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Notes on some hydroids (Cnidaria) from Martinique, with descriptions of five new species

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Abstract: The present report supplements a series of earlier accounts on the hydrozoan fauna of the French Lesser Antilles, and discusses 16 species of hydroids from Martinique. Of these, five are new to science: *Hydractinia promiscua*, *Halecium plicatum*, *Dynamena bimorpha*, *Antennella quaterna* and *Monostaechas bertoti*. The medusoid gonophores of *Ralpharia gorgoniae* Petersen, 1990 are described in detail. The female gonothecae of *Halecium labiatum* Billard, 1933, recorded for the second time, are redescribed. Characters of the trophosome and the cnidome composition allowed a reliable identification of *Halecium lightbourni* Calder, 1991, a species whose previously unknown gonothecae are here described for the first time. A reexamination of the type of *Dynamena tropica* Stechow, 1926 proved that it is conspecific with *D. crisioides* Lamouroux, 1824. *Sertularia notabilis* Fraser, 1947 is included in the synonymy of *S. hattorii* Leloup, 1940, and arguments for doing so are provided. The so called variety *pusilla* Ritchie, 1910, associated for a long time with *Hincksella cylindrica* (Bale, 1888), is raised to species, as *H. pusilla* (Ritchie, 1910), and their distinguishing characters are emphasized. *Clytia edentula* Gibbons & Ryland, 1991 is found for the second time, extending its known range of distribution.

Keywords: Hydrozoa - Lesser Antilles - French West Indies - Caribbean.

INTRODUCTION

The hydrozoan fauna of the French Lesser Antilles, never investigated in the past, has received increasing attention during the last few years, with a number of taxonomical studies that provided the first comprehensive accounts on the species composition of two overseas departments, Guadeloupe and Martinique (Galea, 2008; 2010a; 2013; Galea *et al.*, 2012; Galea & Ferry, 2013).

Additional samples from Martinique were gathered during a recent survey undertaken in January and February 2014. New stations have been explored, and some of those inspected in 2012 (see Galea, 2013) were visited again.

The present study deals with those species that have not been the subject of earlier accounts, as well as with those for which new data became available, such as the finding of fertile specimens, allowing reliable taxonomic determination to be made for materials identified previously to genus only.

MATERIAL AND METHODS

Sampling was done either by scuba diving or snorkeling. Hydroid colonies were carefully removed from their substrate using haemostatic forceps, so as to preserve the integrity of the adjacent fauna. Although some observations were done on living specimens shortly after collection, most of them were carried out on formalin-preserved material, using the methods described in Galea (2007, 2008, 2010a). Samples were deposited in collections of the Muséum d'Histoire Naturelle of Geneva, Switzerland, and registration codes are indicated by MHNG-INVE- followed by numbers. Occasionally, references are made to samples either hosted in the private collection of the senior author of this study (these are indicated by HRG- followed by a four-digit number) or belonging to the British Antarctic Survey (BAS).

TAXONOMY AND RESULTS

Order Anthoathecata Cornelius, 1992
Family Hydractiniidae L. Agassiz, 1862
Genus *Hydractinia* Van Beneden, 1844

***Hydractinia promiscua* Galea & Ferry, sp. nov.**

Figs 1A, B; 3A-E; Table 1

Holotype material: MHNG-INVE-91108; sample #M280; France, Martinique, Le Prêcheur, Babody, 14.78632° -61.21765°, 20 m; 25.01.2014; male colony encrusting the outside of a worm tube and adjacent sponge.

Paratype material: MHNG-INVE-91124; sample #M335; France, Martinique, Le Prêcheur, Babody, 14.78632° -61.21765°, 15-20 m; 25.06.2014; male colony on ascidian.

Diagnosis: Hydractiniid growing on various substrates, with gastro-, gono-, and tentaculozooids. Gonophore a non-liberated medusoid with four radial canals and eight tentacle stumps. Nematocysts comprising desmonemes, two size classes of microbasic euryteles, and three size classes of haplonemes.

Etymology: From the Latin *prōmiscūa*, meaning indiscriminately, for its unselective substrate affinity.

Description: Colony stolonial, with creeping, scarcely branching and anastomosing hydrorhiza. Perisarc thin, smooth to irregularly wrinkled, ending at base of polyps; spines absent; no naked coenosarc. Polyps of three types: gastro-, gono-, and tentaculozooids. Gastrozooids creamy-white in color, clavate, contractile; 12-20 filiform tentacles, amphicoronate in life; hypostome dome shaped, with a wide belt of nematocysts between mouth and insertion of tentacles (Fig. 3A). Gonozooids smaller than their feeding counterparts, with 8-11 filiform tentacles, and a belt of nematocysts around hypostome (Fig. 3B). Gonophores 1-2 per gonozooid, given off laterally from proximal halves of polyps; only males present. Ripe gonophores nearly spherical, width slightly exceeding height (Fig. 3B²); four radial canals and a barely visible circular canal (Fig. 3B¹); manubrium surrounded by apparently four compact, interradian masses of sperm cells; no signs of rudimentary tentacle knobs at this stage (Fig. 3B¹). More advanced medusoids (Fig. 3C), whose gametes had been expelled, are still attached to their corresponding gonozooids; their shape had changed from spherical to oval, their length being greater than the diameter; 8 rudimentary tentacles (four perradial and four interradian), as well as a velum, are present. Tentaculozooids filiform (Fig. 3D), sparsely and irregularly scattered amongst the other zooids; of varied length, sometimes exceeding the size of gastrozooids. Cnidome: 1) desmonemes (Fig. 3E¹); 2, 3) small and large microbasic euryteles (Fig. 3E^{2,3}); 4-6) egg-shaped,

elongate and slender, as well as ovoid haplonemes (Fig. 3E⁴⁻⁶).

Dimensions: Gastrozooids up to 3 mm high; gonozooids up to 1 mm high (preserved material, though not differing much from live material). Unspent gonophore *ca.* 890 μm long and 745 μm wide; spent gonophore *ca.* 915 μm long and 760 μm wide. Desmonemes (6.3-6.8)×(3.4-3.7) μm; small microbasic euryteles (7.4-7.7)×(2.6-2.8) μm; large microbasic euryteles (9.7-10.6)×(3.1-3.4) μm; egg-shaped haplonemes *ca.* 5.1×3.1 μm; elongate and slender haplonemes (9.4-10.3)×(2.3-2.6) μm; ovoid haplonemes (10.0-10.3)×(4.0-4.3) μm.

Distribution: Known only from Martinique (present study).

Type locality: France, Martinique, Le Prêcheur, Babody.

Remarks: Notoriously difficult to identify, the hydractiniid hydroids – especially those producing medusoids – offer few exploitable distinguishing morphological features. In addition, several structures, such as the spines and/or the dactylozooids, occur in certain conditions and, as a consequence, they do not offer enough features to the species that produce them in order to establish reliable comparisons with other congeners.

To compare the present hydroid with its relatives, only the non-calcareous species producing medusoid gonophores with radial canals were considered (see Table 1). Since the genera *Schuchertinia* and *Bouillonactinia* (both introduced by Miglietta *et al.*, 2010) are not well characterized, all nominal species discussed herein are referred to the widely speciose genus *Hydractinia* Van Beneden, 1844.

A considerable impediment concerns the species for which only limited descriptions are available and/or no data on the cnidome composition exist (*e.g.* Clarke, 1882; Sigerfoos, 1899; Broch, 1914; Wedler & Larson, 1986; Hirohito, 1988).

For example, the relationships between *H. arge* (Clarke, 1882) and *H. hooperii* (Sigerfoos, 1899) are unsettled yet. According to Calder (1988), their types are reportedly lost, thus preventing a comparison of their cnidomes. Calder (1971) provided arguments in favor of their specific separation, whereas he united them in a later study (Calder, 1988). The Bermudian specimens assigned to *H. arge* in his latter account may not belong to Clarke's taxon, owing to: 1) their smaller size; 2) their exclusive occurrence on gastropod shells instead of being mainly epiphytic [an occurrence of *H. arge* on the gastropod *Bittium* sp. was noted by Calder (1971)]; 3) the lack of gastrozooid autotomization, as described by both Clarke (1882) and Calder (1971) [note that Bavestrello *et al.* (2000) showed that water movement induced transverse fission in the zooids of *H. pruvoti* (Motz-Kossowska,

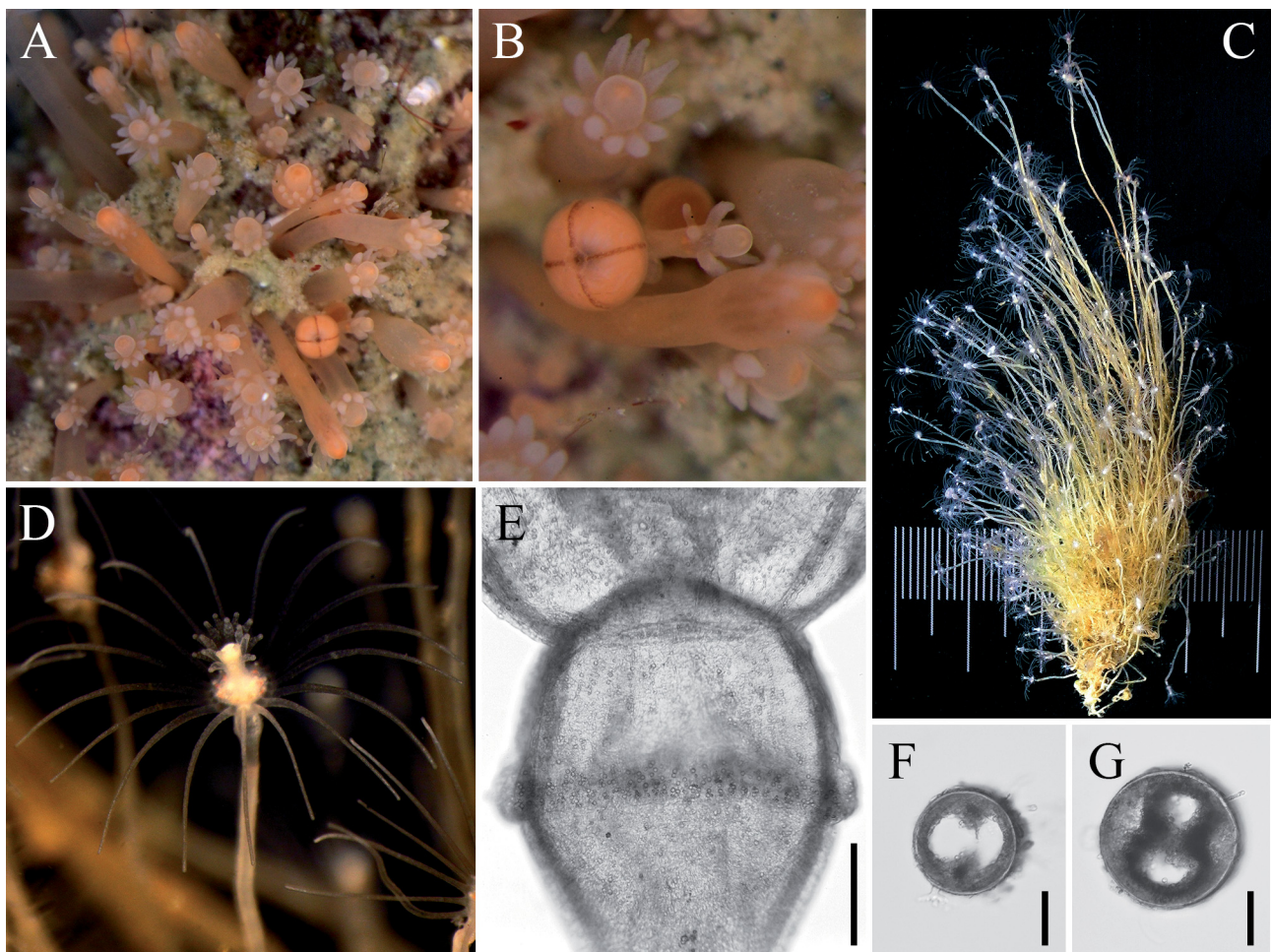


Fig. 1. A, B: *Hydractinia promiscua* sp. nov. (A) Portion of colony growing on worm tube. (B) Detail of a gonozooid carrying a male medusoid. (C-G): *Ectopleura* sp. (C) Whole colony. (D) Hydranth. (E) Detail of the neck region showing belt of nematocysts. (F, G) Cross sections through two stems, showing endodermal ridges. Scale bars: 100 μ m (F, G), 200 μ m (E).

1905), suggesting that the autotomization observed in *H. arge* may not be an intrinsic feature of this species, depending instead on environmental factors].

It is obvious that, for reliable comparisons, the cnidome composition should be emphasized, though it is obvious that this approach has its limits too, due to some variation in size of the capsules from one sample to another, and their assignment to a given type. The following examples are edifying: 1) Namikawa (2000) found differences in the size of nematocysts of *H. misakiensis* from two localities; 2) similar data also emerge from the accounts of Millard (1975) and Vervoort (2006) on *H. multitentaculata*, unless they dealt with different species; 3) one of the size classes of microbasic euryteles reported by Namikawa (1991) in his *H. multigranosi* is said to belong to the haplonemes in a later study (Namikawa, 2000).

In addition, the small size and/or the rare occurrence of some nematocysts could easily lead the examiner to overlook them. It is also likely that capsules of the same type, but belonging to different size classes, were lumped together, as illustrated by the accounts of Millard (1955,

1975) on *Hydractinia altispina* and *H. multitentaculata*, respectively. We agree with Schuchert (P. Schuchert, pers. comm.) that some of these rare capsules, as well as the so called size classes observed in certain categories of nematocysts, might be no more than early and intermediate stages, respectively, in the formation of fully-functional capsules. In order to use them reliably as taxonomic discriminators, their occurrence should be documented carefully in multiple hydroid populations of a given species.

Owing to the taxonomical impediments discussed above, it is likely that molecular techniques may prove to be the only truly reliable method of separating these difficult hydroid species.

Although the available data on all species of medusoid-producing hydractiniids are summarized in Table 1, the present hydroid is compared in more detail to its congeners from the temperate to tropical western North Atlantic. Indeed, due to their mostly epizootic habit, these hydroids are not expected to occur outside their known geographical areas.

Table 1. Comparison between *Hydractinia promiscua* sp. nov. and its medusoid-producing allies. The abbreviations used are as follows: AI (atrichous isorhizas), BI (basitrichous isorhizas), DE (desmonemes), HA (haplonemes), HE (heteronemes), mBE (microbasic euryteles), mBM (microbasic mastigophores), UC (unidentified capsules); N.A. signifies that no information is available.

Species name	Reference(s)	Distribution	Cnidome (μm)	Substrate	Structure, condition of coenosarc	Hydrorhiza	Spines	Types of dactylozooids
<i>H. aculeata</i> (Wagner, 1833)	Schuchert (2008, 2014)	Mediterranean	DE: (5.7.5)×(3.5.4); HE: (14.17)×(3.5.4); mBE: (6.5.8)×(2.5.3)	Gastropod shells inhabited by molluscs or hermit crabs	From reticulate to encrusting		Smooth	Tentaculozooids
<i>H. allmani</i> Bonnevie, 1898	Schuchert (2008)	Arctic to northern boreal	DE: (6.7)×(3.4); UC: (14.16)×(4.5); HE: (9.11)×(3.4)	Gastropod shells	Crustlike with naked coenosarc		Short, conical with rounded tips	Absent
<i>H. altispina</i> Millard, 1955	Millard (1955, 1975)	South Africa	DE: 6×3.6; mBE: (8.4-13.8)×(2.4-5.4) in apparently 2 size classes	Gastropod shell	Hydrorhiza covered with layer of free coenosarc		Long, smooth	Absent
<i>H. arcica</i> (Jäderholm, 1902)	Schuchert (2008)	Greenland	DE: 6×4; mBE: (8.5-9.5)×(2.5-3.0); mBM: (12.14)×(4.5)	Gastropod shells	Hydrorhiza loosely meshed, covered with perisarc		Absent	Absent
<i>H. arge</i> (Clarke, 1882)	Clarke (1882), Calder (1971)	Atlantic coast of N America	N.A.	Mostly epiphytic, also on gastropod shells	“Hydrorhizal mat” covered by coenosarc		Absent	Absent
<i>H. arge</i> (Clarke, 1882) sensu Calder (1988)	Calder (1988)	Bermuda	DE: (5.0-5.7)×(2.8-3.3); HA: (4.9-6.6)×(2.4-2.7); mBE: [(7.3-7.8)×(2.6-2.8)] and [(8.3-10.2)×(2.9-3.7)]	Gastropod shells	Branching, anastomosed stolons		Inconspicuous	Absent
<i>H. arge</i> (Clarke, 1882) sensu Wedler & Larson (1986)	Wedler & Larson (1986)	Puerto Rico	N.A.	Gastropod shell with hermit crab	“Very dense net”		Absent	Absent
<i>H. beikensis</i> (Watson, 1978)	Watson (1978), Bouillon <i>et al.</i> (1997)	Australia	(?) BI: 6.5×2.5; (?) mBE: 4.5×2.5	Gastropod shells	Reticulate		Absent	Absent
<i>H. calderi</i> Bouillon <i>et al.</i> , 1997	Bouillon <i>et al.</i> (1997)	Alboran Sea	DE: (6.3-7.5)×(3.2-3.6); mBE: (8.7-11.0)×3.2	Gastropod shells	Hydrorhiza reticulate		Present	Present, type not stated
<i>H. canalifera</i> Millard, 1957	Millard (1957, 1975)	South Africa	N.A.	Seaweed	Hydrorhiza encrusted in centre of colony, covered with naked coenosarc		Absent	Tentaculozooids
<i>H. cytaeiformis</i> Vervoort, 2006	Vervoort (2006)	Cape Verde	DE: [(3.2-3.6)×(2.7-3.2)] and (ca. 4.9×4.5); mBE: (6.3-8.0)×(3.2-3.6);	Worm tube	Stolons densely packed, intertwined, anastomosing, no naked coenosarc		Absent	Tentaculozooids
<i>H. denhami</i> (Thornely, 1904)	Thornely (1904)	Palk Strait	N.A.	Gastropod shell with hermit crab	“Basal crust”		Present	Absent
<i>H. denhami</i> (Thornely, 1904) sensu Stechow (1912)	Stechow (1912)	Bab-el-Mandeb Strait	N.A.	Gastropod shell with hermit crab	N.A.		N.A.	Absent
<i>H. diogenes</i> Millard, 1959	Millard (1959, 1975)	Mozambique	DE: 5×3.5; mBE: 9×4	Gastropod shells with hermit crabs	Dense mat covered by layer of free coenosarc		Short, smooth	Spiral zooids

