

Research Article

Hydroids (Cnidaria: Hydrozoa: Leptothecata and Limnomedusae) on 2011 Japanese tsunami marine debris landing in North America and Hawai‘i, with revisory notes on *Hydrodendron* Hincks, 1874 and a diagnosis of Plumaleciidae, new family

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Abstract

Twenty-eight species of hydroids are now known from Japanese tsunami marine debris (JTMD) sent to sea in March 2011 from the Island of Honshu and landing between 2012 and 2016 in North America and Hawai‘i. To 12 JTMD hydroid species previously reported, we add an additional 16 species. Fourteen species (50%) were detected only once; given the small fraction of debris sampled, this suggests that the diversity of the total arriving hydroid fauna was likely larger. Our ongoing studies provide the first documentation of these species being rafted from one continental margin to another. *Plumalecium plumularioides* (Clark, 1877) is newly reported for the Japanese hydroid fauna. Fourteen species (52%), held to be either naturally amphi-Pacific or possibly introduced by ships at some earlier date, were already known from the Pacific coast of North America. We suggest that *Obelia griffini* Calkins, 1899, as represented in the JTMD fauna, may be a North Pacific oceanic neustonic species. We propose that *Hydrodendron mirabile* (Hincks, 1866) and its congeners be included in the family Phylactothecidae Stechow, 1921, here emended. We establish a new family, Plumaleciidae Choong and Calder, 2018, to accommodate the genus *Plumalecium* Antsulevich, 1982.

Key words: Pacific distributions, Leptothecata, Limnomedusae, anthropogenic debris, population connectivity, transoceanic dispersal, systematics

Introduction

The Great East Japan Earthquake and Tsunami of March 11, 2011 sent into the North Pacific Ocean

a vast field of floating debris derived from the Tōhoku coastline of northeast Honshu. Rafted objects with living Japanese species began arriving on the shores of North America in the spring and summer

of 2012 and in the Hawaiian Islands in the fall of 2012 (Carlton et al. 2017). One of the most common groups of organisms in the biofouling communities on this debris was hydroids. Choong and Calder (2013) reported on the presence of the Japanese hydroid *Sertularella mutsuensis* Stechow, 1931 on a large dock lost during the tsunami from the Port of Misawa (Aomori Prefecture) that landed 14 months later, in June 2012, on the Oregon coast. Calder et al. (2014) reported upon collections of 11 additional coastal thecate species (and one likely pelagic hydroid, *Obelia griffini* Calkins, 1899) from biofouling on tsunami debris intercepted in 2012 and 2013 landing in Oregon and Washington.

We report here on additional collections of hydroids recovered from Japanese tsunami marine debris collected in Washington, Oregon, California, and Hawai'i between 2012 and 2016, and analyze the total hydroid fauna found to date.

Materials and methods

Morphological analyses

Samples were obtained from JTMD objects (identified as such through multiple lines of evidence; see Carlton et al. 2017) landing in North America and the Hawaiian Islands (Supplementary material Table S1). Each object was assigned a unique identification number preceded by JTMD-BF- (Japanese Tsunami Marine Debris-BioFouling-). Specimens retrieved from the field were either preserved directly in 95% ethanol, or frozen and transferred into ethanol at a later date. All specimens studied here are deposited in the collections of the Invertebrate Zoology Section, Department of Natural History, Royal Ontario Museum (ROMIZ) and the Royal British Columbia Museum (RBCM/BCPM). The classification and implied relationships of hydroids adopted here generally follows Leclère et al. (2009), Maronna et al. (2016), and Cunha et al. (2017). Species descriptions are provided where warranted. Several taxa in this study were described and illustrated in our previous work (Calder et al. 2014).

Genetic analyses

Three approximately 20 × 20 cm scrapings were taken from the sides of a floating dock (JTMD-BF-1) originating from the Port of Misawa, Aomori Prefecture, which landed on the central Oregon coast in early June 2012 (Table S1). The samples were preserved in 70% ethanol and sent to the Geller Laboratory at Moss Landing Marine Laboratories, Moss Landing, California USA. The ethanol was later decanted and samples were rinsed with distilled water, drained,

and homogenized in an IKA (Wilmington, NC, USA) A11 analytical mill. 10 g of homogenate were used in a MoBio PowerSoil DNA extraction kit (Qiagen, Germantown, Maryland, USA). Genomic DNA was quantified using Nanodrop ND-1000 (ThermoFisher, Waltham, Massachusetts USA). 5 ng of each total DNA extraction were amplified in PCR cocktails comprising a final concentration of 1 × Green Go Taq Master Mix, 0.2 mg mL⁻¹ BSA, 1.5 mM MgCl₂, and 0.2 μM of each primer in a 50 μL reaction. We used primers jgHCO2198 and jgLCO1490 from Geller et al. (2013). Reaction conditions consisted of an initial 3 minute melt at 94 °C, followed by 32 cycles of a 1 minute at 95 °C, 45 seconds at 47 °C, and 90 seconds at 72 °C. PCR amplicons were viewed on a 2% agarose gel stained with ethidium bromide. Samples were purified with 1.4 × the sample volume of Agencourt Ampure (Brea, California USA) beads, according to the manufacturer's protocol.

Samples were quantified using Picogreen High sensitivity DNA assay according to the manufacturer's protocol (Qiagen). 100 ng of sample were fragmented with the IonXpress Ion Shear enzyme kit (ThermoFisher). Samples were purified with 1.4 × the sample volume of Agencourt Ampure beads. Samples were then ligated with IonXpress barcodes and sequencing adapters, size selected for ca. 400 bp using an e-gel cassette, purified once more with 1.4 × Ampure beads. Samples were quantified using the Agilent (Santa Clara, California, USA) Bioanalyzer high sensitivity chip assay and combined into an equimolar pool. Samples were run using the Ion Torrent 400 bp sequencing kit and v314 chip according to the manufacturer's protocol, yielding 500,000 reads passing filter. Reads were trimmed of primers and clustered into groups using a 95% similarity threshold using the software package Geneious v9 (Biomatters, Auckland, New Zealand).

Consensus sequences were compared to Genbank for any matches to COI sequences annotated as derived from Hydrozoa. Candidate novel sequences were aligned with hydroid sequences downloaded from Genbank, aligned with MAFFT (Katoh and Standley 2013). Maximum likelihood trees were constructed with FastTree (Price et al. 2010) from within Geneious.

Samples of individual hydroids collected from a wide variety of JTMD objects (below) were also submitted for genetic analysis (by analytical techniques as described in McCuller et al. 2018), but failed to yield useful sequences.

Results

To the 12 hydroid species previously identified on JTMD and believed to originate from the Japanese

coast (based upon evidence reviewed in Calder et al. 2014, and further detailed in the Discussion below), we now add an additional 16 species (Table S2). Two of the 12 taxa reported earlier only to genus, *Phialella quadrata* (Forbes, 1848) and *Plumularia caliculata* Bale, 1888, are now resolved to species level based upon the availability of additional material. Campanulariid hydroids (*sensu lato*, here treated in the families Campanulariidae, Clytiidae, and Obeliidae) are the most diverse group in the JTMD hydroid fauna.

In addition to these species, Calder et al. (2014) found two anthoathecate species (*?Bougainvillia muscus* (Allman, 1863) and *Stylactaria* sp.); additional athecate hydroids are in hand, and these will be treated separately in a subsequent report.

Fourteen of the 28 species collected from JTMD objects (50%) were detected only once (three species reported earlier by Choong and Calder (2013) and Calder et al. (2014), and 11 additional species newly reported herein) (See Table S2). Forty-three percent (six) of these unique species arrived in 2015, in concert with a peak of detected overall JTMD diversity (Carlton et al. 2017).

Of interest (and argued below as partial evidence for the Western Pacific origin of the JTMD hydroid fauna) is that total hydroid diversity per object declined after 2013 (even as unique species continued to arrive and peaked later). On four objects (BF-1, 8, 23, and 40) arriving in Oregon and Washington between summer 2012 and spring 2013, hydroid diversity ranged from four to eight species (excluding *Obelia griffini* Calkins, 1899, as discussed below). Thus, eight species (*Amphisbetia furcata* (Trask, 1857), *Eutima japonica* Uchida, 1925, *Halecium tenellum* Hincks, 1861, *Phialella quadrata*, *Plumularia caliculata*, *Sertularella mutsuensis* Stechow, 1931, *Sertularella* sp., and *Gonionemus vertens* A. Agassiz, 1862) were found on the Misawa dock (BF-1, noted above) that landed in June 2012 in Oregon. Five and six species were found on debris items arriving in Oregon in February 2013 (BF-23) and in Washington in March 2013 (BF-40), respectively: on the former were *Hydrodendron gracile* (Fraser, 1914), *Orthopyxis platycarpa* Bale, 1914, *Plumularia setacea* (Linnaeus, 1758), *Eutima japonica*, and *Stylactaria* sp.; on the latter were *Phialella quadrata*, *Obelia longissima* (Pallas, 1766), *Amphisbetia furcata*, *Plumularia caliculata*, *Plumalecium plumularioides* (Clark, 1877) and *Eutima japonica*. Since spring 2013, most objects arrived with one species, and no object was found with more than two species.

Twenty-four species (89% of the JTMD hydroid fauna) were already reported from Japan (Table S2); two species, *Hydrodendron gracile* and *Plumalecium plumularioides* represent new records for the country

(one reported earlier by Calder et al. 2014), and two, not taken to species level, *Clytia* sp. and *Antennella* sp. are of uncertain geographic distribution. In turn, 14 species (52%) already known from the North East Pacific Ocean (Table S2), are held to be either naturally amphi-Pacific in distribution or possible ship-borne introductions. Twelve taxa are unknown from the Pacific coast of North America. However, they are not treated here as new records for the Eastern Pacific because they are present only on intercepted debris and are not yet known to have established populations. Six hydroid species (*Orthopyxis caliculata* (Hincks, 1853), *Obelia dichotoma* (Linnaeus, 1758), *Amphisbetia furcata*, *Plumularia setacea*, and *Plumalecium plumularioides*) were found on debris arriving in the Hawaiian Islands; two of these (*O. dichotoma* and *P. setacea*) were previously known from Hawai'i, recognized there as introduced and cryptogenic, respectively (Carlton and Eldredge 2009).

Notably, species of *Clytia* Lamouroux, 1812 were absent on JTMD arriving in 2012 and 2013, but began to appear in 2014. *Clytia* sp., whose affinities are discussed below, was found once (BF-363) on an object landing in Washington during early 2015. *Clytia linearis* (Thornely, 1900) was discovered on a derelict vessel (BF-538) arriving in Oregon in spring 2016. *Clytia hemisphaerica* (Linnaeus, 1767) appeared on six items in Oregon and Washington between 2014 and 2015. *Clytia linearis* is a distinctive warm-water species, although Galea (2007) reported it from colder waters of the Subantarctic in the fjords region of southern Chile. Its later appearance on JTMD may be due to a longer, more circuitous route through lower latitudes before the rafted vessel became caught up in ocean currents moving north and east. *Clytia* sp., although currently unidentified, was accompanied by a warm-water, southern species of neustonic bryozoan, *Jellyella eburnea* (Hincks, 1891), also indicating a longer route through lower latitudes (McCuller and Carlton 2018). The six objects on which *C. hemisphaerica* arrived, however, bore no distinctive indication of their route after departure from the Tōhoku coast in March 2011. Finally, the most common hydroid in our samples was *Obelia griffini*. We suggest below that it may be an element of the open ocean neustonic fauna.

Details are provided below on identification, taxonomy, and geographic distribution of 24 species of neritic hydroids on JTMD, and of the putatively pelagic hydroid *Obelia griffini*. Four additional JTMD leptothebate species (*Halecium tenellum*, *Hydrodendron gracile*, *Sertularella mutsuensis*, and *Sertularella* sp.), not represented in the newer samples analyzed here, are recorded in Calder et al. (2014).

Table 1. Comparison between the trophosome in the hydroid stages of *Opercularella lacerata*, *Opercularella rugosa*, *Phialella quadrata*, and JTMD specimen BF-382 (ROMIZ B4107).

	<i>Opercularella lacerata</i> (in Cornelius 1995a)	<i>Opercularella rugosa</i> (from Nutting 1901)	<i>Phialella quadrata</i> (in Cornelius 1995a)	JTMD-BF-382 (ROMIZ B4107)
Colony	Erect, much branched, branches angled at ca 60°	Erect; irregularly branched, branches alternate, geniculate	Erect, branches tending all to be directed upwards	Stolonial and erect, branches directed upwards
Hydrotheca height	300–400 µm	Not given	ca 250 µm	230–260 µm
Hydrotheca shape	Widest in middle	Widest distally (towards aperture or in middle)	Widest distally (towards aperture)	Widest distally (towards aperture)
Operculum	9–12 pointed flaps (cusps)	10–12 pointed flaps	Pleated sheath, ca 10 pleats, not cusped	Pleated, < 10 pleats, not cusped
Pedicel	Typically shorter than hydrotheca	Very short	Often longer than hydrotheca	Often longer than hydrotheca
Stem	Both spirally and transversely grooved (ringed)	Transversely grooved (ringed)	Transversely grooved (ringed)	Transversely grooved (ringed)
Gonophores	Fixed sporosacs	Medusae	Medusae	unknown
Reported distribution	North Atlantic Ocean, Baltic Sea (Schuchert 2001); Indo-Pacific (?) (Cornelius 1995a)	Alaska (Nutting 1901); West Seattle, Washington (Fraser 1946)	Sea of Japan (Naumov 1960); Atlantic and Indo-Pacific (Cornelius 1995a)	N/A

Systematic Account

Order Leptothecata Cornelius, 1992

Family Phialellidae Russell, 1953

Phialella quadrata (Forbes, 1848)

Thaumantias quadrata Forbes 1848: 43, pl. 9, figures. 2a–e [medusa stage].

