

Research Article

Hydroids (Cnidaria, Hydrozoa) from marine fouling assemblages in the Galápagos Islands, Ecuador

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Abstract

An account is given of hydroids collected in 2015 and 2016 from port and harbor fouling communities in the Galápagos Islands. Also included is the hydroid of *Ectopleura media*, discovered on the wreck of the tanker *Jessica* near Isla San Cristóbal in 2001. Among 20 species reported herein were six anthoathecates and 14 leptothecates. Most common in the samples were the kirchenpaueriid *Ventromma halecioides* and the halopteridid *Halopteris alternata*. Eight species (*Bougainvillia muscus*, *Bimeria vestita*, *Clytia elongata*, *C. obliqua*, *C. thornelyi*, *Obelia oxydentata*, *Eucheilota* sp., and *Halecium labiatum*) are reported for the first time from the Galápagos archipelago. Three of them (*Clytia elongata*, *C. thornelyi*, and *Halecium labiatum*) are also new to the eastern Pacific. Seven species treated here are considered introduced by shipping to the islands, bringing to eight the number of introduced hydroids. In addition, we treat four species as cryptogenic, bringing to five the total number of the latter in the Galápagos. The binomen *Obelia thornelyi* Nutting, 1927, *Clytia stolonifera* Blackburn, 1938, and *C. latithecata* Millard and Bouillon, 1973 are regarded as synonyms, with the first of these having nomenclatural priority. Meanwhile, the senior synonym *O. thornelyi* is reassigned to the genus *Clytia* Lamouroux, 1812 as *C. thornelyi*. Another species in the samples, *Dynamena distans* Lamouroux, 1816 (also widely known as *Sertularia distans* and *Tridentata distans*), is combined for the first time with the genus *Amphisbetia* L. Agassiz, 1862, as *A. distans*.

Key words: Hydroidolina, marine invertebrates, Medusozoa, species introductions, cryptogenic, invasion, taxonomy, Tropical Eastern Pacific Realm

Introduction

Hydroids of the Galápagos Islands have received only modest attention. The most comprehensive contributions to knowledge of the group in the region are by Fraser (1938a, b, 1948) on collections acquired in the archipelago

during the Allan Hancock Pacific Expeditions of 1931–1932, 1933, 1934, and 1938. Earlier, Clarke (1907) reported three species collected during the 1904–1905 cruise of the United States Fish Commission Steamer *Albatross*. Hastings (1930) added a new species of zancleid (*Zanclaea protecta*) from James Island (Isla Santiago) and from Pánama (type locality: Isla Taboga). Houvenaghel and Houvenaghel (1974) identified one hydroid (*Dynamena crisioides* Lamouroux, 1824) to species, and mentioned several others that were identified to genus only, in an investigation on vertical zonation of rocky intertidal biota at Isla Santa Cruz. Best known of all hydrozoans in the Galápagos is the family Stylasteridae Gray, 1847. Cairns (1986) reviewed earlier studies on stylasterids from the islands and provided accounts of 14 species, nine of them as new. Cairns (1991) added another new species, but the total number remained at 14, with one earlier species being placed in synonymy. Additions to the general hydroid fauna, and a checklist of species, were provided by Calder et al. (2003). Marshall et al. (2002) and Marshall and Edgar (2003) called attention to hydroids discovered on and adjacent to the wreck of the oil tanker *Jessica* off Isla San Cristóbal in 2001. A Galápagos field guide by Hickman (2008) included accounts of 12 of the more prominent hydroid species. In an overview of the local marine invertebrate fauna (Hickman 2009), bryozoans and hydroids were reported to be two of the more diverse groups. Including 14 stylasterids (Cairns 1991) and 96 others (Calder et al. 2003), 110 species have been recorded from the islands.

Most previous investigations of hydroids in the Galápagos have focused on species from natural habitats. The present study is based primarily on hydroids found as part of fouling communities, particularly those in ports and harbours.

Materials and methods

Hydroids from the Galápagos Islands examined here were obtained during surveys for invasive species in February 2015 and April 2016. Manual collecting from docks and pilings was undertaken in the vicinity of Puerto Ayora (Isla Santa Cruz) and at Isla Baltra (Figure 1). A single sample came from Isla Bartolomé. In addition, in April 2016, fouling panels [14 × 14 cm, 0.5 cm thick, grey polyvinyl chloride (PVC) plates, lightly sanded on the underside to optimize attachment conditions, and suspended horizontally at a depth of 1 m] that had been deployed 14 months or 3 months earlier in February 2015 and January 2016 respectively at (1) the Puerto Ayora main passenger docks, (2) a private dock in Franklin's Bay, Puerto Ayora, both on Santa Cruz Island, and (3) on a Navy floating dock on Baltra Island, were retrieved. Voucher samples of hydroids (and other taxa) were removed and preserved in 95% ethanol. An additional sample of hydroids was collected from the wreck of the oil tanker *Jessica* at Isla San Cristóbal in 2001 by G. Edgar and P. Marshall.

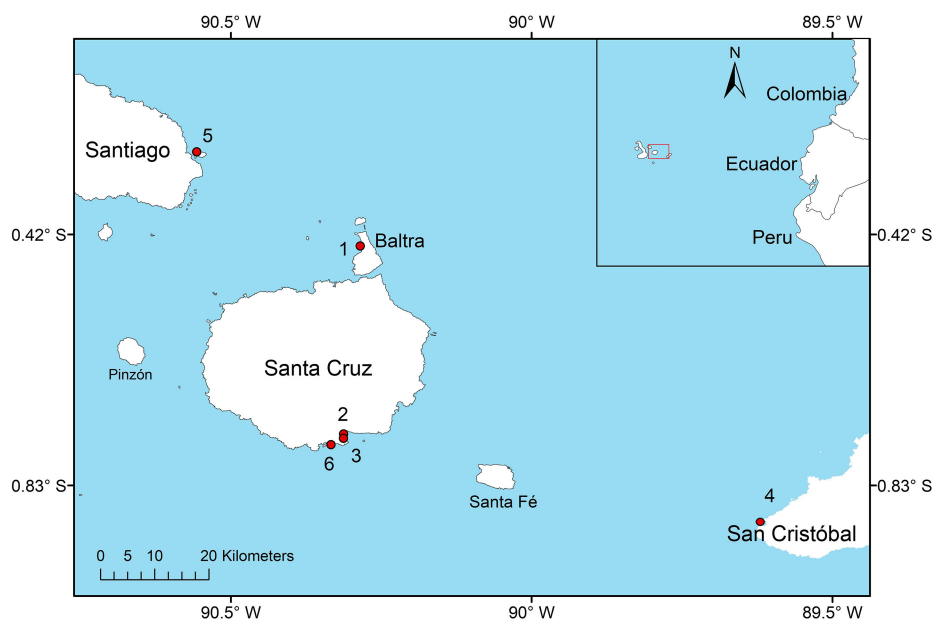


Figure 1. Sampling locations in the Galápagos Islands, Ecuador. Inset shows location of the archipelago, west of continental South America. Station 1, Isla Baltra, navy dock, $-0.436364; -91.297469$; Station 2, Isla Santa Cruz, Puerto Ayora main passenger dock, $-0.747828; -90.312564$; Station 3, Isla Santa Cruz, Franklin's Bay, $-0.755194; -90.312653$; Station 4, Isla San Cristóbal, wreck of tanker *Jessica*, $-0.894728; -89.619889$. Station 5, Isla Bartolomé, $-0.279608; -90.556714$; Station 6, Isla Santa Cruz, Tortuga Bay, $-0.763792; -90.340253$. Map courtesy of Linda McCann.

Collections are deposited at the Smithsonian Environmental Research Station (SERC), Edgewater, Maryland, USA, and at the Charles Darwin Research Station, Puerto Ayora, Santa Cruz Island, Galápagos, Ecuador. Specimens of one species (*Ectopleura media*) are in collections of the Invertebrate Zoology Section at the Royal Ontario Museum.

The classification system adopted here generally follows Schuchert (2012) for anthoathecates and Maronna et al. (2016) for leptothecates. A synonymy list accompanying each species includes the original binominal name together with its author and date, along with citations of any publications providing primary records of hydroids from the Galápagos Islands. All cited references have been examined as part of the study. Illustrations are based entirely on hydroids included herein.

Abbreviations are as follows:

- JJM Hyd. Jenny Mallinson Galápagos hydroid collection, University of Southampton, Southampton, UK
- NMNH National Museum of Natural History, Smithsonian Institution, Washington, DC, USA
- ROMIZ Invertebrate Zoology collections, Royal Ontario Museum, Toronto, Ontario, Canada
- SERC Galápagos collections, Smithsonian Environmental Research Center, Edgewater, Maryland, USA
- WoRMS World Register of Marine Species

Results

Twenty species (six anthoathecates and 14 leptotheccates) are reported here, eight of which are new to the islands (Table 1, Supplementary material Table S1). We note whether species may be cryptogenic or introduced, but otherwise we consider the species treated here as native (although whether they should bear the names of “cosmopolitan” species with type localities in other oceans often remains to be determined).

Unless otherwise stated, all vials referred to are SERC numbers.

Systematic Account

Phylum Cnidaria Verrill, 1865

Class Hydrozoa Owen, 1843

Superorder Anthoathecata Cornelius, 1992a

Order Aplanulata Collins, Winkelman, Hadrys and Schierwater, 2005

Family Tubulariidae Fleming, 1828

Ectopleura media Fraser, 1948

Figure 2a, b

Ectopleura media Fraser 1948: 201, pl. 22, figs. 2a–d.—Marshall et al. 2002: 92, photos 14, 15.—Calder et al. 2003: 1198.—Marshall and Edgar 2003: 294.—Hickman 2008: 124, three unnumbered figs.—Calder et al. 2009: 940.

Material.—Isla San Cristóbal, on wreck of the tanker *Jessica*, 10 May 2001, 1 colony, 2.5 cm high, some hydranths with developing gonophores, coll. G. Edgar and P. Marshall, ROMIZ B3479.

Remarks.—The type locality of *Ectopleura media* Fraser, 1948, presently known only from the Galápagos, is Bindloe Island (Isla Marchena). It has also been reported from Punta Vicente Roca, Isla Isabela (Calder et al. 2003) and Isla San Cristóbal (Marshall et al. 2002; Marshall and Edgar 2003). At the latter location, specimens were found on and adjacent to the wreck of the oil tanker *Jessica*, which grounded off Puerto Baquerizo Moreno on 16 January 2001. By May 2001, when assessments were undertaken by Marshall and colleagues, colonies of the hydroid were a conspicuous component of the fouling assemblage on and adjacent to the wreckage.

Fraser (1948) believed that gonophores of *Ectopleura media* were medusa buds. However, from specimens observed previously in the Galápagos by us, they are medusoids that do not become released as free medusae. In that, they differ from those of the sympatric *E. integra* (Fraser, 1938a), whose type locality is Isla Baltra, Galápagos (Calder et al. 2009). Gonophores of *E. crocea* (L. Agassiz, 1862), reported from Isla Isabela by Fraser (1938a), are sporosacs, with those of the female having 6–8 crest-like processes distally (Schuchert 2010). Fraser’s record of *E. crocea* from the archipelago has been considered doubtful (Calder et al. 2003: 1205), as it is a species more characteristic of cool temperate than tropical waters.

Table 1. Introduced and cryptogenic Hydrozoa of the Galápagos Islands (* treated herein).

