

This article was downloaded by: [University of Bath]

On: 13 February 2014, At: 13:26

Publisher: Taylor & Francis

Informa Ltd Registered in England and Wales Registered Number: 1072954 Registered office: Mortimer House, 37-41 Mortimer Street, London W1T 3JH, UK



Journal of Natural History

Publication details, including instructions for authors and subscription information:

<http://www.tandfonline.com/loi/tnah20>

Revision of *Halisiphonia* Allman, 1888 (Cnidaria, Hydrozoa, Hebellidae), with comments on its taxonomic position

Antonio Carlos Marques^a, Alvaro Luis Peña Cantero^b & Alvaro Esteves Migotto^c

^a Departamento de Zoologia, Instituto de Biociências, Universidade de São Paulo, São Paulo, SP, Brazil

^b Instituto Cavanilles de Biodiversidad y Biología Evolutiva, Universidad de Valencia, Valencia, Spain

^c Centro de Biologia Marinha, Universidade de São Paulo, São Sebastião, SP, Brazil

Published online: 28 Nov 2010.

To cite this article: Antonio Carlos Marques, Alvaro Luis Peña Cantero & Alvaro Esteves Migotto (2006) Revision of *Halisiphonia* Allman, 1888 (Cnidaria, Hydrozoa, Hebellidae), with comments on its taxonomic position, *Journal of Natural History*, 40:17-18, 1047-1062, DOI: [10.1080/00222930600845259](https://doi.org/10.1080/00222930600845259)

To link to this article: <http://dx.doi.org/10.1080/00222930600845259>

PLEASE SCROLL DOWN FOR ARTICLE

Taylor & Francis makes every effort to ensure the accuracy of all the information (the "Content") contained in the publications on our platform. However, Taylor & Francis, our agents, and our licensors make no representations or warranties whatsoever as to the accuracy, completeness, or suitability for any purpose of the Content. Any opinions and views expressed in this publication are the opinions and views of the authors, and are not the views of or endorsed by Taylor & Francis. The accuracy of the Content should not be relied upon and should be independently verified with primary sources of information. Taylor and Francis shall not be liable for any losses, actions, claims, proceedings, demands, costs, expenses, damages, and other liabilities whatsoever or howsoever caused arising directly or indirectly in connection with, in relation to or arising out of the use of the Content.

This article may be used for research, teaching, and private study purposes. Any substantial or systematic reproduction, redistribution, reselling, loan, sub-licensing, systematic supply, or distribution in any form to anyone is expressly forbidden. Terms &

Revision of *Halisiphonia* Allman, 1888 (Cnidaria, Hydrozoa, Hebellidae), with comments on its taxonomic position

ANTONIO CARLOS MARQUES¹, ALVARO LUIS PEÑA CANTERO² & ALVARO ESTEVES MIGOTTO³

¹Departamento de Zoologia, Instituto de Biociências, Universidade de São Paulo, São Paulo, SP, Brazil, ²Instituto Cavanilles de Biodiversidad y Biología Evolutiva, Universidad de Valencia, Valencia, Spain, and ³Centro de Biologia Marinha, Universidade de São Paulo, São Sebastião, SP, Brazil

(Accepted 1 June 2006)

Abstract

The deep-water genus *Halisiphonia* is reviewed, based on redescriptions of all available type specimens of its species. The genus includes four valid species, *H. arctica*, *H. galathea*, *H. megalotheca*, and *H. nana*, and one species inquirenda, *H. spongicola*, for which the type could not be located.

Keywords: Cnidome, deep-water, hydroids, morphometry, systematics, taxonomy

Introduction

The phylogenetic position of the family Hebellidae is disputed. Some authors treat it as a subfamily of the Lafoeidae (e.g. Bouillon 1985; Calder 1991), but there is apparently no synapomorphy uniting the Lafoeidae and the Hebellidae (Schuchert 2001, p 61). The Hebellidae comprises the genera *Bedotella* Stechow, 1913, *Hebella* Allman, 1888, *Scandia* Fraser, 1912, and *Halisiphonia* Allman, 1888 (see reviews in Marques et al. 2004, 2006).

Halisiphonia is a genus of little known and rarely recorded species, and is chiefly characterized by an indistinct demarcation between pedicel and hydrotheca and by having relatively long pedicels in comparison with other Hebellidae. The inconspicuous diaphragm renders some *Halisiphonia* species superficially similar to stolonial colonies of the Lafoeidae genus *Lafoea*, whose members are usually characterized by erect colonies and gonothecae that are aggregated into coppinia.

The *Halisiphonia* species are inhabitants of deep waters, making it difficult to obtain intact specimens and to gather information on their life history. Scarce material also

Correspondence: Antonio Carlos Marques, Departamento de Zoologia, Instituto de Biociências, Universidade de São Paulo, CP 11461, 05422-970, São Paulo, SP, Brazil. Email: marques@ib.usp.br

Published 28 August 2006

ISSN 0022-2933 print/ISSN 1464-5262 online © 2006 Taylor & Francis

DOI: 10.1080/00222930600845259

constrains the understanding on the taxonomy of the genus. Rees and Vervoort (1987) pointed out two better known species of *Halisiphonia* (*H. megalotheca* and *H. galathea*) and “three more, poorly known species in *Halisiphonia*” (Rees and Vervoort 1987, p 34), namely *H. arctica*, *H. nana*, and *H. spongicola*. We have studied the type material of all known species of *Halisiphonia*, except *H. spongicola*, whose type material is presumably lost.

The goal of this study is to redescribe the holotypes of the known species of *Halisiphonia*, in order to clarify the taxonomy of this poorly known hebellid genus and to provide additional morphometric and morphological data (e.g. cnidome). A reliable evaluation of the intra- and interspecific variability is currently not possible and new material might require some of the species to be synonymized.

Material and methods

The material studied belongs to the collections of The Natural History Museum (London, UK), Zoological Museum of the University of Copenhagen (Denmark), Zoologische Staatssammlung München (Germany), and Nationaal Natuurhistorisch Museum (NNM, Leiden, The Netherlands). Types and additional material were examined, measured, and photographed with a compound microscope and a stereomicroscope. The cnidome terminology follows Weill (1934) and Mariscal (1974); measurements of nematocysts were made on non-discharged capsules. Other study methods for Hebellidae and Lafoeidae are given in Peña and García-Carrascosa (1993) and Peña Cantero et al. (1998).

Genus *Halisiphonia* Allman, 1888

Halisiphonia Allman 1888, p 30–31; Stepanjants 1979, p 55.

Type species: *Halisiphonia megalotheca* Allman, 1888, by monotypy.

Diagnosis

Colonies stolonial with creeping hydrorhiza. Hydrothecae tubular or slightly conical, deep, borne on pedicels of varied length; pedicels arising singly from hydrorhiza and almost imperceptibly merging into hydrothecae; diaphragm present, though inconspicuous in some hydrothecae, thin and membranous. Operculum and nematophores absent.

Gonangia developing medusae. Gonothecae solitary, laterally compressed, pedicellate, arising from hydrorhiza.

