

<https://doi.org/10.11646/zootaxa.4441.2.7>
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***Agalma clausi* (Bedot, 1888) (Siphonophora: Physonectae)—complementary description with notes on species distribution and ecology**

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Abstract

Siphonophores are colonial hydrozoans, which in spite of often growing to great lengths are an inconspicuous and under-studied component of pelagic ecosystems. Although they are widely distributed, many species have rarely been collected, or often been misidentified so their taxonomy still requires some clarification. Here we redescribe one such species, *Agalma clausi* Bedot, 1888, supplementing information on its morphology, ecology and distribution based on the material collected in the tropical sector of the Atlantic Ocean and adjacent seas. We also provide comments on the probable status of another *Agalma* species, *A. haekeli* Bigelow, 1911.

Key words: *Agalma clausi*, siphonophore, redescription

Introduction

The first description of the species currently known as *Agalma clausi* (Bedot, 1888) was probably given by Fewkes (1880), under the name *A. sarsi* Kölliker, 1853, a species currently referred to as *A. elegans* (Sars, 1846). Although all he described and figured was a single bract (Fig. 1A), it was very distinctive as it bore, on its outer surface, highly refractive red spots arranged in irregular rows. Indeed, he found that these spots were glands containing dense red pigment that, when released into the sea water, coloured it yellow. Fewkes noted that the longitudinal rows of cells had been described on the bracts of *A. clavatum* Leuckart, 1853, and that that species was generally considered, e.g. Claus (1863), to belong to *A. elegans*. However, as no pigment was found in these spots they cannot be compared with the bract described by Fewkes that, according to Bigelow (1911), belongs to *A. clausi* Bedot, 1888.

Bedot (1888) then described the new species *Agalma clausi*, based on three specimens collected at Villefranche-sur-Mer, in the western Mediterranean Sea. Unfortunately, like many zoologists of the latter part of the 19th century, Bedot concentrated on describing the histology of the colonies and, thus, failed to provide vital information on certain taxonomically significant morphological characters. He gave a pretty, but stylised figure of a complete colony (Fig. 2A), but otherwise gave only a single and poor representation of a nectophore (Fig. 2B). In the text he merely stated that the general shape of nectophores and course of their radial canals resembled those of *Agalmopsis sarsi* [= *A. elegans*] and *Agalma (Cristallodes) rigidum* Haeckel, 1869 [= *A. okenii*, Eschscholtz, 1825]. Since the arrangement of the ridges on the nectophores of these other two species is very distinctive, the only thing that can be gleaned from Bedot's remarks is that the lateral radial canals of *Agalma clausi* were spirally coiled.

With regard to the bracts, however, Bedot (1888) devoted a great deal of space to their description, but mainly with regard to the red-pigmented glands and other clusters of ectodermal cells found on them. However, he appeared to describe only one type of bract (Fig. 1B), and a younger form of it (Fig. 1C), but there are reasons to think otherwise, as will be discussed below. Bedot (1888) noted Leuckart's (1853, 1854) earlier descriptions of four rows of spherical bodies on the bracts of *Agalma clavatum* and compared them with the bracts, presumably larval,

of *A. elegans* and noted no pigmentation nor that the spherical bodies were glands, rather multinucleate structures. Nevertheless, it is difficult to equate the bracts described by Leuckart (1853, 1854) with any other *Agalma* species, particularly pertaining to their mature bracts. Concerning the red spots on the bracts of "*A. Sarsii*" mentioned by Fewkes (1880), Bedot (1888) recognised a similar situation but noted differences in the shape of the bracts (see Fig. 1) and commented that Fewkes' appeared to be made up of single cells, while his glands were multicellular.

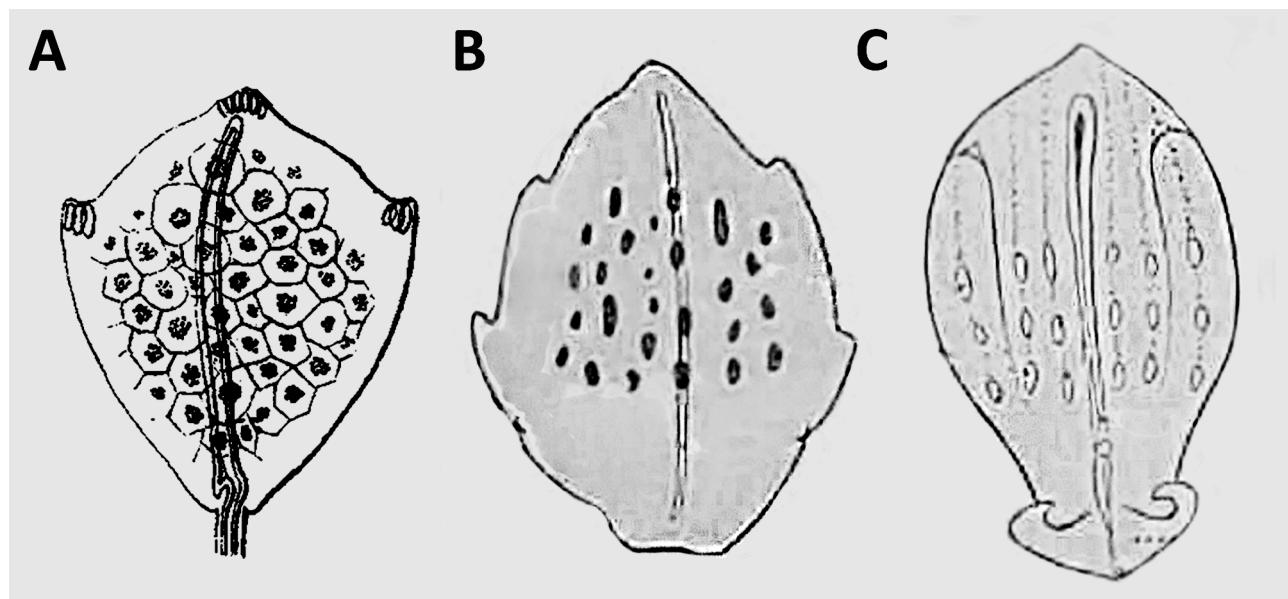


FIGURE 1. A. Fewkes (1880), Plate II, figure 2. "Covering scale of *Agalma Sarsii*"; B. & C. Figures 13 and 25 from Bedot (1888) Plate IV. Proximal at bottom.

When describing the tentilla, Bedot (1888) noted the typical *Agalma*-form with a terminal ampulla and two lateral terminal filaments (Fig. 2C). However, he also noted the large size of the involucrum, from which the cnidoband never emerged, and within which the terminal processes could also be withdrawn. The number of spiral turns in the cnidoband was from 1.5 to 5, and Bedot gave a detailed description of the arrangement and type of nematocysts present therein. Another feature he described is probably one of the most important characters for identifying this species. This is with regard to the palpons (Fig. 2D), or tentacles, as he called them, whose palpacle did not typically arise from its base, but at approximately its mid-length. This is a very distinctive, if not unique character, and it is surprising that neither Bigelow (1911) nor Totton (1965) commented on it.

Finally, in an addendum to his paper, Bedot (1888) pointed out that Haeckel's (1888a) *System der Siphonophoren* had been published while his paper was already in press. He noted that, according to Haeckel's classification, his species, *clausi*, should be placed in the genus *Crystallodes*, but later, for no apparent reason, Bedot (1896) placed it in a new genus *Stephanopsis*.

In his *Challenger Report* published later that year, Haeckel (1888b) described a new species, *Agalma eschscholtzii* that showed certain similarities with Bedot's specimens. Both Haeckel's description and elaborate figures (see Fig. 3) depicted only a single young colony that Haeckel had collected during his stay in Belligemma (Weligama), Sri Lanka. The whole description was brief and the only significant character of the nectophores was that there were three scarlet pigmented spots or ocelli on the ostium, where the upper and lateral radial canals joined the ring canal (Fig. 3B). What else can be gleaned from Haeckel's description will be discussed below when comparisons are made between the present observations and those of Bedot and Haeckel.

Fewkes (1889) noted Bedot's (1888) description of *Agalma clausi*, and he admitted that he might have confused that species with *A. sarsii*. He compared the release of the red pigmentation from the bracts when the colony was disturbed, with a similar release from the mouths of the palpons of *Forskalia* species and concluded that it must be a form of defence. However, Fewkes made no mention of Haeckel's description of *A. eschscholtzii*.

Schneider (1898) briefly reviewed the taxonomy of the family Agalmatidae Brandt, 1834, particularly with regard to the changes made by Haeckel (1888b) and he concluded that many of Haeckel's species were synonyms and, thus, that the number of species could be reduced significantly. However, his final classification was very

confused. For instance, he included the species *Stephanomia Sarsi* (Fewkes, 1880), although he recognised that it was not the same species as *Agalma sarsi* Kölliker, 1853, and synonymised both Bedot's (1888) *A. clausi* and Haeckel's (1888b) *A. eschscholtzii* with it.

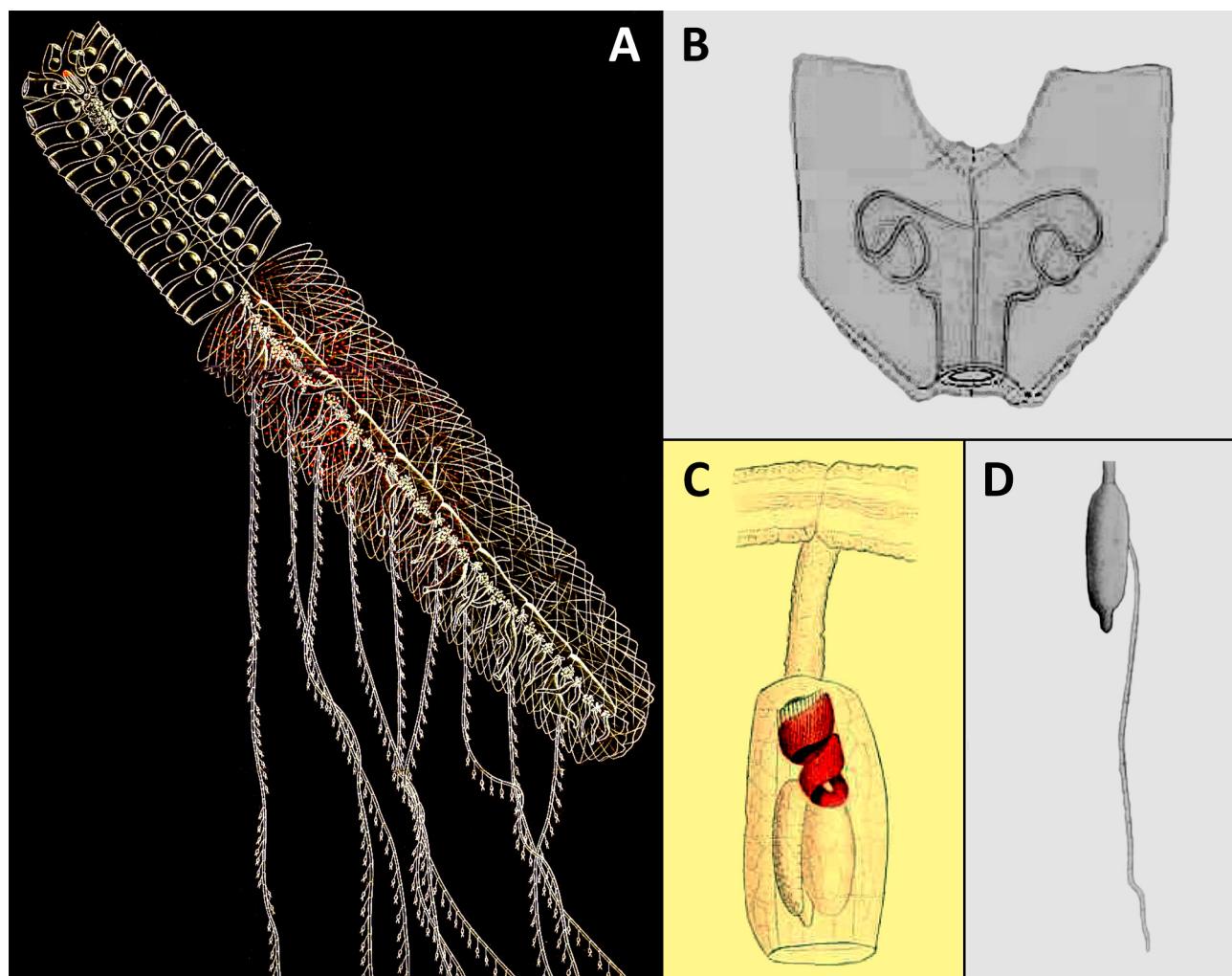


FIGURE 2. **A.** Whole colony of *Agalma clausi* from Bedot (1888) Plate III; **B.** Nectophore; **C.** Tentillum; **D.** Palpon, from Bedot (1888), Plate IV, figs. 6, 3, and 18, respectively.