Species name	Reference(s)	Distribution	Cnidome (μm)	Substrate	Structure, condition of coenosarc	Hydrorhiza	Spines	Types of dactylozooids
<i>H. epiconcha</i> Stechow, 1907	Stechow (1909), Hirohito (1988)	Japan	N.A.	Gastropod shells	Crust-like, covered by naked coenosarc		Two types	Tentaculozooids
<i>H. granulata</i> Hirohito, 1988	Hirohito (1988)	Japan	N.A.	Gastropod shell inhabited by hermit crab	Dense mat covered by naked coenosarc		Smooth or rugose	Spiralzooids + tentaculozooids
<i>H. hooperi</i> (Sigerfoos, 1899)	Sigerfoos (1899)	Vicinity of New York	N.A.	Gastropod shells	Highly ramified and anastomosed, no naked coenosarc		Small	Absent
<i>H. hooperi</i> (Sigerfoos, 1899) sensu Wedler & Larson (1986)	Wedler & Larson (1986)	Puerto Rico	N.A.	Gastropod shell	Reticular		Absent	Absent
<i>H. inermis</i> (Allman, 1872)	Schuchert (2008, 2014)	Mediterranean	DE: (4.5-5) \times 2.5; mBE: [(7.5-8) \times 2.5] and (9 \times 3)	Algae, barnacles, sponge, rocks	Tightly reticulate but never encrusting, covered by perisarc		Absent	Absent
<i>H. kaffaria</i> Millard, 1955	Millard (1955)	South Africa	N.A.	Gastropod shells	Covered with layer of free coenosarc		Absent	Tentaculozooids
<i>H. marsupialia</i> Millard, 1975	Millard (1975)	South Africa	UC: (7.2-10.2) \times (2.7-3.6); UC: 5.4 \times 3.0	Gastropod shells	From perisarc-covered tubes to coalescent and covered with naked coenosarc		Smooth and short	Absent
<i>H. michaelseni</i> Broch, 1914	Broch (1914)	Senegal	N.A.	Gastropod shell with hermit	Naked coenosarc present locally		Present	Spiralzooids
<i>H. misakiensis</i> (Iwasa, 1934)	Iwasa (1934), Hirohito (1988), Namikawa (2000)	Japan	DE: (5.6-7.2) \times (2.8-3.6); mBE: [(7.6-9.2) \times (2.8-3.2)] and [(10.4-14.0) \times (3.2-4.8)]; AI: (4.0-5.6) \times (1.6-2.0)	Gastropod shells inhabited by molluscs or hermit crabs	Closely reticulated, covered by perisarc		Smooth	Tentaculozooids
<i>H. multigranosa</i> (Namikawa, 1991)	Namikawa (1991, 1995)	Japan	DE: (5.7-7.2) \times (2.7-3.9); mBE (?) or HA: [(4.8-5.6) \times (1.6-2.4)]; mBE: [(8.8-9.6) \times (2.8-3.2)] and [(10.4-11.2) \times (3.6-4.0)]	Gastropod shells	Stolonial growth, covered by perisarc		Absent	Tentaculozooids
<i>H. multitentaculata</i> (Millard, 1975)	Millard (1975), Vervoort (2006)	South Africa, Mauritania	DE: (5.4-7.2) \times (3.0-3.6); mBE: (9.0-13.8) \times (2.4-4.2), possibly in two size classes	Gastropod shells	Network of coalesced perisarc tubes covered by layer of free coenosarc		Smooth or slightly corrugated	Spiralzooids
<i>H. paucispinata</i> Vervoort, 2006	Vervoort (2006)	Cape Verde	DE: (3.6-4.1) \times (2.3-2.7); mBE: [(5.0-5.4) \times (2.7-3.2)] and [(7.0-7.5) \times (1.8-2.3)]	Gastropod shells	Stolonial tubes fused forming thin, solid plate, covered by coenosarc		Two sizes	N.A.
<i>H. piscicola</i> (Komai, 1932)	Komai (1932), Yamada (1959), Kubota (1991)	Japan	DE: (5.6-6.6) \times (3.2-3.6); mBE: [(8.6-11.2) \times (2.8-4.0)] and [(11.2-16.0) \times (3.8-4.8)]	Scorpaenid fishes	Loosely reticulated		Occasionally present	Absent
<i>H. proboscidea</i> (Hincks, 1868)	Schuchert (2008)	British Is. to Alboran Sea	DE: (8-9) \times 4; mBE: 12 \times (3-4)	Inert substrates (rocks, laminarians)	Network of perisarc covered stolons		Smooth	Tentaculozooids

Species name	Reference(s)	Distribution	Cnidome (μm)	Substrate	Structure, condition of coenosarc	Hydrorhiza	Spines	Types of dactylozooids
<i>H. promiscua</i> sp. nov.	Present study	Caribbean	DE: (6.3-6.8) \times (3.4-3.7); mBE: [(7.4-7.7) \times (2.6-2.8)] and [(9.7-10.6) \times (3.1-3.4)]; HA: (ca. 5.1 \times 3.1), [(9.4-10.3) \times (2.3-2.6)], and [(10.0-10.3) \times (4.0-4.3)]	Worm tube, ascidian	Loosely reticular hydrorhiza	Absent	Absent	Tentaculozooids
<i>H. pruvoti</i> Motz-Kosowska, 1905	Schuchert (2008)	Mediterranean	DE; two size classes of (?) HE	Gastropod shells	Reticulate stolons or coalescent into crust	Occasionally present, smooth	Occasionally present, smooth	Tentaculozooids
<i>H. sandrae</i> (Wedler & Larson, 1986)	Wedler & Larson (1986)	Puerto Rico	N.A.	Ascidian	"Netlike"	Absent	Absent	Likely absent
<i>H. sinipapillaris</i> (Hirohito, 1988)	Hirohito (1988)	Japan	N.A.	Gastropod shell	Closely reticulated, covered by perisarc	Smooth, nipple-like to conical	Smooth, nipple-like to conical	Tentaculozooids (characteristically short, papillary)
<i>H. sp.</i>	Galea (2013)	Martinique	DE: (6.9-7.2) \times (3.7-4.0); mBE: (8.0-8.5) \times (2.9-3.2); HE: [(9.8-10.4) \times (4.2-4.5)] and [(13.3-14.4) \times (3.7-4.0)]; UC: (6.4-6.6) \times (3.2-3.4)	Limestone and sponge	Creeping, ramified hydrorhiza, no naked coenosarc	Absent	Absent	Tentaculozooids
<i>H. sp.</i> (as <i>Spyactis</i> sp.)	Wedler & Larson (1986)	Puerto Rico	N.A.	Gastropod shell	"Wide-meshed hydrorhizal net"	Absent	Absent	Absent

Species name	Gastrozooids	Gonozooids	Gonophore	Marginal rudimentary tentacles	Oocyte number							
Size (mm)	Tentacle number	Tentacle rows	Nematocysts around hypostome	Tentacle number	Size (mm)	Nematocysts around hypostome	Position of gonophores on zooid	Gonophore nb.	Size (μm)	Radial canals		
<i>H. aculeata</i> (Wagner, 1833)	1.5-2	12-18	2	Present	< 0.6	Present	Upper third	1-6	600-800	4	7-8	30-36, or more
<i>H. almani</i> Bonnevie, 1898	5-15	10-16	1	Present	< 5	Present	Upper third	2	1000-1200	4	8 (periradial longer than interradial)	< 100
<i>H. altispina</i> Millard, 1955	4	5-12	1	N.A.	0.44	N.A.	Near base	N.A.	420 \times 510 (σ^7); 460 \times 360 (σ^8)	4	Absent	ca. 32
<i>H. arctica</i> (Jäderholm, 1902)	2	18-22	2-3	Present	0.5	Present	Just below tentacle whorl	2	N.A.	Possibly present	Absent	ca. 10
<i>H. arge</i> (Clarke, 1882)	< 40	14-20	2	N.A.	< 10	4-13	At 3/4 apically	4-10	ca. 800	4	8	> 10
<i>H. arge</i> (Clarke, 1882) sensu Calder (1988)	2	8-16	2	N.A.	1.7	5-10	Proximal to tentacular whorl	2	ca. 1100 \times 1200	4	8	> 12

Species name	Gastrozooids			Gonozooids			Gonophore						
	Size (mm)	Tentacle number	Tentacle rows	Nematocysts around hypostome	Size (mm)	Tentacle number	Nematocysts around hypostome	Position of gonophores on zooid	Gonophore nb.	Size (µm)	Radial canals	Marginal rudimentary tentacles	Oocyte number
<i>H. arge</i> (Clarke, 1882) sensu Wedler & Larson (1986)	10-20	15-30	2	N.A.	1.5-2.0	5-15	N.A.	Upper half	2-3	N.A.	Presumably 4	N.A.	Likely about 20 or more
<i>H. betkensis</i> (Watson, 1978)	1.2	8-15	1	N.A.	0.65-0.8	ca. 8	N.A.	Below the tentacles	< 5	ca. 400	4	0	12
<i>H. calderi</i> Bouillon <i>et al.</i> , 1997	5	20-40	3	N.A.	0.5-2.5	2-14	N.A.	Upper half	1-3	ca. 800	4	8 (4 small, 4 more developed)	"numerous"
<i>H. canalifera</i> Millard, 1957	2-3.2	10-14	1	N.A.	1.3	6-9	N.A.	Upper half	4-5	< 500	4	Absent	> 50
<i>H. cytaeiformis</i> Vervoort, 2006	0.5-0.9	10-12	1	N.A.	0.22-0.23	0	N.A.	Middle part	1-2	115-160	4	4	ca. 8
<i>H. denhami</i> (Thornely, 1904)	N.A.	ca. 24	N.A.	N.A.	N.A.	4-5	N.A.	Middle part	2	N.A.	4	N.A.	N.A.
<i>H. denhami</i> (Thornely, 1904) sensu Stechow (1912)	N.A.	N.A.	N.A.	N.A.	N.A.	8-10	N.A.	Upper third	4-6	N.A.	4	8	12-20
<i>H. diogenes</i> Millard, 1959	2-3	10-26	N.A.	N.A.	N.A.	5-15	N.A.	Near distal end	< 6	450×460 (♂); 390×430 (♀)	Presumably 4	Absent	5-13
<i>H. epiconcha</i> Stechow, 1907	< 6	8-30 (rarely 50)	2	N.A.	1.5-3	8-10 (or more)	N.A.	Above middle part	2-5	ca. 800×600	4	8	ca. 30
<i>H. granulata</i> Hirohito, 1988	2	< 16	1	N.A.	N.A.	4-10	N.A.	Above middle part	4-5	N.A.	4	8	> 20
<i>H. hooperi</i> (Sigerfoos, 1899)	20-25	15-35	1	N.A.	N.A.	6-15	N.A.	Just below tentacle whorl	1-7	Length ca. 1000	4	8	Manubrium "gorged with sexual cells"
<i>H. hooperi</i> (Sigerfoos, 1899) sensu Wedler & Larson (1986)	15	15-20	1	N.A.	N.A.	4-9	N.A.	Upper half	ca. 3	N.A.	Presumably 4	N.A.	N.A.
<i>H. inermis</i> (Allman, 1872)	2-3	12-22	2	Present	0.5-1	6-16	Present	Middle of body	4-8	N.A.	4	8	10-20
<i>H. kaffaria</i> Millard, 1955	2	8-15	2	N.A.	1.1	5-12	N.A.	Upper third	N.A.	550×500 (♂); 450×400 (♀)	4	"indication" of tentacles	21-32

Species name	Gastrozooids			Gonozooids			Gonophore						
	Size (mm)	Tentacle number	Tentacle rows	Nematocysts around hypostome	Size (mm)	Tentacle number	Nematocysts around hypostome	Position of gonophores on zooid	Gonophore nb.	Size (µm)	Radial canals	Marginal rudimentary tentacles	Oocyte number
<i>H. marsupialia</i> Millard, 1975	1.9	8-16	1	N.A.	0.8	5-9	N.A.	Upper half	< 6	700×600	4	4-8	20-40
<i>H. michaelseni</i> Broch, 1914	4	20-25	2	N.A.	ca. 1	4-6	N.A.	Just below the tentacles	2-4	N.A.	4	4	Unknown
<i>H. misakiensis</i> (Iwasa, 1934)	1-4	< 30	Likely > 1	Present	N.A.	< 20	N.A.	Above middle part	1-5	ca. 500	4	8	> 20
<i>H. multigranosi</i> (Namikawa, 1991)	0.5-2.15	8-16	1	N.A.	0.5-2	4-11	N.A.	Above middle part	1-8	250-350	3-4	Absent	1-6
<i>H. multitentaculata</i> (Millard, 1975)	< 8.0	40-91	Several	N.A.	< 3.2	7-13 (♂)	N.A.	Upper third	3-4 (♂)	660×680 (♂); 700×680 (♀)	4	4 (♀)	ca. 300
<i>H. paucispinata</i> Vervoort, 2006	1.2-1.6	14-16	2	N.A.	N.A.	< 10	N.A.	Upper third	2-3	ca. 500 (♀)	4	Absent	“fairly large”
<i>H. piscicola</i> (Komai, 1932)	10	11-30	1	Present	1.4-3.3	< 12	Present	Upper third	1-3	ca. 400	4	4	ca. 30
<i>H. proboscidea</i> (Hincks, 1868)	1-5	10-32	2-3	Present	0.7	6-12	Present	Upper third	2-10	N.A.	4	4-8 (♀) 8-10 (♂)	16-70
<i>H. promiscua</i> sp. nov.	3	12-20	1	Present	1	8-11	Present	Proximal half	1-2	ca. 890×745 (♂)	4	8	Unknown
<i>H. pruvoti</i> Moitz-Kosowska, 1905	1-6	8-14	1	Absent	N.A.	1-3	Absent	Upper third	3-8	1000×(600-700)	4	4	> 100
<i>H. sandrae</i> (Wedler & Larson, 1986)	2	11-16	1	N.A.	0.5-1.5	4-11	N.A.	Shortly below tentacle whorl	2-3	N.A.	Presumably 4	N.A.	N.A.
<i>H. sinipapillaris</i> (Hirohito, 1988)	1.5	6-12	1	N.A.	< 0.75	0	N.A.	Upper third	2-3	ca. 2000	4	4	Tens ?
<i>H. sp.</i>	N.A.	12-16	1	Present	N.A.	6-12	Present	Above middle part	1	ca. 335×395 (♂)	4	Absent	Unknown
<i>H. sp.</i> (as <i>Shyactis</i> sp.)	2-3	9-13	1	N.A.	N.A.	5-8	N.A.	Upper half	1-3	N.A.	Presumably 4	N.A.	N.A.

Like *H. arge*, the present hydroid possesses gonophores with 4 radial canals and 8 tentacle rudiments, but its gastro- and gonozooids are comparatively smaller, and do not show any tendency to autotomize. The Bermudan material assigned by Calder (1988) to the same taxon comes close to our specimens regarding the size of its zooids, the number of their tentacles, and the structure of its medusoid, but its cnidome seems to possess only one type of haplonemes, whilst two additional ones occur in the Martinican hydroid.

The Puerto Rican material identified as *Stylactis arge* by Wedler & Larson (1986) possesses taller zooids with more numerous tentacles, and its medusoids are apparently devoid of tentacle stumps (possibly immature?). The rather brief description, combined with the absence of data on the cnidome, prevents any further comparison from being established with our material.

Hydractinia hooperii, as described originally, has similar medusoids, but its zooids are much taller and possess comparatively more tentacles, thus differing from our material.

The gonozooids of *H. sandrae* (Wedler & Larson, 1986) are said to exhibit a red pigmentary belt between the whorl of tentacles and the insertion of gonophores, but this was not apparent in our material examined alive (see Pl. 1B). No data on the cnidome of *H. sandrae* were provided by the authors, making impossible any further comparison with our hydroid.

The medusoid-producing *Hydractinia* sp. from Martinique, described earlier by one of us (Galea, 2013), has a different cnidome and, consequently, is not conspecific with the present species.

Last, the as yet unidentified species of *Hydractinia* from Puerto Rico [see Wedler & Larson (1986), p. 95, fig. 10E, as *Stylactis* sp.] is incompletely described, and data on its cnidome is lacking.

In spite of the rather scanty data available, it seems that our material differs morphologically from each of the three nominal species mentioned above, particularly with respect to their original descriptions (subsequent assignments are taken with reserve). According to Schuchert (P. Schuchert, *pers. comm.*), the present species is indistinguishable macroscopically from *H. aculeata* (Wagner, 1833) [see Schuchert (2014)] but, owing to its different substrate selection, remote geographical distribution, and different cnidome composition, it should be kept separate. In addition, none of the remaining species listed in Table 1 is expected to occur in our study area, on the account of their limited dispersal ability due to their characteristic epizoic or epiphytic habit.

Family Tubulariidae Fleming, 1828

Genus *Ectopleura* L. Agassiz, 1862

Ectopleura sp.

Figs 1C-G; 3F-I

Material examined: MHNG-INVE-91110; sample #M294; France, Martinique, Saint Pierre, Tombant de la Galère, 14.75144° -61.18236°, 3 m; 01.02.2014; colony up to 5 cm high with incipient gonophores. – MHNG-INVE-91121; sample #M332; France, Martinique, Saint Pierre, Tombant de la Galère, 14.75144° -61.18236°, 2-4 m; 04.03.2014; colony up to 7 cm high with incipient gonophores.

Description: Stems sparsely branched (no autoepizootic growth), rarely simple, arising in dense clusters from tortuous, tangled mass of stolonial fibers attached to sand grains (Fig. 1C). Perisarc irregularly annulated, with smooth areas between corrugated patches, thinning out distally. Coenosarc with two longitudinal, endodermal ridges which may meet in the centre. Neck region conspicuously swollen, flexible and contractile, covered basally with filmy perisarc; a narrow, but distinct, transversal band of nematocysts (isorhizas) in middle. Hydranths vasiform; aboral tentacles long, 17-21 (commonly 18) in number, monilifiliform, oval in cross section, especially basally. Oral tentacles short, 14-18 in number, not adnate basally to hypostome, semimoniliform, circular in cross section. About 10-14, short, lobed blastostyles arise slightly above the aboral row of tentacles. Gonophores incipient, their type could not be ascertained. Cnidome: large stenoteles (Fig. 3I¹) in oral tentacles; small and rounded stenoteles (Fig. 3I²) in both oral and aboral tentacles; small and ovoid stenoteles (Fig. 3I³) in both oral and aboral tentacles; microbasic basitrichous isorhizas (Fig. 3I⁴) in both oral and aboral tentacles; O-isorhizas (Fig. 3I⁵) in both oral and aboral tentacles; desmonemes (Fig. 3I⁶) in aboral tentacles.