Remarks

Allman (1888, p 30) established the genus *Halisiphonia* based on *H. megalotheca* (see Allman 1888, p 31, Plate 16, Figure 1, 1a), a species he thought lacking a diaphragm, and of which he stated the hydrothecal cavity was “directly continuous with that of the peduncle or stolon”. Therefore, since its erection, the presence of a diaphragm is generally not mentioned in the diagnosis of *Halisiphonia* species. *Halisiphonia nana* Stechow, 1921 was also described as lacking a diaphragm (Stechow 1921, p 228; 1925, p 452, Figure 22). In both cases, however, the diaphragm was originally overlooked: for *H. megalotheca* the presence of a diaphragm was confirmed by Billard (1910, p 5), who examined the holotype; for *H. nana*, we found a very thin, membranous diaphragm, although it was indistinct or even absent in some hydrothecae. Kramp (1932, p 40) comments: “a diaphragm may be more or less distinctly developed or altogether lacking in this genus”. Indeed, Kramp (1937, 1956) described two other species of *Halisiphonia*, *H. arctica* and *H. galathea*, respectively, in which he recognized a diaphragm. For the former, the diaphragm is stated

as being “a very delicate membrane with a central opening” (Kramp 1937, p 38), whereas for the latter, it was said that “a very slight internal thickening may sometimes indicate the base of the hydrotheca, and in a few cases an extremely delicate diaphragm may be discerned” (Kramp 1956, p 17). Similarly, Vervoort (1966, p 121, for *H. galathea*) states, “in some thecae there is an extremely delicate membrane basally of the place of attachment, in some theca present as a hollowed meniscus, in others as a tight membrane. It may represent a very thin diaphragm”. Bouillon (1985) regarded the feature as present in only some species and Calder (1991, p 31) implied the existence of a diaphragm or annular thickening for Hebellinae (his rank), including *Halisiphonia*.

The inconspicuousness of the diaphragm makes some of the *Halisiphonia* species superficially resemble stolonial colonies of *Lafoea*, a genus usually characterized by erect colonies (occasionally stolonial, see Calder 1991, p 36) and gonothecae aggregated into coppinia. Lafoeids with coppinia are included within the subfamilies Lafoeinae A. Agassiz, 1865 and Zygophylacinae Quelch, 1885, although the genus *Cryptolarella*, with single gonothecae, is exceptionally included among the Eulafoeinae [*sic*] sensu Bouillon (1985) (cf. Marques et al. 2005). In the past, lafoeids with solitary gonophores were assigned to the subfamily Hebellinae Fraser, 1912. The subfamily Hebellinae has been raised to family level (e.g. Schuchert 2001, 2003), and kept separate from the Lafoeidae, a hypothesis corroborated by the presence of medusa buds in the gonothecae of *H. arctica* (Schuchert 2001); an opinion with which we concur.

In *H. arctica*, *H. galathea*, and *H. megalotheca* the gonotheca is spatulate, being round or pear-shaped in frontal view, strongly compressed in lateral view, truncated distally, and attached to the hydrorhiza by a short pedicel (see below). However, according to the original description and single record, *H. spongicola* (Haeckel 1889, p 77, Plate 4, Figure 9) has gonotheca “not compressed or spatuliform, with a slit-shaped opening; their transverse section and the distal opening are circular”. Nonetheless, the frontal outline of its gonotheca seems similar to those of the other *Halisiphonia*.

The gonothecal profile of *Halisiphonia* recalls that of *Hebella* and *Scandia*, two genera assigned to the family Hebellidae (plus *Bedotella*, see Marques et al. 2004, 2006); in *Halisiphonia* and *Bedotella*, however, the gonotheca is strongly laterally compressed.

***Halisiphonia arctica* Kramp, 1932**

(Figure 1; Table I)

Halisiphonia arctica Kramp 1932, p 37, Figures 17–20, 31; Kramp 1963, p 53, 106 (incorrectly assigned as “n. sp.”); Schuchert 2001, p 61, Figure 47.

Material examined

Holotype: *Halisiphonia arctica* Kramp, 1932, colony with gonothecae in alcohol (ZMUC no number).

Type locality

Baffin Bay (Greenland), 74°41'N, 70°30'E, 1200 m, 23 August 1928, on *Eudendrium planum* Bonnevill, 1898, “Godthaab” Expedition Sta. 135.

Description of holotype

Colony stolonial, creeping on hydrocaulus of *Eudendrium planum*. Stolonial hydrorhiza—a network of branching and anastomosing tubes of thin perisarc—giving rise to numerous

pedicellate hydrothecae and five gonothecae. Pedicels smooth, with three to six complete basal annuli, 0.36–4.85 mm long, almost cylindrical throughout (0.10–0.13 mm wide where walls are parallel), slightly and progressively widening to base of hydrothecae, merging into it almost imperceptibly. Hydrothecae deep conical to almost cylindrical, 0.67–1.13 mm high (from diaphragm up to distal renovation), 0.11–0.23 mm wide at diaphragm, 0.19–0.38 mm wide at aperture, with straight and smooth walls (sometimes with inconspicuous undulations) and thin perisarc; margin entire, slightly flaring, with up to 13 renovations; aperture perpendicular to long axis of hydrotheca. Diaphragm membranous, transversal; desmocytes small (ca 4 µm in diameter) and inconspicuous, irregularly distributed or forming one or two transversal rows above diaphragm. Hydranths 0.15–0.25 mm high, 0.16–0.22 mm wide at base of tentacles, with 12–16 tentacles, hypostome conical. Retracted hydranths lying over diaphragm. Hydranth regenerations leaving marks outside (margin renovations) and inside the hydrotheca; new diaphragm formed above the preceding one resulting in a fine thickened line around inner side of hydrotheca and corresponding cycles of desmocytes (not always seen); previous diaphragm may disappear. Hydranth base may be marked with several slight constrictions at the place of older diaphragms.

Gonothecae spatulate, rounded basally, truncated apically, a narrow transverse slit as superior aperture, arising singly from hydrorhiza on short, annulated pedicels (two to three rings). Pedicel 0.10–0.13 mm high, 0.10–0.13 mm wide. Gonotheca 2.50–3.42 mm high, 1.45–1.73 mm wide at aperture, 0.40–0.53 mm wide at base. Two gonothecae containing medusa buds, clearly seen through the fine and transparent gonothecal perisarc. Each gonotheca with two buds in a row, occupying only a fraction of gonothecal inner space; distal bud larger and more developed, with recognizable tentacles, manubrium, and umbrella. Umbrella twice as high as wide, mesoglea thin; manubrium tubular, reaching about halfway to bell margin. In both gonothecae, buds enclosed by a mantle. Peduncle

Table I. Morphometric data of the holotype specimen of *Halisiphonia arctica*.

	Mean ± SD (range) (n)
Diameter of hydrorhiza (mm)	0.09–0.11
Diameter of pedicel base (mm)	0.11 ± 0.01 (0.10–0.12) (10)
Diameter of pedicel distal (mm)	0.12 ± 0.01 (0.11–0.13) (10)
Number of annulations	3–6
Length of pedicel (mm)	1.91 ± 1.49 (0.36–4.85) (10)
Diameter at diaphragm (mm)	0.18 ± 0.03 (0.11–0.23) (10)
Length of hydrothecae (mm)	0.93 ± 0.17 (0.67–1.13) (10)
Diameter at aperture (mm)	0.30 ± 0.06 (0.19–0.38) (10)
Number of renovations	0–13
Length of hydranth (mm)	0.19 ± 0.03 (0.15–0.25) (10)
Width of hydranth (mm)	0.20 ± 0.02 (0.16–0.22) (10)
Number of tentacles	12–16
Length of gonotheca pedicel (mm)	0.12 ± 0.01 (0.10–0.13) (5)
Width of gonotheca pedicel (mm)	0.12 ± 0.01 (0.10–0.13) (5)
Length of gonotheca (mm)	3.06 ± 0.37 (2.50–3.42) (5)
Width of gonotheca (mm)	0.46 ± 0.05 (0.40–0.53) (5)
Length of medusa bud (mm)	1.32 (1)
Width of medusa bud (mm)	0.65 (1)
Length of manubrium (mm)	0.50 (1)
Width of manubrium (mm)	0.12 (1)
Heterotrichous microbasic mastigophores	7.40 ± 0.46 × 2.30 ± 0.35 (10)
Heterotrichous ?macrobasic euryteles	11.35 ± 0.71 × 4.90 ± 0.39 (10)

