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## A review of the physonect siphonophore genera *Halistemma* (Family Agalmatidae) and *Stephanomia* (Family Stephanomiidae)

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## Abstract

Re-descriptions are given for all the known species in the siphonophore physonect genera *Halistemma* (Family Agalmatidae) and *Stephanomia* (Family Stephanomiidae fam. nov.) based almost entirely on specimens collected by submersibles or ROVs. A new *Halistemma* species, *H. maculatum* sp. nov., is also described. Until now two of the *Halistemma* species were known only from incomplete specimens, such that for one, *H. cupulifera* Lens & van Riemsdijk, only the tentilla had been described, while for the other, *H. striata* Totton, only the nectophores were known. The species *Stephanomia amphyridis* Lesueur & Petit, originally established on the basis of only an illustration of part of the siphosome, is poorly known and several descriptions in the past have been based on further siphosomal material that actually belonged to a species of *Halistemma*. A specimen of that species, which included the nectosome, was recently described by Mapstone (2004) as *H. amphyridis*, but Pugh (2006) considered that it actually belonged to *H. foliacea* Quoy & Gaimard. That specimen has been re-examined for this study. The taxonomic position of the two genera is discussed. Although only distantly related the species of the two genera have a post-larval form referred to as the *Nectalia* stage. Haeckel (1888b) originally described a specimen at this stage as a separate species, *Nectalia loligo*. *Nectalia* stage specimens of two *Halistemma* species and of *S. amphyridis* were present in the material and their relationship with Haeckel's specimen is discussed.

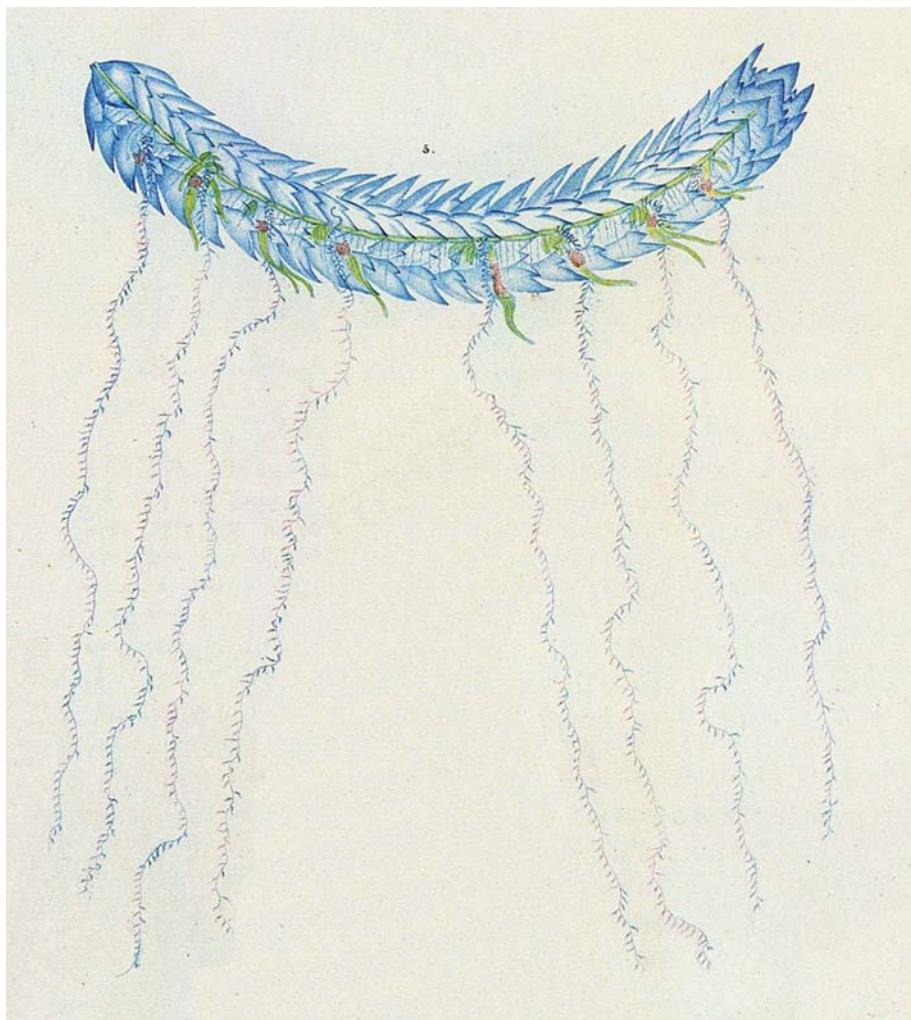
**Key words:** Siphonophora, Physonectae, *Halistemma*, *Stephanomia*, *Nectalia*, Morphology, Taxonomy

## Introduction

Lesueur & Petit (1807, Plate XXIX, fig. 5) (see Figure 1) illustrated, in the Atlas to the "Voyage de découvertes aux Terres Australes", part of the siphosome of a physonect siphonophore, to which they gave the name *Stephanomia Amphyridis*. The exact location where the specimen was collected is unknown and, as Totton (1954) pointed out, according to the narrative of the voyage it could have been anywhere between Le Havre and Mauritius. In the first volume of that narrative Péron & Lesueur (1807, p. 45<sup>1</sup>) said, "What shall I say now of this other species of zoophyte, which, like a beautiful azure-coloured garland of crystal, floats at the surface of the water, regularly

1. Original quote: Que dirai-je maintenant de cette autre espèce de zoophyte, qui, semblable à une belle guirlande de cristal couleur d'azur, se promène à la surface des flots, soulève successivement ses folioles diaphanes, et qui ressemblent à des feuilles de lierre! Ses beaux tentacules couleur de rose sont étendus au loin, cherchant par-tout la proie dont l'animal doit se nourrir. A peine elle est trouvée, que déjà ces tentacules l'ont enveloppée d'un réseau fatal. .... L'animal alors se resserre sur lui-même, en formant une espèce de cercle autour de la pâture qu'il vient de conquérir. Des milliers de suçoirs, semblables à de longues sanguines, s'élancent dans le même instant du dessous des folioles dont je viens de parler, et qui, dans l'état de repos, servent à les recouvrir et à les protéger... Quelques momens à peine se sont écoulés, et déjà la proie la plus volumineuse a disparu.... Dois-je insister sur cette admirable propriété phosphorique commune à la plupart des animaux de cette classe, mais qui dans celui dont je parle, se manifeste plus vive et plus éclatante encore, ce qui le fait paraître au milieu des ténèbres comme une belle guirlande de flammes et de phosphore!

raising its translucent leaflets, which resemble ivy leaves! Its beautiful rose-coloured tentacles have spread widely, ever looking for prey on which the animal feeds. As soon as such was found the tentacles have already wrapped themselves into a deadly network. .... The animal then contracts, forming a kind of circle around the food it had just captured. At the same moment thousands of suckers, like long leeches, shoot out from beneath the leaflets, which I have just mentioned, and which in the resting state, are used to cover and protect them ... Just a few moments have passed, and already the most voluminous prey has disappeared .... Do I need to insist on this wonderful phosphoric property common to most animals of this class, but in that regard, manifests itself more lively and brighter, which makes it appear in the dark like a beautiful garland of flames and phosphorus!"



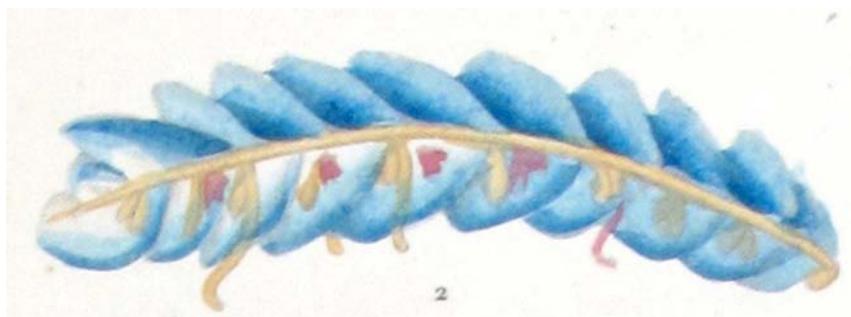
**FIGURE 1.** *Stephanomia amphytridis* from Lesueur & Petit (1807) Plate XXIX figure 5.

This can hardly be considered as a description, but subsequent authors, notably Haeckel (1888b), considered that they could glean sufficient information from the illustration to recognise it as a distinct species. For instance, Haeckel noted that the bracts were tridentate and appeared to be arranged regularly into four longitudinal rows. He also considered that there were free internodes between successive cormidia, i.e. all the components of each cormidium were grouped together around the gastrozooid, and that the siphosomal stem between these groups was devoid of zooids. However, Bedot (1896), for instance, was not convinced with regard to Haeckel's interpretations and, obviously, all these points depend on the accuracy of the original drawing, as will be discussed later.

A second *Stephanomia* species, *S. uvaria* or *uviformis* (see Totton, 1965, p. 45 for further details), was illustrated by Lesueur (? 1815), but soon Eschscholtz (1829) established the genus *Apolemia* to encompass the former specific name, and there it has remained ever since. Chamisso & Eysenhardt (1821, pp. 367–368, Pl. XX<sup>1</sup>XII, fig. 5, A–F) described and figured fragments, including a nectophore, under the name *Stephanomia*

1. Not Plate XXXIII as stated in the text.

*Amphitritis* [sic], but Eschscholtz (1829, p. 152) again considered that it was probably the same as his *Agalma okeni* Eschscholtz, 1825; a conclusion with which we fully concur. However, the genus *Stephanomia* quickly became a catchall for several new physonect siphonophore species. For instance, delle Chiaje (1822, Pl. 50, figs. 7–8; 1829, p. 30) illustrated and briefly described, respectively, the species *Stephanomia ophiura*<sup>1</sup>, which clearly belongs to the currently recognised family Forskaliidae although it is specifically unrecognisable. Quoy & Gaimard (1824, p. 585, Pl. 86, fig. 2) (see Figure 2) added *S. levigata* to the list, but Bedot (1896), in his extensive but not entirely accurate review of the family Agalmatidae, considered that their specimen was an unrecognisable fragment, which indeed it appears to be. Nonetheless, Schneider (1898) identified it as belonging to *S. amphyrtridis*, perhaps because of the apparent blue colouration. Later Quoy & Gaimard (1833, (1834)) briefly described and poorly illustrated ten more *Stephanomia* species, namely *S. helianthus*, *S. melo*, *S. hippopoda*, *S. triangularis*, *S. imbricata*, *S. heptacantha*, *S. foliacea*, *S. alveolata*, *S. tectum*, and *S. cirrhosa*.(see Figures 3 & 4).



**FIGURE 2.** Quoy and Gaimard (1824), Plate 86, fig. 2 "*Stephanomia levigata*".

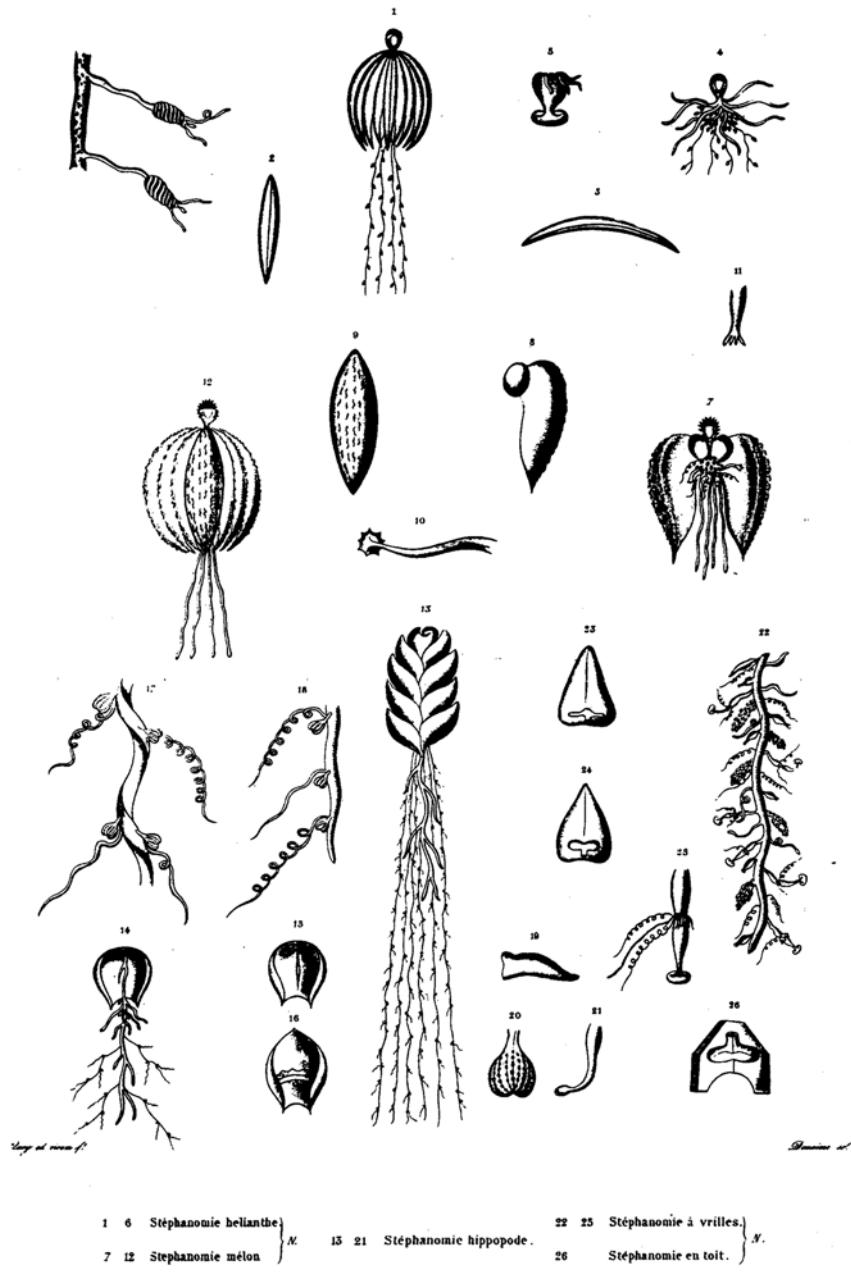
With regard to the first three of Quoy & Gaimard's (1833, (1834)) *Stephanomia* species, Bedot (1896) considered that they "ne sont certainement pas des Agalmides" ["were certainly not agalm(at)ids"]. Indeed, the third species, *S. hippopoda* (Figure 3, nos.13–21) is not a physonect siphonophore, but represents the calycophoran *Hippopodius hippocampus* (Forskål, 1776). Up until recently the other two species, *S. helianthus* and *S. melo* (Figure 3, nos. 1–6 and 7–12, respectively) would have been classified as belonging to the physonect family Athorybiidae. However, recent genetic information (Dunn *et al.*, 2005a) has shown that, despite the obvious differences in form, athorybiid species do in fact form part of the family Agalmatidae. Bedot also correctly surmised that *S. cirrhosa* (Stéphanomie à vrilles, Figure 3, nos. 22–25) belonged to a species of *Forskalia* (family Forskaliidae), but eliminated the single nectophore of *S. Tectum* (Stéphanomie en toit, Figure 3, no. 26) without comment, even though it distinctly resembles one of the two types of nectophore of *Agalma okeni* Eschscholtz, 1825.

For the five species shown in Quoy & Gaimard's (1834) Plate 3 (Figure 4), Bedot (1896) considered them all to be mutilated and incomplete agalmatids of which four, excluding *S. foliacea* (Figure 4, nos. 8–12), were impossible to identify. Again, looking at the shape of the nectophores and bracts of these other four species, one again might hazard a guess that all belong to *Agalma okeni*. Bedot (1896, p. 384<sup>2</sup>) considered that "Only *S. foliacea* can be conserved and classified within the doubtful species, because the particular shape of its bracts will allow it, perhaps, one day to be recognised and then to assign it to a place in the classification of Agalm[at]ids".

It can be seen that Quoy and Gaimard's (1834) illustrations of *Stephanomia* species left a great deal to be desired, and Bedot (1896) noted Haeckel's (1869, p. 47<sup>3</sup>) criticism: "In the case of these arbitrary descriptions/illustrations by Quoy and Gaimard, which additionally involve only mutilated individuals or single fragments, it is indeed totally impossible to determine or to hazard a guess as to which agalmid genus they might be referred. These illustrations are only the useless ballast of science." Haeckel is obviously justified in this statement but, in

1. Totton (1965, p. 97) ascribes the description of this species to "Chiaje, 1831", which appears to be the date when four volumes of the *Memorie su la Storia e Notomia degli Animali senza Vertebre del Regno di Napoli* and the figures were published together. However, the figures (1822) and the volumes (1823, 1825, 1828, 1829) had previously been published separately.
2. Original quote: "Seule, *S. foliacea* peut être conservée; et classée dans les espèces douteuses, car la forme particulière de ses boucliers permettra peut être un jour de la reconnaître et de lui assigner une place dans la classification des Agalmides.
3. Original quote: "Es ist in der That bei jenen willkürlichen Darstellungen von Quoy und Gaimard, die noch dazu meist nur verstümmelte Individuen oder einzelne Bruchstücke betreffen, ganz unmöglich zu bestimmen oder zu errathen, auf welche Agalmiden-Genera dieselben zu beziehen sein könnten. Jene Darstellungen sind nur unnützer Ballast der Wissenschaft."

view of the number of poorly described species and *nomina nuda* that appeared in his 1888 "Challenger" Report (Haeckel, 1888b), and not least those that are pure invention, it does seem somewhat hypocritical. To be fair it should be said that Quoy & Gaimard were medics and not trained naturalists and so their inability to understand the complexity of siphonophores is somewhat understandable. Nonetheless, the fifth species *S. foliacea* will be seen to play an important part, we believe, in the recent history of the genera *Stephanomia* and *Halistemma*.



**FIGURE 3.** Quoy & Gaimard (1834) Plate 2.

Blainville (1834) mentioned and Milne Edwards (1841) described further *Stephanomia* species, but these are not relevant in the present context and so let us pass on to Vogt (1852a, p. 522). He noted "Zwei Arten *Agalma* (ich nenne sie *rubra* und *punctata*)" [Two species of *Agalma* (I call them *rubra* and *punctata*)], but gave no description apart from an illustration of a female gonodendron, and an individual male and female gonophore of the former species. The following year Kölliker (1853) gave a reasonably good description of what he considered to be a new species, namely *Agalmopsis punctata*, and a year later Vogt (1854) then described more fully the two species he had mentioned previously. Rather confusingly, it transpired that Vogt's *Agalma rubra* was the same as Kölliker's

*Agalmopsis punctata*, while Vogt's *Agalma punctata* was clearly a junior synonym of *Apolemia uvaria*. None the less, it is only Vogt's *Agalma rubra* that concerns us as it was the first species of the genus *Halistemma* to be described. However, it should be noted that Vogt (1854) also described and illustrated what he believed to be the post-larval stage of his *Agalma rubra*. But what he described is what is presently called an *Athorybia*-stage and that is now known to be the post-larval stage of *Agalma* species. *Halistemma* species pass through a *Nectalia*-stage (Carré, 1971; present text). Thus Vogt had, inadvertently, described two species under a single specific name.

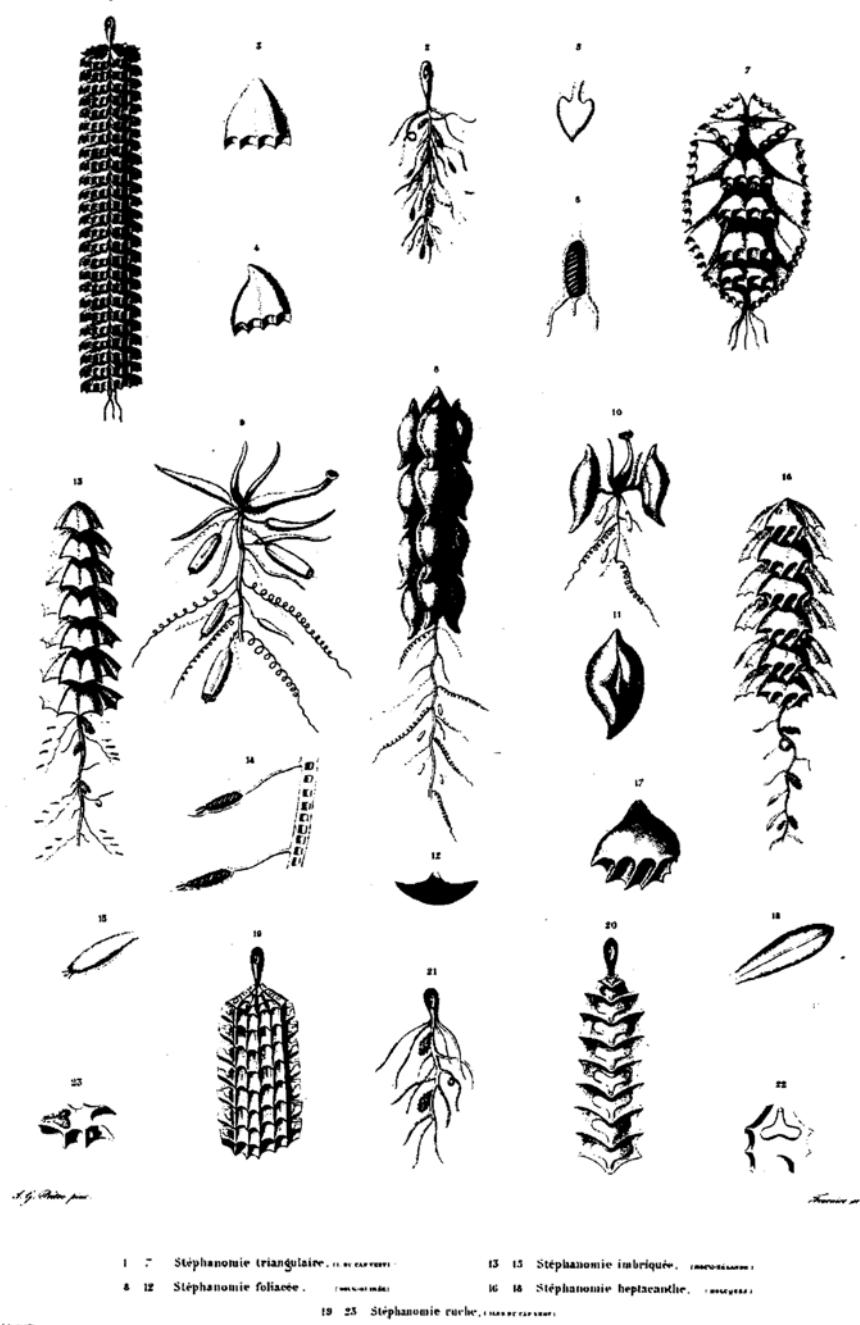
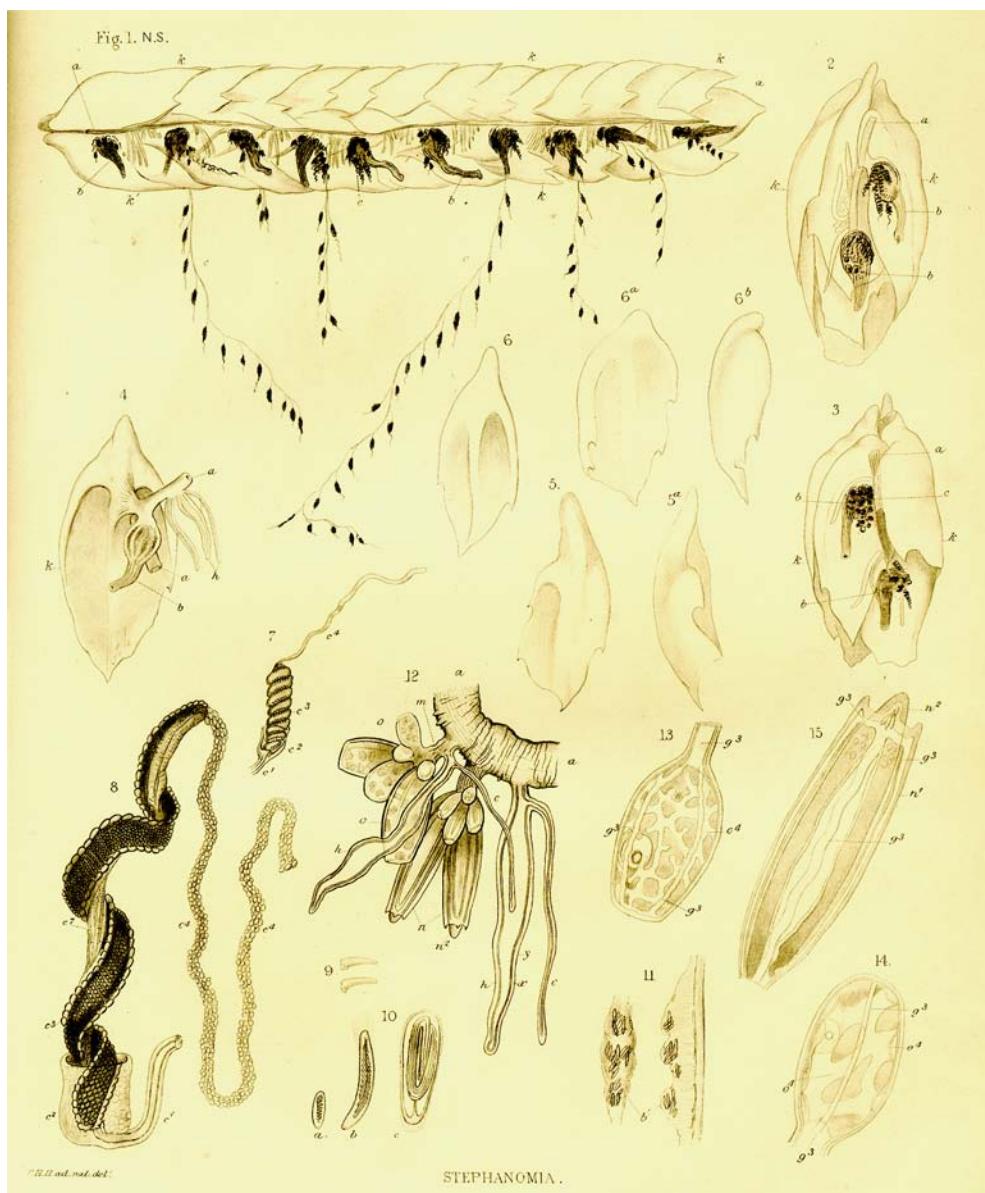


FIGURE 4. Quoy & Gaimard (1834) Plate 3.

Because the tentilla of Vogt's species, *Agalma rubra*, possessed, at the distal end of the cnidoband, a single terminal filament, whereas in *Agalma* species there was a central ampulla and two lateral filaments, Huxley (1859) established a new genus for Vogt's species, namely *Halistemma*, resulting in the specific name becoming *rubrum*. Huxley included this genus, and obviously *Stephanomia*, in his new family, the Stephanomiadæ. The only criterion he used to distinguish these two genera was, according to him, the presence, genus *Stephanomia*, or absence, genus

*Halistemma*, of an involucrum, a covering tissue, at the proximal end of the cnidoband of the tentillum. This differentiation was based on the fact that the specimen he described as *Stephanomia Amphitridis* [sic] possessed an involucrum on each tentillum, while neither Vogt nor Kölliker (1853) had noted the presence of an involucrum on the tentillum of their specimens. However, as will be shown, the reverse is the case as the tentilla of *Halistemma* species do possess an involucrum, albeit almost vestigial in some cases, while the tentilla of the species we now refer to as *S. amphytridis* do not. This obviously means that the specimen Huxley described under that name is actually a *Halistemma* species.



**FIGURE 5.** Huxley's (1859) Plate VI [Not VII as stated in text] of *Stephanomia Amphitridis*.

For Huxley's (1859) redescription of what he called *Stephanomia Amphitridis* (see Figure 5) again he had only a fragment of the siphosome to work with, and his description was brief, although his illustrations were quite detailed. We will draw attention to his statement (*ibid.* p. 72) that "The hydrophyllia [bracts] surrounded the coenosarc in whorls of four (figs. 2, 3) [see Figure 5]; they were attached by triangular, striated processes of the ectoderm, whose base was inserted upon a triangular ridge, which traversed the middle of the internal face of each hydrophyllum (fig. 4). From this a clear linear canal is continued almost to the extremity of the organ. The hydrophyllia were in general leaf-shaped, and it appeared to me that a distinction might be drawn between those which were situated at the sides and those which were superior and inferior; the latter (fig. 5, 5 *a*) being distinguished by a sort of shoulder on one side of their upper extremity, which is absent in the lateral hydrophyllia

(figs. 6, 6 a, 6 b)". However, although the bracts appear to be arranged into four rows, as Haeckel (1888b) interpreted to be the case in Lesueur and Petit's (1807) illustration, it is the morphology of the bracts that is of greatest interest. Also, it should be noted that an involucrum is clearly present on the tentillum of Huxley's specimen (Figure 5, fig. 8), and that Huxley described the presence of palpons with palpacles (Figure 5, fig. 12).

L. Agassiz (1862) seemed to be pre-empting the work of Haeckel (1888b) as he quite unnecessarily complicated the taxonomy of the family Agalmatidae by dividing it into 10 genera, including three new ones of his own and one, *Forskalia*, that actually belongs in the family Forskaliidae. He retained the genus *Halistemma* for Vogt's (1852) *Agalm rubra* and its junior synonym, Kölliker's *A. punctatum*, and *Stephanomia* for *S. amphitridis* (*amphitritis* according to him). But within the genus *Agalmopsis* he included the minor species described by Sars (1846) as *A. elegans*, as well as Kölliker's *A. Sarsii*, and Leuckart's *Agalma clavatum*, which is generally considered to be a junior synonym of *A. elegans*.

Haeckel (1869), not unsurprisingly, disagreed with L. Agassiz (1862) and only retained the four well established agalmatid genera, *Agalma*, *Agalmopsis*, *Halistemma* and *Stephanomia*, together with *Forskalia*, and added a sixth, *Crystallodes* Haeckel that is generally (see Bigelow, 1911) regarded as synonymous with *Agalma*. For the genus *Halistemma*, he agreed with L. Agassiz, but also included in it the species described by A. Agassiz (1865) as *Nanomia cara*. Haeckel (*ibid.* p. 45<sup>1</sup>) made an interesting statement, while describing the attachment of the various zooids to the stem of his new species, *Crystallodes rigidum* (= *Agalma okeni*), that for the siphosome where attached to the ventral side and "in the extension of which is a (ventral) row of nectophores". This must have been a bland assumption, as we know that the nectophores are attached dorsally.

Synopsis of the Genera of Agalmidae.		
I. Subfamily CRYSTALLODINAE.	Cormidia ordinate. Internodes free, covered only with bracts. Palpons and gonostyles at the base of the siphons.	Tentilla with a simple terminal filament, . . . . . 41. <i>Stephanomia</i> . Tentilla tricornuate, with a triple terminal filament, . . . . . 42. <i>Crystallodes</i> .
Siphosome short and rigid, about as long as the necto- some. Trunk of the siphosome stiff, scarcely con- tractile, densely covered with thick prismatic or spher- oidal bracts.	Cormidia loose. Palpons and gonostyles attached to the internodes, between the siphons.	Tentilla with a simple terminal filament, . . . . . 43. <i>Phyllophysa</i> . Tentilla tricornuate, with a triple terminal filament, . . . . . 44. <i>Agalma</i> .
II. Subfamily ANTHEMODINAE.	Cormidia ordinate. Internodes free, covered only with bracts. Palpons and gonostyles at the base of the siphons.	Tentilla with a simple terminal filament, . . . . . 45. <i>Anthemodes</i> . Tentilla tricornuate, with a triple terminal filament, . . . . . 46. <i>Cuneolaria</i> .
Siphosome very long and movable, much longer than the nectosome. Trunk of the siphosome very extensible and contractile, loosely covered with thin scales or folia- ceous bracts (rarely with prismatic bracts).	Cormidia loose. Palpons and go- nostyles attach- ed to the inter- nodes, between the siphons.	Tentilla with a simple terminal filament, { Cnidoband naked, without involu- cre, . . . . . 47a. <i>Halistemma</i> . Cnidoband envelop- ed by a campanu- late involucre, . . . . . 47b. <i>Cupulita</i> . Tentilla tricornuate or multicornuate, with a triple or multiple terminal filament, { Terminal ampulla of the tentilla, with two lateral horns, . . . . . 48. <i>Agalmopsis</i> . Terminal ampulla of the tentilla, with a corona of eight radial horns, . . . . . 49. <i>Lychnagalma</i> .

FIGURE 6. Haeckel's (1888b) key to the genera of the family Agalmatidae.

Haeckel (1888a, b), however, retained 10 genera within the family Agalmatidae, but only six of these were the same. Haeckel based his division of the genera primarily on all eight possible combinations of three characters, i.e.

1. Original quote: "in deren Verlängerung die eine (ventrale) Reihe der Schwimmglocken liegt."

rigid or extensile siphosome, ordinate or loose cormidia, and unicornuate or tricornuate tentilla, with further characters to divide off the two remaining genera (Figure 6). It is a pity that he placed so much emphasis on the first two of these criteria, which are rather dubious, rather than the third, as then the classification would make more sense. Thus a glance at Figure 6 will show that if the structure of the tentillum had been used as the primary taxonomic character, then the genera with tricornuate tentilla, *Agalma*, *Agalmopsis*, *Crystallodes* and *Cuneolaria*, would immediately be separated off from the others. Since, presently, all of these four genera are considered to be synonymous, then the other criteria used by Haeckel to separate them are clearly invalid. This is also the case for the genera with unicornuate tentilla, although in this case four of the genera are considered valid; *Phyllophysa* being a junior synonym of *Halistemma*. But it is still the structure of the tentillum, with particular regard to the involucrum, that characterises each genus.

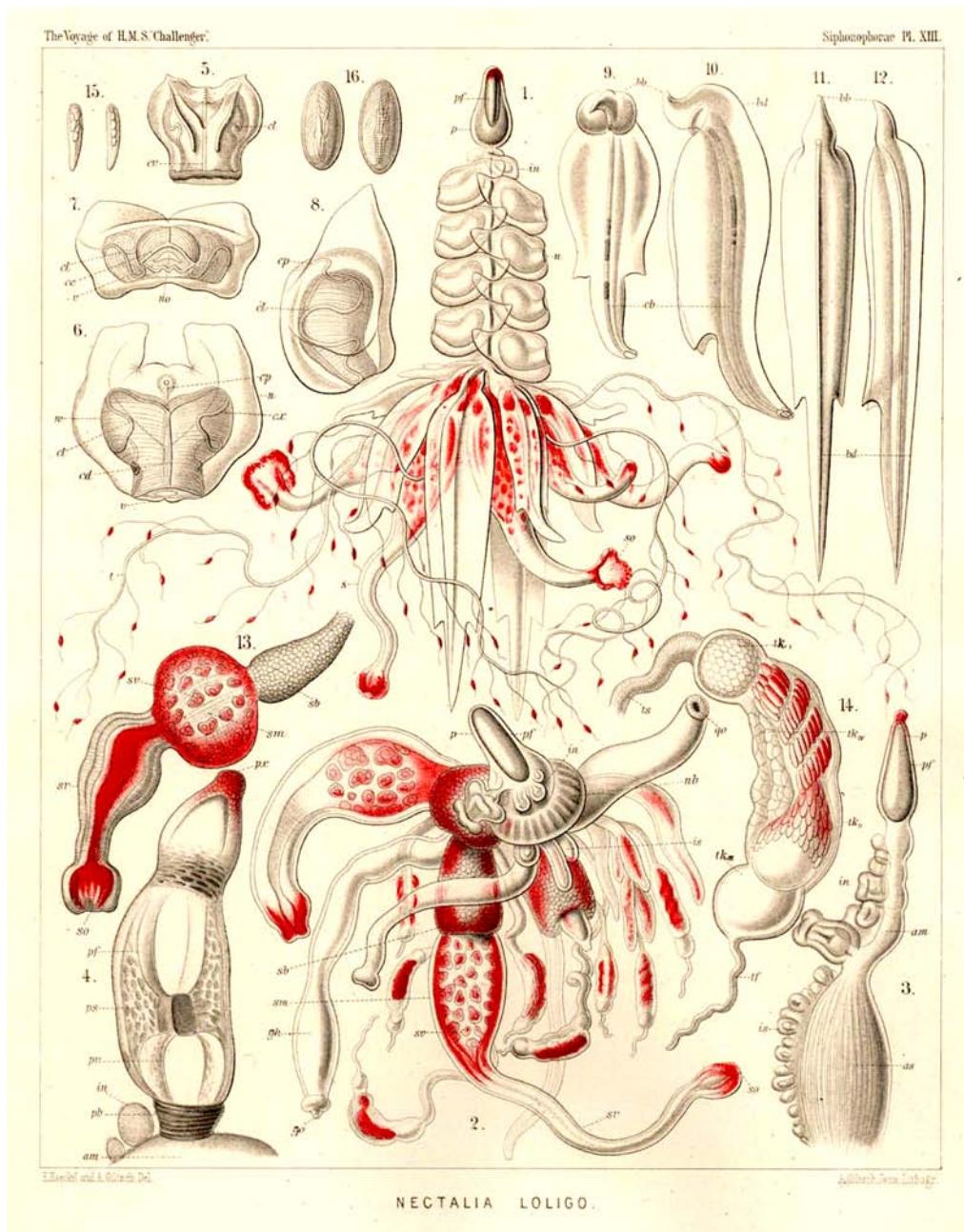
Fortunately, out of these ten genera we only need to consider three. As noted above Haeckel distinguished the genus *Stephanomia* on the basis of its short, rigid stem, its ordinate cormidia, and the presence of a simple terminal filament on the tentillum, but he made no mention as to whether the tentillum possessed an involucrum. He retained only Lesueur & Petit's (1807) *S. amphitridis* in the genus, along with a new species that he called *S. nereidum* Haeckel, which has to become a *nomen nudum* as insufficient information was given. Because he considered that Huxley's specimen of *Stephanomia amphitridis* had loose cormidia, he moved it into the genus *Phyllophysa*, which rather surprisingly considering his views of L. Agassiz's work he retained and also included the species *P. foliacea* of Quoy & Gaimard. In order to avoid confusion he renamed Huxley's *S. amphitridis* as *P. squamacea* Haeckel. Such prescience, although based on a rather dubious distinction, is notable for, as will be shown in the present paper, these two species are actually one and the same, albeit belonging to the genus *Halistemma*. Haeckel retained *H. rubrum* within the genus *Halistemma* and noted the similarities in the structure of the tentilla between that genus and *Cupulita*. He distinguished them on the basis of the absence of an involucrum in *Halistemma* species but, as noted above, this is actually not the case. He suggested another distinction in that he considered the palpons of *Halistemma* to be mouthless, while those of *Cupulita* had a terminal mouth, but that is a fallacy, as all palpons have a mouth opening.

There is, however, another "species" that Haeckel (1888b) described that is particularly relevant to this review. We refer to *Nectalia loligo* Haeckel (see Figure 7) that Haeckel placed in an entirely separate physonect family, the Nectaliidae. The single specimen on which the description was based was hand-collected off Lanzerote, Canary Islands in 1867. Haeckel gave a quite detailed description of the specimen; noting that there were four pairs of mature nectophores arranged biserially, but not stating to which side of the nectosome they were attached. From his Plate XIII, figure 3 (see Figure 7, fig. 3) one might infer that they were attached on the same side as the buds (*is*) on the siphosome (*as*), i.e. ventrally. However, one wonders as to whether this interpretation is correct as, in Haeckel's figure, the siphosomal buds (*is*) lay immediately below the buds of nectophores and there are no signs of the attachment lamellae of the mature nectophores. It seems more likely that the buds (*is*) were actually those lamellae, and that the anterior end of the siphosome was not illustrated. The overall length of the specimen can be estimated from Haeckel's statements that the nectosome measured 20–25 mm, presumably including the pneumatophore, and was about the same length as the longest bract, which was 25 mm long, so that the total length was about 50 mm. Unusually, he devoted several lines to the description of the nectophores, but unfortunately and typically he made no mention of the pattern of ridges, although the upper lateral ridges can clearly be seen on the youngest nectophores (fig. 5 in Figure 7). It is not clear how accurate the depictions of the courses of the lateral radial canals are.

Haeckel (1888b, p. 253), or perhaps his translator, waxed lyrical in his description of the siphosome likening it to "a dichlamydeous flower". The top of the siphosome was surrounded by a corona of elongate bracts to make an "amphithec fundamental form". All the bracts, 8 in number, seemed to have the same basic shape, but varied greatly in size, being up to 25 mm in length. Attached to the siphosome, immediately below the bracts, were the equivalent number of palpons, but Haeckel made no mention of whether they possessed palpacles. But the presence of palpons, if we are to believe Haeckel, is a significant character, as we will come to discuss.

According to Haeckel all of the gastrozooids, which from his illustration appear to have been five in number, bore a long tentacle with side branches (tentilla) of a very strange design (Figure 7, fig. 14). Haeckel (*ibid.* p. 254) described these as having "a long pedicel (*ts*), a large cnidosac (*tk*), and a simple small terminal filament (*tf*). The cnidosac has a peculiar form, being composed of two large subspherical ampullae (one proximal, *tk<sub>I</sub>*, and one distal, *tk<sub>III</sub>*), and between both a cylindrical middle part (*tk<sub>II</sub>*), which contains a large cnidobattery (*tk<sub>IV</sub>*). This latter is a long

spiral riband of four to five coils, composed of innumerable small paliform cnidocysts (fig. 15) and two lateral rows of large ellipsoidal cnidocysts (fig. 16)". It appears that Haeckel believed that the tentacles of all the gastrozooids possessed tentilla of this type, but we are inclined to disbelieve this as they appear to be larval tentilla, and consequently would be found only on the tentacle of the protozooid. Finally, Haeckel described the presence of both male and female gonodendra, but gave few details and did not illustrate them. This is not surprising for, as we shall show, this so-called species *Nectalia loligo* is not a species at all, but a post-larval stage of a *Halistemma* species. Chun (1897) mentioned three further specimens of this "species", but the only part he gave a detailed description of was the pneumatophore.

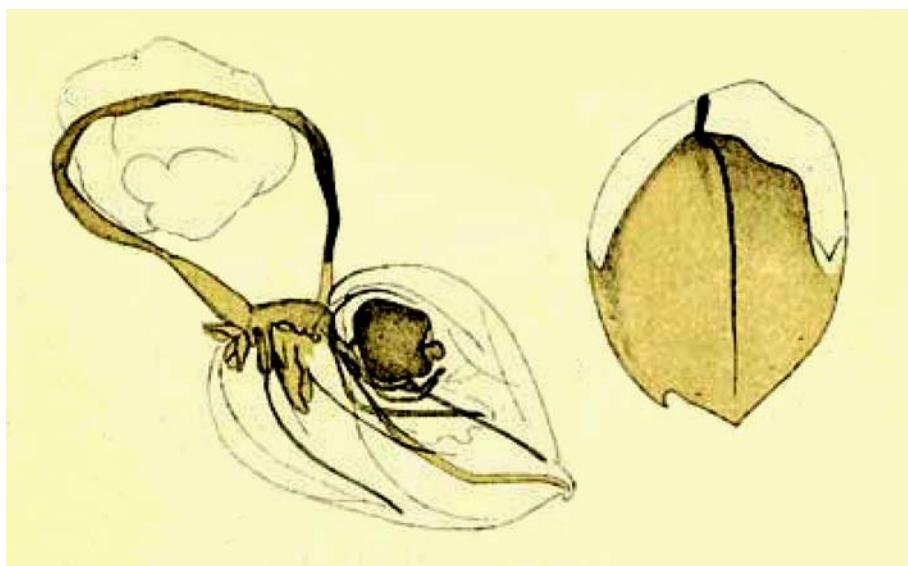


**FIGURE 7.** *Nectalia loligo* Haeckel, 1888b, Plate XIII. (See Haeckel, 1888b for legend and annotations).

Bedot (1896) gave a brief chronological account of almost all the agalmatid species that had been described to date and, in summary, retained eight of Haeckel's ten genera despite the fact that all four of the genera that Haeckel classified as possessing a triple terminal filament on the tentillum (see Figure 6) should clearly, as they are now, be united into a single genus, namely *Agalma*. Additionally, he placed the species that he, previously, had described as *A. clausi* Bedot, 1888, also with trifid tentilla, into a totally unnecessary new genus *Stephanopsis*. He retained the

genus *Halistemma* for *H. rubrum*, but suppressed the genus *Cuneolaria* as he considered it to have little value. He also "strongly" suppressed the genus *Phyllophysa*, which was somewhat strange as throughout the text Bedot had retained Quoy & Gaimard's (1833, 1834) species *Stephanomia foliacea*, which L. Agassiz (1862), followed by Haeckel (1888b), had placed in the genus *Phyllophysa*, but which Bedot eventually concluded was an incompletely known species, which finally he excluded from his classification.

With regard to Lesueur & Petit's (1807) illustration of *Stephanomia amphytridis*, Bedot (1896, p. 382<sup>1</sup>) remarked: "The character drawn from the arrangement of the cormidia—if it has the importance that one wishes to give it—must be established by more accurate observations than those of Peron & Lesueur. Moreover, the illustrator has shown, between the cormidia, all along the stem, a series of small filaments that do not extend beyond the bracts. One can scarcely comprehend their significance, but their presence is sufficient for one not to speak of "free internodes" as Haeckel did. It most probably suggests some tentacles distributed between the gastrozooids. Huxley ... rediscovered much later the *Stephanomia amphytridis* of Peron and Lesueur and gave some interesting details about its structure, principally regarding the tentilla. As a result we must consider this siphonophore to be very closely related to *Cupulita picta* Haeckel [=*Nanomia bijuga*]. It is even probable that these two species are identical. But we await some new studies before definitively uniting them." This is an extraordinary statement as the bracts of the two latter species are completely different. It is to be hoped that the present presentation will completely refute this suggestion.



**FIGURE 8.** *Stephanomia* sp. Plate XV, figs. 113–4 from Lens & van Riemsdijk (1908).

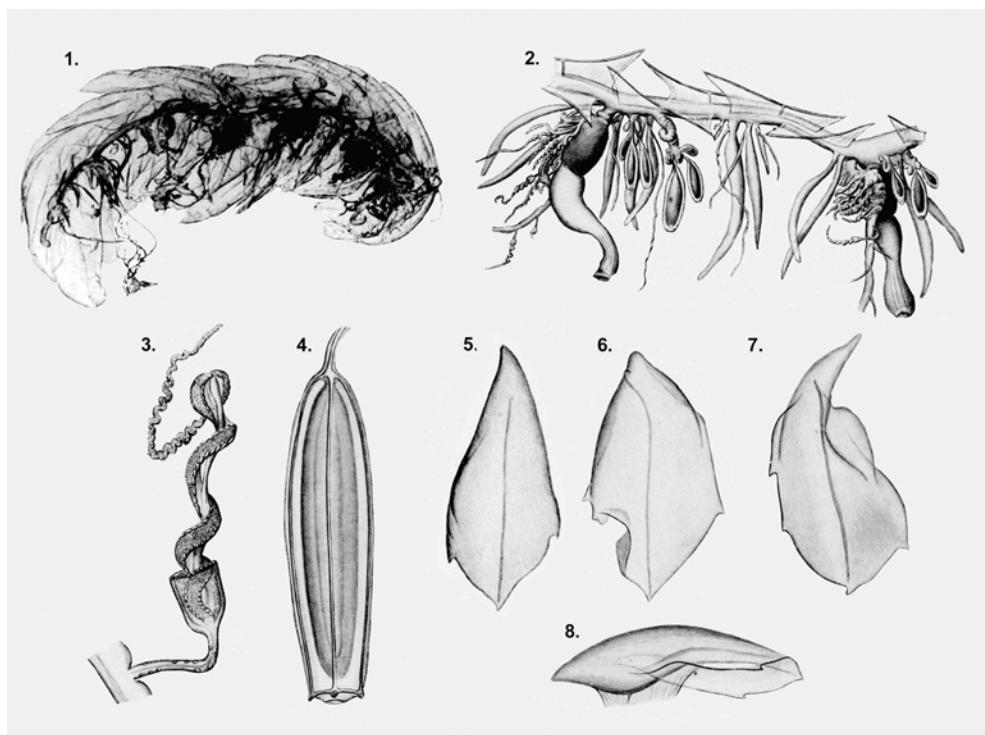
Lens & van Riemsdijk (1908) collected fragments of three physonects, one of which they ascribed to the genus *Stephanomia* and the other two to *Halistemma*, but they only gave one a specific name. The *Stephanomia* sp. specimen (Figure 8) consisted of a fragment of the stem, including a shapeless nectophore and a piece of the siphosome to which some bracts were attached. They noted (*ibid.* p. 84) "Comparing our sketch of the bract (Pl. XV, fig. 114) with HUXLEY'S 59 P1. VI, fig. 6a, 6b, we see there is considerable analogy between the two". This is indeed true, and so we will consider Lens & van Riemsdijk's specimen to be the same as Huxley's (1859) *Stephanomia Amphytridis* but, as we will show, neither specimen actually belong to the species *S. amphytridis*. The *Halistemma* sp. that they described and figured certainly looks like a *Halistemma* but there is too little information

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1. Original quote: "Le caractère tiré de la disposition des cormidia—s'il a l'importance que l'on veut bien lui donner—doit être établi par des observations plus exactes que celles de Peron et Lesueur. Du reste, le dessinateur a représenté entre les cormidia, tout le long de la tige, une série de petits filaments qui ne dépassent pas les boucliers. On n'en comprend guère la signification, mais leur présence suffit pour que l'on ne puisse pas parler de «free internodes», comme le fait Haeckel. Il s'agit très probablement de tentacules disséminés entre les gastrozoïdes. Huxley [XXXI] retrouva plus tard la *Stephanomia amphytridis* de Peron et Lesueur et donna d'intéressants détails sur sa structure et principalement sur les boutons urticants. Il en résulte que l'on doit considérer ce Siphonophore comme très proche parent de *Cupulita picta* Haeckel. Il est même probable que ces deux espèces sont identiques. Mais nous attendrons de nouvelles recherches avant de les réunir définitivement."

to identify it specifically. The other *Halistemma* species they named *H. cupulifera* Lens & van Riemsdijk, 1908. Their description of the specimen will be considered in the section below that deals with that species, and here we will only note that the identification of the specimen as a new species was based entirely on the structure of the tentillum, which they said was involucrate and bore, at the end of its terminal filament, "a small acorn-cup-shaped appendage" (*ibid.* p. 85) from which the specific name was derived.

Bigelow (1911) was the next major reviewer of the family Agalmatidae. He rejected the general characters, such as the contractility of the stem and the shape of the bracts, that Haeckel (1888b) and Bedot (1896) had used to classify the various genera, but noted that the form of the tentillum was an important character. Thus he united Bedot's genera, *Agalma*, *Crystallomia*, *Stephanopsis*, and *Agalmopsis*, as the genus *Agalma*. He recognised the distinctiveness of the genera *Anthemodes* [= *Cordagalma*] and *Lychnagalma*, but considered that the genus *Halistemma* should be united with *Cupulita*, in which Bedot had also included *Stephanomia* species, as a single genus that, according to precedence, he called *Stephanomia*. Although he recognised that the genera *Halistemma* and *Stephanomia* previously had been separated by the absence or presence, respectively, of an involucrum on the tentillum, he noted (*ibid.* p. 274) "But the involucrum is a secondary structure in development and its absence therefore is not sufficiently important to necessitate a separate genus; at most it may indicate a subgenus; and certainly the slight difference in the arrangement of the palpons described by Chun ('88) and by Schneider ('98) is not more than a specific character". Whether or not Bigelow's contention is correct is actually irrelevant in this context as we now know that the species of both genera have an involucrum on their tentilla. Nonetheless, the genera are distinct as has clearly been shown by the molecular studies of Dunn *et al.* (2005),

Bigelow (1911) described two specimens, consisting only of fragments of the siphosome, of what he called *Stephanomia amphitridis* [sic] (see Figure 9). In his list of synonyms he included the specimens recorded by Péron & Lesueur (1807, *S. amphitridis*), Huxley (1859, *S. amphitridis*) and Lens & van Riemsdijk (1908, *Stephanomia* sp.), including their junior synonyms, but he also, questionably, included *S. foliacea* Quoy & Gaimard (1833, 1834). Bigelow (1911, pp. 288–9) noted that the bracts attached to the siphosome were "arranged in four or five irregular somewhat diagonal rows", but noted that there were differences between them according to their position. Thus the dorsal ones were "distally tridentate" (Figure 9, figs. 5 & 8), while the lateral ones were more irregular in shape (Figure 9, fig. 7), and the ventral ones had "a peculiar cup-shaped recess on one of their lateral margins" (Figure 9, fig. 6). This last type of bract is very characteristic as will be shown.



**FIGURE 9.** "*Stephanomia amphitridis*" adapted from Bigelow (1911) Plate 18, fig. 1–8.

Bigelow (1911, p. 288) noted that his specimens gave a better guide to the arrangement of the cormidia than Huxley (1859) had been able to provide. Thus he noted "Proximal to any given siphon there are from 2–5 palpons; distal and close to it are the two gonodendra, ♀ and ♂, and crowded against them 3–6 palpons. On the pairs the ♂ cluster is always next the siphon (Plate 18, fig. 2). Next to the ♀ gonodendron there is a vacant space occupied only by bracts; but midway between every two siphons there is a cluster of 3–6 palpons of different ages. These intermediate groups are clearly shown in Huxley's figure ('59, pl. 6, fig. 1); and they are represented as filaments in the original figure of the species". This, as it happens, is a crucial statement for Bigelow was saying that his specimens were monoecious. Further, he noted that "The tentilla of the "Albatross" specimens, with short involucrum and single terminal filament (Plate 18, fig. 3) agree very well with Huxley's account".

Bigelow (1911) also found a specimen of *Nectalia loligo*, from the Tropical Pacific, which he classified as belonging to the sub-family Nectaliinae, within the family Agalmatidae. His specimen possessed only four nectophores, some bracts and palpons, but only two gastrozooids, and no gonophores. Unfortunately all the developed tentilla had been lost and so Bigelow was unable to verify Haeckel's (1888b) description of them, or whether the tentacles of the two gastrozooids possessed different types of tentilla.

Totton (1936) briefly mentioned the collection of fragments of nine specimens of *Stephanomia amphitridis* [sic] in the Beebe collections from around Bermuda. According to his notes these specimens included nectophores, but unfortunately he never managed to publish a description of them. Kramp (1942) described a new *Stephanomia* species, *S. orthocanna*, but Totton (1954) believed it did not belong to that genus and so moved it into a new one, *Marrus*, but still considered that it belonged to the family Agalmatidae, although the molecular genetic data of Dunn (2005) later showed that it did not.

Kawamura (1954) mentioned the capture of a specimen of *S. amphitridis* [sic] at Misaki, Japan, which unfortunately he did not illustrate. Nectophores were absent from this specimen, but in his brief description he noted that the bracts, like Bigelow's specimens, were arranged in five irregular rows, two lateral and one dorsal. Kawamura actually compared his specimen directly with those of Bigelow (1911), but whereas Bigelow only referred to two specimens collected at Albatross St. 4704 and 4705, Kawamura refers to four specimens, catalogue nos. 498, 28303, 28304 and 28305. However, we know from Mapstone (2004) that the 28303 and 28305 specimens both came from St. 4705, for which Bigelow noted six stem fragments had been collected, so perhaps the no. 498 specimen refers to St. 4704, and all the others to St. 4505. Nevertheless, it seems certain that Kawamura thought his specimen to be of the same species as that which Bigelow had described. It is fortunate that, before his untimely death, Francesc Pagès re-examined Kawamura's specimen and made some rough drawings that will be referred to later.

Leloup (1955, p. 13) also briefly mentioned the collection of a colony of *Stephanomia amphitridis* [sic] at 34°44'N, 47°52'W, in the North west Atlantic during the 1910 Michael Sars Expedition. He remarked "Cet exemplaire a été déterminé par A. K. TOTTON qui, à son sujet, m'a écrit 'Temporarily call it *Stephanomia amphitridis*, but a perusal of my forthcoming report (DISCOVERY Reports) will show that this name cannot be used'"!

