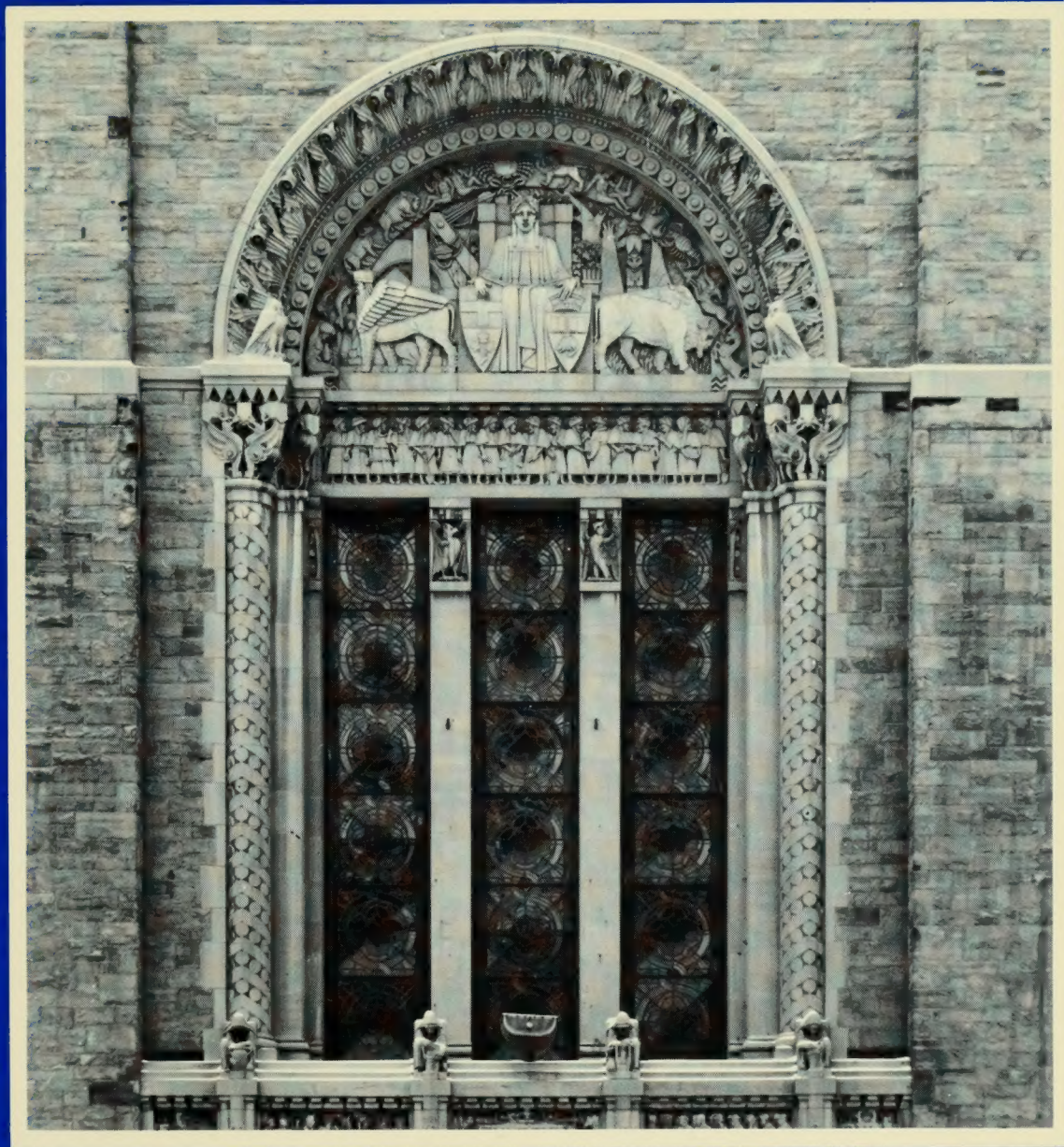


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Shallow-Water Hydroids of Bermuda
The Athecatae

Dale R. Calder

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Shallow-Water Hydroids of Bermuda The Athecatae

Dale R. Calder



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Shallow-Water Hydroids of Bermuda

The Athecatae

Abstract

The shallow-water athecate hydroids known from Bermuda and vicinity, comprising 26 species in 24 genera, are surveyed. Synonymies are updated for each family-, genus-, and species-group taxon represented. Six taxa are described as new to science: *Corydendriinae*, subf. nov., *Rhizorhagiinae*, subf. nov., *Rhizodendrium*, gen. nov., *Rhizodendrium sterreri*, sp. nov., *Eudendrium bermudense*, sp. nov., and *Coryne sargassicola*, sp. nov. *Zyzyzus warreni* is proposed as a replacement name for the junior primary homonym *Tubularia solitaria* Warren, 1906b (not *Tubularia solitaria* Rapp, 1829). The tribe Pachycordylini Cockerell, 1911, is elevated to the rank of subfamily. *Pachycordyle* Weismann, 1883, *Parawrightia* Warren, 1907, and *Stylactaria* Stechow, 1921a, are re-established as the valid names of genera. *Tubularia muscoides* Linnaeus, 1761, is designated as type species of the nominal genus *Fistulana* O. F. Müller, 1776a. A lectotype is designated for the conglomerate *Podocoryne alderi* Hodge, 1861, a nominal species based on hydroid and medusa stages referable to different genera. The invalid name *Bougainvillia ramosa* (van Beneden, 1844a) is replaced with the name *Bougainvillia muscus* (Allman, 1863).

Descriptions and illustrations are provided for each species studied, and data on nematocyst complement and size are given for all but one of them. Of the 26 species discussed, 23 occur elsewhere in the western Atlantic and 9 are reportedly circumglobal in warm waters. Eleven of the 23 previously known species are reported from Bermuda for the first time.

Introduction

Hydroids of the oceanic island of Bermuda have been the subject of several previous investigations. The most comprehensive taxonomic accounts to date have been by Congdon (1907) and Bennett (1922). Hydroids collected by H.M.S. *Challenger* on Challenger Bank in the vicinity of Bermuda were discussed by Allman (1888) and Ritchie (1909). Reports by Verrill (1900, 1907), Smallwood (1910), Stechow (1912), Jäderholm (1920), and Moore (1969) discussed one or more hydroid species from the Bermuda platform. Fraser (1944) included most of the species known from the area, based on literature records. Calder (1986) listed common and otherwise noteworthy hydrozoan species. Hydroids on pelagic *Sargassum* were studied by Burkenroad (*in* Parr, 1939), by Morris and Mogelberg (1973), and by Ryland (1974). Morphological, developmental, and physiological investigations have been undertaken on Bermuda material by Congdon (1906), Cowden (1965a, 1965b), Summers (1972a), Lesh-Laurie (1976), and Clark and Cook (1986). Accounts of the neustonic species *Porpita porpita* (Linnaeus, 1758) and *Velevilla velevilla* (Linnaeus, 1758) in

Bermudian waters have been published by Fewkes (1883), Verrill (1900), Bigelow (1918), Totton (1936), and Calder (1986). *Millepora alcicornis* Linnaeus, 1758, a conspicuous member of the Bermudian coral reef community, has been mentioned in papers such as those of Nelson and Duncan (1876), Moseley (1876, 1879, 1880), Rice (1878), Quelch (1886), Verrill (1900, 1902a, 1902b, 1907), Moore (1969), and Calder (1986).

The purpose of this report was to provide a taxonomic account of the athecate hydroids currently known from Bermuda and vicinity, to a depth of 100 m, based largely on collections made by the author since 1977. The athecate fauna of the study area is rather depauperate, accounting for only about one-quarter of the total number of hydroid species known from Bermuda (Calder, unpublished data). A decision was made early in the study to include as complete a synonymy of each family-, genus-, and species-group taxon as possible. Original spellings of the names of taxa were verified, authorship and dates of these names were rechecked, and matters of nomenclature were con-

sidered according to provisions of the International Code of Zoological Nomenclature (International Commission on Zoological Nomenclature [ICZN], 1985). Some of the nomenclatural problems encountered have been resolved here, while others will require submissions to the commission.

Questions regarding the identity, synonymy, and systematic positions of taxa arose repeatedly during the course of this study. One quandary in particular involved the extent to which nominal species should be combined or divided. The hydrozoan literature is replete with extremes of taxonomic "lumping" and "splitting," and the confusion resulting from both. For example, Duchassaing and Michelotti (1864) viewed practically every morphological form of the hydrocoral *Millepora* Linnaeus, 1758, from the Caribbean as a distinct species, whereas Hickson (1898a, 1898b) recognized only one species in the genus worldwide. Most authors now follow Boschma (1948) in recognizing three species in the Caribbean, and about a dozen worldwide. Nevertheless, determining how far to go in combining or splitting nominal species is largely a matter of personal opinion. Most recent hydrozoan systematists have tended to be "taxonomic lumpers," and generally broad taxa have been recognized here. Reasons why relatively few species of hydroids are believed to exist worldwide were briefly stated by Cornelius (1981).

Related to the question of lumping or splitting of taxa is the interpretation of hydroid species distribution. According to literature records, many species of hydroids are virtually cosmopolitan. Admittedly, certain hydroids are well adapted for long-range dispersal, and their rate of speciation seems to be rather slow (Cornelius, 1981). Yet the question arises whether some species are as widely distributed as records indicate, or whether their reported range is partly an artifact of the hydrozoan taxonomist's inability to discriminate distinct but closely related species.

Hydrozoan classification is complicated by many factors, including the following: (1) the existence of separate

hydroid and medusa generations in many species; (2) the legacy of separate classifications for hydroids and medusae; (3) the production of free medusae and fixed gonophores in closely related species; (4) the differential reduction of male and female gonophores in certain species; (5) the production in some taxa of morphologically dissimilar medusae by virtually indistinguishable hydroids, and vice versa; (6) the morphological variation sometimes displayed within a given taxon; (7) the scarcity of reliable taxonomic characters in various taxa; (8) the general lack of knowledge concerning the biology of these animals, including life cycles of many species. Classification of the order Athecatae Hincks, 1868, in particular is currently in a state of flux. Most authors over the past 30 years have regarded the Capitata Kühn, 1913, as the most primitive suborder of the Hydrozoa, largely following Rees (1957). Athecate classification has been extensively modified recently by Petersen (1979), Werner (1984), and Bouillon (1985). Following the last two authors, families of the suborder Filifera Kühn, 1913, are discussed first here. Yet it is unlikely that a stable classification, accurately reflecting relationships within the Athecatae, has been achieved by the traditional approaches used in studies to date. A re-examination of relationships within athecate hydroids and their medusae, especially using methods of phylogenetic systematics (Wiley, 1981), is greatly needed. The only such study within the Hydrozoa up to now is that by Cairns (1984) for stylasterids. The arrangement of families adopted here, somewhat modified from Werner (1984), is recognized as unsatisfactory. Unfortunately, no demonstrably superior classification exists at present.

The known range given here is based on reported occurrences at Bermuda, and elsewhere in the Atlantic, Pacific, and Indian oceans. In most cases, only one significant record has been cited to document occurrences outside Bermuda.

Materials and Methods

Hydroids were collected during six field trips to the Bermuda Islands, on the following dates: 1–22 September 1977, 26 February–10 March 1982, 17 July–6 August 1982, 15 June–13 July 1983, 20 September–11 October 1984, and 24 September–8 October 1986. Specimens were also obtained on 23–24 May 1979 during a two-day vacation cruise to the islands. Most collections were made by snorkelling, although scuba gear was used on occasional dives. Collecting efforts were concentrated in shallow-water areas of the northeastern half of Bermuda, especially in Flatts Inlet, Castle Harbour, Harrington Sound, and Whalebone Bay (Fig. 1), and only those hydroids taken

in depths of 0–100 m are included in this report. Intensive sampling was undertaken around ledges, bridges, pilings, floats, and moorings; in grass beds; and in ponds and caves. Considerable time was spent searching beaches for stranded specimens of the neustonic hydroids *Porpita* and *Velella*. Large quantities of pelagic *Sargassum* were collected and examined for attached hydroids during each field trip.

Collections at depths of 60–100 m in offshore waters south of Castle Harbour were made by dredging from the M/V *Northstar* (3 September 1977), R/V *Culver* (1 July 1983), and R/V *Weatherbird* (27 September 1984). Dredg-

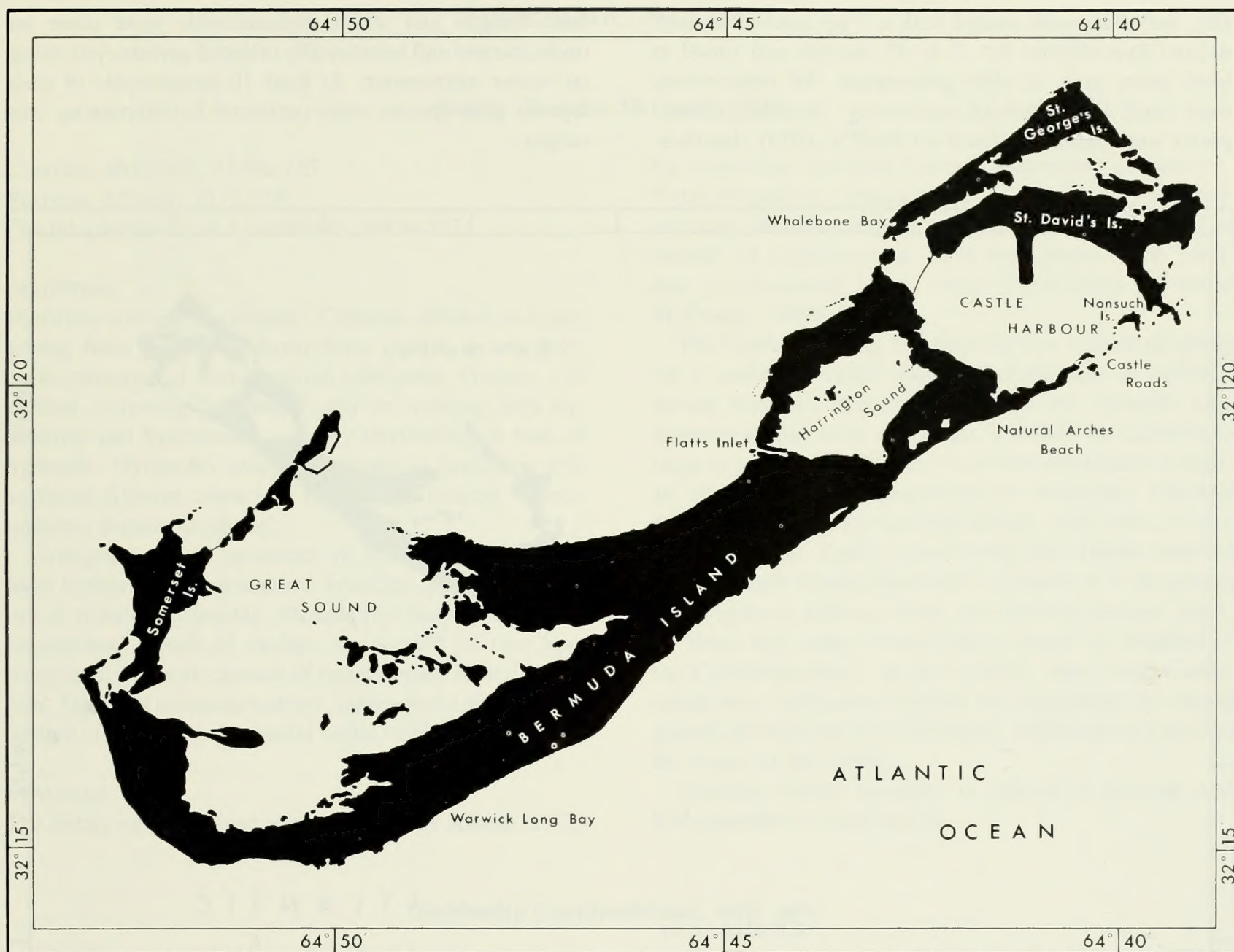


FIG. 1. The Bermuda Islands.

ing in 75 m of water on Challenger Bank, southwest of Bermuda (Fig. 2), was undertaken on 3 October 1984 aboard R/V *BBS II*; on the return cruise from Challenger Bank, a 10-minute plankton tow was made 6 km offshore from Gibbs Hill lighthouse with a plankton net 1 m in diameter.

Hydroids in reference collections at the Bermuda Biological Station were examined. Among these were specimens from (1) buoy chains, collected by Dr John Markham and colleagues between 5 October and 23 December 1976; (2) waters south of Castle Harbour in 60–100 m, collected by Dr Markham using a dredge aboard M/V *Northstar* on 6 August and 27 August 1977; (3) the Castle Harbour area, collected by Prof. H. Mergner on 22 and 24 June 1967; (4) the Castle Harbour area, collected by Dr H. Thiel on 3–4 August 1974; (5) Argus Tower on Plantagenet Bank (Fig. 2), collected by Dr W. Sterrer on 23 April 1976; (6) the wreck *Pelinaion* off St David's Island, collected by

Dr W. Sterrer on 18 August 1974; (7) Castle Harbour, collected by H. E. Lehman in June 1966; (8) surveys of Bermudian caves, collected by Dr T. Iliffe during the summer of 1982.

Specimens collected during this investigation have been deposited in the Department of Invertebrate Zoology, Royal Ontario Museum (ROMIZ). All descriptions and illustrations herein are from Bermuda material, as indicated, except for a paratype of *Coryne sargassicola* from the Gulf Stream off New York City.

As complete a synonymy as possible has been given for each taxon, although many of the lists may be less than exhaustive. Virtually all of the listed synonyms have been verified by examination of cited references.

Nematocysts were examined in preserved material by compressing pieces of tissue, or entire individuals of minute specimens, between a slide and coverslip. Occasion-

ally, materials were treated with a 5 per cent solution of sodium hypochlorite for 15 to 45 seconds and rinsed in fresh water prior to slide preparation. All observations were made by brightfield microscopy. Nematocyst categories were identified based on Weill's (1934) classifica-

tion. Length and width measurements were made on undischarged and horizontally oriented nematocysts using an ocular micrometer. At least 10 nematocysts of each type in each species were measured in determining size ranges.



FIG. 2. Bermuda, Challenger Bank, and Plantagenet Bank.

Systematic Account

Family Clavidae McCrady, 1859a

Clavidae McCrady, 1859a:123.

Turridae Allman, 1872:259.

Cordylophorinae von Lendenfeld, 1885a:221.

DIAGNOSIS

Hydroids solitary or colonial. Colonies stolonial or erect, arising from a creeping hydrorhiza; growth in erect colonies monopodial with terminal hydranths. Perisarc soft or firm, investing hydrorhiza only or covering both hydrorhiza and hydrocaulus, usually terminating at base of hydranth. Hydranths elongate, clavate to fusiform, with scattered filiform tentacles. Hypostome conical. Nematophores present or absent.

Gonophores fixed sporosacs or free medusae, arising from hydrorhiza, hydrocaulus, branches, pedicels, or entire or reduced hydranths. Medusa bell-shaped with short manubrium; mouth of medusa surrounded by four lips, margins of lips with clusters of nematocysts. Radial canals four. Marginal tentacles solitary, numerous in adult. Ocelli present. Gonads on interradial walls of manubrium.

REMARKS

The family name Turridae was constituted by Allman (1872)

for clavid-like hydroids having medusiform gonophores. Taxa referred by Allman to the nominal family are now generally included in the Clavidae McCrady, 1859a. The identity of *Turris* Lesson, 1843, type genus of the Turridae, is discussed below under *Turritopsis nutricula* McCrady, 1859b.

The family Clavidae has been used as a catch-all group for a seemingly rather disparate assemblage of hydroids having scattered filiform tentacles on the hydranth. Differences among taxa within the Clavidae are sufficiently large to warrant recognition of several subfamilies at least. In addition to the nominotypical subfamily Clavinae McCrady, 1859a, the Corydendriinae, subf. nov., is recognized below. Earlier, von Lendenfeld (1885a) founded the subfamily Cordylophorinae, including in it the genera *Cordylophora* Allman, 1844, and *Merona* Norman, 1865. Of these two, only *Cordylophora* should be retained in the Cordylophorinae, in my opinion. One or more additional new subfamilies should be established for clavid genera not represented in Bermuda, but doing so is beyond the scope of this report.

Bouillon (1985) included 11 genera of hydroids and hydromedusae in this family.

Subfamily Corydendriinae, subf. nov.

DIAGNOSIS

Clavid hydroids with stolonial or erect colonies; branches of erect colonies adnate to hydrocaulus for a varying distance basally. Hydranths elongate, more or less cylindrical, not polymorphic; tentacles filiform, scattered over much of hydranth. Nematophores absent.

Gonophores fixed sporosacs or free medusae, arising from hydrorhiza, hydrocaulus, branches, or pedicels, but not from hydranths.

REMARKS

Hydroids of the Corydendriinae, subf. nov., differ from the Clavinae McCrady, 1859a, in having cylindrical instead of club-shaped hydranths, tentacles scattered over much of the hydranth rather than restricted to a bulbous region distally, and gonophores borne on hydrorhiza, stem, or branches instead of on the hydranth. Unlike on the Cordylophorinae von Lendenfeld, 1885a, the branches are adnate for some distance at their origin rather than becoming immediately free, and the hydranths are elongate and tubular rather than spindle-shaped to vasiform. The subfamily Corydendriinae, as defined here, encompasses

the genera *Corydendrium* van Beneden, 1844a, *Turritopsis* McCrady, 1859b, and *Rhizodendrium*, gen. nov. It is possible that the poorly known genus *Tubiclava* Allman, 1863, if it is valid, belongs in this group. *Merona* Norman, 1865, having polymorphic hydranths and nematophores, is excluded; without doubt it should be referred to another new subfamily within the Clavidae.

Genus *Corydendrium* van Beneden, 1844a

Corydendrium van Beneden, 1844a:313.

Soleniopsis Ritchie, 1908:494.

DIAGNOSIS

Clavid hydroids with erect, irregularly branched colonies; hydrocaulus polysiphonic. Branches adnate to hydrocaulus, or to other branches, over part or all of their lengths. Perisarc firm, terminating near hydranth base. Hydranths elongate, tubular; tentacles filiform, scattered over much of hydranth.

Gonophores fixed sporosacs, arising as blind, elongate

sacs of coenosarc below hydranths and within perisarcal tubes of branchlets.

TYPE SPECIES

Sertularia parasitica Linnaeus, 1767, by monotypy.

REMARKS

L. Agassiz (1862) believed that *Corydendrium* van Beneden, 1844a, and *Cordylophora* Allman, 1844, were congeneric, and he referred both to the nominal genus *Syncoryna* Ehrenberg, 1834. Allman (1872) showed why neither should be referred to *Syncoryna*, identical with *Coryne* Gaertner, 1774, and argued that they represented two distinct genera. Colony form, hydranth shape, and characteristics of the gonophores are sufficiently distinctive in *Corydendrium* to warrant its separation from *Cordylophora*.

Ritchie (1908) recognized the similarities between *Corydendrium* and his nominal genus *Soleniopsis*, but he mistakenly believed that the former produced free medusae. Stechow (1911) recognized this error and referred *Soleniopsis* to *Corydendrium*.

Kramp (1935) regarded *Turritopsis* McCrady, 1859b, as congeneric with *Corydendrium*, suggesting that hydroids of the two differed only in the type of gonophore produced. Petersen (1979) seems to have adopted this view, but both genera are recognized as valid here and in most other recent publications. Kramp himself, in later reports (e.g., Kramp, 1959, 1961, 1965, 1968), employed the name *Turritopsis* for the medusa.

Corydendrium parasiticum (Linnaeus, 1767)

Figs. 3, 4

Sertularia parasitica Linnaeus, 1767:1315.

Sertolara parassita—Cavolini, 1785:181; pl. 6, figs. 8–13 [incorrect subsequent spelling].

Pennaria parasitica—Goldfuss, 1820:89.

Sertulariam parasiticam—Ehrenberg, 1834:71 [incorrect subsequent spelling].

Syncoryna parasitica—Ehrenberg, 1834:71.

Corydendrium parasiticum—van Beneden, 1844b:313.

Sertularia (Syncoryne) parasitica—Frey and Leuckart, 1847:30.

Syncoryne parasitica—Allman, 1864a:352.

Clava parasiticum—Bonnievie, 1899a:9.

Clava (Corydendrium) parasiticum—Bonnievie, 1899a:39.

Soleniopsis dendriformis Ritchie, 1908:495; figs. 142, 143; pl. 26, fig. 1.

Corydendrium sessile Ritchie, 1910a:802; pl. 76, figs. 1, 2.

Corydendrium dendriformis—Ritchie, 1910a:803.

Corydendrium dendriforme—Gravelly, 1927:7; pl. 2, fig. 2.

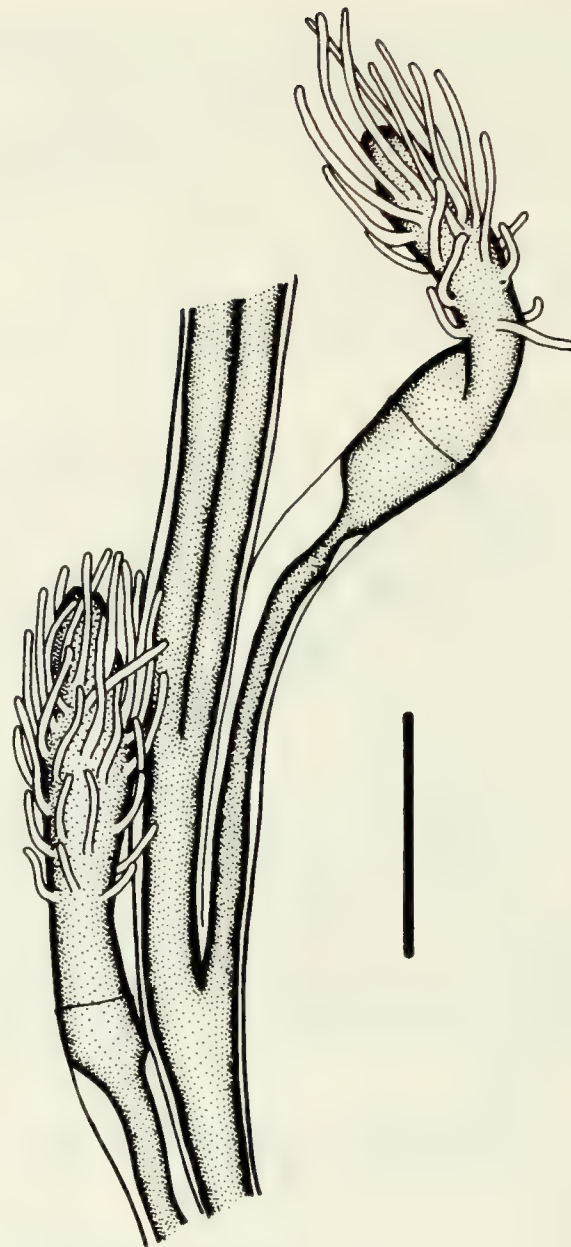


FIG. 3. *Corydendrium parasiticum*, part of hydrocaulus with hydranths, ROMIZ B136. Scale equals 1 mm.

Corydendrium flabellatum Fraser, 1938:11; pl. 1, figs. a, b.

Corydendrium parasticum—Wedler and Larson, 1986:71 [incorrect subsequent spelling].

TYPE LOCALITY

“Habitat in Oceano, saepe in Corallina rubente” (Linnaeus, 1767).

MATERIAL EXAMINED

Flatts Inlet, on underside of large, flat rock, –3 m, 2 August 1982, one colony, 2.2 cm high, without gonophores, ROMIZ B136. Atlantic Ocean, 2 km southeast of Castle Roads, on calcareous rubble, –60 to –90 m, 3 September 1977, one colony, 4.5 cm high, without hydranths and gonophores, ROMIZ B158. Harrington Sound, near Flatts Inlet bridge, on ledge near shore, –1.5 m, 5 March 1982, two colonies, 4 cm high, without gonophores, ROMIZ B173.

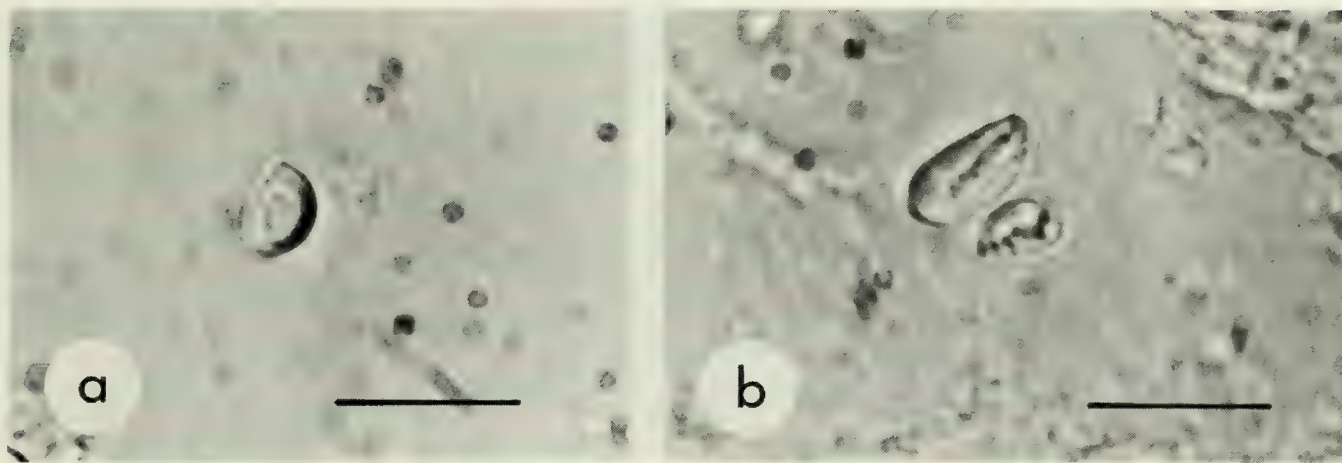


FIG. 4. *Corydendrium parasiticum*, nematocysts of hydranth, ROMIZ B158. Scales equal 10 μm . a, Desmoneme. b, Heterotrichous microbasic eurytele.

DESCRIPTION

Colonies erect, straggly, up to 4.5 cm high, arising from a creeping hydrorhiza. Hydrocaulus polysiphonic in all but very young colonies, individual tubes relatively stout, 0.45 mm in diameter. Branching irregular, in one or more planes, branches adnate to hydrocaulus basally, gradually curving outwards and becoming free distally; secondary branches arising in like manner from primary branches; ultimate branchlets typically alternate. Perisarc moderately thick over most of colony, becoming thin at hydranth base and terminating below tentacles, smooth or with occasional wrinkles but not annulated, clear to straw-coloured, often encrusted with detritus and silt. Hydranths cylindrical through clavate to fusiform, constricted basally below orifice of perisarc tube, up to 2.8 mm long from basal constriction to tip of hypostome, about 0.3–0.5 mm wide. Tentacles filiform, often as many as 40 or more, scattered over distal three-quarters of hydranth, proximal tentacles shorter and more slender than distal ones. Hypostome elongate, conical.

Gonophores not seen.

Nematocysts—

Hydroids: desmonemes 5.3–5.7 μm \times 3.7–3.8 μm ; heterotrichous microbasic euryteles 8.2–8.4 μm \times 3.8–4.3 μm .

REMARKS

Ritchie (1910a) believed that *Corydendrium dendriforme* (Ritchie, 1908) was distinct from *C. parasiticum* (Linnaeus, 1767) in having (1) thicker, more definite stems; (2) branchlets arranged in a pseudopinnate fashion; and (3) the free portion of the pedicels much less elongate. Rees and Thursfield (1965) also considered *C. dendriforme* to be valid. However, the characters used to distinguish them seem variable, and Vervoort (1941) and Millard (1959a, 1975) have been followed in regarding the name *C. dendriforme* as a junior synonym of *C. parasiticum*.

Leloup (1937) regarded *Corydendrium sessile* Ritchie,

1910a, as conspecific with *C. dendriforme*, suggesting that the former was based on a young, immature colony of the latter. Its name, too, is referred to *C. parasiticum* here.

Fraser's (1938) account of *Corydendrium flabellatum* from the Pacific coasts of Mexico and Panama corresponds with *C. parasiticum*, and the former is regarded here as conspecific with the latter. The status of *C. fruticosum* Fraser, 1914, from the Vancouver Island region is unclear. The colony form of this hydroid appears to have resembled that of *C. parasiticum* and other nominal species of the genus, but the species was referred to *Corydendrium* van Beneden, 1844a, with some doubt by Fraser (1914, 1937, 1946) because its gonophores had not been observed. According to Fraser (1914), hydranths of *C. fruticosum* have 12 to 15 tentacles, far fewer than the number usually present in *C. parasiticum*. *Corydendrium fruticosum* merits further study to determine its affinities.

KNOWN RANGE

Bermuda: first record.

Elsewhere: western Atlantic (Wedler, 1975); eastern Atlantic (Ritchie, 1908); Indian Ocean (Millard, 1975); western Pacific (Leloup, 1937); eastern Pacific (Fraser, 1938).

Genus *Turritopsis* McCrady, 1859b

Clavula Wright, 1859:106.

Turritopsis McCrady, 1859b:58.

Dendroclava Weismann, 1883:26.

Turritopsis Wedler and Larson, 1986:71 [incorrect subsequent spelling].

DIAGNOSIS

Clavid hydroids with stolonal or erect and irregularly branched colonies; hydrocaulus monosiphonic or polysiphonic. Branches adnate to hydrocaulus, or to other branches, over part of their length. Perisarc firm, termi-

nating near hydranth base. Hydranths elongate, tubular; tentacles filiform, scattered over much of hydranth calyx.

Gonophores free medusae, developing on pedicels or branches below hydranths. Medusa with eight or more simple, solitary marginal tentacles. Radial canals surrounded by mass of vacuolated cells at apex of stomach. Ocelli present.

TYPE SPECIES

Turritopsis nutricula McCrady, 1859b, by monotypy.

REMARKS

The familiar and widely used name *Turritopsis* McCrady, 1859b, is predated by the nearly forgotten *Clavula* Wright, 1859, and the two are considered synonyms here, as discussed below. Although McCrady's (1859b) paper proposing the generic name *Turritopsis* was presented orally before a meeting of the Elliott Society of Natural History of Charleston, South Carolina, on 1 December 1856, the proceedings of the meeting were not published until 1859. Only the year of publication is indicated on the cover of these proceedings. In the absence of other information, the date must be taken as the last day of the year [Art. 21c (ii)]. Wright's (1859) account of *Clavula*, in the July 1859 issue of the *Edinburgh New Philosophical Journal*, must be interpreted as having been published first. Application will be made to the ICZN to use its plenary powers [Art. 79] to suppress the virtually unused name *Clavula* Wright, 1859, in favour of the well-known *Turritopsis*.

Russell (1953) included *Turris neglecta* Lesson, 1843, as questionably conspecific with *Turritopsis nutricula*, the type species of *Turritopsis*. However, he noted that Lesson's medusa was inadequately described and its identity uncertain. The genus name *Turris* Lesson, 1843, is regarded here as a nomen dubium. Mueller (1766) had earlier applied the name *Turris* to a genus of the Mollusca, but Mueller's publication has been placed on the Official Index of Rejected and Invalid Works in Zoological Nomenclature by the ICZN (Opinion 701).

Turritopsis nutricula McCrady, 1859b

Figs. 5, 6

?*Turris neglecta*—Forbes, 1848:23; pl. 3, figs. 2a–i [medusa] [*Turris neglecta* Lesson, 1843, a nomen dubium].

Clavula gossii Wright, 1859:106; pl. 8, fig. 1.

Oceania (Turritopsis) nutricula McCrady, 1859b:56; pl. 4, figs. 1–10, 12–15, 28a; pl. 5, figs. 11, 16–18, 28b [medusa].

Turritopsis nutricula McCrady, 1859b:58 [medusa].

Turritopsis nutricula—L. Agassiz, 1862:347 [medusa] [incorrect subsequent spelling].

Oceania polycirrho Keferstein, 1863:26; pl. 2, figs. 11–13 [medusa].

Turritopsis polynema Haeckel, 1879:66 [medusa].

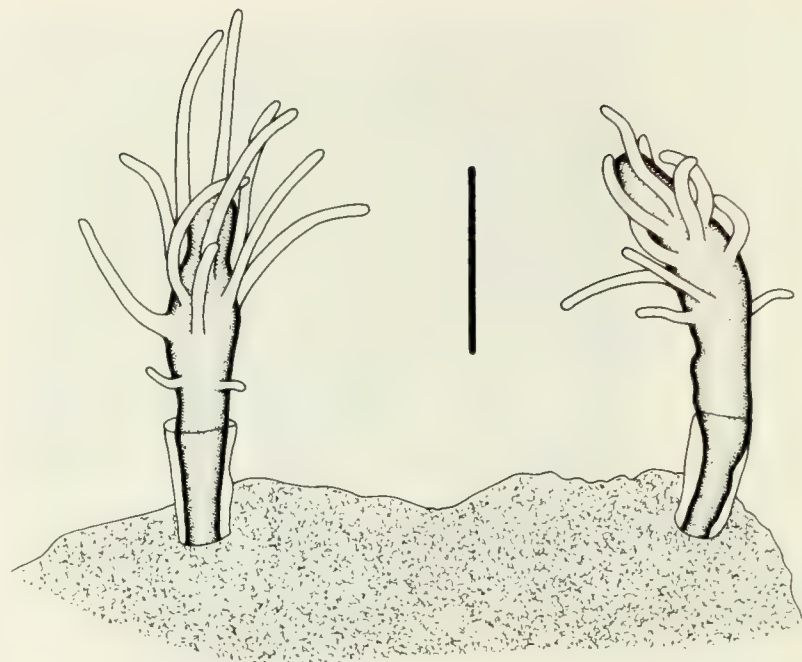


FIG. 5. *Turritopsis nutricula*, two hydranths arising from sponge substrate, ROMIZ B172. Scale equals 0.5 mm.

Modeeria multitentacula Fewkes, 1881:149; pl. 3, figs. 7–10 [medusa].

Modeeria nutricula—Fewkes, 1882:294; pl. 10, fig. 8 [medusa].

Modeeria (Turritopsis) nutricula—Fewkes, 1883:80 [medusa].

Modeeria multitentaculata—Brooks, 1883a:144 [medusa] [incorrect subsequent spelling].

Oceania nutricula—Brooks, 1883b:465 [medusa].

Modeeria nutricula—Brooks, 1886:388 [medusa] [incorrect subsequent spelling].

Turritopsis polycirrho—Hartlaub, 1897:480; pl. 16c, fig. 2 [medusa].

Turritopsis nutricula var. *pacifica* Maas, 1911:14; pl. 1, figs. 6–8; pl. 2, fig. 9 [medusa] [incorrect subsequent spelling].

Corydendrium nutricula—Krampe, 1935:11.

Turritopsis nutricula—Wedler and Larson, 1986:71 [incorrect subsequent spelling].

TYPE LOCALITY

Charleston Harbour, South Carolina, United States.

MATERIAL EXAMINED

Whalebone Bay, on sponge, –1 m, 7 September 1977, two colonies, 5 mm high, without gonophores, ROMIZ B162. Flatts Inlet, on sponge, –2 m, 5 March 1982, one colony, with hydranths extending 1.5 mm above sponge substrate, without gonophores, ROMIZ B172.

DESCRIPTION

Colonies erect, with hydrorhiza and much of hydrocaulus embedded in sponge, sparingly and irregularly branched, reaching 5 mm high. Hydrocaulus monosiphonic, branches

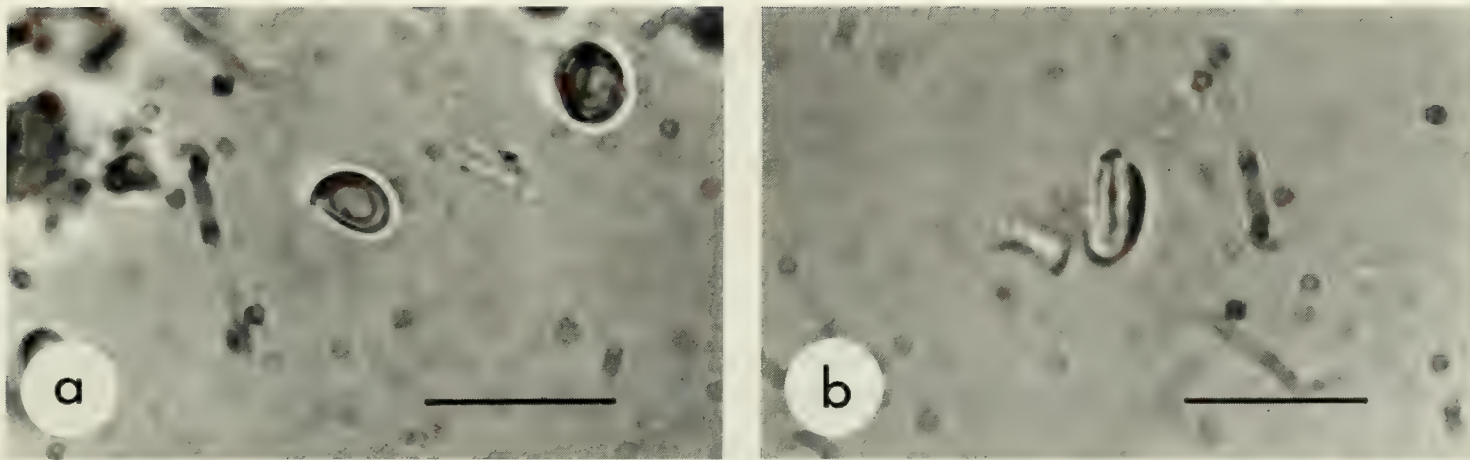


FIG. 6. *Turritopsis nutricula*, nematocysts of hydranth, ROMIZ B172. Scales equal 10 μm . a, Desmoneme. b, Heterotrichous microbasic eurytele.

adnate to hydrocaulus at their origin, curved outwards and becoming free distally; hydrocaulus and branches slender basally, 0.12 mm wide, gradually expanding in diameter distally, reaching 0.23 mm wide at base of hydranth. Perisarc moderately thick, clear to straw-coloured, with fine longitudinal creases and occasional wrinkles but no annulations, terminating below tentacles on hydranth base. Hydranths fusiform, reaching 0.9 mm long from base to tip, 0.2 mm wide. Tentacles filiform, 12 to 20 in number; about 4 in an irregular whorl distally, remainder scattered over distal two-thirds to three-quarters of hydranth, those at proximal end shorter and more slender than those at distal end. Hypostome elongate, conical.

Gonophores not seen.

Nematocysts—

Hydroids: desmonemes 4.6–4.8 μm \times 2.8–3.1 μm ; heterotrichous microbasic euryteles (small) 6.5–6.8 μm \times 3.1–3.3 μm .

REMARKS

Both hydroid and medusa stages of this species have long been known as *Turritopsis nutricula* McCrady, 1859b, but this binomen is actually predated by the virtually forgotten name *Clavula gossii* Wright, 1859. This nomenclatural problem arises in part from Wright's application of a separate name to the hydroid of a medusa he believed was conspecific with *Turris neglecta* Lesson, 1843. His contemporaries (e.g., Allman, 1864a, 1872; Hincks, 1868) realized that this contravened nomenclatural principles, and the name *C. gossii* was included in the synonymy of *T. neglecta* in their monographs. However, *T. neglecta* is now generally considered to be a nomen dubium. According to Russell (1953), Lesson's (1843) description of the medusa was inadequate for positive identification. Russell (1953) believed that the medusa described by Wright (1859) was identical with *T. nutricula*, and he included the name *C. gossii* as its junior synonym. This interpretation of relative priority was based on the widespread but mistaken belief (e.g., see A. Agassiz, 1865; Mayer, 1910;

Fraser, 1944; Russell, 1953; Kramp, 1961; Vervoort, 1968; Millard, 1975) that McCrady's (1859b) original description of *T. nutricula* was published in 1856, as discussed earlier (see p. 8). *Clavula gossii* has not been used as a senior synonym since it was instituted by Wright (1859), to my knowledge. Upon completion of this study, application will be made to the ICZN to use its plenary powers [Art. 79] to suppress the name *Clavula gossii* Wright, 1859, in favour of *Turritopsis nutricula* McCrady, 1859b.

I have followed Mayer (1910) and Russell (1953) in regarding *Oceania polycirra* Keferstein, 1863, *Turritopsis polynema* Haeckel, 1879, and *Modeeria multitentacula* Fewkes, 1881, as conspecific with this species.

Most authors have adopted the view of Stechow (1923a) that *Turritopsis dohrnii* (Weismann, 1883) is conspecific with *T. nutricula*. Hydroids of the two appear to differ in both colony form and habitat. Unlike colonies of *T. nutricula*, which are small with a monosiphonic hydrocaulus and usually found in shallow water, hydroids of *T. dohrnii* are larger with a polysiphonic hydrocaulus and known from deeper waters. Numerous specimens of *T. nutricula* have been observed from shallow-water habitats of Virginia (Calder, 1971) and South Carolina, including the type locality of Charleston Harbour (Calder and Hester, 1978). None of these hydroids were more than a few millimetres in height, and none had polysiphonic stems like *T. dohrnii*. Specimens of *T. nutricula* from nearshore waters of Bermuda resembled those examined from the American east coast in colony form. Both species are recognized as valid here because conclusive evidence that differences in colony form in the two may be environmentally induced is lacking. Young medusae have been described from both species, but a critical comparison of the two has not been made. The adult medusa of *T. dohrnii* is apparently unknown. Specimens identified as *T. dohrnii* (ROMIZ B139) were found on a brachyuran crab collected at a depth of 256 m off Castle Roads, Bermuda, during this study. However, the species has been excluded from this report, which includes hydroids from the upper 100 m only.

Turritopsis fascicularis Fraser, 1943b, collected from a depth of 118 fathoms (216 m) off Florida, appears to be identical in most respects with descriptions of *T. dohrnii*, and is regarded here as conspecific with the latter rather than with *T. nutricula*.

McCrary (1859b) mistook the parasitic actinula larva of the narcomedusa *Cunina octonaria* McCrary, 1859a, a frequent parasite on the medusa stage of *Turritopsis nutricula*, for the hydroid of this species. Excellent descriptions and illustrations of the hydroids and young medusae of *T. nutricula* were given by Brooks (1886).

KNOWN RANGE

Bermuda: Castle Harbour, medusa stage (Fewkes, 1883); in shallow inshore waters and on buoy chains (Calder, 1986).

Elsewhere: western Atlantic (Fraser, 1944); eastern Atlantic (Russell, 1953); Indian Ocean (Millard, 1975); western Pacific (Ralph, 1953); eastern Pacific (Fraser, 1948).

Genus *Rhizodendrium*, gen. nov.

DIAGNOSIS

Clavid hydroids with creeping hydrorhiza and sessile, elongate hydranths. Hydranths invested with thin perisarc proximally, occasionally forming a basal collar; tentacles filiform, as many as 20 or more, arranged in a more or less regular whorl around mouth, scattered or in several irregular whorls proximally, those of distal end longer and stouter than those proximally. Hypostome short, dome-shaped.

Gonophores fixed sporosacs, borne on hydrorhiza, spherical where known.

TYPE SPECIES

Rhizodendrium sterreri, sp. nov., designated herein.

ETYMOLOGY

The name is a combination of parts of the names *Rhizogeton* and *Corydendrium*, and is derived from the Greek words *rhiza* (root) and *dendron* (tree). The gender of the name is neuter.

REMARKS

Rhizodendrium, gen. nov., resembles *Rhizogeton* L. Agassiz, 1862, a genus established to accommodate the hydroid *R. fusiformis* L. Agassiz, 1862, from tide pools on the Massachusetts coast. L. Agassiz (1862) observed that *Rhizogeton* was similar to *Clava* Gmelin, 1790, but differed in having a thin covering of perisarc over the proximal part of the hydranth, a different hydranth shape, and gonophores on the hydrorhiza instead of the hydranth. Examination of type material of the type species, *R. fu-*

siformis (MCZ 52), confirmed Agassiz's original description of *Rhizogeton* in most respects, although the specimens were in rather poor condition. Nevertheless, it was apparent from this examination that *Rhizodendrium* can be held distinct from *Rhizogeton*, on the following characters. The hypostome is short and dome-shaped, instead of very elongate and conical. Tentacles number as many as 20 or more, instead of a maximum of 10. The tentacles are arranged in an oral whorl distally, and sometimes occur in more or less regular whorls elsewhere on the hydranth, instead of being decidedly scattered.

The shape of the hydranth in *Rhizodendrium* is much like that of *Turritopsis* McCrary, 1859b, and somewhat less like *Corydendrium* van Beneden, 1844a. The colony form is strictly stolonial, unlike that of *Turritopsis* and *Corydendrium*, and the gonophores arise from the stolon rather than from branchlets or pedicels. In *Tubiclava* Allman, 1863, gonophores were believed to arise in dense clusters from the hydranth, as in *Clava* (Allman, 1863, 1872), and not from the hydrorhiza, as in *Rhizodendrium*.

Two nominal species referred to *Rhizogeton*—*R. nudus* Broch, 1909, from Spitzbergen and *R. ezoense* Yamada, 1964, from Japan—are transferred here to *Rhizodendrium*. The only species thus remaining in *Rhizogeton* is *R. fusiformis*. *Rhizogeton nematophorus* Antsulevich and Polteva, 1986, from the USSR is a polymorphic species with nematophores, and seems sufficiently distinct to be recognized as a new genus.

Gonophores have not been observed in the type species of *Rhizodendrium*. However, those of *R. nudum* and *R. ezoense* are spherical rather than fusiform, as in *Rhizogeton*.

Rhizodendrium sterreri, sp. nov.

Figs. 7, 8

MATERIAL EXAMINED

Holotype: Whalebone Bay, on pelagic *Sargassum*, 2 September 1977, one colony, 2 mm high, without gonophores, ROMIZ B150. Paratype: Whalebone Bay, on pelagic *Sargassum*, 2 September 1977, one colony, 2 mm high, without gonophores, ROMIZ B305.

DESCRIPTION

Colonies stolonial, with a creeping reticular hydrorhiza bearing sessile hydranths. Perisarc smooth or wrinkled, moderately thin on hydrorhiza, extending up 1 mm or more over base of hydranth or restricted to little more than a short collar between hydranth and hydrorhiza. Hydranths elongate, cylindrical, up to 2.0 mm long, 0.3 mm wide, with as many as 20 or more tentacles. Tentacles filiform, 4 to 6 in an irregular whorl distally, remainder scattered over distal two-thirds to three-quarters of hydranth, those at distal end longer and stouter than those proximally.

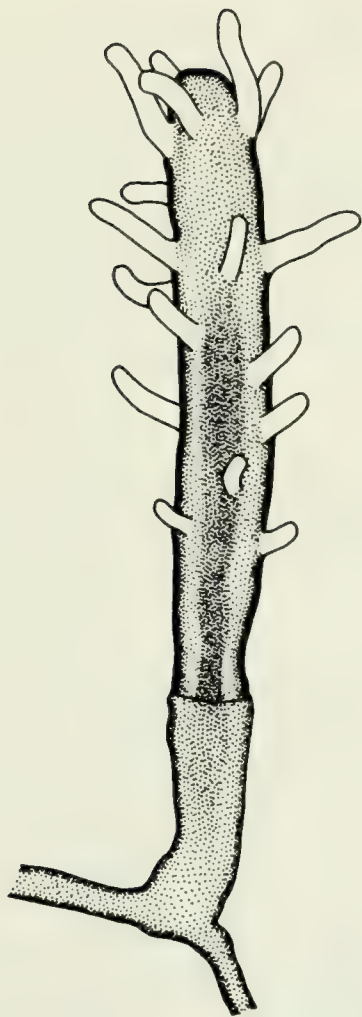


FIG. 7. *Rhizodendrium sterreri*, sp. nov., hydranth from holotype colony, ROMIZ B150. Scale equals 0.5 mm.

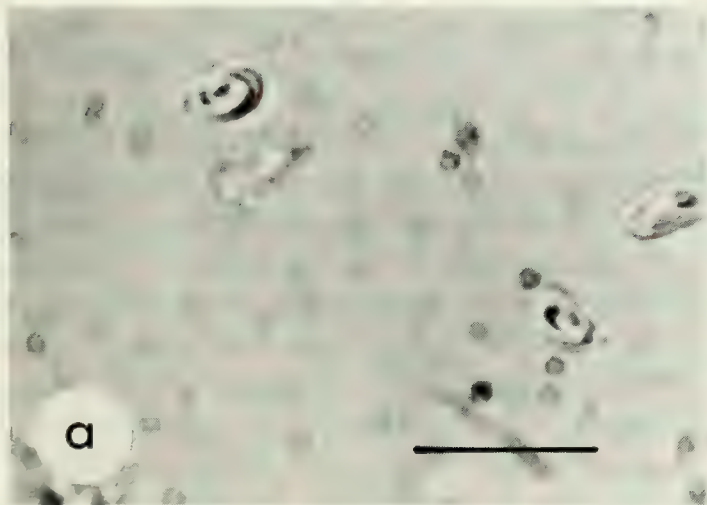


FIG. 8. *Rhizodendrium sterreri*, sp. nov., nematocysts of hydranth of holotype colony, ROMIZ B150. Scales equal 10 μm . a, Desmonemes. b, Heterotrichous microbasic eurytele.

Hypostome dome-shaped.

Gonophores lacking.

Nematocysts—

Hydroids: desmonemes 4.6–5.2 μm \times 2.8–3.1 μm ;
heterotrichous microbasic euryteles 6.6–7.6 μm \times 2.6–
2.9 μm .

REMARKS

Hydranths of *Rhizodendrium sterreri*, sp. nov., are distinct from L. Agassiz's (1862) description and illustrations of *Rhizogeton fusiformis* in having an irregular oral whorl of four to six tentacles instead of widely scattered distal ten-

tacles. They also differ from those of *R. fusiformis* in being much smaller, in possessing more tentacles, and in having longer and stouter tentacles at the distal than at the proximal end.

Rhizodendrium sterreri is very similar to descriptions of its two congeners, *R. nudum* (Broch, 1909) and *R. ezoense* (Yamada, 1964), in hydranth shape and size, as well as in tentacle number, size, and arrangement. However, in *R. sterreri* the base of the hydranth is sheathed in perisarc, as is obvious when the soft tissues are dissolved in sodium hypochlorite, whereas perisarc is reportedly absent from the base in *R. nudum* (Broch, 1909; Dons, 1913).

Hydranths of *R. sterreri* appear to be smaller than those of *R. ezoense*. Nematocyst data exist only from *R. sterreri*, but cnidome and nematocyst size are unlikely to differ much in these hydroids.

