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A re-description of *Frillagalma vityazi* Daniel 1966 (Siphonophorae, Agalmatidae)*

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SUMMARY: Ten complete specimens of *Frillagalma vityazi* Daniel, 1966 (Siphonophorae, Agalmatidae) were collected by the submersibles Johnson-Sea-Link I and II. These have allowed a more detailed description of the species to be made, as it was previously known only by its ill-preserved nectophores and one type of its bracts. The taxonomic status of the species is discussed. In addition much material has been identified from the Discovery collections, and the distribution of the species in the North Atlantic Ocean is considered.

Key words: Siphonophore, Physonect, *Frillagalma,* re-description.

INTRODUCTION

Frillagalma vityazi Daniel, 1966 was originally described from, what was said to be, three mature and one juvenile nectophores collected at "Vityaz" St. 5212 (05°11'S, 91°15'E) using an Indian Ocean Standard net fished over the 200-0 m depth range. The main features of the small nectophores were that all the ridges were flared and frilled, and that there were two pairs of short ridges arising from the apico-laterals. The courses of the lateral radial canals on the nectosac were simple and unlooped. Daniel (1966) considered that her new species most probably belonged in the physonect family Agalmatidae.

Since the original description there have been relatively few further records for this species. Daniel (1973, 1985) and Rengarajan (1975) added a few more records for the Indian Ocean; with an illustration of a possible bract appearing in Daniel (1985). Most other records [Pugh, 1974, 1975 (under the heading "Physonect C"); and Stepanjants, 1975] come from the North Atlantic Ocean. Stepanjants (1975) described and figured some bracts and she drew attention to their structural similarity to those found in the family Forskaliidae. Nonetheless, there were no such similarities amongst the nectophores. Mackie *et al*. (1987) also noted that the bract that Totton (1965, fig. 61) had illustrated under the heading *Forskalia cuneata* Chun, 1888 most probably belonged to *F. vityazi*; again establishing the apparent link with the family Forskaliidae. However, the bract figured by Daniel (1985) was quite different in design. That author likened it to the bracts of *Agalma okeni* Eschscholtz, 1825, but stated that it possessed more spines between the distal facets. Arai *et al*. (1993) briefly mentioned the presence of this species in the North-eastern Pacific Ocean.

There is, thus, some confusion as to the structure of the bracts of this species, and some uncertainty as to its systematic position. As complete specimens

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have been collected recently using the submersible Johnson-Sea-Link (JSL) I and II it is now possible to resolve the bract problem and to give a more detailed description of the species, *Frillagalma vityazi*.

RESULTS

Frillagalma vityazi Daniel, 1966

Diagnosis

Rigid stemmed physonect siphonophore with nectophores arranged biserially on the nectosome. Nectophores with pairs of apico-lateral, infra-lateral and vertical lateral ridges. The former divide close to the ostium. Two pairs of ridges arising from the apico-laterals that extend for a short distance toward the mid-line. In poorly preserved material, all ridges take on a frilled appearance. Course of lateral radial canals, which usually arise from the dorsal canal, relatively simple. Each cormidium on the siphosome bears a gastrozooid and tentacle, three enantiomorphic pairs of bracts, two dactylozooids without palpacles, and several gonophores of both sexes. One pair of bracts is distinctly different from the others. The tentilla on the tentacle are of unique design, with a rudimentary cnidoband and, usually, two superimposed terminal vesicles, the more distal of these bearing a finger-like side branch.

Description

Material examined. Nine of the 10 specimens collected by the JSL I and II submersibles. The station data for these are given in Table 1. In addition, over five thousand nectophores and nearly two thousand bracts have been identified from material in the Discovery Collections (Table 2).

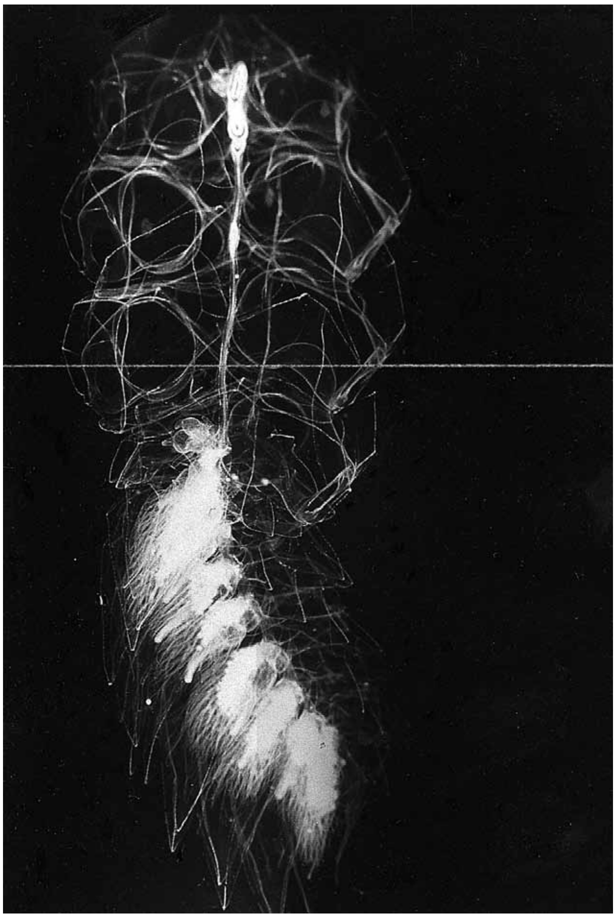

FIG. 1. – *Frillagalma vityazi*. Living specimen, approximately 3.5 cm in length, collected during JSL I Dive 2633. (Photograph: R. Gilmer)

TABLE 1. – Station data for specimens of *Frillagalma vityazi* collected by the submersibles Johnson-Sea-Link I and II.

	Dive No.	Position	Depth (m)
JSL I	2633	26° 14.8'N, 77° 43.7'W	892
	2640*	26° 01.3'N, 77° 30.4'W	830
	2648	26° 30.9'N, 78° 17.8'W	841
	2648	26° 30.9'N, 78° 17.8'W	833
	2649	26° 16.5'N, 77° 43.5'W	784
	2886	26° 31.8'N, 78° 05.6'W	810
	2886	26° 31.8'N, 78° 05.6'W	795
JSL II	1450	24° 38.8'N, 83° 45.3'W	696
	1680	25° 51.1'N, 77° 15.1'W	722
	1680	25° 51.1'N, 77° 15.1'W	683

* Not examined.

General structure (Fig. 1)

The animals are rigid stemmed, like *Agalma okeni*, and measure up to approximately 3.5-4 cm in length. The nectophores are arranged biserially on the nectosome, which usually is slightly shorter than the siphosome. There is no obvious pigmentation on any part of the animal.

