A review of the genus *Bargmannia* Totton, 1954 (Siphonophorae, Physonecta, Pyrostephidae)

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CONTENTS

SYNOPSIS. Two new species of the physonect siphonophore genus *Bargmannia* are described, and *B. elongata* Totton (1954) and *B. lata* (Mapstone, 1998) are redescribed. The status of the genus and its retention within the family Pyrostephidae are discussed.

INTRODUCTION

Totton (1954) established the genus *Bargmannia*, named after his colleague Dr Helene Bargmann, to include the single species, *B. elongata*; nectophores of which he had found in thirteen *Discovery* samples, plus one from the *Michael Sars* Expedition (Leloup, 1955). Because the structure of the nectophores differed so markedly from those of all other known physonect siphonophores, Totton did not give a detailed description of them; remarking only that the lateral radial canals on the nectosac had straight courses. Totton (1965) later noted that, although *B. elongata* was one of the most easily recognised siphonophore species, nothing more had been published on it since its original description. In fact, by the time of publication of Totton's monograph, only Alvariño (1963, 1964) had mentioned it; and then only in lists of siphonophore species collected in the western Pacific. Totton included a brief description of a further specimen collected at *Discovery* St 4246 (37°50'N, 13°22'W), remarking on the orange coloration of the stem.

Since that time several authors have reportedly identified this species from various collections. However, examination of both Totton's material and that from more recent *Discovery* collections (Mackie, Pugh & Purcell, 1987) appeared to indicate that Totton's (1954, 1965) illustrations of *Bargmannia elongata* could be referred to two species, and that his material also included a third species. However, it was not until submersibles collected specimens of this genus that this contention could be proved beyond doubt. Study of this submersible material, together with that from the *Discovery* collections, shows that there are at least four species that may be referred to the genus *Bargmannia*. The second species that Totton illustrated under the name *B. elongata* has recently been described under the name *B. lata*. More detailed descriptions of both these species, together with descriptions of

two previously undescribed species, are given herein.

Totton (1954) did not refer the genus *Bargmannia* to any of the physonect families, although his description appears at the end of a section dealing with various species of the family Agalmatidae. Later, Totton (1965) placed the genus in the family Pyrostephidae, which previously had been monotypic for the species *Pyrostephos vanhoeffeni* Moser, 1925. However, his diagnosis of that family applied only to the genus *Pyrostephos*, and included such features as marked bends in the dorsal and lateral radial canals on the nectosac of the nectophores. This character alone would exclude the genus *Bargmannia*. Since then, Stepanjants (1967) placed the genus in the catch-all family Agalmatidae, whereas Daniel (1974) retained it within the family Pyrostephidae. Now that intact specimens have been collected by submersibles it is possible to review the systematic position of the genus *Bargmannia*. It is concluded that, for the present at least, it should be retained within the family Pyrostephidae, the diagnosis of which is adjusted accordingly.

Family **PYROSTEPHIDAE** Moser, 1925

DIAGNOSIS. Long-stemmed physonect siphonophores. Nectophores with large triangular thrust block; with lateral wedge-shaped processes reduced or absent. With apico-, infra- and vertical (meso-) lateral ridges; apico-laterals divide above ostial level. Adaxial wall of nectosac lacking musculature; deeply hollowed. Long pallial canal; short pedicular canal, giving rise, on nectosac, to only dorsal and ventral radial canals; lateral radial canals arise separately from dorsal. Dorsal and lateral radial canals either looped or straight. Tentillum with straight (or twisted, but not tightly coiled) cnidoband; lacking an involucrum; with terminal filament. Dactylozooids either absent or modified to form peculiar palpacle-less oleocysts. Individual specimens of single sex (dioecious), with gonophores budded

one from another to form a small gonodendron; female gonophores contain two or more eggs.

REMARKS. In *Pyrostephos vanhoeffeni*, the triangular thrust block is best seen on smaller nectophores. On larger, preserved ones it is bent up dorsally (see also Discussion section).

Genus *BARGMANNIA* Totton, 1954

DIAGNOSIS. Pyrostephids with distinctive elongate nectophores. Mature nectophores with large, triangular thrust block; without apical wedge-shaped processes; with extensive ventro-lateral wings. Basic ridge pattern may be augmented by additional ridges branching from apico-laterals. Nectosac basically cylindrical; dorsal and ventral radial canals straight; lateral radial canals arise separately, but in close proximity, from the dorsal canal. Pneumatophore without apical pore.

Siphosome diffuse; devoid of fully formed dactylozooids. Bracts specifically variable in shape. Each cormidium; with simple tentacle-like structure attached to stem midway between successive gastrozooids; with single gonodendron; with four bud-like structures (?vestigial dactylozooids) with sexually dimorphic arrangement. Second tentacle and fifth bud occasionally present proximal to a gastrozooid.

REMARKS. The meso-lateral ridges on the nectophores, as referred to in the above diagnosis, are homologous with the vertical lateral ridges, as defined by Pugh and Youngbluth (1988), found on the nectophores of certain agalmatid species. In these latter species these ridges run vertically, or slightly obliquely, between the apico- and infra-lateral ridges, although they may not reach the latter. However, in *Bargmannia* spp. their arrangement is strikingly different in that they have a very oblique course; and it is the infra-lateral ridges that may or may not join them basally. For these reasons the term meso-lateral ridges will be used herein.

In contrast, the outer of the two branches of the apico-lateral ridges should not be compared with the lateral ridges of agalmatid species, as defined by Pugh and Youngbluth (1988). They more closely resemble the near-ostial branching of the apico-laterals in agalmatid species such as *Lychnagalma utricularia* (Claus, 1879) (see Pugh & Harbison, 1986) and *Halistemma transliratum* Pugh & Youngbluth, 1988, which also possess normal lateral ridges.

The long, median canal that runs up the thrust block (see Figure 2), just below its ventral surface, has been variously referred to as a pallial (e.g. Daniel, 1974) or a pedicular canal (e.g. Daniel, 1985). In accord with the definitions given by Totton (1965) here the canal will be referred to as the pallial canal; and the short canal, passing through the mesogloea from the stem to the nectosac, the pedicular canal.

Recently, it has been brought to my attention (Dr S. Haddock, personal communication) that the generic name *Bargmannia* was used by Herre (1955) in a description of a genus of an extinct salamander. *Bargmannia* Totton, 1954 clearly has priority of publication.
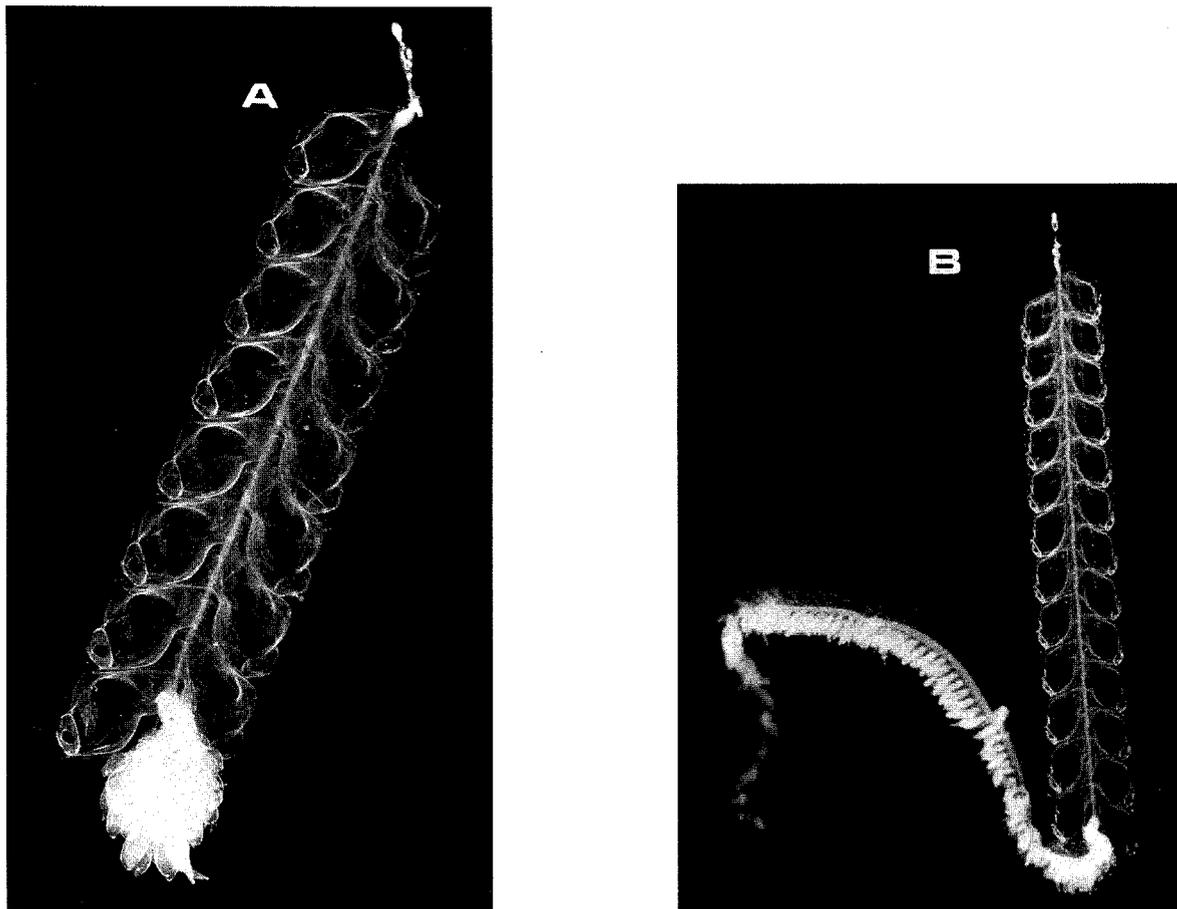

Fig. 1   *Bargmannia elongata*. A. Photograph (reproduced by kind permission of Larry Madin, WHOI) of live specimen collected during *Alvin* Dive 961.
    B. Photograph (reproduced by kind permission of Steve Haddock, UCSB) of live specimen collected during *JSL* I Dive 2673. Nectosomal length c. 9 cm.

Bargmannia elongata Totton, 1954

(Figures 1–5)

Bargmannia elongata Totton 1954 (Text-Figure 28 A–D only); Totton 1965 (Figure 45, A–D only); Kirkpatrick & Pugh, 1984: Figure 11.

HOLOTYPE. BMNH 1952.11.19.7, designated by Totton (1954): one nectophore from *Discovery* II St. 699; 14° 27.3'N, 30° 02.3'W; 14–v–1931; 0–370m. The specimen was figured by Totton (1954, text-Figure 28 C, D; 1965, Figure 45 C, D).

PARATYPES. As designated by Totton (1954): eighteen nectophores from the same sample as the holotype. BMNH 1952.11.19.8–25.

MATERIAL EXAMINED. The holotype and paratype material have been re-examined in order to establish to which of the presently recognised *Bargmannia* spp. the name *elongata* should be applied. Totton's (1954) other material also has been re-examined and, although all the material is in poor condition, it appears that only the nectophores from two other *Discovery* stations belong to this species. These are St. 681 (21°13'S, 29°55.25'W; 1–v–1931) where a TYFV net was fished over a depth range 1500–1000m; and St. 107 (43°03'S, 17°03'E; 4–xi–1926) where the net used was a N450 and the depth range was 850–950m. The nectophore from the former of these stations was figured by Totton (1954, text-Figure 28 A, B; 1965, Figure 45 A, B). The other nectophore, from *Discovery* St. 1769, also illustrated in the same figures (E, F) does not belong to *B. elongata*, but to *B. lata*.

Several nectophores of this species have been found in more recent *Discovery* collections, as is discussed below. However, the major part of the redescription will be based on two specimens collected by DSRV *Alvin* off San Diego, California, U.S.A. in 1979, during Dives 961 (32°14'N 117°22'W; 5–ix–1979; water depth 833m) and 966 (33°04'N 118°16'W; 8–ix–1979; water depth 747m). The *Alvin* Dive 961 specimen, preserved in Steedman's solution, has been deposited in The Natural History Museum London (BMNH 1998.2163). The exact depths of collection for both *Alvin* specimens were not recorded.

DIAGNOSIS. Nectophores with central thrust block broadly rounded or obliquely truncate apically. Pair of short ridges, directed toward mid-line, branch from apico-laterals where latter bend out sharply at a right angle. Outer branches of apico-laterals end, basally, on, or just apical to, enlarged processes lateral to ostium. In preserved specimens ostium opens dorso-basally and nectosac, with apparently dense musculature, has distinct dorso-ventral undulations. The ratio of the overall length of the nectophore to the length of the nectosac averaged 1.31. Delicate, foliaceous bracts; typically with patches of ectodermal cells on distal half of dorsal surface.

DESCRIPTION. A photograph of the living specimen collected during *Alvin* dive 961 is shown in Figure 1A. By the time it was taken, in a tank on board the mother ship, several nectophores had become detached and the siphosomal stem had contracted. A second living specimen, collected during *Johnson-Sea-Link* (*JSL*) I Dive 2673 (27°02.7'N, 85°01.5'W, depth 780m), is shown in Figure 1B.

PNEUMATOPHORE. The pneumatophore measured c. 2.2 mm in length and 1 mm in width, but was distorted and ruptured. No pigmentation was apparent. In the *Alvin* dive 961 specimen, the main gas cavity, the pneumatosaccus (height 1.8 mm), was separated from the small gas secreting region, the pneumadenia, by a narrow collar. Below the pneumatophore was a long stalk, up to 7.6 mm in length. Immediately above the nectosome, this stalk narrowed and was flattened to form a hinge-like structure, which could facilitate the

use of the pneumatophore as a means of orientating the animal.

NECTOPHORE (Figures 2–3). The nectophores had a biserial, staggered arrangement down the nectosome (Figure 1). Forty two nectophores were found with the *Alvin* dive 961 specimen, though many were small or immature; and 26, mostly mature ones, were found with the *Alvin* dive 966 specimen. The mean dimensions, for the fully developed nectophores of each specimen, were:- length: 21.29 ± 0.93 mm and 16.49 ± 0.75 mm; width: 9.58 ± 0.56 mm and 7.40 ± 0.32 mm; and the ratios of total length of the nectophore to the length of the nectosac were 1.29 ± 0.02 and 1.34 ± 0.04, respectively. For net collected nectophores, damage and distortion by preservation, particularly to their basal halves, made it difficult to assess this ratio accurately.

