carolina (Fraser 1912b; Wells *et al*. 1964; Cain 1972) to the southern Caribbean Sea (Leloup 1935; Wedler 1975, as *Laomedea congdoni*), and from there southwards to Brazil in the western South Atlantic (Vannucci 1955).

Among subjective synonyms of *O. hyalina* are *O. congdoni* Hargitt, 1909, *Laomedea sargassi* Broch, 1913, and *Gonothyraea integra* Fraser, 1940, found on sunken *Sargassum* off Block Island, Rhode Island (Calder & Choong 2018). Additional comments on the hydroid of *O. hyalina* are given elsewhere (Calder 2013).

Reported distribution. *Gulf coast of Florida.* Dry Tortugas (Wallace 1909: 137, as *Obelia dichotoma*).—Key West (Fraser 1943: 89).—SW of Key West, Eastern Dry Rocks, on reefs (Fraser 1943: 89).—Key West (Fraser 1944: 161).—Cape San Blas area, on *Syringodium* and *Diplanthera* (=*Halodule*) (Shier 1965: 119).

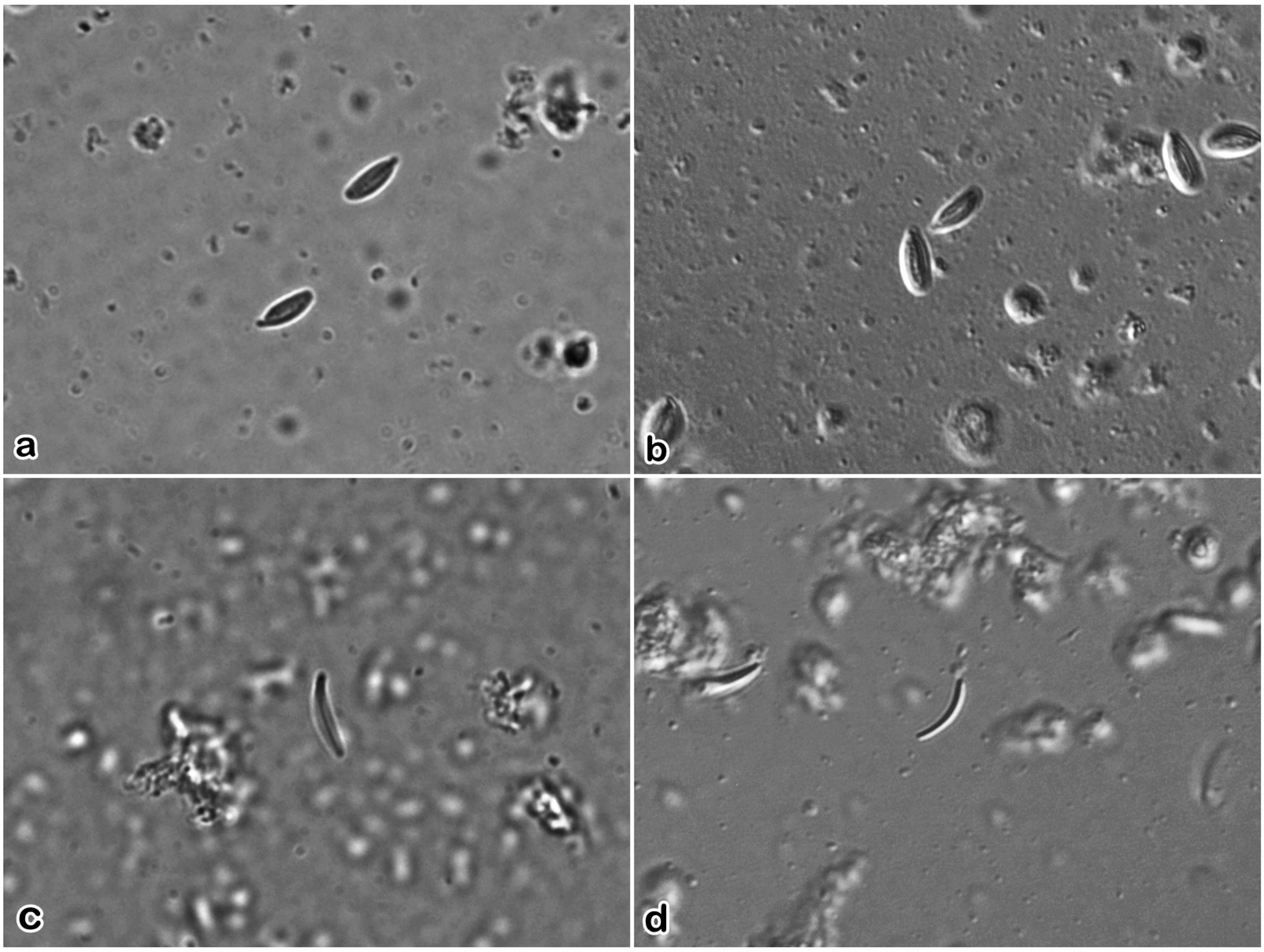

FIGURE 18. ***Obelia hyalina*****:** nematocysts, ROMIZ B4361. **a,** A-type b-mastigophores. **b,** A-type b-mastigophores (?). **c,** I_g-type isorhiza. **d,** I_d-type isorhiza.

Elsewhere in western North Atlantic. Mexico: 10 miles (16 km) N of "Zoblos Island" (= Isla Holbox) (Clarke 1879: 242).—USA: Gulf Stream, unstated location off the southeastern US, on gulfweed (Nutting 1895: 30).—Cuba: near Havana, off Morro Castle, "*Pentacrinus* Grounds", on floating seaweed (Nutting 1895: plate after p. 88, as *Obella hyalina*).—Sargasso Sea: SE of Bermuda, 30°N, 70°W, on floating *Sargassum* (Versluys 1899: 30).—Bermuda: shallow water areas, on sponges, algae, large hydroids (Congdon 1907: 468).—USA: Massachusetts, Woods Hole, on floating gulfweed (Hargitt 1909: 375, as *Obelia congdoni*).—USA: Louisiana, abundant on stranded gulfweed and floating wood in spring (Cary & Spaulding 1909: 6, as *Obelia dichotoma*).—USA: North Carolina, Beaufort area, off Bogue Bank, on *Sargassum* + Marshallberg, pilings, on ascidians + dredged offshore, on sponge (Fraser 1912b: 363).—Cuba: Havana Harbor, on a buoy and a mussel (Stechow 1914: 130, as *Obelia dichotoma*).—USA: North Carolina, Beaufort (Nutting 1915: 76).—Canada: E of Nova Scotia in the Gulf Stream, on *Sargassum* (Fraser 1918: 350).—Bermuda: on floating *Sargassum* + Agar's Island, on a fish-car (Bennitt 1922: 249).—Sargasso Sea, on *Sargassum* (Hentschel 1922: 4, as *Laomedea sargassi*).—Sargasso Sea: numerous stations (23), on *Sargassum* (Timmermann 1932: 297–303).—Bonaire: Plaja Flambaai, on stranded algae (Leloup 1935: 24, as *Laomedea sargassi*).—Aruba: Boca Prins, on stranded *Sargassum* (Leloup 1935: 24, as *Laomedea sargassi*).—Sargasso Sea: 29°N, 44°W, on *Sargassum* + 30°N, 54°W, on *Sargassum* (Leloup 1935: 24, as *Laomedea sargassi*).—North Atlantic Drift: 43.4°N, 31°W, on *Sargassum* (Leloup 1935: 24, as *Laomedea sargassi*).—Sargasso Sea: E of Florida, 29°50'N, 74°W, on floating *Sargassum* + SE of Bermuda, 30°11'N, 71°08'W, on floating *Sargassum* + W of Bermuda, 32°07'N, 66°35'W, on floating *Sargassum* (Leloup 1937: 101, as *Laomedea sargassi*).—USA: Texas, Corpus Christi Bay (Cross & Parks 1937: 9, as *Obelia dichotoma*).—Gulf Stream, on pelagic *Sargassum* + Sargasso Sea, on pelagic *Sargassum* (Burkenroad, in Parr 1939: 24, as *Obelia*).—USA: Rhode Island, Block Island, 1.25 miles (2 km) from North Light, on sunken *Sargassum*, 13 ftm (24 m) (Fraser 1940: 577, as *Gonothyraea integra*).—Gulf Stream: seaward of continental shelf E of Delaware, 130–167 miles (209–269 km) S of Nantucket (Massachusetts), surface, on gulfweed + 100 miles (161 km) E of Cape Hatteras, on *Sargassum* (Fraser 1943: 89).—?USA: New Jersey, on crustaceans parasitic in mouth of the shark *Odontaspis* (Fraser 1943: 89).—Haiti: Jérémie, on gulfweed (Fraser 1943: 89).—Canada: Nova Scotia, S of Cape Sable, 41°43'N, 65°21'50"W, 1309 ftm (2394 m) (on sunken *Sargassum*?) (Fraser 1944: 161).—USA: Massachusetts, S of Marthas Vineyard, 39°57'30"N, 70°51'15"W, 150 ftm (274 m), (on sunken *Sargassum*?) (Fraser 1944: 161).—USA: Massachusetts, S of Nantucket, 38°59'N, 70°07'W, 1544 ftm (2824 m) (?on sunken *Sargassum*?) (Fraser 1944: 161).—USA: Massachusetts, off Marthas Vineyard, 38°25'N, 72°40'W, on floating *Sargassum* (Fraser 1944: 161).—USA: Florida, Florida Straits, on *Sargassum* (Fraser 1944: 161).—Cuba: off Havana, on *Sargassum* (Fraser 1944: 161).—?USA: Louisiana coast (Fraser 1944: 157, as *Obelia equilateralis*).—Sargasso Sea: on *Sargassum* (Vervoort 1946: 346, as *Laomedea sargassi*).—?Panama: Caledonia Bay (Puerto Escoces), on hand line on rocky reef (Fraser 1947b: 7, as *Obelia equilateralis*).—USA: Florida, Biscayne Bay, on boat slips (Weiss 1948: 158).—USA: Texas, off Sabine Pass, on buoys + Galveston Bay, on buoy + Sabine Bank, on buoys + off Freeport, on buoys + Matagorda Island, on buoys + Port Aransas, on driftwood, blue crab, oysters, *Sargassum*, tar + Port Aransas, on south jetty (Deevey 1950: 343, as *Obelia dichotoma*).—USA: Texas, Port Aransas, jetties (Hedgpeth 1950: 73, as *Obelia dichotoma*).—USA: Louisiana, Grand Isle, on *Sargassum* (Behre 1950: 7).—Unstated location: on buoys (Woods Hole Oceanographic Institution 1952: 187).—USA: Mississippi, Mississippi Sound (Fincher 1955: 92, as *Obelia gracilis*).—USA: North Carolina, Core Banks, on *Aequipecten gibbus*, 17–20 ftm (31–37 m) (Wells *et al*. 1964: 566).—Venezuela: "La Guaria" (= La Guaira) (Vervoort 1968: 23, as *Laomedea* (*Obelia*) *congdoni*).—USA: North Carolina, *Lithothamnion* reef S of Cape Lookout (Cain 1972: 80).—USA: Texas, Galveston, on wooden pilings, submerged debris, *Sargassum*, blue crabs, *Thais*, hydroids (Defenbaugh & Hopkins 1973: 86, as *Obelia dichotoma*).—USA: Texas, West Flower Garden Bank, on glass float, float cable, floating *Sargassum* (Defenbaugh 1974: 99, as *Obelia dichotoma*).—Sargasso Sea + Gulf Stream, several stations between Florida and New Jersey, on *Sargassum natans* I, *S. natans* IX, *S. fluitans* III, *S. fluitans*, *S. ramifolium*, *S. filipendula, S. polyceratium*, *S. pteropleuron, S. bermudense*, *Sargassum* sp. (Rackley 1974: 32).—Colombia: Santa Marta area, rocky littoral (Wedler 1975: 340, as *Laomedea congdoni*; Bandel & Wedler 1986: 41, as *Obelia dichotoma*).—Colombia: north coast (Mergner 1977: 122, as *Laomedea* (*Obelia*) *congdoni*; 1987: 187, as *Laomedea* (*Obelia*) *congdoni*).—USA: Florida, southeast coast (Mergner 1977: 122, as *Laomedea* (*Obelia*) *congdoni*; 1987: 187, as *Laomedea* (*Obelia*) *congdoni*).—USA: South Carolina, estuaries, unstated locations (Calder & Hester 1978: 90).—USA: Texas, Buccaneer oil field, on oil platform (Fotheringham 1981: 194).—Belize: Carrie Bow Cay area, on *Thalassia*, mangrove roots, floating *Sargassum*, dead corals and gorgonians (Spracklin 1982: 249, as *Obelia dichotoma*).—USA: continental shelf off South Carolina and Georgia (Wenner *et al*. 1983, as *Obelia dichotoma*).—USA: South Carolina, inner (17–18 m), middle (32–36 m) and outer (46–69 m) continental shelf, + Georgia, inner (17–22 m), middle (23–29 m) and outer (59–67 m) continental shelf (Wenner *et al*. 1984: 20, 39, as *Obelia dichotoma*).—Colombia: Bahía de Cartagena region (Flórez González 1983: 123, as *Obelia dichotoma*).—USA: South Carolina, North Inlet area, Town Creek and tributaries + North Inlet, Baruch Plantation, oyster landing + North Inlet, pilings + Murrells Inlet, jetties + Murrells Inlet, Capt. Dick's marina, floating docks + Charleston area + Breach Inlet, jetties + Isle of Palms, marina, floating docks + Hunting Island, seawalls and rubble + Beaufort area, floating docks (Fox & Ruppert 1985: 61, 76, 84, 93, 104, 141, 167, 177, 226, 232, as *Obelia dichotoma*).—Bermuda: shallow inshore waters, buoy chains (Calder 1986: 136, as *Obelia dichotoma*).—Sargasso Sea: on *Sargassum natans* (Niermann 1986: 347, as *Obelia dichotoma*).—USA: Louisiana, on coastal petroleum platforms (Lewbel *et al*. 1987: 214, as *Obelia dichotoma*).—USA: South Carolina, continental shelf, fouling plates (Van Dolah *et al*. 1988: 684, as *Obelia dichotoma*).—USA: South Carolina and Georgia, inner continental shelf, on artificial reefs (Wendt *et al*. 1989: 1112, as *Obelia dichotoma*).—USA: South Carolina, coastal areas, in stomachs of Atlantic spadefish (Hayse 1990: 81, as *Obelia dichotoma*).—Bermuda: Flatts Inlet, 0.5–2 m, on rock, algae, *Thyroscyphus marginatus*, barnacle + Whalebone Bay, on pelagic *Sargassum* + Ferry Reach, 3 m, on float line + Atlantic Ocean, 2 km SE of Castle Roads, 0–10 m, on pelagic *Sargassum* and polypropylene trap lines + Green Bay Cave, 40 m inside, 5–6 m depth, on *Eudendrium* sp. + Natural Arches Beach, on stranded *Sargassum* (Calder 1990 [1991a]: 73–74, as *Obelia dichotoma*).—Belize: Twin Cays (Calder 1991b: 223, as *Obelia dichotoma*).—Belize: South Water Cay, South Water Cut, on *Thalassia* (Kaehler & Hughes 1992: 331, as *Obelia dichotoma*).—USA: Florida, off Vero Beach, on artificial reef (Nelson *et al*. 1994: 1306).—Bermuda: various locations, on *Sargassum natans*, *S. fluitans* (Calder 1995: as *Obelia dichotoma*).—Cuba: north coast (Ortiz Rosado 2000: 87, as

Obelia dichotoma).—Bermuda: Argus (=Plantagenet) Bank + Challenger Bank (Calder 2000: 1134, as *Obelia dichotoma*).—Cuba: Ciudad de La Habana province, Cojimar, on *Sargassum* (Ortiz 2001a: 64, as *Campanularia* cf. *angulata*).—Panama: Canal Zone, Atlantic side, Buoy #6 + Colón, Fort Sherman dock, wood, 09°22'12"N, 79°56'59"W, 0-2 m + Colón, Club Nautico, steel pilings, 09°21'51"N, 79°53'39"W, 0-1 m + Bocas del Toro area, Crawl Cay, 09°15.261'N, 82°07.787'W, 2–4 m + Bocas del Toro area, Swan's Key, 09°27'12.2"N, 82°18'01.8"W, 1-4 m + Bocas del Toro area, Bastimentos (north), 09°20.898'N, 82°09.959'W, 1–4 m + Bocas del Toro area, Drago 2, 1–2 m + Bocas del Toro area, Drago 2, 2–4 m (Calder & Kirkendale 2005: 487, as *Obelia dichotoma*).—USA: Florida, Canaveral National Seashore, on *Caretta caretta* (Pfaller *et al*. 2008: 1097, as *Obelia dichotoma*; Reich *et al*. 2010: 117, as *Obelia dichotoma*).—French Lesser Antilles: Guadeloupe, Grande-Terre, L'Oeil, 16°26.782'N, 61°32.405'W, 12–15 m, on gorgonian + Grande-Terre, Pointe d'Antigues, 16°26.251'N, 61°32.523'W, 10 m, on gorgonian + Grande-Terre, Passe à Colas, 16°21.269'N, 61°34.193'W, 10–15 m, on sponge (Galea 2010: 9, as *Obelia dichotoma*).—USA: Florida, Fort Pierce, Fort Pierce Inlet State Park, 27°28'29.5"N, 80°17'25.8"W, on stranded *Sargassum fluitans* (Calder 2013: 58).—French Lesser Antilles: Martinique (Galea 2013: 49, as *Obelia dichotoma*).—Caribbean Sea (Wedler 2017b: 96, figs. 87A, B, 88, 89, as *Obelia dichotoma*).—Mexico: Alacranes Reef, on algae, sponges, hydroids, soft corals, ascidians, rock, artificial reef (Mendoza-Becerril *et al*. 2018b: 131, as *Obelia dichotoma*).—Cuba: Havana, coral reef system west of the city (Castellanos *et al*. 2018: 572, Supplementary Table S2, as *Obelia dichotoma*).—Panama: Bocas del Toro area, Punta Hospital + Crawl Cay (Miglietta *et al*. 2018b: 108).

***Obelia oxydentata* Stechow, 1914**

Figs. 17c–f

Obelia(?) *oxydentata* Stechow, 1914: 131, fig. 7.
?*Laomedea bicuspidata*.—Leloup, 1937: 99, figs. 4A, B [not *Obelia bicuspidata* Clark, 1875 = *O. bidentata* Clark, 1875].
Obelia bicuspidata.—Fraser, 1944: 154.—Deevey, 1950: 343; 1954: 270 [not *Obelia bicuspidata* Clark, 1875 = *O. bidentata* Clark, 1875].
Obelia oxydentata.—Joyce, 1961: 56, pl. 12, figs. 1, 2.
Clytia longicyatha.—Shier, 1965: 39, pl. 21 [not *Obelia longicyatha* Allman, 1877].

Type locality. Virgin Islands of the United States: St. Thomas, Charlotte Amalie (Stechow 1914: 131).

Material examined. Caloosahatchee River at Fort Myers, 26°38.788'N, 81°52.356'W, on floating dock, less than 1 m, 25 March 2012, 25° C, 17‰, several colonies, up to 1.2 cm high, with gonophores, coll. D. Calder, ROMIZ B4362.—Caloosahatchee River at Fort Myers, 26°38.790'N, 81°52.354'W, on floating dock, less than 1 m, 18 July 2012, 7‰, several colonies, up to 10 mm high, with gonophores, coll. D. Calder, ROMIZ B4363.—Sanibel Island, beach at Lighthouse Point, 26°26'57"N, 82°01'07"W, on a detached alga, in intertidal pool, 03 August 2014, one colony, 5 mm high, without gonophores, coll. D. Calder, ROMIZ B4364.—Fort Myers Beach, on detached *Thalassia testudinum*, 30 October 2017, one colony, 5 mm high, without gonophores, coll. D. Calder, ROMIZ B4365.—Fort Myers Beach, Salty Sam's Marina, 26°27'21.7"N, 81°56'34.6"W, on floating dock on oyster shells, algae, and *Calyptospadix cerulea*, <0.1 m, 24 C, 22 February 2018, three colonies, up to 1 cm high, without gonophores, coll. D. Calder, ROMIZ B4366.—Sanibel Island, beach at Lighthouse Point, 26°26'57"N, 82°01'06"W, on detached *Thalassia* at water's edge, 13 March 2018, 20° C, 33.5‰, one colony, 4 mm high, without gonophores, coll. D. Calder, ROMIZ B4367.—Caloosahatchee River at Fort Myers, 26°38.788'N, 81°52.356'W, on floating dock, less than 1 m, 29 March 2018, 22° C, 15‰, several colonies, up to 1 cm high, condition very good, without gonophores, coll. D. Calder, ROMIZ B4368.

Remarks. Reasons for recognizing *Obelia oxydentata* Stechow, 1914 as distinct from *O. bidentata* Clark, 1875 have been discussed earlier (Calder 2013, 2017; Calder *et al*. 2019). Supporting evidence exists from differences in colony morphology and geographic distribution, and most recently from the results of molecular studies. Hydroids of *O. bidentata* (type locality: Greenport, Long Island, New York) are large (commonly 5–10 cm but reaching as much as much as 35 cm high) and polysiphonic when fully developed, and they occur in temperate to cool-temperate regions. Those of *O. oxydentata* (type locality: U.S. Virgin Islands) are tiny (usually 1-2 cm high or less) and monosiphonic, even when fertile, and they inhabit tropical and warm-temperate waters. While evidence from molecular studies is thus far indirect (e.g., Govindarajan *et al*. 2006; Leclere *et al*. 2009), populations identified as *O.*

bidentata from North Carolina (but probably referable to *O. oxydentata*) appear to be genetically distinct from those collected in northwest Europe (likely identified correctly as *O. bidentata*).

From the records below, *O. oxydentata* can be regarded primarily as a species of shallow and more or less sheltered inshore waters, including harbours, rivers, canals, bayous, lagoons, seagrass beds, and mangrove swamps. It has also been reported as part of the floating *Sargassum* fauna (e.g., Fraser 1944; Defenbaugh & Hopkins 1973; both as *O. bicuspidata*). In the region studied here, no record of *O. oxydentata* was found below a depth of 18 m and most were much less. *Obelia oxydentata* also is a decidedly euryhaline species, having been collected during this study at salinities as low as 7‰. As a species forming part of the fouling community in harbours (Calder *et al*. 2019), it has likely been transported widely by shipping.

Hydroids identified as *Clytia longicyatha* (Allman, 1877) by Shier (1965) from northern Florida appear to correspond with *O. oxydentata* as understood here, although they were said to be fascicled at the base. They reached a height of only 6–12 mm, yet gonothecae were observed on the colonies. Certain other reports of *C. longicyatha* from the warm western North Atlantic (distribution records listed in Fraser 1944) may also have been based on *O. oxydentata*. *Clytia longicyatha*, dredged off the Florida reef at a depth of 90 fathoms (165 m) (Allman 1877), has incorrectly been considered a synonym of *O. bidentata* in some contemporary works (Calder 1991). The species, described by Allman as being about 2.5 cm high and with a fascicled stem, somewhat resembles both *O. bidentata* and *O. oxydentata*. In particular, marginal cusps of its hydrothecae are bimucronate. However, examination of two colonies or colony fragments of the species from deep water off Bermuda (2 km off Castle Roads, 329 m, on line of a crab trap, 04.iv.1992, coll. D. Calder) essentially confirms Allman's brief account. The colony form is that of a species of *Clytia* Lamouroux, 1812 rather than *Obelia* Péron & Lesueur, 1810, and its hydrothecae are much deeper than those of either *O. bidentata* or *O. oxydentata*. *Clytia longicyatha* is a valid, deep water species.

In the western North Atlantic, *Obelia oxydentata* is believed here to range from Chesapeake Bay (Calder 1971, as *Obelia bicuspidata*) to the tropics. The hydroid is widespread in the Caribbean region, and it occurs southwards at least to southern Brazil (Oliveira *et al*. 2016, as *O. bidentata*). Records of it from cold and deeper waters in southern South America are likely based on other species. It has also been reported in parts of the tropical eastern Pacific (Stechow, 1914; Calder *et al*. 2019) and Indian Ocean (Gravier-Bonnet 1999). As for the cool-temperate *O. bidentata*, it occurs from Minas Basin, Nova Scotia (Calder 2017) at least to South Carolina (Calder & Hester 1978: 90, as *O. longicyatha*).

Reported distribution. ***Gulf coast of Florida.*** ?Off Tampa Bay, 7–10 miles (11–16 km) offshore, 8–10 ftm (15–18 m) (Leloup 1937: 99, as *Laomedea bicuspidata*).—Tampa Bay (Fraser 1944: 154, as *Obelia bicuspidata*).—West coast of Florida (Deevey 1950: 343, as *Obelia bicuspidata*).—Florida Keys (Deevey 1954: 270, as *Obelia bicuspidata*).—Seahorse Key (Joyce 1961: 56).—Cape San Blas area (Shier 1965: 39, as *Clytia longicyatha*).

Elsewhere in western North Atlantic. USA: North Carolina, Beaufort + Bogue Sound, 10 ft (3 m) + North River, 8–10 ft (2–3 m) (Fraser 1912b: 362, as *Obelia bicuspidata*).—Virgin Islands of the United States: St. Thomas, Charlotte Amalie (Stechow 1914: 131; 1919: 50; Ruthensteiner *et al*. 2008: 19).—?Bonaire: Kralendijk, 0.2–0.3 m + northern lagoon ("lagune septentrionale"), 0.2–0.5 m + lagoon, southern coast ("Lagoen, cote meridionale"), 0.3 m (Leloup 1935a: 26, as *Laomedea spinulosa* var. *minor*).—?Aruba: Boca Prins, on stranded *Sargassum* (Leloup 1935a: 26, as *Laomedea spinulosa* var. *minor*).—USA: Louisiana, Grand Isle + Bayou Pass + Bayou de Gettes + Hog island + Barataria Bay (Fraser 1944: 154, as *Obelia bicuspidata*; Behre 1950: 7, as *Obelia bicuspidata*).—USA: Florida, Biscayne Bay (Weiss 1948: 158).—USA: Florida, east coast (Deevey 1950: 343, as *Obelia bicuspidata*).—Bahamas (Deevey 1950: 343, as *Obelia bicuspidata*).—Panama (Deevey 1950: 343, as *Obelia bicuspidata*).—Unstated location: on buoys (Woods Hole Oceanographic Institution 1952: 187).—USA: Mississippi, Mississippi Sound (Fincher 1955: 92).—French Guiana: Cayenne + W of Grand Cermérable (Leloup 1960, as *Laomedea bicuspidata*).—USA: Mississippi, Horn Island (Richmond 1962: 69).—Venezuela: Lake Maracaibo, Isla de Zapara, north coast, shore (Rodriguez 1963: 214).—USA: Virginia, Norfolk, Norfolk Naval Base Pier 12, on fouling panels, 5 m (Calder & Brehmer 1967: 153, as *Obelia bicuspidata*).—Venezuela: La Guaira (Vervoort 1968: 19, as *Laomedea* (*Obelia*) *bicuspidata*).—Guatemala: Puerto Barrios (Vervoort 1968: 19, as *Laomedea* (*Obelia*) *bicuspidata*).—?Panama: Colón (Vervoort 1968: 19, as *Laomedea* (*Obelia*) *longicyatha*).—USA: Virginia, York River at VEPCO (electric power plant) outfall + Hampton Roads, Norfolk Naval Base Pier 12 (Calder 1971: 53, as *Obelia bicuspidata*).—USA: Texas, Galveston (Defenbaugh 1972: 387; Defenbaugh & Hopkins 1973: 84; both as *Obelia bicuspidata*).—Colombia: Ciénaga Grande de Santa Marta, entrance (Wedler 1973: 34, as *Laomedea bicuspidata*).—Colombia: Santa Marta (Wedler 1975: 340, as *Laomedea bicuspidata*).—USA: Florida, Bache Shoal

(Mergner 1977: 122, as *Laomedea* (*Obelia*) *bicuspidata*; 1987: 187, as *Laomedea* (*Obelia*) *bicuspidata*).—USA: South Carolina, estuaries, widespread (Calder & Hester 1978: 90, as *Obelia bidentata*).—Colombia: Ciénaga Grande de Santa Marta (Palacios 1979: 114).—Colombia: Bahía de Cartagena region (Flórez González 1983: 123, as *Obelia bicuspidata*).—USA: South Carolina, Murrells Inlet, Capt. Dick's Marina, floating docks + Charleston area + Folly River area, Oak Island, oyster reefs + Folly River, pilings + Isle of Palms, marina, on floating docks + Beaufort River, oyster reefs + Beaufort area, pilings and seawalls (Fox & Ruppert 1985: 104, 141, 152, 162, 177, 211, 219, as *Obelia bidentata*).—Bermuda: Ferry Reach at Bermuda Biological Station, 0.5 m + Castle Harbour, cave entrance near Tucker's Town Bay, 2 m + Flatts Inlet, 1.5 m (Calder 1990 [1991a]: 71, as *Obelia bidentata*).—Belize: Twin Cays (Calder 1991b: 223, as *Obelia bidentata*).—Panama: Buoy #6, Atlantic side, Canal Zone + Mole Buoy, Atlantic entrance to canal + Colón, Fort Sherman dock, 09°22'12"N, 79°56'59"W, 0–2 m + Colón, bridge near Fort Sherman, 09°17'33"N, 79°55'22"W, 0–2 m + Colón, Fort Sherman dock, marina, 09°20'57"N, 79°54'10"W, 0–2 m + Colón, Club Nautico, steel pilings, 09°21'51"N, 79°53'39"W, 0–1 m + Colón, Isla Margareta, Fort Randolph, shore, 09°23'15"N, 79°53'11"W, 0–1 m + Portobelo Harbor, dock, 09°33'14"N, 79°39'34"W, 0–1 m (Calder & Kirkendale 2005: 487, as *Obelia bidentata*).—Cuba: Playa Baracoa, 2 m (Varela *et al.* 2005: 178, as *Obelia bidentata*).—USA: North Carolina, Beaufort (Govindarajan *et al*. 2006: 823, as *Obelia bidentata*).—French Lesser Antilles: Guadeloupe, Grande-Terre, mangrove, Petit Canal, 16°21.891'N, 61°30.137'W, 0.5 m (Galea 2010: 9, as *Obelia bidentata*).—USA: Florida, Fort Pierce, ship canal at Link Port, 27°32'05"N, 80°20'50"W, 0.1 m (Calder 2013: 59).—French Lesser Antilles: Martinique (Galea 2013: 49, as *Obelia bidentata*).—Caribbean Sea (Wedler 2017b: 94, figs. 85A, B, 86A–C, as *Obelia bidentata*).—Panama: Bocas del Toro area, San Cristóbal + vicinity of Manuguar Cay (Miglietta *et al*. 2018b: 108, as *Obelia bidentata*).

Suborder Macrocolonia Leclère, Schuchert, Cruaud, Couloux & Manuel, 2009

Infraorder Haleciida Bouillon, 1984

Family Haleciidae Hincks, 1868 [1869]

Genus *Halecium* Oken, 1815

Halecium lightbourni Calder, 1990 [1991a]

Fig. 19a

Halecium lightbourni Calder, 1990 [1991a]: 19, figs. 10, 11.

Type locality. Bermuda: Flatts Inlet, 0.5 m (Calder 1990 [1991a]: 19).

Material examined. Fort Myers Beach, on stranded *Idiellana pristis*, 01 March 2013, one colony, 3 mm high, without gonophores, coll. D. Calder, ROMIZ B4377.

Remarks. *Halecium lightbourni* Calder, 1990 [1991a] is an infrequently reported and poorly known species, originally described from Bermuda. It has subsequently been reported from Panama (Calder & Kirkendale 2005), Martinique (Galea & Ferry 2015), and Cuba (Castellanos *et al*. 2018) in the western North Atlantic, and from Brazil (Nogueira *et al*. 1997; Grohmann *et al*. 2003; Oliveira *et al*. 2016) in the western South Atlantic.

Hydroids of *H. lightbourni* resemble those of *H. nanum* Alder, 1859 in habit and in colony size (<1 cm high), but they differ most notably in lacking zooxanthellae. Among other characters differentiating *H. lightbourni*, colonies are less shrubby, hydrothecae tend to be narrower at the margin (129–160 μm vs. 147–182 μm), internodes of hydrocauli and branches are more slender at the nodes (65–86 μm vs. 84–89 μm), and large nematocysts (now considered pesudostenoteles rather than euryteles) are larger (8.3–8.9 μm long x 3.8–4.7 μm wide vs. 6.7–7.4 μm long x 3.1–3.8 μm wide) and somewhat different in shape (Calder 1990 [1991a]). The species has not been reported from pelagic *Sargassum*, a common substrate of *H. nanum*. The cnidome of *H. lightbourni* comprises microbasic mastigophores and small pseudostenoteles in addition to large pseudostenoteles (Calder 1990 [1991a]; Galea & Ferry 2015).

When originally described (Calder 1990 [1991a]), only trophosomes of *H. lightbourni* were available for study.

Gonosomes were discovered and described in material from Martinique by Galea & Ferry (2015). From their account, female gonothecae are sac-shaped to reniform, with a lateral aperture for two gonothecal hydranths. They thus differ from those of *H. nanum*, which have a disto-lateral aperture at the end of two adnate, finely annulated tubes. Male gonothecae are clavate, as in many other species of the genus *Halecium* Oken, 1815. Gonothecae of the two sexes were found by Galea & Ferry on different colonies.

Reported distribution. ***Gulf coast of Florida.*** First record.

Elsewhere in western North Atlantic. Bermuda: Flatts Inlet, 0.5–1.0 m, on *Pennaria disticha* and algae + Harrington Sound, Cripplegate Cave, at entrance, 0.5 m, on *Dynamena crisioides* + Great Sound, on channel buoy, 2.5 m, on ascidians and *Pennaria disticha* (Calder 1990 [1991a]: 19).—Panama: Bocas del Toro, Boca del Drago, 0-3 m (Calder & Kirkendale 2005: 481).—French Lesser Antilles: Martinique, Saint Pierre, Tombant de la Galère, 14.75144, -61.18236, 10–15 m, on *Thyroscyphus marginatus* (Galea & Ferry 2015: 224).—Cuba: Havana, coral reef system west of the city (Castellanos *et al*. 2018: Supplementary Table S2).

Halecium nanum Alder, 1859

Fig. 19b

Halecium nanum Alder, 1859: 355, pl. 14, figs. 1–4.—Leloup, 1935a: 8.—Shier, 1965: 47, pl. 26.
C. markii.—Wallace, 1909: 137 [incorrect subsequent spelling of *Halecium marki* Congdon, 1907].

Type locality. Atlantic Ocean: SW of the Azores, 34°48’N, 34°25’W, “…on Gulf-weed…” (Alder 1859: 355).

Material examined. Sanibel Island, beach at Lighthouse Point, 26°27’00”N, 82°01’01”W, on detached *Thalassia* at water’s edge, 15 March 2018, 18° C, 34‰, one colony, 0.6 mm high, without gonophores, coll. D. Calder, ROMIZ B4378.

Remarks. *Halecium nanum* Alder, 1859 was originally described as an epizoite of gulfweed collected from a location SW of the Azores, in the Sargasso Sea. This epibenthic hydroid comprises part of a remarkable biota that rafts on pelagic *Sargassum* (Timmermann 1932; Burkenroad, in Parr 1939; Morris & Mogelberg 1973; Calder 1995). As such, the species can be expected to occur wherever pelagic *Sargassum* is transported by warm ocean currents in the North Atlantic. *Halecium nanum* was not considered by Cornelius (1995a: 291) to be a normal part of the hydroid fauna of northwest Europe, but it has been reported from warmer waters in the eastern Atlantic and Mediterranean (Medel & Vervoort 2000). Distribution records in the western North Atlantic currently extend from the middle-Atlantic states of the USA (Fraser 1944) to the southern Caribbean Sea (Leloup 1935a). It has also been reported from the Fernando de Noronha Archipelago, Brazil (Amaral *et al*. 2009). As a hydroid harbouring symbiotic zooxanthellae, *H. nanum* is a species of shallow waters, having been reported from the sea surface to a depth of 48 m (Fraser 1944). Fraser believed a collection of the species from 1544 ftm (2824 m) off the east coast of the United States was likely to have been taken from sunken *Sargassum*. The hydroid is brownish in colour when alive due to zooxanthellae in its tissues. The morphologically similar *H. xanthellatum* Galea 2013 also has algal symbionts, but it differs in cnidome, in gonothecal shape, and in having flared hydrothecal margins (Galea 2013). Hydranths of specimens identified as *H. nanum* by Wedler (2017b) from the Colombia were unusual in being white in colour, with green algal symbionts in the coenosarc. Gonothecae of these hydroids were also atypical in morphology and the identification is considered questionable.

Bosc (1797) applied the binomen *Hydra articulata* to a hydroid found on gulfweed during a passage from Bordeaux, France, to Charleston, South Carolina, USA. The species has long been considered indeterminate (e.g., Bedot 1901). Of the hydroids now known to occur on pelagic *Sargassum*, however, it most closely resembles *Halecium nanum*, and *H. articulata* constitutes a nomenclatural threat to that well-known species name. I had earlier intended to seek suppression of the unfamiliar *H. articulata* and to ask for conservation of the better-known *H. nanum* (Calder 1990 [1991a]: 22). Under the current edition of the ICZN, that can be accomplished by applying provisions relating to Reversal of Precedence. In the interests of nomenclatural stability, therefore, the well-known name *Halecium nanum* Alder, 1859 is designated herein as valid and as a nomen protectum, while *Hydra articulata* Bosc, 1797 is relegated to a nomen oblitum following articles of the code (ICZN Art. 2.9.1.1). Reversal of Precedence can be applied in this case because the binomen *Hydra articulata* has been unused as a valid name in zoology after 1899, while *Halecium nanum* has appeared in more than 25 publications by numerous authors (>10) in the past 50 years (e.g., Morris & Mogelberg 1973; Cornelius & Garfath 1980; Boero 1981; Spracklin 1982; Calder 1986, 1990 [1991a], 1991b, c, 1993b, 1995; Boero & Fresi 1986; Cairns *et al*. 1991, 2002; Bouillon *et al*. 1995; Cornelius 1995a; Farnsworth & Ellison 1996; Medel & López-González 1996; Medel & Vervoort 2000; Schuchert 2005; Calder & Kirkendale 2005; Altuna 2007; Oliveira & Marques 2007; Galea 2008; Amaral *et al*. 2009; Gravili *et al.* 2015; Oliveira *et al*. 2016).

