



Some leptothebate hydroids (Cnidaria, Hydrozoa) from Hawaii, mostly from inshore and nearshore waters

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Abstract

This report is based on a small collection of hydroids from the Hawaiian Islands, in the central Pacific Ocean. Most of the examined material was obtained by staff of the Bernice Pauahi Bishop Museum, Honolulu, during surveys for nonindigenous marine species in shallow, sheltered, inshore or nearshore waters, and especially in harbours, bays, and lagoons. In all, 34 species of leptothebate hydroids, assigned to 14 families and 20 genera, were identified and are discussed. One of them, based on a single infertile colony with a damaged hydrotheca, was identified provisionally only to the rank of suborder. Given the limited geographic and bathymetric focus of the surveys, only four of the species, *Clytia thornelyi*, *Halecium sibogae*, *Macrorhynchia balei*, and *M. hawaiiensis*, were collected at depths greater than 25 m. Seven species, *Cirrhoholenia tetranema* Kramp, 1959, *Orthopyxis crenata* (Hartlaub, 1901), *Clytia elongata* Marktanner-Turneretscher, 1890, *C. paulensis* (Vanhöffen, 1910), *Tridentata maldivensis* (Borradaile, 1905), *Monothecha flexuosa* (Bale, 1894), and a hydroid identified only as Eirenida (undetermined), are recorded from Hawaii for the first time. Three others, *Lytocarpia nigra* (Nutting, 1905) *Macrorhynchia balei* (Nutting, 1905), and *M. hawaiiensis* (Nutting, 1905), have their type localities in Hawaii, with the last of these being known to date only from the Hawaiian archipelago. Most of the species are well-known from shallow water areas across the tropical and subtropical Indo-Pacific region, and over half of them have been reported as well from warm waters in the Atlantic Ocean. Their existence in the remote islands of Hawaii is attributed to long-range dispersal by both natural and human-mediated means, including shipping.

Key words: Anthoathecata, Hydroidolina, Leptothebata, marine invertebrates, Medusozoa, taxonomy, zoological nomenclature

Introduction

The oceanic islands of Hawaii, located in the central Pacific Ocean, are singularly remote from continental coasts and even from other Pacific islands. Yet hydroids have likely occupied this volcanic archipelago for aeons, and the

contemporary hydroid fauna is known to be quite diverse. Including the specimens studied here, 108 species have now been reported from the islands. Excluded from that number are two limnopolyps from fresh waters (*Craspedacusta sowerbii* Lankester, 1880 and *Calpasoma dactylopterum* Fuhrmann, 1939), and all hydroids found on Japanese tsunami marine debris that reached Hawaii over the last decade (Choong *et al.* 2018). It is presently unknown whether any of the species transported from Japan will become established in the islands.

Noteworthy taxonomic works on the hydroids of Hawaii include accounts of predominantly deep water offshore species by Nutting (1905), of the shallow inshore fauna by Cooke (1977), of stylasterids by Cairns (1978, 2005, 2017), and of mostly nearshore anthoathecates by Calder (2010). Several published reports of one or a few species of hydroids from Hawaii have been mentioned earlier (Calder 2010).

As with hydroids inhabiting other isolated islands such as the Azores (Cornelius 1992b) and Bermuda (Calder 1993), the shallow-water species of Hawaii are likely to have been introduced largely through long-distance rafting of their benthic stages by natural and human-mediated means. Included as part of the latter is transport of fouling species on hulls of ships, and in ballast water. Carlton & Eldredge (2009) suspected that fouling organisms were likely carried to the Hawaiian Islands early on by Polynesian vessels, and later by ships visiting from European and other worldwide ports. Citing the work of Richards (2000), they noted that over a single 20-year period (1820–1840), whaling ships visited Honolulu more than 1500 times, and trans-ocean traders from around the Pacific Rim arrived in the same port over 400 times. Today, international commercial and military shipping is considered of prime importance in facilitating species invasions of coastal and inland waters, including those of Hawaii (Coles *et al.* 1999, 2002a, 2004; Carlton & Eldredge 2009). Of relevance, a major commercial shipping port occurs in Honolulu Harbor, and nearby Pearl Harbor has long been the site of a large American naval base.

Over a period of two decades around the turn of the current millenium, extensive surveys were undertaken in Hawaii to document occurrences of nonindigenous marine and estuarine species. Fieldwork, as part of those investigations, focused primarily on substrates in harbours (e.g., Honolulu Harbor, Pearl Harbor, Hilo Harbor, Kahului Harbor) and bays (e.g., Kaneohe Bay, Maunaloa Bay), where invasive species were most likely to be found. Reports based on those projects (Coles *et al.* 1999, 2002a, b, 2004, 2006, 2009; Carlton & Eldredge 2009, 2015) included identifications of hydroids. A majority of the thecate species listed in the publications of Coles *et al.* and Carlton & Eldredge are studied and discussed in greater detail here. Anthoathecate hydroids and limnopolyps of Hawaii were addressed earlier (Calder 2010).

Objectives of this study were to report on a collection of leptothecate hydroids, most of them from shallow waters surrounding the main islands of Hawaii (especially Oahu and Maui), at the Royal Ontario Museum. Included with an account of each species is information on type locality, basic taxonomy, and geographic distribution. The Hawaiian hydroid fauna, including the leptothecates, remains little studied and inadequately known.

Materials and Methods

Materials examined here exist in collections of the Invertebrate Zoology Section, Department of Natural History, at the Royal Ontario Museum (Toronto, Canada). Most of the specimens, received for identification from S.L. Coles of the Bernice Pauahi Bishop Museum, Honolulu, were collected during surveys for nonindigenous species in the inshore and nearshore waters of the main Hawaiian Islands. Others, from shallow coastal waters of Oahu and Maui, were donated by J.P. Hoover. Another small collection from inshore waters of the island of Oahu was obtained during my visit to the Bishop Museum in July 2009.

Included in accounts of each species are an abbreviated synonymy list, information on type locality, summaries of examined material, and remarks on taxonomy and nomenclature. Finally, a “Reported Distribution” section for each species includes original published records from the main Hawaiian Islands, followed by a brief overview of the reported distribution elsewhere. Excluded are distribution records from Hawaii based solely on other published accounts.

Synonymy lists are limited to citation of the publication in which a given species name was first made available nomenclaturally, to works providing original records of particular species in Hawaii, and to publications also providing significant information on introduced and cryptogenic marine species of hydroids from Hawaii. Original authorship and dates of all nominal taxa used herein were traced and confirmed. The classification system has been adapted from multiple sources, but especially from Maronna *et al.* (2016).

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

BM	British Museum (Natural History), now the Natural History Museum, London, UK.
BPBM	Bernice Pauahi Bishop Museum, Honolulu, Hawaii, USA.
HURL	Hawaii Undersea Research Laboratory, Honolulu, Hawaii, USA.
ICZN	International Commission on Zoological Nomenclature; <i>International Code of Zoological Nomenclature. Fourth Edition</i> (International Commission on Zoological Nomenclature 1999).
ROM	Royal Ontario Museum, Toronto, Ontario, Canada.
ROMIZ	Invertebrate Zoology collections, Royal Ontario Museum, Toronto, Ontario, Canada.
WoRMS	World Register of Marine Species (http://www.marinespecies.org , last consulted 06 April 2020), with content on Hydrozoa from the World Hydrozoa Database by Peter Schuchert (http://www.marinespecies.org/hydrozoa).
ZSM	Zoologische Staatssammlung München, München, Germany.

Systematic Account

Order Leptothecata Cornelius, 1992a

Family Syntheciidae Marktanner-Turneretscher, 1890

Genus *Synthecium* Allman, 1872

***Synthecium megathecum* Billard, 1925a**

Figs. 1a, b

Sertularia tubitheca.—Pictet, 1893: 51, pl. 2, figs. 44, 45 [not *Sertularia tubitheca* Allman, 1877].

Synthecium tubithecum.—Nutting, 1905: 950 [not *Sertularia tubitheca* Allman, 1877].

Synthecium megathecum Billard, 1925a: 648 [nom. nov. for *Sertularia tubitheca* sensu Pictet, 1893].—Coles *et al.*, 2002a: 318; 2002b: 177.—Carlton & Eldredge, 2009: 37.

Synthecium tubitheca.—Cooke, 1977: 91, fig. 19 [not *Sertularia tubitheca* Allman, 1877].

Type locality. Indonesia: Ambon Bay (Pictet 1893, as *Sertularia tubitheca*).

Material examined. Oahu: Kaneohe Bay, Sta. 7, Pristine Reef, 21°28'42.3"N, 157°49'29.5"W, 19 November 1999, one colony, 1.1 cm high, with gonothecae, coll. R. DeFelice and S.L. Coles, ROMIZ B3306.

Remarks. Species of the genus *Synthecium* Allman, 1872 can be difficult to distinguish, particularly when gonothecae are absent (Billard 1925b). Gravier-Bonnet (1979) has largely been followed here in regarding hydroids assigned to *S. tubithecum* (Allman, 1877) from locations including Hawaii, Japan, and the Indian Ocean to be *S. megathecum* Billard, 1925a instead. Schuchert (2003) suspected that *S. megathecum* might be conspecific with *S. flabellum* Hargitt, 1924. Meanwhile, however, *S. megathecum* has been recognized as valid in works such as those by Rees & Vervoort (1987) and Vervoort & Watson (2003).

The type (and type locality) of the replacement name *Synthecium megathecum* is that of its objective synonym *Sertularia tubitheca* sensu Pictet (1893) (not *S. tubitheca* Allman, 1877) (ICZN Art. 72.7).

Reported Distribution. Hawaii. Molokai, off west coast, R/V *Albatross* Sta. 3819, 21°09'50"N, 157°22'51.6"W, 70 fm (128 m) (Nutting 1905, as *Synthecium tubithecum*).—Island of Hawaii, Hilo Bay, R/V *Albatross* Sta. 4053, 19°45'39.96"N, 155°04'40.8"W, 29 fm (53 m) (Nutting 1905, as *Synthecium tubithecum*).—Oahu, Kaneohe Bay, 1-2 m, on coral rubble (Cooke 1977, as *Synthecium tubitheca*).—Oahu, Kaneohe Bay, Pristine Reef, 21°28'42.3"N, 157°49'29.5"W (Coles *et al.* 2002a).—Oahu, Waikiki, Sta. 4, Tongg's wreck, 21°15'17.4"N, 157°49'19"W, 4 m (Coles *et al.* 2002b).—Oahu, Waikiki, Sta. 5, Aquarium Outside Reef, 21°15'53.5"N, 157°49'36"W, 3 m (Coles *et al.* 2002b).

Elsewhere. Indo-West Pacific, from east Africa to New Zealand (Vervoort & Watson 2003).

Family Hebellidae Fraser, 1912

Genus *Hebella* Allman, 1888

Hebella sp.

Fig. 1c

Anthohebella parasitica.—Coles *et al.*, 2002a: 318; 2002b: 177.—Carlton & Eldredge, 2009: 37.

Material examined. Oahu: Kaneohe Bay, Sta. 25, Moku Manu Island, 26 January 2000, one colony, on *Lytocarpia nigra*, without gonophores, coll. R. DeFelice and S.L. Coles, ROMIZ B3310.

Remarks. The hydroid colony examined here has previously been identified as *Anthohebella parasitica* (Ciamician, 1880), by Coles *et al.* (2002a). Its trophosome resembles both *A. parasitica* and *Hebella furax* Millard, 1957, but the absence of gonophores renders identification of the hydroid uncertain. It has been assigned provisionally here to *Hebella* Allman, 1888.

Reported Distribution. Hawaii. Oahu, Kaneohe Bay, Sta. 25, Moku Manu Island, 18–20 m (Coles *et al.* 2002a, as *Anthohebella parasitica*).—Oahu, Waikiki, Sta. 8, Ala Wai buoy, 21°16'34"N, 157°50'46.7"W, 16.5 m (Coles *et al.* 2002b, as *Anthohebella parasitica*).

Family Cirrholoveniidae Bouillon, 1984

Genus *Cirrholovenia* Kramp, 1959

Cirrholovenia tetranema Kramp, 1959

Fig. 1d

Cirrholovenia tetranema Kramp, 1959: 253, figs. 17a, b [medusa].

Type locality. Solomon Islands: 9°25'S, 160°00'E, 29 m (Kramp 1959).

Material examined. Oahu: Pearl Harbor, Sta. 15, 21°22'19"N, 157°56'09"W, 27 November 2007, one colony, without gonothecae, coll. S.L. Coles, ROMIZ B5283.

Remarks. In having been described originally from several locations in the Indo-West Pacific region, including the Solomon Islands (type locality), the Strait of Malacca, Gulf of Siam (=Gulf of Thailand), the Philippines, and Indonesia, *Cirrholovenia tetranema* Kramp, 1959 might be expected to occur in Hawaii. This is nevertheless the first report of the species from the islands. The hydroid, known initially as *Egmondella amirantensis* Millard & Bouillon, 1973 (type locality: Amirante, Seychelles) and later as *Lafoeina amirantensis*, was linked to the medusa *C. tetranema* by Migotto & Cabral (2005) in Brazil. Brinckmann (1965) had earlier studied the life cycle of the species in the Gulf of Naples, Italy.

Reported Distribution. Hawaii. First record.

Elsewhere. Circumglobal, tropical and warm temperate waters (Xu *et al.* 2014; Calder *et al.* 2019).

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

Eirenida (undetermined)

Fig. 1e

Material examined. Oahu: Pearl Harbor, Sta. 15, 21°22'19"N, 157°56'09"W, 27 November 2007, one colony, without gonothecae, coll. S.L. Coles, ROMIZ B5284.

Remarks. The single colony available for study was sterile and in poor condition. In lacking information on its medusa stage, the hydroid is currently unidentifiable, even to family rank. It has been provisionally assigned here to the suborder Eirenida Maronna *et al.*, 2016. Hydroids of several genera and families within that taxon can be difficult to differentiate based on morphology alone.

Reported Distribution. Hawaii. First record.

Family Campanulariidae Johnston, 1837

Genus *Orthopyxis* L. Agassiz, 1862

Orthopyxis crenata (Hartlaub, 1901)

Figs. 1f, g

Eucopella crenata Hartlaub, 1901: 364, pl. 22, figs. 27–31, 33–35.

Type locality. New Zealand: Cook Strait, French Pass (Hartlaub 1901).

Material examined. Oahu: Kaohikaipu Island, 7 August 2007, one colony, 1.5 mm high, without gonothecae, coll. M. Hutchinson, ROMIZ B5285.

Remarks. This hydroid was assigned to *Orthopyxis crenata* (Hartlaub, 1901) based on the similarity of its hydrothecae to those of Indo-Pacific populations of the species described by authors including Hartlaub (1901), Ralph (1957), Hirohito (1969, 1995), Millard & Bouillon (1973), Millard (1975), Vervoort & Watson (2003), and Watson (2005). The species has also been reported from the Atlantic Ocean and Mediterranean Sea (e.g., Gravili *et al.* 2015; Oliveira *et al.* 2016). No gonothecae were observed in the Hawaiian material available here. While somewhat resembling the Atlantic *O. sargassicola* (Nutting, 1915), the two species are distinct both morphologically and genetically (Cunha *et al.* 2015, 2020). Marginal cusps of *O. crenata* are much shallower than those of *O. sargassicola*, and its gonothecae are erect and smooth to slightly wrinkled instead of annulated and recumbent.

Numerous references to *O. crenata* are cited in the synonymy list of Vervoort & Watson (2003).

Reported Distribution. Hawaii. First record.

Elsewhere. Atlantic, Pacific, and Indian oceans; temperate to tropical waters (Vervoort & Watson 2003).

Family Clytiidae Cockerell, 1911

Genus *Clytia* Lamouroux, 1812

Clytia elongata Marktanner-Turneretscher, 1890

Fig. 2a

?*Clytia elongata* Marktanner-Turneretscher, 1890: 215, pl. 3, fig. 11.

Type locality. New Zealand: Auckland (Marktanner-Turneretscher 1890).

Material examined. Oahu: Pearl Harbor, Rainbow Bay Marina, 21°22'15.45"N, 157°56'16.31"W, <1 m, on dock, 16 July 2009, one colony fragment, 5 mm high, without gonothecae, coll. D.R. Calder, ROMIZ B5286.

Remarks. Hydrothecae of *Clytia elongata* Marktanner-Turneretscher, 1890 are distinctive in being gracile and deep, with gradually tapered walls and low, rounded marginal cusps. Pedicels of the species are slender, with a series of small annulations at the distal end. Conforming with these characters and assigned to the species here is a hydroid colony from a floating dock at the Rainbow Bay Marina in Pearl Harbor (ROMIZ B5286).

Clytia elongata, previously unknown from Hawaii, has seldom been reported anywhere. It was originally described from Auckland, New Zealand (Marktanner-Turneretscher 1890) and has been recorded from an unstated location off the coast of New South Wales, Australia (Ritchie 1911). A report from Cook Strait, New Zealand, by Vervoort & Watson (2003) appears questionable. More recently, the species was identified from marine fouling communities in Franklin's Bay, Puerto Ayora, Galápagos Islands, Ecuador (Calder *et al.* 2019). To date, only the trophosome of this poorly known species is known.

The binomen *Clytia elongata* was applied by Warren (1908) to a different species of hydroid from Natal, South Africa. Stechow (1919) recognized its homonymy with *C. elongata* Marktanner-Turneretscher, 1890, and provided the replacement name *C. warreni* for it.

Reported Distribution. Hawaii. First record.

Elsewhere. New Zealand (Marktanner-Turneretscher 1890), New South Wales, Australia (Ritchie 1911); Galápagos Islands (Calder *et al.* 2019).

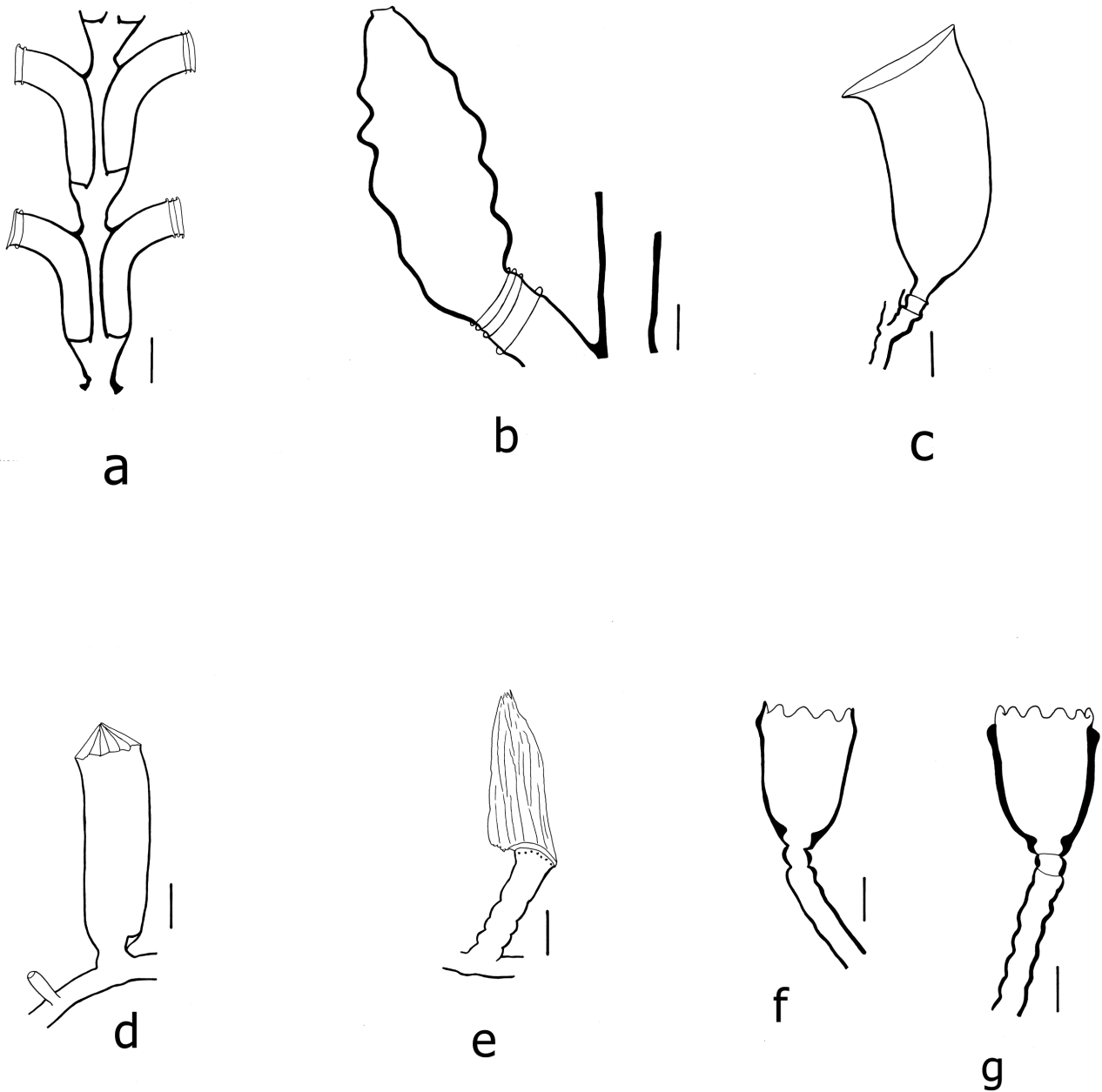


FIGURE 1. **a**, *Synthecium megathecum*: two pairs of hydrothecae, Pristine Reef, Kaneohe Bay, Oahu, ROMIZ B3306. Scale equals 0.2 mm. **b**, *Synthecium megathecum*: gonotheca arising from hydrothecal orifice, Pristine Reef, Kaneohe Bay, Oahu, ROMIZ B3306. Scale equals 0.1 mm. **c**, *Hebella sp.*: hydrotheca, pedicel, and stolon, Moku Manu Island, Kaneohe Bay, Oahu, ROMIZ B3310. Scale equals 0.2 mm. **d**, *Cirrholovenia tetranema*: stolon with hydrotheca and nematotheca, Pearl Harbor, Oahu, ROMIZ B5283. Scale equals 0.05 mm. **e**, *Eirenida* (undetermined): pedicel and damaged hydrotheca, Pearl Harbor, Oahu, ROMIZ B5284. Scale equals 0.1 mm. **f**, *Orthopyxis crenata*: part of pedicel with a hydrotheca, Kaohikaipu Island, Oahu, ROMIZ B5285. Scale equals 0.1 mm. **g**, *Orthopyxis crenata*: part of pedicel, and hydrotheca with more thickened walls, Kaohikaipu Island, Oahu, ROMIZ B5285. Scale equals 0.1 mm.

