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ZOOTAXA



Some shallow-water hydroids (Cnidaria: Hydrozoa) from the central east coast of Florida, USA

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Table of contents

Abstract			
Introduction			
Material and methods			
Systematic account			
ORDER ANTHOATHECATA Cornelius, 1992			
SUBORDER CAPITATA Kühn, 1913			
Family Pennariidae McCrady, 1859			
Pennaria disticha Goldfuss, 1820			
Family Cladocorynidae Allman, 1872.			
Cladocoryne floccosa Rotch, 1871			
Velella velella (Linnaeus, 1758)			
Family Zancleidae Russell, 1953			
Zanclea alba (Meyen, 1834)			
Family Solanderiidae Marshall, 1892			
Solanderia gracilis Duchassaing & Michelin, 1846			
SUBORDER FILIFERA Kühn, 1913			
Family Oceaniidae Eschscholtz, 1829.			
Turritopsis fascicularis Fraser, 1943			
Family Bougainvilliidae Lütken, 1850			
Parawrightia robusta Warren, 1907			
Bimeria vestita Wright, 1859			
Family Eudendriidae L. Agassiz, 1862			
Eudendrium carneum Clarke, 1882			
ORDER LEPTOTHECATA Cornelius, 1992			
SUBORDER CONICA Broch, 1910.			
Family Lovenellidae Russell, 1953			
Lovenella grandis Nutting, 1901.			
Family Phialellidae Russell, 1953			
Plicatotheca anitae Calder & Vervoort, 1986			
Family Lafoeidae A. Agassiz, 1865			
Lafoea intorta sp. nov.			
Family Hebellidae Fraser, 1912b.			
Hebella venusta (Allman, 1877)			
Hebella sp.			
Hebellopsis communis Calder, 1991a			
Hebellopsis gigas (Pieper, 1884)			
Hebellopsis scandens (Bale, 1888)			
Family Zygophylacidae Quelch, 1885.			
Cryptolaria pectinata (Allman, 1888)			
Family Haleciidae Hincks, 1868			
Halecium calderi Galea, 2010			
Halecium tenellum Hincks, 1861b			
Family Thyroscyphidae Stechow, 1920.	22		
Symmetroscyphus intermedius (Congdon, 1907)	22		
Thyroscyphus marginatus (Allman, 1877)	23		
Thyroscyphus ramosus Allman, 1877	24		
Family Sertulariidae Lamouroux, 1812.	24		
Diphasia digitalis (Busk, 1852)	24		
Dynamena crisioides Lamouroux, 1824	26		
Dynamena dalmasi (Versluys, 1899)	26		
Dynamena disticha (Bosc, 1802)	27		
Pasya quadridentata (Ellis & Solander, 1786)	27		
Salacia desmoides (Torrey, 1902)			
Sertularella areyi Nutting, 1904	28		
Sertularella conica Allman, 1877	29		
Sertularella unituba Calder, 1991a	30		
Tridentata distans (Lamouroux, 1816)			
Tridentata loculosa (Busk, 1852)			
Tridentata marginata (Kirchenpauer, 1864)			
Tridentata turbinata (Lamouroux, 1816)			
Family Syntheciidae Marktanner-Turneretscher, 1890	34		

Hincksella brevitheca Galea, 2009
Synthecium tubithecum (Allman, 1877)
Family Plumulariidae McCrady, 1859
Dentitheca dendritica (Nutting, 1900)
Nemertesia simplex (Allman, 1877)
Plumularia floridana Nutting, 1900
Plumularia setacea (Linnaeus, 1758)
Plumularia strictocarpa Pictet, 1893
Family Halopterididae Millard, 1962
Antennella gracilis Allman, 1877
<i>Antennella incerta</i> Galea, 2010
Halopteris alternata (Nutting, 1900)
Halopteris carinata Allman, 1877
Halopteris clarkei (Nutting, 1900)
Halopteris diaphana (Heller, 1868)
Monostaechas quadridens (McCrady, 1859) 44
Family Kirchenpaueriidae Stechow, 1921a
Ventromma halecioides (Alder, 1859)
Family Aglaopheniidae Marktanner-Turneretscher, 1890
Aglaophenia dubia Nutting, 1900
Aglaophenia latecarinata Allman, 1877
Aglaophenia rhynchocarpa Allman, 1877 48
Aglaophenia trifida L. Agassiz, 1862 49
Gymnangium speciosum (Allman, 1877) 49
Macrorhynchia allmani (Nutting, 1900) 50
Macrorhynchia clarkei (Nutting, 1900)
Macrorhynchia philippina Kirchenpauer, 1872 52
SUBORDER PROBOSCOIDEA Broch, 1910
Family Campanulariidae Johnston, 1837
Subfamily Campanulariinae Johnston, 1837
Campanularia macroscypha Allman, 1877
Orthopyxis sargassicola (Nutting, 1915)
Subfamily Clytiinae Cockerell, 1911
Clytia elsaeoswaldae Stechow, 1914
<i>Clytia linearis</i> (Thornely, 1900) 55
Clytia noliformis (McCrady, 1859)
Clytia paulensis (Vanhöffen, 1910)
Subfamily Obeliinae Haeckel, 1879 57
Obelia geniculata (Linnaeus, 1758) 57
Obelia hyalina Clarke, 1879 58
Obelia oxydentata Stechow, 1914
Acknowledgements
References

Abstract

This paper gives a systematic account of 67 species, referable to 22 families and 40 genera, identified in a small collection of hydroids from the central Atlantic coast of Florida between Melbourne and Palm Beach. The fauna mostly comprises an assemblage of tropical western Atlantic species ranging northwards along the southeastern coast of the United States. One new species, Lafoea intorta, is described. Applying Reversal of Precedence provisions in zoological nomenclature, the widely-used generic name Halopteris Allman, 1877 is designated as valid and as a nomen protectum, while its virtually unused senior synonym Halicornaria Hincks, 1865 (not Halicornaria Allman, 1874) is reduced to a nomen oblitum. The genus Pasya Stechow, 1922 is resurrected for the hydroid generally known as Dynamena quadridentata (Ellis & Solander, 1786). Laomedea tottoni Leloup, 1935 is shown to be a junior objective synonym of Clytia fragilis Congdon, 1907, which in turn is a junior subjective synonym of *Clytia linearis* (Thornely, 1900). Obelia oxydentata Stechow, 1914 is recognized as distinct from O. bidentata Clark, 1875. Hincksella brevitheca Galea, 2009, first described from Cuba, is reported for only the second time; records of the species are added here from Grand Cayman Island and the Caribbean coast of Panama as well as from the Atlantic coast of Florida. Also reported for the second time is Antennella incerta Galea, 2010, previously known only from Guadeloupe in the Caribbean Sea. The true Halopteris diaphana (Heller, 1868), known from the Mediterranean Sea and from Brazil, is reported for the first time from the western North Atlantic. Earlier records of the species in the region are based on misidentifications of H. alternata (Nutting, 1900). Male gonothecae of Halecium calderi Galea, 2010 are reported and illustrated for the first time.

Key words: Anthoathecata, Capitata, Carolinian Province, Filifera, Hydroidolina, Leptothecata, marine invertebrates, taxonomy, West Atlantic Tropical Region, zoological nomenclature

Introduction

Taxonomic investigations on hydroids of the Atlantic coast of the United States and Canada have concentrated for the most part on species of New England and the Maritime Provinces, as reflected in both an historical overview and in distribution records by Fraser (1944). More than 75 scientific publications provide information on the fauna of those northern waters (Calder 1975), beginning with a synopsis by Stimpson (1853) of species around Grand Manan Island at the mouth of the Bay of Fundy. By comparison, fewer than half that number have dealt with hydroids occurring south of Cape Hatteras, North Carolina (Calder 1983). One of the least studied areas along the entire eastern seaboard of North America is the central coast of Florida between Cape Canaveral and Palm Beach. Reports of species from inshore and nearshore waters in the area are few and scattered in publications such as those on fouling organisms (Nelson et al. 1994; Pfaller et al. 2008), on a description of a single new species (Thomas et al. 1995), on other invertebrate groups (Clark & Goetzfried 1976; Winston 1982, 2010), and in general identification guides (Humann 1992; Humann & DeLoach 2002). A small number of records from the central Florida coast exist in taxonomic studies on hydroids from Louisiana and Texas (Deevey 1950) and from areas in the Florida Straits and beyond in the Gulf of Mexico (Allman 1877; Bogle 1975). Several species from the region were also mentioned in worldwide accounts on capitate hydroids by Petersen (1990) and on the hydrozoan family Halopterididae by Schuchert (1997). To date, however, no comprehensive taxonomic study on hydroids of the central Florida Atlantic coast has been published. Better known is the fauna at the southern end of the state, including the Straits of Florida and the Dry Tortugas, as well as of the Bahamas to the east and the Gulf of Mexico to the west. Even the deep-sea fauna east of the Florida peninsula, with species recorded by Nutting (1900, 1904, 1915), Fraser (1943, 1944), Bogle (1975), and Henry et al. (2008), among others, is better characterized than that inhabiting the nearby shelf and shore.

The objective of this study was to provide a report on a collection of hydroids from inshore and shallow shelf waters (<120 m) along the central east coast of Florida, based largely on material at the Harbor Branch Oceanographic Institution (now the Harbor Branch Oceanographic Institute of Florida Atlantic University), Fort Pierce. The study area is important biogeographically as a zone of transition between the West Atlantic Tropical Region to the south and the warm-temperate Carolinian Region to the north (Briggs 1974). Some of the material examined here provided data for an earlier biogeographic study on hydroids of the western North Atlantic (Calder 1992), but identifications of species were not given in that paper. This work represents an initial step towards knowledge of the fauna; hydroids of the region are still little studied and poorly known.

Material and methods

Hydroids identified herein are mainly from collections originally held in the museum at the Harbor Branch Oceanographic Institution (HBOI), Fort Pierce, Florida. Many came from dives using *Johnson-Sea-Link* submersibles and from surveys along the east coast of Florida by R/V *Gosnold* in the 1970s. Original examination of collections at HBOI was undertaken 9–23 February 1991. Vouchers of each species, held in collections of the Invertebrate Zoology Section of the Department of Natural History, Royal Ontario Museum, were re-examined here. Materials held at HBOI were supplemented with new material collected from the study area during my visit to Florida in 1991, and again during a trip to Fort Pierce on 14 July 2012. Geographic limits of the current study area extend along the central part of the Atlantic coast of Florida from Melbourne (28°04'N) to Palm Beach (26°41'N), and from inshore waters out onto the continental shelf.

At present, a lack of homogeneity exists in the classification systems adopted for Hydrozoa. Classifications have been changing recently at an unprecedented rate, largely the result of molecular studies on species of this cnidarian class. While resulting taxonomic instability is disadvantageous, significant advances are being made in knowledge of phylogenetic relationships within the group. Rapid change can be expected to continue over the near term. The classification scheme employed here, admittedly an interim one, generally follows that of Schuchert (2012b) for Anthoathecata, and Cornelius (1995) and Calder (2012) for Leptothecata. Historic convention is followed in addressing anthoathecates before leptothecates, although that too may change (see Schuchert 2012b: 21–22).

A "Reported Distribution" section for each species discussed below includes putative worldwide and western Atlantic ranges, as well as records from the Atlantic coast of Florida, defined here as extending from the border between the states of Georgia and Florida at the mouth of the St. Marys River (30°42'30"N, 81°26'30"W) on the north to Key Largo (25°06'N, 80°26'W) on the south. Felder *et al.* (2009) have been followed in taking adjacent areas west of a line between Key Largo, Florida, and Punta Hicacos, Cuba (23°12'N, 81°08'W), to be within the Gulf of Mexico. Synonymy lists are restricted to original accounts of species, together with works providing primary records of species from the Atlantic coast of Florida, as defined above. All citations have been verified. The following abbreviations used in this work refer to the following:

MCZ	Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts, USA
ROMIZ	Invertebrate Zoology collections, Royal Ontario Museum, Toronto, Ontario, Canada
USNM	National Museum of Natural History, Smithsonian Institution, Washington, D.C., USA
ICZN	International Code of Zoological Nomenclature

Systematic account

PHYLUM CNIDARIA Verrill, 1865

SUBPHYLUM TESSERAZOA Salvini-Plawen, 1978 (MEDUSOZOA Petersen, 1979)

CLASS HYDROZOA Owen, 1843

SUBCLASS HYDROIDOLINA Collins, 2000

ORDER ANTHOATHECATA Cornelius, 1992

SUBORDER CAPITATA Kühn, 1913

Family Pennariidae McCrady, 1859

Pennaria disticha Goldfuss, 1820

Fig. 1a

Pennaria disticha Goldfuss, 1820: 89. *Pennaria tiarella.*—Fraser, 1933: 261; 1944: 86.—Weiss, 1947: 57; 1948: 158.—Winston, 1982: 164. *Pennaria* sp.—Cummings, 1994: 1208. *Halocordyle disticha.*—Jones, 2002: 218.

Type locality. Italy: Gulf of Naples. Goldfuss (1820) gave the provenance of this species simply as "Im Mittelmeer," but his record was based on Cavolini's (1785: 134) "*Sertolara pennara*" [not *Sertularia pennaria* Linnaeus, 1758] from the Gulf of Naples area.

Voucher material. Fort Pierce Inlet, north jetty, north side, 27°28'24.2"N, 80°17'20.3"W, 0.1 m, 15.ii.1991, 20° C, collected manually, one colony, 5 cm high, without gonophores, coll. D.R. Calder, ROMIZ B1118.

Remarks. *Globiceps tiarella* Ayres, 1854 (type locality: Sag Harbor, Long Island, New York), Eucoryne elegans Leidy, 1855 (type locality: Point Judith, Rhode Island), *Pennaria gibbosa* L. Agassiz, 1860 (type locality: Key West, Florida; see A. Agassiz 1965) and *P. inornata* Brooks, 1883 (type locality: Fort Macon, North Carolina) are generally considered to be conspecific with *P. disticha* Goldfuss, 1820 from the Mediterranean (e.g. Calder 1988), although molecular work is needed to confirm the supposed synonymy. A large, familiar, and distinctive hydroid, *P. disticha* has often been used in experimental studies (Schuchert 2006). Contact with colonies of this species may result in a relatively painful sting.

Pennaria disticha, prevalent in tropical and warm-temperate areas of the western Atlantic (Fraser 1944; Calder 1988), may become dormant at water temperatures between $15-20^{\circ}$ C (Calder 1990). Colonies from Fort Pierce Inlet, collected during winter at 20° C, were active but lacked gonophores. A euryhaline species, it extends from oceanic salinities to about the 20% isohaline in estuaries (Calder 1976). The form of the colony is strongly influenced by environmental conditions; those from areas exposed to waves are typically small and compact while those from sheltered areas tend to be larger and more slender (Calder 1988). The life cycle includes a short-lived medusoid stage that may or may not be released from the hydroid (Hargitt 1900; Brinckmann-Voss 1970). In the western Atlantic, *P. disticha* has been reported as far north as the coast of Maine (Mayer 1910), where it would be active only during summer. The hydroid is restricted bathymetrically to shallow waters (0–29 m) (Fraser 1944).

Descriptions and recent discussion of the species have been provided by Schuchert (2006) and Calder (2010).

Reported distribution. Atlantic coast of Florida. Talbot Island, from stomach of a Black Scoter (Fraser 1933, 1944, as *Pennaria tiarella*, from "Tablot" Island).—Biscayne Bay (Weiss 1947, 1948, as *Pennaria tiarella*).— Sebastian Inlet (Winston 1982, as *Pennaria tiarella*).—Boca Raton (Cummings 1994, as *Pennaria* sp.).—Biscayne Bay (Jones 2002, as *Halocordyle disticha*).

Western Atlantic. Maine (Mayer 1910, as *Pennaria tiarella*) to Brazil (Oliveira *et al.* submitted), including Bermuda (Calder 1988), the Gulf of Mexico (Calder & Cairns 2009), and the Caribbean Sea (Galea 2008).

Elsewhere. Thought to be circumglobal in tropical and warm-temperate waters (Calder 2010).

Family Cladocorynidae Allman, 1872

Cladocoryne floccosa Rotch, 1871 Fig. 1b

Cladocoryne floccosa Rotch, 1871: 228.

Type locality. UK: Guernsey, Herm, on stones at low tide (Rotch 1871).

Voucher material. Fort Pierce Inlet, north jetty, north side, 27°28'24.2"N, 80°17'20.3"W, 0.1 m, 15.ii.1991, 20° C, collected manually, one stolonal colony, up to 5 mm high, without gonophores, coll. D.R. Calder, ROMIZ B1114.

Remarks. The earliest account of this species, as *Hydra corynaria*, was in an obscure paper by Bosc (1797). The French naturalist discovered the species on pelagic *Sargassum* during a crossing from Bordeaux, France, to Charleston, South Carolina, but the name he applied to it was never adopted. The species has become widely

known instead as *Cladocoryne floccosa* Rotch, 1871. In the interests of nomenclatural stability, the name *C. floccosa* was assigned precedence over its virtually unused senior subjective synonym *H. corynaria* by Calder *et al.* (2003). Under Article 23.9 of the *International Code of Zoological Nomenclature* (ICZN) (International Commission on Zoological Nomenclature 1999), the former becomes a *nomen protectum* and the latter a *nomen oblitum*.

Cladocoryne floccosa has been reported several times from the Caribbean region (e.g., Fraser 1947, as *C. pelagica* Allman, 1876; Wedler & Larson 1986; Galea 2008). Fraser's (1944) record of it from 1544 fathoms (2824 m) at a location south of Nantucket, Massachusetts (as *C. pelagica*) is anomalous and the species must certainly have been growing on floating (or sunken) *Sargassum*, as he speculated. According to Schuchert (2006, 2012b), its bathymetric range is 0–50 m.

Reported distribution. Atlantic coast of Florida. First record.

Western Atlantic. Vineyard Sound, Massachusetts, on floating *Sargassum* (Hargitt 1909, as *C. floccosa* var. *sargassensis*) to Brazil (Migotto 1996), and including the Caribbean Sea (Galea 2008).

Elsewhere. Thought to be circumglobal in tropical and warm-temperate waters (Schuchert 2006, 2012b).

Family Porpitidae Goldfuss, 1818

Velella velella (Linnaeus, 1758) Fig. 1c

Medusa velella Linnaeus, 1758: 660. *Velella mutica.*—L. Agassiz, 1862: 366.—A. Agassiz, 1865: 217.—Fewkes, 1886: 974. *Velella velella.*—Bayer, 1963: 454, figs. 5–7.

Type locality. Mediterranean Sea (Schuchert 2010).

Voucher material. Beach north of Jupiter Inlet, 26°56'45"N, 80°04'16"W, stranded on shore, 20.ii.1991, collected manually, one young colony, left-sailing form, 5 mm long x 2 mm wide, without gonophores, coll. D.R. Calder, ROMIZ B1113.

Remarks. Strandings of the pleustonic hydrozoan *Velella velella* (Linnaeus, 1758) on beaches of south Florida vary from one year to another (Bayer 1963). Bayer noted that strong easterly winds during winter tend to blow this species and the related *Porpita porpita* (Linnaeus, 1758) ashore from the Florida Current just off the coast.

The specimen from the beach at Jupiter Inlet examined here was a left-sailing form, as defined by Edwards (1966). Of more than 2500 specimens from the Tortugas studied by A. Agassiz (1883), all were likewise of the "left-handed" (left-sailing) form, with the sail extending from NW to SE along the longitudinal axis of the float. Distributions of left and right-sailing forms of the species in the Atlantic Ocean and Mediterranean Sea were reviewed by Edwards (1966). Sailing characteristics of the species were investigated in a wind tunnel by Francis (1991).

Early on considered siphonophores and later as "chondrophores," both *V. velella* and *P. porpita* are now classified amongst the hydroids, as anthoathecates (Calder 1988, 2010; Schuchert 2010, 2012a, b). Sometimes reported from Florida as *Velella mutica* Lamarck, 1801, that binomen is considered a junior synonym of *V. velella* (Calder 1988; Schuchert 2010).

Reported distribution. Atlantic coast of Florida. "Coast of Florida" (L. Agassiz 1862, as *Velella mutica*).— Cape Florida (A. Agassiz 1865, as *V. mutica*).—Gulf Stream; Straits of Florida (Fewkes 1886, as *V. mutica*).— Miami area (Bayer 1963).

Western Atlantic. New England (A. Agassiz 1883, as *Velella mutica*) to Argentina (Oliveira *et al.* submitted), including Bermuda (Calder 1988), the Gulf of Mexico (Calder & Cairns 2009), and the Caribbean Sea (Fewkes 1885, as *V. mutica*).

Elsewhere. Circumglobal in tropical and temperate waters (Calder 2010; Schuchert 2012b).



FIGURE 1. a, *Pennaria disticha*: part of hydrocaulus with annulated pedicel and juvenile hydranth, ROMIZ B1118; scale equals 0.5 mm. **b**, *Cladocoryne floccosa*: stem and hydranth, ROMIZ B1114, scale equals 0.5 mm. **c**, *Velella velella*: juvenile, left-sailing form, ROMIZ B1113, scale equals 1 mm. **d**, *Zanclea alba*: pedicel and hydranth, ROMIZ B3961, scale equals 0.25 mm. **e**, *Solanderia gracilis*: tip of branch with three hydranths, ROMIZ B3962, scale equals 0.25 mm. **f**, *Turritopsis fascicularis*: pedicel and hydranth with medusa bud, ROMIZ B1106, scale equals 0.25 mm. **g**, *Parawrightia robusta*: part of pedicel and hydranth, ROMIZ B1110, scale equals 0.25 mm. **h**, *Bimeria vestita*: pedicel and hydranth, ROMIZ B1116, scale equals 0.25 mm. **i**, *Eudendrium carneum*: part of hydrocaulus with pedicel and hydranth, ROMIZ B3960, scale equals 0.25 mm.

Family Zancleidae Russell, 1953

Zanclea alba (Meyen, 1834)

Fig. 1d

Acrochordium album Meyen, 1834: 165, pl. 28, fig. 8.

Type locality. North Atlantic Ocean: near the Azores, on Fucus natans (=Sargassum natans) (Meyen 1834).

Voucher material. Fort Pierce Inlet State Park, 27°28'29.5"N, 80°17'25.8"W, on stranded *Sargassum fluitans*, 14.vii.2012, 28° C, 35‰, collected manually, two colonies, with medusa buds, coll. D.R. Calder, ROMIZ B3961.

Remarks. The generic name Zanclea Gegenbaur, 1856, although predated by Acrochordium Meyen, 1834 and *Mnestra* Krohn, 1853, has been conserved by the International Commission on Zoological Nomenclature (1994). A genus once erroneously thought monospecific (Calder 1988), 14 nominal species have been assigned to it by Bouillon *et al.* (2006) and 34 by Schuchert (2012a). One of these, *Z. alba* (Meyen, 1834), is common on the holopelagic gulfweeds *Sargassum natans* and especially *S. fluitans* in the North Atlantic (Calder 1995), and is recorded here from the study area. Colonies of *Z. alba* usually occur within inner and older parts of the algal thallus (e.g., on "stems"), and especially on colonies of the cheilostome bryozoan *Membranipora tuberculata*. That microhabitat on gulfweed may offer increased shelter and reduced risk of desiccation. Species of *Zanclea* tend to be substrate specialists, occurring in association with bryozoans, bivalves, or corals (e.g., Boero *et al.* 2000; Fontana *et al.* 2012).

The binomen Zanclea alba is still relatively obscure, having been largely overlooked until the late 20th century (Calder 1988). The following original reports of hydroids from *Sargassum* are likely to have been based on this species: *Clava amphorata* Bosc, 1797 from the North Atlantic (Bosc 1797: 9); *Zanclea alba* (Meyen, 1834) from Bermuda (Calder 1988, 1995) and Belize (Calder 1991b, c); *Zanclea costata* Gegenbaur, 1856 from the Tortugas (Mayer 1910: 88), Texas (Deevey 1950: 349; Defenbaugh & Hopkins 1973: 47), Colombia (Fraser 1947: 3), and Belize (Spracklin 1982: 240); *Gemmaria costata* (Gegenbaur, 1856) from North Carolina (Fraser 1912b: 346) and the Atlantic Ocean off both Nantucket and Cape Hatteras (Fraser 1943: 86); *Zanclea gemmosa* McCrady, 1859 from off Martha's Vineyard (Fraser 1944: 44); *Gemmaria gemmosa* (McCrady, 1859) from the Tortugas (Mayer 1900: 35) and from Woods Hole (Hargitt 1908: 105); *Zanclea* sp. from Puerto Rico (Wedler & Larson 1986); *Gemmaria* from the western North Atlantic (Burkenroad, in Parr 1939: 24). So too is Murbach's (1899) mistaken report of *Corynitis agassizii* McCrady, 1859 from pelagic *Sargassum* in Vineyard Sound. Hargitt (1908) correctly determined that Murbach's hydroid was a species of *Gemmaria* McCrady, 1859 (=*Zanclea*) and not *C. agassizii* (=*Sphaerocoryne agassizii*).

