

THREE NEW SPECIES OF PRAYINE SIPHONOPHORE (CALYCOPHORAE, PRAYIDAE) COLLECTED BY A SUBMERSIBLE, WITH NOTES ON RELATED SPECIES

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ABSTRACT

Three new species of siphonophore belonging to the calycophoran sub-family Prayinae are described. The individual specimens of these were collected, in the Bahamas region, by the submersible DSRV JOHNSON-SEA-LINK II, using her sophisticated sampling devices. One of the new species has been ascribed to the genus *Prayola* Carré, 1969. The other two show characters that are intermediate between those found in existing prayine genera and have necessitated the erection of two new genera, *Craseoa* and *Mistoprayina*, to encompass them. The morphological characters that are of taxonomic significance in prayine siphonophores are reviewed, and a reclassification of one existing species, *Rosacea villafrancae* Carré, 1969, is proposed.

Although many species of siphonophores can be collected adequately by net sampling systems, it has become apparent in recent years that there are a large, and ever increasing, number that are not. For instance, SCUBA diving techniques have shown that many of the apparently rare siphonophore species, described in the last century but not seen since, actually are quite common. This apparent paradox is explained easily by the fact that the animals are extremely fragile and, as they would be torn to shreds, do not appear in net collections.

Submersibles, with their sophisticated sampling devices, have made it possible to extend these in situ studies to greater depths, and with significant effect. One important feature of these in situ sampling methods is that the animals are collected individually. In the case of siphonophores, whose stems can stretch out to many meters in length, it is not always possible to capture the whole animal. However, even if only part of the animal is collected and even if, subsequently, this becomes dissociated into its component pieces, one knows unequivocally that all these pieces belong to a single specimen.

During a series of dives (October/November 1984) in the vicinity of the Bahamas, over 130 individual specimens of siphonophores were collected using the submersible DSRV JOHNSON-SEA-LINK II. A full list of these dives and a brief description of the sampling devices used is given in Pugh and Harbison (1986). These devices consist of slurp guns, whereby even 10+ m-long siphonophores can be gently sucked into individual containers, and detritus samplers, into which the required animal is brought by delicate maneuvering of the submersible. More than 30 species of siphonophores were identified from these collections and about half of these were undescribed. Amongst the latter were three, belonging to the calycophoran sub-family Prayinae, which are described here. One species clearly is attributable to the genus *Prayola* Carré, 1969, while the other two show characters that are intermediate between those found in existing genera and have necessitated the erection of two new genera, *Craseoa* and *Mistoprayina*, to encompass them.

CLASSIFICATION

Sub-order Calycophorae Leuckart, 1854

Family Prayidae Kölliker, 1853

Sub-family Prayinae Chun, 1897

Craseoa new genus

Diagnosis.—Prayine siphonophores with an apposed pair of cylindrical nectophores. The somatocyst is simple, without either an ascending or descending branch. The lateral radial canals on the small nectosac are S-shaped. The bracts are rounded and divided into two almost equal lobes by a deep fissure. Six bracteal canals are present. The gonophores are asymmetric in shape with wing-like expansions. The sub-umbrella cavity is relatively small, occupying only part of the lower half of the gonophore. The arrangement of the two mantle canals is slightly asymmetric. Special, asexual nectophores are absent.

Type Species.—*C. lathetica* new species described herein.

Etymology.—The generic name *Craseoa* can be derived from the Greek κρασις, κρασεως meaning a blending, referring to the mixture of prayine characters found in the specimens. It is also an anagram of *Rosacea*.

