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Some anthoathecate hydroids and limnopolyps (Cnidaria, Hydrozoa) from the Hawaiian archipelago

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Abstract

A systematic account is given of 17 families, 25 genera, and 32 species of anthoathecate hydroids and limnopolyps reported from Hawaii. Applying Reversal of Precedence provisions in zoological nomenclature, the familiar hydrozoan genus names *Hydractinia* Van Beneden, 1844a, *Bimeria* Wright, 1859a, and *Porpita* Lamarck, 1801 are designated as valid and as nomena protecta, while seldom-used older names threatening them (the synonyms *Echinochorium* Hassall, 1841 and *Manicella* Allman, 1859a, and the homonym *Porpita* Soldani, 1789 respectively) are relegated to nomena oblita. Also designated a nomen oblitum is the name *Pyxidium* Leuckart, 1856, threatening its junior but widely used synonym *Ectopleura* L. Agassiz, 1862. The species name *Bimeria vestita* Wright, 1859a is rendered valid and a nomen protectum, while its virtually unused senior synonym *Manicella fusca* Allman, 1859 becomes a nomen oblitum. *Hydrodendrium* Nutting, 1905 is reinstated as a valid genus, distinct from *Hydractinia* and replacing its junior objective synonym *Nuttingia* Stechow, 1909. The spelling of Hydrodendridae Nutting, 1905 is emended to Hydrodendriidae, but that family name is retained as a synonym of Hydractiniidae. Usage of the familiar generic name *Sphaerocoryne* Pictet, 1893 is upheld by recognizing it and its former senior subjective synonym *Corynetes* Haeckel, 1879 as valid. The correct spelling of the family name originally founded as Olindiadae Haeckel, 1879 is taken to be Olindiidae, and spelling of the species name *Solanderia misakinensis* (Inaba, 1892), first established as *Dendrocryne* (sic) *misakii*, is stabilized. One new species, *Stylactaria munita*, is described from shallow waters at Hawaii Kai, Oahu. Lectotypes are designated for *Corydendrium corrugatum* Nutting, 1905 and *Corydendrium minor* Nutting, 1905 (=*Turritopsis minor*), both originally described from Hawaii. Type material of *Balea mirabilis* Nutting, 1905 (=*Balella mirabilis*), originally described from waters between the islands of Molokai and Maui, could not be located. Six anthoathecate species [*Corydendrium parasiticum* (Linnaeus, 1767), *Bimeria vestita*, *Amphinema* sp., *Eudendrium carneum* Clarke, 1882, *Ectopleura viridis* (Pictet, 1893), and *Sphaerocoryne bedoti* Pictet, 1893] are recorded from Hawaii for the first time.

Key words: Capitata, Filifera, Hydroidolina, marine biology, oceanic islands, Pacific Ocean, taxonomy, Trachylina, zoological nomenclature

Introduction

Taxonomic information on hydroids of Hawaii, exclusive of stylasterids, is based largely on two publications. Nutting (1905) reported 49 species from offshore waters (10–500 fathoms: 18–914 m), collected during a cruise of the steamer *Albatross* in 1902. Seven of them were anthoathecates. Cooke (1977) included 28 species of hydroids and hydromedusae in an account of the shallow reef and shore fauna of the islands, with 14 of them being anthoathecates. In addition to these two works, records of hydroids from the islands occur in studies on introduced and cryptogenic marine and estuarine biota (Coles *et al*. 1999, 2006; Carlton & Eldredge 2009). Reports of one or a few marine hydrozoans from Hawaii also exist in various papers (Allman 1888; Hartlaub 1901; Edmondson 1930, 1933, 1946; Boone 1938; De Oreo 1946; Chu & Cutress 1954, 1955; Pardy & Lenhoff 1968; Rees *et al*. 1970; Rees 1971; Reed 1971; Pardy 1971; Tusov & Davis 1971; Long 1974; Martin 1975; Eldredge & Devaney 1977; Grovhaug & Rastetter 1980). Hoover (1998, 2006) included several species of hydroids, and provided color photographs of them, in guidebooks. Meanwhile, hydrozoans from limnic waters have been documented by Edmondson (1940), Mumford (1940), Matthews (1963, 1966), Rahat & Campbell (1974), and Bailey-Brock & Hayward (1984).

The objective of this study was to provide a synopsis of the anthoathecate hydroids and limnopolyps currently known from Hawaii, based on both previous records and new collections. Stylasterid hydroids of the islands have been investigated earlier by Cairns (1978, 2005) and are excluded here. No representatives of the family Milleporidae Fleming, 1828 have been reported from the archipelago (Cooke 1977). A total of 32 species, other than stylasterids, are recorded here from the Hawaiian Islands. Several anthoathecate species can be identified only to genus at present, and knowledge of the local hydroid fauna is acutely limited, as it is for much of the Indo–Pacific region.

Fundamental changes are currently underway in hydrozoan systematics, the result of advances made possible by phylogenetic systematics and more recently by molecular methods. Classification of the group is evolving, and is far from having attained a state of stability. Meanwhile, traditional morphology-based species recognition in hydroids, with its acknowledged limitations and subjectivity (Calder 1988: 2), is being complemented by the cogency of genetic analysis. Molecular systematics is a robust new discipline in studies on Hydrozoa, but it needs to be complemented with sound taxonomic and nomenclatural practices.

Material and methods

Materials examined here exist in collections at the Bernice P. Bishop Museum (Honolulu, Hawaii), the National Museum of Natural History (Washington, DC), the Royal Ontario Museum (Toronto, Canada), and the Nationaal Natuurhistorisch Museum Naturalis (Leiden, The Netherlands).

Synonymy lists are limited to the publication in which a given name was first made available nomenclaturally, and to works providing original records of a particular species in Hawaii. Original authorship and dates of all nominal taxa used herein were traced and confirmed. The classification system used herein has been adapted from multiple sources, as credited in the text.

Descriptions of species recorded in the study area from earlier works, but not seen here, are based on accounts in those works except as noted. For example, the account of *Cordylophora caspia* (Pallas, 1771), not seen during this study, is extracted from that in Cooke (1977).

Nematocysts from preserved material were examined, if material was suitable, as outlined elsewhere (Calder 1988).

The term “eumedusoid” in studies of hydrozoans has been applied to a reduced medusa having radial canals, a subumbrellar cavity, a velum, and vestigial or totally reduced marginal tentacles (e.g. Kühn 1913; Millard 1975; Bouillon *et al*. 2006). As noted by Cornelius (1995: 330–331), the word is a misnomer because its etymology suggests “fully medusoid.” Moreover, reduction of sexual stages in hydrozoans is a continuum from only slightly modified medusae to the occurrence of mere “gonads” in the body wall of a polyp. Nevertheless, the term “eumedusoid” as applied to a partially reduced medusa in a given species is useful, widely used, and retained here in its usual sense. It seems undesirable and potentially confusing to replace it with the word “medusoid,” as is sometimes done. The latter term has long been understood to be one of the two basic body forms in the medusozoan life cycle, with the other being the polypoid stage.

Abbreviations used in this work are as follows:

BPBM	Bernice Pauahi Bishop Museum (Honolulu).
CAS	California Academy of Sciences (San Francisco).
HURL	Hawaii Undersea Research laboratory (Honolulu).
ICZN	International Code of Zoological Nomenclature.
NMNH	National Museum of Natural History, Smithsonian Institution (Washington, DC).
RMNH	Nationaal Natuurhistorisch Museum Naturalis (Leiden).
ROMIZ	Invertebrate Zoology collections, Royal Ontario Museum (Toronto).
USNM	United States National Museum (now National Museum of Natural History, NMNH). Collection numbers of material at the NMNH are prefaced by the abbreviation “USNM.”

Systematic account

Phylum Cnidaria Verrill, 1865

Cnidaria Verrill, 1865: 145.

Diagnosis. Metazoan animals with intrinsic nematocysts; body in two basic forms, polyp and medusa, each consisting fundamentally of two dermal layers (epidermis and gastrodermis) separated by mesoglea, enclosing a gastrovascular cavity (coelenteron) with one opening, the mouth; tentacles usually present; symmetry radial or a modification thereof.

Remarks. Verrill (1865: 145) has recently been credited as author of Cnidaria, earlier attributed to Hatschek (1888: 249), although the name was originally established for a taxon at the rank of class. Cnidaria is predated by Coelenterata Frey & Leuckart, 1847: 137, applied to a group that originally included ctenophores as well as cnidarians (it did not originally include sponges, as sometimes claimed). The name Cnidaria gained widespread usage after being adopted in an influential treatise on invertebrate animals (Hyman 1940: 365), and it has now become widely accepted as the name of the phylum. More details are given in a forthcoming publication by Daly *et al*. (in press).

For recent comments on Cnidaria, see Cairns & Fautin (2009) and Collins *et al*. (in press). A contemporary treatise on the phylum is that by Bouillon (1995); current perspectives on phylogeny of the group are given by Daly *et al*. (2007).

Subphylum Medusozoa Petersen, 1979

Medusozoa Petersen, 1979: 105.

Diagnosis. Cnidaria with both polyp and medusa stages in the life cycle, albeit with some species exclusively polypoid, others exclusively medusoid.

Remarks. Petersen (1979) recognized Medusozoa for an assemblage having medusoid as well as polypoid stages in the life cycle within the phylum Cnidaria. Medusozoa now is taken to include the classes Hydrozoa Owen, 1843, Scyphozoa Goette, 1887, Cubozoa Werner, 1973, and Staurozoa Marques & Collins, 2004. The mitochondrial genome of the group has been shown to be composed of linear molecules, and not circular ones as observed in Anthozoa and other metazoans (Bridge *et al*. 1992; Marques & Collins 2004). Results from mtDNA analyses thus support hypotheses that medusozoans are a derived group, that the polyp preceded the medusa in cnidarian evolution, and that Anthozoa is the earliest diverging class in the phylum.

Class Hydrozoa Owen, 1843

Hydrozoa Owen, 1843: 82.

Diagnosis. Medusozoa with acellular mesoglea; polyps lacking a stomodeum (actinopharynx) between coelenteron and mouth; coelenteron lacking gastric filaments, not divided into compartments by mesenteries or septa; medusae craspedote, with velum (craspedon) partially enclosing subumbrellar cavity; gametes usually of ectodermal origin.

Remarks. Owen (1843) established Hydrozoa for "The class of Polypi organized like the Hydra." For a comprehensive overview of the class, see Bouillon *et al*. (2006). Updated classifications of the group are given by Daly *et al*. (2007) and Schuchert (2009). The class Hydrozoa comprises two monophyletic clades, Hydroidolina Collins, 2000 and Trachylina Haeckel, 1879.

Subclass Hydroidolina Collins, 2000

Hydroidolina Collins, 2000: 21.

Diagnosis. Hydrozoa with polyps and medusae as significant and conspicuous stages in the life cycle (although some species exclusively polypoid or medusoid), often metagenetic except in siphonophores; polypoid stages, when present, usually polymorphic; medusae frequently reduced, forming parts of a highly polymorphic colony in siphonophores; medusa stage usually with true tentacular bulbs, ocelli present or absent, free ecto-endodermal statocysts lacking; planula larvae, when present, usually with cnidoblasts, glandular cells, neural cells, and interstitial cells, most often settling and becoming benthic except in Porpitidae and Margelopsidae (Anthoathecata) and holopelagic Siphonophora.

Remarks. For discussion of the subclass Hydroidolina Collins, 2000, and of the subclass Trachylina Haeckel, 1879 as currently used in hydrozoan classification, see Collins (2000), Marques & Collins (2004), Daly *et al*. (2007), and Cartwright *et al*. (2008). Hydroidolina encompasses the hydrozoan orders Anthoathecata Cornelius, 1992, Leptothecata Cornelius, 1992, and Siphonophorae Eschscholtz, 1829.

Order Anthoathecata Cornelius, 1992

Anthoathecata Cornelius, 1992: 246.

Diagnosis. Hydrozoa with colonial or solitary hydroids having hydranths lacking hydrothecae, gonophores lacking gonothecae, and nematophores, if present, lacking nematothecae.

Gonophores fixed sporosacs, eumedusoids, or medusae. Medusae, when present, usually with bell-shaped umbrella; marginal sense organs, when present, comprising ocelli, statocysts and cordyli absent; gonads on manubrium, infrequently extending onto bases of radial canals.

Remarks. Cornelius (1992) proposed Anthoathecata (later spelled Anthoathecatae by Cornelius 1995: 74) as a single replacement name for Athecata Hincks, 1868, established in a monograph on hydroids, and its junior synonym Anthomedusae Haeckel, 1879, used in a systematic account on medusae. The name eliminates vestiges of a much-maligned dual nomenclature for the taxon, including awkward compound names such as “Athecatae/Anthomedusae.” As a term readily applicable to both major stages in the life cycle, it is more inclusive than either of the older names associated primarily or exclusively with either hydroids or medusae. In being applied to a taxon above the rank of family-group, no rules of zoological nomenclature are violated in adopting this recently established name. Anthoathecata, now in widepread use, has been adopted in the World Hydrozoa Database (Schuchert 2009). However, there is evidence from molecular work that Anthoathecata and its suborders Filifera Kühn, 1913 and Capitata Kühn, 1913 are not monophyletic (Cartwright *et al*. 2008), and classification of the entire assemblage must eventually change.

Recognized as an order here, Anthoathecata is essentially equivalent in scope to Gymnoblastea Allman, 1871 as used and defined in older works on hydroids.

Suborder Filifera Kühn, 1913

Filifera Kühn, 1913: 227.

Diagnosis. Anthoathecate hydroids with hydranth tentacles filiform, not capitate or moniliform (an exception is Ptilocodiidae Coward, 1909, having dactylozooids with or usually with capitate tentacles).

Gonophores fixed sporosacs, eumedusoids, or medusae. Medusae, when present, with mouth surrounded by four lips or, if mouth is round and lacks lips, with oral tentacles on or above rim; gonads on manubrium, usually subdivided into perradial, interradial, or adradial masses.

Cnidome usually including desmonemes and euryteles; stenoteles absent.

Remarks. Representatives of the suborder Filifera Kühn, 1913 are distinguished by having filiform tentacles and a cnidome usually including desmonemes and euryteles, but lacking stenoteles. The group is apparently not monophyletic (Daly *et al*. 2007; Cartwright *et al*. 2008). It was assigned to the rank of order and subdivided into two suborders (Margelina Haeckel, 1879 and Pandeida Haeckel, 1879) by Bouillon & Boero (2000) and Bouillon *et al*. (2006) based on differences in attributes of the medusa stage. That classification has not been followed in revisions of European Filifera by Schuchert (2004, 2007, 2008a, b). Meanwhile, ideas about phylogeny of the group continue to evolve, and classification will gradually follow. For example, Cartwright *et al*. (2008) recognized four separate clades in Filifera: Filifera I comprising Eudendriidae L. Agassiz, 1862; Filifera II comprising the genera *Fabienna* Schuchert, 1996, *Proboscidactyla* Brandt, 1835, *Brinckmannia* Schuchert & Reiswig, 2006, and *Hydrichthella* Stechow, 1909; Filifera III comprising Hydractiniidae L. Agassiz, 1862 and Stylasteridae Gray, 1847; and Filifera IV comprising *Dicoryne* Allman, 1859 + Bougainvilliidae Lütken, 1850 + Oceaniidae Eschscholtz, 1829 + Pandeidae Haeckel, 1879 + Rathkeidae Russell, 1953 (with the four included families forming a group termed "Gonoproxima," all having gonophores on hydrocauli, pedicels, or stolons rather than on the hydranth body column).

Currently included in Filifera are 22 families and about 765 species (Daly *et al*. 2007).

Family Oceaniidae Eschscholtz, 1829

Oceanidae Eschscholtz, 1829: 96 [emended to Oceaniidae by Kühn (1913: 233); name placed on Official List of Family-Group Names in Zoology (ICZN Opinion 2166)]

Diagnosis. Filiferan hydroids with stolonal or erect colonies, arising from a creeping hydrorhiza or stolonal mat. Hydrocaulus of erect colonies branched or unbranched, monosiphonic or polysiphonic, growth monopodial with terminal hydranths. Zooids monomorphic, or polymorphic with gastrozooids, gonozooids, and dactylozooids. Perisarc filmy to firm, investing only hydrorhiza or on both hydrorhiza and base of hydranths in stolonal colonies, covering both hydrorhiza and hydrocaulus in erect colonies, usually terminating at base of hydranth. Hydranths or gastrozooids clavate to fusiform, with filiform tentacles scattered over distal third or more of body; hypostome conical to proboscis-shaped. Nematophores present or absent.

Gonophores fixed sporosacs or free medusae, arising variously from hydrorhiza, hydrocaulus, pedicels, gonozooids, or blastostyles. Medusae, when present, bell-shaped with short manubrium; mouth surrounded by four lips, margins of lips fringed with clusters of nematocysts; radial canals four, simple; marginal tentacles solitary, numerous in adult. Ocelli present, adaxial. Gonads interradial, on manubrium.

Remarks. Genera in this family were until recently assigned to Clavidae McCrady, 1859. However, *Clava* Gmelin, 1791, type genus of the family, is now known to be more closely related to *Hydractinia* Van Beneden, 1844a and related genera than to others earlier included in Clavidae (Schuchert 2001a; Miglietta *et al*. 2009). Schuchert (2004) resurrected the name Oceanidae Eschscholtz, 1829 (emended to Oceaniidae by Kühn 1913) to accommodate these genera. Three genera of oceaniids have been reported from Hawaii: *Corydendrium* Van Beneden, 1844a, *Turritopsis* McCrady, 1857, and *Rhizogeton* L. Agassiz, 1862. Nine genera and about 37 species are currently recognized in the group worldwide (Schuchert 2009).

Genus *Corydendrium* Van Beneden, 1844a

Corydendrium Van Beneden, 1844a: 313.
Type species. *Sertularia parasitica* Linnaeus, 1767 [*Corydendrium parasiticum*], by monotypy.

Diagnosis. Oceaniid hydroids sometimes stolonal but usually with erect and irregularly branched colonies. Hydrocaulus polysiphonic or less frequently monosiphonic; hydrocladia, if present, adnate for part or all of their length to hydrocaulus or to other hydrocladia. Perisarc firm, covering hydrocauli and hydrocladia, terminating near hydranth bases; perisarcal tubes of side branches nested. Hydranths club-shaped to elongate-tubular, lacking perisarc; tentacles filiform, scattered over most of hydranth.

Gonophores fixed sporosacs, arising below hydranths as elongate, blind sacs of coenosarc, protected within perisarcal tubes of hydrocladia and hydrocaulus.

Remarks. Taxonomic and nomenclatural accounts of *Corydendrium* Van Beneden, 1844a have been provided by Calder (1988) and Schuchert (2004). Seven species were listed under the genus in the database of Schuchert (2009), with one of those, *Corydendrium corrugatum* Nutting, 1905 from Hawaii, being considered a nomen dubium. It is included as valid here, but further taxonomic appraisal of the species is warranted.

Corydendrium corrugatum Nutting, 1905

Figs. 1, 2

Corydendrium corrugatum Nutting, 1905: 941, pl. 2, fig. 2, pl. 7, figs. 5–7.—Calder, 2004: 20.

Type locality. Hawaii: "south of…Oahu, 319 fathoms" (583 m) (Nutting 1905). This station was actually south of Molokai, not Oahu.

Material examined. Molokai: Albatross Stn. 3828, off south coast, 583 m, 01.iv.1902, one fragmentary colony, about 15 cm high, without gonophores, USNM 22150 [LECTOTYPE; bottle also contains an antipatharian overgrown by an operculate hydroid].–Molokai: Albatross Stn. 3828, off south coast, 583 m, 01.iv.1902, seven colony fragments, up to 9 cm high, without gonophores, USNM 52582 [PARALECTOTYPE; bottle also contains an antipatharian and a lafoeid hydroid].–Maui: Albatross Stn. 4077, off northeast coast, 99 fm (181 m), 21.vii.1902, several colony fragments, largest fragment 2.9 cm high, with poorly preserved hydranths, without gonophores, USNM 22171 [PARALECTOTYPE; this material, identified as *Corydendrium corrugatum*, labelled "cotype," and mentioned by Nutting (1905) under the distribution of that species, is referable instead to *Balella mirabilis* (Nutting, 1905)].–Oahu: Waianae, on Mahi wreck, 60–90 ft (18–27 m), 05.xi.2003, one colony fragment, 6 cm high, without gonophores, coll. S. L. Coles, BPBM (without collection number).–Oahu: Waianae, on Mahi wreck, 60–90 ft (18–27 m), 05.xi.2003, one colony fragment, 5.5 cm high, without gonophores (cormoids of *Monotheca* sp. also present), coll. S. L. Coles, ROMIZ B3819.

Description. Hydroids with erect, robust colonies up to about 15 cm high, arising from a tangled mass of creeping hydrorhizal fibres. Hydrocaulus strongly polysiphonic, up to 6–7 mm thick basally, twisted and root-like in shape, irregularly branched; larger branches polysiphonic and resembling hydrocaulus; smaller, more distal branches tending to be curved, adnate for part of their length to hydrocaulus or to hydrocladia from which they arise, sometimes with a constriction near base, polysiphonic basally, becoming monosiphonic at distal extremity; anterior surface of smaller branches giving off hydrophore-like ultimate branchlets reaching to base of hydranths; ultimate branchlets of varied length but mostly short, alternate, relatively close, adnate to their supporting branch, not annulated but with variably developed concentric wrinkles over much or all of free distal part. Perisarc of moderate thickness, sometimes with wrinkles but mostly smooth except on ultimate branchlets, brown in older parts of colony, becoming straw-coloured distally. Hydranths clavate, retractable into perisarcal sheath of pedicel, about 0.8 mm long, with filiform tentacles scattered over distal half or more of hydranth; tentacles numerous, >20 in number; hypostome elongate to dome-shaped, crater-shaped when wide open.

Gonophores not seen.

Remarks. *Corydendrium corrugatum* Nutting, 1905 was originally described from bathyal waters off Hawaii. Hydroids were distinguished by Nutting (1905) from those of *C. parasiticum* (Linnaeus, 1767) in having a thicker and more rigid hydrocaulus, and in having distinct and decidedly corrugated hydrophores.

The species, provisionally recognised as valid here, has also been reported (or tentatively reported) from Indonesia (Schuchert 2003; Di Camillo *et al*. 2008). Also resembling *C. corrugatum* are hydroids identified as *C. parasiticum* from the Amakusa Islands (Hirohito 1969) and Sagami Bay (Hirohito 1988), Japan, and from northern Australia (Watson 1999: fig. 2). Records from the western Pacific are from much shallower water (<50 m) than the original material from Hawaii.

Nutting (1905) did not designate a holotype for this species. Syntype material from south of Molokai (USNM 22150, USNM 52582) and from northeast of Maui (USNM 22171) exists in the NMNH. A sample from Albatross Station 4135, near Kauai (USNM 22172), has also been listed and marked as type material (it contains a label marked "cotype") of the species, but it was not mentioned by Nutting (1905) and is not considered type material here. In fact, hydroids in both USNM 22171 and USNM 22172, re-examined here, are referable to *Balella mirabilis* Nutting, 1905 and not *C. corrugatum*. To clarify application of the name to a taxon, a large colony from off the south coast of Molokai (USNM 22150) is designated as lectotype of *C. corrugatum*, and colony fragments in another lot from the same station (USNM 52582) comprise paralectotype material. Alhough the paralectotype contains the hydroid fragment illustrated in Nutting's (1905) Plate II, fig. 2, the lectotype colony is larger and overall a better representative of the species in my opinion.

The relationship between *Corydendrium corrugatum* and *C. parasiticum* is open to question. Some corrugations were evident on ultimate branchlets in all hydroids of this genus from Hawaii. It appeared to be more strongly developed in those assigned to *C. corrugatum*, but the difference was not absolute. Two species were recognized here based as much on bathymetry (with *C. parasiticum* in shallow inshore waters and *C. corrugatum* at greater depths) as on the degree of corrugation evident on the ultimate branchlets. Differences in a character such as the robustness of the hydrocaulus, noted by Nutting (1905), would seem to be variable and of limited value in differentiating the two.

Reported distribution. Hawaii. Albatross Stn. 3828, south of Molokai, (583 m); Albatross Stn. 4077, "northeast coast of … Maui, 99 fathoms" (181 m) (Nutting 1905).

Worldwide. Hawaii; (?) Indonesia; (?) Japan; (?) Australia; 16–583 m (Hirohito 1969, as *C. parasiticum*; Watson 1999, as *C. parasiticum*; Schuchert 2003; Di Camillo *et al*. 2008).

Corydendrium parasiticum (Linnaeus, 1767)

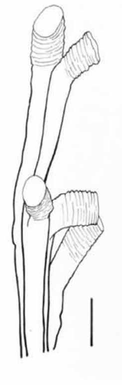
Fig. 3

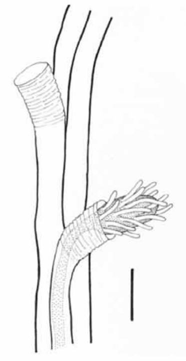
Sertularia parasitica Linnaeus, 1767: 1315.

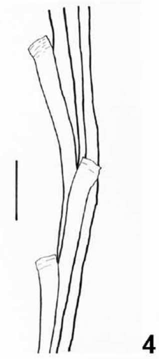
Type locality. "Habitat in Oceano…" (Linnaeus 1767).

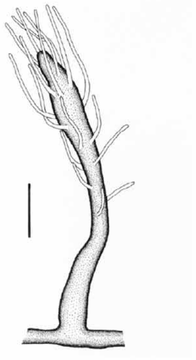
Material examined. Oahu: Pearl Harbor, on boat in drydock, 5.iv.1950, three colony fragments, to 6.2 cm high, without gonophores, BPBM D308.

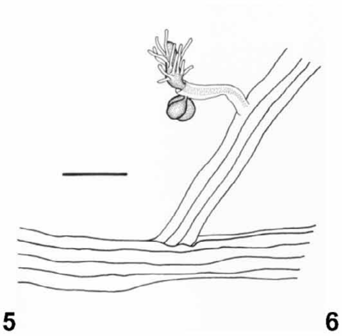
Description. Hydroid colonies erect, straggly, up to 6.2 cm high, arising from a creeping, non-encrusting hydrorhiza. Hydrocaulus and main branches rather crooked, polysiphonic except at distalmost extremities, with stout individual tubes (~0.5 mm in diameter); branching irregular, mostly in one plane; branches adnate to hydrocaulus or to larger branches basally, gradually curving way from supporting stem and becoming free; distalmost branches and branchlets supporting hydranths, tending to be alternate; ultimate branchlets (pedicels) of varied length. Perisarc mostly smooth, mostly of moderate thickness, becoming thin and terminating at end of a tubular ultimate branchlet protecting hydranths, sometimes with striations or wrinkles on branchlets, not annulated, yellowish in older parts of colony, becoming almost clear in younger distal parts, occasionally with adhering silt and detritus. Hydranths clavate to almost cylindrical, about 2 mm long, constricted basally, retractable into perisarcal sheath of varying length; tentacles numerous, filiform, scattered over distal half or more of hydranth, distal ones longer and thicker than those those proximally; hypostome conical, elongate.

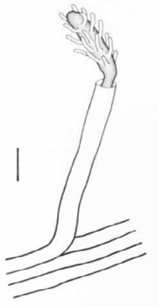


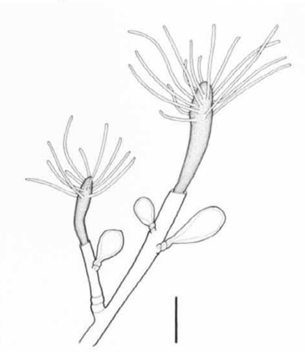


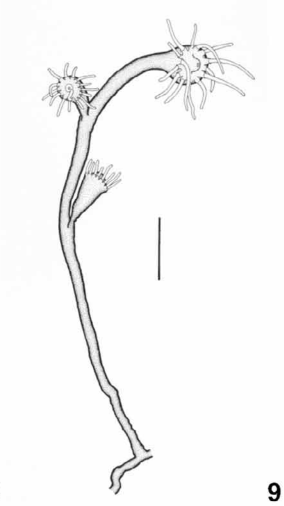


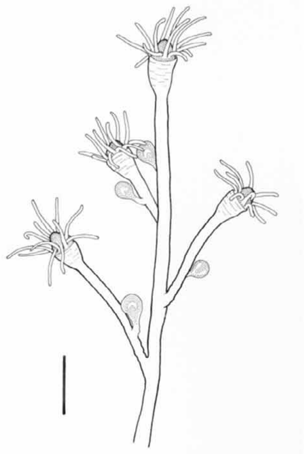












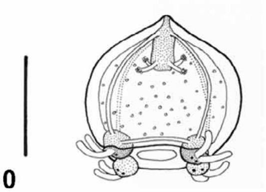


FIGURE 1. *Corydendrium corrugatum*: part of hydrocaulus, hydranths lacking, ROMIZ B3819. Scale equals 0.5 mm.

FIGURE 2. *Corydendrium corrugatum*: part of hydrocaulus of lectotype colony, with a hydranth, USNM 22150. Scale equals 0.5 mm.

FIGURE 3. *Corydendrium parasiticum*: part of hydrocaulus, hydranths lacking, BPBM D308. Scale equals 1 mm.

FIGURE 4. *Rhizogeton* sp.: hydranth, ROMIZ B3833. Scale equals 0.5 mm.

FIGURE 5. *Turritopsis minor*: part of hydrocaulus of lectotype colony, with hydrocladium, hydranth, and gonophores, USNM 22184. Scale equals 0.5 mm.

FIGURE 6. *Turritopsis* cf. *nutricula*: part of colony with a hydranth, ROMIZ B3298. Scale equals 0.25 mm.

FIGURE 7. *Cordylophora caspia*: part of hydrocaulus, with hydranths and gonophores (after Cooke 1977). Scale equals 0.5 mm.

FIGURE 8. *Bimeria vestita*: hydrocaulus with hydranths, ROMIZ B3821. Scale equals 0.5 mm.

FIGURE 9. *Bougainvillia muscus*: part of hydrocaulus with hydranths and medusa buds, ROMIZ B3823. Scale equals 0.5 mm.

FIGURE 10. *Bougainvillia muscus*: newly liberated medusa, ROMIZ B3823. Scale equals 0.5 mm.

Gonophores not seen.

Remarks. The biology and distribution of *Corydendrium parasiticum* (Linnaeus, 1767) has been reviewed by Schuchert (2004), and its synonymy by Calder (1988), Hirohito (1988), and Schuchert (2004). The species is thought to be circumglobal in shallow tropical and subtropical waters, and is widespread in warm regions of the Pacific Ocean (Vervoort 1941; Calder *et al*. 2003; Kirkendale & Calder 2003). The nematocyst complement has been described and illustrated in material from Bermuda by Calder (1988) and from Brazil by Migotto (1996). Lindquist *et al*. (2000) and Stachowicz & Lindquist (2000) identified bioactive secondary metabolites in *C. parasiticum* that acted as deterrents to potential predators.

Reported distribution. Hawaii. Oahu: Pearl Harbor, reported herein.
Worldwide. Circumglobal in warm waters; about 1–90 m (Schuchert 2004).

Genus *Rhizogeton* L. Agassiz, 1862

Rhizogeton L. Agassiz, 1862: 224.
Type species. *Rhizogeton fusiformis* L. Agassiz, 1862, by monotypy.

Diagnosis. Oceaniid hydroids with stolonal colonies. Hydranths arising from hydrorhiza, with thin perisarcal collar at base, varied in shape but nearly cylindrical when extended; tentacles filiform, scattered over much of hydranth; hypostome conical.

Gonophores fixed sporosacs, borne on hydrorhiza.

Remarks. The genus *Rhizogeton* L. Agassiz, 1862 is distinguished from other oceaniid hydroids in having stolonal colonies with fixed gonophores that arise only from the hydrorhiza, and in lacking nematophores. *Rhizodendrium* Calder, 1988 has been considered a synonym (Schuchert 2004; Bouillon *et al*. 2006), and I agree. *Rhizodendrium* was established after comparing *R. sterreri* Calder, 1988 from Bermuda with incompletely described and poorly preserved type material of *Rhizogeton fusiformis* L. Agassiz, 1862, type species of *Rhizogeton*, from Massachusetts. The diagram and description of the hydranth of *R. fusiformis* in L. Agassiz (1862: 224–226, Plate 20) must be considered misleading based on subsequent observations of the species. Abundant fertile colonies identified as *R. fusiformis* from Passamaquoddy Bay, Canada (ROMIZ B3101, ROMIZ B3102) generally overlap *Rhizodendrium sterreri* in important characters such as hypostome shape, tentacle numbers and arrangement, and gonophore morphology, the reasons originally given for establishing *Rhizodendrium* as a distinct genus.

Five species are currently recognized in the genus *Rhizogeton* (Schuchert 2009). Possible undescribed species have been noted in both the Indian Ocean (Gravier-Bonnet & Mioche 1996) and in European waters (Schuchert 2008a: 273–274). Hydroids of *Rhizogeton* are mostly inconspicuous and poorly known, but they now appear to be notably widespread. Representatives have been reported from the Atlantic, Pacific, Indian, and Arctic oceans, and some are known to raft on phoretic substrates such as pelagic *Sargassum* (Calder 1988, 1995).

Rhizogeton sp.

Fig. 4

(?) *Rhizogeton* sp.—Cooke, 1977: 83, fig. 11.

Material examined. Oahu: Kaneohe Bay, south of Kekepa Island, 2 m, 10.iv.1979, on *Porites compressa* in alpheid crevice, 13 colony fragments, without gonophores, coll. W.J. Cooke, BPBM (without catalog number).–Oahu: Kaneohe Bay, south of Kekepa Island, 2 m, 10.iv.1979, on *Porites compressa* in alpheid crevice, several hydranths from sample above, without gonophores, coll. W.J. Cooke, ROMIZ B3833.