Dimensions: Stems up to 7 cm high. Hydranths *ca.* 2.5 mm high, and 7 mm wide between tips of opposite tentacles. Large stenoteles (10.0-10.3)×(8.3-8.6) μm; small and rounded stenoteles (6.6-7.4)×(5.7-6.6) μm; small and ovoid stenoteles (5.7-6.3)× *ca.* 4.8 μm; microbasic basitrichous isorhizas (8.3-9.1)× *ca.* 3.4 μm; O-isorhizas (8.0-8.6)×(7.4-8.0) μm; desmonemes (4.3-4.8)×(3.1-3.7) μm.

Remarks: In the absence of fully formed gonophores, the present material could not be identified reliably to species. According to Petersen (1990), six species of *Ectopleura* with a known hydroid stage occur along the Atlantic coast of North America, *viz.* *E. americana* Petersen, 1990, *E. crocea* (L. Agassiz, 1862), *E. dumortierii* (Van Beneden, 1844), *E. grandis* Fraser, 1944, *E. larynx* (Ellis & Solander, 1786), and *E. mayeri* Petersen, 1990. A seventh species, *E. obypa* Migotto & Marques, 1999, was described from Brazil.

Ectopleura americana could be excluded on account of several distinct features: 1) its aboral tentacles are circular throughout in cross-section; 2) the neck region is finely and longitudinally striated; 3) the cauli are unbranched;

4) the 14-24 blastostyles are long, stout, dichotomously branched, and arranged in up to three whorls (Petersen, 1990).

According to various authors (Deevey, 1950; Defenbaugh & Hopkins, 1973; Petersen, 1990), the reduced number of tentacles (never exceeding 16) even in mature, fertile individuals, is diagnostic for *E. grandis*. Our specimens, provided with up to 18 tentacles in the oral whorl, and up to 21 around the hypostome, would not fit the above diagnosis. However, we believe that the tentacle number alone should not be regarded as a reliable character. Unfortunately, no data are available on the cnidome of *E. grandis*. This species is said to reproduce through medusae, though fully mature specimens have never been seen.

The sympatric *E. mayeri* is equally excluded on the account of the characteristic yellow fluorescent tinge of its living hydranths, and the occurrence of microbasic mastigophores in its cnidome (Galea, 2013).

The cnidome of the present species shows affinities with those of *E. crocea* [see Schuchert (1996)], *E. dumortierii* [see Schuchert (2010)], *E. larynx* [see Östman *et al.* (1995)], and *E. obypa* [see Migotto & Marques (1999)], though additional data are necessary to clarify the precise identity of some of the capsules involved. While *E. larynx* is a temperate to cold water species, not expected to occur in tropical environments, our material comes closest to *E. crocea* (P. Schuchert, *pers. comm.*), a species with considerable spreading capabilities due to anthropic activities. *Ectopleura obypa* is different in forming exclusively unbranched cauli, and in having a higher number of tentacles.

Genus *Ralpharia* Watson, 1980

Ralpharia gorgoniae Petersen, 1990

Fig. 2

Ralpharia gorgoniae – Galea, 2013: 10, pl. 1L-O, fig. 2R.

Material examined: MHNG-INVE-91114; sample #M320; France, Martinique, Case-Pilote, 14.63753° -61.13974°, 3 m; 20.02.2014; 5 fertile polyps, 10 female and 20 male medusoids set free.

Description: See the original account by Petersen (1990) and the additional data provided by Galea (2013).

Dimensions: Male medusoids 890-1060 µm (951±49 µm, n=10) long and 755-900 µm (865±41 µm, n=10) wide; female medusoids 1110-1245 µm (1181±43 µm, n=10) long and 1000-1100 µm (1090±41 µm, n=10) wide.

Distribution: Possibly endemic to the Caribbean Sea. Scattered records from some countries bordering the basin are summarized by Galea (2013), but the species is certainly widely-spread within the whole area.

Remarks: The complex structure of the blastostyle, with the gonophores inserted proximally and clusters of nematophores occurring distally (Fig. 2A), is common to three species of the genus, *viz.* *R. neira* Petersen, 1990, *R. rosetta* Watson, 1999, and *R. sanctisebastiani* (da Silveira & Migotto, 1984). Nothing is known about the blastostyles of *R. parasitica* (Korotneff, 1887), nor about its gonophores.

The gonophores of *R. gorgoniae* were illustrated for the first time by Wedler & Larson (1986, as *Tubularia parasitica*), while a short account is available in Petersen (1990). In the present material, the gonophores were liberated from their corresponding polyps within less than an hour, corresponding to the time elapsed between the sampling and their examination in the laboratory. They apparently belong to both sexes, as suggested by differences in their size and color (Fig. 2B). Their anatomy, as described below, shows that we are dealing with eumedusoids. In both sexes, the umbrella is bell shaped, slightly longer than wide. The mesoglea is rather thin (Fig. 2C) and the endoderm is provided with closely-set circular muscle fibers (Fig. 2H). In contrast with the statement by Petersen (1990), who reported only 4 radial canals in his material, each medusoid in the present collection has generally 4-5 (rarely 3 or 6) radial canals, some of which may give off one or two additional, secondary branches, most often a short distance after their origin from the manubrium, but also more distally, on the sides of the umbrella. The bell margin is provided with a raised, internal, thickened collar (Fig. 2C, D), composed of large, polygonal cells (Fig. 2G). No tentacle bulbs or rudimentary tentacles exist. A cross section through the bell margin reveals that the circular canal, of ovoid shape, passes in the middle of the raised collar (Fig. 2F). There is a well-developed velum (Fig. 2D) which, according to the observations made by Wedler & Larson (1986), helps the medusoid swim actively in the plankton. The manubrium is globular to ovoid, not surpassing half of the subumbrellar cavity, and is devoid of a mouth (Fig. 2E). The gonads could not be distinctly seen around the manubrium, especially in formalin-fixed specimens, though in some gonophores which appear to be female, either several flattened eggs or developing larvae could be seen (it is also likely that the gonophores were partly spent prior to the specimen examination). The bell margin, the radial canals, as well as the gonads in living specimens are bright orange in females and yellow-orange in males (Fig. 2B), due to pigment granules disseminated in their tissues. The whole gonophore is entirely devoid of nematocysts. Gonophores provided with a similar raised, internal collar around the bell margin are also known in *R. magnifica* Watson, 1980, *R. neira*, and *R. sanctisebastiani*, but they are absent in *R. coccinea* Watson, 1984, and – apparently – in *R. rosetta*. Four rudimentary tentacle knobs, as well as nematocysts, are present in the medusoids of *R. magnifica* and *R. coccinea*.

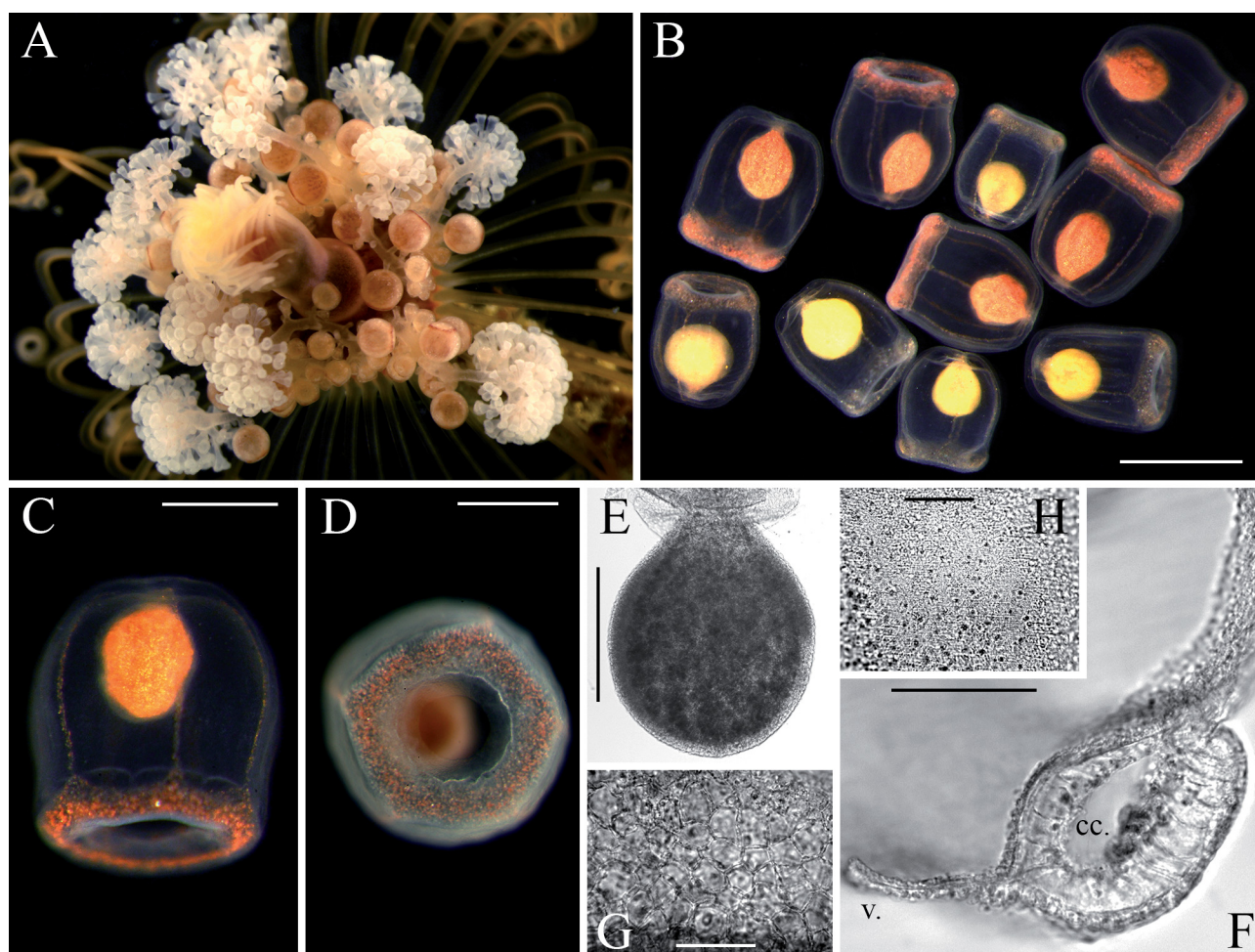


Fig. 2. *Ralpharia gorgoniae* Petersen, 1990. (A) Oral view of a fully fertile polyp. (B) Medusoids of both sexes. (C) Detail of a female medusoid in lateral view. (D) Oral view of a medusoid; note the well-developed velum. (E) Lateral view of a manubrium. (F) Cross section at level of the raised internal collar, showing the velum (v.) and the circular canal (cc.). (G) Microscopical structure of the internal collar, showing accumulation of large, polygonal cells. (H) Microscopical detail of the endoderm, showing closely-set, transverse muscle fibers. Scale bars: 50 μm (H), 100 μm (F, G), 300 μm (E), 500 μm (C, D), and 1 mm (B).

Boero & Bouillon (1989) suggested that, due to their morphological reduction, the gonophores of *R. gorgoniae* could be an example of swimming medusoids among the athecate hydroids. From the available data, it appears that *R. neira*, as well as *R. sanctisebastiani*, satisfy the same condition, in being devoid of marginal bulbs, mouth, and nematocysts.

Order Leptothecata Cornelius, 1992

Family Haleciidae Hincks, 1868

Genus *Halecium* Oken, 1815

***Halecium labiatum* Billard, 1933**

Fig. 3J, K

Halecium labiatum Billard, 1933: 21, fig. 8. – Vervoort, 1967: 30, fig. 4. – Van Praët, 1979: 877, fig. 9. – Rees & Vervoort, 1987: 28, fig. 4C.

Material examined: HRG-1024; sample #M327; France, Martinique, Le Vauclin, Pointe Faula, 14.54064° -60.82837°, 0 m; 23.02.2014; several stems, some bearing female gonothecae, on floating *Sargassum* sp.

Description: See original account by Billard (1933).

Dimensions: Stems 1-2 mm high. Hydrothecae 25-30 μm deep, 95-110 μm wide at base and 115-125 μm wide at rim. Female gonotheca 560-740 μm long. Egg diameter ca. 210 μm .

Distribution: Gulf of Suez (Billard, 1933), and possibly the southern Red Sea (Vervoort, 1967) and the Gulf of Aden (Rees & Vervoort, 1987).

Remarks: The present colony, composed of several minute, irregularly branched stems, is not suitable for a comprehensive redescription of its trophosome.

However, according to Billard (1933) and Van Praët (1979), the stems of *H. labiatum* are up to 2 cm high, monosiphonic throughout, and regularly divided into 660-925 µm long internodes.

The few side branches that exist in our material arise from short lateral apophyses given off just below a stem hydrotheca; they are composed of a single, long and slender internode topped by a hydrotheca. The latter are shallow, with slightly divergent walls and a moderately inwardly rolled margin. Hydranths, when present, badly preserved; the tentacle number and the cnidome composition could not be ascertained properly.

Conversely, the typical morphology of the gonothecae (female in this material) shows that we are undoubtedly dealing with Billard's species. They are given off mostly in pairs (occasionally singly) from below the stem hydrothecae; saccular, with the "dorsal" wall conspicuously bulging, while the "frontal" side is slightly sigmoid. The aperture, placed frontally in the distal half of the gonotheca, is composed of a prominent "lip" recovering a twin hydrotheca from which protrude a couple of hydranths. There are one or two large eggs per gonotheca, and some of them appear to have been fertilized. The lower "lip", according to Billard's wording, is nothing more than the rim of the twin hydrotheca.

The sterile specimens examined by Vervoort (1967) and Rees & Vervoort (1987) possibly belong to the present species, but their occurrence in the same geographical area is not a sufficient argument to justify their identification.

Halecium lightbourni Calder, 1991

Fig. 3L-P

Halecium lightbourni Calder, 1991: 19, figs 10, 11. – ? Grohmann *et al.*, 2003: 6. – Calder & Kirkendale, 2005: 481.

Material examined: MHNG-INVE-91109; sample #M291; France, Martinique, Saint Pierre, Tombant de la Galère, 14.75144° -61.18236°, 10-15 m; 01.02.2014; male and female colonies epizoic on *Thyroscyphus marginatus* (Allman, 1877).

Description: See original account by Calder (1991).

Dimensions: Stems up to 6 mm high. Female gonothecae 605-810 µm long and 345-420 wide. Oocytes 130-210 µm in diameter. Male gonothecae 355-425 µm long and 135-155 µm wide. Microbasic mastigophores *ca.* 6.0×1.7 µm; small pseudostenoteles *ca.* 4.8×2.3 µm; large pseudostenoteles (9.7-10.8)×(4.3-4.6) µm.

Distribution: Bermuda (Calder, 1991), Caribbean coast of Panama (Calder & Kirkendale, 2005). A third record, from Brazil (Grohmann *et al.*, 2003), must be considered as provisional on account of the lack of formal description and figures of the studied material.

Remarks: These small, mostly simple or occasionally branched stems with moderately long and slender internodes and shallow, somewhat flaring hydrothecae, correspond well to the trophosome of *H. lightbourni*, as described by Calder (1991). In addition, the cnidome composition appears to be the same [compare our Fig. 3P with fig. 11 on p. 20 in Calder (1991)]. In our view, the nematocysts are microbasic mastigophores (Fig. 3P¹), as well as small and large pseudostenoteles (Fig. 3P^{2, 3}). The last two capsules, though none were seen discharged, are provided with conspicuously swollen shafts and resemble the pseudostenoteles observed in other species of *Halecium*. In contrast, Calder (1991) identified them as microbasic euryteles.

The present material is fertile, carrying gonothecae of both sexes on different colonies. They are given off either from below a secondary hydrotheca or from within a hydrotheca. The females are saccular to reniform; their aperture, characteristically tilted outward and upward (Fig. 3M¹), is represented by a twin hydrotheca (Fig. 3M²) from which protrude a pair of normal hydranths. There are 5-6 oocytes per gonotheca (Fig. 3N). The male gonothecae are club shaped (Fig. 3O), thus typical of the genus.

Halecium plicatum Galea, sp. nov.

Fig. 4A-I

Holotype material: MHNG-INVE-91117; sample #M327; France, Martinique, Le Vauclin, Pointe Faula, 14.54064° -60.82837°, 0 m; 23.02.2014; female colony on floating *Sargassum* sp.

Paratype material: MHNG-INVE-91118; sample #M327; France, Martinique, Le Vauclin, Pointe Faula, 14.54064° -60.82837°, 0 m; 23.02.2014; male colony on floating *Sargassum* sp. – MHNG-INVE-91111; sample #M303; France, Martinique, Le Vauclin, Pointe Faula, 14.54064° -60.82837°, 0 m; 11.02.2014; female colony on floating *Sargassum* sp.

Diagnosis: Small, monosiphonic stems; internodes moderately long, with a terminal hydrotheca and a lateral, upwardly-curved, small apophysis supporting following internode. Female gonotheca kidney-shaped, perisarc thick on "dorsal" side, pleated on top, a twin gonotheca on "ventral" side. Nematocysts comprising microbasic mastigophores and pseudostenoteles.

Etymology: The specific epithet *plicatum* is the participle of the Latin *plico* (in Greek, πλέχω), meaning pleated, to characterize the appearance of the perisarc on the summit of the female gonotheca.