The nectophores of the dive 966 specimen were noticeably smaller than those from dive 961 but, as will be seen in the description of the following species, the size range of the nectophores can vary greatly between individual specimens. In general, the thrust block was roundly, and often slightly asymmetrically, truncate (Figure 2A, *tb*; 2B), although for a few of the nectophores of the smaller specimen it was distinctly tapered. The latter was also apparent on several net collected nectophores where the apex of the thrust block was drawn out to form a small digitiform process that could be folded over ventrally.
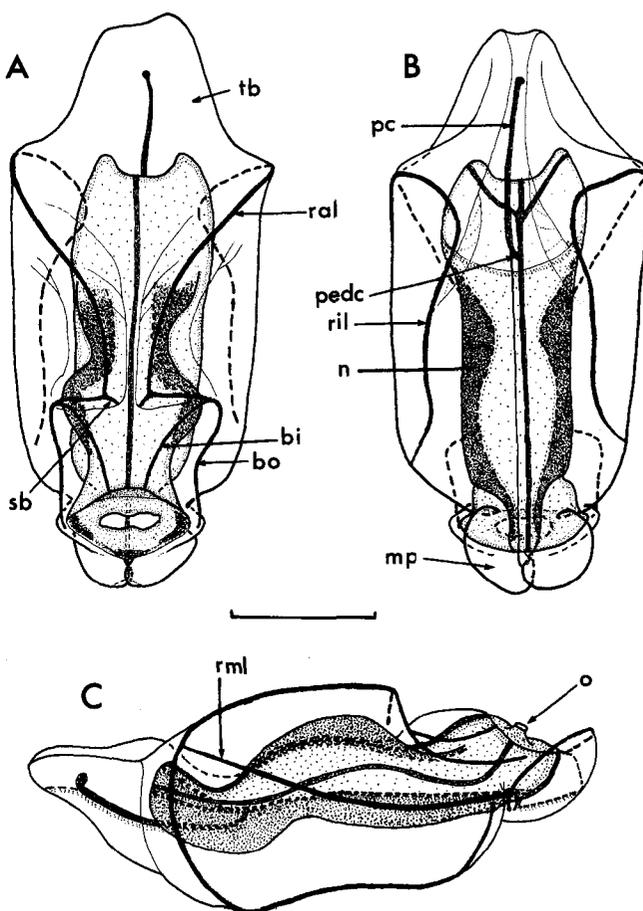

Fig. 2 *Bargmannia elongata*. A. Upper, B. lower, and C. lateral views of mature nectophore. Scale bar = 5 mm. *bi, bo*: inner and outer branches of apico-lateral ridge; *mp*: mouth-plate; *n*: nectosac; *o*: ostium; *pc*: pallial canal; *pedc*: pedicular canal; *ral, ril, rml*: apico-, infra- and meso-lateral ridges; *sb*: side branch; *tb*: thrust block.

The basic *Bargmannia* ridge pattern is supplemented by a pair of short ridges (Figures 2A, *sb*; 3A) that branch from the apico-laterals (Figure 2A, *ral*) at the point where the latter bend sharply, through 90°, away from the mid-line. This sharp bend typically can be seen in less well preserved specimens and is characteristic for this species. The side branches are directed, for a short distance, toward the deep median furrow. In many specimens, particularly net collected material, they were difficult to discern but often can be seen after staining. Basally, the inner branch of each apico-lateral ridge curves inwards and then down to reach the ostium (Figure 2 A, *bi*), except for immature nectophores (Figure 3A) where it ends slightly above that level. Each outer branch (Figures 2A, *bo*; 3C) typically terminates on or just above one of the small, but prominent, lateral processes on either side of the ostium.

Basal extensions of the meso-lateral ridges form the baso-lateral margins of the bilobed mouth-plate (Figure 2B, *mp*; 2C), each lobe being thickened ventrally, particularly toward the mid-line. Basally, the two lobes typically overlap and unite, in the mid-line, at about half the height of the mouth-plate (Figure 3C). The lower nerve tract (see Mackie, 1964), which can be traced down the nectophore, beneath its ventral surface in the mid-line, recurves at this point and

continues obliquely to the baso-ventral margin of the ostium (Figure 3C). In immature nectophores the mouth-plate is not thickened and has a U-shaped emargination in the mid-line (Figure 3A, B) which is deepest in the youngest nectophores.

Above the mouth-plate, the basal extensions of the meso-lateral ridges curve round toward the mid-line, on the ventral surface of the nectophore (Figure 2 B), before looping back outwards as the meso-laterals proper (Figure 2C, *rml*). The infra-laterals are weakly defined in the region where they divide from the meso-laterals, and in younger nectophores clearly terminate before reaching the latter (Figure 3 B). The meso-laterals curve up, obliquely, across the lateral surface to reach the junction with the other main ridges at a level slightly below the apex of the nectosac (Figure 2C). The connection with the other ridges is weak, and often the meso-laterals appear to end slightly below the junction, as was found for younger nectophores (Figure 3 A).

The infra-laterals (Figure 2B, *ril*) demarcate the ventral margins of the thickened walls of the more basal part of the ventro-lateral wings. In lateral view these wings are slightly emarginate in outline. Apical to where the infra-laterals curve up to join the other ridges, the wings remain well developed and are thickened with mesogloea.
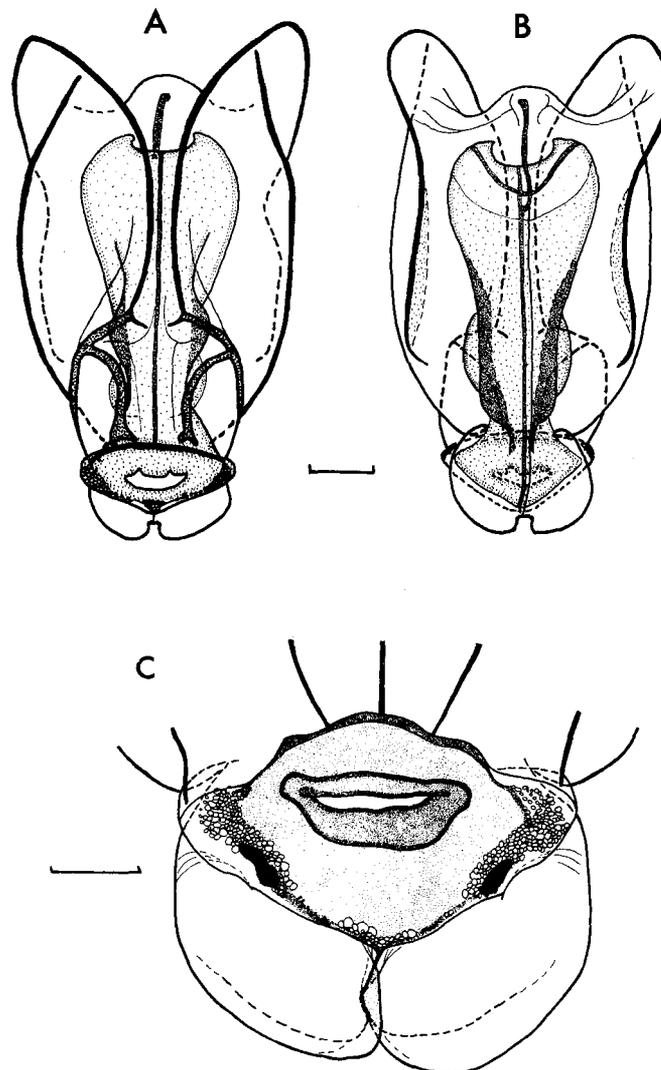

Fig. 3. *Bargmannia elongata*. A. Upper and B. lower views of young nectophore; C. detail of ostial region of mature nectophore. Scale bar = 1 mm.
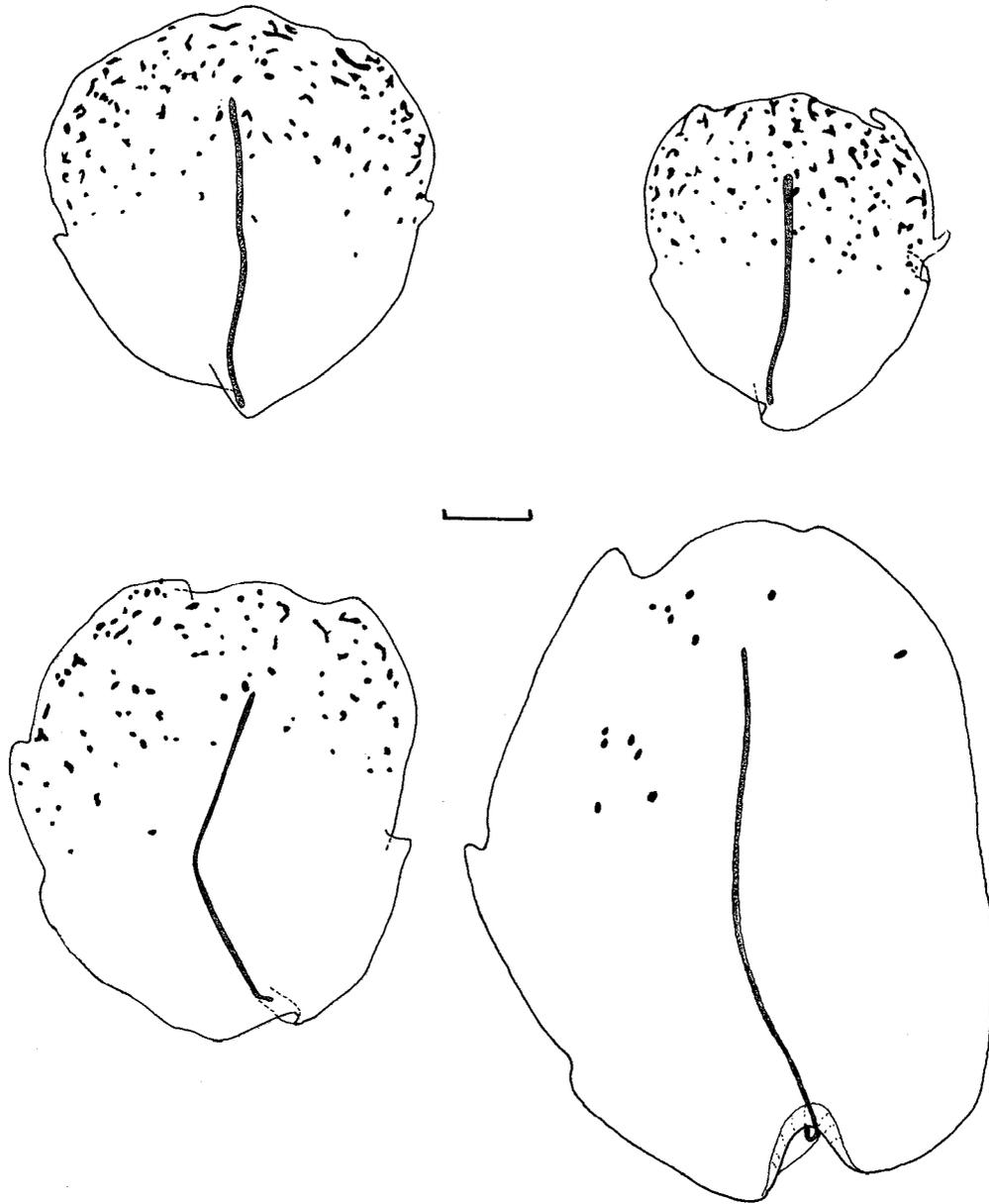
Fig. 4 Bracts of *Bargmannia elongata*. Scale bar = 1 mm.

This thickening diminishes in the region of the thrust block, but there is still a shallow median gutter that enfolds the nectosomal stem in the region of attachment of the nectophore (Figure 2 B).

In the preserved nectophores, the nectosac is a dorso-ventrally undulating tube (Figure 2B, *n*; 2C), with prominent dorso-lateral extensions in the mid region, and ventro-lateral ones both apically and basally. However, this arrangement is not apparent in the nectophores of the living animal (Figure 1). The nectosac is broadest at about two-thirds its length, narrowing slightly towards its apex. It has a distinct apical emargination; U-shaped in the younger nectophores (Figure 3 A). Typically, the ventral, adaxial region towards the apex of the nectosac is distinctly undercut and, from a level just basal to the point of insertion of the pedicular canal, its wall is devoid of musculature (Figure 2 B). The musculature of the remainder of the nectosac appears well developed and gives it a

distinctly opaque appearance. The ostium, in the preserved material, opens onto the dorso-basal (abaxial) surface (Figure 2C, *o*) and is roughly rhomboidal in shape. However, this probably is distortion due to preservation (see Figure 1). In the *Alvin* specimens it has a large velum, with a relatively small central opening, but in net collected material often the velum is destroyed. The lateral walls of the ostium extend out to form lateral processes (Figure 3C) that, typically, are covered by patches of ectodermal cells of varied size. Further such patches are present on the ventral margin of the velum, but not on the dorsal margin, except for the youngest nectophores. Some, if not all, of these cells probably produce bioluminescent material since this has been found to be the case in another *Bargmannia* spp. (Dr S. Haddock, personal communication).

The long pallial canal (Figure 2B, *pc*) extends up into the median thrust block, where it ends with a short dorsal inflection into the
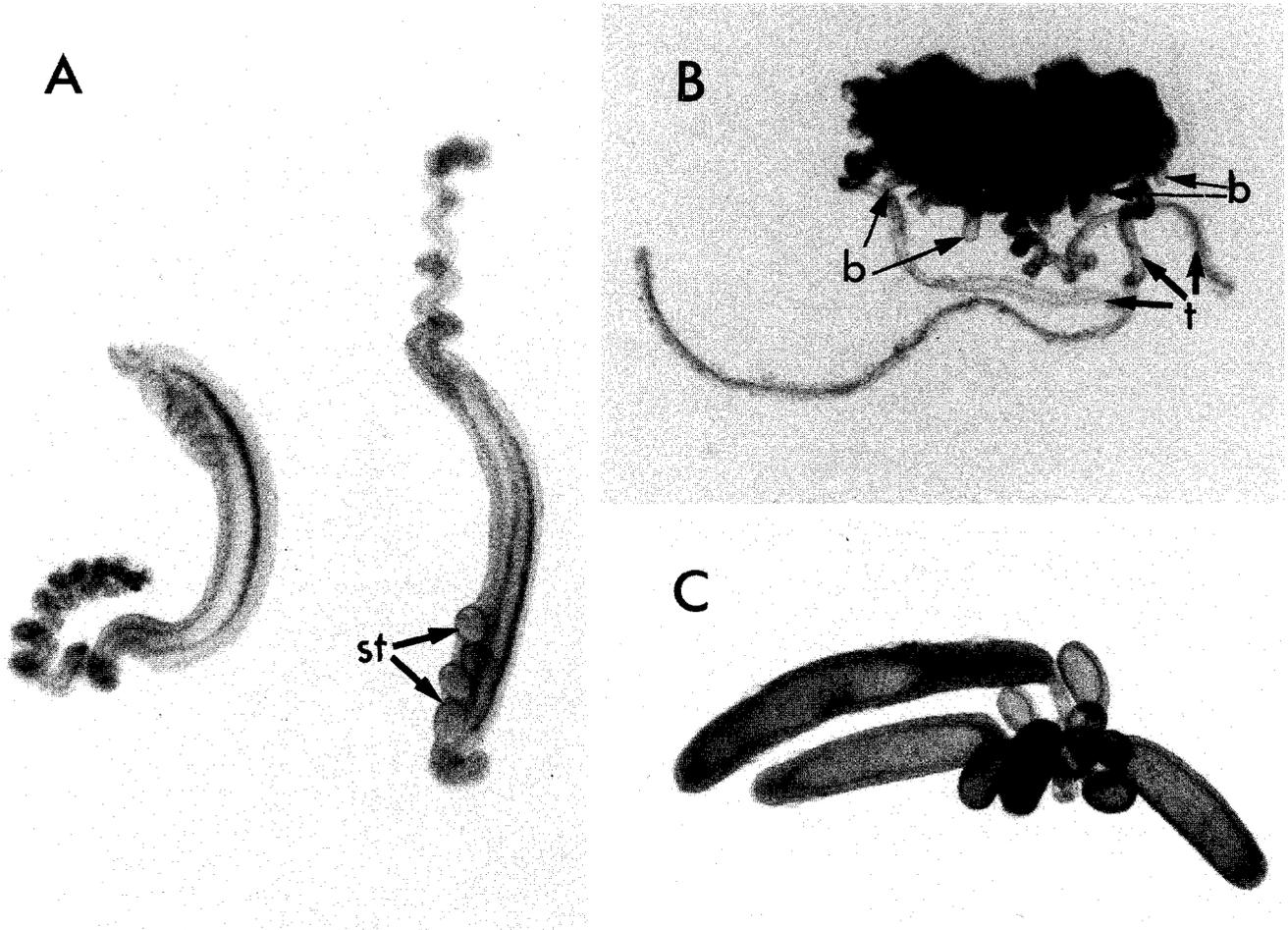
Fig. 5 *Bargmannia elongata.* A. Young tentilla with stenoteles (*st*) at proximal end of cnidoband (magn. 50×); B. Part of siphosome showing three siphosomal tentacles (*t*) and several buds (*b*) (magn. 16×); C. Male gonophores (magn. 30×).

mesogloea. At its base the lower nerve tract can be seen to leave its proximity and to continue down beneath the ventral surface of the nectophore to reach the ostium. The short pedicular canal (Figure 2B, *pedc*) extends through the mesogloea, from the base of the pallial canal, to the nectosac. There it gives rise to only the dorsal and ventral radial canals. The lateral canals arise separately, but in close proximity to each other, from the dorsal canal, and initially are directed toward the apico-lateral margins of the nectosac. They then continue down the lateral margins of the nectosac and, although their courses show undulations (Figures 1C, 2C), they are merely following the dorso-ventral undulations in the nectosac itself; the latter being a preservation artefact.