Material.—Washington, on vessel, stolonial and branching colony, bryozoan *Scruparia ambigua* (d'Orbigny, 1841) epizoid, no gonothecae (JTMD-BF-40), ROMIZ B4175; Washington, on basket, branching colony, no gonothecae, *S. ambigua* epizoid (JTMD-BF-343), RBCM 017-00011-003; California, on the pelagic gooseneck barnacle *Lepas* on crate, no gonothecae (JTMD-BF-382), ROMIZ B4107.

Description.—Colony with both stolonial and erect parts. Stolon smooth, hydrocaulus annulated. Erect hydrocauli flexuous, annulated throughout, branched or unbranched. Branches, when present, angled upwards. Annuli transverse. Hydrotheca operculate, long-conical, widest distally towards aperture, thin-walled, operculum pleated, not demarcated basally by crease line, pedicel ringed. Gonothecae not observed.

Remarks.—In our previous study (Calder et al. 2014) we reported (as *Phialella* sp.) the occurrence of a species, closely resembling *P. quadrata*, on a floating dock (JTMD-BF-1) from Misawa, Japan. It was compared as well with *Opercularella rugosa* (Nutting, 1901) and *O. lacerata* (Johnston, 1847). Specimens in one of our present samples (JTMD-BF-382), growing on young species of *Lepas* Linnaeus, 1758, had both stolonial and erect stems. Stolonial colonies

of *P. quadrata* have been reported in other zoobenthic communities (Voronkov et al. 2010). The JTMD material most closely corresponds to *P. quadrata* in the following ways: (1) branches are directed upwards at a more acute angle than in *O. lacerata* (see Cornelius 1995a, Table 1) (2) hydrothecal pedicels are long (those of *P. quadrata* are often longer than the hydrothecae, while those of *O. lacerata* and *O. rugosa* are mostly shorter), and (3) hydrothecal size and shape differ (in *O. lacerata*, hydrothecae are 300–400 µm high and widest in the middle; those of *P. quadrata* are 230–260 µm high and widest below their opercula). Comparisons with species having similar characters are given in Table 1.

Distribution.—Sea of Japan (Naumov 1960). A well-known European species (Bouillon et al. 2004, and records summarized in Mendoza-Becerril et al. 2009), held to be introduced to Australia (Hewitt et al. 2004) through ship fouling, and thus perhaps to other coasts of the southern hemisphere as well, including New Zealand, Chile, and South Africa.

Family Eirenidae Haeckel, 1879

Eutima japonica Uchida, 1925

Eutima japonica Uchida 1925: 93, figure 17.

Remarks.—Calder et al. (2014) reported this endocommensal hydroid in the mussel *Mytilus galloprovincialis* Lamarck, 1819 from JTMD-BF-8. *Eutima japonica* Uchida, 1925 has also been found in *M. galloprovincialis* in samples from JTMD-BF-1, 6, 23, 40, 43, and 168 (Table S1) (G. Ruiz and J. Geller) based upon morphological and genetic analyses.

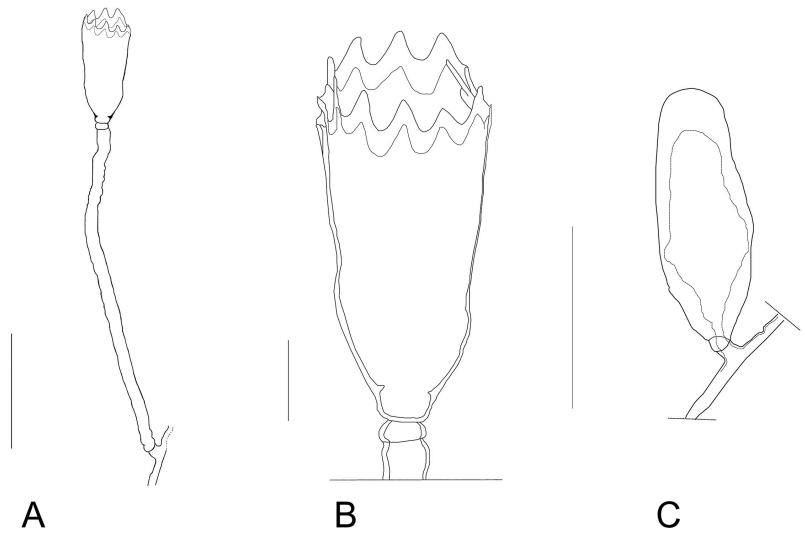


Figure 1. *Campanularia volubilis*: (A) pedicel and hydrotheca. Scale equals 500 μm . (B) detail of hydrotheca. RBCM 017-00006-001. Scale equals 100 μm . (C) gonotheca. RBCM 017-00006-001. Scale equals 500 μm . Del. HHC Choong.

Family Campanulariidae Johnston, 1837

***Campanularia volubilis* (Linnaeus, 1758)**

(Figure 1)

Sertularia volubilis Linnaeus 1758: 811.

Campanularia reduplicata Nutting 1901: 172, pl. 18, figure 1.

Campanularia urceolata.—Nutting 1915: 40, pl. 4, figures 4 and 5.

Campanularia groenlandica.—Hirohito 1995: 54, figure 16a–b [not *Campanularia groenlandica* Levinsen 1893].

Material.—Oregon, on vessel, epizoid on *Scruparia ambigua*, single pedicel with hydrotheca, with ♂ gonothecae (JTMD-BF-201), RBCM 017-00006-001.

Description.—Colony stolonial, pedicel arising from creeping hydrorhiza. Pedicel approximately 3 times length of hydrotheca, perisarc mostly smooth, wrinkled at base, with irregular annulations towards the distal end. Subhydrothecal spherule almost oval. Perisarc slightly thickened. Hydrotheca deeply campanulate, one side somewhat curved to resemble the urceolate form, ca. 400 μm in length from hydrothecal margin to bottom of basal chamber, walls narrowing slightly towards hydrothecal base. Basal chamber 32 μm high. Hydrothecal margin with 11–12 well-demarcated, triangular but slightly rounded cusps, 39 μm in length, separated by rounded embayments. Margin reduplicated. Hydrothecal walls thin to slightly thickened around basal chamber. Gonothecae somewhat cylindrical, ca 725 μm in length, ca 266 μm at widest part, truncated at distal end, on very short pedicel with one spiral twist, arising from stolon. Pedicel length ca 64 μm .

Remarks.—The specimen examined corresponds most closely with accounts of *Campanularia urceolata* Clark, 1877 and *C. reduplicata* Nutting, 1901, both considered conspecific with *C. volubilis* (Calder and

Stephens 1997; Calder 2004). *Campanularia volubilis* and *C. urceolata* were reported from Japan by Yamada (1950). The gonotheca of our specimen closely resembles that reported by Hirohito (1995) as being *C. groenlandica* Levinsen, 1893, but we follow Schuchert (2001) in not considering *Campanularia* cf. *C. groenlandica* sensu Hirohito (1995) to be conspecific with *C. groenlandica* Levinsen, 1893. The gonotheca of our specimen, and that of Hirohito, resembles that of *C. urceolata* figured by Nutting (1915). Gonothecae in *C. volubilis* have no neck when young (Cornelius 1995b). The shape of the hydrotheca in Hirohito's specimen appears to be morphologically closer to *C. volubilis* than *C. groenlandica* as shown by Naumov (1960), and by Schuchert (2001). The pedicel in our specimen and those of Hirohito are not as annulated as in most descriptions of *C. volubilis* but Cornelius (1995b) reported straight to spirally grooved pedicels in this species.

Distribution.—Japan (Fraser 1946; Yamada 1950). Fraser (1946) characterized *C. volubilis* as a naturally circumpolar species, widespread through the North Atlantic and North Pacific Oceans, from the Bering Sea to the Galapagos Islands in the Eastern Pacific (Fraser 1937, 1946), although the conspecificity of warm-temperate and tropical populations is improbable.

***Orthopyxis calculata* (Hincks, 1853)**

Campanularia calculata Hincks 1853: 178, pl. 5, figure B.

Material.—Hawai'i, on buoy, colony arising from hydrorhiza, no gonothecae (JTMD-BF-90), ROMIZ B4098.

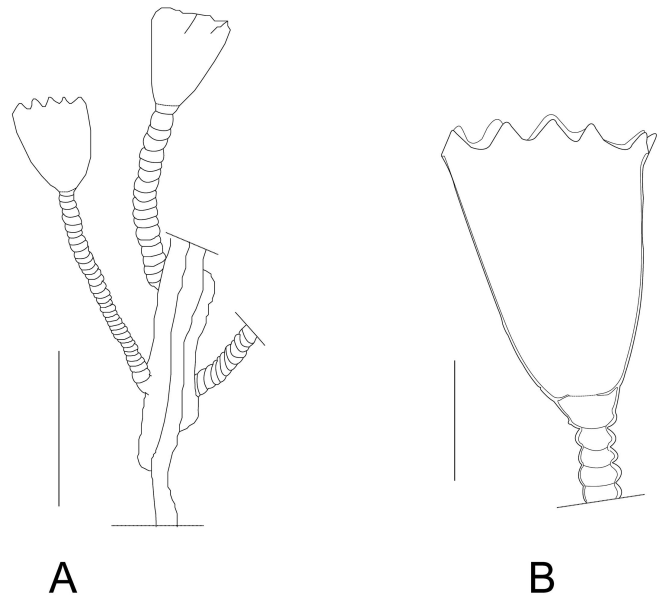


Figure 2. *Clytia* sp.: (A) part of colony. ROMIZ B4156. Scale equals 1000 μ m. (B) detail of hydrotheca. ROMIZ B4156. Scale equals 200 μ m. Del. HHC Choong.

Remarks.—The occurrence of *Orthopyxis caliculata* in JTMD material was reported in our previous study (Calder et al. 2014), along with a detailed discussion of the synonymy of *O. caliculata* into *O. integra* (Macgillivray, 1842) by some workers (e.g. Kramp 1911; Cornelius 1995b; Vervoort and Watson 2003). Following our earlier work, we retain *O. caliculata* as a separate species from *O. integra* based upon observed trophosomal characters, particularly the presence of bilaterally symmetrical hydrothecae in the former, rather than being radially symmetrical as in the latter. The validity of *O. caliculata* as a species has been corroborated through a re-evaluation of morphological diagnostic characters, including differential hydrothecal perisarc thickness resulting in bilateral symmetry, together with molecular analyses (Cunha et al. 2015). Our specimens correspond with Japanese material considered by Hirohito (1995) as *O. caliculata* (although referred by him to the genus *Campanularia* Lamarck, 1816).

Distribution.—Japan (Hirohito 1995); northwest Pacific (Korea, Russia) and northeast Pacific (Fraser 1937, 1946, and records reviewed in Calder et al. 2014); widely reported (often as *Orthopyxis integra*) from the North Atlantic Ocean.

Orthopyxis platycarpa Bale, 1914

Orthopyxis platycarpa Bale 1914: 79, pl. 11, figure 3.
Campanularia platycarpa.—Hirohito 1995: 56, figure 16e–g.

Material.—Oregon, on float, several pedicels with hydrothecae, without gonothecae (JTMD-BF-18),

ROMIZ B4232; Oregon, on vessel, colony with epizoic bryozoan *Scruparia ambigua*, on *Lepas* sp. stalk, without gonothecae (JTMD-BF-23), ROMIZ B4091.

Remarks.—We regard *Orthopyxis platycarpa* as being distinct from *O. integra* based on differences in the morphology of the hydrothecae and gonothecae, including the frequent occurrence of a convex submarginal, basal band of thickened perisarc on the hydrothecae in *O. platycarpa* and gonothecae that are distinctly compressed compared to *O. integra* (Bale 1914; Cunha et al. 2015). Comparisons of some trophosomal characters of specimens of *O. platycarpa*, *O. integra*, and *O. caliculata* from the collections of the Royal Ontario Museum, together with information on *O. platycarpa* from Naumov (1960, as *Campanularia platycarpa*) are provided in Calder et al. (2014).

Distribution.—Western Pacific Ocean (Japan, China, Russia) (Calder et al. 2014).

Family Clytiidae Cockerell, 1911

Clytia sp.

(Figure 2)

Material.—Washington, on plastic bowl, section of colony amongst fouling, without gonothecae (JTMD-BF-363), ROMIZ B4156.

Description.—Colony bushy, partial colony section about 17 mm high, stem and main branches fascicled. Hydrothecal pedicels long, reaching over 2.8 mm,

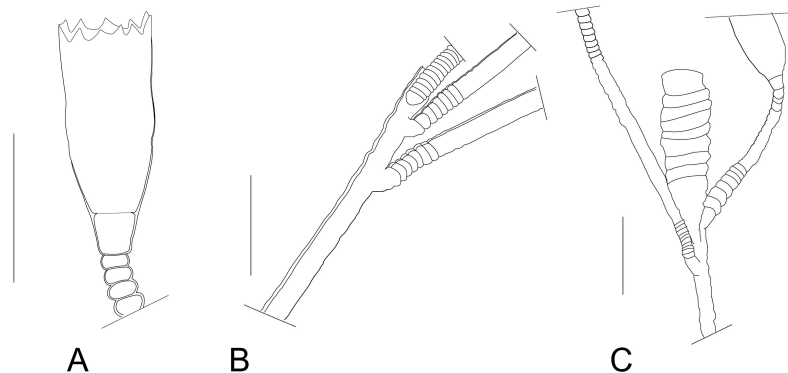


Figure 3. *Clytia hemisphaerica*: (A) detail of hydrotheca. RBCM 017-00016-001. Scale equals 500 μ m. (B) proximal part of pedicel branches. RBCM 017-00016-001. Scale equals 500 μ m. (C) gonotheca. RBCM 017-00016-001. Scale equals 500 μ m. Del. HHC Choong.

arising from main branch and branchlets, annulated throughout or having smooth sections between basal and distal parts. Hydrotheca large, deeply campanulate, up to 470 μ m long and 252 μ m wide at its widest point, with 10–14 prominent, pointed-to-slightly-rounded cusps about 25–30 μ m tall. No gonothecae observed.