Description: Colonies small, upright, arising from creeping, branching and anastomosing hydrorhiza with irregular, internal pegs of perisarc (Fig. 4A). Hydrocauli monosiphonic; basal part composed of 2-3

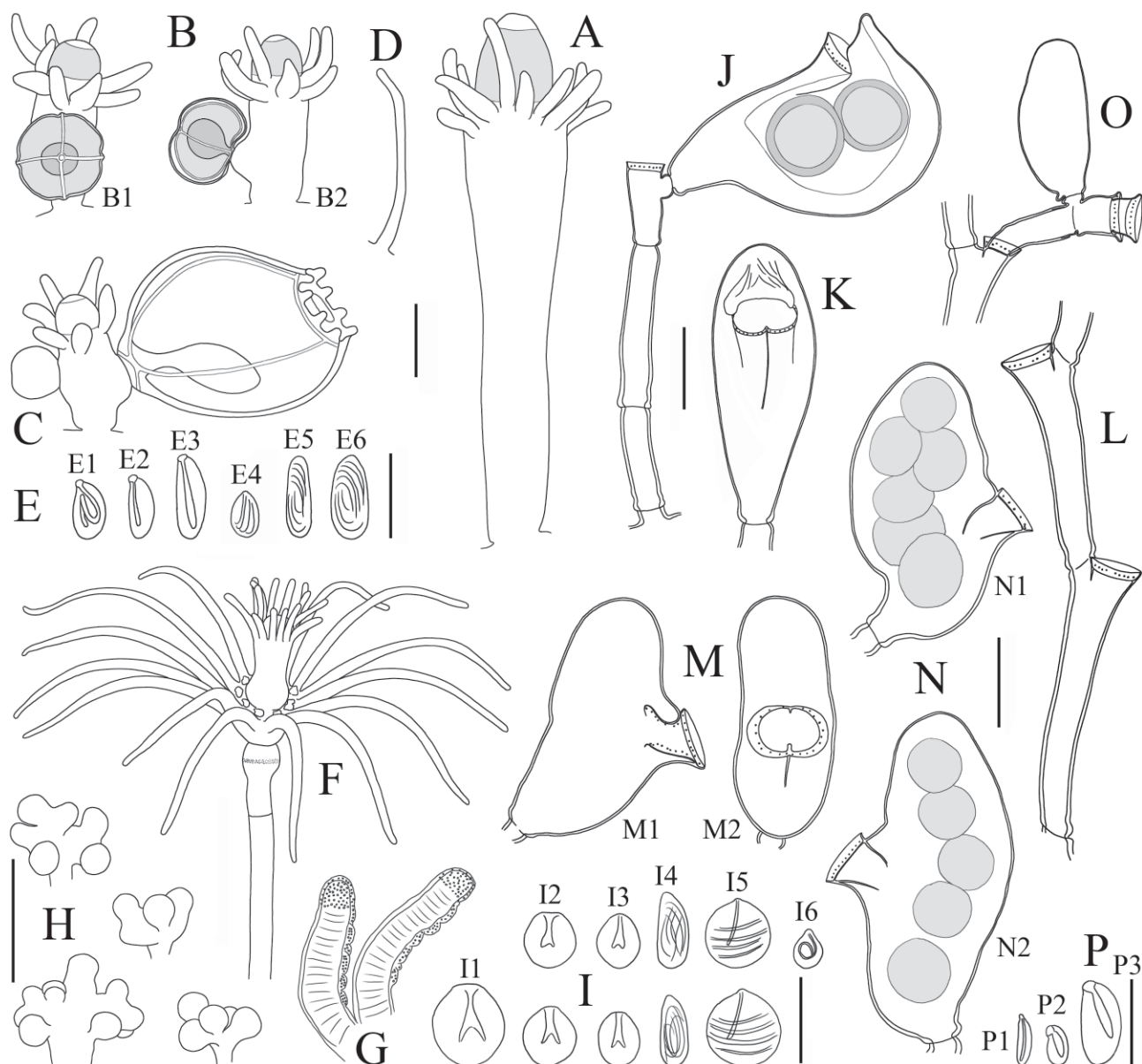


Fig. 3. A-E: *Hydractinia promiscua* sp. nov. (A) Gastrozooid. (B) Same gonozooid with ripe, unspent male gonophore seen both frontally (B¹) and laterally (B²). (C) Gonozooid with spent medusoid in lateral view. (D) Tentaculozooid. (E) Cnidome. F-I: *Ectopleura* sp. (F) Hydranth. (G) Two oral tentacles. (H) Four blastostyles with immature gonophores. (I) Cnidome of both aboral (upper row) and oral (lower row) tentacles. J, K: *Halecium labiatum* Billard, 1933. (J) Female gonotheca in lateral view. (K) Same gonotheca seen frontally. L-P: *Halecium lightbourni* Calder, 1991. (L) Two stem internodes. (M) Same female gonotheca seen both laterally (M¹) and frontally (M²). (N) Two female gonothecae with oocytes. (O) Male gonotheca. (P) Cnidome. Scale bars: 10 μ m (E, I, P), 200 μ m (J-O), 300 μ m (A-D, G, H).

short, cylindrical segments with bulged ends; remainder of cauli divided into slightly geniculate, moderately long and slender internodes, by means of slightly oblique constrictions of the perisarc sloping in alternate directions (Fig. 4B, C); perisarc thin and smooth; each internode swollen basally, with a hydrotheca distally, and 1-2 short, upward-curved apophyses for the insertion of following internodes; apophyses given off from just below the base of a theca. Side branches,

when present, short, composed of only 1-3 internodes (Fig. 4B, C⁶). Short, athecate internodes may be inserted among the normal sequence of thecate internodes (Fig. 4A, B, C¹, C⁶) in various stems. Hydrothecae shallow, walls slightly flaring, rim even, not everted (Fig. 4D); renovations occasional; secondary hydrophores of varied length, basal part with annulated perisarc. Hydranths with *ca.* 20 filiform tentacles surrounding a conical hypostome. Gonothecae arising with no definite

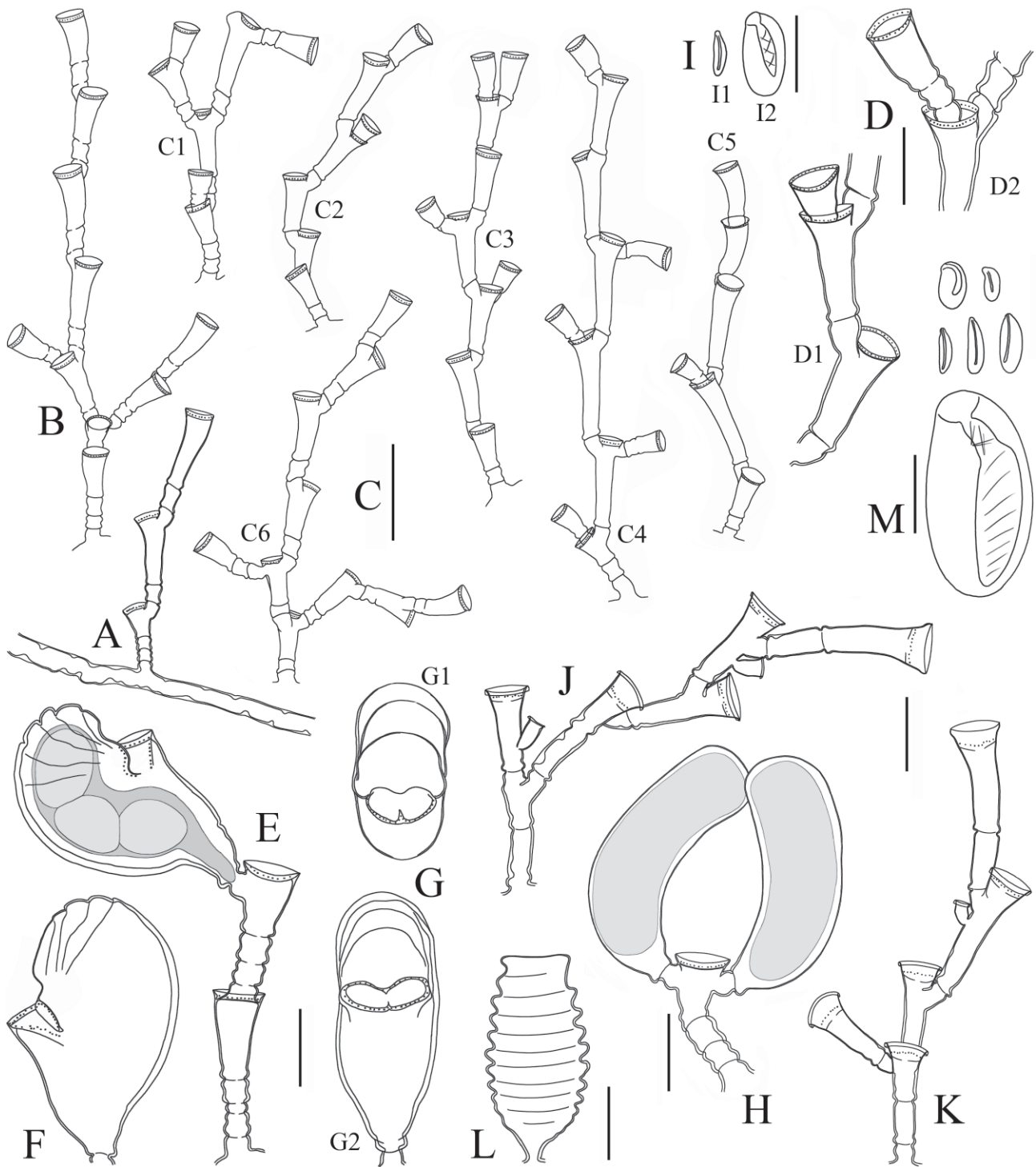


Fig. 4. A-I: *Halecium plicatum* sp. nov. (A) Stolon (note internal pegs) and upright stem. (B) Stem from sample M327. (C) Six stems from sample M303 (note irregular presence of short athecate internodes). (D) Details of internodes with hydrothecae from samples M303 (D¹) and M327 (D²). (E) Female gonotheca, showing oocytes. (F, G) Same female gonotheca seen laterally (F), frontally (G²), and from a plane parallel to the aperture of twin hydrotheca (G¹). (H) Male gonotheca. (I) Cnidome. J-M: *Hydrodendron mirabile* (Hincks, 1866). (J, K) Two erect stems. (L) Male gonotheca. (M) Cnidome. Scale bars: 10 µm (I, M), 200 µm (D-H), 300 µm (J-L), 500 µm (A-C).

pedicel from stem apophyses, similarly to the branches. Female kidney-shaped (Fig. 4E-G), laterally flattened (Fig. 4G²), perisarc thick, especially on “dorsal” side (Fig. 4F), forming apically a number of conspicuous folds; concave side carrying a twin hydrotheca (Fig. 4G²) from which emerges a pair of hydranths; hydrothecae not fused medially, but separated frontally by an internal septum (Fig. 4G¹) plunging, for some distance, into the lumen of gonotheca (Fig. 4F); generally three large eggs per gonotheca. Male gonothecae cylindrical, curved in middle, tapering basally, with rounded top; a compact mass of sperm cells fills nearly completely their lumen (Fig. 4H). Cnidome (Fig. 4I): microbasic mastigophores and likely pseudostenoteles, though none was seen discharged.

Dimensions: Stems up to 3 mm high. Internodes 220–250 µm long and 55–70 µm wide at node. Short athecate internodes (occasionally present) 90–135 µm long. Stem apophyses 80–90 µm long. Hydrothecae *ca.* 30 µm deep, 115–140 µm wide at base, and 125–160 µm wide at aperture. Female gonotheca 560–660 µm long, 385–400 µm wide. Male gonotheca 600–670 µm long, 215–245 µm wide. Microbasic mastigophores (5.5–6.0) × *ca.* 1.7 µm; pseudostenoteles (9.5–9.8) × (4.0–4.3) µm.

Distribution: Known only from Martinique (present study).

Type locality: France, Martinique, Le Vauclin, Pointe Faula.

Remarks: Although the hydrocauli and, when present, the side branches are divided into regular sequences of thecate internodes (Fig. 4C²⁻⁵), short, intermediate athecate internodes may be inserted among them (Fig. 4C^{1, 6}) in some stems, but not in others, as illustrated by the colony from sample M303. Their presence was, however, constant in the colony from sample M327 (Fig. 4A, B).

The specimens of *Halecium* sp. from Guadeloupe [see Galea (2010a), p. 11, Fig. 3P-S], which exhibit a trophosome similar to that of the present species, were re-examined for this study. A more careful analysis of their cnidome revealed that two additional capsules, previously overlooked due to their scarcity, equally occur: a smaller pseudostenotele [(5.9–6.6) × (2.3–2.4) µm], as well as a tubular, slightly curved, heteroneme with rounded ends [(4.7–4.9) × *ca.* 2.4 µm]. No such capsules were observed in any of the available specimens of *H. plicatum*.

Similarly, the trophosome of the as yet unidentified *Halecium*, mentioned by Galea (2013, p. 20, fig. 5J-M), resembles that of the new species. A re-analysis of its cnidome confirmed the previous observations, proving that it is not only distinct from *H. plicatum*, but also from its Guadeloupean relative.

The mode of branching in *H. plicatum* is equally found in a number of congeners, but these exhibit several distinguishing features enabling their separation from

the new species, as follows: 1) *Halecium conicum* Stechow, 1919 has comparatively deeper and flaring hydrothecae, and the female gonothecae are irregularly ovoid, with a small, distal aperture (Motz-Kossowska, 1911, as *H. minutum* sp. nov.); 2) *H. curvicaule* von Lorenz, 1886 has female gonothecae provided with numerous conspicuous transverse ridges on nearly their whole surface (Calder, 1970); 3) small specimens of *H. dichotomum* Allman, 1888 with sympodial growth habit are distinguished through their hydrothecae with everted rim, and the presence of characteristic wrinkles on the “dorsal” surface of the female gonothecae (Galea, 2013); 4) the female gonothecae of *H. expansum* Trebilcock, 1928 have an entirely smooth surface and their aperture is provided with a “large, slit-like opening flanked on each side by [a] gutter-shaped flap supporting a hydranth” (Vervoort & Watson, 2003); 5) *H. fragile* Hodgson, 1950 has exceedingly long and slender internodes (Watson & Vervoort, 2001); 6) *H. interpolatum* Ritchie, 1907 is a large species, with polysiphonic stems, exceedingly long and slender internodes (Peña Cantero, 2014), and its female gonothecae are broadly ovoid, with a rounded, distal aperture (Watson, 2008); 7) the coenosarc of *H. nanum* Alder, 1859 is filled with zooxanthellae, and its female gonothecae have an almost distal aperture, whose closely appressed tubes are finely annulated (Calder, 1991); 8) the hydrothecae of *H. pygmaeum* Fraser, 1911 have everted margins, and its female gonothecae are smooth-walled and contain *ca.* 7 oocytes (Hirohito, 1995); 9) the internodes of *H. scalariformis* Billard, 1929 are very short and annulated basally (Billard, 1929); 10) the female gonothecae of *H. speciosum* Nutting, 1901 are ovoid in general outline and transversely annulated, and the distal part of the internodes may be wrinkled (Nutting, 1901); 11) the internodes of *H. tenellum* Hincks, 1861 are long, slender and strongly geniculate, its hydrothecal rim is greatly outrolled, and the female gonothecae are pear-shaped and contain a larger number of oocytes (Calder, 1991; Galea *et al.*, 2007); 12) the internodes of *H. vagans* Fraser, 1938 are exceedingly long and slender, and the hydrothecal margin is almost flaring (Fraser, 1938). Short, athecate internodes, like those of *H. plicatum*, are also inserted among the thecate internodes of several other species of the genus, but a number of morphological characters distinguish them from the new species, as follows: 1) the hydrothecae of *H. arcticum* Ronowicz & Schuchert, 2007 are comparatively deeper and have an everted margin, and its female gonothecae are discoid, with an apical aperture flanked by two lateral horns (see original description); 2) the stems and branches of *H. lankesterii* (Bourne, 1890) are more irregularly segmented, its coenosarc contains zooxanthellae, and the female gonothecae are smooth-walled (Schuchert, 2005); 3) *H. luteum* Watson, 1975 has strongly fascicled stems, its internodes are short, the hydrothecal rim is outrolled, and there is a “wedge-shaped thickening of the perisarc” below the diaphragm (Watson, 1975).

Female gonothecae with the overall shape of those of *H. plicatum* are present in other species of the genus. The main features allowing their distinction from the new species are as follows: 1) the gonothecae of *H. beanii* (Johnston, 1838) are smooth-walled, and this is a large species with polysiphonic stems, rather short internodes, and apophyses in continuation of the long axis of internode, the hydrotheca being displaced laterally (Hirohito, 1995); 2) *H. bermudense* Congdon, 1907 forms large colonies with polysiphonic stems, its internodes are almost collinear, the apophyses are in continuation of the long axis of internode (the hydrothecae being displaced laterally), the female gonotheca is entirely smooth (Migotto, 1996), and its cnidome is different (Calder, 1991); 3) the gonotheca of *H. bithecum* Watson, 2005 is entirely smooth and its aperture is more tubular, the stems may be slightly polysiphonic, and the hydrothecae are borne on well-developed hydrophores (Watson, 2005); 4) *H. fjordlandicum* Galea, 2007 forms pinnate colonies with polysiphonic stems, the internodes are very long and slender, the cnidome is different (Galea, 2007), and its gonothecae are smooth-walled and much curved (Galea & Schories, 2012); 5) colonies of *H. jaederholmi* Vervoort, 1972 are large and polysiphonic, the hydrothecae are characteristically adnate to their corresponding internodes, and the gonothecae are entirely smooth (Vervoort, 1972; Millard, 1977); 6) *H. macrocephalum* Allman, 1877 has polysiphonic stems, the apophyses are a continuation of the long axis of internode, its hydrothecae being displaced laterally and tilted downwards to about 45°, and the gonothecae have a smooth surface (Allman, 1877; Vervoort *et al.*, 2011); 7) *H. scutum* Clark, 1877 forms large, polysiphonic colonies, its internodes are short, the apophyses are minute, and the gonothecae are entirely smooth, with the aperture “partially covered by a characteristic hood-like process” (Schuchert, 2005); 8) the internodes of the large, polysiphonic *H. sessile* Norman, 1867 are collinear, gradually widening distally, and their gonothecae are smooth-walled (Cornelius, 1975); 9) the gonothecae of *H. tabulatum* Watson, 2005 are smooth, their aperture is a “deep slightly inwardly tilted shelf containing a reduced hydranth”, and its hydrothecae expand to margin, where the rim is weakly everted (Watson, 2005).

Genus *Hyrodendron* Hincks, 1874

Hyrodendron mirabile (Hincks, 1866)

Fig. 4J-M

Material examined: MHNG-INVE-91105; sample #M135; France, Martinique, Anse Dufour, 14.52716° -61.09003°, 0-1 m; 23.01.2014; male colonies on benthic *Sargassum* sp.

Description: See Hirohito (1995).