The youngest nectophores (Figure 3A, B) typically show the absence of a median thrust block, and the apico-lateral margins are demarcated by the apico- and infra-lateral ridges. The basal portions of the apico-lateral ridges are particularly well marked, and the inner branches are distinctly broadened, often appearing almost bifurcate at their basal ends, which lie just above the ostium (Figure 3A). There are two short tracts of cells extending out from the lateral processes of the ostium just ventral to the outer branch of the apico-lateral ridges. These could not be discerned in the mature nectophores.

BRACT (Figure 4). The bracts are extremely delicate, foliaceous structures, the largest of which measures 9 mm in length. The dorsal

surface is slightly convex, the ventral one slightly concave. For many the proximal region is bent up dorsally, or one side is folded over the other resulting in a distinct asymmetry. The bracteal canal extends, approximately in the mid-line and in close proximity to the ventral wall, to about four-fifths the length of the bract. The distal end of the bract is slightly truncate and bears two lateral processes, which vary in shape from merely rounded corners to distinct teeth. The region between them usually is roundly pointed. Additional processes may be present on the lateral margins of the bract. Again these can form distinct teeth, but quite often are indiscernible. The maximum number of lateral processes found was two on one side, and one on the other. The distal half of the dorsal side of the bract is dotted with distinctive patches of small round ectodermal cells. These patches are densely packed on the smallest bracts; but more spread out on the larger ones, where some patches have been lost by abrasion. These cells probably are sites of bioluminescence.

GASTROZOOID AND TENTACLE. The larger gastrozooids in the *Alvin* material measured up to 10 mm in length. They are brown in colour, in their preserved state, and are comprised of a short, narrow basigaster, to the base of which the tentacle is attached; a large, expanded stomach, the inside of which is covered with thickened patches of endodermal cells; and a long proboscis, with longitudinal endodermal hepatic stripes. Several younger, smaller gastrozooids

also are present, which are largely colourless and transparent, with only small patches of endodermal cells in the stomach region.

No mature tentilla remained with the specimens. The immature tentilla (Figure 5A) conformed to the basic *Bargmannia* design, with the cnidoband ranging from being straight to curved or slightly twisted. There was a maximum of only six large nematocysts, probably stenoteles, that measure c. 120 by 80µm, irregularly arranged on the proximal region of the cnidoband. About half the circumference of the cnidoband is covered with rows of two other types of nematocysts; one is ovoid, measuring c. 16 × 11 µm; and the other is spherical, measuring c. 8.5µm in diameter. Similar nematocysts are also present on the terminal filament. It has not been confirmed that these nematocysts are the acrophores and desmonemes that are typically found on the terminal filaments of many physonect species. It is, however, unusual to find such small nematocysts on the cnidoband. The terminal filament obviously can extend to a considerable extent, but in the preserved specimens it is generally tightly coiled.

SIPHOSOMAL TENTACLES AND BUDS (Figure 5B).   Midway between each gastrozooid a peculiar tentacular structure is attached directly to the siphosomal stem. In the preserved specimens they are usually tightly coiled, but some relaxed ones can reach lengths of 8 mm. Along one side there is a biserial arrangement of spherical nematocysts, c. 13 µm in diameter, similar to those on the cnidoband of the tentacle. The gastrovascular canal is lined by an irregular honeycomb of large endodermal cells.

In addition to the siphosomal tentacle, small bud-like structures were noted protruding from the stem. Because the siphosome in both specimens was tightly coiled it was not possible to assess the precise disposition of these buds. However, their arrangement may be similar to that which will be described for the following species.

GONOPHORE (Figure 5C).   Both the *Alvin* specimens are male and bear numerous gonodendra at various stages of development. The gonophores measure up to 4 mm in length, including the pedicel. They appear to bud one from another to form a small gonodendron. If the gonophores becomes detached, their thin-walled pedicels remain, giving the false impression of the presence of gonopalpons. Again, since the stem is highly contracted, it is difficult to ascertain their exact disposition.

REMARKS CONCERNING THE IDENTIFICATION OF *BARGMANNIA ELONGATA*.   Complete and well-preserved specimens of *B. elongata* easily can be distinguished from the other *Bargmannia* spp., particularly as the form of the bracts is very distinctive. For the nectophores, the arrangement of the apico-lateral ridges, with their distinct right-angled bend and the presence of the short extra ridges branching from them, also are characteristic features. However, in the case of net collected material, which is usually damaged or distorted, the nectophores of this species may be difficult to distinguish from those of the following species, as is discussed further after its description.

Bargmannia amoena sp. nov.

HOLOTYPE.   BMNH 1998.2164, preserved in Steedman's solution, collected during *JSL* II Dive 1458 off Dry Tortugas, Florida; 24°00.6'N 82°17.4'W; 3.ix.1987; 841m.
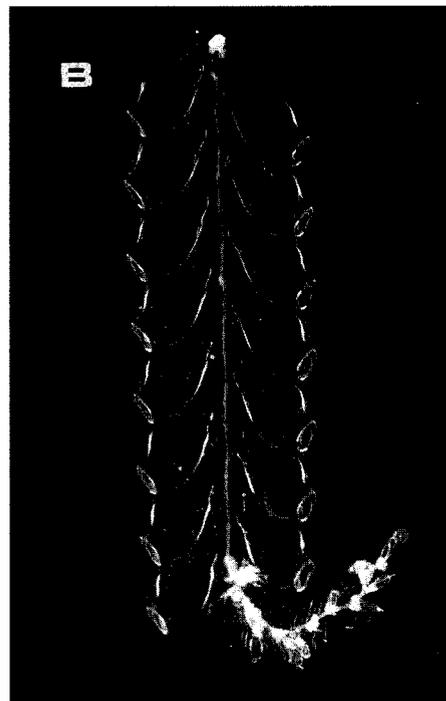

Fig. 6   *Bargmannia amoena* sp. nov.. Photographs (taken by Ron Gilmer) of live specimen collected during JSL II Dives 968 (A) and 1687 (B). Nectosomal lengths: A. c. 5 cm, B. c. 7 cm.
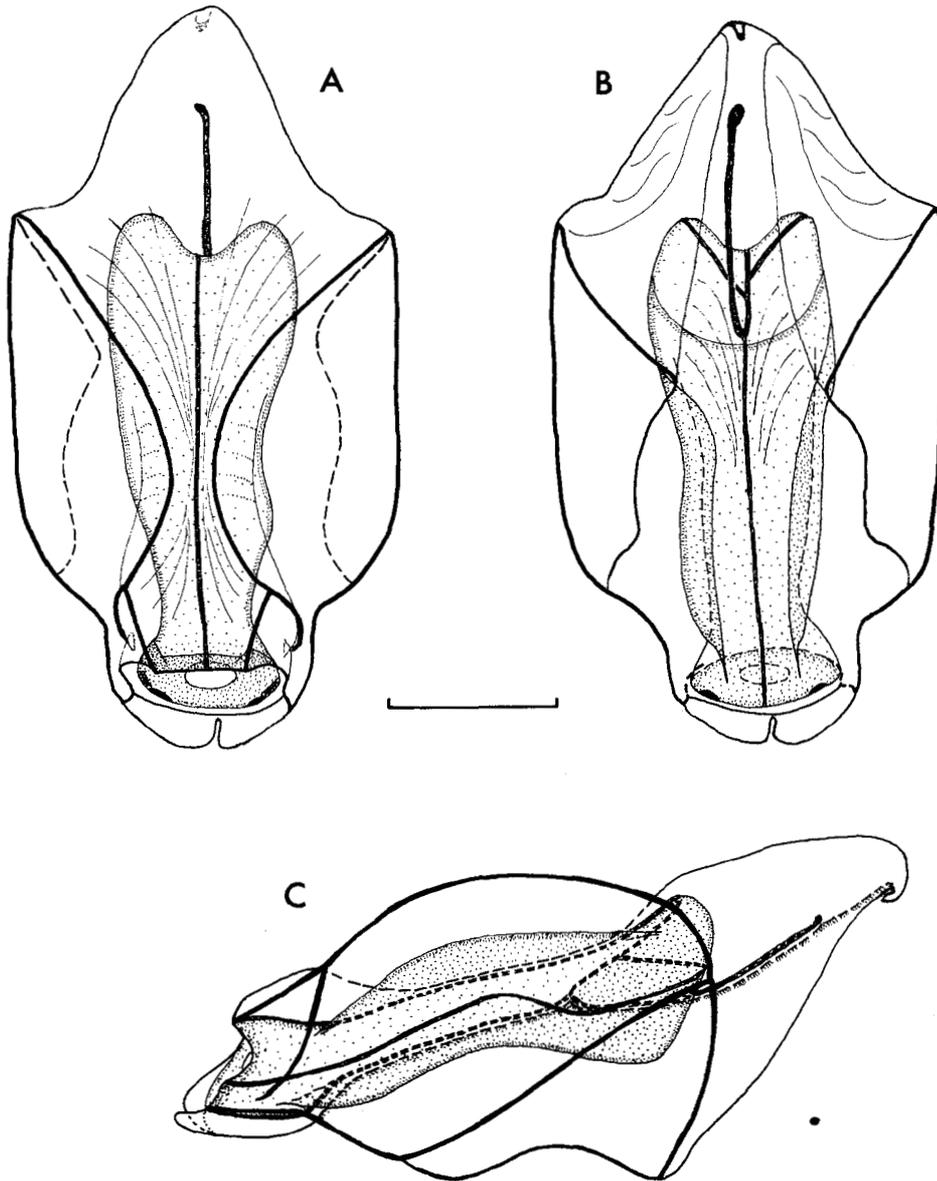
Fig. 7 *Bargmannia amoena* sp. nov. A. Upper, B. lower, and C. lateral views of mature nectophore from type specimen collected during JSL II Dive 1458. Scale bar = 5 mm.

PARATYPE. BMNH 1998.2165, preserved in Steedman's solution, collected during *JSL* I Dive 2636 off The Bahamas; 25°53.2'N 77°48.3'W; 5–xi–1989; 890m.

MATERIAL EXAMINED. 67 specimens have been collected during 40 dives by the submersibles *JSL* I and II. Of these, 52 have been re-examined for this description. Some of the material originally ascribed to *B. elongata* by Totton (1954) probably belongs to this species. In addition, some poorly preserved nectophores have been found in recent *Discovery* collections.

DIAGNOSIS. Apico-lateral ridges of nectophores smoothly curved, without pronounced bends; their outer branches terminating well above the ostium, before reaching the relatively small lateral ostial processes. No additional ridges. In smaller specimens central thrust block pointed with small digitiform process apically; in larger ones, latter folded over ventrally so that, in upper view, thrust block appears roundly truncate. In preserved specimens, ostium opens basally. Nectosac more translucent than that of *B. elongata*. Ratio of overall length of nectophore to that of nectosac averages 1.42, varying slightly according to the size of specimen. Bracts of two types; both delicate and foliaceous, with two pairs of lateral teeth; without patches of large ectodermal cells.

DESCRIPTION. Photographs of living specimens collected during *JSL* II dives 968 and 1687 are shown in Figure 6. The specimens from the *JSL* collections fall within three size classes, based on the length of the mature nectophores, but also reflected by the degree of sexual maturity. All the smaller specimens were colourless, while the largest ones had bright orange-red basigasters; the basal part of the gastrozooid.