Rhizodendrium nudum has been reported several times from warm-water localities, but the records seem questionable on zoogeographic grounds. Ritchie (1910b) identified a hydroid from the Christmas Islands in the Indian Ocean as "*Rhizogeton nudum* Broch (?)," and indicated that his specimens lacked perisarc at the base of the hydranth. Rees and Thursfield (1965) expressed some doubt that Ritchie's specimens were identical with *R. nudum*, and suggested that they might represent a juvenile colony of another species. Mammen (1963) referred specimens from south India to *R. nudum*, but noted that they possibly belonged to another species. Millard and Bouillon (1974) reported *R. nudum* from Mozambique, and stated that their

record confirmed the existence of the species in the Indian Ocean. Their hydroids, unlike those of *R. nudum* described by Broch (1909), had a collar of perisarc at the base of the hydranth. Some, if not all, of these records may be based on specimens of *R. sterreri*.

In a study of the hydroids on pelagic *Sargassum* in the western Atlantic, Burkenroad (*in* Parr, 1939) mentioned finding a hydroid resembling the genus *Clava* Gmelin, 1790. It seems highly probable that it was *R. sterreri*.

ETYMOLOGY

The species is named after Dr Wolfgang Sterrer, former director of the Bermuda Biological Station, who provided the initial stimulus for this study.

KNOWN RANGE

Known only from the type locality.

Family Bougainvilliidae Lütken, 1850

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

Hippocrenidae McCrady, 1859a:158.

Nemopsidae L. Agassiz, 1862:345.

Dicorynidae Allman, 1864a:366.

Atractylidae Hincks, 1868:87.

Bimeridae Allman, 1872:294 (emended to Bimeriidae by Torrey, 1902).

Margelidae Haeckel, 1879:68.

Lizusidae Haeckel, 1879:80.

Thamnostomidae Haeckel, 1879:84.

Pachycordylini Cockerell, 1911:77.

Lizziinae Russell, 1953:144.

Clavopsellidae Thiel, 1962:249.

DIAGNOSIS

Hydroid colonies stolonial or erect, arising from a creeping hydrorhiza; growth monopodial with terminal hydranths. Perisarc on hydrorhiza and hydrocaulus of varied thickness, terminating at base of hydranth or extending over hydranth as a thin, filmy pseudohydrotheca. Hydranths cylindrical through fusiform to vasiform, with one or more whorls of filiform tentacles beneath conical to nipple-shaped hypostome.

Gonophores fixed sporosacs or free medusae, borne on hydrorhiza, hydrocaulus, branches, and pedicels, or on entire or reduced hydranths. Medusae bell-shaped with short manubrium; mouth circular; oral tentacles simple or dichotomously branched, inserted above mouth. Radial canals four. Marginal tentacles either solitary or in clusters, borne on 4, 8, or 16 tentacle bulbs. Ocelli present or absent. Gonads on manubrium, either forming a continuous ring or on interradial, adradial, or perradial axes.

REMARKS

Characters of hydroids belonging to the Bougainvilliidae Lütken, 1850, have recently been reviewed by Millard (1975). She noted (1975:71) that difficulties may be encountered when drawing dividing lines between hydroids of the Clavidae McCrady, 1859a, Hydractiniidae L. Agassiz, 1862, Eudendriidae L. Agassiz, 1862, and Bougainvilliidae. Medusae of the Bougainvilliidae have a number of characteristics, including the presence of oral tentacles, in common with those of the Cytaeididae L. Agassiz, 1862, and Russelliidae Kramp, 1957. Because of these similarities, Petersen (1979) placed the three families together in the superfamily Bougainvillioidea Lütken, 1850.

The family Bougainvilliidae, as currently classified, includes a seemingly disparate assemblage of hydroids and medusae. Russell (1953) recognized three subfamilies, the Bougainvilliinae Lütken, 1850, Lizziinae Russell, 1953, and Thamnostominae Haeckel, 1879, within the group. Four subfamilies are distinguished here among the bougainvilliids of Bermuda. In addition to the Bougainvilliinae, Bimeriinae Allman, 1872, and Pachycordylinae Cockerell, 1911, a new subfamily is recognized and defined, the Rhizorhagiinae. The subfamily Bimeriinae, as used here, is roughly equivalent in scope to the Thamnostominae as defined by Russell (1953). Neither hydroids nor medusae of the Lizziinae have been reported from Bermuda.

According to Haeckel (1879), the family-group names Margelidae, Lizusidae, and Thamnostomidae were first used in his 1877 manuscript "*Prodromus Syst. Medusen.*" However, this was an unpublished document (Kramp, 1961:400), and the three names were not published [Art. 8] until the appearance of the later work (Haeckel, 1879).

Subfamily Pachycordylinae Cockerell, 1911

DIAGNOSIS

Bougainvilliid hydroids with perisarc terminating at base of hydranth. Hydranths club-shaped through spindle-shaped to amphora-shaped; hypostome dome-shaped; tentacles in two or more close whorls.

Gonophores, where known, fixed sporosacs or free but sometimes degenerate medusae.

REMARKS

Whereas hydroids of the subfamily Bougainvilliinae Lütken, 1850, have tentacles arranged more or less in a single whorl on the hydranth, representatives of the tribe Pachycordylini Cockerell, 1911, herein elevated to the rank of subfamily, have tentacles in two or more whorls. Often these whorls are rather indistinct, and the tentacles may be essentially scattered. Nevertheless, the tentacles are restricted to a relatively narrow band on the hydranth and are thereby distinguishable from hydroids of the family Clavidae McCrady, 1859a.

Thiel (1962) established the nominal family Clavopsellidae for *Clavopsella* Stechow, 1919, and *Balella* Stechow, 1919, but Stechow (1922) had earlier constituted the family name Balellidae for the latter genus. Nutting (1905) applied the name Tubidendridae to the Balellidae, but this name is not available because it was not based on a name then valid for a contained genus [Art. 11f (i)(1)]. Little is known about the medusa stages of either of these two genera. All of the species heretofore included in *Clavopsella* possess fixed gonophores or degenerate medusae. Jäderholm (1919) observed medusa buds in *Balella mirabilis* (Nutting, 1905), but was unable to provide information beyond size and presence of short marginal tentacles. *Balella* is regarded here as closer to the Clavidae than to the Bougainvilliidae because tentacles are present on the proximal as well as on the distal part of the hydranth. Accordingly, the family Balellidae is recognized here as a valid taxon. The nominal genus *Clavopsella* is regarded as a junior synonym of *Pachycordyle* Weismann, 1883, in this report, and the name Pachycordylinae has priority over Clavopsellinae.

The affinities of the genus *Silhouetta* Millard and Bouillon, 1973, are uncertain, but it has been included here in the Pachycordylinae because of the scattered arrangement of the tentacles and the peculiar domelike shape of the hypostome.

Representatives of the Pachycordylinae appear intermediate between bougainvilliids and clavids, but they are retained in the Bougainvilliidae here based on characteristics of the medusa of *Silhouetta*. Medusa buds of *Silhouetta uvacarpa* Millard and Bouillon, 1973, were described as being "without doubt" bougainvilliid in character by Millard and Bouillon (1973, 1975).

Genus *Millardiana* Wedler and Larson, 1986

Millardiana Wedler and Larson, 1986:90.

DIAGNOSIS

Hydroid colonies mostly stolonial, with perisarc terminating at hydranth base. Hydranth thick, clavate; tentacles filiform, scattered around distal end of hydranth.

Gonophores sporosacs, borne on gonozooids beneath whorl of four to five tentacles.

TYPE SPECIES

Millardiana longitentaculata Wedler and Larson, 1986, by monotypy.

REMARKS

Millardiana was established by Wedler and Larson (1986) for a hydroid resembling *Pachycordyle* Weismann, 1883, but differing from that genus in having gonophores on gonozooids with four to five tentacles instead of zooids with the normal complement of tentacles. They referred the genus to the family Bougainvilliidae Lütken, 1850. It is tentatively referred here to the Pachycordylinae Cockerell, 1911, although the presence of gonozooids is anomalous. *Millardiana* is a monotypic genus.

Millardiana longitentaculata Wedler and Larson, 1986

Figs. 9, 10

Millardiana longitentaculata Wedler and Larson, 1986:90; figs. 7Ba,b; pl. 1, fig. 8.

TYPE LOCALITY

La Parguera, Puerto Rico.

MATERIAL EXAMINED

Green Bay, Harrington Sound, on shells of *Cerithium literatum* from *Cladophora* bed, -2.5 m, 21 September 1984, colonies without gonophores on four shells, ROMIZ B371.

DESCRIPTION

Colonies stolonial, with hydrorhiza adhering to gastropod shells. Pedicels very short, each bearing a terminal hydranth. Perisarc thin, smooth or slightly wrinkled, terminating at base of hydranth; pseudohydrotheca absent. Hydranths clavate to ovate to nearly fusiform, reaching 1.2 mm long, 0.34 mm wide at widest point, distal end with about 10 to 25 long, filiform tentacles in two to three close whorls, those of one whorl more or less alternating with those of adjacent whorls, proximal tentacles often

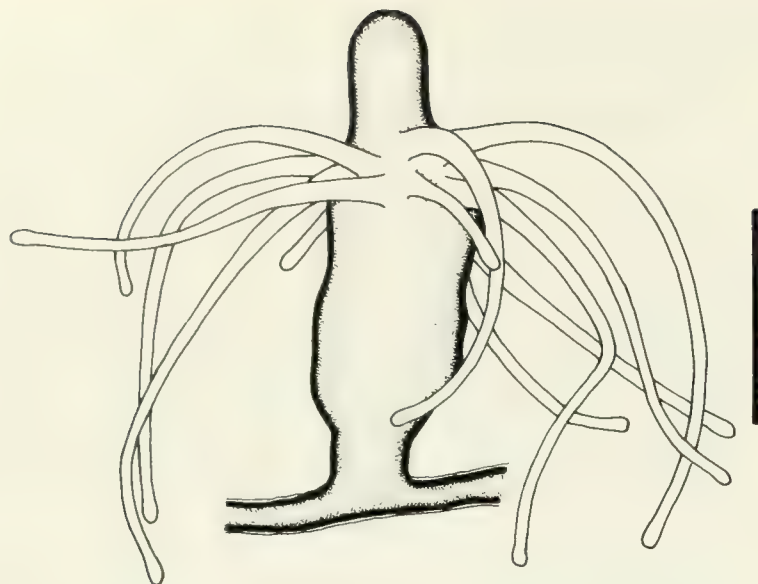


FIG. 9. *Millardiana longitentaculata*, hydranth, ROMIZ B371. Scale equals 0.5 mm.

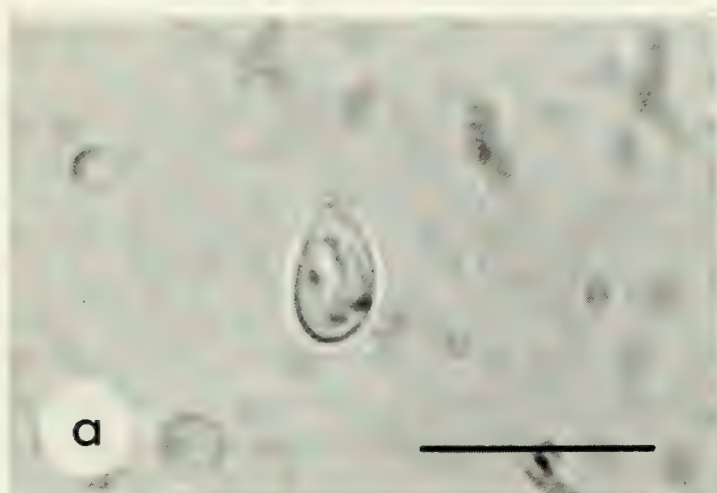


FIG. 10. *Millardiana longitentaculata*, nematocysts of hydranth, ROMIZ B371. Scales equal 10 μm . *a*, Desmoneme. *b*, Heterotrichous microbasic eurytele.

smaller than distal ones. Hypostome prominent, extensible, and proboscis-like. Colour of hydranth deep red in live material.

Gonophores not seen.

Nematocysts—

Hydroids: desmonemes 5.6–6.4 μm \times 3.4–3.8 μm ; heterotrichous microbasic euryteles 7.6–10.4 μm \times 2.8–3.8 μm .

REMARKS

Although superficially similar in colony form to *Pachycordyle napolitana* Weismann, 1883, *Millardiana longitentaculata* Wedler and Larson, 1986, is clearly a distinct species. Characteristics of the latter distinguishing it from the former include the intense red pigmentation of the hydranths and the extremely long tentacles and hypostome. According to Wedler and Larson (1986), gonophores are sporosacs borne on polyps having only four to five tentacles. From their description and illustration, these remarkable polyps somewhat resemble the gonozooids of the family Hydractiniidae L. Agassiz, 1862, and are atypical of hydroids of the Bougainvilliidae Lütken, 1850.

KNOWN RANGE

Bermuda: first record.

Elsewhere: western Atlantic (Wedler and Larson, 1986).

Genus *Pachycordyle* Weismann, 1883

Pachycordyle Weismann, 1883:87.

?*Parvanemus* Mayer, 1904:6.

Pachycordile Lo Bianco, 1909:544 [incorrect subsequent spelling].

Clavopsella Stechow, 1919:21.

DIAGNOSIS

Bougainvilliid hydroids with the characters of the subfamily.

Gonophores fixed sporosacs or free but degenerate medusae. Medusa ephemeral, pyriform, without mouth, radial canals, marginal tentacles, oral tentacles, or ocelli.

TYPE SPECIES

Pachycordyle napolitana Weismann, 1883, by monotypy.

REMARKS

Pachycordyle napolitana Weismann, 1883, and *P. weismanni* Hargitt, 1904a, type species of the nominal genera *Pachycordyle* Weismann, 1883, and *Clavopsella* Stechow, 1919, respectively, are regarded here as conspecific following Picard (1958) and Morri (1981). The name *Clavopsella* can therefore be regarded as a junior subjective synonym of the name *Pachycordyle*, resurrected here.

Picard (1958) and Morri (1981) included *P. napolitana* in the genus *Cordylophora* Allman, 1844. *Pachycordyle* differs from *Cordylophora* in having tentacles arranged in two or more close whorls rather than scattered over much of the hydranth.

Stechow (1919) proposed the generic names *Clavopsella* and *Balella* for species of Filifera having more than one whorl of tentacles on the hydranth. Unlike hydroids of *Balella*, which have two widely separated whorls of tentacles, hydroids of *Clavopsella* (= *Pachycordyle*) have from two to four close whorls of tentacles. This characteristic is shared with *Silhouetta* Millard and Bouillon, 1973, a genus with well-developed medusa buds instead of fixed sporosacs or free but degenerate medusae.

The nominal genus *Clavopsella* was initially referred to the family Bougainvilliidae Lütken, 1850, by Stechow (1919), but was later transferred to the Clavidae McCrady, 1859a, by Stechow (1923a). Thiel (1962) placed *Clavopsella* with *Balella* in a new family, the Clavopsellidae, a family he considered intermediate between the Clavidae and the Bougainvilliidae. As noted above, *Balella* is regarded as closer to the Clavidae than the Bougainvilliidae and is returned here to the family Balellidae. *Clavopsella* (i.e., *Pachycordyle*) is classified among the Bougainvilliidae in this report, following Millard (1975) and Bouillon (1985).

The definition of *Pachycordyle* adopted above differs from that used by Thiel (1962) and Millard (1975) for *Clavopsella*. They included *Clavopsella quadrangularia* Thiel, 1962, and *Rhizorhagium navis* Millard, 1959b, nominal species likely referable to *Aselomaris* Berrill, 1948, in *Clavopsella*. *Aselomaris*, in my opinion, belongs in the subfamily Bougainvilliinae rather than in the Pachycordylinae.

Parvanemus Mayer, 1904, established for a species (*P. degeneratus* Mayer, 1904) whose medusa lacked tentacles, radial canals, marginal sense organs, and presumably a ring canal, was included by Mayer (1910) in the synonymy of *Pachycordyle*.

Pachycordyle napolitana Weismann, 1883

Figs. 11, 12

Pachycordyle napolitana Weismann, 1883:87; pl. 6, fig. 6.

Pachycordyle weismanni Hargitt, 1904a:553; pl. 21, figs. 1–8.

Cordylophora annulata Motz-Kossowska, 1905:66; fig. 5.

Pachycordyle neapolitana—Motz-Kossowska, 1905:70 [incorrect subsequent spelling].

Perigonimus neapolitanus—Motz-Kossowska, 1905:75; fig. 8 [incorrect subsequent spelling] [not *Perigonimus neapolitanus* Hargitt, 1904a].

Pachycordyle weismanni—Lo Bianco, 1909:544 [incorrect subsequent spelling].

Tubiclava annulata—Stechow, 1912:343; pl. 13, fig. 8.

Clavopsella weismanni—Stechow, 1919:22.

Clavopsella annulata—Stechow, 1921a:250.

Rhizorhagium (Pachycordyle) napolitanum—Stechow, 1923a:56.

Cordylophora neapolitana—Picard, 1958:189 [incorrect subsequent spelling].

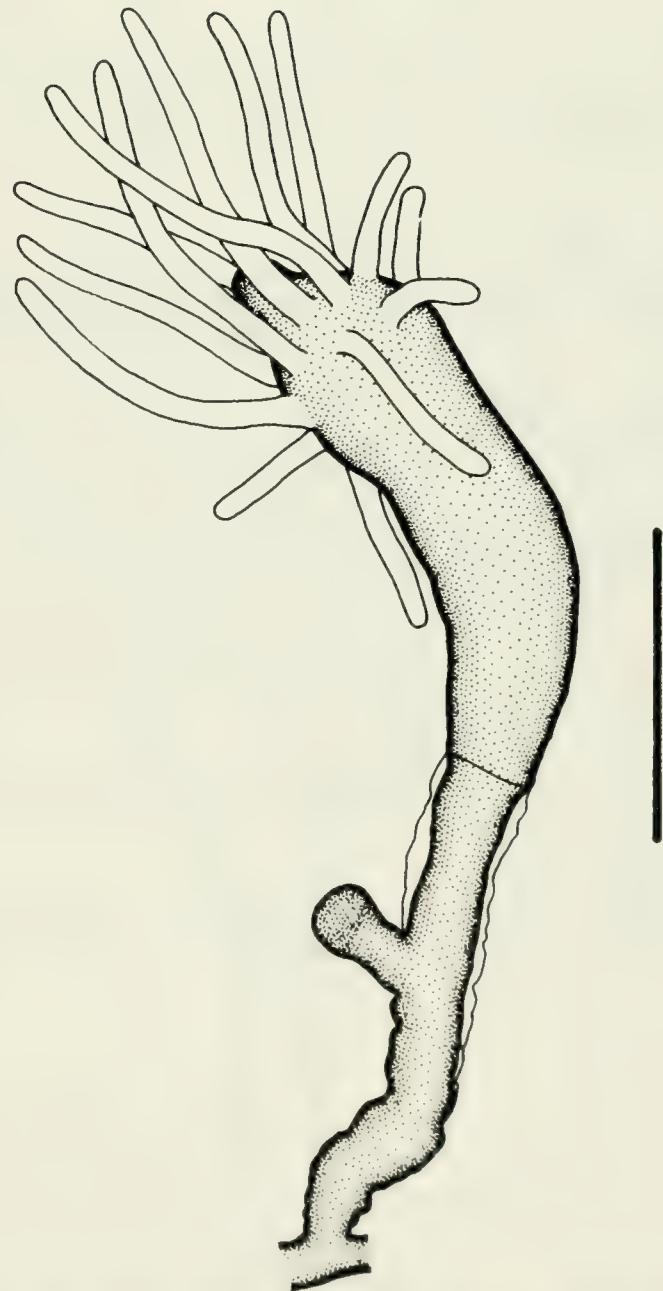


FIG. 11. *Pachycordyle napolitana*, hydranth, ROMIZ B154. Scale equals 0.5 mm.

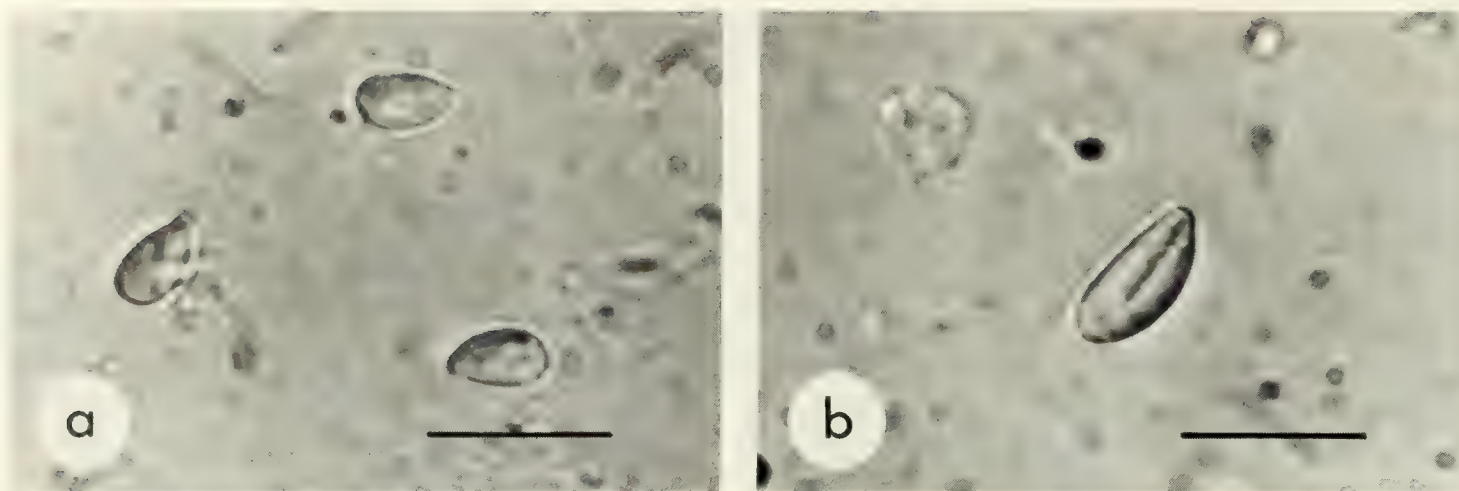


FIG. 12. *Pachycordyle napolitana*, nematocysts of hydranth, ROMIZ B154. Scales equal 10 μm . a, Desmonemes. b, Heterotrichous microbasic eurytele.

TYPE LOCALITY

Naples, Italy.

MATERIAL EXAMINED

Green Bay, Harrington Sound, on gastropod from *Thalassia* bed, - 2 m, 8 March 1982, one colony, 2 mm high, with an incipient gonophore, ROMIZ B154.

DESCRIPTION

Colony stolonial, with reticular hydrorhiza growing over a gastropod shell. Pedicels of varied length but usually less than 1 mm long, slender basally, widening distally, bearing a terminal hydranth. Perisarc moderately thin, wrinkled throughout, terminating at base of hydranth; pseudohydrotheca absent. Hydranths club-shaped to spindle-shaped, reaching 1.0 mm long, 0.45 mm wide at widest point, distal end of fully developed hydranth with about 16 to 20 filiform tentacles in three or four close whorls, tentacles of one whorl alternating with those of adjacent whorls, proximal tentacles often smaller than distal ones. Hypostome dome-shaped.

Incipient gonophore(?) arising singly from hydranth pedicel on short, wrinkled stalk, completely invested with perisarc. Sex indeterminable.

Nematocysts—

Hydroids: desmonemes 5.6–6.0 μm \times 3.0–3.6 μm ; heterotrichous microbasic euryteles 9.1–9.6 μm \times 3.8–4.5 μm .

REMARKS

Thiel (1962) distinguished *Clavopsella weismanni* (Hargitt, 1904a) and *C. annulata* (Motz-Kossowska, 1905) on the basis of hydroid colony shape and presence or absence of radial canals in the medusa. According to his key, the hydrocaulus of *C. weismanni* is slightly branched and its medusa has radial canals, whereas in *C. annulata* the hydrocaulus is unbranched and radial canals are lacking.

Branching of the hydrocaulus is not regarded here as particularly reliable in separation of the two. Radial canals were not reported in the degenerate and ephemeral medusae of either nominal species in earlier descriptions (Hargitt, 1904a; Motz-Kossowska, 1905; Stechow, 1919, 1923a). A vestigial ring canal, observed in the medusa of *Pachycordyle weismanni* by Hargitt (1904a), was not reported in *P. annulata* by Motz-Kossowska (1905). Hydroids and degenerate medusae of both nominal species appear similar based on existing descriptions, and the two have been regarded conspecific by Picard (1958), Morri (1981), and others. I have followed Picard and Morri in regarding both of these as conspecific with *P. napolitana* Weismann, 1883. Picard (1958) included Mediterranean records of *Tubiclava fruticosa* Allman, 1871, under this species as well.

Material from Bermuda discussed here closely resembles specimens (ROMIZ B695) and published descriptions of *Pachycordyle napolitana* from the Mediterranean, and has been identified as such. However, specimens with well-developed gonophores are needed for more definitive identification.

KNOWN RANGE

Bermuda: first record.

Elsewhere: western Atlantic (Wedler and Larson, 1986); Mediterranean Sea (Morri, 1981).

Genus *Silhouetta* Millard and Bouillon, 1973

Silhouetta Millard and Bouillon, 1973:25.

DIAGNOSIS

Hydroid colonies stolonial or erect, with firm perisarc terminating at hydranth base. Hydranths large, amphora-shaped; tentacles filiform, in two or more close whorls, those of one whorl alternating with those of adjacent whorls.

Gonophores free medusae, arising in clusters from stem or branches. Medusae at liberation with four simple or dichotomously branched oral tentacles arising above mouth. Tentacle bulbs four; marginal tentacles four, solitary. Ocelli present.

TYPE SPECIES

Silhouetta uvacarpa Millard and Bouillon, 1973, by monotypy.

REMARKS

The genus *Silhouetta* was founded by Millard and Bouillon (1973) to accommodate the hydroid *S. uvacarpa* Millard and Bouillon, 1973, from the Seychelles. Although they recognized the similarity of their hydroid to specimens previously referred to *Clavopsella* Stechow, 1919, a new genus was established because well-developed medusa buds were present instead of fixed sporosacs or degenerate medusae.

Silhouetta appears to be distinct from *Clavopsella*, and its senior synonym *Pachycordyle* Weismann, 1883, even if gonophore type is not regarded as a valid generic character. Although hydranth shape is typically variable in bougainvilliid hydroids, all the hydranths of *S. uvacarpa* from Bermuda, like those illustrated by Millard and Bouillon (1973) from the Seychelles, had a characteristic amphora shape.

Silhouetta uvacarpa Millard and Bouillon, 1973

Figs. 13, 14

Silhouetta uvacarpa Millard and Bouillon, 1973:25; figs. 3A–D; pls. 2, 3.

Silhouetta puertoricensis Wedler and Larson, 1986:91; figs. 9Aa,b.

TYPE LOCALITY

Silhouette, Seychelles.

MATERIAL EXAMINED

Sailor's Choice Cave, near Walsingham Pond, Hamilton Parish, –1.0 m, 6 July 1982, 16 colonies, 1.0–2.3 cm high, without gonophores, coll. T. Iliffe, ROMIZ B138.

DESCRIPTION

Colonies initially stolonial, later erect, reaching 2.3 cm high, arising from a creeping hydrorhiza. Hydrocaulus monosiphonic in young colonies, polysiphonic in older ones, irregularly branched; primary branches unbranched or irregularly branched; hydrocaulus and branches curved and twisted, imparting a straggly appearance to colony. Perisarc irregularly wrinkled and creased but with annulations absent, moderately thick and golden in colour basally, becoming progressively thinner and more colourless

distally, terminating at hydranth base. Hydranth amphora-shaped, with conical hypostome, wrinkled basally, reaching 1.5 mm long from base to tip of hypostome, up to 0.9 mm wide at widest point, bearing filiform tentacles distally. Young hydranths with about 8 tentacles in two whorls; older hydranths with up to 24 tentacles in four rather close whorls, tentacles of one whorl alternating with those of adjacent whorls, proximal tentacles often shorter and more slender than distal ones.

Gonophores lacking.

Nematocysts—

Hydroids: desmonemes $6.7\text{--}7.6\ \mu\text{m} \times 3.7\text{--}3.9\ \mu\text{m}$; heterotrichous microbasic euryteles $9.6\text{--}12.7\ \mu\text{m} \times 4.4\text{--}5.6\ \mu\text{m}$.

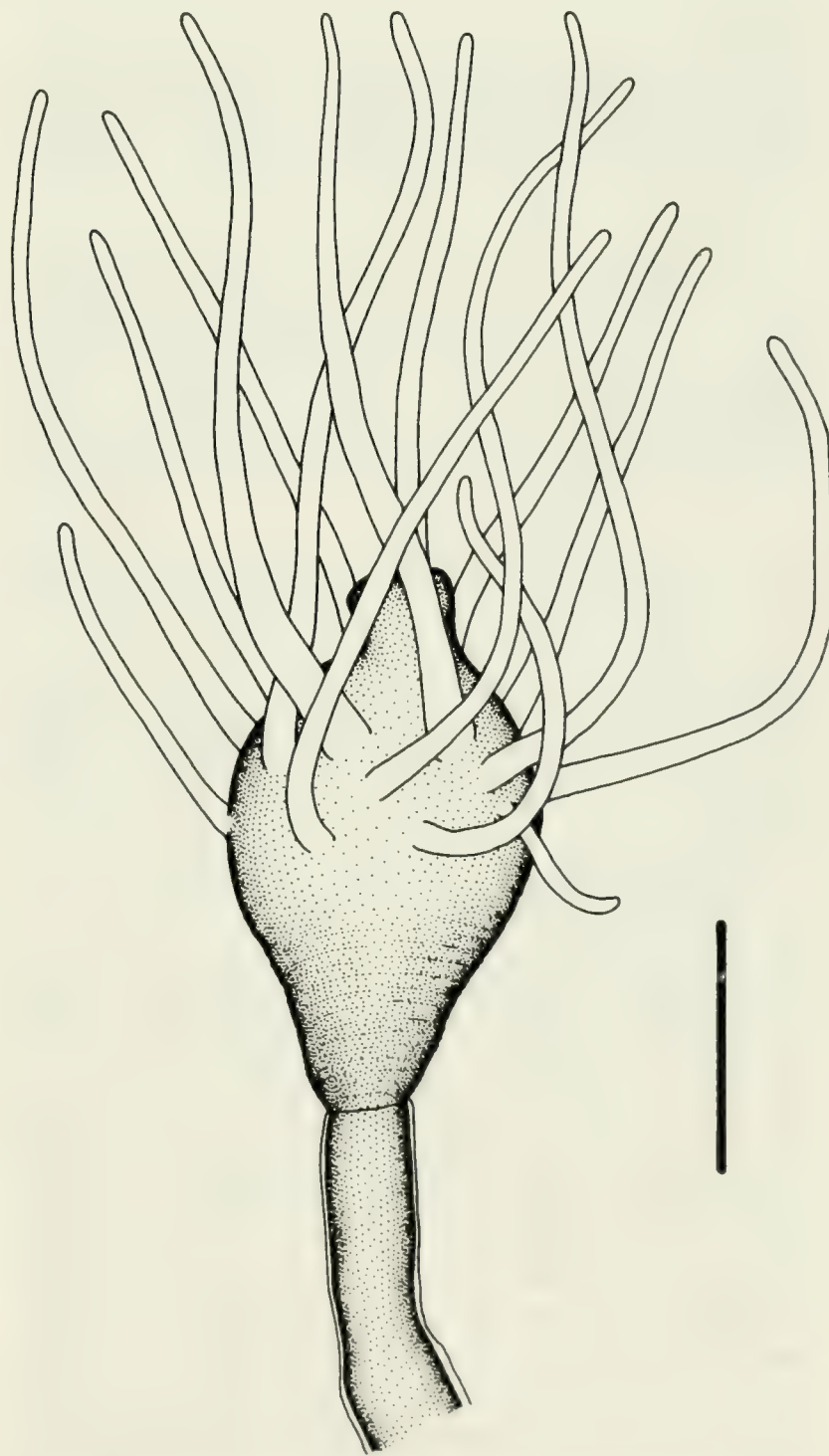


FIG. 13. *Silhouetta uvacarpa*, hydranth, ROMIZ B138. Scale equals 0.5 mm.

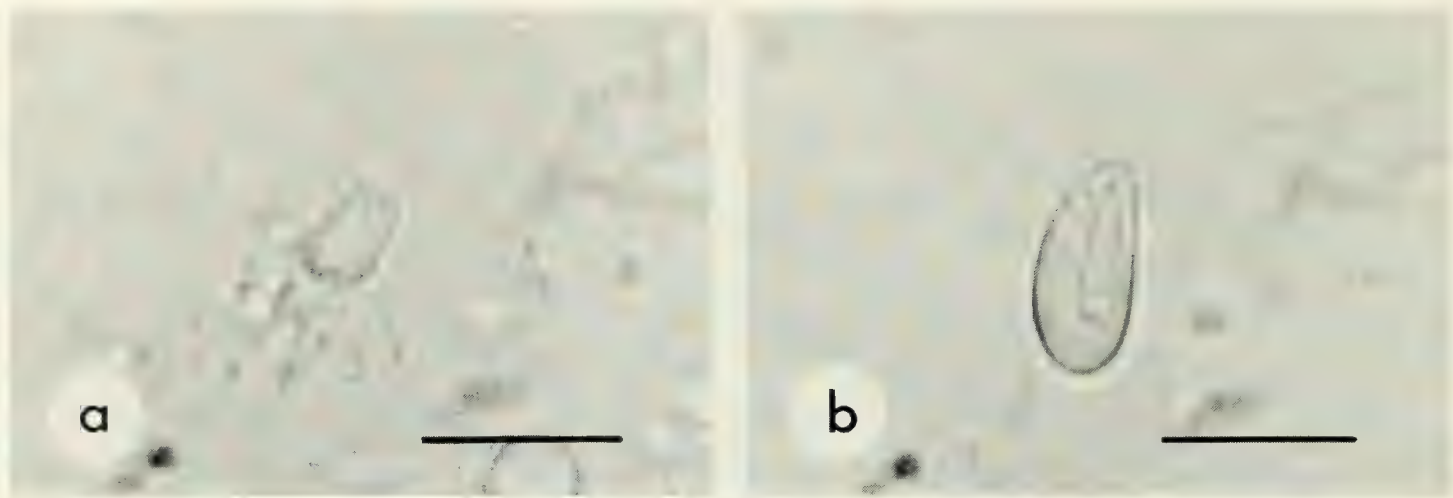


FIG. 14. *Silhouetta uvacarpa*, nematocysts of hydranth, ROMIZ B138. Scales equal 10 μm . *a*, Desmoneme. *b*, Heterotrichous microbasic eurytele.

REMARKS

These hydroids lacked gonophores, but resembled the original description of *Silhouetta uvacarpa* Millard and Bouillon, 1973, in all other major respects, including nematocyst complement and size.

Fully developed medusa buds and newly liberated medusae of *Silhouetta uvacarpa* were described by Millard and Bouillon (1973, 1975). Large medusa buds bore four marginal tentacle bulbs, each with a single tentacle and black ocellus, and simple oral tentacles inserted above the mouth. Newly liberated medusae were 0.9 mm high and

1.0 mm wide, with four dichotomously branched oral tentacles.

Silhouetta puertoricensis, described by Wedler and Larson (1986) from Puerto Rico, is regarded here as conspecific with *S. uvacarpa*. Wedler and Larson established a new species for their material because oral tentacles could not be seen in the medusa buds.

KNOWN RANGE

Bermuda: first record.

Elsewhere: western Atlantic (Wedler and Larson, 1986); Indian Ocean (Millard and Bouillon, 1973).

Subfamily Rhizorhagiinae, subf. nov.

DIAGNOSIS

Bougainvilliid hydroids with perisarc extending as a pseudohydrotheca around hydranth. Hydranths vasiform; hypostome nipple-shaped; tentacles in two or more close whorls.

Gonophores, where known, fixed sporosacs.

REMARKS

The hypostome of the Rhizorhagiinae, subf. nov., is elongate and nipple-shaped instead of dome-shaped as in the Bougainvilliinae Lütken, 1850, Pachycordylinae Cockerell, 1911, and Bimeriinae Allman, 1872. Moreover, the hydranths are decidedly vasiform, resembling those of the Eudendriidae L. Agassiz, 1862, as much or more than those of other subfamilies of the Bougainvilliidae. This is not to imply that the subfamily is especially close to the Eudendriidae. Unlike in eudendriids, in the Rhizorhagiinae the hypostome is not flared or knob-shaped and gonophores do not arise from the hydranths. Like the Pachycordylinae, this subfamily has hydroids with tentacles arranged in two or more close whorls on the hydranth. A pseudohydrotheca is present, but it is not as extensively developed as in the

Bimeriinae, in which perisarc extends as a sheath over the bases of the tentacles and the hypostome.

Included in the subfamily are the genera *Rhizorhagium* M. Sars, 1874, and *Parawrightia* Warren, 1907. Although only *Parawrightia* is represented in Bermuda, *Rhizorhagium* was chosen as the type genus of the taxon because it is better known [Recommendation 64A].

Genus *Parawrightia* Warren, 1907

Parawrightia Warren, 1907:187.

DIAGNOSIS

Bougainvilliidae with branched or unbranched hydrocaulus; perisarc extending as a distinct pseudohydrotheca over base of hydranth nearly to tentacles. Hydranth vasiform; manubrium nipple-shaped; tentacles in several close, alternating whorls.

Gonophores fixed sporosacs, enveloped in perisarc, borne on hydrocaulus and branches.

TYPE SPECIES

Parawrightia robusta Warren, 1907, by monotypy.

REMARKS

Parawrightia Warren, 1907, is recognized as a valid name here, although it has not been widely adopted even for its type species. It bears some resemblance to *Wrightia* Allman, 1872, but the name of the latter is an invalid junior homonym of *Wrightia* L. Agassiz, 1862, a name given to a genus of thecate hydrozoans. Berrill (1948) instituted the new genus *Aselomaris* to accommodate *Atractylis arenosa* Alder, 1862, type species of *Wrightia* Allman, 1872, by monotypy, and for a new species, *A. michaeli*. Neither of the two species originally included was designated by Berrill (1948) as type of his new nominal genus. *Atractylis arenosa* is herein designated as type species of *Aselomaris*. *Wrightia* Allman, 1872 (not *Wrightia* L. Agassiz, 1862) thus becomes an objective synonym of *Aselomaris*, having the same type species. *Aselomaris* differs from *Parawrightia* in having fusiform to clavate hydranths with a dome-shaped hypostome, like hydranths of *Bougainvillia* Lesson, 1830, instead of vasiform hydranths with a nipple-shaped hypostome. Hydranths of many bougainvilliid hydroids are admittedly variable in shape, depending upon degree of expansion, but those of *Parawrightia* are quite consistent in form and clearly distinct from those of *Aselomaris*.

Stechow (1923a), Millard (1975), and Bouillon (1985) included *Parawrightia* as a synonym of *Rhizorhagium* M. Sars, 1874. It is improbable that *R. roseum* M. Sars, 1874, and *P. robusta* Warren, 1907, type species of *Rhizorhagium* and *Parawrightia* respectively, are congeneric. *Rhizorhagium* differs in having simple unbranched stems, tentacles arranged in a single whorl on the hydranth, and gonophores on the hydrorhiza or rhizocaulome rather than on the hydrocaulus (Rees, 1938). Therefore, both genera are recognized as valid here. The name *Rhizorhagium* has on occasion (e.g., Rees, 1938; Millard, 1975) been attributed to M. Sars (1877), but it was actually made available earlier by M. Sars in G. O. Sars (1874). Millard (1975) and Bouillon (1985) mistakenly included *Wrightia* Allman, 1872, as a synonym of *Rhizorhagium*; instead, it is an objective synonym of *Aselomaris*, as noted above.

Stechow (1923a) regarded *Parawrightia* and *Pachycordyle* Weismann, 1883, as synonyms. The genus *Pachycordyle* is poorly understood at present, but it seems highly unlikely that it is congeneric with *Parawrightia*. *Pachycordyle weismanni* Hargitt, 1904a, type species of the nominal genus *Clavopsella* Stechow, 1919, liberates free but degenerate medusae (Hargitt, 1904a; Brinckmann-Voss, pers. comm., 1986); its hydranths are claviform to fusiform, and its hypostome is subconical. Based on such differences, I conclude that *Parawrightia* and *Clavopsella*

are distinct. In this report, *Clavopsella* is regarded as identical with *Pachycordyle*.

Parawrightia shows some remarkable similarities to *Cordylophora* Allman, 1844, a genus usually included in the family Clavidae McCrady, 1859a. In both genera, colonies are typically branched, gonophores are fixed sporosacs occurring on hydrocaulus and branches, and hydranths are similar in shape. Nevertheless, tentacles are somewhat less scattered and a pseudohydrotheca is present in *Parawrightia*, and this genus is considered distinct from *Cordylophora* here.

Finally, *Parawrightia* differs from *Silhouetta* Millard and Bouillon, 1973. Unlike in *Silhouetta*, gonophores of *Parawrightia* are solitary, fixed sporosacs instead of grape-like clusters of medusa buds that become free medusae. In addition, hydranths are vasiform in *Parawrightia* instead of spindle-shaped.

Parawrightia was founded by Warren (1907) for a single new nominal species, *Parawrightia robusta*, and is still monotypic. It seems debatable whether the genus should be referred to the Bougainvilliidae Lütken, 1850, although it is discussed under that family here.

Parawrightia robusta Warren, 1907

Figs. 15, 16

Parawrightia robusta Warren, 1907:187; figs. 1, 2B, 3, 4; pls. 33, 34.

Rhizorhagium robustum—Millard, 1966:452.

Garveia robusta—Wedler and Larson, 1986:90; figs. 8Ba–d; pl. 1, fig. 7.

TYPE LOCALITY

Natal, South Africa.

MATERIAL EXAMINED

Flatts Inlet, on rocks and stems of *Eudendrium carneum*, –1 m, 9 July 1983, several colonies, up to 1.5 cm high, with male gonophores, ROMIZ B357. Flatts Inlet, on *Thyrosocyphus marginatus*, –2 m, 4 July 1983, one colony, up to 1 cm high, with male gonophores, ROMIZ B358.

DESCRIPTION

Colonies stolonial or erect, reaching 1.5 cm high, arising from a creeping hydrorhiza. Hydrocaulus monosiphonic, slender, unbranched or irregularly branched; hydrocaulus and branches usually somewhat crooked; colonies tangled and straggly. Perisarc fairly thick, smooth or wrinkled, extending as a thin pseudohydrotheca over hydranth base nearly to tentacles. Hydranths vasiform, about 1.1 mm long from base to tip of hypostome, 0.5 mm wide at widest point; hypostome conical, elongate. Tentacles filiform, tapering gradually from base to tip, up to about 26 in num-

ber, arranged in two or three close whorls, those of one whorl more or less alternating with those of adjacent whorls, proximal tentacles smaller than distal ones.

Gonophores fixed sporosacs, completely enveloped in thin perisarc, arising singly on short, smooth pedicels from hydrocaulus, or from hydrocaulus and branches.

Nematocysts—

Hydroids: desmonemes $4.8\text{--}5.3\ \mu\text{m} \times 2.7\text{--}2.9\ \mu\text{m}$; heterotrichous microbasic euryteles $7.3\text{--}7.5\ \mu\text{m} \times 3.7\text{--}3.8\ \mu\text{m}$.

REMARKS

Warren (1907) described this hydroid as a new genus and species, naming it *Parawrightia robusta*. Millard (1966, 1975), without comment, placed it in the genus *Rhizorhagium* M. Sars, 1877. According to Rees (1938), *Rhizorhagium* has simple, unbranched stems and tentacles arranged in a single whorl. Warren's hydroid, with typically branched hydrocauli and tentacles in several whorls, is recombined here with *Parawrightia*.

In Bermuda, the hydroid was found on ceilings of cavities in the rocky shoreline near the bridge at Flatts Inlet.

KNOWN RANGE

Bermuda: first record.

Elsewhere: western Atlantic (Florez Gonzalez, 1983); Indian Ocean (Millard, 1975).

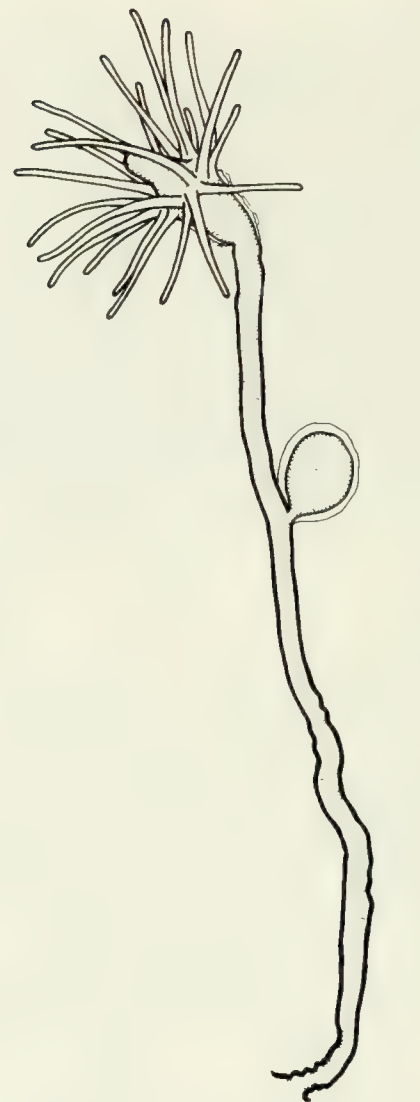


FIG. 15. *Parawrightia robusta*, hydranth and gonophore, ROMIZ B357. Scale equals 1 mm.

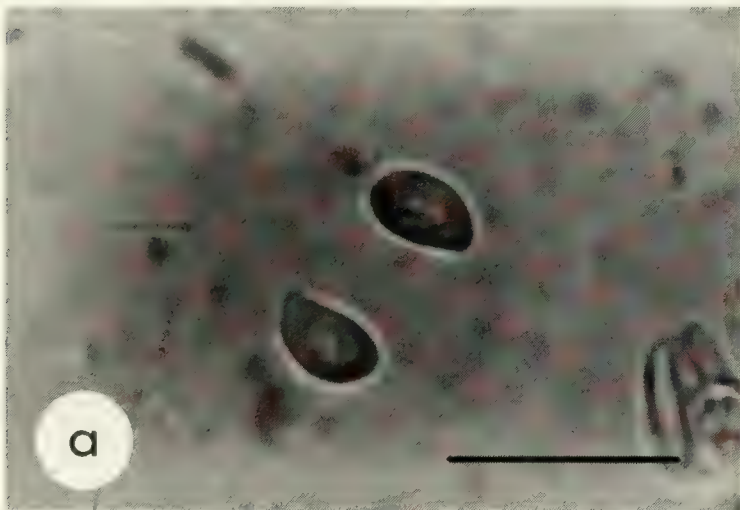


FIG. 16. *Parawrightia robusta*, nematocysts of hydranth, ROMIZ B357. Scales equal $10\ \mu\text{m}$. *a*, Desmonemes. *b*, Heterotrichous microbasic eurytele.

Subfamily Bimeriinae Allman, 1872

DIAGNOSIS

Bougainvilliid hydroids with perisarc enveloping hydranth and extending as a sheath over proximal ends of tentacles. Hydranths ovoid to vasiform; hypostome dome-shaped; tentacles in a single whorl or in two close whorls.

Gonophores fixed sporosacs or free medusae; medusae with characteristics of the family. Marginal tentacles solitary or in eight groups. Oral tentacles dichotomously branched.

REMARKS

Allman (1872) originally included in the family Bimeriidae those genera of bougainvilliids whose hydroids produced fixed sporosacs. This unnatural grouping of taxa was recombined with the Atractylidae Hincks, 1868, by Torrey (1902).

Russell (1953) tentatively referred a hydrozoan to the genus *Thamnostoma* Haeckel, 1879, under the subfamily Thamnostominae Haeckel, 1879. The hydrozoan that Russell studied has since been referred to *Koellikerina* Kramp, 1939, by Petersen and Vannucci (1960). This genus is included in a subfamily with *Bimeria* Wright, 1859, here, under the name Bimeriinae Allman, 1872.

Genus *Bimeria* Wright, 1859

Bimeria Wright, 1859:109.

Manicella Allman, 1859a:51.

DIAGNOSIS

Hydroids with the characters of the subfamily.

Gonophores fixed sporosacs.

TYPE SPECIES

Bimeria vestita Wright, 1859, by monotypy.

REMARKS

The generic names *Bimeria* Wright, 1859, and *Manicella* Allman, 1859a, are simultaneous synonyms, having both been published in July 1859 for the same species. Allman (1864a) seemed uncertain that *Manicella* and *Bimeria* were congeneric. Later, he conceded (Allman, 1872) that the type species of the two genera, *Bimeria vestita* Wright, 1859, and *Manicella fusca* Allman, 1859a, were "almost certainly the same species" and recognized *Bimeria* as the valid name. Hincks (1868), acting as first reviser [Art. 24], had earlier chosen *Bimeria* as the name having precedence.

Life-cycle studies by Brückner (1914) and Rees (1938) showed that hydroids of the medusae of *Perigonimus cidaritis* Weismann, 1883, and *Thamnostoma russelli* Rees,

1938, are similar to those of *Bimeria vestita*, type species of *Bimeria*, although *B. vestita* produces fixed gonophores instead of free medusae. Petersen and Vannucci (1960) referred *P. cidaritis* and *T. russelli*, as well as material identified as *Thamnostoma* sp. by Browne (1905), to *Koellikerina fasciculata* (Péron and Lesueur, 1807). Petersen and Vannucci noted that hydroids of *Thamnostoma* Haeckel, 1879, are unknown.

Rees (1938), Vervoort (1964), and others have pointed to the relationship between hydroids of *Garveia* Wright, 1859, and *Bimeria*. The two have been regarded as congeneric by some authors (e.g., Torrey, 1902; Browne, 1907; Stechow, 1919, 1923a; Bouillon, 1985). *Bimeria* differs from *Garveia* in having a perisarc sheath over the base of the tentacles, and I agree with authors such as Rees (1938), Vervoort (1964), and Millard (1975) that the two should be regarded as distinct. In fact, as reported by Mammen (1963), *Garveia* appears to resemble *Bougainvillia* Lesson, 1830, more than it does *Bimeria*.

Identical accounts of the genus *Bimeria* and its type species, *B. vestita*, were published in two different journals by Wright (1859, 1863a). Also duplicated in these two papers were accounts of the nominal species *Coryne implexa* (Alder, 1856b), *Coryne margarica* Wright, 1859, and *Garveia nutans* Wright, 1859.

Bimeria vestita Wright, 1859

Figs. 17, 18

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

Manicella fusca Allman, 1859a:51.

Bimeria humilis Allman, 1877:8; pl. 5, figs. 3,4.

Perigonimus vestitus—Motz-Kossowska, 1905:74.

not *Bimeria vestita*—Annandale, 1907:141; fig. 3 [= *Garveia franciscana* (Torrey, 1902)].

Bimeria vestita f. *nana* Leloup, 1932:142; fig. 14.

Leuckartiara vestita f. *nana*—Vervoort, 1946a:294.

Leuckartiara vestita—Vervoort, 1946a:295.

Perigonimus vestita—Mammen, 1963:42 [incorrect subsequent spelling].

Garveia humilis—Vervoort, 1968:7.

Bimeria (*Garveia*) *umilis*—Wedler and Larson, 1986:71 [incorrect subsequent spelling].

TYPE LOCALITY

Firth of Forth, Scotland.

MATERIAL EXAMINED

Flatts Inlet, on undersides of flat rocks, - 3 m, 2 August 1982, two colonies, 4 and 5 mm high, without gonophores, ROMIZ B137. Green Bay Cave, Harrington Sound,

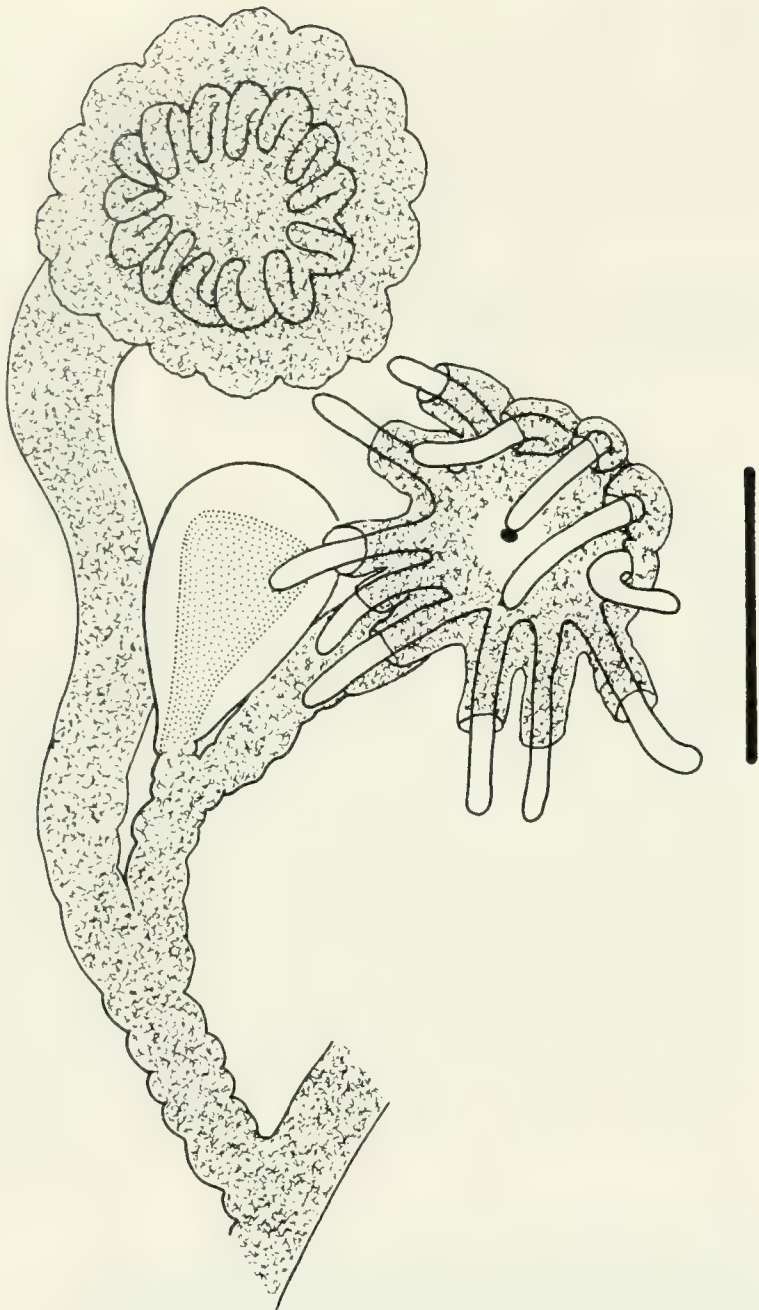


FIG. 17. *Bimeria vestita*, part of hydrocaulus with two hydranths and gonophore, ROMIZ B160. Scale equals 0.25 mm.

on *Eudendrium carneum*, 8 July 1982, one colony, 7 mm high, with male gonophores, ROMIZ B146. Harrington Sound, at Flatts Bridge, on algae, 21 September 1977, one colony, 1.5 mm high, with female gonophores, ROMIZ B160.