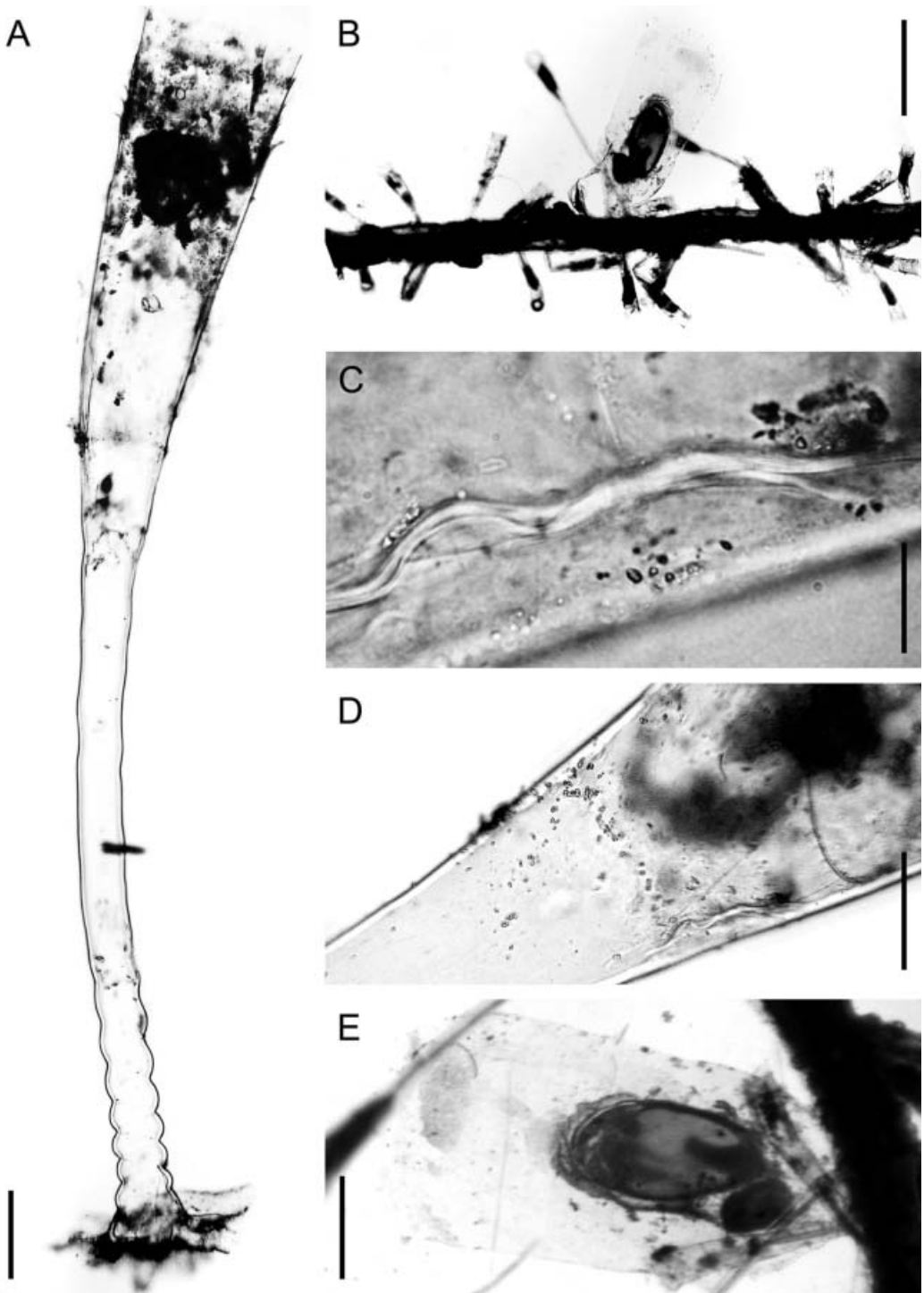


Figure 1. *Halisiphonia arctica* Kramp, 1932. (A) Hydrotheca, lateral view; (B) portion of a colony; (C) hydrothecal diaphragm; (D) base of hydrotheca showing desmocytes; (E) gonothecae, lateral view. Scale bars: 200 μ m (A); 1.0 mm (B); 25 μ m (C); 100 μ m (D); 500 μ m (E).

uniting blastostyle to stem coenosarc broken in both cases. Apparently four tentacles with large bulbs. No nematocysts on the exumbrella or on the mantle. Neither radial canal (at higher magnification, $400\times$) nor sensorial structures (ocelli, statocysts) seen. Absence of gonads indicating that buds possibly represent immature medusae.

Nematocysts of two categories. Heterotrichous microbasic mastigophores (seen discharged), $7.0\text{--}8.0 \times 2.0\text{--}3.0\ \mu\text{m}$, rice grain-shaped, common, ratio shaft/capsule=1:1. Heterotrichous ?macrobasic euryteles (not seen discharged), $10.0\text{--}12.5 \times 4.0\text{--}5.5\ \mu\text{m}$, bean-shaped, common.

Remarks

Halisiphonia arctica has not been recorded again since its original description from Greenland. The species was considered similar to *H. megalotheca* by Schuchert (2001), who notes that the only difference between them is the more elongate hydrotheca of *H. arctica*.

However, concerning gross morphology, *H. arctica* is distinguished from its congeners by the combination of two characters: everted margin and annulated pedicels. *Halisiphonia megalotheca* and *H. nana* have everted margins but both lack annuli in their pedicels. *Halisiphonia arctica* differs from *H. galathea*, with which it shares the presence of annuli in the pedicel, by having everted hydrothecal margin. *Halisiphonia arctica* also shows twice (up to 13) as many renovations as *H. galathea* (up to six) and *H. nana* (up to six), although this may be a variable character. The process of hydranth regeneration of *H. arctica* leaves the scars of the old diaphragms, as described and illustrated by Kramp (1932, p 39, Figures 18–20), a unique feature among the species of the genus.

The medusa of *H. arctica* was previously reported by Schuchert (2001, p 61) from the holotype, the same material being described here. Besides the presence of medusae suggesting affinities with *Hebella* (Schuchert 2001), the morphology of the medusa buds of *H. arctica*, in some aspects (umbrella tall, four tentacles with large bulbs, manubrium cylindrical) comparable to the newly liberated medusae of *Hebella scandens* (Bale, 1888) and *Hebella furax* Millard, 1957 (see Andrade and Migotto 1997; Migotto and Andrade 2000, respectively), indicates affinities between *Halisiphonia* and *Hebella*. Moreover, once this stage becomes better known, there could be a drastic modification on the classification of *Halisiphonia*, and the genus might even fall into synonymy with a medusa-based genus.

Distribution

The species is only known for Greenland, at the depth of 1200 m.

***Halisiphonia galathea* Kramp, 1956**

(Figure 2D; Table II)

Halisiphonia galathea Kramp 1956, p 17–18, Figure 3; Vervoort 1966, p 121–122, Figures 22, 23; Belyaev 1972, p 48.

Material examined

Holotype: *Halisiphonia galathea* Kramp, 1956; colony with gonothecae in alcohol (ZMUC no number).

Type locality

Kermadec Trench (north of New Zealand), $35^{\circ}16'S$, $178^{\circ}40'W$, 8210–8300 m, 14 February 1952, on rock (bottom grey clay with pumice), “Galathea” Expedition Sta. 649.

Table II. Morphometric data of the holotype specimen of *Halisiphonia galathea*.