PNEUMATOPHORE. The pneumatophore measured approximately 3 mm in height and 1.5 mm in width, but was highly distorted and
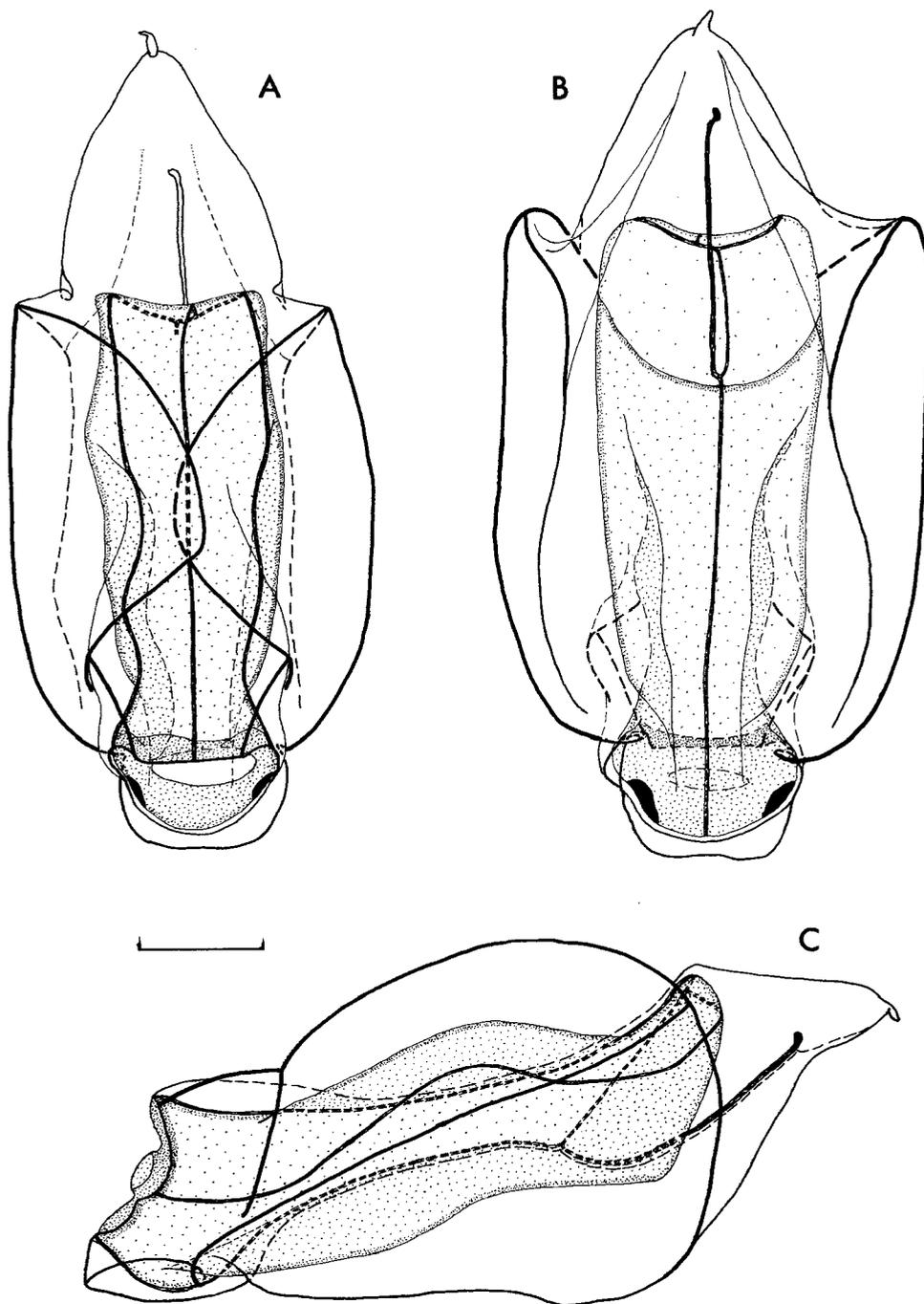
Fig. 8 *Bargmannia amoena* sp. nov. A. Upper, B. lower, and C. lateral views of mature nectophore from small specimen collected during JSL II Dive 976. Scale bar = 1 mm.

ruptured by the expansion of the gas within it. No pigmentation is apparent. The pneumatophore is inserted onto the apical end of a long stalk that, depending on the degree of contraction, can be 5–6 mm in length. As in *B. elongata*, this stalk is flattened at its base, where it joins the nectosome, to form a hinge-like structure.

NECTOPHORE (Figures 7–9). The nectophores had a biserial, staggered arrangement down the nectosome (Figure 6). The number of nectophores found with each specimen varied from 5 to 32. Depending on the mean length of their nectophores, these specimens can be divided into three size categories. Seven specimens, all collected during the same cruise in 1984, bore c. 10 relatively small nectophores whose lengths were less than 8 mm. The mean length, for the mature nectophores, was 7.41 ± 0.43 mm; the mean width 3.10 ± 0.22 mm; and the ratio of the overall length to that of the nectosac averaged 1.41 ± 0.06. None of these specimens was sexually mature. The bulk of the specimens was included in second size category, where the length of the mature nectophores ranged from 9 to 19 mm. These specimens bore distinct, but immature, gonophores. Each specimen averaged about 20 nectophores, whose mean length was 13.70 ±

1.86 mm; mean width 6.71 ± 0.88 mm; and the ratio of the overall length to that of the nectosac averaged 1.42 ± 0.06. Finally six specimens had even larger nectophores and were sexually mature. They averaged 13.5 nectophores, whose mean length was 20.94 ± 2.36 mm; mean width 10.58 ± 2.18 mm; and the ratio of the overall length to that of the nectosac averaged 1.44 ± 0.05.

As was the case for *B. elongata*, the apex of the thrust block of the smaller specimens was drawn out to form a small digitiform process (Figure 8A). In the larger specimens, this process usually became folded over onto the ventral side of the nectophore (Figure 7C), so that, in upper view, the thrust block appeared roundly truncate (Figure 7A).

The apico-lateral ridges are, in their preserved state, smoothly curved and have no pronounced bend or side branches (Figures 7 & 8), as was found for *B. elongata*. After these ridges divide, the inner branches extend obliquely down to reach the ostium; while the outer branches curve down the sides of the nectophore, but peter out well above ostial level. The latter is particularly marked on the smaller nectophores (Figure 8C).

Basal extensions of the meso-lateral ridges form the baso-lateral margins of the mouth-plate (Figures 7 & 8). The structure of the mouth-plate varies with the size of the mature nectophore. In the smallest specimens, the mouth-plate is only slightly truncate basally (Figure 8A). In the middle size range of specimens, the mouth-plate becomes more and more emarginate and, in the largest ones, it has a narrow U-shaped median indentation stretching up to the ostium (Figure 7A). The mouth-plates of the immature nectophores of all sizes of specimens show the same features as the corresponding mature ones (Figure 9).

Above the mouth-plate, in the small and medium sized specimens, the basal extensions of the meso-lateral ridges curve slightly in toward the mid-line (Figure 8B), before curving out again to form the meso-laterals proper. In addition the infra-laterals do not unite with the latter. On the largest specimens, there is no inward curve of the meso-laterals (Figures 7B, 9B), but the infra-laterals have a very weak connection with them (Figure 7B); However, the apical junction of the meso-laterals with the other ridges is always clearly defined. The arrangement of the infra-lateral ridges, in the small (Figure 8C) and medium sized specimens, is very similar to that described for *B. elongata*. However, in the largest specimens, the ventro-lateral wings are more extensive in the region where the infra-laterals curve up to join the other ridges. The ventral margins of these wings are distinctly emarginate.

The nectosac, in its preserved state, appears as a dorso-ventrally undulating tube; but this is probably a preservation artefact. The dorso-lateral extensions, in the mid region of the nectosac, are slightly more extensive than in *B. elongata*. At its apex the nectosac has a shallow U-shaped indentation, and the adaxial wall is distinctly undercut and devoid of musculature. On the remainder of the nectosac the musculature appears much less dense that of *B. elongata*, and the nectosac is considerably more translucent. The arrangement of the pallial and pedicular canals, and the radial canals on the nectosac is similar to that of *B. elongata*.

In the preserved specimens, the ostium opens almost basally and has a large velum. Its lateral walls are only slightly extended to form small lateral processes. The pattern of the patches of ectodermal cells is similar to that of *B. elongata*, but the cells are more uniform in size, and the patches more diffuse laterally. In addition, there are two ventro-lateral patches of deeply granulated cells that are relatively large and almost spherical.

The youngest nectophores (Figure 9) typically show the absence of a median thrust block. The inner branches of the apico-lateral ridges reach the ostium. The degree of emargination of the apex of
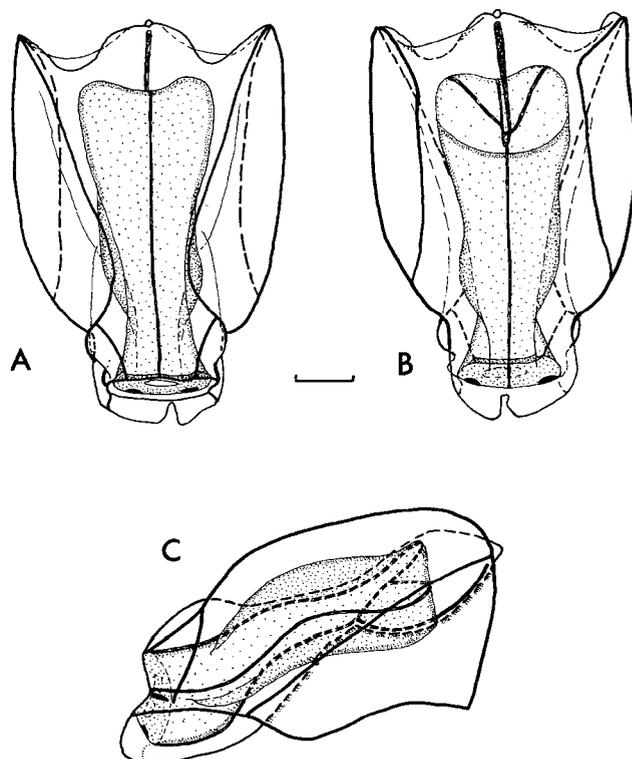

Fig. 9 *Bargmannia amoena* sp. nov. A. Upper, B. lower, and C. lateral views of young nectophore from specimen collected during JSL II Dive 1449. Scale bar = 2 mm.

the nectosac is variable, according to the developmental stage. It ranges from a narrow, median U-shaped indentation to a marked emargination across most of the width of the nectosac. As noted above the shape of the mouth-plate varies according to the size of the specimen. On either side of the ostium there is a tract of small ectodermal cells extending up toward the end of the outer branch of the apico-lateral ridges. These tracts are longer than those seen on the young nectophores of *B. elongata* and, again, are difficult to discern on the adult nectophores.

BRACT (Figure 10). There are three pairs of bracts per cormidium. Each is thin and leaf-like, with a slight thickening in the central region of the proximal half. The dorsal surface is slightly convex, and the ventral one slightly concave. In general their size is in proportion with that of the nectophores, with those of the largest specimens measuring up to 18 mm in length. No patches of ectodermal cells were observed. However, in each cormidium, each successive pair of bracts tends to be slightly larger than the pair proximal to it. The proximal part of each bract is slightly asymmetrical to allow for insertion onto the stem. The bracteal canal extends to about two-thirds to four-fifths the length of the bract. It remains in close contact with the ventral wall of the bract at all times.

There is much variation in the shape and form of the bracts, but two basic types can be distinguished; both having two pairs of lateral teeth. In one type, which make up the first two pairs of bracts in each cormidium, the bracts are relatively symmetrical. The more distal pair of lateral teeth are very variable in shape, ranging from being virtually absent to being quite marked (Figure 10A, B, D). In the second type (Figure 10C, E), which are the distal pair, the bracts are asymmetrical, and the bracteal canal can have a distinct proximal curve. The distal pair of lateral teeth are well developed and closer
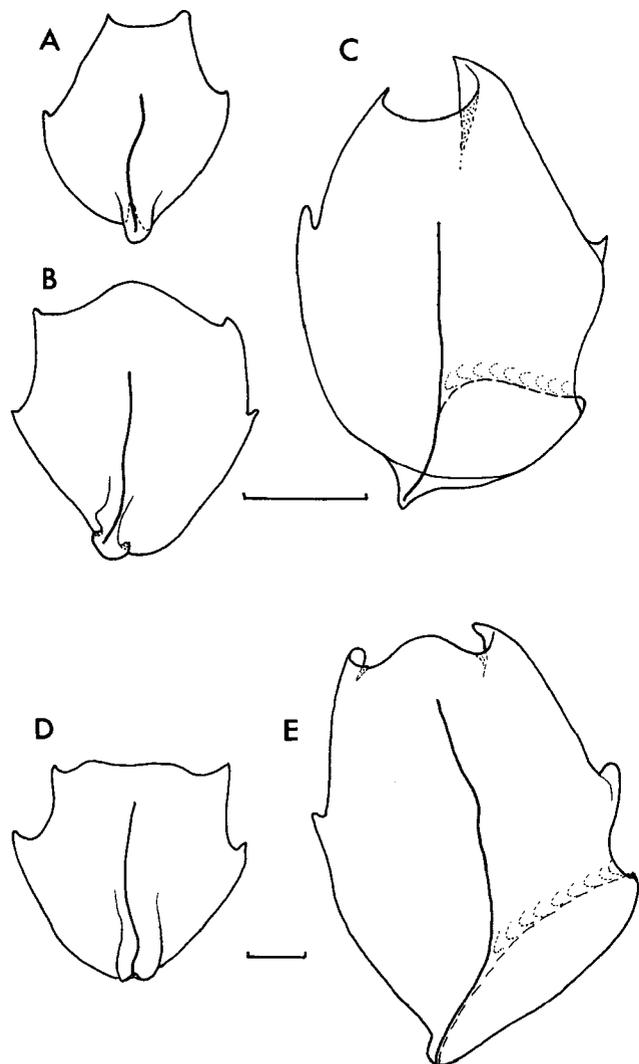
Fig. 10 Bracts of *Bargmannia amoena* sp. nov. Scale bars: A, B, C = 1 mm, D, E = 2 mm.

part, a regularly coiled terminal filament. The cnidoband is a simple tube that, in life, is generally straight or slightly curved, and can extend to a length greater than 0.5 cm. One side of the cnidoband appears to consist of a primitive elastic strand. It is not tightly folded, as is the case in some other physonect species, but a few pleats are present. The other side of the tentillum is comprised of numerous rows of small nematocysts of two types, as was the case in *B. elongata*. These are ovoid, measuring 20×14 μm and 12×11 μm, and occur in roughly equal proportions and possibly in alternating rows, although this could not be determined with certainty. Similar nematocysts are found along the length of the terminal filament. Again, it has not been determined whether these nematocysts are the acrophores and desmonenes found in other physonect siphonophores. At the proximal end of the cnidoband there is a paired series of up to 26 stenoteles that measure 135×105 μm.

SIPHOSOMAL TENTACLES AND BUDS (Figure 11B, C). As several of the siphosomal stems of the specimens examined remained relaxed, it was possible to study the disposition of the siphosomal tentacles and buds in detail. The primary siphosomal tentacle (Figure 11B, *t*) is inserted midway between successive gastrozooids and can be tightly coiled or extend to several millimetres in length. As in *B. elongata*, its surface is covered in large ectodermal cells and there is a paired series of nematocysts along one side.

On each cormidium there are, at least, four solid bud-like structures, whose arrangement is sexually dimorphic. In the female specimens (Figure 11B), the first bud (*b1*) lies a short distance distal to the gastrozooid (*gz1*), while the second (*b2*) is inserted about one quarter the length of the cormidium. The gonodendron is then inserted between the latter and the central siphosomal tentacle (*t*). The third bud (*b3*) lies a short distance distal to this tentacle, and the last (*b4*) is inserted immediately proximal to the next gastrozooid (*gz2*). In the male specimens (Figure 11C), the gonodendron is situated immedietly distal to the gastrozooid. The first bud (*b1*) then lies distal to the gonodendron at about one quarter the length of the cormidium; that is approximately in the same position as the second bud on the female specimens. The second bud lies immediately proximal to the central siphosomal tentacle; and the third midway between that tentacle and the next gastrozooid. The fourth, as in the female specimens, is inserted immediately proximal to the next gastrozooid. These arrangements pertain in the great majority of the specimens examined, but in the largest ones another tentacle, and possibly another bud, are found in close proximity to the fourth bud. Usually, this tentacle is much smaller than the central tentacle, but otherwise appears to be identical; including the double row of nematocysts.

together than on the first type, so that the distal end of the bract is relatively narrow. One of the proximal pair of teeth is usually more developed than the other, and on that side the lateral wall of the proximal part of the bract often extends out as a rounded notch.