Remarks.—We are unable to assign the limited material in hand to a known Japanese species. In many respects, our specimen corresponds to *Clytia universitatis* Torrey, 1904 (see Fraser 1937), particularly in details of the trophosome and fascicled stem. We compared the present material to Fraser's specimen of *C. universitatis* from Isla Partida, Gulf of California, Mexico, in the holdings of the Royal BC Museum (BCPM 976-395-1). Some hydrothecae in our specimen are broader than those in Fraser's material and that illustrated by Torrey (1904), which are uniformly deeply campanulate, and increase in diameter very slightly from base to margin. *Clytia universitatis*, however, is known largely from southern California and Mexico (with reports as far north as San Francisco Bay; Fraser 1946), and the JTMD trajectories do not bring objects past these lower latitudes along the North American coast toward Washington. The absence of any other unique Eastern Pacific species on BF-363 further argues against recruitment in the eastern Pacific Ocean.

Clytia hemisphaerica (Linnaeus, 1767)

(Figure 3)

Medusa hemisphaerica Linnaeus 1767: 1098 [medusa stage].

Clytia minuta.—Nutting 1915: 61, pl. 14, figures 1–4.—Fraser 1937: 76, pl. 15, figure 74a–b.

Clytia edwardsi.—Hirohito 1995: 61, figure 17d–e.

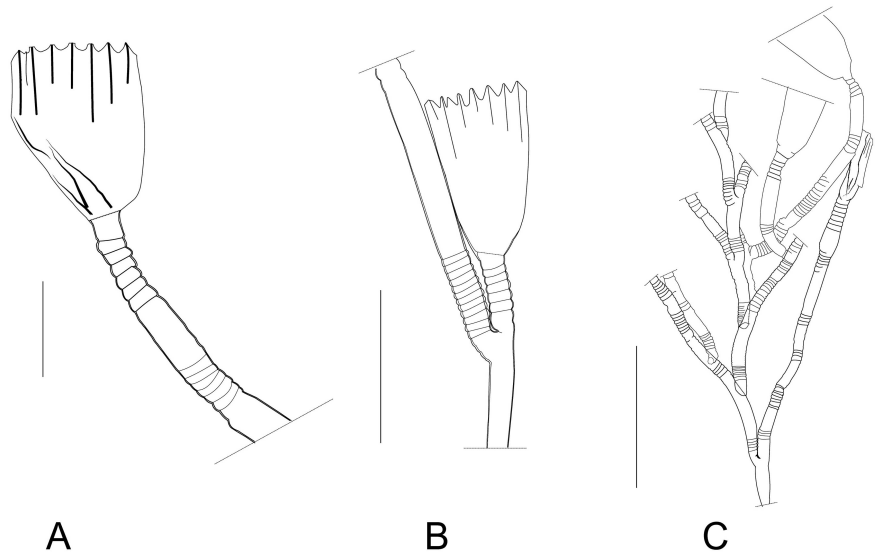
Material.—Oregon, on lid, colony on *Lepas* sp., without gonothecae (JTMD-BF-136), ROMIZ B4099; Oregon, on basket (JTMD-BF-252), ROMIZ B4102; Washington, on basket, colony with gonothecae,

Scruparia ambigua epizoic (JTMD-BF-343), RBCM 017-00011-001; Washington, on tote, colony with gonothecae (JTMD-BF-469), RBCM 017-00016-001; Washington, on basket, colony with hydranths, with gonothecae (JTMD-BF-470), RBCM 017-00016-005; Washington, colony with hydranths, without gonothecae, on tote (JTMD-BF-472), RBCM 017-00016-003.

Description.—Colony arising from creeping stolon, pedicels usually very long, branching several times. Colony height reaching 22 mm, branches reaching as long as half of colony height. Secondary branches may be shorter. Basal region of branch curves upward, branches often aligned parallel with primary pedicel. Main pedicel annulated basally and distally, central portion smooth. Perisarc thin to very slightly thickened. Pedicellate form also present in same colony. Hydrotheca thin-walled, campanulate, 643 μ m high, widest at margin, about 343 μ m, narrowing slightly to 305 μ m at middle. Diaphragm 154 μ m wide. Basal chamber approximately 84 μ m high. Margin with 10–12 prominent, triangular, slightly rounded teeth, approximately 37 μ m high, separated by rounded embayments. Hydrothecal pedicels annulated basally and distally or fully annulated. Gonothecae arising from stolon or stem, on short, annulated pedicels; approximately 901 μ m high, broadly cylindrical, slightly tumid in mid-section; wall with spiral ridges.

Remarks.—The occurrence of *C. hemisphaerica* in JTMD samples is notable because of the presence of morphologically variable colonies. In the material examined, the colonies possess extremely long pedicels and repeated branching, but also possess distinctly annulated gonothecae, suggesting the possibility that populations settling in coastal fouling communities may change morphology as they drift for long periods of time at sea. West and Renshaw (1970) found that branching in *Clytia* sp. can vary in response to food and temperature conditions.

Figure 4. *Clytia linearis*: (A) hydrotheca and part of pedicel. RBCM 017-00022-001. Scale equals 500 μm . (B) portion of stem showing apophyseal region and fold of perisarc projecting inward into internode lumen. RBCM 017-00022-001. Scale equals 1000 μm . (C) part of colony showing branching. RBCM 017-00022-001. Scale equals 2000 μm . Del. HHC Choong.



Clytia hemisphaerica, along with *Obelia dichotoma* and *O. geniculata* (Linnaeus, 1758), which also occur in the JTMD samples, have been found on a wide variety of vertebrate, invertebrate and algal substrates, which phoretic habitat may facilitate dispersal through long-distance transoceanic transport (Cornelius 1982). Our samples are found on various anthropogenic substrates, overgrowing young *Lepas* sp., with *Scruparia ambigua* epizooic.

Distribution.—*Clytia hemisphaerica* was reported from the Tōhoku region by Nishihira (1968) and from Matsuyama by Yamada (1958). This species is reported to be nearly cosmopolitan in coastal waters (Schuchert 2001), and may thus involve a species complex.

Clytia linearis (Thornely, 1900)

(Figure 4)

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

Clytia ? obliqua Clarke 1907: 9, pl. 5, figures 1–4.

Clytia carinadentata Fraser 1938: 28, pl. 7, figure 30.

Clytia linearis.—Lindner and Migotto 2002: 542, figure 2.

Material.—Oregon, on vessel, weathered colonies, without gonothecae (JTMD-BF-538), RBCM 017-00022-001.

Description.—Colony erect, stem flexuous, sympodially branched, stems up to 16.5 mm high. Internode with smooth, upward-curved apophysis. Apophyses alternate left-and-right of stem. Apophyseal region has fold of perisarc projecting inward into internode lumen. Internode supports succeeding internode or distal pedicel. Stem, branches and pedicels with moderately thickened perisarc, variously

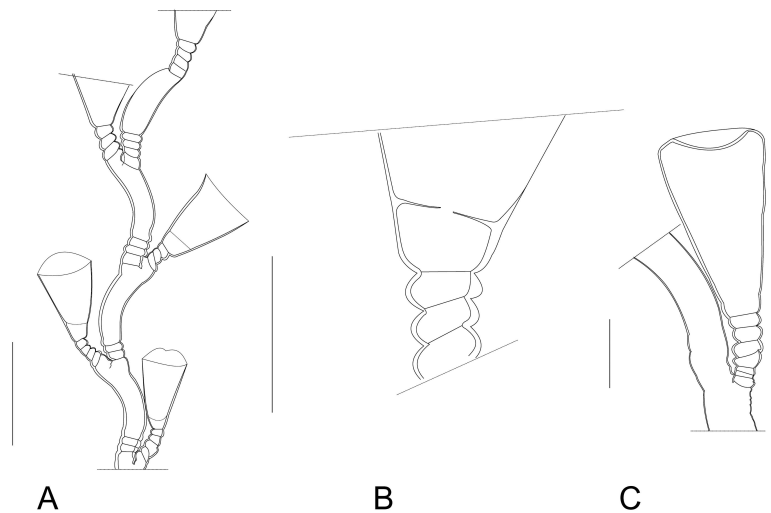
annulated, ranging from almost fully annulated to alternating annulated and smooth sections. Distal portion of pedicel supporting hydrotheca always annulated. Hydrotheca large, cylindrical, 1065–1164 μm long, 660–956 μm wide at margin. Hydrothecal walls almost parallel, occasionally narrowing slightly towards margin. Perisarc thin. Basal chamber 60–114 μm high, diaphragm thin, 194–253 μm wide. Hydrothecal margin with 12–16 pointed to slightly rounded cusps, approximately 54 μm high. Hydrothecal cusps triangular, not narrow; pleated, pleats extending from apex of cusp, occasionally reaching into middle of hydrotheca. Gonothecae not observed.

Remarks.—Our material corresponds to the descriptions of Fraser (1938) and Lindner and Migotto (2002), with the exception of the general shape of the hydrothecal cusps, which resemble those of *Clytia ?obliqua* Clarke, 1907 in being triangular instead of long and narrow. Material with similar cusps is described by Migotto (1996). Cornelius (1982) did not consider the angle of slope of the hydrothecal cusps to be significant, and assigned Clarke's species to *C. linearis*. The fold of the perisarc projecting inward into the internode lumen in the apophyseal region was also observed by Lindner and Migotto (2002). *Clytia linearis* is widely reported in both benthic habitats and in the open ocean on plankton, where, if the same species, it facultatively rafts and disperses as an epizooite on pteropods (Cornelius 1982, 1987).

Clytia linearis is one of two species represented in the JTMD hydroid fauna apparently acquired by tsunami objects south of the Boso Peninsula. While

Figure 5. *Laomedea flexuosa*:

(A) portion of stem with hydrothecae. RBCM 017-00016-004. Scale equals 500 μm .
 (B) basal chamber of hydrotheca. RBCM 017-00016-004. Scale equals 200 μm .
 (C) gonotheca. RBCM 017-00016-004. Scale equals 200 μm . Del. HHC Choong.



many of the other species considered here are regarded as wide ranging from lower-latitude warm climates to sub-boreal if not boreal waters, *C. linearis* is considered a species of warmer waters (Kirkendale and Calder 2003; Calder 2013). JTMD-BF-538, a Japanese vessel washing ashore in spring 2016 in southern Oregon, also had aboard warmer-water western Pacific bivalves, in addition to a typical colder-water fauna representative of the tsunami strike zone of the Tōhoku coast. Many JTMD objects were transported by coastal currents to southern Japan and the South China Sea and acquired species typical of warmer, southern waters, before being re-engaged by ocean currents and being swept north and east to North America (Carlton et al. 2017). Similarly, Boero et al. (2005) recorded the possible colonization and invasion of colder European waters by *C. linearis* as an alien species.

Distribution.—Japan (Yamada 1959; Hirohito 1995). Originally described from Papua New Guinea, it is widely reported from subtropical and tropical waters of the Atlantic, Pacific, and Indian Oceans (Kirkendale and Calder 2003; Calder 2013), and may thus also represent a species complex. Bouillon et al. (2004) suggested that *C. linearis* is a Lessepsian migrant into the Mediterranean through the Suez Canal.

Family Obeliidae Haeckel, 1879

***Laomedea flexuosa* Alder, 1857**

(Figure 5)

Laomedea flexuosa Alder 1857: 122.—Cornelius 1992: 97, figure 19 a–d.—Schuchert 2001: 154, figure 134 a–c.

Material.—Washington, on basket, living colonies with gonangia (JTMD-BF-465), RBCM 017-00016-004.

Description.—Colony erect, unbranched, approximately 2000 μm tall. Stems flexuose, internodes characteristically curved, stem internodes annulated proximally, 2–5 annulations. Perisarc of moderate thickness. Hydrothecae arise out of annulated pedicels given off from distal parts of internodes. Usually one pedicel per internode, very infrequently two, 3–10 or more annuli per pedicel, tapering distally. Central portion of pedicels sometimes smooth. Hydrothecae bell-shaped, perisarc sometimes slightly thickened asymmetrically. Hydrothecal rim entire. Diaphragm thin, transverse or slightly oblique. Gonothecae arising directly from stolon, internodes, or axils, carrot-shaped, truncated distally (♀?), or apex slightly rounded.

Distribution.—Widely reported from the North Atlantic, Arctic, and Europe, as well as from South Africa and New Zealand (Cornelius 1982; Schuchert 2001). Fraser (1944) recorded it from the Gulf of St. Lawrence. Very common intertidally in the Bay of Fundy, on fucoids (Calder 2017). Chaplygina (1992) reported the introduction of *L. flexuosa* to the Sea of Japan.

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

Sertularia dichotoma Linnaeus 1758: 812.

Obelia dichotoma.—Hincks 1868: 156, pl. 28, figure 1a–b.—Cornelius 1995b: 296, figure 69a–k.

Obelia alternata Fraser 1938: 35, pl. 8, figure 38a–b.