Pneumatophore

In the JSL material the small pneumatophore is closely surrounded by the youngest nectophores (Fig. 1). However, in some of the Discovery material, it was found to be borne on a thin stolon, which when relaxed can measure up to 3 mm in length.

TABLE 2. – Latitudinal distribution of *Frillagalma vityazi* in the North Atlantic Ocean. (Discovery Collections material).

Latitudinal Range (°N)	Total n°. of nectophores	Total n°. of bracts	Mean depth (m)	N°. of samples in which it occurred	Total n°. of samples analysed
0-5	1357	364	781	24	44
5-10*	-	-	-	-	-
10-15	470	413	480	24	41
15-20	1166	528	714	29	67
20-25	7	0	539	3	30
25-30	375	195	905	28	48
30-35	1592	408	806	132	307
35-36.28	66	5	844	11	29

*No sampling within this range.

The pneumatophore measures up to 3.5 mm in length and 1.4 mm in diameter. There is no obvious apical pore. However, it is clearly distorted by the expansion of its gas contents as it was brought to the surface. This expansion ruptures the base of the pneumatophore and the gas passes down the gastrovascular canal. No pigmentation is visible, although there is a concentration of ectodermal cells at the apex.

Nectophore (Figs. 1-3)

The nectophores are arranged biserially down the nectosome (Fig. 1), and the maximum number counted was 12, plus a half developed one. The preserved nectophores measure up to c. 8.6 mm in length, 8.0 mm in width, and 7.2 mm in height. The central thrust block is minute in the developing nectophores (Fig. 2a), but in the mature ones it becomes broader (Fig. 3a), but does not extend axially to any great extent. There is no obvious mouth plate at the base of the ostium.

The most obvious difference between the nectophores of the present material and those originally described by Daniel (1966) is the appearance of the ridges. Daniel described them as being frilled or fluted (Fig. 2b, c) but, despite her claim that her material was well preserved, this clearly is a preservation artefact. This would account for why the present material is considerably larger than Daniel's, as clearly her specimens have undergone considerable shrinkage. The ridges on live and, indeed, preserved

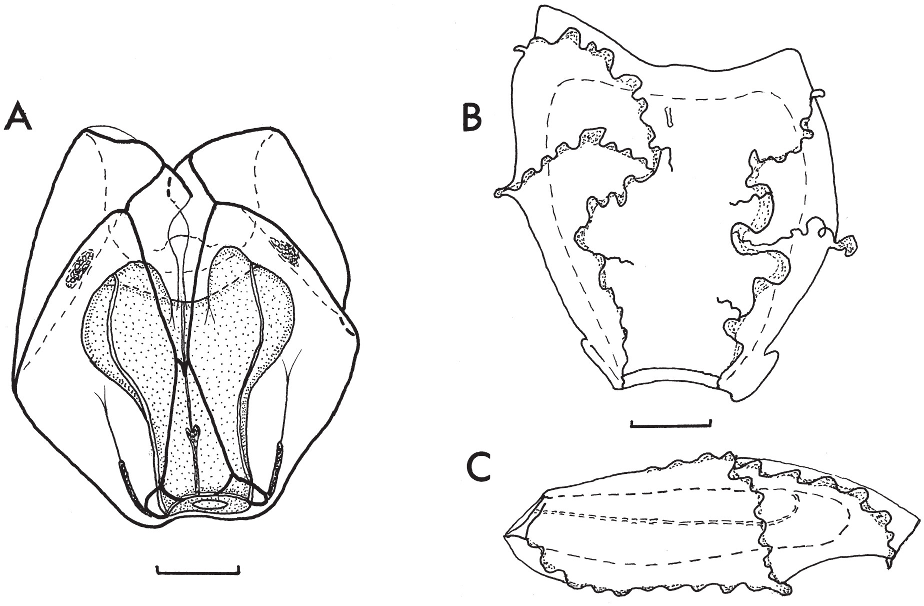

FIG. 2. – *Frillagalma vityazi*. A. Upper view of young nectophore collected during JSL II Dive 1680. (Scale bar = 1 mm); B., C. Upper and lateral views of type nectophore (redrawn from Daniel, 1966). (Scale bar = 0.1 mm).

