The medusae of some species of *Hebella* Allman, 1888, and *Anthohebella* gen. nov. (Cnidaria, Hydrozoa, Lafoeidae), with a world synopsis of species*

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Key words: Cnidaria; Hydrozoa; Hydroidomedusae; Leptomedusae; taxonomy; paedomorphosis; life cycle.
The newly liberated, immature medusae of *H. scandens*, *Hebella furax*, *H. muscensis*, and the liberable eumedusoid of *H. dyssymetra* are described. The taxonomy of the medusa-producing Hebellinae is revised in the light of life cycle features. Due to inconsistencies between skeletal and medusan features, *Hebellopsis* is merged into *Hebella*. The new genus *Anthohebella* is proposed for the hebellids with swimming gonophores. All the nominal species referred to *Hebella* and *Hebellopsis* are discussed; out of the 45 nominal species referred at least once to *Hebella* and *Hebellopsis*, 15 are retained as valid: 11 are referred to *Hebella* and four to *Anthohebella* gen. nov.; 12 nominal species are considered conspecific with currently recognized species referred to the genera *Hebella*, *Scandia* and *Lafoea*; the remaining 18 nominal species are retained as doubtful.

Contents

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Introduction

The genera *Hebella* Allman, 1888, *Halisiphonia* Allman, 1888, *Scandia* Fraser, 1912, *Hebellopsis* Hadzi, 1913, and *Bedotella* Stechow, 1913 (see Bouillon, 1985 for diagnoses) have been referred to the Lafoeidae Hincks, 1868 (sometimes as a subfamily: Hebelli-

nae Fraser, 1912), or to a distinct family, Hebellidae Fraser, 1912. Calder (1991), in a detailed account of this group, accepted its assignment to the Hebellinae (see also Nutting, in Fraser, 1912a; Antsulevich, 1987). Calder (1991) referred the Hebellinae with medusae to *Hebellopsis* and *Hebella*, the distinction being based on diaphragm morphology. The aim of the present paper is to review the available knowledge of Hebellinae with medusae, supplementing it with new data on their life cycles.

The presence of medusae in Hebellinae has been known even before the proposal of the hydroid-based genus *Hebella* by Allman (1888). A. Agassiz (1865a), in fact, described and figured a hebellid hydroid and its newly liberated immature medusa, ascribing them to the medusa-based species *Laodicea calcarata* L. Agassiz, 1862. This action has been disputed by various authors (Browne, 1907; Mayer, 1910; Russell, 1953; Rees & Thursfield, 1965; Calder, 1991) because known *Laodicea* hydroids have operculate hydrothecae, whereas those of *Hebella* have not.

Besides A. Agassiz's observations, the medusae of the Hebellinae have been described while still inside the gonotheca (e.g. Millard, 1975) or when newly liberated (e.g. Hirohito, 1969). But no complete life cycle of *Hebella* has been described so far, with the exception of *Hebella parasitica* (Ciamician, 1880) which, however, was described as producing a peculiar medusoid, possibly interpretable as a swimming gonophore (see Boero, 1980; Boero & Bouillon, 1989, and discussion below).

The medusae or medusa buds of 14 of the 45 nominal species of *Hebella* have been described so far. The published descriptions are mostly fragmentary, but allow recognition of the following categories:

1 - Gonothecae containing mature medusae, with distinguishable gametes.

1 a: gametes on radial canals

Hebella contorta Marktanner-Turneretscher, 1890: medusa buds with four small tentacles and four rows of reproductive organs (see Stechow & Müller, 1923).

1 b: gametes on "manubrium"

Hebella parasitica (Ciamician, 1880): liberation from gonotheca observed by Boero (1980).

Hebella brevitheca Leloup, 1938: medusa buds carefully described by Hirohito (1995), who referred this species to *Scandia*.

Scandia najimaensis Hirohito, 1995: medusa buds reported in the original description.

2 - Gonothecae containing immature medusae, without gametes.

2 a: with ocelli

Hebella calcarata (L. Agassiz, 1862): medusae with two tentacles and eight ocelli on liberation (A. Agassiz, 1865a).

Hebella scandens (Bale, 1888): newly liberated medusae with four perradial bulbs, but only three perradial tentacles (the fourth being not yet developed) four interradial bulbs, and an adaxial ocellus on each bulb (Altuna Prados, 1994).

Hebella muscensis Millard & Bouillon, 1975: "medusa bud with rounded hypostome, at least four marginal tentacles and a varying number of ocelli (usually eight)" (Millard & Bouillon, 1975: 10).

2 b: without ocelli

Hebella calcarata (L. Agassiz, 1862): newly liberated medusa "deeply campanulate, with two long marginal tentacles, and others in course of development, four radial canals and yellow-spotted proboscis" (Nutting, 1901: 353).

Hebella cylindrica (Von Lendenfeld, 1885): medusa buds with marginal tentacles and a short manubrium (Pictet, 1893).

Hebella scandens (Bale, 1888): newly liberated medusa with a simple mouth, two long opposite marginal tentacles and four short interradial tentacles (Hirohito, 1969; Millard, 1975).

Hebella striata Allman, 1888: medusa buds with long manubrium (Hartlaub, 1905).

Hebella plana Ritchie, 1907: medusa buds with four coiled tentacles, 4-12 tentacular bulbs and a short manubrium (Totton, 1930).

Hebella crateroides Ritchie, 1909: medusa buds reported by Ritchie (1910a).

Hebella furax Millard, 1957: medusa buds with three long marginal tentacles and a four-lobed mouth (Millard, 1975).

As briefly pointed out above, different authors described different medusan features for *Hebella scandens* and *H. calcarata*. New material referred to four species of Hebellinae is described here, with information on medusa stages. Furthermore, gonosomal features are described from type material of the nominal species *Hebella brevitheca* and *Scandia tubitheca*, both with a medusa stage. Additional information is given from examination of museum specimens. Based on this information, a world synopsis of the nominal species of Hebellinae with medusae is attempted, together with the proposal of a new genus to accommodate hebellids with swimming gonophores.

Material and methods

Many specimens in liquid or mounted on slides, from the collections of: National Museum of Natural History, Leiden (RMNH); Musée National d'Histoire Naturelle de Paris (MHNP), Zoological Museum of Amsterdam (ZMA), The Natural History Museum, London (NHML), Musée Royal d'Afrique Centrale, Tervuren (MRAC), Institut Royal des Sciences Naturelles de Belgique (IRSNB), South African Museum (SAM), Royal Ontario Museum (ROM), Museum d'Histoire Naturelle de Genève (MHNG).

Living fertile colonies from shallow waters of Papua New Guinea (Laing Island, Bismarck Sea), Japan (Oshoro, Hokkaido, Sea of Japan), and Spain (Blanes, Mediterranean Sea) were kept in the laboratory until medusa liberation. Newly released medusae were transferred into small aquaria and fed with *Artemia* nauplii, their further development was observed as much as possible.

See details under "Material" sections below.

The taxonomy of Hebellinae with medusae

In the following synopsis all nominal species referred to medusa-producing hebellids are treated separately, reporting all citations known to us, even those of no immediate taxonomic relevance.

1 - Valid species

As discussed below, the valid species of Hebellinae with medusae (listed chronologically) are here referred to two genera.

Genus *Hebella* Allman, 1888

Diagnosis.— Colony stolonal, hydrotheca on short pedicel, campanulate to cylindrical, usually with annular thickening, and membranous or perisarc diaphragm. Hydranth with conical hypostome. Gonotheca solitary, with or without opercular flaps, arising from hydrorhiza. Medusae in form of either liberable eumedusoids with mature gametes on radial canals, or liberable but immature medusae, with two to four marginal tentacles, with or without ocelli, with short manubrium with or without oral lips, with four or more radial canals.

Discussion.— Hadzi (1913), and recently Calder (1991), based distinction of *Hebella* from *Hebellopsis* on the presence of a membranous hydrothecal diaphragm and annular thickening in *Hebella* and of a chitinous perisarcal hydrothecal diaphragm in *Hebellopsis*. Such distinction was based on unfertile material.

A similar generic distinction based on diaphragm features was proposed by Levinsen (1893) and Broch (1909) for the Campanulariidae, with the recognition of just two genera: *Laomedea* Lamouroux, 1812, and *Campanularia* Lamarck, 1816. A higher generic diversity in the Campanulariidae was restored by considering gonophore features too (see Cornelius, 1982, and Bouillon, 1985, for definitions of genera). Nutting (1915: 10) studied the histology of the hydrothecal diaphragms of several species of Campanulariidae and, commenting on the use of diaphragm features as a generic character, stated that "this criterion can, therefore, not be regarded as a satisfactory one for dividing the Campanularidae [sic] into generic groups". When skeletal features suggest assignment to one genus, but medusan features indicate a differing affinity, taxonomic decisions usually assign more weight to medusan characters, as done by Cornelius (1982) in the treatment of *Clytia hummelincki* (Leloup, 1935), a campanulariid with sub-hydrothecal spherule (a *Campanularia* character) and a *Clytia* medusa (these features are confirmed by unpublished observations by Boero & Bouillon). Also in the Hebellinae skeletal features should not overweight medusan features. Generic distinction in the Campanulariidae is now based on a blend of medusan and hydroid characters and its application requires life cycle knowledge.

Petersen (1979, 1990) posed the problem of paraphyly and polyphyly when species differing only in the degree of medusa expression are grouped into different genera. Medusa reduction, in fact, often occurred in hydroidomedusan lineages and species with eumedusoids could be the result of parallel paedomorphic events in the same clade. This could well apply to *Hebella dyssymetra* and to *H. tubitheca* (see descriptions of their liberable eumedusoids below). According to pre-Petersen rules they should be ascribed to a genus different from *Hebella*, but we agree with Petersen that, lacking further indications, *Hebella* would become paraphyletic and the new genus could be polyphyletic. Since hebellid life cycle features are still poorly known, we are inclined to avoid generic distinctions based on characters which have been proven as misleading in other families. In the following observations on the medusa

stages of the hebellids, we report *Hebella scandens* (with diaphragm features of "*Hebellopsis*") and *Hebella furax* (with diaphragm features of "*Hebella*") as having similar newly released medusae and we tend to regard this last feature as more important than diaphragm morphology, thus merging *Hebellopsis* into *Hebella*.

The above diagnosis, deriving from the findings reported below, is, however, based on still insufficient knowledge about life cycles. Hirohito (1995: 115-116) summarized the proposal by Stechow (1923c) of considering *Hebella* as identical with *Phortis* McCrady, 1857, and gave sound reasons for discarding it.

Hebella striata Allman, 1888
(fig. 1)

Hebella striata Allman, 1888: 30, pl. 15, figs 3, 3a; Pfeffer, 1890: 567; Pictet & Bedot, 1900: 12; Hartlaub, 1901: 44; Jäderholm, 1903: 262; Jäderholm, 1905: 4, 19, 38; Hartlaub, 1905: 505-506, 508, 554, 586-587, 632, fig. K2; Ritchie, 1907: 521-522, 529-530, pl. 1 figs 7-8; Ritchie, 1909: 67; Vanhöffen, 1910: 272-273, 313, 339; Bedot, 1916: 125; Bedot, 1918: 154; Bedot, 1925: 227; Jäderholm, 1926: 5; Totton, 1930: 156, fig. 12; Leloup, 1960: 231; Rees & Thursfield, 1965: 71-72; Vervoort, 1972: 62-67, fig. 17b, c; Leloup, 1974: 10; Boero, 1980: 134; Calder, 1991: 39-42; Blanco et al. , 1994: 24-26, figs 25-26.
Lafoea striata; Jäderholm, 1904: 275.

Material.— Type mounted on slide, one infertile colony growing on *Lafoea dumosa* (Fleming, 1820) (NHML no. 88.11.13.22.A.), Strait of Magellan; "Challenger" St. 313: one infertile colony mounted on slide, growing on *Grammaria magellanica* Allman, 1888 (NHML no. 90.4.11.2.E.); Mission du Cap Horn, 1882-1883, no. 142: several hydrothecae mounted on slide, det. E. Leloup (IRSNB no. I.G. 22225); Vema 15-107, 54°10.2'S 65°57.5'W, 6.iii.1959, 101 m depth: one infertile colony mounted on slide, growing on *Symplectoscyphus subdichotomus* (Kirchenpauer, 1884) (RMNH Coel. no. 7170); Vema 17-24, 53°37.7'S 69°54.6'W, 29.iii.1961, 42 m depth: one infertile colony mounted on slide, growing on *S. subdichotomus* (RMNH Coel. no. 7407).

Discussion.— Hydrothecae from type material with membranous diaphragm, hydranths with up to 12 tentacles. Hartlaub (1905) described the gonotheca with medusa buds.

Hebella scandens (Bale, 1888)
(fig. 2)

non *Laodicea calcarata*: L. Agassiz, 1860-62, but all subsequent citations of *Hebella calcarata* (L. Agassiz, 1862) (see discussions in section 2).
Lafoea scandens Bale, 1888: 758, pl. 13, figs 16-19; Whitelegge, 1889: 192; Billard, 1904: 481; Billard, 1906c: 174; Warren, 1908: 272, 341-342, 347, 349, fig. 21.
Hebella scandens; Marktanner-Turneretscher, 1890: 214, pl. 3, fig. 16; Pictet, 1893: 42-43; Marktanner-Turneretscher, 1895: 401; von Campenhausen,

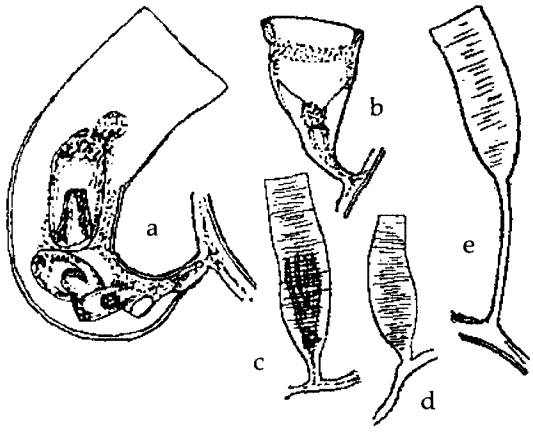


Fig. 1. *Hebella striata*. a: gonotheca with three medusa buds; b: immature gonosome; c, d, e: three hydrothecae. Slightly modified after Hartlaub (1905).

1896a: 104; Farquhar, 1896: 460; von Campenhausen, 1897: 307; Versluys, 1899: 31-32; Hartlaub, 1905: 586-587; Warren, 1908: 341, fig. 21; Bale, 1913: 117-120, pl. 12, fig. 10; Levinsen, 1913: 285; Thornely, 1916: 124; Bedot, 1916: 124; Bedot, 1918: 153; Stechow, 1919: 77-78, fig. 2; Bedot, 1925: 226; Vannucci, 1949: 236-237, pl. 2, figs 22-23; Vannucci, 1950: 85; Vannucci, 1951: 82-83; Deevey, 1954: 270; Vannucci, 1954: 114-115; Millard, 1957: 202; Millard, 1958: 176; Picard, 1958: 1; Vervoort, 1959: 237, fig. 12; Plante, 1961 (1965): 307; Rossi, 1961: 80, fig. 1; Millard, 1964: 11; Mammen, 1965: 4-5, fig. 31; Rees & Thursfield, 1965: 75; Vervoort, 1966: 123; Vervoort, 1967: 31-33, figs 5-6; Millard, 1968: 2, 262; Hirohito, 1969: 14, fig. 11; Vervoort, 1972: 65; Millard, 1973: 59; Millard & Bouillon, 1973: 59-60; Millard, 1975: 182-184, fig. 60 F-G; Millard, 1978: 186; ; Boero, 1980: 134; Gili, 1981: 107; Gili, 1982: 71-72, 144, 174, fig. 32 B; Gili, García & Colomer, 1984: 413, 423; Blanco, 1984: 273-274, pl. 1, fig. 8; Gili & Castello, 1985: 9-10, 13: Gili & García-Rubies, 1985: 43-44, 51, fig. 6 I; Roca & Moreno, 1987: 21, figs 19 b, 33; Gibbons & Ryland, 1989: 38O, 395, 410-411, 414, 427, fig. 14A, B; Gili & Ballestreros, 1991: 247; Genzano & Zamponi, 1992: 16, 60, 79, fig. 25, photo 5; Genzano, 1992: 144-145, fig. 8; Altuna Prados, 1994: 44, 54, fig. 2 B, F; Blanco et al., 1994: 23-24, figs 23-24.

Hebella scandens var. *contorta*: see *Hebella contorta* Marktanner-Turneretscher, 1890.

Lictorella scandens; Borradaile, 1905: 836, 840.

Hebella Michaelseni Broch, 1914 (see discussions at p. 40).

Hebellopsis scandens; Hadzi, 1916: 76; Stechow, 1925: 442; Vervoort, 1941: 197; Gili, 1982: 72; García-Corrales et al., 1979: 12; Calder, 1991: 42-43, 45, 95.

Grammaria scandens; Jäderholm, 1919: 7, 31.

Phortis scandens; Stechow, 1923a: 139.

Hebella spiralis Nutting, 1927 (see discussions at p. 40).

Hebella (?) *eximia* Fraser, 1944 (see discussions at p. 40).

Hebellopsis sinuosa Vannucci, 1949 (see discussions at p. 40).

Hebellopsis besnardi Vannucci, 1950 (see discussions at p. 40).

Hebella scandens var. *michaelseni*; Vervoort, 1959: 238-239, fig. 13; Gili, Vervoort & Pagès, 1989: 72-73, fig. 3.

Hebella urceolata Millard, 1964 (see discussions at p. 40).

Museum Material.— Mergui Archipelago: microslide preparation of stained infertile colony, det. W.J. Rees (NHML no. 1964.8.7.44); var. *contorta*, St. Thomas Sound, 15-19.i.1909: one infertile colony mounted on slide, growing on *Dynamena crisioides* Lamouroux, 1824, Leg. Kükenthal & Hartmeyer (RMNH Coel. no. 3612); var. *contorta*, Bonaire, 9.ix.1948: one fertile colony mounted on slide, growing on *D. crisioides* (RMNH Coel. no. 1535); var. *contorta*, French Polynesia, Moorea Atoll, 9-10 m, 3.viii.73, Leg. P. Vasseur, Det. W. Vervoort: one infertile colony growing on *Synthecium samauense* Billard, 1924 (RMNH Coel. no. 11620).

Living Material.— Laing Island (Papua New Guinea): several fertile colonies growing on sertulariids.

Hydroid.— Hydrotheca with flared margin, mostly oblique, but bent 90° when growing over host hydrothecae, wall smooth to slightly corrugated, asymmetrical, with perisarc diaphragm. Pedicel short, smooth or annulated, hydranth with 12-16 tentacles. Gonotheca bigger than hydrotheca, with undulated walls, four opercular flaps, asymmetrical, truncated distally, tapering towards base, on short pedicel.

Newly liberated medusa.— Bell deep-campanulate, evenly covered by nematocysts, jelly thicker at apex, manubrium short, mouth with four small lips, four radial canals, two perradial tentacles arising from big tentacular bulbs, six smaller atentaculate bulbs, two perradial and four interradial ones. Each bulb with an adaxial ocellus.

Discussion.— The present material agrees with the many available descriptions of *H. scandens* and *H. calcarata* (see p. 33 for the proposed status of this nominal species).

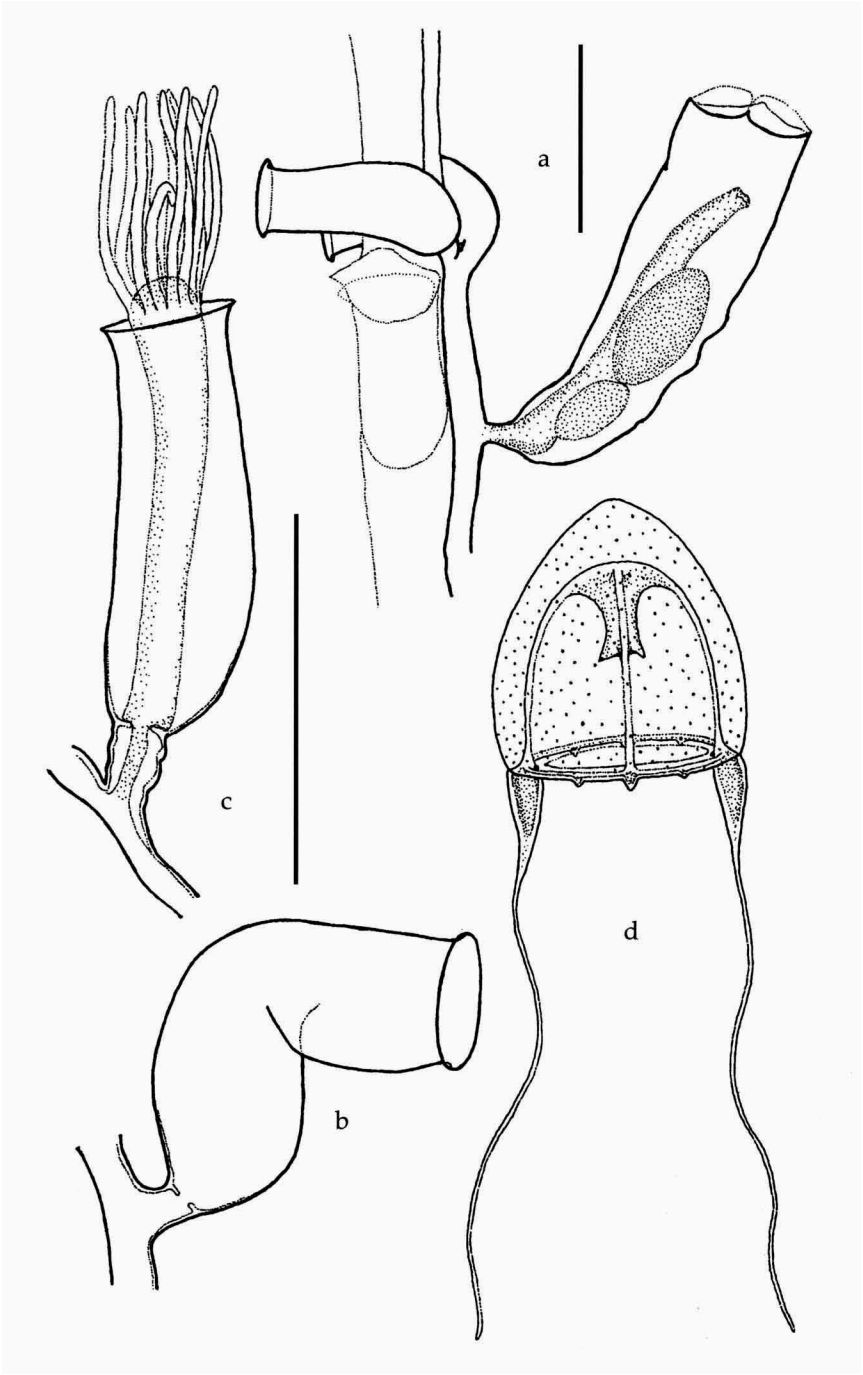


Fig. 2. *Hebella scandens* from Laing Island, Papua New Guinea. a: portion of fertile colony, growing on a sertulariid; b: twisted hydrotheca; c: straight hydrotheca; d: newly liberated medusa, released from a laboratory-reared colony, bell 1 mm high. Scale bars: a, b-c: 0.5 mm.