While the pelagic phaeophytes *Sargassum natans* and *S. fluitans* are important substrates for *H. nanum*, this species is a substrate generalist, occurring also on benthic algae, seagrasses, other hydroids, buoys, and even tarballs (see Reported Distribution below). Taxonomic accounts of this hydroid, including synonymy lists of the species, are given in works such as those of Calder (1990 [1991a]) and Medel & Vervoort (2000).

As noted in the synonymy list above, Wallace (1909) reported this hydroid from the Dry Tortugas simply as “*C. markii*”. He nevertheless clearly intended it for *Halecium* Oken, 1815 and *H. marki* Congdon, 1907 (=*H nanum*).

Reported distribution. ***Gulf coast of Florida.*** Dry Tortugas (Wallace 1909: 137, as *C. markii*).—Dry Tortugas, on *Sertularella* (Leloup 1935a: 9).—Cape San Blas area, on *Syringodium*, *Thalassia*, and *Sargassum* (Shier 1965: 99).

Elsewhere in western North Atlantic. North Atlantic Ocean: off the Antilles, on *Sargassum* (Jäderholm 1903: 267).—Bermuda: on *Sargassum* and large hydroids (Congdon 1907: 474, as *Halecium marki*).—USA: North Carolina, seaward side of Bogue Bank, on floating *Sargassum* (Fraser 1912b: 368).—USA: North Carolina, dredged off Beaufort, on *Pasythea quadridentata* (=*Pasya quadridentata*) (Fraser 1912b: 368, as ?*Halecium repens*).—Mexico: NNE of Yucatan Peninsula, 22°47’N, 86°10’W, on *Sargassum* (Stechow 1914: 135; 1919: 36).—Bermuda: on floating *Sargassum* + Cow Ground Flat, on *Pennaria* (Bennitt 1922: 245).—Sargasso Sea, on *Sargassum* (Hentschel 1922: 4).—Sargasso Sea: 33°19’N, 43°55’W, on *Sargassum* + 31°30’N, 76°00’W, on *Sargassum* + 24°26’N, 64°44’W, on *Sargassum* + 27°20’N, 61°10’W, on *Sargassum* (Timmermann 1932: 298, 301).—USA: South Carolina, off Murrells Inlet, 33°30’N, 79°00’W, on *Sargassum* (Timmermann 1932: 301).—Bonaire: Kralendijk, Pasanggrahan, on algae + De Hoop, on algae + Plaja Oranje Pan, on algae + Zuidpunt, on algae (Leloup 1935a: 8, 9).—Sargasso Sea: NNE of Bermuda, 35°07’N, 63°35’W, on *Sargassum* (Leloup 1935a: 9).—West Indies: between Trinidad and Grenada, on *Sargassum* (Leloup 1935a: 9).—Sargasso Sea: E of the Bahamas, 23°57’N, 67°45’W, on *Sargassum* + 27°13’N, 62°16’W, on *Sargassum* (Leloup 1935b: 4, as *Halecium nanum* var. *alta*).—Sargasso Sea: W of Bermuda, 32°07’N, 66°35’W, on *Sargassum* (Leloup 1937: 96, as *Halecium nanum* var. *alta*).—Atlantic Ocean: Gulf Stream, on pelagic *Sargassum* + Sargasso Sea, on pelagic *Sargassum* (Burkenroad, in Parr 1939: 24).—Gulf Stream: 130-167 miles (209–269 km) S of Nantucket, USA, on *Sargassum* (Fraser 1943: 89).—Atlantic Ocean: E of New Jersey, 38°59’N, 70°07’W, 1544 ftm (2824 m), likely on sunken *Sargassum* (Fraser 1944: 200).—Sargasso Sea: NE of the Bahamas, on *Sargassum* (Fraser 1944: 200).—Puerto Rico: off NE coast, 18°27’35”N, 65°33’55”W, 26 ftm (48 m) (Fraser 1944: 200).—Atlantic Ocean: off the Antilles, on *Sargassum* (Fraser 1944: 200).—USA: Texas, Port Aransas, on *Sargassum* and tar (Deevey 1950: 345).—USA: southern Florida, on buoys (Deevey 1950: 345).—USA: Florida, Florida Current off Miami, on *Sargassum* (Adams 1960: 81).—Sargasso Sea + Gulf Stream, several stations between Florida and New Jersey, on *Sargassum natans*, *S. fluitans* III, *S. fluitans* X, *S. polyceratium*, *S. filipendula* (Rackley 1974: 21).—Belize: Carrie Bow Cay (Spracklin 1982: 240, as *Halecium namum* (sic)).—Sargasso Sea: Hydrostation “S” off Bermuda, *31*°45’N, 64°10’W, on pelagic *Sargassum* (Butler *et al*. 1983: 232).—Bermuda: on *Sargassum* (Calder 1986: 136).—Bermuda: Whalebone Bay, on *Sargassum* and other algae + Flatts Inlet, on *Thalassia* + Natural Arches Beach, on *Sargassum* (Calder 1990 [1991a]: 20).—Belize: Twin Cays, on *Thalassia*, *Sargassum*, benthic algae (Calder 1991b: 223; 1991c: 2068).—Bermuda: on *Sargassum natans* and *S. fluitans* (Calder 1995: 540).—Bonaire (Bouillon *et al*. 1995: 46).—Trinidad (Bouillon *et al*. 1995: 46).—Sargasso Sea (Bouillon *et al*. 1995: 46).—Belize: Spruce Cay + WeeWee Cay + Peter Douglas Cay (Farnsworth & Ellison 1996: 66).—Panama: Colón, Isla Margareta, Fort Randolph, shore, 09°23’15”N, 79°53’11”W, 0-1 m + Bocas del Toro area, Mangrove Inn, 09°19’52.6”N, 82°15’17.7”W, 2-3 m + Bocas del Toro area, Crawl Cay, 09°15.261’N, 82°07.787’W, 2-4 m (Calder & Kirkendale 2005: 481).—French Lesser Antilles: Guadeloupe, Grande-Terre, E of Saint François, 16°15’18.00”N, 61°14’37.00”W, seagrass meadows, on *Thalassia* (Galea 2008: 22, as *Halecium* cf. *nanum*).—French Lesser Antilles: Les Saintes, Terre-de-Haut, Pain de Sucre, 15°51’45”N, 61°35’60”W, rocky shore, on algae (Galea 2008: 22, as *Halecium* cf. *nanum*).—(?)Colombia: Santa Marta + Isla Piedra Ahogada (Wedler 2017b: 110, figs. 105A–C).—Cuba: Havana, coral reef system west of the city (Castellanos *et al*. 2018: Supplementary Table S2).—(?)Panama: Bocas del Toro area, near Bocatorito Bay (Miglietta *et al*. 2018b: 108, as *Halecium* cf. *nanum*).

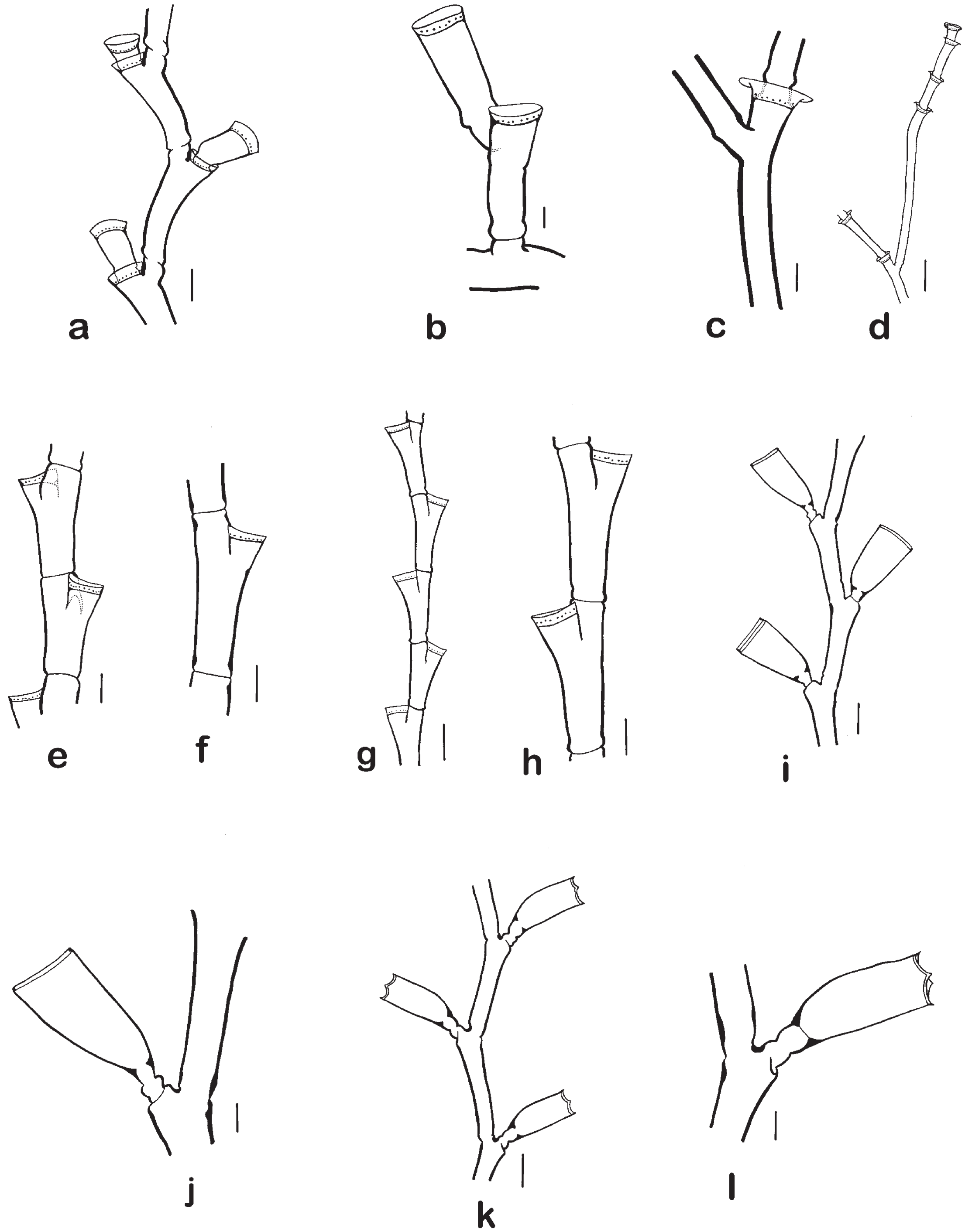

FIGURE 19. a, ***Halecium lightbourni*****:** part of hydrocaulus with hydrothecae, Fort Myers Beach, ROMIZ B4377. Scale equals 0.1 mm. **b,** ***Halecium nanum*****:** stolon with hydrocaulus and two hydrothecae, Sanibel Island, ROMIZ B4378. Scale equals 0.05 mm. **c,** ***Halecium tenellum*****:** part of colony with a hydrotheca, Southwest Florida Shelf, ROMIZ B4379. Scale equals 0.05 mm. **d,** ***Halecium tenellum*****:** part of colony with renovated hydrothecae, Southwest Florida Shelf, ROMIZ B4379. Scale equals 0.2 mm. **e,** ***Halecium*** **sp.:** part of a branch with three hydrothecae, Sanibel Island, ROMIZ B4381. Scale equals 0.1 mm. **f,** ***Halecium*** **sp.:** part of a branch with a hydrotheca, Southwest Florida Shelf, ROMIZ B1594. Scale equals 0.1 mm. **g,** ***Nemalecium lighti*****:** part of colony with five hydrothecae, Fort Myers Beach, ROMIZ B4419. Scale equals 0.2 mm. **h,** ***Nemalecium lighti*****:** two internodes, with hydrothecae, Fort Myers Beach, ROMIZ B4419. Scale equals 0.1 mm. **i,** ***Thyroscyphus marginatus*****:** part of colony with three hydrothecae, Sanibel Island, ROMIZ B4382. Scale equals 0.5 mm. **j,** ***Thyroscyphus marginatus*****:** hydrotheca, Sanibel Island, ROMIZ B4382. Scale equals 0.2 mm. **k,** ***Thyroscyphus ramosus*****:** part of colony with three hydrothecae, Sanibel Island, ROMIZ B4385. Scale equals 0.5 mm. **l,** ***Thyroscyphus ramosus*****:** hydrotheca, Sanibel Island, ROMIZ B4385. Scale equals 0.2 mm.

Halecium tenellum Hincks, 1861

Figs. 19c, d

Halecium tenellum Hincks, 1861: 252, pl. 6, figs. 1–4.—Clarke, 1879: 244.—Leloup, 1935: 9; 1937: 96.—Fraser, 1944: 201.

Type locality. UK: Devon, Salcombe Bay (Hincks 1961: 252).

Material examined. Southwest Florida Shelf, middle shelf west of North Naples, 26°16'15"N, 83°47'00"W, 76.2 m, 04 November 1980, one colony fragment, 4 mm high, without gonophores, coll. Continental Shelf Associates, ROMIZ B4379.—Southwest Florida Shelf, middle shelf west of North Naples, 26°16.72'N, 83°46.82'W, 83 m, 24 July 1981, otter trawl, on *Acryptolaria longitheca*, one colony, 2 mm high, without gonophores, coll. Continental Shelf Associates, ROMIZ B4380.

Remarks. Originally described by Hincks (1861) from Salcombe Bay, England, *Halecium tenellum* has been widely regarded as a virtually cosmopolitan species (Calder 1990 [1991a]; Cornelius 1995; Medel & Vervoort 2000; Schuchert 2001). Given current uncertainty over identifications of this hydroid from high latitudes (Calder 1990 [1991a]; Schuchert 2001; 2005), reports of it from Arctic and subarctic waters of Canada (Verrill, 1879: 152; Fraser 1922: 5, 1931: 481, 1933: 564) have been excluded from distribution records given below. Reports from the boreal western Atlantic have been included, although it is questionable whether they too are reliable. Notwithstanding its type locality in southern England, most collections of *H. tenellum* in the northeastern Atlantic have been to the south of the British Isles (Medel & Vervoort 2000). As stated in previous work (Calder 1990 [1991a]; 2013), *H. tenellum* is believed to be a species occurring mostly in temperate and tropical waters. In the western South Atlantic, it has been reported as far south as Brazil and Argentina (Oliveira *et al*. 2016). Its bathymetric range, according to Oliveira *et al*., extends from the intertidal zone to 835 m. However, records of the species cited below have predominantly been from neritic bottoms. Specimens from the Southwest Florida Shelf examined here fall within that zone.

The two colonies of *H. tenellum* reported above (ROMIZ B4379, ROMIZ B4380) were sterile. Several earlier accounts of the species from the tropical and warm-temperate western North Atlantic were also based on sterile hydroids (Fraser 1912b; Leloup 1935, 1937; Calder 1990 [1991a], 2013; Galea 2010; Castellanos *et al*. 2018). Other reports of *H. tenellum* exist from the region (Clarke 1879; Fraser 1944, 1947b; Cain 1972; Wedler 1975; Calder & Hester 1978; Wenner *et al*. 1984; Wedler & Larson 1986; Calder 1991b, 2000; Calder & Kirkendale 2005; Castellanos *et al*. 2011), but no indication was given in them of the reproductive state of the specimens. While fertile colonies were mentioned by Bennitt (1922) in material from Bermuda, they were neither described nor illustrated by him.

In hydroids currently assigned to the genus *Halecium* Oken, 1815, morphological characters of the female gonothecae are of critical importance in species identification. Those of *H. halecinum* (Linnaeus, 1758), type species of the genus, are irregularly obovate with a tubular and distolateral aperture at the end of a chimney-like tube for one or more gonothecal hydranths. By contrast, those of *H. tenellum*, as described by Cornelius (1975b; 1995b) and others, are much different in shape, being ovate, laterally flattened, and with a simple terminal aperture. Gonophoral hydranths are absent. The possible taxonomic significance of this difference, at the generic level, warrants exploration (Calder 2017: 47).

Medel & Vervoort (2000) provided a detailed synonymy of *H. tenellum*, along with worldwide records of the species. A substantial recent literature on the species from South America has been cited by Oliveira *et al*. (2016).

Reported distribution. ***Gulf coast of Florida.*** SW Florida Shelf, W of the Dry Tortugas, 24°34'N, 83°16'W, 36 ftm (66 m) (Clarke 1879: 244).—Dry Tortugas, 27 ft (8 m), on pebbles (Leloup 1935: 10).—Off Tampa Bay, 7–10 miles (11–16 km) offshore, 8–10 ftm (15–18 m) (Leloup 1937: 96).—Tampa Bay (Fraser 1944: 203).

Elsewhere in western North Atlantic. USA: Maine, Casco Bay, 8–34 ftm (15–62 m) (Verrill 1874c: 364).—USA: Massachusetts, Cashes Ledge, 52–90 ftm (95–165 m) (Verrill 1875a: 414).—Canada: Nova Scotia, NE Georges Bank, 41°25'N, 66°24.8'W, 50 ftm (91 m) (Smith & Harger, 1875: 7).—USA: Massachusetts, Woods Hole (Nutting 1901: 357).—Canada: Quebec, Gaspé (Stafford, 1912a: 59; 1912b: 73).—Canada: New Brunswick, St. Andrews (Stafford, 1912b: 73).—Canada: Quebec, Seven Islands (Sept-Îles) (Stafford 1912b: 73).—USA: North Carolina, Beaufort area (Fraser 1912b: 369).—Canada: Nova Scotia, Canso Banks, 50 ftm (91 m), on ascidian stalks (Fraser, 1913: 169).—Canada: New Brunswick, from N end of Campobello Island to head of Passamaquoddy Bay (Fraser, 1918: 353).—Canada: Nova Scotia, Brier Island (Fraser, 1918: 353).—Canada: Quebec, Seven Islands (Sept-Îles) (Fraser, 1918: 353).—Canada: Newfoundland and Labrador, Bay of Islands (Fraser, 1918: 353).—Bermuda: Somerset Bridge, on *Sargassum* (Bennitt 1922: 246).—Canada: New Brunswick, Miramichi River estuary, outside Portage and Fox islands, 15–40 m (Fraser 1926: 210).—USA: Maine, Mount Desert region, shore to 330 feet (101 m) (Procter 1933: 119).—Bonaire: Zuidpunt, on stranded algae + Lac, mouth, 1 m, on detached algae + Lac, Soerebon, 0.8 m (Leloup 1935: 10).—Curaçao: Boca Grandi, on stranded *Sargassum* (Leloup 1935: 10).—USA: Maine, Casco Bay, 21 ftm (38 m) (Fraser 1944: 202).—USA: off Cape Cod, 41°41'N, 69°47'W, 18 ftm (33 m) (Fraser 1944: 203).—USA: Massachusetts, 5¾ miles (9 km) off Chatham Light, 14 ftm (26 m) (Fraser 1944: 203).—USA: Massachusetts, 11.5 miles (19 km) off Cape Cod Light, 28 ftm (51 m) (Fraser 1944: 203).—Venezuela: off Isla Tortuga, 2–5 ftm (4–9 m) (Fraser 1947b: 9).—Colombia: Santa Marta area, rocky littoral (Wedler 1975: 334, as "*H. tenellum* (?)").—Canada: Quebec, Saguenay Fjord (Fjord de Saguenay) (Brunel, 1970: 18; Drainville *et al*., 1978: 9).—USA: North Carolina, *Lithothamnion* reef S of Cape Lookout (Cain 1972: 80).—USA: South Carolina, Prices Creek (Calder & Hester 1978: 90).—USA: South Carolina, inner (17–18 m), middle (32–36 m) and outer (46–69 m) continental shelf + Georgia, inner (17–22 m), middle (23–29 m) and outer (59–67 m) continental shelf (Wenner *et al*. 1984: 20, 39).—USA: South Carolina, Beaufort River, oyster reefs (Fox & Ruppert 1985: 211).—Virgin Islands of the United States: St. Croix, on algae (Wedler & Larson 1986: 91).—Bermuda: Argus (=Plantagenet) Bank, on Argus Tower, 20 m (Calder 1990 [1991a]: 23).—Belize: Twin Cays (Calder 1991b: 223).—Bermuda: Challenger Bank + Argus (=Plantagenet) Bank (Calder 2000: 1133).—Panama: Galeta, STRI Galeta Laboratory, dock, 09°24'08"N, 79°51'39"W, 0-2 m (Calder & Kirkendale 2005: 481).—Canada: Nova Scotia, Western Bank (Henry *et al*. 2006: 68).—French Lesser Antilles: Guadeloupe, Grande-Terre, Grotte aux Barracudas, 16°27.343'N, 61°32.244'W, 21 m, on *Sertularella diaphana* + Pointe Plate, 16°27.220'N, 61°32.128'W, 15–20 m, on *Thyroscyphus marginatus* + Les Ancres, 16°27.002'N, 61°32.320'W, 15–18 m, on *Sertularella diaphana* (Galea 2010: 11).—Cuba: Golfo de Batabanó, Cayería San Felipe, Cayo Real + Arrecife Punta Francés, Boya 5 (Castellanos *et al*. 2011: 14).—French Lesser Antilles: Martinique (Galea 2013: 49).—USA: Florida, Jeff's Reef off Fort Pierce, 27°32.8'N, 79°58.8'W, 80 m (Calder 2013: 22).—Cuba: Havana, coral reef system west of the city (Castellanos *et al*. 2018: Supplementary Table S2).—Panama: Bocas del Toro area, vicinity of Manuguar Cay (Miglietta *et al*. 2018b: 108).

Halecium sp.

Figs. 19e, f

Material examined. Southwest Florida Shelf, middle shelf west of Gasparilla Island, 26°45.86'N, 83°21.44'W, 50 m, 18 July 1981, triangle dredge, one colony fragment, 3.9 cm high, without gonophores, coll. Continental Shelf Associates, ROMIZ B1594.—Sanibel Island, beach at Lighthouse Point, 26°26'58"N, 82°01'04.5"W, detached and stranded on beach, 21 March 2018, 22° C, 34.5‰, one colony, 7 cm high, with male gonophores, coll. D. Calder, ROMIZ B4381.

Remarks. These hydroids resemble the trophosomes of several species of *Halecium* Oken, 1815 that have been reported from the Gulf of Mexico (Calder & Cairns 2009), including *H. halecinum* (Linnaeus, 1758), *H. beanii* (Johnston, 1838), *H. sessile* Norman, 1867, *H. macrocephalum* Allman, 1877, and *H. bermudense* Congdon, 1907. In lacking female gonophores, the specimens cannot be reliably identified to species. Colonies were strongly polysiphonic, with alternate and predominantly pinnate side branches; hydranths bore 20+ tentacles and the cnidome comprised both pseudostenoteles (10.2–12.0 long x 5.4–7.0 μm wide) and microbasic mastigophores (ca. 6.0 long x 1.8 μm wide).

Genus *Nemalecium* Bouillon, 1986

Nemalecium lighti (Hargitt, 1924)

Figs. 19g, h, 20

Halecium lighti Hargitt, 1924: 489, pl. 4, fig. 13.

Type locality. Philippines: Oriental Mindoro, Puerto Galera (Hargitt 1924: 489, as Port Galera Bay).

Material examined. Fort Myers Beach, 26°27'38.9"N, 81°57'58.4"W, on sponge, stranded on beach, 29° C, 33‰, 27 August 2018, several colony fragments, up to 8 mm high, without gonophores, coll. D. Calder, ROMIZ B4419.

Remarks. A brief history of the hydroid *Nemalecium lighti* (Hargitt, 1924), first described from the Philippines, has been given earlier (Calder 1991b). Originally included in *Halecium* Oken, 1815, the genus *Nemalecium* was established for the species by Bouillon (1986). The most distinctive generic character is the presence of nematodactyls, unique fingerlike defensive structures occurring within the tentacular whorl and curving over the hypostome of the hydranth. Curiously, hydroids of *Nemalecium* had seldom been reported anywhere in the world prior to the mid-1980s. Records now suggest that they are both common and widespread, occurring in warm waters of the Atlantic, Pacific, and Indian oceans (Calder *et al*. 2019). After having been recorded initially in the Atlantic Ocean from Bermuda (Calder 1991b), they have been reported frequently in the Caribbean Sea (see records below), to the south in Brazil (Oliveira *et al*. 2016), and recently from the Gulf of Mexico (Mendoza-Becerril *et al*. 2018b). It is unclear whether *N. lighti* is a recent invasive species or one that had been widely overlooked or misidentified earlier.

Two species of *Nemalecium* have now been reported from the tropical western North Atlantic. Part of the material identified as *N. lighti* by Galea (2008) from the Caribbean Sea was referred by Galea *et al*. (2012) to a new species, *N. gracile*. Primary characters said by them to distinguish it from *N. lighti* include (1) hydranths that constantly forage and are long and nearly transparent, rather than ones that are nearly immobile, shorter, and milky white; (2) tentacles that are raised at different levels rather than being uniform in elevation; (3) internodes that are much more slender in form; (4) primary hydrophores that extend beyond the level of the distal internodes rather than terminating below them; (5) pseudostenoteles that are smaller (capsule length usually <30 µm rather than >30). As noted by Galea *et al*., hydroids assigned to *N. lighti* by Calder (1991b) from Bermuda resemble *N. gracile* and are likely referable to that species. The specific identity of specimens identified as *N. lighti* by Galea (2010: 4, 5), from Guadeloupe, is unclear. Swimming gonophores are produced by both species (Galea *et al*. 2012).

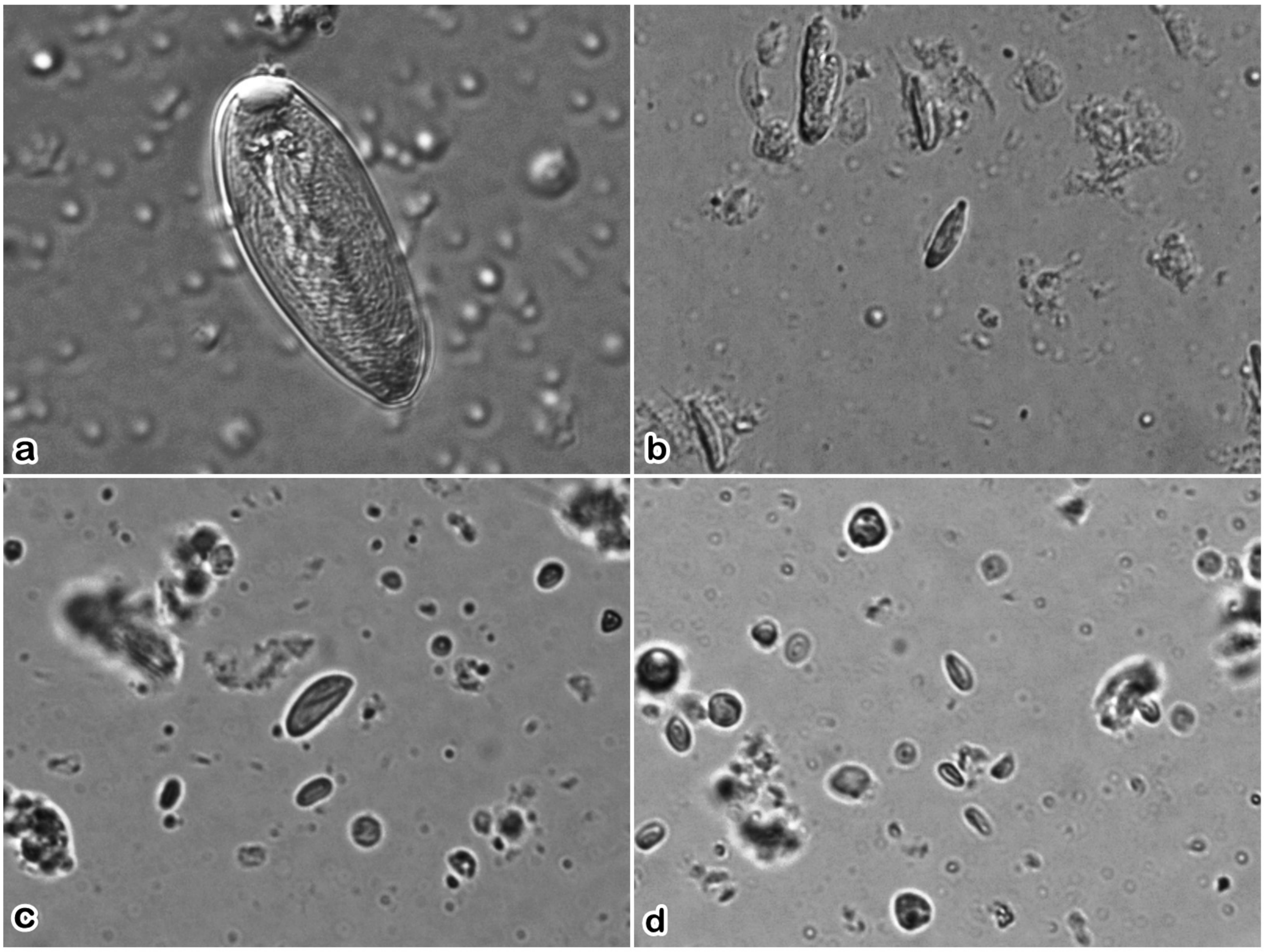

FIGURE 20. ***Nemalecium lighti*****:** nematocysts of hydranth, ROMIZ B4419. **a,** pseudostenotele. **b,** microbasic mastigophores. **c,** microbasic eurytele. **d,** rhopaloid heteronemes.

The cnidome of *N.* cf. *lighti* includes several categories of nematocysts, including pseudostenoteles, microbasic mastigophores, microbasic euryteles, and rhopaloid heteronemes (Galea *et al*. 2012). In material examined here from Florida, the nematocyst complement (Fig. 20) included pseudostenoteles (31.2–34.8 µm long x 13.2–15.8 µm wide, undischarged, n=10, ROMIZ B4419), microbasic mastigophores (6.8–7.3 µm long x 1.8–2.1 µm wide, undischarged, n=10, ROMIZ B4419), microbasic euryteles (7.6–8.8 µm long x 2.6–3.3 µm wide, undischarged, n=10, ROMIZ B4419), and rhopaloid heteronemes (3.8–6.0 µm long x 1.6–3.2 µm wide, undischarged, n=4, ROMIZ B4419). Pseudostenoteles of *N. lighti* are prominent on nematodactyls in the tentacular whorl of the hydranth. The species is known to be venomous to humans. The envenomations of a swimmer in Brazil, stung on the forearms, arms, neck, back, and later the thorax, were described by Marques *et al*. (2002).

While *N. lighti* has been classified as a haleciid based on colony morphology, molecular studies by Maronna *et al*. (2016) suggest that it is part of a different lineage. Their analysis indicated an affinity of the species with those of a new order group, Plumupheniida Maronna *et al*., 2016, but as a taxon *incertae sedis* within that group. More analyses to test that conclusion are warranted, and the species has been provisionally retained here in Haleciidae.

Reported distribution. ***Gulf coast of Florida*.** First record.

Elsewhere in western North Atlantic. Bermuda: Castle Harbour + Town Cut (Calder 1990 [1991a]: 27.—Belize: Twin Cays (Calder 1991b: 223).—Panama: Colón, Fort Sherman dock, wood, 09°22’12”N, 79°56’59”W, 0–2 m + Colón, Fort Sherman dock, marina, 09°20’57”N, 79°54’10”W, 0–2 m + Portobelo Harbor, dock, 09°33’14”N, 79°39’34”W, 0-1 m + Bocas del Toro area, Mangrove Inn, 09°19’52.6”N, 82°15’17.7”W, 2–3 m + Bocas del Toro area, Almirante pilings, 09°16.218’N, 82°23.382’W, 1–10 m + Bocas del Toro area, Hospital Point, 09°20”01.9”N, 82°13’07.7”W, 2–13 m + Bocas del Toro area, Cayo Solarte Sud, 09°18’45.3”N, 82°12’46.6”W, 2–3 m + Bocas del Toro area, Boca del Drago, 09°25’36.3”N, 82°19’30.1”W, 1–3 m + Bocas del Toro area, Cayos Zapotilla, 09°15.564’N, 82°02.750’W, 7–8 m + Bocas del Toro area, near Laguna Bocatorito, 2–4 m + Bocas del Toro area, Drago 2, mangroves, 1–2 m + Bocas del Toro area, Drago 2, 2–4 m (Calder & Kirkendale 2005: 483).—French Lesser Antilles: Les Saintes, Terre-de-Haut, Pompierre Bay, 15°52’25”N, 61°34’15”W, large rocks in seagrass meadows, on algae, concretions, sponge + Pain de Sucre, 15°51’45”N, 61°35’60”W, rocky shore, on sponge (Galea 2008: 24; Galea *et al*. 2012: 47).—Cuba: Golfo de Batabanó, Punta Francés, Boya El Límite (Castellanos *et al*. 2009: 96, 2011: 15).—French Lesser Antilles: Martinique, Les Abîmes, 14.807514, -61.226698, 8 m, on dead gorgonians (Galea *et al*. 2012: 48).—Caribbean Sea (Wedler 2017: 111).—Mexico: Alacranes Reef, on sponges, soft corals (Mendoza-Becerril *et al*. 2018b: 130).—Cuba: Havana, coral reef system west of the city (Castellanos *et al*. 2018: Supplementary Table S2).—Panama: Bocas del Toro area, Smithsonian Tropical Research Station docks/weather station + Isla San Cristóbal + vicinity of Manuguar Cay (Miglietta *et al*. 2018: 105, 106).

Infraorder Sertulariida Maronna, Miranda, Peña Cantero, Barbeitos & Marques, 2016

Family Thyroscyphidae Stechow, 1920

Genus *Thyroscyphus* Allman, 1877

Thyroscyphus marginatus (Allman, 1877)

Figs. 19i, j

Obelia marginata Allman, 1877: 9, pl. 6, figs. 1, 2.—Fewkes, 1881a: 128.
Campanularia insignis.—Wallace, 1909: 137 [not *Campanularia insignis* Fewkes, 1881].
Campanularia marginata.—Nutting, 1915: 45, pl. 6, figs. 5–7.—Fraser, 1943: 88; 1944: 124, pl. 22, figs. 97a–d.—Penner, 1962: 177 [not *Campanularia marginata* Bale, 1884 = *Thyroscyphus macrocytharus* (Lamouroux, 1824)].
Lytoscyphus marginatus.—Leloup, 1935a: 31.
Cnidoscyphus marginatus.—Splettstösser, 1929: 89, figs. 83–87, 88a, b.—Leloup, 1937: 101.—Van Gemerden-Hoogeveen, 1965: 14.

Type locality. USA: Florida, off Loggerhead Key, 9 ftm (16 m) (Allman 1877: 9, as *Obelia marginata*).

Material examined. Fort Myers Beach, 26°27’24”N, 81°57’48”W, washed ashore, 22 January 2013, several colonies and colony fragments, up to 16 cm high, without gonophores, ROMIZ B4412.—Fort Myers Beach, stranded on shore, 01 March 2013, several tangled colony fragments, up to 8 cm high, without gonophores, ROMIZ B4413.—Sanibel Island, beach at Lighthouse Point, detached and stranded in tidepool, 30 March 2013, one colony, 7.3 cm high, without gonophores, coll. D. Calder, ROMIZ B4382.—Sanibel Island, beach at Lighthouse Point, 26°26'57"N, 82°01'06"W, on detached shell fragments at water's edge, 13 March 2018, 20° C, 33.5‰, one colony, 18 cm high, without gonophores, coll. D. Calder, ROMIZ B4383.—Sanibel Island, beach at Lighthouse Point, 26°26'58"N, 82°01'04.5"W, on detached shell debris at water's edge, 21 March 2018, 22° C, 34.5‰, one colony, 2.8 cm high, without gonophores, coll. D. Calder, ROMIZ B4384.

Remarks. *Thyroscyphus marginatus* was originally described from the vicinity of Loggerhead Key, Dry Tortugas, southwest Florida, by Allman (1877, as *Obelia marginata*). The species is large, conspicuous, easily collected, and easily identified from the morphology of its colonies and distinctive hydrothecae. While reported at depths from the lower intertidal zone to 805 m (Nutting 1915, as *Campanularia marginata*), it is primarily a species of relatively shallow waters (Calder 1998, as *Cnidoscyphus marginatus*). The hydroid is a familiar one in southwest Florida and the southern Gulf of Mexico, as well as in the Caribbean region and in shelf waters of the southeastern United States. Its geographic range in the western Atlantic extends from North Carolina (Cain 1972, as *C. marginatus*) to Brazil (Oliveira *et al*. 2016). The species also occurs in warm waters of the eastern Atlantic (Medel & Vervoort 1998, as *C. marginatus*).

Allman (1888) described this species a second time, as *Campanularia insignis* from Challenger Bank near Bermuda, and it was reported under that name in southwest Florida by Wallace (1909). That binomen is invalid as both a junior primary homonym of *Campanularia insignis* Fewkes, 1881 (likely identical with *C. macroscypha* Allman, 1877) and a subjective junior synonym of *Obelia marginata* Allman, 1877 (now *Thyroscyphus marginatus*). Also of note, Nutting (1915), Fraser (1944), and others applied the binomen *Campanularia marginata* to this species, rendering *Campanularia marginata* Bale, 1884 from Australia a junior secondary homonym. A replacement name, *Thyroscyphus balei*, was proposed for Bale's (1884) species by me (Calder 1983), but a senior synonym of both the original and the replacement name, *Clytia macrocythara* Lamouroux, 1824 (=*Thyroscyphus macrocytharus*), has subsequently been discovered by Watson (1994). The original spelling of the specific name of Lamouroux's species was *macrocyttara*, but the change to *macrocythara* by de Blainville (1830) and virtually all subsequent authors is taken to be a justified emendation (ICZN Art. 33.2.3.1).