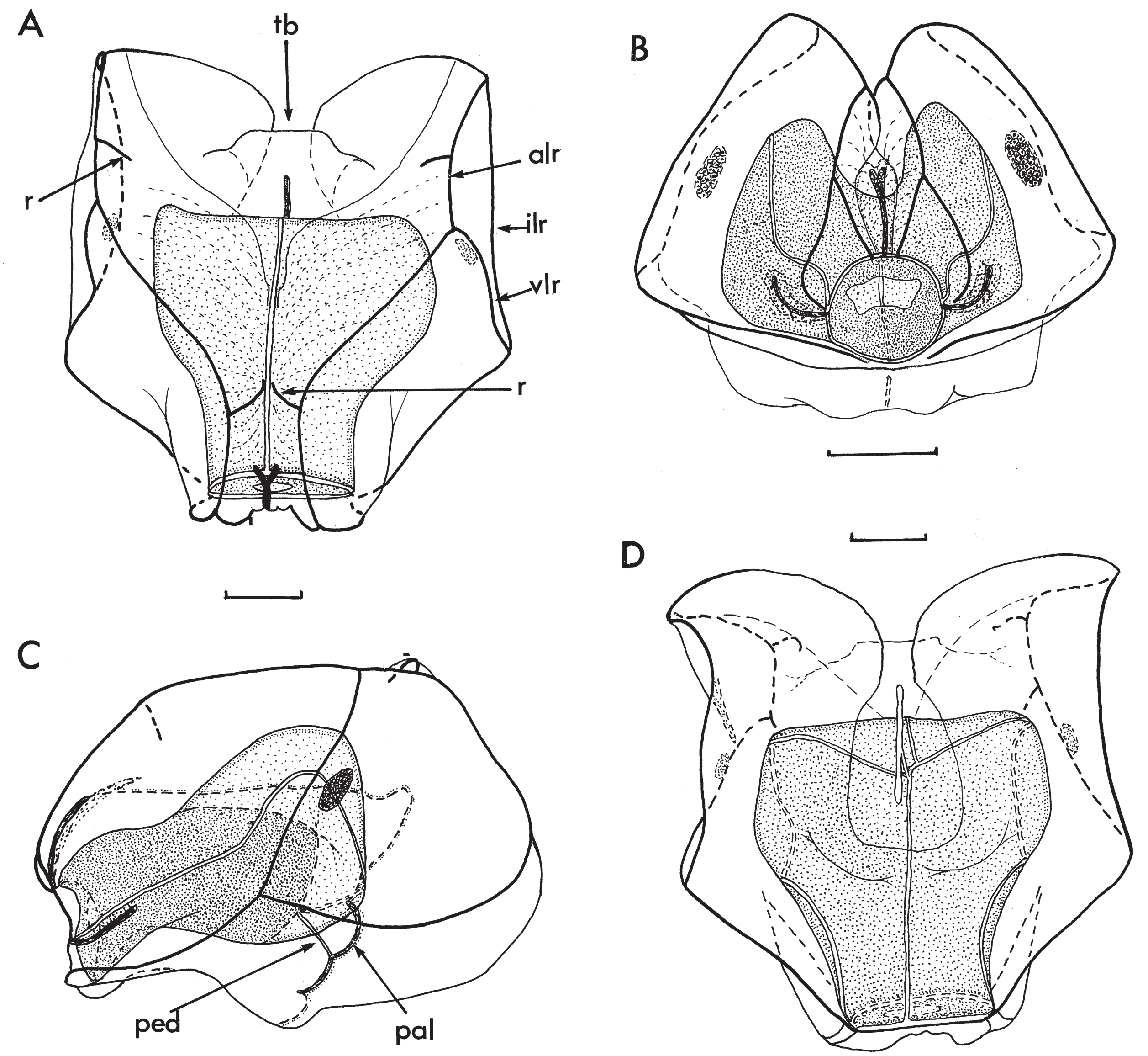

FIG. 3. – *Frillagalma vityazi*. A. Upper, B. ostial, C. lateral, and D. lower views of mature nectophore collected during JSL II Dive 1680. (Scale bar = 1 mm). alr: apico-lateral ridge, ilr: infra-lateral ridge, pal: pallial canal, ped: pedicular canal, r: ridgelet, tb: thrust block, vlr: vertical lateral ridge.

JSL material showed no frilling or fluting (Figs. 2a, 3). However, such frequently has been observed on the specimens in the Discovery Collections, although rarely to the extreme situation illustrated by Daniel (1966). Nonetheless, the highly characteristic arrangement of the ridges is the same in all material and there is no doubt that we are dealing with the same species.

There are three main pairs of ridges that, in accordance with previous descriptions of other physonects (Pugh and Harbison, 1986; Pugh and Youngbluth, 1988) are designated as apico-laterals, vertical laterals and infra-laterals (Fig. 3a). The apico-laterals run up along the adaxial margins of the axial wings and over onto and down the upper surface of the nectophore. For the most part these ridges form crests on relatively narrow processes. Thus, it is easy to envisage, with shrinkage during preservation, how they could become frilled. On the axial wings they extend basad to their junction with the infra-laterals, but there they are not so marked and eventually peter out. On the upper surface of the mature nectophores (Fig. 3a), they remain widely apart until the vertical lateral ridges branch off. They then curve in toward the mid-line, with the deep median groove between them being narrowest in the region where the more ostial pair of ridgelets arises. In the developing nectophores (Fig. 2a) the apico-laterals run much closer to the mid-line, and almost overlap at their closest approach, at the same level as on the mature nectophores. Toward the ostium, the apico-laterals divide (Fig. 3b). One pair of branches runs obliquely in toward the mid-line, terminating approximately above the ostial ring canal. The other pair runs basally and obliquely away from the mid-line, before curving back to end on the lateral sides of the ostium.

Two pairs of short ridges arise from the apico-laterals (Fig. 3a). These run down toward the mid-line on the sides of the deep median furrow. One pair arises at the point where the apico-laterals bend sharply from the axial plane onto the upper surface of the nectophore, that is at the apex of the axial wings. The other pair, as mentioned above, arise closer to the ostium where the apico-laterals make their closest approach toward the mid-line.

The vertical lateral ridges run from the apico-laterals, approximately on a level with the apex of the nectosac, obliquely down the sides of the nectophore (Fig. 3c) to join the infra-laterals. The sides of the nectophore are, thereby, divided into two main facets. The infra-laterals arise, from the apico-laterals, toward the bases of the axial wings and curve basally and then ostially to join with the vertical laterals. In this region the central part of the nectophore is thickened basally, so that the infra-laterals appear to be relatively high up on the sides (Fig. 3c). They then continue toward the ostium and peter out on its baso-lateral margins.

The pallial or mantle canal is long, running from a median pocket, close to the base of the nectophore, up to another pocket at the base of the thrust block (Figs. 3c, d). Frequently, the section of this canal that lies above where the pedicular canal arises is longer than illustrated, and it may be up to twice as long as the lower part. After staining, the lower nerve tract (Mackie, 1964) can clearly be seen extending beyond the basal end of the pallial canal and continuing down to the ostium. This tract has been previously noted by Pugh and Harbison (1986) in *Lychnagalma utricularia* (Claus, 1879) and by Pugh and Youngbluth (1988) in *Halistemma transliratum* Pugh and Youngbluth, 1988, but mistakenly referred to as a canal.

The nectosac stretches to about two-thirds the length of the nectophore, without any obvious median indentation at its apex (Fig. 3a). Nonetheless, its apico-lateral processes are quite pronounced (Fig. 3b, c). The pedicular canal, linking the canal system on the nectosac to the gastrovascular system of the stem, is quite long and ascends obliquely, in the mid-line, from the pallial canal to reach the nectosac just above its baso-ventral margin. On the nectosac it usually gives rise to only the dorsal and ventral canals (Fig. 3d). The ventral canal then runs directly to the ostial ring canal. Immediately above the junction with the pedicular canal, the dorsal canal first gives rise to either the right or left lateral canal. It then bends slightly to the left or right, respectively, and gives rise to the other lateral canal. Finally, it bends back to the mid line and continues over onto the upper side of the nectosac and directly to the ostial ring canal. Both branching arrangements for the lateral canals have been noted on nectophores from the same specimen. The course of the lateral radial canals is very simple (Fig. 3c). They run obliquely upwards and out to the lateral margins on the axial side of the nectosac, and then round onto the lateral sides. In the region where they pass under the vertical lateral ridge, they gradually curve down to the middle of the nectosac, and then continue directly to the ostial ring canal.

The whole of the surface of the nectophore is covered in tiny clumps of minute ectodermal cells that, for clarity, have been omitted from the illustrations. In addition there are five other aggregations of cells on the surface of the nectophores. The most prominent of these is a pair of “spots” lying axial to the vertical lateral ridge at about its mid height (Fig. 3c). These spots are composed of large, roughly hexagonal ectodermal cells, with large densely staining nuclei. These cells can generate bioluminescence (Steve Haddock, pers. comm.). The other three aggregations lie in the vicinity of the ostium and consist of narrow strips of small cells that stretch away from it (Fig. 3b). Two lie laterally, and usually are narrower but denser than the third. This third lies dorsally and it has a Yshaped appearance. All three lie on slightly swollen processes. These too can generate bioluminescence.