Material.—Oregon, on float, several pedicels with hydrothecae, without gonothecae (JTMD-BF-18), ROMIZ B4200; Oregon, on pallet, stem fragments, with gonothecae (JTMD-BF-24), ROMIZ B4190; Hawai‘i, on I-beam, stems arising from stolon, no hydrothecae or gonothecae (JTMD-BF-72), ROMIZ B4197; Washington, on post-and-beam wood, colony,

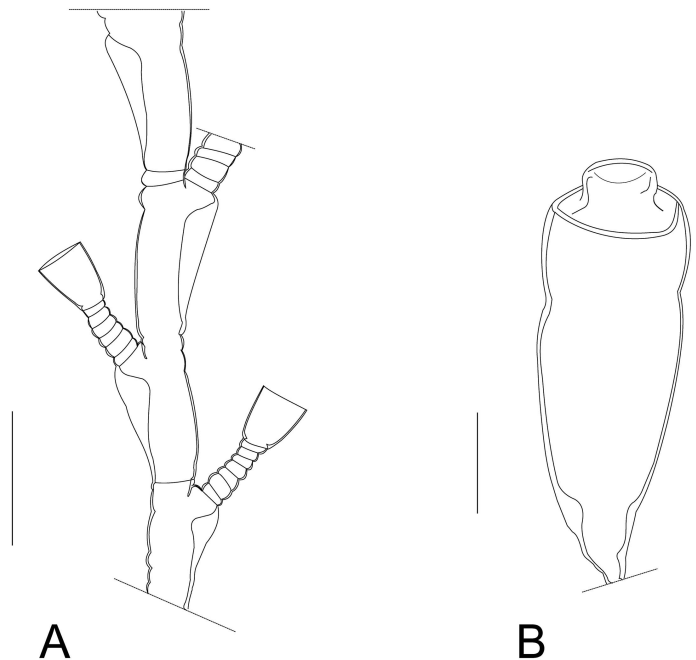


Figure 6. *Obelia geniculata*: (A) portion of stem with hydrothecae. ROMIZ B4181. Scale equals 500 μm . (B) gonotheca. ROMIZ B4181. Scale equals 200 μm . Del. HHC Choong.

no gonothecae (JTMD-BF-97), ROMIZ B4199; Washington, on vessel, stems, no gonothecae (JTMD-BF-131), ROMIZ B4185; Washington, on vessel, colonies covered by fouling, with remnants of coenosarc, without gonothecae (JTMD-BF-134), ROMIZ B4205; Oregon, on vessel, colony fragments, without gonothecae, likely dried out at some point, bryozoans *Scruparia ambigua* / *Aetea* Lamouroux, 1812 epizoic (JTMD-BF-202), ROMIZ B4191; Hawai'i, on vessel, dense colonies, without gonothecae (JTMD-BF-209), ROMIZ B4209; Washington, on tote, partially covered by *S. ambigua*, juvenile *Lepas* sp. also present, no gonothecae (JTMD-BF-464), RBCM 017-00016-002; Washington, colony without gonothecae, on crate (JTMD-BF-473) RBCM 017-00015-001; Japan, Minami-sanriku, Motoyoshi District, Miyagi Prefecture, Tōhoku Coast, August 2016, 3-month test panel, several hydrocauli, without gonothecae (MS-1) RBCM 017-00023-001.

Remarks.—*Obelia dichotoma* remains a problematic taxon due to a high degree of morphological variation in the characters used to delimit the species (Cornelius 1982, 1995b; Calder 2013). Nevertheless, although the non-monophyly of *O. dichotoma* remains problematic (Cunha et al. 2017), some widespread populations appear to be identical based upon nematocyst types and isoenzyme patterns (Östman 1982) and hydranth characters (Cornelius 1987). Despite intraspecific variability, branching pattern

and shape of the hydrothecal rim remain useful in delimiting hydroids attributed to the *O. dichotoma* species complex from its congeners such as *O. geniculata*, *O. longissima* and *O. griffini* (Kubota 1981, 1999; Calder et al. 2014) from Japanese waters. Specifically, we assigned our specimens to *O. dichotoma* based on the presence of hydrothecae with polyhedral margins, and with walls that are polygonal in cross-section, rather than round as in *O. griffini* (Cornelius 1995b; Calder et al. 2014). *Obelia dichotoma* is also less profusely branched than *O. griffini* (Fraser, 1914). Specimens referable to *O. dichotoma* also occurred on a test panel recovered from the Tōhoku Coast in August 2016 (RBCM 017-00023-001).

Distribution.—Japan, where it is the most widely distributed species of *Obelia* (Kubota 1999). A likely cosmopolitan species complex.

Obelia geniculata (Linnaeus, 1758) (Figure 6)

Sertularia geniculata Linnaeus 1758: 812.

Obelia geniculata.—Fraser 1937: 87, pl. 17, figure 89a–b.—Cornelius 1975b: 272, figure 5a–b.—Hirohito 1995: 76, figure 22a–b.

Material.—Washington, Misawa 3 dock, hydrocauli with coenosarc, with gonothecae (JTMD-BF-8), ROMIZ B4181; Washington, Misawa 3 dock, stems and colonies on *Lepas* sp., with gonothecae (JTMD-BF-8), ROMIZ B4188.

Description.—Colony arising from stolon. Hydrocaulus monosiphonic, flexuose, unbranched. Internodes short, curved, usually one annulation basally. Perisarc of internode greatly thickened on side where hydrothecal pedicel originates. Pedicels short, arising from shelf-like lateral processes, 2–5 annulations. Hydrothecae campanulate-to-bell-shaped, margin entire. Annular in apical view and hydrothecal perisarc slightly thickened. Gonothecae arising from axils of hydrothecae, on short pedicels, conical, tapering basally, with distal short, prominent collar.

Remarks.—The samples examined correspond with accounts of *Obelia geniculata* from Japan (Yamada 1958; Hirohito 1995; Kubota 1999) and elsewhere in having thickened perisarc of the stem, only one annulation between the internodes of the stem, and the lack of branching. Our samples contain remnants of coenosarc, but the gonothecae were empty, and the hydrothecal margins showed some damage from weathering the elements.

Distribution.—Japan (Hirohito 1995); nearly cosmopolitan in temperate to cold waters (Cornelius 1975b; Schuchert 2001).

Obelia griffini Calkins, 1899

Obelia griffini Calkins 1899: 357, pl. 4, figs. 18, 18A-C; pl. 6, fig. 18D.

Material.—Hawai'i, fragments of stem and one crushed hydrotheca, no gonothecae (JTMD-BF-21), ROMIZ B4202; Oregon, on pallet, colonies with gonophores (JTMD-BF-24), ROMIZ B4201; Oregon, on pallet, colony with gonothecae (JTMD-BF-24), ROMIZ B4203; Washington, on vessel, colony with gonothecae, *Scruparia ambigua* epizoic (JTMD-BF-40), ROMIZ B4173; Washington, on vessel, colony on pelagic crab *Plagusia* Latreille, 1804, no gonothecae (JTMD-BF-40), ROMIZ B4174; Washington, on vessel, several colonies, no gonothecae (JTMD-BF-40), ROMIZ B4176; Oregon, on vessel, colonies with gonophores (JTMD-BF-50), ROMIZ B4186; Washington, several hydrocauli arising from hydrorhiza, with perisarc, with gonotheca (JTMD-BF-97), ROMIZ B4198; Washington, on vessel, stem fragments, without gonothecae, *S. ambigua* epizoic (JTMD-BF-131), ROMIZ B4184; Washington, amidst fouling on vessel, fragments of hydrocauli with hydrothecae arising from hydrorhiza, without gonothecae (JTMD-BF-134), ROMIZ B4194; Washington, on vessel, colonies with perisarc and gonangia (JTMD-BF-170), ROMIZ B4189; Oregon, on buoy, colony with gonothecae (JTMD-BF-172), ROMIZ B4204; Washington, on vessel, stems arising from hydrorhiza, without hydrothecae or gonothecae, *S. ambigua* epizoic (JTMD-BF-223), ROMIZ B4193; Oregon, on helmet,

colony fragments, with gonothecae, likely dried out at some point (JTMD-BF-241), ROMIZ B4182; Washington, on pallet, several colonies, largely devoid of coenosarc, with gonothecae (JTMD-BF-338), ROMIZ B4150; Washington, on basket, colony with gonothecae, *S. ambigua* epizoic (JTMD-BF-343), RBCM 017-00011-002; Washington, Long Beach, on cap, weathered, empty colonies, stems and branches only, hydrothecae missing, with gonothecae (JTMD-BF-370), ROMIZ B4149; California, on crate, 2 colonies with gonothecae (JTMD-BF-382), ROMIZ B4158; Washington, on vessel, hydrocauli arising from hydrorhiza, with coenosarc, with gonophores, *S. ambigua* epizoic (JTMD-BF-402), ROMIZ B4154.

Remarks.—Following our previous study, we retain *O. griffini* as distinct from generally considered conspecific species such as *O. dichotoma*. *Obelia surcularis* Calkins, 1899 and *O. gracilis* Calkins, 1899 are simultaneous synonyms, with nomenclatural priority having been assigned to the binomen *O. griffini* (see Calder et al. 2014 for discussion and description).

Obelia griffini was found on three of four stranded objects sampled in our previous study (Calder et al. 2014). It is also the most common *Obelia* species found in the present study, and the most abundant hydroid in the JTMD material.

Distribution.—North Pacific Ocean (see discussion, below).

Obelia longissima (Pallas, 1766)

Sertularia longissima Pallas 1766: 119.

Material.—Oregon, on pallet, stem fragments, one hydrotheca (flattened), without gonothecae (JTMD-BF-24), ROMIZ B4187; Washington, on vessel, *Scruparia ambigua* epizoic, no gonothecae (JTMD-BF-40), ROMIZ B4177; Oregon, on vessel, colonies with gonothecae, *S. ambigua* epizoic (JTMD-BF-43), ROMIZ B4207; Oregon, on vessel, colony fragment, without gonothecae (JTMD-BF-58), ROMIZ B4183; Washington, on tote, dried stems and branches, no gonothecae (JTMD-BF-374), ROMIZ B4169; Washington, on tote, dried stems and branches (JTMD-BF-380), ROMIZ B4171; California, on crate, on mussel *Mytilus galloprovincialis*, with remnants of coenosarc, with gonothecae (JTMD-BF-382), ROMIZ B4161; Washington, on basket, stems with few hydrothecae, no gonothecae, likely dried out previously (JTMD-BF-405), ROMIZ B4159; Washington, weathered colony, primarily stems, with few hydrothecae, likely dried out, no gonothecae (JTMD-BF-406), ROMIZ B4172.

Remarks.—Our samples correspond morphologically with *Obelia longissima*, previously reported as originating from Japan (Calder et al. 2014). As in the

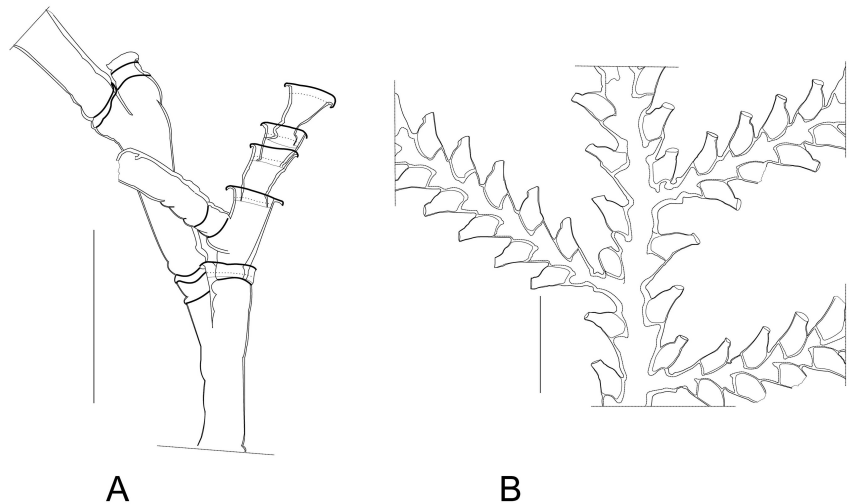


Figure 7. (A) *Halecium delicatulum*: portion of stem and hydrothecae. ROMIZ B4104. Scale equals 500 μm . (B) *Abietinaria inconstans*: section of hydrocaulus and side-branches. ROMIZ B4106. Scale equals 1000 μm . Del. HHC Choong.

previous study, the colonies are also weathered and contain empty gonothecae, indicating that the colonies had persisted on the debris for extended periods.

Distribution.—*Obelia longissima* is a cosmopolitan species, and although more widespread in the Atlantic (Vervoort 1972; Cornelius 1995b; Schuchert 2001), is amph-Pacific in distribution (Fraser 1937; Calder 1970; Park 1990). Hydromedusae of *O. longissima* have been reported from the northwest Sea of Japan (Dautova and Petrova 2010).

Family Haleciidae Hincks, 1868

***Halecium delicatulum* Coughtrey, 1876**

(Figure 7A)

Halecium delicatula Coughtrey 1876: 299.

Halecium flexile var. *japonica* Leloup 1938: 4, figure 1.

Halecium delicatulum.—Ralph 1958: 334, figure 11e, h–n.—Hirohito 1995: 20, figure 5a–c.

Material.—Washington, on vessel, monosiphonic colony, no gonothecae, *Scruparia ambigua* epizoic (JTMD-BF-339), ROMIZ B4104.

Description.—Colony monosiphonic, stolon tubular, creeping, tangled. Hydrocaulus cylindrical, erect, somewhat flexuous, branched. Internodes corrugated, 1–2 oblique twists basally, 1–2 corrugations above each node. Alternate nodes twisted obliquely in opposite directions. Perisarc moderately thickened. Primary hydrophores alternate, length variable, not constricted or delimited by node. Up to four hydrophores in linear series, length of hydrophores as in primary one or longer. Hydrothecae gradually widening, rim everted or rolled, no reduplication, ring of desmocytes below rim, diaphragm distinct.

Occasionally thickening of perisarc below diaphragm, especially on adcauline side, forming pseudodiaphragm. Gonothecae not present.

Remarks.—Although gonothecae are absent, the trophosomes in our material correspond most closely with accounts of *Halecium delicatulum* from Japan (Hirohito 1995) and elsewhere in having erect monosiphonic stems, irregular branching, oblique nodes twisted in opposite directions on successive internodes, and hydrothecal margins everted. Additionally, in our material, the primary hydrophore is short or almost sessile, with the hydrothecal rim very close to touching the internode supported by the apophysis of the hydrophore-bearing internode. Although variable, the length of the primary hydrophores and the strongly everted hydrothecal rim primarily characterize *H. delicatulum* (Vervoort and Watson 2003). A pseudodiaphragm was observed in several hydrothecae (Leloup 1938, as *Halecium flexile* var. *japonica*; Ralph 1958; Hirohito 1995). Hirohito (1995) reported both monosiphonic and polysiphonic colonies from Japan.

The vessel on which *H. delicatulum* was found also bore a southern species of open ocean, neustonic bryozoan, *Jellyella eburnea*, indicating that this raft passed through lower latitude waters in the North Pacific before arriving in Washington (McCuller and Carlton 2018).