Totton (1954, p. 46), in that *Discovery Report*, gave a brief history of the usage of the generic name *Stephanomia* and concluded "There are two courses open to systematists when dealing with this name and with long-stemmed Physonects that have single terminal filaments to their tentilla, The first is to use the name '*Stephanomia*' as a temporary convenience and to acknowledge that *S. amphitridis* of Lesueur & Petit is at present unidentifiable; and therefore cannot be the name of the type of a genus *Stephanomia*. The second course is to abandon the generic name *Stephanomia* and to take instead one that can be used for a species of which topotype specimens, or a type specimen, can be re-examined—specimens, that is, of a long-stemmed form with single terminal filaments. For the present I am taking the first course". However, Totton (1954) did not retain within the genus *Stephanomia* all the species that Bigelow (1911) had included in it. Thus he removed the species *bijuga* and *cara* into the genus *Nanomia*, but retained *S. rubra* [= *Halistemma rubrum*] within it.

Totton (1954, p. 62), while commenting on the post-larval developmental stages of *Agalma elegans*, noted "The buds of the nectophores now grow and begin to function. There is a second smaller gastrozooid and a ring of from four to eight palpons present at this stage, which is prior to the elongation of the siphosome in the reverse direction to that of the nectosome and to the appearance of a succession of secondary stem groups of buds. The stage before the appearance of secondary groups is reminiscent of the adult *Nectalia loligo*, and might be referred to as the 'Nectalia stage' in the same way in which earlier stages are referred to as 'Athorybia larvae' because of their resemblance to miniature specimens of *Athorybia rosacea*. In the 'Nectalia stage' the terminal gastrozooids

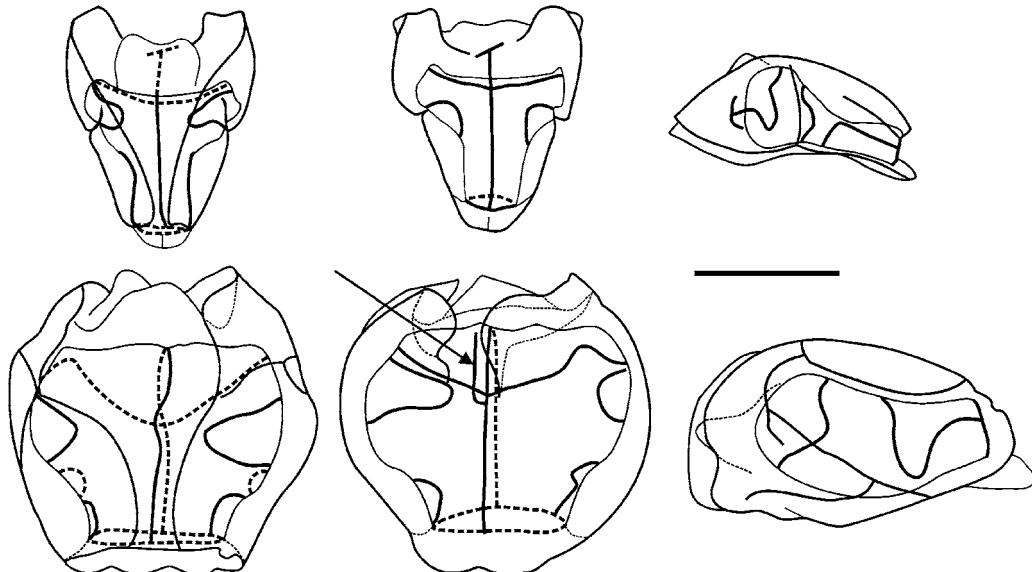
are surrounded, just as they are in *Nectalia loligo*, by a number of long, trifid bracts of the general shape figured by Haeckel (1888b; pl. XIII, figs. 1, 9–12). They are very much like those of *Athorybia rosacea* and, since they are probably pre-cormidal as Garstang suggested, they may be homologous with them and with the larval bracts of *A. okenii* [sic]". This stage was later illustrated by Totton (1955, figs. 8–9; 1965, fig. 20). Totton (1954) also noted that the tentilla of the first gastrozooid, the protozooid, were kidney-shaped and of the larval type. In a footnote on the same page Totton also noted that "Nectalia Haeckel, 1888b, should be accepted with some caution, since specimens with the very peculiar tentilla that Haeckel figured have not certainly been seen again, and his figures are often not dependable. ... I have examined many such specimens taken at Bermuda by Beebe, but a great deal more work has still to be done on the large amount of Agalmid material sent me by Beebe before the question can be resolved. I hope eventually to be able to link up these *Nectalia*-like specimens with a giant form that I provisionally called *Stephanomia amphytridis*. They have a new type of nectophore". He repeated this idea that *Nectalia loligo* was a juvenile form in his 1965 Monograph. It is thus rather strange that Carré (1971, Plate I, fig. 6), in her paper on the larval and post-larval development of *Halistemma rubrum*, showed a photograph of the post-larval form that clearly is at the *Nectalia* stage, but did not refer to it by that name. However, she did (*ibid.* Plate II, fig. 1) show a photograph of the unusual larval tentillum, which differs somewhat from the *N. loligo* tentillum illustrated by Haeckel, (1888b, Plate XIII, fig. 14).

Despite these earlier statements, particularly with regard to *Stephanomia amphytridis*, Totton (1965, p. 56) later abandoned the name *Stephanomia* altogether, and replaced the species *rubra*, *cupulifera*, and a new one, *striata*, in the genus *Halistemma*, which he defined as "with unicornuate tentilla whose cnidoband lacks a marked basal involucrum". Like *H. cupulifera*, *H. striata* was not described from a whole specimen, but only based on a few loose nectophores that none the less are very distinctive. Under the heading of "Indeterminate species" Totton included "? *Halistemma amphytridis*" and he noted (*ibid.* p. 61) "in the absence of data about the nectosomes of these four specimens [presumably, Lesueur & Petit's, Huxley's, and Bigelow's two], it is difficult to base a description of a species on them, although if a complete, well preserved specimen should ever be taken off the east coast of Australia, the details of whose siphosome corresponded with Huxley's (1859) and Bigelow's (1911) figures and material, then we could firmly establish a species *Stephanomia amphytridis* Lesueur & Petit, 1807". But it is clear that Totton knew more about this species as once again he mentioned the Beebe Bermuda specimens as well as more recent ones sent to him by the National Institute of Oceanography (see next paragraph). However, Totton was mistaken in suggesting that another specimen collected in the same vicinity as Huxley's, and conforming to the latter's description, would firmly establish *S. amphytridis* as a valid species, as he himself noted that Lesueur & Petit's original specimen was collected somewhere between Le Havre and Mauritius.

Daniel (1974) described and illustrated two nectophores and a bract under the name ? *Halistemma amphytridis*. The thickened, foliaceous, slightly asymmetrical bract was very large, measuring 29 mm in length and 15 mm in width, with possibly two pairs of lateral teeth. Equally the nectophores, which were in a poor condition, were very large, with the larger measuring 33 mm in height and 25 mm in width. The author noted the presence of large axial wings, or wedge-shaped processes; the fact that the thrust block was deeply divided; and that the lateral radial canals had convoluted courses. But the pattern of ridges could not be discerned. Daniel (1985, p. 76) reiterated her earlier description, but also remarked "The nectophore described below differs a great deal from the typical "*Halistemma*" type of nectophore and warrants a creation of new genus and new species, but in this account it is still retained as *H. amphytridis* (= *Stephanomia amphytridis*)".

Margulis (1976) purportedly described three new physonect genera and species from the north western part of the Indian Ocean, based almost exclusively on their nectophores, all of which she attributed to the family Agalmatidae. The first of these, *Paragalma birsteini* Margulis 1976 (Figure 10, top), according to its ridge pattern and the course of the lateral radial canals, appears to us to belong to the genus *Halistemma* and, as is discussed below, we have assigned it as a questionable junior synonym of *H. cupulifera*.

The second species, *Sphaeragalma rotunda* Margulis, 1976, had nectophores with a characteristic ridge pattern. It is also noticeable that, in the lower view (Figure 10, bottom centre, arrowed), Margulis has only drawn an ascending mantle canal, while a descending mantle canal is present in all known agalmatid species. There is no doubt in our minds, as is discussed below, that these nectophores belong to *Stephanomia amphytridis*. The third species, *Tottonia contorta* Margulis, 1976, also is not an agalmatid, but belongs to the family Apolemiidae, and currently is included in the genus *Apolemia* (Siebert *et al.*, 2013).



**FIGURE 10.** Upper (left), lower (centre) and lateral (right) views of *Paragalma birsteini* (top) and *Sphaeragalma rotunda* (bottom). Redrawn, with a few alterations, from Margulis (1976) figures 1–6. Scale bar 5 mm.

A new species of *Halistemma*, *H. transliratum*, was described by Pugh & Youngbluth (1988), and that description will be dealt with in more detail below.

Mapstone (2004, p. 231) gave what she called the "First full description of the large physonect *Halistemma amphitridis* (Lesueur & Petit, 1807)", based on a specimen collected in the Flores Sea (Indonesia) at 7°55'S, 122°5'E during the *Snellius* Expedition of 1929–30. She directly compared the components of the siphosome (bracts, etc) with those Bigelow's (1911) specimen of *Stephanomia amphitridis* and found that they essentially agreed. However, Mapstone was also able to describe the nectophores, which measured up to 20 mm in height and 22 mm in width; and thus were relatively small in comparison with the ones mentioned by Daniel (1974, 1985). Although she stated that the nectophores were attached to the ventral side of the nectosome, a subsequent examination of the specimen by one of us (PRP) has shown that they were actually attached to the dorsal side. This obviously meant that it belonged to the Family Agalmatidae (see Dunn *et al.*, 2005a), and other characters showed that it was a *Halistemma* species. One of the main characteristics of the nectophores was the ridge pattern, which included two complete pairs of vertical-lateral ridges, and an apparently incomplete pair of lateral ones, although this is very difficult to discern in her illustrations. In addition, it is worth noting that, although Mapstone did not mention it in her text, her figure 3A clearly shows that a small, but reasonably well developed involucrum was present proximal to the cnidoband of the tentillum.

It was thus clear that Mapstone's specimen was the same as the ones that Bigelow's (1911) referred to as *Stephanomia amphitridis* and, by inference from the above comments, we can also add Huxley's (1859) *S. amphitridis*, Lens & van Riemsdijk's (1908) *Stephanomia* sp., and Kawamura's (1954) *S. amphitridis*. But the question remains as to whether all of these specimens were the same as the one figured by Lesueur & Petit (1807). Mapstone (2004, p. 237) took the approach that the "Two large *Halistemma* species noted in earlier literature and tentatively identified as *H. amphitridis* 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 that may be *H. amphitridis*, 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 x 33 mm length by width) than that of *H. amphitridis*, with a vertical lateral ridge which divides into two branches, and the bract is differently shaped". So although Totton (1954, 1965) had ascribed the same material as seen by one of us (PRP) to *H. amphitridis*, Mapstone decided that they belonged to another species.

However, in his Appendix C, Pugh (2006, p. 42) took the completely opposite view. He stated "Nonetheless, it is the structure of the bracts that specifically characterises all these specimens. Huxley (1859, p. 72) described the

bracts as being 'attached by triangular, striated processes from the ectoderm, whose base was inserted on a triangular ridge, which traversed the middle of the inner face.' This triangular structure, it is clearly visible in Bigelow's (1911) Pl. 18, fig. 8 and its presence has been confirmed (Pugh, personal observation) in both Bigelow's and Mapstone's specimens; the latter author referring to it as a 'ventral keel'. Francesc Pagès (personal communication) has also confirmed its presence on the bracts of Kawamura's specimen. Because of this distinctive swelling, in the region of attachment on the lower side of the bract, Pugh (2006) considered that the specimens described by these authors should all be synonymised with *Halistemma (Stephanomia) foliacea* (Quoy and Gaimard). Although Quoy and Gaimard's (1833, 1834) description and figures may not be up to modern day standards, nevertheless the mention of bracts 'munie d'une languette triangulaire en dedans, à l'aide de laquelle ces corps se fixent sur leur axe' (*ibid*, p.75) [provided with a triangular tongue beneath, with which these bodies are fixed to their axis] is a very distinctive character and was, at that time, quite sufficient to establish the species, albeit incompletely known, as Bedot (1896) recognised. Indeed, Bigelow (1911) included *S. foliacea* species as a doubtful synonym of his *S. amphitridis*".

Thus, in this paper we consider Lesueur & Petit's *Stephanomia amphitridis* to be a valid species, different in many ways from *Halistemma* species, although in other ways quite similar. Although this ascription can never be fully proven, as it is presumed that the original specimen is not extant, the numerous recent observations of a very large physonect species clearly establish that a species resembling Lesueur & Petit's illustration does exist. All of the extant *Halistemma* species, with the exception of *H. foliacea*, but including another new species, have been collected over the past 30 years either by manned submersibles or by ROVs and we hope to give fuller descriptions for some of them than have been given in the past.

## Terminology

For the general description of the nectophores we will adopt the basic terminology used by Haddock *et al.* (2005), albeit that it was established for a calycophoran siphonophore of the Family Prayidae. Thus the three main orthogonal axes of the nectophore (see their Figure 1) are: i) the proximal-distal axis representing the line between the point of insertion of the external pedicular canal, which connects with the central gastrovascular cavity of the nectosomal stem, and the centre of the ostial opening of the nectosac; ii) the right to left lateral axis; and iii) the top to bottom, upper to lower axis. Thus, the length of the nectophore lies along the proximal-distal axis, but may extend, proximally, beyond the point of insertion of the external pedicular canal, so as to encompass the axial wings, or lateral wedge-shaped process, which surround the nectosomal stem. The width of the nectophore is the lateral, left to right, axis, and the depth or height lies along the upper to lower axis. Nectophores are often illustrated from the three positions that they most conveniently adopt in a Petri dish; that is lateral, and what approximates to upper and lower, although the two latter may not necessarily lie in exactly the same plane with respect to each other.

The terminology used for the ridges on the nectophores differs from that previously used (Pugh & Youngbluth, 1988) in that we refer to pairs of upper and lower laterals, in place of apico- and infra-laterals respectively, but retain the terms lateral and vertical lateral ridges. This is in accord with the terminology adopted by Haddock *et al.* (2005). We will also use the name mantle canal for the canal that runs along the axial surface of the nectophore in the region where the attachment lamella is present. The systematic importance of this canal, as to whether it has only an ascending branch or both an ascending and a descending branch, has only recently (Dunn *et al.*, 2005a) been appreciated. However, although agreeing that this canal is homologous with the canal running along the median wall of the hydroecium in prayid, hippopodiid and some clausophyid calycophoran siphonophores, we no longer agree with how Haddock *et al.* (2005) interpreted it. Mapstone (2009) has also presented arguments to rename the two branches of the mantle canal as ascending and descending surface diverticula, but we do not see the necessity for this and will retain the term originally established by Leuckart (1854), i.e. *Mantelgefässe* or mantle canals. Haeckel (1888b) was the first to use the term *pallial canal* and it is likely that the person who translated the original text into English derived it from *Mantelgefässe*, via the Latin *pallium* meaning mantle. This point will be considered in more detail in a forthcoming paper on the family Clausophyidae (Pugh, *in prep.*). For a glossary of the other, rather arcane, terminology used in describing siphonophores one is referred to Totton (1965) or Mapstone (2009).

## Family Agalmatidae Brandt, 1835

*Diagnosis:* Physonect siphonophores whose nectophores, when present, are budded off on the dorsal side of the nectosome. Descending mantle canal present on nectophores, when such are developed. Species are monoecious. For most species, with the possible exception of those of the genus *Athorybia*, the adult tentilla are involucrate.

*Genera:* *Agalma*, *Halistemma*, *Nanomia*, *Athorybia* and *Melophysa*, the last two being short-stemmed forms with, in the genus *Athorybia*, the total suppression of the nectosome.

*Remarks:* The family Agalmatidae, based on the genus *Agalma* Eschscholtz, 1825, was established by Brandt (1835); the name coming from the Greek for *glory* or *delight*. However, Poche (1914) pointed out that, because of the Greek declension of the noun, the name of the family should correctly be written as Agalmatidae, and this form has been generally used after it was adopted by Cairns *et al.* (1991).

## Genus *Halistemma* Huxley, 1859

*Diagnosis:* Agalmatid siphonophores with characteristic arrangement of ridges on the nectophores; basically consisting of pairs of upper and lower lateral, lateral, and vertical lateral. Characteristic sinuous arrangement of the lateral radial canals on the nectosac. Adult bracts of at least two different types. In development the colonies pass through a distinctive post-larval *Nectalia* stage. Tentilla with single terminal filament, often ending in a cupulate process. Involucrum vestigial or covering only first one or two spirals of cnidoband.

### *Halistemma rubrum* (Vogt, 1852)

*Agalma rubra* Vogt, 1852a, p. 522, Pl. XIV, figs. 4–5 & 8; 1852b, p. 273, Pl. 5, figs. 10–11, 14; 1854, pp. 62–82, Pls. VII–XI; Sars, 1859, p. 8; Spagnolini, 1869, pp. 631–632;

*Agalmopsis punctata* Kölliker, 1853, pp. 15–18, Pl. IV; Leuckart, 1853, pp. 1–95, Pl. I, figs. 1, 19–20, Pl. II, figs. 1–2, 5–7.

*Agalmopsis rubra* Leuckart, 1853, pp. 1–95, Pl. I, figs. 5–7, 11, Pl. II, figs. 18–19; Schneider, 1898, p. 123; 1899, pp. 41–48, figs. 34–42; 1900, p. 17, figs. 2, 5–15, 30–37, 46–50, 52, 54–71, 75, 80–94, 159–164, 196, 232;

*Agalma rubrum* Leuckart, 1854, pp. 321–331, Pl. XII; Claus, 1860, figs. 8, 28, 32, 35, 39; Keferstein & Ehlers, 1860, p. 261; 1861, pp. 25–26, Pl. I, figs. 14–15, Pl. II, fig. 5; Weissmann, 1883, p. 209–211, Pl. XXII; Delage & Hérouard, 1901, fig. 376.

*Halistemma rubrum* Huxley, 1859, pp. 129–130, pl. XII, fig. 9; L. Agassiz, 1862, p. 369; Metschnikoff, 1874, p. 57–61, Pl. X, Pl. XI, fig. 1; Fewkes, 1880, Pl. II, figs. 3–4; Bedot, 1896, p. 407; Lo Bianco, 1904, fig. 149; Totton, 1965, pp. 56–59, Pl. XII; D. Carré, 1971, p. 77–93, figs. 1–9, Pls. I–III; Daniel, 1974, p. 45–47, text–fig. 3E–G; 1985, p. 71–75, fig. 15a–f; Kirkpatrick & Pugh, 1984, p. 34, fig. 8; Gili, 1986, pp. 273–274, figs. 4.48a, 4.64a–d; Pugh & Youngbluth, 1988, fig. 6D; Gasca, 1990, p. 48, Pl. I, fig. 4; Pagès & Gili, 1992, p. 73, fig. 9; Carré & Carré 1995, figs. 165A, 177A,C, 181F, 189; Pugh, 1999a, p. 482, figs. 3.11, 3.22; Gao *et al.*, 2002, p. 71, fig. 27; Bouillon *et al.*, 2004, p. 211, fig. 123C–G; 2006, figs. 208 I–J, 209A–B; Araujo, 2006, p. 58, Pl. VI, fig. 12.

*Agalma punctatum* Graeffe, 1860, p. 14.

*Agalma minimum* Graeffe, 1860, pp. 15–20, Pls. II, III; Haeckel, 1869, p. 46; 1888b, p. 233.

*Halistemma punctatum* L. Agassiz, 1862, p. 369; Haeckel, 1888b, p. 367

*Stephanomia rubra* Bigelow, 1911, p. 284; 1918, pp. 426–426, Pl. 8, fig. 5; Leloup, 1935, p. 3; Daniel & Daniel, 1963, p. 194, fig. II 9; Alvaríñ, 1981, p. 394, fig. 174–4; Totton, 1954, pp. 47–52, text–figs. 12–13 [*in partim. non* text–figs. 15–18];

*Halistemma rubra* Totton & Fraser, 1955, p. 3, fig. 4; Trégouboff & Rose, 1957, p. 351, Pl. 77, figs. 6–8, Pl. 78, figs. 1–2; Stepanjants, 1967, pp. 128–129, figs. 71–72; Carré, 1974, p. 211, Pl. III, fig. 1;

?non *Halistemma rubrum* Zhang, 2005, pp. 22–24, figs. 2D, 18

The above list refers only to important taxonomic changes or to papers that, in some way, describe the species *Halistemma rubrum*.

*Diagnosis.* Basic *Halistemma* ridge pattern on nectophores, with all pairs of ridges incomplete. Two types of adult bract. Tentilla with very small, almost vestigial involucrum and no terminal cupulate process.

*Material examined.* Five specimens collected by the Johnson-Sea-Link (JSL) submersibles, including 1 *Nectalia* stage (\*); four from the Bahamas and one from the Gulf of Maine, and three specimens collected by the ROV Doc Ricketts (DR) in the southern part of the Gulf of California, Mexico.

JSL II Dive 973-D4*	21 October 1984	26°17.5'N, 77°43.7'W	depth 506 m.
JSL II Dive 1401-D5	30 August 1986	39°51.7'N, 70°22.6'W	depth 640 m.
JSL II Dive 1683-D1	9 October 1988	26°27.0'N, 77°57.4'W	depth 445 m.
JSL I Dive 2656-D3	17 November 1989	26°4.3'N, 77°34.3'W	depth 536 m.
JSL I Dive 2656-D6	17 November 1989	26°4.3'N, 77°34.3'W	depth 527 m.
DR Dive 335-D5	18 February 2012	24°12.7'N, 109°38.4'W	depth 245 m.
DR Dive 339-D12	21 February 2012	23°33.5'N, 106°47.0'W	depth 213 m.
DR Dive 344-D10	26 February 2012	24°30.3'N, 108°14.5'W	depth 297 m.

Thanks to the kindness of Susan Svonthun, from the Video Laboratory at MBARI, a brief video of the specimen of *Halistemma rubrum* collected at 245 m during *Doc Ricketts* Dive 335 will be placed on the website [www.youtube.com/user/MBARIvideo](http://www.youtube.com/user/MBARIvideo).

**Description:** A picture of a specimen collected by the submersible Johnson-Sea-Link I is shown in Figure 11.  
**Pneumatophore:** The exploded pneumatophore measured approximately 1.0 mm in length and 0.75 mm in diameter, and showed no obvious characteristics or pigmentation.



**FIGURE 11.** *Halistemma rubrum*. Tank photograph of JSL I Dive 2656-D3 specimen, approximately 12 cm in length.

**Nectosome:** The nectophores were budded off on the dorsal side of the stem.

**Nectophores:** Thirty detached nectophores were present in association with the largest specimen, from JSL II Dive 1401, together with four attached nectophores and nectophoral buds at varying stages of development. Detached nectophores from the JSL II 1401-D5 and JSL II 2656-D6 specimens were quite variable in shape (see Figures 13–15) and ranged in size from 1.9 x 1.9 mm (length x width) to 7 x 7 mm.

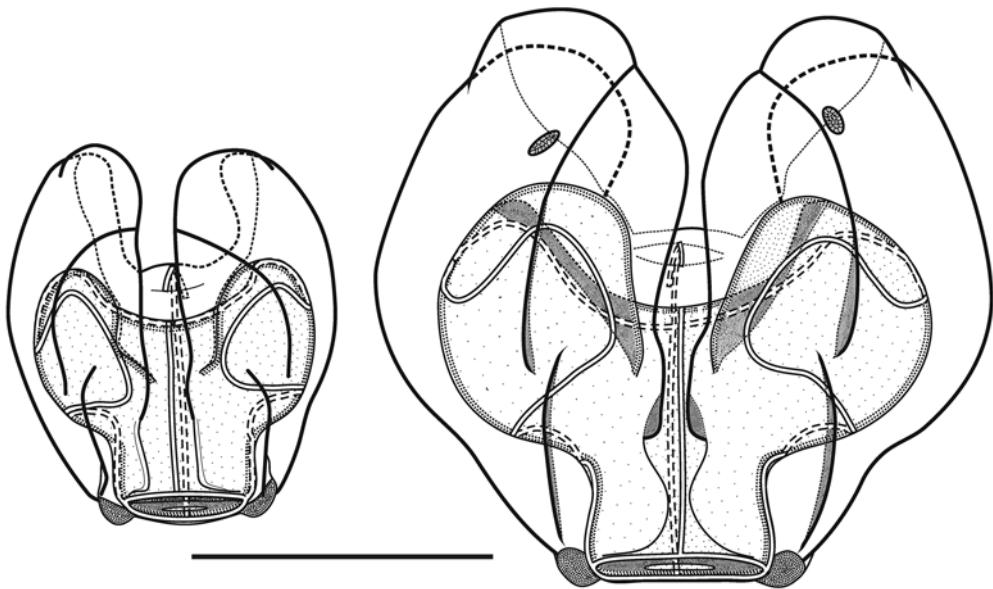
The very young nectophoral bud (Figure 12) clearly showed the pattern of the ridges, with the upper lateral ones bending out, laterally, as they approached the ostium. The relatively large lateral ostial processes were packed with nematocysts, which were also found across the upper margin of the ostium.



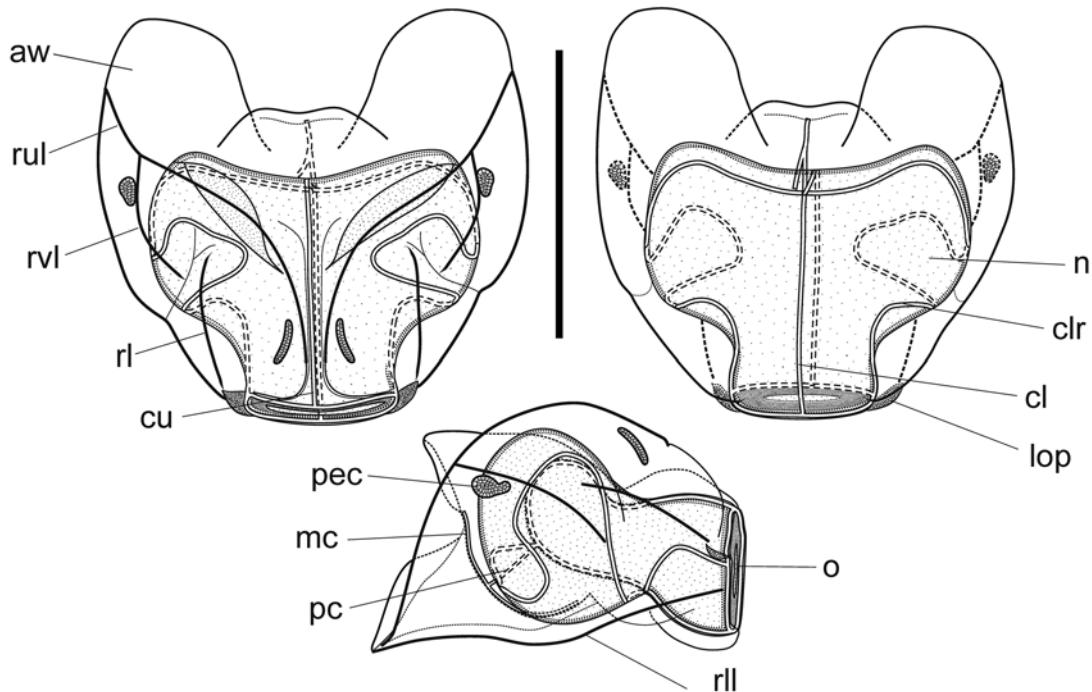
**FIGURE 12.** *Halistemma rubrum*. Nectophoral bud (upper view) from JSL Dive 1401-D5 specimen. Scale bar 0.5 mm.

In the smaller, younger nectophores (Figure 13) the central thrust block was very flat and undeveloped so that the relatively large axial wings extended well beyond it. For most of their length the upper lateral ridges remained close to the median line of the nectophore. They were very pronounced down to the level where the nectosac began to narrow and, in the slightly older nectophore (Figure 13 right); here they formed a distinct flap. They then continued on toward the ostium as only a slightly raised line on the surface of the nectophore, before curving out laterally and petering out close to the lateral margins of the nectosac. The lateral and vertical lateral ridges also formed distinct flaps overhanging the surface of the nectophore. Some, but not all, of the preserved younger nectophores bore a pair of ectodermal cell patches, which lay close to the vertical lateral ridges, but they were very delicate and easily abraded. In addition, nematocysts were still found on the lateral ostial processes, as well as across the upper side of the ostium, of the younger nectophore but they had all but disappeared in the slightly larger ones.

As the nectophores increased in size the central thrust block enlarged and became prominent, although never reaching the level of the apices of the axial wings (Figures 14–15). In the ostial region, a basal mouth plate was absent (even in the younger nectophores). The now relatively small lateral ostial processes, present on either side of the ostium, were covered in small plate-like cells that originally, presumably, lay below the nematocysts, which had been lost by abrasion or usage. There were two pairs of ectodermal cell patches on the upper lateral sides of the nectophore, although some or all of these had been abraded on most nectophores. When present, one pair lay between the lower laterals and the vertical laterals, close to the latter; and the other lay between the upper lateral and lateral ridges, close to the former (Figure 14).



**FIGURE 13.** Upper views of young ectophores of *Halistemma rubrum* from JSI Dives 2646-D6 (left) and 1401-D5 (right). See Figure 14 for annotations. Scale bars 2 mm.

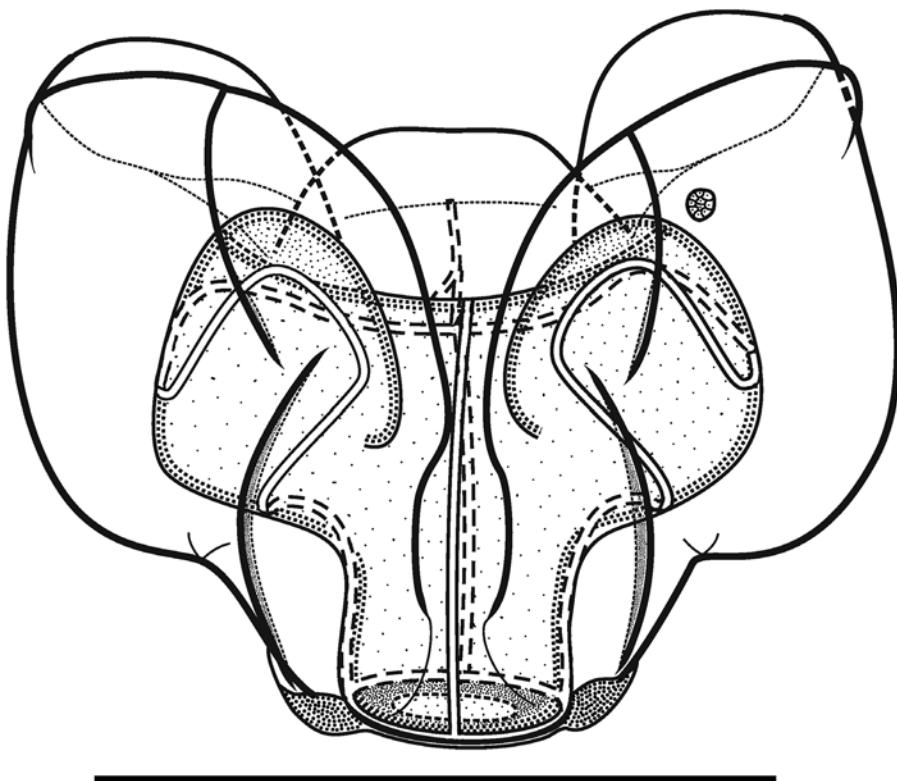


**FIGURE 14.** *Halistemma rubrum*. Upper (top left), lower (top right) and lateral (bottom) views of a mature ectophore from the JSI Dive 2656-D6 specimen. aw: axial wing; cl, clr & cu: lower, lateral and upper canals, respectively; lop: lateral ostial process; mc: mantle canal; n: nectosac; o: ostium; pc: pedicular canal; pec: ectodermal cell patch; rl, rll, rul & rvl: lateral, lower lateral, upper lateral, and vertical later ridges, respectively; tb: thrust block. Scale bar 5 mm.

Although the pattern of the ridges on the ectophores of *Halistemma rubrum* conformed to the basic *Halistemma* arrangement, as described by Totton (1954) and Pugh & Youngbluth (1988), uniquely the pairs of upper laterals, lower laterals and laterals were incomplete at both ends, while the vertical-laterals were incomplete at their lower end and, indeed, their connection with the upper laterals at times was very vague. The upper lateral ridges ran across the upper surface of the ectophore from the apical margins (though never joining the lower laterals) of the axial wings down towards the ostium. However, the upper laterals were only prominent proximally and, at approximately one sixth of the length of the ectophore away from the ostium, they were reduced to slight

prominences on the surface of the nectophore. They continued toward the ostium but, just before reaching it, they curved out and ran parallel to the upper margin of the ostium before petering out. The lateral ridges started on the upper surface of the nectophore, slightly proximal to the distal end of the vertical lateral ridges, and curved outwards slightly as they ran down towards the ostium, petering out just above the lateral ostial processes.

The vertical lateral ridges arose relatively high up the upper lateral ridges, at the level of the apex of the nectosac or above depending on the stage of development. These ridges curved down the lateral surfaces of the nectophore and petered out just distal to the proximal end of the lateral ridges. A strong fold was present in the mesogloea at the distal end of the vertical lateral ridges and the proximal end of the lateral ridges so that these ridges appeared to continue and end in a hook-shaped flap on some nectophores. The lower lateral ridges ran along the entire length of the lower lateral edge of the nectophore from the outer margins of the axial wings to almost the level of the ostium where they petered out and joined the lower margins of the nectophore. There were no distinct ridges on the lower surface of the nectophore. However, in their preserved state, folds ran down the inner apices of the axial wings to just above the level of the nectosac.



**FIGURE 15.** *Halistemma rubrum*. Upper view of mature nectophore from the JSL Dive 1401-D5 specimen. Scale bar 5 mm.

The mantle canal, on the lower median surface of the nectophore, ran from a quarter to a halfway down the central thrust block to just below the central apex of the nectosac. The ascending and descending branches were almost equal in length, so that the pedicular canal arose at its mid-point and extended down to the nectosac, where it gave rise to all four radial canals. The courses of the upper and lower canals were straight. The lateral radial canals extended outwards on a smooth curve following the apical surface of the nectosac. At the lateral margins of the nectosac, they first looped downwards and then upwards, looping onto the upper side of the nectosac. They then ran obliquely down the lateral surface of the nectosac and made a short loop onto the lower surface before returning to the mid height of the nectosac and then running directly to join the ostial ring canal.

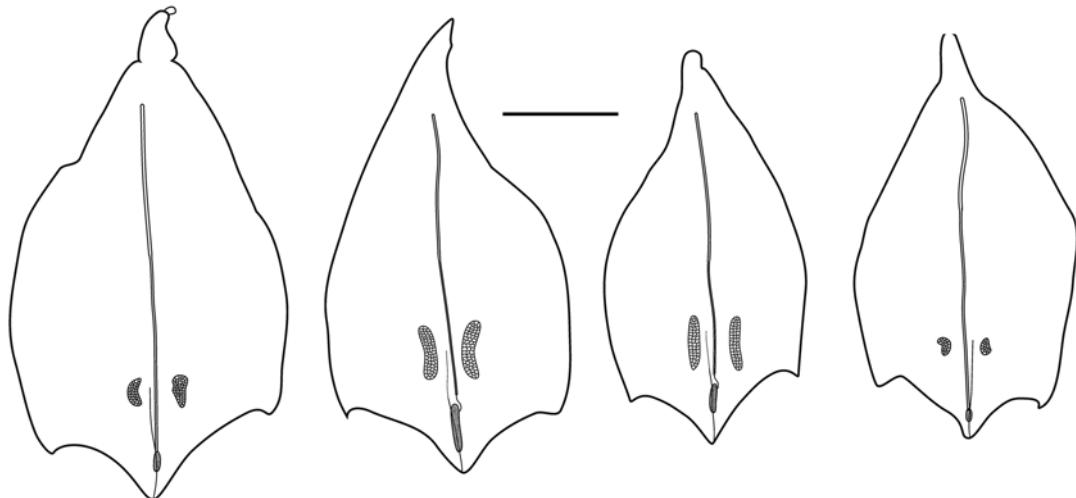
*Siphosome:* The long siphosomal stem was clearly divided into cormidia that, from the anterior end, consisted of a cluster of palpons; male gonophores individually attached to the stem and interspersed with palpons; a further cluster of palpons; a distinct female gonodendron, with the gonophores borne on a thickened stalk; another cluster of palpons; and finally the gastrozooid, with its tentacle bearing tentilla. The exact disposition of the bracts was not determined.

*Bracts:* There were two types of adult bracts, which were quite flimsy, foliaceous and occurred in

enantiomorphic pairs. For the largest specimen, from JSL Dive 1401-D5, the Type A bracts were approximately six times as abundant as the Type B ones, but their arrangement on the stem could not be discerned, although it was thought that the Type A bracts may be inserted laterally, and the Type B ones dorsally.

Type A—These bracts were quite variable in shape and measured up to c. 9 mm in length (Figure 16). Several were shorter and squatter, and in the younger ones the bracteal canal tended to extend further toward the proximal end. The distal end was pointed and there was a pair of, asymmetrically positioned, lateral teeth, of variable size, somewhat proximal to it. The tooth on the inner side was more proximal to the one on the outer side. There was a pair of patches of ectodermal cells on the upper surface, whose size and position could vary quite considerably. Often, these were extremely difficult to see, but they were assumed to be sites of bioluminescence. A short median ridge ran proximally from the distal point to peter out between the pair of ectodermal cell patches.

The bracteal canal originated at a variable distance from the proximal end of the bract. It was thicker in its proximal half, where the bracteal attachment lamella was, and thinner distally. As it approached the distal end of the bract it penetrated into the mesogloea, thinning further, and curved upwards to end somewhat distal to the proximal end of a patch of cells, on the upper surface. Although variable in shape, for the most part these patches were elongate structures (Figure 16), but they never extended as far as the median distal tip of the bract itself. They were comprised of numerous nematocysts, which probably were the same as the microbasic euryteles that Carré (1971) identified on the larval bracts (see below), and other types of cell. These were the bracts that Totton (1954, Text—figs 13–14) illustrated. However, on some bracts these nematocyst patches were less elongate, ending some distance before the distal end of the bract (Figure 16).



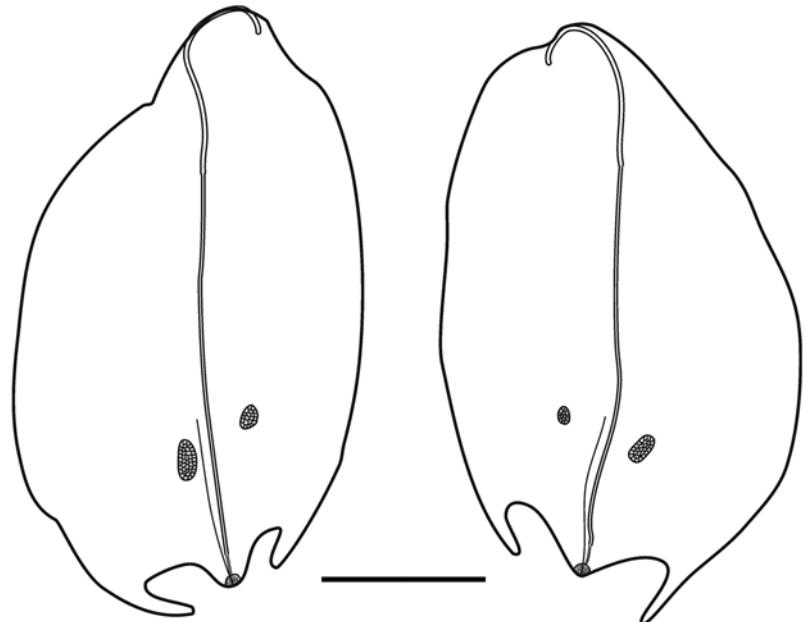
**FIGURE 16.** *Halistemma rubrum*. Type A bracts—upper views. Proximal at top, distal at bottom. Scale bar 2 mm.

Type B—These bracts (Figure 17) were of a similar size to the first type but they had more pronounced lateral teeth that extended beyond the median distal point of the bract and they were more oval in shape. Again the tooth on the inner side was more proximal than the one on the outer side. Two patches of ectodermal cells were present on the upper side of the bract, with the patch on the inner side being noticeably proximal to the other one. Another clear distinguishing feature was the arrangement of the bracteal canal. At the proximal end the canal arose on to the upper side of the bract before curving over onto the lower side and thinning at approximately one third of the way towards the distal end. The canal continued for almost the entire length of the bract before slightly narrowing again and penetrating into the mesogloea to end below a small distal cap-shaped indentation, which also contained the same sort of nematocysts as seen on the Type A bracts.

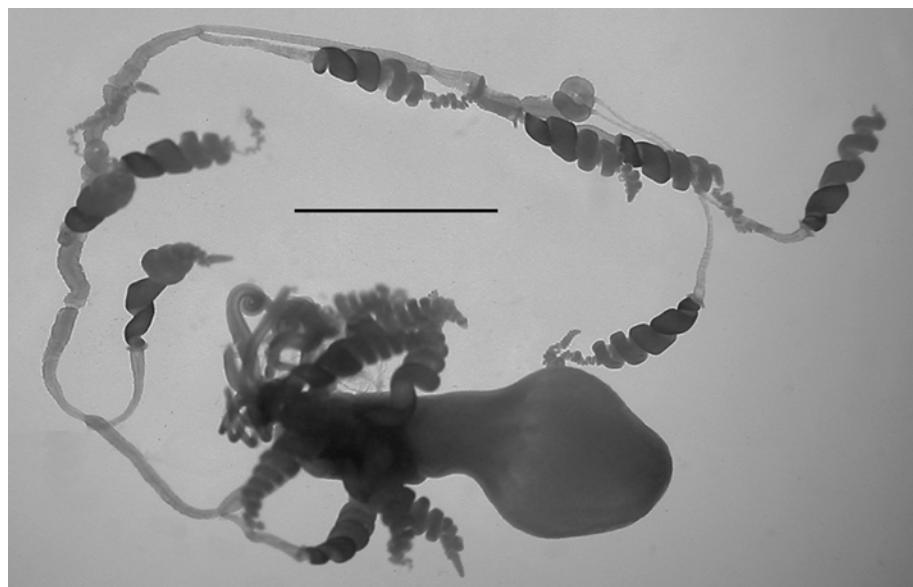
*Gastrozooid and tentacle:* The gastrozooids (Figure 18) were variable in size, with a relatively small basigaster, but otherwise showed no other remarkable features. They were generally colourless or with a faint orange hue.

*Tentilla:* A mature tentillum is shown in Figure 19. The highly extensile pedicel ended in a very small, almost vestigial involucrum, which did not cover even the most proximal part of the cnidoband. The latter consisted of up to eight spiral coils, although 5–6 was more common. Two types of nematocyst were present on the cnidoband; stenoteles and, probably, anisorhizas. Only 40–50 stenoteles, which measured c. 56 µm in length and 17 µm in

diameter, were found in a single row on either side of the proximal part of the first spiral of the cnidoband. The anisorhizas that occupied the remainder of the cnidoband, along with numerous darkly-staining platelets, measured c. 50 µm in length and 8 µm in diameter. The terminal filament contained two types of nematocysts, which were presumed to be acrophores and desmonemes, measuring c. 10 x 13 and c. 14 x 8 µm, as those types have been found on the terminal filaments of other agalmatid species (Purcell. 1984). The loosely and irregularly coiled terminal filament did not end in a cupulate process, but with a tightly coiled tapering section (Figure 19, detail).

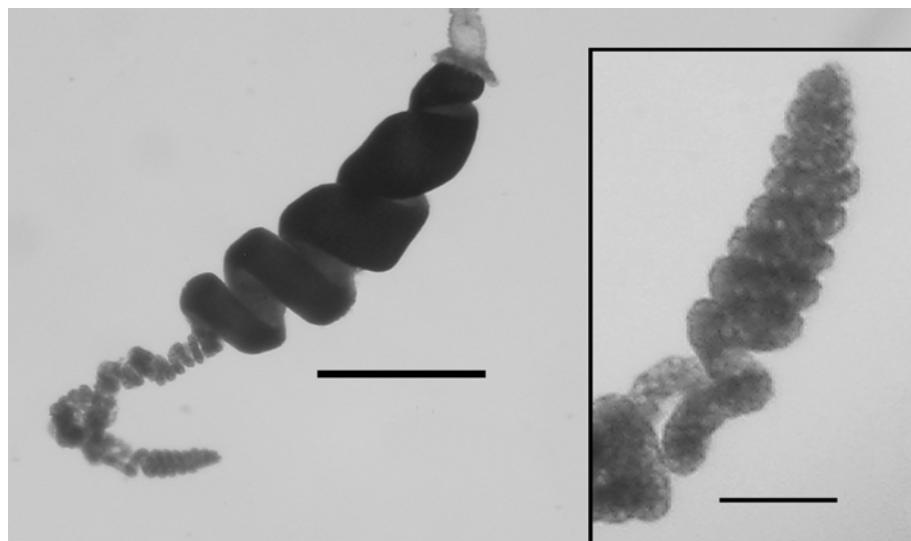


**FIGURE 17.** *Halistemma rubrum*. Type B bracts—upper views. Proximal at top, distal at bottom. Scale 2 bar mm.



**FIGURE 18.** Gastrozooid and tentacle of *Halistemma rubrum* from JSL Dive 1401-DS5 specimen. Scale bar 2 mm.

*Palpons:* The thin-walled palpons (Figure 20) were generally featureless, but with a quite marked distal teat-shaped proboscis and a narrow peduncle. They measured up to 5.5 mm in length. Each had a long, narrow palpacle attached at its base, but no nematocysts were found on it or on the palpon itself.



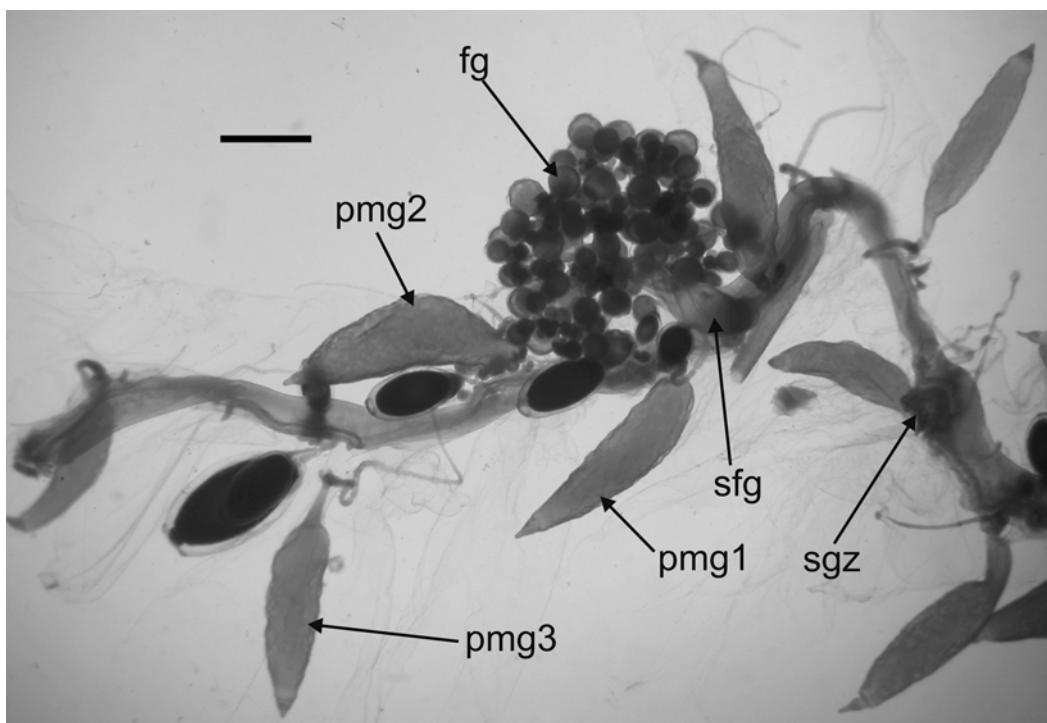
**FIGURE 19.** Tentillum of *Halistemma rubrum*, with (inset) detail of its terminal process. Scale bars 0.5 mm and 0.1 mm, respectively.



**FIGURE 20.** *Halistemma rubrum*. Palpons. Distal end at top. Scale bar 1 mm.

**Gonophores:** Totton (1965, pp. 56 & 58) gave a detailed description of the arrangement of the male and female gonodendra, noting "On each cormidium there are proximally two or three palpons, probably derived from secondary budding. Distal to them there is a larger palpon with a palpacle that measures 15 mm in length, not fully expanded. From the distal side of its base is budded, in the mid-ventral line, the wide muscular stemmed female gonodendron, with its branches and medusoid gonophores resembling a miniature bunch of grapes. When mature it

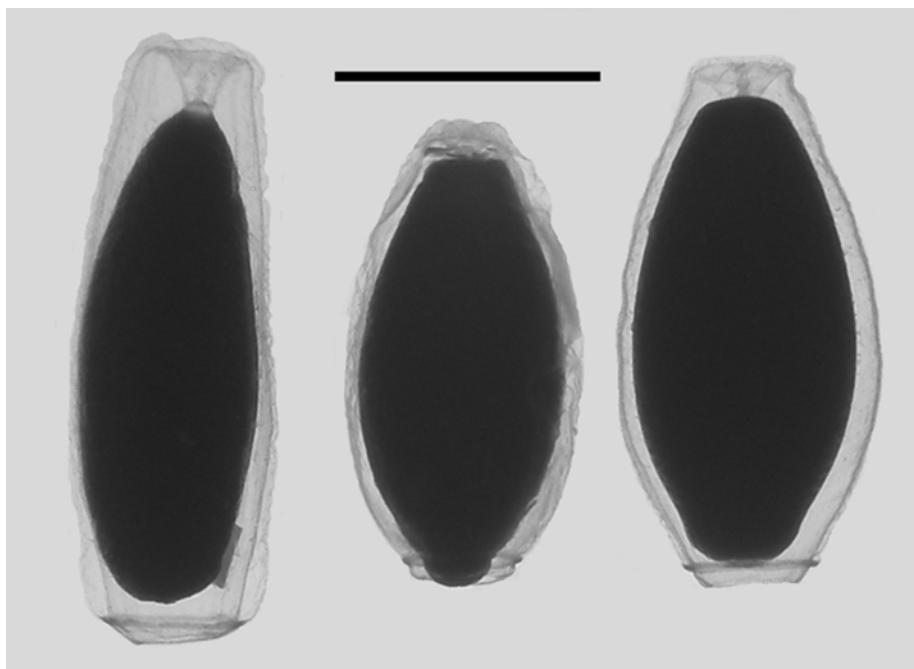
is about 5 mm in diameter, and capable of a great deal of expansion and contraction. It is situated at about one-third the distance from the last gastrozooid to the next one, and bears a number of reinforcing rings in the stem-wall. Distal to the female gonodendron are three other large palpons with palpacles, occupying the middle region of the cormidium. On the distal side of the base of each and in the mid-ventral line of the stem is a reduced male gonodendron ... It has not been sufficiently described hitherto. It can be seen that each of the male gonophores buds off at an angle of rather more than 120° in the transverse plane from the base of its predecessor to form a left-handed spiral. When mature the pedicels of the male gonophores grow to the comparatively enormous length of 5 mm. There may be present on each male gonodendron from eight to ten mature male medusoid gonophores, which start to pulsate whilst still attached, but finally detach themselves to swim away and shed their sperms. They are about 6 mm in length and lack tentacles. Each female gonophore — up to 0.7 mm in diameter — contains a single egg. In the distal region of each cormidium may be found two or three other palpons probably derived from secondary budding. It is not known whether they in turn develop gonodendra".



**FIGURE 21.** *Halistemma rubrum*. Part of the stem of JSL Dive 1401-DS5 specimen showing a female gonodendron and three male gonodendra with associated palpons. **fg**: female gonodendron, borne on a thickened stalk (**sfg**); **pmg1, 2, 3**: palpon associated with each male gonodendron; **sgz**: stalk of detached gastrozooid. Scale bar 1 mm.

This basic arrangement can be seen (Figure 21) for one of the JSL specimens. The racemose female gonodendron (**fg**), with its thickened stalk (**sfg**), bore no palpons. No mature female gonophores were found with any of the specimens examined. The three male gonodendra present in each cormidium, each associated with a palpon (**pmg1-3**), included only a few male gonophores, with a maximum length of 2.3 mm, that were obviously still immature (Figure 22). They had a short, broad stalk through which the gastrovascular canal passed, and a widely opened distal mouth.

*Nectalia*-stage: The specimen from JSL II dive 973-DS4 was young (Figure 23) and, although it had clearly developed beyond the *Nectalia* post-larval stage, it still bore the protozooid, with its tentacle bearing larval tentilla. The JSL Dive 1683-D1 specimen also still possessed six larval bracts, but the protozooid and larval tentilla had been lost. The former specimen included fourteen nectophores, no different from those of the adult specimens, and a couple of nectophoral buds. Only six larval bracts were found, while thirteen Type A bracts were also present. Carré (1971), who studied the larval development of *Halistemma rubrum*, also made brief mention of some young colonies of that species, found in the plankton, but neither referred to them as being at the *Nectalia*-stage nor described them in detail, apart from the larval tentilla. Also, as noted above, the post-larval stage that Vogt (1854) attributed to this species actually is that of an *Agalma* species.



**FIGURE 22.** Male gonophores of *Halistemma rubrum*. Proximal at the top, distal at the bottom. Scale bar 1 mm.

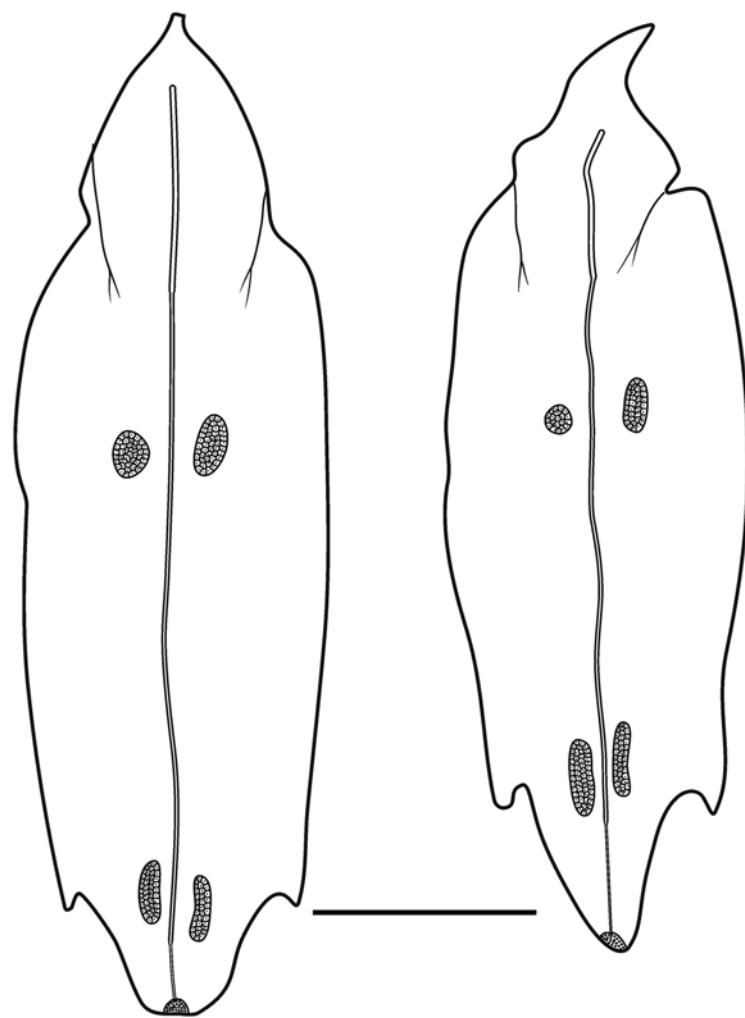


**FIGURE 23.** Tank picture of the JSL Dive 973-DS4 specimen of *Halistemma rubrum*, showing the protozooid (arrowed) with its tentacle bearing larval tentilla. Scale bar 2 mm.

