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Shallow water hydroids (Cnidaria, Hydrozoa) from the 2002 NOWRAMP cruise to the Northwestern Hawaiian Islands

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Abstract

Forty-two species of hydroids, excluding stylasterids, are reported in the present collection from the Northwestern Hawaiian Islands. Of these, four are anthoathecates and 38 are leptothecates. Among the latter, *Sertularella affinicostata* and *Monotheca gibbosa* are described as new species. The binomen *Halopteris longibrachia* is proposed as a new replacement name for *Plumularia polymorpha* var. *sibogae* Billard, 1913, an invalid junior primary homonym of *P. sibogae* Billard, 1911. Based largely on evidence from earlier molecular phylogenies, the genus *Disertasia* Neppi, 1917 is resurrected to accommodate species including *Dynamena crisioides* Lamouroux, 1824, *Sertularia disticha* Bosc, 1802, and *Sia. moluccana* Pictet, 1893. *Sertularella robusta* Coughtrey, 1876 is an invalid junior primary homonym of *Sla. gayi* var. *robusta* Allman, 1874a, and has been replaced here by the binomen *Sla. quasiplana* Trebilcock, 1928, originally described as *Sla. robusta* var. *quasiplana* Trebilcock, 1928. *Clytia hummelincki* (Leloup, 1935) is referred to the synonymy of its senior subjective synonym, *C. brevithecata* (Thornely, 1900). Following Reversal of Precedence provisions in the International Code of Zoological Nomenclature to preserve prevailing usage of binomena, the familiar names *Sia. disticha* Bosc, 1802 (also known as *Dynamena disticha*) and *Lytocarpia phyteuma* (Stechow, 1919b) are designated *nomena protecta* and assigned precedence over their virtually unknown senior synonyms *Hydra quinternana* Bosc, 1797 and *Aglaophenia clavicula* Whitelegge, 1899, respectively, names now reduced to the status of *nomena oblita*. Twenty species are reported for the first time from Hawaii [*Eudendrium merulum* Watson, 1985, Phialellidae (undetermined), *Hebella* sp., *Hebellopsis scandens* (Bale, 1888), *H. sibogae* Billard, 1942, *Clytia brevithecata*, *C. linearis* (Thornely, 1900), *C.* cf. *noliformis* (McCrady, 1859), *Halecium* sp., *Sla. affinicostata*, *Sla. angulosa* Bale, 1894, *Pasya heterodonta* (Jarvis, 1922), *Tridentata orthogonalis* (Gibbons & Ryland, 1989), *Pycnotheca producta* (Bale, 1881), *Monotheca gibbosa*, *H. longibrachia*, *A. postdentata* Billard, 1913, *A. suensonii* Jäderholm, 1896, *A. whiteleggei* Bale, 1888, and *L. flexuosa* (Lamouroux, 1816)]. *Sertularia orthogonalis*, reported for only the third time worldwide, is assigned to the genus *Tridentata* Stechow, 1920. Hydroids of the NOWRAMP 2002 collection consisted largely of presumptive widespread species, with over 75% of them having been reported elsewhere in the tropical Indo-west Pacific region.

Key words: Anthoathecata, Hydroidolina, Leptothecata, marine invertebrates, Medusozoa, Papahānaumokuākea Marine National Monument, taxonomy, tropical Indo-west Pacific region, zoological nomenclature

Introduction

Located in the central Pacific, the oceanic islands of Hawaii are remote from all continents. Far to the west is the so-called Coral Triangle of the tropical Indo-west Pacific, a region of unequalled marine species biodiversity (Sanciangco *et al*. 2013) encompassing the Philippines, eastern Indonesia, Papua New Guinea, the Solomon Islands, and East Timor (Veron *et al*. 2009). The biota of the isolated Hawaiian archipelago, by comparison, is much less diverse. Amongst zooxanthellate corals, Veron *et al*. reported multiple times fewer species from the main Hawaiian Islands (62) and the Northwestern Hawaiian Islands (47) than from locations such as the Celebes Sea (545), the Sulu Sea (540), the southeast Philippines (533) and the north Philippines (510). A biogeographic parallel occurs in the Atlantic, with the marine biota of isolated and subtropical Bermuda representing an attenuated outpost of a much richer tropical one in the Caribbean Sea (Calder 1993). However, distant oceanic islands in both cases have been populated over centuries by invasive species that crossed significant biogeographic barriers, likely in large part via rafting and shipping. Nevertheless, only a fraction of those species inhabiting a centre of diversity are ever transported to and successfully colonize such distant and physically dissimilar new territories. Even for those that survive long-range transport to remote islands, environmental conditions there must be suitable for them to survive and become established. In short, the Hawaiian archipelago neither duplicates the habitat diversity and size, nor the optimal physical environment, of the Coral Triangle region, and its reduced species richness is axiomatic.

While hydroid species numbers are known to be much greater in the Coral Triangle than in Hawaii, with several hundred recorded there to date (e.g., Billard 1913, 1925b; Hargitt 1924; Nutting 1927; Vervoort 1993; Schuchert 2003; Di Camillo *et al*. 2008; Galea 2016), the Hawaiian fauna is nevertheless moderately diverse. Some 117 species, including those identified here, have been reported thus far from the archipelago. The first major inventory of hydroids from the Hawaiian Islands was undertaken by Nutting (1905) after examination of a collection from a cruise of the United States Bureau of Fisheries steamer *Albatross* in 1902. In it, he identified 49 species, mostly from relatively deep waters, with 29 described as new. Before Nutting, Allman (1888) had described two species from Oahu in collections from HMS *Challenger*, and Hartlaub (1901) had reported one from Laysan Island. Later, surveys for invasive species (Coles *et al*. 1999a, b, 2002a, b, 2004, 2006, 2009; DeFelice *et al*. 2002; Menza & Monaco 2009; See *et al*. 2009; Carlton & Eldredge 2009, 2015), and accounts of hydroids predominantly from inshore locations (Cooke 1977; Calder 2010, 2020), added dozens more species to the faunal list of the islands. Other information exists in various reports on one or a few hydrozoans from the state (see Calder 2010: 5).

The hydroids of geographically isolated Hawaii consist largely of widespread species. Overall, affinities of the fauna are closer to species assemblages of the Indo-west Pacific than with those of the west coast of the Americas, as with most other groups of marine invertebrates in the state (Kay & Palumbi 1987). Meanwhile, previous reports of hydroids from the Northwestern Hawaiian Islands are limited in number. Most such records are based on the work of Nutting (1905) and more recently on studies of invasive species (DeFelice *et al.* 2002; Godwin *et al*. 2006; Menza & Monaco 2009; See *et al*. 2009).

The objective of this study was to investigate hydroids collected during the NOWRAMP 2002 cruise to the Northwestern Hawaiian Islands, contained within the Papahānaumokuākea Marine National Monument. The report complements two earlier papers (Calder 2010, 2020) on hydroids of Hawaii, largely comprising species inhabiting the main islands.

Materials and methods

Materials examined here were collected using SCUBA by one of us (AF) during the 2002 NOWRAMP (Northwestern Hawaiian Islands Reef Assessment and Monitoring Program) cruise, aboard R/V *Rapture*, to the Northwestern Hawaiian Islands (Fig. 1). Hydroids were present in collections from eight of the locations surveyed during the cruise, with the maximum depth sampled at each location in parentheses: Nihoa (23 m), French Frigate Shoals (25 m), Gardner Pinnacles (17 m), Laysan Island (16 m), Lisianski Island (22 m), Pearl & Hermes Atoll (26 m), Midway Atoll (19 m), and Kure Atoll (23 m). Initially preserved in formalin, these materials are now in 70% ethanol. Voucher specimens have been deposited in collections at the Bernice Pauahi Bishop Museum, Honolulu, and the Royal Ontario Museum, Toronto.

Accounts of each species include a synonymy list, information on type locality, data on examined material, remarks on taxonomy and nomenclature, and a summary of distribution records. Synonymy lists are limited to a citation of the publication in which a given species name was first made nomenclaturally available, to works providing original records of particular species in Hawaii, and to publications providing significant information on introduced and cryptogenic marine species of hydroids from the state. In a Reported Distribution section, only original records of a species from the Hawaiian archipelago are included. As well, a broad overview of records from other locations worldwide is provided. Line drawings were prepared with Koh-I-Noor Rapidograph pens and ink from pencil sketches made using a camera lucida. Photomicrographs were taken using a Zeiss Axioscop microscope. Illustrations of nematocysts, all to the same magnification, are from photomicrographs originally taken at ×1000.

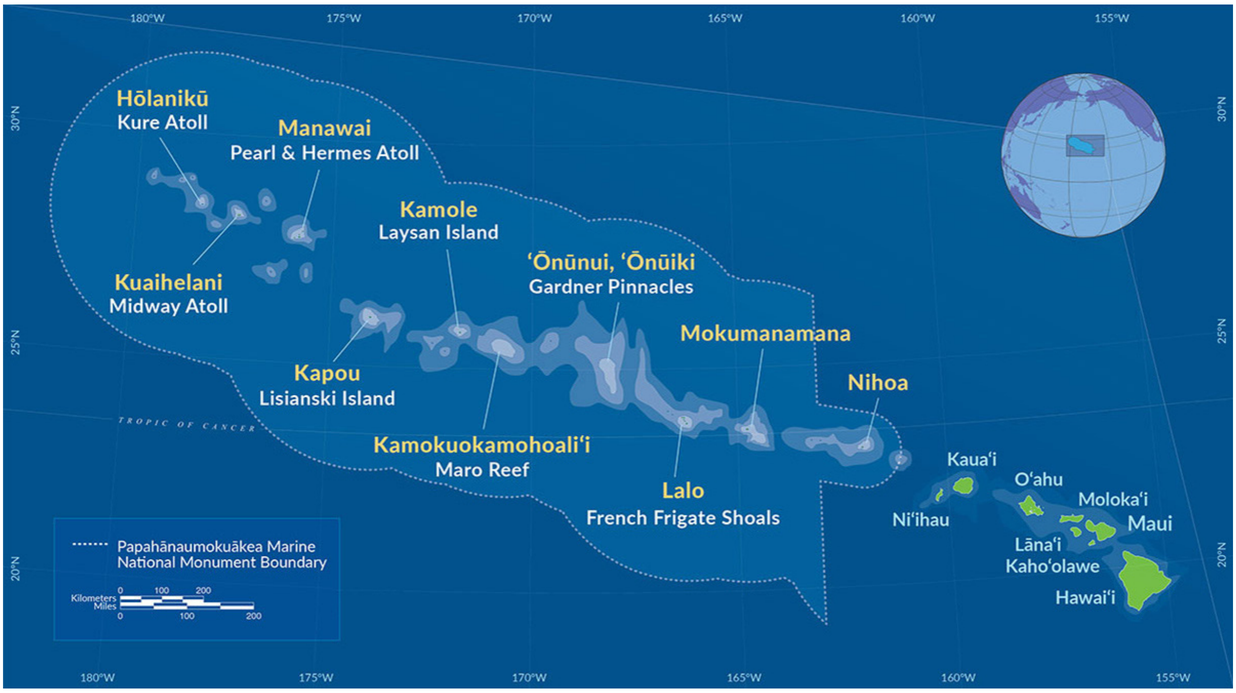

FIGURE 1. Map of the Northwestern Hawaiian Islands, with island names in both English and Hawaiian. Figure courtesy of Kaji Fujii, National Oceanographic and Atmospheric Administration.

Abbreviations used in this work refer to the following:

BPBM	Bernice Pauahi Bishop Museum (Honolulu, HI, USA)
ICZN	International Commission on Zoological Nomenclature; *International Code of Zoological Nomenclature. Fourth Edition* (International Commission on Zoological Nomenclature 1999)
NOWRAMP	Northwestern Hawaiian Islands Reef Assessment and Monitoring Program
ROMIZ	Royal Ontario Museum (Toronto, ON, Canada), Invertebrate Zoology collections
WoRMS	World Register of Marine Species (http://www.marinespecies.org, with content on Hydrozoa from the World Hydrozoa Database by Peter Schuchert (http://www.marinespecies.org/hydrozoa)

Systematic Account

Phylum Cnidaria Verrill, 1865

Subphylum Medusozoa Petersen, 1979

Class Hydrozoa Owen, 1843

Subclass Hydroidolina Collins, 2000

Order Anthoathecata Cornelius, 1992

Clade Capitata Kühn, 1913, *sensu stricto*

Family Pennariidae McCrady, 1859

Genus *Pennaria* Goldfuss, 1820

Pennaria disticha Goldfuss, 1820

Fig. 2a

Pennaria disticha Goldfuss, 1820: 89.—Hoover, 1998: 20, unnumbered figure; 2006: 20, unnumbered figure.—Coles *et al.*, 2002a: 318, 343; 2002b: 21, 25, 32; 2004: 22, 73; 2006: 489, 492, 494; 2009: 59, 69, 76, 82.—DeFelice *et al.*, 2001: 15, two unnumbered photographs; 2002: 25, 50.—Godwin *et al*. 2006: 27.—See *et al.*, 2009: 276, 281.—Calder, 2010: 63, fig. 43.—Miglietta *et al.*, 2015: 5; 2019: 86, 87.

Pennaria sp.—Edmondson, 1933: 23, figs 11, 12a; 1946: 24, figs 12, 13a.

Corydendrium splendidum Boone, 1938: 33, pl. 4.

Pennaria tiarella.—Edmondson & Ingram, 1939: 256.—Chu & Cutress, 1954: 9.—Josephson, 1961: 565.—Pardy & Lenhoff, 1968: 197, figs 1–3.—Banner, 1968: 21.—Mariscal & Lenhoff, 1969: 330.—Rees *et al.*, 1970: 309, figs 1, 2.—Reed, 1971: 48.—Pardy, 1971: 84, figs 1–3.—Rees, 1971: 119, figs 1, 2.—Long, 1974: 27.

Halocordyle disticha.—Cooke, 1977: 80, fig. 8.—Coles *et al.*, 1999a: 194, 205, 209; 1999b: 150.

Pennaria distachia.—Menza & Monaco, 2009: 1 [incorrect subsequent spelling].

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

Voucher material. Pearl & Hermes Atoll, 19.ix.2002, one colony fragment, 6 mm high, with a medusa bud, coll. A. Faucci, ROMIZ B5404.—French Frigate Shoals, 11.ix.2002, four colonies or colony fragments, to 10 cm high, with medusa buds, coll. A. Faucci, ROMIZ B5488.

Remarks. *Pennaria disticha* Goldfuss, 1820 has been reported numerous times from shallow tropical and temperate waters worldwide, although cryptic species seem certain to exist under the name (Miglietta *et al*. 2015, 2019). A taxonomic overview of the species in the Hawaiian Islands has been given earlier (Calder 2010).

The earliest record of *P. disticha* from Hawaii is based on Boone (1938, as *Corydendrium splendidum*), whose material was collected in Kaneohe Bay during 1928. It is now the most frequently reported hydroid species across the Hawaiian archipelago. DeFelice *et al*. (2001) noted that *P. disticha* is common as a fouling organism in harbours of the main islands, as well as in cracks, crevices, and protected areas of reefs. In the Northwestern Hawaiian Islands, it has been reported to date from Necker Island, French Frigate Shoals, Gardner Pinnacles, Maro Reef, Laysan Island, Lisianski Island, Pearl & Hermes Reef, Midway Atoll, and Kure Atoll (See *et al*. 2009). A record of its occurrence at Midway Atoll (Carlton & Eldredge 2009), based on DeFelice *et al*. (1998), could not be confirmed, although it has been reported from there by Godwin *et al*. (2006) and See *et al*. (2009).

Contemporary taxonomic accounts of *Pennaria disticha* are given in works by Calder (1988a, as *Halocordyle disticha*, 2010, 2013, 2019) and Schuchert (2006). DeFelice *et al*. (2001) reported that hydroid populations of the species in Hawaii are capable of inflicting a mild sting.

Reported Distribution. Hawaiian archipelago. Oahu: Kaneohe Bay (Edmondson 1933, 1935, as *Pennaria tiarella*; Boone 1938, as *Corydendrium splendidum*; Edmondson & Ingram 1939, as "probably *Pennaria tiarella*"; Josephson 1961, as *P. tiarella*; Banner 1968, as *P. tiarella*; Pardy & Lenhoff 1968, as *P. tiarella*; Mariscal & Lenhoff 1969, as *P. tiarella*; Rees *et al*. 1970, as *P. tiarella*; Pardy 1971, as *P. tiarella*; Rees 1971, as *P. tiarella*; Reed 1971, as *P. tiarella*; Coles *et al.* 2002a; Calder 2010; Miglietta *et al*. 2015, 2019); Pearl Harbor (Edmondson 1933, as *Pennaria* sp.; Long 1974, as *P. tiarella*; Cooke 1977, as *Halocordyle disticha*; Hoover 1998, 2006; Coles *et al*. 1999b, as *H. disticha*; Coles *et al*. 2009; Calder 2010; Miglietta *et al*. 2015, 2019); Ala Wai Harbor (Cooke 1977, as *H. disticha*; Coles *et al*. 1999a, as *H. disticha*; Calder 2010); Kewalo Basin (Cooke 1977, as *H. disticha*; Coles *et al*. 1999a, as *H. disticha*; Calder 2010; Miglietta *et al*. 2015, 2019); Honolulu Harbor (Cooke 1977, as *H. disticha*; Coles *et al*. 1999a, as *H. disticha*, 2009; Calder 2010); Lanai Lookout (Hoover 1998, 2006); Pearl Harbor (Coles *et al*. 1999b; Calder 2010; Miglietta *et al*. 2019); Waikiki (Coles *et al*. 2002b); Maunalua Bay (Coles *et al*. 2002b); Kuapâ Pond (Coles *et al*. 2002b); Keehi Lagoon/Marina (Coles 2009; Miglietta *et al*. 2015, 2019); Haleiwa (Miglietta *et al*. 2015, 2019).—French Frigate Shoals (DeFelice *et al*. 2002; Godwin *et al*. 2006; See *et al*. 2009).—Kauai: Nawiliwili Harbor Pier 2 (Coles *et al.* 2004); Marriott Hotel Reef (Coles *et al.* 2004, 2006); Port Allen Harbor Main Pier (Coles *et al.* 2004); Port Allen Reef (Coles *et al*. 2004); Port Allen Harbor (Coles *et al*. 2006); Hoai Bay (Coles *et al*. 2006).—Molokai: Hale O Lono Harbor Dock (Coles *et al*. 2004); Kaunakakai Dock (Coles *et al*. 2004).—Maui: Kahului Harbor Pier 1 (Coles *et al*. 2004); Kahului Harbor Pier 2 (Coles *et al*. 2004); Maalaea Small Boat Harbor (Coles *et al*. 2004); Mala Wharf (Coles *et al*. 2006); Maui (Miglietta *et al*. 2015, 2019).—Island of Hawaii: Kawaihae Reef (Coles *et al*. 2004, 2006); Kawaihae Harbor Main Pier (Coles *et al*. 2004); Hilo Harbor Pier 1 (Coles *et al*. 2004).—All of the main islands (DeFelice *et al*. 2001; Carlton & Eldredge 2009).—Laysan Island (Godwin *et al*. 2006; See *et al*. 2009).—Lisianski Island (Godwin *et al*. 2006; See *et al*. 2009; Calder 2010; Miglietta *et al*. 2015, 2019).—Pearl & Hermes Atoll (Godwin *et al*. 2006; See *et al*. 2009; Calder 2010; Miglietta *et al*. 2015, 2019).—Kure Atoll (Godwin *et al*. 2006; See *et al*. 2009).—Midway Atoll (Godwin *et al*. 2006; See *et al*. 2009).—Necker Island (See *et al*. 2009).—Gardner Pinnacles (See *et al*. 2009).—Maro Reef (See *et al*. 2009).—Northwestern Hawaiian Islands (Menza & Monaco 2009, as *Pennaria distachia*).

Elsewhere. Considered circumglobal in tropical and warm-temperate waters (Calder 2010), although cryptic species likely exist (Miglietta *et al*. 2015, 2019).

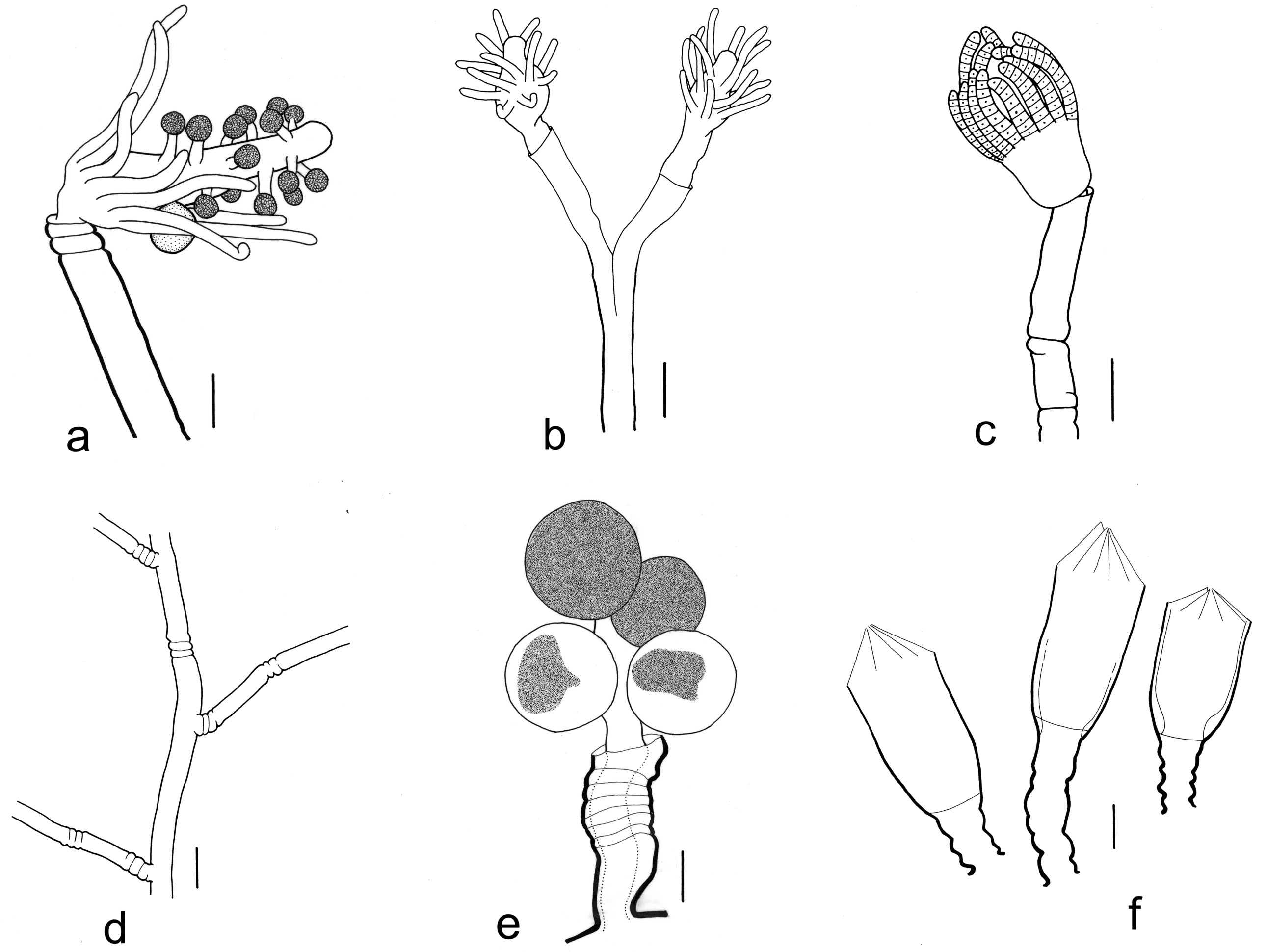

FIGURE 2. Pennariidae, Oceaniidae, Eudendriidae, and Phialellidae. a, *Pennaria disticha* Goldfuss, 1820, hydranth with a medusa bud and part of pedicel, Pearl & Hermes Atoll, ROMIZ B5404**.** Scale equals 0.2 mm. **b, *Turritopsis* sp.**, hydrocaulus with two hydranths, Midway Atoll, ROMIZ B5490. Scale equals 0.2 mm. **c, *Eudendrium merulum* Watson, 1985,** hydranth and part of pedicel, Nihoa, ROMIZ B5405. Scale equals 0.1 mm. **d, *Eudendrium merulum* Watson, 1985,** hydrocaulus and proximal ends of three branches, Nihoa, ROMIZ B5405. Scale equals 0.2 mm**. e, *Eudendrium merulum* Watson, 1985,** female gonophores, Nihoa Island, ROMIZ B5405. Scale equals 0.1 mm**. f. Phialellidae (undetermined),** three hydrothecae, Gardner Pinnacles, ROMIZ B5406. Scales equal 0.05 mm.

Family Sphaerocorynidae Prévot, 1959

Genus *Sphaerocoryne* Pictet, 1893

Sphaerocoryne bedoti Pictet, 1893

Sphaerocoryne bedoti Pictet, 1893: 10, pl. 1 figs 5, 6.—Calder, 2010: 67, figs 44, 45.

Type locality. Indonesia: Moluccas, Ambon (Pictet 1893).

Voucher material. Midway Atoll, on coral rubble, 20.ix.2002, one colony, up to 6 mm high, without medusa buds, coll. A. Faucci, ROMIZ B3830.

Remarks. A hydroid identified as *Sphaerocoryne bedoti* was described and illustrated earlier from the Hawaiian archipelago (Calder 2010), based in part on a specimen from Midway Atoll examined again here (ROMIZ B3830). Recent comments on the species exist in that account, in Schuchert (2010), and in Maggioni *et al*. (2021). Of particular interest in the work of Maggioni *et al.* is discovery of species with hydroids much like those of *S. bedoti*, including *Kudacoryne diaphana* Maggioni, in Maggioni *et al*., 2021 from the Red Sea, Saudi Arabia, and Maldives, *Euphysilla pyramidata* Kramp, 1955, an essentially circumglobal species, and *Euphysilla* sp. from the Caribbean Sea (Martinique and Panama). They noted that hydroids of *S. bedoti* were distinguishable in colouration (hypostome white or yellowish, with a bright red band below it; gastric cavity with broadest part transparent or yellowish, and whitish below) and in having medusa buds in large clusters. Also similar is the hydroid currently known as *Sphaerocoryne agassizii* (McCrady, 1859), although it is distinguished by medusa buds with only two opposite, prominently capitate tentacles.

Reported Distribution. Hawaiian archipelago. Midway Atoll (Calder 2010).
Elsewhere. Considered circumglobal in tropical and warm temperate waters (Calder 2010; Schuchert 2010).

Family Oceaniidae Eschscholtz, 1829

Genus *Turritopsis* McCrady, 1857

Turritopsis sp.

Fig. 2b

Turritopsis nutricula.—Cooke, 1977: 82, fig. 10.—Grovhoug & Rastetter, 1980: 252.—Coles *et al*., 2002a: 206, 31, 343.—Carlton & Eldredge, 2009: 33.
Turritopsis cf. *nutricula*.—Calder, 2010: 16, fig. 6.

Voucher material. Midway Atoll, on calcareous rubble, 23.ix.2002, one colony, 1.75 mm high, without gonophores, coll. A. Faucci, ROMIZ B5490.

Remarks. While species of the genus *Turritopsis* McCrady, 1857 from Hawaii and elsewhere across the Indo-Pacific region have earlier been commonly assigned to *T. nutricula* McCrady, 1857 (e.g., Kramp 1968; Millard & Bouillon 1973, 1974; Millard 1975; Cooke 1977; Hirohito 1988; Park 1993; Bouillon 1995; Schuchert 1996; Watson 1996; Kubota 2005; Calder 2010), molecular investigations contradict that identification. Such studies reveal the existence of a species complex in *T. nutricula* (Miglietta *et al*. 2007, 2019; Miglietta & Lessios 2009). Instead of being cosmopolitan in distribution, Miglietta *et al*. (2007) suggested that *T. nutricula* may be restricted to the western Atlantic Ocean. Little progress has yet been made in resolving the nomenclature of cryptic species within hydroids assigned to the species. As noted by Schuchert (2003), a likely valid species in the tropical Indo-west Pacific region is *T. chevalense* (Thornely, 1904), but others are of probable existence as well. For now, the sterile hydroid colony examined here is identified simply as *Turritopsis* sp.

Molecular phylogenetic studies also indicate that the family Oceaniidae Eschscholtz, 1829, as presently constituted, is polyphyletic (Prudkovsky *et al*. 2016; Schuchert 2016; Maggioni *et al.* 2017). Nevertheless, the type species of *Turritopsis* (*T. nutricula*) and that of *Oceania* Kölliker, 1853 (*O. armata* Kölliker, 1853), the type genus of the family, cluster in close proximity to each other (Prudkovsky *et al*. 2016; Schuchert 2016). Relationships of two other genera usually included in the family, *Rhizogeton* L. Agassiz, 1862 and *Turritopsoides* Calder, 1988b, appear to lie elsewhere. Species assigned to those genera, *R. nudus* Broch, 1910 and *T. marhei* Maggioni, Puce, Galli, Seveso & Montano, 2017, occur in clades remote from *O. armata* (Prudkovsky *et al.* 2016; Maggioni *et al*. 2017). Although substantial data gaps still exist in molecular assessments of the family, *Turritopsis* can confidently be included, with *Oceania*, in Oceaniidae.

Reported Distribution. Hawaiian archipelago. Oahu: Ala Wai Yacht Harbor, on stems of *Pennaria* (Cooke 1977, as *Turritopsis nutricula*).—Pearl Harbor, on test panels (Grovhoug & Rastetter 1980, as *T. nutricula*).—Kaneohe Bay, on test panels (Grovhoug & Rastetter 1980, as *T. nutricula*).—Kaneohe Bay from BPBM-D-457 (“Kaneohe Bay”), Coconut Island, Hawaii Institute of Marine Biology Pier, Kaneohe Yacht Club dock, MCB Fuel Dock, and SAG Harbor (Coles *et al*. 2002a, as *T. nutricula*).—Kaneohe Bay at Kaneohe Yacht Club dock, and Coconut Island and reef, shallow (Calder 2010, as *T.* cf. *nutricula*).

Elsewhere. The relationships and geographic distribution of the hydroid assigned to *Turritopsis* from Hawaii needs to be established by barcoding studies.

Family Eudendriidae L. Agassiz, 1862

Genus *Eudendrium* Ehrenberg, 1834

Eudendrium merulum Watson, 1985

Figs 2c–e, 3

Eudendrium merulum Watson, 1985: 200, figs 53–58.

Type locality. Australia: Victoria, Bass Strait, 0.5 km S of Clonmel Island, 38°45’S, 146°43’E, from wreck of streamer *Blackbird*, 6 m (Watson 1985).

Voucher material. Nihoa, 06.x.2002, three branched colonies or colony fragments, to 8 mm high, one with female gonophores, coll. A. Faucci, ROMIZ B5405.—Kure Atoll, on algae and calcareous rubble, 25.ix.2002, two mostly stolonal colonies, to 5 mm high, without gonophores, coll. A. Faucci, ROMIZ B5476.