Bigelow (1911) attempted to bring some sort of sanity to the classification of the siphonophores but, unfortunately, in this case his reasoning was not always sound. He was convinced that Fewkes' (1880) *Agalma sarsi* [=*Agalmopsis elegans* (Sars, 1846)] and Bedot's (1888) *A. clausi* were synonymous and, since the former name was pre-occupied by *A. sarsi* Kölliker, 1853, then the specific name *clausi* had to be accepted. He noted that Schneider (1898) had also synonymised Haeckel's (1888b) *A. eschscholtzii* with them, but decided (*ibid.* p. 276) that "inasmuch as the nectophores are pigmented in Haeckel's species, and the bracts are not, while the reverse is true in *clausi*, it is better to postpone the union of the two until fresh material from the Indian Ocean (the type locality of *eschscholtzii* is Ceylon) can be studied". However, this statement is inaccurate as Haeckel's (1888b, Plate XIII) clearly shows the presence of red pigmentation on at least some of the bracts, although he did not describe it. Nonetheless, Bigelow (1911) recognised that the name *A. eschscholtzii* was pre-occupied, and so he proposed the specific name *haeckeli* to replace it.

Finally, in his *Synopsis of the Siphonophora*, Totton (1965) decided to follow Bigelow (1911) and accept both the species *Agalma clausi* and *A. haeckeli* although, unlike Bigelow, he did mention the presence of red pigmentation on the bracts of the latter species. He also noted that no colonies of either species had been collected since their original descriptions. Thus, at that time the former species was known only from Villefranche-sur-Mer, in the western Mediterranean Sea, while the latter was found off Sri Lanka.

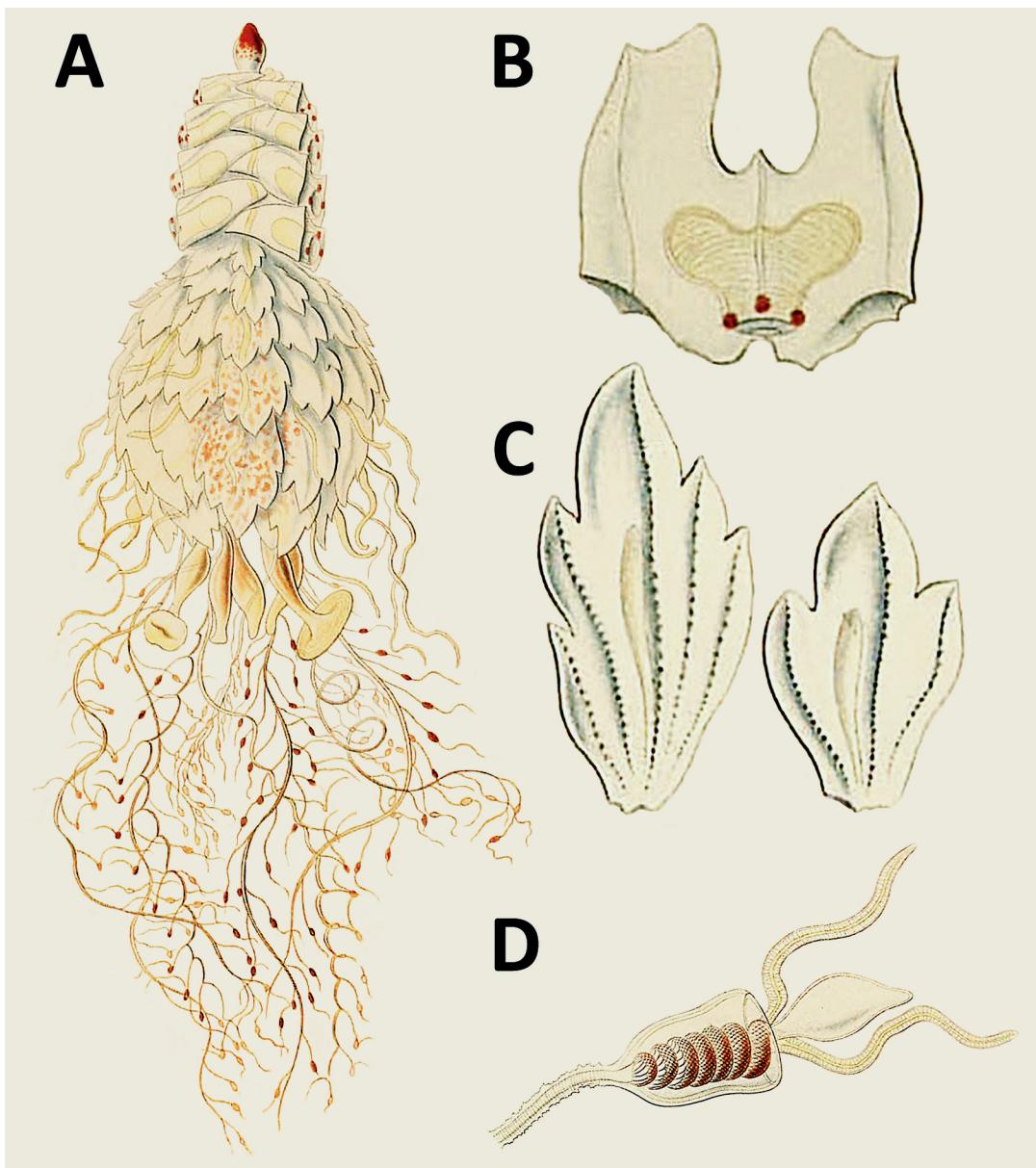


FIGURE 3. *Agalma eschscholtzii* Haeckel. **A.** Whole colony; **B.** Nectophore; **C.** Bracts; **D.** Tentillum. From Haeckel (1888b), Plate XVIII, figs. 8, 9, 10, 11 & 14 respectively.

Although both *Agalma clausi* and *A. haeckeli* share some morphological similarities, especially in terms of presence of red pigmentation on the bracts, there appear to be some fundamental differences between, for instance, the bracts of these species (*cf.* Fig. 3C and Fig. 1B, C). Clearly, the confirmation of the status of both species had to await the collection and examination of fresh material, and such an opportunity arose with the expeditions to the Alborán Sea (Mills *et al.* 1996), close to the type locality of *A. clausi*, and the tropical part of the Atlantic Ocean (see Madin & Harbison 1977). However, despite extensive collections from the Indian Ocean (*e.g.* Daniel 1985) no further specimens of *Agalma* species with red-pigmented bracts have been obtained from that Ocean area. These recent specimens of *A. clausi* are described herein and comparisons are made with the descriptions given by Bedot and Haeckel.

Materials and methods

Material examined. All the specimens of *Agalma clausi* analysed for this study are presently housed in the

personal collections of one of us (PRP) (Tab. 1). They were collected either by the manned submersible *Johnson Sea Link I* (JSL I) or by blue water diving (BWP).

TABLE 1. Examined specimens of *Agalma clausi*.

Specimen	Date of collection	Position
BWP 554-12	17 Mar. 1977	03°36.1'N, 31°54.5'W
BWP 561-8	21 Mar. 1977	06°26.6'N, 38°41.7'W
BWP 565-4	24 Mar. 1977	09°03.2'N, 45°55.9'W
BWP 573-8	28 Mar. 1977	11°46.1'N, 55°17.5'W
BWP 573-15	28 Mar. 1977	11°46.1'N, 55°17.5'W
BWP 1044-11	14 Jul. 1983	03°56.9'N, 37°15.8'W
BWP 1044-15	14 Jul. 1983	03°56.9'N, 37°15.8'W
BWP 1044-16	14 Jul. 1983	03°56.9'N, 37°15.8'W
BWP 1044-22	14 Jul. 1983	03°56.9'N, 37°15.8'W
BWP 1047-27	19 Jul. 1983	02°24.8'N, 35°42.9'W
BWP 1048-1	20 Jul. 1983	03°01.3'N, 33°34.8'W
BWP 1048-7	20 Jul. 1983	03°01.3'N, 33°34.8'W
JSL I Dive 2929-DS1	06 Apr. 1991	35°29.0'N, 4°26.0'W
JSL I Dive 2929-CG4	06 Apr. 1991	35°29.0'N, 4°26.0'W
JSL I Dive 2938-CG4	10 Apr. 1991	35°52.0'N, 3°23.0'W

JSL I specimens were collected over a depth range of 260 to 369 m during a cruise to the Alborán Sea (Western Mediterranean) (Mills *et al.* 1996), while the BWP specimens were collected at depths between the surface and c. 30 m during various Woods Hole Oceanographic Institution cruises to tropical regions of the Western Atlantic Ocean (*e.g.* Harbison *et al.* 1977; Madin & Harbison 1977).

Laboratorial procedures and data processing. Morphological observations, with focus on ontogenetic changes in the morphology of the zooids, were performed using both a stereomicroscope (OLYMPUS SZX12) with an OLYMPUS SC50 camera, and a light microscope (OLYMPUS BX51) with mounted OLYMPUS photographic equipment (SC30, U-CMAD3, U-TV1X-2). Measurements were performed with cellSens Standard 1.12 software (OLYMPUS), or ImageJ (National Institutes of Health).

The distribution map for *Agalma clausi* was drawn with ArcGIS 10.4 software, based on the geographical coordinates of all valid species records that were either extracted from the literature (*e.g.* Bedot 1888; Haeckel 1888b for *A. haeckeli*, *ibid.* as *A. eschscholtzii*; Mills *et al.* 1996) or from GBIF (Global Biodiversity Information Facility).

Terminology. Haddock *et al.* (2005a) provided an overview of siphonophoran colony axes established for the calyptophoran siphonophore of the Family Prayidae. Since some of their terminology does not apply to physonects, we used a modified version introduced by Pugh and Baxter (2014).

Results

Agalma clausi (Bedot, 1888)

Synonyms.

Agalma sarsi (Fewkes, 1880) p. 628.

Crystallodes Clausi (Bedot, 1888, *post-scriptum*) p. 20.

Stephanopsis Clausi (Bedot, 1896) p. 406.

Stephanomia sarsi (Schneider, 1898) p. 121–122.

? *Agalma eschscholtzii* (Haeckel, 1888) p. 226 and Plate XVIII, Fig. 8–17.

? *Agalma haeckeli* (Bigelow, 1911) p. 274–277.

Systematics. *Agalma clausi* belongs to the Family Agalmatidae Brandt, 1834 that is nested within the historically recognized Physonectae, a suborder that groups all siphonophores sharing particular body plan *i.e.*, possessing pneumatophore, nectosome, and siphosome. However, Physonectae were shown to be polyphyletic (Dunn *et al.* 2005) and following the most recent phylogeny (Munro *et al.* 2018) agalmatid siphonophores are placed within a newly erected, monophyletic clade Euphysonectae. Although this phylogenetic hypothesis is well supported, as the International Commission on Zoological Nomenclature (ICZN 1999) does not recognise clades we decided to maintain the name Physonectae throughout this text.

Type specimens. There is no known type specimen, thus we designate the specimen from BWP Dive 1044-15 as a neotype. It will be deposited at the United States National Museum (Smithsonian Institution), Washington, DC under accession number USNM 1422474. It was collected close to the surface by a SCUBA diver on 14th July, 1983 at 3°56.9'N, 37°15.8'W.