GASTROZOOID AND TENTACLE (Figure 11A, C). The largest gastrozooids measure up to 10 mm in length. In the preserved state they are suffused with a brown coloration with, in the largest specimens, the basigaster having bright orange-red pigmentation. The latter (Figure 11C, *bg*), typically, is cup-shaped, enclosing the base of the stomach region, and is covered in large rounded ectodermal cells. The stomach region (Figure 11C, *s*) appears relatively thin and the endodermal hepatic villi can be seen within. The proboscis region can be extended to some distance.

The tentacle can be several centimetres in length. It is a simple, narrow, unsegmented tube, bearing a haphazard and irregular arrangement of the two sorts of small nematocysts that are also found on the tentilla. In the present specimens, only a few tentilla, up to 10, remain attached close to its base. In their preserved state, the tentilla (Figure 11A) typically are highly contracted and are comprised of a short pedicel; an irregularly twisted cnidoband; and, for the most

GONOPHORE. (Figure 11B, C). As noted above, the degree of sexual maturity of the specimens appears to be directly related to their size, as assessed by the length of the nectophores. Thus in the smallest specimens, at most, only gonophore buds can be seen. The major group of medium sized specimens have better developed gonophores, while the largest are obviously sexually mature. All seven of the largest specimens are male.

There is only a single gonodendron per cormidium. In male specimens the gonodendron lies immediately distal to a gastrozooid and proximal to the first siphosomal bud. The mature male gonophores (Figure 11C, *mg*) measure up to 5.5 mm in length and 1.1 mm in diameter. The female gonophores (Figure 11B, *fg*) are attached to the stem by a short stalk that is inserted approximately midway between the second siphosomal bud and the central siphosomal tentacle. Between one and six gonophores, in various stages of development, are attached to it by short pedicels. Each
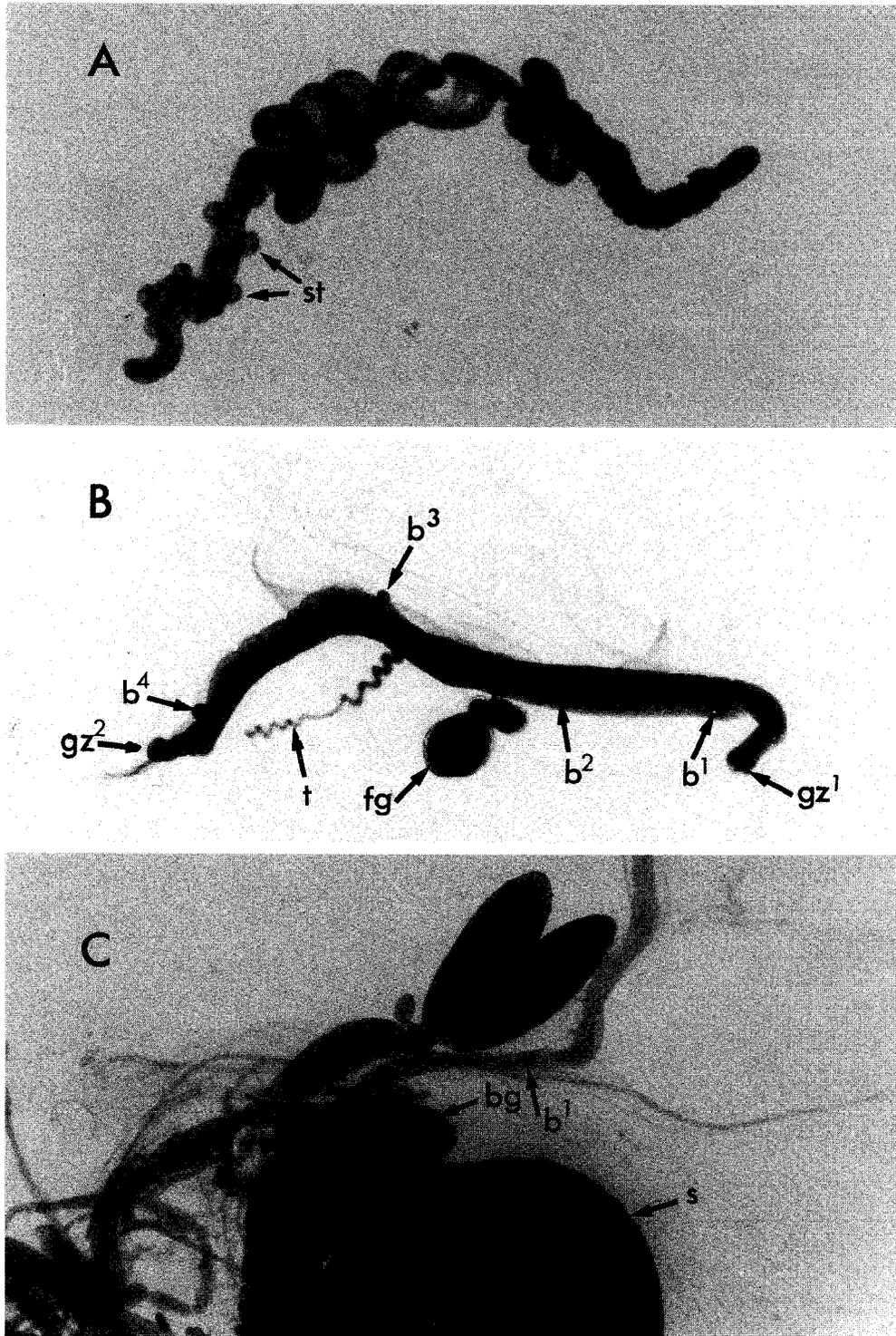
Fig. 11 *Bargmannia amoena* sp. nov. A. Mature tentillum, with stenoteles (*st*) at base of cnidoband (magn. 25×); B. Cormidium of siphosome, with gastrozooids detached (*gz¹* and *gz²* mark their attachment points) showing the siphosomal tentacle (*t*), four buds (*b¹⁻⁴*) and female gonophores (*fg*) (magn. 25×); C. Male gonophores (*mg*) attached just distal to gastrozooid, with its basigaster (*bg*) and stomach (*s*), and proximal to the first bud (*b¹*) (magn. 12.5×).

gonophore contains two eggs. This is a highly unusual situation as, according to Carré and Carré (1995) all other physonect siphono-phores have only one egg in each gonophore. However, Totton (1965) states that the gonophores of *Pyrostephos vanhoeffeni* contain from three to five eggs.

DISTRIBUTION. Much of Totton's (1954, 1965) *Bargmannia* material, from early *Discovery* collections, is so poorly preserved that it is difficult to be certain to which species it belongs. However, as noted earlier, the nectophores from *Discovery* Sts. 699 and 681, from the South and North Atlantic Ocean respectively, belong to *B. elongata*; as does that from *Discovery* St. 107 from south of South Africa. Several other of his nectophores probably belong to *B. amoena*, but this has not been established with certainty.

The great majority of the 8500+ nectophores of *Bargmannia* spp. that have been identified from over 300 recent *Discovery* samples, mainly from the North east Atlantic Ocean, belong to either *B. elongata* or *B. amoena*. However, these identifications were made before it was realised that two similar species were present. A re-examination of some of the material, however, typically showed that the material was too poorly preserved for specific identification. However, it was clear that *B. amoena*, not *B. elongata*, was the predominant species of the genus at c. 44°N, 13°W, where an extensive series of collections was made (Pugh, 1984). Collectively, both species have a widespread distribution in the North-east Atlantic Ocean; from the equator to 60°N, with possibly *B. elongata* being more common at lower latitudes and *B. amoena* at higher ones. Nectophores have been collected at all depths from the surface to 4520 m, but the vast majority were found in samples from between 200 and 600 m.

Most of the 67 specimens of *B. amoena* collected by the sub-mersibles *JSL* I and II came from a relatively small area in the region of The Bahamas, from 25°03' to 26°36'N and 77°23' to 78°44'W. Five others were collected near the Dry Tortugas, between Florida and Cuba, at c. 24°30'N, 83°45'W. All were collected over a wide depth range, from 435 to 910 m, with a mean depth of 625 ± 130 m. This mean depth is slightly deeper than the depth range for both *B. elongata* and *B. amoena* found in *Discovery* net collections. However, both figures probably are biased because, in the case of the submersible, most observations and collections were made within the 600–900 m depth range, while at 44°N, 13°W for instance, most of the net sampling was concentrated in the top 600 m of the water column.

REMARKS CONCERNING THE IDENTIFICATION OF *BARGMANNIA AMOENA*. Complete and well-preserved specimens of *B. amoena* easily can be distinguished from the other *Bargmannia* spp. as they have very distinctive bracts. However, if only poorly preserved nectophores are present, then there may be some difficulty in separating this species from *B. elongata*. They cannot be confused with *B. gigas*, because of the relatively enormous size of the latter's nectophores; and should not be confused with *B. lata*. The much narrower nectosac of the latter species, together with the greater depth of the furrow between its deep lateral wings, should easily distinguish it.

As noted above, the best feature distinguishing *B. elongata* and *B. amoena* is the arrangement of the apico-lateral ridges. In *B. elongata* these have a pair of side branches, running down toward the mid-line, while in *B. amoena* such side branches are absent. In addition, in *B. elongata*, at the point where these side branches arise, the apico-laterals bend sharply outwards, through 90°, while in *B. amoena* the apico-laterals only curve gently away from the mid-line. Unfortunately, it is this region of the nectophore that most often becomes distorted in poorly preserved specimens and these distin-

guishing features can be masked. This can result in the distinct, right-angle bend in the apico-lateral ridges of *B. elongata* coming to resemble the much smoother curve in *B. amoena* or, conversely, those of the latter species becoming distorted to form distinct bends resembling those of the former. The side branches to the apico-laterals in *B. elongata* often are difficult to discern, but usually show up after staining.

Another obvious difference, despite its subjectiveness, is the density of the musculature on the nectosac. Nectophores with almost opaque nectosacs appear to belong to *B. elongata*, while those with translucent nectosacs belong to *B. amoena*. In addition, the ratio of the total length of the nectophore to that of the nectosac may be of use. In *B. elongata* this ratio, in well-preserved specimens, averages 1.31, while in *B. amoena* it averages 1.42. However, with poorly preserved material, particularly when the basal half of nectophore is damaged, both measurements could be underestimated, which would lead to a corresponding increase in the ratio.

Other features of the nectophore that might be considered include the fact that in *B. amoena* the outer branch of the apico-lateral ridges peters out higher above the ostium than in *B. elongata*. Also, the lateral processes to the ostium are much larger in *B. elongata*. In addition, the angle at which the ostium opens is very characteristic in well-preserved material. In *B. elongata* the ostium is directed dorso-basally while in *B. amoena* it opens basally. However, all these features might be difficult to discern in poorly preserved nectophores The structure of the mouth-plate may be important but, as has been shown for *B. amoena*, this may vary according to the size of the specimens. More well preserved specimens of *B. elongata* are needed in order to assess this. Similarly, this applies to the arrangement of the meso-lateral ridges and their basal extensions; and to the profile of the ventral margins of the ventro-lateral wings.

ETYMOLOGY. *Amoena* is Latin for 'pleasing, delightful'.

Bargmannia lata Mapstone 1998

Bargmannia elongata Totton 1954 (partim) (text-Figure 28, E–F only), 1965 (partim) (Figure 45 E–F only).
Bargmannia lata Mapstone 1998: 141–146, figs 1–3.

HOLOTYPE. In the collections of the British Columbia Provincial Museum, BCPM 996-203-1; one nectophore and one bract collected at St. LC10 (48°22.4'N 126°20.2'W; 24–iv–1987; 700–0m) off British Columbia, Canada;

PARATYPES. As designated by Mapstone; 1. 7 nectophores and 7 bracts (BCPM 996-204-1#1), and 2. 6 nectophores and 6 bracts (BCPM 996-205-1#2) from the same sample as the holotype; 3. 11 nectophores (BCPM 996-206-1#3), and 6. 1 bract (BMNH 1996.1239-1240#6) from St.A4 (48°15'N 126°40'W; 21.iii.87; 500 m); 4. 8 nectophores (0–700m; BCPM 996-207-1#4), and 5. 14 nectophores and 2 bracts (BMNH 1996.1234-1238#5) from St. LB17 (47°56.5'N 126°26.1'W; 21.iii.87; 700m).

MATERIAL EXAMINED. One specimen collected during *Alvin* Dive 966 off San Diego, California, U.S.A.; 33°04'N 118°16'W; 8–ix–1979; water depth 747m. The depth of collection of the specimen was not recorded.

Two nectophores collected at *Discovery* St. 1769, and figured by Totton (1954, Text-Figure 28, E, F; 1965, Figure 45, E, F) as *B. elongata*; 33°43.3'S 8°38.5'E; 20–v–1936; 1000–750 m; NHML 1957.5.15.110.

In addition, the specimens that Totton included under the name *B. elongata* have been re-examined. Although not all are in good condition, the following appear to belong to *B. lata*:-

Table 1 Geographical distribution of *Bargmannia lata* from recent *Discovery* collections.

Station	Date	Position	Depth (m)	Nects	Bracts
8565# 1	1–viii–74	3°03.1'N 23°14.3'W	700– 800	5	
6662#37	21–ii–68	10°34.9'N 19°43.7'W	1060–1300	24	16
6662#32	20–ii–68	10°45.3'N 19°51.7'W	1210–1450	3	4
6662#30	19–ii–68	10°47.4'N 19°52.7'W	730– 795	17	
6662#15	16–ii–68	10°57.0'N 19°56.6'W	600– 695	27	
6662#20	17–ii–68	10°57.5'N 19°49.0'W	810– 900	8	
6662#22	17–ii–68	10°57.6'N 19°57.3'W	610– 680	25	3
6662#16	16–ii–68	10°59.4'N 19°52.1'W	810– 890	18	2
7824#39	10–iii–72	11°01.1'N 19°55.8'W	895–1000	5	
6662#10	15–ii–68	11°03.1'N 19°59.2'W	910– 985	4	
6662# 7	14–ii–68	11°04.6'N 19°48.2'W	715– 800	33	
6662# 8	15–ii–68	11°08.2'N 19°47.8'W	910– 985	7	
7831# 1	16–iii–72	13°18.4'N 25°33.2'W	10–1000	12	
7803# 2	19–ii–72	18°06.4'N 25° 8.1'W	1015–1250	13	
11261#16	28–vi–85	31°13.1'N 25°18.3'W	1000–1100	16	
8281#29	17–iii–73	31°42.5'N 63°43.6'W	1259–1500	26	
11794#36	26–vi–88	47°14.2'N 19°31.2'W	1200–1300	10	
11794#83	2–vii–88	47°17.9'N 19°21.4'W	1300–1395	7	
11794#31	26–vi–88	47°27.1'N 19°18.0'W	2500–2750	17	2
12096# 2	3–vi–90	47°57.8'N 16°49.6'W	1100–1200	16	20

4 nectophores from John Murray Expedition St. 34; 13°05.6'N, 46°24.7'E; 16–x–33; 0–1022 m. BMNH 1949.11.10.378; and 4 nectophores from *Discovery* St. 206; 16°36'S, 6°25.1'W; 1–v–37; 1900–1500 m. BMNH 1957.5.15.111.