Cnidome. Microbasic euryteles, small (Fig. 3a), (n=10): 6.4–7.0 µm long × 2.4–2.7 µm wide (undischarged)
Microbasic euryteles, large (Fig. 3b, c), (n=6): 19.0–20.8 µm long × 10.0–11.3 µm wide (undischarged)

Remarks. Approximately 80 species are currently recognized worldwide in the genus *Eudendrium* Ehrenberg, 1834. Hydroids of the group are easily distinguished in having monopodial growth, perisarc reaching to a groove at the base of relatively large, naked, urn-shaped hydranths, a typically flared or knob-shaped hypostome, and solid, filiform tentacles arranged more or less in a single whorl. Their gonophores are also distinctive, arising in a whorl around bases of the hydranths. Those of the male usually comprise a linear series of oval to nearly round chambers, while those of the female initially possess a spadix curving over a single ovum.

While hydroids of *Eudendrium* are distinctive, identification of species assigned to the genus can be particularly troublesome. Within the last few decades, the nematocyst complement and morphology of the gonophores, particularly those of the female, have been emphasized as characters of particular value in the morphological distinction of species.

In terms of the cnidome, all known species of *Eudendrium* have small microbasic euryteles. Most, but not all, of the others also have additional “complementary nematocysts”. While these often comprise nematocysts of an entirely different category, they may simply be microbasic euryteles of a noticeably larger size. The locations of the complementary nematocysts, and the shapes that aggregations of them sometimes create, are also of taxonomic value.

Complementary nematocysts in hydroids examined here consisted solely of large microbasic euryteles (Fig. 3a–c). On hydranths, these were scattered around the base above the perisarc groove and around the rim of the hypostome. In this overall character, they align with some 20 of the known species of the genus (Calder 2017: 34–36), and they conform with a so-called “*Eudendrium ramosum* (Linnaeus, 1758) group”.

Colonies from the present collection were small (up to 8 mm high) and stolonal to alternately branched. One of the specimens nevertheless had female gonophores, indicative of a species having small colonies. Developing female gonophores, with unbranched spadices, were observed on a nearly atrophied hydranth. Fully mature gonophores were present on a blastostyle, lacking tentacles and with expanded and wrinkled pedicel perisarc (Fig. 2e). The perisarc of the hydrocaulus and branches was smooth, except for a few annulations basally and with occasional irregular ones elsewhere. Although hydranths were mostly in poor condition, the best ones bore a single whorl of about 20–23 tentacles.

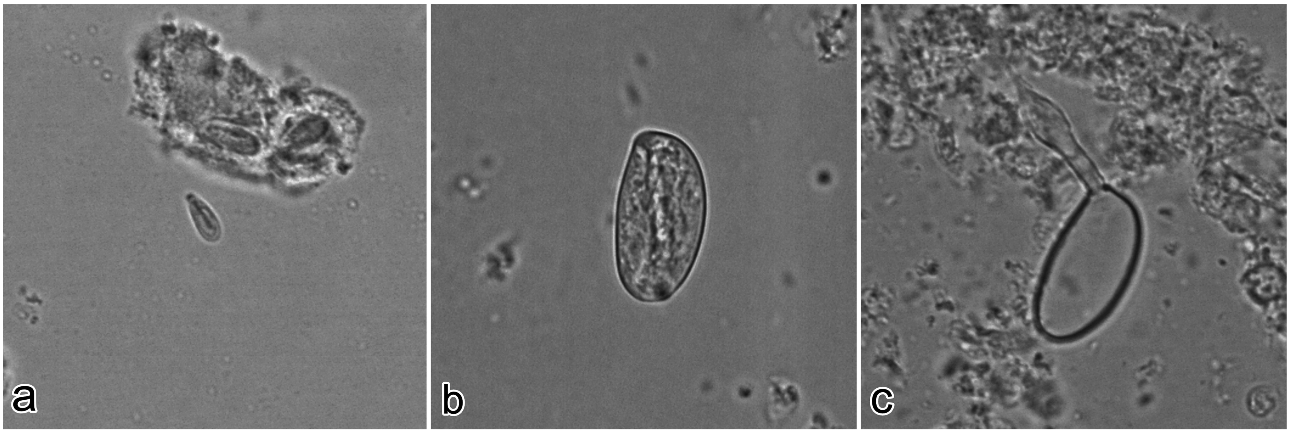

FIGURE 3. Eudendriidae. *Eudendrium merulum* Watson, 1985, nematocysts, material from Nihoa, ROMIZ B5405**. a,** microbasic eurytele, small**,** undischarged**. b,** microbasic eurytele, large, undischarged. **c,** microbasic eurytele, large, discharged.

The characters of these hydroids, together with the presence of large euryteles as complementary nematocysts, most closely resemble *E. merulum* Watson, 1985. While the trophosomes also resemble those of *E. generale* von Lendenfeld, 1885, female gonophores occur on atrophied rather than fully developed hydranths, as in that species (Watson 1985). In addition, complementary euryteles tend to be larger and their shafts are spinier in material examined here. Also similar in morphology are hydroids of *E. pusillum* var. *amoyicum* Hargitt, 1927 [=*E. generale amoyicum*], and *E. kirkpatricki* Watson, 1985. Colonies of the first of these species appear to be more profusely branched (Ling 1938; Xu *et al*. 2014a), while complementary nematocysts of the second are larger and possess a longer, less spiny shaft (Watson 1985). Hydroids from Fiji having a similar colony form were identified as *Eudendrium* sp. by Gibbons & Ryland (1989). Finally, stolonal colonies of this hydroid resemble *E. breve* Fraser, 1938a, but the complementary microbasic euryteles were much larger than even the largest of those reported in that species (13.0–14.6 × 5.8–6.8 µm) (Calder *et al*. 2021). While specimens from this collection have been assigned here to *E. merulum*, DNA analyses are needed to sort out the taxonomy of this and related species (Schuchert 2008).

Hydroids of *E. merulum* may be restricted to the Pacific Ocean. Schuchert (2008) found that hydroids identified as this species from the eastern Atlantic Ocean, Mediterranean Sea, and Black Sea all represented distinct genetic lineages, and that they likely differ from the Australian population.

Reported Distribution. Hawaiian archipelago. First record.

Elsewhere. Australia (Watson 1985); Yemen (Marques *et al*. 2000). As noted above, records of the species from the eastern Atlantic and adjacent seas are likely erroneous (Schuchert 2008).

Order Leptothecata Cornelius, 1992

Family Phialellidae Russell, 1953

Phialellidae (undetermined)

Fig. 2f

Voucher material. Gardner Pinnacles, on *Halopteris longibrachia*, nom. nov., 14.ix.2002, one colony, 0.35 mm high, without gonothecae, coll. A. Faucci, ROMIZ B5406.

Remarks. The single, sterile, stolonal colony examined here occurred as a tiny epizoite on the hydroid *Halopteris longibrachia*, nom. nov. Although referable to the family Phialellidae Russell, 1953, and likely to either *Oper-*

cularella Hincks, 1869 or *Phialella* Browne, 1902, neither the specific nor generic identity of the hydroid could be categorically established. Given a paucity of species-specific characters, and in the absence of gonophores, distinguishing hydroids of these two genera is difficult. The specimen from Gardner Pinnacles has therefore been identified here simply as Phialellidae (undetermined).

The trophosome of this hydroid resembles those of species such as ?*Phialella quadrata* (Forbes, 1848) from the Seychelles (Millard & Bouillon 1973) and *Opercularella* sp. from the coast of Ecuador (Calder *et al*. 2021). Some 10 species are currently assigned to *Phialella* in WoRMS (Schuchert 2021b). Distinguished by characters of the medusa stage, their trophosomes are likely all much alike. Notably, hydroids assigned to three species of *Phialella* from California were found to be essentially indistinguishable (Boero 1987), and Watson (1994b) reported that colonies of *P. quadrata* and *P. fragilis* (Uchida, 1938) were identical. A hydroid tentatively assigned by Galea *et al*. (2014) to *P. falklandica* Browne, 1902, the type species of *Phialella*, resembles that of *Opercularella lacerata* Johnston, 1847, but it differs in having gonothecae with rounded longitudinal ridges rather than smooth to wavy walls.

Morphologically similar to *P. quadrata*, *P. falklandica*, and related species are hydroids included in *Opercularella*, with some four species recognized in WoRMS (Schuchert 2021a). Indeed, molecular data in Maronna *et al*. (2016) indicate that *P. quadrata* is genetically close to *Campanularia lacerata*, the type species of *Opercularella*. Even closer to *P. quadrata* in their phylogram is *Opercularella pumila* S.F. Clark, 1875, misassigned to *Campanulina* Van Beneden, 1847 in that work and certain others (e.g., Cornelius 1995; Bouillon *et al*. 2006; Schuchert 2021a).

As presently defined, hydroids assigned to *Opercularella* are said to have fixed gonophores while those referred to *Phialella* liberate a medusa (Cornelius 1995; Bouillon *et al*. 2006). Should the two genera prove to be identical, the name *Opercularella* would have nomenclatural priority.

Reported Distribution. Hawaiian archipelago. First record.

Family Hebellidae Fraser, 1912

Genus *Hebella* Allman, 1888

Hebella furax Millard, 1957

Fig. 4a

Hebella furax Millard, 1957: 200, fig. 8A–C.
Anthohebella parasitica.—Coles *et al*., 2002a: 34, 318, 344; 2002b: 21, 25, 177 [not *Lafoea parasitica* Ciamician, 1880].
Hebella sp.—Calder, 2020: 205, fig. 1c.

Type locality. South Africa: False Bay, off Swartklip, 34°5.5′S, 18°39′E, 15–18 m (Millard 1957).

Voucher material. Midway Atoll, on *Antennella secundaria*, 23.ix.2002, one colony, 0.8 mm high, without gonothecae, coll. A. Faucci, ROMIZ B5407.—Gardner Pinnacles, on *Macrorhynchia phoenicea*, 14.ix.2002, one colony, 1.3 mm high, without gonothecae, coll. A. Faucci, ROMIZ B5408.—Midway Atoll, on *M. phoenicea* and *Aglaophenia whiteleggei*, 23.ix.2002, two colonies, to 1.0 mm high, without gonothecae, coll. A. Faucci, ROMIZ B5409.

Remarks. These hydroids closely resembled *Lafoea parasitica* Ciamician, 1880 (type locality: Adriatic Sea), *Hebella dyssymetra* Billard, 1933 (type locality: Gulf of Suez), and *H. furax* Millard, 1957 (type locality: South Africa). All three species have been reported from warm-waters of the Pacific Ocean. Vervoort & Vasseur (1977) noted that there was little to separate *H. dyssymetra* and *H. furax*, but both were upheld pending examination of additional material. With trophosomes that are all much alike, these species are most reliably distinguished by their gonosomes. Those of *L. parasitica* release "swimming gonophores" with gonads on the manubrium, those of *H. dyssymetra* liberate medusoids with gonads on radial canals, and those of *H. furax* release immature medusae (Boero *et al*. 1997). Based on the character of its gonophores, *L. parasitica* was referred by them to new genus, *Anthohebella* Boero, Bouillon & Kubota, 1997.

During identification of material examined here, *H. dyssymetra* was dismissed because hydrothecae were not markedly bent (Hirohito 1995), and hydrothecal pedicels were distinctly developed rather than being indistinct (Boero *et al*. 1997). Unlike *H. furax*, with occasional colonies said to be parasitic, all colonies in the collection were epizoites on plumularioid hydroids. Nevertheless, hydroids of the species are predominantly free-living, and Boero *et al*. (1997) suspected that records of *Anthohebella parasitica* in the Pacific were based instead on *H. furax*. Following their assumption, and considering the type locality and center of distribution of *A. parasitica*, specimens from Midway Atoll and Gardner Pinnacles have been assigned to *H. furax*. Hydroids identified as *Hebella* sp. from Hawaii by Calder (2020) are here considered conspecific.

The taxonomy of the family Hebellidae Fraser, 1912, and current concepts of genera assigned to it, remain unsettled. For example, life cycle studies (Migotto & de Andrade 2000) reveal that the adult medusa of *H. furax* shares characters with *Toxorchis kellneri* Mayer, 1910 [=*Staurodiscus kellneri*] (formerly in family Laodiceidae L. Agassiz, 1862). Peña Cantero *et al*. (2010) pointed to an affinity between *Anthohebella parasitica* and *Stegopoma plicatile* (M. Sars, 1863) (family Tiarannidae Russell, 1940). Marques *et al*. (2006) suggested that *Hebella* Allman, 1888 (type species: *Hebella striata* Allman, 1888) and *Anthohebella* (type species: *Lafoea parasitica* Ciamician, 1880) were either sister groups or congeneric. Investigations by Moura *et al*. (2012) and Maronna *et al*. (2016) indicate that *A. parasitica* is close genetically to *Hebella venusta* (Allman, 1877). Their studies also establish that the family Hebellidae as presently constituted is polyphyletic and in need of revision.

DNA barcoding of *H. striata* will be needed to better resolve the taxonomy of the genus *Hebella*, the family based on it, and affinities of species assigned to it. A detailed morphological account of the species has been given by Vervoort (1972). Also called for is a molecular analysis of *Campanularia mutabilis* Ritchie, 1907, type species of *Scandia* Fraser, 1912, to establish its systematic relation with *Hebella*.

Reported Distribution. Hawaiian archipelago. Oahu: Kaneohe Bay, Moku Manu Island (Coles *et al*. 2002a, as *Anthohebella parasitica*; Calder 2020, as *Hebella* sp.); Waikiki, Ala Wai buoy (Coles *et al*. 2002b, as *A. parasitica*).

Elsewhere. ?Japan (Stechow 1913b, as *Hebella parasitica*; Hirohito 1995, as *H. parasitica*); ?Indochina (Dawydoff 1952, as *H. parasitica*); South Africa (Millard 1957, and others); Seychelles (Millard & Bouillon 1973; Boero *et al*. 1997); Australia (Watson 1975); Moorea, French Polynesia (Vervoort & Vasseur 1977, as *H. parasitica*); Mediterranean Sea (Garcia Corrales *et al*. 1979, and others); Papua New Guinea (Boero *et al*. 1997); Indonesia (Di Camillo *et al*. 2008); Brazil (Migotto and de Andrade 2000; Oliveira *et al*. 2016, and others); Maldives (Gravier-Bonnet & Bourmaud 2012); St. Helena (Galea 2015).

***Hebella* sp.**

Fig. 4b

Voucher material. Midway Atoll, on a hydroid stem, 23 ix.2002, one colony, with two hydrothecae, 1.3 mm high, without gonothecae, ROMIZ B5493.

Remarks. This hydroid could not confidently be assigned to any known species of the family Hebellidae Fraser, 1912. Its characters are closest to those of the hebellid genera *Hebella* Allman, 1888 (type species: *Hebella striata* Allman, 1888) and *Anthohebella* Boero, Bouillon & Kubota, 1997 (type species: *Lafoea parasitica* Ciamician, 1880), purportedly distinguished by the morphology of their liberated gonophores. Although gonophores of *H. striata* are certainly medusoids or medusae (Hartlaub 1905), their anatomy after liberation has yet to be described. Thus, the molecular phylogenetic relationship of *H. striata* and *H. parasitica* needs study to determine whether the two nominal genera they nomenclaturally typify are indeed distinct. The species examined here has therefore been provisionally assigned to *Hebella*. Given the absence of gonosomes, our specimen is best not dealt with as an undescribed species. It is different from a hydroid reported earlier by Calder (2020) from Oahu as *Hebella* sp., identified above as *Hebella furax* Millard, 1957, and the species it represents is new to Hawaii.

In having a distinct, annulated pedicel, a deeply campanulate to almost cylindrical hydrotheca, hydrothecal walls with modest transverse annulations, a strongly flaring hydrothecal rim, and a ring of thickened perisarc at the hydrothecal base, this species most closely resembles *Hebella venusta* (Allman, 1877). However, it differs in having fewer and less distinct annulations on the hydrothecal wall. Moreover, its hydrothecae are larger (ca. 1000 µm long × 400 µm wide) than those of *H. venusta* as measured by Calder (1991a: to 650 µm long × 300 µm wide) and Galea (2010: 470–545 µm long × 265–315 µm wide). In terms of biogeography, *H. venusta* may be endemic to the Atlantic Ocean; records of it from the Indian Ocean (Ritchie 1910, as *Lafoea venusta*) and the Red Sea (Mergner & Wedler 1977) are regarded here as questionable.

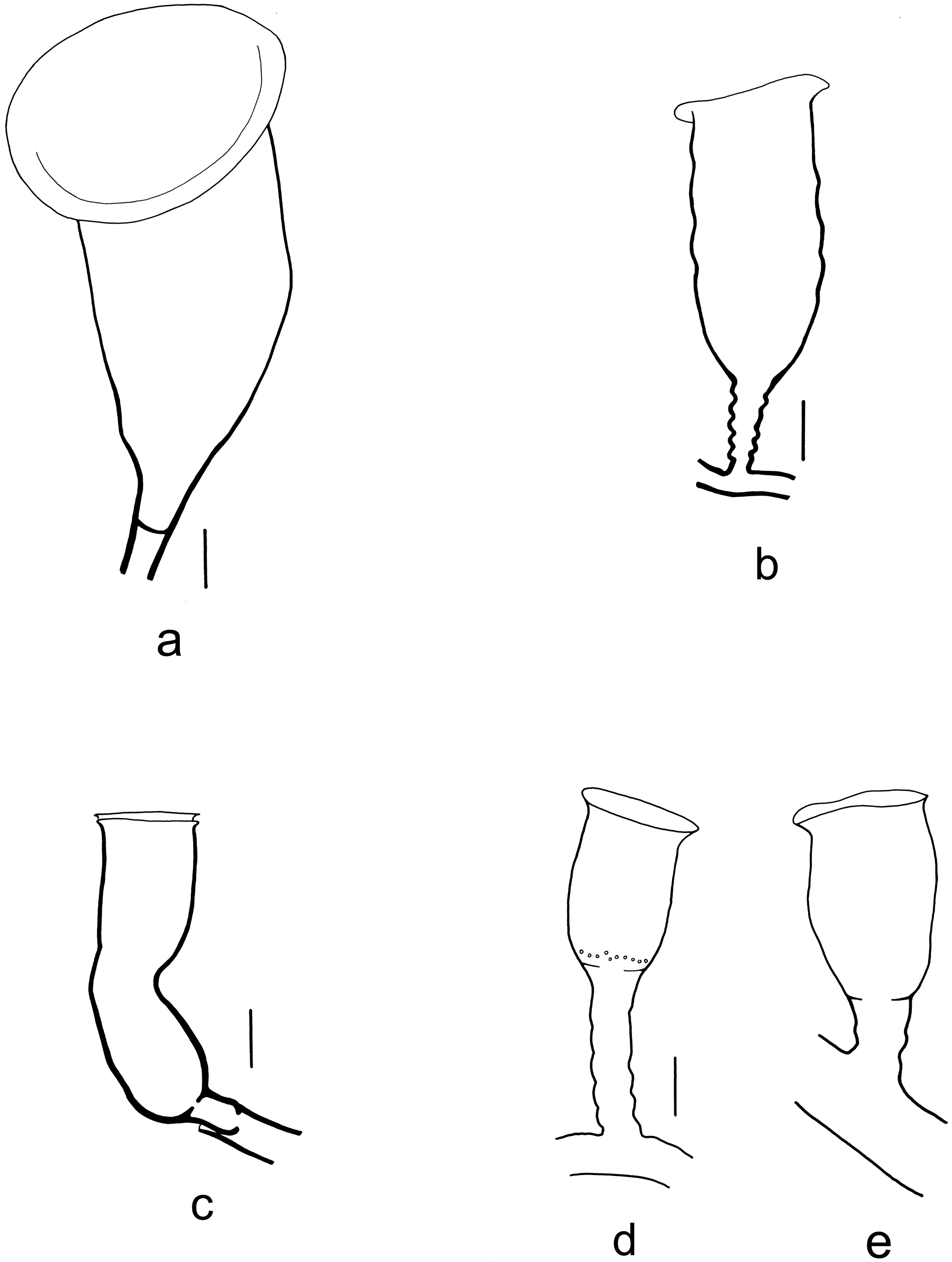

FIGURE 4. Hebellidae. a, ***Hebella furax*** **Millard, 1957**, hydrotheca, Midway Atoll, ROMIZ B5407. Scale equals 0.1 mm. **b.** ***Hebella*** **sp.,** hydrotheca, pedicel, and stolon, Midway Atoll, ROMIZ B5493. Scale equals 0.2 mm**. c,** ***Hebellopsis scandens*** **(Bale, 1888)**, hydrotheca and pedicel, Pearl & Hermes Atoll, ROMIZ B5413. Scale equals 0.1 mm. **d,** ***Hebellopsis sibogae*** **Billard, 1942**, hydrotheca and pedicel, Pearl & Hermes Atoll, ROMIZ B5410. Scales equal 0.1 mm. **e,** ***Hebellopsis sibogae*** **Billard, 1942**, hydrotheca and pedicel, Pearl & Herme**s** Atoll, ROMIZ B5411. Scale equal 0.1 mm. *e,*

In the molecular barcoding studies of Moura *et al*. (2012) and Maronna *et al*. (2016), *H. venusta* and *A. parasitica* have been shown to be very close. Gonothecae of the two also appear to be morphologically similar (Boero *et al*. 1997; Galea 2010), although the medusoid or medusa stage of *H. venusta* is unfortunately still unknown.

Reported Distribution. Hawaiian archipelago. First record.

Genus *Hebellopsis* Hadži, 1913

Hebellopsis scandens (Bale, 1888)

Fig. 4c

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

Type locality. Australia: Port Stephens; Port Jackson (Bale 1888, as *Lafoea scandens*).

Voucher material. Pearl & Hermes Atoll, on *Pasya heterodonta*, 28.ix.2002, three colonies, to 0.5 mm high, without gonothecae, coll. A. Faucci, ROMIZ B5413.

Remarks. *Hebellopsis scandens* Bale, 1888 is common as an epizoite on other hydroids, especially sertulariids and syntheciids. In typically curving from back to front of the substrate, its long, slender, and nearly cylindrical hydrothecae tend to be variously contorted.

Taxonomic and nomenclatural accounts of this species have been given in works including Calder (1991a), Boero *et al*. (1997, as *Hebella scandens*), and Vervoort & Watson (2003). In having a distinct diaphragm rather than a variably developed annular perisarcal thickening at the base of the hydrotheca, the species is assigned here to *Hebellopsis* Hadži, 1913 rather than to *Hebella* Allman, 1888. Meanwhile, confusion over the names *H. scandens* and *Hebella calcarata* (A. Agassiz, in L. Agassiz, 1862), as applied to this species, has been addressed in the works by Calder (1991a) and Boero *et al*. (1997).

Of the putative hebellids included in the molecular study of Maronna *et al*. (2016), *H. scandens* was closest genetically to *Staurodiscus gotoi* (Uchida, 1927). By contrast, it was distant from *Hebella venusta* (Allman, 1877) and *H. parasitica* (Ciamician, 1880). Similar results had been reported earlier by Moura *et al*. (2012).

A juvenile medusa has been described in the life cycle of *H. scandens* (e.g., Altuna 1996; Boero *et al*. 1997), but the identity of the adult stage is as yet unresolved. Thus, the nomenclature of this hydrozoan remains unsettled at the rank of both species and genus.

Reported Distribution. Hawaiian archipelago. First record.

Elsewhere. Considered circumglobal, temperate to tropical waters: western Pacific (Xu *et al*. 2014b, as *Hebella scandens*); central Pacific (Vervoort & Vasseur 1977, as *H. scandens* var. *contorta*; Coles *et al*. 2003); eastern Pacific (Fraser 1948, as *Hebella calcarata*); western Atlantic (Calder 2013); eastern Atlantic (Altuna 1996, as *H. scandens*); Indian Ocean (Millard 1975, as *H. scandens*).

Hebellopsis sibogae Billard, 1942

Fig. 4d, e

Hebellopsis sibogae Billard, 1942: 70, fig. 8.

Type locality. Indonesia: Siboga Expedition Sta. 129, Sulawesi, Karkaralong group, anchorage off Kawio and Kamboling, 04°40′19″N, 125°24′05″E (Billard 1942; van Soest 1976).

Voucher material. Pearl & Hermes Atoll, on *Macrorhynchia philippina*, 19.ix.2002, two hydrothecae and pedicels, to 0.55 mm high, without gonothecae, coll. A. Faucci, ROMIZ B5410.—Pearl & Hermes Atoll, on calcareous rubble, 28.ix.2002, one colony, 0.55 mm high, without gonothecae, coll. A. Faucci, ROMIZ B5411.—Kure Atoll, on sponge, 25.ix.2002, one colony, 0.6 mm high, without gonothecae, coll. A. Faucci, ROMIZ B5412.—Kure Atoll, 25.ix.2002, one colony, 1 mm high, without gonothecae, coll. A. Faucci, ROMIZ B5482. Gardner Pinnacles, on calcareous rubble, 14.ix.2002, one colony, 3.5 mm high, without gonophores, ROMIZ B5494.

Remarks. Hydroids examined here closely resemble those of *Lafoea gigas* Pieper, 1884 (type locality: Adriatic Sea), *Laomedea michaelsarsi* Leloup, 1935 (type locality: Tortugas, Florida, USA), and *Hebellopsis sibogae* Billard, 1942 (type locality: Indonesia). Morphological differences between the three are presently unclear. The first of these, well-known in the Mediterranean Sea and vicinity, has been reported infrequently elsewhere (Peña Cantero & García Carrascosa 2002; Galea 2008). The second has been reported from the western and eastern North Atlantic (Leloup 1935; Vervoort 1959). The only record of either one in the Pacific Ocean is that of *L. michaelsarsi* from Darwin Island, Galapagos Islands (Calder *et al*. 2003, as *Hebellopsis michaelsarsi*). Reports of *Hebella pocillum* (Hincks, 1869) from the west coast of North America by Fraser (1937a, 1947) have occasionally been included with question in the synonymy of *L. gigas* (e.g., Peña Cantero & García Carrascosa 2002, as *Scandia gigas*), but such inclusion seems erroneous. The third species is known only from Indonesia, based on the original account of Billard (1942). As for the first two, they may be conspecific (Galea 2008).

With reference to the generic assignment of these species, the well-known *L. gigas* has been referred at various times to *Lafoea* Lamouroux, 1821, *Hebella* Allman, 1888, *Scandia* Fraser, 1912, *Hebellopsis* Hadži, 1913, and *Croatella* Hadži, 1915. Its characters clearly differentiate it from *Lafoea* in having stolonal rather than erect colonies, and isolated rather than aggregated gonophores. Unlike the hebellid genera *Hebella*, *Scandia*, and *Anthohebella* Boero, Bouillon & Kubota, 1997, a well-developed hydrothecal diaphragm rather than a rounded annular thickening is present at the base of the hydrotheca. This species has usually been misassigned in current literature to *Scandia*, as *S. gigas*, but its gonosomal characters clearly differ from those of *S. mutabilis* (Ritchie, 1907), type species of that genus. Female gonothecae are pumpkin-shaped (Peña Cantero & García Carrascosa 2002) to spherical (Gravili *et al*. 2015) rather than sac-shaped, somewhat corrugated, and distally truncate (Fraser 1944), while those of the male are fusiform (Peña Cantero & García Carrascosa 2002) rather than resembling hydrothecae in shape and size (Fraser 1944). The species was assigned to *Hebellopsis* by Calder (2013) based on the character of its hydrothecal diaphragm, but that too is taken here to be incorrect given its unusual gonothecae. It diverges from the putative hebellid genera *Bedotella* Stechow, 1913a in lacking nematophores and nematothecae, and from *Halisiphonia* Allman, 1888 in lacking laterally flattened and fan-shaped gonothecae. Hydroids of *Staurodiscus* Haeckel, 1879 are as yet scarcely known.

In a molecular study by Maronna *et al*. (2016), "*Scandia gigas*" was considered a "rogue taxon" and included as "Leptothecata *incertae sedis*" because of its unexpected and isolated placement in phylograms. Excluded from Hebellidae in their analyses, it has been provisionally retained in the family here pending further study. In appearing to be genetically remote from other known hebellids, however, and in having what appear to be morphologically distinctive gonophores, we conclude that the species should be assigned at least to a different genus. It is therefore returned here to *Croatella*, a taxon originally based primarily on *L. gigas* but also provisionally including *Campanularia corrugata* Thornely, 1904 (Hadži 1915: 78). Hadži distinguished the genus largely by the morphology of its diaphragm, which was said to be two-layered with a peripheral cleft.

Given all this, specimens from the Northwestern Hawaiian Islands have been assigned, largely on zoogeographic grounds, to the western tropical Pacific hydroid *H. sibogae*. This is only the second collection record of the species. With no information yet available on either the gonosome or the molecular phylogeny of the species, however, it is kept here in *Hebellopsis* rather than being assigned to *Croatella*. The holotype (Van Soest 1976), on an alga (Billard 1942), is now at the Naturalis Biodiversity Center, Leiden, the Netherlands (ZMA.COEL.5224).

Reported Distribution. Hawaiian archipelago. First record.

Elsewhere. Indonesia (Billard 1942).

Family Clytiidae Cockerell, 1911

Genus *Clytia* Lamouroux, 1812

Clytia brevithecata (Thornely, 1900)

Fig. 5a

Campanularia brevithecata Thornely, 1900: 454, pl. 44 figs 8, 8a, b.

Type locality. Papua New Guinea: New Britain, Blanche Bay (Thornely 1900, as *Campanularia brevithecata*).

Voucher material. Nihoa, on calcareous rubble, 06.x.2002, one colony, 1.25 mm high, without gonothecae, coll. A. Faucci, ROMIZ B5414.—Pearl & Hermes Atoll, on *Halimeda* sp., 19.ix.2002, one colony, 3 mm high, without gonothecae, ROMIZ B5480.

Remarks. The hydroid of *Clytia brevithecata* (Thornely, 1900), type locality Papua New Guinea, appears indistinguishable morphologically from that of *Clytia hummelincki* (Leloup, 1935), type locality Bonaire, in the Caribbean Sea. Both have very shallow, cup-shaped hydrothecae with an entire margin, a subhydrothecal spherule, and unbranched pedicels with annulations at the base and occasionally elsewhere. Their gonothecae also seem indistinguishable. Connections between Indo-Pacific and Atlantic populations appear to exist, given Millard's (1966a, 1975) record of *C. hummelincki* from Agulhas Bank at the southern tip of Africa. Based on morphology, the two are taken here to be conspecific, with the name *C. brevithecata* having nomenclatural priority. Galea & Ferry (2015: 241) had suggested earlier that the two might be conspecific. Confirmation of their synonymy through DNA studies of topotypic material of the two would be germane. Of note already, however, hydroids identified as *C. hummelincki* from South Africa, Italy, and Belize are genetically close (Cunha *et al*. 2017). Synonyms or not, the name of the Pacific species has been adopted for the specimen recorded here from Nihoa.

Hydroids identified as *C. hummelincki* have been shown to be genetically distant from certain other species assigned to *Clytia* Lamouroux, 1812. Cunha *et al*. (2017) debated the ambiguous inclusion of the species in Clytiidae, but its medusa is typical of the group (Gravili *et al*. 2008) and it has been retained here in both the family Clytiidae and the genus *Clytia*.