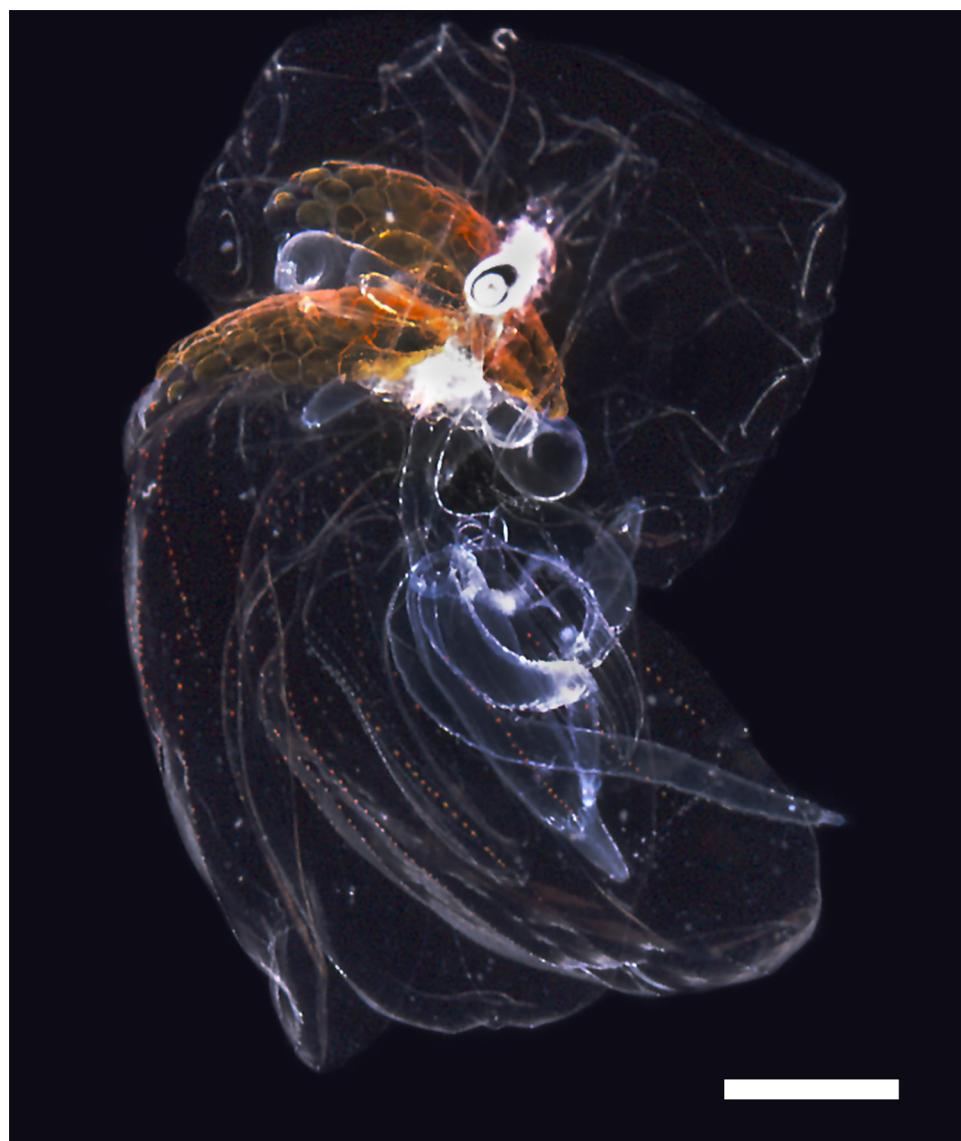


FIGURE 4. *In situ* photograph of specimen BWP 1048-7. Scale bar: 0.5 mm. (With grateful thanks to Ron Gilmer).

Diagnosis. Rigid-stemmed, monoecious agalmatid siphonophore of prismatic appearance, with nectophores arranged biserially and some bracts showing carmine pigmentation in living animal. Nectophores with short axial wings and size-dependent ridge pattern, incomplete laterals discernible only in younger zooids, but upper and lower lateral ridges present throughout development, but very weak in largest nectophores. No vertical lateral ridges. Thrust block small on mature nectophores; lateral ostial processes also small and packed with nematocysts. Typical *Agalma* course of lateral radial canals. Cormidia bearing gastrozooids (often flask-shaped), with tentacle,

several gonophores of both sexes, bracts and palpons. Involucrum of tentillum voluminous, able to contain the cnidoband, the two terminal filaments and the central ampulla. Palpacle of palpon originates not at its base but, on the fully mature palpon, almost at its mid-length. Six types of bracts, of which one is able to discharge a coloured, probably fluorescent, fluid when stimulated.

Description

General structure (Fig. 4) *Agalma clausi* had a rigid stem, and bore numerous foliaceous bracts. The longest specimen examined here (JSL I Dive 2929-DS1) had a total length of 10 cm with a nectosome of 4 cm.

Living animals had distinctive patches of glands on the outer surface of the bract that were able to release orange fluid upon stimulation (Fig. 4). Besides mentioned structures, preserved colonies were mostly transparent with brownish to reddish pigmentation of the stem and of some zooids (mainly gastrozooids).

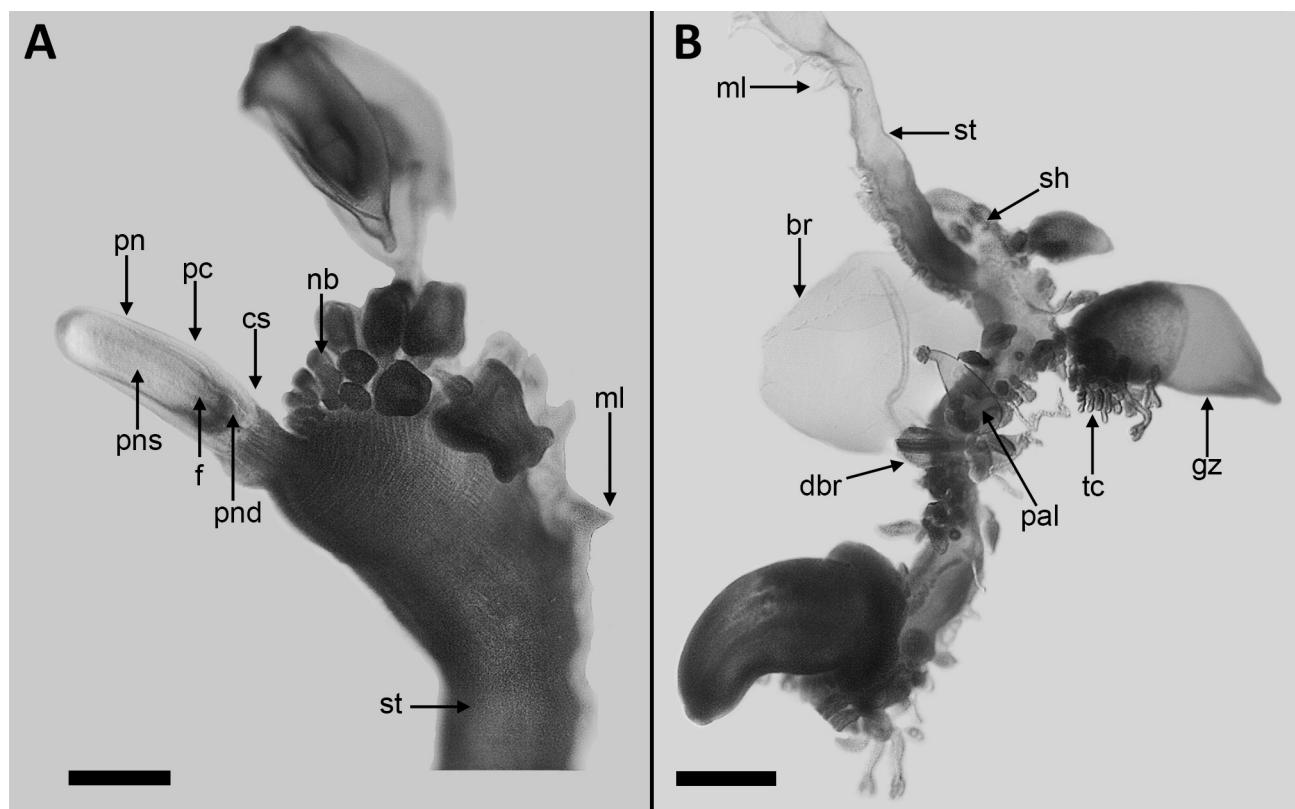


FIGURE 5. A. Pneumatophore and nectosomal growth zone of specimen JSL I Dive 2929-DS1; B. Siphosomal stem from specimen BWP 1044-22. *br*—bract, *cs*—chitin septa, *dbr*—developing bract, *f*—funnel, *gz*—gastrozooid, *ml*—muscular lamella of nectophore, *nb*—nectophoral buds, *pal*—palpon, *pc*—pericystic cavity, *pn*—pneumatophore, *pnd*—pneumadenia, *pns*—pneumatosaccus, *sh*—siphosomal horn, *st*—stem, *tc*—tentacle. Scale bars: A. 2.5 mm; B. 1 mm.

Stem. In its preserved state, the nectosomal stem was thinner than that of the siphosome, and bore no zooids other than nectophores. Nectophores were budded off dorsally (Fig. 5B). Siphosome was highly contracted, and in all specimens examined, most zooids had become detached or lost during collection, which hampered analysis of their arrangement in each cormidium (Fig. 5B). The siphosomal stem bore up to 9 cormidia (in specimen JSL I Dive 2929-DS1), each of which comprised a single gastrozooid, numerous bracts, variable numbers of male and female gonophores, and some palpons with particularly long palpacles.

Pneumatophore and nectosomal growth zone. The size of the pneumatophore varied greatly between specimens. In specimen JSL I Dive 2929-DS1 it was 4 mm long and 1 mm wide (with a 1 mm long stalk) (Fig. 5A), while in specimen BWP 1044-22 this zooid was much smaller (1.1 mm long, and 0.8 mm wide, with a 0.4 mm long stalk). The size variation was reflected in the variety of shapes of the pneumatophore (from elongated to roundish).

The pneumatophore did not overtop the nectophores, and was borne on a short stalk (Fig. 4, 5A). At its anterior

end, it had pigmented tissue (presumably red/orange in living specimens, but still discernible in the fixed ones). The nectosomal growth zone was considerably more voluminous than other parts of nectosomal stem (Fig. 5A). Nectophoral buds were attached by the relatively long stalks that shortened with growth.

Nectophores. The nectophores of *Agalma clausi* reached maximal dimensions of 15.8 mm in width and 16.6 mm in length in specimen JSL I Dive 2929-DS1. The maximal number of mature nectophores in specimens examined was 30 in specimen JSL I Dive 2929-DS1 (all were detached).

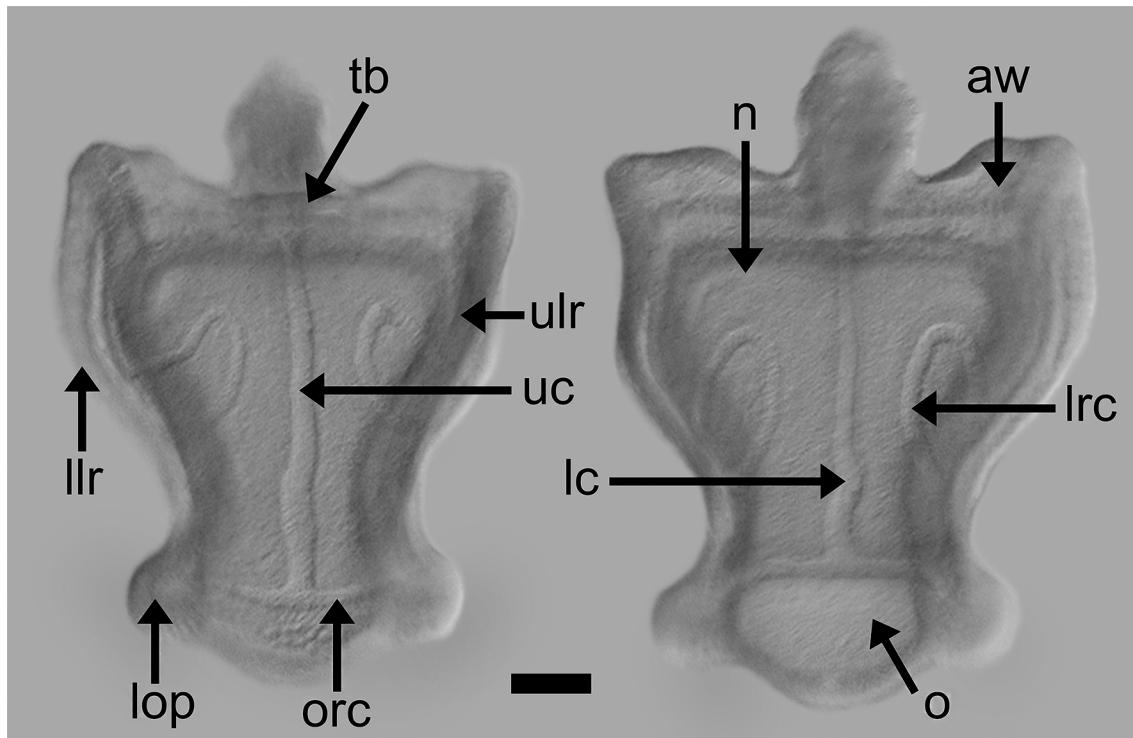


FIGURE 6. Morphology of *Agalma clausi* nectophoral bud in upper (left) and lower (right) views. *aw*—axial wing, *lc*—lower canal, *llr*—lower lateral ridge, *lop*—lateral ostial process, *lrc*—lateral radial canal, *n*—nectosac, *o*—ostium, *orc*—ostial ring canal, *tb*—thrust block, *uc*—upper canal, *ulr*—upper lateral ridge. Scale bar: 200 µm.

