



## First full description of the large physonect siphonophore *Halistemma amphytridis* (Lesueur & Petit, 1807)

Gillian M. Mapstone

Department of Zoology, The Natural History Museum, Cromwell Road, London SW7 5BD, UK  
E-mail: mapstone@btinternet.com

**Key words:** Cnidaria, Hydrozoa, Siphonophora

### Abstract

The physonect siphonophore *Halistemma amphytridis* (Lesueur & Petit, 1807), previously known as *Stephanomia amphytridis*, was originally described in part from siphosomal material only. This paper demonstrates that the siphosome of a large mature *Halistemma* colony, collected during the 'Snellius' Expedition to Indonesia, is conspecific with two siphosomal samples of the above species taken by Bigelow on the 'Albatross' Expedition to the eastern tropical Pacific. Furthermore, a gap in the literature is filled herein with the first description of a *H. amphytridis* nectosome. The nectophores are larger and more prismatic than those of other published *Halistemma* species, with two vertical-lateral ridges, an incomplete lateral ridge, lateral radial canals of the nectosac more extensively looped, and a pallial canal with short diverticulum into the mesoglea. Siphosomal zooids including gastrozooids, palpons, bracts and gonophores are redescribed. The mature tentillum (on the gastrozoid tentacle) is unicornuate, with a vestigial involucre, a cnidoband with 4–5 coils which is more extended than in other *Halistemma* species (except *H. cupulifera* Lens & van Riemsdijk, 1908), and a terminal filament without a swollen terminal process at the tip.

### Introduction

A large, well-preserved physonect siphonophore collected from the surface of the Flores Sea, Indonesia, during the Dutch 'Snellius' I Expedition is identified as a giant specimen of the agalmatid genus *Halistemma*. Since the siphosome is comparable with material of *Stephanomia amphytridis* in the Smithsonian Institution collected by Bigelow (1911), this 'Snellius' specimen is here referred to *H. amphytridis* (Lesueur & Petit, 1807). *H. amphytridis* nectophores are here described and illustrated for the first time, and siphosomal zooids are re-described.

### Material and methods

Material examined includes:

The subject specimen of this paper from the Museum Naturalis, Leiden, The Netherlands,

collected 22.08.1930 in the Flores Sea, Indonesia, from 7° 55.0' S, 122° 12.5' E (Station 317a) (Goodman, personal communication) during the 'Snellius' I Expedition 1929–1930, and preserved in formalin.

Two samples of siphosomal material from the Smithsonian Institution, Washington (USNM 28303 and 28305), collected 28.12.1904 in the eastern tropical Pacific Ocean circa 600–0 m from 15° 05' 00" S, 99° 19' 00" W (Station 4705) during the 'Albatross' Expedition 1904–1905, identified by H. B. Bigelow as *Stephanomia amphitridis*, and preserved in alcohol.

Other material registered as *Halistemma* from The Natural History Museum, London (NHM) (Reg. Nos. 1949.11.10, 1949.11.10.14–16, 1959.8.10.80–82, 1974.4.26.5, 1974.7.11.1, 1986.1.6.15) and several unregistered *Halistemma* specimens (none referable to *H. amphytridis*) together with *Halistemma rubrum* (Vogt, 1852) from the

Mediterranean Sea (Reg. Nos. 1952.9.23.285-294, 1952.9.23.297-300, 1952.9.23.304, 1952.9.23.305-311, 1953.7.2.23), *H. striata* Totton, 1954, from the Atlantic Ocean (Reg. No. 1973.4.26.5), all identified by A.K. Totton, and a paratype of *Halistemma transliratum* Pugh & Youngbluth, 1988, from the Atlantic Ocean (Reg. No. 1987.4.1.1).

Specimens were transferred either to a petri dish and examined under a Zeiss binocular microscope, or to a cavity slide and examined using an Olympus CH 30 microscope, and illustrated using an attached camera lucida. Terminology for the descriptions is taken mainly from Mapstone (2003), with ridge names from Pugh & Youngbluth (1988).

Abbreviations in the present Figures are: alr – apico-lateral ridge; alr<sub>1</sub> – inner branch of alr; alr<sub>2</sub> – outer branch of alr; alr<sub>t</sub> – tooth on alr; anb – apical nematocyst button; axp – axial process of nectosac; axw – axial wing; ba – basigaster of gastrozoid (cnidogenic band); bc – bracteal canal; bcs – bracteal canal scar; bl – bracteal lamella; br – bract; cb – cnidoband; chr – ostial chromatophore; co – column of gastrozooids; cp – cupulate process; df – dorsal furrow; dg – dorsal groove; div – diverticulum (of pallial canal); doa – dorsal opaque area; drc – dorsal radial canal; dt – dorsal tooth; el – elastic ligaments; fgd – female gonodendron; fgo – female gonophore; gmo – gastrozoid mouth; go – gonophore; grc – gonophore radial canal; gzt – gastrozoid tentacle; hs – hepatic stripe; ib – immature bract; ig – immature gastrozoid; ilr – infra-lateral ridge; inv – involucre; itt – immature tentillum; lf – lateral furrow; lr – lateral ridge; lrc – lateral radial canal; lrc-abl – abaxial loop of lrc; lrc-axl – axial loop of lrc; lrc-dl – dorsal loop of lrc; lrc-ll – lateral loop of lrc; lrc-ol – ostial loop of lrc; lrc-vl – ventral loop of lrc; mgo – male gonophore; mp – mouthplate; n – nectophore; nb – nectophore bud; nbz – nectosomal budding zone; nem – nematocyst; nml – nectophoral muscular lamellae; no – notch; ns – nectosac; nst – nectosomal stem; odf – ostio-dorsal furrow; olf – ostio-lateral furrow; orc – ostial ring canal; ot – ostium; pal – palpon; pal<sub>1</sub>, pal<sub>2</sub> – palpons identified in Figure 3j; pas – pallial canal scar; pcl – palpacle; pcl<sub>1</sub> – palpacle of pal<sub>1</sub>; pdv – proximal diverticulum (of bracteal canal); pe – pedicel of tentillum; pec – pedicular canal; peg – pedicel of female gonodendron; pem – pedicel of male gon-