Several nectophores and bracts also have been identified from more recent *Discovery* material from the N.E. Atlantic (Table 1).

DIAGNOSIS. Nectophores with relatively long median thrust block; with extensive ventro-lateral wings, emarginate on ventral margins. Nectosac a relatively short, narrow tube without any pronounced dorso-ventral undulations; squarely truncate apically. Ratio of overall length of nectophore to that of nectosac, on average, exceeds 1.59. Bracts large, robust, distally truncate; with semicircular dorsal ridge connecting tips of baso-lateral processes and delimiting a dorso-basal facet; with prominent tooth on outer lateral margin.

DESCRIPTION. A photograph of the live specimen collected by *Alvin* and taken on board the mother ship is shown in Figure 12. Unfortunately, prior to photography, several nectophores had become detached and the siphosomal stem had contracted. No pigmentation is apparent in the preserved specimen, but the original colour photograph indicates that the whole of the endodermal lining of the stem was suffused with an orange-red colour.

PNEUMATOPHORE. The highly distorted pneumatophore of the *Alvin* specimen measured 2 mm in height. It is borne on a very short, but probably highly contracted, stalk.

NECTOPHORE (Figures 13–15). A total of 16 nectophores was found with the *Alvin* specimen. The mean dimensions for the fully developed nectophores of this specimen were:- length 19.44 ± 2.73 mm (range 14.79–23.86 mm); width 9.72 ± 1.07 mm, and the ratio of total length to that of the nectosac was 1.59 ± 0.09. Nectophores of the earlier *Discovery* material, in the NHM, are somewhat larger with an average length of 24.94 ± 6.02 mm (range 17.74–31.94 mm). The ratio of total length to that of the nectosac also was slightly greater ratio (1.67 ± 0.10; n = 10); the same as that for Mapstone's (1998) material. Similarly, the nectophores of more recent *Discovery* material also are larger: length 22.89 ± 4.04 mm (range 15.8–29.6 mm; n = 48). These nectophores have the greatest length:nectosac-length ratio of 1.73 ± 0.11. However, this increase in ratio probably
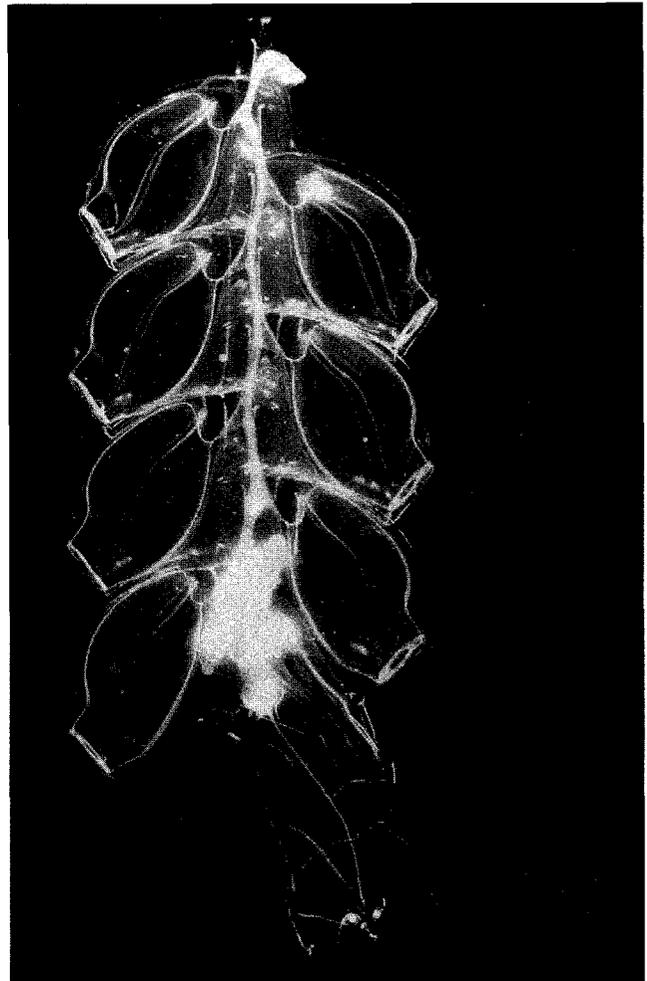

Fig. 12 *Bargmannia lata*. Photograph (reproduced by kind permission of Larry Madin, WHOI) of live specimen collected during *Alvin* Dive 966. Nectosomal length c. 5 cm.
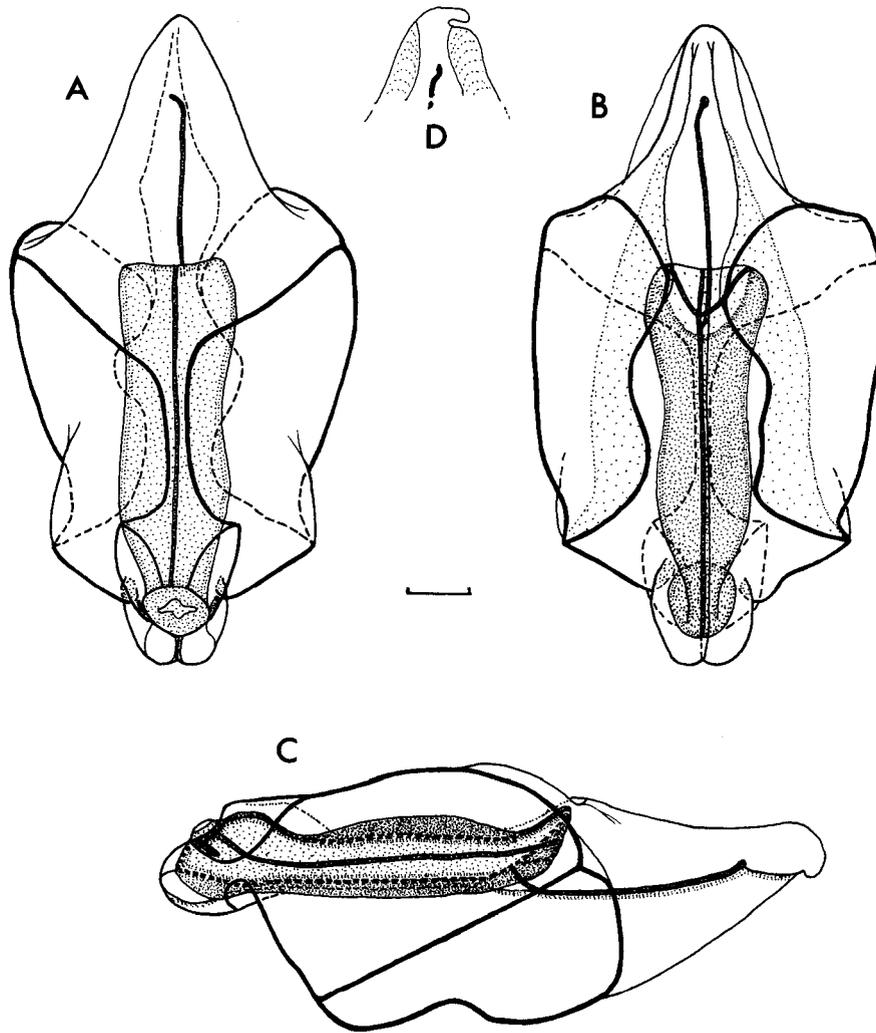
Fig. 13 *Bargmannia lata.* A. Upper, B. lower, and C. lateral views of mature nectophore collected during DSRV *Alvin* Dive 966. D. Ventral view of the apex of another nectophore. Scale bar = 2 mm.

is due to the fact that the base of the nectophore frequently is damaged, resulting in an underestimate of both measurements, and a consequent increase in their ratio.

The central thrust block forms an extensive triangular process whose apex is often roundly pointed Figure 13A). However, on several nectophores one side is drawn out to form a small digitiform process that may be folded over laterally or ventrally (Figure 13D). The ridge pattern conforms to the basic *Bargmannia* design, with no extra ridges being present.

From their junction with the meso- and infra-lateral ridges on the 'shoulder' of the nectophore, the apico-laterals are directed obliquely toward the mid-line. They closely approach each other, and continue for some distance in a basal direction; leaving a narrow median furrow between them. At about one quarter the length of the nectophore, in the *Alvin* material, they rapidly curve out laterally, before giving rise to the typical inner and outer branches (Figures 13–15). The inner branch curves obliquely toward the mid-line and joins the ostium on its dorsal surface. The outer branch curves down and then round and ends on the lateral margin of ostium, although it can be difficult to discern basally. The angle between the apico-lateral ridge and its inner branch is acute (Figure 13A). However, in

less well preserved nectophores, this pronounced angle is not always apparent (Figure 14B) and the inner branch can appear as a simple continuation of the main ridge.

The mouth-plate is small and made up of two rounded lobes that unite in the mid-line, slightly basal to the ostium. The ventro-lateral margins of these lobes are, as usual, formed by basal extensions of the meso-lateral ridges. Above the ostium, on the ventral surface of the nectophore, these basal extensions curve round toward the mid-line, before looping back out as the meso-laterals proper and continuing apically. After a relatively long distance, in comparison with *B. elongata* and *B. amoena*, the infra-laterals branch from them (Figures 13C, 15C). The meso-laterals then continue obliquely up and across the lateral margins of the nectophore to join the apico- and infra-laterals on the 'shoulder' of the nectophore. The junctions with the other ridges, both apically and basally, are obvious, unlike in *B. elongata*.

In the basal two-thirds of the nectophore, the infra-lateral ridges form the ventral margins to the ventro-lateral wings (Figure 13C, 15C). These wings are relatively large in comparison with those of *B. elongata* and *B. amoena*, occupying more than half the depth of the nectophore. They are distinctly emarginate in the mid region of
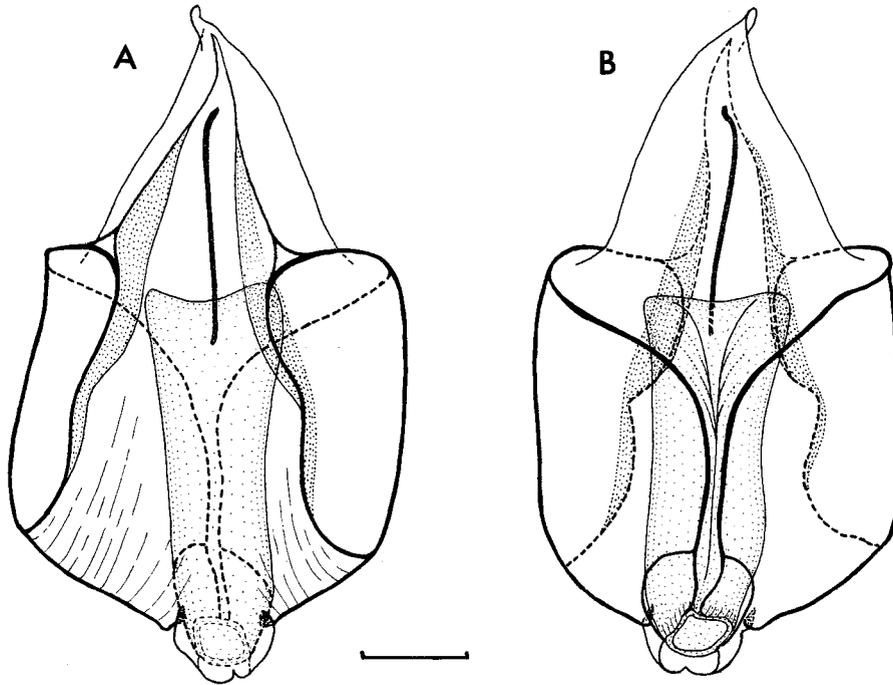
Fig. 14 *Bargmannia lata.* A. Lower and B. upper views of nectophore from *Discovery* St. 1769. Scale bar = 5 mm.
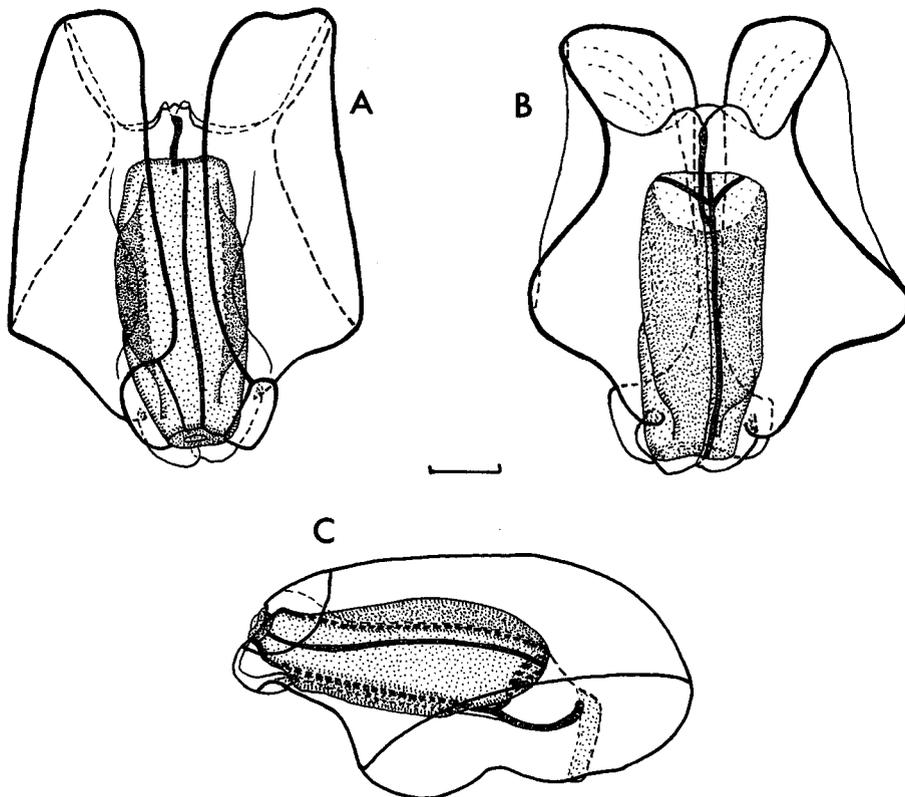
Fig. 15 *Bargmannia lata.* A. Upper, B. lower and C. lateral views of young nectophore collected during DSRV *Alvin* Dive 966. Scale bar = 1 mm.

the nectophore. In the region where the infra-laterals leave the ventral margins of the ventro-lateral wings, the latter begins to thicken toward the mid-line. These thickened, rounded, unridged lateral walls continue up to the apex of the nectophore and, on the thrust block, delimit a narrow gutter that enfolds the nectosomal stem (Figures 13B, 14A).