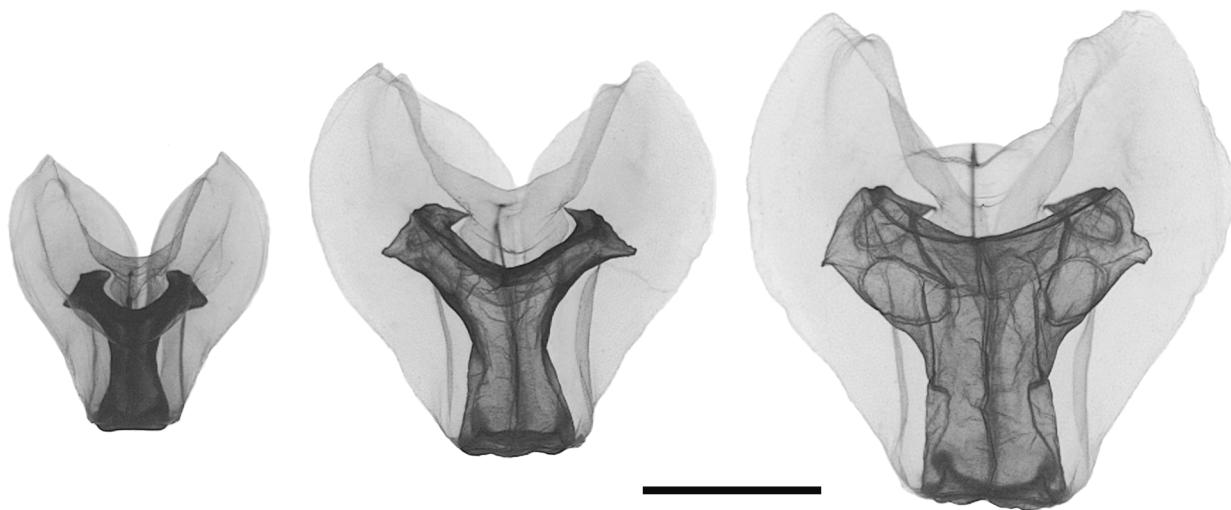


FIGURE 7. Lower views of different sized nectophores of JSL I Dive 2919-DS1 specimen showing the Y-shaped nectosac. Scale bar: 2 mm.

The nectophoral buds were very small, with wide radial canals having a typical *Agalma* course, but with a more pronounced loop of lateral radial canal and short axial wings (Fig. 6). Both newly-budded and adult

nectophores had their lateral ostial processes, as well as the upper surface of the ostial opening of the nectosac, packed with nematocysts, but none were observed elsewhere on the nectophore surface. The nectosac occupied most of the nectophore. The lower and upper lateral ridges were complete and easily discernible on the bud, but became less obvious in mature nectophores (Fig. 8). In contrast, the lateral ridge, although incomplete, could only be identified on older nectophores.

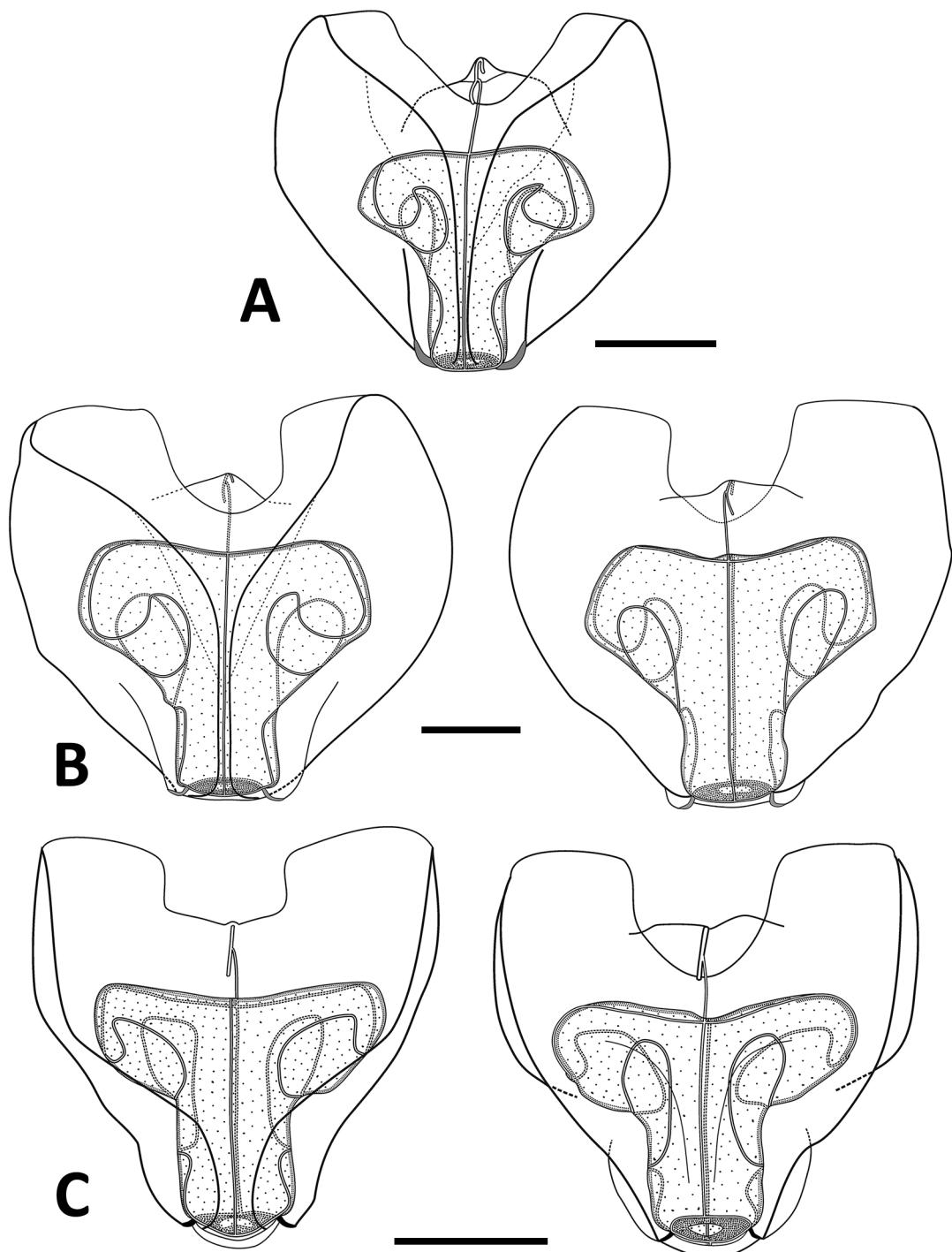


FIGURE 8. Nectophores of *Agalma clausi* drawn at different developmental stages, based on specimen JSL I Dive 2929-DSI. **A.** Young nectophore; **B.** Upper (left) and lower (right) views of medium-sized nectophore; **C.** Upper (left) and lower (right) views of largest nectophore. Scale bars: A. 2 mm; B. 2 mm; C. 5 mm.

During the next stages of development of the nectophores, they took on a very characteristic and rather unexpected shape (Fig. 7). The axial wings rapidly increased in size, so that at an early stage they formed almost half the height of the nectophore (Fig. 7 left), before the main body increased at a faster rate. The most obvious feature is that the nectosac becomes distinctly Y-shaped with the lateral tips truncated in a characteristic way. Nectophores that displayed this stage of development were present in almost all the specimens examined, whether they were collected at depth (JSL) or at the surface (BWP).

With further development of the nectophores (Fig. 8A) the upper lateral ridges remained close to each other for most of their length; the thrust block was not very prominent; and the axial wings were relatively short. As the nectophores matured (Fig. 8B, C), the upper lateral ridges moved further and further apart, while neither the thrust block nor the axial wings changed proportions significantly, although the latter tended to be more broadly truncated proximally. Both ascending and descending mantle canals, of similar lengths, were present, and the pedicular canal branched off perpendicularly and ran to the nectosac, where it gave rise to all four radial canals. Lower and upper radial canals ran straight to the ostial ring canal, while the lateral branches formed pronounced loops, first on the upper surface of the nectosac, and then on the lower. Then, instead of running straight along the lateral surface of nectosac to the ostial ring canal, they formed an additional loop on the upper nectosac surface.

Bracts. Six types of bracts were identified, differing in the presence, placement and shape of the transverse ridge, number of cusps and additional features, such as the presence of patches of nematocysts or glands discharging pigmented fluid (Fig. 9). Each bract type also possessed lines of opaque tissue on the distal portion of the upper surface (Fig. 9). All types of bracts were observed in broad size ranges and in each colony of *Agalma clausi*, confirming that they were actually different bract types rather than developmental variants of the same type. Bract of the Types A & B, and C & D, probably represent two dissimilar enantiomorphic pairs, as is often the case for species of the physonect genus *Forskalia* (see Pugh, 2003). The potential spatial restriction of different bract types along the stem could not be elucidated, because most bracts became detached upon fixation and storage.

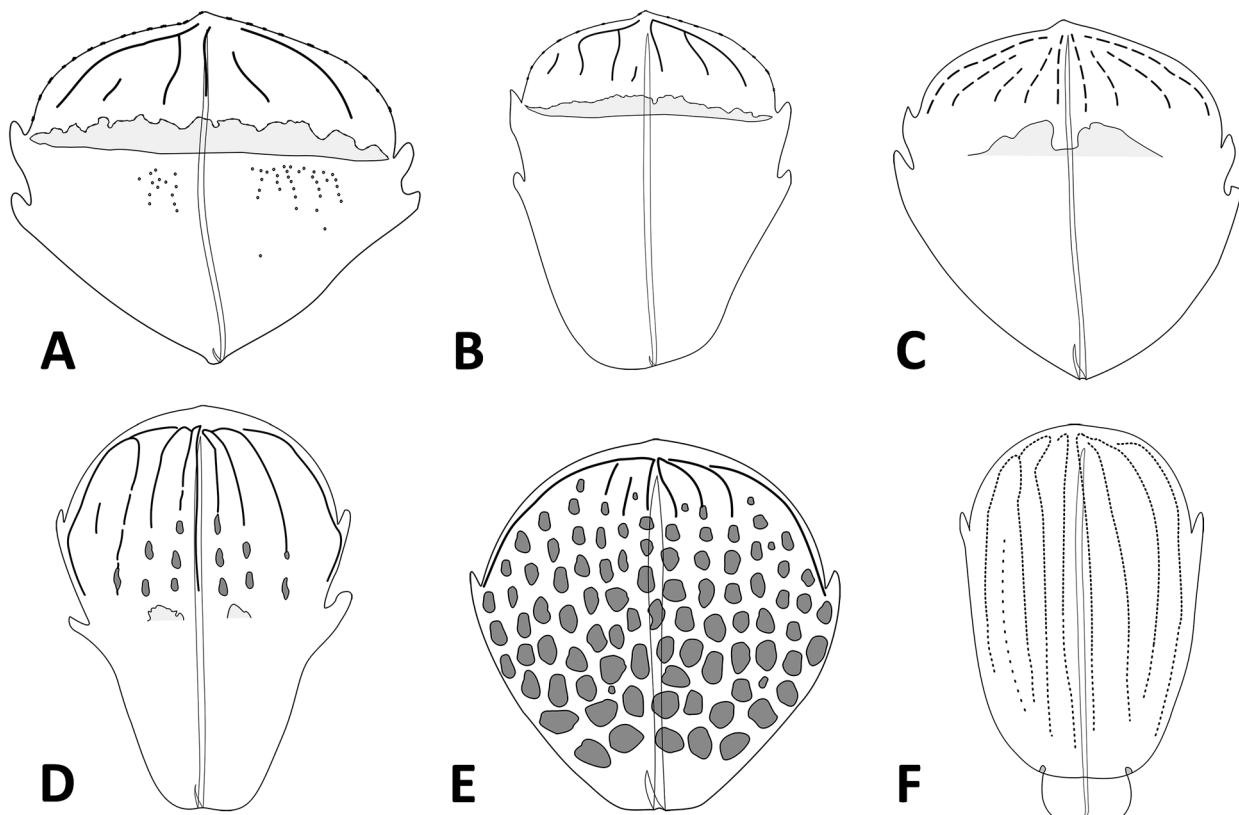


FIGURE 9. Different types (A–F) of *Agalma clausi* bracts. All drawings represent bracts of similar size i.e., 3.0 ± 0.5 cm in length except for type E bracts, which measured c. 1.3 cm in length.

