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Research Article

Additions to the hydroids (Cnidaria, Hydrozoa) of marine fouling communities on the mainland of Ecuador and in the Galapagos Islands

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Abstract

Hydroids were examined from surveys of marine fouling communities undertaken during 2018 in Ecuador. Specimens were collected on settlement panels in harbours at Salinas and La Libertad on the mainland, and at Isla San Cristóbal in the Galapagos Islands. Of 27 species in the samples, 18 were present in collections from the mainland and 14 from San Cristóbal. Most frequent in samples from the mainland were *Bougainvillia* cf. *muscus* (20 samples), *Obelia microtheca* (20), *Clytia delicatula* (19) and *Pennaria disticha* (10). In collections from San Cristóbal, most frequent were *Obelia alternata* (27), *Bougainvillia* cf. *muscus* (16), *Ectopleura crocea* (13) and *Cirrholovenia tetranema* (11). Based on genetic evidence, *Ectopleura media* Fraser, 1948 is assigned to the synonymy of *E. crocea* (L. Agassiz, 1862). In addition, a COI reference sequence is deposited for the first time for *Tridentata turbinata.* Male gonophores of *Eudendrium breve*, previously unknown, were discovered and illustrated. The cnidome of the species comprises small and large microbasic euryteles. Five of the species have not been reported before from the Tropical Eastern Pacific. Of these, three (*Amphinema* cf. *rugosum, Egmundella humilis,* and Campanulinida, undetermined) were found only in the Galapagos, one (*Clytia delicatula*) occurred at both mainland sites and the Galapagos, and one (*Opercularella* sp.) was collected only from a station on the mainland. Six other species [*Ectopleura integra*, *Coryne repens*, *Clytia irregularis*, *C. seriata*, *Obelia alternata* (resurrected here from the synonymy of *O. dichotoma*), and *O. microtheca*] are known only from the Tropical Eastern Pacific. Three of them, *E. integra, C. irregularis,* and *C. seriata*, are new to the Ecuadorian mainland. Species numbers were similar (range of 6 to 11 taxa) across all stations. One-third (nine species) were found only in Galapagos samples, whereas nearly half (13 species) were found only at mainland sites. More than half (15 species) were restricted to a single station. Previous studies, together with this work, bring the total of introduced and cryptogenic hydroid species in the Galapagos Islands to 12 (previously eight) and nine (previously five) taxa, respectively. We recognize four introduced and eight cryptogenic hydroid species from the coast of mainland Ecuador.

Key words: Hydroidolina, Isla San Cristóbal, La Libertad, Salinas, species invasions, cryptogenic species, Tropical Eastern Pacific

Introduction

Much of what is currently known about the taxonomy and distribution of hydroids in the Tropical Eastern Pacific is recorded in a series of papers by Fraser (1938a, b, c, 1939, 1948). His studies were based on large and important collections acquired in the 1930s during several Allan Hancock Pacific Expeditions to the region. The bulk of those hydroid collections, including primary types of new species, are now at the Santa Barbara Museum of Natural History (Santa Barbara, California, USA). Other parts of the Hancock hydroid collections are at the National Museum of Natural History, Smithsonian Institution (Washington, DC, USA), and in the Fraser Hydroid Collection at the Royal British Columbia Museum (Victoria, British Columbia, Canada). With a few notable exceptions (e.g., Humara-Gil and Cruz-Gómez 2018; Mendoza-Becerril et al. 2020a), hydroids of the region have been neglected in the decades since Fraser's publications, and the fauna remains poorly known. Meanwhile, many of Fraser's new species from Hancock collections need to be re-examined and described in greater detail. Lectotypes of them occur in the collections at Santa Barbara (Calder et al. 2009).

Underscoring the importance of investigations on taxonomy and distribution of hydroids in the region is the rapid shift in global patterns of species distributions due to increased coastal development and the resulting abundance of anthropogenic structures and materials for substrates, coupled with climate change and long-range dispersal mechanisms such as shipping (Carlton et al. 2019). Furthermore, coastal infrastructure such as harbors, marinas, and piers are highly susceptible to biological invasions as they increase the total area for fouling benthic species recruitment (Oricchio et al. 2019) and may provide novel hard-bottom habitat in otherwise predominately soft-sediment environments. Hydroids are an important component of marine fouling communities, and this study continues a recent investigation of specimens collected from the Galapagos Islands (Isla Santa Cruz, Isla Baltra, Isla Bartolomé, Isla San Cristóbal), Ecuador (Calder et al. 2019). The present paper is an account of species from both the Galapagos archipelago (Isla San Cristóbal) and mainland Ecuador (Salinas and La Libertad).

Materials and methods

Field methods

Collections of fouling organisms colonizing settling plates were made on the mainland coast of Ecuador and in the Galapagos Islands. Plates of grey polyvinyl chloride (PVC), measuring 14 × 14 cm and 0.5 cm thick, were suspended horizontally at depths of 1 m. These substrates were deployed in February 2018 and retrieved in May 2018, for a three-month exposure time.

On the mainland (Figure 1), plates were deployed at two locations in the province of Santa Elena: (1) Salinas (three stations: at the Naval Base pier

Figure 1. Map of research sites in Salinas and La Libertad, Ecuador.

[*muelles*], at Salinas Yacht Club, and at Capitania Salinas and (2) the CEPE (Corporación Estatal Petrolera Ecuatoriana, now Petroecuador) pier at La Libertad. Docks at the Naval Base, Yacht Club, and Capitania are floating structures, whereas that at La Libertad is a fixed cement oil dock. In the Galapagos (Figure 2), plates were deployed in Puerto Baquerizo Moreno, Isla San Cristóbal (the easternmost island of the archipelago), at three stations: buoys (*boyas*) in Wreck Bay, the old passenger dock, and the new passenger dock Tiburon Martillo.

Surface temperature and salinity data were obtained with a YSI SCT meter. A HOBO U22-001 (Onset Computer Corporation) temperature logger was placed on the plate array, at a depth of 1 m, at San Cristóbal, Salinas Yacht Club, and La Libertad. The HOBO logger at the latter site was lost.

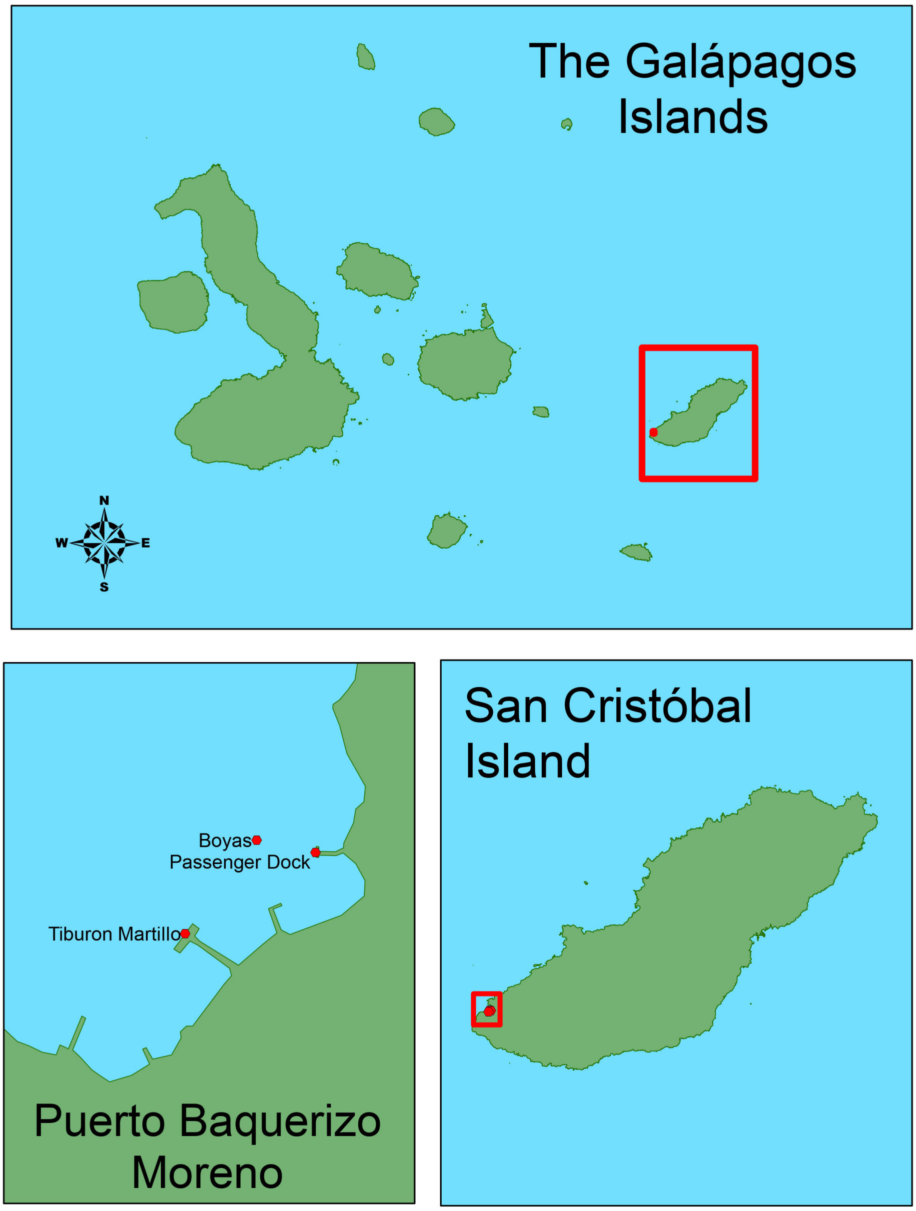

Figure 2. Map of research sites on San Cristóbal Island, Galapagos, Ecuador.

Laboratory Methods

Voucher samples of hydroids and all other macroscopic taxa on the panels were collected and preserved in either 95% ethanol or 10% seawater formalin. SERC (Smithsonian Environmental Research Center, Edgewater, Maryland, USA) vial numbers accompany all collection records herein. Collections are deposited at SERC and at the Charles Darwin Research Station, Puerto Ayora, Santa Cruz Island, Galapagos.

For molecular genetic analyses, specimens were shipped to the Moss Landing Marine Laboratories (California State University) in Moss Landing, California. DNA was extracted from ~ 25 mg tissue subsamples using the DNeasy Blood & Tissue Kit (Qiagen, Catalog No. 69504) following the manufacturer's protocol. A fragment of the COI gene was amplified by polymerase chain reaction (PCR) using conditions described in Geller et al.

(2013). PCR products were purified using Agencourt AMPure beads (Beckman Coulter, Catalog No. A63880) according to the manufacturer's protocol and sent to Elim Biopharmaceuticals (Hayward, California, USA) for dideoxy chain termination sequencing. Forward and reverse sequences were assembled and primer sequences removed using Geneious 10.1 (Biomatters, Auckland, New Zealand). Sequences were compared to the GenBank database.

Taxonomic and Biogeographic Classifications

The classification system adopted herein is based largely on that of Schuchert (2012) for anthoathecates and Maronna et al. (2016) for leptothecates. Synonymy lists provide the original scientific name and author of each species, together with citations of any publications providing primary records and collection data on hydroids from Ecuador. All cited references have been examined, and illustrations are based entirely on specimens examined during this study. Nematocyst classification used herein follows Weill (1934) and Östman (1979a, b, 1982, 1999). Illustrations of nematocysts, all to the same magnification, are from photomicrographs originally taken at 1000× using a Zeiss Axioscop microscope.

The Tropical Eastern Pacific Biogeographic Region is taken to extend from the Gulf of California (Mar de Cortés) to northern Peru (Hastings 2000). Within that region, the Panamic Province extends from the Pacific coast of Honduras, at the Golfo de Fonseca, to northern Peru, at the southern end of the Golfo de Guayaquil. The coast of Ecuador falls within that province, while biota of the Galapagos Islands is considered sufficiently divergent to warrant recognition of the archipelago as a distinct Galapagos Province.

Abbreviations are as follows:

BCPM British Columbia Provincial Museum (now Royal British Columbia Museum), Victoria, British Columbia, Canada
ROM Royal Ontario Museum, Toronto, Ontario, Canada
ROMIZ Invertebrate Zoology collections, Royal Ontario Museum, Toronto, Ontario, Canada
SBMNH Santa Barbara Museum of Natural History, Santa Barbara, California, USA
SERC Ecuador hydroid collections, Smithsonian Environmental Research Center, Edgewater, Maryland, USA
WoRMS World Register of Marine Species (http://www.marinespecies.org, last consulted 7 December 2020), with content on Hydrozoa from the World Hydrozoa Database by Peter Schuchert (http://www.marinespecies.org/hydrozoa).

Results

Salinity and Temperature Regime

On retrieval in May 2018, surface temperature and salinity measured 27 °C and 30.2‰ at Salinas Yacht Club on the mainland, and 22 °C and 31.6‰ at Isla San Cristóbal. Averaged temperature logger data for February–May 2018 were 24.5 °C for Salinas and 18.2 °C for San Cristóbal. Water temperatures at San Cristóbal reflect the typically cooler conditions around the Galapagos Islands, impacted by the northbound Humboldt (Peru) Current.

General diversity patterns

Twenty-seven species of hydroids, comprising nine anthoathecates and 18 leptothecates, are reported here from fouling communities on experimentally deployed panels in mainland Ecuador and in the Galapagos Islands (Table 1). Of the seven families of anthothecates, only Tubulariidae was represented by more than one species. The leptothecates were represented by nine families (and two taxa of uncertain family affinity), of which two, Clytiidae and Obeliidae, account for half (nine) of the species. One of these, *Obelia alternata*, is resurrected out of synonymy with the putatively cosmopolitan *O. dichotoma*.

Numbers of species were relatively uniform (range of 6 to 11 taxa) across all stations (Table 1), with the highest diversity in samples from the Salinas Yacht Club. One third of all taxa (nine species) were found only in samples from the Galapagos, whereas nearly half (13 species) were found only at sites on the mainland. Five species were found both on the mainland and on San Cristóbal. More than half (15 species) were found at only one station (nine unique to individual mainland stations, and six unique to island stations) (Table 1).

Eighteen species were present in collections from the mainland (17 from the Salinas area, and one additional species, *Ectopleura* sp., found only at La Libertad) and 14 species from San Cristóbal. The most frequent mainland species were *Bougainvillia* cf. *muscus* (20 samples), *Obelia microtheca* (20), *Clytia delicatula* (19) and *Pennaria disticha* (10). Most frequent at San Cristóbal were *Obelia alternata* (27 samples), *Bougainvillia* cf. *muscus* (16), *Ectopleura crocea* (13) and *Cirrholovenia tetranema* (11).

Native, Introduced and Cryptogenic Species

Seven species (*Ectopleura integra, Coryne repens, Clytia irregularis, C. seriata, Obelia alternata*, *O. microtheca*, and Campanulinida, undetermined) from the samples are known only from the Tropical Eastern Pacific. Of these, *C. repens* and *O. alternata* may be Galapagos Islands endemics. Three species that we take to be native are first records for the mainland of Ecuador: *E. integra, C. irregularis*, and *C. seriata* (Table 2).

Table 1. Hydroid species found in Salinas and La Libertad, Ecuador, and San Cristóbal Island, Galápagos, Ecuador, by sample station.

