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

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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. galatheae*, *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 stolonal 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
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. galatheae*) 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 stolonal 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. galatheae*, 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. galatheae) 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 stolonal colonies of Lafoea, a genus usually characterized by erect colonies (occasionally stolonal, 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. galatheae, 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 hydrothiza 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_ Bonnevie, 1898, “Godthaab” Expedition Sta. 135.

**Description of holotype**

Colony stolonal, creeping on hydrocaulus of _Eudendrium planum_. Stolonal hydrothiza—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 μm (A); 1.0 mm (B); 25 μm (C); 100 μm (D); 500 μm (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 (celli, statocysts) seen. Absence of gonads indicating that buds possibly represent immature medusae.

Nematocysts of two categories. Heterotrichous microbasic mastigophores (seen discharged), $7.0–8.0 \times 2.0–3.0\mu m$, rice grain-shaped, common, ratio shaft/capsule $=1:1$. Heterotrichous ?macrobasic euryteles (not seen discharged), $10.0–12.5 \times 4.0–5.5\mu m$, 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. galatheae_, 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. galatheae_ (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 galatheae_** Kramp, 1956

(Figure 2D; Table II)

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

Material examined

Holotype: _Halisiphonia galatheae_ Kramp, 1956; colony with gonothecae in alcohol (ZMUC no number).

Type locality

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

Colony stolonal, 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 membraneous, 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 × 2.0–3.0 μm, rice grain-shaped, common.

Remarks

Kramp’s (1956) description of *H. galatheae* 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. galatheae* is a well-characterized species due to the straight hydrothecal margin (not everted) and longer pedicels. Rees and Vervoort (1987, p 34) regarded *H. galatheae* 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. galatheae* have much longer and more slender

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

| Character                      | Mean ± SD (range) (n) |
|-------------------------------|-----------------------|
| Diameter of hydrorhiza (mm)   | 0.12–0.16             |
| Diameter of pedicel base (mm) | 0.12 ± 0.02 (0.10–0.16) (6) |
| Diameter of pedicel distal (mm)| 0.12 ± 0.02 (0.10–0.16) (6) |
| Number of annulations         | 2–6                   |
| Length of pedicel (mm)        | 5.84 ± 2.16 (3.96–11.00) (9) |
| Diameter at diaphragm (mm)    | 0.25 ± 0.07 (0.16–0.36) (6) |
| Length of hydrothecae (mm)    | 0.94 ± 0.18 (0.70–1.20) (6) |
| Diameter at aperture (mm)     | 0.38 ± 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 ± 0.42 × 2.38 ± 0.44 (8) |
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. galatheae* 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. galatheae* in this aspect. On the contrary, *H. galatheae* 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. galatheae*, having comparable long pedicels and straight margins. The type specimens of *H. galatheae* and *H. megalotheca* also differ in the presence of annuli on the pedicel and non-flaring hydrothecal rim of the former.

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 galatheae* Kramp, 1956: gonotheca, lateral view. Scale bars: 800 µm (A); 500 µm (B); 25 µm (C); 450 µm (D).
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.

_Lafœa (Halisiphonia) megalotheca_: Levinsen 1893, p 165; Broch 1917, p 14.

_Lafœa 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 stolonal, with two empty hydrothecae (remains of tissue are present inside pedicels and base of hydrotheca) 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), 15–17 × 2–4 µm \( (15.75 \pm 0.76 \times 2.94 \pm 0.78, n=8) \), 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°40’S, 77°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. galatheae* 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. galatheae*. 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. galatheae*”. Yet, the margin of the hydrotheca of *H. galatheae* 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. galatheae* 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. galatheae*, 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. galatheae*, 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. galatheae* 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.

| Measurement                              | 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 diaphrag (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) |
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 (6–7 × 2.0 μm).
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 stolonal, 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.

|                | *H. articata* Kramp, 1931 (holotype—present description) | *H. nana* Stechow, 1921 (holotype—present description) | *H. megalotheca* Allman, 1888 (holotype—present description) | *H. galatheae* Kramp, 1956 (Vervoort 1972) | *H. galatheae* Allman, 1888 (Vervoort 1966) | *H. galatheae* Kramp, 1956 (original description) | *H. galatheae* ?Vervoort 1987—as *H. megalotheca* | *H. nana* Stechow, 1921 (Blanco 1984) |
|----------------|--------------------------------------------------------|----------------------------------------------------|------------------------------------------------------|---------------------------------|---------------------------------|---------------------------------|-------------------------------------------------|---------------------------------|
| **Pedicel**    |                                                        |                                                    |                                                      |                                 |                                 |                                 |                                                 |                                 |
| 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                       |
| 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                       |
| Number of annulations | 3–6 (complete annuli)                        | 0 (maximally constricted at base)                  | 0                                                   | 2–6 (complete annuli)           | Not seen                        | 0.080                                          | 0.080                                          | 0.044–0.056                      |
| **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                                                | 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                       |
| Margin         | Everted                                                | Everted                                            | Everted                                             | Straight                        | Everted                        | Straight                                       | Everted                                       | Present                         |
| Margin renovations | Up to 11                                             | Up to 6                                            | Absent                                              | Up to 6                         |                                 |                                                 |                                                 |                                 |
| **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                   | One type seen                   |                                                 |                                                 |                                 |
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