Types A & B. These enatinomorphic bract types were the most abundant ones, and were characterized by the presence of two pairs of lateral cusps, and a long, almost complete transverse ridge at the same level as the distal pair (Fig. 9A & B). This ridge formed an extensive, irregularly frilled flap. Cell clusters, probably including nematocysts, were dispersed fairly evenly along the edge of the transverse flap and on the distal edge of the bract. On the upper side of the distal facet there were from five to nine lines of superficial cells organised into a regular pattern. There were often gaps in these lines, and some parts appeared wider than others, probably caused by abrasion of the cells. Bracts of Type A differed from B in the presence of nematocysts patches identified on the upper surface of the bract, and in the dimensions of bracts, with Type A being wider than long, while Type B were longer than wide.

Types C & D. Another enantiomorphic pair of bracts, similar to those of Type A and B, with two pairs of lateral cusps, but with a less complete transverse ridge, restricted to the central part of the upper side of the bract. For both types, this was usually situated on a level with the distal pair of cusps, but sometimes were slightly more proximal, but never as far as to be on a level with the proximal pair of cusps. No cell clusters (e.g. nematocysts) were found either on the distal edge of bracts or on the surface and edge of flaps. The flap itself was comprised of either two interconnected flaps with irregular edges (Type C; Fig. 9C), or two smaller and separate flaps (Type D; Fig. 9D). Each bract examined had lines of opaque tissue, that in Type C were always nine in number, and sometimes were discontinuous, probably due to cell abrasion (Fig. 9C), while in Type D these lines were bolder, and acquired a gland-like appearance in their more proximal regions (Fig. 9D).

Type E. These bracts were the smallest of all the types of bract present (Fig. 9E), and possessed only a single pair of lateral cusps. The lines formed by the opaque tissue were short. Observed bracts had prominent glands slightly embedded in the mesogloea, which presumably were responsible for producing and discharging the coloured fluid in the living colonies (Fig. 10). Bracts, whose upper surface resembled bubble wrap were found occasionally. They appeared to be intact and so, probably, were Type E bracts that had lost their pigmentation upon preservation or fluid discharge (*cf.* Fig. 4).

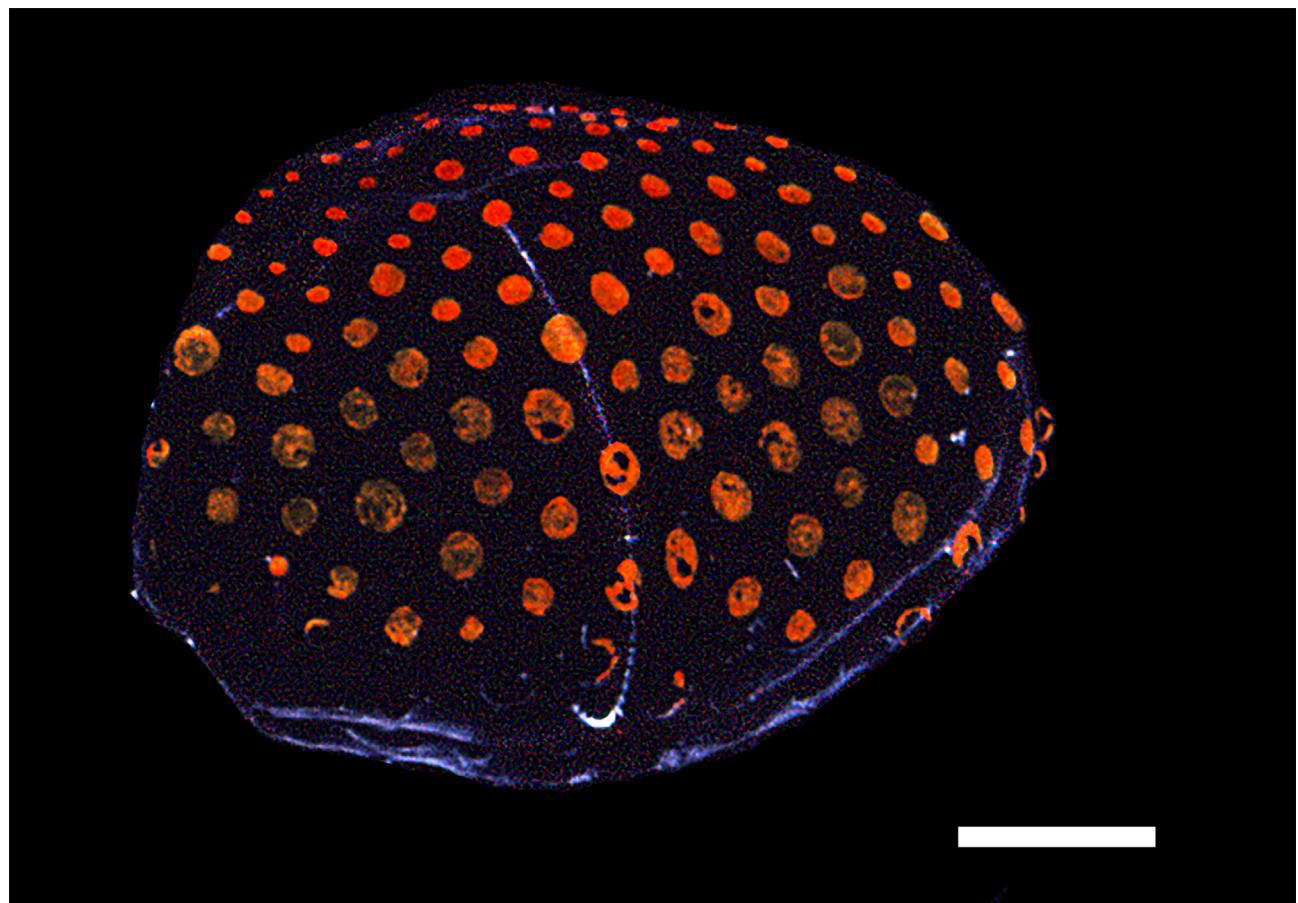


FIGURE 10. Loose Type D bract of *Agalma clausi* from BWP Dive 1044-11. Scale bar: 1 mm. (With grateful thanks to Ron Gilmer).

Type F. These bracts were characterised by a thickened swelling on their lower sides at the proximal end (Fig. 9F), while the remainder of the bract was thin and leaf-like. On the younger bracts this protuberance partially projected out from the proximal end of the bract with the more distal part separated from the main body of the bract by a shallow lateral furrow. These young bracts were frequently folded in half, longitudinally, with their sides defining a deep, but narrow, gutter along the lower side. Toward the distal end there was a pair of prominent lateral cusps. As they enlarged, the bracts tended to flatten out, and the thickened protuberance no longer protruded proximally, but formed part of the main body of the bract. At the same time the two distal lateral cusps were resorbed into the bract forming two marked swellings on the lower side. The bracteal canal originated on the proximal protuberance and passed, distally over it, in a very shallow furrow, before continuing along the mid-line beneath the lower wall of the bract. It ended close to the distal end of the bract, without penetrating into the mesogloea. There were nine irregular longitudinal rows of ectodermal cells on the upper surface of the bract, which were not the same as the opaque tissues identified on the other types of bract.

Palpons. The most distinctive zooid of *Agalma clausi* was the palpon, with its elongate shape (up to 10.6 mm length for specimen JSL I Dive 2929-DS1), with the palpacle attached, not at the base, but laterally at a variable length, up to half the length, but on average at one third the length of the palpon (Fig. 11). Such a position was already established in the youngest palpons (Fig. 11A), and was maintained throughout zooid development (Fig. 11E).

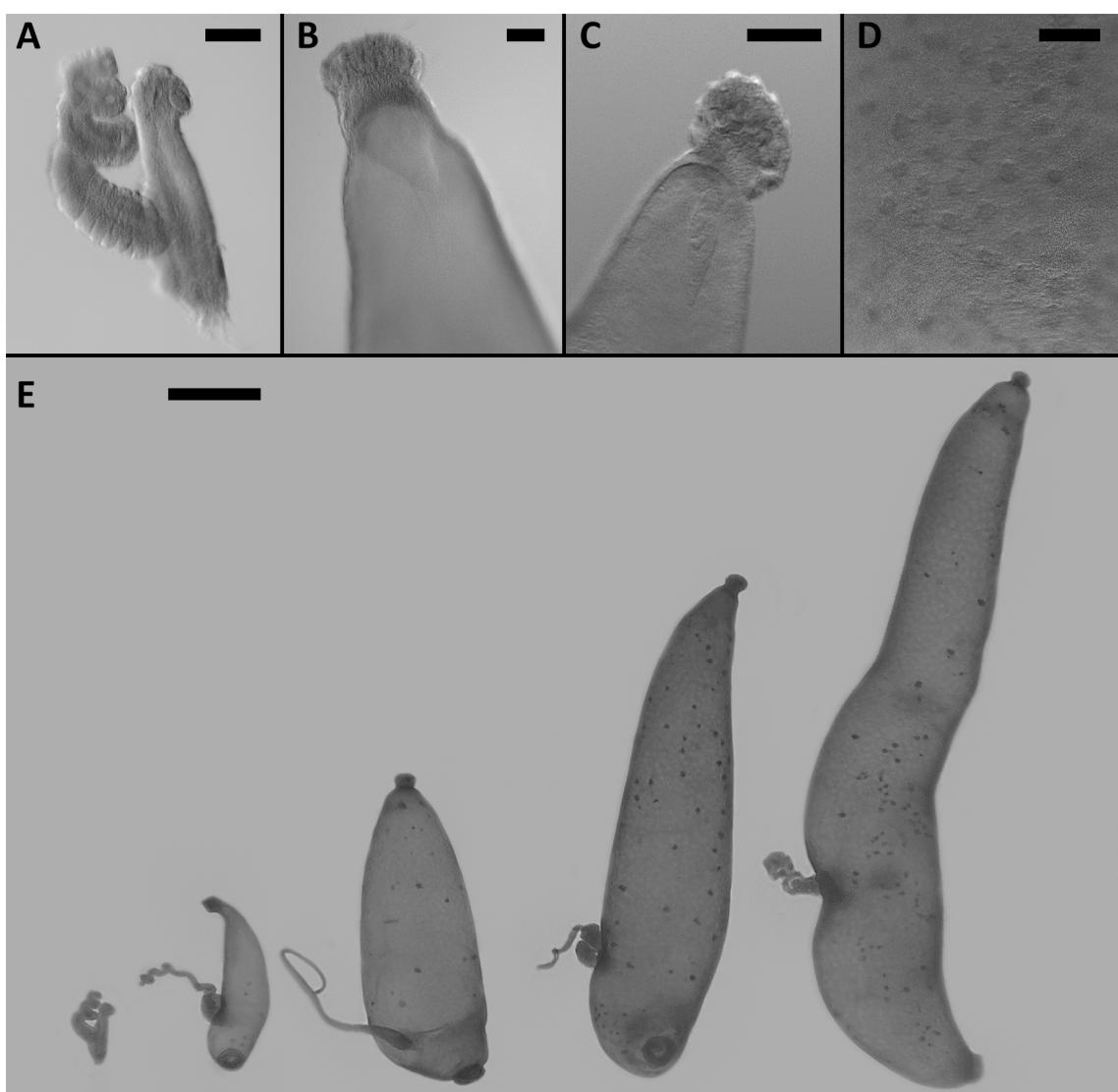


FIGURE 11. Palpons of *Agalma clausi*. **A.** Early bud; **B.** Tip of mature palpon with amorphous droplet; **C.** Tip of mature palpon with nematocysts arranged differently; **D.** Surface of mature palpon with regularly scattered opaque cells; **E.** Developmental sequence of palpons of specimen BWP 1044-22. Scale bars: A. 100 µm; B. 100 µm; C. 200 µm; D. 100 µm; E 50 µm.

Large palpons appeared to be filled with a dense amorphous substance, while the younger ones were more transparent, with a milky-white appearance (Fig. 11B, C). In some specimens, there were opaque cells either randomly scattered in the ectoderm (Fig. 11D) or packed in clusters (Fig. 11E). The distal region of the palpon, around the mouth, was always packed with nematocysts of unknown type, more numerous in younger zooids (Fig. 11). These were quite variable in size, ranging from $56 \times 29 \mu\text{m}$ to $75 \times 42 \mu\text{m}$. They appeared to be different from the types of nematocyst found in the cnidoband of the tentillum but, as no discharged ones were observed, their identity could not be determined. No nematocysts were found elsewhere on the palpons or the palpacles, with the exception of specimen BWP 1044-22 in which one palpon had three nematocysts in its epidermis. Small nematocysts, c. $9 \times 6 \mu\text{m}$, were scattered along the length of the palpacle. They could not be identified with certainty, but they appeared to differ from those found on the terminal filament of the tentillum.