ophore; pn – pneumatophore; pnd – pneumadenia (gas gland); pns – pneumatosaccus; pp – proximal point (of bract); sbz – siphosomal budding zone; sst – siphosomal stem; t – tooth; tb – thrust block; tf – terminal filament; tr – tentacle rudiment; tt – tentillum; ve – velum; vf – ventral furrow; vk – ventral keel; vlf – vertical-lateral furrow; vlr<sub>1-2</sub> – vertical lateral ridges 1 and 2; v – ventral ridge; vrc – ventral radial canal.

*Taxonomic account:* *Halistemma amphitridis* (Lesueur & Petit, 1807), Figures 1–3

*Stephanomia amphitridis* Lesueur & Petit, 1807: pl. 29, figure 5 (description of figure 5 in Péron, 1807, p. 45); Totton, 1954: 46.

? *Stephanomia foliacea* Quoy & Gaimard, 1833: 74, pl. 13, figures 8–12.

*Stephanomia amphitridis* Huxley, 1859: 72, pl. 6; Schneider, 1898: 118; Bigelow, 1911: 287, pl. 18, figures 1–8; Kawamura, 1953: 110.

*Stephanomia amphitritidis* Agassiz, 1862: 368.

? *Phyllophysa foliacea* Agassiz, 1862: 369.

? *Stephanomia nereidum* Haeckel, 1888a: 40; 1888b: 221.

*Phyllophysa squamacea* Haeckel, 1888a: 40; 1888b: 225.

*Cupulita amphitrites* Bedot, 1896: 408.

? *Stephanomia* sp. Lens & van Riemsdijk, 1908: 84, pl. 15, figures 113–114.

*Halistemma amphitridis* Totton, 1965: 60; Bonnemains & Carré, 1991: 54, figures 1 and 12; (non Daniel, 1974: 47, figure 3h–j; Daniel, 1985: 75, figure 16a, b; Mackie et al., 1987: 117).

### Diagnosis

Halistemmid with prismatic dorso-ventrally flattened nectophores having two complete vertical lateral ridges and incomplete lateral ridge; lateral radial canals with six loops; bract with distal tip of canal terminating in small circular apical nematocyst swelling; terminal process of unicornuate tentillum with small cupulate process.

### Description of 'Snellius' specimen

A schematic representation of the whole colony of *Halistemma amphitridis* is illustrated in Figure 1a.

### *Pneumatophore*

3 mm × 1.25 mm, with numerous endodermal septa enclosing upper gas cavity (pneumatocyst), with red pigmented apex and lower gas gland (pneumadenia) (Fig. 2b).

### *Nectosome*

Nectosomal stem orange, much contracted at 31 mm long, 3.5 mm diameter (Fig. 2b); ventral nectosomal budding zone with numerous buds and several immature attached nectophores, largest with two prominent swellings, probably chromatophores; main stem with dorsal groove and 43 identifiable contracted nectophoral muscular lamellae in ventral mid-line.

### *Nectophores*

Forty one detached matures and two detached immatures. Matures typically 20 mm × 22 mm length by width (upper view) (maximum length 23 mm), 9 mm height (lateral view), with paired ridges and wedge-shaped axial wings; mouthplate with small median notch, protruding <2 mm from nectosac (Fig. 1b and c). Apico-lateral ridge 'alr' delimits dorsal (upper) and lateral surfaces, rises to high point marked by small tooth 'alr<sub>1</sub>', and divides at ostium into inner branch alr<sub>1</sub> and outer branch alr<sub>2</sub> (Figs 1b, d and 2d); infra-lateral ridge 'ilr' delimits ventral (lower) and lateral surfaces and merges imperceptibly with edge of mouthplate ostially (Figs 1c, d and 2d); two