The hydrothecae can be almost symmetrical, or sharply asymmetrical, according to their position on the sertulariid hosts. The asymmetry is maximal when the hydrothecae originating from hydrorhizae developed on one side of the host's stem grow above the host's own hydrothecae, reaching the opposite side of the host's stem. Such hydrothecae are almost identical with those described in *H. contorta, H. sinuosa, H. spiralis, H. besnardi,* and *H. urceolata.* Asymmetrical and almost symmetrical hydrothecae were present in the same colony, so that this character cannot be considered as having a specific value.

The hydroid and newly liberated medusa of *Hebella scandens* described here, look identical in all anatomical details to those described and figured by A. Agassiz (1865a) as *Lafoea (Laodicea) calcarata.* The description by A. Agassiz is thus confirmed by our specimens. However, the further development of the medusa described by him is still to be considered as doubtful because it was inferred from a series of animals collected in the plankton, and not from continuous rearing of medusae under laboratory conditions. As remarked by Calder (1991), the specific name *calcarata* was coined for a *Laodicea* medusa, but has subsequently been applied to the hydroid on the basis of A. Agassiz's (1865a) description of what he considered to be the hydroid stage of *Laodicea calcarata* (L. Agassiz, 1862).

The original description of *Hebella scandens* by Bale (1888) suggests the presence of immature medusae in the gonotheca, a feature further confirmed by various authors, as mentioned below. The presence of adradial ocelli in the medusa of hebellid hydroids indicates affinity between *Hebella* and the Laodiceidae. Hirohito (1969) cited the description of the medusa of *Laodicea calcarata* by A. Agassiz (1865a), but he did not discuss it. Probably, Hirohito checked this character in his material due to the report of ocelli in the newly released medusa by Agassiz. In fact, Hirohito explicitly stated that there were no ocelli. Usually ocelli are evident even when the medusae are still in the gonotheca as buds, but we describe below that the newly released medusae of *Hebella furax* had no evident ocelli, whereas these became evident one day after liberation. Millard (1975: 182) described the medusa of *H. scandens* as having "a simple mouth, two long, opposite marginal tentacles, and rudiments of two other perradial tentacles and four interradial tentacles", so being similar to the one described by Hirohito (1969), though the latter was round in shape, possibly due to contraction. Altuna Prados (1994) was the first to cite medusae of *H. scandens* as having ocelli at liberation, but this feature had been recorded previously by A. Agassiz (1865a) in the newly liberated medusae of *H. calcarata,* here considered as conspecific with *H. scandens.*

Material from Bonaire, labelled as *H. scandens* var. *contorta* has gonothecae containing ocellate medusa buds and is referred to *Hebella scandens* (see below for discussion of *Hebella contorta*).

Hebella contorta Marktanner-Turneretscher, 1890
(fig. 3)

Hebella contorta Marktanner-Turneretscher, 1890: 215, pl. 3, fig. 17a, b; Pictet, 1893: 43: Marktanner-Turneretscher, 1895: 401; von Campenhausen, 1896a: 104; von Campenhausen, 1896b: 306-307, 317; Billard, 1904: 481; Billard, 1906b: 174; Levinsen, 1913: 285, pl. 5, figs 16-17; Bedot, 1916: 124; Bedot, 1918: 153; Bedot, 1925: 225; Hargitt, 1924: 488; Nutting, 1927: 207; Rees & Thursfield, 1965: 73; Boero, 1980: 134; Gili, 1982: 72; Rees & Vervoort, 1987: 35; Calder, 1991: 43-44.

Hebella calcarata var. *contorta*; Bale, 1915: 253-254; Ritchie, 1910b: 810; Bale, 1915: 253-254; Briggs, 1918: 35-36; Leloup, 1937a: 4, 26-27, fig. 17; Vervoort, 1946: 305; Hodgson, 1950: 13-14, fig. 24; Dawydoff, 1952: 55; Pennycuik, 1959: 151, 188.

Hebellopsis contorta; Stechow & Müller, 1923: p. 464, pl. 3, fig. 5.

Phortis contorta; Stechow, 1923a: 139.

Hebella scandens var. *contorta* (in part); Vervoort, 1959: 239, fig. 14; Vervoort, 1968: 25-26, 100, fig. 10; Gravier, 1970: 116; Rho & Chang, 1972: 100, pl. 2, figs 6-9; Rho & Chang, 1974: 133, 138; Rho, 1977: 255, 415, pl. 73, fig. 6; Vervoort & Vasseur, 1977: 13-14, figs 4, 12a; Rees & Vervoort, 1987: 35-36, fig. 6d; Park, 1992: 286; Park, 1993: 264.

Hebellopsis scandens (in part); Calder, 1991: 43-44.

Discussion.— Many authors considered this nominal species as conspecific with *Hebella scandens* or with *H. calcarata*. On the one hand, this proposal could be accepted in the light of the degree of variation observed for *H. scandens*. Gonosome described by Stechow & Müller (1923) as gonotheca with already ripe eumedusoids. They pro-

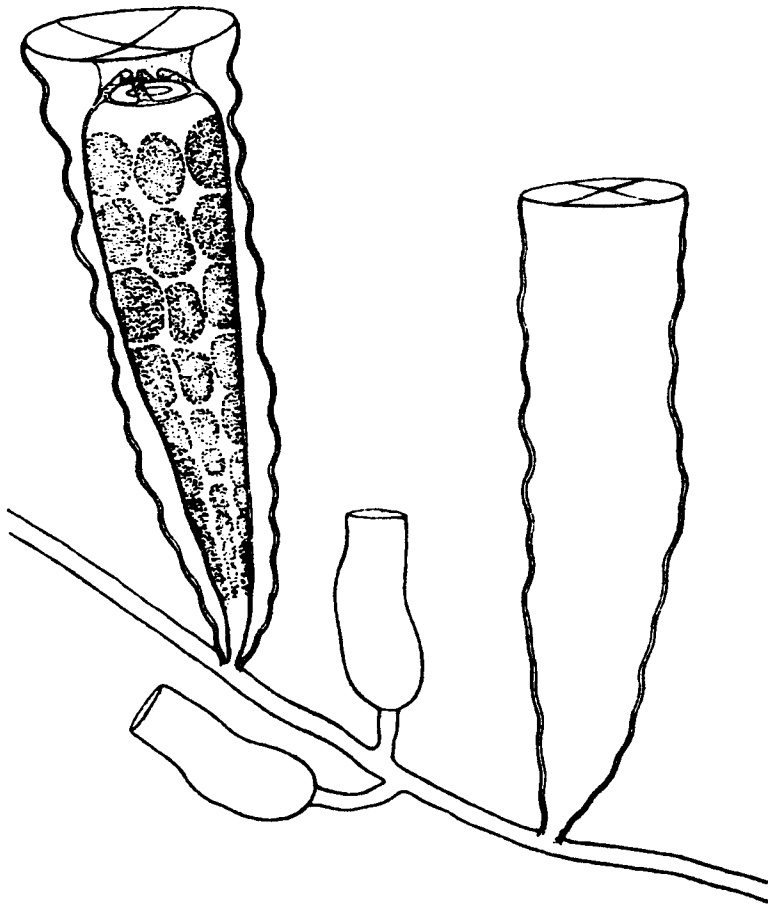


Fig. 3. *Hebella contorta*. Portion of colony with two hydrothecae and two gonothecae, one containing a "medusoid" with mature gonads. After Stechow & Müller (1923).

vided a detailed figure of a medusoid with gonads "following the radial canals", a velum, and tentacle rudiments. On the basis of such features Rees & Thursfield (1965) retained *H. contorta* as distinct from *H. scandens*. Infertile material of *H. scandens* and of *H. contorta* is, however, indistinguishable. The absence of information on the gonosome in the original description of *H. contorta* could mean that this nominal species has been based on material of *H. scandens*. In the interest of stability of nomenclature we suggest accepting *H. contorta* as a valid species, instead of proposing a new name and consider *contorta* as doubtful. The case of *H. scandens* and *H. contorta* shows that hebellid species with almost identical hydroids can have quite different medusa stages, as already proved for *H. muscensis* and *H. tubitheca* by Millard & Bouillon (1975).

Hebella plana Ritchie, 1907
(fig. 4)

Hebella striata var. *plana* Ritchie, 1907: 530, pl. 1, fig. 8; Ritchie, 1909: 67; Vanhöffen, 1910: 314; Billard, 1914: 9; Jäderholm, 1926: 4.

Hebella plana; Totton, 1930: 156, fig. 12 A-B; Briggs, 1939: 23; Rees & Thursfield, 1956: 74; Boero, 1980: 134; Blanco et al., 1994: 21-23, figs 21-22.

Material.— "Terra Nova" Expedition St. 355: a fertile colony mounted on slide, (NHML no. 29.10.28.58) (figured by Totton, 1930).

Discussion.— Totton (1930) described the gonothecae and the medusa buds. *Hebella plana* resembles *H. striata* in having a long cylindrical hydrotheca which, however, is not striated as that of *H. striata*. Observed material has membranous diaphragm, some hydrothecae have a slight annular thickening. Following Totton (1930), we consider it a valid species.

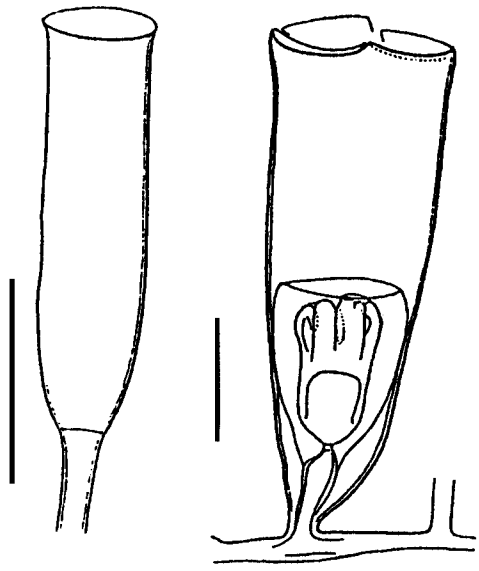


Fig. 4. *Hebella plana*. Left: hydrotheca, right: gonotheca containing one medusa bud. Scale bars: 0.5 mm. After Totton (1930).

Hebella crateroides Ritchie, 1909
(fig. 5)

Hebella crateroides Ritchie, 1909: 524; Ritchie, 1910a: 6-7, pl. 4, fig. 1; Ritchie, 1910b: 800-801, 810; Jarvis, 1922: 336; Briggs & Gardiner, 1931: 189, fig. 2; Pennycuick, 1959: 151, 188; Rees & Thursfield, 1965: 73; Boero, 1980: 134; Calder, 1991: 39-40.

Material.— Type mounted on slide: a fertile colony, growing on *Macrorhynchia phoenicea* (Busk, 1852) (NHML no. 1964.8.7.42).

Discussion.— Observation of type material confirms Ritchie's descrip-

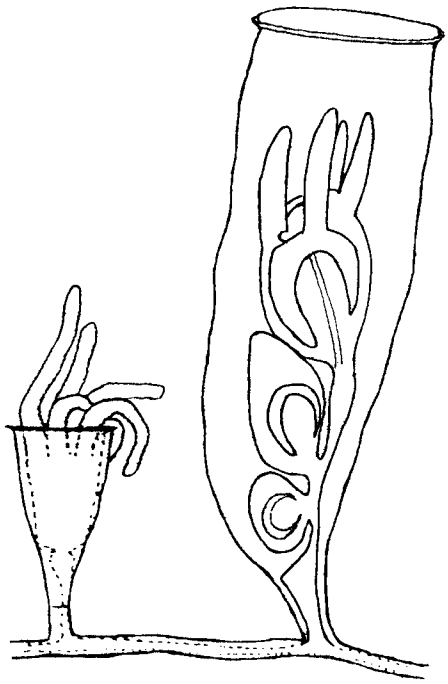


Fig. 5. *Hebella crateroides*. Hydrotheca and gonotheca with medusa buds. After Ritchie (1910a).

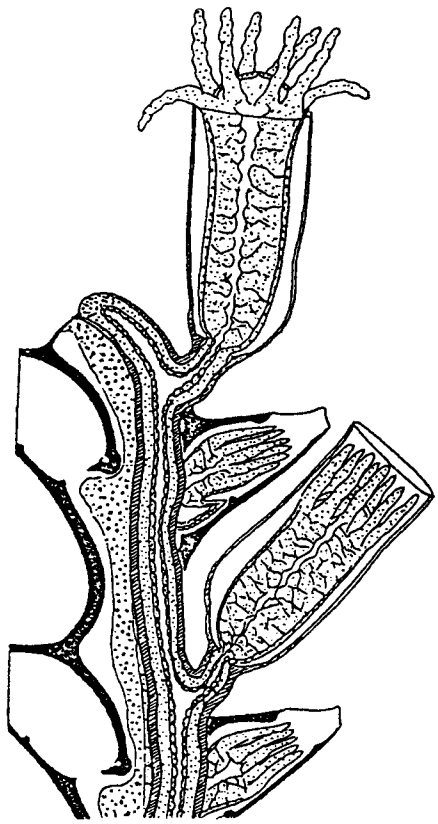


Fig. 6. *Hebella dispolians*. Portion of colony with two hydrothecae, growing on *Amphisbetia maplestonei* (Bale, 1844). After Warren (1909).

tions (Ritchie, 1909, 1910 a, b) reporting a membranous diaphragm, the absence of a perisarc diaphragm, and a hydranth with 6-8 tentacles. Gonotheca with four-tentacled, immature medusa buds. Rees & Thursfield (1965) remarked that this species might be removed from *Hebella* on description of the mature medusa, but did not comment on the hydrotheca. *Hebella crateroides* differs from other hebellids in having no marked constriction between the hydrotheca and the pedicel, its hydrotheca resembling that of *Laomedea* spp. However, the sub-hydrothecal chamber or the spherule typical of the Campanulariidae are lacking. These features are distinct enough to retain this species as valid and referable to *Hebella*.

Hebella dispolians (Warren, 1909)
(fig. 6)

Lafoea dispolians Warren, 1909: 105-112, pl. 1, figs 1-2.
Phortis dispolians; Stechow, 1923a: 139.
Hebella thankasseriensis Mammen, 1965: 5-6, figs 32-33. n. syn. (see discussion in section 2).
Hebella dispolians; Millard, 1975: 180, fig. 59 E; Boero, 1980: 134.

Discussion.— The peculiar parasitic habit of this species, in which the hydranth can make use of the hydrotheca of the host, is rather distinctive (see Millard, 1975, for discussion) and, in spite of lack of knowledge on reproduction, we provisionally consider this species as valid.

Hebella brochii (Hadzi, 1913)
(fig. 7)

Hebellopsis brochii Hadzi, 1913: 188-193, figs 30-33; Hadzi, 1916: 27; Calder, 1991: 42-43.
Hebella (*Hebellopsis*) *brochi*; Stechow, 1919: 78.
Hebellopsis brochi; Stechow, 1923a: 139.
Phortis brochi; Stechow, 1923a: 139.
Hebella brochi; Leloup, 1934: 8; Picard, 1951: 261; Boero, 1980: 134; Boero & Fresi, 1986: 143.
Lafoea parasitica (excl. syn); Broch, 1912: 40, fig. 12 (see discussion in section 2).
non *Hebellopsis brochi*; Da Cunha, 1950: 132, fig. 4.
non *Hebella brochi*; Hirohito, 1995: 116-118, Fig. 33 a-c.

Material.— Portofino (Genova, Italy, Ligurian Sea), 5 m depth: several infertile colonies growing on *Synthecium evansi* (Ellis & Solander, 1786), (RMNH Coel. 14404).

Discussion.— Gonotheca unknown. This is the type species of the genus *Hebellopsis*. It is endemic to the Mediterranean and has been reported as exclusively epizoic on *Synthecium evansi*. The figure given by Da Cunha (1950) of material from Portugal on *Sertularella mediterranea* Hartlaub, 1901, suggests that his specimens were actually *Hebella scandens*. Hirohito (1995) referred to *H. brochii* a hydroid with thecae lacking a peridermal thickening, the character on which Hadzi (1913) based the genus *Hebellopsis*. For this reason Hirohito's material cannot be identified as *H. brochii*. Hirohito (1995) also described a gonotheca with medusa buds, but the reported features seem still unsufficient to allow specific identification. *Hebella brochii* has corrugated hydrothecal walls, the base of the hydrotheca is wider or as wide as the opening, the pedicel is very short to indistinct, and a perisarc diaphragm is evident.

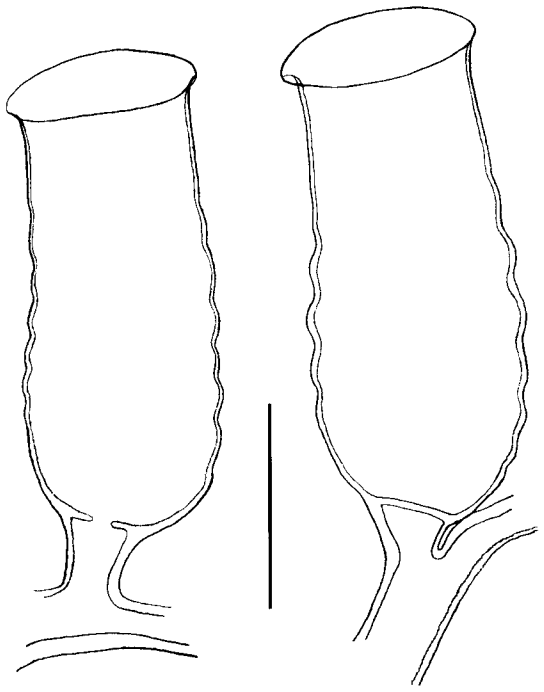


Fig. 7. *Hebella brochii*. Two hydrothecae from Portofino, Ligurian Sea, in optical section. Scale bar: 0.25 mm.

Hebella dyssymetra Billard, 1933
(fig. 8)

Hebella dyssymetra Billard, 1933: 6, fig. 1 A-C; Vervoort, 1967: 33, fig. 7; Millard & Bouillon, 1973: 57-59, fig. 8A-C; Van Praët, 1979: 882, fig. 20; Antsulevich, 1983: 1141-1143, fig. 1A; Antsulevich, 1987: 46-47, fig. 10; Gibbons & Ryland, 1989: 380, 393-394, fig. 12A-B; Calder, 1991: 39-41, fig. 24; Ryland & Gibbons, 1991: 544, 551; Hirohito, 1995: 120-122, fig. 34 a-f (in part).
Hebella dyssymmetra var. *trigona* Billard, 1942: 68; Pennycuik, 1959: 151, 188-189; Van Soest, 1976: 80.
Hebella dyssymmetra var. *undulosa* Billard, 1942: 69, fig. 5.
Hebella dyssymmetra var. *minor* Billard, 1942: 69; Van Soest, 1976: 80; Van Praët, 1979: 282.
Hebella dyssymmetra var. *monogona* Billard, 1942: 69, fig. 4.
Hebella dyssymmetra; Pennycuik, 1959: 188.
Hebella dyssymetra var. *monogona*; Van Soest, 1976: 80; Van Praët, 1979: 883.
Hebella dyssymetra var. *undulata*; Van Soest, 1976: 80-81.
Hebella dyssymmetrica; Boero, 1980: 134.

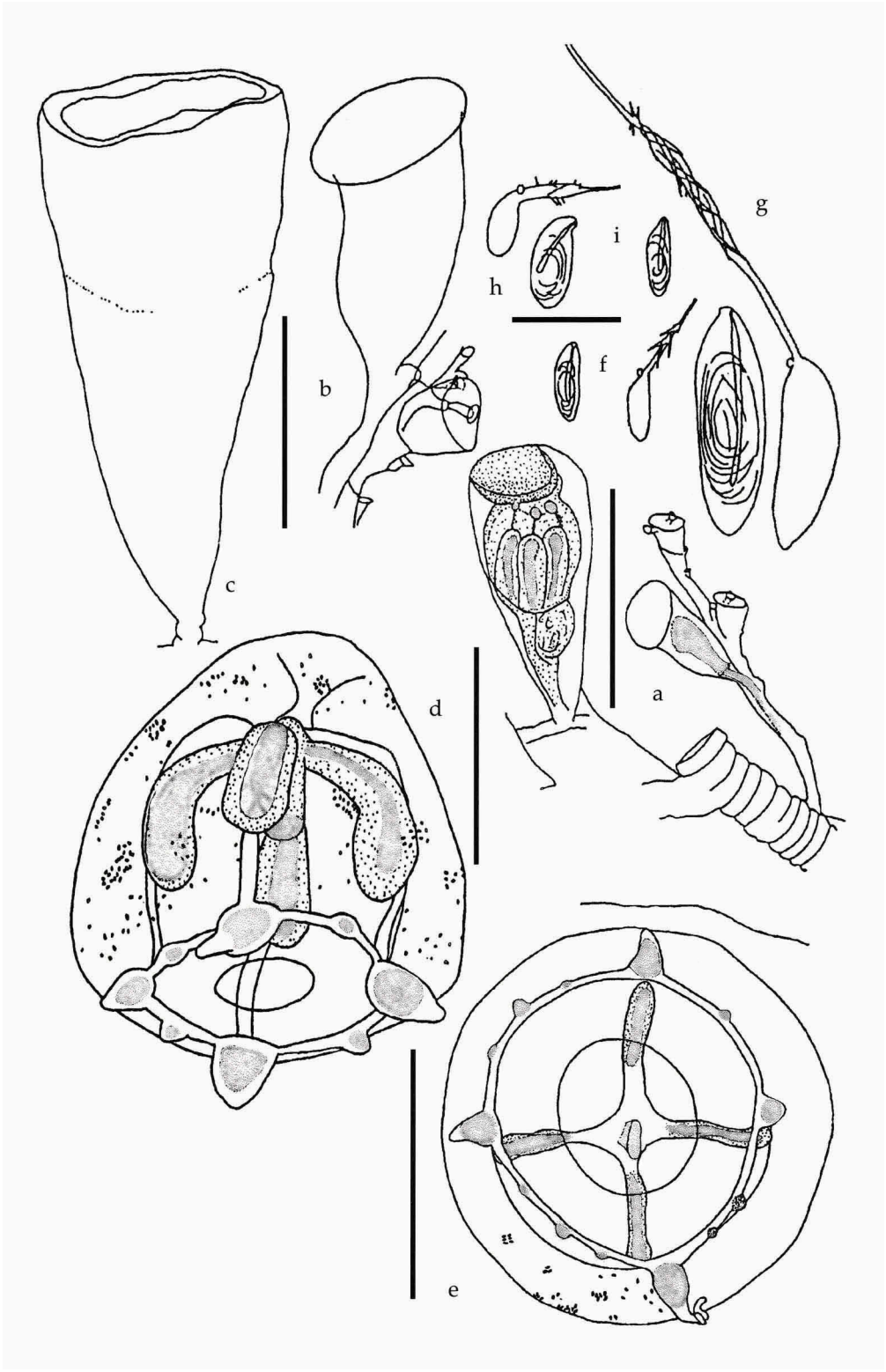
Material.— Gulf of Suez, St. XVII bis: syntype, fertile colonies mounted on slides growing on *Macrorhynchia philippina* (Kirchenpauer, 1872), (MHNP no. HL 191, 192, 193); Dahlak Archipelago, Cundabilu, Israel Southern Red Sea Expedition, 4.iv.62 (E 62/3902): fertile colonies growing on *Gymnangium gracilicaule* (Jäderholm, 1903) (RMNH Coel. no. 3704); var. *monogona*, Siboga Expedition St. 273: syntype, numerous fertile colonies growing on *Macrorhynchia philippina* (ZMA Coel. no. 5229); var. *undulosa*, Siboga Expedition, St. 213: syntype, colonies on *Macrorhynchia philippina* (ZMA Coel. no. 5178); var. *trigona*, Siboga Expedition St. 77: holotype, one fertile colony on *Antennella secundaria* (Gmelin, 1789) (ZMA Coel. no. 5177); var. *minor*, Siboga Expedition St. 152: holotype, one colony on *Antennella balei* (Billard, 1911) (ZMA Coel. no. 5230).