Remarks.—The outward appearance of the nectophores of *C. lathetica*, in that they are cylindrical and possess relatively small nectosacs, is similar to that in the species of two other prayine genera, *Rosacea* and *Desmophyes*. However, the absence of both an ascending and descending branch to the simple somatocyst, together with the S-shaped course of the lateral radial canals on the nectosac, are important morphological characters (see Table 1) and prevent the inclusion of *C. lathetica* in either of these genera. Nonetheless, these characters apply also to the species of the genus *Prayola*, but the shape of the nectophore, and particularly

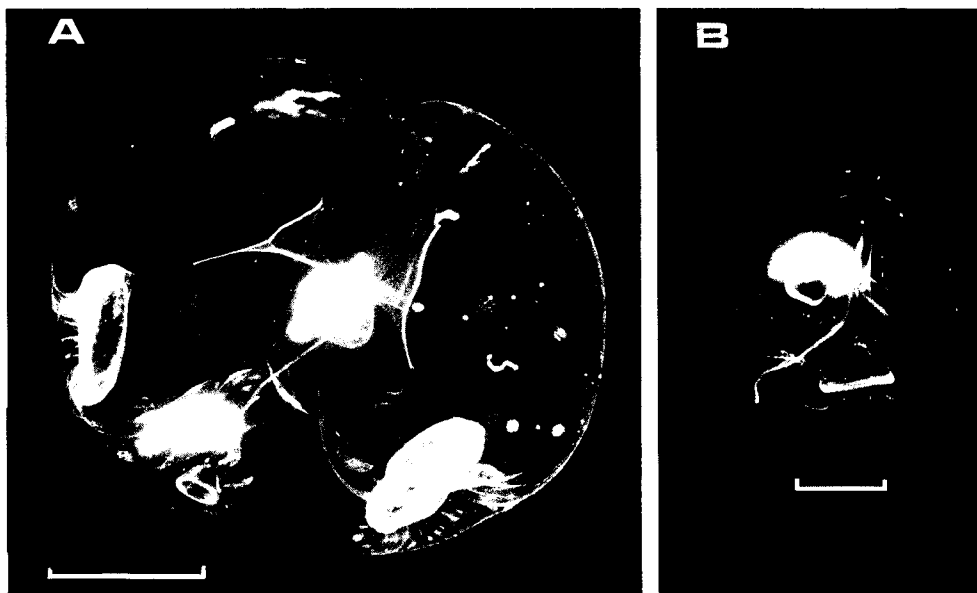


Figure 1. *Craseoa lathetica*. Photographs of the living holotype specimen. A. Nectosome. Scale = 5 mm; B a cormidial group. Scale = 2 mm. Photos by R. W. Gilmer.