Clytia elsaeoswaldae Stechow, 1914

Figs. 2b, c

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

Clytia cf. *gracilis*.—Coles *et al.*, 2009: 59, 68, 72, 76, 82, 85.

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

Material examined. Oahu: Pearl Harbor, Sta. 15, 21°22'19"N, 157°56'09"W, 27 November 2007, five colonies or colony fragments, to 1.1 cm high, with gonothecae, coll. S.L. Coles, ROMIZ B5287.—Oahu: Pearl Harbor, 21°20'40"N, 157°58'31"W, 31 January 2008, one colony fragment, to 5 mm high, without gonothecae, coll. S.L. Coles, ROMIZ B5288.—Oahu: Pearl Harbor, Rainbow Bay Marina, 21°22'15.45"N, 157°56'16.31"W, <1 m, on dock, 16 July 2009, one colony, 5 mm high, on sponge, with gonothecae, coll. D.R. Calder, ROMIZ B5289.

Remarks. The distinction between *Clytia elsaeoswaldae* Stechow, 1914 and *C. gracilis* (M. Sars, 1850), often considered conspecific in the past, is now becoming more clear (Lindner *et al.* 2011; Calder 2013, 2019; Cunha *et al.* 2020). Characters said by Lindner *et al.* to distinguish *C. elsaeoswaldae* from *C. gracilis* include a colony form that is stolonial or mostly so rather than branched, and gonothecae that arise from the hydrorhiza rather than from the pedicels. From morphometric studies by Cunha *et al.* (2020), hydroids of *C. elsaeoswaldae* also differ from those of *C. gracilis* in having hydrothecae that are usually broader and hydrothecal bases that tend to be more distinctly rounded. Recognition of *Clytia elsaeoswaldae* as a distinct species is also supported by the multigene phylogenetic analyses of Leclère *et al.* (2009), Lindner *et al.* (2011), and Cunha *et al.* (2017). These same studies also confirm that both *C. elsaeoswaldae* and *C. gracilis* (and its cryptic species) are distinct from *C. hemisphaerica* (Linnaeus, 1767). Hydroids of the latter species differ morphologically from those related congeners in having hydrothecal cusps that are rounded and erect rather than pointed and inclined to the right (when viewed laterally), and gonothecae that are spirally ribbed rather than smooth (Cornelius 1995b; Lindner *et al.* 2011; Calder 2019).

Stechow (1914) named two putatively distinct species, *Clytia elsae-oswaldae* and *Thaumantias (?) elsae-oswaldae*, after his wife, Elsa Oswald. Nomenclatural confusion exists because both are now assigned to *Clytia* Lamouroux, 1812. Given their secondary homonymy, precedence was assigned to the first of these names, under the First Reviser Principle (ICZN Art. 24.2), by Calder (1991). Type material of that species included both trophosome and gonosome. The identity of the second species, based on an apparent juvenile, is a *species inquirenda* (Calder 2019).

The hydroid from Hawaii examined during this study corresponds in morphology with the concept of *C. elsaeoswaldae* and is assigned to it here. The species has only recently been reported from the Pacific Ocean (Balboa, near Newport Beach, California, and Bahía de los Ángeles, Mexico), as the medusa stage (Bryant & Arehart 2019). However, certain records of *C. gracilis* from locations in the Pacific Ocean are also believed referable to it, including ones from Hawaii (Coles *et al.* 2009, as *Clytia* cf. *gracilis*).

Reported Distribution. Hawaii. Oahu, Pearl Harbor, Sta. 2, West Loch entrance channel, 21°20.636'N, 157°58.497'W (Coles *et al.* 2009, as *Clytia* cf. *gracilis*).—Oahu, Pearl Harbor, Sta. 6A, Hospital Point South, 21°20.624'N, 157°57.927'W (Coles *et al.* 2009, as *Clytia* cf. *gracilis*).—Oahu, Pearl Harbor, Sta. 15, Rainbow Bay Marina, 21°22.321'N, 157°56.182'W, floating buoys and docks (Coles *et al.* 2009, as *Clytia* cf. *gracilis*).—Oahu, Keehi Lagoon, Sta. KL18, marina docks, 21°19.183'N, 157°53.663'W (Coles *et al.* 2009, as *Clytia* cf. *gracilis*).

Elsewhere. Warm-temperate and tropical waters of the western Atlantic, including the Caribbean Sea (Calder 2019); warm eastern Pacific (medusa stage) (Bryant & Arehart 2019).

Clytia paulensis (Vanhöffen, 1910)

Figs. 2d–g

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

Type locality. French Southern and Antarctic Lands: Île Saint-Paul, in the crater basin, shallow water (Vanhöffen 1910).

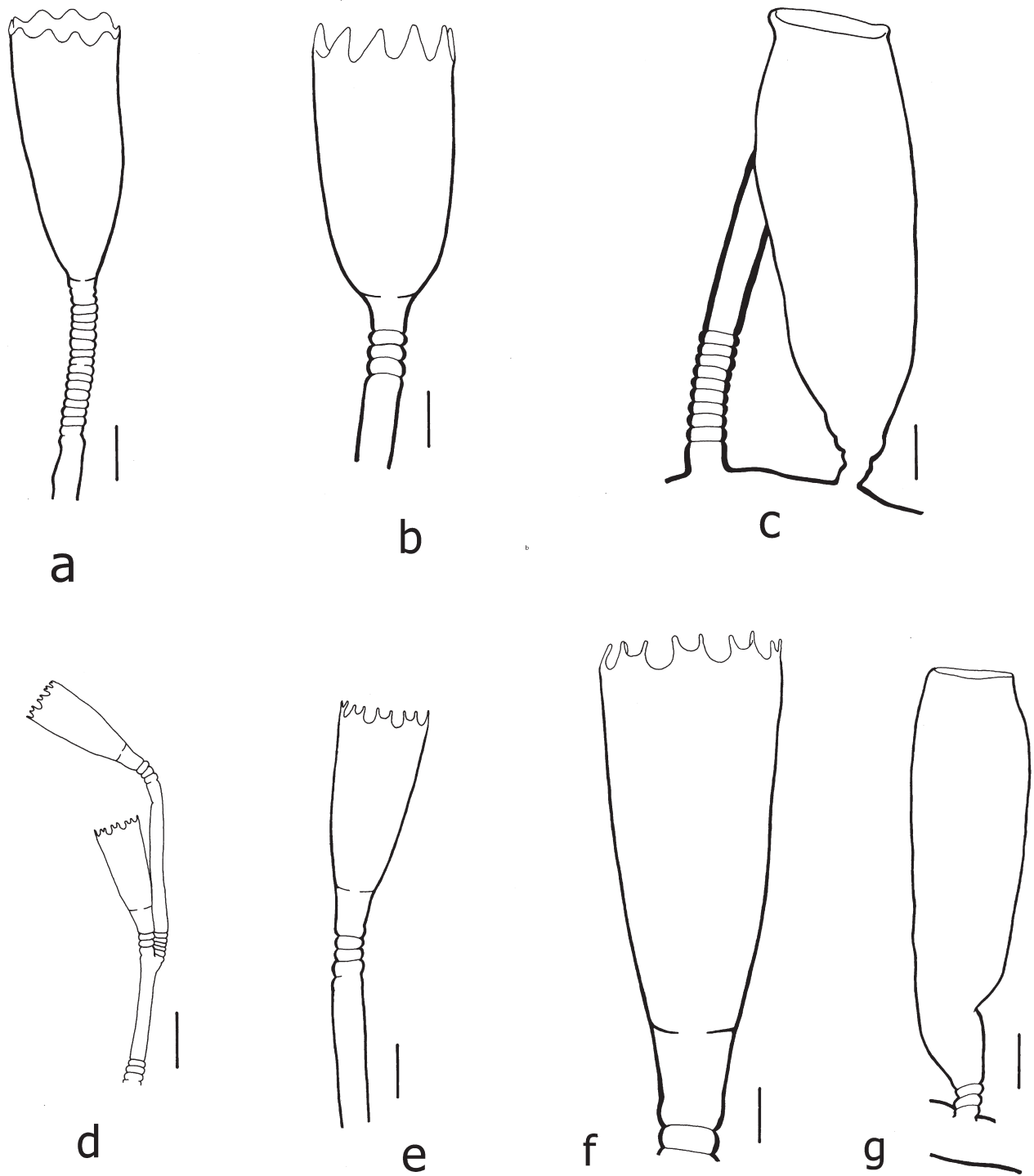


FIGURE 2. **a**, *Clytia elongata*: part of pedicel with a hydrotheca, Rainbow Bay Marina, Pearl Harbor, Oahu, ROMIZ B5286. Scale equals 0.1 mm. **b**, *Clytia elsaeoswaldae*: part of pedicel with a hydrotheca, Rainbow Bay Marina, Pearl Harbor, Oahu, ROMIZ B5289. Scale equals 0.1 mm. **c**, *Clytia elsaeoswaldae*: part of a stolon and pedicel, with a gonotheca, Rainbow Bay Marina, Pearl Harbor, Oahu, ROMIZ B5289. Scale equals 0.1 mm. **d**, *Clytia paulensis*: part of colony with two hydrothecae, Rainbow Bay Marina, Pearl Harbor, Oahu, ROMIZ B5290. Scale equals 0.2 mm. **e**, *Clytia paulensis*: part of pedicel with a hydrotheca, Rainbow Bay Marina, Pearl Harbor, Oahu, ROMIZ B5290. Scale equals 0.1 mm. **f**, *Clytia paulensis*: hydrotheca, Rainbow Bay Marina, Pearl Harbor, Oahu, ROMIZ B5290. Scale equals 0.05 mm. **g**, *Clytia paulensis*: gonotheca, Rainbow Bay Marina, Pearl Harbor, Oahu, ROMIZ B5290. Scale equals 0.1 mm.

Material examined. Oahu: Pearl Harbor, Rainbow Bay Marina, 21°22'15.45"N, 157°56'16.31"W, <1 m, on dock, 16 July 2009, eight colony fragments, to 3 mm high, on sponge, with two gonothecae, coll. D.R. Calder, ROMIZ B5290.

Remarks. *Clytia paulensis* (Vanhöffen, 1910) has been reported from warm-temperate and tropical locations in the western and eastern Pacific, the western and eastern Atlantic, and the Indian Ocean (Calder 2019). It is also known from oceanic islands and seamounts such as Île Saint-Paul (Vanhöffen 1910), the Seychelles (Millard & Bouillon 1973), Madeira, the Canary Islands, the Islas Selvagens, and the Cape Verde Islands (Medel & Vervoort 2000), and Challenger Bank near Bermuda (Calder 2000). Although previously unreported in Hawaii, its discovery at Oahu is therefore unsurprising. The colonies reported here were found as part of the fouling community on a floating dock in Pearl Harbor.

The hydroid of *C. paulensis* is distinguished by a combination of characters including its stolonial or sparsely branched colonies, its slender pedicels, its slim and cylindrical hydrothecae, and its bimucronate hydrothecal margin (Cornelius 1995b; Cunha *et al.* 2020). Gonothecae are smooth. Its medusa is typical of those observed in other species of the genus *Clytia* Lamouroux 1812 (Gravili *et al.* 2015). Overviews of this species are given in works by Cornelius (1995b), Medel & Vervoort (2000), Gravili *et al.* (2015), and Calder (2019).

Reported Distribution. Hawaii. First record.

Elsewhere. Atlantic, Pacific, and Indian oceans; temperate and tropical waters (Medel & Vervoort 2000).

***Clytia thornelyi* (Nutting, 1927)**

Figs. 3a–e

Obelia serrulata.—Thornely, 1900: 453 [not *Obelia serrulata* Bale, 1888].

Obelia thornelyi Nutting, 1927: 202.

Clytia latitheca.—Coles *et al.*, 2002a: 318; 2009: 59, 68, 72. —Carlton & Eldredge, 2009: 37.

Type Locality. Papua New Guinea: New Britain, Blanche Bay, 40 fm (73 m), on ropes and fish baskets (Thornely 1900, as *Obelia serrulata*).

Material examined. Oahu: Kaneohe Bay, Floating City, 10 November 1999, one colony, 7 mm high, without gonothecae, coll. R. DeFelice and S. Coles, ROMIZ B3302.—Oahu: Pearl Harbor, Sta. PH10B, 21°21'19"N, 157°57'07"W, 26 February 2008, two colony fragments, to 8 mm high, with gonothecae, coll. S. Coles, ROMIZ B5291.—Maui, HURL Sta. P5-739, 20°56'27.6"N, 156°45'39.6"W, 88 m, 07 April 2009, two colonies or colony fragments, to 2 cm high, with gonothecae, ROMIZ B5292.—Oahu: Pearl Harbor, near Rainbow Bay Marina, 21°22'16.52"N, 157°56'19.75"W, 1 m, on buoy, 16 July 2009, one colony, 3.0 cm high, with gonothecae, coll. D.R. Calder, ROMIZ B5293.

Remarks. The nomenclature of this hydroid is gradually being resolved, with recognition that the binomina *Clytia thornelyi* (Nutting, 1927), *C. stolonifera* Blackburn, 1938, and *C. latitheca* Millard & Bouillon, 1973 all subjectively refer to the same species (Calder *et al.* 2019). Nutting (1927) had recognized that a hydroid identified by Thornely (1900) as *Obelia serrulata* Bale, 1888, from Papua New Guinea, was misidentified and constituted a new species. He thereupon named it *Obelia thornelyi* in honour of L.R. Thornely. The species, currently assigned to *Clytia* Lamouroux, 1812 based on colony form and character of its gonophores (e.g., Millard & Bouillon 1973; Millard 1975; Watson 2005; Calder *et al.* 2019), is now known to have a wide geographic distribution in warm waters. It was reported earlier from Hawaii as *C. latitheca* (Coles *et al.* 2002a, 2009). Somewhat resembling hydroids examined here is a species from the Red Sea that Thornely (1908) identified as *Campanularia denticulata* Clark, 1877. It is unlikely that her hydroid from that location is conspecific with the species of Clark, originally described from the cold waters of Alaska.

Of note, Laura Roscoe Thornely (1860–1951) was a respected British taxonomist of hydroids and bryozoans around the turn of the 20th century. While she published on collections of hydroids from the U.K. (Thornely 1894, 1897), she is best known for her research on species from the Indo-West Pacific region (Sri Lanka, India, the Sudanese Red Sea, Papua New Guinea, Loyalty Islands, and New Caledonia) (Thornely 1900, 1904, 1908, 1916).

Hydrothecal cusps in specimens examined here from Rainbow Bay Marina, Pearl Harbor (ROMIZ B5293), were remarkable in being broadly triangular and sharp-pointed (Figs. 3a, b). In this, they are identical with those illustrated by Thornely (1900) in her account of the species (as *Obelia serrulata*).

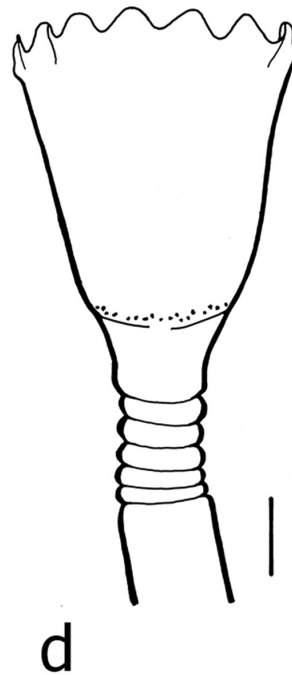
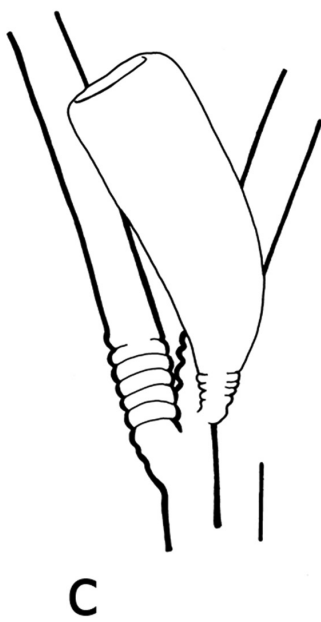
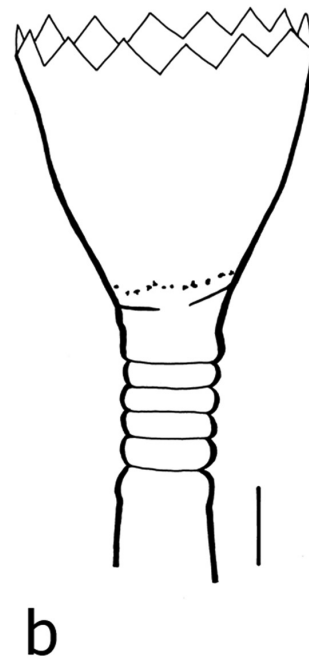
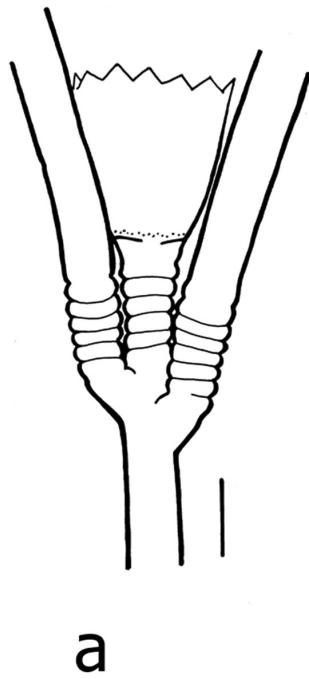


FIGURE 3. **a**, *Clytia thornelyi*: part of hydrocaulus with a hydrotheca, Rainbow Bay Marina, Pearl Harbor, Oahu, ROMIZ B5293. Scale equals 0.2 mm. **b**, *Clytia thornelyi*: part of pedicel with a hydrotheca, Rainbow Bay Marina, Pearl Harbor, Oahu, ROMIZ B5293. Scale equals 0.1 mm. **c**, *Clytia thornelyi*: part of hydrocaulus with a gonotheca, Rainbow Bay Marina, Pearl Harbor, Oahu, ROMIZ B5293. Scale equals 0.2 mm. **d**, *Clytia thornelyi*: part of pedicel with a hydrotheca, off Maui, 20°56'27.6"N, 156°45'39.6"W, ROMIZ B5292. Scale equals 0.1 mm. **e**, *Clytia thornelyi*: part of hydrocaulus with a gonotheca, 20°56'27.6"N, 156°45'39.6"W, off Maui, ROMIZ B5292. Scale equals 0.2 mm.

Reported Distribution. Hawaii. Oahu, Kaneohe Bay, Sta. 14, Floating City, 21°26'23.1"N, 157°47'30.2"W (Coles *et al.* 2002a, as *Clytia latitheca*).—Oahu, Pearl Harbor, Sta. 10A, Southeast Loch Dock, 21°21.359'N, 157°57.131'W (Coles *et al.* 2009, as *Clytia latitheca*).

Elsewhere. Western Atlantic (Calder & Kirkendale 2005, as *Clytia stolonifera*; Oliveira *et al.* 2016, as *Clytia stolonifera*), eastern Pacific (Calder *et al.* 2019), western Pacific (Kirkendale & Calder 2003, as *Clytia latitheca*), and Indian Ocean (Millard 1975, as *Clytia latitheca*); tropical and subtropical waters.