The nectosac is a relatively short and narrow tube without any marked dorso-ventral undulations (Figures 13, 14) in the preserved specimens. Its apex lies approximately on a level with the 'shoulder' of the nectophore. The nectosac occupies only c. 38% of the width of the nectophore, as measured across its 'shoulder'. This results from the fact that the extensive ventro-lateral wings not only increase the depth of the nectophore, but also increase its relative width. The apex of the nectosac is squarely truncate, without any marked indentation. Its adaxial surface is distinctly undercut and, typically, is devoid of musculature. The remaining musculature on the nectosac appears much less dense in comparison with that of *B. elongata*.

The canal system follows the basic *Bargmannia* plan. The long pallial canal ends, apically, with a short dorsad inflection into the mesogloea. On the nectosac the pedicular canal gives rise to only the dorsal and ventral radial canals. In contrast to *B. elongata* and *B. amoena*, in the preserved material the lateral radial canals have straight courses down the lateral margins of the nectosac. However,

in life, their courses appeared to be slightly undulating (Figure 12). In the original colour photograph there are indications that the pallial, dorsal, ventral, ostial ring, and proximal parts of the lateral canals were suffused with a light orange-red colour.

The ostial opening, in the preserved nectophores, typically is displaced slightly dorsad and has a well-developed velum, but no pronounced lateral processes. There are no marked patches of ectodermal cells, although some nectophores show a single row around the basal half of the ostium and/or a short, narrow band of small cells that lies just dorsal to the outer branch of the apico-lateral ridge. These cells, again, are presumed to be sites of bioluminescence.

BRACT (Figure 16).   Only seven bracts were retained with the *Alvin* material. However, because of their very characteristic shape, several more have been identified from recent *Discovery* material. The bracts measured from 13.5 to 27 mm in length and were remarkably robust. They had a convex dorsal and a concave ventral surface. In the *Alvin* specimen, there were two types of bract, with one type being represented by only a single small bract. The key feature that distinguishes them is the presence of only a single lateral tooth on the outer margin (Figure 16A, B) of the larger ones; while the smaller one has lateral processes on both sides (Figure 16C). The
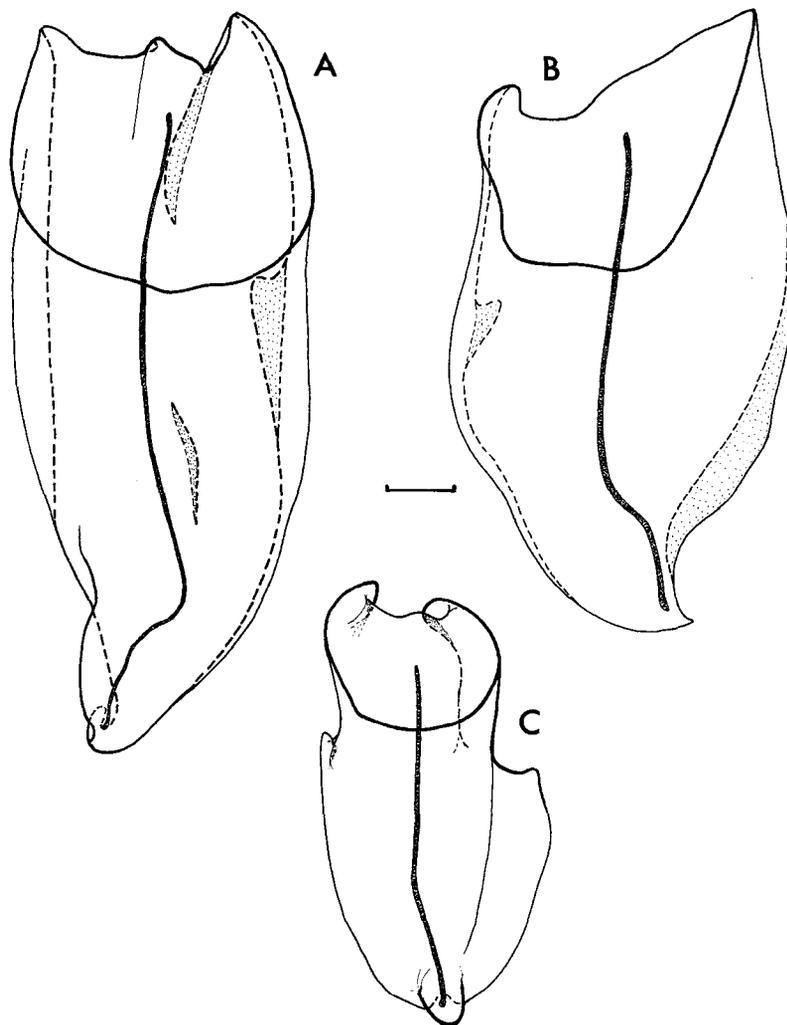

Fig. 16   Bracts of *Bargmannia lata* collected during DSRV *Alvin* Dive 966. Scale bar = 2 mm.

larger ones also were distinctly asymmetric proximally; and the bracteal canal made a right-angled bend. These differences may be just the result of growth, or may related to their point of attachment on the cormidium, as was noted for *B. amoena*. Both types of bract are distally truncate, and possess a semicircular dorsal ridge that delimits a rounded distal facet. The ridge connects the tips of two distal processes.

The shape of the distal margin of the larger bracts varied considerably. On some, the inner margin of one of the distal process extended up the ventral side of the bract forming a flap-like structure; while on others this flap was absent. Another small ventral flap can be present, approximately in the mid line, in the proximal half of the bract. The bracteal canal lies just above the ventral surface of the bract and ends close to its distal margin. The original colour photograph of the *Alvin* dive 966 specimen indicated that, in life, some of the bracteal canals had an orange-red pigmentation like that of the remainder of the stem.

GASTROZOOID AND TENTACLE.   Only a small portion of the proximal end of the siphosome was preserved from the *Alvin* specimen, so that only a few young gastrozooids were present. These measured up to 7 mm in length, and showed no distinguishing features. No pigmentation is apparent in the preserved material, but in life they had a deep red pigmentation.

The tentacles attached to the gastrozooids mainly bore young tentilla; with a c. 1 mm pedicel; a 2.5 mm cnidoband, apparently devoid of large nematocysts; and a c. 4 mm uncoiled terminal filament, apparently without a terminal process. However, a few more mature tentilla had cnidobands extending to more than 8 mm, with 4–6, possibly more, large nematocysts (stenoteles), arranged biserially and arranged alternately, at their proximal ends. Small nematocysts, possibly of two types, are present throughout the cnidoband and terminal filament.

SIPHOSOMAL TENTACLES AND BUDS.   The peculiar tentacular processes, previously noted in specimens of *B. elongata* and *B. amoena*, are present on the small part of the siphosomal stem remaining but, because of the contracted state of the latter, it was not possible to ascertain their exact disposition. They are narrow, delicate structures, measuring up to c. 4 mm in length, and are covered in large, rounded ectodermal cells. Small nematocysts are present but, without destroying the tentacle, it was no possible to assess whether they had a biserial arrangement, as noted for the previously described species. Siphosomal buds also appear to be present, but their arrangement could not be discerned.

GONOPHORE.   A few loose male gonophores are present with the *Alvin* material. They are identical to those previously described for *B. elongata* and *B. amoena*.

DISTRIBUTION.   A total of 288 nectophores and 27 bracts of *B. lata* have been found in recent *Discovery* collections (Table 1). The data indicated that, in the North-east Atlantic Ocean, *B. lata* was more commonly collected at lower latitudes and at deeper mesopelagic depths; with a mean depth of c. 1000 m. Totton's material came from two sites in the South Atlantic Ocean and one in the Gulf of Aden; the *Alvin* material came from off San Diego, California, USA; and Mapstone's (1998) from off British Columbia, Canada; thus indicating a widespread geographical distribution for this species.

REMARKS CONCERNING THE IDENTIFICATION OF *BARGMANNIA LATA*. *B. lata* can now be easily distinguished from other *Bargmannia* spp. The nectophores are relatively broad, with extensive ventro-lateral wings, that are markedly emarginate along their ventral margins. The median thrust block is relatively long so that the ratio of the total

length of the nectophore to that of the nectosac is high, c. 1.6, or more for net collected material, as compared with c.1.31 in *B. elongata* and c. 1.41–1.44 in *B. amoena*. The nectosac appears as a relatively short, narrow, straight-sided tube, without any pronounced dorso-ventral undulations, and squarely truncate apically. It occupies only c. 38% of the width of the nectophore, as compared with 45% in *B. elongata*. The large, robust bract, with a semicircular dorsal ridge connecting the tips of the baso-lateral processes, also is distinctive.

Despite these differences it is clear that Totton (1954, 1965), had little reason to suspect that he was dealing with at least two *Bargmannia* spp., particularly as he had so few, poorly preserved nectophores. However, with the collection of complete specimens of *Bargmannia* spp. by submersibles the specific differences between the various types of nectophore that Totton illustrated can now be established.

Bargmannia gigas sp. nov.

HOLOTYPE.   BMNH 1998.2166 one nectophore, preserved in Steedman's solution, collected at *Discovery* St. 8560#2 (0°03.1'N, 22°44.2'W; 27–vii–1974; 1510–2000 m; RMT8 net).

PARATYPES.   Three nectophores, preserved in Steedman's solution, from the same *Discovery* sample. BMNH 1998.2167–69.

MATERIAL EXAMINED.   The type and paratypes, and a further ten nectophores from the same station, which are retained in the *Discovery* collections at the Southampton Oceanography Centre. All the nectophores are presumed to have originated from a single specimen.

DIAGNOSIS.   Nectophores relatively enormous, up to 52 mm in length; with large ventro-lateral wings; with small mouth-plate deeply divided. Basic ridge pattern supplemented by three pairs of ridges, all dividing from apico-laterals; two pairs short, directed toward mid-line; third pair directed laterally. Nectosac without dorso-ventral undulations; apex only slightly emarginate; ostial opening large. Ratio of overall length of nectophore to that of nectosac averages 1.63.

DESCRIPTION. NECTOPHORES (Figures 17 and 18).   The relatively enormous nectophores varied in size from 14.5 × 8 mm (length × width) for the smallest, immature one, to 52 × 20 mm, respectively, for the largest. The mean dimensions for the fully developed nectophores were length: 41.0 ± 6.96 mm and width: 19.1 ± 2.52 mm, and the ratio of total length to that of the nectosac was 1.63 ± 0.10. The nectophores, in their present state of preservation, are devoid of pigmentation and, in most cases, the muscular lining of the nectosac has become detached and/or lost. The large, thickened, central thrust block is roundly truncate.

The basic pattern of the prominent ridges conforms with that of the genus, and both the inner and outer branches of the apico-laterals appear to reach the dorso-lateral margins of the ostium. In addition there are three pairs of ridges that branch from the apico-laterals (Figures 17A, 18). Two of these pairs of ridges are very short and run down into the shallow median gutter, towards the mid-line. One pair arises at a level of about two-fifths the length of the nectosac, while the other originates from the inner branches of the apico-laterals, close to the ostium. The other pair arises from the outer branches of the apico-laterals and extends up the sides of the nectophore between the apico- and meso-laterals. These ridges peter out approximately at the mid-length of the mature nectophore. Below them the lateral walls of the nectophore often show prominent thickenings (Figure 17C).
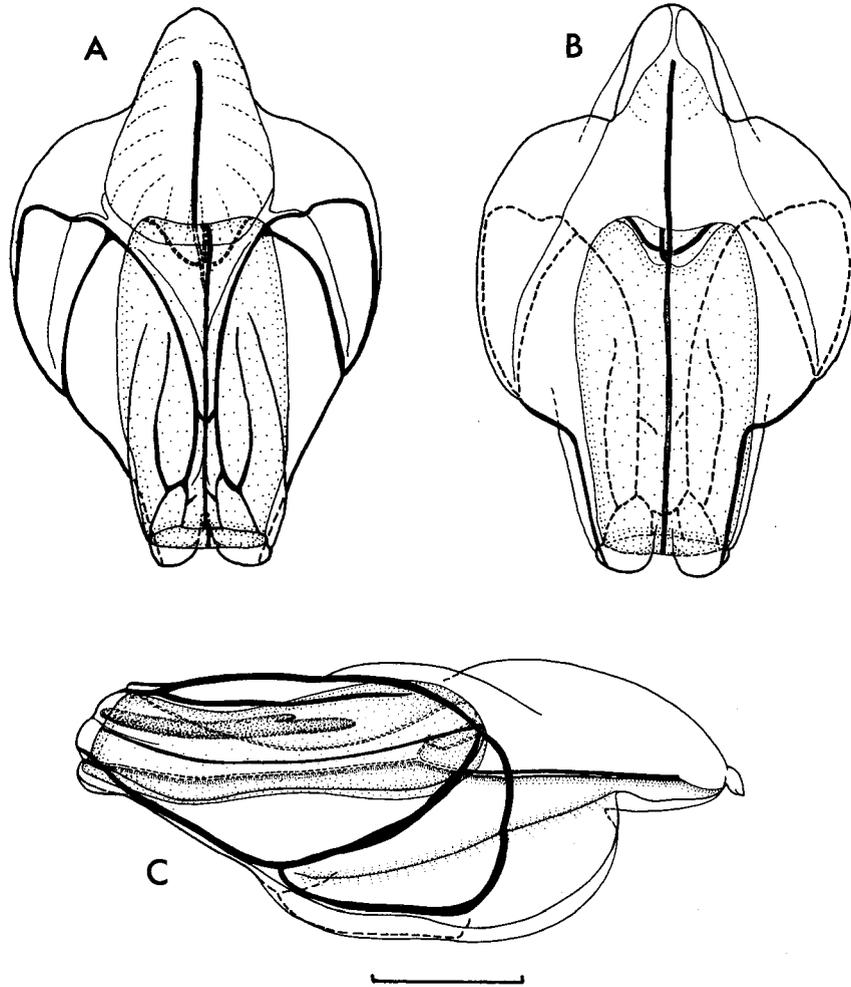
Fig. 17 *Bargmannia gigas* sp. nov. A. upper, B. lower, and C. lateral views of mature nectophore. Scale bar = 1 cm.
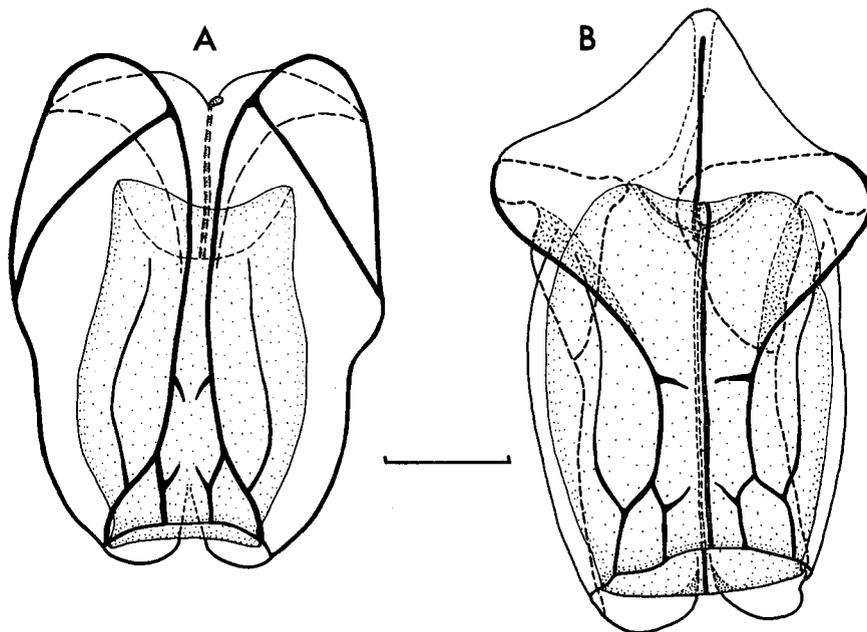

Fig. 18 *Bargmannia gigas* sp. nov. Upper views of A. smallest, and B. slightly larger nectophores. Scale bar = 0.5 cm.