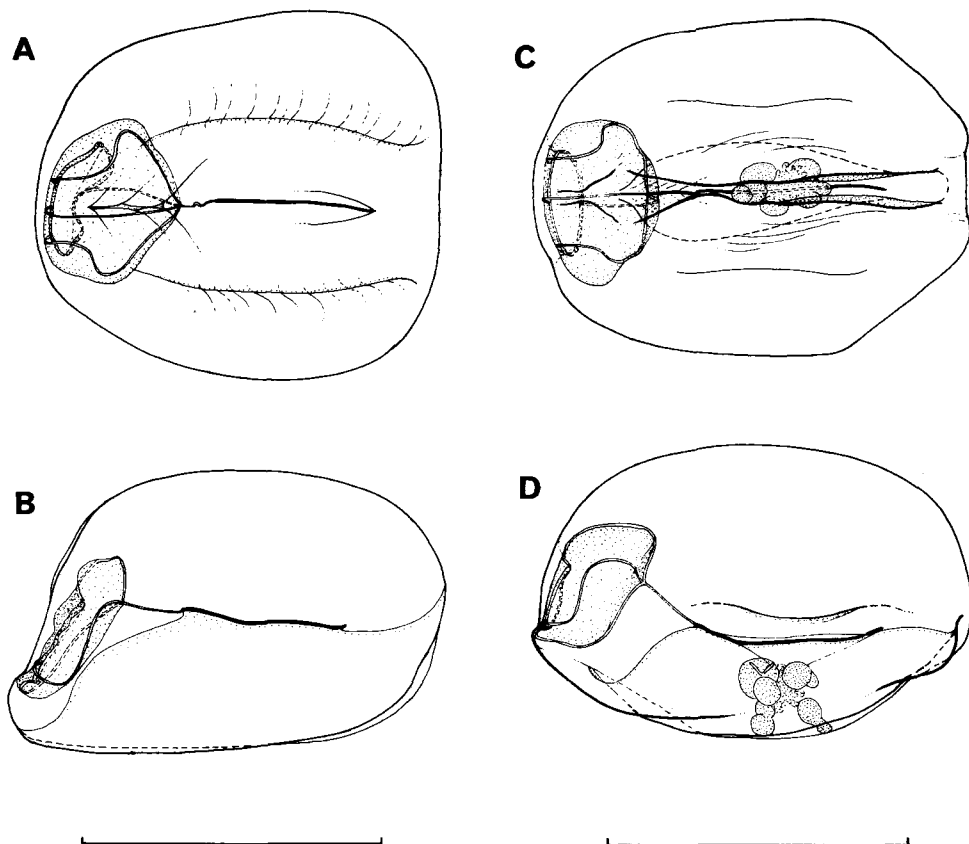


Figure 2. Nectophores of *Craseoa lathetica* (JSL 996 specimen): A. Ventral and B. Lateral views of the N_1 nectophore. C. Ventral and D. Lateral views of the N_2 nectophore. Scale = 1 cm.

the nectosac, is very different and *Prayola* species are the only prayine siphonophores to have only five canals in their bracts, the dorsal one being absent. The stem groups of *C. lathetica* differ from all other prayine species in that the gonophores have a relatively small sub-umbrella cavity. All these characters together necessitate the establishment of a new genus, *Craseoa*; to include the new species which is described below.

Craseoa lathetica new species

Figures 1–5

Material Examined.—Three specimens collected in the region of the Bahamas by the submersible JOHNSON-SEA-LINK II in 1984.

Holotype.—Specimen collected at a depth of 607 m using a detritus sampler during JSL dive 996. (31 October 1984; 25°22.5'N, 77°54.9'W). Preserved in 5% formalin. Presented to the British Museum (Natural History) and entered as Regd. No. 1986-6-1-1.

Paratypes.—Individual specimens collected during JSL dives 959 and 998. JSL dive 959: 17 October 1984; 26°25.6'N, 78°44.5'W; Detritus sampler; Depth of collection: 715 m. JSL dive 998: 31 October 1984; 25°22.0'N, 77°51.6'W; Slurp gun; Depth of collection: 659 m; Temperature: 10.3°C. These two specimens are housed in the biological collections of the Institute of Oceanographic Sciences, Wormley.

Diagnosis.—A monotypic genus and species of prayine siphonophore, whose principal characters have been given in the diagnosis of the genus. In this species the