The larval bracts (Figure 24) measured up to 15 mm in length. They were thickest at their proximal ends, thinning distally, with the upper surface convex and the lower one concave. The distal end was roundly pointed, and slightly proximal to it there were two rounded, lateral teeth. On the upper surface of the bract there were two pairs of patches of ectodermal cells, usually slightly asymmetrically placed and varying in size. Often these patches had been rubbed off but, usually, their outlines could be seen. The cells within these patches possessed densely staining nuclei, and were presumed to be sites of bioluminescence.

The bracteal canal followed the contours of the lower, median wall of the bract from close to its proximal end to almost its distal end. The canal was thickened in the proximal region, where the attachment lamella was present, but distally it was distinctly thinner. It continued along the median wall, but shortly before the distal end of the

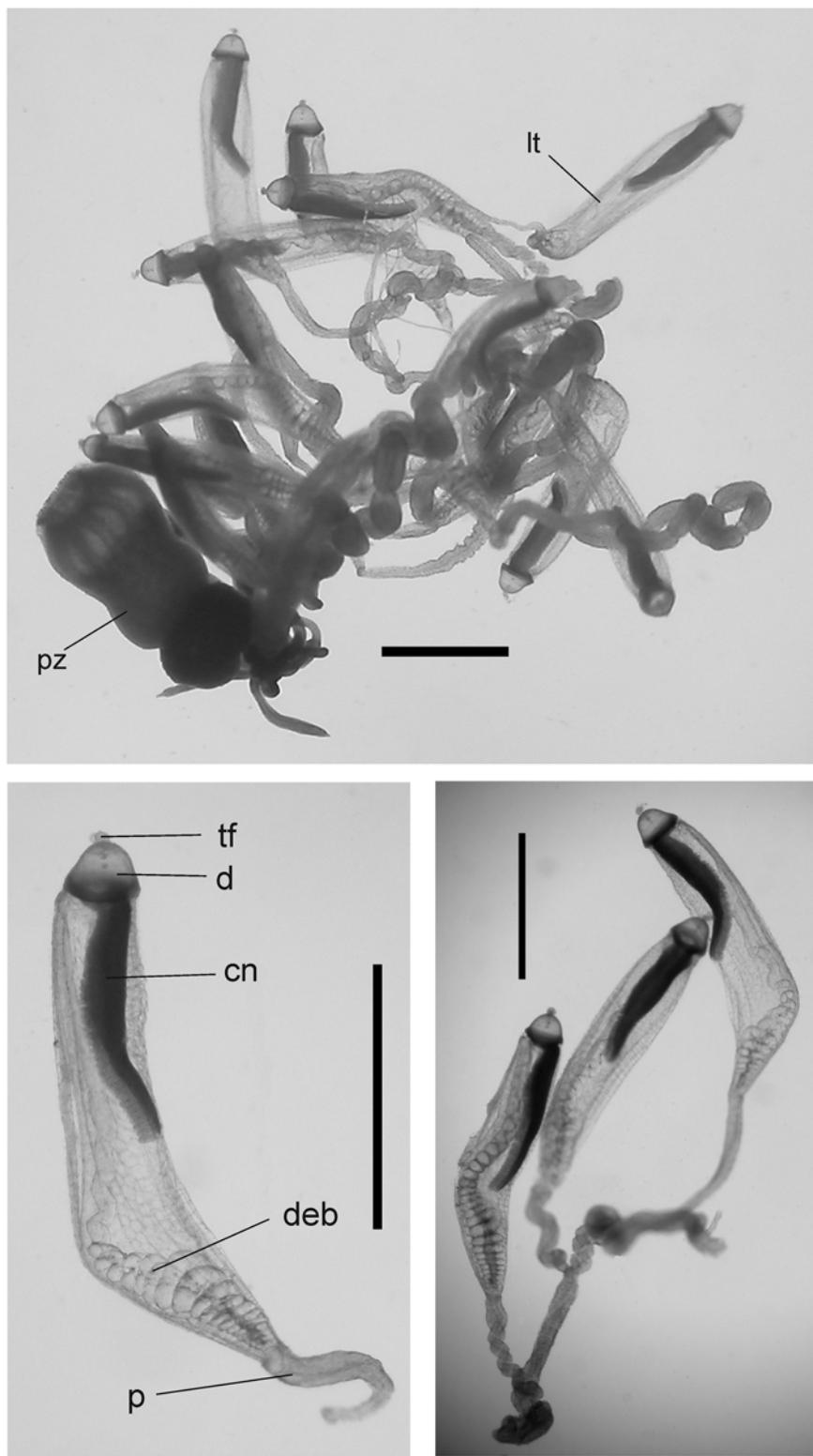
bract it penetrated into the mesogloea and continued, as a thin canal, to end below a cup shaped indentation filled with nematocysts. These nematocysts were identified by Carré (1971) as microbasic euryteles, but we were not able to confirm this.



**FIGURE 24.** *Halistemma rubrum*. Upper views of *Nectalia*-stage larval bracts from JSL Dive 973-DS4 specimen. Proximal at top, distal at bottom. Scale bar 2 mm.

The protozooid (Figure 25) showed no great differences from the adult gastrozooids, with all three main regions, proximal basigaster, stomach and distal proboscis, being of approximately the same length and diameter.

The larval tentilla, which were first described and illustrated by Keferstein & Ehlers (1861, Plate II, figs. 12–15, 17), were distinctly different from the adult forms. They consisted of a long, highly contractile proximal pedicel, and a long sac-like structure capped, distally, by a hemispherical dome from the centre of which projected a short terminal filament. There were no signs of any nematocysts on either the majority of the dome or the terminal filament. Two main structures were present in the sac. The double elastic band ran the entire length of the sac, and was particularly noticeable in its proximal region, where the coiling of the two bands around each other was obvious. The other structure was the cnidoband, the proximal end of which lay distally in the sac at the base of the domed terminal process. It extended to approximately half the length of the sac. Stenoteles and anisorhizas, as identified by Carré (1971), were present in the cnidoband, but whereas the latter occurred throughout, the former were restricted to each side of the distal three-quarters of its pendulous section. There were about 80 stenoteles present, measuring c.  $70 \times 23 \mu\text{m}$ , which was slightly larger than those on the adult tentilla. However, the anisorhizas were slightly smaller, measuring c.  $40 \times 9 \mu\text{m}$ . The number of stenoteles present was considerably higher than the dozen that Carré (1971) found on each side of the cnidoband of her specimens. Whether this difference can be accounted for by the differences in age of the specimens cannot be determined at present.



**FIGURE 25.** *Halistemma rubrum*. Top: Protozooid (pz) and tentacle, with larval tentilla (lt) from JSL Dive 973-DS4 specimen. Bottom: Individual larval tentilla. **cn**: cnidoband; **d**: dome-like structure; **deb**: double elastic band; **tf**: terminal filament. Scale bars 1 mm.

*Remarks:* The nectophores of *Halistemma rubrum* are easily distinguished from those of all other *Halistemma* species by the incompleteness of the basic ridge system. The absence of a mouth plate is also a useful diagnostic character, although it is not unique to this species. In addition, the almost vestigial involucrum at the base of the

cnidoband of the tentillum, and the presence of a tightly coiled tapering process at the end of the terminal filament, rather than a cupulate process, help to distinguish *H. rubrum* from other *Halistemma* species.

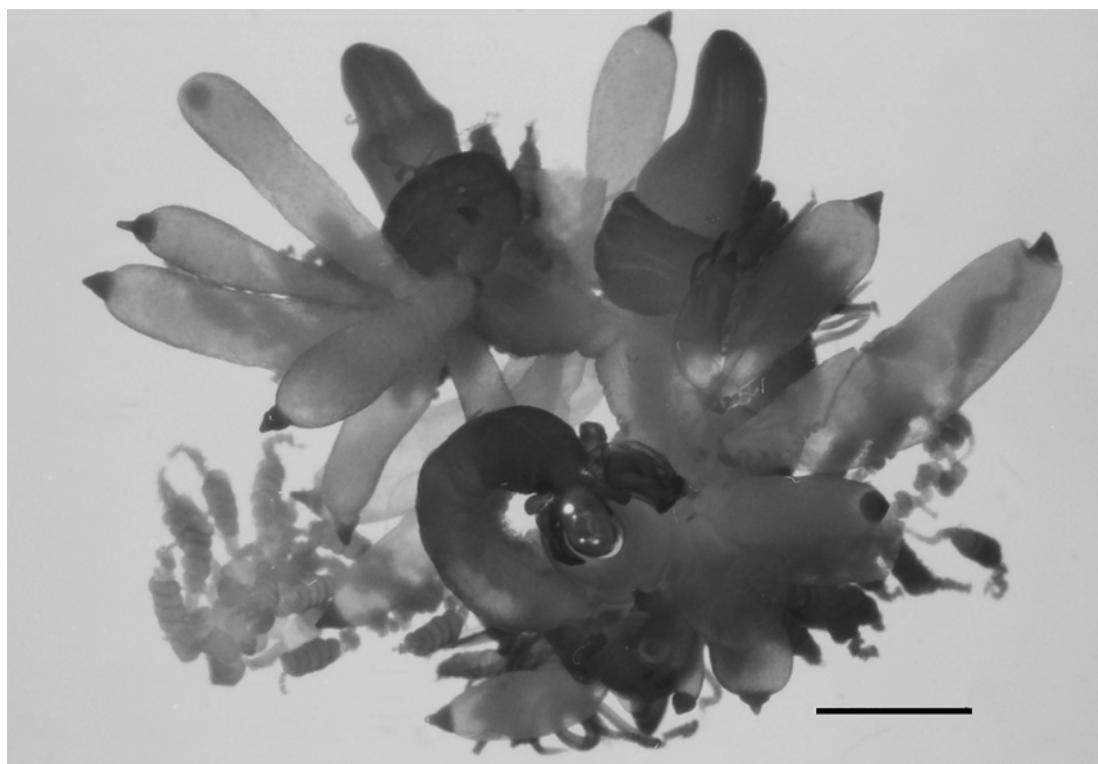
**Distribution:** There have been numerous records for *Halistemma rubrum* since Vogt (1852a) first described it; the most reliable of which come from the Mediterranean Sea as, to date, it is the only *Halistemma* species that has been found there. Most records are from the western basin (e.g. Carré, 1971, Bouillon *et al.*, 2004) but there are a few from the eastern basin, including the Adriatic Sea (e.g. Gamulin & Kršinić, 2000) and off Lebanon (e.g. Lakkis & Zeidane 1997).

Since the nectophores of *Halistemma cupulifera* have not until now been described, and together with the discovery recently of two new species, *H. transliratum* Pugh & Youngbluth, 1988 and *H. maculatum* sp. nov., all records from other regions need to be treated with some caution. For instance, as we will show, the type "e" and "f" nectophores that Totton (1954) ascribed to *H. rubrum* actually belong to other *Halistemma* species, namely *H. cupulifera* and *H. maculatum* sp. nov., respectively.

The present records for the North Atlantic Ocean came from the Gulf of Maine and the Bahamas. There are several other unverified records for the western North Atlantic, and Leloup (1936), for one, also cites its presence at various positions in the eastern North Atlantic. These records, if true, indicate that *Halistemma rubrum* appears to have a widespread distribution in that region, including the Gulf of Mexico (Pugh & Gasca, 2009) and Caribbean (Stepanjants, 1975).

In the South Atlantic Ocean *Halistemma rubrum* has been reported from off South Africa and Namibia (e.g. Pagès & Gili, 1992) and off Brazil (Nogueira & Oliveira 1991). Margulis (1969) found it to be the second commonest physonect in samples collected throughout the Atlantic Ocean, and found that its most northerly occurrence was at 50°22'N, 21°13'W, the most southerly at 42°04'S, 38°58.9'W, being present at all depths between the surface and 1700 m.

*Halistemma rubrum* has also been recorded on a number of occasions throughout the Indian Ocean but, as noted above, some of Totton's (1954) records belong to different species. Daniel (1985) gives the most comprehensive data for that region, with further data from the eastern Indian Ocean being given by Musayeva (1976).



**FIGURE 26.** *Halistemma cupulifera*. JSLII Dive 1450 specimen. Scale bar 2 mm.

Although Stepanjants (1967, 1977a, b) states that *H. rubrum* has a fairly widespread distribution in the warmer waters of the Pacific Ocean, most other records are concentrated in three areas; in the Humboldt Current, off Chile (Pagès *et al.*, 2001); in western waters from the Moluccas (Bedot, 1896), Vietnam (Leloup, 1956), Taiwan (Yu, 2006), and Chinese waters (e.g. Zhang, 2005); and finally off southern California and Baja California (Alvariño, 1967, 1991). However, some of these identifications must be doubtful. For instance Zhang, whose fig 2D of *H. rubrum*, shows a nectophore with a large mouth plate, which is not a character for this species. Nonetheless, three of the specimens examined in this study came from the southern end of the Gulf of California. Four other specimens of *Halistemma* sp. collected during the same cruise probably belonged to *H. rubrum*, but they were not examined,. Two of these also came from DR0335, at 284 and 198 m depth; one was collected during DR0340 ( $23^{\circ}41.6'N$ ,  $106^{\circ}05'W$ ) at 201 m; and another during DR0341 ( $24^{\circ}18.9'N$ ,  $109^{\circ}11.9'W$ ) at 217 m.

### ***Halistemma cupulifera* Lens & van Riemsdijk, 1908**

*Halistemma cupulifera* Lens & van Riemsdijk, 1908, p. 85, pl. XVI; Pugh & Youngbluth, 1988, p. 10, fig. 6C.

*Stephanomia cupulita* Kawamura, 1954, p. 112.

*Halistemma rubrum* Totton, 1954 (*in partim*) Text—fig. 16, A, B, E.

? *Paragalma birsteini* Margulis, 1976, p. 1244, figs. 1–3.

**Diagnosis:** Basic *Halistemma* ridge pattern on nectophores, with pair of complete vertical-laterals and laterals arising from upper laterals and ending just above the large lateral ostial processes. Up to five types of bract. Tentilla with small, cup-shaped involucrum covering at most the first two spirals of the cnidoband, and a large cupulate terminal process to the terminal filament.

*Material examined:*

JSL II Dive 1450—CG4	28 August 1987	$24^{\circ}38.8'N$ $83^{\circ}45.3'W$	depth 683 m
<i>Atlantis</i> 2 St. 101	25 June 1978	$40^{\circ}04.6'N$ $54^{\circ}31.4'W$	depth unknown
<i>Discovery</i> St. 3185	14 November 1954	$40^{\circ}47'N$ $12^{\circ}05'W$	depth 0 m
<i>Discovery</i> 7089#13	14 November 1969	$17^{\circ}48'7''N$ $25^{\circ}28.7'W$	depth 515–600 m

**Holotype:** *Siboga* St. 244. Lat.  $4^{\circ}25.7'S$ ,  $130^{\circ}3.7'E$ . 2991m. Housed in the Zoölogisch Museum, Amsterdam, COEL 4516.

**Description:** This description will be based mainly on the JSLII Dive 1450 specimen (Figure 26), which consisted of the stem with the pneumatophore, the largely denuded nectosome and parts of the siphosome, together with some detached nectophores and bracts.

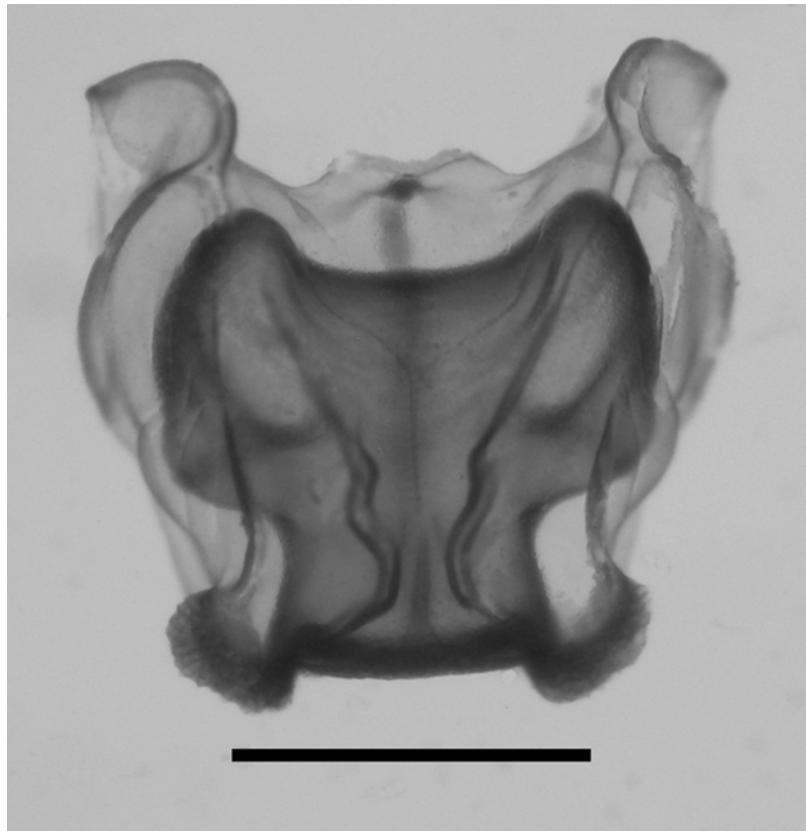
**Pneumatophore:** The pneumatophore measured 1.7 mm in length, and 0.6 mm in diameter. There was a distinct patch of cells at the apex that may have been pigmented. Whatever pigmentation there might have been had leached away during preservation.

**Nectosome:** The nectophores were budded off on the dorsal side of the stem.

**Nectophores:** Eighteen detached nectophores were present in association with the JSLII Dive 1450 specimen, together with some nectophoral buds, at varying stages of development, and attachment lamellae. Detached nectophores ranged in size from  $1.9 \times 1.7$  mm (height x width) to  $9.5 \times 9.0$  mm. The upper view of the largest nectophoral bud (Figure 27) clearly showed the upper lateral ridges curving outwards just above the ostium, and also giving rise to the lateral and vertical lateral ridges. The relatively enormous lateral ostial processes had numerous elongate nematocysts projecting out from them. Both the axial wings and the central thrust block were only slightly developed, and there was no obvious mouth plate.

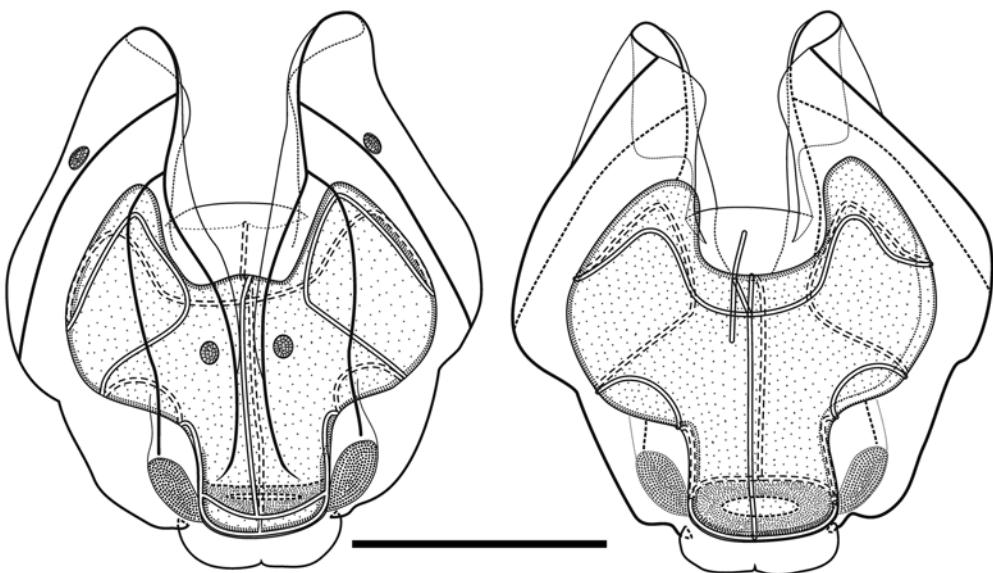
In the smaller, younger nectophores (Figure 28) the central thrust block was still quite flat and underdeveloped, but the axial wings had considerably enlarged and extended well beyond it. In the ostial region, a mouth plate had begun to develop, which was slightly emarginated in the mid-line. The lateral ostial processes were still relatively large, but most of the nematocysts by now had been lost, at least in the preserved material, and so these processes were covered in small plate-like cells. No nematocysts were ever seen in this region on fully developed

nectophores. Totton (1965), for *Halistemma striata*, described these lateral processes as ostial chromatophores, but clearly this was not their original function and, in addition, they do not appear to be pigmented. Whether, once the nematocysts are lost, they become sites of bioluminescence is not clear. However, there were two pairs of oval, occasionally elongate, patches of ectodermal cells on the upper lateral sides of the nectophore that almost certainly were sites of bioluminescence. One pair lay close to the junction of the upper lateral and vertical lateral ridges, on the upper side of the latter; and the other lay close to the upper lateral ridges, between them and the lateral ridges. These patches were easily abraded and generally were not seen in the net collected material.

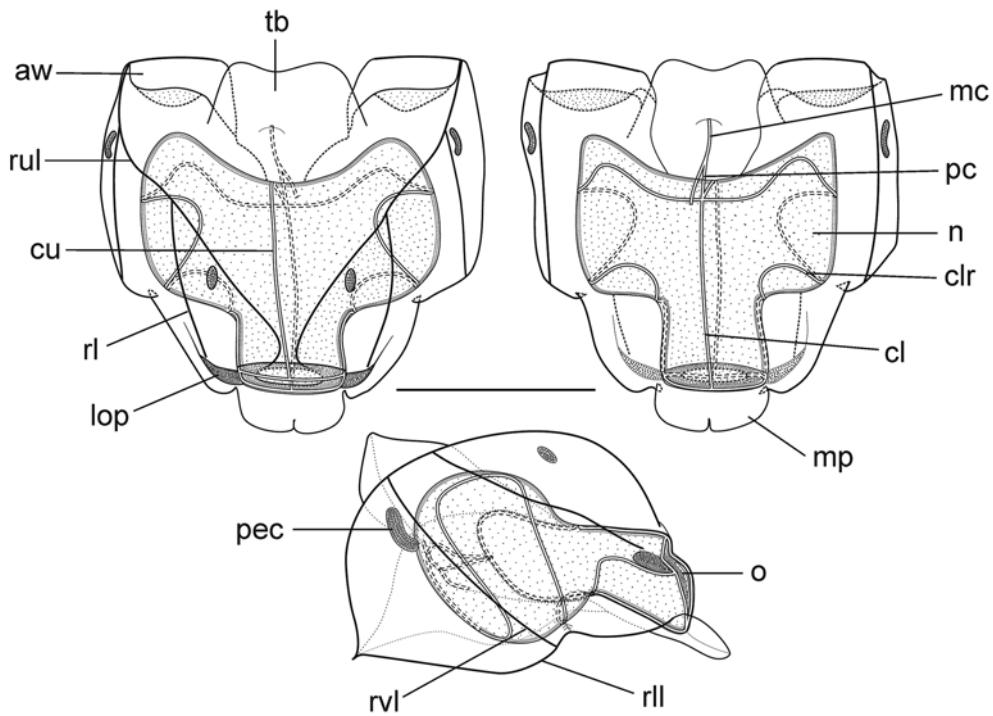


**FIGURE 27.** *Halistemma cupulifera*. Upper view of very young nectophore. Scale bar 0.5 mm.

As the nectophores increased in size the central thrust block became more and more developed and ultimately reached to the same level or slightly above the now squared-off, slightly outward-sloping axial wings (Figure 29). The mouth plate also increased in size, but still remained only slightly emarginated in the midline. The typical *Halistemma* arrangement of the ridges on the nectophores of *H. cupulifera* was present. The upper lateral ridges (Figure 29) ran from the apical margins of the axial wings distally toward the ostium. At first they were widely apart, but after they had given rise to the vertical lateral ridges they curved inward and continued obliquely toward the midline. Their closest approach was slightly above the ostium, but then they curved out and continued laterally, gradually petering out. The lateral ridges branched from the upper lateral ridges at approximately half the latter's length (but higher up in the younger nectophores) and ran obliquely down the lateral surfaces of the nectophore towards the ostium. However, they also petered out, and on a level with the upper laterals, ended just above the lateral ostial processes. The vertical lateral ridges extended from the upper laterals, at approximately the level of the top of the nectosac in mature nectophores (Figure 29), and well above the nectosac in the younger ones (Figure 28), obliquely downwards and almost parallel to the laterals until they joined the lower lateral ridges. These lower lateral ridges ran along the entire length of the lower lateral edge of the nectophore from the outer margins of the axial wings, where they joined with the apico-laterals, to below the ostium where they joined with the lateral margins of the mouth plate. The proximal and distal parts of these ridges slightly overlapped each other at about one-third the height of the nectophore. There were no distinct ridges on the lower surface of the nectophore; however, in the preserved material folds ran down the inner apices of the axial wings to just above the upper-mid line of the nectosac below the region of the central thrust block.



**FIGURE 28.** *Halistemma cupulifera*. Young nectophores from JSLII Dive 1450 specimen. Scale bar 2 mm.

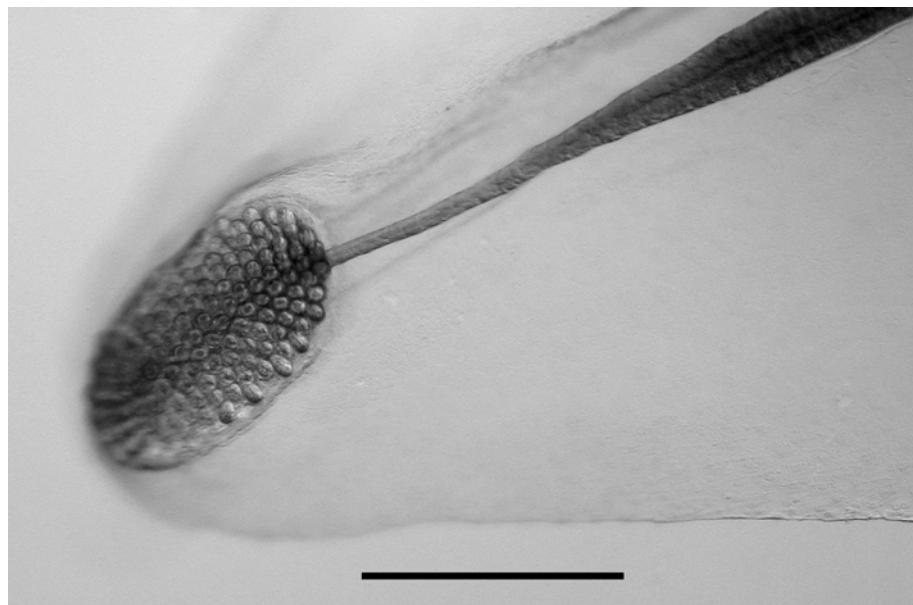


**FIGURE 29.** *Halistemma cupulifera*. Upper (top left), lower (top right) and lateral (bottom) views of mature nectophore. For legend see Figure 14. mp: mouth plate. Scale bar 5 mm.

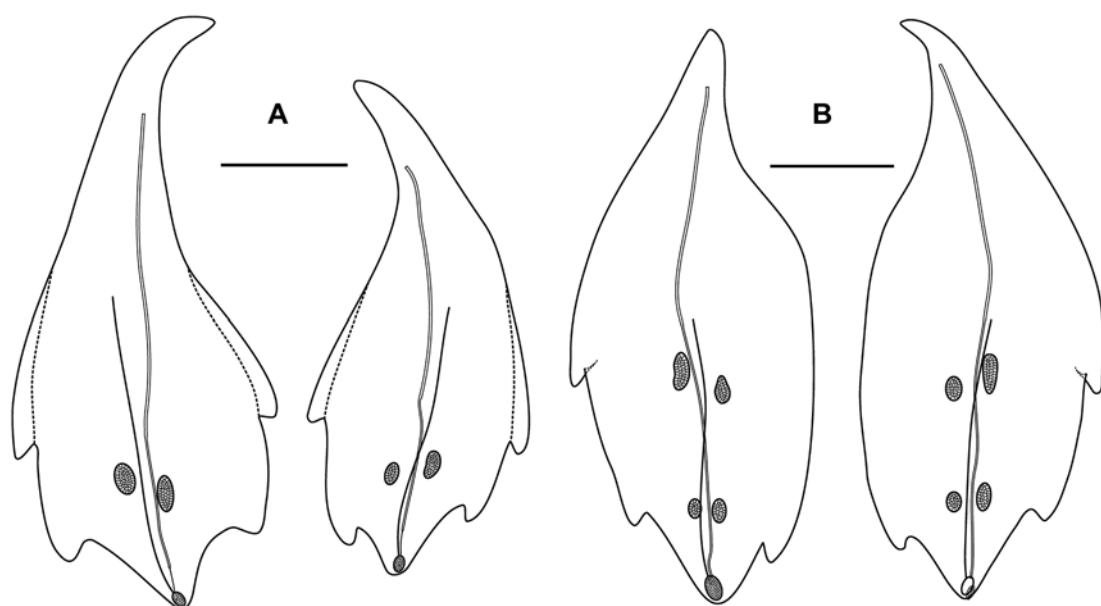
The ascending and descending branches of the mantle canal, on the proximal median surface of the nectophore, were of almost equal length, so the pedicular canal arose at its mid-length and extended down to the nectosac. There it gave rise to all four radial canals. The courses of the upper and lower canals were straight. The lateral radial canals extended out laterally and formed a loop before reaching the lateral margins of the nectosac. They then looped up onto the upper side of the nectosac, and then back down the lateral surface and onto the lower surface, before returning back to the lateral surface of the nectosac and curving round to run directly to the lateral margins of the ostium, where they joined the ring canal.

*Siphosome:* In all the specimens examined the siphosome was greatly contracted and it was not possible to determine accurately the organisation of the individual cormidia.

*Bracts*: Fifty-seven, generally foliaceous bracts were found with the JSLII Dive 1450 specimen and these could be divided into five categories on the basis of their general morphology, which included the number of lateral teeth and ectodermal cell patches on the outer surface. The latter were undoubtedly sites of bioluminescence, as Mr. Peter David observed brilliant bluish bioluminescence being emitted by them when he hand-collected the Discovery St. 3185 specimen. The bracteal canal lay just within the lower surface of the bract for most of the length, only entering the mesogloea and sloping up towards the upper surface close to the distal end. The canal ended below a cup-shaped oval hollow on the upper surface that, in the younger bracts at least, was filled with tightly packed elongate nematocysts (Figure 30). Like those on the lateral ostial processes on the nectophore, these nematocysts had generally disappeared in the fully-grown bracts.



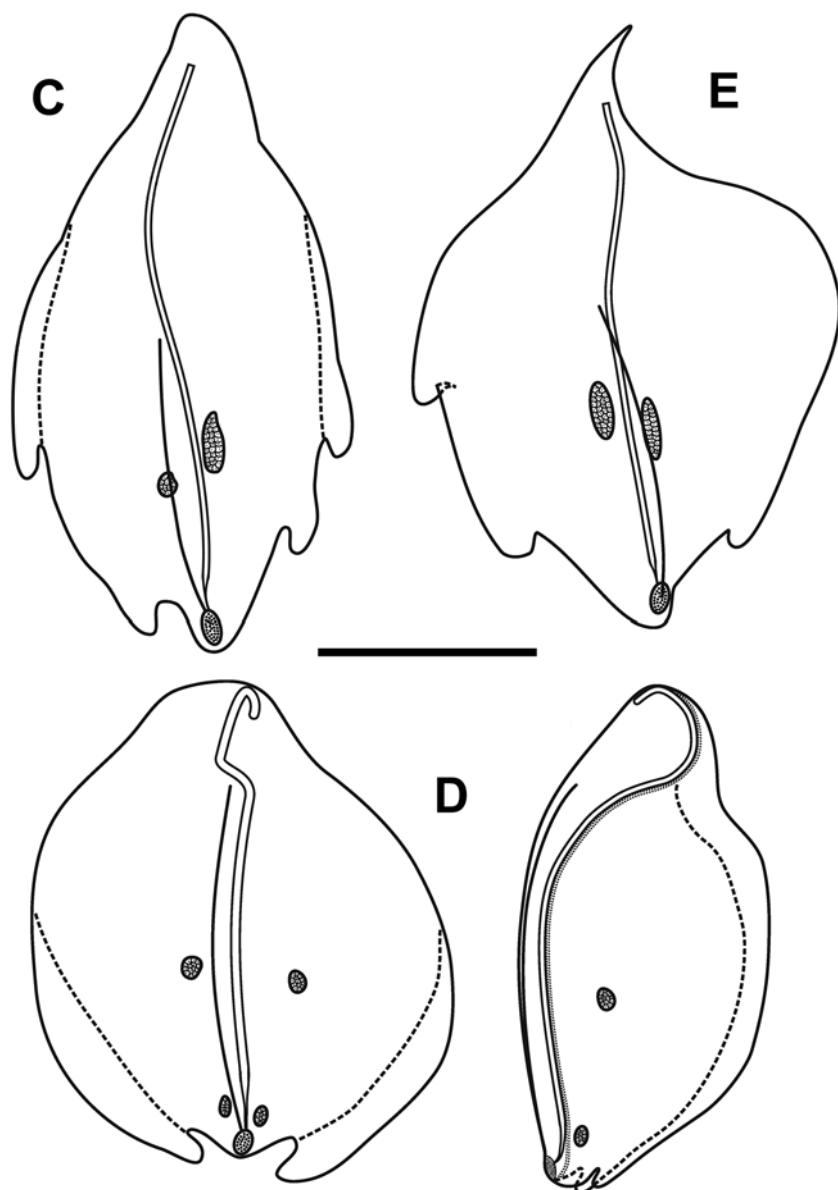
**FIGURE 30.** *Halistemma cupulifera*. Nematocyst-covered process on the distal bract tip from JS1450 specimen. Scale bar 0.5 mm.



**FIGURE 31.** *Halistemma cupulifera*. Upper views of Type A and B bracts. Proximal at top, distal at bottom. Scale bar 5 mm.

Type A—Twenty-eight bracts of this type were found in association with this specimen, the most numerous bracts present (Figure 31). These bracts were elongate, with a distinctly tapered proximal end that bent toward the inner side, and were present in enantiomorphic pairs. They ranged in length from 14.5 to 24 mm and from 6 to 12

mm in width at the widest part (between the proximal pair of lateral teeth). They bore two distinct pairs of lateral teeth, and a median ridge on the upper surface that was most distinct in the distal half of the bract. The mesogloea was markedly thickened in the proximal part of the bract, where the lower part of the bract showed no concavity. At approximately the same level as the origin of the canal the thickness of the mesogloea began to reduce, at first only in the central part of the lower surface, but then gradually the concavity on that side widened and deepened so that at the distal end of the bract the mesogloea was very thin. The bracteal canal remained in contact with the lower wall throughout most of its length, but at a level just proximal to the proximal pair of teeth, it showed a marked narrowing. Close to its distal end the canal penetrated into the mesogloea and ran obliquely toward the upper surface. There was only one pair of oval ectodermal patches, toward the distal end of the upper side of the bract, which were slightly misaligned and occasionally quite elongate.



**FIGURE 32.** *Halistemma cupulifera*. Upper view of Type C, Type D in upper (left) and lateral (right) view, and upper view of Type E bracts. Proximal at top, distal at bottom. Scale bar 5 mm.

Type B—Eleven bracts of this kind were present in enantiomorphic forms (Figure 31). They were also quite large, elongate and asymmetrical, measuring from 9.2 to 22.5 mm in length and from 6 to 8.5 mm in width. There were three lateral teeth. A single more proximal one on the outer lateral edge of the bract, which extended slightly on to the upper surface, and an asymmetric pair of more distal lateral ones. There were two pairs of ectodermal cell patches. A median ridge stretched from approximately the mid-length of the upper surface of the bract to almost the

distal end. The bracteal canal, which originated closer to the proximal end of the bract than for the Type *A* bracts, but still some distance from it, had a similar arrangement as found in the Type *A* bracts; thinning on a level with the proximal end of the median ridge; entering the mesogloea close to the distal tip; and running up to end below the cupulate structure on the upper side of the bract.

Type *C*—Nine bracts of this type were found (Figure 32). This asymmetrical type appeared to be intermediate in form between the Type *A* and *B* bracts. They were smaller with two pairs of lateral teeth, the more distal pair being very asymmetrically arranged, and just one pair of ectodermal patches. They ranged from 8 to 17 mm in length and from 5.5 to 11.5 mm in width. The bracteal canal extended almost to the proximal point of the bract and in young bracts, the canal remained thick for almost the entire length, tapering only towards the distal end when it entered the mesogloea. In the larger bracts of this type, the canal thinned at the same level as the proximal end of the median dorsal ridge.

Type *D*—Seven, very rounded bracts of this type were found. They did not seem to be present in enantiomorphic pairs and appear to be characteristic for this species (Figure 32). They measured from 10.5 to 15 mm in length and from 10 to 14 mm in width. The mesogloea of the proximal end of the bract was extremely thick, but its thickness rapidly decreased on the lower side, and it remained relatively thin for most of the length of the bract. This, combined with the fact that the bracts were extremely concavo-convex, resulted in most of the bracts observed being folded in two longitudinally. There was one pair of rounded lateral teeth that extended beyond the median distal point of the bract in upper view. They possessed two small pairs of ectodermal cell patches, which were quite even in size and shape (small ovals) on all bracts. The bracteal canal originated almost on the upper side of the bract, running down, within a shallow central furrow, the proximal end and then along the lower surface of the bract until the distal end where it entered the mesogloea as in the other bract types. In younger bracts, the canal remained thick for almost the entire length, tapering only at the point of sloping into the mesogloea where as in older bracts, the canal thinned just over a quarter of the way down from the proximal end. A median lateral ridge also started at this point and petered out over the distal cupulate process, as with the other types of bract.

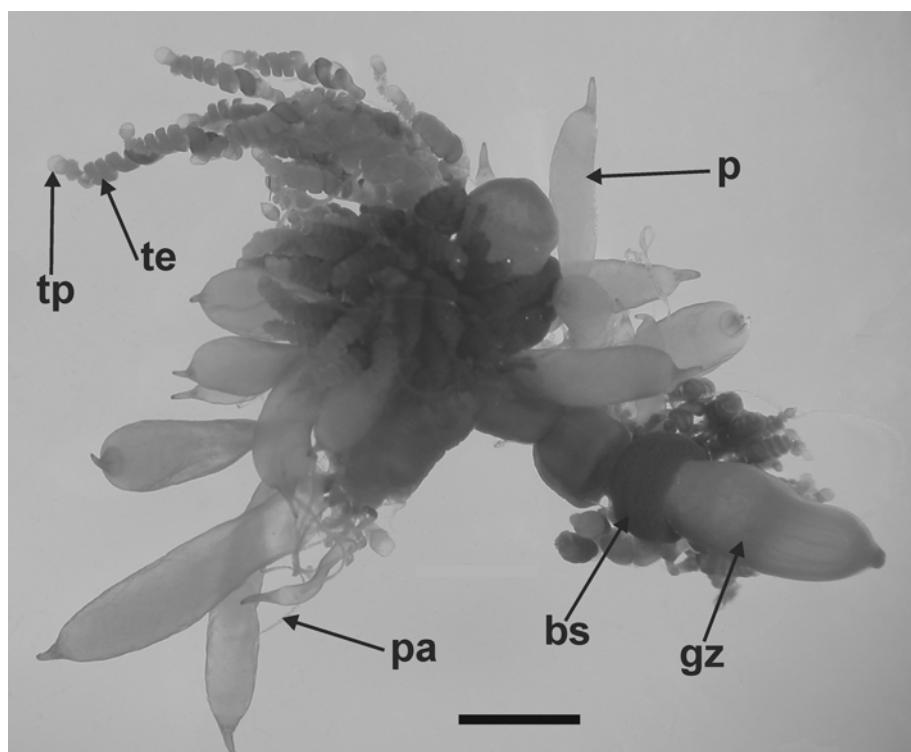
Type *E*—Only two small bracts of this type were found (Figure 32). They measured 9 and 7 mm in length and 13.2 and 9 mm in width and were present in the same asymmetrical morph. The proximal ends of the bracts were extremely pointed and the mesogloea much thickened in that region. However, at about one third the length of the bract the mesogloea suddenly thinned on the inner side resulting in a marked change of direction of the bracteal canal. This canal remained thick along almost its entire length, only tapering when it entered the mesogloea distally. This might indicate that the bracts were not fully developed, as was seen for some of the other types of bract. There was a pair of distal lateral teeth, but only one more proximal one on the outer lateral side. The median ridge on the upper side ran from just under half the length of the bract, just proximal to the level of the proximal tooth. There was one pair of quite elongate ectodermal cell patches on the upper surface of each bract.

Bigelow (1911), in his description of *Halistemma foliacea* under the name *Stephanomia amphitridis*, noted that the bracts on his specimens appeared to be arranged in four or five irregular rows. He also mentioned dorsal, lateral and ventral types of bract. Kawamura (1954), who re-examined Bigelow's material, considered that there were five rows, one dorsal and two laterals on each side. Assuming that the latter two types were different and occurred in enantiomorphic pairs on either side of the stem, then this would suggest five rows of bracts of three types. It is difficult to reconcile that with our present findings of five types of bract. It is very likely that the Type *D* bracts represent the dorsal ones, as they did not appear to occur in enantiomorphic pairs. It is possible that the Type *C* bracts, with four lateral teeth and a pair of ectodermal patches on the upper surface, may be a young form of the Type *A* bracts, which also share the same characters. However, although both the Type *B* and Type *E* bracts have three lateral teeth, the former has two pairs of ectodermal patches, while the latter only has one. As noted above the two Type *E* bracts were small and probably not fully developed, but the absence of the second pair of ectodermal patches is striking.

*Gastrozoid and tentacle:* The gastrozooids, up to 6 mm in length, showed no particular diagnostic features (Figure 33). There was a cupulate basigaster proximally, a variously expanded, central stomach region, and an extremely variable distal proboscis. Any pigmentation that might have been present in life had been leeched out during preservation.

*Tentilla:* Only the mature tentilla were looked at in detail (Figure 34). They were borne on highly contractile pedicels, at the distal end of which was an involucrum. This involucrum varied in size from a simple enlarged ring around the pedicel to a cup-shaped structure covering at least the first two spirals of the cnidoband. These

differences did not appear to be developmental stages, but probably were caused by damage to the fragile structure. The cnidoband had up to seven closely wound spirals, on which two types of nematocyst were found on their outer surfaces. The vast majority of the nematocysts, arranged in many rows, were banana-shaped, measuring c. 48 µm in length and 6.5 µm in diameter. No discharged ones were noted and so their identity was not ascertained, but presumably they were anisorhizas (see Carré, 1971). On either side of these nematocysts, in the most proximal part of the cnidoband, was a single row of stenoteles; there being about 50 on each side. These measured c. 67 µm in length and 26 µm in diameter. Large numbers of c. 12 µm diameter platelets were also apparent in the cnidoband. The terminal filament arose at the distal end of the cnidoband and clearly could reach a considerable length when fully extended. Two types of nematocyst were present, although their exact arrangement was not apparent. These were probably acrophores, which measured 19.5–25 µm in length and 10.5–12 µm in diameter, and desmonemes, c. 25 x 10.5 µm respectively. At the end of the terminal filament was a large cupulate terminal process, which measured 250–315 µm in length and 200–300 µm in diameter. The distal part bore no nematocysts, but was covered in round or ovoid platelets, ranging from 18 to 23 µm in length. The proximal part bore nematocysts similar to those of the terminal filament, but generally smaller. The ratio between the proximal and distal parts of the terminal process was somewhat variable, ranging from c. 2:1 to 1:2.

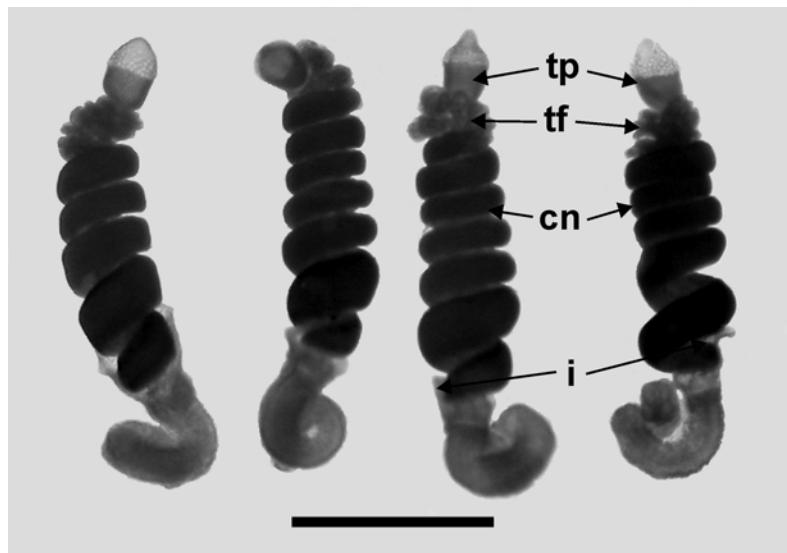


**FIGURE 33.** *Halistemma cupulifera*. Part of siphosomal stem from JSLII Dive 1450 specimen. **bs:** basigaster; **gz:** gastrozooid; **p:** palpon; **pa:** palpacle; **te:** tentillum; **tp:** terminal process. Scale bar 2 mm.

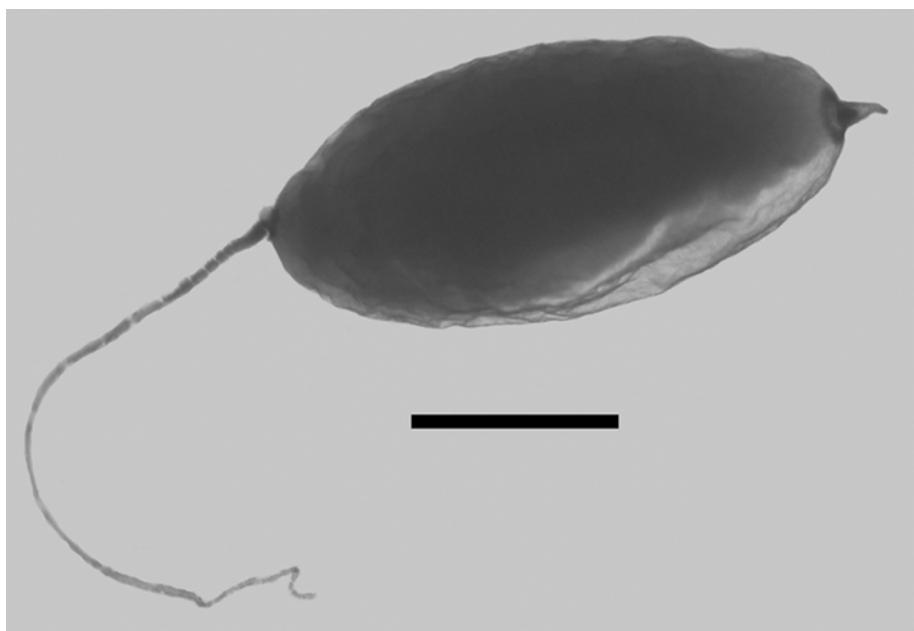
**Palpon:** Most of the palpons remained attached to the siphosomal stem fragments of the JSLII Dive 1405 specimen (Figure 33), but a few larger ones were detached and these measured up to 6.3 mm in length and 2.7 mm in diameter (Figure 35). These larger ones appeared to be filled with a dense amorphous substance, while the younger ones on the stem were more translucent with a milky-white appearance. All had a more or less extended narrow distal proboscis, and a long thin palpacle, attached proximally. Although there was a regular arrangement of the cells on the palpacle, no nematocysts were found on it or, indeed, on the palpon itself.

**Gonophore:** No gonophores were found with the JSLII 1405 specimen, but the *Atlantis* 2 St. 101 one showed some developing ones (Figure 36). Both the male and the female gonodendra were attached to a distinct inflation on the ventral side of the siphosome, with the male one anterior to the female. The female gonophores formed a racemose cluster borne on a distinct thickened stalk. Between them were attached two palpons, one of which had broken off, but its peduncle was still visible.

**Nectalia stage:** None of the specimens examined were at this stage, and no larval bracts or tentilla were observed.



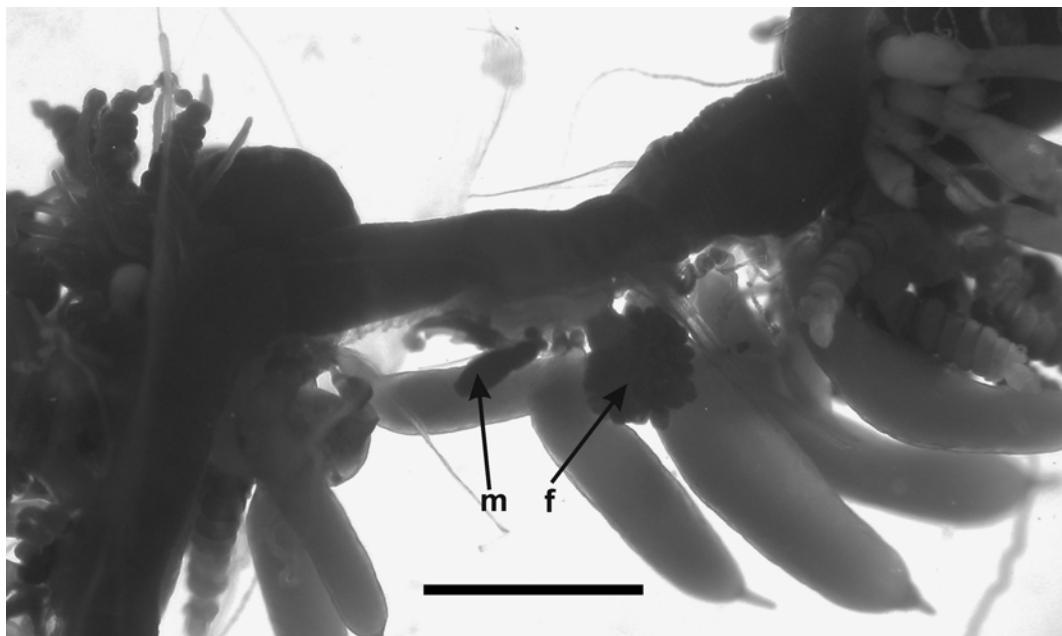
**FIGURE 34.** *Halistemma cupulifera*. Four tentilla from the JSLII Dive 1450 specimen. **cn:** cnidoband; **i:** involucrum; **tf:** terminal filament; **tp:** terminal process. Scale bar 1 mm.



**FIGURE 35.** *Halistemma cupulifera*. Palpon from JSL1450 specimen. Scale bar 2 mm.

*Remarks:* As noted above, Lens & van Riemsdijk (1908) described a new species of *Halistemma*, *H. cupulifera*, based on a single, imperfect specimen consisting of a pneumatophore, a nectosome denuded of all mature nectophores, and a part of the siphosome with some zooids still attached (see Figure 37). The size of the pneumatophore was not given, but the contracted nectosome measured 4 mm in length and 1.5 mm in diameter, and included a few buds of nectophores at its apical end. The short piece of siphosome included some fully developed female gonophores and four (+) gastrozooids, three of which were said to have tentacles with mature tentilla. The latter were described as having a cnidoband with 4–5 spiral turns, with the first two spirals containing ensiform nematocysts, but a proximal involucrum was said to be absent. The contracted terminal filament bore, at its distal end, (*ibid.* p. 85) "a small acorn-cup-shaped appendage (*cupulifera*) the basal part consisting of ... an agglomeration of the small circular cnidocysts of the terminal filament and proximally of many delicate ectoderm-cells". "Elongate, cylindrical, not quite transparent but more whitish opaque" (*ibid.* p. 86) palpons were present, which were without palpacles, but the authors correctly surmised that they had probably become detached. There were only two bracts, of which the larger was in very poor condition. The smaller was 5 mm in length and had a

foliaceous appearance, with (*ibid.* p. 86) "two small incisions occur on both sides, which even on the right side attain the appearance of a lobe". On the upper surface there were two oval patches of ectodermal cells. They mention that microscopically small filaments arose from some of these cells, which might indicate that they were nematocysts, but they also described small canals, directed proximally, from each patch that eventually united. These must be artefacts. Although they describe two incisions on each side of the bract, their figure only shows three individual teeth. The bract most resembles our Type E bract, but because of the thickness of the canal it is almost certainly immature, which was the conclusion reached above.

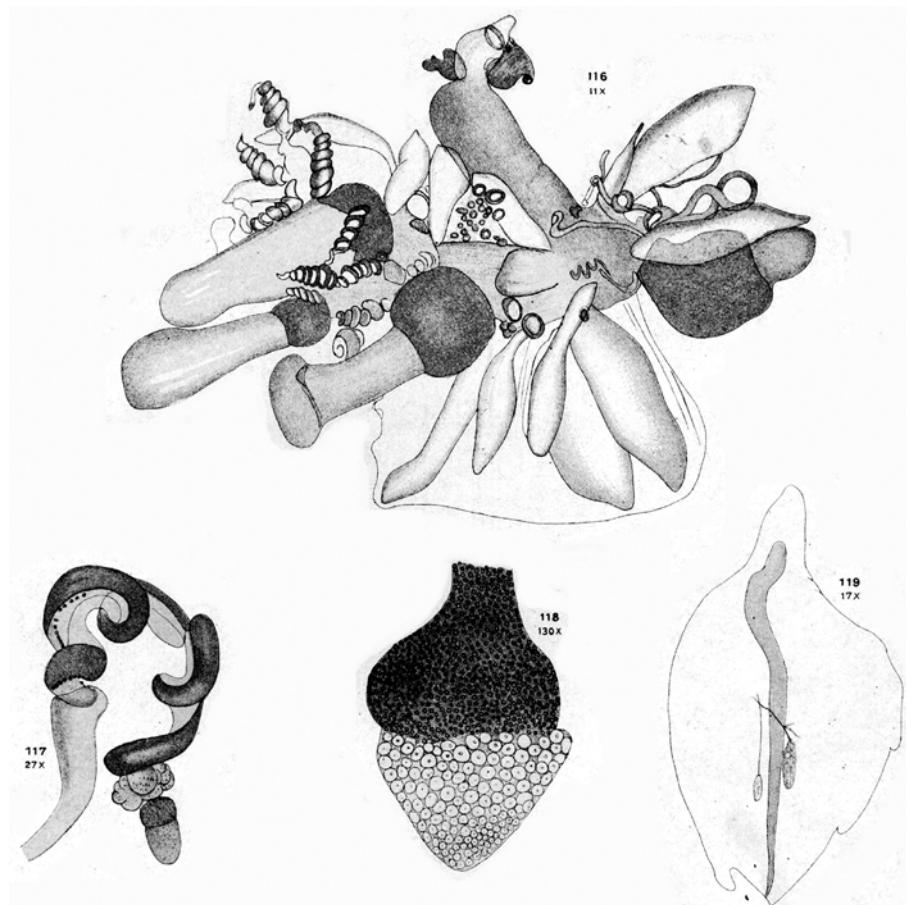


**FIGURE 36.** *Halistemma cupulifera*. Detail of siphosome from *Atlantis* 2 specimen showing young ♂ (m) and ♀ (f) gonophores. Scale bar 2 mm.