The hydrozoan assigned the binomen *C. hummelincki* has been considered a likely invasive species in the Mediterranean (Gravili *et al*. 2008). Invasive or not, its known distribution has expanded considerably since the mid-20th century. From the original description of the species in the Caribbean Sea (Leloup 1935), its reported range now extends to the Florida Keys, USA (Deevey 1954), Ghana, west Africa (Buchanan 1957, as *Laomedea hummelincki*), Agulhas Bank, South Africa (Millard 1966a, 1975), Bermuda and adjacent banks (Calder 1991a, 2000), Brazil (Migotto 1996; Oliveira *et al*. 2016), the Mediterranean Sea (Boero *et al*. 1997; Gravili *et al*. 2008, 2015), the Galapagos Islands (Calder *et al*. 2003), Papua New Guinea (Boero & Bouillon, unpublished, cited in Gravili *et al*. 2008), Guadeloupe, Martinique, and Panama, in the Caribbean Sea (Galea 2008, 2013; Miglietta *et al*. 2018), Indonesia (Di Camillo *et al*. 2008), Cuba (Castellanos-Iglesias *et al*. 2009, 2018), Baa Atoll (Gravier-Bonnet & Bournaud 2012), and Belize (Cunha *et al.* 2017). A record from Pakistan (Moazzam & Moazzam 2006) was likely based on a misidentification of *C. edentula* Gibbons & Ryland, 1989. Records of *C. hummelincki* from the Indo-Pacific region (Calder *et al*. 2003; Di Camillo *et al*. 2008; Gravier-Bonnet & Bourmaud, 2012; Boero & Bouillon, unpublished) are taken here to have been based on *C. brevithecata*.

Reported Distribution. Hawaiian archipelago. First record.

Elsewhere. Circumglobal in tropical and warm-temperate waters (see Remarks above).

Clytia elsaeoswaldae Stechow, 1914

Fig. 5b, c

Clytia elsae-oswaldae Stechow, 1914: 125, fig. 4.
Clytia cf. *gracilis*.—Coles *et al*., 2009: 59, 68, 72, 76, 82, 85 [not *Clytia gracilis* (M. Sars, 1850)].
Clytia elsaeoswaldae.—Calder, 2020: 208, fig. 2b, c.

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

Voucher material. Midway Atoll, on algae, 23.ix.2002, one colony, 2 mm high, with a gonotheca, coll. A. Faucci, ROMIZ B5415.

Remarks. Hydroids from our collections corresponded closely with original descriptions of two warm-water species of the genus *Clytia* Lamouroux, 1812, *C. obliqua* (Clarke, 1907) and C. *elsaeoswaldae* Stechow, 1914. Colonies of both appear to be stolonal or mostly so rather than erect and branched, hydrothecae are relatively broad with rounded bases, and hydrothecal cusps slant to the right rather than being regularly triangular when viewed laterally (Clarke 1907; Stechow 1914; Lindner *et al*. 2011; Cunha *et al*. 2020). Gonothecae were lacking in Clarke's (1907) specimens of *C. obliqua*, but those of C. *elsaeoswaldae* had smooth to slightly undulating walls, a constriction below the truncated distal end, and they usually arose from the hydrorhiza (Lindner *et al*. 2011; Stechow 1914). Such characters correspond with material examined here. From these descriptions the two species seem much alike and, if conspecific, the binomen *C. obliqua* would have priority.

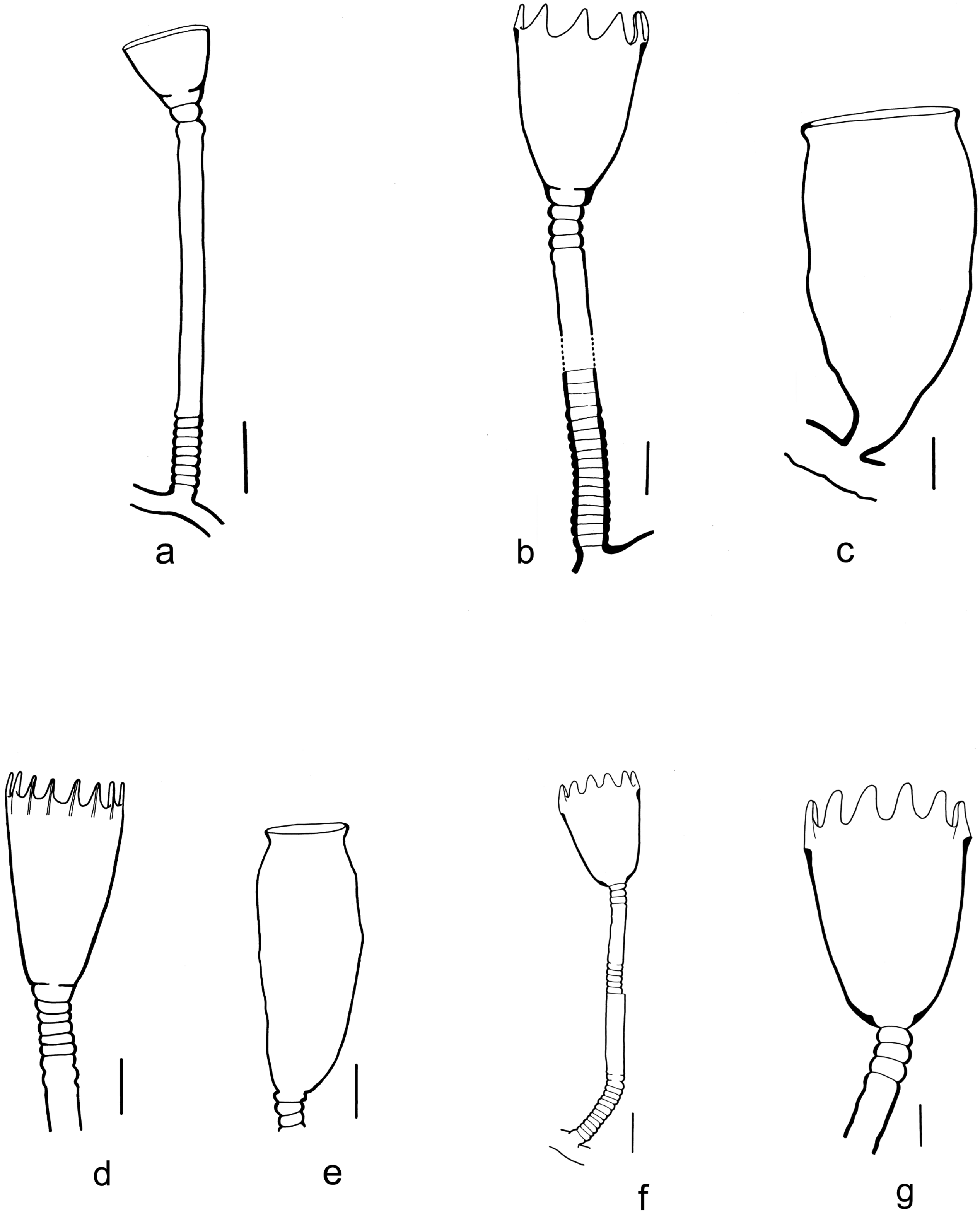

FIGURE 5. Clytiidae. a, ***Clytia brevithecata*** **(Thornely, 1900)**, hydrotheca and pedicel, Nihoa, ROMIZ B5414. Scale equals 0.2 mm. **b,** ***Clytia elsaeoswaldae*** **Stechow, 1914**, hydrotheca and pedicel, Midway Atoll, ROMIZ B5415. Scale equals 0.1 mm. **c,** ***Clytia elsaeoswaldae*** **Stechow, 1914**, gonotheca, Midway Atoll, ROMIZ B5415. Scale equals 0.1 mm. **d,** ***Clytia linearis*** **(Thornely, 1900)**, hydrotheca and distal end of pedicel, Gardner Pinnacles, ROMIZ B5418. Scale equals 0.2 mm. **e,** ***Clytia linearis*** **(Thornely, 1900)**, gonotheca, Laysan Island, ROMIZ B5417. Scale equals 0.2 mm. **f,** ***Clytia*** **cf.** ***noliformis*** **(McCrady, 1859)**, hydrotheca and pedicel, Pearl & Hermes Atoll, ROMIZ B5419. Scale equals 0.2 mm. **g,** ***Clytia*** **cf.** ***noliformis*** **(McCrady, 1859)**, hydrotheca and distal end of pedicel, Pearl & Hermes Atoll, ROMIZ B5419. Scale equals 0.1 mm.

However, the identity of *C. obliqua* is uncertain based on subsequent accounts of the species. After examining type material of the species, Cornelius (1982) concluded that it was conspecific with *C. linearis* (Thornely, 1900). That synonymy was followed in several other works (e.g., Gibbons & Ryland 1989; Calder 1991a; Watson 2000; Xu *et al*. 2014b; Wedler 2017; Choong *et al*. 2019). However, unlike material examined here, hydroids of *C. linearis* are mostly erect and branched, and their hydrothecal cusps are slender and regularly triangular, with an internal keel-like thickening of perisarc.

Meanwhile, Gibbons & Ryland (1989) discussed the identity of a hydroid from Fiji that closely resembled Clarke's (1907) illustration of *C. obliqua* (although hydrothecal cusps were shown with a slant to the left rather than the right in their illustrations). They nevertheless followed Cornelius (1982) in concluding that *C. obliqua* was conspecific with *C. linearis*, and identified their hydroids as *C. ?gracilis* instead. A syntype of *C. obliqua* (USNM 29616) examined during their deliberations was said to be branched, with tall hydrothecae. That seems at least somewhat at variance with the original account of Clarke (1907), who described the species as "…a small creeping form with peduncles from 1 mm to 1½ mm in height." The specimens portrayed in Clarke's illustrations were stolonal, and hydrothecae were not particularly deep. Moreover, unlike in *C. linearis*, Gibbons & Ryland observed no keel-like thickening on the inner edge of the cusps in the type. Given the conflicting accounts of *C. obliqua*, along with the lack of gonophores in Clarke's material, the species is regarded here as a *species inquirenda*. The type of *C. obliqua* at the NMNH was unavailable for examination during this study because of the pandemic outbreak in 2019. Hydroids examined here have therefore been assigned to C. *elsaeoswaldae*.

Clytia elsaeoswaldae is morphologically close to the much better-known *C. gracilis* (M. Sars, 1850), type locality Lofoten, Norway. Progress has been made in distinguishing the tropical to warm-temperate C. *elsaeoswaldae* from the boreal *C. gracilis* based on characters noted above (Lindner *et al*. 2011; Cunha *et al*. 2020). Records of *C. gracilis* from the tropical Pacific Ocean, including the Hawaiian Islands (Coles *et al*. 2009), are therefore believed to have been based on misidentifications of the present species. Its is likely much more widespread than currently recognized.

Reported Distribution. Hawaiian archipelago. Oahu: Pearl Harbor, West Loch entrance channel (Coles *et al*. 2009, as *Clytia* cf. *gracilis*; Calder 2020); Pearl Harbor, Hospital Point South (Coles *et al*. 2009, as *C.* cf. *gracilis*); Pearl Harbor, Rainbow Bay Marina, floating buoys and docks (Coles *et al*. 2009, as *C.* cf. *gracilis*; Calder 2020); Keehi Lagoon, marina docks (Coles *et al*. 2009, as *C.* cf. *gracilis*); Pearl Harbor, Rainbow Bay Marina, <1 m, on dock (Calder 2020).

Elsewhere. Tropical and warm-temperate waters of the western Atlantic, including the Caribbean Sea (Stechow 1914; Lindner *et al*. 2011; Calder 2019) and the warm eastern Pacific (Bryant & Arehart 2019, medusa stage). If *C. obliqua* is conspecific, the species has also been reported from Panama, Pacific coast (Clarke 1907), Japan (Fraser 1936; Hirohito 1969, 1995), California, USA (Fraser 1948), and Ecuador (Calder *et al*. 2019). A report of *C. obliqua* from the Mediterranean coast of France (Picard 1950) seems questionable.

Clytia linearis (Thornely, 1900)

Fig. 5d, e

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

Type locality. Papua New Guinea: New Britain, Blanche Bay (Thornely 1900, as *Obelia linearis*).

Voucher material. Laysan Island, on coralline algae, 18.ix.2002, three colonies or colony fragments, to 7 mm high, without gonothecae, coll. A. Faucci, ROMIZ B5416.—Laysan Island, on *Halimeda* sp., 17.ix.2002, one colony, 1.7 cm high, with gonothecae, coll. A. Faucci, ROMIZ B5417.—Gardner Pinnacles, 14.ix.2002, two colonies or colony fragments, to 6 mm high, without gonothecae, coll. A. Faucci, ROMIZ B5418.—Laysan Island, on *Halimeda* sp., 17.ix.2002, one colony, 3 mm high, with gonothecae, coll. A. Faucci, ROMIZ B5423.

Remarks. These records of *Clytia linearis* (Thornely, 1900) constitute the first reports of the species from the Hawaiian Islands. This well-known hydrozoan has been reported elsewhere from tropical and warm-temperate waters across the Indian and Pacific oceans [Millard 1975, as *Clytia gravieri* (Billard, 1904); Mergner 1977, as *Campanularia* (*Clytia*) *gravieri*; Mergner & Wedler 1977, as *C. gravieri*; Rees & Vervoort 1987; Gibbons & Ryland 1989; Hirohito 1995; Watson 2000; Schuchert 2003; Xu *et al*. 2014b; Mendoza-Becerril *et al*. 2020]. It is widespread in the Atlantic Ocean as well (e.g., Calder 1991a, 2013; Altuna Prados 1994; Migotto 1996; Lindner & Migotto 2002; Gravili *et al*. 2015; Oliveira *et al*. 2016).

Clytia linearis occurs in a clade linked to another that includes *C. hemisphaerica* (Linnaeus, 1767), taken to be conspecific with *C. johnstoni* (Alder, 1856), the type species of *Clytia* Lamouroux, 1812 (e.g., Govindarajan *et al*. 2006; Leclère *et al*. 2009; Lindner *et al*. 2011; Zhou *et al*. 2013; He *et al*. 2015; Maronna *et al*. 2016; Cunha *et al*. 2017, 2020). These molecular studies also confirm the wide geographic distribution of the species, with specimen vouchers from Brazil (São Sebastião), Italy (Torre Inserraglio) and the USA (Beaufort, North Carolina) being very close genetically. Analyses of specimens from the Indo-Pacific region are needed to confirm the putative worldwide distribution of the species.

The original date of publication of the work by Thornely, in which this binomen appeared (as *Obelia linearis*), has commonly been cited as both 1899 and 1900. Rees & Vervoort (1987: 199) indicated that its publication date was "v-1900". That coincides with the date "May, 1900" on the Title Page of Willey, A., *Zoological results based on material from New Britain, New Guinea, Loyalty Islands and elsewhere. Part IV* that included the paper by Thornely. Her work has therefore been cited herein as "Thornely (1900)". Another error in the literature warranting attention has been the frequent misspelling of Thornely's name as "Thorneley". A synonymy list of *C. linearis* has been given elsewhere (Calder 1991a).

Reported Distribution. Hawaiian archipelago. First record.

Elsewhere. Circumglobal, tropical to warm-temperate waters (Lindner & Migotto 2002).

Clytia cf. *noliformis* (McCrady, 1859)

Fig. 5f, g

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

Type locality. Bermuda: Castle Harbour, on a dead octocoral (based on a neotype; Opinion 1986, International Commission on Zoological Nomenclature 2002).

Voucher material. Pearl & Hermes Atoll, on *Aglaophenia whiteleggei* and adhering algae, 28.ix.2002, one colony, 2.8 mm high, without gonothecae, coll. A. Faucci, ROMIZ B5419.—Laysan Island, on *Halimeda* sp. and *Tridentata orthogonalis*, 17.ix.2002, two colonies, to 3 mm high, without gonothecae, coll. A. Faucci, ROMIZ B5420.

Remarks. These hydroids resemble *Clytia noliformis* (McCrady, 1859), and are provisionally assigned to that species here. Hydrothecae appear to be slightly longer, and embayments separating hydrothecal cusps somewhat deeper, than usual in *C. noliformis* (e.g., Nutting 1915; Calder 1991a, 2013). As such, they are essentially identical to specimens identified as *C. noliformis* from the tropical eastern Pacific by Calder *et al*. (2021). While hydroids from both locations also resemble *Orthopyxis crenata* (Hartlaub, 1901) in hydrothecal outline, they differ from that species in having thinner hydrothecal walls, deeper cusps, and regularly annulated rather than sinuous pedicels. When present, gonosomes readily distinguish the two as well, with *C. noliformis* liberating a free medusa and *O. crenata* releasing a medusoid. However, our material was sterile.

Lindner & Migotto (2001) discovered an unusual category of nematocysts in *C. noliformis*, the merotrichous isorhiza. Nematocysts resembling them in shape and size were present in specimens examined here, but all were undischarged and their identity could not be determined with certainty.

Characters of both hydroid and medusa stages, as well as DNA barcoding (e.g., Maronna *et al*. 2016), support the inclusion of *C. noliformis* in the genus *Clytia* Lamouroux, 1812. To date, no genetic comparisons have been undertaken of hydroids assigned to the species from the Atlantic and Pacific or Indian oceans. Past uncertainty over the specific identity of *C. noliformis* has been resolved by the designation of a neotype (International Commission on Zoological Nomenclature 2002). The type locality of the species is Bermuda.

Clytia noliformis is a widely distributed species in warm waters of the Atlantic Ocean (e.g., Nutting 1915; Fraser 1944; Lindner & Migotto 2002; Calder 2013; Galea 2013; Gravili *et al*. 2015; Oliveira *et al*. 2016), and it is a major epibiont there on pelagic *Sargassum* (Ryland 1974; Calder 1991a; 1995; Mendoza Becerril *et al*. 2020). The species has been recorded earlier in the Pacific from the coast of Ecuador (Fraser 1948; Calder *et al*. 2021), from Guam (Kirkendale & Calder 2003), the Korea Strait (Lee *et al*. 2018, 18S rDNA sequences of plankton) and from

Tahiti (Pearman *et al*. 2020, metabarcoding of plankton). A record of it from Chile by Leloup (1974) was discounted by Galea and Schories (2012) as an unidentified species of *Clytia*. In the Indian Ocean, records of it exist from India (Leloup 1932; Panikkar & Aiyar 1937; Mammen 1965; Sarma 1974, 1975; Pati *et al*. 2014, 2015), the Andaman and Nicobar Islands (Leloup 1932; Deepa *et al*. 2015); Myanmar (Leloup 1932), Madagascar (Gravier 1970, Gravier-Bonnet 1999), La Réunion (Bourmaud 2003) and Pakistan (Moazzam & Moazzam 2006). Collections from the Northwestern Hawaiian Islands constitute the first records of *C. noliformis*, or of a species resembling it, in the central North Pacific Ocean.

Reported Distribution. Hawaiian archipelago. First record.

Elsewhere. Considered circumglobal in warm-temperate to tropical waters: western Pacific (Kirkendale & Calder 2003); eastern Pacific (Fraser 1948; Calder *et al*. 2021), western Atlantic (Calder 2013; Oliveira *et al*. 2016); eastern Atlantic (Faucci & Boero 2000); Indian Ocean (Mammen 1965; Bourmaud 2003).

Family Haleciidae Hincks, 1869

Genus *Halecium* Oken, 1815

Halecium sp.

Fig. 6a, b

Voucher material. Pearl & Hermes Atoll, on calcareous rubble, 28.ix.2002, two colonies or colony fragments, to 4 mm high, without gonothecae, coll. A. Faucci, ROMIZ B5421.—Nihoa, on calcareous rubble, 06.x.2002, one colony, 9 mm high, without gonothecae, coll. A. Faucci, ROMIZ B5422.

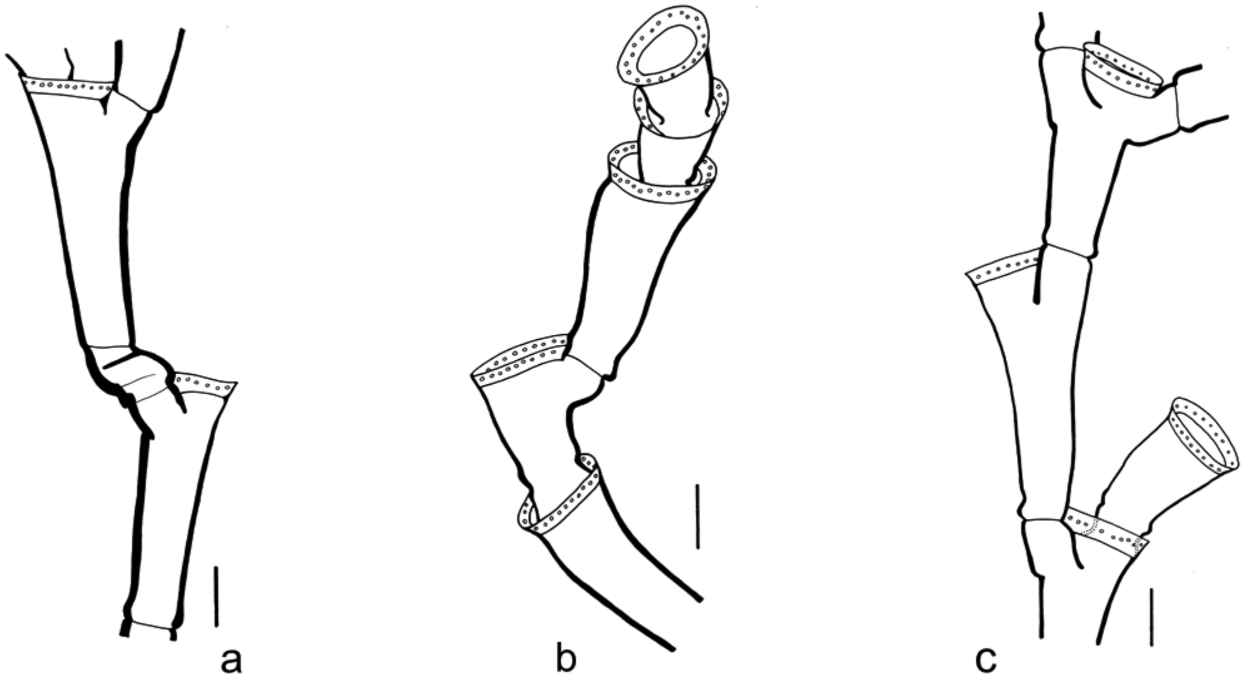

FIGURE 6. Haleciidae. a, *Halecium* sp., part of colony with two hydrothecae, Pearl & Hermes Atoll, ROMIZ B5421. Scale equals 0.1 mm. **b, *Halecium* sp.**, part of colony with five hydrothecae, Pearl & Hermes Atoll, ROMIZ B5421**.** Scale equals 0.1 mm. **c, *Nemalecium lighti* (Hargitt, 1924)**, part of hydrocaulus, with four hydrothecae, Kure Atoll, ROMIZ B5424**.** Scale equals 0.1 mm.

Remarks. In overall colony form, hydroids examined here resemble those identified as *Halecium* sp. 2 from Fiji by Gibbons & Ryland (1989). Their colonies, collected from both the Suva barrier reef and the Great Astrolabe reef, were rarely more than 5 mm high. Ours were also small, attaining a maximum height of 9 mm. Likewise of similar morphology are hydroids identified as *Halecium lankesterii* (Bourne, 1890) from locations including the tropical west coast of Africa (Vervoort 1959) and South Africa (Millard 1975). However, hydranths of that species may contain zooxanthellae (Schuchert 2005), unlike those examined here. Moreover, that species, originally described from Plymouth, UK, seems unlikely to occur in the tropical central Pacific. Another allied species is *H. plicatum* Galea, in Galea & Ferry, 2015 from Martinique in the Caribbean Sea. Unlike in that species, no internal pegs of perisarc were present in the hydrorhiza. *Nemalecium lighti* (Hargitt, 1924), common in Hawaii, was discounted as a possibility because both nematodactyls and large pseudostenotele nematocysts were absent. Given the absence of gonophores, and especially those of the female, these hydroids could not be positively identified.

Reported Distribution. Hawaiian archipelago. First record.

Elsewhere. ?Fiji (Gibbons & Ryland 1989, as *Halecium* sp. 2).

Genus *Nemalecium* Bouillon, 1986

Nemalecium lighti (Hargitt, 1924)

Fig. 6c, pl. 4, fig. 13

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*., 1999a: 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; 2020: 214, fig. 4g, h.

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

Voucher material. Kure Atoll, on algae and detached, 25.ix.2002, three colonies or colony fragments, to 1.6 cm high, without gonothecae, coll. A. Faucci, ROMIZ B5424.

Remarks. *Nemalecium* Bouillon, 1986 is a remarkable genus of hydroids. Its species are readily distinguished by having 1–2 curved, finger-like nematodactyls (Bouillon 1986) in addition to typical tentacles in the tentacular whorl of the hydranth. Immense pseudostenotele nematocysts (>25 µm long) are borne on these nematodactyls. To date, two species, *N. lighti* (Hargitt, 1924) and *N. gracile* Galea, Ferry & Bertot, 2012, have been described and assigned the genus. Of these, only *N. lighti* has been reported to date from the Pacific and Indian oceans, although undescribed species are believed to occur there (Gravier-Bonnet & Migotto 2000; Gravier-Bonnet & Bourmaud 2006, 2012; Di Camillo *et al*. 2008; Galea *et al*. 2012; Boissin *et al*. 2018). Records of *N. gracile* to date are restricted to the Atlantic Ocean, while *N. lighti* is taken to be circumglobal in shallow, warm waters. In Hawaii, the species is well-represented in nearshore habitats (Calder 2020). It was misidentified in early records from the islands as *Halecium beanii* (Johnston, 1838), a species inhabiting cool to cold rather than tropical waters (Fraser 1947; Cornelius 1995a, Schuchert 2005; Antsulevich 2015). Moreover, those first Hawaiian reports were of a species that was venomous (De Oreo 1946; Chu & Cutress 1954). *Nemalecium lighti* is known to sting humans (Marques *et al*. 2002; Santhanam 2020), while *H. beanii* is likely innocuous.

Taxonomically, Maronna *et al*. (2016) disputed the inclusion of *Nemalecium* in Haleciidae Hincks, 1869 based on molecular data, referring it instead to the order Plumupheniida Maronna *et al*., 2016. Until its family-group affinities are resolved, however, we continue to assign it to Haleciidae Hincks, 1869 given its haleciid-like morphological characters.

Recent reviews of *N. lighti* have been given elsewhere (Calder 2019; Calder *et al*. 2019).

Reported Distribution. Hawaiian archipelago. Oahu: near Honolulu, human envenomations (De Oreo 1946, as *Halecium* (*beani*?)); Maunalua Bay, on rubble (Cooke 1977, as *H. beani*); Barbers Point Harbor, barge pier (Coles *et al*. 1999, as *Halecium* sp.); Honolulu Harbor, wood block, coll. 1945, Bishop Museum, BPBM-D-260 (Coles *et al*. 1999, as *Halecium* sp.; Carlton & Eldredge 2009, as *H. beanii*); Kaneohe Bay, coll. 1963, Bishop Museum, BPBM-D-349 (Coles *et al*. 2002a, as *Halecium* sp.); Kaneohe Bay, Sag Harbor (Coles *et al*. 2002a, as *Halecium* sp.); Pearl Harbor, entrance channel (Coles *et al*. 2009, as *Halecium* sp.); Pearl Harbor, West Loch entrance channel (Coles *et al.* 2009, as *Halecium* sp.); Pearl Harbor, Hospital Point south (Coles *et al.* 2009, as *Halecium* sp.); Pearl Harbor, Utah Memorial (Coles *et al.* 2009, as *Halecium* sp.); Pearl Harbor, Hawaiian Electric Company discharge (Coles

et al. 2009, as *Halecium* sp.); Honolulu Harbor, Piers 40–41 (Coles *et al.* 2009, as *Halecium* sp.); Keehi Lagoon, marina docks (Coles *et al.* 2009, as *Halecium* sp.); Keehi Lagoon, barge wreck (Coles *et al.* 2009, as *Halecium* sp.); Keehi Lagoon, stream mouth (Coles *et al.* 2009, as *Halecium* sp.); north shore, in alphaeid crevices on corals (Calder 2010).—Hawaiian Islands: no specific location (Chu & Cutress 1954, as *H. beani*).—Kauai: Nawiliwili Harbor (Coles *et al*. 2004, as *Halecium* sp.).—Molokai: Kaunakakai main dock (Coles *et al*. 2004, as *Halecium* sp.).—Maui: Kahului Harbor Pier 1 (Coles *et al*. 2004, as *Halecium* sp.).
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 affinicostata, sp. nov.

Figs 7a–e, 8

Sertularella costata.—Calder *et al*., 2003: 1190, fig. 14a, b [not *Sertularella costata* Leloup, 1940].

Type locality. Ecuador: Galapagos Islands, Darwin Island, within SCUBA depth, on barnacle cluster (Calder *et al*. 2003, as *Sertularella costata*).

Etymology. The specific name is derived from the Latin adjective *affinis* (akin to) and the name *costata*, given its resemblance to *Sertularella costata*.

Voucher material. HOLOTYPE: Ecuador: Galapagos Islands, Isla Darwin, SCUBA depth, on barnacle cluster, 26 January 1999, one colony, 1.5 mm high, with gonothecae, coll. K. Collins, ROMIZ B3339.

PARATYPES: Ecuador: Galapagos Islands, Cousin Rock, 10 m, on sponge, 17 June 2001, one colony, 5.2 mm high, without gonothecae, coll. D. Calder, ROMIZ B3409.—Ecuador: Galapagos Islands, Marchena Island, Punta Espejo, ca. 8 m, 18 June 2001, four colonies, to 5 mm high, without gonothecae, coll. L. Garske, ROMIZ B3418.—French Frigate Shoals, on calcareous rubble, 13.ix.2002, one colony, 2 mm high, without gonothecae, coll. A. Faucci, ROMIZ B5486.

OTHER MATERIAL: Ecuador: Galapagos Islands, Wolf Island, 6 m, on algae, November 1992, two colonies, to 0.55 mm high, without gonothecae, coll. P. Humann, ROMIZ B3315.—Ecuador: Galapagos Islands, Wolf Island, on stolon of *Aglaophenia* sp., 25 January 1999, one colony, 1.1 mm high, without gonothecae, coll. J. Mallinson, ROMIZ B3318.

Description. Holotype colony unbranched, diminutive, with cauli reaching 1.5 mm high, arising from a hydrorhiza overgrowing cluster of small barnacles. Paratype colonies unbranched to occasionally with a branch or two, with cauli reaching 5.2 mm high, overgrowing a sponge. Basal stolons without internal pegs, diameter 59–83 µm; cauli mostly erect, caulus bearing a maximum of three hydrothecae in holotype, occasionally with a single hydrotheca borne on a short internode in parts of colony, paratypes with as many as 13 cauline hydrothecae (ROMIZ B3418). Hydrocaulus monosiphonic, nearly straight to irregular, length of first internode from insertion with hydrorhiza to base of first hydrotheca 0.14–0.35 mm, smooth to slightly wrinkled but without regular annulations, expanding gradually in circumference distally, hydrocaulus beyond first hydrotheca divided into typically short internodes, with first of these growing out directly from base of hydrotheca without nodes or annulations, more distal internodes separated by oblique nodes sloping alternately in opposite directions; internodes 322–423 µm long, 73–88 µm wide at nodes, 128–151 µm wide at base of hydrotheca, often with an annulation or slight swelling at proximal end, mostly smooth elsewhere, widening gradually from proximal end to base of hydrotheca, then tapering again to distal node, every internode bearing a hydrotheca; perisarc of moderate thickness. Hydrothecae sessile, alternate, typically biseriate but sometimes given off in multiple planes, quite deep, barrel-shaped, extending upwards and outwards, arranged alternately on opposite sides of hydrocaulus, adnate to internode for 1/3 or less of their length, with axis oblique to that of hydrocaulus; hydrothecal walls with about 10–14 sharp-edged horizontal ridges, widest near mid-point, tapering towards proximal and distal ends, narrowest at base, slightly constricted just below margin, then expanding to rim, length abcauline wall 338–377 µm, length adcauline wall adnate 72–99 µm, length adcauline wall free 279–310 µm, maximum diameter 189–218 µm, both adcauline and abcauline walls convex over much of their length, slightly concave at distal end; hydrothecal base 90–118 µm wide. Hydrothecal rim quadrangular, with four distinct, pointed, equally developed cusps separated by shallow embayments, no evidence of renovations in present material; hydrothecal orifice 150–183 µm wide; hydrothecal cavity enclosed by an operculum of four triangular valves; submarginal cusps three, one being abcauline and two latero-adcauline. Hydranths with an abcauline diverticulum.