Species	Status I, Introduced C, Cryptogenic	Galápagos collection records	Possible Origin	Remarks
Bougainvilliidae				
* <i>Bougainvillia muscus</i>	I	2016 (Baltra)	North Atlantic?	Mills et al. (2007) and Carlton and Eldredge (2009, 2015) regard it as an introduction to the northeast Pacific Ocean and to the Hawaiian Islands, respectively, as well
* <i>Bimeria vestita</i>	C	2016 (Santa Cruz)	unknown	Considered cryptogenic because of a possible global species complex; reported from 1930s collections from Ecuador, Panamá, and Mexico (see text); introduced to the Hawaiian Islands (Carlton and Eldredge 2015; see also Calder 2010)
Cirrholoventiidae				
* <i>Cirrholovenia tetranema</i>	C	1992 (Daphne Chica, Española); 1994 and 2015 (Santa Cruz); 2000 (Isabela)	Indo-west Pacific?	Considered cryptogenic because of a possible global species complex
Clytiidae				
* <i>Clytia elongata</i>	I	2016 (Santa Cruz)	Australia-New Zealand	First report from the eastern Pacific Ocean; reported as <i>Clytia ? elongata</i> (identified by P.M. Ralph) on New Zealand ship hulls (Skerman 1960)
* <i>Clytia thornelyi</i>	I	2016 (Baltra, Santa Cruz)	western Pacific or western Atlantic	First report from the eastern Pacific Ocean
<i>Clytia hummelincki</i>	I	1992 (San Cristobal), 2000 (Wolf)	Caribbean (via the Panama Canal) or the Indo-west Pacific	Reported earlier from the Galápagos Islands (Calder et al. 2003). A species demonstrating an invasion propensity (Gonzalez-Duarte et al. 2016), having arrived in the Mediterranean in the 1990s; records since the 1980s from the Indo-west Pacific (summarized in Gonzalez-Duarte et al. 2016) may represent recent introductions as well
Obeliidae				
* <i>Obelia dichotoma</i>	C	1930s (Floreana, Baltra, Isabela); later collections from Fernandina, Espanola, Santa Cruz	unknown	Considered cryptogenic because of a possible global species complex
* <i>Obelia oxydentata</i>	I	2016 (Santa Cruz)	western Atlantic or western Pacific	Previously known from the eastern Pacific based on a Panamá record from 1904–1905
Haleciidae				
* <i>Halecium labiatum</i>	I	2016 (Baltra)	western Indian Ocean	
* <i>Nemalecium lighti</i>	I	2005–2007 (Wolf, Darwin, Marchena); 2016 (Santa Cruz)	Indo-west Pacific or western Atlantic	
Pennariidae				
<i>Pennaria disticha</i>	C	1930s (Wolf, Floreana); 1992 (San Cristobal), 1994 (Tortuga), 1998–99 (Marchena, Espanola); 2005–2007 (Darwin, Marchena)	unknown	1930s–1990s records: Calder et al. 2003; 2005–07 record: Banks et al. 2009. Considered cryptogenic because of a possible global species complex; Carlton and Eldredge (2009), review its previous designations as cryptogenic or introduced in the Pacific theater
Kirchenpaueriidae				
* <i>Ventromma halecioides</i>	C	1999 (Fernandina); 2016 (Santa Cruz)	unknown	Considered cryptogenic because of a possible global species complex; Carlton and Eldredge (2009) also considered it cryptogenic in the Hawaiian biofouling fauna
Halopterididae				
* <i>Halopteris alternata</i>	I	2016 (Santa Cruz)	Atlantic Ocean	

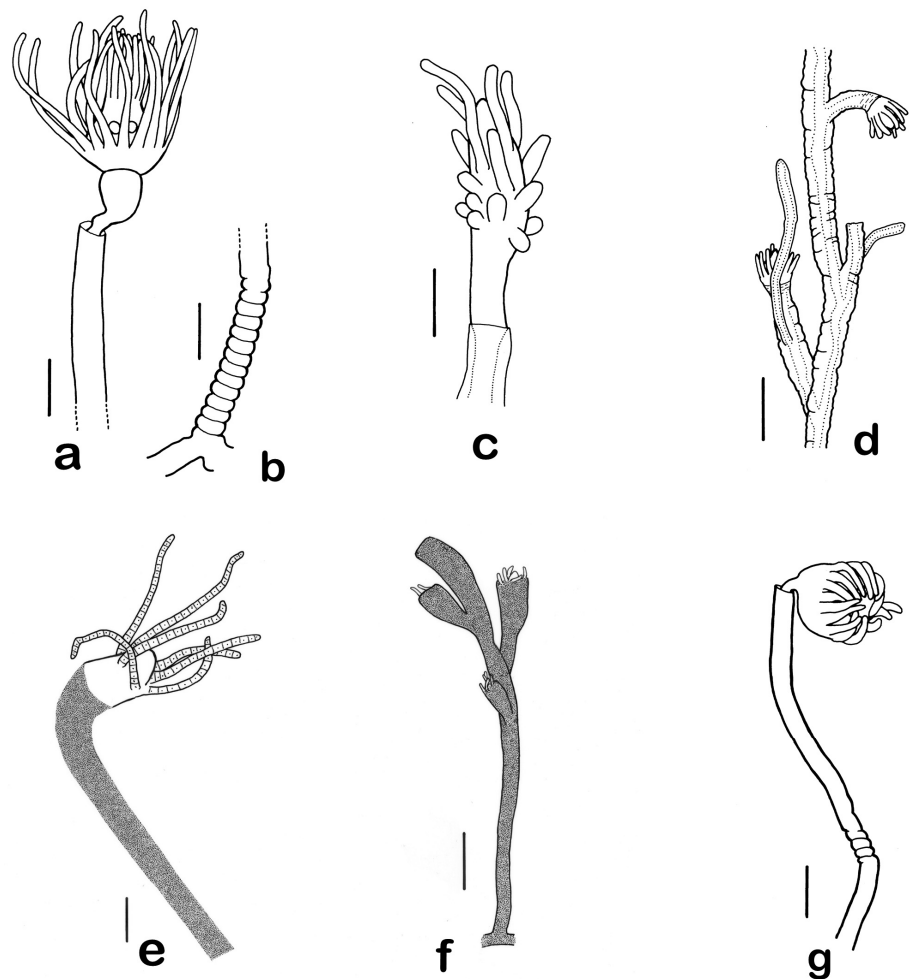


Figure 2. Anthoathecata: families Tubulariidae, Oceaniidae, Bougainvilliidae, and Eudendriidae. a, *Ectopleura media*, hydranth and distal end of hydrocaulus, Isla San Cristóbal, ROMIZ B3479, scale equals 0.5 mm. b, *Ectopleura media*, proximal end of hydrocaulus, showing annulated base, ROMIZ B3479, scale equals 0.5 mm. c, *Turritopsis* sp., hydranth, Isla Santa Cruz, Puerto Ayora, main passenger dock, SERC #234288, scale equals 0.2 mm. d, *Bougainvillia muscus*, part of colony, with two hydranths and two stolons, Isla Baltra, navy dock, SERC #232848, scale equals 0.25 mm. e, *Bougainvillia* sp., hydranth and distal end of pedicel, Isla Santa Cruz, Puerto Ayora, main passenger dock, JJM Hyd. 4, scale equals 0.1 mm. f, *Bimeria vestita*, colony with three hydranths, Isla Santa Cruz, SERC #02611, scale equals 0.2 mm. g, *Eudendrium* (?) *breve*, hydranth and pedicel, Isla Santa Cruz, Tortuga Bay, scale equals 0.2 mm.

Order Filifera Kühn, 1913

Family Oceaniidae Eschscholtz, 1829

?*Turritopsis* sp.

Figure 2c

Material.—Isla Santa Cruz, Puerto Ayora, main passenger dock, on fouling plate deployed 27 February 2016, retrieved April 2016, 2 colonies, up to 3 mm high, without gonophores, coll. K Larson, vial 234288.

Remarks.—Although these specimens lacked gonophores and appear to have been quite young, they are unmistakably oceaniids. The colonies are similar to stolonal hydroids from Fiji that Gibbons and Ryland (1989) identified as *Tubiclava* sp. They also resemble *Tubiclava triserialis* Fraser, 1938a, a *species inquirenda* originally described from the Islas Revillagigedo

of Mexico in the warm eastern Pacific. As for *Tubiclava* Allman, 1863, Schuchert (2004) justifiably regarded it as a genus of doubtful identity that should no longer be recognized as valid. Another hydroid of somewhat similar morphology is that of *Oceania armata* Kölliker, in Gegenbaur et al., 1853. While the medusa stage of that species is widely distributed and well-known, its hydroid had until recently been known only as juveniles from laboratory cultures of Mediterranean material (Metschnikoff 1886; Schuchert 2004). However, the medusa of *O. armata* has now been linked by Schuchert (2016) to the hydroids of *Turritopsis chevalense* (Thornely, 1904) and *T. fascicularis* Fraser, 1943 via DNA barcoding. Hydroids of both nominal species are relatively large and polysiphonic, and distinct from the miniscule ones observed here. There is no record of this hydromedusa, or of the hydroids above, in the tropical eastern Pacific.

In having clavate hydranths with scattered filiform tentacles, a prominent hypostome, and an exoskeleton comprising non-nested tubes of perisarc, we have assigned our specimens with question to the oceaniid genus *Turritopsis* McCrady, 1857. Further identification to species level on the basis of morphology is inadvisable based on the available material. The oceaniid *T. nutricula* McCrady, 1857 has been recorded earlier in the Galápagos from Isla Isabela (Fraser 1938a) and Isla Wolf (Calder et al. 2003). If our hydroid is indeed *T. nutricula*, a species originally described from Charleston, South Carolina, USA, and reported worldwide in temperate and tropical waters, shipping would be a likely means of introduction.

As for *Turritopsis nutricula*, molecular studies now indicate the probable existence of a species complex hidden under that name. According to Miglietta et al. (2007) and Miglietta and Lessios (2009), the hydrozoan originally assigned that binomen may be restricted in distribution to the western Atlantic Ocean. Related species originally described from the Indo-Pacific region, and their type localities, include *T. rubra* (Farquhar, 1895) from Wellington Harbour, New Zealand, *T. lata* von Lendenfeld, 1885 from Port Jackson, Australia, *T. pacifica* Maas, 1909 from Sagami Bay, Japan, *T. chevalense* from Sri Lanka (Gulf of Manaar), and *T. minor* Nutting, 1905 from Maui, Hawaii. Of these, molecular sequencing has been undertaken to date on *T. rubra*, *T. lata*, and *T. chevalense* (= *Oceania armata*). Species limits and distributions within the genus remain obscure, and our sterile material is identified here simply as ?*Turritopsis* sp.

Family Bougainvilliidae Lütken, 1850

***Bougainvillia muscus* (Allman, 1863)**

Figure 2d

Perigonymus muscus Allman 1863: 12.

Material.—Specimens collected in April 2016 from fouling plates deployed at the Isla Baltra navy dock, 15 January 2016, coll. K. Larson: 1 colony

fragment, 3 mm high, without gonophores, vial 234218; 3 colony fragments, up to 5.5 mm high, without gonophores, vial 232875; 3 colony fragments, up to 5 mm high, without gonophores, vial 232858; 10 colony fragments, up to 10 mm high, without gonophores, vial 232848; 2 colony fragments, up to 7 mm high, without gonophores, vial 234192; 1 colony fragment, 4 mm high, without gonophores, vial 232869.

Remarks.—These hydroids, although sterile, were assigned to *Bougainvillia muscus* (Allman, 1863) based on their similarity to colonies studied earlier in Hawaii (Calder 2010). The latter specimens had been identified after examination of both hydroid and medusa stages. As noted earlier, *B. muscus* is presumably a eurytopic Atlantic species (type locality: Devon, England) that has also been reported in temperate and tropical waters of the Pacific and Indian oceans. Molecular data revealing low divergence values between populations from Europe and New Zealand (Schuchert 2007) support the conclusion that the species is widely distributed. Its hydroid is sometimes part of the fouling community in ports and canals (Billard 1926, as *B. ramosa muscus*; Millard 1959, as *B. ramosa*; Schuchert 1996; Calder 2010), as in this study, suggesting that long-range transport has been effected by shipping. Reports of the species from several other remote oceanic islands, including Bermuda (Calder 1988), New Zealand (Schuchert 1996), and Hawaii (Calder 2010), also provide evidence of its capacity for human-mediated dispersal. The medusa stage of *B. muscus* is also known to have a wide geographic range. While most accounts of it are from the eastern North Atlantic and Mediterranean Sea (Kramp 1961, as *B. ramosa*), records also exist from the Pacific and Indian oceans (Bouillon 1980, as *B. ramosa*; Navas-Pereira and Vannucci 1991, as *B. ramosa*; Schuchert 1996; Santhakumari and Nair 1999, as *B. ramosa*; Xu et al. 2014a).