DESCRIPTION

Colonies minute, stolonal or erect, arising from a creeping hydrorhiza. Hydrocaulus monosiphonic, slender basally, gradually expanding distally, either unbranched or sparingly and more or less alternately branched. Perisarc of moderate thickness, annulated or wrinkled at base of hydrocaulus and branches, becoming encrusted with silt and detritus in older colonies, extending as a filmy covering over hydranth and around base of hypostome, forming tubular sheaths around bases of tentacles. Hydranth vaseiform, merging almost imperceptibly with pedicel; hypostome conical, tentacles 9 to 16 in number, filiform, in two close whorls.

Nematocysts—

Hydroids: desmonemes $3.8\text{--}4.7\ \mu\text{m} \times 2.6\text{--}2.9\ \mu\text{m}$; heterotrichous microbasic euryteles $6.6\text{--}7.3\ \mu\text{m} \times 3.7\text{--}4.5\ \mu\text{m}$.

Gonophores fixed sporosacs lacking radial canals and tentacular rudiments, completely enveloped in perisarc, arising singly on short, annulated or wrinkled pedicels from hydrocaulus and branches, less frequently from hydrorhiza. Female gonophores pear-shaped, each bearing a single egg or embryo. Male gonophores pear-shaped to elongate-oval.

REMARKS

Bimeria vestita Wright, 1859, and *Manicella fusca* Allman, 1859a, are simultaneous synonyms, as noted above

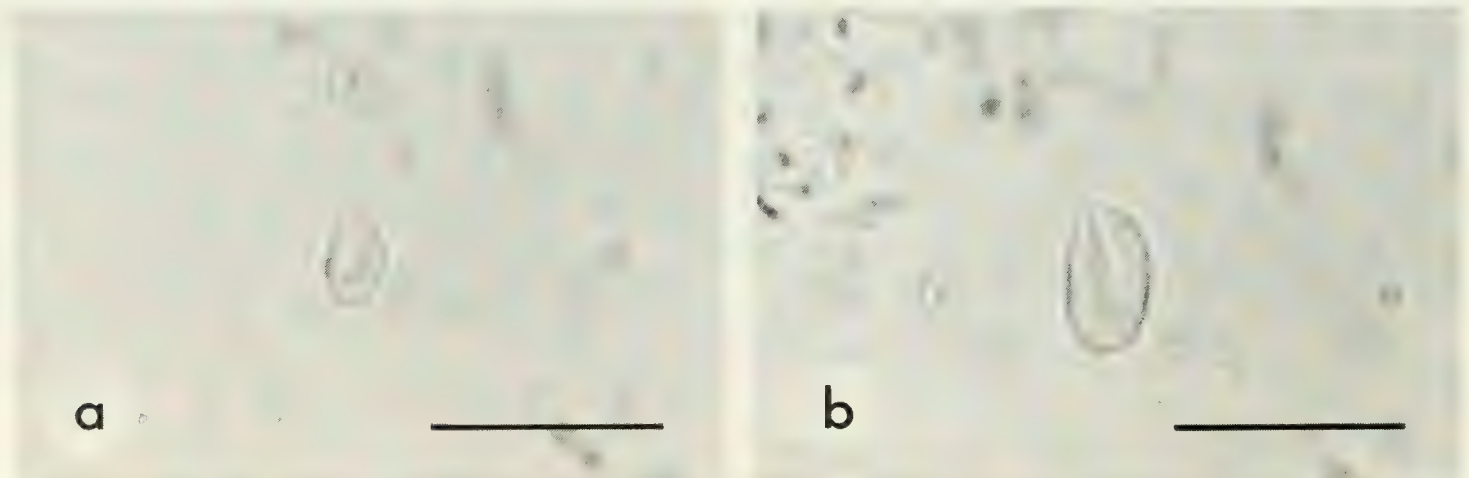


FIG. 18. *Bimeria vestita*, nematocysts of hydranth. Scales equal $10\ \mu\text{m}$. *a*, Desmoneme, ROMIZ B160. *b*, Heterotrichous microbasic eurytele, ROMIZ B137.

under discussion of the genus *Bimeria* Wright, 1859. Hincks (1868), the first reviser [Art. 24], chose *B. vestita* as having precedence over *M. fusca*.

Allman (1877) introduced the name *Bimeria humilis* for certain hydroids dredged in shallow water off the Tortugas, Florida. He indicated that these specimens differed from *B. vestita* in having "massive hydranths" and a somewhat less branched hydrocaulus. The two nominal species are nevertheless regarded as conspecific here.

Bimeria vestita has been reported from Bermuda before by Congdon (1907), Bennitt (1922), and Calder (1986),

as *B. humilis*. Congdon observed dense growths of this hydroid on species of *Eudendrium* Ehrenberg, 1834, and *Halocordyle* Allman, 1872, as well as on sponges.

KNOWN RANGE

Bermuda: on hydroids and sponges. (Congdon, 1907); listed, with no comment (Bennitt, 1922); in shallow inshore waters, and on wrecks and buoy chains (Calder, 1986).

Elsewhere: western Atlantic (Vervoort, 1968); eastern Atlantic (Picard, 1958); Indian Ocean (Millard, 1975); western Pacific (Leloup, 1937); eastern Pacific (Fraser, 1948).

Subfamily Bougainvilliinae Lütken, 1850

DIAGNOSIS

Bougainvilliid hydroids with perisarc terminating at base of hydranth, or extending upwards as a pseudohydrotheca. Hydranth fusiform to clavate; hypostome dome-shaped; tentacles more or less in a single whorl.

Gonophores fixed or motile sporosacs, or free medusae; medusae with characteristics of the family. Marginal tentacles in four perradial groups. Oral tentacles almost always dichotomously branched.

REMARKS

The subfamily Bougainvilliinae Lütken, 1850, as defined here, encompasses hydroids and medusae of the genera *Bougainvillia* Lesson, 1830, and *Nemopsis* L. Agassiz, 1849, as well as hydroids of the genera *Dicoryne* Allman, 1859b, *Garveia* Wright, 1859, and *Aselomaris* Berrill, 1948. Of these, only *Bougainvillia* is known at present from Bermuda.

Genus *Bougainvillia* Lesson, 1830

Bougainvillia Lesson, 1830:118.

Hippocrene Brandt, 1835:29 [invalid junior homonym of *Hippocrene* Oken, 1817 (Mollusca)].

Perigonimus M. Sars, 1846:8.

Bougainvillea Forbes, 1848:61 [incorrect subsequent spelling].

Perigonymus Forbes, 1848:81 [incorrect subsequent spelling].

Margelis Steenstrup, 1850:35.

Atractylis Wright, 1858a:447.

Bourgainvillea Wright, 1858a:449 [incorrect subsequent spelling].

Perigommus Allman, 1871:24 [incorrect subsequent spelling].

Parigonimus Allman, 1872:325 [incorrect subsequent spelling].

Bourgainvillia Allman, 1872:433 [incorrect subsequent spelling].

Atractilis Allman, 1872:433 [incorrect subsequent spelling].

Lizusa Haeckel, 1879:80.

Bougainvilleia Brooks, 1883b:468 [incorrect subsequent spelling].

Perigonemus Fewkes, 1891:29 [incorrect subsequent spelling].

Perigonismus Möbius, 1893:89 [incorrect subsequent spelling].

Lizuza Delage and Hérouard, 1901:56 [incorrect subsequent spelling].

Bougainvillia Hargitt, 1902:13 [incorrect subsequent spelling].

Perigominus Hartlaub, 1905:533 [incorrect subsequent spelling].

Hypocrene Bedot, 1912:259 [incorrect subsequent spelling].

DIAGNOSIS

Bougainvilliidae with colonies stolonal or erect, with monosiphonic or polysiphonic hydrocaulus. Perisarc soft or firm, terminating at hydranth base or forming a pseudohydrotheca. Hydranth with a single distal whorl of filiform tentacles; hypostome conical.

Gonophores free medusae, arising singly or in clusters from hydrocaulus, branches, or hydrorhiza. Medusae with short manubrium; oral tentacles perradial, usually branched dichotomously. Radial canals four; ring canal present. Marginal tentacles all alike in structure, arising in clusters from four tentacle bulbs. Ocelli usually present. Gonads on manubrium; medusa buds occasionally produced.

TYPE SPECIES

Bougainvillia macloviana Lesson, 1830, by monotypy.

REMARKS

The name *Bougainvillia* has been attributed by many au-

thors to Lesson (1836), although it was actually founded in an earlier paper by the same author (Lesson, 1830). Likewise, there has been confusion over the name of the type species of the genus because Lesson (1830) first referred to it as *Cyanaea bougainvillii*. Below this name, but on the same page, Lesson commented that his medusa was not at all a "cyanée" but the type of a new genus named *Bougainvillia*. He then applied the name *B. macloviana* to the species, making *C. bougainvillii* and *B. macloviana* simultaneous synonyms. Lesson (1836), acting as first reviser [Art. 24], chose the name *B. macloviana* for the species. *Bougainvillia macloviana* is the type species of the genus, not *B. ramosa* (van Beneden, 1844b) as designated by Allman (1872).

Rees (1938) demonstrated that *Perigonimus* M. Sars, 1846, is a junior subjective synonym of *Bougainvillia* because the hydroid of its type species, *P. muscoides* M. Sars, 1846, gives rise to medusae referable to *Bougainvillia*. In a revision of the genus *Perigonimus*, Rees (1956a) noted that nearly 40 other nominal species had been referred to *Perigonimus* at one time or another. These were shown to belong not only to a number of genera, but to at least six families.

Totton (1930) designated *Eudendrium ramosum* sensu van Beneden, 1844b (not *Sertularia ramosa* Linnaeus, 1758), referred to *Bougainvillia*, as type species of *Atractylis* Wright, 1858a. As noted by Totton (1930) and Rees (1938), *Atractylis* is, therefore, a subjective synonym of *Bougainvillia*.

Margelis principis Steenstrup, 1850, which is type species of *Margelis* Steenstrup, 1850, and the two originally included nominal species of *Lizusa* Haeckel, 1879, are now all included in *Bougainvillia*. The names *Margelis* and *Lizusa* are, therefore, synonyms of *Bougainvillia*.

Vannucci and Rees (1961) noted that hydroids of the various species of *Bougainvillia* are difficult to separate; they differ little from each other, yet are greatly influenced by environmental factors. Vannucci and Rees concluded from their review of the genus that many of the nominal species are of questionable validity. The same opinion was expressed many years earlier by Mayer (1910).

Of the numerous incorrect subsequent spellings [Art. 33c] of the name *Bougainvillia* and its synonyms, the most commonly encountered is *Bougainvillea*, first used by Forbes (1848). The list given here should not be considered complete; I was unable to trace and verify several others listed by Neave (1939, 1940a, 1940b).

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

Figs. 19, 20

Eudendrium ramosum—van Beneden, 1844b:56; pl. 4, figs. 1–13 [hydroid and medusa] [not *Eudendrium ramosum* (Linnaeus, 1758)].

not *Tubularia* (*Sertularia*) *ramosa*—Dalyell, 1847:64; pl. 11, figs. 1–8 [= ?*Bougainvillia pyramidata* (Forbes and Goodsir, 1851)].

Atractylis ramosa—Wright, 1858a:449 [not *Eudendrium ramosum* (Linnaeus, 1758)].

Bougainvillea britannica—Wright, 1858a:449 [medusa] [incorrect subsequent spelling] [not *Bougainvillia britannica* (Forbes, 1841)].

Podocoryne alderi Hodge, 1861:82; pl. 2, figs. 11–15 [medusa, not hydroid].

Margelis ramosa—L. Agassiz, 1862:344 [hydroid and medusa] [not *Eudendrium ramosum* (Linnaeus, 1758)].

Perigonimus muscus Allman, 1863:12 [incorrect subsequent spelling].

Perigonimus ramosus—Allman, 1863:12 [incorrect subsequent spelling] [not *Eudendrium ramosum* (Linnaeus, 1758)].

Atractylis (*Eudendrium*) *ramosa*—Wright, 1863b:35 [not *Eudendrium ramosum* (Linnaeus, 1758)].

Corynopsis alderi—Allman, 1864a:354 [medusa, not hydroid].

Bougainvillia ramosa—Allman, 1864a:366 [not *Eudendrium ramosum* (Linnaeus, 1758)].

Bougainvillia muscus—Allman, 1864a:366.

Bougainvillia fruticosa Allman, 1864a:366 [nomen nudum].

Bougainvillia fruticosa Allman, 1864b:58.

Lizusa octocilia—Haeckel, 1879:80 [part] [not *Medusa octocilia* Dalyell, 1847 = ?*Bougainvillia pyramidata* (Forbes and Goodsir, 1851)].

Bougainvillea ramosa—Pictet, 1893:11 [incorrect subsequent spelling] [not *Eudendrium ramosum* (Linnaeus, 1758)].

Bougainvillea muscus—Pictet, 1893:11 [incorrect subsequent spelling].

Bougainvillea (*Margelis*) *ramosa*—Garstang, 1894:214 [medusa] [not *Eudendrium ramosum* (Linnaeus, 1758)].

Bougainvillia flavida Hartlaub, 1897:456; pl. 14, fig. 5 [female medusa only].

Bougainvillia autumnalis Hartlaub, 1897:465; pl. 15, figs. 11–13 [medusa].

Lizusa octociliata—Aurivillius, 1898:114 [medusa] [incorrect subsequent spelling].

Lizusa 8-ciliata—Aurivillius, 1898:424 [medusa] [incorrect subsequent spelling].

?*Bougainvillia v. benedenii* Bonnevie, 1898:468.

?*Bougainvillia benedenii* Bonnevie, 1898:484; pl. 26, figs. 34,35 [hydroid and medusa].

?*Bougainvillia vanbenedeni*—Bonnevie, 1899a:43 [incorrect subsequent spelling].

Bougainvillia gibbsi Mayer, 1900a:5; pl. 4, figs. 14,15 [medusa].

Margelis autumnalis—Browne, 1900:708 [medusa].

?*Bougainvillia van benedeni*—Jäderholm, 1909:46; pl. 3, fig. 5 [incorrect subsequent spelling].

?*Bougainvillia van benedenii*—Broch, 1909:198.
Bougainvillia ramosa var. *nana* Hartlaub, 1911:189
 [medusa].
Bougainvillia triestina Hartlaub, 1911:154; fig. 138
 [medusa].
Bougainvillia ramosa var. *minima* Kramp and Damas,
 1925:254 [medusa].
Bougainvillia autumnalis var. *magna* Babnik, 1948:290;
 fig. 2 [medusa].
Bougainvillia ramosa f. *musca*—Millard, 1975:99.
Bougainvillia ramosa f. *fruticosa*—Millard, 1975:99.
Bougainvillia ramosa f. *ramosa*—Millard, 1975:99.
Bougainvillia ramosa f. *vanbenedenii*—Millard, 1975:99.

TYPE LOCALITY

Torquay (Torbay), Devon, Great Britain.

MATERIAL EXAMINED

Green Bay Cave, Harrington Sound, on survey line 40 m from entrance, -6 m, 3 March 1982, three colonies, 6-14 mm high, with medusa buds, coll. T. Iliffe, ROMIZ B152. Flatts Inlet, on *Cliona* sp., -0.5 m, 27 February 1982, one colony, 4 mm high, without medusa buds, ROMIZ B153. St George's Island, north shore, on oyster on mooring chain, -2 m, 5 October 1976, one colony, 10 mm high, without medusa buds, coll. J. Markham, L. Coen, ROMIZ B163. Flatts Inlet, on sponge, -1.5 m, 5 March 1982, one colony, 7 mm high, without medusa buds, ROMIZ B169. Flatts Inlet, on rocks and *Eudendrium carneum*, -2 m, 4 July 1983, three colonies, up to 13 mm high, with medusa buds, newly liberated medusae, and laboratory-reared adult medusae, ROMIZ B328.

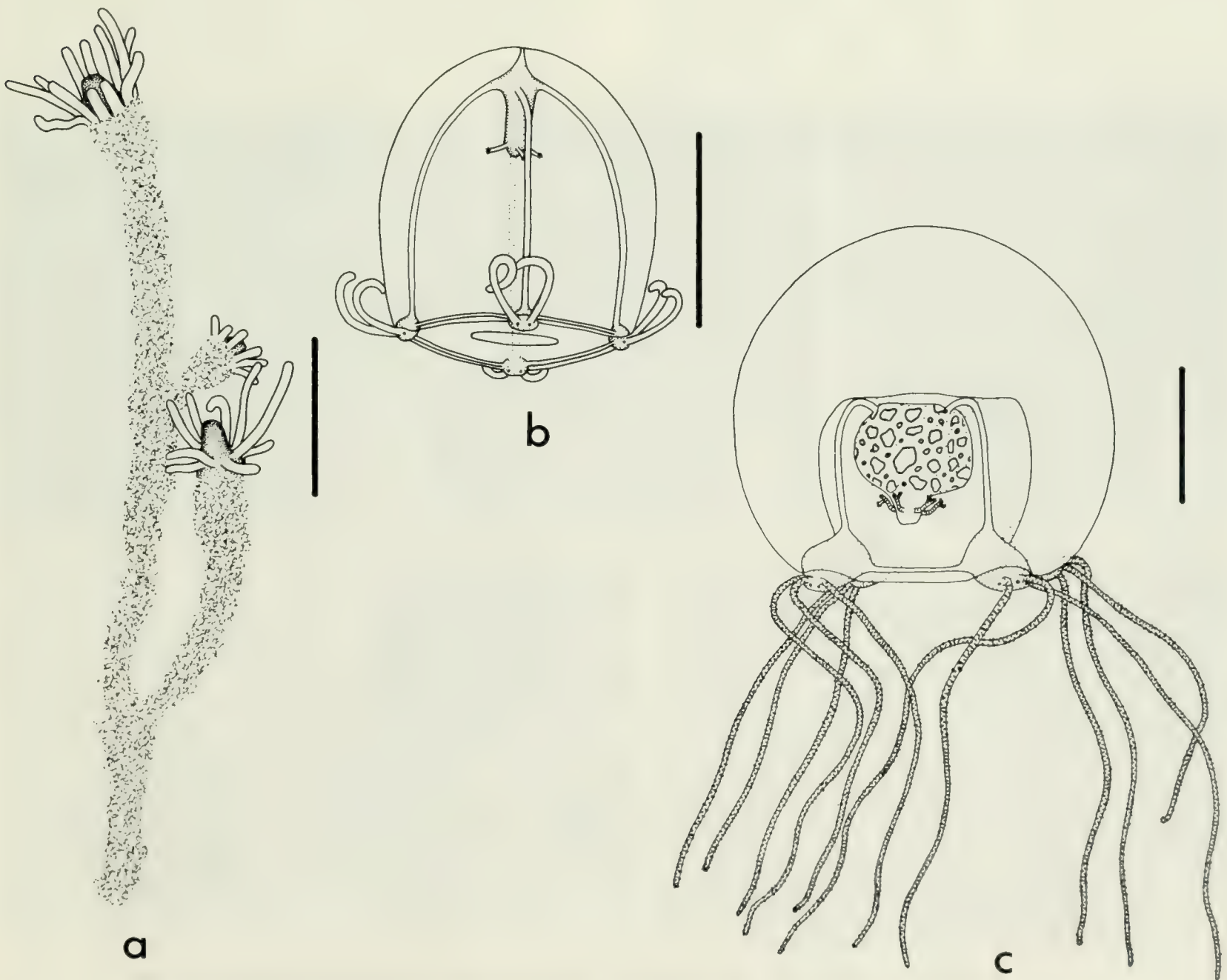


FIG. 19. *Bougainvillia musca*. Scales for *a* and *b* equal 0.5 mm; scale for *c* equals 1 mm. *a*, Hydroid colony, ROMIZ B152. *b*, Newly liberated medusa, ROMIZ B328. *c*, Three-day-old adult female medusa, ROMIZ B328.

DESCRIPTION

Hydroid colony initially stolonial, later erect, reaching 14 mm high, growing from a creeping hydrorhiza. Hydrocaulus slender, monosiphonic, profusely and more or less alternately branched; primary branches unbranched or somewhat regularly branched; terminal branchlets slender basally, gradually increasing in diameter distally; hydrocaulus and branches curved and twisted, occasionally exhibiting stolonial growth. Perisarc of moderate thickness, smooth or irregularly wrinkled (especially at bases of branches) but not annulated, heavily encrusted with particles of silt and detritus, and extending over base of hydranth as a pseudohydrotheca; pseudohydrotheca cup-shaped in retracted hydranths; perisarc not investing tentacles or hypostome. Hydranth cylindrical when extended, fusiform when contracted, with conical hypostome, bearing tentacles distally. Tentacles slender, filiform, in two close whorls, 10 to 16 in number.

Nematocysts—

Hydroids: desmonemes $3.9\text{--}4.6\ \mu\text{m} \times 2.7\text{--}3.0\ \mu\text{m}$; heterotrichous microbasic euryteles $5.7\text{--}6.5\ \mu\text{m} \times 2.8\text{--}3.4\ \mu\text{m}$.

Medusa buds globular, arising singly on stalks of moderate length from pedicels below hydranths, completely invested with perisarc. Newly liberated medusae thimble-shaped, 0.8 mm high, 0.7 mm wide; mesoglea of moderate thickness; umbilical canal present; peduncle lacking. Exumbrella with four distinct interradiial longitudinal furrows and four somewhat less distinct perradiial longitudinal furrows; exumbrellar nematocysts lacking. Manubrium small, tubular, with simple quadrate mouth; oral tentacles four, unbranched, inserting just above mouth, each oral tentacle terminating with small cluster of nematocysts. Radial canals four, joining a narrow ring canal. Marginal bulbs conical, rounded basally, each with two tentacles and two conspicuous black ocelli, each ocellus occurring at base

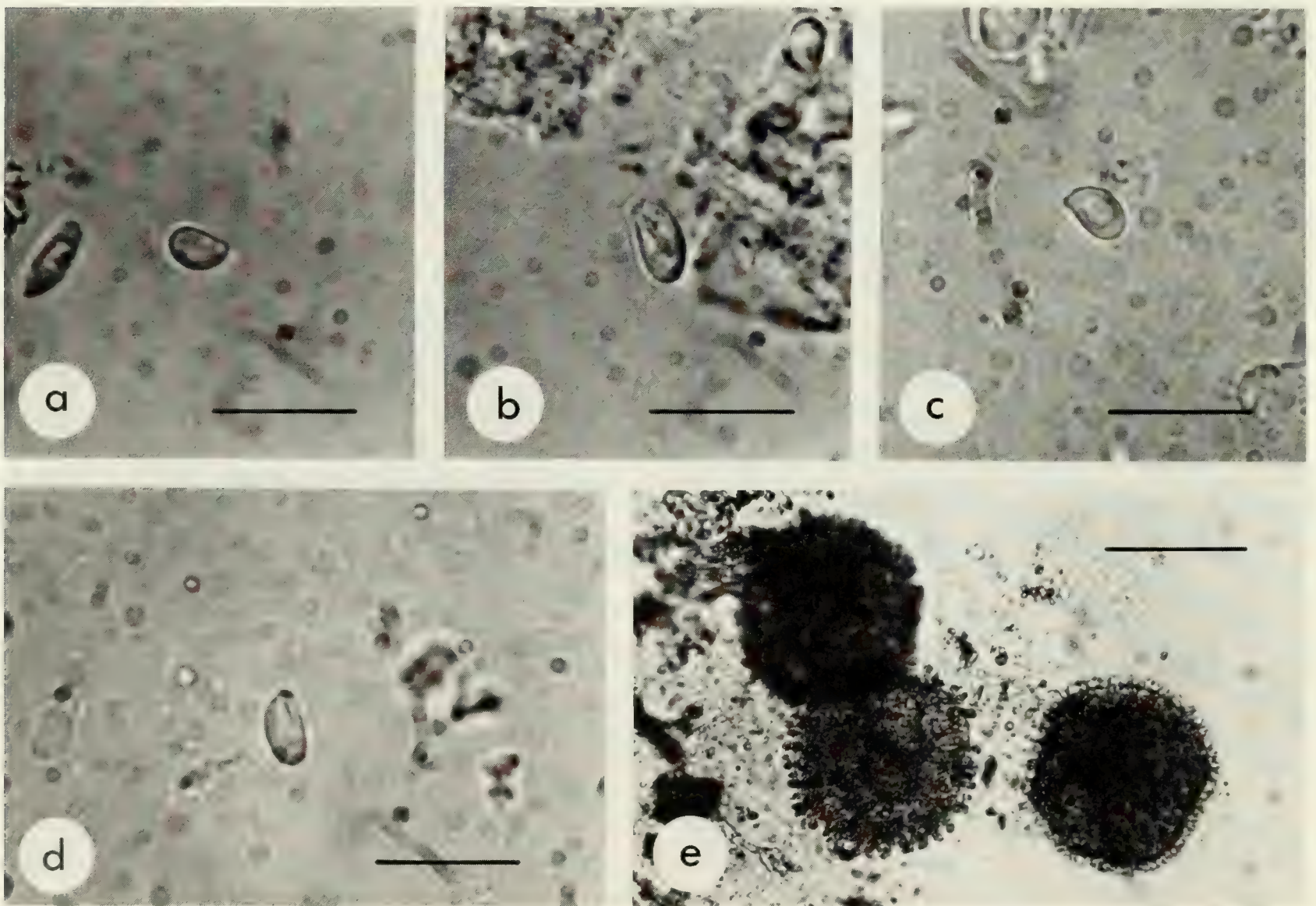


FIG. 20. *Bougainvillia muscus*, nematocysts, ROMIZ B328. Scales for *a*–*d* equal $10\ \mu\text{m}$; scale for *e* equals $100\ \mu\text{m}$. *a*, Desmoneme of hydroid. *b*, Heterotrichous microbasic eurytele of hydroid. *c*, Desmoneme of medusa. *d*, Heterotrichous microbasic eurytele of medusa. *e*, Eggs, each with outer envelope of heterotrichous microbasic euryteles.

of a tentacle. Velum broad. Endoderm of manubrium and tentacle bulbs cream-coloured.

Nematocysts—

Medusae: desmonemes $4.5\text{--}5.1\ \mu\text{m} \times 3.0\text{--}3.5\ \mu\text{m}$; heterotrichous microbasic euryteles $5.3\text{--}6.5\ \mu\text{m} \times 2.9\text{--}3.4\ \mu\text{m}$.

One day after liberation, medusae 1.2 mm high, 1.1 mm wide; mesoglea thicker, especially at apex. One medusa with an incipient third tentacle on one of four marginal bulbs, incipient tentacle lacking an ocellus basally. Two days after liberation, medusae about 1.5 mm high and wide, oral tentacles distally bifurcated, and gonads present interradially on manubrium. Each tentacle bulb with a developing third tentacle, varying in length from about half that of original pair to a mere stub. Developing tentacles without ocelli initially, later with ocelli. Three days after liberation, medusae about 2.0 mm high and wide, oral tentacles divided once, marginal tentacles 12 in number, 3 on each tentacle bulb, and ocelli 10 to 12 in number. Gonads large, mature eggs present, ova with an outer envelope bearing numerous heterotrichous microbasic euryteles ($6.5 \times 3.6\ \mu\text{m}$).

REMARKS

The invalid name *Bougainvillia ramosa* (van Beneden, 1844b) has been extensively applied to this species in the literature of both hydroids and hydromedusae (e.g., see Hincks, 1868; Allman, 1872; Stechow, 1919; Vervoort, 1946b; Russell, 1953; Kramp, 1961; Vannucci and Rees, 1961; Millard, 1975; and numerous others). Van Beneden (1844b) applied the name *Eudendrium ramosum* to a bougainvilliid hydrozoan in the mistaken belief that it was conspecific with *Tubularia ramosa* Linnaeus, 1758, a species now referred to the genus *Eudendrium* Ehrenberg, 1834. Even though the hydrozoan studied by van Beneden has since been referred to a different genus from the true *Eudendrium ramosum* (Linnaeus, 1758), the name *B. ramosa* cannot be retained for the species [Art. 49]. The name *B. ramosa* is replaced here with its oldest available synonym, *Bougainvillia muscus* (Allman, 1863).

Russell (1953) noted that the synonymy of this species is in doubt because several different hydroid growth forms apparently produce similar medusae. It is still unresolved whether these different hydroid growth forms belong to a single, variable species, or to more than one species. The list of synonyms given here, taken largely and selectively from Bedot (1905, 1910, 1912, 1916, 1918), Russell (1953), Kramp (1961), and Vannucci and Rees (1961), is provisional and not intended to be exhaustive. A thorough taxonomic reassessment of the species is needed.

Records of the hydroid *Tubularia* (*Sertularia*) *ramosa* and the hydromedusa *Medusa oclia* (*M. octocilia*, *M. sexdecilia*, *M. duodecilia*) by Dalyell (1847) have been excluded from the synonymy of this species based on the

conclusions of Edwards (1966a), who suggested that they were likely referable to *Bougainvillia pyramidata* (Forbes and Goodsir, 1851). Edwards noted that Dalyell's illustration of the hydroid, found on a sea pen, closely resembled specimens of *B. pyramidata* from the same substrate examined by Edwards (1964a). Wright (1858a) thought that the medusa of this hydroid was identical with *B. britannica* (Forbes, 1841), and Mayer (1910) among others regarded the two as conspecific. However, these are now considered to be different species (e.g., see Russell, 1953; Kramp, 1961; Vannucci and Rees, 1961; Edwards, 1964b, 1966a).

The nominal species *Podocoryne alderi* Hodge, 1861, was almost certainly based on a hydroid belonging to *Podocoryna* M. Sars, 1846, and a medusa belonging to *Bougainvillia muscus* (Vannucci and Rees, 1961; Edwards, 1966a, 1972). Allman (1864a) proposed the generic name *Corynopsis* for the conglomerate *P. alderi*. Hodge (1861) reported sending "two or three depauperated specimens," along with some sketches, to J. Alder for identification. This material, labelled "*Podocoryne alderi* Seaham H" (Seaham Harbour, northeast England), and relabelled "*Corynopsis alderi* Hodge," is represented in the Alder Collection at the Hancock Museum, Newcastle upon Tyne. The hydroid colony consists of a branching and anastomosing stolon network, with occasional short spines and a few hydractiniid hydranths, growing over serpulid polychaete tubes. Since the more widely used name *B. muscus* is predated by Hodge's (1861) nominal species, the name *P. alderi* is restricted here to the hydroid only; the above-cited material from the Hancock Museum is designated as the lectotype [Art. 74]. The name *P. alderi* thus is restricted to *Podocoryna*, and no longer threatens the name *B. muscus*. Moreover, the generic name *Corynopsis* Allman, 1864a, becomes a junior subjective synonym of *Podocoryna*, instead of *Podocoryna* in part and *Bougainvillia* in part. Edwards (1972) included *P. alderi* as a questionable synonym of *P. borealis* (Mayer, 1900a), which in turn was viewed as a questionable synonym of *P. tubulariae* M. Sars, 1857.

Bougainvillia flavida Hartlaub, 1897, has been regarded as a synonym, or a synonym in part, of this species (e.g., see Hartlaub, 1911; Kramp, 1937; Vannucci and Rees, 1961). Edwards (1964a, 1964b) concluded that Hartlaub's (1897) hydroid of *B. flavida* was referable to *B. britannica*, his male medusae to *B. pyramidata*, and his female medusa to "*B. ramosa*." *Bougainvillia autumnalis* Hartlaub, 1897, is also a synonym, at least in part, of this species (e.g., see Russell, 1953; Kramp, 1961; Vannucci and Rees, 1961). *Bougainvillia vanbenedenii* Bonnevie, 1898, has been included as a questionable synonym here following Vannucci and Rees (1961), although these authors left open the possibility that Bonnevie's species might be identical with *B. superciliaris* (L. Agassiz, 1849). However, the

hydroid of *B. superciliaris* is now known to be stolonal (Werner, 1961; Edwards, 1966a).

Hydroids examined here from Bermuda bear considerable resemblance to the description of *Bougainvillia longicirra* Stechow, 1914, from the Caribbean. Like *B. muscus*, Stechow's (1914) colonies were small but often extensively branched, the hydrocaulus was monosiphonic, the perisarc was wrinkled and encrusted with particles of silt and detritus, a pseudohydrotheca was present, and the tentacles numbered about 16. Medusa buds were present on Stechow's hydroids, but the newly liberated medusa was not observed. Fraser (1944) was almost certain that *B. longicirra* was conspecific with *B. superciliaris*, but Vannucci and Rees (1961) correctly disputed this, noting that the latter is a boreal species occurring well to the north of the locality where *B. longicirra* was found. As noted above, the hydroid of *B. superciliaris* is now known to be stolonal. Stechow (1914) indicated that *B. longicirra* might represent the hydroid of the medusa *B. niobe* Mayer, 1894. Vannucci and Rees (1961) stated that this was based on surmise, and noted that the type locality of Charlotte Amalie in the West Indies is within range of *B. frondosa* Mayer, 1900b, as well as that of *B. niobe*. I have not regarded *B. longicirra* as conspecific with *B. muscus* because of a lack of knowledge about its medusa stage.

Medusae described here were isolated and reared in the laboratory following liberation from the hydroid. Specimens were maintained at 28–29° C in covered fingerbowls containing natural seawater, and fed pieces of newly hatched

nauplii of *Artemia* several times daily. Observations were made on both living and preserved material. Sexual maturity was attained about three days after liberation, when eggs were observed being shed from the gonads of female medusae; none of the medusae reared to maturity were male. The eggs were surrounded by an envelope containing nematocysts, as reported previously for this species (Russell, 1953). Of several dozen medusae isolated initially, none survived longer than 3.5 days in the laboratory. A short life span in medusae of this species might partly explain Russell's (1953) observation that they are scarce in the plankton around the British Isles, considering the abundance of the hydroid there.

Neither hydroid nor medusa of *Bougainvillia muscus* has been reported previously from Bermuda, but two other species of medusae belonging to this genus have been reported from the area. Bigelow (1918, 1938) identified *B. niobe* in collections of hydromedusae from Bermuda, and Moore (1949) noted that the species was an abundant winter form there. *Bougainvillia platygaster* (Haeckel, 1879) has been recorded from a number of areas in the western North Atlantic, including the Sargasso Sea near Bermuda (Kramp, 1959).

KNOWN RANGE

Bermuda: first record.

Elsewhere: western Atlantic (Mayer, 1910, as *B. autumnalis*); eastern Atlantic (Russell, 1953); Indian Ocean (Millard, 1975); western Pacific (Yamada, 1959).

Family Cytaeidae L. Agassiz, 1862

Cytaeidae L. Agassiz, 1862:341 [emended to Cytaeidae by Kramp, 1961].

DIAGNOSIS

Hydroid colonies stolonal; hydranths arising from a creeping hydrorhiza. Perisarc covering hydrorhiza, terminating at base of hydranths, often in form of a collar. Hydranths columnar; tentacles filiform, in one more or less regular oral whorl; hypostome conical.

Gonophores free medusae or fixed sporosacs, arising from hydrocaulus on stalks. Medusa bell-shaped; manubrium bulbous, with simple, circular mouth and four or more unbranched oral tentacles inserting above mouth. Radial canals four. Marginal tentacles solid, four or exceptionally eight, each arising from a tentacle bulb. Ocelli absent. Gonads on manubrium.

REMARKS

Rees (1962) recognized three genera of hydroids in the family Cytaeidae L. Agassiz, 1862. All species having

free medusae were included in *Cytaeis* Eschscholtz, 1829. Species with fixed gonophores were placed in *Perarella* Stechow, 1922, except for the poorly known *Stylactis vermicola* Allman, 1888, which was retained in *Stylactella* Haeckel, 1889.

The diagnosis of the family Cytaeidae given here encompasses the recently described *Paracytaeis* Bouillon, 1978a, but excludes *Cnidostoma* Vanhöffen, 1911, following Picard (*in* Kramp, 1961:444) and Rees (1962).

Haeckel (1889) believed that *Stylactella*, *Stylactis* Allman, 1864a, and *Hydranthea* Hincks, 1868, were related genera, and stated, "Perhaps *Stylactella* and the allied genera may represent together a distinct family, the Stylactidae." Although the poorly known genus *Stylactella* is apparently a cytaeid, the nominal family Stylactidae is not a synonym of the Cytaeidae, as implied by Rees (1962). The name Stylactidae is derived from the nominal genus *Stylactis* rather than *Stylactella*, and the former is therefore type genus of the family [Art. 63]. The nominal genus *Stylactis*, and Haeckel's Stylactidae, are included

here in the Hydractiniidae L. Agassiz, 1862. *Hydranthea* is now included in the family Haleciidae Hincks, 1868 (e.g., see Cornelius, 1975; Bouillon, 1985).

Genus *Cytaeis* Eschscholtz, 1829

Cytaeis Eschscholtz, 1829:104.

Cytacis de Blainville, 1834:284 [incorrect subsequent spelling].

Cyteis van Beneden, 1867:18 [incorrect subsequent spelling].

Cytheis van Beneden, 1867:18 [incorrect subsequent spelling].

Nigritina Haeckel, 1879:73.

Cytaeidium Haeckel, 1879:75.

Cytaesis Bouillon, 1978a:129 [incorrect subsequent spelling].

DIAGNOSIS

Hydroids with characters of the family.

Gonophores free medusae, arising on stalks from hydrorhiza. Medusa with characters of the family, with only four marginal tentacles.

TYPE SPECIES

Cytaeis tetrastyla Eschscholtz, 1829, by monotypy.

REMARKS

Haeckel (1879) established two subgenera within the genus *Cytaeis* Eschscholtz, 1829, *Nigritina* for those species lacking a gastric peduncle and *Cytaeidium* for those having a peduncle. He attributed *Nigritina* to J. Steenstrup, but apparently the name was derived from an unpublished manuscript by that author. Neither nominal subgenus is recognized in the recent literature on *Cytaeis* (e.g., Kramp, 1959, 1961, 1965; Rees, 1962; Uchida, 1964; Vervoort, 1967; Millard, 1975; Hirohito, 1977; Bouillon, 1978a, 1980, 1985). Kramp (1961) regarded *Cytaeis pusilla* Gegenbaur, 1857, type species of *Cytaeidium*, as doubtfully conspecific with *Cytaeis tetrastyla* Eschscholtz, 1829.

Mayer (1910) included the nominal genus *Cubogaster* Haeckel, 1879 (original spelling *Cybogaster* Haeckel, 1864), in the synonymy of *Cytaeis*. However, *Cybogaster gemmascens* Haeckel, 1864, type species of *Cybogaster* by monotypy, was regarded by Russell (1953) as conspecific with *Lizzia blondina* Forbes, 1848, type species of the bougainvilliid genus *Lizzia* Forbes, 1846. Thus, neither *Cybogaster* nor its junior objective synonym *Cubogaster* [Art. 33a (ii)] can be regarded as synonymous with *Cytaeis*.

Stylactella Haeckel, 1889, and *Perarella* Stechow, 1922, are distinguished from *Cytaeis* largely by the type of gonophore produced (Rees, 1962), a practice criticized by Petersen (1979). However, the relationships of these nominal genera are unclear and they have not been combined here.

Komai (1931) was the first to link hydroid and medusa stages of *Cytaeis*, working with what he thought was *C. japonica* Uchida, 1927. Rees (1962) regarded Komai's hydrozoan as a distinct species and named it *C. uchidae*.

Worldwide, three nominal species of *Cytaeis* medusae were listed by Kramp (1961). Six species, including the hydroids of five of these, were included in the genus by Rees (1962). Rees suggested that more than one species may have been combined under *C. tetrastyla* by Kramp (1961).

Cytaeis sp.

Figs. 21, 22

MATERIAL EXAMINED

Green Bay, Harrington Sound, on shell of *Cerithium litteratum* from *Cladophora* bed, -2.5 m, 21 September 1984, one colony, with medusa buds, two medusae liberated in laboratory from hydroid, ROMIZ B353.

DESCRIPTION

Colony stolonial, with hydrorhizal network adhering to gastropod shell. Perisarc smooth, thin, terminating at base of hydranth, not dilated in form of cup-shaped collar. Spines absent. Hydranths all gastrozooids, clavate to nearly columnar, up to 0.6 mm long, 0.2 mm wide, with four to five tentacles in each of two closely placed oral whorls, those of one whorl alternating with those of adjacent whorl. Tentacles filiform, but with nematocyst batteries arranged in more or less distinct rings medially and distally. Hypostome dome-shaped.

Nematocysts—

Hydroids: desmonemes $5.0\text{--}5.8\ \mu\text{m} \times 3.3\text{--}3.8\ \mu\text{m}$; heterotrichous microbasic euryteles $7.4\text{--}8.3\ \mu\text{m} \times 3.5\text{--}3.8\ \mu\text{m}$.

Medusa buds pear-shaped to globular, arising singly on relatively long stalks from hydrorhiza, completely invested in perisarc. Newly liberated medusae bell-shaped, about 0.4 mm high and wide; mesoglea thin. Exumbrella with four distinct perradial longitudinal furrows and four less distinct interradianal furrows in preserved and contracted material; scattered exumbrellar nematocysts present. Manubrium tubular to somewhat fusiform, extending about halfway to velar opening; mouth simple; oral tentacles four, unbranched, inserted just above mouth, each with a small terminal cluster of nematocysts. Radial canals four; narrow ring canal present. Tentacle bulbs four, perradial, subspherical, each with a single contracted filiform tentacle. Ocelli absent. Gonads undeveloped.

REMARKS

This hydrozoan cannot be assigned at present, with any degree of confidence, to any of the nominal species cur-

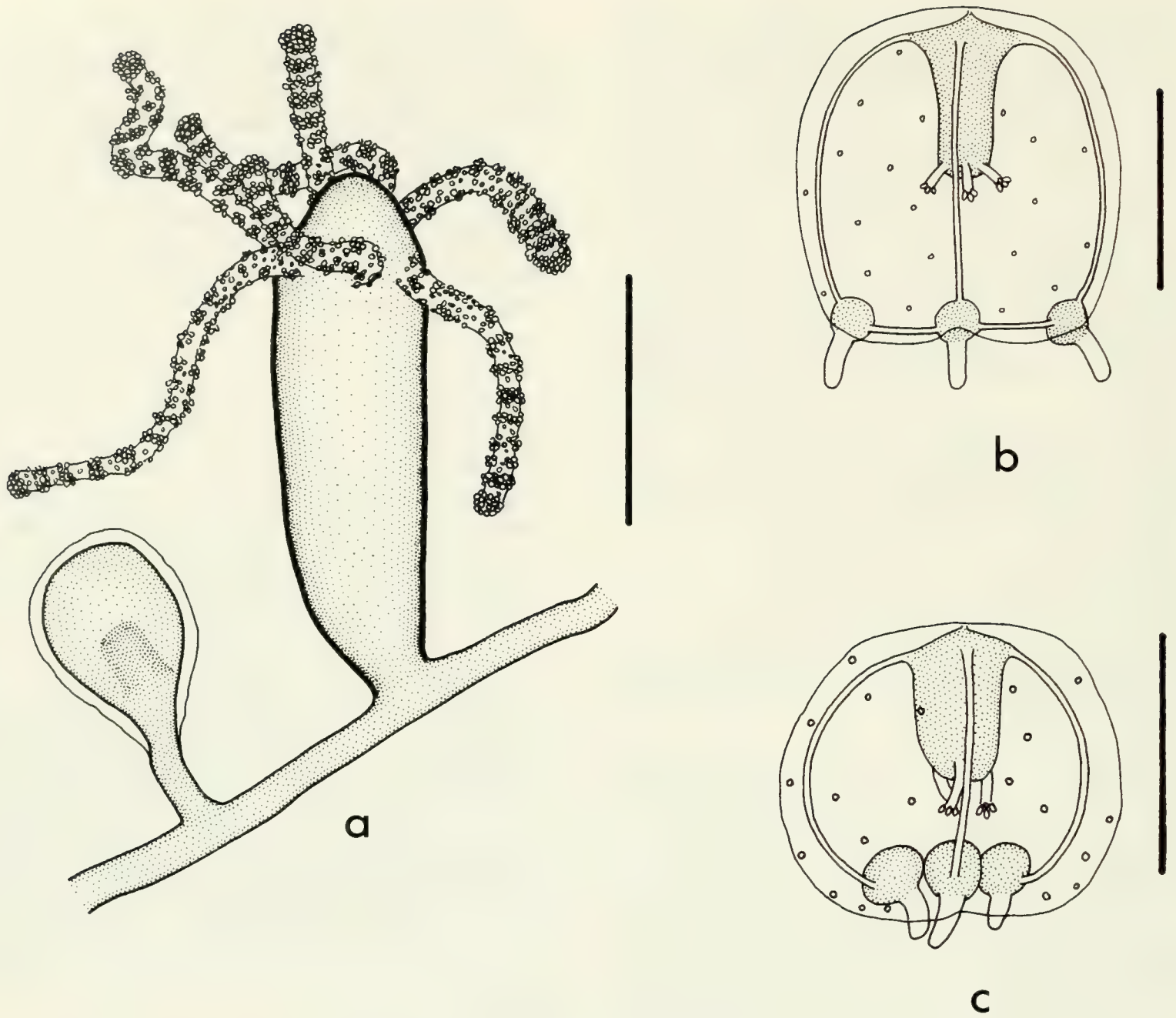


FIG. 21. *Cytæis* sp., ROMIZ B353. Scales equal 0.25 mm. *a*, Hydranth and gonophore. *b*, Newly liberated, living medusa. *c*, Newly liberated, preserved medusa.

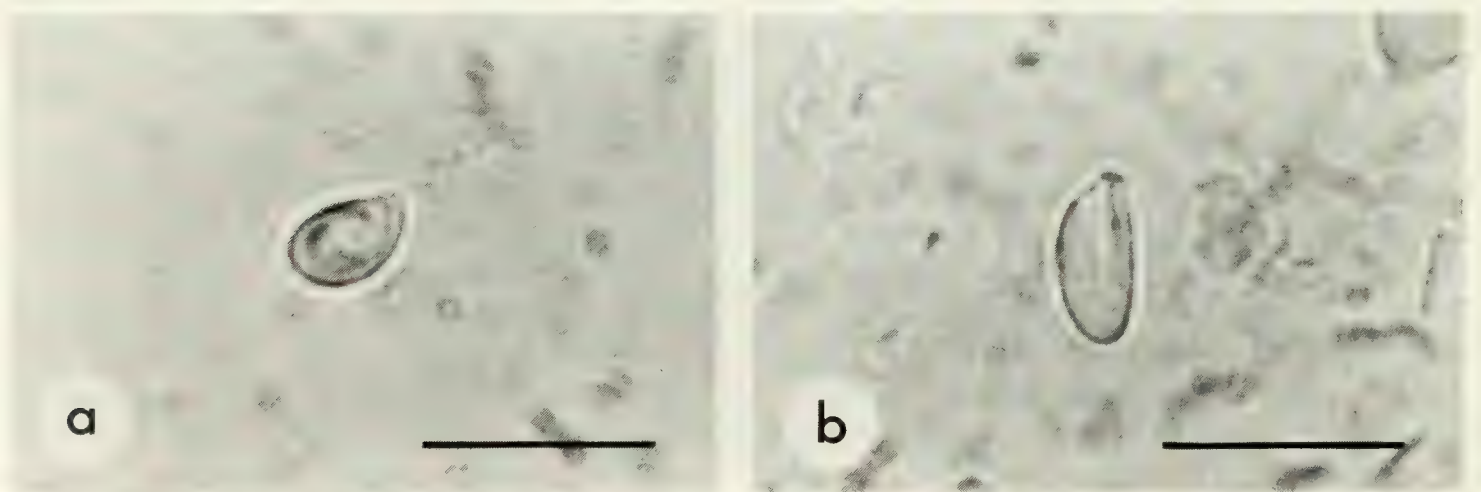


FIG. 22. *Cytæis* sp., nematocysts of hydranth, ROMIZ B353. Scales equal 10 μ m. *a*, Desmoneme. *b*, Heterotrichous microbasic eurytele.

rently referred to *Cytaeis* Eschscholtz, 1829. While bearing considerable resemblance to *C. nassa* (Millard, 1959a), Bermuda specimens have not been referred to that species for several reasons. First, hydranths were smaller than those of *C. nassa* described by Vervoort (1967) and Millard and Bouillon (1973), and much smaller than those measured by Millard (1959a) and Rees (1962). Admittedly, hydranth measurements in the literature on *C. nassa* are quite varied, and differences noted here may be taxonomically insignificant. Secondly, Millard (1959a) reported that young hydranths of *C. nassa* had 8 tentacles in a single verticil, while older ones had 16 tentacles in two alternating verticils. The smaller hydranths of *Cytaeis* sp. studied here had 4 to 5 tentacles in each of two closely placed whorls. This seeming difference may also be taxonomically unimportant, because Vervoort's (1967) material of *C. nassa* had 4 tentacles per whorl on the majority of hydranths. Finally, the manubrium of the young medusa in present collections was proportionately smaller than that described or illustrated in *C. nassa* by Millard (1959a, 1975), Rees (1962), and Millard and Bouillon (1973). As in *C. niotha* (Pennycuik, 1959), an inadequately known nominal species from Australia, hydranths of *C. nassa* appear to have been substantially larger than those of Bermudian specimens. Gonophores of *C. niotha*, although arising from the hydrorhiza, were unlike my material in being clustered around the bases of the hydranths. *Stylactis indica* Stechow, 1920, referred to *Cytaeis* by Rees (1962), is likewise poorly known; questions remain as to the nature of its gonophores and to its generic identity. Bermuda specimens differ from *C. uchidae* Rees, 1962, and *C. nuda* Rees, 1962, in having undeveloped instead of developed gonads in the newly liberated medusa. My material is

similar to descriptions of *C. imperialis* Uchida, 1964, from Japan, but has not been identified as that species largely on zoogeographic grounds. ROM specimens may well belong to *Cytaeis tetrastyla* Eschscholtz, 1829, an epipelagic medusa known to occur near Bermuda (Bigelow, 1918). However, such an identification cannot be established at present because of lack of information on the life cycle of *C. tetrastyla*. Rearing of the medusa of Bermudian material will likely be necessary to ascertain whether it belongs to any of the previously named species of *Cytaeis*, or to an undescribed species.

The status of the various nominal species of *Cytaeis* is in need of clarification. Confusion exists in particular over *C. japonica* Uchida, 1927. It seems uncertain whether *C. japonica* is identical with *C. uchidae* (alternative spelling *C. uchidai*, as emended by Kramp, 1965). Rees (1962) believed that the two were distinct, while Uchida (1964) regarded them as conspecific. If they are conspecific, the specific name *japonica* has priority [Art. 23] and cannot be abandoned in favour of the name *uchidae*, as proposed by Uchida (1964). The name *C. japonica* originally encompassed at least two and possibly three different species of medusae. Uchida (1930) realized that what he originally thought (Uchida, 1927) was the young medusa with medusa buds of *C. japonica* was identical with *Podocoryna simplex* Kramp, 1928, instead. In addition, he later indicated (Uchida, 1964) that the name *C. japonica* encompassed *C. imperialis* as well. Kramp (1961, 1965) regarded *C. japonica* as a synonym of *C. tetrastyla*. Further research is needed to clarify the relationships of the Japanese species of *Cytaeis*.

Hydroids of the genus *Cytaeis* have not been reported before from Bermuda.

Family Hydractiniidae L. Agassiz, 1862

Hydractinidae L. Agassiz, 1862:339 [emended to Hydractiniidae by Hincks, 1868:18].

Podocorynidae Allman, 1864a:353.

Stylactidae Haeckel, 1889:79.

Janariidae Stechow, 1921b:29.

DIAGNOSIS

Hydroid colonies stolonal. Hydrorhiza consisting of tubes covered with chitinous perisarc, or an encrustation of naked coenosarc with or without a calcareous skeleton, frequently with spines, less frequently with calcareous branches. Hydranths sessile, naked, polymorphic, as gastrozooids, gonozooids, and occasionally dactylozooids. Gastrozooids of one or more types, usually with one or more close whorls of filiform tentacles encircling a conical to club-shaped hypostome; gonozooids with or without filiform

tentacles; dactylozooids elongate, lacking tentacles.

Gonophores fixed sporosacs or free medusae, usually borne on gonozooids. Medusa well developed to degenerate, more or less bell-shaped. Manubrium tubular to sac-shaped, with or without a peduncle; rim of manubrium tubular or with four branched or unbranched lips, having terminal batteries of nematocysts; mouth present or absent. Radial canals four. Marginal tentacles solid, four, eight, or more. Ocelli present or absent. Gonads on manubrium, sometimes extending along proximal portions of radial canals.

REMARKS

Rees (1962) provided the first clear distinction between hydroids of the closely related families Hydractiniidae L. Agassiz, 1862, and Cytaeididae L. Agassiz, 1862. Ac-

ording to his diagnosis, followed here, cytaeid hydroids differ from hydractiniids in completely lacking spines on the hydrorhiza, and in having gonophores on the hydrorhiza instead of on gonozooids. The status of the nominal family Stylactidae Haeckel, 1889, referred to the Hydractiniidae here, is discussed under the family Cytaeididae elsewhere in this report (see pp. 28–29).

Bouillon (1978b) briefly discussed the Hydractiniidae, including it together with the families Stylasteridae Gray, 1847, Ptilocodiidae Coward, 1909, and Rhysiidae Brinckmann, 1965, in a newly recognized superfamily Hydractinioidea L. Agassiz, 1862 [Art. 36].

Generic limits within the Hydractiniidae are problematic (Motz-Kossowska, 1905; Goette, 1916; Stechow, 1923a; Kramp, 1932; Iwasa, 1934; Rees, 1962; Bouillon, 1971, 1985; Millard, 1975). Stechow (1923a), for example, recognized 14 recent (nonfossil) genera in his classification of the subfamily Hydractiniinae. In a re-examination of Stechow's classification, Kramp (1932) included no more than five of these in the group: he combined seven within *Hydractinia* (*Halerella* Stechow, 1922, *Stylactis* Allman, 1864a, *Cionistes* Wright, 1861, *Podocoryna* M. Sars, 1846, *Hydronema* Stechow, 1921a, *Hydractinia* van Beneden, 1841, and *Hydrissa* Stechow, 1921a), excluded four from discussion (*Clavactinia* Thornely, 1904, *Rhizohydra* Cope, 1884, *Hydrocorella* Stechow, 1921b, and *Hydractomma* Stechow, 1921a), and dismissed the remaining three as pandeids (*Perigonella* Stechow, 1921c, *Podocorella* Stechow, 1921c, and apparently *Clavopsis* Graeffe, 1883). Kramp recognized two subgenera, *Hydractinia* and *Stylactis*, within the genus *Hydractinia*. More recently, Bouillon (1985) included the nominal genera *Clavactinia*, *Hansiella* Bouillon, 1980, *Hydractinia*, *Hydrocorella*, *Janaria* Stechow, 1921b, *Kinetocodium* Kramp, 1921, *Podocoryna* (as *Podocoryne*; but *Podocoryne* is an incorrect subsequent spelling of *Podocoryna*, first used by Lütken, 1850), *Stylactis*, and *Tregoubovia* Picard, 1958, in the Hydractiniidae. *Kinetocodium* possesses characters of both the Hydractiniidae and the Cytaeididae, and its systematic position is unclear at present. *Stylactis* is a synonym of *Hydractinia*, as noted by Stechow (1923a) and others, and *Stylactis* auct., to which Bermuda material belongs, is replaced here by *Stylactaria* Stechow, 1921a. Much confusion remains at the generic level within this family, and taxonomic revision is badly needed.