Living material.— Oshoro, Hokkaido, Sea of Japan: several living fertile colonies growing on *Antennella secundaria* (Gmelin, 1791) and *Eudendrium boreale* Yamada, 1954.

Hydroid.— Hydrotheca curved, with slightly everted margin. Diaphragm or peridermal thickening absent. Hydranth milky white, with conical hypostome and up to 20 tentacles. Pedicel indistinct, without annulation. Gonotheca smooth, about twice the size of the hydrotheca, wider at its truncated end and tapering basally, with a short corrugated pedicel. Up to two medusa buds at different growth stages in each gonotheca. Mature gonads already visible in medusa buds. Nematocysts: microbasic mastigophores of two sizes.

Medusa.— Medusa already mature at liberation. Four radial canals, each with a gonad on the proximal portion, 4 perradial atentaculate bulbs, 4 smaller interradial marginal bulbs. Manubrium short, tubular; mouth and gastral cavity present. Exumbrellar nematocysts abundant. During life span (max. 10 days) three tentacles grew from three of the initial perradial bulbs, with many cilia and scarce nematocysts on outer surface. Up to three marginal bulbs grew in some quadrants. Nematocysts:

Fig. 8. *Hebella dyssymetra* from Oshoro, Hokkaido, Japan. a: portion of colony, growing on *Antennella secundaria* and *Eudendrium boreale*; b: hydrotheca; c: gonotheca after release of a medusoid; d: newly released medusoid with mature male gonads; e: spent 3-day-old medusa reared in the laboratory (exumbrellar nematocysts only partly drawn); f: undischarged and discharged microbasic mastigophores on tentacles of hydroid; g - h: two types of microbasic mastigophores on exumbrella of medusoid; i: microbasic mastigophore on tentacles of medusoid. Scale bars: a: 1 mm; b-c, d-e: 0.5 mm; c: 1 mm; f-i: 10 μm.


c
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microbasic matigophores of three sizes: small ones on tentacles, identical to those of the hydroid, medium and larger ones disposed in patches on exumbrella. No nematocysts found on manubrium and tentacular bulbs.

Discussion.— The living material from Japan differs from other descriptions of *H. dyssymetra* in not having a distinct membranous diaphragm. Gibbons & Ryland (1989: 393), however, reported on specimens of this nominal species as having "a thin, delicate, often indistinct, diaphragm". In the same colony from syntype material are present both hydrothecae with slight or no annular thickening and with diaphragm thin or apparently absent. Gonothecae of this material contain eumedusoids with long gonads on radial canals, similar to those that gave rise to liberated eumedusoids in the present study. The four varieties described by Billard (1942) were based on size, number of medusa buds in gonotheca, and presence of wrinkled hydrotheca. Such character states are within intra-colony variations and the four varieties are not recognized as valid.

Hebella dyssymetra resembles many nominal species of *Hebella*. Calder (1991), for instance, reported it as having already been regarded as similar to *Hebella brevitheca*, *H. parasitica* (in part), *H. laterocaudata* and *H. furax*. The observation of a newly liberated medusa with already mature gonads recalls the description of *H. brevitheca* by Leloup (1938), in which the presence of mature gametes was similarly reported. But examination of type material of *H. brevitheca* showed that the gonotheca contains a medusoid with gonads on the "manubrium". Furthermore, the hydranth of *H. brevitheca* has 8-10 short, thick tentacles, whereas that of the *H. dyssymetra* has up to 20 tentacles. So these two nominal species cannot be considered conspecific as suggested by Antsulevich (1983, 1987). The other *Hebella* species known to have gonads on the radial canals of the medusa bud is *H. contorta* described by Stechow & Müller (1923) and it is retained as distinct from *H. dyssymetra*, as discussed above.

Hirohito (1995) reported on material identifiable as the present species, but with gonothecae containing immature medusa buds with four long tentacles. This suggests that almost indistinguishable hydroids might produce quite different medusae. At least part of Hirohito's material should not be included in *H. dyssymetra*.

Hebella laterocaudata Billard, 1942
(fig. 9)

Hebella laterocaudata Billard, 1942: 69, fig. 7; Van Praët, 1979: 883, fig. 21; van Soest, 1976: 81; Boero, 1980: 134; Calder, 1991: 39-40.

Discussion.— Insertion of the pedicel on one side of the hydrotheca is here provisionally considered a specific character, even though some colonies in other species may have at least some hydrothecae with this feature (see, for instance, some of the morphological variations of *Hebella parasitica* figured by Hadzi, 1913).

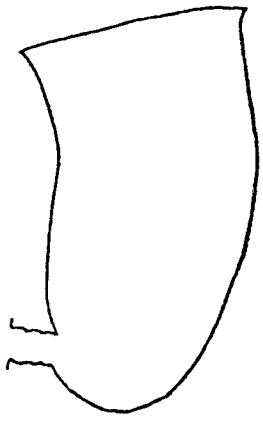

Fig. 9. *Hebella laterocaudata*. Hydrotheca. After Billard (1942).

Hebella furax Millard, 1957
(figs 10, 11)

Hebella furax Millard, 1957: 200, fig. 8; Millard, 1964: 10, fig. 2 B, D; Millard & Bouillon, 1973: 59; Millard, 1975: 181, fig. 60A-C; Watson, 1975: 159, fig. 2; Vervoort & Vasseur, 1977: 12; García Corrales et al., 1979: 14-15, fig. 5; Boero, 1980: 34; Gili, 1982: 152.

? *Hebella parasitica*; Hirohito, 1995: 122-123, fig. 34 g-i.

Material.— Mahé, Ile Ronde, Seychelles: several fertile colonies growing on *Macrorhynchia* sp. (det. Millard & Bouillon) (MRAC no. 2.740).

Living material. — Laing Island (Papua New Guinea): several living fertile colonies growing on aglaopheniids.

Hydroid.— Hydrothecae almost conical when growing on upper part of the host, cylindrical when growing on lower part of the same host, asymmetrical to symmetrical, with everted margin, sharply or slightly oblique, with short to long, wrinkled or annulated pedicels, with a membranous diaphragm (sometimes absent) and an annular thickening. Hydranth with 20-26 tentacles. Gonotheca as big as or slightly bigger

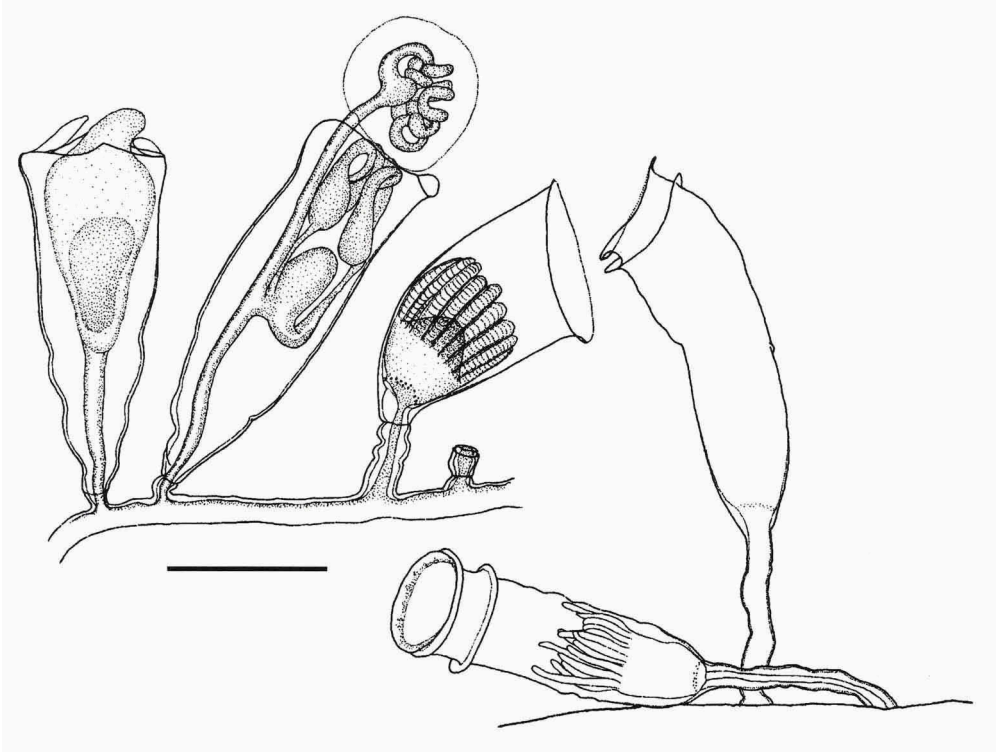

Fig. 10. *Hebella furax* from Laing Island, Papua New Guinea. Left: portion of colony with one hydrotheca and two gonothecae, growing in beween aglaopheniid hydrocladia. Right: two hydrothecae on base of hydrocaulus of aglaopheniid host (the hydrorhiza is behind the host's hydrocaulus). Scale bar: 0.5 mm.

than hydrotheca, with four opercular flaps, on short pedicel, slightly undulated walls, truncated distally, tapering at base. Opercular flaps sometimes lost after medusa liberation.

Newly liberated medusa.— Bell almost quadrate, evenly covered with nematocysts (two types of microbasic mastigophores), jelly of uniform thickness, manubrium short, widest at base, mouth with four lips, four radial canals, four perradial tentacular bulbs, two opposite ones bearing a long tentacle each, the other two bearing one short tentacle each (one shorter than the other), four small atentaculate interradial bulbs. No ocelli.

One-day-old medusa.— Bell spherical, new tentacles developing from interradial bulbs, eighth adradial atentaculate bulbs, each perradial and interradial bulb with an evident adaxial ocellus, ocelli appearing also on some of adradial bulbs. Manubrium widening at base, with the four lips more pronounced than in newly liberated medusa. Exumbrellar nematocysts almost absent.

Two-day-old medusa.— Bell spherical, four well developed perradial tentacles, four developing interradial tentacles, eight adradial atentaculate bulbs. Four additional radial canals in differing states of development (one almost complete) starting from interradial sides of the manubrium. One developing adradial radial. Manubrium cruciform, with four pouches corresponding to the lips.

Discussion.— Great care has been given to the identification of variations of the hydrothecae within colonies. The almost all-embracing description of the hydroid stage given above is due to the fact that the hydrothecae growing at the base of the stem of the aglaopheniid hosts are sharply cylindrical and have a long pedicel, being so different from the ordinary hydrothecae that they might be referred to different species (or even to the genus *Scandia*) in the absence of a common hydrorhiza. Some hydrothecae have a membranous diaphragm, but some have not.

The incomplete development of the medusae did not allow referral to a medusa-based genus with certainty, but did confirm the presence of ocelli in some medusae of the Hebellinae. In the present material some small dark pigment spots were visible in the bulbs of the newly-released medusa, but they were so scattered to be visible only at high magnification. After one day the spots converged and formed a clearly visible adaxial ocellus on each of the main tentacular bulbs. New atentaculate bulbs had ocelli too.

This inconspicuousness of the ocelli in the medusa buds and in the newly liberated medusae could explain why ocelli were not observed in the specimens of *Hebella scandens* examined by Hirohito (1969) and Millard (1975). The presence or absence of ocelli could so be due to differences in development of the medusa and, therefore, the absence of ocelli in newly liberated medusae cannot be regarded as a reliable character if further development is not observed.

In the light of the features of the two-day-old medusa of *Hebella furax* described here, the fully developed medusae of the Hebellinae could be referred to one of the leptomedusan genera having ocelli and multiple radial canals but with unknown hydroids, namely: *Melicertissa* (Laodiceidae) or *Orchistomella* (Melicertidae) (see Bouillon, 1985, for diagnoses).

The growth of the stolon in the hydrocaulus of the host (not observed in the presently examined specimens), is similar to that of *Hebella dispolians* (Warren, 1909),

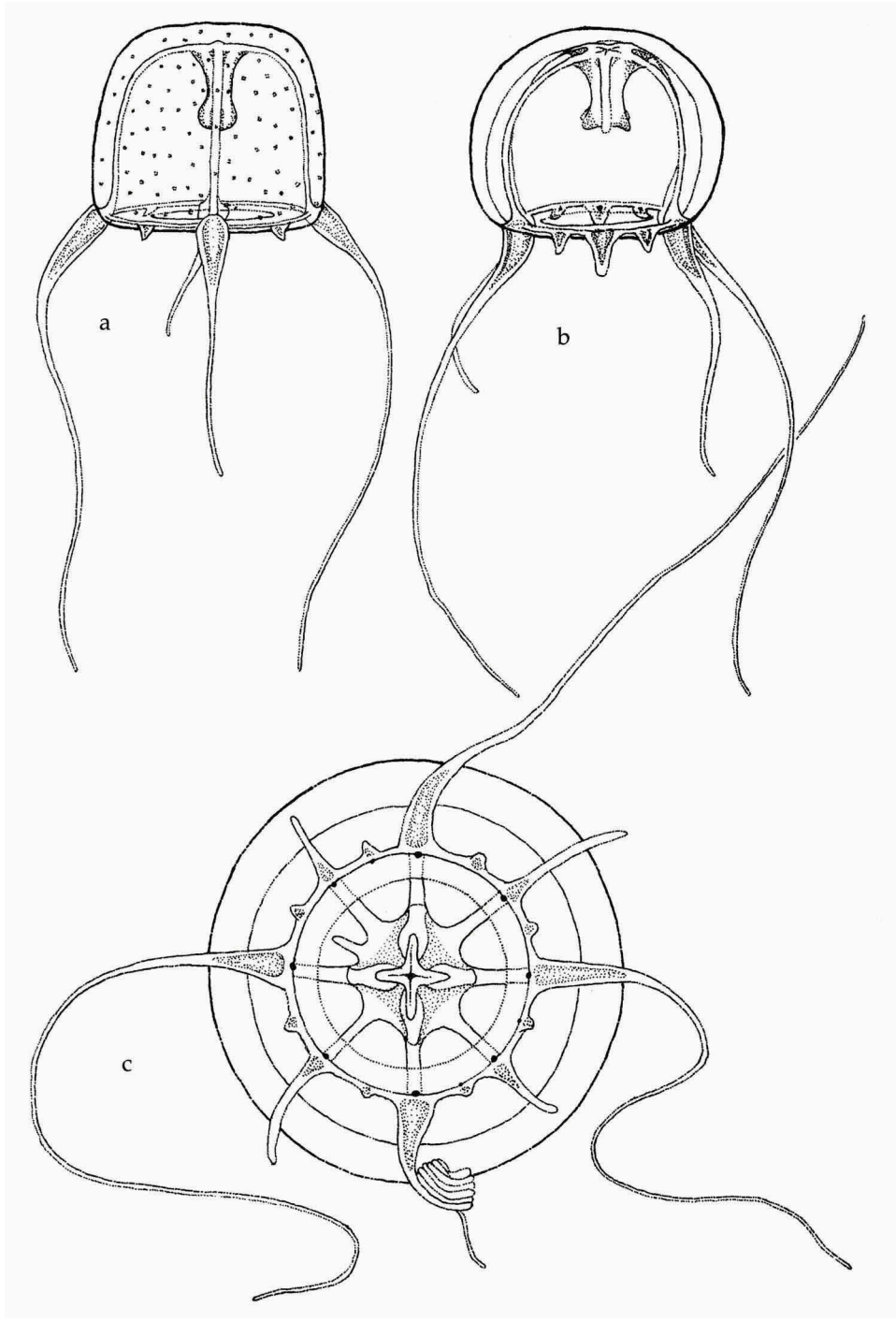

Fig. 11. *Hebella furax* from Laing Island, Papua New Guinea. a: newly released medusa from laboratory-reared colony, diameter of bell: 0.4 mm; b: 1-day-old medusa, diameter of bell: 0.5 mm; c: 2-day-old medusa, diameter of bell: 0.7 mm.

though less developed. Millard (1975) based the separation between the two species on both size and degree of integration with the host colony.

As noted by Vervoort & Vasseur (1977), the hydroid is similar to that of *Hebella parasitica* and has probably been reported as such in many accounts of Pacific hydroids. *Hebella parasitica*, however, was described by Ciamician (1880) from the Mediterranean Sea, where it has since been shown to produce medusoids with gonads on the manubrium (see Boero, 1980). Due to differences in the medusa stage, the present material cannot be *H. parasitica*. Possibly, records of *H. parasitica* from the Pacific are referable to *H. furax*, in particular those of Hirohito (1995) who reported medusa buds with three long tentacles from Japanese material, distinguishing it from *H. furax* by the absence of opercular flaps in the gonotheca, a feature here demonstrated as having poor diagnostic value.

Hebella muscensis Millard & Bouillon, 1975
(fig. 12)

Hebella muscensis Millard & Bouillon, 1975: 10, fig. 3 A, B; Boero, 1980: 134; Calder, 1991: 39, 41.
non *Campanularia corrugata* Thornely, 1904: 114-115, pl. 1, fig. 2 (see section 2).

Material.— Mahé, Anse de la Mouche, Seychelles: several fertile colonies growing on *Synthecium* spec. det. Millard & Bouillon (MRAC no. 3.551).

Living Material.— Laing Island (Papua New Guinea): several fertile living colonies growing on aglaopheniids.

Hydroid.— Most hydrothecae cylindrical, with everted, oblique margin, basally asymmetrical, with membranous diaphragm and a slight annular thickening. Hydrothecal walls with 5-10 annuli. Pedicel short, smooth to ringed. Hydranth with 12-16 tentacles. Gonotheca same size as hydrotheca, with four opercular flaps, bent over hydrorhiza, asymmetrical, with up to 11 rings, truncate distally, tapering towards base, on short pedicel.

Newly liberated medusa.— Bell spherical, evenly covered with nematocysts (microbasic mastigophores of three sizes), jelly uniform in thickness, manubrium short, mouth with no evident lips, four radial canals, four perradial tentacular bulbs, each bearing a long tentacle, four small atentaculate interradial bulbs. Each bulb with an adaxial ocellus.

Discussion.— The present material agrees with the descriptions of both hydroid and medusa buds given by Millard & Bouillon (1975). The presence of ocelli is confirmed in the liberated medusa, reinforcing the above-mentioned assumption that hebellid medusae may have some affinity with medusae of the Laodiceidae (but also with other Leptomedusae with ocelli).

The two nominal species *Campanularia corrugata* Thornely and *Campanularia costata* Bale were regarded as identical by several authors, but Millard & Bouillon (1975) showed that the descriptions of each of these species could apply to two species with indistinguishable hydroids but with different gonothecal content: one with infertile medusa buds and the other with already distinguishable sex cells (interpreted by them as a fixed gonophore). They retained both *C. corrugata* and *C. costata* as doubtful

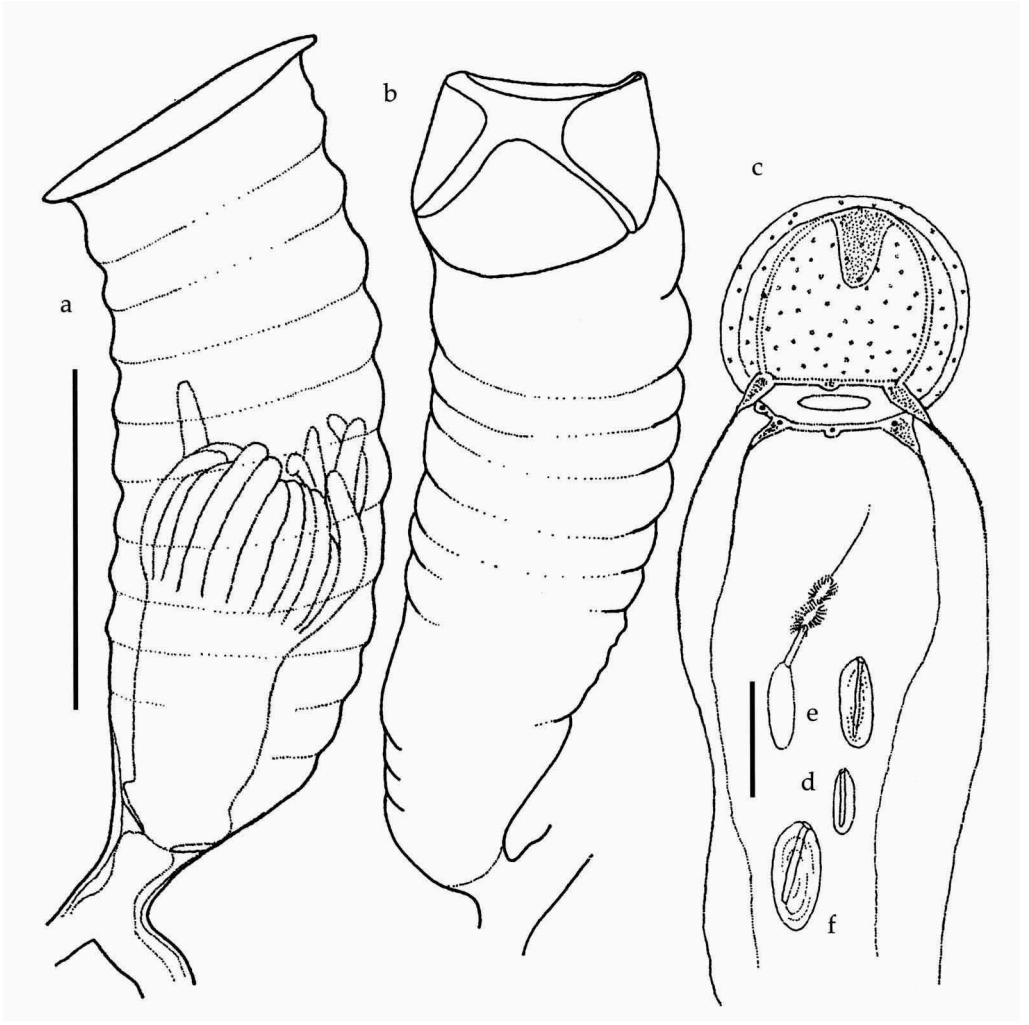

Fig. 12. *Hebella muscensis* from Laing Island, Papua New Guinea. a: hydrotheca; b: gonotheca; c: newly released medusa, diameter of bell: 0.5 mm; d-f three types of microbasic mastigophores on exumbrella. Scale bars: a-b: 0.5 mm; d-f: 10 μm.

due to the incompleteness of the descriptions, and named the material with medusa buds *Hebella muscensis* spec. nov., and the material with fixed gonophores *Scandia tubitheca* spec. nov. (see below for discussion of *Anthohebella tubitheca*).