Species	Sample Stations						
	Mainland Ecuador				Galápagos Islands		
	La Libertad pier	Salinas			Isla San Cristóbal		
		Capitania Salinas pier	Naval Base Salinas	Salinas Yacht Club	Buoys	Passenger dock	Tiburon Martillo pier
Ectopleura integra			x				
Ectopleura crocea				x		x	x
Ectopleura sp.	x						
Tubulariidae (unidentified)			x	x	x	x	x
Coryne repens					x		
Pennaria disticha	x	x	x	x			
Turritopsis sp.		x	x	x			
Bougainvillia cf. *muscus*	x	x	x	x		x	x
Amphinema cf. *rugosum*					x	x	
Eudendrium breve							x
Cirrholovenia tetranema	x	x			x	x	x
Egmundella humilis							x
?*Opercularella* sp.	x						
Campanulinida, undet.					x		
Clytia delicatula	x	x	x	x	x		x
Clytia irregularis				x			
Clytia linearis	x	x	x			x	
Clytia noliformis			x				
Clytia seriata	x			x			
Clytia sp.						x	
Obelia alternata					x	x	x
Obelia microtheca	x	x	x	x			
Obelia oxydentata				x		x	
Nemalecium lighti				x			
Tridentata turbinata						x	
Halopteris alternata				x			
Ventromma halecioides				x			
Plumularia floridana			x				
Total species (excluding unidentified Tubulariidae; see text)	9	7	9	11	6	9	7
Species Unique to a Given Station	2	–	3	4	2	2	2

Four species were detected for the first time in the Tropical Eastern Pacific (Tables 2 and 3). Two of these (*Amphinema* cf. *rugosum* and *Egmundella humilis*) were found only in the Galapagos Islands, one (*Clytia delicatula*) occurred both on mainland and Galapagos sites, and one (*Opercularella* sp.) was found only on the mainland. We suggest that the first four are probable introductions, via shipping, to the Eastern Pacific (Tables 2 and 3).

Table 3 presents a summary of the introduced and cryptogenic hydroids of the Galapagos Islands and the mainland coast of Ecuador. The Galapagos fauna has benefitted from assessments of introduced and cryptogenic hydrozoans (Calder et al. 2019; Carlton et al. 2019), but no such analyses are available for the Ecuadorian mainland. Previous (Calder et al. 2019) and current (this paper) studies bring the total number of introduced and cryptogenic hydroid species in the Galapagos Islands to 12 (previously eight) and nine (previously five) taxa respectively, with *B. muscus* now re-assigned, as discussed below, to cryptogenic status. Five introduced and eight cryptogenic hydroid species are recognized herein from the Ecuador mainland.

Table 2. Biogeographic status, probable origin if introduced, and current or previous distribution status of 2018 biofouling species.

Species	Status (see text): Native (N) Introduced (I) Cryptogenic (C) Unknown (U)	Probable Origin if Introduced	Mainland Ecuador (present survey)	Previously known from mainland?	Galápagos (present survey)	Previously known from Galápagos?	Remarks
Ectopleura integra	N		x	no		yes	new record for mainland Ecuador
Ectopleura crocea	I	North Atlantic	x	no	x	yes	new record for mainland Ecuador
Ectopleura sp.	U		x	–			not identifiable to species
Coryne repens	N				x	yes	apparent island endemic
Pennaria disticha	C		x	yes		yes	species complex (see text)
Turritopsis sp.	U		x	yes		yes	
Bougainvillia cf. *muscus*	C		x	no	x	yes	
Amphinema cf. *rugosum*	I	North Atlantic Ocean or Indo-West Pacific			x	no	
Eudendrium breve	N				x	yes	
Cirrholovenia tetranema	C		x	no	x	yes	
Egmundella humilis	I	Northwest Pacific?			x	no	
?Opercularella sp.	U		x	no			new record for the Tropical Eastern Pacific
Campanulinida undet.	I				x	no	
Clytia delicatula	I	Indo-West Pacific	x	no	x	no	
Clytia irregularis	N		x	no			new record for mainland Ecuador
Clytia linearis	C		x	yes	x	yes	
Clytia noliformis	C		x	yes			
Clytia seriata	N		x	no			new record for Ecuador mainland
Clytia sp.	U				x	–	not identifiable to species
Obelia alternata	N				x	yes	apparent island endemic
Obelia microtheca	N		x	yes			
Obelia oxydentata	I	Western Atlantic	x	no	x	yes	
Nemalecium lighti	I	Indo-West Pacific or Western Atlantic	x	no	x	yes	
Tridentata turbinata	C				x	yes	
Halopteris alternata	I	Atlantic Ocean	x	no		yes	
Ventromma halecioides	C		x	no		yes	
Plumularia floridana	C		x	yes		yes	

Table 3. Introduced and cryptogenic hydroids of the Galapagos Islands and the Ecuador mainland: summary of previously recognized, new records, and re-assigned taxa. * – not found in the 2018 panel deployments.

Location	Introduced Species		Cryptogenic Species		
	Previously recognized (Calder et al. 2019)	New records or newly recognized (herein)	Previously recognized (Calder et al. 2019)	New records (herein)	Previously known, but here newly considered cryptogenic
Galapagos Islands	**Clytia elongata*	*Amphinema* cf. *rugosum*	**Pennaria disticha*		*Bougainvillia muscus* (as introduced in Calder et al. 2019)
	**Clytia thornelyi*	*Egmundella humilis*	*Cirrholovenia tetranema*		*Clytia linearis*
	**Clytia hummelincki*	Campanulinida, undet.	**Ventromma halecioides*		**Tridentata turbinata*
	Obelia oxydentata	*Clytia delicatula*	**Obelia dichotoma*		**Plumularia floridana*
	**Halecium labiatum*	*Ectopleura crocea* (see text; first collected 1934)	**Bimeria vestita*		
	Nemalecium lighti				
	Halopteris alternata				
Ecuador mainland		*Obelia oxydentata*	**Bimeria vestita*	*Bougainvillia* cf. *muscus*	*Clytia noliformis*
		Clytia delicatula		*Cirrholovenia tetranema*	*Clytia linearis*
		Nemalecium lighti		*Ventromma halecioides*	*Plumularia floridana*
		Halopteris alternata			*Pennaria disticha* (as introduced in Cardenas-Calle et al. 2019)

Systematic Account

Phylum Cnidaria Verrill, 1865
Subphylum Medusozoa Petersen, 1979
Class Hydrozoa Owen, 1843
Subclass Hydroidolina Collins, 2000
Order Anthoathecata Cornelius, 1992
Suborder Aplanulata Collins, Winkelman, Hadrys & Schierwater, 2005
Family Tubulariidae Fleming, 1828
Genus *Ectopleura* L. Agassiz, 1862

Ectopleura integra **(Fraser, 1938a)**

Figure 3a

Tubularia integra Fraser 1938a: 26, pl. 5, fig. 24.–Calder et al. 2009: 941.

Ectopleura integra.–Calder et al. 2003: 1198.–Hickman 2008: 123, three unnumbered figs. –Calder et al. 2009: 941.

Type locality.—Ecuador: Galapagos Islands, Isla Baltra (South Seymour Island) (Fraser 1938a; Calder et al. 2009).

Material.—Salinas, Salinas Naval Base, 1 colony fragment, 8 mm high, with medusa buds, 255044.

Remarks.—The condition of the colony examined here was poor, but its gonophores were medusa buds with four slightly developed tentacular protuberances as in *Ectopleura integra* (Fraser, 1938a). Originally assigned to *Tubularia* Linnaeus, 1758 by Fraser (1938a), this species was combined instead with the genus *Ectopleura* L. Agassiz, 1862 by Calder et al. (2003). This is the first report of *E. integra* from the mainland of Ecuador, although it is known elsewhere in the Tropical Eastern Pacific from the Galapagos Islands and from Panama (Fraser 1938a).

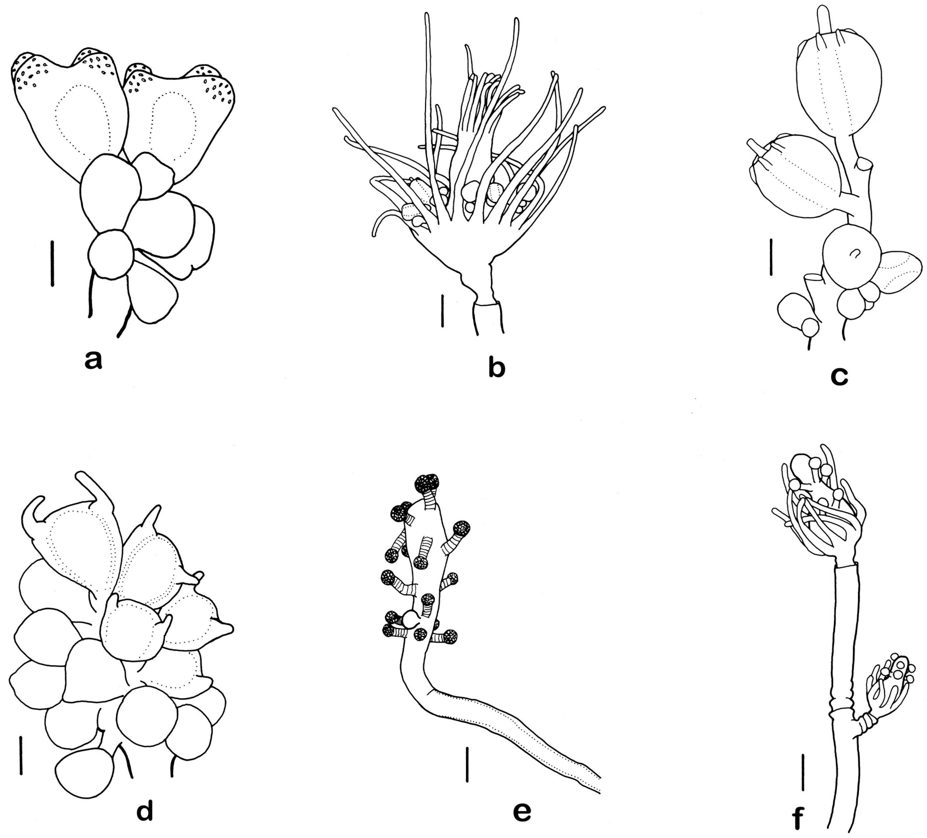

Figure 3. Anthoathecata, families Tubulariidae, Corynidae, and Pennariidae. a, *Ectopleura integra*, blastostyle with developing medusa buds, 255044, scale equals 0.05 mm. b, *Ectopleura crocea*, hydranth with gonophores, 303803, scale equals 0.50 mm. c, *Ectopleura crocea*, blastostyle with male gonophores, 303803, scale equals 0.20 mm. d, *Ectopleura* sp., blastostyle with developing medusa buds, 253919, scale equals 0.05 mm. e, *Coryne repens*, hydranth with developing gonophore, 254810, scale equals 0.25 mm. f, *Pennaria disticha*, tip of a hydrocaulus with two hydranths, 253937, scale equals 0.20 mm.

Reported Distribution.—*Tropical Eastern Pacific:* Galapagos Islands, Ecuador (Fraser 1938a; Calder et al. 2003; Hickman 2008); Isla Pacora and Isla Medidor, Panama (Fraser 1938a).

Worldwide: known only from the Tropical Eastern Pacific.

Ectopleura crocea (L. Agassiz, 1862)

Figure 3b, c

Parypha crocea L. Agassiz 1862: 249, pl. 23, figs. 1–26, pl. 23a, figs. 1–7.

Tubularia crocea.–Fraser 1938a: 26.

Ectopleura media Fraser 1948: 201, pl. 22, figs. 2a–d.–Marshall et al. 2002: 83, photos 14, 15. –Calder et al. 2003: 1198.–Marshall and Edgar 2003: 290.–Hickman 2008: 124, three unnumbered figures.–Calder et al. 2009: 940; 2019: 24, figs. 2a, b.

Type locality.—USA: Massachusetts, Boston Harbor, on floating timbers (L. Agassiz 1862).

Material.—Galapagos, San Cristóbal, passenger dock, 7 colonies or colony fragments, to 1.8 cm high, with well-developed gonophores, 254064. –San Cristóbal, Tiburon Martillo, several colony fragments, to 2.5 cm high, with gonophores, 254193.–San Cristóbal, passenger dock, 2 stems, to 3.5 cm high, with gonophores, 254676.–San Cristóbal, Tiburon Martillo, 1 colony, 9 mm high, with gonophores, 261196.–San Cristóbal, passenger dock, 3 colonies or colony fragments, to 2.5 cm high, with gonophores, 254675. –San Cristóbal, passenger dock, 2 colonies or colony fragments, to 1.8 cm high, with gonophores, 303803.–San Cristóbal, Tiburon Martillo, 4 colonies or colony fragments, 1.9 cm high, with gonophores, 261195.–San Cristóbal, passenger dock, 1 colony, 2 cm high, with gonophores and actinulae, 306601. –San Cristóbal, passenger dock, 2 colony fragments, to 1.5 cm high, with incipient gonophores, 261131.–San Cristóbal, Tiburon Martillo, 8 colonies or colony fragments, to 3.4 cm high, with gonophores, 254724.–San Cristóbal, passenger dock, 3 colonies or colony fragments, to 2.2 cm high, without gonophores, 261134.–San Cristóbal, Tiburon Martillo, 9 colony fragments, to 2.2 cm high, with developing gonophores, 254094.–San Cristóbal, Tiburon Martillo, 3 colony fragments, to 2.6 cm high, with nascent gonophores, 254093.–Salinas, Salinas Yacht Club, 1 colony, 1.3 cm high, with incipient gonophores, 306583 (a fragment of the colony of this mainland Ecuador material was a 100% sequence match to GenBank *E. crocea* sequence MH80965.1; see below).

Remarks.—These hydroids were initially identified as *Ectopleura media* (Fraser, 1948), a species thought endemic to the Galapagos Islands. Morphologically similar to *E. crocea* (L. Agassiz, 1862), barcoding revealed that a specimen from San Cristóbal (306601) was genetically identical to GenBank MH888021.1 (based on collections from New York State); this sequence has been deposited in GenBank as Accession Number MT949544. Based on the molecular analyses, and on the morphologically similar accounts of the two, we refer *E. media* to the synonymy of *E. crocea*, a species originally described from Boston Harbor, Massachusetts, USA. *Ectopleura crocea*, a common fouling organism in harbours and on ships (Woods Hole Oceanographic Institution 1952), has been considered circumglobal in temperate waters (Schuchert 2010). We consider this species to be non-native in the Galapagos, likely introduced many years ago by shipping. Fraser (1938a) had reported the species, as *Tubularia crocea*, from material collected in Tagus Cove, Isla Isabela, at a depth of 30 fathoms (55 m). Given the cool-temperate type locality of the species, Fraser's record of it from the Tropical Eastern Pacific Region had been considered doubtful in earlier works (Calder et al. 2003, 2019). A detailed overview of the biology of *E. crocea* has been given by Schuchert (2010).

Ectopleura crocea was collected during this study from both Isla San Cristóbal, Galapagos Islands, and from Salinas on the mainland, the latter identified genetically, as the specimen (306583) lacked gonophores. It is thus possible that other unidentifiable tubulariid specimens (below) from Salinas are also *E. crocea*. While the Galapagos archipelago offers cooler than usual tropical waters, warmer waters prevail on the mainland coast. Whether this range of thermal tolerance reflects the presence of warmtolerant clades of this generally more temperate species remains to be investigated. Regardless, *E. crocea* now adds to the growing list of invasions in the islands that have been able to colonize natural, open-ocean environments (Carlton et al. 2019).