Gastrozooid and tentacle. Feeding polyps were clearly divided into a narrower distal part – the stomach region, bearing hepatic stripes, and an expanded proximal part, the basigaster, composed of nematogenic tissue (Fig. 12). At the very tip of this zooid type there was a small, pyramidal proboscis bearing the mouth. The gastrozooids measured up to 6.8 mm in length, and up to 2.7 mm width, at the widest point of the basigaster. Notably, the gastrozooids were often flask-shaped, but this may be a preservation artefact.

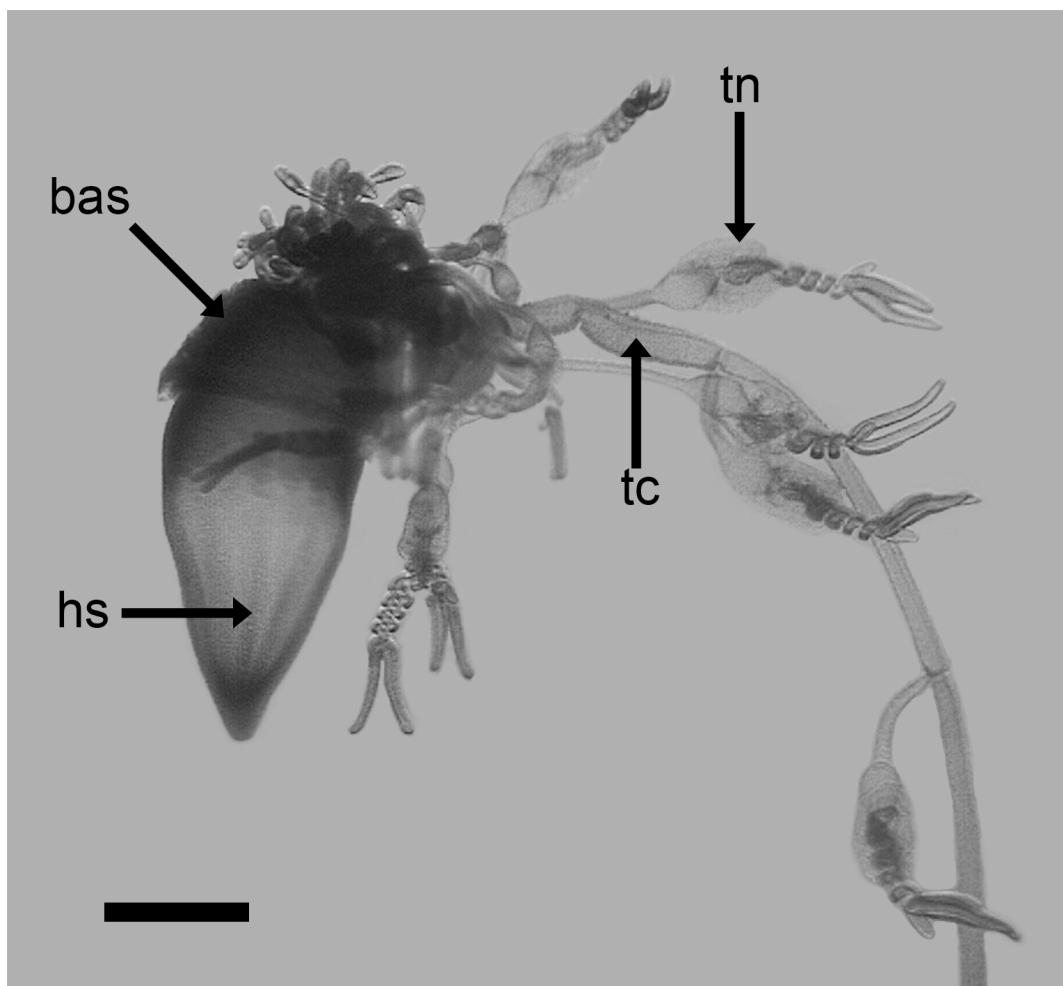


FIGURE 12. Morphology of gastrozooid. *bas*—basigaster, *hs*—hepatic stripes, *tc*—tentacle, *tn*—tentillum. Scale bar: 500 μm .

During the growth of the gastrozooid, the most apparent change was a reduction in the proportional length of the basigaster with respect to that of the whole gastrozooid. Concomitant with this was an increase in the length of the tentacle (Fig. 13). The latter arose from the base of the basigaster and, at a very early stage of development, appeared to be spiralled, with regularly spaced buds of tentilla.

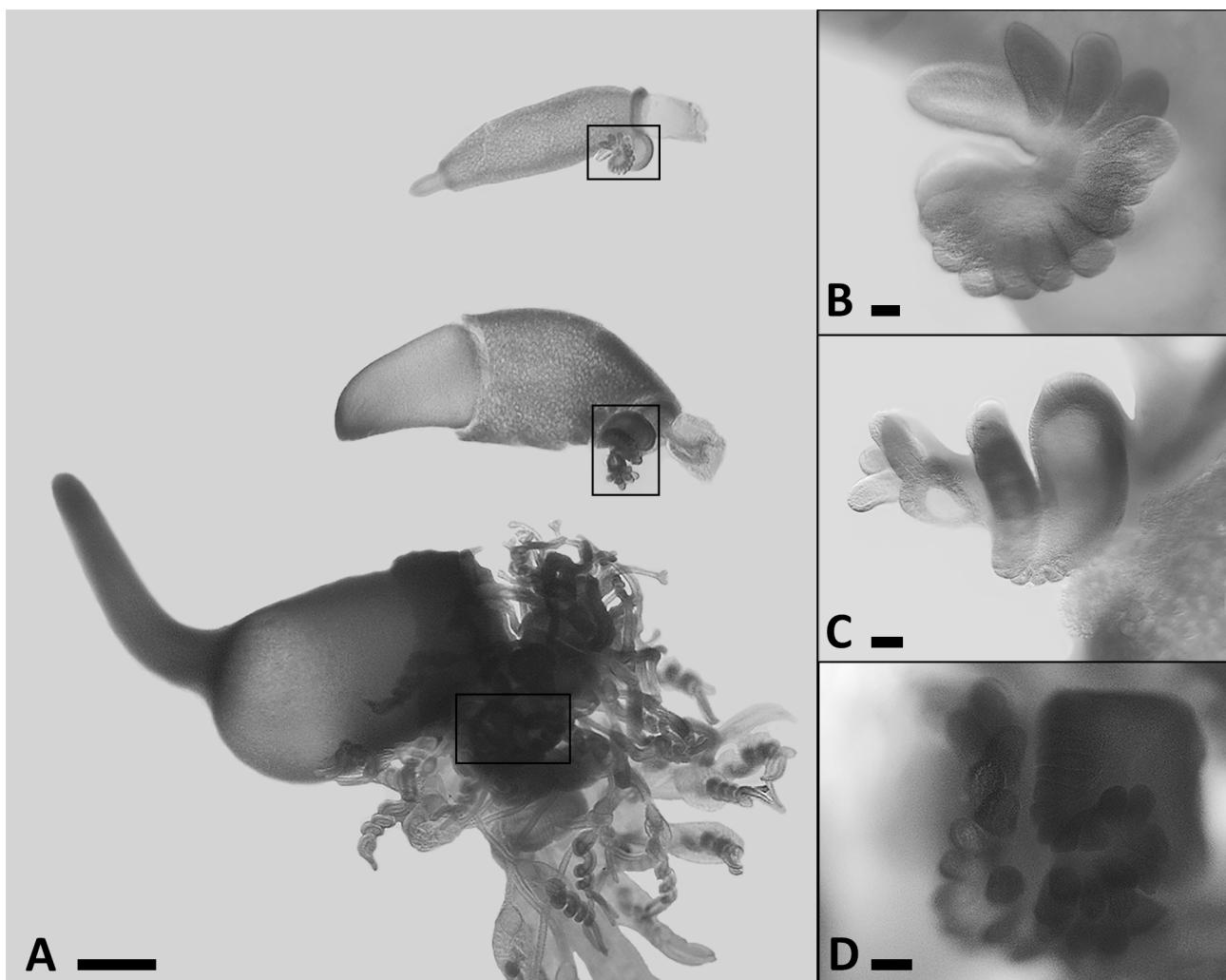


FIGURE 13. Developmental sequence of gastrozooids (A), showing tentacle bud for each of the gastrozooid growth stage respectively (B–D). Scale bars: A. 500 μm ; B. 50 μm ; C. 100 μm ; D. 200 μm .

Tentillum. As it developed, the primarily oval bud of the tentillum elongated and a small vesicle appeared at its distal end; the primordial ampulla (Fig. 13B, 14A, *pa*), on either side of which could be seen the rudiments of the terminal filaments (Fig. 14A, *tf*). These quickly increased in size and the distal end of the cnidoband, apparently devoid of all nematocysts, formed a single spiral turn (Fig. 14B). The cnidoband continued to elongate, adding further loose spirals distally, while at its proximal end a spiral cluster of elongated (up to 150 μm in length) nematocysts developed (Fig. 14A, *nc*). These appeared to be microbasic mastigophores (C. Östman, pers. comm.). They remained in the same position, and did not appear to be augmented throughout the remainder of the development of the tentillum.

At the same time, the distal end of the pedicle of the tentillum began to change. The gastrovascular canal increased considerably in size, eventually forming a large spherical vesicle before shrinking back to its original size, once the tentillum had reached maturity. At the same time, the ectoderm toward the distal end of the pedicle began to grow out into a cupulate process that would develop into the involucrum (Fig. 14B, *inv*). The margin of the involucrum, then, gradually elongated distally, to form a sheath that, eventually, could totally enclose the cnidoband and the terminal processes, when these were totally contracted. Up until now the cnidoband had been only loosely coiled, but now, starting from its distal end, the spiralling began to consolidate. As it approached maturity, the cnidoband had several spiral coils (up to 5), but after the involucrum expanded to the point when it was able to contain both terminal filaments and the ampulla, the number of coils decreased to c. 2 while the width of each spiral widened (Fig. 14B). Throughout the development of the tentillum, the gastrovascular canal ran through the cnidoband to its distal end. At first, it was straight and then followed the spiralling of the cnidoband. In the latter stages, it also coiled up on itself, like a spring.

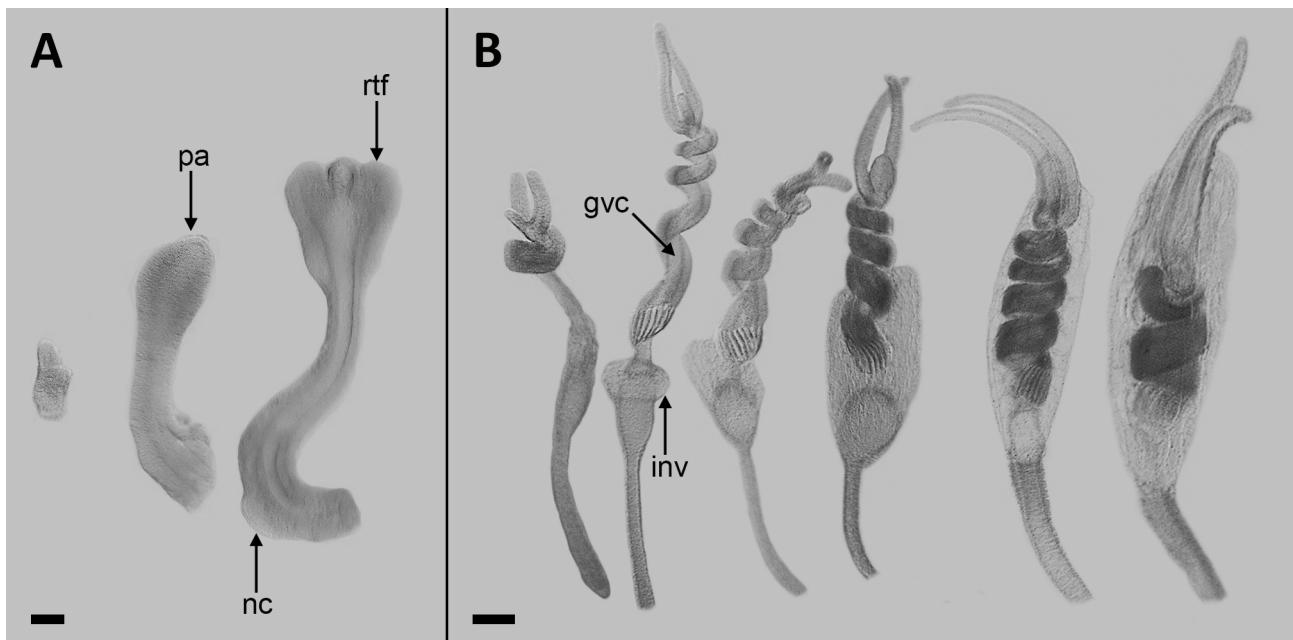


FIGURE 14. Development of tentillum. **A.** Early stages; **B.** Later stages. *gvc*—gastrovascular canal, *inv*—involuticum, *nc*—nematocyst cluster, *pa*—primordial ampulla, *rtf*—rudiment of terminal filament Scale bars: A. 50 µm; B. 200 µm.