The life cycle of Zanclea alba includes a medusa having two well-developed tentacles, with cnidophores, at liberation (Calder 1988). At that stage, gonads were undeveloped. Medusae have not been reared further in the laboratory, and hydroids of Z. alba have not been clearly linked as yet to any known adult medusa. While such medusae must exist in the Sargasso Sea, given the abundance and pelagic substrate of the hydroid, no medusoid species of Zanclea were reported from the oceanic realm of the North Atlantic by Kramp (1959, 1961). Medusae described as Zanclea costata from the plankton at the Tortugas by Mayer (1910) may be Z. alba, but they could also be from hydroids of another species of Zanclea in the region.

The nematocyst complement of this hydroid comprises stenoteles of two size classes, while that of its juvenile medusa includes stenoteles and macrobasic euryteles (Calder 1988; Galea 2008).

Reported distribution. Atlantic coast of Florida. First record.

Western Atlantic. New England, on floating *Sargassum* (Hargitt 1908, as *Gemmaria gemmosa*), to the Caribbean Sea (Calder 1991c), including Bermuda (Calder 1988) and the Gulf of Mexico (Defenbaugh & Hopkins 1973, as *Zanclea costata*).

Elsewhere. Eastern Atlantic, near the Azores (Meyen 1834).

Family Solanderiidae Marshall, 1892

Solanderia gracilis Duchassaing & Michelin, 1846

Fig. 1e

Solanderia gracilis Duchassaing & Michelin, 1846: 219.

Type locality. Caribbean Sea: Guadeloupe (Duchassaing & Michelin 1846).

Voucher material. Off Jupiter Inlet, 26°57.1'N, 79°59.6'W, 56 m, 06.v.1976, *Johnson-Sea-Link*, JSL 2043, diver lockout, one young colony, 1.5 cm high, without gonophores, coll. D. Girardin, ROMIZ B3962.

Remarks. Records of *Solanderia gracilis* Duchassaing & Michelin, 1846, endemic to the western Atlantic Ocean and the only species of the genus known to occur in the region (Bouillon *et al.* 1992), have been summarized in Larson (1987). Most accounts of this warm-water hydroid have been from the Caribbean Sea, although it has also been found off North Carolina. The latter record was based on a specimen collected from the continental shelf off Cape Fear (33°31'N, 77°25'W, 29 m, 18° C, ROMIZ B489), an area influenced by the warm Gulf Stream.

The hydroid from Florida examined here constitutes the second record of this shallow-water species from the east coast of the United States, and extends its known depth range to 56 m. Now preserved in 70% ethanol, the colony is small, very young, and straw-coloured rather than purplish to brownish-red as in larger, older colonies.

A detailed account of *Solanderia gracilis*, based largely on material from St. John in the Virgin Islands, was given by Vervoort (1962). Absence of *Solanderia gracilis* from mainland areas and larger islands in the Caribbean Sea was attributed by Larson (1987) to sedimentation, a factor he considered important in limiting its distribution.

Reported distribution. Atlantic coast of Florida. First record.

Elsewhere. North Carolina (Larson 1987) to Bahia, Brazil (Bouillon *et al.* 1992), including the Caribbean Sea (Larson 1987).

SUBORDER FILIFERA Kühn, 1913

Family Oceaniidae Eschscholtz, 1829

Turritopsis fascicularis Fraser, 1943 Fig. 1f

Turritopsis fascicularis Fraser, 1943: 76, pl. 15, figs. 1a, b.

Type locality. USA: Florida, off Alligator Reef, 24°41'45"N, 80°27'45"W, 118 fathoms (216 m) (Fraser 1943: 76).
Voucher material. Off Vero Beach, 27°41.2'N, 80°14.5'W, 17 m, 13.ii.1974, small biological dredge, R/V *Gosnold* Station 220/226, one erect and fascicled colony, in poor condition, 1.9 cm high, without gonophores, ROMIZ B1075.—Off St. Lucie Inlet, 27°10.8'N, 80°00.8'W, 44 m, 19.iv.1977, *Johnson-Sea-Link*, JSL 2187, diver lockout, one colony, up to 1.1 cm high, with medusa buds, coll. L. Edmiston, ROMIZ B1106.

Remarks. Earlier, I regarded *Turritopsis fascicularis* Fraser, 1943 as conspecific with *T. dohrnii* (Weismann, 1883) from Europe (Calder 1988: 10). In the absence of information on life histories and relationships between European and American populations, however, they are maintained here as distinct species. Unlike *T. nutricula* McCrady, 1857, colonies of both nominal species are erect, polysiphonic, and branched.

Colonies identified as *Turritopsis fascicularis* from deep waters off Bermuda (Calder 1998: 10) have fixed gonophores rather than free medusae, as originally described in this species by Fraser (1943), and may represent an undescribed species.

Fraser's (1943) type material of *Turritopsis fascicularis* from the Florida Keys was collected within the Gulf of Mexico, as defined above.

Reported distribution. Atlantic coast of Florida. First record.

Western Atlantic. South Atlantic Bight (Wendt et al. 1989) to the Caribbean Sea (Calder 1991b).

Family Bougainvilliidae Lütken, 1850

Parawrightia robusta Warren, 1907

Fig. 1g

Parawrightia robusta Warren, 1907: 187, text-figs. 1, 2B, 3A,B, 4A,B, pls. 33, 34.—Jones, 2002: 217.

Type locality. South Africa: Natal, "...Park Rynie...Isipingo and Scottsburg" (Warren 1907).

Voucher material. Fort Pierce Inlet, north jetty, north side, 27°28'24.2"N, 80°17'20.3"W, low water, 20.ii.1991, collected manually, one colony, on *Thyroscyphus ramosus*, up to 5 mm high, without gonophores, coll. D.R. Calder, ROMIZ B1110.

Remarks. Records of *Parawrightia robusta* Warren, 1907 indicate that it is a shallow-water hydroid, occurring from low-water to about 12 m (Grohmann *et al.* 2003). It has been found on substrates such as seaweeds, sponges, and other hydroids. Although reported infrequently, its occurrence on the east coast of Florida is not surprising given its known distribution from Bermuda to Brazil in the western Atlantic (see below). Justification for recognition of the genus *Parawrightia* Warren, 1907 has been given earlier (Calder 1988).

Reported distribution. Atlantic coast of Florida. Biscayne Bay (Jones 2002).

Western Atlantic. Florida to Brazil (Grohmann *et al.* 2003), including Bermuda (Calder 1988) and the Caribbean Sea (Wedler & Larson 1986, as *Garveia robusta*; Calder & Kirkendale 2005).

Elsewhere. Indian Ocean (Millard 1975, as Rhizorhagium robustum).

Bimeria vestita Wright, 1859

Fig. 1h

Bimeria vestita Wright, 1859:109, pl. 8, fig. 4.

Type locality. UK: Scotland, Firth of Forth, North Queensferry and Inch Garvie (Inchgarvie) (Wright 1859).

Voucher material. Fort Pierce Inlet, north jetty, north side, 27°28'24.2"N, 80°17'20.3"W, low water, 15.ii.1991, 20° C, collected manually, four colonies, up to 8 mm high, without gonophores, coll. D.R. Calder, ROMIZ B1116. Fort Pierce Inlet, north jetty, north side, 27°28'24.2"N, 80°17'20.3"W, 0.1 m, on *Pennaria disticha*, 15.ii.1991, 20° C, collected manually, one colony, 4 mm high, without gonophores, coll. D.R. Calder, ROMIZ B1118.

Remarks. *Bimeria humilis* Allman, 1877 (type locality: Tortugas, Florida) has been regarded as conspecific with *B. vestita* Wright, 1859 from Scotland (Calder 1988; Marques *et al.* 2000; Schuchert 2007). Synonymy of the two names needs to be confirmed given the widely-separated provenances of the populations they denote and the significant hydrographic differences between them. Recent accounts of hydroids attributed to the species have been given by Genzano & Zamponi (1999), Marques *et al.* (2000), Schuchert (2007), and Calder (2010).

Reported distribution. Atlantic coast of Florida. First record.

Western Atlantic. Continental shelf of South Carolina and Georgia (Wenner *et al.* 1984, as *Bimeria humilis*) to Argentina (Genzano & Zamponi 1999), including Bermuda (Calder 1988), the Gulf of Mexico (Calder & Cairns 2009, as *B. humilis*), and the Caribbean Sea (Calder & Kirkendale, 2005).

Elsewhere. Considered essentially circumglobal in tropical and temperate waters (Calder 2010).

Family Eudendriidae L. Agassiz, 1862

Eudendrium carneum Clarke, 1882 Fig. 1i

Eudendrium carneum Clarke, 1882: 137, pl. 7, figs. 10-17.-Winston, 1982: 160; 2010: 232.-Jones 2002: 218.

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

Voucher material. Fort Pierce Inlet, north jetty, north side, 27°28'24.1"N, 80°17'21.2"W, intertidal zone, on rocks, 14.vii.2012, 28° C, 35‰, collected manually, five colonies, up to 3.4 cm high, without gonothecae, coll. D.R. Calder, ROMIZ B3960.

Remarks. Colonies of the eurytopic hydroid *Eudendrium carneum* Clarke, 1882 are large, conspicuous, and widespread in shallow temperate and tropical waters. Female colonies are particularly distinctive in bearing fenestrated embryo-bearing perisarcal capsules along ultimate branchlets. Winston (1982) found it to be abundant during warmer months of the year at coastal sites in the Indian River region of Florida, where it provided substrate for bryozoans.

Evidence suggests that shipping has played a significant role in dispersal of *Eudendrium carneum* globally (Watson 1985; Calder 2010). In the western North Atlantic, Fraser's record of the species from 75 fathoms (137 m) off Cape Canso, Nova Scotia, is regarded as erroneous based on known temperature tolerances (Calder 1990) and overall distribution of this warm-water hydrozoan.

Reported distribution. Atlantic coast of Florida. Indian River area (Winston 1982, 2010).—Biscayne Bay (Jones 2002).

Western Atlantic. South coast of Cape Cod, Massachusetts (Fraser 1944) to Brazil (Oliveira *et al.* submitted), including Bermuda (Calder 1988), the Gulf of Mexico (Calder & Cairns 2009), and the Caribbean Sea (Calder & Kirkendale 2005).

Elsewhere. Circumglobal in tropical and warm-temperate waters (Schuchert 2008; Calder 2010).



FIGURE 2. a, *Lovenella grandis*: hydrocaulus with two hydrothecae and a gonotheca, ROMIZ B1076, scale equals 0.5 mm. b, *Lovenella grandis*: hydrocaulus with pedicel and hydrotheca, ROMIZ B1076, scale equals 0.25 mm. c, *Plicatotheca anitae*: part of hydrocaulus with two hydrothecae, ROMIZ B1072, scale equals 0.25 mm. d, *Plicatotheca anitae*: gonotheca, ROMIZ B1072, scale equals 0.25 mm. e, *Lafoea intorta*, sp. nov.: part of hydrocaulus with five hydrothecae, ROMIZ B1098, scale equals 0.25 mm. f, *Lafoea intorta*, sp. nov.: part of hydrocaulus with a hydrotheca, ROMIZ B1098, scale equals 0.10 mm.

ORDER LEPTOTHECATA Cornelius, 1992

SUBORDER CONICA Broch, 1910

Family Lovenellidae Russell, 1953

Lovenella grandis Nutting, 1901 Fig. 2a, b

Lovenella grandis Nutting, 1901: 353, fig. 45.

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

Voucher material. Off St. Lucie Inlet, 27°08.5'N, 80°01.6'W, 32 m, 26.ii.1974, Smith-McIntyre grab, R/V *Gosnold* Station 222/266E, four colony fragments, one on small shell fragment, up to 4.3 cm high, with gonophores, ROMIZ B1076.

Remarks. Material examined here could not be distinguished in any significant way from accounts of *Lovenella grandis* Nutting, 1901, a species first described from New England. Gonothecae in specimens from Florida had a distinct collar terminally instead of being truncate, but this is taken to be merely a developmental difference in a poorly-known species.

Primary records of *Lovenella grandis* are few in number (e.g., Nutting 1901; Hargitt 1908; Sumner *et al.* 1913; Fraser 1941; Defenbaugh 1972; Defenbaugh & Hopkins 1973) and are limited to the east and gulf coasts of the United States. Of the hydroids examined in this collection, *L. grandis* is unusual in apparently being a temperate species at the southern limits of its range rather than a tropical-subtropical species extending northwards into the southeastern United States. Other lots of this species in collections at the ROM are from South Carolina (Murrells Inlet, Main Creek, 33°32'51"N, 79°01'27"W, 22.v.1975, coll. D. Calder, ROMIZ B1549; Murrells Inlet, Main Creek, 33°33'14"N, 79°01'20"W, 22.v.1975, coll. D. Calder, ROMIZ B1553) and Massachusetts (Nantucket Sound off Martha's Vineyard, east of East Chop Lighthouse, 41°27.425'N, 70°31.591'W, 12 m, 15.x.2001, on shell, coll. D. Calder, ROMIZ B3500).

Little is yet known about the life cycle of *Lovenella grandis*, although gonothecae observed here, first described by Fraser (1941), contained medusa buds rather than fixed sporosacs. In his original description of the species, Nutting (1901) reported that gonophores produced "free, bell-shaped medusae with 8 tentacles in two sets, and 4 lithocysts."

Reported distribution. Atlantic coast of Florida. First record.

Western Atlantic. Massachusetts (Hargitt 1908, Sumner *et al.* 1913) to Florida (this study); northern Gulf of Mexico (Defenbaugh & Hopkins 1973).

Family Phialellidae Russell, 1953

Plicatotheca anitae Calder & Vervoort, 1986

Fig. 2c, d

Plicatotheca anitae Calder & Vervoort, 1986: 2022, figs. 1-4.

Type locality. Bermuda: 2 km southeast of Castle Roads, 60–90 m (Calder & Vervoort 1986).

Voucher material. Off Sebastian Inlet, 27°52.5'N, 79°57.5'W, 75–98 m, 28.ii.1974, Smith-McIntyre grab, R/ V *Gosnold* Station 222/274D, six colony fragments, up to 1.5 cm high, with two gonothecae, ROMIZ B1072.

Remarks. *Plicatotheca anitae* Calder & Vervoort, 1986 appears to be widely distributed, having been reported from the Pacific and Indian oceans as well as the western and eastern Atlantic. Although Bermuda is the type locality of the species, this is only the second record of it in the western Atlantic. It is a species of deeper waters, having a reported bathymetric distribution of 60–1480 m (Vervoort 2006). Specimens examined here were collected at the upper end of this range, on the outer edge of the continental shelf off the east coast of Florida.

Gonothecae of *Plicatotheca anitae* are reported here for the second time. They correspond with the description

of Gili *et al.* (1989), based on material from Guinea Bissau, western Africa, in being laterally flattened and triangular in shape. As with the specimens of Gili *et al.*, gonothecae observed here were empty and the nature of the gonophore could not be determined.

Plicatotheca anitae resembles *Campanulina denticulata* Clarke, 1907, originally described from abyssal depths (2845 fathoms = 5203 m) off Peru. In addition to trophosomal differences between the two noted earlier (Calder 1991a), the gonotheca of *P. anitae* is now known to be triangular rather than long and irregularly cylindrical as in *C. denticulata. Campanulina indivisa* Fraser, 1948 from 267–347 fathoms (488–634 m) off Catalina Island, California, regarded as conspecific with *C. denticulata* by Vervoort (1966), was referred to *Plicatotheca* Calder & Vervoort, 1986 by Calder *et al.* (2009). That generic assignment is doubtful if gonothecae of *C. indivisa*, presently unknown, prove identical with those of *C. denticulata*.

Reported distribution. Atlantic coast of Florida. First record.

Western Atlantic. Bermuda (Calder 1991a) to Florida (this study).

Elsewhere. Atlantic and Indo-Pacific regions, from deeper neritic to bathyal depths (Vervoort 2006).

Family Lafoeidae A. Agassiz, 1865

Lafoea intorta, sp. nov.

Figs. 2e, f, 3, 4

? Lafoea gracillima.—Clarke, 1879: 243.—Fraser 1944: 225 [part].



FIGURE 3. Lafoea intorta, sp. nov.: a, part of hydrocaulus with two hydrothecae, ROMIZ B1098; b, hydrotheca, with diaphragm marked by an arrow, ROMIZ B1098.

Type material. Holotype: off St. Lucie Inlet, 27°11.8'N, 79°57.3'W, 87 m, 04.x.1986, *Johnson-Sea-Link*, J028/ JSL 2132, one colony, 2.5 cm high, without coppiniae, coll. R. Roesch, ROMIZ B1098.

Etymology. The specific name *intorta* is taken from the Latin word for "twisted" or "tangled," in reference to the bushy and tangled appearance of the hydroid colony.

Description. Colony erect, profusely tangled, about 3 cm high, arising from a creeping and somewhat wrinkled hydrorhiza, comprising several hydrocauli. Larger hydrocauli polysiphonic throughout most of length, becoming progressively more slender distally, monosiphonic at distal end, irregularly branched; larger branches resembling hydrocauli, polysiphonic except at extremities; smaller and younger branches monosiphonic throughout; perisarc of stem and branches thickest basally, thinning out distally. Hydrothecal pedicels 130–210 μ m in length, sometimes almost straight but usually with a curve or loose twist basally, diameter of pedicels 60–70 μ m

and remaining nearly uniform throughout length, arising directly from all sides of hydrocaulus and branches, never adnate basally, most given off at an angle of 45 degrees or more from stem and branches. Hydrothecae deeply conical and with smooth walls, sometimes nearly symmetrical but more often somewhat curved with abcauline wall less convex than adcauline side, length abcauline wall 380–500 μ m, length adcauline wall 420–550 μ m; base of hydrotheca with an irregular whorl of punctae just above a filmy diaphragm, then merging almost imperceptibly with pedicel; diameter across diaphragm 65–85 μ m; hydrothecal margin entire, distinctly everted, occasionally renovated in older parts of colony; orifice round, 150–165 μ m in diameter, without an operculum. Nematothecae absent. Hydranths with about 12 filiform tentacles.

Gonophores not seen.

Nematocysts (Fig. 4): microbasic mastigophores (5.5–6.4 μ m long x 2.1–2.6 μ m wide; n = 10), abundant on tentacles; holotrichous isorhizas (23.2–24.5 μ m long x 9.0–10.0 μ m wide; n = 10), common on hydranth body and in coenosarc. Identifications of nematocyst categories are tentative; discharged threads were too indistinct in ethanol-preserved material for certain designation.



FIGURE 4. *Lafoea intorta*, sp. nov., nematocysts, ROMIZ B1098: a, microbasic mastigophores, from tentacle; b, holotrichous isorhiza, from hydranth; c, holotrichous isorhiza, partially discharged.

Remarks. The warm-water *Lafoea intorta*, **sp. nov.**, resembles *Lafoea dumosa* (Fleming, 1820), *L. fruticosa* (M. Sars, 1850), and *L. gracillima* (Alder, 1856), cold-water species found at higher latitudes or at greater depths further south. While species of *Lafoea* Lamouroux, 1821 are difficult to identify because of their morphological variability, and their taxonomy is therefore unsettled, material examined here can nevertheless be distinguished from each of these putative species. In *L. intorta*, pedicels are longer and more obviously twisted than those of *L. dumosa*, a species with hydrothecae that appear almost sessile. Conversely, its pedicels are shorter and have fewer twists than in either *L. fruticosa* or *L. gracillima*. Unlike in *L. gracillima*, its hydrothecae are deep-cone-shaped rather than decidedly narrow and cylindrical, and the hydrothecal margin is distinctly flared instead of straight or slightly flared. Hydrothecae of *L. intorta* are smaller than those of *L. dumosa* and *L. fruticosa*. A filmy, vestigial diaphragm was observed in some of the empty hydrothecae (Fig. 3b), a structure said to be absent in the genus (Millard 1975; Cornelius 1995a; Bouillon *et al.* 2006).

On biogeographic grounds, material identified as *Lafoea gracillima* by Clarke (1879) from shelf waters of southwest Florida and by Fraser (1944) from northwest of the Dry Tortugas (Florida) may have been *L. intorta*. Existence of the Arctic-boreal species *L. gracillima* in the subtropical southeastern Gulf of Mexico where these sites are located is improbable. A colony identified as *Lafoea fruticulosa* (sic) by Wenner *et al.* (1984) from a reef on the outer continental shelf off Charleston, South Carolina (32°29.5'N, 78°49.5'W, 50 m, 5.v.1981, R/V *Dolphin*, Cerame-Vivas dredge, without gonophores, ROMIZ B1916) was re-examined here and found to be identical with *L. intorta*. That specimen is designated here as a paratype of the species.

The cnidome of *Lafoea intorta* includes what are believed to be microbasic mastigophores and holotrichous isorhizas. Other nematocyst categories were observed as well, but it was unclear whether they were part of the cnidome or simply exogenous ones. Study material long preserved in alcohol rendered nematocyst examination difficult.

Reported distribution. South Carolina (Wenner *et al.* 1984, as *Lafoea fruticulosa*) to the central east coast of Florida (this study).

Family Hebellidae Fraser, 1912b

Hebella venusta (Allman, 1877) Fig. 5a

Lafoea venusta Allman, 1877: 11, pl. 6, figs. 2, 3.

Type locality. USA: Florida, Loggerhead Key (Allman 1877).

Voucher material. Bethel Shoal off Vero Beach, 27°42.6'N, 80°06.8'W, 24 m, on *Thyroscyphus marginatus*, 18.ii.1976, *Johnson-Sea-Link*, JSL 328, diver lockout, one colony, without gonothecae, coll. S. Nelson, ROMIZ B1097.

Remarks. *Hebella venusta* (Allman, 1877) appears to be common in the Caribbean region (Fraser 1944, as *Lafoea venusta*; Vervoort 1968; Galea 2010; Castellanos Iglesias 2011). The species was collected on Challenger Bank near Bermuda in 1873 during the voyage of H.M.S. *Challenger* (Ritchie 1909, as *Lafoea venusta*; Calder 1991a), but it has not been seen in that region since then and appears to have become locally extinct (Sterrer 1998; Calder 2000). Records from the Indian Ocean (Ritchie 1910, as *Lafoea venusta*; Mergner & Wedler 1977) need to be verified.

Gonothecae of *H. venusta* were first described by Galea (2010), but the character of the gonophores is still unknown.

Reported distribution. Atlantic coast of Florida. First record.

Western Atlantic. North Carolina (Cain 1972) to Brazil (Oliveira *et al.* submitted), including Bermuda (Calder 1991a), the Gulf of Mexico (Calder & Cairns 2009), and the Caribbean Sea (Galea 2010).



FIGURE 5. a, *Hebella venusta*: pedicel and hydrotheca, ROMIZ B1097, scale equals 0.20 mm. **b**, *Hebella* sp.: pedicel and hydrotheca, ROMIZ B1132, scale equals 0.25 mm. **c**, *Hebellopsis communis*: pedicel and hydrotheca, ROMIZ B1100, scale equals 0.10 mm. **d**, *Hebellopsis gigas*: pedicel and hydrotheca, ROMIZ B1082, scale equals 0.25 mm. **e**, *Hebellopsis scandens*: pedicel and hydrotheca, ROMIZ B1091, scale equals 0.10 mm. **f**, *Cryptolaria pectinata*: distal part of a hydrocladium, ROMIZ B1120, scale equals 0.25 mm.

Hebella sp.

Fig. 5b

Voucher material. Off St. Lucie Inlet, 27°10.7'N, 80°02.7'W, on *Aglaophenia latecarinata*, 23 m, vii.1975, *Johnson-Sea-Link*, JSL 274, one colony, without gonophores, coll. T. Askew, ROMIZ B1132.

Remarks. The hydroid colony examined here was small, with only two hydrothecae, and it lacked gonothecae. Its hydrothecae resemble those of a number of hebellid species, including *Scandia mutabilis* (Ritchie, 1907), *Anthohebella parasitica* (Ciamician, 1880), and *Hebella furax* Millard, 1957. The first of these three species has fixed gonophores (Fraser 1912b), while the other two liberate a medusa (Boero 1980; Migotto & de Andrade 2000). In the absence of knowledge about its gonophores, however, present material cannot be identified to species with any degree of certainty and is even assigned to the genus *Hebella* Allman, 1888 with question.