In addition to the record by Fraser (1938a) from Isla Isabela, this species has been reported previously in the archipelago, as *E. media*, from Isla Marchena in 1935 (Fraser 1948), Isla San Cristóbal (Marshall et al. 2002; Marshall and Edgar 2003; Calder et al. 2019), and Isla Isabela (Calder et al. 2003).

Reported Distribution.—*Tropical Eastern Pacific:* Galapagos Islands, Ecuador (Fraser 1938a, as *Tubularia crocea*; 1948, as *Ectopleura media*; Marshall et al. 2002, as *E. media*; Calder et al. 2003, 2019, as *E. media*; Marshall and Edgar 2003, as *E. media*; Hickman 2008, as *E. media*); Salinas (new record for mainland Ecuador, herein); Isla Jicarón, Panama (Fraser 1938a, as *Tubularia crocea*).

Worldwide: Circumglobal in temperate waters (Schuchert 2010).

***Ectopleura* sp.**

Figure 3d

Material.—La Libertad, CEPE, 6 colony fragments, to 1.2 cm high, with medusa buds, 253919.

Remarks.—These specimens were in poor condition and could not be identified to species. Unlike in *Ectopleura crocea* (L. Agassiz, 1862), gonophores of these hydroids were medusa buds with two opposite tentacles, resembling those of species such as *E. viridis* Pictet, 1893, *E. minerva* Mayer, 1900b, *E. sacculifera* Kramp, 1957, and others (Xu et al. 2014). While *E. sacculifera* was described from 02°52′18″S; 82°19′30″W in waters off Santa Elena, Ecuador, the species was described from a single medusa and there is insufficient evidence to link hydroids from La Libertad to it. They differ from *Ectopleura integra* (Fraser, 1938a), medusa buds of which have four rudimentary tentacular processes.

Tubulariidae (unidentifiable)

Material.—Salinas, Salinas Naval Base, 5 colonies or colony fragments, to 1 cm high, with nascent gonophores, 254630.–Galapagos, San Cristóbal, *boyas*, 5 colony fragments, to 1 cm high, with deteriorated hydranths and gonophores, 254183.–San Cristóbal, Tiburon Martillo, 1 colony fragment, 2 cm high, with a deteriorated hydranth, 255112.–Salinas Naval Base, 5 colony fragments, to 1.7 cm high, without gonophores, 261077.–Salinas Naval Base, 1 stem, 1 cm high, without gonophores, 303310.–San Cristóbal, passenger dock, 1 colony, 1.7 cm high, without gonophores, 261159.–Salinas Naval Base, 2 colony fragments, to 8 mm high, without gonophores, 261100. –San Cristóbal, passenger dock, 1 colony, 8 mm high, without gonophores, 261133.

Remarks.—These specimens were unidentifiable because of their poor condition and lack of adequate gonophore development. It seems unlikely, however, that they are referable to species other than the three tubulariids listed above.

Suborder Capitata Kühn, 1913
Family Corynidae Johnston, 1837
Genus *Coryne* Gaertner, 1774

Coryne repens **Fraser, 1938a**

Figure 3e

Coryne repens Fraser 1938a: 13, pl. 1, figs. 6a, b.–Calder et al. 2003: 1198, fig. 17; 2009: 928.

Type locality.—Ecuador: Galapagos Islands, Isla Floreana (Charles Island), off Black Beach, 01°16′40″S; 90°29′46″W, 5 m (Fraser 1938a; Calder et al. 2009).

Material.—Galapagos, San Cristóbal, *boyas*, 1 colony, 5 mm high, with gonophores, 254810.

Remarks.—*Coryne repens* Fraser, 1938a differs little in morphology from the widely-distributed *C. pusilla* Gaertner, 1774, but it has been held separate on zoogeographic grounds (Schuchert 2001). Comparisons of the two, especially by barcoding, are therefore needed, especially since a species complex likely exists in hydroids identified as *C. pusilla* (Schuchert 2010). Axillar gonophores were present on the colony examined here.

Distribution records to date suggest that *C. repens* is endemic to the Galapagos Islands. It has been reported from Isla Floreana (Fraser 1938a), Isla Fernandina (Calder et al. 2003), and Isla San Cristóbal (this study). Additional records from the Galapagos can be added here from specimens in ROM collections:

ROMIZ B3477. Isla San Cristóbal, near wreck of the tanker "Jessica", 10 May 2001, with axillary gonophores, coll. G. Edgar and P. Marshall.

ROMIZ B3432. Isla Marchena, NW side, tidepool, 18 June 2001, with axillary gonophores, coll. D. Calder.

ROMIZ B3437. Isla Isabela, Punta Vicente Roca, rocky wall, 6 m, 19 June 2001, with axillary gonophores, coll. D. Calder.

ROMIZ B3448. Isla Isabela, Punta Vicente Roca, rocky wall, 15 m, 19 June 2001, on barnacle shell, with axillary gonophores, coll. D. Calder.

Reported Distribution.—*Tropical Eastern Pacific*: Galapagos Islands, Ecuador (Fraser 1938a; Calder et al. 2003).

Worldwide: known only from the Galapagos Islands.

Family Pennariidae McCrady, 1859
Genus *Pennaria* Goldfuss, 1820

Pennaria disticha **Goldfuss, 1820**

Figure 3f

Pennaria disticha Goldfuss 1820: 89.–Marshall et al. 2002: 83, photo 3.–Calder et al. 2003: 1198.–Marshall and Edgar 2003: 290.–Hickman 2008: 125, three unnumbered figs.–Banks et al. 2009: 56, 59.–Cárdenas-Calle et al. 2018a: 72; 2018b: 398; Cárdenas-Calle et al. 2019: 455.

Pennaria tiarella.–Fraser 1938a: 25; 1938c: 132; 1948: 200.
Pennaria sp.–Witman and Smith 2003: 29.

Type locality.—Italy: Gulf of Naples (Goldfuss 1820).

Material.—Salinas, Salinas Yacht Club, 4 colony fragments, up to 2.2 cm high, without gonophores, 254584.–Salinas, Capitania, 4 colonies or colony fragments, to 2.7 cm high, with gonophores, 260970.–La Libertad, CEPE, 1 colony fragment, 4 mm high, without gonophores, 253937.–La Libertad, CEPE, 1 colony, 5 mm high, without gonophores, 260947.–Capitania, 1 colony, 5 mm high, without gonophores, 260994.–Salinas Yacht Club, 1 colony, 1.7 cm high, with incipient gonophores, 261068.–Capitania, 2 colonies or colony fragments, to 2.7 cm high, with gonophores, 254010.–Salinas, Salinas Naval Base, 1 colony fragment, 1.1 cm high, without gonophores, 254061.–Capitania, 3 colonies or colony fragments, to 3.3 cm high, with deteriorated gonophores, 254002.–Capitania, 3 colonies or colony fragments, to 2.1 cm high, with gonophores, 303299 (a sequence of which has been deposited as GenBank Accession Number MT949547).

Remarks.—The hydroid of *Pennaria disticha* Goldfuss, 1820 was found as part of fouling assemblages during this study only on the Ecuadorian mainland (Salinas and La Libertad). Fraser (1948) had also reported the species, as *Pennaria tiarella* (Ayres, 1852), from La Libertad. Cárdenas-Calle et al. (2019) recorded it from three coastal provinces of the country (Manabí, Santa Elena, El Oro). While *P. disticha* did not recruit to fouling panel deployments on Santa Cruz Island in 2015–2016 (Calder et al. 2019) nor in the current (2018) study on San Cristóbal Island, it has been reported since the 1930s from the Galapagos (Calder et al. 2003, 2019); if introduced, it may have arrived centuries earlier. It is widespread in open ocean environments throughout the Archipelago (Keith 2016) as well as in more protected shallow bays, such as Franklin's Bay in the Puerto Ayora region (JTC, *personal observations*, 2015). Moreover, *P. disticha* was observed during fieldwork from 16–22 June 2001 to be one of the most abundant and conspicuous species on exposed rocky coasts from near-surface waters to depths of 7–8 m (DRC, *personal observations* at Rocas Gordon, Daphne Meñor, Rábida, Cousin's Rock, Marchena, Punta Vicente Roca on Isla Isabela, and Pinzón). According to Hickman (2008), colonies from wave-swept areas tend to be smaller and more compact than those from sheltered waters.

Detailed taxonomic accounts of this well-known species have been given elsewhere (e.g., Schuchert 2006; Calder 2010). In terms of its biogeographic status, Cranfield et al. (1998) treat it as introduced to New Zealand, with a European origin. Paulay et al. (2002) treat this species as cryptogenic in Guam, whereas Carlton and Eldredge (2009) treat it as introduced to the Hawaiian Islands. Calder et al. (2019) classified *P. disticha* as cryptogenic in the Galapagos Islands due to it being a possible global species complex, whereas Cárdenas-Calle et al. 2019 treat it as introduced on the Ecuador mainland. Miglietta et al. (2015, 2019) have shown that *P. "disticha"* consists of at least two or three distinct clades, whose origins remain to be determined. Two of these clades (1 and 2D) have been found on the Pacific coast of Panama. The genetic identity of mainland Ecuador and Galapagos material remains to be determined. Given this complexity, it seems best to treat *Pennaria* in the tropical Eastern Pacific at this time as cryptogenic; it may consist of both native and introduced populations if not species. While the observed habitat diversity of *P. disticha* in, for example, the Galapagos Islands, ranging from inshore bays to exposed rocky coasts, may reflect this taxonomic diversity, known introduced species have also invaded the open ocean environments in the Galapagos (Carlton et al. 2019).

Reported Distribution.—*Tropical Eastern Pacific:* Oaxaca, Mexico (Humara-Gil and Cruz-Gómez 2018) to Bahía Santa Elena, Ecuador, and the Galapagos Islands (Fraser 1938a, c, 1948, as *Pennaria tiarella*; Marshall et al. 2002; Calder et al. 2003; Marshall and Edgar 2003; Witman and Smith 2003, as *Pennaria* sp.; Hickman 2008; Banks et al. 2009).

Worldwide: commonly taken to be circumglobal in warm-temperate and tropical waters.

Suborder Filifera Kühn, 1913
Family Oceaniidae Eschscholtz, 1829
Genus *Turritopsis* McCrady, 1857

?*Turritopsis* sp.

Figure 4a

Turritopsis nutricula.–Fraser 1938a: 12.–Calder et al. 2003: 1194.
?*Turritopsis* sp.–Calder et al. 2019: 26, fig. 2c.

Material.—Salinas, Salinas Yacht Club, 1 colony, 5 mm high, without gonophores, 254027.–Salinas Yacht Club, 5 colonies or colony fragments, to 1.4 cm high, with many medusa buds, 261020.–Salinas Yacht Club, 6 colonies or colony fragments, to 1 cm high, without gonophores, 261055. –Salinas, Salinas Naval Base, 1 colony, 1 mm high, without gonophores, 261100.–Salinas, Capitania, 1 colony, 3 mm high, without gonophores, 260989.

Remarks.—The hydroid *Turritopsis nutricula* McCrady, 1857 has been reported from Ecuador (Fraser 1938a; Calder et al. 2003) and elsewhere in the tropical Eastern Pacific (Fraser 1938a, b, 1948). Lacking knowledge of both the medusa stage and the genetic barcode of present material, however, the hydroids collected here can be reliably identified only to genus. The best of these specimens, with medusa buds, were found at the Salinas Yacht Club (261020).

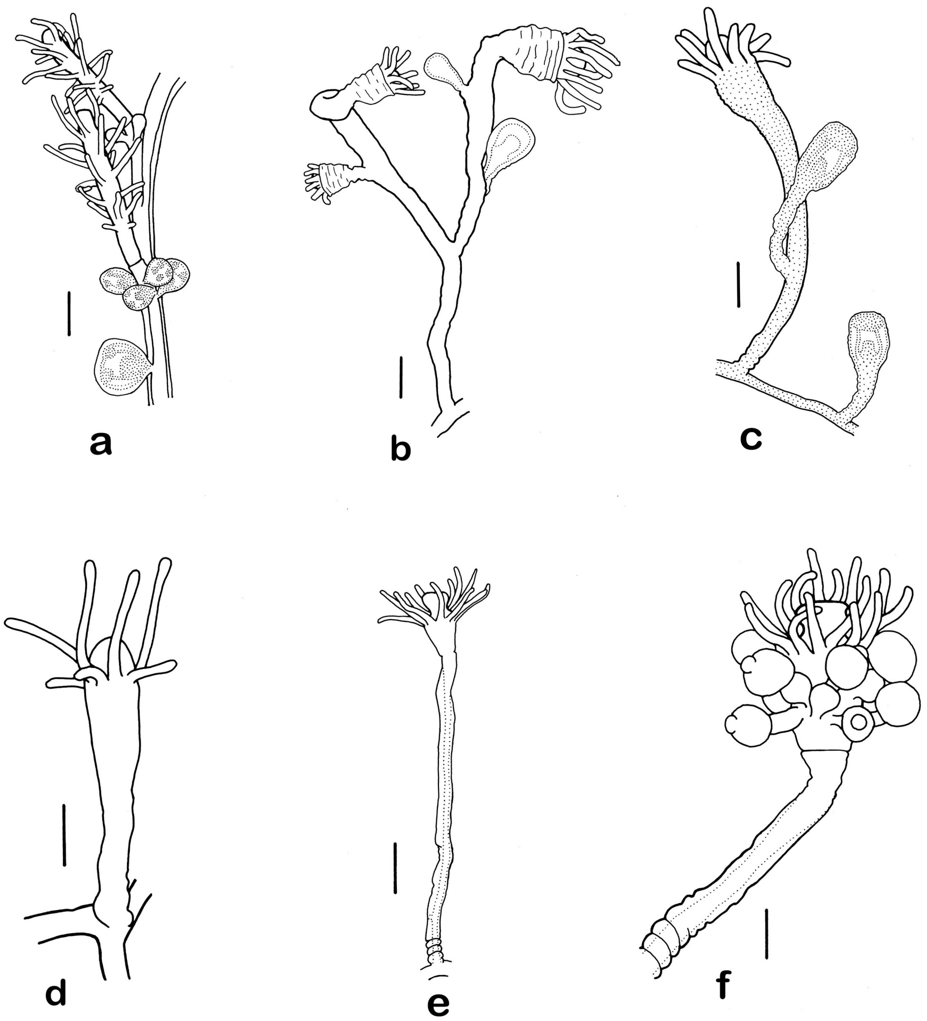

Figure 4. Anthoathecata, families Oceaniidae, Bougainvilliidae, Pandeidae, and Eudendriidae. a, *Turritopsis* sp., hydrocaulus with two hydranths and developing medusa buds, 261020, scale equals 0.30 mm. b, *Bougainvillia* cf. *muscus*, hydrocaulus with hydranths and a medusa bud, 303803, scale equals 0.15 mm. c, *Amphinema cf. rugosum*, part of colony with a hydranth and two medusa buds, 303816, scale equals 0.15 mm. d, *Amphinema* cf. *rugosum*, young hydranth, 261154, scale equals 0.10 mm. e, *Eudendrium breve*, pedicel and hydranth, 261196, scale equals 0.25 mm. f, *Eudendrium breve*, hydranth with male gonophores, 261196, scale equals 0.10 mm.