Information on the biology of *Bougainvillia muscus* has been summarized by Schuchert (2007). This constitutes the first record of the species, a likely introduction, from the Galápagos Islands.

?*Bougainvillia* sp.

Figures 2e; 5a

Material.—All but the last are specimens from fouling plates retrieved in April 2016 at the main passenger dock, Puerto Ayora, Isla Santa Cruz, coll. K. Larson: plate deployed 27 February 2015, 1 colony fragment, 3 mm high, without gonophores, vial 234289; plate deployed 15 January 2016, 1 colony, 2 mm high, without gonophores, vial 234057; plate deployed 15 January 2016, 1 colony fragment, 2 mm high, without gonophores, vial 234064.—Isla Santa Cruz, Puerto Ayora, port, 26 April 2016, 1 colony, 2 mm high, without gonophores, coll. J. J. Mallinson, JJM Hyd. 4.

Remarks.—This miniscule hydroid appears to be a species of *Bougainvillia* Lesson, 1830, or at least a bougainvilliid. A note by one of us (JJM) indicates

that in life it had a “tall hypostome”. In preserved material, the hypostome was dome-shaped. The colony was stolonial, and hydranth pedicels tapered very gradually from distal to proximal end. In lacking gonophores, identification to species is impossible based on morphology.

***Bimeria vestita* Wright, 1859**

Figure 2f

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

Material.—Isla Santa Cruz, Puerto Ayora, Puerto Ayora dock, fouling community on floats, 22 February 2015, 8 colony fragments, up to 6 mm high, with gonophores, coll. G. Ruiz and M. Torchin. –Isla Santa Cruz, Tortuga Bay, from rotten wood on beach, February 2015, 4 colony fragments, up to 8 mm high, without gonothecae, coll. L. McCann and J.T. Carlton, SERC field catalog #02611. –Isla Santa Cruz, Puerto Ayora, fouling on docks, February 2015, 9 colony fragments, up to 4 mm high, without gonophores, coll. J.T. Carlton, G. Ruiz and L. McCann, SERC field catalog #02013. –Isla Santa Cruz, Puerto Ayora, main passenger dock, collected April 2016 from fouling plate deployed 27 February 2015, 2 colonies, up to 7 mm high, one with gonophores, coll. K. Larson, vial 233131.

Remarks.—These hydroids are referable to the genus *Bimeria* Wright, 1859, and they correspond morphologically with *B. vestita* Wright, 1859. Earlier, Fraser (1938a, b) reported the species from the coast of Ecuador, as well as from the Pacific coasts of Mexico and Panamá. This is the first record of the species, or one like it, from the Galápagos. A distinct variety of the species (*B. vestita* forma *nana*) was described from Sri Lanka by Leloup (1932), and he identified it again from Vietnam (Leloup 1937). Confirmation is needed whether populations identified as *B. vestita* from warm waters of the Pacific are the same as Wright’s (1859) species from the Firth of Forth, Scotland. Worldwide distribution records are summarized by Schuchert (2007), with reports of the species from temperate and tropical waters of the Atlantic, Pacific, and Indian oceans. We consider *B. vestita* to be cryptogenic in the Galápagos.

Fraser (1938a) reported three species of *Bimeria* from the Galápagos (*B. gracilis* Clark, 1876; *B. tenella* Fraser, 1925; *B. laxa* Fraser, 1938a), but all have been reassigned to the genus *Garveia* Wright, 1859 (Calder et al. 2003).

Family Eudendriidae L. Agassiz, 1862

***Eudendrium* (?) *breve* Fraser, 1938a**

Figure 2g

Eudendrium breve Fraser 1938a: 18, pl. 3, fig. 13. –Calder et al. 2003: 1194. –Calder et al. 2009: 933.

Material.—Isla Santa Cruz, Tortuga Bay, fouling community on dead intertidal mangrove roots, 23 February 2015, 2 colony fragments, up to 5 mm high, without gonophores, coll. J.T. Carlton. –The following specimens

collected April 2016 from fouling plates deployed at Puerto Ayora main passenger dock, Isla Santa Cruz, 27 February 2015, coll. K. Larson: 1 colony fragment, 5 mm high, without gonophores, vial 233131; 3 colony fragments, 12 mm high, without gonophores, vial 234122; 1 colony, 2 mm high, without gonophores, vial 233133; the same, but plates deployed 15 January 2016: 1 colony fragment, 6 mm high, without gonophores, vial 234098; 1 colony, 1 mm high, without gonophores, vial 233016; 1 colony, 3 mm high, without gonophores, vial 232765; 1 colony, 7 mm high, without gonophores, vial 234099. –Isla Baltra, navy dock, collected April 2016 from fouling plate deployed 15 January 2016, 3 colony fragments, up to 3.5 mm high, without gonophores and 1 colony, 1 mm high, without gonophores, both sets of Baltra material coll. K. Larson, vials 234198 and 232869 respectively.

Remarks.—These hydroids generally corresponded with Fraser’s (1938a) brief original account of *Eudendrium breve* from Charles Island (Isla Floreana), Galápagos. The species has also been reported from Isla Española in the archipelago (Calder et al. 2003). Unlike the original description of Fraser’s hydroid, pedicels in our specimens were annulated at the base, and several bore one or more branches rather than being completely stolonial. They appear very close also to hydroids identified as the presumably cosmopolitan *E. capillare* Alder, 1856 (type locality: Embleton Bay, Northumberland, England) at other locations in the Pacific including Enewetak Atoll, Marshall Islands (Cooke 1975), Sagami Bay, Japan (Hirohito 1988), and Hawaii (Calder 2010). As with *E. capillare*, our specimens lacked complementary nematocysts in addition to small microbasic euryteles. If the Pacific population of hydroids assigned to *E. capillare* is indeed identical with that of the Atlantic, Fraser’s *E. breve* is likely conspecific.

Knowledge of the gonophores, and especially those of female colonies, is now considered critical in the characterization of species of *Eudendrium* Ehrenberg, 1834. So too is knowledge of the cnidome. *Eudendrium breve* constitutes a *species inquirenda* because type material was sterile and its nematocyst complement has yet to be unequivocally established. Large isorhizas in addition to microbasic euryteles were found in specimens assigned with question to *E. breve* by Cooke (1975) from Enewetak Atoll. Such nematocysts were not observed in material examined here. Re-examination and redescription of type material (SBMNH 345383, SBMNH 345384, SBMNH 346372) of the species, in collections at the Santa Barbara Museum of Natural History, Santa Barbara, California, is needed. Our specimens are assigned to *E. breve* with question given the inadequate knowledge of the species, and with nothing but sterile material available in the present collection.

In addition to records from the Galápagos and Enewetak Atoll, *Eudendrium breve* has also been reported from Baja California (Fraser 1948).

Superorder Leptothecata Cornelius, 1992b

Order Statocysta Leclère, Schuchert, Cruaud, Couloux and Manuel, 2009

Family Cirrholoveniidae Bouillon, 1984

***Cirrholovenia tetranema* Kramp, 1959**

Figure 3a

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

Egmondella amirantensis Millard and Bouillon 1973: 40, figs. 5a–d [hydroid].

Lafoeina amirantensis.—Calder et al. 2003: 1180, fig. 5.

Material.—Isla Santa Cruz, Puerto Ayora, Franklin’s Bay, fouling community on floats, epizoic on hydroid *Nemalecium lighti*, 27 February 2015, several colonies, up to 2.5 mm high, without gonophores, coll. J. T. Carlton.

Remarks.—The hydroid known as *Egmondella amirantensis* Millard and Bouillon, 1973 was shown, through life cycle studies by Migotto and Cabral (2005), to be conspecific with the medusa *Cirrholovenia tetranema* Kramp, 1959. The latter name has nomenclatural priority and is accepted as valid in WoRMS (Schuchert 2018).

The medusa of *Cirrholovenia tetranema*, originally described by Kramp (1959) from the Solomon Islands (holotype) and from several other localities in the Indo-Pacific, is now known from coastal and shelf waters of the Atlantic, Pacific, and Indian oceans (Migotto and Cabral 2005). Based on the known distribution of its medusa, Kramp (1968: 190) suspected that *C. tetranema* was native to the Indo-Malayan region. The hydroid stage, first described as *E. amirantensis* from Amirante, Seychelles (Millard and Bouillon 1973), is also taken to be circumglobal in tropical and warm temperate waters (Migotto and Cabral 2005). Other hydroids are a common substrate of the species, although colonies have also been found on bryozoans, macroalgae, and rocks.

Hydroids of this cryptogenic species have been reported earlier from the Galápagos at Isla Daphne Chica, Isla Española, Isla Santa Cruz, and Isla Isabela (Calder et al. 2003, as *Lafoeina amirantensis*).

Family Eucheilotidae Bouillon, 1984

***Eucheilota* sp.**

Figure 3b

Material.—Isla Santa Cruz, Puerto Ayora, Franklin’s Bay, 27 April 2016, on leg of spider crab *Teleophrys cristulipes*, coll. J. T. Carlton, JJM Hyd. 13.

Remarks.—The shallow hydrothecal vestiges of this hydroid superficially resemble those of haleciids. However, in having a filmy curtain of perisarc hanging down over the hydrophores, it corresponds instead with accounts of various species of *Eucheilota* McCrady, 1859 by Werner (1968), Russell (1970), Cornelius (1995a), Altuna (2008, 2009), and others. In species of that genus, diaphanous hydrothecae resembling those of *Aequorea* Péron and