Hebellopsis communis Calder, 1991a

Fig. 5c

Hebellopsis communis Calder, 1991a: 42, Figs. 26 a, b.

Type locality. Bermuda: 2 km off Castle Roads (Calder 1991a).

Voucher material. Bethel Shoal off Vero Beach, 27°42.6'N, 80°06.8'W, 24 m, on *Thyroscyphus marginatus*, 18.ii.1976, *Johnson-Sea-Link*, JSL 328, diver lockout, one colony, without gonothecae, coll. S. Nelson, ROMIZ B1100.

Remarks. *Hebellopsis communis* Calder, 1991a resembles *H. scandens* (Bale, 1888), but differs in having: (1) hydrothecae that are deeper (>500 μ m vs. <500 μ m) and deeply campanulate rather than cylindrical and often markedly curved, (2) hydrothecal pedicels that are spirally annulated and of varied length (up to 400 μ m long) rather than smooth and short (up to 130 μ m long), and (3) hydrothecal orifices with larger openings (diameter 256–280 μ m vs. 160–191 μ m). Hydrothecae resemble those of *Hebella furax* Millard, 1957 but lack a rounded annular ring basally. *Hebellopsis gigas* (Pieper, 1884) is also similar, but it has longer pedicels and hydrothecae with a more pronounced distal flare.

This species, usually epizoic on other hydroids (especially *Thyroscyphus marginatus* Allman, 1877), is known only from the warm western Atlantic (Calder 1991a, 2000; Castellanos Iglesias *et al.* 2011; Oliveira *et al.* submitted). Its gonophores have yet to be described.

Reported distribution. Atlantic coast of Florida. First record.

Western Atlantic. Bermuda (Calder 1991a) to Brazil (Oliveira et al. submitted).

Hebellopsis gigas (Pieper, 1884)

Fig. 5d

Lafoea gigas Pieper, 1884: 165.

Type locality. Adriatic Sea: east coast (Pieper 1884).

Voucher material. Off Melbourne, 28°04.0'N, 80°12.8'W, 25 m, 01.iii.1974, R/V *Gosnold* Station 222/281B, Smith-McIntyre grab, one colony, on a bivalve shell, 3 mm high, without gonophores, ROMIZ B1082.

Remarks. Galea (2008) presented evidence that *Laomedea michaelsarsi* Leloup, 1935, originally from the Tortugas, Florida, and *Lafoea gigas* Pieper, 1884, first described from the Adriatic Sea, are conspecific. His conclusion is followed here, although a molecular comparison of material from the two regions is needed to confirm synonymy of the two names.

Few morphological characters exist in hydroid stages of taxa currently assigned to Hebellidae Fraser, 1912b, and classification within the family overall remains flawed. Efforts to resolve relationships from molecular work have only just begun, although both Hebellidae and the supposedly related Lafoeidae A. Agassiz, 1865 appear to be polyphyletic (Peña Cantero *et al.*, 2010; Moura *et al.* 2012). Relationships to other families, including Laodiceidae L. Agassiz, 1862, Zygophylacidae Quelch, 1885, and Tiarannidae Russell, 1940, are still unclear. Disagreement continues over the number and scope of genera within Hebellidae.

As for the present species, its frequent referral to *Scandia* Fraser, 1912b is incorrect in my opinion. *Scandia*, as defined by its type species *S. mutabilis* Ritchie, 1907, is characterized by having a rounded annular perisarcal thickening at the base of the hydrotheca, a feature lacking in both *Lafoea gigas* Pieper, 1884 and its putative synonym *Laomedea michaelsarsi* Leloup, 1935. For the same reason this species is not referable to *Staurodiscus*

Haeckel, 1879, *Hebella* Allman, 1888, or *Anthohebella* Boero, Bouillon & Kubota, 1997 (distinguished from *Hebella* in having swimming gonophores instead of eumedusoids or medusae). For now I continue to recognize *Hebellopsis* Hadži, 1913 (type species: *Hebellopsis brochii* Hadži, 1913) as valid, distinguishing it amongst genera of this group in having a distinct diaphragm rather than a rounded annular thickening at the base of the hydrotheca, as in those genera above. In possessing that character, *Lafoea gigas* conforms with *Hebellopsis* and is referred to it here. As for the type species of the genus, Hadži (1913) spelled the specific name of the type species of the genus as both *brochi* (in the title, and in captions to figs. 30–32) and *brochii* (p. 188) in the original description. Under the First Reviser Principle, the name *brochii*, more widely used of the two in recent key works (Bouillon *et al.* 2006; Schuchert 2012a), is taken as the correct original spelling.

Detailed recent accounts of this species are given by Peña Cantero & García Carrascosa (2002) based on collections from the Mediterranean, and by Galea (2008) from Caribbean material.

Reported distribution. Atlantic coast of Florida. First record.

Western Atlantic. Bermuda area (Calder 1998, 2000, as *Hebellopsis michaelsarsi*) to the Caribbean Sea (Galea 2008, as *Scandia gigas*).

Elsewhere. Eastern Atlantic (Altuna Prados 1994, as *Scandia gigas*) and Mediterranean (Broch 1933; Peña Cantero & García Carrascosa 2002, as *S. gigas*); Galápagos (Calder *et al.* 2003, as *H. michaelsarsi*).

Hebellopsis scandens (Bale, 1888)

Fig. 5e

Lafoea scandens Bale, 1888: 758, pl. 13, figs. 16-19.

Type locality. Australia: Port Stephens and Port Jackson (Bale 1888).

Voucher material. Bethel Shoal off Vero Beach, 27°42.6'N, 80°06.8'W, 24 m, on *Pasya quadridentata*, 18.ii.1976, *Johnson-Sea-Link*, JSL 328, diver lockout, four colony fragments, without gonothecae, coll. S. Nelson, ROMIZ B1091.

Remarks. This widespread species, common as an epizoite on other hydroids, has been reported along the east coast of the United States as *Hebella calcarata* A. Agassiz, 1865 by authors including Fraser (1944). Confusion over that binomen, now included in the synonymy of *Laodicea undulata* (Forbes & Goodsir, 1853), has been reviewed earlier (Calder 1991a). It is especially frequent in the region south of Cape Hatteras (Fraser 1912b, as *H. calcarata*; Calder & Hester 1978, as *Hebella scandens*; Wenner *et al.* 1983, 1984, as *H. scandens*). Records of this species in boreal waters north of Cape Cod, listed in Fraser (1944) are considered doubtful.

The medusa stage of this species was raised in the laboratory from the hydroid and described by Altuna Prados (1996).

Reported distribution. Atlantic coast of Florida. First record.

Western Atlantic. New England (Fraser 1944, as *Hebella calcarata* A. Agassiz, 1865) to Argentina (Oliveira *et al.* submitted, as *H. scandens*), including Bermuda (Calder 1991a), the Gulf of Mexico (Calder & Cairns 2009), and the Caribbean Sea (Vervoort 1968, as *H. scandens* var. *contorta*).

Elsewhere. Circumglobal in tropical, subtropical and temperate waters (Vervoort & Watson 2003).

Family Zygophylacidae Quelch, 1885

Cryptolaria pectinata (Allman, 1888)

Fig. 5f

Perisiphonia pectinata Allman, 1888: 45, pl. 21, figs. 2, 2a-b.

Type locality. New Zealand: Challenger Station 169 (37°34'S, 179°22'E) (Allman 1888).

Voucher material. Off St. Lucie Inlet, 27°11.8'N, 79°57.3'W, 87 m, 04.x.1986, *Johnson-Sea-Link*, J028/JSL 2132, one colony, 2.5 cm high, without coppiniae, coll. R. Roesch, ROMIZ B1120.

Remarks. This species was first reported in the western Atlantic, as Eucryptolaria pinnata Fraser, 1938 (type

locality: Galápagos Islands), by Fraser (1943). Following examination of its type material, *E. pinnata* was included in the synonymy of *Cryptolaria pectinata* (Allman, 1888) by Calder *et al.* (2009). The monotypic genus *Eucryptolaria* Fraser, 1938 had been referred earlier to *Cryptolaria* Busk, 1857 by Rees & Vervoort (1987).

Evidence from recent cladistic (Marques *et al.* 2006) and molecular (Moura *et al.* 2012) studies demonstrate that *Cryptolaria* should be assigned to the same family-group cluster as *Zygophylax* Quelch, 1885 and *Abietinella* Levinsen, 1913. Moura *et al.* also contended that Zygophylacinae Quelch, 1885, usually included as a subfamily within Lafoeidae A. Agassiz, 1865 for this group of genera, merited recognition as a distinct family. Their recommendation is adopted here. Moreover, they also found evidence of cryptic diversity within eastern Atlantic populations of *Cryptolaria pectinata*. Comparisons of hydroids assigned to *C. pectinata* from the western Atlantic with those from the type locality of New Zealand, and elsewhere, appear warranted.

The hydroid examined here was collected at a depth of 87 m near the edge of the continental shelf, east of St. Lucie Inlet. No coenosarc or hydranths were present, and the colony appeared to be recently dead.

Reported distribution. Atlantic coast of Florida. First record.

Western Atlantic. Cape Fear, North Carolina (Henry *et al.* 2008) to the Caribbean Sea (Fraser 1943, as *Eucryptolaria pinnata*) and Gulf of Mexico (Calder & Cairns 2009).

Elsewhere. Circumglobal at lower latitudes in deeper waters (49–1280 m) (Vervoort & Watson 2003).

Family Haleciidae Hincks, 1868

Halecium calderi Galea, 2010

Fig. 6a–c

Halecium calderi Galea, 2010: 9, figs. 3A-J.

Type locality. Guadeloupe: Grande-Terre, Les Ancres (16° 27.002 N, 61° 32.320 W) (Galea 2010).

Voucher material. Off St. Lucie Inlet, 27°12.8'N, 80°01.2'W, 39 m, 17.v.1976, *Johnson-Sea-Link*, JSL 2046, diver lockout, two colonies, up to 2 cm high, with gonophores, coll. J. Reed, ROMIZ B1094.—Off St. Lucie Inlet, 27°11.8'N, 80°00.6'W, 42 m, on *Oculina varicosa*, 17.v.1976, *Johnson-Sea-Link*, JSL 2047, diver lockout, one colony, 4 cm high, with gonophores, coll. G. Melton, ROMIZ B1124.

Remarks. This is the second record of a species recently described from Guadeloupe by Galea (2010), extending its known range northwards to Florida from the Caribbean Sea. Male gonothecae are illustrated for the first time (Fig. 6c). They differ from those of the female (Fig. 6b) in having fewer lateral crests and in being approximately 30% smaller.



FIGURE 6. a, *Halecium calderi*: part of hydrocaulus with hydrothecae, ROMIZ B1094, scale equals 0.25 mm. b, *Halecium calderi*: female gonotheca, ROMIZ B1094, scale equals 0.25 mm. c, *Halecium calderi*: male gonotheca, ROMIZ B1124, scale equals 0.20 mm. d, *Halecium tenellum*: a, part of hydrocaulus with hydrothecae, ROMIZ B1105, scale equals 0.25 mm.

Morphologically, *Halecium calderi* Galea, 2010 closely resembles *Halecium sibogae* Billard, 1929 (type locality: Indonesia) and *H. sibogae marocanum* Billard, 1934 (type locality: Morocco). Relationships of these nominal species-group taxa remain unresolved. For now, the binomen established by Galea (2010) for the warm western North Atlantic population is adopted.

Reported distribution. Atlantic coast of Florida. First record.

Western Atlantic. Florida (this record) to Guadeloupe (Galea 2010).

Halecium tenellum Hincks, 1861b

Fig. 6d

Halecium tenellum Hincks, 1861b: 252, pl. 6, figs. 1-4.—Jones, 2002: 216.

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

Voucher material. Jeff's Reef off Fort Pierce, 27°32.8'N, 79°58.8'W, 80 m, 15.iv.1977, *Johnson-Sea-Link*, JSL 2184-A, diver lockout, one colony, 1.3 cm high, without gonophores, coll. F. Stanton, ROMIZ B1105.

Remarks. The morphology of the hydroid examined here approaches accounts of *Halecium delicatulum* Coughtrey, 1876 (type locality: Upper Harbour, Dunedin, New Zealand) and *H. mediterraneum* Weismann, 1883 (type locality: Naples, Italy) in having typically long primary hydrophores. However, no pseudodiaphragm such as that often reported in both of those species (e.g., Schuchert 2005) was present in hydrophores of the colony from Florida. It was also small (1.3 cm high) and its hydrocaulus monosiphonic except at the base, as is typical of *Halecium tenellum* Hincks, 1861b.

In the western North Atlantic, Fraser (1944) included distribution records of *Halecium tenellum* from Hudson Strait to the Caribbean Sea. At least some reports of the species from high latitudes have been based on misidentifications (Hamond 1957; Cornelius 1975; Calder 1991a; Schuchert 2005). The species is more likely restricted to temperate and tropical waters. An extensive list of literature pertaining to *H. tenellum* was given by Medel & Vervoort (2000).

Reported distribution. Atlantic coast of Florida. Biscayne Bay (Jones 2002).

Western Atlantic. Possibly from southern New England (Fraser 1944) to Argentina (Oliveira *et al.* submitted), including Bermuda (Calder 1991a), the Gulf of Mexico (Calder & Cairns 2009), and the Caribbean Sea (Galea 2010).

Elsewhere. Considered a cosmopolitan species by Medel & Vervoort (2000), but see Remarks above.

Family Thyroscyphidae Stechow, 1920

Symmetroscyphus intermedius (Congdon, 1907)

Fig. 7a, b

Thyroscyphus intermedius Congdon, 1907: 482, figs. 33-36.

Type locality. Bermuda: Mangrove Bay, 32°18'10"N, 64°51'30"W (Congdon 1907).

Voucher material. Bessie Cove, north of St. Lucie Inlet, 27°11'07"N, 80°09'41"W, on seagrass, <0.5 m, 19.ii.1991, collected manually, one colony in two fragments, up to 4 mm high, without gonophores, coll. D.R. Calder, ROMIZ B1117.

Remarks. A taxonomic account of *Symmetroscyphus intermedius* (Congdon, 1907) has been given earlier (Calder 1991a). Occurring in shallow-waters with algal symbionts in its tissues, this species is found on substrates such as seagrasses, algae, prop roots of red mangroves, and other hydroids (Calder 1991c; Kaehler & Hughes 1992; Galea 2008; Castellanos Iglesias *et al.* 2011). Gonophores of *S. intermedius* remain undescribed.

Reported distribution. Atlantic coast of Florida. First record.

Western Atlantic: Bermuda (Calder 1991a) to the Caribbean Sea (Calder & Kirkendale 2005; Castellanos Iglesias *et al.* 2011).



FIGURE 7. a, *Symmetroscyphus intermedius*: part of erect colony, ROMIZ B1117, scale equals 0.5 mm. b, *Symmetroscyphus intermedius*: part of colony with two hydrothecae, ROMIZ B1117, scale equals 0.25 mm. c, *Thyroscyphus marginatus*: part of hydrocaulus with three hydrothecae, ROMIZ B3963, scale equals 0.5 mm. d, *Thyroscyphus marginatus*: pedicel and hydrotheca, ROMIZ B3963, scale equals 0.25 mm. e, *Thyroscyphus ramosus*: part of hydrocaulus with four hydrothecae, ROMIZ B1133, scale equals 0.5 mm. f, *Thyroscyphus ramosus*: pedicel and hydrotheca, ROMIZ B1133, scale equals 0.5 mm. f, *Thyroscyphus ramosus*: pedicel and hydrotheca, ROMIZ B1133, scale equals 0.25 mm.

Thyroscyphus marginatus (Allman, 1877)

Fig. 7c, d

Obelia marginata Allman, 1877: 9, pl. 6, figs. 1, 2. *Thyroscyphus marginatus.*—Cummings, 1994: 1208.—Jones, 2002: 218.

Type locality. USA: Florida, off Loggerhead Key (Allman 1877).

Voucher material. Bethel Shoal off Vero Beach, 27°42.6'N, 80°06.8'W, 24 m, 18.ii.1976, *Johnson-Sea-Link*, JSL 328, diver lockout, one colony fragment, 3 cm high, without gonothecae, coll. S. Nelson, ROMIZ B3963.

Remarks. *Thyroscyphus marginatus* (Allman, 1877) is a conspicuous species, forming large colonies that reach as much as nine inches (23 cm) high (Allman 1877). It is easily distinguished from the sympatric *T. ramosus* Allman, 1877 in having an entire (non-cuspate) rather than a four-cusped hydrothecal margin, and a single operculum that is shed rather than a persistent one of four valves.

In some earlier papers (Calder 1993, 1998, 2000; Calder & Kirkendale 2005; Calder & Cairns 2009) I assigned this species to *Cnidoscyphus* Splettstösser, 1929, a genus originally established with three included species (*Laomedea torresii* Busk, 1852; *Obelia marginata* Allman, 1877; and *Thyroscyphus aequalis* Warren, 1908). No type species was designated for it until Vervoort (1993: 104) chose *L. torresii* Busk, 1852 as the name-bearing type. *Cnidoscyphus* was founded on an invalid character (presence of large nematocysts in the mantle lining of the hydrotheca, now known in several thyroscyphid and sertulariid genera) and it is currently regarded as a junior synonym of *Thyroscyphus* Allman, 1877 (Bouillon *et al.* 2006).

This hydroid species is widely reported in the tropical western Atlantic (see records in Fraser 1944, as *Campanularia marginata*; Vervoort 1968, as *Cnidoscyphus marginatus*; Calder & Kirkendale 2005, as *C. marginatus*; Galea 2008; Castellanos Iglesias *et al.* 2011). It extends northwards into shelf waters of the southeastern United States (Cain 1972, as *C. marginatus*; Wenner *et al.* 1983, 1984; Cummings 1994) and Gulf of Mexico (Calder & Cairns 2009, as *C. marginatus*), but is infrequent in estuaries of the region (Calder 1983).

Reported distribution. Atlantic coast of Florida. Boca Raton (Cummings 1994).—Biscayne Bay (Jones 2002).

Western Atlantic. North Carolina (Cain 1972, as *Cnidoscyphus marginatus*) to Brazil (Oliveira *et al.* submitted), including Bermuda (Calder 1991a), the Gulf of Mexico (Calder & Cairns 2009, as *C. marginatus*), and the Caribbean Sea (Galea 2008).

Elsewhere. Eastern Atlantic (Vervoort 1959, as C. marginatus; Medel & Vervoort 1998, as C. marginatus).

Thyroscyphus ramosus Allman, 1877

Fig. 7e, f

Thyroscyphus ramosus Allman, 1877: 11, pl. 6, figs. 5, 6.—Winston, 1982: 116; 2010: 231.

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

Voucher material. Off Fort Pierce, 27°29.6'N, 80°17.0'W, 7–8 m, SCUBA, one fragmentary colony, 4 cm high, without gonophores, coll. F. Stanton, ROMIZ B1133.—Fort Pierce Inlet, north jetty, 13.iii.1975, collected manually, one colony, 14 cm high, without gonophores, coll. J.E. Winston, ROMIZ B1926.

Remarks. *Thyroscyphus ramosus* Allman, 1877 is widely reported in the Caribbean region (Vervoort 1968; Calder & Kirkendale 2005; Galea 2008; Castellanos Iglesias *et al.* 2011). Shimabukuro & Marques (2006) provided a detailed account of its morphology based on material from Brazil.

According to Winston (1982), *Thyroscyphus ramosus* is abundant year-round on the North Beach breakwater at Fort Pierce, Florida, within the study area, although colonies she observed there were dormant during January. A large hydroid extending bathymetrically into the intertidal zone, it was an important substrate for bryozoans in the area. In turn, it grows on a variety of substrates, both animate (e.g., algae, sponges) and inanimate (e.g., artificial reefs, rocks, sand, pilings) (Oliveira *et al.* submitted). Although usually recorded from relatively shallow waters, Nutting (1915) reported *T. ramosus* from 100–250 fathoms (183–457 m) off Morro Castle, Cuba.

Reported distribution. Atlantic coast of Florida. Indian River area (Winston 1982, 2010).

Western Atlantic. Sebastian Inlet, Florida (Winston 1982: 116) to Brazil (Oliveira *et al.* submitted), and including the Gulf of Mexico (Calder & Cairns 2009) and the Caribbean Sea (Galea 2008).

Elsewhere. Eastern Atlantic (Vervoort 1959); ?Indian Ocean (Leloup 1932).

Family Sertulariidae Lamouroux, 1812

Diphasia digitalis (Busk, 1852) Fig. 8a

Sertularia digitalis Busk, 1852: 393.

Type locality. Australia: Torres Strait, Prince of Wales Channel (Busk 1852: 393).



FIGURE 8. a, *Diphasia digitalis*: part of a hydrocladium with hydrothecal pairs, ROMIZ B3964, scale equals 0.25 mm. b, *Dynamena crisioides*: part of hydrocaulus with basal part of a hydrocladium and hydrothecae, ROMIZ B3965, scale equals 0.25 mm. c, *Dynamena dalmasi*: part of hydrocaulus with two hydrothecal pairs, ROMIZ B1081, scale equals 0.25 mm. d, *Dynamena disticha*: part of hydrocaulus with two hydrothecal pairs, ROMIZ B3966, scale equals 0.20 mm. e, *Pasya quadridentata*: part of hydrocaulus with three hydrothecal pairs, ROMIZ B1085, scale equals 0.25 mm. f, *Pasya quadridentata*: gonotheca, ROMIZ B1085, scale equals 0.25 mm. g, *Salacia desmoides*: part of hydrocaulus with two hydrothecal pairs, ROMIZ B1085, scale equals 0.25 mm. f, *Pasya quadridentata*: gonotheca, ROMIZ B1085, scale equals 0.25 mm. h, *Sertularella areyi*: part of hydrocaulus with two hydrothecae, ROMIZ B1135, scale equals 0.5 mm. i, *Sertularella conica*: part of hydrocaulus with three hydrothecae, ROMIZ B1087, scale equals 0.25 mm.

Voucher material. West Palm Beach, on reef seaward of the Breakers Hotel, 45 feet (13.7 m), together with *Halopteris carinata*, January 1991, SCUBA, one colony, 2.5 cm high, without gonophores, coll. P. Humann, ROMIZ B3964.

Remarks. *Diphasia digitalis* (Busk, 1852) was first reported in the western Atlantic by Allman (1877) from Key West, Florida, although he assigned it to a new genus and species (*Desmoscyphus longitheca*). Soon after, Allman (1888) reported it from Bahia, Brazil, but described it as a new species (*Desmoscyphus acanthocarpus*). Nutting (1904) concluded that *Desmoscyphus longitheca* Allman, 1877 and *D. acanthocarpus* Allman, 1888 were identical after examining types of the two nominal species, and assigned both to the synonymy of *Diphasia digitalis*.

Bale (1884: 101) noted that colonies of this species appear "dark gray, almost black." Others have described them as dark brown (e.g., Morri *et al.* 2009). The colouration is due to blackish pigment granules in epidermal layers of the coenosarc (Schuchert 2003). Material examined here, in fair condition, had obvious black pigment granules in the coenosarc.

The known range of *Diphasia digitalis* in the western Atlantic is extended slightly to the north, having been reported earlier from the Florida Keys (Fraser 1944).

Reported distribution. Atlantic coast of Florida. First record.

Western Atlantic. West Palm Beach area, Florida (reported herein) to Brazil (Oliveira *et al.* submitted), and including the Gulf of Mexico (Calder & Cairns 2009) and the Caribbean Sea (Vervoort 1968).

Elsewhere. Circumglobal in tropical and subtropical waters (Millard 1975; Schuchert 2003).

Dynamena crisioides Lamouroux, 1824

Fig. 8b

Dynamena crisioides Lamouroux, 1824: 613, pl. 90, figs. 11, 12.

Type locality. Indonesia: Moluccas (Lamouroux 1824).

Voucher material. Off Palm Beach, 26°48.4'N, 79°58.6'W, 37 m, 16.ix.1975, *Johnson-Sea-Link*, JSL 288, one colony, 4.5 cm high, without gonophores, coll. S. Nelson, ROMIZ B1089.—Fort Pierce Inlet, north jetty, north side, 27°28'24.1"N, 80°17'21.2"W, intertidal zone, on rocks, 14.vii.2012, 28° C, 35‰, collected manually, seven cormoids, up to 3.7 mm high, two with gonothecae, coll. D.R. Calder, ROMIZ B3965.