Detailed accounts of *T. marginatus* are given elsewhere (Splettstösser 1929, as *Cnidoscyphus marginatus*; Vervoort 1968, as *C. marginatus*; Calder 1991b, 2013; Medel & Vervoort 1998, as *C. marginatus*). The hydroid was reported to be venomous by Penner (1962).

Reported distribution. ***Gulf coast of Florida.*** Off Loggerhead Key, 9 ftm (16 m) (Allman 1877: 9, as *Obelia marginata*).—Off Sand Key, 15 ftm (27 m), on a telegraph cable (Fewkes 1881a: 128, as *Obelia marginata*).—Dry Tortugas (Wallace 1909: 137, as *Campanularia insignis*).—S of St. George Island, 28°46'N, 84°49'W, 26 ftm (48 m) + S of Alligator Point, 28°28'N, 84°25'W, 21 ftm (38 m) + W of Marco Island, 26°N, 82°57'30"W, 24 ftm (44 m) (Nutting 1915: 45, as *Campanularia marginata*).—Dry Tortugas (Splettstösser 1929: 89, as *Cnidoscyphus marginatus*).—Dry Tortugas, 25 feet (8 m) (Leloup 1935a: 31, as *Lytoscyphus marginatus*).—Off Tampa Bay, 7–10 miles (11–16 km) offshore, 8–10 ftm (15–18 m) (Leloup 1937: 101, as *Cnidoscyphus marginatus*).—Salt Key Bank, 24°36'40"N, 83°02'20"W, W of Loggerhead Key, 16 ftm (29 m) + Eastern Dry Rocks, off Key West + Key West, off South Beach, 5 ftm (9 m) + W of North Naples, 26°16'10"N, 82°25'40"W, 20 ftm (37 m) (Fraser 1943: 88, as *Campanularia marginata*).—Off Sand Key + off Dry Tortugas (Fraser 1944: 126, as *Campanularia marginata*).—Dry Tortugas (Van Gemerden-Hoogeveen 1965: 15, as *Cnidoscyphus marginatus*).—Key West (Penner 1962: 177, as *Campanularia marginata*).

Elsewhere in western North Atlantic. Mexico: off Zoblos Island (=Isla Holbox) (Clarke 1879: 241, as *Obelia marginata*).—Bermuda: Challenger Bank, 30 ftm (55 m) (Allman 1888: 19, as *Campanularia insignis*).—Cuba: off Morro Castle, 100–250 ftm (183–457 m) (Nutting 1895: 87, as *Obelia marginata*).—Bahamas: ridge between Eleuthera and Little Cat Island (Nutting 1895: 223, as *Obelia marginata*).—Venezuela: near Los Testigos Islands, 11 m (Versluys 1899: 30, as *Obelia marginata*).—Anguilla: 100–150 ftm (183–274 m) (Jäderholm 1903: 270, as *Obelia marginata*).—Bermuda: "…along the shores…plentiful" (Congdon 1907: 468, as *Campanularia insignis*).—Bermuda: Challenger Bank, 30 ftm (55 m) (Ritchie 1909: 250, as *C. insignis*).—Cuba: off Havana, 23°10'42"N, 82°18'24"W, 67 ftm (123 m) (Nutting 1915: 45, as *Campanularia marginata*).—USA: Georgia, slope off southern Cumberland Island, 30°44'N, 79°26'W, 440 ftm (805 m) (Nutting 1915: 45, as *Campanularia marginata*).—Barbados (Nutting 1919: 116, as *Campanularia marginata*).—Bermuda: Bailey's Bay (Splettstösser 1929: 89, as *Cni-*

doscyphus marginatus).—Virgin Islands of the United States: St. Thomas + St. John (Splettstösser 1929: 89, as *Cnidoscyphus marginatus*).—Bermuda: Challenger Bank (Splettstösser 1929: 89, as *Cnidoscyphus marginatus*).—Venezuela: near Islas Los Tortuguillos (Leloup 1937: 101, as *Cnidoscyphus marginatus*).—Anguilla: inside Sombrero Island (Fraser 1943: 88, as *Campanularia marginata*).—USA: South Carolina, continental slope E of Hilton Head Island, 32°07'N, 78°37'30"W, 229 ftm (419 m) (Fraser 1944: 126, as *Campanularia marginata*).—Puerto Rico: Puerto Rico, including Culebra (Fraser 1944: 126, as *Campanularia marginata*).—Bermuda: (Challenger Bank?), 30 ftm (55 m) (Fraser 1944: 126, as *Campanularia marginata*).—Aruba: 8 miles (13 km) SW of Sint Nicolaas Baai, 23–24 ftm (42–44 m) Fraser 1947b: 5, as *Campanularia marginata*).—Unstated location: on buoys (Woods Hole Oceanographic Institution 1952: 186, as *Campanularia marginata*).—Curaçao: Knip Baai (Van Gemerden-Hoogeveen 1965: 14, as *Cnidoscyphus marginatus*).—Bahamas: North Bimini (Van Gemerden-Hoogeveen 1965: 15, as *Cnidoscyphus marginatus*).—Virgin Islands of the United States: St. Thomas (Vervoort 1968: 33, as *Cnidoscyphus marginatus*).—USA: North Carolina, *Lithothamnion* reef S of Cape Lookout (Cain 1972: 80, as *Cnidoscyphus marginatus*).—Colombia: widespread (Wedler 1975: 340; Flórez González 1983: 123; Bandel and Wedler 1987: 41; all as *Cnidoscyphus marginatus*).— USA: Florida, southeast coast (Mergner 1977: 122, as *Cnidoscyphus marginatus*; 1987: 187, as *Cnidoscyphus marginatus*).—USA: South Carolina, Prices Creek, 8 m (Calder & Hester 1978: 91, as *Cnidoscyphus marginatus*; Calder 1983: 16).—Belize: Carrie Bow Cay, 5–31 m (Spracklin 1982: 249, as *Cnidoscyphus marginatus*).—USA: continental shelf of South Carolina and Georgia (Wenner *et al*. 1983: 151).—Dominican Republic: south coast (Williams *et al*. 1983: 43, as *Cnidoscyphus marginatus*).—USA: South Carolina, inner (17–18 m), middle (32–36 m) and outer (46–69 m) continental shelf + Georgia, inner (17–22 m), middle (23–29 m) and outer (59–67 m) continental shelf (Wenner *et al*. 1984: 21, 40).—USA: Texas, Flower Garden Bank (Rezak *et al*. 1985: 224).—Puerto Rico: La Parguera (Wedler & Larson 1986: 89, as *Cnidoscyphus marginatus*).—Bermuda: shallow inshore and deeper offshore waters, common (Calder 1986: 137).—Puerto Rico: Mona Island + Desecheo Island (Larson 1987: 514).—British Virgin Islands: Virgin Gorda Island (Larson 1987: 514).—Bermuda: Flatts Inlet, 0.5–2 m + Harrington Sound, Cripplegate Cave, 0.5 m + Whalebone Bay, 1.5–4 m + 2 km SE of Castle Roads, 60–90 m (Calder 1990 [1991a]: 79).—USA: Florida, off Boca Raton, on artificial reef (Cummings 1994: 1208).—Cuba: north coast (Ortiz Rosado 2000: 87, as *Campanularia marginata*).—Bermuda: Argus (=Plantagenet) Bank, on Argus Tower, 20 m (Calder 2000: 1136, as *Cnidoscyphus marginatus*).—Costa Rica, near Limón, 1–2 m (Kelmo & Vargas 2002: 605).—Panama: Bocas del Toro, Hospital Point, 09°20'00.7"N, 82°13'06.8"W, 0–2 m + Hospital Point, 09°20'01.9"N, 82°13'07.7"W, 2–13 m + Swan's Key, 09°27'12.2"N, 82°18'01.8"W, 1–4 m + Bastimentos (north), 09°20.898'N, 82°09.959'W, 1–4 m (Calder & Kirkendale 2005: 484, as *Cnidoscyphus marginatus*).—Cuba: Alamar, east coast of Havana (Ortea & Caballer 2007: 122).—French Lesser Antilles: Guadeloupe, Basse-Terre, N of Malendure, 16°10'25.00"N, 61°46'58.00"W, rocky shore (Galea 2008: 37).—French Lesser Antilles: Guadeloupe, Grande-Terre, Les Arches, 16°27.529'N, 61°32.021'W, 17 m + Grotte aux Barracudas, 16°27.343'N, 61°32.244'W, 21 m + Pointe Plate, 16°27.220'N, 61°32.128'W + Les Ancres, 16°27.002'N, 61°32.320'W, 15–18 m + Pointe d'Antigues, 16°26.251'N, 61°32.523'W (Galea 2010: 3, 4).—Cuba: Golfo de Batabanó (Castellanos-Iglesias *et al*. 2011: 20).—French Lesser Antilles: Martinique, Le Diamant, 14.442310, -61.039697, 10–13 m + Le Prêcheur, La Perle, 14.841853, -61.227858, 13 m + Le Prêcheur, Les Jardins des Abîmes, 14.809044, -61.228853, 10–15 m + Le Prêcheur, Pointe Lamare, 14.780461, -61.211935, 10–17 m + Case-Pilote, Anse Batterie, 14.643113, -61.141711, 6–8 m + Case-Pilote, Case-Pilote, 14.637536, -61.139743, 9–15 m (Galea 2013: 11, 14, 15, 18, 29, 35).—USA: Florida, Bethel Shoal off Vero Beach, 27°42.6'N, 80°06.8'W, 24 m (Calder 2013: 23).—Colombia: Guajira, on gas platforms (Gracia *et al*. 2013: 385).—French Lesser Antilles: Martinique, Saint Pierre, 14.75144, -61.18236, 10–15 m + Case-Pilote, 14.63753, -61.13974, 9–15 m (Galea & Ferry 2015: 224, 237).—Caribbean Sea (Wedler 2017b: 136, figs. 147, 148, 149A–G, 150A, B, 151A, B).—Mexico: Alacranes Reef, on sponges, corals, molluscs, rocks (Mendoza-Becerril *et al*. 2018b: 130).—Panama: Bocas del Toro area, Crawl Cay (Miglietta *et al*. 2018b: 108).

Thyroscyphus ramosus **Allman, 1877**

Figs. 19k, l

Thyroscyphus ramosus Allman, 1877: 11, pl. 6, figs. 5, 6.—Wallace, 1909: 137.—Splettstösser, 1929: 55.—Fraser, 1943: 91.—Van Gemerden-Hoogeveen, 1965: 15.

Type locality. USA: Florida, south of Sand Key, 10 fathoms (18 m) (Allman 1877: 11).

Material examined. Sanibel Island, beach at Lighthouse Point, 26°26'57"N, 82°01'07"W, detached, in intertidal pools, 03 August 2014, one colony fragment, 2.1 cm high, without gonophores, coll. D. Calder, ROMIZ B4385.

Remarks. *Thyroscyphus ramosus* Allman, 1877 is another species originally described from collections made in the Straits of Florida by L.F. de Pourtalès. While its colony form resembles that of *T. marginatus* (Allman, 1877), hydrothecae of the two species are quite different. In *T. ramosus*, the hydrothecal margin is quadricuspate and bears an operculum of four valves, while in *T. marginatus* it is entire and open, with the operculum having been shed. *Thyroscyphus longicaulis* Splettstösser, 1929 from the Caribbean Sea resembles *T. ramosus*, but its hydrothecae are longer and more slender, marginal cusps are more deeply incised, and a somewhat more developed pedicel is present (Vervoort 1968). Also similar is *T. fruticosus* (Esper, 1791 [1793]) from the Indo-Pacific region. Its marginal cusps appear to be shallower than those of *T. ramosus*, and its pedicels are even less well developed.

As with *T. marginatus*, *T. ramosus* is predominantly a hydroid of warm and shallow waters. Of the two species, *T. ramosus* has been reported less frequently and its distribution is more limited. It has not been reported in the northern Gulf of Mexico and does not occur as far north on the American Atlantic coast. The known range in the Americas currently extends from the continental shelf off South Carolina (Wenner *et al*. 1984) to Brazil (Oliveira 2016). An amphi-Atlantic species, it has also been reported from Freetown, Sierra Leone, in the tropical eastern Atlantic (Vervoort 1959). A record from the Gulf of Mannar in the Indian Ocean by Leloup (1932) seems questionable.

Other detailed accounts of *T. ramosus* include those of Splettstösser (1929), Fraser (1944), Vervoort (1968), Migotto (1996), Shimabukuro & Marques (2006), Galea (2008), and Calder (2013).

Reported distribution. ***Gulf coast of Florida.*** South of Sand Key, 10 fathoms (18 m) (Allman 1877: 11).—Dry Tortugas (Wallace 1909: 137; Splettstösser 1929: 55; Van Gemerden-Hoogeveen 1965: 15).—Inside Florida Reef, 4 ftm (7 m) (Fraser 1943: 91).

Elsewhere in western North Atlantic. Cuba: off Morro Castle, 100–250 ftm (183–457 m) (Nutting 1895: 87).–Venezuela: near Los Testigos Islands, 11 m (Versluys 1899: 31).—Saint-Barthélemy: 2 ftm (4 m) (Jäderholm 1903: 273).—Haiti: Port du Paix (Splettstösser 1929: 55).— Virgin Islands of the United States: St. John, "Loango Westindien" (=Lovango Cay) (Splettstösser 1929: 55).—Bahamas: off Orange Key, 9 ftm (16 m) (Fraser 1943: 91).—Trinidad: Maguaripe Bay (=Macqueripe Bay) (Fraser 1943: 91).—Anguilla: off Sombrero, 240 ftm (439 m) (Fraser 1943: 91).—Puerto Rico: north coast, 18°30'30"N, 66°23'05"W, 40 ftm (73 m) (Fraser 1944: 183).—Puerto Rico: off Culebra Island, 18°19'10"N, 65°19'40"W, 10 ftm (18 m) (Fraser 1944: 183).—St. Eustatius: Oranjestad, near Billy Gut, tidal zone (Van Gemerden-Hoogeveen 1965: 15).—Colombia: widespread (Van Gemerden-Hoogeveen 1965: 15; Wedler 1975: 340; Flórez González 1983: 123; Bandel and Wedler 1987: 41).—Haiti: St. Marc (Vervoort 1968: 33).—Barbados (Vervoort 1968: 33).—Venezuela: La Guaira (Vervoort 1968: 33).—Virgin Islands of the United States: St. Thomas, sound + Savannah Passage (Vervoort 1968: 33).—Virgin Islands of the United States: St. John, south coast (Vervoort 1968: 33).—USA: Florida, Indian River region, Sebastian Inlet + Fort Pierce breakwater (Winston 1982: 164, 165; 2009: 231).—USA: South Carolina, middle continental shelf E of Cape Island, 32–36 m (Wenner *et al*. 1984: 40).—Puerto Rico: Mona Island and Desecheo Island (Larson 1987: 514).—Colombia: Bahía de Chengue, on *Rhizophora* (Reyes & Campos 1992: 108).—Costa Rica: near Limón, 9–20 m (Kelmo & Vargas 2002: 606).—Panama: Bocas del Toro, Swan's Key, 09°27'12.2"N, 82°18'01.8"W, 1–4 m + Boca del Drago, 0–3 m + Drago 2, 2–4 m (Calder & Kirkendale 2005: 484).—French Lesser Antilles: Les Saintes, Terre-de-Haut, Pain de Sucre, 15°51'45"N, 61°35'60"W, rocky shore (Galea 2008: 39).—Mexico: Campeche (López Garrido 2008: 168).—French Lesser Antilles: Guadeloupe, Grande-Terre, Les Ancres, 16°27.002'N, 61°32.320'W, 15–18 m + L'Oeil, 16°26.782'N, 61°32.405'W, 12–17 m + Pointe d'Antigues, 16°26.251'N, 61°32.523'W (Galea 2010: 4).—Cuba: Golfo de Batabanó (Castellanos-Iglesias *et al*. 2011: 20).—French Lesser Antilles: Martinique (Galea 2013: 50).—USA: Florida, off Fort Pierce, 27°29.6'N, 80°17.0'W, 7–8 m + Fort Pierce Inlet, north jetty (Calder 2013: 24).—Caribbean Sea (Wedler 2017b: 138, figs. 152–155A, B, 156).—Panama: Bocas del Toro area, Swan's Cay (Miglietta *et al*. 2018b: 108).

Family Sertulariidae Lamouroux, 1812

Genus *Amphisbetia* L. Agassiz, 1862

Amphisbetia distans **(Lamouroux, 1816)**

Figs. 21a, b

Dynamena distans Lamouroux, 1816: 180, pl. 5, figs. 1a, B.
Sertularia stookeyi.—Joyce, 1961: 66, pl. 16, figs. 3, 4.—Shier, 1965: 55, pls. 27, 30.

Type locality. Atlantic Ocean: “Sur le *Fucus natans* (*Sargassum natans*) et quelques autres productions marines…” (Lamouroux 1816: 180).

Material examined. Sanibel Island, beach at Lighthouse Point, 26°26’57”N, 82°01’06”W, on detached *Syringodium* at water’s edge, 13 March 2018, 20° C, 33.5‰, one colony, up to 7 mm high, with gonophores, coll. D. Calder, ROMIZ B4386.—Sanibel Island, beach at Lighthouse Point, 26°26’58”N, 82°01’04.5”W, on detached *Thalassia* at water’s edge, 21 March 2018, 22° C, 34.5‰, two colonies, up to 5 mm high, without gonophores, coll. D. Calder, ROMIZ B4387.—Sanibel Island, beach at Lighthouse Point, 26°26’38”N, 82°01’36”W, on stranded *Thalassia* and *Syringodium*, 28 March 2018, 21° C, 35‰, three colonies, up to 7 mm high, without gonophores, coll. D. Calder, ROMIZ B4388.

Remarks. The hydroid described by Lamouroux (1816) as *Dynamena distans* is now widely known as either *Sertularia distans* or *Tridentata distans*. As noted in previous works (Calder 2013; Calder *et al.* 2019), molecular phylogenetic studies (Moura *et al*. 2011; Maronna *et al*. 2016) reveal that the species is more closely related to *Sertularia operculata* Linnaeus, 1758, type species of *Amphisbetia* L. Agassiz, 1862, than to either *Sertularia argentea* Linnaeus, 1758, type species of *Sertularia* Linnaeus, 1758 or *Sertularia perpusilla* Stechow, 1919, type species of *Tridentata* Stechow, 1920. The binomen *Amphisbetia distans* has therefore been applied to it here, following Calder *et al*. (2019). *Sertularia stookeyi* Nutting, 1904 is a subjective junior synonym (Calder 1983, 1990 [1991a]).

Records below indicate that *A. distans* is widely distributed in shallow tropical and temperate waters of the western North Atlantic. It has been reported from many locations in the Caribbean Sea, and its known range extends as far north as southern Massachusetts on the east coast of the United States (Fraser 1944). A eurytopic species (Calder 1976, 1990), it is particularly abundant and widespread in estuaries of South Carolina (Calder 1983). The hydroid was also found all seasons of the year on the shallow continental shelf nearby (Wenner *et al*. 1984). By contrast, records so far from the Gulf of Mexico are relatively few. While a substrate generalist, the hydroid is well-known as an epibiont on pelagic *Sargassum*. As such, it occurs in surface waters of the Sargasso Sea, and is transported northwards on gulfweed in the Gulf Stream. Elsewhere, the range of the species extends southwards to Brazil in the western Atlantic (Oliveira *et al*. 2016), and it is reported to be circumglobal in tropical and temperate waters (Calder 2013). While the hydroid of *A. distans* has been identified from bottoms as deep as 826 m (Ramil & Vervoort 1992), it is predominantly a species of shallow waters (<60 m) (Cornelius 1995b). *Amphisbetia distans* has also been found in the intertidal zone (Calder 2013).

Detailed taxonomic accounts of this species include those of Calder (1990 [1991a], 2013, as *Tridentata distans*), Cornelius (1995b, as *T. distans*), Medel and Vervoort (1998, as *Sertularia distans*), and Calder *et al*. (2019).

Reported Distribution. *Gulf coast of Florida.* Seahorse Key, on *Thalassia* and *Syringodium* (Joyce 1961: 66, as *Sertularia stookeyi*).—Cape San Blas area (Shier 1965: 55, as *Sertularia stookeyi*).

Elsewhere in western North Atlantic. USA: Massachusetts, off Hyannis, on *Sargassum* (Verrill 1875b: 43, as *Sertularia gracilis*).—USA: Massachusetts, Naushon Island (Nutting 1904: 57, as *Sertularia gracilis*).—Bahamas: Great Bahama Bank, on floating seaweed (Nutting 1904: 60, as *Sertularia stookeyi*).—USA: Massachusetts, Vineyard Sound, Naushon Island, outside Tarpaulin Cove, 7–8 ftm (13–15 m), on *Fucus*, *Thuiaria argentea* (=*Sertularia argentea*) (Fraser 1912a: 47, as *Sertularia stookeyi*).—USA: North Carolina, Beaufort area, on floating gulfweed and seaweed + Bogue Sound, 10 ft (3 m) + North River, 10 ft (3 m) + Straits, 10 ft (3 m) + offshore, on sponge (Fraser 1912b: 375, as *Sertularia stookeyi*).—Bermuda: off north shore, on floating *Sargassum* + Hamilton Harbour, on floating *Sargassum* (Bennitt 1922: 251, as *Sertularia stookeyi*).—Bermuda: on floating *Sargassum* (Prat 1935: 127, as *Sertularia gracilis*; 1940: 272, as *Sertularia gracilis*).—Bonaire: Plaja Oranje Pan, on stranded algae + Boca Onima, on stranded *Sargassum* (Leloup 1935: 48, as *Sertularia distans* var. *gracilis*).—Bonaire: Lac, mouth, back of reef, 1.5 m, on detached *Sargassum* (Leloup 1935: 48, as *Sertularia distans* var. *gracilis* forme *peculiaris*).—Curaçao: Boca Grandi, on stranded *Sargassum* + Boca Grandi, on deteriorated, floating *Sargassum* (Leloup 1935: 48, as *Sertularia distans* var. *gracilis*).—Aruba: Boca Prins, on stranded *Sargassum* (Leloup 1935: 48, as *Sertularia distans* var. *gracilis*).—Sargasso Sea: 39°N, 41°W, W of the Azores, on floating *Sargassum* (Leloup 1935: 48, as

Sertularia distans var. *gracilis*).—Sargasso Sea: 32°07'N, 66°35'W, W of Bermuda, on floating *Sargassum* (Leloup 1937: 105, as *Sertularia distans* var. *gracilis*).—Gulf Stream and Sargasso Sea: on *Sargassum natans* and *S. fluitans* (Burkenroad, in Parr 1939: 23, as *Sertularia flowersi*). —USA: Florida, between Biscayne and Duck keys (Fraser 1943: 93, as *Sertularia stookeyi*).—Trinidad & Tobago: Trinidad, Maguaripe Bay (=Macqueripe Bay) (Fraser 1943: 93, *Sertularia stookeyi*).—USA: Massachusetts, Nantucket Sound, 18 ftm (33 m) + Vineyard Sound, near West Chop Light, 14 ftm (26 m) + Vineyard Sound, Naushon Island, off Tarpaulin Cove, 14 ftm (26 m) (Fraser 1944: 289, as *Sertularia stookeyi*).—Gulf Stream: S of Marthas Vineyard (Massachusetts), 39°56'N, 70°46'W (probably on *Sargassum*) (Fraser 1944: 289, as *Sertularia stookeyi*).—Panama: Caledonia Bay (Puerto Escoces), on floating *Sargassum* (Fraser 1947b: 11, as *Sertularia stookeyi*).—Venezuela: Isla Cubagua, shore (Fraser 1947b: 11, as *Sertularia stookeyi*).—Aruba: Boca Prins, on stranded *Sargassum* (Van Gemerden-Hoogeveen 1965: 36, as *Sertularia distans* var. *gracilis*).—Curaçao: Boca Grandi, on stranded *Sargassum* (Van Gemerden-Hoogeveen 1965: 36, as *Sertularia distans* var. *gracilis*).—Bonaire: Kralendijk, Pasanggrahan, on wood fragments + Oranjepan, on stranded *Sargassum* + Boca Washikemba, on stranded brown algae (Van Gemerden-Hoogeveen 1965: 36, as *Sertularia distans* var. *gracilis*).—Trinidad & Tobago: Tobago, Rockley Bay (=Rockly Bay), on *Sargassum* (Van Gemerden-Hoogeveen 1965: 36, as *Sertularia distans* var. *gracilis*).—Venezuela: Islote Aves, northern lagoon, near low water (Van Gemerden-Hoogeveen 1965: 36, as *Sertularia distans* var. *gracilis*).—Antigua and Barbuda: Antigua, Deep Bay at Fort Barrington, on *Sargassum* (Van Gemerden-Hoogeveen 1965: 36, as *Sertularia distans* var. *gracilis*).—Antigua and Barbuda: Barbuda, Martello Tower Beach, near low tide (Van Gemerden-Hoogeveen 1965: 36, as *Sertularia distans* var. *gracilis*).—St. Kitts and Nevis: St. Kitts, Frigate Bay, near low tide, on *Sargassum* (Van Gemerden-Hoogeveen 1965: 36, as *Sertularia distans* var. *gracilis*).—Saint-Barthélemy: Public, tidal zone, on *Sargassum* (Van Gemerden-Hoogeveen 1965: 36, as *Sertularia distans* var. *gracilis*).—Bahamas: North Bimini, 1 km offshore (Van Gemerden-Hoogeveen 1965: 36, as *Sertularia distans* var. *gracilis*).—Sargasso Sea: 43°04'N, 31°W, N of the Azores (Van Gemerden-Hoogeveen 1965: 36, as *Sertularia distans* var. *gracilis*).—Sargasso Sea + Gulf Stream, stations between Florida and South Carolina, on *Sargassum polyceratium*, *S. filipendula* (Rackley 1974: 39, as *Sertularia stookeyi*).—USA: South Carolina, inshore waters, abundant, especially on *Leptogorgia* (Calder & Hester 1978: 91, as *Sertularia stookeyi*).—Belize: Carrie Bow Cay, on *Thalassia* (Spracklin 1982: 246, as *Sertularia stookeyi*).—USA: South Carolina estuaries, Bulls Bay, 4–5 m + Sewee Bay, 2–4 m + Prices Creek, 8 m + Inlet Creek, 4 m + Charleston Harbor, entrance, 10 m + Charleston Harbor, Rebellion Reach, 12 m + Stono Inlet, 7–10 m + Kiawah River, 6 m + Dawho River, 7–10 m + North Edisto River, Bear's Bluff, 7 m + North Edisto River, Toogoodoo Creek, 4 m + North Edisto River, Steamboat Creek + North Edisto River, Wadmalaw Island, 8 m + North Edisto River, Point of Pines, 8 m + North Edisto River, Deveaux Bank, 10 m + South Edisto River, Bay Point + Beaufort River, 6 m + Colleton River, 6 m + Port Royal Sound, 8 m + Calibogue Sound, 7 m (Calder 1983: 13, as *Sertularia distans*).—USA: South Carolina, inner (17–18 m) and middle (32–36 m) continental shelf + Georgia, inner (17–22 m), middle (23–29 m) and outer (59–67 m) continental shelf (Wenner *et al*. 1984: 21, 40, as *Sertularia distans*).—USA: Texas, mid-continental shelf (Rezak *et al*. 1985: 224, as *Sertularia distans*).—USA: South Carolina, coastal areas, in stomachs of Atlantic spadefish (Hayse 1990: 81, as *Sertularia distans*).—Bermuda: Harrington Sound, Stream Passage Cave, inside entrance, 0.5 m, on rock + Castle Harbour, near Castle Island, on *Thyroscyphus marginatus*, 5 m + Harrington Sound, Cripplegate Cave, entrance, 0.5 m, on rock + Flatts Inlet, on algae, 2–3 m + Natural Arches Beach, on stranded *Sargassum* (Calder 1990 [1991a]: 105, 106, as *Tridentata distans*).—Belize: Twin Cays, on *Rhizophora*, *Thalassia*, other invertebrates (Calder 1991b: 223, 1991c: 2068, as *Tridentata distans*).—Bermuda: Harrington Sound, just below tidal level (Thomas 1996: 758, as *Sertularia distans*).—Cuba: Golfo de Batabanó, Cayo Real, 21°57'42.5"N, 83°32'06.2"W, 0 m + Cayo Los Indios, 22°02'28.9"N, 82°50'55.4"W, 0.5 m (Castellanos *et al*. 2011: 22, as *Tridentata distans*).—Cuba: Isla de la Juventud, wreck of *Las Calderas*, 21°29'57.5"N, 82°38'57.3"W, 6 m (Castellanos *et al*. 2011: 22, as *Tridentata distans*).—USA: Florida, Fort Pierce Inlet, north jetty, on *Thyroscyphus ramosus*, intertidal (Calder 2013: 30, as *Tridentata distans*).—French Lesser Antilles, Martinique: Le Vauclin, Pointe Faula, 14.54064, -60.82837, 0 m, on floating *Sargassum* (Galea & Ferry 2015: 234, as *Sertularia distans*).—Mexico: Alacranes Reef, on shipwreck (Mendoza-Becerril *et al*. 2018b: 130, as *Sertularia distans*).—Cuba: Havana, coral reef system west of the city (Castellanos *et al*. 2018: Supplementary Table S2, as *Sertularia distans*).—Panama: Bocas del Toro area, near Bocatorito Bay (Miglietta *et al*. 2018b: 108, as *Sertularia distans*).

Genus *Dynamena* Lamouroux, 1812

Dynamena disticha (Bosc, 1802)

Fig. 21c

Sertularia disticha Bosc, 1802: 101, pl. 29, fig. 2.
Sertularia cornicina.—Nutting, 1904: 58.—Fraser, 1943: 92; 1944: 279.
Sertularia mayeri.—Nutting, 1904: 58.—Leloup, 1935a: 49.—Fraser, 1943: 93.—Shier, 1965: 51, pl. 28.
Sertularia exigua.—Fraser, 1944: 281.
Sertularia erasmoi.—Joyce, 1961: 67, pl. 17, figs. 1, 2.
Dynamena cornicina.—Van Gemerden-Hoogeveen, 1965: 25.
Dynamena mayeri.—Van Gemerden-Hoogeveen, 1965: 30.
Sertularia sp.—Shier, 1965: 52, pl. 29.

Type locality. Atlantic Ocean: "...sur le *fucus natans* (*Sargassum natans*) dans la haute mer…" (Bosc 1802: 101).

Material examined. Sanibel Island, beach at Lighthouse Point, 26°26'57"N, 82°01'07"W, on detached *Thalassia* in water along shore, 21 February 2013, one colony, 9 mm high, with gonothecae, coll. D. Calder, ROMIZ B4410.—Sanibel Island, beach at Lighthouse Point, detached and stranded in tidepool, 30 March 2013, one colony, 8 mm high, without gonophores, coll. D. Calder, ROMIZ B4411.—Sanibel Island, beach at Lighthouse Point, 26°26'55"N, 82°01'08"W, on detached *Thalassia* in water along shore, 21° C, 34.5‰, 19 March 2018, three colony fragments, up to 8 mm high, with gonothecae, coll. D. Calder, ROMIZ B4408.—Sanibel Island, beach at Lighthouse Point, 26°26'58"N, 82°01'04.5"W, on detached *Idiellana pristis* at water's edge, 21 March 2018, 22° C, 34.5‰, three colony fragments, up to 1.1 cm high, without gonophores, coll. D. Calder, ROMIZ B4407.

Remarks. Hydroids identified under either the binomen *Dynamena disticha* (Bosc, 1802) or one of its various synonyms are widespread and of frequent occurrence in the tropical and warm-temperate western North Atlantic. The reported range of the species extends from southern New England (Nutting 1904) and Bermuda (Calder 1990 [1991a]) to the Caribbean coast of northern South America (Wedler 1975), and on to Argentina in the southwest Atlantic (Oliveira *et al*. 2016). Well-known as part of the *Sargassum* fauna, it is found in the Sargasso Sea and the Gulf of Mexico, and is carried far northwards in the warm Gulf Stream on gulfweed to waters east of Atlantic Canada (Fraser 1918). As apparent from distribution records below, it has been collected several times previously on the Gulf coast of Florida. *Dynamena disticha* has been reported over a bathymetric range of 0–256 m (Fernandez & Marques 2018), but the species is much more frequent in near-surface waters.

Molecular analyses (Moura *et al*. 2011; Maronna *et al*. 2016) reveal that *Dynamena* Lamouroux, 1812 as presently constituted is polyphyletic and in need of significant revision. Indeed, *Dynamena disticha* is shown in such studies to be genetically distant from the type species of the genus, *D. pumila* (Linnaeus, 1758). *Sertularia quadridentata* Ellis & Solander, 1786, another species likewise remote from *D. pumila* but formerly included in *Dynamena*, was referred earlier (Calder 2013) to *Pasya* Stechow, 1922, as *P. quadridentata*. *Dynamena disticha* needs to be reassigned, along with any closely related species, to another genus. Such re-classification needs careful consideration and is beyond the scope of this study.

Moura *et al*. (2011) detected potential cryptic species within populations identified as *D. disticha* from western Europe. Questions also exist about possible taxonomic differences between two forms assigned to the species in the western Atlantic (Calder 2013). One of these, a stunted form usually 1 cm high or less, is common on pelagic *Sargassum* as originally described by Bosc (1802). The other morphotype, more robust and reaching 5 cm high, has been reported largely from inshore waters on various benthic substrates.

Hydroids of *D. disticha* are typically bright yellow in colour (Bosc 1802; Calder 1971, 1983). While seldom branched, a single hydrocladium may occur on large colonies (Calder 1971). In this character it differs from the closely related but alternately branched *D. moluccana* (Pictet, 1893). *Dynamena dimorpha* Galea, in Galea & Ferry 2015, a species much resembling *D. disticha*, has recently been described from Martinique in the Caribbean Sea. It differs in having both unbranched and pinnately branched colonies, thicker and less collapsable perisarc, and hydrothecae that are shallower and wider (Galea & Ferry 2015). From the original account of that species, symbiotic zooxanthellae may be present.

Gonothecae in *D. disticha*, resembling inverted Chinese lanterns, usually occur on the hydrorhiza. They may also arise from internodes of the hydrocaulus or even from old hydrothecae (Calder 1971; Galea 2008). In the latter case, their morphology is atypical in being sac-shaped with a rounded distal end, they vary in length and width, and their walls are smooth or only slightly undulated (Galea 2008).

While believed to be a substrate generalist (Calder 1971, 1991c; Oliveira 2016), this hydroid often occurs on seagrasses and especially on pelagic *Sargassum*. If estuarine populations have been correctly assigned to this species, *D. disticha* is both euryhaline and eurythermal. It extends from coastal waters up-estuary to about the 18‰ isohaline (Calder 1976), and it tolerates temperatures as low as about 9° C before becoming dormant (Calder 1990). Hydroids, including *D. cornicina* (=*D. disticha*), were found to be the primary food of Atlantic spadefish (*Chaetodipterus faber*) in estuarine areas and offshore reefs of South Carolina (Hayse 1990).

The nomenclature of *D. disticha* has been reviewed elsewhere (Calder 1990 [1991a]). A detailed synonymy of the species exists in Medel & Vervoort (1998).

Reported distribution. ***Gulf coast of Florida.*** Pourtales Plateau (Nutting 1904: 58, as *Sertularia cornicina*).—Off Cape San Blas, 29°16'30"N, 85°32'W (*Albatross* Station 2369), 26 ftm (48 m) (Nutting 1904: 59, as *Sertularia mayeri*).—Off Cape Romanes (Cape Romano) (Nutting 1904: 59, as *Sertularia mayeri*).—Dry Tortugas, 27 ft (8 m) (Leloup 1935a: 49, as *Sertularia mayeri*).—W of Florida, 20 ftm (37 m) (Fraser 1943: 92; 1944: 280, as *Sertularia cornicina*, "robust type").—Dry Tortugas (Fraser 1943: 93, as *Sertularia mayeri*).—Between Biscayne and Duck keys, on *Sargassum* (Fraser 1943: 93, as *Sertularia mayeri*).—W of Cape Romano, 2 miles (3 km) (Fraser 1944: 282, as *Sertularia exigua*).—Seahorse Key, on *Sargassum* (Joyce 1961: 67, as *Sertularia erasmoi*).—Dry Tortugas, on shells, coral debris (Van Gemerden-Hoogeveen 1965: 25, as *Dynamena cornicina*).—Dry Tortugas (Van Gemerden-Hoogeveen 1965: 30, as *Dynamena mayeri*).—Cape San Blas area (Shier 1965: 51, as *Sertularia mayeri*).—Cape San Blas area, on *Syringodium*, *Thalassia*, *Sargassum*, *Diplanthera* (=*Halodule*), and *Codium* (Shier 1965: 99, as *Sertularia* sp.).