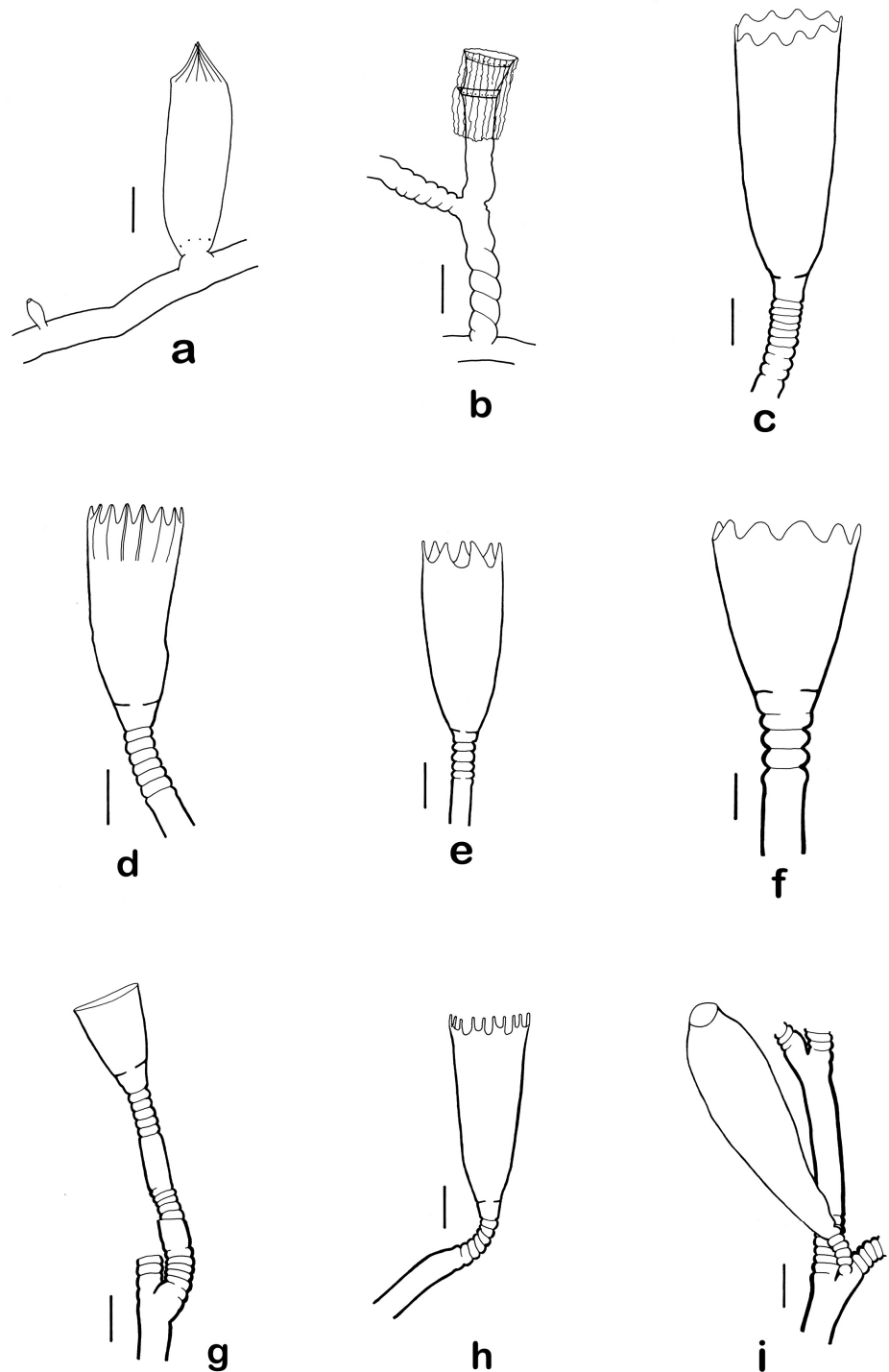


Figure 3. Leptothecata: families Cirrholoveniidae, Eucheilotidae, Clytiidae, and Obeliidae. a, *Cirrholovenia tetranema*, part of colony, with a hydrotheca and a nematotheca, Isla Santa Cruz, Franklin's Bay, scale equals 0.05 mm. b, *Eucheilota* sp., part of colony, with collapsed wall of hydrotheca, Isla Santa Cruz, Puerto Ayora, Franklin's Bay, JJM Hyd. 13, scale equals 0.1 mm. c, *Clytia elongata*, hydrotheca and distal end of pedicel, Isla Santa Cruz, Franklin's Bay, JJM Hyd. 16, scale equals 0.1 mm. d, *Clytia linearis*, hydrotheca and distal end of pedicel, Isla Baltra, navy dock, SERC #232841, scale equals 0.2 mm. e, *Clytia obliqua*, hydrotheca and distal end of pedicel, Isla Santa Cruz, Puerto Ayora, main passenger dock, JJM Hyd. 2, scale equals 0.1 mm. f, *Clytia thorneleyi*, hydrotheca and distal end of pedicel, Isla Santa Cruz, Franklin's Bay, JJM Hyd. 11, scale equals 0.1 mm. g, *Obelia dichotoma*, part of colony, with renovated pedicel and hydrotheca, Isla Santa Cruz, Franklin's Bay, fouling community on floats, scale equals 0.1 mm. h, *Obelia oxydentata*, hydrotheca, Isla Santa Cruz, Franklin's Bay, fouling community on floats, scale equals 0.1 mm. i, *Obelia oxydentata*, part of hydrocaulus, with a gonotheca, Isla Santa Cruz, Franklin's Bay, fouling community on floats, scale equals 0.1 mm.

Lesueur, 1810 collapse as hydranths develop, leaving a wrinkled skirt of perisarc hanging from the hydrothecal bases. The presence of punctae above a basal diaphragm reinforces the impression of a haleciid. Our hydroid may be referable to *Euceilota comata* (Bigelow, 1909), the medusa stage of which occurs in the tropical eastern Pacific, but definitive identification is impossible in the absence of life cycle or genetic information. Reduction of the hydrotheca accompanying growth of the hydranth also occurs in several other species of leptothebate genera including *Eutonina* Hartlaub, 1897, *Eirene* Eschscholtz, 1829, and *Eutima* McCrady, 1859.

In some works, *Euceilota* and Euceilotidae Bouillon, 1984 have been included in Lovenellidae Russell, 1953. Bouillon (1984) and Cornelius (1995a), among others, are followed here in recognizing Euceilotidae as a distinct family. The hydroid stages of euceilotids, where known, are much different morphologically from those of lovenellids (see Cornelius 1995a), evidence that these families are distinct. Molecular studies (e.g. Leclère et al. 2009; Maronna et al. 2016) that have explicitly or implicitly sunk Euceilotidae in the synonymy of Lovenellidae have misinterpreted relationships of the two because certain included species were assigned to the wrong genus. For presumed relationships of these families to be based on sound evidence, genetic comparisons of the type species of their type genera, *Euceilota* and *Lovenella* Hincks, 1868 (*Euceilota ventricularis* McCrady, 1859 and *Campanularia clausa* Lovén, 1836, respectively), are warranted.

No hydroids resembling *Euceilota* sp. have been reported before from the Galápagos.

Family Clytiidae Cockerell, 1911

***Clytia elongata* Marktanner-Turneretscher, 1890**

Figure 3c

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

Material.—All but the last are specimens from fouling plates retrieved April 2016 which had been deployed at Franklin’s Bay, Puerto Ayora, Isla Santa Cruz, 27 February 2015, coll. K. Larson: 5 colony fragments, up to 4 mm high, without gonophores, vial 234138; 5 colony fragments, up to 6 mm high, without gonophores, vial 234236; 1 colony fragment, 3.5 mm high, without gonophores, vial 234237; 1 colony fragment, 2 mm high, without gonophores, vial 234921; 1 colony, 2.5 mm high, without gonophores, vial 232798. –Isla Santa Cruz, Puerto Ayora, Franklin’s Bay, epizoic on bryozoan *Amathia verticillata*, 28 April 2016, 3 colony fragments, up to 4 mm high, without gonophores, coll. K. Collins, JJM Hyd. 16.

Remarks.—A rare and poorly known species, *Clytia elongata* Marktanner-Turneretscher, 1890 is nevertheless distinctive in the morphology of its trophosome. As the specific name implies, its hydrothecae are deep and

slender. Also noteworthy are the low, rounded cusps on the hydrothecal rim. While thereby resembling *C. noliformis* (McCrary, 1859) and *C. thornelyi* (Nutting, 1927), hydrothecae of *C. elongata* are much deeper and more cylindrical than in either of those species. Meanwhile, marginal cusps are not truncated as in *C. macrotheca* (Perkins, 1908) and *C. reloncavia* Galea and Schories, 2012. Gonophores and gonothecae of the species have yet to be described, and none were observed here. Specimens from the Galápagos corresponded closely in both shape and size (Figure 3c) with the original account and illustration of the hydroid by Marktanner-Turneretscher (1890) and with a subsequent overview of the species by Ralph (1957).

Clytia elongata, a probable introduction to the tropical eastern Pacific, is previously known only from the western Pacific. Originally described from Auckland, New Zealand, it has been reported elsewhere from New South Wales, Australia (Ritchie 1911) and Cook Strait, New Zealand (Vervoort and Watson 2003). Rees and Thursfield (1965) re-examined Ritchie's Australian specimens and found that they "...agree well with the figure given by Marktanner-Turneretscher...". By contrast, Vervoort and Watson expressed uncertainty that specimens examined by them from Cook Strait were the same species. In their illustration of the hydrotheca, marginal cusps are more deeply incised than shown by Marktanner-Turneretscher, and the hydrothecae are much larger. Those characters also differ from specimens examined here. *Clytia elongata* Warren, 1908, a name applied to a different species from Natal, South Africa, is an invalid junior primary homonym. That binomen has been replaced by the name *C. warreni* Stechow, 1919.

Hydroids of *Clytia elongata* from the Galápagos were found on *Amathia verticillata*, a ctenostome bryozoan that is also non-native to the archipelago (McCann et al. 2015).

***Clytia linearis* (Thornely, 1900)**

Figure 3d

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

Clytia acutidentata Fraser 1938a: 28, pl. 7, figs. 29a, b. –Calder et al. 2003: 1210.

?*Clytia carinadentata* Fraser 1938a: 29, pl. 7, fig. 30. –Calder et al. 2003: 1210.

Clytia linearis.–Calder et al. 2003: 1202.

Material.—Specimens collected April 2016 from fouling plates deployed at the Isla Baltra navy dock 15 January 2016, coll. K. Larson: 5 fragments, up to 7 mm high, without gonothecae, vial 232841; 1 colony fragment, 7 mm high, without gonothecae, vial 233083; 4 colony fragments, up to 4 mm high, without gonothecae, vial 232880; 4 colony fragments, up to 6 mm high, without gonothecae, vial 232867.

Remarks.—These hydroids correspond with *Clytia linearis* (Thornely, 1900) in having a keel-like perisarcal thickening extending from the apex of each pointed marginal cusp downwards onto the distal wall of the hydrotheca. This thickening, on the inner surface of the hydrotheca,

appears microscopically as a distinctive vertical line. The cusps and distal end of the hydrotheca are also pleated in cross-section. Fully-developed colonies usually exhibit sympodial growth. The taxonomy and nomenclature of the species have been reviewed earlier (Calder 1991a), and its life cycle was described by Lindner and Migotto (2002).

Clytia linearis, taken to be circumglobal in tropical and subtropical waters (Medel and Vervoort 2000), was reported earlier from the Galápagos by Calder et al. (2003). Included in the synonymy of the species by Calder et al. (2009) were *C. acutidentata* Fraser, 1938a from the Galápagos (Isla Floreana) and the Pacific coast of Mexico (Barra de Potosi), *C. carinadentata* Fraser, 1938a from the Galápagos (Isla Isabela), and *Gonothyraea serialis* Fraser, 1938a from the Pacific coast of Colombia (Puerto Utria). Also included in the synonymy of *C. linearis* is *Obelia striata* Clarke, 1907 from two locations in the tropical eastern Pacific (Rees and Vervoort 1987; Calder 1991a). Although one of these records was based on a colony from a trawl sample made at a depth of 2320 fm (4243 m), the specimen was found on a pteropod likely picked up in much shallower water. Another record of the species in the warm eastern Pacific is that of Calder (1996) from Rocas Alijos, west of Baja California, Mexico.

While *Clytia linearis* is a substrate generalist (Calder 1991a, b), it is also known to be frequent on shells of certain species of pteropods (Rees and Vervoort 1987). Such an association might account, at least in part, for the wide distribution of this hydroid. Alternatively, a circumglobal distribution may indicate existence of a species complex under the name.

***Clytia obliqua* (Clarke, 1907)**

Figure 3e

Campanularia (?) *obliqua* Clarke, 1907: 9, pl. 5, figs. 1–4.

Material.—Isla Santa Cruz, Puerto Ayora, Puerto Ayora dock, 25 April 2016, on stem of the hydroid *Halopteris alternata*, 1 colony, 2 mm high, without gonophores, coll. J.J. Mallinson, JJM Hyd. 2.

Remarks.— In the morphology of its trophosome, the hydroid examined here corresponds with species from the Indo-Pacific region that have been identified as *Clytia gracilis* (M. Sars, 1850) (e.g. Gibbons and Ryland 1989; Schuchert 2003), and as *C. warreni* Stechow, 1919 (e.g. Millard 1975; Watson 2000). The type localities of those two species are Lofoten, Norway, and Algoa Bay, South Africa, respectively. More likely, hydroids from the Galápagos are conspecific with the morphologically similar *Campanularia* (?) *obliqua* Clarke, 1907, originally described from Isla Perico, Panamá. Clarke's species is referable to *Clytia*, as first suggested by Fraser (1936) and repeated later by Hirohito (1995). In an earlier work (Calder 1991a), *Clytia obliqua* was included in the synonymy of *C. linearis* (Thornely, 1900), but we regard them as distinct because of differences in

the morphology of their marginal cusps. In *C. obliqua*, there are no keel-like thickenings of perisarc on the inner edge of each cusp as in *C. linearis*. A degree of uncertainty in our identification arises because species of the genus *Clytia* Lamouroux, 1812 are often inadequately distinguished and in need of revision. Identification of our specimens is also hindered by the absence of gonothecae.

Clytia obliqua has been reported from Japan (e.g. Fraser 1936; Yamada 1959; Hirohito 1995) and from California (Fraser 1948) in addition to the type locality of Panamá. Hirohito expressed uncertainty whether hydroids from Japan were actually conspecific with those reported by Fraser from the eastern Pacific.