Gonophores fixed sporosacs. Gonothecae of holotype colony male, containing spermatocytes, borne on a short, smooth pedicel arising from hydrorhiza or from base of hydrocaulus adjacent to a hydrotheca, nearly circular in cross-section, elongate-oval in lateral view, with rounded base and distal taper to a narrow neck, 0.8–1.0 mm long from base to orifice, maximum diameter 0.45–0.60 mm; margin entire, 0.15–0.18 mm wide, orifice round or nearly so. Gonothecal walls with seven to eight transverse, rounded ridges, those at distal end prominently developed, those at proximal end flattened, less pronounced; perisarc quite thick.

Remarks. Of the many described species of *Sertularella* Gray, 1848, these hydroids resemble several in a group bearing numerous sharp-edged horizontal ridges around walls of the hydrothecae. Amongst them, it appears closest to *S. costata* Leloup, 1940, originally described from Sagami Bay, Japan. The hydroid examined here is nevertheless readily distinguished from that species in having fewer ridges, with ca. 10–14 instead of ca. 20 (Leloup, 1940; Hirohito 1983, 1995). Its hydrothecae also differ in being barrel-shaped rather than distinctly tapered distally, and a smooth part just below the rim is more elongated. Moreover, the basal-most internode of the hydrocaulus is typically short rather than forming a long, slender, smooth peduncle as in *S. costata*, and cauline internodes are shorter and thicker. Given these differences, the hydroid is considered distinct from *S. costata*, as described by Leloup (1940) and Hirohito (1983, 1995), and from other known species of *Sertularella*. It has therefore been described here as new, under the binomen *S. affinicostata*. Of note, specimens from French Frigate Shoals are morphologically indistinguishable from colonies identified as *S. costata* from the Galapagos Islands by Calder *et al*. (2003). Those specimens, like the colony examined here, differ from *S. costata* in the characters noted above, and are taken here to have been misidentified. All are taken to be referable to the same species, *S. affinicostata*.

In being sterile, the single colony from French Frigate Shoals has been designated as a paratype (ROMIZ B5486). Selected as the holotype (ROMIZ B3339) is a fertile colony of the species from Darwin Island, Galapagos Islands, erroneously assigned to *S. costata* by Calder *et al*. (2003). Additional paratypes include previously unrecorded specimens from the Galapagos (ROMIZ B3409, ROMIZ B3418) in collections at the ROM. Cauli of these colonies are noteworthy in being taller (to 5.2 mm vs. 2 mm high), and they bear more hydrothecae (as many as 13 vs. 5) than those from either Darwin Island (ROMIZ B3339) or French Frigate Shoals (ROMIZ B5486). Other specimens from the Galapagos Islands (ROMIZ B3315, ROMIZ B3318), assigned to *S. costata* by Calder *et al*. (2003) but here considered conspecific with *S. affinicostata*, are too miniscule to be considered adequate type material.

Similar hydrothecal ornamentation appears on the hydrothecal walls of several other species of *Sertularella*, including *S. mirabilis* Jäderholm, 1896 and *S. sinensis* Jäderholm, 1896. Hydroids of those species differ in morphology from S. *affinicostata*, with colonies of *S. mirabilis* forming three-dimensional lattices and resembling sponges, and those of *S. sinensis* being bushy (Jâderholm 1896; Vervoort 1993; Hirohito 1995; Schuchert 2015). Stems of both species diverge from those of the hydroids described here in being repeatedly branched, and their colonies are larger (to 5 cm or more high). *Sertularella crenulata* Nutting 1905, a species originally described from Hawaii, differs in having finer and more numerous hydrothecal ridges (>30). Its colonies are also significantly larger (to 7.5 cm high) and more robust, with basally polysiphonic cauli (Nutting 1905, Vervoort 1993). Two tropical western Pacific species, *S. paucicostata* Vervoort, 1993 and *S. pseudocostata* Vervoort, 1993, are immediately distinguishable from *S. affinicostata* in lacking intrathecal cusps. Their hydrothecae are also considerably larger, with a total depth × maximum diameter of 715–825 µm × 305–390 µm in *S. paucicostata*, and 1105–1300 µm × 540–585 µm in *S. pseudocostata*. Others of the genus with similar hydrothecal ornamentation include *S. patagonica* (d'Orbigny, 1842), with 6–8 transverse ridges, *S. peculiaris* Leloup, 1935, with about five ridges, *S. helenae* Vervoort, 1993, with 8–9 ridges encircling cylindrical hydrothecae, and *S. fraseri* Galea, 2010, with 5–6 ridges.

Sertularella affinicostata is unusual in being a species from the Hawaiian Archipelago that is currently known elsewhere only from the eastern Pacific rather than the Indo-west Pacific region. Both poorly known and easily overlooked, it undoubtedly occurs elsewhere in the tropical Pacific Ocean.

Reported Distribution. Hawaiian archipelago. First record.

Elsewhere. Galapagos Islands, Wolf and Darwin islands (Calder *et al*. 2003, as *Sertularella costata*).

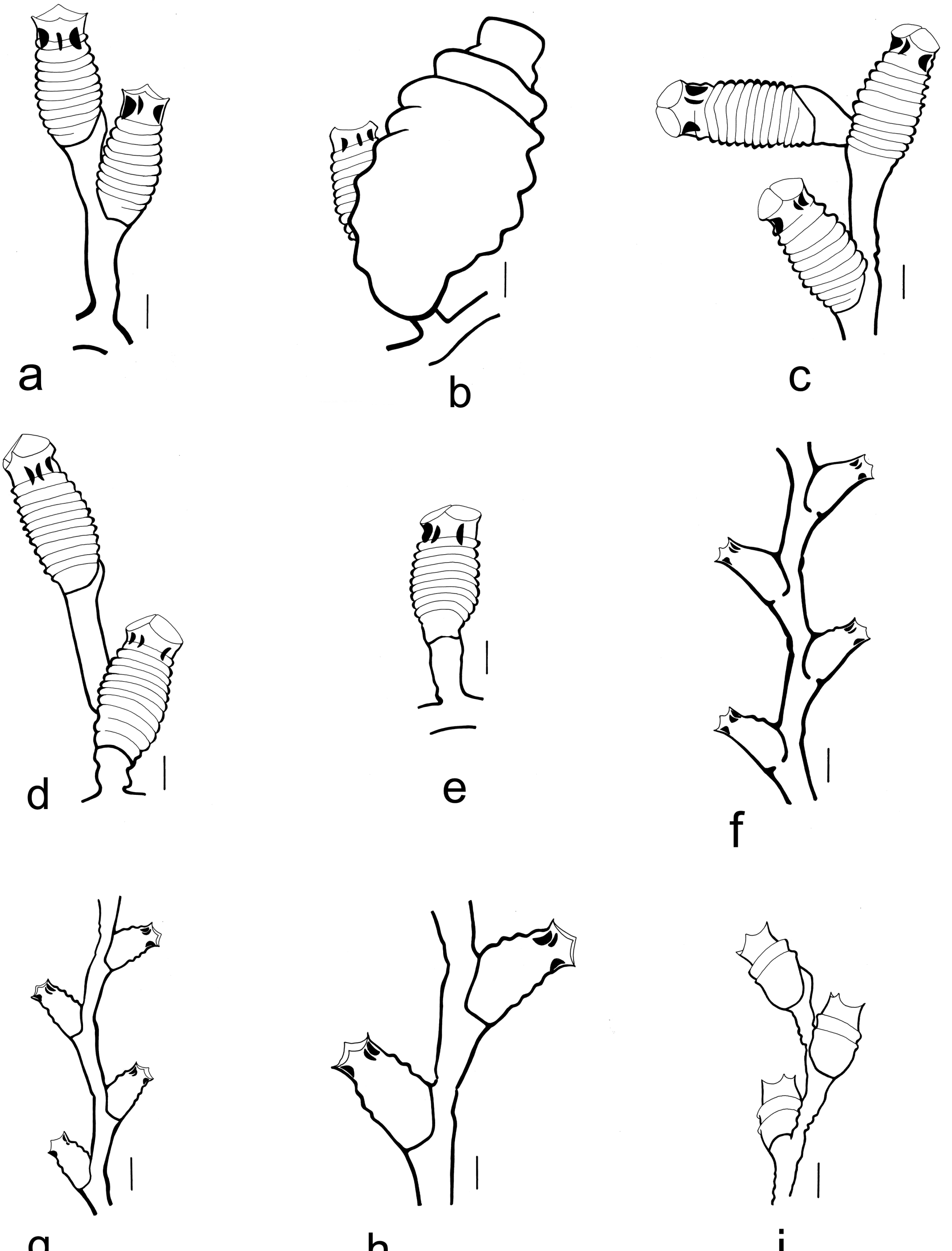

FIGURE 7. Sertularellidae. a, *Sertularella affinicostata*, sp. nov., holotype, hydrocaulus with two hydrothecae, Darwin Island, Galapagos Islands, Ecuador, ROMIZ B3339. Scale equals 0.1 mm. **b, *Sertularella affinicostata*, sp. nov.,** holotype, hydrocaulus with male gonotheca and a hydrotheca, Darwin Island, Galapagos Islands, Ecuador, ROMIZ B3339. Scale equals 0.1 mm. **c, *Sertularella affinicostata*, sp. nov.,** paratype, hydrocaulus with three hydrothecae, French Frigate Shoals, ROMIZ B5486. Scale equals 0.1 mm. **d, *Sertularella affinicostata*, sp. nov.,** paratype, hydrocaulus with two hydrothecae, French Frigate Shoals, ROMIZ B5486. Scale equals 0.1 mm. **e, *Sertularella affinicostata*, sp. nov.,** paratype, hydrocaulus with a single hydrotheca, French Frigate Shoals, ROMIZ B5486. Scale equals 0.1 mm. **f, *Sertularella angulosa* Bale, 1894**, part of hydrocaulus with four hydrothecae, French Frigate Shoals, ROMIZ B5477. Scale equals 0.2 mm. **g, *Sertularella angulosa* Bale, 1894**, part of hydrocaulus with four hydrothecae, Kure Atoll, ROMIZ B5425. Scale equals 0.1 mm. **h, *Sertularella angulosa* Bale, 1894**, part of hydrocaulus with two hydrothecae, Kure Atoll, ROMIZ B5425. Scale equals 0.1 mm. **i, *Sertularella areyi* Nutting, 1904**, part of hydrocaulus with three hydrothecae, Nihoa, ROMIZ B5478. Scale equals 0.2 mm.

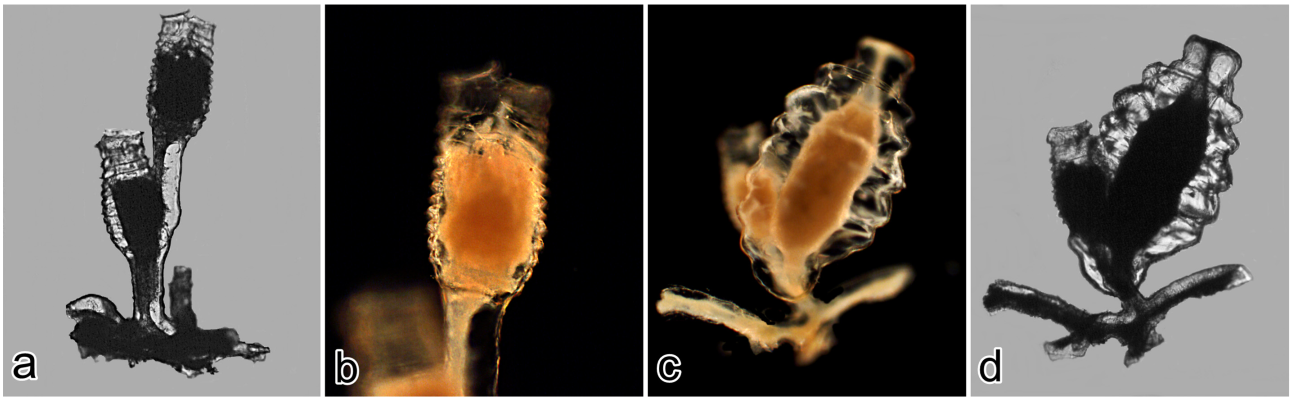

FIGURE 8. Sertularellidae. *Sertularella affinicostata*, sp. nov., holotype, Isla Darwin, Galapagos Islands, Ecuador, ROMIZ B3339. **a,** hydrocaulus and hydrorhiza, with two hydrothecae. **b,** a single hydrotheca, darkfield illumination. **c,** hydrocaulus and hydrorhiza, with a male gonotheca and a hydrotheca, darkfield illumination. **d,** hydrocaulus and hydrorhiza, with a male gonotheca and a hydrotheca.

Sertularella angulosa Bale, 1894
Fig. 7f–h

Sertularella angulosa Bale, 1894: 102, pl. 4 fig. 6.

Type locality. Unknown, but likely Australia (Bale 1894).

Voucher material. Kure Atoll, on algae and a bryozoan, 26.ix.2002, two colonies, to 5 mm high, without gonothecae, coll. A. Faucci, ROMIZ B5425.—French Frigate Shoals, on hydroid stem, 12.ix.2002, one colony, 7 mm high, without gonothecae, coll. A. Faucci, ROMIZ B5477.

Remarks. These small hydroid colonies appear closest in morphology to accounts of *Sertularella angulosa* Bale, 1894 from Indonesia by Billard (1925b) and Vervoort & Vasseur (1977), the latter in a discussion of *S. robusta* Coughtrey, 1876 from Moorea, French Polynesia. Indeed, the two have generally been considered conspecific (Hodgson 1950; Vervoort & Vasseur 1977; Hirohito 1995; Vervoort & Watson 2003). However, specimens examined here have been excluded from *S. robusta*, the putative senior synonym, largely on zoogeographic grounds. Originally described from Foveaux Strait at the southern tip of New Zealand (Coughtrey 1876), and with a centre of distribution in cold waters elsewhere in the Southern Hemisphere (Leloup 1960, 1974; Blanco 1968; Vervoort 1972; Vervoort & Watson 2003; Galea 2007; Galea *et al.* 2009; El Beshbeeshy 2011; Galea & Schories 2012; Oliveira *et al*. 2016; Galea *et al*. 2017), it seems improbable that *S. robusta* extends into tropical and warm-temperate parts of the Pacific and Indian oceans. Hydroids assigned to it from such areas (Pennycuik 1959; Vervoort & Vasseur 1977; Hirohito 1983, 1995; Gravier-Bonnet & Bourmaud 2012) are likely to have been misidentified. Thus, *S. angulosa* has been taken here to be valid, and populations inhabiting lower latitudes in the Pacific, including Kure Atoll, are more likely referable to it than to *S. robusta*. In addition to the original account of *S. angulosa* by Bale (1894), thorough accounts of its trophosome and gonosome have been given by Billard (1925b) and by Vervoort & Vasseur (1977, partly under the binomen *S. robusta*). Uncertainties nevertheless remain over the identity of the species. Bale's (1894) type material of *S. angulosa* was sterile, and while his collections were almost certainly from Australia, the exact type locality and original habitat of the species are unknown.

Also included in the synonymy of *S. robusta* by Vervoort & Vasseur (1977) was *S. microgona* von Lendenfeld, 1885. From accounts of it by Billard (1925b) and Vervoort & Vasseur (1977, as *S. robusta*, in part), the species differs from *S. angulosa* in having hydrothecae that are more slender and more tapered towards the distal end. Vervoort & Vasseur also compared the type of *S. inconstans* Billard, 1925b with their *S. robusta*. Differences between them were said to include the larger colony size, smaller submarginal cusps, and remarkably thick stem perisarc of *S. inconstans*. Finally, hydrothecae of the similar *S. keiensis* Billard, 1925b are slenderer at the distal end, and four submarginal cusps are present (Billard 1925b; Hirohito 1995; Xu *et al*. 2014b) rather than three, as in *S. microgona, S. angulosa*, and *S. robusta*.

As for *S. robusta* Coughtrey, 1876, its binomen is a permanently invalid junior primary homonym of *S. gayi* var. *robusta* Allman, 1874a (ICZN 1999, Art. 57.2), originally described from the Faroe-Shetland Trough in the North Atlantic Ocean. It is nomenclaturally inconsequential that Allman's name was introduced as a variety (ICZN 1999, Art. 45.6.4). Moreover, Reversal of Precedence provisions cannot be applied (ICZN 1999, Art. 23.9.1.1) to validate the junior homonym as a *nomen protectum* because its senior homonym has been used as a valid name after 1899, including in certain recent works (e.g., Nutting 1904: 79; Billard 1906a: 331; 1906b: 185; Bedot 1925: 370; Vervoort 1972: 118; Ramil & Vervoort 1992: 223; Calder & Vervoort 1998: 39, with a synonymy list; Henry *et al*. 2008: 794; Gil & Ramil 2017: 428). The junior homonym *S. robusta* Coughtrey, 1876 is replaced here by the binomen *S. quasiplana* Trebilcock, 1928, originally described as *S. robusta* var. *quasiplana* Trebilcock, 1928. The name of that variety qualifies as a replacement (ICZN 1999, Art. 60.2) in being considered a synonym of *S. robusta* by Vervoort & Watson (2003). As with the *S. robusta* of Coughtrey, it was originally described from New Zealand (Island Bay). Also described as a variety of the same species by Trebilcock (1928) was *S. robusta* var. *flucticulata*. Although sharing the same general type locality (Bluff, in Foveaux Strait, New Zealand) with *S. robusta*, it was excluded from consideration as a replacement name because it has been included in the synonymy of *S. integra* Allman, 1876 (Vervoort & Watson 2003). With respect to authorship and date of the Atlantic species, now regarded in some works as distinct from *S. gayi* (Lamouroux, 1821) (Moura *et al*. 2011), it should be credited to Allman (1874a) and not Coughtrey (1876).

The name *Sertularella polyzonias* var. *robusta* as utilized by Verrill (1873a:10) was not accompanied by a description, illustration, or indication, and is a *nomen nudum*. The trinomen *S. polyzonias* f. *robusta* appeared again in Kirchenpauer (1884) for hydroids "…mit viel dickeren Stämmen und Zweigen und grösseren Hydrotheken…" from the Cape of Good Hope, South Africa. That hydroid was briefly mentioned in the work of Hartlaub (1901), and an illustration of it was provided, but its nomenclature was left unsettled. The name *S. polyzonias* var. *robusta* was listed by Bedot (1916, 1918, 1925), but in reference to the hydroid of Verrill (1873a), not Kirchenpauer (1884). The nomenclature of Kirchenpauer's junior homonym was finally settled by Millard (1964). She recognized it as distinct from *S. polyzonias* (Linnaeus, 1758), and linked it instead to *S. megista* Stechow, 1923b. Finally, another junior homonym of both *S. gayi* var. *robusta* Allman, 1874a and *S. robusta* Coughtrey, 1876 is *S. robusta* Clark, 1877. That binomen has been replaced by the name *S. albida* Kirchenpauer, 1884.

Material assigned to *S. angulosa* by Billard (1925b) was collected at depths between 59 m and 90 m at several locations in Indonesia. Billard believed that hydroids identified by Jäderholm (1905) as *S. tenella* (Alder, 1856), from Tierra del Fuego, were conspecific. Given the cold Southern Hemisphere collection locale of Jäderholm's material, however, it is more likely referable to *S. robusta* (=*S. quasiplana*), as indicated by Galea *et al*. (2017).

Vervoort & Vasseur (1977) found *S. angulosa* (as *S. robusta*) to be the most common hydroid on the entire Tiahura barrier reef at Moorea. It extended from the reef flat, at 1 m, to the spur and groove zone at 20 m, and reached peak abundance in cavities on the reef flat.

Reported Distribution. Hawaiian archipelago. First record.

Elsewhere. Indian Ocean (Millard & Bouillon 1973, as *Sertularella robusta*; Gravier-Bonnet & Bourmaud 2012, as *S. robusta*), western Pacific Ocean (Pennycuik 1959, as *S. robusta*; Vervoort & Vasseur 1977, as *S. robusta*; Hirohito 1983, 1995, as *S. robusta*).

Sertularella areyi Nutting, 1904

Fig. 7i

Sertularella areyi Nutting, 1904: 83, pl. 17 fig. 6.—Coles *et al*., 2002a: 318; 2002b: 177.—Carlton & Eldredge, 2009: 38.—Calder, 2020: 216, fig. 5a.

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

Material examined. Nihoa, on algae, 06.ix.2002, 2 colonies or colony fragments, to 5 mm high, without gonothecae, coll. A. Faucci, ROMIZ B5478.

Remarks. Discovery of *Sertularella areyi* Nutting, 1904 from inshore waters of Hawaii in the central Pacific (Calder 2019, 2020), and from diving depths at Nihoa in this study, is surprising given the type locality of the species. The hydroid was originally described by Nutting (1904) from outer neritic and upper bathyal waters (100–200 ftm = 182–364 m) off Cuba, in the western North Atlantic. Records of it from the Atlantic to date have mainly been at intermediate depths, although the species appears to be quite eurybathic. *Sertularella areyi* has been most widely reported in the western Pacific, with records from Japan (Yamada 1959; Hirohito 1995), Korea (Rho & Chang 1974), the Philippines (Vervoort 1993), New Caledonia (Vervoort 1993), the Loyalty Islands (Vervoort 1993), New Zealand (Vervoort & Watson 2003), and China (Xu *et al*. 2014b; Song 2019). When subjective synonyms of the species are included, its range also includes Australia (*Sertularella annulaventricosa* Mulder & Trebilcock, 1915, from Queenscliff, Victoria), Tasmania (*Sertularia undulata* Bale, 1915, from South Cape), Indonesia (*Sertularella tricincta* Billard, 1939, from the Kei Islands), and South Africa (*Sertularella capensis delicata* Millard, 1964, from Natal). Molecular comparisons of populations across its reported distribution will therefore be enlightening. In the western Atlantic Ocean, its putative range extends from Plantagenet Bank near Bermuda (Calder 2000) and from shelf waters off South Carolina (Wenner *et al*. 1984) in the north to Brazil (Oliveira *et al*. 2016) in the south.

Type material of *S. areyi* was collected off Cuba during the Bahama Expedition of 1893, led by Charles Cleveland Nutting (1858–1927) of the State University of Iowa (now the University of Iowa). Nutting (1904) named the species in honour of Melvin Franklin Arey (1844–1931), Professor of Natural Sciences at the Iowa State Normal School (now the University of Northern Iowa), a participant in the expedition, and a veteran of the American Civil War (https://scua.library.uni.edu/university-archives/historical-information-and-essays/lincoln-civil-war-and-uni). An engaging narrative of the Bahama Expedition appears in Nutting (1895).

Detailed accounts of *S. areyi* from the western Pacific Ocean appear in the major works of Vervoort (1993) and Vervoort & Watson (2003).

Reported Distribution. Hawaiian archipelago. Oahu: Kaneohe Bay, Moku Manu Island (Coles *et al*. 2002a; Calder 2020); Waikiki, Kapua Channel (Coles *et al*. 2002b).

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

Family Sertulariidae Lamouroux, 1812

Genus *Disertasia* Neppi, 1917

Disertasia crisioides (Lamouroux, 1824), comb. nov.

Fig. 9a, b

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.—Calder, 2020: 218, fig. 5e, f.

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

Type locality. Indonesia: Moluccas (Lamouroux 1824).

Voucher material. Lisianski Island, 01.x.2002, one young colony, 2 cm high, without gonothecae, coll. A. Faucci, ROMIZ B5426.—Gardner Pinnacles, on calcareous rubble, 14.ix.2002, two colonies or colony fragments, 2.8 cm high, one with gonothecae, coll. A. Faucci, ROMIZ B5427.

Remarks. This hydroid, widely known as *Dynamena crisioides* Lamouroux, 1824, is a common and relatively well-known shallow-water hydroid with a worldwide distribution in tropical and subtropical waters. It has been reported several times earlier from the Hawaiian Islands (Cooke 1977; Coles *et al*. 1999a; Coles *et al*. 2002a; Carlton & Eldredge 2009; Calder 2020).

Based on molecular data, *D. crisioides* must unfortunately be removed from the polyphyletic genus *Dynamena* Lamouroux, 1812 and assigned elsewhere. In the phylogenetic analyses of Moura *et al*. (2011), Maronna *et al*. (2016), and Song (2019), the species appears closest to *Dy. disticha* (Bosc, 1802) and *Dy. moluccana* (Pictet, 1893), with all three being genetically distant from *Dy. pumila* (Linnaeus, 1758), the type species of *Dynamena*. They are here referred instead to a resurrected genus *Disertasia* Neppi, 1917, type species *Disertasia cavolini* Neppi, 1917. Inclusion of *D. crisioides* in the genus, as *Disertasia crisioides*, comb. nov., warrants further assessment, however, as it is slightly separated from its two known congeners. Further comments on *Disertasia* are included in the Remarks section of *Di. disticha* immediately below. As for the specific name of its type species, *Di. cavolini*, it was formed as a noun in apposition and is the correct original spelling. Such formation of specific names is nevertheless discouraged by the code (ICZN 1999, Recommendation 31A).

For taxonomic and biological information on this species, see Millard (1975), Vervoort & Vasseur (1977), Gibbons & Ryland (1989), Calder (1991a, b, 2013), and Schuchert (2003), all under the binomen *Dynamena crisioides*.

Reported Distribution. Hawaiian archipelago. Oahu: Kewalo Basin (Cooke 1977, as *Dynamena crisioides*); Honolulu Harbor (Cooke 1977, as *Dy. crisioides*); Honolulu Harbor, Pier 29 (Coles *et al*. 1999a, as *Dy. crisiodes*, sic); Honolulu Harbor, Snug Harbor (Coles *et al*. 1999a, as *Dy. crisiodes*, sic); Honolulu Harbor, Sand Island Coast Guard Station (Coles *et al*. 1999a, as *Dy. crisiodes*, sic); Honolulu Harbor, Sand Island Park (Coles *et al*. 1999a, as *Dy. crisiodes*, sic); Keehi Lagoon, Airport Rescue Dock (Coles *et al*. 1999a, as *Dy. crisiodes*, sic); Kewalo Basin, Fisherman's Wharf (Coles *et al*. 1999a, as *Dy. crisiodes*, sic); Barbers Point, coal pier (Coles *et al*. 1999a, as *Dy. crisiodes*, sic); Kaneohe Bay, Sag Harbor (Coles *et al*. 2002a, as *Dy. crisioides*; Calder 2020, as *Dy. crisioides*); Honolulu Harbor, in collections at the Bishop Museum (Carlton & Eldredge 2009, as *Dy. crisioides*).—Kauai: Port Allen Harbor (Coles *et al*. 2006, as *Dy. crisioides*).

Elsewhere. Circumglobal, shallow tropical and subtropical waters (Calder 2013, as *Dy. crisioides*).

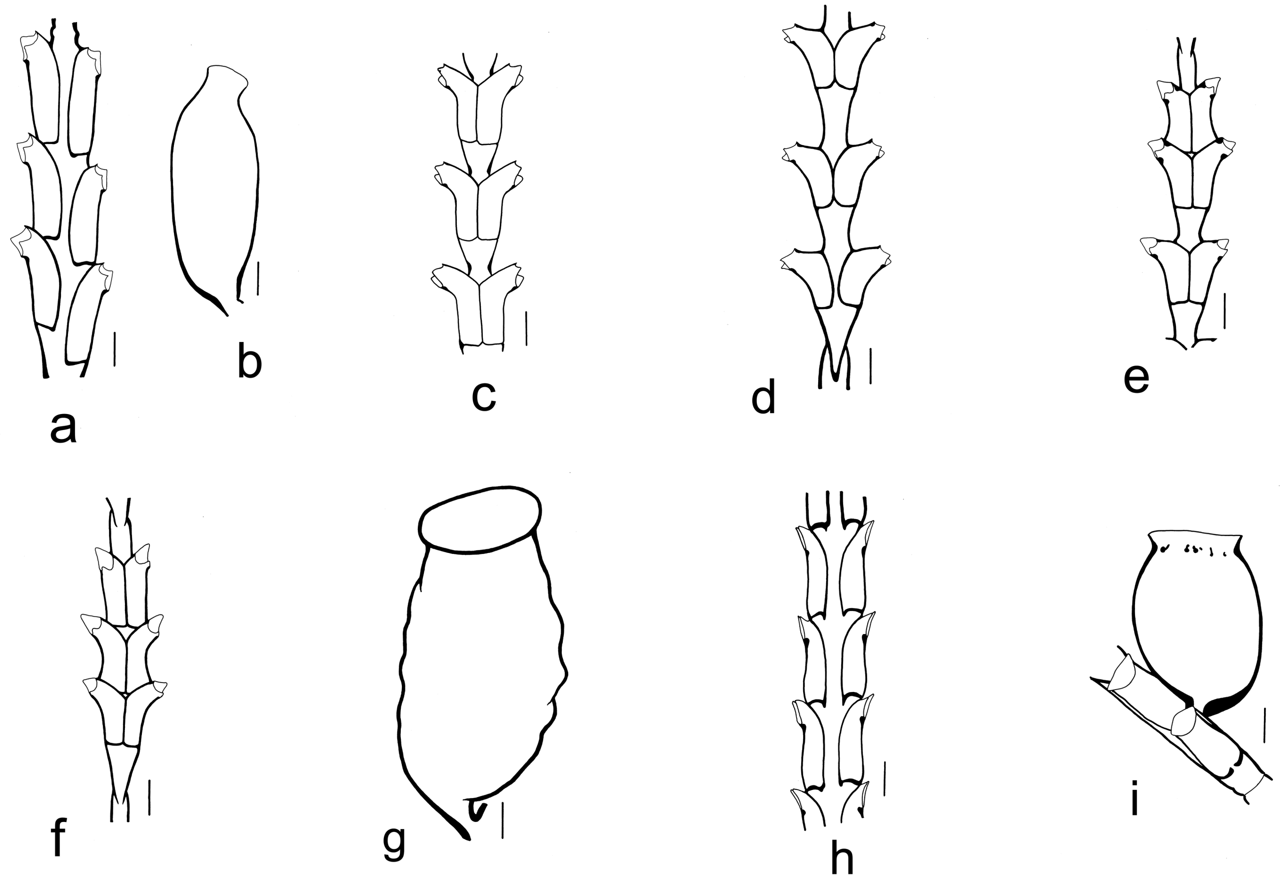

FIGURE 9. Sertulariidae. a, *Disertasia crisioides* (Lamouroux, 1824), part of hydrocladium with three hydrothecal pairs, Gardner Pinnacles, ROMIZ B5427. Scale equals 0.2 mm. **b, *Disertasia crisioides* (Lamouroux, 1824)**, gonotheca, Gardner Pinnacles, ROMIZ B5427. Scale equals 0.2 mm. **c, *Disertasia disticha* (Bosc, 1802)**, part of hydrocaulus with three hydrothecal pairs, Pearl & Hermes Atoll, ROMIZ B5428. Scale equals 0.2 mm. **d, *Pasya heterodonta* (Jarvis, 1922),** proximal end of hydrocaulus, with three hydrothecal pairs, Pearl & Hermes Atoll, ROMIZ B5436. Scale equals 0.2 mm. **e, *Pasya heterodonta* (Jarvis, 1922),** distal end of hydrocaulus, with three hydrothecal pairs, two pairs being stacked, Kure Atoll, ROMIZ B5491. Scale equals 0.2 mm. **f, *Pasya heterodonta* (Jarvis, 1922),** distal end of hydrocaulus, with three stacked hydrothecal pairs, Pearl & Hermes Atoll, ROMIZ B5485. Scale equals 0.2 mm. **g, *Pasya heterodonta* Jarvis, 1922),** gonotheca, Kure Atoll, ROMIZ B5491. Scale equals 0.1 mm. **h, *Salacia tetracythara* Lamouroux, 1816**, part of hydrocladium with three hydrothecal pairs, Lisianski Island, ROMIZ B5429. Scale equals 0.2 mm. **i, *Salacia tetracythara* Lamouroux, 1816**, gonotheca from same colony, Lisianski Island, ROMIZ B5429. Scale equals 0.2 mm.