Genus *Anthohebella* gen. nov.

Diagnosis.— Colony stolonal, hydrotheca on short pedicel, campanulate, usually with annular thickening and thin membranous diaphragm. Hydranth with conical hypostome. Gonotheca solitary, originating from hydrorhiza, with or without opercular flaps. Swimming gonophores with a velum, four radial canals, four marginal atentaculate bulbs, and gametes on the spadix ("manubrium").

Etymology.— from *Antho-*, with reference to Anthomedusae, and *Hebella*, a genus of Hebellinae.

Type species: *Lafoea parasitica* Ciamician, 1880. Type locality: Rovinj, northern Adriatic Sea.

Discussion.— Boero (1980) described the liberated medusoid of the nominal species *Hebella parasitica* and suggested that the abnormal position of the gonads, typical of the Anthomedusae, might require assignment of the species to a separate genus. This exceptional feature is the only character that distinguishes the newly proposed genus from *Hebella*. Boero & Bouillon (1989) tried to solve the systematic problem of thecate (leptomedusan) hydroids producing medusae with gonads on the manubrium, and so similar to Anthomedusae, by interpreting such liberated structures as swimming gonophores, combining characters of medusae and fixed gonophores. In their interpretation, the so-called manubrium should be a spadix. Petersen's (1979, 1990) argument that genera identified only on the basis of the presence of fixed gonophores or liberable eumedusoids are probably polyphyletic because such structures can originate independently by paedomorphosis within the same clade, is accepted here. The origin of such specialized morphs as swimming gonophores, however, presumably involved a more complex series of changes than simple medusa reduction, and its parallel occurrence in a clade is here considered as unlikely, even though monophyly of *Anthohebella* remains a matter of speculation.

In both *Anthohebella parasitica* and *A. brevitheca* a mouth has been observed (see below for references and descriptions), whereas spadices usually lack a mouth. However, in the haleciids, for instance, the female blastostyle can have mouth and tentacles (Billard, 1904a), so the presence of a mouth has been recorded in other leptomedusan gonophores.

Anthohebella parasitica (Ciamician, 1880)
(fig. 13)

Lafoea parasitica Ciamician, 1880: 673, fig. 39; Jickeli, 1883: 629, pl. 27, figs 21-25; Graeffe, 1884: 355-357; Von Lendenfeld, 1884: 912; Schneider, 1897: 483; Babic, 1904: 212; Babic, 1910: 210; Vanhöffen, 1910: 314.

Hebella parasitica; Marktanner-Turneretscher, 1890: 213; Carus, 1884: 10; Babic, 1911: 227-230, figs 1-2; Hadzi, 1913: 201-210; Stechow, 1913: 103-105, figs 75-78; Bedot, 1916: 124; Bedot, 1918: 153; Stechow, 1919: 76-77; Neppi, 1921: 19-20, fig. 13; Stechow, 1923d: 9; Bedot, 1925: 226; Leloup, 1934: 8; Perrier, 1936: 22; Leloup, 1937a: 4, 28; Leloup, 1938: 8, fig. 5; Da Cunha, 1941: 1-5, figs 1-2; Da Cunha, 1944: 42-43, fig. 20; Da Cunha, 1950: 124; Rossi, 1950: 217-218, fig. 12b; Picard, 1951a,: 347, 349; Dawydoff, 1952: 55; Yamada, 1958: 51, 55; Yamada, 1959: 45; Riedl, 1959: 646; Ito & Inoue, 1962: 449, 457, figs 78-79; Hadzi, 1965: 187, fig. 34; Riedl, 1970: 150, fig. 41; Vervoort, 1972: 64; Mergner & Wedler, 1977: 16, pl. 2, fig. 15; Vervoort & Vasseur, 1977: 12-13; García Corrales et al., 1979: 11-16, fig. 6; Boero, 1980: 133-136, figs 1-7; Boero, 1981b: 109, fig. 1; Gili, 1981: 107; Gili, 1982: 71-72, 144, 174, fig. 32; Florez-Gonzalez, 1983: 119, 123; Gili et al., 1984: 413, 422; Gili & García-Rubies, 1985: 43, 51, fig. 4h; Izquierdo et al., 1986: 85, fig. 3; Llobet et al., 1986: 38, fig. 4 C; Boero & Fresi, 1986: 143; Rees & Vervoort, 1987: 36, fig. 6d; Roca & Moreno, 1987: 20, figs 19, 32; Boero & Bouillon, 1989: 37; Gibbons & Ryland, 1989: 380, 394-395; Ryland & Gibbons, 1991: 527, 559; Park, 1993: 264-265, fig. 2; Vervoort, 1993: 544; Altuna Prados, 1994: 44, fig. 2 B, C.

?*Lafoeina parasitica*; Nutting, 1900: 9, 13, 28.
non *Lafoea parasitica*; Broch, 1912: p. 40, fig. 12.
non *Hebella parasitica*; Hirohito, 1995: 122-123, fig. 34 g-i.

Material.— Pontetto, Genova, Italy (Ligurian Sea) (RMNH Coel. no. 13083), and Blanes, Spain (Western Mediterranean): many fertile colonies growing on aglaopheniids .

Discussion.— See Boero (1980) for the description of hydroid and swimming gonophore. See also discussion on *Hebella furax*. Several specimens of newly liberated swimming gonophores collected from Blanes had a gastric cavity and were able to ingest *Artemia* eggs whose shells had been removed with the aid of fine needles.

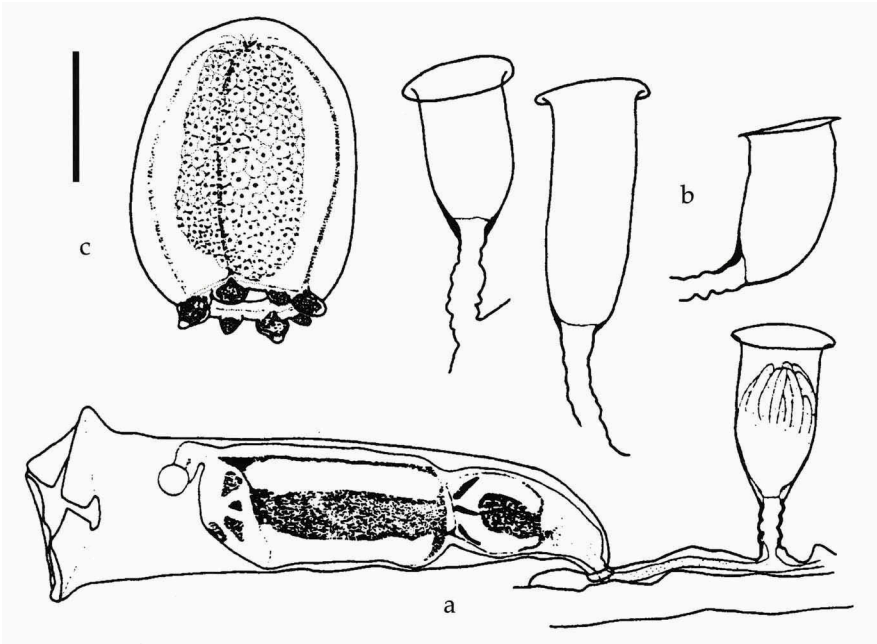

Fig. 13. *Anthohebella parasitica*. a: portion of colony with one hydrotheca and one gonotheca containing two swimming gonophores; b: three hydrothecae; c: female swimming gonophore. Scale bar: 0.5 mm. After Boero (1980).

Anthohebella brevitheca (Leloup, 1938)
(fig. 14)

Hebella brevitheca Leloup, 1938: 7, fig. 4, pl. 1, fig. 3; Boero, 1980: 134; Antsulevich, 1983: 1141-1143, fig. 9; Antsulevich, 1987: 46-47, fig. 10; Calder, 1991: 39-40.
Scandia brevitheca; Hirohito, 1995: 129-131, fig. 37 a-f.

Material.— Northern part of Sagami Bay, Japan: type series, five microslide preparations of fertile colonies growing on *Macrorhynchia phoenicea* (Busk, 1852) (IRSNB no. I.G. 11891).

Hydroid.— Examination of type material confirmed the original description by Leloup (1938) as far as the perisarcal structures and the hydranth are concerned, but

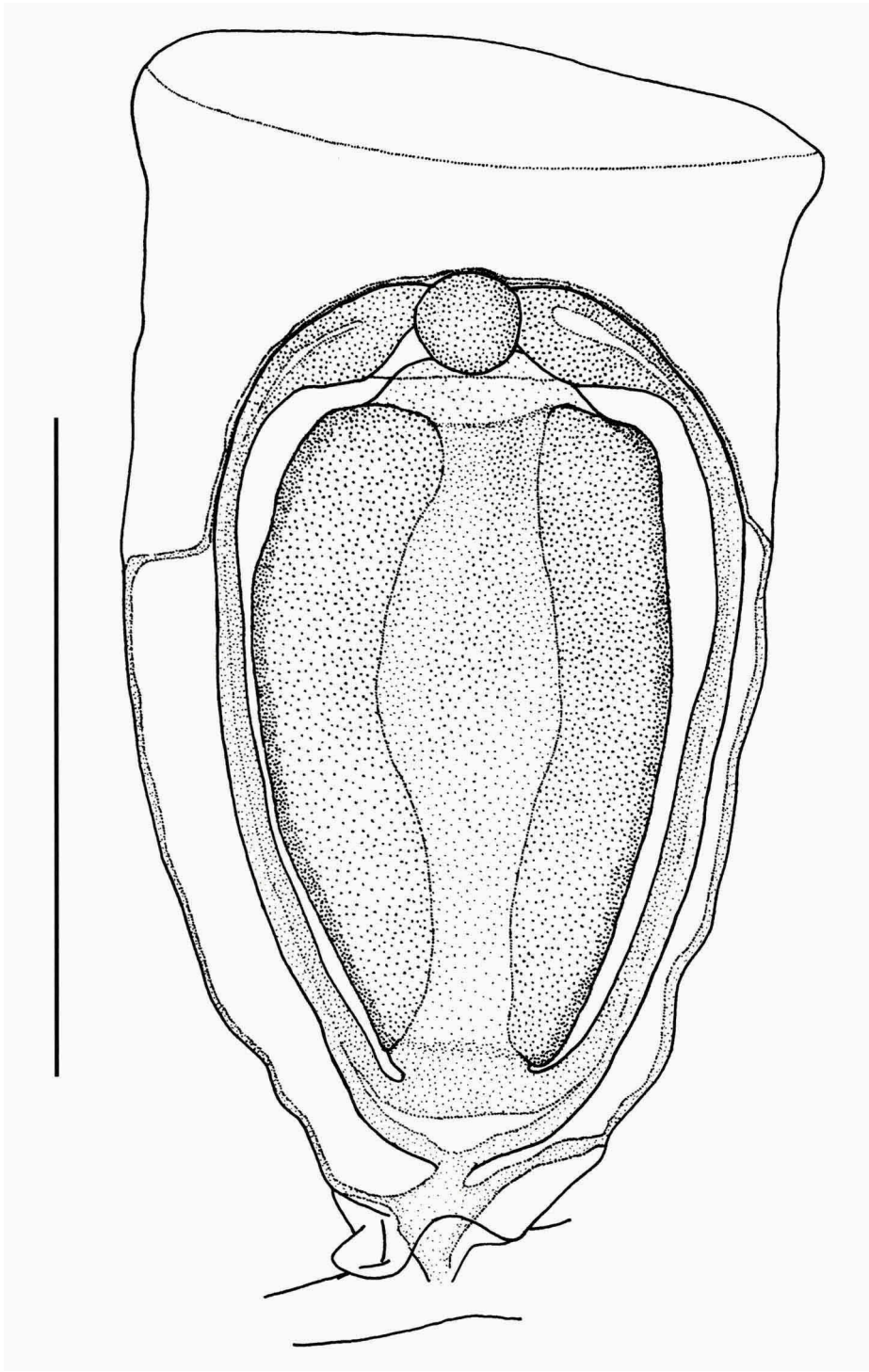

Fig.14. *Anthohebella brevitheca*. Type material from Sagami Bay, Japan. Gonotheca containing one swimming gonophore. Scale bar: 0.5 mm.

allowed recognition of distinctive features in the gonosome, simply described by him as "containing male cells" and figured poorly. The following description of the gonosome of type material integrates the original description by Leloup (1938).

Gonosome.— Gonotheca with simple, wide opening, cylindrical for upper half of its length, tapering and bending basally. A single medusa bud, enveloped in an ectodermal sheath ending as a terminal plate closing the gonothecal opening. In the umbrella of the medusa bud striated muscles are recognizable, together with four radial canals, leading to four large, atentaculate bulbs. Velum present, with velar opening. Spadix large, occupying most of subumbrellar cavity, with four distinct interradial rows of male cells. In one specimen a mouth is evident.

Discussion.— The striated muscle of the subumbrella, the presence of radial canals, bulbs and velum suggest that this medusa bud is a swimming gonophore. The "history" of the description of the present species clearly reflects the attitude of one-stage (hydroid or medusa) oriented scientists. Leloup (1938) prepared extremely good slides, on which gonosomal structures are easily detectable after almost 60 years since preparation. He merely described the presence of male cells, without mentioning the type of the gonosome.

The present description can be expanded by the one given by Hirohito (1995: 129), who reported the gonothecae as containing "Medusoids with well developed manubrium, without mouth opening, with mature gonad around manubrium, with four radial canals and a ring canal, with eight short marginal tentacles, without statocysts". The proposal by Hirohito (1995) to include this species in *Scandia* (a genus identified by the presence of fixed gonophores), however, cannot be accepted.

Anthohebella tubitheca (Millard & Bouillon, 1975) (fig. 15)

Scandia corrugata; Millard & Bouillon, 1973: 60, fig. 8D-F.
Scandia tubitheca Millard & Bouillon, 1975: 10; Hirohito, 1995: 133-134, fig. 39 a-e.
non *Campanularia corrugata* Thornely, 1904: 114-115, pl. 1.

Material.— Seychelles: holotype mounted on slide, one fertile colony with gonothecae (SAM no. SAM-H 2919).

Discussion.— Millard and Bouillon (1975) recognized two hebellid species with identical hydroids but with different gonosomal contents. They proposed the name *Hebella muscensis*, for the material with immature medusae and the name *Scandia tubitheca* for the material with fixed gonophores (see *Hebella muscensis* on p. 22). Their drawing of the gonophore shows the presence of sex cells, but re-examination of type material allowed recognition of a medusoid structure with gonads around a "manubrium", here identified as a swimming gonophore. *Scandia tubitheca* was reported as growing on other hydroids by Millard & Bouillon (1975), but *Scandia* hydroids are usually epiphytic, whereas *Hebella* colonies have been recorded living only on other hydroids. Furthermore, *Scandia* hydroids have long pedicels and *Hebella* hydroids short ones, and "*Scandia*" *tubitheca* has short pedicels. The gonotheca too, with its four opercular flaps, is typically hebellid, and different from the gonothecae reported for *Scandia*, which are usually dimorphic (e.g. Broch, 1933; Boero, 1981a). Therefore, we

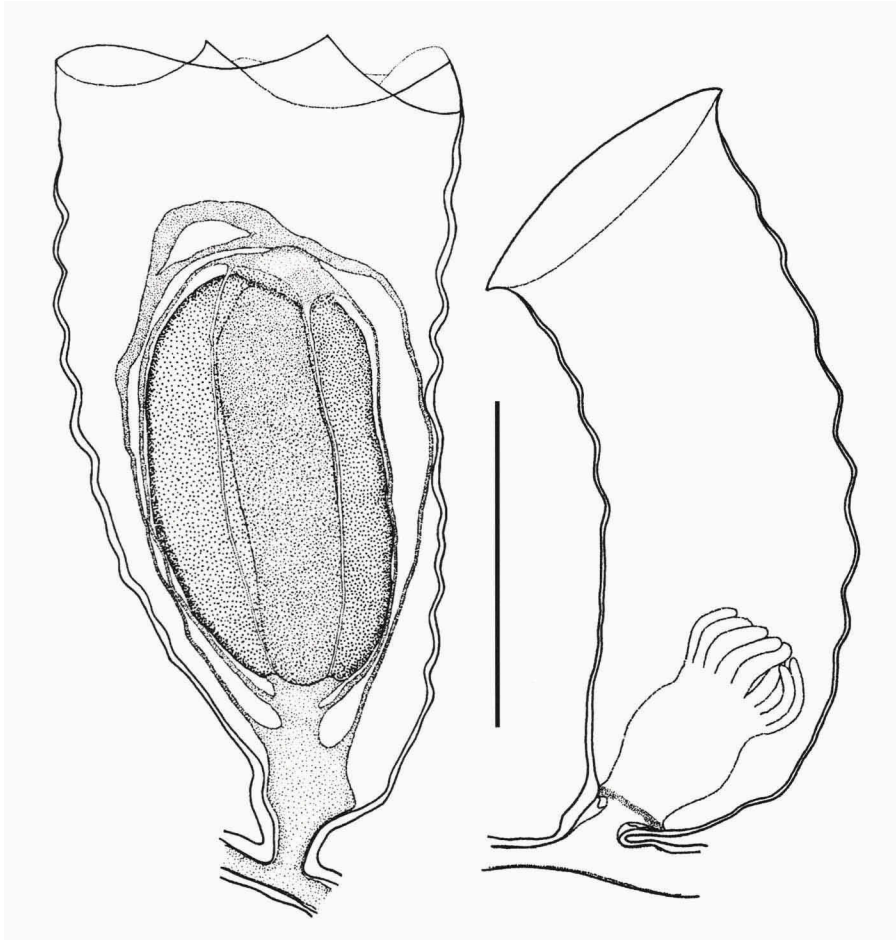

Fig. 15. *Anthohebella tubitheca*. Type material from the Seychelles, optical section. Right: hydrotheca; left: gonotheca containing one swimming gonophore. Scale bar: 0.5 mm.

here transfer *Scandia tubitheca* to the genus *Anthohebella*. Hirohito (1995) reported the medusoids of *S. tubitheca* as having gametes on the radial canals. If this feature will be confirmed, the species should be transferred to *Hebella*. Locating gametes in ripe medusoids inside the gonotheca may be difficult due to tissue packing.

Anthohebella najimaensis (Hirohito, 1995)
(fig. 16)

Scandia najimaensis Hirohito, 1995: 131, fig. 38 a-e, pl. 8 fig. B

Discussion.— Hirohito (1995: 131) reported this species as growing on other hydroids and described the gonophores as "medusoids, with manubrium surrounded by gonad, without radial canals, ring canal or marginal tentacles", also suggesting that "radial canals and a ring canal might have been reduced with the maturation of the gonad". These features match the diagnosis of *Anthohebella*.

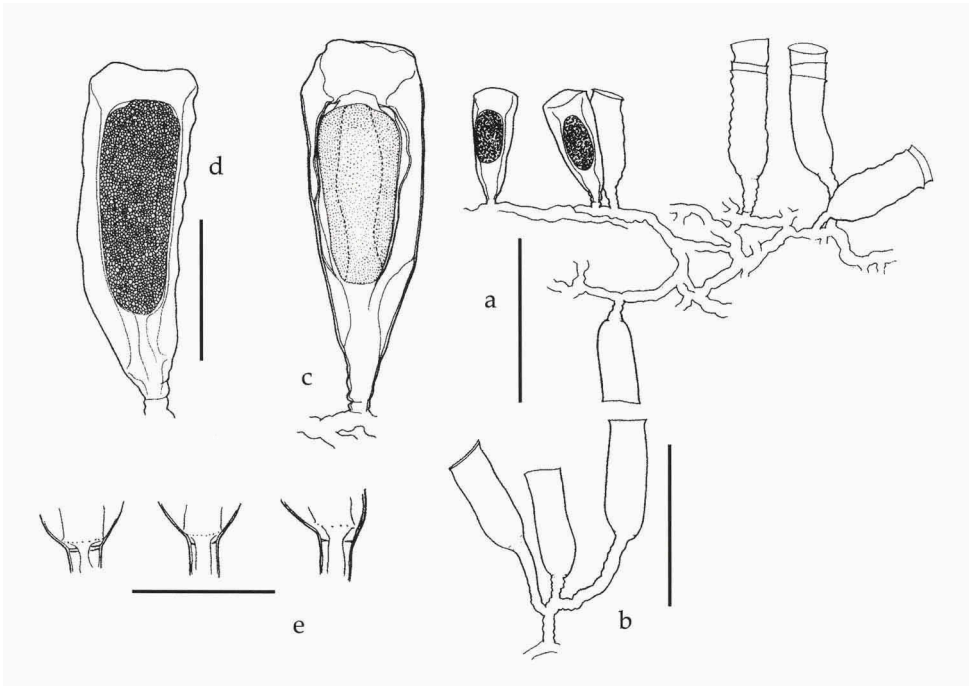

Fig. 16. *Anthohebella najimaensis*. a: part of colony with gonophores; b: hydrothecae; c - d: gonophores; e: bases of hydrothecae. Scale bars: a - b: 1.5 mm; c - e: 0.5 mm. Redrawn after Hirohito (1995).

2 - Nominal species considered conspecific with currently recognized species

All nominal species accommodated at least once in *Hebella* or *Hebellopsis* are listed chronologically below, and the names retained as valid are given in bold. When a species has been occasionally referred to a genus of medusa-producing hebellids by a few authors and to other genera by all other authors, only the records of medusa-producing hebellids are listed.

Hebella pocillum (Hincks, 1868) = ***Lafoea dumosa* (Fleming, 1820)**

Lafoea pocillum Hincks, 1868: 204-205, pl. 40, fig. 2; Bedot, 1918: 175; Bedot, 1925: 266; Vervoort, 1946: 201; Naumov, 1960 (1969): 9, 61, 65, 116, 273-274, fig. 161; Rees & Thursfield, 1965: 80.

Hebella pocillum; Nutting, 1901: 159, 175; Jäderholm, 1909: 19, 71; Ritchie, 1911: 33; Fraser, 1911: 51; Fraser, 1918: 353; Fraser, 1921: 166; Bedot, 1925: 261; Fraser, 1927: 326; Fraser, 1931: 481; Fraser, 1937: 114, pl. 24, fig. 130; Fraser, 1944: 207; Fraser, 1946: 57, 189-190; Yamada, 1955: 122, fig. 1B; Patriti, 1970: 27, fig. 27; Rees & Vervoort, 1987: 41.

Hebella (*Lafoea*) *pocillum*; Torrey, 1902: 12, 22; Hartlaub, 1905: 587.

non *Hebella pocillum* v. *adriatica*; Babic, 1910: 213, pl. 1, figs 2 a, b.

Lafoea fruticosa f. *pocillum*; Vervoort, 1949: 148.

non *Scandia pocillum*; Picard, 1951: 349; Picard, 1951b: 261; Picard, 1955: 187; Rossi, 1961: 81, fig. 2; García Corrales et al., 1979: 23-24, fig. 10; Gili, 1982: 72-73, fig. 33; Gili et al., 1984: 422.

non "*Scandia pusillum*"; Gili et al., 1984: 414.