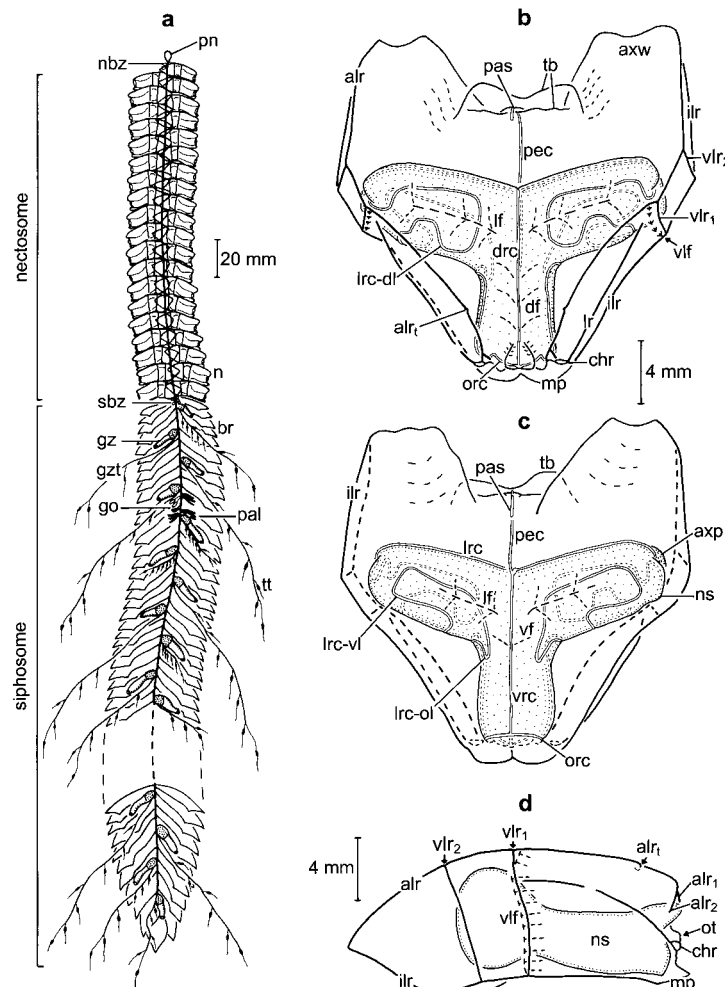


Figure 1. *Halitemma amphitridis*. (a) Schematic representation of whole colony with gonophores and palpons shown in one cormidium only. (b and c) Upper and lower views of mature nectophore. (d) Lateral view of mature nectophore to show ridges. Abbreviations listed under section Materials and methods'.

complete vertical-lateral ridges 'vlr<sub>1</sub>, vlr<sub>2</sub>' connect apico-lateral and infra-lateral ridges (Figs 1b and d); lateral ridge 'lr' extending from vertical lateral furrow to swollen ostial chromatophore plaque, course parallel to apico-lateral ridge (Figs 1a, d and 2d); short ventral ridge from junction of apico-lateral and infra-lateral ridge along edge of wedge-shaped axial wing (Fig. 2c).

Surface with furrows including dorsal furrow in dorsal mid-line from ostium, dividing at mid-nectophore height into two diagonal lateral furrows (Figs 1b and 2d); short ventral furrow in ventral mid-line arises some distance from ostium and divides into two short lateral furrows (Fig. 1c); thin opaque line from notch of mouth-plate to base of ventral furrow (not illustrated); prominent vertical lateral furrow on each lateral surface, adjacent to (and ostial of) vlr<sub>1</sub> ridge (Figs

1b, d and 2a); two short ostio-dorsal furrows above ostium on each side of dorsal opaque area (Fig. 2d); two small ostio-lateral furrows on lateral sides of ostium separate chromatophore swelling from alr<sub>2</sub> (Fig. 2d).

Thrust block between axial wings broad, bilobed in upper and lower views, typically shorter than wings (Fig. 1b and c), atypically longer, and undercut axially; pallial canal in mid-line on axial surface with short blind-ending diverticulum into mesoglea from upper end (Fig. 2e), connecting via long pedicular canal to radial canals of nectosac (Figs 1a, b, 2c and e). Nectosac T-shaped with two broad axial processes (Fig. 1b and c) and thick musculature; radial canals thin, arise together from pedicular canal, with dorsal and ventral straight, laterals each straight to axial nectosac process, then with six loops and short straight

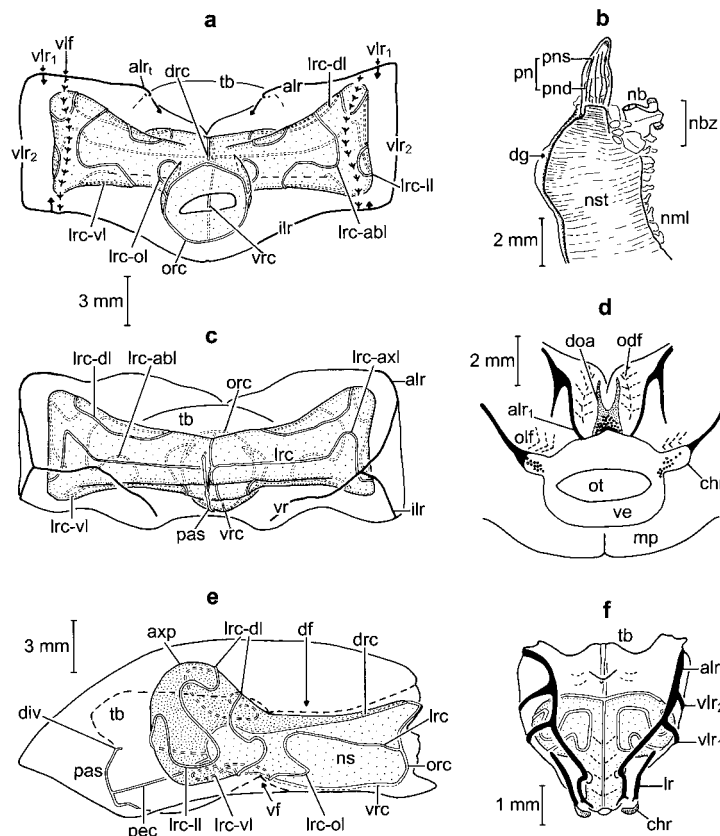


Figure 2. *Halistemma amphytridis*. (a and c). Abaxial and axial views of mature nectophore to illustrate the course of lateral, radial, and other canals (some ridges omitted from a). (b) Apex of nectosome, lateral view. (d) Detail of ostial region of mature nectophore. (e) Lateral view of nectophore to illustrate the course of radial canals. (f) Upper view of immature nectophore. Abbreviations listed under Materials and methods.