	Mean \pm SD (range) (n)
Diameter of hydrorhiza (mm)	0.12–0.16
Diameter of pedicel base (mm)	0.12 \pm 0.02 (0.10–0.16) (6)
Diameter of pedicel distal (mm)	0.12 \pm 0.02 (0.10–0.16) (6)
Number of annulations	2–6
Length of pedicel (mm)	5.84 \pm 2.16 (3.96–11.00) (9)
Diameter at diaphragm (mm)	0.25 \pm 0.07 (0.16–0.36) (6)
Length of hydrothecae (mm)	0.94 \pm 0.18 (0.70–1.20) (6)
Diameter at aperture (mm)	0.58 \pm 0.19 (0.28–0.80) (7)
Number of renovations	0–6
Length of gonotheca pedicel (mm)	(0.40–0.50) (2)
Width of gonotheca pedicel (mm)	(0.10–0.14) (2)
Length of gonotheca (mm)	(1.80–2.04) (2)
Width of gonotheca at aperture (mm)	(1.44–1.48) (2)
Width of gonotheca at base (mm)	(0.16–0.26) (2)
Heterotrichous ?microbasic mastigophores	9.56 \pm 0.42 \times 2.38 \pm 0.44 (8)

Description of holotype

Colony stolonial, with many hydrothecae and two gonothecae arising from hydrorhiza. Hydrorhiza 0.12–0.16 mm wide, forming a sparse network of branching tubes of thin perisarc. Pedicel straight, cylindrical, elongated, 3.96–11.00 mm long, 0.10–0.16 mm wide, smooth but with two to six complete basal annuli; slightly and progressively widening to base of hydrotheca, merging into it almost imperceptibly. Hydrotheca deep conical, 0.70–1.20 mm high (from diaphragm up to distal renovation), 0.16–0.36 mm wide at diaphragm, 0.28–0.80 mm wide at aperture, with straight and smooth walls, and thin perisarc; margin entire, not flaring, with up to six renovations; aperture perpendicular to long axis of hydrotheca. Diaphragm membranous, transversal, not conspicuous and sometimes lacking; desmocytes not seen. Hydranths not present.

Gonothecae spatulate, laterally compressed, rounded basally, truncated apically, with a narrow transverse slit as superior aperture, arising singly from hydrorhiza on short, annulated pedicels. Pedicel 0.40–0.50 mm high, 0.10–0.14 mm wide. Gonotheca 1.80–2.04 mm high, 1.44–1.48 mm wide at aperture, 0.16–0.26 mm wide at base.

Nematocysts of one category, heterotrichous ?microbasic mastigophores (not seen discharged), 9.0–10.0 \times 2.0–3.0 μ m, rice grain-shaped, common.

Remarks

Kramp’s (1956) description of *H. galathea* is brief, particularly with regard to colony dimensions; the range of variation or average values of important characters are not given. Kramp (1956, p 17–18) did not recognize gonothecae in the holotype and overlooked that the hydrothecal pedicels are annulated at their bases. He reported pedicels much longer (25 mm) than those found by us (11 mm), but the other measurements given by him are within the range of variation we obtained, except the width of the pedicel, which is slightly thinner than the ones we measured. Nonetheless, *H. galathea* is a well-characterized species due to the straight hydrothecal margin (not everted) and longer pedicels. Rees and Vervoort (1987, p 34) regarded *H. galathea* as conspecific with *H. megalotheca*, due to the existence of intermediate specimens, regarding the pedicel length, and the similarity of their gonothecae. Contrary to their argument, *H. galathea* have much longer and more slender

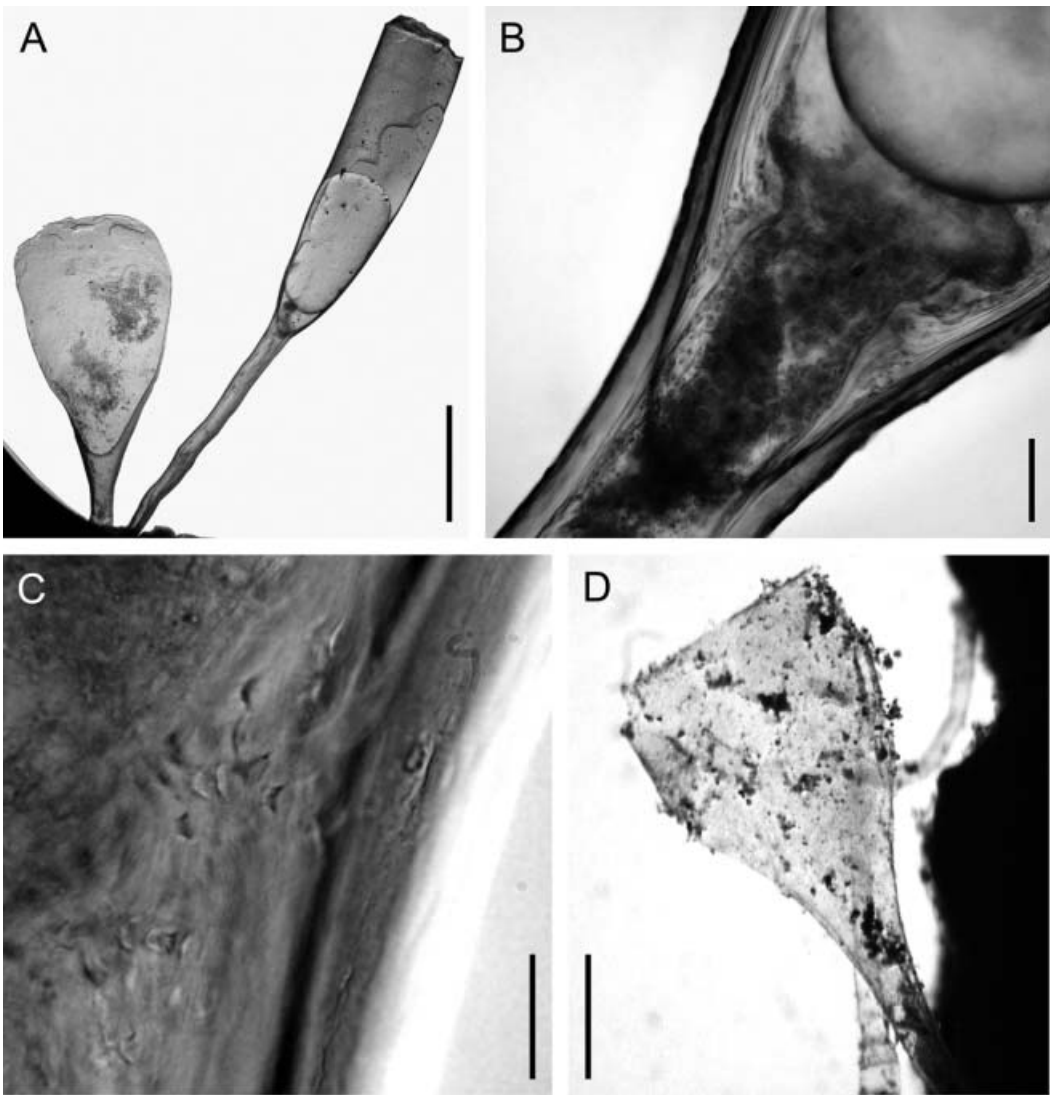


Figure 2. (A–C) *Halisiphonia megalotheca* Allman, 1888: (A) gonotheca (left) and hydrotheca, lateral view; (B) base of hydrotheca; (C) base of hydrotheca showing desmocytes; (D) *Halisiphonia galathea* Kramp, 1956: gonotheca, lateral view. Scale bars: 800 μm (A); 500 μm (B); 25 μm (C); 450 μm (D).

pedicels than those studied by them or by previous authors (Rees and Vervoort 1987, p 33, Table 4). Moreover, the demarcation between pedicel and hydrotheca in *H. galathea* is indistinct, whereas in the holotype of *H. megalotheca* hydrotheca and pedicel are clearly distinct. The illustrations of material identified as *H. megalotheca* by Vervoort (1972, p 60, Figure 17a) and Rees and Vervoort (1987, p 31, Figure 6a, b) are also distinct from *H. galathea* in this aspect. On the contrary, *H. galathea* assigned by Vervoort (1966, p 122, Figure 24), later considered as *H. megalotheca* by Rees and Vervoort (1987), agrees well with the holotype of *H. galathea*, having comparable long pedicels and straight margins. The type specimens of *H. galathea* and *H. megalotheca* also differ in the presence of annuli on the pedicel and non-flaring hydrothecal rim of the former.