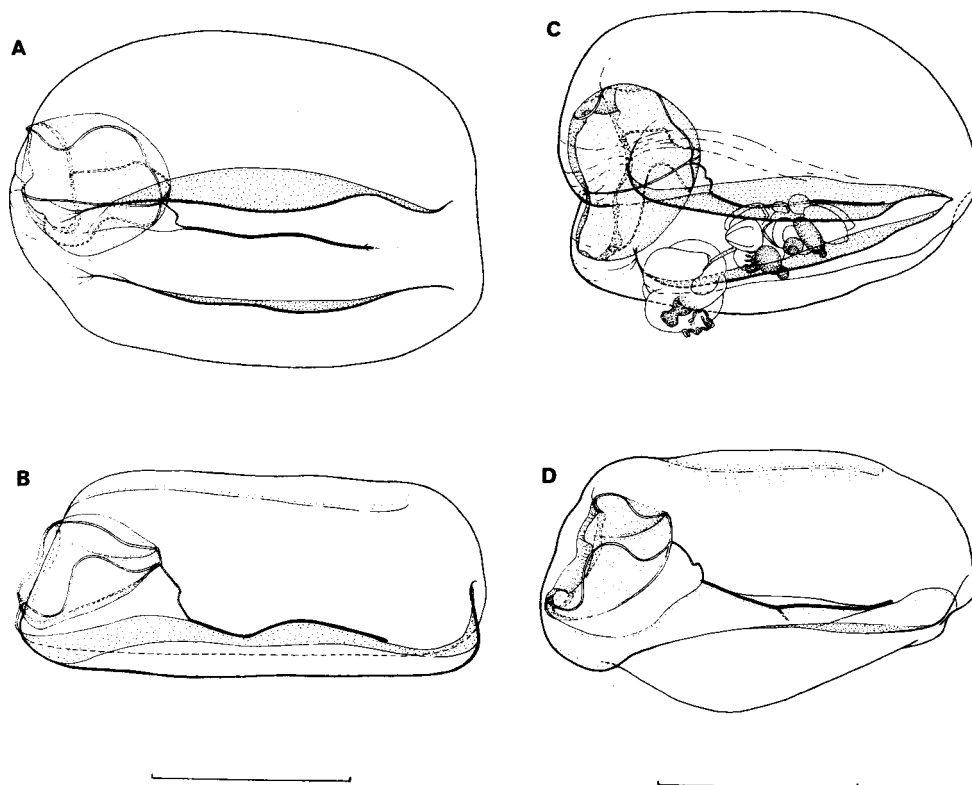


Figure 3. Nectophores of *Craseoa lathetica* (JSL 959 specimen): A. Ventro-lateral and B. Lateral views of N_1 nectophore. C. Ventro-lateral and D. Lateral views of N_2 nectophore. Scale = 1 cm.

dorsal bracteal canal arises from the distal end of the right (posterior) longitudinal canal.

Description. — NECTOPHORES (Figs. 1A, 2, 3). Each specimen possesses two apposed nectophores (N_1 and N_2) (Fig. 1A). The nectophores are rounded, cylindrical and bear no pronounced ridges or visible pigmentation. The N_1 nectophores vary in size from 14.5 mm in length by 12.5 mm in width (JSL 996 specimen) to 23.5 by 19.5 mm (JSL 959); the N_2 nectophore from 14.5 \times 11 mm (JSL 996) to 21.5 \times 18 mm (JSL 959).

The hydroecium of the N_1 nectophore is a broad gutter extending along the entire length of the ventral surface, although appearing only as a very slight indentation at the apical and basal ends (Figs. 2A, 3A). In the N_2 nectophore the hydroecium is narrower and encloses the budding zone of the siphosome. It does not reach to the apex of the nectophore as the sides unite together, in a broad curve, just below that point (Figs. 2C, 3C). In the largest specimen, the depth of the hydroecium decreases rapidly towards the base of the N_2 nectophore as a result of a sharp incurving of its lateral flaps (Fig. 3C).

In both types of nectophore (N_1 and N_2) the somatocyst lies in the midline, above the central part of the dorsal wall of the hydroecium, and ends at about $\frac{1}{2}$ th the height of the nectophore. It is unbranched, without terminal swellings, and has neither an ascending (apically into the mesogloea) nor a descending (basally beyond the point of origin of the pedicular canal) branch (Figs. 2B, D; 3B, D).