Siphosome

The siphosome (Fig. 1) is compact and rigid. It bears up to c. twenty cormidia. This compactness makes it difficult to study an individual cormidium in detail, but each is comprised of a gastrozooid with a branched tentacle; two dactylozooids without palpa-

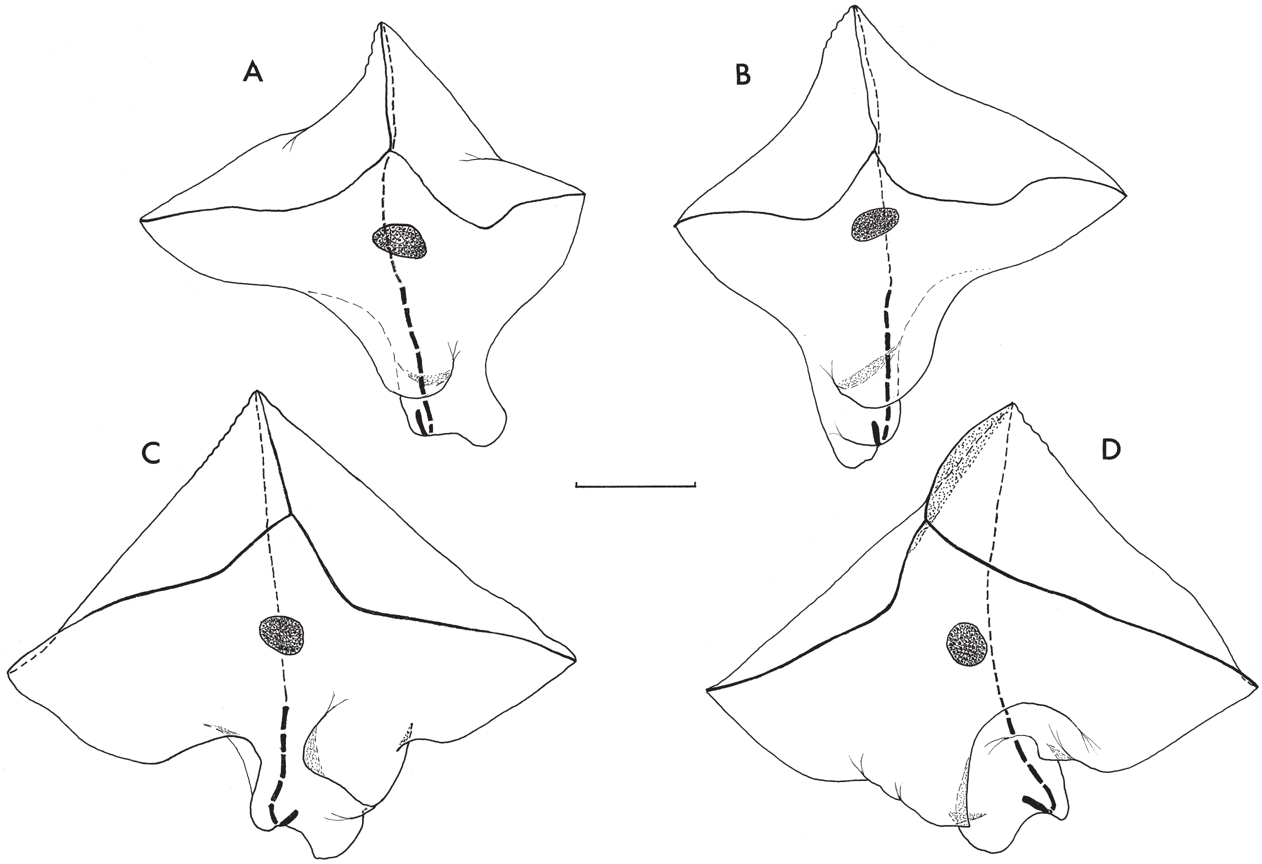

FIG. 4. – *Frillagalma vityazi*. Upper views of A. left-hand side and B. right-hand side dorsal bracts; C. left-hand side and D. right-hand side lateral bracts. (Scale bar = 1 mm).

cles; six bracts; and some gonophores of both sexes. No pigmentation was apparent on any structure.

Bracts (Figs. 4, 5)

Each cormidium bears six bracts that form three enantiomorphic pairs and are arranged in an alternating overlapping sequence around the entire stem. They are attached to a swollen part of the stem, at least in the preserved specimens, that lies immediately proximal to a gastrozooid. The two pairs of bracts that lie laterally and dorsally are very similar in shape, although they can be distinguished. They bear a superficial resemblance to the bract that Daniel (1985, fig.19d) ascribed to this species, but the later has four distal facets and more closely resembles the adult bracts of *Agalma okeni*. The third pair, which lies ventrally, is very distinctive and closely resembles the one figured by Totton (1965, fig. 61), under the heading *Forskalia cuneata*, and those described and illustrated by Stepanjants (1975, fig. 2) as belonging to *Frillagalma vityazi*.

The dorsal bracts (Fig. 4a, b) measure up to c. 3.7 mm in length by 3.9 mm in width. The lateral bracts (Fig. 4c, d) are slightly larger measuring up to c. 4.0 mm in length and 4.7 mm in width. Both types of bract are roughly rhomboidal in shape. Their dorsal sides are divided into three facets by two ridges, which run straight across from the lateral corners before curving distad and uniting, forming a single ridge that runs to the distal end of the bract. The surfaces of the two distal facets are concave. The bracteal canal runs the full length of the bract. Distally it is a thin canal that runs through the mesogloea, while proximally, in the region of attachment to the stem, it is thickened and runs along the ventral surface of the bract and ultimately curves up toward the dorsal surface. There is a large patch of ectodermal cells, which are known to bioluminesce, approximately in the middle of the dorsal surface.

The main difference between these two types of bract is that the sides of the lateral bracts are roughly equal in size, whereas one side is wider than the other on the dorsal ones. This wider side extends laterally and overlies the corresponding distal facet of the lateral bract next to it. The surface of the proximal half of this wider side is distinctly hollowed and this gives rise to a prominent dorso-lateral, flap-like protuberance situated well above the proximal end of the bract. On the lateral bracts, the proximal part of the corresponding side is less emarginated so that the dorso-lateral protuberance is more rounded and swollen, and is situated close to or at the proximal end of the bract. The shape of both dorsal and lateral bracts can be quite variable, particularly in their proximal regions.

Mature ventral bracts (Fig. 5) measure up to c. 8 mm in length and 3.6 mm in height. They are flattened laterally so that the lateral wings enclose a long, deep, but narrow ventral cavity, which extends to the proximal end of the bract.