section to ostial ring canal (Figs 1b, c, 2a, c and e); loops include small upward axial loop 'lrc-axl' on axial process of nectosac (Fig. 2c), larger downward loop 'lrc-ll' on flattened lateral end of axial process (Fig. 2e), extensive dorsal loop 'lrc-dl' on dorsal nectosac surface (Figs. 1b, 2a and c), small abaxial loop 'lrc-abl' on abaxial nectosac surface (Fig. 2a), extensive ventral loop 'lrc-vl' on ventral nectosac surface (Figs 1c, 2b, c and e), and final small upward ostial loop 'lrc-ol' on lateral nectosac surface (Fig. 2e); ostial ring canal wavy in lateral view, follows contours of ostial end of nectosac (Figs 1b and 2e).

Immature nectophores 4.5–4 mm × 14.5–17.5 mm length by width; ridges prominent, axial wings short and level with thrust block (Fig. 2f); furrows absent in smallest nectophore, vertical lateral furrow deep in larger immature; apico-lateral ridges deviate around tooth  $alr_1$  before reaching ostium; ostial chromatophores prominent.

#### *Siphosome*

Siphosomal stem orange, much contracted, including one length contiguous with nectosome

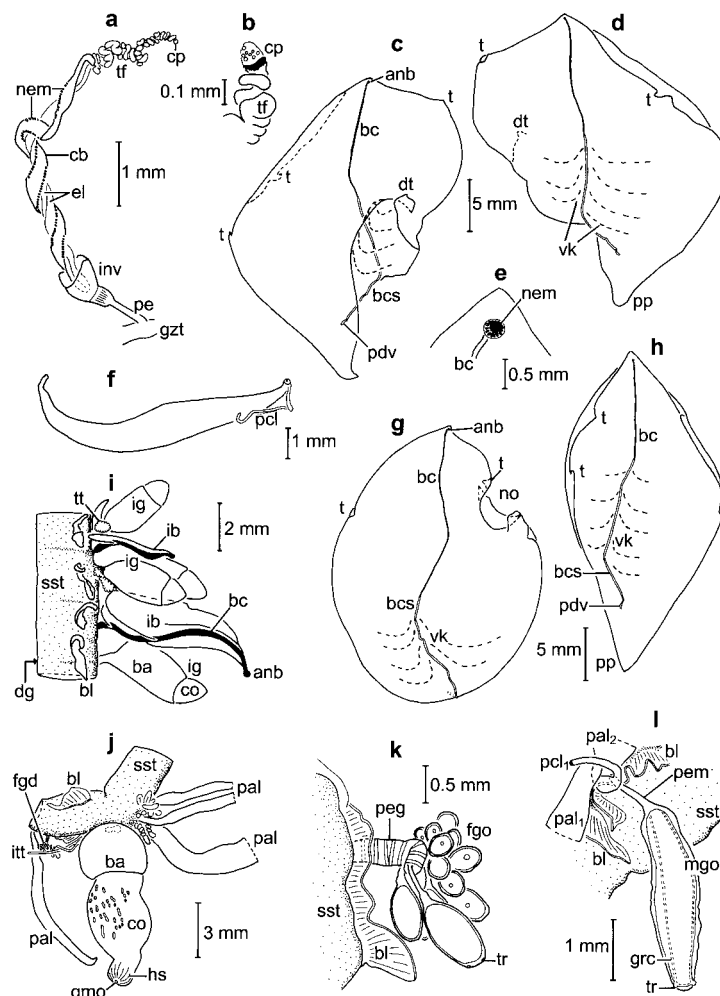


Figure 3. *Halistemma amphitridis*. (a) Mature tentillum. (b) Detail of cupulate process. (c and d) Upper and lower views of lateral bract with dorsal concavity. (e) Detail of tip of mature bract to show apical nematocyst pit. (f) Palpon. (g) Lower view of ventral bract. (h) Lower view of dorsal bract. (i) Lateral view of siphosomal stem below budding zone to show attached siphosomal elements. (j) Gastrozoid attached to stem. (k) Gonodendron. (l) One attached male Gonophore. Abbreviations listed under section Materials and methods'.

having short budding zone at apex, and four separate lengths, with total contracted length of approximately 155 mm; three contiguous cormidia on one fragment, 4–6 mm in length, marked by three contiguous gastrozooids.

#### *Bracts*

217 loose bracts and many small attached immature bracts, translucent with mesoglea thicker proximally than distally; mature bracts typically flaccid, immature bracts turgid; three types identified including 161 detached ‘dorsal’ bracts, 44 ‘lateral’ bracts, and 12 ‘ventral’ bracts; small number with characters intermediate between dorsal and lateral types; average length of matures 24–26 mm.