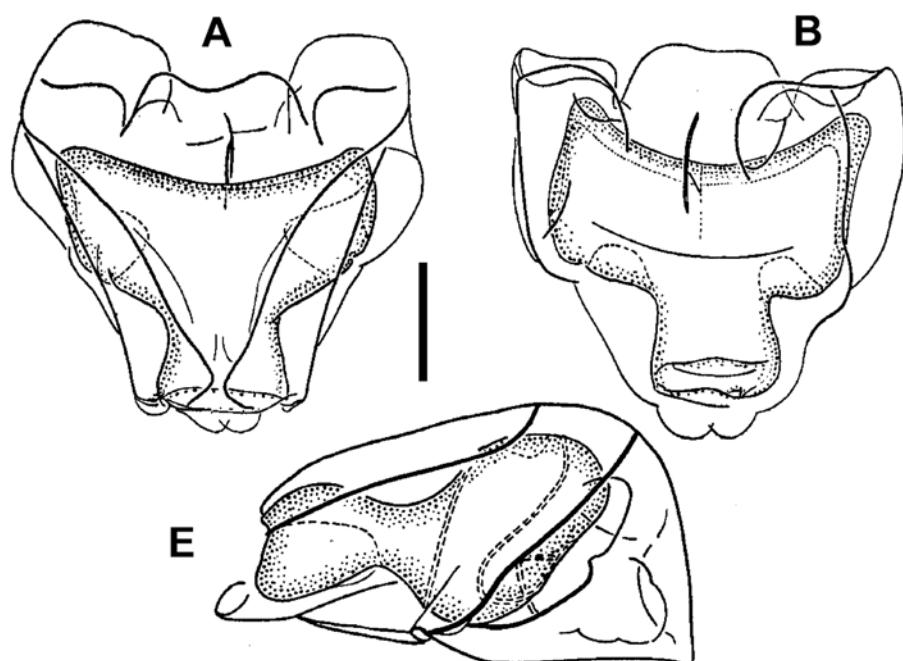
Lens & van Riemsdijk's specimen was re-examined by one of us (PRP) many years ago. It seemed to have deteriorated over the years possibly because the tube it was contained in probably had once been stoppered with cotton wool, as such fibres were very prevalent. This is one of the worst things that you can do to a siphonophore specimen as the finer parts tend to become entangled in the wool and are difficult to recover. It appears that with regard to the specimen of *Halistemma cupulifera* no attempt was made to retrieve the entangled pieces, as there were no signs of any tentilla whatsoever with the type specimen. In addition only one mutilated bract was found, which bore no resemblance to that which they illustrated. Nonetheless there were several gastrozooids and numerous palpons, many of which possessed an obvious palpacle, so it is unclear why Lens & van Riemsdijk did not notice them. Some developing female gonophores were also present.

Thus, unfortunately, it was not possible to confirm the two most characteristic features of the specimen as described by Lens & van Riemsdijk (1908), that is the structure of the tentillum and of the bract. So we will have to rely on what the authors originally said. The acorn-like structure of the terminal process of the tentillum is, indeed, very distinctive and, although other *Halistemma* species have been found to have a similar structure, it is not as large as in this species. The only major difference between our material and that of Lens & van Riemsdijk is that whereas they considered that an involucrum was absent on their tentilla it is clearly present on ours (see Figure 34), although barely covering the most proximal spiral of the cnidoband. However, if one looks closely at Lens & van Riemsdijk's Plate XVI, figure 117 (see Figure 37, bottom left), and we are grateful to one of the referees for pointing this out, there does appear to be a small flap of tissue covering the base of the cnidoband. Nonetheless, the involucrum is a very delicate structure and, as noted above, several earlier authors failed to note its presence in *H. rubrum*. Thus, we are satisfied that the specimens that we have described here belong to *Halistemma cupulifera*. Although this is the first time that the nectophores of *Halistemma cupulifera* have been described under that specific name, they have probably been illustrated previously by Totton (1954, Text—fig. 16, A, B, E) as his "e-type" *H. rubrum*. Comparisons between his illustrations (see Figure 38) and our Figure 29 will demonstrate the

many similarities, for instance the sizes and relationships of the axial wings and the thrust block, and the way that the lateral ridge distinctly diverges away from the vertical lateral one, with both being joined to the apico-lateral one.



**FIGURE 37.** *Halistemma cupulifera* Lens & van Riemsdijk (1908). Figures 116–119 from their Plate XVI.



**FIGURE 38.** "e-type" nectophores, probably of *Halistemma cupulifera*, from Totton (1954, Text—fig. 16, A, B, E). Scale bar 2 mm.

We also believe that a nectophore of this species was described and illustrated by Margulis (1976) under the name *Paragalma birsteini*. This species undoubtedly shows characters of the genus *Halistemma*, particularly with regard to the arrangement of the lateral radial canals and ridges. Although her illustrations (see Figure 10) showed neither the lateral nor the vertical lateral ridges reaching the upper lateral one, while in several *Halistemma* species, including *H. cupulifera*, they both do, the general morphology of the nectophore, particularly the mouth plate, has led us to conclude that it most likely belongs to *H. cupulifera*, and accordingly we consider it to be a questionable junior synonym of that species.

**Distribution:** The type specimen of *Halistemma cupulifera*, from *Siboga* St. 244, was collected just south of the Moluccas in Indonesia. The JSL specimen came from the Gulf of Mexico, west of the Dry Tortugas, while the four other specimens examined came from the North Atlantic Ocean; one at the shelf break to the south west of Ireland, one from off Portugal, one from the mid-Atlantic at 40°N, and one from the Cape Verde Islands. In addition, another North Atlantic specimen was collected by a SCUBA diver at 20 m depth in the Sargasso Sea (24°52.13'N, 60°29.32'W) (Pagès & Madin, 2010). Johnsen & Widder (1998) mentioned three specimens of *H. cupulifera* caught by a Tucker trawl in the eastern Gulf of Mexico, but the provenance of their identifications is not known.

Kawamura (1954) mentioned having caught a single specimen, which he referred to as *Stephanomia cupulita* off Misaki, Japan in April 1909, which had six fully-grown nectophores, and bracts 10–13 mm long and 6–8 mm wide but, apart from mentioning the distinctive terminal processes to the terminal filaments of the tentilla, that was the extent of his description. It is a pity that this was not one of Kawamura's specimens re-examined by Pagès (2002). Dhugal Lindsay (personal communication) noted that *Halistemma cupulifera* was present in large numbers north of Osprey Reef (off Queensland, Australia) in late July, 2012.

The "e-type" *Halistemma rubrum* that Totton (1954) illustrated came from *Discovery* St. 1585 at 0°06'S, 49°45.4'E, between Somalia and the Seychelles in the western Indian Ocean. It is not clear whether Totton's other Indian Ocean specimens of *H. rubrum* also belong to this species, with the exception of that from *Discovery* St. 1586, which belongs to the new *Halistemma* species described herein. The other Indian Ocean specimen that we, questionably, ascribe to this species, the *Paragalma birsteini* of Margulis (1976) came from *Petr Lebedev* St. 11 at 7°39'N, 87°54'E, which Margulis said was in the North western Indian Ocean. However, the position given is midway between Sri Lanka and the Nicobar Islands, which would be difficult to classify in the terms used by Margulis.

Alvariño *et al.* (1990), as referenced by Pugh (1999a), claimed to have identified specimens of *H. cupulifera* collected at epipelagic depths off Chile at c. 40°S, between 81 and 90°W, and between Chile and the Antarctic Peninsula. However, like all Alvariño's identifications, these must be treated with a great deal of caution, and need confirmation if the specimens still exist.

Thus, leaving apart the questionable records of Alvariño *et al.* (1990), *Halistemma cupulifera* has been collected in three very disparate regions; in the western Pacific regions of Indonesia, the Coral Sea and Japan; in the western Indian Ocean; and in the North Atlantic Ocean and the Gulf of Mexico.

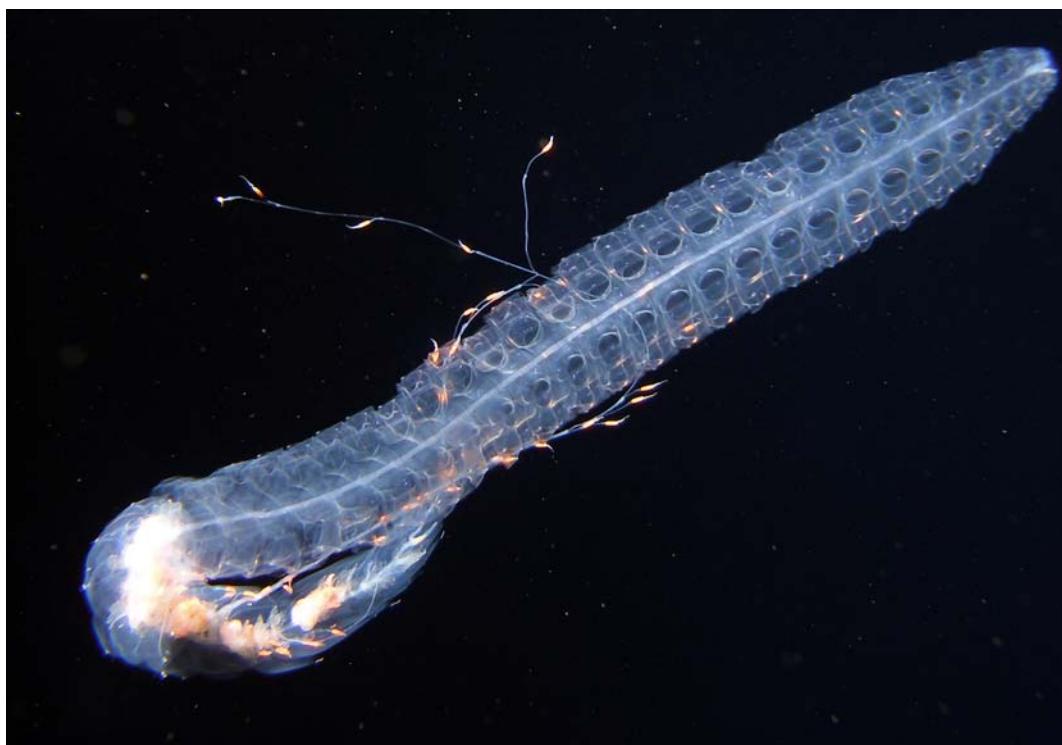
### ***Halistemma striata* Totton, 1965**

*Halistemma striata* Totton, 1965, pp. 59–60, text.—fig. 24; Margulis, 1969, p. 23, fig. 2 (4,5); Stepanjants, 1977b, p. 61, fig. 3В–Д ; Pugh, 1999a, p. 482, fig. 3.12.

**Diagnosis.** Nectophores with four pairs of vertical lateral ridges. The proximal three are complete, uniting with both the upper and lower lateral ridges, while the most distal arises from the lateral ridge, a short distance after the latter divides from the upper lateral ridge, and does not join with the lower lateral ridge. The lateral ridge is complete, reaching the ostium. Close to the ostium the upper lateral ridges diverge and run laterally before petering out. Two types of adult bract, with the Type A bracts having two different forms. Tentilla with small involucrum covering the proximal 1.5 spirals of the cnidoband. Terminal filament without cupulate process at distal end.

**Material examined:** Two specimens collected by the Johnson-Sea-Link (JSL) submersibles; one from the Bahamas and from off the Florida coast in the Gulf of Mexico.

JSL II 990-SS12	29 October 1984	25°22.5'N 77°54.5'W	depth 706 m
JSL I 2664-DS8	16 September 1995	c.27°0.0'N c85°0.0'W	No depth recorded



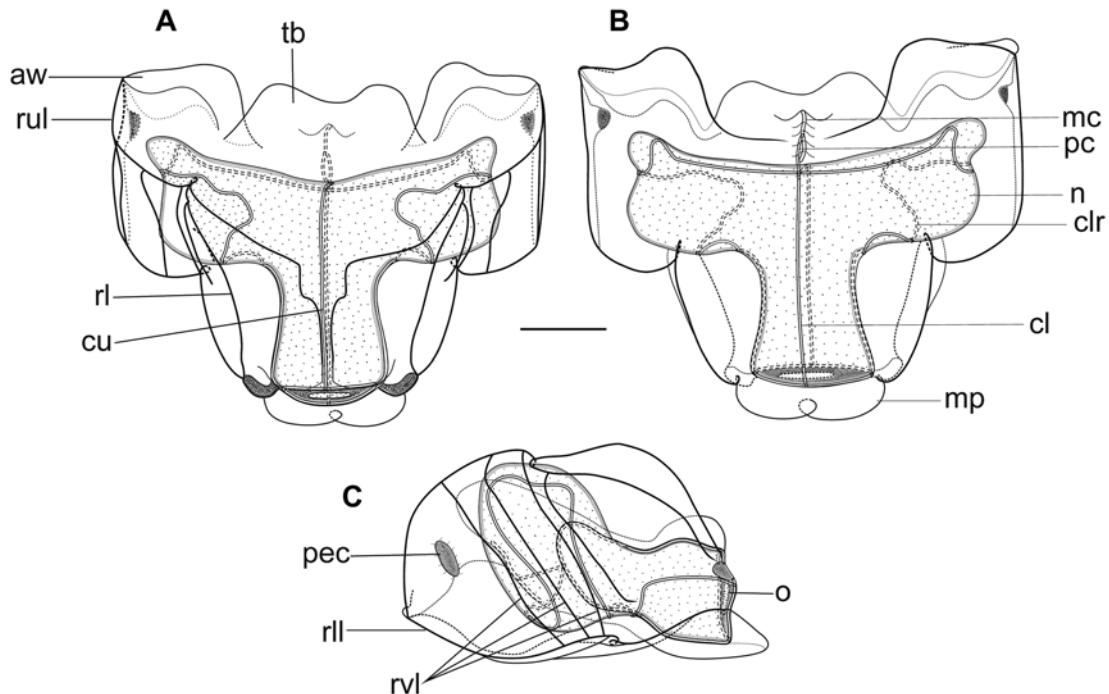
**FIGURE 39.** A probable specimen of *Halistemma striata*. Scale not known. © Dr. Mark Benfield and the Gulf SERPENT Project.

**Description:** The description will be based entirely on the JSL II Dive 990-SS12 specimen, although not all of the specimen was preserved, as the other is even less complete and in poor condition. Photographs of this specimen were taken, but they are not good enough to reproduce. However, an *in situ* photograph of what most likely is *Halistemma striata*, although it was not collected, was kindly sent to me by Dr. Mark Benfield and is reproduced as Figure 39. It was taken in the Gulf of Mexico at 26°52.69'N, 93°16.13'W at 768 m, during the Gulf SERPENT Project. The whole specimen and, in particular, the robustness of the bracts, together with the long patches of nematocysts at their distal tips bears a close resemblance to the photographs of the JSL II Dive 990-SS12 specimen. Although the bracts of *H. rubrum* also have relatively long patches of nematocysts the bracts are small and less robust (see video).

**Nectosome:** The nectosome and pneumatophore for both specimens was not found with the preserved material and so it was not possible to confirm that nectophores were budded off on the dorsal side of the stem. However, at least six specimens of *Halistemma striata* were collected at Discovery St. 10523#6 (see below) and these had pneumatophores measuring c. 1.45 mm in length and 0.75 mm in diameter, and it was also clear that the nectophores were attached to the dorsal surface of the stem.

**Nectophores:** No nectophoral buds or young nectophores were found with the specimen, and the eighteen preserved nectophores were all of a similar size, with a maximum length of 23 mm and a maximum width of 25 mm (Figure 40). The ridge pattern is characteristic for the species. There were four vertical lateral ridges on each side. The three more proximal ridges were complete, running obliquely down the lateral sides of the nectophore from the upper lateral ridge to the lower one at an angle of c. 30°, as Totton (1965) noted. The most proximal bent slightly distad close to its junction with both the upper and lower lateral ridges. The next bent distad close to the upper lateral ridge, while the third was almost straight. In the preserved state, this pair of ridges was found in the depths of furrows running down the sides of the nectophore, but this was probably a preservation artefact. The distal-most ridge that branched from the upper lateral soon bifurcated to form the fourth vertical lateral ridge and

the lateral one. The vertical lateral one continued obliquely down the side of the nectophore but before reaching the lower lateral it curved toward the ostium and petered out. The lateral ridge ran in a broad arc toward the ostium, and formed part of the edge of the large lateral ostial process.



**FIGURE 40.** Upper (A), Lower (B), and Lateral (C) views of a mature nectophore of *Halistemma striata*. For Legend see Figures 14 and 29. Scale bar 5mm.

The axial wings were prominent, but quite short, and were truncated proximally, while laterally they were triangular in shape. Approximately in the middle of this lateral facet was an elongate concavity that was lined with ectodermal cells, which probably were sites of bioluminescence. These were the only patches of cells found on the nectophores. The broad thrust block did not extend, proximally, as far as the axial wings and had a wide median emargination.

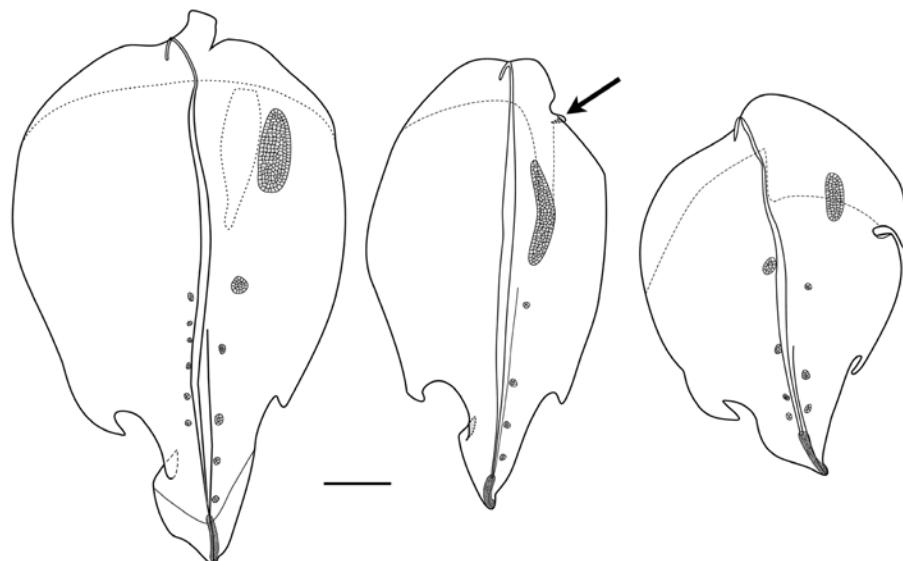
The ascending branch of the mantle canal was slightly longer than the descending one, and in the preserved state it ran along a raised process on the lower side of the thrust block. The pedicular canal was about half its length. The latter reached the nectosac on its lower side, just below its apex, and immediately gave rise to the four radial canals. The lateral radial canals followed the typical *Halistemma* course, looping outward and slightly downwards toward the lateral sides of the nectosac; then looping up and down the lateral sides, passing briefly onto the lower side of the nectosac, before looping up to the mid height of the nectosac and travelling directly to join the ostial ring canal. Minor sub-loops were noted in several specimens.

**Siphosome:** The siphosome was relatively wide and robust, with the large bracts entirely covering the other zooids. The cormidia, even in the contracted state, were quite clearly separated from each other; although the arrangement of the zooids within each cormidium was difficult to discern.

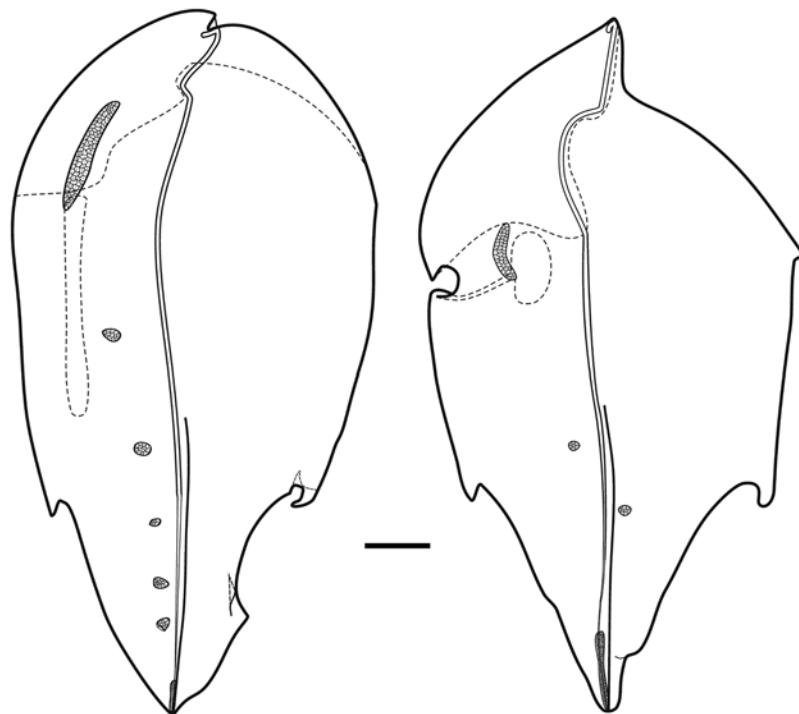
**Bracts:** There were basically two types of bract, although one, the Type A was present in two forms.

**Type A**—These bracts were robust measuring up to 63 mm in length and 32 in width (Figures 41–42). They were widest toward the proximal end, while the distal end came to a point. Both forms of this bract had a weak median ridge in the distal half, where a pair of prominent, asymmetrically placed lateral teeth was present. There was a large patch of ectodermal cells, probably sites of bioluminescence, on one side of the bract in its proximal half, and up to six pairs of smaller rounded patches on either side of the mid-line in the distal half. At the distal end of the bract in the mid-line, there was a long narrow strip of nematocysts. The bracteal canal ran the full length of the bract and, particularly in the younger bracts (Figure 41C) it was thickened for most of its length, but narrowed both proximally and distally. Proximally it ran up onto the upper side of the bract for a short distance and remained in contact with the lower wall of the bract for most of its length. Just before reaching the level of the proximal end

of the patch of nematocysts it penetrated into the mesogloea and as a narrow canal continued obliquely upwards to the upper surface, where it continued below the nematocysts to the distal tip.



**FIGURE 41.** *Halistemma striata*. Upper views of young Type A bracts. Type A-1 (left and centre), Type A-2 (right). Proximal at top, distal at bottom. Scale bar 5 mm.

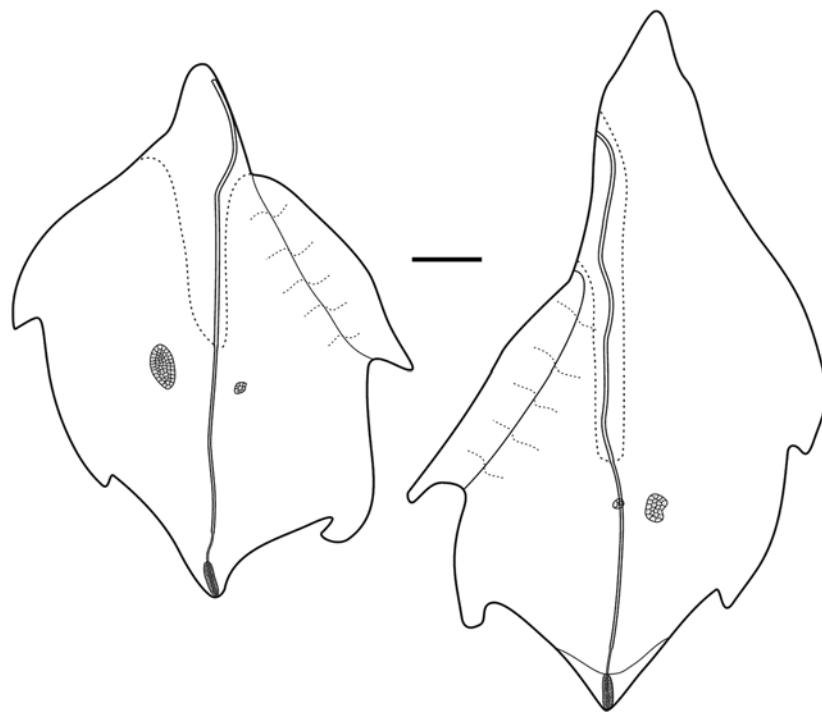


**FIGURE 42.** *Halistemma striata*. Upper views of mature Type A-1 (left) and A-2 (right) bracts. Proximal at top, distal at bottom. Scale bar 5 mm.

Type A-1. In addition to the pair of lateral teeth, on one side of the triangular distal process there was a distinct point, where the lateral walls of the bract overlapped each other. Usually the proximal patch of ectodermal cells was more elongate and less wide than that on the Type A-2 bracts. On the lower side of the bract the mesogloea was distinctly thickened close to the proximal end, being more extensive on the side where the ectodermal patch was present on the upper side. There was also a distal extension of thickened mesogloea on that side that continued for some distance down the bract; either forming part of the proximal thickening or completely separate from it. The distal strip of nematocysts was shorter than in the Type A-2 bracts.

One of the younger bracts (Figure 41 centre, arrowed) had a small, lateral cusp-like structure close to the proximal end, which somewhat resembled the situation in the *Type A-2* bracts. However, this was unusual and, by the distal lateral process, it clearly was a *Type A-1* bract.

*Type A-2*. The main difference that these bracts showed from the previous ones was the presence, proximally and on one side, of a distinctive circular indentation. The thickening of the mesogloea on the lower side was also arranged differently, being also exclusively on the same side as the indentation and proximal to it. A shorter distal extension was also present, but it lay closer to the mid-line.



**FIGURE 43.** *Halistemma striata*. Type B bracts—upper views. Proximal at top, distal at bottom. Scale 5 mm.

**Type B**—These bracts measured up to 52 mm in length and 29 mm in width (Figure 43). They were distinctly asymmetrical, foliaceous and pointed at both ends. There were two pairs of large asymmetrical lateral teeth, and a pair of ectodermal cells, of distinctly different sizes on the upper side in its distal half. The inner side of the bract, from distal to the origin of the bracteal canal to the more proximal lateral tooth, was distinctly thinner than the rest of the bract and formed a flap. The bracteal canal arose on one side of the pointed proximal end and, as with the Type A bracts it ran along the median lower surface for most of its length, before narrowing and running obliquely up through the mesogloea to reach the relatively short strip of nematocysts, under which it continued to the distal tip. The type of nematocysts present was not investigated. In the proximal half of the bract, the canal was raised on a thickened mesogloal process.

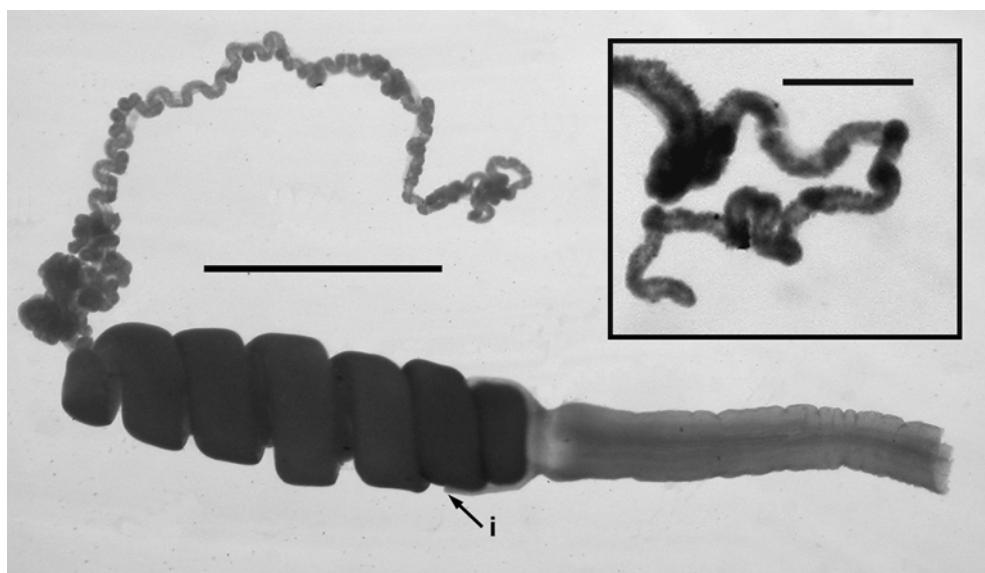
**Gastrozooid and tentacle:** The large gastrozooids showed no unusual features, while the tentacles, in their preserved and contracted state, were relatively thickened with musculature (Figure 44). The photographs of the JSL II Dive 990-SS12 specimen show that the basigaster was deep red in colour, while the stomach region was milky white.

**Tentilla:** A mature tentillum is shown in Figure 45. In life the cnidobands were orange in colour, while the terminal filaments were white. The long, thick, rigid in preservation, pedicel ended distally in a small involucrum, which covered the proximal 1.5 spirals of the cnidoband (Figure 45 i). The latter consisted of up to ten spiral coils, particularly in the JSL Dive 2664 specimen, although c. 7 was more common in the JSL Dive 990 one. There were relatively few, but large stenoteles, measuring c. 92 x 40 µm, confined to the sides of the proximal end of the cnidoband. The remainder of the cnidoband was filled with innumerable banana-shaped nematocysts, presumably anisorhizas that measured c. 81 x 12.5 µm. Within the cnidoband the double elastic band was very prominent. The terminal filament contained two types of nematocysts, which as discussed above were presumably acrophores and

desmonemes, measuring c.  $31 \times 11$  and c.  $25 \times 10.5 \mu\text{m}$ , respectively. The long, loosely and irregularly coiled terminal filament did not end, distally, in a cupulate process, but was just rounded off (Figure 45, inset).



**FIGURE 44.** *Halistemma striata*. Thickened tentacle bearing tentilla on long pedicels. Scale bar 5 mm.



**FIGURE 45.** *Halistemma striata*. Individual tentillum (scale bar 5 mm), with (inset) detail of terminal filament (scale bar 2 mm.) i indicates the distal most tip of the involucrum.

**Palpons:** The thin-walled palpons (Figure 46) were generally featureless, but were clearly divided into a narrow tubular proximal region and an expanded distal part, with a distinct terminal proboscis surrounding the terminal opening. In their preserved state many palpons exceeded 15mm in length. At their base they bore a long palpacle. No nematocysts were found on either the palpon or the palpacle.

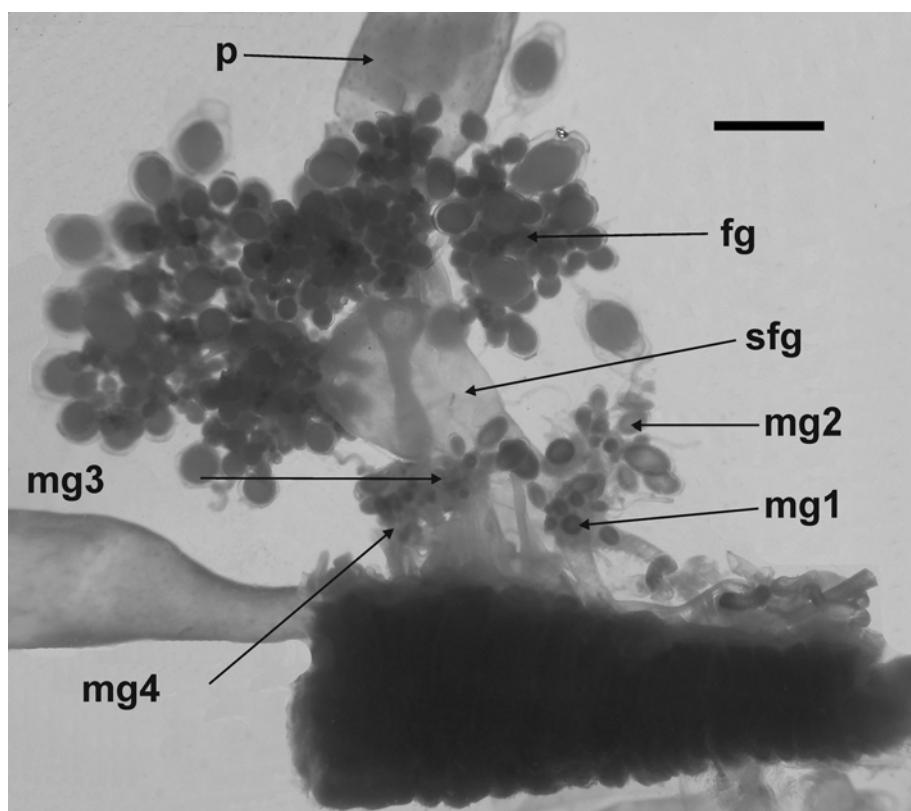
**Gonophores:** The female gonodendron was borne on a very broad, long but thin-walled stalk (Figure 47), with strengthening rings towards its base. This usually divided into two main branches on which the racemes of female gonophores were arranged. Mature female gonophores were quite variable in shape measuring up to 3 mm in length and 2 mm in width, and had a broadly open distal orifice (Figure 48).

There were four male gonodendra in each cormidium, which is the most that have been observed for any

*Halistemma* species. *H. rubrum* is the next most complex (see also the discussion regarding gonodendra in *H. foliacea*), which has three. All the other species, where known have a single male and a single female gonodendron, with the male one anterior to the female. For *H. striata* there is one male gonodendron anterior to the female one, alongside which sits the second male one. Then there are two further male gonodendra posterior to the female one.



**FIGURE 46.** *Halistemma striata*. Palpon and palpacle. Scale bar 5 mm.



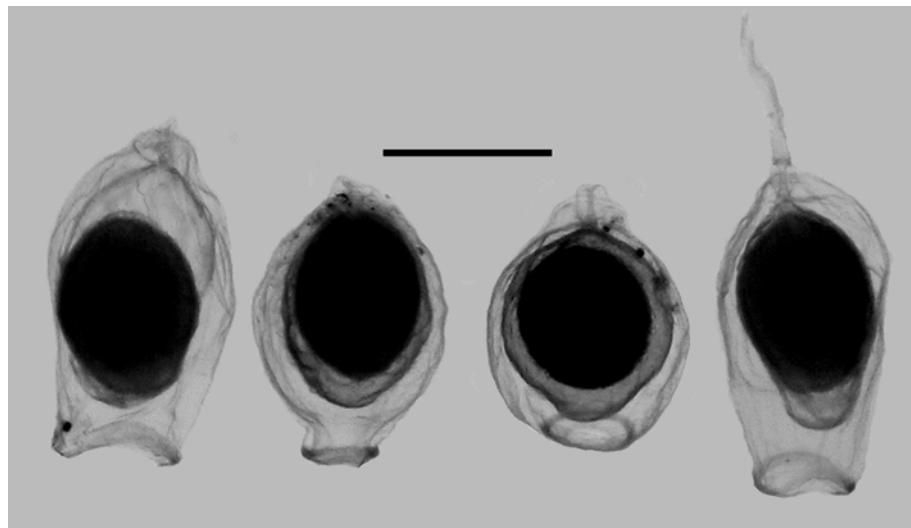
**FIGURE 47.** *Halistemma striata*. Part of partially denuded siphosome (anterior to the right). fg: female gonodendron, with gonophores borne on a broad thin stalk (sfg); mg: male gonodendra 1, 2, 3 and 4; p: palpon. Scale bar 2 mm.

The male gonophores were long and cylindrical, measuring up to 4.5 mm in length and 1.6 mm in diameter (Figure 49), and possessed long proximal pedicels. Distally the mouth opening was wide open, like that of the female gonophores. The gonodendral cluster usually consisted of a small bundle of gonophores, usually consisting of a mature one distally and a group of developing gonophores proximally.

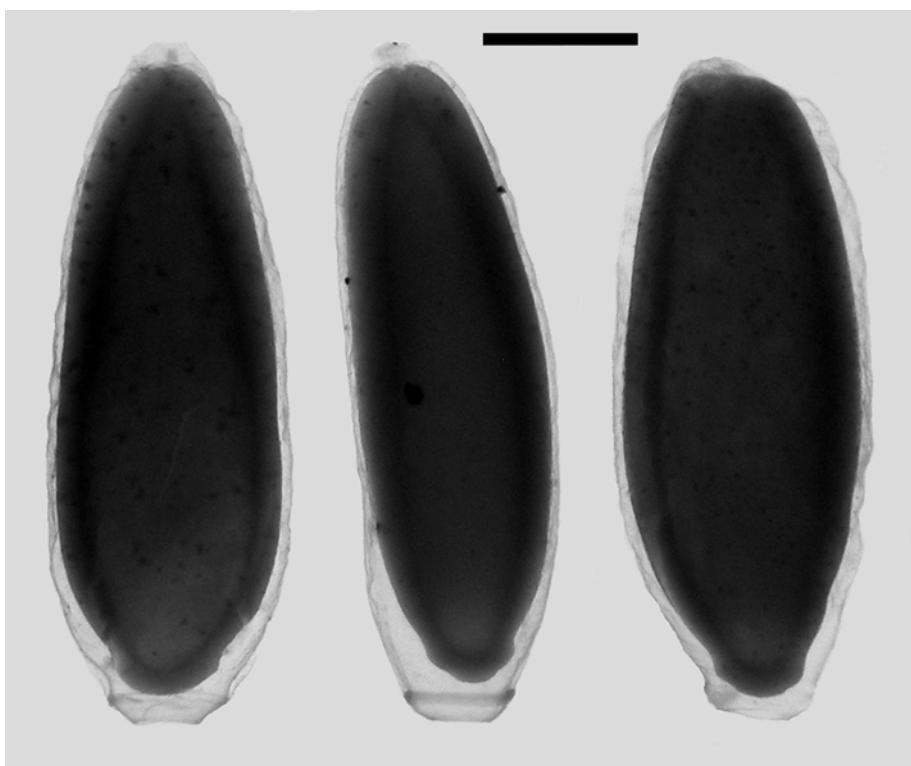
*Nectalia*-stage: Neither of the JSL specimens was at the *Nectalia* post-larval stage.

*Remarks:* The nectophores of *Halistemma striata* are easily identified by the presence of four pairs of vertical lateral ridges. They are also the largest of any *Halistemma* species, and the largest nectophores in the present

material, measuring 25 m in width, were considerably larger than the range of 8–19 mm for Totton's (1965) original material. They are slightly larger than the nectophores of *H. foliacea*, but that species has just two pairs of vertical lateral ridges. The Type A-2 bracts are also very distinctive, as is the distal end of the terminal filament of the tentillum. In most *Halistemma* species there is a cupulate process present, which differs morphologically from species to species. In *H. rubrum* the terminal filament ends in a tightly coiled tapering process, while in *H. striata* no distinct process is present.



**FIGURE 48.** *Halistemma striata*. Individual female gonophores. Scale bar 1 mm.



**FIGURE 49.** *Halistemma striata*. Individual male gonophores. Scale bar 1 mm.

*Distribution:* Totton's (1965) original material came from the Beebe collections centred around 32°12'N, 64°36'W south of Bermuda, and two *Discovery* stations, in the central south (*Discovery* St. 81, 32° 45'S, 8° 47'W), and equatorial north Atlantic (*Discovery* St. 704, 3° 37'7"N, 29° 14'W). Margulis (1969) found *Halistemma striata* at 18 sites throughout the Atlantic Ocean, all but two of which were found between 40°N and 20°S; the others

being at c. 56°N, 21.5°W and 42°S, 38.5'W. Stepanjants (1975) had another Atlantic record, from north of Puerto Rico. It has also been found in eight recent *Discovery* samples, shown in decreasing latitudinal order:

Station	Nect	Bract	Date	Latitude	Longitude	Depth Range (m)
7711#09	5		18-May-1971	52°50.5'N	20°09.3'W	605–700
9791#10	4	12	06-May-1978	49°28.5'N	14°00.8'W	500–600
53305#32	1		21-Apr-1994	49°14.1'N	12°15.2'W	200–310
11058#03	1		11-Apr-1984	45°34.9'N	13°36.4'W	95–200
8508#33	48	107	16-Apr-1974	44°04.8'N	13°07.6'W	302–400
7800#02	55	138	18-Feb-1972	19°46.7'N	22°32.7'W	0–1000
7089#23	29		16-Nov-1969	17°40.7'N	25°19.7'W	110–200
6662#11	102	271	15-Feb-1968	11°03.0'N	19°52.6'W	510–590
10523#06	139	232	10-May-1982	05°41.9'S	00°29.4'E	400–500

The Beebe collections, from Bermuda, contain at least four specimens, namely:

Specimen No. 29365	600 fm	22 nectophores
Specimen No. 29372	700 fm	23 nectophores
Specimen No. 301371	600 fm	1 nectophore.
Specimen No. 312196	600 fm	6 nectophores, 2 bracts.

Stepanjants (1977a) gave the first Pacific Ocean record, from south-east of the Solomon Islands, and Margulis (1987) gave the second from the region of 41–48°S 106–110°W. Recently, Yu (2006) has added a record from Taiwanese waters, and it has also been found from Japanese waters (Dhugal Lindsay, personal communication). It has not been noted during the extensive observations in the Monterey Bay, California, region, nor in the Gulf of California. In conclusion, it appears that *Halistemma striata* is a rare species with an extensive geographical distribution, generally in the warmer waters of the World's oceans.

### ***Halistemma transliratum* Pugh & Youngbluth, 1988**

*Halistemma transliratum* Pugh & Youngbluth, 1988, pp. 1–14, figs. 1–6, 6A, 7.

**Diagnosis:** Nectophores without mouth plate. One pair of complete vertical lateral ridges. Lateral ridges extending from apico-laterals almost to ostium, ending on lateral ostial processes. Apico-laterals divide close to the ostium, the inner pair continuing on to the ostium, while the outer pair runs out laterally. Several patches of ectodermal cells on upper and lateral surfaces. Four types of adult bract, three of which have a characteristic transverse ridge. Terminal filament of tentillum ends in small glandiform process.

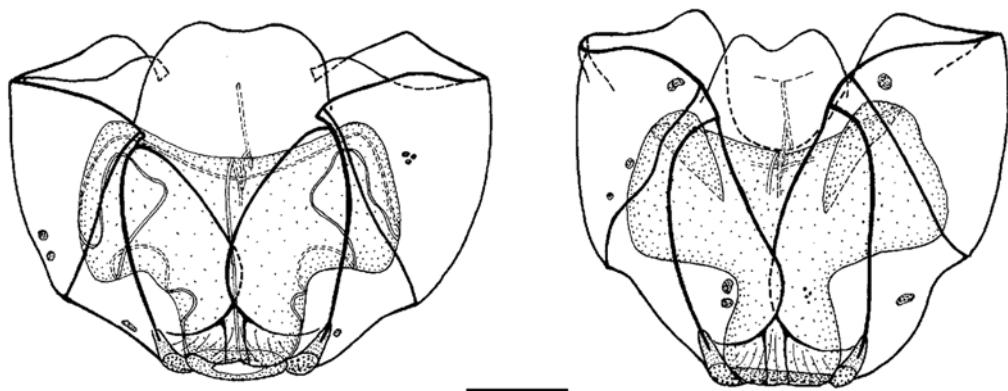
**Holotype:** Specimen collected at a depth of 472 m during JSLI Dive 628 (3 October 1981; 26°13.5'N, 77°41.8'W). Preserved in 5% buffered formalin and presented to the United States National Museum (Smithsonian Institution), USNM 78496.

**Paratype:** Specimen collected during JSLII Dive 972 at a depth of 563 m (21 October 1984; 26°24.3' N, 77°49.8'W). Presented to the British Museum (Natural History), Regd. No. 1987.4.1.1.

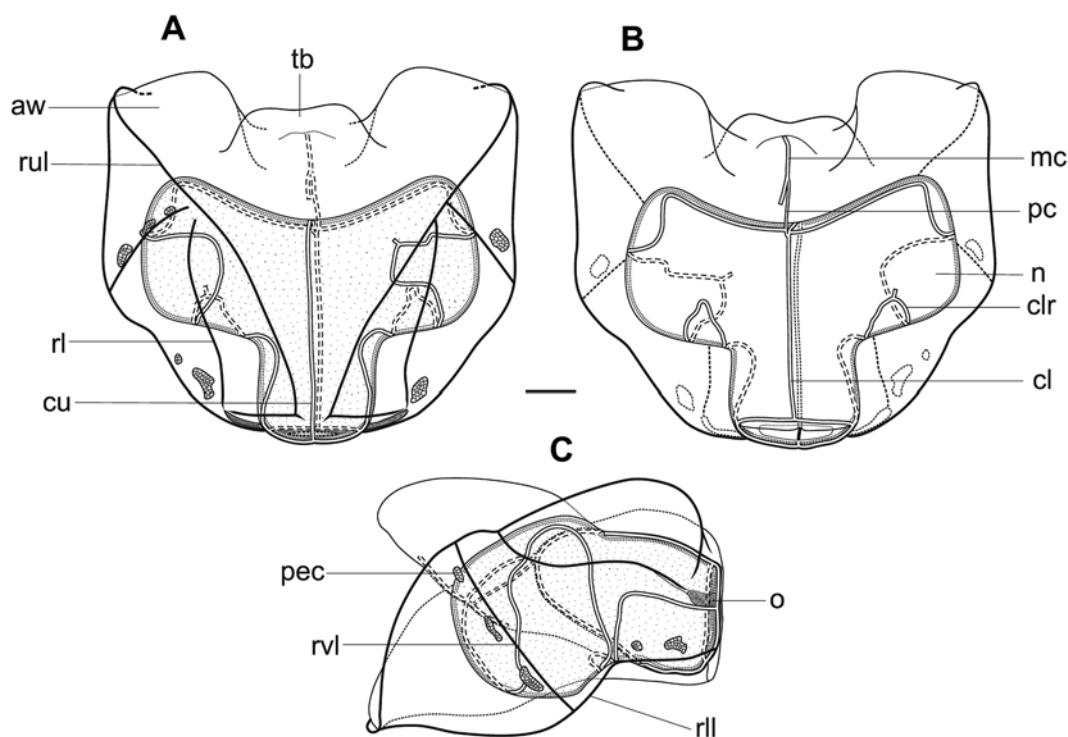
**Material examined.** The paratype specimen has been re-examined, together with pieces of other specimens found in 25 recent *Discovery* hauls (see below).

#### *Description.*

**Pneumatophore:** Borne on a long stalk, with no characteristic features.



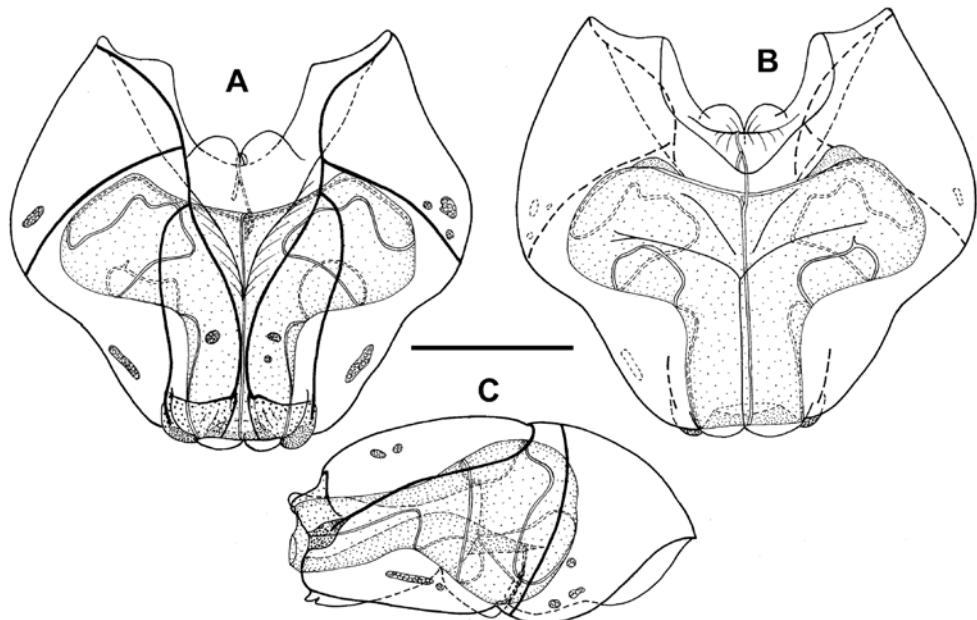
**FIGURE 50.** *Halistemma transliratum* Upper views of mature nectophore from holotype. Scale bar 3 mm. From Pugh & Youngbluth (1988).



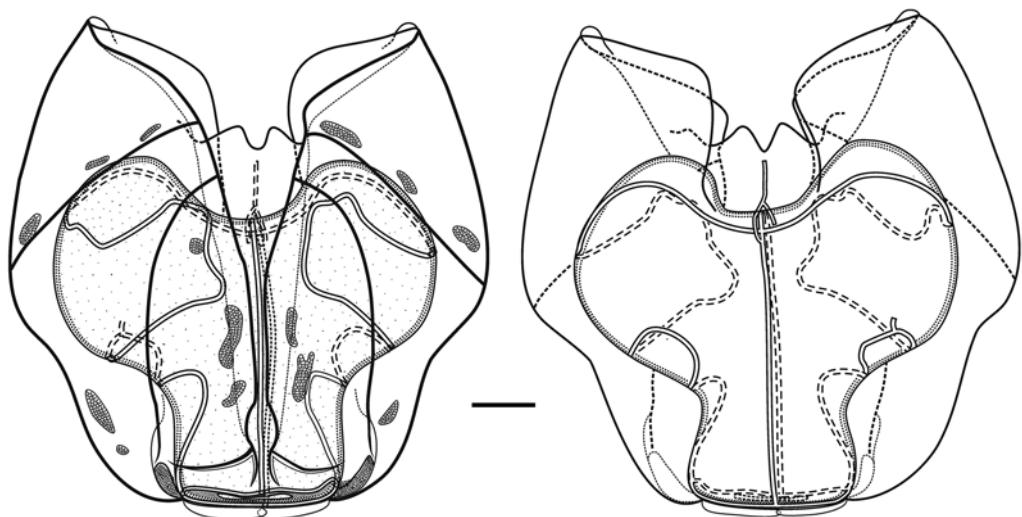
**FIGURE 51.** *Halistemma transliratum*. Upper (A), lower (B) and lateral (C) views of mature nectophore from paratype specimen. For Legend see Figure 14. Scale bar 1 mm.

**Nectophores.** (Figures 50–53) Fifteen nectophores, which measured up to 13 mm in length and 13.4 mm in width, were present with the holotype, and seven with the paratype. The number of nectophores found in individual *Discovery* samples ranged from 1 to 93 (see Table 1 below), but it was impossible to say exactly how many specimens were present in each of the 25 samples collected. The basic *Halistemma* ridge pattern was present. The pairs of upper and lower laterals joined at the lateral corners of the axial wings and continued for a short distance as a single ridge. The upper laterals converged as they passed over the upper surface of the nectophore and in many of those from the holotype specimen, shortly above the ostium, they overlapped one another before diverging again (Pugh & Youngbluth, 1988). A short distance above the ostial level they divided, giving off a long lateral branch and a much shorter descending one. In the original description Pugh & Youngbluth (1988) suggested that the latter branch continued down to the ostium, but the recent examination of the paratype suggests that this is an artefact, and that the ridge is very short (Figures 50 & 51). The lateral branch passed outwards, parallel to the ostium and petered

out just before reaching the tips of the lateral ostial processes. During their course the pair of upper lateral ridges gave rise to the vertical lateral and lateral ridges. Each vertical lateral ridge ran, slightly diagonally, down the lateral margin of the nectophore to join with the corresponding lower lateral ridge. Similarly, each lateral ridge ran obliquely toward the ostium and ended at the tip of the corresponding enlarged lateral ostial process. The lower lateral ridges, from their junction with the upper laterals, ran along the lower lateral margin of the nectophore to reach the ostium.



**FIGURE 52.** *Halistemma transliratum*. Young nectophore from holotype. A. upper, B. Lower, and C. Lateral views. Scale bar 3 mm. From Pugh & Youngbluth (1988).



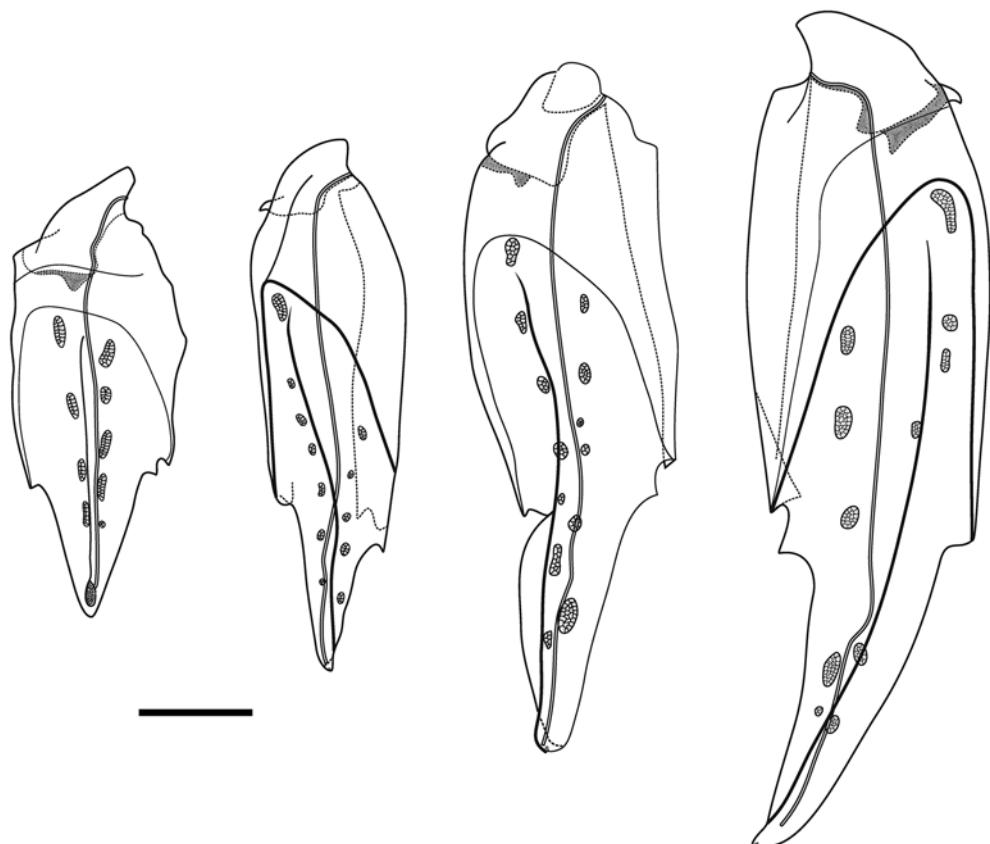
**FIGURE 53.** *Halistemma transliratum*. Upper (left) and lower (right) views of a younger nectophore from the paratype specimen. Scale bar 1 mm.

In young nectophores the thrust block was small and deeply emarginated centrally (Figures 52 & 53). However, as the nectophores matured the thrust block increased considerably in both width and height and could extend further than the axial wings, which did not increase much in size as the nectophore enlarged. A small mouth plate was present on the lower side of the ostium in the younger nectophores, but this virtually disappeared as the nectophores matured. The lateral ostial processes were quite extensive, but it is not known if these bore nematocysts as very young buds of nectophores were not found. The patches of ectodermal cells were more numerous on the young nectophores of the paratype specimen than those previously described from the holotype. A

row of up to five patches was arranged parallel to the vertical lateral ridges. In addition, a pair of patches, often quite elongated, appeared above the infra-lateral ridge on the lateral sides close to the ostium, and several patches could occur just lateral to the apico-lateral ridges in the distal half of the nectophore. All these patches became very indistinct on the mature nectophores of the paratype.

The ascending branch of the mantle canal was approximately twice the length of the descending one. Pugh & Youngbluth (1988) noted what they thought to be a thin canal arising from the base of the descending mantle canal, which ran along the mid-line of the lower side of the nectophore apparently to reach the ostial ring canal. This, of course, is not a canal but a giant nerve fibre that, for instance, Mackie (1973) described in the nectophore of *Nanomia bijuga*.

The long pedicular canal reached the nectosac on its lower side just below its median apex, but did not give rise directly to all four radial canals, only the upper and lower ones. The lateral radial canals arose a short distance along the upper canal either together, as in the younger nectophores of the paratype, or asymmetrically, as for the more mature ones. For the paratype nectophores (Figure 53) the course of the lateral radial canals was often quite irregular and, occasionally, small diverticula could be seen branching off at various places along their length. At first the lateral canals were directed out toward the lateral margins of the nectosac but, before they reached it, they made a short loop down toward the ostium, before looping out and up on to the lateral surfaces of the nectosac. There they made a large loop up and down, followed by a small loop on the lower surface before returning to the mid-height of the nectosac and then running directly to join the ostial ring canal.