These bracts can undergo considerable distortion, particularly in net collected material, so that they often appear kinked (cf. Totton, 1965, fig. 61). In the distal half of the bract there is a median dorsal ridge (Fig. 5a) whose edge is more or less serrated. At about the mid-height of the bract this ridge divides and, together with a cross ridge, delimits a rounded, roughly triangular dorsal facet. In many bracts the cross ridge may be indistinct. The dorsal facet (Fig. 5a) partially overhangs the lateral surface that abuts with its neighbouring lateral bract. On the other side, the branch of the median dorsal ridge curves round and joins a distinctly toothed lateral longitudinal ridge that runs down to rejoin the median ridge at the distal tip of the bract (Fig. 5a). The lateral sides of the bract are slightly asymmetrical. On the side that abuts with the other ventral bract (Fig. 5c, d), the ventro-lateral margin merges with the lateral toothed ridge a sort distance above the distal tip of the bract; while on the other side it extends to the distal tip (Fig. 5b, e). On both sides there is a distinct tooth, occasionally more than one, on the ventro-lateral margin at about one third the length of the bract from the distal tip (Fig. 5a, d).

The bracteal canal arises on the outer side of the lateral facet that abuts with the other ventral bract, at a short distance from the proximal end of the bract. It quickly runs over onto the inner surface of that facet and continues obliquely up the lateral wall of the ventral cavity to reach the dorsal wall of the latter. It then penetrates into the mesogloea, continuing its obliquely dorsad course, before bending through 90° and continuing down to the distal tip of the bract.

Gastrozooid and tentacle (Figs. 6, 7)

Typically the gastrozooid can be divided into three parts. Proximally there is a short, saddle-shaped basigaster covered in large ectodermal cells and to which the tentacle is attached. The inflated

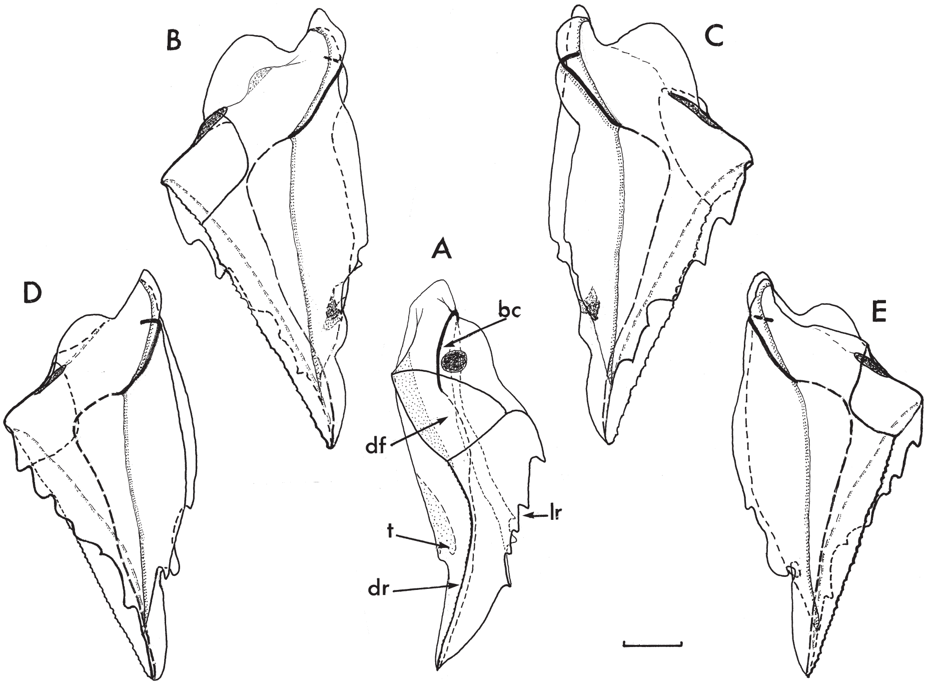

FIG. 5. – *Frillagalma vityazi*. Ventral bracts. A. dorsal view; B., C. lateral views of left-hand side bract; D., E. lateral views of right-hand side bract. (Scale bar = 1 mm). bc: bracteal canal, lr: longitudinal ridge, dr: dorsal ridge, t: tooth, df: dorsal facet.