Family Bougainvilliidae Lütken, 1850

Genus *Bougainvillia* Lesson, 1830

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

Figure 4b

Eudendrium ramosum.–Van Beneden 1844: 56, pl. 4, figs. 1–13 [not *Eudendrium ramosum* (Linnaeus, 1758)].

Perigonymus muscus Allman 1863: 12 [incorrect subsequent spelling of *Perigonimus* M. Sars, 1846].

Bougainvillia muscus.–Calder et al. 2019: 27, fig. 2d.

Type locality.—UK: Devon, Torquay (Allman 1863).

Material.—Salinas, Capitania, 1 colony, 2 mm high, without gonophores, 253991.–Capitania, several colony fragments, to 1 cm high, without gonophores, 260971.–Galapagos, San Cristóbal, passenger dock, 1 colony, 2 mm high, on stem of *Ectopleura crocea*, without gonophores, 254064.

–Salinas, Salinas Yacht Club, 1 colony, 2.5 mm high, on *Pennaria disticha*, without gonophores, 254584.–Salinas Yacht Club, 5 colonies or colony fragments, to 1.7 cm high, with gonophores, 261021.–La Libertad, CEPE, 1 colony, 1.4 cm high, without gonophores, 303783.–San Cristóbal, Tiburon Martillo, 3 colonies or colony fragments, to 4 mm high, without gonophores, 261197.–Salinas Yacht Club, 2 colonies, to 5 mm high, without gonophores, 254571.–La Libertad, CEPE, several colonies, to 6 cm high, without gonophores, 260957.–Salinas Yacht Club, 2 colonies, to 1 cm high, without gonophores, 261055.–San Cristóbal, passenger dock, 2 colonies, to 1 cm high, without gonophores, 261130.–Salinas Yacht Club, 1 colony, 2 mm high, without gonophores, 254019.–Salinas Yacht Club, 1 colony, 7 mm high, without gonophores, 254568.–Salinas Yacht Club, 1 colony, 1 mm high, on *Nemalecium lighti*, without gonophores, 261018.–Salinas, Salinas Naval Base, 5 colonies or colony fragments, to 1.1 cm high, without gonophores, 303310.–San Cristóbal, Tiburon Martillo, 1 colony, 2 mm high, with gonophores, 254725.–San Cristóbal, passenger dock, 2 colonies or colony fragments, to 3 mm high, with medusa buds, 303803.–San Cristóbal, passenger dock, 1 colony, 2 mm high, without gonophores, 261159. –Capitania, 2 colonies or colony fragments, to 2 cm high, without gonophores, 260993.–San Cristóbal, Tiburon Martillo, 2 colonies or colony fragments, to 2 mm high, without gonophores, 254130.–San Cristóbal, passenger dock, 5 colonies or colony fragments, to 4 mm high, without gonophores, 261131.–San Cristóbal, passenger dock, 4 colonies or colony fragments, to 3 mm high, without gonophores, 261160.–Capitania, 2 colonies or colony fragments, to 8 mm high, without gonophores, 254998.–Capitania, 3 colonies or colony fragments, to 8 mm high, with medusa buds, 254009.–Capitania, 1 colony, 2 mm high, on a bryozoan, without gonophores, 260992.–San Cristóbal, Tiburon Martillo, 2 colonies or colony fragments, to 5 mm high, without gonophores, 254742.–Capitania, 3 colonies or colony fragments, to 6 mm high, without gonophores, 254002.–Capitania, 2 colonies or colony fragments, to 8 mm high, without gonophores, 254507.–La Libertad, CEPE, 1 colony, 1 cm high, without gonophores, 253970.–San Cristóbal, passenger dock, 3 colonies or colony fragments, to 4 mm high, without gonophores, 261134.–San Cristóbal, passenger dock, 1 colony, 4 mm high, without gonophores, 254071.–San Cristóbal, Tiburon Martillo, 3 colonies or colony fragments, to 3 mm high, without gonophores, 254093.–San Cristóbal, passenger dock, 3 colonies, to 4 mm high, on *Ectopleura crocea*, without gonophores, 254676.–San Cristóbal, Tiburon Martillo, 1 colony, 2 mm high, without gonophores, 261196.–San Cristóbal, passenger dock, 4 colonies or colony fragments, to 2 mm high, without gonophores, 254675. –Salinas Yacht Club, 2 colonies, to 1.1 cm high, on bryozoans, without gonophores, 254564.

Remarks.—These hydroids have been assigned to *Bougainvillia* Lesson, 1830 and, with some uncertainty, to *B. muscus* (Allman, 1863). Identification of the species is facilitated by knowledge of its medusa stage, and only polyps were available in present collections. *Bougainvillia muscus*, known to be widespread in distribution and frequent in harbours (Schuchert 2007), has been reported earlier from the region (Calder et al. 2019). Because of our hesitancy to assign the material in hand definitively to *B. muscus*, we treat it here as cryptogenic, although categorized earlier by us as introduced in the Galapagos in Calder et al. (2019).

Fraser (1938a) described *Bougainvillia crassa* from several locations in the Tropical Eastern Pacific, including the vicinity of Bahía Santa Elena, Ecuador. That location (02°12′23″S; 81°00′05″W) was later designated as the type locality of the species (Calder et al. 2009). Its hydroid appears to be more robust, coarser and intensely polysiphonic, more branched, and more flabellate in appearance than material examined here.

Reported Distribution.—*Tropical Eastern Pacific:* Isla Baltra, Galapagos Islands, Ecuador (Calder et al. 2019).

Worldwide: taken to be essentially circumglobal in tropical and temperate waters (Schuchert 2007).

Family Pandeidae Haeckel, 1879

Genus *Amphinema* Haeckel, 1879

***Amphinema* cf. *rugosum* (Mayer, 1900a)**

Figure 4c, d

Stomotoca rugosa Mayer 1900a: 4, pl. 5, fig. 2 [medusa stage].

Type localities.—USA: Rhode Island, Newport; South Carolina, Charleston; Florida, Tortugas (Mayer 1900a).

Material.—Galapagos, San Cristóbal, passenger dock, 1 colony, 1.5 mm high, without gonophores, 261154.–San Cristóbal, passenger dock, 3 colonies or colony fragments, to 2.5 mm high, without gonophores, 303803.–San Cristóbal, *boyas*, 2 colonies or colony fragments, to 3 mm high, with medusa buds, 303816 (a sequence of which has been deposited, as *Amphinema* sp., as GenBank Accession Number MT949545.–San Cristóbal, *boyas*, 4 colonies or colony fragments, to 2 mm high, with medusa buds, 254166.–San Cristóbal, *boyas*, 3 colonies or colony fragments, to 2 mm high, without gonophores, 254798.–San Cristóbal, passenger dock, 2 colonies, to 2 mm high, on *Tridentata turbinata*, without gonophores, 255078.–San Cristóbal, *boyas*, 3 colonies or colony fragments, to 4 mm high, with a few gonophores, 261242.–San Cristóbal, *boyas*, 2 colonies, to 2 mm high, without gonophores, 261233.

Remarks. In having medusa buds on both hydranth pedicels and stolons, these hydroids have been provisionally assigned to *Amphinema rugosum* (Mayer, 1900a). Largely on the basis of its medusa stage, the species has been considered circumglobal (Schuchert 2007), although it has not been reported before from the Tropical Eastern Pacific. Given the previous absence

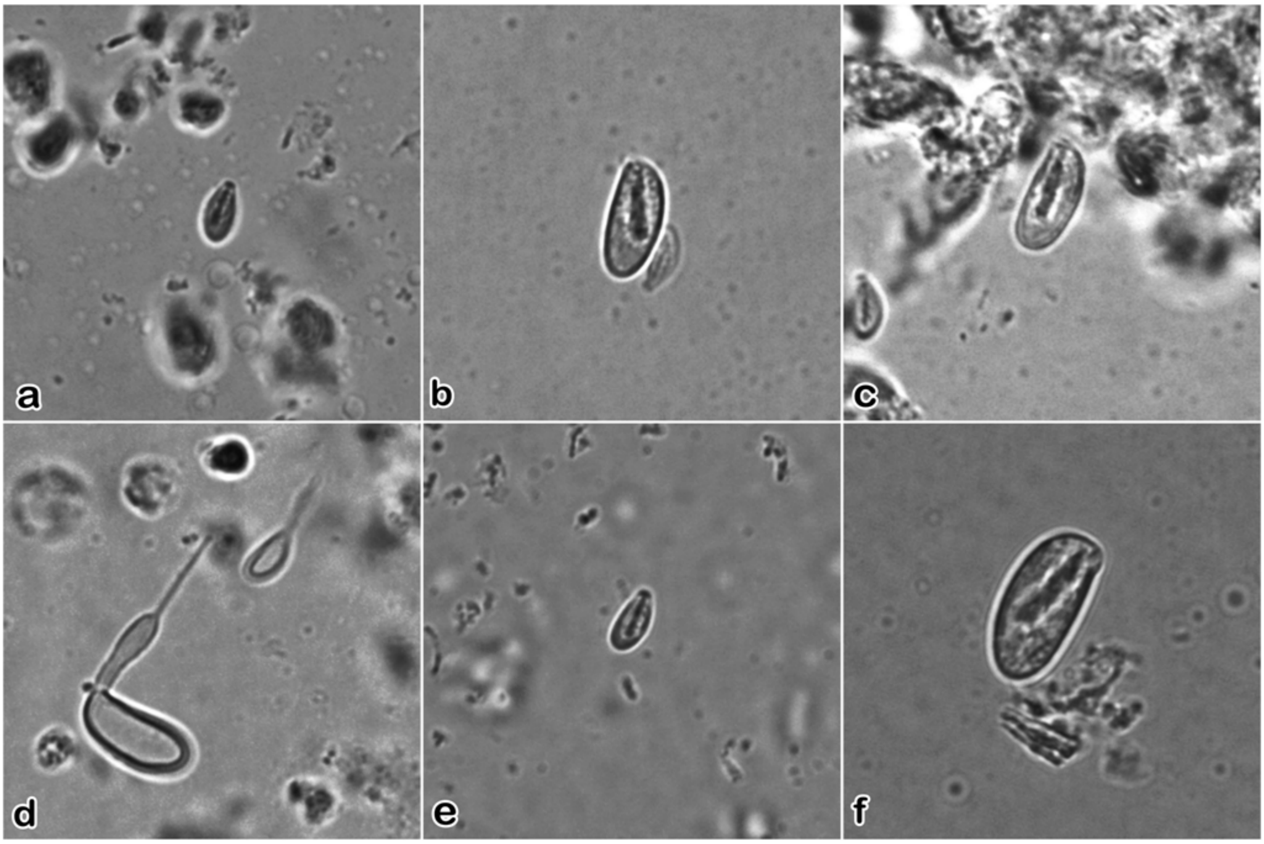

Figure 5. *Eudendrium breve*: nematocysts. a, small microbasic eurytele, undischarged, San Cristóbal, 261196. b, large microbasic eurytele, undischarged, San Cristóbal, 261196. c, large microbasic eurytele, undischarged, San Cristóbal, 261196. d, large and small microbasic euryteles, discharged, San Cristóbal, 261196. e, small microbasic eurytele, undischarged, Marchena, ROMIZ B3427. f, large microbasic eurytele, undischarged, Marchena, ROMIZ B3427. Photomicrographs by D.R. Calder.

of Eastern Pacific records of this species and its biofouling habit in a port environment in the Galapagos, we tentatively regard it as introduced to the islands.

Reported Distribution.—*Tropical Eastern Pacific:* first record.

Worldwide: considered circumglobal (Schuchert 2007).

Family Eudendriidae L. Agassiz, 1862

Genus *Eudendrium* Ehrenberg, 1834

***Eudendrium breve* Fraser, 1938a**

Figures 4e, f, 5a–f

Eudendrium breve Fraser 1938a: 18, pl. 3, fig. 13.–Fraser 1948: 196.–Calder et al. 2003: 1194; 2009: 933.

Eudendrium (?) *breve*.–Calder et al. 2019: 29, fig. 2g.

Type locality.—Ecuador: Galapagos Islands, Isla Floreana (Charles Island), Black Beach, 01°16′40″S, 90°29′46″W, 5 m (Fraser 1938a; Calder et al. 2009).

Material.—Galapagos, San Cristóbal, Tiburon Martillo, 2 colonies, to 5 mm high, with male gonophores, 261196.

Remarks.—Fraser (1938a) described *Eudendrium breve* from colonies lacking gonophores. Subsequent reports of the species (Fraser 1948; Cooke

1975; Calder et al. 2003, 2009, 2019) have likewise been based on sterile specimens. Male gonophores, present in material examined during this study, are illustrated for the first time herein (Figure 3f). They were borne on hydranths that were but little reduced, clearly distinguishing *E. breve* from the similar and widespread *E. capillare* Alder, 1856. Female gonophores of the species have yet to be described.

Additional material of *E. breve* from the Galapagos, with abundant male gonophores, exists in ROM collections:

Isla Marchena, NW side, subtidal rocky ledges, 8 m, 21.5 °C, on barnacle shell, 18 June 2001, coll. D. Calder, ROMIZ B3427.

Hydroids of *E. breve* examined here from San Cristóbal had a cnidome comprising two size classes of microbasic euryteles (Figure 5a–d). Small ones (5.1–5.6 × 2.2–2.7 um), well represented on the tentacles, were most abundant. Larger ones (9.8–11.0 × 4.2–4.8 um) were most prevalent around the basal region of the hydranth. Specimens from Isla Marchena (ROMIZ B3427), noted above, had an equivalent cnidome (Figure 5e, f), although the large euryteles were much bigger (small euryteles 5.3–5.8 × 2.2–2.6 um; large euryteles 13.0–14.6 × 5.8–6.8 um).

Reported Distribution.—*Tropical Eastern Pacific:* Galapagos Islands, Ecuador (Fraser 1938a, 1948; Calder et al. 2003, 2019).

Worldwide: reported from San Eugenio Point (Punta San Eugenio), west coast of Baja California, Mexico (Fraser 1948) and the Galapagos Islands (Fraser 1938a, 1948; Calder et al. 2003, 2019), with a questionable record from Enewetak Atoll, Marshall Islands (Cooke 1975).

Order Leptothecata Cornelius, 1992
Family Cirrholoveniidae Bouillon, 1984
Genus *Cirrholovenia* Kramp, 1959

***Cirrholovenia tetranema* Kramp, 1959**

Figure 6a

Cirrholovenia tetranema Kramp 1959: 253, figs. 17a, b [medusa].–Calder et al. 2019: 31, fig. 3a.
Egmundella amirantensis Millard and Bouillon 1973: 40, figs. 5A–D [hydroid].
Lafoeina amirantensis.–Calder et al. 2003: 1180, fig. 5.