Family Obeliidae Haeckel, 1879

Genus *Obelia* Péron & Lesueur, 1810

Obelia cf. *dichotoma* (Linnaeus, 1758)

Figs. 4a, b

Obelia dichotoma Linnaeus, 1758: 812.—Cooke, 1977: 89, fig. 16.—Grovhoug, 1979: 40.—Grovhoug & Rastetter, 1980: 44.—Coles *et al.*, 2002a: 206; 2002b: 32, 234; 2004: 22, 72; 2009: 59.—Godwin, 2003: 128.—Carlton & Eldredge, 2009: 37.—Choong *et al.*, 2018: 51, 52.

Type Locality. “In Oceano” (Linnaeus 1758); restricted to coast of southwest England by Cornelius (1975).

Material Examined. Oahu: Kaneohe Bay, Sag Harbor, Sta. 24, 21°27'03.3"N, 157°46'42"W, 25 January 2000, one colony, 1 cm high, without gonothecae, coll. R. DeFelice and S.L. Coles, ROMIZ B3309.

Remarks. Although hydroids of *Obelia dichotoma* (Linnaeus, 1758) are reported to be widespread across several oceans (Cornelius 1995b), it is unclear whether the Hawaii population is conspecific with that species, originally described from the eastern North Atlantic. Cryptic lineages have been discovered in clades assigned to *O. dichotoma* (Cunha *et al.* 2017, 2020). Specimens examined here have been provisionally assigned to the species, but eventual revision of the identification is likely. Traditional taxonomy at this point is simply inadequate to resolve the question of its identity.

Reported Distribution. Hawaii. Oahu, Kaneohe Bay (Cooke 1977).—Oahu, Pearl Harbor (Grovhoug 1979; Grovhoug & Rastetter 1980).—Oahu, Kaneohe Bay, Sta. 24, Sag Harbor, 21°27'03.3"N, 157°46'42.0"W (Coles *et al.* 2002a).—Oahu, Hawaii Kai, Sta. 4, Maunalua Bay, 21°16'56.5"N, 157°42'54.4"W (Coles *et al.* 2002b).—Oahu, on hull fouling (Godwin 2003).—Maui, Kahului Harbor, Sta. MA1, Pier 1, 20°54'00.5"N, 156°28'09.8"W, concrete pilings (Coles *et al.* 2004).—Island of Hawaii, Hilo Harbor, Sta. HA4, Pier 1, 19°44'05"N, 155°03'25.1"W (Coles *et al.* 2004).—Oahu, Pearl Harbor, Sta. PH14, Hawaiian Electric Company discharge, 21°23.218'N, 157°57.632'W (Coles *et al.* 2009).—Oahu, Pearl Harbor, Sta. 15, Rainbow Bay Marina, 21°22.321'N, 157°56.182'W (Coles *et al.* 2009).—Oahu, Kaneohe Bay (Bishop Museum, BPBM-D458) (Carlton & Eldredge 2009).—Oahu, Punaluu, on Japanese tsunami marine debris (I-beam, JTMD-BF-72) (Choong *et al.* 2018).—Oahu, on Japanese tsunami marine debris (skiff, JTMD-BF-209), offshore, towed in to Haleiwa (Choong *et al.* 2018).

Elsewhere. Supposed, at present, to be nearly cosmopolitan in nearshore waters (Cornelius 1995b).

Obelia oxydentata Stechow, 1914

Fig. 4c

?*Campanularia spinulosa*.—Nutting, 1905: 943.

Obelia(?) *oxydentata* Stechow, 1914: 131, fig. 7.

Obelia bidentata(?).—Grovhoug, 1979: 40.

Obelia bidentata.—Coles *et al.*, 2002a: 318; 2002b: 234; 2009: 76, 82, 85.—Carlton & Eldredge, 2009: 37.

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

Material examined. Oahu: Kaneohe Bay, Sta. 15, Coconut Island Reef, 21°26'38.5"N, 157°47'47.2"W, 8 November 1999, one colony, 7 mm high, with gonothecae, coll. R. DeFelice and S.L. Coles, ROMIZ B3301.—Oahu: Honolulu Harbor, Sta. 20, 21°19'52"N, 157°53'36"W, 22 April 2008, one colony, 8 mm high, without gonothecae, coll. S.L. Coles, ROMIZ B5294.

Remarks. Over the last few decades, *Obelia oxydentata* Stechow, 1914 (type locality: St. Thomas, U.S. Virgin Islands) has commonly been taken to be conspecific with *O. bidentata* Clark, 1875 (type locality: Long Island, New York, USA). A case has been made recently that they are indeed distinct, with *O. oxydentata* being recognized again as a valid species (Calder 2013, 2019; Calder *et al.* 2019). *Obelia bidentata*, taken to be a temperate to cool-temperate species with large (to 15 cm or more), extensively branched, and polysiphonic colonies, differs from the tropical to warm-temperate *O. oxydentata*, having small (usually 1 cm or less), unbranched, and monosiphonic colonies. Molecular approaches to date on this taxonomic issue have been inconclusive (Govindarajan *et al.* 2006; Leclère *et al.* 2009; Cunha *et al.* 2020), and further assessment is needed, preferably based on topotypic material of the two putative species.

In an account on the hydrozoans of Chesapeake Bay (Calder 1971), I confounded these species, identifying *O. oxydentata* as *O. bicuspidata* Clark, 1875 and *O. bidentata* as *O. longicyatha* Allman, 1877. In that study, hydrothecal dimensions of the two morphotypes differed, with those of “*O. longicyatha*” (= *O. bidentata*) being larger and proportionately deeper than those of “*O. bicuspidata*” (= *O. oxydentata*). As for the oft-misidentified *Obelia longicyatha*, it is now known (Allman, 1877; Calder 2019: 66) to be a deep-water species, referable to *Clytia* Lamouroux, 1812. While it too has bimucronate cusps on the hydrothecal rim, its branching is of the clytiid rather than the obeliid type and its hydrothecae are much deeper and more tapered than those of either *O. oxydentata* or *O. bidentata*.

Nutting (1905) reported a fragmentary colony of *Campanularia spinulosa* Bale, 1888 from a depth of 52 fathoms (95 m) off Maui, Hawaii. Bale’s Australian hydroid, having hydrothecae with bicuspid margins, is now taken to be conspecific with *O. bidentata*. While the identity of Nutting’s specimen (in collections at the National Museum of Natural History, Smithsonian Institution, USNM 22195) is presently questionable, it was found in waters much deeper than usual for the typically shallow, inshore *O. oxydentata*. Should Bale’s *C. spinulosa* prove identical with *O. oxydentata*, however, it would have priority as the valid name of the species. Clearly, the nomenclature of this species remains unsettled.

Reported Distribution. Hawaii. ?Maui, north of Kahului Harbor, *Albatross* Sta. 4071, 20°58′0.12″N, 156°26′34.8″W, 52 fm (95 m) (Nutting 1905, as *Campanularia spinulosa*).—Oahu, Pearl Harbor, fouling panels (Grovhoug 1979, as *Obelia bidentata*?).—Oahu, Kaneohe Bay, Sta. 8, Kahaluu Pier, 21°27′48.7″N, 157°50′01.5″W, old pier pilings (Coles *et al.* 2002a, as *Obelia bidentata*).—Oahu, Kaneohe Bay, Sta. 15, Coconut Island Reef, 21°26′38.5″N, 157°47′47.2″W (Coles *et al.* 2002a, as *Obelia bidentata*).—Oahu, Hawaii Kai, Sta. 2, under the Marina Outlet Bridge (Coles *et al.* 2002b, as *Obelia bidentata*).—Oahu, Keehi Lagoon, Sta. KL20, Moanalua stream mouth, 21°19.910′N, 157°53.586′W, prop roots of *Rhizophora mangle* (Coles *et al.* 2009, as *Obelia bidentata*).

Elsewhere. Western Atlantic (Calder 2019); eastern Pacific (Stechow 1914; Calder *et al.* 2019); western Pacific (Hirohito 1969; ?Gibbons & Ryland 1989, as *Obelia bidentata*; Xu *et al.* 2014, as *Obelia bidentata*); Indian Ocean (Gravier-Bonnet 1999).

Family Haleciidae Hincks, 1869

Genus *Halecium* Oken, 1815

Halecium sibogae Billard, 1929b

Figs. 4d–f

Halecium sibogae Billard, 1929b: 307, Fig. 1B.—Carlton & Eldredge, 2009: 35.

Type locality. Indonesia (Billard 1929b).

Material examined. Oahu: Palea Point, 50 ft (15 m), on coral slab, 23 September 1996, coll. J. Hoover, ROMIZ B3036.—Oahu: Waianae, *Mahi* wreck, on hull, 60–90 ft (18–27 m), 05 November 2003, one colony, 5 cm high, with female gonothecae, coll. S.L. Coles, ROMIZ B3867.—Oahu: off Sandy Beach, 19 m, on basaltic substrate, 27 May 2009, one colony, 2.5 cm high, with male gonothecae, coll. S.L. Coles, ROMIZ B5295.

Remarks. This identification is based on the original account of *Halecium sibogae* by Billard (1929b), but especially on that of Gibbons & Ryland (1989). The species differs from *Diplocyathus sibogae* Billard, 1929a (= *Hydrodendron sibogae*) most notably in lacking nematophores and nematothecae. Given their identical specific names and superficial resemblance, potential confusion exists over the identity of the two.

The known distribution of *H. sibogae* in the Pacific Ocean is limited to Indonesia (Billard 1929b; Di Camillo *et al.* 2008), Fiji (Gibbons & Ryland 1989), and Hawaii (Carlton & Eldredge 2009). *Halecium corpulatum* Watson, 2012 from northwestern Australia (eastern Indian Ocean) may be conspecific. A related species appears to be *H. calderi* Galea, 2010 from Guadeloupe (Galea 2010) and Florida (Calder 2013) in the warm western Atlantic. *Halecium sibogae marocanum* Billard, 1934 has been reported in the eastern North Atlantic and Mediterranean (Medel & Vervoort 2000).

Reported Distribution. Hawaii. Oahu, wreck of the *Mahi*, 20–30 m (Carlton & Eldredge 2009).

Elsewhere. Indonesia (Billard 1929b; Di Camillo *et al.* 2008); Fiji (Gibbons & Ryland 1989); ?western Australia (Watson, 2012, as *Halecium corpulatum*). *Halecium sibogae marocanum* Billard, 1934 has been reported from the eastern North Atlantic Ocean and the Mediterranean Sea (e.g., Medel & Vervoort 2000).

Genus *Nemalecium* Bouillon, 1986

Nemalecium lighti (Hargitt, 1924)

Figs. 4g, h

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

Halecium (beani?).—De Oreo, 1946: 645, figs. 7–9 [not *Halecium beanii* (Johnston, 1838)].

Halecium beani.—Chu & Cutress, 1954: 9 [not *Halecium beanii* (Johnston, 1838)].

?*Halecium beani*.—Cooke, 1977: 87, fig. 15.—Coles *et al.* 1999: 120, 194, 209 [not *Halecium beanii* (Johnston, 1838)].

Halecium sp.—Coles *et al.*, 2002a: 206, 318; 2004: 73; 2009: 59, 76.

Halecium beanii.—Carlton & Eldredge, 2009: 35 [not *Halecium beanii* (Johnston, 1838)].

Nemalecium lighti.—Calder 2010: 53.

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

Material examined. Oahu: Kaneohe Bay, Sta. 8, Kahaluu Landing, 21°27'48.7"N, 157°50'01.5"W, 02 November 1999, three colonies or colony fragments, to 2 cm high, without gonothecae, coll. R. DeFelice and S.L. Coles, ROMIZ B3296.—Oahu: Pearl Harbor, Sta. 2, 21°20'40"N, 157°58'31"W, 31 January 2008, one colony, 2.4 cm high, without gonophores, coll. S.L. Coles, ROMIZ B5296.—Oahu: Honolulu Harbor, Keehi Lagoon, 21°19'10"N, 157°53'36"W, 22 April 2008, six colonies or colony fragments, to 2.8 cm high, with gonothecae, coll. S.L. Coles, ROMIZ B5297.—Oahu: Pearl Harbor, Sta. 14, 21°23'10"N, 157°57'34"W, 04 March 2008, one colony fragment, 1.2 cm high, with empty gonothecae, coll. S.L. Coles, ROMIZ B5298.—Oahu: Honolulu Harbor, La Mariana Sailing Club, 21°19'17.68"N, 157°53'36.37"W, 1 m, on an ascidian on dock, 16 July 2009, two colonies, to 2.5 cm high, without gonophores, coll. D.R. Calder, ROMIZ B5299.—Oahu: Pearl Harbor, Rainbow Bay Marina, 21°22'15.45"N, 157°56'16.31"W, on dock, <1 m, 16 July 2009, one colony, 4.7 cm high, without gonophores, coll. D.R. Calder, ROMIZ B5300.

Remarks. Records included herein suggest that *Nemalecium lighti* (Hargitt, 1924) is both frequent and widespread in shallow waters of Hawaii. A common fouling organism (Calder *et al.* 2019), it is known to be venomous to humans (Marques *et al.* 2002). Hydroids responsible for several envenomations near Honolulu, identified as a species of *Halecium* in De Oreo (1946), are believed here to have been *N. lighti* instead. Illustrations in De Oreo's paper correspond with colonies of that venomous species. Hydroids in other collections from Hawaii, variously identified as *Halecium beani*, *H. beanii* or *Halecium* sp. (Chu & Cutress 1954; Cooke 1977; Coles *et al.* 1999, 2002a, 2004, 2009; Carlton & Eldredge 2009), are also believed referable to *N. lighti*.

Hydroids of *Nemalecium* Bouillon, 1986 are noteworthy in having modified tentacles or nematodactyls, armed with large pseudostenotele nematocysts, on the hydranths. Swimming gonophores are released from the gonothecae (Gravier-Bonnet & Migotto 2000). While usually assigned to Haleciidae Hincks, 1869, Maronna *et al.* (2016) expressed some uncertainty about the family affinities of the genus. Recent accounts of *N. lighti* include those of Galea (2008), Galea *et al.* (2012), Calder (2019), and Calder *et al.* (2019).

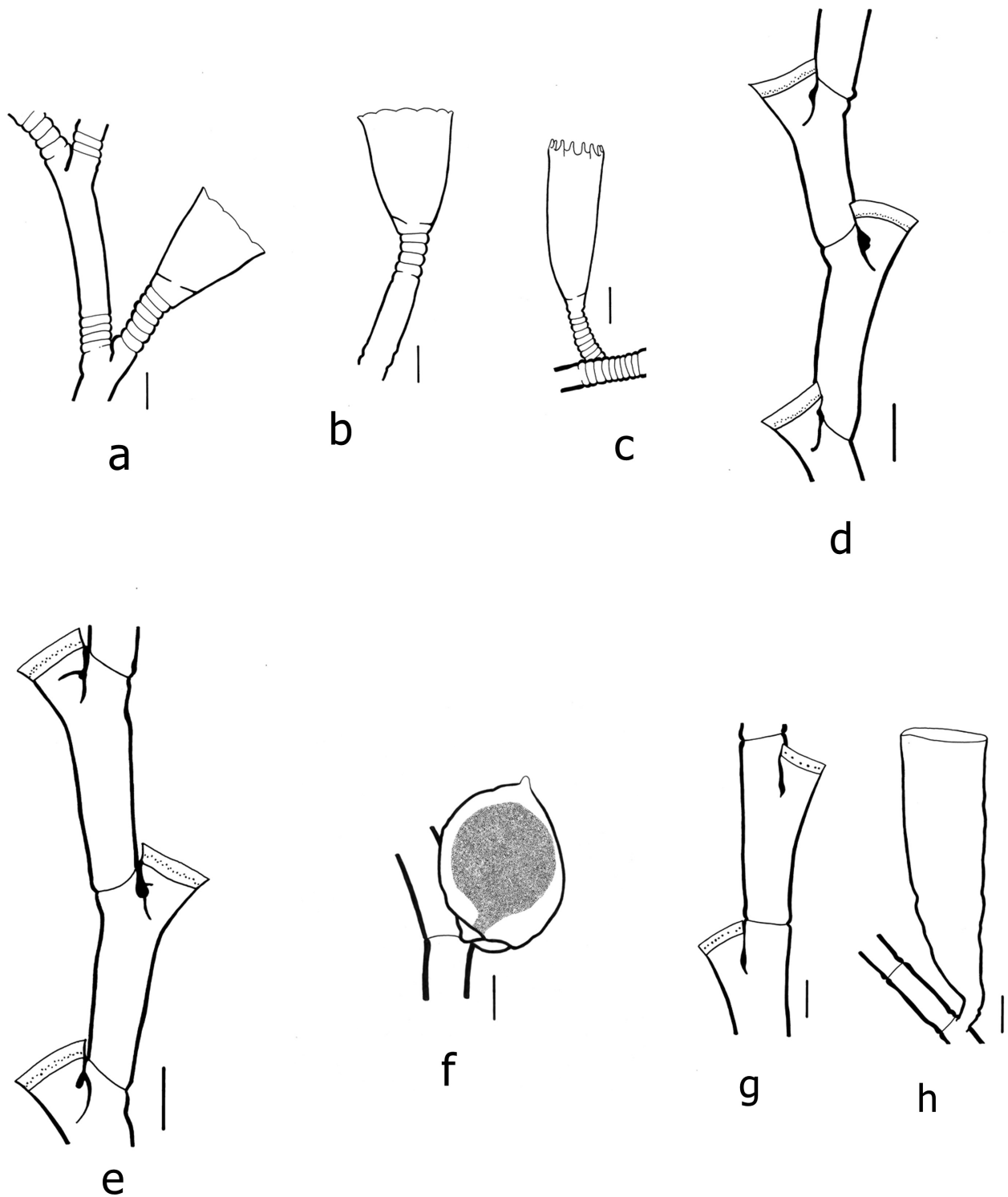


FIGURE 4. **a**, *Obelia dichotoma*: part of hydrocaulus with hydrotheca and pedicel, Sag Harbor, Kaneohe Bay, Oahu, ROMIZ B3309. Scale equals 0.1 mm. **b**, *Obelia dichotoma*: part of pedicel with a hydrotheca, Sag Harbor, Kaneohe Bay, Oahu, ROMIZ B3309. Scale equals 0.1 mm. **c**, *Obelia oxydentata*: part of hydrocaulus with hydrotheca and pedicel, Honolulu Harbor, Oahu, ROMIZ B5294. Scale equals 0.1 mm. **d**, *Halecium sibogae*: part of hydrocaulus with three hydrothecae, Palea Point, Oahu, ROMIZ B3036. Scale equals 0.2 mm. **e**, *Halecium sibogae*: part of hydrocaulus with three hydrothecae, off Sandy Beach, Oahu, ROMIZ B5295. Scale equals 0.2 mm. **f**, *Halecium sibogae*: part of branch with a male gonotheca, off Sandy Beach, Oahu, ROMIZ B5295. Scale equals 0.2 mm. **g**, *Nemalecium lighti*: part of a branch with two hydrothecae, La Mariana Sailing Club, Honolulu Harbor, Oahu, ROMIZ B5299. Scale equals 0.1 mm. **h**, *Nemalecium lighti*: part of colony with a gonotheca, Keehi Lagoon, Honolulu Harbor, Oahu, ROMIZ B5297. Scale equals 0.2 mm.

Reported Distribution. Hawaii. Oahu, near Honolulu, human envenomations (De Oreo 1946, as *Halecium beani*?).—Hawaii, no specific location (Chu & Cutress 1954, as *Halecium beani*).—Oahu, Maunalua Bay, 30 ft (9 m), on rubble (Cooke 1977, as *Halecium beani*).—Oahu, Barbers Point Harbor, Sta. 32, 21°19'19.8"N, 158°07'16.7"W, barge pier (Coles *et al.* 1999, as *Halecium sp.*).—Oahu, Honolulu Harbor, 5 m, wood block, coll. 1945, Bishop Museum, BPBM-D-260 (Coles *et al.* 1999, as *Halecium sp.*; Carlton & Eldredge 2009, as *Halecium beanii*).—Oahu, Kaneohe Bay, coll. 1963, Bishop Museum, BPBM-D-349 (Coles *et al.* 2002a, as *Halecium sp.*).—Oahu, Kaneohe Bay, Sta. 24, Sag Harbor, 21°27'03.3"N, 157°46'42.0"W (Coles *et al.* 2002a, as *Halecium sp.*).—Kauai, Sta. KA1, Nawiliwili Harbor (Coles *et al.* 2004, as *Halecium sp.*).—Molokai, Sta. MO4, Kaunakakai Main Dock, 21°05'05.0"N, 157°01'54"W (Coles *et al.* 2004, as *Halecium sp.*).—Maui, Sta. MA1, Kahului Harbor Pier 1, 20°54'00.5"N, 156°28'09.8"W (Coles *et al.* 2004, as *Halecium sp.*).—Oahu, Pearl Harbor, Sta. PH1, entrance channel, 21°19.468'N, 157°58.218'W (Coles *et al.* 2009, as *Halecium sp.*).—Oahu, Pearl Harbor, Sta. PH2, West Loch entrance channel, 21°20.636'N, 157°58.497'W (Coles *et al.* 2009, as *Halecium sp.*).—Oahu, Pearl Harbor, Sta. PH6A, Hospital Point South, 21°20.624'N, 157°57.927'W (Coles *et al.* 2009, as *Halecium sp.*).—Oahu, Pearl Harbor, Sta. PH13, Utah Memorial, 21°22.137'N, 157°57.736'W (Coles *et al.* 2009, as *Halecium sp.*).—Oahu, Pearl Harbor, Sta. PH14, Hawaiian Electric Company discharge, 21°23.218'N, 157°57.632'W (Coles *et al.* 2009, as *Halecium sp.*).—Oahu, Honolulu Harbor, Sta. HH11, Pier 40-41, 21°19.033'N, 157°52.936'W (Coles *et al.* 2009, as *Halecium sp.*).—Oahu, Keehi Lagoon, KL18, Marina Docks, 21°19.183'N, 157°53.663'W (Coles *et al.* 2009, as *Halecium sp.*).—Oahu, Keehi Lagoon, KL19, Barge Wreck, 21°19.087'N, 157°54.446'W (Coles *et al.* 2009, as *Halecium sp.*).—Oahu, Keehi Lagoon, KL20, stream mouth, 21°19.910'N, 157°53.586'W (Coles *et al.* 2009, as *Halecium sp.*).—Oahu, north shore, in alpheid crevices on corals (Calder 2010).