*Dorsals*: 88 matures, up to 32 mm × 19 mm length by width, leaf-shaped with acute angle to pointed distal tip and with proximal point; typically two pairs of approximately symmetrical lateral teeth (Fig. 3h), atypically with staggered teeth; lower surface with downward projecting ventral keel in proximal part, typically flanked by two shallow concavities, and with elongate bracteal canal scar; origin of scar slightly offset from midline, being closest to lateral surface flanking stem in life; scar with short diverticulum penetrating into mesoglea from proximal end; bracteal canal thin, typically straight, close to lower (ventral) surface, deviating through mesoglea to upper (dorsal) surface apically and terminating as small swollen apical button in cup-shaped depression filled with nematocysts (Fig. 3e); upper surface typically flat, atypically with weak mid-dorsal ridge extending short distance proximally from apical nematocyst button. Fifteen immatures < 27 mm × 17 mm length by width; with teeth either present and typically symmetrical, or represented by swellings only; thick prominent bracteal canal with prominent apical nematocyst button (Fig. 3i), thick scar and very short proximal diverticulum, origin of scar somewhat asymmetric.

*Laterals*: 31 matures, up to 31 mm × 20 mm length by width, typically concave, markedly asymmetric and probably attached to stem in enantiomorphic (mirror-image) pairs, but specific pairs not identifiable in present material; obtuse angle to distal tip (marked by apical nematocyst button) and with proximal point; ventral keel dis-

placed either to right or left and flanked by concavities (Fig. 3d); teeth asymmetric, typically two on outer lateral border (furthest from stem), and 1–2 on inner border; in bracts with only one lateral tooth on stem side, a second tooth is displaced onto upper surface adjacent to deep dorsal concavity (Fig. 3c); in bracts with two teeth on stem side, teeth closer to apex than those on outer lateral margin and upper surface smooth (not illustrated); ventral keel with elongate bracteal canal scar and short proximal diverticulum into mesoglea; bracteal canal thin with apical nematocyst button. Fifteen immatures < 23 mm × 14 mm length by width, markedly asymmetric, with thick bracteal canal, typically large apical button; other variations as for mature bracts.

*Ventrals*: 10 matures, up to 27 mm × 22 mm length by width, thick and proximally rounded, with distal pointed tip and deep < 3 mm wide notch on one side (Fig. 3g); large tooth at each end of notch, sometimes with 1–2 extra teeth at proximal end; typically single small tooth on outer margin; bract with smooth upper surface, typically concave and with bracteal canal scar originating on upper surface (no proximal diverticulum identifiable), passing over thickened proximal end of bract and onto ventral keel; latter with deep concavity on each side; bracteal canal thin, terminating in small apical button. Two immatures < 15 mm × 13 mm length by width, with thick bracteal canal and scar, latter with short proximal diverticulum.

#### *Gastrozoid, tentacle, and tentilla*

Mature gastrozoid < 9 mm × 2 mm length by width, column opaque and yellowish to translucent with hepatic stripes around mouth; basal basigaster pink, typically swollen (Fig. 3j); thick pinkish-grey annulate tentacle attached to basigaster on one side, with small white oval basal disc adjacent; tentacle much coiled, precluding measurement of length, and bearing large number of filamentous immature and mature tentilla (mostly obscured by siphosomal stem and basigaster in Fig. 3j); each mature tentillum arising from one annulus of tentacle, with cnidoband of 4–5 coils, sometimes quite loose, and single much coiled terminal filament with minute acorn-shaped cupulate process at tip (Fig. 3b); younger tentilla with more closely coiled cnidoband. Immature

gastrozooids 5 mm × 2 mm length by width, with basigaster longer relative to column (Fig. 3i).

#### *Palpon and palpacle*

Yellowish white < 15 mm × 2 mm length by width, typically with small swelling below tip, and collar of refringent nematocysts at tip (Fig. 3f); small proximal basal disc; palpacles of detached palpons mostly short and broken, longest measured 6 mm.

#### *Gonophores and gonodendra*

Regularly arranged on stem with 8–12+ male gonophores immediately distal of gastrozoid, then female gonodendron with 10–15+ female gonophores in each cormidium; palpons attached with gonophores. Male gonophores pink, with thin long pedicel when mature, largest approximately 3 mm long (Fig. 3l), four radial canals and four small tentacular buds (with nematocysts) at ostium. Female gonophores white, arranged in gonodendra, each connected to stem by thick pink gonodendron pedicel with opaque strengthening rings; approximately 15 gonophores per gonodendron, at varying stages of development and with nucleus discernible in some (Fig. 3k); gonophores ovoid, elongate with small ostium and four small tentacular buds; radial canals not discernible.

### Discussion

The siphosome of the present ‘Snellius’ specimen of *Halistemma amphytridis* can be directly compared with those of the ‘Albatross’ specimens of *Stephanomia amphytridis* (Bigelow, 1911), as already noted above. These similarities, together with the newly described nectophores of *H. amphytridis*, are discussed and contrasted with the nectophores and siphosomal zooids, where known, of *H. cupulifera*, *H. rubrum*, *H. striata*, and *H. transliratum*.

*Halistemma amphytridis* nectophores are larger (20 × 22 mm length by width) than those of *H. rubrum* (13.0 mm × 10.5 mm length by width, Totton, 1965) and *H. transliratum* (13.0 mm × 13.4 mm length by width, Pugh & Youngbluth, 1988), and exhibit two vertical lateral

ridges instead of one. In *H. rubrum* the single ridge passes diagonally from the apico-lateral ridge towards the infra-lateral ridge, but does not reach it (Totton, 1965, Fig. 21a), whereas in *H. transliratum* the single ridge joins the infra-lateral (Pugh & Youngbluth, 1988). In *H. amphytridis* the lateral ridge is incomplete, as it is in *H. rubrum*, but in the latter species the vertical lateral furrow, where the ‘free end’ of the lateral ridge originates, has a more diagonal alignment in lateral view (personal observation). In *H. transliratum* the lateral ridge is complete and arises from the apico-lateral ridge (Pugh & Youngbluth, 1988, Figs 1–3), whereas only a weak U-shaped and diagonally aligned vertical lateral furrow is discernible in the nectophores of the paratype (personal observation).