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

Material.—Salinas, Capitania, 3 colonies or colony fragments, on stems of *Bougainvillia* and *Clytia*, without gonothecae, 260971.–La Libertad, CEPE, 2 colonies, without gonothecae, 253965.–Galapagos, San Cristóbal, Tiburon Martillo, 1 colony, on stem of tubulariid, without gonothecae, 255112.–San Cristóbal, Tiburon Martillo, 1 colony, without gonothecae, 261197.–La Libertad, CEPE, 2 colonies or colony fragments, without gonothecae, 253959.–San Cristóbal, passenger dock, 1 colony, on *Tridentata turbinata*, without gonothecae, 261156.–San Cristóbal, Tiburon Martillo, 1 colony, without gonothecae, 261195.–San Cristóbal, Tiburon Martillo,

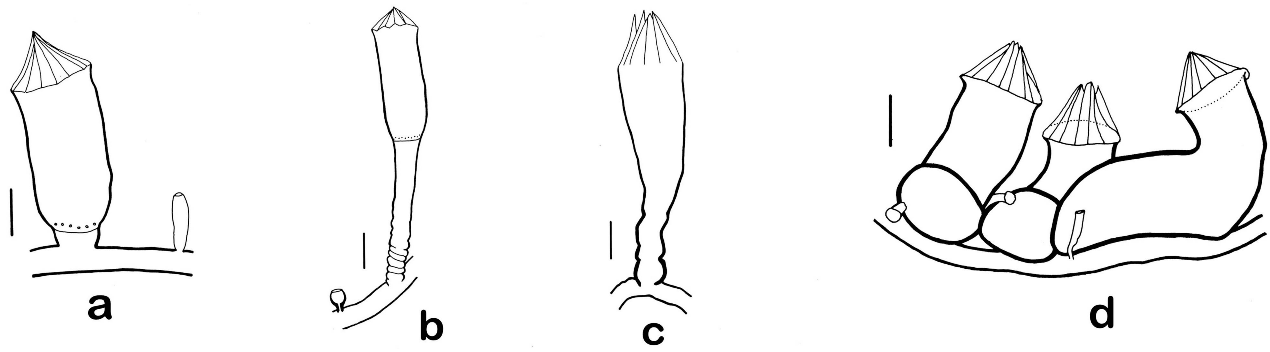

Figure 6. Leptothecata, families Cirrholoveniidae and incertae sedis. a, *Cirrholovenia tetranema*, part of colony with hydrotheca and nematotheca, 254724, scale equals 0.05 mm. b, *Egmundella humilis*, part of colony with hydrotheca and nematotheca, 261195, scale equals 0.10 mm. c, *Opercularella* sp., part of colony with hydrotheca, 260950, scale equals 0.05 mm. d, Campanulinida, undetermined, part of colony with three hydrothecae and nematothecae, 254810, scale equals 0.10 mm.

1 colony, without gonothecae, 254131.–San Cristóbal, *boyas*, 3 colonies, on bryozoans, without gonothecae, 254159.–Capitania, 1 colony, without gonothecae, 254009.–San Cristóbal, *boyas*, 3 colonies or colony fragments, without gonothecae, 254166.–San Cristóbal, Tiburon Martillo, 1 colony, without gonothecae, 254742.–San Cristóbal, Tiburon Martillo, 1 colony, without gonothecae, 255113.–San Cristóbal, Tiburon Martillo, 3 colonies, without gonothecae, 254724.–San Cristóbal, passenger dock, 1 colony, without gonothecae, 254071.

Remarks.—Neither the hydroid nor the medusa of this species was recognized and characterized as a species until the latter half of the 20th century. Kramp (1959) was first to describe the medusa, as *Cirrholovenia tetranema*, from specimens collected during the Galathea Expedition at several locations in the Indo-west Pacific region [Strait of Malacca; Gulf of Siam (Gulf of Thailand); Philippines; Bali; type locality: Solomon Islands]. Later, Millard and Bouillon (1973) described the hydroid, as *Egmundella amirantensis*, from the Seychelles. Migotto and Cabral (2005) linked hydroid and medusa stages of the species through life cycle studies, with the binomen *Cirrholovenia tetranema* having nomenclatural priority. The species is now known to be widely distributed in warm waters of the Atlantic, Pacific, and Indian oceans. It was first reported in the Tropical Eastern Pacific from four islands in the Galapagos (Daphne Chica, Española, Santa Cruz, Isabela) by Calder et al. (2003, as *Lafoeina amirantensis*). It was found there again, in a fouling community at Isla Santa Cruz, by Calder et al. (2019).

Reported Distribution.—*Tropical Eastern Pacific:* Galapagos Islands, Ecuador (Calder et al. 2003, as *Lafoeina amirantensis*; Calder et al. 2019).

Worldwide: essentially circumglobal in tropical and temperate waters (Migotto and Cabral 2005).

Family Incertae Sedis
Genus *Egmundella* Stechow, 1921b

***Egmundella humilis* Fraser, 1936**
Figure 6b

Egmundella humilis Fraser 1936: 50, pl. 1, figs. 2a–d.

Type locality.—Japan: Sagami Bay (Fraser 1936; Calder and Choong 2018).

Material.—Galapagos, San Cristóbal, Tiburon Martillo, 1 colony, 1 mm high, without gonothecae, 261195.

Remarks.—Fraser (1936) established the binomen *Egmundella humilis* for a species of hydroid collected by Emperor Hirohito in Sagami Bay, Japan. In common with that species, as described and illustrated by Fraser (1936) and Hirohito (1995), the colony from San Cristóbal examined here was stolonal, pedicels were of varied length and wrinkled to annulated at the base, hydrothecae were essentially cylindrical and operculate, opercula were cone-shaped with multiple flaps and faintly demarcated from the hydrotheca, and nematothecae were bulbous, solitary, and restricted to the hydrorhiza. As with specimens described by Galea (2013) from Martinique in the Caribbean Sea, a ring of desmocytes and a thin diaphragm were present at the base of the hydrotheca. Ours is the first report of *E. humilis* from the Galapagos and the Tropical Eastern Pacific.

Galea (2013) noted that the trophosome of *Egmundella modesta* Millard & Bouillon, 1975 is morphologically indistinguishable from that of *E. humilis*, although he hesitated in concluding that they are conspecific. That species, gonophores of which are as yet undescribed, has been reported from the Indian Ocean (Millard and Bouillon 1975) and the eastern North Atlantic (Vervoort 2006).

Reported Distribution.—*Tropical Eastern Pacific:* new record.

Worldwide: Japan (Fraser 1936; Hirohito 1995), off Martinique (Galea 2013), and questionably from the Seychelles (Millard and Bouillon 1975, as *Egmundella modesta*) and Mauritania (Vervoort 2006, as *E. modesta*).

Genus *Opercularella* Hincks, 1869

?*Opercularella* sp.
Figure 6c

Material.—La Libertad, CEPE, 1 colony, on stolons of *Clytia* sp. 1, without gonothecae, 260950.

Remarks.—This tiny hydroid colony was assigned to *Opercularella* Hincks, 1869 in having: (1) a stolonal colony form; (2) pedicellate hydrothecae; (3) a cone-shaped operculum of multiple segments (> 4), and without a crease line at its base; (4) no detectable diaphragm; (5) no nematothecae. Gonophores were absent. Hydroids of the genus are thought to differ little from those of *Phialella* Browne, 1902, and the generic identity of the species is therefore uncertain. However, the type species of *Phialella*, *P. falklandica* Browne, 1902, was based on a medusa with an as yet unknown hydroid (Galea et al. 2014). *Opercularella* was established by Hincks (1869) for a known hydroid, *Campanularia lacerata* Johnston, 1847, with characters similar in several respects to those of the species examined here.

No hydroids corresponding to this species have been reported previously from the Tropical Eastern Pacific region. A hydroid described by Fraser (1938c) as *Lovenella rugosa* from Tenacatita Bay, Mexico, is superficially similar, but its operculum is separated from the hydrothecal wall by a crease line. The two are therefore considered distinct. More alike morphologically are hydroids identified as either *Opercularella belgicae* (Hartlaub, 1904) or *Phialella belgicae* from the Antarctic and the coast of Chile (Leloup 1974; Galea 2007; Peña Cantero et al. 2013). That species forms erect colonies, and is an unlikely inhabitant of the warmer waters of coastal Ecuador.

Campanulinida, undetermined species

Figure 6d

Material.—Galapagos, San Cristóbal, *boyas*, 1 colony, 1 mm high, with gonothecae, 254810.

Remarks.—The condition of our specimen was unsatisfactory and its morphology was difficult to observe. Initially thought conspecific with *Nicoliana gravierae* (Millard, 1975), that identification was abandoned after examining photographs of the species (provided courtesy of Horia Galea). We regard the Ecuador species as unidentifiable at present.

Reported Distribution.—*Tropical Eastern Pacific:* first record. Given the lack of previous Eastern Pacific records of any hydroid resembling this species, as well as its biofouling habit in the Galapagos, we regard it as introduced to the islands.

Family Clytiidae Cockerell, 1911

Genus *Clytia* Lamouroux, 1812

***Clytia delicatula* (Thornely, 1900)**

Figure 7a–d

Obelia delicatula Thornely 1900: 453, pl. 44, fig. 7.

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

Material.—Salinas, Capitania, 3 colonies, to 6 mm high, without gonothecae, 254506.–Salinas, Salinas Naval Base, 1 colony, 2 mm high, without gonothecae, 254630.–Capitania, 1 colony, 5 mm high, without gonothecae, 260971.–Salinas Naval Base, 2 colony fragments, to 5 mm high, on tubulariid stems, without gonothecae, 261077.–La Libertad, CEPE, 3 colonies or colony fragments, to 4 mm high, without gonothecae, 254453.

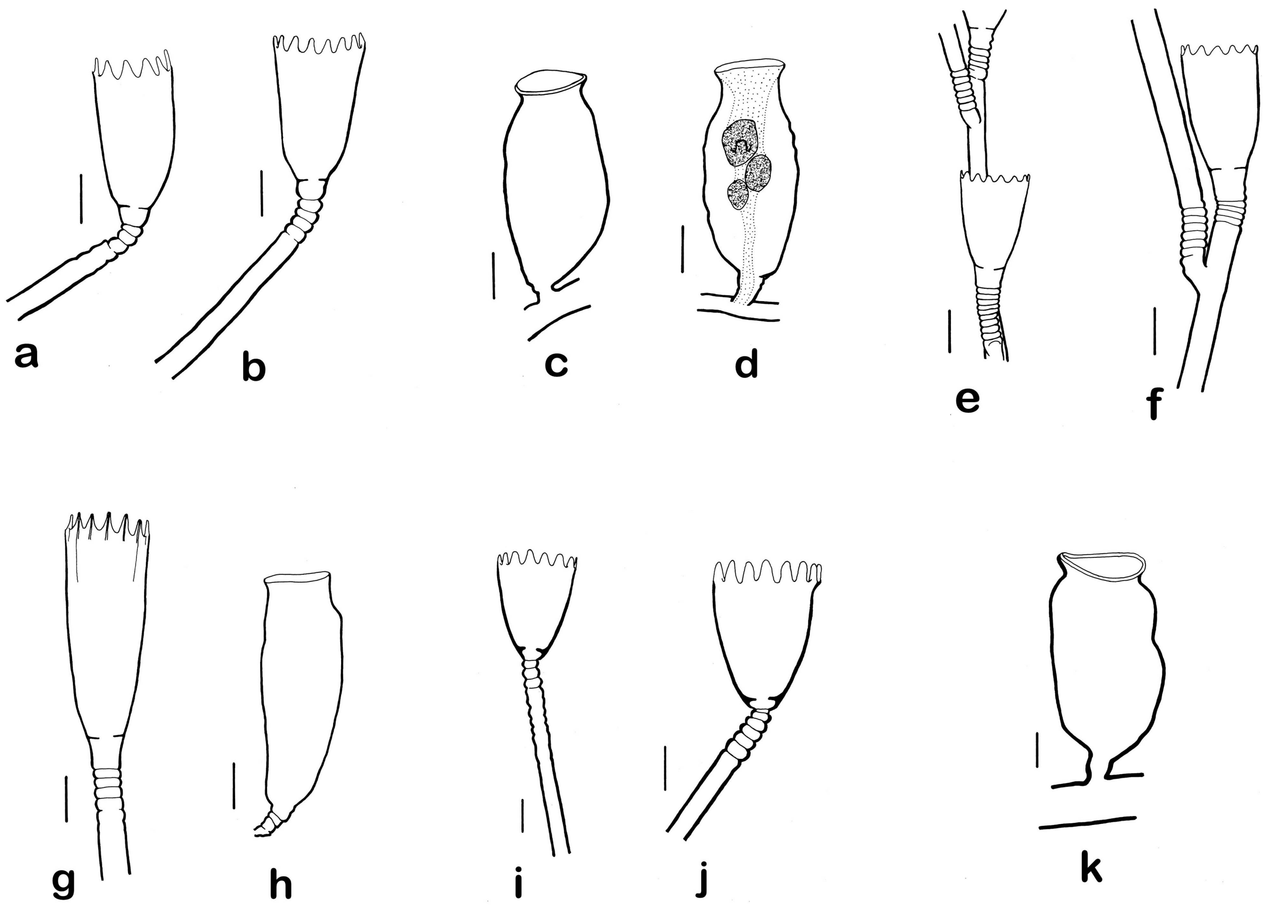

Figure 7. Leptothecata, family Clytiidae. a, *Clytia delicatula*, hydrotheca and distal end of pedicel, 254506, scale equals 0.20 mm. b, *Clytia delicatula*, hydrotheca and distal end of pedicel, 260942, scale equals 0.20 mm. c, *Clytia delicatula*, gonotheca, 260942, scale equals 0.20 mm. d, *Clytia delicatula*, gonotheca with medusa buds, 260950, scale equals 0.20 mm. e, *Clytia irregularis*, part of hydrocaulus with a hydrotheca, 261022, scale equals 0.25 mm. f, *Clytia irregularis*, part of hydrocaulus with a hydrotheca, 261022, scale equals 0.20 mm. g, *Clytia linearis*, hydrotheca and distal end of pedicel, 253965, scale equals 0.20 mm. h, *Clytia linearis*, gonotheca, 253965, scale equals 0.20 mm. i, *Clytia noliformis*, hydrotheca and distal end of pedicel, 255036, scale equals 0.20 mm. j, *Clytia noliformis*, hydrotheca and distal end of pedicel, 261083, scale equals 0.20 mm. k, *Clytia noliformis*, gonotheca, 261083, scale equals 0.10 mm.

–La Libertad, CEPE, several colony fragments, to 5 mm high, without gonothecae, 260957.–Salinas Naval Base, 2 colonies or colony fragments, 3 mm high, without gonothecae, 261076.–Galapagos, San Cristóbal, Tiburon Martillo, 1 colony, 3.5 mm high, without gonothecae, 261196.–La Libertad, CEPE, 8 colonies or colony fragments, to 1 cm high, with gonothecae, 260950.–Salinas, Salinas Yacht Club, 2 colonies, to 7 mm high, without gonothecae, 261018.–Salinas Yacht Club, 6 colonies or colony fragments, to 5 mm high, without gonothecae, 261054.–Salinas Naval Base, 1 colony, 5 mm high, without gonothecae, 303310.–La Libertad, CEPE, 1 colony, 2 mm high, on *Obelia microtheca*, without gonothecae, 253920.–Salinas Naval Base, 2 colonies or colony fragments, to 6 mm high, without gonothecae, 261107.–La Libertad, CEPE, ca. 8 colonies or colony fragments, to 6 mm high, with gonothecae, 260942.–Capitania, 1 colony, 5 mm high, without gonothecae, 260993.–Salinas Yacht Club, 1 colony, 3 mm high, without gonothecae, 255017.–San Cristóbal, *boyas*, 2 colonies, to 4 mm high, on bryozoans, without gonothecae, 254159.–Capitania, 1 colony, 3 mm high, without gonothecae, 254998.–Capitania, 1 colony, 3 mm high, without gonothecae, 260992.–San Cristóbal, *boyas*, 1 colony, 2 mm high, without gonothecae, 254166.–Capitania, 1 colony, 2 mm high, without gonothecae, 254002.–Salinas Naval Base, 5 colonies or colony fragments, to 4 mm high, without gonothecae, 254632.