**FIGURE 54.** *Halistemma transliratum*. Type A bracts—upper views. Scale 5 mm. Redrawn from Pugh & Youngbluth (1988).

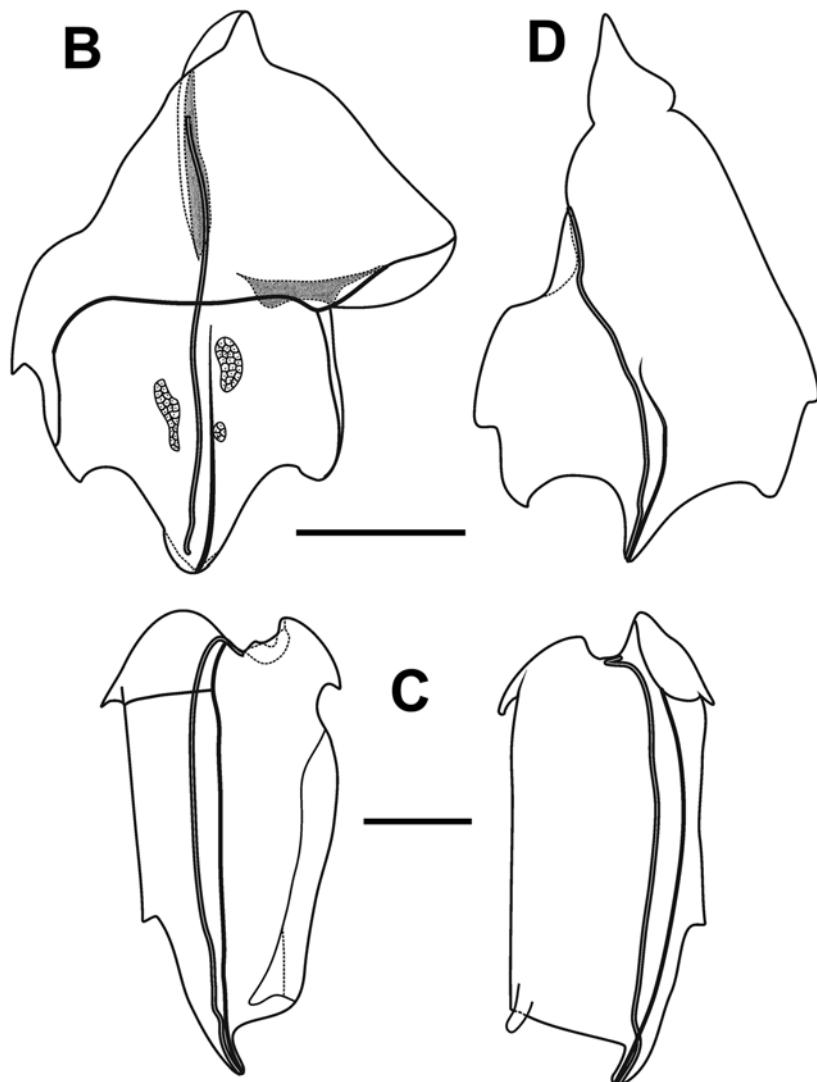
#### *Siphosome:*

*Bracts.* At least four kinds of adult bract were found with the holotype specimen.

Type A bracts (Figure 54) were elongate and lanceolate, measuring up to 41 mm in length. They resembled the larval bracts of other species, but were easily distinguished by the inverted U-shaped ridge running transversely across the upper surface. There was also a median ridge on the upper surface running from just distal to the transverse ridge down to the distal tip of the bract. In addition, toward the proximal end of the bract there was a small flap on one side on its lower side. Numerous patches of ectodermal cells were found on the upper surface,

often with an almost biserial arrangement. The distal portion of the bract, which was triangular in cross section, was a long tapering process that occupied about the distal third of the total length. Its proximal end was demarcated by a pair of lateral teeth and a third tooth, on the inner side, was present.

The bracteal canal ran from close to the proximal end of the bract down to the tip of the long distal process. It penetrated into the mesogloea about half way down the distal process and ended below a small, terminal cup-shaped indentation. No nematocysts were noted amongst the cells present in this indentation, but their presence could not be ruled out.



**FIGURE 55.** Bracts of *Halistemma transliratum*. Upper views of Type B, Type C, and Type D. Scale bars 3 mm. Redrawn from Pugh & Youngbluth (1988).

Although these bracts resembled the larval bracts of other species, they were by far the commonest of all the types of bract, which suggests that they may be present on all cormidia. At least three specimens were collected at Discovery St. 11794#27, and of the 100 bracts found 64 were Type A, 20 Type B, 2 Type C, and 14 Type D.

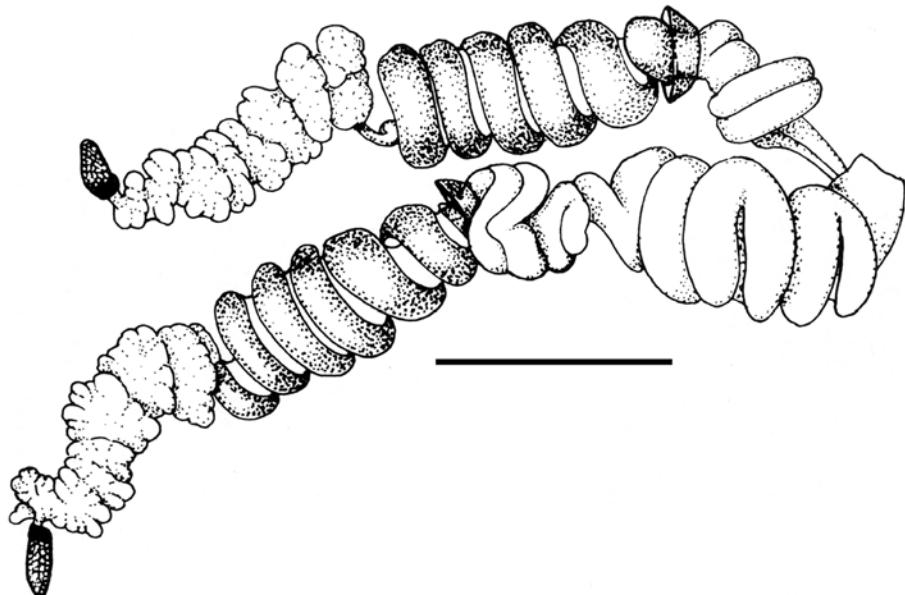
Type B bracts (Figure 55) measured up to 12.6 mm in length and occurred in enantiomorphic pairs. They were distinctly asymmetrical, with a transverse ridge on the upper side, delimiting a thickened distal facet. On one side, the ridge continued out laterally, but less distinctly, to reach the side of the bract, while on the other side there was a lateral cusp. On either side, a branch of the transverse ridge ran distally, gradually becoming less distinct. A symmetrical pair of rounded lateral cusps was present distally, with a short distal process between them. A median ridge ran, on the upper surface, from just distal to the transverse ridge to the distal end of the bract. Patches of ectodermal cells were present on the upper side of the distal facet. On the lower surface there were two flaps. One transverse one at the same level as the transverse ridge, and a median longitudinal flap in the proximal half of the bract.

The bracteal canal commenced within the groove formed by the median flap on the lower side of the bract. It penetrated into the mesogloea, roughly on a level with the two lateral, distal cusps and ran obliquely up to end below a small cup-shape indentation on the upper side of the bract close to its distal extremity. Again, this indentation contained cells, some of which may have been nematocysts.

Type C bracts (Figure 55) were the least common, and the two found with the type specimen probably represented an enantiomorphic pair, although they were by no means mirror images of each other. They measured up to 13.5 mm in length. An asymmetrically placed longitudinal ridge ran most of the length of the bract, but was indistinct proximally, where an additional, ridge ran out to one of a pair of proximal lateral cusps. Another pair of cusps, asymmetrically arranged, was present on the distal half of the bract. No patches of ectodermal cells were noted.

The bracteal canal arose in a central indentation at the proximal end of the bract and ran down to the tip of the distal process, having penetrated into the mesogloea slightly proximal to this process.

Type D bracts (Figure 55) measured up to 13.1 mm in length, and formed enantiomorphic pairs. In outline they appeared almost symmetrical, and distally there were two pairs of rounded lateral cusps, and a short median ridge on the upper side. However, the bracteal canal did not run down the centre of the bract, but arose on the inner lateral margin of the bract at about one-third to one-half its length. It then ran down to the end of the pointed distal process. A single patch of ectodermal cells was found on the upper surface of one of the three bracts of this type found with the type specimen, but Pugh & Youngbluth (1988) did not state its position, and none was present on the *Discovery* material.



**FIGURE 56.** *Halistemma transliratum* tentilla. Scale bar 1 mm.

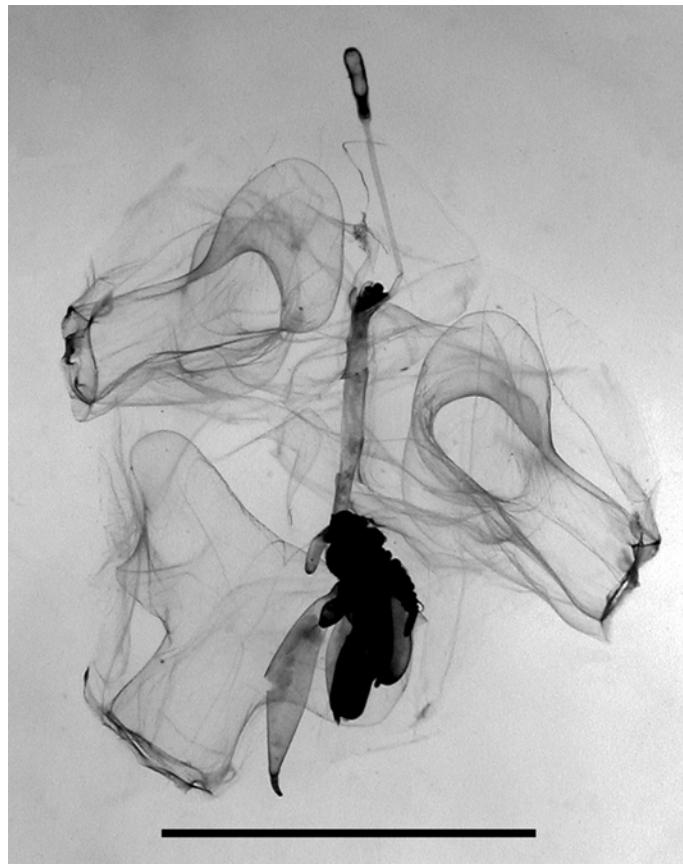
**Tentillum.** Each tentillum (Figure 56) consisted of a long pedicel, a coiled cnidoband, usually with 6 coils, and a very long terminal filament that ended in a characteristically shaped terminal process. A cup-shaped process at the base of the cnidoband represented the vestigial involucrum. The cnidoband, in life deep orange-red in colour, contained a few stenoteles, usually confined to the first few coils, and numerous anisorhizas. The terminal filament and the proximal cupulate part of the terminal process contained acrophores and desmonemes, while the distal part of the latter was devoid of any nematocysts, but included numerous platelets.

**Palpon:** Long, thin, transparent, featureless palpons borne on long peduncles. Long palpacle. No sign of nematocysts on either structure.

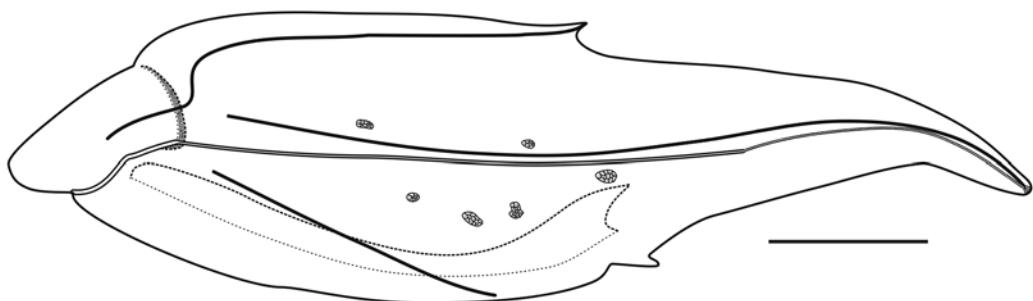
**Gonophores:** Only developing male gonophores, of typical form, were found on the siphosomal stem of the holotype specimen, and no gonophores were present with the paratype.

**Nectalia-stage:** It is probable that the paratype specimen was at the *Nectalia* post-larval stage (Figure 57), as the stem bore only a single gastrozooid and a few palpons together with seven nectophores and a Type B bract (Figure 58). The pneumatophore was c. 1.3 mm in length and 0.3 mm in diameter, with the pneumatosaccus and

gas gland clearly visible. It was borne on a long, narrow stalk, over 4 mm in length. Two other bracts were found in association with the specimen, which both resembled the Type A bract apart from the arrangement of the U-shaped transverse ridge. On the larger one (Figure 58) the transverse ridge was incomplete, and there was a distinct flap on the lower and inner side of the bract. The bracteal canal entered the mesogloea at about half the length of the distal, triangular process and ended below a small cupulate process that contained small nematocysts. The canal was thickest proximally in the region of attachment, then thinned as it continued along the lower surface of the bract, and again as it penetrated into the mesogloea and ran to the distal end. The smaller of the loose bracts had a complete transverse ridge, with the proximal end of the upper, median, longitudinal ridge joining it.



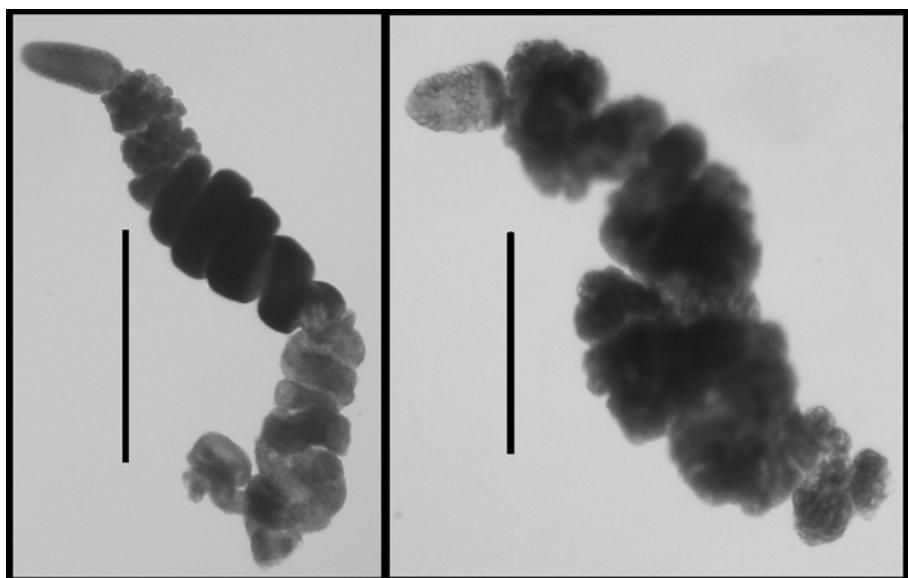
**FIGURE 57.** *Halistemma transliratum* Nectalia-stage paratype specimen from JSLII Dive 972. Scale bar 5 mm.



**FIGURE 58.** *Halistemma transliratum*. Nectalia-stage bract from JSLII Dive 972. Proximal to the left, distal to the right. Scale bar 5 mm.

At first glance, it appeared that the gastrozooid bore a few adult type tentilla, as they had a spiral cnidoband, but on closer examination, they were found to be somewhat different (Figure 59). Although they possessed a long pedicel, a rudimentary involucrum, a coiled cnidoband with 4 turns, and a long, coiled terminal filament. However, the terminal process was not of the adult-type as it consisted of a long, hollow tube devoid, as far as could be seen,

of nematocysts. The form of these tentilla is quite different from the larval tentilla found with other *Halistemma* species but, at present, we cannot be certain that this type of tentillum is a true larval one, or a stage in the development of the adult form.



**FIGURE 59.** Left. Young tentillum of *Halistemma transliratum* from the JSLII Dive 972 specimen. Scale bar 1 mm. Right. Detached terminal filament. Scale bar 0.5 mm.

*Distribution:* The two JSL specimens came from the Bahamas and were collected at depths of 628 and 563 m. Several specimens have been identified from recent *Discovery* collections:

Discovery Station	Nects	Bracts	Date	Latitude N	Longitude W	Depth range (m)
10105#23	25	24	03-Sep-1979	54°51.3'	13°09.5'	100–200
10115#23	32	39	12-Sep-1979	49°49.5'	14°07.0'	195–300
10115#07	41	26	11-Sep-1979	49°43.8'	14°05.9'	500–600
53318#04	53	48	30-Apr-1994	49°27.5'	11°32.9'	505–600
53304#18	53	35	16-Apr-1994	49°17.7'	12°50.5'	200–300
53305#02	14	14	19-Apr-1994	49°17.2'	12°17.7'	300–410
53305#32	19	8	21-Apr-1994	49°14.1'	12°15.2'	200–310
53305#23	34	19	20-Apr-1994	49°13.9'	12°17.0'	200–300
53305#35	7	1	21-Apr-1994	49°12.9'	12°16.8'	798–900
53305#31	53	26	21-Apr-1994	49°12.3'	12°17.9'	100–200
53304#28	1		17-Apr-1994	49°10.7'	12°53.6'	500–605
11794#51	32	24	28-Jun-1988	47°29.8'	19°07.4'	200–300
11794#50	42	14	28-Jun-1988	47°27.9'	19°08.3'	110–205
11794#46	2	1	27-Jun-1988	47°20.7'	19°14.8'	300–405
11794#17	40	16	24-Jun-1988	47°18.5'	19°30.9'	500–600
11794#27	84	102	25-Jun-1988	47°16.4'	19°31.1'	400–490
11794#26	19	10	25-Jun-1988	47°13.0'	19°32.6'	300–400
11058#03	40	66	11-Apr-1984	45°34.9'	13°36.4'	95–200

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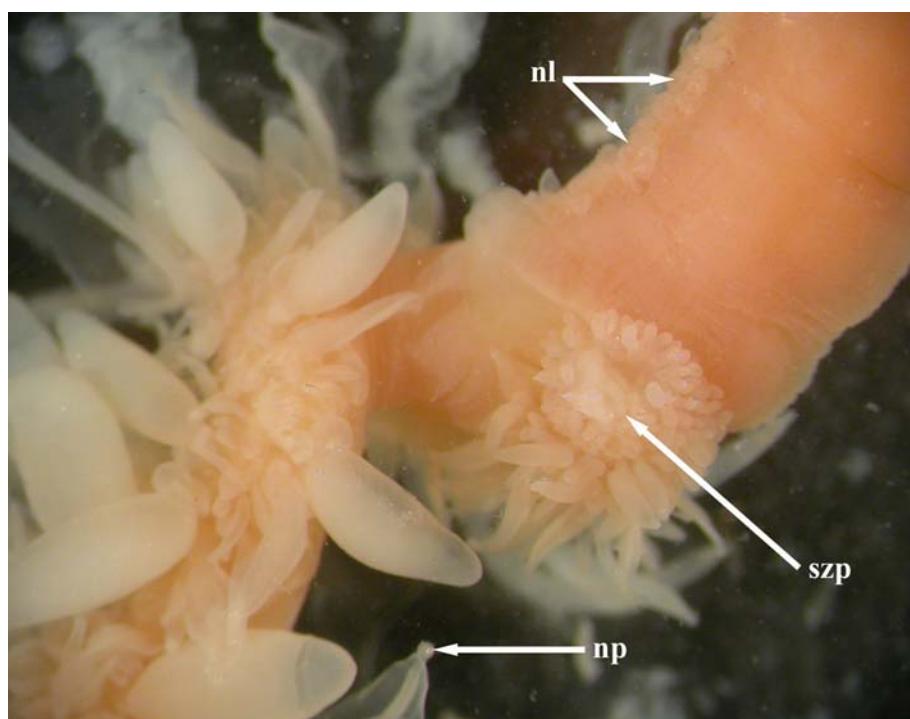
(Continued)

Discovery Station	Nects	Bracts	Date	Latitude N	Longitude W	Depth range (m)
8517#01	93	165	14-Jun-1974	44°28.9'	12°51.7'	400–500
8507#42	29	41	02-Apr-1974	44°14.9'	12°57.2'	900–1000
8507#55	26	21	07-Apr-1974	44°03'	12°46.8'	90–110
11120#02	71	64	27-May-1984	43°00.6	20°56.6'	100–550
10523#13	11	10	12-May-1982	4°54.1'S	0°23.7'	995–1100

Many of these specimens were collected in the region of the Porcupine Seabight and Goban Spur off Ireland (c. 49°N, 13°W), or at 47°N, 19–20°W (Pugh, 1990), and mainly in the 100–600 m depth range. One specimen, however, was collected in the Gulf of Guinea (c. 5°S, 0.4°W) between 995 and 1100 m. There are no other known published records, but Dr Dhugal Lindsay (personal communication) has caught a specimen of *Halistemma transliratum* in Sagami Bay, Japan. Thus the species appears to have quite a wide distribution in tropical, subtropical and temperate waters, and may exist at deeper depths in warmer waters throughout the World's oceans.

### *Halistemma foliacea* (Quoy & Gaimard, 1833 (1834))

*Stephanomia foliacea* Quoy & Gaimard, 1833 (1834), p. 74, Pl. 3, figs. 8–12; Blainville, 1834, p. 119; Lamarck, 1840, p. 28; Huxley, 1859, p. 136; Haeckel, 1888b, p. 225; Bedot, 1896, p. 384; Bigelow, 1911b, p. 355; *Stephanomia amphitridis* Huxley, 1854, p. 72, Pl. 6; Bigelow, 1911b, p. 287, Pl. 18, figs. 1–8; Kawamura, 1954, p. 110. *Phyllophysa foliacea* L. Agassiz, 1862, p. 368; Haeckel, 1888a, p. 40; 1888b, p. 225; Bedot, 1896, p. 399. *Phyllophysa squamacea* Haeckel, 1888b, p. 225. *Halistemma amphytridis* Mapstone, 2004, p. 232, figs. 1–3. *Halistemma foliacea* Pugh, 2006, p. 42. ? *Stephanomia nereidum* Haeckel, 1888b, p. 221.



**FIGURE 60.** *Halistemma foliacea*. Junction between nectosome and siphosome, with the nectophoral attachment lamellae (**nl**) on the dorsal side of the nectosome, and the zone of proliferation of the siphosome (**szp**) ventral. The distal tip of a young "dorsal" bract, showing the nematocyst-containing process (**np**), can also be seen.

*Diagnosis.* Nectophores with two, complete pairs of vertical lateral ridges. The lateral ridges do not connect with the upper lateral ones. Four types of bract, all, to a varying degree, with a distinct median keel on the lower side. The "ventral" bracts have a very characteristic semicircular indentation on their inner side of the distal half. Terminal filament of mature tentilla with small cupulate process.

*Material examined.* Specimen collected at *Snellius* I Station 317a at 7°55.0'S, 122°12.5'E, to the north of Flores, Indonesia, on the 22<sup>nd</sup> August 1930. The specimen probably was collected in a 50 cm diameter opening plankton net, 1 m in length towed at the surface. The water depth was 2350 m.

*Description.*

*Pneumatophore.* The small pneumatophore was greatly distorted and bore an apical cap of dark red pigmentation

*Nectosome.* Typically the nectophores were budded off on the dorsal side of the nectosome (Figure 60), despite Mapstone's (2004) statement to the contrary. The nectosome and siphosome were a brownish orange colour in their preserved state.

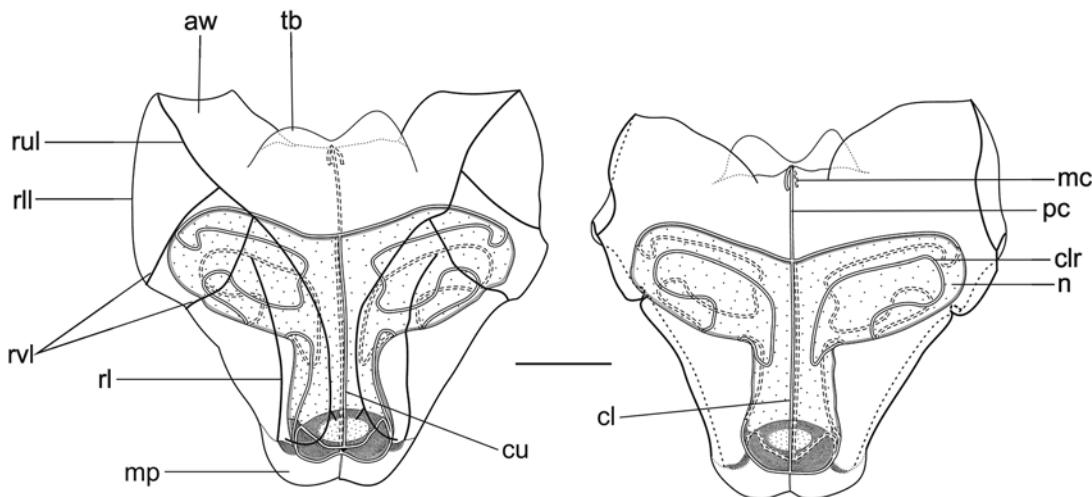


**FIGURE 61.** *Halistemma foliacea*. Upper view of a very young nectophore. **lop:** lateral ostial process; **rul** and **rvl:** upper and vertical lateral ridges. Scale bar 1 mm.

*Nectophores:* The *Snellius* specimen included 45 mature nectophores and a very young one. The mature nectophores were, generally, in a poorish condition, as one might expect from net collected material. No patches of ectodermal cells were noted on the lateral surfaces of any of the nectophore, but one cannot be certain that they are truly absent. The very young nectophore (Figure 61) clearly showed the characteristic feature of the nectophores of *Halistemma foliacea*, that was the two pairs of vertical lateral ridges. The upper lateral ridges reached to the ostium and, at this stage, had a slight kink proximal to the ostium. The lateral ostial processes were relatively large but there were no obvious large nematocysts.

The adult nectophores (Figure 62) were very flimsy, often damaged, and many had the lining of the nectosac completely detached. The upper and lower lateral ridges met at the outer proximal tips of the axial wings. The

upper laterals ran obliquely inwards toward the ostium, but the degree to which they approached each other was quite variable. Shortly above the ostium they began to diverge and each gave rise to a short inner branch, while the outer branch continued out laterally and eventually petered out in the region of the lateral ostial processes. The lower lateral ridges continued down the lower sides of the nectophore and eventually merged with the mouth plate. The rounded, relatively small mouth plate had a central, broad emargination, and the "ventral nerve tract" (see Mackie 1973) could clearly be seen running in the mid-line to join the ostium. The two pairs of vertical lateral ridges were distinct and complete. There was a furrow paralleling the more distal pair of ridges, but such furrows, particularly on the upper surface, are usually preservation artefacts. The pair of lateral ridges ran proximally and obliquely up from the ends of the lateral ostial processes, but did not connect with any other ridge.



**FIGURE 62.** *Halistemma foliacea*. Upper (left) and lower (right) views of a mature nectophore. Scale bar 5 mm.

The central thrust block was broad, but not greatly developed. It had a broad central emargination. The axial wings were proximally truncated, particularly in upper view. They too were not greatly developed and varied in the extent to which they projected from the main body of the nectophore. Most often they projected beyond the top of the thrust block, but not uncommonly they were virtually non-existent, with the thrust block extending beyond their proximal ends

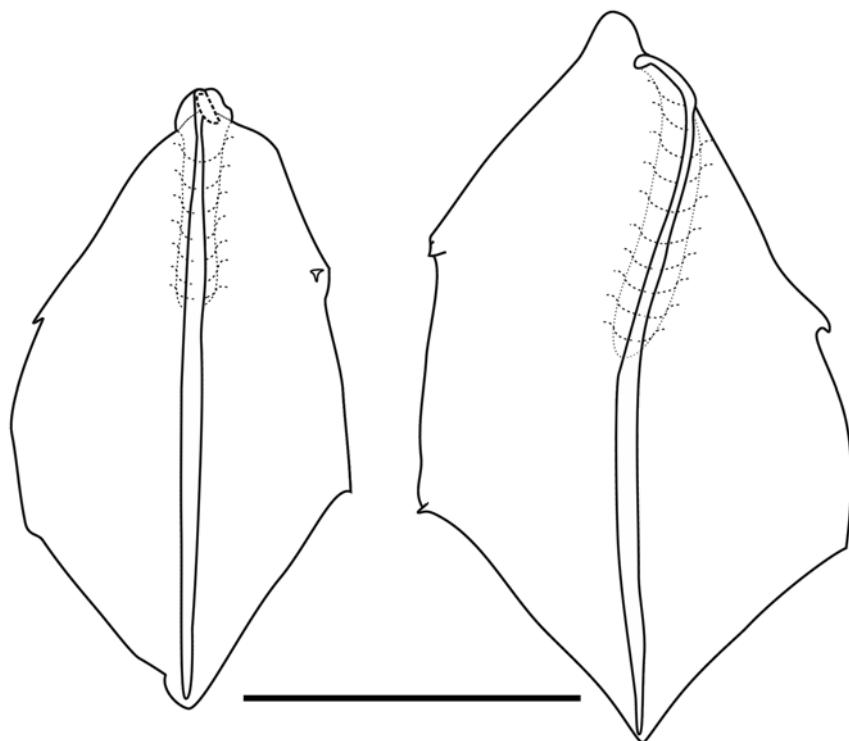
The nectosac was roughly T-shaped, with a relatively narrow neck; although this probably was a preservation artefact due to the poor state of the nectophores. The ascending and descending branches of the mantle canal were quite short and of approximately the same length. The long pedicular canal ran down from the lower side of the thrust block to the top of the nectosac, where it gave rise to all four radial canals. The upper and lower canals ran straight down to the ostial ring canal. The course of the lateral radial canals was the most complex of all the *Halistemma* species and is better illustrated (Figure 62) than described in detail. There was a small patch of ectodermal cells on the velum close to where the upper canal joined the ring canal. The two lateral ostial processes were relatively small, and were covered by distinctive cells. These processes had usually become detached, except by the ostium, so that they appeared as flaps.

*Siphosome*. Bigelow (1911, p. 288) gave a description of the arrangement of the zooids in each cormidium of his specimens of *Stephanomia amphitridis* [sic], noting that "The cormidia have been described by Huxley, but the location of the various zooids is more precise than he supposed. In the present series there are nineteen siphons, with corresponding segments of stem, and in all of them the arrangement is as follows:—Proximal to any given siphon there are from 2–5 palpons; distal and close to it are the two gonodendra, ♀ and ♂, and crowded against them 3–6 palpons. On the pairs the ♂ cluster is always next the siphon ... Next to the ♀ gonodendron there is a vacant space occupied only by bracts; but midway between every two siphons there is a cluster of 3–6 palpons of different ages". This basic arrangement has been confirmed for the present specimen as is discussed below.

*Bracts*. Huxley (1859) thought for his specimen of "*Stephanomia amphitridis*" that there were two types of bracts arranged in four whorls, with pairs of laterals differing from the identical dorsals and ventrals (see Figure 5). Bigelow (1911, pp. 287–8), however, considered the bracts to be arranged into "four or five irregular somewhat diagonal rows", and "that their external location does not necessarily indicate the level at which their supporting

lamellae join the stem". Nevertheless, he noted three types of bract that he designated "dorsal", "lateral" and "ventral"; a convention followed by Mapstone (2004). For the *Snellioides* specimen she counted 161 "dorsal", 44 "lateral", and 12 "ventral" bracts. However, if the bracts had been arranged into four or more rows then one might expect the number of lateral bracts to be at least twice that of the other types. Thus, judging by the relative numbers found with the *Snellioides* specimen, one wonders if Bigelow's designations were entirely correct, but unfortunately he gave no numbers for each type. Nevertheless we will follow his designations here, although we consider that there are two types of lateral bracts.

*"Dorsal"* bracts: Most of these bracts were in poor condition. They measured up to 32 mm in length by 19 mm in maximum width. At all stages of development the bracts distal end came to a median point, and up to two, slightly asymmetrical pairs of lateral teeth were present; although they were always very small and indistinct, often appearing just as small notches.

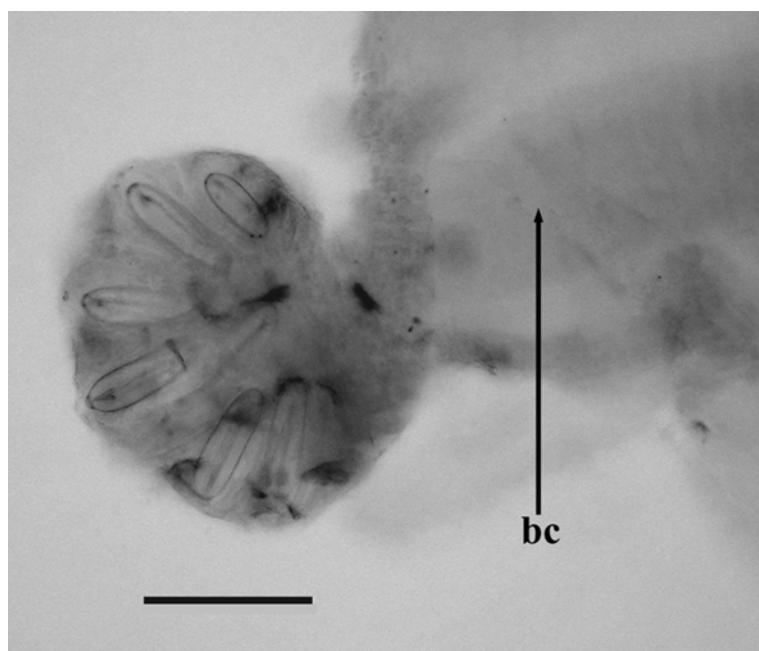


**FIGURE 63.** *Halistemma foliacea*. Lower views of young "dorsal" bracts. Scale bar 5 mm..

The younger "dorsal" bracts (Figure 63) were flattened in the upper/lower plane, but with a small median enlarged region, like a keel at the proximal end on the lower surface. The broad bracteal canal was widest in its central region and narrowed in both the proximal and distal directions. At the proximal end it curved over the thickened keel and up toward the upper side of the bract. At the distal end it might have been inflected slightly into the mesogloea, but the latter was very thin in that region. Although Mapstone (2004, p. 236) stated that the distal end of the bracteal canal was "terminating as small swollen apical button in cup-shaped depression filled with nematocysts" this was not found to be the case by the present authors. A single young "dorsal" bract, out of all the detached bracts of the three different types, showed that the bracteal canal ended, distally, below a ball of tissue that protruded out from the tip of the bract, in which nematocysts, probably stenoteles, were embedded, (Figure 64). A close study of the anterior end of the siphosomal stem shows that there are still some young "dorsal" bracts attached and showing this sphere of nematocysts at their distal tip (see Figure 60, np). However, more posteriorly, for the more developed "dorsal" bracts, this sphere of nematocysts has become detached, leaving a small, empty cup-shaped depression. No young bracts of the other types were seen on the siphosomal stem and so it is unclear whether they also develop such a sphere of nematocysts, but there was no evidence for it on the detached bracts.

As the bracts grew the proximal keel on the lower side of the bract became more prominent and gradually the bracteal canal narrowed (Figure 65). Firstly, the keel became displaced toward the inner side of the bract, and no longer reached to the proximal tip, which had begun to elongate so that the bracteal canal usually remained on the

lower side of the bract. At some stage, but not necessarily concomitant with the proximal elongation, the proximal region of the bract began to become thickened with mesogloea. Thus in some cases (Figure 65 A, left) the bracteal canal continued to the proximal end and up toward the upper surface, and on its outer side (right in figure) the proximal end of the bract became thickened, while the other side was distinctly thinner, so that the narrow keel, in the preserved state at least, often formed a flap partially covering it. In another (Figure 65 A, right) the proximal end of the bract had begun to elongate and its central part was thickened, still with the distinctive keel running over it. In the fully developed bract (Figure 65 B) the entire proximal end of the bract became thickened with mesogloea and formed a cone shaped structure, while the whole bract resembled a rhomb. However, in the mid region of the bract, on the inner side, the extent and appearance of the mesogloal thickening could be very variable. The distal end always remained thin and, as above, it was difficult to decide whether the bracteal canal actually penetrated into the mesogloea before terminating.

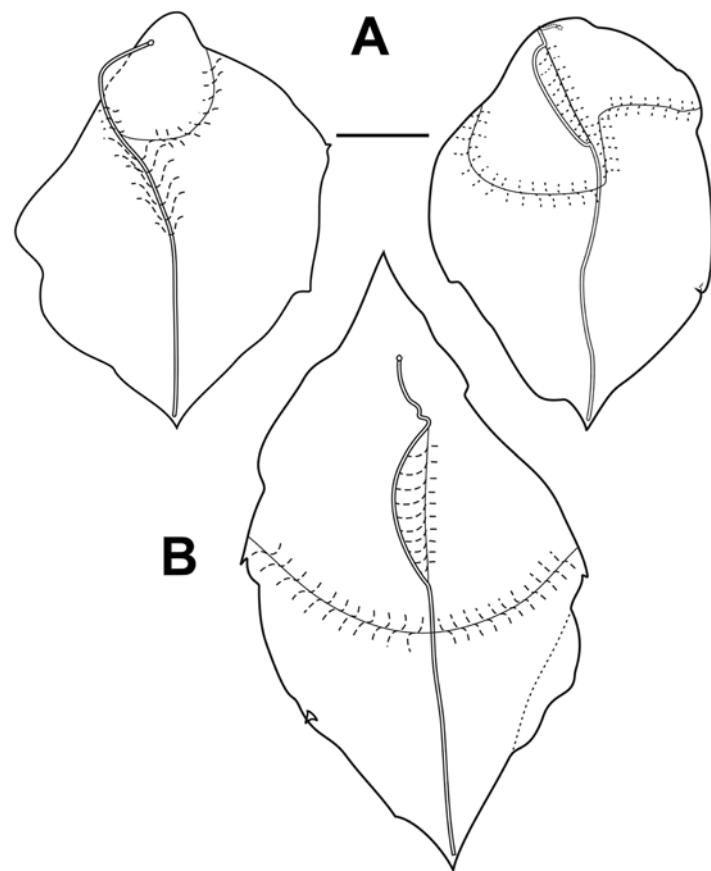


**FIGURE 64.** Detail of distal tip of young "dorsal" bract of *Halistemma foliacea*, showing the spherical extension containing nematocysts. **bc:** bracteal canal. Scale bar 1 mm.

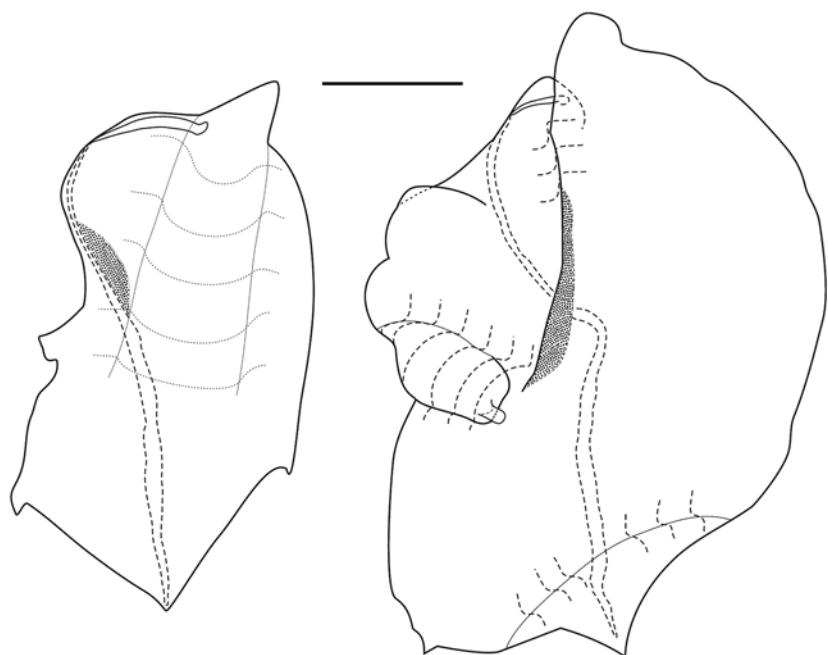
Although not noticeable in the youngest bracts, as the bracts mature the proximal tip of the bracteal canal tended to enlarge slightly. Sometimes this was an internal swelling without affecting the width of the canal, sometimes it was expanded laterally and often it was slightly inflected into the mesogloea.

*"Lateral" bracts:* Although Mapstone (2004, p. 238) noted that there were two types of lateral bract she illustrated only of them in her Figure 3, and based the differentiation of the two types mainly on the distribution of the lateral teeth. However, there appear to be more substantial differences between them. Both types measured up to c 30 mm in length, but the second type tended to be wider than the first. At all stages of development both types were distinctly asymmetrical and occurred in enantiomorphic forms.

The Type I bracts (Figures 66 left, 67), which were about twice as common as the other type, were distinctly convex on their upper sides, particularly in the central part of the proximal half. For the younger bracts (Figure 66, left), the distal end was pointed, while the proximal end was formed by a rounded cone like process. Toward the distal end there was a pair of lateral teeth; slightly asymmetrical in position and size. On the inner side there was an additional lateral process at about the mid-height of the bract. The proximal end of the bracteal canal often was slightly enlarged and inflected into the mesogloea. It then ran along the upper side before running over the inner lateral side, on to the lower side, and ran distally, initially over the edge of a slightly thickened keel, which at one point overhung the lower side, forming a small cavity. It was greatly thickened in its mid region tapering down both proximally and, particularly, distally. The canal ended at the distal tip of the bract, where there was no sign of an accumulation of nematocysts.



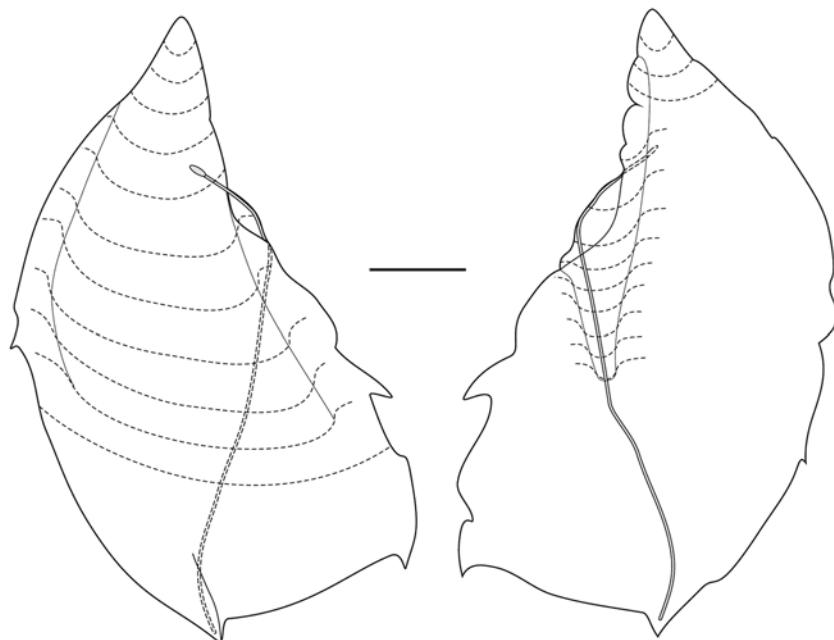
**FIGURE 65.** Lower views of maturing (A) and mature (B) "dorsal" bracts of *Halistemma foliacea*. Proximal at top, distal at bottom. Scale bar 5 mm.



**FIGURE 66.** *Halistemma foliacea*. Upper views of young "lateral" bracts. Type I (left) and Type II (right). Scale bar 3 mm.

For the mature Type I bracts (Figure 67) the convexity of the upper surface was very obvious in its proximal two-thirds, as indicated by the dotted lines in Figure 67 (left).. The pair of lateral teeth was distinctly asymmetrical in their positioning, with the one on the inner side being larger than the other. The lateral process, on the inner side,

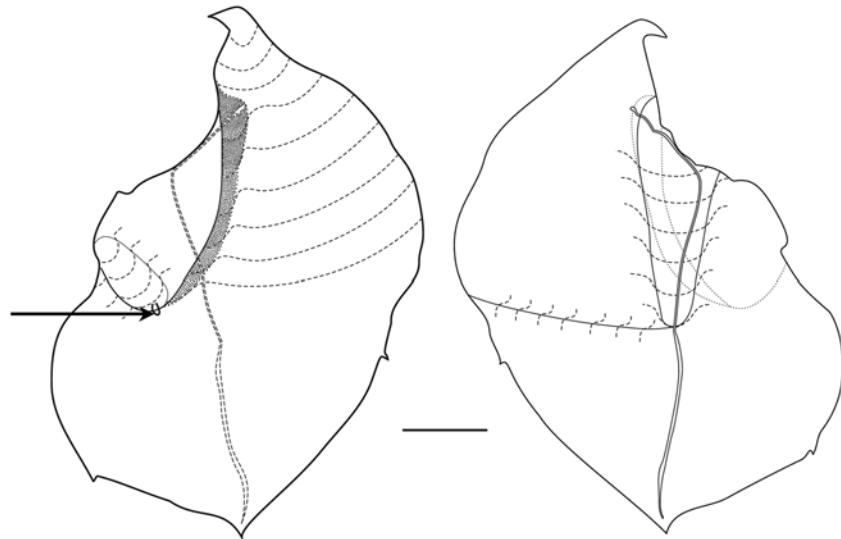
was prominent and now resembled an enlarged tooth or cusp. The bracteal canal, now narrow and of equal diameter, lay almost exclusively on the lower side of the bract. Proximally, however, it originated on the upper side of the bract and usually began with a small swelling that could be inflected into the mesogloea. As with the younger bract, the proximal part of the canal ran over the edge of the now thickened keel, which extended more laterally than the upper side of the bract and to above the mid-height of the bract (Figure 67, right). There was an indication of a short median ridge descending from the distal end of the bract on the upper side (Figure 67, left).



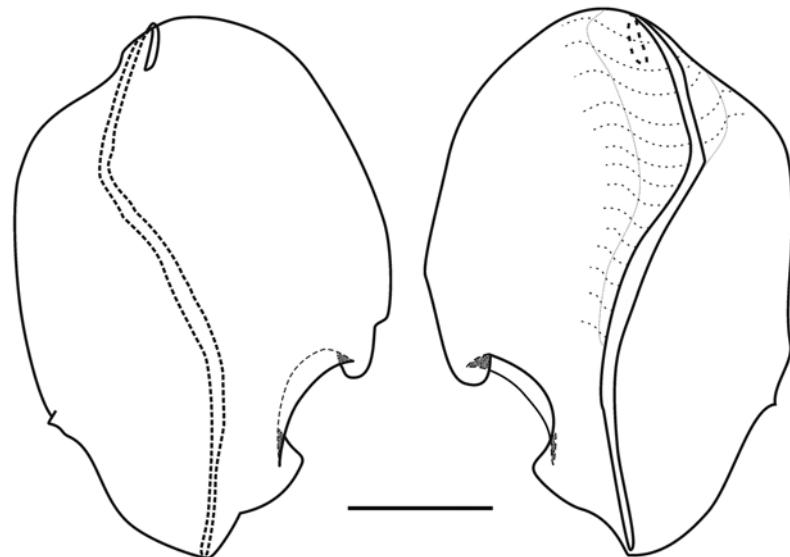
**FIGURE 67.** *Halistemma foliacea*. Mature Type I "lateral" bract. Upper (left) and lower (right) views. Proximal at top, distal at bottom. Scale bar 5 mm.

The Type II "lateral" bracts (Figures 66 (right), 68) differed markedly from the Type I ones in having a large excavated area on the upper and inner side of the bract, where the mesogloea between the upper and lower sides was quite thin. Both the distal and proximal ends of the bract were pointed, although the proximal end often was bent to one side. The excavated region was demarcated by a median, slightly elevated ridge running distally from the rounded proximal process to about the mid-height of the bract. It overhung the excavated upper side for most of its length. The distal border of the excavated area was formed by a thickened cushion of mesogloea whose distal side was demarcated by a shallow gutter. On the side of the cushion closest to the mid-line there was a distinct, but small, flap or rounded cusp (Figure 68 left, arrowed). Proximally, the bracteal canal lay entirely on the upper side of the bract and ended in a slight swelling, often inflected into the mesogloea, that lay beneath the overhanging median ridge. About halfway across the excavated region it passed over onto the lower side of the bract and ran distally over a marked, but fairly shallow, keel that extended to about half the length of the bract. It then continued toward the distal end but terminated before reaching it, and again without any sign of a patch of nematocysts being present. The proximal part of the bract, on its lower side was more thickened with mesogloea than the distal part and, particularly for the younger bracts, the distal tip was very thin. In addition the younger bracts tended to have only one small lateral tooth, distally, while the mature ones has a pair, arranged asymmetrically.

*"Ventral" bracts:* These were the most distinctive of all the bract types and the least common. They measured up to 27 mm in length and 22 mm in maximum width. At all developmental stages they had an obtuse distal tip, while the proximal end was rounded. On their outer sides the bracts were distinctly emarginated to form a hemispherical indentation, partially overlain by a flap on the upper surface. Although not visible on the younger bracts (Figure 69), the older ones (Figure 70) usually possessed a small tooth immediately above and below the indentation, on the upper surface of the bract. There was also a relatively large process on the outer surface of the mature bracts, just proximal to the indentation, which was represented by only a small notch in the younger ones. At all developmental stages there was another small tooth on the opposite, inner side of the bract at approximately the same level as the indentation.



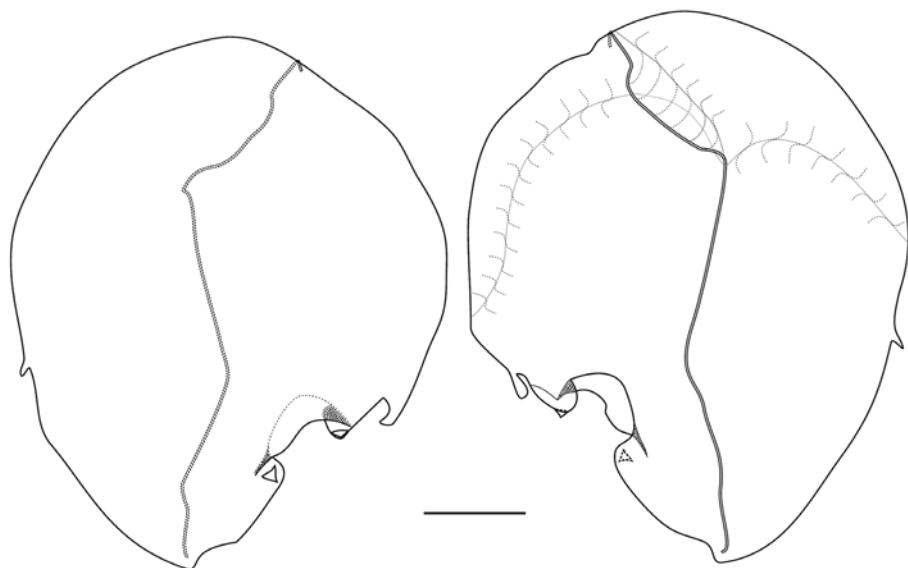
**FIGURE 68.** *Halistemma foliacea*. Mature Type II "lateral" bract. Upper (left) and lower (right) views. Proximal at top, distal at bottom. Scale bar 5 mm.



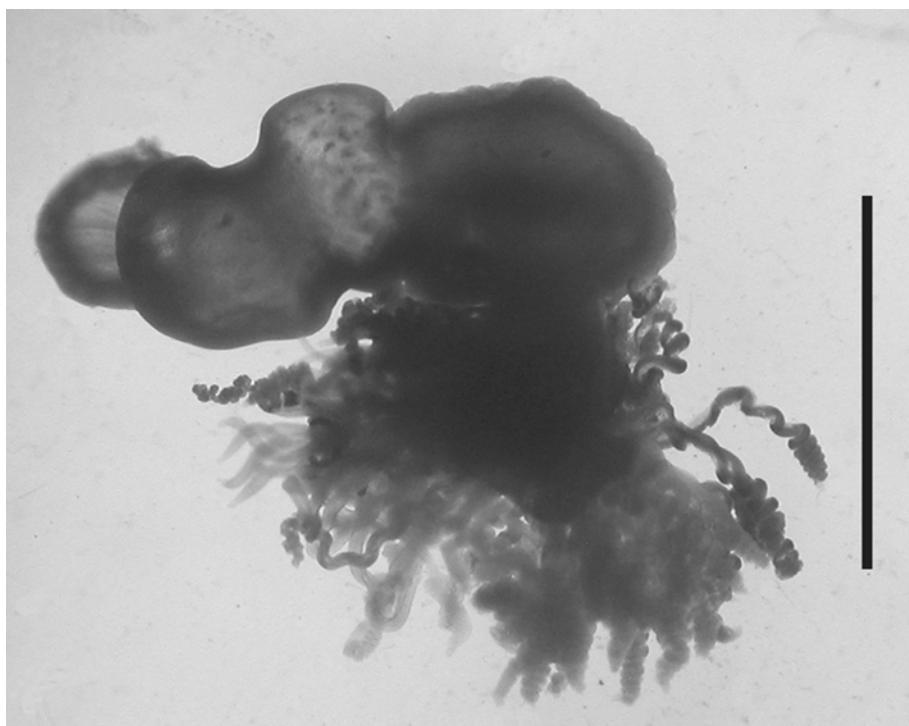
**FIGURE 69.** Young "ventral" bracts of *Halistemma foliacea*. Upper (left) and lower (right) views. Proximal at top, distal at bottom. Scale bar 5 mm.

The younger bracts (Figure 69) possessed a shallow but broad keel in the proximal half on the lower surface. On the mature bracts this keel was relatively short and narrow, but much more pronounced, such that in the preserved specimens it often bent over the inner side of the bract forming a sort of flap. Also on the lower surface the proximal end of the bract was distinctly thickened with mesogloea. This thickening was more pronounced on the outer side. The proximal end of the canal lay on the upper side of the bract; a feature more obvious in the younger ones. There was no obvious swelling or inflection into the mesogloea. It then passed onto the lower side and ran distally over the middle of the keel and, with a zig and a zag extended to close to the distal end of the bract. In the younger bracts the canal was thickened, particularly in its central region, and tapered down toward the distal end. Very close to its distal end the canal penetrated through the thin layer of mesogloea to end on the upper surface; occasionally below a small cavity, but there was no indication of the presence of nematocysts.

*Gastrozooid and tentacle.* The gastrozooid (Figure 71) was fairly cylindrical with a large basigaster occupying one quarter to one third its length. The stomach and proboscis regions were not well distinguished and narrow hepatic stripes could be seen ascending from the mid-height of the gastrozooid to the distal mouth. The tentacle was annulated, with each tentillum arising in the restriction between each segment.

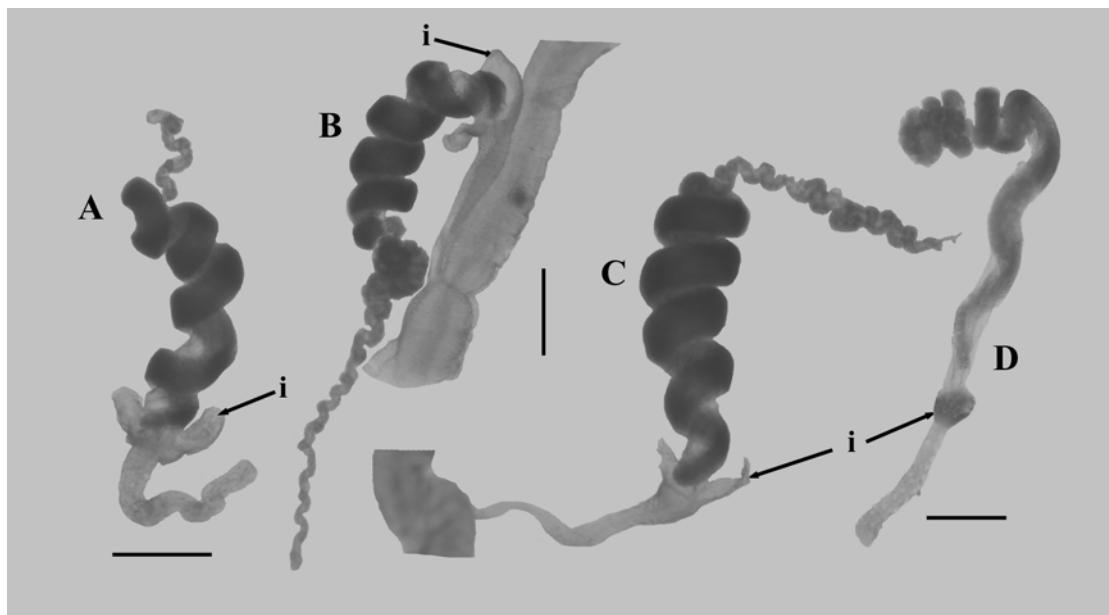


**FIGURE 70.** *Halistemma foliacea*. Mature "ventral" bracts. Upper (left) and lower (right) views. Proximal at top, distal at bottom. Scale bar 5 mm.