The nectophores of *Halistemma amphytridis* are only slightly larger than those of *H. striata* (16 mm × 19 mm length by width). In the latter species there is an extra complete vertical lateral ridge, and a weak vertical lateral furrow separating the most ostial vertical lateral ridge from the lateral ridge in the NHM material. A similar furrow is also figured in *H. striata* nectophores from the South Atlantic (Pugh, 1999, Fig. 3.12). In *H. striata* the lateral ridge divides into two branches; an upper branch passes to the lateral ostial chromatophore and a lower branch continues towards, but does not reach, the infra-lateral ridge. The course of this ridge is well shown by Totton (1965, Fig. 24b). Also in the NHM *H. striata* specimens, the two most ostially situated vertical lateral ridges reunite just before the junction with the infra-lateral ridge.

Two large *Halistemma* species noted in earlier literature and tentatively identified as *H. amphytridis* seem more likely referable to other species. Firstly, a 28–33 mm long nectophore illustrated by Daniel (1974, Fig. 3h) shows different proportions to the present nectophores, and the thrust block is narrow and divided, indicating that it might be an immature nectophore of another giant agalmatid. Secondly, Totton (1965) mentions material collected by Beebe and by the ships of the National Institute of Oceanography which may be *H. amphytridis*, quoted again in Mackie et al. (1987). However, in figures drawn from some of this material and supplied to the author by P. R. Pugh, the nectophore is much larger (< 33 mm × 33 mm length by width) than that of *H. amphytridis*, with

a vertical lateral ridge which divides into two branches, and the bract is differently shaped.

The course of the lateral radial canals over the nectosac in *Halistemma amphitridis* is more complex than in any other described species of the genus. In *H. transliratum* the dorsal loop is quite extensive (Pugh & Youngbluth, 1988), but neither it nor the ventral loop are as complex as the loops of *H. amphitridis* with their 'geometric' appearance and dorsal loop with an extra 'loop within a loop' (Figs 1b and c). In *H. rubrum* (Totton, 1954, Fig. 12) and *H. striata* (Pugh, 1999, Fig. 3.12) the course of the lateral radial canals is simpler. In *H. amphitridis* the nectosac widens ostially, and the upper part juts out over the lower region (Figs 1b and 2e) in a manner not apparent in other *Halistemma* species. The small ostio-lateral furrows in *H. amphitridis* (Fig. 2d) also occur in the *H. transliratum* paratype, and are similar to those observed in *Lychnagalma utricularia* (Pugh & Harbison, 1986, Fig. 2a).

Comparison of the two 'Albatross' specimens with the present siphosome confirms the identity of the present 'Snellius' specimen with *Stephanomia amphitridis* of Bigelow (1911). The dimensions and morphology of the 'Snellius' siphosomal elements, and their arrangement on the siphosomal stem fall within the range found in the 'Albatross' material, and fit the description and illustrations of Bigelow (1911). The bracts in Bigelow's pl. 18 Figures 5 and 8 correspond to the present dorsal bracts (Fig. 3h), the bract in pl. 18 Figure 7 corresponds to the present lateral bracts with a dorsal concavity (Fig. 3c and d), and the bract in pl. 18 Figure 6 has the same notch as the present ventral bracts, though it also has a proximal point. Furthermore, the eight ventral bracts identified in the two loaned USNM specimens have rounded proximal ends identical to those of the 'Snellius' ventral bracts (Fig. 3g). Lateral bracts in the loaned 'Albatross' material include both types found in the 'Snellius' specimen.

In the 'Albatross' material, the stem, basigasters of the gastrozooids and gonophores are varied shades of brown, whereas in the 'Snellius' specimen they are orange (stem, basigasters), pink (male gonophores), or white (female gonophores). This is probably due to preservation of the 'Albatross' specimens in alcohol, whereas in formalin pigment leaches out more readily (Map-

stone, 2003), although a considerable amount still remains in the 'Snellius' specimen.

The arrangement of zooids within a single cormidium is more easily discerned in the 'Albatross' *Stephanomia amphitridis* specimens due to greater stem extension, but is identical to that in the more contracted 'Snellius' specimen. Bigelow clearly shows and describes in his text the sequence of zooids (excluding bracts) in one cormidium as follows: proximal gastrozooid (siphon) – male gonophores – female gonodendron (together with three-six associated palpons) – 3-6 mid-way palpons – 2-5 palpons proximal to next (more distal) gastrozooid – gastrozooid, or siphon (see Bigelow, 1911, pl. 18, Fig. 2 & p. 288). Bigelow (1911) also provides an excellent figure of a mature male gonophore (pl. 18, Fig. 4) which clearly shows the four tentacular rudiments on the bell margin. In the 'Snellius' specimen, there are four similar smaller rudiments around the ostium of the female gonophore (two are shown, but not labelled, in Fig. 3k). Although four radial canals are identified in the umbrella of the largest 'Snellius' male gonophores, they are omitted from Figure 3l.