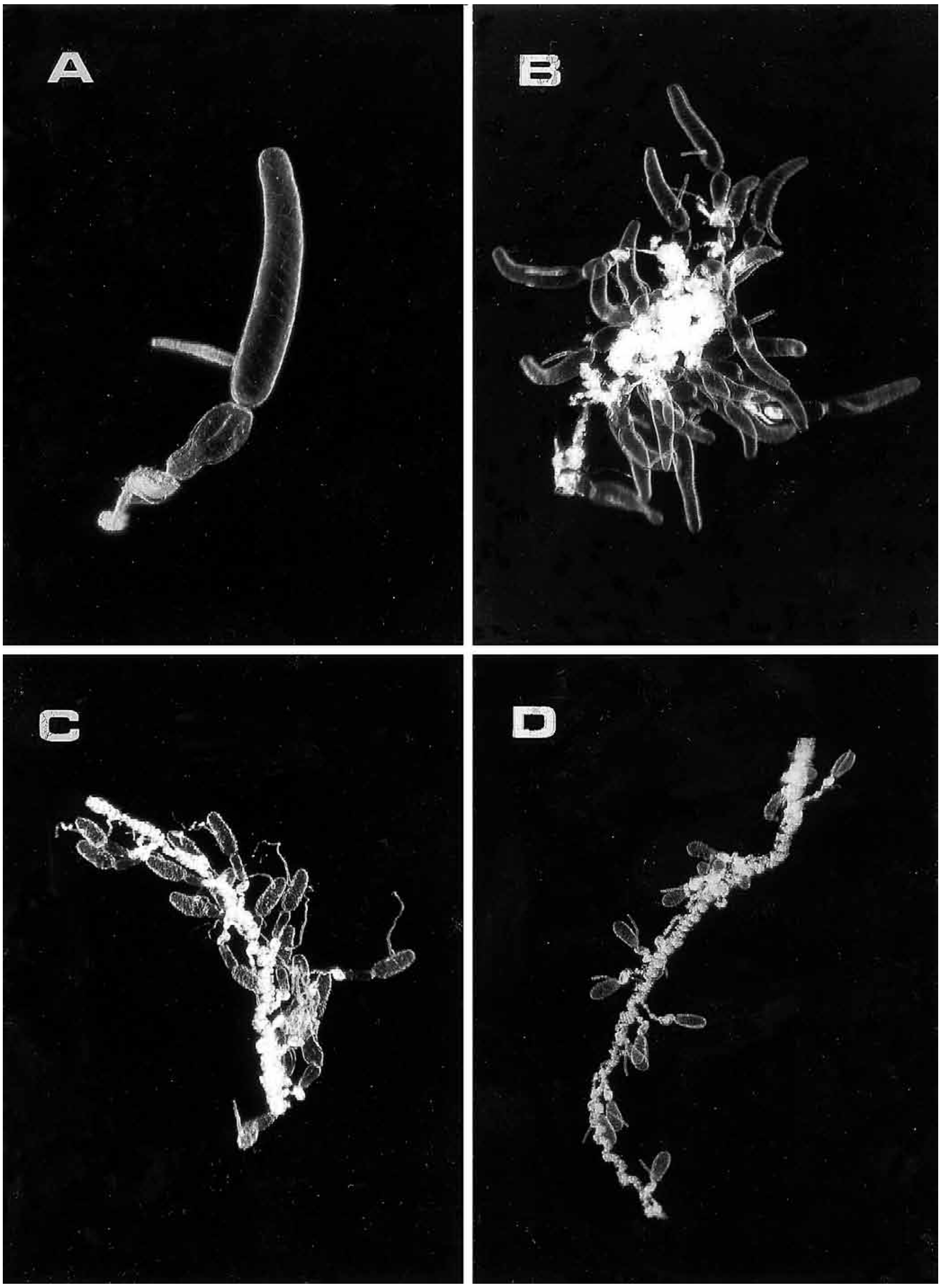

FIG. 6. – *Frillagalma vityazi*. Tentilla from A., B. a JSL Dive 1680 specimen; C. the JSL II Dive 1450 specimen; and D. another specimen from JSL Dive 1680. (For sizes see text).

stomach region is usually fairly spherical but can be elongated. There are obvious signs of hepatic stripes. Distally there is a more or less extended proboscis, which can stretch out to a length greater than that of the stomach region, with a terminal mouth. On the main stem, distal to each gastrozooid, there is a short internode where nothing is attached to the stem.

The tentacle bears numerous tentilla that are of a very characteristic and peculiar design (Fig. 6). The proximal part of the tentillum (Fig. 7) consists of a highly coiled pedicel that presumably could, when relaxed in life, extend for a considerably distance. Beyond this there is a relatively long section that appears to consist almost entirely of a folded up, in a zigzag fashion, elastic strand, with the narrow gas-

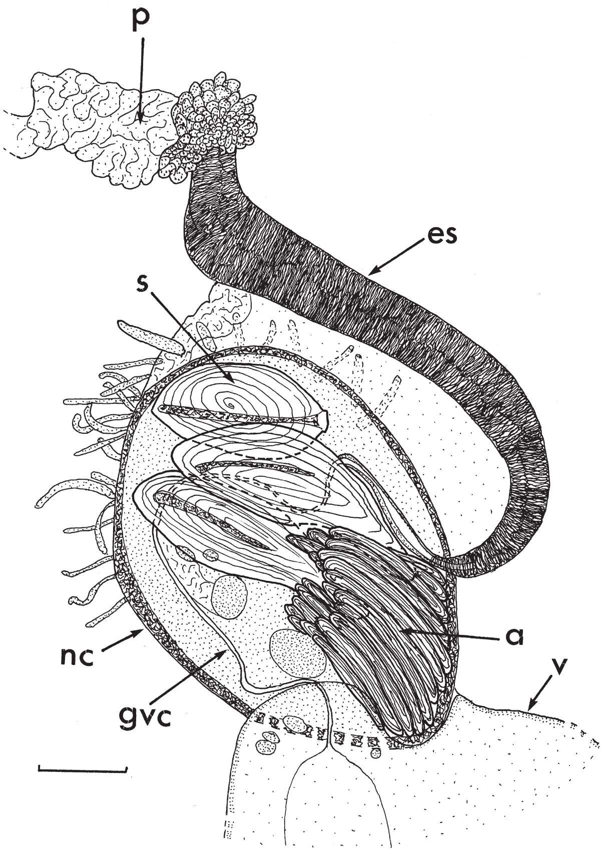

FIG. 7. – *Frillagalma vityazi*. Detail of the proximal region of a tentillum, showing the folded elastic strand and the nematocyst capsule. Scale bar = 50 μm. a: anisorhiza, el: elastic strand, gvc: gastro-vascular canal, nc: nematocyst capsule, p: pedicel, s: stenotele, v: vesicle.

trovascular canal running through the middle of it. This elastic strand can be made to unfold if pressure is applied to it. Most of this section of the tentillum is loosely attached to a capsule containing nematocysts. The elastic strand appears to end as the capsule is reached, but the gastrovascular canal can be seen to loop through it and connect with the vesicle beyond. The nematocyst capsule (Fig. 7) is by no means organised into a cnidoband that, as a coiled structure, is so characteristic of many agalmatid species. It also contains relatively few nematocysts. In its proximal half are found just three large nematocysts. The most proximal of these is an ovoid structure, measuring c. 90 × 50 μm, with a distinct cap. The other two are more elongate, measuring c. 150 × 50 μm, with no distinctive cap. Despite these differences, all three nematocysts appear to be stenoteles. In the distal half of the capsule, on one side only, is a bank of c. 30-35 anisorhizas measuring c. 70 × 7 μm. The remainder of the capsule is filled with relatively amorphous material. A band of hair-like, solid protuberances (?cnidocils) is attached to one side of the proximal part of the capsule. The function of these is not known.

Distal to the nematocyst capsule are, usually, two fluid-filled vesicles (Fig. 6) separated by a narrow constriction. In most of the JSL specimens examined, the proximal vesicle measures about 0.55 × 0.25 mm; while the distal one is typically about 1.1 × 0.25 mm (Fig. 6a, b). The gastrovascular cavity does not occupy the whole of the proximal vesicle, but at first the canal expands into a wide funnel-shaped structure, surrounded by mesogloea. A superficial annular constriction then usually marks the point at which it expands to fill the whole. The gastrovascular cavity fills the whole of the distal vesicle. Both are sparsely, and randomly, covered in rounded, amorphous, patches that protrude from their surface. They are definitely not nematocysts, and their function is unknown. An extraordinary feature of the distal vesicle is that on one side, usually toward its base, there is an apparently solid, finger-like protuberance. This side branch often appears annulated, and also bears rounded or conical, amorphous protuberances from its surface. It is usually fairly stiff and of variable length, up to c. 0.4 mm.

Amongst the JSL specimens there are two exceptions to this basic arrangement of the terminal vesicles of the tentillum. In one, from JSL II Dive 1450, the vast majority of the tentilla have smaller vesicles; the proximal one being c. 0.4 × 0.17 mm and the distal one c. 0.7 × 0.26 mm (Fig. 6c). In addition, the side branch from the distal vesicle arises at about the mid-height of the latter and, usually, is greatly extended and less rigid than the previously described ones. This branch can reach lengths in excess of 1.4 mm. The other exception was found on one of the specimens from JSL II Dive 1680 (Fig. 6d) where only a single, relatively small (c. 0.34 × 0.17 mm) vesicle was present. A side branch was present close to its base, thus resembling the distal vesicle of the other forms. The smallness of the tentilla suggests that they are immature, and have yet to develop the proximal vesicle. However, all the cormidia bore tentilla of this type, and only an occasional more usual tentillum was noted.