Elsewhere in western North Atlantic. Atlantic Ocean: high seas, on *Fucus natans* (=*Sargassum natans*) (Bosc 1802: 101, as *Sertularia disticha*).—USA: South Carolina, Charleston Harbor (McCrady 1859: 204, as *Dynamena cornicina*).—USA: South Carolina, Charleston (A. Agassiz 1865: 142, as *Dynamena cornicina*).—USA: North Carolina, coast (Verrill 1872: 437, as *Dynamena cornicina*).—USA: Massachusetts, Vineyard Sound, on *Halecium* and floating *Zostera*, 1–8 ftm (2–15 m) (Verrill 1874d: 733, as *Sertularia cornicina*).—USA: North Carolina, off Cape Fear, 9 ftm (16 m) (Allman 1877: 24, as *Sertularia exigua*).—USA: North Carolina, Fort Macon area (Coues & Yarrow 1878: 308, as *Sertularia cornicina*).—Mexico: Yucatan, on an alga (Clarke 1879: 246, as *Sertularia complexa*).—USA: North Carolina, Beaufort (Brooks 1882: 142, as *Dynamena bilatteralis*; 1884: 711, as *Dinamena bilateralis*).—USA: Massachusetts, Woods Hole area (Nutting 1901: 359, as *Sertularia cornicina*).—USA: Massachusetts, Woods Hole area + near Nobska Point, on seaweed (Nutting 1901: 360, as *Sertularia complexa*).—Atlantic Ocean: beyond the Antilles, on *Sargassum* (Jäderholm 1903: 287, as *Sertularia exigua*).—USA: Massachusetts, Woods Hole area (Nutting 1904: 58, as *Sertularia cornicina*).—Bahamas: between Eleuthera and Little Cat islands, shoal water + Great Bahama Bank, on floating seaweed (Nutting 1904: 59, as *Sertularia mayeri*).—USA: North Carolina, off Cape Fear, 33°37'30"N, 77°36'30"W, 14 ftm (26 m) (Nutting 1904: 59, as *Sertularia mayeri*).—USA: North Carolina, Bogue Sound, on floating algae and *Sargassum* + North River + Straits, 10 ft (3 m) + off Beaufort, on sponge (Fraser 1912b: 374, as *Sertularia cornicina*).—USA: Massachusetts, Georges Bank, floating colonies (Fraser 1915: 308, as *Sertularia cornicina*).—Gulf Stream: E of Nova Scotia, on *Sargassum* (Fraser 1918: 359, as *Sertularia cornicina*).—Bermuda: Agar's Island, on ledges and *Sargassum* + Somerset Bridge, on ledges and *Sargassum* + Challenger Bank, on a gorgonian, 32 ftm (59 m) (Bennitt 1922: 251, as *Sertularia cornicina*).—Sargasso Sea, on *Sargassum* (Hentschel 1922: 4, as *Sertularia mayeri*).—Bonaire: Kralendijk, Pasanggrahan, 0.2 m, on algae + Plaja Witte Pan, on stranded algae + Plaja Oranje Pan, on stranded algae + Lac, mouth, back of reef, on detached *Sargassum*, 1.5 m + Boca Washikemba, on stranded algae + Boca Onima, on stranded *Sargassum* (Leloup 1935a: 40, as *Dynamena cornicina*).—Curaçao: Boca Grandi, on *Sargassum* (Leloup 1935a: 40, as *Dynamena cornicina*).—Aruba: Boca Prins, on stranded *Sargassum* (Leloup 1935a: 40, as *Dynamena cornicina*).—Sargasso Sea: on pelagic *Sargassum*, 23°57'N, 67°45'W + 27°13'N, 62°16'W (Leloup 1935b: 4, as *Dynamena cornicina*).—Bahamas: Elbow Cay, south coast (Leloup 1937: 106, as *Dynamena cornicina*).—Atlantic Ocean: Gulf Stream, on pelagic *Sargassum* + Sargasso Sea, on pelagic *Sargassum* (Burkenroad, in Parr 1939: 23).—Trinidad & Tobago: Trinidad, Maguaripe Bay (=Macqueripe Bay) (Fraser 1943: 93, *Sertularia mayeri*).—Sargasso Sea: NE of the Bahamas, on *Sargassum* (Fraser 1944: 280, as *Sertularia cornicina*).—USA: North Carolina, offshore (Fraser 1944: 280, as *Sertularia cornicina*).—Sargasso Sea: 34°N, 38°W, on *Sargassum* (Vervoort 1946: 307, as *Dynamena cornicina*).—Aruba: 8 miles (13 km) SW of San Nicolaas Bay (Sint Nicolaas Baai), 23–24 ftm (42–44 m) (Fraser 1947b: 10, as *Sertularia cornicina*).—Colombia: 2 miles (3 km) off Bahía Honda, 9 ftm (16 m) (Fraser 1947b: 10, as *Sertularia exigua*).—Venezuela: off Isla Tortuga (Fraser 1947b: 10, as *Sertularia exigua*).—USA: Texas, Port

Isabel + Port Aransas, on *Sargassum* (Deevey 1950: 346, as *Sertularia cornicina*).—Aruba: Boca Prins, on stranded *Sargassum* (Van Gemerden-Hoogeveen 1965: 25, as *Dynamena cornicina*).—Curaçao: Klein Curaçao, western shore, on *Sargassum* (Van Gemerden-Hoogeveen 1965: 25, as *Dynamena cornicina*).—Bonaire: Kralendijk, Pasanggrahan, near low tide, on small stone + De Hoop, 1–3 m + Punt Vierkant, on algae, coral, & detached, low tide to 2 m + Oranjepan, on *Sargassum* + Boca Washikemba, on stranded brown algae + Boca Onima, on *Sargassum* (Van Gemerden-Hoogeveen 1965: 25, as *Dynamena cornicina*).—Venezuela: Isla La Blanquilla, Playa Valuchu, 2.5 m, on wood fragments + Islas Los Frailes, La Pecha, SW shore, 1–2 m, on algae + Islas Los Testigos, Puerto Tamarindo, ca. 2 m, on seaweed (Van Gemerden-Hoogeveen 1965: 25, as *Dynamena cornicina*).—Trinidad & Tobago: Trinidad, Monos, Avalon Bay, ca. 1 m, on stones, shells + Tobago, Buccoo Bay, 2 m, on coral (Van Gemerden-Hoogeveen 1965: 25, as *Dynamena cornicina*).—Grenada: between Grenada and Trinidad, on floating *Sargassum* (Van Gemerden-Hoogeveen 1965: 25, as *Dynamena cornicina*).—St. Kitts & Nevis: St. Kitts, Frigate Bay, near low tide, on algae and other hydroids (Van Gemerden-Hoogeveen 1965: 25, as *Dynamena cornicina*).—Sint Maarten: Simson Lagoon, outlet, near low tide, on algae (Van Gemerden-Hoogeveen 1965: 65, as *Dynamena cornicina*).—USA: Virginia, York River (Tue Marsh Light; Perrin; Gloucester Point; Page's Rock) + James River (Hampton Bar) + southern Chesapeake Bay (Little Creek jetty; Cape Charles) (Calder 1971: 70, as *Dynamena cornicina*).—USA: Virginia, York River, Big Mumford Island, 37°16'N, 76°31'W, on *Zostera* (Marsh 1973: 93, as *Dynamena cornicina*).—USA: Texas, Galveston, front beach, on floating *Sargassum* (Defenbaugh & Hopkins 1973: 107, as *Sertularia mayeri*).—USA: Texas, West Flower Garden Bank, on floating *Sargassum* (Defenbaugh 1974, as *Sertularia mayeri*).—Sargasso Sea + Gulf Stream, several stations between Florida and North Carolina, on *Sargassum fluitans* III, *S. fluitans* X, *S. pteropleuron* (Rackley 1974: 35, as *Dynamena mayeri*).—Colombia: Santa Marta area, rocky littoral (Wedler 1975: 340, as *Dynamena cornicina*).—USA: Florida, southeast coast (Mergner 1977: 122, as *Dynamena cornicina*; 1987: 187, as *Dynamena cornicina*).—USA: South Carolina, numerous areas across the coastal zone (Calder & Hester 1978: 91, as *Dynamena cornicina*).—Belize: Carrie Bow Cay (Spracklin 1982: 246, as *Dynamena cornicina*).—Barbados: on *Thalassia* (Lewis & Hollingworth 1982: 43, as *Sertularia mayeri*).—?Colombia: Bahía de Cartagena (Flórez González 1983: 123, as *Dynamena cornicina*).—USA: South Carolina, Murrells Inlet, 1–3 m + Sewee Bay, 2–4 m + Bulls Bay, 5 m + Prices Creek, 8 m + Inlet Creek, 4 m + Charleston Harbor entrance, 10 m + Kiawah River, 2–6 m + North Edisto River, 7–10 m + South Edisto River, 7 m + Beaufort River, 6 m (Calder 1983: 10, as *Dynamena cornicina*).—USA: continental shelf of South Carolina and Georgia (Wenner *et al*. 1983: 148, as *Dynamena cornicina*).—USA: South Carolina, inner (17–18 m), middle (32–36 m) and outer (46–69 m) continental shelf + Georgia, inner (17–22 m), middle (23–29 m) and outer (59–67 m) continental shelf (Wenner *et al*. 1984: 21, 40, as *Dynamena cornicina*).—USA: South Carolina, North Inlet area, Town Creek and tributaries + Murrells Inlet, jetties + Charleston area + Folly River area, Oak Island, oyster reef + Breach Inlet, jetties (Fox & Ruppert 1985: 61, 92, 140, 152, 167, as *Dynamena cornicina*).—Bermuda: inshore shallow waters + reefs + offshore banks + pelagic *Sargassum* (Calder 1986: 137).—Colombia, Santa Marta area, rocky littoral, near low tide, on algae, other hydroids, *Thalassia*, *Syringodium* (Bandel & Wedler 1987: 42, as *Dynamena cornicina*).—USA: South Carolina and Georgia, inner continental shelf, on artificial reefs (Wendt *et al*. 1989: 1112, as *Dynamena cornicina*).—USA: South Carolina, coastal areas, in stomachs of Atlantic spadefish (Hayse 1990: 81, as *Dynamena cornicina*).—Bermuda: Flatts Inlet, on *Thalassia*, 1 m + Whalebone Bay, on algae, 1–4 m + Natural Arches Beach, on *Sargassum* (Calder 1990 [1991a]: 93, 94).—Belize: Twin Cays (Calder, 1991b: 223).—USA: North Carolina, Onslow Bay, in fish stomachs (Pike & Lindquist 1994: 366, as *Dynamena cornicina*).—Bermuda: on pelagic *Sargassum fluitans* (Calder 1995: 540).—Bermuda: Challenger Bank + Argus (=Plantagenet) Bank (Calder 2000: 1133).—Cuba: Ciudad de La Habana province, Cojimar, on *Sargassum* (Ortiz 2001a: 64, as *Dynamena cornicina*).—Costa Rica: Limón, Isla Uvita, 09°59'40"N, 83°00'50"W (Kelmo & Vargas 2002: 607).—Panama: Colón, Isla Margareta, Fort Randolph, shore, 09°23'15"N, 79°53'11"W, 0-1 m + Bocas del Toro area, Hospital Point, 09°20'01.9"N, 82°13'07.7"W, 2-13 m + Bocas del Toro area, Boca del Drago, 09°25'36.3"N, 82°19'30.1"W, 1-3 m + Bocas del Toro area, Cayos Zapotilla, 09°15.564'N, 82°02.750'W, 7-8 m + Bocas del Toro area, Crawl Cay, 09°15.261'N, 82°07.787'W, 2-4 m + Bocas del Toro area, near Laguna Bocatorito, 2-4 m + Bocas del Toro area, Bastimentos (front), 09°20.898'N, 82°09.959'W, 1-4 m + Bocas del Toro area, Boca del Drago, 0-3 m + Bocas del Toro area, "Emelio's Beach," 09°22.027'N, 82°14.336'W + Bocas del Toro area, Drago 2, 2-4 m (Calder & Kirkendale 2005: 485).—French Lesser Antilles: Guadeloupe, Grande-Terre, E of Saint François, 16°15'18.00"N, 61°14'37.00"W, seagrass meadows, on *Thalassia* + Basse-Terre, N of Malendure, 16°10'25.00"N, 61°46'58.00"W, rocky shore, on sponge, algae, rock + Basse-Terre, Petite Anse, 16°05'47.00"N, 61°46'17.00"W, rocky shore, on algae, concretions + Basse-Terre, Anse à la Barque, 16°05'21"N, 61°46'00"W, rocky shore, dock, pilings, on ascidian (Galea 2008: 30, 31).—French Lesser Antilles: Les Saintes, Terre-de-Haut, Pompierre Bay, 15°52'25"N, 61°34'15"W, large rocks in seagrass meadows, on *Halimeda*, *Thalassia* + Terre-de-Haut, Pain de Sucre, 15°51'45"N, 61°35'60"W, rocky shore, on algae, sponge, concretions, bivalve shell (Galea 2008: 31).—Cuba (Castellanos *et al*. 2009: 99, as *Dynamena cornicina*).—French Lesser Antilles: Guadeloupe, Grande-Terre, Les Arches, 16°27.529'N, 61°32.021'W, 17 m + Grande-Terre, Pointe d'Antigues, 16°26.251'N, 61°32.523'W (Galea 2010: 3, 4).—French Lesser Antilles: Les Saintes, Terre-de-Haut, Pointe Morel, 15°53.050'N, 61°34.410'W, 6–11 m (Galea 2010: 5).—USA: Florida: Fort Pierce Inlet State Park, 27°28'29.5"N, 80°17'25.8"W, on stranded *Sargassum* (Calder 2013: 27).—French Lesser Antilles: Martinique (Galea 2013: 50).—Caribbean Sea (Wedler 2017b: 125, figs. 125, 126A, B).—Mexico: Alacranes Reef, on algae, seagrass, corals, artificial reefs (Mendoza-Becerril *et al*. 2018b: 130).—Cuba: Havana, coral reef system west of the city (Castellanos *et al*. 2018: Supplementary Table S2).—Panama: Bocas del Toro area, Crawl Cay (Miglietta *et al*. 2018b: 108).

Dynamena pourtalesi **(Nutting, 1904), comb. nov.**

Fig. 21d

Sertularia distans Allman, 1877: 25, pl. 16, figs. 9, 10.—Clarke, 1879: 246.—Nutting, 1895: 179 [junior primary homonym of *Sertularia distans* Lamouroux, 1816].

Sertularia pourtalesi Nutting, 1904: 59, pl. 5, fig. 5 [*nomen novum* for *Sertularia distans* Allman, 1877].

Type locality. USA: Florida, Tennessee Reef, 21 ftm (38 m) (Allman 1877: 25, as *Sertularia distans*).

Material examined. Southwest Florida Shelf, middle shelf west of Gasparilla Island, 26°45.86'N, 83°21.44'W, 50 m, 18 July 1981, triangle dredge, four colony fragments, up to 6.4 cm high, without gonophores, coll. Continental Shelf Associates, ROMIZ B306.—Southwest Florida Shelf, middle shelf west of North Naples, 26°16.83'N, 83°23.81'W, 59.5 m, 19 July 1981, triangle dredge, eight colony fragments, up to 3.4 cm high, without gonophores, coll. Continental Shelf Associates, ROMIZ B1965.

Remarks. This species was originally described as *Sertularia distans* by Allman (1877) from the Tennessee Reef off Long Key, Florida. Nutting (1895: footnote, p. 179) recognized that the binomen was a junior primary homonym of *Sertularia distans* Lamouroux, 1816, and later (Nutting 1904) proposed *S. pourtalesi* as a replacement name for it. No new records of this species have been reported since Nutting's monograph.

Allman's species has been regarded as a synonym of *Amphisbetia distans* (Lamouroux, 1816) in some works (Cornelius 1979, as *Sertularia distans*; Garcia *et al*. 1980, as *S. distans*; Calder 1983, as *S. distans*), and of *Dynamena disticha* (Bosc, 1802) in others (Calder 1990 [1991]; Medel & Vervoort 1998). Its colonies are much more robust than the exceptionally fine ones of *T. distans*, its hydrothecae are larger and more tubular, and its hydrothecal pairs are more adnate. Conspecificity of the two is considered improbable. In this work, *S. pourtalesi* is also held to be distinct from *D. disticha*, a smaller species in which hydrothecae are more cylindrical and only 2/3 as large, and hydrothecal pairs that are much closer together given the significantly shorter length of the internodes. In being a species of the continental shelf, it also appears to occur in deeper waters than *D. disticha*, a species most often found within a few metres of the surface. *Dynamena dalmasi* (Versluys, 1899) is somewhat similar in general colony form, but its hydrothecal walls are much more constricted distally and its hydrothecal pairs tend to be less adnate.

In lacking an abcauline diverticulum, *S. pourtalesi* is combined here with *Dynamena* Lamouroux, 1812 instead of *Sertularia* Linnaeus, 1758 or *Tridentata* Stechow, 1920. Marktanner-Turneretscher (1890) had earlier included the species in the same genus, although under the binomen *Dynamena distans* (not *D. distans* Lamouroux, 1816) and on the basis of a misidentification, as noted below. Also in accord with the diagnosis of *Dynamena*, the hydrothecal margin of *D. pourtalesi* is tridentate, with two large lateral cusps and a smaller median adcauline one. Nutting (1904) and Fraser (1944) were mistaken in describing the margin as having only two cusps.

Two distribution records of *Dynamena pourtalesi* have been discounted here. Nutting (1904, as *Sertularia pourtalesi*) reported it from 45°35'N, 55°01'W, 67 ftm (123 m), a location in cold waters south of Placentia Bay, Newfoundland, and an unlikely environment for this warm-temperate to tropical species. In addition, Marktanner-Turneretscher (1890: 239, as *D. distans*) recorded it on algae from the Sargasso Sea. After examining his description and illustrations of the species, that account is taken to be a misidentification of the similar *D. disticha*, a common species on pelagic *Sargassum*.

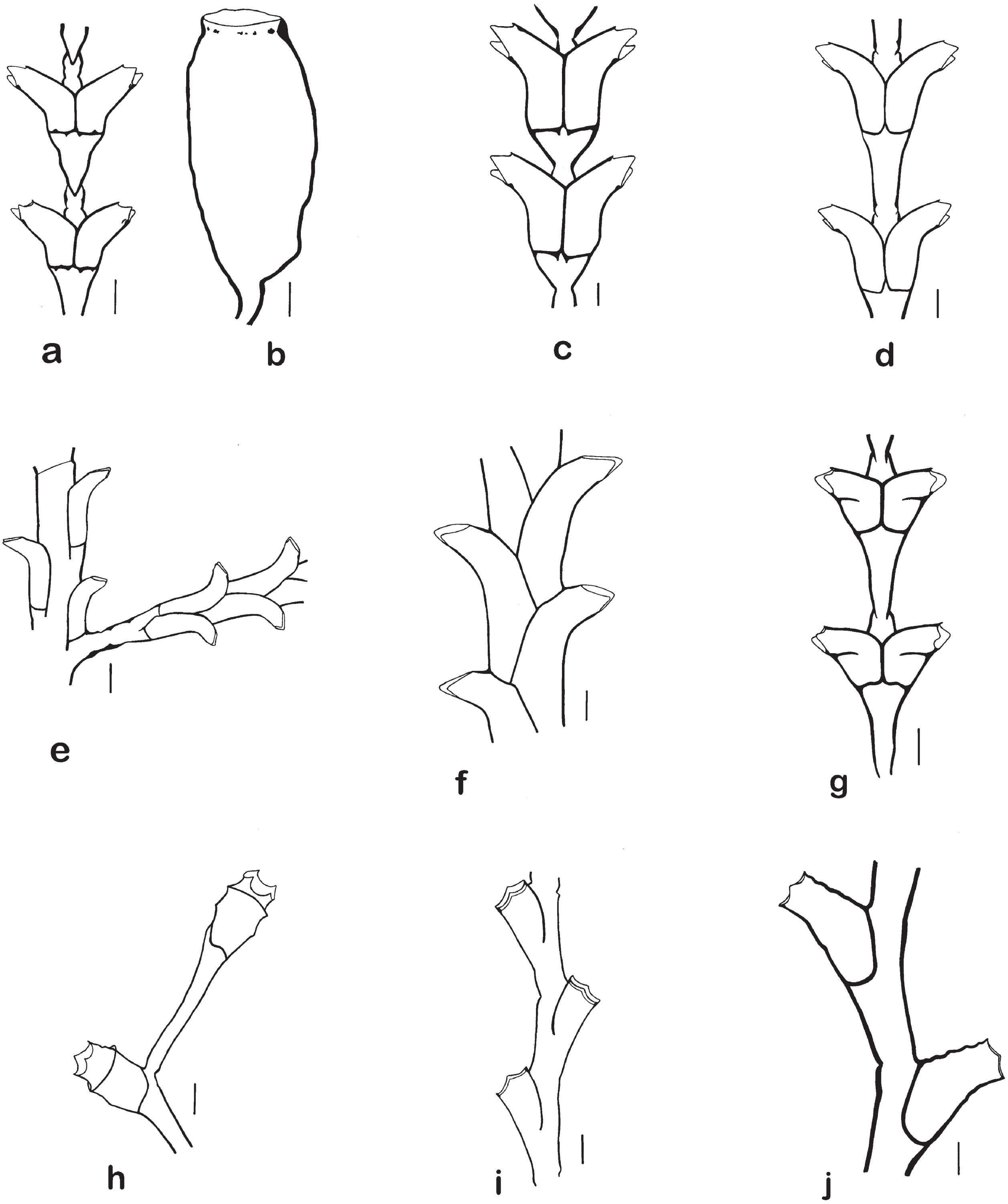

FIGURE 21. a, ***Amphisbetia distans*****:** part of hydrocaulus with two hydrothecal pairs, Sanibel Island, ROMIZ B4387. Scale equals 0.1 mm. **b,** ***Amphisbetia distans*****:** gonotheca, Sanibel Island, ROMIZ B4386. Scale equals 0.1 mm. **c,** ***Dynamena disticha*****:** part of hydrocaulus with two hydrothecal pairs, Sanibel Island, ROMIZ B4410. Scale equals 0.1 mm. **d,** ***Dynamena pourtalesi*****:** part of hydrocaulus with two hydrothecal pairs, Southwest Florida Shelf, ROMIZ B306. Scale equals 0.2 mm. **e,** ***Idiellana pristis*****:** base of hydrocaulus with a branch, Sanibel Island, ROMIZ B4390. Scale equals 0.2 mm. **f,** ***Idiellana pristis*****:** part of branch with hydrothecae, Sanibel Island, ROMIZ B4390. Scale equals 0.1 mm. **g,** ***Tridentata turbinata*****:** part of hydrocaulus with two hydrothecal pairs, Sanibel Island, ROMIZ B4393. Scale equals 0.2 mm. **h,** ***Sertularella areyi*****:** part of colony with two hydrothecae, Southwest Florida Shelf, ROMIZ B1978. Scale equals 0.2 mm. **i,** ***Sertularella diaphana*****:** part of colony with three hydrothecae, Southwest Florida Shelf, ROMIZ B4392. Scale equals 0.2 mm. **j,** ***Sertularella unituba*****:** part of colony with two hydrothecae, Southwest Florida Shelf, ROMIZ B2001. Scale equals 0.2 mm.

Dynamena pourtalesi is a rarely reported species with a known distribution largely restricted to the shelf waters of southwest Florida. The only other records of it are those of Fewkes (1881, as *Sertularia distans*) from the Caribbean island of St. Vincent and Wells *et al*. (1964) from Core Banks, North Carolina. Its gonosome remains unknown.

Reported distribution. ***Gulf coast of Florida.*** Tennessee Reef, 21 ftm (38 m) (Allman 1877: 25, as *Sertularia distans*).—WNW of the Dry Tortugas, 24°46'N, 83°16'W, 36 ftm (66 m) (Clarke 1879: 246, as *Sertularia distans*).—Pourtalès Plateau (Nutting 1895: 179, as *Sertularia distans*).—Off Cape San Blas, 29°16'30"N, 85°32'W, 26 ftm (48 m) (Nutting 1904: 59, as *Sertularia pourtalesi*).—S of Key West, 24°26'N, 81°48'15"W, 37 ftm (68 m) (Nutting 1904: 59, as *Sertularia pourtalesi*).—W of Venice, 27°04'N, 83°21'15"W, 26 ftm (48 m) (Nutting 1904: 59, as *Sertularia pourtalesi*).

Elsewhere in western North Atlantic. St. Vincent, 114 ftm (208 m) (Fewkes 1881a: 128, as *Sertularia distans*).—USA: North Carolina, Core Banks, on *Aequipecten gibbus*, 17–20 ftm (31–37 m) (Wells *et al*. 1964: 566).

Genus *Idiellana* Cotton & Godfrey, 1942

Idiellana pristis (Lamouroux, 1816)

Figs. 21e, f

Idia pristis Lamouroux, 1816: 199, pl. 5, figs. 5a, B—E.
Idia.—Nutting, 1895: 180.
Idiella pristis.—Leloup, 1935a: 37, figs. 19–21.
Idiellana pristis.—Van Gemerden-Hoogeveen, 1965: 16.

Type locality. Indonesia: "Côtes de la Nouvelle-Hollande" (Lamouroux 1816: 199, as *Idia pristis*).

Material examined. Fort Myers Beach, stranded on shore, 16 February 2013, several colonies, up to 9.5 cm high, without gonophores, ROMIZ B4414.—Fort Myers Beach, stranded on shore, 16 February 2013, one colony, 11 cm high, without gonophores, ROMIZ B4415.—Fort Myers Beach, stranded on shore, 01 March 2013, several colonies, up to 13 cm high, without gonophores, ROMIZ B4416.—Sanibel Island, beach at Lighthouse Point, detached and stranded in tidepool, 30 March 2013, one colony, 4.8 cm high, without gonothecae, coll. D. Calder, ROMIZ B4389.—Sanibel Island, beach at Lighthouse Point, 26°26'57"N, 82°01'07"W, detached, in intertidal pool, 03 August 2014, one juvenile colony, 1.6 cm high, without gonophores, coll. D. Calder, ROMIZ B4390.—Sanibel Island, beach at Lighthouse Point, 26°26'58"N, 82°01'04.5"W, on detached shell debris at water's edge, 21 March 2018, 22° C, 34.5‰, one colony, 7 mm high, without gonophores, coll. D. Calder, ROMIZ B4391.

Remarks. Records of *Idiellana pristis* (Lamouroux, 1816) in the western North Atlantic have mostly been from the Caribbean region. Even there, they have been quite limited in number, with reports from Martinique (Fraser 1944, as *Idiella pristis*), Puerto Rico (Fraser 1944, as *Idiella pristis*), St. Thomas (Vervoort 1968), and Colombia (Wedler 1975, as *Idiella pristis*; Flórez González 1983; Bandel & Wedler 1987; Quiceno & Palacio 2008, as *Idiella pristis*; Wedler 2017b). To the north, records exist from both the Dry Tortugas and Key West, Florida (Nutting 1895, as *Idia*; Leloup 1935a, as *Idiella pristis*; Van Gemerden-Hoogeveen 1965), and from the northeast coast of Cuba (Varela & Cabrales 2010). The species has yet to be reported along the east coast of the United States. Present records extend the known range northwards to Sanibel Island, Florida, in the southeastern Gulf of Mexico.

Elsewhere, hydroids of *I. pristis* have been reported several times from Brazil (Oliveira *et al*. 2016), although a report in that work of the species from "La Tortuga Island", Venezuela, is believed here to be a misinterpretation of records from the Dry Tortugas, Florida. The species has a wide geographic range over tropical and subtropical areas of the Atlantic, Pacific, and Indian oceans (Vervoort 1993; Vervoort & Watson 2003), but it has yet to be reported from the eastern Pacific. Its known bathymetric range is from 0 m to 183 m (Fraser 1944; Calder & Cairns 2009; Fernandez & Marques 2018), with most records being from intermediate depths (Vervoort 1993).

The hydroid is distinctive in having unbranched hydrocladia with a double row of alternate, adnate, distally projecting hydrothecae (Schuchert 2003). The specific name of the species is derived from the resemblance of these hydrocladia to the rostrum of the sawfish, *Pristis pristis* (Linnaeus, 1758) (Lamouroux 1816: 199; Millard 1975: 270).

Earlier generic names applied to this species, *Idia* Lamouroux, 1816 and its replacement name *Idiella* Stechow, 1919, are invalid in being junior homonyms of *Idia* Hübner, 1813 (Lepidoptera) and *Idiella* Brauer & Bergenstamm, 1890 (Diptera) respectively. Hübner had used the name *Idia* even earlier (1808), but it appeared in a pamphlet (*Erste Zuträge zur Sammlung exotischer Schmetterlinge*) that has been rejected for nomenclatural purposes (ICZN 1966, Opinion 789) in failing to meet Criteria of Publication in Zoological Nomenclature (ICZN Art. 8). That pamphlet is listed as Title Number 72 in the Official Index of Rejected and Invalid Works in Zoological Nomenclature. In the same ruling (Opinion 789), *Idia* Hübner, 1808 (Name No. 1863) and *Idia* Lamouroux, 1816 (Name No. 1864) were both placed on the Official Index of Rejected and Invalid Generic Names in Zoology. The replacement name *Idiellana*, proposed by Cotton & Godfrey (1942), is in current use supplanting the junior homonym *Idiella* Stechow, 1919.

Molecular data confirm the inclusion of *Idiellana* in Sertulariidae Lamouroux, 1812. Its assignment to a separate family (Idiidae Allman, 1888) or even to a distinct taxon of higher rank (legion Thalamophora Allman, 1888), as proposed by Allman (1888: lii, 82, 83), is unwarranted. The phylograms of Maronna *et al*. (2016) include *Idiellana pristis* in a clade with several species of the sertulariid genus *Dynamena* Lamouroux, 1812, especially *D. moluccana* (Pictet, 1893).

Reported distribution. ***Gulf coast of Florida.*** Key West area, shallow water (Nutting 1895: 180, as *Idia*).—Dry Tortugas (Leloup 1935a: 39, as *Idiella pristis*; Van Gemerden-Hoogeveen 1965: 16).

Elsewhere in western North Atlantic. French Lesser Antilles: Martinique (Fraser 1944: 312, as *Idiella pristis*).—Puerto Rico: north coast, 18°31'N, 66°10'15"W, 38 ftm (69 m) + 18°30'30"N, 66°23'05"W, 40 ftm (73 m) + 18°30'24"N, 66°04'15"W, 100 ftm (183 m) + 18°30'N, 66°12'20"W, 46–56 ftm (84–102 m) + 18°23'35"N, 65°37'10"W, 10 ftm (18 m) (Fraser 1944: 312, as *Idiella pristis*).—Virgin Islands of the United States: St. Thomas, Sound + Savannah Passage (Vervoort 1968: 36, 37).—Colombia: Santa Marta area, rocky littoral (Wedler 1975: 340, as *Idiella pristis*; Bandel & Wedler 1987: 41).—Colombia: Bahía de Cartagena, Ciénaga del Picón, mangroves, 0.2–2 m (Flórez González 1983: 123).—Colombia: Ciénaga de La Boquilla, mangroves (Quiceno & Palacio 2008: 71, as *Idiella pristis*).—Cuba: Bahía de Puerto Padre, entrance channel, 5 m (Varela & Cabrales 2010: 105).—Caribbean Sea (Wedler 2017b: 128, figs. 128, 129).

Genus *Tridentata* Stechow, 1920

Tridentata turbinata (Lamouroux, 1816)

Fig. 21g

Dynamena turbinata Lamouroux, 1816: 180.
Sertularia turbinata.—Leloup, 1935a: 50.—Van Gemerden-Hoogeveen, 1965: 38.

Type locality. Australasia: on "*Fucus*" (Lamouroux 1816: 180, as *Dynamena turbinata*).

Material examined. Sanibel Island, beach at Lighthouse Point, 26°26'58"N, 82°01'04.5"W, on stranded *Sargassum pteropleuron*, 21 March 2018, 22° C, 34.5‰, two colonies, up to 9 mm high, without gonophores, coll. D. Calder, ROMIZ B4393.

Remarks. *Tridentata turbinata* is a species of tropical and subtropical waters that has been recorded but few times along the Atlantic and Gulf coasts of the United States. In inshore waters, it has not been reported north of Florida along the east coast except as colonies transported northwards on pelagic *Sargassum* by the Gulf Stream (e.g., Stachowicz & Lindquist 1997). It has been reported twice from Louisiana in the northern Gulf of Mexico, although one of those occurrences was based on specimens from gulfweed (pelagic *Sargassum*) (Cary & Spaulding 1909). Most distribution records listed below of *T. turbinata* in the North Atlantic are from the Caribbean region, although the species is also well-known from Bermuda and the Bahamas. To the south, records of the species are frequent in warm waters of coastal Brazil (Oliveira *et al*. 2016). As records below also indicate, it is most common in shallow waters.

This species has long been misassigned to a non-monophyletic genus *Sertularia* Linnaeus, 1758 instead of *Tridentata* Stechow, 1920. As documented earlier (Calder 1990 [1991a]: 104, 2013: 33; Calder *et al*. 2019), significant morphological differences exist between those two genera in both trophosome and gonosome. Molecular phylograms such as those in Moura *et al*. (2011) and Maronna *et al*. (2016) reveal that *T. turbinata* is very close genetically to *T. perpusilla* (Stechow, 1919), type species of *Tridentata*, and that both species are remote from *S. argentea* Linnaeus, type species of *Sertularia*. It bears repeating, once again, that the valid name of the species should be *Tridentata turbinata*.

The hydroid of *T. turbinata* is relatively common in shallow waters of the Atlantic, Pacific, and Indian oceans, yet specimens with gonothecae have been reported infrequently. Humara-Gil & Cruz-Gómez (2018: 466, figs. 8B, E) recently discovered fertile colonies from Oaxaca, Mexico, as did Galea & Ferry (2015: 235, fig. 6G, as *Sertularia turbinata*) from Guadeloupe. Earlier accounts of colonies with gonothecae include those of Stechow (1919: 93, fig. H^1, as *Sertularia brevicyathus*) from the Tonga Islands, Vervoort (1959: 277, figs.36b, c, as *Sertularia turbinata*) from off Freetown, Sierra Leone, Millard (1975, 310, fig. 100E, as *Sertularia turbinata* forma *acuta*) from South Africa, and Hirohito (1995:217, figs. 73e, f, as *Sertularia turbinata*) from Sagami Bay, Japan. Colonies examined here were sterile.

Detailed taxonomic and nomenclatural accounts of this species include those of Calder (1990 [1991a]) and Medel & Vervoort (1998, as *Sertularia turbinata*).

Reported distribution. ***Gulf coast of Florida.*** Dry Tortugas: Loggerhead Key, on algae (Leloup 1935a: 51, as *Sertularia turbinata*; Van Gemerden-Hoogeveen 1965: 38, as *Sertularia turbinata*).—Dry Tortugas: S of Loggerhead Key (Van Gemerden-Hoogeveen 1965: 38, as *Sertularia turbinata*).