Genus *Stylactaria* Stechow, 1921a

Stylactaria Stechow, 1921a:250.

DIAGNOSIS

Hydractiniidae with reticular hydrorhiza; hydrorhizal stolons covered with perisarc; hydrorhiza not encrusting, nor

covered with naked coenosarc, nor forming a calcareous skeleton. Hydrorhizal spines present or absent. Hydranths typical of the family.

Gonophores fixed sporosacs or free but degenerate medusae, borne on gonozooids beneath whorl of oral tentacles; newly liberated medusa sac-shaped. Manubrium simple, tubular, without mouth, oral lips, or oral tentacles. Tentacles 8 to 10 in number, rudimentary. Radial canals four. Ocelli absent. Gonad surrounding manubrium.

TYPE SPECIES

Stylactis inermis Allman, 1872, by monotypy.

REMARKS

The nominal genus *Stylactis* Allman, 1864a, was constituted to accommodate two species, *Podocoryne sarsii* Steenstrup, 1850, and *Podocoryna fucicola* M. Sars, 1857. A retiform hydrorhiza, consisting of anastomosing tubes covered with perisarc, was regarded as diagnostic of the genus (Allman, 1864a). Bonnevie (1898) discovered that the hydrorhiza in type material of *P. sarsii* was encrusting and covered with naked coenosarc. She did not, as suggested by Iwasa (1934) and others, mention examining material of *P. fucicola* as well. However, the hydrorhiza of *P. fucicola* also appears to be encrusting with naked coenosarc (see Castric-Fey, 1970). I concur with Goette (1916), Stechow (1923a), Iwasa (1934), and others that these two species, with their encrusting hydrorhizae, are best referred to the genus *Hydractinia* van Beneden, 1841. The type species of *Stylactis* must be one of these two originally included species [Art. 69], not one subsequently referred to the genus such as *Stylactis inermis* Allman, 1872 (see Millard, 1975). Mayer (1910) designated *P. fucicola* (misspelled as *Stylactis fuciola*) type species of *Stylactis*. *Podocoryna fucicola* is referred to *Hydractinia* (e.g., see Stechow, 1923a; Iwasa, 1934; Castric-Fey, 1970), and the name *Stylactis* is a junior subjective synonym of *Hydractinia*, as noted earlier by Stechow (1923a).

Stechow (1923a) suggested, incorrectly, that the name *Stylactella* Haeckel, 1889, be used for species of *Stylactis* auct. Three nominal species were originally included in *Stylactella* by Haeckel (1889), *S. abyssicola* Haeckel, 1889, *S. spongicola* Haeckel, 1889, and *S. vermicola* Allman, 1888. Gonophores in all three reportedly arise from the hydrorhiza and not from gonozooids (Allman, 1888; Haeckel, 1889; Iwasa, 1934; Rees, 1962); they should be included in the family Cytaeididae rather than in the Hydractiniidae (Rees, 1962). Thus, the name *Stylactella* cannot replace *Stylactis* auct., species of which have gonophores on gonozooids. Rees (1962) regarded *Stylactella* as an insufficiently described genus of cytaeid, and included *S. vermicola* as its type and only known species. He transferred both *S. spongicola* and *S. abyssicola* to *Perarella* Stechow, 1922, also included in the family Cytaeididae.

Stechow (1921a) proposed that the new name *Stylactaria* be applied to those species of *Stylactis* auct. with gonophores on gonozooids, if such hydroids were to be recognized as a distinct genus, and designated *Stylactis inermis* Allman, 1872, as type species of the genus. *Stylactaria* is recognized here as the valid name of the genus. *Stylactaria inermis* reportedly produces fixed sporosacs (Bouillon, 1971), while some species of *Stylactis* sensu Mayer (1910) may liberate degenerate medusae. Given the variation of gonophore development among species of the group, a separate genus for those liberating a degenerate medusa seems unjustified.

Stechow (1923a) included the nominal genus *Clavopsis* Graeffe, 1883, characterized by the presence of free but degenerate medusae, in the Hydractiniidae L. Agassiz, 1862. He believed that *Stylactis* sensu Mayer (1910) corresponded with that nominal genus. However, Graeffe's account of the type species of *Clavopsis*, *C. adriatica* Graeffe, 1883, was of a hydroid that was more likely a pandeoid or possibly a bougainvillioid than a hydractiniid. The hydranth pedicel of *C. adriatica* was enveloped in thin perisarc, and there was no clear evidence given of polymorphism in the species. *Clavopsis* is certainly not a synonym of *Stylactis* sensu Mayer (1910), and hence not of *Stylactaria* either.

Stylactaria differs from *Hydractinia*, *Podocoryna* M. Sars, 1846, *Clavactinia* Thornely, 1904, *Hydractomma* Stechow, 1921a, and *Hydrissa* Stechow, 1921a, in having a reticular, nonencrusting hydrorhiza devoid of naked coenosarc. The hydrorhiza does not form a calcareous skeleton, as in *Hydrocorella* Stechow, 1921b, and *Janaria* Stechow, 1921b. Unlike *Podocoryna*, which liberates a well-developed medusa, *Stylactaria* has fixed gonophores or a degenerate, short-lived medusa. *Stylactaria* differs from *Kinetocodium* Kramp, 1921, in having well-developed instead of reduced oval tentacles, and gonophores arising from gonozooids rather than from the hydrorhiza.

Species assigned to *Stylactaria* here, in addition to *S. inermis*, are *S. arge* (Clarke, 1882), *S. arctica* (Jäderholm, 1902), *S. ingolfi* (Kramp, 1932), *S. pisicola* (Komai, 1932), *S. yerii* (Iwasa, 1934), *S. carcinicola* (Hiro, 1939), and *S. claviformis* (Bouillon, 1971). I have not included *Hydractinia pruvoti* Motz-Kossowska, 1905, in the genus because of its hydrorhiza, which is encrusting rather than reticular. Moreover, its medusa is campanulate instead of sac-shaped, and four tentacles are present instead of eight. It was included by Stechow (1921a) as the only species in his new genus *Hydractomma*.

***Stylactaria arge* (Clarke, 1882), comb. nov.**

Figs. 23, 24

Stylactis arge Clarke, 1882:135; pl. 8, figs. 18–20.

Sytlactis arge Clarke, 1882:138 [lapsus].

Stylactis hooperii Sigerfoos, 1899:802; figs. 1–5.

Stylactis hooperi—Hargitt, 1901a:311 [incorrect subsequent spelling].

Stylactis hoopei—Komai, 1932:451 [incorrect subsequent spelling].

Stylactis sp. Crowell, 1947:206.

Hydractinia arge—Calder, 1971:31; pl. 2, fig. B; pl. 7, fig. A.

Stylactis hooperi var. *minor* Wedler and Larson, 1986:94; fig. 10c [incorrect subsequent spelling].

TYPE LOCALITY

Crisfield, Maryland, on Chesapeake Bay, United States.

MATERIAL EXAMINED

Green Bay, Harrington Sound, on shell of *Cerithium litteratum* from *Cladophora* bed, –2 m, 11 July 1983, 1 colony, with gonozooids and male gonophores, two medusae liberated in laboratory from hydroid, ROMIZ B354. Green Bay, Harrington Sound, on shells of *C. litteratum* from *Cladophora* bed, –3 m, 11 July 1983, 2 colonies, one male and one female, with gonozooids and gonophores, ROMIZ B355. Green Bay, Harrington Sound, on shells of *C. litteratum* from *Cladophora* bed, –1.5 m, 27 June 1983, 13 colonies, with gonozooids and gonophores, ROMIZ B356. Green Bay, Harrington Sound, on shells of *C. litteratum* from *Cladophora* bed, –3 m, 4 October 1986, 2 colonies, with gonozooids and gonophores, ROMIZ B367.

DESCRIPTION

Colony stolonial, with branching and anastomosing hydrorhizal stolons adhering to gastropod shell. Perisarc thin, smooth or with irregular wrinkles, terminating at base of hydranth, not dilated as cup-shaped collar. Spines chitinous, simple, inconspicuous in unstained material, up to 0.3 mm high, arising from hydrorhizal stolons. Polyps of two types, gastrozooids and gonozooids. Gastrozooids contractile, variable in shape but generally clavate, up to 2 mm high, 0.3 mm wide, somewhat bulbous and rugose beneath tentacular whorl, slightly to distinctly constricted at insertion with hydrorhiza. Tentacles filiform, 8 to 16 in number on fully developed gastrozooids, in two closely placed whorls, those of upper whorl held somewhat more erect than those of lower whorl in life. Hypostome dome-shaped to clavate to knob-shaped. Gonozooids columnar, contractile, up to 1.7 mm high, 0.2 mm wide; region beneath tentacular whorl smooth and slender. Tentacles filiform, 5 to 10 in number, in one whorl. Medusa buds arising proximal to tentacular whorl, usually with two buds on opposite sides of gonozooid. Hypostome bulbous to dome-shaped. Sexes separate.

Nematocysts—

Gastrozooids: desmonemes 5.0–5.7 μm \times 2.8–3.3 μm ;

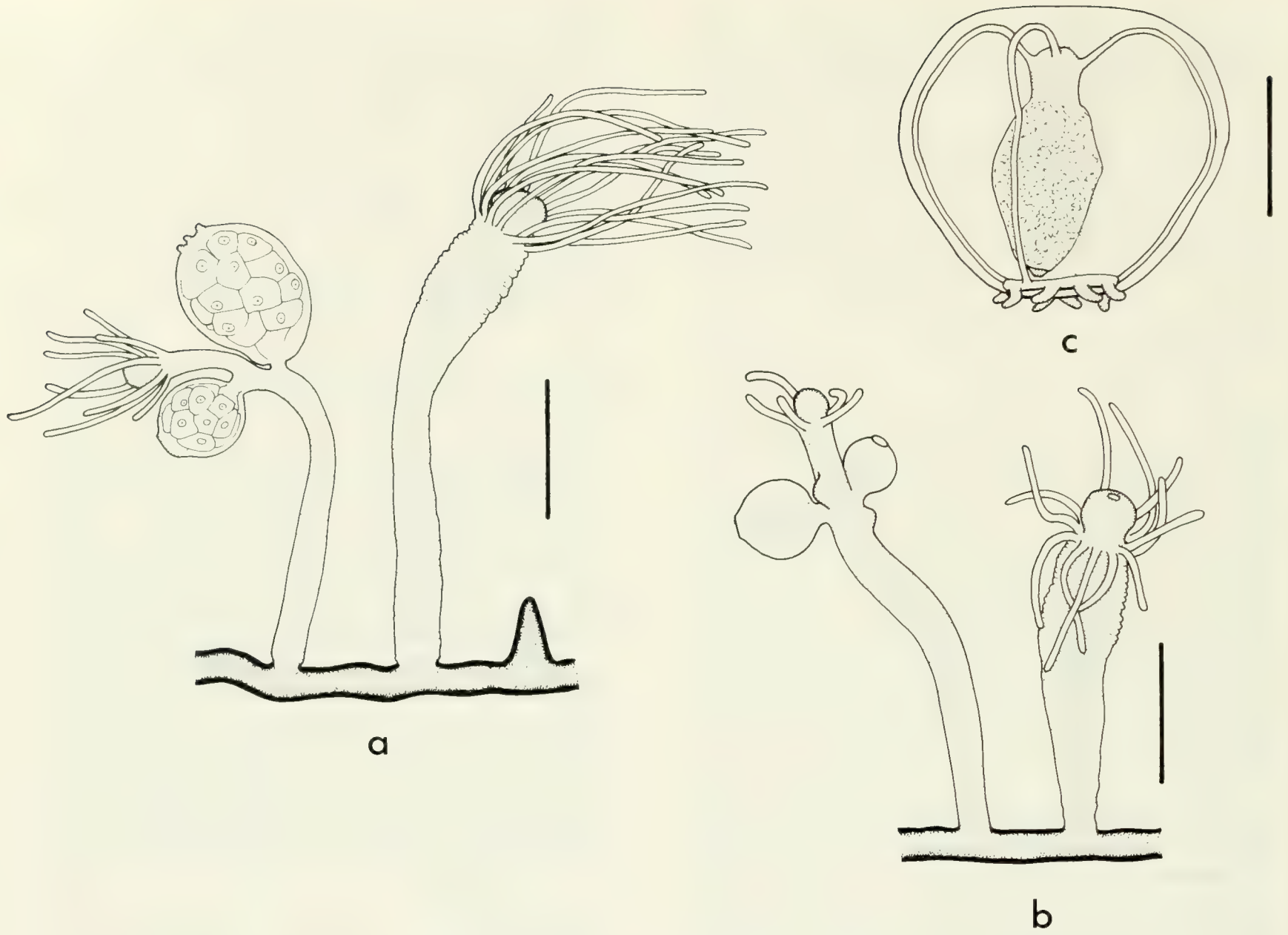


FIG. 23. *Stylactaria arge*. Scales equal 0.5 mm. *a*, Gastrozoid, and gonozoid with female medusa buds, ROMIZ B355. *b*, Gastrozoid, and gonozoid with male medusa buds, ROMIZ B354. *c*, Male medusa, one to two hours old, ROMIZ B354.

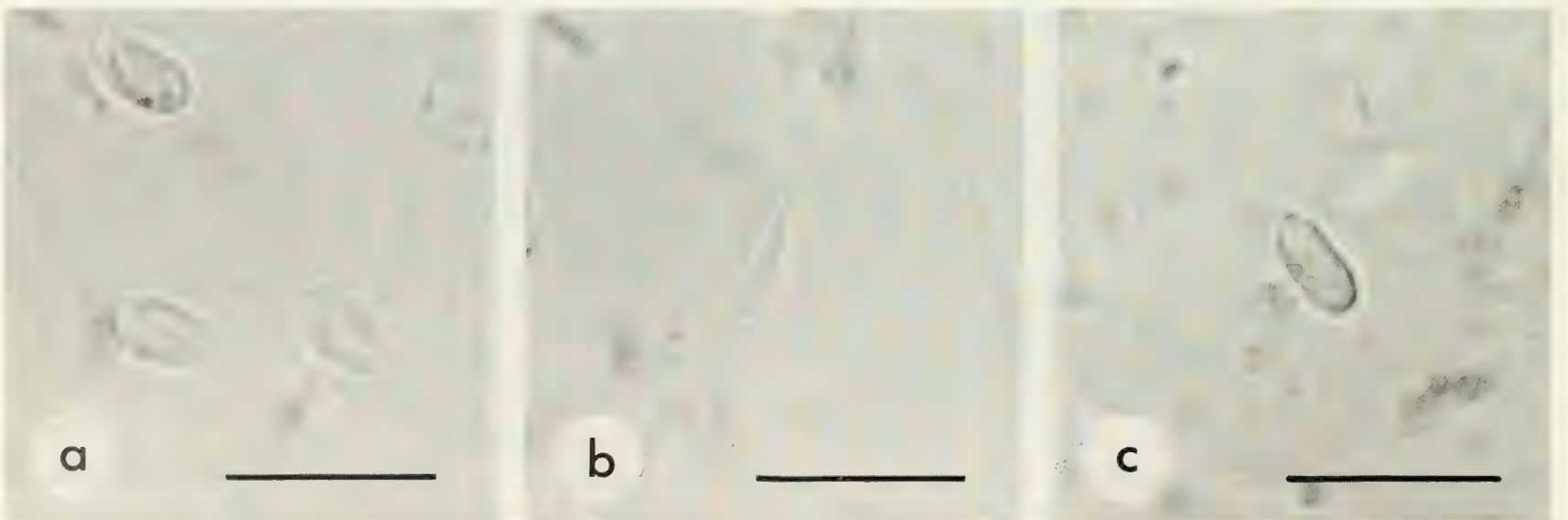


FIG. 24. *Stylactaria arge*, nematocysts of gastrozoid and gonozoid. Scales equal 10 μm . *a*, Desmonemes of gastrozoid, ROMIZ B354. *b*, Heterotrichous microbasic eurytele of gastrozoid, ROMIZ B354. *c*, Haploneme of gonozoid, ROMIZ B367.

heterotrichous microbasic euryteles 7.3–7.8 μm \times 2.6–2.8 μm .

Gonozooids: desmonemes 5.5–6.5 μm \times 3.0–3.8 μm ; haplonemes 4.9–6.6 μm \times 2.4–2.7 μm ; heterotrichous microbasic euryteles 8.3–10.2 μm \times 2.9–3.7 μm .

Medusa sac-shaped, degenerate, about 1.1 mm high and 1.2 mm wide in formalin-preserved specimens; mesoglea thin. Manubrium tubular, extending nearly to velar opening; mouth, oral arms, and oral tentacles lacking. Radial canals four; narrow ring canal present. Tentacles eight in number, rudimentary. Ocelli absent. Gonads encircling manubrium, fully developed prior to liberation of medusa.

Nematocysts—

Medusae: desmonemes 4.8–5.6 μm \times 2.6–3.0 μm ; heterotrichous microbasic euryteles 5.9–6.9 μm \times 2.4–2.9 μm .

REMARKS

Medusae of *Stylactaria arge* (Clarke, 1882) and *S. hooperii* (Sigerfoos, 1899) are inseparable from existing descriptions (Clarke, 1882; Sigerfoos, 1899). Accounts of their hydroids differ only in minor respects (Fraser, 1944; Crowell, 1947; Calder, 1971, 1975). From the original descriptions (Clarke, 1882; Sigerfoos, 1899), *S. hooperii* seems to differ from *S. arge* in having (1) somewhat smaller

gastrozooids, (2) gastrozooids that do not reproduce asexually by autotomy, (3) gastrozooid tentacles in a single row rather than in two closely placed whorls, and (4) spines on the hydrorhiza. I have been unable to locate type material of either nominal species for comparison. Apparent differences such as those noted above are interpreted here as nothing more than variation that might be expected within a single species, and *S. hooperii* is regarded here as conspecific with *S. arge*. Both nominal species were originally described from eelgrass beds on the middle Atlantic coast of the United States. Calder (1971, 1975) earlier referred Crowell's (1947) report of *Stylactis* sp. to this species.

Specimens referred here to *Stylactaria arge* were less robust than the hydroids described by Clarke (1882) and Sigerfoos (1899), as also were colonies described earlier (ROMIZ B666) from Chesapeake Bay (Calder, 1971). There seems little likelihood, from their overall similarity to *S. arge*, that the specimens from Bermuda represent a distinct species. As in material from the United States, medusae were degenerate, short-lived, sexually mature at release, and liberated from the hydroids only at dusk.

KNOWN RANGE

Bermuda: first record.

Elsewhere: western Atlantic (Calder, 1975).

Superfamily Pandeoidea Haeckel, 1879

?Trichydridae Hincks, 1868:215.

Tiaridae Haeckel, 1879:40 [invalid name, type genus a junior homonym].

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

Amphinemidae Haeckel, 1879:46.

Protiaridae Haeckel, 1879:46.

Bythotiaridae Maas, 1905:434.

Calycopsidi Mayer, 1910:104.

Stomotocini Cockerell, 1911:79.

Hydrichthyinae Stechow, 1922:142.

?Timoididae Kramp, 1961:138.

Niobiidae Petersen, 1979:133.

Halimedusidae Arai and Brinckmann-Voss, 1980:62.

DIAGNOSIS

Hydroid colonies stolonial or erect, with a creeping hydrorhiza; some taxa ectoparasitic on fishes and ichthyoparasitic copepods, arising from a basal plate embedded in tissues of host. Perisarc variably developed; pseudo-hydrotheca present or absent. Hydranths of free-living forms with a single, oral whorl of filiform tentacles surrounding

a conical hypostome; those of parasitic forms elongate, degenerate, lacking tentacles.

Gonophores free medusae, arising from hydrorhiza, hydrocaulus, branches, pedicels, or hydranths. Medusae bell-shaped, with or without an apical projection; manubrium quadrate, with or without a peduncle; oral tentacles absent; mouth surrounded by four, or infrequently eight, lips with or without marginal nematocyst batteries. Radial canals four, or infrequently eight; centripetal canals usually absent. Marginal tentacles hollow, two, four, or more, with or without conical basal bulbs. Ocelli present or absent. Gonads on manubrium, extending outwards along radial canals in some species.

REMARKS

Pelagiana trichodesmiae Borstad and Brinckmann-Voss, 1979, is evidently referable to the superfamily Pandeoidea Haeckel, 1879, but the family to which it should be referred is uncertain at present. Accordingly, only the superfamily for this species is given here.

Classification of the Pandeoidea is based largely on the medusa stage because hydroids of most genera within the

superfamily are unknown. A thorough revision of the Pandeidae by Hartlaub (1914) improved taxonomic understanding of the family, though he retained the name Tiaridae Haeckel, 1879, for the group. The name Tiaridae Haeckel, 1879, is invalid (Bigelow, 1913) because *Tiara* Lesson, 1843, its nominal type genus, is a junior homonym of *Tiara* Swainson, 1832, a mollusc [Art. 39]. Bigelow's (1913) use of the name Pandeidae for the family has been widely followed in the subsequent literature (e.g., Bigelow, 1918; Russell, 1953; Rees, 1956a; Yamada, 1959; Kramp, 1961; Goy, 1972; Millard, 1975; Petersen, 1979; Arai and Brinckmann-Voss, 1980; Bouillon, 1980, 1985).

Medusa taxonomists have recently recognized that the family Pandeidae, as envisaged earlier this century, encompassed a mixed assemblage of genera. Some authors (e.g., Russell, 1953; Arai and Brinckmann-Voss, 1980) have divided the Pandeidae into a number of subfamilies. Petersen (1979) recognized a group of families, including the Calycopsidae Mayer, 1910, Protiaridae Haeckel, 1879, Pandeidae, and Niobiidae Petersen, 1979, within a superfamily, the Pandeoidea. The Trichydridae Hincks, 1868, and Halimedusidae Arai and Brinckmann-Voss, 1980, were also included in this superfamily by Bouillon (1985). However, if the Trichydridae is included in this taxon, the superfamily name Trichydroidea Hincks, 1868, would predate the name Pandeoidea Haeckel, 1879 [Arts. 23a, 36]. It seems likely that further refinements to the classification of the group will become necessary as knowledge of these hydrozoans advances.

Stechow (1922) established the subfamily Hydrichthyinae based on the parasitic hydroid genus *Hydrichthys* Fewkes, 1887. Fraser (1944) recognized the group as a distinct family, the Hydrichthyidae. Millard (1975) included *Hydrichthys* in the Pandeidae based on the morphology of its medusa stage. Through life-cycle studies, Larson (1982) identified the medusa of a *Hydrichthys* hydroid as *Stomotoca pterophylla* Haeckel, 1879, a pandeid. The family-group name Hydrichthyinae is, therefore, included here within the synonymy of the Pandeoidea. Larson (1982) concluded that the genus name *Hydrichthys* was a synonym of *Stomotoca* L. Agassiz, 1862, but Arai (in press) disagreed. She noted that medusae of the genus *Stomotoca* possess two tentacles, whereas immature medusae of *Hydrichthys mirus* Fewkes, 1887, type species of *Hydrichthys*, have four tentacles (Fewkes, 1887).

Bouillon (1980) observed that the gonads of *Timoides agassizii* Bigelow, 1904, arose from the manubrium of the medusa rather than from the radial canals as believed earlier, and placed the family name Timoididae Kramp, 1961, in synonymy with the Pandeidae.

Hydroids of several pandeoid medusa genera have been placed in the nominal genus *Perigonimus* M. Sars, 1846. However, *Perigonimus* is a junior subjective synonym of *Bougainvillia* Lesson, 1830 (see p. 24).

Genus *Pelagiana* Borstad and Brinckmann-Voss, 1979

Pelagiana Borstad and Brinckmann-Voss, 1979:1233.

DIAGNOSIS

Hydroids on planktonic blue-green "algae" (*Trichodesmium thiebautii*); body globular with conical hypostome. Tentacles filiform, in an oral whorl; tentacular nematocysts arranged in two spiral bands.

Gonophores free medusae, arising from hydranth proximal to tentacular whorl. Young medusa thimble-shaped, with four radial canals. Mouth quadrate, without(?) clusters of nematocysts or oral tentacles. Tentacle bulbs four, triangular, with one opposite pair larger than the other; marginal tentacles two, solitary, filiform, arising from the larger pair of tentacle bulbs. Ocelli absent. Adult medusa unknown.

TYPE SPECIES

Pelagiana trichodesmiae Borstad and Brinckmann-Voss, 1979, by original designation.

REMARKS

Borstad and Brinckmann-Voss (1979) tentatively referred their nominal genus *Pelagiana* to the family Pandeidae Haeckel, 1879. They noted that the young medusa of *P. trichodesmiae* Borstad and Brinckmann-Voss, 1979, type species of the genus, resembles the Pandeidae in having large, triangular tentacle bulbs, filiform tentacles, four radial canals, and a four-cornered mouth. The hydroid also has a number of characters found in pandeids: it is monomorphic, and it has a single whorl of filiform tentacles and a conical hypostome. Nevertheless, the systematic position of this species is uncertain because its medusa has yet to be reared to maturity, and in the absence of more detailed information it is referred here only to the superfamily Pandeoidea.

Borstad and Brinckmann-Voss (1979) observed that pandeid medusae undergo considerable morphological change during development, and suggested that life-cycle studies may demonstrate that this hydrozoan belongs to a species that is already known.

Pelagiana trichodesmiae Borstad and Brinckmann-Voss, 1979

Figs. 25, 26

Pelagiana trichodesmiae Borstad and Brinckmann-Voss, 1979:1233; figs. 1–3 [hydroid and young medusa].

TYPE LOCALITY

Barbados, West Indies.

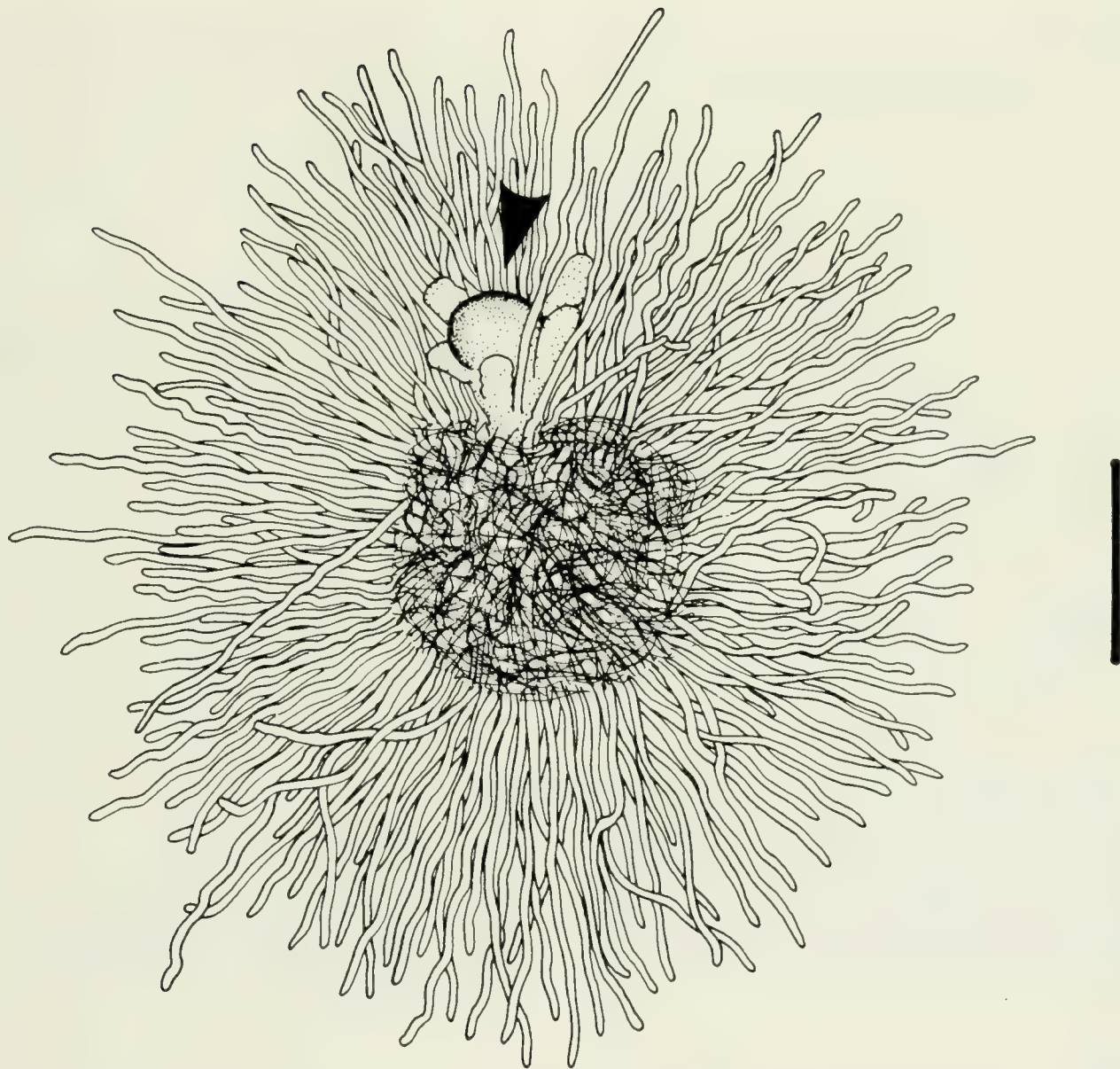


FIG. 25. *Pelagiana trichodesmiae*, hydroid on clump of *Trichodesmium thiebautii*, ROMIZ B352. Scale equals 0.25 mm.

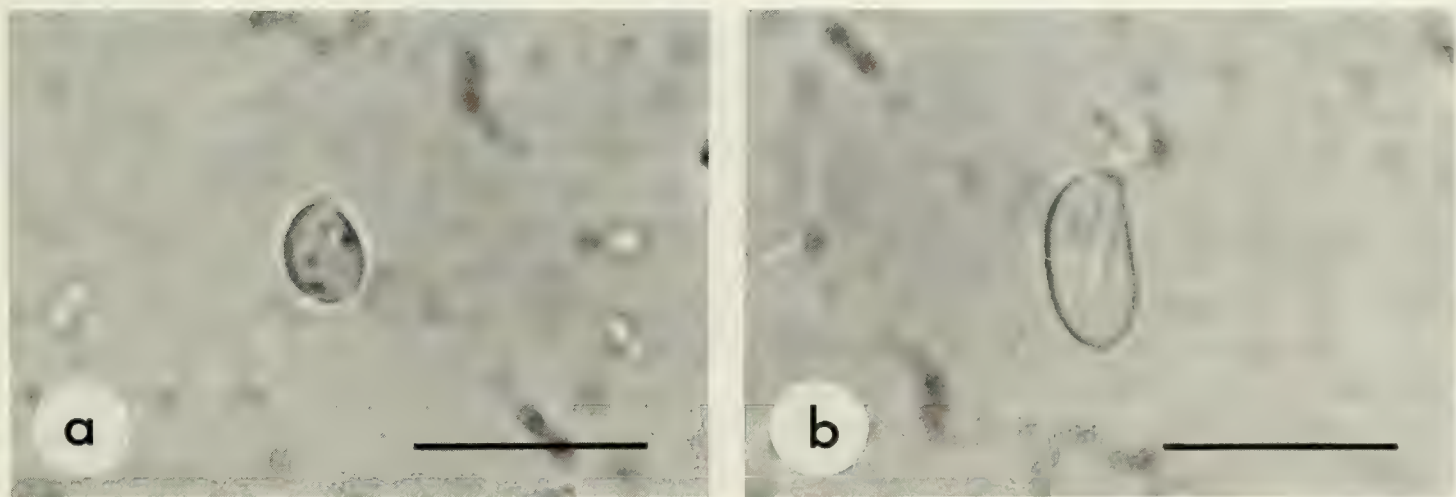


FIG. 26. *Pelagiana trichodesmiae*, nematocysts of hydranth, ROMIZ B352. Scales equal 10 μ m. *a*, Desmoneme. *b*, Heterotrichous microbasic eurytele.

MATERIAL EXAMINED

Atlantic Ocean, 6 km southwest of Gibbs Hill lighthouse, on *Trichodesmium thiebautii*, - 1 m, 3 October 1984, two colonies, 0.3 mm high, without gonophores, ROMIZ B352.

DESCRIPTION

Hydroids minuscule, inconspicuous, solitary or forming stolonial colonies of a few hydranths; hydrorhiza with thin perisarc, embedded in filamentous tufts of planktonic *Trichodesmium thiebautii*. Hydranths sac-shaped to pear-shaped, up to 345 μm high, 195 μm wide, constricted at juncture with hydrorhiza. Tentacles four to five in number, filiform, in an oral whorl. Hypostome relatively large, dome-shaped, with terminal mouth.

Gonophores not seen.

Nematocysts—

Hydroids: desmonemes 4.6–5.2 μm \times 3.4–3.8 μm ; heterotrichous microbasic euryteles 6.8–7.9 μm \times 3.0–4.0 μm .

REMARKS

Geiselman (1977) collected hydroids of this species in plankton samples from the subtropical Atlantic, but did not name them. Borstad and Brinckmann-Voss (1979) described and named *Pelagiana trichodesmiae* from material collected at Barbados. Its hydroid has been reported only on *Trichodesmium thiebautii*, an oceanic blue-green "alga."

Borstad and Brinckmann-Voss (1979) described the medusa of *Pelagiana trichodesmiae* from a single specimen newly liberated from its hydroid, and did not find this stage in the plankton. Clarification of the possible synonymy of this species awaits the rearing of its medusa to a more advanced stage.

Although the hydroid of *Pelagiana trichodesmiae* is inconspicuous and poorly known, it appears to be relatively common. Geiselman (1977) found it in about 40 per cent of her near-surface collections of *Trichodesmium thiebautii* from the subtropical North Atlantic. Borstad and Brinckmann-Voss (1979) found it every month of the year at Barbados between August 1974 and June 1976. It was immediately located in a plankton sample taken off Bermuda during this study. Given the occurrence of *T. thiebautii* in all tropical oceans, Borstad and Brinckmann-Voss hypothesized that the species may have a wide distribution.

Hydroids of this species were collected by Geiselman (1977) during a cruise "from Spain to Bermuda," but the closest of her records to Bermuda was in mid-North Atlantic near 30° N, 44° W.

KNOWN RANGE

Bermuda: first record.

Elsewhere: western Atlantic (Borstad and Brinckmann-Voss, 1979); eastern Atlantic (Geiselman, 1977).

Family Eudendriidae L. Agassiz, 1862

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

Myrionemidae Pictet, 1893:18.

DIAGNOSIS

Hydroid colonies usually erect with branched hydrocauli, arising from a creeping hydrorhiza; growth monopodial with terminal hydranths. Perisarc firm, reaching to groove at base of hydranth. Hydranth often large, urn-shaped to elongate; hypostome typically flared, flexible. Tentacles filiform, in a single whorl or in two or more close whorls.

Gonophores fixed sporosacs, originating on hydranth beneath tentacles, often arranged in a whorl, reproductive hydranth often reduced to a blastostyle. Male gonophore with one or more bulbous chambers, successive chambers in a linear series. Female gonophore initially with curved spadix, each spadix supporting a single egg.

REMARKS

Species of the family Eudendriidae L. Agassiz, 1862, are immediately distinguishable from other athecate hydroids by the shape of the hypostome, which is large, flexible,

and usually flaring distally. The classification of the Eudendriidae has been spared the dual nomenclature found in many other families of athecate hydroids because all known species reproduce sexually by fixed sporosacs. The sexes are usually on separate colonies, although *Eudendrium motzkossowskiae* Picard, 1951, is reportedly hermaphroditic (Picard, 1951).

The family comprises two genera. *Eudendrium* Ehrenberg, 1834, a well-known genus with a worldwide distribution, includes many nominal species. *Myrionema* Pictet, 1893, has been reported infrequently, is apparently restricted to shallow-water habitats in the tropics and subtropics, and includes only three nominal species. Both genera are found in Bermuda.

Genus *Eudendrium* Ehrenberg, 1834

Calamella Oken, 1815:55 [invalid name, published in work rejected for nomenclatural purposes by the ICZN, Opinion 417].

Eudendrium Ehrenberg, 1834:72.

Corymbogonium Allman, 1861:171.

Edendrium Allman, 1872:295 [incorrect subsequent spelling].

Erudendrium Thompson, 1899:583 [incorrect subsequent spelling].

DIAGNOSIS

Eudendriidae with calyx of hydranth moderately short, urn-shaped. Tentacles in one whorl, of varied number but usually fewer than 35.

TYPE SPECIES

Tubularia ramosa Linnaeus, 1758, by subsequent designation by Allman (1872).

REMARKS

Cornelius (1976) noted that the widely used generic name *Eudendrium* Ehrenberg, 1834, was threatened by the infrequently used name *Thoa* Lamouroux, 1816. Two species had originally been included in *Thoa* by Lamouroux (1816), *T. savignii* Lamouroux, 1816, and *Sertularia halecina* Linnaeus, 1758. The former is a junior objective synonym of *Tubularia ramea* Pallas, 1766, a species now referred to *Eudendrium*. *Sertularia halecina* had commonly been referred to *Halecium* Oken, 1815, a generic name invalidated (Opinion 417) because it was originally published in a work that was not consistently binominal. As a solution to these nomenclatural problems, Lemche (1976) recommended that the ICZN (1) validate, under the plenary powers, the generic name *Halecium* Oken, 1815, as requested by Cornelius (1976), and (2) designate *Sertularia halecina* Linnaeus, 1758, as the type species of *Thoa*. This proposal was adopted (Opinion 1220), with *Thoa* becoming a junior objective synonym of the valid name *Halecium*.

Another threat to *Eudendrium* has been removed elsewhere in this report (p. 64) by designating *Tubularia muscoides* Linnaeus, 1761, as the type species of *Fistulana* O. F. Müller, 1776a. In so doing, *Fistulana* becomes a junior subjective synonym of *Coryne* Gaertner, 1774.

The genus *Eudendrium* comprises a common and distinctive group of hydroids. However, there are many nominal species in the genus that are by no means easily distinguished, and a large number of these are of questionable validity. Fraser (1944) noted that descriptions of many of the 22 nominal species of *Eudendrium* reported from the western North Atlantic are meagre and based on incomplete specimens. The taxonomy of the genus has been further complicated because species have often been described on the basis of taxonomically unreliable characters. In addition, there has been little evidence, particularly in the older literature, of an appreciation of the considerable range of colony form that can occur within a species.

Watson (1985) emphasized the value of the cnidome in identification of species of *Eudendrium* from Australia. Interspecific differences that were noted by Watson in the complement of nematocyst categories present, and in the length-width ratios of nematocyst capsules of a given category, could be used as a taxonomic character.

Eudendrium bermudense, sp. nov.

Figs. 27–29

MATERIAL EXAMINED

Holotype: Sailor's Choice Cave, Hamilton Parish, on ledge at entrance, – 1.5 m, 30 June 1983, one colony, 2.0 cm high, with female gonophores, ROMIZ B333. Paratypes: Sailor's Choice Cave, Hamilton Parish, on ledges and survey line at entrance, – 1 to – 2 m, 30 June 1983, two colonies, 3.2 and 3.8 cm high, with male gonophores; one colony, 2.0 cm high, with female gonophores; ROMIZ B334. Sailor's Choice Cave, Hamilton Parish, on ledges at entrance, – 1 m, 27 June 1983, three colonies, 2.0–3.5 cm high, with female gonophores, ROMIZ B335. Castle Harbour, under causeway near halfway point, on rocks and shells, – 1 m, 1 October 1986, five colonies, up to 6.6 cm high, with female gonophores; four colonies, up to 4.6 cm high, with male gonophores; one sterile colony, 3.5 cm high; ROMIZ B360.

DESCRIPTION

Colonies slender, straggly, up to 3.8 cm high, arising from a creeping hydrorhiza. Hydrocaulus upright, monosiphonic or slightly polysiphonic basally, more or less alternately branched in one plane, branches similarly rebranched or with alternate pedicels. Perisarc of moderate thickness, horn-coloured to dark brown basally, becoming progressively thinner and more colourless towards extremities, terminating at groove around base of hydranth, annulated at bases of hydrocaulus, branches, and pedicels, with occasional irregularly placed annulations elsewhere

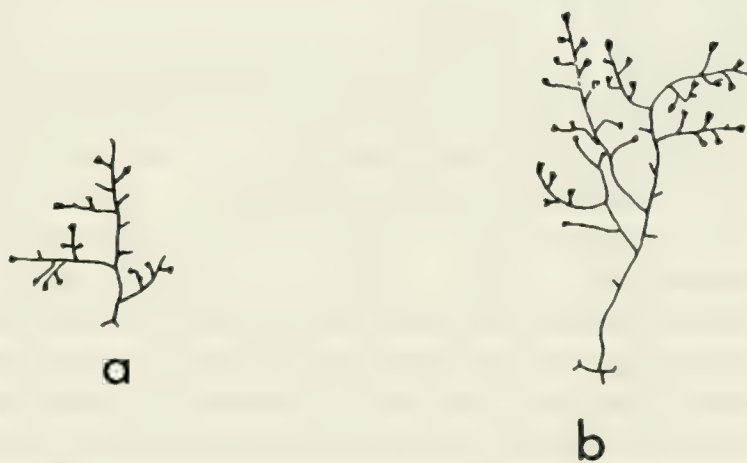


FIG. 27. *Eudendrium bermudense*, sp. nov., colony form. Natural size. a, Holotype, ROMIZ B333. b, Paratype, ROMIZ B334.

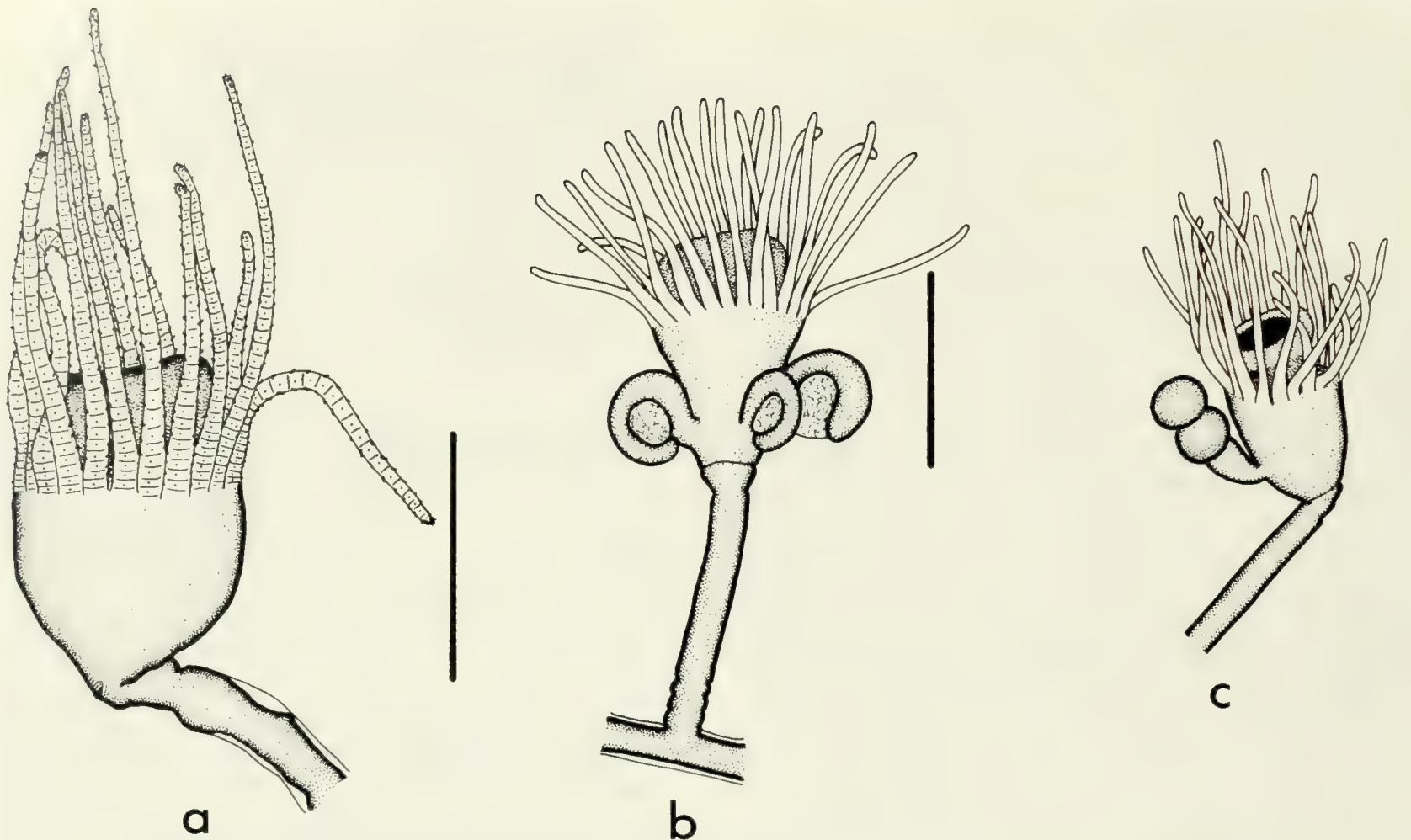


FIG. 28. *Eudendrium bermudense*, sp. nov., hydranths and gonophores. Scales equal 0.5 mm. *a*, Hydranth, holotype colony, ROMIZ B333. *b*, Hydranth with female gonophores, holotype colony, ROMIZ B333. *c*, Hydranth with male gonophores, paratype colony, ROMIZ B334.

but mostly smooth. Hydranths urn-shaped, 447–638 μm long from proximal end to base of hypostome when fully developed, 298–532 μm wide, with a shallow but distinct perisarc groove basally; hypostome large, knob-shaped to flared. Tentacles 21 to 26 in number, solid, filiform, in one whorl.

Gonophores fixed sporosacs, originating distal to perisarc groove on hydranth. Female gonophores borne in a whorl on entire hydranths, spadix unbranched, curving over egg. Male gonophores with one or two chambers, borne on entire hydranths.

Nematocysts—

Hydroids: macrobasic euryteles (on hypostome, hydranth base, coenosarc) 29.4–34.5 μm \times 12.3–14.0 μm ; heterotrichous microbasic euryteles (on tentacles, hypostome, hydranth, coenosarc) 8.0–8.4 μm \times 3.4–3.7 μm .

REMARKS

Eudendrium bermudense, sp. nov., differs from its Bermudian congeners in having macrobasic euryteles in addition to microbasic euryteles. In possessing nematocysts of the former category, *E. bermudense* resembles *E. infundibuliforme* Kirkpatrick, 1890, *E. glomeratum* Picard, 1951, and *E. motzkossowskiae* Picard, 1951, as well as

Myrionema amboinense Pictet, 1893. Unlike *E. infundibuliforme*, hydranth pedicels of *E. bermudense* are not expanded distally. In contrast with *E. glomeratum*, macrobasic euryteles of *E. bermudense* are scattered rather than being aggregated in dome-shaped batteries on the hydranth column. There is no evidence that the gonophores of *E. bermudense* are hermaphroditic, as has been reported in *E. motzkossowskiae* (e.g., see Motz-Kossowska, 1905; Picard, 1951; Millard, 1975; Boero, 1981). *Eudendrium bermudense* is immediately distinguishable from *M. amboinense* in having more regularly branched colonies, smaller hydranths, and fewer tentacles, and in lacking algal symbionts. The hydroids resemble descriptions of *E. angustum* Warren, 1908, which has large nematocysts of uncertain identity (Millard, 1975), but the hypostome of the latter is reportedly “blocked” by a solid plug of endodermal cells (Warren, 1908; Millard, 1975). No such plug was apparent in specimens of *E. bermudense*. Finally, large nematocysts, believed by Watson (1985) to be macrobasic euryteles, occur in *E. aylingae* Watson, 1985, and *E. currumbense* Watson, 1985. However, *E. aylingae* is apparently a much smaller species than *E. bermudense*, and the macrobasic euryteles(?) of *E. currumbense* are considerably smaller than those of *E. bermudense*.

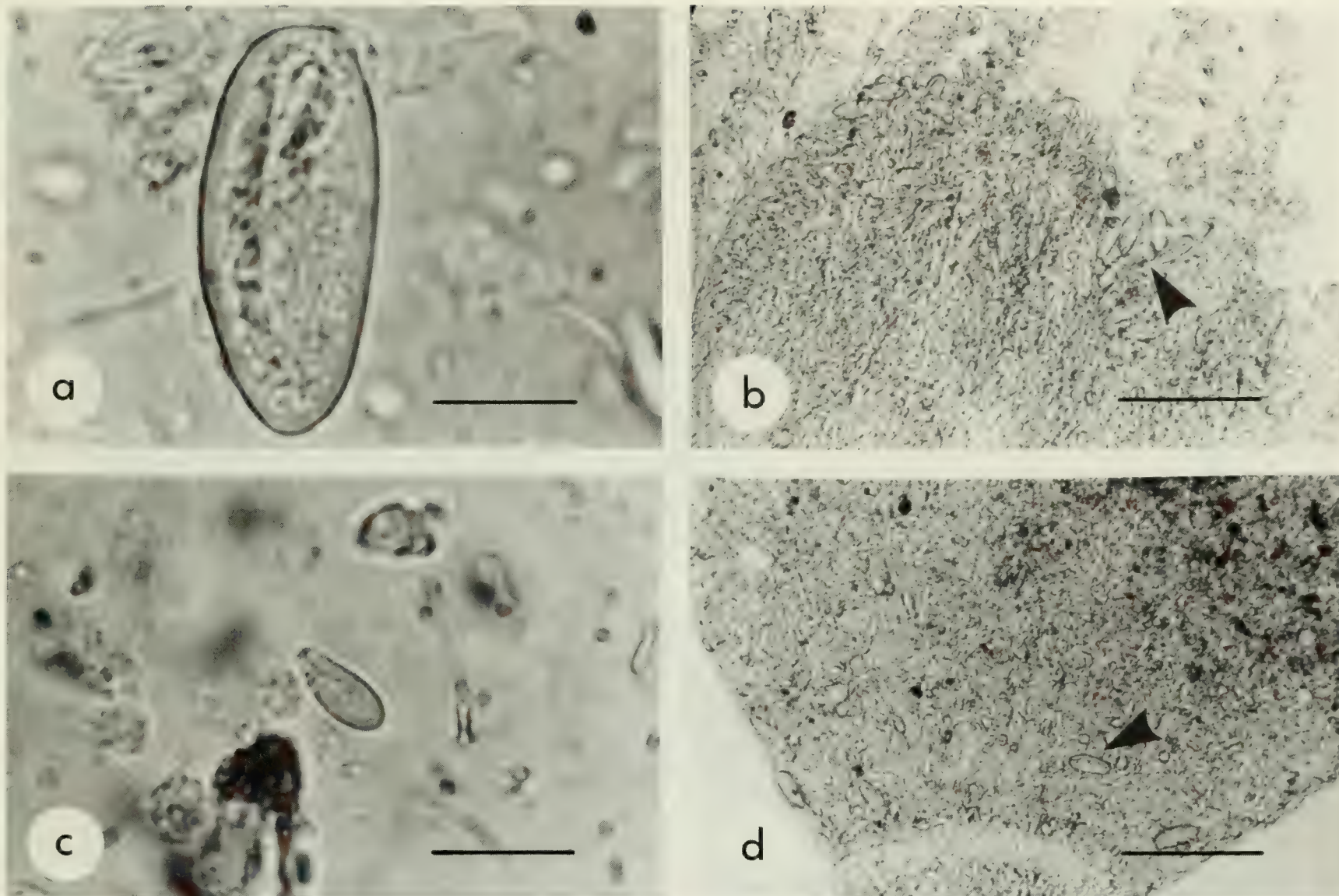


FIG. 29. *Eudendrium bermudense*, sp. nov., nematocysts of hydranth, ROMIZ B333. Scales for *a* and *c* equal 10 μm ; scales for *b* and *d* equal 100 μm . *a*, Macrobasal eurytele. *b*, Hypostome with macrobasal euryteles. *c*, Heterotranchous microbasal eurytele. *d*, Hydranth base with macrobasal euryteles.

ETYMOLOGY

The specific name refers to the occurrence of the species in Bermuda.

KNOWN RANGE

Known only from the type locality.

Eudendrium capillare Alder, 1856a

Figs. 30–32

Eudendrium capillare Alder, 1856a:355; pl. 12, figs. 9–12.

Corymbogonium capillare—Allman, 1861:171.

Dicoryne capillare—Alder, 1862:230.

Eudendrium tenue A. Agassiz, 1865:160; fig. 250.

Eudendrium capillare var. *mediterranea* Neppi, 1917:30.

Eudendrium parvum Warren, 1908:272; fig. 1; pl. 45, figs. 1–4.

not *Eudendrium* ?*capillare*—Millard, 1966:454 [= *Eudendrium ramosum* (Linnaeus, 1758)].

TYPE LOCALITY

Embleton Bay, Northumberland, Great Britain.

MATERIAL EXAMINED

Castle Island, Castle Harbour, on underside of flat rocks, –2 m, 30 July 1982, one colony, 13 mm high, with male gonophores; two colonies, 6–13 mm high, without gonophores; ROMIZ B142. Hungry Bay, on underside of flat rocks, –1.5 m, 6 September 1977, two colonies, 11–17 mm high, with female gonophores, ROMIZ B161.

DESCRIPTION

Colonies small, slender, straggly, up to 17 mm high, arising from a creeping hydrorhiza. Hydrocaulus upright, monosiphonic, 100–125 μm wide, irregularly to more or less alternately branched; branches in turn alternately to irregularly branched; pedicels often long and bent. Perisarc relatively thick and golden-coloured at base of colony, becoming progressively thinner and colourless towards extremities, terminating at groove around base of hydranth.



FIG. 30. *Eudendrium capillare*, colony form, ROMIZ B142.
Natural size.