Dactylozooid (Fig. 8a)

There are two large dactylozooids per cormidium that do not have a palpacle attached at their bases. They are attached proximally on either side of the

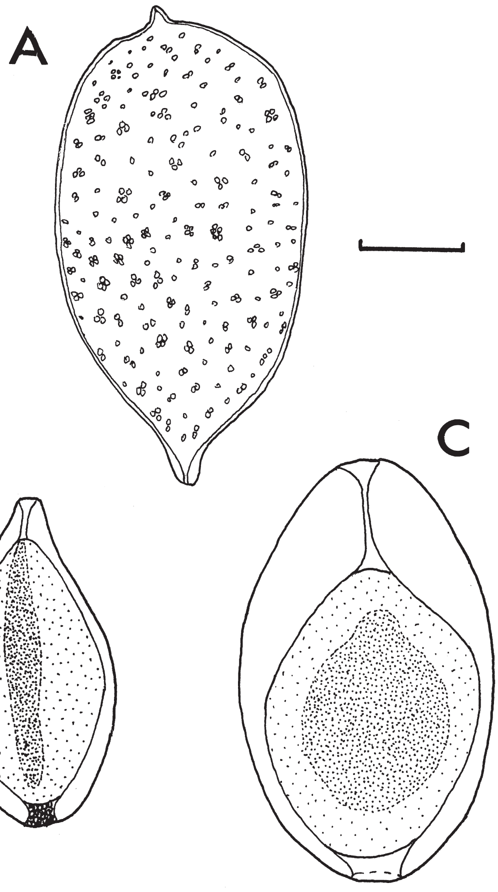

FIG. 8. – *Frillagalma vityazi*. A. Dactylozooid; B. male and C. female gonophores. (Scale bar = 0.5 mm).

swollen part of the stem where the bracts are inserted. Each is a simple inflated, thin-walled bag, borne on a short peduncle and bearing a short, more or less pronounced, terminal proboscis that opens via a pore. They measure up to 2.5 mm in length and c. 1 mm in width. The endoderm often has a milky-white appearance, while the external surface is covered in an irregular pattern of groups of from one to four large ectodermal cells. These cells are of variable size and shape, although generally rounded. These dactylozooids resemble the cystons described by Haeckel (1888), although he found only one such structure per cormidium.

Gonophore (Fig. 8b, c)

The gonophores are attached to the stem between the two dactylozooids, at the proximal end of the stem swelling. Both sexes are present in each cormidium, and it appears that each is associated with one of the dactylozooids. It also appears that the sexes alternate from side to side in successive cormidia, although the crowding of the siphosome makes this difficult to verify absolutely. Gonophores at all stages of maturity are present on each cormidium.

The mature male gonophore (Fig. 8b) is borne on a short pedicle and measures c. 1.8 mm in length and 0.8 mm in width with a prominent spadix. The mature female gonophore (Fig. 8c) measures up to c. 2.0 mm in length and 1.25 mm in width. In the developing female gonophore the egg occupies most of the volume, but as it reaches maturity the mesogloea at the proximal end of the gonophore thickens.

Bioluminescence

As noted above there are distinctive patches of ectodermal cells on both the nectophores and bracts that have been found to be sites of bioluminescence (S. Haddock, pers. comm.). One interesting feature was that this bioluminescence could be either blue or green, and that, in some specimens, the nectophores might produce bioluminescence of one colour, while the bracts produced the other. It is to be hoped that this phenomenon can be investigated further in the future.

Distribution

Almost all of the previous records for *Frillagalma vityazi* come from two main areas, the Indian and North Atlantic Oceans. However, it is said to be common off British Columbia (NE Pacific) (Arai *et al.*, 1993), although no details are given. The records of Daniel (see Daniel, 1985) are widely distributed throughout the Indian Ocean, from higher latitudes in the Arabian Sea (c. 25°N, 68°E), and the Bay of Bengal, to off the west coast of Australia (c. 32°S, 110°E). Most of her c. 65 nectophores appear to have collected by nets fished over the 0-200 m depth range. However, as no nets seem to have been fished at deeper depths, these data do not give a clear indication of its overall depth distribution. This is borne out by the fact that Stepanjants' (1975) specimens, from the Puerto Rican Basin (North Atlantic Ocean) and the Caribbean Sea, were found in the 2000-1000 and 1000-500 m depth ranges, respectively.

The most detailed assessment of the depth distribution of *Frillagalma vityazi* (Physonect "C") was given by Pugh (1974) from samples taken in the vicinity of the Canary Islands (c. 28°N, 14°W). He found his 65 nectophores and 63 bracts in 14 hauls at depths ranging from 660 to 950 m, with the bulk of them appearing in the 750-800 m depth range. In addition to this material, there are records for a further 5033 nectophores and 1913 bracts found in 252 samples collected in the North Atlantic Ocean (Table 2) (Pugh, unpublished data). These data show that *F. vityazi* occurs only in warmer waters, ranging from the equator to c. 36°N. Although greatest numbers of nectophores were found in the samples collected between 32 and 36°N, if the fishing effort at the various latitudes is taken into account, then *F. vityazi* is most abundant at the equator.

These data also indicate that *Frillagalma vityazi* has been found in all depth horizons from the surface to 2000 m, together with a single record from the 3330-3910 m depth range. Nonetheless, it was mainly found between 600 and 1500 m, with a mean depth, for the nectophores, of 753 m. There appears to be some latitudinal change in the depth distribution with the shallowest mean depth (480 m) being found between 10 and 15°N, and the deepest (905 m) between 25 and 30°N. These latitudinal depth changes appear to related to the prevailing hydrographical conditions (see Fasham and Angel, 1975; Mackie *et al.*, 1987). *F. vityazi* appears, for the most part, to be confined to deeper South Atlantic Central Water (mixed with Antarctic Intermediate Water) and the boundary between this water mass and North Atlantic Central Water, to the north, may be acting as a barrier to its distribution. If this is the case then one would expect this species would be common in the South Atlantic. In actuality, the distribution of siphonophores in the warmer waters of that region is little known, but specimens of *F. vityazi* have recently been found in the vicinity of 38-39°S, 18-19°E (Pugh, unpublished data).

The depths of collection for the ten specimens collected by submersible ranged from 683 to 892 m (Table 1) and, thus, are very consistent with the mean depths noted above for the net collected material. All but one of these specimens was collected in the region of the Bahamas; the one (JSL II Dive 1450) coming from the region of the Dry Tortugas in the Gulf of Mexico.

DISCUSSION

Based on the structure of the nectophores alone, Daniel (1966) erected a new genus, *Frillagalma*, for her new species, *F. vityazi*, and included it within the family Agalmatidae. Stepanjants (1975) also noted that the frilled ridges on the nectophores instantly distinguished this species from any other known physonect. In addition, she correctly associated some peculiar bracts with the species. She also commented that, although Daniel (1966) had placed *F. vityazi* in the family Agalmatidae, the bracts that she had found were more reminiscent of those found in the family Forskaliidae. Thus, she was uncertain as to the exact taxonomic status of the species.