Elsewhere in western North Atlantic. Bahamas: between Eleuthera and Little Cat islands + near Spanish Wells (Nutting 1904: 60, as *Sertularia brevicyathus*).—Bermuda: various locations, abundant, on sponges, seaweeds, large hydroids (Congdon 1907: 481, as *Sertularia brevicyathus*).—USA: Louisiana, occasional, on gulfweed (Cary & Spaulding 1909: 6, as *Sertularia brevicyanthus* (sic)).—Bermuda: Challenger Bank, 31–70 ftm (57–128 m), on a gorgonian and algae + Agar's Island, on *Sargassum* (Bennitt 1922: 250, as *Sertularia brevicyathus*).—Bonaire: Lac, mouth, back of reef, on detached *Sargassum* + Boca Washikemba, on stranded algae + Lagoen, north coast, on stranded *Sargassum* (Leloup 1935: 51, as *Sertularia turbinata*).—Aruba: Boca Prins, on stranded *Sargassum* (Leloup 1935: 51, as *Sertularia turbinata*).—Bahamas: Cay Sal Bank, 5–7 ftm (9–13 m), on benthic algae (Leloup 1937: 106, as *Sertularia turbinata*).—Atlantic Ocean: Gulf Stream, on pelagic *Sargassum* + Sargasso Sea, on pelagic *Sargassum* (Burkenroad, in Parr 1939: 23, as *Sertularia brevicyathus*).—Puerto Rico: northeast coast, 18°27'35"N, 65°33'35"W, 26 ftm (48 m) + 18°24'30"N, 65°38'30"W, 9 ftm (16 m) + 18°23'35"N, 65°37'10"W, 10 ftm (18 m) (Fraser 1944: 291, as *Sertularia turbinata*).—Panama: Caledonia Bay (Puerto Escoces), on floating *Sargassum* (Fraser 1947b: 11, as *Sertularia turbinata*).—Venezuela: off Isla Tortuga, 2–5 ftm (4–9 m) (Fraser 1947b: 11, as *Sertularia turbinata*).—Colombia: La Goajira, Rio Hacha (=Riohacha), on algae (Van Gemerden-Hoogeveen 1965: 38, as *Sertularia turbinata*).—Aruba: Boca Prins, on *Sargassum* + wharf of Arend Petroleum Co., on iron beam (Van Gemerden-Hoogeveen 1965: 38, as *Sertularia turbinata*).—Bonaire: Oranjepan, on stranded *Sargassum* + Boca Washikemba, on stranded brown algae + Playa Grandi, on *Sargassum* (Van Gemerden-Hoogeveen 1965: 38, as *Sertularia turbinata*).—Tobago: Rockley Bay (=Rockly Bay) on *Sargassum* (Van Gemerden-Hoogeveen 1965: 38, as *Sertularia turbinata*).—West Indies: between Trinidad and Grenada (Van Gemerden-Hoogeveen 1965: 38, as *Sertularia turbinata*).—Antigua: Deep Bay, at Fort Barrington, on algae, sponge (Van Gemerden-Hoogeveen 1965: 38, as *Sertularia turbinata*).—Sint Maarten: Simson Lagoon, bridge, on algae (Van Gemerden-Hoogeveen 1965: 38, as *Sertularia turbinata*).—Virgin Islands of the United States: St. Thomas, Sound, on other hydroids (Vervoort 1968: 52, as *Sertularia turbinata*).—Colombia: off Santa Marta (Wedler 1975: 340, as *Sertularia turbinata*).—USA: Florida, southeast coast (Mergner 1977: 122, as *Sertularia turbinata*; 1987: 187, as *Sertularia turbinata*).—Belize: Carrie Bow Cay, 0–10 m, on dead corals, gorgonians (Spracklin 1982: 246, as *Sertularia turbinata*).—Colombia: vicinity of Bahía de Cartagena (Flórez González 1983: 120, as *Sertularia turbinata*).—Bermuda: inshore, shallow waters + offshore, on banks, buoy chains (Calder 1986: 139, as *Sertularia turbinata*).—USA: Louisiana, on a coastal petroleum platform, 46 m (Lewbel *et al*. 1987: 214, as *Sertularia turbinata*).—Belize: Twin Cays (Ellison & Farnsworth 1990: 96, as *Sertularia turbinata*).—Bermuda: Whalebone Bay, 1 m, on ledge + Flatts Inlet, on rocks, *Thyroscyphus marginatus*, 2 m (Calder 1990 [1991a]: 111).—Belize: Twin Cays, on *Rhizophora*, benthic algae, sponges, other invertebrates (Calder 1991b: 223; 1991c: 2068).—Belize: Lark Cay, on *Rhizophora* +Northeast Cay, on *Rhizophora* + Twin Cays, on *Rhizophora* (Ellison & Farnsworth 1992: 90, as *Sertularia turbinata*).—Bermuda: Walsingham Pond (Thomas *et al*. 1992: 139, 152, as *Sertularia turbinata*).—Bermuda: Harrington Sound, just below tidal level (Thomas 1996: 758, as *Sertularia turbinata*).—USA: North Carolina, off Cape Lookout in Gulf Stream, 34°10'N, 76°13'W, on *Sargassum* (Stachowicz & Lindquist 1997: 116).—Bermuda: Argus (=Plantagenet) Bank, on Argus Tower, 20 m (Calder 2000: 1135, 1136).—Panama: Bocas del Toro area, Boca del Drago, 09°25'36.3"N, 82°19'30.1"W, 1-3 m + Bocas del Toro area, Cayos Zapotilla, 09°15.564'N, 82°02.750'W, 7-8 m + Bocas del Toro area, Swan's Key, 09°27'12.2"N, 82°18'01.8"W, 1-4 m + Bocas del Toro area, Drago 2, mangrove, 1–2 m + Bocas del Toro area, Drago 2, 2–4 m (Calder & Kirkendale 2005: 486).—French Lesser Antilles: Guadeloupe, Basse-Terre, N of Malendure, 16°10’25.00”N, 61°46’58.00”W, on algae (Galea 2008: 37, as *Sertularia turbinata*).—French Lesser Antilles: Les Saintes, Terre-de-Haut, Pain de Sucre, 15°51’45”N, 61°35’60”W, on *Dictyota*, *Thyroscyphus ramosus* (Galea 2008: 37, as *Sertularia turbinata*).—USA: Florida: Fort Pierce Inlet, 27°28’24.1”N, 80°17’21.2”W, north jetty, intertidal, on benthic algae (Calder 2013: 33).—French Lesser Antilles: Martinique (Galea 2013: 50, as *Sertularia turbinata*).—French Lesser Antilles: Martinique, Le François, Pointe Jacob, 14.58552, -60.84993, 0 m, on floating *Sargassum* (Galea & Ferry 2015: 235, as *Sertularia turbinata*).—Caribbean Sea (Wedler 2017b: 134, figs. 141A, B, 142, 143, as *Sertularia turbinata*).—Mexico: Alacranes Reef, on shipwreck (Mendoza-Becerril *et al*. 2018b: 130, as *Sertularia turbinata*).

Family Sertularellidae Maronna, Miranda, Peña Cantero, Barbeitos & Marques, 2016

Genus *Sertularella* Gray, 1848

Sertularella areyi Nutting, 1904

Fig. 21h

Sertularella areyi Nutting, 1904: 83, pl. 17, fig. 6.

Type locality. Cuba: near Havana, 100–200 ftm (183–366 m) (Nutting 1904: 83).

Material examined. Southwest Florida Shelf, outer shelf west of Sanibel Island, 26°16.67’N, 84°04.08’W, 137 m, 25 July 1981, triangle dredge, one colony fragment, 5 mm high, without gonophores, coll. Continental Shelf Associates, ROMIZ B1978.

Remarks. Hydroids of *Sertularella areyi* Nutting, 1904 are small (usually less than 1 cm high) but quite striking in colony morphology. Long, slender internodes bear largely exserted and barrel-shaped hydrothecae having 1–3 annular ribs and a thickened hydrothecal rim. It has been reported few times in the western Atlantic, and gonothecae have yet to be described in specimens from the region. Although the type locality is off the north coast of Cuba, in the Gulf of Mexico, the species has been recorded much more frequently in the western Pacific (Korea, Japan, the Philippines, New Caledonia, Loyalty Islands, Australia, New Zealand), with fertile colonies having been described from there (Vervoort 1993; Hirohito 1995; Vervoort & Watson 2003). Elsewhere, records of *S. areyi* exist from Hawai‘i, surprisingly from the inshore waters of Kâne‘ohe Bay and Waikîkî (Carlton & Eldredge 2009). As well, Vervoort (1993) included *S. capensis delicata* Millard, 1964 from the east and south coasts of South Africa in the synonymy of the species.

In the western North Atlantic, *S. areyi* is a species inhabiting waters of the continental shelf and upper slope, having been reported over a depth range between 17–366 m. Geographically, it is known from offshore waters of South Carolina and Bermuda (Plantagenet Bank) in the north to Cuba (Nutting, 1904; Wenner *et al*. 1984; Calder 2000) in the south. The species has also been reported from Brazil (Oliveira *et al*. 2016). The only previous record from the Gulf of Mexico is Nutting’s (1904) original account of the species from the north coast of Cuba. This is the first report of the species from the Gulf coast of Florida. Lack of any records of *S. areyi* from the Caribbean Sea may be due to the paucity of deep-water collecting in the region to date.

Sertularella areyi has been discussed in detail by Vervoort (1993), based on collections from the Philippines, New Caledonia, and the Loyalty Islands. That work includes a detailed synonymy, a description, illustrations, and distribution records of the species. An update was provided by Vervoort & Watson (2003) in a study on hydroids of New Zealand. The extent of genetic divergence between hydroids assigned to *S. areyi* from the western North Atlantic and those from other oceans is as yet unknown.

Reported distribution. ***Gulf coast of Florida.*** First record.

Elsewhere in western North Atlantic. Cuba: near Havana, 100–200 ftm (183–366 m) (Nutting 1904: 83).—USA: South Carolina, outer continental shelf, 46–69 m + Georgia, inner (17–22 m), middle (23–29 m) and outer (59–67 m) continental shelf (Wenner *et al*. 1984: 21, 40).—Bermuda: Argus (=Plantagenet) Bank (Calder 2000: 1134).—USA: Florida, outer continental shelf off Sebastian Inlet, 27°52.5’N, 79°57.5’W, 75–98 m (Calder 2013: 28).

Sertularella diaphana **(Allman, 1885)**

Fig. 21i

Thuiaria distans Allman, 1877: 27, pl. 17, figs. 1, 2 [not *Sertularella distans* (Lamouroux, 1816)].
Sertularella distans.—Nutting, 1904: 88.—Wallace, 1909: 137 [not *Sertularella distans* (Lamouroux, 1816)].
Thuiaria diaphana Allman, 1885: 145, pl. 18, figs. 1–3.
Sertularella speciosa.—Fraser, 1943: 92.

Type locality. Australia: Queensland, Moreton Bay (Allman 1885: 145, as *Thuiaria diaphana*).

Material examined. Southwest Florida Shelf, middle shelf west of North Naples, 26°16'15"N, 83°47'00"W, 76.2 m, 04 November 1980, on *Nemertesia sinuosa*, two juvenile colony fragments, 9 mm and 13 mm high, without gonophores, coll. Continental Shelf Associates, ROMIZ B4392.

Remarks. *Sertularella diaphana* (Allman, 1885) has been collected most often in the western North Atlantic from offshore locations within the neritic zone, although exceptions occur. For example, Congdon (1907) found this species in shoal waters at the entrance of a cave in Castle Harbour, Bermuda. Its reported bathymetric distribution extends from shallow subtidal waters (Allman, 1877, as *Thuiaria pinnata*) to a depth of 1408 m (Fernandez & Marques 2018). In the western Atlantic, it ranges from the Bermuda area (Calder 1990 [1991a], 2000) and from shelf waters off South Carolina (Wenner *et al*. 1984, as *Sertularella pinnigera*) to Brazil (Oliveira *et al*. 2016). Records suggest that *S. diaphana* is widespread in the Caribbean region, and it is known as well from several locations in the Gulf of Mexico (Calder & Cairns 2009; Castellanos *et al*. 2011; Mendoza-Becerril *et al*. 2018b). Elsewhere, it is believed to be essentially circumglobal in tropical and subtropical waters (Millard 1975; Vervoort 1993; Schuchert 2003; Vervoort & Watson 2003; Galea 2010). With good reason, however, Galea noted the possibility that cryptic species exist among hydroids identified as *S. diaphana*, and DNA barcoding of geographically separated populations is needed to complement morphological accounts.

Only limited molecular data are available on hydroids of the speciose genus *Sertularella* Gray, 1848, including *S. diaphana*. Based on current evidence, phylogenetic affinities of the species are somewhat unclear. Phylograms in Maronna *et al*. (2016) reveal that the species is quite divergent genetically from others of the genus included in the study, including the type species *Sertularella polyzonias* (Linnaeus, 1758). Their analysis was based on specimens of *S. diaphana* from Brazil. Again, additional molecular studies of this hydroid are warranted.

Gonophores in this species are liberated as medusoids from hydroids that appear to be dioecious (Gravier-Bonnet & Lebon 2002). Actively swimming gonophores were shed, one per gonotheca, early in the morning, and gametes were released over a life span of 2–3 hours.

The complex synonymy and nomenclature of *S. diaphana*, as presently understood, has been reviewed in works such as those of Calder (1990 [1991a]) and Vervoort (1993).

Reported distribution. ***Gulf coast of Florida.*** Dry Tortugas, shallow water (Allman 1877: 27, as *Thuiaria distans*).—North of Dry Tortugas, 25°04'30"N, 82°59'15"W, 26 ftm (48 m) (Nutting 1904: 88, as *Sertularella distans*).—Dry Tortugas (Wallace 1909: 137, as *Sertularella distans*).—Between Key West and Dry Tortugas, 24°24'N, 82°24'30"W, 34 ftm (62 m) (Fraser 1943: 92, as *Sertularella speciosa*).

Elsewhere in western North Atlantic. Bahamas: Cay Sal Bank, Double-Headed Shot Key (Cay), 3–4 ftm (5–7 m) (Allman 1877: 278, as *Thuiaria pinnata*).—Barbados: 56 ftm (102 m) (Fewkes 1881a: 128, as *Thuiaria pinnata*).—Bahamas: between Eleuthera and Little Cat islands, shallow water (Nutting 1895: 224, as *Thuiaria distans*).—Cuba: off Havana, 23°10'25"N, 82°20'24'"W, 33 ftm (60 m) (Nutting 1904: 88, as *Sertularella distans*).—Mexico: off Yucatan, near Arrowsmith Bank, 20°59'N, 86°23'W, 167 ftm (305 m) (Nutting 1904: 88, as *Sertularella distans*).—Bermuda: Castle Harbour, 32°20'30"N, 64°42'10"W, entrance of a cave (Congdon 1907: 476, as *Sertularella speciosa*).—Montserrat: off SW coast, 16°41'54"N, 62°13'24"W, 88 ftm (161 m) (Fraser 1943: 92, as *Sertularella speciosa*).—Puerto Rico: north coast, 18°30'30"N, 66°23'05"W, 40 ftm (73 m) (Fraser 1944: 260, as *Sertularella distans*).—Virgin Islands of the United States: St. John, south coast (Vervoort 1968: 44, as *Sertularella speciosa*).—Colombia: Santa Marta area (Wedler 1975: 340, as *Sertularella speciosa*).—Belize: Carrie Bow Cay (Spracklin 1982: 246, as *Sertularella speciosa*).—Dominican Republic: south coast (Williams *et al*. 1983: 43, as *Sertularella speciosa*).—Colombia: vicinity of Bahía de Cartagena, coastal areas, offshore islands (Flórez González 1983: 121, as *Sertularella speciosa*).—USA: South Carolina, inner (17–18 m) and middle (32–36 m) continental shelf + Georgia, middle continental shelf, 23–29 m (Wenner *et al*. 1984: 21, 40, as *Sertularella pinnigera*).—Puerto Rico: Mona Island + Desecheo Island (Larson 1987: 514, as *Sertularella speciosa*).—British Virgin Islands: Virgin Gorda (Larson 1987: 514, as *Sertularella speciosa*).—Colombia: Santa Marta area (Bandel & Wedler 1987: 38, as *Sertularella speciosa*).—Bermuda: Challenger Bank, 59 m, small colony on *Aglaophenia rhynchocarpa* (Calder 1990 [1991a]: 101).—Costa Rica: northern Punta Mona, Refugio Nacional de Vida Silvestre Gandoca-Manzanillo, 09°37'45"N, 82°37'07"W, 9 m (Kelmo & Vargas 2002: 608).—Bermuda: Challenger Bank (Calder 2000: 1134).—Mexico: Veracruz area, Arrecife La Blanquilla + Arrecife Anegada de Adentro (Jones *et al*. 2008, as *Sertularella speciosa*).—French Lesser Antilles: Guadeloupe, Grande-Terre, Grotte aux Barracudas, 16°27.343'N, 61°32.244'W, 21 m + Grande-Terre, Les Ancres, 16°27.002'N, 61°32.320'W, 15–18 m + Grande-Terre, L'Oeil, 16°26.782'N, 61°32.405'W, 12–17 m + Grande-Terre, Pointe d'Antigues, 16°26.251'N, 61°32.523'W + Grande-Terre, L'Avion, 16°25.610'N, 61°32.561'W, 15–25 m (Galea 2010: 16, 17).—Cuba: Golfo de Batabanó, Boya El Límite, Punta Francés + Cayo Campos, Archipiélago de los Canarreos, reef (Castellanos *et al*. 2011: 23).—French Lesser Antilles: Les Saintes, Terre-de-Haut, Pointe à Cabrit, 15°52.645'N, 61°36.125'W, 10–15 m (Galea 2010: 17).—French Lesser Antilles: Martinique, Le Prêcheur, Anse Céron, 14.837414°N, 61.223930°W (Galea 2013: 17).—Caribbean Sea (Wedler 2017b: 129, figs. 130–134).—Mexico: Alacranes Reef, on rocks (Mendoza-Becerril *et al*. 2018b: 130).—Panama: Bocas del Toro area, the wall (25 m)/Pandora (20 m) (Miglietta *et al*. 2018b: 108).

***Sertularella unituba* Calder, 1990 [1991a]**

Fig. 21j

Sertularella conica.—Van Gemerden-Hoogeveen, 1965: 32, fig. 7.—Leloup 1935: 44 [not *Sertularella conica* Allman, 1877].
Sertularella gayi unituba Calder, 1990 [1991a]: 103, figs. 54a, b.

Type locality. Bermuda: 2 km SE of Castle Roads, 50-80 m (Calder 1990 [1991a]: 103, as *Sertularella gayi unituba*).

Material examined. Southwest Florida Shelf, middle shelf west of Gasparilla Island, 26°45.86'N, 83°21.44'W, 50 m, 18 July 1981, triangle dredge, one colony, 5.5 cm high, without gonophores, coll. Continental Shelf Associates, ROMIZ B2001.

Remarks. This hydroid was originally described from Bermuda as a subspecies of *Sertularella gayi* (Lamouroux, 1821). Medel & Vervoort (1998) examined material of *S. gayi unituba* Calder, 1990 [1991a], including the holotype, and elevated the subspecific name to specific rank. Corroborating this change, Moura *et al*. (2011) found that a hydroid consistent with the phenotype of *S. unituba* from the Azores was indeed close to *S. gayi*, but genetically distinct from it. As for *S. gayi*, difficulties exist in identification of the species even within its main center of distribution in northwestern Europe (Cornelius 1995b: 72). Characters distinguishing *S. unituba* from *S. gayi* and *S. gayi robusta* Allman, 1874a were reviewed by Medel & Vervoort (1998: 54). The trinomen *S. gayi robusta* had been used earlier by Allman (1873), as "*Sertularella gayii*…variety *robusta*", but as a nomen nudum.

Hydroids identified as *S. gayi* have been reported from the Caribbean Sea and Gulf of Mexico a number of times (see Nutting 1904; Fraser 1944; Deevey 1950; Vervoort 1968). Given the incertitude surrounding identification of the species noted above, confirmation is needed that *S. gayi* actually exists in the warm western Atlantic. While it is likely that some records of the species were based on *S. unituba*, existing descriptions and illustrations of them are insufficient to establish which ones. However, it is much more certain that hydroids assigned to *S. conica* Allman, 1877 by Leloup (1935) and Van Gemerden-Hoogeveen (1965) were misidentified specimens of *S. unituba*. Although Leloup did not describe or illustrate his specimens, the same material was examined later by Van Gemerden-Hoogeveen. Her description and illustrations of the species conform to *S. unituba*, not *S. conica*.

Regarded as synonyms of *S. unituba* by Medel & Vervoort (1998) were two older names, *Sertularia exigua* Allman, 1888 and *S. laxa* Allman, 1888, applied to hydroids from bathyal waters in the Azores. However, both names are invalid as junior primary homonyms. Shortly before publication, Allman (1888) recognized that his *Sertularia exigua* was predated by *Sertularia exigua* Allman, 1877, and he proposed *S. laxa* as a replacement name for it in the same work. However, that binomen is also predated, by *S. laxa* Lamarck, 1816. *Sertularella unituba* thus stands the valid name of the species. I cannot agree with Galea (2013: 24) that *S. unituba* and *S. conica* are conspecific.

In addition to the original description of *S. unituba*, the species has been described and discussed at length by Medel & Vervoort (1998) from material collected in the Cape Verde Islands. Besides inspecting the holotype of the species, syntypes of *Sertularia exigua* (and its replacement name *S. laxa*) from the Azores were examined by them as well. New material of *S. unituba* from the Cape Verde region was studied and discussed by Vervoort (2006).

Sertularia unituba has most often been collected at intermediate depths. In the western North Atlantic, it has been reported over a bathymetric range of 24–274 m (Leloup 1935, as *Sertularella conica*; Van Gemerden-Hoogeveen 1965: 32, as *Sertularella conica*; Calder 1990 [1991a], as *Sertularella gayi unituba*; Medel & Vervoort 1998; Calder 2013). Records from the eastern North Atlantic extend from 61–1200 m, although most specimens were collected at depths between 61–250 m (Medel & Vervoort 1998; Vervoort 2006). Allman's (1888) specimens of *S. exigua*/*S. laxa* from the Challenger Expedition came from a depth of 450 ftm (823 m) off the Azores.

Reported distribution. ***Gulf coast of Florida.*** Dry Tortugas, 25–45 ftm (46–82 m) (Leloup 1935: 44, as *Sertularella conica*).—Dry Tortugas, 25 ftm (46 m) (Van Gemerden-Hoogeveen 1965: 32, as *Sertularella conica*).

Elsewhere in western North Atlantic. Bermuda: 2 km SE of Castle Roads, 50–80 m, on calcareous rubble (Calder 1990 [1991a]: 103, as *Sertularella gayi unituba*; Medel & Vervoort 1998: 58).—Bermuda: 2 km S of "Castle Rock" (Castle Roads), on a crab pot line, 274 m (Medel & Vervoort 1998: 60).—Bermuda: Argus (=Plantagenet) Bank (Calder 2000: 1134, as *Sertularella gayi*).—USA: Florida, off St. Lucie Inlet, 27°11.6'N, 80°00.7'W, 41 m + off Vero Beach, Bethel Shoal, 27°42.6'N, 80°06.8'W, 24 m (Calder 2013: 30).

Infraorder Plumupheniida Maronna, Miranda, Peña Cantero, Barbeitos & Marques, 2016

Family Aglaopheniidae Marktanner-Turneretscher, 1890

Genus *Aglaophenia* Lamouroux, 1812

Aglaophenia dubia Nutting, 1900

Fig. 22a

Aglaophenia gracilis Allman, 1877: 42, pl. 25, figs. 1–4.—Clarke, 1879: 248 [invalid junior primary homonym of *Aglaophenia gracilis* Lamouroux, 1816].
Aglaophenia dubia Nutting, 1900: 92, pl. 18, fig. 5 [replacement name for *Aglaophenia gracilis* Allman, 1877].
Aglaophenia flowersi Nutting, 1900: 93, pl. 19, figs. 1, 2.
Aglaophenia (?) *allmani*.—Leloup, 1935a: 57 [part] [not *Aglaophenia allmani* Nutting, 1900].
Aglaophenia elongata.—Leloup, 1937: 112.—Van Gemerden-Hoogeveen, 1965: 79, fig. 44.—Bogle, 1975: 101, figs. 7A–C. [not *Aglaophenia elongata* Meneghini, 1845].

Type locality. USA: Florida, off Carysfort Reef, 52 ftm (95 m) (Allman 1877: 43, as *Aglaophenia gracilis*).

Material examined. Southwest Florida Shelf, middle shelf west of North Naples, 26°17'00"N, 83°24'00"W, 55 m, 05 November 1980, one colony, 16.5 cm high, without corbulae, coll. Continental Shelf Associates, ROMIZ B2147.

Remarks. As apparent from the synonymy list above, several binomena have been applied to this species in southwest Florida (and elsewhere in the western North Atlantic). Allman (1877) first described it, as *Aglaophenia gracilis*, from specimens collected off Carysfort Reef, Straits of Florida. That name, a junior primary homonym of *Aglaophenia gracilis* Lamouroux, 1816, has been supplanted by the replacement name *A. dubia* Nutting, 1900. *Aglaophenia flowersi* Nutting, 1900, from the Sand Key area, Straits of Florida, is taken to be conspecific with it. Of the two simultaneous synonyms, precedence has been assigned to *A. dubia* under the First Reviser Principle in nomenclature (Calder 1997). Meanwhile, this species has also frequently been assigned to *A. elongata* Meneghini, 1845 (type locality, from a neotype: SW of Banjole Island, Rovinj, Croatia). Based on morphological differences noted in hydroids of *A. dubia* and *A. elongata* (Calder 1997), however, the two are considered distinct here. Indeed, *A. elongata* is thought to be limited in distribution to the Mediterranean Sea (Svoboda & Cornelius 1991; Gravili *et al*. 2015). Finally, part of the hydroid material identified as *Aglaophenia* (?) *allmani* by Leloup (1935a), specifically a colony fragment in collection No. 71, Sta. 210 from the Dry Tortugas, was found by Van Gemerden-Hoogeveen (1965: 79) to have been based on "*A. elongata*" (actually *A. dubia*).

Aglaophenia dubia, typically a species of shelf waters, is discussed in greater detail elsewhere (Calder 1997, 2013).

Reported distribution. ***Gulf coast of Florida.*** Off Carysfort Reef, 52 ftm (95 m) (Allman 1877: 43, as *Aglaophenia gracilis*).—Southwest Florida Shelf, W of the Dry Tortugas, 24°43'N, 83°25'W, 37 ftm (68 m) (Clarke 1879:

248, as *Aglaophenia gracilis*).—Southwest Florida Shelf, W of North Captiva Island, 26°34'N, 83°16'W, 27 ftm (49 m) (Nutting 1900: 92).—Southwest Florida Shelf, W of Naples, 26°00'N, 82°58'W, 24 ftm (44 m) (Nutting 1900: 92).—Florida Keys, 100 ftm (183 m) (Nutting 1900: 92).—Off Sand Key, 116 ftm (212 m) (Nutting 1900: 93, as *Aglaophenia flowersi*).—Dry Tortugas, 27 ft (8 m) (Leloup 1935a: 57, as *Aglaophenia* (?) *allmani*).—Tampa Bay, 7–10 miles (11–16 km) offshore, 8–10 ftm (15–18 m) (Leloup 1937: 112, as *Aglaophenia elongata*).—Dry Tortugas, 8 m (Van Gemerden-Hoogeveen 1965: 79, as *Aglaophenia elongata*).—USA: Florida, southern Straits of Florida, 24°21.5'N, 82°26.7'W, 58–60 m + 24°17.7'N, 82°32'W, 223–229 m + 24°51'N, 80°35'W, 64–69 m (Bogle 1975: 103, as *Aglaophenia elongata*).

Elsewhere in western North Atlantic. French Lesser Antilles: Martinique, 96 ftm (176 m) (Fewkes 1881a: 127, as *Aglaophenia gracilis*).—Cuba: Straits of Florida (Nutting 1895: 179, as *Aglaophenia gracilis*).—Cuba: off Havana, 150 ftm (274 m) (Nutting 1900: 92).—Bahamas: off Little Cat Island, 6 ftm (11 m) (Nutting 1900: 92).—Anguilla: 100–150 ftm (183–274 m) (Jäderholm 1903: 294, as *Aglaophenia flowersi*).—Bermuda: Challenger Bank, 32 ftm (59 m) (Bennitt 1922: 252, as *Aglaophenia lophocarpa*).—USA: Texas, West Flower Garden Bank (Defenbaugh 1974: 101, as *Aglaophenia elongata*).—Colombia: Santa Marta area (Wedler 1975: 332, as *Aglaophenia elongata*).—USA: Florida, northern Straits of Florida, 25°47.6'N, 80°05'W, 55 m + 25°46'N, 80°05'W, 57 m + 25°14'N, 80°09'W–25°16'N, 80°09'W, 91 m + 25°17'N, 80°05'W, 174 m + 25°35'N, 80°05'W, 55 m (Bogle 1975: 102, as *Aglaophenia elongata*).—USA: South Carolina, inner (17–18 m), middle (32–36 m) and outer (46–69 m) continental shelf + Georgia, inner (17–22 m), middle (23–29 m) and outer (59–67 m) continental shelf (Wenner *et al*. 1984: 21, 40, as *Aglaophenia elongata*).—USA: northern Gulf of Mexico, outer shelf edge banks (Rezak *et al*. 1985: 224, as *Aglaophenia elongata*).—USA: Louisiana, shelf hard bottoms, 29°06'11"N, 92°40'27"W, 22 m + 28°50'40"N, 92°44'33"W, 27 m (Putt *et al*. 1986: 54, as *Aglaophenia elongata*).—USA: Florida, Biscayne Bay (Jones 1992: 215, as *Aglaophenia elongata*).—Bermuda: 2 km to 2.5 km SE of Castle Roads, 50–91 m + 2.5 km E of St. David's Lighthouse, 85 m + 4 km NW of North Rock, 62–70 m + 2–2.5 km SSE of Castle Roads, 60–91 m + 5 km SSE of Castle Roads, 85 m (Calder 1997: 51).—Bermuda: Argus (=Plantagenet) Bank (Calder 2000: 1134).—Panama: Bocas del Toro area, Hospital Point, 09°20'01.9"N, 82°13'07.7"W, 2-13 m (Calder & Kirkendale 2005: 483).—Colombia: off Manaure, 22 and 70 m (Posada *et al*. 2010: 75, as *Aglaophenia elongata*).—USA: Florida, off St. Lucie Inlet, 27°11.8'N, 80°00.6'W, 42 m + 27°10.8'N, 80°00.8'W, 44 m + off Jupiter Inlet, 26°57.6'N, 79°59.4'W, 48 m (Calder 2013: 46).—Caribbean Sea (Wedler 2017b: 143, figs. 162, 163).

Aglaophenia latecarinata Allman, 1877

Fig. 22b

Aglaophenia pelasgica.—A. Agassiz, 1865: 139 [incorrect subsequent spelling].
Aglaophenia late-carinata Allman, 1877: 56; 1885: 151, pl. 23, figs. 5–6.—Fraser, 1943: 94; 1944: 378, pl. 82, figs. 368a–e.
Aglaophenia perpusilla Allman, 1877: 48, pl. 29, figs. 5–7.—Wallace, 1909: 137.
Aglaophenia minuta.—Wallace, 1909: 137.
Aglaophenia mammillata.—Wallace, 1909: 137.
Aglaophenia latecarinata.—Bogle, 1975: 34, figs. 1A–D, maps 1, 2.

Type locality. USA: Gulf of Mexico, on gulfweed (Allman 1877: 56).

Material examined. Fort Myers Beach, 26°27'18"N, 81°57'38"W, on stranded *Sargassum fluitans*, 11 February 2012, 18° C, one colony or colonies, up to 9 mm high, without corbulae, coll. D. Calder, ROMIZ B4402.

Remarks. *Aglaophenia latecarinata* was originally described, on "Gulf Weed" (*Sargassum*) from the Gulf of Mexico, in a brief footnote by Allman (1877). A fuller account of the species was given later (Allman 1885) based on dry specimens from the same collection, that of "Miss H. Gatty" (Horatia Katherine Frances Gatty, 1846–1945). It was said by him to be "…quite a characteristic form of the hydroid fauna of the floating Sargasso field of the North Atlantic." Indeed, *A. latecarinata* is the principal hydroid dominant on *Sargassum fluitans*, with hydroids being a prime component of the pelagic *Sargassum* fauna (Morris & Mogelberg 1973; Calder 1995). Originally spelled *late-carinata*, the specific name has been corrected to *latecarinata* (ICZN Art. 32.5.2.3). A. Agassiz (1865) had earlier reported this species, from the Dry Tortugas, as *Aglaophenia pelasgica*. It was unclear whether he was assigning it to *Hydra pelagica* Bosc, 1797 or *Aglaophenia pelagica* Lamouroux, 1816. In any case, both are *species inquirenda*.

Aglaophenia latecarinata is a hydroid species inhabiting surface and relatively shallow waters, and records of it from bathyal and abyssal depths are certainly based on specimens captured near-surface during deployment of sampling gear (Vervoort 1972: 204, as *Aglaophenia* cf. *perpusilla*) or on sunken *Sargassum* (Fraser 1944: 380). Meanwhile, *A. latecarinata* has often been reported from benthic habitats as well as from gulfweed, the substrate of the species as described by Allman (1877). A genetic comparison of truly bottom-dwelling specimens with those on pelagic seaweeds is warranted. The need for such an appraisal is highlighted by recent molecular analyses. Moura *et al*. (2012) concluded that benthic specimens assigned to *A. latecarinata* from Brazil were genetically distinct from other species assigned to the genus. They proposed that *Aglaophenia* as presently constituted is polyphyletic when that benthic population is assigned to it. In an earlier account (Leclère *et al*. 2007) based on the same material, however, the genus was said to be monophyletic even though *A. latecarinata* was quite divergent from other included species.

Strandings of pelagic *Sargassum* are infrequent on beaches of southwest Florida, and *A. latecarinata* was found only once during this study. Recent studies on seasonal movements of floating *Sargassum* provide an explanation for this scarcity. Data from satellite imagery suggest that an expanding accumulation of these algae in the northwest Gulf of Mexico during winter is advected by the Loop Current into the Gulf Stream and on into the Atlantic during summer (Gower & King 2011). Inasmuch as the Loop Current remains well to the west of the southwest Florida coast, little pelagic *Sargassum* normally washes ashore here. The data of Sanchez-Rubio *et al*. (2018) also reflect the relative paucity of these macroalgae nearshore in the study area.

Detailed accounts of this diminutive species, comprising an important part of the "displaced benthos" (Hedgpeth 1957) on pelagic gulfweed, are given elsewhere (e.g., Bogle 1975; Calder 1995, 1997, 2013; Ansín Agís *et al*. 2001).

Reported distribution. *Gulf coast of Florida.* Dry Tortugas (A. Agassiz 1865: 139, as *Aglaophenia pelasgica*; Wallace 1909: 137, as *Aglaophenia minuta*, *A. perpusilla*, and *A. mammillata*; Fraser 1943: 94, as *Aglaophenia late-carinata*; 1944: 380, as *Aglaophenia late-carinata*).—The Quicksands (Allman 1877: 48, as *Aglaophenia perpusilla*).—Eastern Dry Rocks off Key West, on reefs (Fraser 1944: 380, as *Aglaophenia late-carinata*).—Southern Straits of Florida, 24°17'N, 82°34'W, 320–437 m + 24°24'N, 80°52'W, 221–231 m (Bogle 1975: 36).