Remarks. *Dynamena crisioides* Lamouroux, 1824 is a conspicuous and well-known intertidal and shallow subtidal species occurring at lower latitudes worldwide. It was found here off the east coast of Florida at a depth of 37 m (ROMIZ B1089), as well as intertidally on jetty rocks at Fort Pierce Inlet (ROMIZ B3965). Taxonomic (Calder 1991a) and ecological (Calder, 1991d) accounts of the species have been given earlier.

Reported distribution. Atlantic coast of Florida. First record.

Western Atlantic. Bahamas, Florida Keys (Fraser 1944), and Dry Tortugas (Van Gemerden-Hoogeveen 1965) to Brazil (Oliveira *et al.* submitted), including Bermuda (Calder 1991a), the Gulf of Mexico (Calder & Cairns 2009), and the Caribbean Sea (Galea 2008).

Elsewhere. Circumglobal in shallow waters of the tropics and subtropics (Calder, 1991a; Schuchert 2003).

Dynamena dalmasi (Versluys, 1899)

Fig. 8c

Desmoscyphus dalmasi Versluys, 1899: 38, figs. 6-8.

Type locality. Haiti: "... pres de l'île Tortuga..." (Versluys 1899: 40).

Voucher material. Off Melbourne, 28°04.0'N, 80°12.8'W, 25 m, 01.iii.1974, R/V *Gosnold* Station 222/281B, Smith-McIntyre grab, one colony, 10 mm high, without gonophores, ROMIZ B1081.

Remarks. This hydroid species was first described and named by Allman (1877), as *Thuiaria sertularioides*, from Pourtalès Gulf Stream exploration collections off south Florida. As discussed in greater detail elsewhere (Calder 1991a), that name was rejected prior to 1961 as a junior secondary homonym and it has now been replaced

by the binomen *Dynamena dalmasi* (Versluys, 1899). Typically found on coastal reefs and banks (e.g., Cain 1972, as *Sertularia dalmasi*; Defenbaugh 1974, as *S. dalmasi*; Wenner *et al.* 1984; Rezak *et al.* 1985; Calder 1991a, 2000; Grohmann *et al.* 2003, 2011; Hajdu & Teixeira 2011), the reported depth range of *D. dalmasi* is from 8–366 m (Calder & Cairns 2009).

Reported distribution. Atlantic coast of Florida. First record.

Western Atlantic. North Carolina (Cain 1972) to Brazil (Oliveira *et al.* submitted), including Bermuda (Calder 1991a), the Gulf of Mexico (Calder & Cairns 2009), and the Caribbean Sea (Vervoort 1968, as *Sertularia dalmasi*).

Elsewhere. Tropical and subtropical parts of the western and eastern Atlantic and Pacific oceans (Medel & Vervoort 1998).

Dynamena disticha (Bosc, 1802)

Fig. 8d

Sertularia disticha Bosc, 1802: 101, pl. 29, fig. 2.

Type locality. Atlantic Ocean: "...sur le *fucus natans*..." (Sargassum natans) (Bosc 1802).

Voucher material. Fort Pierce, Fort Pierce Inlet State Park, 27°28'29.5"N, 80°17'25.8"W, on stranded *Sargassum* sp., 14.vii.2012, 28° C, 35‰, collected manually, one colony, 4 mm high, without gonophores, coll. D.R. Calder, ROMIZ B3966.

Remarks. Hydroids referred to *Dynamena disticha* (Bosc, 1802) in the western Atlantic occur in two forms, a stunted one (<1 cm high) found on floating *Sargassum* and a much larger one (up to 5 cm high) on a variety of benthic substrates. It remains to be confirmed whether they are actually conspecific. Specimens observed here, growing on a species of *Sargassum*, were of the stunted variety as originally described by Bosc (1802).

Comments on the taxonomy of this species have been given earlier (Calder 1991a). Included in the synonymy of *D. disticha* therein were the following, all originally described from the western North Atlantic: *Sertularia exigua* Allman, 1877, *S. distans* Allman, 1877, *S. complexa* Clarke, 1879, *Dynamena bilatteralis* Brooks, 1883, *Sertularia mayeri* Nutting, 1904, *S. pourtalesi* Nutting, 1904, and with question *Dynamena cornicina* McCrady, 1859. An extensive list of literature on *D. disticha* was given in Medel & Vervoort (1998).

Reported distribution. Atlantic coast of Florida. First record.

Western Atlantic. Massachusetts (Nutting 1901, as *Sertularia cornicina* and *S. complexa*) to Argentina (Oliveira *et al.* submitted), including Bermuda (Calder 1991a), the Gulf of Mexico (Calder & Cairns 2009), and the Caribbean Sea (Calder & Kirkendale 2005; Galea 2008). The species has been reported on *Sargassum* in the Gulf Stream as far north as Nova Scotia (Fraser 1918, as *S. cornicina*).

Elsewhere. Circumglobal in tropical, subtropical and temperate waters (Peña Cantero & García Carrascosa 2002).

Pasya quadridentata (Ellis & Solander, 1786)

Fig. 8e, f

Sertularia quadridentata Ellis & Solander, 1786: 57, pl. 5, figs. g, G. Dynamena quadridentata.—Jones, 2002: 218.

Type locality. South Atlantic Ocean, on algae "...not far from the island of Ascension" (Ellis & Solander 1786).

Voucher material. Off Fort Pierce, 27°10.8'N, 80°02.5'W, 21.6 m, on benthic algae, 24.vii.1975, R/V *Johnson* and *Johnson-Sea-Link*, JSL 273, one colony, up to 6 mm high, with gonophores, coll. T. Askew, ROMIZ B1085.

Remarks. This hydroid has commonly been known as *Dynamena quadridentata* (Ellis & Solander, 1786) (synonymy in Vervoort & Watson 2003). However, molecular studies by Moura *et al.* (2011) indicate that the nominal genus *Dynamena* Lamouroux, 1812 is polyphyletic, and that *D. quadridentata* is genetically distant from *D. pumila* (Linnaeus, 1758), its type species. *Pasya* Stechow, 1922 (type species: *Sertularia quadridentata* Ellis & Solander, 1786), generally regarded as a synonym of *Dynamena*, is resurrected here for the species. The specific

name *quadridentata* has also been combined in the past with *Pasythea* Lamouroux, 1812, but that nominal genus is now restricted to Bryozoa (type species: *Cellaria tulipifera* Ellis & Solander, 1786). Additional discussion of nomenclature relevant to these names has been given earlier (Calder 1991: 89).

Pasya quadridentata, common in the Caribbean Sea region (Vervoort 1968; Calder & Kirkendale 2005, as *Dynamena quadridentata*), ranges northwards to the Carolinas along the east coast of the United States (Cain 1972; Calder 1983, as *D. quadridentata*). The species is transported to even higher latitudes in the Gulf Stream on floating *Sargassum* (Fraser 1912b; Burkenroad, in Parr 1939, as *Pasythea quadridentata*), including New England (Hargitt 1908, as *Pasythea nodosa*).

Reported distribution. Atlantic coast of Florida. Biscayne Bay (Jones 2002, as Dynamena quadridentata).

Western Atlantic. Woods Hole region, Massachusetts (Hargitt 1908, as *Pasythea nodosa*) to Brazil (Oliveira *et al.* submitted, as *D. quadridentata*), including Bermuda (Calder, 1991a, as *D. quadridentata*), the Gulf of Mexico (Calder & Cairns 2009, as *D. quadridentata*), and the Caribbean Sea (Calder & Kirkendale 2005, as *D. quadridentata*).

Elsewhere. Circumglobal in temperate and tropical waters (Vervoort 1968; Vervoort & Watson 2003).

Salacia desmoides (Torrey, 1902)

Fig. 8g

Sertularia desmoidis Torrey, 1902: 65, pl. 8, figs. 70–72 [the specific name desmoidis deemed to be an incorrect original spelling (ICZN Art. 33.2.3.1) and emended by Nutting (1904) to desmoides].

Type locality. USA: southern California (San Diego, San Clemente Island, San Pedro) (Torrey 1902).

Voucher material. Off St. Lucie Inlet, 27°11.8'N, 79°57.3'W, 87 m, 04.x.1986, *Johnson-Sea-Link*, J028/JSL 2132, six colony fragments, up to 2.5 cm high, without gonothecae, coll. R. Roesch, ROMIZ B3967.

Remarks. Originally described from southern California, *Salacia desmoides* (Torrey, 1902) has been reported from tropical and subtropical regions worldwide, including both eastern and western Atlantic (e.g., Grohmann *et al.* 2003; Vervoort 2006). Although specimens from Florida examined here indeed correspond morphologically with the species, and the name *S. desmoides* is maintained for them here, on biogeographic grounds their identity needs verification. As for European populations, molecular studies by Moura *et al.* (2011) indicate a close genetic relationship amongst hydroids assigned to the species from Portugal, the Azores, and the Mediterranean Sea (Banyuls-sur-Mer, France). Particularly needed now, however, are analyses of specimens from the type locality of southern California (and from the western Atlantic).

In first describing this species, Torrey (1902) spelled the specific name as *desmoidis* in both text and figure captions. While incorrectly formed, there is no evidence of an inadvertent error, such as a lapsus calami or a printer's or copyist's error, having been made (ICZN Art. 32.5.1). The subsequent spelling of the name as *desmoides*, first introduced by Nutting (1904), might thus appear under the code to be an unjustified emendation. However, that spelling, in prevailing usage (see recent synonymy in Vervoort & Watson 2003) and even adopted by Torrey (1904), is deemed here to be a justified emendation (ICZN Art. 33.2.3.1).

Reported distribution. Atlantic coast of Florida. First record.

Western Atlantic. Continental shelf of South Carolina and Georgia (Wenner *et al.* 1984) to Brazil (Grohmann *et al.* 2003).

Elsewhere. Tropical and subtropical regions of the Atlantic, Pacific, and Indian oceans (Medel & Vervoort 1998).

Sertularella areyi Nutting, 1904

Fig. 8h

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

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

Voucher material. Off Sebastian Inlet, 27°52.5'N, 79°57.5'W, 75–98 m, 28.ii.1974, Smith-McIntyre grab, R/ V *Gosnold* Station 222/274C, one colony, 7 mm high, without gonophores, ROMIZ B1135.

Remarks. *Sertularella areyi* Nutting, 1904 was found in a sample from the outer continental shelf mid-way along the Atlantic coast of Florida. Originally described from Cuba, it has been reported from deeper neritic and upper bathyal bottoms in tropical and subtropical regions of the Atlantic, Pacific, and Indian oceans. Detailed taxonomic accounts of this small but morphologically striking species, based on material from the western Pacific, are given by Vervoort (1993) and Vervoort & Watson (2003). The latter authors noted that it often grows on larger hydroids.

Reported distribution. Atlantic coast of Florida. First record.

Western Atlantic. South Carolina/Georgia continental shelf (Wenner *et al.* 1984) to Brazil (Oliveira *et al.* submitted), including Bermuda (Calder 2000) and the Gulf of Mexico (Calder & Cairns 2009).

Elsewhere. Indian Ocean (Millard 1975, as *Sertularella annulaventricosa* Mulder & Trebilcock, 1915); western Pacific (Vervoort 1993; Hirohito 1995; Vervoort & Watson 2003).

Sertularella conica Allman, 1877

Fig. 8i

Sertularella conica Allman, 1877: 21, pl. 15, figs. 6, 7.

Type locality. USA: Florida, southwest of Tortugas, 60 fathoms (110 m) (Allman 1877).

Voucher material. Off Fort Pierce, 27°10.8'N, 80°02.5'W, 22 m, 24.vii.1975, R/V *Johnson* and *Johnson-Sea-Link*, JSL 273, several fragments of one colony, up to 8 mm high, without gonophores, coll. T. Askew, ROMIZ B1087.

Remarks. Valid questions about the identity of Allman's (1877) original material of *Sertularella conica* have been raised by Galea (2008), who suggested that it appeared more like *S. unituba* Calder, 1991a than the *S. conica* of Calder (1991a) and Migotto (1996). Uncertainty exists because Allman's account of the species was brief and his illustration somewhat generalized. An earlier attempt (Calder 1991a) to examine and better characterize the type of *S. conica* was unsuccessful because the specimen could not be found at the Museum of Comparative Zoology. For now, the concept of *S. conica* adopted in earlier papers (Calder 1983, 1991a) is maintained in this work. In my opinion, hydrothecae of *S. conica* as briefly described and illustrated by Allman more closely resemble those in specimens attributed to that species in my earlier works (Calder 1983, 1991a) than to *S. unituba*, but discovery and redescription of type material would help resolve the issue.

Specimens assigned here to *Sertularella conica* somewhat resemble *Sertularella peculiaris* Leloup, 1935 from the Caribbean, but are fundamentally different from that species in having colonies that are erect instead of stolonal or mostly stolonal. Erect colonies of *S. peculiaris* essentially comprise a series of pedicellate hydrothecae (e.g., Leloup 1935, fig. 26, as *S. tenella* forme *peculiaris;* Galea 2008, Fig. 6B) rather than having a typical leptothecate hydrocaulus made up of regular internodes each bearing a disto-lateral hydrotheca, as in *S. conica*. I therefore disagree with the opinion of Galea (2008) that material identified as *S. conica* by me (Calder 1991a) is referable to *S. peculiaris*. A record of *S. conica* from Brazil by Migotto (1996), based on a very small colony (2.7 mm high), needs reassessment.

Reports of this tropical-subtropical species from cold waters of Nova Scotia in the boreal western North Atlantic (e.g., Fraser 1944), from the west coast of North America (e.g., Fraser 1937a), and from the Southern Ocean (e.g., Vervoort 1972; Stepanjants 1979) are considered misidentifications (Calder 1991a). So too are records by Fraser (1938a, b, 1948) from the tropical eastern Pacific (Calder *et al.* 2003: 1212) and by Van Gemerden-Hoogeveen (1965) from the Dry Tortugas. Specimens from the latter location more closely resemble *Sertularella unituba*.

Reported distribution. Atlantic coast of Florida. First record.

Elsewhere. North Carolina (Fraser 1912b) to Argentina (Oliveira *et al.* submitted), including Bermuda (Calder 1991a), the Gulf of Mexico (Calder & Cairns 2009), and the Caribbean Sea (Fraser 1947).

Elsewhere. Questionably reported from the eastern Atlantic (Stechow 1920) and the Indian Ocean (Jarvis 1922).

Fig. 9a, b

Sertularella gayi unituba Calder, 1991a: 103, fig. 54.

Type locality. Bermuda: 2 km southeast of Castle Roads (Calder 1991a).

Voucher material. Off St. Lucie Inlet, 27°11.6'N, 80°00.7'W, 41 m, 18.v.1976, *Johnson-Sea-Link*, JSL 2048, two colony fragments, up to 2.3 cm high, without gonophores, coll. J. Reed, ROMIZ B1093.—Bethel Shoal off Vero Beach, 27°42.6'N, 80°06.8'W, 24 m, 18.ii.1976, *Johnson-Sea-Link*, JSL 328, diver lockout, five colonies and colony fragments, up to 4 cm high, two with gonothecae, coll. S. Nelson, ROMIZ B1099.

Remarks. Originally described as *Sertularella gayi unituba* by Calder (1991a), the subspecific name was elevated to specific rank by Medel & Vervoort (1998). Their taxonomic judgment was followed by Vervoort (2006) and is accepted here. Its recognition as a species distinct from *S. gayi* Lamouroux, 1821 is supported by the molecular studies of Moura *et al.* (2011).

Sertularella unituba has been regarded as likely conspecific with hydroids that Allman (1888) initially described under the name *Sertularia exigua* (not *Sertularia exigua* Allman, 1877; not *Sertularella exigua* Thompson, 1879), and on discovering the homonymy renamed in a plate caption as *Sertularia laxa* (not *Se*

As noted above in remarks on *Sertularella conica* Allman, 1877, questions remain over the identity of that species, and whether it and *S. unituba* may be conspecific.

Reported distribution. Atlantic coast of Florida. First record.

Western Atlantic. Bermuda (Calder 1991a) to the Dry Tortugas (Van Gemerdeen-Hoogeveen 1965, as *Sertularella conica*).

Elsewhere. Eastern Atlantic (Allman 1888, as Sertularella exigua; Medel & Vervoort 1998; Vervoort 2006).

Tridentata distans (Lamouroux, 1816)

Fig. 9c

Dynamena distans Lamouroux, 1816: 180, pl. 5, figs. 1a, B. Sertularia stookeyi.—Fraser, 1943: 93. Sertularia gracilis.—Jones, 2002: 215.

Type locality. Atlantic Ocean, on Fucus natans (=Sargassum natans) and other flotsam (Lamouroux 1816: 180).

Voucher material. Fort Pierce Inlet, north jetty, north side, 27°28'24.1"N, 80°17'21.2"W, intertidal zone, on stem of *Thyroscyphus ramosus*, 14.vii.2012, 28° C, 35‰, collected manually, one colony, 5 mm high, without gonothecae, coll. D.R. Calder, ROMIZ B3968.

Remarks. Billard (1906) noted that the original description of *Tridentata distans* by Lamouroux (1816, as *Dynamena distans*) was inadequate, and he justifiably described illustrations of the species in that initial account as "gross." Nevertheless, he was able to confirm the identity of the species after examining Lamouroux's type at l'Institut Botanique de Caen. That identification, upheld in a subsequent review of Lamouroux's types (Billard 1909), is the foundation of the current concept of the species.

Recently, the possible existence of cryptic species in *T. distans* has been raised on the basis of molecular studies (Moura *et al.* 2011, as *Sertularia distans*). Moreover, the generic affinity of the species needs clarification. Moura *et al.* showed that the species was genetically closer to *Sertularia operculata* Linnaeus, 1958, type species of *Amphisbetia* L. Agassiz, 1862, than to *Sertularia perpusilla* Stechow, 1919, type species of *Tridentata* Stechow, 1920. Differences in morphology support such a possibility. For example, gonothecal walls in *T. distans* are ovate and smooth rather than barrel-shaped with transverse ribs as in *S. perpusilla*.

Tridentata distans is a eurytopic hydroid with a wide latitudinal range, occurring from temperate regions to the tropics. In the southeastern United States it is frequent both inshore (Calder 1983, as *Sertularia distans*) and on hard bottoms of the continental shelf (Wenner 1984, as *S. distans*). Live colonies were found in estuaries of South Carolina at salinities of 20–34‰ (Calder 1976, as *S. stookeyi* Nutting, 1904) and temperatures of 8–32° C (Calder

1990, as *S. distans*). It is also a component of the pelagic *Sargassum* fauna (e.g., Lamouroux 1816, as *Dynamena distans*; Fraser 1944, as *S. stookeyi*; Calder 1991a).

This species is noteworthy for the minuteness of its hydrothecae.

Reported distribution. Atlantic coast of Florida. Between Biscayne and Duck Keys (Fraser 1943, as *Sertularia stookeyi*); Biscayne Bay (Jones 2002, as *S. gracilis* Hassall, 1848).

Western Atlantic. Massachusetts (Fraser 1912a, as *S. stookeyi*) to Brazil (Oliveira *et al.* submitted, as *S. distans*), including Bermuda (Calder 1991a), the Gulf of Mexico (Calder & Cairns 2009), and the Caribbean Sea (Fraser 1943, as *S. stookeyi*).

Elsewhere. Circumglobal in tropical, subtropical, and temperate waters (Vervoort & Watson 2003, as *S. distans*).

Tridentata loculosa (Busk, 1852)

Fig. 9d

Sertularia loculosa Busk, 1852: 393.

Type locality. Australia: Bass Strait (Busk 1852: 393).

Voucher material. Off Fort Pierce Inlet, 27°28.8'N, 80°14.5'W, 15 m, 13.ii.1974, R/V *Gosnold* Station 220/224, 10-foot otter trawl, four colony fragments, on bryozoans and algae, up to 1.3 cm high, without gonophores, ROMIZ B1078.

Remarks. Contrary to information in synonymy lists of several papers reporting on this species, the original description of *Sertularia loculosa* by Busk (1852) was not accompanied by illustrations. Busk's unfortunate omission of them led to much confusion over the identity and synonymy of the species. The first published figures of *S. loculosa* were by Bale (1884: pl. 4, figs. 5–6, pl. 9, fig. 12, pl. 19, fig. 9), drawn from sketches sent to him by Busk, but they too were misleading in that they showed pronounced marginal cusps bordering the rim of each hydrotheca. Those inaccurate drawings led Billard (1909) to mistakenly assume that *S. loculosa* was conspecific with *S. turbinata* (Lamouroux, 1816). A more representative drawing of *S. loculosa*, based on type material, was not published until later (Bale 1913, pl. 12, fig. 6, under *S. turbinata*). Problems surrounding the history and synonymy of the species were reviewed and clarified by Billard (1927), who concluded that *S. loculosa* was indeed valid and that *S. ligulata* Thornely, 1904 was identical to it. Migotto (1996) examined type material and confirmed the identity and validity of the species.

A strap-like "ligula" or nematophore, extending from the adcauline side of the hydranth and curving towards the hydrothecal orifice, is diagnostic of the species. It was poorly preserved in most hydranths of the colony examined here.

Sertularia loculosa has been assigned here provisionally to *Tridentata* Stechow, 1920. Besides the presence of a characteristic ligula, marginal cusps are inconspicuous and the valves of the operculum differ greatly in size, as noted by Schuchert (2003). Molecular studies are needed to better establish its generic identity. It is clearly not congeneric with *Sertularia argentea* Linnaeus, 1758, type species of *Sertularia* Linnaeus, 1758.

Reported distribution. Atlantic coast of Florida. First record.

Western Atlantic. Florida (this study) to Brazil (Oliveira *et al.* submitted, as *Sertularia loculosa*), including Bermuda (Calder 2000) and the Caribbean Sea (Calder & Kirkendale 2005; Galea 2008, as *S. loculosa*).

Elsewhere. Warm eastern Atlantic; Indo-Pacific (Schuchert 2003, S. loculosa).

Tridentata marginata (Kirchenpauer, 1864)

Fig. 9e, f

Dynamena marginata Kirchenpauer, 1864: 13, figs. 8a–c. *Tridentata marginata*.—Jones, 2002: 218.

Type locality. "Mare pacificum," on Sargassum (Kirchenpauer 1864).



FIGURE 9. a, Sertularella unituba: part of hydrocaulus with two hydrothecae, ROMIZ B1099, scale equals 0.25 mm. b, Sertularella unituba: gonotheca, ROMIZ B1099, scale equals 0.25 mm. c, Tridentata distans: part of hydrocaulus with four hydrothecal pairs, ROMIZ B3968, scale equals 0.20 mm. d, Tridentata loculosa: part of hydrocaulus with two hydrothecal pairs, ROMIZ B1078, scale equals 0.20 mm. e, Tridentata marginata: part of hydrocaulus with two hydrothecal pairs, ROMIZ B3969, scale equals 0.35 mm.; f, Tridentata marginata: gonotheca, ROMIZ B3969, scale equals 0.25 mm. g, Tridentata turbinata: part of hydrocaulus with two hydrothecal pairs, ROMIZ B3969, scale equals 0.25 mm. hydrochecal pairs, ROMIZ B3970, scale equals 0.25 mm. hydrocladium with hydrothecae, ROMIZ B1079, scale equals 0.25 mm. i, Synthecium tubithecum: part of hydrocladium with two hydrothecal pairs, ROMIZ B1074, scale equals 0.25 mm.

Voucher material. Bethel Shoal off Vero Beach, 27°42.6'N, 80°06.8'W, 24 m, 18.ii.1976, *Johnson-Sea-Link*, JSL 328, diver lockout, two plumes, up to 4 cm high, without gonothecae, coll. S. Nelson, ROMIZ B1095.—Fort Pierce, Fort Pierce Inlet State Park, 27°28'29.5"N, 80°17'25.8"W, on stranded *Sargassum* sp., 14.vii.2012, 28° C, 35‰, collected manually, one colony, 1.5 cm high, with gonophores, coll. D.R. Calder, ROMIZ B3969.

Remarks. *Tridentata marginata* (Kirchenpauer, 1864) and *Desmoscyphus inflatus* Versluys, 1899 (also known as *Sertularia inflata* and *Tridentata inflata*) are held to be conspecific here. The hydroid is common in shallow-waters of the southeastern United States on both benthic substrates and floating *Sargassum*. It is one of the few species of sertulariid hydroids known to liberate a free medusoid (Migotto 1998).