Disertasia disticha **(Bosc, 1802), comb. nov.**

Fig. 9c

Sertularia disticha Bosc, 1802: 101, pl. 29 fig. 2.
Dynamena cornicina.—Cooke, 1977: 95, fig. 21.—Coles *et al*., 2002a: 207; 2004: 73.—Carlton & Eldredge, 2009: 38.

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

Voucher material. Pearl & Hermes Atoll, on algae, 28.ix.2002, one colony, 9 mm high, without gonothecae, coll. A. Faucci, ROMIZ B5428.

Remarks. This hydroid conforms with traditional taxonomic accounts of *Dynamena disticha* (Bosc, 1802), and it has been provisionally assigned to that species here. However, evidence from both morphology and DNA barcoding (Moura *et al.* 2011) indicates the likely existence of a species complex under that name. The hydroid from Pearl & Hermes Atoll may be specifically distinct from that of Bosc, and changes in nomenclature might be expected.

The species of Bosc (1802) was described from material collected on pelagic *Sargassum* in the open Atlantic Ocean. Colonies from that substrate are small (1 cm high or less), gracile, and unbranched (Calder 1991a). Another morphotype from a variety of substrates along the shallow Atlantic coast are larger in size (up to 5 cm high), more robust, and an essentially perpendicular branch may infrequently be present (Fraser 1944, as *Sertularia cornicina*; Calder 1971, as *Dynamena cornicina*). The overall morphology of their trophosomes and gonosomes are otherwise much alike, and the colour of both is bright yellow. Comparisons of them are warranted to establish if observed differences are attributable to genetics or environment.

Molecular studies by Moura *et al*. (2011), Maronna *et al*. (2016), and Song (2019) confirm that *Dynamena* Lamouroux, 1812 is polyphyletic. Indeed, *Dy. disticha* has been shown by them in all phylograms to be genetically distant from *Sertularia pumila* Linnaeus, 1758, type species of the genus. The species also appears too remote from *Tridentata* Stechow, 1920, type species *Sertularia perpusilla* Stechow, 1919b, to be assigned there. Instead, as noted above, the genus *Disertasia* Neppi, 1917 has been resurrected here from the synonymy of *Dynamena* to accommodate this and closely related species. Of particular note, the type species of *Disertasia* by monotypy, *Di. cavolini* Neppi, 1917, is taken to be conspecific with *Dy. disticha* (Picard 1958; Calder 1991a; Medel & Vervoort 1998; Gravili *et al*. 2015). The present species is thus assigned the binomen *Disertasia disticha*, comb. nov. Also assigned here to *Disertasia*, based on their proximity in molecular phylograms to *Di. disticha*, are *Dy. moluccana* (Pictet, 1893) and, with somewhat less certainty, *Dy. crisioides* Lamouroux, 1824. Meanwhile, it is unclear if any of the sampled populations of *Di. disticha* included in molecular analyses were from pelagic *Sargassum*, as with the original account of the species by Bosc (1802).

In an obscure paper on hydroid epibionts from pelagic *Sargassum* in the North Atlantic, Bosc (1797) described, as *Hydra quinternana*, a small yellow sertulariid likely to have been identical with *Disertasia disticha*. It therefore constitutes a nomenclatural threat to the now widely used species name *Dy. disticha* (=*Sertularia disticha* Bosc, 1802). In the interests of nomenclatural stability, Reversal of Precedence provisions in the code (ICZN 1999, Art. 23.9) are followed here to designate *Di. disticha* (Bosc, 1802) as valid and a *nomen protectum*, and to relegate *H. quinternana* Bosc, 1797 to a *nomen oblitum.* Reversal of Precedence is applicable in this case because the binomen *H. quinternana* has not been used as a valid name in zoology after 1899, while *Dy. disticha* has appeared in more than 25 publications by numerous authors (>10) in the past 50 years (e.g., Boero 1981; Calder 1991a, 1995, 2013, 2019; Cornelius 1992; Migotto 1996; Grohmann *et al.* 1997; Medel & Vervoort 1998; Faucci & Boero 2000; Peña Cantero & García Carrascosa 2002; Kirkendale & Calder 2003; Schuchert 2003; Calder & Kirkendale 2005; Bouillon *et al*. 2006; Vervoort 2006; Gravier-Bonnet 2007; Galea 2008, 2010; Cunha & Jacobucci 2010; Moura *et al*. 2011; Xu *et al*. 2014b; Galea & Ferry 2015; Gravili *et al*. 2015; Oliveira *et al*. 2016; Maronna *et al*. 2016; Mendoza-Becerril *et al*. 2018; Miglietta *et al*. 2018).

For much of the 20th century, this species was assigned to *Dynamena cornicina (=Sertularia cornicina* McCrady, 1859). The actual identity of *Dy. cornicina* is ambiguous at present, however, and its binomen is now taken to be a *nomen dubium*. McCrady's (1859) original description of the species, from Charleston Harbor, South Carolina, USA, was lacking in detail, no illustrations of it were provided, and no types are known to exist. His account applies equally to two abundant species in the Charleston area (Calder 1991a), *Di. disticha* and *Amphisbetia distans* (=*Dynamena distans* Lamouroux, 1816). As for hydroids assigned to *Dy. cornicina* auct. during the period, most are taken to have been identical with *Di. disticha* rather than *A. distans*. Specimens identified as *Sertularia cornicina* from Charleston exist in collections at the MCZ (MCZ IZ 175, MCZ IZ 176), but they were collected by Louis Agassiz rather than John McCrady (Adam Baldinger, personal communication, 15 April 2021). The identity of *S. cornicina* may therefore be suspected, but not unequivocally proven, from those collections.

Reported Distribution. Hawaiian archipelago. Oahu: Kaneohe Bay, Coconut Point (Cooke 1977, as *Dynamena cornicina*).—Kauai: Nawiliwili main dock, concrete pier pilings; Port Allen main dock, concrete pier pilings (Coles *et al*. 2004, as *Dy. cornicina*).—Molokai: Kaunakakai Harbor main dock, main pier, concrete pier pilings (Coles *et al*. 2004, as *Dy. cornicina*).—Maui: Kahului Harbor, Pier 1, concrete pilings (Coles *et al*. 2004, as *Dy. cornicina*).

Elsewhere. Reported to be circumglobal in shallow waters, from tropical to temperate zones (Calder 2013).

Genus Pasya Stechow, 1922

Pasya heterodonta (Jarvis, 1922), comb. nov.

Fig. 9d–g

Pasythea heterodonta Jarvis, 1922: 344, pl. 24 figs 11A–B, 12.

Type locality. Republic of Mauritius: Cargados (=Cargados Carajas Shoals), 24 fm (44 m) (Jarvis 1922).

Voucher material. Pearl & Hermes Atoll, on calcareous rubble, 28.ix.2002, three colonies, to 9 mm high, without gonothecae, coll. A. Faucci, ROMIZ B5436.—Midway Atoll, on *Halimeda* sp., 20.ix.2002, one colony, 8 mm high, without gonothecae, coll. A. Faucci, ROMIZ B5437.—Pearl & Hermes Atoll, 19.ix.2002, three colony fragments, 8.5 mm high, without gonothecae, coll. A. Faucci, ROMIZ B5438.—Pearl & Hermes Atoll, on calcareous rubble, 19.ix.2002, one colony, 8 mm high, without gonothecae, coll. A. Faucci, ROMIZ B5485.—Kure Atoll, on calcareous rubble, 25.ix.2002, five colonies or colony fragments, to 9 mm high, with gonothecae, ROMIZ B5491.

Remarks. *Pasya heterodonta* (Jarvis, 1922) resembles the much better-known *P. quadridentata* (Ellis & Solander, 1786) in having stacked hydrothecal pairs on the stems (Fig. 9e, f). It differs, however, in having stacked pairs only at the extreme distal ends the cauli. Indeed, such groups are sometimes entirely lacking in present material, likely occurring in younger and earlier developmental stages of a given caulus. While gonothecae of the two species are fundamentally alike, suggestive of a close relationship, those of *P. heterodonta* appear to have fewer and less pronounced ridges. Grouping of hydrothecal pairs may occasionally occur as well in *P. obliqua* (Lamouroux, 1816), but hydrothecae of that species are more swollen and internodes are much shorter and stouter.

In reporting *P. heterodonta* from Moorea, French Polynesia, Vervoort & Vasseur (1977, as *Dynamena heterodonta*) provided a description and illustrations of type material of the species. Unlike in *P. quadridentata*, hydrothecae were said to have a longer free portion that curved away from the internode, the operculum was more acute, and intrathecal cusps were well-developed. Similar differences in hydrothecal morphology had convinced Billard (1925) earlier to recognize *P. heterodonta* as distinct from *P. quadridentata*. Gibbons & Ryland (1989) acknowledged the distinct appearance of two equivalent morphotypes from Fiji, but nevertheless questioned the validity *P. heterodonta*. They suggested that perceived differences might not exceed the range of morphological variability within *P. quadridentata*. Given its distinct morphology, including the relative paucity of contiguous hydrothecal groups and their limitation to the distal end of the stems, *P. heterodonta* is taken here to be a species of the tropical Indo-Pacific, distinct from *P. quadridentata* (type locality: "...coast of Africa, not far from the island of Ascension"). *Pasya heterodonta* has also been recognized recently as valid by Galea (2016, as *Dynamena heterodonta*) in material from Indonesia.

Cauli of *P. heterodonta* lacking stacked pairs of hydrothecae closely resemble those of both *Thuiaria maldivensis* Borradaile, 1905 and *Sertularia borneensis* Billard, 1925. Given their similarity, Schuchert (2003) suspected that the latter two might be conspecific. While gonothecae of *T. maldivensis* are still undescribed, Gibbons & Ryland (1989) and Schuchert (2003) provided descriptions and illustrations of gonothecae of *S. borneensis* based on specimens from Verde Island, the Philippines, and the Kei Islands, Indonesia, respectively. They differ from those of *P. heterodonta* in being strongly ridged. Moreover, Gibbons and Ryland noted the existence of two lateral horns that arose from a distal gonothecal collar, as in species assigned to *Tridentata* Stechow, 1920 (type species *S. perpusilla* Stechow, 1919b).

As for *Pasya* Stechow, 1922, the genus has recently been resurrected as valid (Calder 2013) given the genetic distance of its type species, *Sertularia quadridentata* (Ellis & Solander, 1786), from that of *Sertularia pumila* Linnaeus, 1758, type species of a currently polyphyletic genus *Dynamena* Lamouroux, 1816. The extent of their separation is apparent in phylograms such as those of Moura *et al*. (2011) and Song (2019). *Pasya* was proposed by Stechow (1922) as a replacement name for use in Hydrozoa of *Pasythea* Lamouroux, 1812 (type species: *Cellaria tulipifera* Ellis & Solander, 1786), now restricted to Bryozoa. *Tuliparia* de Blainville, 1830 has the same type species (Stechow 1922) and is a junior objective synonym of *Pasythea.*

Development of the intrathecal cusps varied considerably within colonies of *P. heterodonta* examined here (Fig. 9d–f). Disparities in their development were noted earlier by Billard (1925) and are apparent in illustrations of the species by Galea (2016: fig. 1L, N). Only slight variations in cusp development were noted by Vervoort & Vasseur (1977).

Reported Distribution. Hawaiian archipelago. First record.

Elsewhere. French Polynesia: Tuamotu Archipelago, Gambier Island (Billard 1905, as *Sertularia gracilis*).—Indonesia: Makassar Strait, 2°25′S, 117°43′E; E of Sumbawa, 34–36 m, Billard 1925, as *Dynamena heterodonta*).—New Caledonia: Ile des Pins (Redier 1966, as *D. heterodonta*; Gravier Bonnet 2007, as *D. heterodonta*).—South Africa (Millard 1975, as *Dynamena quadridentata*, in part, Fig. 87H).—Moorea (Vervoort & Vasseur 1977, as *D. heterodonta*).—Fiji (Gibbons & Ryland 1989, as *D. quadridentata*, type B).—Indonesia: Arafura Sea (Galea 2016).

Genus *Salacia* Lamouroux, 1816

Salacia tetracythara Lamouroux, 1816

Fig. 9h, i

Salacia tetracythara Lamouroux, 1816: 214, pl. 6 fig. 3a, B, C [correct original spelling].
Salacia tetracyttara Lamouroux, 1816: 553 [incorrect original spelling].
Thuiaria fenestrata.—Nutting, 1905: 950.

Type locality. Australasia? (Lamouroux 1816).

Voucher material. Lisianski Island, 01.x.2002, two colonies, to 3.4 cm high, one with gonothecae, coll. A. Faucci, ROMIZ B5429.—Pearl & Hermes Atoll, 28.ix.2002, three colonies, to 5.5 cm high, without gonothecae, coll. A. Faucci, ROMIZ B5430.—Laysan Island, 18.ix.2002, one colony, 1.5 cm high, without gonothecae, coll. A. Faucci, ROMIZ B5431.—Kure Atoll, detached, 25.ix.2002, one colony, 2.3 cm high, without gonothecae, coll. A. Faucci, ROMIZ B5432.—Laysan Island, 17.ix.2002, two colonies, to 5.2 cm high, without gonothecae, coll. A. Faucci, ROMIZ B5433.

Remarks. As shown in the synonymy list above, the specific name of this species was spelled two different ways (as *tetracythara* and *tetracyttara*) in the original work by Lamouroux (1816). Rees & Vervoort (1987: 103), Acting as First Revisers (ICZN 1999, Art. 24.2.3), selected *tetracythara* as correct. Cornelius (1975: 381) noted that *Salacia tetracythara* Lamouroux, 1816 is the type species, by monotypy, of the genus *Salacia* Lamouroux, 1816. He provided a historical account of the synonymy of the genus and species, and noted that its type was destroyed during World War II. Billard (1909b) had earlier examined the type and found that it corresponded well with *Thuiaria fenestrata* Bale, 1884 from Australia. The two are now widely considered conspecific, and the account of Bale (1884) facilitates identification of the species. Also taken to be a synonym is *Calyptothujaria opposita* von Campenhausen, 1896 from Ternate, Indonesia.

Salacia and *Thuiaria* Fleming, 1828 have at times been regarded as congeners (Stechow 1922, 1923c; Rees & Thursfield 1965; Cornelius 1979), although they are currently held to be distinct (Cornelius 1995b; Hirohito 1995; Bouillon *et al*. 2006; Song 2019). A key difference in terms of morphology is the presence of an abcauline diverticulum or caecum (Millard 1975, fig. 81A) in *Thuiaria* and its absence in *Salacia*. A molecular analysis of *S. tetracythara*, needed to clarify relationships of *Salacia*, have yet to be undertaken. *Sertularia desmoides* Torrey 1902, subjectively assigned at present to the same genus, has been shown to be genetically distant from *Thuiaria thuja* (Moura *et al*. 2011; Maronna *et al*. 2016; Song 2019), the type species of *Thuiaria*.

Salacia tetracythara is widely distributed across the tropical and subtropical Indo-Pacific region (Rees & Vervoort 1987), and it has recently been reported from Brazil in the Atlantic Ocean (Mendonça *et al*. 2021). The hydranth and modified tentacles of this hydroid were studied and described by Gravier-Bonnet (2008).

Reported Distribution. Hawaiian archipelago. Laysan Island: north of the island, 20 fathoms (37 m) (Nutting 1905, as *Thuiaria fenestrata*).—Maui: NE of the island, 14 fathoms (26 m) (Nutting 1905, as *T. fenestrata*).

Elsewhere. Tropical and subtropical Indo-Pacific, from the Mozambique Channel and the Gulf of Aden to Hawaii (Lamouroux 1816; Billard 1909b, as *Thuiaria tetracythara*; Pennycuik 1959; Mammen 1965; Rees & Vervoort 1987; Gibbons & Ryland 1989; Hirohito 1995; Watson 2000; Schuchert 2003; Gravier-Bonnet 2007, 2008; Di Camillo *et al*. 2008; Gravier-Bonnet & Bourmaud 2012; Preker & Lawn 2012; Song 2019).—Atlantic Ocean, Brazil (Mendonça *et al*. 2021).

Genus *Tridentata* Stechow, 1920

Tridentata loculosa (Busk, 1852)

Fig. 10a, b

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.—Calder, 2020: 221, fig. 6f.

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

Voucher material. Midway Atoll, 23.ix.2002, five colony fragments, to 1.3 cm high, with gonothecae, coll. A. Faucci, ROMIZ B5434.—Gardner Pinnacles, on calcareous rubble, 14.ix.2002, one colony, 4 mm high, without gonothecae, coll. A. Faucci, ROMIZ B5435.

Remarks. DNA sequences are as yet unavailable for *Tridentata loculosa* (Busk, 1852), and its genetic affinities remain uncertain. Following previous work (Calder 2013, 2020), it has been assigned temporarily here to *Tridentata* Stechow, 1920 given the general resemblance of its trophosome and gonosome to species of that genus (including its type species, *Sertularia perpusilla* Stechow, 1919b). Its indistinct marginal cusps, markedly dissimilar upper and lower opercular valves, and presence of a ligula (an intrathecal modification of the mantle, resembling a nematophore), set it apart from them. In particular, the taxonomic significance of the ligula is uncertain. Given its unusual characters, Hirohito (1974) suggested that a new genus might be warranted for the species, but later (Hirohito 1995) retained it in *Sertularia* Linnaeus, 1758 following Vervoort & Vasseur (1977). With respect to its generic name, this species bears little morphological resemblance to *Sertularia argentea* Linnaeus, 1758, type species of *Sertularia*. Thus, it can certainly be excluded from that genus (Calder 2013, 2020), where it has usually been assigned.

Taxonomic reviews of *T. loculosa* were provided by Migotto (1996, as *Sertularia loculosa*) and Calder (2013). Of note, *Sertularia ligulata* Thornely, 1904 was shown by Billard (1927) to be conspecific with *S. loculosa*. Although widely distributed and possibly circumglobal in tropical and subtropical waters, this species has not been recorded to date in the eastern Pacific Ocean. Colonies examined here from Midway Atoll (ROMIZ B5434), collected during September 2002, bore gonothecae.

Reported Distribution. Hawaiian archipelago. Oahu: Kaneohe Bay, 2 m, on *Porites lobata* (Cooke 1977, as *Sertularia ligulata*); Kaneohe Bay, Waiahole Reef (Coles *et al*. 2002a, as *S. ligulata*; Calder 2020); Waikiki, Aquarium Outside Reef, 3 m (Coles *et al*. 2002b, as *Tridentata ligulata*); Waikiki, *Atlantis* wreck, 20–30 m (Coles *et al*. 2002b, as *T. ligulata*).

Elsewhere. Warm waters of the Indian Ocean (Millard 1975, as *S. ligulata*), western and central Pacific (Hirohito 1995, as *S. ligulata*; Schuchert 2003, as *S. ligulata*; Calder 2020), and western and eastern Atlantic (Vervoort 1959, as *S. ligulata*; Calder 2013).

Tridentata orthogonalis (Gibbons & Ryland, 1989), comb. nov.

Fig. 10c

Sertularia orthogonalis Gibbons & Ryland, 1989: 423, fig. 38A–D.

Type locality. Fiji: Viti Levu, Pacific Harbor, Ndeumba Island, Ndeumba fringing reef (Gibbons & Ryland 1989, as *Sertularia orthogonalis*).

Voucher material. Laysan Island, 18.ix.2002, one colony, 6 mm high, without gonothecae, coll. A. Faucci, ROMIZ B5439.—Laysan Island, on *Halimeda* sp. and unattached, 17.ix.2002, four colonies or colony fragments, 6–14 mm high, with gonothecae, coll. A. Faucci, ROMIZ B5440.

Remarks. *Tridentata orthogonalis* (Gibbons & Ryland, 1989), comb. nov., originally described from Fiji, is a morphologically striking but little-known species. To date, the only other published records of it are those Coles *et al*. (2003, as *Sertularella orthogonalis*) from American Samoa and Hewitt & Campbell (2010, as *Sertularia orthogonalis*) from Australia.

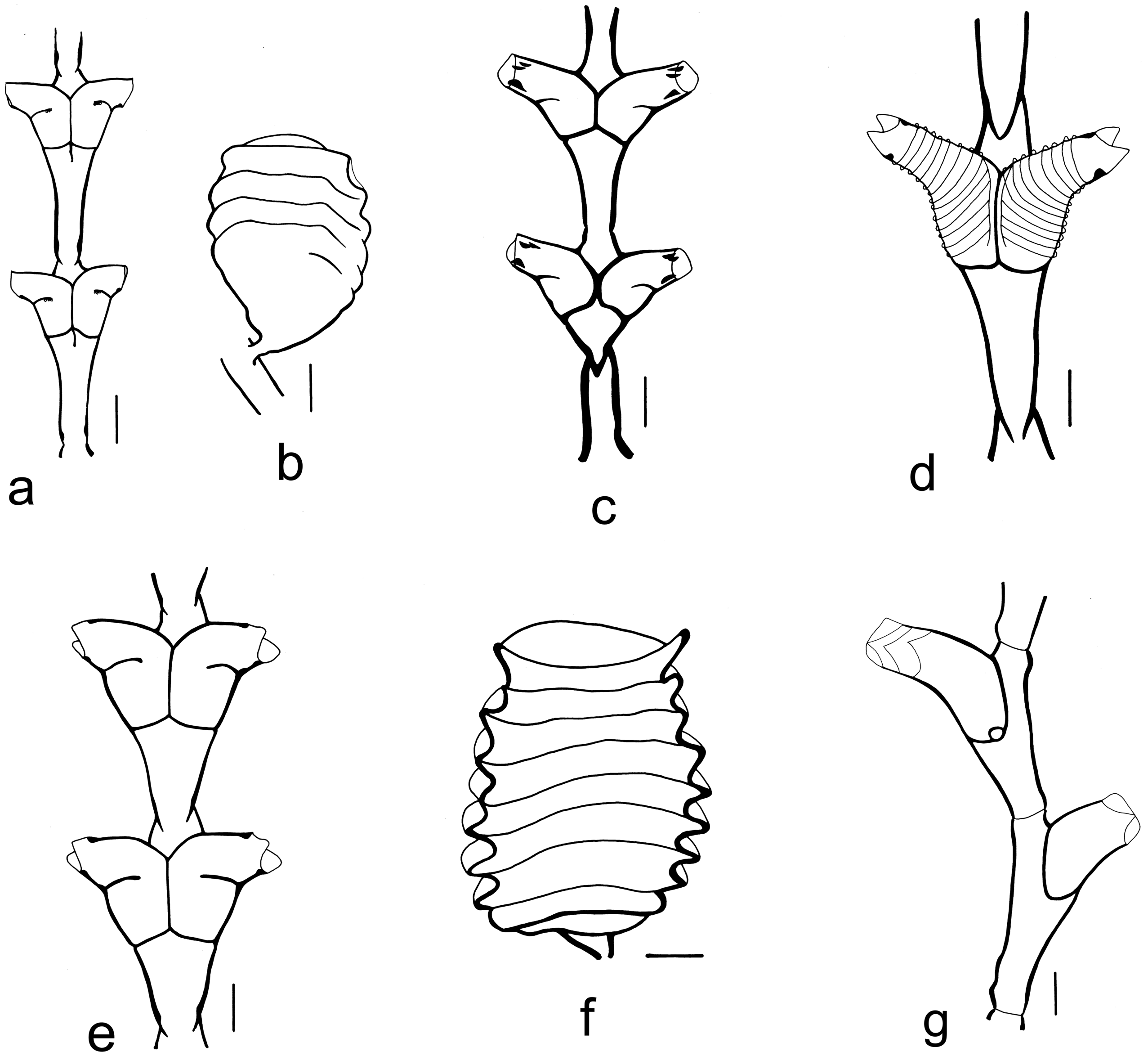

FIGURE 10. Sertulariidae and Symplectoscyphidae. a, *Tridentata loculosa* (Bale, 1852), part of hydrocaulus with two hydrothecal pairs, Midway Atoll, ROMIZ B5434. Scale equals 0.2 mm. **b, *Tridentata loculosa* (Bale, 1852)**, gonotheca, Midway Atoll, ROMIZ B5434. Scale equals 0.2 mm. **c, *Tridentata orthogonalis* (Gibbons & Ryland, 1989)**, part of hydrocaulus with two hydrothecal pairs, Laysan Island, ROMIZ B5440. Scale equals 0.2 mm. **d, *Tridentata rugosissima* (Thornely, 1904),** part of hydrocaulus with one hydrothecal pair, Laysan Island, ROMIZ B5489. Scale equals 0.1 mm. **e, *Tridentata turbinata* (Lamouroux, 1816)**, part of hydrocaulus with two hydrothecal pairs, Pearl & Hermes Atoll, ROMIZ B5444. Scale equals 0.1 mm. **f, *Tridentata turbinata* (Lamouroux, 1816)**, gonotheca, Pearl & Hermes Atoll, ROMIZ B5444. Scale equals 0.2 mm. **g, *Bicaularia tongensis* (Stechow, 1919b)**, part of hydrocaulus with two hydrothecae, Midway Atoll, ROMIZ B5445. Scale equals 0.1 mm.

Gibbons & Ryland (1989) noted the general resemblance of their hydroid to *Sertularia tongensis* Stechow, 1919b from Tonga. They distinguished it from that species in that each hydrotheca has an abcauline intrathecal ridge and three distinct intrathecal cusps. Colonies from Laysan Island conform well with the original account of *S. orthogonalis* and have been identified as such here. Based on characters of both the trophosome and gonosome of the species, it has been transferred in this work from *Sertularia* Linnaeus, 1758 to *Tridentata* Stechow, 1920.

As for *S. tongensis*, it somewhat resembles *S. borneensis* Billard, 1925a, and was considered a questionable synonym of that species by Schuchert (2003). In turn, *S. borneensis* was considered conspecific with *Tridentata maldivensis* (Borradaile, 1905) by Calder (2010), although it now seems better to maintain them as separate species until their gonosomes can be compared and their genetic affinities determined. Galea (2010) assigned the replacement name *Sertularia ephemera* to *S. tongensis*, considering it referable to the same genus as *Sertularella tongensis* Stechow, 1919b, a different species. However, the latter hydroid is now assigned to *Bicaularia* Song, Lyu, Ruthensteiner, Wang & Gravili, 2019, and homonymy between *Sertularella tongensis* (=*Bicaularia tongensis*) and *Sertularia tongensis* (=*Tridentata tongensis*) no longer exists.

This report extends the known distribution of *T. orthogonalis* to the central North Pacific Ocean.

Reported Distribution. Hawaiian archipelago. First record.

Elsewhere. Fiji (Gibbons & Ryland 1989, as *Sertularia orthogonalis*); American Samoa (Coles *et al*. 2003, as *Sertularella orthogonalis*); Australia (Hewitt & Campbell 2010, as *Sertularia orthogonalis*).

Tridentata rugosissima (Thornely, 1904)

Fig. 10d

Sertularia rugosissima Thornely, 1904: 118, pl. 2 fig. 4.
Sertularia subtilis.—Cooke, 1977: 97, fig. 25.—Carlton & Eldredge, 2009: 39.
Tridentata humpferi.—Coles *et al*., 2002a: 318; 2002b: 177, 234 [incorrect subsequent spelling].
Tridentata hupferi.—Carlton & Eldredge, 2009: 39.
Tridentata rugosissima.—Calder, 2020: 222, fig. 6g.

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

Material examined. Laysan Island, on *Halimeda* sp., 17 ix.2002, one colony, 4.5 mm high, without gonothecae, coll. A. Faucci, ROMIZ B5489.

Remarks. An account of *Tridentata rugosissima* (Thornely, 1904) from Hawaiian waters has been provided earlier (Calder 2020). The species has been reported there several times from locations around the island of Oahu (Cooke 1977, as *Sertularia subtilis*; Coles *et al*. 2002a, as *Tridentata humpferi*; Coles *et al*. 2002b, as *T. humpferi*; Calder 2020).

Hydroids of *T. rugosissima* are morphologically distinctive in having hydrothecal walls ringed by about 12 or more transverse ridges. Also present are distinct abcauline and less distinct adcauline intrathecal cusps. Subjective synonyms of the species, based on studies by Migotto (1996), include *Sertularia hupferi* Broch, 1914 from Ghana, *S. subtilis* Fraser, 1937b from Puerto Rico, and *Geminella subtilis* Vannucci Mendes, 1946 from Brazil.

While reported from the Indo-Pacific, central Pacific, and both eastern and western Atlantic, genetic comparisons of widely separated populations of hydroids assigned to *T. rugosissima* are warranted. Also needed is confirmation of the generic identity of the species, based to date only on morphology (Stechow 1923c; Calder & Choong 2018; Calder 2020). Assigning it to *Sertularia* Linnaeus, 1758, as in most works to date (including WoRMS), is clearly incorrect because *T. rugosissima* is morphologically remote from *Sertularia argentea* Linnaeus, 1758, type species of that genus. It has been referred here to *Tridentata* Stechow, 1920 based on characters of both the trophosome and the gonothecae, which generally conform with those of the type species of the genus, *Sertularia perpusilla* Stechow, 1919b. Vannucci Mendes (1946, as *Geminella subtilis*) appears to have been first in describing the gonotheca of *T. rugosissima*.

Reported Distribution. Hawaiian archipelago. Oahu: Kahe Point reef, 2 m, on coral rubble (Cooke 1977, as *Sertularia subtilis*); Kaneohe Bay, Pristine Reef (Coles *et al*. 2002a, as *Tridentata humpferi*; Calder 2020); Waikiki, Canoes (Coles *et al*. 2002b, as *T. humpferi*); Waikiki, Kapua Channel, 5 m (Coles *et al*. 2002b, as *T. humpferi*); Waikiki, Kaiser's Channel (Coles *et al*. 2002b, as *T. humpferi*); Hawaii Kai, Channel Marker 1, Maunalua Bay, 4 m (Coles *et al*. 2002b, as *T. humpferi*).