Elsewhere in western North Atlantic. Haiti (A. Agassiz 1865: 139, as *Aglaophenia pelasgica*).—USA: North Carolina, 100 miles (161 km) S of Cape Hatteras (A. Agassiz 1865: 139, as *Aglaophenia pelasgica*).—USA: Gulf of Mexico (Allman 1877: 56, as *Aglaophenia late-carinata*; 1885: 152, as *Aglaophenia late-carinata*).—USA: South Carolina, E of Charleston, 32°43'25"N, 77°20'30"W, 233 ftm (426 m), on (sunken) algae (Fewkes 1881a: 132, as *Aglaophenia minuta*).—Gulf Stream, on gulfweed (Nutting 1895: 30, as as *Aglaophenia minuta*).—Bahamas: Great Bahama Bank (Nutting 1895: 30, as *Aglaophenia minuta*; Nutting 1900: 97, as *Aglaophenia minuta*).—Sargasso Sea, 30°N, 70°W, on *Sargassum* (Versluys 1899: 47, as *Aglaophenia late-carinata*).—USA: Gulf Stream E of Delaware, 38°31'N, 69°08'W + Gulf Stream E of New Jersey, 39°09'N, 72°17'W (Nutting 1900: 97, as *Aglaophenia minuta*).—Bahamas: near Little Cat Island (Nutting 1900: 98, as *Aglaophenia minima*).—USA: off South Carolina, 33°38'N, 77°36'W, 15 ftm (27 m) (Nutting 1900: 98, as *Aglaophenia mammillata*).—Sargasso Sea, 28°46'N, 55°10'W + 30°25'N, 56°09'W + 35°18'N, 41°00'W (Jäderholm 1903: 294, as *Aglaophenia minuta*).—Bermuda, on *Sargassum* (Congdon 1907: 483, as *Aglaophenia minuta*; Smallwood 1910: 137, as *Aglaophenia minuta*).—USA: Massachusetts, Woods Hole + Vineyard Sound, on *Sargassum* (Hargitt 1908: 109, as *Aglaophenia minuta*).—USA: Louisiana, very common on gulfweed (Cary & Spaulding 1909: 6, as *Agalaophenia minuta*).—USA: North Carolina, Bogue Bank, on *Sargassum* (Fraser 1912b: 378, as *Aglaophenia minuta*).—Mexico: Yucatan Channel, 22°47'N, 86°10'W, on *Sargassum* (Stechow 1912: 370, as *Aglaophenia late-carinata*).—USA: Louisiana, south of Marsh Island, 27°10'N, 91°50'W, on *Sargassum* (Stechow 1912: 370, as *Aglaophenia late-carinata*).—Cuba: Straits of Florida, 23°14'N, 84°08'W, on *Sargassum* (Stechow 1912: 370, as *Aglaophenia late-carinata*).—Bahamas: Straits of Florida, 25°52'N, 79°35'W, on *Sargassum* (Stechow 1912: 370, as *Aglaophenia late-carinata*).—USA: Florida, Straits of Florida, 26°14'N, 79°48'W, on *Sargassum* (Stechow 1912: 370, as *Aglaophenia late-carinata*).—Sargasso Sea: 36°52'N, 43°50'W, on *Sargassum* (Stechow 1912: 370, as *Aglaophenia late-carinata*).—Sargasso Sea: on floating seaweed (Broch 1913: 7, as *Aglaophenia late-carinata*).—Sargasso Sea: 30°21'N, 45°20'W, on *Sargassum* (Ferdinandsen & Winge 1920: 103).—North Atlantic Drift: 40°39'22"N, 36°58'30"W to 42°02'26"N, 41°45'15"W (Bedot 1921: 40).—Sargasso Sea: 31°38'N, 42°38'W (Bedot 1921: 40).—Bermuda: on floating *Sargassum* + Agar's Island + Challenger Bank (Bennitt 1922: 252, as *Aglaophenia minuta*).—Sargasso Sea: on *Sargassum* (Hentschel 1922: 4, as *Aglaophenia late-carinata*).—Gulf Stream (?): on *Sargassum* (Leloup 1932:

164).—Sargasso Sea: on *Sargassum*, 34°25’N, 40°05’W + 33°19’N, 43°55’W + 31°56’N, 48°25’W + 30°20’N, 53°10’W + 20°05’N, 71°20’W + 23°50’N, 66°46’W + 25°10’N, 64°56’W + 27°09’N, 61°23’W + 30°50’N, 54°35’W + 41°31’N, 41°56’W + 33°30’N, 60°30’W + 31°25’N, 73°35’W + 39°30’N, 34°00’W + 40°00’N, 40°00’W + 24°00’N, 43-44°W + 24°30’N, 38°00’W (Timmermann 1932: 298–303, as *Aglaophenia late-carinata*).—Guatemala: off Puerto Barrios, on *Sargassum* (Timmermann 1932: 299, as *Aglaophenia late-carinata*).—USA: South Carolina, off Murrells Inlet, 33°30’N, 79°00’W, on *Sargassum* (Timmermann 1932: 301, as *Aglaophenia late-carinata*).—Bonaire: Plaja Oranje Pan + Zuidpunt (Leloup 1935a: 57).—Curaçao: Boca Grandi, on *Sargassum* (Leloup 1935a: 57).—Aruba: Boca Prins, on *Sargassum* (Leloup 1935a: 57).—Sargasso Sea: 30°N, 54°W + 35°07’N, 63°35’W (Leloup 1935a: 57).—North Atlantic Drift: 43°04’N, 31°W (Leloup 1935a: 57; Van Gemerden-Hoogeveen 1965: 76).—USA: Florida, off Hollywood, on *Sargassum* (Leloup 1935a: 57).—Sargasso Sea: on pelagic *Sargassum*, 23°57’N, 67°45’W + 27°13’N, 62°16’W (Leloup 1935b: 4).—Bahamas: Cay Sal Bank, on benthic algae (Leloup 1937: 113).—Sargasso Sea: on *Sargassum*, 29°50’N, 74°W + 30°11’N, 71°08’W + 32°07’N, 66°35’W (Leloup 1937: 113).—Gulf Stream, on pelagic *Sargassum* + Sargasso Sea, on pelagic *Sargassum* (Burkenroad, in Parr 1939: 23, as *Aglaophenia minuta*).—USA: Gulf Stream, 130–167 miles (209–269 km) S of Nantucket Island, on gulfweed (Fraser 1943: 94, as *Aglaophenia late-carinata*).—USA: North Carolina, E of Cape Hatteras (Fraser 1943: 94, as *Aglaophenia late-carinata*).—Haiti: Jérémie, on gulfweed (Fraser 1943: 94, as *Aglaophenia late-carinata*).—USA: Rhode Island, Block Island, near North Light, 13 ftm (24 m) (Fraser 1944: 380, as *Aglaophenia late-carinata*).—USA: Gulf Stream off mid-Atlantic states, 39°57’50”N, 70°51’15”W, 150 ftm (274 m) + 39°05’30”N, 70°44’30”W, 1525 ftm (2789 m) + 39°58’N, 70°06’W, on *Sargassum* + 38°25’N, 72°40’W, on *Sargassum* +38°59’N, 70°07’W, 1544 ftm (2824 m) (Fraser 1944: 380, as *Aglaophenia late-carinata*).—USA: Florida, off Hollywood, on *Sargassum* (Fraser 1944: 380, as *Aglaophenia late-carinata*).—USA: Louisiana, Grand Isle, on *Sargassum* (Fraser 1944: 380, as *Aglaophenia late-carinata*; 1945: 22, as *Aglaophenia late-carinata*).—USA: Texas, Gulf coast, on *Sargassum* (Fraser 1944: 380, as *Aglaophenia late-carinata*).—Sargasso Sea: on *Sargassum* (Vervoort 1946: 338).—USA: Louisiana, Grand Isle, on *Sargassum* (Behre 1950: 7, as *Aglaophenia minuta* and *A. late-carinata*).—USA: Texas, St. Joseph Island, on *Sargassum* + Port Aransas, on *Sargassum* and tar (Deevey 1950: 347, as *Agaophenia perpusilla*).—Unstated location: on buoys (Woods Hole Oceanographic Institution 1952: 185, as *Aglaophenia late-carinata*).—USA: Mississippi, Mississippi Sound, on floating *Sargassum* (Fincher 1955: 92 as *Aglaophenia late-carinata*).—USA: Florida, Florida Current off Miami (Adams 1960: 81, as *Aglaophenia latecerinata*).—French Guiana: on a hydroid (Leloup 1960, as *Aglaophenia latecarinata*).—USA: Texas, Lower Laguna Madre, on *Sargassum* (Breuer 1961: 166, as *Aglaophenia late-carinata*).—Venezuela: Sucre, Chacopata (Van Gemerden-Hoogeveen 1965: 76).—Aruba: Boca Prins, on *Sargassum* (Van Gemerden-Hoogeveen 1965: 76).—Curaçao: Boca Grandi, on *Sargassum* (Van Gemerden-Hoogeveen 1965: 76).—Klein Bonaire: East Coast Landing (Van Gemerden-Hoogeveen 1965: 76).—Bonaire: Punt Vierkant, on *Sargassum* (Van Gemerden-Hoogeveen 1965: 76).—Venezuela: Islote Aves, northern lagoon (Van Gemerden-Hoogeveen 1965: 76).—St. Eustatius, Schildpaddenbaai, on *Sargassum* (Van Gemerden-Hoogeveen 1965: 76).—Saint-Barthélemy: Fourche, Five Island (Van Gemerden-Hoogeveen 1965: 76).—Sargasso Sea, 35°07’N, 63°35’W, on *Sargassum* (Van Gemerden-Hoogeveen 1965: 76).—Virgin Islands of the United States: St. Thomas (Vervoort 1968: 72).—Virgin Islands of the United States: St. Croix, Frederiksted (Vervoort 1968: 72).—USA: Gulf Stream (Weis 1968: 556, as *Aglaophenia*).—USA: Texas, Galveston, on *Sargassum* (Defenbaugh 1972: 388, as *Aglaophenia late-carinata*; Defenbaugh & Hopkins 1973: 117, as *Aglaophenia late-carinata*).—USA: Texas, Flower Garden Bank (Defenbaugh 1974: 101, as *Aglaophenia late-carinata*).—Colombia: Santa Marta area (Wedler 1975: 340; Bandel & Wedler 1987: 42).—Sargasso Sea + Gulf Stream, several stations between Florida and New Jersey, on *Sargassum natans* I, *S. natans* VIII, *S. fluitans* III, *S. fluitans* X, *S. filipendula, S. polyceratium*, *S. pteropleuron*, *Sargassum* sp. (Rackley 1974: 49).—Bahamas: Little Bahama Bank, on *Sargassum* (Bogle 1975: 35).—Northern Straits of Florida, on *Sargassum* (Bogle 1975: 35).—Mexico: Arrowsmith Bank (Bogle 1975: 36).—USA: Florida, southern Straits of Florida (Bogle 1975: 36).—Belize: Carrie Bow Cay, on *Sargassum* (Spracklin 1982: 250).—Colombia: Bahía de Cartagena (Flórez González 1983: 123).—Sargasso Sea: Hydrostation “S” off Bermuda, 31°45’N, 64°10’W, on pelagic *Sargassum* (Butler *et al*. 1983: 231, as *Aglaeophenia latecarinata*).—USA: South Carolina, inner (17–18 m), middle (32–36 m) and outer (46–69 m) continental shelf + Georgia, inner (17–22 m), middle (23–29 m) and outer (59–67 m) continental shelf (Wenner *et al*. 1984: 21, 40).—Bermuda: on *Sargassum* (Calder 1986: 139).—Belize: Twin Cays (Calder 1991b).—Bermuda: on *Sargassum*, Natural Arches Beach + 2 km SE of Castle Roads + Church Bay (Calder 1995: 540).—Bermuda: Whalebone Bay, on *Sargassum* + Town Cut + Shelly Bay Beach, on *Sargassum* and plastic + Atlantic Ocean 2 km off Natural Arches Beach + Challenger Bank + Flatts Inlet, on *Sargassum* + Fort St. Catherine's Beach, on *Sargassum* (Calder 1997: 55).—USA: North Carolina, near 34°10'N, 76°13'W, on *Sargassum* (Stachowicz & Lindquist 1997: 116).—Bermuda: Challenger Bank + Argus (=Plantagenet) Bank (Calder 2000: 1134).—Cuba: Archipiélago Sabana-Camagüey, cayos Esquivel and Mendoza, 1 m + Ciudad de La Habana province, Cojimar, on *Sargassum* (Ortiz 2001a: 64, as *Aglaophenia* cf. *latecarinata*).—Panama: Bocas del Toro area, Hospital Point, 09°20'01.9"N, 82°13'07.7"W, 2–13 m + Cayo Solarte Sud, 09°18'45.3"N, 82°12'46.6"W, 2–3 m + Boca del Drago, 09°25'36.3"N, 82°19'30.1"W, 1–3 m + Cayos Zapotilla, 09°15.564'N, 82°02.750'W, 7–8 m + Swan's Key, 09°27'12.2"N, 82°18'01.8"W, 1–4 m (Calder & Kirkendale 2005: 483).—Cuba: Playa Antonio (Península de Guanahacabibes), on *Sargassum* (Varela *et al*. 2005: 178).—French Lesser Antilles: Guadeloupe, Grande-Terre, Pointe Plate, 16°27.220'N, 61°32.128'W, 15–20 m, on sponge + Grande-Terre, Les Ancres, 16°27.002'N, 61°32.320'W, 15–18 m, on bivalve shells (Galea 2010: 31).—Colombia: offshore waters (Posada *et al.* 2010: 75, 77).—Cuba: Golfo de Batabanó (Castellanos-Iglesias *et al*. 2011: 24).—USA: Florida, off St. Lucie Inlet + Fort Pierce, Fort Pierce Inlet State Park, on *Sargassum* (Calder 2013: 46).—French Lesser Antilles: Martinique (Galea 2013: 50).—Caribbean Sea (Wedler 2017b: 144, figs. 164–166A, B).—Mexico: Alacranes Reef, on algae, sponges (Mendoza-Becerril *et al*. 2018b: 130).—Panama: Bocas del Toro area, STRI (Smithsonian Tropical Research Station) docks/weather station (Miglietta *et al*. 2018b: 108).

Genus *Gymnangium* Hincks, 1874

Gymnangium sinuosum (Fraser, 1925)

Fig. 22c

Halicornaria sinuosa Fraser, 1925: 171, figs. 7A–C.
Aglaophenia (?) *allmani*.—Leloup, 1935a: 57 [part] [not *Macrorhynchia allmani* (Nutting, 1900)].
not *Halicornaria sinuosa*.—Leloup, 1937: 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 sinuosum.—Bogle, 1975: 271, figs. 23A, B.

Type locality. USA: Florida, Gulf Stream off Cape Florida, 2-1/8 miles (3.4 km) SSE of Fowey Rocks Lighthouse, 45 ftm (82 m) (Fraser 1925: 172, as *Halicornaria sinuosa*).

Material examined. Southwest Florida Shelf, middle shelf west of North Naples, 26°16'15"N, 83°47'00"W, 76 m, 04 November 1980, one fragment, 4.0 cm high, plus broken stem, without gonophores, coll. Continental Shelf Associates, ROMIZ B2203.

Remarks. *Gymnangium sinuosum* (Fraser, 1925) has been discussed in detail elsewhere (Bogle 1975; Calder 1997; Ansín Agís *et al.* 2001). While much like the essentially sympatric *G. speciosum* (Allman, 1877), the two have been distinguished to date mainly on the basis of a single morphological character. The hydrothecal margin in *G. sinuosum* has a single embayment on each side rather than two. According to Bogle (1975), the length of the median inferior nematotheca is much less variable in *G. sinuosum* as well. Although she examined material of both species (including type specimens) and considered them to be distinct, examination of the two morphotypes using molecular methods would nevertheless be worthwhile. Hydroids conforming to the concepts of *G. allmani* (Marktanner-Turneretscher, 1890) and *G. longicaudum* (Nutting, 1900), species or putative species from the Caribbean Sea with particularly long median inferior nematothecae, might well be included in any such studies.

As noted earlier (Bogle 1975; Calder 1997; Ansín Agís *et al.* 2001), part of the material assigned to *Gymnangium speciosum* by Nutting (1900, as *Halicornaria speciosa*), specifically that from the Straits of Florida south of Carysfort Reef (25°05'N, 80°15'W), is referable instead to *G. sinuosum*. In addition, part of the material identified as *Aglaophenia* (?) *allmani* by Leloup (1935a), namely several colonies in collection No. 71, Sta. 210 from the Dry Tortugas, was assigned by Van Gemerden-Hoogeveen (1965: 79) to *Halicornaria hians* var. *balei* (Marktanner-Turneretscher, 1890). From her description and illustrations (figs. 39–41), however, it is clear that they are referable to *G. sinuosum* (Bogle 1975; Calder 1997). Finally, as apparent from his illustration, Leloup's (1937, fig. 13) record of *Halicornaria sinuosa* (=*G. sinuosum*) from shelf waters off Tampa Bay is based on a misidentification of *G. speciosum* (Bogle 1975; Calder 1997).

The name *Halicornaria* Allman, 1874a, sometimes applied to this genus in the past, is a junior synonym of *Gymnangium* Hincks, 1874 (Stechow 1921b; Calder 1997, 2013). Evidence now exists for subdivision of *Gymnangium* into two taxa. Ronowicz *et al*. (2017) studied nine species assigned to the genus from the Indian Ocean, utilizing both morphological and molecular methods. In addition to maintenance of *Gymnangium*, their results support recognition of *Taxella* Allman, 1874b, long held to be its congener. As for *G. sinuosum*, the species studied here, it remains in *Gymnangium*. From current knowledge of this hydroid and its distribution, it is another species typical of shelf waters in the warm western Atlantic.

Reported distribution. ***Gulf coast of Florida.*** Dry Tortugas, 27 ft (8 m) (Leloup 1935a: 57, as *Aglaophenia* (?) *allmani*; Van Gemerden-Hoogeveen 1965: 70, as *Halicornaria hians* var. *balei*).—Straits of Florida, E of Alligator Reef, 24°51’N, 80°35’W, 64–69 m (Bogle 1975: 272).

Elsewhere in western North Atlantic. USA: Florida, Straits of Florida, 25°05’N, 80°15’W, south of Carysfort Reef, 56 ftm (102 m) (Nutting 1900: 127, as *Halicornaria speciosa*; Bogle 1975: 271).—USA: Florida, Gulf Stream off Cape Florida, 2-1/8 miles (3.4 km) SSE of Fowey Rocks Lighthouse, 45 ftm (82 m) (Fraser 1925: 172, as *Halicornaria sinuosa*; Bogle 1975: 271, syntypes).—USA: Florida, Straits of Florida, E of Cape Florida, 25°43’N, 80°04’W–25°44’N, 80°04’W, 137–174 m (Bogle 1975: 271).—USA: South Carolina, inner (17–18 m), middle (32–36 m) and outer (46–69 m) continental shelf + Georgia, inner (17–22 m) and middle (23–29 m) continental shelf (Wenner *et al*. 1984: 21, 40).—Bermuda: 2.5 km E of St. David’s Lighthouse, 85 m (Calder 1997: 43).

Genus *Lytocarpia* Kirchenpauer, 1872

Lytocarpia tridentata (Versluys, 1899)

Fig. 22d

Aglaophenia tridentata Versluys, 1899: 47, figs. 16–18.
Aglaophenia contorta Nutting, 1900: 96, pl. 20, figs. 5–7.—Wallace, 1909: 137.

Type locality. Venezuela: Los Testigos Islands, 11 m (Versluys 1899: 49, as *Aglaophenia tridentata*).

Material examined. Florida Keys, Bahia Honda Channel, 24°39.489’N, 81°17.198’W, 6 m, 16 June 2008, on limestone, three colony fragments, up to 14.5 cm high, with gonophores, ROMIZ B3806.—Fort Myers Beach, stranded intertidally on detached octocoral, 16 February 2013, one colony, 2.9 cm high, without gonophores, coll. D. Calder, ROMIZ B4403.

Remarks. Versluys (1899) provided the first account of this species, as *Aglaophenia tridentata*, based on sterile colonies from the Archipiélago de Los Testigos in the southeastern Caribbean Sea. It was described again by Nutting (1900), as *A. contorta*, from fertile specimens taken near Key West, Florida. On recognizing that hydroids in the two accounts were conspecific, Stechow (1923b) followed the Principle of Priority and adopted the senior name for the species. Totton (1926) assigned it to *Thecocarpus* Nutting, 1900 based on the morphology of corbulae from material collected in Brazil. With *Thecocarpus* now held to be a junior synonym of *Lytocarpia* Kirchenpauer, 1872, the valid name of the species is *Lytocarpia tridentata*.

Lytocarpia tridentata is most readily distinguished by the morphology of its saddle-shaped hydrothecae. These consist of a somewhat bulbous base having an adcauline intrathecal ridge and supporting a large and projecting median inferior nematotheca, a somewhat constricted mid-region, an expanded distal end flanked by a pair of horn-shaped lateral nematothecae, and a margin with three cusps, one well-developed median and two blunt laterals. Colonies are erect, with a monosiphonic and unbranched hydrocaulus reaching as much as 18 cm high (Migotto 1996). Hydrocladia, occurring in a distal plume on larger colonies, are alternate and unbranched.

Detailed accounts of the taxonomy of this species include those of Vervoort (1968, as *Aglaophenia tridentata*), and Migotto (1996, as *Lytocarpia tridentata*), with the latter study based on material from Brazil. Records of *L. tridentata* in the tropical northwest Atlantic have been fewer in number than those to the south in Brazil (Oliveira *et al*. 2016). As noted by Vervoort (1968) and confirmed by the collection data of Migotto (1996) and others, this hydroid is predominantly a species of shallow waters. Its known bathymetric range extends from the intertidal zone (Migotto 1996) to 70 m (Grohmann *et al*. 2003; Posada *et al*. 2010), with most reports at depths of less than 20 m.

Reported distribution. ***Gulf coast of Florida.*** Off Key West, 5½ ftm (10 m) (Nutting 1900: 96, as *Aglaophenia contorta*).—Off Marco Island, 2 ftm (4 m) (Nutting 1900: 96, as *Aglaophenia contorta*).—Dry Tortugas (Wallace 1909: 137, as *Aglaophenia contorta*).

Elsewhere in western North Atlantic. Venezuela: Los Testigos Islands, 11 m (Versluys 1899: 49, as *Aglaophenia tridentata*).—Virgin Islands of the United States: St. Thomas, Sound + Savannah Passage (Vervoort 1968: 76, as *Aglaophenia tridentata*).—Costa Rica: off Limón, 10°01'10"N, 83°04'45"W (Kelmo & Vargas 2002: 616).—Colombia: Golfo de Salamanca, 70 m (Posada *et al*. 2010: 79, as *Aglaophenia tridentata*).—Caribbean Sea (Wedler 2017b: 148, fig. 177).

Genus *Macrorhynchia* Kirchenpauer, 1872

Macrorhynchia allmani (Nutting, 1900)

Fig. 22e

Aglaophenia ramosa Allman, 1877: 39, pl. 23, figs. 1–4 [junior secondary homonym of *Aglaophenia ramosa* (Busk, 1852); replaced before 1961 by a substitute name in current use (ICZN Art. 59.3)].

Aglaophenia allmani Nutting, 1900: 100, pl. 22, figs. 2–3 [*nomen novum* for *Aglaophenia ramosa* Allman, 1877].—Van Gemerden-Hoogeveen, 1965: 78, fig. 43.

Aglaophenia (?) *allmani*.—Leloup, 1935a: 57 [part].

?*Aglaophenia mercatoris* Leloup, 1937: 113, figs. 15A–D.

Type locality. USA: Florida, Florida Reef, 2–3 ftm (4–6 m) (Allman 1877: 40, as *Aglaophenia ramosa*).

Material examined. Southwest Florida Shelf, middle shelf west of Gasparilla Island, 26°45.86'N, 83°21.44'W, 50 m, 18 July 1981, triangle dredge, one colony fragment, 5.6 cm high, without phylactocarps, coll. Continental Shelf Associates, ROMIZ B2187.

Remarks. The binomen *Aglaophenia allmani* was proposed by Nutting (1900) as a replacement name for *A. ramosa* Allman, 1877, a junior secondary homonym of *A. ramosa* (Busk, 1852). The species is now assigned to *Macrorhynchia* Kirchenpauer, 1872 based on characters of both trophosome and gonosome, with the latter having recently been described by Galea (2013). An earlier account of the gonophores of *Macrorhynchia allmani* by Wedler (2004) has been discounted (Calder 2013), having been based on a different species, likely *M. furcata* (Nutting, 1900).

As highlighted by Galea (2013), uncertainty has persisted in the formulation of taxonomically significant differences between *M. allmani* and several morphologically similar species (*Nematophorus grandis* Clarke, 1879, *Pleurocarpa ramosa* Fewkes, 1881, *Lytocarpus racemiferus* Allman, 1883, *L. clarkei* Nutting, 1900, *Aglaophenia mercatoris* Leloup, 1937, and *A. longiramosa* Fraser, 1945) from the warm western North Atlantic. Comparisons of some of these species have been reviewed in previous papers (Calder 1997, 2013; Galea 2013). Two of them from the Gulf coast of the United States (*A. mercatoris* from near Tampa Bay; *A. longiramosa* from the coast of Alabama) were included by me (Calder 1997) as synonyms or questionable synonyms of *M. allmani*, although both have been provisionally recognized as valid by Galea (2013). Studies are needed to better establish relationships in this entire group of species.

Several records of *M. allmani* in the western North Atlantic that have been corrected or clarified in earlier work warrant review here. Congdon (1907) reported *Lytocarpus philippinus* (=*Macrorhynchia philippina*) from Bermuda, but his illustration of it was based on *M. allmani*. Stechow (1920) recognized the error but compounded it by providing an unnecessary replacement name for the species (*M. bermudensis*). From current knowledge of the hydroids of Bermuda, it seems highly likely that Congdon combined two species under a single name, with specimens reportedly found along shallow shores indeed being *M. philippina* and the others (illustrated in fig. 37), from deeper waters on Challenger Bank, being *M. allmani*. Reports of *M. clarkei* from Challenger Bank (Bennitt 1922, as *Lytocarpus clarkei*) and from waters around Bermuda (Calder 1986), a species not reliably known from the region, were almost certainly based on material of the abundant *M. allmani* (Calder 1997). Van Gemerden-Hoogeveen (1965) discovered that material identified by Leloup (1935a) as *Aglaophenia* (?) *allmani* (=*M. allmani*) from the Dry Tortugas, Florida, included two additional species, "*Aglaophenia elongata*" (actually *A. dubia*) and "*Halicornaria hians* var. *balei*" (actually *Gymnangium sinuosum*). Finally, as noted above, the hydroid from Colombia identified as *M. allmani* by Wedler (2004) appears to have been *M. furcata* (Nutting, 1900).

Macrorhynchia allmani is a robust species most often encountered in open coastal waters.

Reported distribution. *Gulf coast of Florida.* Florida Reef, 2–3 ftm (4–6 m) (Allman 1877: 40, as *Aglaophe-*

nia ramosa).—Dry Tortugas, 27 ft (8 m) and 45 ftm (82 m) (Leloup 1935a: 57, as *Aglaophenia* (?) *allmani*; Van Gemerden-Hoogeveen 1965: 78, as as *Aglaophenia allmani*).—?Off Tampa Bay, 7–10 miles (11–16 km) offshore, 8–10 ftm (15–18 m) (Leloup 1937: 113, as *Aglaophenia mercatoris*).

Elsewhere in western North Atlantic. St. Vincent: 95 ftm (174 m) (Fewkes 1881a: 127, as *Aglaophenia ramosa*; Fraser 1944: 366, as *Aglaophenia allmani*).—Colombia: el Golfo de Darién*,* 09°30'N, 76°20'W, 42 ftm (77 m) (Nutting 1900: 100, as *Aglaophenia allmani*).—Bermuda: Challenger Bank (Congdon 1907: 484 [part], as *Lytocarpus philippinus*).—Barbados: 33 ftm (60 m) (Nutting 1919: 100, as *Aglaophenia allmani*).—Bermuda: Challenger Bank, 31–70 ftm (57–128 m) (Bennitt 1922: 254, as *Lytocarpus clarkei*).—Barbados: 100 ftm (183 m) (Fraser 1943: 93, as *Aglaophenia allmani*).—Virgin Islands of the United States: St. Croix, 17°37'55"N, 64°54'20"W, 115 ftm (210 m) (Fraser 1943: 93, as *Aglaophenia allmani*).—USA: Alabama, 29°58'N, 88°03'W, 16 ftm (29 m) (Fraser 1945: 21, as *Aglaophenia longiramosa*).—Aruba: 8 miles (13 km) SW of Sint Nicolaas Bay, 23–24 ftms (42–44 m) (Fraser 1947b: 14, as *Aglaophenia allmani*).—Virgin Islands of the United States: St. John, south coast (Vervoort 1968: 68, as *Aglaophenia* (?) *allmani*).—Virgin Islands of the United States: St. Thomas, Savannah Passage (Vervoort 1968: 68, as *Aglaophenia* (?) *allmani*).—USA: South Carolina, inner (17–18 m) and middle (32–36 m) continental shelf + Georgia, inner (17–22 m), middle (23–29 m) and outer (59–67 m) continental shelf (Wenner *et al*. 1984: 21, 40, as *Aglaophenia allmani*).—Bermuda: inshore and offshore waters (Calder 1986: 139, as *Macrorhynchia clarkei*).—Puerto Rico: Mona Island and Virgin Gorda Island (Larson 1987: 20, as *Aglaophenia allmani*).—?Colombia: Santa Marta area (Bandel & Wedler 1987: 117, as *Lytocarpus* (*Aglaophenia*) *allmani*).—Bermuda: 2.5 km SE of Castle Roads, 60–90 m + 1 km NE of Town Cut, 20 m + Challenger Bank, 60–70 m + 2 km S of St. David's Lighthouse, 90 m + 2.5 km 2.5 km SSE of Castle Roads, 60 m (Calder 1997: 64, 65).—Bermuda: Challenger Bank + Argus (=Plantagenet) Bank (Calder 2000: 1133).—Colombia: Golfo de Salamanca, 70 m + off Tolú, 70 m & 270 m + off Puerto Escondido, 70 m (Posada *et al*. 2010: 79).—Cuba: Golfo de Batabanó (Castellanos-Iglesias *et al*. 2011: 24).—USA: Florida, Bethel Shoal off Vero Beach, 27°42.6'N, 80°06.8'W, 24 m (Calder 2013: 50).—French Lesser Antilles: Martinique, Le Prêcheur, 14.841853, -61.227858, 10–15 m + Le Diamant, 14.442310, -61.039697, 10–13 m (Galea 2013: 41).—Caribbean Sea (Wedler 2017b: 149, figs. 178A, B, 179, 180, 181A, B, 182).

Macrorhynchia philippina **Kirchenpauer, 1872**

Fig. 22f

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.
Lytocarpus philippinnus.—Wallace, 1909: 137 [incorrect subsequent spelling].

Type locality. Philippines: Manila (Kirchenpauer 1872: 45, as *Aglaophenia philippina*).

Material examined. Sanibel Island, beach at Lighthouse Point, 26°26'57"N, 82°01'07"W, detached and in water along shore, 21 February 2013, one colony, 18 cm high, without phylactocarps, coll. D. Calder, ROMIZ B4404.—Sanibel Island, beach at Lighthouse Point, detached and stranded in tidepool, 30 March 2013, one colony, 8 cm high, without phylactocarps, coll. D. Calder, ROMIZ B4405.—Sanibel Island, beach at Lighthouse Point, 26°26'59"N, 82°01'03"W, on detached shell fragments at water's edge, 13 March 2018, 20° C, 33.5‰, one colony, 15 cm high, with gonophores, coll. D. Calder, ROMIZ B4406.

Remarks. *Macrorhynchia philippina*, considered distinctive in traditional taxonomy largely on the basis of hydrothecal characters (Fig. 22f), is thought to be essentially circumglobal in warm neritic waters (Calder 2013). Molecular work on this hydroid has been limited, but thus far it seems to support the likelihood of a wide geographic range. Moura *et al*. (2012) discovered the same 16S genotype in hydroids identified as this species from two widely separated locations in the Atlantic Ocean (Brazil and Madeira). In another analysis, the phylogram of Postaire *et al*. (2016), shows little intraspecific divergence in specimens assigned to this species from Moorea in the tropical western Pacific, from Juan de Nova Island in the Indian Ocean, and from the two Atlantic populations mentioned above.

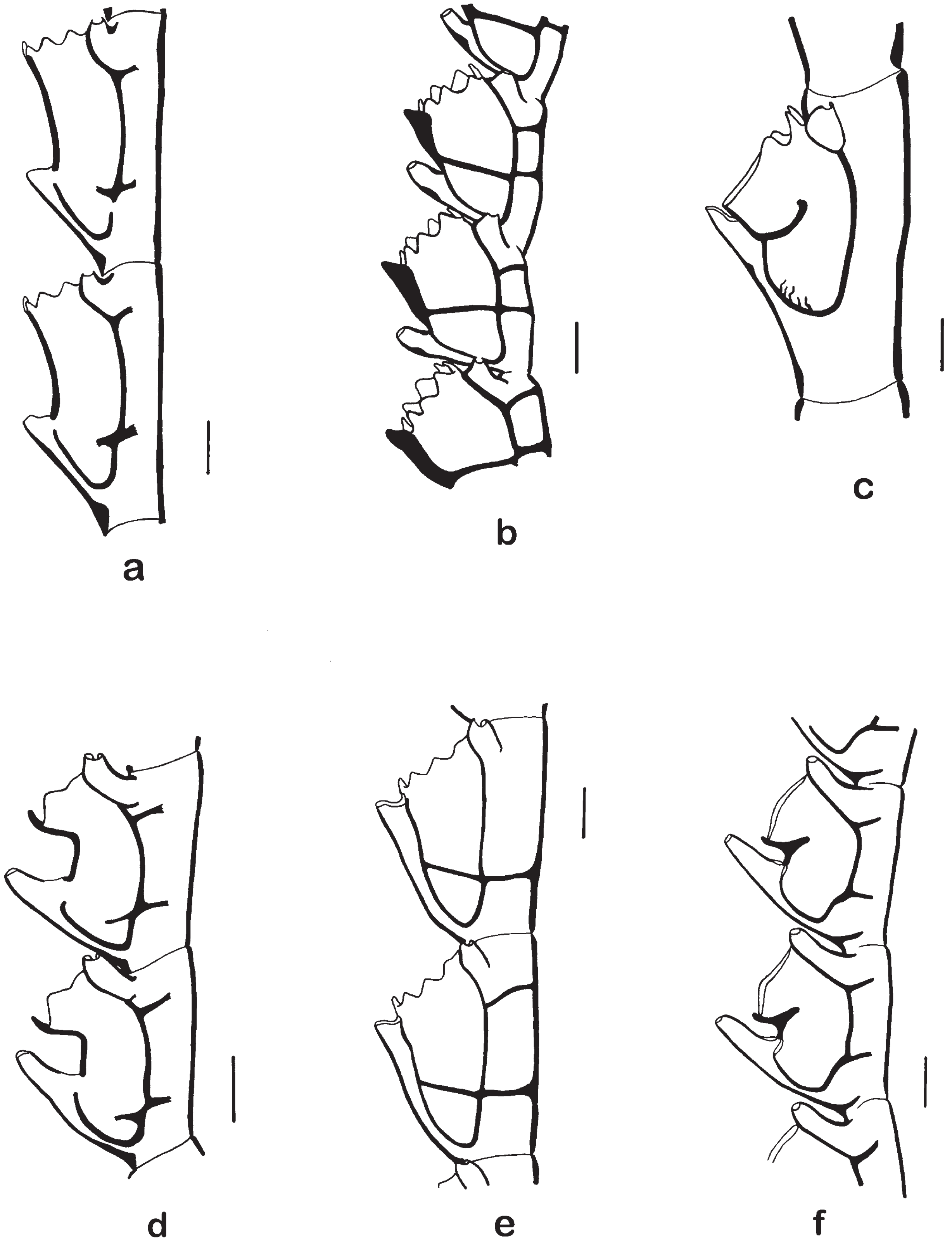

FIGURE 22. a, ***Aglaophenia dubia*****:** part of a hydrocladium with two hydrothecae, Southwest Florida Shelf, ROMIZ B2147. Scale equals 0.1 mm. **b,** ***Aglaophenia latecarinata*****:** part of a hydrocladium with three hydrothecae, Fort Myers Beach, ROMIZ B4402. Scale equals 0.1 mm. **c,** ***Gymnangium sinuosum*****:** part of a hydrocladium with one hydrotheca, Southwest Florida Shelf, ROMIZ B2203. Scale equals 0.1 mm. **d,** ***Lytocarpia tridentata*****:** part of a hydrocladium with two hydrothecae, Florida Keys, Bahia Honda Channel, ROMIZ B3806. Scale equals 0.1 mm. **e,** ***Macrorhynchia allmani*****:** part of a hydrocladium with two hydrothecae, Southwest Florida Shelf, ROMIZ B2187. Scale equals 0.1 mm. **f,** ***Macrorhynchia philippina*****:** part of a hydrocladium with two hydrothecae, Sanibel Island, ROMIZ B4405. Scale equals 0.1 mm.

Several records of *M. philippina* from the western North Atlantic require comment. Although the species is known to occur in Bermuda (Calder 1997), Congdon's (1907) record of it from there (as *Lytocarpus philippinus*) is based, at least in part, on a misidentification (Bale 1919: 352; Stechow 1920: 44; Calder 1997: 68). As evidence of this, an illustration of the species (Congdon 1907, fig. 37) portrays *M. allmani* (Nutting, 1900) instead. It is likely that specimens collected nearshore were *M. philippina*, while those from Challenger Bank were *M. allmani*. Records of *M. philippina* from Bermuda by Smallwood (1910) and Bennitt (1922) are somewhat uncertain given earlier confusion over the species in the area. Nutting (1900) reported *M. philippina* from Panama, but he failed to indicate whether the hydroids he examined were from the Atlantic or Pacific coast of that country.

More detailed accounts of this species in the western North Atlantic are given elsewhere (Calder 1997, 2013). An extensive synonymy list under *M. philippina* appears in Ansín Agís *et al*. (2001). Gonophores are liberated as short-lived medusoids (Gravier 1970; Migotto 1996; Bourmaud & Gravier-Bonnet 2004; Galea 2018).

Reported distribution. ***Gulf coast of Florida.*** Dry Tortugas (Wallace 1909: 137, as *Lytocarpus philippinus*).

Elsewhere in western North Atlantic. Jamaica (Nutting 1900: 123, as *Lytocarpus philippinus*).—?Panama (Nutting 1900: 123, as *Lytocarpus philippinus*).—Bermuda: shore areas (Congdon 1907: 484 [part], as *Lytocarpus philippinus*).—Bermuda: Fairyland Point (Smallwood 1910, as *Lytocarpus philippinus*).—USA: North Carolina, Bogue Sound, 10 ft (3 m) + Shackleford Banks, shallow water (Fraser 1912b: 379, as *Lytocarpus philippinus*).—?Bermuda: Somerset Bridge (Bennitt 1922: 254, as *Lytocarpus philippinus*).—USA: Florida, Biscayne Bay (Weiss 1948: 158, as *Lytocarpus philippinus*).—USA: unstated location: on buoys (Woods Hole Oceanographic Institution 1952: 187, as *Lytocarpus philippinus*).—USA: Florida, Biscayne Bay, Soldier Key (Voss & Voss 1955: 223, as *Lytocarpus filippinus*).—USA: Mississippi, Mississippi Sound (Fincher 1955: 92, as *Lytocarpus philippinus*).—Sint Maarten: Great Bay, NE shore, tidal zone (Van Gemerden-Hoogeveen 1965: 74, as *Lytocarpus philippinus*).—Venezuela: Puerto Cabello (Vervoort 1968: 88, as *Lytocarpus philippinus*).—Colombia; Santa Marta area (Wedler 1975: 333, as *Lytocarpus philippinus*).—Mexico, Arrowsmith Bank, 21°07'N, 86°21'W, 49–55 m (Bogle 1975: 61).—USA: Florida, Sebastian Inlet, 1.0–1.5 m (Clark & Goetzfried 1976: 477, as *Lytocarpus* sp.).—USA: South Carolina, Bulls Bay, 5 m + Prices Creek, 8 m + Capers Inlet, 3 m + Beaufort River, 6 m + Chechessee River, 9 m (Calder & Hester 1978: 91, as *Lytocarpus philippinus*; Calder 1983: 23).—Colombia: Bahia de Cartagena area, Bocachica + Obelisco + Chamba + Faro de Salmedina (Flórez González 1983: 123, as *Lytocarpus philippinus*).—Colombia: Santa Marta area (Bandel & Wedler 1987: 38, as *Lytocarpus philippinus*).—Bermuda: various localities (Calder 1986: 139).—USA: Florida, artificial reef off Boca Raton (Cummings 1994: 1208, as *Lytocarpus philippinus*).—Bermuda: Flatts Inlet, 2 m + Harrington Sound, entrance of Cripplegate Cave, 1 m (Calder 1997: 66).—USA: Florida, Biscayne Bay (Jones 2002: 218, as *Macrorynchia philippina*).—Panama: Bocas del Toro area, Swan's Key, 09°27'12.2"N, 82°18'01.8"W, 1–4 m (Calder & Kirkendale 2005: 483).—French Lesser Antilles: Guadeloupe, Grande-Terre, Les Arches, 16°27.529'N, 61°32.021'W, 17 m + L'Oeil, 16°26.782'N, 61°32.405'W, 12–17 m + Pointe d'Antigues 16°26.251'N, 61°32.523'W (Galea 2010: 34).—French Lesser Antilles: Les Saintes, Terre-de-Haut, La Baleine du Large, 15°52.820'N, 61°35.226'W, 20 m (Galea 2010: 34).—Cuba: Ciego de Ávila, Cayo Guillermo, 5 m (Varela 2012: 6).—USA: Florida, Bethel Shoal off Vero Beach, 27°42.6'N, 80°06.8'W, 24 m (Calder 2013: 52).—French Lesser Antilles: Martinique (Galea 2013: 50).—Caribbean Sea (Wedler 2017b: 152, figs. 185A, B, 186, 187).

Family Halopterididae Millard, 1962

Genus *Halopteris* Allman, 1877

Halopteris alternata (Nutting, 1900)

Figs. 23a–c

Plumularia alternata Nutting, 1900: 62, pl. 4, figs. 1, 2.—Wallace, 1909: 136.—Fraser, 1943: 96.

Plumularia diaphana.—Fraser, 1944: 343.—(?)Joyce, 1961: 72, pl. 18, fig. 3.—(?)Shier, 1965: 59, pl. 32 [not *Plumularia diaphana* (Heller, 1868)].

Halopteris diaphana diaphana.—Vervoort, 1968: 58, figs. 27a, b.

Halopteris alternata.—Schuchert, 1997: 42.

Type locality. Bahamas: Barracuda Rocks (Nutting 1900: 62, as *Plumularia alternata*).

Material examined. Fort Myers Beach, stranded intertidally on detached *Idiellana pristis*, 16 February 2013, three colony fragments, up to 8 mm high, without gonophores, coll. D. Calder, ROMIZ B4400.