The broad, but relatively short, mouth-plate consists of two rounded processes whose basal margins are marked by basal extensions of the meso-lateral ridges. These ridges peter out, without apparently uniting, on the lower surface of the nectophore a short distance above ostial level. The infra-lateral ridges branch from the meso-laterals approximately on a level with the mid-length of the nectosac. The meso-laterals then run obliquely up the sides of the nectophore to join the other ridges, approximately on a level with the top of the nectosac. The infra-laterals form the ventral margins of the ventro-lateral wings up to a level just above the top of the nectosac. They then bend through 90° and run up to join the apico- and meso-laterals (Figure 17C). The thickened ventro-lateral wings are well developed and enclose a deep groove, which at its deepest occupies half the height of the nectophore (Figure 17C). They are roundly truncate apically at about four-fifths the length of the nectophore.

The nectosac is a long tube, with only a slight apical emargination, that occupies most of the main body of the nectophore, and has no obvious dorso-ventral undulations. It is distinctly undercut adaxially and is presumed to have a muscle-free zone in that region, although this could not be established with certainty. The ostial opening is very large and is only slightly directed towards the upper surface. The pedicular canal (Figure 17B) typically only gives rise to the dorsal and ventral radial canals. The course of all the canals is straight.

Typically, the youngest nectophores show the absence of a central thrust block (Figure 18A), but with a clearly defined ridge pattern. A slightly larger nectophore shows the gradual development of the thrust block and the ventro-lateral wings (Figure 18B).

REMARKS CONCERNING THE IDENTIFICATION OF *BARGMANNIA GIGAS*. *B. gigas* is known only from the nectophores of what is presumed to be a single specimen, collected in the equatorial Atlantic at a depth of 1510–2000m. The nectophores easily can be distinguished from other *Bargmannia* sp. by their incredible size and the distinctive pattern of ridges.

ETYMOLOGY. The specific name *gigas* refers to the giant size of the nectophores.

DISCUSSION

As was noted in the Introduction, the content of the genus *Bargmannia* is debated. Although Totton (1965) included it in the family Pyrostephidae, some of the characters that he listed in his diagnosis of that family apply exclusively to the scope accorded to the genus *Pyrostephos*, which is monotypic for *P. vanhoeffeni*. In particular, these are the looping of the lateral radial canal on the nectosac of the nectophore, and the three to four marked bends of the dorsal canal. In *Bargmannia* all the canals are held to be straight, or only slightly sinuous. Other characters, such as the number of tentilla on the tentacle, and the structure of the bracts and gastrozooids probably are more specific than familial. However, in both genera the nectosome is long but again this is not a good familial character.

At first glance, the nectophores of *Pyrostephos vanhoeffeni* (see Totton, 1965, Figure 41) and *Bargmannia* species look strikingly different. However, there are several similarities. Specimens of *P. vanhoeffeni* have been collected recently by SCUBA divers (G.R. Harbison, personal donation) and by net (Pagès, Pugh & Gili, 1994). It is apparent from these that the mature nectophores can vary greatly in size; ranging from 8 × 5 mm (length × width) in the SCUBA collected material (Figure 19B) to 15 ×18 mm, respectively, in the net collected specimens (Figure 19C). Such large size ranges of the mature nectophores of physonect species have not often been observed,

although such is so in *Nanomia bijuga* (delle Chiaje, 1841) (Pugh, *pers. obs.*). It is also known to be so in at least two *Bargmannia* spp. In *B. amoena* (Figure 19A), the size variation of mature nectophores is even greater than that of *P. vanhoeffeni*, ranging from c. 6 × 3 mm (length × width) to 25.5 × 12.5 mm respectively. Although the general shape of mature *Bargmannia* nectophores does not change with size, it appears that that of *P. vanhoeffeni* does. In the smaller specimens of the latter (Figure 19B) there is a large triangular thrust block, reminiscent of that on mature *Bargmannia* nectophores. However, in the larger, preserved specimens (Figure 19C) the thrust block is folded upwards producing a deep transverse furrow on the dorsal surface, just basal to it. Neither *P. vanhoeffeni* nor *Bargmannia* spp. have large apico-lateral processes.

The nectophores of both genera have the same basic ridge pattern; comprising apico-, infra, and vertical (meso-) laterals, but no lateral ridges. In addition, in both, the apico-laterals divide into two branches close to the ostium. The inner branch ('frontal ridge') of the larger nectophores of *Pyrostephos vanhoeffeni* (see Totton, 1965, Figure 40) is relatively short, in comparison with *Bargmannia* spp., and directed only toward the mid-line. However, the present material, particularly that of the smaller specimens, shows that these ridges can curve round basally and continue for a short distance towards the ostium before petering out. Nonetheless, the species of these two genera are not the only physonects to show this basic pattern of ridges. It is also found on the nectophores of two others namely, *Frillagalma vityazi* Daniel, 1966 (see Pugh, 1998) and *Erenna richardi* Bedot, 1904 (P.R.Pugh, personal observation). In addition, an even simpler arrangement, in which the vertical lateral ridges are absent, is found in two *Marrus* species, namely *M. antarcticus* Totton, 1954 and *M. orthocanna* Kramp (1942). For these, the branching of the apico-lateral ridges is weak and difficult to discern. A third species, namely *M. orthocannoides*, that Totton (1954) include in the latter genus probably does not belong there as its nectophores do not have an adaxial muscle-free zone on the nectosac.

Species referred to both *Bargmannia* and *Pyrostephos* have an adaxial zone on the nectosac of the nectophore that is muscle-free and deeply embayed. In addition, the lateral radial canals arise separately from the dorsal canal. These appear to be important characteristics. Of the other species previously mentioned *Marrus antarcticus* and *M. orthocanna* show all of these characters. However, in *Frillagalma vityazi*, there is no deeply embayed, muscle-free adaxial zone; although the lateral radial canals do arise separately from the dorsal one, albeit very close to the point of insertion of the pedicular canal (Pugh, 1998). Further, this species has many marked differences from the others under consideration and need not be considered further in this discussion. *Erenna richardi* does have a muscle-free zone, but it lies at the apex of the nectosac, which is not deeply embayed adaxially. Thus, from the basic arrangement of the ridges and nectosac, the nectophores of *Bargmannia*, *Pyrostephos* and *Marrus* species are very similar. Another common feature is that they all have relatively short pedicular and relatively long, ascending pallial canals. But how do their siphosomal elements compare?

Most siphonophores are believed to be hermaphrodite (monoecious), bearing both male and female gonophores. However, specimens of *Physalia*, the Portuguese Man O'War, and probably all other cystonect siphonophores, are single sexed (dioecious). It should be noted that Mackie, Pugh & Purcell (1987, p.100) used the terms monoecious and dioecius erroneously. In physonect siphonophores, species of the benthic family Rhodaliidae appear to be dioecious (Pugh, 1983), as are *Marrus antarcticus*, *Pyrostephos vanhoeffeni* (Totton, 1965), and from the present study *Bargmannia* spp. According to Andersen (1981) *M. orthocanna* is monoecious, but the male gonophores he illustrated were only minute, bud-like
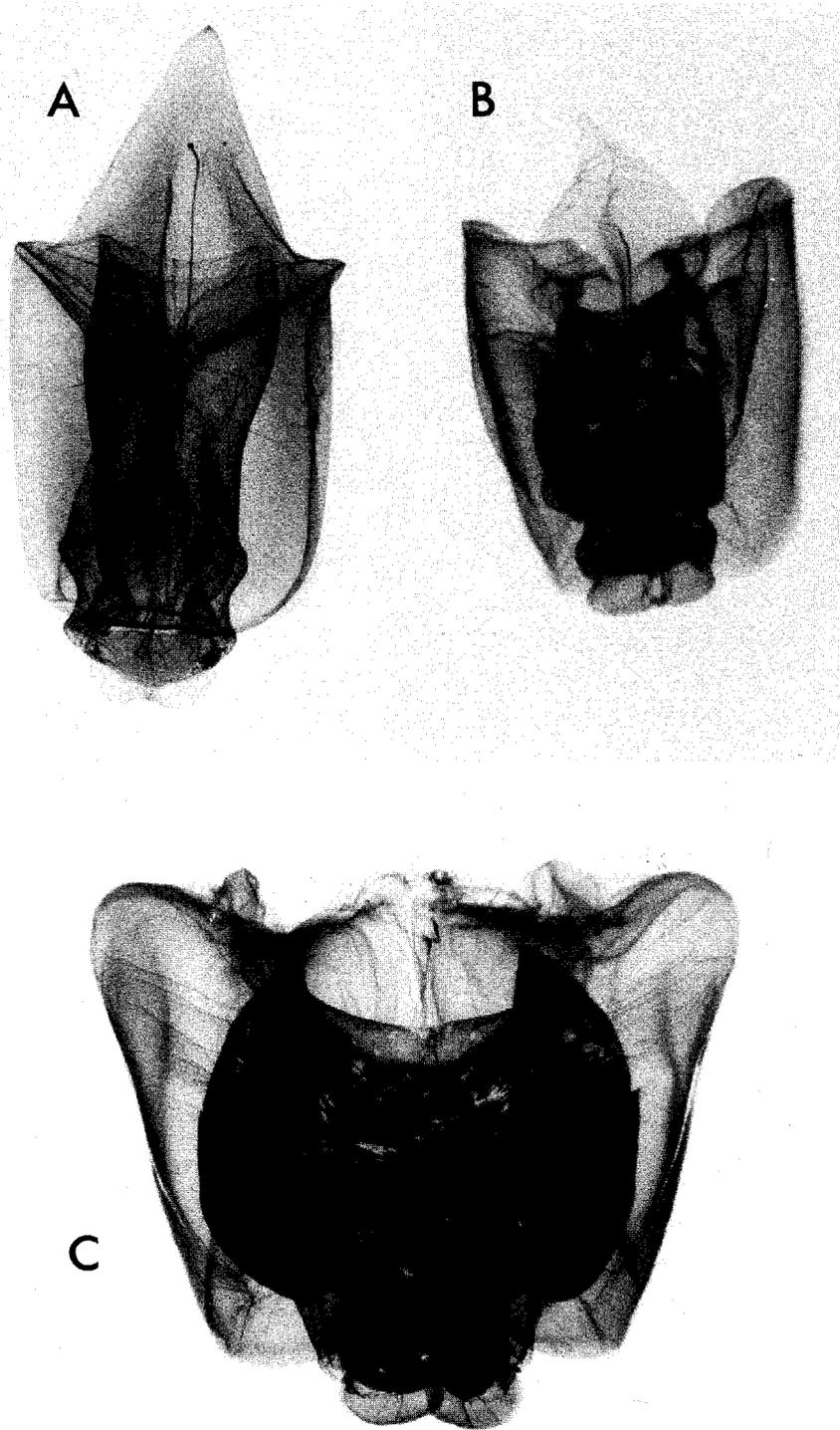
Fig. 19 Nectophores of A. *Bargmannia amoena* sp. nov. (magn. 10); B, C. *Pyrostephos vanhoeffeni* collected by SCUBA (B, magn. 11x) and by net (C, magn. 7.5x).

structures. Since only female gonophores could be identified on submersible collected specimens, this point could not be checked (P.R.Pugh, personal observation). Whether *Erenna richardi* is monoecious or dioecious remains unknown. Nonetheless, it is of interest to note that, of the physonect species whose female gonophores are known, only those of *P. vanhoeffeni* and *B. amoena* contain more than one egg; 3–5 in the former species (Totton,

1965) and two in the latter.

The structure of the tentillum is another feature in which close similarities between *Bargmannia* species and *Pyrostephos vanhoeffeni* appear. In both the cnidoband is straight, or slightly twisted, but not tightly coiled, and is without a basal involucrum. In addition, they both have long terminal filaments. Even more striking is the presence of large nematocysts, probably stenoteles, only in the

proximal region of the cnidoband of both species. However, those of *Bargmannia* spp. are considerably larger than those of *P. vanhoeffeni*, which measure c. 40 × 28 mm. Further, the other nematocysts present on the cnidoband and terminal filament are very similar. Two types of small nematocysts were found in *Bargmannia* spp. and similar ones, measuring 13–17 × 9.5–10.5 μm and 6.5 × 6.5 μm, were found in *P. vanhoeffeni*. Although the tentillum of *Erenna* has a straight cnidoband, and that of *Marrus* is loosely coiled or straight, the types and distribution of the nematocysts are quite different. The cnidoband of *Erenna* is massively armed with two types of elongate nematocysts, measuring c. 160 × 37 μm and c. 35 × 18 μm, while the terminal process appears to be devoid of any nematocyst. The cnidoband of *Marrus* contains heteronemes and haplonemes, measuring c. 55 × 20 μm and c. 35 × 7 μm of the type often seen in other agalmatid species. The terminal filament of the latter species contains only small nematocysts, probably desmonemes, acrophores or anacrophores, measuring c. 16 × 9.5 μm and c. 10 × 10 μm. These differences in the nematocyst types alone seem sufficient to indicate that *Bargmannia* and *Pyrostephos* are more closely related to each other than either is to *Marrus* or *Erenna*.

Despite all these similarities between *Bargmannia* spp. and *Pyrostephos vanhoeffeni*, there are at least two major differences: *Bargmannia* spp. are the only physonect siphonophores known to have siphosomal tentacles, though apolemiid species have nectosomal ones; they also lack dactylozooids, although the bud-like structures may be vestigial ones. In addition, *P. vanhoeffeni* is the only species known to have highly modified dactylozooids, the oleocysts, without palpacles. The only other species in which dactylozooids are thought to be absent is *Marrus orthocanna* (Andersen, 1981). However, Totton (1965) reported that palpons are present on the gonodendra of *M. antarcticus*. Further work needs to be carried out on well-preserved specimens of these *Marrus* species in order to investigate this apparent difference, and whether each is monoecious or dioecious.

Although there are major differences between *Bargmannia* spp. and *Pyrostephos vanhoeffeni*, there appear to be sufficient similarities to warrant the retention of the genus *Bargmannia* in the family Pyrostephidae. The alternative would be to propose a new family for it, since the genus certainly does not fit neatly into the family Agalmatidae. This might also apply to the genera *Marrus* and *Erenna* but their species are too little known.

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