Hydrothecae of *Tridentata marginata* resemble those of *T. turbinata* (Lamouroux, 1816), including the presence of a horseshoe-shaped ridge of perisarc on the internal surface of the abcauline wall below the orifice. The species differs from *T. turbinata* in having alternately branched instead of unbranched colonies. Although very young colonies of *T. marginata* may be unbranched as in *T. turbinata*, they can be distinguished from that species in having much smaller hydrothecae (e.g., diameter at base 75–98 µm vs. 121–149 µm).

This species has often been assigned to *Sertularia* Linnaeus, 1758 instead of *Tridentata* Stechow, 1920. Major differences separate the two genera, apparent from a comparison of *Sertularia argentea* Linnaeus, 1758, type species of *Sertularia*, and *Sertularia perpusilla* Stechow, 1919, type species of *Tridentata*. Evidence of their distinctive morphological differences, briefly noted earlier (Calder 1991a: 104) has also been supported by molecular data (Moura *et al.* 2011). Although it may be polyphyletic as presently constituted, recognition of the genus *Tridentata* is, once again, upheld here. As for *T. marginata*, it was shown by Moura *et al.* to be very close genetically to *T. perpusilla*, type species of that genus.

Reported distribution. Atlantic coast of Florida. Biscayne Bay (Jones 2002).

Western Atlantic. North Carolina (Fraser 1944, as *Sertularia inflata*) to Brazil (Oliveira *et al.* submitted, as *S. marginata*), including Bermuda (Calder 1991a), the Gulf of Mexico (Calder & Cairns 2009), and the Caribbean Sea (Galea 2008, as *S. marginata*). The species is carried north of Cape Hatteras to New England on pelagic *Sargassum* in the Gulf Stream (Hargitt 1908, as *S. versluysi* Nutting, 1904).

Elsewhere. Circumglobal in tropical and warm-temperate waters (Migotto 1998, as *S. marginata*; Vervoort & Watson 2003, as *S. marginata*).

Tridentata turbinata (Lamouroux, 1816)

Fig. 9g

Dynamena turbinata Lamouroux, 1816: 180.

Type locality. "Sur les Fucus de l'Australasie" (Lamouroux 1816).

Voucher material. Fort Pierce Inlet, north jetty, north side, 27°28'24.1"N, 80°17'21.2"W, intertidal zone, on benthic algae, 14.vii.2012, 28° C, 35‰, collected manually, about four colonies, up to 1.1 cm high, without gonothecae, coll. D.R. Calder, ROMIZ B3970.

Remarks. This species has sometimes been identified as *Sertularia brevicyathus* (Versluys, 1899) in the western North Atlantic. However, most authors have followed Billard (1925) in assigning that binomen to the synonymy of *Dynamena turbinata* Lamouroux, 1816. As in earlier work (Calder 1991a), the species is referred herein to the genus *Tridentata* Stechow, 1920. Detailed taxonomic accounts of *T. turbinata* have been given elsewhere (e.g., Calder 1991a; Medel & Vervoort 1998, as *Sertularia turbinata*).

Reports of *T. turbinata* have been based most often on sterile material, and gonophores were lacking in present material from the east coast of Florida. Gonothecae of the species are barrel-shaped with transverse ridges, and with a wide terminal aperture (e.g., Stechow 1919, as *Sertularia brevicyathus*; Millard 1975, as *S. turbinata*; Hirohito 1995, as *S. turbinata*).

Tridentata turbinata is a hydroid of tropical and subtropical waters, extending northwards in the western North Atlantic to the Tortugas (Leloup 1935, as *Sertularia turbinata*), the Bahamas (Leloup 1937, as *S. turbinata*), and Bermuda (Calder 1991a). It has also has been reported as part of the *Sargassum* fauna in the region (Burkenroad, in Parr 1939, as *S. brevicyathus*).

Reported distribution. Atlantic coast of Florida. First record.

Western Atlantic. Fort Pierce, Florida (this study) to Brazil (Oliveira et al. submitted, as Sertularia turbinata),

including Bermuda (Calder 1991a), the Gulf of Mexico (Calder & Cairns 2009), and the Caribbean Sea (Calder & Kirkendale 2005).

Elsewhere. Circumglobal in tropical and subtropical waters (Millard 1975, as S. turbinata).

Family Syntheciidae Marktanner-Turneretscher, 1890

Hincksella brevitheca Galea, 2009

Fig. 9h

Hincksella brevitheca Galea, 2009: 61, figs. 1B, 2A-I.

Type locality. Cuba: off Cayo Largo (21°35'06"N, 81°35'19" W), 15 m (Galea 2009).

Voucher material. Palm Beach, 0.75 miles (1.2 km) offshore, 29 m, 22.vii.1974, *Johnson-Sea-Link*, JSL 1173, diver lockout, one colony, 2.3 cm high, without gonophores, coll. J. Prentice, ROMIZ B1079.

Remarks. *Hincksella brevitheca* Galea, 2009, recently described from Cuba, is reported for only the second time. Similar nominal species in the western Atlantic include *Sertularella formosa* Fewkes, 1881 and *S. hartlaubi* Nutting, 1904, both of which are referable to Syntheciidae Marktanner-Turneretscher, 1890 and to the genus *Hincksella* Billard, 1918, as currently defined. Galea (2009) examined type material of *Hincksella hartlaubi* and concluded that it was conspecific with *H. formosa*, a conclusion also held by Vervoort (1959).

As with the original account of *Hincksella brevitheca* by Galea (2009), material from Florida had (1) stem internodes each with three hydrothecae and an apophysis bearing a hydrocladium, (2) hydrocladia with few or no nodes, (3) shallow and deeply immersed hydrothecae, each thickened at the margin and given off at an angle of about 30° with the stem. These characters distinguish the species from others of the genus.

Although previously known only from southern Cuba, Galea (2009: 63) noted that the species presumably occurs throughout the Caribbean Basin. In support of his view, two additional records of it from the Caribbean can be added here based on material in collections at the Royal Ontario Museum (Cayman Islands: Grand Cayman Island, caves in coral reef west side, just north of Georgetown, 10 m, 26.xi.1980, one colony, without gonophores, coll. A. Logan, ROMIZ B1990; Panama: Bocas del Toro area, Swan's Key, 09°27'12.2"N, 82°18'01.8"W, 1–4 m, 07.viii.2004, two colonies, without gonophores, coll. L. Kirkendale, no collection number). The specimens from Panama were reported as *Sertularella hartlaubi* by Calder & Kirkendale (2005).

Gonophores of the species have yet to be described.

Reported distribution. Atlantic coast of Florida. First record.

Western Atlantic. Florida (reported herein) to the Caribbean Sea (Galea 2009; Calder & Kirkendale 2005, as *Sertularella hartlaubi*).

Synthecium tubithecum (Allman, 1877)

Fig. 9i

Sertularia tubitheca Allman, 1877: 24, pl. 16, figs. 5, 6.

Type locality. USA: Florida, Tortugas (Allman 1877).

Voucher material. Palm Beach, 0.75 miles (1.2 km) offshore, 29 m, 22.vii.1974, *Johnson-Sea-Link*, JSL 1173, diver lockout, one colony, 2 cm high, without gonophores, coll. J. Prentice, ROMIZ B1074.

Remarks. *Synthecium tubithecum* (Allman, 1877) is widespread in tropical and subtropical regions of the western Atlantic (e.g., Nutting 1904; Fraser 1944; Vervoort 1968; Wenner *et al.* 1984; Galea 2010; Oliveira *et al.* submitted). Its occurrence outside the region has been questioned (Calder 1991a).

Reported distribution. Atlantic coast of Florida. First record.

Western Atlantic. Continental shelf of South Carolina (Nutting 1904) to Brazil (Oliveira *et al.* submitted), including Bermuda (Calder 1991a), the Gulf of Mexico (Calder & Cairns 2009), and the Caribbean Sea (Galea 2010).

Elsewhere. Questionably from the Gold Coast (Ghana), eastern Atlantic (Buchanan 1957).

Family Plumulariidae McCrady, 1859

Dentitheca dendritica (Nutting, 1900)

Fig. 10a

Plumularia dendritica Nutting, 1900: 67, pl. 8, figs. 4-6.—Jones, 2002: 217.

Dentitheca dendritica.—Humann, 1992: 73, middle photograph.—Humann & DeLoach, 2002: 73, middle photograph.— Cairns et al., 2002: 55.

Type locality. Bahamas: near Little Cat Island (Nutting 1900: 67).

Voucher material. Palm Beach, 1.42 miles (2.3 km) offshore, 30.5 m, 23.vii.1974, *Johnson-Sea-Link*, JSL1174, diver lockout, one colony fragment, 7 cm high, without gonophores, coll. J. Prentice, ROMIZ B1127.— Palm Beach Inlet, 80 feet (24 m), February 1991, sandy flat, two colony fragments, up to 13 cm high, without gonophores, coll. P. Humann, ROMIZ B1130.

Remarks. *Dentitheca dendritica* Nutting, 1900 is, as its specific name implies, tree-like in colony form. Hydroids are robust, arborescent, and reach nearly a half-metre high (Nutting 1900), and as noted two paragraphs below it may grow even taller. According to Humann (1992) and Humann & DeLoach (2002), it is found on reef tops, outcroppings along walls, and flat substrates, particularly in areas swept by currents. The plane of the colony is oriented perpendicular to the direction of water flow.

Sphaerocystis heteronema Fraser, 1943, originally described from the Bahamas, is considered identical with *Dentitheca dendritica* (Calder 1997: 8; Galea 2010: 28). The tropical Indo-Pacific *D. habereri* (Stechow, 1909) has generally been maintained as a distinct species (e.g., Ryland & Gibbons 1991; Hirohito 1995; Schuchert 2003; Kirkendale & Calder 2003; Di Camillo *et al.* 2010). Nutting (1927) found that specimens from the Philippines "agree very exactly" with descriptions, illustrations, and type material of *D. dendritica*, and he identified them as such. However, Galea *et al.* (2012) established that gonothecae of *D. dendritica* originate as replacements of nematothecae adjacent to hydrothecae or on the apophyses, whereas those of *D. habereri* arise in axils of internode apophyses. *Dentitheca bidentata* (Jäderholm, 1920) from Brazil is a much smaller species than *D. dendritica*, with colonies reaching only about 4 cm high (Migotto & Marques 1999). Cusps on the hydrothecal margin of that species are both more pronounced and more distant from the hydrocladial axis than in *D. dendritica*, and hydrothecae are not as deep.

Zoanthids are commonly associated with these large hydroids. Two species were reported by Swain (2009) on *Dentitheca dendritica* in the western Atlantic, *Hydrozoanthus tunicans* (Duerden, 1900) and the newly described *H. antumbrosus* (Swain, 2009), while both *Hydrozoanthus gracilis* (Lwowsky, 1913) and *Parazoanthus* sp. (probably *Hydrozoanthus* sp.) have been reported on *D. habereri* in the Indo-west Pacific (Di Camillo *et al.* 2010). Noteworthy is Duerden's (1900) account of *Parazoanthus tunicans* (now *Hydrozoanthus*), found on a species of hydroid from Jamaica that was likely *D. dendritica*. The hydroid reached "...as much as 100 cm. high."

Gonothecae of *Dentitheca dendritica* were unknown until being discovered and illustrated recently by Wedler (2004, in hydroids identified as *D. habereri*). Even more recently, Galea *et al.* (2012) found that gonophores of both sexes are cryptomedusoids retained within the pear-shaped to conical gonothecae. By contrast, gonothecae of *D. habereri* are described as bell-shaped (Hirohito 1995; Schuchert 2003; Di Camillo *et al.* 2010), and the gonophores of *D. bidentata* are short-lived medusoids (Migotto & Marques 1999). According to both Wedler and Galea *et al.*, the duration of gonophore production in *D. dendritica* appears to be very brief.

Colonies of Dentitheca dendritica are reported to sting bare skin (Humann 1992; Humann & DeLoach 2002).

Reported distribution. Atlantic coast of Florida. Palm Beach (Humann 1992; Humann & DeLoach 2002, based on material listed above; Cairns *et al.* 2002).—Biscayne Bay (Jones 2002, as *Plumularia dendritica*).

Western Atlantic. Florida (Humann 1992) and the Bahamas (Vervoort 1968, as *Plumularia dendritica*) to the Caribbean Sea (Galea 2010).

Elsewhere. If *Dentitheca habereri* is conspecific, the species also inhabits the tropical western Pacific and Indian oceans (Di Camillo *et al.* 2010).



FIGURE 10. a, *Dentitheca dendritica*: part of hydrocladium with two hydrothecae, ROMIZ B1130, scale equals 0.10 mm. b, *Nemertesia simplex*: apophysis and basal part of hydrocladium, ROMIZ B1121, scale equals 0.20 mm. c, *Nemertesia simplex*: part of hydrocladium with hydrotheca, ROMIZ B1121, scale equals 0.10 mm. d, *Plumularia floridana*: part of hydrocaulus with basal parts of two hydrocladia, and three hydrothecae, ROMIZ B1080, scale equals 0.25 mm. e, *Plumularia setacea*: part of hydrocaulus with basal parts of two hydrocladia, a female gonotheca, and a hydrotheca, ROMIZ B1111, scale equals 0.20 mm. f, *Plumularia strictocarpa*: part of hydrocaulus with basal parts of two hydrocaulus and three hydrothecae, ROMIZ B3971, scale equals 0.20 mm.

Nemertesia simplex (Allman, 1877)

Fig. 10b, c

Antennularia simplex Allman, 1877: 34, pl. 21, figs. 1, 2.

Type locality. USA: Florida, off Alligator Reef, 86 fathoms (157 m) (Allman 1877: 34).

Voucher material. Hoskin Reef off Vero Beach, 27°41.4'N, 79°59.1'W, 65 m, 02.vi.1982, *Johnson-Sea-Link I*, JSL 1197, one colony, up to 9 cm high, without gonophores, 3.7 cm high, without gonothecae, coll. C. Hoskin, ROMIZ B1121.—Off Sebastian Inlet, 27°47.2'N, 79°57.2'W, 110–99 m, 28.vi.1978, 10-foot try net, one colony, up to 46 cm high, with gonophores, coll. J. Miller, ROMIZ B1122.

Remarks. *Nemertesia simplex* (Allman, 1877) is poorly known. The only original records of the species other than that of Allman (1877), from the Alligator Reef area in the Straits of Florida, are those of Nutting (1900). He reported *N. simplex* in collections taken off Cape Henry, Virginia, Cape Hatteras, North Carolina, and Havana, Cuba, during *Albatross* cruises, and from the Pourtalès Plateau (Straits of Florida) in material from the 1893 Bahamas Expedition of the State University of Iowa. Moreover, the only illustrations of the species prior to now are the two of Allman (1877). Nutting included a copy of Allman's magnified figure of the species in his monograph on plumularioids but gave no illustrations of his own material. The present record from the east coast of Florida falls within the stated geographic and bathymetric range (48–373 fathoms = 88–682 m) of the species.

Characters differentiating *N. simplex* from its congeners were tabulated by Ramil & Vervoort (2006). They upheld opinions of Allman (1877) and Nutting (1900) that it has affinities with *N. ramosa* (Lamarck, 1816). Both
have monomeric or mostly monomeric hydrocladia. Morphological differences distinguishing *Nemertesia simplex* from *N. ramosa* include the following: (1) the hydrocaulus is monosiphonic and unbranched or only slightly branched rather than polysiphonic and much branched; (2) hydrothecal margins tend to slope at an oblique angle to the axis of the hydrocladium rather than being perpendicular to it. Gonothecae, of the usual type in this genus (Ramil & Vervoort 2006), are quite small, ovoid, and with an oblique aperture (Nutting 1900). They arise from apophyses of the hydrocladia.

Reported distribution. Atlantic coast of Florida. First record.

Western Atlantic. Offshore waters of Virginia to the Gulf of Mexico (Nutting 1900).

Plumularia floridana Nutting, 1900

Fig. 10d

Plumularia floridana Nutting, 1900: 59, pl. 2, figs. 4-5.—Jones, 2002: 217.

Type locality. USA: Florida, "two miles west of Cape Romano..." (Nutting 1990: 59).

Voucher material. Off Vero Beach, 27°41.2'N, 80°14.5'W, 17 m, 13.ii.1974, small biological dredge, R/V *Gosnold* Station 220/226, four colony fragments, up to 1.9 cm high, without gonophores, ROMIZ B1080.

Remarks. Material examined here came from a station on the inner continental shelf off Vero Beach. With the exception of its occurrence on floating *Sargassum* (Fraser 1944), *Plumularia floridana* Nutting, 1900 is a species more frequently recorded inshore than offshore along the southeastern United States. While common in estuaries of South Carolina (Calder & Hester 1978; Calder 1983), it has not yet been reported from hard bottom areas on the shelf between North Carolina and Florida (Cain 1972; Wenner *et al.* 1984). As noted earlier (Calder 1997), the species is eurytopic, surviving temperatures down to 10° C and salinities as low as 25‰.

An extensive synonymy of this species is listed in Ansín Agís *et al.* (2001), who described material from the Canary Islands.

Reported distribution. Atlantic coast of Florida. Biscayne Bay (Jones 2002).

Western Atlantic. South Carolina (Calder 1983) to Brazil (Oliveira *et al.* submitted), including Bermuda (Calder 1997) and the Gulf of Mexico (Calder & Cairns 2009). It extends northwards to New England on *Sargassum* (Fraser 1944).

Elsewhere. Believed to be circumglobal, mostly in tropical and warm-temperate waters (Ansín Agís *et al.* 2001).

Plumularia setacea (Linnaeus, 1758)

Fig. 10e

Sertularia setacea Linnaeus, 1758: 813. Plumularia setacea.—Deevey, 1950: 347, fig. 6.

Type locality. UK: Brighton ("Brighthelmstone") and Whitstable (Ellis 1755: 19, as *Corallina setacea*). Linnaeus (1758) gave the binomen *Sertularia setacea* to the species described by Ellis, listing its locality only as "Habitat in Oceano."

Voucher material. Off Vero Beach, 27°41.2'N, 80°14.5'W, 17 m, 13.ii.1974, small biological dredge, R/V *Gosnold* Station 220/226, several colony fragments, up to 2.4 cm high, without gonophores, ROMIZ B1077.—Fort Pierce Inlet, north jetty, north side, 27°28'24.2'N, 80°17'20.3"W, low water, on polychaete tubes, 15.ii.1991, 20° C, collected manually, six colony fragments, up to 2.1 cm high, with gonophores, coll. D.R. Calder, ROMIZ B1111.

Remarks. *Plumularia setacea* (Linnaeus, 1758) and *P. strictocarpa* Pictet, 1893 are generally said to be indistinguishable morphologically in the absence of reproductive structures. Part of the material examined here (ROMIZ B1111) bore gonophores protected by fusiform gonothecae, typical of *P. setacea*. Specimens from shelf waters off Vero Beach (ROMIZ B1077), although sterile, were assigned to the same species based on the size of the

colonies, larger than normally found in *P. strictocarpa*, and their identical appearance to colonies from Fort Pierce Inlet (ROMIZ B1111) having gonophores.

Also somewhat resembling *Plumularia setacea* are three less well known species originally described from the Straits of Florida region, *P. filicula* Allman, 1877, *P. attenuata* Allman, 1877, and *P. megalocephala* Allman, 1877. As noted earlier (Calder 1997), all appear to differ from the present species in having hydrocladial apophyses with pronounced cylindrical extensions distal to the mamelon, and in bearing a nematotheca on the proximalmost (ahydrothecate) internode of each hydrocladium. Moreover, gonothecae of *P. filicula*, as described and illustrated by Allman (1877), have a wide, oblique aperture rather than a small circular one at the end of a narrow neck as in *P. setacea*. In *P. attenuata*, all hydrocladial internodes beyond the proximalmost one are hydrothecate instead of being alternately hydrothecate and athecate. Hydrocauli of *P. megalocephala* were described by Allman as being irregularly branched, whereas those of *P. setacea* are usually unbranched or only sparingly branched. In some respects these hydroids resemble species of *Nemertesia* Lamouroux, 1812, but further study is needed to confirm their generic affinities.

Thorough taxonomic accounts of *Plumularia setacea* are given by Ansín Agís *et al.* (2001) and Schuchert (2013).

Reported distribution. Atlantic coast of Florida. Central east coast of Florida (Deevey 1950, distribution map).

Western Atlantic. Marthas Vineyard (Fraser 1944) to Argentina (Oliveira *et al.* submitted), including Bermuda (Calder 1997), the Gulf of Mexico (Calder & Cairns 2009), and the Caribbean Sea (Galea 2010).

Elsewhere. Cosmopolitan except for polar regions (Ansín Agís et al. 2001; Schuchert 2013).

Plumularia strictocarpa Pictet, 1893

Fig. 10f

Plumularia strictocarpa Pictet, 1893: 55, pl. 3, figs. 47-49.—Jones, 2002: 218.

Type locality. Indonesia: "Baie d'Amboine" (Pictet 1893).

Voucher material. Beach north of Jupiter Inlet, 26°56'45"N, 80°04'16"W, washed ashore on a tarball, 20.ii.1991, collected manually, one colony, up to 6 mm high, without gonophores, coll. D.R. Calder, ROMIZ B1109.—Sebastian Inlet, 27°51'43"N, 80°26'47"W, washed ashore on *Sargassum*, 19.ii.1991, collected manually, one colony, up to 8 mm high, without gonophores, coll. D.R. Calder, ROMIZ B3971.—Fort Pierce, Fort Pierce Inlet State Park, 27°28'29.5"N, 80°17'25.8"W, on stranded *Sargassum fluitans*, 14.vii.2012, 28° C, 35‰, collected manually, two colonies, up to 6 mm high, without gonophores, coll. D.R. Calder, ROMIZ B3972.

Remarks. *Plumularia strictocarpa* Pictet, 1893 resembles *P. setacea* (Linnaeus, 1758), but its gonothecae are barrel- to cocoon-shaped with spiral annulations instead of being fusiform with smooth walls. Its colonies also tend to be much smaller. It is one of the more abundant species on pelagic *Sargassum* in the western North Atlantic (Calder, 1995, 1997).

Reported distribution. Atlantic coast of Florida. Biscayne Bay (Jones 2002).

Western Atlantic. From the Gulf Stream off Nova Scotia (Fraser 1918, on *Sargassum*, as *Plumularia setaceoides* Bale, 1882) to Brazil (Oliveira *et al.* submitted), including Bermuda (Calder 1991a), the Gulf of Mexico (Calder & Cairns 2009), and the Caribbean Sea (Calder & Kirkendale 2005).

Elsewhere. Circumglobal, tropical and subtropical waters (Kirkendale & Calder 2003).

Family Halopterididae Millard, 1962

Antennella gracilis Allman, 1877 Fig. 11a, 12

Antennella gracilis Allman, 1877: 38, pl. 22, figs. 6, 7. *Antennella secundaria.*—Schuchert 1997: 14, fig. 4d, e [part].



FIGURE 11. a, *Antennella gracilis*: part of hydrocaulus with two hydrothecae, ROMIZ B1090, scale equals 0.25 mm. **b**, *Antennella incerta*: front view of hydrotheca, showing laterally-displaced axillar nematotheca, ROMIZ B3973, scale equals 0.25 mm. **c**, *Antennella incerta*: hydrocaulus with three hydrothecae, ROMIZ B3973, scale equals 0.25 mm. **d**, *Halopteris alternata*: part of hydrocaulus with a hydrocladium and two hydrothecae, ROMIZ B3974, scale equals 0.20 mm. **e**, *Halopteris alternata*: part of hydrocladium with two hydrothecae, ROMIZ B3974, scale equals 0.20 mm. **f**, *Halopteris carinata*: part of hydrocladium with two hydrothecae, ROMIZ B1128, scale equals 0.20 mm. **g**, *Halopteris carinata*: male gonotheca, ROMIZ B1128, scale equals 0.25 mm. **h**, *Halopteris carinata*: female gonotheca with two nematothecae, ROMIZ B1128, scale equals 0.25 mm.



FIGURE 12. *Antennella gracilis*, nematocysts, ROMIZ B1090. **a**, seed-shaped heteroneme, from tentacle; **b**, microbasic mastigophore, from tentacle; **c**, merotrichous isorhiza, from nematophore; **d**, discharged merotrichous isorhiza; **e**, part of thread of merotrichous isorhiza, showing mid-portion of thread with spines.

Type locality. USA: Florida, off Carysfort Reef (Allman 1877: 38).

Voucher material. Off St. Lucie Inlet, 27°11.8'N, 79°57.3'W, 87 m, 04.x.1986, *Johnson-Sea-Link*, J028/JSL 2132, submersible lockout, one colony, up to 2.3 cm high, without gonophores, coll. R. Roesch, ROMIZ B1090.