Description. Hydroid colonies stolonal, arising from a creeping hydrorhiza usually obscured by algal mat on coral substrate. Perisarc of hydrorhiza thin, translucent, smooth to wrinkled but not annulated, extending over base of hydranth as an almost invisible, filmy, close-adhering sheath (apparent after dissolving a hydranth in sodium hypochlorite). Hydranths essentially sessile, clavate to elongate and almost cylindrical, when extended up to 4 mm long, 0.25 mm wide; tentacles filiform, up to about 25 in number, scattered over distal half to three-quarters of hydranth, distal ones longer, thicker, and closer together than those basally; hypostome conical to proboscis-like. Colour of live hydranths brownish-red, with distinct white spots located at bases of tentacles.

Gonophores not seen.

Remarks. Hydroids assigned to *Rhizogeton* L. Agassiz, 1862 (as *Rhizogeton* sp. and *R. nudum* Broch, 1909) have been reported from a number of locations in warm waters of the Pacific and Indian oceans, including Mozambique (Millard & Bouillon 1974; Millard 1975), La Réunion (Gravier-Bonnet & Mioche 1996), south India (Mammen 1963), Christmas Island (Ritchie 1910b), Enewetak Atoll (Cooke 1975), and Hawaii (Cooke 1977). It is improbable that the cold-water *R. nudum* is present in the tropical and subtropical Indo-Pacific, and records of the species from the region are believed to be based on misidentified material. Hirohito (1988) reported that specimens from Sagami Bay, Japan, identified as *R. ezoense* Yamada, 1964 (type locality: Hokkaido, Japan), resembled those of Millard & Bouillon (1974) from Mozambique.

A hydroid species identified as *Rhizogeton* sp. is frequent in Hawaii inside alpheid crevices on the scleractinian corals *Porites lobata* and *P. compressa* (Cooke 1977; personal observations). Gonophores have yet to be discovered in material from the region. The species is possibly identical with hydroids identified as *Rhizogeton* sp. from shrimp crevices on reef flats in the Indian Ocean at La Réunion by Gravier-Bonnet & Mioche (1996). Their hydrozoan is now considered an undescribed species, fertile colonies have been found, and it has been collected on other islands in the Indian Ocean (Nicole Gravier-Bonnet, pers. comm., 3 July 2009). The coral substrates of the hydroid in Hawaii are abundant and widespread (Maragos 1977).

Reported distribution. Hawaii. No location given, on *Porites lobata*, in alpheid crevices (Cooke 1977). Material examined during this study was collected around Oahu: from Kekepa Island (10.iv.1979, coll. W.J. Cooke); other specimens were observed on similar substrates at Haleiwa Beach (12.vii.2009), and off Kailua Beach (26.vii.2009) (personal observations).

Genus *Turritopsis* McCrady, 1857

Turritopsis McCrady, 1857: 58.
Type species. *Turritopsis nutricula* McCrady, 1857, by monotypy.

Diagnosis. Oceaniid hydroids sometimes stolonal but usually with erect and irregularly branched colonies. Hydrocaulus polysiphonic or less frequently monosiphonic, branched or less often simple; hydrocladia, if present, adnate to hydrocaulus or to other hydrocladia over part of their length basally. Perisarc with firm outer primary and more filmy inner secondary layers, covering hydrocauli and hydrocladia, terminating near hydranth bases. Hydranths club-shaped, lacking perisarc; tentacles filiform, scattered over most of hydranth.

Gonophores, where known, free medusae, borne on pedicels or branches. Medusa thimble-shaped; radial canals surrounded by mass of vacuolated cells at apex of manubrium; marginal tentacles solitary, simple, eight or more; ocelli present.

Remarks. With the publication date of McCrady's account of *Turritopsis* established as 1857 instead of 1859 (Calder *et al*. 1992), earlier concerns (Calder 1988) that this familiar generic name was threatened by the nearly forgotten *Clavula* Wright, 1859a are removed.

Transformation of medusae into polyps has been described in species of this genus (Bavastrello *et al*. 1992; Piraino *et al*. 1996). Although reported relatively infrequently, this peculiar phenomenon has been known for more than a century. Hincks (1865) reported it in a hydractiniid, and other early accounts of such "retrograde metamorphosis" were reviewed by Hincks (1868: xxviii–xxix).

Turritopsis minor **(Nutting, 1905)**

Fig. 5

Corydendrium minor Nutting, 1905: 941, pl. 2, fig. 1, pl. 7, figs. 8, 9.
Turritopsis minor.—Calder, 2004: 20.

Type locality. Hawaii: "north coast of Maui, 95 fathoms" (174 m) (Nutting 1905).

Material examined. Maui: Albatross Stn. 4098, off north coast, 95 fm (174 m), fragments of a colony, to 1.4 cm high, with hydranths and medusa buds, USNM 22184 [LECTOTYPE; labelled "TYPE"].–Maui: Albatross Stn. 4077, off northeast coast, 99 fm (181 m), several colony fragments, to 1.4 cm high, with shriveled hydranths and gonophores (sample appears to have been dry at some time), USNM 22164 [PARALECTOTYPE; labelled "TYPE;" sample also contains a species of *Lafoea*].–Oahu: off Haleiwa, 60 fm (110 m), R/V Valiant Maid (no other collection data), on anthozoan axis, three colony fragments, to 3.1 cm high, with gonophores, BPBM (without collection number).–Oahu: off Haleiwa, 60 fm (110 m), R/V Valiant Maid (no other collection data), on anthozoan axis, small fragment of sample above, ROMIZ B3832.

Other type material. Maui: CAS syntype 018683 (PARALECTOTYPE; Fautin & Weitbrecht 1985).

Description. Hydroid colonies erect, bushy, reaching 3.1 cm high, arising from a dense hydrorhizal mat. Hydrocaulus strongly polysiphonic with slender individual tubes (<0.2 mm in diameter), irregularly and frequently branched, mostly in one plane; main branches resembling hydrocaulus, polysiphonic to strongly polysiphonic basally, gradually becoming thinner and monosiphonic distally, bearing more or less alternate branchlets; ultimate branchlets monosiphonic, slender, of varied length, adnate to stem for some distance basally, then abruptly curving outwards and becoming free distally, often constricted or wrinkled near insertion with stem, supporting a hydranth distally. Perisarc moderately thick, terminating on pedicels below hydranths; colour brownish-yellow in older parts, becoming almost clear distally. Hydranths elongate, clavate to fusiform, about 0.4 mm long, with about 12–16 filiform tentacles scattered over much of hydranth body, with distal ones longer than those at proximal end; hypostome elongate.

Gonophores free medusae. Medusa buds ovoid, attached to ultimate branchlets by short pedicels, one or more per branchlet, enclosed in a thin perisarcal capsule. According to Nutting (1905), manubrium apparently short; mouth quadrate; radial canals four, unbranched; marginal tentacles distinct, numerous but number and arrangement undetermined.

Remarks. Nutting (1905) referred this species to *Corydendrium* Van Beneden, 1844a, but noted that it produces medusae instead of fixed gonophores. It was assigned to the genus *Turritopsis* McCrady, 1857 by Calder (2004). Although Miglietta *et al*. (2007) treated it as valid, they remarked that it was insufficiently characterized because its life cycle was incompletely known. Additional knowledge of the medusa stage, and its reproductive biology, is needed to clarify relationships of the species with other species of the genus. Hydroid populations of a species from shallow waters in Hawaii (see *Turritopsis nutricula* McCrady, 1857 below) seem to differ in colony form from those of the deeper *T. minor* (Nutting, 1905) in being less robust, less branched, and less strongly polysiphonic.

No holotype was designated for *Turritopsis minor* by Nutting (1905). Syntype material from the northeast and north coasts of Maui (USNM 22164, USNM 22184, respectively) exists in the National Museum of Natural History, Washington, DC. Additional syntype material, not examined here, exists at the California Academy of Sciences (CAS syntype 018683, Maui, one colony, IZ164; Fautin & Weitbrecht 1985). A fragmentary colony bearing intact hydranths and medusa buds (USNM 22184) has been chosen here as the lectotype to objectively define the species. Hydroid fragments in USNM 22164, designated as paralectotype material, are shrivelled, and the sample may have been dry sometime in the past. CAS syntype 018683 also comprises paralectotype material.

Reported distribution. Hawaii. Albatross Stn. 3859, "between … Molokai and Maui, 138 fathoms" (252 m); Albatross Stn. 4077, "northeast coast of Maui, 99 fathoms" (181 m); Albatross Stn. 4098, "north coast of Maui, 95 fathoms" (174 m) (Nutting 1905).
Worldwide. Known only from Hawaii.

***Turritopsis* cf. *nutricula* McCrady, 1857**

Fig. 6

Oceania (*Turritopsis*) *nutricula* McCrady, 1857: 56, pl. 4, figs. 1–10, 12–15, 28a; pl. 5, figs. 11, 16–18, 28b.
Turritopsis nutricula.–Cooke, 1977: 82, fig. 10.–Grovhoug & Rastetter, 1980: 252.

Material examined. Oahu: Kaneohe Bay, shallow water, x.1972, six colony fragments, now in poor condition, up to 1.6 cm high, with medusa buds (and medusae in second vial), coll. W.J. Cooke, BPBM D456.–Oahu: Kaneohe Bay, Kaneohe Yacht Club, dock (Stn. 20); 5.xi.1999, one colony, 1.9 cm high, with medusa buds, coll. R. DeFelice and S. Coles, ROMIZ B3298.–Oahu: Kaneohe Bay, Coconut Island reef, 8.xi.1999, two fragmentary colonies, 0.8 and 0.6 cm high, with medusa buds, coll. R. DeFelice and S. Coles, ROMIZ B3300.–Oahu: Kaneohe Bay, Coconut Island, 24.vii.2009, on sponges, two colonies, to 1.9 cm high, with medusa buds, coll. D.R. Calder, ROMIZ B3820.

Description. Hydroid colonies erect, up to 1.9 cm high, arising from a creeping hydrorhiza. Hydrocaulus and main branches polysiphonic over most of length in larger colonies, smaller colonies less strongly so, becoming monosiphonic at distal extremities, irregularly branched; branches adnate basally, curving gradually to abruptly outwards and becoming free distally. Perisarc moderately thin, terminating at hydranth base below tentacles, never annulated, clear to yellowish, outer layer mostly smooth, inner layer with wrinkles and creases; pedicels of nearly equal diameter throughout. Hydranths clavate to nearly spindle-shaped, up to 1.4 mm long, 0.2 mm wide; tentacles filiform, 14–24 in number, scattered over distal three-quarters or more of hydranth, distal ones longer and thicker than those basally; hypostome conical to proboscis-like.

Gonophores free medusae. Medusa buds globular, enveloped in filmy perisarc, attached by short pedicels to stem and branches, most frequent on ultimate branchlets below hydranths, often with as many as 7–8 buds in close proximity and at various stages of development surrounding a branchlet, manubrium short; radial canals four; tentacles retracted into subumbrellar cavity.

Remarks. The identity of this hydrozoan in Hawaiian waters, generally assigned in the past to *Turritopsis nutricula* McCrady, 1857, cannot be established with certainty on the basis of its hydroid trophosome alone. Knowledge about morphology and reproductive strategies of its virtually unstudied medusa stage is necessary, but such information is presently lacking. The prevailing identification is provisionally retained here until the taxonomy of the species is better resolved.

Miglietta *et al*. (2007) referred Cooke's (1977) report of *Turritopsis nutricula* from Ala Wai Yacht Harbor, Oahu, to the offshore Hawaiian species *T. minor* Nutting, 1905 solely on zoogeographic grounds. However, comparisons of shallow inshore and deeper water offshore populations of the genus *Turritopsis* McCrady, 1857 from the region are needed before it can be determined whether or not they are conspecific. This hydrozoan also shares some characters with the widespread *T. dohrnii* (Weismann, 1883), *T. polycirrha* (Keferstein, 1862) from Europe, and *T. rubra* (Farquhar, 1895) from Tasmania and New Zealand, as well as *T. nutricula* from the east coast of the Americas. Differences among these species were summarized in Schuchert (2004), who discovered that European populations previously thought conspecific with the oviparous *T. nutricula* were referable instead to either *T. dohrnii* or especially to the larviparous *T. polycirrha*. Indeed, Miglietta *et al*. (2007) suggested on the basis of molecular studies that *T. nutricula* was restricted to the western Atlantic

Ocean. More evidence is needed to support that claim, but their results establish that other species have frequently been misidentified as *T. nutricula*, especially in the Mediterranean Sea and in Japanese waters.

Meanwhile, Carlton & Eldredge (2009) believed *T. nutricula* had been introduced to Hawaii, possibly from the North Atlantic and likely by shipping. Extensive naval and merchant ship activities have been carried out for decades between Honolulu and ports on the Atlantic and Gulf coasts of the United States, where *T. nutricula* is common (Calder 1971; Calder & Cairns 2009). Moreover, American oysters (*Crassostrea virginica*), a known substrate of *T. nutricula* (Calder 1971: 31), were introduced to Hawaii several times during the late 19th and early 20th centuries (Carlton & Eldredge 2009). Yet hydroids from Hawaii appear to be unlike *T. nutricula* from the type locality of Charleston Harbor on the Atlantic coast of the United States in having colonies of moderate size (often 1–2 cm or more in height) that are branched and polysiphonic rather than small (less than 1 cm), sparingly branched or unbranched, and monosiphonic. *Turritopsis dohrnii* is also known to be invasive, having recently been reported from worldwide loactions (Miglietta & Lessios 2009). As for the shallow-water species of *Turritopsis* from Hawaii, research on the medusa stage and its modes of reproduction, molecular investigations, or both are needed to establish its identity.

Material above catalogued as BPBM D456 contained two vials, one with hydroids and a second labelled "*T. nutricula* medusae." Medusae are no longer present in this vial.

Reported distribution. Hawaii. Oahu: Ala Wai Yacht Harbor, on stems of *Pennaria* (Cooke 1977). Worldwide. Western Atlantic; reports from elsewhere including Hawaii need verification (Miglietta *et al*. 2007; Miglietta & Lessios 2009).

Family Cordylophoridae von Lendenfeld, 1885

Cordylophorinae von Lendenfeld, 1885: 221.

Diagnosis. Filiferan hydroids with erect, monopodial colonies; arising from a creeping hydrorhiza. Hydrocaulus branched, with hydrocladia given off immediately from hydrocaulus rather than being adnate to it for a varying distance basally; perisarc enveloping hydrocauli, hydrocladia, pedicels, and hydrorhiza, not extending over hydranths as a pseudohydrotheca. Hydranths spindle-shaped; tentacles filiform, scattered over hydranth body; hypostome conical to nipple-shaped.

Gonophores fixed sporosacs, borne on hydrocladia and hydranth pedicels; spadix branched.

Remarks. Cordylophoridae von Lendenfeld, 1885 was originally established as a subfamily (Cordylophorinae) within Clavidae McCrady 1859. Two genera were originally included in it, *Cordylophora* Allman, 1843 and *Merona* Norman, 1865. In having polymorphic hydranths and nematophores, however, *Merona* differs significantly from *Cordylophora* and was removed from Cordylophorinae (Calder 1988). The single remaining genus *Cordylophora* has been assigned in most recent works to Oceaniidae Eschscholtz, 1829. Cordylophoridae has been recognized as valid in the World Hydrozoa Database, but its recognition may be temporary because molecular studies on *Cordylophora* suggest an affinity with Bougainvilliidae Lütken, 1850 (Schuchert 2009). As for Clavidae, its type genus (*Clava* Gmelin, 1791) is now known to be a hydractiniid (see Remarks above under family Oceaniidae).

Genus *Cordylophora* Allman, 1843

Cordylophora Allman, 1843: 395.

Type species. *Cordylophora lacustris* Allman, 1843, a junior subjective synonym of *Tubularia caspia* Pallas, 1771 [*Cordylophora caspia*], by monotypy.

Diagnosis. With characters of the family.

Remarks. The author and date of the generic name *Cordylophora* is customarily cited as Allman (1844). However, as shown earlier by Sherborn (1925) and Neave (1939a), the name was made available the previous year by Allman (1843).

Cordylophora caspia (Pallas, 1771)

Fig. 7

Tubularia caspia Pallas, 1771: 479.
Cordylophora caspia.—Cooke, 1977: 81, fig. 9.

Type locality. "In Mari Caspio…" (Pallas 1771).

Material examined. None.

Description. (From Cooke 1977: 81–82): "This rather large hydroid is characterized by irregular loosely branched stems up to 15 mm tall and 0.2 to 0.25 mm in diameter with polyps given off semialternately and terminally… The polyps are 1 mm to 2 mm in total length with 10 to 20 scattered filiform tentacles and are dull red distally. The perisarc of the stem ends well beneath the body of the polyp. Many gonophores are present on the colony, two to four (no more) on the stem, usually 1 mm or so below the terminal polyps (not as low on the side polyps). The orange gonophores are covered by the perisarc and are elongate-oval in shape, 1 mm long (including pedicel) by 0.3 mm maximum diameter."

Remarks. An overview of *Cordylophora caspia* (Pallas, 1771) and its biology has recently been given by Schuchert (2004). He provided a synonymy list, taxonomic comments, information on ecology and distribution, and an overview of morphological variation in the species. This hydroid is believed to have originated in the Ponto-Caspian region (Folino-Rorem *et al*. 2009), and is currently the focus of numerous studies as an invasive species (see *Zoological Record*).

Cordylophora caspia in the recent past has generally been regarded as conspecific with *C. lacustris* Allman, 1843 (Cairns *et al*. 2002). However, molecular studies now provide evidence of the existence of multiple cryptic species in *C. caspia* (Schable *et al*. 2008). Folino-Rorem *et al*. (2009) identified several lineages of these hydroids, each having different salinity tolerances. Some lineages had wide geographic ranges, yet different lineages were also frequently sympatric. Dispersal is thought to have occurred by shipping. No hydroids from Hawaii were included in the analyses of Folino-Rorem *et al*. (2009), and genetic affinity of the local population is unknown.

Hydroids assigned to the genus *Cordylophora* Allman, 1843 are circumglobal in brackish waters (Schuchert 2004), and they penetrate into limnic biotopes, even those with soft water and low alkalinity (Smith *et al*. 2002). Specimens have been widely utilized in experimental work on cnidarians (Vervoort 1995), and are readily cultured (Kinne 1977: 656). Optimum conditions for colony development under laboratory conditions (Kinne 1956) are reportedly in waters of low salinity (2–18‰) and moderate temperature (11–18° C). In nature, colonies are frequently found at salinities of 7‰ or lower (Vervoort 1946; Calder 1976). Hydroids become dormant during winter in regions with colder climates (Smith 2001). Sexual reproduction occurs by fixed gonophores. According to Bouillon (1985), larvae may develop within the gonophores to an advanced stage, occasionally even to the young polyp stage.

This species was discovered on algae growing in anchialine waters (Halua Pond) on Cape Kinau, Maui, during the summers of 1974 and 1975 (Cooke 1977; Carlton & Eldredge 2009). No material of *C. caspia* was found in collections at the Bishop Museum.

Reported distribution. Hawaii. Maui: Cape Kinau, in an anchialine pond on the chlorophyte *Caulerpa serrulata* (Cooke 1977).

Worldwide. Circumglobal in temperate and tropical brackish to fresh waters; 0–85 m (Fraser 1944, as *Cordylophora lacustris*; Vervoort 1946; Naumov 1960; Smith 2001; Smith *et al*. 2002; Schuchert 1996, 2004).

Family Bougainvilliidae Lütken, 1850

Bougainvilleae Lütken, 1850:29 [emended to Bougainvilliidae by Allman (1876)].

Diagnosis. Filiferan hydroids colonial, stolonal or erect; arising from a creeping hydrorhiza; growth monopodial with terminal hydranths. Perisarc thin to thick, enveloping hydrocauli, hydrocladia, pedicels, and hydrorhiza, terminating at bases of hydranths or extending upwards as a pseudohydrotheca. Hydranths club-shaped to vasiform; tentacles filiform, in one or more distal whorls; hypostome conical to nipple-shaped.

Gonophores fixed sporosacs or free medusae. Medusae, when present, bell-shaped, with typically short manubrium and circular mouth; oral tentacles simple or dichotomously branched, rarely lacking; radial canals four; marginal tentacles solitary or in clusters, borne on 4, 8, or 16 tentacle bulbs; gonads on manubrium.

Remarks. For comments on the family Bougainvilliidae Lütken, 1850, see Calder (1988) and Schuchert (2007). It presently comprises 15 genera and about 100 species (Schuchert 2009).

Genus *Bimeria* Wright, 1859a

Bimeria Wright, 1859a: 109.
Type species. *Bimeria vestita* Wright, 1859a, by monotypy.

Diagnosis. Bougainvilliid hydroids stolonal or erect and more or less alternately branched, arising from a creeping hydrorhiza. Erect colonies with monosiphonic hydrocaulus. Perisarc filmy to firm, covering hydrorhiza, hydrocauli, hydrocladia, and pedicels, enveloping hydranth and extending as a sheath over bases of tentacles and around periphery of hypostome. Hydranths ovoid to vasiform; tentacles filiform, in a distal whorl; hypostome dome-shaped.

Gonophores fixed sporosacs, arising from hydranth pedicels.

Remarks. *Bimeria* Wright, 1859a and *Manicella* Allman, 1859 have long been regarded as simultaneous synonyms because both were published in July issues of journals that year (Calder 1988). Precedence was assigned to the name *Bimeria* by Hincks (1868), acting as First Reviser. Even Allman (1872) eventually accepted the relative priority of the two. However, Allman's (1859) account of *Manicella* appeared in an issue of the *Annals and Magazine of Natural History* that can now be dated as 1 July 1859 (Evenhuis 2003). The dating of Wright's (1859a) account of *Bimeria* is less certain. In the journal itself, only the month of publication (July) is given, and publication date can only be taken here as 31 July 1859 (ICZN Art. 21.3.1). Wright's (1859b) later claim of priority for *Bimeria* and the species name *B. vestita* Wright, 1859a was based on having found the hydroid first and having presented the names before a meeting of the Royal Physical Society of Edinburgh in January 1859. Such claims have no standing in zoological nomenclature, and the two names were not made available until they appeared in print in Wright's (1859a) article. Nomenclatural stability is threatened when the virtually unknown *Manicella* and its type species by monotypy *M. fusca* Allman, 1859 become senior synonyms of the now widely used *Bimeria* and its type species *B. vestita*. Using Reversal of Precedence under the current code (ICZN Art. 23.9), *Bimeria* and *B. vestita* are designated here as valid and as nomena protecta, while *Manicella* and *M. fusca* are relegated to nomena oblita. First, the names *Manicella* and *M. fusca* have not been used as valid names in zoological nomenclature after 1899 (ICZN Art. 23.9.1). Meanwhile, *Bimeria* and the species name *B. vestita* have been used in at least 25 works by more than 10 authors in the past 50 years (ICZN Art. 23.9.2): Millard (1975), Calder (1988, 1993, 1998, 2009), Hirohito

(1988), Medel & López-González (1996), Migotto (1996), Grohmann *et al*. (1997), Rajagopal *et al*. (1997), Genzano & Rodriguez (1998), Genzano & Zamponi (1999), Cairns *et al*. (2002), Migotto *et al*. (2002), Kelmo *et al*. (2003), Bouillon *et al*. (2004, 2006), Calder & Kirkendale (2005), Shimabukuro *et al*. (2006), Vervoort (2006), Altuna (2007), Galea (2007), Oliveira & Marques (2007), Schuchert (2007), Morri *et al*. (2009).

Hydroids of *Bimeria* and *Koellikerina* Kramp, 1939 are distinctive in having tentacles ensheathed basally in a tube of perisarc. While their trophosomes are similar, gonophores are fixed sporosacs in *Bimeria* and free medusae in *Koellikerina*. Both genera were assigned earlier to the subfamily Bimeriinae Allman, 1872 (Calder 1988). The hydroid stage is not reliably known in *Thamnostoma* Haeckel, 1879, a related genus (Petersen & Vannucci 1960; Schuchert 2007).

Taxonomic reviews of *Bimeria* have been given previously in reports by Calder (1988) and Schuchert (2007). The genus was also included in the synopsis of Bouillon *et al*. (2006), although its scope therein overlaps *Garveia* Wright, 1859a, assigned to a different subfamily (Bougainvilliinae Lütken, 1850). Of nine species listed under *Bimeria* in that work, at least three, *Bimeria cerulea* [=*Calyptospadix cerulea* Clarke, 1882], *B. tunicata* Fraser, 1943, and *B. robusta* Torrey, 1902, are referable to *Garveia* (Vervoort 1964; Cairns *et al*. 2002). As well, the genus *Calyptospadix* Clarke, 1882, included by Bouillon *et al*. (2006) as a synonym of *Bimeria*, has been combined instead with *Garveia* (Calder 1971). The type species of *Calyptospadix*, *C. cerulea*, may be conspecific with *G. franciscana* (Torrey, 1902) (Cairns *et al*. 2002). *Bimeria rigida* Warren, 1919, an outlier in the genus, has a preoral cavity in the hydranth and close-fitting perisarc around each tentacle instead of a loose tube. Its taxonomy merits closer study.

***Bimeria vestita* Wright, 1859a**

Fig. 8

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

Type locality. Firth of Forth, Scotland (Wright 1859a).

Material examined. Oahu: Hawaii Kai, on pilings of bridge over Highway 72, 21º17'06.60"N, 157º43'07.21"W, 0.1 m, 27.vii.2009, on small oyster shell, one colony, with stems up to 4 mm high, without gonophores, coll. D.R. Calder, ROMIZ B3821.

Description. Hydroid colony up to 4 mm high, with both simple and sparsely branched stems, arising from a creeping hydrorhiza. Hydrocaulus monosiphonic, unbranched or with a few irregular, short, cone-shaped branches each with a single terminal hydranth, narrowest at base, gradually expanding distally. Perisarc quite thick at base of hydrocaulus and on stolons of hydrorhiza, becoming thinner distally, irregularly smooth to wrinkled, nowhere regularly annulated, almost completely obscured by encrusting silt and other dirt, covering hydranth except for mouth region on hypostome, extending as tubular sheaths over proximal ends of tentacles. Hydranths vasiform, about 0.3 mm long, merging almost imperceptably with supporting hydrocaulus or branch; tentacles filiform, amphicoronate, in two close but distinctly separated whorls, about 14–15 in number, emerging through perisarcal sheath covering hydranth; hypostome low, conical.

Gonophores not seen.

Remarks. The taxonomy, nomenclature, and general biology of *Bimeria vestita* Wright, 1859a have been reviewed in a number of previous works, including Calder (1988), Hirohito (1988), Genzano & Zamponi (1999), Marques, Mergner *et al*. (2000), Vervoort (2006), and Schuchert (2007). Although small and inconspicuous, it has been reported over a wide area geographically and is considered to be essentially circumglobal in shallow, warm to temperate waters.

Reported distribution. Hawaii. New record.

Worldwide. Western and eastern Pacific; western and eastern Atlantic; Indian Ocean; 0–200 m (Fraser 1938a; Millard 1975; Calder 1988; Hirohito 1988; Vervoort 2006; Schuchert 2007).

Genus *Bougainvillia* Lesson, 1830

Bougainvillia Lesson, 1830: 118.
Type species. *Bougainvillia macloviana* Lesson, 1830, by monotypy.

Diagnosis. Bougainvilliid hydroids sometimes stolonal but usually erect and irregularly branched, arising from a creeping hydrorhiza. Erect colonies with monosiphonic or polysiphonic hydrocaulus. Perisarc filmy or firm, covering hydrorhiza, hydrocauli, hydrocladia, and pedicels, terminating near hydranth bases or forming a pseudohydrotheca, not enveloping bases of tentacles. Hydranths club-shaped to fusiform; tentacles filiform, amphicoronate, in a distal whorl; hypostome conical to dome-shaped.

Gonophores predominantly free medusae, exceptionally as eumedusoids, borne singly or in clusters on hydrocauli, hydrocladia, pedicels, or hydrorhiza. Medusae bell-shaped; manubrium short; oral tentacles four, perradial, usually branched dichotomously; radial canals four; tentacle bulbs four; marginal tentacles all filiform, clustered on tentacle bulbs; ocelli usually present; gonads on manubrium; medusa buds sometimes produced.

Remarks. Species of *Bougainvillia* Lesson, 1830 occur worldwide. Their hydroids can be difficult to identify, often resembling one another in colony form and varying in morphology under different environmental conditions (Vannucci & Rees 1961). One species of the genus is known to occur in Hawaii.

Bougainvillia muscus (Allman, 1863)

Figs. 9–11

Perigonymus muscus Allman, 1863: 12 [incorrect subsequent spelling of *Perigonimus* M. Sars, 1846].
Bougainvillia sp.—Tusov & Davis, 1971: 52.
Garveia sp.—Cooke, 1977: 84, fig. 12.
Bougainvillia ramosa.—Cooke, 1977: 84, fig. 13.
Garveia humilis.—Grovhoug & Rastetter, 1980: 252.

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

Material examined. Oahu: Honolulu Harbor, 26.vi.1945, several tangled colonies with entoprocts, to 2.5 cm high, with gonophores, BPBM D258.–Oahu: Honolulu Harbor, 2.vii.1945, several tangled colonies, to 5.3 cm high, without hydranths and gonophores, BPBM D261.–Oahu: Pearl Harbor, Dry Dock #2, 29.iii.1948, >100 colony fragments, to 6 cm high, with gonophores, BPBM D288.–Oahu: Honolulu Harbor, Ala Wai Yacht Harbor, 1 m, on stems of *Pennaria disticha*, no date, one colony, to 1 cm high, with medusa buds, identified as *Garveia humilis*, BPBM (without collection number).–Oahu: Pearl Harbor, Station 15, 21º22’19” N, 157º56’09” W, 27.xi.2007, one colony, to 1.8 cm high, with medusa buds, coll. S.L. Coles, ROMIZ B3822.–Oahu: Honolulu Harbor, La Mariana Sailing Club dock, 21º19’16.90” N, 157º53’37.95” W, 16.vii.2009, 3 colony fragments, to 4.5 cm high, with medusa buds (and medusae liberated in laboratory), coll. D.R. Calder, ROMIZ B3823.

Description. Hydroid colonies erect, up to 6 cm high, arising from a creeping hydrorhiza. Hydrocaulus monosiphonic, somewhat crooked, irregularly branched, widest at base, narrowest distally; perisarc of hydrocaulus golden-colored, relatively thick basally, thinner elsewhere, with sporadic wrinkles but otherwise essentially smooth; main branches tortuous, more slender than hydrocaulus; perisarc of main branches wrinkled basally, tending to be crinkled elsewhere, not annulated; terminal branchlets slender basally, shorter ones gradually increasing in diameter distally, longer ones tending to be cylindrical beyond base, extreme proximal end wrinkled to spirally twisted; perisarc of branchlets crinkly, extending distally as a cup-shaped pseudohydrotheca over base of contracted hydranth, not extending as a sheath over bases of tentacles or over hypostome. Hydranths cylindrical to fusiform; tentacles filiform, 12–16 in number, amphicoronate, arranged in two close whorls around distal end of hydranth; hypostome conical. Endoderm of hydranths ochre-coloured in life.

Gonophores free medusae. Medusa buds pear-shaped, invested with thin perisarc, arising via short stalks on terminal branchlets below hydranths. Newly liberated medusae thimble-shaped, umbrella 0.6–0.7 mm high, 0.5–0.6 mm wide; mesoglea moderately thick; umbilical canal present at apex; vestige of pedicel attaching medusa bud to hydroid sometimes forming an apical wart or small cone, peduncle lacking; manubrium short, small, tubular, with simple mouth; oral tentacles four, unbranched, inserted on manubrium just above mouth, appearing slightly capitate with a small cluster of nematocysts at distal end; radial canals four; ring canal present; tentacle bulbs four, conical, base rounded; marginal tentacles filiform, eight, with two per tentacle bulb; ocelli eight, conspicuous, dark red, one at base of each tentacle; velum broad; endoderm of manubrium and tentacle bulbs cream to orange-coloured. One-day-old laboratory-raised medusae about 1 mm high and wide; oral tentacles unbranched; marginal tentacles two per tentacle bulb; gonads beginning development interradially on manubrium. Three-day-old medusae about 1.3 mm high and wide; oral tentacles unbranched; marginal tentacles 12, with three per tentacle bulb; ocelli eight; exumbrellar surface dotted with minute batteries of nematocysts; gonads well-developed, one with mature egg bearing an outer envelope armed with numerous heterotrichous microbasic euryteles.

Remarks. Cooke (1977) reported this species from Hawaii, as *Bougainvillia ramosa* (Van Beneden, 1844b). That name was later shown to be invalid (Calder 1988) and has been replaced by the binomen *B. muscus* (Allman, 1863). Cooke believed that the hydroid reported from the same area by Tusov & Davis (1971) as *Bougainvillia* sp. was conspecific with his material, and I agree. Hydroids from Ala Wai Yacht Harbor, Oahu, identified by Cooke (1977) as *Garveia* sp., are also regarded here as small colonies of *B. muscus*. So too are the records of *Garveia humilis* (Allman, 1877) from Pearl Harbor and Kaneohe Bay by Grovhoug & Rastetter (1980). The complicated taxonomy of *Bougainvillia muscus* has been reviewed recently by Calder (1988) and Schuchert (2007).

It seems remarkable zoogeographically that a species originally described from southern England might occur in Hawaii and elsewhere in the central and western Pacific. While *Bougainvillia muscus* is reportedly widespread in coastal waters of the Atlantic, Pacific, and Indian oceans (e.g. Millard 1975; Calder 1988; Schuchert 1996), the probability that such a wide range actually exists is given more credibility in light of 16S sequence data by Schuchert (2007). Divergence values of European and New Zealand populations were found to be quite low, suggesting that they are indeed conspecific.