Distribution: Numerous records assigned to *H. mirabile* and its putative synonym, *H. caciniiformis* (Ritchie, 1908), are mostly based on sterile specimens whose specific identity could not be ascertained properly (Galea *et al.*, 2014). Records based on fertile material corresponding to the concept of *H. mirabile* defined by Galea *et al.* are from the Mediterranean, Caribbean (present report), Korea (Rho & Park, 1980), and Japan (Hirohito, 1974; 1995).

Remarks: A recent account on the present material, including a comparison with Mediterranean specimens of *H. mirabile*, is provided by Galea *et al.* (2014).

Family Sertulariidae Lamouroux, 1812

Genus *Dynamena* Lamouroux, 1812

Dynamena bimorpha Galea, sp. nov.

Fig. 5A-F, Table 2

? *Dynamena cornicina* – Millard, 1964: 29, fig. 9; 1975: 261, fig. 86A-E (not *Dynamena cornicina* McCrady, 1859).

Holotype material: MHNG-INVE-91119; sample #M327; France, Martinique, Le Vauclin, Pointe Faula, 14.54064° -60.82837°, 0 m; 23.02.2014; sterile colony with simple and pinnately-branched stems, on floating *Sargassum* sp.

Diagnosis: Simple and pinnate stems within the same colony; cladia alternate; stem internodes with a basal, lateral apophysis, an axillar hydrotheca, as well as two hydrothecae alternately-placed above; hydrothecae on cladia in strictly opposite pairs; gonothecae transversely ribbed.

Etymology: From the Latin *bis*, meaning double, and the Greek μορφή, meaning shape, to make an allusion to the co-occurrence of two growth forms in this species.

Description: Colonies erect, arising from a creeping, branching stolon. Stems either simple (Fig. 5A) or pinnately-branched (Fig. 5B). Simple stems with a short basal part devoid of hydrothecae, ending in oblique node; above, stem divided into up to 12 internodes by collar-like constrictions of the perisarc; each internode with a pair of opposite hydrothecae, these separated in basalmost internodes, becoming gradually contiguous distally; adnate for half their adaxial length; pairs of hydrothecae fairly close along internode. Abcauline wall thickened just below margin.

Pinnate stems with a basal, athecate part ending in an oblique hinge joint, or with an additional segment bearing one or two pairs of subalternate hydrothecae. Above, stem divided into up to 10 regular internodes by transverse constrictions of the perisarc. Internodes geniculate, with a proximal apophysis supporting a cladium, and three hydrothecae: one in the axil formed by the apophysis with the internode, and two alternate

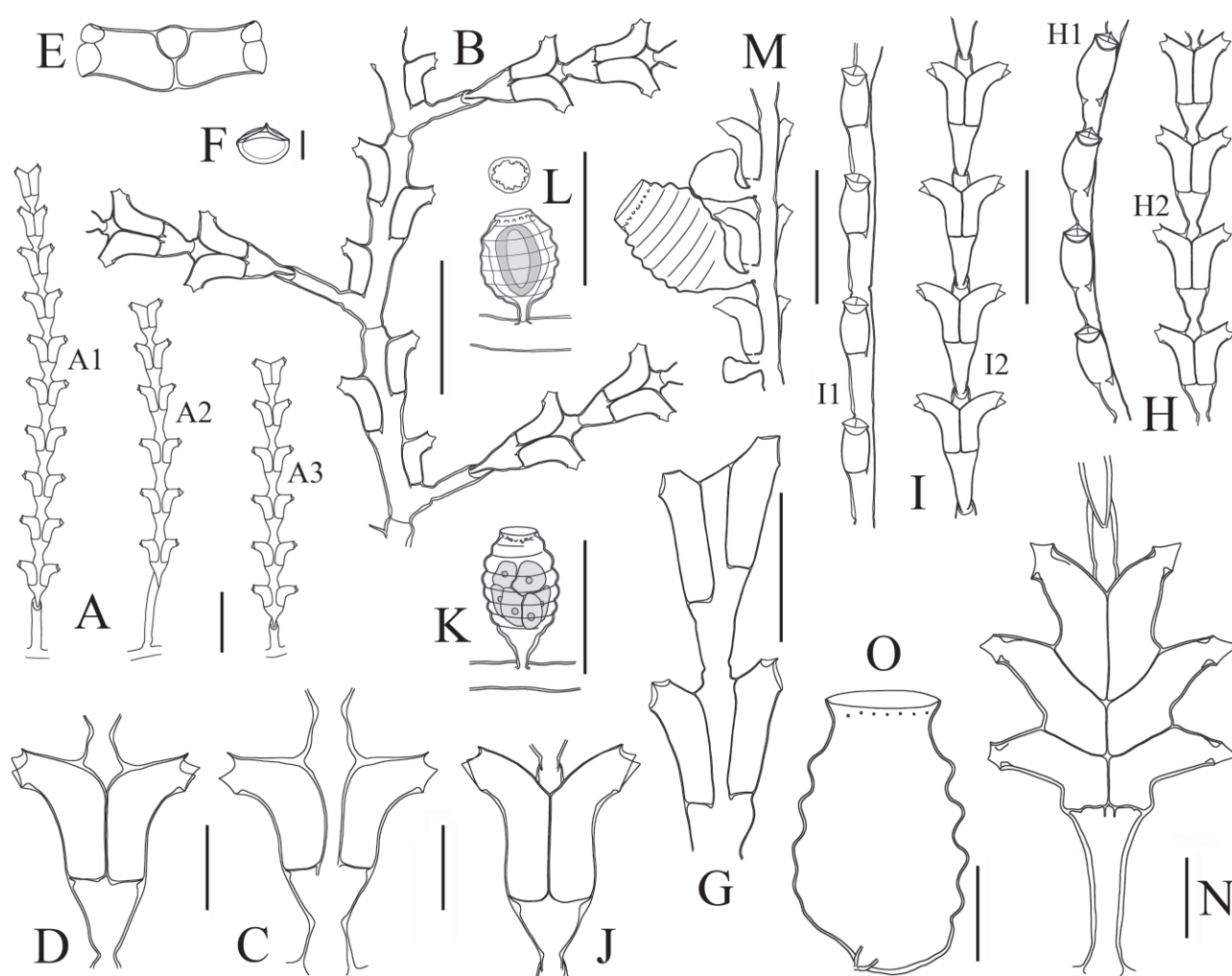


Fig. 5. A-F: *Dynamena bimorpha* sp. nov. (A) Three simple stems. (B) Detail of a pinnate stems, showing the stem internodes and the basal parts of three cladia. (C, D) Hydrothecal pairs from basalmost internode (C) and from a more distal internode (D) of a simple stem, and comparison with hydrothecae of *D. disticha* (Bosc, 1802) (J). (E) Hydrothecal pair seen from above, showing small, adaxial teeth. (F) Aperture of a hydrotheca seen frontally, showing pleated adaxial opercular flap, and a slightly larger, abaxial flap. G: Type material of *D. tropica* Stechow, 1926. H-M: *D. disticha*. (H, I) Stem from Martinique in lateral (H¹) and frontal (H²) aspect compared with stem from the Mediterranean in lateral (I¹) and frontal (I²) views. (K, L) Female (K) and male (L) gonothecae from Martinican material. (M) Gonotheca on basal part of stem from the Mediterranean. N, O: *Dynamena quadridentata* (Ellis & Solander, 1786). (N) Internode with stacked hydrothecae. (O) Gonotheca. Scale bars: 100 μ m (E, F), 200 μ m (N), 300 μ m (C, D, J, O), 500 μ m (G), and 1 mm (A, B, H, I, K-M).

above; apophyses prominent, given off alternately from opposite sides of caulus. Cladia unbranched, straight; left and right rows of cladia coplanar; there is a basal, atecate internode separated by a transverse node from the apophysis, and by an oblique node distally; remainder of cladium with exactly the same structure as the simple stems; with up to 10 pairs of hydrothecae. Stem hydrothecae adnate for two-thirds their adcauline length; abaxial wall straight basally and convex distally; adaxial wall convex medially, straight to curved in its immersed portion, then nearly straight distally. Perisarc of hydrotheca thickened toward aperture, especially on abaxial side. Aperture ovoid, facing outward and

slightly upward; margin with two prominent lateral pointed cusps, and a smaller median one adaxially. Operculum composed of a large, abaxial valve and a slightly smaller one, divided medially by crease line. Hydranth with no abaxial caecum. Gonothecae absent.

Dimensions: Simple stems up to 8 mm high; internodes 650-855 μ m long and 75-125 μ m wide at nodes; free adcauline wall of hydrotheca 175-240 μ m, adnate adcauline part 400-455 μ m, abcauline wall 340-390 μ m long, base width 130-155 μ m, aperture 125-140 μ m wide. Pinnate stems up to 2 cm high; internodes 1295-1545 μ m long and 135-220 μ m wide at nodes; apophyses 170-210 μ m long; first cladial segments 430-

Table 2. Comparison between *Dynamena bimorpha* sp. nov. and its congeners. The abbreviations used are as follows: for the stems, H (height); for the hydrotheca, AA (adnate adaxial side), FA (free adaxial side), Ad (whole adaxial side), Ab (whole abaxial side), ϕ (diameter at aperture), ϕ (diameter at aperture), L (length), W (maximum width), ϕ (diameter at aperture).

Species name	Reference(s)	Condition of stem	Stem internodes	Cladial internodes	Particulars of hydrotheca	Gonotheca	Distribution
<i>D. anceps</i> (Fraser, 1938)	Fraser (1938), Calder <i>et al.</i> (2009)	Pinnate (opposite cladia), H < 4 cm	Regular, (?) with two pairs of successive hydrothecae	No data available	Opposite though not in contact, long, tubular, adnate for 1/3 their length	Unknown	Pacific off Ecuador, Panama, Mexico
<i>D. bilamellata</i> Watson, 2000	Watson (2000)	Simple, H < 10 mm, ca. 11 pairs of hydrothecae	Each with one pair of hydrothecae, L = 336-440 μ m	No cladia	Opposite, in contact in front of stem, > 1/2 adnate, 2 prominent internal shelves, AA = 92-136 μ m, FA = 80-96 μ m, Ab = 144-160 μ m, ϕ = 60-64 μ m	Unknown	N Australia
<i>D. bimorpha</i> sp. nov.	Present study, Millard (1975)	Simple, H < 8 mm; pinnate (alternate cladia), H < 2 cm	With a proximal apophysis, an axillary hydrotheca, and 2 other subopposite thecae above	Each with a pair of opposite hydrothecae	Pairs separated to contiguous in simple stems; contiguous on cladia, FA = 175-240 μ m, AA = 400-455 μ m, Ab = 340-390 μ m, ϕ = 125-140 μ m	Unknown	Caribbean, South Africa
<i>D. brevis</i> (Fraser, 1935)	Fraser (1935), Hirohito (1995)	Simple, occasionally a branch, H < 7 mm	Each with a pair of hydrothecae	No cladia	Opposite, adnate for < 1/2, bending outward nearly at right angle with stem, AA = 180-220 μ m, ϕ = 80-100 μ m	Unknown	Japan
<i>D. cristoides</i> Lamouroux, 1824	Calder (1991)	Regularly pinnate (alternate), H < 5 cm	With a proximal apophysis, an axillary hydrotheca, and 1-3 pairs of subopposite thecae above	Of varied length, with 1-3 pairs of hydrothecae	Subopposite on cladia, elongate, tubular, deeply immersed, AA = 336-503 μ m, FA = 75-196 μ m, Ab = 317-419 μ m, ϕ = 112-121 μ m	Unknown	Circumglobal in tropical and subtropical waters
<i>D. dalmasi</i> (Versluys, 1899)	Medel & Vervoort (1998), Calder (1991)	Simple or occasionally and irregularly branched, H < 7.6 cm	Long (947-1106 μ m), with 1 opposite pair of hydrothecae distally	Structure as the stem	Pairs either separated or contiguous, cylindrical, curved outwards, Ad = 461-504 μ m, Ab = 266-336 μ m, internal cusps distinct or not	Unknown	Circumglobal in tropical and subtropical waters
<i>D. decipiens</i> (Levinson, 1913)	Levinson (1913), Watson (2000), as <i>D. mertoni</i>	Regularly pinnate (alternate), H < 2.2 cm	With a basal apophysis, an axillary hydrotheca, and two other alternating thecae above, L = 720-1160 μ m	With grouped, overlapping, multiple pairs of hydrothecae	Opposite on cladia, long, tubular, AA = 400-544 μ m, FA = 168-200 μ m, Ab = 520-544 μ m, ϕ = 120-156 μ m	Grouped on proximal stem, barrel shaped, L = 1700-1780 μ m, W = 800-900 μ m, ϕ = 480-496 μ m, corrugated to almost smooth, a slightly everted collar	India, N Australia
<i>D. dispar</i> (Fraser, 1938)	Fraser (1938), Calder <i>et al.</i> (2009)	Simple, H < 1 cm	Each with a pair of medially placed hydrothecae	No cladia	Opposite, stout for their reduced length, with fine striations	On basal part of stems, barrel shaped, L = ca. 1200 μ m, W = ca. 800 μ m, walls transversely ringed, distally truncate, aperture wide	Pacific off Ecuador, Baja California
<i>D. disticha</i> (Boss, 1802)	Calder (1991), present study	Simple, H < 1 cm	Each with a pair of hydrothecae, L = 401-895 μ m	No cladia	Cylindrical, curving outwards distally, with or without internal cusps, AA = 130-363 μ m, FA = 205-354 μ m, Ab = 270-446 μ m, ϕ = 98-140 μ m	Vasiform L = 880-1015 μ m (ϕ) and 725-815 μ m (δ), W = 545-605 μ m (ϕ) and 565-605 μ m (δ), with 5-6 spiral grooves, aperture wide, on short collar	Circumglobal in temperate to tropical seas
<i>D. fissa</i> (Thornely, 1904)	Thornely (1904), Billard (1925)	Branching irregular to dichotomous, H < 7.6 cm	No nodes, hydrothecae in well separated pairs or triplets, branches given off from before and behind a pair of thecae	Structure as the stem	Opposite, contiguous or not, stout for their reduced length, AA = 310-340 μ m, FA = 230-285 μ m, Ab = 355-385 μ m, ϕ = 105-115 μ m	On stem and branches, broadly ovoid, strongly annulated aperture large, on broad neck	Sri Lanka, Indonesia

Species name	Reference(s)	Condition of stem	Stem internodes	Cladial internodes	Particulars of hydrotheca	Gonotheca	Distribution
<i>D. griffini</i> (Hargitt, 1924)	Hargitt (1924)	Mostly simple, occasionally branched, H < 9 mm	With more than one pair of hydrothecae	When present, presumably as the stem	Cylindrical, curving outward distally, adnate for 2/3, generally in groups of two	Borne on stem internodes, urn-like, tapering below, a narrow neck, aperture rather small for the genus	Philippines
<i>D. heterodonta</i> (Jarvis, 1922)	Jarvis (1922), Billard (1925)	Simple, H < 15 mm	With one (proximally) or more (distally) pairs of opposite hydrothecae	No cladia	Cylindrical, strongly curving outwards, AA = 215-250 µm, FA = 160-240 µm, φ = 70-90 µm, submarginal cusps	Below proximal pair of hydrothecae, vasiform, with ca. 5 annular ridges, truncate distally	Cargados, Gambier, Borneo, Sumbawa
<i>D. japonica</i> Stechow, 1920	Hirohito (1995)	Pinnate (opposite), H < 20 cm	Each with a pair of cladial apophyses and 3-4 pairs of opposite hydrothecae	Varied length, 1-3 pairs of opposite hydrothecae	Pairs not contiguous, tubular, almost fully immersed in internode, Ad = 550-600 µm, φ = 200-250 µm	On hydrocladia, elongate, L = 1500-1600 µm, W = 700-800 µm, tapering below, aperture wide, on short collar	Japan
<i>D. moluccana</i> (Pictet, 1893)	Billard (1925), as <i>D. cornicina</i> ; Schuchert (2003)	Pinnate (alternate), H < 6 cm	Each with a lateral apophysis and 3 alternate hydrothecae	Each with a pair of opposite hydrothecae	Long, tubular, adnate for 2/3, AA = 375-515 µm, FA = 215-265 µm, φ = 125-180 µm, axillar hydrotheca exceedingly curved outward	On stems and stolons, urn-shaped, L = ca. 1000 µm, W = ca. 700 µm, walls smooth to undulated, aperture wide, on short distal neck	From South Africa to Marshall islands
<i>D. nanshaensis</i> Tang, 1991	Tang (1991)	Simple, H < 10 mm	Each with generally one (occasionally 2) pair(s) of hydrothecae, L = 520-540 µm	No cladia	Long, tubular, with parallel walls basally, adnate for 1/2-3/4, distal part curved outwards, AA = 210-280 µm, FA = 70-150 µm, Ab = 240-320 µm, φ = 90-110 µm	Unknown	Southern China
<i>D. obliqua</i> Lamouroux, 1816	Millard (1958, 1975), Hirohito (1995)	Simple, H < 17 mm	Irregular, each bearing generally 1 (but up to 4) pairs of opposite hydrothecae	No cladia	Opposite, less tendency towards grouping, moderately long, swollen, AA = 270-380 µm, FA = 120-160 µm, φ = 120-140 µm, submarginal cusps occasionally present	Near base of stem, barrel-shaped, with 5-8 transverse annulations, aperture broad on short neck, L = 1400-1600 µm (♀ > ♂), W = 650-700 µm	Australia, Indonesia, S Africa
<i>D. ogasawarana</i> Hirohito, 1974	Hirohito (1974)	Simple, H = ca. 2.5 mm, with 7-8 pairs of hydrothecae	Each with a pair of hydrothecae, L = ca. 300 µm	No cladia	Opposite, adnate for 1/2, free part at 60° to internode, 2 internal inconspicuous cusps, AA = 110-160 µm, FA = 110-150 µm, φ = 50-60 µm	On proximal internodes, ovoid, L = ca. 500, W = ca. 300 µm, walls smooth, distal end truncate, aperture wide, on short collar	Japan
<i>D. pumila</i> (Linnaeus, 1758)	Cornelius (1979)	Unbranched to sparsely and irregularly branched, H < 7.5 cm	Each with 1-3 pairs of hydrothecae, L = 600-920 µm (one pair)	Structure as the stem	Opposite to sub-opposite, tubular, curved outwards, 2/3 adnate	Borne on stems and branches, ovoid, wall sometimes slightly undulated, aperture wide on short neck, L = 1200-1400 (♀) and 1400-1500 µm (♂), W = 620-670 (♀) and 570-600 (♂)	Cool to temperate N Atlantic
<i>D. quadridentata</i> (Ellis & Solander, 1786)	Calder (1988), present study	Simple, H < 13 mm	Varied in length, with 1-7 pairs of hydrothecae	No cladia	Pairs of hydrothecae stacked in groups, usually with internal cusps, Ab = 168-289 µm, φ = 84-98 µm	Urn-shaped, L = 865-1000 µm, W = 500-600 µm, 4-5 transverse ridges, aperture wide (360-400 µm), on short collar	Circumglobal in tropical and subtropical waters
<i>D. spinea</i> Watson, 2005	Watson (2005)	Simple, H < 6 mm	Of varied length, comprising a succession of subopposite hydrothecae	No cladia	Pairs widely separated frontally, flask-shaped, narrowing to margin, adnate for > 1/2, AA = 137-152 µm, FA = 98-105 µm, Ab = 172-195 µm, φ = 98-105 µm	Urn-shaped, L = 1098-1235 µm, W = 672-896 µm, walls smooth, aperture flanked by two opposite horns	W Australia

545 µm long; free adcauline wall of hydrotheca 175–205 µm, base of hydrotheca 110–120 µm wide, aperture 120–135 µm wide; adnate wall of hydrotheca 330–365 µm in axillar thecae, and 415–450 µm in the others; abcauline wall of hydrotheca 275–310 µm in axillar thecae, and 340–380 µm in the others.