The cnidome of the tentillum appeared to include four different nematocyst types, two in the terminal filaments, and two in the cnidoband. For the former, there were spherical desmonemes (measuring 9.63 ± 0.31 µm, $n = 12$) and acrophores (measuring $10.9 \pm 1.34 \times 4.1 \pm 1.34$ µm, $n = 6$), with the desmonemes being far more numerous. These were illustrated by Bedot (1888, Pl. III, figs. 21 & 23). Unfortunately, nematocyst identification in the cnidoband was unsuccessful because of the lack of discharged ones. However, the vast majority were small nematocysts ($28.63 \pm 1.63 \times 5.75 \pm 0.84$ µm, $n = 12$) that, according to Purcell (1984), were haplonemes, possibly anisorhizas. The less abundant larger ones ($167.25 \pm 12.18 \times 23.92 \pm$ µm, $n = 12$) were concentrated at the proximal end of the cnidoband. Both types were illustrated by Bedot (*ibid.* Figs. 29–31), including an evaginated nematocyst of the larger type (*ibid.* Fig. 30), which closely resembles a microbasic mastigophore.

Gonophores. Both male and female reproductive zooids were attached to gonodendra via pedicles, forming clusters of gonophores of one sex (Fig. 15). There were usually a few palpons closely associated with each gonodendra, although their exact number could not be determined. Male gonophores were elongated when mature, growing up to 4.3 mm in length and becoming completely opaque, but roundish, with very thin mesogloea in young specimens (Fig. 15B).

Female gonodendra bore more numerous gonophores than male ones (Fig. 15C, D). The gonodendra, when budded off, had a trifid structure that was retained through the development (Fig. 15C). During growth of the gonophores their shape changed from spherical to oval, while their medusae bell became significantly enlarged, so that in mature gonophores the radial canals were distinct (Fig. 15D).

Distribution. Bedot's (1888) specimens came from superficial waters of the Bay of Villefranche in the North-western Mediterranean Sea. The bay is a well-known place for research on siphonophores, but since then no other specimens of this species have been encountered there (e.g. Leloup 1935; Carré & Carré 1995). The only other records of *A. clausi* from the Mediterranean come from Mills *et al.* (1996), who found this species during an expedition to its western part, the Alborán Sea. These authors collected six specimens at depths ranging from 260 m to 369 m at three different sites.

All other records of *Agalma clausi* come from the western North Atlantic Ocean (Fig. 16). The northernmost specimen was captured by Casey W. Dunn during blue water diving in the Gulf Stream at $37^{\circ}26'N$, $72^{\circ}41'W$. All the remaining specimens collected by SCUBA divers, including several that were not used for this description as they were in poor condition or had been discarded, came from equatorial waters, between 2 and $12^{\circ}N$ and 33 and $45^{\circ}W$, some of which were reported by Madin & Harbison (1977) and Harbison *et al.* (1977).

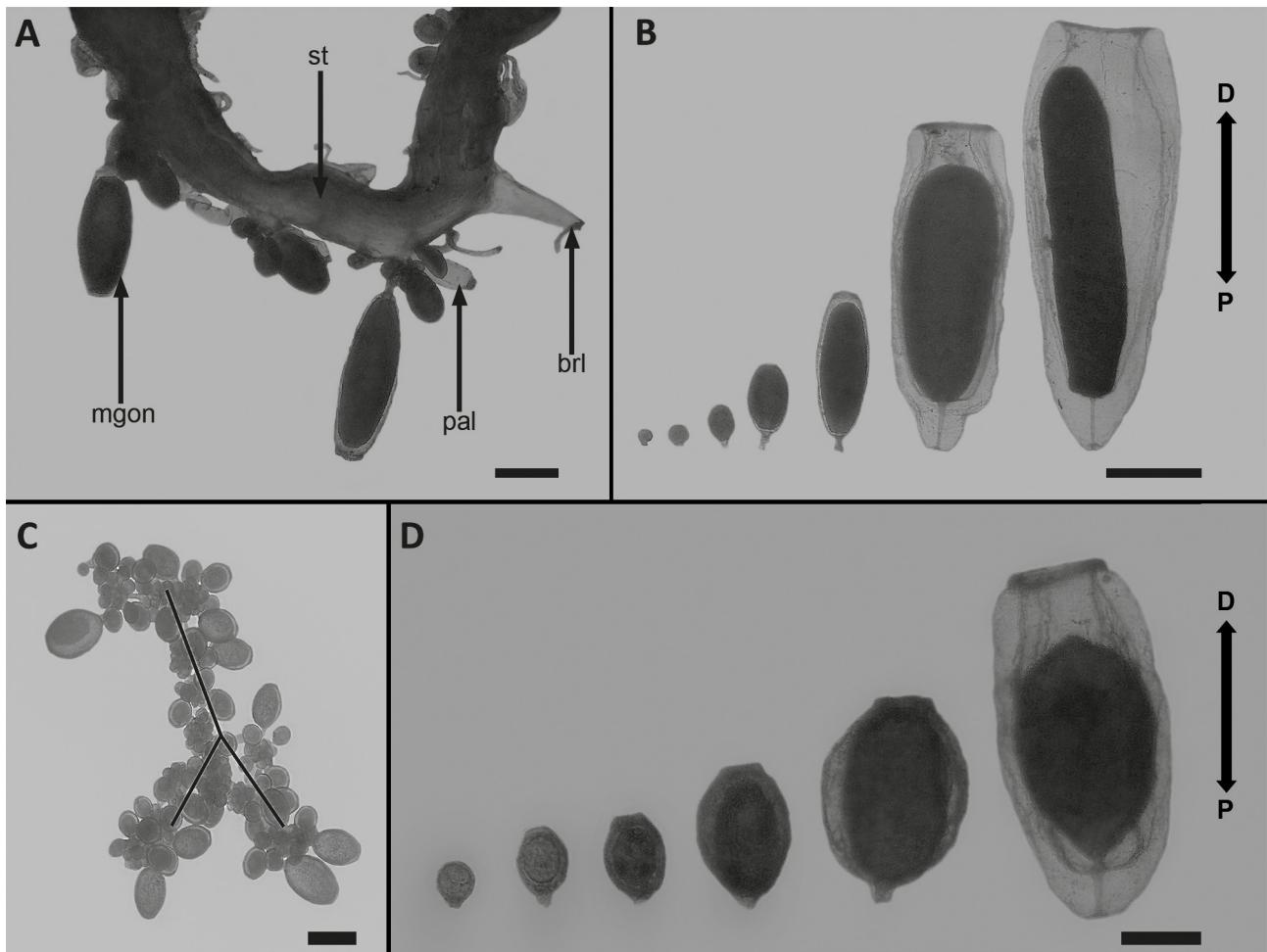


FIGURE 15. Gonophores of *Agalma clausi*. **A.** Portion of stem showing arrangement of male gonophores; **B.** Developmental sequence of male gonophores with zooid axis; **C.** Mature female gonodendron showing gonophores at different stages of development being arranged along three axes; **D.** Growth sequence of female gonophores with zooid axis. *brl*—bracteal lamella, *D*—distal, *mgon*—male gonophores, *P*—proximal, *pal*—palpon, *st*—stem. Scale bars: A., B. 0.8 mm; C., D. 0.5 mm.

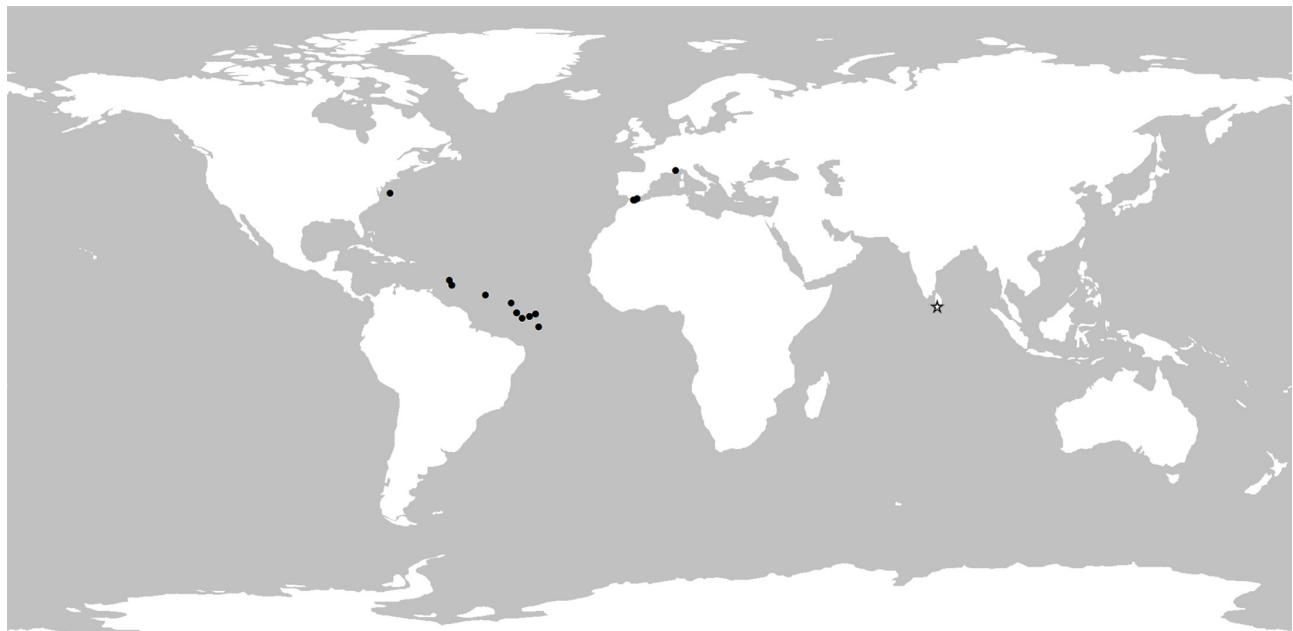


FIGURE 16. Distribution map of *Agalma clausi* (dots) and *A. haeckeli* (star).

Discussion

Status of *Agalma clausi* and *A. haackeli*. Making comparisons between our material and that described by Bedot (1888) and Haeckel (1888b) is difficult, particularly with regard to the nectophores, for which their descriptions appear to be inaccurate. When identifying a physonect siphonophore, the most important morphological characters of taxonomic interest usually are the structure of the nectophore, with the notable exception of *Athorybia* species (no nectophores) and rhodaliids (nectophores not known to have specific characteristics), and the bract. Of subsidiary interest are the structure of the tentillum and, very occasionally, the palpon. In the present case, the lack of detail in Bedot's and Haeckel's descriptions of the nectophore means that no thorough comparisons can be made. As for the tentillum, their descriptions agreed that it had the typical *Agalma*-type form, with a terminal ampulla and two lateral terminal filaments, as indeed was the case for our specimen. The cnidoband of Haeckel's tentilla was said to include 2–8 spiral turns (see Fig. 3D), while Bedot's had 1.5 to 5 (see Fig. 2C). For our specimens, the number of spiral turns reached a maximum of c. 5 before becoming fully mature, then reducing to c. 2. Therefore, no conclusions can be drawn from this.

The structure of the palpon usually has little taxonomic value, with the notable exception of *Physophora* species, but the presence or absence of a tentacle-like structure, a palpacle, can have generic significance. However, the palpacle, like the tentacle on the gastrozooid, usually arises at the proximal end of the palpon. Uniquely, Bedot (1888, Pl. III, fig. 18) illustrated a palpon with the palpacle arising at its mid-length, and he drew attention to this in the text. The palpae present in our material obviously resemble very closely those described by Bedot. Haeckel (1888b, p. 228), however, only briefly described the palpae of his specimen, and said "From their [the palpae] tapering base arises usually (or always?) a long palpacle". If this statement proves to be true then it would indicate a clear difference between the two species.