Hydroids of *Bougainvillia muscus* were frequent on floating docks in sheltered waters of Honolulu Harbor and Pearl Harbor, Hawaii, during July 2009. Medusae liberated from these colonies were raised to maturity in the laboratory during this study. Specimens were kept at room temperature (21º C) in a covered beaker containing natural seawater, and fed newly hatched *Artemia* twice a day. Water was changed after each feeding. Development was somewhat slower than described in medusae of this species from Bermuda (Calder 1988). While gonads began to appear at about the same time (two days after liberation), development of a third marginal tentacle per tentacle bulb was observed in three-day-old medusae, a day later than those from Bermuda. Branching of oral tentacles was also delayed, with most still unbranched even after four days. Differences are attributed to different culture conditions. Specimens from Bermuda were raised at warmer temperatures (28–29º C) and fed several times a day instead of just twice. Medusae of this species are thought to be short-lived; of those raised in Bermuda, none lived longer than 3.5 days. Those raised in Hawaii were preserved at maturity after four days.

Information on ecology and distribution of this species is given by authors including Peña Cantero & García Carrascosa (2002), Vervoort (2006), and Schuchert (2007). *Bougainvillia muscus* appears to be nearly cosmopolitan in warm and temperate regions.

Reported distribution. Hawaii. Oahu: Kaneohe Bay (Tusov & Davis 1971); Kaneohe Bay, on stems of *Halocordyle* [=*Pennaria disticha*] (Cooke 1977, as *B. ramosa*); Ala Wai Yacht Harbor (Cooke 1977, as *Garveia* sp.); Pearl Harbor and Kaneohe Bay (Grovhoug & Rastetter 1980, as *Garveia humilis*).

Worldwide. Western and eastern Pacific; western and eastern Atlantic; Indian Ocean; 0–100 m, doubtful to 1193 m (Calder 1988; Peña Cantero & García Carrascosa 2002; Schuchert 2007; Mills *et al*. 2007).

Family Pandeidae Haeckel, 1879

Pandaeidae Haeckel, 1879: 46 [emended to Pandeidae by Bigelow (1913)].

Diagnosis. Filiferan hydroids colonial, generally stolonal, a few having small, erect cormoids, rarely with polysiphonic hydrocaulus; arising from a creeping hydrorhiza, or, in taxa ectoparasitic on fishes and ichthyoparasitic copepods, from a basal plate embedded in tissues of host. Perisarc varying in development; pseudohydrotheca present or absent. Hydranths club-shaped to vasiform to bulbous to tubular; tentacles filiform, usually in one whorl, some taxa with 2–3 whorls, or scattered, or absent; hypostome usually conical; hydranths of parasitic forms degenerate, elongate, atentaculate, and lacking perisarc.

Gonophores usually free medusae, exceptionally as fixed gonophores in certain parasitic forms. Medusae, when present, bell-shaped; apical projection present or absent. Manubrium large, quadrate, with or without peduncle; mouth usually bordered by four lips; oral tentacles absent. Radial canals usually four, rarely eight; centripetal canals usually absent; mesenteries present or absent. Marginal tentacles hollow, filiform, two, four, or more; basal bulbs and ocelli present or absent. Gonads on manubrium, occasionally extending onto radial canals.

Remarks. A taxonomic discussion of the family Pandeidae Haeckel, 1879, and superfamily Pandeoidea Haeckel, 1879, has been given previously (Calder 1988). Bouillon *et al*. (2006) assigned 25 genera to the family, with 10 of those known only as the medusa stage. Diagnoses of the family and of some 12 genera assigned to it were given by Schuchert (2007), who remarked on the need for a comprehensive phylogenetic review of pandeid genera. Where described, pandeid hydroids are mostly small and quite simple polypoid forms, and offer a paucity of morphological characters for differentiation. Pandeidae, comprising some 75 species, is “probably not monophyletic” (Daly *et al*. 2007).

Genus *Amphinema* Haeckel, 1879

Amphinema Haeckel, 1879: 49.

Type species. *Oceania dinema* Péron & Lesueur, 1810 [*Amphinema dinema*], by subsequent designation by Rees & Russell (1937).

Diagnosis. Pandeid hydroids stolonal (unless *Bimeria biscayana* Browne, 1907 is included; see Schuchert 2007), arising from a creeping hydrorhiza. Hydrocaulus simple, slender, of moderate length, often annulated basally, gradually expanding in diameter distally. Perisarc covering hydrorhiza and hydrocaulus, terminating below hydranth base; pseudohydrotheca absent. Hydranths clavate; tentacles filiform, amphicoronate, eight or more, in a distal whorl; hypostome dome-shaped.

Gonophores free medusae; medusa buds borne on short pedicels arising from hydrorhiza, or caulus, or both. Medusae bell-shaped, usually with large apical process, gastric peduncle absent; manubrium broad at base; oral lips four, simple, little or not crenulated; mesenteries between manubrium and radial canals present or absent; radial canals four; marginal tentacles two, opposite, perradial, large; tentaculae or marginal warts present or absent; ocelli present or absent; gonads adradial, interradial, or perradial, sometimes extending onto radial canals.

Remarks. The genus *Amphinema* Haeckel, 1879 was founded for two nominal species, *Saphenia titania* Gosse, 1853 and *S. apicata* McCrady, 1859. Both are now generally included in the synonymy of *Oceania dinema* Péron & Lesueur, 1810 (=*Amphinema dinema*) (Mayer 1910a; Russell 1953; Kramp 1961; Schuchert 2007). However, Haeckel's (1879) account of *S. titania* was evidently based in part on a species not described until later, *Stomotoca rugosa* Mayer, 1900a (=*Amphinema rugosum*) (Rees & Russell 1937; Russell 1953).

Some misinformation exists in the literature about the type species of *Amphinema*. Rees & Russell (1937: 70) stated that Haeckel (1879) had fixed *Amphinema titania* as "genotype," but Haeckel in fact did not designate a type species for the genus. After providing a new definition of *Amphinema*, Rees & Russell (1937: 70) chose *A. dinema* as type species. Their designation is valid because (1) no previous type species designation exists for the genus (ICZN Art. 69.1), and (2) *O. dinema* was included in *Amphinema* by Haeckel (1879) as a synonym of *A. titania* (ICZN Art. 67.2). This type fixation has been accepted as valid by authors including Russell (1953), Kramp (1961), and Schuchert (2007).

Amphinema sp.

Fig. 12

Material examined. Oahu: Hawaii Kai, on pilings of bridge over Highway 72, 21º17'06.60"N, 157º43'07.21"W, 0.1 m, 27.vii.2009, on small oyster shell, one colony, to 2.5 mm high, without gonophores, coll. D.R. Calder, ROMIZ B3824.

Description. Hydroid colonies stolonal, small, up to about 2.5 mm high, arising from a creeping hydrorhiza. Hydrocaulus simple, of varied length, exceedingly slender basally, gradually increasing in diameter towards terminal hydranth. Perisarc investing hydrorhiza and hydrocaulus thin, clear to straw-coloured, smooth except for a few wrinkles or annulations at base of hydrocaulus, ending perceptibly or almost imperceptibly below hydranth base; hydranths club-shaped, reaching about 1 mm long, widest at tentacular whorl, narrowest at base; tentacles filiform, amphicoronate, in two close whorls around distal end of hydranth, about 12–14 in number; hypostome dome-shaped to elongate. Endoderm of hydranths a conspicuous orange-red colour in life. When disturbed, hydranths bend over sharply, as noted in other described species of the genus.

Medusa buds not seen.

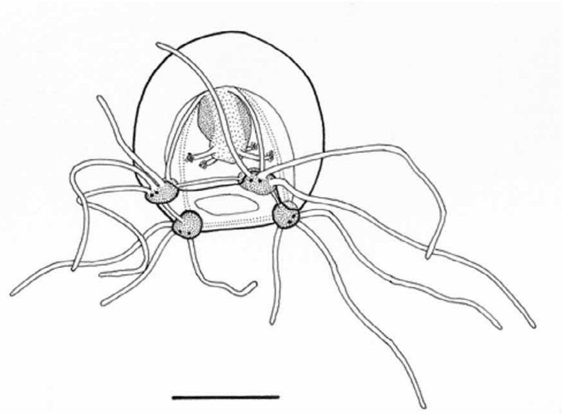
Remarks. Hydroids are known for only three of about 12 currently recognized species of the genus *Amphinema* Haeckel, 1879. The specimens from Hawaii Kai cannot reliably be identified to species, especially in the absence of gonophores and information on their life cycle. Trophosomes are essentially identical with those of *A. dinema* (Péron & Lesueur, 1810) and *A. rugosum* (Mayer, 1900a), two species that are morphologically indistinguishable in the absence of medusa buds (Russell 1953; Schuchert 2007). Also similar is the hydroid of *Amphinema* sp. from Bodega Bay, California, described by J.T. Rees (2000). Unlike *A. rollinsi* Widmer, 2007 from deep waters of the Monterey Bay Submarine Canyon, California, colonies are strictly stolonal and perisarc investing the hydrocaulus is smooth and more slender. Hydroids referable to the genus *Amphinema* have not been reported before from Hawaii.

Reported distribution. Hawaii. New record.

Genus *Hydrichthys* Fewkes, 1887

Hydrichthys Fewkes, 1887: 604.
Type species. *Hydrichthys mirus* Fewkes, 1887, by monotypy.

Diagnosis. Pandeid hydroids with colonies ectoparasitic on fishes and on ichthyoparasitic copepods. Zooids monomorphic or dimorphic, atentaculate, clavate to tubular, arising from a basal encrusting plate or reticular hydrorhiza; perisarc absent.



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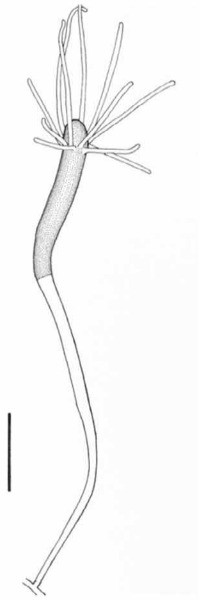

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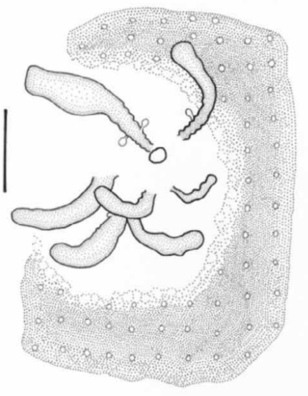

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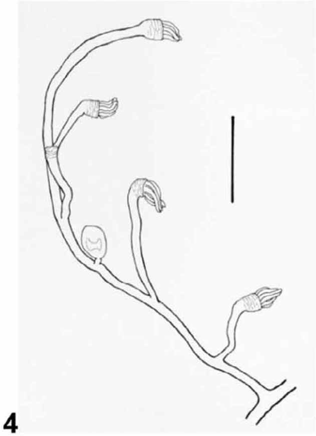

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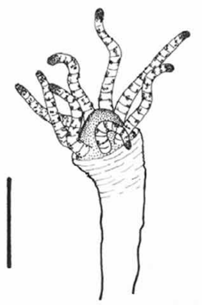

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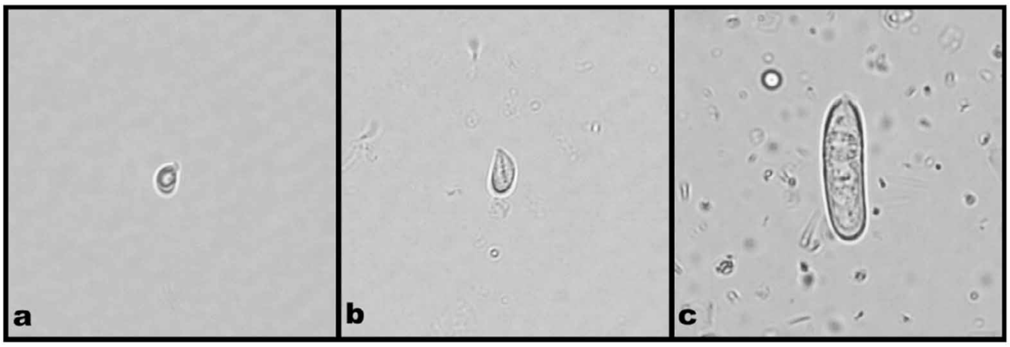

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FIGURE 11. *Bougainvillia muscus*: three-day-old medusa, ROMIZ B3823. Scale equals 0.5 mm.

FIGURE 12. *Amphinema* sp.: hydrocaulus and hydranth, ROMIZ B3824. Scale equals 0.5 mm.

FIGURE 13. *Hydrichthys pietschi*: part of colony on skin of host fish, *Ceratias holboelli* (after Martin 1975). Scale equals 60 µm.

FIGURE 14. (?)*Merga* sp.: hydrocaulus with hydranths and a medusa bud, USNM (without collection number). Scale equals 1.0 mm.

FIGURE 15. (?)*Merga* sp.: hydranth, USNM (without collection number). Scale equals 0.25 mm.

FIGURE 16. (?)*Merga* sp.: nematocysts, USNM (without collection number). a, desmoneme. b, heterotrichous microbasic eurytele. c, foreign nematocyst on colony.

Gonophores fixed sporosacs or free medusae, arising from hydranths or from gonostyles. Medusae, when present, with bell-shaped umbrella having an apical projection. Manubrium cruciform in cross-section; mouth with four prominent lips; radial canals jagged, four or more; mesenteries present. Newly liberated medusae with two opposite marginal tentacles; older medusae with up to six; tentacle bulbs conical. Gonads on interradii of manubrium, forming eight adradial masses. Ocelli absent.

Remarks. Diagnosis of the polyphyletic genus *Hydrichthys* Fewkes, 1887 as given here follows that in Bouillon *et al*. (2006) and Schuchert (2007). Bouillon *et al*. recognized seven species in this genus of parasitic hydroids, including *Hydrichthys pietschi* Martin, 1975 from Hawaii.

Hydroid species currently assigned to *Hydrichthys* are known to liberate medusae referable to several genera (Schuchert 2007), and the genus is in need of revision.

Hydrichthys pietschi Martin, 1975

Fig. 13

Hydrichthys pietschi Martin, 1975: 4, figs. 3–5.

Type locality. USA: Hawaii, off Oahu, ca. 95 m (Martin 1975).

Type material. University of Southern California, Hancock Parasitology Collection, No. 7115 (HOLOTYPE) (not seen).

Description. (From Martin 1975, with measurements in microns): “ Polyps project from basal plate, some bearing buds on the aboral half of body… Polyp 490–1010 long, 112–168 wide. Ectoderm thin (about 3) endoderm 809 thick enclosing many granules 0.8–.9 in diameter. Nematocysts and mesoglea not seen. Medusa bud … stalked, 87–106 long, 58 wide. Mass of cells at distal end probably developing manubrium. Bud endoderm also contains granules. Bud stalk 40–50 long; 47 wide.

Basal plate …approximately 4,800 in diam. with outer thin, 3, and inner thick, 16–22, ectoderm. Thickened inner ectoderm contains granules and may function in digestion … Endoderm thickness 8–25, with numerous granules, encloses shallow gastrovascular cavity. Maximum plate thickness 137 … about equal to the greatest penetration into the host. In this penetration the pigmented epidermis and some of the underlying tissues of the host are eroded. The granules of the hydroid and of the host epidermis are very nearly the same size. Possibly the hydroid obtains its granules from the host. There is a definite tissue response of the host to the parasite with a massing of cells beneath the inner ectoderm .… which is not seen in uninfected skin…”

Remarks. Martin (1975) described *Hydrichthys pietschi* as a parasite on the myctophid fish *Ceratias holboelli* from waters off Oahu. It is known only from the type locality, and only from the original description. This parasitic species was reported to lack both nematocysts and mesoglea. It would be remarkable indeed if nematocysts are completely lacking in polyps of this cnidarian, and the claim needs verification. While not found elsewhere on the polyp, euryteles and desmonemes were reported from the mouth region in a species of *Hydrichthys* from Papua New Guinea (Boero *et al*. 1991: 191). While scarce or sometimes apparently absent, nematocysts have also been reported in hydroids of both *H. sarcotretis* (Jungersen, 1911) and *H. cyclothonis* Damas, 1934 from Europe (Jungersen 1913; Schuchert 2007).

Reported distribution. Hawaii. Oahu: leeward side, 95 m (Martin 1975).

Worldwide. Known only from Hawaii.

Genus *Merga* Hartlaub, 1913

Merga Hartlaub, 1913: 249.

Type species. *Pandea violacea* A. Agassiz & Mayer, 1899 [*Merga violacea*], by monotypy.

Diagnosis. Pandeid hydroids stolonal or with small, erect, and slightly branched cormoids, arising from a creeping hydrorhiza. Erect colonies with monosiphonic hydrocaulus. Perisarc filmy to firm, covering hydrorhiza, hydrocauli, hydrocladia, and pedicels, terminating near hydranth base or forming a pseudohydrotheca, not enveloping bases of tentacles. Hydranths club-shaped to fusiform; tentacles filiform, amphicoronate, in a distal whorl; hypostome conical to dome-shaped.

Gonophores where known free medusae, borne on hydrocauli or hydrorhiza. Medusae bell-shaped, with or without apical process; manubrium of moderate length, not twisted, cruciform in cross-section at base, perradial edges with mesenteries extending to radial canals, oral lips four, simple to slightly folded; radial canals four; marginal tentacles four, eight, or more, all filiform; rudimentary tentacle bulbs and tentaculae present or absent; ocelli present or absent; gonads adradial or interradial, smooth or granulate, on manubrium, not located on folds or pits of manubrial wall.

Remarks. Hartlaub (1913) established *Merga* to accommodate *Pandea violacea* A. Agassiz & Mayer, 1899, a pandeid medusa having gonads without folds. By mid-20th century four species were included in the genus (Kramp 1961: 106–107, 444), and the number is currently nine (Schuchert 2009). Most are known only as the medusa stage. Where described, hydroids are small and have few distinguishing morphological characters. The genus *Merga* has been reviewed and revised a number of times, most recently by Schuchert (1996, 2007) and Brinckmann-Voss & Arai (1998).

(?)*Merga* sp.

Figs. 14–16

Material examined. Northwest Hawaiian Islands, north of French Frigate Shoals: HURL #P5-696-specimen-6, 24 23.9'N, 166 04"E, ca. 1485 m, 11.viii.2007, on unknown tubes and sponge spicules, colony with stems up to about 8 mm high, with medusa buds, USNM (without collection number).

Description. Hydroid colonies small, with stolonal or erect cormoids, up to about 8 mm high, arising from a creeping and anastomosing hydrorhiza. Hydrocaulus monosiphonic, somewhat crooked, narrowest at base, irregularly giving off terminal branchlets and sometimes branches, all partly obscured by patches and crusts of particulate and other adhering matter; terminal branchlets and branches tortuous, slender basally, resembling hydrocaulus; perisarc golden-colored, quite thick basally, thinner elsewhere, with occasional bulges and wrinkles but smooth for the most part (even at bases of hydrocaulus, branches, and branchlets), annulations absent, extending distally as a cup-shaped and wrinkled pseudohydrotheca over base of hydranth, not extending as a sheath over bases of tentacles or over hypostome. Hydranths fusiform; tentacles filiform, quite robust for size of hydranth in preserved material, about 8 in number, apparently amphicoronate and in two close whorls around distal end of hydranth, but difficult to be sure given preservation state of specimens; each tentacle comprising a linear series of large cells armed with nematocysts and with an especially dense cluster at tip; hypostome conical.

Gonophores apparently free medusae. Medusa buds oviform, about 0.35 mm long (excluding pedicel), 0.25 mm wide, invested with thin perisarc, arising via short stalks from hydrocaulus and hydrorhiza.

Remarks. Identification of this hydroid is based solely on molecular barcoding information. That of material examined here, performed by Allen Collins (pers. comm., 3 September 2009), indicates a close relationship to a medusa, provisionally considered a species of *Merga* Hartlaub, 1913 but possibly representing a new genus, being described by Dhugal Lindsay (pers. comm., 30 October, 2009). Specimens from Hawaii have gonophores that are almost certainly liberated as free medusae, but only preserved material was available for study.

This bathyal hydroid resembles that of *Merga galleri* Brinckmann, 1962, a neritic species from the Mediterranean Sea, but it differs in having hydranths with about eight tentacles instead of 4–6, and in having medusa buds on both hydrocaulus and hydrorhiza. Colonies are not strictly stolonal as in *Merga tergestina* (Neppi & Stiasny, 1912), another neritic species reported from the Mediterranean and from Papua New Guinea (Vannucci & Yamada 1959; Schuchert 2007). Hydroids of *M. tergestina* also lack pseudohydrothecae around the hydranths, as in *Merga* (?) sp. This may be an undescribed species, but more information is needed on its life cycle.

The cnidome consists of desmonemes and microbasic heterotrichous euryteles (Fig. 16a, b). Other large (about 20 µm long) nematocysts were present on the hydroids (Fig. 16c) but they are likely from siphonophores or other medusozoans taken in the sample with this species.

Reported distribution. Hawaii. Northwest Hawaiian Islands, north of French Frigate Shoals.

Family Balellidae Stechow, 1922

Tubidendridae Nutting, 1905: 940.
Balellidae Stechow, 1922: 142.

Diagnosis. Filiferan hydroids with erect, irregularly branched, polymorphic colonies. Hydrocaulus polysiphonic. Hydrorhiza, hydrocaulus, and hydrocladia covered with perisarc, although naked coenosarc may also be present. Gastrozooids club-shaped to pyriform; tentacles filiform, in two widely separated whorls, one proximally and another mid-distally on hydranth; hypostome elongate. Gonozooids small, slender, with one or no tentacles; bearing medusa buds. Dactylozooids present on hydrocaulus and hydrocladia, digitate, solid, lacking perisarc over most or all of length.

Gonophores free medusae, borne on gonozooids; radial canals four; marginal tentacles four, solitary, short.

Remarks. The name Tubidendridae, first applied to this family by Nutting (1905), is not available [ICZN Art. 11.7.1.1] because it was not formed from the stem of an available generic name included in the taxon when it was established (Calder 1988). It was replaced by the name Balellidae by Stechow (1922).

Affinities and classification of Balellidae have been difficult to resolve because little is known about the life cycle in species of the group. Jäderholm (1919) and Schuchert (2003) established the presence of medusa buds arising from gonozooids in *Balella mirabilis* (Nutting, 1905), but the adult medusa has yet to be described. Gonophores have not been observed in the only other putative species in the family, *B. irregularis* (Fraser, 1938a). Stechow (1923b) included the taxon as a subfamily of Clavidae McCrady, 1859, while authors including Millard (1975), Hirohito (1988), and Bouillon (1995) included it in Bougainvilliidae Lütken, 1850. Calder (1988) regarded it as a distinct family, closer to Clavidae [now Oceaniidae Eschscholtz, 1829] than to Bougainvilliidae. Recent authors have also recognized it as a distinct family (Calder *et al*. 2003; Schuchert 2003; Bouillon *et al*. 2006). Schuchert (2003), and Nutting (1905) earlier, suggested that affinities of the family were with Hydractiniidae L. Agassiz, 1862, given the polymorphic character of zooids and the occurrence of naked coenosarc on stems of both *B. mirabilis* and *B. irregularis*.

Balellidae includes the single genus *Balella* Stechow, 1919, and two species.

Genus *Balella* Stechow, 1919

Balea Nutting, 1905: 940 [invalid junior homonym of *Balea* Gray, 1824 (Mollusca)]
Balella Stechow, 1919: 154 [replacement name for *Balea* Nutting, 1905].
Type species. *Balea mirabilis* Nutting, 1905 [*Balella mirabilis*], by monotypy.

Diagnosis. Filiferan Hydrozoa with characters of family Balellidae.

Remarks. The generic name *Balella* Stechow, 1919 is a replacement name for *Balea* Nutting, 1905, an invalid junior homonym of *Balea* Gray, 1824 (Mollusca)].

***Balella mirabilis* (Nutting, 1905)**
Fig. 17

Balea mirabilis Nutting, 1905: 940, pl. 2, fig. 3, pl. 7, figs. 3, 4.
Balella mirabilis.—Calder, 2004: 20.

Type locality. USA: Hawaii, between Molokai and Maui, 232 m (Nutting 1905).

Material examined. Maui: Albatross Stn. 4077, off northeast coast, 99 fm (181 m), 21.vii.1902, several colony fragments, largest fragment 2.9 cm high, with poorly preserved hydranths, without gonophores, USNM 22171 [originally identified as *Corydendrium corrugatum* and labelled "cotype"].–Kauai: Albatross Stn. 4135, 225–294 fm (411–538 m), 01.viii.1902, fragments of at least three colonies, largest fragment 6 cm high, with poorly preserved hydranths, without gonophores, USNM 22172 [originally identified as *Corydendrium corrugatum*, labelled "cotype," and in a vial together with USNM 22171].

Description. Hydroid colonies erect, robust, polymorphic, reaching to 6 cm high, arising from a tangled hydrorhizal tuft, apparently anchoring colony on a sedimentary substrate. Hydrocaulus polysiphonic with tubes interconnecting, naked coenosarc occurring in grooves parallel to tubes, stem quite rigid, irregularly branched in one plane, nearly straight, diameter gradually decreasing distally; branches straight to slightly curved, little branched or unbranched, polysiphonic to extreme ends but gradually tapering distally. Hydrocaulus and branches densely armed with small dactylozooids. Perisarc sometimes forming a shallow, thin, cup-shaped collar at base of hydranths; colour dark brown in older and thicker parts of colony, becoming straw-coloured in younger distal parts. Hydranths naked except for small basal collar of perisarc, arising at irregular intervals, most frequent on branches, clavate to pyriform with an elongate and relatively slender aboral stalk; tentacles filiform, in two distinct whorls; proximal whorl of tentacles somewhat smaller, about 12–16 in number; mid-distal whorl of tentacles tending to be larger, about 8–12; hypostome elongate. Dactylozooids largely or entirely naked, digitate, solid, with outer ectoderm and inner endodermal core.

Gonophores not seen.

Remarks. *Balella mirabilis* (Nutting, 1905) was originally described from the Hawaiian Islands. Type material of the species was never received at the NMNH (Geoff Keel, pers. comm., 01 September 2009) and apparently has been lost. A neotype is needed, preferably from the same general locality. While one of the lots listed above might serve the purpose, neither is in good condition and it seems better to defer action in the hope that a better colony will eventually be found.

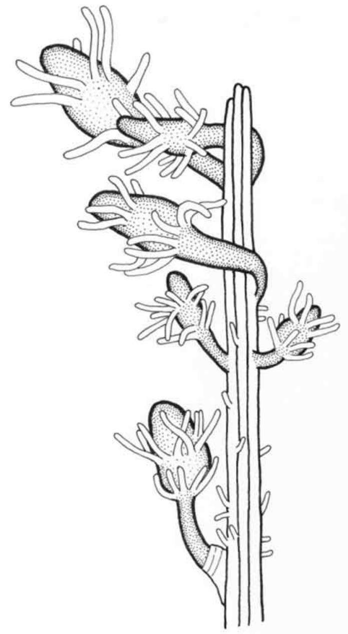
Although Nutting's (1905) hydroid was infertile, colonies of the species with medusa buds, arising from gonozooids, were described later from Japan (Jäderholm 1919) and Indonesia (Schuchert 2003). Gonozooids described by Jäderholm lacked tentacles, while those studied by Schuchert usually had a single filiform tentacle. The hydroid has not yet been linked to a known medusa, and the life cycle of the species remains obscure.

Balella irregularis (Fraser, 1938a) from the Galápagos Islands was considered conspecific with *B. mirabilis* by Calder *et al*. (2003). Although subsequently treated as valid (Calder *et al*. 2009) because of apparent differences in development of proximal tentacles on the hydranth, such differences may represent intraspecific variation and a reassessment of the two forms is needed.

As noted earlier by Schuchert (2003), the dense basal tuft of hydrorhizal fibres suggests that this species grows on sedimentary substrates. *Balella irregularis* was also found on a substrate of sand and coralline red algae (Calder *et al*. 2009).

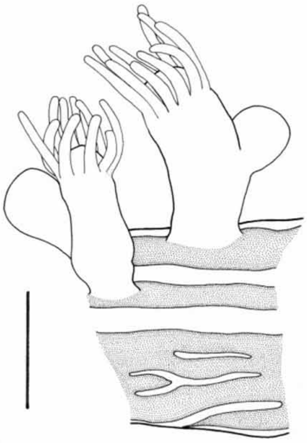
Reported distribution. Hawaii. Albatross Stn. 3856, "between Molokai and Maui…, 127 fathoms" (232 m) (Nutting 1905).

17



18

19



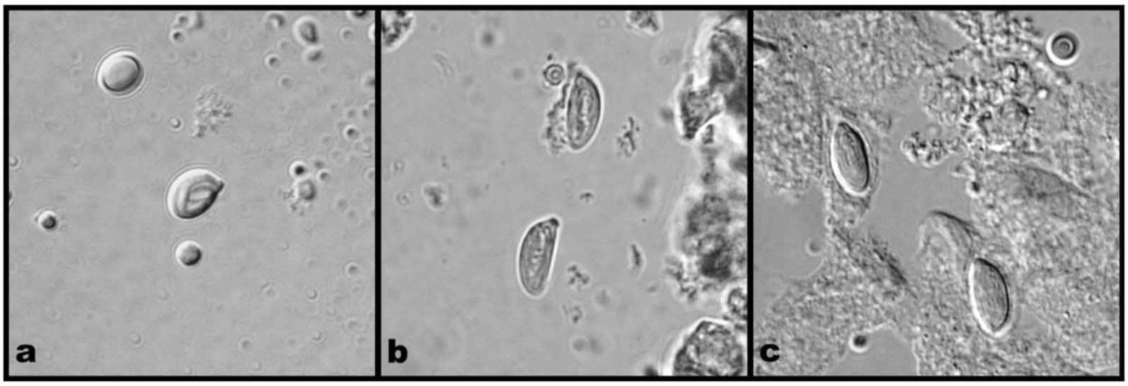


FIGURE 17. *Balella mirabilis*: part of hydrocaulus with hydranths (after Nutting 1905).

FIGURE 18. *Hydrodendrium gorgonoides*: habit of 21-cm-high colony, BPBM D522.

FIGURE 19. *Hydrodendrium gorgonoides*: part of branch with two hydranths, each bearing a gonophore, BPBM D521. Scale equals 0.5 mm.

FIGURE 20. *Hydrodendrium gorgonoides*: nematocysts, BPBM D521. a, desmoneme. b–c, heterotrichous microbasic euryteles.

Worldwide. Hawaii; Japan; Indonesia; (?)Galápagos Islands, as *B. irregularis*; 49–232 m (Nutting 1905; Hirohito 1988; Schuchert 2003; Calder *et al*. 2009).

Family Hydractiniidae L. Agassiz, 1862

Hydractinidae L. Agassiz, 1862: 339 [emended to Hydractiniidae by Hincks (1868)].

Diagnosis. Filiferan hydroid colonies with sessile zooids; hydrorhiza comprising either perisarc-covered stolons, or an encrusting mat of coalesced coenosarc that may be naked or perisarc-covered, with or without a calcareous skeleton; usually stolonal but in some species forming erect pillars, or branches, or arborescent colonies; chitinous or calcareous spines frequently present; protective tubes sometimes overgrowing hydranths. Zooids naked, either polymorphic, with gastrozooids, gonozooids, and sometimes dactylozooids, or less often monomorphic. Gastrozooids with filiform tentacles in a single whorl, or in two or more close whorls, or scattered over distal half of body, infrequently with just one or two filiform tentacles. Gonozooids with filiform tentacles in one or more whorls, or as blastostyles lacking both tentacles and mouth; dactylozooids, if present, lacking tentacles.

Gonophores fixed sporosacs, fixed or liberable eumedusoids, or free medusae, usually borne on gonozooids. Medusae, when present, bell-shaped; radial canals four, ring canal present; manubrium sac-shaped to tubular, not reaching beyond subumbrellar cavity, oral region with four unbranched or branched lips with terminal batteries of nematocysts; marginal tentacles solid, solitary; ocelli present or absent; gonads interradial, on manubrium, sometimes extending along proximal reaches of radial canals.

Remarks. The diagnosis of Hydractiniidae L. Agassiz, 1862 adopted here is essentially as given by Schuchert (2008a) in a review of recent genera and species of the family in European waters. His work is followed in regarding Hydrodendridae Nutting, 1905 [emended here to Hydrodendriidae] as a synonym of Hydractiniidae. The diagnosis of the family has been modified slightly to accommodate the genus *Hydrodendrium* Nutting, 1905.