Remarks. The nomenclature of the hydroid now known once again as *Halopteris alternata* (Nutting, 1900) was resolved by Schuchert (1997). For a time during the mid- and late 20th century, this hydroid was thought to be conspecific with the mostly European *H. diaphana* (Heller, 1868). As noted by Schuchert, and reiterated elsewhere (Calder 2013), morphological differences distinguishing *H. alternata* from its congener include (1) the usual presence of an axillar nematotheca beneath hydrothecae on the hydrocaulus, (2) hydrocladia with homomerous rather than heteromerous segmentation, (3) athecate hydrocladial internodes with one rather than two or three nematothecae, (4) female gonothecae that are fusiform and essentially straight rather than cornucopia-shaped. Taxonomic confusion over the two species, both of which occur in the tropical western Atlantic, makes it difficult to untangle their distribution records. Of the two, however, *H. alternata* is by far the more frequently encountered species.

Halopteris alternata is widespread in shallow waters throughout the tropical western North Atlantic. It extends from the Caribbean coast of South America (Vervoort 1968, as *Halopteris diaphana diaphana*) northwards to shelf waters of South Carolina (Wenner *et al*. 1984, as *H. diaphana*) and seawards to Bermuda (Calder 1997, as *H. diaphana*). A population on pelagic *Sargassum* believed to be the same species is carried northwards by the Gulf Stream (Fraser 1912b, as *Plumularia alternata*) and into the central North Atlantic Ocean by the North Atlantic Drift (Timmermann 1932, as *Plumularia catharina*).

Approaching the northern geographic range of *H. alternata* is the southern limit of *Halopteris tenella* (Verrill, 1874d), a species of the temperate zone in eastern North America. It is the most abundant plumularioid found in inshore waters, including estuaries, from southern New England (Nutting 1901; Petersen 1964; both as *Schizotricha tenella*) to South Carolina (Calder & Hester 1978; Calder 1983; both as *S. tenella*). While the two species are somewhat similar in morphology and could easily be confused, *H. tenella* differs from *H. alternata* in having (1) heteromerously rather than homomerously segmented hydrocauli, (2) hydrocladia that are branched rather than unbranched, and with two kinds of athecate hydrocladial internodes, long nematothecate ones and very short anematothecate ones, (3) female gonothecae that are cornucopia-shaped instead of fusiform or nearly so. Colonies of *H. tenella* also attain a much larger size, reaching 10 cm high (Calder 1971). Fraser (1944) believed that this species extended to the Caribbean region, having included Leloup's (1935a) reports of *Antennella diaphana* from Bonaire and Aruba in the synonymy of *H. tenella*. That synonymy is not upheld here, and the southern limit of *H. tenella* is taken to be the southeastern United States (Calder 1983). It is known to occur as far north as the Damariscotta River estuary, Maine (personal unpublished observations). The only record of the species from the Gulf of Mexico to date is a questionable one from Louisiana by Fraser (1944, as *Schizotricha tenella*). Also of uncertain identity is the species identified as *Plumularia diaphana* from Seahorse Key, on the Gulf coast of Florida, by Joyce (1961). His illustration of the trophosome, and especially the hydrocladia (pl. 18, fig. 3) appears as much like *H. tenella* or *H. diaphana* as *H. alternata*. Likewise uncertain is the identity of material included in *P. diaphana* by Shier (1965) from the Cape San Blas area of Florida. Hydrocauli were described as being heteromerously segmented, as in *H. tenella* and *H. diaphana*. The hydroids of both Joyce and Shier were unfortunately sterile.

One of the three colony fragments in material of *H. alternata* examined here (ROMIZ B4400) constituted an "*Antennella* form" (Fig. 23c), although a developing apophysis and hydrocladium was present.

Schuchert (1997) provided a fuller account of *H. alternata*, and compared it with related species.

Reported distribution. ***Gulf coast of Florida.*** Dry Tortugas (Wallace 1909: 136, as *Plumularia alternata*; Fraser 1943: 96, as *Plumularia alternata*; Fraser 1944: 343, as *Plumularia diaphana*; Schuchert 1997: 43).—?Seahorse Key (Joyce 1961: 72, as *Plumularia diaphana*).—?Cape San Blas area (Shier 1965: 59, as *Plumularia diaphana*).—Dry Tortugas, Loggerhead Key, tidal zone (Vervoort 1968: 59, as *Halopteris diaphana diaphana*).

Elsewhere in western North Atlantic. Bahamas: Barracuda Rocks (Nutting 1900: 62, as *Plumularia alternata*).—Bermuda: on floating *Sargassum* (Congdon 1907: 484, as *Plumularia alternata*).—USA: Louisiana, Gulf of Mexico off Marsh Island, 27°10'N, 91°50'W (Stechow 1912: 363, as *Plumularia alternata*).—Cuba: W of Havana, 23°14'N, 84°08'W (Stechow 1912: 363, as *Plumularia alternata*).—USA: North Carolina, Beaufort area, on floating *Sargassum* and *Turbinaria* (Fraser 1912: 381, as *Plumularia alternata*).—Sargasso Sea: east of New Jersey, on floating seaweed (Broch 1913: 4, as *Plumularia catharina*).—Bermuda: on floating *Sargassum* (Bennitt 1922: 255, as *Plumularia diaphana*).—Sargasso Sea, on *Sargassum*, 34°25'N, 40°05'W + 31°56'N, 48°25'W + 30°20'N, 53°10'W + 27°20'N, 61°10'W (Timmermann 1932: 298, 301, as *Plumularia catharina*).—Dominican Republic: off

Monte Cristi, on *Sargassum* (Timmermann 1932: 299, as *Plumularia catharina*).—North Atlantic Drift: 41°00'N, 34°00'W, on *Sargassum* (Timmermann 1932: 301, as *Plumularia catharina*).—Aruba: Boekoeti Reef, 0.2 m (Leloup 1935a: 52, as *Antenella diaphana* forme *typica*).—Sargasso Sea: 29°N, 44°W, on *Sargassum* (Leloup 1935a: 52, as *Antenella diaphana* forme *typica*).—Atlantic Ocean: Gulf Stream, on pelagic *Sargassum* + Sargasso Sea, on pelagic *Sargassum* (Burkenroad, in Parr 1939: 24, as *Plumularia catharina*).—Trinidad & Tobago: Trinidad, Maguaripe Bay (=Macqueripe Bay) (Fraser 1943: 96, as *Plumularia alternata*).—USA: Louisiana, Grand Isle, on floating *Sargassum* (Fraser 1944: 343, as *Plumularia diaphana*).—Aruba: 8 miles (13 km) SW of San Nicolaas Bay (Fraser 1947b: 13, as *Plumularia diaphana*).—Trinidad & Tobago: Tobago, Buccoo Bay, shore (Fraser 1947b: 13, as *Plumularia diaphana*).—USA: Florida, Biscayne Bay (Weiss 1948: 158, as *Plumularia diaphana*).—USA: Louisiana, Grand Isle, on *Sargassum* (Behre 1950: 7, as *Plumularia alternata*).—Unstated location: on buoys (Woods Hole Oceanographic Institution 1952: 188, as *Plumularia diaphana*).—USA: Mississippi, Mississippi Sound, on *Sargassum* (Fincher 1955: 92, as *Plumularia diaphana*).—Aruba: Boekoeti, northern sea side, on coral fragments, tidal zone (Van Gemerden-Hoogeveen 1965: 49, as *Antennella diaphana diaphana*).—Bonaire: Klein Bonaire, east coast landing, on *Sargassum*, sponge, and stone, tidal zone (Van Gemerden-Hoogeveen 1965: 49, as *Antennella diaphana diaphana*).—Bonaire: Palu Lechi, on sponge, low tide (Van Gemerden-Hoogeveen 1965: 49, as *Antennella diaphana diaphana*).—St. Kitts & Nevis: St. Kitts, Frigate Bay, tidal zone (Van Gemerden-Hoogeveen 1965: 49, as *Antennella diaphana diaphana*).—Sint Maarten: Simpson Lagoon, W shore of Little Key, on algae, tidal zone (Van Gemerden-Hoogeveen 1965: 49, as *Antennella diaphana diaphana*).—Virgin Islands of the United States: St. John, Turner Bay, on *Turbinaria*, tidal zone (Van Gemerden-Hoogeveen 1965: 49, as *Antennella diaphana diaphana*).—Jamaica: Kingston, on *Halocordyle disticha* (=*Pennaria disticha*) (Vervoort 1968, as *Halopteris diaphana diaphana*).—Colombia: Puerto Colombia, jetty (Vervoort 1968, as *Halopteris diaphana diaphana*).—USA: Texas, West Flower Garden Bank, on floating *Sargassum* (Defenbaugh 1974: 102, as *Plumularia diaphana*).—Gulf Stream, several stations between Florida and New Jersey, on *Sargassum natans* I, *S. polyceratium*, *S. pteropleuron, S. bermudense* (Rackley 1974: 43, as *Halopteris diaphana*).—Colombia: Santa Marta area (Wedler 1975: 340, as *Halopteris diaphana*; Bandel & Wedler 1987: 38, as *Halopteris diaphana*).—Jamaica: south coast (Mergner 1977: 122, as *Halopteris diaphana*; 1987: 187, as *Halopteris diaphana*).—Belize: Carrie Bow Cay (Spracklin 1982: 246, as *Halopteris diaphana*).—Colombia: Bahía de Cartagena (Flórez González 1983: 123, as *Halopteris diaphana diaphana*).—USA: South Carolina, middle continental shelf E of South Santee River, 32–36 m (Wenner *et al.* 1984: 40, as *Halopteris diaphana*).—?USA: Texas, banks on the continental shelf (Rezak *et al*. 1985: 224, as *Halopteris catharina*).—Bermuda: common inshore, and on pelagic *Sargassum* (Calder 1986: 139, as *Halopteris diaphana*).—USA: South Carolina and Georgia, inner continental shelf, on artificial reefs (Wendt *et al.* 1989: 1119, as *Halopteris diaphana*).—Belize: Twin Cays (Calder 1991b: 223, as *Halopteris diaphana*).—Colombia: Bahía de Chengue, on *Rhizophora* (Reyes & Campos 1992: 108, as *Halopteris diaphana*).—Bermuda: on pelagic *Sargassum* (Calder 1995: 540, as *Halopteris diaphana*).—Belize: Turin Cays (=Twin Cays) (Schuchert 1997: 43).—Bonaire: Klein Bonaire (Schuchert 1997: 43).—Jamaica: Kingston (Schuchert 1997: 43).—Colombia: Puerto Colombia (Schuchert 1997: 43).—Aruba: Boekoeti reef (Schuchert 1997: 43).—Sint Maarten: Simpson Lagoon (Schuchert 1997: 43).—St. Kitts & Nevis: St. Kitts, Frigate Bay (Schuchert 1997: 43).—Virgin Islands of the United States: St. John (Schuchert 1997: 43).—Bonaire: Poeloe Lechi (Schuchert 1997: 43).—Bermuda: Whalebone Bay, on *Thyroscyphus marginatus*, *Pennaria disticha*, and pelagic *Sargassum*, 0–1.5 m + Castle Harbour, W of Castle Roads, on algae + Harrington Sound, Stream Passage Cave, on rock, 1 m + Atlantic Ocean, 2 km SE of Castle Roads, on coral rubble and algae, 70–73 m + Flatts Inlet, on pelagic *Sargassum* + Atlantic Ocean, 2.5 km SSE of Castle Roads, on rhodoliths, 60 m (Calder 1997: 36, as *Halopteris diaphana*).—Bermuda: Challenger Bank + Argus (=Plantagenet) Bank (Calder 2000: 1133).—Panama: Colón, Club Nautico, steel pilings, 09°21'51"N, 79°53'39"W, 0–1 m + Galeta, STRI Galeta Laboratory, dock, 09°24'08"N, 79°51'39"W, 0–2 m + Bocas del Toro area, Hospital Point, 09°20'00.7"N, 82°13'06.8"W, 0–2 m + Bocas del Toro area, Mangrove Inn, 09°19'52.6"N, 82°15'17.7"W, 2–3 m + Bocas del Toro area, Boca del Drago, 09°25'36.3"N, 82°19'30.1"W, 1–3 m + Bocas del Toro area, Cayos Zapotilla, 09°15.564'N, 82°02.750'W, 7–8 m + Bocas del Toro area, Crawl Cay, 09°15.261'N, 82°07.787'W, 2–4 m + Bocas del Toro area, near Laguna Bocatorito, 2–4 m + Bocas del Toro area, Swan's Key, 09°27'12.2"N, 82°18'01.8"W, 1–4 m + Bocas del Toro area, Bastimentos, 09°20.898'N, 82°09.959'W, 1–4 m + Bocas del Toro area, "Emelio's Beach", 09°22.027'N, 82°14.336'W + Bocas del Toro area, Drago 2, mangrove, 1–2 m (Calder & Kirkendale 2005: 483).—French Lesser Antilles: Guadeloupe, Basse-Terre, N of Malendure, 16°10'25.00"N, 61°46'58.00"W, rocky shore + Basse-Terre, Petite Anse, 16°05'47.00"N, 61°46'17.00"W, rocky shore + Basse-Terre, Anse à la Barque, 16°05’21”N, 61°46’00”W, rocky shore, dock, pilings (Galea 2008: 41).—French Lesser Antilles: Les Saintes, Terre-de-Haut, Pompierre Bay, 15°52’25”N, 61°34’15”W, large rocks in seagrass meadows + Terre-de-Haut, Pain de Sucre, 15°51’45”N, 61°35’60”W, rocky shore (Galea 2008: 41).—French Lesser Antilles: Guadeloupe, Grande-Terre, Pointe Plate, 16°27.220’N, 61°32.128’W + Grande-Terre, L’Oeil, 16°26.782’N, 61°32.405’W, 12–17 m + Grande-Terre, Passe à Colas, 16°21.269’N, 61°34.193’W, 10–15 m (Galea 2010: 3, 4).—French Lesser Antilles: Les Saintes, Terre-de-Haut, Pointe Morel, 15°53.050’N, 61°34.410´W, 6–11 m + Terre-de-Haut, Pointe à Cabrit, 15°52.645’N, 61°36.125’W, 10–15 m (Galea 2010: 5).—Cuba: Golfo de Batabanó, Cayo Campos (Castellanos-Iglesias *et al*. 2011: 16).—USA: Florida, off West Palm Beach, 13.7 m (Calder 2013: 42).—French Lesser Antilles: Martinique (Galea 2013: 50).—Caribbean Sea (Wedler 2017b: 155, figs. 190A, B, 191–193).—Mexico: Alacranes Reef, on shipwreck (Mendoza-Becerril *et al*. 2018b: 130, as *Halopteris diaphana*).—Cuba: Havana, coral reef system west of the city (Castellanos *et al*. 2018: Supplementary Table S2).—Panama: Bocas del Toro area, Punta Caracol + Punta Hospital + near Bocatorito Bay (Miglietta *et al*. 2018b: 108).

***Halopteris clarkei* (Nutting, 1900)**

Fig. 23d–f

Plumularia gracilis Clarke, 1879: 246, pl. 5, figs. 29, 30, 30b, c [junior primary homonym of *Plumularia gracilis* Murray, 1860].
Plumularia clarkei Nutting, 1900: 61, pl. 3, fig. 5 [*nomen novum* for *Plumularia gracilis* Clarke, 1879].
Antennella diaphana diaphana.—Van Gemerden-Hoogeveen, 1965: 49, figs. 23–28 [part; not *Antennella diaphana* (Heller, 1868) (=*Halopteris diaphana*)].
Halopteris gracilis.—Schuchert, 1997: 110, figs. 39a–d (right), e, g.

Type locality. Cuba: off Havana, 175 ftm (320 m) (Clarke 1879: 247, as *Plumularia gracilis*).

Material examined. Southwest Florida Shelf, middle shelf west of North Naples, 26°16’30”N, 83°42’30”W, 80.5 m, 03 November 1980, one colony fragment, 2.6 cm high, with one male gonotheca, coll. Continental Shelf Associates, ROMIZ B2097.—Southwest Florida Shelf, middle shelf west of North Naples, 26°16.83’N, 83°23.81’W, 59.5 m, 19 July 1981, triangle dredge, two colony fragments, up to 3.1 cm high, without gonophores, coll. Continental Shelf Associates, ROMIZ B2096.

Remarks. *Plumularia gracilis,* the name initially applied to this species by Clarke (1879), is an invalid junior primary homonym of *Plumularia gracilis* Murray, 1860. Nutting (1900) recognized the homonymy and proposed *P. clarkei* as a replacement name for it. Following current usage, the species is assigned here to the genus *Halopteris* Allman, 1877. However, revision of *Halopteris* is warranted and it is unlikely that *H. clarkei* will prove to be congeneric with *H. carinata* Allman, 1877, the type species of the genus.

Halopteris clarkei falls within a group of species currently assigned to *Halopteris* that have hydrocladia arranged in opposite pairs (Schuchert 1997). Others in the group include *H. catharina* (Johnston, 1833) and *H. geminata* (Allman, 1877) from the Atlantic Ocean, *H. plagiocampa* (Pictet, 1893) from the western Pacific, *H. opposita* (Mulder & Trebilcock, 1911) and *H. zygocladia* (Bale, 1914) from Australia, and *H. gemellipara* Millard, 1962 from South Africa. *Halopteris enersis* Galea, 2006 from Chile has subsequently been added to this group. Characters used to differentiate these species have been outlined by Schuchert (1997) and Galea (2006).

The hydroid of *H. clarkei* is much like *H. geminata*, originally described from a site off Sand Key in the Straits of Florida. Nutting (1900: 61) pondered whether *H. clarkei* and *H. geminata*, along with *H. catharina*, might prove conspecific, but in the end recognized all three as valid. Fraser (1944: 347) saw little justification for combining them. Schuchert (1997: 115) suspected that *H. clarkei* (as *H. gracilis*) and *H. geminata* might be conspecific, but recognized both given the need for more evidence that they were identical. He considered them distinct from *H. catharina*, a species differing in having two pairs of lateral nematothecae instead of a single pair and in lacking axillar nematothecae (Schuchert 1997: 113). Hydrothecae of *H. clarkei* also usually overtop the transverse node of the hydrocladial internodes (Fraser 1946 [1947a]: 366–367), whereas those of *H. catharina* do not quite reach the node (Cornelius 1995b, figs. 29B–D; Schuchert 1997, figs. 38b, c). Hydroids of *H. clarkei* appear to differ from those of *H. geminata* in having (1) an unbranched rather than a dichotomously branched hydrocaulus, (2) one rather than two or three nematothecae on athecate hydrocladial internodes, and (3) lateral nematothecae with bulbous rather than straight walls (Schuchert 1997:

114). As with *H. clarkei*, *H. geminata* is poorly known and infrequently observed, although it was recently identified in several collections from slope waters off the southeastern United States by Henry *et al*. (2008).

Schuchert (1997) discovered that some of the material from the Dry Tortugas identified as *Antennella diaphana diaphana* by Van Gemerden-Hoogeveen (1965) was referable instead to *H. gracilis* (=*H. clarkei*). Records of the species from near St. Lucie Inlet, on the Atlantic coast of Florida, by Schuchert (1997) and Calder (2013) are based on the same collection (ROMIZ B1096).

Halopteris clarkei has been reported only from shelf and upper slope waters of the western North Atlantic between North Carolina (Wells *et al*. 1964, as *Plumularia clarkei*) and Cuba (Schuchert 1997, as *Halopteris gracilis*). Further details on the species are given by Schuchert (1997, as *H. gracilis*) and Calder (2013).

Reported distribution. *Gulf coast of Florida.* Dry Tortugas, 46–49 m (Van Gemerden-Hoogeveen 1965: 49, as *Antennella diaphana diaphana* (part); Schuchert 1997: 111, as *Halopteris gracilis*).

Elsewhere in western North Atlantic. Cuba: off Havana, 175 ftm (320 m) (Clarke 1879: 247, as *Plumularia gracilis*; Nutting 1900: 61, as *Plumularia clarkei*).—Cuba: off Havana, 23°11’45”N, 82°17’54”W, 182 ftm (333 m) (Nutting 1900: 61, as *Plumularia clarkei*).—USA: North Carolina, Core Banks, on *Aequipecten gibbus*, 17–20 ftm (31–37 m) (Wells *et al*. 1964: 566, as *Plumularia clarkei*).—USA: South Carolina, inner (17–18 m) and outer (46–69 m) continental shelf + Georgia, inner (17–22 m) and outer (59–67 m) continental shelf (Wenner *et al*. 1984: 21, 40).—Cuba: off Havana (Schuchert 1997: 110, as *Halopteris gracilis*).—USA: Florida, off St. Lucie Inlet, 27°11.8’N, 79°57.3’W, 87 m (Schuchert 1997: 110, as *Halopteris gracilis*; Calder 2013: 43).

Genus *Monostaechas* Allman, 1877

Monostaechas quadridens (McCrady, 1859)

Fig. 23g

Plumularia quadridens McCrady, 1859: 199.—A. Agassiz, 1865: 140.
Monostaechas ? *quadrideus*.—Wallace, 1909: 137 [incorrect subsequent spelling].
Monostaechas quadridens.—Leloup, 1937: 108, fig. 10A.—Fraser, 1943: 95.—Vervoort, 1968: 61, figs. 28a, b.

Type locality. USA: South Carolina, Charleston (McCrady 1959: 199).

Material examined. Southwest Florida Shelf, middle shelf west of Gasparilla Island, 26°45.86’N, 83°21.44’W, 50 m, 18 July 1981, triangle dredge, one colony, 4.3 cm high, without gonophores, coll. Continental Shelf Associates, ROMIZ B2100.—Sanibel Island, beach at Lighthouse Point, 26°26’58”N, 82°01’04.5”W, on stranded *Sargassum pteropleuron*, 21 March 2018, 22° C, 34.5‰, one colony, 7 mm high, without gonophores, coll. D. Calder, ROMIZ B4401.

Remarks. The reported range of *Monostaechas quadridens* in the western Atlantic is from southern New England (Nutting 1900, 1901) to northern Argentina (Oliveira *et al*. 2016), including the Gulf of Mexico (Deevey 1950, 1954; Calder & Cairns 2009). It is particularly common in the southeastern United States on reefs and banks of the continental shelf. Reports of the species from shallow inshore waters in the region have usually been of detached colonies (McCrady 1859; Calder 1983) that were probably carried landwards into estuarine areas by water currents. Based on its known distribution, this hydroid is considered here to be a warm-temperate to tropical species, usually found at moderate depths within the neritic zone. Current records suggest that *M. quadridens* is circumglobal (Schuchert 1997), but its occurrence beyond the Atlantic Ocean needs confirmation.

Shuchert (1997) discovered that hydroids from the Bahamas, identified as *Antennella diaphana diaphana* by Van Gemerden-Hoogeveen (1965), were referable to this species. His account of *M. quadridens*, and that of Ansín Agís *et al*. (2001), provide further discussion, illustrations, and synonymy lists of the species. *Monostaechas dichotoma* Allman, 1877 from off Pacific Reef in the Straits of Florida is considered a synonym (e.g., Nutting 1900; Fraser 1944; Vervoort 1968; Schuchert 1997; Ansín Agís *et al*. 2001).

Reported distribution. *Gulf coast of Florida.* Florida Ship Channel (A. Agassiz 1865: 140, as *Plumularia quadridens*).—Florida Reef (A. Agassiz 1865: 223, as *Plumularia quadridens*).—Dry Tortugas (Wallace 1909: 137, as *Monostaechas* ? *quadrideus* “or some related species”).—Off Tampa Bay, 7–10 miles (11–16 km) offshore, 8–10 ftm (15–18 m) (Leloup 1937: 108).—Off Dry Tortugas, 24°36’40”N, 83°02’20”W, 16 ftm (29 m) (Fraser 1943: 95).—Dry Tortugas, Bird Key reef + SW Channel, 10–12 ftm (18–22 m) (Vervoort 1968: 61).

Elsewhere in western North Atlantic. USA: South Carolina, Charleston, floating in water (McCrady 1859: 199, as *Plumularia quadridens*).—USA: Florida, off Pacific Reef, 283 ftm (518 m) (Allman 1877: 37, as *Monostaechas dichotoma*).—Mexico: Yucatan Bank, 50 ftm (91 m) (Fewkes 1881a: 128, as *Monostaechas dichotoma*).—Barbados: 76 ftm (139 m) (Nutting 1900: 76).—USA: Massachusetts, near Martha's Vineyard, 22 ftm (40 m) (Nutting 1900: 76; 1901: 365).—West Indies (Nutting 1901: 365).—USA: North Carolina, near Beaufort (Fraser 1912b: 380).—USA: Florida, east coast, 15–20 miles (24–32 km) offshore, 20–30 ftm (32–48 m) (Leloup 1937: 108, as *Monostaechas quadridens* forme *fisheri*).—Barbados: 100 ftm (183 m) (Fraser 1943: 95).—USA: South Carolina, Charleston, off the bar (Fraser 1943: 95).—USA, North Carolina, off Cape Hatteras, 14 ftm (26 m) (Fraser 1944: 335).—USA: South Carolina, Blackfish Bank (Fraser 1945: 21).—USA: Texas, Port Isabel, on *Podochela sidneyi* (Deevey 1950: 347).—USA: North and South Carolina, reefs on continental shelf (Pearse & Willams 1951: 136).—Bahamas: New Providence (Van Gemerden-Hoogeveen 1965: 49, as *Antennella diaphana diaphana* (part); Schuchert 1997: 130).—Virgin Islands of the United States: St. Thomas, Savannah Passage + Sound + south coast (Vervoort 1968: 62).—USA: North Carolina, *Lithothamnion* reef S of Cape Lookout (Cain 1972: 80).—?USA: Texas, West Flower Garden Bank, 156 ft (48 m) (Defenbaugh 1974: 101, as *Monostaechas* sp.).—USA: South Carolina, Port Royal Sound, Chechessee River, 32°17'30"N, 80°45'00"W, 9 m, unattached (Calder & Hester 1978: 91; Calder 1983: 17).—Belize: Carrie Bow Cay (Spracklin 1982: 246).—USA: South Carolina, ledges, inner continental shelf (Calder 1983: 18).—USA: South Atlantic Bight, between South Carolina and northern Florida (Wenner *et al*. 1983: 148).—Colombia: Bahía de Cartagena (Flórez González 1983: 123).—USA: South Carolina, inner (17–18 m), middle (32–36 m) and outer (46–69 m) continental shelf + Georgia, inner (17–22 m), middle (23–29 m) and outer (59–67 m) continental shelf (Wenner *et al*. 1984: 21, 40).–USA: Texas, shelf edge banks (Rezak *et al*. 1985: 224).—USA: South Carolina, continental shelf, fouling plates (Van Dolah *et al*. 1988: 694).—USA: South Carolina and Georgia, inner continental shelf, on artificial reefs (Wendt *et al.* 1989: 1112).—USA: South Carolina, coastal areas, in stomachs of Atlantic spadefish (Hayse 1990: 81).—Belize: South Water Cay, on *Thalassia* (Kaehler & Hughes 1992: 331).—USA: Florida, St. Lucie Inlet, 27°10.8'N, 80°00.8'W, 44 m (Schuchert 1997: 130; Calder 2013: 45).—USA: South Carolina, inner continental shelf SE of Charleston, 32°30.0'N, 79°42.3'W, 18 m (Schuchert 1997: 130).—Bahamas: New Providence (Schuchert 1997: 130).—Bermuda: Argus (=Plantagenet) Bank (Calder 2000: 1135).—French Lesser Antilles: Guadeloupe, Grande-Terre, Pointe Plate, 16°27.220'N, 61°32.128'W, 15–20 m (Galea 2010: 26).—Cuba: Punta Francés, Boya 56 (Castellanos *et al*. 2009: 96, 2011: 18).—French Lesser Antilles: Martinique (Galea 2013: 50).—Mexico: Alacranes Reef, on sponges, corals, rocks (Mendoza-Becerril *et al*. 2018b: 130).

Family Kirchenpaueriidae Stechow, 1921a

Genus *Ventromma* Stechow, 1923b

Ventromma halecioides (Alder, 1859)

Figs. 23h, i

*Plumularia halecioide*s Alder, 1859: 353, pl. 12, figs. 1–5.—Van Gemerden-Hoogeveen, 1965: 64.
Plumularia mermis.—Wallace, 1909: 136 [incorrect subsequent spelling].
Ventromma halecioides.—Leloup, 1935a: 51.
Plumularia inermis.—Shier, 1965: 62, pl. 34.

Type locality. UK: England, Cullercoats and Roker (Alder 1859: 353).

Material examined. Fort Myers Beach, Salty Sam's Marina, 26°27'21.7"N, 81°56'34.6"W, on floating dock on oyster shell, <0.1 m, 19 C, 05 February 2018, one colony, 1.1 cm high, without gonophores, coll. D. Calder, ROMIZ B4394.—Sanibel Island, beach at Lighthouse Point, 26°26'55"N, 82°01'08"W, on detached *Syringodium* in water along shore, 21° C, 34.5‰, 19 March 2018, one colony, 9 mm high, without gonothecae, coll. D. Calder, ROMIZ B4395.—Fort Myers Beach, Salty Sam's Marina, 26°27'21.7"N, 81°56'34.6"W, on floating dock on oyster shell, <0.1 m, 20° C, 33‰, 24 March 2018, one large colony, in several pieces, 1.7 cm high, without gonophores, coll. D. Calder, ROMIZ B4396.

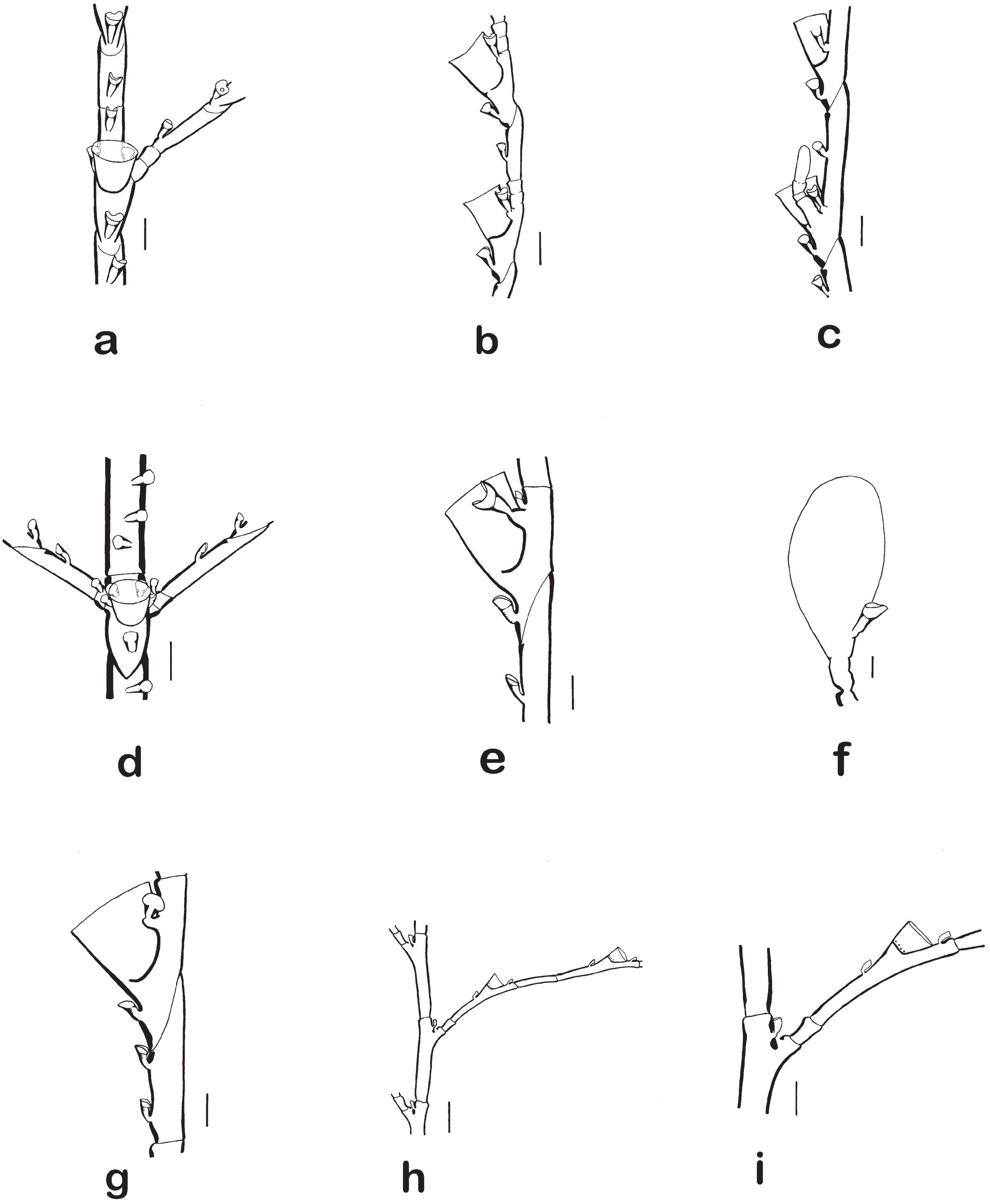

FIGURE 23. a, ***Halopteris alternata*****:** part of a hydrocaulus with proximal end of a hydrocladium, Fort Myers Beach, ROMIZ B4400. Scale equals 0.1 mm. **b,** ***Halopteris alternata*****:** part of a hydrocladium with two hydrothecae, Fort Myers Beach, ROMIZ B4400. Scale equals 0.1 mm. **c,** ***Halopteris alternata*****:** part of hydrocaulus of an "*Antennella* form" with a developing hydrocladium, Fort Myers Beach, ROMIZ B4400. Scale equals 0.1 mm. **d,** ***Halopteris clarkei*****:** part of hydrocaulus with proximal ends of two hydrocladia, Southwest Florida Shelf, ROMIZ B2097. Scale equals 0.1 mm. **e,** ***Halopteris clarkei*****:** hydrocladial hydrotheca and nematothecae, Southwest Florida Shelf, ROMIZ B2097. Scale equals 0.1 mm. **f,** ***Halopteris clarkei*****:** male gonotheca with a nematotheca, Southwest Florida Shelf, ROMIZ B2097. Scale equals 0.05 mm. **g,** ***Monostaechas quadridens*****:** part of colony with a hydrotheca and nematothecae, Southwest Florida Shelf, ROMIZ B2100. Scale equals 0.1 mm. **h,** ***Ventromma halecioides*****:** part of hydrocaulus with a hydrocladium, Sanibel Island, ROMIZ B4395. Scale equals 0.2 mm. **i,** ***Ventromma halecioides*****:** part of hydrocaulus with proximal end of a hydrocladium, Sanibel Island, ROMIZ B4395. Scale equals 0.1 mm.

Remarks. *Ventromma halecioides* is a species of tropical and warm-temperate waters, with a range in the western Atlantic from North Carolina (Fraser 1912b, as *Plumularia inermis*) to Brazil (Oliveira *et al*. 2016). As reflected in the distribution records below, it is particularly widespread in the Caribbean region. It is also thought to be widespread in warm water regions elsewhere in the Atlantic, as well as in the Pacific and Indian oceans (Calder 2013; Humara-Gil & Cruz-Gómez 2018). Within the Atlantic Ocean at least, the phylograms of Maronna *et al*. (2016) show little genetic distance between populations of this species from France and Brazil.

An extensive synonymy, detailed description, and discussion of this species has been given by Ansín Agís *et al*. (2001, as *Kirchenpaueria halecioides*). As reviewed elsewhere (Calder 2013), molecular evidence now lends support for recognition of *Ventromma* Stechow, 1923b as distinct from *Kirchenpaueria* Jickeli, 1883, and for recognition of this species under the binomen *V. halecioides*. *Plumularia inermis* Nutting, 1900, originally described from the Bahamas and recognized as valid by Fraser (1944), is taken to be conspecific.

Colonies of the hydroid stage of *V. halecioides* are quite small and usually found in shallow, sheltered inshore waters. Its gonophores, thought earlier to be fixed sporosacs (Calder 1997), are liberated as free-swimming medusoids (Galea 2018).

Reported distribution. *Gulf coast of Florida.* Dry Tortugas (Wallace 1909: 136, as *Plumularia mermis*; Leloup 1935a: 51; Van Gemerden-Hoogeveen 1965: 65, as *Plumularia halecioides*).—Cape San Blas area, on ascidians & oysters (Shier 1965: 62, as *Plumularia inermis*).