Distribution

The species is known from north of New Zealand (Kramp 1956) and Celebes Sea (Vervoort 1966), at depths varying from 4940 (Vervoort 1966) to 8300 m (Kramp 1956).

***Halisiphonia megalotheca* Allman, 1888**

(Figure 2A–C)

Halisiphonia megalotheca Allman 1888, p 31, Plate 16, Figure 1, 1a; Murray 1896, p 357; Kramp 1932, p 40; Kramp 1951, p 123; Vervoort 1966, p 122–123, Figure 24; Vervoort 1972, p 60, Figure 17a; Stepanjants 1979, p 55–56, Plate 9, Figure 11; Rees and Vervoort 1987, p 31; Dawson 1992, p 15.

?*Halisiphonia megalotheca*: Stechow 1925, p 452.

Laföea (Halisiphonia) megalotheca: Levinsen 1893, p 165; Broch 1917, p 14.

Laföea megalotheca: Marktanner-Turnerestcher 1895, p 404; Billard 1910, p 5–6.

Material examined

Holotype: single slide, BMNH 1888.11.13.20, two empty hydrothecae and one empty gonotheca.

Additional material

Single slide, five hydrothecae and one young gonotheca rising from a stolon creeping on a Hexactinellid, Vema Expedition, Sta. 14–29, 30 March 1958, South Africa, 41°03'S, 07°49'E, 4961 m (deposited in the collection of the NNM = RMNH—coel. 7406).

Type locality

South of Australia, 42°42'S, 134°10'E, 2600 fathom (=4755 m), “Challenger” Expedition Sta. 160.

Description of holotype

Colony stolonial, with two empty hydrothecae (remains of tissue are present inside pedicels and base of hydrothecae) and one empty gonotheca arising from hydrorhiza ca 0.12 mm wide. Pedicel smooth, without annulations or constrictions, 1.25–1.90 mm long, almost cylindrical (0.14–0.15 mm wide at base; 0.16–0.18 mm wide distally) except near hydrotheca, where it expands, merging into base of hydrotheca. Walls of pedicel uniformly thick (25–30 µm); annular thickening of perisarc suggesting a feeble diaphragm; several rows of desmocytes (ca 5 µm in diameter) above annular thickening (more conspicuous in one hydrotheca). Hydrothecae campanulate, 2.10–2.60 mm high, 0.22–0.24 mm wide at base, 0.65–0.67 mm wide at aperture. Margin of hydrotheca entire, without renovation; aperture round, inconspicuously everted, perpendicular to long axis of hydrotheca. Hydrothecal wall smooth, with thick perisarc, though thinning distally (20 µm at base; 10–12 µm at middle; 7–10 µm near aperture). Hydranths not present.

Gonothecae spatulate, laterally compressed, rounded basally, truncated apically, with a narrow transverse slit as superior aperture, arising singly from hydrorhiza on short, smooth pedicels. Pedicel ca 0.20 mm long and 0.18 mm wide at base. Gonotheca 2.38 mm total height (including pedicel), 1.16 mm maximal width, ca 0.90 mm wide at apex, 0.61 mm wide at base.

Only one category of nematocysts observed, heterotrichous ?microbasic mastigophores (not seen discharged), $15\text{--}17 \times 2\text{--}4 \mu\text{m}$ ($15.75 \pm 0.76 \times 2.94 \pm 0.78$, $n=8$), rice grain-shaped common.

Additional data

Vervoort (1972, p 60) described specimens from the South Atlantic (4961 m), noting the presence of “spatulate, very compressed body that might represent young gonotheca”. Rees and Vervoort (1987, p 34) described deep-water material from off Oman, in the Arabian Sea, with “one well preserved hydranth found, attached deep inside hydrotheca, just above ‘diaphragm’; 14 tentacles”.

Remarks

Halisiphonia megalotheca has the largest hydrothecae so far described for the genus (at least twice as long; see Table IV). The two hydrothecae present in the holotype are similar in dimensions with the values given by Allman (1888, p 31; “hydrothecae measure about one-tenth of an inch in length”; see Table I), but his illustration (Allman 1888, Plate 16, Figure 1) depicts hydrothecae with a greater length/width ratio than those presently found in the holotype. Stechow (1925, p 452) reports the species for the Indian Ocean ($38^{\circ}40'S$, $77^{\circ}38.6'E$, 672 m deep) creeping on *Symplectoscyphus paulensis* Stechow, 1923 and *Sertularella valdiviae* Stechow, 1923, remarking on its somewhat thinner pedicels and absence of diaphragm, although the place where the hydranth base was attached to the hydrotheca could be determined. The material described by Stechow (1925) presents characteristics intermediate between *H. galathea* and *H. megalotheca*, with hydrothecal length closer to the former and pedicel length closer to the latter. This possibly led Rees and Vervoort (1987, p 31–34, reporting *H. megalotheca*) to consider *H. megalotheca* conspecific with *H. galathea*. Previous authors (e.g. Vervoort 1966, 1972), primarily on the basis of the much longer pedicels of the former, recognized both as separate species. Rees and Vervoort (1987, p 34) justified their decision based on the apparent existence of intermediate specimens, varying from the “short stalked *H. megalotheca*” to the “long stalked *H. galathea*”. Yet, the margin of the hydrotheca of *H. galathea* is straight while that of *H. megalotheca* is everted, although only slightly. Also, we could confirm that Kramp (1956) did not notice that the pedicels of *H. galathea* are annulated basally (see above), contrasting with those of *H. megalotheca* that are completely smooth. As the specimens studied by Vervoort (1972) and Rees and Vervoort (1987) include hydrothecae with both straight and everted margins, but without annulated pedicels, we do not regard them as conspecific with *H. galathea*, although some of them could be assigned to *H. megalotheca*. This species was originally described based on few hydrothecae only, certainly not representing the range of variation of morphometrical characters possibly exhibited by the species. The material identified by Vervoort (1966) as *H. galathea*, but later considered conspecific with *H. megalotheca* by Rees and Vervoort (1987), has straight walls and long pedicels (up to 15 mm long) with “some indistinct rings or wrinkles” (Vervoort 1966, p 121). Vervoort’s (1966, Figure 22) illustration and description of the gonotheca of *H. galathea* appear to be similar in shape and size to those we found in the holotype of the species, suggesting his identification was possibly correct (see above).

Distribution

The species is known from the south of Australia (Allman 1888), South Africa (Vervoort 1972), off Oman (Rees and Vervoort 1987) at depths varying from 692 (Stechow 1925) to 4961 m (Vervoort 1962). We consider the record from St Paul (Stechow 1925) as doubtful.

Halisiphonia nana Stechow, 1921
(Figure 3; Table III)

Halisiphonia nana Stechow 1921, p 227–228; Stechow 1925, p 452–453, Figure 22; Kramp 1932, p 41; Stepanjants 1979, 56, Plate 9, Figure 10; Blanco 1984, p 273, Figure 7; Blanco, Zamponi and Genzano 1994, p 20–21, Figure 20; Rees and Vervoort 1987, p 34–35; Peña Cantero and Gili 2006.
? *Halisiphonia* ? *nana*; Millard 1977, p 14, Figure 3C.