As for *Hydractinia*, type genus of the family, authorship and date of the name has been widely credited to Van Beneden (1841). However, the name therein was only the vernacular “Hydractinie,” and it was not until later (Van Beneden 1844a) that it was made available as *Hydractinia* (ICZN Art. 11). Nomenclatural problems arise as a result, with *Hydractinia* Van Beneden, 1844a being a junior synonym of the virtually unused name *Echinochorium* Hassall, 1841. In the interests of nomenclatural stability, the well-known name *Hydractinia* is designated here as valid and as a nomen protectum, while *Echinochorium* is relegated to a nomen oblitum by applying Reversal of Precedence provisions (ICZN Art. 23.9). First, *Echinochorium* has not been used as a valid name in zoology after 1899 (ICZN Art. 23.9.1.1). In contrast, *Hydractinia* has been used in more than 25 works by numerous authors (>10) in the past 50 years (ICZN Art. 23.9.1.2): (e.g. Millard 1975; Bouillon 1985; Hirohito 1988; Buss & Yund 1989; Bouillon *et al.* 1997, 2006; Brinckmann-Voss 1996; Schuchert 1996, 2008a; Boero *et al*. 1998; Cairns *et al*. 2002; Migotto *et al*. 2002; Peña Cantero & García Carrascosa 2002; Cunningham & Buss 1993; Watson 2003; Stampar *et al*. 2006; Miglietta 2006; Vervoort 2006; Xu & Huang 2006; Galea *et al*. 2007; Mills *et al*. 2007; Altuna 2008; Ferrell 2008; Puce *et al*. 2008; Miglietta *et al*. 2009; Calder *et al*. 2009). The generic name *Dysmorphosa* Philippi, 1842 also predates *Hydractinia*, but it is more likely a senior synonym of *Podocoryna* M. Sars, 1846. Its type species, *D. conchicola* Philippi, 1842, is of uncertain identity but possibly conspecific with *Podocoryna exigua* (Haeckel, 1879) (Schuchert 2008a).

Hydractiniid hydroids can be difficult to delimit from those of anthoathecate families such as Oceaniidae Eschscholtz, 1829, Cytaeididae L. Agassiz, 1862, Bougainvilliidae Lütken, 1850, Pandeidae Haeckel, 1879, and Rhysiidae Brinckmann, 1965. Moreover, concepts of genera within Hydractiniidae have varied widely, with as many as 14 (Stechow 1923b) and as few as five (Kramp 1932; Bouillon *et al*. 2006) recent ones being recognized in various classifications. Eleven genera were recognized as valid by Schuchert (2009), but he noted earlier (Schuchert 2008a) that current subdivision of the family at the generic level is provisional and certain to change. Miglietta *et al*. (2009) observed that the current practice of collapsing *Podocoryna* M. Sars, 1846 and *Stylactaria* Stechow, 1921a into *Hydractinia* is impractical. Comprehensive taxonomic revision of the family, involving both molecular biology and alpha-taxonomy, is clearly needed. The sometimes-overlooked genus *Hydrodendrium* Nutting, 1905, represented in Hawaii by *H. gorgonoides* Nutting, 1905, is included here in Hydractiniidae, but its family affinities need to be more clearly resolved.

Stampar *et al*. (2006) listed nearly 100 species in a broadly defined genus *Hydractinia* that also encompassed *Podocoryna* and *Stylactaria*, and Daly *et al*. (2007) reported that about 100 species of hydractiniids were known overall. In light of the degree of crypsis now thought to occur in the family, and in hydrozoans generally, that number will likely prove to be conservative. Indeed, additional new nominal species of hydractiniids continue to be described (e.g. Lin *et al*. 2010).

Genus *Hydrodendrium* Nutting, 1905

Hydrodendrium Nutting, 1905: 936.
Nuttingia Stechow, 1909: 10 [invalid replacement name for *Hydrodendrium* Nutting, 1905].
Type species. *Hydrodendrium gorgonoides* Nutting, 1905, by monotypy.

Diagnosis. Hydractiniid hydroids with erect colonies, comprising a massive, arborescent, spongy, branched hydrocaulus with a skeletal axis of intertwining and anastomosing chitinous fibres penetrated internally and invested externally by naked coenosarc; spines and hydrophores absent. Hydranths monomorphic, sessile, naked, anemone-like, arising from bands of coenosarc at surface, not embedded in skeleton; tentacles filiform, in a single distal whorl; hypostome flattened to dome-like.

Gonophores fixed sporosacs, arising as sac-shaped evaginations of hydranth body wall; colonies monoecious.

Remarks. *Hydrodendrium* Nutting, 1905 has seldom been used as a valid genus name. Stechow (1909) instituted *Nuttingia* as a replacement name for it after incorrectly considering *Hydrodendrium* a homonym of *Hydrodendron* Hincks, 1874 (see also Stechow 1923b). The two are not homonyms (ICZN Art. 56), and *Nuttingia* is an invalid junior objective synonym of *Hydrodendrium*. Both *Hydrodendrium* and *Nuttingia* were included in the synonymy of *Hydractinia* Van Beneden, 1844a by authors including Bouillon (1985), Bouillon *et al*. (1997) and Schuchert (2008a).

The genus *Hydrodendrium* is maintained here based on a unique combination of characters outlined in the diagnosis above. It is distinguished from *Hydractinia* in having monomorphic, stout hydranths with a low hypostome that arise from an erect and arborescent chitinous skeleton lacking spines, and gonophores that are fixed sporosacs arising as hernia-like protuberances from the walls of unmodified (Nutting 1905) or only slightly shrunken hydranths. The growth form of the skeletal axis superficially resembles that of *Solanderia* Duchassaing & Michelin, 1846 or even an octocoral.

Hydrodendrium or its junior objective synonym *Nuttingia* have been assigned at various times to the families Hydrodendriidae Nutting, 1905 (Nutting 1905), Podocorynidae Allman, 1864 (Hickson & Gravely 1907), Bougainvilliidae Lütken, 1850 (Stechow 1909), Clathrozoidae Stechow, 1921a (Stechow 1921a), and Hydractiniidae L. Agassiz, 1862 (Bouillon *et al*. 1997). Affinities of the genus appear to be with Hydractiniidae, as noted by authors such as Schuchert (2008a).

Hydrodendrium gorgonoides Nutting, 1905
Figs. 18–20

Hydrodendrium gorgonoides Nutting, 1905: 936, pl. 1, figs. 1–6, pl. 7, figs. 1, 2.

Type locality. USA: Hawaii, between Honolulu and Kauai, 541 m (Nutting 1905).

Material examined. Kauai: Albatross Stn. 3991, off Molokea Point, 22º25.6944’ N, 159º 38.7500’ W, 497–541 m, 12.vi.1902, one fragmentary colony, with fragments to 15 cm high, with gonophores, USNM 22167 [HOLOTYPE].–Oahu: off Kaena Point, 21º37.4’N, 158º 22.3’W, 337–403 m, SANGO III, haul #2, tangle nets, 30.ix.1970, one fragmentary branched colony, 7.9 cm high, with hydranths, without gonophores, coll. R. Grigg, BPBM D520.–Oahu: off Kaena Point, 21º35.9’N, 158º 23.5’W, 380–415 m, SANGO III, haul #2, tangle nets, 9.viii.1970, one fragmentary branched colony, 11.3 cm high, with hydranths and gonophores, coll. R. Grigg, BPBM D521.–No collection data, one dried colony, 21 cm high, coll. R. Grigg, BPBM D522.

Other type material. Kauai: Mokolea Point, 22.256944’ N, 159.387500’ W, 497–541 m, 12.vi.1902, one branch, Albatross Stn. 3991, CAS IZ163 (syntype) [PARALECTOTYPE; Fautin & Weitbrecht 1985].

Description. Hydroid colonies fragmentary, robust, erect, dendritic, irregularly branched in one plane, reaching to 21 cm high, 1.9 cm wide. Hydrocaulus and branches forming a thick, woody, spongy, chitinous axis penetrated and overlaid by naked coenosarc; chitinous fibers of axis somewhat twisted, branched, running parallel or nearly so to axis of hydrocaulus and branches, appearing twisted. Hydranths in preserved material columnar, stout throughout, fairly short, to about 0.7 mm high, lacking perisarc, arising from coenosarcal strands overlying grooves in chitinous matrix, scattered irregularly over hydrocaulus and branches but most numerous in axils of branches; tentacles filiform, solid, about 10–13 in number, arranged in one whorl around hypostome, bearing warts and incomplete rings formed by batteries of nematocysts, hypostome dome-shaped to almost flattened, with central round mouth. Colour of preserved colony tan, hydranths and gonophores cream.

Gonophores styloid sporosacs, arising from essentially normal to slightly shrunken hydranths as sac-shaped outgrowths of hydranth wall, with one per hydranth, becoming very large, laterally flattened, spade-shaped, with wide base connected to hydranth by a thick pedicel, round-pointed apex pointing away from hydranth, lacking spadix, radial canals, tentacle bulbs, and tentacles.

Nematocysts. desmonemes (5.6–6.1 µm long × 3.9–4.1 µm wide)

Heterotrichous microbasic euryteles (8.5–9.2 µm long × 3.8–4.0 µm wide)

Remarks. *Hydrodendrium gorgonoides* Nutting, 1905 was described from Hawaii on the basis of what appear to be fragments of a single colony. While the tallest intact specimen observed here (BPBM D522) was 21 cm high, Nutting believed that the hydroid may reach as much as a foot (30 cm) or more in height, based on fragments in his sample. Colonies are octocoral-like in colony form, as its specific name suggests.

In an earlier work (Calder 2004: 20), this species was listed under the binomen *Hydractinia gorgonoides*. For reasons given immediately above, it is removed from *Hydractinia* Van Beneden, 1844a here and returned to *Hydrodendrium* Nutting, 1905. Stechow (1923b: 71) had included it as *Nuttingia gorgonoides*.

Hydrodendrium gorgonoides, currently known only from Hawaii, is a poorly known species. Material examined here represents only the second published record of the species. The scarcity of records may be due in part to difficulties of sampling its rocky, rugged, deep-water habitat.

Although not unique among hydractiniids, it is unusual in being monomorphic and in having a massive, erect, porous skeletal axis formed of chitin and covered with naked coenosarc. A detailed account of the structure of its hydrocaulus was given by Nutting (1905). Gonophores of the species differ from other hydractiniids in being hernia-like sporosacs arising from the walls of normal hydranths. Colonies are said to be monoecious (Nutting 1905).

Several other species of hydractiniids are known to have an erect and chitinous skeleton invested with coenosarc, including *Hydractinia angusta* Hartlaub, 1904, *H. dendritica* Hickson & Gravely, 1907, *H. sodalis* Stimpson, 1858, *H. rugosa* Fraser, 1938b and its likely synonym, *H. prolifica* Fraser, 1948 (Calder *et al.* 2009), *H. bayeri* Hirohito, 1984, *H. cryptogonia* Hirohito, 1988, and *H. antonii* Miglietta, 2006. All of these but *H. cryptogonia* differ from *Hydrodendrium gorgonoides* in having polymorphic rather than monomorphic colonies. Moreover, the chitinous skeletons of all but *H. dendritica* and *H. cryptogonia* bear large, jagged spines instead of being smooth. *Hydractinia arborescens* Carter, 1878 has a similar colony form, but that species was described from poor material and is known only from its skeleton. Based on current knowledge, it is considered a nomen dubium. The provenance of its type material was uncertain, possibly somewhere in Polynesia (Carter 1878).

As for *H. sodalis*, Stimpson (1858) has consistently been cited as author of the name. It might be debated whether that author's brief mention of it meets criteria of availability under Art. 12 of the ICZN. In describing a new pagurid crab (*Eupagurus constans*) from "Hakodadi" (Hakodate, Hokkaido, Japan), he wrote: "Carcinoecium corneum spirale, base convolutum, muricatum, a polypo hydroideo (*Hydractinia sodalis*, nob.) constructum…" (Stimpson 1858: 249). That perfunctory account has nevertheless been sufficient for the species to be recognizable, so prevailing authorship and date of the name have been retained here. A few more details of the hydroid, including an illustration, were provided by Stimpson (1907: 219, pl. 24, fig. 3) in a posthumous publication. Stechow (1907) provided the first detailed description of *H. sodalis*, now quite familiar in waters of Japan (Hirohito 1988).

All eight gonophores examined microscopically by me from a single colony (BPBM D521) were male, but both male and female gonophores were reported on the same colony by Nutting (1905).

This hydroid has sometimes been overlooked in species lists and other accounts of Hydractiniidae L. Agassiz, 1862. One of the colonies studied here (BPBM D521) had been examined and identified earlier as this species by both W.J. Cooke and W. Vervoort (from information on labels contained in the bottle). A dried colony also exists at the Bishop Museum (BPBM D522). Although likely from the Hawaiian islands, its provenance is not known. Collection data record the collector as R. Grigg of Hawaii, and the identifier as W. Vervoort. It is much branched and root-like in shape, measuring 21 cm high and 1 cm in diameter at the base (Fig. 18).

Reported distribution. Hawaii. Albatross Stn. 3991, "between Honolulu and Kauai…, 296 fathoms" (541 m) (Nutting 1905).

Worldwide. Known only from Hawaii.

Genus *Stylactaria* Stechow, 1921a

Stylactaria Stechow, 1921a: 250.
Type species. *Stylactis inermis* Allman, 1872 [*Stylactaria inermis*], by monotypy.

Diagnosis. Hydractiniid hydroids with colonies exclusively stolonal. Polyps sessile, naked, polymorphic, with gastrozooids, gonozooids, and sometimes dactylozooids, arising from a creeping hydrorhiza comprising hydrorhizal stolons covered with perisarc; hydrorhiza not encrusting, calcareous, or covered with naked perisarc; spines present or absent. Gastrozooids, gonozooids, and dactylozooids as for family.

Gonophores fixed sporosacs or fixed or free eumedusoids, developing on gonozooids proximal to whorl of tentacles. Fully developed medusoids sac-shaped; manubrium simple, tubular, lacking mouth, oral lips, and oral tentacles; marginal tentacles rudimentary, 8–10 in number; radial canals four; ocelli absent. Gonad surrounding manubrium.

Remarks. As noted above, classification of Hydractiniidae L. Agassiz, 1862 at the generic level remains unsettled. The genus *Stylactaria* Stechow, 1921a has recently been treated both as a synonym of *Hydractinia* Van Beneden, 1844a (e.g. Bouillon *et al*. 1997, 2006; Boero *et al*. 1998; Cairns *et al*. 2002; Stampar *et al*. 2006; Schuchert 2008a) and as distinct (Calder 1988; Namikawa 1991; Miglietta *et al*. 2009). In this work, *Stylactaria* is once again recognized as valid pending a more detailed taxonomic reappraisal of the family. Investigations on the nature of stolonal versus mat growth forms in Hydractiniidae, and the influence of genetics and environmental effects on them (Ferrell 2008), may prove relevant in taxonomy as well as ecology.

The taxonomy and nomenclature of *Stylactaria* (including *Stylactis* auct.) has been reviewed in a previous work (Calder 1988). Earlier detailed accounts of the genus include those of Iwasa (1934), Bouillon (1971), and Hirohito (1988). Subsequent reviews have been provided by Namikawa (1991) and Bouillon *et al*. (1997), who summarized the characters of 29 nominal species and another five unnamed species assigned to the genus. Schuchert (2008a) reviewed species in European waters under the genus *Hydractinia*. The greatest diversity within the genus is known from Japan, with 14 species reported from that country. The most frequent substrates of known species are shells of gastropods, with or without pagurid crabs (Bouillon *et al*. 1997).

Species assigned to *Stylactaria* are morphologically quite homogeneous and difficult to distinguish. Characters utilized in the taxonomy of the genus were recently reviewed and evaluated by Bouillon *et al*. (1997). Understanding of the group is likely to advance once more molecular work has been completed, as in the related genus *Hydractinia*. Greater attention to nematocyst complement and distribution may also aid in species differentiation, as in the genus *Eudendrium* Ehrenberg, 1834.

Medusoids in certain species of *Stylactaria* are known to be liberated at dusk or soon after dark (Sigerfoos 1899; Calder 1971, 1988), as in *Pennaria disticha* Goldfuss, 1820.

***Stylactaria munita*, sp. nov.**

Figs. 21–23

Material examined. Oahu: Hawaii Kai, on pilings of bridge over Highway 72, 21º17’06.60”N, 157º43’07.21”W, 0.1 m, 28.vii.2009, on small oyster shell, one colony, to 1.6 mm high, without gonophores, coll. D.R. Calder, ROMIZ B3825 [HOLOTYPE].

Etymology. The specific name is taken from the Latin word “*munitus*,” meaning fortified, armed, or protected, in reference to distinctive nematocyst batteries arming the body together with a dense band of nematocysts around the hypostome of gastrozooids.

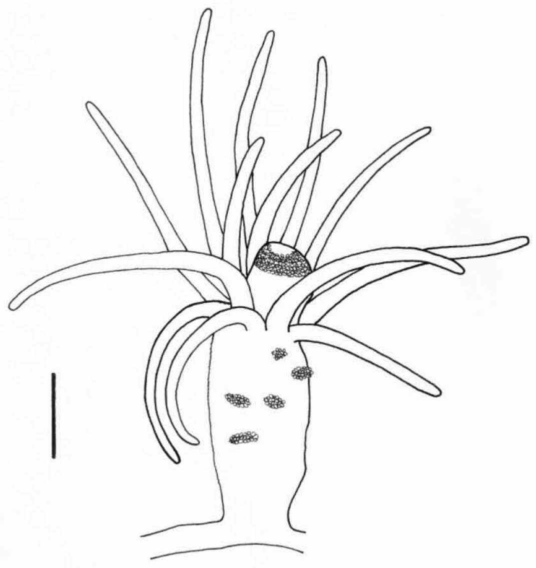
Description. Hydroid colonies stolonal, polymorphic, inconspicuous, with zooids arising from a creeping hydrorhiza growing over an oyster shell; stolons of hydrorhiza branching and anastomosing in a loose meshwork. Perisarc thin, investing hydrorhiza, terminating at base of zooids, not forming prominent cup-shaped perisarcal collar; spines absent. Polyps in present material of two types, gastrozooids and dactylozooids (occurring as tentaculozooids). Gastrozooids small, widely spaced, varied in shape from bowling pin-shaped to almost columnar, up to 0.75 mm high, 0.30 mm wide; body column with oval warts containing dense aggregations of nematocysts (comprising large heterotrichous microbasic euryteles only), each aggregation usually containing >25 nematocysts; hypostome dome-shaped to bulbous to almost cylindrical, distal end with a dense refringent band of nematocysts (all large heterotrichous microbasic euryteles); tentacles gradually tapering from base to tip, amphicoronate, in two close whorls around distal end of hydranth, about 10–16 in number. Tentaculozooids frequent, slender, elongate, each resembling an exceedingly long tentacle, tapering gradually from base to distal end, appearing slightly enlarged at tip due to an especially dense aggregation of nematocysts (heterotrichous microbasic euryteles), up to 1.6 mm long in preserved material, usually located near a gastrozooid. Colour of gastrozooids white when alive.

Gonozooids and gonophores not seen.

Nematocysts. Gastrozooids (tentacles):
desmonemes (4.9–5.2 µm long × 3.0–3.2 µm wide)
heterotrichous microbasic euryteles (7.3–8.5 µm long × 2.6–3.1 µm wide)
Gastrozooids (hypostome):
heterotrichous microbasic euryteles (9.2–10.0 µm µm long × 3.3–3.9 µm wide)
Gastrozooids (body nematocyst patches):
heterotrichous microbasic euryteles (9.0–10.0 µm long × 3.0–4.0 µm wide)

Dactylozooids (tentaculozooids):
desmonemes (4.5–5.2 µm long × 2.7–3.3 µm wide)
heterotrichous microbasic euryteles (7.0–9.0 µm long × 3.0–3.9 µm wide)

Remarks. *Stylactaria munita*, **sp. nov.**, differs from other known species of hydractiniids in having gastrozooids with nematocyst warts on the body wall as well as a refringent band of nematocysts on the hypostome. Nematocysts arming both hypostome and body wall are large heterotrichous microbasic euryteles.



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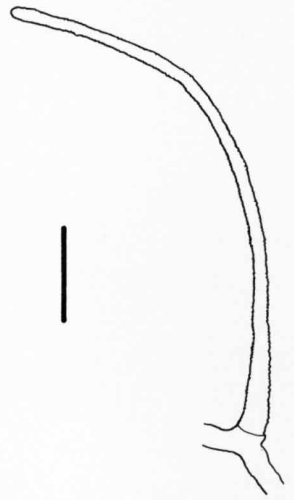

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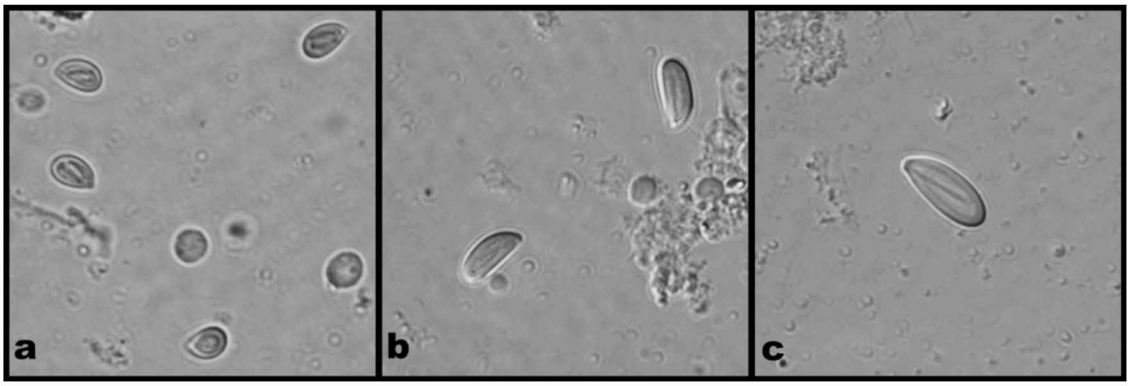

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FIGURE 21. *Stylactaria munita*, **sp. nov.**: gastrozooid from holotype colony, ROMIZ B3825. Scale equals 0.25 mm.
FIGURE 22. *Stylactaria munita*, **sp. nov.**: tentaculozooid from holotype colony, ROMIZ B3825. Scale equals 0.25 mm.
FIGURE 23. *Stylactaria munita*, **sp. nov.**: nematocysts from gastrozooid of holotype colony, ROMIZ B3825. a, desmonemes from tentacle. b, small heterotrichous microbasic euryteles from tentacle. c, large heterotrichous microbasic eurytele from hypostome.

As with 29 other species of hydractiniids assigned or provisionally assigned to *Stylactaria* Stechow, 1921a (Bouillon *et al*. 1997), *S. munita*, **sp. nov.**, possesses a hydrorhiza that consists predominantly of perisarc-covered stolons rather than an encrusting mat of coalesced coenosarc. Of these, *S. munita* closely resembles two Mediterranean species, *S. aculeata* (Wagner, 1833) and *S. pruvoti* (Motz-Kossowska, 1905). In the three species, tentaculozooids as well as gastrozooids are present, and spines are either absent or small and only occasionally present. *Stylactaria munita* and *S. aculeata* differ from *S. pruvoti* in having gastrozooids with a refringent band of nematocysts on the hypostome. In turn, *S. munita* and *S. pruvoti* differ from *S. aculeata* in having clusters of heteronemes on the hydranth body, with those of *S. munita* occurring as slightly elevated warts. Of these species, *S. munita* is the only one known from a substrate other than gastropod shells occupied by snails or pagurid crabs, and its hydrorhiza is not known to be encrusting. Peña Cantero & García Carrascosa (2002) described and illustrated a hydroid identified as *Hydractinia carnea* (M. Sars, 1846) from the Mediterranean Sea that also had nematocyst patches on the body column, but no mention was made of a dense band of nematocysts on the hypostome of their species.

The band of nematocysts that surrounds the hypostome in *Stylactaria munita* may be a more widespread character among species of the genus than currently recognized. It is known to be shared with several other hydractiniids besides *Stylactaria aculeata*, including *S. proboscidea* (Hincks, 1868), *S. inermis* (Allman, 1872), *S. arctica* (Jäderholm, 1902), *S. claviformis* Bouillon, 1971, *S. otagoensis* Schuchert, 1996, *Hydractinia sarsii* (Steenstrup, 1850), *H. fucicola* (M. Sars, 1857), and *H. allmanii* Bonnevie, 1898 (Schuchert 1996, 2008a). Nevertheless, all of them differ from *S. munita* in one or more characters besides having larger gastrozooids: *S. proboscidea* has tentaculozooids shorter than gastrozooids; *S. inermis* lacks tentaculozooids; *S. arctica* has zooids with basal perisarcal collars and lacks tentaculozooids; *S. claviformis* lacks nematocyst warts on the body column of gastrozooids; *S. otagoensis* has hydrorhizal spines and larger nematocysts; *H. sarsii* and *H. fucicola* have encrusting hydrorhizae with naked coenosarc, and hydrorhizal spines.

The closest known species to *S. munita* geographically is *S. mar* Gasca & Calder, 1993 from the Pacific coast of Mexico (Bahía de Manzanillo). That species differs from *S. munita* by having long spines, zooids with distinct basal perisarcal collars, and larger gastrozooids (to 3 mm high) with haploneme nematocysts as well as euryteles and desmonemes. It was found on tubes of a sabellid polychaete.

Stylactaria munita is one of the smallest species of the genus described to date, with the largest gastrozooids observed measuring a mere 0.75 mm high. Only *Hydractinia cytaeiformis* Vervoort, 2006 (referred to here as *Stylactaria cytaeiformis*, comb. nov.) from deep waters (1200 m) off Cape Verde Island, and the poorly known *Stylactaria siphonis* (Stechow, 1921b), reported once off Plettenberg Bay, South Africa (see Millard 1975), are equally small (0.5 to 0.8–0.9 mm high). However, *S. siphonis* differs from *S. munita* in having fewer tentacles (8–10), in lacking tentaculozooids, in kind of substrate (occurring in the siphon of a gastropod instead of a bivalve), and in bathymetric provenance (500 m instead of 0.1 m). The bathyal *S. cytaeiformis* most notably lacks the dense nematocyst armature of hypostome and body column seen in *H. munita*, but its tentaculozooids also differ in being small and capitate.

The presence of tentaculozooids, together with the absence of both spines and a perisarcal collar at the bases of gastrozooids, is shared with *Stylactaria multigranosi* Namikawa, 1991 from Japan. Gastrozooids of *S. munita* differ from that species in the dense band of nematocysts on the hypostome and nematocyst warts on the body column. *Stylactaria multigranosi* is also thought to be substrate specific on shells of the gastropod *Nassarius multigranosus* (Namikawa 1991). As for tentaculozooids, their abundance is related in certain species, at least in part, to the proximity of space competitors (Namikawa *et al*. 1992).

Material of *Stylactaria munita* examined here lacked both gonozooids and gonophores, and the nature of the life cycle is as yet unknown.

Reported distribution. Known only from the type locality.

Family Eudendriidae L. Agassiz, 1862

Eudendroidae L. Agassiz, 1862: 342 [emended to Eudendriidae by Hincks (1868)].

Diagnosis. Filiferan hydroids colonial, sometimes stolonal but usually erect and branched; hydrocaulus monosiphonic or polysiphonic, arising from a creeping hydrorhiza; growth monopodial with terminal hydranths. Perisarc usually firm, enveloping hydrocaulus, hydrocladia, pedicels, and hydrorhiza, extending upward to groove at hydranth base. Hydranths urn-shaped, often large; tentacles filiform, usually in one whorl but with two or more very close whorls in some taxa; hypostome large, flexible, knob-shaped to flared.

Gonophores fixed sporosacs, arising from hydranth proximal to tentacles; reproductive hydranths sometimes reduced. Male gonophores with from one to several bulbous chambers in a linear series. Female gonophores, with one exception (*Eudendrium vervoorti* Marques & Migotto, 1998), having a curved spadix enclosing an egg.

Remarks. The family Eudendriidae L. Agassiz, 1862 presently comprises two genera, the ubiquitous, familiar, and species-rich *Eudendrium* Ehrenberg, 1834, and the circumtropical but much less frequently encountered *Myrionema* Pictet, 1893, with its four nominal species (now including *Perigonimus multicornis* Allman, 1876: see Schuchert 2008b). The number of valid species of eudendriids has been estimated at about 85 (Daly *et al*. 2007), all of them having fixed gonophores. The family and its two genera are thought to be monophyletic (Marques, Mergner *et al*. 2000). A detailed review of the family, and of species occurring in European waters, has been given recently by Schuchert (2008b).

Eudendriids are easy to recognize by the distinctive morphology of their hydranths and gonophores. Hydranths tend to be large and urn-shaped to barrel-shaped, with a prominent, pedunculated, knobbed to strongly flared hypostome apically and a shallow perisarc groove basally. Gonophores are styloid and arise from the gastric column of normal to reduced hydranths. Those of the male often comprise a linear series of bead-like chambers, while those of the female consist initially of a spadix enveloping a single egg (*Eudendrium vervoorti* Marques & Migotto, 1998 is an exception, reportedly having gonophores that lack a spadix).

Hydroids referable to *Myrionema* differ from those of the better-known *Eudendrium* in having more elongated hydranths with a greater number of tentacles, often 40 or more in several close whorls. Zooxanthellae are present in the tissues (Calder 1988) of *Myrionema,* but such symbionts are also known to occur in a species of *Eudendrium* (*E. moulouyensis* Marques, Peña Cantero, & Vervoort, 2000 from the Mediterranean Sea). Of the two genera, only *Eudendrium* is currently known from Hawaii, although colonies of *Myrionema* might eventually be discovered there in shallow, sheltered environments.

Genus *Eudendrium* Ehrenberg, 1834

Eudendrium Ehrenberg, 1834: 319.
Type species. *Tubularia ramosa* Linnaeus, 1758 [*Eudendrium ramosum*], by subsequent designation by Allman (1872).

Diagnosis. Eudendriid hydroids with hydranths having a relatively short calyx; tentacles filiform, varied in number but usually fewer than 35, in one whorl.

Remarks. The hydrozoan genus *Eudendrium* Ehrenberg, 1834 is distinctive morphologically and well-defined taxonomically, but identification of the numerous species assigned to it can be decidedly difficult. A number of them were founded on the basis of taxonomically unreliable characters and on incomplete specimens, and are of doubtful validity. The extent of morphological similarity among species of the genus further complicates the taxonomy of the group (Watson 1985). Significant phenotypic variation also exists in certain species of *Eudendrium,* and the existence of sibling species is possible (Oliveira *et al*. 2000). Characters currently considered important in distinguishing species of the genus include reproductive structures, fate of reproductive hydranths, and nematocyst complement (cnidome), in addition to general morphology (Watson 1985; Calder 1988; Marques, Mergner *et al*. 2000, Marques, Peña Cantero *et al*. 2000; Schuchert 2008b). A detailed discussion of the utility of the cnidome in the taxonomy of *Eudendrium*, together with the morphology, size, location, and relative abundance of nematocyst categories present, was given by Watson (1985). Given the importance of gonophore morphology in the taxonomy of the group, identification of sterile material by traditional means may in many cases be all but impossible.

Colony size in species of *Eudendrium* varies from about 0.5 cm high in *E. fragile* Motz-Kossowska, 1905 (=*E. album* Nutting, 1896: see Schuchert 2008b) to as much as 30 cm high in *E. rameum* (Pallas, 1766) (Oliveira *et al*. 2000). Eudendriids are often relatively large and conspicuous. Major contemporary reviews of species include works by Watson (1985) on 17 species from Australia, by Marques, Mergner *et al*. (2000) on 25 species from various locations representing all oceans, by Marques, Peña Cantero *et al*. (2000) on 13 species from the Mediterranean Sea, and by Schuchert (2008b) on 20 species known from European waters.

Earlier nomenclatural threats to the familiar name *Eudendrium* by *Thoa* Lamouroux, 1816 and *Fistulana* O. F. Müller, 1776a have been removed, as discussed earlier (Calder 1988).

Eudendrium capillare **Alder, 1856**

Figs. 24, 25

Eudendrium capillare Alder, 1856: 355, pl. 12, figs. 9–12.–Nutting, 1905: 939.
Eudendrium sp.—Cooke, 1977: 87.

Type locality. UK: Northumberland, Embleton Bay (Alder 1856).

Material examined. Oahu: Kaneohe Bay, pier at Hawaii Institute of Marine Biology, 2 m, on wood pilings, no date, two colony fragments, to 0.6 cm high, with male gonophores, BPBM (without collection number).—Oahu: Kaneohe Bay, pier at Hawaii Institute of Marine Biology, 2 m, on wood pilings, no date, fragment of colony above, with male gonophores, ROMIZ B3834.–Oahu: Hawaii Kai, on pilings of bridge over Highway 72, 21º17'06.60"N, 157º43'07.21"W, 0.1 m, 27.vii.2009, on small oyster shell, one colony, with cormoids up to 0.5 cm high, without gonophores, coll. D. R. Calder, ROMIZ B3826.

Description. Colonies small, with both stolonal and erect forms, up to 0.6 cm high, arising from a creeping hydrorhiza; colonies with erect hydrocaulus sparsely and irregularly to more or less alternately branched. Hydrocaulus monosiphonic, branched or simple, when branched with branches and ultimate branchlets relatively long, straight to sometimes contorted, resembling hydrocaulus. Perisarc relatively firm, becoming thinner in younger parts, terminating at perisarc groove on base of hydranths, annulated at bases of hydrocaulus, branches and ultimate branchlets, a few annulations and wrinkles elsewhere but mostly smooth. Hydranths urn-shaped, up to 0.35 mm long from base to hypostome, 0.30 mm wide; base with perisarc groove; gastroderm with numerous black pigment spots; ring of nematocysts above perisarc groove lacking; hypostome large, knob-shaped to flared. Tentacles solid, filiform, in one whorl, about 18–22 in number.

Gonophores fixed sporosacs, borne on atrophied blastostyles. Male gonophores with one chamber or a linear pair of two chambers; terminal chamber with an apical tubercle; blastostyles with a tuft of as many as 20 strings of gonophores. Female gonophores not seen.

Nematocysts. Heterotrichous microbasic euryteles (7.0–7.7 µm long × 2.8–3.3 µm wide).

Remarks. Material with male gonophores, corresponding with the characters of *Eudendrium capillare* Alder, 1856, were present in collections at the Bishop Museum (BPBM, without collection number) from shallow waters in Kaneohe Bay. Cooke (1977) also found minute specimens in shallow waters that resembled *E. capillare*, but he concluded that species identification was impossible in the absence of gonophores. From his description, these hydroids are thought to be the same species as specimens examined here. The Hawaiian population and should be studied further, however, because a preponderance of colonies from the region were stolonal rather than erect as usual in the species.