Elsewhere. Atlantic, Pacific, and Indian oceans; warm waters (Calder *et al.* 2019).

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

Genus *Sertularella* Gray, 1848

Sertularella areyi Nutting, 1904

Fig. 5a

Sertularella areyi Nutting, 1904: 83, pl. 17, fig. 6.—Coles *et al.*, 2002a: 318; 2002b: 177.—Carlton & Eldredge, 2009: 38.

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

Material examined. Oahu: Kaneohe Bay, Sta. 25, Moku Manu Island, 26 January 2000, two colony fragments, to 5 mm high, without gonothecae, coll. R. DeFelice and S.L. Coles, ROMIZ B3312.

Remarks. Discovery of *Sertularella areyi* Nutting, 1904 in shallow nearshore locations at Oahu, Hawaii, was unexpected. Originally described from deep water (183–366 m) off the north coast of Cuba, this hydroid appears to be widespread on outer neritic and upper bathyal bottoms in parts of the western Pacific, including Australia, Indonesia, Japan, Korea, the Philippines, New Caledonia, the Loyalty Islands, and New Zealand (Vervoort 1993; Vervoort & Watson 2003). Elsewhere, it is known from the Indian Ocean (Millard 1975, as *Sertularella annulaventricosa*), and from South Carolina and Bermuda southwards to Brazil in the western Atlantic (Calder 2019). Vervoort & Watson (2003) are followed in considering *S. annulaventricosa* Mulder & Trebilcock, 2015 from Australia and elsewhere the Indo-West Pacific region to be conspecific with *S. areyi*.

Sertularella areyi is a small but striking species, with barrel-shaped hydrothecae encircled by two prominent circular (not spiral) flanges (Vervoort & Watson 2003). Its gonothecae resemble Chinese lanterns, with about 7–10 transverse flanges (Vervoort 1993; Hirohito 1995; Galea 2016). Detailed accounts of this hydroid, based on colonies from the western Pacific Ocean, have been provided by Vervoort (1993) and Vervoort & Watson (2003).

Reported Distribution. Hawaii. Oahu, Kaneohe Bay, Sta. 25, Moku Manu Island (Coles *et al.* 2002a).—Oahu, Waikiki, Sta. 10, Kapua Channel, 21°15'34.8"N, 157°49'39.7"W (Coles *et al.* 2002b).

Elsewhere. Atlantic, Pacific, and Indian oceans, at lower latitudes (Vervoort & Watson 2003).

Sertularella diaphana (Allman, 1885)

Fig. 5b

Thuiaria diaphana Allman, 1885: 145, pl. 18, figs. 1–3.

Sertularella torreyi Nutting, 1905: pl. 4, fig. 4, pl. 11, figs. 2, 3.

Sertularella speciosa.—Cooke, 1977: 96, fig. 22.

Sertularella diaphana.—Hoover, 1998: 21, unnumbered figure; 2006: 21, unnumbered figure.—Carlton & Eldredge, 2009: 38.—Wagner *et al.*, 2016: 57, two unnumbered figures.

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

Material examined. Oahu: Palea Point, just outside Hanauma Bay, 25 ft (8 m), 08 October 1996, two colonies, to 4.9 cm high, without gonothecae, coll. J. Hoover, ROMIZ B2902.

Remarks. *Sertularella diaphana* (Allman, 1885) was originally described from a collection made available to G.J. Allman by Horatia Gatty (1846–1945). Hydroids in it were dry but in mostly good condition (Allman 1885). Illustrations of *S. diaphana* by Allman reflect the quality of the specimen he examined, and the species is recognizable from his account of it. The holotype colony was 9 inches (23 cm) high, with four alternate branches each resembling the main hydrocaulus, with intact hydrothecae, and with large, cylindrical, longitudinally ribbed gonothecae. As noted earlier (Calder 2015), much of the Gatty hydroid collection is now at the Weston Park Museum, Sheffield, England, with other parts at the Natural History Museum, London.

Allman's type of *S. diaphana* was from Queensland, Australia. With the species now known to be widespread across the Indo-Pacific (Billard 1925b; Millard 1975; Gibbons & Ryland 1989; Vervoort 1993; Hirohito 1995; Vervoort & Watson 2003; Schuchert 2003; Di Camillo *et al.* 2008; Galea 2016), its occurrence in Hawaii was to be expected. This hydroid has also been reported frequently in warm parts of the Atlantic as well (Calder 2019).

Sertularella torreyi Nutting, 1905, described from Hawaii as a new species, is now considered conspecific with *S. diaphana* following Billard (1925b). Nutting (1905) reported it from collections made off Molokai and Kauai by the *Albatross*, but the online database of the NMNH currently indicates that the specimens were from W of Laysan Island (USNM 22152) and the Kaulakahi Channel between Kauai and Niihau (USNM 70814). *Sertularella diaphana* has not been found as part of the fouling community in harbours of Hawaii.

Reported Distribution. Hawaii. Laysan Island, off west coast, *Albatross* Sta. 3949, 25°47'44.88"N, 171°52'33.6"W, 70 fm (128 m) (Nutting, 1905, as *Sertularella torreyi*).—Kauai, off west coast, *Albatross* Sta. 4003, 22°13'54.84"N, 159°51'25.2"W, 751–406 fm (1373–742 m) (Nutting, 1905, as *Sertularella torreyi*).—Oahu, Kaneohe Bay, shallow water (Cooke 1977, as *Sertularella speciosa*).—Oahu, Palea Point, 25 ft (8 m) (Hoover 1998, 2006).—Papahânaumokuâkea Marine National Monument, mesophotic coral ecosystems (Wagner *et al.* 2016).

Elsewhere. Reported to be eurybathic and essentially circumglobal in tropical and subtropical regions (Fernandez & Marques 2018; Calder 2019).

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

Genus *Bicaularia* Song, Lyu, Ruthensteiner, Wang, & Gravili, 2019

Bicaularia tongensis (Stechow, 1919)

Figs. 5c, d

Sertularella tongensis Stechow, 1919: 89, figs. F¹, G¹.—Coles *et al.*, 2002a: 318.—Carlton & Eldredge, 2009: 38.

Type locality. Tonga Islands (Kingdom of Tonga) (Stechow 1919).

Material examined. Oahu: Kaneohe Bay, Sta. 25, Moku Manu Island, 26 January 2000, one colony, in several fragments, to 5 mm high, with gonothecae, coll. R. DeFelice and S.L. Coles, ROMIZ B3313.

Remarks. The hydroid of *Bicaularia tongensis* (Stechow, 1919) is distinctive in having two opercular flaps, each one pleated along its median line, together with branches and gonothecae (when present) that arise from within the cavities of hydrothecae borne on the hydrocaulus (Galea 2010, 2016; Song *et al.* 2019). Uncertainty has existed in the past over generic affinities of this diminutive species, and it has been variously assigned to *Sertularia* Lin-

naeus, 1758, *Sertularella* Gray, 1848, and *Symplectoscyphus* Marktanner-Turneretscher, 1890. Analyses by Song *et al.* reveal that it is sufficiently distinct morphologically and genetically to justify assignment to a new genus, *Bicaularia* Song, Lyu, Ruthensteiner, Wang, & Gravili, 2019.

As reported by Galea (2010) and Song *et al.* (2019), synonyms of the binomen *B. tongensis* include *Sertularella thecocarpa* Jarvis, 1922 from the Chagos Archipelago, *S. minuscula* Billard, 1925a [not 1924 as often cited, see References] from Indonesia, *S. parvula* Mammen, 1965 from India, and *Sertularia stechowii* Hirohito, 1995 from Japan. In addition, *Sertularella exilis* Fraser, 1938a from the west coasts of Panama and Mexico was regarded as a possible synonym by Song *et al.* Of note, the name *Sertularia tongensis* Stechow, 1919 applies to a different species from *Sertularella tongensis* Stechow, 1919 (= *Bicaularia tongensis*) and no homonymy exists because the two are not congeneric. As for *Sertularia tongensis*, its generic affinities are presently unresolved. Its assignment to *Sertularia* is based on a widespread erroneous concept of that genus that is not founded on its type species (*S. argentea* Linnaeus, 1758).

A thorough account of the systematics, general ecology, and distribution of *Bicaularia tongensis* has been given by Song *et al.* (2019). A lectotype (ZSM 20041539) was selected by them from available syntypes.

The record of *Bicaularia tongensis* herein is based on the same colony reported earlier by Coles *et al.* (2002a, as *Sertularella tongensis*) from Hawaii.

Reported Distribution. Hawaii. Oahu, Kaneohe Bay, Sta. 25, Moku Manu Island (Coles *et al.* 2002a, as *Sertularella tongensis*).

Elsewhere. Indo-Pacific (main center of distribution); Caribbean Sea; Mediterranean Sea (Song *et al.* 2019). Its occurrence in the eastern Pacific needs verification.

Family Sertulariidae Lamouroux, 1812

Genus *Dynamena* Lamouroux, 1812

Dynamena crisioides Lamouroux, 1824

Figs. 5e, f

Dynamena crisioides Lamouroux, 1824: 613, pl. 90, figs. 11, 12.—Cooke, 1977: 93, fig. 20.—Coles *et al.*, 2002a: 318; 2006: 492.—Carlton & Eldredge, 2009: 38.

Dynamena crisioides.—Coles *et al.*, 1999: 194 [incorrect subsequent spelling].

Type locality. Indonesia: Moluccas (Lamouroux 1824).

Material examined. Oahu: Kaneohe Bay, Sta. 24, Sag Harbor, 21°27'03.30"N, 157°46'42"W, three colony fragments, to 1.7 cm high, with one gonotheca, ROMIZ B3308.

Remarks. *Dynamena crisioides* Lamouroux, 1824 is a widely distributed and frequently encountered species in tropical and subtropical waters, distinctive in the subopposite arrangement and complete separation of its hydrothecal pairs (Millard 1975; Calder 1991; Hirohito 1995; Schuchert 2003). Its hydroid, commonly found intertidally but also present in shallow subtidal waters, is reported here from Sag Harbor, Kaneohe Bay, Oahu. It has been reported previously in the Hawaiian Islands by Cooke (1977), Coles *et al.* (1999, 2002a, 2006), and Carlton & Eldredge (2009).

Detailed accounts of this species include those of Millard (1975), Calder (1991), Hirohito (1995), and Schuchert (2003).

Reported Distribution. Hawaii. Oahu, Kewalo Basin (Cooke 1977).—Oahu, Honolulu Harbor (Cooke 1977).—Oahu, Honolulu Harbor, Pier 29, Sta. 8, 21°18'39.4"N, 157°52'24.3"W (Coles *et al.* 1999, as *Dynamena crisioides*).—Oahu, Honolulu Harbor, Snug Harbor, Sta. 12, 21°18'55.5"N, 157°53'12.3"W (Coles *et al.* 1999, as *Dynamena crisioides*).—Oahu, Honolulu Harbor, Sand Island Coast Guard Station, Sta. 13, 21°18'24.7"N, 157°52'19.5"W (Coles *et al.* 1999, as *Dynamena crisioides*).—Oahu, Honolulu Harbor, Sand Island Park, Sta. 14, 21°18'08.0"N, 157°52'09.4"W (Coles *et al.* 1999, as *Dynamena crisioides*).—Oahu, Keehi Lagoon, Airport Rescue Dock, Sta. 17, 21°18'42.2"N, 157°55'09.3"W (Coles *et al.* 1999, as *Dynamena crisioides*).—Oahu, Kewalo Basin, Fishermans Wharf, Sta. 23, 21°17'38.9"N, 157°51'26.6"W (Coles *et al.* 1999, as *Dynamena crisioides*).—Oahu, Barbers Point, coal pier, Sta. 30, 21°19'18.5"N, 158°07'11.2"W (Coles *et al.* 1999, as *Dynamena crisioides*).—

Oahu: Kaneohe Bay, Sag Harbor, 21°27'03.30"N, 157°46'42.0"W (Coles *et al.* 2002a).—Kauai, Port Allen Harbor, 21°54'3.5"N, 159°35'49.9"W (Coles *et al.* 2006).—Oahu, Honolulu Harbor, in collections at the Bishop Museum (Carlton & Eldredge 2009).

Elsewhere. Circumglobal, shallow tropical and subtropical waters (Calder 2013).

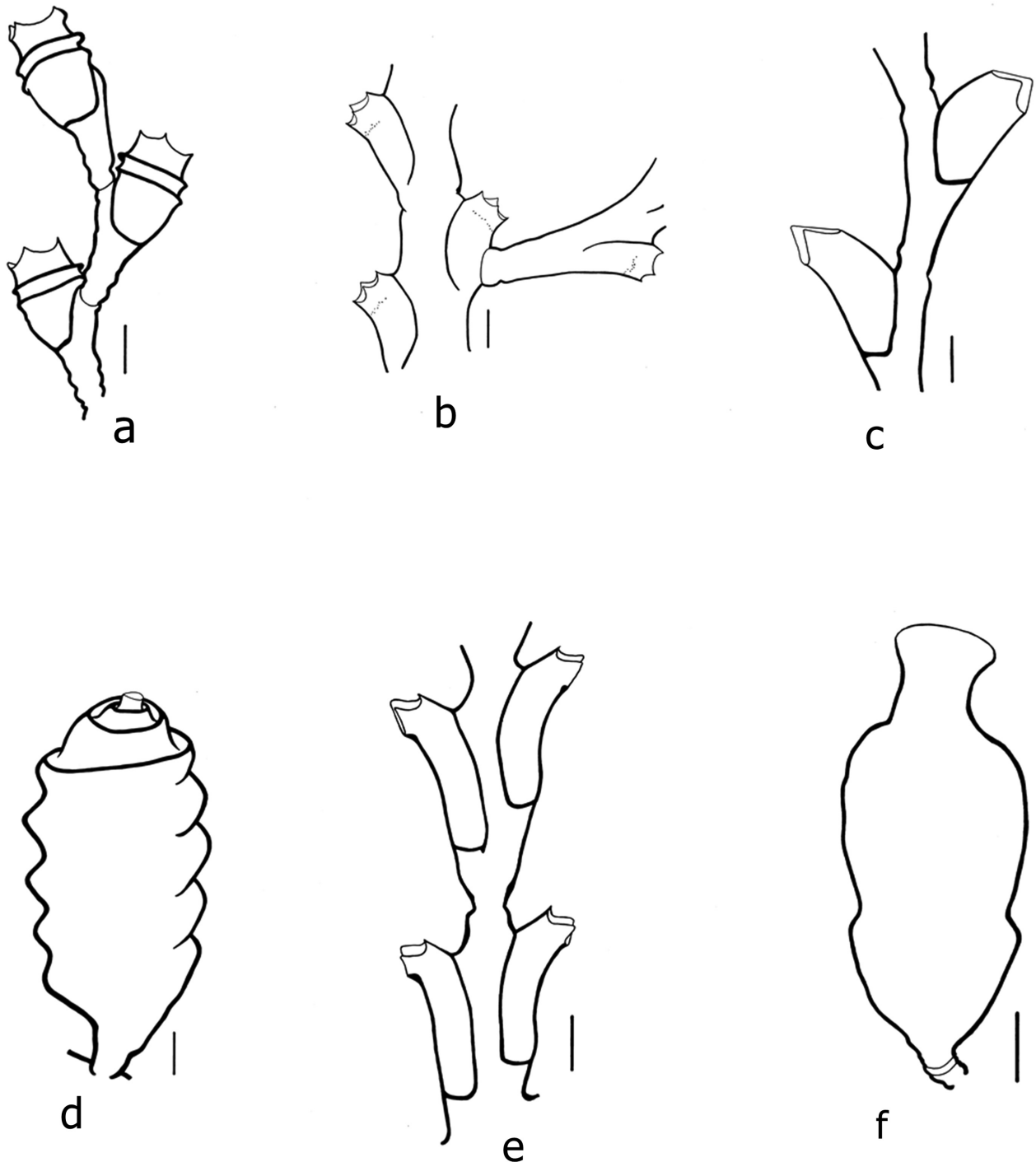


FIGURE 5. **a**, *Sertularella areyi*: part of colony with three hydrothecae, Moku Manu Island, Kaneohe Bay, Oahu, ROMIZ B3312. Scale equals 0.2 mm. **b**, *Sertularella diaphana*: part of hydrocaulus with three hydrothecae, and base of a branch with one hydrotheca, Palea Point, Oahu, ROMIZ B2902. Scale equals 0.2 mm. **c**, *Bicaularia tongensis*: part of hydrocaulus with two hydrothecae, Moku Manu Island, Kaneohe Bay, Oahu, ROMIZ B3313. Scale equals 0.1 mm. **d**, *Bicaularia tongensis*: gonotheca, Moku Manu Island, Kaneohe Bay, Oahu, ROMIZ B3313. Scale equals 0.1 mm. **e**, *Dynamena crisioides*: part of a branch with two hydrothecal pairs, Sag Harbor, Kaneohe Bay, Oahu, ROMIZ B3308. Scale equals 0.2 mm. **f**, *Dynamena crisioides*: gonotheca, Sag Harbor, Kaneohe Bay, Oahu, ROMIZ B3308. Scale equals 0.2 mm.

Dynamena moluccana (Pictet, 1893)

Figs. 6a, b

Sertularia moluccana Pictet, 1893: 50, pl. 2, figs. 42, 43.

Dynamena sp.—Hoover, 1998: 20, unnumbered figure; 2006: 20, unnumbered figure.

Dynamena mollucana.—Hoover, 1998: 20; 2006: 20 [incorrect subsequent spelling].

Type locality. Indonesia: Ambon Bay (Pictet 1893, as *Sertularia moluccana*).

Material examined. Maui: Makena, 20°39'N, 156°26'W, 12 m, 07 December 1997, six colonies or colony fragments, to 6.1 cm high, without gonothecae, coll. J. Hoover, ROMIZ B3035.—Maui: Molokini outer rim, 31 May 2007, three colonies or colony fragments, to 2.5 cm high, without gonothecae, collector unrecorded, ROMIZ B5301.

Remarks. The shape and arrangement of the hydrothecae in *Dynamena moluccana* (Pictet, 1893) resemble those of *D. disticha* (Bosc, 1802) or its synonym *D. cornicina* auct. in some respects, and the two were often considered conspecific in the past (e.g., Billard 1925b; Vervoort 1993). However, colonies of *D. moluccana* tend to be regularly and alternately branched while those of *D. disticha* are unbranched or sparsely and irregularly branched. They are now taken to be distinct species (Calder 1991; Schuchert 2003). Major differences in hydrothecal arrangement and gonothecal morphology in the two were also noted by Schuchert, in a careful study of the species. He observed that hydrothecae in branched colonies of *D. disticha* were in opposite, contiguous pairs on both the hydrocaulus and the hydrocladia. In *D. moluccana*, hydrothecae were in opposite, contiguous pairs on hydrocladia but not on the hydrocaulus. There, each internode typically bore three hydrothecae, a distal subopposite to nearly alternate pair and a proximal, axillary one that was strongly recurved and largely free. All hydrothecae were separated on both front and back. Gonothecae of *D. moluccana* were said to be smooth, moderately annulated, or transversely ribbed, and more oblong than the nearly spherical and strongly annulated ones of *D. disticha*.

Desmoscyphus palkensis Thornely, 1904 from Palk Bay, Sri Lanka, and *Sertularia cornicina* var. *pinnata* Jarvis, 1922 from the Saya de Malha Bank in the Indian Ocean were included in the synonymy of *D. moluccana* by Schuchert (2003). A phylogram in Leclère *et al.* (2009) indicates that *D. moluccana* is relatively distant genetically from *D. pumila* (Linnaeus, 1758), type species of *Dynamena* Lamouroux, 1812. Its affinities therefore warrant further consideration.