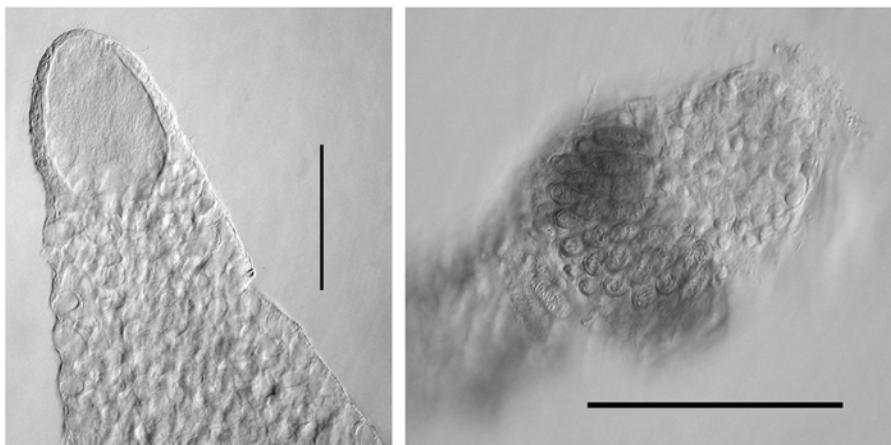


**FIGURE 71.** *Halistemma foliacea*. Gastrozooid and contracted tentacle. Scale bar 5 mm.

**Tentilla.** The tentilla possessed an involucrum at the proximal end of the cnidoband (Figure 72) that consisted of two lobes, either symmetrical (Figure 72 A) or asymmetrical (Figure 72 B, C). During development these lobes were thickened and quite prominent, but as the tentilla matured they expanded into thin sheets, surrounding the proximal end of the cnidoband, that were extremely flimsy and easily torn, such that only a vestige of them may remain (Figure 72, D). At earlier stages of development the cnidoband was usually quite tightly coiled into c. 5 spirals, but as it matured the proximal coils straightened, although the spiralling could still be discerned. The double elastic band ran through the interior of the cnidoband. The long terminal filament ended in a small cupulate process (Figure 73, right). In the youngest tentilla (Figure 73, left) this process was formed by an acorn-shaped process, devoid of nematocysts. However, when mature the base of the acorn-shaped process, itself still devoid of nematocysts, was surrounded by a cupulate swelling that included nematocysts, mainly desmonemes.



**FIGURE 72.** *Halistemma foliacea*. Tentilla at various stages in their development. Scale bars 5 mm.



**FIGURE 73.** Distal ends of tentilla of *Halistemma foliacea*. Left: young tentillum; right: mature tentillum. Scale bar 100 µm.

Two types of nematocyst were present on the cnidoband; stenoteles and anisorhizas. There were over 200 stenoteles arranged in two rows on either side of the proximal part of the cnidoband. They measured c. 70 µm in length and 25 µm in diameter. The myriad of anisorhizas were banana-shaped, broader at the cap end and roundly pointed at the other, and measured c. 47 µm in length and 9 µm in diameter. The terminal filament had the usual desmonemes and acrophores. The desmonemes measured c. 22 µm in length and 10 µm in diameter; while the acrophores were slightly smaller, measuring c. 21 µm by 9 µm.

**Palpons.** The featureless palpons measured up to 17 mm in length (Figure 74). They were mainly cylindrical, but tapered at each end, with at the distal end a narrow, short proboscis, which occasionally possessed a swollen middle region. The palpacle arose at the base of the palpon and presumably was quite long in life, but in the preserved state most of them were broken off and quite short. They bore occasion annulations. No nematocysts were found on the palpacle, but stenoteles were occasionally found scattered sparsely over the surface of the palpon itself. A maximum of six was observed. Mapstone (2004) mentioned a collar of nematocysts close to the distal tip of the palpon, but this was not observed on the palpons looked at during the present study.

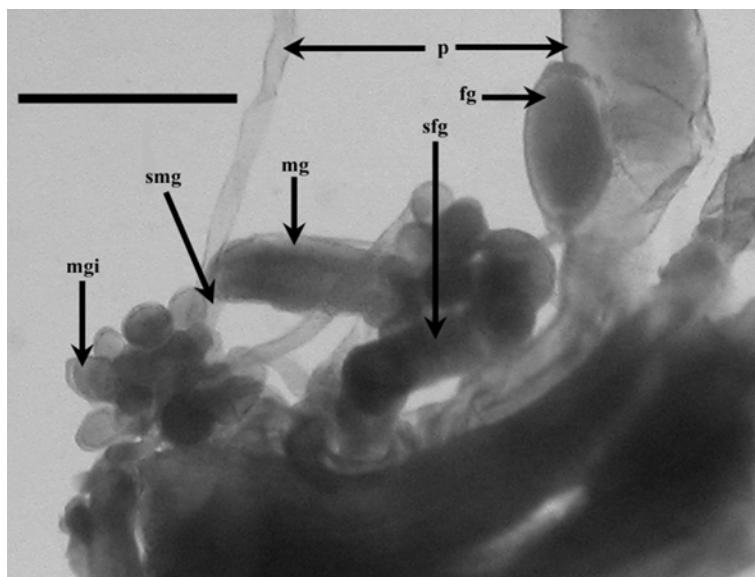
**Gonophores:** In each cormidium the male gonodendron (Figure 75) was attached to the siphosome immediately posterior to a gastrozooid, followed quite closely by the female one. The male gonophores, at various stages in development, appeared to be attached to a broad stalk, as noted by Huxley (1859), or at least a swelling from the siphosomal wall. Young palpons were also attached to this process. The female gonodendron, however,

had a very distinct, elongate, thickened stalk (Figure 75, **sfg**), with marked annular strengthening rings. Again the gonophores were at various stages in development, but no palpons appeared to be attached to the gonodendron.



**FIGURE 74.** Detached palpons of *Halistemma foliacea*. Scale bar 5 mm.

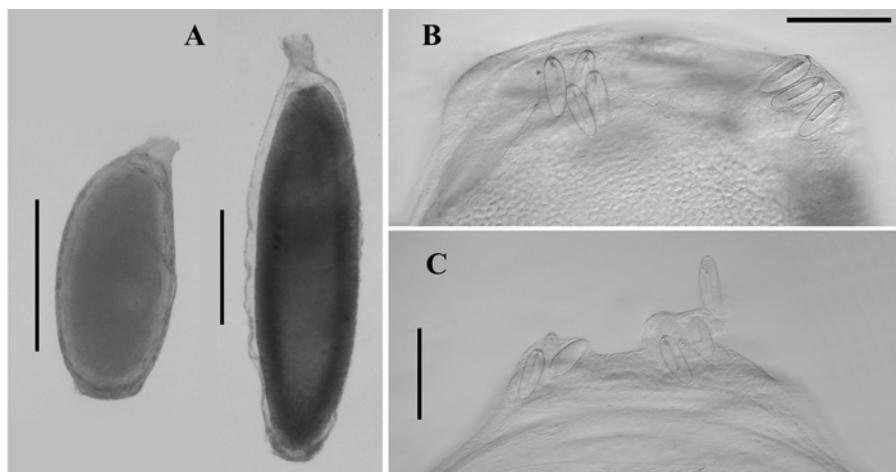
Mapstone (2004) noted that this arrangement of the gonodendra in each cormidium differed from that of *Halistemma rubrum*, as described by Totton (1965), in that, for the latter species, there were three male gonodendra. However, she did not point out the more important difference in that in *H. rubrum* the female gonodendron was anterior to the male ones, while in *H. foliacea* the single male gonodendron was anterior to the female one.



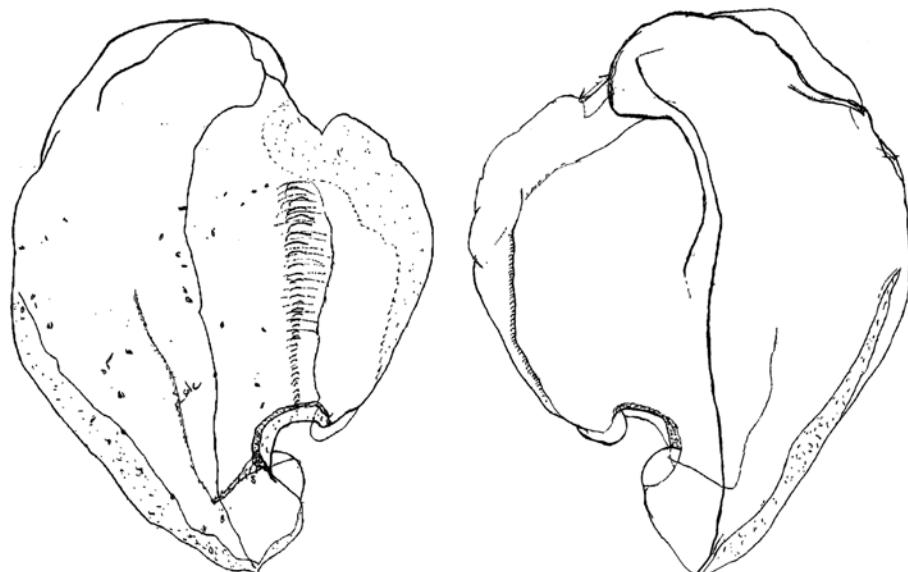
**FIGURE 75.** Part of siphosome of *Halistemma foliacea* showing male and female gonodendra. **fg.** female gonophore, with its thickened stalk (**sfg**); **mg.** mature male gonophore, with its narrow stalk (**smg**); **mgi.** immature male gonophore; **p.** palpon. Scale bar 1 mm.

The mature male gonophores measured up to c. 3 mm in length and were narrow cylindrical structures borne on short stalks. The female ones were broader and shorter (Figure 76). Mapstone (2004, p. 237) mentioned "four

small tentacular buds" around the ostium of both the male and female gonophores, which in the former case at least contained nematocysts. This is in line with Huxley (1859, p. 73) who said "The calyx of the androphore is terminated by four obtuse elevations, containing large thread-cells", although he neither described nor illustrated such elevations on the female gonophores. Similarly, Bigelow (1911) described and illustrated tentacular rudiments around the ostium of the male gonophore, but made no mention of such on the female gonophores. Many of the gonophores, of both sexes (Figure 76, A), did not show these knobs, but the most mature ones did (Figure 76, B,C). They were four small excrescences around the distal ostium, although they do not appear tentacular as Mapstone (2004) suggested. Each of these contained up four or five stenoteles, measuring c. 70 x 20  $\mu\text{m}$ .



**FIGURE 76.** *Halistemma foliacea*. **A.** Female (left) and male (right) gonophores. Scale bar 0.5 mm. **B.** distal end of male and **C.** female gonophores, showing patches of nematocysts. Scale bars 100  $\mu\text{m}$ .



**FIGURE 77.** *Halistemma foliacea*. Sketches of "ventral" bracts from Kawamura's (1954) specimens of "*Stephanomia amphitridis*" made by Francesc Pagès. No scale given.

*Nectalia stage:* The post-larval *Nectalia* stage of *Halistemma foliacea* has yet to be collected or identified.

*Remarks.* As noted in the Introduction, the species *Stephanomia amphitridis* was first illustrated by Lesueur & Petit (1807). Further descriptions, under the name *S. amphitridis*, were given by Huxley (1859), Bigelow (1911) and Kawamura (1954); but were all based, like the original illustration, on only siphosomal fragments. Mapstone (2004) published what she said was "The first full description of ... *Halistemma amphitridis*", based on a specimen that was fairly complete, including the nectosome and nectophores. Kawamura had compared his material with that of Bigelow, and Mapstone did the same for her specimen, and it was clear that they all belonged to the same

species. This can be further proven by the fact that the late Frances Pagès re-examined Kawamura's material and produced some preliminary drawings (Figure 77) of the "ventral" bracts that had the same characteristic lateral indentation. A comparison of the illustrations of Bigelow and Mapstone with those of Huxley also shows that Huxley's specimen belonged to the same species.

However, do all these specimens belong to the species *Stephanomia amphytridis*? As we have already discussed in the Introduction it is our contention that none of the specimens mentioned in the previous paragraph belong to *S. amphytridis* and that should all be referred to as *Halistemma foliacea*.

*Halistemma foliacea* shows several distinctive characters that make it easy to identify. The presence of two vertical lateral ridges on the nectophores is a unique character among *Halistemma* species, as is the presence of a distinct keel on the lower side of all types of bract. The distinct semicircular incision on the inner side, in the distal half, of the "ventral" bracts is also a unique character.

During the present study of the same material as that which Mapstone (2004) described a few differences have emerged. The fact that Mapstone described the nectophores as being budded off on the ventral side of the nectosome was clearly an oversight on her part, as in all agalmatids with the exception of species of the genus *Athorybia*, which do not develop them, the nectophores are budded off on the dorsal side. However, this fact was not fully established until after her publication, by Dunn *et al.* (2005a), and further by Pugh (2006). Although Mapstone noted differences among the "lateral" bracts she did not clearly divide them into two types; perhaps to stay in line with Bigelow (1911). None the less, it is clear that there are two types distinguished by the presence/absence of a deeply excavated area on the proximal, upper, inner surface of the bract. Mapstone also seemed to believe that patches of nematocysts were present at the distal end of the bracteal canal in all forms of bracts, but no evidence for this could be found for all but the "dorsal" ones. In that case the nematocysts were aggregated into a spherical ball extending from the distal tip of the bract but it was usually broken off and could only be seen on the youngest forms.

*Distribution.* As noted above, there appear to be only five known records for *Halistemma foliacea*. Quoy & Gaimard's (1833, (1834)) original specimen was collected to the north of New Guinea, in the equatorial region between 135 and 145°E. Huxley's (1859) specimen was collected off the east coast of Australia, for which Mapstone (2004) gives the position as 32°S, 155°07'E, almost half way between Sydney and Brisbane. Neither of these specimens is thought to be still in existence. However, Bigelow's (1911) specimens are housed at the Smithsonian Institution, Washington, D.C. and were collected in the eastern tropical Pacific Ocean at c. 17°S, 100.7°W (St. 4704) and 15°05'S, 99°19' W (Station 4705) during the 'Albatross' Expedition 1904–1905. Kawamura's (1954) small specimen was from Misaki, Japan and the one from Snellius Expedition (St. 317a at 7°55.0'S, 122°12.5'E) from north of Flores Island, Indonesia.

Dr Dhugal Lindsay (personal communication) has informed us that he found *Halistemma foliacea* to be common in the northern part of the Coral Sea; quite close to where Huxley collected his specimen. Thus the known specimens have all been found in the Pacific Ocean and, apart from Bigelow's specimens, within a somewhat restricted area. However, it probably has a much wider distribution and, because of the distinctiveness of its bracts, particularly the "ventral" ones, and the presence of two complete vertical lateral ridges on the nectophores, it should be easy to identify.



**FIGURE 78.** *Halistemma maculatum* sp. nov. Tank photograph of specimen collected during JSLII Dive 1673. Length not recorded.

## *Halistemma maculatum* sp. nov.

*Halistemma rubrum* Totton, 1954 (*in partim*) Text—fig. 16, A, D, F.

Material examined:

Dive	Date	Position	Depth
JSLII 716	12 May 1983	c. 25°19.5'N 76°55'W	? 122 m.
JSL II 983-CGP8	26 October 1984	25°6.8'N 77°23.1'W	568 m*.
JSL II 996-CGP4	31 October 1984	25°22.5'N 77°54.9'W	610 m*.
JSL II 1411-DS8	6 September 1986	39°56.4'N 70°14.3'W	640 m.
JSL II 1673-CG9	4 October 1988	26°27.9'N 78°2.9'W	828 m.
JSL II 1675-CG1	5 October 1988	26°25.6'N 77°52.8'W	777 m.
JSL II 1679-CG11	7 October 1988	25°50.3'N 77°14.8'W	753 m*.
JSL II 1679-CG12	7 October 1988	25°50.3'N 77°14.8'W	depth not recorded*.
JSL II 1679-DS6	7 October 1988	25°50.3'N 77°14.8'W	720 m*.
JSL II 1681-CG9	8 October 1988	26°25.0'N 77°52.6'W	800 m.
<b>JSL II 1685-CG4</b>	<b>10 October 1988</b>	<b>26°27.8'N 77°58.9'W</b>	<b>837 m.</b>
JSL II 1687-DS4	11 October 1988	26°23.0'N 78°35.6'W	715 m.
JSL I 2634-DS3	4 November 1989	26°14.1'N 77°43.9'W	799 m.
JSL I 2646-CG3	10 November 1989	26°3.0'N 77°32.0'W	792 m.
JSL I 2652-CG3	15 November 1989	26°0.1'N 77°28.2'W	606 m.
JSL I 2652-CG4a	15 November 1989	26°0.1'N 77°28.2'W	604 m*.

\* indicates specimens at the post-larval *Nectalia*-stage. Emboldened—holotype specimen

**Holotype:** The JSLII Dive 1685-CG4 specimen has been designated the holotype and has been donated to the National Museum of Natural History, Smithsonian Institution, Washington, D.C., U.S.A.

**Diagnosis:** Basic *Halistemma* ridge pattern on nectophores, with complete vertical-laterals, joining both the upper and lower laterals at a right-angle. Lateral ridges join upper laterals. Mouth plate present and deeply divided. Three types of bract, with the Type *A* having multiple patches of ectodermal cells on the upper surface and, uniquely for this species, a distal bump on the inner lateral edge. Tentilla with reduced, almost vestigial, involucrum that does not completely cover the first spiral of the cnidoband, and a small acorn-shaped terminal process to the terminal filament.

**Description:** The description will be based largely on the type specimen from JSL II Dive 1685, unless otherwise stated. Unfortunately, this specimen was not photographed after capture, but a tank photograph of the specimen collected during JSLII Dive 1673 is shown in Figure 78.

**Pneumatophore:** The pneumatophore measured 1.5 mm in length, and 0.8 mm in diameter. There was a small cluster of brownish cells at its anterior end, which suggests that it might have had a reddish cap in life.

**Nectosome:** The nectophores were budded off on the dorsal side of the stem.

**Nectophores:** Thirty-nine detached nectophores were present in association with the type specimen, while the nectosome bore several nectophoral buds, at varying stages of development, and the attachment lamellae of the detached nectophores. Detached nectophores ranged in size from 5.5 x 4.5 mm (length x width) to 11 x 10 mm.

For the very young nectophoral buds (Figure 79) the ridges stood out distinctly, as did the two lateral pairs of ectodermal cell patches, and particularly the relatively enormous lateral ostial processes that were packed with nematocysts.



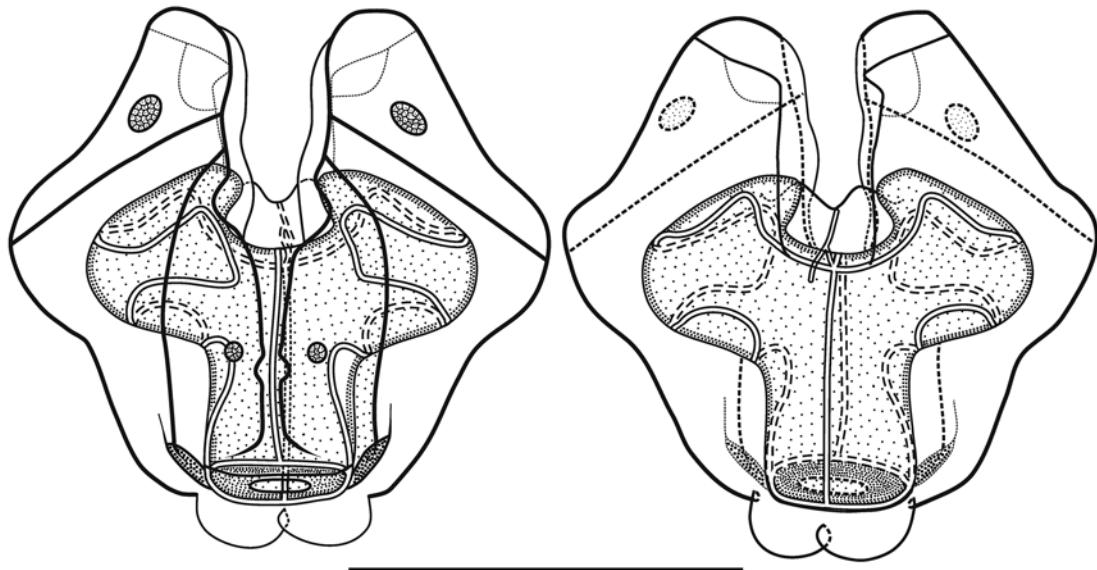
**FIGURE 79.** *Halistemma maculatum* sp. nov. Very young nectophore from JSLII Dive 1679-CG12 specimen. Scale bar 1 mm.

For the younger nectophores (Figure 80) the central thrust block was quite small and under-developed, so that the pointed axial wings extended well beyond it. As the nectophores increased in size the central thrust block became more developed and although it only reached to the same level or slightly above the now squared-off, slightly outward and downward-sloping axial wings (Figure 81). In the ostial region, the distal mouth plate enlarged proportionally with the size of the nectophores, and the left and right sides overlapped extensively in the mid-line. The lateral ostial processes gradually diminished in relative size and began to lose their nematocysts, either through abrasion or having been used and subsequently discarded. These processes were then covered in small plate-like cells. There were two pairs of almost circular patches of ectodermal cells on the upper lateral sides of the nectophore that almost certainly were sites of bioluminescence. One pair lay close to the centre of the triangular facet on each side between the upper and lower lateral, and the vertical lateral ridges; and the other pair in the middle of the facets demarcated by the upper and lateral ridges.

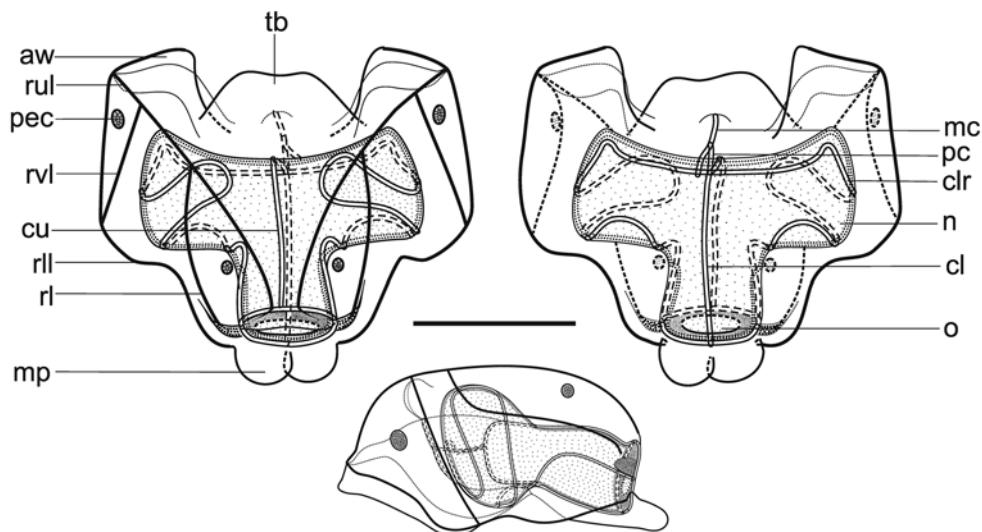
The general arrangement of the ridges on the nectophores of *Halistemma maculatum* sp. nov. was similar to that of all *Halistemma* species as described by Totton (1954) and Pugh & Youngbluth (1988). The pair of upper lateral ridges ran across the upper surface of the nectophore from the apical margins of the axial wings obliquely toward the ostium. They closely approached each other slightly above the ostium, but then curved out laterally and petered out before reaching it.

The vertical lateral ridges arose relatively high up on the upper lateral ridges, above the apex of the nectosac, and ran obliquely down the sides of the nectophore to join with the lower lateral ridges. These lower lateral ridges ran along the entire length of the lower lateral edge of the nectophore from the outer margins of the axial wings, where they joined with the upper laterals, to below the ostium where they petered out and joined with the lateral margins of the mouth plate. There were no distinct ridges on the lower surface of the nectophore; however, folds ran down the inner apices of the axial wings to just above the apex of the nectosac.

The lateral ridges branched from the upper lateral ridges at a quarter to one third of the way along the latter's length from the apices of the axial wings. Their course was initially almost parallel to that of the vertical lateral ridges, but quite soon they curved and ran directly toward the ostium. They did not reach the latter but petered out on a level with the upper laterals, ending just over the large lateral ostial processes.



**FIGURE 80.** *Halistemma maculatum* sp. nov. Upper (left) and lower (right) views of young nectophore from type specimen. Scale bar 5 mm.

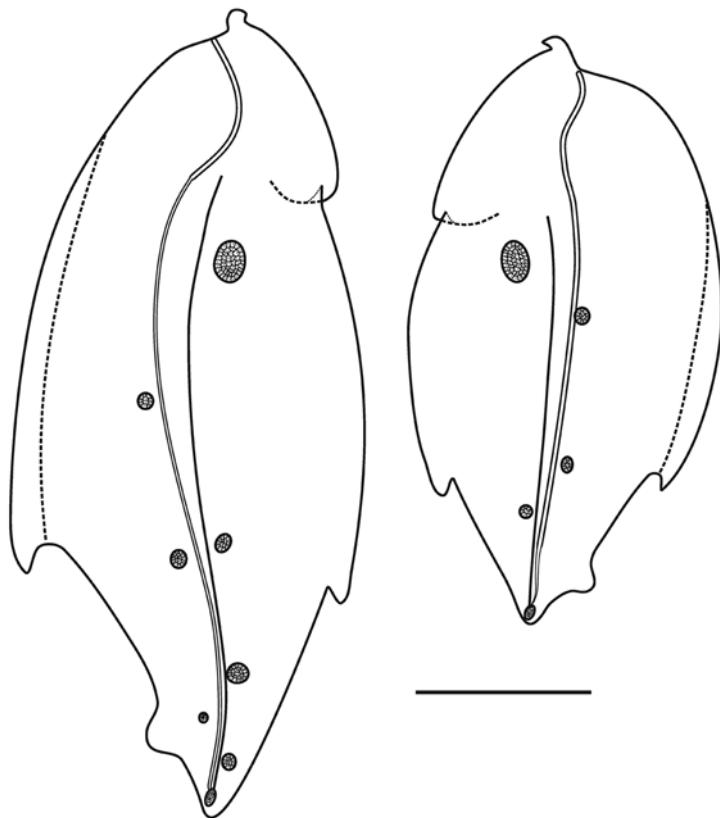


**FIGURE 81.** *Halistemma maculatum* sp. nov. Upper (top left), lower (top right) and lateral (bottom) views of a mature nectophore from type specimen. Scale bars 5mm.

The mantle canal on the proximal or axial surface of the nectophore ran from mid-way down the central thrust block to just below the central apex of the nectosac, in the region where the nectophore had been attached to the stem. The ascending and descending branches were almost equal in length, so the pedicular canal arose at its mid-point and reached the nectosac just below the apex of the nectosac, on its lower side. There it gave rise to all four radial canals. The courses of the upper and lower canals were straight. The lateral radial canals extended out laterally and on the lower surface quite close to the top of the nectosac. Towards the lateral margins of the nectosac the lateral radial canals formed a relatively sharp hump and then formed a loop up the lateral surfaces of the nectosac. From there, they looped back down to the lower surface where they formed another loop before returning to the lateral surface of the nectosac and running down directly to the lateral margins of the ostial ring canal.

*Siphosome:* In each cormidium immediately anterior to the gastrozoid, which lies posterior-most, were several palpons, and anterior to them a very distinct, single stalked, female gonodendron bearing a cluster of gonophores (Figure 87). Two or more palpons separated it from the male gonophores that were attached directly to the stem, and anterior to them was another cluster of palpons, at least five in number. The disposition of the bracts was could not be determined.

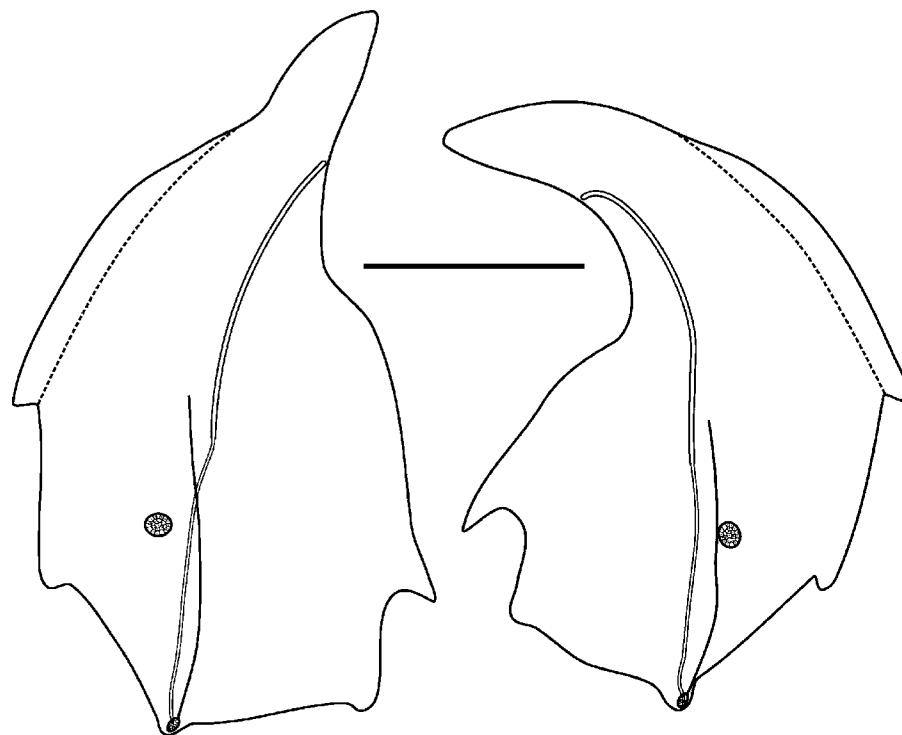
*Bracts*: Ninety-nine detached, foliaceous bracts were associated with the type specimen and these could be divided into three categories on the basis of their general morphology, which included the numbers of lateral teeth and ectodermal cell patches on the upper surface. The bracteal canal lay just within the lower surface of the bract for most of the length, only entering the mesogloea and sloping up towards the upper surface close to its distal end. It ended below a small cup-shaped oval hollow on the upper surface that, in the younger bracts at least, was filled with tightly packed elongate nematocysts. Like those on the lateral ostial processes on the nectophore, these nematocysts had generally disappeared in the fully grown bracts.



**FIGURE 82.** *Halistemma maculatum* sp. nov. Upper views of Type A bracts. Proximal at top, distal at bottom. Scale bar 5 mm.

*Type A*—Twenty-seven bracts of this type were found in association with the type specimen and were present in enantiomorphic forms (Figure 82). These distinctive bracts were elongate and fairly oval, but tapered to rounded points both proximally and distally. They ranged in length from 16.5 to 24.5 mm in length and from 8 to 11.5 mm in width at their widest part. Each bore an asymmetrical pair of lateral teeth approximately at two thirds of the length of the bract from the proximal end, and a third, reduced tooth on the outer side at about one-third the length. A very characteristic feature was a pronounced bump on the inner lateral edge towards the distal end of the bract (Figure 82). A median ridge on the upper surface was present in the distal two thirds of the bract. The mesogloea was markedly thickened in the proximal third of the bract, but rapidly decreased in thickness on a level with the proximal end of the median ridge, where the lower surface of the bract became concave. For the remainder of the length of the bract the mesogloea was slightly thickened on the outer side, while on the inner side it was very thin, often resulting in that side folding inwards. The bracteal canal originated on the inner side of the bract, very close to the proximal end. In mature bracts (Figure 82, left) it was thickened in the proximal third of the bract. At approximately the same level as the proximal end of the median ridge, and at the level of the reduced inner tooth, the canal decreased noticeably in diameter, but remained in contact with the lower wall of the bract. Thus as the thickness of the mesogloea and the bract itself decreased the canal followed the contour of the lower surface and curved upwards. In younger bracts (Figure 82, right), however, the canal remained thickened for most of the length of the bract, tapering only towards the distal end. The bracteal canal remained in contact with the lower wall throughout most of its length, but close to its distal end it penetrated into the mesogloea and ran obliquely toward the upper surface, where it ended below a small oval processes, on the upper side of the bract close to its distal tip.

It is presumed that a cluster of small nematocysts once occupied this area, but on most bracts they been detached. Between 3 and 7 oval ectodermal patches of differing size were observed, distributed randomly (not paired) on the upper surface on either side of the mid-line, although due to their tendency of being abraded, their number varied somewhat.

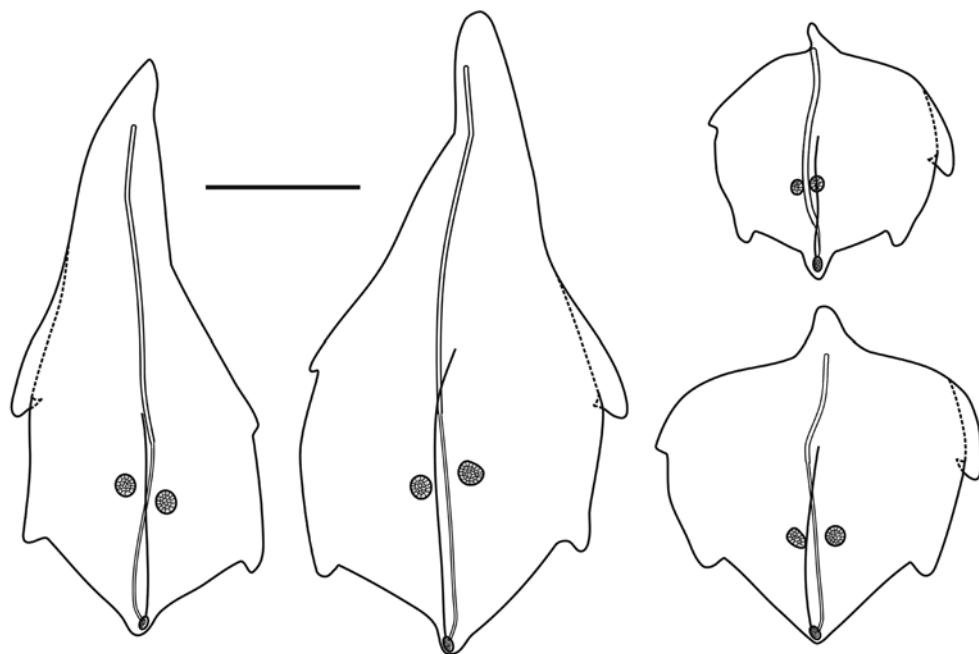


**FIGURE 83.** *Halistemma maculatum* sp. nov. Upper views of Type B bracts. Proximal at top, distal at bottom. Scale bar 5 mm.

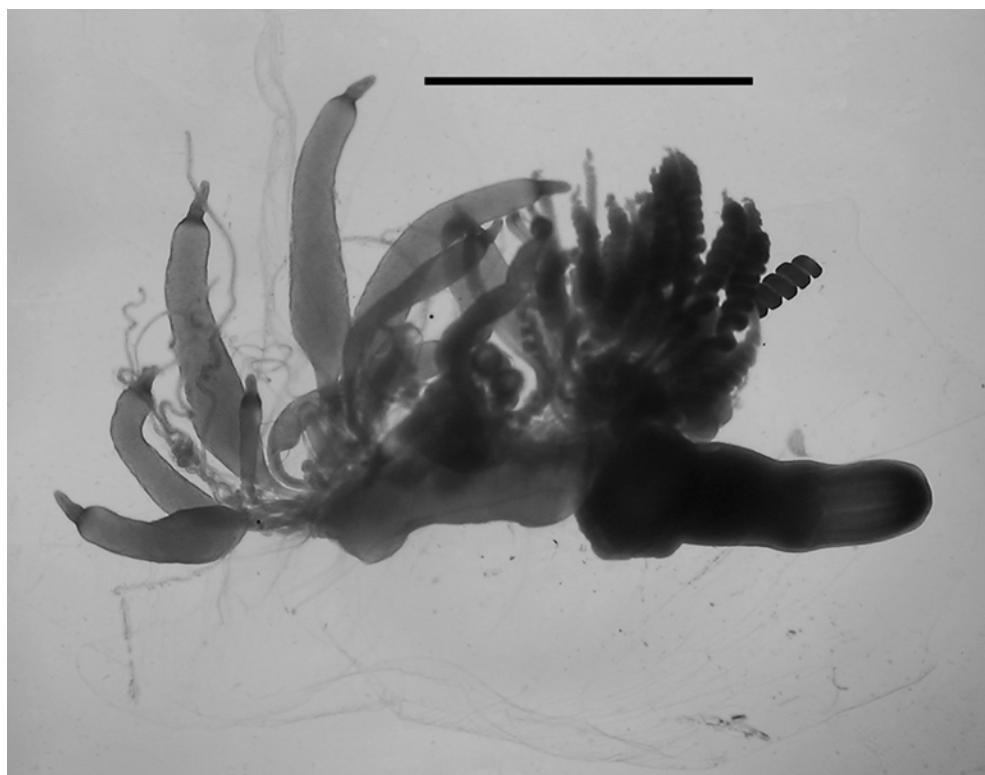
*Type B*—This was the most numerous type with forty-five bracts in enantiomorphic forms being present with the holotype (Figure 83). They were quite elongate, asymmetrical and widened at the distal end, measuring from 9 to 20.5 mm in length and from 5.5 to 12 mm in width. There were four lateral teeth that were asymmetrical and misaligned. The inner proximal one was longer and more pointed than the others, while the inner distal one was often reduced to a slight bump. There was only one ectodermal cell patch on the outer half of the upper surface of the distal part of each bract. A distinct conical, pointed process formed the proximal end of the bract. A medial ridge stretched from approximately the mid-length of the bract to almost the distal end on its upper surface. The bracteal canal originated at approximately one sixth of the length of the bract, from its proximal end, and on the inner lateral surface. It narrowed on a level just below the proximal end of the median ridge, but only penetrated into the mesogloea close to the distal tip, where it ran diagonally up to end below a small cupulate structure on the upper side of the bract. In the proximal region of the bract the mesogloea on the outer half of the bract was thickened. This thickening continued, in the central region of the bracts, around the mid-line, and thinning towards the lateral edges forming a thin and flimsy convexo-concave surface on the under side. The bracteal canal ran down the middle of this thickening and so there was no marked change in its course as found in the type A bracts.

*Type C*—These bract, twenty-seven in number, were somewhat similar to the previous type but less asymmetrical and with a pair of ectodermal patches on the upper surface, in the distal half (Figure 84). They were also the most variable in shape, which appears to be age related, with the smaller ones being more rounded, while the larger older ones were elongate. They ranged in size from 5.5 to 22 mm in length and from 3.5 to 10 mm in width. There were two pairs of slightly misaligned lateral teeth, with the inner proximal tooth being somewhat smaller than the others and there was a small infolding at the level of the outer proximal one. A median ridge, on the upper surface, extended from just below the distal end for just under half of the length of the bract. Proximal to the origin of the bracteal canal, on the inner side of the bract, the mesogloea was relatively thick and formed a cylindrical process. Distal to this the mesogloea was thicker in the outer half, but also tapered down distally, so that the bracteal canal formed a smooth upward curve as it ran distally. In the larger bracts the thickened portion

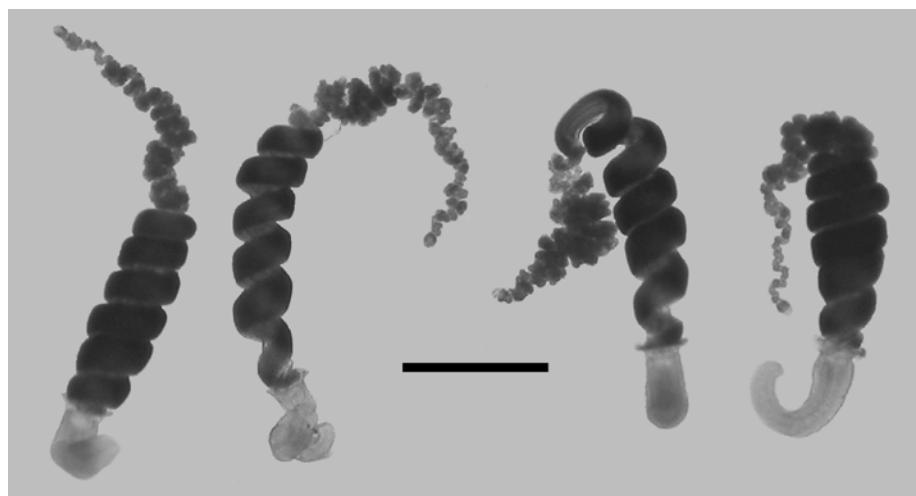
extended to approximately the same level as the proximal inner tooth, while in the younger ones it remained thickened for most of its length, only tapering when it entered the mesogloea before ending below the small cupulate process on the upper surface.



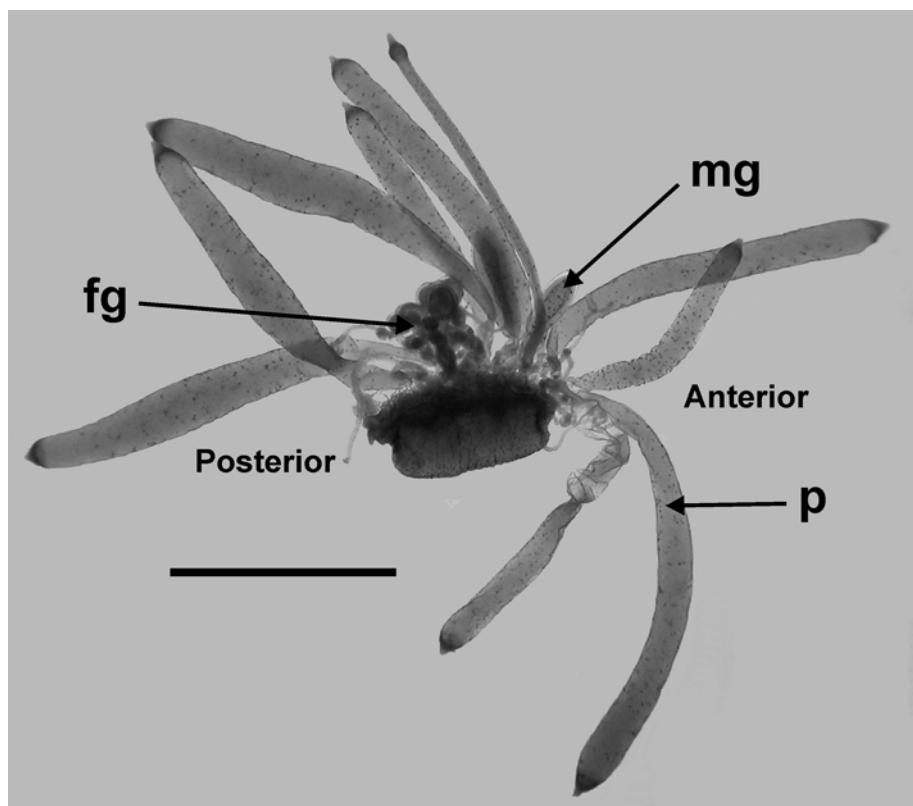
**FIGURE 84.** *Halistemma maculatum* sp. nov. Upper views of Type C bracts. Proximal at top, distal at bottom. Scale bar 5 mm.



**FIGURE 85.** *Halistemma maculatum* sp. nov. Piece of siphosomal stem from holotype, showing a gastrozooid and tentacle, and several palpons with palpacles. Scale bar 5 mm.



**FIGURE 86.** *Halistemma maculatum* sp. nov. Mature tentilla from type specimen. Proximal at top, distal at bottom. Scale bar 1 mm.



**FIGURE 87.** *Halistemma maculatum* sp. nov. Piece of stem from JSLII Dive 2646-CG3 specimen. **fg:** female gonophores; **mg:** male gonophore; **p:** palpon. Scale bar 5 mm.

*Gastrozoid and tentacle:* The gastrozooids (Figure 85) were variable in form and measured up to c. 5.5 mm in length. There was a distinct basigaster.

*Tentilla:* The mature tentilla are shown in Figure 86. At the distal end of the highly contractile pedicel was a very small, almost vestigial involucrum, which hardly covered any of the cnidoband. The cnidoband usually consisted of six spiral coils, which were usually closely wound but occasionally somewhat looser. Two types of nematocysts were present; stenoteles and, probably, anisorhizas. The stenoteles, whose capsules measured 68 x 25  $\mu\text{m}$ , were few in number and were found only on the outer edges of the proximal one or two spirals of the cnidoband. The other banana-shaped nematocysts were variable in size ranging from 39 to 69  $\mu\text{m}$  in length and 6.5 to 9  $\mu\text{m}$  in diameter. Large numbers of platelets, 8–9  $\mu\text{m}$  in diameter, were visible on the cnidoband. The long

terminal filament bore two types of nematocysts; probably acrophores, c. 18.5 x 9  $\mu\text{m}$ , and desmonemes, c. 22 x 9  $\mu\text{m}$ , as discussed above. The terminal filament ended in a process that was acorn-shaped, with a cupulate proximal part. This process was considerably smaller than that found on the tentilla of *Halistemma cupulifera*, and measured c. 180  $\mu\text{m}$  in length and 100  $\mu\text{m}$  in diameter, with the cupulate proximal part occupying slightly under half the length. This part contained small nematocysts, c. 14 x 9  $\mu\text{m}$ , while the distal part was covered in platelets, about 16  $\mu\text{m}$  in diameter.

*Palpon:* The thin-walled, narrow palpons were featureless apart from a darker papilliform distal end (Figures 85, 87). They measured up to 6.5 mm in length. They possessed a long narrow palpacle, but no nematocysts were found on it or on the palpon itself.



**FIGURE 88.** *Halistemma maculatum* sp. nov. Male (top) and female (bottom) gonophores from JSLII Dive 2646-CG3 specimen. Proximal at top, distal at bottom. Scale bar 1 mm.

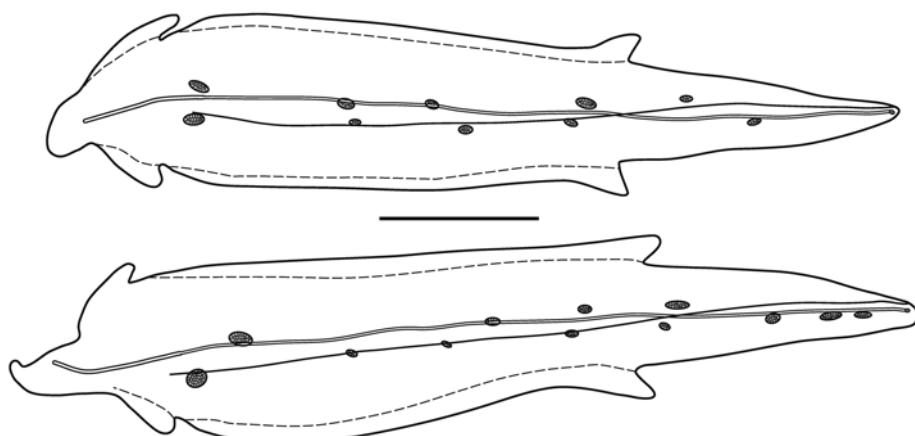
*Gonophore:* The single male gonodendron was attached immediately posterior to a gastrozooid and the female one, with its thickened stalk, immediately followed it. The mature male gonophores were elongate structures (Figure 88) measuring up to 3 mm in length and 0.9 mm in diameter. The female gonophores (Figure 88) were almost spherical, with a short triangular pedicel and a widely open mouth. They measured up to 1.2 mm in length and 1 mm in diameter. No nematocysts were found on the gonophores of either sex.



**FIGURE 89.** *Nectalia* stage of *Halistemma maculatum* sp. nov. from JSL II Dive 1679. Scale bar 5 mm.

*Nectalia*-stage: Five of the specimens of *Halistemma maculatum* sp. nov. were at the post-larval *Nectalia*-stage of development (see *Material examined*), of which three were collected during a single dive. One of these, with a nectophore and a C-type bract still attached is shown in Figure 89. The nectosome bore up to eighteen nectophores that did not differ from those of adult specimens. The short siphosome, in live, bore a corona of long larval bracts (Figures 90, 91) that, in their preserved state measured up to 32.5 mm in length. They bore two pairs of distinct

lateral teeth, and a series of irregularly sized and positioned ectodermal patches was present on the upper side of the bract for much of its length (Figure 90). However, abrasion often made these patches difficult to see. There was a median longitudinal ridge on the upper side of these bracts that ran from their distal end to the approximate level of the proximal pair of lateral teeth. However, in the proximal half of the bract this ridge was only weakly defined. The mesogloea was thickest at the proximal and distal ends of the bract, and in the central part of the bract the lateral sides delimited a distinct concave cavity. The distal end of the bract was triangular in cross section. The bracteal canal originated close to the proximal end of the bract and followed the median line on the lower side of the bract; thereby firstly curving slightly upwards and then downwards. It entered the mesogloea close to the distal tip of the bract, curling upwards and then straight toward the distal point ending below a small cupulate process. Only in this final section did the canal show signs of narrowing. The cupulate process was relatively large in the younger bracts, and was filled with nematocysts; but when the latter were lost or used up the cavity decreased in size. Adult bracts were often found, in small numbers, with these *Nectalia*-stage specimens, and were either of the A- or, more commonly, the C-type.



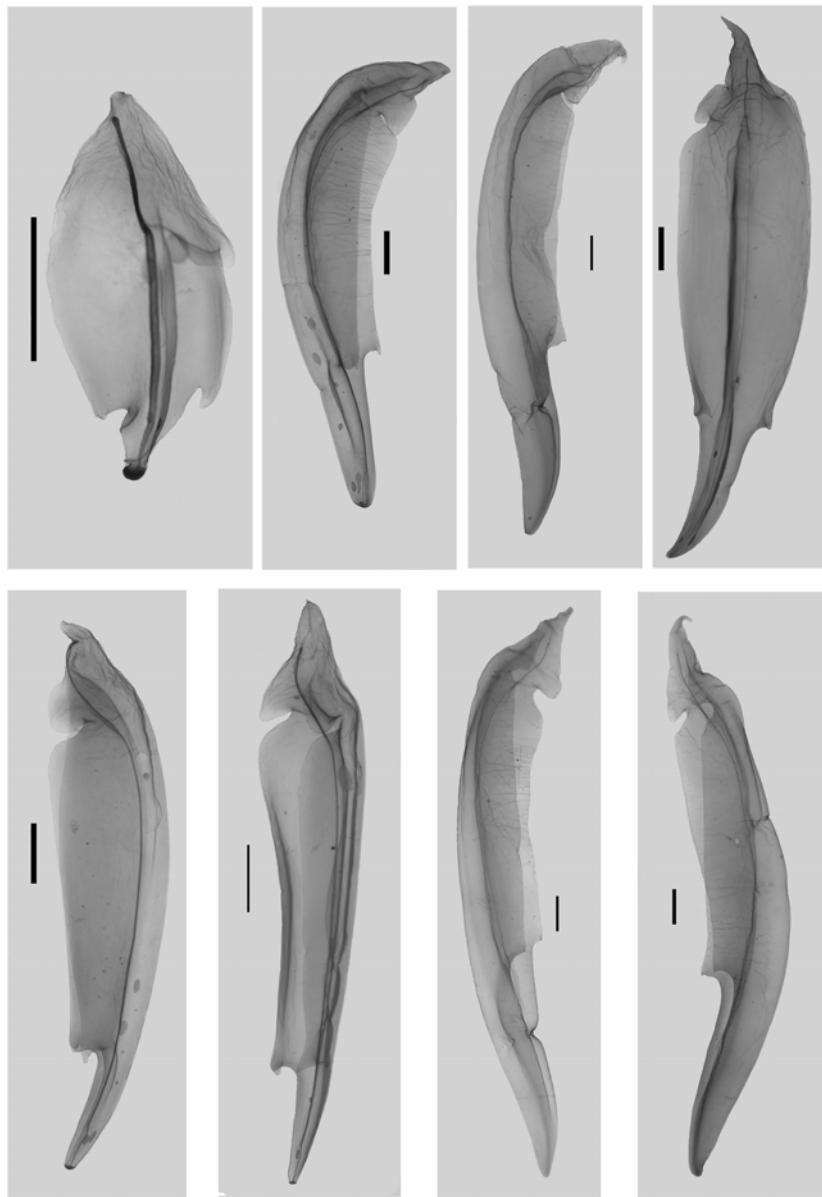
**FIGURE 90.** *Halistemma maculatum* sp. nov. Upper views of *Nectalia*-stage bracts of JSLII Dive 996-SS4 specimen. Proximal to the left. Scale bar 5 mm.

The short siphosomal stem typically bore two or three gastrozooids, including the protozooid, and a number of palpons, usually about five per gastrozooid. Larval type tentilla branched from the tentacle of the protozooid, while the other gastrozooids had tentacles with adult type tentilla. The larval tentilla (Figure 92, A) somewhat resembled those that D. Carré (1971, Plate II, fig. 1) illustrated for *Halistemma rubrum*, but there were certain notable differences. The tentilla were borne on long contractile pedicels and consisted of a sac, enclosing the cnidoband and a double elastic band, with a domed terminal process, with a short terminal filament projecting out from its distal summit.

The terminal process and filament bore no nematocysts, and the former often was annulated. Immediately proximal to the terminal process a dark band formed the beginning of the cnidoband, which stretched down one side of the enclosing sac for about two-thirds of its length. Two types of nematocysts were found. A row of about 25 stenoteles was present on either side of the cnidoband, but only on its distal two-thirds, that is the part closer to the pedicel. These stenoteles measured c. 65 µm in length and 27.5 µm in diameter. The remainder of the cnidoband was filled with banana-shaped nematocysts, probably anisorhizas, which measured c. 40 µm in length and 6.5 µm in diameter.

In some, but not all, of the *Nectalia*-stage specimens of *Halistemma maculatum* sp. nov. the palpons (Figure 92, B) showed certain differences from the ones found on the adult specimens. The distal proboscis region was often more pronounced, with a dark subterminal annular structure. In addition and usually, but not always, at the proximal end of the palpon there were included darker structures that were made up of variously sized oil globules. On occasion these structures projected out from the side of the palpon.

*Remarks:* As noted in the remarks on *Halistemma cupulifera*, Totton (1954) found two forms of nectophores, which he called "e-type" and "f-type", and which he ascribed to *Halistemma rubrum*. We believe that the "e-type" nectophores belong to *H. cupulifera*, and that the "f-type" ones (Figure 93) belong to this new species, *H. maculatum* sp. nov., although it is difficult to be certain of this.



**FIGURE 91.** Upper view of Type A (top left) and various views of *Nectalia*-stage larval bracts (all others) of *Halistemma maculatum* sp. nov. from JSLII 1679-CG12 specimen. Proximal at top, distal at bottom. Scale bars 2 mm.

Nevertheless, the nectophores of *Halistemma cupulifera* and *H. maculatum* sp. nov. are of a similar size. For both a mouth plate is present and the vertical lateral ridges are complete. The main difference between them is that in *H. cupulifera* the axial wings are squarely truncated and the thrust block extends to the same level, whereas in *H. foliacea* the axial wings are obliquely truncated and the broader thrust block does not extend to their level. However, such differences would probably not be apparent on specimens that were collected and probably mutilated by nets, such as Totton's specimens (Figure 93).