Remarks.—This species was distinctive during preliminary sorting in having tumbler-shaped hydrothecae with an abrupt basal taper and a rather large chamber below the diaphragm (Figure 7a, b). Its identity was nevertheless obscure until fertile colonies were discovered. While gonothecae generally conform with those observed in many other species of *Clytia* Lamouroux, 1812, they are nevertheless distinctive in being shaped like an ovoid neck amphora (Figure 7c, d). Both trophosome and gonosome thus correspond closely in morphology with the original account of *Clytia delicatula* by Thornely (1900). Colonies of the species are mostly stolonal, and gonothecae arise from the hydrorhiza.

Clytia delicatula was not included in Fraser's (1938a, b, c, 1948) accounts of hydroids from Allan Hancock Expeditions and is new to the Tropical Eastern Pacific. Like *Clytia linearis* (Thornely, 1900), another hydroid originally described from Blanche Bay, Papua New Guinea, it was well represented in the samples, and especially in those from the mainland of Ecuador.

Reported Distribution.—*Tropical Eastern Pacific:* new record.

Worldwide: warm western Pacific (Hirohito 1995).

***Clytia irregularis* Fraser, 1938a**

Figure 7e, f

Clytia irregularis Fraser 1938a: 31, pl. 8, fig. 32.

Type locality.—Mexico: Oaxaca, Bahía Tangolunda (Tangola Tangola Bay), 15°45′37″N, 96°05′24″W, shallow water (Fraser 1938a; Calder et al. 2009).

Material.—Salinas, Salinas Yacht Club, 3 colonies or colony fragments, to 5 mm high, without gonothecae, 261022.–Salinas Yacht Club, 3 colonies, to 3 mm high, without gonothecae, 254017.–Salinas Yacht Club, 3 colonies or colony fragments, to 7 mm high, without gonothecae, 261053.–Salinas Yacht Club, 6 colonies or colony fragments, to 6 mm high, without gonothecae, 254562.

Remarks.—These hydroids corresponded with Fraser's (1938a) account of *Clytia irregularis*. The margin of the hydrotheca bears about 12 pointed cusps, and the chamber below the diaphragm is deep. No gonothecae were observed.

The distribution of the species is extended southwards from Mexico to Ecuador.

Reported Distribution.—*Tropical Eastern Pacific:* Gulf of California to Bahía Tangolunda (Tangola Tangola Bay), Mexico (Fraser 1938a, 1948).

Worldwide: known only from the Tropical Eastern Pacific.

Clytia linearis **(Thornely, 1900)**

Figure 7g, h

Obelia linearis Thornely 1900: 453, pl. 44, fig. 6.
Clytia acutidentata Fraser 1938a: 28, pl. 7, figs. 29a, b.
Clytia carinadentata Fraser 1938a: 29, pl. 7, fig. 30.
Clytia linearis.–Calder et al. 2003: 1202; 2019: 34, fig. 3d.

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

Material.—Salinas, Capitania, one colony, 6 mm high, on sponge, without gonothecae, 253991.–Capitania, 1 colony, 2 mm high, without gonothecae, 254506.–La Libertad, CEPE, 7 colonies or colony fragments, to 7 mm high, with gonothecae, 253965.–Capitania, 4 colonies or colony fragments, to 4 mm high, without gonothecae, 253988.–Capitania, 2 colonies, to 5 mm high, without gonothecae, 260970.–La Libertad, CEPE, 2 colonies or colony fragments, to 4 mm high, with gonothecae, 253959.–Salinas, Salinas Naval Base, 1 colony, 6 mm high, without gonothecae, 261076.–La Libertad, CEPE, 7 colonies or colony fragments, to 1 cm high, with gonothecae, 253937.–Galapagos, San Cristóbal, passenger dock, 3 colonies or colony fragments, to 1 cm high, without gonothecae, 261133.–Capitania, 3 colonies or colony fragments, to 7 mm high, with gonothecae, 260972.

Remarks.—*Clytia linearis* (Thornely, 1900) is both widespread and frequently reported. Recent accounts of the species in the Tropical Eastern Pacific include those by Humara-Gil and Cruz-Gómez (2018), Calder et al. (2019), and Mendoza-Becerril et al. (2020a).

Reported Distribution.—*Tropical Eastern Pacific:* Rocas Alijos, Mexico (Calder 1996) and La Paz Bay, Gulf of California, Mexico (Mendoza-Becerril et al. 2020a) to the Galapagos Islands, Ecuador (Fraser 1938a, as *Clytia acutidentata* and *C. carinadentata*; Calder et al. 2003, 2019).

Worldwide: circumglobal in tropical and warm-temperate waters (Medel and Vervoort 2000; Lindner and Migotto 2002).

Clytia noliformis **(McCrady, 1859)**

Figure 7i–k

Campanularia noliformis McCrady 1859: 194, pl. 11, fig. 4.
Clytia noliformis.–Fraser 1948: 209.

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

Material.—Salinas, Salinas Naval Base, 1 colony and fragments, 3 mm high, without gonothecae, 255036.–Salinas Naval Base, 1 colony, 4 mm high, with gonothecae, 261083.

Remarks.—Hydroids of *Clytia noliformis* (McCrady, 1859) are distinctive in morphology. Colonies of the species are strictly stolonal, hydrothecae are shallow and cup-shaped, marginal cusps tend to be shallow and blunt, hydrothecal walls usually have somewhat thickened perisarc, the hydrothecal diaphragm is thick, the chamber below the diaphragm is small and oval in outline, and a subhydrothecal spherule is present. Gonothecae are sac-shaped with a wide aperture, and may be laterally flattened.

The center of distribution of *C. noliformis* appears to be the warm western Atlantic region (Calder 1991), where it is a dominant hydroid on *Sargassum natans* (Ryland 1974; Calder 1995; Mendoza-Becerril et al. 2020b). The life cycle of the species was reviewed by Lindner and Migotto (2002).

Reported Distribution.—*Tropical Eastern Pacific:* Solango Island (Isla Salango), Ecuador (Fraser 1948).

Worldwide: western and eastern Atlantic, Indian Ocean, eastern Pacific, tropical and warm-temperate waters (Calder 1991; Lindner and Migotto 2002).

Clytia seriata Fraser, 1938a

Figure 8a, b

? *Clytia seriata* Fraser 1938a: 33, pl. 8, figs. 35a, b.

Type locality.—Mexico: Oaxaca, between Bahía Santa Cruz and Bahía Tangolunda (Santa Cruz Bay and Tangola Tangola Bay), 15°45′N; 96°06′12″W, 27–37 m (Fraser 1938a; Calder et al. 2009).

Material.—Salinas, Salinas Yacht Club, 4 colony fragments, to 5 mm high, with gonothecae, 254023.–La Libertad, CEPE, 7 colonies or colony fragments, to 1 cm high, with gonothecae, 253917.–Salinas Yacht Club, 1 colony fragment, 4 mm high, with a gonotheca, 255014.

Remarks.—Hydrothecal margins in *Clytia seriata* Fraser, 1938a are unusual for species of the genus in being entire rather than cusped, a character shared with congeners or supposed congeners including *C. hummelincki* (Leloup, 1935), *C. pearsonensis* Watson, 1973, and *C. edentula* Gibbons & Ryland, 1989. Fraser (1938a, 1947) was uncertain of its generic assignment, not having seen gonothecal contents, but material examined here contained medusa buds of the type occurring in *Clytia* Lamouroux, 1812. As noted in both the original description of Fraser and in an examination of specimens on a paralectotype slide (BCPM-976-394-1), successive pedicels (internodes) of this species are arranged very nearly in a straight line. Hydrothecae are deep funnel-shaped with almost straight walls, and the chamber below the diaphragm is large.

Clytia seriata has been reliably reported before only from the type locality (Fraser 1938a) and from the lagoon at Bahía Tenacatita (Tenacatita

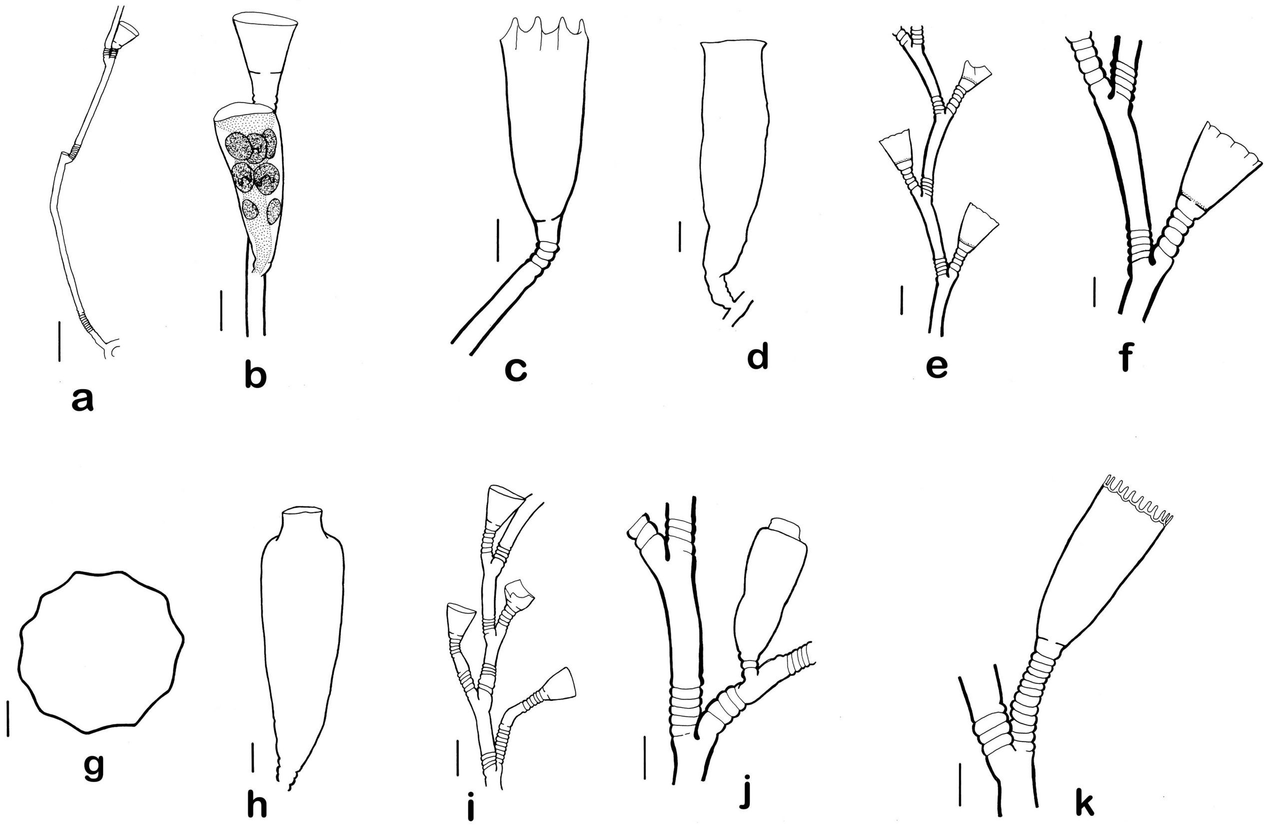

Figure 8. Leptothecata, families Clytiidae and Obeliidae. a, *Clytia seriata*, part of colony with hydrotheca, 253917, scale equals 0.75 mm. b, *Clytia seriata*, part of colony with hydrotheca and gonotheca containing medusa buds, 255014, scale equals 0.25 mm. c, *Clytia* sp., hydrotheca and distal end of pedicel, 303803, scale equals 0.10 mm. d, *Clytia* sp., gonotheca, 303803, scale equals 0.10 mm. e, *Obelia alternata*, part of hydrocaulus with hydrothecae, 261196, scale equals 0.20 mm. f, *Obelia alternata*, part of hydrocaulus with a hydrotheca, 261196, scale equals 0.10 mm. g, *Obelia alternata*, cross section of hydrothecal rim, 261196, scale equals 0.04 mm. h, *Obelia alternata*, gonotheca, 261196, scale equals 0.10 mm. i, *Obelia microtheca*, part of hydrocaulus with hydrothecae, 254002, scale equals 0.25 mm. j, *Obelia microtheca*, part of hydrocaulus with gonotheca, 254454, scale equals 0.15 mm. k, *Obelia oxydentata*, part of hydrocaulus with pedicel and hydrotheca, 261054, scale equals 0.10 mm.

Bay), Mexico (Fraser 1938c). Reports of it from the coast of Central America (Colombia) by Fraser (1948) and Schmitt (1948) appear to have been based on an erroneous collection number (see Calder et al. 2009).

Reported Distribution.—*Tropical Eastern Pacific:* Bahía Tenacatita, Mexico (Fraser 1938c) to the coast of Ecuador (this study).

Worldwide: known only from the Tropical Eastern Pacific.

***Clytia* sp.**

Figure 8c, d

Material.—Galapagos, San Cristóbal, passenger dock, 1 colony, 2 mm high, with one gonotheca, 303803.

Remarks.—We have been unable to identify this species, even though our material contained a gonotheca with medusa buds. Hydrothecae were quite deep, with about eight pointed cusps around the margin, and the distal end was decidedly wavy in cross-section. The specimen resembled *Clytia linearis* (Thornely, 1900), but the marginal cusps were fewer in number and lacked perisarcal keels along their inner sides. Hydrothecae and the gonotheca were also much smaller than those of *C. linearis*. We report this hydroid simply as *Clytia* sp.

Family Obeliidae Haeckel, 1879
Genus *Obelia* Péron and Lesueur, 1810

Obelia alternata **Fraser, 1938a**
Figure 8e–h

Obelia alternata Fraser 1938a: 35, pl. 8, figs. 38 a, b; 1948: 212.–Calder et al. 2009: 956.
Obelia dichotoma.–Hickman 2008: 130, three unnumbered figs. [not *Obelia dichotoma* (Linnaeus, 1758)].

Type locality.—Ecuador: Galapagos, Isla Floreana (Charles Island), Post Office Bay, 01°14′37″S; 90°28′08″W, 27 m (Fraser 1938a; Calder et al. 2009).