With the identity of a hydroid identified as *D. cornicina* by Cooke (1977) from Kaneohe Bay, Hawaii, being uncertain, it is not included with *D. moluccana* here. Colonies were described as mostly unbranched, and hydrothecae were shown as being opposite and contiguous as in *D. disticha*. A gonotheca of the species was shown as being oblong and transversely ribbed. Verified records of *D. moluccana* from Hawaii are those of Hoover (1998, 2006, as *Dynamena* sp. and *D. mollucana*), based on the same specimens examined here (ROMIZ B3035).

A note stating “green hydroid” exists with one of the collections examined here (ROMIZ Bxxxx). Stems of the species were described as being “yellowish” by Kirkendale & Calder (2003).

Reported Distribution. Hawaii. Maui, Molokini Islet, back wall, 40 ft. (12 m) (Hoover 1998, 2006, as *Dynamena* sp.).

Elsewhere. Indo-West Pacific (Schuchert 2003).

Genus *Tridentata* Stechow, 1920

Tridentata maldivensis (Borradaile, 1905)

Figs. 6c–e

Thuiaria maldivensis Borradaile, 1905: 842, pl. 69, figs. 6a, b.

Type locality. Republic of Maldives: Suvadiva Atoll, 31 fm (57 m) (Borradaile 1905).

Material examined. Maui: Kanaio, 20°33'N, 156°22'W, 40 ft (12 m), November 1996, fragments of one colony, 9 mm high, without gonothecae, ROMIZ B5311.

Remarks. From current morphological accounts, hydroids originally assigned the names *Thuiaria maldivensis* Borradaile, 1905 and *Sertularia borneensis* Billard, 1925a appear indistinguishable. If conspecific, as seems likely,

the name *T. maldivensis* is older and would have priority. Schuchert (2003) suspected that they were identical, but retained the name of the somewhat better known *S. borneensis* for material from the Kei Islands, Indonesia. Gravier-Bonnet & Bourmaud (2012) believed that *T. maldivensis* differed from its congener in having the adnate part of the adcauline hydrothecal wall of a hydrothecal pair about equal to or shorter in length than the free part. Unfortunately, that does not match an account of the type of *S. borneensis* examined by Vervoort & Vasseur (1977). In turn, Vervoort & Vasseur were mistaken in considering the hydroid to be conspecific with *T. turbinata* (Lamouroux, 1816). For clarification, the type of *T. maldivensis*, in collections at the Natural History Museum, London, UK, needs to be redescribed, illustrated, and compared with that of *S. borneensis*. Gonothecae were lacking in the type material of both nominal species, further limiting their characterizations. Neither one can validly be assigned to *Sertularia* Linnaeus, 1758, or to *Thuiaria* Fleming, 1828, as defined by their type species. They correspond more closely with *Tridentata* Stechow, 1920 and are assigned to that genus here. As discussed several times earlier (Calder 2013: 33; 2019: 86; Calder *et al.* 2019: 44), morphological and molecular evidence both confirm that *Tridentata* is clearly distinct from *Sertularia*.

Confusion thus persists over the identity and status of these two putative species, and the colony from Hawaii examined here could be assigned at the moment to either of them. It has been referred to *T. maldivensis*, as *Tridentata maldivensis*, both because that name is the older of two likely synonyms and because hydrothecae more closely resembled those illustrated by Borradaile (1905) than those in figures of *T. borneensis* by Billard (1925b). No illustrations of the latter species were provided by Billard (1925a) in its original description. Meanwhile, relationships of these hydroids to *Tridentata tumida* (Allman, 1877) from Florida, USA, *T. tongensis* (Stechow, 1919) from the Kingdom of Tonga, *T. westindica* Stechow 1920 from Martinique, and *Sertularia malayensis* var. *sorongensis* Leloup, 1930 from New Guinea need to be resolved.

Reported Distribution. Hawaii. First record.

Elsewhere. Maldives (Borradaile 1905; Gravier-Bonnet & Bourmaud 2012). If *Tridentata borneensis* is conspecific, the range is extended into the tropical western Pacific (Schuchert 2003).

***Tridentata loculosa* (Busk, 1852)**

Fig. 6f

Sertularia loculosa Busk, 1852: 393.

Sertularia ligulata.—Cooke, 1977: 97, fig. 24.—Coles *et al.*, 2002a: 318.

Tridentata ligulata.—Coles *et al.*, 2002b: 177.

Tridentata loculosa.—Carlton & Eldredge, 2009: 39.

Type locality. Australia: Bass Strait, 45 fm (82 m) (Busk 1852).

Material examined. Oahu: Kaneohe Bay, Sta. 5, Waiahole Reef, 21°29'14.6"N, 157°49'55.8"W, 17 November 1999, one colony, in fragments, 5 mm high, on a bryozoan, without gonothecae, coll. R. DeFelice and S.L. Coles, ROMIZ B3299.

Remarks. Confusion over the identity and synonymy of the hydroid described as *Sertularia loculosa* Busk, 1852 has been resolved (Billard 1927a; Calder 1991, 2013; Migotto 1996; Schuchert 2003). Now considered valid, it can readily be distinguished from species such as *Tridentata turbinata* (Lamouroux, 1816) and *T. marginata* (Kirchenpauer 1864). While the species is distinctive, particularly in possessing a strap-like nematophore (ligula) extending from the adcauline wall of the hydranth to the hydrothecal orifice, its generic assignment is still unclear. In sharing certain characters with species of *Tridentata* Stechow, 1920, it has been referred temporarily to that genus here. However, sequences of the hydroid are needed to determine its affinities. It is certainly not referable to *Sertularia*, as defined by the type species of that genus (*Sertularia argentea* Linnaeus, 1758). The two are decidedly dissimilar in the morphology of their trophosomes and gonosomes.

This hydroid has been reported before from Hawaii as both *Sertularia ligulata* (or *Tridentata ligulata*) (Cooke 1977; Coles *et al.* 2002a, 2002b) and as *S. loculosa* (Carlton & Eldredge 2009). Billard (1927a) concluded that *S. ligulata* Thornely, 1904, from the Gulf of Manaar (=Gulf of Mannar), was conspecific with *S. loculosa*. That conclusion has become widely adopted over the last three decades. Thus far, *T. loculosa* has not been reported east of Hawaii in the Pacific Ocean.

Hydroids of this species liberate swimming gonophores, as do those of both *T. marginata* and *T. turbinata* (Galea 2018).

Reported Distribution. Hawaii. Oahu, Kaneohe Bay, 2 m, on *Porites lobata* (Cooke 1977, as *Sertularia ligulata*).—Oahu, Kaneohe Bay, Sta. 5, Waiahole Reef, 21°29'14.6"N, 157°49'55.8"W (Coles *et al.* 2002a, as *Sertularia ligulata*).—Oahu, Waikiki, Sta. 5, Aquarium Outside Reef, 21°15'53.5"N, 157°49'36"W, 3 m (Coles *et al.* 2002b, as *Tridentata ligulata*).—Oahu, Waikiki, Sta. 6, *Atlantis* wreck, 21°15'37.6"N, 157°50'15.3"W, 20–30 m (Coles *et al.* 2002b, as *Tridentata ligulata*).

Elsewhere. Indo-West Pacific (Schuchert 2003); warm western and eastern Atlantic (Calder 2013). The species has yet to be recorded from the eastern Pacific.

***Tridentata rugosissima* (Thornely, 1904)**

Fig. 6g

Sertularia rugosissima Thornely, 1904: 118, pl. 2, fig. 4.

Sertularia subtilis.—Cooke, 1977: 97, fig. 25.—Carlton & Eldredge, 2009: 39.

Tridentata hupferi.—Coles *et al.*, 2002a: 318; 2002b: 177, 234 [incorrect subsequent spelling].

Tridentata hupferi.—Carlton & Eldredge, 2009: 39.

Type locality. Sri Lanka: “Gulf of Manaar” (=Gulf of Mannar), on algae (Thornely 1904, as *Sertularia rugosissima*).

Material examined. Oahu: Kaneohe Bay, Sta. 7, Pristine Reef, 21°28'42.3"N, 157°49'29.5"W, 19 November 1999, one colony fragment, 6 mm high, without gonothecae, coll. R. DeFelice and S.L. Coles, ROMIZ B3305.

Remarks. This species was first described by Thornely (1904), from Sri Lanka, as *Sertularia rugosissima*. Following Migotto (1996), *Sertularia hupferi* Broch, 1914 from the Gold Coast (=Ghana), *S. subtilis* Fraser, 1937 from Puerto Rico, and *Geminella subtilis* Vannucci Mendes, 1946 from Brazil are now taken to be conspecific. In resolving their identities, Migotto examined types of all but *S. hupferi*, the hydroid of which had nevertheless been adequately described by Broch (1914). Trophosomes of the species are noteworthy, and striking, in having approximately a dozen or more closely-spaced transverse ridges on walls of the hydrothecae. In examinations of Thornely's type (BM 1907.8.27.6), Gibbons & Ryland (1989, as *S. hupferi*) and Migotto (1996) also noted the presence of a prominent abcauline submarginal cusp and a fainter adcauline one inside the hydrothecae. Both cusps were evident in specimens examined here from Hawaii (Fig. 6g).

Gonothecae of *S. rugosissima* have been described infrequently. Fertile colonies were found in collections from Brazil by Vannucci Mendes (1946, as *Geminella subtilis*) and from Eniwetak Atoll by Cooke (1975, as *S. subtilis*). In those works, gonothecae were described and illustrated as ovoid with a wide orifice and with about 9–12 distinct transverse ridges. Given the characters of both its trophosome and gonosome, this species is allied to *Tridentata perpusilla* (Stechow, 1919), the type species of *Tridentata* Stechow, 1920, and it is assigned to that genus here following Stechow (1923) and Calder & Choong (2018) earlier. Other morphologically allied species include *T. turbinata* (Lamouroux, 1816), *T. marginata* (Kirchenpauer, 1864), and *T. tumida* (Allman, 1877), with these three also clustering as a monophyletic group in phylograms of Maronna *et al.* (2016).

As with the previous species, *T. rugosissima* has not yet been reported east of Hawaii in the Pacific Ocean.

Reported Distribution. Hawaii. Oahu, Kahe Point reef, 2 m, on coral rubble (Cooke 1977, as *Sertularia subtilis*).—Oahu, Kaneohe Bay, Sta. 7, Pristine Reef, 21°28'42.3"N, 157°49'29.5"W (Coles *et al.* 2002a, as *Tridentata hupferi*).—Oahu, Waikiki, Sta. 7, Canoes, 3.5 m, 21°28'42.3"N, 157°49'42.5"W (Coles *et al.* 2002b, as *Tridentata hupferi*).—Oahu, Waikiki, Sta. 10, Kapua Channel, 5 m, 21°15'34.8"N, 157°49'39.7"W (Coles *et al.* 2002b, as *Tridentata hupferi*).—Oahu, Waikiki, Sta. 11, Kaiser's Channel, 21°16'26.5"N, 157°50'26.1"W (Coles *et al.* 2002b, as *Tridentata hupferi*).—Oahu, Hawaii Kai, Sta. 3, Channel Marker 1, Maunalua Bay, 4 m, 21°16'28.0"N, 157°43'09.7"W (Coles *et al.* 2002b, as *Tridentata hupferi*).

Elsewhere. Indian Ocean (Thornely 1904, 1916; Millard & Bouillon 1973, as *Sertularia hupferi*); western Pacific (Jäderholm 1919, as *Sertularia rugosissima*; Cooke 1975, as *Sertularia subtilis*; Yamada & Kubota 1987, as *Sertularia rugosissima*; Gibbons & Ryland 1989, as *Sertularia hupferi*); western Atlantic (Fraser 1937, as *Sertularia subtilis*; Migotto 1996, as *Sertularia rugosissima*; Galea 2008, *Sertularia rugosissima*; Oliveira *et al.* 2016); eastern Atlantic (Broch 1914, as *Sertularia hupferi*).

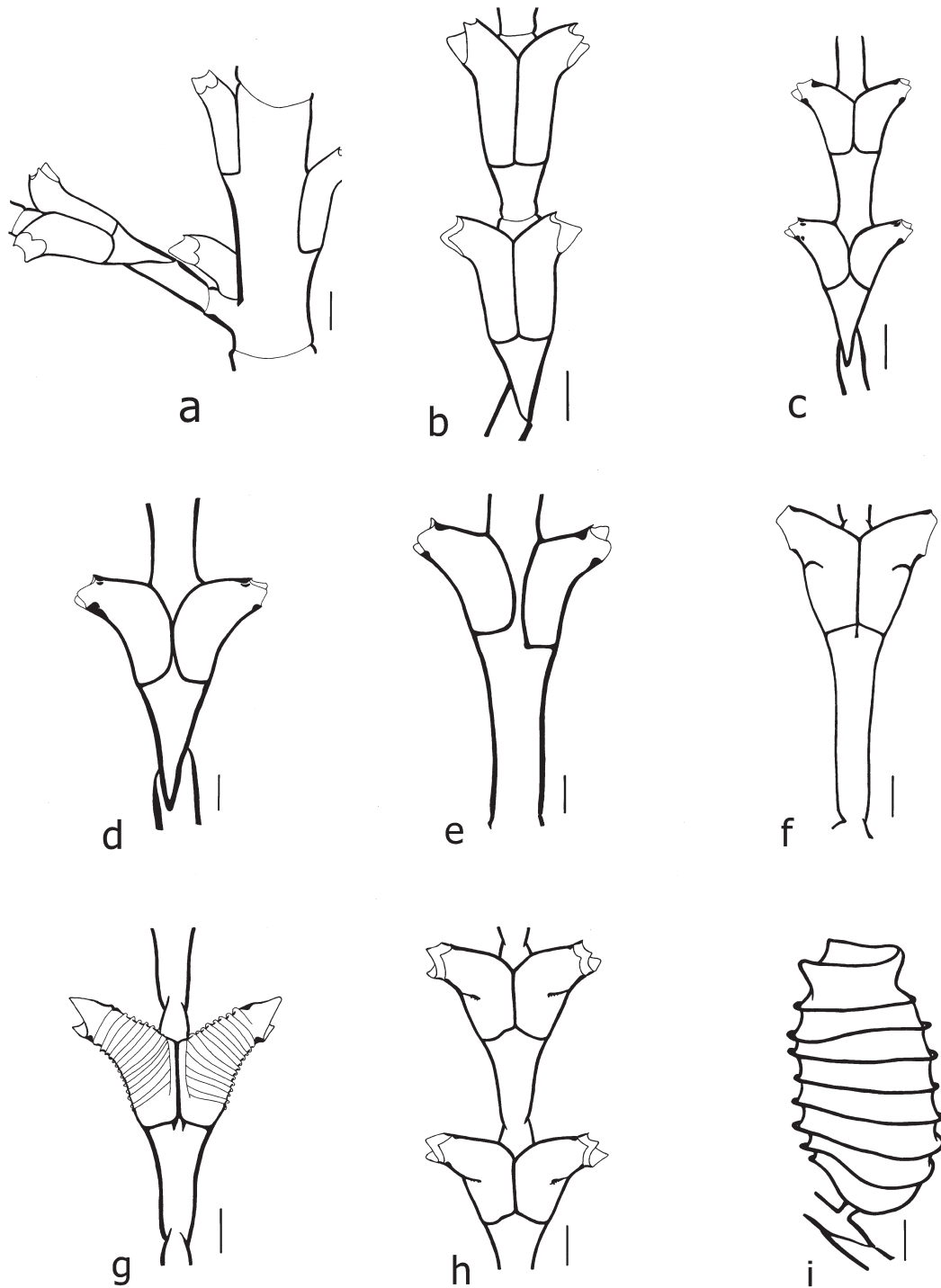


FIGURE 6. **a**, *Dynamena moluccana*: part of hydrocaulus and base of a hydrocladium, with five hydrothecae, Makena, Maui, ROMIZ B3035. Scale equals 0.2 mm. **b**, *Dynamena moluccana*: basal part of a hydrocladium, with two hydrothecal pairs, Makena, Maui, ROMIZ B3035. Scale equals 0.2 mm. **c**, *Tridentata maldivensis*: part of hydrocaulus with two hydrothecal pairs, Kanaio, Maui, ROMIZ B5311. Scale equals 0.2 mm. **d**, *Tridentata maldivensis*: part of hydrocaulus with one pair of contiguous hydrothecae, Kanaio, Maui, ROMIZ B5311. Scale equals 0.1 mm. **e**, *Tridentata maldivensis*: part of hydrocaulus with a separated hydrothecal pair, Kanaio, Maui, ROMIZ B5311. Scale equals 0.1 mm. **f**, *Tridentata loculosa*: part of hydrocaulus with one hydrothecal pair, Waiahole Reef, Kaneohe Bay, Oahu, ROMIZ B3299. Scale equals 0.1 mm. **g**, *Tridentata rugosissima*: part of hydrocaulus with one hydrothecal pair, Pristine Reef, Kaneohe Bay, Oahu, ROMIZ B3305. Scale equals 0.1 mm. **h**, *Tridentata turbinata*: part of hydrocaulus with two hydrothecal pairs, Molokini outer rim, Maui, ROMIZ B5302. Scale equals 0.1 mm. **i**, *Tridentata turbinata*: base of hydrocaulus with a gonotheca, Molokini outer rim, Maui, ROMIZ B5302. Scale equals 0.2 mm.

***Tridentata turbinata* (Lamouroux, 1816)**

Figs. 6h, i

Dynamena turbinata Lamouroux, 1816: 180.

Tridentata turbinata.—Coles *et al.*, 2002b: 177.—Carlton & Eldredge, 2009: 39.

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

Material examined. Maui: Molokini outer rim, 31 May 2007, several colony fragments, to 7 mm high, with gonothecae, Coll. M. Hutchinson, ROMIZ B5302.

Remarks. Misunderstandings over the identity and scope of *Tridentata turbinata* (Lamouroux, 1816), briefly mentioned in remarks above on *Tridentata loculosa* (Busk, 1852), now seem settled. Differences of opinion nevertheless remain over generic assignment of the species, whether to *Sertularia* Linnaeus, 1758 or *Tridentata* Stechow, 1920. Justifications for referring it to the latter genus have been provided elsewhere (Calder 1991, 2013, 2019; Calder *et al.* 2019).

Tridentata turbinata is a widespread and frequently reported species in shallow, tropical to warm-temperate waters throughout the Indo-Pacific and Atlantic regions (see Millard 1975, as *Sertularia turbinata*; Hirohito 1995, as *S. turbinata*; Medel & Vervoort 1998, as *S. turbinata*; Oliveira *et al.* 2016, as *S. turbinata*; Calder 2019). The gonosome of this hydroid has nevertheless been reported infrequently. Gonothecae observed here were similar to those described by Vervoort (1959, as *S. turbinata*), Millard (1975, as *S. turbinata*), Hirohito (1995, as *S. turbinata*), Galea & Ferry (2015, as *S. turbinata*), and Humara-Gil & Cruz Gomez (2018). In being barrel-shaped with transverse ridges and a large distal orifice, they resemble those occurring in a group of related species including *T. marginata* (Kirchenpauer, 1864), *T. tumida* (Allman, 1877), *T. rugosissima* (Thornely, 1904), and *T. perpusilla* (Stechow, 1919).

A detailed synonymy of this species has been given by Medel & Vervoort (1998, as *Sertularia turbinata*).

Reported Distribution. Hawaii. Oahu, Waikiki, Sta. 2, Outside Pop’s, 21°16′10.8″N, 157°50′01.3″W, 6 m (Coles *et al.* 2002b).—Oahu, Waikiki, Sta. 3, Atlantis Submarine site, 21°15′44.8″N, 157°50′09.9″W, 20 m (Coles *et al.* 2002b).—Oahu, Waikiki, Sta. 8, Ala Wai Buoy, 21°16′34.0″N, 157°50′46.7″W (Coles *et al.* 2002b).—Oahu, Waikiki, Sta. 10, Kapua Channel, 21°15′34.8″N, 157°49′39.7″W, 5 m (Coles *et al.* 2002b).

Elsewhere. Circumglobal in warm, shallow waters (Millard 1975, as *Sertularia turbinata*; Rees & Vervoort 1987, as *Sertularia turbinata*; Calder 1991, 2019; Hirohito 1995, as *Sertularia turbinata*; Medel & Vervoort 1998, as *Sertularia turbinata*; Schuchert 2003, as *Sertularia turbinata*; Calder *et al.* 2003, 2019).

Family Kirchenpaueriidae Stechow, 1921

Genus *Ventromma* Stechow, 1923

***Ventromma halecioides* (Alder, 1859)**

Figs. 7a–c

Plumularia halecioides Alder, 1859: 353, pl. 12, figs. 1–5.

Ventromma halecioides.—Coles *et al.*, 2002a: 318; 2002b: 243; 2004: 73; 2009: 77, 82, 85.—Carlton & Eldredge, 2009: 36.

Type Locality. UK: England, Cullercoats (Northumberland) and Roker (Durham) (Alder 1859).