The *Stephanomia amphitridis* specimen described by Huxley (1859) is similar to the 'Snellius' material, and Huxley's Figures of detached bracts can be equated with the 'Snellius' dorsal (pl. 6, Fig. 6), lateral (pl. 6 Figs 5, 5a and 6), and ventral (pl. 6, Fig. 6b) bracts. *S. amphitridis* is thus here also considered a synonym of *Halistemma amphitridis*, in agreement with Bigelow (1911) and Totton (1965). In *S. nereidum*, Haeckel's description of 3-5 teeth on the bracts and their 'less regular' arrangement on the stem correspond closely to the 'Snellius' specimen, as do the nectophores (see above). The 'free internodes' noted by Haeckel are probably due to greater relaxation of his specimen.

Huxley's *Stephanomia amphitridis* specimen was collected from off the east coast of Australia at 32° S, 155° 7' E (J. Goodman, personal communication), a relatively temperate location. In contrast, both the 'Albatross' and 'Snellius' specimens come from tropical waters, as well as another specimen, recorded as *Cupulita amphitrites* by Bedot (1896), from the Bay of Ambon, off Ceram. Other specimens recorded as *H. amphitridis* not yet reliably identified as the present species, come from areas as far apart as Bermuda (Totton, 1936),



the Bahamas (Haddock & Case, 1999), and Sagami Bay, Japan (Hunt & Lindsay, 1999). It is therefore inappropriate to suggest a distributional range for *Halistemma amphytridis* at this time.

The siphosomal zooids of *Halistemma amphytridis* show several differences to those of other *Halistemma* species. In *H. rubrum* the bracts are smaller, tridentate, and have an elongate apical pit of nematocysts on the upper surface, as shown by Totton (1954, Fig. 13). The cormidial arrangement is also different, with male gonophores arising in three gonodendra at the bases of three palpons, distal to a single female gonodendron arising from the base of a single more proximal palpon (Totton, 1965). The tentillum of *H. rubrum* has a small cone-shaped coil at the tip of the terminal process, illustrated in detail by Pugh & Youngbluth (1988, Fig. 6d), and in relation to a whole gastrozoid tentacle by Vogt (1854, pl. 8, Fig. 6). In *H. transliratum* four bract types are identified by Pugh & Youngbluth (1988). One is the elongate immature nectalia-type not found in the mature 'Snellius' *H. amphytridis* specimen. The other three types are smaller, of which two have a transverse ridge unique to *H. transliratum*. The third bract type is superficially similar to the lateral bracts of *H. amphytridis*, but has an acutely pointed apex and more prominent lateral teeth than in *H. amphytridis*. Since only two specimens of *H. transliratum* have so far been described (Pugh & Youngbluth 1988), with male gonophores found only in the more mature holotype, it is possible that in this specimen the female gonophores had not yet formed. *H. transliratum* may eventually prove to be monoecious, like *H. rubrum* and *H. amphytridis*.

The tentillum of *Halistemma transliratum* bears a small swelling at the tip of the terminal filament. A larger acorn-like (cupulate) swelling or process is the only distinguishing character of the incompletely known species *H. cupulifera* (Lens & van Riemsdijk, 1908). In *H. transliratum*, the dark nematocyst-bearing basal portion of this process is smaller than the pale platelet-covered upper portion (Pugh & Youngbluth, 1988, Figs 6a and 7), whereas in *H. cupulifera* the basal portion is larger and the process is bigger (Pugh & Youngbluth, Fig. 6b). The slightly swollen tip of the terminal filament of *H. amphytridis* constitutes a similar, but smaller, bipartite cupulate process, with platelets distally and nematocysts basally

(Fig. 3b). In *H. rubrum* and *H. transliratum* the cnidoband has 8–10 and 5–6 coils respectively (Totton, 1965; Pugh & Youngbluth, 1988), whereas in *H. amphytridis* it has only 4–5 (Fig. 3a). In the former two species these cnidobands appear to remain tightly coiled when mature, whereas in *H. amphytridis* the cnidoband becomes stretched at maturity to reveal two elastic ligaments (see also Bigelow, 1911, pl. 18, Fig. 3). These ligaments are also observed in *H. cupulifera* (Lens & van Riemsdijk, 1908).

## Conclusions

The present 'Snellius' *Halistemma* specimen is referred to *H. amphytridis* because of the similarity of its siphosome with those of the 'Albatross' specimens. The nectophores are distinctive with two complete vertical lateral ridges and particularly complex lateral radial canals. The tentillum has a very small cupulate process at the tip of the terminal filament, smaller than found in other *Halistemma* species, and different also from the spiral tip to the terminal process of *H. rubrum*.

## Acknowledgments

I extend thanks to Dr Leen van Ofwegen of the Museum Naturalis, Leiden, for loan of the 'Snellius' specimen, to Dr Stephen Cairns of the Smithsonian Institution for loan of the 'Albatross' material, to Professor Philip Rainbow (Keeper of Zoology) of the NHM for provision of facilities, to Dr Philip Pugh for Figures and information on halistemmid material held at Southampton Oceanography Centre, to Dr Jordan Goodman of University College London for providing the grid reference for Huxley's specimen, and to my husband for encouragement and reading the manuscript.

## References

- Agassiz, L., 1862. Part IV. Hydroidæ. Contributions to the Natural History of the United States of America. Second monograph. Little, Brown & Company, Boston; Trübner & Company, London: 183–371.