Remarks. Antennella gracilis Allman, 1877, originally described from the southeast coast of Florida, has been regarded in several contemporary works (e.g., Cornelius 1995b; Calder 1997; Schuchert 1997; Cairns *et al.* 2002; Ansín Agís *et al.* 2001; Vervoort & Watson 2003) as coterminous with *A. secundaria* (Gmelin, 1791), a Mediterranean species with a supposed worldwide distribution. The two appear much alike. However, Schuchert (1997: 15–18) recently discovered that the voucher material listed above (ROMIZ B1090), while identified as and resembling *A. secundaria*, differed from European and Indian Ocean material of that species in both cnidome and in morphology of lateral nematothecae. Large nematocysts were elongate and nearly cylindrical, and thought to be macrobasic mastigophores (19–23 μ m x 5.5–6.5 μ m), rather than elongate-oval microbasic mastigophores (10.5–

13.5 μ m x 4.0–5.0 μ m). As for lateral nematothecae, the upper chamber was conical and emarginated rather than conical with innerside significantly lowered, while the cavity of the lower chamber was marked by perisarcal ridges rather than appearing smooth. Schuchert noted that the examined material from Florida might belong to a different species, a suggestion taken here to be correct. Rather than assigning it to a new species, however, the material is referred to a resurrected *A. gracilis*, partly on morphological grounds (it corresponds in most respects with the description by Allman 1877) and partly on zoogeographic grounds (the collection site is within two degrees of latitude of the type locality of the species off the southeast coast of Florida).

The type of *Antennella gracilis* (MCZ, no catalog number) was examined earlier by both Calder (1997) and Schuchert (1997). It appears to have been dry at some time in the past, and has also been combined in the same bottle with specimens of *Monostaechas quadridens* McCrady, 1859. While the material is in unsatisfactory condition, a small axillary nematotheca is present contrary to the report of Fraser (1944: 315), who indicated that it was of normal size and situated some distance from the hydrotheca. Fraser was misled by an imperfect illustration of the species by Allman (1877).

Three kinds of nematocysts, namely seed-shaped heteronemes, microbasic mastigophores, and what are believed to be merotrichous isorhizas (but considered macrobasic mastigophores by Schuchert 1997), were observed in material examined here (Fig. 12).

Due to the brief description and imprecise illustration of *Antennella gracilis* by Allman (1877), as well as its subsequent confusion with *A. secundaria*, the distribution of this species is uncertain.

Reported distribution. Atlantic coast of Florida. Off Carysfort Reef (Allman 1877).—Off St. Lucie Inlet (Schuchert 1997, as *Antennella secundaria*).

Western Atlantic. North Carolina (Nutting 1900) to the Caribbean Sea (Vervoort 1968; Bandel & Wedler 1987), including Bermuda (Calder 1997, as *Antennella secundaria*) and the Gulf of Mexico (Calder & Cairns 2009, as *A. secundaria*).

Elsewhere. Records from the Indian Ocean (Thornely 1904), western Pacific (Stechow 1913; Hargitt 1924), and eastern Pacific (Fraser 1948) need verification.

Antennella incerta Galea, 2010

Fig. 11b, c

Antennella incerta Galea, 2010: 25, figs. 6H¹, J, K.

Type locality. Guadeloupe: Grande-Terre, L'Oeil (16°26.782'N, 61°32.405'W) (Galea 2010: 4).

Voucher material. West Palm Beach, on reef seaward of the Breakers Hotel, 45 feet (13.7 m), on stems of *Halopteris carinata*, January 1991, SCUBA, two colonies, up to 2.5 mm high, without gonophores, coll. P. Humann, ROMIZ B3973.

Remarks. Cormoids of *Antennella incerta* Galea, 2010 are remarkably small and slender, and specimens might easily be overlooked or mistaken for juveniles of another species. Colonies of *A. incerta* are distinguished in particular by having a single, laterally-displaced axillar nematotheca distal to each hydrotheca (Fig. 11b), and a pair of lateral nematothecae that are mug-shaped and deeply emarginated on the adcauline side, each borne on a long apophysis that reaches nearly to the hydrothecal margin (Fig. 11c). A perisarcal thickening marks the inner abcauline wall of the hydrotheca just above the base. Thecate internodes are saddle-shaped, and the terminal one of a hydrocladium does not extend beyond the axil between it and the hydrotheca or the bases of the nematothecal apophyses.

This is only the second report of *A. incerta*, extending its known range northwards from the Caribbean Sea.

Reported distribution. Atlantic coast of Florida. First record.

Western Atlantic. Florida (this study) to Guadeloupe (Galea 2010).

Halopteris alternata (Nutting, 1900)

Fig. 11d, e

Plumularia alternata Nutting, 1900: 62, pl. 4, figs. 1, 2. *Plumularia diaphana.*—Weiss, 1948: 158 [not *Plumularia diaphana* (Heller, 1868)]. Type locality. Bahamas: Barracuda Rocks (Nutting 1900: 62).

Voucher material. West Palm Beach, on reef seaward of the Breakers Hotel, 45 feet (13.7 m), together with *Halopteris carinata*, January 1991, SCUBA, one colony, 2.5 cm high, without gonophores, coll. P. Humann, ROMIZ B3974.

Remarks. *Halopteris alternata* (Nutting, 1900) was originally described from material collected by Alexander Agassiz and party during the cruise of the steamer *Wild Duck* to the Bahamas in 1893. Most authors during the twentieth century followed Bedot (1914) in regarding it as coterminous with *H. diaphana* (Heller, 1868), a species originally described from the Adriatic Sea. However, several characters distinguishing *H. alternata* from *H. diaphana* were documented by Schuchert (1997): (1) an axillar nematotheca is usually present distal to cauline hydrothecae; (2) segmentation of the hydrocaulus is homomerous rather than heteromerous; (3) hydrocladial internodes usually have one rather than 2–3 nematothecae; (4) female gonothecae are fusiform and straight rather than being cornucopia-shaped. Based on such differences, *Halopteris alternata* is now taken to be a valid species, and material examined above is assigned to it.

Reported distribution. Atlantic coast of Florida. Biscayne Bay (Weiss 1948, as Plumularia diaphana).

Western Atlantic. South Carolina (Wenner *et al.* 1984, as *Halopteris diaphana*) to Brazil (Oliveira *et al.* submitted), including Bermuda (Calder 1997, as *H. diaphana*), the Gulf of Mexico (Calder & Cairns 2009), and the Caribbean Sea (Galea 2008). It is carried northwards to North Carolina (and probably beyond) on *Sargassum* and *Turbinaria* (Fraser 1912b, as *Plumularia alternata*).

Elsewhere. Eastern Atlantic (Ansín Agís *et al.* 2001). Records from the Pacific and Indian oceans are questionable (see Ansín Agís *et al.* 2001; Galea 2008).

Halopteris carinata Allman, 1877

Fig. 11f-h

Halopteris carinata Allman, 1877: 33, pl. 19, figs. 3–7.—Humann, 1992: 75, middle photograph.—Humann & DeLoach, 2002: 75, middle photograph.—Schuchert, 1997: 123, fig. 45.

Type locality. USA: Florida, off Carysfort Reef (Allman 1877).

Voucher material. Off Palm Beach, 26°48.4'N, 79°58.6'W, 36.6 m, *Johnson-Sea-Link*, JSL 288, 16.ix.1975, one colony, 9 cm high, without gonophores, coll. S. Nelson, ROMIZ B1084.—West Palm Beach, on reef seaward of the Breakers Hotel, 45 feet (13.7 m), January 1991, SCUBA, fragments of one or more large colonies, cormidia up to 11 cm high, with gonophores, coll. P. Humann, ROMIZ B1128.

Remarks. Significant taxonomic and nomenclatural problems exist within the genus Halopteris Allman, 1877. First, the name is threatened by a seldom-used senior synonym (Halicornaria Hincks, 1865; type species Plumularia catharina Johnston, 1833, by monotypy; not Halicornaria Allman 1874 = Gymnangium Hincks, 1874). In the interests of nomenclatural stability, the well-known name *Halopteris* is designated herein as valid and as a nomen protectum, while Halicornaria Hincks, 1865 (not Halicornaria Allman, 1874) is relegated to a nomen oblitum by adopting Reversal of Precedence provisions (ICZN Art. 23.9.1.1). Thus, Halicornaria sensu Hincks has not been used as a valid name in zoology after 1899, whereas Halopteris has been utilized in more than 25 works by numerous authors (>10) in the past 50 years (e.g., Vervoort 1968, 2006; Millard 1975; Rees & Vervoort 1987; Gili et al. 1989; Cornelius 1995b; Hirohito 1995; Migotto 1996; Calder 1997; Schuchert 1997, 2003; Watson 2000; Ansín Agís et al. 2001; Cairns et al. 2002; Peña Cantero & García Carrascosa 2002; Grohmann et al. 2003; Vervoort & Watson 2003; Calder & Kirkendale 2005; Bouillon et al. 2006; Galea 2006, 2008, 2010; Altuna Prados 2007; Henry et al. 2008; Castellanos Iglesias et al. 2011). Second, misgivings were expressed earlier (Calder 1997: 33) about the overly broad scope of *Halopteris* as currently recognized and defined. Its type species, *Halopteris* carinata Allman, 1877, is decidedly different in hydrothecal and gonothecal morphology from other species presently assigned to the genus (see Schuchert 1997: 125). No changes to the existing classification and nomenclature of the genus are introduced here, but revision of Halopteris is warranted.

Gonothecae of both sexes were present on some cormidia in part of the material (ROMIZ B1128). Smaller male gonothecae were present on hydrocladia and larger female ones on hydrocauli (Figs. 11g, h).

One part of the material examined here (ROMIZ B1128) has been illustrated (as photographs) in the

guidebooks of Humann (1992) and Humann & DeLoach (2002), and the other (ROMIZ B1084) has been described by Schuchert (1997).

Reported distribution. Atlantic coast of Florida. Off Carysfort Reef (Allman 1877).—off Palm Beach area (Humann 1992; Schuchert 1997; Humann & DeLoach 2002).

Western Atlantic. South Florida and the Bahamas (Fraser 1944) to Brazil (Oliveira *et al.* submitted), including Bermuda (Calder 1997), the Gulf of Mexico (Calder & Cairns 2009), and the Caribbean Sea (Calder & Kirkendale 2005; Galea 2010; Castellanos Iglesias *et al.* 2011).

Elsewhere. Cape Verde Islands (Ansín Agís et al. 2001; Vervoort 2006).

Halopteris clarkei (Nutting, 1900)

Fig. 13a

Plumularia gracilis Clarke, 1879: 246, pl. 5, figs. 29, 30 [permanently invalid junior primary homonym of *Plumularia gracilis* Murray, 1860].

Plumularia clarkei Nutting, 1900: 61, pl. 3, fig. 5 [replacement name for *Plumularia gracilis* Clarke, 1879]. *Halopteris gracilis*.—Schuchert, 1997: 110, fig. 39.

Type locality. Cuba: off Havana, 175 fathoms (320 m) (Clarke 1879: 247).

Voucher material. Off St. Lucie Inlet, 27°11.8'N, 79°57.3'W, 87 m, 04.x.1986, *Johnson-Sea-Link*, J028/JSL 2132, one colony with several cormidia, up to 3.3 cm high, without gonophores, coll. R. Roesch, ROMIZ B1096.

Remarks. This species was originally described as *Plumularia gracilis* by Clarke (1879). That binomen, a junior primary homonym of *Plumularia gracilis* Murray, 1860, is permanently invalid (ICZN Art. 57.2). Nutting (1900) proposed *Plumularia clarkei* as a replacement name for the species, now currently assigned to *Halopteris* Allman, 1877 as *H. clarkei*. Nutting provided a new name in the belief that the binomen *P. gracilis* was preoccupied in works by Blainville (1834: 479) and Lamarck (1836: 167). However, the species referred to as *P. gracilis* in both of those works, and earlier in Blainville (1830: 443), was originally founded as *Aglaophenia gracilis* Lamouroux, 1816, and secondary homonymy with Clarke's (1879) *P. gracilis* no longer exists. Nutting, and later Stechow (1923), overlooked the more nomenclaturally important primary homonymy of *P. gracilis* Clarke, 1879 with Murray's (1860) use of the same binomen for a species from California.

A detailed account of this hydroid (as *Halopteris gracilis*) is given by Schuchert (1997), whose material included the colonies from Florida examined here (ROMIZ B1096). *Halopteris clarkei* has been reported infrequently, and it is known only from the warm western North Atlantic. It is immediately distinguished from the sympatric *H. diaphana* (Heller, 1868) and *H. alternata* (Nutting, 1900) in having opposite instead of alternate hydrocladia.

Reported distribution. Atlantic coast of Florida. Off St. Lucie Inlet (Schuchert 1997).

Western Atlantic. Continental shelf of Georgia (Wenner *et al.* 1984) to Cuba (Clarke 1879), and including the southeastern Gulf of Mexico (Calder & Cairns 2009).

Halopteris diaphana (Heller, 1868)

Fig. 13b–d

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

Type locality. Croatia: Capocesto (Primošten) (Heller 1868: 42).

Voucher material. Off Melbourne, 28°04.0'N, 80°12.8'W, 25 m, 01.iii.1974, R/V *Gosnold* Station 222/281B, Smith-McIntyre grab, several fragments of a colony, on a bivalve shell, up to 7 mm high, with gonophores, ROMIZ B3975.

Remarks. Material examined here was small and exceedingly slender, and its identity at first seemed uncertain. Within the genus *Halopteris* Allman, 1877, however, these specimens are clearly referable to the *H*. *diaphana* (Heller, 1868) group as recognized by Schuchert (1997). Amongst species of that group, they most closely resemble *H. diaphana*, *H. tenella* (Verrill, 1874), *H. alternata* (Nutting, 1900), and *H. violae* Calder,

Mallinson, Collins, & Hickman, 2003. Specimens resemble those of *H. diaphana, H. tenella*, and *H. violae* in the usual sequential segmentation of hydrocladia, with the first segment being very short and anematothecate, the second longer and nematothecate, and the third long and both nematothecate and hydrothecate. Female gonothecae are cornucopia-shaped, as in *H. diaphana* and *H. tenella*, rather than fusiform or nearly so as in both *H. alternata* and *H. violae*. Unlike in *H. alternata*, axillar nematothecae are absent on hydrocauli. Cauline internodes generally bear two nematothecae, as in *H. diaphana* and *H. tenella*. Most importantly, hydrocauli are heteromeric (including some cormoid stems that are unbranched, as in *Antennella* Allman, 1877), unlike any species in the group except *H. diaphana*. Based on Schuchert's (1997: 42) tabular comparison of species in the group, material at hand fully corresponds with characters of *H. diaphana* and is assigned to that species here. *Halopteris diaphana* has been justifiably reported before in the western Atlantic only from Brazil (Schuchert, 1997).

A revision of the taxonomy of *Halopteris diaphana* as now conceived is given by Schuchert (1997). In the western Atlantic, hydroids referable to *H. alternata* (Nutting, 1900) have often been misidentified as this species. **Reported distribution.** Atlantic coast of Florida. First record.

Western Atlantic. Melbourne, Florida (reported herein) and Brazil (Schuchert 1997).

Elsewhere. Mediterranean Sea (Schuchert 1997).



FIGURE 13. a, *Halopteris clarkei*: part of hydrocaulus with two hydrocladia and three hydrothecae, ROMIZ B1096, scale equals 0.25 mm. **b**, *Halopteris diaphana*: part of hydrocaulus with a hydrocladium and a hydrotheca, ROMIZ B3975, scale equals 0.20 mm. **c**, *Halopteris diaphana*: part of a hydrocladium with a hydrotheca and nematothecae, ROMIZ B3975, scale equals 0.10 mm. **d**, *Halopteris diaphana*: part of hydrocaulus with a hydrotheca and female gonotheca, ROMIZ B3975, scale equals 0.10 mm. **e**, *Monostaechas quadridens*: part of a hydrocladium with two hydrothecae and a female gonotheca, ROMIZ B1102, scale equals 0.25 mm. **f**, *Ventromma halecioides*: part of hydrocaulus with a hydrocladium and two hydrothecae, ROMIZ B1108, scale equals 0.20 mm.

Monostaechas quadridens (McCrady, 1859)

Fig. 13e

Plumularia quadridens McCrady, 1859: 199. *Monostaechas quadridens.*—Leloup, 1937: 108, figs 10A, B.—Schuchert, 1997: 130, fig. 47b–e. Type locality. USA: South Carolina, Charleston Harbor area, "floating in the water" (McCrady 1859: 199).

Voucher material. Off St. Lucie Inlet, 27°10.8'N, 80°00.8'W, 44 m, 21.vi.1977, *Johnson-Sea-Link*, diver lockout, JSL 2230-c, two colony fragments, 1.5 and 2 cm high, one with gonothecae, ROMIZ B1102.

Remarks. Originally described from South Carolina, *Monostaechas quadridens* McCrady, 1859 is ubiquitous in coastal waters off the southeastern United States (e.g., Fraser 1912b, 1943, 1944; Leloup 1937; Cain 1972; Wenner *et al.* 1983, 1984; Wendt *et al.* 1989; Schuchert 1997). Wenner *et al.* reported it as frequent in dredge (47%) and trawl (35%) samples from nine hard bottom sites on inner (17–22 m), middle (23–38 m), and outer (47–67 m) continental shelf areas of South Carolina and Georgia. In estuaries within the region, however, it has been found only as detached colonies (McCrady 1859; Calder 1983).

Detailed taxonomic accounts of *Monostaechas quadridens* include those of Schuchert (1997), whose material included the specimens from off St. Lucie Inlet examined here (ROMIZ B1102), and Ansín Agís *et al.* (2001), whose material came from the Canary Islands and the Cape Verde Islands.

Reported distribution. Atlantic coast of Florida. Off Miami and Jacksonville (Leloup 1937).—Off St. Lucie Inlet (Schuchert 1997).

Western Atlantic. Massachusetts (Nutting 1900, 1901) to Argentina (Oliveira *et al.* submitted), including Bermuda (Calder 2000), the Gulf of Mexico (Calder & Cairns 2009), and the Caribbean Sea (Galea 2010).

Elsewhere. Circumglobal, tropical and temperate waters (Schuchert 1997).

Family Kirchenpaueriidae Stechow, 1921a

Ventromma halecioides (Alder, 1859) Fig. 13f

Plumularia halecioides Alder, 1859: 353, pl. 12, figs. 1–5. *Ventromma halecioides.*—Jones, 2002: 218.

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

Voucher material. Fort Pierce, ship canal at Link Port, 27°32'05"N, 80°20'50"W, 0.1 m, 17.ii.1991, on prop roots of *Rhizophora mangle*, 15° C, 22‰, collected by snorkeling, 10 cormoids, up to 1.3 cm high, without gonophores, coll. D.R. Calder, ROMIZ B1108.

Remarks. Differences between the genera *Kirchenpaueria* Jickeli, 1883 and *Ventromma* Stechow, 1923 appear slight morphologically, and the two are frequently regarded as congeneric. The trophosome of *Ventromma* is distinguished by having nematophores with nematothecae, lacking in *Kirchenpaueria*. *Ventromma* is retained in this work based largely on evidence from molecular work (Leclère *et al.* 2007; Moura *et al.* 2008; Peña Cantero *et al.* 2010), showing that *V. halecioides* (Alder, 1859), its type species, is genetically distant from *Kirchenpaueria pinnata* (Linnaeus, 1758), type species of *Kirchenpaueria*.

A species often found inshore in quiet-water areas, *Ventromma halecioides* (Alder 1859) was found here on red mangroves bordering the canal leading into the harbor at the Harbor Branch Oceanographic Institution, Fort Pierce.

Reported distribution. Atlantic coast of Florida. Biscayne Bay (Jones 2002).

Western Atlantic. North Carolina (Fraser 1912b, as *Plumularia inermis* Nutting, 1900) to Brazil (Oliveira *et al.* submitted), including Bermuda (Calder 1997), the Gulf of Mexico (Calder & Cairns 2009), and the Caribbean Sea (Galea 2008, as *Kirchenpaueria halecioides*).

Elsewhere. Believed to be circumglobal in shallow tropical and warm-temperate waters (Calder 1997).

Family Aglaopheniidae Marktanner-Turneretscher, 1890

Aglaophenia dubia Nutting, 1900

Fig. 14a

Aglaophenia gracilis Allman, 1877: 42, pl. 25, figs. 1–4 [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 elongata*.—Bogle, 1975: 101, fig. 7.—Jones 2002: 218 [not *Aglaophenia elongata* Meneghini, 1845].

Type locality. USA: Florida, off Carysfort Reef (Allman 1877: 43, as Aglaophenia gracilis).

Voucher material. Off St. Lucie Inlet, 27°11.8'N, 80°00.6'W, 137 feet (42 m), 17.v.1976, *Johnson-Sea-Link*, JSL 2047, three cormoids, up to 8.8 cm high, without gonophores, coll. G. Melton, ROMIZ B1125.—Of Jupiter Inlet, 26°57.6'N, 79°59.4'W, 48 m, 17.i.1974, R/V *Gosnold* Station 216/128, 20-foot otter trawl, two cormoids, up to 4.8 cm high, without gonophores, ROMIZ B3976.—Off St. Lucie Inlet, 27°10.8'N, 80°00.8'W, 44 m, 03.ii.1977, *Johnson-Sea-Link*, JSL 2161, one cormoid, 1.6 cm high, without gonophores, coll. F. Stanton, ROMIZ B3977.

Remarks. This species was originally described from southeastern Florida as *Aglaophenia gracilis* by Allman (1877). That name is a permanently invalid junior primary homonym of *Aglaophenia gracilis* Lamouroux, 1816 (ICZN Art. 57.2). Nutting (1900) recognized the homonymy and proposed *Aglaophenia dubia* as a replacement name for Allman's species.

Aglaophenia dubia was referred to the synonymy of *A. elongata* Meneghini, 1845, a Mediterranean species, by Bedot (1921). Some subsequent authors who studied the species adopted that proposed synonymy (Leloup 1937; Van Gemerden-Hoogeveen 1965; Bogle 1975; Wedler 1975; Wenner *et al.* 1984; Jones 2002), while others did not (Fraser 1944; Deevey 1954; Rees & Thursfield 1965; Vervoort 1968). Bogle (1975) noted several differences between her material from the Straits of Florida and the original account of *A. elongata* by Meneghini (1845), but with considerable reservation retained that name for the western Atlantic species. Hydroids of the same morphotype from Bermuda were compared by me (Calder 1997) with accounts of the Mediterranean species by Svoboda & Cornelius (1991), as well as with material of *A. elongata* from Capo d'Enfola, Elba, Italy (ROMIZ B1231). A number of differences in the two were noted, particularly in corbula morphology. Corbulae of hydroids from Bermuda were elongate rather than egg-shaped, there were 6–14 instead of 4–6 pairs of nematocladia, free ribs were frequent instead of being absent, and peduncles bore 1–3 hydrothecae instead of just one. I therefore concluded that *A. dubia* was valid. Moreover, Svoboda and Cornelius noted that records of *A. elongata* outside the Mediterranean seemed erroneous.

Aglaophenia dubia and *A. flowersi* Nutting, 1900, the latter originally described from near Sand Key, Florida, have been considered identical (Leloup 1937; Bogle 1975; Calder 1997), and as such are simultaneous synonyms. Precedence was assigned to the name *A. dubia* following the First Reviser Principle (ICZN Art. 24.2) in nomenclature (Calder 1997). Additional taxonomic remarks on *A. dubia* are given in Bogle (1975, as *A. elongata*) and Calder (1997).

This species is usually found at intermediate depths in the warm western Atlantic. Its known bathymetric range is 11–274 m (Bogle 1975, as *A. elongata*).

Reported distribution. Atlantic coast of Florida. Off Carysfort Reef (Allman 1877, as *Aglaophenia gracilis*).—Straits of Florida (Bogle 1975, as *A. elongata*).—Biscayne Bay (Jones 2002, as *A. elongata*).

Western Atlantic. South Carolina/Georgia continental shelf (Wenner *et al.* 1984, as *A. elongata*) to Brazil (Oliveira *et al.* submitted), including Bermuda (Calder 1997), the Gulf of Mexico (Calder & Cairns 2009), and the Caribbean Sea (Bogle 1975, as *A. elongata*).

Elsewhere. Questionably reported from the Galápagos Islands (Fraser 1938b).

Aglaophenia latecarinata Allman, 1877

Fig. 14b

Aglaophenia late-carinata Allman, 1877: 56 [incorrect original spelling]. *Aglaophenia latecarinata.*—Leloup, 1935: 57.—Fraser, 1944: 378.