Material Examined. Oahu: Kaneohe Bay, Sta. 8, Kahaluu Landing, 21°27′48.7″N, 157°50′01.5″W, 02 November 1999, three colony fragments, to 8 mm high, without gonothecae, coll. R. DeFelice and S.L. Coles, ROMIZ B3297.—Oahu: Honolulu Harbor, Sta. 18, Keehi Lagoon, 21°19′10″N, 157°53′36″W, 22 April 2008, one colony, 1.5 cm high, with gonothecae, coll. S. Coles, ROMIZ B5303.—Oahu: Honolulu Harbor, Sta. 18, Keehi Lagoon, 21°19′10″N, 157°53′36″W, 22 April 2008, three colony fragments, to 1.8 cm high, with gonothecae, coll. S. Coles, ROMIZ B5304.—Oahu: Heeia Kia Boat Harbor, 21°26′36.31″N, 157°48′37.31″W, at surface, on rope, 11 July 2009, one colony, 2.0 cm high, without gonothecae, coll. D.R. Calder, ROMIZ B5305.—Oahu: Honolulu Harbor, La Mariana Sailing Club, 21°19′16.90″N, 157°53′37.95″W, <1 m, on an ascidian on dock, 16 July 2009, one colony, 2.1 cm high, with gonothecae, coll. D.R. Calder, ROMIZ B5306.

Remarks. In some works, *Ventromma halecioides* (Alder, 1859) has been assigned to *Kirchenpaueria* Jickeli, 1883. Evidence from molecular studies (Leclère *et al.* 2007; Moura *et al.* 2008, 2018, 2019; Peña Cantero *et al.* 2010; Maronna *et al.* 2016) reveals that *Ventromma* Stechow, 1923 (type species: *Plumularia halecioides* Alder, 1859) is clearly divergent from *Kirchenpaueria* Jickeli, 1883 (type species: *Sertularia pinnata* Linnaeus, 1758). *Ventromma halecioides* is therefore taken here to be the valid name of the species.

Ventromma halecioides is one of the few species of hydroids that thrives in quiet water areas. In Hawaii, it was found at several locations sheltered from water currents and significant wave action, including Kahaluu Landing in Kaneohe Bay (ROMIZ B3297), Heeia Kia Boat Harbor (ROMIZ B5305), and Keehi Lagoon (ROMIZ B5303, ROMIZ B5304) and La Mariana Sailing Club (ROMIZ B5306) in Honolulu Harbor. A common fouling species (Woods Hole Oceanographic Institution 1952, as *Plumularia halecioides*; Morri & Boero 1986; Cornelius 1992b; Calder *et al.* 2019), the hydroid has been reported in shallow waters from the tropics to warm temperate areas worldwide (Ansin Agís *et al.* 2001, as *Kirchenpaueria halecioides*; Calder 2019). Moura *et al.* (2019, as *K. halecioides*) confirmed that haplotypes of this species are widely distributed, believing that dispersal of its hydroid has been due to shipping.

Detailed descriptions and general accounts of this species include those of Cornelius (1995b), Ansin Agís *et al.* (2001, as *Kirchenpaueria halecioides*), and Gravili *et al.* (2015).

Reported Distribution. Hawaii. Oahu, Kaneohe Bay, Sta. 8, Kahaluu Pier, 21°27'48.7"N, 157°50'01.5"W (Coles *et al.* 2002a).—Oahu, Hawaii Kai area (Coles *et al.* 2002b).—Kauai, Sta. KA3, Port Allen Main Dock, 21°54'09.9"N, 159°35'31.3"W, concrete pier pilings (Coles *et al.* 2004).—Oahu, Keehi Lagoon, Sta. KL18, Marina Docks, 21°19.183'N, 157°53.663'W (Coles *et al.* 2009).

Elsewhere. Circumglobal; temperate and tropical waters (Ansin Agís *et al.* 2001, as *Kirchenpaueria halecioides*; Calder *et al.* 2019).

Family Plumulariidae McCrady, 1859

Genus *Monotheca* Nutting, 1900

Monotheca flexuosa (Bale, 1894)

Figs. 7d–f

Plumularia flexuosa Bale, 1894: 115, pl. 5, figs. 6–10.

Type locality. Australia: Victoria, “mouth of Snowy River and Cape Lefebvre” (Bale 1894, as *Plumularia flexuosa*).

Material examined. Oahu: Palea Point, just outside Hanauma Bay, 25 ft (8 m), 08 October 1996, on *Sertularella diaphana*, one colony, in six fragments, to 5 mm high, without gonothecae, coll. J. Hoover, ROMIZ B5307.—Maui: Kanaio, 20°33'N, 156°22'W, 40 ft (12 m), November 1996, three colonies or colony fragments, to 6 mm high, without gonothecae, ROMIZ B5310.—Oahu: Palea Point, just outside Hanauma Bay, 30 ft (9 m), 06 October 1996, on *Lytocarpia nigra* and algae, two colonies, to 4 mm high, without gonothecae, coll. J. Hoover, ROMIZ B5308.

Remarks. *Monotheca* Nutting, 1900 is recognized here as distinct from *Plumularia* Lamarck, 1816 because their type species (*Monotheca margaretta* Nutting, 1900 and *Sertularia setacea* Linnaeus, 1758, respectively) are significantly different genetically (Leclère *et al.* 2007, 2009; Moura *et al.* 2008, 2018; Maronna *et al.* 2016) as well as morphologically. Both genera are considered polyphyletic at present, and revision of them is needed. In reviewing species of the genus from Australia, Watson (2011) included *Monothecella* Stechow, 1923 (type species: *Plumularia compressa* Bale, 1882) as a synonym of *Monotheca*.

Of a dozen or more species that have been assigned to *Monotheca*, colonies observed here correspond most closely with *M. flexuosa* (Bale, 1894) from southeastern Australia, as described by Watson (2011). She reported it to be the most abundant and widespread species of the genus in that country. While resembling the Atlantic *M. margaretta*, the hydrocaulus is more flexuous and lateral nematothecae appear sessile rather than arising from distinct pedicels. Gonothecae of the two species also differ (Calder 1997; Watson 2011).

This is the first record of *M. flexuosa* from Hawaii, and from the central to eastern Pacific Ocean. Reports of this species outside the Pacific Ocean are regarded here as questionable, although Watson (2011) suspected that the species might prove to be cosmopolitan.

Reported Distribution. Hawaii. First record.

Elsewhere. Australia (Watson 2011); ?South Africa (Stechow 1925; Millard 1975, as *Monothecha pulchella*); Japan (Hirohito 1974, as *Monothecha flexiosa*); New Zealand (Vervoort & Watson 2003, as *Monothecha pulchella*); ?Strait of Gibraltar (Medel & Vervoort 1995, as *Monothecha pulchella*); ?Vema Seamount (Millard 1966, as *Monothecha pulchella*).

Genus *Plumularia* Lamarck, 1816

Plumularia floridana Nutting, 1900

Fig. 7g

Plumularia floridana Nutting, 1900: 59, pl. 2, figs. 4, 5.—Coles *et al.*, 2002a: 318; 2004: 73; 2006: 492.—Carlton & Eldredge, 2009: 36.

Plumularian hydroid.—Edmondson, 1946: 26, fig. 13d.

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

Material examined. Oahu: Kaneohe Bay, Sta. 5, Waiahole Reef, 21°29'14.6"N, 157°49'55.8"W, 17 November 1999, two colony fragments, to 1.3 cm high, one with gonophores (male?), coll. R. DeFelice and S.L. Coles, ROMIZ B3303.

Remarks. Hydroids matching accounts of *Plumularia floridana* Nutting, 1900 are reported herein from Oahu, Hawaii. Earlier records of the species from the islands include those of Coles *et al.* (2002a) from Oahu, and Coles *et al.* (2004, 2006) from the Island of Hawaii. In addition, illustrations of an unidentified “plumularian hydroid” from Waikiki, Oahu, by Edmondson (1946) resemble this species.

Originally described from the Cape Romano area of southwest Florida, *P. floridana* has been taken to be essentially circumglobal in distribution (Ansín Agís *et al.* 2001; Calder 2013). However, cryptic diversity evidently occurs in hydroids identified as that species, with two lineages detected in the Caribbean and two others in the tropical eastern Pacific (Moura *et al.* 2018). These lineages all need to be explored further and compared with topotypic material of *P. floridana* from Florida. Several similar species were described by Fraser (1938a, b) from the tropical eastern Pacific, and others were collected to the north of that area. Perhaps the closest of these to *P. floridana* is *P. sinuosa* Fraser, 1948 from the Revillagigedo Islands, Mexico. However, that species, based on a sterile and possible juvenile type specimen (Calder *et al.* 2009), is insufficiently known. Two others, *P. propinqua* Fraser, 1938a and *P. micronema* Fraser, 1938b, approach *P. floridana* in morphology but differ most notably in having monomerously rather than heteromerously segmented hydrocladia. Also similar are *P. alicia* Torrey, 1902, originally described from California, *P. alicia* var. *minuta* Billard, 1927b from Cameroon, west Africa, and *P. pennycuikae* Millard & Bouillon, 1973 from the Seychelles. These have been viewed as conspecific or questionably conspecific with *P. floridana* in some works (Calder 1997). With the identities and relationships of these hydroids currently being unsettled, the binomen *P. floridana* is maintained for the species reported here from Hawaii. Moreover, given the volume of commercial and naval ship activity in the islands, the local hydroid population is of unknown origin at present.

Additional information on *P. floridana* is given in works such as those by Migotto (1996), Calder (1997, 2019), and Ansín Agís *et al.* (2001).

Reported Distribution. Hawaii. Oahu, Waikiki Reef, underside of stones (Edmondson 1946, as “plumularian hydroid”).—Oahu, Kaneohe Bay, Sta. 3, Hakipuu Reef Flat, 21°30'03.9"N, 157°50'25.7"W (Coles *et al.* 2002a).—Island of Hawaii, Kawaihae Reef, Sta. HA1, 20°01'55.5"N, 155°50'09.4"W, just seaward of Kawaihae Harbor (Coles *et al.* 2004).—Island of Hawaii, Sta. 1, Kawaihae Reef, 20°01'55.5"N, 155°50'09.4"W (Coles *et al.* 2006).—Island of Hawaii, Sta. HA6, Red Hill, 19°30'28.8"N, 155°57'19.5"W (Coles *et al.* 2006).

Elsewhere. Circumglobal, inshore and nearshore waters of the tropical, subtropical, and temperate zones (Ansín Agís *et al.* 2001; Calder 2019).

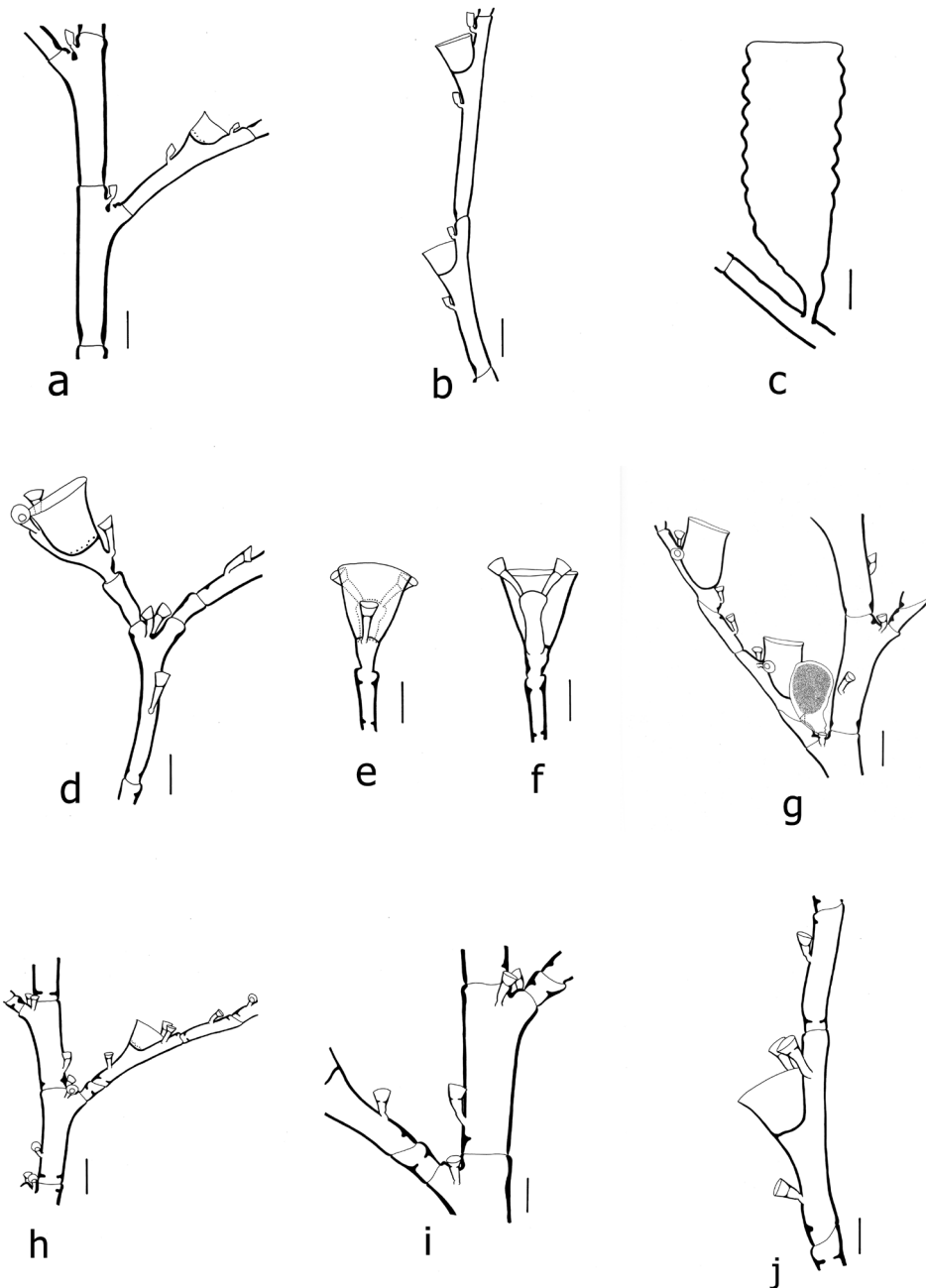


FIGURE 7. **a, *Ventromma halecioides*:** part of hydrocaulus with proximal ends of two hydrocladia, and one hydrotheca, La Mariana Sailing Club, Honolulu Harbor, Oahu, ROMIZ B5306. Scale equals 0.1 mm. **b, *Ventromma halecioides*:** part of hydrocladium with two hydrothecae, La Mariana Sailing Club, Honolulu Harbor, Oahu, ROMIZ B5306. Scale equals 0.1 mm. **c, *Ventromma halecioides*:** proximal end of hydrocaulus with a gonotheca, La Mariana Sailing Club, Honolulu Harbor, Oahu, ROMIZ B5306. Scale equals 0.2 mm. **d, *Monotheca flexuosa*:** part of hydrocaulus with a hydrocladium, nematothecae, and a cladial hydrotheca, Palea Point, Oahu, ROMIZ B5307. Scale equals 0.05 mm. **e, *Monotheca flexuosa*:** part of hydrocladium and front view of a hydrotheca, Palea Point, Oahu, ROMIZ B5307. Scale equals 0.05 mm. **f, *Monotheca flexuosa*:** part of hydrocladium and back view of a hydrotheca, Palea Point, Oahu, ROMIZ B5307. Scale equals 0.05 mm. **g, *Plumularia floridana*:** part of hydrocaulus with proximal ends of two hydrocladia, nematothecae, two cladial hydrothecae, and a cladial gonotheca (male?), Waiahole Reef, Kaneohe Bay, Oahu, ROMIZ B3303. Scale equals 0.1 mm. **h, *Plumularia strictocarpa*:** part of hydrocaulus with a hydrocladium, nematothecae, and a hydrotheca, Palea Point, Oahu, ROMIZ B5309. Scale equals 0.1 mm. **i, *Plumularia strictocarpa*:** part of hydrocaulus with proximal ends of two hydrocladia, and nematothecae, Palea Point, Oahu, ROMIZ B5309. Scale equals 0.05 mm. **j, *Plumularia strictocarpa*:** two cladial internodes, with nematothecae and a hydrotheca, Palea Point, Oahu, ROMIZ B5309. Scale equals 0.05 mm.

Plumularia strictocarpa Pictet, 1893

Figs. 7h–j

Plumularia strictocarpa Pictet, 1893: 55, pl. 3, figs. 47–49.—Coles *et al.*, 2002a: 318; 2002b: 177, 234; 2004:73; 2006: 492.—Carlton & Eldredge, 2009: 36.
? *Plumularia setacea*.—Cooke, 1977: 101, fig. 28.—Bailey-Brock, 1989: 591.—Carlton & Eldredge, 2009: 36 [?not *Plumularia setacea* (Linnaeus, 1758)].

Type locality. Indonesia: Ambon Bay, on sponges, shells; shallow water (Pictet 1893).

Material examined. Oahu: Palea Point, just outside Hanauma Bay, 25 ft (8 m), 08 October 1996, on *Sertularella diaphana*, one colony, 5 mm high, without gonothecae, coll. J. Hoover, ROMIZ B5309.

Remarks. Trophosomes of *Plumularia strictocarpa* Pictet, 1893 (type locality: Indonesia) closely resemble those of *P. setacea* (Linnaeus, 1758) (type locality: England), and *P. warreni* Stechow, 1919 (type locality: South Africa). Although colonies of *P. strictocarpa* tend to be smaller with more slender stem internodes in my experience, no trophosomal characters have yet been noted that definitively separate these species. Instead, they are most reliably distinguished by the shape of their gonothecae. Those of *P. strictocarpa* are cocoon-shaped with spirally annulated walls, those of *P. setacea* are fusiform with smooth walls and a tubular neck, and those of *P. warreni* are dimorphic, with females being oval to sac-shaped and males elongated and curved. Of note, *P. setacea* is the type species of the genus *Plumularia* Lamarck, 1816 (ICZN 1998).

Additional issues confound the taxonomy of these species. Schuchert (2014) and Moura *et al.* (2018) discovered unexpectedly high genetic diversity in hydroids assigned to *P. setacea*. Multiple lineages were distinguished that could be considered cryptic species under a genealogical species concept. Genetic diversity also occurred in *P. strictocarpa*, albeit to a much lesser extent. Moura *et al.* recognized three lineages within that species, one from the Maldives and SW Indian Ocean, another from Brazil, and a third from Moorea in the central Pacific, south of Hawaii.

Based on the results of Schuchert (2014) and Moura *et al.* (2018), it seems unlikely that hydroids from Hawaii in the tropical Pacific are conspecific with those of *P. setacea* from its type locality in temperate northwestern Europe. As for *P. warreni*, reliable distribution records for it appear limited to South Africa and the Indian Ocean (Millard 1975). By contrast, *P. strictocarpa*, originally described from Indonesia, appears to be widely distributed in the tropical Pacific (Pictet 1893; Hirohito 1974, 1995; Ryland & Gibbons 1991; Kirkendale & Calder 2003; Calder *et al.* 2003; Schuchert 2014; Moura *et al.* 2018). Given such information on hydroid distributions, the specimen examined here (ROMIZ B5309) though sterile, has been referred to *P. strictocarpa*. The colony also corresponded with accounts of that species, with its typically small trophosome (Calder 1997, 2013) as in the original description (Pictet 1893). Colonies with gonophores are needed to confirm the existence of *P. strictocarpa* in Hawaii.

Reports of *P. setacea* from Hawaii (Cooke 1977; Bailey-Brock 1989; Carlton & Eldredge 2009) are believed here to have been based instead on *P. strictocarpa*.

Reported Distribution. Hawaii. ?Oahu, Kaneohe Bay, on a variety of substrates (Cooke 1977, as *P. setacea*).—Oahu, Kaneohe Bay, Sta. 1, North Channel, 21°30'22.1"N, 157°50'57.1"W (Coles *et al.* 2002a).—Oahu, Kaneohe Bay, Sta. 7, Pristine Reef, 21°28'42.3"N, 157°49'29.5"W (Coles *et al.* 2002a).—Oahu, Kaneohe Bay, Sta. 14, "Floating City", 21°26'23.1"N, 157°47'30.2"W (Coles *et al.* 2002a).—Oahu, Kaneohe Bay, Sta. 25, Moku Manu Island (Coles *et al.* 2002a).—Oahu, Waikiki, Sta. 7, Canoes, 21°28'42.3"N, 157°49'42.5"W, 3.5 m (Coles *et al.* 2002b).—Oahu, Waikiki, Sta. 8, Ala Wai Buoy, 21°16'34.0"N, 157°50'46.7"W (Coles *et al.* 2002b).—Oahu, Waikiki, Sta. 11, Kaiser's Channel, 21°16'26.5"N, 157°50'26.1"W (Coles *et al.* 2002b).—Oahu, Hawaii Kai, Sta. 3, Maunalua Bay, Channel Marker 1, 21°16'28.0"N, 157°43'09.7"W (Coles *et al.* 2002b).—Oahu, Hawaii Kai, Sta. 4, Maunalua Bay, Koko Marina Nearshore, 21°16'56.5"N, 157°42'54.4"W, 1.5 m (Coles *et al.* 2002b).—Maui, Sta. MA3, Maalaea Reef, near Maalaea Harbor, 20°47'31.6"N, 156°30'45.8"W (Coles *et al.* 2004).—Island of Hawaii, Sta. HA6, Red Hill, 19°30'28.8"N, 155°57'19.5"W (Coles *et al.* 2006).