Material examined

Holotype: *Halisiphonia nana* Stechow, 1921; colony with many hydrothecae and without gonothecae in four slides and alcohol (ZSM no number).

Additional material

XXI/2 German Antarctic expedition, Bouvet Island, four hydrothecae on *Sertularella* sp., PS65/029, 25 November 2003, 54°31.59'–54°31.51'S, 03°13.05'–03°12.84'E, 377–365 m, leg. R. V. Polarstern.

Type locality

East of Bouvet Island, South Atlantic, 54°28.7'S, 03°30'E, 457 m, 28 November 1898, “Valdivia” Expedition Sta. 131.

Description of holotype

Colony stolonal, with hydrorhiza creeping on spicules of sponges and other material aggregated on a polychaete tube, and on hydrorhiza and hydrocaulus of *Eudendrium antarcticum* Stechow, 1921. Hydrorhiza smooth, 0.037–0.075 mm in diameter. Pedicel

Table III. Morphometric data of the holotype specimen of *Halisiphonia nana*.

	Mean ± SD (range) (n)
Diameter of hydrorhiza (mm)	0.049 ± 0.008 (0.037–0.075) (16)
Diameter of pedicel base (mm)	0.048 ± 0.005 (0.040–0.062) (16)
Length of pedicel (mm)	0.303 ± 0.076 (0.195–0.462) (16)
Diameter at diaphragm (mm)	0.070 ± 0.008 (0.052–0.087) (16)
Length of hydrothecae (to first aperture) (mm)	0.525 ± 0.100 (0.230–0.715) (16)
Diameter at aperture (terminal or first) (mm)	0.137 ± 0.011 (0.107–0.162) (16)
Diameter at aperture (last renovation) (mm)	0.137 ± 0.005 (0.127–0.147) (5)
Length of first renovation (mm)	0.086 ± 0.052 (0.040–0.260) (6)
Length of second renovation (mm)	0.027–0.082 (3)
Length of third renovation (mm)	0.037 (1)
Length of fourth renovation (mm)	0.077 (1)
Length of fifth renovation (mm)	0.055 (1)
Length of sixth renovation (mm)	0.017 (1)
Length of hydrothecae (total) (mm)	0.592 ± 0.082 (0.352–0.750) (16)

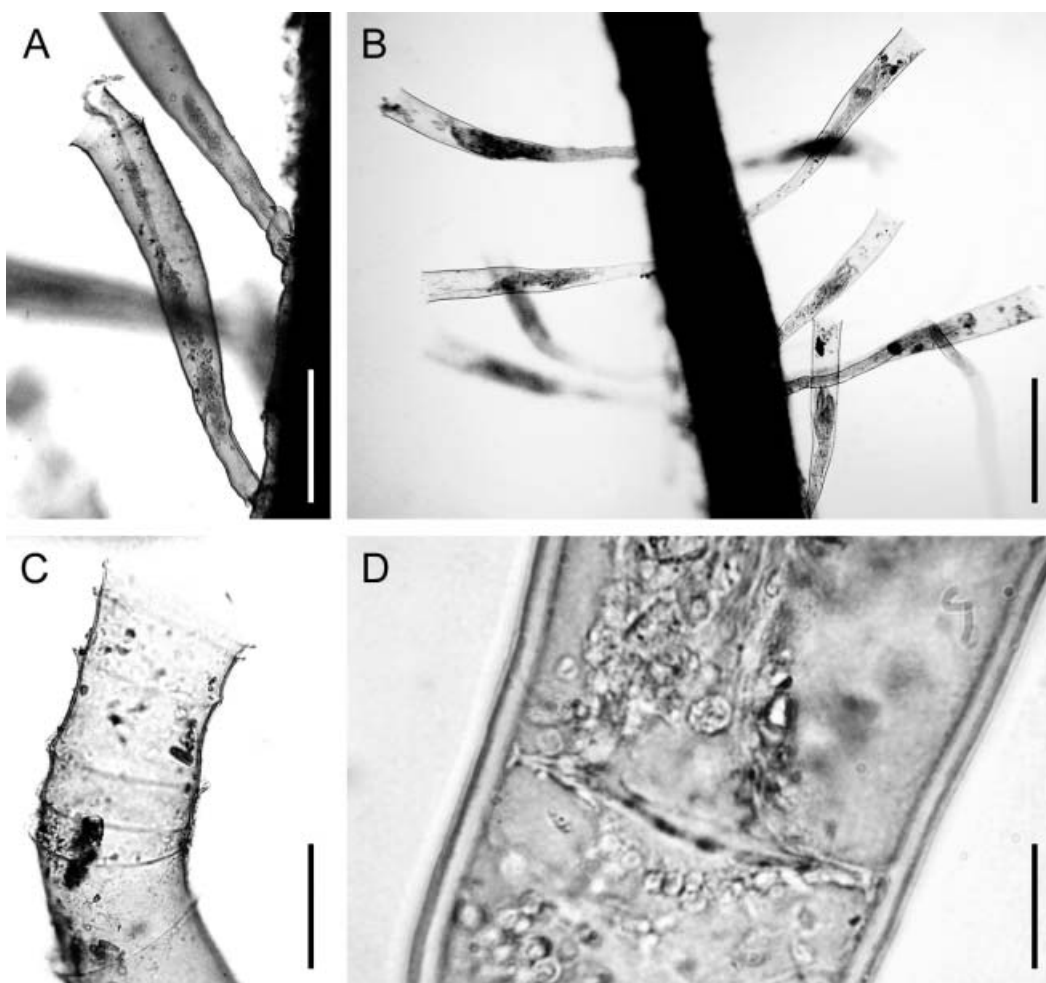


Figure 3. *Halisiphonia nana* Stechow, 1921. (A) Hydrothecae, lateral view; (B) portion of a colony; (C) terminal part of hydrotheca with renovations; (D) base of hydrotheca, showing diaphragm. Scale bars: 250 μm (A); 125 μm (B); 100 μm (C); 25 μm (D).

smooth, with thin perisarc, without annulations (usually with a constriction at base), 0.040–0.062 mm wide at base, slightly and progressively widening to base of hydrothecae, merging into it almost imperceptibly. Base of hydrothecae either with or without a thin, almost undetectable membranous diaphragm; few desmocytes present above diaphragm in some hydrothecae. Distance between hydrorhiza and diaphragm 0.195–0.462 mm. Hydrotheca almost cylindrical, slightly widening towards aperture, 0.352–0.750 mm long, with thin perisarc and smooth walls; margin entire, slightly flaring, with up to six renovations (though usually without renovations); aperture round, 0.107–0.162 mm in diameter. Hydrotheca usually slightly curved to one side; aperture perpendicular or slightly inclined to concave side. Without operculum and nematothecae. Hydranth with about 10 filiform tentacles in one whorl; tentacles with rings of nematocysts; hypostome dome-shaped. Gonotheca not present.

Nematocysts apparently of one category, rice grain-shaped, on tentacles ($6\text{--}7 \times 2.0 \mu\text{m}$).