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

Voucher material. Off St. Lucie Inlet, 27°10.8'N, 80°02.5'W, 21.6 m, 24.vii.1975, on algae, one colony, cormoids up to 1.4 cm high, without gonophores, coll. T. Askew, ROMIZ B1086.—Fort Pierce, Fort Pierce Inlet State Park, 27°28'29.5"N, 80°17'25.8"W, on stranded *Sargassum fluitans*, 14.vii.2012, 28° C, 35‰, collected manually, two colonies, up to 7 mm high, without gonophores, coll. D.R. Calder, ROMIZ B3978.



FIGURE 14. a, *Aglaophenia dubia*: part of a hydrocladium with two hydrothecae, ROMIZ B1125, scale equals 0.10 mm. b, *Aglaophenia latecarinata*: part of a hydrocladium with two hydrothecae, ROMIZ B1086, scale equals 0.10 mm. c, *Aglaophenia rhynchocarpa*: part of a hydrocladium with two hydrothecae, ROMIZ B1083, scale equals 0.10 mm. d, *Aglaophenia trifida*: part of a hydrocladium with three hydrothecae, ROMIZ B1086, scale equals 0.10 mm. e, *Gymnangium speciosum*: part of a hydrocladium with three hydrothecae, ROMIZ B1086, scale equals 0.10 mm. f, *Macrorhynchia allmani*: part of a hydrocladium with three hydrothecae, ROMIZ B1131, scale equals 0.20 mm. f, *Macrorhynchia clarkei*: part of a hydrocladium with two hydrothecae, ROMIZ B3982, scale equals 0.10 mm. g, *Macrorhynchia clarkei*: part of a hydrocladium with two hydrothecae, ROMIZ B1129, scale equals 0.10 mm. h, *Macrorhynchia clarkei*: a single phylactogonium from a pseudocorbula, ROMIZ B1129, scale equals 0.25 mm. i, *Macrorhynchia philippina*: part of a hydrocladium with three hydrothecae, ROMIZ B1092. Scale equals 0.10 mm.

Remarks. Although often reported from hard bottoms, *Aglaophenia latecarinata* Allman, 1877 is also a conspicuous epibiont of the pelagic gulfweed species *Sargassum fluitans* (Calder 1995). As such it is ubiquitous in the Caribbean Sea (e.g., Leloup 1935; Van Gemerden-Hoogeveen 1965), Gulf of Mexico (e.g., Fraser 1944; Defenbaugh & Hopkins 1973), Florida Current (e.g., Nutting 1895, as *Aglaophenia minuta*; Bogle 1975), Gulf Stream (e.g., Burkenroad, in Parr 1939, as *A. minuta*; Rackley 1974), and Sargasso Sea (e.g., Broch 1913; Leloup 1937). Colonies on gulfweed are stunted, as with certain other *Sargassum* associates (Adams 1960), and they typically reach only about a centimeter in height on that substrate. While the species tends to be a dominant hydroid on *S. fluitans*, it is much less frequent on *S. natans*, the other holopelagic species of gulfweed in the North Atlantic (Calder 1995). Hydroids of *A. latecarinata* are known to occur as well on flotsam such as plastics (Calder 1997).

The troubled nomenclature and extensive synonymy of this species have been reviewed elsewhere (Bogle 1975; Calder 1997; Ansín Agís *et al.* 2001). The last group of authors also provided detailed distribution records.

Reported distribution. Atlantic coast of Florida. Hollywood, near Miami (Leloup 1935; Fraser 1944).

Western Atlantic. New England, on pelagic *Sargassum* (Fraser 1944), to Brazil (Oliveira *et al.* submitted), and including Bermuda and the Sargasso Sea (Jäderholm 1896; Calder 1993), the Gulf of Mexico (Calder & Cairns 2009), and the Caribbean Sea (Galea 2010).

Elsewhere. Warm waters of the eastern Atlantic, Indian Ocean, and western Pacific (Ansín Agís *et al.* 2001; Park 2012).

Aglaophenia rhynchocarpa Allman, 1877

Fig. 14c

Aglaophenia rhynchocarpa Allman, 1877: 40, pl. 23, figs. 5-8.—Bogle, 1975: 59, fig. 3.

Type locality. USA: Florida, Key West, Triangle Shoal (Allman 1877: 40).

Voucher material. Palm Beach, 1.42 miles (2.3 km) offshore, 30.5 m, 23.vii.1974, *Johnson-Sea-Link*, JSL1174, diver lockout, two colony fragments, up to 4 cm high, without gonophores, coll. J. Prentice, ROMIZ B1083.—West Palm Beach, on reef seaward of the Breakers Hotel, 45 feet (13.7 m), January 1991, SCUBA, four cormoids, up to 2.0 cm high, without gonophores, coll. P. Humann, ROMIZ B3979.

Remarks. Remarks on taxonomy of *Aglaophenia rhynchocarpa* Allman, 1877 include those of Bogle (1975) and Calder (1997). Both considered *A. cylindrata* Versluys, 1899 from the Testigos Islands, West Indies, to be conspecific, following Bedot (1925) and Vervoort (1968) earlier. Added to the synonymy of *A. rhynchocarpa* in my 1997 report were *A. rathbuni* Nutting, 1900 from "Caravellas" (Caravelas), Brazil, and *A. insolens* Fraser, 1943 from Maguaripe Bay, Trinidad. Bogle regarded the latter two as coterminous, and indicated that they were merely variants of *A. rhynchocarpa*. *Aglaophenia gracillima* Fewkes, 1881, originally described from Martinique, West Indies, resembles *A. rhynchocarpa* but differs in having a median abcauline carina that extends well beyond the rim of the hydrotheca. Moreover, the peduncle of its corbula bears 3–4 hydrothecate internodes (cormidia) instead of one.

Palm Beach, Florida, currently appears to represent the northern range limit of *Aglaophenia rhynchocarpa*. The species was reported from Challenger Bank, near Bermuda, in collections from the *Challenger* Expedition (Ritchie 1909, as *Aglaophenia cylindrata* Versluys, 1899; Calder 1997). However, it has not been seen again anywhere around Bermuda or on nearby banks, in spite of extensive hydroid collecting in the area during the late 20th century. As with *Hebella venusta* (Allman, 1877), noted earlier, it may have become locally extinct (Sterrer 1998; Calder 2000). By contrast, the species was particularly well-represented in samples from Arrowsmith Bank, Yucatan Channel, examined by Bogle (1975).

Reported distribution. Atlantic coast of Florida. Carysfort Reef (Bogle 1975).

Western Atlantic. Palm Beach, Florida (reported herein) to Brazil (Oliveira *et al.* submitted), and including the Gulf of Mexico (Calder & Cairns 2009) and Caribbean Sea (Vervoort 1968; Galea 2010).

Elsewhere. Eastern Atlantic (Vervoort 1959, as Aglaophenia latecarinata, in part).

Aglaophenia trifida L. Agassiz, 1862

Fig. 14d

Aglaophenia cristata McCrady, 1859: 202 [not *Aglaophenia cristata* (Lamarck, 1816) = *Aglaophenia pluma* (Linnaeus, 1758)]. *Aglaophenia trifida* L. Agassiz, 1862: 358.

Type locality. USA: South Carolina, Sullivan's Island (stranded on the beach) and Charleston (McCrady 1859: 203, as *Aglaophenia cristata*).

Voucher material. Off Sebastian Inlet, 27°51.5'N, 80°09.5'W, 26 m, 01.iii.1974, Smith-McIntyre grab, R/V *Gosnold* Station 222/276E, one colony, 8.5 cm high, without gonophores, ROMIZ B1126.—Nearshore off Fort Pierce, 27°29.6'N, 80°17.0'W, 5–8 m, 02.v.1975, one colony, 4.5 cm high, without gonophores, coll. F. Stanton, ROMIZ B3980.—Nearshore off Fort Pierce, 27°29.6'N, 80°17.0'W, 7–8 m, 10.vii.1975, SCUBA, one colony, 4.2 cm high, without gonophores, coll. F. Stanton, ROMIZ B3981.

Remarks. This hydroid was first described as *Aglaophenia cristata* (Lamarck, 1816) by McCrady (1859). He suspected it was distinct from that European species, now known as *Aglaophenia pluma* (Linnaeus, 1758), but had no material of the eastern Atlantic form to verify his conjecture. The binomen *A. trifida* was applied to the species a short time later by L. Agassiz (1862). Although Agassiz neither described nor illustrated it, the specific name *trifida* is nevertheless available from that work because a bibliographic reference to McCrady's earlier description (ICZN Art. 12.2) was provided.

Aglaophenia rigida Allman, 1877, described from material collected during explorations of the Gulf Stream region by L.F. de Pourtalès, is morphologically similar to A. *trifida*. The two had been distinguished by Fraser (1944) based on the number of cusps on the hydrothecal margin, with eight reported in A. *rigida* and nine in A. *trifida*. After examinating type material of A. *rigida* and finding nine rather than eight cusps to be present, I synonymized the two names (Calder 1983).

Aglaophenia trifida resembles *A. pluma*, a European species re-described on the basis of a neotype by Svoboda & Cornelius (1991). Median inferior nematothecae extend a greater distance along the abcauline wall of the hydrotheca in *A. pluma*, and its corbulae are shorter (usually with about 5–10 ribs instead of 12–14). *Aglaophenia trifida* is held to be distinct here.

Nutting (1900) found Aglaophenia rigida (= A. trifida) to be abundant along the Carolina coast south of Cape Hatteras in Albatross collections, and concluded that it was likely the most abundant species of the genus Aglaophenia Lamouroux, 1812 on the American Atlantic seaboard. Fraser's (1912b) report of this rather large species (as A. rigida) from Sargassum near Beaufort, North Carolina, is regarded here as a misidentification. Records of A. trifida from areas outside the southern United States need verification.

Reported distribution. Atlantic coast of Florida. First record.

Western Atlantic. North Carolina (Nutting 1900, as *Aglaophenia rigida*) to Brazil (Oliveira *et al.* submitted), and including the Gulf of Mexico (Calder & Cairns 2009) and the Caribbean Sea (Fraser 1944, as *Aglaophenia rigida*).

Elsewhere. Questionably reported from the eastern Pacific (Fraser 1948, as Aglaophenia rigida).

Gymnangium speciosum (Allman, 1877)

Fig. 14e

Halicornaria speciosa Allman, 1877: 54, pl. 34, figs. 1–5.
not Halicornaria speciosa.—Nutting, 1900: 127 (part) [=Gymnangium sinuosum (Fraser, 1925)].
Gymnangium speciosum.—Humann, 1992: 69, middle photograph.—Humann & DeLoach, 2002: 69, middle photograph.

Type locality. Bahamas: Double-Headed Shot Key (Allman 1877: 55).

Voucher material. West Palm Beach, on reef seaward of the Breakers Hotel, 45 feet (13.7 m), January 1991, SCUBA, fragments of one dead colony, c. 19.5 cm high, with empty gonothecae, coll. P. Humann, ROMIZ B1131.

Remarks. This species was originally described by Allman (1877) as *Halicornaria speciosa*. *Halicornaria* Allman, 1874 was widely used as a generic name until it was a shown to be a junior synonym of *Gymnangium* Hincks, 1874 by Stechow (1921b). He noted that Allman's (1874) account of *Halicornaria* appeared in April 1874,

whereas its subjective synonym *Gymnangium* was made available by Hincks (1874) earlier that year (February). Moreover, the name *Halicornaria* Allman, 1874 is now known to be an invalid junior homonym of *Halicornaria* Hincks, 1865 (Calder 1997). The status of the senior homonym is discussed above under *Halopteris carinata* Allman, 1877. Although the name *Gymnangium* is now well-established, the genus-group it represents is thought to be polyphyletic (Leclère *et al.* 2007).

Of the four putatively valid species of *Gymnangium* in the tropical western Atlantic, *G speciosa* differs from *G arcuatum* (Lamouroux, 1816) in having unbranched colonies and in possessing an intrathecal septum, from *G longicaudum* (Nutting, 1900) in having median inferior nematothecae that extend a relatively short distance beyond the hydrothecal rim instead of well beyond it, and from *G sinuosum* (Fraser, 1925) in having two embayments on each side of the hydrothecal rim instead of one. More detailed accounts of these species are given by Bogle (1975) and Calder (1997).

Nutting's (1900) report of this species (as *Halicornaria speciosa*) from *Albatross* Station 2640 (25°05'N, 80°15'W) south of Carysfort Reef, Florida, was assigned instead to *Gymnangium sinuosum* by Bogle (1975: 271) after an examination of Nutting's specimens (USNM 18703, 18704). The misidentified record was repeated in Fraser (1944).

The photograph of *Gymnangium speciosum* in Humann (1992) and Humann & DeLoach (2002) shows the same colony examined here.

Reported distribution. Atlantic coast of Florida. Off West Palm Beach (Humann 1992; Humann & DeLoach 2002).

Western Atlantic. Southeastern Florida, Bahamas, Gulf of Mexico, and Arrowsmith Bank in the northwestern Caribbean Sea (Bogle 1975) to Barbados (Fraser 1944) and Colombia (Wedler 1975). The species is also known from Bermuda (Calder 1997).

Macrorhynchia allmani (Nutting, 1900)

Fig. 14f

Aglaophenia ramosa Allman, 1877: 39, pl. 23, figs. 1–4 [permanently invalid 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 [replacement name for Aglaophenia ramosa Allman, 1877].

Type locality. USA: Florida, "Florida reef, from a depth of from 2 to 3 fathoms" (3.7–5.5 m) (Allman 1877: 40, as *Aglaophenia ramosa*).

Voucher material. Bethel Shoal off Vero Beach, 27°42.6'N, 80°06.8'W, 24 m, on shell fragments, 18.ii.1976, *Johnson-Sea-Link*, JSL 328, diver lockout, three cormoids, up to 4.2 cm high, without gonothecae, coll. S. Nelson, ROMIZ B3982.

Remarks. Fully-developed colonies of *Macrorhynchia allmani* Nutting, 1900 reach as much as 28 cm high (Calder 1997). Those examined here were much smaller, but they otherwise correspond in morphology with earlier accounts of the species.

Macrorhynchia allmani resembles the sympatric *M. clarkei* Nutting, 1900, and the two have sometimes been confused, as noted earlier (Calder 1997). The most obvious difference between them macroscopically is colour, with colonies of *M. allmani* appearing brownish and those of *M. clarkei* black. Microscopically, hydrocladial internodes of *M. allmani* usually have two internal perisarcal ridges while those of *M. clarkei* have only one. Other differences are reported in remarks on the latter species immediately below.

Reproductive structures of this species have yet to be described. In their absence, *M. allmani* is referred to the aglaopheniid genus *Macrorhynchia* Kirchenpauer 1872 based on trophosomal characters identified by Bogle (1975) and reiterated by Calder (1997). As in that genus, the hydrocaulus is polysiphonic and repeatedly branched, cauline nematothecae are large and triangular, median inferior nematothecae are largely adnate to the abcauline hydrothecal wall, and hydrothecae are of moderate depth. Wedler (2004) described gonophores in a hydroid identified as this species, but in my opinion his specimens are referable to *M. furcata* (Nutting, 1900) instead. Lateral nematothecae visible in his Fig. 3c are forked, as in that species.

Reported distribution. Atlantic coast of Florida. First record.

Western Atlantic. Continental shelf of South Carolina and Georgia (Wenner et al. 1984, as Aglaophenia

allmani) to Brazil (Oliveira *et al.* submitted) including Bermuda (Calder 1997), the Gulf of Mexico (Calder & Cairns 2009), and the Caribbean Sea (Vervoort 1968, as *Aglaophenia* (?) *allmani*).

Macrorhynchia clarkei (Nutting, 1900)

Fig. 14g, h

Lytocarpus clarkei Nutting, 1900: 124, pl. 32, figs. 5-7.

Macrorhynchia robusta.—Humann, 1992: 75, top photograph.—Humann & DeLoach, 2002: 75, top photograph [not Macrorhynchia robusta (Fewkes, 1881)].

Type locality. Bahamas: off Little Cat Island (Little San Salvador Island), on a submerged bank connecting it and Eleuthera (Nutting 1900). Syntype material, comprising three slides, is in the National Museum of Natural History, Smithsonian Institution (USNM 18698).

Voucher material. West Palm Beach, on reef seaward of the Breakers Hotel, 45 feet (13.7 m), January 1991, SCUBA, fragments of one colony, c. 15 cm high, with phylactogonia forming pseudocorbulae, but without gonophores, coll. P. Humann, ROMIZ B1129.

Remarks. The coenosarc of *Macrorhynchia clarkei* Nutting, 1900 contains numerous "black pigment cells," as noted in the original description of the species, and colonies appear almost black macroscopically. The common name "black bush hydroid" is appropriate for this hydroid.

In a previous work (Calder 1997: 65) I considered it likely that Macrorhynchia clarkei was conspecific with M. grandis (Clarke, 1879). The same opinion had been expressed earlier by Bogle (1975: 297). The two are held distinct here given apparent differences between them in both morphology and bathymetric distribution. For example, median inferior nematothecae extend beyond hydrothecal margins in *M. grandis* but not in *M. clarkei*. As for their type localities, M. grandis came from bathyal depths (339 fathoms = 620 m) in the Straits of Florida (24°08'N, 82°51'W) while M. clarkei was from much shallower waters (5-24 m) in the Bahamas. Although additional records of the two have extended their reported depth ranges, M. clarkei still appears to be a species more typical of shallow waters and *M. grandis* one of deeper regions. There is also no mention of the black pigment granules in M. grandis that are so conspicuous in M. clarkei. For the same reasons given above, M. clarkei is considered distinct from *M. ramosa* (Fewkes, 1881), originally described from St. Vincent in the Caribbean. Illustrations of type material portraying some characters of these three similar species are provided elsewhere (Calder 1997: Fig. 20 a-c). Macrorhynchia allmani (Nutting, 1900) from the warm western Atlantic also resembles M. clarkei but has been distinguished by having more widely spaced hydrocladia, longer hydrocladial internodes, deeper hydrothecae, and shorter median inferior nematothecae (Calder, 1997). It also has two internal ridges per hydrocladial internode rather than one, with one beneath the intrathecal ridge and another beneath the lateral nematothecae. Nevertheless, as noted by Bogle (1975), careful study of the various nominal species assigned to Macrorhynchia Kirchenpauer 1872 is needed to sort out the taxonomy of this difficult group. Some recent authors (Ansín Agís et al. 2001; Vervoort 2006) have recognized Nematophorus Clarke, 1879 as a genus distinct from Macrorhynchia, having a pseudocorbula instead of single phylactogonia, and have assigned M. clarkei to it.

Records of this species from Bermuda (Bennitt 1922, as *Lytocarpus clarkei*; Calder 1986, as *Macrorhynchia clarkei*) are misidentifications of *Macrorhynchia allmani* Nutting, 1900 (see Calder 1997). Conversely, the hydroid from Florida illustrated by Humann (1992: 75) and Humann & DeLoach (2002: 75) and identified as *Macrorhynchia robusta* (Fewkes, 1881) is referable to *M. clarkei*. That misidentification is entirely due to an error on my part, and was based on the voucher material above. The colony in their photograph is the same one examined here. Hydrothecal cusps are much more deeply cut in *M. robusta* than in *M. clarkei*.

Reported distribution. Atlantic coast of Florida. West Palm Beach (Humann 1992; Humann & DeLoach 2002).

Western Atlantic. Florida and the Bahamas to the Caribbean Sea in the western Atlantic (Vervoort 1968, as *Lytocarpus clarkei*; Galea 2010).

Elsewhere. Cape Verde Islands (Vervoort 1959, as *L. clarkei;* Ansín Agís *et al.* 2001, as *Nematophorus clarkei*; Vervoort 2006, as *N. clarkei*).

Macrorhynchia philippina Kirchenpauer, 1872

Fig. 14i

Macrorhynchia philippina Kirchenpauer, 1872: 19.
Aglaophenia philippina Kirchenpauer, 1872: 45, text-fig. p. 17; pl. 1, fig. 26, pl. 2, figs. 26 a–b; pl. 7, fig. 26.
Lytocarpus philippinus.—Weiss, 1948: 158.—Cummings, 1994: 1208.
Lytocarpus filippinus.—Voss & Voss, 1955: 223 [incorrect subsequent spelling].
Lytocarpus sp.—Clark & Goetzfried, 1976: 477.
Macrorynchia philippina.—Jones, 2002: 218 [incorrect subsequent spelling].

Type locality. Philippines: Manila (Kirchenpauer 1872: 45).

Voucher material. Bethel Shoal off Vero Beach, 27°42.6'N, 80°06.8'W, 24 m, 18.ii.1976, *Johnson-Sea-Link*, JSL 328, diver lockout, one colony fragment, 3.7 cm high, without gonothecae, coll. S. Nelson, ROMIZ B1092.

Remarks. A thorough taxonomic account of *Macrorhynchia philippina* Kirchenpauer, 1872, including both a synonymy list and detailed distribution records, has been given by Ansín Agís *et al.* (2001). Additional synonyms of this widespread species are listed in Calder (1997).

Although the reported bathymetric range of *Macrorhynchia philippina* extends from surface waters to 411 m (Ansín Agís *et al.* 2001), the species is most often encountered at shallow depths (<25 m). In the southeastern United States it penetrates a short distance inside bays, inlets, creeks, and rivers (Fraser 1912b; Calder & Hester 1978; Calder 1983), but only into environments that are typically euhaline (30–40‰).

Variously known as "fire weed" or "fire fern" (Rifkin *et al.* 1993), or "white stinger" (Cairns *et al.* 2002), colonies of *Macrorhynchia philippina* are venomous to humans. A large (20 cm), venomous hydroid identified by Clark & Goetzfried (1976) as *Lytocarpus* sp. from the jetty at Sebastian Inlet, Florida, was likely this species. They described a new species of opisthobranch mollusc (*Lomanotus stauberi*) associated with it. Contact with the hydroid caused an intense sting, and nematocysts were also thought to be present in mucus released into the water from the colony. Those hydroids were reported by Clark & Goetzfried to be seasonal in occurrence in the area, being present from June through November and occasionally into December.

Macrorhynchia philippina liberates a medusoid stage as part of its life cycle (e.g., Gravier 1970; Migotto 1996; Bourmaud & Gravier-Bonnet 2004).

Reported distribution. Atlantic coast of Florida. Biscayne Bay (Weiss 1948, as *Lytocarpus philippinus*; Voss & Voss 1955, as *Lytocarpus filippinus*; Jones 2002).—(?) Sebastian Inlet (Clark & Goetzfried 1976, as *Lytocarpus* sp.).—Boca Raton (Cummings 1994, as *L. philippinus*).

Western Atlantic. North Carolina (Fraser 1912b, as *Lytocarpus philippinus*) to Brazil (Oliveira *et al.* submitted), including Bermuda (Calder 1997), the Gulf of Mexico (Calder & Cairns 2009), and the Caribbean Sea (Galea 2010).

Elsewhere. Circumglobal in warm neritic waters (Ansín Agís et al. 2001; Schuchert 2003).

SUBORDER PROBOSCOIDEA Broch, 1910

Family Campanulariidae Johnston, 1837

Subfamily Campanulariinae Johnston, 1837

Campanularia macroscypha Allman, 1877

Fig. 15a, b

Campanularia macroscypha Allman, 1877: 11, pl. 8, figs. 1, 2.—Fraser, 1943: 88.

Type locality. USA: Florida, off Sand Key, 120 fathoms (219 m) (Allman 1877).

Voucher material. Off St. Lucie Inlet, 27°10.8'N, 80°02.5'W, on *Eudendrium carneum*, 22 m, 24.vii.1975, *Johnson-Sea-Link*, JSL 273, one colony, up to 2 mm high, without gonophores, coll. T. Askew, ROMIZ B1088.— Off St. Lucie Inlet, 27°11.4'N, 80°00.9'W, 42 m, 18.v.1976, *Johnson-Sea-Link*, diver lockout, one colony, up to 4 mm high, without gonophores, coll. M. Flake, ROMIZ B1101.—Off St. Lucie Inlet, 27°10.8'N, 80°00.8'W, 43 m, 24.viii.1977, *Johnson-Sea-Link*, JSL 1439, diver lockout, one colony, up to 1.1 cm high, without medusa buds, coll. J. Reed, ROMIZ B1104.