Nutting's (1905) hydroids from Albatross Stn. 3854 were infertile, and he assigned them to *Eudendrium capillare* with considerable reservation. They are regarded as a different species herein, identified as *Eudendrium* sp. 2.

The cnidome of *Eudendrium capillare* is usually thought to comprise only heterotrichous microbasic euryteles. Schuchert (2008b) also discovered small isorhizas in material from Europe, although numbers varied and they were sometimes absent. I was unable to confirm the presence of isorhizas in material from Hawaii.

Reported distribution. Hawaii. Oahu: Kaneohe Bay and Honolulu Harbor (Cooke 1977).
Worldwide. Virtually cosmopolitan in warm and temperate waters; 0–82 m (Fraser 1946; Calder 1988; Schuchert 2008b).

Eudendrium carneum Clarke, 1882

Figs. 26, 27

Eudendrium carneum Clarke, 1882: 137, pl. 7, figs. 10–17.

Type locality. USA: Virginia, Hampton Roads, Fort Wool (Clarke 1882).

Material examined. Oahu, Pearl Harbor, on boat in dry dock, 5.iv.1950, 16 colony fragments in fair to poor condition, up to 10 cm high, eight with female gonophores, five with male gonophores, three without gonophores, BPBM D307.–Oahu, Pearl Harbor, Alpha Docks, 25.vii.1976, ~5 m, on *Schizoporella*, five colony fragments, to 7 cm high, with female gonophores, coll. P.Z. Langford, BPBM (without collection number).–Oahu: Honolulu Harbor, Pier 20, 16.ix.1997, one colony, 9 cm high, with male gonophores, coll. R. DeFelice and S. Coles, BPBM D1083.

Description. Colonies erect, up to 10 cm high, arising from a hydrorhizal mat or broken off near base, straggly in form; branching in some parts occasionally regular and alternate but predominantly irregular. Hydrocaulus polysiphonic basally, monosiphonic distally; main branches long, most of them monosiphonic, typically quite straight, resembling hydrocaulus. Perisarc in older parts of colony thick, dark brown, becoming thinner and golden-coloured in younger parts, terminating at perisarc groove on base of hydranths, mostly smooth but with annulations at bases of branches and pedicels, a few annulations elsewhere on hydrocaulus, branches and pedicels. Hydranths urn-shaped, in preserved material up to about 0.6 mm long from base to hypostome, 0.3 mm wide; base ringed by perisarcal groove and band of heterotrichous anisorhizas; hypostome large, knob-shaped to flared. Tentacles solid, filiform, in one whorl, about 25 in number.

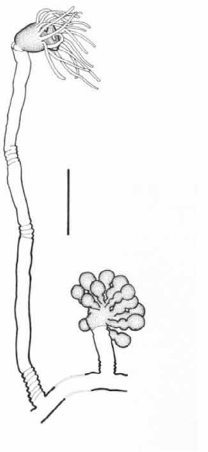
Gonophores fixed sporosacs, borne on atrophied blastostyles. Female gonophores with bifid spadix curving over egg; each spadix secreting a perisarcal capsule around embryo before being shed; clusters of embryos in perisarcal capsules scattered along ultimate branchlets; perisarc of these branchlets becoming wrinkled proximally. Male gonophores comprising a linear series of up to five chambers; each distal chamber armed with heterotrichous anisorhizas; blastostyles with as many as 10 strings of gonophores.

Nematocysts. Heterotrichous microbasic euryteles (abundant on tentacles; present on hydranths and male gonophores)

Heterotrichous anisorhizas (occurring in a ring around hydranth base; also present on hypostome and at tips of male gonophores)

Remarks. *Eudendrium carneum* Clarke, 1882 is widespread and well-known. Detailed accounts of its taxonomy and natural history are given by authors including Millard (1975), Watson (1985), Calder (1988), Marques, Mergner *et al*. (2000); Marques, Peña Cantero *et al*. (2000), and Schuchert (2008b), and need not be repeated here. Its occurrence in many areas has been attributed to shipping (Watson 1985), and discovery of *E. carneum* in collections from the ports of Pearl Harbor and Honolulu Harbor in Hawaii accord with this hypothesis.

Although reported here for the first time from Hawaii, *Eudendrium carneum* has been established in waters of the state for more than 50 years based on previously unidentified material examined here (BPBM D307).



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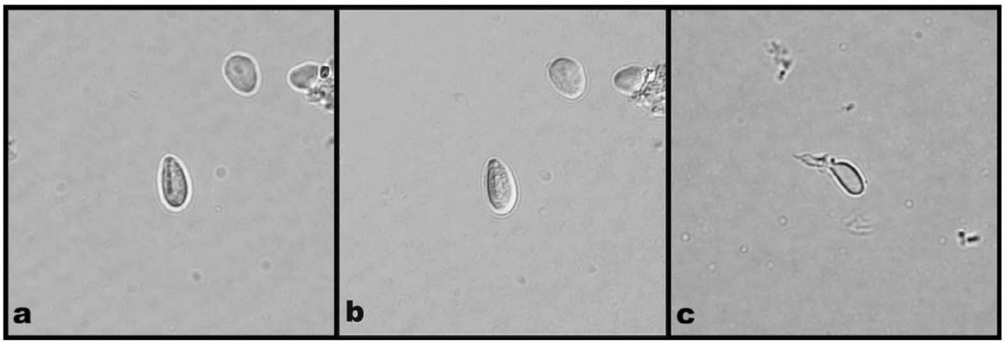

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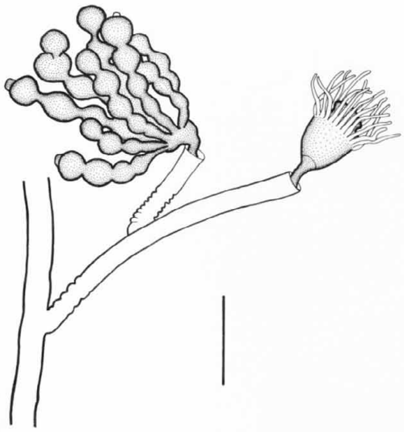

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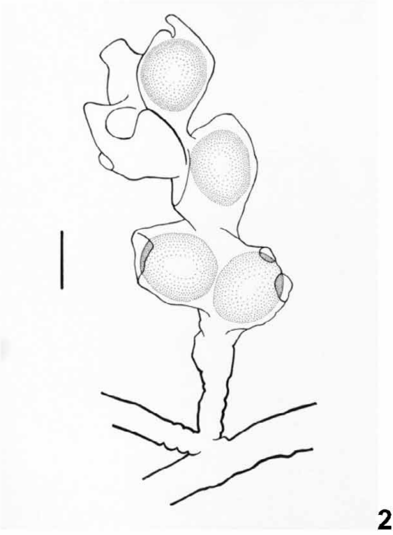

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FIGURE 24. *Eudendrium capillare*: part of colony with hydranth and male gonophore, ROMIZ B3834. Scale equals 0.5 mm.

FIGURE 25. *Eudendrium capillare*: nematocysts, ROMIZ B3826. a–b, heterotrichous microbasic euryteles (undischarged). c, heterotrichous microbasic eurytele (discharged).

FIGURE 26. *Eudendrium carneum*: part of colony with hydranth and male gonophores, BPBM D1083. Scale equals 0.5 mm.

FIGURE 27. *Eudendrium carneum*: part of female colony with encapsulated embryos, BPBM D307. Scale equals 0.25 mm.

The cnidome of this species is as described earlier (Calder 1988).

Reported distribution. Hawaii. New record.

Worldwide. Circumtropical; 0–137 m, but usually in the upper 20 m (Fraser 1946; Watson 1985; Marques, Mergner *et al*., 2000; Marques, Peña Cantero *et al*. 2000; Schuchert 2008b).

***Eudendrium* sp. 1**

Figs. 28, 29

Eudendrium rameum.—Nutting, 1905: 939 [not *Eudendrium rameum* (Pallas, 1766)].

Material examined. Kauai: Albatross Stn. 4135, off Wailua, 22.076389º N, 159.323611º W, 1.viii.1902, 411–538 m, two colony fragments, to 6.8 cm high, hydranths in poor condition, apparently without gonophores (colonies possibly dry at some time), labelled *Eudendrium rameum*, USNM 22223.–Maui: Albatross Stn. 4077, NE of Kahului Harbor, 21.016667º N, 156.404167º W, 21.vii.1902, 181–194 m, one colony, in fragments, largest fragment 3.5 cm high, with numerous hydranths in rather poor condition, with female gonophores, labelled *Eudendrium rameum*, USNM 22267.–Niihoa: Albatross Stn. 4150, 23.1º N, 161.9º W, 5.viii.1902, 130-293 m, four colony fragments, to 5.8 cm high, one with female gonophores, labelled *Eudendrium arbuscula*, USNM22270.

Description. Colonies erect, up to 6.8 cm high, broken off near base, densely branched in one plane, dendritic, branching irregular proximally, more or less regular and alternate distally. Hydrocaulus strongly polysiphonic, up to 2 mm thick basally, irregularly twisted or curved; largest branches resembling hydrocaulus; ultimate branches much more slender, monosiphonic or weakly polysiphonic basally, hydranth-bearing branchlets monosiphonic. Perisarc in older parts of colony thick, brown to light brown in colour, becoming thinner and golden to almost glassy, terminating at base of hydranths; annulated at bases of ultimate branches and branchlets, smooth or with scattered wrinkles elsewhere. Hydranths small, about 0.3 mm long, with a single whorl of about 22 filiform tentacles, otherwise too poorly preserved to adequately describe.

Gonophores fixed sporosacs. Female gonophores occurring at distal end of branchlet, sometimes associated with a partially atrophied hydranth with a cluster of stubby tentacles and lacking a hypostome; spadix unbranched, curving over egg, 1–3 gonophores per branchlet; male gonophores not seen.

Remarks. Nutting (1905) identified this hydroid as *Eudendrium rameum* (Pallas, 1766). Like that species, colonies from Hawaii are robust, strongly polysiphonic, and profusely branched, but the identification seems uncertain. The specimens also resemble *Eudendrium arbuscula* Wright, 1859a in colony form, and a colony from Niihoa in NMNH collections (USNM 22270) is labelled and catalogued as such. Given the poor condition of the hydranths, the absence of male gonophores, inadequate knowledge of the cnidome, and the remoteness of Hawaii from the predominantly eastern North Atlantic distribution of *E. arbuscula*, identification of present material to that species on current evidence seems questionable.

Reported distribution. Hawaii. Albatross Stn. 4077, “off … Maui, 99 fathoms” (181 m); Albatross Stn. 4135, off … Kauai, 225 fathoms” (411 m) (Nutting 1905, as *Eudendrium rameum*).

***Eudendrium* sp. 2**

?*Eudendrium capillare*.—Nutting, 1905: 939.

Material examined. None.

Remarks. Nutting (1905) assigned a sterile colony of *Eudendrium* Ehrenberg, 1834 from bathyal waters off Hawaii, with question, to *E. capillare* Alder, 1856. No description of the species was given, other than its general size ("…somewhat larger than British specimens"; Nutting, 1905: 939), and no illustration was provided. The material is listed in the NMNH catalog (Molokai: Albatross Stn. 3854, south of Kamalo, 20.995833º N, 156.861111º W, 9.iv.1902, 238–245 m, without gonophores, labelled *Eudendrium capillare*, USNM 22216), but it could not be located for this study (Geoff Keel, pers. comm., 05 April 2010). The identity of the species remains doubtful.

Reported distribution. Hawaii. Albatross Stn. 3854, "off the south coast of … Molokai, 134 fathoms" (245 m) (Nutting 1905, as ?*Eudendrium capillare*).

Suborder Capitata Kühn, 1913

Capitata Kühn, 1913: 228.

Diagnosis. Anthoathecate hydroids with some or all hydranth tentacles capitate or moniliform.

Gonophores fixed sporosacs, fixed or liberable eumedusoids, or medusae. Medusae, when present, with mouth usually simple, circular; gonads on manubrium, ordinarily surrounding it entirely.

Cnidome including stenoteles.

Remarks. Hydrozoans assigned to Capitata Kühn, 1913 are distinguished by having capitate or moniliform tentacles, and a cnidome that includes stenoteles. Major revisions of the group have been undertaken by Rees (1957a) and Petersen (1990), the latter providing a phylogenetic analysis. The suborder currently includes 26 families and about 375 species, but molecular evidence suggests that the suborder Capitata is paraphyletic and comprises two clades, Capitata *sensu stricto* and Aplanulata Collins, Winkelmann, Hadrys & Schierwater, 2005 (Collins *et al*. 2005; Daly *et al*. 2007; Cartwright *et al*. 2008; Nawrocki *et al*. 2010). Although no formal redefinition of the Capitata has yet been proposed, the order of families herein reflects the two clades believed to exist within Capitata.

Clade Aplanulata Collins, Winkelman, Hadrys, & Schierwater, 2005

Aplanulata Collins *et al*. 2005: 95.

Diagnosis. Capitata with direct development, lacking a planula stage in the life cycle.

Remarks. Originally included in Aplanulata Collins *et al*., 2005 were Hydridae Dana, 1846, Candelabridae Stechow, 1921a, Corymorphidae Allman, 1872, and Tubulariidae Fleming, 1828. Certain other capitate families may also prove to be referable to this group (Collins *et al*. 2006; Daly *et al*. 2007; Cartwright *et al*. 2008).

Family Hydridae Dana, 1846

Hydridae Dana, 1846: 116.

Diagnosis. Aberrant capitate freshwater hydroids with solitary hydranths, occasionally appearing colonial because of asexual budding from lower walls. Hydranths varied in shape, elongate and cylindrical or with central bulge when extended, barrel-shaped when contracted, with pedal disc basally and whorl of tentacles distally; pedal disc with central pore; tentacles hollow, filiform to slightly moniliform distally, in one whorl around hypostome; hypostome dome-shaped; perisarc absent except on embryothecae.

Gonophores completely reduced and medusa suppressed; gametes produced within wart-like protuberances in ectoderm of hydranth wall; planula stage absent; sexes hermaphroditic or gonochoric; when hermaphroditic, 'testis' occurring distally and 'ovary' proximally on hydranth column.

Remarks. The family Hydridae Dana, 1846 is now generally thought to contain a single genus, *Hydra* Linnaeus, 1758 (Petersen 1990; Bouillon *et al*. 2006; Daly *et al*. 2007; Hemmrich *et al*. 2007; Schuchert 2010). Of some 80 described species, fewer than 15 are considered valid (Jankowski *et al.* 2008).

Polyps of species of *Hydra* resemble filiferans, particularly in having tentacles that appear filiform. However, their affinities with Capitata Kühn, 1913 are reflected in the cnidome (comprising stenoteles, desmonemes, and haplonemes) and in overall development (Petersen 1990). They were regarded by Petersen as being closely related to Moerisiidae Poche, 1914, with the two having similar cnidomes and aflagellate planulae. Bouillon *et al*. (2006) suggested that Hydridae might warrant classification as a distinct order, but included them, together with Moerisiidae and four other families, in the capitate suborder Moerisiida Poche, 1914. Collins *et al*. (2005) included Hydridae in Aplanulata Collins *et al*., 2005.

The taxonomy and nomenclature of Hydridae have long been in disarray. Although *Hydra* was established by Linnaeus (1758) with 11 included nominal species, none of the original names is in current use (Campbell 1989). Some of the originally included taxa have been assigned to other groups, while any conforming with the current concept of the genus have unfortunately been given replacement names that have become more familiar than now-abandoned original ones. Campbell (1989) discussed some of the confusion over names and identifications in the group.

Genus *Hydra* Linnaeus, 1758

Hydra Linnaeus, 1758: 816.
Type species. None validly designated.

Diagnosis. With the characters of the family.

Remarks. Confusion exists over the type species of *Hydra* Linnaeus, 1758, in part because of significant nomenclatural problems mentioned above. That designation has been assigned to *Hydra viridis* Linnaeus, 1767 by Annandale (1911), to *H. vulgaris* Pallas, 1766 by Apstein (1915), and to *Hydra oligactis* Pallas, 1766 by Petersen (1990), but all are ineligible because they were not among the originally included nominal species in the genus when it was founded by Linnaeus (1758).

Campbell (1989) provided a history of research on *Hydra* and reviewed European species of the genus. While this fresh water genus is represented on few oceanic islands (Jankowski *et al.* 2008), it has long been known to occur on Hawaii (Mumford 1940).

Hydra sp.

Figs. 30, 31

Hydra.—Mumford, 1940: 243.
Hydra sp.—Bailey-Brock & Hayward, 1984: 199, fig. 1B.

Material examined. Kauai: AMFAC–Kekaha, from prawn ponds, associated with *Hyalinella vaihiriae* (Bryozoa), viii.1982, several hundred polyps, to 1 mm high (preserved), many with buds, coll. J. Brock, BPBM (without collection number).–Kauai: AMFAC–Kekaha, from prawn ponds, associated with *Hyalinella vaihiriae* (Bryozoa), viii.1982, several polyps from sample above, to 1 mm high (preserved), many with buds, coll. J. Brock, ROMIZ B3831.

Description. Hydroids solitary, with flattened basal disc; algal symbionts absent. Hydranths columnar to bulbous in preserved material, up to about 1 mm high, lacking perisarc, with a distal whorl of 5–7 filiform tentacles; hypostome flattened and usually indistinct. Contracted tentacles tapering distally, heavily armed with nematocysts. Many polyps with lateral buds arising from lower hydranth wall, often with more than one per individual; tentacles on buds formed synchronously.

Gonads not seen.

Nematocysts (Fig. 31).

desmonemes (6.0–6.7 µm long × 4.3–4.9 µm wide)
atrichous isorhizas (6.8–7.2 µm long × 3.0–4.0 µm wide)
holotrichous isorhizas (8.0–9.4 µm long × 3.9–4.3 µm wide)
stenoteles (10.0–15.8 µm long × 8.0–13.1 µm wide)

Remarks. In an overview of animal distributions on oceanic islands, Mumford (1940) noted that "*Hydra*" had been collected near the University of Hawaii and from other localities on the island of Oahu. Bailey-Brock & Hayward (1984) also discovered *Hydra* sp. in Hawaii, growing on the freshwater bryozoan *Hyalinella vaihiriae* Hastings, 1929 in prawn ponds on Kauai in 1982. The aquaculture farm where specimens were found was later closed and there have been no subsequent published reports of *Hydra* sp. from the Hawaiian Islands. Material from that source was deposited in collections at the Bishop Museum and was examined here. Many of the specimens were undergoing asexual budding, but no gonads were observed and identification to species was not possible from preserved material. From the morphology of the holotrichous isorhizas (Fig. 31d), however, the species appears to belong to a clade that includes *H. vulgaris* Pallas, 1766 and *H. carnea* L. Agassiz, 1850, among others (Hemmrich *et al.* 2007).

A species thought referable to *Hydra* Linnaeus, 1758 (described as a "pink hydra") was collected from a stream on the Island of Hawaii in 2006 (Lucius Eldridge, pers. comm., 2 May 2006). No specimens from that discovery were found in collections at the Bishop Museum and nothing more is known here about the record.

Family Tubulariidae Fleming, 1828

Tubulariadae Fleming, 1828: 552 [emended to Tubulariidae by Hincks (1868)].

Diagnosis. Capitate hydroids solitary or colonial. Hydrocaulus erect, branched or unbranched, usually long and cylindrical, infrequently short and thick, arising from creeping hydrorhiza, basal disc, or tuber- to rhizoid-like processes proximally, distal end with bulbous to tapered neck region supporting a hydranth; perisarc cylindrical, often thick and rigid over hydrocaulus, thin over neck region, extending to hydranth base; annulations present or absent. Hydranths flask-shaped to barrel-shaped, with thickened parenchymatic cushion basally, bearing tentacles at aboral and oral ends. Aboral tentacles long, tapering, in one whorl; oral tentacles shorter, in one or several close whorls, usually filiform but sometimes pseudofiliform, moniliform, or capitate.

Gonophores fixed sporosacs or free medusae, borne on blastostyles arising in a whorl from hydranth just above aboral tentacles; planula stage absent. Fixed sporosacs, when present, often with actinula larvae. Medusae, if present, bell-shaped, symmetrical with straight margin or bilaterally symmetrical with more or less oblique margin, exumbrella with or without 5–8 meridional tracks of nematocysts; manubrium usually quite small; mouth simple, circular; radial canals four; marginal tentacles 1–4, perradial; ocelli absent; gonads surrounding manubrium; medusae sometimes producing actinulae.

Remarks. Authorship of the family-group name Tubulariidae has been credited to Fleming (1928). Goldfuss (1818) and Fischer von Waldheim (1823) used the name "Tubulariae" earlier (Calder 1988), but in what is interpreted as a descriptive term for a group of genera excluding *Tubularia* Linnaeus, 1758, and as such neither is available (ICZN Art. 11.7). Goldfuss included the genera *Clava* Gmelin, 1791, *Coryne* Gaertner, 1774, *Calamella* Oken, 1815, and *Sertularia* Linnaeus, 1758 in Tubulariae, but he assigned the genus name *Tubularia* to a different family ("Polypi") within a different order ("Infusoria"). Likewise, Fischer von Waldheim used the name "Tubulariae" for a group that did not include *Tubularia*.

The diagnosis of Tubulariidae given above has been adapted from Calder (1988), who reviewed the nomenclatural history of the family, from Petersen (1990), who revised diagnoses of included genera, from Bouillon *et al*. (2006), who provided a list of included species, and from Schuchert (2010), who recently revised the European species. Tubulariidae presently comprises 10 genera and about 75 species, and is thought to be monophyletic (Daly *et al*. 2007; Schuchert 2009). Of the included genera, only *Ectopleura* L. Agassiz, 1862 has been reported from Hawaii.

Marques & Migotto (2001) recognized two subfamilies in Tubulariidae, namely Tubulariinae Fleming, 1828 (including *Tubularia*, *Hybocodon* L. Agassiz, 1862, *Zyzzyzus* Stechow, 1921a, *Ralpharia* Watson, 1980, and *Bouillonia* Petersen, 1990) and the newly established Ectopleurinae Marques & Migotto, 2001 (including *Ectopleura* L. Agassiz, 1862 and *Pinauay* Marques & Migotto, 2001). A new genus established recently, *Lobataria* Watson, 2008, is referable to Tubulariinae.

Genus *Ectopleura* L. Agassiz, 1862

Ectopleura L. Agassiz, 1862: 342.

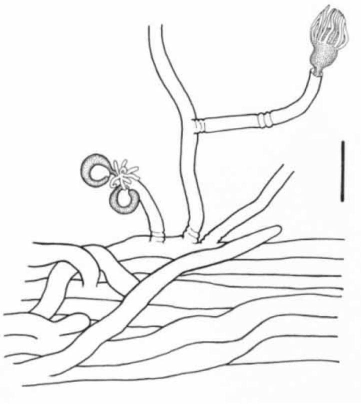
Type species. *Tubularia dumortierii* Van Beneden, 1844b [*Ectopleura dumortierii*], by subsequent designation by Mayer (1910a).

Diagnosis. Tubulariid hydroids solitary or colonial. Hydrocaulus erect, long, cylindrical, with open lumen, usually with two longitudinal V-shaped endodermal ridges, rarely with five, arising from a creeping hydrorhiza or hydrothizal mat; neck region bulbous, with perisarc groove around widest part; perisarc over neck region thin. Hydranths with oral tentacles usually filiform, rarely moniliform or capitate, in a single whorl, aboral tentacles essentially filiform.

Gonophores free medusae, eumedusoids, or sporosacs, borne on dichotomously branched or unbranched blastostyles just above aboral tentacles. Medusae when present bell-shaped, radially symmetrical; exumbrella with four pairs of meridional nematocyst tracks; marginal tentacles four perradial or two opposite, equally developed, moniliform or with abaxial nematocyst clusters; manubrium short, extending at most to velar opening; radial canals four; gonads encircling manubrium.

Remarks. The widely-used generic name *Ectopleura* L. Agassiz, 1862 is threatened by several older but now unused senior subjective synonyms, including *Pyxidium* Leuckart, 1856, *Vorticlava* Alder, 1856, *Parypha* L. Agassiz, 1860, and *Thamnocnidia* L. Agassiz, 1860. Of these threats to nomenclatural stability, only that represented by *Pyxidium* can be resolved here.

The type species of *Pyxidium*, *P. truncatum* Leuckart, 1856 (by monotypy), is of questionable identity. It was included by L. Agassiz (1862) in *Parypha* (see also A. Agassiz 1865: 194), a senior subjective synonym of *Ectopleura*. Haeckel (1879) listed it in an index of obsolete names. Reversal of Precedence (ICZN Art. 23.9) can be applied to relegate *Pyxidium* to the status of nomen oblitum. That name has been not been used as valid in zoology after 1899 (ICZN Art. 23.9.1.1). Meanwhile, *Ectopleura* has been used in over 25 works by more than 10 authors in the past 50 years (Art. 23.9.1.2) (e.g. Kramp 1961; Brinckmann-Voss 1970; Millard 1975; Bouillon 1978b; Wedler & Larson 1986; Calder 1988; Hirohito 1988; Petersen 1990; Migotto 1996; Calder & Vervoort 1998; Bouillon & Boero 2000; Faucci & Boero 2000; Marques & Migotto 2001; Cairns *et al*. 2002; Peña Cantero & García Carrascosa 2002; Kirkendale & Calder 2003; Schuchert 2003, 2009; Calder & Kirkendale 2005; Bouillon *et al*. 2006; Galea *et al*. 2007; Xu *et al.* 2007; Altuna 2008; Watson 2008; Guenther *et al*. 2010). Accordingly, *Ectopleura* is herein assigned precedence over *Pyxidium* whenever the two are considered congeneric.



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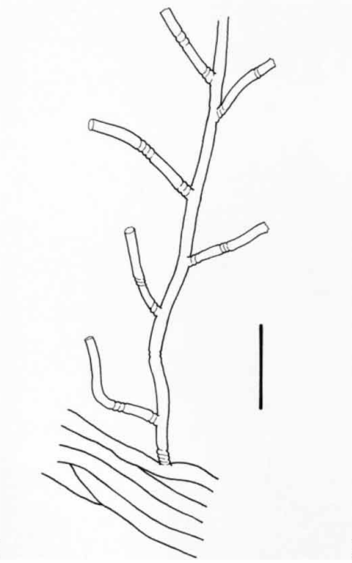

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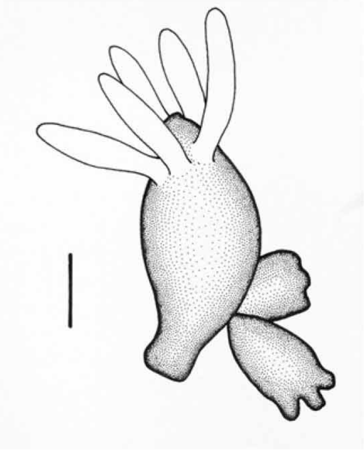

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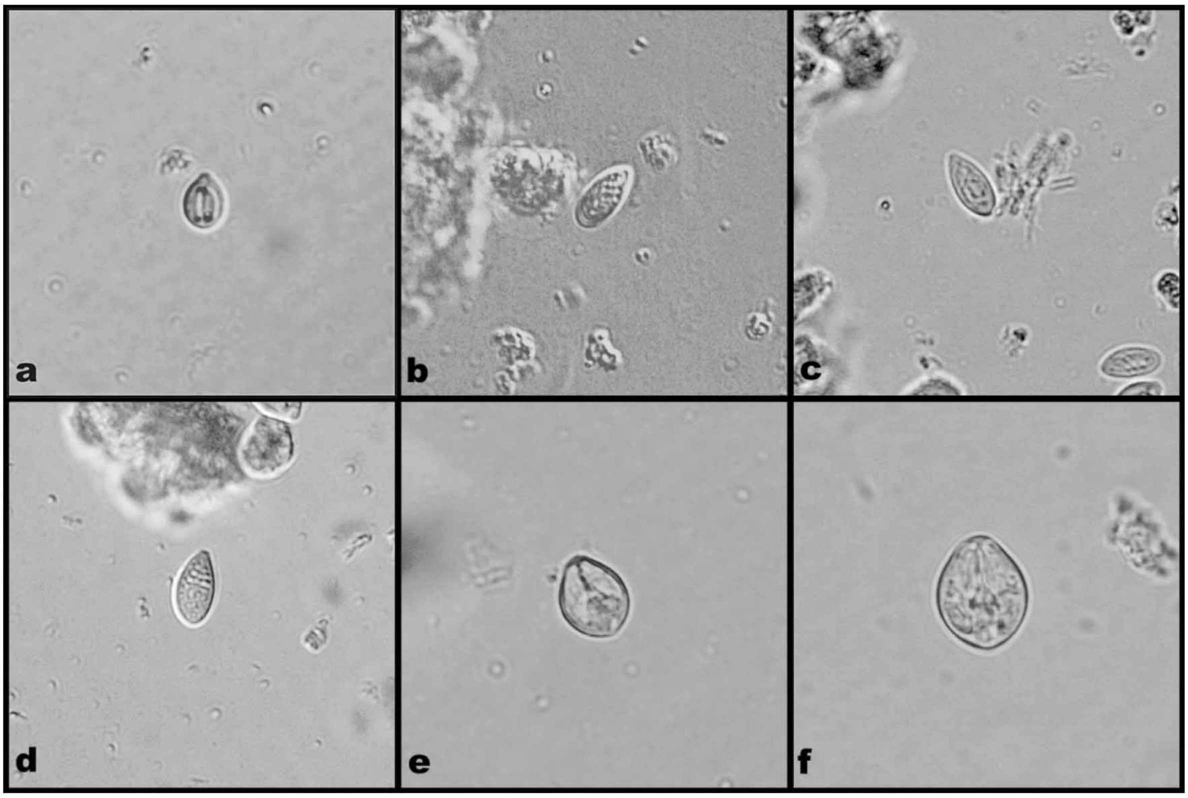

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FIGURE 28. *Eudendrium* sp. 1: part of hydrocaulus bearing a hydranth and a blastostyle with female gonophores, USNM 22270. Scale equals 0.5 mm.

FIGURE 29. *Eudendrium* sp. 1: part of hydrocaulus with a branch; hydranths lacking, USNM 22270. Scale equals 1 mm.

FIGURE 30. *Hydra* sp.: polyp with two lateral buds, ROMIZ B3831. Scale equals 0.25 mm.

FIGURE 31. *Hydra* sp.: nematocysts, ROMIZ B3831. a, desmoneme. b–c, atrichous isorhizas. d, holotrichous isorhiza. e, small stenotele. f, large stenotele.

The identity of *Vorticlava* is fixed by its type species by monotypy, *V. humilis* Alder, 1856, now regarded as a junior subjective synonym of *Ectopleura larynx* Ellis & Solander, 1786 (Vervoort 1946; Cornelius & Garfath 1980). The threat of *Vorticlava* to *Ectopleura* cannot be removed by Reversal of Precedence because the senior name was used as valid several times during the first half of the 20th century (ICZN Art. 23.9.1.1) (e.g. Bedot 1910, 1912, 1916, 1918, 1925; Rees 1937).

Parypha and *Thamnocnidia* were both initially introduced without included species. However, brief definitions of them were given (L. Agassiz, 1860: 45, 46), thereby making the names available (ICZN Art. 12.1). In a subsequent work (L. Agassiz 1862: 342), several nominal species were assigned to each one. Included under *Parypha* were *Pyxidium truncatum* Leuckart, 1856, *Tubularia cristata* McCrady, 1859, and *Parypha crocea* L. Agassiz, 1862. Species referred to *Thamnocnidia* were *Tubularia coronata* Abildgaard, in Müller, 1806, *T. calamaris* sensu Van Beneden, 1844b (non Pallas, 1766), *Thamnocnidia spectabilis* L. Agassiz, 1862, and *T. tenella* L. Agassiz, 1862. No type species were designated for either genus, but all of them are referable or questionably referable to *Ectopleura*, as currently defined. Reversal of Precedence cannot be applied to assign priority to *Ectopleura* over *Thamnocnidia* and *Parypha* because both of the latter have been used as valid since 1900 (e.g. *Thamnocnidia* was used as a genus name by Whiteaves 1901: 20, and as a subgenus name by Fenchel 1905: 573; *Parypha* was employed by Allen 1900: 291). Other instances of their usage early in the 20th century are listed in Bedot (1925).

In the interests of nomenclatural stability, a case to the International Commission on Zoological Nomenclature is needed requesting conservation of the widely used name *Ectopleura* in place of its essentially abandoned senior subjective synonyms *Vorticlava*, *Parypha*, and *Thamnocnidia*. In the meantime, existing usage is maintained here.

The diagnosis of *Ectopleura* given above, modified from that proposed by Petersen (1990), Bouillon *et al*. (2006), and Schuchert (2010), reflects the current concept of the genus. Additional characters are from a cladistic analysis of Tubulariidae Fleming, 1828 by Marques & Migotto (2001). In the classification of the family by Marques & Migotto, species earlier assigned to *Ectopleura* that had (1) fixed gonophores, (2) sexually dimorphic blastostyles, and (3) oral tentacles adnate to hypostome, were assigned to *Pinauay* Marques & Migotto, 2001 (type species *Tubularia larynx* Ellis & Solander, 1786, by original designation). However, *Pinauay* is predated by *Vorticlava*, *Parypha*, and *Thamnocnidia*, and was not recognized as distinct from *Ectopleura* by Schuchert (2009, 2010).

***Ectopleura* cf. *viridis* (Pictet, 1893)**

Figs. 32, 33

Tubularia viridis Pictet, 1893: 17, pl. 1, figs. 10, 11.