Remarks

Halisiphonia nana was redescribed by Stechow (1925) on the same original material, asserting the absence of a diaphragm. Nevertheless, in the holotype of *H. nana*, which includes plenty of material with well-preserved hydrothecae and hydranths, we found hydrothecae with diaphragm clearly recognizable as a very thin, transversal membrane at the base of the hydrotheca, although it was indistinct or even absent in some. The diaphragm is better seen at its insertion with the hydrothecal wall. Millard (1977, p 14) doubtfully assigned material from off Crozet Island (Indian Ocean) to the species. We agree with Rees and Vervoort (1987, p 31–34) in considering Millard's record dubious. Besides the absence of “diaphragm or annular thecal thickening”, the specimens described by Millard (1977) are larger, with the diameter of the hydrothecae at the margin twice as wide (0.14–0.23 diameter at margin) as *H. nana* (see above and Table IV). The general dimensions, the everted hydrothecal margin, and the absence of a diaphragm indicate that Millard's specimens are possibly part of a stolonial, young colony of *Lafoea*. The absence of gonophores, however, hinders any better conclusion. Blanco (1984) recorded the species from off South Georgia (54°08'S, 36°02'W, 180 m deep) and also remarked on the absence of a diaphragm or thecal thickening, though her drawing suggests, at least, the presence of desmocytes marking the base of the hydrotheca.

Distribution

The species is known from off Bouvet Island (Stechow 1921; Peña Cantero and Gili 2006), off South Georgia (Blanco 1984), and a doubtful record from off Kerguelen (Millard 1977) at depths varying from 180 (Blanco 1984) to 457 m (Stechow 1921).

***Halisiphonia spongicola* Haeckel, 1889**

Halisiphonia spongicola Haeckel 1889, p 77–78, Plate 4 Figure 9; Kramp 1932, p 40–41; Kramp 1951, p 123; Rees and Vervoort 1987, p 34.

Type specimen

Rees and Vervoort (1987) made no remarks on the type series of the species. The material is not in the museum collections that we consulted and in which it could have been deposited. We believe the type material is lost.

Type locality

Original data are “Challenger” Sta. 241, northwestern Pacific, off Yokohama, 35°41'N, 157°42'E, 4206 m, and “Challenger” Sta. 272, ESE of Christmas Island, 03°48'S, 152°56'W, 4755 m, both on keratose sponges (see Rees and Vervoort 1987, p 34).

Remarks

Halisiphonia spongicola differs from all other species of *Halisiphonia* in the shape of the gonothecae, “not compressed or spatuliform, with a slit-shaped opening; their transverse section and the distal opening are circular” (Haeckel 1889, p 77, Plate 4 Figure 9). The frontal outline of the gonotheca, however, appears similar to those of the other *Halisiphonia* species. Because the type material is likely lost and its original description does not include crucial details, we presently consider *Halisiphonia spongicola* as *species inquirenda*, and suspect that it could even belong to a different genus.

Table IV. Comparative morphological and morphometric data of *Halisiphonia* spp.

	<i>H. artica</i> Kramp, 1931 (holotype—present description)	<i>H. nana</i> Stechow, 1921 (holotype—present description)	<i>H. megalotheca</i> Allman, 1888 (holotype—present description)	<i>H. galathea</i> Kramp, 1956 (holotype—present description)	<i>H. megalotheca</i> Allman, 1888 (Vervoort 1972)	<i>H. galathea</i> Kramp, 1956 (original description)	<i>H. galathea</i> Kramp, 1956 (Vervoort 1966)	? <i>H. galathea</i> Kramp, 1956 (Rees and Vervoort 1987—as <i>H. megalotheca</i>)	<i>H. nana</i> Stechow, 1921 (Blanco 1984)
Pedicle									
Total length	0.36–4.85	0.19–0.46	1.25–1.90	3.96–11.00	1.32–2.60	Up to 20.00–25.00	8.00–15.00	1.50–9.00	0.90–1.26 (including hydrotheca)
Diameter	0.10–0.13	0.04–0.062	0.14–0.18	0.10–0.16	0.12–0.16	0.080	0.12–0.14	0.10–0.16	0.044–0.056
Number of annulations	3–6 (complete annuli)	0 (maximally constricted at base)	0	2–6 (complete annuli)		Not seen			
Hydrotheca									
Length	0.67–1.13	0.35–0.75	2.10–2.60	0.70–1.20	1.9–2.0	1.20	1.2–1.6	1.70–2.30	
Width at base	0.11–0.23	0.05–0.87	0.22–0.24	0.16–0.36	0.16–0.20		0.14–0.16	0.18–0.28	
Desmocytes present	Yes	Yes	Yes	No	?	–	No	?	?
Width at aperture	0.19–0.38	0.10–0.16	0.65–0.67	0.28–0.80	0.48–0.65	0.04	0.64–0.66	0.48–0.88	0.14–0.18
Margin	Everted	Everted	Everted	Straight	Everted	Straight	Straight	Straight	Everted
Margin renovations	Up to 11 (Kramp)/up to 13 (present)	Up to 6	Absent	Up to 6					Present
Gonotheca									
Total length	2.50–3.42		2.30	1.80–2.04	1.35		2.20		
Maximum width	0.40–0.53		1.16	1.44–1.48	1.04		1.16		
Perisarc (hydrotheca + pedicel)	Thin	Thin	Thick	Thin					
Diaphragm	Membraneous	Membraneous	Feeble	Membraneous, sometimes lacking					
Nematocysts	Two types seen	One type seen	One type seen	One type seen					

Acknowledgements

The authors wish to thank Prof. Wim Vervoort (Nationaal Natuurhistorisch Museum, Leiden, The Netherlands) for his help with the bibliography, and Dr. AM García-Carrascosa (Universidad de Valencia, Spain) for hosting us in his laboratory for part of the studies. The project had financial support from Fundação de Amparo à Pesquisa do Estado de São Paulo (FAPESP 2001/02626-7, 2001/10677-0, 2003/02432-3, and 2004/09961-4), by a research contract funded by the Ministerio de Ciencia y Tecnología and the Universidad de Valencia, Spain (Ramón y Cajal Program), a research project (CGL2004-04684/ANT), funded by the Ministerio de Educación y Ciencia of Spain and the Fondo Europeo de Desarrollo Regional (FEDER), and support from the National Museum of Natural History, Department of Invertebrate Zoology, United States Antarctic Program funded by the National Science Foundation (OPP-9509761). ACM and AEM also have financial support from the Conselho Nacional de Desenvolvimento Científico e Tecnológico (CNPq; 302596/2003-8 and 300194/1994-3, respectively).