Remarks. *Campanularia macroscypha* Allman 1877 is distinguished by having long, cylindrical hydrothecae with a dozen or more deeply-cut, linguiform cusps, and irregularly-segmented pedicels. It is known only from the southeastern United States and Gulf of Mexico. A hydroid of relatively deep waters, its previously-known bathymetric range is 84–1119 m (Henry *et al.* 2008). Voucher material above from St. Lucie Inlet was from shallower depths of 22–43 m. Specimens reported from a station (Stn. 117, 32°04.03'N, 65°02.48'W) on Challenger Bank, off Bermuda (Calder 2000) were collected at 49 m.

Gonothecae of this species remain undescribed.



FIGURE 15. a, *Campanularia macroscypha*: part of colony with hydrotheca, ROMIZ B1101, scale equals 0.5 mm. b, *Campanularia macroscypha*: hydrotheca and distal part of pedicel, ROMIZ B1101, scale equals 0.20 mm. c, *Orthopyxis sargassicola*: hydrotheca and distal part of pedicel, ROMIZ B1123, scale equals 0.20 mm. d, *Orthopyxis sargassicola*: gonotheca, ROMIZ B1123, scale equals 0.20 mm. e, *Clytia elsaeoswaldae*: part of a colony with hydrotheca and gonotheca, ROMIZ B1134, scale equals 0.25 mm. f, *Clytia linearis*: hydrotheca and distal part of pedicel, ROMIZ B134, scale equals 0.25 mm.

Reported distribution. Atlantic coast of Florida. First record.

Western Atlantic. Cape Lookout, North Carolina (Henry *et al.* 2008) to the Gulf of Mexico north of Yucatan (Fraser 1944), as well as Bermuda (Calder 1998, 2000).

Orthopyxis sargassicola (Nutting, 1915)

Fig. 15c, d

Clytia sargassicola Nutting, 1915: 57, pl. 12, figs. 8, 9.

Type locality. Bahamas: "...southern edge of the Gulf Stream" (Nutting 1915).

Voucher material. Seminole Shores, just north of St. Lucie Inlet, 19.ii.1991, on stranded *Sargassum*, one colony, up to 3 mm high, with gonophores, coll. D.R. Calder, ROMIZ B1123.

Remarks. Although first reported on *Sargassum* from the Gulf Stream in the western North Atlantic, most records of *Orthopyxis sargassicola* (Nutting, 1915) to date have been from Brazil, where it appears to be common. There, Oliveira *et al.* (submitted) included records of it from algae, barnacles, and mussels. A shallow water species, it has been recorded from the intertidal zone to a depth of about 20 m (Migotto 1996).

Orthopyxis sargassicola resembles *O. tincta* Hincks, 1861a from Australia in having laterally compressed, strongly ribbed, and partially recumbent gonothecae, together with thickened and distinctly cuspate hydrothecae. However, its gonothecae are much less tapered distally and they have only about a half-dozen ribs instead of a dozen or more. Gonophores of *O. sargassicola* are liberated as reddish-coloured eumedusoids, lacking both tentacles and manubrium (Migotto 1996).

Reported distribution. Atlantic coast of Florida. First record.

Western Atlantic: Gulf Stream east of Cape Hatteras (Fraser 1943, as *Eucopella sargassicola*) southwards to Brazil (Oliveira *et al.* submitted), including Bermuda (Calder 1991a) and the Caribbean Sea (Leloup 1935, as *Campanularia sargassicola*). Leloup also recorded it from pelagic *Sargassum* in the central North Atlantic (29°N, 44°W) over the western side of the Mid-Atlantic Ridge.

Subfamily Clytiinae Cockerell, 1911

Clytia elsaeoswaldae Stechow, 1914 Fig. 15e

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

Type locality. U.S. Virgin Islands: St. Thomas, Charlotte Amalie (Stechow 1914).

Voucher material. Off St. Lucie Inlet, 27°10.7'N, 80°02.7'W, on *Eudendrium carneum*, 23 m, vii.1975, *Johnson-Sea-Link*, JSL 274, one colony, up to 4 mm high, with gonophores, coll. T. Askew, ROMIZ B1134.

Remarks. Lindner *et al.* (2011) have been followed in recognizing *Clytia elsaeoswaldae* Stechow, 1914 (type locality: St. Thomas) as distinct from *Clytia gracilis* (M. Sars, 1850) (type locality: Norway). Suspicions had been raised earlier, on zoogeographic grounds, that the two might be distinct (Calder 1991a: 57). As with material of Lindner *et al.* from Brazil and type material from the U.S. Virgin Islands, gonothecae of hydroids from Florida examined here were borne on the stolons or mostly so. The species appears to be endemic to shallow-waters of the warm western Atlantic. Material earlier identified as *C. gracilis* by me (Calder 1991a) from Bermuda is referable to the same species. A phylogenetic analysis by Lindner *et al.* (2011) indicates that *C. elsaeoswaldae* is related phylogenetically to *C. hemisphaerica* (Linnaeus, 1758) and to several species resembling *C. gracilis*.

Clytia elsaeoswaldae is distinguished in part by the following combination of characters: (1) colonies are stolonal, or erect with monosiphonic and dichotomously branched hydrocauli; (2) hydrothecae have about 9-14 cusps that are usually inclined to the right when viewed laterally; (3) gonothecae tend to arise from the hydrorhiza, and have smooth to slightly undulated walls (Lindner *et al.* 2011).

The hydroid examined here was growing as an epizoite on a stem of *Eudendrium carneum* Clarke, 1882. Its stolons were entangled with those of a colony of *C. linearis* (Thornely, 1900), discussed below.

Reported distribution. Atlantic coast of Florida. First record.

Western Atlantic. Bermuda (Calder 1991a, as *Clytia gracilis*) to Brazil (Oliveira *et al.* submitted), and including the Caribbean Sea (Stechow 1914).

Clytia linearis (Thornely, 1900) Fig. 15f

Obelia linearis Thornely, 1900: 453, pl. 44, fig. 6.

Type locality. Papua New Guinea: New Britain, Blanche Bay (Thornely 1900).

Voucher material. Off St. Lucie Inlet, 27°10.7'N, 80°02.7'W, on *Eudendrium carneum*, 23 m, vii.1975, *Johnson-Sea-Link*, JSL 274, fragments of one colony, up to 9 mm high, without gonophores, coll. T. Askew, ROMIZ B3983.

Remarks. Comments are warranted on nomenclature of *Clytia linearis* (Thornely, 1900). Leloup (1935) referred *Obelia fragilis* Calkins, 1899 and *Clytia fragilis* Congdon, 1907 to the genus *Laomedea* Lamouroux, 1812. To remove supposed homonymy between the two when thus assigned, he proposed *C. tottoni* as a substitute name for Congdon's species. However, no homonymy currently exists because the two species are now assigned once again to *Obelia* Péron & Lesueur, 1810 and *Clytia* Lamouroux, 1812, respectively, where they are considered synonyms of other species (Cairns *et al.* 2002). In being a replacement name for *C. fragilis* Congdon, 1907, the name *C. tottoni* Leloup, 1935 is by definition a junior objective synonym of it, having the same name-bearing type (ICZN Art. 67.8, 72.7). In turn, both binomena are considered here to be junior subjective synonyms of *C. linearis*, as discussed earlier (Calder, 1991a). If Atlantic and Pacific populations are ever shown to be different species, however, the name *C. fragilis* will need to be resurrected for the former.

It is improbable that Leloup's (1935) species, discussed under the name *Laomedea tottoni*, is the same as Congdon's *Clytia fragilis*, i.e., I believe he misidentified his hydroid. Indeed, it seems much more like *C. laxa* Fraser, 1937b in lacking the prominent pleat extending down from each marginal cusp and in being polysiphonic rather than monosiphonic (or even partly stolonal). Hydroids from Guadeloupe recently described by Galea (2010) as *Clytia tottoni* also resemble *C. laxa*. In summary, the binomen *C. tottoni* is a junior objective synonym of *C. fragilis* (considered here a junior synonym of *C. linearis*), while Leloup's *C. tottoni* was in fact a different species, likely identical to *C. laxa*. Hydroids reported as *C. laxa* by Nelson *et al.* (1994) from artificial reefs off Vero Beach, Florida, are assumed here to have been correctly identified and not based on *C. linearis*.

Discussion of *C. linearis*, based on material from Bermuda (type locality of *C. fragilis*), is given in an earlier work (Calder 1991a). Lindner & Migotto (2002) provided additional information on the species, including development of its medusa stage.

Reported distribution. Atlantic coast of Florida. First record.

Western Atlantic. Cape Hatteras (Nutting 1915, as *Clytia fragilis* Congdon, 1907) to Brazil (Oliveira *et al.* submitted), including Bermuda (Calder 1991a), the Gulf of Mexico (Calder & Cairns 2009), and the Caribbean Sea (Calder & Kirkendale 2005).

Elsewhere. Circumglobal in shallow warm waters (Lindner & Migotto 2002).

Clytia noliformis (McCrady, 1859)

Fig. 16a, b

Campanularia noliformis McCrady, 1859: 194, pl. 11, fig. 4.

Type locality. Bermuda: Castle Harbour, on a dead octocoral (International Commission on Zoological Nomenclature 2002); based on a neotype.

Voucher material. Fort Pierce, Fort Pierce Inlet State Park, 27°28'29.5"N, 80°17'25.8"W, on stranded *Sargassum natans*, 14.vii.2012, 28° C, 35‰, collected manually, two colonies, with gonophores, coll. D.R. Calder, ROMIZ B3984.



FIGURE 16. a, *Clytia noliformis*: hydrotheca and distal part of pedicel, ROMIZ B3984, scale equals 0.10 mm. b, *Clytia noliformis*: gonotheca, ROMIZ B3984, scale equals 0.10 mm. c, *Clytia paulensis*: part of colony with hydrotheca and pedicel, ROMIZ B1103, scale equals 0.20 mm. d, *Clytia paulensis*: hydrotheca and distal part of pedicel, ROMIZ B1103, scale equals 0.10 mm. e, *Obelia geniculata*: part of hydrocaulus with three hydrothecae, ROMIZ B1119, scale equals 0.25 mm. f, *Obelia hyalina*: part of colony with three hydrothecae, ROMIZ B3985, scale equals 0.25 mm. g, *Obelia oxydentata*: part of colony with three hydrothecae, ROMIZ B3985, scale equals 0.25 mm.

Remarks. The hydroid species recorded here, widely known for a century as *Clytia noliformis* (McCrady, 1859), has been objectively defined recently by a neotype (International Commission on Zoological Nomenclature 2002). Evidence had arisen that the binomen *C. noliformis* was likely applied by McCrady (1859) to a different species (Calder 1991a; Lindner & Calder 2000), more closely resembling *C. hemisphaerica* (Linnaeus, 1767). A neotype was therefore needed to conserve prevailing usage of the name. McCrady's hydrozoan types (including any of *C. noliformis*) are believed to have been destroyed during the American Civil War (Stephens & Calder 1992).

Clytia noliformis is an abundant epibiont on pelagic *Sargassum*, and especially so on *S. natans* (Burkenroad, in Parr 1939; Calder 1995). Colonies grow quickly outwards onto new phylloids (leaflets) and bladders of these fucoids, and are least abundant on the oldest and innermost parts of the thalli (Ryland 1974). Niermann (1986) reported that *C. noliformis* was more prevalent on *S. natans* north of a thermal front in the Sargasso Sea than south of it. The difference was attributed to greater water stratification in the south and to a lower nutrient supply, resulting in less food (nannoplankton) for the hydroid.

A combination of morphological characters can be used to distinguish *Clytia noliformis* from its congeners (colonies stolonal; hydrothecae about equal in height and breadth at the margin; marginal cusps triangular; basal chambers of hydrothecae shallow; subhydrothecal spherule present; coenosarc and hydranths yellowish), and merotrichous isorhiza nematocysts are diagnostic (Lindner & Migotto 2001, 2002). As for gonothecae, they are

urn-shaped, arise from the hydrorhiza, have walls that are slightly undulated and cylindrical to laterally compressed, and the distal end bears a tubular neck (Calder 1991a). The cnidome of *C. noliformis* includes microbasic b-mastigophores as well as merotrichous isorhizas.

The life cycle of *C. noliformis* has been followed in the laboratory from hydroid to adult medusa stages (Lindner & Migotto 2002). A detailed taxonomic account of the species has been given earlier (Calder 1991a).

Reported distribution. Atlantic coast of Florida. First record.

Western Atlantic. Nova Scotia, on *Sargassum* (Fraser 1918), to Brazil (Oliveira *et al.* submitted), and including Bermuda (Calder 1991a), the Gulf of Mexico (Calder & Cairns 2009), and the Caribbean Sea (Vervoort 1968, as *Campanularia* (*Clytia*) noliformis).

Elsewhere. Sargasso Sea (Niermann 1986); warm waters of the eastern Atlantic (Rees & White 1966; Wirtz 2007) including the Mediterranean Sea (Faucci & Boero 2000), Indian Ocean (Mammen 1965), western Pacific (Kirkendale & Calder 2003), and eastern Pacific (Fraser 1948).

Clytia paulensis (Vanhöffen, 1910)

Fig. 16c, d

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

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

Voucher material. Off St. Lucie Inlet, 27°10.8'N, 80°00.8'W, 44 m, 03.ii.1977, *Johnson-Sea-Link*, diver lockout, JSL 2161, two colonies, up to 2 mm high, without gonophores, coll. F. Stanton, ROMIZ B1103.

Remarks. Although *Clytia paulensis* (Vanhöffen, 1910) is distinctive, presumably widespread, and now quite frequently reported (see synonymy list in Medel & Vervoort 2000), it was not described until the early twentieth century. Also surprising given its ubiquity is its remote type locality, a small volcanic island in the southern Indian Ocean. Fraser (1937a, 1944, 1946, 1948) did not mention it from the Americas, although *Clytia longitheca* (Fraser 1914) from the west coast is considered a synonym (Schuchert 2012). It has now been reported from both Atlantic and Pacific coasts of the American continents (Cairns *et al.* 2002; Oliveira *et al.* submitted).

Recent taxonomic accounts of *C. paulensis* include those of Medel & Vervoort (2000) and Peña Cantero & García Carrascosa (2002); the latter authors add notes on ecology of the species.

Reported distribution. Atlantic coast of Florida. First record.

Western Atlantic. Chesapeake Bay (Calder 1971) to Brazil (Oliveira *et al.* submitted), and from Challenger Bank near Bermuda (Calder 2000), the Gulf of Mexico (Calder & Cairns 2009), and the Caribbean Sea (Calder & Kirkendale 2005).

Elsewhere. Considered to be almost circumglobal in temperate and tropical waters (Cornelius 1995b; Ramil *et al.* 1998; Medel & Vervoort 2000; Peña Cantero & García Carrascosa 2002).

Subfamily Obeliinae Haeckel, 1879

Obelia geniculata (Linnaeus, 1758)

Fig. 16e

Sertularia geniculata Linnaeus, 1758: 812.

Type locality. UK: Dover. According to Cornelius (1975), Linnaeus (1758) is likely to have established this species based on an illustration of material from Dover, England, by Ellis (1755).

Voucher material. Off Fort Pierce, between Capron Shoal and the beach, on *Thyroscyphus ramosus*, 09.v.1974, SCUBA, two colonies, up to 7 mm high, with one empty gonotheca, coll. D. Biggs and D. Mook, ROMIZ B1073.—Hutchinson Island, Walton Rocks area, 27°20'19"N, 80°13'59"W, on algae, 17.ii.1991, collected manually, one colony, up to 5 mm high, with gonophores, coll. D.R. Calder, ROMIZ B1107.—Fort Pierce Inlet, north jetty, north side, 27°28'24.2"N, 80°17'20.3"W, on *Thyroscyphus ramosus*, 0.1 m, 15.ii.1991, 20° C, collected manually, two colonies, up to 8 mm high, with gonophores, coll. D.R. Calder, ROMIZ B1115.—Sebastian Inlet,

27°51'43"N, 80°26'47"W, washed ashore on *Sargassum*, 19.ii.1991, collected manually, one colony, up to 5 mm high, without gonophores, coll. D.R. Calder, ROMIZ B1119.

Remarks. While often thought to be virtually cosmopolitan in shallow waters, molecular studies (Govindarajan *et al.* 2005) suggest the existence of cryptic species in hydroids of the *Obelia geniculata* (Linnaeus, 1758) morphotype. Moreover, the reported latitudinal distribution of *O. geniculata*, from the subarctic to the tropics, also appears to be exceptionally wide for a single species. Within that geographic range, local morphological variants have been noted. In one example, populations from Chesapeake Bay lack the usual asymmetrical development of perisarc on internodes of the hydrocaulus (Calder 1971), considered characteristic of the species (Cornelius 1995b). Hydroids from Florida examined here had the typical asymmetric thickening of perisarc on stem internodes beneath the distal hydrotheca on each, but colonies appeared to be stunted compared with those from boreal waters of the western and eastern North Atlantic (Calder 1975, 2012).

Reported distribution. Atlantic coast of Florida. First record.

Western Atlantic. Hudson Strait (Fraser 1944) to Argentina (Oliveira *et al.* submitted), and from the Gulf of Mexico (Joyce 1961; Calder & Cairns 2009) and Caribbean Sea (Vervoort 1968, as *Laomedea* (*Obelia*) *geniculata*).

Elsewhere. Considered essentially cosmopolitan in neritic waters (Vervoort & Watson 2003).

Obelia hyalina Clarke, 1879

Fig. 16f

Obelia hyalina Clarke, 1879: 241, pl. 4, fig. 21.—Fraser, 1944: 160.

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

Voucher material. Fort Pierce, Fort Pierce Inlet State Park, 27°28'29.5"N, 80°17'25.8"W, on stranded *Sargassum fluitans*, 14.vii.2012, 28° C, 35‰, collected manually, one colony, 7 mm high, without gonophores, coll. D.R. Calder, ROMIZ B3985.

Remarks. The species originally regarded as *Obelia hyalina* Clarke, 1879 was generally considered valid for more than half of the 20th century, as reflected in works such as those of Stechow (1912), Nutting (1915), Fraser (1944), Deevey (1950), Rees & Thursfield (1965), and Vervoort (1968, as *O. congdoni*). Over the most recent 4–5 decades, however, it has been widely regarded as conspecific with *O. dichotoma* (Linnaeus, 1758). Evidence is now apparent from life cycle, nematocyst, and molecular studies that lumping in hydroid taxonomy during that period was excessive, including within the genus *Obelia* Péron & Lesueur, 1810. This species has traditionally been distinguished from *O. dichotoma* in having hydrocauli that are monosiphonic and relatively little branched, and hydrothecal margins that are entire and not plicated (Nutting 1915; Fraser 1944). Accordingly, *Obelia hyalina* is once again recognized as valid in this work. Colonies are usually much smaller in size (usually 15–20 mm) than those of *O. dichotoma* (as much as 50–350 mm) as described by Cornelius (1995b). It is also a species of tropical and warm-temperate rather than of boreal and mostly cool-temperate regions, where *O. dichotoma* was originally found.

Clarke (1879), in the original account of *O. hyalina*, made no mention of either substrate or depth of collection. Many subsequent records of the species have been based on specimens from *Sargassum* (e.g., Nutting 1895, 1915; Versluys 1899; Fraser 1912b, 1918, 1943, 1944; Broch 1913, as *Laomedea sargassi*; Bennitt 1922; Leloup 1935, 1937, as *L. sargassi*; Rees & Thursfield 1965), the substrate of colonies examined here. It appears that the common species of *Obelia* on pelagic *Sargassum* in the North Atlantic is *O. hyalina*, and gulfweed would be of common occurrence at its type locality in the southern Gulf of Mexico. *Obelia hyalina* is found on both *Sargassum natans* and *S. fluitans*, and it is one of the most frequent hydroid species on those holopelagic fucoids (Calder 1995, as *O. dichotoma*).

The name *Laomedea sargassi* Broch, 1913 has sometimes been applied to this species (e.g., Leloup, 1935, 1937). Broch (1913) had considered both *Obelia hyalina* Clarke 1879 and *Gonothyraea hyalina* Hincks, 1866 referable to genus *Laomedea* Lamouroux, 1812, and proposed *L. sargassi* as a replacement name for the supposed junior homonym. No homonymy currently exists because the two species are again referred to different genera, and the binomen *L. sargassi* is an invalid junior objective synonym of *O. hyalina*. Somewhat less certain is the identity

of *Obelia congdoni* Hargitt, 1909. It was described from material found on *Sargassum* in the Woods Hole region, Massachusetts. Hargitt (1909) had considered it identical with material that Congdon (1907) had identified as *O. hyalina* from Bermuda, but he believed both his hydroids and those of Congdon were different from Clarke's (1879) species. The origins of branches were thought to differ, gonothecae were said to be large with a terminal neck instead of small and rounded distally, and colonies were larger (20–30 mm instead of 12 mm high). Nutting (1915), Fraser (1944), and Vervoort (1968) are probably correct that *O. congdoni* and *O. hyalina* are conspecific.

According to Clarke (1879), *Obelia hyalina* was obtained north of "Zoblos Island," which I have been unable to locate. Nutting (1900: 91) gave coordinates of "lat.N.24°8', long.W.28°51'" for a station said to be 10 miles north of Zoblos Island, but that is in the eastern North Atlantic off the coast of Africa. In a narrative of cruises including the one during which Clarke's material was collected, Alexander Agassiz made no mention of "Zoblos" Island. However, one of the transects surveyed during the work extended from "...the north side of the Yucatan Bank to Alacran Reef, and from there in a south-east direction into 20 fathoms off the Joblos Islands..." (A. Agassiz 1888: ix). Isla Holbox (roughly pronounced "hole-bosch"), at the northeastern tip of the Yucatan Peninsula, Mexico, corresponds with Agassiz's account and is taken to be the site. The station off "Zoblos Island" (Isla Holbox) is the type locality of three other nominal species (*Eudendrium distichum, Campanularia coronata, Nematophorus grandis*) of hydroids described by Clarke (1879).

Reported distribution. Atlantic coast of Florida. Straits of Florida (Fraser 1944).

Western Atlantic. Gulf Stream east of Nova Scotia, on *Sargassum* (Fraser 1918), to Brazil (Vannucci 1949), and including the Sargasso Sea (Leloup 1937, as *Laomedea sargassi*), the Caribbean Sea (Leloup 1935, as *L. sargassi*), and the Gulf of Mexico (Fraser 1944).

Elsewhere. Eastern Atlantic (Rees & White 1966); questionable records exist from the tropical eastern Pacific (Fraser 1948) and Indian Ocean (Thornely 1904).

Obelia oxydentata Stechow, 1914

Fig. 16g

Obelia(?) *oxydentata* Stechow, 1914: 131, fig. 7. *Obelia oxydentata.*—Weiss, 1948: 158.

Type locality. Virgin Islands: St. Thomas, Charlotte Amalie (Stechow 1914).

Voucher material. Fort Pierce, ship canal at Link Port, 27°32'05"N, 80°20'50"W, 0.1 m, 17.ii.1991, on prop roots of *Rhizophora mangle*, 15° C, 22‰, collected by snorkeling, several colony fragments, up to 9 mm high, without gonophores, coll. D.R. Calder, ROMIZ B1112.

Remarks. Specimens referred here to *Obelia oxydentata* Stechow, 1914 were all small (<1 cm high) with monosiphonic hydrocauli. Hydroids with the same characters have been reported elsewhere from shallow waters of the tropical and subtropical western Atlantic as *O. bidentata* Clark, 1875 (e.g., Bermuda: Calder 1991a; Brazil: Migotto 1996; Guadeloupe: Galea 2010). Such specimens contrast with the original descriptions of *O. bidentata* (colonies polysiphonic and up to 15 cm high) and its subjective synonym *O. bicuspidata* Clark 1875 (colonies polysiphonic and up to 8 cm high), both from temperate waters in the Long Island Sound area. While I earlier considered *O. oxydentata* to be conspecific with *O. bidentata* (e.g., Calder 1991a), it appears to be a different species. *Obelia longicyatha* Allman, 1877 from 90 fathoms (165 m) off Florida Reef, with small (< 2.5 cm) but partly polysiphonic colonies, has also been regarded in many recent works as conspecific with *O. bidentata*. Comparisons are warranted to determine whether the supposedly shallow-water *O. oxydentata* is identical with it.

Reported distribution. Atlantic coast of Florida. Biscayne Bay (Weiss 1948).

Western Atlantic. Florida (this report) to Brazil (Vannucci Mendes 1946), and including the Caribbean Sea (Stechow 1914; Fraser, 1944). Its range will likely prove to be much more extensive once it can be reliably distinguished from *Obelia bidentata* Clark 1875.

Elsewhere. Tropical eastern Pacific (Stechow 1914).

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