From the available information, one might hope that the bracts would shed the most light on the relations between the specimens under investigation but, unfortunately, they did not. Haeckel considered that the bracts were thickened and wedge-shaped, with the distal part either three- or five-lobed, and with the same number of longitudinal ridges ending in the middle of each lobe on the upper side of the bract (see Fig. 3C). Along each ridge was a series of large nematocysts. He made no mention of the presence of any red pigmentation on these bracts, despite the fact that such can clearly be seen on his figure of the entire specimen (see Fig. 3A). Haeckel (1888b, p. 228) also stated "The form of the larger bracts is rather regular and symmetrical; there are, however, intermingled, mainly in the proximal part of the siphosome, numerous smaller bracts which have a more irregular form, and partly fill up the void intervals between the former". Thus, Haeckel appeared to indicate the presence of, at least, another type of bract, which he did not describe. From other statements that Haeckel made, one forms the impression that his single specimen disintegrated very quickly, allowing him time for only the most superficial of observations.

Bedot's (1888) extensive description of the bracts of *Agalma clausi* was mainly concerned with the structure of the pigmented glands and other groups of ectodermal cells found, presumably, on the upper surface of the bract. However, he also stated that a very large number of bracts were present with his specimens, two of which he figured (see Fig. 1B and C). He considered the latter to be a young form of the former. If one compares these figures with the six types of bract found in our specimens (Fig. 9) one sees that there is a certain similarity between Bedot's mature bract (Figure 1B) and the present Type E bract. Both are covered with large pigmented patches, or glands, although their extent on the latter is far greater than the former, and is more like that illustrated by Fewkes (1880) (see Fig. 1A). Indeed, Fewkes' bract, like our Type E, had only one pair of lateral cusps, while Bedot's had two. As for Bedot's young bracts (Fig. 1C), there is a certain similarity with our Type F bract, particularly "un petit bonnet" (*ibid.* p. 82) at the proximal end of the bract that corresponds to the thickened proximal process found on our Type F bracts. The longitudinal lines of cells are also very similar, except that Bedot believed that they were the exploded remnants of the pigmented "glands". In addition, although not obvious from the figure, Bedot (*ibid.*) also remarked presence of "lobes latéraux", that, presumably, are comparable with the small pair of lateral cusps seen on the Type F bracts. However, we found no evidence for the distinct pair of cusps that Bedot associated with these processes. Nevertheless, Bedot also described two lateral lobes toward the distal end of the bract (see Fig. 1C) and these can be equated with the distal pair of lobes on our younger bracts that later became resorbed into the main body forming two thickened processes.

In one paragraph, Bedot (1888) firstly stated that the largest bract measured about 4 cm in length, and referred

to his figure of the mature bracts (*cf.* Fig. 1B), with, as aforementioned, the two pairs of lateral cusps. However, later on in that paragraph he said, that in the majority of cases there was a transverse ridge running between the more distal pair of lateral cusps. Thus, almost certainly, Bedot's specimens included our Type B bracts.

With this additional piece of information, there can be little doubt that the material we have studied belongs to Bedot's species, *Agalma clausi*. The case of the species described by Haeckel (1888b) is, however, far more complicated. Based on the morphology of the tentillum, *A. haeckeli* clearly belongs to the genus *Agalma*, unfortunately his description of the structure of the nectophore provided no taxonomically useful information. However, if the palpacle does arise at the proximal end of the palpon, then this would be a clear distinguishing feature. Bracts of his species are very different from any described *Agalma* species, most closely resembling those of *A. elegans*, but with the presence of ridges. On the other hand, the unmentioned presence of red pigmentation on the bracts closely allies Haeckel's specimen with *A. clausi*. Unfortunately, Bigelow (1911) did not note that fact and considered Haeckel's specimen to lack pigmentation on the bracts, while noting the presence of the three pigment spots on the nectophores that Bedot did not describe. This led him to retain the species *A. haeckeli* until fresh material from the Indian Ocean was available for study. Thus, although Mills *et al.* (1996) concluded that *A. haeckeli* should be considered as a junior synonym of *A. clausi*, in light of the present investigation and with particular reference to the bracts, we consider that *A. haeckeli* should be retained as a *species inquirendum* until Bigelow's suggestion is fulfilled.

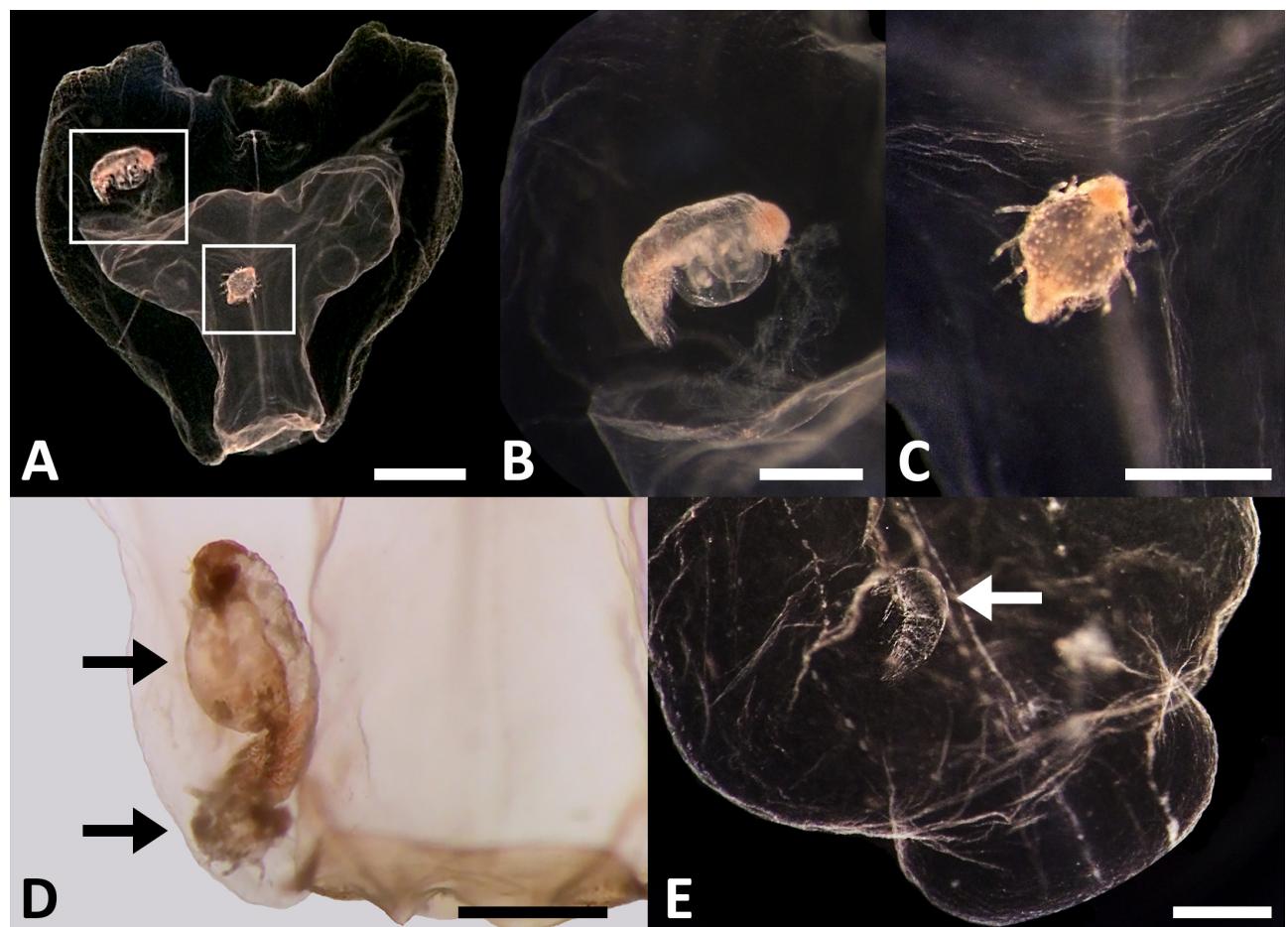


FIGURE 17. Details of amphipod placements within zooids of *Agalma clausi* specimen BWP 1044-22. **A.** Two *Eupronoe* sp. (squared) living inside nectophore mesoglea; **B.** Close-up of picture A showing one of *Eupronoe* sp. in the axial wing of the *Agalma clausi* nectophore, and the damage it caused to the radial canal; **C.** Close up of picture A showing another *Eupronoe* sp. that lives in the central part of the nectophore, presumably ingesting pre-digested food directly from the radial canal; **D.** Two *Eupronoe* sp. (arrowed) living in the lateral part of the nectophore, close to the ostium; **E.** Exuviae of an amphipod (arrowed) inside the *Agalma clausi* bract. Scale bars: A. 1 mm; B., C., D. 500 µm; E. 250 µm.

Ecology. With the singular exception of the specimen from the Gulf Stream, the few known specimens have been found in warm waters of two disparate areas, the western Mediterranean and superficial equatorial waters of the western North Atlantic, where the species was frequently encountered.

As Purcell (1980) pointed out, *Agalma* species use a form of aggressive mimicry in their attempts to catch prey. The expanded tentillum, with its red cnidoband and two extended lateral terminal filaments, can take on the semblance of a copepod that, when contracted and relaxed, acts as a lure to entice its prey. Further examples of aggressive mimicry have recently been found for species of the genus *Erenna* (Haddock *et al.* 2005b; Pugh & Haddock 2016). Purcell (1981) also found that the preferred prey of *A. elegans* and *A. okenii* was largely shrimp or small fish, with an occasional, presumably carnivorous, copepod. Although no prey items were identified from the gastrozooids, based on the typical *Agalma*-like morphology of an *A. clausi* tentillum, it can be assumed that the diet of these species is similar.

Bedot (1888) stated that the release of clouds of red pigmentation from the glands on the Type D bracts was very reminiscent of the release of similar material from the palpons of some *Forskalia* species. Although the material appeared not to be bioluminescent (see Mills *et al.* 1996) it is possible that it was similarly fluorescent, and presumably its release was a defensive reaction if the colony was disturbed.

One noticeable feature of the specimens caught close to the surface, by SCUBA divers, and those collected at depth, by the JSL submersible, was that the former were heavily infested with amphipods (Fig. 17) while, for the deeper living JSL specimens only a single amphipod was found free in the nectosac of a nectophore from specimen 2929-DS1. Harbison *et al.* (1977) made a detailed study on the association of amphipods with siphonophores, and found that many of these were species specific. For *Agalma clausi* they found *Paralycea gracilis* Claus 1879, and juveniles of *Eupronoe* and other pronoids. A single specimen of *P. gracilis* was found sitting within the nectosac of a nectophore, but immediately swam off when disturbed. Juveniles of platysceloid amphipods were also found "encysted" within the tissue of the nectophores and bracts (Fig. 17D). These juveniles bore into the tissue, and excavated a chamber that bordered on one of the canals in the nectophore, or the bracteal canal (Fig. 17A, B, C). This is then bitten into and the cavity is then constantly flushed with the fluid circulating in the gastrovascular canal system of the colony. As was previously reported for other gelatinous organisms (Gasca *et al.* 2007), including siphonophores (Mańko *et al.* 2017), some crustaceans require gelatinous hosts in their life cycle, as indicated here by the presence of amphipod exuviae buried in the mesoglea of *A. clausi* (Fig. 17E). Specimens of another amphipod species, *Parascelus edwardsi* Claus 1879, were recently identified from the specimen BWP 1055-15, however, there is no information as to their exact placement within the colony, since they became separated from the colony after preservation.

Acknowledgements

We thank the pilots of the *JSL* submersibles for their expertise in collecting the specimens, the crews of the WHOI and HBOI vessels, and the scientific complement during the cruises where specimens were collected for all their help in collecting the specimens used in this study. PRP also particularly wishes to thank the late Richard Harbison and Edie Widder for inviting him to participate on two of the cruises when specimens of *Agalma clausi* were collected. Also thanks to Ron Gilmer for taking some of the photographs and to Michael Thurston for identifying some of the amphipods. MKM would like to express his gratitude to Sławek Kwaśniewski (Institute of Oceanology, Polish Academy of Sciences) for allowing the use of his laboratory equipment, and to Carina Östman for confirming nematocyst identification. This project benefited from the financial support from the SYNTHESYS grant (GB-TAF-5264) awarded to MKM and Gillian M. Mapstone. We greatly thank Dhugal Lindsay and an anonymous reviewer for their helpful comments that improved the manuscript.

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