Despite the fact that the living nectophores do not have frilled ridges, *Frillagalma vityazi* does show several morphological characters that, in combination, are highly distinctive and are quite sufficient to justify Daniel's (1966) establishment of a separate genus. In particular, these are the structure of the nectophore and the course of the radial canals on its nectosac; the different types of bract; the presence of only a pair of dactylozooids in each cormidium; and the structure of the tentillum with its nematocyst capsule (? rudimentary cnidoband). The resemblance of the ventral bracts of *F. vityazi* to the "knee-shaped" bracts of *Forskalia* species is striking, as Stepanjants (1975) noted. This similarity also led Totton (1965) tentatively to ascribe some loose bracts, that are now ascribed to *F. vityazi*, to a little known species *Forskalia cuneata* Chun, 1888. However, with the present knowledge of the morphology of *F. vityazi*, it is apparent that this is where the similarity ends. In *Forskalia* species the apico-basally flattened nectophores are arranged multiserially; palpons are present; and the tentilla have a distinctly coiled cnidoband. There are three basic types of bract, but they are arranged quite differently. In each cormidium, a pair of enantiomorphic leaf-like bracts are attached directly to the stem. All the others are attached to the elongated peduncle of the gastrozooid. At the base of this peduncle there is a pair of bolster-shaped bracts, and distal to these is a succession, up to ten, of knee-shaped ones.

Does, then, *Frillagalma vityazi* belong in the family Agalmatidae? The main problem here is that the Agalmatidae is probably a composite family containing those species that do not have the distinctive characters of the other extant physonect families. There is no doubt that its taxonomy needs revising. As Daniel (1966) pointed out, there is a clear similarity between the pattern of ridges on the nectophores of *F. vityazi* and those of species belonging to the genera *Agalma*, *Halistemma* and

Nanomia with, in addition, the genus *Lychnagalma*. However, this does not apply to the course of the lateral radial canals on the nectosac. Further, the species of these four genera bear palpons with palpacles, and have very different tentilla. In combination, the characteristic features of these four genera set them apart from all other genera presently included in the family Agalmatidae.

The structure of the tentillum is probably one of the most important characters in establishing groupings within the Agalmatidae. The tentilla of the aforementioned four genera are involucrate and possess a well developed, tightly coiled cnidoband. There is, however, one similarity with *Frillagalma vityazi* in that the tentilla of *Agalma* and *Lychnagalma* species also have a terminal vesicle, with two or eight, respectively, lateral filaments arising from their bases. Purcell (1980) suggested that in the case of *Agalma* species aggressive mimicry was being used to enhance prey capture. When "fishing" the two processes at the base of the terminal vesicle of the tentillum are spread out laterally and, in combination with the red-coloured cnidoband, take on the superficial appearance of a copepod. In addition, the pedicle of each tentillum is periodically contracted, mimicking the darting movement of a copepod. Similarly, Pugh and Harbison (1986) suggested that the tentillum of *L. utricularia* (Claus, 1879) might resemble a small jellyfish. The terminal vesicle floats upwards and the eight lateral processes are spread out to resemble tentacles. It is possible that the structure of the tentillum of *F. vityazi* is another instance of aggressive mimicry, but it is unclear as to exactly what is being mimicked.

With reference to the other genera within the Agalmatidae, *Marrus* appears to have more in common with *Bargmannia*, which Totton (1965) placed in the family Pyrostephidae. However, in the species of both genera, excluding *M. orthocannoides* Totton, 1954, which most probably does not belong to the genus, the lateral radial canals on the nectosac of the nectophores arise from the dorsal canal and, in the two *Marrus,* at a considerable distance from the point of insertion of the pedicular canal. Nonetheless this is not an uncommon feature amongst physonects and can also been seen in species of the families Apolemiidae and Pyrostephidae, and, in addition to *Frillagalma vityazi*, in other agalmatid species, such as *Halistemma transliratum*. Thus such an arrangement of the radial canals does no imply any close relationship.

Of the three remaining agalmatid genera, ignoring the poorly known ones recently described by Margulis (1976, 1982a,b), *Erenna* and *Moseria* each has very distinctive features. This leaves *Cordagalma* as the only other comparable genus within the family. Based on the course of the radial canals alone, Daniel (1966) noted a similarity between *Frillagalma vityazi* and *C. cordiforme* Totton, 1932. At that time both of these species were known only by their nectophores. However, *C. cordiforme* has ridgeless heart-shaped nectophores that are very different from those of *F. vityazi*. As Stepanjants (1977) points out, it is the basal part of the nectophore of *C. cordiforme* that is enlarged, in contrast to the apical part in other agalmatids, including *F. vityazi*. Despite these differences, later information makes a comparison between the two species of interest. Carré (1968) gave a full description of *C. cordiforme* based on several complete specimens. He found that each cormidium on the long, nonrigid siphosome consisted of a gastrozooid, with its tentacle; a single dactylozooid devoid of a palpacle and comparable with the cystons described by Haeckel (1888); several gonophores of both sexes; and six to eight similar bracts attached at the bases of the other organs. The tentilla on the tentacles were of peculiar design and possessed only a rudimentary cnidoband. Carré (1968) likened them to the larval tentilla of certain other physonect siphonophores. Thus in the possession of larval-type tentilla and dactylozooids without palpacles, although the number per cormidium differs, there are similarities between the two species.

A second species of *Cordagalma* recently has been described, *C. tottoni* Margulis, 1993. The lateral radial canals on the nectosac of the typically heart-shaped nectophores of this species apparently arise from the ventral canal, below the point of insertion of the pedicular canal. This is an unusual, if not unique, situation amongst the physonect siphonophores, for they usually either arise at the point of insertion of the pedicular canal or above it, from the dorsal canal, as noted above. Fragments of stem, also found in the same sample and attributed to the same species, suggested that true palpons, with, albeit short, palpacles, were present; although not all the dactylozooids possessed this structure. This is in contrast to the situation in *C. cordiforme* as is the structure of the tentillum which is said to have a cnidoband. Thus the aforementioned similarities between *Frillagalma vityazi* and *C. cordiforme* do not exist for this species.

In conclusion it appears that, on the basis of the tentilla, with their rudimentary cnidobands, and the presence of only palpacle-less dactylozooids on each cormidium, one might consider *Frillagalma vityazi* and *Cordagalma cordiforme* to be close relatives. However, there are also striking differences between them, particularly in the structure of the nectophore, so that there is no reason to consider them congeneric. At present it appears that *F. vityazi* should still be considered as an agalmatid siphonophore although, as mentioned above, the family Agalmatidae is in need of revision.

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