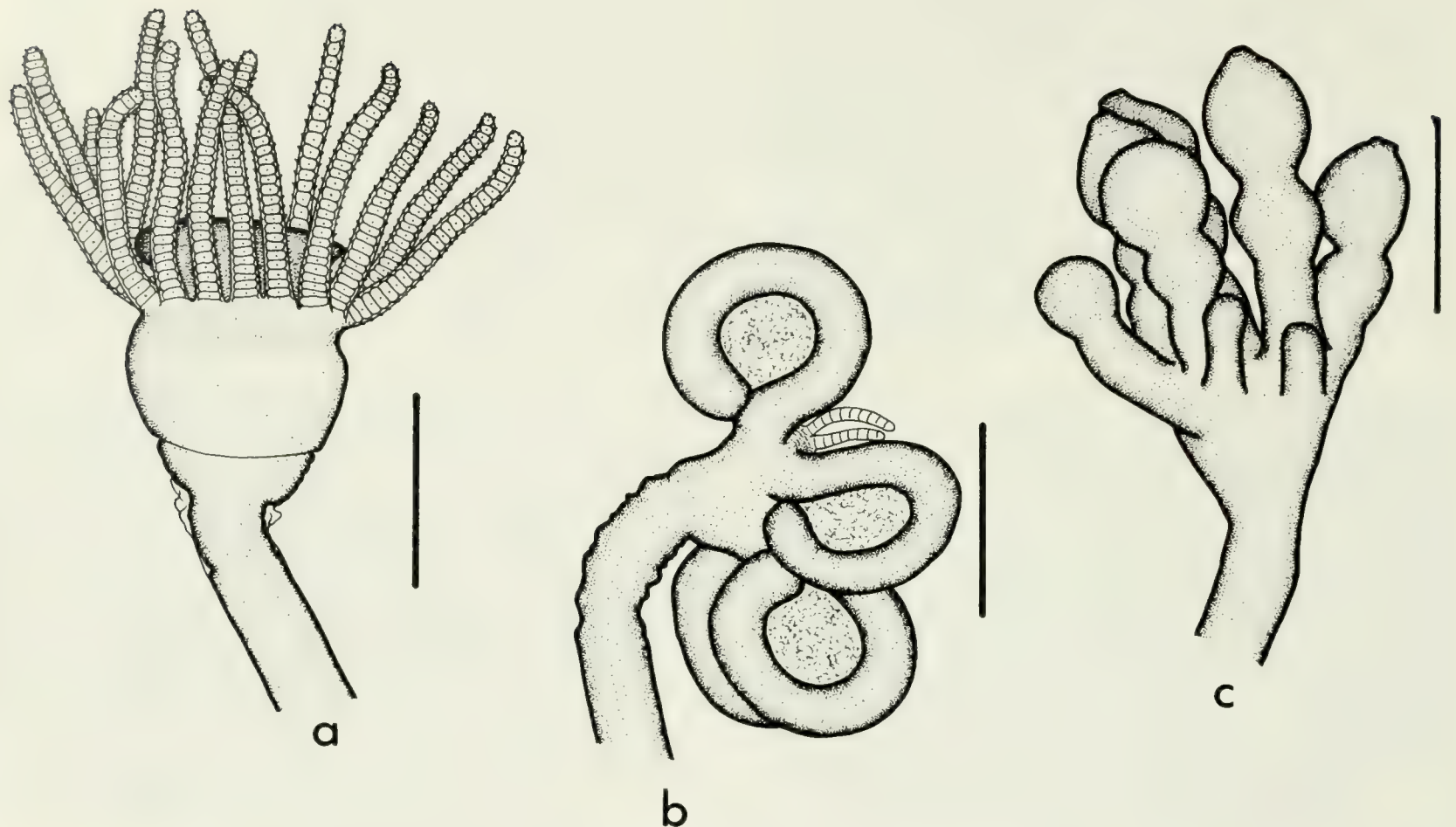


FIG. 31. *Eudendrium capillare*, hydranths and gonophores. Scales equal 0.25 mm. *a*, Hydranth, ROMIZ B142. *b*, Reduced hydranth with female gonophores, ROMIZ B161. *c*, Reduced hydranth with male gonophores, ROMIZ B142.

annulated at bases of hydrocaulus, branches, and pedicels, and with irregularly placed annulations frequent elsewhere. Hydranths urn-shaped, 295–385 μm long from proximal end to base of hypostome, 250–340 μm wide, with a shallow but distinct perisarc groove basally. Hypostome large, flared. Tentacles 15 to 20 in number, solid, filiform, in one whorl.

Gonophores fixed sporosacs, originating distal to perisarc groove on hydranth. Female gonophores borne in a whorl on hydranths with partially atrophied tentacles; spadix unbranched, curving over egg. Male gonophores with up to three chambers each, borne on atrophied hydranths; terminal chamber with an apical tubercle.

Nematocysts—

Hydroids: heterotrichous microbasic euryteles (on tentacles, hydranth, and elsewhere) 7.1–8.0 μm \times 3.0–3.2 μm .

REMARKS

Records suggest that *Eudendrium capillare* Alder, 1856a, is widely distributed (Vervoort, 1959), but Millard (1975)

cautioned that most records provide insufficient information to verify identification. Although the species has been frequently recorded from warm waters (e.g., Fraser, 1912, 1948; Mammen, 1963; Millard and Bouillon, 1974; Cooke, 1975; Millard, 1975), hydroids from Bermuda were nevertheless referred to *E. capillare* with some reservation given the northerly type locality of this species. Unfortunately, type material of *E. capillare* could not be located (Cornelius and Garfath, 1980), but specimens from Bermuda corresponded with Alder's (1856a) figures and brief description of the species. Bermuda specimens are also identical in all major respects, including the complement and arrangement of nematocysts, with more detailed accounts of the species given by Millard and Bouillon (1974) from East Africa and by Millard (1975) from South Africa.

A small hydroid somewhat resembling *Eudendrium capillare* in colony form was described and named *E. tenellum* by Allman (1877) from material collected at a depth of 471 fathoms (861 m) off Florida. Hydranths and gonophores, both of which are now generally regarded as essential for diagnosis of any species of the genus *Eudendrium*



FIG. 32. *Eudendrium capillare*, heterotrichous microbasic eurytele from hydranth, ROMIZ B161. Scale equals 10 μ m.

Ehrenberg, 1834, were lacking in Allman's material. In fact, Allman was not certain that his specimen belonged to *Eudendrium*. He stated (1877:8): "Its reference to this genus is probably correct, but as neither hydranths nor gonophores were present in the specimen, it may possibly have its true place in some other." Nonetheless, many authors have identified small hydroids of this genus as *E. tenellum*, and the species has been reported from Atlantic, Pacific, Arctic, and Indian oceans (e.g., Stechow, 1923a; Fraser, 1937, 1944, 1948; Kramp, 1943; Yamada, 1959; Calder, 1972; Hirohito, 1977). It is unfortunate that the name *E. tenellum*, based on unrecognizable material and regarded here as a nomen dubium, should subsequently have been applied to what is seemingly a recognizable species. It is not possible to ascertain whether any of the later records of *E. tenellum* are actually conspecific with the hydroid upon which the name is based. These records are founded on one or more species of *Eudendrium*, apparently differing from *E. capillare* in having gonophores on entire rather than on atrophied hydranths. Naumov (1960) regarded *E. tenellum* auct. as a synonym of *E. capillare*, and Christiansen (1972) concurred with this view. Calder (1972), Hirohito (1977), and others have regarded the two as distinct based on differences in colony form and degree of reduction of hydranths bearing gonophores. Naumov (1960) also regarded *E. hyalinum* Bonnevie, 1899b, as conspecific with *E. capillare*. Bonnevie's (1899b) material was sterile and her description was so general that the identity of her hydroid is uncertain, although it could be identical with the *E. tenellum* of some authors. I have,

therefore, not regarded it as conspecific with *E. capillare*.

Hincks (1868) regarded *Eudendrium tenue* A. Agassiz, 1865, as possibly conspecific with *E. capillare*. Vervoort (1946b) thought likewise, and I concur. *Eudendrium parvum* Warren, 1908, also seems conspecific with *E. capillare*, for reasons given by Millard (1966).

KNOWN RANGE

Bermuda: first record.

Elsewhere: western Atlantic (Fraser, 1944); eastern Atlantic (Hincks, 1868); Indian Ocean (Millard, 1975); western Pacific (Yamada, 1959); eastern Pacific (Fraser, 1937).

Eudendrium carneum Clarke, 1882

Figs. 33–35

Eudendrium ramosum—McCrary, 1859a:166. —A. Agassiz, 1865:160. —Congdon, 1906:27; figs. 1–4; 1907:464. —Fraser, 1912:349; figs. 8A–C; 1943:87. —Bennett, 1922:245 [not *Eudendrium ramosum* (Linnaeus, 1758)].

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

Eudendrium cunninghami Kirkpatrick, 1910:127; pl. 7, figs. 1–3.

TYPE LOCALITY

Fort Wool, Hampton Roads, Virginia, United States.

MATERIAL EXAMINED

Hamilton Harbour, on mooring chain, –2.5 m, 12 November 1976, two colonies, 6.4 cm high, with female gonophores, coll. J. Markham, L. Coen, G. Rupp, ROMIZ B134. Flatts Inlet, on concrete pier, –2 m, 24 May 1979, five sterile colonies, up to 6 cm high; seven colonies, up to 6 cm high, with male gonophores; five colonies, up to 10 cm high, with female gonophores; ROMIZ B135. Castle Grotto, Castle Harbour, on cave wall 25–50 m from entrance, –1 m, 20 July 1982, one sterile colony, 5.8 cm high, ROMIZ B148. Flatts Inlet, on rocks, –0.5 m, 27 February 1982, one colony, 9.3 cm high, with male gonophores, ROMIZ B166. Ferry Reach, St George's Island, on rope, –0.5 to –2 m, 2 September 1977, one male colony, 3.6 cm high; one sterile colony, 10.5 cm high; ROMIZ B176. Somerset Bridge, on concrete wall, –2 m, 15 September 1977, one male colony, 10 cm high, ROMIZ B178.

DESCRIPTION

Colony extensively branched and bushy, up to 10.5 cm high, arising from a creeping mass of hydrorhizal stolons. Hydrocaulus upright, polysiphonic, more or less alternately branched; primary branches also polysiphonic and

alternately or somewhat irregularly branched; secondary branches often polysiphonic basally and branched in like manner. Perisarc thick and brownish-coloured in older parts of colony, thinner and paler towards extremities, annulated or wrinkled at bases of branches and hydranth pedicels, with occasional annulations elsewhere but mostly smooth, terminating almost imperceptibly at groove around hydranth base. Hydranths urn-shaped, about 0.8 mm long from proximal end to base of hypostome, 0.65 mm wide, with a shallow perisarc groove and a ring of anisorhiza nematocysts basally; hypostome very large, flared to knob-shaped. Tentacles about 27 to 32 in number, solid, filiform, in one whorl.

Gonophores fixed sporosacs, developing on hydranth distal to perisarc groove. Female gonophores on reduced hydranths with partially atrophied tentacles; spadix bifid, curving over egg. During development, spadices shed, embryos borne in perisarc-covered capsules arranged irregularly along pedicel, perisarc of gonophore pedicel extensively wrinkled, terminal hydranth eventually lost. Male gonophores with up to five chambers each, borne on atrophied hydranths; distal end of gonophore with scattered anisorhiza nematocysts.

Nematocysts—

Hydroids: heterotrichous anisorhizas (on hydranth base, hypostome, and tips of male gonophores) 20.3–23.0 μm \times 9.4–11.3 μm ; heterotrichous microbasic euryteles (on tentacles, hydranth, and elsewhere) 8.3–9.4 μm \times 3.6–4.0 μm .

REMARKS

Allman (1877) described and named eight new nominal species of *Eudendrium* Ehrenberg, 1834, from the southeastern United States, where *E. carneum* Clarke, 1882, is now known to be frequent (Fraser, 1944; Calder and Hester, 1978). One of these, *E. tenellum*, was discussed earlier. Of the remaining seven, all differ from *E. carneum* in one or more respects. The hydrocaulus was described as monosiphonic, rather than polysiphonic, in *E. attenuatum*, *E. laxum*, and *E. cochleatum*. The number of tentacles borne by the hydranth was reported to be only about 20, instead of 25 or more, in *E. eximium*, *E. exiguum*, and *E. fruticosum*. Annulations at the bases of branches and pedicels, well marked in *E. carneum*, were faint or even absent in *E. eximium*, *E. fruticosum*, and *E. gracile*. Reproductive hydranths, reduced or aborted in *E. carneum*, were little if at all aborted in *E. eximium*, *E. fruticosum*, and *E. laxum*. Unfortunately, gonophores were lacking in Allman's material of *E. exiguum* and *E. gracile*, and both gonophores and hydranths were lacking in his specimens of *E. attenuatum*. Characters such as tentacle number, degree of atrophy of reproductive hydranths, extent of perisarc annulation, and number of tubes comprising the hydrocaulus are known to vary intraspecifically in



FIG. 33. *Eudendrium carneum*, colony form, ROMIZ B135. Natural size.

Eudendrium, but all Allman's species appear to have been different from *E. carneum*. So does *E. distichum*, described by Clarke (1879) from material obtained southwest of Key West, Florida, in 339 fathoms (620 m) of water. Although *E. distichum* appears to have resembled *E. carneum* in colony size and general shape, it seems to have had only 16 to 20 tentacles on the hydranth. Some of Allman's (1877) species were evidently distinguished on the basis of relatively minor differences, and their status needs to be re-evaluated.

In Bermuda, *Eudendrium carneum* was abundant during warm months in areas swept by strong tidal currents, such as Flatts Inlet and the Somerset Bridge area. Specimens with active hydranths and gonophores were also collected in Flatts Inlet at 18° C during the winter of 1982 (ROMIZ B166).

Eudendrium carneum has been reported previously from Bermuda as *E. ramosum* (Linnaeus, 1758) by Congdon (1906, 1907) and Bennett (1922). Records of *E. ramosum* from the southeastern United States by McCrady (1859a), A. Agassiz (1865), and Fraser (1912, 1943b) were also likely based on material of *E. carneum*. Ultrastructural studies on spermatozoa of *E. carneum* were conducted in Bermuda by Summers (1972a), again on hydroids misidentified as *E. ramosum*.

KNOWN RANGE

Bermuda: no specific locality given (Congdon, 1906, 1907); Hamilton Harbour (Bennett, 1922); Flatts Inlet (Summers, 1972a); shallow inshore waters (Calder, 1986). Elsewhere: western Atlantic (Fraser, 1944); eastern Atlantic (Kirkpatrick, 1910); Indian Ocean (Millard, 1975); eastern Pacific (Fraser, 1948).

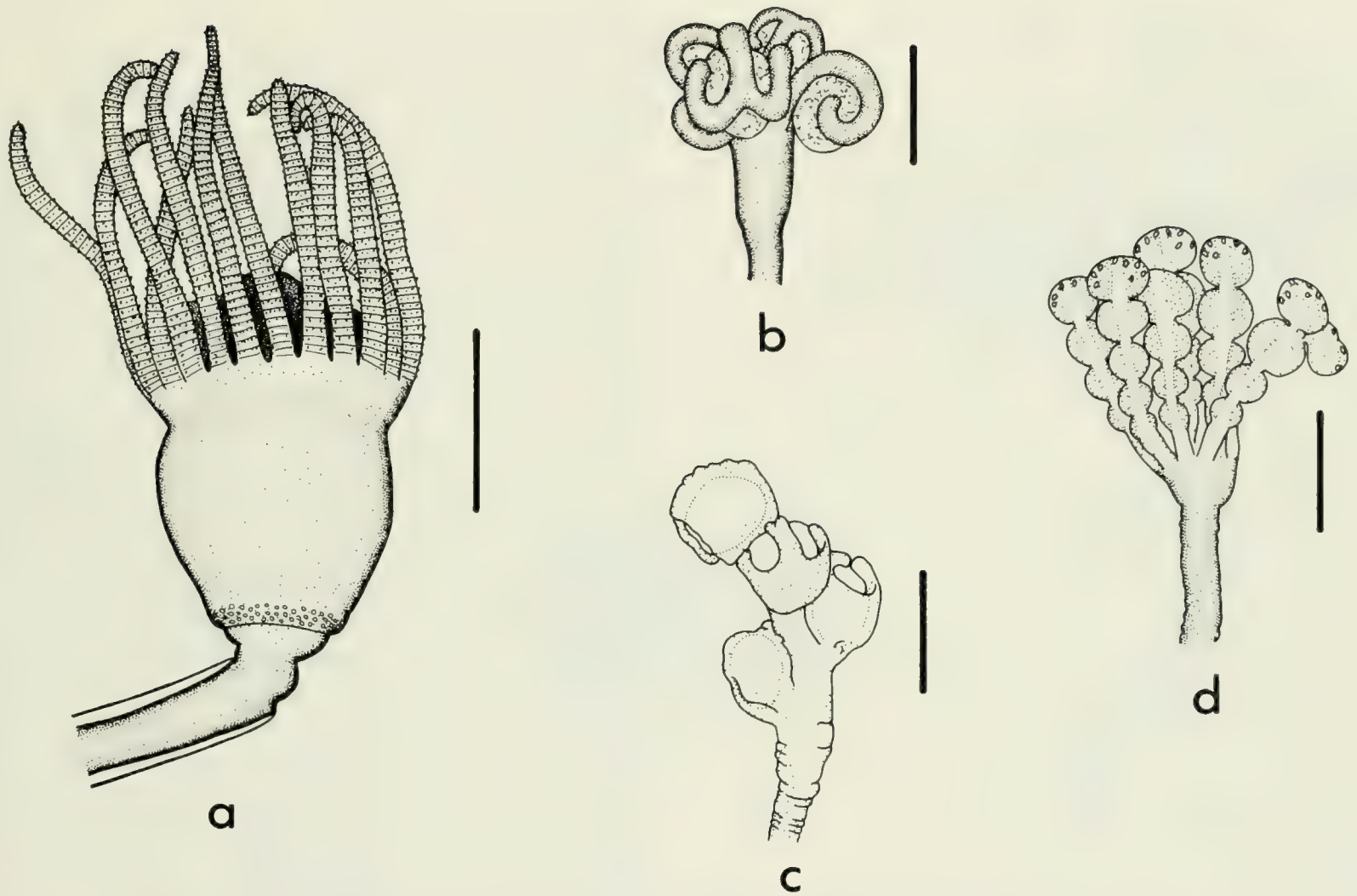


FIG. 34. *Eudendrium carneum*, hydranths and gonophores, ROMIZ B135. Scales equal 0.5 mm. *a*, Hydranth. *b*, Reduced hydranth with female gonophores. *c*, Pedicel with capsules containing embryos. *d*, Reduced hydranth with male gonophores.

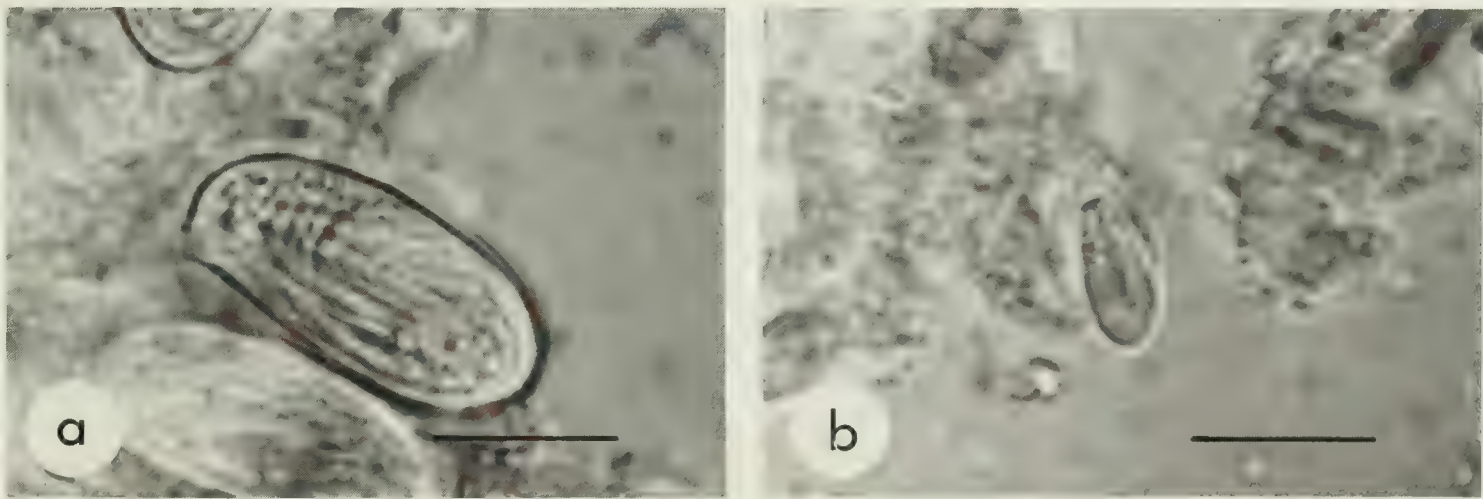


FIG. 35. *Eudendrium carneum*, nematocysts of hydranth, ROMIZ B135. Scales equal 10 μ m. *a*, Heterotrichous anisorhiza. *b*, Heterotrichous microbasic eurytele.

Genus *Myrionema* Pictet, 1893

Myrionema Pictet, 1893:18.

DIAGNOSIS

Eudendriidae with calyx of hydranth elongate, often columnar below tentacles. Tentacles in two or more close whorls, number varied but commonly 40 or more.

TYPE SPECIES

Myrionema amboinense Pictet, 1893, by monotypy.

REMARKS

This genus was instituted by Pictet (1893) for a new species, *Myrionema amboinense*, from the western Pacific. The greater number of tentacles, which occur in several close whorls, and the elongate calyx of the hydranth distinguish hydroids of this genus from the more familiar *Eudendrium* Ehrenberg, 1834. Hydroids of this genus contain symbiotic zooxanthellae in their tissues and are apparently restricted to shallow water.

Myrionema amboinense Pictet, 1893

Figs. 36, 37

Myrionema amboinensis Pictet, 1893:19, 62; pl. 1, figs. 12,13; pl. 3, figs. 55,56.

Eudendrium hargitti Congdon, 1906:27; figs. 5–11.

“*Eudendrium*” *hargettii*—Wallace, 1909:137 [incorrect subsequent spelling].

Eudendrium griffini Light, 1913:333; figs. 1–5; pls. 1, 2.

Eudendrium amboinensis—Leloup, 1932:143; fig. 15; pl. 16, fig. 1.

Myrionema amboinense—Briggs and Gardner, 1931:184; pl. 1, figs. 1–3.

Myrionema hargitti—Spracklin, 1982:240; fig. 114b.

Myrionema griffini—Watson, 1985:180.

TYPE LOCALITY

Baton-Mera, Ambon, Moluccas, Indonesia.

MATERIAL EXAMINED

Tucker's Town Bay, Castle Harbour, on pontoon anchor chain, –1 m, 23 July 1982, one colony, 3.5 cm high, with male gonophores, ROMIZ B141. Tucker's Town Bay, Castle Harbour, on pontoon anchor chain, –0.5 m, 5 March 1982, three colonies, 3.5–5.6 cm high, without gonophores, ROMIZ B171. Walsingham Pond, on rocky cliff, –2 m, 5 September 1977, one colony, 3.4 cm high, without gonophores, ROMIZ B179. Whalebone Bay, on rocks in *Thalassia* bed, –0.5 m, 24 June 1983, seven colonies, 1.3–4.0 cm high, with female gonophores, ROMIZ B329.

DESCRIPTION

Colonies straggly, growing in clumps up to 5.6 cm high; hydrorhiza creeping. Hydrocaulus monosiphonic, 0.16–0.25 mm in diameter, sparingly and irregularly branched; primary branches unbranched or irregularly branched, often directed upwards and resembling hydrocaulus in appearance and size. Perisarc thin, flexible, straw-coloured to virtually colourless, usually annulated or faintly wrinkled at bases of branches, mostly smooth elsewhere, terminating at groove around hydranth base. Hydranth reaching about 1.7 mm long from proximal end to base of hypostome, urn-shaped to club-shaped with a long, cylindrical calyx, widest at tentacle-bearing region, with a shallow perisarc groove and a ring of macrobasic eurytele nematocysts basally. Hypostome large, flared to knobbed. Tentacles up to 2 mm long, about 35 to 60 in number, solid, filiform, in two or more close whorls. Hydranth and tentacles bearing large numbers of zooxanthellae.

Gonophores fixed sporosacs, originating on hydranth proximal to tentacles. Male gonophores with one to four chambers, borne on entire hydranths. Female gonophores borne in a whorl of as many as eight or more on entire hydranths; spadix unbranched, curving over egg. During development, spadices shed, embryos borne in perisarc-covered capsules arranged irregularly along pedicel.

Nematocysts—

Hydroids: macrobasic euryteles (on hydranth base, hypostome) 21.8–23.4 μm \times 9.7–11.3 μm ; heterotrichous microbasic euryteles (on tentacles, hydranth, and elsewhere) 8.5–9.4 μm \times 3.5–3.8 μm .

REMARKS

Morphological differences between *Myrionema hargitti* (Congdon, 1906) from the tropical western Atlantic and *M. amboinense* Pictet, 1893, from the Indo-west Pacific appear to be negligible. Hydroids of both are shallow-water inhabitants harbouring large numbers of algal symbionts, and are brownish in colour when alive. Specimens of *M. amboinense* illustrated by Millard and Bouillon (1973) have longer calyces than hydroids referred to *M. hargitti*, but calyx length is highly variable in this genus. So too is tentacle number, although counts have usually been higher in *M. amboinense*. In *M. hargitti*, tentacle number has been reported as 35 to 45 (Congdon, 1907) and 35 to 60 (Bennett, 1922). Tentacle number in *M. amboinense*, with which *M. griffini* (Light, 1913) is conspecific, has been reported as 80 to 120 (Pictet, 1893), 50 to 70 (Light, 1913), 40 to 50 (Hargitt, 1924), and 70 to 90 (Millard and Bouillon, 1973). Nematocyst types and sizes appear to be similar in the two. In proposing *M. griffini*, Light (1913) noted that the tentacles were heavily armed with nematocysts. Congdon (1906, 1907) reported that nematocysts were few in number on the tentacles of *M. hargitti*. An

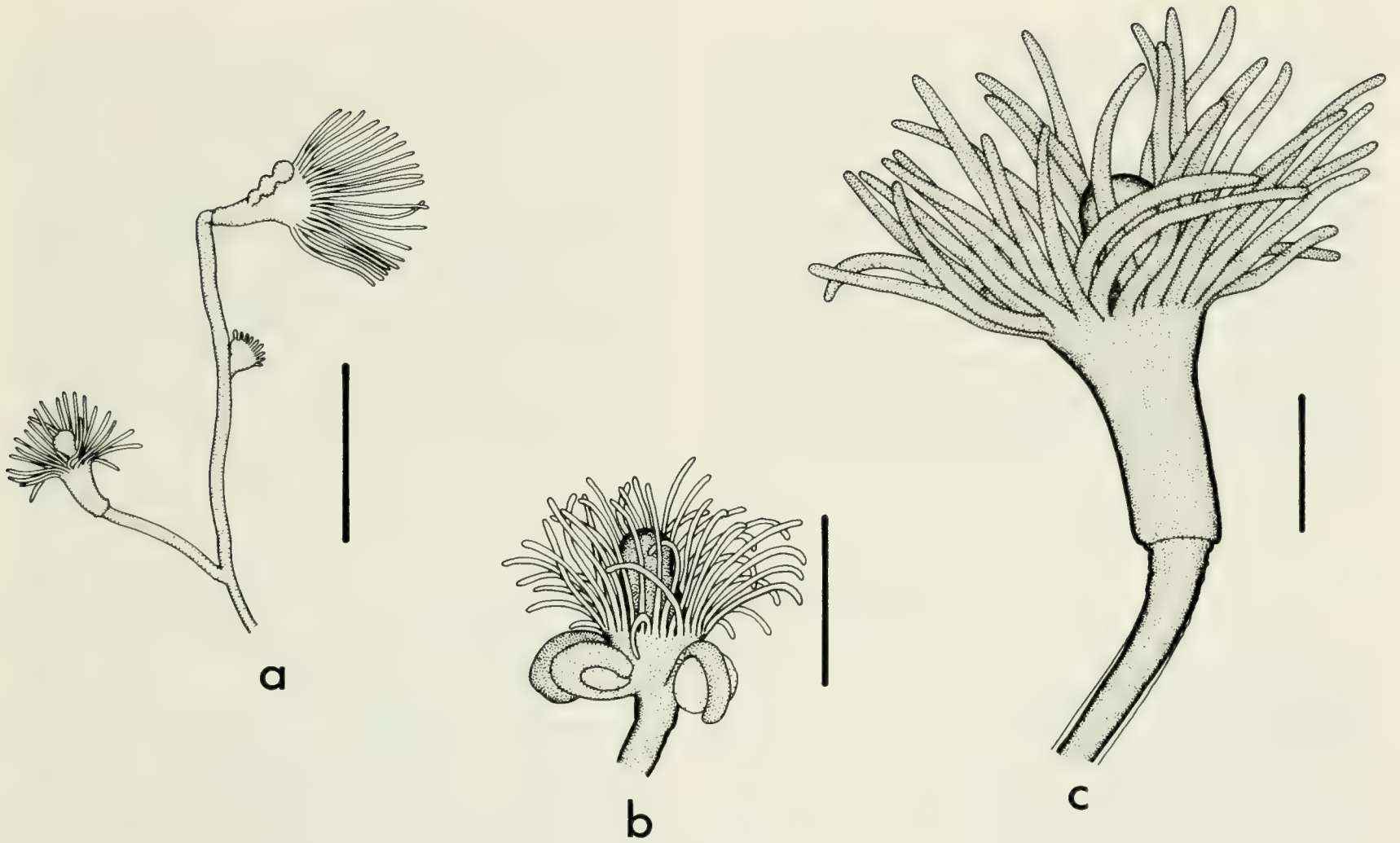


FIG. 36. *Myrionema amboinense*. Scale for *a* equals 3 mm; scale for *b* equals 1 mm; scale for *c* equals 0.5 mm. *a*, Hydrocaulus and hydranths, with a male gonophore, ROMIZ B141. *b*, Hydranth, with female gonophores, ROMIZ B329. *c*, Hydranth, ROMIZ B141.

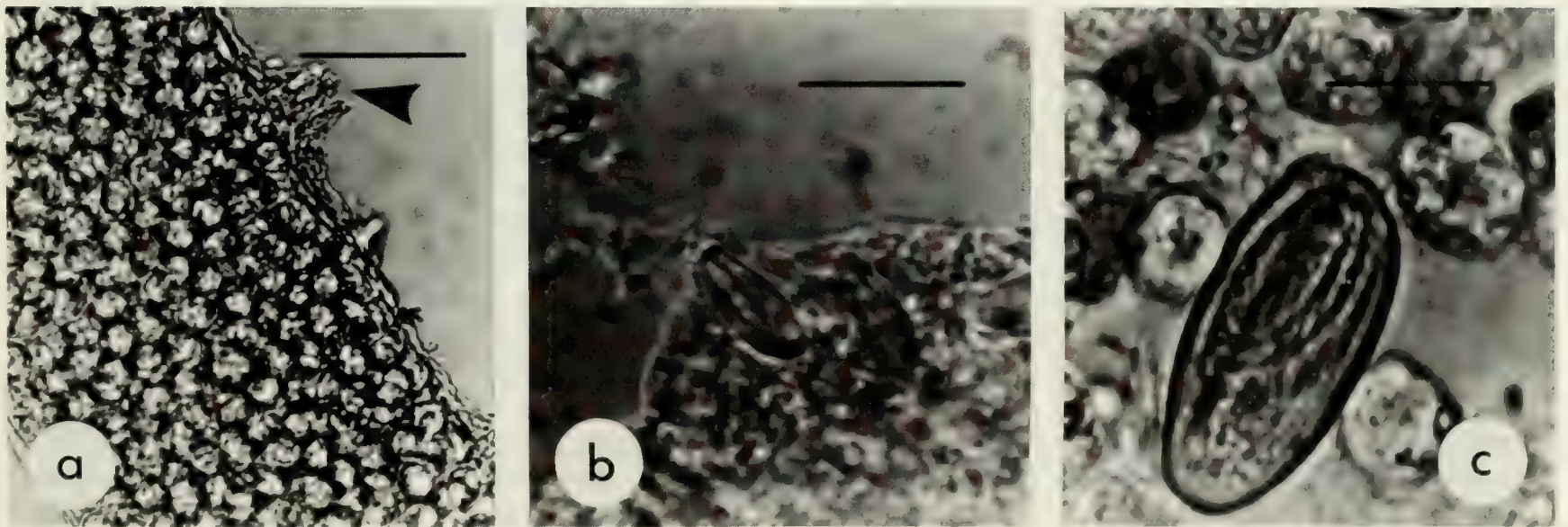


FIG. 37. *Myrionema amboinense*, ROMIZ B171. Scale for *a* equals 40 μm ; scales for *b* and *c* equal 10 μm . *a*, Part of a tentacle, with nematocyst battery (arrow) and algal symbionts. *b*, Heterotrichous microbasic eurytele. *c*, Macrobasic eurytele.

examination of the tentacles of Bermuda specimens of *M. amboinense* during this study revealed that nematocysts were present in moderate numbers (Fig. 37a). Although hydroids of the two nominal species are isolated geographically, I regard *M. hargitti* as conspecific with *M. amboinense*.

Myrionema amboinense was observed in Bermuda during this study only in shallow waters of relatively sheltered areas such as Tucker's Town Bay. It was also one of the few hydroid species collected in the quiet waters of Walsingham Pond. Bennett (1922) reported this hydroid to be extremely abundant in Hungry Bay on the south shore of Bermuda, where it was first observed by Congdon (1906,

1907) and later seen by Smallwood (1910). Bennett also located it just below low tide on buoys, timbers, ledges, and turtle grass throughout Hamilton Harbour and Great Sound.

KNOWN RANGE

Bermuda: no specific locality given (Congdon, 1906); inlet on south shore (Congdon, 1907); Hungry Bay (Smallwood, 1910); Hungry Bay, Hamilton Harbour, Great Sound (Bennett, 1922); quiet inshore waters (Calder, 1986). Elsewhere: western Atlantic (Fraser, 1944); eastern Atlantic (Picard, 1958); Indian Ocean (Millard and Bouillon, 1973); western Pacific (Pennycuik, 1959).

Family Corymorphidae Allman, 1872

Corymorphidae Allman, 1872:386.

Monocaulidae Allman, 1872:395.

Amaltheidae Haeckel, 1879:37.

Steenstrupiini Cockerell, 1911:78.

Branchiocerianthidae Broch, 1916:21.

Paragotoeidae Ralph, 1959:176.

DIAGNOSIS

Hydroids solitary. Hydrocaulus upright, more or less cylindrical, invested with thin, flexible perisarc; usually with papillae and anchoring filaments basally. Hydranths terminal, flask-shaped, with oral and aboral bands of tentacles; oral tentacles capitate or filiform, in one or more close whorls; aboral tentacles filiform, in one whorl.

Gonophores fixed sporosacs or free medusae, generally borne on blastostyles arising from hydranth just distal to aboral tentacles. Medusa, when present, bell-shaped; exumbrella without tracks of nematocysts; manubrium short, with simple, circular mouth. Radial canals four. Marginal tentacles one to four. Ocelli absent. Gonads surrounding manubrium.

REMARKS

Allman (1872) established the family Corymorphidae to accommodate *Corymorpha* M. Sars, 1835, and several other nominal genera now considered identical with it. In the same publication, he founded the Monocaulidae to include *Monocaulus* Allman, 1864a. For much of the present century, the genera *Monocaulus* and *Corymorpha*, and the two families based on them, have been regarded as identical. The name Monocaulidae has fallen into disuse in favour of the name Corymorphidae, but to my knowledge criteria of the First Reviser Principle in nomenclature [Art. 24] have never been met in this case. The two are considered synonyms here, and the name Corymorphidae

is assigned precedence over Monocaulidae in the interests of nomenclatural stability.

Rees (1957) recognized four subfamilies within the Corymorphidae. "Lower corymorphines," such as *Euphysa* Forbes, 1848, *Hypolytus* Murbach, 1899, and possibly *Gymnogonos* Bonnevie, 1898, were grouped in the Euphysinae Haeckel, 1879. "Higher corymorphines," including *Corymorpha*, were placed in the Corymorphinae. *Boreohydra* Westblad, 1937, considered an aberrant corymorphine by Rees, was retained in the Boreohydrinae Westblad, 1947. *Branchiocerianthus* Mark, 1898, viewed as a corymorphine with secondarily acquired bilateral symmetry, was placed in the Branchiocerianthinae Broch, 1916. Although there has been little outright criticism of this classification, Millard (1975) cautioned that subdivision of the family is still not settled. For example, Calder (1974) suggested that *Boreohydra* may be better referred to the family Myriothelidae Hincks, 1868 (= Candelabridae Stechow, 1921a) rather than to the Corymorphidae, and Petersen (1979) elevated the Euphysinae to the rank of family. Bouillon (1985) recognized the Euphysidae and Boreohydridae as distinct families.

The family-group names Amaltheidae Haeckel, 1879, and Steenstrupiini Cockerell, 1911, are synonyms of the Corymorphidae because their type genera, *Amalthea* Schmidt, 1852, and *Steenstrupia* Forbes, 1846, are now generally considered congeneric with *Corymorpha* (e.g., see Broch, 1916; Brinckmann-Voss, 1970; Millard, 1975; but also see Rees and Thursfield, 1965; Bouillon, 1985). Brinckmann-Voss (1970) has been followed in regarding the Paragotoeidae Ralph, 1959, as identical with the Corymorphidae. The family Euphysidae, including the Trichorhizini Cockerell, 1911, and Hypolytidae Fraser, 1943a, was considered valid by Petersen (1979) and Bouillon (1985).

Hydroids of the families Corymorphidae and Tubulariidae Goldfuss, 1818, are obviously related, and several authors (e.g., Broch, 1916; Stechow, 1923a; Russell, 1953; Naumov, 1960; Kramp, 1961) have united the two. Differences between them are usually more pronounced in the hydroid stage than in the medusa. The family Corymorphidae is recognized as a distinct taxon in this report, a position held previously by authors such as Kramp (1949), Rees (1957), Brinckmann-Voss (1970), Vervoort (1972), Calder (1975), Millard (1975), Petersen (1979), and Bouillon (1985).

Genus *Zyzyzus* Stechow, 1921a

Zyzyzus Stechow, 1921a:249.

Zyzygus Neave, 1940a:712 [incorrect subsequent spelling].

Zyzyzuz Bouillon, 1985:243 [incorrect subsequent spelling].

DIAGNOSIS

Corymorphid hydroids epizoic on sponges. Hydrocaulus parenchymatous, with endodermal canals, with rooting processes present basally, covered with thin perisarc. Hydranths radially symmetrical, with two whorls of tentacles; aboral tentacles long, filiform, in one whorl; oral tentacles relatively short, capitate in young hydroids, otherwise filiform, forming a band around hypostome.

Gonophores fixed sporosacs, arising from blastostyles distal to aboral tentacles, forming actinulae; hydroids monoecious.

TYPE SPECIES

Tubularia solitaria Warren, 1906b (not *Tubularia solitaria* Rapp, 1829), by monotypy.

REMARKS

Stechow (1921a) founded *Zyzyzus* to accommodate *Tubularia solitaria* Warren, 1906b (not *Tubularia solitaria* Rapp, 1829), a hydroid having characteristics of both the Corymorphidae Allman, 1872, and Tubulariidae Goldfuss, 1818. The genus was referred to the subfamily Corymorphinae, within the family Tubulariidae, by Stechow (1923a). Kramp (1933) initially regarded *Zyzyzus* as congeneric with *Corymorpha* Allman, 1872, but concluded later (Kramp, 1949) that the genus was based on a species of *Tubularia* Linnaeus, 1758, which was adapted for life as an epizoite on sponges. Millard (1975), Watson (1978), Petersen (1979), and Bouillon (1985) recognized *Zyzyzus* as valid, but referred it to the Tubulariidae rather than the Corymorphidae.

Zyzyzus resembles *Tubularia* and the Tubulariidae mainly in having an actinula larva in its life cycle (Warren, 1906b), but in most other respects it resembles *Corymorpha* and

the Corymorphidae in my opinion. For example, the hydroid is strictly solitary; the hydrocaulus is thick and parenchymatous, with well-developed endodermal canals; the perisarc is thin, soft, and flexible; and the internal anatomy of the hydranth is more like that of *Corymorpha* M. Sars, 1835 (Allman, 1872; Rees, 1957) than that of *Tubularia* or the "lower corymorphines" (Grönberg, 1897; Rees, 1957). The gastrovascular cavity of the hydranth in *Zyzyzus* is separated into oral and aboral chambers by a well-developed diaphragm (Fig. 38). For these reasons, the genus is included here in the Corymorphidae.

The absence of papillae on the hydrocaulus, the presence of one or more anchoring stolons basally, and the existence of an actinula larva in its life cycle distinguish *Zyzyzus* from *Corymorpha*.

Zyzyzus warreni, nom. nov.

Figs. 38–40

Tubularia solitaria Warren, 1906b:83; pls. 10, 11 [invalid junior primary homonym of *Tubularia solitaria* Rapp, 1829 (not a hydroid)].

Zyzyzus solitarius—Stechow, 1921a:249.

Corymorpha solitaria—Kramp, 1933:12.

TYPE LOCALITY

Natal, South Africa.

MATERIAL EXAMINED

Flatts Inlet, on sponge, – 1 to – 2 m, 13 September 1977, several small hydroids, up to 5 mm high, some with developing blastostyles, ROMIZ B133. Flatts Inlet, on sponges and *Eudendrium carneum* on underside of flat rock, – 3 m, 2 August 1982, several hydroids, up to 10 mm high, with developing blastostyles, ROMIZ B147. Castle Grotto, Castle Harbour, about 25 m inside cave entrance, on sponge, – 1 m, 20 July 1982, several hydroids, up to 11 mm high, with gonophores, ROMIZ B165. Stream Passage Cave, Harrington Sound, 3 m inside cave entrance, on sponge, – 1 m, 20 June 1983, several hydroids, up to 17 mm high, with gonophores, ROMIZ B370.

DESCRIPTION

Hydroids solitary, up to 17 mm high, usually embedded in sponge tissue basally. Base bulbous, lacking papillae but with one or more stout anchoring stolons of varying length. Hydrocaulus parenchymatous, with branching and anastomosing endodermal canals, reaching 1.5 mm wide basally, tapering distally. Perisarc thin, flexible, terminating just below hydranth in a distinct circular perisarc groove. Hydranths up to 1.7 mm high, 1.5 mm wide, distinctly demarcated from hydrocaulus, vasiform with two whorls of tentacles. Aboral tentacles filiform, reaching

3 mm long; oral tentacles much shorter, capitate in young polyps, otherwise filiform; tentacle number varying with hydranth size, larger hydranths with 22 to 25 aboral and 15 to 20 oral tentacles.

Blastostyles short, arising just distal to aboral tentacles, bearing clusters of fixed, cryptomedusoid gonophores. In examined specimens, gonophores incompletely developed, lacking actinulae.

Nematocysts—

Hydroids: desmonemes $3.7\text{--}4.2\ \mu\text{m} \times 2.8\text{--}2.9\ \mu\text{m}$; isorhizas (ovate) $6.6\text{--}7.5\ \mu\text{m} \times 2.8\text{--}3.7\ \mu\text{m}$; ?isorhizas (reniform) $6.4\text{--}7.3\ \mu\text{m} \times 1.9\text{--}2.1\ \mu\text{m}$; ?mastigophores $6.8\text{--}8.2\ \mu\text{m} \times 4.3\text{--}5.4\ \mu\text{m}$; microbasic euryteles $9.5\text{--}10.8\ \mu\text{m} \times 4.9\text{--}6.1\ \mu\text{m}$; stenoteles (small) $5.5\text{--}5.7\ \mu\text{m} \times 4.5\text{--}4.7\ \mu\text{m}$; stenoteles (medium) $6.7\text{--}7.3\ \mu\text{m} \times 5.7\text{--}6.4\ \mu\text{m}$; stenoteles (large) $9.6\text{--}12.2\ \mu\text{m} \times 8.7\text{--}11.2\ \mu\text{m}$.

REMARKS

The name *Tubularia solitaria* Warren, 1906b, is an invalid junior primary homonym of *Tubularia solitaria* Rapp, 1829, and must be replaced [Art. 52]. *Zyzyzus warreni* is proposed here as a new replacement name for Warren's taxon.

Zyzyzus warreni resembles descriptions and illustrations of *Tubularia spongicola* von Lendenfeld, 1885b, by von Lendenfeld (1885b) and Watson (1978). According to Watson, *Z. warreni* differs from *Z. spongicolus* in having male and female gonophores on separate blastostyles instead of on the same ones. From existing descriptions, the two seem otherwise remarkably similar and may prove conspecific. According to Watson (1978), von Lendenfeld's (1885b) description and figure of *Z. spongicolus* do not correspond well with the type material, which she re-examined.

In Bermuda, this hydroid is usually, but not exclusively, epizoic on sponges. A few specimens were found attached to the hydrocaulus of the hydroid *Eudendrium carneum* Clarke, 1882, during this study (ROMIZ B147).

Zyzyzus warreni is evidently dormant during winter in Bermuda. No specimens were observed on a collecting trip in February and March 1982, although it was specifically looked for in areas where it was known to occur earlier and where it was collected on subsequent summer trips.

ETYMOLOGY

The replacement name for this species honours Ernest Warren, who first discovered and named this species, and who contributed significantly to knowledge of the hydroids of Natal.

KNOWN RANGE

Bermuda: first record.

Elsewhere: western Atlantic (Millard, 1975); eastern Atlantic (Ritchie, 1908); Indian Ocean (Millard, 1975).

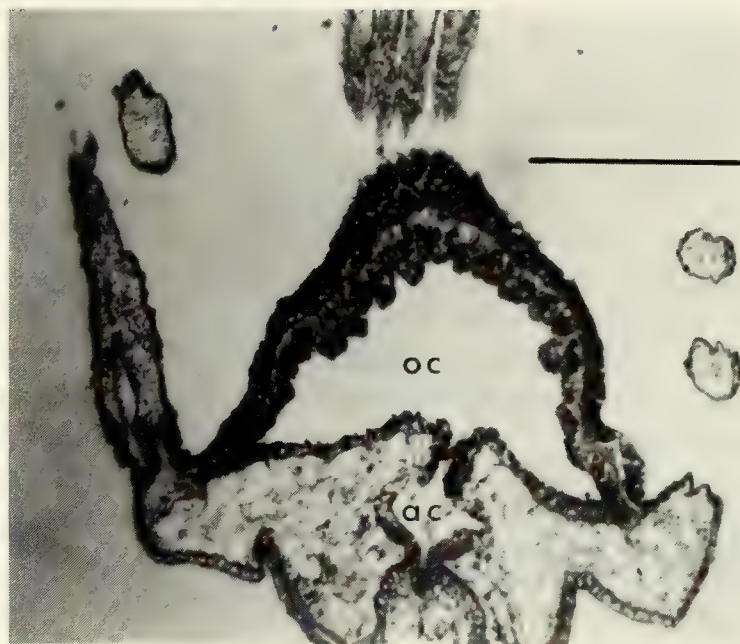


FIG. 38. *Zyzyzus warreni*, photomicrograph of cross-section of hydranth, showing oral (oc) and aboral (ac) chambers separated by a well-developed diaphragm, ROMIZ B147. Scale equals 250 μm .

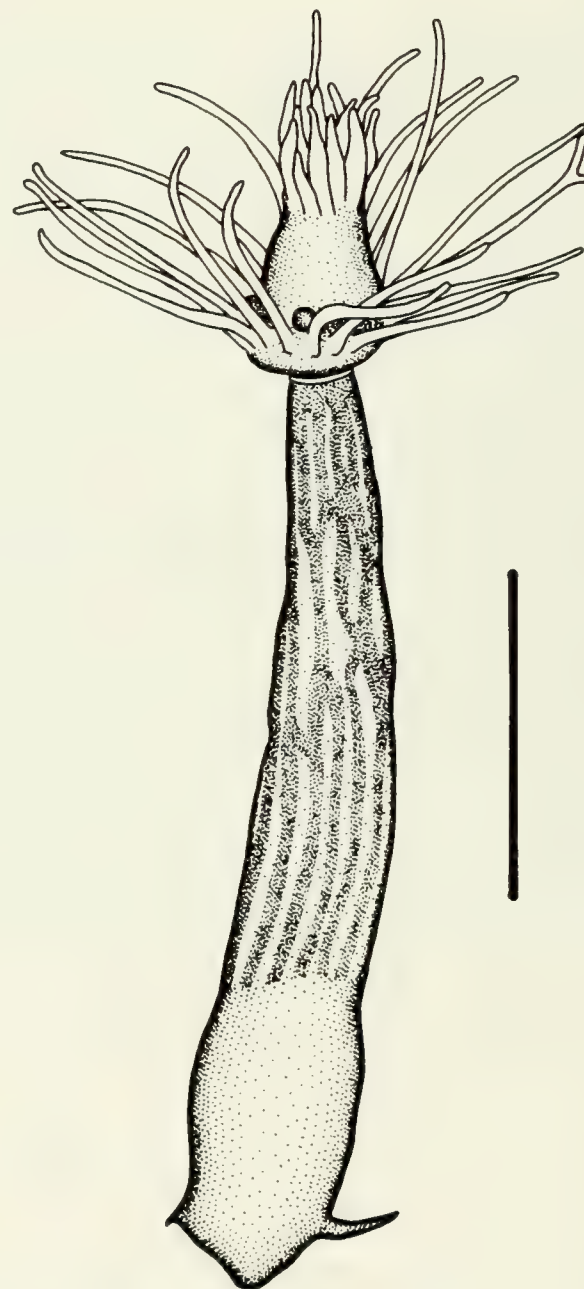


FIG. 39. *Zyzyzus warreni*, hydroid, ROMIZ B147. Scale equals 2 mm.

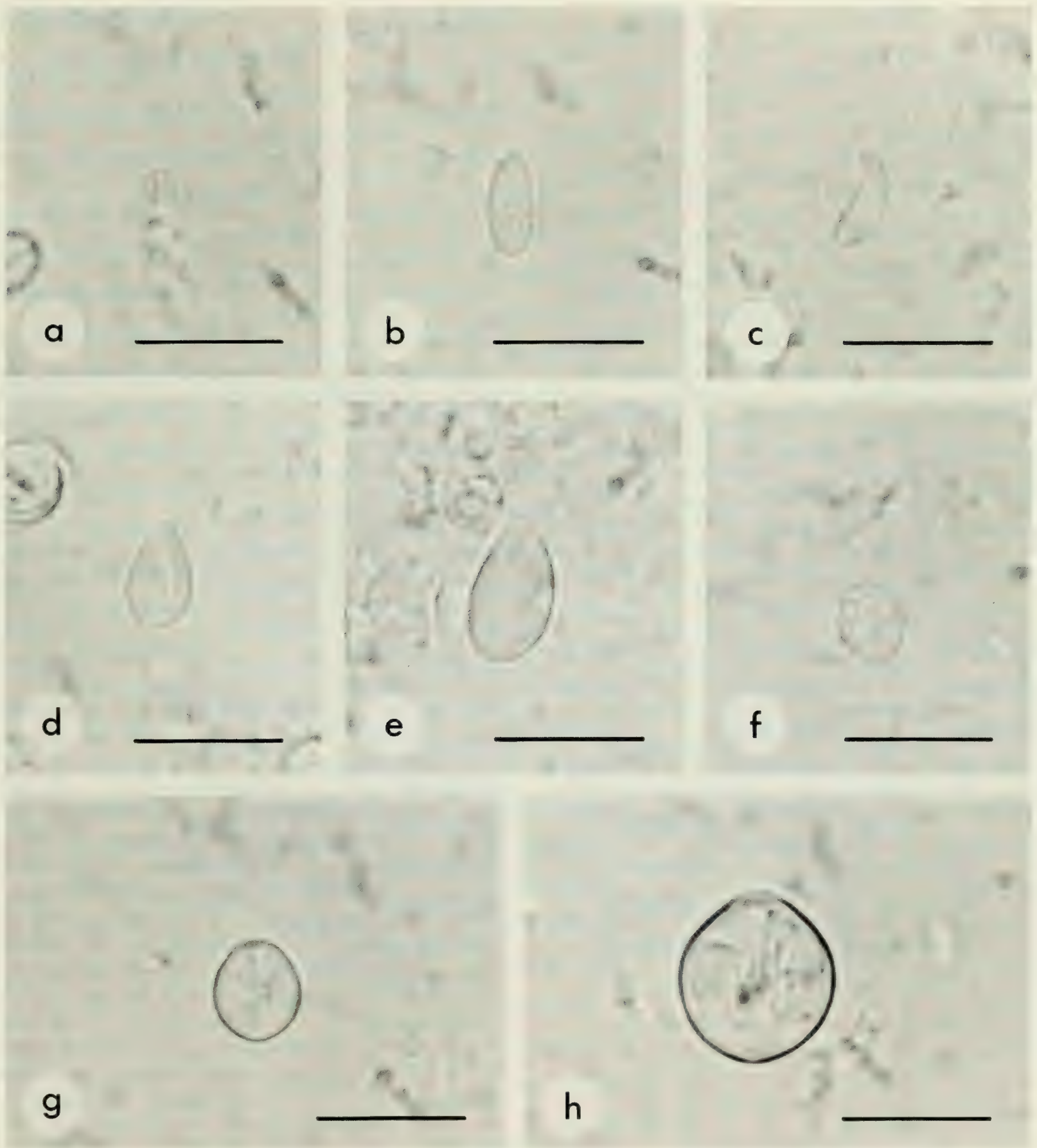


FIG. 40. *Zyzzyzus warreni*, nematocysts of hydranth, ROMIZ B165. Scales equal 10 μ m. *a*, Desmoneme. *b*, Ovate isorhiza. *c*, Reniform isorhiza. *d*, ?Mastigophore. *e*, Microbasic eurytele. *f*, Small stenotele. *g*, Medium stenotele. *h*, Large stenotele.

Family Tubulariidae Fleming, 1828

Tubulariadae Fleming, 1828:552 [corrected to Tubulariidae by Hincks, 1868].

Hybocodonidae Allman, 1872:421.

Hybdocoridae Pennington, 1885:71 [incorrect subsequent spelling of Hybocodonidae Allman, 1872].

DIAGNOSIS

Hydroids solitary or colonial. Hydrocaulus upright, cylindrical, invested with thick, rigid perisarc. Hydranths terminal, flask-shaped, with oral and aboral whorls of tentacles. Oral tentacles relatively small, usually filiform in mature hydranths, capitate in immature ones; aboral tentacles large, filiform, in one whorl.

Gonophores fixed sporosacs or free medusae, borne on blastostyles arising from hydranth just distal to aboral tentacles; developmental stages including an actinula larva. Medusa, when present, bell-shaped; exumbrella with or without tracks of nematocysts; manubrium short, with simple, circular mouth. Radial canals four. Marginal tentacles one to four. Ocelli absent. Gonads surrounding manubrium.

REMARKS

Goldfuss (1818) appears to have been the first to establish a family-group taxon under the name "Tubulariae." Four genera were included in the group, *Clava* Gmelin, 1790, *Coryne* Gaertner, 1774, *Calamella* Oken, 1815, and *Sertularia* Linnaeus, 1758. The name, based on a genus excluded from the group, does not meet the criteria of availability [Art. 11f (i)(1)]. Goldfuss recognized the genus *Tubularia* Linnaeus, 1758, as valid, but it was included with a heterogeneous assemblage of invertebrate genera in another family, named the Polypi. Fischer von Waldheim (1823) also recognized a family "Tubulariae," but did not include *Tubularia* in the group. The family-group name Tubulariidae was first made available by Fleming (1828), as the Tubulariadae.