Distribution.—Japan (Hirohito 1995); considered circumglobal in tropical, subtropical and boreal waters (Vervoort and Watson 2003). Described originally from Dunedin harbor, New Zealand, it may be introduced to the southwest Pacific (Hewitt et al. 2004), or may represent a global species complex (Schuchert 2005; Galea et al. 2014).

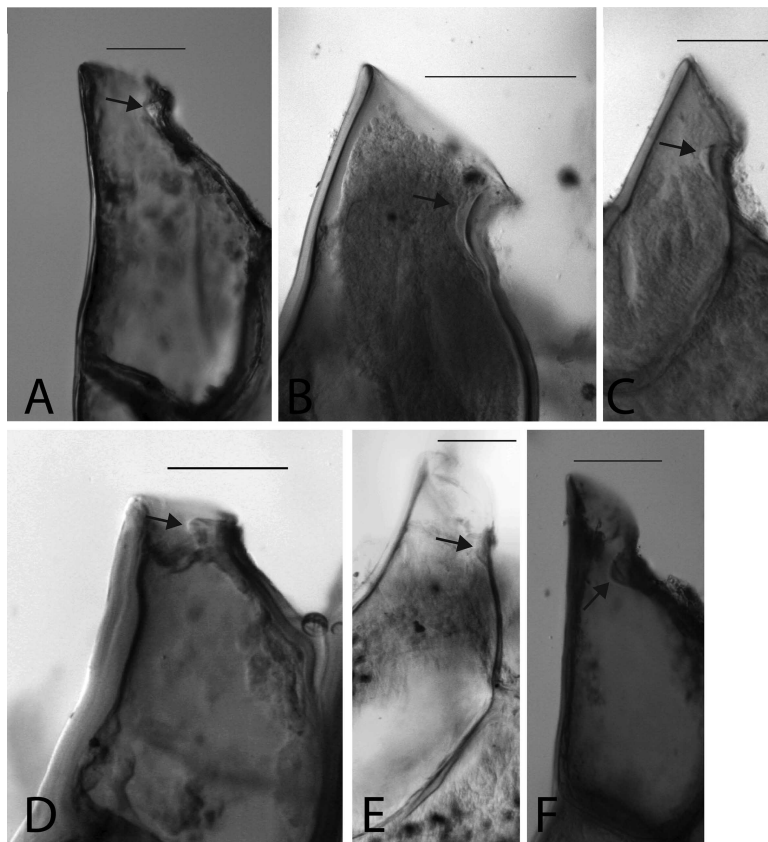


Figure 8. Submarginal intrathecal projection in hydrotheca of *Abietinaria* spp.: (A) *A. inconstans*. ROMIZ B4106. Scale equals 100 μ m. (B) *A. abietina*. BCPM 976-515-1. Scale equals 200 μ m. (C) *A. anguina*. BCPM 976-520-1. Scale equals 100 μ m. (D) *A. inconstans*. BCPM 976-530-1. Scale equals 100 μ m. (E) *A. amphora*. BCPM 976-519-1. Scale equals 100 μ m. (F) *A. costata*. BCPM 976-521-1. Scale equals 100 μ m. Photomicrographs by HHC Choong.

Family Sertulariidae Lamouroux, 1812

***Abietinaria inconstans* (Clark, 1877)**

(Figure 7B, 8A)

Sertularia inconstans Clark 1877: 222, pl. 15, figures 51–52.
Thuiaria costata Nutting 1901: 187, pl. 26, figures 4–9.
Abietinaria inconstans.—Nutting 1904: 116, pl. 33, figures 1–2.—
 Fraser 1937: 133, pl. 29, figure 153a–c.

Material.—Washington, on buoy, section of hydrocaulus with hydrocladia, without gonothecae, *Symplectoscyphus tricuspидatus* (Alder, 1856) epizoic (JTMD-BF-342), ROMIZ B4106.

Description.—Colony imperfectly pinnate, main stem straight. Basal-most portion of stem deeply annulated. Main branches secondarily unbranched, alternate, coplanar, pointing laterally and upwards at angles between 45–75 degrees, Wide angles proximally, more acute distally, one or two internodes between successive branches, 3–4 hydrothecae between branches on same side of stem. Perisarc of stem thickened. Base of branches with 1–2 spiral twists. Internode length variable. Cauline nodes with single constriction. Perisarc of branches slightly thickened. Axillary hydrothecae present. Hydrothecae flask-shaped, 1/3–1/2 adnate, swollen basally, perisarc of

adaxial wall of basal part of hydrothecae forming chitinous projection downwards at junction with hydrothecal base. Distal portion of hydrothecae gradually narrowing towards aperture, flattening somewhat on adcauline side, forming pronounced neck. Aperture oval, facing upwards, occasionally forming indistinct gutter on adaxial side. Submarginal intrathecal projection occasionally present on adaxial side of hydrothecae. Gonothecae not present.

Remarks.—We follow Ansulevich's concept of the species, and include *A. amphora* and *A. costata* in the synonymy of *A. inconstans*. Ansulevich (1987) considered *A. inconstans* to be identical to *A. costata* Nutting (= *Thuiaria costata* Nutting, 1901), and *A. amphora* Nutting, 1904 based upon similarities in colony form, structure of the hydrothecae and gonothecae, as well as geographical distribution. Nutting noted similarities between the hydrothecae of *A. inconstans* and *A. costata*, including the presence of an abcauline, sub-marginal intrathecal projection in *A. inconstans* (Nutting 1901, 1904), but kept the two species separate based on trophosomal differences (*A. inconstans* being less robust), and the gonosome (greater variation in *A. inconstans*, although he did not examine the gonothecae). Ansulevich (1987)

provided a diagnosis for the gonothecae of *A. costata* and its congeners: gonothecae oval, short neck, small pedicel; aperture circular, without cusps or internal projections; gonothecal wall wavy, 4–6 longitudinal ribs; gonothecae may be irregular due to deformation, without the neck, and underdeveloped or curved ribs. According to Antsulevich, the variability in the gonosome of *A. inconstans* is due to deformation when the gonothecae are densely packed.

Neither Nutting (1904) nor Fraser (1937) noted the presence of an adcauline, sub-marginal intrathecal projection in *A. amphora*, but it is present in Fraser's specimen of *A. amphora* (BCPM976-519-1) examined by one of us (HHCC). This submarginal projection is also present in specimens of *A. abietina* (Linnaeus, 1758) (BCPM 976-515-1) and *A. anguina* (Trask, 1857) (BCPM 976-520-1) examined here, as well as *A. pacifica* Stechow, 1923. However, the shape of the projection differs in being long and narrow in *A. abietina* (Figure 8B), and rounded in *A. anguina* (Figure 8C) while it is more triangular in our specimen (ROMIZ B4106) (Figure 8A), and Fraser's other specimens of *A. inconstans* (BCPM 976-530-1) (Figure 8D), *A. amphora* (BCPM 976-519-1) (Figure 8E), and *A. costata* (BCPM 976-521-1) (Figure 8F). Stechow (1923) and Fraser (1937) did not illustrate the adcauline submarginal projection in *A. pacifica*.

Distribution.—Reported by Kostina and Tsurpalo (2016) from the South Kurile Islands bordering northern Japan, and by Stepanjants (2013) in Japanese waters. Widespread along the North American coast from Alaska to Mexico (Mills et al. 2007).

Amphisbetia furcata (Trask, 1857)

Sertularia furcata Trask 1857: 101, pl. 5, figure 2a–e.—Fraser 1937: 162, pl. 37, figure 195a–e.

Material.—Washington, on vessel, two fragments of stems arising from stolon, without gonothecae (JTMD-BF-40), ROMIZ B4094; Washington, on tray, hydrocauli, with gonothecae (JTMD-BF-328), ROMIZ B4140; Hawai'i, on vessel, colony on *Lepas* sp., with gonothecae (JTMD-BF-329), ROMIZ B4103; Washington, on buoy, colonies on young *Lepas* sp., with gonothecae (JTMD-BF-386), ROMIZ B4108; Washington, on float, scraped from colony growing on mussel *Mytilus galloprovincialis* shell, fragments of hydrocauli arising from stolon, no gonothecae (JTMD-BF-609), RBCM017-00017-001.

Remarks.—The occurrence of *Amphisbetia furcata* originating in Japan was discussed in our previous study (Calder et al. 2014). We follow Antsulevich (1987) in regarding *A. furcata* originally described from San Francisco Bay, California, and *A. pacifica* Stechow, 1931, type locality Mutsu Bay, Japan, as

conspecific. Yamada (1959) distinguished *A. pacifica* from *A. furcata* by the presence of two distinct spiral constrictions at the base of the stem, and in having gonothecae which are not globular but elongated-oval with indistinct shoulders. However, illustrations of *A. furcata* from California by Torrey (1902) and of *A. pacifica* from Japan by Hirohito (1995) show that the gonothecae of both putative species to be very similar, and correspond to those present in our material. The spiral twists at the base of the stem described by Yamada are clearly visible in Fraser's specimen of *A. furcata* (BCPM 976-652-1) (Fraser 1937 as *Sertularia furcata*) examined by one of us (HHCC) as well as in our material.

Distribution.—Kurile Islands to the Sea of Japan, Japan, and Yellow Sea (Antsulevich 2011); in north-east Pacific from British Columbia to Ecuador (Fraser 1937, 1946).

Family Symplectoscyphidae Maronna et al., 2016

Symplectoscyphus tricuspoidatus (Alder, 1856)

Sertularia tricuspoidata Alder 1856: 356, pl. 13, figures 1–2.
Sertularella tricuspoidata.—Fraser 1937: 159, pl. 36, figure 191a–c.

Material.—Washington, on buoy, fragment of colony epizoic on hydrocaulus and branch of *Abietinaria inconstans*, without gonothecae (JTMD-BF-342), ROMIZ B4106.

Description.—Stolon creeping, hydrocaulus arising from stolon, bearing two hydrothecae, two transverse annuli on basal part of hydrocaulus. Second hydrotheca arising on transverse plane to first hydrotheca on oblique annulation. Stolon tubular, robust, perisarc slightly thickened. One end of stolon branched dichotomously, bearing solitary, deformed hydrothecae arising directly from each branch. Hydrothecae on hydrocaulus tubular, slightly tumid at base, smooth walled, 2–3 times longer than wide. Abcauline side of hydrothecae forming continuous curve with hydrocaulus. Hydrothecal aperture with three prominent, equal-sized cusps, deeply emarginated between cusps. Margin of aperture flared, single renovation visible on one hydrotheca. Hydrothecal perisarc very slightly thickened. Gonothecae not present.

Remarks.—Our sample is an epizoan with creeping stolon on *Abietinaria inconstans*. Second-level epizoic hydroids are facultative epizoites, and have been observed as creeping colonies with solitary zooids in contrast to their usual erect colony structure (Orlov 1997). Although the colonial structure exhibits great plasticity, the hydrothecae observed in our material correspond with accounts of *Symplectoscyphus tricuspoidatus* by Fraser (1937), Cornelius (1979), and Hirohito (1995).

Distribution.—Circumpolar in distribution in Arctic to northern boreal waters (Broch 1918; Naumov 1960; Cornelius 1979). Northeast Pacific from Alaska to San Diego (Fraser, 1937 as *Sertularella tricuspidata*) and Japan (Yamada 1950; Hirohito 1995).

Family Aglaopheniidae Lamouroux, 1812

***Aglaophenia* aff. *pluma* (Linnaeus, 1758)**
(Figure 9A, 10A, 10B)

Aglaophenia pluma.—Fraser 1937: 179, pl. 41, figure 217 a–c.—Svoboda and Cornelius 1991: 30, figures 10–24.

Material.—Washington, on vessel, plumes with corbulae (JTMD-BF-532), RBCM 017-00019-001; Washington, on vessel, colonies with corbulae (JTMD-BF-532), RBCM 017-00019-002; Hawai'i, on rope and buoy mass, colonies with corbulae (JTMD-BF-667), ROMIZ B4233.

Description.—Colony unbranched, reaching 41 mm tall. Two cauline nematothecae and one abortive hydrotheca on each stem internode. Hydrotheca cup-shaped, 9 cusps of varied length, outermost longest. Median cusp sharp, straight or recurved, angled towards adaxial side. Intrathecal ridge present but not developed into intrathecal septum dividing hydrotheca. Supracalycine nematothecae extending past hydrothecal margin, covering adaxial-most cusps in side-view. Hydrothecal length/breadth ratio 1.7–1.9. Mesial nematotheca large, adaxial wall arising from upper third of hydrotheca, not reaching its margin. Free part approximately 88 μm , gutter-shaped, not tubular, foramen to hydrotheca visible. Corbula three times longer than height, with one basal hydrotheca, 9–15 pairs of unfused ribs, with narrow openings in between.

Remarks.—Identification of *Aglaophenia* aff. *pluma* is difficult due to the lack of specific diagnostic characters (Cornelius 1995a), and 16S rRNA analyses of north-east Atlantic and west Mediterranean specimens strongly suggests that *A. pluma* is likely a species complex including *A. pluma*, *A. tubiformis* Marktanner-Turneretscher, 1890, and *A. octodonta* Heller, 1868 (Leclère et al. 2009; Moura et al. 2012). These three species show extremely low levels of 16S sequence divergence, and probably reflect intra-specific variation, with the name *A. pluma* having priority (Moura et al. 2008). *Aglaophenia tubiformis* was recorded in the eastern Atlantic and the Mediterranean Sea and *A. octodonta* from the Mediterranean and adjacent Atlantic (Svoboda and Cornelius 1991). Assessment of the true distribution is difficult (Cornelius 1995b). Our material closely corresponds with Fraser's specimen from England (BCPM 976-797-1) and the descriptions of *A. pluma* by Cornelius (1995b), Fraser (1937), and Svoboda and

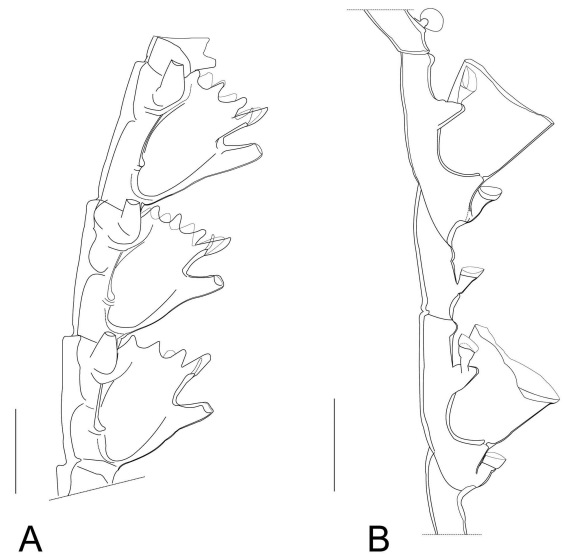


Figure 9. (A) *Aglaophenia* aff. *pluma*: portion of cladium showing three cormidia. RBCM 017-00019-002. Scale equals 200 μm . (B) *Antennella* sp.: section of stem. ROMIZ B4105. Scale equals 200 μm . Del. HHC Choong.