Discussion.— Cornelius (1975), after examination of type material, considered *Lafoea pocillum* Hincks, 1868, as conspecific with *Lafoea dumosa* (Fleming, 1820).

Hebella gigas (Pieper, 1884) = ***Scandia gigas* (Pieper, 1884)**

Lafoea gigas Pieper, 1884: 165; Carus, 1884: 10; Schneider, 1897: 483, 503, 508; Babic, 1904: 211-212; Bedot, 1916: 141; Bedot, 1918: 175; Bedot, 1925: 261.
Lafoea pocillum f. *adriatica*; Babic, 1910: 213, fig. 2 a, b.
?*Hebella gigas*; Hadzi, 1913: 209, figs 34-35.
Croatella gigas; Hadzi, 1915: 64-78, figs 22-27; Stechow, 1923a: 139.
Hebella gigas; Stechow, 1919: 76; Leloup, 1934: 8.
Hebellopsis gigas; Broch, 1933: 61-62, fig. 22.
Scandia gigas; Boero, 1981a: 190, fig. 6; Gili & Castello, 1985: 9-14; Gili & García Rubies, 1985: 45, 51, fig. 6 E-F; Gili, 1986: 171, fig. 4, 27B-C; Llobet, et al., 1986: 35, 39, fig. 4H.

Living material.— Portofino, Genova, Italy (Ligurian Sea): several fertile colonies growing on algae.

Discussion.— Authors working in the Mediterranean area used the name *Scandia pocillum* for *Lafoea gigas* Pieper (1884) (see under *Hebella pocillum*). Boero (1981a) reintroduced the name *S. gigas* since Cornelius (1975) showed that *L. pocillum* is conspecific with *L. dumosa*. Hadzi (1915) based his genus *Croatella* on material he considered identical with that described by Pieper as *L. gigas*. *Scandia* Fraser, 1912 predates *Croatella* Hadzi, 1915.

Hebella neglecta Stechow, 1913 = ***Scandia neglecta* (Stechow, 1913)**

Hebella neglecta Stechow, 1913a: 139; Stechow, 1913b: 108, fig. 83; Hadzi, 1916: 26-27; Jäderholm, 1919: 10, pl. II, fig. 5; Stechow, 1923a: 138; Nutting, 1927: 208; Boero, 1980: 134; Calder, 1991: 39.
Croatella neglecta; Stechow, 1923d: 9.
Scandia neglecta; Fraser, 1936: 50, fig. 3; Hirohito, 1995: 131-133, fig. 38 f-i.

Discussion.— Hirohito (1995) described the gonophores as styloids, thus confirming assignment of this species to the genus *Scandia*, as suggested by Fraser (1936). Specimens of this species, however, have always been reported as growing on other hydroids, a substrate typical for both *Hebella* and *Anthohebella*. If further studies will reveal the presence of swimming gonophores in the gonotheca, this species should be assigned to *Anthohebella*.

Hebella michaelseni Broch, 1914 = ***Hebella scandens* (Bale, 1888)**

Hebella Michaelseni Broch, 1914: 32, fig. 7, pl. 1, fig. 2; Stechow, 1925b: 522.
Phortis michaelseni; Stechow, 1923a: 139.
Hebella scandens var. *michaelseni*; Vervoort, 1959; 238-239, fig. 13; Gili, Vervoort & Pagés, 1989: 72-73, fig. 3.

Material.— Mussera, Kinsembo, Ambrizette (Angola): type series, five slides with infertile colonies growing on *Sertularella polyzonias* (Linnaeus, 1758), det. H. Broch (IRSNB, no. I.G. 11365); *Hebella scandens* var. *michaelseni*, W coast of Africa, 5°37'N 0°38'E, 50 m depth, St. 85, 30.i.1946, Atlantide Expedition St. 85: one infertile colony mounted on slide, growing on *Sertularella undulitheca* Vervoort, 1959 (RMNH Coel. no. 1289).

Discussion.— Gonosome unknown. Stechow (1925b) considered *Hebella michaelseni* as identical with *H. calcarata*. Vervoort (1959) and Gili et al. (1989) considered *H. michaelseni* as conspecific with *Hebella scandens*, ranking it at variety level due to differences in size and corrugation of the hydrothecal wall. Such features are quite varied even within the same colony, so that *H. michaelseni* is considered conspecific with *H. scandens*.

Hebella spiralis Nutting, 1927 = ***Hebella scandens* (Bale, 1888)**

Hebella spiralis Nutting, 1927: 208-209, pl. 40, figs 4-6; Vervoort & Vasseur, 1977: 13; Rees & Vervoort, 1987: 35-36; Calder, 1991: 43-44.

Discussion.— Gonosome unknown. Hydrothecae of *Hebella scandens* can have a morphology similar to that of the present nominal species which, thus, could prove to be identical with *H. scandens*, as already proposed by Calder (1991) and also Vervoort & Vasseur (1977), who treated it as a variety of *H. scandens*.

Hebella michaelsarsi (Leloup, 1935) = ***Scandia michaelsarsi* (Leloup, 1935)**

Campanularia (?) *mutabilis*; Broch, 1914: 10, fig. 13.
Laomedea michael-sarsi Leloup, 1935: 22, fig. 9.
Scandia mutabilis; Fraser, 1944: 208, pl. XXXIX, fig. 187.
Hebella michael-sarsi; Vervoort, 1959: 242-243, fig. 16; Vervoort, 1968: 100; Boero, 1980: 134.
Scandia michael-sarsi; García Corrales, et al., 1979: 20-21, fig. 9.
Hebellopsis michaelsarsi Calder, 1991: 45-46.

Material.— Dry Tortugas (Florida): syntype mounted on slide, fragments of colonies, (IRSNB, no. I.G. 10.497); Atlantic Ocean 10°22'N 16°22'W, 17.xii.1945, Atlantide Exp. St. 44: one infertile colony in spirit, growing on *Idiellana pristis* (Lamouroux, 1816) (RMNH).

Discussion.— Gonosome unknown. This nominal species has been referred to *Laomedea* (Leloup, 1935), then to *Hebella* (Vervoort, 1959), *Scandia* (García Corrales et al., 1979) and *Hebellopsis* (Calder 1991). Fraser (1944) considered this species as conspecific with *Scandia mutabilis*. The original description by Leloup (1935) reports on a long and branched pedicel, a feature not shared by any other species of *Hebella* and typical of the genus *Scandia*. Contrary to what was stated by Calder (1991), who retained this species as valid due to the presence of a thick diaphragm, Leloup (1935) described the diaphragm as "mince" (thin). Vervoort (1959) reported on material growing loosely on *Idiellana pristis*, having a different habit from other *Hebella* species. Examination of syntype material, however, confirmed the presence of a diaphragm similar to that of *Scandia gigas*. We concur with Calder (1991) in retaining this species as distinct from *Scandia mutabilis* since this last species has an annular thickening and no diaphragm and, for the reasons given above, with García Corrales et al. (1979) in referring it to *Scandia*.

Hebella corrugata (Fraser, 1938) = ***Scandia corrugata* Fraser, 1938**

Scandia corrugata Fraser, 1938a: 46, pl. 11, fig. 52; Fraser, 1938b: 110; Fraser, 1938c: 133; Fraser, 1946: 58, 192.

Hebella corrugata; Cairns et al., 1991: 24.

Discussion.— Described as a species of *Scandia* by Fraser (1938a) and transferred to *Hebella* by Cairns et al. (1991). The figure given by Fraser shows characteristic gonothecae, much different from those of other *Hebella* species. The difference consists in them not being truncated distally and being smaller than the hydrotheca. Fraser (1938a) did not report about the type of gonophore. However, he based the genus *Scandia* Fraser, 1912 (Fraser, 1912a) on the presence of fixed gonophores, as opposed to *Hebella*, characterized by free medusae. His inclusion of the material in *Scandia*, thus, should implicitly mean that he considered the gonothecae as containing a fixed gonophore. The transfer of *Scandia corrugata* to *Hebella*, as proposed by Cairns et al. (1991), causes homonymy because there is another *Hebella* with the same name: *Hebella corrugata* (Thornely, 1904). We provisionally include the present species in *Scandia*.

Hebella (?) *eximia* Fraser, 1944 = ***Hebella scandens* (Bale, 1888)**

Hebella (?) *eximia* Fraser, 1944: 207, pl. 39, fig. 185; Fraser, 1946: 58, 190; Vervoort, 1968: 100; Boero, 1980: 134.

Discussion.— Gonosome unknown. Characterized by long, cylindrical hydrothecae. According to Fraser (1946: 190) "the nature of the trophosome should place this species with *H. calcarata*, and the distribution fits in perfectly, but judgement must be withheld until the gonosome is obtained". We agree with Fraser (1946) and consider *H. eximia* as conspecific with the nominal species *H. calcarata*, and so with *H. scandens*.

Hebella sinuosa (Vannucci, 1949) = ***Hebella scandens* (Bale, 1888)**

Hebellopsis sinuosa Vannucci, 1949: 237, pl. 2, fig. 24; Calder, 1991: 43-45.
Hebella sinuosa; Boero, 1980: 134.

Discussion.— Gonosome unknown. Calder (1991) tentatively considered *Hebellopsis sinuosa* as conspecific with *Hebella scandens*, a view we agree with.

Hebella besnardi (Vannucci, 1950) = ***Hebella scandens* (Bale, 1888)**

Hebellopsis besnardii Vannucci, 1950: 85, pl. 1, fig. 3; Calder, 1991: 43-45.
Hebella besnardi; Boero, 1980: 134.

Discussion.— Gonosome unknown. This nominal species has been already tentatively considered as identical with *H. scandens* by Calder (1991). We agree with this decision, due to insufficient knowledge of the variation and reproduction and resemblance of the drawings in the original description with some of the many different morphotypes of the hydrothecae of *H. scandens*.

Hebella urceolata Millard, 1964 = ***Hebella scandens* (Bale, 1888)**

Hebella urceolata Millard, 1964: 11-13, fig. 2 A; García Corrales, et al., 1979: 17, fig. 7.

Discussion.— Considered as conspecific with *H. scandens* by Millard (1975) and Calder (1991), a decision we concur with. García Corrales et al. (1979), considered it as valid, but similar to *H. scandens*, without noting the comments of Millard (1975) on its status.

Hebella thankasseriensis Mammen, 1965 = ***Hebella dispolians* (Warren, 1909)**

Hebella thankasseriensis Mammen, 1965: 5-6, figs 32-33: Boero, 1980: 134; Gibbons & Ryland, 1989: 395.

Discussion.— Gonosome unknown. Mammen (1965) did not cite the other two species of hebellids known to have stolons penetrating the tissues of their hosts (namely *H. furax* and *H. dispolians*), and considered this species as new due to this particular habit. His description and figures look similar to those of *H. dispolians*, so *H. thankasseriensis* is considered conspecific with it.

3 - Doubtful species

Most of the following species (listed alphabetically) have been based on insufficient diagnostic features, their descriptions being too general and the material, when available, being of uncertain identification. The treated species have been referred at least once to *Hebella* or to *Hebellopsis*. Since we retain *Hebellopsis* as identical with *Hebella*, we will refer all the folowing nominal species to *Hebella*.

Hebella calcarata (L. Agassiz, 1862)

Medusa:

Laodicea calcarata L. Agassiz, 1860-62: 350 (adult medusa); A. Agassiz, 1865a: 122-124, 126, 131-132, 138, 224, figs 184-189, 194 (adult medusa); A. Agassiz, 1865b: 91 (adult medusa); Claus, 1881: 89; Mayer, 1910: 204; Bigelow, 1914: 12. [= *L. cruciata* Forskål, 1775 = *L. undulata* (Forbes & Goodsir, 1853); Kramp, 1961: 14; Rees & Thursfield, 1965: 76.

non *Laodice (Lafoea) calcarata*; Metschnikoff, 1886: 83, pl. 4, figs 17-31, pl. 5, fig. 1.

non *Laodice calcarata*; Browne, 1907: 460, 463, 465-466.

Phortis calcarata; Stechow, 1923a: 139.

Hydroid:

Lafoea calcarata; auct. [not *Lafoea calcarata* (A. Agassiz, 1865a) = *Laodicea undulata* (Forbes and Goodsir, 1853)]; A. Agassiz, 1865a: 124-126, 132, figs 190-193 (hydroid and young medusa); Coues & Yarrow, 1878: 308; Levinsen, 1893: 170; Nutting, 1899: 748; Hargitt, 1901: 387, 568, figs 24, 50; Hargitt, 1902a: 14; Hargitt, 1902b: 554; Schydlowsky, 1902: 152; Billard, 1904: 481; Hargitt, 1904: 43; Hartlaub, 1905: 587; Billard, 1906a: 330; Billard, 1906b: 173-174, 177; Billard, 1906c: 157, 174; Browne, 1907: 463, 465-466; Congdon, 1907: 467; Mayer, 1910: 204.

Hebella calcarata; Nutting, 1901: 342, 352-353, 359, 369-370, 378, figs 56, 94; Nutting, 1904: 58; Thornely, 1904: 108, 116; Billard, 1907: 337, 339-340; Ritchie, 1909: 524; Kingsley, 1910: 28, pl. 5, fig. 43; Mayer, 1910: 202; Ritchie, 1910: 7; Ritchie, 1911: 800-801, 810; Fraser, 1912a: 371, fig. 34; Bale, 1913: 118-120; pl. 12, fig. 10; Levinsen, 1913: 284-285; Stechow, 1913: 105, fig. 79; Bale, 1915: 251-253; Fraser, 1918: 253; Jäderholm, 1920: 3; Fraser, 1921: 166; Jarvis, 1922: 332, 336; Bennitt, 1922: 149; Stechow, 1923a: 138-139; Bale, 1924: 235; Trebilcock, 1928: 4; Billard, 1933: 6; Leloup, 1937b: 96; Fraser, 1938a: 46; Fraser, 1939: 159, 165; Leloup, 1940: 8; Kramp, 1943: 23-40; Fraser, 1944: 205; pl. 39, fig. 183; Vervoort, 1946: 304; Fraser, 1947: 9; Fraser, 1948: 227; Picard, 1951: 161; Buchanan,

1957: 362; Ralph, 1958: 306-308, fig. 1 a-s; Pennycuick, 1959: 151, 188; Ralph, 1961: 236; Vervoort, 1968: 100; Hirohito, 1969: 14-16, fig. 11; Vervoort, 1972: 65; Leloup, 1974: 9, fig. 6; García Corrales et al., 1979: 11-14, fig. 4; Gili, 1982: 152; Spracklin, 1982: 246-249, fig. 115 e; Izquierdo et al., 1986: 86-88, fig. 4; Yamada & Kubota, 1987: 39; Gibbons & Ryland, 1989: 395; Hirohito, 1995: 118-120, fig. 33 d-h.

Hebella calcarata var. *contorta*: see *Hebella contorta*.

Hebellopsis calcarata; Yamada, 1959: 46.

Discussion.— Further rearing of the medusae with ocelli obtained from the hydroid of *Hebella scandens* might prove that the medusa described as *Laodicea calcarata* by L. Agassiz (1862) has a hebellid hydroid. If this were so, *H. calcarata* (L. Agassiz, 1862) would have priority over *H. scandens* (Bale, 1888), but such decision is premature with the presently poor state of knowledge. All records of *H. calcarata* hydroids do not refer to the original description of this medusa-based species, but to inference about its life cycle, and should be ascribed to *H. scandens*. The medusa-based nominal species *Laodicea calcarata* is currently regarded conspecific with *L. undulata* (Forbes & Goodsir, 1853) (see Bigelow, 1914; Kramp, 1961), and the hydroids of *Laodicea* are known to be operculated (see Metschnikoff, 1886; Russell, 1936; Russell, 1953 for *L. undulata*; Bouillon et al., 1991, for *L. indica* Browne).

For further discussion see remarks on *Hebella scandens*.

Hebella communis Calder, 1991

Hebella communis Calder, 1991: 42-45, fig. 26.

Material.— Atlantic Ocean, 2 km off Castle Rock (Bermuda): holotype in spirit, one infertile colony growing on *Thyroscyphus marginatus*, 60 to 90 m depth, 3.ix.1977 (ROM no. ROMIZ B293).

Discussion.— Gonosome unknown. The present nominal species was proposed with caution by Calder (1991: 43) who distinguished it from *Hebella scandens* "as having larger, less cylindrical hydrothecae and longer, distinctly annulated pedicels". The present evaluation of diagnostic characters of hebellid species showed that features such as those invoked by Calder (1991) to identify *Hebella communis* can be highly varied even within the same colony (see *H. furax* above) so that knowledge of the gonosome, especially when other distinctive characters are lacking, is essential. Furthermore, hebellids can show much modified morphologies according to the host on which they grow and to their position on it. *Hebella scandens*, being one of the most catholic hebellids in host choice, is thus a much varied species. *Hebella communis*, being based on insufficiently distinctive characters, is provisionally regarded as doubtful or, possibly, as conspecific with *H. scandens*.

Hebella corrugata (Thornely, 1904)

Campanularia corrugata Thornely, 1904: 114-115, pl. 1, fig. 2; Ritchie, 1907: 341; Ritchie, 1910a: 2, 4, 11; Ritchie, 1910b: 800-801, 809, 816; Ritchie, 1910c: 286, 830; Vanhöffen, 1910: 314.

Hebella corrugata; Vanhöffen, 1910: 271-314; Stechow, 1913: 105, figs 80-82; Broch, 1914: 30, fig. 6; Jäderholm, 1919: 11, fig. 6; Stechow, 1923a: 139-140; Stechow & Müller, 1923: 462, fig. 2; Hargitt, 1924: 487-488; Trebilcock, 1928: 4; Billard, 1941: 13, figs 3-4; Rees & Thursfield, 1965: 72-73; Mam-

men, 1965: 3, fig. 3O; Millard & Bouillon, 1975: 9.
Croatella corrugata; Hadzi, 1916, p. 26.
Halicornaria plumosa (gonotheca); Armstrong, 1879: 101.
Hebella costata corrugata; Billard, 1941: 13, figs 3-4.

Material.— Philippines, Cebu City, piers of harbour, 1976: one fertile colony in spirit, leg. M. Lourdes, det. W. Vervoort (RNHM Coel. no. 8129).

Discussion.— Gonosome unknown. Systematic position discussed by Millard & Bouillon (1975). Here considered as a doubtful species (see discussion of *H. costata, H. muscensis* and *Anthohebella tubitheca*).

The material from the Philippines bears gonothecae with medusa buds and closely resembles *H. furax*.

Hebella costata (Bale, 1884)

Campanularia costata: Bale, 1884: 56, pl. 1, fig. 3; Bale, 1888: 757; Billard, 1941: 13-14, figs 2-3; Ralph, 1958: 308-309, fig. 1; Pennycuick, 1959: 151, 188.

Material.— Madagascar, Isle Europe, 50 m depth, St. P. 9: one infertile colony mounted on slide, growing on *Plumularia* spec., leg. P. Vasseur, det. W. Vervoort (RMNH Coel. no. 8129); Comores, Mayotte Island, Dzaudzi reef, 2 m depth, 7. 1964; one infertile colony in spirit, growing on *Synthecium patulum* (Busk, 1852), leg. P. Vasseur, det. W. Vervoort (RMNH Coel. no. 8152).

Discussion.— Gonosome unknown. Millard & Bouillon (1975) suggested that the original description of this nominal species could apply to hydroids with medusae or with fixed gonophores and considered *H. costata* as a *nomen oblitum*. We consider it as doubtful.

Hebella cylindrata Marktanner-Turneretscher, 1890

Hebella cylindrata Marktanner-Turneretscher, 1890: 214, pl. 3, fig. 15; Pictet, 1893: 42; Marktanner-Turneretscher, 1898: 401; Versluys, 1899: 31-32; Jäderholm, 1904: 274; Billard, 1904b: 481; Billard, 1906c: 174-175; Babic, 1910: 210; Levinsen, 1913: 285; Bedot, 1916: 124; Bedot, 1918: 153; Bedot, 1925: 226; Vervoort, 1959: 241-242, fig. 15; De Haro, 1965: 108-109, fig. 3; Vervoort, 1966: 123; Vervoort, 1968: 100; Vervoort, 1972: 65-66; García et al., 1980: 12-13; Gili, 1982: 72.
Phortis cylindrata; Stechow, 1923a: 139.

Material.— Albatross collection D 3727: one infertile colony mounted on slide, growing on a hydroid labelled *Macrorhynchia phoenicea* (NHML no. 1970.3.3.48).

Discussion.— Gonosome unknown. This nominal species has been alternately included in and removed from the synonymy of *Hebella scandens* and *H. calcarata* by many authors, almost all of them stressing the necessity of knowledge of the gonosome for a final decision (see Vervoort, 1959). The original description did not report on features which could allow its distinction from other hebellids.

Hebella cylindrica (Von Lendenfeld, 1885)

Lafoea cylindrica Von Lendenfeld, 1885a: 908, 912, pl. 40, figs 4-5; Von Lendenfeld, 1885b: 690; Von Lendenfeld, 1887: 18; Farquhar, 1896: 461; Billard, 1904: 481; Jäderholm, 1904: 274; Billard, 1906d: 74; Warren, 1908: 342-343.

Hebella cylindrica; Marktanner-Turneretscher, 1890: 214; Pictet, 1893: 2, 41, 43, pl. 2, fig. 36; Vesluys, 1899: 29-31, fig. 1; Weltner, 1900: 585-587; Jäderholm, 1904: 271; Hartlaub, 1905: 586-588; Billard, 1907: 339; Warren, 1908: 342-343; Bale, 1913: 120, fig. 10; Levinsen, 1913: 284-285; Bedot, 1916: 124; Bedot, 1918: 153; Jarvis, 1922: 336; Stechow & Müller, 1923: 242; Bedot, 1925: 226; Totton, 1930: 155; Billard, 1942: 67, fig. 1; Fraser, 1944: 206, pl. 39, fig. 184; Fraser, 1946: 190; Vervoort, 1946: 305; Ralph, 1958: 308, fig. 1t; Vervoort, 1966: 123, fig. 25; Vervoort, 1972: 66; van Soest, 1976: 80; Boero, 1980: 134; Calder, 1991: 43-44: Cairns et al., 1991: 43-44.

Hebella cylindrica var. *elongata* Billard, 1942: 67, fig. 1; Vervoort, 1966: 123, fig. 25; van Soest, 1976: 80; Van Praët, 1979: 882.

Material.— *H. cylindrica* var. *elongata*. Siboga Expedition St. 257: syntype, numerous infertile colonies on *Sertularella moluccana* (von Campenhausen, 1896) (ZMA Coel. no. 5184, 5232); Siboga Expedition St. 257: syntype, one infertile colony mounted on slide, growing on *Sertularella moluccana* (MNHNP no. HL 190); *H. cylindrica* var. *elongata*. Acapulco, Panama, Galathea Expedition St. 716, 7°25'N 89°32'W, 6.v.1952, 3570 m depth: one infertile colony mounted in slide, growing on a bryozoan (?) (RMNH Coel. no. 3759).