Allman (1872) founded the family Hybocodonidae to accommodate *Hybocodon* L. Agassiz, 1862, but the genus is now generally referred to the Tubulariidae (e.g., Millard, 1975; Petersen, 1979; Bouillon, 1985). Pennington (1885) incorrectly spelled this nominal family "Hybdocoridae."

There has been disagreement among hydrozoan systematists as to whether hydroids with fixed gonophores should be recognized as different genera from those producing free medusae, when other criteria supporting generic separation are lacking. The view that hydroids should not be referred to different genera if they differ only in gonophore type has been advocated by authors such as Levinsen (1893), Broch (1916), Kramp (1949), and Petersen (1979). Conversely, Rees (1957:498) reviewed various points of view in the debate and concluded that "the use of separate genera is justifiable and the only suitable course for the

vast majority of species in the present state of our knowledge."

The matter is of relevance in delimitation of several genera within the Tubulariidae. In most contemporary classifications, *Ectopleura* L. Agassiz, 1862, and *Hybocodon* L. Agassiz, 1862, are distinguished from *Tubularia* Linnaeus, 1758, chiefly in having free medusae instead of fixed gonophores. *Ectopleura* and *Hybocodon* in turn are distinguished on the basis of differences in the morphology of their medusae. These three genera were redefined by Petersen (1979) in a step towards a single classification system for the athecate hydroids and their medusae. Gonophores were considered in his scheme, but the presence or absence of a free medusa was not viewed as a diagnostic character at the generic level. He included in *Tubularia* those solitary species of tubularian hydroids producing either asymmetrical fixed gonophores or asymmetrical medusae. Under such a redefinition of the genus, *Hybocodon* becomes congeneric with *Tubularia*. Primitively colonial tubularian hydroids, having either symmetrical fixed gonophores or symmetrical medusae, were referred to the genus *Ectopleura*. Petersen's proposal eliminates vestiges of the illogical dual classification for hydroids and medusae in the Tubulariidae, and makes it possible to refer hydroids and medusae, independently of each other, to the appropriate genus. Further evaluation is needed to test whether it is tenable for all species of the family, and whether it constitutes a natural classification.

Significant advances have been made over the past three decades towards achieving a single classification of the Hydrozoa. Nevertheless, there is at present little alternative but to retain separate genera for many hydroids and hydromedusae until the identity and affinities of the two generations are resolved through life-cycle and systematic studies. Even when life cycles are known, serious difficulties may arise in formulating a single natural classification (Rees, 1957).

The definition adopted for *Ectopleura*, the only genus of the Tubulariidae known from Bermuda, is the conventional one followed by authors such as Brinckmann-Voss (1970), Millard (1975), and Bouillon (1985).

Genus *Ectopleura* L. Agassiz, 1862

Ectopleura L. Agassiz, 1862:342.

Acharadria Wright, 1863c:378.

Acharadrium Allman, 1872:376 [incorrect subsequent spelling].

Acharadia Brinckmann-Voss, 1970:25 [incorrect subsequent spelling].

Archardia Bouillon, 1985:112 [incorrect subsequent spelling].

DIAGNOSIS

Primitively colonial hydroids, with the characters of the family.

Gonophores free medusae, with the characters of the family. Medusa radially symmetrical; exumbrella with eight longitudinal tracks of nematocysts; marginal tentacles two or four.

TYPE SPECIES

Tubularia dumortierii van Beneden, 1844b, by subsequent designation by Mayer (1910).

REMARKS

The genus *Ectopleura* was established by L. Agassiz (1862) to accommodate *Tubularia dumortierii* van Beneden, 1844b, and four other nominal species, including corynids as well as tubulariids. Agassiz did not designate a type species for the genus, but *E. dumortierii* was later so designated by Mayer (1910).

Brinckmann-Voss (1970) obtained medusae referable to *Ectopleura* from the hydroid of *Acharadria larynx* Wright, 1863c, type species of *Acharadria*. The name *Acharadria* Wright, 1863c, is, therefore, a junior synonym of *Ectopleura*.

Ectopleura pacifica Thornely, 1900

Figs. 41, 42

Ectopleura sp. Fewkes, 1883:85; pl. 1, fig. 11 [medusa].

Ectopleura pacifica Thornely, 1900:452; pl. 44, figs. 1, 1a.

Ectopleura minerva Mayer, 1900b:31; pl. 16, fig. 38; pl. 37, fig. 125 [medusa].

?*Tubularia pacifica*—Borradaile, 1905:838.

TYPE LOCALITY

Blanche Bay, New Britain, Papua New Guinea.

MATERIAL EXAMINED

Stream Passage Cave, Harrington Sound, on limestone wall, -1.5 m, 27 July 1982, one hydroid, 2.3 cm high, with blastostyles, ROMIZ B140. St George's Island, north shore, on mooring chain, -9 m, 5 October 1976, one colony, 2.5 cm high, with well-developed medusa buds, coll. J. Markham, L. Coen, ROMIZ B164. Stream Passage Cave, Harrington Sound, on rock, -1 m, 20 June 1983, one hydroid, 3.0 cm high, with medusa buds, ROMIZ B369.

DESCRIPTION

Hydroids with creeping, branched hydrorhiza invested with thick, straw-coloured, smooth or occasionally wrinkled perisarc, giving rise to upright hydrocauli. Hydrocauli up to 2.5 cm high, 0.7 mm wide, invested with perisarc, widely separated or in small clumps, each with a single terminal

hydranth. Perisarc straw-coloured, moderately thick basally, tapering to thin distally, terminating just below hydranth base. Hydranth vasiform, up to 1.8 mm high, 1.0 mm wide, bearing two whorls of tentacles. Aboral tentacles filiform, numbering 17 to 22 in mature hydranths, reaching 2 mm long; oral tentacles capitate, numbering 15 to 20 in mature hydranths, 0.3 mm long.

Gonophores free medusae, arising in clusters from short, slender blastostyles on hydranth just distal to aboral tentacles. Well-developed medusa buds dome-shaped, 2.8 mm high, 2.5 mm wide, with an apical projection; exumbrella with eight meridional tracks of nematocysts; mesoglea thin. Manubrium simple, tubular, reaching two-thirds distance to velar opening. Radial canals four. Tentacle bulbs four; two of these, opposite each other, bearing well-developed, capitate marginal tentacles.

Nematocysts—

Hydroids: desmonemes (on hydranths, medusa buds)

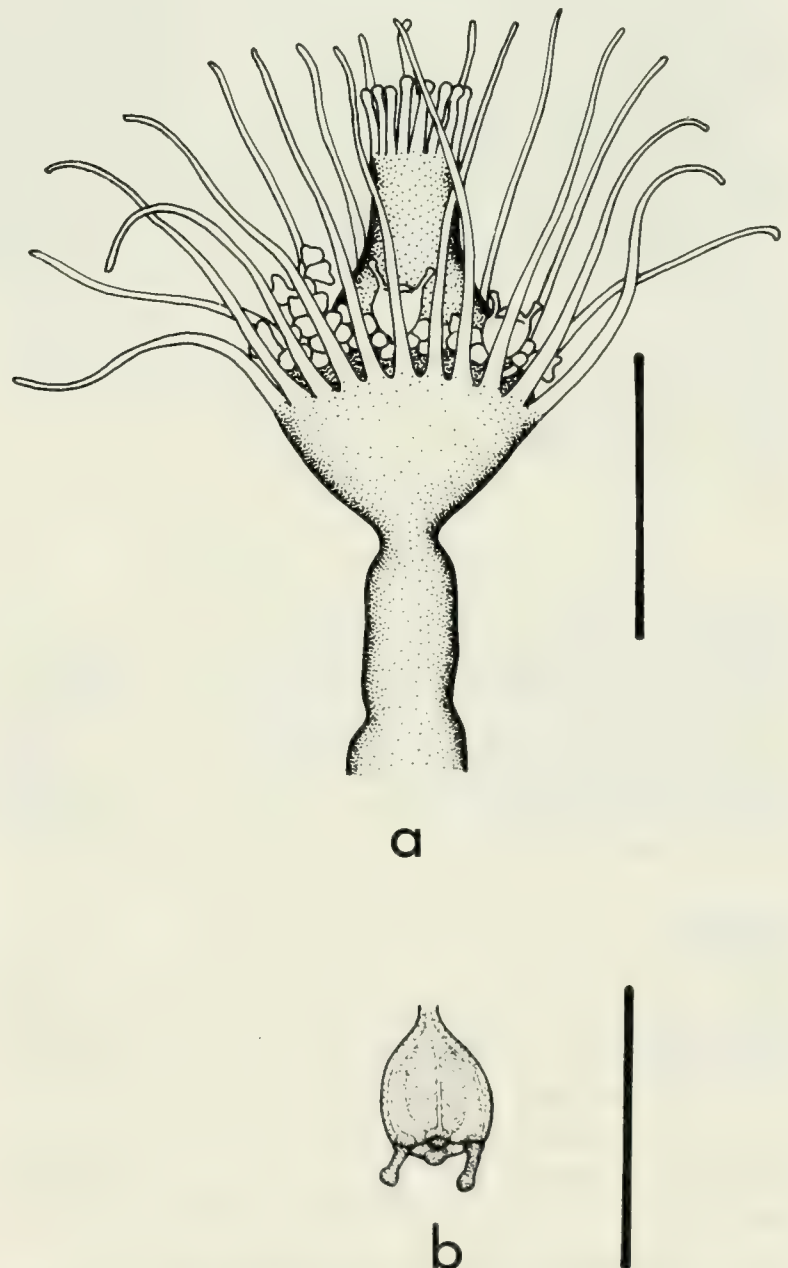


FIG. 41. *Ectopleura pacifica*, ROMIZ B164. Scale for *a* equals 1 mm; scale for *b* equals 0.5 mm. *a*, Hydranth with medusa buds. *b*, Medusa bud.

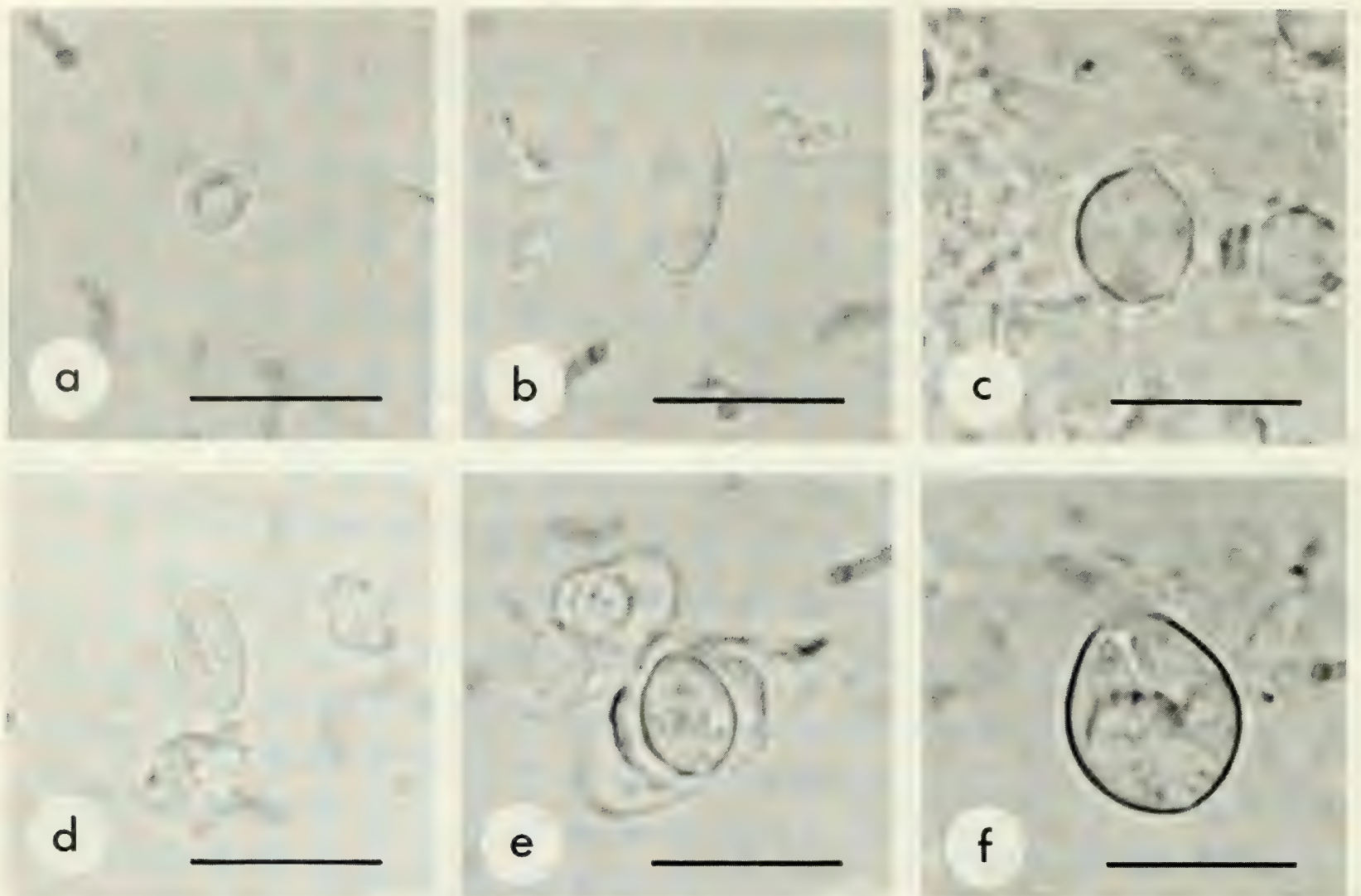


FIG. 42. *Ectopleura pacifica*, nematocysts of hydranth and medusa bud, ROMIZ B369. Scales equal 10 μm . *a*, Desmoneme of hydranth. *b*, ?Basitrichous isorhiza of hydranth. *c*, Heterotrichous anisorhiza of medusa bud. *d*, ?Microbasic mastigophore of medusa bud. *e*, Small stenotele of hydranth. *f*, Medium stenotele of hydranth.

4.6–4.9 μm \times 3.3–3.6 μm ; ?basitrichous isorhizas (on hydranths) 8.3–9.1 μm \times 3.7–4.0 μm ; heterotrichous anisorhizas (on medusa buds) 7.3–7.8 μm \times 6.1–6.7 μm ; ?microbasic mastigophores (on medusa buds) 6.8–7.5 μm \times 3.4–3.8 μm ; stenoteles (small) (on hydranths, medusa buds) 6.5–7.3 μm \times 4.9–6.6 μm ; stenoteles (medium) (on hydranths, medusa buds) 9.3–11.9 μm \times 8.0–9.8 μm .

REMARKS

Thornely (1900) described *Ectopleura pacifica* from a hydroid collected off New Britain in the western Pacific. Hydroids from Bermuda correspond in all respects to Thornely's original description of this species. While recognizing that major zoogeographic barriers separate these Bermudian hydroids from the type locality of *E. pacifica* (see Ekman, 1953; Briggs, 1974), I nevertheless regard them as conspecific based on morphological evidence.

Mayer (1900b) applied the name *Ectopleura minerva* to medusae collected at the Tortugas, Florida. The same species had earlier been reported from Bermuda by Fewkes

(1883), as *Ectopleura* sp. Neither Mayer nor Fewkes observed the hydroid of *E. minerva*, but their descriptions of the medusa are applicable to medusa buds in present material (ROMIZ B164) and to Thornely's (1900) description of *E. pacifica*, and the two are regarded here as conspecific. The name *E. pacifica* has priority over *E. minerva* because Thornely's (1900) account of the former appeared in May, while Mayer's (1900b) report of the latter appeared in July.

Free medusae ascribed to *Ectopleura pacifica* have been reported in the literature only by Mammen (1963) and Calder (1986), the latter based on Fewkes's (1883) record of *Ectopleura* sp. from Bermuda. Mammen's identification is believed to be wrong because his medusa bore four equally developed tentacles instead of two, and the oral tentacles of his hydroid were filiform instead of capitate. Notably, however, medusae identified as *E. minerva* have been reported from several locations in the Indian Ocean and the western Pacific (Nair, 1951; Kramp, 1965, 1968; Sugiura, 1977; Bouillon, 1978a, 1978c).

Hydroids of *Ectopleura pacifica* resemble descriptions of *E. larynx* (Wright, 1863c). In both species, hydroids are small and "primitively" colonial with capitate oral tentacles, and the medusa buds have two tentacles instead of four. In spite of these similarities, the two are regarded as separate species here because of apparent differences in their morphology. In hydroids of *E. larynx*, only 2 to 8 oral tentacles and 4 to 16 aboral tentacles have been observed on the hydranth (Wright, 1863a, 1863c; Brinckmann-Voss, 1970), far fewer than in *E. pacifica*.

Family Halocordylidae Stechow, 1921a

Halocordylidae Stechow, 1921a:249.

DIAGNOSIS

Colonial, capitate hydroids with creeping hydrorhiza and upright, pinnately branched hydrocaulus bearing branches on upper side only. Perisarc tubular, thick, and firm. Hydranths terminal, clavate to pear-shaped, each with an aboral whorl of long, filiform or slightly capitate tentacles, an oral whorl of short capitate tentacles, and one or more distinct or indistinct whorls of short capitate tentacles between.

Gonophores borne just distal to aboral tentacles, either liberated as short-lived medusae or remaining attached to hydranth as eumedusoids. Medusa thimble-shaped with thin mesoglea; manubrium short; mouth lacking. Radial canals four. Tentacle bulbs four; tentacles rudimentary or absent. Ocelli present or absent. Gonads surrounding manubrium.

REMARKS

Stechow (1921a) proposed that the name Pennariidae McCrady, 1859a, as applied to this taxon, be replaced for reasons elaborated upon in subsequent publications (Stechow, 1922, 1923a). In these last two papers, he noted that the type genus *Pennaria* Oken, 1815, originally included eight species, five of which were thecates and the other three of which were of indeterminable identity. Stechow noted that the name *Pennaria* should not have been applied later by Goldfuss (1820) to two species of athecate hydroids, including the familiar *Pennaria disticha*. He recognized *Halocordyle* Allman, 1872, as the valid name of the genus, and established the name Halocordylidae for the family. This family name has now gained widespread use (e.g., Rees, 1957; Pennycuik, 1959; Vervoort, 1959; Mammen, 1963; Calder, 1971; Cooke, 1975; Millard, 1975; Hirohito, 1977; Petersen, 1979; Bouillon, 1985; Garcia-Corrales and Aguirre, 1985). The family names Pennariidae and Halocordylidae cannot be regarded as synonyms because the nominal genera *Pennaria* and *Halocordyle* are not even in the same order.

Brinckmann-Voss (1970) believed that *E. larynx* and *E. minerva* were different species based on the shape of the medusa.

KNOWN RANGE

Bermuda: Castle Harbour, medusa stage (Fewkes, 1883); inshore on floats and offshore on buoy chains (Calder, 1986).

Elsewhere: western Atlantic (Mayer, 1900b); Indian Ocean (Jarvis, 1922); western Pacific (Sugiura, 1977).

Pennaria Oken, 1815, is invalid on grounds in addition to those noted by Stechow (1922, 1923a). Oken's (1815) publication has been rejected for nomenclatural purposes by the ICZN (Opinion 417) because it did not consistently adhere to the Principle of Binominal Nomenclature [Art. 5a].

Halocordyle Allman, 1872, type genus of the family Halocordylidae, is regarded as congeneric with *Eucoryne* Leidy, 1855. For reasons noted below (see p. 56), usage of the junior synonym *Halocordyle* as the name of the genus is maintained in this report. The name Halocordylidae is retained as the valid name of the family.

Ten genera were included in the family Halocordylidae by Stechow (1923a). With the exception of the type genus, all have since been transferred to other families (Mammen, 1963). Hydroids of this family are unusual among the Athecatae in their regularly pinnate colony form (Brinckmann-Voss, 1970; Millard, 1975).

Genus *Halocordyle* Allman, 1872

Pennaria auct. [not *Pennaria* Oken, 1815:93 (invalid name, published in a work rejected for nomenclatural purposes by the ICZN, Opinion 417)].

Globiceps Ayres, 1854:193 [invalid junior homonym of *Globiceps* Le Peletier de Saint-Fargeau and Serville, 1825 (Hemiptera)].

Eucoryne Leidy, 1855:136.

Eucoryna van Beneden, 1867:17 [incorrect subsequent spelling].

Halocordyle Allman, 1872:368.

Halocordile Wedler and Larson, 1986:69 [incorrect subsequent spelling].

DIAGNOSIS

With the characters of the family.

TYPE SPECIES

Globiceps tiarella Ayres, 1854, by monotypy, a junior subjective synonym of *Pennaria disticha* Goldfuss, 1820.

REMARKS

The invalid name *Pennaria* Oken, 1815, came into widespread use for this genus after Goldfuss (1820) referred his familiar species *P. disticha* to it. As noted above, *Pennaria* originally included five thecate species and three other species of indeterminable identity (Stechow, 1922, 1923a).

The binomen "*Sertolara pennara*" had earlier been applied by Cavolini (1785) to the hydroid referred to by Goldfuss (1820) as *Pennaria disticha*. Cavolini obviously believed his material was conspecific with *Sertularia pennaria* Linnaeus, 1758, but the latter is now known to be a species of thecate hydroid (see p. 57). *Sertolara* as used by Cavolini is an incorrect subsequent spelling of *Sertularia* Linnaeus, 1758. As such, it is an unavailable name [Art. 33c] and cannot be used as the name of this genus.

Ayres (1854) founded the name *Globiceps tiarella* for an American hydroid now generally regarded as conspecific with *Pennaria disticha*. The name *Globiceps* Ayres, 1854, cannot replace *Pennaria* auct. because it is an invalid junior homonym of *Globiceps* Le Peletier de Saint-Fargeau and Serville, 1825, a name applied to a hemipteran (L. Agassiz, 1862; Allman, 1872).

One year after the publication of the name *Globiceps tiarella*, Leidy (1855) described the same species under the name *Eucoryne elegans*. L. Agassiz (1862) and Allman (1872) believed that the name *Eucoryne* Leidy, 1855, was preoccupied by *Eucorynus* Schoenherr, 1823, a coleopteran. Allman (1872) proposed *Halocordyle* as a substitute name for *Globiceps* Ayres, 1854, and *Eucoryne* Leidy, 1855. However, *Eucoryne* Leidy, 1855, and *Eucorynus* Schoenherr, 1823, are not homonyms [Art. 56b]. *Eucoryne*, seldom used as a valid name since it was published (e.g., see Bedot, 1910, 1912, 1916, 1918, 1925), is nonetheless available as a senior synonym of *Halocordyle*, now in widespread use (e.g., see the 11 works cited above to demonstrate widespread use of the family name Halocordylidae). In the interests of nomenclatural stability, a submission will be made to the ICZN requesting suppression of the genus name *Eucoryne* Leidy, 1855, and placement of the name *Halocordyle* Allman, 1872, on the Official List of Generic Names in Zoology.

Halocordyle disticha (Goldfuss, 1820)

Figs. 43–45

Sertolara pennara—Cavolini, 1785:134; pl. 5, figs. 1–6 [incorrect subsequent spelling] [not *Sertularia pennaria* Linnaeus, 1758].

Sertularia pennaria—Gmelin, 1790:3856 [not *Sertularia pennaria* Linnaeus, 1758].

Pennaria disticha Goldfuss, 1820:89.

Plumularia pennaria—de Blainville, 1830:442.

Pennaria cavolinii Ehrenberg, 1834:297.

Aglatophenia pinnaria—Costa, 1839:185 [incorrect subsequent spelling].

Pennaria caulini delle Chiaje, 1841:145.

Anisocalyx pinnarium—Costa, 1842:18.

Globiceps tiarella Ayres, 1854:193.

Eucoryne elegans Leidy, 1855:136; pl. 10, figs. 1–5.

?*Euphysa globator* Leuckart, 1856:28; pl. 2, fig. 4 [medusa].

Pennaria tiarella—McCrary, 1859a:153.

Pennaria gibbosa L. Agassiz, 1860, pl. 15, figs. 1,2.

Pennaria disticha—L. Agassiz, 1862:344 [incorrect subsequent spelling].

Eucoryna elegans—van Beneden, 1867:17 [incorrect subsequent spelling].

Pennaria cavolini—van Beneden, 1867:50 [incorrect subsequent spelling].

Halocordyle tiarella—Allman, 1872:369.

Pennaria symmetrica Clarke, 1879:240; pl. 1, figs. 2,3.

Globiceps globator—Haeckel, 1879:40 [medusa].

Pennaria inornata Brooks, 1883a:144.

Pennaria australis Bale, 1884:45.

Pennaria rosea von Lendenfeld, 1885b:594; pl. 24, figs. 40–42.

Pennaria adamsia von Lendenfeld, 1885b:595; pl. 25, figs. 45–48; pl. 26, fig. 49.

Pennaria pennaria—Marktanner-Turneretscher, 1890:201.

Halocordyle australis Bale, 1894:94.

Pennaria cavolina—Spencer, 1892:13 [incorrect subsequent spelling].

Halocordyle cooperi Warren, 1906a:73; pl. 9.

Pennaria pacifica Clarke, 1907:6; pl. 1, figs. 1–6.

Pennaria australis var. *cooperi*—Warren, 1908:282.

Pennaria australis—Warren, 1908:283.

Pennaria disticha var. *australis*—Ritchie, 1910a:806.

Pennaria wilsoni Bale, 1913:116.

Halocordyle disticha—Stechow, 1923a:48.

Halocordyle australis—Stechow, 1923a:48.

Halocordyle wilsoni—Stechow, 1923a:48.

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

Halocordyle disticha var. *australis*—Vervoort, 1941:192.

Halocordyle fragilis Vannucci, 1951:76; pl. 1, figs. 2,3.

Halocordyle pennaria var. *australis*—Mammen, 1963:54; figs. 22–24.

Pennaria "*americana*" Garcia-Corrales and Aguirre, 1985:86 [nomen nudum].

Pennaria (*Halocordyle*) *tiarella*—Garcia-Corrales and Aguirre, 1985:86.

Pennaria "*europa*" Garcia-Corrales and Aguirre, 1985:86 [nomen nudum].

Pennaria (*Halocordyle*) *disticha*—Garcia-Corrales and Aguirre, 1985:86.

Pennaria symetrica—Garcia-Corrales and Aguirre, 1985:86 [incorrect subsequent spelling].

Halocordyle disticha—Wedler and Larson, 1986:69 [incorrect subsequent spelling].

TYPE LOCALITY

Gulf of Naples, Italy.

MATERIAL EXAMINED

Castle Harbour near Tucker's Town, on patch reef, -7 m, 3 August 1982, two colonies, 6.7 and 10.2 cm high, with well-developed medusa buds, ROMIZ B131. Flatts Inlet, on underside of flat rocks, -3 m, 2 August 1982, one colony, 2.2 cm high, without gonophores, ROMIZ B143. Whalebone Bay, on ledges at entrance, -1 m, 4 March 1982, two colonies, 2.6 and 3.1 cm high, without gonophores, ROMIZ B167.

DESCRIPTION

Colonies erect, arising from a creeping, branching hydrorhiza; growth monopodial with terminal hydranths. Hydrocaulus monosiphonic, reaching about 0.4 mm wide, zigzag to nearly straight, annulated basally, divided at more or less regular intervals by one or more well-developed annulations; internodes 0.6–4.0 mm long, each typically supporting a branch distally. Perisarc thick, black through brown to deep horn-coloured basally, becoming progressively thinner and lighter coloured distally, terminating abruptly below hydranths of hydrocaulus, branches, and ramuli. Branches up to 27 mm long, annulated basally, given off alternately from opposite sides of hydrocaulus, curved outwards, divided into internodes; these internodes 1.5–4.0 mm long, marked by distinct to rather faint annulations proximally and distally; each internode giving rise to a ramulus from both its upper surface and its distal end. Ramuli unbranched, annulated basally or throughout entire length, each terminating in a hydranth. Hydranths clavate to pear-shaped, up to 1.7 mm long, 0.3 mm wide; with a whorl of about 10 to 16 long, filiform or faintly knobbed tentacles aborally; a varied number of short, capitate tentacles in one or more regular or irregular verticils medially; and a whorl of about four to six short, capitate tentacles orally. Hypostome dome-shaped.

Nematocysts—

Hydroids: desmonemes $4.5\text{--}5.3\ \mu\text{m} \times 3.3\text{--}3.8\ \mu\text{m}$; basitrichous haplonemes $5.7\text{--}9.4\ \mu\text{m} \times 2.5\text{--}3.6\ \mu\text{m}$; heterotrichous microbasic euryteles $10.8\text{--}13.6\ \mu\text{m} \times 6.1\text{--}6.8\ \mu\text{m}$; stenoteles (very small) $5.7\text{--}6.6\ \mu\text{m} \times 4.3\text{--}4.6\ \mu\text{m}$; stenoteles (small) $7.4\text{--}7.8\ \mu\text{m} \times 5.5\text{--}5.7\ \mu\text{m}$; stenoteles (medium) $14.2\text{--}17.7\ \mu\text{m} \times 10.0\text{--}12.0\ \mu\text{m}$; stenoteles (large) $28.1\text{--}39.8\ \mu\text{m} \times 16.3\text{--}20.2\ \mu\text{m}$.

Gonophores free but degenerate medusae, those of a given colony either all male or all female, arising on short pedicels just distal to aboral tentacles. Well-developed medusa buds elongate-oval, about 0.9 mm high, 0.6 mm wide, covered with an ectodermal sheath; mesoglea thin; manubrium simple, tubular, reaching nearly to velar opening. Radial canals four. Tentacle bulbs four, reduced; tentacles

reduced. Ocelli lacking. Gonads surrounding manubrium, filling subumbrellar cavity.

Nematocysts—

Medusa buds: heterotrichous microbasic euryteles $7.5\text{--}8.3\ \mu\text{m} \times 3.1\text{--}4.0\ \mu\text{m}$.

REMARKS

There has been some question as to whether *Sertularia pennaria* Linnaeus, 1758, may belong to the same species as this hydroid (e.g., see Cavolini, 1785; L. Agassiz, 1862; Marktanner-Turneretscher, 1890; Bedot, 1901; Mayer, 1910). Bedot (1912) reported that the Linnaean species is an *Aglaophenia* Lamouroux, 1812, rather than an athecate hydroid. Examination of the Linnaean type has confirmed Bedot's (1912) conclusion (P. F. S. Cornelius, pers. comm.) that it is an aglaopheniid.

The oldest available specific name for this well-known species is that of Goldfuss (1820), who applied the name *Pennaria disticha* to Cavolini's (1785) "*Sertolara pennaria*." Cavolini's hydroid was identical with what is widely referred to today as *Halocordyle disticha* (Goldfuss, 1820) and *Pennaria tiarella* (Ayres, 1854), rather than Linnaeus's (1758) *Sertularia pennaria*.



FIG. 43. *Halocordyle disticha*, colony form. Natural size. *a*, Colony from exposed area, ROMIZ B167. *b*, Colony from sheltered area, ROMIZ B131.

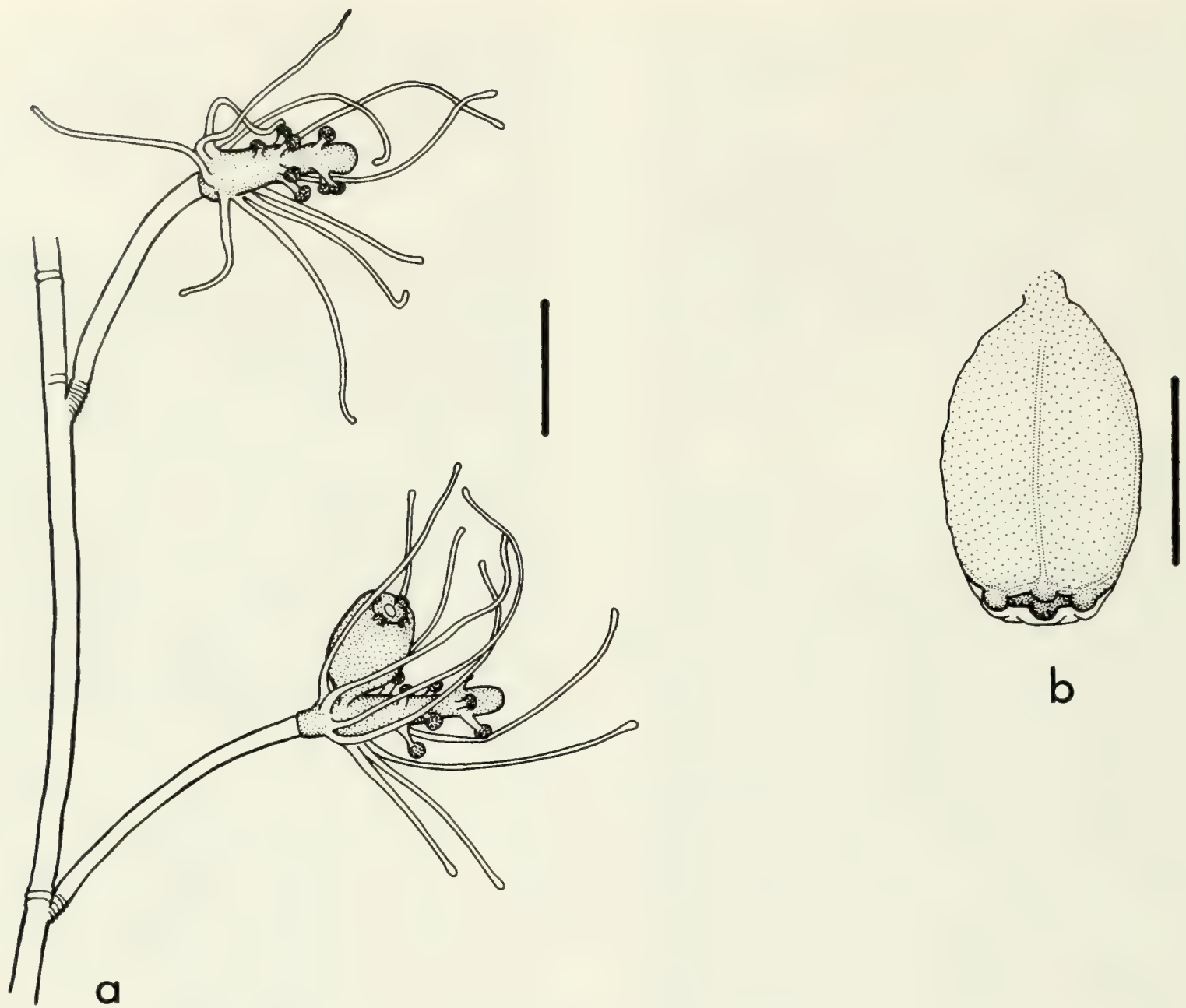


FIG. 44. *Halocordyle disticha*, ROMIZ B131. Scale for *a* equals 1 mm; scale for *b* equals 0.5 mm. *a*, Hydrocaulus and hydranths. *b*, Medusa bud.

The synonymy list provided above has been taken largely from Bedot (1901, 1905, 1910, 1912, 1916, 1918, 1925), Mayer (1910), Millard (1975), Cooke (1977), Hirohito (1977), and Garcia-Corrales and Aguirre (1985). The last two papers included extensive discussion of the synonymy of *Halocordyle disticha*, and the matter will not be repeated here. In neither paper, however, was it noted that Bale (1894) had described *Halocordyle australis* as a different species from *Pennaria australis* Bale, 1884. Both nominal species are included here in the synonymy of *Halocordyle disticha*.

Colonies of *Halocordyle disticha* displayed considerable variation in form from one location to another in Bermudian waters (Fig. 35). Specimens from sheltered waters near the base of a patch reef in Castle Harbour (ROMIZ B131) were large and gracile. Internodes of both hydrocaulus and branches were long and slender, and the branches and ramuli were elongate. Specimens from wave-swept

ledges at the entrance of Whalebone Bay (ROMIZ B167), as well as those subjected to strong tidal currents near the bridge at Flatts Inlet (ROMIZ B143), were small and compact. Internodes of the hydrocaulus and hydrocladia in these colonies were thicker and much shorter, and the branches and ramuli were relatively stunted. The degree of annulation on stem and branches, a variable character in this species (Millard, 1975), did not appear to differ significantly from one colony form to another in Bermudian material.

Hydroids of *Halocordyle disticha* are inactive during colder months in temperate areas (Hargitt, 1900; McDougall, 1943; Brinckmann-Voss, 1970; Calder, 1971). In Bermuda, a few colonies with active hydranths were found in winter even at water temperatures as low as 17°C, but the species was observed in far greater abundance during the warmer seasons.

Medusae of this species are short-lived and are liberated

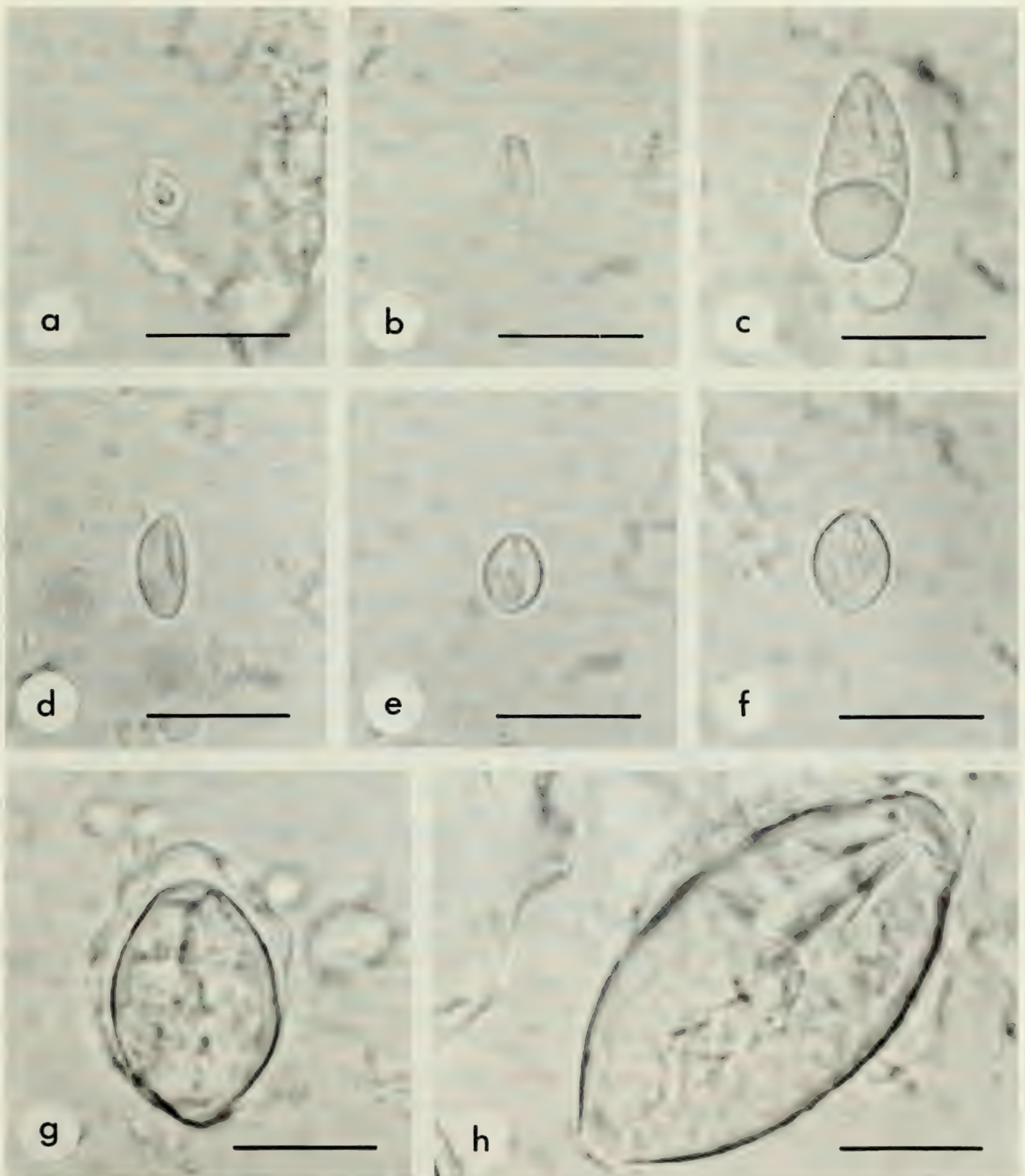


FIG. 45. *Halocordyle disticha*, nematocysts of hydranth and medusa bud. Scales equal 10 μ m. a, Desmoneme of hydranth, ROMIZ B143. b, Basitrichous haploneme of hydranth, ROMIZ B143. c, Heterotrichous microbasic eurytele of hydranth, ROMIZ B143. d, Heterotrichous microbasic eurytele of medusa bud, ROMIZ B131. e, Very small stenotele of hydranth, ROMIZ B143. f, Small stenotele of hydranth, ROMIZ B143. g, Medium stenotele of hydranth, ROMIZ B167. h, Large stenotele of hydranth, ROMIZ B167.

in the evening in Bermuda (Weill, 1937a), as noted in specimens from Chesapeake Bay (Calder, 1971). Brinckmann-Voss (1970) and others noted that medusa buds of *Halocordyle disticha* often shed their gametes while attached to the hydroid and are sometimes not released. The phenomenon of egg release by attached medusa buds in this species was described by Cavolini (1785), as noted by Cornelius (1977).

According to Weill (1934), the cnidome of hydroids of this species included desmonemes, stenoteles, microbasic mastigophores, and heteronemes of an undetermined category. Bouillon (1985) has been followed here in regarding the last two of these as microbasic euryteles and basitrichous haplonemes. The nematocyst complement of medusa buds in Bermudian material typically consisted of microbasic euryteles, although a few stenoteles and haplonemes were observed in some specimens. Euryteles of medusa buds almost always lacked the spherical inclusions found in those of the hydroid.

This species has been reported from Bermuda several

times previously (Verrill, 1900; Congdon, 1907; Bennett, 1922; Calder, 1986). It has also been utilized in morphological and developmental studies conducted at the Bermuda Biological Station (Weill, 1937a; Cowden, 1964, 1965a, 1965b; Summers and Haynes, 1969; Summers, 1970, 1972b; Lesh-Laurie, 1976; Clark and Cook, 1986).

KNOWN RANGE

Bermuda: no specific locality given (Verrill, 1900; Congdon, 1907; Weill, 1937a); Hamilton Harbour and Great Sound (Bennett, 1922); near the Bermuda Biological Station (Cowden, 1964, 1965a, 1965b); Flatts Inlet (Summers and Haynes, 1969; Summers, 1970, 1972b; Lesh-Laurie, 1976); inshore in shallow water and offshore on buoy chains (Calder, 1986).

Elsewhere: western Atlantic (Fraser, 1944); eastern Atlantic (Brinckmann-Voss, 1970); Indian Ocean (Millard, 1975); western Pacific (Yamada, 1959); eastern Pacific (Fraser, 1948).

Family Sphaerocorynidae Prévot, 1959

Sphaerocorynidae Prévot, 1959:108.

DIAGNOSIS

Hydroids colonial, with creeping stolons and upright, unbranched or sparingly branched hydrocauli with terminal hydranths. Perisarc moderately thin, reaching to hydranth base. Hydranths pyriform, with bulbous base and conical hypostome. Tentacles capitate, scattered in an irregular band about bulbous hydranth base.

Gonophores free medusae, arising from hydranth on short pedicels among or distal to tentacles. Medusae bell-shaped, with or without exumbrellar nematocyst tracks; manubrium tubular in juveniles, cruciform in cross-section in adults, not extending beyond velar opening; mouth simple. Radial canals four. Marginal tentacles two or four, capitate. Ocelli present. Gonads on perradii of manubrium.

REMARKS

Sphaerocoryne Pictet, 1893, and *Linvillea* Mayer, 1910, the latter a genus formerly included in the family Corynidae Johnston, 1836, were grouped by Petersen (1979) in the Sphaerocorynidae Prévot, 1959. Petersen noted that these genera differ in several respects from typical corynid hydrozoans. Tentacles in the hydroid stage are restricted to the expanded basal region of the hydranth, and medusa buds arise among or distal to the tentacles. Gonads in the medusa do not surround the manubrium but are located perradially on it. Finally, the nematocyst complement of both hydroid and medusa includes stenoteles and desmo-

nemes. Petersen believed that this family was more closely related to the Moerisiidae Poche, 1914, than to the Corynidae as suggested by Prévot (1959).

Genus *Sphaerocoryne* Pictet, 1893

Sphaerocoryne Pictet, 1893:9.

DIAGNOSIS

Hydroids with the characters of the family.

Medusa buds arising in clusters on hydranth just distal to tentacles. Medusae with scattered exumbrellar nematocysts; manubrium of adult somewhat cruciform in cross-section. Marginal tentacles four, capitate or moniliform, equally developed at liberation.

TYPE SPECIES

Sphaerocoryne bedoti Pictet, 1893, by monotypy.

REMARKS

The hydroids of *Sphaerocoryne* Pictet, 1893, and *Linvillea* Mayer, 1910, resemble one another morphologically. Yamada and Konno (1973) reported finding only minor differences in a comparison of *Sphaerocoryne multitentaculata* (Warren, 1908) (= *S. bedoti* Pictet, 1893) from Japan and *Linvillea agassizii* (McCrary, 1859a) from Virginia, United States. Medusa buds in *L. agassizii* arise among the tentacles on the hydranth, while they occur distal to the ten-

tacles in *S. bedoti*. Differences are more pronounced in medusae of the two species. In *L. agassizii*, medusae have eight exumbrellar nematocyst tracks, the manubrium is distinctly cruciform in cross-section in the adult, and two of the four marginal tentacles are undeveloped in young medusae. In *S. bedoti*, medusae have scattered exumbrellar nematocysts, the manubrium is less distinctly cruciform in cross-section than in *L. agassizii*, and the four marginal tentacles are equally developed at all stages of growth.

Adult medusae of *Sphaerocoryne peterseni* Bouillon, 1984a, have adaxial batteries of nematocysts along each of four marginal tentacles, and an abaxial ocellus is present on each tentacle bulb. The hydroid stage of this species is unknown.

***Sphaerocoryne bedoti* Pictet, 1893**

Figs. 46, 47

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

Clavatella multitentaculata Warren, 1908:278; pl. 45, figs. 7-9.

Sphaerocoryne multitentaculata—Stechow, 1921a:248.

Eleutheria multitentaculata—Bedot, 1925:179.

Sphaerocoryne sp.—Gravelly, 1927:8; pl. 2, fig. 3.

Coryne (?) *multitentaculata*—Pennycuik, 1959:158.

TYPE LOCALITY

Ambon, Moluccas, Indonesia.

MATERIAL EXAMINED

Major's Bay, Harrington Sound, on sponge, -2 m, 13 September 1977, several hydranths with medusa buds, and several newly liberated medusae, ROMIZ B132. Major's Bay, Harrington Sound, on sponge, -2 m, 13 September 1977, several hydranths with medusa buds, ROMIZ B177. Walsingham Pond area, cave entrance, on underside of rock, -1 m, 29 June 1983, two hydranths, 1 cm high, without gonophores, ROMIZ B331.

DESCRIPTION

Hydrorhiza embedded in sponge. Hydrocaulus monosiphonic, unbranched, about 1 cm high, 120 μm wide, supporting a terminal hydranth. Perisarc rather thin, hyaline, smooth or with a few wrinkles; distinct annulations not apparent. Hydranths pyriform, 0.8 mm high, 0.5 mm wide, with an elongate hypostome. Tentacles capitate, of varying length, about 30 in number, scattered in a narrow band around bulbous hydranth base.

Nematocysts—

Hydroids: desmonemes 12.4-13.2 μm \times 5.6-5.9 μm ; stenoteles (small) 11.2-12.2 μm \times 7.7-9.2 μm ; stenoteles (large) 24.4-26.3 μm \times 16.8-18.0 μm .

Gonophores developing in small clusters, borne on hydranth just distal to tentacles. Well-developed medusa buds and newly liberated medusae thimble-shaped, 450 μm high, 350 μm wide in alcohol-preserved specimens; exumbrella with scattered nematocysts; mesoglea thin; manubrium simple, conical, reaching about halfway to velar opening. Radial canals four. Tentacle bulbs four, equally developed; marginal tentacles scarcely if at all developed. Ocelli and gonads undeveloped.

Nematocysts—

Medusae: desmonemes 8.3-9.5 μm \times 3.8-4.5 μm ; basitrichous haplonemes 9.2-10.8 μm \times 7.9-9.4 μm ; stenoteles (small) 9.1-9.7 μm \times 6.5-7.5 μm ; stenoteles (large) 12.4-13.6 μm \times 8.8-10.5 μm .

REMARKS

Three nominal species of the genus *Sphaerocoryne* Pictet, 1893, *S. bedoti* Pictet, 1893, *S. multitentaculata* (Warren, 1908), and *S. peterseni* Bouillon, 1984a, have been described in the literature. Only the medusa stage of *S. peterseni* is known. Hydroids of the other two, found on sponges, are virtually inseparable based on currently available descriptions. Yamada and Konno (1973) preferred to

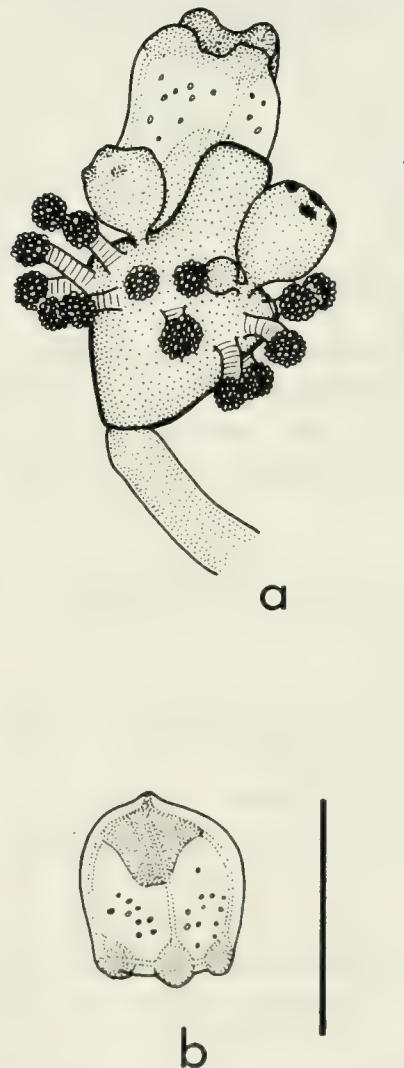


FIG. 46. *Sphaerocoryne bedoti*. Scales equal 0.5 mm. a, Part of hydrocaulus, and hydranth, ROMIZ B177. b, Newly liberated medusa, ROMIZ B132.

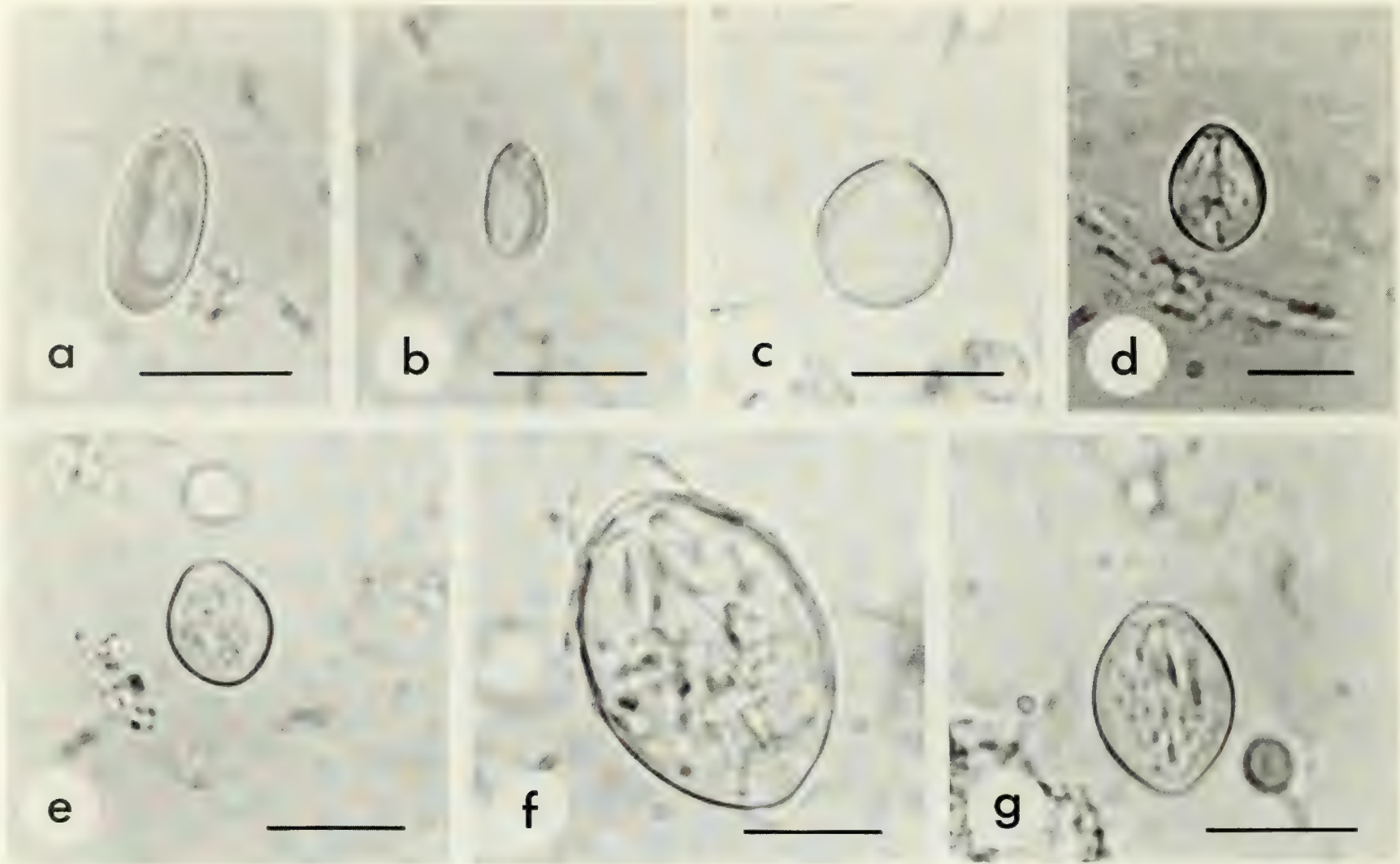


FIG. 47. *Sphaerocoryne bedoti*, nematocysts of hydranth and medusa bud. Scales equal 10 μm . *a*, Desmoneme of hydranth, ROMIZ B331. *b*, Desmoneme of medusa bud, ROMIZ B132. *c*, Basitrichous haploneme of medusa bud, ROMIZ B132. *d*, Small stenotele of hydranth, ROMIZ B331. *e*, Small stenotele of medusa bud, ROMIZ B132. *f*, Large stenotele of hydranth, ROMIZ B331. *g*, Large stenotele of medusa bud, ROMIZ B132.

recognize *S. multitentaculata* as a valid species because of a general lack of information on living material from areas other than Japan, but Mammen (1963) and Millard (1975) have been followed here in regarding it as conspecific with *S. bedoti*.