Cornelius (1991). The number of leaves reported in the corbulae of *A. pluma* is quite varied, ranging from nine in Fraser (1937) to 5–10 (or more) by Svoboda and Cornelius (1991). Corbulae in our samples varied in length within a colony, from 9–15 leaves (Figure 10).

Distribution.—*Aglaophenia pluma* was reported from Japan as *A. pluma* var. *dichotoma* M. Sars, 1857 (Rees and Thurfield 1965); the variety was included in *A. pluma* by Svoboda and Cornelius (1991). Fraser (1946) noted records from Vancouver Island and Mexico, both of which would require confirmation. The true distribution of this European boreal species remains unclear, as reliable records from elsewhere have yet to be confirmed (Svoboda and Cornelius 1991).

Family Halopterididae Millard, 1962

***Antennella* sp.**
(Figure 9B)

Material.—Oregon, on vessel, colony arising from hydrorhiza, without gonothecae (JTMD-BF-210), RBCM 017-00007-001; Washington, on buoy, colony arising from hydrorhiza, without gonothecae (JTMD-BF-341), ROMIZ B4105.

Description.—Unbranched, erect, monosiphonic stem arising directly from anastomosing hydrorhiza, individual hydrocauli < 10 mm long. Segmentation heteromerous; alternating transverse and oblique nodes. Basal part of stem divided into segments (two or more) divided by transverse nodes, distal-most segment with

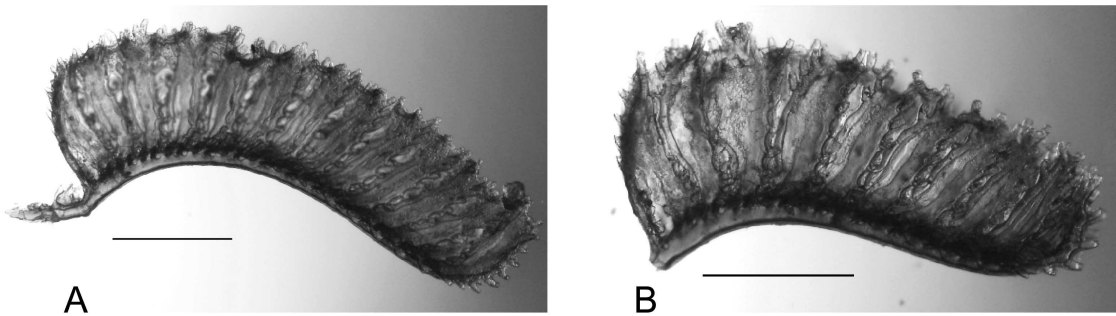


Figure 10. (A) *Aglaophenia* aff. *pluma*: corbula. RBCM 017-00019-002. Scale equals 1000 μm . (B) another corbula from same colony. RBCM 017-00019-002. Scale equals 1000 μm . Photomicrographs by HHC Choong.

oblique node. Hydrothecate and ahydrothecate internodes present. Hydrothecae confined to middle part of internodes, cup-shaped, abcauline wall straight in side view, rim even, hydrothecal opening approximately 50° with main axis, adcauline side adnate for approximately $1/3$ its length. Hydrotheca surrounded by three nematothecae: one median inferior, conical with rim of upper chamber lowered adaxially, outer side often reaching or exceeding hydrothecal base; and two laterals, placed on short apophyses, one on each side of hydrothecal aperture, not fused to hydrotheca, not reaching hydrothecal margin, two-chambered, conical with inner side lowered. No axillar nematothecae. Ahydrothecate internodes with one median nematotheca. Gonothecae not present.

Remarks.—In having no axillar nematothecae behind the free adcauline wall of the hydrothecae, our species differs from other Japanese species such as *A. quadriaurita* Ritchie, 1909 (= *A. variabilis* Fraser, 1936 from Japan, which also has two pairs of lateral nematothecae); *A. varians* (Billard, 1911), with two pairs of lateral nematothecae and regular absence of median inferior nematothecae; or *A. secundaria* (Gmelin, 1791), with median nematothecae on the upper part of the oblique node. *Antennella avalonia* Torrey, 1902 reported from the west coast of North America by Fraser (1946) is likely conspecific with *A. secundaria* (Calder 1997; Schuchert 1997), although it is currently accepted as valid in WoRMS. Our samples were mostly devoid of coenosarc and appeared weathered.

Halopteris aff. *campanula* (Busk, 1852)

(Figure 11)

Material.—Washington, on vessel, sections of branched hydrocauli with hydrocladia, and fragments of hydrocauli, with gonothecae (JTMD-BF-449), RBCM 017-00008-001.

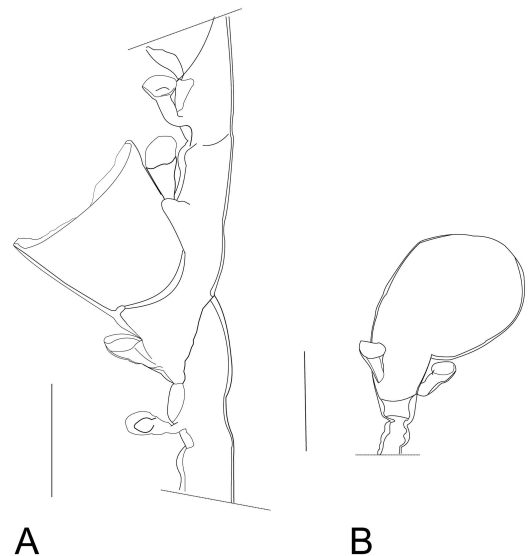


Figure 11. *Halopteris* aff. *campanula*: (A) section of hydrocladium. RBCM 017-00008-001. Scale equals 200 μm . (B) gonotheca. RBCM 017-00008-001. Scale equals 200 μm . Del. HHC Choong.

Description.—Cormoids pinnate. Hydrocladia homomerously segmented. Internodes with hydrocladia alternate left and right. Perisarc of hydrocaulus and hydrocladia slightly thickened, particularly around nodes. Each internode with one hydrotheca and its 3–4 nematothecae: one median inferior, not reaching hydrotheca, two laterals placed on short apophyses, one on each side of the hydrothecal aperture, short, two-chambered, adaxial wall of upper chamber reduced, not reaching hydrothecal margin; occasionally one superior nematotheca on separate intersegment in distal part of caulus. Apophysis of hydrocladial insertion indistinct, without nematothecae. First node of hydrocladium without hydrotheca but with one nematotheca, proximal node transverse,

distal node oblique. Hydrotheca cup-shaped, rim even, slightly flaring, reaching much higher than lateral nematothecae, adaxial and abaxial walls straight in side view, 1/3–1/2 of adaxial wall adnate. Perisarc of abaxial wall slightly thickened. Hydrothecal aperture approximately 50° with main axis. Gonothecae pear-shaped, approximately 500 µm long (♀?), flattened laterally, arising from base of hydrothecae, two nematothecae on basal part, on pedicel with two sometimes, quadrangular segments separated by somewhat oblique nodes.

Remarks.—Due to the fragmentary nature of the sample, we consider our identification as tentative, pending further analysis. The available trophosome and gonothecae of this hydroid generally correspond in morphology with accounts of *Halopteris campanula* by Hirohito (1995) and Schuchert (1997) in the number and position of the nematothecae, shape and position of the gonothecae and associated pedicel, hydrothecal shape and thickening of the abaxial wall of the hydrotheca. However, it differs in the following respects: the outer wall of the lateral nematothecae lacks the distinct emargination over half its height (spanner-type) as described in Schuchert (1997), i.e., the apical chamber is conical, not globular; the gonothecae are slightly smaller in our material than in Schuchert (1997) at 900 µm. We are unable to determine if the branched colony is polysiphonic from the available material.

Distribution.—Japan: Sagami Bay south to Kagoshima Prefecture (Hirohito 1995); widespread through the Indo-West Pacific to the Red Sea, as well as Australia and New Zealand (Schuchert 1997). As JTMD-BF-449 did not have otherwise a clear signature of warmer-water, southern species, this vessel may have proceeded along slightly south of the Boso Peninsula in order to acquire this hydroid, which has not yet been reported from the Tōhoku coast.

Family Plumulariidae McCrady, 1859

***Plumularia caliculata* Bale, 1888**

Plumularia caliculata Bale 1888: 780, pl. 20, figures 9, 10.—Hirohito 1995: 271, figure 92a–e.

Plumularia sp. Calder et al. 2014: 434, figures 5e–f.

Material.—Washington, on vessel, colony fragment, remnants of coenosarc in hydrothecae and nematothecae, no gonothecae (JTMD-BF-40), ROMIZ B4234; Oregon, on vessel, several broken plumes attached to hydrotheca, without gonangia (JTMD-BF-533), RBCM 017-00021-002.

Remarks.—This material corresponds in morphology to the specimen examined previously (Calder et al. 2014: 434, figures 5e–f) through its hydrothecae with a convex abaxial wall, which distinguishes it from *P. setacea* (Linnaeus, 1758). In *P. setacea* the

abcauline wall is straight or occasionally curved inward in the middle, never curved outwards (Schuchert 2013). Although the previous specimen could not be differentiated with certainty from *Plumularia lagenifera* Allman, 1885 due to its condition and the lack of gonothecae, the substrate and collection date of that sample (the floating dock from Misawa, Honshu, Japan, JTMD-BF-1, 05 June 2012) pointed to *P. caliculata* of Japanese origin. The present material also supports the identification of this species as *P. caliculata*; in the cauline internodes in our samples we observed two nematothecae associated with the apophysis bearing the hydrocladium. While apophyses with two nematothecae were observed occasionally in northeastern Pacific and Atlantic *P. setacea*, this character seems to be invariable in *P. lagenifera* in the northeastern Pacific (one nematotheca only) (Schuchert 2013). As our specimens possess hydrothecae with inwardly curved abaxial wall and two apophyseal nematothecae were observed, we assign them to *P. caliculata*.

Distribution.—Australia, its type locality; Japan, and likely Korea (Calder et al. 2014).

***Plumularia setacea* (Linnaeus, 1758)**

Sertularia setacea Linnaeus 1758: 813.

Material.—Hawai'i, on buoy, remnants of hydrotheca, several cormoids with hydrocauli and several hydrocladia, without gonothecae (JTMD-BF-144), ROMIZ B4100; Oregon, on vessel, several plumes, with gonangia, *Scruparia ambigua* epizoid (JTMD-BF-356), RBCM 017-00012-001; Oregon, on vessel, several plumes, with coenosarc and gonangia, partially covered by *S. ambigua* (JTMD-BF-356), RBCM 017-00020-001; Washington, on float, several plumes, with male and female gonangia (JTMD-BF-462), RBCM 017-00009-001; Oregon, on buoy, several plumes, with gonangia (JTMD-BF-531), RBCM 017-00018-001; Oregon, on vessel, several weathered and broken plumes, without gonangia, (JTMD-BF-533), RBCM017-00021-001.

Remarks.—In our previous study (Calder et al. 2014) we reported *Plumularia setacea* from JTMD. The present material also corresponds morphologically to other accounts of *P. setacea* in having a straight outer wall of the hydrotheca, one nematotheca associated with the apophysis bearing the hydrocladium, and a nematotheca on the ahydrothecate internode of the hydrocladia, as well as nematothecae on the internodes of the hydrocaulus (Calder 1997; Schuchert 2013). Gonothecae were observed arising from apophyses via short pedicels, fusiform in shape. Both male and female gonothecae are present. Our material was in good condition, with

a significant amount of coenosarc present, partially overgrown by the bryozoan *Scruparia ambigua*.

Distribution.—Japan (Hirohito 1995); Pacific coast of North America from Alaska to southern California (Fraser 1937), and reported from all oceans; almost certainly a species complex (Mills et al. 2007; Schuchert 2014).

Family Phylactothecidae Stechow, 1921

Diagnosis (emended) and Systematic Discussion.—Colonies stolonial or erect, arising from creeping hydrorhiza; hydrocauli monosiphonic or polysiphonic; hydrothecae shallow to bell-shaped, sessile or pedicellate, basal region with delicate diaphragm, with or without desmocytes; hydranths usually much larger than hydrothecae, with or without an intertentacular web. Nematophores present, with variably reduced nematothecae. Gonophores fixed sporosacs; gonothecae solitary or aggregated to form a glomulus.

Watson (1969) noted the need for revision of nominal genera of nematophore-bearing hydroids in Haleciidae, which was reiterated by Cornelius (1975a) who recognized the arbitrary nature of the limits of these genera. The inclusion of the genus *Hydrodendron* Hincks, 1874 within the family Haleciidae is indeed problematic, as shown by phylogenetic analysis using 16S as well as combined 16S, 18S, and 28S rRNA data; *Hydrodendron* shows a marked divergence from the *Halecium* species studied (Moura et al. 2008; Leclère et al. 2009; Maronna et al. 2016). Rees and Vervoort (1987) had previously noted the usefulness of gonosomal characters in separating *Hydrodendron* from *Halecium*. *Hydrodendron mirabile* shares the presence of nematophores and nematothecae with Plumularioidea. Maronna et al. (2016) proposed the taxon Plumupheniida (which includes the families within Plumularioidea) to accommodate *H. mirabile*. There is some support for the inclusion of *Hydrodendron* within Plumularioidea, suggesting that the presence of nematothecae in Plumularioidea and *Hydrodendron* is not due to convergence, and that defensive polyps (dactylozoids) were acquired only once within Macrocolonia in the ancestor of Plumularioidea (Leclère et al. 2009). Nematophore-bearing haleciid species were included under *Hydrodendron*, *Ophiodissa* Stechow, 1919 and *Phylactotheca* Stechow, 1913 (the latter two currently included as synonyms of *Hydrodendron*) to accommodate forms having shallow to deeply campanulate hydrophores (Watson 1969). We propose that Phylactothecinae Stechow, 1921 be elevated to full family rank, and that *Hydrodendron mirabile* and its congeners are included in the family Phylactothecidae Stechow, 1921 within the superfamily Plumularioidea.