Elsewhere. Indian Ocean (Thornely 1904, 1916, as *Sertularia rugosissima*; Millard & Bouillon 1973, as *S. hupferi*); western Pacific (Jäderholm 1919, as *S. rugosissima*; Cooke 1975, as *S. subtilis*; Yamada & Kubota 1987, as *S. rugosissima*; Gibbons & Ryland 1989, as *S. hupferi*); western Atlantic (Fraser 1937b, as *S. subtilis*; Migotto 1996, as *S. rugosissima*; Calder & Kirkendale 2005, as *Tridentata. subtilis*; Galea 2008, as *S. rugosissima*; Oliveira *et al*. 2016, as *S. rugosissima*; Miglietta *et al*. 2018, as *S. rugosissima*); eastern Atlantic (Broch 1914, as *S. hupferi*).

Tridentata turbinata **(Lamouroux, 1816)**

Fig. 10e, f

Dynamena turbinata Lamouroux, 1816: 180.
Tridentata turbinata.—Coles *et al*., 2002b: 177.—Carlton & Eldredge, 2009: 39.—Calder, 2020: 224, fig. 6h, i.

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

Voucher material. Laysan Island, on *Halimeda* sp., 18.ix.2002, two colonies or colony fragments, to 6 mm high, without gonothecae, coll. A. Faucci, ROMIZ B5441.—Laysan Island, on *Halimeda* sp., 17.ix.2002, one colony, 5 mm high, with gonothecae, coll. A. Faucci, ROMIZ B5442.—Laysan Island, on *Halimeda* sp., 17.ix.2002, three colonies or colony fragments, to 3.5 mm high, with gonothecae, coll. A. Faucci, ROMIZ B5443.—Pearl & Hermes Atoll, on *Macrorhynchia philippina*, 19.ix.2002, one colony, 6 mm high, with gonothecae, coll. A. Faucci, ROMIZ B5444.

Remarks. The hydroid *Tridentata turbinata* (Lamouroux, 1816) is widespread and relatively well-known in shallow, tropical to subtropical waters. Worldwide, it has been reported from the Pacific, Atlantic, and Indian oceans (Redier 1971, as *Sertularia turbinata*; Millard 1975, as *S. turbinata*; Rees & Vervoort 1987, as *S. turbinata*; Gibbons & Ryland 1989, as *S. turbinata*; Calder 1991a, 2020; Hirohito 1995, as *S. turbinata*; Migotto 1996, as *S. turbinata*; Medel & Vervoort 1998, as *S. turbinata*; Schuchert 2003, as *S. turbinata*; Humara-Gil & Cruz-Gómez 2018).

In terms of relationships, the molecular phylogenies of Maronna *et al*. (2016), Song (2019), and Galea & Maggioni (2021) combine *T. turbinata* in a clade with *T. marginata* (Kirchenpauer, 1864), *T. tumida* (Allman, 1877), and *T. perpusilla* (Stechow, 1919b), with the last of these being the type species of the genus *Tridentata* Stechow, 1920. Added to that clade by Galea & Maggioni was *Sertularia trigonostoma* Busk, 1852. In another clade relatively close to them are species here assigned to *Disertasia* Neppi, 2017, including *Dynamena crisioides* Lamouroux, 1824, *Sertularia disticha* Bosc, 1802 and *S. moluccana* Pictet, 1893. In a series of clades more distant from them in the phylograms are *Sertularia pumila* Linnaeus, 1758, type species of *Dynamena* Lamouroux, 1812, *S. operculata* Linnaeus, 1758, type species of *Amphisbetia* L. Agassiz, 1862, and *Sertularia argentea* Linnaeus, 1758, type species of *Sertularia* Linnaeus, 1758.

Discussion of the hydroid *T. turbinata* in Hawaiian waters has been given elsewhere (Calder 2020). In being a predominantly shallow-water species, it was not reported by Nutting (1905) in collections from mostly deep waters of the state by the United States Bureau of Fisheries steamer *Albatross*.

Reported Distribution. Hawaiian archipelago. Oahu: Waikiki, Outside Pop's, 6 m (Coles *et al*. 2002b); Waikiki, *Atlantis* Submarine site, 20 m (Coles *et al*. 2002b); Waikiki, Ala Wai buoy (Coles *et al*. 2002b); Waikiki, Kapua Channel, 5 m (Coles *et al*. 2002b).—Maui: Molokini outer rim (Calder 2020).
Elsewhere. Circumglobal in shallow, tropical and subtropical waters (Calder 2019, 2020).

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

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

Bicaularia tongensis **(Stechow, 1919b)**

Fig. 10g

Sertularella tongensis Stechow, 1919b: 89, figs F^1, G^1.—Coles *et al*., 2002a: 318.—Carlton & Eldredge, 2009: 38.
Bicaularia tongensis.—Calder, 2020: 217, fig. 5c, d.

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

Voucher material. Midway Atoll, on a bryozoan, 23.ix.2002, one colony, 3.5 mm high, without gonothecae, coll. A. Faucci, ROMIZ B5445.—Laysan Island, on *Halimeda* sp., 17.ix.2002, one colony, 5 mm high, with gonothecae, coll. A. Faucci, ROMIZ B5446.

Remarks. A taxonomic account of *Bicaularia tongensis* (Stechow, 1919b) in Hawaii has been given earlier (Calder 2020). New records of the species from the region are added here from Midway Atoll and Laysan Island.

A thorough account of this species, accompanied by a synonymy list, has been provided by Song (2019) and Song *et al*. (2019).

Reported Distribution. Hawaiian archipelago. Oahu: Kaneohe Bay, Moku Manu Island (Coles *et al*. 2002a, as *Sertularella tongensis*; Calder 2020).

Elsewhere. Indo-Pacific; Caribbean Sea; Mediterranean Sea (Song *et al*. 2019). If *Sertularella exilis* Fraser, 1938 is conspecific, the species also occurs in the eastern Pacific (Fraser 1938, 1948).

Family Plumulariidae McCrady, 1859

Genus *Monotheca* Nutting, 1900

Monotheca flexuosa (Bale, 1894)

Fig. 11a

Plumularia flexuosa Bale, 1894: 115, pl. 5 figs 6–10.
Monotheca flexuosa.—Calder, 2020: 225, fig. 7d–f.

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

Voucher material. Kure Atoll, on algae, 26.ix.2002, one colony, 2.5 mm high, without gonothecae, coll. A. Faucci, ROMIZ B5447.

Remarks. Originally described from Australia, *Monotheca flexuosa* (Bale, 1894) was recently reported in the central North Pacific from the main Hawaiian Islands of Oahu and Maui (Calder 2020). While its overall distribution is still uncertain, Watson (2011a) suspected that the species might be cosmopolitan.

In having slender colonies and cup-shaped hydrothecae with essentially straight margins, *M. flexuosa* resembles *M. margaretta* Nutting, 1900, the type species of *Monotheca* Nutting, 1900. Unlike in *M. margaretta*, however, its stems are more flexuous, lateral nematothecae appear sessile rather than pedicellate, and hydrothecae lack a median adaxial notch. Another similar species is *M. pulchella* (Bale, 1881), but its stem is robust with stronger perisarcal ridges, and hydrocladia arise midway along much shorter cauline internodes (Bale 1894; Watson 2011a). As for *M. obliqua* (Johnston, 1847), its margin is more sinuous, and female gonothecae appear to be smooth (Cornelius 1995b) rather than transversally ridged, as in *M. margaretta* (Calder 1997), or smooth to faintly undulated, as in *M. flexuosa* (Watson 2011a).

Evidence for recognition of *Monotheca* as distinct from *Plumularia* Lamarck, 1816 has been made elsewhere on the basis of both morphology (Calder 1997) and genetics (Moura *et al*. 2018). Species currently assigned to the genus are small and often epiphytic, although *M. obliqua*, *M. flexuosa*, *M. margaretta*, and *M. bergstadi* Gil & Ramil, 2021 are or appear to be substrate generalists (Watson 2011a; Gravili *et al*. 2015; Calder 2019; Gil & Ramil, 2021).

Reported Distribution. Hawaiian archipelago. Oahu: Palea Point, just outside Hanauma Bay, 8 m (Calder 2020).—Maui: Kanaio, 12 m (Calder 2020).

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

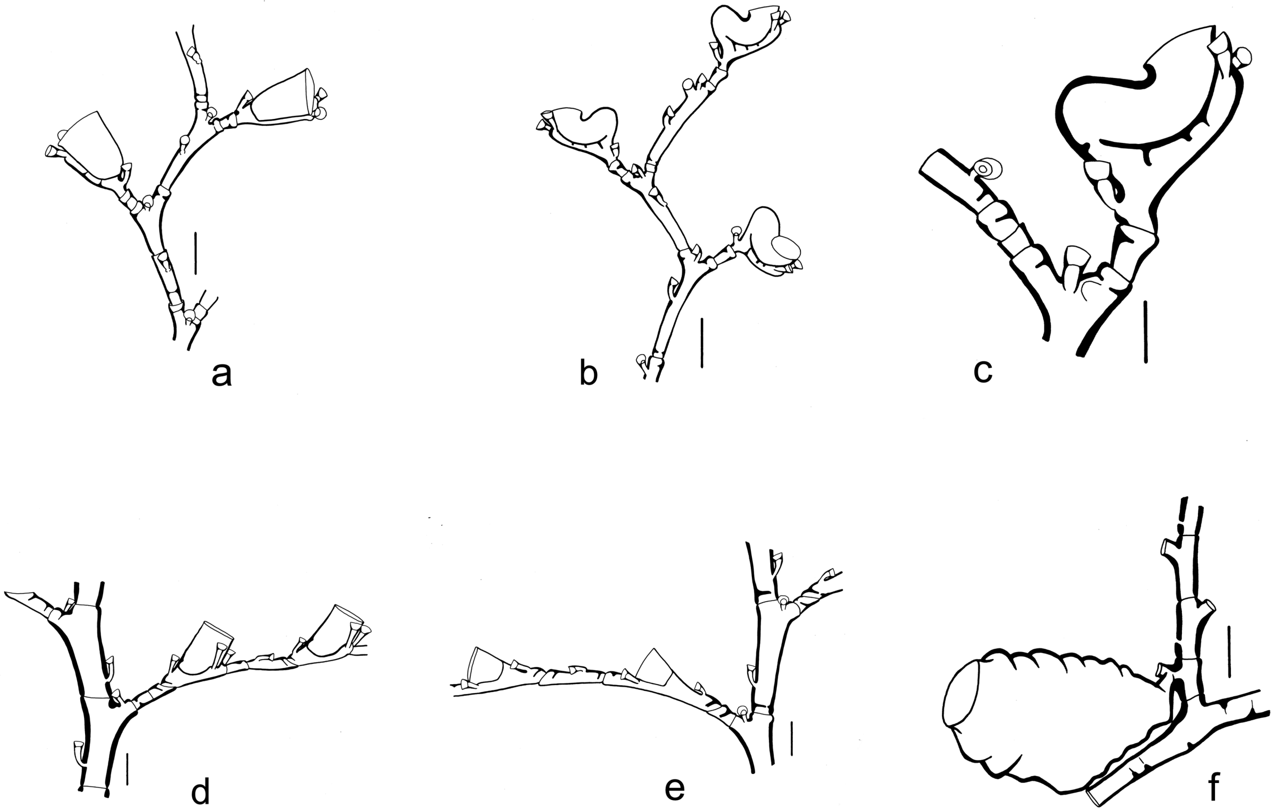

FIGURE 11. Plumulariidae. a, *Monotheca flexuosa* (Bale, 1894), part of hydrocaulus with two hydrocladia, each with a hydrotheca, Kure Atoll, ROMIZ B5447. Scale equals 0.1 mm. **b, *Monotheca gibbosa,*** sp. nov., holotype, part of hydrocaulus with hydrocladia and three hydrothecae, Laysan Island, ROMIZ B5448. Scale equals 0.1 mm. **c, *Monotheca gibbosa,*** sp. nov., holotype, part of hydrocaulus, and a hydrocladium with one hydrotheca, Laysan Island, ROMIZ B5448. Scale equals 0.05 mm. **d, *Plumularia floridana* (Nutting 1900)**, part of hydrocaulus with bases of two hydrocladia, one with two hydrothecae, Gardner Pinnacles, ROMIZ B5449. Scale equals 0.1 mm. **e, *Plumularia strictocarpa* Pictet, 1893**, part of hydrocaulus with bases of two hydrocladia, one with two hydrothecae, Kure Atoll, ROMIZ B5453. Scale equals 0.1 mm. **f, *Plumularia strictocarpa* Pictet, 1893**, part of hydrorhiza, and proximal end of hydrocaulus with a gonotheca, Kure Atoll, ROMIZ B5453. Scale equals 0.2 mm.

Monotheca gibbosa, sp. nov.

Figs 11b, c, 12

Plumularia margaretta.—Cooke, 1977: 100, fig. 27 (not *Monotheca margaretta* Nutting, 1900).

Type locality. USA: Hawaii, Laysan Island, at SCUBA depth, on calcareous rubble.

Etymology. The specific name is derived from the Latin adjective *gibbus*, meaning “bulging”, “protuberant”, or “hunpbacked”, in allusion to the prominent hump at the base of the hydrotheca.

Voucher material. HOLOTYPE: Laysan Island, on a small piece of calcareous rubble, 18.ix.2002, three fragments of a colony, to 2 mm high, without gonothecae, coll. A. Faucci, ROMIZ B5448.
PARATYPE: Laysan Island, on algae, 18.ix.2002. two colonies or colony fragments, to 2 mm high, without gonothecae, coll. A. Faucci, ROMIZ B5492.

Description. Colonies minuscule, inconspicuous, with erect cormoids reaching 2 mm high, arising from a creeping hydrorhiza having occasional internal perisarcal spurs in its lumen. Hydrocaulus monosiphonic, strongly geniculate distal to a straight pedicellate base of varied length, unbranched, divided at regular intervals into long, slender, ahydrothecate internodes by distinct, transverse nodes; cauline internodes relatively straight, 180–230 µm long beyond basal region, 19–25 µm wide at nodes, with firm perisarc and internal perisarcal ridges at proximal and distal ends, each internode with one nematotheca in axil of a distal apophysis and one about midway on internode on side opposite apophysis. Apophyses with a mamelon and a distal perisarcal ridge, given off alternately from opposite sides of hydrocaulus, bearing short, unbranched hydrocladia each with a single distal hydrotheca. Hydrocladia 140–190 µm long, with one proximal athecate internode and a longer distal thecate internode; nodes nearly straight; athecate internodes short, lacking nematothecae, 35–40 µm long, narrowest proximally, widest distally, with a distal perisarcal ridge; thecate internodes 120–150 µm long, saddle-shaped in lateral view, each with a hydrotheca, a median inferior nematotheca, two lateral nematothecae, and usually with three internal perisarcal ridges beneath hydrotheca, terminating in a blunt and short central point between lateral nematothecae, ending proximal to adaxial wall of hydrothecal orifice. Nematothecae bithalamic, movable, conical; cauline nematothecae 45 µm long; median nematothecae 30–40 µm long, not reaching base of hydrotheca, rim sloping only slightly downwards from abaxial to adaxial wall; lateral nematothecae 35–45 µm long, arising from slight lateral bulges at distal end of internode, not reaching hydrothecal orifice. Hydrothecae prostrate, with base elevated on raised subhydrothecal chamber of internode, creating a prominent basal hump, proportionately deep, with maximum depth 125–145 µm, slender and cylindrical but with a pronounced U-shaped bend, perisarc firm relative to thecal size; adaxial wall concave, adnate to internode except free at distal end; abaxial wall strongly convex except becoming strongly concave below margin; rim nearly circular, entire, facing obliquely upwards, aperture diameter 65–67 µm; base with a ring of desmocytes; intrathecal ridge lacking.

Gonothecae not seen.

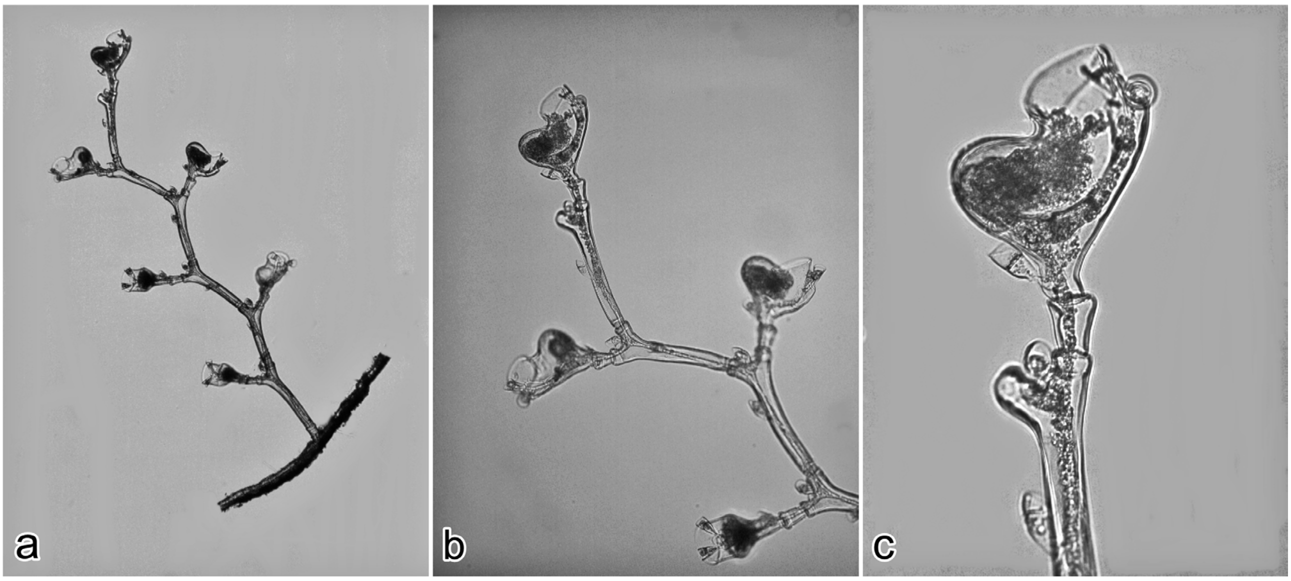

FIGURE 12. Plumulariidae. *Monotheca gibbosa*, sp. nov., holotype, Laysan Island, ROMIZ B5448**. a,** part of colony, with hydrorhiza, hydrocaulus, six hydrocladia, and six hydrothecae**. b,** distal end of hydrocaulus, with four hydrocladia and four hydrothecae. **c,** distal end of hydrocaulus, with hydrocladium and a hydrotheca.

Remarks. *Monotheca gibbosa*, **sp. nov.**, is immediately distinguishable from all other species currently assigned to *Monotheca* Nutting, 1900 in the distinctive shape of its hydrothecae. These are proportionately elongate, slender, and bent in the shape of a curved cylinder, with the abaxial wall having a prominent basal hump. In this, they somewhat resemble an inchworm (caterpillar of a geometrid moth) in motion. By contrast, hydrothecae in other species of the genus, namely *M. obliqua* (Johnston, 1847), *M. australis* (Kirchenpauer, 1876), *M. hyalina* (Bale, 1881), *M. pulchella* (Bale, 1881), *M. spinulosa* (Bale, 1881), *M. flexuosa* (Bale, 1894), *M. margaretta* Nutting, 1900, *M. posidoniae* Picard, 1951, *M. togata* Watson, 1973, *M. amphibola* Watson, 2011a, *M. bergstadi* Gil & Ramil, 2021, are shaped like a cup, bowl, scoop, cowl, or bonnet. Also differing in the same way are other species that have been assigned at times to *Monotheca*, including *Plumularia excavata* (Mulder & Trebilcock, 1911), *P. crateriformis* (Mulder & Trebilcock, 1911), *P. vervoorti* (Leloup, 1971), *P. epibracteolosa* Watson 1973, and *P. meretricia* Watson, 1973. More closely resembling hydrothecae of *M. gibbosa* are those of *Plumularia goldsteini* Bale, 1881. However, each hydrocladium in that species bears 3–4 hydrothecae rather than one, and the aperture of the hydrotheca is vertical rather than oblique in orientation.

Other noteworthy characters also set *M. gibbosa* apart from its congeners. For example, there are no abaxial and adaxial flanges on the hydrothecae, as in *M. amphibola*. Thecate internodes of the species end in an inconspicuous point, while those of *M. spinulosa* terminate in a prominent spine (Bale 1881; Watson 2011a). Hydrothecae lack an intrathecal ridge, such as that present in both *M. australis* and *M. spinulosa*. Nematothecae are not adaxially excavated like those in *M. spinulosa* and *M. togata*, and median nematothecae are neither adaxially excavated nor immovable as in *M. australis* and *M. amphibola* (Watson 2011a). The hydrothecal rim is entire rather than being indented by a median adaxial notch as in *M. margaretta*. Characters of the gonothecae are also of value in distinguishing species of *Monotheca*, but those of *M. gibbosa* are as yet unknown.

Although described here as a new species, this is the second report of *M. gibbosa* from Hawaii. Cooke (1977) reported it, as *Plumularia margaretta*, from red algae (*Amansia* sp.) on the Kahe Point Reef, Oahu. As noted above, the Atlantic *M. margaretta* differs in having hydrothecae that are cup-shaped and shallow rather than being elongate and in the form of a curved cylinder.

Hydroid colonies of *M gibbosa* are exceptionally minuscule and inconspicuous. Of all the species in a genus having diminutive cormoids, it is perhaps the smallest. Colonies described here were only 2 mm in height, and specimens reported from Kahe Point Reef, Oahi, by Cooke (1977, as *M. margaretta*) were likewise 1–2 mm high. Other species of *Monotheca* with colonies less than 5 mm high include *M. togata* and *M. amphibola* (Watson 2011a). The largest colonies of the genus appear to be those of *M. obliqua*, which can reach 4 cm high (Gravili *et al*. 2015).

Although most species of *Monotheca* are believed to be epiphytic (Watson 2011a), hydroids of *M. gibbosa* examined here occurred on a fragment of calcareous rubble as well as on algae. Of 11 species recognized in the genus in this work (*M. obliqua*, *M. australis*, *M. hyalina*, *M. spinulosa, M. pulchella*, *M. flexuosa*, *M. margaretta*, *M. posidoniae*, *M. togata*, *M. amphibola*, and *M. bergstadi*), only four appear to be substrate generalists. The predominantly European *M. obliqua* has been reported from algae, sponges, hydroids, bryozoans, cirripedes, and rocks (Cornelius 1995b; Gravili *et al*. 2015). In the Pacific, *M. flexuosa* has been found on red and green algae, mussels, ascidians, and polychaete tubes (Watson 2011a). The common Atlantic hydroid *M. margaretta* has most often been observed on algae (e.g., *Sargassum*, *Turbinaria*) and seagrasses (*Thalassia*), but it also occurs on invertebrates and inanimate substrates (Galea 2010, as *Plumularia margaretta*; Mendoza-Becerril *et al*. 2018; Calder 2019). The recently described *M. bergstadi* was found on algae and a bryozoan (Gil & Ramil 2021).

Reported Distribution. Hawaiian archipelago. Oahu: Kahe Point Reef (Cooke 1977, as *Plumularia margaretta*).

Genus *Plumularia* Lamarck, 1816

Plumularia floridana Nutting, 1900

Fig. 11d

Plumularia floridana Nutting, 1900: 59, pl. 2 figs 4, 5.—Coles *et al*., 2002a: 318; 2004: 73; 2006: 492.—Carlton & Eldredge, 2009: 36.—Calder, 2020: 226, fig. 7g.
Plumularian hydroid.—Edmondson, 1946: 26, fig. 13d.

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

Voucher material. Gardner Pinnacles, on rubble, 14.ix.2002, one colony, 4.5 mm high, without gonothecae, coll. A. Faucci, ROMIZ B5449.

Remarks. *Plumularia floridana* Nutting, 1900 was originally described from the Atlantic Ocean off the southwest coast of Florida (Nutting 1900). From identifications based on morphology, the species has subsequently been reported worldwide in shallow tropical to temperate waters, including Hawaii (Calder 2020). Cryptic diversity likely exists in hydroids assigned that binomen. With molecular work needed to sort out the taxonomy of this morphotype, current usage of the name *P. floridana* has been maintained for the colony from Gardner Pinnacles examined here.

Information on hydroids identified as *P. floridana* are provided in works such as those by Calder (1997, 2019, 2020), Ansín Agís *et al.* (2001), and Calder *et al*. (2021).

Reported Distribution. Hawaiian archipelago. Oahu: Waikiki Reef, underside of stones (Edmondson 1946, as "plumularian hydroid"); Kaneohe Bay, Hakipuu Reef Flat (Coles *et al*. 2002a); Kaneohe Bay, Waiahole Reef (Calder 2020).—Island of Hawaii, Kawaihae Reef, just seaward of Kawaihae Harbor (Coles *et al*. 2004, 2006); Red Hill (Coles *et al*. 2006).

Elsewhere. Circumglobal in the neritic zone of tropical, subtropical, and temperate waters (Ansín Agís *et al.* 2001; Calder 2020).

Plumularia strictocarpa Pictet, 1893

Fig. 11e, f

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.—Calder, 2020: 228, fig. 7h–j.

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; shallow water (Pictet 1893).

Voucher material. Midway Atoll, on rubble, 23.ix.2002, three colonies or colony fragments, to 1.3 cm high, with developing gonothecae, coll. A. Faucci, ROMIZ B5450.—Laysan Island, 18.ix.2002, four colonies or colony fragments, to 2.5 cm high, without gonothecae, coll. A. Faucci, ROMIZ B5451.—Laysan Island, on *Halimeda* sp., 17.ix.2002, one colony, 2.5 cm high, without gonothecae, coll. A. Faucci, ROMIZ B5452.—Kure Atoll, on *Halimeda* sp., 25.ix.2002, three colonies or colony fragments, to 6 mm high, with gonothecae, coll. A. Faucci, ROMIZ B5453.

Remarks. In terms of morphology, *Plumularia strictocarpa* Pictet, 1893 can be difficult to separate from *P. setacea* (Linnaeus, 1758), with the latter being taxonomically important as the type species of *Plumularia* Lamarck, 1816 (International Commission on Zoological Nomenclature 1998, Opinion 1886). While colonies of *P. strictocarpa* are typically smaller and finer, the two species are most readily distinguished by their gonosomes. Fertile colonies from Kure and Midway atolls were therefore helpful in establishing identifications, with gonothecae of specimens examined here conforming with those of *P. strictocarpa*. Thus, they were typical of the species in being cocoon-shaped with spirally annulated walls (Fig. 11f), instead of being fusiform with a tubular neck and smooth walls, as in *P. setacea*. They also differed from gonothecae of the similar *P. warreni* Stechow, 1919b, which lack annulated walls (Millard 1975). Notably, these three species fall within the same clade in DNA barcoding studies (Moura *et al.* 2018), but were considered "likely good biological species" by Schuchert (2014).

Originally described from Ambon Bay, Indonesia (Pictet 1893), *P. strictocarpa* has been widely reported across the tropical and subtropical Pacific Ocean. The species has been reported to be circumglobal in distribution (Calder 2020), although evidence of genetic diversity now exists (Schuchert 2014; Moura *et al*. 2018). Schuchert identified at least two and possibly three distinct lineages in specimens from locations in the Indian (Mayotte, Maldives), Pacific (French Polynesia), and Atlantic (Brazil) oceans. Moura *et al*. concluded that these constitute three putative species.

Identifications from this study confirm the occurrence of *P. strictocarpa* in the Hawaiian region, and it is likely common in occurrence there. As implied earlier (Calder 2020), reports of the temperate *P. setacea* from Hawaii have probably been based on misidentifications of *P. strictocarpa*.

Reported Distribution. Hawaiian archipelago. Oahu: Kaneohe Bay, on a variety of substrates (Cooke 1977, as *Plumularia setacea*); 2.4 km off SE coast, 20 m, on PVC settlement plates (Bailey-Brock 1989, as *P. setacea*); Kaneohe Bay, North Channel (Coles *et al*. 2002a); Kaneohe Bay, Pristine Reef (Coles *et al*. 2002a); Kaneohe Bay, "Floating City" (Coles *et al*. 2002a); Kaneohe Bay, Moku Manu Island (Coles *et al*. 2002a); Waikiki, Canoes, 3.5 m (Coles *et al.* 2002b); Waikiki, Ala Wai buoy (Coles *et al.* 2002b); Waikiki, Kaiser's Channel (Coles *et al.* 2002b); Hawaii Kai, Maunalua Bay, Channel Marker 1 (Coles *et al.* 2002b); Hawaii Kai, Maunalua Bay, Koko Marina nearshore, 1.5 m (Coles *et al.* 2002b); Palea Point, just outside Hanauma Bay, 8 m (Calder 2020).—Maui, Maalaea Reef, near Maalaea Harbor (Coles *et al*. 2004).—Island of Hawaii, Red Hill (Coles *et al*. 2006).

Elsewhere. Reportedly circumglobal, tropical and subtropical waters (Pictet 1893; Millard & Bouillon 1973; Hirohito 1974, 1995; Millard 1975; Ryland & Gibbons 1991; Migotto 1996; Calder 1997, 2013, 2020; Calder *et al.* 2003; Kirkendale & Calder 2003; Coles *et al*. 2003; Calder & Kirkendale 2005; Galea & Ferry 2015; Oliveira *et al*. 2016).

Family Kirchenpaueriidae Stechow, 1921

Genus *Pycnotheca* Stechow, 1919b

Pycnotheca producta (Bale, 1881)

Fig. 13a

Plumularia producta Bale, 1881: 39, pl. 15 fig. 3.

Type locality. Australia: Victoria, Queenscliff (Bale 1881).

Voucher material. Laysan Island, on algae, 13.ix.2002, four colonies or colony fragments, to 6 mm high, without gonothecae, coll. A. Faucci, ROMIZ B5481.

Remarks. The generic name *Pycnotheca* Stechow, 1919b was proposed as a replacement name for *Diplocheilus* Allman, 1883, an invalid junior homonym of *Diplocheilus* van Hasselt & Temminck, 1823 (Pisces). The type species of the genus, by subsequent designation by Stechow (1923c: 215), is *Diplocheilus mirabilis* Allman, 1883. Molecular phylogenetic studies (Maronna *et al*. 2016; Moura *et al*. 2018) confirm the close phylogenetic relationship of *Pycnotheca* to kirchenpaueriid genera including *Kirchenpaueria* Jickeli, 1883 and *Oswaldella* Stechow, 1919a.

Watson (1990) provided a review of characters useful in distinguishing the three currently recognized species of *Pycnotheca*. *Pycnotheca mirabilis* (Allman, 1883) differs from *P. producta* (Bale, 1881) and *P. biseptata* (Blackburn, 1938) in having stems that are longer (up to 35 mm rather than to 10–15 mm), hydrocladia that arise at a more acute angle and are both long and flexuous rather than short and stiffer, hydrothecae that are decidedly scoop-shaped rather than jug- or bowl- shaped, and gonothecae that are large and usually erect rather than small and typically adherent to the hydrorhiza or substrate. In life, hydranths of *P. producta* were said by Watson to be a luminescent bluish–white in colour. *Pycnotheca biseptata* differs from both *P. mirabilis* and *P. producta* in having a rudimentary septal ridge passing from the hydrocladial internode into the adcauline wall of the hydrotheca. Watson also provided measurements of major morphological characters of each species. In terms of substrate preferences, *P. mirabilis* was reported by Vervoort & Watson (2003) to be predominantly an epizoite and *P. producta* an epiphyte. Nonetheless, Vervoort & Watson noted that differences between *P. producta* and *P. mirabilis* were not clearly resolved. If the two should prove conspecific, the name *P. producta* was described first and would have nomenclatural priority. Based on Watson's (1990) characterization of the three species, specimens from Laysan most closely correspond with *P. producta* and have been assigned to that species here.