Material.—Galapagos, San Cristóbal, passenger dock, 4 colonies, to 6 mm high, with gonothecae, 254678.–San Cristóbal, *boyas*, 1 colony, 2.5 mm high, without gonothecae, 254183.–San Cristóbal, passenger dock, 7 colony fragments, to 5 mm high, with gonothecae, 254677.–San Cristóbal, passenger dock, 2 colonies, to 9 mm high, on bryozoans, with gonothecae, 261155.–San Cristóbal, passenger dock, 3 colonies, to 3 mm high, on *Tridentata turbinata*, without gonothecae, 254065.–San Cristóbal, *boyas*, 3 colonies or colony fragments, to 2 mm high, without gonothecae, 254798. –San Cristóbal, passenger dock, 2 colonies, to 5 mm high, without gonothecae, 261130.–San Cristóbal, passenger dock, 2 colony fragments, to 6 mm high, with gonothecae, 255066.–San Cristóbal, Tiburon Martillo, 5 colonies or colony fragments, to 7 mm high, with gonothecae, 261196.–San Cristóbal, Tiburon Martillo, 14 colonies or colony fragments, to 1.1 cm high, with gonothecae, 254725.–San Cristóbal, Tiburon Martillo, 1 colony, 4 mm high, without gonothecae, 261195.–San Cristóbal, *boyas*, 6 colonies or colony fragments, to 6 mm high, with gonothecae, 254803.–San Cristóbal, *boyas*, 6 colonies or colony fragments, to 6 mm high, with gonothecae, 303803.–San Cristóbal, *boyas*, 1 colony, 2 mm high, without gonothecae, 303816.–San Cristóbal, passenger dock, 1 colony, 3 mm high, without gonothecae, 261159.–San Cristóbal, passenger dock, 3 colonies or colony fragments, to 5 mm high, with gonothecae, 261186.–San Cristóbal, *boyas*, 1 colony fragment, 3 mm high, without gonothecae, 254801.–San Cristóbal, *boyas*, 8 colonies, to 3 mm high, on bryozoans, with gonothecae, 254159.–San Cristóbal, passenger dock, 2 colonies or colony fragments, to 4 mm high, without gonothecae, 261160.–San Cristóbal, *boyas*, 1 colony, 2 mm high, without gonothecae, 261234.–San Cristóbal, *boyas*, 7 colonies or colony fragments, to 3 mm high, without gonothecae, 254796.–San Cristóbal, passenger dock, 1 colony, 3 mm high, without gonothecae, 261133.–San Cristóbal, Tiburon Martillo, 4 colonies or colony fragments, to 9 mm high, with gonothecae, 254116.–San Cristóbal, Tiburon Martillo, 3 colonies or colony fragments, to 7 mm high, with gonothecae, 254745.–San Cristóbal, Tiburon Martillo, 3 colonies or colony fragments, to 2 mm high, without gonothecae, 254724.–San Cristóbal, passenger dock, 1 colony, 2 mm high, without gonothecae, 261134.–San Cristóbal, *boyas*, 4 colonies or colony fragments, to 3.5 mm high, with a gonotheca, 261233.

Remarks.—Species diversity within the genus *Obelia* Péron and Lesueur, 1810 is certain to have been materially underestimated by hydroid taxonomists over the last quarter of the 20th century. Hydroids assigned here to *Obelia alternata* Fraser, 1938a would have been identified during that period as *O. dichotoma* (Linnaeus 1758), influenced in part by Cornelius' (1975) recognition of only a few globally-distributed species of *Obelia*. As with that Linnaean species, hydrothecal margins in our material were slightly crenate and polygonal in cross-section, and gonothecae were deeply conical with a terminal collar (Figure 8e–h). Yet our specimens, in common both with the account of *O. alternata* by Fraser and with paralectotype specimens of the species examined here (BCPM 976-407-1), appear distinctive. Stems were decidedly geniculate rather than being predominantly straight. In being strongly flexuose, they resembled those of *O. geniculata* (Linnaeus, 1758) but lacked the asymmetric perisarcal thickening of the internodes typical of that species. Hydrothecal pedicels were short and usually annulated throughout. Overall, colonies were small (to 1.1 cm high, but usually much less) and little if at all branched rather than larger (as much as 35 cm) and typically branched as in *O. dichotoma* (Cornelius 1995). Specimens in our collections as small as 3 mm high bore gonothecae, as with the small (7 mm high) fertile lectotype colony (SBMNH 347065). We have therefore recognized *O. alternata*, known only from the Galapagos Islands (Calder et al. 2009), as a valid species.

On the same fouling plate as *Obelia alternata*, specimen 254803, was a campanularioid (254805) that appeared morphologically similar to *O. alternata*, and which was removed as a "sister" sample to 254803 for molecular analysis. This appeared to be the sole campanularioid species present on the plate. The only other hydroids on this plate were *Coryne repens* Fraser, 1938a and Campanulinida, undetermined. However, a portion of 254803 itself was not taken for molecular analysis. Campanularioid 254805, a sequence of which has been deposited as GenBank Accession Number MT949549,, matched none of the many sequences of *Obelia dichotoma* on GenBank.

All collections of the species in this study were from Isla San Cristóbal. *Obelia alternata* has been reported earlier in the Galapagos archipelago from Charles Island (Isla Floreana), South Seymour Island (Isla Baltra), and Albemarle Island (Isla Isabela) by Fraser (1938a, 1948).

Reported Distribution.—*Tropical Eastern Pacific:* Galapagos Islands, Ecuador (Fraser 1938a, 1948).

Worldwide: known only from the Galapagos Islands.

Obelia microtheca **Fraser, 1938a**

Figure 8i, j

Obelia microtheca Fraser 1938a: 37, pl. 9, figs. 40a–d.–Calder et al. 2009: 958.

Type locality.—Ecuador: Santa Elena Bay, 02°08′20″S; 81°00′15″W, 15–18 m (Fraser 1938a; Calder et al. 2009).

Material.—Salinas, Capitania, 1 colony, 5 mm high, on sponge, with gonothecae, 253991.–Capitania, 5 colonies or colony fragments, to 6 mm high, without gonothecae, 254506.–Capitania, 2 colonies, to 5 mm high, without gonothecae, 260971.–Capitania, 3 colonies or colony fragments, to 4 mm high, without gonothecae, 253988.–La Libertad, CEPE, 1 colony, 6 mm high, with a gonotheca, 254454.–Capitania, 2 colonies, to 4 mm high, without gonothecae, 260970.–Salinas, Salinas Naval Base, 1 colony, 2 mm high, without gonothecae, 261076.–La Libertad, CEPE, 3 colonies or colony fragments, to 1 cm high, without gonothecae, 260950.–Salinas, Salinas Yacht Club, 2 colonies, to 7 mm high, on *Nemalecium lighti*, without gonothecae, 261018.–La Libertad, CEPE, 2 colonies or colony fragments, to 7 mm high, without gonothecae, 253920.–Capitania, 1 colony, 6 mm high, without gonothecae, 260994.–Capitania, 1 colony, 3 mm high, without gonothecae, 260993.–Salinas Naval Base, 1 colony, 2 mm high, without gonothecae, 261100.–Capitania, 1 colony, 5 mm high, without gonothecae, 254009.–Salinas Yacht Club, 1 colony, 3 mm high, without gonothecae, 254562.–La Libertad, CEPE, 3 colonies or colony fragments, to 4 mm high, without gonothecae, 260933.–Capitania, 4 colonies or colony fragments, to 5 mm high, without gonothecae, 260992.–Capitania, 1 colony, 7 mm high, without gonothecae, 254002.–Capitania, 1 colony, 3 mm high, without gonothecae, 254507.–Capitania, 1 colony, 6 mm high, without gonothecae, 260972.

Remarks.—As with *Obelia alternata* Fraser, 1938a, discussed above, *O. microtheca* has often been included earlier in the synonymy of *Obelia dichotoma* (Linnaeus, 1758). This is another diminutive species, with specimens in our collections ranging from 2–10 mm in colony height. Indeed, the lectotype colony of *O. microtheca*, with gonothecae, was only 3 mm high (Calder et al. 2009). In present material, as with paralectotype specimens examined here (BCPM 976-437-1; BCPM 976-437-2), stems were predominantly straight rather than strongly flexuose as in *O. alternata*. Hydrothecal pedicels were often long and annulated either throughout or at proximal and distal ends only. Hydrothecae were funnel-shaped with nearly straight sides, and hydrothecal margins were entire and nearly round in cross-section rather than crenate and polygonal in cross-section. Gonothecae were deeply conical, with a terminal collar. While in some characters these hydroids resembled both *O. alternata* and *O. dichotoma*, they corresponded most closely in morphology with Fraser's (1938a) original account of *O. microtheca* and we assign them to that species here. Calder et al. (2009) had earlier maintained the species as valid.

Collections of *O. microtheca* were obtained during this study only from sites on the mainland coast of Ecuador, just inshore of the type locality off Salinas. It has been reported previously from the coast of Panama to Independencia Bay, southern Peru (Fraser 1938c).

Reported Distribution.—*Tropical Eastern Pacific:* Panama to Peru (Fraser 1947).

Worldwide: known only from the Tropical Eastern Pacific.

Obelia oxydentata **Stechow, 1914**

Figure 8k

Obelia(?) *oxydentata* Stechow 1914: 131, fig. 7.
Obelia oxydentata.–Calder et al. 2019: 38, figs. 3h, i.

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

Material.—Salinas, Salinas Yacht Club, 2 colonies or colony fragments, to 8 mm high, without gonothecae, 261022.–Salinas Yacht Club, 3 colonies, up to 2.5 mm high, on *Pennaria disticha*, without gonothecae, 254584. –Salinas Yacht Club, 1 colony, 2 mm high, on hydroid stem, without gonothecae, 254019.–Salinas Yacht Club, 3 colonies or colony fragments, to 8 mm high, without gonothecae, 261054.–Salinas Yacht Club, 1 colony, 4.5 mm high, without gonothecae, 261053.–Galapagos, San Cristóbal, passenger dock, 1 colony, 5 mm high, without gonothecae, 261160.–Salinas Yacht Club, 1 colony, 8 mm high, without gonothecae, 306583.–San Cristóbal, passenger dock, 1 colony, to 3 mm high, without gonothecae, 261134.–San Cristóbal, passenger dock, 1 colony, 4 mm high, without gonothecae, 254071.

Remarks.—*Obelia oxydentata* Stechow, 1914 appears at present to be a common constituent of fouling assemblages in the study area. Nine collections of the species are recorded here from Ecuador, with six inshore from Salinas and three from Isla San Cristóbal, Galapagos. Another three collections were reported from Isla Santa Cruz, Galapagos, by Calder et al. (2019). The only likely record of the species from the Tropical Eastern Pacific prior to that report is that of Clarke (1907, as *Obelia* (?) sp.) from Isla Perico in the Gulf of Panama. It was not found in the extensive hydroid collections of various Allan Hancock Pacific Expeditions to the region (Fraser 1938a, b, c, 1948). The species was also absent in a collection of hydroids from coastal waters of the Galapagos made by one of us (DRC) in 2001. Its center of distribution is believed here to be the warm western Atlantic.

A detailed account of *Obelia oxydentata*, considered in this work to be distinct from *Obelia bidentata* Clark, 1875, has been given earlier (Calder et al. 2019). Appearing very similar to both *O. bidentata* and *O. oxydentata* from existing descriptions is *O. spinulosa* (Bale, 1888), originally described from Port Jackson, Australia. That species has occasionally been reported

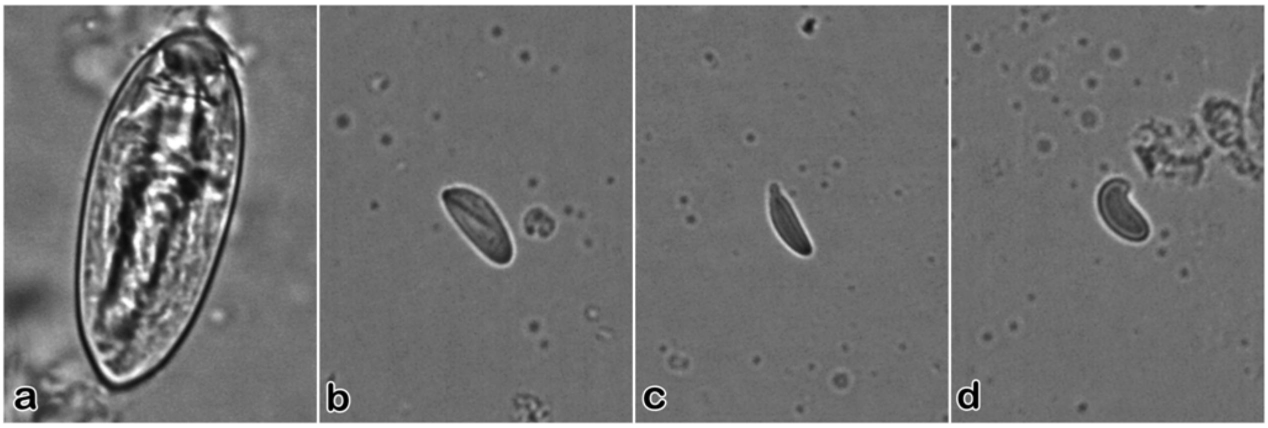

Figure 9. *Nemalecium lighti*: nematocysts (all to same scale), 261018. a, pseudostenotele, undischarged. b, microbasic eurytele, undischarged. c, microbasic mastigophore, undischarged. d, rhopaloid heteroneme, undischarged. Photomicrographs by D.R. Calder.

from the Indo-west Pacific region (e.g., Annandale 1915, as *Obelia spinulosa*; Ritchie 1910, as *Campanularia* (?) *spinulosa*; Leloup 1932, as *Laomedea* (*Obelia*) *spinulosa* var. *minor*), but not from Australia in recent times (Jeanette Watson, *personal communication*, 25 July 2019). Usually treated as a synonym of *O. bidentata* (e.g., Calder 1991; WoRMS), it is treated here as a *species inquirenda*. If conspecific with *O. oxydentata*, the binomen *O. spinulosa* would have priority.

Reported Distribution.—*Tropical Eastern Pacific:* Panama and the Galapagos Islands, Ecuador (Calder et al. 2019).

Worldwide: temperate and tropical western Atlantic (Calder 2013, 2019), western, central, and eastern Pacific (Hirohito 1969; Xu et al. 2014, as *Obelia bidentata*; Calder et al. 2019; Calder 2020), Indian Ocean (Gravier-Bonnet 1999), and possibly Fiji (Gibbons and Ryland 1989, as *O. bidentata*); probably circumglobal.

Family Haleciidae Hincks, 1869

Genus *Nemalecium* Bouillon, 1986

***Nemalecium lighti* (Hargitt, 1924)**

Figures 9a–d, 10a

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

Nemalecium lighti.–Hickman 1908: 129, three unnumbered figs.–Banks et al. 2009: 51, 53, 56, 59.–Calder et al. 2019: 41, figs. 4c, d, 5b, c.

Type locality.—Republic of the Philippines: Oriental Mindoro, Puerto Galera Bay (Hargitt 1924).

Material.—Salinas, Salinas Yacht Club, 1 colony, 1.2 cm high, without gonothecae, 261022.–Salinas Yacht Club, 2 colony fragments, to 1.7 cm high, without gonothecae, 261021.–Salinas Yacht Club, 1 colony, 1.2 cm high, without gonothecae, 261020.–Salinas Yacht Club, 3 colonies, to 1.5 cm high, without gonothecae, 254568.–Salinas Yacht Club, 8 colonies or colony fragments, to 1.7 cm high, without gonothecae, 261018.–Salinas Yacht Club, 1 colony, 1.8 cm high, without gonothecae, 255020.