Yamada and Konno (1973) described the hydroid of this species and outlined the development of the medusa from liberation to maturity. They found that the four marginal tentacles developed concurrently in the medusa, and that an abaxial ocellus appeared on each tentacle bulb about 8 to 10 days after liberation. Medusae raised on *Artemia* in the laboratory were mature two weeks after release from the hydroid. Male medusae were ovoid, 2.5–3.5 mm high, 2.0–3.0 mm wide, and possessed a manubrium two-thirds to four-fifths the length of the subumbrellar cavity. Female medusae were conical, 3.0–4.5 mm high, 2.0–3.0 mm wide, and bore a manubrium about two-thirds the length of the subumbrellar cavity. These laboratory-reared specimens have not been identified with any previously named species of medusa.

Bermudian hydroids of *Sphaerocoryne bedoti* tended to

be slightly smaller than those described from Indonesia (Pictet, 1893), South Africa (Warren, 1908), India (Mammen, 1963), and Japan (Yamada and Konno, 1973). However, the range of hydranth size and shape in this species is reflected in both living and preserved material examined by Mammen (1963). Tentacle number is likely to vary somewhat with hydranth size, and tentacle arrangement appears to differ depending upon the degree of expansion or contraction of the hydranth. Newly liberated medusae of this species from Bermuda, measured after five years in preservative, were decidedly smaller than those described by Yamada and Konno (1973). Part of this difference may be attributable to contraction of my specimens on preservation, and their subsequent shrinkage in the alcohol preservative.

KNOWN RANGE

Bermuda: inshore, on sponges (Calder, 1986).

Elsewhere: western Atlantic (Mergner and Wedler, 1977); Indian Ocean (Millard and Bouillon, 1974); western Pacific (Yamada and Konno, 1973).

Family Corynidae Johnston, 1836

Corynidae Johnston, 1836:107.
Sarsiadae Forbes, 1848:54.
Syncorynidae Allman, 1872:274.
Codonidae Haeckel, 1879:9.

DIAGNOSIS

Hydroid colonies stolonial or erect, with creeping hydro-rhiza and upright, unbranched or irregularly branched hydrocaulus. Perisarc firm. Hydranths variable in shape but often clavate, with an oral whorl of capitate tentacles, frequently with scattered or verticillate capitate tentacles extending proximally over hydranth, and with or without an aboral whorl of reduced filiform tentacles. Hypostome dome-shaped to conical.

Gonophores fixed sporosacs or free medusae, borne on hydranth proximal to or among capitate tentacles. Medusae, when present, bell-shaped, without exumbrellar nematocyst tracks; manubrium tubular, short and enclosed within subumbrellar cavity or long and extending beyond velar opening; mouth simple, circular. Radial canals four. Marginal tentacles four. Ocelli present. Gonads surrounding manubrium, arranged in one or more rings.

REMARKS

The scope of the family Corynidae Johnston, 1836, adopted here encompasses only the genera *Coryne* Gaertner, 1774, *Sarsia* Lesson, 1843, and *Dipurena* McCrady, 1859a. The poorly known genus *Dicodonium* Haeckel, 1879, has generally been regarded as a corynid, but apparently is not (Brinckmann-Voss, 1970). Accordingly, the name of the tribe Dicodoniini, established for this genus by Cockerell (1911), is excluded from the synonymy of the Corynidae given above. Petersen (1979) has been followed in referring *Sphaerocoryne* Pictet, 1893, and *Linvillea* Mayer, 1910, to the Sphaerocorynidae Prévot, 1959, as well as *Dicylocoryne* Annandale, 1915, and *Bicorona* Millard, 1966, to the Dicylocorynidae Petersen, 1979. Earlier, Rees (1957) removed *Hydrocoryne* Stechow, 1907, to a new family, the Hydrocorynidae. Among other nominal genera frequently encountered in discussions of corynids, *Syncoryna* Ehrenberg, 1834, and *Staurocoryne* Rotch, 1872, are regarded as congeneric with *Coryne* (e.g., see Millard, 1975), and *Stauridiosarsia* Mayer, 1910, is considered to be congeneric with *Sarsia* (e.g., see Brinckmann-Voss, 1970; Millard, 1975; Arai and Brinckmann-Voss, 1980; Bouillon, 1985). The systematic affinities of *Sarsiella* Hartlaub, 1907, and *Bibrachium* Stechow, 1919, are unclear, although both were included in the Corynidae by Bouillon (1985). The family-group name Codonidae Haeckel, 1879 (correctly spelled Codoniidae) is included as a synonym of the name Corynidae because its type genus,

Codonium Haeckel, 1879, is congeneric with *Sarsia* (Mayer, 1910).

The corynid genera *Coryne*, *Sarsia*, and *Dipurena* were recently redefined by Petersen (1979). In his classification, tentacle arrangement and gonophore location on the hydranth of the hydroid, as well as manubrium length, extent of the manubrium functioning as a "stomach," and position of the gonad on the manubrium in the medusa, were used to distinguish genera. It is possible, following Petersen's diagnoses, to refer corynid hydroids to genus in the absence of information on type of gonophore produced. It remains to be determined whether this classification is more "natural" than the one adopted by most other current authors.

The filiform tentacles of corynid hydroids, which may be present or absent even within a given species, were regarded as evolutionary vestiges by Rees (1957). Edwards and Harvey (1983) disputed this, suggesting instead that they are highly specialized sense organs used for detection of prey as indicated by Tardent and Stössel (1971), Stössel and Tardent (1971), and Tardent and Schmid (1972).

Genus *Coryne* Gaertner, 1774

Coryne Gaertner, 1774:40.
Fistularia O. F. Müller, 1776a:254 [invalid junior homonym of *Fistularia* Linnaeus, 1758 (Pisces)].
Fistulana O. F. Müller, 1776a:282.
Capsularia Modeer, 1793:256 [nomen nudum].
Capsularia Cuvier, 1798:665.
Corine Cuvier, 1798:656 [incorrect subsequent spelling].
Coryna Bosc, 1802:238 [incorrect subsequent spelling].
Corina Schweigger, 1820:409 [incorrect subsequent spelling].
Stipula M. Sars, 1829:4.
Syncoryna Ehrenberg, 1834:294.
Hermia Johnston, 1838:111.
Syncoryne Steenstrup, 1842:10 [incorrect subsequent spelling].
Halybotrys de Filippi, 1866:383.
?*Actinogonium* Allman, 1871:95 [invalid junior homonym of *Actinogonium* Schomburgk, 1847 (?Protozoa)].
Syncorine Spagnolini, 1871:211 [incorrect subsequent spelling].
Staurocoryne Rotch, 1872:126.
Halobotrys Carus, 1885:2 [incorrect subsequent spelling].
Eucoryne Broch, 1909:138 [invalid junior homonym of *Eucoryne* Leidy, 1855 (Hydrozoa)].
Halybothrys Bedot, 1910:310 [incorrect subsequent spelling].
?*Actigia* Stechow, 1921a:248.

DIAGNOSIS

Corynid hydroids with stolonal or erect and branching colonies. Hydranths with several more or less distinct whorls of capitate tentacles distally, those of one whorl often alternating with those of adjacent whorls; hydranths occasionally with a whorl of reduced filiform tentacles proximally.

Gonophores fixed sporosacs, arising on hydranth either in axils of capitate tentacles or just proximal to capitate tentacles.

TYPE SPECIES

Coryne pusilla Gaertner, 1774, by monotypy.

REMARKS

The diagnosis of *Coryne* Gaertner, 1774, given above is similar to that adopted by Brinckmann-Voss (1970), Millard (1975), Bouillon (1985), and others. It differs from the definition of the genus proposed by Petersen (1979), who included in *Coryne* those species of corynids having a stolonal or erect and branching colony form; capitate tentacles alternating in successive whorls; filiform tentacles either present or absent; gonophores arising either in the axils of the tentacles or in a whorl replacing the lowest verticil of capitate tentacles; and medusae, when present, with a short manubrium completely or almost completely surrounded by the gonad. Although not followed in this report, Petersen's ideas concerning the scope of the genus merit further evaluation.

The name of this genus was originally spelled *Coryne* by Gaertner (1774); *Corine* Cuvier, 1798, *Coryna* Bosc, 1802, and *Corina* Schweigger, 1820, are incorrect subsequent spellings. Broch (1909) founded the subgenus *Eucoryne* within the genus, but that name is an invalid junior homonym of *Eucoryne* Leidy, 1855.

Although the name *Fistularia* had been applied to a genus of fishes by Linnaeus (1758), O. F. Müller (1776a) applied the same name to a genus of hydroids. Later in the same publication, Müller employed the name *Fistulana* as a replacement name for *Fistularia* O. F. Müller, 1776a. One of the hydroids included in *Fistulana* by Müller was *Tubularia ramosa* Linnaeus, 1758, the type species of *Eudendrium* Ehrenberg, 1834. Had this species been designated type species of Müller's nominal genus, the virtually forgotten name *Fistulana* would be a senior objective synonym of the widely used name *Eudendrium*. To my knowledge, no type species has ever been designated for *Fistulana*. Accordingly, *Tubularia muscoides* Linnaeus, 1761, another species included by Müller (1776a) in his genus but now included in *Coryne*, is hereby designated as type species of *Fistulana*. The name *Fistulana* thus becomes a junior subjective synonym of *Coryne*, and its potential nomenclatural threat to *Eudendrium* is removed.

Van Beneden (1844b) identified as *Syncoryna pusilla*

Gaertner, 1774, a hydroid that was subsequently shown by Hincks (1868) and Allman (1872) to be a different species. Hincks (1868) proposed the name *Coryne vanbenedenii* for this hydroid. Allman (1871, 1872) removed it to a new nominal genus, *Actinogonium*, chiefly because an actinula larva was reported in its life cycle, and he renamed the species *A. pusillum*. Stechow (1921a) noted that *Actinogonium* Allman, 1871, is a junior homonym of *Actinogonium* Schomburgk, 1847, a protozoan, and proposed *Actigia* as a replacement name. Brinckmann-Voss (1970) listed the species from the Mediterranean, based on a questionable record by Schneider (1898a), under the genus *Coryne*.

Stechow (1923a) has been followed in regarding *Stipula* M. Sars, 1829, *Syncoryna* Ehrenberg, 1834, *Hermia* Johnston, 1838, and *Halybotrys* de Filippi, 1866, along with *Fistularia* O. F. Müller, 1776a, *Fistulana*, *Capsularia* Cuvier, 1798, and *Eucoryne* Broch, 1909, as congeneric with *Coryne*. Stechow also regarded *Acrochordium* Meyen, 1834, as a synonym of *Coryne*, but it belongs in the Zancleidae Russell, 1953 (see p. 69). *Staurocoryne* Rotch, 1872, has been regarded as congeneric with *Coryne*, following Millard (1975), Edwards and Harvey (1983), and Bouillon (1985). Under the definition of this genus proposed by Petersen (1979), *Stauridia* Wright, 1858b [not *Stauridia* Forbes, 1848], *Stauridiosarsia* Mayer, 1910, and *Perinema* Stechow, 1921c, would be congeneric with *Coryne*. They are regarded here as congeneric with *Sarsia* Lesson, 1843.

Coryne sargassicola, sp. nov.

Figs. 48, 49

Syncoryne mirabilis—Fraser, 1912:347; fig. 3 [not *Sarsia mirabilis* L. Agassiz, 1849 (= *Sarsia tubulosa* (M. Sars, 1835))].

Syncoryne sp. Burkenroad in Parr, 1939:23.

Syncoryne (*Sarsia*) *mirabilis*—Morris and Mogelberg, 1973:10; fig. 2.

MATERIAL EXAMINED

Holotype: Natural Arches Beach, washed ashore on pelagic *Sargassum*, 8 March 1982, one colony, 2.7 mm high, without gonophores, ROMIZ B159. Paratypes: Whalebone Bay, on pelagic *Sargassum*, 6 September 1977, one colony, 2.7 mm high, without gonophores, ROMIZ B156; Natural Arches Beach, washed ashore on pelagic *Sargassum*, 8 March 1982, one colony, 2.5 mm high, without gonophores, ROMIZ B302; Gulf Stream, east-southeast New York City, 40°02' N, 70°50' W, on pelagic *Sargassum*, 1 October 1969, one colony, 4.5 mm high, with gonophores, coll. M. Fine on R/V *Eastward*, ROMIZ B490.



FIG. 48. *Coryne sargassicola*, sp. nov., part of colony with hydrorhiza, hydrocaulus, and hydranth, ROMIZ B302. Scale equals 0.5 mm.



FIG. 49. *Coryne sargassicola*, sp. nov., nematocysts of hydranth, ROMIZ B302. Scale equals 10 μm . a, Small stenotele. b, Large stenotele.

DESCRIPTION

Hydroid colonies typically stolonial, occasionally with an irregular branch; pedicels arising from a creeping hydrorhiza. Pedicels up to 3 mm long, 0.12 mm wide, supporting terminal hydranth. Perisarc of moderate thickness basally, thinning out distally, smooth or with a few wrinkles but not annulated, terminating below tentacles on hydranth. Hydranth elongate-oval, reaching 1 mm long, 0.3 mm wide; tentacles arranged in whorls of four to six each, with those of one whorl alternating with those of adjacent whorls; oral tentacles capitate, with terminal knobs 65–85 μm in diameter; aboral tentacles capitate, in one to four whorls, with terminal knobs of lowest whorl 55–60 μm in diameter; basal whorl of reduced filiform tentacles present or absent. Hypostome conical, moderately elongate.

Nematocysts—

Hydroids: stenoteles (small) 11.7–12.2 μm \times 6.7–7.3 μm ; stenoteles (large) 19.9–20.8 μm \times 14.1–15.1 μm .

Gonophores presumably fixed sporosacs, arising from hydranth in axils of proximal tentacles.

REMARKS

This species has been referred to *Coryne* Gaertner, 1774, rather than to *Sarsia* Lesson, 1843, or *Dipurena* McCrady,

1859a, because gonophores in paratype material (ROMIZ B490) appear to be fixed sporosacs arising from the axils of the tentacles. It also corresponds with the genus *Coryne* as defined by Petersen (1979).

Coryne sargassicola, sp. nov., is regarded as conspecific with the corynids reported earlier from *Sargassum* by Fraser (1912) and Morris and Mogelberg (1973) as *Syncoryne mirabilis* (L. Agassiz, 1849), and by Burkenroad in Parr (1939) as *Syncoryne* sp. Following Kramp (1928), *S. mirabilis* is now generally regarded as a synonym of *Sarsia tubulosa* (M. Sars, 1835). It is improbable that the boreal *S. tubulosa* ranges into the warm waters where pelagic *Sargassum* is normally found, and where the present species occurs.

Hydroids of *Sarsia tubulosa* and *Coryne sargassicola* are similar in colony form and in having smooth perisarc. However, filiform tentacles, observed on some hydranths of *C. sargassicola* (ROMIZ B156, ROMIZ B302), are lacking in *S. tubulosa* (e.g., see Edwards, 1978, 1983; Brinckmann-Voss, 1985). Moreover, the hydroid of *S. tubulosa* produces free medusae instead of fixed sporosacs. It is unclear whether Fraser (1912) actually observed liberation of gonophores in the hydroid he identified as *Syncoryne mirabilis*, or whether he simply assumed they would be released.

He noted that the "medusae" of his specimens were sexually mature before liberation.

L. Agassiz (1849), Mayer (1910), and Berrill (1953) reported that free medusae were produced by hydroids of *Sarsia tubulosa* at certain times of year, and fixed eumedusoids at other times. Edwards (1978) found no such variation in gonophore type in cultures of *S. tubulosa* maintained in the laboratory. Hydroids of that species cultured at various temperatures by Edwards all released their medusae, and none of the medusae bore gonads at liberation. Likewise, Edwards demonstrated that temperature variation had no influence on the type of gonophore produced by either *Sarsia occulta* Edwards, 1978, or *Sarsia lovenii* (M. Sars, 1846). In the former species, gonads were partially developed in the medusa prior to its liberation. In *S. lovenii*, gonophores ripened on the hydranth and were not released as free medusae. Edwards concluded that L. Agassiz, Mayer, and Berrill had confused more than one valid taxon for a single species.

Hydroids of *Coryne sargassicola* resemble those of *C.*

pintneri Schneider, 1898a, and of *C. filiformis* (Rees, 1936), but are smaller and lack annulations on the perisarc. They also resemble the cold-water *C. hincksii* Bonnevie, 1898, but dimensions of the latter given by Rees (1956b) and Calder (1972) indicate that it is a more robust species than *C. sargassicola*.

Observations on live material are needed to clarify the life cycle of this hydrozoan, and to confirm its generic identity.

ETYMOLOGY

The specific name is derived from a combination of the generic name *Sargassum* plus the Latin suffix *cola*, a dweller, in reference to the algal substrate of this species.

KNOWN RANGE

Bermuda: on pelagic *Sargassum* (Burkenroad in Parr, 1939, as *Syncoryne* sp.).

Elsewhere: western Atlantic (Fraser, 1912, as *Syncoryne mirabilis*).

Family Cladonematidae Gegenbaur, 1857

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

Stauridiidae Hincks, 1868:61.

Dendronemidae Haeckel, 1879:107.

DIAGNOSIS

Hydroid colonies with creeping stolons and short, unbranched or sparingly branched hydrocauli with terminal hydranths. Perisarc of moderate thickness, terminating at hydranth base. Hydranths clavate, with an oral whorl of capitate tentacles, usually with an aboral whorl of reduced filiform tentacles.

Gonophores free medusae, arising from hydranth just distal to filiform tentacles; medusae creeping or swimming. Manubrium with radial pouches; these pouches short and enclosed within subumbrellar cavity or moderately long and extending beyond velar opening; mouth with oral tentacles bearing nematocyst clusters. Radial canals bifurcated or simple, number variable. Marginal tentacles hollow, equal in number to radial canals, branching, bearing organs of adhesion. Ocelli present. Gonads surrounding manubrium.

REMARKS

Prévot (1959), Naumov (1960), and Millard (1975) believed that differences between the Cladonematidae Gegenbaur, 1857, and the Eleutheriidae Stechow, 1923a, were insufficient to warrant recognition of both families. Although the two families are acknowledged here to be

closely related, the Eleutheriidae are regarded as distinct from the Cladonematidae largely on the basis of differences in the medusa. These differences include the presence of a nematocyst ring around the umbrella margin, the lack of oral tentacles, the location of the gonads, and the reduced umbrella in the Eleutheriidae.

Hydroids of this family resemble those of the Corynidae Johnston, 1836. Their medusae share with those of the Corynidae characters such as the presence of ocelli and the location of the gonad in a ring around the manubrium, but are otherwise rather highly specialized.

Genus *Cladonema* Dujardin, 1843a

stauridie Dujardin, 1843a:1133.

Cladonema Dujardin, 1843a:1134.

Stauridia Forbes, 1848:81 [emendation of stauridie Dujardin, 1843a].

Stauridium Krohn, 1853a:137 [emendation of stauridie Dujardin, 1843a].

Stauridia Wright, 1858b:284 [invalid junior homonym of *Stauridia* Forbes, 1848 (Hydrozoa)].

DIAGNOSIS

With the characters of the family.

TYPE SPECIES

Cladonema radiatum Dujardin, 1843a, by monotypy.

REMARKS

The genus *Cladonema* and its type species, *C. radiatum*, were described in two separate but essentially identical papers by Dujardin (1843a, 1843b). One of these papers (Dujardin, 1843a) appeared in the January-June issue of the *Comptes Rendus Hebdomadaires des Séances de l'Académie des Sciences*. The other (Dujardin, 1843b) was published in the December issue of the *Annales des Sciences Naturelles*. Accordingly, the former is taken as the first publication of the generic name *Cladonema* and of its type species, *C. radiatum*.

The name "stauridie," applied by Dujardin (1843a, 1843b) to the hydroid of the medusa *Cladonema radiatum*, is not available [Art. 11]. The name of Dujardin's (1843a, 1843b) hydroid, stauridie, was emended to *Stauridia* by Forbes (1848). Wright (1858b), apparently unaware that Forbes had emended the name, also proposed the name *Stauridia* for this hydroid genus and included a new species, *S. producta*, in it. However, *S. producta* produces medusae referable to the family Corynidae Johnston, 1836, as first shown by Hincks (1862), and is not congeneric with the hydroid described by Dujardin (1843a, 1843b). Mayer (1910) removed *S. producta* to a new genus, *Stauridiosarsia*, a name considered synonymous with *Sarsia* Lesson, 1843.

Dendronema Haeckel, 1879, is similar to *Cladonema*, but was recognized as a valid genus by Bouillon (1985).

Cladonema radiatum Dujardin, 1843a

Fig. 50

stauridie Dujardin, 1843a:1133.

Cladonema radiatum Dujardin, 1843a:1134 [medusa].

Coryne stauridia Gosse, 1853:260.

Coryne stauridiae Gosse, 1853, pl. 16, figs. 1–5 [lapsus].

Syncoryne stauridium Krohn, 1853a:420.

Cladonema radiatum gegenbauri Haeckel, 1879:109 [medusa].

Cladonema radiatum krohnii Haeckel, 1879:109 [medusa].

Cladonema radiatum dujardinii Haeckel, 1879:109 [medusa].

Cladonema radiatum allmani Haeckel, 1879:109 [medusa].

Stauridium cladonema Haeckel, 1879:109.

Cladonema sp. Fewkes, 1883:87 [medusa].

Cladonema sp. Perkins, 1902:25 [medusa].

Cladonema radiata—Johansen and Levinsen, 1903:278 [medusa].

Cladonema perkinsii Mayer, 1904:18; pl. 4, fig. 35 [medusa].

Cladonema mayeri Perkins, 1906:118 [medusa and hydroid].

Cladonema allmani—Perkins, 1908:138 [medusa].

Cladonema dujardinii—Perkins, 1908:138 [medusa].

Cladonema gegenbauri—Perkins, 1908:140 [medusa].

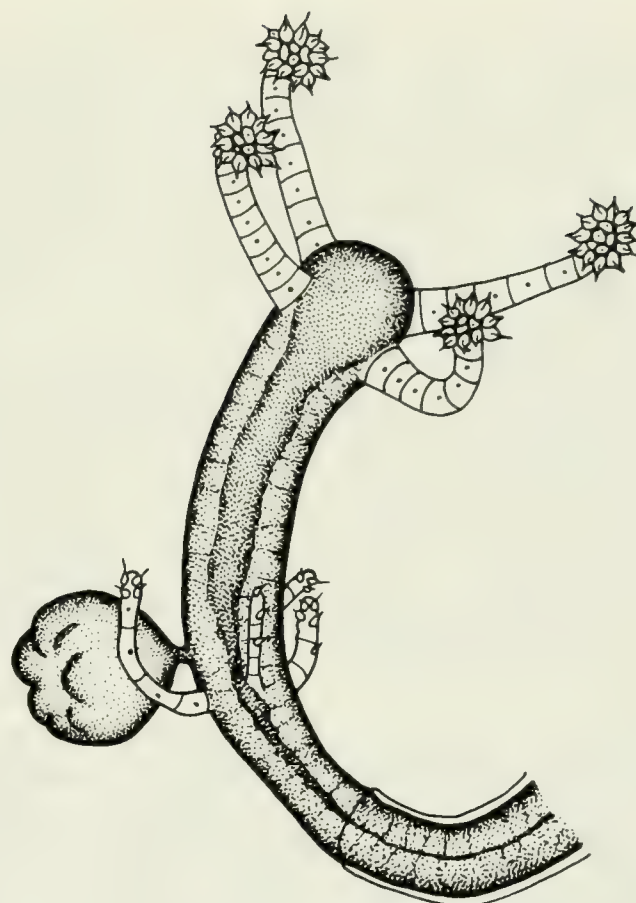


FIG. 50. *Cladonema radiatum*, part of hydrocaulus, and hydranth with medusa bud, ROMIZ B144. Scale equals 0.25 mm.

Cladonema krohnii—Perkins, 1908:140 [medusa].

Stauridia radiatum—Mayer, 1910:100.

Eleutheria radiata—Lengerich, 1922:210; fig. 1 [medusa].

Eleutheria perkinsii—Lengerich, 1922:211 [medusa].

not *Cladonema radiatum* var. *mayeri* Uchida, 1925:81; fig. 7 [= *Cladonema uchidai* Hirai, 1958].

Cladonema dujardini—Bedot, 1925:486 [medusa] [incorrect subsequent spelling].

Cladonema perkinsii—Bedot, 1925:486 [medusa] [incorrect subsequent spelling].

TYPE LOCALITY

Mediterranean Sea.

MATERIAL EXAMINED

Ferry Reach, St George's Island, opposite Whalebone Bay, on *Thalassia*, – 1.5 m, 26 July 1982, two hydranths, with medusa buds, ROMIZ B144; medusa, newly liberated, obtained in laboratory from one of the hydranths above, ROMIZ B151. Whalebone Bay, on *Thalassia*, – 2 m, 8 September 1977, one hydranth, ROMIZ B157.

DESCRIPTION

Hydroid colonies with unbranched pedicels arising from a creeping hydrorhiza. Pedicels up to 4 mm long but usually much shorter, 75 μ m wide, supporting a terminal hydranth. Perisarc smooth, of moderate thickness, terminating a short distance below filiform tentacles on hydranth. Hydranths clavate, reaching 638 μ m long, 128 μ m

wide, with an oral whorl of four capitate tentacles and an aboral whorl of four filiform tentacles. Capitate tentacles solid, 326 μm long, 47 μm wide at base, tapering distally, with seven to nine endodermal cells; terminal knobs about 75 μm wide, button-shaped. Filiform tentacles solid, 168 μm long, 33 μm wide, with four to six endodermal cells, alternating with capitate tentacles. Hypostome rounded, with an oral, ectodermal cavity.

Medusa buds developing on short stalks just distal to filiform tentacles. Newly liberated medusa dome-shaped, 319 μm high and 426 μm wide in contracted, formalin-preserved specimen; mesoglea thin; manubrium short, wide, nearly spherical in longitudinal section. Radial canals nine. Tentacle bulbs nine, each with a single, reddish abaxial ocellus. Marginal tentacles nine, each with an adhesive organ and several bulbous clusters of nematocysts.

REMARKS

Hydroids of the various nominal species of *Cladonema* Dujardin, 1843a, are similar morphologically. Those of *C. myersi* Rees, 1949, and *C. uchidai* Hirai, 1958, apparently both lack the whorl of filiform tentacles found in other species of the genus (Rees, 1949; Hirai, 1958; Naumov, 1960), and Rees (1979) suggested that the two might be conspecific. *Cladonema radiatum* Dujardin, 1843a, and *C. californicum* Hyman, 1947, each possess both capitate and filiform tentacles and are virtually inseparable from one another in existing descriptions. However, Rees (1979), who first described the hydroid of *C. californicum*, did not include macrobasic mastigophores as part of the cnidome of this species. Nematocysts of this category have been reported from *C. radiatum* by Brinckmann and Petersen (1960), although they are not always present (Bouillon, 1971). Bouillon observed that when macrobasic mastigophores are present in *C. radiatum*, they occur principally in the stolons, rarely in the body of the hydranth, and never on the tentacles.

Hydroids of *Cladonema radiatum* also resemble those of *Dipurena reesi* Vannucci, 1956, and *D. strangulata* McCrady, 1859a. Brinckmann and Petersen (1960) found

that *C. radiatum* differed from *D. reesi* in several respects, including the shape of the knobs and number of endodermal cells in the capitate tentacles, the presence of a slight terminal swelling on the filiform tentacles, the position of these tentacles on the hydranth, the shape of the stenoteles, and the presence of macrobasic mastigophores in addition to stenoteles. Calder (1970) reported that *D. strangulata* resembled *C. radiatum* in a number of these characters, such as the location of the filiform tentacles and the number of endodermal cells in the capitate tentacles, but differed in lacking the slight terminal swelling of the filiform tentacles. Macrobasic mastigophores were also lacking in *D. strangulata*. Bouillon (1971) found that the three species were distinguishable by the structure of the hypostome. Ectodermal gland cells in the hypostome form a dome in *D. strangulata* and several related species; a button in *D. reesi*; and a cavity in *Cladonema* as well as species of *Staurocladia* Hartlaub, 1918, and *Eleutheria* de Quatrefages, 1842.

Weill (1936) found medusae of *Cladonema radiatum* in Bermuda, and examined their nematocyst complement. Later, Weill (1937b) published observations on 106 specimens collected near the Bermuda Biological Station. These medusae encompassed the characteristics of *C. radiatum*, *C. perkinsii*, and *C. mayeri*. Weill concluded that the three nominal species were no more than varieties of one rather variable species, as Mayer (1910) had suggested earlier.

In Bermuda, the hydroid of *Cladonema radiatum* was observed only during the warmer months of the year.

KNOWN RANGE

Bermuda: no specific locality given (Weill, 1936); near the Bermuda Biological Station (Weill, 1937b); on *Thalassia* (Calder, 1986).

Elsewhere: western Atlantic (Mayer, 1910); eastern Atlantic (Brinckmann-Voss, 1970). In his monographs on medusae, Kramp (1961, 1968) regarded *Cladonema uchidai* as conspecific with *C. radiatum*. If this interpretation is correct, the known range of *C. radiatum* extends to the northwestern Pacific Ocean.

Family Zancleidae Russell, 1953

Zancleidae Russell, 1953:98.

DIAGNOSIS

Hydrorhiza creeping, with or without perisarc. Hydranths with tentacles scattered. Tentacles capitate, or virtually filiform, or of both types.

Gonophores free medusae, arising from hydranths. Medusa bell-shaped with a simple, circular mouth; exumbrella with or without oval or clavate patches or elongate tracks

of specialized nematocyst-bearing tissue. Radial canals four. Marginal tentacles, when present, two or four, solid, each bearing abaxial cnidophores. Ocelli lacking. Gonads interradial, on manubrium.

REMARKS

Several names were proposed for this family before Russell (1953) established the Zancleidae, namely the Orthocorynidae by A. Agassiz (1865) and the Corynpteridae and

Clavipteridae by Weill (1934). However, these latter three names do not meet the criteria of availability for family-group names [Art. 11f (i)(1)], and do not take authorship and date [Art. 10a]. If the nominal families Zancleidae and Pteronematidae Haeckel, 1879, are eventually shown to be identical, as believed by Picard (1955, 1957, 1958) but disputed by Rees (1957), Bouillon (1974), and others, the latter name would have priority. Vervoort (1966:390) suggested that *Pteronema darwinii* Haeckel, 1879, might be "a mistreated and misjudged zancleid medusa," but he maintained the Zancleidae and Pteronematidae as separate families. Bouillon (1985) included the genus *Pteronema* Haeckel, 1879, in the family Asyncorynidae Kramp, 1949, rather than in the Zancleidae.

Bouillon (1974) broadened the definition of this family to include a new genus and species of hydroid and medusa, *Teissiera milleporoides*, from the Seychelles. Unlike other representatives of the Zancleidae, hydroids of *T. milleporoides* possess an encrusting skeleton instead of creeping stolons, and the polyps are polymorphic, with both gastrozooids and dactylozooids. The medusa generally resembles those of other genera within the Zancleidae except in having ocelli. Bouillon included four genera in this revised family, *Zanclaea* Gegenbaur, 1857, *Pteroclava* Weill, 1931, *Rosalinda* Totton, 1949, and a new genus, *Teissiera*. Millard (1975) adopted this revised definition of the family. Later, Bouillon (1978c) erected a new family, the Teissieridae, to accommodate *T. milleporoides* and two new species of medusae referred to *Teissiera*, namely *T. australe* and *T. medusifera*. The definition of the Zancleidae was thus returned by Bouillon essentially to that outlined by Russell (1953) and Kramp (1959, 1961, 1968). *Rosalinda*, which shares many characteristics with *Teissiera* (Bouillon, 1974; Petersen, 1979), cannot be retained in the Zancleidae. Instead, the new family Rosalindidae was constituted for the genus by Bouillon (1985). As currently defined, the Zancleidae once again includes the genera *Zanclaea* and *Pteroclava*, and possibly also *Ctenaria* Haeckel, 1879, and *Oonautes* Damas, 1936.

Genus *Zanclaea* Gegenbaur, 1857

- Acrochordium* Meyen, 1834:165.
Mnestra Krohn, 1853b:281.
Zanclaea Gegenbaur, 1857:229.
Gemmaria McCrady, 1859a:151.
Halocharis L. Agassiz, 1862:239.
Gymnocoryne Hincks, 1871:75.
Gemellaria Allman, 1871, pl. 7 [incorrect subsequent spelling].
Zanlcea Allman, 1872:290 [incorrect subsequent spelling].
Guentherella Weill, 1934:417.
Zanklea Riedl, 1963:126 [incorrect subsequent spelling].

DIAGNOSIS

Hydroid colonies stolonial, with perisarc covering hydrorhiza and hydrocaulus. Hydranth elongate. Tentacles capitate, scattered except for those in an oral whorl.

Gonophores free medusae, arising either from hydranth proximal to or among lower tentacles or, rarely, from hydrorhiza; hydranths with medusa buds occasionally reduced to blastostyles. Medusa bell-shaped, with exumbrellar nematocysts; mouth simple, circular. Radial canals four. Marginal tentacles, when present, numbering two or four, with abaxial cnidophores. Ocelli lacking. Gonads interradial.

TYPE SPECIES

Zanclaea costata Gegenbaur, 1857, by monotypy.

REMARKS

The genus-group name *Zanclaea* Gegenbaur, 1857, extensively used in the literature of both hydroids and medusae for more than a century (e.g., Hincks, 1868; Mayer, 1910; Fraser, 1944; Russell, 1953; Kramp, 1961; Brinckmann-Voss, 1970; Millard, 1975; Petersen, 1979; Bouillon, 1985; Calder, 1986), is a junior synonym of the virtually forgotten name *Acrochordium* Meyen, 1834. In the influential works of L. Agassiz (1862), Bedot (1905), and Stechow (1923a), *Acrochordium* was mistakenly regarded as a junior synonym of *Coryne* Gaertner, 1774. A re-examination of Meyen's (1834) account of *Acrochordium* here indicates that it is congeneric with *Zanclaea* rather than with *Coryne*.

Mnestra parasites Krohn, 1853b, and *Zanclaea costata* Gegenbaur, 1857, type species of *Mnestra* Krohn, 1853b, and *Zanclaea* respectively, are regarded as conspecific (Rees, 1953; Picard, 1957; Martin and Brinckmann, 1963). Thus, *Zanclaea* is also a junior synonym of the infrequently used name *Mnestra*, a nominal genus with a single nominal species based on a parasitically deformed medusa (Ankel, 1952; Martin and Brinckmann, 1963). Picard (1957) remarked that he planned to submit an application to the ICZN, requesting that its plenary powers be used to suppress the name *Mnestra* in favour of *Zanclaea*. To my knowledge, however, the application was never published in the *Bulletin of Zoological Nomenclature*.

In the interests of nomenclatural stability, the commission will be requested, in a future submission, to use its plenary powers to suppress the genus-group names *Acrochordium* and *Mnestra* for the Principle of Priority, and to place the name *Zanclaea* on the Official List of Generic Names in Zoology.

Zanclaea alba (Meyen, 1834), comb. nov.

Figs. 51, 52

Acrochordium album Meyen, 1834:165; pl. 28, fig. 8.

Coryne sessilis Gosse, 1853:208; pl. 14, figs. 1-3.

Mnestra parasites Krohn, 1853b:281 [parasitized medusa].
Tubularia implexa Alder, 1856b:439.
Zanclaea costata Gegenbaur, 1857:229; pl. 8, fig. 4 [medusa].
Coryne pelagica Alder, 1857:103; pl. 7, figs. 1,2.
Zanclaea gemmosa McCrady, 1859a:151; pl. 8, figs. 4,5 [medusa].
Coryne briareus Allman, 1859a:54.
Coryne implexa—Wright, 1859:107.
Coryne (margarica) implexa—Wright, 1859:108.
Halocharis spiralis L. Agassiz, 1862:239; pl. 20, figs. 10,10a-c.
Zanclaea implexa—Allman, 1864a:357 [medusa and hydroid].
Halocharis (Corynitis) spiralis—Allman, 1864a:358.
Corynitis agassizii—A. Agassiz, 1865:183 [part]. —Allman, 1872:287 [part]. —Bumpus, 1898:857. —Murbach, 1899:354; pl. 34, fig. 12. —Nutting, 1901:329; fig. 4. —Hargitt, 1901a:307. —Hargitt, 1901b:584; fig. 48. —Hargitt, 1904b:42. [medusa] [not *Corynitis agassizii* McCrady, 1859a]
Gemmaria gemmosa—A. Agassiz, 1865:184; fig. 306 [medusa].
Gemmaria cladophora A. Agassiz, 1865:184; figs. 307–310 [medusa].
Gymnocoryne coronata Hincks, 1871:76; pl. 5, figs. 1,1a.
Gemellaria implexa—Allman, 1871, pl. 7, figs. 1–10 [incorrect subsequent spelling].
Gemmaria implexa—Allman, 1872:290.
Gemmaria sagittaria Haeckel, 1879:103; pl. 7, figs. 3,4 [medusa].
Corynetis agassizii—Brooks, 1883a:136 [incorrect subsequent spelling] [not *Corynitis agassizii* McCrady, 1859a].
Zanclaea inflexa—Pennington, 1885:51 [incorrect subsequent spelling].
Zanclaea hargitti Hartlaub, 1907:119; fig. 109.
Zanclaea sagittaria—Hartlaub, 1907:124.
Zanclaea cladophora—Hartlaub, 1907:121; figs. 112, 113 [medusa].
Gemmaria sagittata—Hargitt, 1908:119 [incorrect subsequent spelling].
Gemmaria costata—Fraser, 1912:346, fig. 2.
Gemmaria implexa var. *neapolitana* Brückner, 1914:460; figs. 7–24.
Halocharis gemmosa—Stechow, 1923b:2.
Gemmaria sp. Timmermann, 1932:296.
Guentherella implexa—Weill, 1934:417.
Zanclaea sessilis—Russell and Rees, 1936:124.
Mnestra implexa—Picard, 1958:188.
Zanclaea costata—Riedl, 1963:126 [incorrect subsequent spelling].

TYPE LOCALITY

Atlantic Ocean, in the vicinity of the Azores, on *Sargassum natans*.

MATERIAL EXAMINED

Atlantic Ocean, 2 km southeast of Castle Roads, on floating *Sargassum*, 24 July 1982, one colony, up to 3 mm high, with medusa buds, ROMIZ B145. Whalebone Bay, on floating *Sargassum*, 2 September 1977, one colony, up to 2 mm high, with medusa buds, ROMIZ B155. Whalebone Bay, on floating *Sargassum*, 27 February 1982, one colony, up to 2 mm high, with medusa buds, ROMIZ B168. Natural Arches Beach, on stranded *Sargassum*, 8 March 1982, several colonies, up to 3 mm high, with medusa buds, ROMIZ B170. St George's Island, beach near Fort St Catherine's, on stranded *Sargassum*, 15 June 1983, several medusae, liberated in laboratory from hydroid, ROMIZ B332. Green Bay, Harrington Sound, on shell of *Cerithium litteratum* from *Cladophora* bed, -2 m, 26 September 1986, one colony, up to 2 mm high, without gonophores, ROMIZ B359.

DESCRIPTION

Hydroid colonies with creeping hydrorhiza and upright, unbranched pedicels. Pedicels up to 1.3 mm long, about 70 μm wide basally, expanding distally, bearing a terminal hydranth. Perisarc of variable thickness, annulated at base of hydrocaulus, smooth distally, terminating at hydranth base. Hydranth nearly cylindrical, reaching 1.6 mm long, 150 μm wide; hypostome dome-shaped. Tentacles as many as 40 or more, all capitate, scattered except for about 5 to 7 in an oral whorl, solid, with about six endodermal cells each, short and relatively stout in preserved material, about 75 μm long, 50 μm wide at base, tapering distally, terminating in a knob of nematocysts; knobs 35–50 μm wide, nearly spherical.

Nematocysts—

Hydroids: stenoteles (small) 6.7–7.0 μm \times 4.9–5.3 μm ; stenoteles (large) 9.6–10.4 μm \times 8.3–8.6 μm .

Medusa buds arising in clusters on short stalks among proximal tentacles on hydranth. Well-developed medusa buds bell-shaped, with thin mesoglea; exumbrella with nematocyst patches; manubrium short, conical to tubular. Radial canals four. Marginal bulbs four; opposite two well developed and bearing tentacles with cnidophores.

Nematocysts—

Medusae: macrobasic euryteles 6.4–7.1 μm \times 3.6–4.4 μm ; stenoteles 6.8–9.2 μm \times 5.8–7.5 μm .

REMARKS

These *Sargassum*-borne specimens are almost certainly identical with *Acrochordium album* Meyen, 1834, a small athecate hydroid found on "*Fucus natans* L." off the Azores. Meyen's (1834) hydroid, a stolonial species with numerous capitate tentacles scattered over an elongate hydranth, is not referable to *Coryne* Gaertner, 1774, as indicated in earlier literature (see p. 64). Instead, it conforms to the current concept of the genus *Zanclaea* Gegenbaur,

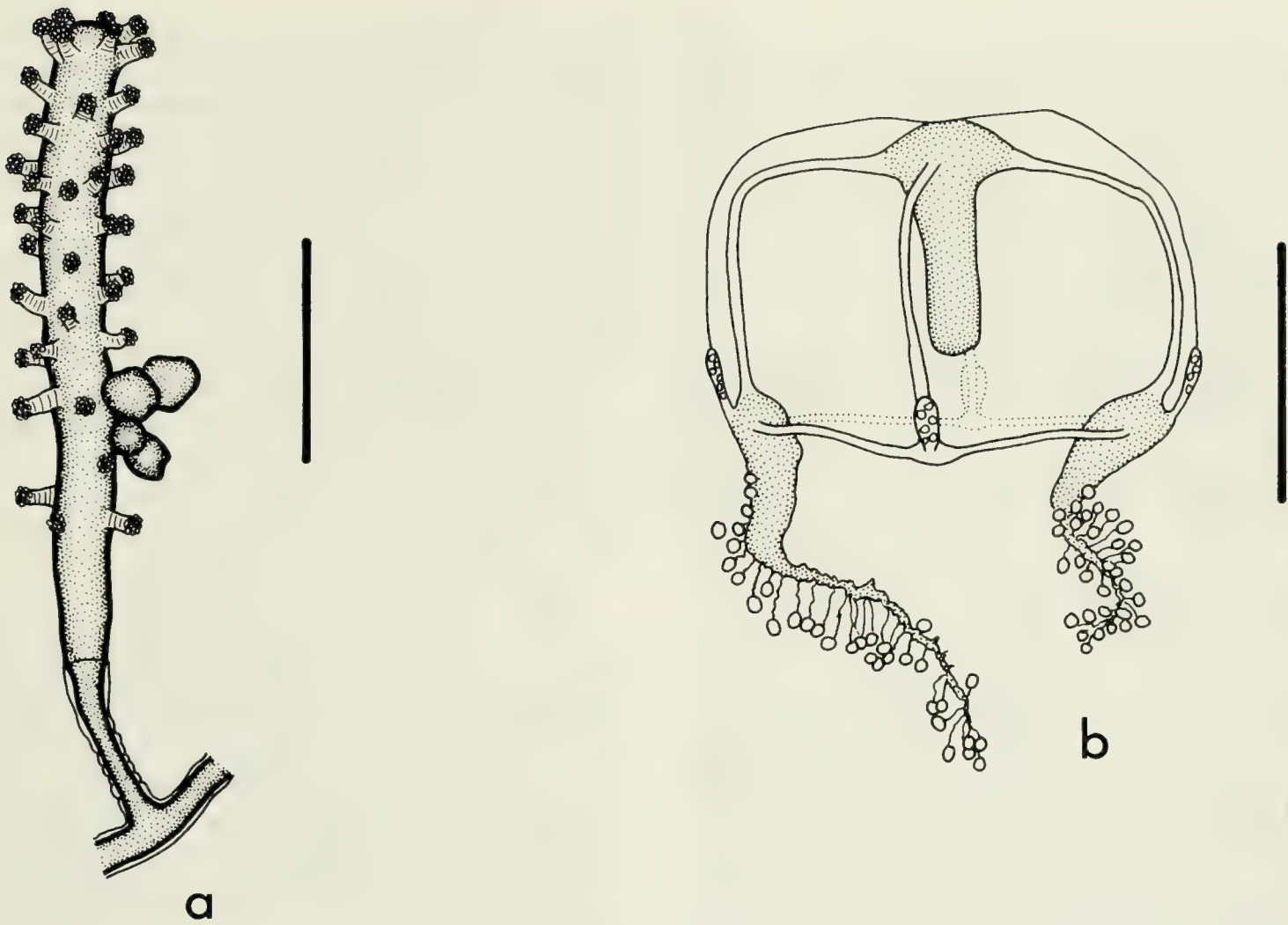


FIG. 51. *Zanclea alba*. Scale for *a* equals 0.5 mm; scale for *b* equals 0.25 mm. *a*, Part of colony with hydrorhiza, hydrocaulus, and hydranth, ROMIZ B145. *b*, Newly liberated medusa, ROMIZ B332.

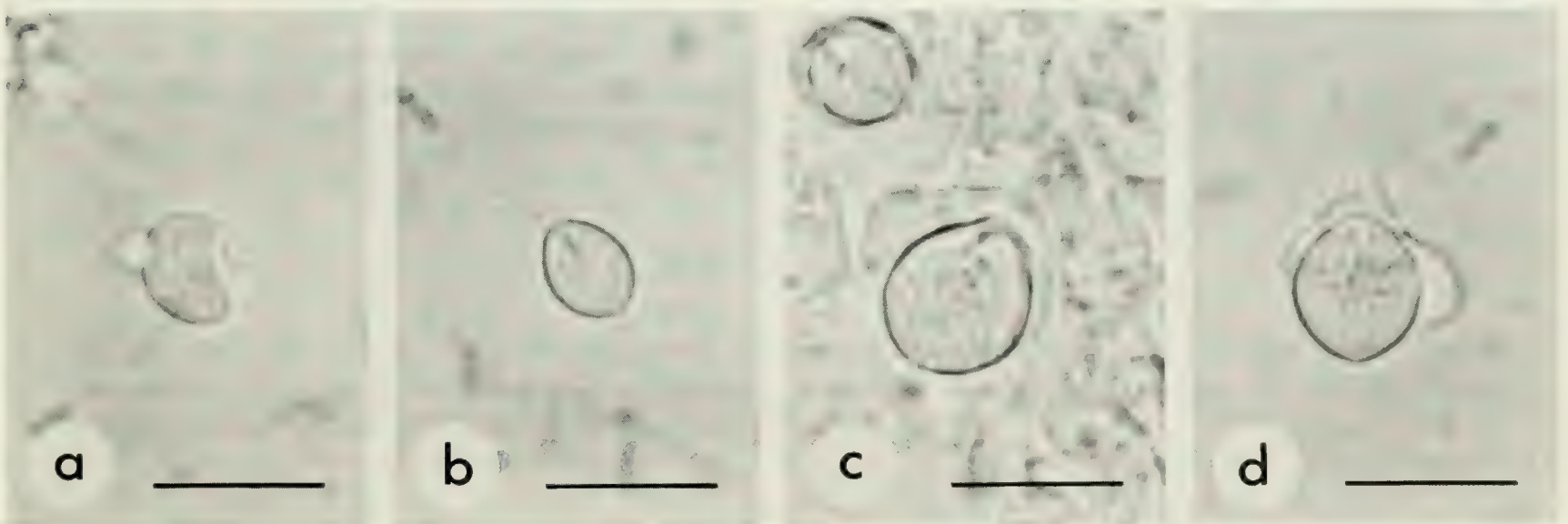


FIG. 52. *Zanclea alba*, nematocysts of hydranth and young medusa. Scales equal 10 μ m. *a*, Macrobasic eurytele of medusa bud, ROMIZ B332. *b*, Small stenotele of hydranth, ROMIZ B170. *c*, Large stenotele of hydranth, ROMIZ B170. *d*, Stenotele of medusa bud, ROMIZ B332.

1857, and to the species commonly named *Z. costata* Gegenbaur, 1857. Uncertainty lingers about the scope of *Z. costata* (e.g., see Picard, 1957), and this name is predated by four other names as given in the synonymy list above. Accordingly, the species-group name *album* (as used in the binomen *Acrochordium album* by Meyen, 1834) is retained, notwithstanding its infrequent use in the literature, and the name *Zanclaea alba*, comb. nov., is recognized here as the valid name of the species.

Russell and Rees (1936) cultured hydroids ascribed to *Zanclaea implexa* (Alder, 1856b) in the laboratory and reared medusae, albeit with difficulty. They showed that a number of differences, formerly used to separate what were believed to be species and even genera, were based on characters that varied with stage of development. In the hydroid, presence or absence of visible perisarc on the hydrorhiza and hydrocaulus was found to vary with age and development of the colony. Likewise, the exact location of medusa-bud formation was shown to be highly variable. In the medusa, arrangement of the nematocyst armature on the exumbrella and thickness of the mesoglea were shown to vary during development. Russell and Rees concluded that the North American *Zanclaea gemmosa* McCrady, 1859a, should be united with the European *Z. implexa* (Alder, 1856b), and they provided a list of synonyms. They provisionally retained *Zanclaea costata* Gegenbaur, 1857, as a separate species because of the presence of four marginal tentacles in the medusa instead of two. However, *Z. implexa* and *Z. costata* were later united by Russell (1953). *Coryne sessilis*, a hydroid described by Gosse (1853) as having tentacles in whorls, was listed by Russell and Rees (1936) as questionably conspecific with *Z. implexa*. Brinckmann-Voss (1970) noted a tendency for

the tentacles to occur in verticils in hydroids ascribed to *Z. costata* from the Mediterranean; it seems likely that Gosse exaggerated this in his illustrations and description of *Z. sessilis*. Picard (1957) believed that *Z. costata* and *Z. gemmosa* were distinct from *Z. sessilis*, but I have followed Brinckmann-Voss (1970) in regarding the three as conspecific. *Zanclaea sessilis* was regarded as conspecific with *Coryne pusilla* Gaertner, 1774, by Vervoort (1946b), but this seems quite unlikely considering the small size of Gosse's hydroids (about 1.5 mm high) and the large number of tentacles present (at least 45).

Hargitt (1908) and Bedot (1925) noted that this species had been misidentified on numerous occasions as *Corynitis agassizii* McCrady, 1859a (= *Linvillea agassizii*). Bedot provided an extensive synonymy list to sort out the nomenclatural confusion.

Weill (1934) reported that the cnidome of a medusa identified as *Gemmaria gemmosa* (McCrady, 1859a) included atrichs as well as macrobasic euryteles and stenoteles. No atrichs were observed in newly liberated medusae of *Zanclaea alba* from Bermuda.

This species, listed under the name *Zanclaea costata*, was reported to be common on pelagic *Sargassum* by Morris and Mogelberg (1973). Hydroids of *Z. alba* were common to abundant on pelagic *Sargassum* at Bermuda during this study.

KNOWN RANGE

Bermuda: on pelagic *Sargassum* (Calder, 1986).

Elsewhere: apparently circumglobal in tropical and temperate waters (Russell and Rees, 1936; Fraser, 1944; Yamada, 1959; Kramp, 1959, 1961, 1965, 1968; Brinckmann-Voss, 1970; Bouillon, 1978c).

Family Milleporidae Fleming, 1828

Milleporadae Fleming, 1828:528 [emended to Milleporidae by Milne Edwards and Haime, 1849].

DIAGNOSIS

Hydroid colonies forming massive, calcareous exoskeletons of varied shape. Coenosteum with a complex network of coenosarc tubes internally, covered externally by a thin epidermal layer, with surface perforated by pores; margins of pores not protruding from surface of coenosteum; larger gastropores surrounded by smaller dactylopores, forming indistinct cyclo systems. Gastrostyles and dactylostyles lacking. Polyps polymorphic; gastrozooids relatively short and stout, with four to seven short capitate tentacles, and arising within gastropores; dactylozooids long, slender, mouthless, with scattered capitate tentacles, and arising from dactylopores.

Gonophores free but reduced medusae, arising from coenosarc within ampullae in coenosteum. Medusae with exumbrellar nematocyst patches; velum and tentacles lacking. Gonads on manubrium.

REMARKS

Species of the family Milleporidae Fleming, 1828, have been recognized as hydrozoans since the work of L. Agassiz (1858), but their systematic position within the class Hydrozoa has been a matter of longstanding debate. Moseley (1880) referred this family, along with the Stylasteridae Gray, 1847, to the suborder Hydrocorallinae. The great differences separating milleporids and stylasterids were pointed out by S. J. Hickson (in a note in Delage and Hérouard, 1901), and he placed the former in a new order, the Milleporina.

Separation of these two families was upheld by Broch (1914) and Stechow (1923a), but they maintained that milleporids were capitate hydroids related to the Corynidae Johnston, 1836. According to a number of recent authors, including Bouillon (1974, 1985) and Petersen (1979), available evidence from hydranth morphology and nematocyst complement suggests that the family has affinities with the Teissieridae Bouillon, 1978c, Zancleidae Russell, 1953, and Cladocorynidae Allman, 1872. Further details on history of the classification of the Milleporidae, together with a taxonomic assessment of the fossil species referred to the family, are given by Boschma (1951, 1956).

Genus *Millepora* Linnaeus, 1758

Millepora Linnaeus, 1758:790.

Palmipora de Blainville, 1830:356.

DIAGNOSIS

With the characters of the family.

TYPE SPECIES

Millepora alcicornis Linnaeus, 1758, by subsequent designation by Apstein (1915).

REMARKS

The genus *Millepora* Linnaeus, 1758, originally included a conglomeration of species only one of which, *M. alcicornis* Linnaeus, 1758, is referred to the genus as it is understood at present (Boschma, 1948). There is even some uncertainty about the identity of *M. alcicornis*, which may have been a species of scleractinian and not a hydrozoan. However, Boschma (1948) indicated that there is support for the belief that the *M. alcicornis* sensu Linnaeus was the branched West Indian hydrozoan currently assigned that name. The colony form of this hydrozoan often bears a resemblance to an elk's horn, as reflected in the etymology of the specific name. Moreover, the definition of *M. alcicornis* by Linnaeus (1767) almost certainly refers to the hydrozoan genus *Millepora* as understood at present, and not to a scleractinian.