Type locality. Indonesia: “Port d’Amboine…” (Pictet 1893).

Material examined. Oahu: Kaneohe Bay, anchor cable, 3 m, 4.i.1978, one large clump, 15 cm in diameter, with medusa buds, coll. W.J. Cooke, BPBM (without collection number).–Oahu: Kaneohe Bay, anchor cable, 3 m, 4.i.1978, one small fragment of sample above, with medusa buds, coll. W.J. Cooke, ROMIZ B3827.

Description. Hydroids colonial, forming a dense aggregation of hydrocauli with numerous hydranths, arising from a hydrorhizal mat. Hydrorhizae creeping, wrinkled to smooth. Hydrocauli smooth, unbranched, up to 3.5 cm high, 0.6 mm wide, tangled together basally, free elsewhere, nearly straight to variously contorted, each terminating distally with a bulbous neck region supporting a hydranth. Perisarc of hydrorhiza thick; that on hydrocauli fairly thick basally, becoming thinner distally, filmy over neck region, terminating at base of hydranth; light straw-coloured, essentially clear in thin areas. Hydranths 3 mm high from basal constriction to mouth, 2.5 mm wide, vase-shaped, with proximal half bulbous, distal half tapering, becoming slender orally; bearing one aboral and one oral whorl of tentacles. Aboral tentacles of mature hydranths gradually tapering from base to tip, to 6 mm long, about 25–30 in number, in a single whorl; oral tentacles filiform, digitate, up to 0.9 mm long, about 25 in number, in a single whorl, bases adnate to hypostome, forming longitudinal ridges on it.

Gonophores free medusae. Medusa buds developing in clusters on short, slender blastostyles arising on hydranth immediately distal to aboral tentacles. Well-developed medusa buds thimble-shaped, 0.3 mm high, 0.25 mm wide, with an apical stalk attached to blastostyle; mesoglea thin; exumbrella with eight meridional tracks of nematocysts; manubium simple, large, tubular, stubby, reaching about ¾ distance to velar opening; radial canals four; tentacle bulbs four, with an opposite pair having well-developed marginal tentacles, each with a terminal knob and a single abaxial nematocyst cluster.

Remarks. Identification of hydroids of *Ectopleura* L. Agassiz, 1862 having medusa buds with two opposite tentacles is virtually impossible based on current limited knowledge of the group. Although assigned provisionally to *Ectopleura viridis* (Pictet, 1893), the identity of the hydroid studied here is uncertain in the absence of information on its medusa stage. Several species of *Ectopleura* besides *E. viridis* have medusa buds or medusae with two opposite tentacles (Petersen 1990; Xu *et al.* 2007), but life cycles are unknown or inadequately known for all of them. Medusa buds and trophosomes in specimens examined here generally correspond with those ascribed to *E. minerva* Mayer, 1900b by Hirohito (1988). However, that species was originally described from the Atlantic Ocean (Florida) and records of it from the Pacific Ocean are considered doubtful.

Ectopleura viridis, apparently endemic to the Indo-west Pacific region (see Reported Distribution below), has been reported infrequently. Schuchert (2003, 2009) has been followed in regarding *Ectopleura pacifica* Thornely, 1900 as a synonym of it. A record of *E. pacifica* from India by Mammen (1963) is erroneous because medusa buds were described as having four tentacles rather than two. It was considered a new species, *E. indica*, by Petersen (1990).

The colony examined here, a clump reaching almost 15 cm in diameter, is much larger than specimens of *E. viridis* described previously by Pictet (1893), Thornely (1900, as *E. pacifica*), Borradaile (1905, as *E. pacifica*), Billard (1905), and Schuchert (2003), as well as those ascribed to *E. minerva* by Hirohito (1988). Individual hydrocauli were up to 3.5 cm in length.

Hirohito (1988) and Calder (1988) considered *E. pacifica* and *E. minerva* to be conspecific, but Xu *et al.* (2007) recognized both as valid based on differences in the medusa stage.

Reported distribution. Hawaii. New record.

Worldwide. Indonesia (Pictet 1893; Schuchert 2003), Papua New Guinea (Thornely 1900, as *Ectopleura pacifica*), Mangareva, French Polynesia (Billard 1905), Suvadiva Atoll, Maldives (Borradaile 1905, as *Tubularia pacifica*); 1–68 m.

Clade Capitata Kühn, 1913, *sensu stricto*

Capitata Kühn, 1913: 228.

Diagnosis. Capitata with a planula stage in the life cycle.

Remarks. Planulate Capitata were retained in Capitata Kühn, 1913, *sensu stricto*, by Cartwright *et al.* (2008). To avoid confusion, this name should be changed. Molecular studies by Nawrocki *et al.* (2010) suggest the presence of two clades within the group, namely the Corynida (including Corynidae Johnston, 1836 and Cladonematidae Gegenbaur, 1857) and Zancleida (including Hydrocorynidae Rees, 1957a, Pennariidae McCrady, 1859, Moerisiidae Poche, 1914, Sphaerocorynidae Prévot, 1959, Porpitidae Goldfuss, 1818, Zancleidae Russell, 1953, Asyncorynidae Kramp, 1949, Milleporidae Fleming, 1828, Cladocorynidae Allman, 1872, and Solanderiidae Marshall, 1892).

Family Corynidae Johnston, 1836

Corynidae Johnston, 1836: 107.

Diagnosis. Capitate hydroids with stolonal or erect colonies, arising from creeping hydrorhiza or encrusting base; erect colonies unbranched or irregularly branched. Perisarc covering hydrorhiza, hydrocaulus, and hydrocladia. Hydranths frequently clavate but varied in shape, with an oral whorl of capitate tentacles, additional capitate tentacles often present below this whorl, these either scattered or in verticils; with or without an aboral whorl of reduced filiform sensory tentacles; hypostome conical to dome-shaped, with or without button-like aggregation of mucous gland cells. Colonies polymorphic in *Nannocoryne* Bouillon & Grohmann, 1994, with gametes arising in walls of gonozooids.

Gonophores fixed sporosacs, eumedusoids, or medusae. Medusae, when present, with characters of the order; umbrella bell-shaped, lacking exumbrellar nematocyst tracks; manubrium tubular, varying from short to long, sometimes extending beyond velar opening; radial canals four; marginal tentacles four, capitate; ocelli present. Gonads in one or more rings on manubrium.

Remarks. A revision of the family Corynidae Johnston, 1836 was undertaken by Schuchert (2001b). Until recently, nine genera (*Coryne* Gaertner, 1774, *Sarsia* Lesson, 1843, *Dipurena* McCrady, 1859, *Dicodonium* Haeckel, 1879, *Sarsiella* Hartlaub, 1907, *Dicyclocoryne* Annandale, 1915, *Bicorona* Millard, 1966, *Cladosarsia* Bouillon, 1978a, and *Nannocoryne* Bouillon & Grohmann, 1994) and about 85 species were recognized in the family (Schuchert, 2009).

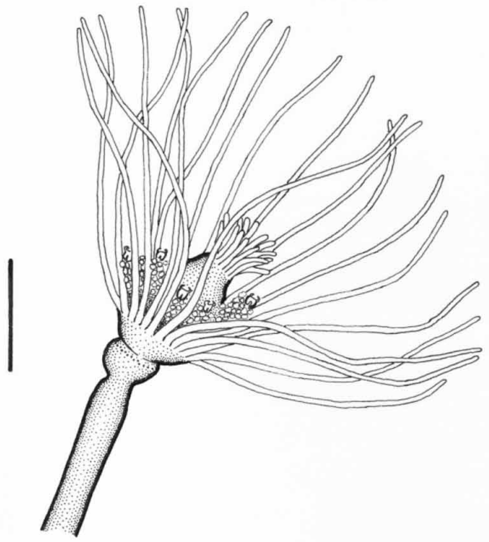
However, major revision of the family and its genera now appears warranted based on the work of Nawrocki *et al*. (2010). Most notably, their analysis indicated that the genus *Polyorchis* A. Agassiz, in L. Agassiz, 1862 should be included in the group. To accommodate results from that study, a step towards a new classification was undertaken by Schuchert (2010), who included the following genera besides *Polyorchis* in the family: *Coryne, Sarsia, and Scrippsia* Torrey, 1909, the reintroduced genera *Stauridiosarsia* Mayer, 1910a and *Codonium* Haeckel, 1879, and an extensively revised *Slabberia* Forbes, 1846, replacing its junior objective synonym *Dipurena.* Mayer (1910b: 719) had adopted the name *Dipurena* in place of *Slabberia* Forbes, 1846 because the latter was predated by *Slabberia* Oken, 1815. However, Schuchert correctly noted that Oken's (1815) work has been rejected for nomenclatural purposes by the International Commission on Zoological Nomenclature (Opinion 417), removing the threat to *Slabberia* Forbes, 1846, a name in use until Mayer's (1910b) replacement of it (see Hartlaub 1907: 62–66; Mayer 1910a: 73–79).

Further changes to the classification of Corynidae can be expected in the near future. Meanwhile, the diagnosis given above reflects the traditional concept of the family.

Genus *Coryne* Gaertner, 1774

Coryne Gaertner, 1774: 40.
Type species. *Coryne pusilla* Gaertner, 1774, by monotypy.

Diagnosis. Corynid hydroids stolonal or with erect and branched hydrocaulus, arising from a creeping hydrorhiza. Hydranths club-shaped, bearing capitate tentacles over distal half or more, filiform tentacles present or absent at proximal end; capitate tentacles surrounding hypostome in an oral whorl, those lower on hydranth scattered or in two or more irregular whorls; hypostome without distinct button-like mucous gland cell aggregation. Cnidome comprising stenoteles.



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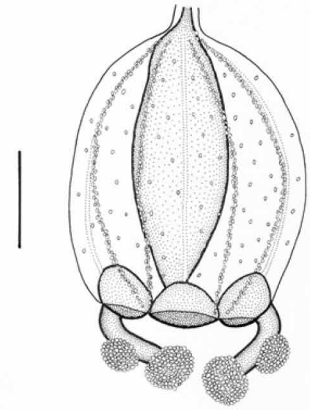

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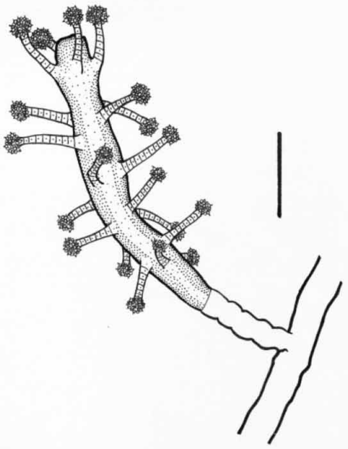

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FIGURE 32. *Ectopleura* cf. *viridis*: hydranth with medusa buds, BPBM (without collection number). Scale equals 2 mm.

FIGURE 33. *Ectopleura* cf. *viridis*: medusa bud, ROMIZ B3827. Scale equals 0.1 mm.

FIGURE 34. *Coryne* sp. 1: part of stolonal colony with hydranth, ROMIZ B3828. Scale equals 0.25 mm.

FIGURE 35. *Coryne* sp. 1: nematocysts, ROMIZ B3828. a, mastigophore (?). b, small stenoteles. c, large stenotele.

Gonophores fixed sporosacs or free medusae, arising either in upper axils of lower capitate tentacles or at level of proximal-most capitate tentacles, the latter sometimes becoming reduced with advancing gonophore development. Free medusae, when present, thimble-shaped with unbranched tentacles; manubrium short, contained within subumbrellar cavity; gonad forming a wide single band on manubrium, not covering oral end. Oblong isorhizas absent in both hydroid and medusa stages. Cnidome comprising stenoteles and desmonemes; occasionally with heteronemes.

Remarks. The concept of the genus *Coryne* Gaertner, 1774 maintained here was proposed by Petersen (1979, 1990) and adopted in most subsequent works (e.g. Brinckmann-Voss 2000; Schuchert 2001b; Bouillon *et al.* 2006). In addition to being more reflective of presumed phylogeny than previous views of the genus, the classification made it possible to differentiate hydroids of the corynid genera *Coryne* and *Sarsia* Lesson, 1843 even when the type of gonophore produced is not known. In earlier classifications, species with fixed sporosacs had been assigned to *Coryne* and those with free medusae to *Sarsia*. As defined here, gonophores in *Coryne* arise either in the axils of lower capitate tentacles or in the region of the hydranth wall where proximal-most capitate tentacles exist or were originally present. By contrast, gonophores in *Sarsia* develop below the level of the capitate tentacles. In adult medusae, the manubrium in *Coryne* is short and contained within the subumbrellar cavity while that in *Sarsia* is long and extends beyond the subumbrellar cavity. A number of characters can be used to differentiate *Coryne* from other genera in the family (Schuchert 2001b; Bouillon *et al.* 2006).

Petersen's (1979, 1990) classification of Corynidae Johnston, 1836, having gained widespread support, has now been challenged by the recent phylogenetic analysis of the family by Nawrocki *et al*. (2010), as noted above. However, changes in the scope of *Coryne* from their analysis are relatively modest (Schuchert 2010), and the diagnosis given above is based on the pre-2010 concept of the genus.

The traditional taxonomy and nomenclature of *Coryne* has been summarized in earlier work (Calder 1988; Schuchert 2001b).

Coryne sp. 1

Figs. 34, 35

Syncoryne mirabilis.—Chu & Cutress, 1955: 403, fig. 3 [not *Sarsia mirabilis* L. Agassiz, 1849 (=*Sarsia tubulosa* (M. Sars, 1835)].

Material examined. Oahu: Hawaii Kai, on pilings of bridge over Highway 72, 21º17'06.60"N, 157º43'07.21"W, 0.1 m, 27.vii.2009, on algae, two colonies, to 2 mm high, without gonophores, coll. D.R. Calder, ROMIZ B3828.

Description. Hydroid colonies mostly stolonal, up to 2 mm high, arising from a creeping hydrorhiza. Hydrocaulus monosiphonic, short, unbranched or with an irregular branch, bearing a terminal hydranth. Perisarc transparent, with that on hydrorhiza mostly smooth and of moderate thickness, that on hydrocauli thinner, smooth to wrinkled almost throughout, not regularly annulated, terminating at base of hydranth below tentacles. Hydranths when extended elongate, cylindrical to clavate, to about 1 mm high and 0.15 mm wide; when contracted oval, much shorter and wider; tentacles all capitate, about 20 in number, with four in an oral whorl, the remainder in about four irregular whorls over remainder of hydranth body, each whorl usually with four tentacles, those of one whorl alternating with tentacles in adjacent whorls; terminal knobs about 60 µm in diameter; hypostome prominent, dome-shaped to cap-shaped.

Gonophores not seen.

Remarks. Hydroid colonies identified here as *Coryne* sp. 1, from a small inlet into the western harbor at Hawaii Kai, on Oahu, are believed to be conspecific with specimens identified as *Syncoryne mirabilis* (L. Agassiz, 1849) from the mouth of the Wailoa River, Hilo Harbor, Island of Hawaii, by Chu & Cutress (1955).

From their illustration and brief description, the hydroids from Hilo Harbor are also believed to be a species of *Coryne* Gaertner, 1774. In morphology they resemble colonies examined here, and they were collected from a similar environment. Hydranths in material from Hilo Harbor arose from creeping stolons, and bore 15 or more scattered capitate tentacles. Medusae, formed on a part of the body column where the proximal-most tentacles would have occurred, were reported to be mature before liberation from the hydroid. The species was thought by Chu & Cutress to be responsible for cases of dermatitis in workers constructing a pier in the area. Of the described species of Corynidae (Schuchert 2001b), none has the characters shared by hydroids from Hawaii Kai and Hilo Harbor. This hydroid may be a new species, but more information on the life cycle is needed before describing it as such.

Cooke (1977) provided a brief description and sketch of a corynid hydroid found in alpheid crevices on the coral *Porites lobata* in Hawaii, and suggested that it might be the same as that identified as *Syncoryne mirabilis* by Chu & Cutress (1955). Gonophores were not observed on his hydroids, and no material of the species exists in collections at the Bishop Museum. Cooke's specimens had fewer tentacles (no more than 12) than those of Chu & Cutress (15 or more) and of the hydroid colonies described above from Hawaii Kai. Given apparent differences in morphology and habitat, Cooke's corynid is treated as a different species (*Coryne* sp. 2) here.

Coryne sp. 1 was found in very shallow waters on algae attached to the piling of a bridge over a small inlet leading into the western harbor of Hawaii Kai. Tidal flow of water moves through the inlet and ample hard substrate is present (rocks, concrete pilings, mollusc shells, algae, bryozoans, etc.), making it a favourable location for hydroids. The species is small and inconspicuous.

Reported distribution. Hawaii. Oahu: Hawaii Kai (this study).

Coryne sp. 2

Fig. 36

Sarsia mirabilis (?)—Cooke, 1977: 77, fig. 4 [not *Sarsia mirabilis* L. Agassiz, 1849 (=*Sarsia tubulosa* (M. Sars, 1835)].

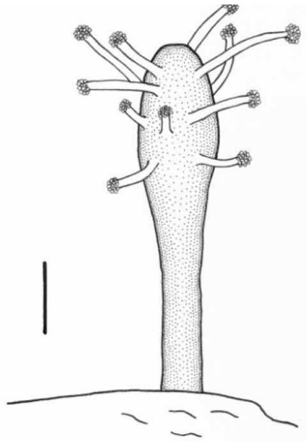
Material examined. None.

Description. (From Cooke 1977: 75): "The polyps are small, 0.5 mm in height, with at most 12 scattered tentacles… The polyps are light brown and either arise singly or form small, irregularly branched colonies… all specimens examined have been sterile…"

Remarks. Cooke (1977) assigned corynid hydroids from an unspecified geographic location in Hawaii, with question, to *Sarsia mirabilis* L. Agassiz, 1849. Colonies of it were found on the coral *Porites lobata*, in burrows of the shrimp *Alpheus deuteropus*. For reasons given in a discussion of the preceding species, these hydroids are not regarded here as conspecific those identified as *Syncoryne mirabilis* [=*Sarsia mirabilis*] by Chu & Cutress (1955) and as *Coryne* sp. 1 above. As for *Sarsia mirabilis*, it is now generally regarded as a synonym of *S. tubulosa* (M. Sars, 1835), an inhabitant of boreal waters in the North Atlantic and North Pacific (Schuchert 2001b). That species does not penetrate into tropical or subtropical waters such as those around Hawaii.

Two other hydroid species besides this corynid have been observed in alpheid crevices on corals around Hawaii, *Rhizogeton* sp. (reported by Cooke 1977, and herein) and *Nemalecium lighti* (Hargitt, 1924), the latter a leptothecate collected during this study. The microhabitat and associated species provide evidence as to the possible identity of *Coryne* sp. 2. In a study of hydroids inhabiting shrimp crevices on corals of a reef flat at La Réunion, Indian Ocean, Gravier-Bonnet & Mioche (1996) also found three species, *Rhizogeton* sp., *N. lighti*, and *Coryne nipponica* (Uchida, 1927). The corynid found by Cooke may prove to be *C. nipponica* or a close relative, but additional knowledge of its life cycle will be necessary before a reliable identification can be made. Its known habitat on perhaps the most ubiquitous and abundant scleractinian coral species in Hawaii (Maragos 1977) should facilitate rediscovery, although it was not found even after several searches for it during this study.

Reported distribution. Hawaii. No location given, on *Porites lobata*, in burrows of the decapod *Alpheus deuteropus* (Cooke 1977).



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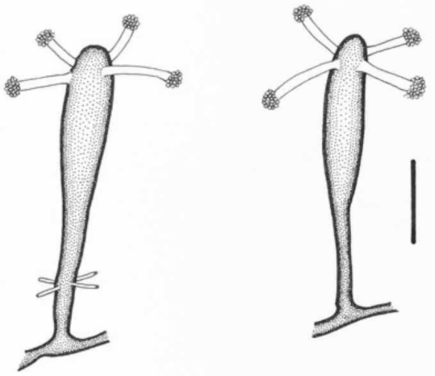

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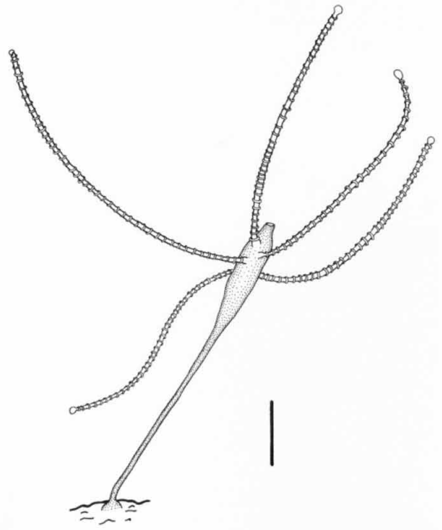

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FIGURE 36. *Coryne* sp. 2: hydranth (after Cooke 1977). Scale equals 0.1 mm.
FIGURE 37. *Cladonema radiatum*: two hydranths, one with filiform tentacles and one without (after Cooke 1977). Scales equal 0.25 mm.
FIGURE 38. *Moerisia horii*: hydranth (after Cooke 1977). Scale equals 1.0 mm.

Family Cladonematidae Gegenbaur, 1857

Cladonemiden Gegenbaur, 1857: 220 [emended to Cladonematidae by Poche (1914: 70)].

Diagnosis. Capitate hydroids stolonal, or with upright, sparingly branched colonies, arising from creeping hydrorhiza. Perisarc covering hydrorhiza and pedicels, reaching to base of hydranths. Hydranths clavate, with an oral whorl of capitate tentacles, with or without an aboral whorl of filiform sensory tentacles; hypostome conical to dome-shaped, appearing button-like, enclosing a pre-oral chamber lined with ectodermal gland cells.

Gonophores free medusae; medusa buds without a perisarcal covering, borne on hydranth proximal to capitate tentacles, and distal to filiform tentacles when present. Medusae creeping or swimming; umbrella margin with or without a ring of nematocysts; manubrium cylindrical, with or without radial pouches; apical chamber above manubrium present or absent; radial canals varying in number, bifurcated or simple. Marginal tentacles hollow, branching, usually equal in number to radial canals, bearing knobs of nematocysts and organs of adhesion. Abaxial ocelli present. Gonads surrounding manubrium, or in brood pouches, or on subumbrella.

Remarks. Petersen (1990), Bouillon *et al*. (2006), Schuchert (2006, 2009), and others are followed here in regarding Cladonematidae Gegenbaur, 1857 and Eleutheriidae Stechow, 1923b as identical. I had earlier held them to be distinct based on characters of the medusa stage (Calder 1988).

Genera traditionally recognized in Cladonematidae (*Eleutheria* Quatrefages, 1842a, *Cladonema* Dujardin, 1843, *Dendronema* Haeckel, 1879, and *Staurocladia* Hartlaub, 1917) are distinguished on the basis of differences in the medusa stage (see Schuchert 2006; Bouillon *et al.* 2006). *Stauridium* Krohn, 1853 is a synonym of *Cladonema*. For detailed discussion of the family, of genera assigned to it, and of taxonomic problems remaining in the group, see Schuchert (2006). A recent molecular study by Nawrocki *et al*. (2010) suggests that *Staurocladia* is congeneric with *Eleutheria*. About 20–23 species are currently recognized in Cladonematidae (Daly *et al*. 2007; Schuchert, 2009).

Two accounts of *Eleutheria* were published by Quatrefages (1842a, b), and it has been unclear in which of them the name was first made available. The paper containing a full account of the taxon (Quatrefages 1842a) is considered here to have been published first. It appeared in the November 1842 issue of *Annales des Sciences Naturelles*. This conclusion coincides with information on publication of the generic name *Eleutheria* in Neave (1939b). While results in Quatrefages (1842b) were presented at a meeting of the Académie des Sciences on 25 July 1842, the abbreviated summary appearing in *Comptes Rendus Hebdomadaires des Séances de l'Académie des Sciences* is undated except for the year and its publication date is taken as the end of 1842 (ICZN Art. 21.3).

Edmondson (1930) described four new species of medusae from Hawaii in the genus *Eleutheria* (*E. acuminata*, *E. alternata*, *E. bilateralis*, and *E. oahuensis*) that have been assigned in subsequent works to *Staurocladia*. They were distinguished on the basis of differences in arrangement of nematocyst clusters on the tentacles, a character now reported to vary considerably (Cooke 1977). Kramp (1961) provided accounts of the four, and Cooke (1977) illustrated and briefly described medusae that he assigned with hesitation to *S. bilateralis* and *S. oahuensis*. Hydroids of Edmondson's four nominal species are unknown, and they are not considered further here.

Genus *Cladonema* Dujardin, 1843

Cladonema Dujardin, 1843: 1134.
Type species. *Cladonema radiatum* Dujardin, 1843, by monotypy.

Diagnosis. Cladonematid hydroids typically stolonal; hydranth with an oral whorl of capitate tentacles, usually with an aboral whorl of filiform sensory tentacles proximally.

Gonophores free medusae; medusa buds given off singly from hydranth distal to filiform sensory tentacles. Medusae as for family; apical chamber above manubrium absent; umbrella bell-shaped; marginal tentacles with several branches, each bearing knobs of nematocysts and organs of adhesion.

Remarks. The taxonomy and nomenclature of *Cladonema* Dujardin, 1843 has been reviewed in Calder (1988) and Schuchert (2006).

Hydroids of *Cladonema* are virtually indistinguishable morphologically from those of *Staurocladia* Hartlaub, 1917 (a genus regarded as identical with *Eleutheria* Quatrefages, 1842a by Nawrocki *et al*. 2010) and separation of the genera is based on characters of medusa buds and medusae (Bouillon *et al*. 2006). Moreover, species of both *Cladonema* and *Staurocladia* strongly resemble certain species of corynids (Brinckmann & Petersen 1960; Calder 1970; Bouillon 1971), often rendering identification of sterile material difficult.

Cladonema radiatum Dujardin, 1843

Fig. 37

Cladonema radiatum Dujardin, 1843: 1134.
Cladonema radiatum.—Cooke, 1977: 77, figs. 5a–c.

Type locality. Mediterranean Sea (Dujardin 1843).

Material examined. None.

Description. (From Cooke 1977: 77–78): "The hydroid stage consists of polyps approximately 1 mm high which arise singly from a creeping stolon… These polyps have four capitate tentacles arranged at right angles just below the mouth and four short, stiff filiform tentacles lower on the body."

Remarks. Cooke (1977) reported *Cladonema radiatum* Dujardin, 1843 from Hawaii, but without locality information. He noted that medusae of the species were frequent in relatively quiet water areas on the chlorophyte *Ulva*. Sketches were provided of both medusa and hydroid stages, and his account of the hydroid of *C. radiatum* was based on specimens collected in Hawaiian waters (W.J. Cooke, pers. comm., 4 November 2009). No hydroids of *C. radiatum* were found in collections at the Bishop Museum.

A thorough review of the species, including a synonymy list, was provided recently by Schuchert (2006).

Reported distribution. Hawaii: No location given (Cooke 1977).

Elsewhere. Reportedly circumglobal in shallow temperate and tropical waters (Millard & Bouillon 1973; Calder 1988; Hirohito 1988; Migotto 1996; Schuchert 2006; Mills *et al.* 2007).

Family Moerisiidae Poche, 1914

Moerisiidae Poche, 1914: 66.

Diagnosis. Capitate hydroids with solitary hydranths, or with simple stolonal colonies having a rudimentary creeping hydrorhiza; podocysts often present. Hydranths club-shaped to bulbous; tentacles moniliform to capitate, scattered over body or restricted to a band below hypostome; sometimes with polyp buds forming proximally; hypostome elongate.

Gonophores free medusae, borne on hydranth amongst or below tentacles. Medusa bell-shaped; radial canals four, simple, unbranched; marginal tentacles solitary, 4 or more and sometimes numerous, moniliform or with transverse clasps of nematocysts; tentacle bulbs with abaxial ocelli; statocysts absent. Manubrium typically cruciform to quadrate, extending outwards as perradial manubrial lobes over proximal ends of radial canals. Gonads on manubrium and manubrial lobes.

Remarks. Authors of recent systematic works (e.g. Petersen 1990; Cairns *et al.* 2002; Bouillon *et al.* 2006; Schuchert 2010) have followed Rees (1957b, 1958) in assigning Moerisiidae Poche, 1914 to Capitata Kühn, 1913 based on nematocyst complement and medusa morphology. The presence of stenoteles and desmonemes in particular indicates a closer relationship to capitate hydroids and medusae than to Limnomedusae

Kramp, 1938, where this family had been assigned earlier (Naumov 1960; Kramp 1961). This relationship has also been confirmed by molecular data (Collins *et al.* 2006). Petersen (1979, 1990) included two genera in Moerisiidae, *Moerisia* Boulenger, 1908 and *Odessia* Paspalew, 1937, relegating *Ostroumovia* Hadži, 1928 to the synonymy of *Moerisia*. Bouillon *et al.* (2006) included a third genus, *Halmomises* von Kennel, 1891, in Moerisiidae but regarded its type species by monotypy, *H. lacustris* von Kennel, 1891 (which they misspelled as *H. ancestries*), as of doubtful status. Three genera (*Moerisia*, *Odessia*, and *Halmomises*) and 12 species are assigned to the family in the World Hydrozoa Database (Schuchert 2009). Taxonomic knowledge of Moerisiidae is still rudimentary, and current concepts of genera and species need reexamination.

Genus *Moerisia* Boulenger, 1908

Moerisia Boulenger, 1908: 358.
Type species. *Moerisia lyonsi* Boulenger, 1908, by monotypy.

Diagnosis. Moerisiid hydroids with moniliform, hollow tentacles.

Moerisiid medusae with moniliform tentacles; gonads smooth, forming a continuous mass extending from central manubrium to manubrial lobes.

Remarks. The brackish-water genus *Moerisia* Boulenger, 1908 as presently constituted is widespread and relatively familiar, but most nominal species assigned to it are poorly understood taxonomically. In the Indo-west Pacific region, only the species currently known as *Moerisia horii* (Uchida & Uchida, 1929) has been thoroughly studied in all phases of its life cycle. Nevertheless, relationships of that species to *M. gemmata* (Ritchie, 1915) and *M. gangetica* Kramp, 1958, both described from the same general region of India, or to other nominal species currently assigned to the genus (*Moerisia lyonsi* Boulenger, 1908, *Caspionema pallasi* Derzhavin, 1912, *Moerisia inkermanica* Paltschikowa-Ostroumowa, 1925, *Moerisia alberti* Leloup, 1938, and *Moerisia carine* Bouillon, 1978b), have not been adequately explored. Moreover, a number of moerisiid records worldwide attributed to *M. lyonsi*, including accounts of mine (Calder 1971; Calder & Burrell 1967; Sandifer *et al.* 1974), have been based on adult medusae with numerous (>20) marginal tentacles. As originally described by Boulenger (1908), however, mature medusae of that species normally have four tentacles. Rees & Gershwin (2000), working with *Moerisia* sp. from California, believed that only one or two morphologically variable species may prove to exist in Moerisiidae Poche, 1914. Confusion and uncertainty prevails in the taxonomy of the genus at present, and a revision of *Moerisia* and its species is needed. As for *M. gemmata*, Rees & Thursfield (1965) included it in the synonymy of *M. inkermanica* (as *Ostroumovia inkermanica*).

Although restricted to environments of low salinity, species of *Moerisia* are well-known to be invasive (Purcell *et al.* 1999; Rees & Gershwin 2000; Ma & Purcell 2005a, b). Notably, resistant podocysts are known to occur in the life cycle, and may facilitate dispersal of these hydrozoans.

Fewer than 10 species are currently included in the genus *Moerisia* (Bouillon *et al.* 2006; Schuchert 2009). One of these, *M. horii*, has been reported from Hawaiian waters (Cooke 1977).

Moerisia horii (Uchida & Uchida, 1929)
Fig. 38

Laccocoryne horii Uchida & Uchida, 1929: 158, figs. 1–3.
Ostroumovia horii.—Cooke, 1977: 73, figs. 1a, b.

Type locality. Japan: Kahoku and Ochi, in brackish waters (Uchida & Uchida 1929).

Material examined. None.

Description. (From Cooke 1977: 73): "The polyp is as long as 2 cm, with most of the length a highly contractile stalk… The hydranth itself is 1 mm to 2 mm long with 4 to 15 tentacles (the number increasing with age) and a well defined hypostome. The tentacles bear the nematocyst rings characteristic of the group and are also slightly capitate. The nematocyst rings are not quite complete, failing to fully encircle the tentacle, although this can be confirmed only in extended live individuals. Scattered among the tentacles of older individuals are medusae buds, as many as 10 in number, in all stages of development. The most complete medusae appear close to release. These are about 0.5 mm tall and 0.4 mm in diameter and bear four moniliform tentacles. Asexual budding occurs with new hydranths being formed from the lower part of the hydranth and stalk. No basal perisarc or chitinous disk was observed…"

Remarks. Uchida & Uchida (1929) described, as *Laccocoryne horii*, a hydroid from two brackish coves (Kahoku and Ochi) on the west coast of Japan. The hydroid, growing on *Potamogeton*, was reported to be solitary. No gonophores were observed on their specimens, even though hydroids were kept in culture for at least several weeks. Later, the complete life cycle of the species, including a description of the medusa, was described by Uchida & Nagao (1959). They assigned the species to *Ostroumovia* Hadži, 1928, and it was later transferred to *Moerisia* Boulenger, 1908 by Kramp (1961: 445). Recent authors, including Petersen (1990) and Bouillon *et al*. (2006), have applied the binomen *Moerisia horii* to it.

Cooke (1977) studied living and preserved moerisiid hydroids from the Island of Hawaii that were similar to those described by Uchida & Uchida (1929) from Japan, and referred them to *Ostroumovia horii*. Medusa buds, present in his material, were about 0.5 mm in height and 0.4 mm in diameter prior to release, and four moniliform tentacles were present. New hydranths arose by budding from the stalk and proximal end of the hydranth. Illustrations were provided of two polyps of this species, drawn from living material. No specimens of this species were found in collections at the Bishop Museum.