Distribution: Martinique (present study) and, possibly, South Africa (Millard, 1975).

Type locality: France, Martinique, Le Vauclin, Pointe Faula.

Remarks: This species was first mistaken for a peculiar variant of *D. disticha* in which, in addition to the commonest, simple stems, a pinnate growth form was also present. Both species co-occurred at the same station and on the same substrate, a floating *Sargassum*. However, a careful examination revealed that the coenosarc of the former is bright yellow, even in fixed material (a supposedly positive reaction with iodine was obtained, suggesting that it may carry zooxanthellae), while it is white to transparent in *D. disticha* [however, this species may also carry symbiotic algae, as the living specimens originally described by Bosc (1802, p. 101) exhibited a yellow tinge: “*Le tout de couleur jaune*”]. In addition, its perisarc is comparatively thicker and not collapsible like that of *D. disticha*, and its hydrothecae are less deep and much wider than in Bosc’s species (compare Fig. 5C, D with Fig. 5J).

True branched colonies were never reported in *D. disticha*, and all records assigned to this species, especially those from the Indo-Pacific, should be referred, with little doubt, to *D. moluccana* (Pictet, 1893), as already stated by Schuchert (2003). Only aberrant ramifications, but not pinnate stems, have been rarely observed in *D. disticha*, and these were given off either from within the hydrothecae (Vannucci Mendes, 1946) or from the stem, below a hydrothecal pair (Schuchert, 2003). There are, to our knowledge, two additional and rather curious records of specimens assigned to *D. disticha*, in which sparingly branched colonies occurred: one is from off the Western Sahara (Leloup, 1937) and the other from off Senegal (Picard, 1951). However, the scant data available from these accounts proved inconclusive, but one can imagine that the formation of aberrant branches, similar to those described by Vannucci Mendes and Schuchert, may have been involved.

The South African material with rather tall (up to 6 cm high), pinnate stems described by Millard (1975) under *D. cornicina* McCrady, 1859 is indistinguishable from the present species. In the specimens with simple stems studied by Millard (1964), the shape of the hydrotheca (especially its degree of curvature) varies between the basalmost and the distalmost internodes, exactly as in our material. Though not clearly stated by Millard (1975), it is assumed that gonothecae were only found in her colonies with simple stems [note that fig. 9D in Millard

(1964) was reproduced subsequently as fig. 86E in her 1975 monograph]. Reportedly, the gonothecae arise from the hydrorhiza or occasionally from the stem bases; “ovate, transversely annulated, with broad aperture and flat operculum, reaching 1.4 mm in length and 0.9 mm in maximum diameter” (Millard, 1975).

The main distinguishing features between *D. bimorpha* and its relatives are summarized in Table 2.

Unlike *D. bimorpha*, two congeners, *D. anceps* (Fraser, 1938) and *D. japonica* Stechow, 1920, form pinnate stems with opposite side branches. In contrast, three other species form pinnate colonies with alternate side branches: *D. crisioides* Lamouroux, 1824, *D. decipiens* (Levinsen, 1913), and *D. moluccana* (Pictet, 1893). In the former, the hydrothecae are alternately placed on the hydrocladia, and not oppositely, as in the present hydroid; in the second, the two rows of cladial hydrothecae are displaced to one side, recalling the genus *Hydrallmania* Hincks, 1868 [see also below the remarks on the material assigned to *Sertularia mertonii* Stechow, 1923 by Watson (2000)]; in the third, the axillar hydrotheca is conspicuously bent outwards, the stem internodes are longer, as well as the distance between the hydrothecae they carry (Galea, personal observations on Indonesian material).

The typically dichotomous branching pattern of the stems of *D. fissa* (Thornely, 1904) gives the colonies the appearance of loose, tangled masses (Billard, 1925). Although the stems of *D. pumila* (Linnaeus, 1758) may adopt a simple appearance, they are mostly branched irregularly to occasionally loosely pinnately, and the hydrothecae are set in strictly opposite pairs on both the stems and side branches (Cornelius, 1979).

Unlike *D. bimorpha*, the following nominal species with exclusively simple stems show a more or less pronounced tendency for grouping of their pairs of hydrothecae: *D. obliqua* Lamouroux, 1816, *D. nanshaensis* Tang, 1991, *D. griffini* (Hargitt, 1924), *D. heterodonta* (Jarvis, 1922), and *D. quadridentata* (Ellis & Solander, 1786). Their taxonomic status, especially with respect to the latter nominal species, is uncertain, as most exhibit more or less pronounced morphological intergradations, with no clear cut distinction between them.

The hydrothecae of *D. bilamellata* Watson, 2000 are characterized by the presence of two conspicuous, internal, ad- and abcauline shelves (Watson, 2000).

According to the latest available description (Hirohito 1995), the hydrothecae of *D. brevis* (Fraser, 1935) appear comparatively smaller and less deep than those of *D. bimorpha*; though generally unbranched, a specimen with a lateral branch, given off from below a pair of stem hydrothecae and similar in structure to the caulus, was reported by Hirohito.

The most distinctive feature of *D. dalmasi* (Versluys, 1899) lies in its long stem internodes, each bearing a hydrothecal pair distally (Vervoort, 1959, as *D. mayeri*; Calder, 1991; Medel & Vervoort, 1998). Some colonies

may be branched irregularly (Medel & Vervoort, 1998). The original account on *D. dispar* (Fraser, 1938) offers few distinguishing traits for this species, except perhaps the fact that the hydrothecae are stout for their length, apparently less deep than those of *D. bimorpha* [compare fig. 62A, B in Fraser (1938) with our Figs 5A-D]. Calder *et al.* (2009), who reexamined the type, added that their surface was covered with fine striae.

Dynamena ogasawarana Hirohito, 1974 is a much smaller species (see Table 2), and its gonothecae are smooth-walled, thus differing from those illustrated by Millard (1964).

Dynamena spinea Watson, 2005 lacks regular nodes, each equivalent of internode being rather long, increasing in diameter distally, where it merges imperceptibly into a pair of subopposite hydrothecae. The laterally flattened gonotheca exhibits two peculiar, lateral horns flanking a distal aperture (Watson, 2005), suspiciously recalling the gonotheca of *Amphisbetia olsenii* Watson, 1973 (see original description of the latter; note also several common features of their respective trophosomes).

Through the courtesy of B. Ruthensteiner of the Zoologische Staatssammlung of Munich, Germany, one of us (HRG) was provided with several photomicrographs of the type of *D. tropica* Stechow, 1926 (a line drawing derived from one of them is illustrated here in Fig. 5G). There is no doubt that these two pairs of hydrothecae belong to a colony of *D. crisioides*. Consequently, *D. tropica* should be regarded as a junior synonym of Lamouroux' (1824) species.

As a final remark, we would like to draw readers' attention concerning a possible misidentification of a poorly known species, *D. decipiens*, mentioned above in this work. Indeed, Watson (2000) assigned material from North Australia to *Sertularia mertoni* Stechow, 1923, using a genus transfer to *Dynamena* Lamouroux, 1812. However, according to Stechow, his species gives off only a few cladia, and this in a very irregular manner (every 8-35 stem hydrothecae, a 6-cm high stem having at most 4 cladia), while the Australian material possesses stems with a regular structure, each internode bearing 3 hydrothecae and a cladial apophysis. In addition, Stechow stated that there was apparently an abaxial caecum, which justifies the assignment of his species to *Sertularia*. His measurements of the hydrothecae suggest that they are about two times smaller than those in Watson's material. Only the structure of cladia, characterized by a *Hydrallmania*-like insertion of the hydrothecae, is shared by the two species. It is likely that Watson's material belongs instead to *D. decipiens* (Levinsen, 1913), originally described from India. Indeed, among their common features, the following ones are noteworthy: 1) colonies in both materials have the same size (*ca.* 2 cm high); 2) the stems are regularly pinnate, each internode bearing a lateral apophysis and 3 hydrothecae; 3) there is often one pair (occasionally two) of opposite cladia in the basalmost segmented part

of the stem; 4) the cladial internodes are composed of 1-4 hydrothecae; 5) the thecae are characteristically stacked and shifted on to one side of the internode; they are long, tubular, adnate for 2/3rd their length, their free part curving outwards. No morphological differences could be noted between Watson's fig. 12 C & D and Levinsen's figs 12 & 11 (Pl. IV), respectively. Note also that there is at least another, earlier record of *D. decipiens* from Australia (Jäderholm, 1916).

Dynamena disticha (Bosc, 1802)

Fig. 5H-M

Material examined: HRG-0868; sample #M153; France, Martinique, Schoelcher, off Madiana Beach, 14.61142° -61.09922°, 2-4 m; 06.02.2012; male and female colonies on *Syringodinium* sp. – HRG-0869; sample #M314; France, Martinique, Le François, Pointe Jacob, 14.58552° -60.84993°, 0 m; 18.02.2014; fertile colonies, sex undeterminable (gonothecae already spent), on floating *Sargassum* sp. – HRG-0573; France, Cassis, Port Pin creek, 43.20323° 5.51105°, 0-1 m; 13.07.2011; fertile colony (sex undeterminable, gonothecae spent) on mineral concretions and algae.

Description: Refer to Calder (1991).

Dimensions: Female gonotheca 880-1015 µm high, 545-605 µm in maximum diameter, 245-280 µm wide at aperture. Male gonotheca 725-815 µm high, 565-605 µm in maximum diameter, 265-290 µm wide at aperture.

Distribution: Circumglobal in tropical, subtropical and temperate waters (Peña Cantero & García Carrascosa, 2002). The Caribbean records are summarized by Calder & Kirkendale (2005).

Remarks: Galea (2008) described aberrant gonothecae arising from within the hydrothecae in specimens from Guadeloupe. Subsequently, fertile material of both sexes became available from Martinique. There is a slight sexual dimorphism in the gonothecae, with the females being a bit longer than the males (see measurements below).

It is interesting to note that, in the populations of *D. disticha* from the western Atlantic, the gonothecae arise in groups from the stolons, close to the origin of stems, as illustrated by specimens from Brazil (Miranda *et al.*, 2011), Colombia (Flórez González, 1983, as *D. cornicina*), Caribbean Sea (Leloup, 1935, as *D. cornicina*; present study, Fig. 5K, L), Gulf of Mexico (Defenbaugh & Hopkins, 1973), and the Atlantic coast on North America (Nutting, 1904; Fraser, 1912; 1944; all as *Sertularia cornicina*). Some records from the eastern Pacific, as for instance those from California (Fraser, 1937a, as *S. cornicina*), equally mention stolonial gonothecae.

Conversely, in the populations from the eastern side of the Atlantic, the gonothecae appear to be given off mostly from the lower stem internodes, as illustrated by specimens from Mediterranean (Neppi, 1917, as *Disertasia cavolini*; Peña Cantero & García Carrascosa, 2002; present study, Fig. 5M), the Strait of Gibraltar (Medel Soteras *et al.*, 1991), Mauritania (Medel & Vervoort, 1998), and Morocco (Patrioti, 1970, as *D. cornicina*).

Only in rare instances, gonothecae on both the stolon and the basal part of the stems were reported, as in material from Mediterranean (Gili i Sardà, 1986, as both *D. cornicina* and *D. cavolinii*; Vervoort, 1993a), Brazil (Migotto, 1996), and Japan (Hirohito, 1995). However, none of these accounts states whether or not the gonothecae occurred simultaneously at both sites within the same or on different colonies.

A comparison of stems from Martinique (Fig. 5H) and the Mediterranean (Fig. 5M) failed to show any significant morphological difference, except perhaps for slight variations in the length of internodes and the dorsal immersion of the hydrothecae in their corresponding internodes, but these variations are far from unusual in this rather variable species.

Dynamena quadridentata (Ellis & Solander, 1786)

Fig. 5N, O

Material examined: MHNG-INVE-91112; sample #M314; France, Martinique, Le François, Pointe Jacob, 14.58552° -60.84993°, 0 m; 18.02.2014; sterile and fertile (sex undeterminable, gonothecae spent) colonies on floating *Sargassum* sp.

Description: See Millard (1975).

Distribution: Circumglobal in tropical, subtropical and temperate waters (Vervoort 1993b). The Caribbean records are summarized by Calder & Kirkendale (2005).

Remarks: For a redescription of this species, refer to Millard (1975) and Hirohito (1995).

Genus *Sertularia* Linnaeus, 1758

Sertularia distans (Lamouroux, 1816)

Fig. 6A-C

Material examined: MHNG-INVE-91120; sample #M327; France, Martinique, Le Vauclin, Pointe Faula, 14.54064° -60.82837°, 0 m; 23.02.2014; male colony on floating *Sargassum* sp.

Description: See Calder (1991).

Distribution: Circumglobal in tropical, subtropical, and temperate waters (Calder, 2013).

Remarks: For a description of this species, refer to Calder (1991) and Hirohito (1995).

Sertularia hattorii Leloup, 1940

Fig. 6D, E

Sertularia hattorii Leloup, 1940: 3, fig. 3. – Yamada, 1959: 71. – Okada *et al.*, 1965: 206, fig. 136. – Rho & Chang, 1972: 8, pl. 5 figs 18-20; 1974: 144. – Park & Rho, 1986: 24. – Park, 1992: 291; 1993: 269; 2010: 112, fig. 62. – Hirohito, 1995: 209, fig. 69.

Sertularia notabilis Fraser, 1947: 11, pl. 2 fig. 5. – Migotto & Vervoort, 1998: 89, figs 1-14. – Galea, 2008: 35, fig. 6J, K.

Caminothuiaria moluccana – Vannucci Mendes, 1946: 569, fig. 39 (not *Caminothuiaria molukkana* Von Campenhausen, 1896).

Material examined: MHNG-INVE-91115; sample #M324; France, Martinique, La Trinité, Anse Cosmy, 14.75829° -60.96594°, 0 m; 23.02.2014; fertile colony (gonothecae spent, sex unidentifiable, stems with 1-4 pairs of hydrothecae) on floating *Sargassum* sp. – HRG-0104; France, Guadeloupe, Les Saintes, Terre-de-Haut, 15.862500° -61.59972°, 0.5 m; 25.03.2008; sterile colony on alga.

Description: For a comprehensive account, see Migotto & Vervoort (1998).

Distribution: Japan (Hirohito, 1995), Korea (Park, 2010), Brazil (Migotto & Vervoort, 1998), Caribbean Sea (present study).

Remarks: The characteristic shape of the hydrothecae and the presence of internal, submarginal cusps, allowed Galea (2008) to find sterile specimens from Guadeloupe in complete agreement with a redescription of *Sertularia notabilis* Fraser, 1947 by Migotto & Vervoort (1998), based on specimens from Brazil. The occurrence of gonothecae in the present material from Martinique, and its comparison with the former, sterile sample, confirms that both are conspecific.

Migotto & Vervoort raised the question about the relationships between Fraser's hydroid and the nominal species *S. hattorii* Leloup, 1940. The former was described based on specimens from the Caribbean, while the second was based on Japanese material. Both exhibit several common features: 1) the basal stem internodes bear either an unpaired hydrotheca or subopposite (or even alternate) hydrothecae; 2) the remainder of cauli bear internodes with a rather typical shape, conferred by the proximal placement of the hydrothecal pair; 3) the thecae characteristically narrow from base to aperture, and face obliquely upwards; 4) the gonothecae are huge, deeply ringed, and curved in middle.

Despite these evidences, Migotto & Vervoort refrained from synonymizing both nominal species, on account of the absence of intrathecal cusps and the occasional presence of side branches in Asian specimens (Leloup, 1940; Hirohito, 1995).