***Clytia thornelyi* (Nutting, 1927), comb. nov.**

Figure 3f

Obelia thornelyi Nutting 1927: 202.

Material.—Isla Baltra, navy dock, collected April 2016 from fouling plate deployed 15 January 2016, 10 colony fragments, up to 20 mm high, with gonothecae, coll. K. Larson, vial 233083. –Isla Santa Cruz, Puerto Ayora, Franklin’s Bay, fouling community on a pontoon, 27 April 2016, 6 colony fragments, up to 5 mm high, without gonophores, coll. J. Geller, JJM Hyd. 11.

Remarks.—These specimens corresponded with accounts of *Clytia latithecata* Millard and Bouillon, 1973, a distinctive clytiid hydroid originally described from the Seychelles. The species is unusual in having hydrothecae with strongly flaring hydrothecal walls, resembling a shallow funnel. While hydrothecae somewhat resemble those of the Atlantic *C. noliformis* (McCrary, 1859), they differ in having a thin diaphragm and in lacking a distinct subhydrothecal spherule. Well-developed, fertile colonies were found on fouling plates immersed at the Baltra navy dock (SERC 233083). Gonothecae were paddle-shaped in lateral view, with smooth walls and a truncate distal end.

As for *Clytia latithecata*, it has been considered identical with a hydroid from Papua New Guinea identified by Thornely (1900) as *Obelia serrulata* (Bale, 1888) (see Kirkendale and Calder 2003). Working on specimens from the Philippines, Nutting (1927) justifiably argued that Thornely’s identification was incorrect and recognized her hydroid as a new species, *O. thornelyi*. *Clytia latithecata* has also been regarded as a junior synonym of *C. stolonifera* Blackburn, 1938, an Australian species (Watson 2005). The senior synonym and valid name of the species is therefore *O. thornelyi*, here assigned to *Clytia*. While the specific name should have been spelled *thornelyae*, in recognition of Laura Roscoe Thornely (1860–1951), the original spelling is to be maintained (ICZN Art. 32.3; Brandon-Jones et al. 2007).

Clytia thornelyi has not been reported before from the Galápagos. Although still a relatively obscure species, it appears to be widespread, with

scattered records from the tropical and subtropical western Atlantic (e.g. Calder and Kirkendale 2005, as *C. stolonifera*; Oliveira et al. 2016, as *C. stolonifera*), the west and central Pacific (e.g. Thornely 1900, as *Obelia serrulata*; Nutting 1927, as *O. thornelyi*; Kirkendale and Calder 2003, as *C. latithecata*; Di Camillo et al. 2008, as *C. latithecata*; Carlton and Eldredge 2009, as *C. latithecata*) and Indian (e.g. Millard and Bouillon 1973, as *C. latithecata*) oceans. We suggest that this species is a likely introduction to the Galápagos from either the western Pacific or the western Atlantic Ocean.

Family Obeliidae Haeckel, 1879

***Obelia dichotoma* (Linnaeus, 1758)**

Figure 3g

Sertularia dichotoma Linnaeus 1758: 812.

Obelia dichotoma.—Fraser 1938a: 36; 1938b: 133. —Calder et al. 2003: 1202. —Hickman 2008: 130, three unnumbered figs.

Material.—Isla Santa Cruz, Puerto Ayora, Franklin’s Bay, fouling community on floats, epizoic on *Nemalecium lighti*, 1 colony, 5 mm high, without gonothecae, 27 February 2015, coll. J. T. Carlton. —Isla Santa Cruz, Puerto Ayora, Franklin’s Bay, collected April 2016 from fouling plate deployed 27 February 2015, 1 colony fragment, 14 mm high, without gonophores, coll. K. Larson, vial 234926. —Isla Baltra, navy dock, collected April 2016 from fouling plate deployed 15 January 2016, 1 colony, 7 mm high, without gonophores, coll. K. Larson, vial 232869.

Remarks.—It seems almost certain that a species complex exists under the binomen *Obelia dichotoma* (Linnaeus, 1758). With a type locality on the coast of southwest England (Cornelius 1975), the species has long been considered abundant in many areas and virtually cosmopolitan in distribution. It has been reported across the tropical and temperate Indo-Pacific region (e.g. Fraser 1937; Millard 1975; Cooke 1977; Hirohito 1995; Vervoort and Watson 2003; Watson 2005; Xu et al. 2014b), including the Galápagos (Fraser 1938a, b; Calder et al. 2003; Hickman 2008). Affinities of local populations remain to be determined, along with their origin. Of note, *Obelia dichotoma* is considered a common component of marine fouling assemblages (Woods Hole Oceanographic Institution 1952; Millard 1959; Standing 1976; Carlton and Eldredge 2009; Karlson and Osman 2012), having been reported on various substrates including test panels, buoys, water pipes, and hulls of ships. Long-range transport by shipping is therefore likely. It may thus be that open ocean, sublittoral populations of what are now called *O. dichotoma* in the tropical eastern Pacific (including the Galápagos) will prove to be an endemic species, whereas *O. dichotoma* found in ports and harbors in the same region will be found to be members of a global “harbor clade”, whose origin may, after centuries of global shipping, be difficult to determine. Pending global genetic dissection of this species, we regard *O. dichotoma* in the islands as cryptogenic.

***Obelia oxydentata* Stechow, 1914**

Figure 3h, i

Obelia oxydentata Stechow 1914: 131, fig. 7.

Material.—Isla Santa Cruz, Tortuga Bay, epizoic on bryozoan *Amathia verticillata*, 21 February 2015, 3 colony fragments, up to 6 cm high, with gonothecae, coll. J. T. Carlton. –Isla Santa Cruz, Puerto Ayora, Franklin’s Bay, fouling community on floats, 1 colony, 9 mm high, with gonothecae, 27 February 2015, coll. J. T. Carlton. –Isla Santa Cruz, Puerto Ayora, Franklin’s Bay, 30 April 2016, 1 colony fragment, 5 mm high, without gonophores, coll. K. Collins, JJM Hyd. 19.

Remarks.—No hydroids such as these, resembling the widely reported *Obelia bidentata* Clark, 1875 (type locality: Long Island Sound, USA) and especially the much less familiar *O. oxydentata* Stechow, 1914 (type locality: St. Thomas, Virgin Islands), have been reported before from the Galápagos Islands. Elsewhere in the eastern Pacific, hydroids similar to these two species have been reported to the east from Isla Perico, Gulf of Panama (Clarke, 1907, as *Obelia* (?) sp.), to the north in San Francisco Bay, California (Fraser 1937, as *O. bicuspidata*; Mills et al. 2007, as *O. bidentata*), and to the south in the fjords region of southern Chile (Galea et al. 2009, as *O. bidentata*). Gibbons and Ryland (1989) remarked that hydroids from Fiji resembled *O. oxydentata* (as illustrated by Hirohito 1969), but assigned them instead to *O. bidentata* following Cornelius (1975). Gravier-Bonnet (1999) applied the binomen *O. oxydentata* to similar hydroids from seagrass beds in Madagascar. Specimens from the Galápagos are much the same as those from Fiji and Madagascar, although gonothecae differ somewhat in tapering distally rather than having a distinct terminal collar.

Over the last four decades, *Obelia oxydentata* has generally been taken to be a synonym of *O. bidentata* (e.g. Cornelius 1975; Calder 1991a; WoRMS), a supposedly cosmopolitan species (Medel and Vervoort 2000; Peña Cantero and Gili 2006). Under that broad concept, however, *O. bidentata* likely comprises a species complex (see Calder 2013, 2017). If hydroids identified as *O. bidentata* across the warm Indo-Pacific region are indeed identical with those of Clark (1875) from the cool-temperate western North Atlantic, genetic confirmation is needed. Morphologically, Clark’s robust specimens were as much as 15 cm high and had polysiphonic stems, unlike the diminutive (< 1 cm high), monosiphonic colonies examined here. Instead, our small specimens closely resemble accounts of *O. oxydentata* from warm waters of the Caribbean (Stechow 1914) and Florida (Calder 2013). Stechow (1914) included Clarke’s (1907) *Obelia* (?) sp. collected in 1904–1905 (before the 1914 opening of the Panama Canal) from the Gulf of Panama, tropical eastern Pacific, in the synonymy of his new species *O. oxydentata*. Unusual even in an era when global distributions of species were widely accepted, Stechow was struck by finding the same hydroid species on both

sides of the Isthmus of Panama: “*Die Auffindung dieser pacifischen Art nunmehr hier auf der atlantischen Seite Amerikas ist außerordentlich bemerkenswert*” (The discovery of this Pacific species now, here on the Atlantic side of America, is extraordinarily remarkable).

Obelia oxydentata is therefore known from the warm western Atlantic (Stechow 1914; Calder 2013), the Indian Ocean (Gravier-Bonnet 1999) and, very likely, Fiji (Gibbons and Ryland 1989). Until now, the sole eastern Pacific record consisted of Clarke’s 1904–1905 material from Isla Perico, an important Pacific Panamá port of the era. Once clearly distinguished morphologically from *O. bidentata*, records of *O. oxydentata* are likely to expand, perhaps significantly. At least some records of *O. bidentata* or another of its many synonyms, *O. bicuspidata* Clark, 1875, from tropical and warm temperate regions of the world, based on small, monosiphonic hydroids (e.g. Millard and Bouillon 1973; Gibbons and Ryland 1989; Calder 1991a, b; Migotto 1996; Kirkendale and Calder 2003; Calder and Kirkendale 2005; Carlton and Eldredge 2009; Galea 2010), may represent *O. oxydentata*.

While *Obelia oxydentata* has almost certainly been introduced to the Galápagos, the source of eastern Pacific populations is unclear, as the species may originate in either the tropical Indo-west Pacific or in the tropical western Atlantic. Once many *Obelia* species can be assessed phylogenetically, we predict that *O. oxydentata* will group with species endemic to one of these two regions.

Order Macrocolonia Leclère, Schuchert, Cruaud, Couloux and Manuel, 2009
 Family Haleciidae Hincks, 1868

***Halecium labiatum* Billard, 1933**

Figure 4a, b

Halecium labiatum Billard, 1933: 21, figs. 8K–M.

Material.—Specimens collected April 2016 from fouling plates deployed at the Isla Baltra navy dock, 15 January 2016, coll. K. Larson: 3 colony fragments, up to 4 mm high, without gonophores, vial 232885; 7 colony fragments, up to 4 mm high, with female gonophores, vial 234225; 4 colony fragments, up to 7 mm high, without gonophores, specimens dry at some point, vial 234190; 1 colony, 6 mm high, without gonophores, vial 232895; 6 colony fragments, up to 5 mm high, with female gonophores, vial 232882; 2 colony fragments, up to 6.5 mm high, without gonophores, vial 232875; 8 colony fragments, up to 9 mm high, with female gonophores, vial 232848; 3 colony fragments, up to 6 mm high, with female gonophores, vial 234201; 6 colony fragments, up to 5 mm high, without gonophores, vial 234222.