Moerisiid hydroids are anatomically simple, morphologically variable, inadequately studied, and difficult to identify. The value of some characters used to distinguish taxa, such as solitary or primitively colonial polyps, developmental complexity of the pedal disc, and formation and arrangement of podocysts, is open to question. Life cycle studies and molecular analyses will be necessary to establish whether populations of this hydrozoan from Hawaii are indeed conspecific with those of *Moerisia horii* from Japan or with another nominal species. In the meantime, the identification made by Cooke (1977) is maintained here in the interests of nomenclatural stability.

Whatever its identity and name, occurrence of this invasive species in Hawaii is a biogeographic enigma. How this brackish water hydrozoan was transported to a pond on a remote oceanic island system in mid-Pacific Ocean is at present a matter of pure conjecture. Carlton & Eldredge (2009) considered it cryptogenic in Hawaii.

Reported distribution. Hawaii. Island of Hawaii: Honokohau, brackish pond in a lava flow (Cooke 1977).

Worldwide. Japan and Hawaii; shallow waters (Uchida & Uchida 1929; Uchida & Nagao 1959; Cooke 1977).

Family Solanderiidae Marshall, 1892

Solanderiidae Marshall, 1892: 8.

Diagnosis. Capitate hydroids forming large, erect, branched, bushy to fan-shaped to tangled colonies, arising from a flattened mass of hydrorhizal tubes. Hydrocaulus and hydrocladia with a skeletal axis of intertwining and anastomosing chitinous fibres, forming a trabecular network; chitinous hydrophores present or absent;

naked coenosarc covering skeleton and filling interstices. Hydranths clavate, arising from superficial coenosarc, bearing an oral whorl of capitate tentacles, additional capitate tentacles scattered over hydranth body; hypostome dome-shaped.

Gonophores fixed sporosacs or eumedusoids, given off from outer layer of coenosarc.

Remarks. The taxonomic history of Solanderiidae Marshall, 1892 has been reviewed by Vervoort (1962) and Bouillon *et al*. (1992). Colonies are supported by a chitinous skeleton that is ectodermal, as in other hydroids (Vervoort 1966). Bouillon *et al*. (1992) included scanning electron micrographs of skeletons of various solanderiid species.

Only one genus, *Solanderia* Duchassaing & Michelin, 1846, has been recognized in this family in recent works. *Chitina* Carter, 1873, regarded as a doubtful solanderiid genus by Vervoort (1962), was considered valid by Bouillon & Cornelius (1988) but as congeneric with *Solanderia* by Schuchert (1996, 2009) and Bouillon *et al*. (2006). Seven species are currently recognized in the family (Daly *et al.* 2007; Schuchert 2009), with two of them known from Hawaii.

Genus *Solanderia* Duchassaing & Michelin, 1846

Solanderia Duchassaing & Michelin, 1846: 219.
Type species. *Solanderia gracilis* Duchassaing & Michelin, 1846, by monotypy.

Diagnosis. Capitate Hydrozoa with characters of family Solanderiidae.

Remarks. In a revision of the genus *Solanderia* Duchassaing & Michelin, 1846, Bouillon *et al*. (1992) recognized six species as valid worldwide. A seventh, *Chitina ericopsis* Carter, 1873, was recently added to the group (Bouillon *et al*. 2006; Schuchert 1996, 2009). Two species of the genus are included in the fauna of Hawaii, as discussed below.

Solanderia secunda (Inaba, 1892)

Figs. 39, 40

Dendrocoryne secunda Inaba, 1892: 99, figs. 111–113.
Ceratella fusca.—Nutting, 1905: 939 [not *Ceratella fusca* Gray, 1868].
Solanderia (?) *minima*.—Cooke, 1977: 73.
Solanderia minima.—Bouillon *et al*., 1992: 6.
Solanderia secunda (f. *minima*).—Bouillon *et al.*, 1992: pl. 14, fig. 5.
Solanderia secunda.—Cooke, 1977: 74.—Hoover, 1998: 22, fig.; 2006: 22, fig.

Type locality. Japan: Misaki (Inaba 1892).

Material examined. Maui: Albatross Stn. 4072, 56 fm (102 m), one fragmentary colony, 6.6 cm high, with hydranths, gonophores not seen, USNM 22271.–Oahu: Waikiki, W end of natatorium, 8 ft (2 m), viii.1963, one colony (dry), 6.4 cm high × 9.4 cm wide, coll. G. Cooper, BPBM D356.–Oahu: off Barber’s Point, 90–100 ft (27–30 m), 6.ii.1965, one colony (dry), 3.8 cm high × 7.9 cm wide, coll. D.P. Fellows, BPBM D405.–Oahu: Kaneohe Bay, off Kipapa Island, 3–4 m, in cave, one colony, 13 cm high, 9.5 cm wide, with few hydranths, without gonophores, coll. R. Grigg, BPBM D519.–Hawaiian islands: trawl, “Valiant Maid” (no other locality data), one colony, 5 cm high, 6 cm wide, without hydranths and gonophores, BPBM D518.–Island of Hawaii: 19º11’N, 155º24.5’W, 260 fm (475 m), on lava, pipe dredge with tangles, R/V Proteus, Sn. 107, Stanford Oceano. Exped. 23, leg 2, 6.ix.1971, one colony, 5.5 cm high by 5.9 cm wide, without hydranths and gonophores, BPBM (without collection number).–Island of Hawaii: Puako, on dropoff directly in front of #45 Puako Road, from roof of fairly bright cave, 40 ft (12 m), two colonies, 4.5 cm high × 5.5 cm wide and

6.0 cm high × 7.0 cm wide, without gonophores, coll. E.D. Chave, BPBM (without collection number).–Oahu: inside Mokumanu Islands, 21º27.82’N, 157º43.09’W, 45 ft (14 m), on ledges, 2.xi.1976, one colony, 5.0 cm high × 4.3 cm wide, hydranths distended, with gonophores, coll. W.J. Cooke, BPBM (without collection number).–Oahu: Lanai Lookout, in cave, 20 ft (6 m), 25.i.1997, one colony, 3.5 cm high × 8.6 cm wide, with gonophores, coll. J.P. Hoover, ROMIZ B3038.–Kahoolawe: Kuheia Bay offshore, 10 m, under ledge, 13.i.1998, one colony, 4.3 cm high × 7.6 cm wide, with hydranths and male gonophores, coll. R. DeFelice, S. Coles and J. Smith, BPBM (without collection number).

Description. Hydroid colonies erect, robust, fan-shaped to shrubby, extensively branched in one plane, reaching 13 cm high, 9.5 cm wide, arising from a flattened base with an outward-extending rootlike system of trabecular hydrorhizae. Hydrocaulus and hydrocladia thick, gradually thinning distally, round to irregularly round in cross-section, comprising a woody, spongy, trabecular network of chitinous fibers permeated by and overlaid with naked coenosarc; chitinous hydrophores and spines present. Hydrophores irregularly spaced and variably developed, most occurring on opposite sides of hydrocladia, comprising a pair of thorns flanking a hydranth; thorns triangular with apex blunt to pointed, sometimes reduced to low ridges on trabeculae. Spines slender, fragile, of varied length, particularly abundant and conspicuous on hydrorhizae, occasionally present elsewhere. Hydranths arising from coenosarc, most frequent on opposite sides of hydrocladia, clavate with dome-shaped hypostome, about 0.4–1.0 mm high; oral region with a whorl of 3–5 capitate tentacles; body with a varied number (ca. 8–12) of scattered capitate tentacles. In ethanol-preserved material, older and thicker parts of colony dark brown; younger and distalmost parts golden to whitish; coenosarc, hydranths, and sporosacs white.

Gonophores fixed sporosacs arising singly on short pedicels from coenosarc adjacent to hydranths, usually occurring amongst hydranths on opposite sides of hydrocladia; tentacles undeveloped.

Nematocysts (Vervoort 1962; Millard 1975; Bouillon *et al.* 1992; Watson 1999):
stenoteles: large (12.0–17.5 µm long × 10.0–14.0 µm wide)
stenoteles: small (6.3–9.4 µm long × 4.5–8.0 µm wide)
“glutinants:” (9.0 µm long × 3.0 µm wide)
isorhizas (?): (6–10 µm long × 7–9 µm wide)

Remarks. *Solanderia secunda* (Inaba, 1892), *Solanderia minima* (Hickson, 1903) and *S. crosslandi* (Thornely, 1908), of the tropical and subtropical Indo-Pacific region, have been differentiated largely on the basis of supposed differences in distal skeletal structure and prominence of lateral hydrophore thorns. After examining extensive material encompassing these three morphotypes, Bouillon *et al*. (1992) concluded that they represent forms or varieties of a single species, *S. secunda*, and their opinion is adopted here. Vervoort & Vasseur (1977) had earlier suggested that the three might represent a single variable species. Specimens from Hawaii conform most closely with *Solanderia secunda* var. *minima* (Cooke 1977; Bouillon *et al.* 1992).

Bouillon *et al*. (1992) considered records of *Solanderia fusca* (Gray, 1868) outside of Australia, including Nutting’s (1905) report of *Ceratella fusca* from Hawaii, to be doubtful. Nutting’s hydroid, from the north coast of Maui (USNM 22271), was re-examined here and identified as *S. secunda*.

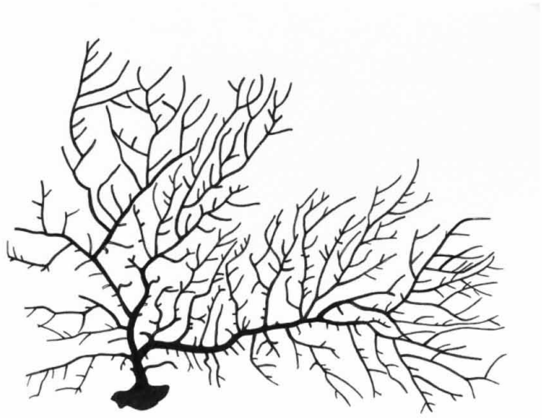
Detailed synonymy lists of this species have been given by Bouillon *et al*. (1992) and Watson (1999). *Solanderia secunda* can be distinguished from other currently recognized species of the genus in having a hydrophore with a pair of lateral thorns. However, these thorns vary considerably in development from one colony to another (Vervoort & Vasseur 1977). The species is dioecious (Vervoort 1962; Bouillon *et al*. 1992), and growth is evidently quite rapid (Watson 1999).

The hydroid has been reported from cryptic habitats including overhangs, crevices in walls, and caves (Cooke 1977; Vervoort & Vasseur 1977; Hoover 1998, 2006; Kirkendale & Calder 2003). Most materials from Hawaii examined here were from similar environments. Depth records of the species in Hawaii range from 2–475 m, but material from deep waters (BPBM, without collection number) lacked hydranths and gonophores.

The color of larger branches of this species vary from purple and deep purple to chocolate brown to ochre. Smaller branches may be mauve, creamy, or yellowish-brown. Hydranths are white; male gonophores are scarlet (Millard 1975; Bouillon *et al.* 1992; Watson 1999).

Reported distribution. Hawaii. Maui: north coast, 56 fm (102 m) (Nutting 1905, as *Ceratella fusca*); no location, 120 m, as *S. secunda* (Cooke 1977).–Oahu: Kipapa Island, Kaneohe Bay, underwater cave, 3–4 m, as *S.* (?) *minima* (Cooke 1977); Kipapa Island, Kaneohe Bay, as *S. minima* (Bouillon *et al.* 1992); Lanai Lookout, 15 ft (5 m) (Hoover 1998, 2006).

Worldwide. Tropical and subtropical Indo-Pacific, from the Red Sea eastward to French Polynesia; 2–475 m (Vervoort 1962; Cooke 1977; Vervoort & Vasseur 1977; Hirohito 1988; Bouillon *et al.* 1992; Watson 1999; Schuchert 2003; Kirkendale & Calder 2003).



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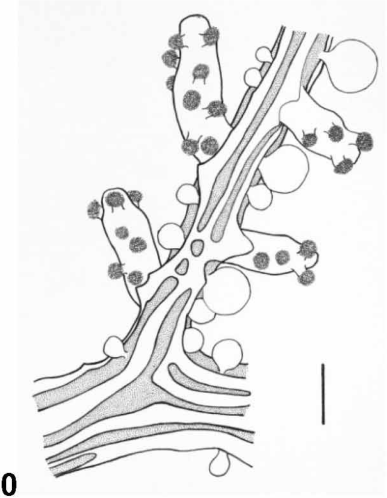

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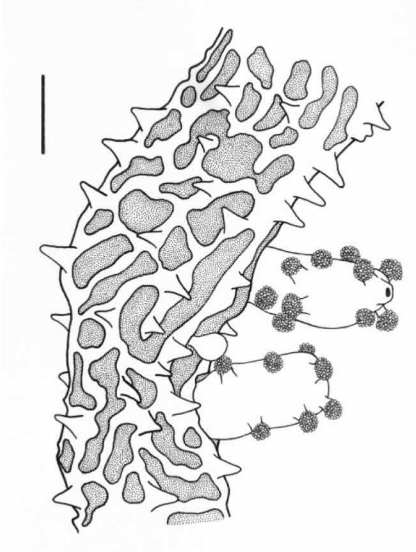

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FIGURE 39. *Solanderia secunda*: colony form, BPBM D356.

FIGURE 40. *Solanderia secunda*: branch with hydranths and gonophores, BPBM (without collection number). Scale equals 0.25 mm.

FIGURE 41. *Solanderia misakinensis*: form of a 5.7 cm high portion of a colony, RMNH 3575.

FIGURE 42. *Solanderia misakinensis*: branch with hydranths and a small gonophore, RMNH 3575. Scale equals 0.25 mm.

Solanderia misakinensis (Inaba, 1892)

Figs. 41, 42

Dendrocryne misakii Inaba, 1892: 97, figs. 106–110 [*Dendrocryne* an inadvertent error for *Dendrocoryne*].
Solanderia misakinensis.—Cooke, 1977: 75, figs. 2, 3.

Type locality. Japan: Misaki (Inaba 1892).

Material examined. Oahu: off Halona Blowhole, under ledge, 7 m, one fragmentary colony, 5.7 cm high, with hydranths and gonophores, RMNH 3575.

Description. Fragment of hydroid colony erect, robust, shrubby, branched in one plane, 5.7 cm high, 2.3 wide, cut off at base. Hydrocaulus and hydrocladia thick, gradually thinning distally, irregularly round in cross-section, comprising a woody, spongy, trabecular network of chitinous fibers permeated by and overlaid with naked coenosarc; chitinous spines present, hydrophores absent. Spines slender, fragile, of varied length, abundant on hydrocaulus and hydrocladia. Hydranths arising from coenosarc, most frequent on opposite sides of hydrocladia, clavate with dome-shaped to flattened hypostome, about 0.5 mm high; oral region with a whorl of 4 capitate tentacles; body with a varied number (ca. 10–14) of scattered capitate tentacles. In ethanol-preserved material, older and thicker parts of colony brown, perisarc reddish orange under microscope; younger and distalmost parts golden; coenosarc, hydranths, and sporosacs white.

Gonophores fixed sporosacs arising singly from coenosarc adjacent to hydranths, usually occurring amongst hydranths on opposite sides of hydrocladia; tentacles undeveloped.

Remarks. There has been confusion over spelling of the specific name of this species. In the original description of Inaba (1892) it was spelled *misakii*. The name was modified to *misakinensis* by Goto (1897), and that spelling was adopted by Stechow (1909, 1923a), Bedot (1918, 1925), Jäderholm (1919), Vervoort (1962), and most subsequent authors. The name has also been spelled *misakiensis*, most notably by Hirohito (1988). In a revision of the genus *Solanderia* Duchassaing & Michelin, 1846, Bouillon *et al*. (1992) discussed the species under the name *S. misakinensis*, but in their key it was spelled *misakiensis*. Although different from the original spelling (as *misakii*), *misakinensis* is in prevailing usage as reflected in the synonymy list in Bouillon *et al*. (1992), is herein deemed to be the correct original spelling, and is attributed to Inaba (1892) [ICZN Art. 33.3.1].

Bouillon *et al*. (1992) did not mention Cooke's (1977) report of *Solanderia misakinensis* from Hawaii, giving the distribution of the species as Japan, Korea, New Zealand, and Russia (Sea of Japan). The record from New Zealand was shown by Schuchert (1996) to have been based on a misidentification. Material reported by Cooke from Oahu was identified by Willem Vervoort, and the record has been confirmed as valid on re-examination here. The absence of hydrophores, the distinctive reticulated perisarc of the skeleton, and the numerous perisarcal spines on hydrocaulus and hydrocladia distinguish *S. misakinensis* from *S. secunda* (Inaba, 1892). Although colony form is a variable character, that of *S. misakinensis* examined here is coarser, and its height to width ratio greater, than *S. secunda* from Hawaii. The overall form more closely resembles that of certain octocorals.

Reported distribution. Hawaii. Oahu: Halona Blowhole, under ledge, ca. 7 m (Cooke 1977).

Worldwide. Hawaii (Cooke 1977); Japan, Korea, Russia (Sea of Japan) (Bouillon *et al.* 1992); 2–100 m.

Family Pennariidae McCrady, 1859

Pennaridae McCrady, 1859:148 [emended to Pennariidae by Hincks (1868)].

Diagnosis. Capitate hydroids with erect colonies; stems monosiphonic, pinnately branched, with branches giving rise to hydranth pedicels on upper side only; perisarc firm. Hydranths naked, clavate, with an aboral whorl of long, filiform or slightly capitate tentacles, an oral whorl of short, capitate tentacles, and one or more intermediate whorls of capitate tentacles.

Gonophores eumedusoids, borne on hydranth just distal to aboral tentacles, sometimes liberated and sometimes not. Eumedusoids with short manubrium; radial canals four; tentacle bulbs four; marginal tentacles rudimentary or absent; gonads surrounding manubrium.

Remarks. The name Halocordylidae Stechow, 1921a had earlier been applied by many authors to this taxon. With current acceptance of the generic name *Pennaria* Goldfuss, 1820 as valid and predating *Halocordyle* Allman, 1872, the family name Pennariidae McCrady, 1859 has precedence over Halocordylidae and is used here.

Pennariidae presently includes a single genus, *Pennaria*, with eight species (Schuchert 2009).

Genus *Pennaria* Goldfuss, 1820

Pennaria Goldfuss, 1820: 89.
Type species. *Pennaria disticha* Goldfuss, 1820, by subsequent designation by Bedot (1901).

Diagnosis. Capitate Hydrozoa having characters of the family Pennariidae.

Remarks. Confusion over the taxonomic status of the name *Pennaria*, the authorship of which is now attributed to Goldfuss (1820), was clarified by Gibbons & Ryland (1989). *Halocordyle* Stechow, 1921a is thus regarded as a junior synonym. Other issues surrounding the taxonomy and nomenclature of the genus were discussed by Calder (1988).

Numbers of species currently recognized worldwide in the genus *Pennaria* vary from eight (Bouillon *et al.* 2006; Schuchert 2009) to two (Daly *et al.* 2007), the latter estimate presumably referring to the hydroid stage only.

Pennaria disticha Goldfuss, 1820

Fig. 43

Pennaria disticha Goldfuss, 1820: 89.—Hoover, 1998: 20, fig.; 2006: 20, fig.–Coles *et al.*, 2006: 494.
Pennaria sp.—Edmondson, 1933: 23, figs. 11, 12a; 1946: 24, figs. 12, 13a.
Corydendrium splendidum Boone, 1938: 33, pl. 4.
Pennaria tiarella.—Edmondson & Ingram, 1939: 256.–Chu & Cutress, 1954: 9.—Josephson, 1961: 565.—Mariscal & Lenhoff, 1969: 330.—Pardy & Lenhoff, 1968: 197, figs. 1–3.—Rees *et al.*, 1970: 309, figs. 1, 2.—Reed, 1971: 48.—Pardy, 1971: 84, figs. 1–3.—Rees, 1971: 119, figs. 1, 2.—Long, 1974: 27.
Halocordyle disticha.—Cooke, 1977: 80, fig. 8.—Coles *et al.*, 1999: 150.

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

Material examined. Oahu: Kaneohe Bay, 29.x.1929, indeterminable number of colonies and colony fragments (dry), coll. C.H. Edmondson, BPBM D182.–Oahu: Pearl Harbor, 30.xi.1929, about 20 colonies and colony fragments, up to 7 cm high, detached, without gonophores, coll. C.H. Edmondson, BPBM D183.–Oahu: Kaneohe Bay, 1936 (no month or day given), one colony with numerous stems, to 12 cm high, with gonophores, BPBM D216.–Oahu: Kaneohe Bay, 1939 (no month or day given), seven colony fragments, up to 10 cm high, with gonophores, BPBM D230.–Oahu: Honolulu Harbor, 5.v.1944, 14 colony fragments, to 13 cm high, with gonophores, coll. C.H. Edmondson, BPBM D251.–Oahu: Honolulu Harbor, 8.xi.1944, >25 colony fragments, in poor condition, to 5 cm high, with a few gonophores, coll. C.H. Edmondson, BPBM D254.–Oahu: Honolulu Harbor, 2.vi.1945, 8 colony fragments, to 8.5 cm high, without gonophores, BPBM D259.–Oahu: Honolulu Harbor, 5.vi.1945, 3 colony fragments, to 3 cm high, without gonophores, BPBM D264.–

Oahu: Honolulu Harbor, 9.iv.1946, four colony fragments, in poor condition, to 11 cm high, gonophores not apparent, BPBM D270.–Oahu, Honolulu Harbor, 16.vii.1946, indeterminable number of colonies and colony fragments (dry), coll. C.H. Edmondson, BPBM D273.–Oahu: Honolulu Harbor, 11.xi.1947, one large colony with many stems, to 11.5 cm high, with gonophores, coll. C.H. Edmondson, BPBM D279.–Oahu: Honolulu Harbor, 3.xii.1947, on test blocks, one large colony with several stems, in poor condition, to 12 cm high, without apparent gonophores, coll. C.H. Edmondson, BPBM D282.–Oahu: Pearl Harbor, 15.iv.1948, on bottom of motile dry dock, five colony fragments, up to 12 cm high, with gonophores, coll. C.H. Edmondson, BPBM D289.–Oahu: Honolulu Harbor, Pier 28, 6.iii.1952, one colony with several stems, to 12.5 cm high (label states: "Growth Record—5 inches in 90 days"), with gonophores, BPBM D325.–Oahu: Kaneohe Bay, Checker Reef, 2 m, 19.v.1976, three fouled colony fragments in poor condition, up to 4.5 cm high, removed from *Porites*, with a few gonophores, coll. J.G. Grovhoug, BPBM (without collection number).–Oahu: Kaneohe Bay, Checker Reef, 2 m, 21.v.1976, two fouled colony fragments in poor condition, up to 5 cm high, removed from *Porites*, with a few gonophores, coll. J.G. Grovhoug, BPBM (without collection number).–Oahu: Pearl Harbor, Rainbow Bay Marina, docks and shoreline, 0–1 m, 11.i.1996, three colony fragments, without gonophores, coll. R. DeFelice, BPBM D1043.–Oahu: Pearl Harbor, N side of entrance channel, 0.5–3 m, 13.ii.1996, one colony with three stems, to 5 cm high, without gonophores, coll. R. DeFelice, BPBM D1045.–Oahu: Pearl Harbor, sheet piling in thermal discharge from Hawaiian Electric Company (HECO) Waiau plant, 0–1.5 m, 21.iii.1996, six colony fragments, to 10 cm high, all dead, coll. R. DeFelice, BPBM D1050.–Oahu: Pearl Harbor, Middle Loch, on hull of floating drydock USS "Machinist", 0.5–5 m, 27.iii.1996, two colony fragments, to 8 cm high, lacking hydranths and gonophores (vial also contains a colony of *Bougainvillia muscus*), coll. R. DeFelice, BPBM D1052.–Oahu: Pearl Harbor, SE Loch, E of drydock area, 0.5–6 m, 3.iv.1996, 16 colony fragments, to 8 cm high, all dead, coll. R. DeFelice, BPBM D1056.–Oahu: Pearl Harbor, N side of SE Loch entrance, 0.5–3 m, 2.iv.1996, one colony in two parts, with few hydranths, 7 cm high, no gonophores, coll. R. DeFelice, BPBM D1058.–Oahu: Pearl Harbor, adjacent to Hospital Point Drydock Number 4, 0.5–3 m, 30.iv.1996, four colony fragments, to 4 cm high, in poor condition, no gonophores, coll. R. DeFelice, BPBM D1062.–Oahu: Kewalo Basin, Fisherman's Wharf, 16.vii.1998, one colony with numerous stems, to 14.5 cm high, with gonophores, coll. R. deFelice and S. Coles, BPBM (without collection number).–Oahu: Ala Wai Harbor, Hilton Lagoon discharge pipe, 30.vii.1998, >30 colonies and colony fragments, up to 11 cm high, detached, with a few gonophores, coll. R.C. DeFelice and S.L. Coles, BPBM D1110.–Lisianski, Northwest Hawaiian Islands: LIS–10, 16.ix.2002, about 25 colonies and colony fragments, up to 6 cm high, detached, with gonophores, BPBM D1173.–Pearl and Hermes Reef, Northwest Hawaiian Islands: PHR–24, 26.ix.2002, six colonies and colony fragments with few hydranths, up to 7.5 cm high, detached, with a few gonophores, BPBM D1178.–Lisianski, Northwest Hawaiian Islands: LIS–11, 29.ix.2002, about 10 colonies and colony fragments, up to 8 cm high, detached, with gonophores, BPBM D1182.–Oahu: Pearl Harbor, Rainbow Bay Marina, 21º22'16.52"N, 157º56"19.75" W, on buoy out from docks, 1 m, 16.vii.09, one colony with two stems, 4.5 cm high, with developing gonophores, coll. D.R. Calder, ROMIZ B3829.

Description. Hydroids colonial, erect, large, up to 22 cm high, arising from a creeping and twisted hydrorhiza. Hydrocaulus monosiphonic, alternately branched, straight to slightly curved, annulated just above each hydrocladium, otherwise smooth. Hydrocladia nearly straight to curved, annulated at proximal end and distal to each ultimate branchlet; ultimate branchlets of varied length but usually quite short, annulated basally, straw-coloured, bearing a neck region with a hydranth at distal end. Perisarc quite thick except at distal ends of hydrocaulus, hydrocladia, and ultimate branchlets, terminating at hydranth base. Hydranths bowling-pin-shaped with rounded base, about 1.5 mm high, 0.5 mm wide, bearing a single whorl of long, slender, slightly capitate tentacles aborally, remainder of hydranth armed with much shorter, strongly capitate tentacles, 4–6 of these being arranged in an oral whorl; aboral tentacles reaching to 2 mm long, usually 12–16 in number; hypostome large, knob-shaped. Hydranth body orangy with scattered ochre patches, especially above aboral tentacle whorl; hypostome whitish; hydrocaulus black except at distal extremity; hydrocladia black basally, straw-coloured to clear distally.

Gonophores eumedusoids, arising just distal to aboral tentacles. Eumedusoids thimble-shaped; radial canals four; tentacle bulbs four, rudimentary; manubrium simple, tubular, reaching nearly to velar opening; gonads on manubrium, filling subumbrellar cavity when mature.

Remarks. *Pennaria disticha* Goldfuss, 1820 is one of the most conspicuous shallow-water hydroids in the Hawaiian archipelago, and it is the most frequently reported species from the islands. It occurs on all the main islands of Hawaii, and extends westward to Midway Atoll (Carlton & Eldredge 2009). As is apparent from the material examined above, colonies are active in waters of the region throughout the year.

The taxonomy and general biology of this large, distinctive, and relatively well-known hydroid have recently been reviewed by Schuchert (2006). A synonymy list of the species, under the name *Halocordyle disticha*, has been given in an earlier report (Calder 1988). The cnidomes of both hydroid and attached medusoid stages were described in the same report. Numerous other accounts of the nematocyst complement of *P. disticha* exist, including those by Weill (1934), Millard (1975), García-Corrales & Aguirre (1985), da Silveira & Migotto (1991), Östman *et al.* (1991), Schuchert (1996), and Watson (1999).

Occurring in shallow tropical and temperate areas worldwide, this highly successful invasive species has been reported across the Indo-Pacific on continental shores from South Africa (Millard 1975) and the Red Sea (Hirohito 1977) to the west coast of the Americas (Fraser 1946), and on islands such as Zanzibar and Pemba (Jarvis 1922), Juan de Nova Island (Gravier-Bonnet & Bourmaud 2006), Madagascar (Gravier 1970), the Seychelles (Millard & Bouillon 1973), the Mergui Archipelago (Ritchie 1910a), Christmas Island (Ritchie 1910b), Indonesia (Pictet 1893; Vervoort 1941; Schuchert 2003), the Philippines (Hargitt 1924), Japan (Yamada 1959; Hirohito 1969, 1974, 1988), Palau (Hirohito 1977: 9), Guam (Kirkendale & Calder 2003), Enewetak Atoll (Cooke 1975), New Caledonia (Gravier-Bonnet 2007), New Zealand (Schuchert 1996), Fiji (Gibbons & Ryland 1989), Hawaii (Cooke 1977), and the Galápagos (Fraser 1938a; Calder *et al.* 2003), among others.

The hydroid of *Pennaria disticha* is widely known to be eurytopic. It thrives in oceanic salinities but also penetrates into estuaries approximately to the 20‰ isohaline (Calder 1976). While hydroids may be active throughout the year in tropical and subtropical regions (Schuchert 2006), they become dormant during cold periods in temperate regions (Hargitt 1900; Brinckmann-Voss 1970; Calder 1990). Bathymetrically, *P. disticha* is generally restricted to waters of less than 30 m, and is most abundant in the immediate subtidal region. In Bermuda, it was one of the most common species of hydroids in samples from 0–25 m, but it was absent in all samples below that depth range (Calder 1998). Gonophores are eumedusoids, sometimes remaining fixed and sometimes liberated from the hydroid (Hargitt 1900; Brinckmann-Voss 1970). When released, the free eumedusoids are short-lived (surviving a few hours at most) and liberated during evening hours (Hargitt 1900; Baker 1936; Brinckmann-Voss 1970; Calder 1988; Genzano & Kubota 2003). Hoover (1998, 2006) reported that colonies reach about 12 inches (30 cm) high in Hawaii, and specimens up to 22 cm high were observed during this study on a pier at the Hawaii Institute of Marine Biology on Coconut Island in Kaneohe Bay.

Pennaria disticha has been utilized frequently in morphological and experimental studies on invertebrates (Schuchert 2006), often under the name *P. tiarella*. Its hydroid is venomous to humans (Halstead 1988).

Pennaria wilsoni Bale, 1913 of Australia (Watson 1996), Fiji (Gibbons & Ryland 1989) and Guam (Kirkendale & Calder 2003) somewhat resembles *P. disticha*, but differs in having a single distal whorl of capitate tentacles on the hydranths, and in having hydrocladia that are spirally branched and not pinnate (Hirohito 1988: 30, fig. 9e).

Recorded distribution: Hawaii. Oahu: Kaneohe Bay (Boone 1938, as *Corydendrium splendidum*). Oahu: Kaneohe Bay (Mariscal & Lenhoff 1969). Oahu: Kaneohe Bay (Josephson 1961). Oahu: Kaneohe Bay (Pardy & Lenhoff 1968; Pardy 1971; Reed 1971; as *Pennaria tiarella*). Oahu: Kaneohe Bay (Rees *et al.* 1970, as *Pennaria tiarella*). Oahu: Pearl Harbor, off Ewa Beach, and off Barber's Point (Long 1974, as *Pennaria* *tiarella*). Oahu: Kaneohe Bay; Ala Wai Yacht Harbor, Kewalo Basin, Honolulu Harbor, Keehi Marina (Cooke 1977). Oahu: Kaneohe Bay and Lanai Lookout, 20 ft (6 m) (Hoover 1998, 2006). Oahu: Pearl Harbor (Coles *et al.* 1999, as *Halocordyle disticha*).

Worldwide. Circumglobal in tropical and warm temperate waters; 0–29 m (Millard 1975; Calder 1988; Watson 1999; Schuchert 2006; Calder & Cairns 2009).

Family Sphaerocorynidae Prévot, 1959

Sphaerocorynidae Prévot, 1959: 108.

Diagnosis. Capitate hydroids almost always stolonal with terminal hydranths; stems monosiphonic, arising from a creeping hydrorhiza. Perisarc covering hydrorhiza, hydrocaulus, and hydrocladia (if present), terminating at hydranth base. Hydranths pyriform, with bulbous base and elongate, proboscis-like hypostome; tentacles all capitate, solid, either simple or with both simple and trifid ones present, arranged in a narrow band around broadest part of hydranth.

Gonophores eumedusoids or free medusae, arising on hydranth among or just distal to tentacles. Medusae, when present, with bell-shaped umbrella; exumbrellar nematocyst tracks present or absent; manubrium flask-shaped in juveniles, becoming quadrate to cruciform in cross-section in adults, not extending beyond velar opening; radial canals four; marginal tentacles two or four, with intermediate wart-like clusters or spiral rings of nematocysts, terminating in an oval capitulum armed with nematocysts; marginal bulbs large, adhering to exumbrella, expanded adaxially; abaxial ocelli present. Gonads confluent on perradii of manubrium.