However, it should be noted that the material inspected by Migotto & Vervoort (1998) comprised only minute stems

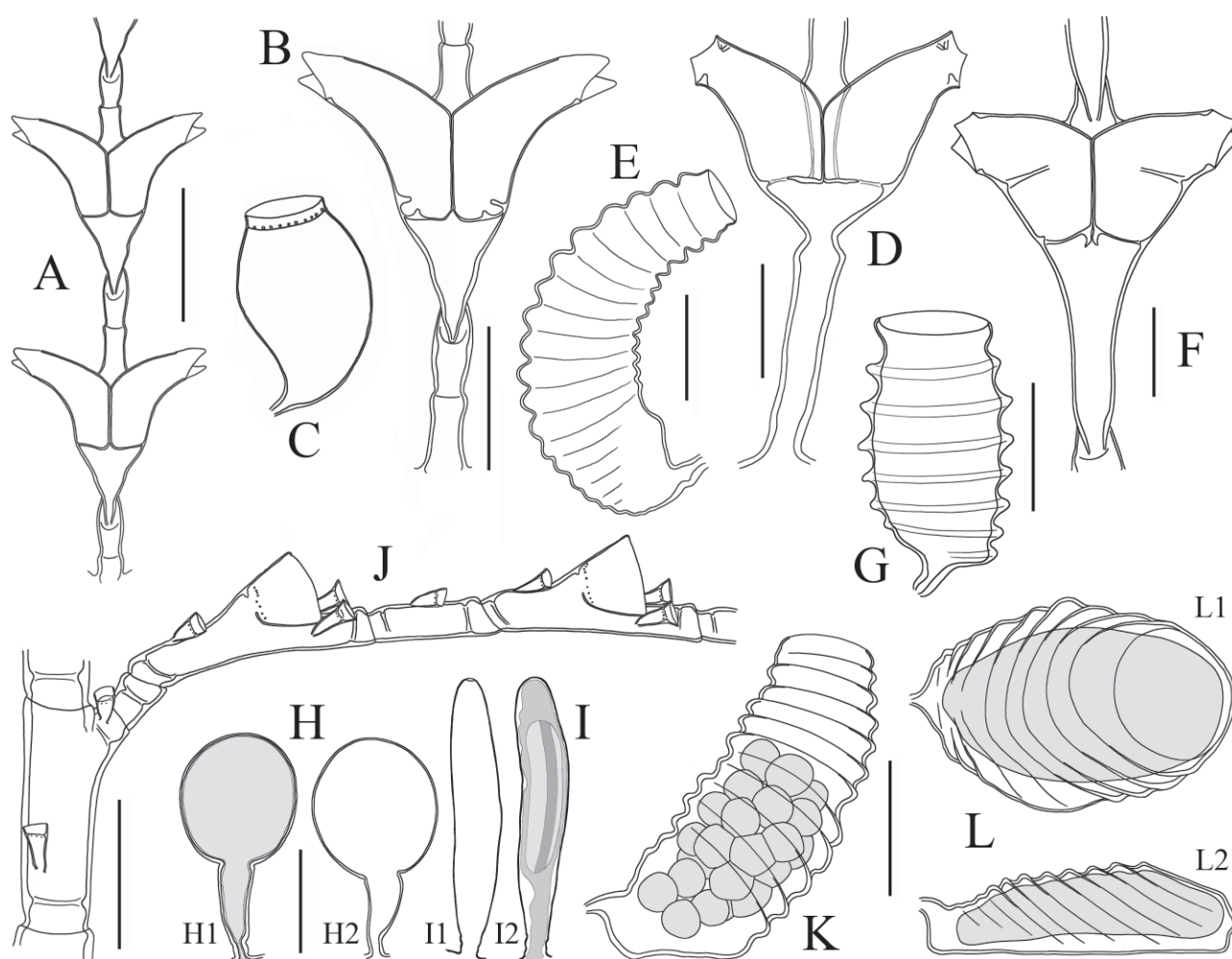


Fig. 6. A-C: *Sertularia distans* (Lamouroux, 1816). (A) Two stem internodes. (B) Detail of an internode, showing hydrothecal pair. (C) Gonotheca. D, E: *Sertularia hattorii* Leloup, 1940. (D) Internode with hydrothecal pair. (E) Gonotheca. F, G: *Sertularia turbinata* (Lamouroux, 1816). (F) Internode with hydrothecal pair. (G) Gonotheca. H, I: *Hincksella pusilla* (Ritchie, 1910). (H) Two female gonothecae, one of them showing its gonophore (H¹). (I) Two male gonothecae, one of them showing its gonophore (I²). J-L: *Plumularia strictocarpa* Pictet, 1893. (J) Stem internode and basal part of a cladium. (K) female gonotheca in lateral view. (L) Male gonotheca seen from above (L¹) and laterally (L²). Scale bars: 200 μ m (B, D, F, J), 300 μ m (A, C), 500 (E, G-I, K, L).

bearing generally 2-5 (at most 8) pairs of hydrothecae, and it is not surprising that no lateral branches were formed in such small colonies. Conversely, Leloup had material with slightly taller stems, bearing up to 10 internodes, in which sparing, incipient side branches appeared. Even taller stems were present in the material studied by Hirohito (according to his fig. 69A, the highest stems must have had at least 13 hydrothecae), and some of them exhibited distinct side branches, although their presence was, by far, not the rule.

As for the presence or absence of intrathecal cusps, this is possibly not a species-specific feature. Indeed, such variations are well documented, not only among other members of the genus {e.g. *S. distans* (Lamouroux, 1816) [see Millard (1975)]}, but also within the family Sertulariidae {e.g. *Dynamena crisioides* Lamouroux,

1824 [see Millard (1975)]; *D. disticha* (Bosc, 1802) [see Calder (1991)]; *Symplectoscyphus unilateralis* (Lamouroux, 1824) [see Galea *et al.* (2014)]}.

In view of the arguments provided above, we believe that the occurrence of intrathecal cusps alone does not justify the specific separation of *S. notabilis* from *S. hattorii*, the latter nominal species having priority.

Sertularia turbinata (Lamouroux, 1816)

Fig. 6F, G

Material examined: MHNG-INVE-91113; sample #M314; France, Martinique, Le François, Pointe Jacob, 14.58552° -60.84993°, 0 m; 18.02.2014; fertile colony (sex unidentifiable) on floating *Sargassum* sp.

Description: See Millard (1975).

Distribution: Guadeloupe and Martinique should be added to the previous Caribbean records given by Calder & Kirkendale (2005). Worldwide, the species occurs in warm waters of the Atlantic, Pacific and Indian oceans (Calder *et al.*, 2003).

Remarks: Only sterile material assigned to this species was reported earlier by one of us (Galea, 2008) from Guadeloupe. The finding of fertile material in Martinique, and comparison with the former specimens, confirms the previous identification. In spite of the numerous world records of this species [see Medel & Vervoort (1998)], its gonothecae were reported only a few times in the literature, *e.g.* Vervoort (1959), Millard (1975), Hirohito (1995).

**Family Syntheciidae Marktanner-Turneretscher,
1890**

Genus *Hincksella* Billard, 1918

***Hincksella pusilla* (Ritchie, 1910)**

Fig. 6H, I

Sertularella cylindrica var. *pusilla* Ritchie, 1910: 817, pl. 77 fig. 9.

Hincksella cylindrica. – Galea, 2010a: 20, fig. 5N-P (synonymy) (not *Sertularella cylindrica* Bale, 1888: 765, pl. 16 fig. 7).

Material examined: HRG-0900; sample #M235; France, Martinique, Le Diamant, 14.44231° -61.03969°, 10-13 m; 20.02.2012; female colony on sponge. – HRG-0901; sample #M326; France, Martinique, Le Vauclin, Pointe Faula, 14.54064° -60.82837°, 0 m; 23.02.2014; male colony on floating *Sargassum* sp.

Description: The trophosome of this species is accurately described by Calder (1991).

Dimensions: Male gonothecae 1030-1360 µm long and 210-260 µm wide. Female gonothecae 625-675 µm long and 565-600 µm wide; pedicel 430-440 µm high.

Distribution: A comprehensive list of world records is given in Galea (2010a). *Hincksella cylindrica* sensu stricto is known exclusively from Australia (Bale, 1888; Ritchie, 1911; Pennycuik, 1959; Watson, 2002; Precker & Lawn, 2010).

Remarks: In the absence of critical comparisons with specimens of *Hincksella cylindrica* (Bale, 1888) from Australia, many accounts, including recent ones (*e.g.* Calder, 1991; Galea, 2010), have considered the widespread variety *pusilla* Ritchie, 1910 as a dwarfed form of the nominal species. Recently, we came across a paper by Precker & Lawn (2010) which includes a modern redescription and a photomicrograph of *H. cylindrica*, supplementing an earlier account by

Watson (2002). This prompted us to raise awareness of the taxonomic status of Bale's species.

Indeed, the hydrothecae of *H. cylindrica* sensu stricto are large [see Ritchie (1911); Precker & Lawn (2010)], stout, and adnate for at least half their adcauline length, while those of the "variety" *pusilla* are comparatively slender, more elongate, and adnate for only one-third to one-quarter [see measurements in Galea (2010a), p. 22, Table 2]. In our opinion, these are sufficient arguments to raise the variety *pusilla* to species, as *H. pusilla* (Ritchie, 1910).

Precker & Lawn provided the first description of the gonothecae of *H. cylindrica* sensu stricto which, in their material, arose from within the hydrothecae, with only their distalmost part becoming free from the theca. Their club shaped appearance (*ca.* 1280 µm long and 280 µm wide) suggests that they were probably male.

Although Precker & Lawn were able to note obvious morphological differences between their specimens of *H. cylindrica* and *H. cylindrica pusilla* from Moreton Bay, Queensland, they refrained from separating them specifically, on account of the absence of gonothecae in specimens of the latter. However, descriptions and/or morphometric data are available in several works, *e.g.* Torrey (1902; 1904, both as *Sertularella halecina*), Hirohito (1969; 1995), Millard & Bouillon (1975).

Similar data are also gathered from the examination of the material in hand, which comprises colonies of both sexes. The male gonothecae (Fig. 6I) arise from the stolon and are club shaped; their perisarc is very thin and easily collapsible. The female gonothecae (Fig. 6H), also arising from the stolon, are mounted on long pedicels, and are slightly ovoid to nearly spherical; their perisarc is comparatively thicker, and their lumen contains a single, large oocyte occupying the whole cavity of the theca.

Male gonothecae of the so called variety *pusilla* arising from within the hydrothecae [Torrey (1902, pl. 7 fig. 56B; 1904, fig. 14), Hirohito (1969, fig. 12B)] do not differ in shape from those of *H. cylindrica*, as described and illustrated by Precker & Lawn, and their dimensions are also similar [*e.g.* (630-1500) × (180-380) µm, according to Hirohito (1969)].

Consequently, it is realized that the male gonothecae in both species do not offer sufficient morphological criteria to allow a specific separation. The discovery of female gonothecae in *H. cylindrica* will possibly provide an additional discriminating factor but, for the time being, the characters of the hydrotheca appear sufficient enough to allow reliable identifications.

Family Plumulariidae McCrady, 1859
Genus *Plumularia* Lamarck, 1816

***Plumularia strictocarpa* Pictet, 1893**

Fig. 6J-L

Plumularia sp. – Galea, 2008: 46, fig. 9J.

Material examined: MHNG-INVE-91106; sample #M274; France, Martinique, Anse Dufour, 14.52716° -61.09003°, 0-1 m; 12.01.2014; male and female colonies on benthic *Sargassum* sp.

Description: See Hirohito (1995) and Migotto (1996).

Distribution: Circumglobal in tropical and subtropical seas. The Caribbean records are summarized by Calder & Kirkendale (2005).

Remarks: Comparison of the present material with the infertile stems of *Plumularia* sp., described and figured by Galea (2008, p. 46, fig. 9J) from Guadeloupe, showed that both are conspecific. The male gonothecae are fully appressed to their substrate (Fig. 6L²), while only the basal part of the female is in contact with it (Fig. 6K).

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

***Antennella quaterna* Galea, sp. nov.**

Fig. 7A-G

Antennella gracilis (pro parte). – Nutting, 1900: 77 (not *A. gracilis* Allman, 1877).

Antennella quadriaurita. – Stechow, 1919: 113. – Deevey, 1954: 271. – Spracklin, 1982: 246, fig. 116I. – Lalana *et al.*, 2001: 160. – Castellanos Iglesias *et al.*, 2009: 98. – Henry, 2011: 69.

Antennella aff. *quadriaurita*. – Galea, 2013: 29, fig. 7K-N.

not *Antennella quadriaurita*. Ritchie, 1909: 92, fig. 9.

not *Antennella quadriaurita*. – Calder, 1997: (= ? *Monostaechas* sp.).

Holotype material: MHNG-INVE-91103; sample #M076; France, Martinique, Case-Pilote, 14.63753° -61.13974°, 9-15 m; 27.01.2012; fertile (female) colony on stem of *Thyroscyphus marginatus* (Allman, 1877).

Paratype material: MHNG-INVE-91104; sample #M076; France, Martinique, Case-Pilote, 14.63753° -61.13974°, 9-15 m; 27.01.2012; sterile colonies on three stems of *T. marginatus*.

Additional material: MHNG-INVE-91125; part of sample H5 GS08; United Kingdom, Gough Island, -40.34485° -9.87765°, 10-17 m; 29.01.2014; part of a male colony with stems up to 5 cm high growing on cluster of serpulid tubes. – MHNG-INVE-91126; part of sample #BAS JR287 DB 12-0293; United Kingdom, offshore station between Inaccessible and Nightingale islands, -37.31° -12.49°, 200 m; 23.05.2013; up to 5.5 cm high stems on gorgonian axis, some bearing either female or both male and female gonothecae. – MHNG-INVE-91127; part of sample #BAS JR287 DB 12-0420; United Kingdom, off the eastern coast of Tristan da Cunha, -37.12° -12.21°, 90 m; 25.05.2013; up to 3.5 cm high stems on octocoral, some bearing

female gonothecae. – BAS JR287 DB 12-0073; United Kingdom, off the northern coast of Gough Island, -40.26° -9.93°, 120 m; 20.05.2013; female colony with 7-8 cm high stems, on shell gravel; – BAS JR287 DB 12-0260; United Kingdom, offshore station between Inaccessible and Nightingale islands, -37.34° -12.5°, 180 m; 23.05.2013; female colony composed of up to 6 cm high stems, on dead gorgonian.

Diagnosis: *Antennella* with heteromerous segmentation of stem; hydrothecate internodes short, carrying a hydrotheca, a mesial nematotheca, as well as two pairs of laterals; ahydrothecate internodes comparatively longer, with 3-4 frontal nematothecae in 2 parallel, closely-set rows. Gonothecae typical of the genus. Cnidome comprising a seed-shaped heteroneme, a microbasic mastigophore, and a large, ovoid heteroneme.

Etymology: From the Latin *quaterni*, *ae*, *a*, meaning constantly four, with reference to the presence of a double pair of lateral nematothecae flanking each hydrotheca.

Description: Colonies comprising short, upright shoots arising from creeping hydrorhiza. Basal part of stems of varied length, composed of 1-3 internodes delimited by transverse constrictions of the perisarc, distalmost node oblique; a varied number of frontal nematothecae in two parallel, closely-set rows. Remainder of stem heteromerously segmented by alternating oblique and transverse nodes, the latter slightly marked. Hydrothecate internodes, up to 6 per stem, with proximal oblique and distal transverse nodes; short, so as to accommodate a hydrotheca placed in middle, and its 5 associated nematothecae: a mesial one, far below the hydrothecal base, and two pairs of laterals. External pair borne on well-developed apophyses; trumpet-shaped, basal chamber high, upper chamber shallow, rim sinuous adaxially. Internal pair sessile, rim of upper chamber even. Hydrotheca cup-shaped, axis oblique to that of internode; perisarc thin; adcauline wall adnate for 2/3rd its length; free part and abcauline wall parallel; margin circular, rim even. Ahydrothecate internodes comparatively longer than their hydrothecate counterparts; proximal node transverse, distal node oblique; 3-4 frontal nematothecae in two parallel, closely-set rows. Gonothecae, female in present material, pear shaped, given off singly from below a hydrotheca through a short apophysis, followed by a quadrangular segment; basal part tapering abruptly, provided with two bithalamic nematothecae; aperture distal, rounded, closed by watch glass-shaped lid. Nematocysts: seed-shaped heteronemes, microbasic mastigophores, as well as large, ovoid heteronemes with shaft spanning about half the length of the capsule.

Dimensions: Stems up to 5 mm high. Thecate internodes 270-310 µm long, athecate internodes 340-

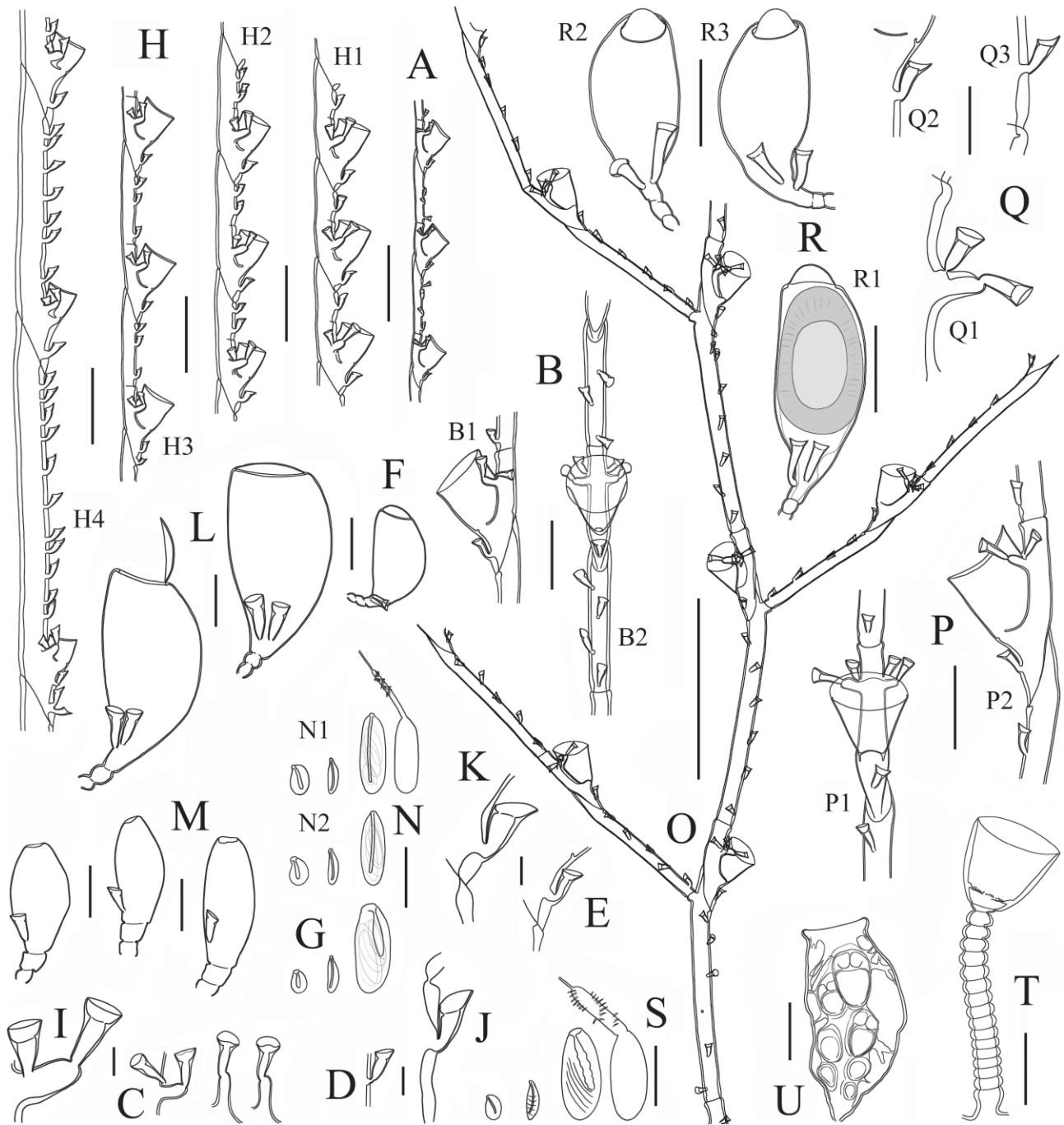


Fig. 7. A-G: *Antennella quaterna* sp. nov. (A) Fragment of stem compared with its homologues from *A. quadriaurita* Ritchie, 1909 [samples H5-GS08 (H¹⁻²), DB 12-0260 (H³), and DB 12-0073 (H⁴)]. (B) Hydrothecate segment in lateral (B¹) and frontal (B²) views. (C-E) Lateral (C), caulinar (D), and mesial (E) nematothecae compared with their homologues from *A. quadriaurita* (I, J, and K, respectively). (F) Female gonotheca compared with two female (L, both from sample DB 12-0260) and three male (M, all from sample H5-GS08) gonothecae of *A. quadriaurita*. (G) Cnidome compared to that of two samples of *A. quadriaurita* [H5-GS08 (N¹) and DB 12-0420 (N²)]. O-S: *Monostaechas bertoti* sp. nov. (O) Fragment of cormoid, showing the heteromerous segmentation of both caulus and cladia. (P) Hydrothecate internode in frontal (P¹) and lateral (P²) views. (Q) Nematothecae: pair of laterals (Q¹), mesial (Q²), and from cauline ahydrothecate internode (Q³). (R) Three gonothecae, one of which containing a female gonophore (R¹). (S) Cnidome. T, U: *Clytia edentula* Gibbons & Ryland, 1989. (T) Hydrotheca atop its pedicel. (U) Gonotheca carrying medusa buds. Scale bars: 10 μ m (G, N, S), 50 μ m (C-E, I-K), 100 μ m (Q), 200 μ m (B, F, L, M, P, R), 300 μ m (T, U), 500 μ m (A, H), 1 mm (O).