While the family name Hydrodendriidae (see Nutting 1905) exists, it is based on the genus *Hydrodendrium* Nutting, 1905. *Phylactotheca* is the type genus of the subfamily Phylactothecinae. The name is currently included as a synonym of Haleciidae, but from the evidence in Maronna et al. (2016), outlined above, this synonymy is incorrect. Although its type genus (*Phylactotheca*) is a junior subjective synonym of *Hydrodendron*, the name is not thereby invalidated under the code (ICZN Art. 40.1). Under the Principle of Coordination in nomenclature, Stechow (1921) is credited as author of the family name as well as the subfamily name. Further analysis which includes the other species of *Hydrodendron*, and especially its type species *H. gorgonoide* (G.O. Sars, 1874), is required to clarify the taxonomic position of *H. mirabile* and its congeners, but clearly *Hydrodendron* is shown to be remote from Haleciidae and merits assignment to its own family.

Hydrodendron mirabile (Hincks, 1866) (Figure 12)

Ophiodes mirabilis Hincks 1866: 422, pl. 14, figures. 1–5.

Material.—Washington, colony with some coenosarc remaining, amidst fouling, without gonothecae (JTMD-BF-402), ROMIZ B4110; Washington, no gonothecae, *Scruparia ambigua* epizoic (JTMD-BF-402), ROMIZ B4109; Washington, on vessel, colony with remnants of hydranths and coenosarc present, amidst fouling, without gonothecae (JTMD-BF-402), ROMIZ B4155; Washington, colony with some coenosarc remaining, amidst bryozoan *Aetea* sp., amphipod *Jassa marmorata* Holmes, 1905, and algal colonies, without gonothecae (JTMD-BF-402), ROMIZ B4170; Washington, hydrocauli arising from hydrorhiza, with coenosarc, without gonothecae, *S. ambigua* epizoic (JTMD-BF-402), ROMIZ B4235.

Description.—Hydrorhiza stolonial, irregularly branched. Stolon wrinkled, perisarc moderately thickened, occasionally projecting internally. Stem segmented, monosiphonic or loosely fasciated at base, irregularly branched; perisarc of stem and branches thickened. Internodes smooth or with one basal wrinkle. Hydrotheca borne on long internode process, shallow, widening moderately towards hydrothecal opening.

Occasionally secondary hydrophores present. Hydrothecal rim entire, often everted, no reduplication; perisarc slightly thickened, but not as thick as in stems and branches. Desmocytes large, refringent, about middle of hydrotheca. Nematothecae sessile, dispersed, often on node processes, occasionally on stolon, large, cone-shaped, margin flared; conspicuous, irregular refringent ring of desmocytes on upper third. Nematophore long, filiform. No gonothecae.

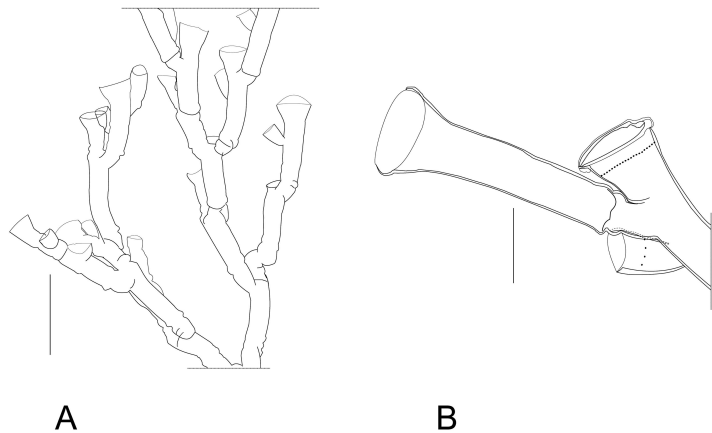


Figure 12. *Hyrodendron mirabile*: (A) part of colony. ROMIZ B4155. Scale equals 500 μm . (B) hydrothecae. ROMIZ B4155. Scale equals 200 μm . Del. HHC Choong.

Table 2. Trophosomal dimensions of *Hyrodendron mirabile* compared to JTMD specimen BF-402 (ROMIZ B4155).

	<i>Hyrodendron mirabile</i> (in Cornelius 1995b)	<i>Hyrodendron mirabile</i> (in Preker and Lawn 2010)	<i>Hyrodendron mirabile</i> (in Hirohito 1995)	<i>Hyrodendron mirabile</i> (in Millard 1975, as <i>H. caciniiformis</i>)	JTMD-BF-402 (ROMIZ B4155)
Colony height	20–50 mm (small colonies stolonal, large colonies polysiphonic basally)	5.1 mm (small colonies, stolonal or erect)	> 10 mm (stolonal, larger colonies polysiphonic basally)	> 10 mm	~ 10 mm (polysiphonic basally)
Hydrotheca height	40–120 μm	95–130 μm	160–320 μm	50–120 μm	104–125 μm
Hydrothecal width at rim	150–250 μm	220–240 μm	190–220 μm	140–200 μm	199–234 μm
Hydrothecal width at base	90–230 μm	Not provided	Not provided	Not provided	120–150 μm
Nematotheca length	20–200 μm	128–136 μm	120–170 μm	Not provided	142–149 μm
Nematotheca width (at rim unless stated otherwise)	60–90 μm (maximum width only; width at rim not given)	40–120 μm	60–100 μm (given as width)	Not provided	69–100 μm
Internode length	370–750 μm	480–760 μm	Not given	Not given	253–694 μm

Remarks.—The trophosome of our material agrees with accounts of *Hyrodendron mirabile* by Cornelius (1995b), Hirohito (1995), and Preker and Lawn (2010). The adcauline peridermal thickening or pseudo-diaphragm, sometimes present near the base of the hydrophore in *H. caciniiformis* (Hincks, 1866) (now reduced to a synonym of the present species; see Cornelius 1975a) observed by Millard (1975) and Vervoort (1959), was not mentioned by Hirohito (1995) in *H. mirabile* from Japan, nor was it observed in our samples. Cornelius (1975a, 1995b) considered larger colonies (in growth length) of *H. caciniiformis* (= *O. caciniiformis*) to be due to intra-specific population variation. Size comparisons of some characters of *H. mirabile* given in various accounts are summarized in Table 2. Our material corresponds to that of Hirohito (1995) in general dimensions, and in

the occasional presence of secondary hydrophores. No gonothecae were seen in our material.

Distribution.—Japan (Hirohito 1995). *Hyrodendron mirabile* has been reported circumglobally from tropical, subtropical, and temperate waters (Kirkendale and Calder 2003; Preker and Lawn 2010), including the oceanic islands of Guam, Bermuda, the Azores, and the Cape Verdes (Calder 2000; Medel and Vervoort 2000; Kirkendale and Calder 2003). Reported in South Africa (as *H. caciniiformis*) by Millard (1975).

Family Plumaleciidae Choong and Calder, **fam. nov.**

Diagnosis.—Colonies erect, arising from a stolonal hydrotheca; hydrocauli unbranched, divided into internodes, giving rise to hydrocladia from alternate

or mostly alternate apophyses, cauline hydrothecae absent; hydrocladia dichotomously or irregularly branched, or unbranched, divided into internodes, often with terminal hydrothecae; hydrothecae uniseriate, sessile, small, cup-shaped, relatively shallow, free of hydrothecial internode or not completely adnate; radially symmetrical; margin entire; operculum absent. Nematophores and nematothecae absent.

Gonophores presumably fixed sporosacs; gonothecae solitary, conical, without nematothecae, arising from apophyses of hydrocaulus; phylactocarps absent.

Plumalecium plumularioides (Clark, 1877)

(Figure 13)

Halecium (?) *plumularioides* Clark 1877: 217, pl. 10, figures. 16, 17.
Plumularia plumularioides.—Nutting 1900: 62, pl. 4, figure. 3.—Cairns et al. 1991: 28.
 not *Plumularia plumularioides*.—Torrey 1902: 78, pl. 11, figures. 103, 104.—Fraser 1911: 84; 1918: 136, pl. 2, figures. 5A–C; 1937: 190, pl. 44, figures. 230a–c; 1947: 92, 363. [Incorrect subsequent spelling]
 not *Plumularia plumularioides*.—Torrey 1904: 38.—Fraser 1935: 145.
Plumalecium plumularioides.—Antsulevich 1982: 71, figures, A, B; 2015: 561, figure 282a–b.
Halecium plumularioides.—Antsulevich 1987: 112, figures, 31A, B.
 not *Kirchenpaueria plumularioides*.—Brinckmann-Voss 1996: 96. [Incorrect subsequent spelling]
Kirchenpaueria plumularioides.—Cairns et al. 2002: 20, 55.—Calder and Stephens 1997: 31.
Ventromma plumularioides Bouillon et al. 2006: 335.
 not *Kirchenpaueria plumularioides*.—Marques et al. 2007: 131, pl. 45, figure. C.—Mills et al. 2007: 161.

Material.—Washington, on vessel, colonies with gonothecae (JTMD-BF-40), ROMIZ B4095; Washington, on vessel, section of hydrocaulus with perisarc, no gonothecae (JTMD-BF-40), ROMIZ B4178; Washington, on vessel colonies with gonothecae (JTMD-BF-40), ROMIZ B4192; Washington, on vessel, colonies without gonothecae (JTMD-BF-40), ROMIZ B4193; Washington, on vessel, section of hydrocaulus with hydrothecae, without gonothecae (JTMD-BF-40), ROMIZ B4237; Oregon, on vessel, dense colonies, overgrowing *Lepas* sp. without gonothecae (JTMD-BF-50), ROMIZ B4196; Hawai‘i, on vessel, found live, scraped off *Mytilus galloprovincialis* shell, without gonothecae (JTMD-BF-87), ROMIZ B4097; Washington, amidst fouling on vessel, fragment of stem with several hydrothecae, with remnants of coenosarc, without gonothecae (JTMD-BF-134), from ROMIZ B4236; Oregon, on buoy, colony arising from hydrorhiza, with remnants of perisarc, overgrowing gooseneck barnacle *Lepas* sp., without gonothecae (JTMD-BF-207), ROMIZ B4101; Washington, on vessel, colonies growing on styrofoam, with gonothecae, *Lepas* sp. also present (JTMD-BF-352), RBCM 017-00010-001; Japan: Miyako, Iwate Prefecture, Tōhoku Coast, November

2015, 3-month test panel, colony arising from stolon, without gonothecae (M12) RBCM 017-00014-001; Japan: Miyako, Iwate Prefecture, Tōhoku Coast, September 2015, 1-month test panel, colony arising from stolon, with gonothecae (M19) RBCM 017-00013-001.

Description.—Colony up to 12 mm high, arising from stolon. Hydrocaulus monosiphonic, erect, usually straight but occasionally slightly geniculate, 1–3 transverse annulations at base, divided into regular internodes, each segment bearing one hydrocladial apophysis distally, hydrocladia alternate. Perisarc moderately thickened. Hydrothecae uniseriate, 1–3 or more per hydrocladium, cup-shaped, tapering slightly to base, margin entire. Gonothecae solitary, conical, with rounded apices, borne on axils of hydrocladial apophyses.

Remarks.—Our material is referable to *Plumalecium plumularioides*, based on trophosomal and gonosomal characters. This species was well-represented on JTMD that stranded on the coasts of Washington, Oregon, and Oahu, Hawai‘i. It was found as well on test panels immersed at Miyako, Iwate Prefecture, Tōhoku region, Japan. The only reliable previous records of *P. plumularioides* are those of Clark (1877) from the type locality (Alaska, Nunivak Island, 15–18 m) and Antsulevich (1982) from the Kurile Islands, Russian Federation (near Kunashir Island, 6 m). As noted by Antsulevich (2015), several records of *P. plumularioides* from the west coast of North America have been based on misidentified hydroids possessing mesial nematothecae (Torrey 1902, as *Plumularia plumularioides* (*sic*); Fraser 1918, as *Plumularia plumularioides* (*sic*), 1935, as *Plumularia plumularioides*; Brinckmann-Voss 1996, as *Kirchenpaueria plumularioides* (*sic*); Mills et al. 2007, as *Kirchenpaueria plumularioides*). The species in all of these reports is likely a *bona fide* kirchenpaueriid and not *P. plumularioides*. This is the first record of its presence in Japan (from test panels recovered from the coast of Tōhoku). While infrequently reported, it is possible that hydroids of *P. plumularioides* from the North Pacific have at various times been misidentified as one or more species of *Halecium*.

Distribution.—Japan (new record, herein). Kurile Islands (Antsulevich 2015) and Bering Sea (Clark 1877).