The form of the different types of bract for each of these two species is very different and should clearly distinguish them, as might the arrangement of the gonodendra. However, the clear distinguishing feature is the structure of the tentilla. The terminal filament of the tentillum of *Halistemma cupulifera* ends in a very large cupulate process, while the terminal process on the filament of *H. maculatum* sp. nov. is very small (cf. Figures 34 and 86).

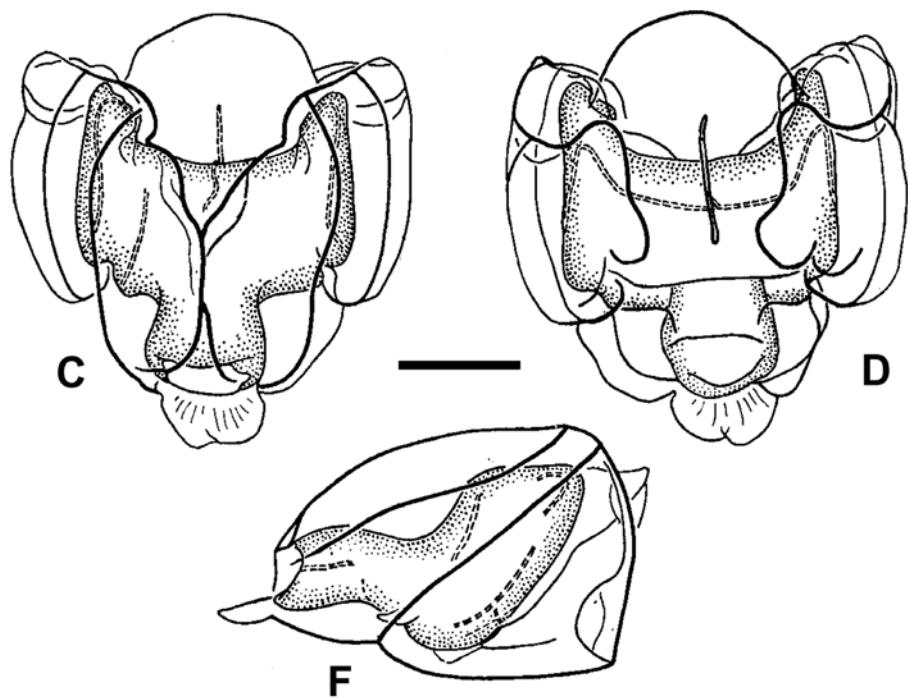
*Distribution:* All the specimens were collected in the region of the Bahamas, within an area only slight over a degree square. As well as the specimens examined, two others, from the same region, are known. These are:

JSLI Dive 2631-DS6, 2 November 1989, 26°22.5'N 78°38.3'W, depth 777m

JSLI Dive 2634-DS7, 4 November 1989, 26°14.1'N 77°43.9'W, depth 806 m.



**FIGURE 92.** *Halistemma maculatum* sp. nov. **A.** Larval tentilla, and **B.** palpons from JSLII 1679-D6 *Nectalia*-stage specimen. Scale bars 1 mm.



**FIGURE 93.** "F-type" nectophores, probably of *Halistemma maculatum* sp. nov., from Totton (1954, Text—fig. 16, C, D, F) Scale bar 2 mm.

Apart from the specimens from JSLII Dive 716 and 1679-CG12—the former's depth of collection being rather dubious and the latter's unrecorded; all the specimens were collected with the moderately narrow depth range of 568 to 837 m. The mean depth for all the specimens was  $727 \pm 91.45$  m, with the five "Nectalia" stage specimens tending to be among the shallower occurring ones (mean depth  $651 \pm 80.5$  m).

Totton's (1954) "f-type" nectophores of *Halistemma rubrum* came from *Discovery* St. 1586 at  $2^{\circ}39.4'N$   $50^{\circ}46.4'E$ , in the Indian Ocean off Somalia and possibly also from *Mahabiss* St. 145 at  $4^{\circ}59'S$   $73^{\circ}16'E$ , central Indian Ocean to the south of the Maldives.

*Etymology:* The species is named for the ectodermal patches or maculae found on the nectophores and bracts.

## Family Stephanomiidae Huxley, 1859

Huxley (1859) established the Family Stephanomiadæ to include four genera, namely *Halistemma*, *Forskalia*, *Stephanomia*, and *Agalma*. He differentiated between the various genera primarily on the presence or absence of an involucrum at the proximal end of the cnidoband of the tentillum. As noted above, he believed that such a structure was absent on the species of both the genera *Halistemma* and *Forskalia*, while it was present for the other two. Huxley then distinguished between the latter two genera on the basis of the unicornuate (*Stephanomia*) or tricornuate (*Agalma*) arrangement of the tentillum.

As the recent studies by Dunn *et al.* (2005a) have shown the grouping of these four genera together into a single family is no longer tenable. *Halistemma* and *Agalma* belong to the family Agalmatidae as their nectophores are budded off on the dorsal side of the stem. Although, like these two genera, *Forskalia* is monoecious and has both ascending and descending mantle canals, its nectophores are borne on the ventral side of the stem and, because of their multiserial arrangement, the genus has long been considered to belong to a distinct family, the Forskaliidae Kölleker, 1853. The genus *Stephanomia* stands alone. It belongs to the dioecious group of physonect siphonophores, with only an ascending mantle canal. The studies by Dunn *et al.* (2005a) required considerable changes to the systematics of physonect siphonophores, and resulted in several genera, previously included in the catch-all family Agalmatidae, having an uncertain systematic position (see Pugh, 2006). Although the data clearly indicated that *Stephanomia* belonged in the dioecious clade of physonects, the position of certain genera, for instance *Marrus*, remain uncertain as they were not included in the original analysis. The genus has been included (Pugh, 2006) within the dioecious clade despite the fact that specimens of one species appear to be monoecious. This has also been found to be the case for certain undescribed *Bargmannia* species (Pugh, personal information). The taxonomic position of *Marrus* was further discussed by Dunn *et al.* (2005b), who noted that there were important variations in some of the more general characters across the known species, including the absence of a muscle-free zone on the nectosac of *M. orthocannoides* Totton, which was present in the other species. It seems clear, therefore, that some of the species presently included in the genus *Marrus* may not belong there, as is the case for several undescribed species that have tentatively been associated with that genus. More morphological and genetic studies are required before the systematic position of that genus can be properly established.

However, there are certain characters of *Stephanomia amphyridis* that clearly distinguish it from all other physonects, and these are deemed of sufficient importance to warrant the re-establishment of the family Stephanomiidae. The very distinctive ridge pattern on the nectophores sets this species apart, as does the course of the lateral radial canals on the nectosac. Almost all of the known dioecious physonect species have straight lateral radial canals; the exception being *Pyrostephos vanhoeffeni* Moser. But that species has other characters that clearly set it apart. Palpons are present on specimens of *S. amphyridis* but are often absent on other dioecious species. For many species the cnidoband of the tentillum is straight, e.g. families Erennidae and Pyrostephidae, although for *Marrus* they, like *S. amphyridis*, are loosely coiled, without an involucrum and with a single terminal filament.

## Genus *Stephanomia* Lesueur & Petit, 1807

Monotypic for *Stephanomia amphyridis* Lesueur & Petit, 1807.

*Diagnosis:* (see under *Stephanomia amphyridis*).

*Remarks:* As noted in the Introduction a variety of physonect siphonophoran species have been described

under the generic name *Stephanomia*, first established by Lesueur & Petit (1807) based on a drawing of part of the siphosome of a, presumably, large physonect that they called *S. amphytridis*. Further authors have described specimens, again usually of only siphosomal fragments, that they believed belonged to this species but, as has been discussed above, many of these descriptions can actually be attributed to a little known species, *Halistemma foliacea*, that was briefly described and poorly illustrated by Quoy and Gaimard (1833, 1834). Thus the detailed descriptions of the siphosome *Stephanomia amphytridis* [sic] given by Huxley (1859) and Bigelow (1911), and another mentioned by Kawamura (1954) have all now been associated with *H. foliacea*, as has that of *S. amphytridis* given by Mapstone (2004).

As will be discussed below, although the specimens that we here attribute to *Stephanomia amphytridis* are indeed large, there appear to have been few previous records, e.g. Totton (1936, 1965) and Daniel (1974, 1985), and only the latter author has given any illustrations, although Totton had started on a manuscript to describe the species. These authors, questionably, attributed the species to the genus *Halistemma* although, as noted above, Daniel (1985) did comment that her nectophore differed considerably from a typical *Halistemma* nectophore. None the less, as we shall see, *S. amphytridis* does have some characters in common with *Halistemma* species, not least the fact that they both go through a post-larval *Nectalia-* stage.

### ***Stephanomia amphytridis* Lesueur & Petit, 1807**

*Stephanomia amphytridis* Lesueur & Petit, 1807, pl. 29, fig. 5; Lamarck, 1816, p. 462; 1840, p. 25; Bedot, 1896, p. 382; Totton, 1954, p. 46; Bonnemains & Carré, 1991, fig. 1 (5); Dunn *et al.*, 2005a, p. 2005; Dunn & Wagner, 2008, p. 752; Lindsay, 2006, p. 105; Pugh, 2006, p. 42; Burton & Lundsten, 2008, p. 30 (fig.); Cartwright *et al.*, 2008, p. 4 Lindsay & Miyake, 2009, p. 419; Pugh & Gasca, 2009, p. 399.  
*Stephanomia amphitritis* Tilesius, 1814, p. 181; Cuvier, 1817, p. 65; 1830, p. 288; 1843, p. 206; Eschscholtz, 1825, p. 744; 1829, p. 155; Lesson, 1830, p. 62; Griffith & Pidgeon, 1834, p. 492; Oken, 1825, p. 744; 1835, p. 197; Leuckart, 1854, p. 321; L. Agassiz, 1862, p. 368; Claus, 1878, p. 272.  
? *Stephanomia levigata* Quoy & Gaimard, 1825, p. 585, Pl. 86, fig. 2.  
*Stephanomia amphitrides* Blainville, 1830, p. 108; 1834, p. 119.  
*Stephanomia amphitridis* Lesson, 1843, p. 476, Pl. 10, fig. 1; 1841, p. 197; Leuckart, 1861, p. 197; Schneider, 1898, p. 118; Totton, 1936, p. 236; Leloup, 1955, p. 13.  
*Stephanomia Amphitritidis* Leuckart, 1854, p. 341; 1875, p. 455.  
*Stephanomia amphitrites*; Haeckel, 1869, p. 45; 1888a, p. 40; 1888b, p. 184, p. 221; Claus, 1872, p. 190.  
*Cupulita amphitrites*, Bedot, 1896, p. 408.  
*Halistemma Amphitrites* Claus, 1876, p. 238  
"? *Halistemma amphytridis*" Totton, 1965, p. 60; Daniel, 1974, p. 47, text—fig. 3, H–J;  
*Halistemma amphytridis* Daniel, 1984, p. 75, fig. 16, a–b; Bonnemains & Carré, 1991, fig. 12; Carré & Carré, 1995, p. 565; Haddock & Case, 1999, p. 575; Hunt & Lindsay, 1999, p. 80, figure 5A; Poupin *et al.*, 1999, p. 20.  
*Halistemma amphytridis* Daniel, 1973, p. 867; Ortman *et al.*, 2010, p. 2150; Bucklin *et al.*, 2010, p. 2238.  
*Halistemma amphytridens* Stepanjants, 1967, p. 127; 1977a, p. 55.  
*Halistemma aff. amphytridis* Lindsay & Hunt, 2005, p. 506.  
? *Stephanomia* sp. Lens & van Riemsdijk, 1908, p. 84, Pl. XV, figs. 113–114.  
non *Stephanomia Amphitritis* Chamisso & Eysenhardt, 1821, Pl. XXXII, fig. 5 = *Agalma okeni*.  
non *Stephanomia amphytridis* Huxley, 1859, p. 72, Pl. 6; Bigelow, 1911, p. 287, pl. 18, figs. 1–8; Kawamura, 1954, p. 110 = *Halistemma foliacea*.  
non *Stephanomia nereidum* Haeckel, 1888a, p. 40, 1888b, p. 221 = *nomen nudum*.  
non *Halistemma amphytridis* Mapstone, 2004, p. 231, figs. 1–3; Araujo, 2006, p. 49 = *Halistemma foliacea*.

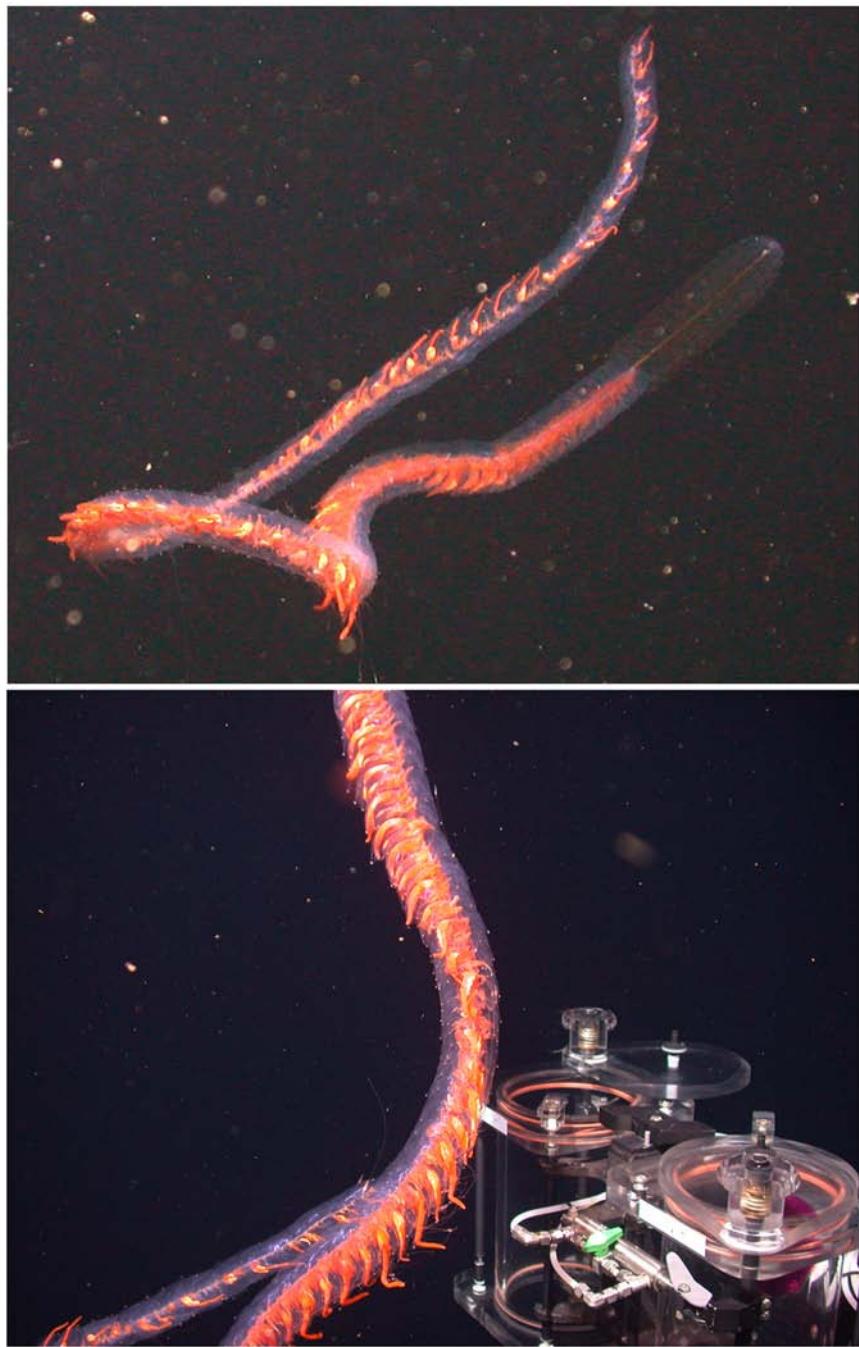
The family Stephanomiidae fam. nov., monotypic for the species *Stephanomia amphytridis*, belongs to the dioecious clade of physonect siphonophores (Dunn *et al.*, 2005). That clade is characterised by the following characters:

Each colony is of a single sex; although there appear to be exceptions to this in the genera *Marrus* and *Bargmannia*;

The nectophores have only an ascending mantle canal;

The nectophores, with the exception of the family Rhodaliidae, possess a muscle-free zone at the proximal end of the nectosac; usually more prominent on the lower side;

The lateral radial canals on the nectosac are usually without major loops; with the major exception being *Stephanomia amphytridis*;



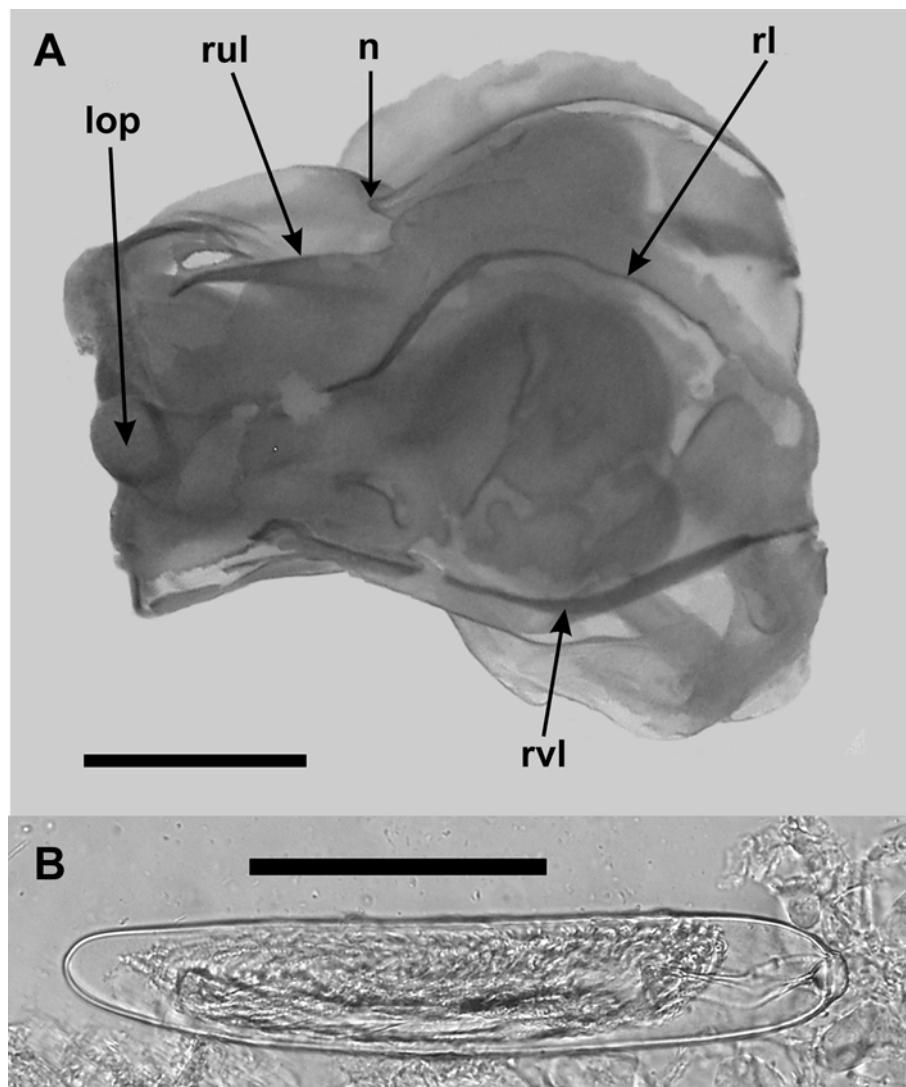
**FIGURE 94.** *Stephanomia amphyridis*. *In situ* photographs of specimen from Tiburon Dive 746. The length of the "detritus" sampler in view, including the lids, is 12 inches. (Photographs courtesy of Dr. S.H.D. Haddock, © MBARI.)

The nectophores are budded off on the ventral side of the nectosome.

Other characters, such as the ridge pattern on the nectophore, the structure of the tentillum, and the presence or absence of palpons, are often of familial or generic significance.

*Diagnosis:* *Stephanomia amphyridis* is dioecious; its nectophores are budded off on the ventral side of the stem, and the mature ones have an extensive muscle-free zone on the proximal, lower side of the nectosac. Only an ascending mantle canal is present. The sinuous course of the lateral radial canals is very characteristic; as is the ridge pattern that, uniquely, includes a divided vertical lateral ridge complex.

The presence of palpons, and a tentillum, with a loosely coiled cnidoband, without involucrum, and a single terminal filament are characters that help to separate this genus from certain other dioecious genera.



**FIGURE 95.** *Stephanomia amphyridis*. A. Lateral view of nectophoral bud from Tiburon Dive 746 specimen. lop. lateral ostial process; rl, rul, and rvl lateral, upper lateral, and vertical lateral ridges, respectively; n. notch. Scale bar 2 mm. B. Nematocyst from lateral ostial process. Scale bar 100 µm

*Material examined:*

JSL II Dive 1457-DS8	3 <sup>rd</sup> September 1987	24°00.7'N	82°16.6'W	Depth 829 m.*
JSL II Dive 1685-CG5	10 <sup>th</sup> October 1988	26°27.8'N	77°58.9'W	Depth 846 m.*
JSL I Dive 2138-DS2	2 <sup>nd</sup> August 1987	39°56.7'N	70°14.9'W	Depth 777 m.*
JSL I Dive 2644-CG2	9 <sup>th</sup> November 1989	26°02.0'N	77°32.0'W	Depth 869 m.*
JSL II Dive 2667-DS8	17 <sup>th</sup> September 1995	c. 27°N	c. 85°W	Depth unknown
JSL II Dive 2677-DS4	22 <sup>nd</sup> September 1995	c. 27°N	c. 84°W	Depth unknown
JSL I Dive 3272-DS1	No Station data available			
Tiburon Dive 746-D4	6th October 2004	35°28.8'N	123°51.9'W	Depth 1161 m.†
Tiburon Dive 1074- SS9	23rd January 2007	35°50.1'N	122°40.1'W	Depth 1158 m.*†
Tiburon Dive 1110-SS12	1st August 2007	35°23.0'N	122°40.0'W	Depth 1401 m. †

\* Nectalia stage. † *in situ* frame grabs.

Thanks to the kindness of Susan Svonthun, from the Video Laboratory at MBARI, a brief video of the specimen of *Stephanomia amphytridis* collected at 1401 m during Tiburon Dive 1110 will be placed on the website [www.youtube.com/user/MBARIvideo](http://www.youtube.com/user/MBARIvideo).

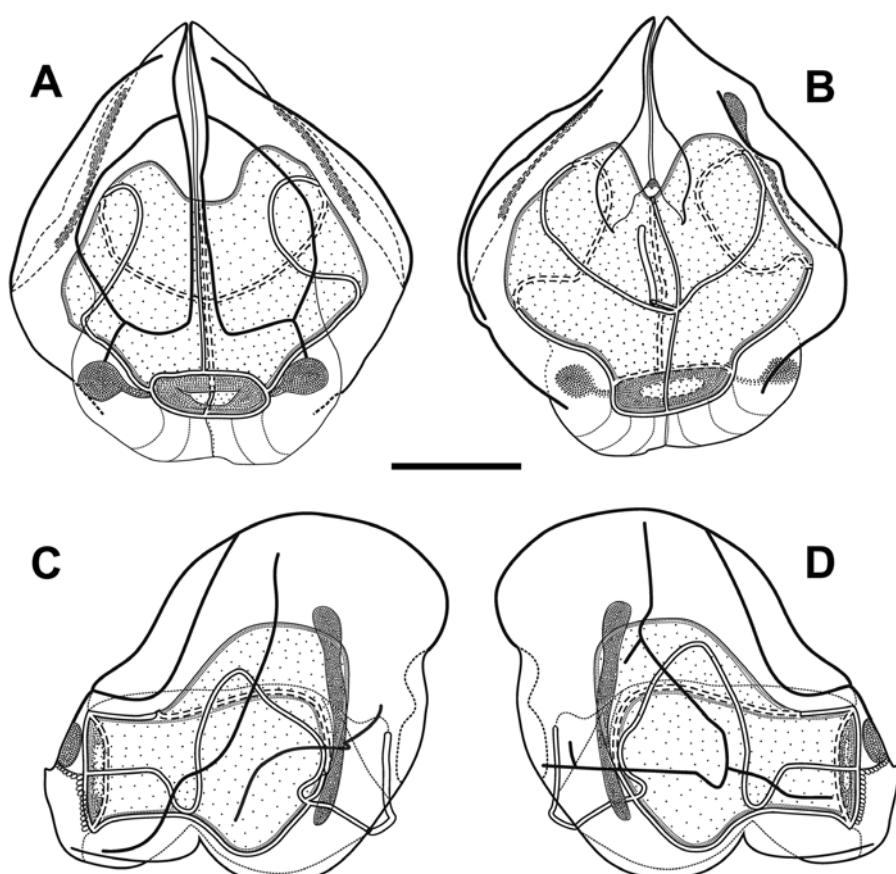
**Description:** Two photographs of a large specimen, part of which was collected during Tiburon Dive 746, are shown in Figure 94. The specimen was probably c. 5 metres long and was very robust, with a rigid siphosome and over 25 large nectophores in the nectosome.

**Pneumatophore:** The pneumatophore was featureless and bore no signs of pigmentation. In its preserved state it measured c. 7.6 mm in length and 3.8 mm in diameter. It was borne on a very muscular stalk that clearly could relax and extend itself considerably so that the pneumatophore would appear well above the nectosome.

**Nectosome:** The very large nectophores were budded off on the ventral side of the nectosome and, usually, there were numerous nectophoral buds at its anterior end.

**Nectophores:** The basic ridge pattern on the nectophores was very similar to that of *Halistemma* species, and consisted of pairs of upper and lower laterals, laterals and what will be referred to as the "vertical lateral ridge complex".

At the bud stage (Figure 95A) these ridges were very distinct and all were completely separate from each other. The upper laterals had a distinct notch in them. The nectosac filled almost the entire nectophore, with the axial wings being undeveloped and the thrust block very small. The mantle and pedicular canals were very prominent. The lateral ostial processes were extremely well-developed, forming hemispherical structures comprised of numerous darkly-staining ectodermal cells that surrounded a central core of 40–50 nematocysts (Figure 95B). These nematocysts measured c. 260 x 50  $\mu\text{m}$  and possibly were the same as those found at the tips of the bracts (see below).



**FIGURE 96.** *Stephanomia amphytridis*. **A.** Upper, **B.** lower and **C.** left and **D.** right lateral views of small nectophore From JSLI Dive 2138. Scale bar 2 mm.

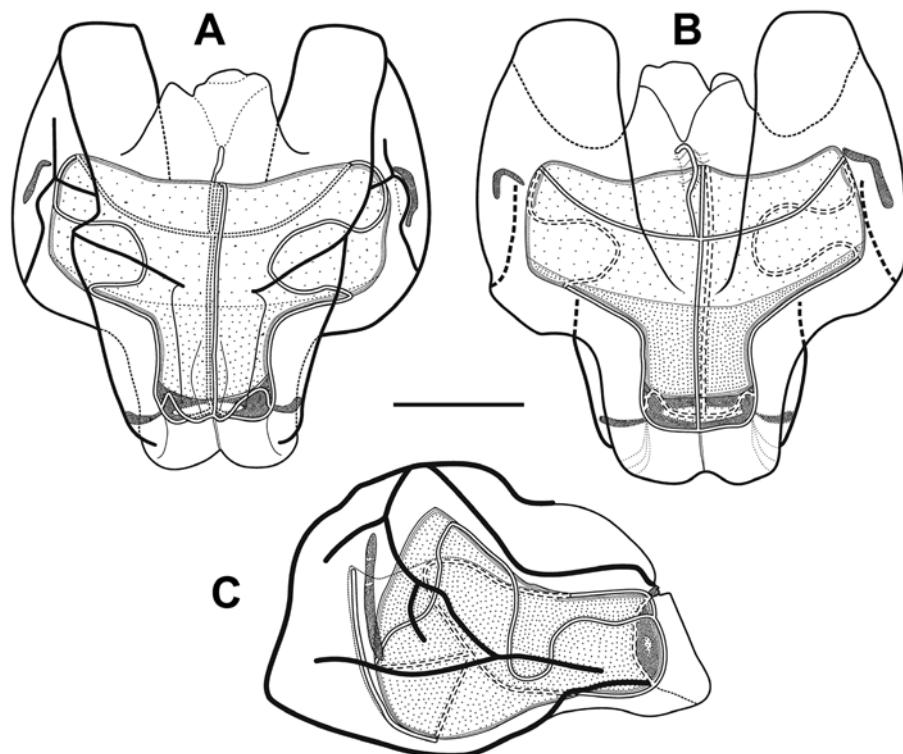
A very young nectophore, measuring 6.5 mm in all directions, is shown in Figure 96. The narrow axial wings were closely apposed to each other, and the thrust block remained as a small process on a mesogloal swelling. The

upper and lower lateral ridges merged at the proximal end of the nectophore. The latter ran down the lower side, at first close together, but then diverging, before petering out at about half the height of the nectophore (Figure 96B). The upper laterals also remained together for most of their course but, slightly above the ostial level, they curved outwards through 90° and continued laterally until they joined the lateral ridges. The lateral ridges branched from the upper laterals above the apex of the nectosac and were first directed obliquely downwards before curving through 90° and running parallel to the nectosac. After the upper laterals had joined them they continued to end just above the much reduced lateral ostial processes.

What we will refer to as the vertical lateral ridge complex appeared to become more complex as the nectophores developed. In fact, for the very small nectophore shown in Figure 96, that on the right side of the nectophore differed from that of the left. On the left side (Figure 96C) there were two entirely separate ridges, neither of which connected with any other ridge. The more proximal one lay in the lower half of the nectophore, while the more distal one was longer and extended from a short distance away from the upper lateral obliquely down to end almost below the ostium. On the right side (Figure 96D) the two ridges had become joined together and each bore an additional side branch.

The canal system was very characteristic. There was an ascending mantle canal extending down from just below the apex of the thrust block along a mesogloal protuberance, until it gave rise to the pedicular canal. This ran directly to the lower proximal side of the nectosac where it gave rise directly to all four radial canals. The upper and lower canals had a straight course to the ostial ring canal, while the laterals first ran upwards and slightly proximally to the lateral sides of the nectosac. There they formed a broad loop upwards and then downwards, to the lower side of the nectosac, before looping back up to its mid-height and then curving and running directly to the ostial ring canal. At this stage of development there was no sign of a muscle-free zone on the nectosac.

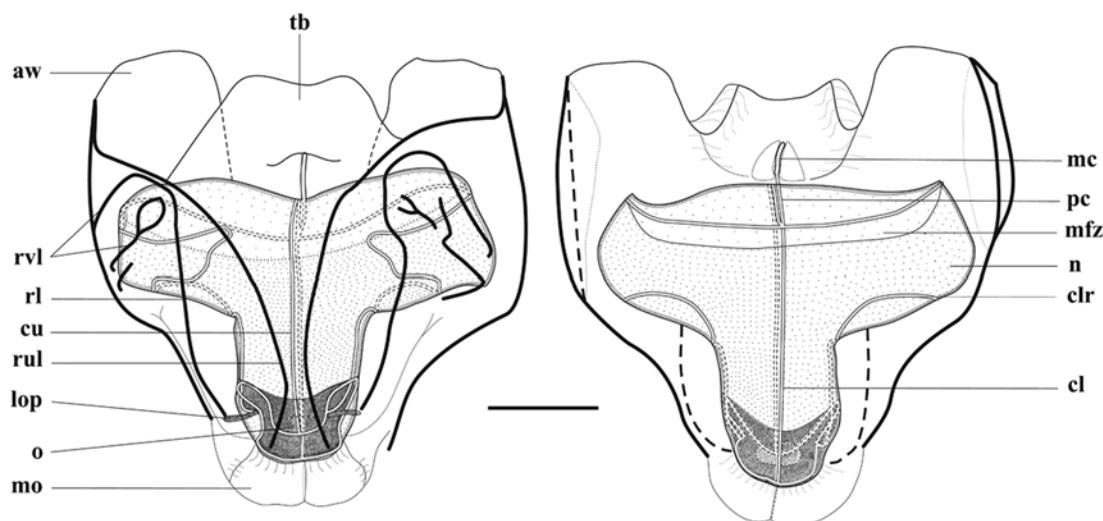
The mouth plate was a thickened structure surrounding the basal half of the ostium. The lateral ostial processes were circular areas with a stalk-like area connecting them to the ostium. They no longer bore nematocysts, just darkly staining ectodermal cells that possibly were sites of bioluminescence. Large, totally transparent cells were present in a single row below the point of insertion of the lateral radial canals onto the ostial ring canal. There was also, on each side, a long patch of ectodermal cells, which was easily detached, on the lateral sides of the nectophore in its proximal half.



**FIGURE 97.** Upper (A), lower (B), and lateral (C) views of medium-sized nectophore of *Stephanomia amphyridis* from T1074-SS9 specimen. Scale bar 5 mm.

A medium-sized nectophore is shown in Figure 97. The ridge pattern was now clearly defined with the upper laterals uniting with the lower laterals at the proximal end of the axial wings. The upper laterals remained widely apart in the proximal half of the nectophore, and then began to approach each other rapidly, before turning toward the ostium. From then on they were considerably narrowed and much less obvious. The lower laterals extended along the lower lateral side of the nectophore to end at the base of the mouth plate. The vertical lateral and lateral ridges arose separately, but quite close together, from the upper lateral ridges. The laterals were first directed obliquely downwards and then curved to run distad to the thickened sides of the mouth plate. The vertical lateral ridge complex was now more clearly defined and consisted of an oblique ridge extending down from the upper lateral ridge to join a longitudinal ridge on the lower lateral side of the nectophore. During its course it gave off two separate branches.

The course of the radial canals was almost the same as that described above. The long ascending mantle canal ran over the surface of a pronounced mesogloal thickening before giving rise to the pedicular canal. The latter did not give rise directly to all four radial canals, as the upper canal arose a short distance along the right lateral canal. By this stage the nectosac clearly had a muscle-free zone on its lower side in its proximal half, although this was not apparent in lateral view. The mouth plate was well developed and thickened laterally, with a pronounced median indentation. The giant ganglion could clearly be seen traversing the mouth plate and extending to the lower side of the ostium.



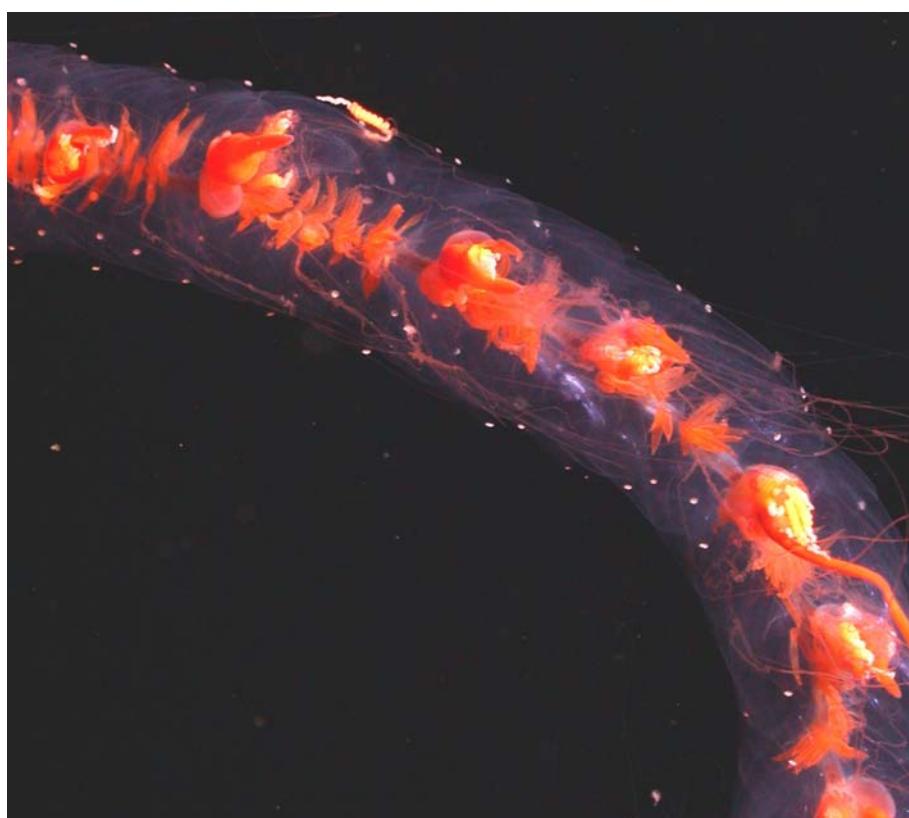
**FIGURE 98.** *Stephanomia amphytridis*. Upper (left) and lower (right) views of mature nectophore. Scale bar 1 cm.

The fully mature nectophores (Figure 98) measured, in their preserved state, up to 55 mm in length and 45 mm in width, thereby exceeding the largest previously known nectophores belonging to *Bargmannia gigas* Pugh (see Pugh, 1999b). They possessed well-defined, proximal truncated, axial wings, and a large central thrust block with a shallow, but broad central emargination. On the lower side of the nectophore the thrust block was hollowed out centrally and laterally thickened and, at its base, were two roundly triangular mesogloal swellings, between which ran the mantle canal. This canal was quite short and soon gave rise to the pedicular canal that connected with the radial canals on the nectosac in the middle of the muscle-free zone on the lower side of the nectosac. There were slight, but not consistent, variations with regard to the origin of each radial canal. The courses of the upper and lower canals remained straight, and the lateral radial canals had the same looping course as described above. The mouth plate was still well developed and slightly emarginated distally in the mid-line,. It was thickened with mesogloea, particularly at the lateral margins.

The arrangement of the upper and lower lateral ridges remained much the same as described above, but the lateral and vertical lateral complex became further developed. The main feature was that the two ridges became totally, or so it appears, separated from the upper lateral ridges, but ran parallel with the latter for a short distance. There were indications of a further continuation, proximally, of the ridges but they never were seen to unite with the upper laterals. The vertical lateral complex appeared to break up into a number of separate ridges that had a very variable arrangement even, as noted above, on the different sides of the same nectophore. In general, a

proximal vertical lateral ridge extended down, to a variable extent, from the lateral ridge, often curving distad toward its lower end. There was a separate ridge distal to this that again was very variable, but often took on a Y-shaped appearance (Figure 98 (left), on right-hand side of nectophore). On some occasions there was a complete loop, while on others the lower distal extension of the ridge shown in Figure 97C was associated with it. There was usually a further vertical, usually short, ridge distal to this, and again of varying design. It is probable that the ridge pattern could be better seen in fresh material, as shrinkage gives rise to a very complex pattern of ridges and excrescences in the preserved material.

*Siphosome*: In life the siphosome, like the nectosome, appeared to be almost rigid but the *in situ* pictures of the specimen from Tiburon Dive 746 (cf. Figures 94 (lower) and 99) showed that the stem could undergo a modicum of relaxation, as the gastrozooids were more spread out in the latter than in the former. The gastrozooids always appeared as discrete entities as did the clusters of palpons, of which up to four appeared to be present in each cormidium. However, it was not clear where the gonodendron was attached in each cormidium. The foliaceous bracts thickly covered the siphosome, particularly dorsally and laterally.



**FIGURE 99.** *Stephanomia amphytridis*. Detail of siphosome, ventral view, from *in situ* photograph of specimen from Tiburon Dive 746. (Photograph courtesy of Dr. S.H.D. Haddock, © MBARI.)

*Bracts*: There were two basic types of bract, both of which were large and quite solid, occurring in enantiomorphic pairs. The Type A bracts were far more abundant than the other type, which probably means that they formed paired lateral rows.

Type A—The mature bracts of this type were extremely asymmetrical, extending proximally only on one side (Figure 100). They measured up to 6.5 cm in both length and width. Typically on the foreshortened side of the bract there was a lateral tooth but, in the younger bracts particularly, another tooth could be present on the opposite side. The proximal tip of the bract was often swollen with mesogloea on the upper side, and distally on the same side there was a median mesogloal thickening. On the bracts, particularly the younger ones, there were occasional small patches of ectodermal cells, either just one or a pair on either side of the mid-line.

The bracteal canal arose on the upper side of the bract but soon traversed onto the lower side and continued straight toward the distal tip. The attachment lamella would have been present for about half its length. The canal remained in contact with the lower surface of the bract until close to the distal tip. In the younger bracts the canal often was greatly expanded in this region and, in the youngest, the proximal regions also were inflated. The canal

then ran obliquely through the mesogloea to end below a small cupulate process at the distal end of the mesogloea thickening. In the youngest bracts it appeared that nematocysts were present in the cupule but, in general, it was just an empty hollow.

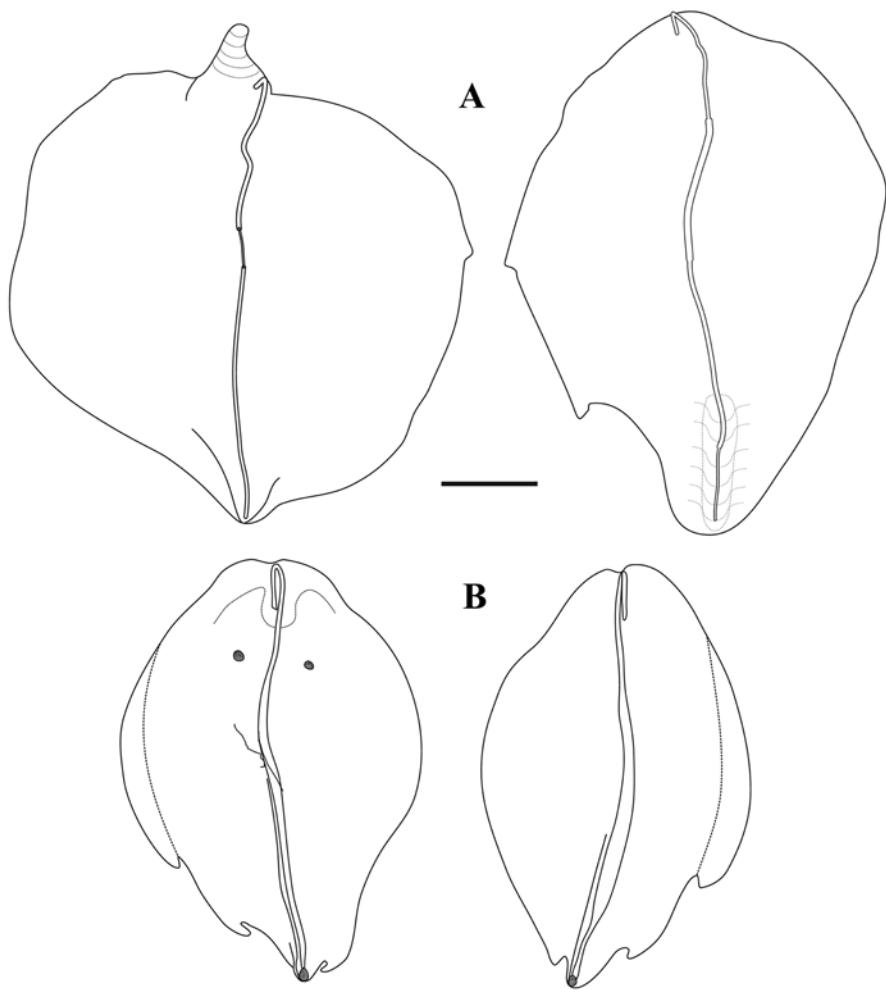


**FIGURE 100.** *Stephanomia amphytridis*. Type A bracts. **A.** Mature, and **B.** young bracts. Proximal at top, distal at bottom. Scale bars **A.** 10 & **B.** 5 mm.

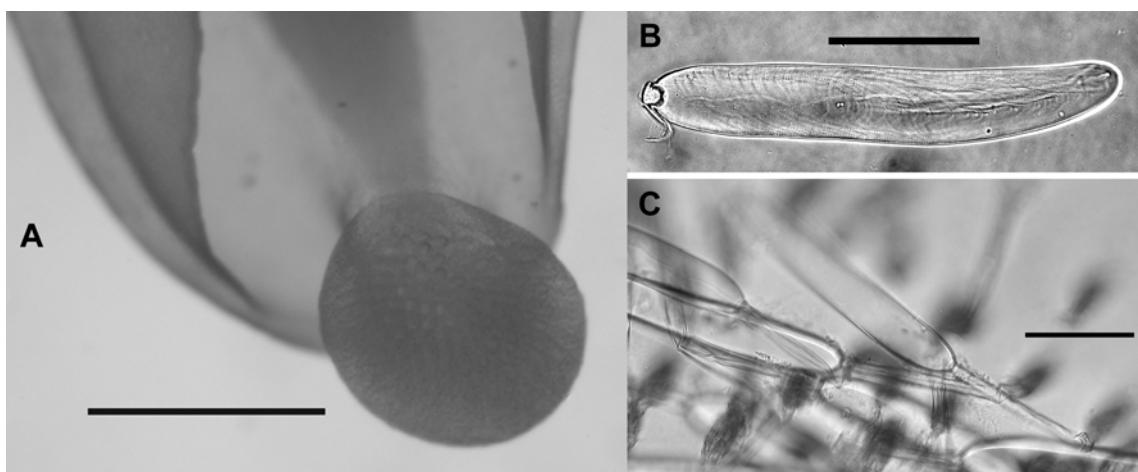
Type B—These bracts were more symmetrical and slightly smaller, measuring up to 5 cm in length and 4.5 mm in width (Figure 101). They were quite variable in their form; some being almost rounded with a swollen proximal region, while others bore lateral or distal teeth in varying numbers. About 40% of the bracts bore no teeth, and a slightly lower number had just one lateral tooth. The remainder were made up of bracts with 2 lateral teeth, or 1 or two distal teeth, or two lateral and one distal, or two lateral and two distal. The degree to which these teeth were developed also varied considerably. The bracteal canal again arose proximally on the upper side and, particularly in the younger bracts, could have a variable thickness. The region of attachment extended to about a third of the length of the bract and in this region the canal ran along the near surface of a narrow mesogloea ridge. As in the Type A bracts the canal continued in close contact with the lower surface of the bract until close to the distal tip, where it similarly ran obliquely through the mesogloea to end below a somewhat large cupulate process. Instead of this process containing nematocysts, in this case it formed the socket for a large spherical ball packed full of nematocysts (Figure 102A). However, apart from the very youngest bracts, this ball of nematocysts had become detached.

The hundreds of nematocysts in this distal ball were all of one type, which measured in their undischarged state c. 210 µm in length and 55 µm in diameter (Figure 102B). A bract was found (Figure 102C) where some of these nematocysts had discharged into it. These showed a short shaft that was obviously grooved, but no spines could be discerned. Once again we are uncertain as to the identity of these nematocysts.

*Gastrozooid and tentacle:* The preserved gastrozooids were relatively large measuring about 3 cm in length with the basigaster occupying the proximal third. However, such sizes are meaningless as they only represent the contracted size in preservation. The tentacles were extremely long bearing numerous large tentilla.

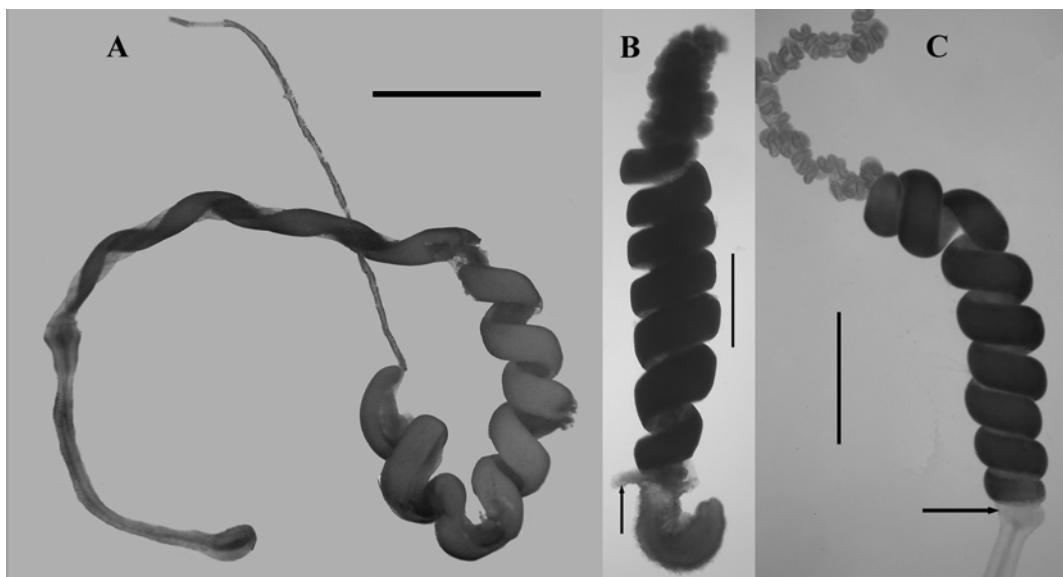


**FIGURE 101.** *Stephanomia amphyridis*. A. and B. Two forms of mature Type B bracts. Proximal at top, distal at bottom. Scale bar 1 cm.



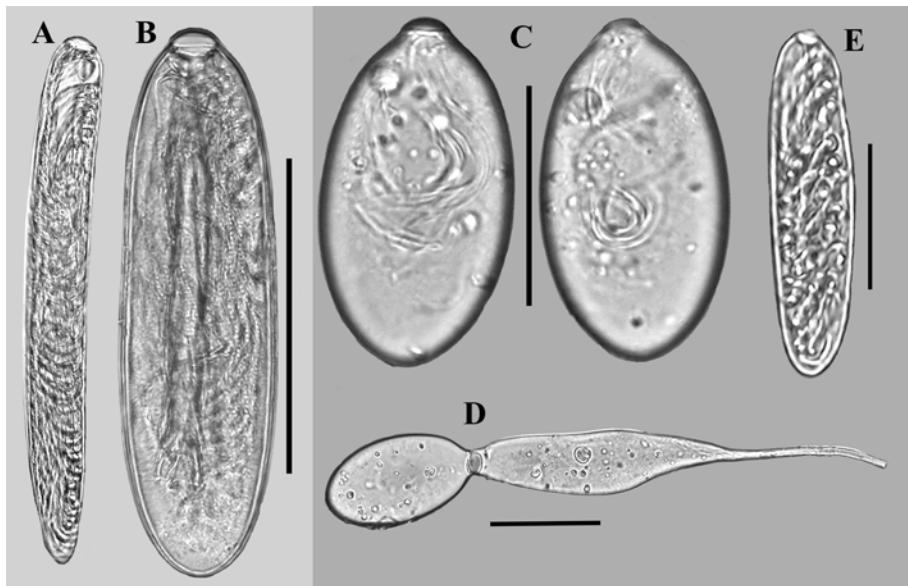
**FIGURE 102.** *Stephanomia amphyridis*. A. Detail of nematocyst cluster at distal tip of young Type B bract. Scale bar 1 mm. B. Undischarged and C. discharged nematocysts from Type B bract. Scale bars 100 µm.

**Tentilla:** Mature preserved tentilla (Figure 103A) consisted of a relatively short pedicle, a long, loosely coiled cnidoband and a long terminal filament. The cnidoband was made up of a broad band of nematocysts and a double elastic band attached firmly to its distal end. When fully stretched out the cnidoband extended to c. 7.5–8 cm in length. Although there was a slight swelling at the junction between the pedicle and the cnidoband no distinct involucrum was apparent.



**FIGURE 103.** *Stephanomia amphytridis*. **A.** Mature tentillum and **B, C** young tentilla from the tentacle of the first adult gastrozooid of the *Nectalia* post-larval stage. (C. © Stefan Siebert). For **B & C** proximal at top, distal at bottom. Scale bars 5 mm.

However, on the younger tentilla (Figure 103 B,C) attached to the tentacle of the first adult gastrozooid of the *Nectalia* post-larval stage, the preserved material (Figure 103B, arrowed) gave the impression that an incomplete horse-shoe shaped involucrum was present. However, this was probably a preservation artefact as a photograph of a similar tentillum from a living specimen (Figure 103C, arrowed) showed just a small swelling. For these younger tentilla the cnidoband was more obviously spirally wound, with 7–9 whorls.



**FIGURE 104.** *Stephanomia amphytridis*. Nematocysts from the cnidoband (**A, B**, scale bar 100  $\mu$ m) and terminal filament (**C–E**, scale bars 50  $\mu$ m) of the tentillum.

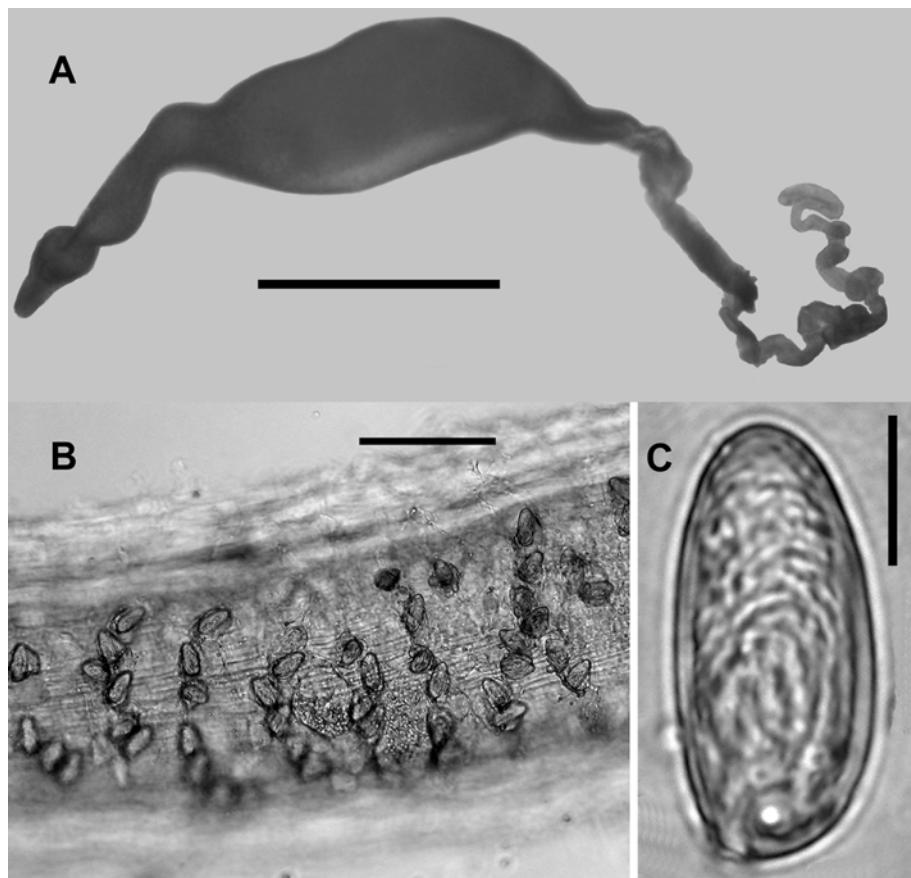
On the cnidoband there were two types of nematocyst, with one type occurring in a wide range of sizes. These (Figure 104A) measured from c. 140 to 195  $\mu$ m in length and from c. 15 to 32  $\mu$ m in diameter. They were by far the more numerous nematocyst and were arranged in numerous (30+) rows across the cnidoband. There was an indication that they gradually decreased in size from the sides toward the middle. Unfortunately no discharged nematocysts of this type were found and so it was not possible to determine their exact type.

The second type of nematocyst (Figure 104B) were of about the same length as the others (c. 175  $\mu$ m), but

were considerably broader (c. 50 µm in diameter). They were probably stenoteles although, again, no discharged ones were found. These nematocysts occupied the lateral margins of the cnidoband, but not in a regular fashion. There were none at the very proximal end of the cnidoband, but after a short distance distally they began to form a tightly packed single row on each side. Distally their number began to increase so that they formed two alternating rows. At about a third of the length of the cnidoband their numbers began to decrease, so that again a single row was present distally. The distance between the individual nematocysts then gradually increased so that at the distal end of the cnidoband these nematocysts were infrequently found.