Remarks. Prévot (1959) established Sphaerocorynidae for *Sphaerocoryne* Pictet, 1893, a genus previously included in Corynidae Johnston, 1836. The concept of the family adopted here is as proposed by Petersen (1990), who referred two genera to it (*Sphaerocoryne* and *Heterocoryne* Wedler & Larson, 1986). The principal difference distinguishing them is the presence of both trifid and simple capitate tentacles in *Heterocoryne*, and simple capitate tentacles only in *Sphaerocoryne*. Where known, gonophores are free medusae in *Sphaerocoryne* and eumedusoids in *Heterocoryne*. Although Petersen (1990) suggested that the two genera “could be merged,” he treated them both as valid. Petersen’s classification of the group has been followed by authors including Cairns *et al*. (2002), Bouillon *et al*. (2006), Daly *et al*. (2007), and Schuchert (2009).

As discussed below, *Sphaerocoryne* sensu Petersen (1990) is divided into two genera here, *Sphaerocoryne* sensu stricto and *Corynetes* Haeckel, 1879.

The cnidome in Sphaerocorynidae comprises both desmonemes and stenoteles. Five species are currently assigned to the family (Schuchert 2009).

Genus *Sphaerocoryne* Pictet, 1893

Sphaerocoryne Pictet, 1893: 9.
Type species. *Sphaerocoryne bedoti* Pictet, 1893, by monotypy.

Diagnosis. Sphaerocorynid hydroids stolonal, usually with long hydrocauli; hydranths with capitate tentacles all simple.

Gonophores free medusae, arising in clusters on hydranth just distal to tentacles. Medusae with exumbrellar nematocysts scattered; manubrium of adult quadrate in cross-section; marginal tentacles four, capitate, equally developed at liberation, with intermediate nematocyst aggregations in bands.

Remarks. Petersen (1990) assigned *Linvillea* Mayer, 1910b, a replacement name for *Corynitis* McCrady, 1859 (an invalid junior homonym of *Corynitis* Geyer, 1832 [Lepidoptera] and *Corynitis* Menge, 1854 [Araneae]), to the synonymy of *Sphaerocoryne* Pictet, 1893. A problem arises from that proposed synonymy because the widely overlooked *Corynetes* Haeckel, 1879, an unjustified emendation of *Corynitis* McCrady, 1859 but nevertheless an available name [ICZN Art. 33.2] and with the same type species (ICZN Art. 67.8), is a senior objective synonym of *Linvillea* and a name with priority over *Sphaerocoryne* when the two are considered congeneric. Reversal of Precedence (ICZN Art. 23.9) cannot be applied to conserve *Sphaerocoryne* in this case because *Corynetes* has been used as a valid name at least once since 1899 (e.g. by Hartlaub 1913: 242). An earlier usage of the name *Corynetes* exists for a coleopteran by Paykull (1798), but that name has been entered in the Official Index of Rejected and Invalid Generic Names in Zoology (ICZN Opinion 604). In being no longer available, *Corynetes* Paykull, 1798 does not invalidate *Corynetes* Haeckel, 1879.

Two solutions exist in resolving the nomenclatural threat to *Sphaerocoryne*. If it and *Corynetes* are considered congeneric, a case should be submitted to the International Commission on Zoological Nomenclature asking for a ruling on the merits of conserving *Sphaerocoryne*. If not, *Corynitis agassizii* McCrady, 1859 can be removed from *Sphaerocoryne* and reassigned to *Corynetes*. *Corynitis agassizii* is known to differ from *Sphaerocoryne bedoti* Pictet, 1893, type species of *Sphaerocoryne*, as follows: (1) medusa buds arise amongst rather than distal to tentacles on hydranths of hydroids; (2) nematocysts on the exumbrella of medusae are arranged in eight exumbrellar tracks rather than being scattered; (3) advanced medusa buds and juvenile medusae have only two opposite tentacles rather than four equally developed ones; (4) nematocysts on tentacles of medusae are aggregated in the form of warts rather than in bands; (5) the manubrium is reportedly more distinctly cruciform in adult medusae; (6) abaxial ocelli of medusae appear before or shortly after liberation instead of much later in development (Yamada and Konno 1973; Calder 1988). By restricting *Sphaerocoryne* to *S. bedoti* Pictet, 1893, type species of the genus, and provisionally to *S. peterseni* Bouillon, 1984a (a species known only from its medusa stage), the genus can be retained as valid. That provisional step is taken here, and the diagnosis of *Sphaerocoryne* given above reflects the change. Affinities of *Corynetes arcuata* Haeckel, 1879, an inadequately characterized species known only from the medusa, are unclear. It has been considered of doubtful validity (Kramp 1961; Bouillon *et al.* 2006). *Sarsia coccometra* Bigelow, 1909 from the eastern tropical Pacific, a medusa regarded as a species of *Sphaerocoryne* by Petersen (1990: 213), was retained in the corynid genus *Sarsia* Lesson, 1843 by Schuchert (2009).

Sphaerocoryne bedoti **Pictet, 1893**

Figs. 44, 45

Sphaerocoryne bedoti Pictet, 1893: 10, pl. 1, figs. 5, 6.

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

Material examined. Midway Atoll: on coral rubble, 20.ix.2002, one colony, up to 6 mm high, without medusa buds, coll. A. Faucci, BPBM (without collection number).–Midway Atoll: on coral rubble, 20.ix.2002, one colony, up to 6 mm high, without medusa buds, coll. A. Faucci, ROMIZ B3830.

Description. Hydroid colonies stolonal, up to 6 mm high, arising from a hydrorhiza creeping over reef rubble. Hydrocaulus monosiphonic, unbranched, reaching just over 5 mm high, bearing a terminal hydranth. Perisarc transparent, with that on hydrorhiza of moderate thickness, mostly smooth but with occasional wrinkles and twists, that on hydrocauli tending to be thinner, smooth or with a few wrinkles, especially at proximal end, not regularly annulated, terminating at base of hydranth well below tentacles. Hydranths pyriform to top-shaped, about 0.8 mm high, 0.5 mm wide; tentacles all capitate, about 22 in number, of varied length, scattered in a narrow band around widest part of hydranth; terminal knobs varied in size, reaching about 110 µm in diameter; hypostome elongate, proboscis-like.

Gonophores not seen.

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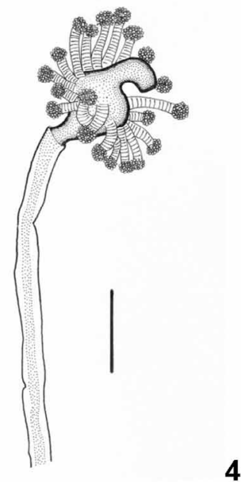

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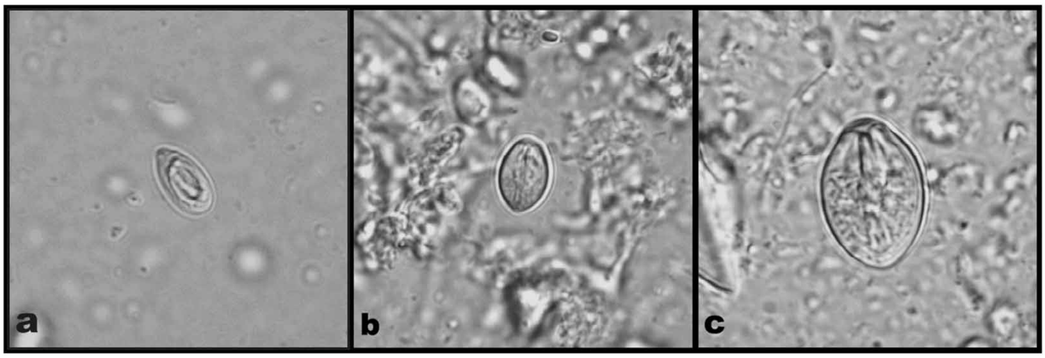

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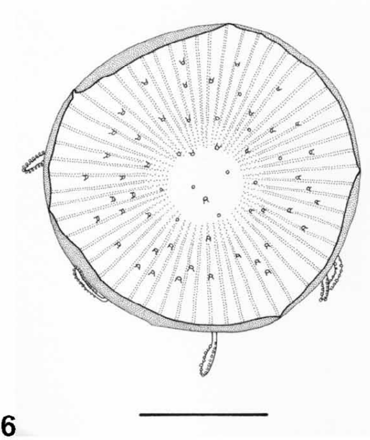

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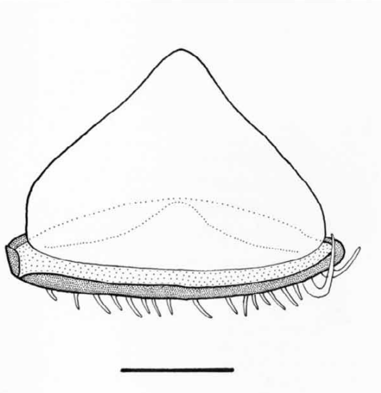

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FIGURE 43. *Pennaria disticha*: hydrocaulus, branch, and two hydranths with developing eumedusoids, ROMIZ B3829. Scale equals 1mm.

FIGURE 44. *Sphaerocoryne bedoti*: part of hydrocaulus and hydranth, ROMIZ B3830. Scale equals 0.5 mm.

FIGURE 45. *Sphaerocoryne bedoti*: nematocysts, ROMIZ B3830. a, desmoneme. b, small stenotele. c, large stenotele.

FIGURE 46. *Porpita porpita*: upper surface of float and mantle, BPBM D452. Scale equals 1 cm.

FIGURE 47. *Velella velella*: lateral view of float, mantle, and sail, BPBM D453. Scale equals 5 mm.

Remarks. Information on the taxonomy, life cycle, and cnidome of *Sphaerocoryne bedoti* Pictet, 1893 has been provided earlier (Calder 1988). A more recent overview of the species is given by Schuchert (2010). Authors including Mammen (1963), Millard (1975), Hirohito (1988), Schuchert (2010) and others are followed in regarding *Sphaerocoryne multitentaculata* (Warren, 1908) as conspecific with this species.

Records of the hydroid stage of *Sphaerocoryne bedoti* are commonly but not exclusively associated with sponge substrates (e.g. Pictet 1893; Mammen 1963; Millard 1975; Hirohito 1988; Calder 1988, 1991; Calder *et al.* 2003; Galea 2008; Schuchert 2010). Material examined here, the first record of the species from Hawaii, occurred on calcareous reef rubble.

The cnidome of hydroids from Hawaii examined here corresponded with that of material from Bermuda (Calder 1988). Elongate-oval desmonemes, and small and large stenoteles, were present (Fig. 45).

Reported distribution. Hawaii. New record.

Worldwide. Circumglobal in warm waters; 0–13 m (Pictet 1893; Millard & Bouillon 1974; Millard 1975; Wedler & Larson 1986; Hirohito 1988; Petersen 1990; Calder *et al.* 2003; Calder & Kirkendale 2005; Bouillon *et al.* 2004; Galea 2008; Schuchert 2010).

Family Porpitidae Goldfuss, 1818

Porpitae Goldfuss, 1818:1012 [emended to Porpitidae by Guilding (1828)].

Diagnosis. Capitate hydroids regarded as polymorphic floating colonies, specialized for life at ocean surface. Each colony comprising an internal float and external mantle above a large central gastrozooid, a medial ring of gonozooids, and a peripheral ring of dactylozooids. Colonies a striking blue colour in life.

Gonophores free medusae. Medusa bell-shaped; exumbrella with perradial nematocyst rows; manubrium small; radial canals four or eight; tentacle bulbs four or eight; tentacles usually two or four, with terminal knobs; ocelli lacking.

Remarks. Porpitids are now known to be anthoathecate hydrozoans instead of siphonophores or a distinct hydrozoan group, the "chondrophores" (see Edwards 1966; Brinckmann-Voss 1970; Bouillon 1985; Calder 1988; Petersen 1990; Bouillon *et al.* 2006; Daly *et al.* 2007). Bouillon (1974) concluded that the group is related to Zancleidae Russell, 1953 based on characters of morphology, histology, and nematocyst complement. That opinion, reviewed in greater detail elsewhere (Calder 1988), has been adopted here. In a molecular study, porpitids were included by Cartwright *et al*. (2008) in a group with Zancleidae, Solanderiidae Marshall, 1892, and Cladocorynidae Allman, 1872. The name Velellidae Eschscholtz, 1829, sometimes applied to this taxon, is predated by the name Porpitidae Goldfuss, 1818.

The family comprises two well-known genera, *Porpita* Lamarck, 1801 and *Velella* Lamarck, 1801. *Porpema* Haeckel, 1888, is recognized as a valid genus by some authors (Bigelow 1911; Schuchert 2009) and as a congener of *Porpita* by others (Totton 1954; Bouillon *et al.* 2006; Schuchert 2010). Three species were considered valid in the family by Daly *et al.* (2007).

Genus *Porpita* Lamarck, 1801

Porpita Lamarck, 1801: 355.
Type species. *Porpita indica* Lamarck, 1801, a junior subjective synonym of *Medusa porpita* Linnaeus, 1758 [*Porpita porpita*], by monotypy.

Diagnosis. Porpitid hydroids with disc-shaped mantle and internal float; upper surface nearly flat or with central bulge, sail absent. Dactylozooids with capitate tentacles in three vertical rows.

Porpitid medusae with eight radial canals when mature; adults with one or two slender capitate marginal tentacles, young medusae lacking tentacles; algal symbionts usually present, aggregated in endodermal cells bordering radial canals.

Remarks. The widely used name *Porpita* Lamarck, 1801 (Hydrozoa) is a junior homonym of *Porpita* Soldani, 1789 (Protozoa), as noted in an earlier work (Calder 1988). Reversal of Precedence can be applied in this case under provisions of the current code (ICZN Art. 23.9), with *Porpita* Lamarck, 1801 being designated as both valid and a nomen protectum and *Porpita* Soldani, 1789 being relegated to a nomen oblitum. First, the senior homonym has not been used as a valid name in zoology after 1899 to my knowledge (ICZN Art. 23.9.1.1). Second, *Porpita* Lamarck, 1801 has been used in at least 25 works by more than 10 authors in the past 50 years (ICZN Art. 23.9.1.2) (Brinckmann-Voss 1970, 1987; Herring 1971; Bouillon 1974, 1984b, 1985; Eldredge & Devaney 1977; Calder 1988, 1993; Petersen 1990; Cairns *et al.* 1991, 2002; Medel & López-González 1996; Schuchert 1996; Kelmo & Santa-Isabel 1998; Hoover 1998; Bullard & Hay 2002; Kirkendale & Calder 2003; Anderson *et al.* 2004; Oiso *et al.* 2005; Dunn *et al.* 2005; Shimabukuro *et al.* 2006; Bouillon *et al.* 2006; Gravier-Bonnet 2007; Daly *et al.* 2007).

More than 20 nominal species have been assigned at various times to this genus worldwide (Calder 1988). Over the past century, most authors have recognized no more than three of these as valid: *Porpita porpita* (Linnaeus, 1758) from the Indian Ocean, *P. umbella* (O.F. Müller, 1776b) from the Atlantic Ocean, and *P. pacifica* Lesson, 1826 from the Pacific Ocean. Moser (1925) and Totton (1954) have been followed here in regarding these three as conspecific, with the name *P. porpita* having priority. For reviews of the taxonomy and nomenclature of this genus, see Bigelow (1911) and Calder (1988).

***Porpita porpita* (Linnaeus, 1758)**

Fig. 46

Medusa porpita Linnaeus, 1758: 659.
Porpita pacifica.—Eldredge & Devaney, 1977: 107, fig. 2.—Hoover, 1998: 23, fig.; 2006: 23, fig.

Type locality. “Habitat in India” (Indian Ocean) (Linnaeus 1758).

Material examined. Oahu: Lanikai Beach, shore, 22.vi.1972, low tide, one colony, 2.6 cm in diameter, coll. Frances Frazier, BPBM D452.

Description. Hydroid colony pleustonic, polymorphic, with disc-shaped mantle overlying a chitinous float. Upper surface of mantle and float slightly concave, with scattered hollow papillae, central pore and peripheral stigmata indistinct; lower surface with one short, broad central gastrozooid, a medial ring of gonozooids, and a peripheral ring of dactylozooids, with most gonozooids and dactylozooids missing in present material. Gonozooids vermiform to club-shaped, with nematocyst knobs scattered over body and arranged in a whorl at distal end. Dactylozooids club-shaped, somewhat triangular in cross-section distally, with short capitate tentacles in three vertical rows over body and arranged in a whorl at distal end. Nematocyst reservoir disc-shaped, internal, between gastrozooid and float.

Gonophores free medusae, arising in clusters from base of gonozooids.

Remarks. The taxonomy of this hydrozoan was thoroughly reviewed by Bigelow (1911). While he recognized *Porpita pacifica* Lesson, 1826 as the valid name for the species in the Pacific Ocean, Moser (1925) and Totton (1954) have been followed here in considering it synonymous with *P. porpita* (Linnaeus, 1758). An account of the cnidome has been given in a previous report (Calder 1988). Additional information on the species is given by Schuchert (2010).

The hydroid stage of *Porpita porpita* is a component of the open ocean pleuston, and specimens occasionally wash ashore in Hawaii (Eldredge & Devaney 1977; Hoover 1998, 2006). Colonies are deep blue in colour when alive. Besides hydroid and medusa, the life cycle includes several juvenile stages, including a rataria "larva" and a young pleustonic hydroid stage.

Recorded distribution. Hawaii. Oahu: off the windward coast (Eldredge & Devaney 1977, as *Porpita pacifica*). Maui: Molokini Islet (Hoover 1998, 2006, as *Porpita pacifica*).
Worldwide. Circumglobal, tropical and temperate waters; pleustonic (Calder 1988; Schuchert 2010).

Genus *Velella* Lamarck, 1801

Velella Lamarck, 1801: 355.
Type species. *Medusa velella* Linnaeus, 1758 [*Velella velella*], by absolute tautonymy.

Diagnosis. Porpitid hydroids with mantle and internal float oval in shape; upper surface with erect, triangular sail oriented diagonally to long axis of float. Dactylozooids with bands and patches of nematocysts; tentacles lacking.

Porpitid medusae with four radial canals; tentacle bulbs four, one opposite pair lacking tentacles and the other pair with 1–2 capitate tentacles each; algal symbionts usually present, aggregated near radial canals and ring canal.

Remarks. Many nominal species of this genus have been described from tropical and temperate oceans worldwide. At present, however, all are believed referable to one species, *Velella velella* (Linnaeus, 1758) (Calder 1988; Bouillon *et al.* 2006; Schuchert 2010).

Velella velella (Linnaeus, 1758)

Fig. 47

Medusa velella Linnaeus, 1758: 660.
Velella pacifica.—Edmondson, 1933: 27; 1946: 28.–Reed, 1971: 49.
Velella velella.—Eldredge & Devaney, 1977: 107, fig. 1b.–Hoover, 1998: 23, fig.; 2006: 23, fig.

Type locality. "Habitat in Pelago. Loefling. In Mari Mediterraneo. Brander" (Linnaeus 1758). The Mediterranean Sea may be taken as the type locality of the species (Schuchert 2010).

Material examined. Pearl and Hermes Reef, Northwest Hawaiian Islands: iv.1927, nine colonies, all left-sailing forms, up to 4 cm long × 2.5 cm wide, coll. T. Dranga, BPBM D145.–Maui: Makena, 1926, one colony, right-sailing form, 2.9 cm long × 1.8 cm wide, coll. J.K. Skinner, BPBM D146.–Oahu: Wianae coast, 04.vi.1941, 1 specimen (dry), BPBM D237.–Oahu: Kaneohe Bay, land side of Chinaman's Hat Islet, 03.x.1971, two colonies, both right-sailing forms, 1.5 cm long × 0.7 cm wide, coll. D.M. Devaney, BPBM D453.

Description. Hydroid colonies pleustonic, polymorphic, with soft mantle overlying an oval chitinous float. Upper surface of mantle with an erect, triangular sail reinforced internally by triangular extension of float; hydroids in two enantiomorphic forms, with sail of some oriented along the NW to SE diagonal and others oriented along the NE to SW diagonal when long axis of float positioned N and S. Lower surface with one long, broad, essentially tubular central gastrozooid, a medial ring of gonozooids, and a peripheral ring of dactylozooids. Gonozooids club-shaped, with nematocyst knobs scattered over body and arranged in a whorl at distal end. Dactylozooids tentacle-like in form, oval in cross section, lacking tentacles. Nematocyst reservoir elongate-oval, internal, between gastrozooid and float.

Gonophores free medusae, arising in clusters from blastostyles near base of gonozooids.

Remarks. Information on synonymy, cnidome, and development of *Velella velella* (Linnaeus, 1758) has been summarized earlier (Calder 1988). Further details on the biology of the species are summarized in Schuchert (2010).

The life cycle of *V. velella* is metagenetic, with both hydroid and medusa stages. From the research of Woltereck (1904, 1905) in the Mediterranean, early development occurs in deep water as a conaria larva. Very young conaria larvae have a rudimentary fluid-filled float, a mouth, and two tentacles. As development proceeds, an organ called the crimson cone appears, which secretes oil droplets as a means of flotation. Conaria rise to the surface and gradually metamorphose into rataria larvae having an air-filled float, developing zooids, and a nascent sail; meanwhile, the crimson cone is lost. With continued development, the rataria becomes the floating colony more immediately recognizable as *V. velella*.

There has been confusion over terminology applied to the dimorphic forms of *Velella velella*. Right-sailing and left-sailing types described here are as defined by Edwards (1966). Thus, with the longitudinal axis of the float oriented north and south, the sail runs from NW to SE in left-sailing forms and from NE to SW in right-sailing forms.

According to Edmondson (1933, 1946), *Velella pacifica* [*V. velella*] is frequently stranded on Hawaiian shores by strong winds. By contrast, Hoover (1998, 2006) noted that the species is uncommon in Hawaii. Colonies are deep blue in colour when alive.

Recorded distribution. Hawaii. No specific location given (Edmondson 1933, 1946). Oahu, Kaneohe Bay (Reed 1971). No location given (Eldredge & Devaney 1977). Oahu: Kahuku (Hoover 1998, 2006). Worldwide. Circumglobal, tropical and temperate waters; pleustonic (Calder 1988; Schuchert 2010).

Subclass Trachylina Haeckel, 1879

Trachylinae Haeckel, 1879: 2.

Remarks. Trachylina Haeckel, 1879 encompasses the hydrozoan orders Actinulida Swedmark & Teissier, 1959, Limnomedusae Kramp, 1938, Narcomedusae Haeckel, 1879, and Trachymedusae Haeckel, 1879 (Collins 2000; Daly *et al.* 2007; Collins *et al.* 2008). Details on the phylogeny of the group are provided in Collins *et al*. (2008).

Order Limnomedusae Kramp, 1938

Limnomedusae Kramp, 1938: 107.

Diagnosis. Hydrozoa with polyps solitary or primitively colonial; hydranths small to minute, morphologically simple, sessile, lacking hydrothecae; hypostome, mouth, and gastric cavity present or absent; tentacles and perisarcal sheath present or absent; asexual reproduction frequent, by frustules, or frustule-like buds, or cysts.

Gonophores fixed or free eumedusoids, or medusae. Medusae, when present, with hemispherical to discoidal umbrella; tentacles hollow, lacking basal bulbs; marginal sense organs, when present, comprising internal statocysts; gonads on radial canals or manubrium.

Remarks. The history and phylogeny of Limnomedusae Kramp, 1938 has been reviewed by Daly *et al*. (2007) and Collins *et al*. (2008). Bouillon *et al*. (2006) included 21 genera in the family, many of them poorly known (Jankowski 2001) and over half (12) being monotypic.

Family Olindiidae Haeckel, 1879

Olindiadae Haeckel, 1879: 252 [emended to Olindiidae by Bigelow (1909: 101)].

Diagnosis. Limnomedusoid polyps small, solitary or colonial; hydrorhiza present or absent. Hydranths atentaculate, or with one tentacle, or with a distal whorl or tuft of tentacles, conical to club-shaped, usually naked; mouth and gastric cavity present; asexual reproduction frequently occurring by frustules, or fission, or cysts.

Gonophores, where known, fixed or free eumedusoids, or medusae. Medusae, when present, typically dome-shaped to flattened; radial canals simple, unbranched; centripetal canals present or absent; sense organs internal marginal vesicles; gonads on radial canals (except on manubrium in *Limnocnida* Günther, 1893).

Remarks. Olindiidae Haeckel, 1879, the largest family in the order Limnomedusae Kramp, 1938 with about 18 genera and 50 species (Schuchert 2009), is considered paraphyletic (Daly *et al*. 2007). Several taxa are obscure and of uncertain status. Jankowski (2001) suggested that freshwater medusae and their marine relatives are both polyphyletic and relatively recent in origin. Collins *et al.* (2006) found a single origin of the freshwater Limnomedusae (*Craspedacusta* Lankester, 1880 + *Limnocnida* Günther, 1893 + *Astrohydra* Hashimoto, 1981), with the brackish genus *Maeotias* Ostroumoff, 1896 as the sister lineage.

There has been inconsistency in the spelling of the name of this family, as Olindiadae, Olindiidae, Olindiadidae, and Olindiasidae, because of uncertainty as to the stem of the type genus *Olindias* F. Müller, 1861 originally used in forming the name. According to Commissioner Miguel Alonso-Zarazaga of the International Commission on Zoological Nomenclature (personal communication, 16 April 2010), the name *Olindias* is a Greek-like word of unknown origin, regarded as a “nomen proprium” (Haeckel 1879; Moreira and Yamashita 1972). The stem of this name for the purposes of the code is that adopted by the author who established the new family (ICN Art. 29.3.3). Haeckel (1879) founded this family as Olindiadae, yet he formed other family-group names in his monograph by adding the suffixes –IDAE or -INAE to the stems of their type genera. It is thus unclear from Haeckel’s work whether he intended the stem to be Olindi-, or as a Greek substantive having the stem Olindiad-. The names Olindiadae and Olindiasidae, the latter suggested by Moreira and Yamashita (1972), are nomenclaturally incorrect. The spelling adopted here is the more widely used Olindiidae, as emended by Bigelow (1909).

The gender of the genus name *Olindias* was not specified by F. Müller (1861), and it cannot be determined from the only originally included species (*O. sambiquensis* F. Müller, 1861). Thus, the name is to be treated as masculine (ICZN Art. 30.2.3). This is of relevance in the correct spelling of certain species-group names combined with *Olindias* [e.g. *O. formosa* (Goto, 1903), should be *O. formosus*].

Genus *Craspedacusta* Lankester, 1880

Craspedacusta Lankester, 1880: 147.
Type species. *Craspedacusta sowerbii* Lankester, 1880, by monotypy.

Diagnosis. Olindiid polyps solitary or primitively colonial. Hydranths atentaculate, athecate, club-shaped to cylindrical; distal end a knob-shaped capitulum, bearing an apical mouth surrounded by nematocysts; hydranth base with attachment region surrounded by thin perisarc; asexual reproduction by frustulation, cyst formation, or fission.

Gonophores medusae, arising from gastric column of hydranth. Medusae hemispherical to dome-shaped, with marginal nematocyst ring; radial canals four; centripetal canals absent; manubrium quadrate, moderately short, gastric peduncle absent; tentacles evenly spaced, of one type, lacking adhesive disks; statocysts in vesicles on velum; gonads sac-shaped, on radial canals.

Remarks. Bouillon *et al*. (2006) listed eight nominal species in *Craspedacusta* Lankester, 1880, but speculated that they might all be conspecific with *C. sowerbii* Lankester, 1880. Earlier, He *et al*. (2000) had recognized six species, while Dumont (1994) reported that four species were considered valid by most workers. Jankowski (2001) and Jankowski *et al*. (2008) believed there were as many as four species endemic to the Yangtze River Basin in China, the likely origin of the genus. Several species of the genus appear valid from molecular data (Collins *et al*. 2008; Zhang *et al*. 2009). The species taxonomy of this enigmatic fresh water genus remains unsettled.

Craspedacusta sowerbii **Lankester, 1880**

Fig. 48

Craspedacusta sowerbii Lankester, 1880: 148.
Craspedacusta sowerbyi.—Edmondson, 1940: 314 [medusa only].—Matthews, 1963: 18, figs. 1, 2; 1966: 246, figs. 1–5.

Type locality. UK: London, Regent's Park, "…in the tank in the water-lily house…" (Lankester 1880: 147).

Material examined. None.

Description. As for diagnosis of genus.

Remarks. *Craspedacusta sowerbii* Lankester, 1880 is a well-known freshwater species with a wide geographic range (Kramp 1961; Dumont 1994). Edmondson (1940) first reported the species from Hawaii, based on medusae found at Maliko Gulch, Maui. Both medusa and polyp stages were later reported from Honolulu in aquaria by Matthews (1963, 1966). No specimens of the hydroid were found in collections at the Bishop Museum, and it is not currently known to occur in limnic aquaria and culture systems at the Waikiki Aquarium (Gerald Crow & Kelley Lam, pers. comm., 30 July 2009).

A review of the global distribution, dispersal, and feeding ecology of *C. sowerbii* and other freshwater medusae is given by Dumont (1994).

Reported distribution. Hawaii. Maui: Maliko Gulch [medusa only] (Edmondson 1940).–Oahu: Honolulu, in aquaria (Matthews 1963, 1966).

Worldwide. All continents except Antarctica, in shallow subtropical and temperate fresh waters (Kramp 1961; Dumont 1994; Jankowski 2001; Jankowski *et al*. 2008; Zhang *et al*. 2009).

Genus *Calpasoma* Fuhrmann, 1939

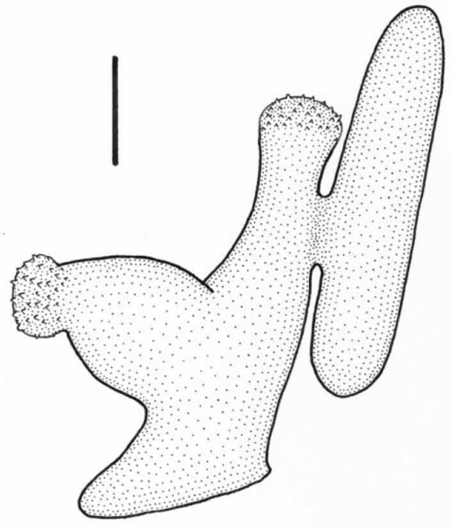
Calpasoma Fuhrmann, 1939: 363.
Type species. *Calpasoma dactylopterum* Fuhrmann, 1939, by monotypy.

Diagnosis. Olindiid polyps solitary, although bipolar or tripolar forms sometimes present. Hydranths minute, athecate, sausage-shaped to cylindrical, with distal mouth but without prominent capitulum; tentacles usually present distally, appearing to arise in two close whorls or irregularly arranged, each tentacle a slender and filiform protrusion of an epithelial tentaculocyte; several nematocysts on distal end of each tentacle, scattered elsewhere; asexual reproduction by frustulation or budding.

Gonophores not known.

Remarks. *Calpasoma* Fuhrmann, 1939 is a peculiar freshwater hydrozoan genus, sometimes believed to be merely a tentaculate form of *Craspedacusta* Lankester, 1880. Studies such as those of Matthews (1966), and Rahat & Campbell (1974), support recognition of the two as distinct, although Jankowski (2001) considered at least one form of *Calpasoma* to be congeneric with *Craspedacusta*. *Astrohydra* Hashimoto, 1981 appears similar, but the genus (and its type species, *A. japonica* Hashimoto, 1981) is not well-known.

The generic name *Calpasoma* is neuter (ICZN Art. 30.1.2), and the specific name of its single contained species should be spelled *dactylopterum*, not *dactyloptera* as originally formed.



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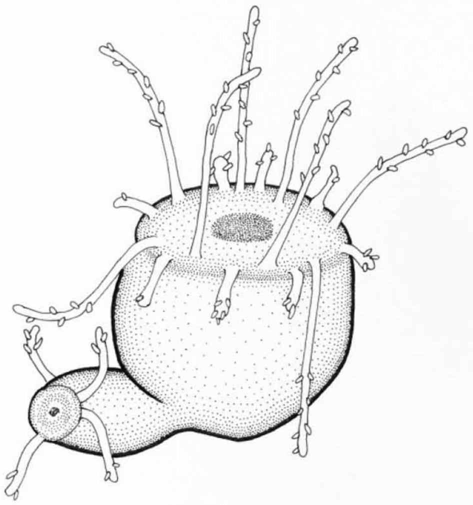

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FIGURE 48.*Craspedacusta sowerbii*: two hydranths and a frustule (after Matthews 1966). Scale equals 100 µm.
FIGURE 49. *Calpasoma dactylopterum*: tentaculate polyp (after Matthews 1966).

Calpasoma dactylopterum Fuhrmann, 1939

Fig. 49

Calpasoma dactyloptera Fuhrmann, 1939: 363, figs. 3–6.–Matthews, 1966: 256.

Type locality. Switzerland: Neuchâtel, alongside *Craspedacusta sowerbii* in aquaria at the university (Fuhrmann 1939).

Material examined. None.

Description. (After Jankowski 2001): "Polyp…0.1–0.4 mm long; transparent to whitish; 8–32 (to 54) tentacles, 68–234 µm long and 8–15 µm wide; each tentacle contains 5–20 non grouped nematocyts (*sic*) (0.14 µm)."

Remarks. Matthews (1966), working in Hawaii, reported *Calpasoma dactylopterum* Fuhrmann, 1939 on the aquatic tracheophyte *Elodea canadensis*, purchased from an unstated source. Specimens of this freshwater cnidarian were not represented in collections at the Bishop Museum, and it was not observed during this study.

The cnidome of *Calpasoma dactylopterum* comprises heterotrichous microbasic euryteles, and reproduction occurs by formation of frustules (Rahat & Campbell 1974).

There is disageement at present whether this is simply a form of *Craspedacusta sowerbii* Lankester, 1880.

Reported distribution. Hawaii. Oahu: Honolulu, in aquaria on *Elodea canadensis* (Matthews 1966). Worldwide. Holarctic, shallow fresh waters (Jankowski *et al*. 2008).

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