Remarks.—In being unfamiliar to us at first, these tiny specimens were compared with accounts of all 140 species currently recognized in the genus *Halecium* Oken, 1815. They are closest morphologically to a group of

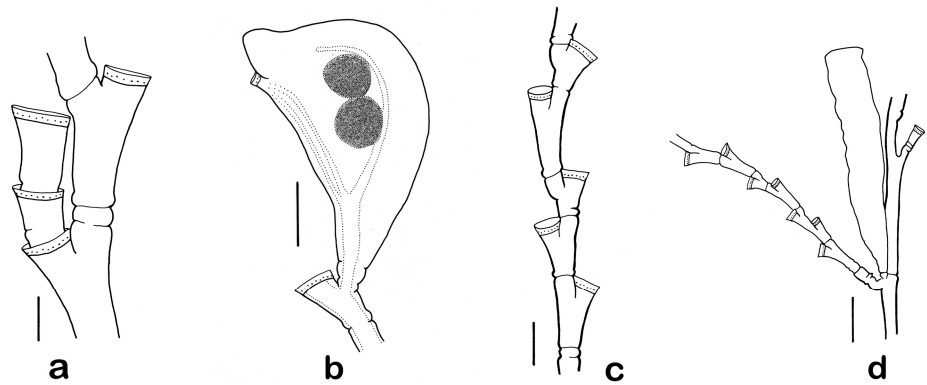


Figure 4. Leptothecata: family Haleciidae. a, *Halecium labiatum*, part of hydrocaulus, with hydrothecae, Isla Baltra, navy dock, SERC # 232882, scale equals 0.1 mm. b, *Halecium labiatum*, part of colony with female gonotheca, Isla Baltra, navy dock, SERC # 232882, scale equals 0.2 mm. c, *Nemalecium lighti*, part of a hydrocladium, with internodes and hydrothecae, Isla Santa Cruz, Franklin's Bay, fouling community on floats, scale equals 0.2 mm. d, *Nemalecium lighti*, part of hydrocaulus, with a branch, hydrothecae, and a gonotheca, Isla Santa Cruz, Franklin's Bay, fouling community on floats, scale equals 0.5 mm.

about 40 species, including the type species *H. halecinum* (Linnaeus, 1758), having female gonothecae of a fundamentally similar form (symmetry bilateral; outline irregularly obovate in lateral view; aperture lateral rather than terminal, with one or more gonophoral hydranths). Within that group, characters of both trophosome and gonosome conformed closest with those of *H. labiatum* Billard, 1933.

Halecium labiatum is very poorly known. The species was originally described by Billard (1933) from material collected at a depth of 36–55 m in the northern Gulf of Suez, Egypt. Subsequent published reports have been from the Dahlak Archipelago in the southern Red Sea (Vervoort 1967), the Gulf of Aden (Rees and Vervoort 1987), and (to where it may also be introduced) Martinique, French Lesser Antilles (Galea and Ferry 2015). Although seldom reported, it seems probable that this small hydroid has on occasion been overlooked, misidentified, identified only to genus, or simply ignored. At least some records of *H. lankesterii* (Bourne, 1890) are likely to have been based on *H. labiatum* (in particular, see Millard 1968, 1975). Misidentifications of Bourne's species have been noted earlier (Peña Cantero and García Carrascosa 2002), although some reports of it from the eastern Atlantic region were likely based on a species other than *H. labiatum*. *Halecium lankesterii* is notable in being one of only a few species of the genus having symbiotic zooxanthellae (Peña Cantero and García Carrascosa 2002). Such symbionts are absent in *H. labiatum*.

Colonies of *H. labiatum* are small, with few distinguishing characters beyond the singular shape of their female gonothecae. As described best by Galea and Ferry (2015), these structures are saccular in form, with a bulging convex wall, a slightly sigmoid concave wall, and there provided with a lateral aperture with a pair of adjoining hydrothecae towards the distal end, a prominent lip protruding over the aperture, and two defensive hydranths. Gonothecae often occur in pairs, as was usually the case in our

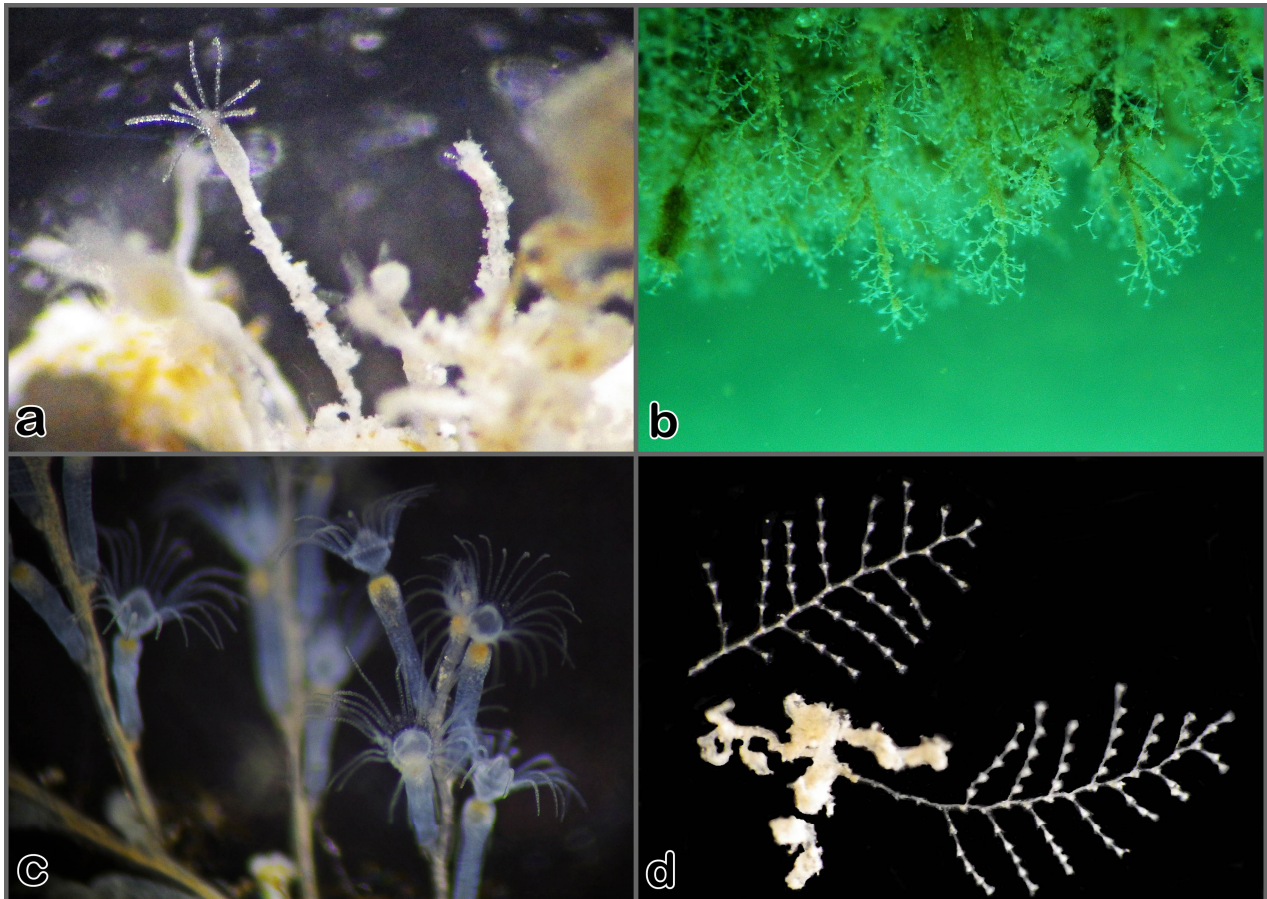


Figure 5. Photographs of hydroids from life. a, *?Bougainvillia* sp., part of colony with a hydranth, Isla Santa Cruz, Puerto Ayora, main passenger dock, JJM Hyd. 3. b, *Nemalecium lighti*, colonies hanging from underside of a boat, Isla Santa Cruz, Puerto Ayora, Franklin's Bay, JJM Hyd. 10. c, *Nemalecium lighti*, hydranths of colonies fouling same boat, Isla Santa Cruz, Puerto Ayora, Franklin's Bay, JJM Hyd. 10. Nematodactyls of the species are not distinct in the photograph but were visible under a microscope. d, *Halopteris alternata*, two colonies, Isla Santa Cruz, Puerto Ayora, main passenger dock, JJM Hyd. 1. Photographs by J.J. Mallinson.

specimens. Material examined by Galea and Ferry had 1–2 large eggs per gonotheca, while the usual number in ours was three. Curiously, all fertile colonies examined here were female.

This species is recorded for the first time anywhere in the Pacific Ocean. Specimens were quite frequent, and well-developed, on fouling plates immersed at the Baltra navy dock. Transport to the Galápagos by shipping therefore seems probable, given the location, but the source of these populations is obscure.

Nemalecium lighti (Hargitt, 1924)

Figures 4c, d; 5b, c

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

Nemalecium lighti.—Hickman 2008: 129, three unnumbered figs. —Banks et al. 2009, pp. 51, 53, 56, 59.

Material.—Isla Santa Cruz, Puerto Ayora, Franklin's Bay, fouling community on floats, 27 February 2015, 10 colony fragments, up to 2.5 cm high, with gonophores, coll. J.T. Carlton. —Isla Santa Cruz, Puerto Ayora, Franklin's Bay, collected April 2016 from fouling plate deployed 27 February 2015,

2 colony fragments, up to 5 mm high, without gonophores, coll. K. Larson, vial 232925. –Isla Santa Cruz, Puerto Ayora, main passenger dock, collected April 2016 from fouling plate deployed 27 February 2015, 6 colony fragments, up to 7 mm high, without gonophores, coll. K. Larson, vial 234261. –Isla Santa Cruz, Puerto Ayora, Franklin’s Bay, collected April 2016 from fouling plate deployed 27 February 2015, 2 colony fragments, up to 4 mm high, without gonophores, coll. K. Larson, vial 234148. –Isla Santa Cruz, Puerto Ayora, Franklin’s Bay, on mooring rope, 27 April 2016, 8 colony fragments, up to 2.5 cm high, without gonophores, coll. J.J. Mallinson, JJM Hyd. 10.

Remarks.—Originally described from Puerto Galera Bay, Mindoro, Philippines (Hargitt 1924), *Nemalecium lighti* was first reported in the eastern Pacific from the Galápagos based upon 2005–2007 collections from Islas Wolf, Darwin, and Marchena (Banks et al. 2009; see also Hickman 2008, for color illustrations).

The species has been reported elsewhere in both the Indo-west Pacific region (e.g. Pennycuik 1959, as *Halecium sessile* Norman, 1867; Gravier-Bonnet and Migotto 2000; Kirkendale and Calder 2003; Galea et al. 2012) and the warm western Atlantic (e.g. Calder 1991a; Migotto 1996; Galea 2008; Oliveira et al. 2016). A second species of *Nemalecium* Bouillon, 1986, *N. gracile*, was recently described from the Caribbean region (Galea et al. 2012). It is uncertain how many records of *N. lighti* from the Atlantic might be referable to *N. gracile* instead. Meanwhile, Gravier-Bonnet and Migotto (2000) and Galea et al. (2012) have noted that additional species of *Nemalecium* may exist in the Indo-Pacific. Colonies examined here were particularly noteworthy for the great length and slenderness of their gonothecae. Some of them measured more than 2.5 mm from base to apex, while being less than 0.5 mm in diameter (Figure 4d). The largest ones included in a table by Galea et al. 2012 (those of *N. cf. lighti* from Brazil, described by Migotto 1996), were 1.9 mm long and 0.8 mm in diameter. Additional taxonomic investigations on the population in the Galápagos are warranted. We tentatively assign an introduced status to *N. lighti*, with possible origins in either the Indo-west Pacific or the western Atlantic.

Although traditionally assigned to Haleciidae, and so classified here, *Nemalecium lighti* now appears misplaced in that family. Evidence from molecular data indicates that the species is not a haleciid, and Maronna et al. (2016) included it in a new leptothecate suborder, Plumupheniida. As noted by them, research is needed to better resolve its systematic position.

Family Sertulariidae Lamouroux, 1812

***Amphisbetia distans* (Lamouroux, 1816), comb. nov.**

Figure 6a, b

Dynamena distans Lamouroux 1816: 180, pl. 5, figs. 1a, B.

Sertularia stookeyi.—Fraser 1938: 55; 1948: 250.

Tridentata distans.—Calder et al. 2003: 1203.