Boschma (1948) recounted the differing views concerning species limits in *Millepora*. These views have ranged from that of Duchassaing and Michelotti (1864), who regarded almost every different growth form as a distinct species, to that of Hickson (1898a, 1898b), who believed that the genus contained a single species, *M. alcicornis*. Hickson's concept of a single species displaying different growth forms or "facies" was widely, although on occasion somewhat grudgingly, accepted through the early decades of the present century. The opinion was gradually superseded by the conclusion that some of the "growth

forms" were indeed distinct species. Boschma (1948), in an extensive and influential review of the species problem in *Millepora*, recognized 10 rather well defined species and discussed the characters used for specific distinction.

De Weerd (1981) noted that the species of *Millepora* are currently distinguished principally on the growth form of the corallum and geographic distribution, but growth form is highly influenced by environmental factors such as water movement and turbidity. The taxonomic value of characters such as texture of the corallum surface, size and shape of the gastropores and dactylopores and their distribution over various parts of the corallum, extent to which cyclo-systems are isolated, presence or absence of ampullae, morphology of the soft parts, and stinging properties has largely been discounted. However, de Weerd concluded that such characters, including the shape and size of ampullae, may be of more value taxonomically than supposed and merit re-examination.

Millepora alcicornis Linnaeus, 1758

Figs. 53–55

Millepora alcicornis Linnaeus, 1758:791.

Millepora alcicornis digitata Esper, 1790:197; pl. 5, figs. 1,2.

Millepora alcicornis corniculata Esper, 1790:197; pl. 6.

Millepora alicornis—Esper, 1790:197 [incorrect subsequent spelling].

Millepora alcicornis ramosa Esper, 1790:198; pl. 7.

?*Millepora alcicornis crustacea* Esper, 1790:200 [not *Millepora crustacea* Linnaeus, 1758].

Millepora alcicornis—Bosc, 1802:288 [incorrect subsequent spelling].

Palmipora alcicornis—de Blainville, 1834:391; pl. 58, fig. 2.

Millepora moniliformis Dana, 1848:544 [not *Millepora moniliformis* Rafinesque, 1820].

Millepora ramosa—Dana, 1848:544.

Millepora pumila Dana, 1848:545; pl. 52, fig. 4 [not *Millepora pumila* Pallas, 1766].

Palmipora fasciculata Duchassaing, 1850:18.

Palmipora parasitica Duchassaing, 1850:18.

Millepora forskali Milne Edwards, 1860:228.

Millepora fasciculata—Milne Edwards, 1860:228 [not *Millepora fasciculata* Lamarck, 1816].

Millepora gothica Duchassaing and Michelotti, 1860:84; pl. 10, figs. 9,10.

Millepora schrammi Duchassaing and Michelotti, 1864:100; pl. 11, fig. 9.

Millepora esperi Duchassaing and Michelotti, 1864:100.

Millepora crista-galli Duchassaing and Michelotti, 1864:101; pl. 11, fig. 7 [not *Millepora crista galli* Morren, 1828].

Millepora delicatula Duchassaing and Michelotti, 1864:101; pl. 11, fig. 10.

Millepora candida Duchassaing and Michelotti, 1864:101.

Millepora digitata—Duchassaing and Michelotti, 1864:102.

Millepora carthaginiensis Duchassaing and Michelotti, 1864:102; pl. 11, fig. 6.

Millepora trinitatis Duchassaing and Michelotti, 1864:102.

Millepora fenestrata Duchassaing and Michelotti, 1864:103; pl. 11, fig. 1.

Millepora nitida Verrill, 1868:362.

Millepora alcicornis var. *cellulosa* Verrill, 1868:363.

Millepora alcicornis var. *fenestrata*—Verrill, 1868:364.

Montipora gothica—Dollfus, 1936:515.

TYPE LOCALITY

Not specified by Linnaeus (1758); subsequently given as "O. Indiae utriusque" (Linnaeus, 1767).

MATERIAL EXAMINED

Whalebone Bay, on ledges at entrance, -4 m, 4 March 1982, one fragmentary colony, 1.5 cm high, ROMIZ B175. Hall's Island, Harrington Sound, on rocks, -1 m, 13 September 1977, one fragmentary colony, 6.2 cm high, liberating medusae when alive, coll. W. Sterrer, ROMIZ B180. Whalebone Bay, on ledges at entrance, -2 m, two fragmentary colonies, 2.0–4.5 cm high, ROMIZ B181. Flatts Inlet, on shells and rubble, -4 m, 5 March 1982, one colony, 7.0 cm high, ROMIZ B304. Flatts Inlet, on rubble, -3 m, 9 July 1983, one colony, 1.7 cm high, ROMIZ B312.

DESCRIPTION

Colonies initially consisting of an encrusting base and fingerlike upright projections; older colonies with extensive upright branches of varied shape. Branches irregularly rebranched, generally in one plane; branchlets fused to varying degrees basally, with tips usually free and digitate. Coenosteum consisting of a framework of anastomosing calcareous trabeculae, interstices occupied by a network of coenosarc tubes, surface covered with an epidermal layer and perforated by pores. Gastropores 0.35 mm in diameter; dactylopores 0.25 mm in diameter; cyclosystems distinct to indistinct, with five to nine dactylopores surrounding each gastropore. Gastrostyles and dactylostyles absent. Gastrozooids relatively stout, reaching about 1 mm above surface of coenosteum when extended, with an oral whorl of four to seven short, capitate tentacles. Dactylozooids long and slender when extended, reaching 1.0–1.5 mm above surface of coenosteum, with short, capitate tentacles grouped at distal end and scattered elsewhere.

Nematocysts—

Gastrozooids: microbasic mastigophores 30.0–31.9 μm \times 24.5–26.3 μm ; stenoteles (small) 8.3–8.9 μm \times 5.7–

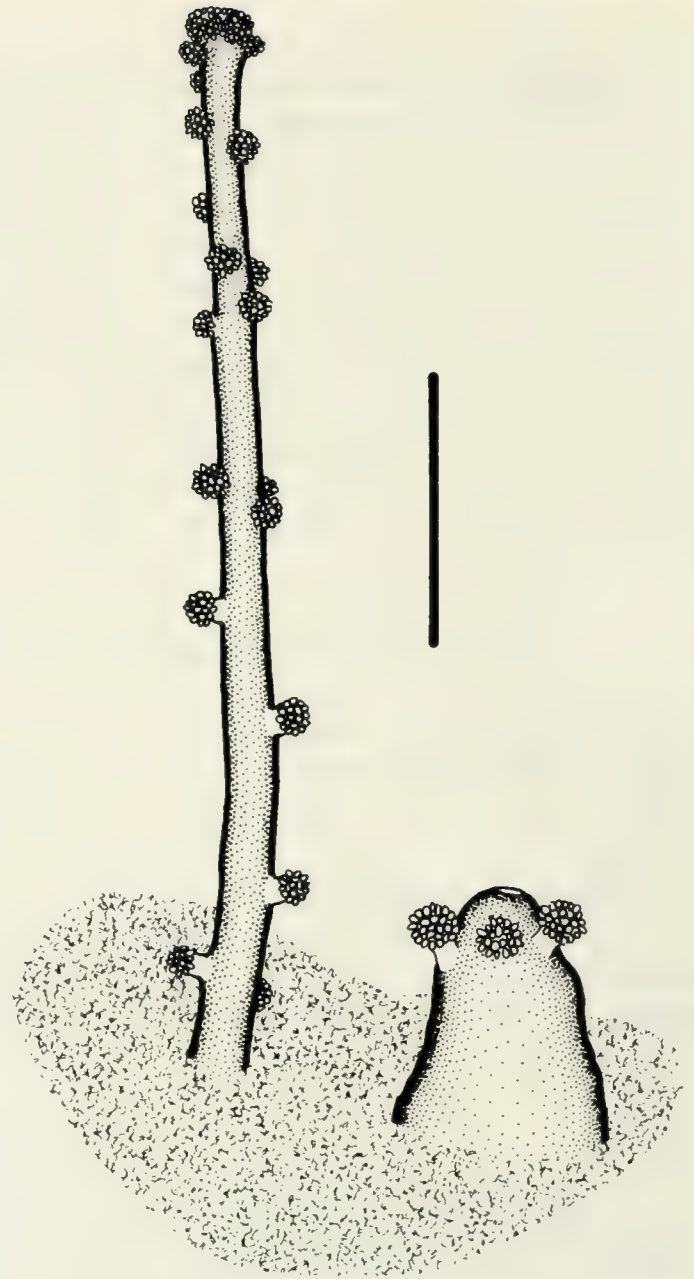


FIG. 53. *Millepora alcicornis*, dactylozooid and gastrozooid extending above coenosteum, ROMIZ B312. Scale equals 0.25 mm.

6.6 μm ; stenoteles (medium) 15.9–17.6 μm \times 12.9–14.2 μm ; stenoteles (large) 21.6–24.7 μm \times 15.9–18.7 μm .

Dactylozooids: stenoteles (small) 8.3–8.6 μm \times 5.9–6.5 μm .

REMARKS

The synonymy of this species is long and complex. The simplified list given here largely follows that of Boschma (1948).

Millepora alcicornis Linnaeus, 1758, is the only species of its genus known to occur in Bermuda, although two other species, *M. complanata* Lamarck, 1816, and *M. squarrosa* Lamarck, 1816, have been reported elsewhere in the western North Atlantic. Colonies of *M. alcicornis* are highly varied in shape, but they are distinguishable from those of *M. complanata* and *M. squarrosa* in being composed of branches rather than of vertical plates

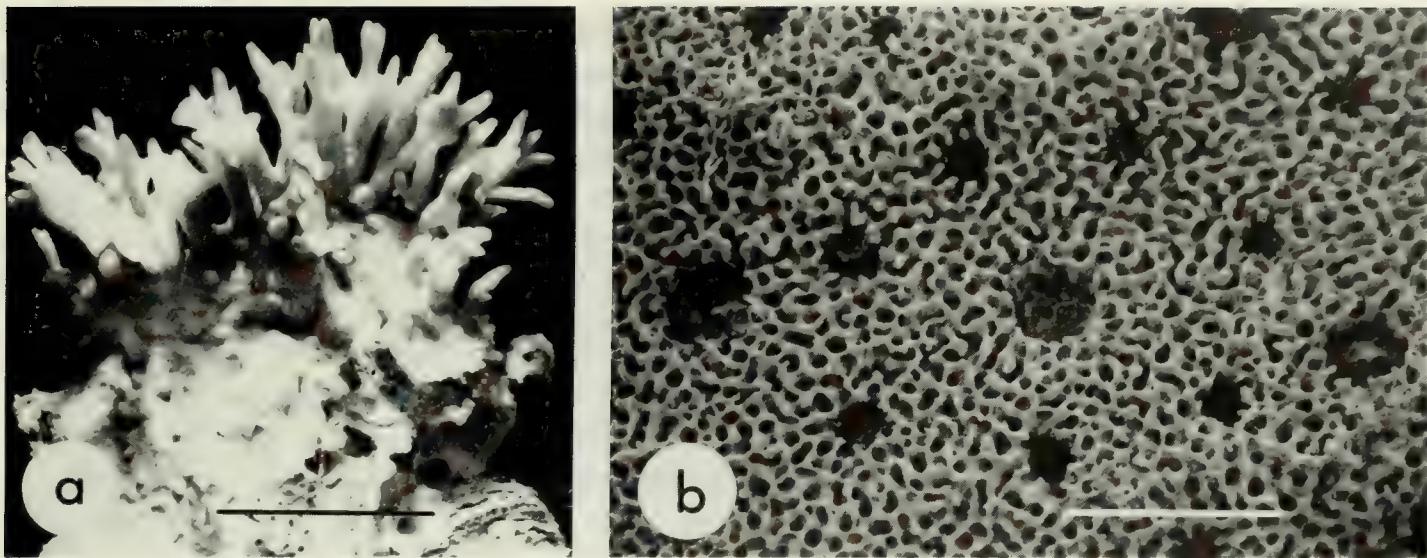


FIG. 54. *Millepora alcicornis*, coenosteum. Scale for *a* equals 5 cm; scale for *b* equals 100 μ m. *a*, Young colony encrusting bivalves and coral rubble, ROMIZ B304. *b*, SEM micrograph of part of coenosteum, showing a cyclosystem, ROMIZ B304.

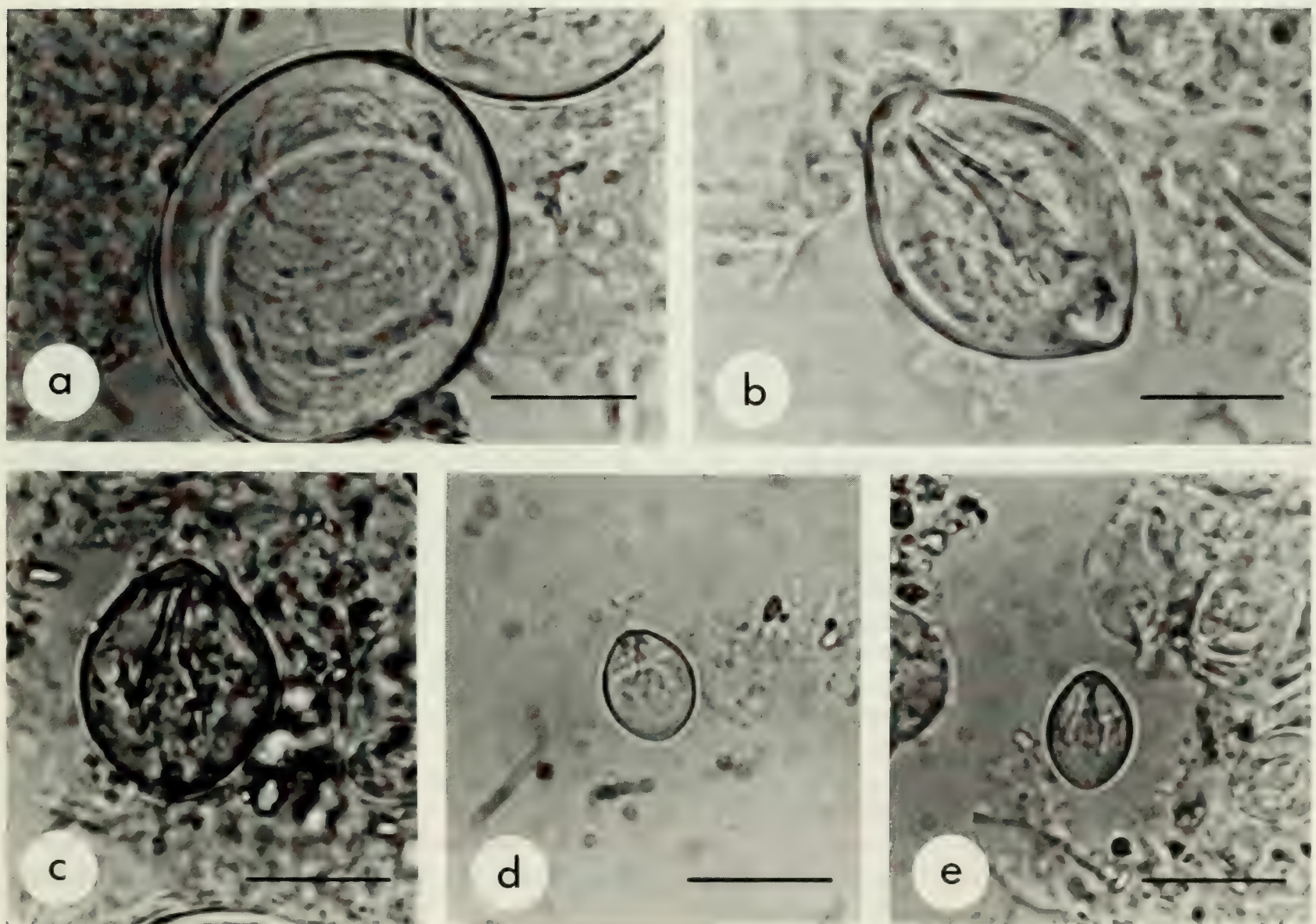


FIG. 55. *Millepora alcicornis*, nematocysts, ROMIZ B312. Scales equal 10 μ m. *a*, Microbasic mastigophore of gastrozoid. *b*, Large stenotele of gastrozoid. *c*, Medium stenotele of gastrozoid. *d*, Small stenotele of gastrozoid. *e*, Small stenotele of dactylozoid.

(Boschma, 1948). The vertical plates of *M. complanata* are truncated distally and united only at their bases, while those of *M. squarrosa* are frilled distally and often united above their bases.

Verrill (1907) reported colonies of *Millepora alcicornis* as large as 4–6 feet (1.2–1.8 m) across and 1–2 feet (0.3–0.6 m) high at Bermuda. He commented that it was the most abundant “coral” on outer reefs and on inner rocks and ledges around the islands, ranging from the shallows to a depth of 5–8 fathoms (9–15 m). When alive, the species is brownish in colour because of the presence of symbiotic zooxanthellae in the tissues. *Millepora alcicornis*,

in common with other species of the genus, is venomous to humans (Verrill, 1907).

A description of the medusa stage of this species is given by Mayer (1910).

KNOWN RANGE

Bermuda: on reefs, ledges, rocks, and other substrates around the entire Bermuda Platform (Nelson and Duncan, 1876; Moseley, 1876, 1879, 1880; Rice, 1878; Quelch, 1886; Verrill, 1900, 1902a, 1902b, 1907; Moore, 1969; Calder, 1986).

Elsewhere: western Atlantic (Boschma, 1948).

Family Porpitidae Goldfuss, 1818

Porpitae Goldfuss, 1818:1012 [emended to Porpitidae by Guilding 1828:403].

Veilellidae Eschscholtz, 1829:165.

Discalidae Haeckel, 1888a:29.

Porpalidae Haeckel, 1888b:57.

Porpitellidae Haeckel, 1888b:63.

DIAGNOSIS

Hydroids polymorphic, highly specialized, adapted for life at sea surface. Float and mantle with or without upright sail; undersurface with a large central gastrozoid, a ring of gonozooids, and a peripheral ring of dactylozooids.

Gonophores free medusae. Medusae thimble-shaped with perradial exumbrellar nematocyst rows; mouth simple, circular. Radial canals four. Tentacle bulbs four. Ocelli lacking. Gonad not completely encircling manubrium.

REMARKS

The family name Porpitidae is frequently attributed to Brandt (1835), but the name was apparently first employed by Goldfuss (1818) as the Porpitae. This name, emended to Porpitidae by Guilding (1828), thus predates the name Veilellidae Eschscholtz, 1829, and must be given priority when the two nominal families are combined. I concur with Brinckmann-Voss (1970) and others that the Porpitidae and Veilellidae can be contained in a single family.

Chamisso and Eysenhardt (1821) included various nominal species of *Porpita* Lamarck, 1801, and *Veilella* Lamarck, 1801, under the name Chondrophorae (as “Medusae Chondrophorae”), but it is unclear whether they intended Chondrophorae to be a family-group name. In any case, the name Chondrophorae does not meet the criteria of availability for family-group names [Art. 11f (i)(1)], either in its original form or in any of its subsequently emended spellings.

Members of this family have been variously treated as siphonophores (e.g., Eschscholtz, 1829; Huxley, 1859; L.

Agassiz, 1862; Haeckel, 1888a, 1888b; Bigelow, 1911; Moser, 1925), as athecate hydroids (e.g., Kölliker, 1853; Vogt, 1854; McCrady, 1859a; A. Agassiz, 1883; Edwards, 1966b; Brinckmann-Voss, 1970), and as a separate order of Hydrozoa, the Chondrophora (e.g., Totton, 1954; Rees, 1957). The concensus among contemporary workers is that they are highly specialized athecate hydroids (see Edwards, 1966b; Brinckmann-Voss, 1970; Fields and Mackie, 1971; Bouillon, 1974, 1985; Petersen, 1979; Arai and Brinckmann-Voss, 1980; Kirkpatrick and Pugh, 1984; Calder, 1986).

Opinions have differed widely concerning their systematic position within the athecate hydroids. Leloup (1929, 1954), Garstang (1946), Totton (1954), Mackie (1959, 1960), and Daniel (1976), among others, have suggested that they are most closely related to the Corymorphidae Allman, 1872, and Tubulariidae Fleming, 1828. Fields and Mackie (1971) regarded *Veilella* as a large, floating tubulariid hydranth and placed the nominal family Veilellidae, together with the Corymorphidae, Tubulariidae, and Margelopsidae Uchida, 1927, in the superfamily Tubularioidea Fleming, 1828. Picard (1955, 1957) and Prévot (1959) included *Veilella* and *Porpita*, along with the Zancleidae Russell, 1953, in the Pteronematoidea Haeckel, 1879. Brinckmann (1964) believed that their affinities were with the tubularians and placed them in a superfamily, the Chondrophoroidea, in the order Anthomedusae. Later, she suggested that they should be placed between the Capitata and Filifera (Brinckmann-Voss, 1970). Based on the morphology and histological structure of their polyps and medusae, as well as their nematocyst complement, Bouillon (1974) argued that *Veilella* and *Porpita* had undeniable affinities with the Zancleidae. Petersen (1979) treated them as a superfamily within the Zancleida, a suborder encompassing the Cladocorynidae Allman, 1872, Zancleidae, Teissieridae Bouillon, 1978c, and Milleporidae Fleming, 1828.

Most of the available evidence points to the Porpitidae as having an affinity with taxa of the superfamily Zancleidea Russell, 1953. If such an interpretation is correct, it follows that *Porpita* and *Verella* should be interpreted as colonies rather than as individual floating hydranths and that their zooids are true polyps, as argued by Edwards (1966b).

Genus *Porpita* Lamarck, 1801

- Porpita* Lamarck, 1801:355.
Polybrachionia Guilding, 1828:403.
Ratis Lesson, 1830:60.
Acies Lesson, 1830:61.
Chrysomitra Gegenbaur, 1857:232.
Disconalia Haeckel, 1888a:30.
Porpitella Haeckel, 1888a:30 [invalid junior homonym of *Porpitella* Pomel, 1883 (Echinodermata)].

DIAGNOSIS

Porpitud hydroids with disc-shaped float and mantle; float flat or with central bulge; sail lacking. Dactylozooids with three vertical rows of short, capitate tentacles.

Medusae with small manubrium. Juvenile specimens without marginal tentacles; adults with one to two slender, decidedly capitate tentacles; endodermal cells along radial canals bearing algal symbionts.

TYPE SPECIES

Medusa porpita Linnaeus, 1758, by absolute tautonymy.

REMARKS

Bigelow (1911) retained the name *Porpita* Lamarck, 1801, for this genus instead of employing *Medusa* Linnaeus, 1758. Apparently, a type species has never been designated for *Medusa*, a nominal genus originally containing species of Hydrozoa, Scyphozoa, and Ctenophora, and the name has been scarcely used this century.

The widely used name *Porpita* Lamarck, 1801, is a junior homonym of *Porpita* Soldani, 1789 (Protozoa), a name apparently all but abandoned in the recent zoological literature. Application will be made to the ICZN to place *Porpita* Lamarck, 1801, on the Official List of Generic Names in Zoology, and *Porpita* Soldani, 1789, on the Official Index of Rejected and Invalid Generic Names in Zoology.

The names *Porpita* Lamarck, 1801, and *Verella* Lamarck, 1801, are threatened by *Phyllidoce* Modeer, 1790, a nominal genus originally including three nominal species, *P. denudata* (Forskål, 1775), *P. porpita* (Linnaeus, 1758), and *P. verella* (Linnaeus, 1758). In the interests of nomenclatural stability, the ICZN will be asked in the ap-

plication referred to above to use its plenary powers to suppress the seldom-used genus-group name *Phyllidoce* for the purposes of the Principle of Priority, and to place that name on the Official Index of Rejected and Invalid Generic Names in Zoology. The name *Phyllidoce* was first used by Browne (1789) for the hydroid known today as *Verella verella* (Linnaeus, 1758), but Browne's work has been suppressed for nomenclatural purposes by the ICZN (Opinion 89).

Bigelow (1911) recognized *Porpema* Haeckel, 1888a, as distinct from *Porpita*, while Totton (1954) believed that the two were congeneric. The taxa appear sufficiently distinct, based on present understanding of their morphology (Bigelow, 1911), to warrant recognition of both as valid genera. Bigelow (1911) regarded *Porpalia* Haeckel, 1888a, as a synonym of *Porpema*. Acting as first reviser, he chose *Porpema* as the valid name of the genus. *Discalia* Haeckel, 1888a, is probably a synonym of *Porpema* as well. Haeckel's (1888a) nominal genera *Disconalia* and *Porpitella* were regarded by Bigelow as congeneric with *Porpita*.

Porpita porpita (Linnaeus, 1758)

Figs. 56, 57

- Medusa porpita* Linnaeus, 1758:659.
Holothuria denudata Forskål, 1775:103.
Holothurio denudata Forskål, 1776, pl. 26, figs. L, 1 [lapsus].
Medusa umbella O. F. Müller, 1776b:297; pl. 9, figs. 2, 3.
Holothuria nuda Gmelin, 1790:3143.
Phyllidoce denudata—Modeer, 1790:201.
Phyllidoce porpita—Modeer, 1790:203.
Porpita indica Lamarck, 1801:355.
Porpita appendiculata Bosc, 1802:155; pl. 18, figs. 5, 6.
Porpita radiata Bory de St Vincent, 1804:99; pl. 5, figs. 2A–D.
Porpita gigantea Péron and Lesueur, 1807, pl. 31, figs. 6, 6a–e.
Porpita forskalea Oken, 1815:111 [name published in a work rejected for nomenclatural purposes by the ICZN (Opinion 417)].
Porpita nuda—Lamarck, 1816:484.
Porpita glandifera Lamarck, 1816:485.
Porpita granulata Cranch, 1818:418.
Porpita coerulea Eschscholtz, 1825:744.
Porpita globosa Eschscholtz, 1825:744.
Porpita ramifera Eschscholtz, 1825:745.
Porpita chrysocoma Lesson, 1826, pl. 7, figs. 1, 1'.
Porpita atlantica Lesson, 1826, pl. 7, fig. 2.
Porpita pacifica Lesson, 1826, pl. 7, figs. 3, 3'.
Porpita moneta Risso, 1826:304.
Medusa nuda—Bory de St Vincent, 1827:139; pl. 90, figs. 3–5.

Medusa glandifera—Bory de St Vincent, 1827:139; pl. 90, figs. 6,7.
Polybrachionia linnaeana Guilding, 1828:404; pl. 10, figs. 1,2.
Porpita forskahli de Haan, 1827:493.
Porpita reinwardtii de Haan, 1827:493.
Porpita kuhlii de Haan, 1827:494.
Porpita mediterranea Eschscholtz, 1829:177.
Porpita umbella Eschscholtz, 1829:179.
Ratis medusae Lesson, 1830:60.
Acies palpebrans Lesson, 1830:61.
Porpita lutkeana Brandt, 1835:41.
Porpita linnaeana—Lesson, 1843:588.
Chrysomitra striata Gegenbaur, 1857:232; pl. 7, figs. 10,11 [medusa].
?Discalia primordialis Haeckel, 1888a:30 [nomen nudum].
Disconalia pectyllis Haeckel, 1888a:30 [nomen nudum].
Disconalia gastroblasta Haeckel, 1888a:30 [nomen nudum].
Porpitella caerulea—Haeckel, 1888a:30 [incorrect subsequent spelling].
Porpitella radiata—Haeckel, 1888a:30.
?Discalia primordialis Haeckel, 1888b:46.
Disconalia pectyllis Haeckel, 1888b:48.
Disconalia gastroblasta Haeckel, 1888b:48; pl. 49, figs. 7–12; pl. 50, figs. 1–10.
Porpitella pectanthis Haeckel, 1888b:64; pl. 46.
Porpita fungia Haeckel, 1888b:67; pl. 45.
Disconalia ramifera Haeckel, 1888b:357.
Porpitella coerulea—Haeckel, 1888b:358.
Porpita porpita—Schneider, 1898b:194.
Phyllocladice denudata—Bigelow, 1911:352 [incorrect subsequent spelling].

TYPE LOCALITY

“Habitat in India” (Linnaeus, 1758).

MATERIAL EXAMINED

Building’s Bay, St George’s Island, washed ashore, 7 October 1984, one colony, 7 mm in diameter, ROMIZ B347. Atlantic Ocean, 10 km south of Nonsuch Island, 7 May 1984, one colony, rataria stage, 3 mm in diameter, coll. Paul Bennett, ROMIZ B350.

DESCRIPTION

Hydroid pleustonic, with disc-shaped mantle and internal float; upper surface of mantle and float slightly convex, with a central pore and numerous peripheral stigmata. Mantle 7 mm wide, with radiating gastrodermal canals; margin soft, flexible; central region firm, with an internal chitinous float consisting of a series of concentric air chambers; a disc-shaped reservoir of nematocytes and nematocysts lying between float and central gastrozoid. Undersurface with a single large, central gastrozoid, a medial band of gono-

zooids, and a peripheral band of dactylozooids. Central gastrozoid short and broad with a terminal mouth; tentacles and prominent nematocyst batteries lacking. Dactylozooids tentaculate, with a distal whorl of four capitate tentacles; body with varying numbers of short, small, capitate tentacles in three vertical rows; mouth lacking. Gonozooids clavate, lacking tentacles but with prominent nematocyst batteries encircling mouth, additional nematocyst batteries scattered over body; medusa buds given off in clusters basally.

Nematocysts—

Hydroids: atrichous isorhizas (on gastrozooids, dactylozooids, gonozooids; in nematocyst reservoir) 9.3–13.2 μm \times 4.2–5.0 μm ; haplonemes (on gastrozooids, dactylozooids) 10.8–14.1 μm \times 5.6–6.6 μm ; stenoteles (small) (on gastrozooids, dactylozooids, gonozooids; in nematocyst reservoir) 15.6–16.7 μm \times 10.5–11.5 μm ; stenoteles (large) (on gastrozooids, gonozooids; in nematocyst reservoir) 27.5–30.0 μm \times 21.8–25.3 μm ; stenoteles (bulbous) (on medusa buds) 15.2–16.2 μm \times 12.7–13.9 μm .

Rataria “larva” planktonic, with swollen, subspherical central gastrozoid, a medial ring of gonozooids, a peripheral ring of tentaculate dactylozooids, and a small disc-shaped float and mantle.

Medusae not seen.

REMARKS

Porpidid taxonomy has advanced relatively little since Bigelow’s (1911) insightful study of the group. The synonymy list here is taken in part from Bigelow’s work, although Moser (1925) and Totton (1954) have been followed in regarding *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 as conspecific.

The development of *Porpita porpita* is known to pass through stages somewhat resembling those of *Velella velella* (Linnaeus, 1758). Various stages in the life history of this species, including the medusa, rataria “larva,” and young pleustonic hydroid, have been described by A. Agassiz (1883), Bigelow (1911), Delsman (1923), and Bouillon (1984b). The medusa, at an advanced stage of its development, has euryteles as part of its cnidome (Bouillon, 1984b, 1985).

A. Agassiz (1883) commented that few specimens of *Porpita porpita* are stranded on beaches compared with *Velella velella*. Only one specimen was found on Bermuda beaches during this study, although considerable time was spent looking for the species during four field trips. *Porpita porpita* has been reported previously from Bermuda by Verrill (1900, as *P. linnaeana*), and by Totton (1936, as *P. umbella*).

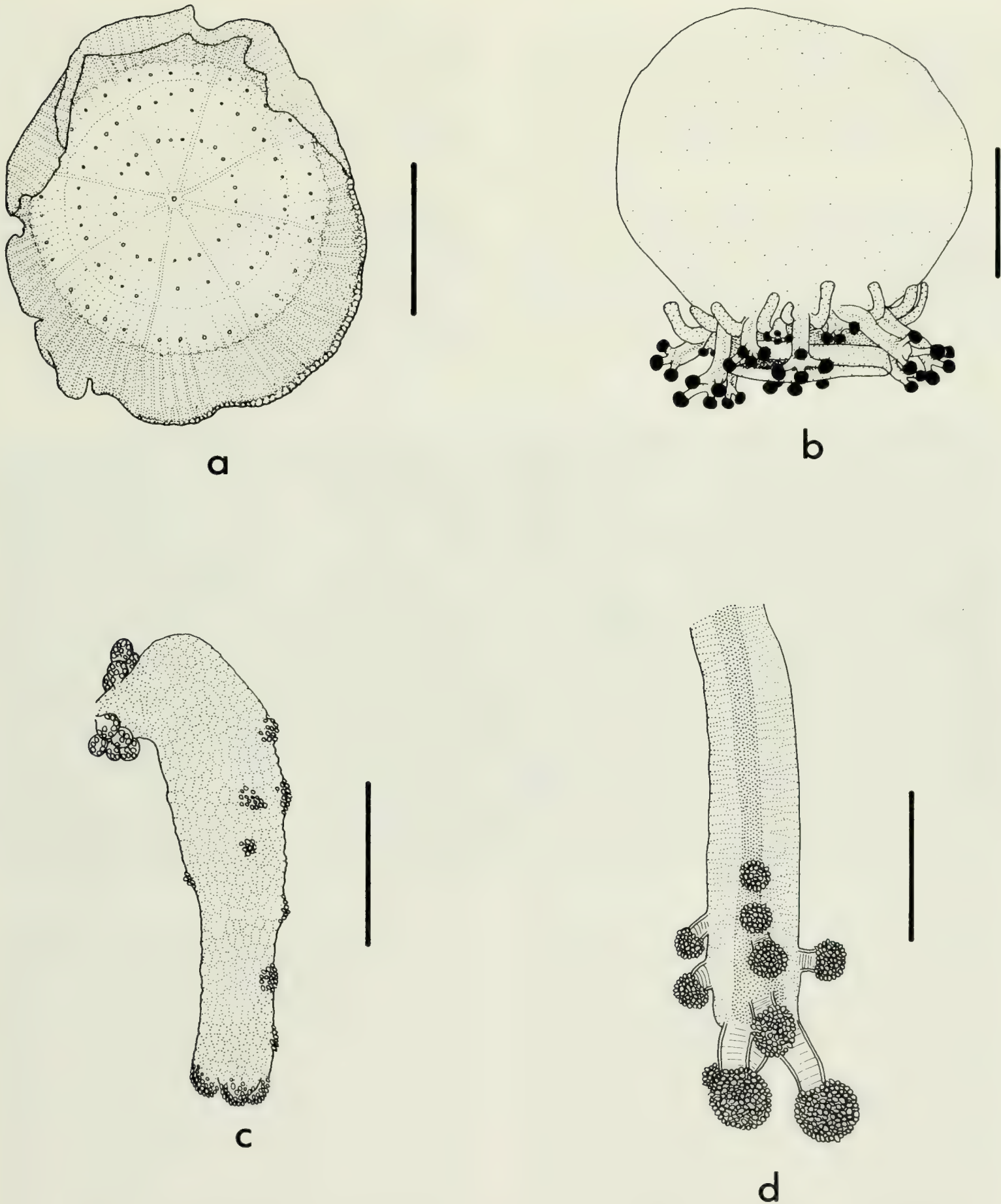


FIG. 56. *Porpita porpita*. Scale for *a* equals 2.5 mm; scale for *b* equals 1 mm; scales for *c* and *d* equal 0.5 mm. *a*, Upper surface of float and mantle, ROMIZ B347. *b*, Ratoria larva, ROMIZ B350. *c*, Gonozoid, with medusa buds, ROMIZ B347. *d*, Dactylozoid, ROMIZ B347.

KNOWN RANGE

Bermuda: no specific locality given (Verrill, 1900; Calder, 1986); 14 km southeast of Nonsuch Island (Totton, 1936). Elsewhere: circumglobal, tropical and temperate waters (Moser, 1925; Brinckmann-Voss, 1970).

Genus *Verella* Lamarck, 1801

Phyllidoce Browne, 1789:387 [invalid name, published in a work suppressed under the plenary powers for nomenclatural purposes by the ICZN (Opinion 89)].
Verella Lamarck, 1801:355.

Vellela Bory de St Vincent, 1827:139 [incorrect subsequent spelling].

Rataria Eschscholtz, 1829:166.

Armenistarium Costa, 1841:187.

Velaria Haeckel, 1888a:31.

Armenista Haeckel, 1888b:83.

DIAGNOSIS

Porpitud hydroids with oval float and mantle and with upright, triangular sail set diagonal to long axis of float. Dactylozooids with nematocyst patches.

Medusae with short, conical manubrium. Tentacle bulbs four, one opposite pair lacking tentacles, each bulb of re-

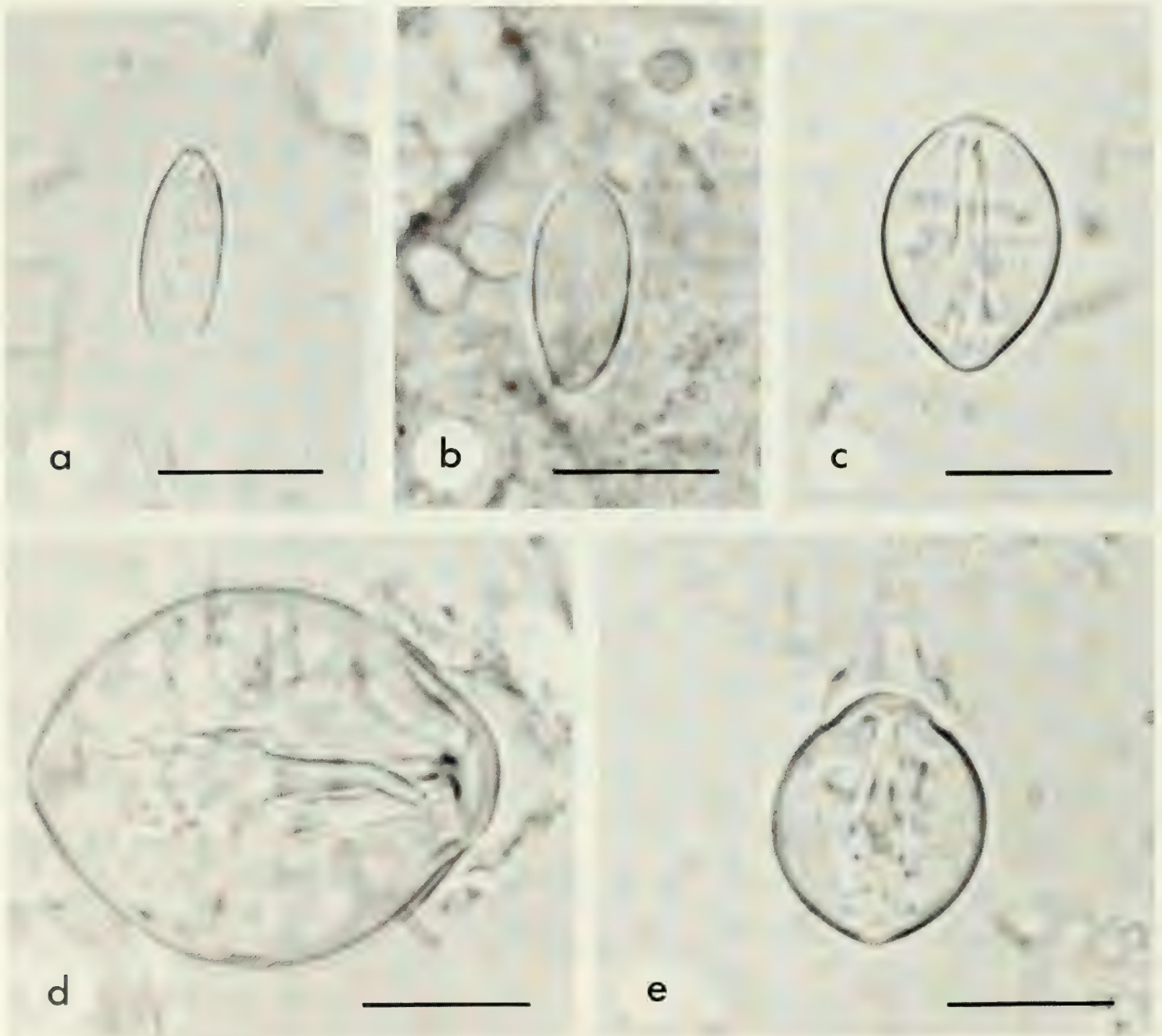


FIG. 57. *Porpita porpita*, nematocysts of hydroid and medusa bud, ROMIZ B347. Scales equal 10 μm . *a*, Atrichous isorhiza of dactylozooid. *b*, Haploneme of gastrozooid. *c*, Small stenotele of dactylozooid. *d*, Large stenotele of gonozooid. *e*, Bulbous stenotele of medusa bud.

maintaining pair with one or two capitate tentacles; zooxanthellae concentrated near radial canals and ring canal.

TYPE SPECIES

Medusa verella Linnaeus, 1758, by absolute tautonymy.

REMARKS

Numerous nominal species of *Verella* Lamarck, 1801, have been described over the years from Atlantic, Pacific, and Indian oceans. All of these are currently believed to belong to a single species, *V. verella* (Linnaeus, 1758) (Schneider, 1898b; Bigelow and Sears, 1937; Totton, 1954; Daniel and Daniel, 1963; Brinckmann-Voss, 1970; Daniel, 1976; Arai and Brinckmann-Voss, 1980; Kirkpatrick and Pugh, 1984).

Verella verella (Linnaeus, 1758)

Figs. 58, 59

Medusa verella Linnaeus, 1758:660.

Holothuria spirans Forskål, 1775:104.

Holothurio spirans Forskål, 1776, pl. 26, figs. K,k1–3 [lapsus].

Phyllidoce verella—Modeer, 1790:194.

Verella mutica Lamarck, 1801:355.

Verella tentaculata Lamarck, 1801:355.

Verella scaphidia Péron and Lesueur, 1807; pl. 30, figs. 6,6a.

Medusa pocillum Montagu, 1815:201; pl. 14, fig. 4.

Verella limbosa Lamarck, 1816:482.

Verella pyramidalis Cranch, 1818:419.

Verella sinistra Chamisso and Eysenhardt, 1821:363; pl. 32, fig. 1.

Verella oblonga Chamisso and Eysenhardt, 1821:364; pl. 32, figs. 2A–C.

Verella lata Chamisso and Eysenhardt, 1821:364; pl. 32, figs. 3A–B.

Verella emarginata Quoy and Gaimard, 1824:586; pl. 86, fig. 9.

Verella cyanea Lesson, 1826, pl. 6, figs. 3,4.

Verella australis de Haan, 1827:489.

Verella pacifica de Haan, 1827:490.

Verella radackiana de Haan, 1827:490.

Verella sandwichiana de Haan, 1827:491.

Vellela limbosa—Bory de St Vincent, 1827:139; pl. 90, figs. 1,2 [incorrect subsequent spelling].

Verella pocillum—Fleming, 1828:500.

Rataria cordata Eschscholtz, 1829:167; pl. 16, fig. 1.

Rataria pocillum—Eschscholtz, 1829:168.

Rataria mitrata Eschscholtz, 1829:168; pl. 16, fig. 2.

Verella aurora Eschscholtz, 1829:171.

Verella septentrionalis Eschscholtz, 1829:171; pl. 15, fig. 1.

Verella spirans—Eschscholtz, 1829:172.

Verella caurina Eschscholtz, 1829:173; pl. 15, fig. 2.

Verella tropica Eschscholtz, 1829:174; pl. 15, fig. 3.

Verella indica Eschscholtz, 1829:175; pl. 15, fig. 5.

Verella antarctica Eschscholtz, 1829:175.

Verella patellaris Brandt, 1835:38.

Verella oxyothone Brandt, 1835:39.

Verella oxyothone var. *brachyothone* Brandt, 1835:39.

Verella oxyothone var. *oxyothone* Brandt, 1835:39.

Armenistarium verella—Costa, 1841:187; pl. 13, fig. 3.

Rataria cristata Haeckel, 1888a:31 [nomen nudum].

Velaria mutica—Haeckel, 1888a:31.

Velaria oblonga—Haeckel, 1888a:31.

Velaria indica—Haeckel, 1888a:31.

Rataria cristata Haeckel, 1888b:79; pl. 44.

Verella patella—Haeckel, 1888b:83 [incorrect subsequent spelling].

Armenista sigmoides Haeckel, 1888b:84; pl. 43.

Armenista mutica—Haeckel, 1888b:84.

Armenista antarctica—Haeckel, 1888b:84.

Armenista indica—Haeckel, 1888b:84.

Armenista lata—Haeckel, 1888b:84.

Armenista lobata Haeckel, 1888b:84 [nomen nudum].

Verella meridionalis Fewkes, 1889:112; pl. 1, figs. 1–3; pl. 2, fig. 3.

Verella verella—Schneider, 1898b:194.

Verella spiralis—Martin, 1904:27 [incorrect subsequent spelling].

Verella subemarginata—Stephens, 1905:65 [incorrect subsequent spelling].

Phyllodice verella—Bigelow, 1911:353 [incorrect subsequent spelling].

TYPE LOCALITY

“Habitat in Pelago. Loeffling. In Mari Mediterraneo. Brander” (Linnaeus, 1758).

MATERIAL EXAMINED

Warwick Long Bay, washed ashore, 7 March 1982, 30 left-sailing forms, 5–22 mm long, 3–14 mm wide, and three right-sailing forms, 11–31 mm long, 9–20 mm wide, ROMIZ B174.

DESCRIPTION

Hydroids pleustonic, with flattened, oval mantle and internal float; upper surface of mantle and float with upright, triangular sail. Specimens occurring in two mirror-image forms, with sail lying along either of two diagonals of mantle and float. Sail with branched and anastomosing radial canals, rather rigidly erect, supported internally by slender, triangular, chitinous extension of float. Mantle coursed by radiating gastrodermal canals having short, lateral diverticulae; margin soft, flexible, bearing large numbers of algal symbionts; central region firm, with an

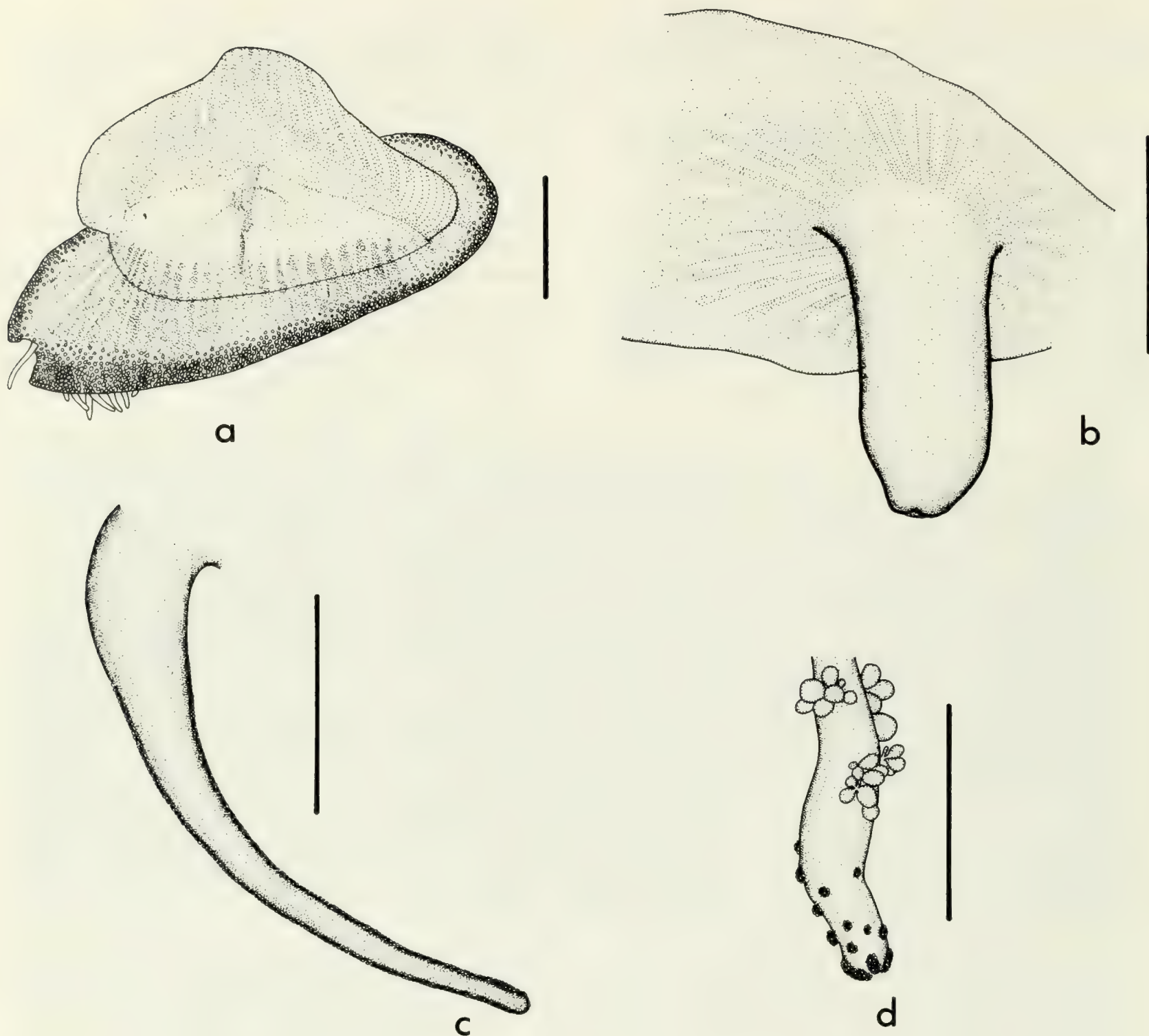


FIG. 58. *Velella velella*, ROMIZ B174. Scale for *a* equals 3 mm; scales for *b-d* equal 2 mm. *a*, Lateral view of float, mantle, and sail. *b*, Gastrozoid. *c*, Dactylozoid. *d*, Gonozoid, with medusa buds.

internal chitinous float consisting of a series of concentric air chambers; an elongate-oval reservoir of nematocytes and nematocysts lying between float and central gastrozoid. Undersurface with a single central gastrozoid, a medial band of gonozooids, and a peripheral band of dactylozooids. Central gastrozoid long and tubular distally with terminal mouth, broad and oval basally, lacking both tentacles and prominent nematocyst batteries; gastrodermis with a series of longitudinal folds. Gonozooids clavate, occurring in various developmental stages, lacking tentacles but with prominent batteries of nematocysts about mouth, additional nematocyst batteries scattered over body; blastostyles given off proximally, each bearing clusters of

medusa buds. Dactylozooids tentacle-shaped, oval in cross-section, each bearing a band of nematocysts along the two narrow edges; nematocyst band typically extending up one side and across distal end of dactylozoid, and continuing down opposite side; band often becoming broken up into discontinuous patches proximally; mouth lacking.

Nematocysts—

Hydroids: atrichous isorhizas (on gastrozooids, dactylozooids, gonozooids; in nematocyst reservoir) $8.5-13.6 \mu\text{m} \times 3.8-4.7 \mu\text{m}$; haplonemes (on gastrozooids) $12.7-14.1 \mu\text{m} \times 6.8-7.6 \mu\text{m}$; stenoteles (small) (on gastrozooids, dactylozooids, gonozooids; in nematocyst reservoir) $12.2-15.1 \mu\text{m} \times 9.2-11.4 \mu\text{m}$; stenoteles (large)



FIG. 59. *Verella verella*, nematocysts of hydroid, ROMIZ B174. Scales equal 10 μm . *a*, Atrichous isorhiza of gastrozoid. *b*, Haploneme of gastrozoid. *c*, Small stenotele of dactylozoid. *d*, Large stenotele of dactylozoid. *e*, Bulbous stenotele of gonozoid.

(on gastrozooids, dactylozooids, gonozooids; in nematocyst reservoir) 18.8–21.2 μm \times 13.3–15.0 μm ; stenoteles (bulbous) (on gastrozooids, dactylozooids, gonozooids, medusa buds; in nematocyst reservoir) 18.8–23.4 μm \times 16.0–21.5 μm .

Medusae not seen.

REMARKS

Hydroids of *Verella verella* (Linnaeus, 1758) occur in two enantiomorphic forms. Edwards (1966b) noted that differing and sometimes conflicting terminology has been used for these two. Edwards has been followed here in designating these as left-sailing and right-sailing forms.

The left-sailing form, which drifts to the left in the downwind direction, corresponds to A. Agassiz's (1883) left-handed form, Chun's (1897a) "SW" form, and Totton's (1954) "NW" form. The right-sailing form, which drifts to the right in the downwind direction, corresponds to Chun's (1897a) "NW" form and Totton's (1954) "SW" form. Both left-sailing and right-sailing forms were observed washing ashore at Bermuda on 7 March 1982 after several days of strong southerly winds.

The development of the hydroid of *Verella verella* was described by Woltereck (1904, 1905) and reviewed by Garstang (1946). Woltereck found young larvae of this species in deep water off Villefranche, the youngest of

which possessed a rudimentary, fluid-filled float; two short, solid tentacles; and a rudimentary mouth. Garstang regarded this larva as an actinula, homologous with that of tubularians. Brinckmann-Voss (1970) questioned this, noting that the only similarity between this larva and an actinula was its possession of two aboral tentacles. Growth of this larva, known as a conaria, was accompanied by the development of a nettle-ring (the incipient nematocyst reservoir known as the "centradenia") and a crimson aboral cone of endoderm. Oil droplets, serving as a temporary method of flotation, are secreted by the crimson cone, and the conaria rises to the surface. Upon reaching the surface, fluid in the rudimentary float of the conaria is expelled and replaced by air, and the crimson cone disappears. At this stage, the larva is known as a rataria. In the rataria, the float enlarges and becomes lined with chitin, the nematocyst reservoir or centradenia becomes solid, zooids begin development, and the sail appears. Continued growth of the rataria leads to the familiar hydroid of this species.

Despite the abundance of the hydroid stage and the large numbers of medusa buds produced by each colony, medusae of this species have seldom been collected in nature. Although they have zooxanthellae and are probably epipelagic, the medusae are small and likely easily overlooked. The largest specimen collected to date was only 2.8 mm high and 2.0 mm wide (Larson, 1980). Brinckmann (1964) and Brinckmann-Voss (1970) described the

development of the medusa in the laboratory.

Rhythmic synchronous contractions, referred to as "concerts" by Fields and Mackie (1971), occur in hydroids of *Velella velella* (Vogt, 1854; Chun, 1897b; Fields and Mackie, 1971). During a contraction, dactylozooids are flexed towards the central gastrozoid, gonozooids shorten, and the mantle is contracted downwards. Immediately after a contraction, the flexed and contracted parts relax and return to their original state. Fields and Mackie (1971) noted that such contractions may occur singly or in a series, and that concert periodicity in *V. velella* varied from one to three minutes. The function of such behaviour remains enigmatic. Garstang (1946) suggested that it might facilitate the spreading of mucus threads used in prey capture. Fields and Mackie did not attribute such movements either to feeding, as suggested by Garstang, or to locomotion. Because of the presence of large numbers of zooxanthellae in the tissues, they suggested that Chun's (1897b) hypothesis that it is a respiratory movement warranted further evaluation.

KNOWN RANGE

Bermuda: Castle Harbour (Fewkes, 1883); 14 km south-east of Nonsuch Island (Totton, 1936); no specific locality given (Calder, 1986).

Elsewhere: circumglobal, tropical and temperate waters (Totton, 1954; Edwards, 1966b; Brinckmann-Voss, 1970).

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