There were also two types of nematocyst found on the terminal filament. The first type (Figure 104C, D) were arranged in three alternating rows along one side of the filament, while the second type (Figure 104E) were far more numerous and covered the remaining surface. The first type measured, in the undischarged state, c. 80 µm in length and 45 µm in diameter. Quite unusually, when compressed these nematocysts tended to discharge and evaginated a bottle-like structure with a long, narrow distal process, without any obvious spines and apparently open at its tip. It is not clear what type of nematocyst this represents, and no one on the Cnidaria Network has responded to our request for information. Apart from the apparent absence of spines, microbasic euryteles appear to be the most closely related, although ours have a very short tubule. Although Werner (1965) suggests that such nematocysts are absent from siphonophores, more recently Carré (1969) has found them to be present on the tentilla of *Rosacea villafrancae*, a calycothoridan, and Carré (1980) on the tentilla of *Agalma elegans*, but neither look anything like the present ones. They might also be strange acrophores, which are usually found on the tentilla of physonects, but they are usually small and their distal tip is closed, while that of the present material appeared to be open.

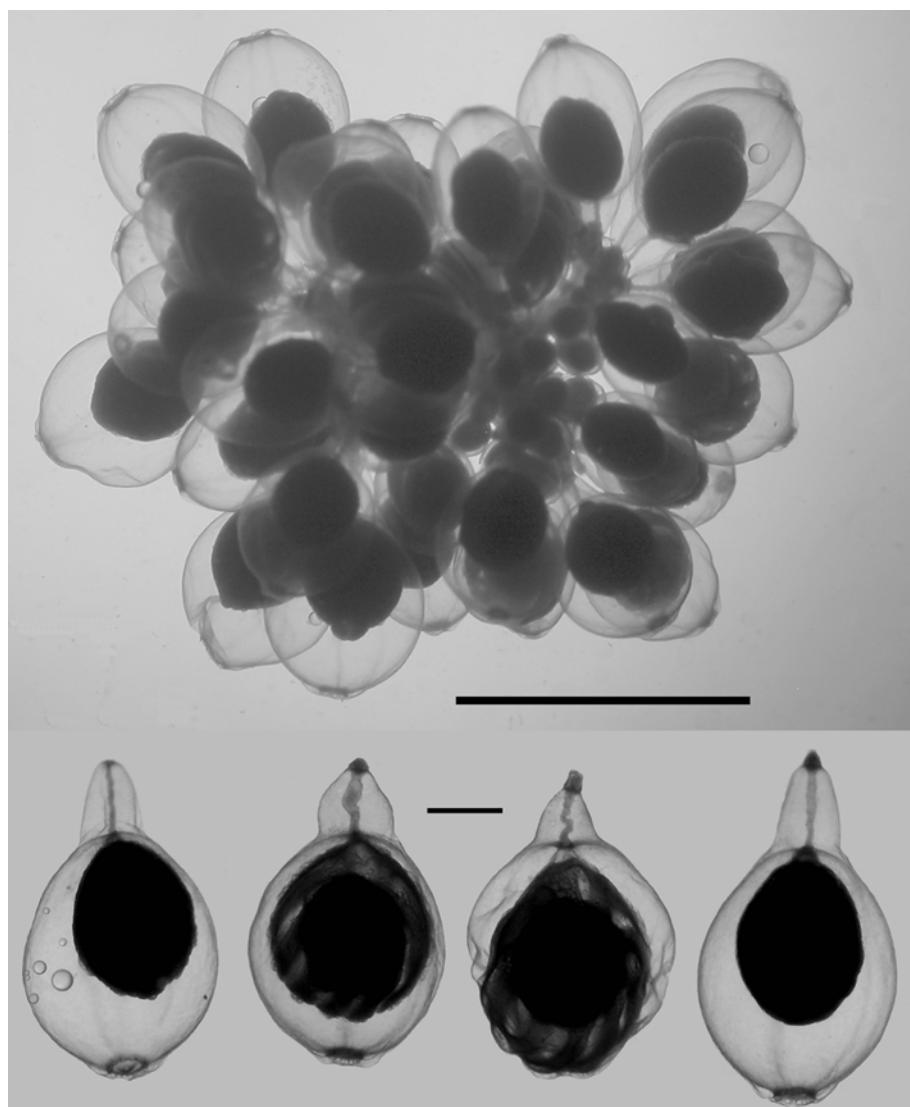
The second, more abundant, type of nematocyst on the terminal filament (Figure 104E) measured c. 62 µm in length and 20 µm in diameter. No discharged nematocysts of this type were found and so, again, we cannot be sure as to which type of nematocyst they belong. As noted above, acrophores along with desmonemes are usually found on the terminal filaments of the tentilla of physonect siphonophores, but these did not resemble either of those types.



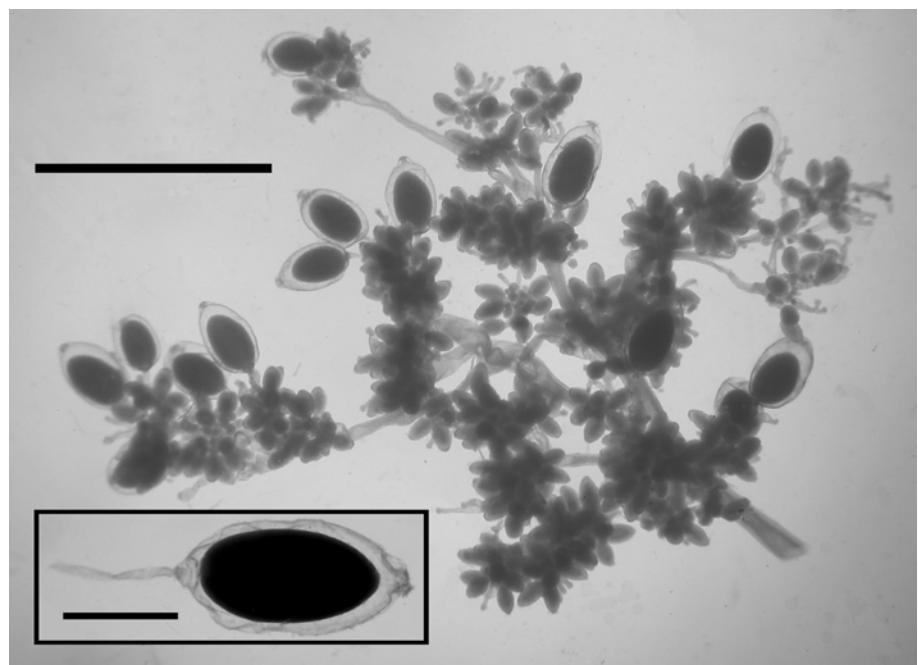
**FIGURE 105.** *Stephanomia amphytridis*. A. Palpon and palpacle. Scale bar 5 mm. B. Portion of palpacle showing attached nematocysts. Scale bar 100 µm. C. Nematocyst. Scale bar 10 µm.

*Palpons*: The palpons (Figure 105A) were simple bag-like structures up to c. 25 mm in length. Usually there was a long, narrow proximal section, an inflated middle part, and a nozzle-shaped distal proboscis terminating in an opening. No nematocysts were found anywhere on its surface. At the proximal end of the narrowed basal region a long semi-annulated palpacle was attached. Nematocysts were scattered randomly along one, somewhat flattened side (Figure 105B). These nematocysts (Figure 105C) measured c. 30 µm in length and 14 µm in diameter and, from their appearance, were probably haplonemes, although none were found discharged. They resembled the second type of nematocyst (Figure 104B) found on the terminal filament of the tentillum, but they were only half the length and relatively broader.

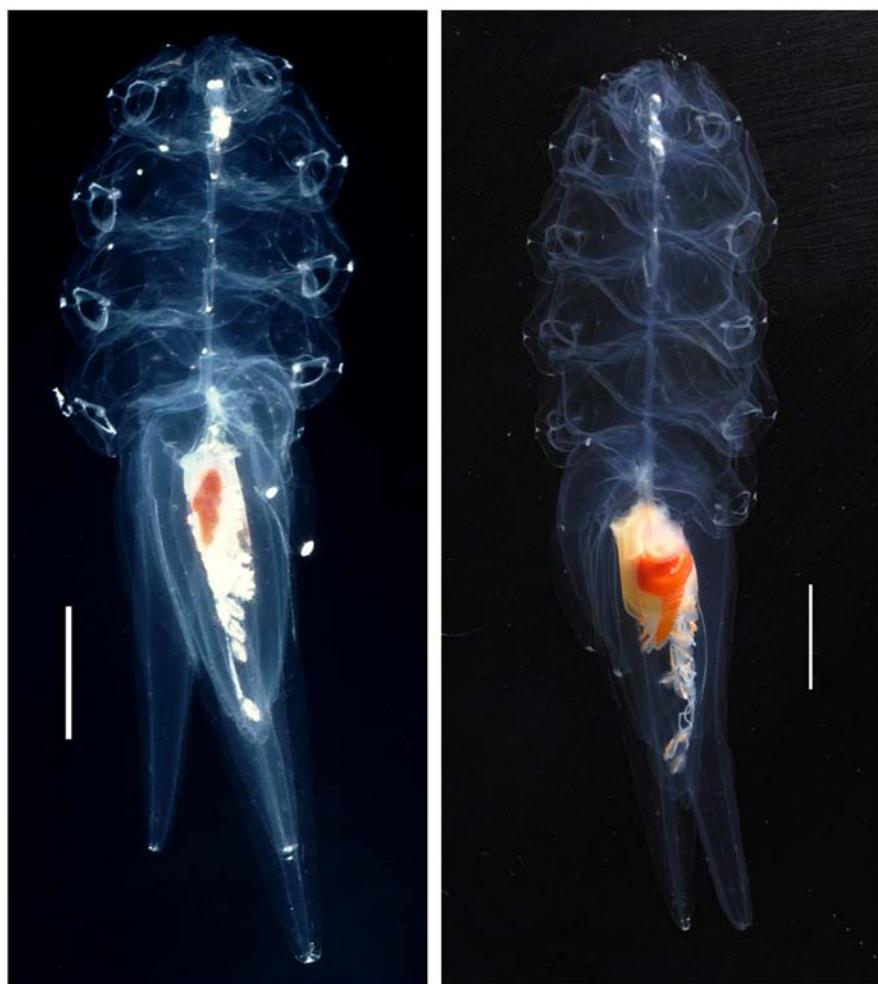
*Gonophores*: Each colony is dioecious and, as for *Apolemia* species, it is difficult to find mature gonophores as, usually, it is only the anterior end of these large colonies that is collected, where all the gonophores are immature. Each cormidium possessed a single gonodendron, with potentially hundreds of gonophores branching from a single gonostyle. A female gonodendron and some, probably, immature female gonophores are shown in Figure 106. The gonophores had a broad, proximally tapering, pedicle and a large bell in which the four lateral radial canals could clearly be seen. They measure up to 4.5 mm in length and c. 2.75 mm in diameter, but that probably misrepresented their mature size. Several clear oil droplets were found in the subumbrella cavity.



**FIGURE 106.** *Stephanomia amphytridis*. Part of female gonodendron (Upper), and some individual female gonophores (Lower). Scale bars 5 and 1 mm, respectively.



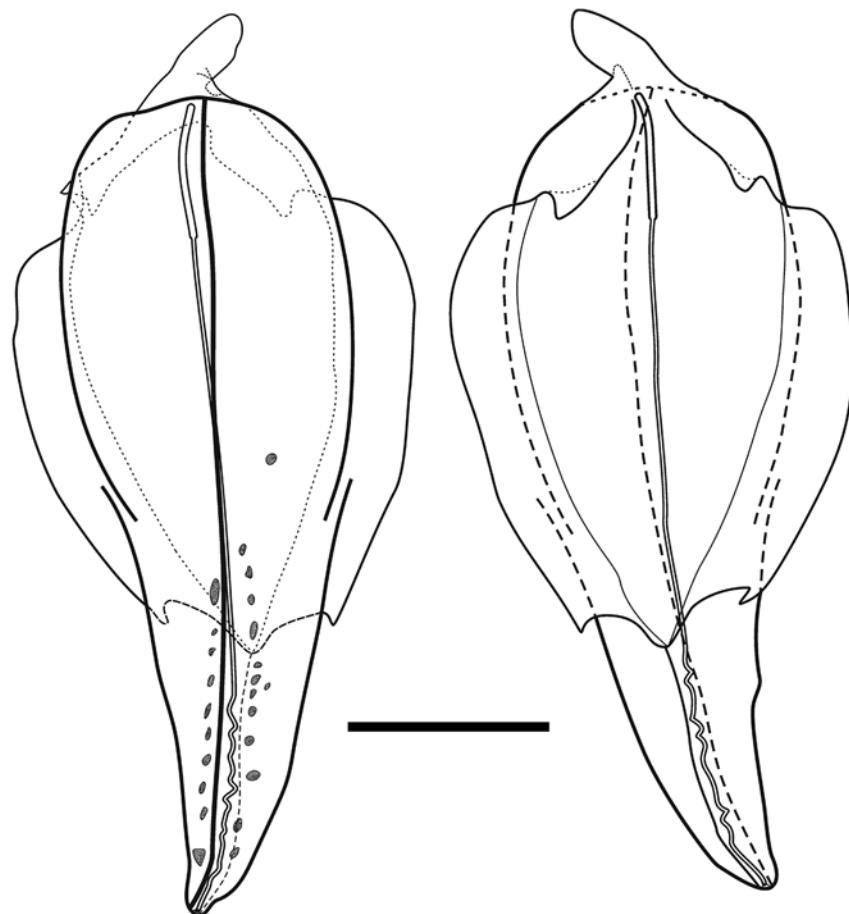
**FIGURE 107.** *Stephanomia amphytridis*. Part of a male gonodendron from T1110-SS12 specimen, with (inset) individual male gonophore. Scale bars 5 and 1 mm, respectively.



**FIGURE 108.** *Stephanomia amphytridis* Nectalia-stages from JSL Dive 1685 (left) and Tiburon Dive 1074 (right). Scale bar 1 cm.

The male gonodendra (Figure 107) probably included hundreds of male gonophores, but the only ones found were very young and hardly developed. The oldest of these gonophores were borne on a long narrow pedicle, about as long as the bell itself. The latter measured c. 2.1 mm in length and 1 mm in diameter, but they almost certainly grew to a much greater size when mature.

*Nectalia*-stage: Of all the specimens of *Stephanomia amphytridis* examined for this study five were at the *Nectalia* post-larval stage, and two of these are shown in Figure 108.



**FIGURE 109.** Upper (left) and lower (right) views of a larval bract of *Stephanomia amphytridis* from JSI I Dive 2138 specimen. Proximal at top, distal at bottom. Scale bar 5 mm.

*Larval bract:* The fully formed larval bracts (Figure 109) were elongate with a distinct distal extension, measured up to 60 mm in length, and usually numbered two or three. These were surrounded anteriorly by up to four smaller bracts at various stages in development (Figure 110). On the upper side of the bract there was a median longitudinal ridge that ran almost the entire length of the mature bract. Proximally, a pair of lateral ridges arose from it and demarcated the lateral margins of the upper side of the bract. Proximal to them the thickness of the bract decreased sharply so that the digitate mesogloal extension lay on the lower side. In the younger bracts these lateral ridges varied considerably in the degree to which they extended distally, and in the youngest they merely curved out laterally. On the mature bracts they extended down to about the mid-point and then petered out. Their places were taken by a separate pair of lateral ridges that, at first, ran parallel with the other pair, but then continued to the distal tip of the bract and joined with the median longitudinal ridge.

The lower side of the youngest bracts (Figure 110, top left) was quite flat apart from in the region of attachment where a distinct central keel was formed, with the bracteal canal following its contours. With age the lower side developed a pair of lateral flaps that arose separately at the proximal end but joined together, distally in the mid-line. Shortly before uniting, for the mature bracts, each gave rise to a pronounced tooth; although they were not present on the more developed of the younger bracts (Figure 109, right). A similar pair of flaps was present proximally. When fully developed the flaps enclosed a deep cavity on the inner side of the bract. From the

junction point of the lateral flaps, which was raised above the lower wall of the more distal part of the bract, there arose a median ridge that also ran to the distal tip, so that the distal extension of the bract had four regular facets.



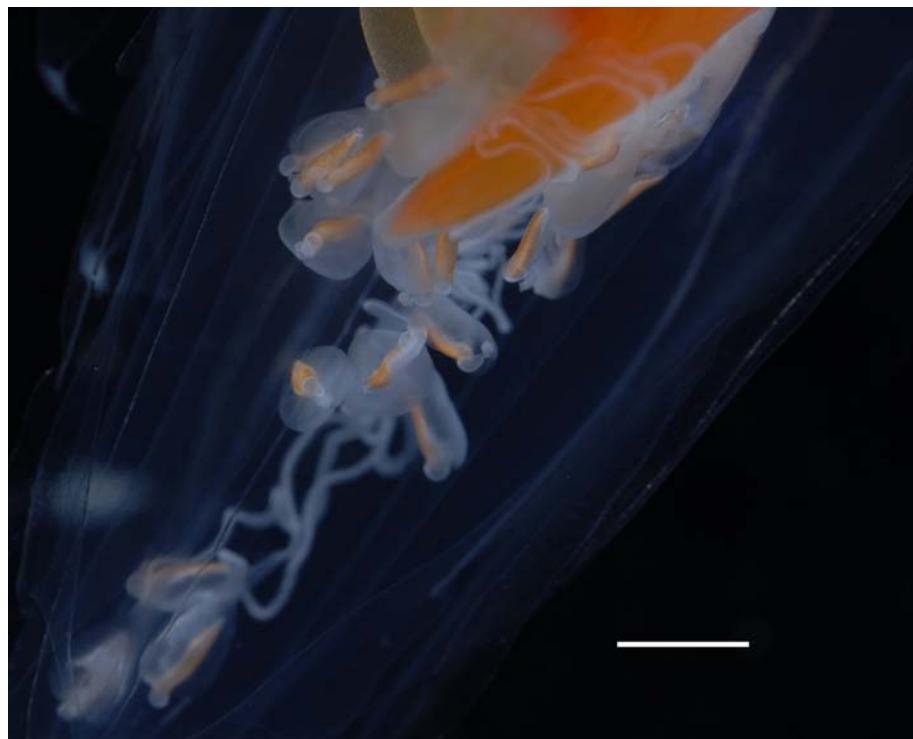
**FIGURE 110.** Upper views of young larval bracts of *Stephanomia amphyridis* from JSL I Dive 2138 specimen. Proximal at top, distal at bottom. Scale bar 5 mm.

On the upper surface of the bracts there were numerous small, rounded spots (not illustrated) that were distributed randomly throughout. There were also larger patches of ectodermal cells that usually, in the younger bracts, formed long slightly curved structures distal to the origin of the lateral ridges; rather like the pair of patches on the nectophores. On the older bracts small patches could occur, particularly on the distal extension, but they were easily detached and their presence difficult to detect.

The canal arose on the lower side of the bract at the same level as the junction between the median and lateral ridges on the upper side. In the region of attachment it was thickened and, as noted above, in the younger bracts ran over a distinct keel. However, in the adult bracts that keel had all but disappeared. After a short distance the canal turned abruptly upwards and penetrated into the mesogloea. In this region the walls of the canal may have had small outward processes. The canal then bent through another right angle and proceeded toward the distal end of the bract. In the distal extension the canal might have had a very wavy course. Just before it terminated, particularly in the younger bracts, it slightly increased its diameter. It ended below a small concavity in the distal tip of the bract. In the mature bracts this concavity was usually empty, but in the younger ones it was found to contain a number of large ectodermal cells along with, in the central region, up to ten large nematocysts, measuring c. 133 x 34  $\mu\text{m}$ .

*Larval tentillum:* The larval tentillum of *Stephanomia amphyridis* (Figures 111, 112) was quite different from that of *Halistemma* species. It was borne on a long, narrow pedicel and consisted of a large featureless sac, a cnidoband and a short "terminal" filament. At an early stage of development the sac, about 2.5 mm in length and with a maximum width of 1.8 mm, was laterally flattened and somewhat heart-shaped, with a shallow median indentation distally (Figure 112A). The cnidoband, total length 2.5 mm, was positioned on one side with a portion, with a reduced compliment of nematocysts, extending distally and from which arose the "terminal filament". In life

(Figure 111) the cnidoband bore orange pigmentation, apart from the "distal" portion, which was colourless. When fully developed (Figure 112B,C) the cnidoband extended from the distal end of the more inflated sac. In actuality, the cnidoband was attached to the sac by a broad tube that ran up one side of the cnidoband to the portion with a reduced nematocyst compliment (Figure 113, arrowed). The tube, much convoluted, could be traced down one side of the sac and appeared to arise slightly proximal to the sac's mid height. The nematocysts on the cnidoband were positioned so that they abutted this tube. This must mean that for them to come into effect the "proximal" end of the cnidoband must break free (see Figure 112B) and, presumably by means of hydrostatic pressure, the cnidoband would be flipped through 180° in order to bring the nematocyst batteries into contact with a prey item. The "terminal" filament would then lie between the sac and the cnidoband.



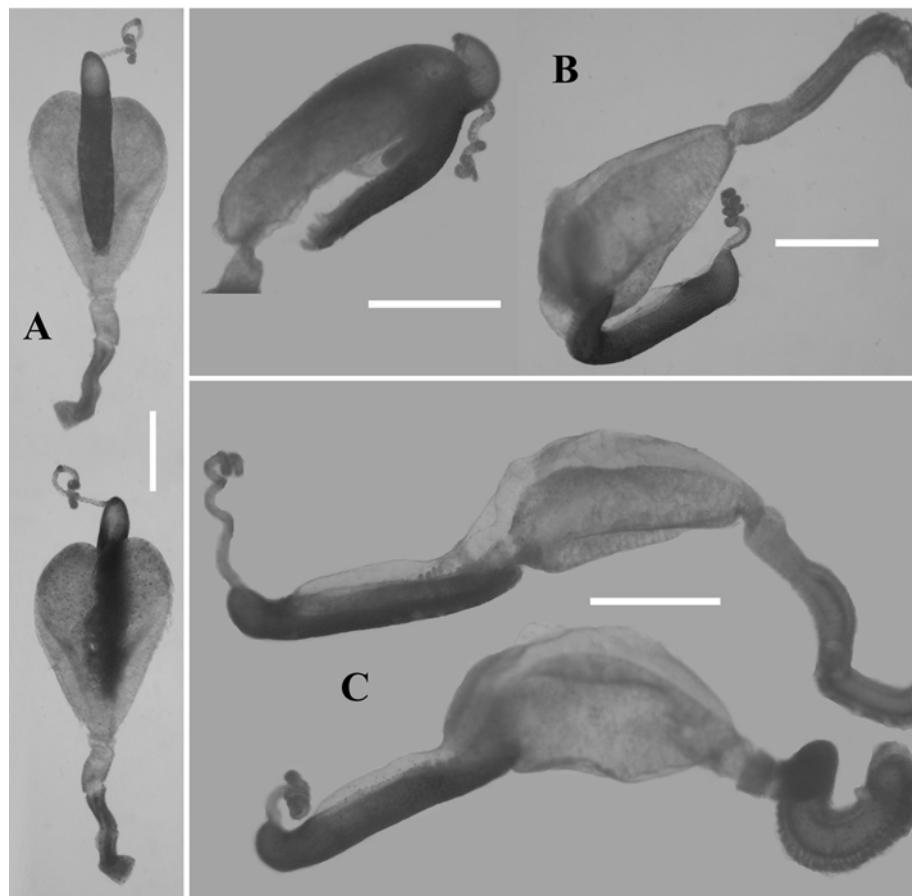
**FIGURE 111.** Nectalia stage of *Stephanomia amphytridis* from Tiburon Dive 1074. Detail of gastrozoooid and larval tentilla. Scale bar 2.5 mm.

Two types of nematocyst were found in the cnidoband (Figure 114A,B). About 20 pairs of the larger ones (Figure 114A), measuring c. 132 x 45 µm, were situated on either side of the cnidoband at its "proximal" end, relative to the unactivated state of the cnidoband. Unfortunately, no discharged nematocysts of any type were found and so their true identity remains unknown. However, in most physonect cnidobands these few, large nematocysts are usually heteronemes (Purcell, 1984) and as the present ones do not have the appearance of stenoteles it is presumed that they may be mastigophores.

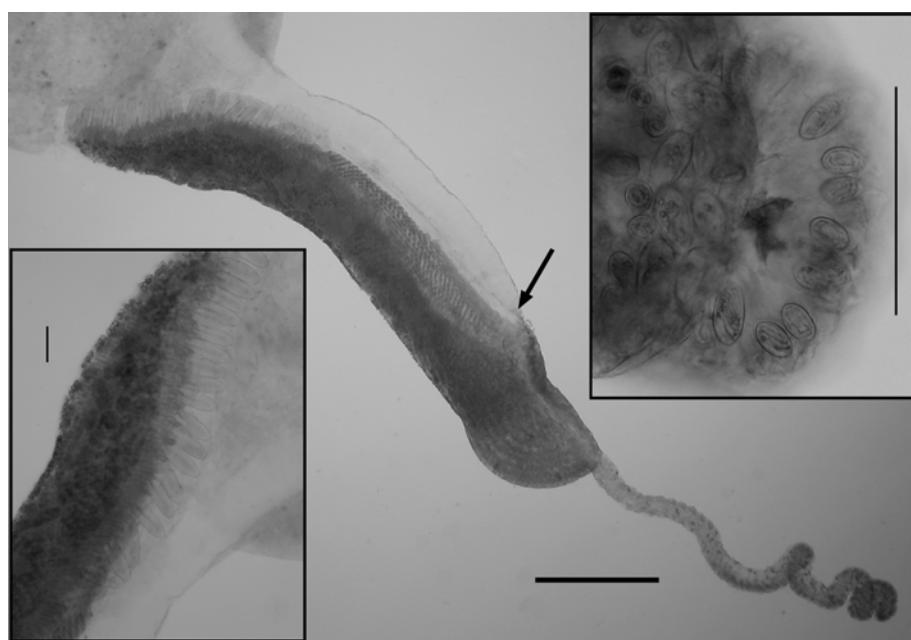
The second type (Figure 114B), measured c. 72 x 15 µm, and were present in great numbers. They filled most of the remainder of the cnidoband on one side. The number of rows of them increased from both the distal and proximal ends. In the "distal" portion, from which the "terminal" filament arose, they were largely confined to the outer walls, with no central concentration, as in the remainder of the cnidoband. These nematocysts are presumed to be haplonemes that, according to Werner (1965), are most likely to be monotrichous anisorhizas.

Three types of nematocyst were found on the "terminal" filament (Figure 114C). The largest of these, measuring c. 34 x 17 µm, were ovoid capsules containing, along with the invaginated tubule, 4 or 5 spherical inclusions. The tubule itself occupied less than half the volume of the capsule. The middle sized nematocysts, measuring c. 30 x 15 µm, were also ovoid and the highly coiled tubule filled the capsule. The smallest, measuring c. 19 x 12 µm, were almost spherical and again the tubule filled most of the capsule. In many physonect species the terminal filament of the adult-type tentillum usually contains two types of nematocysts, acrophores and desmonemes. But without any discharged nematocysts to look at it is futile to speculate on the identity of these

three types. It was difficult to discern the arrangement of the nematocysts in the "terminal" filament (see insert to Figure 113), but there was some indication that the middle sized ones formed outside pairs, with the larger and then smaller ones arranged between them.



**FIGURE 112.** Larval tentilla of *Nectalia* post-larval stage *Stephanomia amphytridis* from Tiburon Dive 1074. **A.** younger tentilla; **B.** intermediate tentilla; **C.** Older tentilla. Scale bars 1 mm.



**FIGURE 113.** Cnidoband and terminal filament of older tentillum of *Stephanomia amphytridis* (scale bar 500 µm), with detail (top right) of nematocysts on terminal filament, and (bottom left) of large nematocysts at proximal end of cnidoband. Scale bars 100 µm.



**FIGURE 114.** *Stephanomia amphytridis* *Nectalia*-stage. Types of nematocyst found on larval tentilla. **A.** at proximal end of cnidoband (scale bar 100 µm); **B.** throughout cnidoband (scale bar 100 µm); and **C.** the three types found on the terminal filament (scale bar 25 µm).

*Remarks:* It is hoped that the present description firmly establishes the species *Stephanomia amphytridis* as a valid species although, of course, we can never be absolutely sure that it is the same as that originally figured by Lesueur & Petit (1807). It is regrettable that Totton did not publish a description of the species, as that would then have avoided some of the confusion that has more recently arisen. We have already established that the three main re-descriptions attributed to this species, i.e. Huxley (1859), Bigelow (1911) and Kawamura (1954), together with Mapstone (2004) can now all be referred to the species *Halistemma foliacea*. After Totton's (1965) doubtful attribution of the species to the genus *Halistemma*, Daniel (1974) described and illustrated two nectophore and a single bract from the Indian Ocean. The nectophores measured 28 and 33 mm in length and 25 mm in width, but clearly were in poor condition, as no ridge pattern could be discerned.

Daniel (1985, p. 76) reproduced her earlier figures under the name *Halistemma amphytridis*, but she remarked "The nectophore described below differs a great deal from the typical "*Halistemma*" type of nectophore and warrants a creation of new genus and new species, but in this account it is still retained as *H. amphytridis* (=*Stephanomia amphytridis*)". Unfortunately she did not say what these distinguishing features were, and one can only presume that it was based on the arrangement of the lateral radial canals. However, her figure did appear to indicate the presence of only an ascending mantle canal, but Daniel drew no attention to this significant feature.

We have already remarked in the Introduction (see Figure 10) that the species *Sphaeragalma rotunda* described by Margulis (1976) most certainly belongs to *Stephanomia amphytridis* as the pattern of the ridges and the lateral radial canals certainly shows, as well as the presence of only an ascending mantle canal, although the nectophores were clearly very young as they only measured 1.1–1.2 cm in length.

*Distribution:* The locality where the original specimen figured by Lesueur & Petit (1807) was collected remains uncertain; the report indicating only that it was collected somewhere between Le Havre and Mauritius. As noted above, the four main re-descriptions of specimens attributed to this species by Huxley, (1859), Bigelow (1911), Kawamura (1954) and Mapstone (2004) in actuality all refer to the species *Halistemma foliacea*.

The first records for specimens that are now attributed to this species appear to come from Totton (1936), who found several specimens in the Beebe Collections from the south-east of Bermuda, and he also listed several specimens of *Nectalia loligo*, which may well be the post larval stages of that species. Later, Leloup (1955) recorded a specimen from the Michael Sars Expedition at c. 35°N, 48°W. There are several more recent records from the North Atlantic, e.g. Haddock & Case (1999) recorded a specimen from the Bahamas; Dunn (2005) from 40°18.6'N 68°07.8'W at a depth of 800m; Bucklin *et al.* (2010) and Ortman *et al.* (2010) from 33°38.5'N 69°47.7'W and 14°05.8'N 54°46.8'W, with a further record from the Gulf of Maine (Pagès, personal communication). Several specimens have also been collected by the JSL submersibles in the vicinity of the Bahamas and the Dry Tortugas (see Table 1). In addition, specimens have been collected at several *Discovery* station in the North Atlantic Ocean, together with further specimens just south of the equator (see Table 2).

**TABLE 1.** Additional records for *Stephanomia amphytridis* collected or observed by MBARI ROVs or Johnson-Sea-Link (JSL) submersibles, in latitudinal order.

<i>Tiburon</i> 1150	4-Nov-2007	36°36.61'N	122°09.52'W	1103 m Nectalia
<i>Tiburon</i> 0260	27-Feb-2001	36°34.20'N	122°31.20'W	1192 m
<i>Tiburon</i> 1110	1-Aug-2007	36°22.47'N	122°40.07'W	1401 m
<i>Tiburon</i> 0962	6-Apr-2005	36°19.78'N	122°53.97'W	1372 m Nectalia
<i>Doc Ricketts</i> 0026	27-May-2009	36°06.98'N	122°45.20'W	1993 m
<i>Doc Ricketts</i> 0105	13-Dec-2009	36°04.07'N	122°17.92'W	1983 m
<i>Doc Ricketts</i> 0101	10-Dec-2009	36°04.14'N	122°17.89'W	1319 m
<i>Doc Ricketts</i> 0030	20-May-2009	35°56.66'N	123°57.35'W	1227 m Nectalia
<i>Doc Ricketts</i> 0030	20-May-2009	35°56.51'N	123°57.20'W	1434 m
<i>Doc Ricketts</i> 0555	21-Nov-2013	36°04.12'N	122°17.84'W	1168 m
<i>Tiburon</i> 0949	2-Feb-2006	35°45.66'N	122°42.16'W	1304 m
<i>Tiburon</i> 0949	2-Feb-2006	35°45.66'N	122°42.16'W	1130 m Nectalia
<i>Tiburon</i> 1074	23-Jan-2007	35°50.22'N	122°40.07'W	1178 m Nectalia
<i>Doc Ricketts</i> 0029	29-May-2009	35°29.79'N	125°00.53'W	1066 m Nectalia
JSL II 2666	17-Sep-1995	c. 27°0.0'N	c. 85°0.0'W	Depth unknown
JSL II 2677	22-Sep-1995	c. 27°0.0'N	c. 85°0.0'W	Depth unknown
<i>Doc Ricketts</i> 0370	31-Mar-2012	26°44.99'N	111°09.71'W	1388 m Nectalia
JSL I 2648	12-Nov-1989	26°30.9'N	78°17.8'W	899 m
JSL I 2888	19-Dec-1990	26°22.8'N	78°46.3'W	761 m.
<i>Tiburon</i> 1040	1-Oct-2006	24°17.41'N	124°03.12'W	1368 m

**TABLE 2.** Records for *Stephanomia amphytridis* at Discovery Stations, in latitudinal order.

Station	Nect	Bract	Date	Latitude	Longitude	Depth Range (m)
7709#44	33	273	30-Apr-1971	60°07.6'N	19°39.4'W	1250–1500
10115#19	14	18	12-Sep-1979	49°36.7'N	14°03.8'W	1100–1300
53305#34	42	76	21-Apr-1994	49°14.5'N	12°14.6'W	700–810
9801#19	26	139	14-May-1978	41°57.8'N	17°00.0'W	1100–1280
7406#29	14	69	05-Oct-1970	40°00.6'N	20°00.9'W	805–900
7480#01	4	5	07-Nov-1970	39°55.2'N	20°07.3'W	1250–1510
10376#34	8	6	29-May-1981	33°12.1'N	33°32.8'W	1100–1200
10382#12	14	14	22-Jun-1981	32°33.5'N	32°06.9'W	900–1000
8277#00	10	6	08-Mar-1973	32°05.4'N	57°40.0'W	0–1000
8281#01	9	5	13-Mar-1973	31°55.3'N	63°52.0'W	905–1000
8281#12	26	17	14-Mar-1973	31°51.9'N	63°51.6'W	1000–1250
8281#14	9	10	15-Mar-1973	31°51.0'N	63°44.2'W	1010–1250
8281#03	22	40	13-Mar-1973	31°46.8'N	63°39.1'W	910–1000
8281#29	1	44	17-Mar-1973	31°42.5'N	63°43.6'W	1250–1500
7856#04	3	2	31-Mar-1972	29°45.0'N	23°05.3'W	795–900
7803#01	10	7	19-Feb-1972	18°01.8'N	25°02.2'W	0–1000

.....continued on the next page

**TABLE 2.** (Continued)

Station	Nect	Bract	Date	Latitude	Longitude	Depth Range (m)
7089#09	13	4	13-Nov-1969	17°52.6'N	25°25.5'W	610–700
7089#16	7		15-Nov-1969	17°48.8'N	25°17.2'W	610–700
7833#02	12	15	17-Mar-1972	14°47.9'N	26°25.3'W	10–1000
7832#01	16	33	16-Mar-1972	13°49.7'N	25°52.0'W	30–1000
7831#01	49	106	16-Mar-1972	13°18.4'N	25°33.1'W	10–1000
6662#08	43	426	15-Feb-1968	11°08.2'N	19°47.8'W	910–985
6662#07	52	101	14-Feb-1968	11°04.6'N	19°48.1'W	715–800
6662#16		52	16-Feb-1968	10°59.4'N	19°52.0'W	810–890
6662#22	16	34	17-Feb-1968	10°57.6'N	19°57.2'W	610–680
6662#20	36	433	17-Feb-1968	10°57.5'N	19°49.0'W	810–900
6662#30	33	132	19-Feb-1968	10°47.4'N	19°52.6'W	730–795
10523#12	46	600	12-May-1982	5°07.5'S	0°27.0'E	895–1000
10523#01	24	248	10-May-1982	6°36.0'S	0°30.7'E	500–600

In the Indian Ocean Daniel (1973, 1974, 1985) found occasional well dispersed specimens, from off South Africa, the Arabian Sea, and off the west coast of Australia. The specimen of *Sphaeragalma rotunda* (Margulies, 1976) was collected in the southern Bay of Bengal, east of Sri Lanka (07°39'N, 87°54').

In the Pacific Ocean, several further specimens have been observed from submersibles in the vicinity of Monterey Bay (see Table 1), and Burton & Lundsten (2008) picture a specimen close to the sea bed on Davidson Seamount, 120 km SW of Monterey, California, at a depth of 1304m. Hunt & Lindsay (1999), Lindsay (2006) and Lindsay & Miyake (2009) have recorded specimens from the North West Pacific in Japanese waters, but there appears to be no records from the South Pacific Ocean.

## Conclusions

In this paper we have given the first full description of what we consider to be the species *Stephanomia amphyridis*, and have established it as the type and only species of the family Stephanomiidae fam. nov. We have shown that most of the descriptions purporting to be of that species, particularly those of Huxley (1959), Bigelow (1911), Kawamura (1954), and Mapstone (2004), actually should be referred to a species belonging to the genus *Halistemma*, namely *H. foliacea*. However, we realise that, as the specific name was established for an illustration of part of the siphosome of a large physonect, without any but the most basic of descriptions, it is impossible to absolutely sure of our ascription.

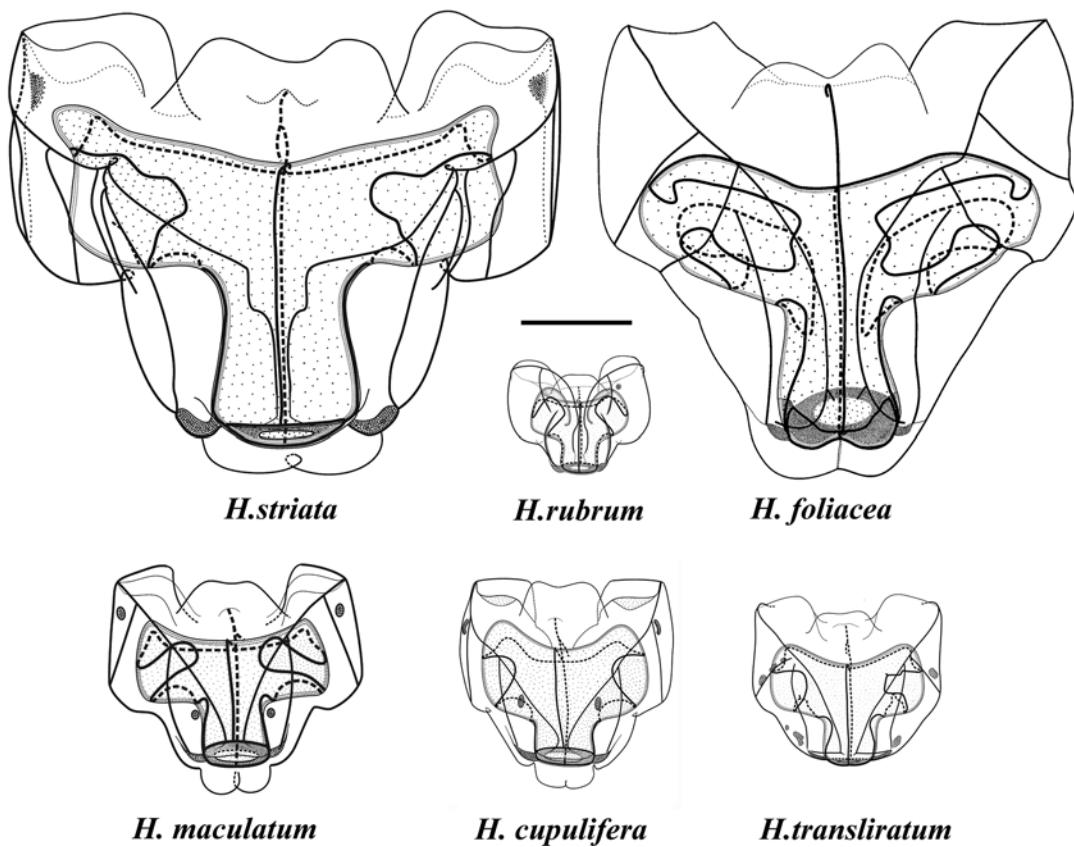
As noted above, during the description of *Stephanomia amphyridis*, the family Stephanomiidae belongs to the dioecious clade off physonect siphonophores characterised, not only by the dioecism of the species, with some exceptions, but by the presence in the nectophores of only an ascending mantle canal. The nectophores, with the exception of the Rhodaliidae, also have a muscle-free zone on their nectosacs. The last two characters contrast with the situation in monoecious species where a descending branch to the mantle canal is also present, and the nectophores do not have a muscle-free zone on their nectosacs. The family Agalmatidae, including the genus *Halistemma*, is further distinguished from other monoecious families by the fact that the nectophores are budded off on the dorsal side of the stem.

Thus, although the genera *Stephanomia* and *Halistemma* are taxonomically quite distinct, there is one interesting feature that connects them, that is that they both pass through a *Nectalia* post-larval stage, characterised by the presence of elongate, lanceolate bracts. Of course, we know little about the larval development of most siphonophore species, so such similarities may be more common than we are currently aware of.

In addition to the description of *Stephanomia amphyridis*, we have also given descriptions of six *Halistemma* species, including one new one. To date only three of the six *Halistemma* species had been described in any detail,

*H. rubrum* (Vogt, 1852), *H. transliratum* Pugh & Youngbluth, 1988, and *H. foliacea* (Quoy & Gaimard, 1833 (1834)), which was recently re-described by Mapstone (2004) but, mistakenly, under the name *Stephanomia amphyridis*. For the other two extant species the identification of *H. cupulifera* Lens & van Riemsdijk, 1908 was based entirely on the structure of the tentillum, the terminal filament of which terminated in a relatively large cupulate process. No other parts of the colony had subsequently been described although, as noted above, Totton (1954) inadvertently illustrated a nectophore, under the name *Stephanomia rubra*, that probably belongs to that species. Totton also described some distinctive nectophores of a new species under the name *H. striata*, which had multiple vertical lateral ridges. The present material has allowed us to improve considerably the descriptions of the last two species, and has allowed the establishment of a further species *H. maculatum* sp. nov.

We have already dealt with the characters that distinguish *Stephanomia amphyridis*, and so it is now only necessary to deal with those that distinguish the six *Halistemma* species. As noted above the primary diagnostic character for the genus *Halistemma* is the fact that the tentillum is unicornuate and possesses an involucrum at the proximal end of the cnidoband, albeit almost vestigial. The nectophores also have a characteristic combination of ridges, consisting of pairs of upper, lower, lateral, and vertical laterals. Neither one of these characters alone characterises the genus, but in combination they do. Nevertheless, the molecular data of Dunn *et al.* (2005) clearly distinguish between the agalmatid genera studied, including *Halistemma*.



**FIGURE 115.** Upper views of nectophores of *Halistemma* species at the same scale. Scale bar 5 mm.

#### Key to the species of the genus *Halistemma*

1. Nectophores with 1 pair of vertical lateral ridges. .... 2
- Nectophores with more than 1 pair of vertical lateral ridges. .... 5
2. Vertical lateral ridges complete, joining both upper and lower lateral ridges. .... 3
- Vertical lateral ridges incomplete, not joining lower lateral ridges; mouth plate absent. .... *Halistemma rubrum* (Vogt, 1852)
3. Mouth plate absent. .... *Halistemma transliratum* Pugh & Youngbluth, 1988
- Mouth plate present. .... 4
4. Mouth plate only slightly emarginated in mid-line. .... *Halistemma cupulifera* Lens & van Riemsdijk, 1908
- Mouth plate deeply divided in mid-line. .... *Halistemma maculatum* sp. nov.

5. Nectophore with 2 pairs of vertical lateral ridges. .... *Halistemma foliacea* (Quoy & Gaimard, 1833)  
 - Nectophores with 3 pairs of vertical lateral ridges. .... *Halistemma striata* Totton, 1965

On the basis of the nectophores alone it is somewhat difficult to distinguish the species *Halistemma cupulifera* and *H. maculatum* sp. nov. from each other, but the differences in the mouth plate and the fact that, in general, the thrust block of *H. cupulifera* extends to the level of the sharply truncated axial wings (see Figure 115) also help to distinguish it from *H. maculatum* sp. nov. The size of the cupulate process at the distal end of the terminal filament of the tentillum also helps to distinguish the two species.

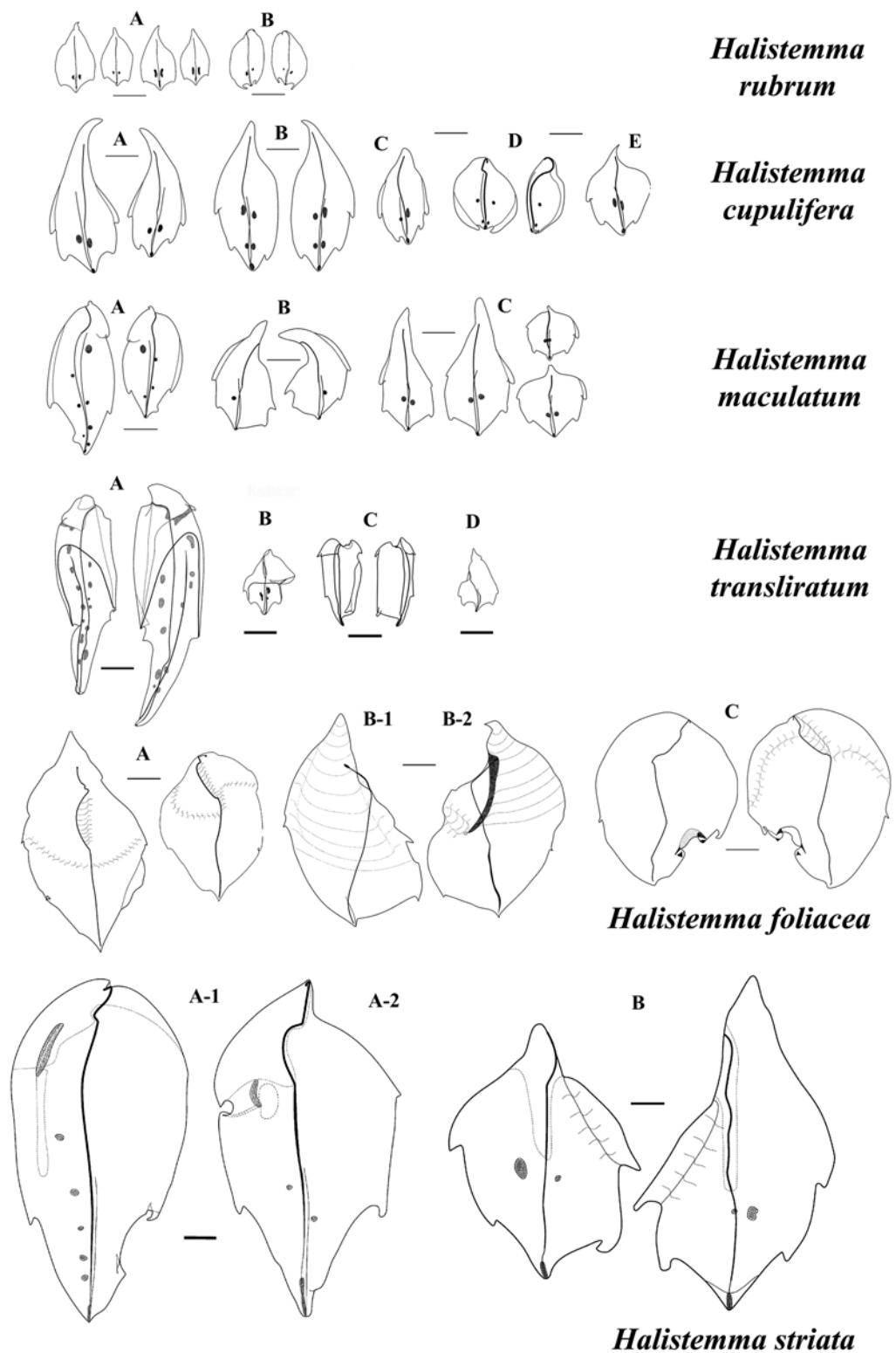
The mature nectophores of the six *Halistemma* species basically fall into three size ranges (Figure 115), with those of *Stephanomia amphyridis* clearly outstripping all of them. *H. striata* and *H. foliacea* have the largest nectophores, but they are easily distinguished by the number of vertical lateral ridges. *H. rubrum* is easily the smallest, but again *H. cupulifera* and *H. maculatum* sp. nov. are the most similar and, despite the differences between them noted above, it is doubtful whether the nectophores of these two species could be distinguished in net collected material. *H. transliratum*, although of similar size, can clearly be distinguished by the absence of a mouth plate.

Although morphological differences between the nectophores are usually the primary characters for the identification of all siphonophore species, the morphology of the bracts, particularly for physonect species, occasionally is of use for specific identifications. This is particularly so for the species of the genera *Athorybia* which do not develop nectophores. The bracts of the six *Halistemma* species are compared in Figure 116. As with the nectophores they fit into three basic size ranges, with the largest ones, belonging to *H. foliacea* and *H. striata*, showing obvious specific differences. For the other species, the bracts of *H. transliratum* are clearly different from all the other species. Those of the remaining three species, however, show some basic similarities with those of *H. rubrum* appearing as smaller forms of the various types of the other two species. Some of the types of bracts of *H. cupulifera* and *H. maculatum* sp. nov. are very similar to each other. For instance, the Type E bracts of *H. cupulifera* are similar to the younger Type C bracts of *H. maculatum* sp. nov., as are, respectively, the Type A and Type C bracts. However, the Type A bracts of *H. maculatum* sp. nov. are very distinctive in that the proximal end is thickened and does not taper to a point. They were the commonest of the different bracteal types. For *H. cupulifera* the fourth most abundant bract, Type D, was very distinctive with its pair of blunt distal teeth and its tendency to fold in half; characters that might help in the identification of that species.

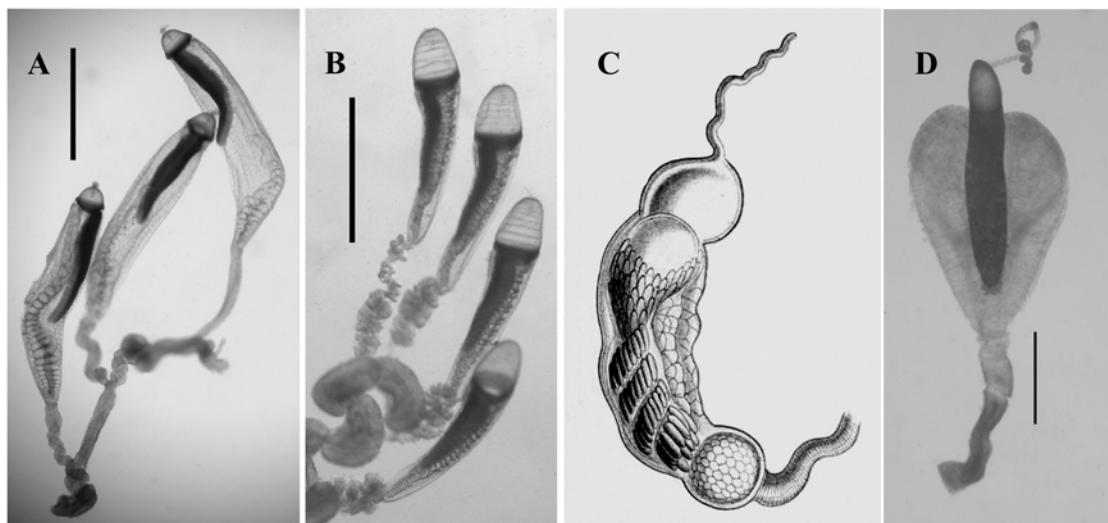
As noted above both *Halistemma* and *Stephanomia* species pass through a *Nectalia* post-larval stage, characterised by the development of long, lanceolate bracts. In the present studies the *Nectalia*-stage was found and described for three *Halistemma* species, *H. rubrum*, *H. transliratum* and *H. maculatum* sp. nov., along with that of *S. amphyridis*. The availability of these specimens allows us to shed some light on the identity of the *Nectalia loligo* described and illustrated (see Figure 7) by Haeckel (1888b). Although Haeckel's illustrations are often stunningly beautiful, all too often they are totally inadequate with regard to important morphological details. In the present case, this is true for both the nectophores and the bracts. We are, thus, left with only the structure of the larval tentillum with which comparisons can be made. In Figure 117 the larval tentilla of two *Halistemma* species and *Stephanomia amphyridis* are compared with Haeckel's drawing from his Plate XIII, figure 14. It is immediately clear that Haeckel's larval tentillum more closely resembles that of *Halistemma* species than that of *S. amphyridis*. The presence of an inflated distal terminal process is a common feature, although the long terminal filament was not found for either of the *Halistemma* species. One major difference is the presence of a proximal inflation of the cnidoband of *Nectalia loligo*. Nonetheless, one must always return to the great deal of artistic licence that Haeckel took with his illustrations.

Assuming that Haeckel's (1888b) *Nectalia loligo* is actually a post-larval stage of a *Halistemma* species, then one other way to home in on a specific identity might be to compare the size of the larval bracts, although it must be remembered that intraspecifically these can be quite variable in length. We know from the present descriptions that the larval bracts measured up to 15 mm in length for *Halistemma rubrum*, and for both *H. transliratum* and *H. maculatum* sp. nov. they were up to 32.5 mm in length. Haeckel (1888b) stated that his bracts were up to 25 mm in length. This indicates that Haeckel's specimen might belong to either of the last two species mentioned or, perhaps *H. cupulifera*. Haeckel's specimen came from the Canary Islands, in the N.E. Atlantic; while all the known specimens of *H. maculatum* sp. nov. came from the Bahamas. *H. transliratum* was also collected also from the Bahamas, but other specimens have been found in the N.E. Atlantic, north of the Canary Islands; with one specimen from just south of the equator. The records for *H. cupulifera* are very patchy and many are difficult to verify, but it is known

to occur in the Sargasso Sea. Thus, although we have little doubt that Haeckel's *Nectalia loligo* is the post-larval form of a *Halistemma* species, without knowledge of the post-larval stages of the other four *Halistemma* species it is not possible to assign it definitively to any known *Halistemma* species.



**FIGURE 116.** Comparison of the various types of bracts of *Halistemma* species. Scale bars 5 mm.



**FIGURE 117.** Comparison of larval tentilla from *Nectalia* post-larval stages of **A.** *Halistemma rubrum*, **B.** *Halistemma maculatum* sp. nov., **C.** *Nectalia loligo* Haeckel (1888b), and **D.** *Stephanomia amphytridis*. Scale bars, where known, 1 mm.

One possible way to home in on an identity might be to compare the size of the larval bracts, although it must be remembered that intraspecifically these can be quite variable in length. We know from the present descriptions that these larval bracts measured up to 15 mm in length for *Halistemma rubrum*, for both *H. transliratum* and *H. maculatum* sp. nov. they were up to 32.5 mm in length, while Haeckel (1888b) stated that his bracts were up to 25 mm in length. This indicates that Haeckel's specimen might belong to either of the last two species mentioned or, perhaps *H. cupulifera*. Haeckel's specimen came from the Canary Islands, in the N.E. Atlantic; while all the known specimens of *H. maculatum* sp. nov. came from the Bahamas. *H. transliratum* was also collected from The Bahamas, but other specimens have been found in the N.E. Atlantic, north of the Canary Islands; with one specimen from just south of the equator. The records for *H. cupulifera* are very patchy and many are difficult to verify, but it is known to occur in the Sargasso Sea. Thus, although there can be little doubt that Haeckel's *Nectalia loligo* is the post-larval form of a *Halistemma* species, probably we will never be able to establish to which species it belonged.

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