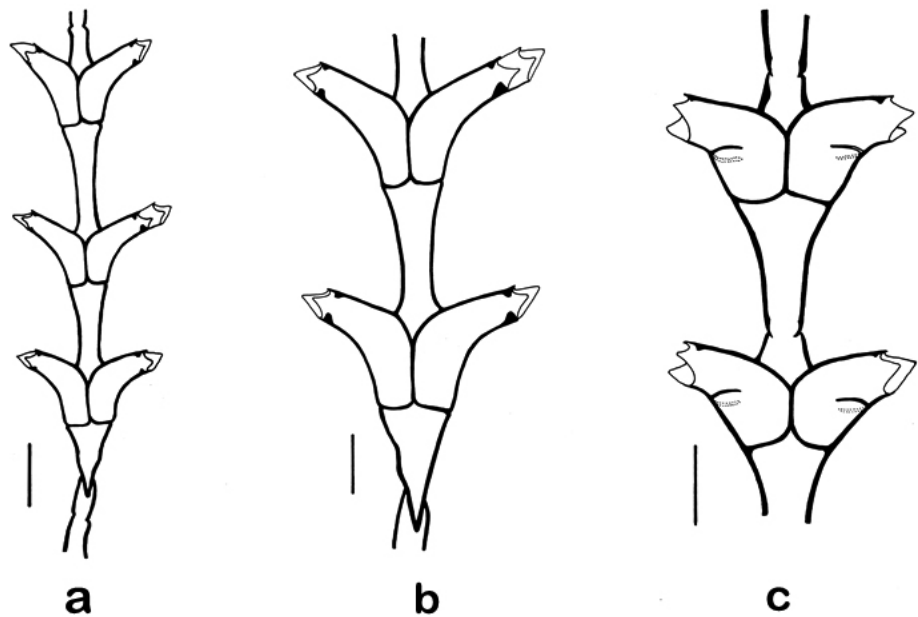


Figure 6. Leptothecata: family Sertulariidae. a, *Amphisbetia distans*, part of colony, with three hydrothecal pairs, Isla Bartolomé, JJM Hyd. 17, scale equals 0.2 mm. b, *Amphisbetia distans*, part of colony, with two hydrothecal pairs, Isla Bartolomé, JJM Hyd. 17, scale equals 0.1 mm. c, *Tridentata turbinata*, part of colony, with two hydrothecal pairs, Isla Santa Cruz, Puerto Ayora, main passenger dock, JJM Hyd. 21, scale equals 0.25 mm.

Material.—Isla Bartolomé, 12.2 m, 29 April 2016, on large red tunicate *Halocynthia dumosa*, 6 colony fragments, up to 1 cm high, without gonophores, coll. G. Lambert, JJM Hyd. 17.

Remarks.—*Dynamena distans* Lamouroux, 1816, also known as *Sertularia distans*, *Tridentata distans*, and *Sertularia stookeyi* Nutting, 1904, among others (see synonymy in Medel and Vervoort 1998), is assigned here to *Amphisbetia* L. Agassiz, 1862 on the basis of molecular evidence. Phylograms in Moura et al. (2011) and Maronna et al. (2016) reveal that the species is much closer genetically to *Sertularia operculata* Linnaeus, 1758 (type species of *Amphisbetia* L. Agassiz, 1862) than to either *Sertularia argentea* Linnaeus, 1758 (type species of *Sertularia* Linnaeus, 1758) or *Sertularia perpusilla* Stechow, 1919 (type species of *Tridentata* Stechow, 1920). In terms of morphology, gonothecae of the species resemble those of *S. operculata* more closely than those of *S. perpusilla* in being ovate with smooth walls instead of barrel-shaped with transverse ribs (Calder 2013). They are also much different from those of *S. argentea*, particularly in lacking one or more disto-lateral horns.

Originally reported from pelagic *Sargassum* and other floating objects in the Atlantic Ocean (Lamouroux 1816), *Amphisbetia distans* is believed to be circumglobal in distribution. A species with distinctively tiny and slender hydrothecae, it appears to be common in the Galápagos. To date, *A. distans* has been reported from the following islands in the archipelago: Wolf (Fraser 1938a, as *Sertularia stookeyi*; Calder et al. 2003, as *Tridentata distans*), Isabela (Fraser 1938a, as *S. stookeyi*), Seymour Norte (Fraser 1948,

as *S. stookeyi*), San Cristóbal (Fraser 1948, as *S. stookeyi*), and Bartolomé (this study). Moura et al. (2011) suggested that cryptic species may exist within *Sertularia distans* (= *A. distans*), at least in the Atlantic Ocean.

Detailed accounts of this species have been given earlier (Calder 1991a, 2013, as *Tridentata distans*; Cornelius 1995b, as *T. distans*; Hirohito 1995, as *Sertularia distans*; Medel and Vervoort 1998, as *S. distans*).

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

Figure 6c

Dynamena turbinata Lamouroux 1816: 180.

Tridentata turbinata.—Calder et al. 2003: 1194, fig. 16.—Hickman 2008: 132, three unnumbered figs.

Material.—Isla Baltra, 28 April 2016, on a weight, 5 colony fragments, up to 8 mm high, without gonophores, coll. J.J. Mallinson, JJM Hyd. 23. —Isla Santa Cruz, Puerto Ayora, Puerto Ayora dock, 2 May 2016, 7 colony fragments, up to 1.6 cm high, without gonophores, coll. J.J. Mallinson, JJM Hyd. 21.

Remarks.—As reflected in an exhaustive synonymy list of this species by Medel and Vervoort (1998, as *Sertularia turbinata*), *Tridentata turbinata* (Lamouroux, 1816) has usually been assigned to *Sertularia* Linnaeus, 1758 under the binomen *S. turbinata*. Molecular data compiled by Maronna et al. (2016) reveal that it is genetically remote from *Sertularia argentea* Linnaeus, 1758, type species of the Linnean genus, and that it is phylogenetically closest to *S. perpusilla* Stechow, 1919, type species of *Tridentata* Stechow, 1920. *Tridentata turbinata* and *T. perpusilla*, together with *T. marginata* (Kirchenpauer, 1864) and *T. tumida* (Allman, 1877), cluster as a monophyletic group in the phylograms of Maronna et al. Morphological evidence exists as well for recognition of *Tridentata* (Calder 1991a, 2013), particularly in the shape of the gonothecae as described below, and *T. turbinata* is upheld here as the valid name of this species.

Fertile colonies of *T. turbinata* have seldom been observed (Calder 2013; Galea and Ferry 2015, as *S. turbinata*), and hydroids examined here were also sterile. As described by Vervoort (1959, as *S. turbinata*), Millard (1975, as *S. turbinata*), Hirohito (1995, as *S. turbinata*), Galea and Ferry (2015, as *S. turbinata*), and Humara-Gil and Cruz-Gómez (2018, as *Tridentata turbinata*), however, gonothecae are similar in morphology to those of *T. perpusilla* and *T. marginata* in being barrel-shaped with about 5–8 prominent transverse ribs. The aperture is terminal and wide in diameter. Gonothecae of the closely related *T. tumida* have yet to be reliably described.

Originally discovered in “Australasia” (Lamouroux 1816), *T. turbinata* is now considered circumglobal in tropical and subtropical waters. The species has been identified previously from the Galápagos at Isla Tortuga (Calder et al. 2003). Hickman (2008) also reported it from the islands, but did not specify a location.

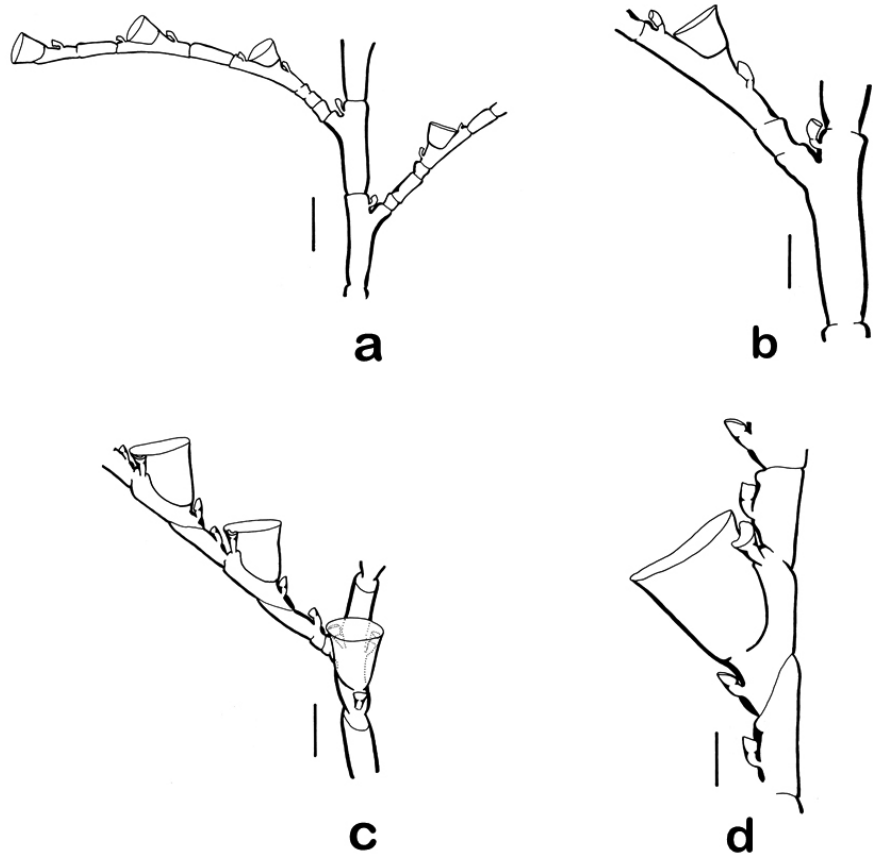


Figure 7. Leptothecata: families Kirchenpaueriidae and Halopterididae. a, *Ventromma halecioides*, part of hydrocaulus, with two hydrocladia, Isla Santa Cruz, Puerto Ayora, main passenger dock, JJM Hyd. 7, scale equals 0.20 mm. b, *Ventromma halecioides*, part of hydrocaulus, with a hydrocladium, nematothecae, and a hydrotheca, Isla Santa Cruz, Puerto Ayora, main passenger dock, JJM Hyd. 7, scale equals 0.1 mm. c, *Halopteris alternata*, part of hydrocaulus, with a hydrocladium, nematothecae, and three hydrothecae, Isla Santa Cruz, Puerto Ayora, main passenger dock, JJM Hyd. 1, scale equals 0.2 mm. d, *Halopteris alternata*, part of a hydrocladium, with nematothecae and a hydrotheca, Isla Santa Cruz, Puerto Ayora, main passenger dock, JJM Hyd. 1, scale equals 0.1 mm.

Family Kirchenpaueriidae Stechow, 1921

Ventromma halecioides (Alder, 1859)

Figure 7a, b

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

Plumularia inermis.—Fraser 1938a: 64, p. 15, figs. 74a, b.

Ventromma halecioides.—Calder et al. 2003: 1200.

Material.—Specimens collected April 2016 from fouling plates deployed at Franklin’s Bay, Puerto Ayora, Isla Santa Cruz, 27 February 2015, coll. K. Larson: 2 colony fragments, up to 6 mm high, without gonophores, vial 234138; 1 colony, 3 mm high, without gonophores, vial 234266; 1 colony, 6 mm high, without gonophores, vial 234236; 2 colony fragments, up to 7 mm high, without gonophores, vial 234244; 1 colony fragment, 11.5 mm high, without gonophores, vial 234245; 3 colony fragments, up to 13 mm high, without gonophores, vial 233108. —Specimens from fouling plates deployed at the main passenger dock, Puerto Ayora, Isla Santa Cruz, 27 February 2015, coll. K. Larson: 2 colony fragments, up to 7 mm high, without

gonophores, vial 234261; 3 colony fragments, up to 13 mm high, without gonophores, vial 232956; 2 colony fragments, up to 6 mm high, without gonophores, vial 234288; 1 colony fragment, 7 mm high, without gonophores, vial 233137; 8 colony fragments, up to 27 mm high, without gonophores, vial 310276; 1 colony fragment, 9 mm high, without gonophores, vial 234122. –Isla Santa Cruz, Puerto Ayora, main passenger dock, collected April 2016 from fouling cage (?) deployed 27 February 2015, 1 colony fragment, 6 mm high, without gonophores, coll. K. Larson, vial 232796. –Isla Santa Cruz, Puerto Ayora, main passenger dock, collected April 2016 from fouling plate deployed 15 January 2016, 2 colony fragments, up to 11 mm high, without gonophores, coll. K. Larson, vial 234056. –Isla Santa Cruz, Puerto Ayora, Puerto Ayora dock, 27 February 2015, on fouling panel rope, 6 colony fragments, up to 2.5 cm high, without gonophores, coll. J.J. Mallinson, JJM Hyd. 7. –Isla Santa Cruz, Puerto Ayora, Puerto Ayora dock, 25 April 2016, on fouling panel rope, 1 colony, 2.4 cm high, without gonophores, coll. J.J. Mallinson, JJM Hyd. 8. –Isla Santa Cruz, Puerto Ayora, Puerto Ayora dock, 26 April 2016, 7 colony fragments, up to 3 cm high, one colony with a gonophore, coll. J.J. Mallinson, JJM Hyd. 7a.