Discussion.— Considered by many authors as conspecific with either *Hebella calcarata* or *H. scandens*, though Calder (1991) excluded it from the synonymy of *H. scandens*. In the original description Von Lendenfeld (1885a: 912) noted that "Near the bottom, which appears semi-spherical we find a perforated disc, forming a ring near the base of hydrotheca", a sentence which strongly suggests the presence of a perisarc diaphragm. Syntype material of *Hebella cylindrica* var. *elongata* consists of hydrothecae elongated due to rim renovation and, contrary to what is suggested by the original description, with a membranous diaphragm. The gonosome is absent in this syntype material, and features are insufficient for its identification.

The material described as *H. cylindrica* var. *elongata* by Vervoort (1966) is reported to grow on a bryozoan. The architecture of the supporting animal, however, is similar to that of erect hydroid colonies. If proven to be a bryozoan, this should be the only case of a *Hebella* not growing on hydroids. The thecae of the Galathea material are very narrow at the base; this feature may prove to be of specific value. Pictet (1893) described the gonotheca with medusa buds from material he referred to *H. cylindrica*. Due to the high degree of variation within the same colony, he considered the three nominal species *H. cylindrata* Marktanner-Turneretscher, 1890, *H. contorta* Marktanner-Turneretscher, 1890, and *H. scandens* (Bale, 1888) (but this last species with some doubt) as conspecific with *H. cylindrica* (Von Lendenfeld, 1885). Ralph (1958: 308), however, mentioned that no other record from the type locality (nor from New Zealand) was known and that the status of *H. cylindrica* was doubtful. If considered as conspecific with *H. scandens* (Bale, 1888), the name *H. cylindrica* (Von Lendenfeld, 1885) should have priority, as already suggested by Pictet (1893) who refrained from taking such a decision only due to incomplete knowledge of the gonosome of *H. scandens*. At present, materials referred to both *H. scandens* or *H. cylindrica* are known to produce free medusae, so that Pictet's caution could be removed and the two species

might be considered identical. Following Ralph's opinion on the identity of type material of *H. cylindrica*, we suggest regarding this nominal species as insufficiently described.

Hebella expansa (Fraser, 1938)

?*Scandia expansa* Fraser, 1938 b: 140, pl. 20, fig. 8; Fraser, 1946: 58, 191-192.
Hebellopsis expansa; Cairns et al., 1991: 24.

Discussion.— Gonosome unknown. The species is characterized by a ringed hydrotheca, a feature shared with other species of *Hebella*. Millard & Bouillon (1975) demonstrated that the absence of gonophores makes identification of hebellids unreliable when recognized only on such a feature.

Hebellopsis hartmeyeri Stechow & Müller, 1923

? *Lictorella halecioides*; Borradaile, 1905: 836-840, fig. 3 (gonotheca).
Hebellopsis hartmeyeri Stechow & Müller, 1923: 463, fig. 4; Stechow, 1924: 69; Stechow, 1925: 213-214, fig. F.

Material.— NNE of Heirisson Pong: one infertile colony on unidentified hydroid, mounted on slide, det. E. Stechow, redet. E. Leloup (IRSNB no. I.G. 11365).

Discussion.— Gonosome unknown. *Hebella hartmeyeri* is characterized by having a cylindrical, long and narrow hydrotheca, with a perisarc diaphragm. Such features, however, have been reported for *Hebellopsis ritchiei, Hebella plana, H. cylindrica* var. *elongata, H. communis, H. eximia,* and *H. sinuosa.* All are based on slight variations in much-varied characters such as the flaring of the hydrothecal rim or the length of the pedicel.

Hebella indica Stechow, 1922

Desmoscyphus humilis; Armstrong, 1879: 101 (gonotheca).
Hebella indica Stechow, 1922: 146; Stechow, 1923a: 138; Boero, 1980: 134.

Discussion.— Gonosome unknown. Stechow (1922) apparently never saw material of this species, describing it from a figure given by Armstrong (1879) of a gonotheca of *Desmoscyphus humilis* (= *Sertularia armstrongi* Bedot, 1925). The difference from *H. scandens*, according to Stechow (1922), should be the length of the pedicel.

Hebella lata Pictet, 1893

Hebella lata Pictet, 1893: 2, 40, pl. 2, figs 34-35; Ritchie, 1910: 7; Levinsen, 1913: 284; Bedot, 1918: 159; Bedot, 1925: 226.

Material.— Amboina: holotype, infertile colonies growing on fragments of stem of plumulariid (indicated as *Lytocarpus philippinus* in the original description, but as "tronc de Plumularien" on the label) (MHNG no. C 11/21).

Discussion.— Gonosome unknown. *Hebella lata* resembles other species with wide and short hydrothecae, and its description could apply to a generalized hebellid. Different hydrothecae from type material could be identified as *Anthohebella parasitica*, *Hebella furax* or *Hebella dyssymetra*, but lack of a gonosome makes identification impossible.

Hebella longa Stechow, 1926

Hebella longa Stechow, 1926: 98-99. Based on descriptions of ?*Lafoea pocillum*; Clark, 1876: 215, fig. 21, and ?*Lafoea sibirica*; d'Arcy Thompson, 1887: 393, fig. 2.

Discussion.— Gonosome unknown. Described without figure by Stechow (1926), it could be any of the hebellids with long hydrothecae.

Hebella parvula (Hincks, 1853)

Campanularia parvula Hincks, 1853: 178, pl. 4, fig. A.
Lafoea parvula; Hincks, 1868: 203, fig. 24, pl. 40, fig. 1; Bedot, 1910: 323; Bedot, 1912: 314; Bedot, 1916: 141; Bedot, 1918: 175; Bedot, 1925: 256.
Hebella parvula; Jäderholm, 1909: 19, 71; Stechow, 1923a: 139; Stechow, 1923b: 106; Stechow, 1925b: 441, fig. 16; Millard & Bouillon, 1973: 60; Millard, 1975: 182, fig. 59D; Boero, 1980: 134.
Lafoea pocillum var. *parvula*; Naumov, 1969: 274.

Discussion.— Gonosome unknown. The figures and description by Hincks (1853) give no indication of the presence of a diaphragm, suggesting assignment of this nominal species to *Lafoea*, an opinion already expressed by Naumov (1969). Cornelius (1975) could not locate the type material, but found contemporary specimens labelled *Lafoea parvula* in the collections of the Natural History Museum (London) and identified them as *Calicella syringa* with missing operculum, stating that the species could have been based on such material. The pedicel figured by Hincks (1868) has more marked annulations than present in *Lafoea*. Stechow (1925b) reported *Hebella parvula* from South Africa (see also Millard, 1975), but his figures and descriptions could be referable to *H. scandens*.

Hebella pusilla Stechow, 1923

Hebella pusilla Stechow, 1923a: 135; Stechow, 1923c: 5; Calder, 1991: 43.

Discussion.— Gonosome unknown. Stechow (1923a) described this species on the basis of a figure of *Sertularella quadrata* Nutting, 1895 published by Nutting (1904) in which an epizoic hydroid was shown. Calder (1991) tried to locate Nutting's material but found no epizoic hydroids, so that he considered this nominal species as dubious.

Hebella pygmaea (Alder, in Hincks, 1868)

Lafoea pygmaea Alder in Hincks, 1868: 205, pl. 40, fig. 3.
Hebella pygmaea; Nutting, 1901: 353, fig. 44; Kingsley, 1910: 28, pl. 5, fig. 44.

Discussion.— Cornelius (1975) identified the type material as a *Calicella*, a genus with much different features from those reported in the description given by Hincks (1868). On the one hand, this incongruence might be due to mislabeling of type material. On the other hand, no *Hebella* species are currently reported from the British Isles (see Cornelius, 1975), so that, if Hincks' material was really a *Hebella*, it has never been found again in the type locality. Actually, no records of *Hebella* species are available from the boreal and arctic region. The referral of *Lafoea pygmaea* to the genus *Hebella* by Nutting (1901) and Kingsley (1910) is possibly due to misinterpretation of the original description when identifying material other than the type.

Hebella ritchiei Vervoort, 1959

Lafoea tenellula; Ritchie, 1911: 820, pl. 88, fig. 5.
Hebella ritchiei Vervoort, 1959: 244-245, fig. 17; Rees & Thursfield, 1965: 74-75, 197; Vervoort, 1966: 123-124, fig. 26; Boero, 1980: 134.

Discussion.— Gonosome unknown. This species resembles other hebellids with elongated hydrothecae (see discussion of *H. hartmeyeri*) and cannot be recognized by any particular feature.

Hebella sibogae (Billard, 1942)

Hebellopsis sibogae Billard, 1942: 70, fig. 8; van Soest, 1976: 81.
Hebella sibogae; Boero, 1980: 134.

Material.— Siboga Expedition St. 129, holotype, one infertile colony growing on algae (ZMA Coel. no. 5224).

Discussion.— Gonosome unknown. Billard (1942) reported this species as growing on algae, an unusual substrate for *Hebella*, but common for *Scandia*. The short description could apply to any hebellid and the figure resembles a species of *Scandia* in the shape of the theca and the length of the pedicel. These features were confirmed by inspection of holotype material. We consider it a doubtful species referable to *Scandia*.

Hebella venusta (Allman, 1877)

Lafoea venusta Allman, 1877: 10-11, pl. 6, figs 3-4; Clarke, 1879: 239, 241, 243; Allman, 1888: 29; Nutting, 1895: 88, fig. 2b; Jäderholm, 1904: 270-274; Ritchie, 1909: 260-263; Ritchie, 1910a: 800-802, 815, pl. 76, figs 5-6; Levinsen, 1913: 285; Bedot, 1912: 316; Bedot, 1916: 142; Bedot, 1918: 176; Bennitt, 1922: 249; Bedot, 1925: 267; Fraser, 1943: 91; Fraser, 1944: 227, pl. 47, fig. 212; Fraser, 1946: 57, 181; Deevey, 1954: 270.
Hebella venusta; Stechow, 1921b: 227; Leloup, 1935: 15, fig. 5; Leloup, 1937b: 97, 117; Vervoort, 1968: 26-28, 100, fig. 11; Mergner & Wedler, 1977: 16, pl. 2, fig. 16; pl. 7, fig. 47; Spracklin, 1983: 246, 249, fig. 115; Florez Gonzalez, 1983: 119, 123, figs 17-18; Calder, 1991: 41-42, fig. 25.
Lafoesa venusta; Billard, 1941: 14.

Material.— Challenger St. 36: one infertile colony mounted on slide (NHML, no. 88.11.13.12.A); St.

Thomas Sound, 18.i.1907, one infertile colony mounted on slide, growing on *Cnidoscyphys marginatus* (Allman, 1877), Leg. Kükenthal & Hartmeyer, det. W. Vervoort (RMNH Coel. no. 3614).

Discussion.— Gonosome unknown. The available descriptions could apply to *Hebella muscensis* and *Anthohebella tubitheca*. However, due to the different features of the medusa stages in hebellids with ribbed hydrothecae shown by Millard & Bouillon (1975), we consider this species as doubtful due to insufficient description.

Hebella westindica Stechow, 1921

Hebella westindica: Stechow, 1921a: 897; Stechow, 1921b: 227; Stechow, 1923a : 135.

Discussion.— Gonosome unknown. As for several other nominal species of *Hebella*, Stechow (1921) described *H. westindica* from a figure published by another author, in this case Nutting (1904). Several authors considered this nominal species as conspecific with *H. venusta* (see discussion for *H. venusta*).

General discussion

The present findings confirm that similar hebellid hydroids can produce quite different medusae or medusoids. Furthermore, their hydrothecae can be widely varied in shape even within the same colony (fig. 2). Most of the nominal species of *Hebella* (and of the alternately recognized or discarded *Hebellopsis*) might either have been based on unreliable characters, within the range of variation of previously described species, or could be species with similar hydroids producing much different medusae, as is the case with *Hebella furax* vs *Anthohebella parasitica* and *Hebella muscensis* vs *Anthohebella tubitheca*. In most original descriptions no information is given on intracolony variation, which, in our experience, can be so great that single hydrothecae of the same colony might be assigned to different nominal species if based on previously accepted distinctions.

Our studies on living material and museum specimens led to the recognition of 11 valid species of *Hebella* and four valid species of *Anthohebella* out of the 45 nominal species of medusa-producing hebellids reported in the literature. Among the remaining ones, 18 are considered doubtful, whereas 12 are considered conspecific with currently recognized species in the genera *Hebella*, *Scandia* and *Lafoea*.

The types of reproductive stages reported in the introduction are emended as follows in the light of the present knowledge:

1 - Liberable eumedusoids with gametes on radial canals:
- *Hebella contorta* Marktanner-Turneretscher, 1890, described by Stechow & Müller (1923) from inside the gonotheca.
- *Hebella dyssymetra* Billard, 1933, described in the present paper for the first time and recognized also from type material.

2 - Medusae released as immature, with or without ocelli (this feature being variable according to state of development at liberation).
- *Hebella striata* Allman, 1888, described by Hartlaub (1905) from inside the gonotheca.

- *Hebella scandens* (Bale, 1888), described by Hirohito (1969), Millard (1975), Altuna Prados (1994) and in the present paper. Pictet's (1893) description of gonothecae containing medusa buds of the nominal species *H. cylindrica* could be referable to *H. scandens*. Possibly the medusae of this species were described by A. Agassiz (1865a) as *Laodicea calcarata*, and by Nutting (1901) as *H. calcarata*.
- *Hebella plana* Ritchie, 1907, described from inside the gonotheca by Totton (1930).
- *Hebella crateroides* Ritchie, 1909, figured by Ritchie (1910a) as immature medusa buds into the gonotheca.
- *Hebella furax* Millard, 1957, described as liberated medusa in the present paper for the first time.
- *Hebella muscensis* Millard & Bouillon, 1975. Described as liberated medusa in the present paper for the first time.

3 - Swimming gonophores:

- *Anthohebella parasitica* (Ciamician, 1880), originally described by Boero (1980).
- *Anthohebella brevitheca* (Leloup, 1938), redescribed in the present paper from inside gonothecae of type material.
- *Anthohebella tubitheca* (Millard & Bouillon, 1975), identified as such by the present study of type material.
- *Anthohebella najimaensis* (Hirohito, 1995).

4 - Recognized species with unknown gonophores:

- *Hebella dispolians* (Warren, 1909).
- *Hebella brochii* (Hadzi, 1913).
- *Hebella laterocaudata* Billard, 1942.

We stress again that many nominal species of *Hebella* are based on unreliable characters or on insufficient life-cycle knowledge. As suggested by almost all authors, the gonosome is of crucial importance for species distinction. A formerly accepted taxonomic character, diaphragm architecture, proved to be not consistent with medusan features, since *Hebella scandens* (with medusae) and *H. contorta* (with eumedusoids) have a perisarc diaphragm, while *H. muscensis* and *H. furax* (both with medusae) and *Anthohebella tubitheca* and *A. parasitica* (both with swimming gonophores) have a membranous diaphragm, so that species with almost identical hydroids can have different types of reproduction and species with similar newly liberated medusae or eumedusoids have different diaphragm architecture.

Neither diaphragm nor medusan features are consistent enough to allow assignment of medusa-producing hebellids to separate genera. The only generic characters here accepted to exclude a *Hebella*-like species from *Hebella* are the presence of swimming gonophores in *Anthohebella* and the presence of fixed gonophores, branched pedicels and non-obligate epizoic life on other hydroids in *Scandia*. The morphological difference between *Scandia* and *Hebella* resides almost exclusively in their gonothecal content and in much varied features such as length of pedicels. From an ecological point of view *Scandia* is mostly epiphytic, whereas *Hebella* is exclusively epizoic on hydroids. It seems possible that *Hebella* species evolved from an ancestor with medusae which became obligatory epizoic on hydroids, and that parallel events of ecological shifts from epizoism to epiphytism (and so from *Hebella*-like hydroids to *Scandia*-like hydroids) led to medusa suppression and loss of features directly linked to epizo-

ic life on hydroids (such as twisted hydrothecae, short pedicels, asymmetries in skeleton). Millard (1973), for instance, remarked how auto-epizoic hydroids show "stunted" morphologies if compared to those of non-auto-epizoic specimens of the same species. The above described variations of *Hebella furax* further demonstrate how hebellids can change morphology according to the site of growth, so that hydroids growing at the base of the supporting hydroid colony resemble *Scandia*, whereas those in between hydrocladia are typical *Hebella*-like. It is thus possible that *Scandia* is a polyphyletic genus, accommodating *Hebella* species which independently lost both epizoic habit and medusae. If this were true, *Hebella* would be paraphyletic. The only reasonable solution would then be to merge all "hebelliform" species into *Hebella*, retaining *Scandia* as polyphyletic. Such a solution seems too extreme to be taken at the present state of knowledge and would lead to overlumping, causing great nomenclatural changes, especially when keeping in mind that improvements in knowledge of species of *Scandia*, *Hebella* or *Anthohebella* could lead to further taxonomic alteration. Medusae of the same family, for instance, can be similar at liberation and become much different during development, so that it is still possible that *Hebella* will have to be split again when complete life cycles will be described. Such general problems were recently addressed by de Queiroz & Gauthier (1994), who, however, did not yet propose a straightforward transformation of Linnean nomenclature into a "phylogenetic system of biological nomenclature", even though the provisional solutions they propose could apply to the cases presented here.

Conclusion

The taxonomic study of the medusae of hebellids is far from being concluded due to difficulties in rearing their medusae to maturity. It is quite possible that the medusae of some hydroid-based species of *Hebella* have been described as distinct medusa-based taxa. However, we are still unable to refer with certainty a single hydroid-based species to the corresponding medusa-based species. The present treatment is thus not conclusive and the generic limitations are, at present, more linked to convenience than to phylogenetic affinities. The insufficient knowledge of life cycle features makes a phylogenetic analysis of hebellids impracticable.

A general outcome of the present account is that similar hydroids can produce much different medusae and vice-versa. This is usually linked to differential paedomorphosis, so that phylogenetic affinities leading to generic distinctions must be evaluated case by case, considering additional characters to medusa reduction (see Boero et al., 1996). At present the recognition of many species of hebellids is impossible if the mature or well-developed gonosome is not known. Future work on hebellid genera should avoid proposal of new species and identification of infertile hydroid colonies based on features now considered unreliable.

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References

Agassiz, A., 1865a. North American Acalephae.— Illustrated Catalogue of the Museum of Comparative Zoology, at Harvard College, 2: 1-234.

Agassiz, A., 1865b. On the mode of development of the marginal tentacles of the free medusae of some hydroids.— Proc. Boston Soc. nat. Hist. (1862-1863) 9: 88-101.

Agassiz, L., 1860-1862. Contributions to the natural history of the United States of America. 4: 1-380.— Boston, Little, Brown & Co.

Allman, G.J., 1864. On the construction and limitation of genera among the Hydroida.— Ann. Mag. Nat. Hist. (Ser. 3) 13: 345-380.

Allman, G. J., 1877. Report on the Hydroida collected during the exploration of the Gulf Stream by L. F. de Pourtalès, assistant United States Coast Survey.— Mem. Mus. Comp. Zool. Harvard College 5 (2): 1-66.

Allman, G.J., 1888. Report on the Hydroida dredged by H.M.S. Challenger during the Years 1873-76. Part II. The Tubularinae, Corymorphinae, Campanularinae, Sertularinae and Thalamophora.— Rep. Scient. Res. Voy. H. M. S. Challenger during the years 1873-76. Zoology 23: 1-90.

Altuna Prados, A., 1994. Observaciones biogeograficas sobre los cnidarios bentonicos de la costa vasca.— KOBIE (Serie Ciencias Naturales), Bilbao, 22: 41-57.

Antsulevich, A.E., 1983. Novye dlya fauny SSSR gidroidy iz pribrezhnykh vod Yaponskogo Morya.— Akad. Nauk SSSR, Zool. Zh. 62 (8): 1141-1147.

Antsulevich, A.E., 1987. Gidroidy shelfa Kurilskikh Ostrovov. Leningrad.— Akad. Nauk SSSR, Zool. Inst.: 1-163.

Armstrong, J., 1879. A description of some new species of hydroid zoophytes from the Indian coasts and seas.— J. Asiatic. Soc. Bengal 48 (2): 98-103.

Babic, K., 1904. Üebersicht der Hydroidpolypen des Adriatischen Meeres.— Gl. hrv. Nar. Dr. 15: 201-220.

Babic, K., 1910. Prilog fauni Jadranskoga mora.— Rad. jug. Akad. Znan. Umye. 183: 207-236.

Babic, K., 1911. Zur bionomie von *Hebella parasitica*.— Zool. Anz. 38: 226-230.

Bale, W. M., 1884. Catalogue of the Australian Hydroid Zoophytes.— Sydney, Australian Museum, Catalogue 8: 1-198.

Bale, W.M., 1888. On some new and rare Hydroida in the Australian Museum collection.— Proc. Linn. Soc. New S. Wales (Ser. 2) 3: 745-799.

Bale, W.M., 1913. Further notes on Australian Hydroids. II.— Proc. Roy. Soc. Victoria, n.s. 26: 114-147.

Bale, W.M., 1915. Report on the Hydroida collected in the Great Australian Bight and other Localities. Part III.— Biological Results of the Fishing Experiments carried on by the F.I.S. "Endeavour", 1909-14, 3 (5): 241-336.

Bale, W.M., 1924. Report on some hydroids from the New Zealand coast, with notes on New Zealand Hydroida generally, supplementing Farquhar's list.— Trans. Proc. N. Z. Inst. 55: 225-268.

Bedot, M., 1912. Matériaux pour servir à l'histoire des hydroïdes. 4me période (1872 à 1880).— Revue suisse Zool. 20(6): 213-469.

Bedot, M., 1916. Matériaux pour servir à l'histoire des hydroïdes. 5me période (1881 à 1890).— Rev. suisse Zool. 24: 1-349.

Bedot, M., 1918. Matériaux pour servir à l'histoire des hydroïdes. 6me période (1891 à 1900).— Rev. suisse Zool. 26 (Fasc. Suppl. 1): 1-376.

Bedot, M., 1923. Notes systématiques sur les plumularides. 3me partie.— Rev. Suisse Zool. 30: 213-243.

Bedot, M., 1925. Matériaux pour servir à l'histoire des hydroïdes. 7me. période (1901-1910).— Rev. suisse Zool. 32 (Fasc. Suppl. 1): 1-657.

Bennitt, R., 1922. Additions to the hydroid fauna of the Bermudas.— Proc. Amer. Acad. Arts Sci. 57: 241-259.

Bigelow, H.B., 1914. List of the Medusae Craspedotae, Siphonophorae, Scyphomedusae, Ctenophorae.— In: Fauna of New England. 12. Occ. Papers Boston Soc. nat. Hist. 7: 1-37.

Billard, A., 1904a. Contribution à l'étude des hydroïdes (multiplication, régénération, greffes, variations).— Ann. Sci. Nat. 20 (8°sér.): 1-251.

Billard, A., 1904b. Hydroïdes récoltés par M. Ch. Gravier dans le Golfe de Tadjourah.— Bull. Mus. Hist. nat. 10: 480-485.

Billard, A., 1906a. Note sur les Hydroïdes du Travailleur et du Talisman.— Bull. Mus. Hist. nat. 12: 329-334.

Billard, A., 1906b. Hydroïdes. In: Mission des pêcheries de la côte occidentale d'Afrique. III.— Actes Soc. linn., Bordeaux. 61: 173-180.