References

- Allman GJ. 1888. Report on the Hydroida dredged by H.M.S. Challenger during the years 1873–76. Part II—the Tubulariinae, Corymorphinae, Campanulariinae, Sertulariinae, and Thalamophora. Report on the scientific results of the voyage of H.M.S. Challenger during the years 1873–76 23(70):i–xix, 1–90, Plates 1–40.
- Andrade LP de, Migotto AE. 1997. Is there a link between *Hebella* hydroids (Hydrozoa, Lafoeidae) and *Staurodiscus* medusae (Hydrozoa, Laodiceidae)? Resumos Expandidos do VII COLACMAR—Congresso Latino-Americano sobre Ciências do Mar, Santos, SP 1:35–36.
- Bale WM. 1888. On some new and rare Hydroida in the Australian Museum collection. Proceedings of the Linnean Society of New South Wales (Series 2) 3:745–799, Plates 12–21.
- Belyaev GM. 1972. Hadal bottom fauna of the world oceans. Jerusalem: Israel Program for Scientific Translations. 199 p, 46 figures, 51 tables.
- Billard A. 1910. Revision d'une partie de la collection des hydroïdes du British Museum. Annales des Sciences Naturelles, Zoologie (Série 9) 11:1–67.
- Blanco OM. 1984. Adición a los hidrozoos argentinos. II. Revista del Museo de La Plata 13(147):269–282, Figures 1–16, Plates 1, 2.
- Blanco OM, Zamponi MO, Genzano GN. 1994. Lafoeidae de la Argentina (Coelenterata, Hydrozoa, Hydroida). Naturalia Patagónica, Ciencias Biológicas 2:1–31, Figures 1–28.
- Bonnevie K. 1898. Zur Systematik der Hydroiden. Zeitschrift für Wissenschaftliche Zoologie 63:465–495, Plates 25–27.
- Bouillon J. 1985. Essai de classification des hydropolypes-hydromeduses (Hydrozoa-Cnidaria). Indo-Malayan Zoology 2:29–243.
- Broch H. 1917. Hydroidenuntersuchungen. V. Studien über die Coppinia von *Grammaria abietina*. Kongelige Norske Videnskabers Selskab 1916:1–16, Plates 1, 2.
- Calder DR. 1991. Shallow-water hydroids of Bermuda. The Thecatae, exclusive of Plumularioidea. Royal Ontario Museum, Life Sciences Contributions 154:i–iv + 1–140, Figures 1–60.
- Dawson EW. 1992. The Coelenterata of the New Zealand region: a handlist for curators, students and ecologists. Occasional Papers of the Hutton Foundation, New Zealand 1:1–68.
- Fraser CM. 1912. Some hydroids of Beaufort, North Carolina. Bulletin of the Bureau of Fisheries, United States 30:337–387.
- Haeckel E. 1889. Report on the deep-sea Keratosa collected by H.M.S. Challenger during the years 1873–76. Report on the scientific results of the voyage of H.M.S. Challenger during the years 1873–1876, Zoology 32:1–92, Plates 1–8.
- Kramp PL. 1932. The Godthaab Expedition 1928. Hydroids. Meddelelser om Grønland 79(1):1–86, Figures 1–34.
- Kramp PL. 1937. Polypdyr (Coelenterata), II. Gopler. Danmarks Fauna 43:1–223, Figures 1–90.
- Kramp PL. 1951. Hydrozoa and Scyphozoa. Reports of the Swedish Deep-Sea Expedition, 1947–1948 10:121–127, Plate 1.
- Kramp PL. 1956. Hydroids from depths exceeding 6000 meters. Galathea Report 2:17–20, Figures 1–7.

- Kramp PL. 1963. Summary of the zoological results of the “Godthaab” expedition: 1928. The Godthaab Expedition 1928. Meddelelser om Grønland 81:1–115.
- Levinsen GMR. 1893. Meduser, Ctenophorer og Hydroider fra Grønlands vestkyst, tilligemed Bemaerkninger om Hydroidernes Systematik. Videnskabelige Meddelelser fra Dansk Naturhistorisk Forening i Kjøbenhavn 5:143–212, 215–220, Plates 5–8.
- Mariscal RN. 1974. Nematocysts. In: Muscatine L, Lenhoff HM, editors. Coelenterate biology: reviews and new perspectives. New York: Academic Press. p 129–178.
- Marktanner-Turneretscher G. 1895. Hydroiden, in Zoologische Ergebnisse der im Jahre 1889 auf Kosten der Bremer geographischen Gesellschaft von Dr. Willy Kükenenthal und Dr. Alfred Walter ausgeführten Expedition nach ost-Spitzbergen. Zoologische Jahrbücher, Abteilung Systematik 8:391–438, Plates 11–13.
- Marques AC, Altuna A, Peña Cantero AL, Migotto AE. 2004. Re-description of *Bedotella armata* from Biscay Bay, northern Spain, the type species of *Bedotella* Stechow, 1913 (Cnidaria, Hydrozoa, Lafoeidae), with comments on its taxonomic position. Hydrobiologia 530/531:223–230.
- Marques AC, Peña Cantero AL, Migotto AE. 2005. Revision of the genus *Cryptolarella* Stechow, 1913 (Lafoeidae, Leptothecata, Hydrozoa). Journal of Natural History 39:709–722.
- Marques AC, Peña Cantero AL, Migotto AE. 2006. An overview of the phylogeny of the families Lafoeidae and Hebellidae (Hydrozoa, Leptothecata), their composition and classification. Invertebrate Systematics 20:43–58.
- Migotto AE, Andrade LP de. 2000. The life cycle of *Hebella furax* (Cnidaria: Hydrozoa): a link between a lafoeid hydroid and a laodiceid medusa. Journal of Natural History 34:1871–1888.
- Millard NAH. 1957. The Hydrozoa of False Bay, South Africa. Annals of South African Museum 43:173–243.
- Millard NAH. 1977. Hydroids from the Kerguelen and Crozet shelves, collected by the cruise MD.03 of the Marion Dufresne. Annals of South African Museum 73:1–47.
- Murray J. 1896. On the deep and shallow water marine fauna of the Kerguelen region of the Great Southern Ocean. Transactions of the Royal Society of Edinburgh 38(2)(10):343–500, 1 map.
- Peña (Cantero) AL, García-Carrascosa AM. 1993. The coppinia of *Abietinella operculata* (Lafoeidae: Hydrozoa Leptomedusae) and its systematic position. Journal of Natural History 27:1003–1011.
- Peña Cantero AL, García Carrascosa AM, Vervoort W. 1998. On the species of *Filellum* Hincks, 1868 (Cnidaria: Hydrozoa) with the description of a new species. Journal of Natural History 32:297–315.
- Peña Cantero AL, Gili JM. 2006. Benthic hydroids (Cnidaria, Hydrozoa) from off Bouvet Island (Antarctic Ocean). Polar Biology 29:764–771.
- Quelch JJ. 1885. On some deep-sea and shallow-water Hydrozoa. Annals and Magazine of Natural History 16:1–20, Plates 1, 2.
- Rees WJ, Vervoort W. 1987. Hydroids from the John Murray Expedition to the Indian Ocean, with revisory notes on *Hydrodendron*, *Abietinella*, *Cryptolaria* and *Zygophylax* (Cnidaria: Hydrozoa). Zoologische Verhandelingen 237:1–209.
- Schuchert P. 2001. Hydroids of Greenland and Iceland (Cnidaria, Hydrozoa). Meddelelser om Grønland, Bioscience 53:1–184, Figures 1–138, Appendices 1–3.
- Schuchert P. 2003. Hydroids (Cnidaria, Hydrozoa) of the Danish expedition to the Kei Islands. Steenstrupia 27:137–256, Figures 1–82, Appendices 1, 2.
- Stechow E. 1913. Neue Genera thecater Hydroiden aus der Familie der Lafoeiden und neue Species von Thecaten aus Japan. Zoologischer Anzeiger 43:137–144.
- Stechow E. 1921. Ueber Hydroiden der Deutschen Tiefsee-Expedition, nebst Bemerkungen über einige andre Formen. Zoologischer Anzeiger 53:223–236.
- Stechow E. 1923. Neue Hydroiden der Deutschen Tiefsee Expedition, nebst Bemerkungen über einige andre Formen. Zoologischer Anzeiger 56:1–20.
- Stechow E. 1925. Hydroiden der Deutschen Tiefsee-Expedition. Wissenschaftliche Ergebnisse der Deutschen Tiefsee-Expedition auf dem Dampfer “Valdivia” 1898–1899 17:383–546, Figures 1–54.
- Stepanjants SD. 1979. Gidroidy vod Antarktikh I Subantarktikh. Rezultaty Biologicheskikh Issledovaniy Sovetskikh Antarkticheskikh Ekspeditsiy, Akademiya Nauk SSSR, Leningrad 22(30):1–200, Figures 1–9, Plates 1–25, 3 colour figures on 2 plates.
- Vervoort W. 1966. Bathyal and abyssal hydroids. Galathea Report 8:97–173.
- Vervoort W. 1972. Hydroids from the Theta, Vema and Yelcho cruises of the Lamont-Doherty Geological Observatory. Zoologische Verhandelingen 120:1–247.
- Weill R. 1934. Contribution à l'étude des cnidaires et de leurs nématocystes. I. Recherches sur les nématocystes. Morphologie—Physiologie—Développement. II. Valeur taxonomique du cnidome. Travaux de la Station Zoologique de Wimereux 11:1–701.