The geographic distribution of *P. producta* is uncertain because it and *P. mirabilis* may have been confused in some works (Watson 1990). To date, the species has been reported from locations in both the western and eastern Pacific, although the report of it from California by Torrey (1902, as *Halicornaria producta*) needs confirmation. If *P. mirabilis* is conspecific, the range of the species is extended to many locations across the Indo-west Pacific (Ansín Agís *et al*. 2014), as well as to False Bay, South Africa (Millard 1957), Vema Seamount (Millard 1966b), and Brazil (Oliveira *et al*. 2016) in the Atlantic.

The publication of Bale (1881) in which *P. producta* was first described is usually dated as 1882. Evidence exists that it appeared as a separate in 1881 (see comment in References section).

Reported Distribution. Hawaiian archipelago. First record.

Elsewhere. Australia (Bale 1881, as *Plumularia producta*; Watson 1990, 1997); Japan (Inaba 1892, as *P. producta*); ? California, USA (Torrey 1902, *Halicornaria producta*).

Family Halopterididae Millard, 1962

Genus *Antennella* Allman, 1877

Antennella cf. *secundaria* (Gmelin, 1791)

Fig. 13b–d

Sertularia secundaria Gmelin, 1791: 3854.

Antennella secundaria.—Coles *et al*., 2002a: 318; 2002b: 177; 2004: 73.—Carlton & Eldredge, 2009: 36.
Monostaechas quadridens.—Calder, 2020: 230, fig. 8h, i [not *Monostaechas quadridens* (McCrady, 1859)].

Type locality. "Habitat in mari mediterraneo" (Gmelin 1791, as *Sertularia secundaria*).

Voucher material. Midway Atoll, on algae, 23.ix.2002, one unbranched colony, 3 mm high, without gonothecae, coll. A. Faucci, ROMIZ B5454.—Midway Atoll, 23.ix.2002, one branched colony, 6.5 mm high, without gonothecae, coll. A. Faucci, ROMIZ B5455.—Kure Atoll, on algae, 25.ix.2002, one unbranched colony, 4 mm high, without gonothecae, coll. A. Faucci, ROMIZ B5456.—Nihoa, 06.x.2002, two branched colonies or colony fragments, to 6 mm high, without gonothecae, coll. A. Faucci, ROMIZ B5457.

Remarks. Originally described from the Mediterranean Sea, *Antennella secundaria* (Gmelin, 1791) has now been reported numerous times from tropical to temperate waters worldwide (Cornelius 1995b). This is reflected in the extensive distribution records and lengthy synonymy list of the species provided by Ansín Agís *et al.* (2001). It nevertheless appears certain now that cryptic species exist in hydroids assigned to *A. secundaria*, with multiple lineages having been distinguished through barcoding sequences (Moura *et al*. 2018, 2019). Indeed, Cornelius (1995b) had suspected, based on observed morphological differences, that more than one species was represented under the name. Given their wide separation geographically, hydroids from the Hawaiian Islands may well be distinct from those of the Mediterranean. However, with the current taxonomy of *A. secundaria* being unsettled, traditional nomenclature has been maintained here.

Of multiple cryptic species identified by Moura *et al*. (2018) within the *A. secundaria* complex, one lineage, conjointly with *A. confusa* Ansín Agís, Ramil & Vervoort, 2001, clustered with the genus *Monostaechas* Allman, 1877. Differences between *Antennella* Allman, 1877 and *Monostaechas* therefore need to be explored, and if valid the two genera may need to be redefined. If congeneric, precedence would have to be established according to the First Reviser Principle in nomenclature (ICZN 1999, Art. 24.2) inasmuch as they were described in the same work by Allman (1877). As for the species *A. secundaria* and *Monostaechas quadridens*, little doubt exists that they are distinct.

While hydroids of *A. secundaria* are usually unbranched and arise directly from the hydrorhiza, occasional colonies of the species are branched in the form of a helicoid sympodium. Accounts of the branched form have been given in various works including those of Billard (1913), Van Gemerden-Hoogeveen (1965), Millard & Bouillon (1973), Millard (1975), Vervoort & Vasseur (1977), Ryland & Gibbons (1991), Calder (1997), and Schuchert (2003). Both unbranched (ROMIZ B5454; ROMIZ B5456) and branched (ROMIZ B5455; ROMIZ B5457) colonies were represented in the present collection.

In a previous paper on hydroids from the main islands of Hawaii (Calder 2020), branched colonies of *A. secundaria* were misidentified as *M. quadridens*. Indeed, several records of *M. quadridens* in the Pacific and Indian oceans may likewise have been based on such misidentifications. Accounts of *M. quadridens* from the vicinity of its type locality near Charleston, South Carolina, USA, indicate that branching in the species is extensive and differs in typically being truly dichotomous. In it, the basal hydrocaulus usually gives rise to a pair of opposite and upward-directed branches, with the continuation of the main stem often similarly re-branched (Nutting 1900; Calder 1983). Branches are then re-branched in the form of a helicoid sympodium. Colonies of the species attain a height of as much as 15 cm (Nutting 1900; Fraser 1944) and are light mahogany in colour. By contrast, the number of branches in colonies of *A. secundaria*, if there are any at all, are almost always limited to four or fewer (Ryland & Gibbons 1991), colonies seldom reach 5 cm high, and the colour is greenish-yellow to red (Cornelius 1995b; Gravili *et al*. 2015).

Nomenclaturally, the type species of *Antennella* Allman, 1877, by monotypy, is *A. gracilis* Allman, 1877. It, in turn, has been considered a junior subjective synonym of *A. secundaria*. That putative synonymy may need reassessment in light of the genetic diversity discovered in this morphospecies.

Reported Distribution. Hawaiian archipelago. Oahu: Kaneohe Bay, North Channel (Coles *et al*. 2002a); Pristine Reef (Coles *et al*. 2002a; Calder 2020, as *Monostaechas quadridens*); Waikiki, Outside Pop's, scoured reef, 6 m (Coles *et al.* 2002b); Waikiki, *Atlantis* submarine artificial reef, 20 m (Coles *et al.* 2002b); Waikiki, Ala Wai buoy (Coles *et al.* 2002b); Waikiki, Kapua Channel, 5 m (Coles *et al.* 2002b).—Molokai: Kaunakakai Harbor main dock (Coles *et al*. 2004).

Elsewhere. Considered cosmopolitan in temperate to tropical waters (Millard 1975; Ansín Agís *et al.* 2001), but this is likely subject to revision.

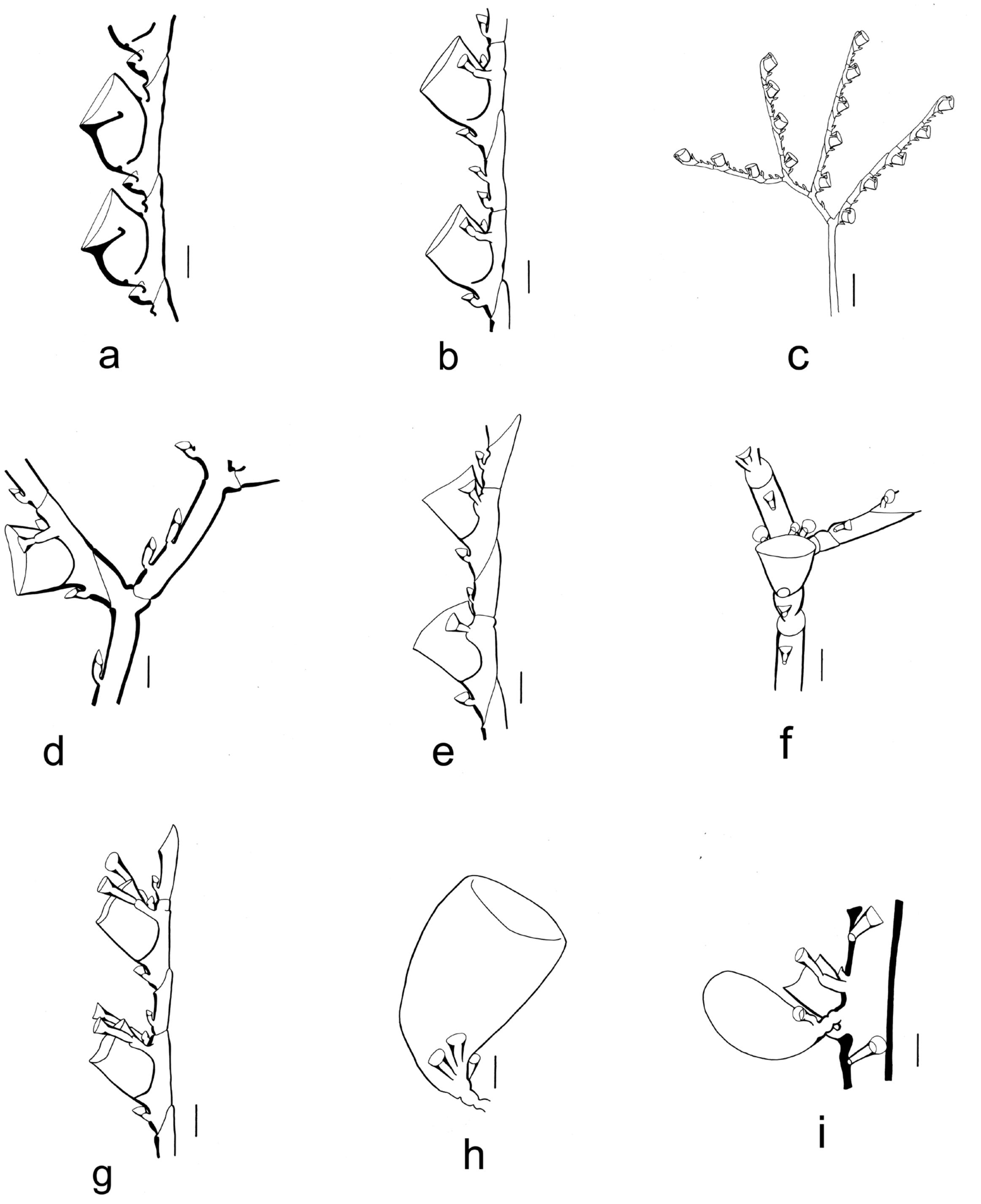

FIGURE 13. Kirchenpaueriidae and Halopterididae. a, ***Pycnotheca producta*** **(Bale, 1881),** part of a hydrocladium with two hydrothecae, Laysan Island, ROMIZ B5481. Scale equals 0.1 mm. **b,** ***Antennella secundaria*** **(Gmelin, 1791)**, part of hydrocaulus with two hydrothecae, Midway Atoll, ROMIZ B5454. Scale equals 0.1 mm. **c,** ***Antennella secundaria*** **(Gmelin, 1791)**, part of a colony to show branching, Midway Atoll, ROMIZ B5455. Scale equals 0.5 mm. **d,** ***Antennella secundaria*** **(Gmelin, 1791)**, part of hydrocaulus, and base of a hydrocladium with a hydrotheca, Midway Atoll, ROMIZ B5455. Scale equals 0.1 mm. **e,** ***Halopteris alternata*** **(Nutting, 1900)**, part of a hydrocladium with two hydrothecae, Laysan Island, ROMIZ B5458. Scale equals 0.1 mm. **f,** ***Halopteris alternata*** **(Nutting, 1900)**, part of hydrocaulus, with a cauline hydrotheca and proximal end of a hydrocladium, Laysan Island, ROMIZ B5458. Scale equals 0.1 mm **g,** ***Halopteris longibrachia,*** **nom. nov.**, part of a hydrocladium with two hydrothecae, Gardner Pinnacles, ROMIZ B5459. Scale equals 0.1 mm. **h,** ***Halopteris longibrachia,*** **nom. nov.**, female gonotheca, Pearl & Hermes Atoll, ROMIZ B5461. Scale equals 0.1 mm. **i,** ***Halopteris longibrachia,*** **nom. nov.**, part of hydrocaulus with a male gonotheca, Gardner Pinnacles, ROMIZ B5459. Scale equals 0.1 mm.

Genus *Halopteris* Allman, 1877

Halopteris alternata (Nutting, 1900)

Fig. 13e, f

Plumularia alternata Nutting, 1900: 62, pl. 4 figs 1, 2.
Halopteris diaphana.—Cooke, 1977: 99, fig. 26.—Carlton & Eldredge, 2009: 36 [not *Halopteris diaphana* (Heller, 1868)].
Halopteris diaphena.—Coles *et al*., 2004: 73 [incorrect subsequent spelling; not *Halopteris diaphana* (Heller, 1868)].

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

Voucher material. Laysan Island, on hydroid stem, 18.ix.2002, two colonies or colony fragments, to 8 mm high, without gonothecae, coll. A. Faucci, ROMIZ B5458.

Remarks. Hydroids examined here were referable to *Halopteris* Allman, 1877, and to the "*H. diaphana*" species group recognized within that genus by Schuchert (1997). Included in the group by him were *H. diaphana* (Heller, 1868), *H. tenella* (Verrill, 1873b), *H. alternata* (Nutting, 1900), *H. billardi* (Vannucci, 1951), and *H. platygonotheca* Schuchert, 1997. *Halopteris violae* Calder *et al*. 2003 has subsequently been assigned to the same group. Within that assemblage, specimens examined here from Laysan Island are closest to *H. alternata*. Characters distinguishing the species from others in the cluster have been reviewed by Schuchert (1997) and Calder *et al*. (2019).

For much of the 20th century, *H. alternata* was included in the synonymy of *H. diaphana*. Confusion over the status of two species was addressed and resolved by Schuchert (1997). He resurrected *H. alternata* as valid based on its distinctive trophosomal and gonosomal characters. DNA barcoding has confirmed that the two are distinct species (Moura *et al*. 2018; Galea *et al*. 2018). In *H. alternata*, an axillar nematotheca is usually present behind each cauline hydrotheca, one nematotheca rather than two or three is present on the athecate hydrocladial internodes, and female gonothecae are fusiform and mostly straight rather than cornucopia-shaped. Additional characters distinguishing the two were noted by Ansín Agís *et al.* (2001). In *H. alternata*, colonies were often found to be geniculate rather than straight, especially in younger parts. Also, they found segmentation of the hydrocaulus to be homomerous in basal parts but heteromerous in younger and apical parts, rather than being completely heteromerous as in *H. diaphana*. *Halopteris vervoorti* Galea, 2008, another similar species, differs from *H. alternata* in having paired rather than single cauline axillar nematothecae (Galea 2008; Galea *et al.* 2018; Calder 2020).

Halopteris alternata is widely distributed in warm parts of the western North Atlantic (Oliveira *et al*. 2016; Calder 2019), and it has been reported as well from the eastern Atlantic (Ansín Agís *et al.* 2001). In the Pacific, records of the species exist from Ecuador (Calder *et al*. 2019, 2021), and hydroids from Hawaii that have been identified earlier as the mostly European *H. diaphana* are taken here to have been based instead on *H. alternata*.

Obvious cryptic diversity has been identified within the *H. alternata* complex by Moura *et al*. (2018).

Reported Distribution. Hawaiian archipelago. Oahu: Kaneohe Bay (Cooke 1977, as *Halopteris diaphana*).—Maui: Kahului Harbor, Pier 1 (Coles *et al*. 2004, as *H. diaphena* sic); Kahului Harbor, Pier 2 (Coles *et al*. 2004, as *H. diaphena* sic).

Elsewhere. Western Atlantic (Oliveira *et al*. 2016; Calder 2019); eastern Atlantic (Ansín Agís *et al.* 2001); eastern Pacific (Calder *et al*. 2019, 2021); central Pacific (Cooke 1977, as *Halopteris diaphana*); possibly Indian Ocean (Jarvis 1922, as *Plumularia alternata*; Gravely 1927, as *Plumularia* sp. nr. *alternata*).

Halopteris longibrachia, nom. nov.

Fig. 13g–i

Plumularia polymorpha var. *sibogae* Billard, 1913: 25, fig. 16.

Type locality. Indonesia: Raja Ampat, 1°42.5'S, 130°47.5'E, 32 m (Billard 1913).

Voucher material. Gardner Pinnacles, on rubble, 14.ix.2002, two colonies or colony fragments, to 1.5 cm high, with gonothecae, coll. A. Faucci, ROMIZ B5459.—Gardner Pinnacles, on *Macrorhynchia phoenicea*, 14.ix.2002, two colonies, to 7 mm high, without gonothecae, coll. A. Faucci, ROMIZ B5460.—Pearl & Hermes Atoll, 19.ix.2002, four colonies or colony fragments, to 1.7 cm high, one colony with female gonothecae, coll. A. Faucci, ROMIZ B5461.

Etymology. The replacement specific name *longibrachia* is derived from the Latin words *longus*, meaning long, and *brachium*, meaning arm, in reference to the exceptionally long, arm-like lateral nematothecae that distinguish this species.

Remarks. Originally described as *Plumularia polymorpha* var. *sibogae* Billard, 1913, this species was recently elevated to species rank by Galea *et al*. (2018), as *Halopteris sibogae* (Billard, 1913). The species is a morphologically striking one in having unusually long lateral nematothecae that extend well beyond the rim of the hydrothecae. Other morphological differences setting it apart from *H. polymorpha* Billard, 1913 include an interesting colour difference in living specimens (Galea *et al*. 2018). While hydranths of *H. polymorpha* are yellow everywhere, those of the so-called *H. sibogae* are mostly yellow on the stems but white on the cladia. The distinctness of the species has been further confirmed by 16S DNA sequences (Galea *et al*. 2018). It occurs in a clade well-separated from *H. polymorpha* and close to *H. vervoorti* Galea, 2008.

Nomenclaturally, however, *Plumularia polymorpha* var. *sibogae* (=*Plumularia sibogae*; *Halopteris sibogae*) is a permanently invalid junior primary homonym of *Plumularia sibogae* Billard, 1911, a different species now assigned to *Antennella* Allman, 1877 (ICZN, 1999, Art. 57.2). With no available and potentially valid synonyms in existence for the rejected junior primary homonym *Plumularia sibogae*, *Halopteris longibrachia* is proposed here as a new replacement name for it.

Other halopteridids with exceptionally long lateral nematothecae and nematothecal apophyses include *Corhiza valdiviae* (Stechow, 1925), assigned to the new genus *Thamnopteros* by Galea, in Galea & Maggioni, 2020, and *T. uniserius* Galea, in Galea & Maggioni, 2020. However, colonies of the latter two differ greatly from those of *H. longibrachia* in being much larger (to 40 cm in *T. valdiviae*; to 17.2 cm in *T. uniserius*; to 2.5 cm high in *H. longibrachia*) and in having polysiphonic stems (Stechow 1925; Millard 1975; Schuchert 1997, Galea, in Galea & Maggioni 2020). Other characters distinguishing *T. valdiviae*, reported from South Africa and Mozambique, are provided by Stechow (1925), Millard (1975), and Schuchert (1997). Characters distinguishing *T. uniserius*, described from New Caledonia, have been summarized by Galea, in Galea & Maggioni (2020). *Halopteris infundibulum* Vervoort, 1966 also has a pair of long lateral nematothecae, but adjacent to each one, at the base of the same apophysis, is a smaller, much shorter nematotheca. Its hydrocladia differ in appearing essentially unsegmented. The species is known from bathyal depths off New Zealand, the Chatham Islands, and New Caledonia (Vervoort 1966; Vervoort & Watson 2003; Ansín Agís *et al*. 2009).

Although *H. longibrachia* ranges at least from the Seychelles (Millard & Bouillon, 1973, as *H. polymorpha* var. *sibogae*) to the Hawaiian Archipelago (this report), it has been reported infrequently. The type material of Billard (1913, as *Plumularia polymorpha* var. *sibogae*) consisted of two colonies from Raja Ampat, Indonesia, collected during the *Siboga* Expedition. Schuchert (1997, as *H. polymorpha* var. *sibogae*) examined those types, along with specimens from the Seychelles reported by Millard & Bouillon. Horia Galea collected numerous fertile colonies from two shipwrecks at Bali, Indonesia (Galea *et al*. 2018, as *H. sibogae*). Others examined in the same report were found on a reef north of Hoga Island in the Tukang Besi Archipelago, Indonesia, by G. Allard. A record from Japan by Hirohito (1983, as *H. polymorpha* var. *sibogae*) has been viewed with uncertainty (Galea *et al*. 2018). Specimens examined here from the Northwestern Hawaiian Islands were found at Gardner Pinnacles and Pearl & Hermes Atoll.

Reported Distribution. Hawaiian archipelago. First record.

Elsewhere. Western Pacific (Galea *et al*. 2018, as *Halopteris sibogae*); Indian Ocean (Millard & Bouillon 1973, as *H. polymorpha* var. *sibogae*).

Family Aglaopheniidae Marktanner-Turneretscher, 1890

Genus *Aglaophenia* Lamouroux, 1812

Aglaophenia postdentata Billard, 1913

Fig. 14a

Aglaophenia postdentata Billard, 1913: 100, fig. 89A–C.

Type locality. Indonesia: Makassar and vicinity; Baie de Wunoh, NW de l'Île Waigeu (=Wunoh Bay, NW of Waigeo Island) (Billard 1913).

Voucher material. Gardner Pinnacles, on *Halimeda* sp., 14.ix.2002, one colony, 2.6 mm high, without corbulae, coll. A. Faucci, ROMIZ B5462.—Gardner Pinnacles, on *Halimeda* sp., 14.ix.2002, one colony, 2.0 mm high, without corbulae, coll. A. Faucci, ROMIZ B5487.

Remarks. The hydroid of *Aglaophenia postdentata* Billard, 1913 is delicate, diminutive, and inconspicuous, with the single sterile colony observed here reaching a height of only 2.6 mm. Colonies of the species are commonly reported to be 5.0–8.5 mm high (Billard 1913; Jäderholm 1920; Vervoort 1941; Redier 1966; Millard & Bouillon 1973; Ryland & Gibbons 1991; Watson 2005; Moura 2020), although they are said to attain a height of about 1 cm (Watson 1994b; Galea 2010).

Morphological accounts of this species include those of Billard (1913), Jäderholm (1920), Vervoort (1941), Redier (1966), Millard & Bouillon (1973), Ryland & Gibbons (1991), Watson (1994b, 2005), Galea (2010), and Moura (2020). The open corbula of the species has been described by Millard & Bouillon (1973), Watson (1994b), and Moura (2020). Hydroid specimens examined by Watson (1994b) were yellow in life, with pink gonophores.

The hydrotheca of *A. postdentata* is small, with its distalmost adaxial quarter free from the internode. An intrathecal ridge extends from the adaxial to the abaxial wall, and the ridge continues partway into the adjoining internode in the examined specimen. Ten quite sharp cusps occur on the rim, comprising single abaxial and adaxial cusps together with four laterals on each side. The adaxial cusp is prominent, unlike the shallow, broad equivalent sometimes seen in the similar *A. pluma* var. *sibogae* Billard, 1913 (Schuchert 2003).

The center of distribution of this infrequently reported little species appears to be the tropical Indo-west Pacific region. However, it is now known to be widely distributed (Moura *et al*. 2018, 2019). In addition to its discovery in the central Pacific Ocean (this study), it has recently been reported from various locations in the Caribbean Sea (Galea 2010; Moura *et al*. 2018, 2019), the Gulf of Guinea in the eastern Atlantic Ocean (Moura *et al*. 2018), and from Brazil (Moura 2020). Of note, the molecular phylogenies of Moura *et al.* indicate that populations of the species across its range are genetically quite close. However, such studies also reveal that *A. postdentata* is distant from *Sertularia pluma* Linnaeus, 1758 (=*Aglaophenia pluma*), the type species of *Aglaophenia* Lamouroux, 1812. Based on evidence from molecular phylogenetic studies, its inclusion in the genus has been justifiably questioned by Postaire *et al*. (2016b).

The reported depth distribution of the species is from 3 m (Moura *et al*. 2018) to 102 m (Moura 2020). In studies undertaken at Juan de Nova Island, Gravier-Bonnet & Bourmaud (2006) found it to be a species of the reef platform (< 20 m).

Reported Distribution. Hawaiian archipelago. First record.

Elsewhere. Indo-west Pacific (Billard 1913; Jäderholm 1920; Vervoort 1941; Redier 1966; Millard & Bouillon 1973; Ryland & Gibbons 1991; Watson 1994b, 1996, 2005; Gravier-Bonnet & Bourmaud 2006, 2012; Moura *et al*. 2018); western Atlantic (Galea 2010; Moura *et al*. 2018; Moura 2020); eastern Atlantic (Moura *et al*. 2018).

Aglaophenia suensonii Jäderholm, 1896

Fig. 14b, c

Aglaophenia suensonii Jäderholm, 1896: 18, pl. 2 fig. 9.

Type locality. Japan: Hirudostrasse (=Hirado Strait), 33°10′N, 129°16′E (Jäderholm 1896).

Voucher material. Laysan Island, detached, 17.ix.2002, three unbranched, monosiphonic cormoids, to 2.4 cm high, one with a corbula, coll. A. Faucci, ROMIZ B5463.

Remarks. Trophosomes of these hydroids conform most closely with accounts of *Aglaophenia suensonii* Jäderholm, 1896 by authors including Jäderholm (1896), Stechow (1909, 1913b, 1923c), Rho (1967), Hirohito (1995), and Xu *et al*. (2014b). Corbulae resemble those in type material of the species in being moderately long, with about 11 pairs of fused corbulacostae. Jäderholm did not include an illustration of the corbula in describing *A. suensonii*, but one was provided later by Stechow (1909: 91, fig. 6) based on an examination of the type. It was elongate, with about 16 pairs of fused corbulacostae that lacked basal hydrothecae. Some subsequent illustrations of corbulae attributed to the species have been shorter, with about 5–8 pairs of ribs (Stechow 1913; Rho 1967; Hirohito 1995).

Aglaophenia suensonii somewhat resembles the temperate to boreal *A. pluma* (Linnaeus, 1758) of Europe and possibly elsewhere (Svoboda & Cornelius 1991; Cornelius 1995b). It is distinguished by corbulae that reach to a greater length (Stechow, 1923c), and by the shape of the marginal cusps of the hydrothecae. Unlike in *A. pluma*, the median abaxial hydrothecal cusp in *A. suensonii* is turned sharply inwards and is partly hidden in lateral view by a pair of large, arrowhead-shaped lateral cusps flanking it. In this, it approaches *A. parvula* Bale, 1881, but differs in having nine rather than 10 marginal cusps. Moreover, the four pairs of lateral cusps are regularly wavy in shape and are mostly similar in size, rather than being irregular in both shape and size as in *A. parvula*. As for *A. pluma*, it has been considered a species complex based on 16S rRNA sequences by Moura *et al*. (2012, 2018, 2019).

Aglaophenia suensonii is a little-known species, reported elsewhere from warm waters of the western Pacific. The specific name has been spelled *suensoni* in some works, but *suensonii* is the original and correct spelling (ICZN 1999, Art. 32.2).

Reported Distribution. Hawaiian archipelago. First record.

Elsewhere. Southern Japan (Hirohito 1995); southern South Korea (Park 1995); East China Sea (Xu *et al*. 2014).

***Aglaophenia whiteleggei* Bale, 1888**

Fig. 14d

Aglaophenia (?) *whiteleggei* Bale, 1888: 794, pl. 21 fig. 8.

Type locality. Unknown (Bale 1888); possibly Australia.

Voucher material. Pearl & Hermes Atoll, 28.ix.2002, two colonies, to 3.5 cm high, without corbulae, coll. A. Faucci, ROMIZ B5464.—Midway Atoll, 23.ix.2002, one colony, 2 cm high, without corbulae, coll. A. Faucci, ROMIZ B5465.—Kure Atoll, 25.ix.2002, one colony, 8 mm high, without corbulae, coll. A. Faucci, ROMIZ B5466.—Laysan Island, detached, 17.ix.2002, one branched colony, 1.8 cm high, without corbulae, coll. A. Faucci, ROMIZ B5467.

Remarks. The identity of *Aglaophenia whiteleggei* Bale, 1888 is somewhat in doubt. In describing this hydroid, Bale (1888) noted that the single, incomplete colony available to him was sterile, and its collection location was unknown ("*Hab*.—?"). Subsequent reports of the species have been from Japan (Stechow 1913b, 1923a; Jäderholm 1919; Stechow & Uchida 1931; Uchida 1958; Hirohito 1969; 1983; 1995), China (Hargitt 1927, as *Lytocarpus nuttingi*; Ling 1938, as *L. nuttingi*; Wei 1959; Huang 1988; Xu *et al.* 2014b), South Korea (Rho 1969; Rho & Park 1986), and Australia (Watson 1994a, 2011b). As for *Lytocarpus nuttingi* Hargitt, 1927, it has been included in the synonymy of *A. whiteleggei* by Huang (1988), Vervoort & Watson (2003), and Xu *et al*. (2014). Concurrently, it is accepted as a valid species (*Macrorhynchia nuttingi*) in WoRMS (Schuchert 2021c).

Ensuing descriptions of the reproductive structures of *A. whiteleggei* differ significantly. For example, Stechow (1913b), Hargitt (1927, as *Lytocarpus nuttingi*), Rho (1969) and Hirohito (1995) described them as forming an open corbula, as in certain species of *Aglaophenia* Lamouroux, 1812. By contrast, Watson (2011b) considered them to be phylactogonia in her material, and she transferred the species to *Macrorhynchia* Kirchenpauer, 1872. In her account, Watson neither cited records of the species from locations outside Australia nor mentioned any of the earlier accounts of the reproductive structures of *A. whiteleggei*. She thus considered her description to be the first account of them. Given material differences in these accounts, it appears certain that two different species have been reported under the binomen *A. whiteleggei*. To establish the likely identity of the species, and of specimens from the Northwestern Hawaiian Islands, accounts of the species by the various authors were compared here with the original description of Bale (1888).

In terms of cormidial structure, specimens from the Northwestern Hawaiian Islands corresponded quite closely with the accounts of Stechow (1913b), Ling (1938, as *L. nuttingi*), Hirohito (1995), and particularly Jäderholm (1919). These all appear more like those described and illustrated by Bale (1888) than those of Watson (2011b), and are taken here to represent *A. whiteleggei*. As with those multiple accounts, the outline of the hydrothecal margin beyond the first pair of cusps is wavy to slightly crooked rather than distinctly cuspate, and the mesial nematotheca diverges at an angle from the axial line of the hydrotheca over its distal third rather than following it. Marginal cusps illustrated by Rho (1969) were as distinct as those in figures by Watson, but they differ in being pointed rather than blunt. While cormidia illustrated by Huang (1988) are close in morphology to those described here, the first pair of cusps were low, with the largest pair being located midway along the lateral sides of the rim. Mesial nematothecae were similar in shape, but were less divergent from the hydrothecae. The perisarc of the cormidia was illustrated as being more thickened, but the overall pattern of the internodal ridges was essentially identical. As with material examined here, the intrathecal ridge is shown to be incomplete by Bale (1888), Stechow (1913), Jäderholm (1919), Rho (1969), Huang (1988), and Hirohito (1995), but complete in Ling (1938), Wei (1959), and Watson (2011). However, that character may vary depending upon the age of the colony part examined. Otherwise, our cormidia are much as described by Bale, Stechow, Jäderholm, Ling, Wei, Huang, and Hirohito. Specimens examined here have therefore been assigned to *A. whiteleggei*. Nevertheless, the identity of the species warrants additional consideration.