Elsewhere in western North Atlantic. Bahamas: Exuma, Barracuda Rocks (=Barracouta Rocks) (Nutting 1900: 63, as *Plumularia inermis*).—USA: North Carolina, Bogue Bank, on *Turbinaria* (Fraser 1912b: 382, as *Plumularia inermis*).—Bermuda: Fairyland Creek, on *Thalassia* (Bennitt 1922: 255, as *Plumularia inermis*).—Bermuda: Hamilton Harbour, on floating buoy (Bennitt 1922: 252, as *Antennularia pinnata*).—Bonaire: Klein Bonaire, west coast, 0.3 m, on algae (Leloup 1935a: 51).—Bonaire: Lac, 0.2–0.8 m, on dead branch, *Rhizophora*, and *Thalassia* + lagoon, 0.3–0.8 m, on *Rhizophora* and *Sargassum* (Leloup 1935a: 51).—Aruba: Boca Prins, on *Sargassum* (Leloup 1935a: 51).—Curaçao: Boca Grandi, on stranded *Sargassum* + Plaja Hoeloe (Playa Hulu), near low tide, on coral debris + Piscadera Baai, near low tide, various substrates (Van Gemerden-Hoogeveen 1965: 64, as *Plumularia halecioides*).—Bonaire: Klein Bonaire, east coast landing, near low tide, on sponge + De Hoop, near high tide + Punt Vierkant, 1–2 m, on algae + Lac Poejito, near low tide, on wood & *Thalassia* + Lac Cay, tidal zone, on wood and algae + Lagoen, near low tide, on wood and rock (Van Gemerden-Hoogeveen 1965: 64, as *Plumularia halecioides*).—Venezuela: Tortuga, SW coast, near low tide, on *Rhizophora* and coral debris (Van Gemerden-Hoogeveen 1965: 65, as *Plumularia halecioides*).—Antigua and Barbuda: Barbuda, Martello Tower Beach, near low tide, on algae (Van Gemerden-Hoogeveen 1965: 65, as *Plumularia halecioides*).—St. Kitts and Nevis: St. Kitts, Frigate Bay, near low tide, on algae and sponge (Van Gemerden-Hoogeveen 1965: 65, as *Plumularia halecioides*).—Sint Eustatius: Gallows Bay, 1–2 m (Van Gemerden-Hoogeveen 1965: 65, as *Plumularia halecioides*).—Sint Maarten: Great Bay, on wood + Simson Lagoon, near low tide, on *Rhizophora* and algae (Van Gemerden-Hoogeveen 1965: 65, as *Plumularia halecioides*).—Virgin Islands of the United States: St. Croix, Krause Lagoon, near low tide, on *Thalassia* + St. John, bay south of Cruz Bay, near low tide, on *Sargassum* (Van Gemerden-Hoogeveen 1965: 65, as *Plumularia halecioides*).—Bahamas: North Bimini, on pelagic *Sargassum* (Van Gemerden-Hoogeveen 1965: 65, as *Plumularia halecioides*).—Venezuela: Higuerote (Hirohito 1974: 45).—Colombia: Santa Marta area (Wedler 1975: 332, as *Plumularia halecoides*; Bandel & Wedler 1987: 42, as *Plumularia halecoides*).—Belize: Carrie Bow Cay (Spracklin 1982: 246, as *Plumularia haleciodes*).—Colombia, Bahía de Cartagena (Flórez González 1983: 121, as *Plumularia halecioides*).—Belize: Twin Cays, shallow water, on *Rhizophora*, *Sargassum*, *Turbinaria*, algae, hydroids, molluscs, wooden test panels (Calder 1991b: 223; 1991c: 2068).—Belize: South Water Cay, on *Thalassia* (Kaehler & Hughes 1992: 331).—Colombia: Bahía de Chengue, on *Rhizophora* (Reyes & Campos 1992: 108, as *Plumularia halecioides*).—Bermuda: Ferry Reach, 0.5 m, on rope + Whalebone Bay, 1 m, on *Thalassia* + Castle Harbour near Tucker's Town, 5 m, patch reef + Green Bay, 1 m, on algae + Walsingham Bay, 0.5 m, on *Rhizophora* + Pilchard Bay, 0.5 m, on *Rhizophora* (Calder 1997: 5).—Cuba: Ciudad de La Habana province, Cojimar, on *Sargassum* (Ortiz 2001a: 64, as *Plumularia* cf. *halecioides*).—USA: Florida, Biscayne Bay (Jones 2002: 218).—Panama: Colón, Fort Sherman dock, marina, 09°20'57"N, 79°54'10"W, 0–2 m + Colón, Isla Margareta, Fort Randolph, shore, 09°23'15"N, 79°53'11"W, 0–1 m + Portobelo Harbor, dock, 09°33'14"N, 79°39'34"W, 0–1 m + Bocas del Toro area, Cayo Solarte Sud, 09°18'45.3"N, 82°12'46.6"W, 2–3 m + Bocas del Toro area, Drago 2, mangrove, 1–2 m (Calder & Kirkendale 2005: 482).—French Lesser Antilles: Guadeloupe, Grande-Terre, E of Saint François, 16°15'18.00"N, 61°14'37.00"W, on *Thalassia* + Basse-Terre, N of Malendure, 16°10'25.00"N, 61°46'58.00"W, on algae + Basse-Terre, Petite Anse, 16°05'47.00"N, 61°46'17.00"W, on algae (Galea 2008: 44, as *Kirchenpaueria halecioides*).—French Lesser Antilles: Les Saintes, Terre-de-Haut, Pompierre Bay, 15°52'25"N, 61°34'15"W, on *Halimeda* + Terre-de-Haut, Pain de Sucre, 15°51'45"N, 61°35'60"W, on algae (Galea 2008: 44, as *Kirchenpaueria halecioides*).—French Lesser Antilles: Guadeloupe, Grande-Terre, harbor of Port-Louis, 16°24.720'N, 61°31.910'W, 0.2 m (Galea 2010: 4, as *Kirchenpaueria halecioides*).—French Lesser Antilles: Les Saintes, Terre-de-Haut, Pointe Morel, 15°53.050'N, 61°34.410'W, 6–11 m (Galea 2010: 5, as *Kirchenpaueria halecioides*).—Cuba: Golfo de Batabanó, Cayo Real, Cayería San Felipe, on rocks (Castellanos-Iglesias *et al*. 2011: 24).—French Lesser Antilles: Martinique, Case-Pilote, Anse Batterie, 14.643113, -61.141711 (Galea 2013: 14).—USA: Florida, Fort Pierce, ship canal at Link Port, 27°32'05"N, 80°20'50"W, on *Rhizophora*, 0.1 m (Calder 2013: 45).—Caribbean Sea (Wedler 2017b: 158, figs. 197, 198, as *Kirchenpaueria halecioides*).—Mexico: Alacranes Reef, on *Thalassia* (Mendoza-Becerril *et al*. 2018b: 130, as *Kirchenpaueria halecioides*).—Cuba: Havana, coral reef system west of the city (Castellanos *et al*. 2018: Supplementary Table S2).—Panama: Bocas del Toro area, STRI (Smithsonian Tropical Research Station) docks/weather station + Punta Hospital + near Bocatorito Bay (Miglietta *et al*. 2018b: 108, as *Kirchenpaueria halecioides*).

Family Plumulariidae McCrady, 1859

Genus *Monotheca* Nutting, 1900

Monotheca margaretta Nutting, 1900

Fig. 24a

Monotheca margaretta Nutting, 1900: 72, pl. 11, figs. 1–3.—Wallace, 1909: 137.
Plumularia margaretta.—Joyce, 1961: 70, pl. 18, figs. 1, 2.—Shier, 1965: 64, pl. 35.

Type locality. Bahamas: near Little Cat Island, shallow water (Nutting 1900: 72).

Material examined. Florida Keys, Bahia Honda Channel, 24°39.489'N, 81°17.198'W, 6 m, 16 June 2008, on *Lytocarpia tridentata*, one colony, 4 mm high, without gonophores, ROMIZ B4397.—Sanibel Island, beach at Lighthouse Point, 26°26'57"N, 82°01'06"W, on detached *Thalassia* in water along shore, 24°C, 35‰, 03 April 2018, fragments of one colony, 4 mm high, without gonothecae, coll. D. Calder, ROMIZ B4398.

Remarks. The genus *Monotheca* Nutting, 1900 has been regarded as congeneric with *Plumularia* Lamarck, 1816 in some works, and as valid in others (Calder 1997: 10). While the genus as presently constituted may be polyphyletic, so too is *Plumularia* (Moura *et al*. 2008: 98). Herein, certain constituent species sometimes assigned to *Monotheca* are considered sufficiently unique morphologically to be recognized as generically discrete. Molecular studies provide evidence in support of that conclusion. Phylograms such as those of Leclère *et al*. (2007, 2009), Moura *et al*. (2008), and Maronna *et al*. (2016) reveal that *Monotheca margaretta* Nutting, 1900, type species of *Monotheca*, is clearly divergent genetically from *Plumularia setacea* (Linnaeus, 1758), type species of *Plumularia*. While a re-definition and revision of the genus appear necessary, its validity is upheld here. The present species is therefore retained in this work under the binomen *M. margaretta*.

Monotheca margaretta is predominantly a hydroid of near-surface waters, and a species of tropical and warm-temperate waters. From collection records listed below, it is especially frequent in beds of the seagrass *Thalassia* and on algae including detached *Turbinaria*. It is also a constituent of the hydroid assemblage found on pelagic *Sargassum* in the open North Atlantic Ocean, the Caribbean Sea, and the Gulf of Mexico. Dispersal of the species has likely been facilitated by rafting on such substrates. While best known from shallow depths, the hydroid has also been found on bottoms as deep as 73 m. Other than its transport to relatively high latitudes on pelagic *Sargassum* in the Gulf Stream and North Atlantic Current, the known geographic range of *M. margaretta* in the western Atlantic extends from South Carolina (Wenner *et al*. 1984) and Bermuda (Calder 1997) to the southern Caribbean Sea (Van Gemerden-Hoogeveen 1965), and southwards to Brazil (Oliveira *et al*. 2016). The species is amphi-Atlantic in distribution, having been reported from locations on the eastern side of the ocean including the Azores, the Canary Islands, the Strait of Gibraltar, the Mediterranean Sea, Senegal, and Ghana (Ansín Agís *et al*. 2001). While this hydroid was collected in shelf waters off South Carolina by Wenner *et al*. (1984), it was never found in estuaries of the state during eight years of field work (Calder & Hester 1978; Calder 1983).

Detailed taxonomic accounts of *M. margaretta* include those of Calder (1997) and Ansín Agís *et al.* (2001). Gonophores of this species are thought to be fixed sporosacs, although those of a closely related species from Europe, *M. obliqua* (Johnston, 1847), are liberated as very short-lived medusoids (Motz-Kossowska 1907). The type of gonophore produced by *M. margaretta* thus needs to be determined.

Reported distribution. ***Gulf coast of Florida.*** Dry Tortugas (Wallace 1909: 137).—Seahorse Key, on *Thalassia* (Joyce 1961: 70, as *Plumularia margaretta*).—Cape San Blas area, on *Thalassia* (Shier 1965: 64, as *Plumularia margaretta*).

Elsewhere in western North Atlantic. Bahamas: near Little Cat Island, shallow water (Nutting 1900: 72).—USA: North Carolina, off Bogue Bank, on floating *Sargassum* (Fraser 1912b: 381).—Bermuda: Challenger Bank, on *Campanularia insignis* (=*Thyroscyphus marginatus*), 55 m (Stechow 1912: 361).—Bermuda: on floating *Sargassum* (Bennitt 1922: 254).—Bonaire: Boca Washikemba, on stranded algae + Lagoen, north coast, on stranded *Sargassum* (Leloup 1935a: 54, as *Plumularia margaretta*).—Curaçao: Boca Grandi, on drifting *Sargassum* (Leloup 1935a: 54, as *Plumularia margaretta*).—Aruba: Boca Prins, on stranded *Sargassum* (Leloup 1935a: 54, as *Plumularia margaretta*).—Atlantic Ocean: Gulf Stream, on pelagic *Sargassum* + Sargasso Sea, on pelagic *Sargassum* (Burkenroad, in Parr 1939: 23).—Sargasso Sea: on *Sargassum*, 34°25'N, 40°05'W + 30°50'N, 54°35'W (Timmermann 1932: 298, 300).—Dominican Republic: Monte Cristi, on *Sargassum* (Timmermann 1932: 299).—USA: Massachusetts, Gulf Stream off Martha's Vineyard, 39°58'N, 70°06'W, on floating *Sargassum* (Fraser 1944: 349, as *Plumularia margaretta*).—Puerto Rico, northeast coast, 18°23'35"N, 65°37'10"W, 10 ftm (18 m) + 18°24'30"N, 65°38'30"W, 9 ftm (16 m) (Fraser 1944: 349, as *Plumularia margaretta*).—Puerto Rico: off Culebra Island, 18°19'10"N, 65°19'40"W, 10 ftm (18 m) (Fraser 1944: 349, as *Plumularia margaretta*).—Colombia: 2 miles (3 km) off Bahía Honda, 9 ftm (16 m) (Fraser 1947b: 14, as *Plumularia margaretta*).—Unstated location: on buoys (Woods Hole Oceanographic Institution 1952: 188, as *Plumularia margaretta*).—USA: Florida, Florida Current off Miami (Adams 1960: 81, as *Monotheca margaritta* (sic)).—Aruba: North of Punta Braboe (=Punta Brabo), on *Thalassia* (Van Gemerden-Hoogeveen 1965: 69, as *Plumularia margaretta*).—Bonaire: Oranjepan (=Oranje Pan), on stranded *Sargassum* (Van Gemerden-Hoogeveen 1965: 69, as *Plumularia margaretta*).—Venezuela: Islote Aves, northern lagoon, on algae, near low water (Van Gemerden-Hoogeveen 1965: 69, as *Plumularia margaretta*).—Barbuda: Martello Tower Beach, on algae (Van Gemerden-Hoogeveen 1965: 69, as *Plumularia margaretta*).—St. Kitts & Nevis: St. Kitts, Frigate Bay, on algae, tidal zone (Van Gemerden-Hoogeveen 1965: 69, as *Plumularia margaretta*).—Sint Maarten: Great Bay, on algae, ca. 2 m (Van Gemerden-Hoogeveen 1965: 69, as *Plumularia margaretta*).—Virgin Islands of the United States: St. John, Turner Bay, on *Turbinaria*, tidal zone (Van Gemerden-Hoogeveen 1965: 69, as *Plumularia margaretta*).—USA: Texas, West Flower Garden Bank, on floating *Sargassum* (Defenbaugh 1974: 102, as *Plumularia margaretta*).—Gulf Stream, several stations between Florida and New Jersey, on *Sargassum polyceratium*, *S. pteropleuron, Sargassum* sp., and *S. ramifolium* (Rackley 1974: 45, as *Plumularia margaretta*).—Colombia: Santa Marta area (Wedler 1975: 340, as *Monotheca margareta*; Bandel & Wedler 1987: 42, as *Monotheca* (*Plumularia*) *margaretta*).—Belize: Carrie Bow Cay (Spracklin 1982: 246, as *Plumularia margaretta*).—Colombia: Bahía de Cartagena (Flórez González 1983: 121, as *Plumularia margaretta*).—USA: South Carolina, middle continental shelf (Wenner *et al*. 1984: 21, 40, as *Plumularia margaretta*).—USA: Georgia, inner continental shelf (Wenner *et al*. 1984: 40, as *Plumularia margaretta*).—Belize: Twin Cays (Calder 1991b: 223).—Belize: South Water Cut, South Water Cay, on *Thalassia* (Kaehler & Hughes 1992: 331).—Colombia: Bahía de Chengue, on *Rhizophora* (Reyes & Campos 1992: 108, as *Plumularia margaretta*).—Bermuda: on pelagic *Sargassum fluitans* and *S. natans* (Calder 1995: 540).—Bermuda: Natural Arches Beach, on stranded *Sargassum fluitans* + Castle Harbour, W of Castle Roads, on *Thalassia*, 2–3 m + Whalebone Bay, on stranded *Sargassum fluitans* + St. Catherine's Beach, on stranded *Sargassum fluitans* + Atlantic Ocean, 2 km off Castle Roads, on rubble, 73 m + Burchall's Cove, on stranded *Sargassum fluitans* + Atlantic Ocean, 2 km off Natural Arches Beach, on rhodolith, 70 m (Calder 1997: 11).—Bermuda: Argus (=Plantagenet) Bank + Challenger Bank (Calder 2000: 1133).—Cuba: Ciudad de La Habana province, Playa Mégano, 0.5 m (Ortiz 2001a: 64).—Panama: Bocas del Toro area, Boca del Drago, 09°25'36.3"N, 82°19'30.1"W, 1-3 m + Bocas del Toro area, Cayos Zapotilla, 09°15.564'N, 82°02.750'W, 7-8 m + Bocas del Toro area, Swan's Key, 09°27'12.2"N, 82°18'01.8"W, 1-4 m + Bocas del Toro area, Bastimentos (front), 09°20.898'N, 82°09.959'W, 1-4 m + Bocas del Toro area, Bastimentos (north), 09°20.898'N, 82°09.959'W, 1-4 m (Calder & Kirkendale 2005: 482).—French Lesser Antilles: Guadeloupe, Grande-Terre, Les Arches, 16°27.529'N, 61°32.021'W, 17 m + Grande-Terre, Pointe d'Antigues, 16°26.251'N, 61°32.523'W, 10–15 m, on an alga + Grande-Terre, harbor of Port-Louis, 16°24.720'N, 61°31.910'W, on red algae (Galea 2010: 29, as *Plumularia margaretta*).—Cuba: Golfo de Batabanó, Cayo Real, Cayería San Felipe (Castellanos-Iglesias *et al*. 2011: 25).—French Lesser Antilles: Martinique (Galea 2013: 50, as *Plumularia margaretta*).—Caribbean Sea (Wedler 2017b: 163, figs. 206A, B, 207A, B, 208).—Mexico: Alacranes Reef, on algae, soft coral (Mendoza-Becerril *et al*. 2018b: 131).—Panama: Bocas del Toro area, near Bocatorito Bay (Miglietta *et al*. 2018b: 108, as *Plumularia margaretta*).

Genus *Nemertesia* Lamouroux, 1812

Nemertesia nigra (Nutting, 1900)

Figs. 24b, c

Antennopsis nigra Nutting, 1900: 74, pl. 12, figs. 5, 6.

Type locality. Cuba: off Havana, *Albatross* Station 2330, 23°11'N, 82°19'W, 121 ftm (221 m) (Nutting 1900: 74).

Material examined. Southwest Florida Shelf, middle shelf west of North Naples, 26°16'15"N, 83°47'00"W, 76.2 m, 04 November 1980, four colony fragments, up to 7.5 cm high, without gonophores, coll. Continental Shelf Associates, ROMIZ B2138.

Remarks. Nutting (1900) founded as distinct species two very similar plumulariid hydroids from upper bathyal waters in the southern Straits of Florida. *Antennopsis nigra*, based on a colony reaching 14 cm high, was collected off Havana, Cuba (*Albatross* Station 2330: 23°11'N, 82°19'W, 221 m). *Antennopsis longicorna*, described from an incomplete colony reaching 5 cm high, came from a station less than 2 km away (*Albatross* Station 2335: 23°11'N, 82°20'W, 373 m). While acknowledging that *A. longicorna* was "very near *A. nigra* and may be identical with it", Nutting nevertheless considered it a distinct species based on the particularly long apophyses found in the fragmentary type specimen. With the character used to separate them likely being at least somewhat variable, *A. nigra* and *A. longicorna* are treated here as conspecific. Of the two simultaneous synonyms, nomenclatural precedence is assigned to the binomen *A. nigra* under the First Reviser Principle (ICZN Art. 24.2) for two reasons. The valid name is based on a more complete type colony, and the specific name is more applicable inasmuch as both hydroids have black or nearly black hydrocauli and main branches. With *Antennopsis* Allman, 1877 currently being considered a subjective junior synonym of *Nemertesia* Lamouroux, 1812 (Bouillon 1985: 170), the correct binomen of the species is *N. nigra*, as applied to it by Calder (2004b: 18) and Ramil & Vervoort (2006: 124).

The original description of *Antennopsis sinuosa* Fraser, 1947b from Aruba, in the southern Caribbean Sea (SW of San Nicolaas Bay, 42–44 m), differs little from that of *Nemertesia nigra*. Secondary accounts of the two in Ramil & Vervoort (2006) also provide no conclusive way of distinguishing them. Type material of *A. sinuosa* at the Santa Barbara Museum of Natural History (SBMNH 347081; SBMNH 36946) was examined and briefly described by Calder *et al*. (2009), but no characters differentiating the species from *N. nigra* were mentioned. The two are taken here to be conspecific. Other than under the names of its two synonyms, *N. nigra* has not been reported since its original description until now.

Nutting (1900) described a third species that he assigned to *Antennopsis* from waters off Havana (*Albatross* Station 2322: 23°11'N, 82°18'W, 210 m). *Antennopsis distans* was distinguished in having widely separated hydrothecae that were said to occur towards the distal ends of long, slender internodes. Hydrocladia were also described as having 2–3 athecate internodes basally, but with the remaining internodes being mostly thecate. These characters, if constant, seem to differentiate the species from *N. nigra*. It is therefore retained as valid here, although uncertainty of its distinctness remains. More material is needed to determine the extent of intraspecific variation within this group of hydroids, and whether a single variable species is represented. Gonothecae were present in Nutting's type of *A. distans*.

A character apparently overlooked in earlier descriptions of *Nemertesia nigra*, but noted in material examined here, is a pronounced thickening of the perisarc over the inner 2/3–3/4 or so of the hydrothecae, especially in older ones. The hydrothecal wall then thins abruptly and remains slender the rest of the way to the rim. When viewed laterally, the hydrotheca is marked by a faint line at the point of transition between thick and thin perisarc. The species is also distinctive in colony form, having a polysiphonic, non-canaliculated, strongly geniculate hydrocaulus with alternate or mostly alternate branches that are branched a second and sometimes a third time, with branching sometimes appearing to be dichotomous. Hydrocladia are heteromerously segmented and arise from the secondary and tertiary branches. Gonothecae of this species have yet to be described.

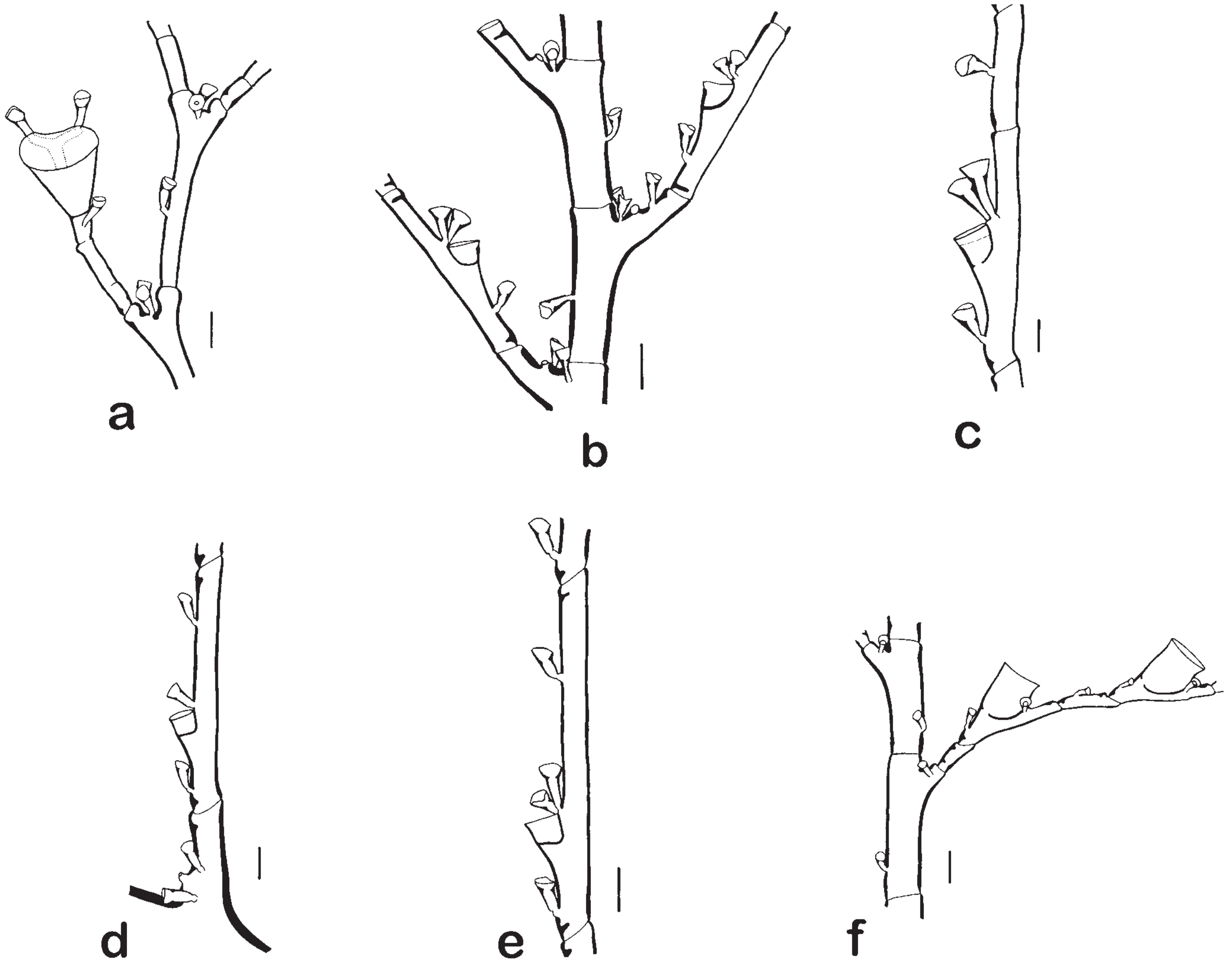

FIGURE 24. a, ***Monotheca margaretta*****:** part of a hydrocaulus with a hydrocladium and hydrotheca, Florida Keys, Bahia Honda Channel, ROMIZ B4397. Scale equals 0.05 mm. **b,** ***Nemertesia nigra*****:** part of hydrocaulus and proximal ends of hydrocladia, Southwest Florida Shelf, ROMIZ B2138. Scale equals 0.1 mm. **c,** ***Nemertesia nigra*****:** part of a hydrocladium with a hydrotheca and nematothecae, Southwest Florida Shelf, ROMIZ B2138. Scale equals 0.05 mm. **d,** ***Nemertesia simplex*****:** apophysis of hydrocaulus and proximal end of a hydrocladium, Southwest Florida Shelf, ROMIZ B2113. Scale equals 0.1 mm. **e,** ***Nemertesia simplex*****:** part of a hydrocladium with a hydrotheca and nematothecae, Southwest Florida Shelf, ROMIZ B2113. Scale equals 0.1 mm. **f,** ***Plumularia floridana*****:** part of a hydrocaulus with proximal end of a hydrocladium and two hydrothecae, Fort Myers Beach, ROMIZ B4399. Scale equals 0.1 mm.

Nemertesia nigra is little-known, having been reported to date only from the southeastern Gulf of Mexico, and if the synonymy with *N. sinuosa* is correct from the southern Caribbean Sea. This is the first record of the species from Florida. Its known bathymetric range is from 42 m (Fraser 1947b, as *Antennopsis sinuosa*) to 373 m (Nutting 1900, as *Antennopsis longicorna*).

Reported distribution. ***Gulf coast of Florida.*** First record.

Elsewhere in western North Atlantic. Cuba: off Havana, 23°11'N, 82°19'W, 121 ftm (221 m) (Nutting 1900: 74, as *Antennopsis nigra*).—Cuba: off Havana, 23°11'N, 82°20'W, 204 ftm (373 m) (Nutting 1900: 74, as *Antennopsis longicorna*).—Aruba: 8 miles (13 km) southwest of San Nicolaas Bay, 23–24 ftm (42–44 m) (Fraser 1947b, as *Antennopsis sinuosa*).

Nemertesia simplex (Allman, 1877)

Figs. 24d, e

Antennularia simplex Allman, 1877: 34, pl. 21, figs. 1, 2.—Nutting, 1900: 70, pl. 9, fig. 5.

Type locality. USA: Florida, off Alligator Reef, 86 ftm (157 m) (Allman 1877: 34, as *Antennularia simplex*).

Material examined. Southwest Florida Shelf, outer shelf NW of the Dry Tortugas, 25°16.83'N, 83°57.35'W, 127 m, 03 August 1981, triangle dredge, one colony, with stems to 14 cm high, without gonophores, coll. Continental Shelf Associates, ROMIZ B2113.

Remarks. Allman (1877) briefly described this hydroid, as *Antennularia simplex*, from material collected off Alligator Reef, Florida. The gonosome of the species was not observed by him, but the trophosome was said to be much like that of *A. ramosa* Lamarck, 1816. Nutting (1900) provided a second account of the species based on additional specimens, and described its gonosome from fertile material. *Antennularia* Lamarck, 1816 is now recognized as a junior synonym of *Nemertesia* Lamouroux, 1812, with the binomen *N. simplex* first being adopted for this species by Bedot (1912: 325).

Ramil & Vervoort (2006) provided a table of characters distinguishing this species from others in the genus, including the morphologically similar *N. ramosa*. *Nemertesia simplex* differs from that congener in having (1) hydrocauli that are monosiphonic and unbranched or slightly branched rather than polysiphonic and much branched, and (2) hydrothecal margins that usually slope at an oblique angle to the hydrocladial axis instead of being perpendicular to it (Calder 2013: 37).

Nemertesia simplex has been reported only a few times, all from the mid- to outer continental shelf and upper continental slope of eastern North America. However, the species may not actually be especially rare. In addition to its type locality in the Straits of Florida (Allman 1877, as *Antennularia simplex*, 157 m), it has been reported southwards to Cuba (Nutting 1900, as *A. simplex*, 368 m) and northwards off the Atlantic coast of the United States to Florida (Calder 2013, 65–110 m), to Georgia and South Carolina (Wenner *et al*. 1984, 32-69 m), to North Carolina (Nutting 1900, as *A. simplex*, 88–219 m) and to Virginia (Nutting 1900, as *A. simplex*, 128–682 m). It is reported here from the Southwest Florida Shelf northwest of the Dry Tortugas (127 m). In their study of hard-bottom habitats off South Carolina and Georgia, Wenner *et al*. (1984) found *N. simplex* at both of their stations on the outer shelf (OS01, OS06) all four seasons of the year, but at one of two stations on the mid-shelf (MS06) only in autumn. Depths at the latter station (32–36 m) likely approach the upper bathymetric limit of the species. Hydroids of *N. simplex* were absent in samples from a second mid-shelf station (MS02, 23–29 m), and from both inner shelf stations (IS01, 17–18 m; IS02, 17–22 m).

Reported distribution. ***Gulf coast of Florida.*** Florida Keys, off Alligator Reef, 86 ftm (157 m) (Allman 1877: 34, as *Antennularia simplex*).—Pourtalès Plateau, 70–80 ftm (128–146 m) (Nutting 1900: 70, as *Antennularia simplex*).

Elsewhere in western North Atlantic. USA: Virginia, off Cape Charles, 37°08'N, 74°36'W, 70 ftm (128 m) + off Cape Henry, 36°41'N, 74°39'W, 373 ftm (682 m) (Nutting 1900: 70, as *Antennularia simplex*).—USA: North Carolina, off Cape Hatteras, 35°13'N, 75°05'W, 48 ftm (88 m) + 35°02'N, 75°12'W, 120 ftm (219 m) (Nutting 1900: 70, as *Antennularia simplex*).—Cuba: off Havana, 23°11'N, 82°20'W, 201 ftm (368 m) (Nutting 1900: 70, as *Antennularia simplex*).—USA: South Carolina, middle (32–36 m) and outer (46–69 m) continental shelf + Georgia, outer (59–67 m) continental shelf (Wenner *et al*. 1984: 21, 40).—USA: Florida, Hoskin Reef off Vero Beach, 27°41.4'N, 79°59.1'W, 65 m (Calder 2013: 36).—USA: Florida, off Sebastian Inlet, 27°47.2'N, 79°57.2'W, 110–99 m (Calder 2013: 36).

Genus *Plumularia* Lamarck, 1816

Plumularia floridana Nutting, 1900

Fig. 24f

Plumularia floridana Nutting, 1900: 59, pl. 2, figs. 4, 5.—Shier 1965: 61, pl. 33.
Plumularia florida.—Wallace 1909: 137 [incorrect subsequent spelling].

Type locality. USA: Florida, "two miles (3.2 km) west of Cape Romano..." (Nutting 1900: 59).

Material examined. Fort Myers Beach, on stranded *Idiellana pristis*, 01 March 2013, three colonies or colony fragments, up to 1 cm high, without gonophores, coll. D. Calder, ROMIZ B4399.

Remarks. *Plumularia floridana* Nutting, 1900 was originally described from the vicinity of Cape Romano, on the southwest coast of Florida. It is a relatively well-known species in warm-temperate to tropical waters of the western Atlantic, with an inshore range extending from southern Massachusetts (Fraser 1944) to Brazil (Oliveira *et al*. 2016). It has also been reported in offshore waters along the eastern United States on pelagic *Sargassum* in the Gulf Stream (Fraser 1944).

Hydroids of *P. floridana* seem quite distinctive. Colonies are small (usually <2 cm high), with relatively large, nearly cylindrical hydrothecae that are free from the hydrocladia for 1/3 or more of their length. Even more distinctive is the gonosome, with gonothecae that are small, thin, filmy, and oval to nearly round. These structures collapse once the gonothecal contents are released.

While *P. floridana* has been found in open ocean environments such as the tops of Challenger and Plantagenet banks off Bermuda (Calder 2000), it has been reported most often from nearshore environments. In coastal South Carolina colonies are widespread across the state, occurring from euhaline waters (>30‰) to about the 25‰ isohaline upestuary (Calder 1976, 1983; Calder & Hester 1978). As for seasonality in the same region, active colonies were found from mid-March through early January, over a temperature range from 10–32° C (Calder 1990). Its reported bathymetric range extends from the surface, on pelagic *Sargassum* (Fraser 1944), to a depth of at least 73 m (Calder 1997).

Plumularia floridana is thought to be circumglobal in warm-temperate and tropical waters (Ansín Agís *et al.* 2001; Calder 2013), although confirmation is needed. More information on the species is given in Migotto (1996), Calder (1997), and Ansín Agís *et al.* (2001).

Reported distribution. ***Gulf coast of Florida.*** SW Florida shelf, 2 miles (3.2 km) west of Cape Romano (Nutting 1900: 59).—Dry Tortugas (Wallace 1909: 137, as *Plumularia florida*).—Cape San Blas area (Shier 1965: 61).

Elsewhere in western North Atlantic. USA: North Carolina, off Bogue Bank, on floating *Sargassum* (Fraser 1912b: 381).—USA: North Carolina, 100 miles (161 km) east of Cape Hatteras, on *Sargassum* (Fraser 1943: 96).—USA: New Jersey, continental slope east of the Jersey shore, 39°05’30”N, 70°44’30”W, 1525 ftm (2789 m) + 38°59’N, 70°07’W, 1522 ftm (2783 m); both almost certainly on sunken *Sargassum* (Fraser 1944: 345).—USA: Maryland, Gulf Stream off the Delmarva Peninsula, 38°25’N, 72°40’W, on pelagic *Sargassum* (Fraser 1944: 346).—USA: Massachusetts, off Nobska Light, 12.5 ftm (23 m) (Fraser 1944: 346).—USA: Louisiana, Grand Isle, on *Sargassum* (Fraser 1944: 346; Behre 1950: 7).—USA: Texas, Galveston, on *Sargassum* (Defenbaugh & Hopkins 1973: 112).—USA: South Carolina, estuaries, widespread, 2–20 m (Calder & Hester 1978: 91; Calder 1983: 20).—Belize: Carrie Bow Cay (Spracklin 1982: 246, as *Plumularia* sp.).—Colombia: Cartagena, Punta Gigante & Playa Blanca (Flórez González 1983: 121, as *Plumularia* sp.).—USA: South Carolina, North Inlet area, Town Creek and tributaries + Folly River area, Oak Island, oyster reef + Beaufort River, oyster reefs (Fox & Ruppert 1985: 61, 152, 211).—USA: South Carolina and Georgia, inner continental shelf, on artificial reefs (Wendt *et al*. 1989: 1119).—Bermuda: Hungry Bay, 1 m + Whalebone Bay, on *Thalassia*, 1 m + 2 km SE of Castle Roads, 73 m + 2 km off Natural Arches Beach, 70 m (Calder 1997: 15).—Bermuda: Challenger Bank + Argus (=Plantagenet) Bank (Calder 2000: 1133).—Panama: Bocas del Toro area, Hospital Point, 09°20’01.9”N, 82°13’07.7”W, 2–13 m + Boca del Drago, 09°25’36.3”N, 82°19’30.1”W, 1–3 m + Crawl Cay, 09°15.261’N, 82°07.787’W, 2–4 m (Calder & Kirkendale 2005: 482).—French Lesser Antilles: Les Saintes, 15°52’25”N, 61°34’15”W, on *Thalassia* (Galea 2008: 46).—French Lesser Antilles: Guadeloupe, Grande-Terre, 16°21.269’N, 61°34.193’W, 10–15 m (Galea 2010: 4).—Cuba: Golfo de Batabanó, Punta Francés, Boya El Límite (Castellanos-Iglesias *et al*. 2011: 24).—USA: Florida, off Vero Beach, 27°41.2’N, 80°14.5’W, 17 m (Calder 2013: 37).—French Lesser Antilles: Martinique (Galea 2013: 50).—Caribbean Sea (Wedler 2017b: 160, figs. 199A–C, 200).—Mexico: Alacranes Reef, on algae, sponges, seagrass, soft corals (Mendoza-Becerril *et al*. 2018b: 131).—Cuba: Havana, coral reef system west of the city (Castellanos *et al*. 2018: Supplementary Table S2).—Panama: Bocas del Toro area, vicinity of Manuguar Cay (Miglietta *et al*. 2018b: 108).

Acknowledgements

Hydroids in this collection from the Southwest Florida Shelf were sent to the Royal Ontario Museum (ROM) for identification by staff of Continental Shelf Associates, with particular thanks being extended to Neal W. Phillips, David A. Gettleson, and Keith D. Spring. Other material, from the Florida Keys, was provided by Karen DeMaria.

Maureen Zubowski provided collections-related assistance at the ROM. I am grateful to Henry Choong and Hugh MacIntosh of the Royal British Columbia Museum for arranging a loan of paratype material of *Clytia laxa*, and to Dorte Janussen, Saskia Dimter, and Angelika Brandt of the Senckenberg Forschungsinstitut und Naturmuseum for a loan of specimens of *Clytia colombiana*. Assistance with taxonomic questions were provided by Horia R. Galea and Eberhard Wedler, and PDF copies of some inaccessible papers were provided by Susel Castellanos-Iglesias, Horia R. Galea, Priscila A. Grohmann, and Jeanette E. Watson. Sincere thanks are extended to María A. Mendoza-Becerril and Jeanette W. Watson for constructive reviews of an especially burdensome manuscript, and to Bastian Bentlage for seeing it through the editorial process. Financial support for parts of the project was provided by the Natural Sciences and Engineering Research Council of Canada, the United States National Science Foundation program Partnerships for Enhancing Expertise in Taxonomy (PEET), and the Royal Ontario Museum.

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