560 μm long and 45-60 μm wide at node. Abcauline wall of hydrotheca 130-175 μm long, free part of adcauline wall 90-95 μm , adnate part 140-160 μm ; diameter at rim 175-185 μm . Gonotheca 400-415 μm long and *ca.* 200 μm wide; aperture *ca.* 100 μm wide; pedicel 30-40 μm long. Seed-shaped heteronemes *ca.* 4.2 \times 2.6 μm ; microbasic mastigophores *ca.* 6.4 \times 2.2 μm ; large, ovoid heteronemes 14.08-16.05 μm long (14.83 \pm 0.54 μm , n=20) and 5.63-6.61 μm wide (5.99 \pm 0.28 μm , n=20).

Distribution: Cuba (Stechow, 1919), Gulf of Mexico (Deevey, 1954), Belize (Spracklin, 1982; Henry, 2011), Cuba (Lalana *et al.*, 2001; Castellanos Iglesias *et al.*, 2009), and Martinique (present study).

Type locality: France, Martinique, Case-Pilote.

Remarks: Stechow (1919), who reexamined Nutting's (1900) Cuban material assigned to *A. gracilis* Allman, 1877, noted that two pairs of lateral nematothecae flanked each hydrotheca ("überall zwei Nematophoren nebeneinander saßen"). He found that material in perfect agreement with *A. quadriaurita* Ritchie, 1909, and identified it as so. There is neither a description nor figures for the Cuban material but, owing its geographical distribution, it is thought to belong to *A. quaterna* sp. nov.

In a recent paper, one of us (Galea, 2013) assigned, with a query, the present material to Ritchie's species, pending a wider study based on specimens from the type locality (Gough Island), as well as from various locations around the world, in order to clarify the taxonomic status of those records. A first comparison with a specimen of *A. quadriaurita* from Inaccessible Island (see Galea, 2010b) made it possible to point out differences in the size of hydro- and nematothecae, as well as a dissimilar cnidome composition (Galea, 2013).

By a fortuitous coincidence, one of us (HRG) was entrusted for identification with several hydroid samples from both shallow- and deep-water stations around the Tristan da Cunha group of islands, among which several contain fertile specimens of *A. quadriaurita*. As noted by Ritchie (1909), the stems of his species grow in dense tufts from a reduced base, being characteristically "hairlike and stand out rigidly from a creeping stolon like a group of stiff bristles". Their height may reach as much as 7-8 cm high.

Microscopically, their internodes, hydrothecae, and gonothecae are comparatively of larger proportions than those of *A. quaterna*. The colonies from littoral stations (*e.g.* H5 GS08) have short (210-395 μm) ahydrothecate internodes carrying one or two nematothecae (Fig. 7H¹), while those from deep-water localities (*e.g.* DB 12-0260) possess longer (320-890 μm) internodes, bearing 3-4 nematothecae in two parallel, closely-set rows (Fig. 7H³). An extreme situation is met with in sample DB 12-0073, in which several consecutive basal ahydrothecate

internodes are exceedingly long (up to 1690 μm) and carry up to 12 nematothecae (Fig. 7H⁴).

The hydrothecae are large, with an abcauline wall 220-275 μm long, a free adcauline wall 90-120 μm long, an adnate part 170-220 μm long, and an aperture 200-270 μm wide (pooled data from measurements taken from several samples). The female gonothecae (Fig. 7L) are borne on short (75-90 μm), quadrangular pedicels, and are 725-780 μm long and 350-460 μm wide, with a 200-250 μm wide aperture. The male gonothecae (Fig. 7M) are also borne on short pedicels (75-90 μm), and are 390-515 μm long and 170-235 μm wide; they carry generally a single nematotheca basally, but either none or up to two may occur in rare instances.

Besides the seed-shaped microbasic heteronemes and the banana-shaped microbasic mastigophores, also common to *A. quaterna*, the cnidome of *A. quadriaurita* comprises a large, ovoid heteroneme, 11.26-13.94 μm long (12.74 \pm 0.75 μm , n=20) and 3.66-4.36 μm wide (4.01 \pm 0.24 μm , n=20), with a long, diagonal shaft spanning the whole length of the capsule. These capsules are more tubular and comparatively smaller than those of the new species (compare Fig. 7G and 7N), and their shaft is almost as long as the capsule itself.

Taken together, the features listed above show that *A. quadriaurita* is a species of larger proportions and has a cnidome that is different from that of the Martinican hydroid, thus justifying their specific separation. In addition, it appears that – besides their general resemblance – both species could confidently be separated only using morphometric data and through the study of their cnidomes. It becomes therefore obvious that the actual geographical distribution of *A. quadriaurita* could not be evaluated properly, with the exception of the West and South African records, but perhaps not of those from India, Korea, Japan or New Zealand [a list of world records is summarized by Vervoort & Watson (2003)]. For the time being, only the records from the Caribbean and the Gulf of Mexico that were assigned earlier to Ritchie's species are kept in *A. quaterna*.

The Brazilian material assigned to *A. quadriaurita* by Grohmann *et al.* (2003) has stems reaching up to 4.8 cm high and its cnidome contains the same heteronemes as the specimens from Tristan da Cunha area (P. Grohmann, *pers. comm.*). In addition, the dimension of its hydrothecae, calculated from their fig. 2, corresponds to the present concept of Ritchie's species.

Genus *Monostaechas* Allman, 1877

Monostaechas bertoti Galea & Ferry, sp. nov.

Fig. 7O-S

Holotype material: MHNG-INVE-91122; sample #M334; France, Martinique, Case-Pilote, Fond Boucher, 14.65536° -61.15657°, 12-14 m; 24.06.2014; fertile

colony on alga, some stems with female gonothecae, mostly immature, though some ripe are also present.

Paratype material: MHNG-INVE-91123; sample #M334; France, Martinique, Case-Pilote, Fond Boucher, 14.65536° -61.15657° 12-14 m; 24.06.2014; colonies on three fragments of algae, some stems with female gonothecae, as above.

Diagnosis: *Monostaechas* with monosiphonic stems, giving off laterally to irregular or alternately-placed cladia; segmentation heteromerous on both stem and cladia; hydrothecae with two pairs of lateral nematothecae; cauline intersegments with 4-8 nematothecae in two closely-set rows; cladial intersegments with 4-6 nematothecae in one row; gonothecae ovoid, with two long, basal nematothecae and a dome-shaped lid.

Etymology: This new species is named in honor of our friend Jean-Marie Bertot, a marine fauna enthusiast who explored the reefs of Martinique for almost two decades. He accompanied us during numerous dives and participated to the collecting effort.

Description: Colony arising from creeping, branching hydrorhiza, apparently devoid of nematothecae. Stems simple, monosiphonic, slender, straight to slightly geniculate (Fig. 70). Shortly above the origin from stolon, a transverse node indicates the beginning of the stem; occasionally, a basal part, composed of one or two rectangular segments of varied length and carrying up to two nematothecae, is present; otherwise, stem divided heteromerously by alternation of straight and oblique nodes. Ahydrothecate segments long and slender, delimited proximally by transverse node and distally by oblique node; distally, a short, lateral apophysis supporting a cladium; generally 5-6 (rarely 4, and up to 8, or even 12 in the basalmost segment) nematothecae in two closely-set, parallel rows. Hydrothecate internodes up to 13 per stem; basally an oblique node, distally a transverse one; short, so as to accommodate a hydrotheca in middle and 5 nematothecae: a mesial one, far below the base of hydrotheca, as well as two pairs of laterals flanking the theca; external pair borne on tall apophyses; internal pair inserted on both sides of the axil made by the adaxial wall of the theca with the internode behind. Cladia, up to 7 per cormoid, widely spaced, given off laterally either alternately or irregularly left and/or right; structure similar to stem, except for the presence of only 4-5 (rarely 6) nematothecae in one row on each ahydrothecate internode; up to 11 hydrothecate internodes per cladium; some cladia branched once through a lateral apophysis given off from the distal part of an ahydrothecate segment. Hydrothecae from stem and cladia alike; moderately deep, tubular, adnate for two thirds their adaxial length, walls parallel, margin slightly scooped in lateral view, rim even, not everted (Fig. 7P²). All

nematothecae bithalamic and movable (Fig. 7Q); basal chamber comparatively taller than upper one; aperture with even rim. Gonothecae borne on stems and cladia, given off through short, lateral apophyses below a hydrotheca; basally a short, rectangular segment; overall shape of gonotheca ovoid, basally curved and tapering, distally truncate and bearing a large, rounded aperture; the latter closed by a dome-shaped lid. All gonothecae presumably female. Nematocysts (Fig. 7S): three size classes of microbasic mastigophores (seed-shaped, banana-shaped, as well as large and ovoid capsules).

Dimensions: Stems up to 2 cm high, apophyses for cladia 30-45 µm long. Width of caulis 50-90 µm, and of cladia 40-50 µm (both at nodes). Length of hydrothecate segments 320-400 µm (cauline) / 320-370 µm (cladial). Length of ahydrothecate segments 735-1155 µm (cauline) / 615-775 µm (cladial). First cladial segment 650-920 µm long. Free adaxial wall of hydrotheca 80-90 µm, adnate part 155-170 µm, abcauline wall 180-200 µm long, aperture 175-190 µm wide. Gonotheca 415-510 µm long, 210-225 µm wide in middle and 85-110 µm at aperture; apophysis 25-30 µm long; small, rectangular segment 35-50 µm long. Caulinar, cladial, and mesial nematothecae 65-75 µm long and 30-40 µm wide at rim. External pair of lateral nematothecae 60-90 µm long, 35-40 µm wide at aperture; apophyses 50-60 µm long. Inner pair of lateral nematothecae 50-65 µm long, 25-30 µm wide at rim. Gonothecal nematothecae 90-140 µm long, 45-50 µm wide at rim. Nematocysts: seed-shaped capsules (4.0-4.3) × ca. 2.4 µm, banana-shaped capsules (6.4-6.7) × (2.1-2.3) µm, large capsules (14.2-15.6) × (5.9-6.2) µm.

Distribution: Known only from Martinique (present study).

Type locality: France, Martinique, Case-Pilote, Fond Boucher.

Remarks: Three members of the genus possess two pairs of lateral nematothecae flanking the hydrothecae, viz. *M. faurei* Millard, 1958, *M. natalensis* Millard, 1958, and *M. providentiae* (Jarvis, 1922). The two former build colonies with thick, polysiphonic stems, whose complex structure was described in detail by Millard (1958). Only *M. providentiae* comes close enough to the present species, but it exhibits the following distinguishing features: 1) its stems and cladia are divided homomerously instead of heteromerously; 2) there are only 2-3 nematothecae per internode, rather than commonly 5-6 (but up to 8 possible) on the cauline internodes, and 4-5 (occasionally 6) on the cladial ones of *M. bertoti*; 3) the cladia are reportedly given off from one side of the stem (Jarvis, 1922), rather than more or less regularly alternate, as in the new species.

Family Campanulariidae Johnston, 1836
Genus *Clytia* Lamouroux, 1812

***Clytia edentula* Gibbons & Ryland, 1989**
 Fig. 7T, U

Clytia edentula Gibbons & Ryland, 1989: 398, fig. 17.

Material examined: MHNG-INVE-91107; sample #M276; France, Martinique, Anse Dufour, 14.52716° -61.09003°, 0-1 m; 12.01.2014; fertile colonies on fragments of benthic *Sargassum* sp.

Description: See the original account by Gibbons & Ryland (1989).

Dimensions: Pedicel 840-3290 µm high, 70-115 µm wide. Hydrotheca 355-420 µm high, 310-445 µm wide at aperture. Gonotheca ca. 1000 µm high, 525 µm in maximum diameter, and 355 µm wide at aperture.

Distribution: Previously known only from Fiji (Gibbons & Ryland, 1989); this is the first record from the Caribbean.

Remarks: These hydrothecae with even rim, mounted on almost ringed pedicels, leave little doubt about the identity of this hydroid. As already underlined by Gibbons & Ryland (1989), *Cytia hummelincki* (Leloup, 1935) has comparatively shallower and wider hydrothecae, a subhydrothecal spherule is present, and the gonothecae are devoid of a collar. These features are also evident from the account of Galea (2008), and are further supported by the co-occurrence in the present collection of fertile colonies of *C. hummelincki*.

Gibbons & Ryland assumed that the wide gonothecal aperture is evidence that the gonophores are free swimming medusa. Their hypothesis is actually confirmed upon examination of the present material, in which several medusa buds can be observed within the gonotheca.

It is worthwhile noting that the nominal species *C. hummelincki* is, very likely, nothing more than a junior synonym of *Campanularia brevithecata* Thornely, 1900. Colonies of the latter form simple, unbranched stems, annulated basally and occasionally elsewhere, and are provided distally with a characteristic spherule below a very shallow hydrotheca. All these are features met with in Leloup's species. In addition, nothing distinguishes the shape of the gonotheca illustrated by Thornely from those examined by Millard (1975) in her material from the Indian Ocean assigned to *C. hummelincki*. Moreover, the presence in each gonotheca of *C. brevithecata* of one or two gonophores with four radial canals (there is no mention of discernible gonads), is in conformity with several convergent observations on *C. hummelincki* (Millard, 1975; Gravili *et al.*, 2008; present study). It is obvious that the occurrence of a subhydrothecal spherule and the lack of knowledge of the nature of the gonophores mislead Thornely with respect to the genus in which she included her new species.

***Clytia laxa* Fraser, 1937b**

Clytia laxa Fraser, 1937b: 1, pl. 1 fig. 1. – Spracklin, 1982: 246, fig. 115B.

Laomedea tottoni – ? Wedler, 1973: 34, fig. 4.

Clytia tottoni. – Galea, 2010a: 7, fig. 2C-H.

not *L. tottoni* Leloup, 1935: 26, figs 11, 12 = replacement name for *Clytia fragilis* Congdon, 1907: 470, fig. 13 = *Clytia linearis* (Thornely, 1900).

not *Laomedea (Phialidium) tottoni*. – Vervoort, 1968: 17, fig. 6 [= *Clytia linearis* (Thornely, 1900)].

not *Laomedea tottoni*. – Leloup, 1974: 21, fig. 17 (= *Clytia* sp.).

not *Obelia tottoni*. – Park, 1998: 60, fig. 1 (= *Clytia* sp.).

Clytia arborescens. – Billard, 1906: 167. – Medel & Vervoort, 2000: 30, figs 7-8 (not *Clytia arborescens* Pictet, 1893: 33, pl. 2 figs 28, 29).

Description: For the latest description of this species, see Galea (2010a).

Distribution: Reliable records are from the Dry Tortugas (Leloup, 1935, as *Clytia tottoni*), Puerto Rico (Fraser, 1937b), Guadeloupe (Galea, 2010a, as *C. tottoni*), Martinique (Galea, unpublished data), and Madeira [Billard, 1906; Medel & Vervoort, 2000; both as *C. arborescens* (Pictet, 1893)].

Remarks: Leloup (1935) proposed the replacement name *Laomedea tottoni* for *Clytia fragilis* Congdon, 1907 to avoid secondary homonymy with *Obelia fragilis* Calkins, 1899 when both are placed in the genus *Laomedea* Lamouroux, 1812. According to Calder (1991), *C. fragilis* is coterminous with *Clytia linearis* (Thornely, 1900), and *L. tottoni* therefore automatically becomes a synonym of Thornely's species as well.

In being a replacement name for *C. fragilis*, *L. tottoni* has the same type as that of Congdon's species (ICZN Art. 72.7), and the two binomina are objective synonyms. However, Caribbean material described by Leloup under the name *L. tottoni* differs morphologically from *C. linearis* [see descriptions given by both Leloup (1935) and Galea (2010a)], conforming instead with *Clytia laxa* Fraser, 1937b.

The material from Madeira assigned by Medel & Vervoort (2000) to *C. arborescens* (Pictet, 1893) is a misidentification of *C. laxa*. Indeed, Schuchert (2003), who examined not only the type of Pictet's hydroid, but also additional material from the Kei Islands, noted that the hydrothecal cusps in this species are sinusoid and symmetric, thus differing from the triangular ones, inclined to one side, present in the material examined by Medel & Vervoort. An earlier record, equally attributed to *C. arborescens*, from the same area (Billard, 1906), most probably belongs to the present hydroid as well.

Due to their geographical remoteness, the Chilean (Leloup, 1974) and Korean (Park, 1998) records assigned to *C. tottoni* are thought to belong to different taxa.

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