Watson (1911) concluded from collection records in the Australian Museum, Sydney, and Museum Victoria, Melbourne, that the type material of Bale (1888) came from Port Jackson, Australia. Stranks (1993) had concluded that different material from an unknown locality might be the type. We simply follow Bale (1888) in concluding that the collection locality of *A. whiteleggei* is unknown.

Reported Distribution. Hawaiian archipelago. First record.

Elsewhere. Unknown location, possibly Australia (Bale 1888); South Korea (Rho 1969); Okinawa (Yamada & Kubota 1987); Japan (Hirohito 1995); China (Huang 1988; Xu *et al*. 2014).

Genus *Lytocarpia* Kirchenpauer, 1872

Lytocarpia flexuosa (Lamouroux, 1816)

Fig. 14e

Aglaophenia flexuosa Lamouroux, 1816: 167.

Type Locality. "Indes Orientales" (Lamouroux 1816).

Voucher material. Pearl & Hermes Atoll, unattached, 19.ix.2002, two colonies, to 4.4 cm high, without corbulae, coll. A. Faucci, ROMIZ B5479.

Remarks. Most records of *Lytocarpia flexuosa* (Lamouroux, 1816) to date have been from locations in the western Indian Ocean (e.g., Billard 1907, as *Thecocarpus giardi*; Millard 1975, as *T. flexuosus flexuosus*; Gravier-Bonnet 1979, as *T. flexuosus*; Rees & Vervoort 1987; Gravier-Bonnet & Bourmaud 2006). Rees & Vervoort (1987) considered reports of the species from the East Indies by Lamouroux (1916, as *Aglaophenia flexuosa*) and from Australia by Kirchenpauer (1872, as *A. flexuosa*) to be dubious inasmuch as it has not been recorded again from the Tropical Western Pacific. Its discovery far to the east at Pearl & Hermes Atoll in this study may reduce some of the doubt. The reported range of the species now extends from South Africa (Millard 1975) and the Red Sea (Mergner & Wedler 1977) to the Northwestern Hawaiian Islands.

Considerable variation in colony form and hydrothecal morphology has been described in hydroids assigned to *L. flexuosa* (Millard 1958, as *T. giardi*, 1962, as *T. flexuosus*, 1975, as *T. flexuosus*). In particular, branching of the colony may be in the form of a spiral or an umbel. Hinge joints vary in location, and hydrocladia may be short or long. The abcauline marginal cusp may be solid or hollow, and it may be simple or bifurcated. One pair or more of the lateral cusps are usually bifid, but not always. The existence of intermediate forms led Millard (1962, 1975) to regard the variants as subspecies of *L. flexuosa*.

Rees & Vervoort (1987: 175) provided a synonymy list for *L. flexuosa*. Included in it was *Thecocarpus giardi* Billard, 1907 and, with question, *Aglaophenia bifida* Stechow, 1923b. They suspected that none of the various subspecies of *L. flexuosa* recognized by Millard (1962, 1975), including *T. flexuosus plumiferus* (Kirchenpauer, 1872), *T. flexuosus solidus* (Millard, 1958), and *T. flexuosus umbellatus* Millard 1962, would prove to be valid. Their material most closely resembled that of the nominotypical subspecies, *T. flexuosus flexuosus* (Lamouroux, 1816). So, too, do specimens examined here from Pearl & Hermes Atoll.

As for *T. flexuosus plumiferus*, Kirchenpauer (1872) spelled its original species-group name two ways, as *Aglaophenia plumifera* in the text and as *A. plumulifera* in the figure captions. Under the Principle of the First Reviser (ICZN 1999, Art. 24.2) in nomenclature, Bedot (1912: 252) cited the two names together and selected *A. plumifera* as the correct original spelling.

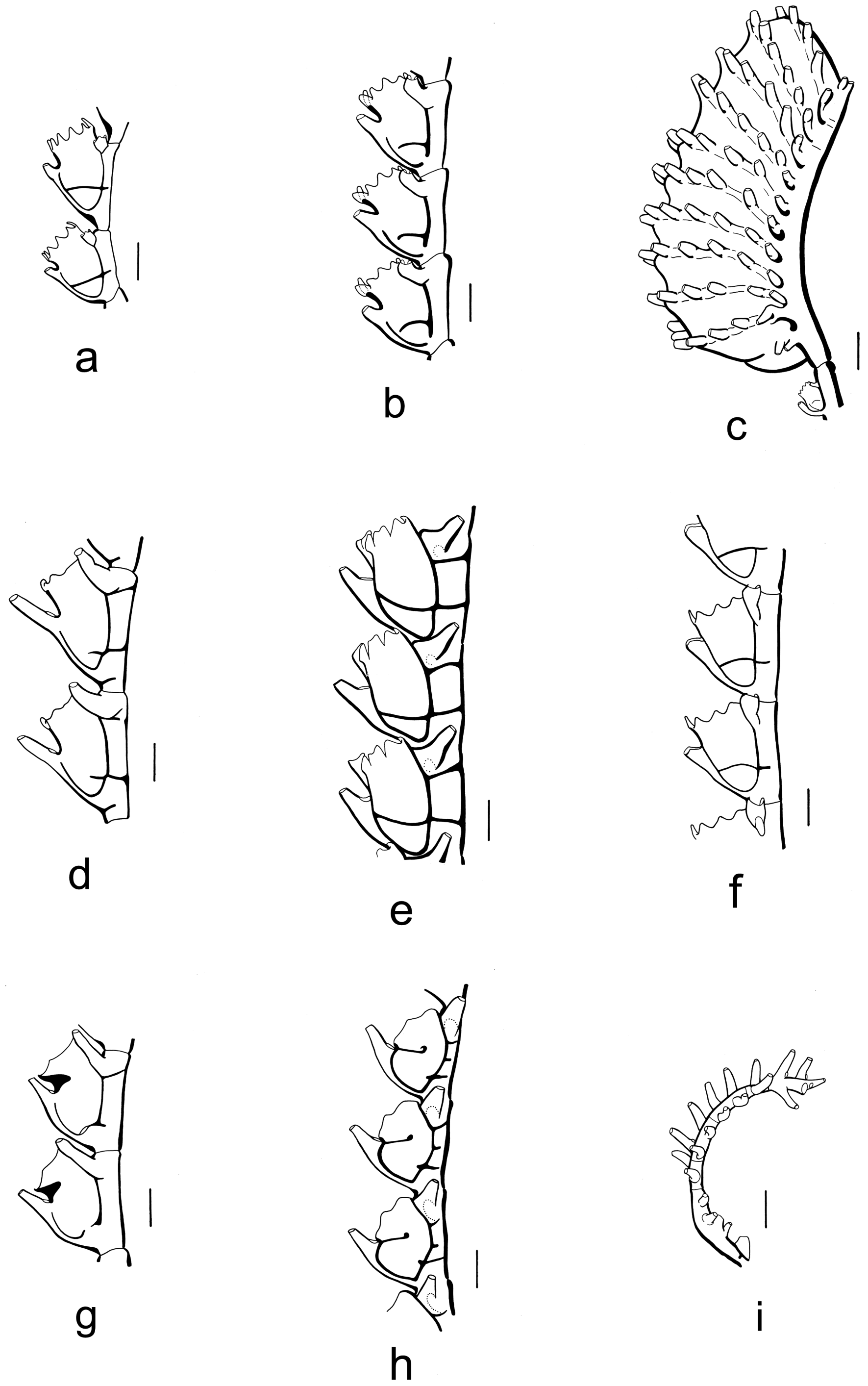

FIGURE 14. Aglaopheniidae. a, ***Aglaophenia postdentata*** **Billard, 1913**, part of a cladium with two hydrothecae, Gardner Pinnacles, ROMIZ B5462. Scale equals 0.1 mm. **b,** ***Aglaophenia suensonii*** **Jäderholm, 1896**, part of a cladium with three hydrothecae, Laysan Island, ROMIZ B5463. Scale equals 0.1 mm. **c,** ***Aglaophenia suensonii*** **Jäderholm, 1896**, corbula, Laysan Island, ROMIZ B5463. Scale equals 0.2 mm. **d,** ***Aglaophenia whiteleggei*** **Bale, 1888**, part of a cladium with two hydrothecae, Pearl & Hermes Atoll, ROMIZ B5464. Scale equals 0.1 mm. **e,** ***Lytocarpia flexuosa*** **(Lamouroux, 1816),** part of a cladium with three hydrothecae, Pearl & Hermes Atoll, ROMIZ B5479. Scale equals 0.1 mm. **f,** ***Lytocarpia phyteuma*** **(Stechow, 1919b)**, part of a cladium with two hydrothecae, Pearl & Hermes Atoll, ROMIZ B5468. Scale equals 0.1 mm. **g,** ***Macrorhynchia philippina*** **Kirchenpauer, 1872**, part of a cladium with two hydrothecae, Midway Atoll, ROMIZ B5470. Scale equals 0.1 mm. **h,** ***Macrorhynchia phoenicea*** **(Busk, 1852)**, part of a cladium with three hydrothecae, Gardner Pinnacles, ROMIZ B5475. Scale equals 0.1 mm. **i,** ***Macrorhynchia phoenicea*** **(Busk, 1852)**, one phylactocarp, without gonothecae, Gardner Pinnacles, ROMIZ B5475. Scale equals 0.2 mm.

In a study of hydroids on reefs at Juan de Nova Island, Gravier-Bonnet & Bourmaud (2006) found *L. flexuosa* only on the outer slope at 30 m. While the substrate of that biotope comprised a large amount of dead stony corals, it supported a diverse hydroid fauna of some 58 species. Specimens collected there occurred on hard substrates, algae, and sessile benthic invertebrates. Aglaopheniids, with 16 species, were well-represented, as were solanderiids.

Hydroids of *L. flexuosa* were described by Lamouroux (1816) as having a shiny fawn colour ("couleur fauve brillant").

Reported Distribution. Hawaiian archipelago. First record.

Elsewhere. "East Indies" (Lamouroux 1816, as *Aglaophenia flexuosa*); Australia (Kirchenpauer, 1872, as *A. flexuosa*); Madagascar (Billard 1907, as *Thecocarpus giardi*; Gravier-Bonnet 1979, as *T. flexuosus*); South Africa (Millard 1975, as *T. flexuosus flexuosus*), including Agulhas Bank (Stechow 1923b, as *Aglaophenia* (?) *bifida*; Millard 1975, as *T. flexuosus solidus*); Mozambique (Millard 1975, as *T. flexuosus flexuosus*); Red Sea (Mergner & Wedler 1977, as *T. flexuosus* var. *flexuosus*); Gulf of Aden (Rees & Vervoort 1987); Oman (Rees & Vervoort 1987); Juan de Nova Island (Gravier-Bonnet & Bourmaud 2006).

Lytocarpia phyteuma **(Stechow, 1919b)**

Fig. 14f

Aglaophenia phyteuma Kirchenpauer, 1876: 23, 33 [*nomen nudum*].
Thecocarpus phyteuma Stechow, 1919b: 139, figs C^2, D^2.
Lytocarpia phyteuma.—Coles *et al*., 2002b: 90, 177.—Carlton & Eldredge, 1009: 36.

Type locality. Tonga (Stechow 1919b, as *Thecocarpus phyteuma*).

Voucher material. Pearl & Hermes Atoll, 19.ix.2002, one colony, 2.4 cm high, without gonophores, coll. A. Faucci, ROMIZ B5468.—Pearl & Hermes Atoll, 19.ix.2002, two colonies or colony fragments, to 3.5 cm high, one with a developing corbula, coll. A. Faucci, ROMIZ B5483.—Pearl & Hermes Atoll, 19.ix.2002, four colonies or colony fragments, to 4.8 cm high, with corbulae, coll. A. Faucci, ROMIZ B5484.

Remarks. The hydroid examined here from Pearl & Hermes Atoll is essentially indistinguishable from accounts of *Lytocarpia phyteuma* (Stechow, 1919b) by Stechow (1919b), Millard & Bouillon (1973), Watson (2000), and Di Camillo *et al*. (2011). It also resembles the original descriptions of *Thecocarpus leopoldi* Leloup, 1930a from West Papua, Indonesia, and especially *Aglaophenia clavicula* Whitelegge, 1899, from Funafuti, Tuvalu, both now regarded as conspecific with *L. phyteuma* (Pennycuik 1959; Vervoort & Vasseur 1977; Watson 2000; Schuchert 2003; Vervoort & Watson 2003; Di Camillo *et al*. 2011). Watson (2000) and Di Camillo (2011) questioned the identity of hydroids from Moorea assigned to this species by Vervoort & Vasseur (1977) given their longer hydrothecae and downward angle of the lateral nematothecae. In those characters they are also unlike the specimen examined here.

The specific name of this species first appeared, as *Aglaophenia* (*Calathophora*) *phyteuma*, in a work by Kirchenpauer (1876: 23, 33). It is therefore almost universally credited to him in current literature on hydroids. Nomenclaturally, however, Kirchenpauer provided neither a description, nor an illustration, nor an "indication" to accompany the name (Calder & Brinckmann-Voss 2011), rendering it a *nomen nudum* (ICZN, 1999, Art. 12.1), indistinguishable from a group of 12 other associated species in his work. The name was first made available by Stechow (1919b), as *Thecocarpus phyteuma*, in an examination of Kirchenpauer's material. Both the trophosome and the corbula of the species were described and illustrated in that work by Stechow. In having a hydrotheca at the base of each rib, this species is referable under current hydrozoan classification to *Lytocarpia* Kirchenpauer, 1872. *Thecocarpus* Nutting, 1900, a name utilized by Stechow and by many others long after, is an objective junior synonym of *Lytocarpia* in that the type species of both genera is *Sertularia myriophyllum* Linnaeus, 1758. *Lytocarpus*, another name often encountered in older literature, is an unjustified emendation of *Lytocarpia* introduced by Allman (1883). It was accompanied by a redefinition that created taxonomic confusion by altering the concept of the genus (Calder 1997).

In not having been made nomenclaturally available until the work of Stechow (1919b), the familiar binomen *Aglaophenia phyteuma* is threatened by *Aglaophenia clavicula* Whitelegge, 1899, a little-known senior subjective synonym. In the interests of nomenclatural stability, Reversal of Precedence provisions under the code (ICZN 1999, Art. 23.9) have been applied here to preserve current usage. Thus, while the senior synonym (*A. clavicula*) has been unused as a valid name in zoology since its original description in a work by Whitelegge (1899) (ICZN 1999, Art. 2.9.1.1), its junior synonym (*Thecocarpus phyteuma* Stechow, 1919b) has been used for a particular taxon, as its presumed valid name, in at least 25 publications by 10 or more authors in the past 50 years, and encompassing a time interval of not less than 10 years (ICZN 1999, Art. 2.9.1.2) (e.g., Millard & Bouillon 1973; Vervoort & Vasseur 1977; Ryland & Gibbons 1991; Bouillon *et al*. 1995; Watson 2000; Coles *et al*. 2002b, 2003; Schuchert 2003; Vervoort & Watson 2003; Preker & Lawn 2005; Leclère *et al*. 2007; Moura *et al*. 2008, 2012, 2018, 2019; Di Camillo *et al*. 2008, 2011; Carlton & Eldredge 2009; Reijnen *et al*. 2011; Calder & Brinckmann-Voss 2011; Gravier-Bonnet & Bourmaud 2012; Maronna *et al*. 2016; Postaire *et al*. 2016a, b; Boissin *et al*. 2018; Mulochau *et al*. 2020).

Lytocarpia phyteuma is currently taken to be a species of the tropical Indo-west Pacific and central Pacific. Its reported range extends from waters off east Africa (Postaire *et al*. 2016b; Boissin *et al*. 2018; Mulochau *et al*. 2020) to Moorea, French Polynesia (Postaire *et al*. 2016b). Records of it from the Mediterranean Sea (Garcia-Corrales *et al.* 1978, as *Thecocarpus phyteuma*; Boero & Bouillon 1993, as *T. phyteuma*) were based on *Aglaophenia kirchenpaueri* (Heller, 1868) (Vervoort & Watson 2003).

Yet, recent molecular phylogenetic studies reveal that *L. phyteuma* is polyphyletic (Maronna *et al*. 2016; Postaire *et al.* 2016b; Moura *et al*. 2019), comprising at least six putative species, with three lineages in each of two sister clades (Moura *et al*. 2018). One of these is a tropical Pacific clade, with one lineage from New Caledonia and two from Moorea. The other is a predominantly Indian Ocean clade, although a population from the Bonin Islands, Japan, exists in one of its three lineages. There is also agreement in such studies that *L. phyteuma* is separated phylogenetically from *Sertularia myriophyllum*, type species of *Lytocarpia*, while being proximate to several species of *Aglaophenia* Lamouroux, 1812, including its type species, *Sertularia pluma* Linnaeus, 1758 (Postaire *et al.* 2016b; Moura *et al*. 2018). While this has potential implications for nomenclature, current classification is maintained for now in utilizing the binomen *L. phyteuma* for the species.

The genus *Lytocarpia* has likewise been shown to be polyphyletic, with multiple lineages occurring at relatively distant phylogenetic positions (Postaire *et al*. 2016b; Moura *et al*. 2018). Based on current evidence from genetic studies, *Lytocarpia* is closest to *Aglaophenia*, *Macrorhynchia* Kirchenpauer, 1872, and *Taxella* Allman, 1874b (Moura *et al*. 2018). The need for an assessment of taxonomically sound morphological characters in the Aglaopheniidae Marktanner-Turneretscher, 1890, and a generic revision of the family, is therefore obvious.

Reported Distribution. Hawaiian archipelago. Oahu: Waikiki, *Atlantis* wreck, 20–30 m (Coles *et al*. 2002b). Elsewhere. Tropical Indo-west Pacific (Leloup 1930a, b, as *Thecocarpus leopoldi*; Pennycuik 1959, as *T. phyteuma*; Millard & Bouillon 1973, as *T. phyteuma*; Watson 2000; Schuchert 2003; Leclère *et al*. 2007; Moura *et al*. 2008, 2012, 2018, 2019; Di Camillo *et al*. 2008, 2011; Gravier-Bonnet & Bourmaud 2012; Maronna *et al*. 2016; Postaire *et al*. 2016b; Boissin *et al*. 2018; Mulochau *et al*. 2020); central Pacific (Whitelegge 1899, as *Aglaophenia clavicula*; Stechow 1919b, as *T. phyteuma*; ? Vervoort & Vasseur 1977, as *T. phyteuma*; Ryland & Gibbons 1991; Vervoort & Watson 2003; Coles *et al*. 2003; Postaire *et al*. 2016b; Moura *et al*. 2018).

Genus *Macrorhynchia* Kirchenpauer, 1872

Macrorhynchia philippina Kirchenpauer, 1872

Fig. 14g

Macrorhynchia philippina Kirchenpauer, 1872: 19.—Hoover, 1998: 21, unnumbered figure; 2006: 21, unnumbered figure.—Coles *et al*., 2004: 72.—Calder, 2020: 235, fig. 9g.
Aglaophenia philippina Kirchenpauer, 1872: 45, text-fig. p. 17; pl. 1 fig. 26; pl. 2 fig. 26a–b; pl. 7 fig. 26.

Type locality. Philippines: Manila (Kirchenpauer 1872).

Voucher material. Pearl & Hermes Atoll, 28.ix.2002, one fragmentary colony, 3 cm high, without gonophores, coll. A. Faucci, ROMIZ B5469.—Midway Atoll, detached, 20.ix.2002, two colony fragments, to 4.5 cm high, without gonophores, coll. A. Faucci, ROMIZ B5470.

Remarks. In the original description of this species by Kirchenpauer (1872), its binomen was introduced as both *Macrorhynchia philippina* and *Aglaophenia philippina*, with a full account under the latter name. *Macrorhynchia* Kirchenpauer, 1872 was proposed in that work as a subgenus of *Aglaophenia* Lamouroux, 1812, and later elevated to generic rank by Stechow (1920). Currently included as subjective synonyms of *M. philippina* are *A. urens*

Kirchenpauer, 1872, *Lytocarpus crosslandi* Ritchie, 1907, and *L. philippinus atlanticus* Billard, 1913 (Calder 1997; Ansín Agís *et al*. 2001). As for the names *Aglaophenia perforata* and *Aglaophenia* (*Macrorhynchia*) *perforata* used by Kirchenpauer (1872) and Stechow (1919b), both are nomenclaturally unavailable (Calder 1997). With *M. philippina* and *A. urens* being simultaneous synonyms, their relative precedence was established by Bale (1919), as First Reviser (ICZN 1999, Art. 24.2.2). *Macrorhynchia philippina* was chosen by him as the valid name of the species.

Based on traditional taxonomic investigations, *M. philippina* is thought to have an exceptionally wide geographic distribution in shallow tropical to warm-temperate waters (e.g., Millard 1975, as *Lytocarpus philippinus*; Calder 1983, 2013; Hirohito 1995; Migotto 1996; Watson 2000; Ansín Agís *et al*. 2001; Schuchert 2003; Vervoort & Watson 2003; Di Camillo *et al*. 2009; Chakraborty & Raghunathan 2020). That conclusion has now been generally supported by molecular phylogenetic studies (Moura *et al*. 2012, 2018, 2019; Postaire *et al*. 2016b; Boissin *et al*. 2018). Of two putative species detected under the binomen by Moura *et al*. (2018), one extended from the southwest Indian Ocean to the tropical west Pacific, and the other was taken to be circumglobal in tropical and subtropical waters. In a study of some 198 putative species of plumularioids by Moura *et al*. (2019), only *M. philippina* and a clade of *Halopteris* cf. *alternata* displayed corresponding 16S haplotypes in the Atlantic and the eastern Pacific oceans on either side of the Central American Isthmus. Transport of the species across this and other biogeographic barriers has been attributed to either human-mediated dispersal or rafting, or both (Moura *et al*. 2012, 2018, 2019; Boissin *et al*. 2018). *Macrorhynchia philippina* is known to liberate actively swimming medusoids (Gravier 1970; Migotto 1996; Watson 2000; Bourmaud & Gravier-Bonnet 2004; Galea 2018). However, in being very short-lived (ca. 2 hours) and negatively buoyant (Gravier 1970; Gravier-Bonnet & Migotto 2000), their capacity for dispersal appears decidedly limited. An account of the colonization and expansion of this invasive species on Gran Canaria Island, Canary Islands, in the eastern North Atlantic, has been described by Espino *et al*. (2020).

Lytocarpus balei Nutting, 1905 from waters off Molokai, Hawaii, at first thought by Billard (1907) to be conspecific with *M. philippina*, is now considered a valid species (Stechow 1907, 1909; Billard 1913; Schuchert 2003, 2015, 2021d; Calder 2020). Currently assigned the binomen *Macrorhynchia balei*, it differs from *M. philippina* in having nematopores on cladial internodes below the hydrothecae, and on primary and auxiliary tubes of the hydrocauli. Other differences distinguishing the two species have been noted by Schuchert (2003). Molecular studies (Moura *et al*. 2019) further support recognition of both species.

Macrorhynchia philippina is a typically large, branched species. Although colonies are usually smaller than 15 cm high, they may attain heights of as much as two feet (61 cm) (Pictet 1893). Identification of *M. philippina* in the field is facilitated by its colony morphology, its dark stems and branches, and especially its salient white to translucent cladia. Hydroids of the species have long been known to be venomous to humans (Kirchenpauer 1872, as *Aglaophenia urens*; Gravely 1927, as *Lytocarpus philippinus*; Halstead 1988, as *L. philippinus*; Rifkin *et al*. 1993, as *L. philippinus*; Santhanam 2020).

Reported Distribution. Hawaiian archipelago. Oahu: Palea Point, 30 ft (9 m) (Hoover 1998, 2006; Calder 2020).—Molokai: Hale O Lono Reef (Coles *et al*. 2004).

Elsewhere. Circumglobal in shallow tropical, subtropical, and warm-temperate seas (Calder 1997, 2013, 2019; Ansín Agís *et al*. 2001; Schuchert 2003; Xu *et al*. 2014b; Moura *et al*. 2018, 2019; Chakraborty & Raghunathan 2020).

Macrorhynchia phoenicea **(Busk, 1852)**

Fig. 14h, i

Plumularia phoenicea Busk, 1852: 398.
Lytocarpus phoeniceus.—Nutting, 1905: 954.
Macrorhynchia phoenicea.—Di Camillo *et al*., 2009: 218, figs 2H–I, 6, 9.

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

Voucher material. Gardner Pinnacles, 14.ix.2002, three colonies or colony fragments, to 4.4 cm high, with developing phylactogonia but no gonothecae, coll. A. Faucci, ROMIZ B5471.—Midway Atoll, 23.ix.2002, two colonies, to 2.5 cm high, without gonophores, coll. A. Faucci, ROMIZ B5472.—Midway Atoll, 20.ix.2002, one colony, 1.5 cm high, without gonophores, coll. A. Faucci, ROMIZ B5473.—Midway Atoll, unattached, 20.ix.2002, three colonies or colony fragments, to 1.2 cm high, without gonophores, coll. A. Faucci, ROMIZ B5474.—Gardner

Pinnacles, 14.ix.2002, three colonies or colony fragments, to 4.3 cm high, without gonophores, coll. A. Faucci, ROMIZ B5475.

Remarks. The species name *Plumularia phoenicea* was made nomenclaturally available through a brief, unillustrated account by British naturalist George Busk (1852). Bale (1884) provided the first detailed description and illustrations of it, under the binomen *Aglaophenia phoenicea*, based in part on material provided by Busk.

In an examination of Busk's specimens at the British Museum, Billard (1909a) concluded that *Plumularia aurita* Busk, 1852 was conspecific with *L. phoeniceus*. Acting as First Reviser (ICZN 1999, Art. 24.2.2), he united the simultaneous synonyms under the binomen *L. phoeniceus*. Precedence was assigned to the specific name *phoeniceus* because it had taken on current usage while *auritus* had not subsequently been reported. If the demoted name was to be recognized as a variety, Billard (1910) proposed *L. phoeniceus auritus* for it, but that trinomen has not gained acceptance. Also assigned to the synonymy of *M. phoenicea* by Schuchert (2003) were *Aglaophenia rostrata* Kirchenpauer, 1872, *Lytocarpus spectabilis* Allman, 1883, and with question *A. disjuncta* Pictet, 1893. Di Camillo *et al*. (2009) regarded *A. rostrata*, *Lytocarpus sibogae* Billard, 1913 and, with question, *A. disjuncta* as synonyms or questionable synonyms of the species. *Lytocarpus spectabilis* (=*Macrorhynchia spectabilis*) was recognized by Di Camillo *et al*. as distinct, although its validity has been questioned by Postaire *et al*. (2016b) and Moura *et al*. (2018) based on molecular data. Meanwhile, the proposed synonymy of *L. sibogae* and *M. phoenicea* has been supported by results from 16S rRNA sequences by Postaire *et al*. As for *A. disjuncta* [=*Macrorhynchia disjuncta*], Galea (2020) found that it differed morphologically in several respects from *M. phoenicea*. Colonies were said to be more delicate, cladia were comparatively longer and more separated, cormidia were longer, and hydrothecae were slightly larger. He therefore recognized *M. disjuncta* as valid and provided a redescription of it.

Hydroids assigned to *M. phoenicea* have long been characterized as decidedly varied in morphology (e.g., Bale 1884, *as Aglaophenia phoenicea*; Marktanner-Turneretscher 1890, as *Lytocarpus phoeniceus*; Billard 1910, 1913, as *L. phoeniceus*; Stechow 1913b, as *L. phoeniceus*; Jarvis 1922, as *L. phoeniceus*; Vervoort 1946, as *L. phoeniceus*; Ryland & Gibbons 1991; Schuchert 2003; Di Camillo *et al*. 2009). Evidence from several molecular studies now indicate the existence of crypsis within the morphological concept of the species (e.g., Postaire *et al*. (2016a, b, 2017; Moura *et al*. 2018). From studies in the southwestern Indian Ocean, Postaire *et al*. (2016a) detected at least two biological species under *M. phoenicea*. These were distinguished morphologically, in terms of grey nomenclature (Minelli 2017), as "morpho types" A and B, and subsequently referred in Postaire *et al*. (2017) to *M. phoenicea* α and β. Hydroids of *M. phoenicea* α were typically tall (to 10 cm high), stiff, black and white in colour, and inhabitants of well-lighted locations swept by strong water currents. Those of *M. phoenicea* β were more gracile, usually brownish-orange in colour, and found under sheltered cliff edges. Their geographic distributions also differed (Postaire *et al*. 2017), with *M. phoenicea* α occurring the western Indian Ocean and the Tropical Southwestern Pacific (as two lineages) and *M. phoenicea* β inhabiting the western Indian Ocean.

Such cryptic diversity was deemed by Postaire *et al*. (2016a) to be widespread in aglaopheniids. They attributed it largely to reduced gene flow due to a low capacity for dispersal (Postaire *et al*. 2017). In *M. phoenicea*, for example, reproduction was reported to occur asexually by stolonization and sexually by brooded, short-lived larvae, thereby limiting propagule transport to short distances. Nevertheless, occasional dispersal of these hydroids by rafting and shipping is likely to occur.

Hydroids of *M. phoenicea sensu lato* are pinnate, often conspicuous, and of varied size, occasionally becoming quite large. Millard (1975) noted that magnificent flabelliform colonies up to 200 mm in height had been reported, likely based on the account of Billard (1913). Meanwhile, Kirkendale & Calder (2003) reported hydroids of the species from Guam that reached about 30 cm high. The synonymy lists of Vervoort & Watson (2003), Di Camillo *et al*. (2009), and Chakraborty & Raghunathan (2020) indicate how frequently hydroids of the morphospecies have been reported across the tropical Indo-Pacific. In Hawaii, Nutting (1905) described it as one of the most common hydroids in R/V *Albatross* collections from the islands. Specimens from waters off Kauai (USNM 22214) and Maui (USNM 22194) in that collection were re-examined and discussed by Di Camillo *et al*. (2009).

As with *M. philippina* Kirchanpauer, 1872, this species has been reported as venomous to humans (Santhanam 2020).

Reported Distribution. Hawaiian archipelago. Oahu: S coast, 229 m (Nutting 1905, as *Lytocarpus phoeniceus*); off Diamond Head, 519 m (Nutting 1905, as *Lytocarpus phoeniceus*).—Molokai: S coast, 110–134 m (Nutting 1905, as *L. phoeniceus*).—Laysan Island: to the N, 298 m (Nutting 1905, as *L. phoeniceus*).—Bird Island (=Nihoa): to the S, 59–708 m (Nutting 1905, as *L. phoeniceus*).—Kauai: to the N, 101 m (Nutting 1905, as *L.*

phoeniceus; Di Camillo *et al*. 2009).—Maui: to the N, 95–102 m (Nutting 1905, as *L. phoeniceus*; Di Camillo *et al*. 2009).

Elsewhere. Tropical Indo-Pacific, from coral reef depths to 708 m (Nutting 1905; Vervoort & Watson 2003), with a reported range from Natal, South Africa (Millard 1975) in the southwestern Indian Ocean to the central Pacific (Nutting 1905; Ryland & Gibbons 1991; Di Camillo *et al*. 2009).

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