Systematic discussion.—Clark (1877) first described this species, as *Halecium* (?) *plumularioides*, from Cape Etolin, Nunivak Island, Alaska. The uniserial arrangement of the hydrothecae, and absence of gonothecae, left him uncertain how it should be classified. He noted the resemblance of its trophosome to that of plumulariid hydroids, but provisionally

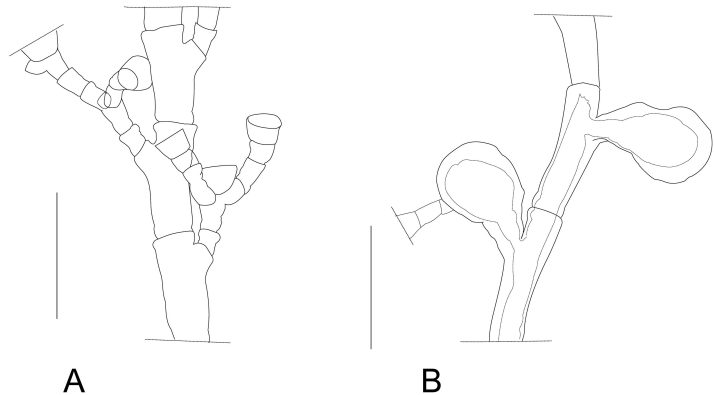


Figure 13. *Plumalecium plumularioides*:
(A) section of hydrocaulus and hydrocladia.
ROMIZ B4101. Scale equals 500 μ m.
(B) gonothecae. ROMIZ B4095. Scale
equals 500 μ m. Del. HHC Choong.

assigned it instead to the genus *Halecium* Oken, 1815 because colonies lacked nematophores, although also absent is the ring of desmocytes consistent with diagnoses of the taxon. Nutting (1900) saw no new material but referred the species instead to *Plumularia* Lamarck, 1816, and to the family Plumulariidae McCrady, 1859, concluding that the absence of nematophores was merely accidental or temporary, notwithstanding the fact that nematophores with well-developed nematothecae are essential character states in that family. Studies by Antsulevich (1982, 1987, 2015), based on specimens from the Kurile Islands, Russian Federation, discounted Nutting's conclusion about the existence of nematophores (and nematothecae) in the species. As originally described by Clark (1877), and later by Antsulevich (1982, 1987, 2015), they are indeed lacking. Our specimens fully correspond with theirs in this character. Given the distinctive morphology of its trophosome, Antsulevich (1982) established *Plumalecium* as a new genus to accommodate the species. While he abandoned the genus shortly after (Antsulevich 1987), including it in the synonymy of *Halecium*, *Plumalecium* was recognized as valid again by him in a later work (Antsulevich 2015). We likewise recognize the validity of the genus, and include the species here under the binomen *Plumalecium plumularioides*.

Clark's species has been included as *Plumularia plumularioides* in Cairns et al. (1991), as *Kirchenpaueria plumularioides* in Cairns et al. (2002) and in the World Register of Marine Species (<http://www.marinespecies.org/aphia.php?p=taxdetails&id=284919>), and as *Ventromma plumularioides* in Bouillon et al. (2006). Classification of this species at the rank of family has also been unsettled. Authors including Cairns et al. (2002), Bouillon et al. (2006), and Antsulevich (2015) referred *P. plumularioides* to Kirchenpaueriidae Stechow, 1921. While kirchenpaueriids lack paired lateral nematothecae, mesial

nematophores (either naked or with reduced nematothecae) occur below each hydrotheca (Leclère et al. 2007; Maronna et al. 2016). Such nematothecae are lacking in *P. plumularioides*.

Plumalecium Antsulevich, 1982 (type species: *Halecium plumularioides* Clark, 1877) appears referable to superfamily Plumularioidea based on trophosomal characters, notwithstanding the lack of nematothecae. We propose that the diagnosis of Plumularioidea be amended to accommodate this species lacking nematothecae. In that character it differs from all known families of plumularioids, as defined in works such as those of Cornelius (1995b), Calder (1997), Bouillon et al. (2006), Leclère et al. (2007), and Maronna et al. (2016). A new family, Plumaleciidae, is thus proposed herein to accommodate the genus. *Plumalecium* is currently monotypic, with *P. plumularioides* as its only known species. *Halecium linkoi* Antsulevich, 1980 resembles *P. plumularioides*, but it seems to differ (Antsulevich 2015: 366) in having hydrocladia that are repeatedly and consistently branched rather than being branched or unbranched, with hydrothecae in the latter case being arranged in a straight series.

Order Limnomedusae Kramp, 1938

Family Olindiidae Haeckel, 1879

***Gonionemus vertens* A. Agassiz, 1862**

Gonionemus vertens A. Agassiz 1862: 350

Material.—BF1: A community metabarcoding sequence with 98.4% pairwise identity to Genbank sequences (over 311 bp) from Japan (KY43780, Okirai Bay) and Russia (KY437948 and KY437951, from Amur Bay and Vostok Bay, respectively) as well as to introduced populations in New England (for example, KY437814, KY437864, and KY437898), as studied and deposited by Govindarajan et al. (2017).

Remarks.—No additional specimens of *Gonionemus* were recovered from the Misawa fisheries dock (JTMD-BF-1) that landed in June 2012 in central Oregon. However “Misawa 1” supported vast bio-fouling communities (exceeding 75 square meters), only a small portion of which was sampled, and it is thus not surprising that the small polyyps of this species were not recovered. Our material aligns with the toxic clade of *Gonionemus vertens* from the Northwest Pacific Ocean, which is distinct from the non-toxic clade of *G. vertens* known from the Northeast Pacific Ocean (Govindarajan et al. 2017). The toxic Western Pacific clade was recently introduced to New England (Govindarajan et al. 2017).

Discussion

Biogeographic sources of JTMD hydroid fauna

We suggest that all of the species reported here, with the exception of *Obelia griffini* (discussed in detail below), originate from the coast of Japan (or, in the case of *Clytia linearis* discussed earlier, slightly farther south). In concert with the findings of Elvin et al. (2018) and Cordell (2018), reporting on JTMD sponges and copepods, respectively, we also found that diversity per object declined over time. As suggested by Elvin et al. (2018) and Cordell (2018), if species were being regularly acquired by JTMD after entering the coastal zone of North America or Hawai‘i, there would be no reason for diversity to decline over time. Rather, this decline suggests a steady attrition of species richness per object raft originating from Japan, as would be expected from the challenges of long-term survival by coastal species rafting for years in an oceanic environment. It is possible that survival in many species may have been prolonged through resting stages (menonts). However, we also observed (in the present study and in Calder et al. 2014) large, weathered colonies with empty gonothecae in some species such as *Obelia longissima*, suggesting persistence of these colonies on the debris for extended periods. In addition, a number of JTMD species arriving in North America, including *Orthopyxis caliculata*, *O. dichotoma*, *Amphisbetia furcata*, *Aglaophenia* aff. *pluma*, and *Plumalecium plumularioides*, were found on debris arriving in Hawai‘i. As none of these species are known from Hawai‘i, their only source is the Western Pacific Ocean.

Finally, as noted by Calder et al. (2014), Carlton et al. (2017), and Elvin et al. (2018), if JTMD objects were being typically colonized after arrival in the Eastern Pacific, it would be highly unlikely that the only species to do so would also be those occurring

in Japanese or other Western Pacific waters. We documented no hydroid species believed to be unique to North America or the Hawaiian Islands on JTMD.

Obelia griffini as a potential member of the North Pacific Oceanic Fauna

We propose that the abundant hydroid *Obelia griffini* may be a member of the poorly known North Pacific open ocean neustonic fauna. *Obelia griffini* was described from either Bremerton or Port Townsend, Washington, without habitat data, by Calkins (1899). Two species described in the same paper are now held to be synonyms of *O. griffini*: *Obelia gracilis*, “on grasses” from Scow Bay, Port Townsend Harbor, and *Obelia surcularis*, on “water grasses” from the same location. *O. griffini* was first synonymized with *Obelia dichotoma* by Cornelius (1975b), but we regard it as a distinct species, as noted earlier, based upon morphological criteria (Calder et al. 2014).

As reviewed by Calder et al. (2014), *O. griffini* has also been reported (as *O. gracilis*) from benthic habitats in China and the South Kurile Islands. In contrast, we find *O. griffini* to be not only the most common hydroid on tsunami debris, but also to be the only species (or in sole company with the native oceanic gooseneck barnacle *Lepas* spp.) often on marine debris (JTMD as well as non-Japanese tsunami debris). Of interest in this regard is Cornwall’s (1927) report that hydroids on the whale barnacle *Coronula diadema* (Linnaeus, 1767) (taken from a humpback whale off Vancouver Island) were identified by Charles H. O’Donoghue as *O. griffini*. The populations of *O. griffini* on JTMD are typically too expansive to have been acquired in the nearshore Eastern Pacific by debris in the brief time most of this debris field is believed to have rafted along the coast prior to landing, especially considering (as discussed above) that no uniquely Eastern Pacific hydroid species were found on any of these objects. Further, *O. griffini* is found on JTMD arriving in the Hawaiian Islands, where no members of this species-group are known to occur, thus making it unlikely that the populations were acquired there.

Finally, neither *O. griffini*, *O. gracilis*, nor *O. surcularis* have been reported from the Japanese hydroid fauna. While it may be that since 1976 populations matching the morphology of these species have been assigned by Japanese workers to *O. dichotoma* following Cornelius (1975b, but not issued until November 1975), *O. griffini* and *O. gracilis* were in regular use prior to that date, *O. gracilis* in particular having been identified in other Asian hydroid studies, and with other workers in the Western Pacific continuing to recognize *O. griffini*

after 1975 as well (for example, Antsulevich 1992). While we report here and in Calder et al. (2014) other less common hydroid species that we interpret as new records for Japan, the abundance and ubiquity of *O. griffini* on JTMD make it difficult to imagine that it has been overlooked in the Japanese coastal fauna. Rather, we suggest that JTMD acquired *O. griffini* during the North Pacific transit, and that this is a native high-seas species.

This said, the presence of oceanic, neustonic species—such as *Obelia griffini*, as well as the gooseneck barnacle *Lepas*, the crabs *Planes* spp. and *Plagusia* spp., the nudibranch *Fiona pinnata* (Eschscholtz, 1831) and the polychaete worm *Amphinome rostrata* (Pallas, 1766), all of which have been found on JTMD (Carlton et al. 2017)—in benthic habitats in China, Russia, or the Pacific Northwest would be highly anomalous. While all of these oceanic species may be found on occasion washed ashore, they are not regular members of coastal benthic communities. Thus, *Obelia griffini* may represent a cryptic species complex, with apparently morphologically identical benthic and pelagic clades. Molecular genetic studies are called for to clarify the status of purported oceanic and shore populations. If the pelagic taxon were to be found to represent a distinct taxon, it would likely require a new name.

A number of species of hydroids are regarded as naturally occurring in both benthic and pelagic habitats (such as *Clytia hemisphaerica* and *Clytia linearis*, both treated herein; see also Calder 1995, for species from the Sargasso Sea, many of which are also reported from nearshore benthic communities). While all or most of these species likely represent species complexes as well, in the case of *O. griffini*, we underscore the observation that this abundant species is not known from the Tōhoku source region of JTMD, thus making its high seas acquisition *en route* through the Pacific Ocean more probable. While hydroids have been previously reported on debris drifting in the North Pacific Ocean (Calder et al. 2014; Goldstein et al. 2014), they have not been regarded as part of the naturally occurring neustonic fauna.

There is some evidence in our material for direct settlement of *Obelia griffini* larvae on *Lepas* or other substrates in the open ocean (that is, sexually produced colonies as opposed to clonally produced colonies or stolonial extension of colonies growing originally on Japanese substrates). For example, runner-like hyperplastic stolons exhibiting directional growth were observed on an *O. griffini* colony on the pelagic crab *Plagusia* sp. (ROMIZ B4174), which colony is small and relatively sparse, indicating that larval recruitment is probable. Production of hyperplastic

stolons exhibiting directional growth have been observed in sexually produced colonies of *Hydractinia symbiolongicarpus* Buss and Yund, 1989 (Van Winkle and Blackstone 2002). The presence of these colonies, in addition to tightly packed “sheets” indicating later development of stolonial mats (also present in our material) supports the argument for open larval recruitment and persistence of these colonies. It is possible that the availability of planulae of *O. griffini*, as well as those species such as *Amphisbetia furcata*, which is probably not part of the oceanic neustonic fauna *sensu stricto*, may be mediated by the release of mature medusae which do not need to feed or by release of larval stages from fixed gonophores. This life cycle plasticity has been observed in *Clytia linearis*, *Obelia* sp., and *A. operculata* (Lindner and Migotto 2002; Genzano et al. 2008).

Conclusions: JTMD hydroid diversity and transoceanic dispersal

Campanularioid hydroids in the genera *Campanularia*, *Orthopyxis*, *Clytia*, *Laomedea*, and *Obelia*, are frequent and well-known members of ship fouling (Hutchins 1952; Zvyagintsev 2003, 2005), harbor fouling (Karlson and Osman 2012), and, often, rafting (Thiel and Gutow 2005; Farrapeira 2011) communities. Not surprisingly, 10 species in these genera comprise the most diverse group of JTMD hydroids. Thiel and Gutow (2005) summarized records of hydroids reported in the literature as rafting species. Other than taxa associated with the drifting brown alga *Sargassum* in the North Atlantic’s Sargasso Sea (Calder 1995), they noted five species whose association with rafting was based only upon circumstantial evidence or distributional inference, rather than direct observation, and an additional four species reported from local or regional coastal debris. Goldstein et al. (2014) reported three species, *Clytia gregaria* (Agassiz, 1862), *Obelia* sp., and *Plumularia setacea* from marine debris collected floating in the North Pacific. The present report represents the first documentation of the 28 species reported here and earlier (Choong and Calder 2013; Calder et al. 2014) as rafting from one continental margin to another.

That half of the species found in our collections occurred only once speaks to the strong probability that JTMD hydroid diversity is far greater than reported here. Only a small fraction of Japanese tsunami marine debris was sampled (Carlton et al. 2017), suggesting that the many thousands of objects not intercepted and studied may have transported many more hydroid species to the Central and Eastern Pacific.

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Supplementary material

The following supplementary material is available for this article:

Table S1. JTMD Objects: BF numbers, landing site locations, dates and object types, and prefecture and city origins if known.

Table S2. Summary of North Pacific distribution of hydroids originating from the Japanese coast and found on tsunami marine debris between 2012 and 2016.

This material is available as part of online article from:

http://www.aquaticinvasions.net/2018/Supplements/AI_2018_JTMD_Choong_etal_SupplementaryTables.xlsx