Elsewhere. Currently considered circumglobal in tropical and subtropical waters (Pictet 1893; Millard & Bouillon 1973; Hirohito 1974, 1995; Millard 1975; Ryland & Gibbons 1991; Migotto 1996; Calder 1997, 2013; Calder *et al.* 2003; Kirkendale & Calder 2003; Calder & Kirkendale 2005; Galea & Ferry 2015; Oliveira *et al.* 2016).

Family Halopterididae Millard, 1962

Genus *Halopterus* Allman, 1877

Halopterus plagiocampa (Pictet, 1893)

Figs. 8a–c

Plumularia plagiocampa Pictet, 1893: 56, pl. 3, fig. 50.

Halopterus plagiocampa.—Coles *et al.*, 2009: 76, 82, 85.—Carlton & Eldredge, 2015: 29.

Type locality. Indonesia: Ambon Bay (Pictet 1893, as *Plumularia plagiocampa*).

Material examined. Oahu: Honolulu Harbor, 21°18'37"N, 157°52'22"W, 17 April 2008, seven colonies or colony fragments, to 3.5 cm high, some with female gonothecae, coll. S.L. Coles, ROMIZ B5312.

Remarks. In having hydroids with hydrocladia arranged in opposite pairs, *Halopterus plagiocampa* (Pictet, 1893) has been grouped with others sharing the same character, viz.: *H. catharina* (Johnston, 1833), *H. geminata* (Allman, 1877), *H. clarkei* (Nutting, 1900), *H. opposita* (Mulder & Trebilcock, 1911), *H. zygocladia* (Bale, 1914), *H. gemellipara* Millard, 1962, and *H. enersis* Galea, 2006 (Schuchert 1997; Galea 2006; Calder 2019). The species is distinguished by having the following combination of characters (Schuchert 1997, 2003; Galea 2006): (1) stolons with nematothecae; (2) hydrocaulus unbranched, with both heteromeric and homomeric segmentation; (3) lateral nematothecae occurring as a single pair, each with two chambers; rim deeply inrolled; (4) internal hydrothecal ridge lacking; (5) axillar nematothecae lacking; (6) female gonothecae cornucopia-shaped.

Schuchert (2003) located the type of *H. plagiocampa*, which could not be distinguished from new material being reported by him from the Kei Islands, Indonesia. A few corrections were made from his earlier account of the hydroid (Schuchert 1997), including segmentation of the hydrocaulus (with both heteromeric and homomeric parts) and deep emargination of the lateral nematothecae. His description and illustrations provide a full account of the species.

Thus far, *H. plagiocampa* has been reported only from the western and central Pacific Ocean, with Hawaii being its easternmost known outpost.

Reported Distribution. Hawaii. Oahu, Honolulu Harbor, Sta, HH08, Kapalama Channel, 21°18.660'N, 157°52.419'W (Coles *et al.* 2009).—Oahu, Honolulu Harbor, Sta, HH14, Sand Island Park, 21°18.140'N, 157°52.165'W (Coles *et al.* 2009).

Elsewhere. Indonesia (Pictet 1893; Billard 1913; Schuchert 1997, 2003); Bonin Islands, Japan (Jäderholm 1919); northern Australia (Watson 2000); Guam (Kirkendale & Calder 2003).

Halopterus vervoorti Galea, 2008

Figs. 8d–g

Halopterus polymorpha.—Coles *et al.* 2002a: 318; 2002b: 177; 2004: 73.—Carlton & Eldredge, 2009: 36 [not *Halopterus polymorpha* (Billard, 1913)].

Halopterus vervoorti Galea, 2008: 42, figs. 9A–F.

Type locality. Guadeloupe: Basse-Terre, Petite Anse, 16°05'47.00"N, 61°46'17.00"W, rocky shore (Galea 2008).

Material examined. Oahu: Palea Point, just outside Hanauma Bay, 06 October 1996, one colony, 1.4 cm high, with male gonophores, coll. J. Hoover, ROMIZ B2905.—Oahu: Kaneohe Bay, Sta. 25, Moku Manu Island, 26 January 2000, one colony, 7 mm high, without gonophores, coll. R. DeFelice and S.L. Coles, ROMIZ B3314.

Remarks. Hydroids from Hawaii identified earlier as the morphologically varied *Halopterus polymorpha* (Billard, 1913) have now been recognized instead as *Halopterus vervoorti* Galea, 2008. The two species are similar in morphology, with differences between them having been discovered only recently (Galea 2008; Galea *et al.* 2018). In particular, *H. vervoorti* possesses cauline axillar nematothecae in pairs while in *H. polymorpha* they occur singly. Although first described from Guadeloupe in the Caribbean Sea, *H. vervoorti* is now known from warm waters worldwide (Galea *et al.* 2018), except the tropical eastern Pacific. A detailed account of this species has been given by Galea *et al.* (2018), complementing the original description (Galea 2008). Included in the more recent of these two papers was an appendix summarizing differences between *H. vervoorti* and related species.

As noted by Galea *et al.* (2018), *H. vervoorti* resembles *H. liechtensternii* (Marktanner-Turneretscher, 1890), *H. sibogae* (Billard, 1913), *H. australis* Galea, in Galea *et al.*, 2018, and *H. brasiliensis* Galea, in Galea *et al.*, 2018 in having paired cauline axillar nematothecae as well as heteromerously segmented hydrocladia. Noteworthy differences distinguishing *H. vervoorti* from these other species, according to Galea *et al.*, are as follows. Unlike in *H. liechtensternii*, stem internodes are shorter, a single axillar nematotheca per hydrocladial hydrotheca is present rather than two, cauline superior nematothecae occur in a single rather than in two distinct rows, female gonothecae are ovoid rather than almost cylindrical, and male gonothecae are elongate-ovoid and large rather than sac-shaped and much smaller. In contrast to *H. sibogae* and *H. australis*, lateral nematothecae are of normal rather than of exceptional length. Hydrothecal margins are also not sinuated, as in *H. australis*. Compared with *H. brasiliensis*, a larger and more robust species, cormoids are shorter, hydrocauli and hydrocladia are thinner, hydrothecae are narrower, and cauline superior nematothecae occur in a single row rather than in two longitudinal rows.

Of biogeographic note, little genetic distance exists between populations of *H. vervoorti* from the Maldives in the Indian Ocean and Martinique and Curaçao in the Caribbean Sea (Galea *et al.* 2018). Their analyses also reveal that the species is close to *H. sibogae* (Billard, 1913), and not far removed from *H. liechtensternii* and *H. carinata* Allman, 1877, with the latter being the type species of the genus *Halopteris* Allman, 1877.

Reported Distribution. Hawaii. Oahu, Kaneohe Bay, Sta. 1, North Channel, 21°30'22.1"N, 157°50'57.1"W (Coles *et al.* 2002a, as *Halopteris polymorpha*).—Oahu, Kaneohe Bay, Sta. 25, Moku Manu Island (Coles *et al.* 2002a, as *Halopteris polymorpha*).—Oahu, Waikiki, Sta. 6, *Atlantis* wreck, 21°15'37.6"N, 157°50'15.3"W, 20–30 m (Coles *et al.* 2002b, as *Halopteris polymorpha*).—Maui, Sta. MA1, Kahului Harbor Pier 1, 20°54'00.5"N, 156°28'09.8"W (Coles *et al.* 2004, as *Halopteris polymorpha*).—Maui, Sta. MA2, Kahului Harbor Pier 2, 20°53'53.5"N, 156°28'13.2"W (Coles *et al.* 2004, as *Halopteris polymorpha*).—Island of Hawaii, Sta. HA4, Hilo Harbor, Pier 1, 19°44'00.5"N, 155°03'25.9"W (Coles *et al.* 2004, as *Halopteris polymorpha*).

Elsewhere. Lesser Antilles, Cape Verde, Red Sea, Madagascar, Maldives, and Indonesia; possibly also from Australia, Japan, and Fiji (Galea *et al.* 2018).

Genus *Monostaechas* Allman, 1877

Monostaechas quadridens (McCrary, 1859)

Figs. 8h, i

Plumularia quadridens McCrary, 1859: 199.

Monostaechas quadridens.—Nutting, 1905: 952.

Type locality. USA: South Carolina, Charleston Harbor area (McCrary 1859: 199).

Material examined. Oahu: Kaneohe Bay, Sta. 7, Pristine Reef, 21°28'42.3"N, 157°49'29.5"W, 18 November 1999, three colony fragments, to 7 mm high, without gonothecae, coll. R. DeFelice and S.L. Coles, ROMIZ B3307.

Remarks. Two species of hydroids from relatively deep waters off Hawaii were assigned by Nutting (1905) to the genus *Monostaechas* Allman, 1877. Most of his specimens of both of them are now in collections at the National Museum of Natural History, Smithsonian Institution. One of the species, identified as *M. quadridens* (McCrary, 1859), came from R/V *Albatross* stations 3854 (south of Molokai, 20.9958°, -156.861°, 238–245 m, USNM 22228) and 3859 (south of Molokai, 21.0444°, -156.739°, 252–256 m, USNM 70804). He was unable to distinguish these hydroids from colonies assigned to *M. quadridens* from the Atlantic coast. The other, taken to be a new species described as *M. fisheri* Nutting, 1905, was found in collections from R/V *Albatross* stations 3936 (off Laysan Island, not currently listed in the NMNH online database), 3949 (west of Laysan Island, 25.7958°, -171.876°, 108–278 m, USNM 22173 (syntype)), and 4072 (north of Maui, 20.975°, -156.444°, 102–108 m, USNM 22146 (syntype); ditto USNM 70740). Other collections of these species from Hawaii exist as well at the NMNH (USNM 70640, USNM 96362).

Hydroids of *M. fisheri* have been distinguished from those of *M. quadridens* in having a long, straight hydrocaulus bearing lateral hydrocladia (Schuchert 1997). By contrast, the hydrocaulus of *M. quadridens* is short, and at its distal end it either divides dichotomously or develops into a scorpioid symposium. Nutting (1905) added that

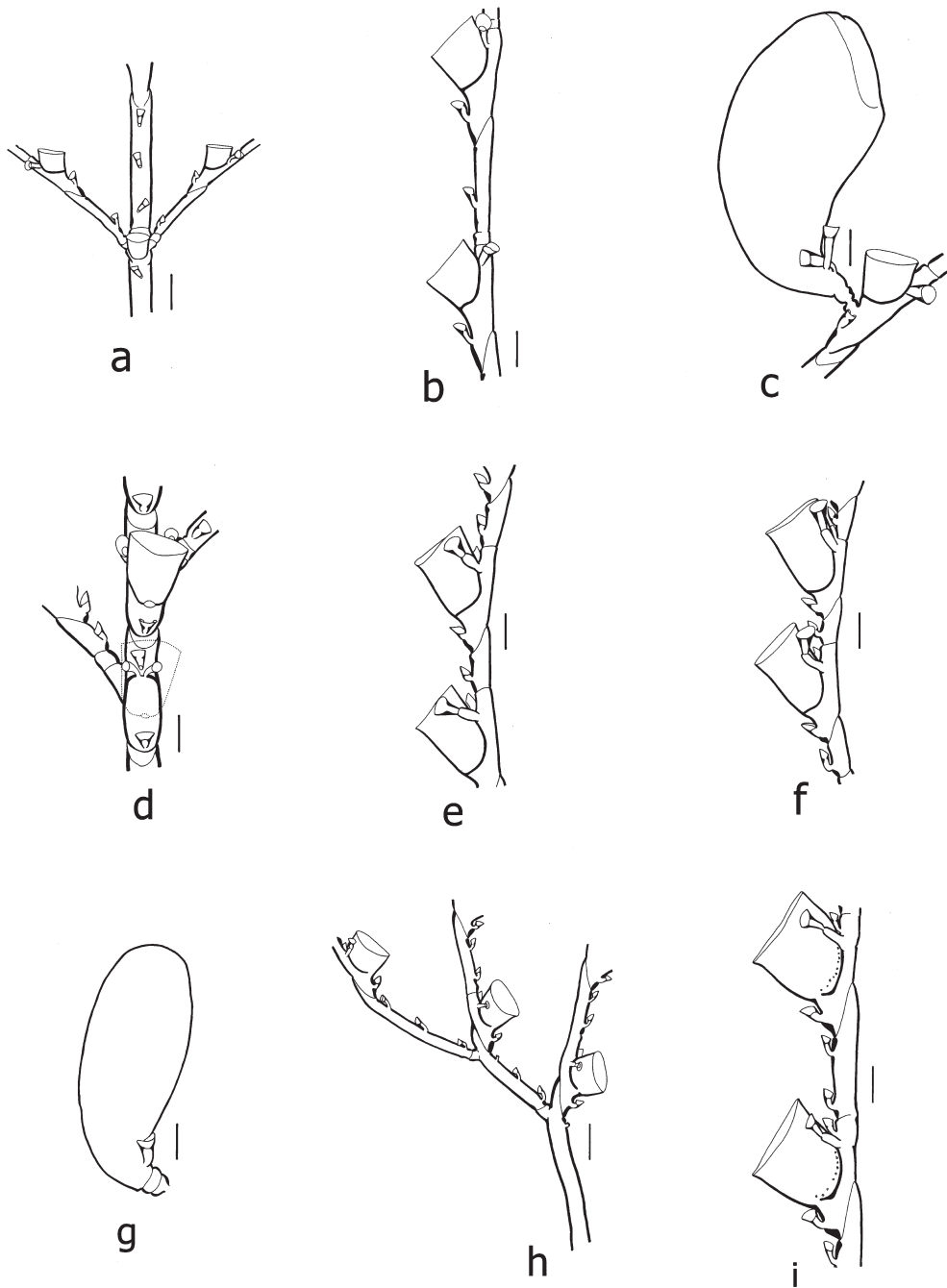


FIGURE 8. **a, *Halopteris plagiocampa*:** part of hydrocaulus with proximal ends of two hydrocladia, with nematothecae and three hydrothecae, Honolulu Harbor, Oahu, ROMIZ B5312. Scale equals 0.2 mm. **b, *Halopteris plagiocampa*:** part of hydrocladium with nematothecae and two hydrothecae, Honolulu Harbor, Oahu, ROMIZ B5312. Scale equals 0.1 mm. **c, *Halopteris plagiocampa*:** part of hydrocaulus with a hydrotheca, a gonotheca, and nematothecae, Honolulu Harbor, Oahu, ROMIZ B5312. Scale equals 0.1 mm. **d, *Halopteris vervoorti*:** part of hydrocaulus, with proximal ends of two hydrocladia, nematothecae, and two cauline hydrothecae; proximal hydrotheca outlined in dots to show paired axial nematothecae; distal hydrotheca illustrated with lateral nematothecae, Moku Manu Island, Kaneohe Bay, Oahu, ROMIZ B3314. Scale equals 0.1 mm. **e, *Halopteris vervoorti*:** part of hydrocladium, with nematothecae and two hydrothecae, Palea Point, Oahu, ROMIZ B2905. Scale equals 0.1 mm. **f, *Halopteris vervoorti*:** part of hydrocladium, with nematothecae and two hydrothecae; Moku Manu Island, Kaneohe Bay, Oahu, ROMIZ B3314. Scale equals 0.1 mm. **g, *Halopteris vervoorti*:** gonotheca, Palea Point, Oahu, ROMIZ B2905. Scale equals 0.1 mm. **h, *Monostaechas quadridens*:** part of branched colony, with nematothecae and hydrothecae, Pristine Reef, Kaneohe Bay, Oahu, ROMIZ B3307. Scale equals 0.2 mm. **i, *Monostaechas quadridens*:** part of hydrocladium, with nematothecae and hydrothecae, Pristine Reef, Kaneohe Bay, Oahu, ROMIZ B3307. Scale equals 0.1 mm.

hydranths of *M. fisheri* contained a dark pigment and appeared almost black. Schuchert (1997) questioned the validity of *M. fisheri*, noting that it was much like *M. quadridens*. While maintaining it as a distinct species, he noted that others (Bedot 1921; Vervoort 1968) had also expressed doubts or questions about differences between the two. Leloup (1935) concluded that they were conspecific.

While *M. quadridens* has generally been taken to be essentially circumglobal in the past, Moura *et al.* (2018) distinguished five putative species in specimens assigned to it. Hydroids of the five lineages came from the Pacific coast of Central America, from Brazil, from Madeira, and from two locations in the Caribbean region. Their analyses also revealed that the genus *Monostaechas*, as presently constituted, is polyphyletic. Indeed, its validity had been questioned earlier (Schuchert 2003: 208). Given the unsettled taxonomy of this group, specimens recorded here from Hawaii are retained under the binomen *M. quadridens*.

Extensive traditional taxonomic accounts of *M. quadridens* include those of Schuchert (1997) and Ansín Agís *et al.* (2001).

Reported Distribution. Hawaii. Molokai, off south coast, *Albatross* Sta. 3854, 20°59'44.88"N, 156°51'39.6"W, 134 fm (245 m) (Nutting (1905).—Between Molokai and Maui, *Albatross* Sta. 3859, 21°02'39.84"N, 156°44'20.4"W, 138 fm (252 m) (Nutting, 1905).

Elsewhere. Provisionally taken to be circumglobal in tropical, subtropical, and temperate waters (Schuchert 1997; Ansín Agís *et al.* 2001, 2009; Vervoort & Watson 2003; Calder 2019).

Family Aglaopheniidae Marktanner-Turneretscher, 1890

Genus *Gymnangium* Hincks, 1874

Gymnangium hians (Busk, 1852)

Fig. 9a

Plumularia hians Busk, 1852: 396.

Halicornaria flava Nutting, 1905: 955, pl. 6, fig. 2, pl. 13, figs. 11, 12.

Gymnangium hians.—Hoover, 1998: 21, unnumbered figure; 2006: 21, unnumbered figure.—Coles *et al.*, 2004: 72.

Type locality. Australia: Torres Strait, Prince of Wales Channel, 9 fm (16 m) (Busk 1852).

Material examined. Oahu: Palea Point, just outside Hanauma Bay, 30 ft (9 m), 05 October 1996, one colony, 4.7 cm high, with gonophores, coll. J. Hoover, ROMIZ B2903.

Remarks. In a report on the hydroids of Hawaii, Nutting (1905) described two new species that he assigned to *Halicornaria* auct. (= *Gymnangium* Hincks, 1874). The first of these, *Halicornaria flava* Nutting, 1905, is now taken to be conspecific with *Gymnangium hians* (Busk, 1852), a species reported herein from Oahu. The second, *H. bryani* Nutting 1905, is currently maintained as valid (Ronowicz *et al.* 2017), under the binomen *G. bryani*. Although its hydroid differs from that of *G. hians* in being epizoic, small (even when fertile), and non-featherlike, Ronowicz *et al.* (2017) suggested that it might simply be an epizoic morphotype of *G. hians*.

Ronowicz *et al.* (2017) undertook a review of *Gymnangium* utilizing methods of both traditional taxonomy and molecular systematics. Their study revealed that the genus warranted being split into two, and both *Gymnangium* and *Taxella* Allman, 1874 were recognized as valid. In *Gymnangium*, the hydrocaulus is monosiphonic or rarely polysiphonic, hydrothecae are cup-shaped, and an abcauline intrathecal septum may be present. In *Taxella*, the hydrocaulus is polysiphonic, hydrothecae are elongate, and an abcauline intrathecal septum is absent (Ronowicz *et al.* 2017). Following Schuchert (2020), 38 species are now recognized as valid in *Gymnangium* and five in *Taxella*. *Gymnangium hians*, reported here, is morphologically and genetically close to *Halicornaria montagui* Billard, 1912, the type species of *Gymnangium*, and it remains assigned to that genus. Its hydroid is known to be morphologically variable (Rees & Thursfield 1965; Ronowicz *et al.* 2017).

Hydroids of *G. hians* are reported to be widespread and locally abundant across the tropical and subtropical Indo-Pacific (Stechow 1923; Rees & Thursfield 1965; Vervoort & Vasseur 1977; Rho & Park 1986; Ryland & Gibbons 1991; Hirohito 1995; Watson 2000; Kirkendale & Calder 2003; Gravier-Bonnet & Bourmaud 2012; Ronowicz *et al.* 2017; Chakraborty & Raghunathan 2020), ranging from the Red Sea (Mergner & Wedler 1977) to Hawaii (Hoover 1996, 2006; Coles *et al.* 2004). Its gonophores are liberated as free medusoids (Ronowicz *et al.* 2017).