Remarks.—Originally described as *Plumularia halecioides* by Alder (1859) from the northeast coast of England, opinions currently differ over the generic assignment of this species. Although no longer considered a species of *Plumularia* Lamarck, 1816, it has been combined in some works with *Kirchenpaueria* Jickeli, 1883, and in others with *Ventromma* Stechow, 1923. Morphological differences between the two genera are minor, with nematophores being naked in *Kirchenpaueria* and protected by nematothecae in *Ventromma*. More conclusively, molecular studies (Leclère et al. 2007; Moura et al. 2008; Peña Cantero et al. 2010; Maronna et al. 2016) have demonstrated that *P. halecioides*, the type species of *Ventromma*, is highly divergent genetically from *Kirchenpaueria pinnata* (Linnaeus, 1758), type species of *Kirchenpaueria*. Support for recognition of the genus *Ventromma* is most recently provided by 16S sequence data showing *Kirchenpaueria halecioides* forming a sister clade to other taxa of Kirchenpaueriidae (Moura et al. 2018). We therefore adopt *Ventromma halecioides* as the valid name of the species.

Although confirmation is needed, hydroids of *V. halecioides* are currently believed to be circumglobal in warm-temperate and tropical waters (Calder 2013). The species has been reported earlier from the Galápagos at Isla Fernandina (Calder et al. 2003). Another record, from Isla Floreana (Fraser 1938a, as *Plumularia inermis* Nutting, 1900), is likely based on a misidentification. While *P. inermis* is a junior subjective synonym of *V. halecioides*, Fraser's material differs in having homomerously segmented hydrocladia. Moreover, gonothecae were elongated and obovate with smooth walls and with a rounded distal end instead of being deep cone-shaped with distinct transverse ridges and with a truncate distal end, as in *V. halecioides*.

Clarke (1907) identified a hydroid from bathyal waters (1063 m) off the Pacific coast of Panamá as *Plumularia helleri* Hincks, 1872, a name now included in the synonymy of *Kirchenpaueria pinnata* (Linnaeus, 1758). Clarke's illustration shows that his species, a kirchenpaueriid with nematothecae, is referable instead to *Ventromma*, but not to *V. halecioides* or any other known species of the genus. While its hydrocladia are heteromerously segmented, the adcauline wall of the hydrotheca is about one-third free (Clarke 1907: pl. 15, figs. 1–6). This deep-water species, deemed herein to be new, warrants redescription and naming. Material to serve as a holotype exists at the NMNH (USNM 29620, as *Plumularia helleri*, R/V *Albatross* Station Number 4622, United States Fish Commission Eastern Pacific Expedition, centroid latitude 6.5167, centroid longitude –81.7333, south of Coiba Island, Panamá, 21 October 1904).

Ventromma halecioides, cryptogenic in the islands, is frequent in areas of quiet, shallow water (Calder 2013), as with the dock areas sampled in Puerto Ayora. It is known to be a component of certain fouling communities, occurring on ships and buoys (Woods Hole Oceanographic Institution 1952, as *Plumularia halecioides*) and in ports (Cornelius 1992b).

Family Halopterididae Millard, 1962

***Halopteris alternata* (Nutting, 1900)**

Figures 5d; 7c, d

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

Not *Plumularia alternata*. –Fraser 1938a: 62, pl. 14, figs. 71a, b.

Material.—Specimens collected April 2016 from fouling plates deployed at Franklin's Bay, Puerto Ayora, Isla Santa Cruz, 27 February 2015, coll. K. Larson: 3 colony fragments, up to 15 mm high, without gonophores, vial 234130; 1 colony, 8 mm high, with gonophores, vial 234154; 6 colony fragments, up to 9 mm high, without gonophores, vial 232798; 2 colony fragments, up to 4.5 mm high, without gonophores, vial 232812; 5 colony fragments, up to 18 mm high, without gonophores, vial 232823; 9 colony fragments, up to 15 mm high, without gonophores, vial 234265; 6 colony fragments, up to 18 mm high, without gonophores, vial 232928. –Isla Santa Cruz, Puerto Ayora, Franklin's Bay, 30 April 2016, on fouling panel, 5 colony fragments, up to 9 mm high, without gonophores, coll. G. Ruiz, JJM Hyd. 18a. –Specimens collected April 2016 from fouling plates deployed 27 February 2015 at main passenger dock, Puerto Ayora, Isla Santa Cruz, coll. K. Larson: 2 colony fragments, up to 8 mm high, without gonophores, vial 232790; 4 colony fragments, up to 9 mm high, without gonophores, vial 233075; same, collections made April 2016 from fouling panels deployed at main passenger dock but on 15 January 2016: 2 colony fragments, up to 11 mm high, without gonophores, vial 232746; 3 colony fragments, up to 10 mm high, without gonophores, vial 233011; 1 colony fragment, 6 mm high, without

gonophores, vial 233028. –Isla Santa Cruz, Puerto Ayora, Puerto Ayora dock, 25 April 2016, on fouling panel, 10 colony fragments, up to 18 mm high, without gonophores, coll. L. McCann, JJM Hyd. 1. –Isla Santa Cruz, Puerto Ayora, Puerto Ayora dock, 02 May 2016, on sponge, 7 colony fragments, up to 13 mm high, without gonophores, coll. N de Voogd, JJM Hyd. 22.

Remarks.—In being referable to the genus *Halopteris* Allman, 1877, these hydroids fall within the “*H. diaphana*” group of species recognized by Schuchert (1997). Of that group, they most closely resemble *H. alternata* (Nutting, 1900) from the tropical and subtropical Atlantic Ocean and are assigned to that species. Unlike *H. billardi* (Vannucci, 1951), *H. diaphana* (Heller, 1868), *H. tenella* (Verrill, 1873), *H. platygonotheca* Schuchert, 1997, and *H. violae* Calder et al., 2003 of that particular assemblage, axillar nematothecae are present or often present above the cauline hydrothecae in our material. They also differ from *H. billardi* in having monosiphonic hydrocauli, from *H. diaphana* in having much coarser internodes on both hydrocaulus and hydrocladia, from *H. tenella* in having unbranched hydrocladia, and from *H. violae* in lacking disto-lateral nematothecae on cauline internodes. Unlike in *H. diaphana*, *H. tenella*, and *H. violae*, hydrocladial internodes are of two types only; short anematothecate internodes are never present distal to a hydrothecate internode. Although similar to hydroids identified as *H. polymorpha* (Billard, 1913), they differ in lacking axillar nematothecae above hydrocladial hydrothecae.

Halopteris alternata was reported in the Galápagos from Isla Wolf and Isla Floreana by Fraser (1938a, as *Plumularia alternata*), but Schuchert (1997) believed that those records were based on a different, undetermined species. Unlike the spindle-shaped gonothecae of *H. alternata*, as described by Schuchert, those of colonies described by Fraser were in the shape of curved cornucopiae.

Originally described from the Bahamas (Nutting 1900), the range of *H. alternata* extends from North Carolina and Bermuda to Brazil in the western Atlantic, and from the vicinity of Madeira, the Canary Islands, and the Cape Verde Islands in the eastern Atlantic (Ansín Agís et al. 2001). It is reported here as a probable introduction for the first time from the Galápagos Islands. Earlier records of the species from various locations across the Pacific Ocean are considered doubtful (Schuchert 1997). *H. alternata* is widespread in the Caribbean (Calder and Kirkendale 2005) and may have been transported into the eastern Pacific from the Caribbean region via the Panama Canal.

Discussion

Constraining the detection of introduced hydroids in regions such as the Galápagos Islands is the reported natural cosmopolitan, and especially tropicopolitan, distribution of a great many species of shallow-water

hydroids, most or all of which, if not transported around the world by centuries of shipping, may prove to be species complexes. This said, for many marine taxa, the Central American Land Barrier has served to isolate Caribbean and eastern Pacific biotas for millions of years (James 1991; Hickman 2009), making it unlikely that the same species now naturally occur on either side of the Isthmus of Panama. Global shipping since the 1500s has, however, served to disperse many marine invertebrates, algae, and fishes across and between oceans (Carlton 2009) such that the appearance of, for example, Caribbean or western Pacific hydroid species in the Galápagos Islands would not be unexpected.

Regionally, the Panama Canal may have served as an important corridor since 1914 for Caribbean hydroids entering the tropical eastern Pacific Ocean (Cohen 2006). Although the freshwater Gatun Lake would appear to be a barrier to the dispersal of marine species, shipping has nevertheless likely transported many hydroid species from the Atlantic to the Pacific (and vice-versa). Dormant stages exist in their life cycles that could survive temporarily unfavourable environmental conditions encountered over the short distance and travel time required in crossing through Panamá. Perhaps more important, however, is the presence of both medusae and polyp stages of hydrozoans in ships' ballast water (Carlton and Geller 1993; Smith et al. 1999, J. T. Carlton, *personal observations*), such that species transported inside vessels would pass imperviously through the Panama Canal and be released on the Central American Pacific coast.

We conservatively recognize here eight introduced and five cryptogenic species of hydroids (Table 1). The introduced species are recognized through their remarkable disjunct distributions, making natural distribution and dispersal unlikely. The cryptogenic species are primarily so designated because they may be members of world-wide species complexes, within which endemic tropical eastern Pacific species may reside. To the species treated here, we add one introduced species reported earlier (Calder et al. 2003) of either Caribbean or Indo-west Pacific origin, *Clytia hummelincki* (Leloup, 1935), and one cryptogenic species of unknown origin, *Pennaria disticha* Goldfuss, 1820. Calder et al. (2003) recorded additional species of hydroids in the open ocean, sublittoral Galápagos fauna that were previously known either from the Atlantic or the western Pacific, but whose biogeography and taxonomy require further investigation.

Of the introduced species, two (*Bougainvillia muscus* and *Halopteris alternata*) may be from the Atlantic Ocean, and two from the broad Indo-Pacific theater (*Halecium labiatum* and *Clytia elongata*). The remaining four (*Clytia thornelyi*, *C. hummelincki*, *Obelia oxydentata*, and *Nemalium lighti*) may originate from either the warm waters of the western Atlantic or the western Pacific. Genetic analyses seeking centers of haplotype diversity, phylogenetic analyses grouping sibling species, or both, may

eventually point to the origins of these species. No introduced species known only from the tropical eastern Atlantic have yet been detected in the Galápagos.

The 2016 dates of first collection of seven of the hydroid species newly added here as introductions or cryptogens to the Galápagos marine fauna do not likely represent new invasions; that is, these records should not be interpreted as part of a new wave of invasions now occurring in the archipelago. Rather, there have been few historical investigations of the biofouling communities in Galápagos ports and harbors (Carlton et al. 2019). While the present investigations (Carlton et al. 2019) thus form a baseline of the diversity of these communities, we do not know when these species first arrived. Given that vessels have been visiting the Galápagos since the 1500s, we have little doubt that with further study, and with resolution of the biogeography of many other species, the list of non-native hydroids will grow considerably.

Finally, we note that the present 2015 and 2016 collections took place during a strong El Niño episode (Stramma et al. 2016) in the equatorial eastern Pacific. With no seasonal or long-term data available on the diversity and distribution of hydroids in the Galápagos Archipelago, it is difficult to interpret what effect these unusually warm seawater temperatures may have had on the fauna. It may be that future studies will be able to place the current collections in a broader temporal framework.

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Supplementary material

The following supplementary material is available for this article:

Table S1. Occurrences of Hydrozoa at sampling locations in the Galápagos Islands, 2001–2016.

This material is available as part of online article from:

http://www.aquaticinvasions.net/2019/Supplements/AI_2019_Calder_etal_Table_S1.xlsx