Billard, A., 1906c. Hydroïdes.— Expéditions Scientifiques du Travailleur et du Talisman. 8: 153-243.

Billard, A., 1907. Hydroïdes de Madagascar et du Sud-Est de l'Afrique.— Arch. Zool. expér. gén. 7 (8): 335-396.

Billard, A., 1914. Hydroïdes.— Deuxième expédition Antarctique Française (1908-1910), commandée par le Dr. Jean Charcot. Paris. (Masson et Cie): 1-34.

Billard, A., 1933. Les Hydroïdes des Golfes de Suez et d'Akaba.— Mém. Inst. Egypt. 21: 1-30.

Billard, A., 1941. Note sur les Hydroïdes *Hebella costata* (Bale) et *Hebella corrugata* (Thornely).— Bull. Soc. Zool. Fr. 66: 13-15.

Billard, A., 1942. Note sur quelques espèces et varietés des genres *Hebella* et *Hebellopsis* (Hydroïdes).— Bull. Soc. Zool. Fr. 67: 67-70.

Blanco, O., 1984. Adición a los hidrozoos argentinos. II.— Rev. Mus. La Plata 13 (Zool.) 147: 269-282.

Blanco, O., M.O. Zamponi & G.N. Genzano, 1994. Lafoeidae de la Argentina (Coelenterata, Hydrozoa, Hydroida).— Naturalia Patagónica, Ciencias Biologicas 2: 1-131.

Boero, F., 1980. *Hebella parasitica* (Cnidaria, Hydroida): a thecate polyp producing an anthomedusa.— Mar. Biol. 59: 133-136.

Boero, F., 1981a. Systematics and ecology of the hydroid populations of two *Posidonia oceanica* meadows.— P.S.Z.N. I: Marine Ecology 2 (3): 181-197.

Boero, F., 1981b, Osservazioni ecologiche sugli idroidi della fascia a mitili della Riviera Ligure di levante.— Cah. Biol. Mar. 22: 107-117.

Boero, F. & J. Bouillon, 1989. An evolutionary interpretation of anomalous medusoid stages in the life cycles of some Leptomedusae (Cnidaria). In: J.S. Ryland & P. A. Tyler (eds), Reproduction, Genetics and Distributions of Marine Organisms.— Olsen & Olsen, Fredensborg: 37-41.

Boero, F., J. Bouillon & C. Gravili, 1991. The life cycle of *Hydrichthys mirus* (Cnidaria: Hydrozoa: Anthomedusae: Pandeidae).— Zool. J. Linn. Soc. 101: 189-199.

Boero F., J. Bouillon & S. Piraino. 1996. Classification and phylogeny in the Hydroidomedusae (Hydrozoa, Cnidaria). Sci. Mar. 60: 7-16.

Boero, F. & E. Fresi, 1986. Zonation and evolution of a rocky bottom hydroid community.— P. S. Z. N. I: Marine Ecology 7 (2): 123-150.

Borradaile, L.A., 1905. Hydroids.— In: Stanley Gardner (ed.), Fauna and Geography of the Maldive and Laccadive Archipelagoes 2 (4): 836-845. University Press, Cambridge.

Bouillon, J., 1985. Essai de classification des Hydropolypes-Hydroméduses (Hydrozoa-Cnidaria).— Indo-Malayan Zool. 1: 29-243.

Bouillon, J., F. Boero & S. Fraschetti, 1991. The life cycle of *Laodicea indica* (Laodiceidae, Leptomedusae, Cnidaria).— Hydrobiologia 216/217: 151-157.

Briggs, E.A., 1918. Descriptions of two new hydroids, and a revision of the hydroid-fauna of Lord Howe Island.— Rec. Aust. Mus. 12 (3): 27-47.

Briggs, E.A., 1939. Hydroida.— Sci. Reps. Australasian Antarc. Exp. (1911-1914) 9 (4): 1-46.

Briggs, E.A. & V. Gardner, 1931. Hydroida.— Scient. Repts Great Barrier Reef Exped. 1828-29 4 (6): 181-196.

Broch, H., 1909. Die Hydroiden der arktischen Meere.— Fauna arct. 5: 127-248.

Broch, H., 1912. Hydroiduntersuchungen. III. Vergleichende Studien an Adriatischen Hydroiden.— Kgl. Norske Vidensk. Selsk. Skr. 1911(1): 1-65.

Broch, H., 1914. Hydrozoa benthonica In: Beiträge zur Kenntnis der Meeresfauna Westafrikas. Hrsg. v. W. Michaelson.— Hamburg (L. Friederichsen & Co): 19-56.

Broch, H., 1933. Zur Kenntnis der Adriatischen Hydroidenfauna von Split.— Skr. Norske-vidensk. Akad Oslo 4: 3-115.

Browne, E.T., 1907. A revision of the Medusae belonging to the family Laodiceidae.— Ann. Mag. nat. Hist. 20 (7): 457-480.

Buchanan, J. B., 1957. The Hydroid Fauna of the Gold Coast.— Rev. Zool. Bot. Afr. 56: 349-372.

Cairns, S., D.R. Calder, A. Brinckmann-Voss, C.B. Castro, P.R. Pugh, C.E. Cutress, W.C. Jaap, D.G. Fautin, R.J. Larson, G.R. Harbison, M.N. Arai, D.M. Opresko, 1991. Common and scientific names of aquatic invertebrates from the United States and Canada: Cnidaria and Ctenophora.— Am. Fish. Soc. Spec. Publ. 22: 1-75.

Calder, D.R., 1991. Shallow-water hydroids of Bermuda: the Thecatae, exclusive of Plumularioidea.— Life Sci. Contr. R. Ont. Mus. 154: 1-140.

Campenhausen, B. von, 1896a. Hydroiden von Ternate, nach den Sammlungen Prof. W. Kükenthal's.— Zool. Anz. 19: 103-107.

Campenhausen, B. von, 1896b. Hydroiden von Ternate. In: Kükenthal W., Ergebnisse einer zoologischen Forschungsreise in den Molluken und in Borneo, Theil 2.— Abh. senckenberg. naturf. Ges. 23: 297-320.

Campenhausen, B. von, 1897. Beitrage zur Systematik der Hydroiden.— Zool. Inst. der Univ. Jena: 297-317.

Carus, J. V., 1884. Prodromus faunae mediterraneae. Pars I.— Stuttgart, E. Schweizerbart'sche Verlagshandlung: 1-524.

Chas Brinquez, J. & C.R. Babio, 1977. Contributión al conocimiento de los Hidropólipos del litoral Gallego. In: Fauna marina de Galicia.— Univ. de Santiago de Campostela 1: 11-43.

Ciamician, J., 1880. Ueber *Lafoea parasitica* n. sp.— Zeitsch. f. wiss. Zool. 33: 673-676.

Clark, S.F., 1876. Report on the hydroids collected on the coast of Alaska and the Aleutian Islands by W. H. Dall; U. S. Coast Survey, and party, from 1871 to 1874 inclusive.— Proc. Acad. Nat. Sci. Philadelphia 1876: 209-235.

Clarke, S.F., 1879. Report on the Hydroida collected during the exploration of the Gulf-Stream and Gulf of Mexico, by Alexander Agassiz. 1877-1878.— Bull. Mus. Comp. Zool. Harvard College. 5: 239-252.

Congdon, E.D., 1907. The Hydroids of Bermuda.— Proc. Amer. Acad. Arts Sc. 42: 463-485.

Claus, C., 1881. Beitrage zur Kenntniss der Geryonopsiden- und Eucopiden-Entwicklung.— Arb. zool. Inst. Univ. Wien 3 (3): 283-312.

Cornelius, P.F.S., 1975. A revision of the species of Lafoeidae and Haleciidae (Coelenterata: Hydroida) recorded from Britain and nearby seas.— Bull. Br. Mus. (Nat. Hist.) (Zool.) 28 (8): 373-426.

Cornelius, P.F.S., 1982. Hydroids and medusae of the family Campanulariidae recorded from the eastern North Atlantic, with a world synopsis of genera.— Bull. Br. Mus. nat. Hist., Zool. 42 (2): 37-148.

Coues, E. & H.-C. Yarrow, 1878. Notes on the natural history of Fort Macon, N. C. and its vicinity.— Proc. Acad. nat. Sci. Philadelphia 1878: 297-330.

d'Arcy Thompson, W., 1887. The Hydroida of the Vega Expedition.— Vega Expeditionens Vetenskapliga Arbeten 4: 387-400.

Da Cunha, A., 1941. Nota sôbre o hidróide "*Hebella parasitica*" (Ciamician) das costas de Portugal.— Archos Mus. Bocage 12: 1-5.

Da Cunha, A., 1944. Hidropólipos das costas de Portugal.— Mem. Mus. Zool. Univ. Coimbra 161: 1-101.

Da Cunha, A., 1950. Nova contribuição para o estudo dos Hidropólipos das costas de Portugal.— Arch. Mus. Bocage 21: 121-144.

Dawydoff, C., 1952. Contribution à l'étude des invertébrés de la faune marine bentique de l'Indochine.— Bull. biol. Fr. Belg., 37, suppl.: 1-158. (Coelenterata: 52-78).

De Haro, A., 1965. Hidroideos del litoral de Blanes (Gerona).— P. Inst. Biol. Apl. 38: 105-122.
Deevey, E.S., 1954. Hydroids of the western Gulf of Mexico. In: P.S. Galtsoff, ed., Gulf of Mexico. Its origin, waters, and marine life.— Fishery Bull. Fish Wildl. Serv. U. S. 55: 267-272.
de Queiroz, K. & J. Gauthier, 1994. Toward a phylogenetic system of biological nomenclature.— Trends Ecol. Evol. 9 (1): 27-31.
Farquhar, H., 1896. List of New Zealand Hydroida.— Trans. Proc. New Zealand Inst. 28: 459-468.
Florez Gonzalez, L., 1983. Inventario preliminar de la fauna hydroide de la Bahía de Cartagena y areas adyacentes.— Boln Mus. Mar. Bogota 11: 112-140.
Forbes, E. & J. Goodsir, 1853. On some remarkable marine invertebrata new to the British seas.— Trans. Roy. Soc. Edinb. 20: 307-315.
Forskål, P., 1775. Descriptiones animalium avium, amphibiorum, piscium, insectorum, vermium; quae in itinere orientali observavit Petrus Forskål.— Hauniae: 1-164.
Fraser, C., 1911. The Hydroids of the West Coast of North America, with special reference to those of Vancouver Island region.— Iowa Bull. Lab. Nat. Hist. Univ. Iowa 6: 3-91.
Fraser, C., 1912a. Some Hydroids of Beaufort, North Carolina.— Bull. U.S. Bur. Fish. 30: 337-387.
Fraser, C., 1912b. Notes on New England Hydroids.— Bull. Lab. Nat. Hist. Univ. Iowa 6: 39-48.
Fraser, C., 1918. Hydroids of Eastern Canada.— Contrib. Canadian Biol. 1917-1918: 329-366.
Fraser, C., 1921. Hydroids. Key to the hydroids of eastern Canada. In: Canadian Atlantic Fauna, 3a.— Contr. Can. Biol. Fish. 17: 137-180, figs 101-107.
Fraser, C., 1927. The hydroids of the Chetcamp Expedition of 1917.— Contr. Can. Biol. Fish., n. ser. 3 (12): 323-330.
Fraser, C., 1931.Hydroids of Hudson Bay and Hudson Strait. In: Biological and Oceanographic conditions in Hudson Bay.— Contr. Can. Biol. Fish., n. ser. 6 (24): 475-481.
Fraser, C., 1936. Some Japanese hydroids, mostly new.— Trans. roy. Soc. Canada Sect. 3, 30: 49-54.
Fraser, C., 1937. Hydroids of the Pacific coast of Canada and the United States.— Univ. Toronto Press, Toronto: 1-208.
Fraser, C., 1938a. Hydroids of the 1934 Allan Hancock Pacific Expedition.— Allan Hancock Pac. Exped. 4 (1): 1-105.
Fraser, C., 1938b. Hydroids of the 1932, 1933, 1935, and 1938 Allan Hancock Pacific expeditions.— Allan Hancock Pac. Exped. 4 (3): 129-153.
Fraser, C., 1938c. Hydroids of the 1936 and 1937 Allan Hancock Pacific Expeditions.— Allan Hancock Pac. Exped. 4 (2): 107-127.
Fraser, C., 1939. Hydroids of the western Canadian Arctic region, 1935-1937.— Can. J. Res., (D, zool. Sci.) 17: 59-61.
Fraser, C., 1943. Distribution records of some hydroids in the collection of the Museum of Comparative Zoology at Harvard College, with description of new genera and new species.— Proc. New Engl. zool. Cl. 22: 75-98.
Fraser, C., 1944. Hydroids of the Atlantic coast of North America.— Univ. Toronto Press, Toronto: 1-451.
Fraser, C., 1946. Distribution and relationship in American Hydroids.— Univ. Toronto Press, Toronto: 1-464.
Fraser, C., 1947. Hydroids of the 1939 Allan Hancock Caribbean Sea Expedition.— Allan Hancock Atl. Exped. 4: 1-24.
Fraser, C., 1948. Hydroids of the Allan Hancock Pacific Expeditions since March, 1938.— Allan Hancock Pac. Exped. 4 (5): 179-343.
García-Corrales, P., Buencuerpo Arcas V., M.V. Peinado De Diego, 1979. Contribucion al conocimiento de los hidrozoos de las costas Españolas. Parte II: "Lafoeidae", "Campanulinidae" y "Syntheciidae".— Bol. Inst. esp. Oceanogr. 5 (3): 3-39.
Genzano, G.N., 1992. La fauna de hidropòlipos (Cnidaria) del litoral de Buenos Aires, Argentina. I.— Neotropica 38 (100): 141-148.
Genzano G.N. & M.O. Zamponi, 1992. Los hidrozoos bentonicos de la costa de Mar del Plata.— Universidad Nacional de Mar del Plata, Mar del Plata: 1-90.

Gibbons, M.J. & J.S. Ryland, 1989. Intertidal and shallow water hydroids from Fiji. I. Athecata to Sertulariidae.— Mem. Qd Mus. 27 (2): 377-432.

Gili, J.-M., 1980. Estudio sistemático y ecológico de los cnidarios bentónicos de las islas Medes (Girona).— Tesis de Licenciatura, Universidad Autónoma de Barcelona.

Gili, J.-M., 1981. Estudio bionómico y ecológico de los cnidarios bentónicos de las islas Medes (Girona).— Oecol. aquat. 5: 105-123.

Gili, J.-M., 1982. Fauna de cnidaris de las illes Medes.— Treb. Inst. Cat. Hist. nat. 6: 9-127.

Gili, J.-M., 1986. Estudio sistemático y faunístico de los cnidarios de la costa catalana.— PhD Thesis, Universidad Autònoma de Barcelona: 1-565.

Gili, J.-M. & E. Ballesteros, 1991. Structure of cnidarian populations in Mediterranean sublittoral benthic communities as a result of adaptation to different environmental conditions. In: J.D. Ros & N. Prat, eds., Homage to Ramon Margalef; or, Why there is such pleasure in studying nature.— Oecol. aquat. 10: 243-254.

Gili, J.-M. & C. Castelló, 1985. Hidropólipos de la costa norte del Cabo de Creus (N.E. Cataluña).— Miscellanéa Zool. Mus. Barcelona 9: 7-24.

Gili, J.-M., A. García & P.L. Colomer, 1984. Els cnidaris bentónics de les illes Medes. in: Els sistemes naturals de les Illes Medes. J. Ros, I. Olivella & J.-M. Gili (eds).— Institut d'Estudis Catalans, Barcelona: 407-427.

Gili, J.-M. & A. García-Rubies, 1985. Contribution à la connaissance de la faune d'hydropolypes de l'île de Majorque.— Anales de Biol., 3, secc. Biol. anim. I: 37-53.

Gili, J.-M., W. Vervoort & F. Pagès, 1989. Hydroids from the West African coast: Guinea Bissau, Namibia and South Africa.— Sci. Mar. 53 (1): 67-112.

Goette, A., 1880. Ein neuer Hydroid-Polyp mit einer neuen Art der Fortpflanzung.— Zool. Anz. 3: 352-358.

Graeffe, E., 1884. Uebersicht der Seethierfauna des Golfes von Triest, nebst Notizen über Vorkommen Lebensweisse, Erscheinungs und Fortpflanzung der einzelnen Arten.III Coelenteraten.— Arb. zool. Inst. Univ. Wien 5: 333-362.

Gravier, N., 1970. Étude des hydraires épiphytes des phanérogames marines de la région de Tulear (sud-ouest de Madagascar).— Recl Trav. Stn mar. Endoume, n. ser., suppl. 10: 111-161.

Hadzi, J., 1913. Poredbena hidroidska istraivanja. I. *Hebella parasitica* (Ciamician). (S. dodatkom: *Hebellopsis brochi* g. et sp. n.: *Hebella* (?) *gigas* Pieper).— Rad. jugosl. Akad. Znan. Umjetn. 198, Mat. Prir. Razr.: 105-210.

Hadzi, J., 1915. O regeneraciji (renovaciji) hidranta u tekatnih hidroida.— Rad. jugosl. Akad. Znan. Umjetn. 208, Mat. Prir. Razr.: 113-210.

Hadzi, J., 1916. Rezultati biolokih istraivanja Jadranskoga mora. Hidroidi I. Ergebnisse biologischer Erforschungen des adriatischen Meeres. Hydroiden I. *Camella vilae-velebiti* g. n., sp. n. *Croatella* g. n.— Prirod. Istra. hrv. slav., mat.-prirod. Razreda (= Bull. Trav. Cl. Sci. Mat. Nat.) 7: 23-81.

Hadzi, J., 1965. Polip kot temeljna in prvotna o blika knidarijev. The polyp as the fundamental and primary form of Cnidaria.— Razpr. Slov. Akad. Znan. Umietn. (4) 8: 101-153.

Haeckel, E., 1879. Das System der Medusen. Erster Theil einer Monographie der Medusen (Craspedotae).— Denksch. med. naturw. Ges. Jena: 1-360.

Hargitt, C.W., 1901. Synopses of North-American Invertebrates. XIV. The Hydromedusae. Parts I-III.— Am. Nat. 35: 301-315, 379-385, 575-595.

Hargitt, C.W., 1902 a. Notes on a few medusae new to Woods Hole.— Biol. Bull. 4: 13-23.

Hargitt, C. W., 1902 b. Notes on the coelenterate fauna of Woods Hole.— Am. Nat. 36: 549-560.

Hargitt, C.W., 1904. The Medusae of the Woods Hole region.— Bull. U.S. Bur. Fish. Washington 24: 21-79.

Hargitt, C. W., 1924. Hydroids of the Philippine Islands.— Phil. Journ. Sci. 24 (4): 467-505.

Hartlaub, C., 1901. Revision der *Sertularella* Arten.— Abh. Nat. Ver. Hamburg 16: 1-143.

Hartlaub, C., 1905. Die Hydroiden der magalhaensischen Region und chilenischen Küste. In: Fauna Chilensis.— Zool. Jahrb. Suppl. VI. 3: 497-714.

Hincks, T., 1853. Further notes on British zoophytes, with description of new species.— Ann. Mag. nat. Hist. 11 (2): 178-185.

Hincks, T., 1868. A history of the British hydroid zoophytes: 1-338.— London: Van Voorst.
Hirohito, 1969. Some Hydroids of the Amakusa Islands.— Biol. Lab. Imperial Household, Tokyo: 1-32.
Hirohito, 1995. The hydroids of Sagami Bay II, Thecata.— Biol. Lab. Imperial Household, Tokyo: 1-355.
Hodgson, M.M., 1950. A revision of the Tasmanian Hydroida.— Pap. Proc. Roy. Soc. Tasm. 1949: 1-65.
Ito, T. & K. Inoue, 1962. Nematocysts of Gymnoblastea and Calyptoblastea. In: Systematic studies on the nematocysts of Cnidaria.— Mem. Ehime Univ. 4: 445-460.
Izquierdo, M.S., P. García-Corrales & J.J. Bacallado, 1986. Contribucíon al conocimento de los hidrozoos caliptoblástidos del Archipiélago Canario. Parte I: Haleciidae, Lafoeidae, Campanulariidae y Syntheciidae.— Bol. Inst. esp. Oceanogr. 3 (1): 81-94.
Jäderholm, E., 1903. Aussereuropaische Hydroiden im schwedischen Reichsmuseum.— Ark. Zool. 1: 259-312.
Jäderholm, E., 1905. Hydroiden aus antarktischen und subantarktischen Meeren gesammelt von der schwedischen Südpolarexpedition.— Wiss. Ergebn. Schwed. Südpolarexpedition 5: 1-41.
Jäderholm, E., 1909. Northern and Arctic invertebrates in the collections of the Swedish State Museum (Riksmuseum). IV Hydroiden.— K. svenska Vetensk Akad. Handl. 45: 1-124.
Jäderholm, E., 1919. Zur Kenntnis der Hydroidenfauna Japans.— Ark. Zool. 12 (9): 1-34.
Jäderholm, E., 1920. On Some Exotic Hydroids in the Swedish Zoological State Museum.— Ark. Zool. 13 (3): 1-10.
Jäderholm, E., 1926. Über einige antarktische Hydroiden.— Ark. Zool. 18 A 1: 1-7.
Jarvis, F.E., 1922. The hydroids from the Chagos, Seychelles and other islands and from the coasts of British East Africa and Zanzibar. In: Reports of the Percy Sladen Trust Expedition to the Indian Ocean in 1905, under the leadership of Mr. J. Stanley Gardiner, M.A.— Trans. Linn. Soc. London, Zool. (2) 18 (1): 331-360.
Jickeli, C.F., 1883. Der Bau der Hydroidpolypen. II.— Morphol. Jahrb. 8: 580-680.
Kingsley, J.S., 1910. A synopsis of the fixed Hydroids of New England.— Tufts Coll. Stud. 3: 13-38.
Kramp, P.L., 1943. Hydroida. In: The Zoology of East Greenland.— Meddr Grönland 121(11): 1-52.
Kramp, P.L., 1961. Synopsis of the medusae of the world.— J. mar. biol. Ass. U.K. 40: 1-469.
Leloup, E., 1934. Note sur les hydropolypes de la rade de Villefranche-sur-Mer (France).— Bull. Mus. r. Hist. nat. Belg. 10 (31): 1-18.
Leloup, E., 1935. Hydraires calyptoblastiques des Indes Occidentales.— Mém. Mus. r. Hist. nat. Belg. 2 (2): 1-73.
Leloup, E., 1937a. Hydropolypes et Scyphopolypes recueillis par C./S. Dawydoff sur les côtes de l'Indochine francaise.— Mém Mus. r. Hist. nat. Belg. 12: 1-73.
Leloup, E., 1937b. Résultats scientifiques des croisières du navire-école belge "Mercator".VI. Hydroidea, Siphonophora, Ceriantharia.— Mém. Mus. r. Hist. nat. Belg. 9 (2): 91-127.
Leloup, E., 1938. Quelques Hydropolypes de la baie de Sagami, Japon.— Bull. Mus. r. Hist. nat. Belg. 14 (28): 1-22.
Leloup, E., 1940. Hydropolypes provenant des croisières du Prince Albert Ier de Monaco.— Rés. Camp. scient. Albert Ier Prince de Monaco 104: 1-38.
Leloup, E., 1960. Hydropolypes du Muséum National d'Histoire Naturelle de Paris.— Mém. Mus. nat. Hist. nat. Paris 17 (4): 217-241.
Leloup, E., 1974. Hydropolypes calyptoblastiques du Chili. Report n° 48 of the Lund University Chile expedition, 1948-1949.— Sarsia 55: 1-62.
Levinsen, G.M.R., 1893. Meduser, Ctenophorer og Hydroider fra Grønlands Vestkyst, tilligemed Bemaerkninger om Hydroidernes Systematik.— Vidensk. Meddr. dansk. naturh. Foren 4: 143-212.
Levinsen, G.M.R., 1913. Systematic studies on the Sertulariidae.— Vidensk. Meddr. dansk. naturh. Foren 64: 249-323.
Llobet, I., J.-M. Gili & M. Barangé, 1986. Estudio de una poblacion de Hidropólipos epibiontes de *Halimeda tuna*.— Misc. Zool. 10: 33-43.