- Bedot, M., 1896. Les siphonophores de la Baie d'Amboine. Etude suivie d'une revision de la famille des Agalmidae. *Review Suisse de Zoologie* 3: 367–414.
- Bigelow, H. B., 1911. Reports on the scientific results of the expedition to the eastern tropical Pacific, in charge of Alexander Agassiz, by the U. S. Fish Commission Steamer 'Albatross', from October, 1904, to March, 1905, Lieut.-Commander L. M. Garrett, U. S. N., commanding. XXIII. The Siphonophorae. *Memoirs of the Museum of Comparative Zoölogy at Harvard College* 38: 171–401.
- Bonnemains, J. & C. Carré, 1991. Siphonophores et vélèles (1). Observes par F. Péron et C.-A. Lesueur au debut de 19e siècle. *Bulletin trimestriel de la Société Géologique de Normandie et des Amis du Muséum du Havre* 78: 33–82.
- Daniel, R., 1974. Siphonophora from the Indian Ocean. *Memoirs of the Zoological Survey of India* 15: 1–242.
- Daniel, R., 1985. The fauna of India and the adjacent countries. Coelenterata: Hydrozoa, Siphonophora. Publication Zoological Survey of India, Calcutta.
- Haddock, S. H. D. & J. F. Case, 1999. Bioluminescence spectra of shallow and deep-sea gelatinous zooplankton: ctenophores, medusae and siphonophores. *Marine Biology* 133: 571–582.
- Haeckel, E., 1888a. System der Siphonophoren auf phylogenetischer Grundlage entworfen. *Jenaische Zeitschrift für Naturwissenschaft* 22: 1–46.
- Haeckel, E., 1888b. Report on the Siphonophorae collected by H. M. S. Challenger during the years 1873–1876. Report on the scientific results of the voyage of H. M. S. Challenger during the years 1873–76. *Zoology* 28: 1–383.
- Hunt, J. C. & D. J. Lindsay, 1999. Methodology for creating an observational database of midwater fauna using submersibles: Results from Sagami Bay, Japan. *Plankton Biology & Ecology* 46: 75–87.
- Huxley, T. H., 1859. The Oceanic Hydrozoa. A description of the Calycophoridae and Physophoridae observed during the Voyage of H.M.S. "Rattlesnake" in the years 1846–1850. Ray Society, London.
- Kawamura, T., 1954. A report on Japanese siphonophores with special reference to new and rare species. *Journal of the Shiga Prefectural Junior College Series A* 2: 99–129.
- Lens, A. D. & T. van Riemsdijk, 1908. The Siphonophora of the 'Siboga' Expedition. *Siboga Expedition* 9: 1–130.
- Lesueur, C. A. & N. M. Petit, 1807. Voyage découvertes aux terres australes. Atlas. Imprimerie Impériale, Paris.
- Mackie, G. O., P. R. Pugh & J. E. Purcell, 1987. Siphonophore biology. In Blaxter, J. H. & A. J. Southward (eds), *Advances in Marine Biology* 24: 97–262.
- Mapstone, G. M., 2003. Redescriptions of two physonect siphonophores, *Apolemia uvaria* (Lesueur, 1815) and *Tottonia contorta* Margulis, 1976, with comments on a third species *Ramosia vittazi* Stepanjants, 1967 (Cnidaria: Hydrozoa: Apolemiidae). *Systematics and Biodiversity* 1: 181–212.
- Péron, F., 1807. Voyage de découvertes aux terres australes sur les corvettes le *Géographe* et le *Naturaliste* et la goëlette le *Casuarina* pendant les Années 1800–1804. Historique. Vol. 1. Imprimerie Impériale, Paris.
- Pugh, P. R., 1999. Siphonophorae. In Boltovskoy, D. (ed.), *South Atlantic Zooplankton I*. Backhuys Publishers, Leiden, The Netherlands.
- Pugh, P. R. & G. R. Harbison, 1986. New observations on a rare physonect siphonophore, *Lychnagalma utricularia* (Claus, 1879). *Journal of the Marine Biological Association of the United Kingdom* 66: 695–710.
- Pugh, P. R. & M. J. Youngbluth, 1988. A new species of *Halistemma* (Siphonophora: Physonectae: Agalmidae) collected by submersible. *Journal of the Marine Biological Association of the United Kingdom* 68: 1–14.
- Quoy, J. R. C. & J. P. Gaimard, 1833. Voyage de découvertes de l'*Astrolabe* exécuté par ordre du Roi, pendant les années 1826–1827–1828–1829, sous le commandement de M.J. Dumont D'Urville. Zoologie. IV. Atlas Zoophytes. J. Tastu, Paris.
- Schneider, K. C., 1898. Mittheilungen über Siphonophoren. III. Systematische und andere Bemerkungen. *Zoologischer Anzeiger* 21: 51–57, 73–97, 114–133, 153–173, 185–200.
- Totton, A. K., 1936. Plankton of the Bermuda Oceanographic Expeditions. VII. Siphonophora taken during the year 1931. *Zoologica* (New York) 21: 231–240.
- Totton, A. K., 1954. Siphonophora of the Indian Ocean together with systematic and biological notes on related specimens from other oceans. *Discovery Reports* 27: 1–162.
- Totton, A. K., 1965. A Synopsis of the Siphonophora. British Museum (Natural History), London.
- Vogt, C., 1852. Ueber die Siphonophoren. *Zeitschrift für Wissenschaftliche Zoologie* 3: 522–525.
- Vogt, C., 1854. Recherches sur les animaux inférieurs de la Méditerranée. 1. Sur les Siphonophores de la mer de Nice. *Mémoires de l'Institut National Genévois* 1: 1–164.