Reported Distribution. Hawaii. Laysan Island, off north coast, *Albatross* Sta. 3939, 25°52'35.04"N, 171°42'28.8"W, 163 fm (298 m) (Nutting 1905, as *Halicornaria flava*).—Oahu, Palea Point, 30 ft (9 m) (Hoover 1998, 2006).—Kauai, Sta. KA3, Port Allen Main Dock, 21°54'09.9"N, 159°35'31.3"W (Coles *et al.* 2004).—Island of Hawaii, Sta. HA4, Hilo Harbor, Pier 1, 19°44'00.5"N, 155°03'25.9"W (Coles *et al.* 2004).

Elsewhere. Tropical and subtropical Indo-Pacific (Ronowicz *et al.* 2017; Chakraborty & Raghunathan 2020).

Genus *Lytocarpia* Kirchenpauer, 1872

Lytocarpia nigra (Nutting, 1905)

Figs. 9b, c

Thecocarpus niger Nutting, 1905: 953, pl. 5, fig. 5, pl. 13, figs. 1–6.—Randall, 1975: 226.

Lytocarpia nigra.—Hoover, 1998: 22, unnumbered figure; 2006: 22, unnumbered figure.—Coles *et al.*, 2002a: 318.—Wagner *et al.*, 2016: 58, two unnumbered figures.

Type locality. USA: Hawaii, *Albatross* Sta. 3939, north of Laysan Island, 163 fm (298 m); *Albatross* Sta. 3955, northeast of Laysan Island, 20 fm (37 m); *Albatross* Sta. 3961, south of Laysan Island, 19 fm (35 m); *Albatross* Sta. 3962, south of Laysan Island, 16 fm (29 m) (Nutting 1905, as *Thecocarpus niger*).

Material examined. Oahu: Palea Point, just outside Hanauma Bay, 30 ft (9 m), 06 October 1996, five colonies or colony fragments, to 4 cm high, without gonophores, coll. J. Hoover, ROMIZ B2906.—Maui: Kanaio coast, 40 ft (12 m), three colonies, to 5.8 cm high, without gonophores, coll. P. Fiene-Severns, ROMIZ B3037.—Oahu: Kaneohe Bay, Sta. 25, Moku Manu Island, 26 January 2000, two colonies or colony fragments, to 1.8 cm high, without gonophores, coll. R. DeFelice and S.L. Coles, ROMIZ B3311.

Remarks. *Lytocarpia nigra* (Nutting, 1905) was originally described from locations off Laysan Island (Kauō or Kamole, in Hawaiian) in the Northwestern Hawaiian Islands. As suggested by the specific name, its hydroids are black in colour due to dense pigment occurring throughout the colony (Nutting 1905; Stechow 1913; Schuchert 2015; Galea 2020). The guidebooks of Hoover (1998, 2006) and Wagner *et al.* (2016) provide colour photographs of the species, and a detailed description of it has been given by Galea (2020).

In addition to its occurrence in the Hawaiian Islands, this species has been reported several times from locations in the western Pacific (Stechow 1913; Rho 1967; Hirohito 1969, 1983, 1995; Yamada 1981; Schuchert 2015; Galea 2020). Recent molecular studies have incorporated data on material attributed to *L. nigra* from the islands of Europa and Juan de Nova in the Mozambique Channel, from New Caledonia, and from Okinawa (Postaire *et al.* 2016; Ronowicz *et al.* 2017; Moura *et al.* 2018, 2019). Results of these studies indicate that this hydroid has a much closer relationship to species of *Macrorhynchia* Kirchenpauer, 1872 and *Taxella* Allman, 1874 than to *Lytocarpia myriophyllum* (Linnaeus, 1758), type species of *Lytocarpia* Kirchenpauer, 1872, and others of that genus. With possible relationships and taxonomy of this species as yet unsettled, however, the binomen *L. nigra* has been retained for it here.

As with certain other species of aglaopheniids (see Millard 1975: fig. 139C), lateral nematothecae at the distal end of a hydrocladium are directed upward (Fig. 9c) while those at the proximal end may face backward (Fig. 9b).

Yamada (1981) included *L. nigra* among a list of hydroid species found as part of the fouling community in Japan.

Reported Distribution. Hawaii. Laysan Island, off north coast, *Albatross* Sta. 3939, 25°52'35.04"N, 171°42'28.8"W, 163 fm (298 m) (Nutting 1905, as *Thecocarpus niger*).—Laysan Island, off west coast, *Albatross* Sta. 3955, 25°44'09.96"N, 171°51'57.6"W, 20 fm (37 m) (Nutting 1905, as *Thecocarpus niger*).—Laysan Island, off north coast, *Albatross* Sta. 3961, 25°47'25.08"N, 171°44'45.6"W, 19 fm (35 m) (Nutting 1905, as *Thecocarpus niger*).—Laysan Island, off north coast, *Albatross* Sta. 3962, 25°48'50.04"N, 171°43'44.4"W, 16 fm (29 m) (Nutting 1905, as *Thecocarpus niger*).—Oahu, Haleiwa, ca. 84 m, in stomach of filefish (Randall 1975, as *Thecocarpus niger*).—Niihau, Lehua Rock, 40 ft (12 m) (Hoover 1998, 2006, as *Lytocarpia nigra*).—Oahu, Kaneohe Bay, Sta. 25, Moku Manu Island (Coles *et al.* 2002a, as *Lytocarpia nigra*).—Papahānaumokuākea Marine National Monument, mesophotic coral ecosystems (Wagner *et al.* 2016, as *Lytocarpia nigra*).

Elsewhere. Korea (Rho 1967, as *Lytocarpia niger*; Park 1993, as *Lytocarpia nigra*); Japan, including Okinawa (Hirohito 1995; Schuchert 2015); South China Sea (Xu *et al.* 2014); New Caledonia (Galea 2020); provisional re-

cords from the Mozambique Channel and New Caledonia (Postaire *et al.* 2016; Ronowicz *et al.* 2017; Moura *et al.* 2018, 2019).

Genus *Macrorhynchia* Kirchenpauer, 1872

Macrorhynchia balei (Nutting, 1905)

Fig. 9d

Lytocarpus balei Nutting, 1905: 954, pl. 6, fig. 1, pl. 13, figs. 7, 8.

Macrorhynchia balei.—Schuchert, 2003: 226.—Wagner *et al.*, 2016: 57, two unnumbered figures.

Type locality. USA: Hawaii, *Albatross* Station 3852, off south coast of Molokai, 20°58'30"N, 156°54'21.6"W, 47–115 fm (86–210 m) (Nutting 1905, as *Lytocarpus balei*).

Material examined. Between Maui, Molokai and Lanai islands: deep reefs, 40–100 m, HURL submersible, 12 July 2007, one colony, 5 cm high, with phylactocarps, Holly Bolick, ROMIZ B3804.

Remarks. Nutting (1905) illustrated and briefly described *Macrorhynchia balei* (as *Lytocarpus balei*) from *Albatross* Sta. 3852, located south of the island of Molokai, Hawaii. The colony examined here (ROMIZ B3804) can be considered topotypic in being from the same general area.

Material listed as a “type” of *M. balei* exists in collections at the NMNH (USNM 22220). It is presently unclear whether Nutting (1905) described the species from a single colony, or from more than one. The NMNH online database lists the specimen count as “1 ca.”. Schuchert (2003) examined this type and described it as a fragmented colony. While it is likely the holotype by monotypy, it is left for a future examiner of the type to confirm whether this is so.

A detailed taxonomic account of *M. balei* has been given by Schuchert (2003). In addition to the type specimen from Hawaii, he also studied new material from Indonesia as well as colonies from the Philippines (USNM 68534) that Nutting (1927) had assigned to the species. Di Camillo *et al.* (2009) concluded that Nutting’s Philippine specimens of *M. balei*, but not the type of the species from Hawaii, were referable to *M. spectabilis* (Allman, 1883). However, *Macrorhynchia spectabilis* has been regarded as conspecific with *M. phoenicea* (Busk, 1852) by Schuchert (2003, 2015, 2020).

The hydroid of *M. balei* is distinctive in having nematopores on hydrocladial internodes beneath the hydrothecae (Fig. 9d), as well as on both primary and auxiliary tubes of the hydrocaulus (Schuchert 2003, 2015). Large isorhiza nematocysts may protrude from these pores. They were first detected in the species by Schuchert (2003), who noted that nematopores may be absent on distal internodes of a hydrocladium. Other characters distinguishing *M. balei* from the morphologically similar *M. philippina* Kirchenpauer, 1872 and *M. phoenicea* (Busk, 1852) have been noted by Schuchert (2003). These three species have been shown to be close genetically (Moura 2018, 2019) as well as morphologically.

Reported Distribution. Hawaii. Molokai, off south coast, *Albatross* Sta. 3852, 20°58'30"N, 156°54'21.6"W, 47–115 fm (86–210 m) (Nutting 1905, as *Lytocarpus balei*; Schuchert 2003).—Papahānaumokuākea Marine National Monument, Northwestern Hawaiian Islands (Wagner *et al.* 2016).

Elsewhere. Japan (Stechow 1907, 1909), including Okinawa (Schuchert 2015); Indonesia (Billard 1913; Schuchert 2003); ?Philippines (Nutting 1927; Schuchert 2003).

Macrorhynchia hawaiiensis (Nutting, 1905)

Figs. 9e, f

Lytocarpus hawaiiensis Nutting, 1905: 954, pl. 5, fig. 6, pl. 12, figs. 10–13.

Macrorhynchia hawaiiensis.—Wagner *et al.*, 2016: 57, two unnumbered figures.

Type locality. USA: Hawaii, *Albatross* Sta. 3848, south of Molokai, 20°57'50.04"N, 156°56'60"W, 44–73 fm (80–134 m); *Albatross* Sta. 3853, Molokai, south coast, 20°59'49.92"N, 156°52'40.8"W, 115 fm (210 m); *Albatross* Sta. 3875, between Maui and Lanai, 20°54'45"N, 156°46'08.4"W, 65 fm (119 m); (Nutting 1905, as *Lytocarpus hawaiiensis*).

Material examined. Between Maui, Molokai and Lanai islands: deep reefs, 40–100 m, HURL submersible, 12 July 2007, one colony, 2.1 cm high, without gonophores, Holly Bolick, ROMIZ B3805.

Remarks. *Macrorhynchia hawaiiensis* (Nutting, 1905) is currently known only from Hawaii. Following the original description of it by Nutting (1905) from locations around the main islands, the species has been reported again only by Wagner *et al.* (2016), from the Northwestern Hawaiian Islands. They found it in shaded parts of reefs (inside crevices and under overhangs). It is recorded again here from Hawaii for the third time.

Nutting's (1905) account of *M. hawaiiensis* was based on specimens, at least some of them fertile, from three stations (3848, 3853, 3875) occupied by R/V *Albatross* in Hawaiian waters. Material from two of these stations is currently listed, as *Lytocarpus hawaiiensis* (sic), in the NMNH online catalog: USNM 22186, Hawaii, R/V *Albatross* Sta. 3848, Molokai Island, 20.9639°, -156.95°, 80–134 m, 08 April 1902, specimen count 1 (syntype); USNM 22197, Hawaii, R/V *Albatross* Sta. 3875, Auau Channel, Maui Island, west of Lahaina, 20.9125°, -156.769°, 62–119 m, 12 April 1902, specimen count 1 (syntype).

Galea (2020) included *M. hawaiiensis* in a group of 13 species assigned to *Macrorhynchia* Kirchenpauer, 1872 that are distinguished by having sac- or cup-shaped hydrothecae, and adaxial but no abaxial intrathecal septa. In *M. hawaiiensis*, unlike others of its group, the mesial nematotheca becomes free at the mid-point of the hydrotheca, the tip of the mesial nematotheca does not reach the hydrothecal aperture, and the hydrothecal rim bears a single median abaxial cusp and two pairs of small, uneven lateral cusps. As for an intrathecal septum in *M. hawaiiensis*, it was described by Nutting (1905) as “obsolete”, and it was undeveloped in specimens examined here (Fig. 9f).

Reported Distribution. Hawaii. Molokai, off south coast, *Albatross* Sta. 3853, 20°59'49.92"N, 156°52'40.8"W, 115 fm (210 m) (Nutting 1905, as *Lytocarpus hawaiiensis*).—Between Maui and Lanai, *Albatross* Sta. 3875, 20°54'45"N, 156°46'08.4"W, 65 fm (119 m) (Nutting 1905, as *Lytocarpus hawaiiensis*).—Molokai, off south coast, *Albatross* Sta. 3848, 20°57'50.04"N, 156°56'60"W, 44–73 fm (80–134 m) (Nutting 1905, as *Lytocarpus hawaiiensis*).—Papahānaumokuākea Marine National Monument, Northwestern Hawaiian Islands (Wagner *et al.* 2016). Elsewhere. No reports.

Macrorhynchia philippina Kirchenpauer, 1872

Fig. 9g

Macrorhynchia philippina Kirchenpauer, 1872: 19.—Hoover, 1998: 21, unnumbered figure; 2006: 21, unnumbered figure.—Coles *et al.*, 2004: 72.

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

Type locality. Philippines: Manila (Kirchenpauer 1872).

Material examined. Oahu: Palea Point, just outside Hanauma Bay, 30 ft (9 m), 05 October 1996, one colony, to 3.2 cm high, without gonophores, coll. J. Hoover, ROMIZ B2904.

Remarks. *Macrorhynchia philippina* Kirchenpauer, 1872 has been regarded as circumglobal in shallow waters of the tropics, subtropics, and warm-temperate regions (e.g., Nutting 1900, as *Lytocarpus philippinus*; Billard 1913, as *L. philippinus*; Fraser 1938a, 1944, 1948, as *L. philippinus*; Vervoort 1968, as *L. philippinus*; Millard 1975, as *L. philippinus*; Ryland & Gibbons 1991; Migotto 1996; Calder 1997, 2013; 2019; Watson 2000; Ansín Agís *et al.* 2001; Schuchert 2003; Kirkendale & Calder 2003; Calder *et al.* 2003; Galea 2010; Oliveira *et al.* 2016; Chakraborty & Raghunathan 2020). Reflecting its capacity for dispersal, its reported distribution also includes several remote oceanic islands (Kirkendale & Calder 2003). Hydroids of *M. philippina* have been recorded earlier from Hawaii by Hoover (1998, 2006) and Coles (2004), and the colony examined here is one of those collected and reported by John P. Hoover.

The barcoding study by Moura *et al.* (2018) confirms the widespread distribution of hydroids identified as *M. philippina*. Nevertheless, two lineages under that name were identified in their study. Even though genetic datasets are still quite limited, Lineage 1 indeed appears to be circumglobal in being based on specimens from the SW Pacific (Moorea), NE Pacific (Panama and Costa Rica, Pacific coasts), SW Atlantic (Brazil), NW Atlantic (Panama, Caribbean coast), NE Atlantic (Azores; Madeira), SE Atlantic (Principe; Sierra Leone), and SW Indian Ocean (Europa and Juan de Nova islands). Lineage 2 was derived from a more limited number of locations, but the lineage was still widespread, with barcodes of hydroids collected in the SW Indian Ocean (Europa Island) and the SW Pacific (New Caledonia). If these lineages constitute two distinct species, questions remain which one constitutes the *M.*

philippina of Kirchenpauer from the Philippines. A study of material from the vicinity of Manila, the type locality of the species, would therefore be constructive.

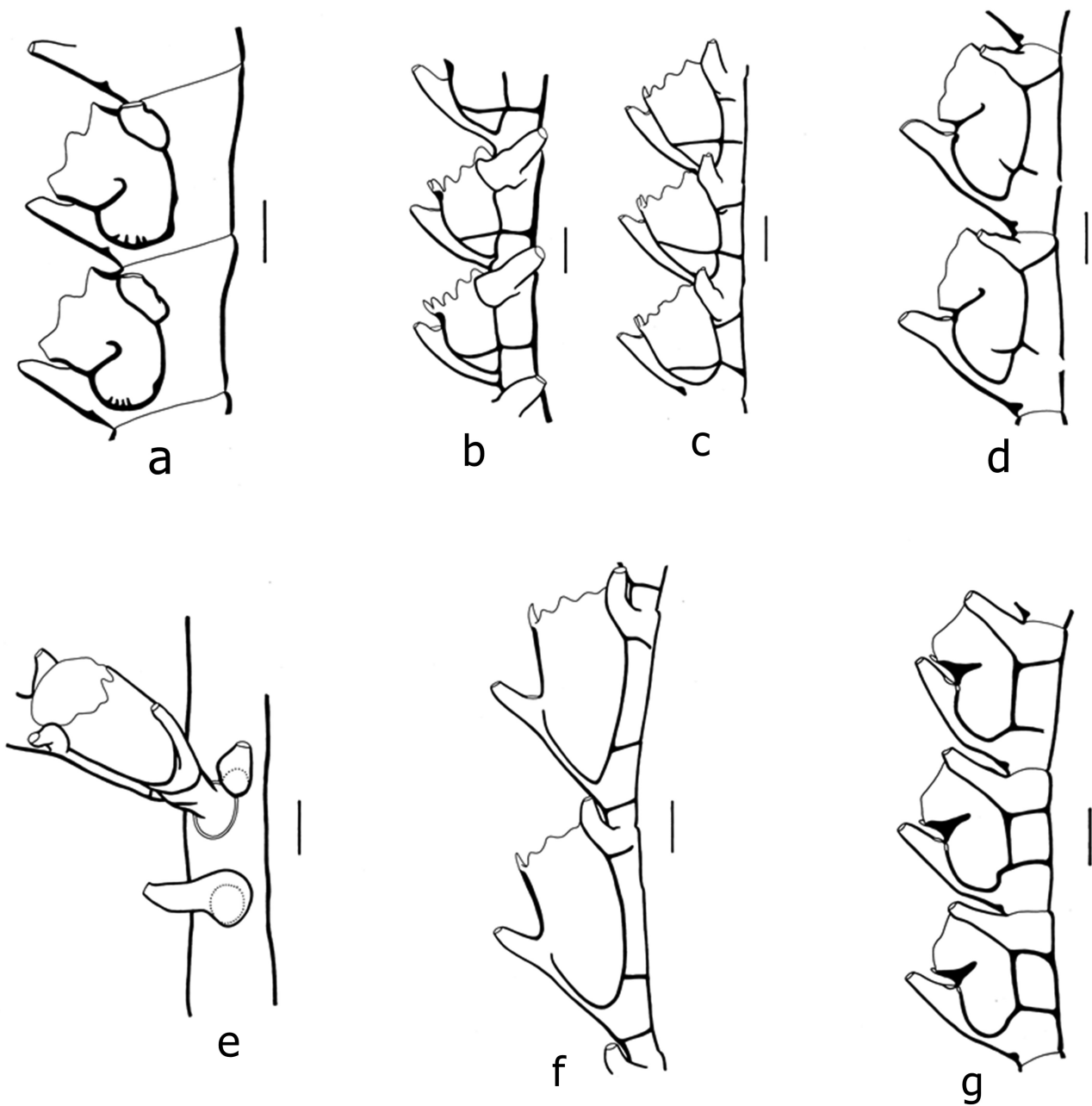


FIGURE 9. **a**, *Gymnangium hians*: part of a hydrocladium, with nematothecae and two hydrothecae, Palea Point, Oahu, ROMIZ B2903. Scale equals 0.1 mm. **b**, *Lytocarpia nigra*: part of a hydrocladium, near proximal end, with nematothecae and two hydrothecae, lateral nematothecae facing downward, Palea Point, Oahu, ROMIZ B2906. Scale equals 0.1 mm. **c**, *Lytocarpia nigra*: part of a hydrocladium, near distal end, with nematothecae and three hydrothecae, Palea Point, Oahu, ROMIZ B2906. Scale equals 0.1 mm. **d**, *Macrorhynchia balei*: part of a hydrocladium, with nematothecae, internodal nematopores, and two hydrothecae, deep reefs between Maui, Molokai, and Lanai, ROMIZ B3804. Scale equals 0.1 mm. **e**, *Macrorhynchia hawaiiensis*: part of a hydrocaulus with cauline nematothecae and proximal end of a hydrocladium, with nematothecae and a hydrotheca, deep reefs between Maui, Molokai, and Lanai, ROMIZ B3805. Scale equals 0.1 mm. **f**, *Macrorhynchia hawaiiensis*: part of a hydrocladium, with nematothecae and two hydrothecae, deep reefs between Maui, Molokai, and Lanai, ROMIZ B3805. Scale equals 0.1 mm. **g**, *Macrorhynchia philippina*: part of a hydrocladium, with nematothecae and three hydrothecae, Palea Point, Oahu, ROMIZ B2904. Scale equals 0.1 mm.

A detailed synonymy and description of *M. philippina* has been given by Ansín Agís *et al.* (2001).

Reported Distribution. Hawaii. Oahu, Palea Point, 30 ft (9 m) (Hoover 1998, 2006).—Molokai, Sta. MO2, Hale O Lono Reef, 21°05'01.4"N, 157°14'57.7"W (Coles *et al.* 2004).

Elsewhere. Circumglobal in shallow tropical, subtropical, and warm-temperate seas (Ansín Agís *et al.* 2001; Schuchert 2003; Xu *et al.* 2014; Moura *et al.* 2018, 2019; Chakraborty & Raghunathan 2020).

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