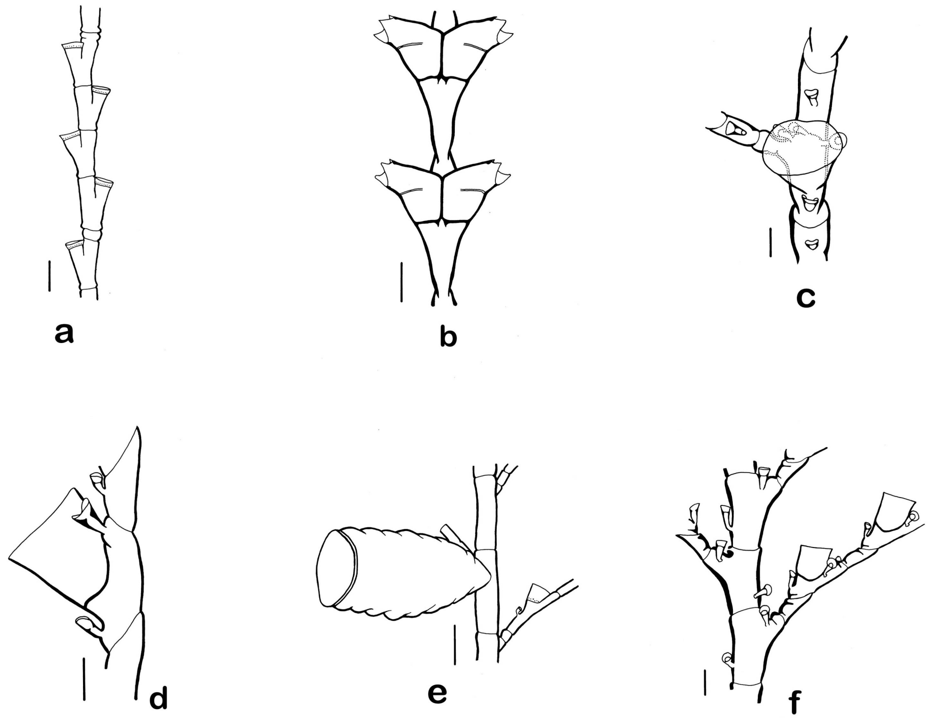

Figure 10. Leptothecata, families Haleciidae, Sertulariidae, Halopterididae, Kirchenpaueriidae, and Plumulariidae. a, *Nemalecium lighti*, part of hydrocaulus with hydrothecae, 261018, scale equals 0.20 mm. b, *Tridentata turbinata*, part of hydrocaulus with two hydrothecal pairs, 254677, scale equals 0.20 mm. c, *Halopteris alternata*, part of hydrocaulus with nematothecae, a cauline hydrotheca, and basal part of a hydrocladium, 254565, scale equals 0.10 mm. d, *Halopteris alternata*, part of hydrocladium with hydrotheca and nematothecae, 254565, scale equals 0.10 mm. e, *Ventromma halecioides*, part of hydrocaulus with gonotheca, and base of a hydrocladium with a hydrotheca, 254565, scale equals 0.20 mm. f, *Plumularia floridana*, part of hydrocaulus and basal parts of three hydrocladia, with hydrothecae and nematothecae, 303801, scale equals 0.10 mm.

Remarks.—Characters of the chitinous exoskeleton in this hydroid are essentially indistinguishable from those occurring in various species of the genus *Halecium* Oken, 1815. Colonies examined here were identified as a species of *Nemalecium* Bouillon, 1986 after discovery of nematodactyls, armed with large pseudostenotele nematocysts (Figure 9a), within the tentacular whorl of the hydranth. The cnidome of the species also includes microbasic euryteles, microbasic mastigophores, and a category thought to be rhopaloid heteronemes (Figure 9b–d).

Nemalecium lighti (Hargitt, 1924), now widely reported (Calder 2019, 2020), has been found earlier in the Galapagos Islands at Wolf (Hickman 2008; Banks et al. 2009), Darwin (Banks et al. 2009) Marchena (Banks et al. 2009), and Santa Cruz (Calder et al. 2019). It was collected here at Salinas on the mainland of Ecuador.

Reported Distribution.—*Tropical Eastern Pacific:* Galapagos Islands, Ecuador (Hickman 2008; Banks et al. 2009; Calder et al. 2019).

Worldwide: Indo-west Pacific, eastern Pacific (Galapagos Islands) and warm western Atlantic (Calder 2019, 2020).

Family Sertulariidae Lamouroux, 1812
Genus *Tridentata* Stechow, 1920

***Tridentata turbinata* (Lamouroux, 1816)**
Figure 10b

Dynamena turbinata Lamouroux 1816: 180.
Tridentata turbinata.–Calder et al. 2003: 1194, fig. 16; 2019: 44, fig. 6c.–Hickman 2008: 132, three unnumbered figs.–Calder et al. 2019: 44, fig. 6c.

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

Material.—Galapagos, San Cristóbal, passenger dock, 2 colonies or colony fragments, to 7 mm high, without gonothecae, 254678.–San Cristóbal, passenger dock, 1 colony, 5 mm high, without gonothecae, 254064.–San Cristóbal, passenger dock, 12 colony fragments, to 1.4 cm high, without gonothecae, 254677.–San Cristóbal, passenger dock, 4 colony fragments, to 9 mm high, without gonothecae, 255068.–San Cristóbal, passenger dock, 9 colony fragments, to 1.8 cm high, without gonothecae, 254065.–San Cristóbal, passenger dock, 6 colony fragments, without gonothecae, 261156.–San Cristóbal, passenger dock, 7 colony fragments, to 1.5 cm high, without gonothecae, 255078.–San Cristóbal, passenger dock, 7 colony fragments, to 1.7 cm high, without gonothecae, 261131.–San Cristóbal, passenger dock, 1 colony, 7 mm high, without gonothecae, 261133.–San Cristóbal, passenger dock, 8 colonies or colony fragments, to 1.8 cm high, without gonothecae, 306600; a sequence of this hydroid has been deposited as GenBank Accession Number MT949546).

Remarks.—The hydroid *Tridentata turbinata* (Lamouroux, 1816) was found during this study only in samples from the passenger dock at Isla San Cristóbal, Galapagos. This essentially circumtropical species has been reported and discussed from the Galapagos archipelago in earlier works (Calder et al. 2003, 2019; Hickman 2008). Inclusion of the species in *Tridentata* Stechow, 1920 rather than *Sertularia* Linnaeus, 1758 is in accord with both morphological and molecular evidence (Calder 2019).

Our COI reference sequence is the first to be deposited for *Tridentata turbinata*.

Reported Distribution.—*Tropical Eastern Pacific:* Oaxaca, Mexico (Humara-Gil and Cruz-Gómez 2018) to the Galapagos Islands, Ecuador (Calder et al. 2003, 2019; Hickman 2008).

Worldwide: circumglobal in tropical and subtropical waters (Calder et al. 2019; Calder 2020).

Family Halopterididae Millard, 1962
Genus *Halopteris* Allman, 1877

***Halopteris alternata* (Nutting, 1900)**
Figure 10c, d

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

not *Plumularia alternata* Fraser 1938a: 62, pl. 14, figs. 71a, b.
Halopteris alternata.–Calder et al. 2019: 47, figs. 5d, 7c, d.

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

Material.—Salinas, Salinas Yacht Club, 2 colonies or colony fragments, to 8 mm high, without gonothecae, 254565.

Remarks.—These hydroids appear identical morphologically with those identified as *Halopteris alternata* (Nutting, 1900) in earlier fouling samples from Isla Santa Cruz, Galapagos (Calder et al. 2019). One of the most common species at that location, it was collected only once during this study, from the mainland of Ecuador at Salinas. Earlier records of the hydroid from Isla Wolf and Isla Floreana in the Galapagos by Fraser (1938a, as *Plumularia alternata*) are thought to have been based on a misidentification (Schuchert 1997).

The hydroid of *H. alternata* is widely distributed in the western North Atlantic (Calder 2013, 2019; Galea 2013). It had commonly been misidentified earlier in the region as *H. diaphana* (Heller, 1868), a species best known in waters of Europe.

Reported Distribution.—*Tropical Eastern Pacific:* Galapagos Islands, Ecuador (Calder et al. 2019).

Worldwide: western Atlantic, eastern Atlantic, eastern Pacific, warm waters (Calder 2019; Calder et al. 2019).

Family Kirchenpaueriidae Stechow, 1921a
Genus *Ventromma* Stechow, 1923

***Ventromma halecioides* (Alder, 1859)**
Figure 10e

Plumularia halecioides Alder 1859: 353, pl. 12, figs. 1–5.
Ventromma halecioides.–Calder et al. 2003: 1200; 2019: 45, figs. 7a, b.

Type locality.—UK: England, Cullercoats and Roker (Alder 1859, as *Plumularia halecioides*).

Material.—Salinas, Salinas Yacht Club, 2 colonies or colony fragments, to 1.2 cm high, with gonothecae, 254565.–Salinas Yacht Club, 2 colonies or colony fragments, to 9 mm high, without gonothecae, 261052.

Remarks.—*Ventromma halecioides* (Alder, 1859), reported earlier to be abundant in fouling communities at Isla Santa Cruz, Galapagos Islands (Calder et al. 2019), was found during this study only at Salinas on the mainland of Ecuador. It is typically a species of shallow, sheltered, quiet water environments.

Comments on the taxonomy and distribution of the species have been given earlier (Calder et al. 2019). Notably, Fraser's (1938a) Galapagos record of *Plumularia inermis* Nutting, 1900, a hydroid regarded as conspecific with *V. halecioides*, is likely to have been based on a misidentification. This species is now included in *Ventromma* Stechow, 1923 rather than *Kirchenpaueria* Jickeli, 1883 based on both morphological and molecular evidence (Calder 2013).

Reported Distribution.—*Tropical Eastern Pacific:* La Paz Bay, Gulf of California, Mexico (Mendoza-Becerril 2020a) to the Galapagos Islands, Ecuador (Calder et al. 2003, 2019).

Worldwide: circumglobal in tropical and warm-temperate waters (Calder 2013, 2020).

Family Plumulariidae McCrady, 1859

Genus *Plumularia* Lamarck, 1816

***Plumularia floridana* Nutting, 1900**

Figure 10f

Plumularia floridana Nutting 1900: 59, pl. 2, figs. 4, 5.–Fraser 1938a: 64.–Calder et al. 2003: 1200.–Hickman 2008: 134, two unnumbered figs.–Banks et al. 2009: 53, 59.

?*Plumularia sinuosa* Fraser 1938a: 67, pl. 15, fig. 77.

Type locality.—USA: Florida, two miles (3 km) W of Cape Romano (Nutting 1900).

Material.—Salinas, Salinas Naval Base, 9 colonies or colony fragments, to 2.1 cm high, without gonothecae, 303801 (a sequence of this hydroid has been deposited as GenBank Accession Number MT949548).–Salinas Naval Base, 2 colonies or colony fragments, to 1 cm high, without gonothecae, 261087.

Remarks.—*Plumularia sinuosa* Fraser, 1938a, originally described from the Galapagos and the Islas Revillagigedo, Mexico, has been regarded in some works as conspecific with *P. floridana* Nutting, 1900 (Calder 1997; Calder et al. 2003). We include it here as a questionable synonym. Collected here from the naval base at Salinas, *P. floridana* has been reported before on the mainland of Ecuador from Bahía Santa Elena (Fraser 1938a). Offshore in the Galapagos, it has been recorded from Isla Isabela (Fraser 1938a, Calder et al. 2003), Isla Fernandina (Calder et al. 2003), Sombrero Chino (Calder et al. 2003), and Isla Santa Cruz (Fraser 1938a, as *Plumularia sinuosa*).

A sequence of our material has been deposited in GenBank (see above). While in a clade with two other hydroids identified as *P. floridana*, based on GenBank COI molecular data, our specimens did not match those sequences, which are based on populations from the Atlantic (STRI CJM86, Isla Escudo de Veraguas) and Pacific (STRI CJM47, Taboguilla, off Panama City) coasts of Panama. No molecular data are available for *P. floridana* from its type locality in southwest Florida (off Cape Romano), and Panamic material may represent one or two different species. Our sequence also groups closely with Tropical Eastern Pacific sequences identified as *P.* cf. *propinqua* Fraser, 1938a (STRI CJM46, Valladolid, off

Panama City) and *P. micronema* Fraser, 1938c (STRI CJM52, Frailes Island, Panama). These two species are similar to *P. floridana,* but differ morphologically in having homomerously rather than heteromerously segmented hydrocladia. Given that cryptic diversity has been reported by Moura et al. (2018) to occur in hydroids identified as *P. floridana*, and given what we consider to be a morphological match of the present material to material of *P. floridana* from Florida, South Carolina, Bermuda, Hawaii, and elsewhere, we retain the name here for the Ecuador material, pending further resolution.

Reported Distribution.—*Tropical Eastern Pacific:* Gulf of California (Fraser 1948, as *P. sinuosa*; Mendoza-Becerril 2020a) to Bahía Santa Elena and the Galapagos Islands, Ecuador (Fraser 1938a; Calder et al. 2003; Hickman 2008; Banks et al. 2009).

Worldwide: circumglobal in tropical and warm-temperate waters (Ansín Agís et al. 2001; Calder 2020).

Discussion

Elucidating the native, introduced, or cryptogenic status of many biofouling invertebrates, especially in tropical regions lacking historical baseline biodiversity studies, is rife with challenges (Carlton 2009). Hydroids, which have had less global taxonomic subscription than many other marine invertebrate groups, are no exception to these difficulties. Many hydroid species have been assigned circumglobal distributions: examples in the present collections include *Pennaria disticha, Bougainvillia muscus, Amphinema rugosum, Cirrholovenia tetrenema, Clytia linearis, Tridentata turbinata, Ventromma halecioides,* and *Plumularia floridana*. Most such species may fall into a *pseudocosmopolitan* category, defined by Darling and Carlton (2018) as "A taxon composed of two or more lineages (which may be native, introduced, or cryptogenic) but retaining a single binomial name with an illusory 'cosmopolitan' biogeographic status." Such taxa, when investigated at a more fine-grained morphological level, through molecular techniques, or both, may then resolve into more refined categories, including *regionally indigenous (provincial)* species, *neocosmopolitan* species (species dispersed by anthropogenic activities in historical time), or, indeed, conceivably *eucosmopolitan* (naturally cosmopolitan) species (Darling and Carlton 2018). However, only a few hydroid taxa have now been extensively investigated to reveal potential global species complexes and resulting delimitations. Examples include species in the hydroid genera *Obelia* (Govindarajan et al. 2005), *Cordylophora* (Folino-Rorem et al. 2008), *Clytia* (Lindner et al. 2011), *Plumularia* (Schuchert 2014), *Lytocarpia* (Postaire et al. 2017), and *Pennaria* and *Turritopsis* (Miglietta et al. 2019). These and other studies uniformly reveal multiple distinct, apparently species-level clades, which may or may not be accompanied by distinct morphological characters.

We predict that it is among these pseudocosmopolitan and unresolved cosmopolitan (Darling and Carlton 2018) taxa that additional endemic species, now hidden under cosmopolitan nomenclature, such as the insular *Obelia alternata* recognized here, will be revealed. We further predict that potentially many more non-indigenous species will be detected on both the Ecuador mainland and in the Galapagos Islands, given the long-term exposure, commencing in the 1500s, of these regions to international shipping traffic.

The temporally short (90-day) and spatially limited studies reported here revealed the presence of five additional hydroid species in the Tropical Eastern Pacific biota, including four presumptive newly-detected introductions in the Galapagos Islands, as well as four introductions in mainland Ecuador, three ostensibly native species as new records for mainland Ecuador, and the addition of several cryptogenic species for both the mainland and the Galapagos. As noted above, an impressive 15 species were found at only one station in either the mainland or on San Cristobal Island, suggesting that sampling over longer time periods and more seasons, and at additional locations, will greatly increase our knowledge of hydroid diversity in Ecuador.

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Ethics and Permits

All institutional and national policies were complied with during the course of this research. No experimental studies were conducted. Collecting permits are on file with the Galapagos National Park.

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