Mammen, T.A., 1965. On a collection of Hydroids from South India. II. Suborder Thecata (excluding family Plumulariidae).— J. mar. biol. Ass. India 7 (1): 1-57.

Marktanner-Turneretscher, G., 1890. Die Hydroiden des k.k. naturhistorischen Hofmuseums.— Annh. naturh. Mus. Wien 5: 195-286.

Marktanner-Turneretscher, G., 1895. Hydroiden. In: Zoologische Ergebnisse der im Jahre 1889 auf Kosten der Bremer geographischen Gesellschaft von Dr. Willy Kükenthal und Dr. Alfred Walter ausgefuhrten Expedition nach Ost-Spitzbergen.— Zool. Jahrb. 8: 391-438.

Mayer, A.G., 1910. Medusae of the world.— Carnegie Inst. Washington. Publ. 109: 1-735.

Mergner, H. & E. Wedler, 1977. Über die Hydroidpolypenfauna des Roten Meeres und seiner Ausgange.— "Meteor" forschungs-ergebn. (Biol.) 24: 1-32.

Metschnikoff, E., 1886. Embriologische Studien auf Medusen. Ein Beitrag zur Genealogie der Primitiv Organe: 1-159.— Holder, Wien.

Millard, N.A.H., 1957. The Hydrozoa of False Bay, South Africa.— Ann. S. Afr. Mus. 43 (4): 173-243.

Millard, N.A.H., 1958. Hydrozoa from the coasts of Natal and Portuguese East Africa. Part I. Calyptoblastea.— Ann. S. Afr. Mus. 44 (5): 165-226.

Millard, N.A.H., 1964. The Hydrozoa of the south and west coast of south Africa. Part II. The Lafoeidae, Syntheciidae and Sertulariidae.— Ann. S. Afr. Mus. 48 (1): 1-56.

Millard, N.A.H., 1968. South-African Hydroids from Dr. Th. Mortensen's Java-South Africa expedition 1929-1930.— Vidensk. Meddr. dansk. naturh. Foren. 131: 251-288.

Millard, N.A.H., 1973. Auto-epizoism in South African hydroids.— Publ. Seto Mar. Biol. Lab. 20 (Proc. Second Internat. Symp. Cnidaria): 23-34.

Millard, N.A.H., 1975. Monograph on the Hydroida of Southern Africa.— Ann. S Afr. Mus. 68: 1-513.

Millard, N.A.H., 1978. The geographical distribution of southern African hydroids.— Ann. S. Afr. Mus. 74 (6): 159-200.

Millard, N.A.H. & J. Bouillon, 1973. Hydroids from the Seychelles (Coelenterata).— Ann. Mus. r. Afr. Centr. 206: 1-106.

Millard, N.A.H. & J. Bouillon, 1975. Additional hydroids from the Seychelles.— Ann. S. Afr. Mus. 69 (1): 1-15.

Naumov, D.V., 1969. Hydroids and Hydromedusae of the USSR: 1-631.— Israel Program for scientific translations, Jerusalem.

Neppi, V., 1921. Nuove osservazioni sui polipi idroidi del golfo di Napoli.— Pubbl. Staz. zool. Napoli 3: 1-31.

Nutting, C., 1895. Narrative and preliminary report of Bahama Expedition.— Bull. Lab. nat. Hist. State Univ. Iowa 3: 1-251.

Nutting, C., 1899. Hydroida from Alaska and Puget Sound.— Proc. U. S. Natnl Mus. 21: 741-753.

Nutting, C., 1900. American hydroids Part.I. The Plumularidae.— Spec. Bull. U.S. nat. Hist. Mus.: 1-285.

Nutting, C., 1901. The hydroids of the Woods Hole region.— Bull. U. S. Fish. Commission 1899 19: 325-386.

Nutting, C., 1904. American Hydroids.Part.II. The Sertularidae.— Spec. Bull. U.S. nat. Hist. Mus.: 1-325.

Nutting, C., 1915. American hydroids. Part III. The Campanulariidae and the Bonneviellidae.— Spec. Bull. U. S. natn. Mus.: 1-126.

Nutting, C., 1927. Report on the Hydroida collected by the United States fisheries steamer "Albatros" in the Philippine region, 1907-1910.— Bull. U. S. Nat. Mus. 63: 195-242.

Park, J.H., 1992. Zoogeographical distribution of marine hydroids (Cnidaria: Hydrozoa: Hydroida) in Korea.— Kor. Journ. Syst. Zool. 8 (2): 279-300.

Park, J.H., 1993. Marine hydroids (Cnidaria: Hydrozoa: Hydroida) from Cheju Island, Korea.— Kor. Journ. Syst. Zool. 9 (2): 261-280.

Patriti, G., 1970. Catalogue des cnidaires et cténaires des côtes atlantiques marocaines.— Trav. Inst. sci. chérif. fac. sci. (Zool.) 35: 1-144.

Pennycuick, P.R., 1959. Faunistic records from Queensland. Part V. Marine and brackish water Hydroids.— Univ. Qd. Pap (Zool.) 1 (6): 141-210.

Perrier, R., 1936. La faune de la France. I A - Coelentérés, Spongiaires, Echinodermes: 1- 118.— Libraire Delagrave, Paris.

Petersen, K., 1979. Development of coloniality in Hydrozoa. In G. Larwood & B. R. Rosen (eds): Biology and systematics of colonial organisms.— Systematic Association special volume 11: 105-139. London & New York, Academic Press.

Petersen, K., 1990. Evolution and taxonomy in capitate hydroids and medusae.— Zool. J. Linn. Soc. 100: 101-231.

Pfeffer, G., 1890. Die niedere Thierwelt des antarktischen Ufergebietes. In: Die intern. Polarforschung 1882-1883.— Die deutschen Expeditionen und ihre Ergebnisse herausg. von G. Neumayer. 5 (2): 455-572.

Picard, J., 1951a. Note sur les hydraires littoraux de Banyuls-sur-Mer.— Vie Milieu 1 (3): 338-349.

Picard, J., 1951b. Les hydraires des formations coralligènes des côtes françaises de la Méditerranée.— Vie Milieu 2 (2): 255-261.

Picard, J., 1955. Hydraires des environs de Castiglione (Algérie).— Bull. Stn Aquicult. Pêche Castiglione n. ser. 7: 177-199.

Picard, J., 1958. Notes sur une collection d'hydroïdes provenant des côtes méditerranéennes d'Israel.— Bull. Sea Res. Fish. Stn Israel 15: 1-3.

Pictet, C., 1893. Etude sur les Hydraires de la Baie d'Amboine. in: M. Bedot & C. Pictet. Voyage dans l'Archipel Malais.— Rev. Suisse Zool. 1: 1-64.

Pictet, C. & M. Bedot, 1900. Hydraires provenant des campagnes de l'"Hirondelle" (1886-1888).— Rés. Camp. sc. Albert Ier, Prince de Monaco. 18: 1-59.

Pieper, F.W., 1884. Erganzungen zu "Heller's Zoophyten etc. des Adriatischen Meeres".— Zool. Anz. 5 (7): 148-221.

Plante, R., 1961 (1965). Contribution à l'étude des peuplements de hauts niveaux sur substrats solides non récifaux dans la région de Tuléar (Madagascar).— Recl Trav. Stn mar. Endoume h. sér., suppl. 2: 205-312.

Ralph, P.M., 1958. New Zealand thecate hydroids. Part II. Families Lafoeideae, Lineolariidae, Haleciidae and Syntheciidae.— Trans. Roy. Soc. N. Z. 85 (2): 301-356.

Ralph, P.M., 1961. A checklist of the hydroid fauna of the Chatham Islands. In: Biological Results of the Chatham Islands 1954 Expedition, part 5.— Mem. N.Z. oceanogr. Inst., 13 (= Bull. N.Z. Dep. indust. scient. Res. 139(5)): 235-238.

Rees, W. & S. Thursfield, 1965. The hydroid collections of James Ritchie.— Proc. Roy. Soc. Edimb. (B) 69 (1-2) (2): 34-220.

Rees, W. & W. Vervoort, 1987. Hydroids from the John Murray Expedition to the Indian Ocean, with revisory notes on *Hydrodendron, Abietinella, Cryptolaria* and *Zygophylax* (Cnidaria: Hydrozoa).— Zool. Verh. 237: 3-209.

Rho, B.J., 1977. Porifera, Hydrozoa & Ascidiacea.— In: Illustrated Flora and Fauna of Korea 20: 1-470 (Korean with English summary).

Rho, B.J & S.R. Chang 1972. A taxonomic study of the marine hydroids in Korea. 3. Marine hydroids from Jeju-do and Chuja-kundo.— J. Korean Res. Inst. Better Living, Ewha Womans University 9: 97-112 (Korean with English summary).

Rho, B.J. & S.R. Chang, 1974. On the classification and the distribution of the marine benthic animals in Korea. I. Hydroids.— J. Korean Res. Inst. Better Living, Ewha Womans University 12: 133-158.

Riedl, R., 1959. Die Hydroiden des Golfes von Neapel und ihr Anteil an der Fauna unterseeischen Höhlen. In: Ergebnisse der österreichischen Tyrrhenia-Expedition 1952, Teil xvi.— Pubbl. Staz. zool. Napoli 30, suppl.: 591-755.

Riedl, R., 1970. Fauna und Flora der Adria, ed. 2.— Verlag Paul Parey, Hamburg & Berlin: 1-640.

Ritchie, J., 1907. The hydroids of the Scottish National Antarctic Expedition.— Trans. R. Soc. Edinb. 45: 519-545.

Ritchie, J., 1909. New species and varieties of Hydroida Thecata from the Andaman Island— Ann. Mag. Nat. Hist. 3: 524-528.

Ritchie, J., 1910a. The Hydroids of the Indian Museum. I. The deep-sea collection.— Rec. Ind. Mus. 5: 1-30.

Ritchie, J., 1910b. The marine fauna of the Mergui Archipelago, Lower Burma, collected by J.J. Simpson and R.M. Rudmose-Brown. The Hydroids.— Proc. zool. Soc. London 1910: 799-825.

Ritchie, J., 1910c. Hydroids from Christmas Island, Indian Ocean, collected by C.W. Andrews, D. Sc., F.R.S., F.Z.S., in 1908.— Proc. Zool. Soc. London 1910: 826-836.

Ritchie, J., 1911. Hydrozoa (Hydroid Zoophytes and Stylasterina) of the "Tethis" Expedition.— Mem. Aust. Mus. 4: 807-869.

Roca, I. & I. Moreno, 1987. Hidropòlipos de las familias Haleciidae Lafoeidae y Hebellidae. In: Claves para la identificacion de la fauna espanola.— Univ. de le Illes Balears 30: 1-23.

Rossi, L., 1950. Celenterati del Golfo di Rapallo (Riviera Ligure).— Boll. Ist. Mus. Zool. Univ. Torino 2 (4): 193-235.

Rossi, L., 1961. Idroidi viventi sulle scogliere del promontorio di Portofino (Golfo di Genova).— Ann. Mus. St. Nat. Genova 72: 69-85.

Russell, F. S., 1936. On the hydroid of *Laodicea undulata*.— J. mar. biol. Ass. U.K. 20 (3): 581-588.

Russell, F.S., 1953.The medusae of the British Isles. Anthomedusae, Leptomedusae, Limnomedusae, Trachymedusae and Narcomedusae.— Cambridge University Press, London: 1-530.

Ryland, J.S. & M.J. Gibbons, 1991. Intertidal and shallow water hydroids from Fiji. II. Plumulariidae and Aglaopheniidae.— Mem. Qd Mus. 30 (3): 525-560.

Schneider, K. I, 1897. Hydropolypen von Rovigno, nebst Üebersicht über das System der Hydropolypen im Allgemeinen.— Zool. Jahrb. 10: 472-555.

Schydlowsky, A., 1902. The hydroids of the White Sea along the coasts of the Solowetzky Islands. (in Russian).— Trav. Soc. Natur. Kharkow 36: 1-277.

Spracklin, B.W., 1982. Hydroidea (Cnidaria: Hydrozoa) from Carrie Bow Bay, Belize. — In: K. Rutzler & I.G. MacIntyre, eds., The Atlantic Reef Ecosystem at Carrie Bow Bay, Belize, 1: Structure and communities.— Smithson. Contr. mar. Sci. 12: 239-251.

Stechow, E., 1913a. Hydroidpolypen der japanischen Ostküste. II. Teil: Campanularidae, Halecidae, Lafoeidae, Campanulinidae und Sertularidae, nebst Ergänzungen zu den Athecata und Plumularidae. In: F. Doflein, Beiträge zur Naturgeschichte Ostasiens.— Abh. Math.-Phys. Kl. Kön. Bayer. Akad. Wiss., suppl. 3 (2): 1-162.

Stechow, E., 1913b. Neue Genera thecater Hydroiden aus der Familie der Lafoeiden und neue Species von Thecaten aus Japan.— Zool. Anz. 43 (3): 137-144.

Stechow, E., 1919a. Zur Kenntis der Hydroidenfauna des Mittelmeeres, Amerikas und anderer Gebiete, nebst Angaben über einige Kirchenpauer'sche Typen von Plumulariden. — Zool. Jb. Syst. 42(1): 1-172.

Stechow, E., 1921a. Neue Ergebnisse auf dem Gebiete der Hydroidenforschung II, III.— München. mediz. Wochenschr. 1921(1): 30, 897.

Stechow, E., 1921b. Üeber Hydroiden der Deutschen Tiefsee-Expedition, nebst Bemerkungen über einige andere Formen.— Zool. Anz. 53 (9-10): 223-236.

Stechow, E., 1922. Zur Systematik der Hydrozoen, Stromatoporen, Anthozoen und Ctenophoren.— Arch. Naturg. 88 (3): 141-155.

Stechow, E., 1923a. Neue Hydroiden der Deutschen Tiefsee-Expedition, nebst Bemerkungen über einige andere Formen.— Zool. Anz. 56: 1-20.

Stechow, E., 1923b. Üeber Hydroiden der Deutschen Tiefsee-Expedition, nebst Bemerkungen über einige andere Formen.— Zool. Anz. 56: 97-119.

Stechow, E., 1923c. Zur kenntis der Hydroidenfauna des Mittelmeeres, Amerikas, und anderer gebiete. II.— Zool. Jb. Syst. 47: 29-270.

Stechow, E., 1923d. Die Hydroidenfauna der japanischen Region.— J. Coll. Sci. Imperial Univ. Tokyo 44 (8): 1-23.

Stechow, E., 1924. Diagnosen neuer Hydroiden aus Australien.— Zool. Anz. 59 (3-4): 57-69.

Stechow, E., 1925a. Hydroiden von West- und Südwestaustraliën nach den Sammlungen von Prof. Dr. Michaelsen und Prof. Dr. Hartmeyer.— Zool. Jb., Syst. 50 (2): 191-270.

Stechow, E., 1925b. Hydroiden der Deutschen Tiefsee-Expedition.— Wiss. Ergebn. dt. Tiefsee-Exped. 'Valdivia' 1898-1899 27: 383-546.

Stechow, E., 1926. Einige neue Hydroiden aus verschiedenen Meeres-gebieten.— Zool. Anz. 68: 96-168.

Stechow, E. & H.I. Müller, 1923. Hydroiden von den Aru-Inseln.— Abh. Senckenb. naturf. Ges. 35 (4): 459-478.

Thornely, L.R., 1904. Report on the Hydroida collected by Prof. Herdman, at Ceylon, in 1902.— Report to the Government of Ceylon on the Pearl Oyster Fisheries of the Gulf of Manaar, Supplementary Reports 8: 107-126.

Thornely, L.R., 1916. Report on the Hydroida and Polyzoa collected by Mr. James Hornell at Okhamandel in Kattiawar in 1905-06.— In: J. Hornell, Report to the Government of Baroda on the Marine Zoology of Okhamandal in Kattiawar, Part II: 147-150.

Torrey, H.B., 1902. The hydroids of the Pacific coast of north America.— Univ. California Publ. Zool. 1: 1-104.

Totton, A.K., 1930. Coelenterata. Part V.- Hydroida.— Nat. Hist. Rep. Br. Antarct. ('Terra Nova') Exped., 1910, Zool. 5 (5): 131-252.

Trebilcock, R.E., 1928. Notes on New Zealand Hydroida.— Proc. R. Soc. Vict., n. ser. 41 (1): 1-31

Van Praët, M., 1979. Les types de polypes d'Hydraires conservés au Muséum National d'Histoire Naturelle de Paris.— Bull. Mus. natn. Hist. nat. Paris (4) 1, section A (4): 871-940.

Van Soest, R.W.M., 1976. A catalogue of the coelenterate type specimens of the Zoological Museum of Amsterdam. II. Benthic Hydrozoa.— Beaufortia 25 (323): 79-95.

Vanhöffen, E., 1910. Die Hydroiden der Deutschen Südpolar-Expedition 1901-1903.— Deutsche Südpol. Exped. 11, Zool. 3: 269-340.

Vannucci, M., 1949. Hydrozoa do Brasil.— Bolm Fac. Filos. Ciênc. Letr. Univ. São Paulo, 99, Zool. 14: 219-266.

Vannucci, M., 1950. Resultados cientificas do Cruzeiro do "Baependi" e do "Vega" à Ihla da Trindade.— Bolm Inst. Paulista Oceanogr. 1 (1): 81-96.

Vannucci, M., 1951. Hydrozoa e Scyphozoa existente no Instituto Paulista de Oceanografia.— Bolm Inst. Paulista Oceanogr. 2 (1): 69-100.

Vannucci, M., 1954. Hydrozoa e Scyphozoa existentes no Instituto Oceanográfico.— Bol. Inst. Oceanogr. S. Paulo. 5 (1-2): 95-149.

Versluys, J.J., 1899. Hydraires calyptoblastes recueillis dans la mer des Antilles, pendant l'une des croisières accomplies par le comte R. de Dalmas sur son yacht "Chazalie".— Mém. Soc. Zool. France 12: 29-58.

Vervoort, W., 1941. The Hydroida of the Snellius Expedition (Milleporidae and Stylasteridae excluded). Biological results of the Snellius Expedition XI.— Temminckia 6: 186-240.

Vervoort, W., 1946. Exotic hydroids in the collections of the Rijksmuseum van Natuurlijke Historie and the Zoological Museum at Amsterdam.— Zool. Meded. Leiden 26 (1-4): 287-351.

Vervoort, W., 1949. Notes on a small collection of hydroids from Jersey (Channel Islands).— Zool. Meded. Leiden 30 (11): 133-162.

Vervoort, W., 1959. The Hydroida of the tropical west coast of Africa. — Atlantide Report. Scient. Res. Danish Exped. coasts trop. W. Afr., 1945-1946 5: 211-325.

Vervoort, W., 1966. Bathyal and abyssal hydroids.— Galathea Report, Scient. Res. Danish Deep-Sea Exped., 1950-1952 8: 97-173.

Vervoort ,W., 1967. The Hydroida and Chondrophora of the Israel South Red Sea Expedition, 1962. In: Israel South Red Sea Expedition, 1962, Reports, No. 25.— Bull. Sea Fish. Res. Stn Israel 43: 18-54.

Vervoort, W., 1968. Report on a collection of Hydroida from the Caribbean region, including an annotated checklist of Caribbean hydroids.— Zool. Verh. Leiden 92: 1-124.

Vervoort, W., 1972. Hydroids from the Theta, Vema and Yelcho cruises of the Lamont-Doherty geological observatory.— Zool. Verh. Leiden 120: 1-247.

Vervoort, W., 1993. Report on hydroids (Hydrozoa, Cnidaria) in the collection of the Zoological Museum, University of Tel-Aviv, Israel.— Zool. Meded. Leiden 67 (40): 537-565.

Vervoort, W. & P. Vasseur, 1977. Hydroids from French Polynesia with notes on distribution and ecology.— Zool. Verh. Leiden 159: 3-98.

Von Lendenfeld, R., 1884. The Australian Hydromedusae.— Proc. Linn. Soc. N. S. W. 9: 206-241, 345-353, 401-420, 467-492, 581-634.

Von Lendenfeld, R., 1885a. Addenda to the Australian Hydromedusae.— Proc. Linn. Soc. N. S. W. 9: 908-924, 984.

Von Lendenfeld, R., 1885b. Über Coelenteraten der Sudsee. V. Die Hydromedusen des Australischen gebiete.— Z. wiss. Zool. 41: 616-672.

Von Lendenfeld, R., 1887. Descriptive catalogue of the Medusae of the Australian Seas, Pt. 2. Hydromedusae.— Sydney, Australian Museum: 1-49.

Warren, E., 1908. On a collection of hydroids, mostly from the Natal coast.— Ann. Natal Mus. 1: 269-355.

Warren, E., 1909. On *Lafoea dispolians* sp. n. a hydroid parasitic on *Sertularia bidens* Bale.— Ann. Natal Mus. 2 (1): 105-112.

Watson, J., 1975. Hydroids of Bruny Island, southern Tasmania.— Trans. R. Soc. S. Aust. 99 (4): 157-176.

Weltner, W., 1900. Hydroiden von Amboina und Thursday Island. In: R. Semon (ed.), Zoologische Forschungsreise in Australien und dem Malayischen Archipel, Bd. 5.— Denschr. Med. Naturwiss. Ges. Jena 8: 583-590.

Whitelegge, T., 1889. The Hydrozoa, Scyphozoa, Actinozoa and Vermes of Funafuti.— Mem. Aus. Mus. Sydney 3: 371-394.

Yamada, M., 1955. Some hydroids from Agattu, in the Aleutian Islands.— Annot. zool. Japon. 28(2): 121-125.

Yamada, M., 1958. Hydroids from the Japanese Inland Sea, mostly from Matsuyama and its vicinity.— J. Fac. Sci. Hokkaido Univ. (6) 14 (1): 51-63.

Yamada, M., 1959. Hydroid fauna of Japanese and its adjacent waters.— Publs Akkeshi mar. biol. Stn 9: 1-101.

Yamada, M. & S. Kubota, 1987. Preliminary report on the marine hydroid fauna in Okinawa Islands.— Galaxea 6: 35-42.

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