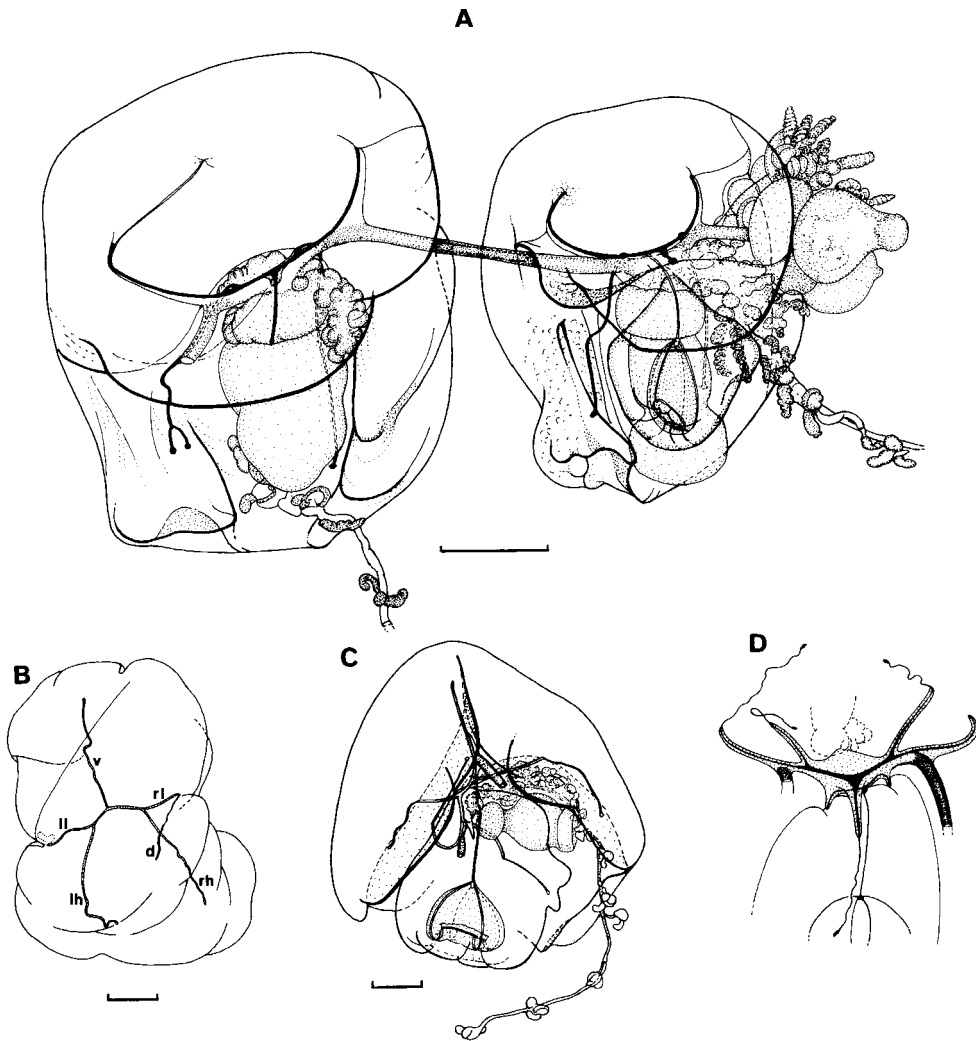


Figure 4. Stem groups of *Craseoa lathetica*: A. Two attached stem groups viewed ventrally. B. Dorsal view of older bract. C. Side (proximal) view of young stem group. D. Detail of arrangement of bracteal and gonophoral canals in the stem attachment region. A. and B. from JSL 998 specimen; C. and D. from JSL 996 specimen. Scale = 0.1 cm. In Figure 3B the bracteal canals are: d: dorsal; v: ventral; l.h. and r.h.: left and right hydroecial; and l.l. and r.l.: left and right longitudinal.

The nectosac is relatively small, extending to about one quarter the height of the nectophores. The ostial opening is basal, but the ventral part of the nectosac is more extensive than the dorsal part (Fig. 1A). The radial canals arise together from the pedicular canal. The dorsal and ventral canals usually run straight to the circular canal around the ostium, but in one specimen (JSL 959) the dorsal canal of both nectophores is slightly S-shaped (Fig. 3). The lateral radial canals in all nectophores are broadly S-shaped (Figs. 2, 3).

The whole surface of the nectophore is covered by minute papillae.

Siphosome. The maximum number of stem groups caught in association with the nectophores was four. It is very likely that others were lost during collection (see Introduction), as most related species usually have between 30 and 100 stem

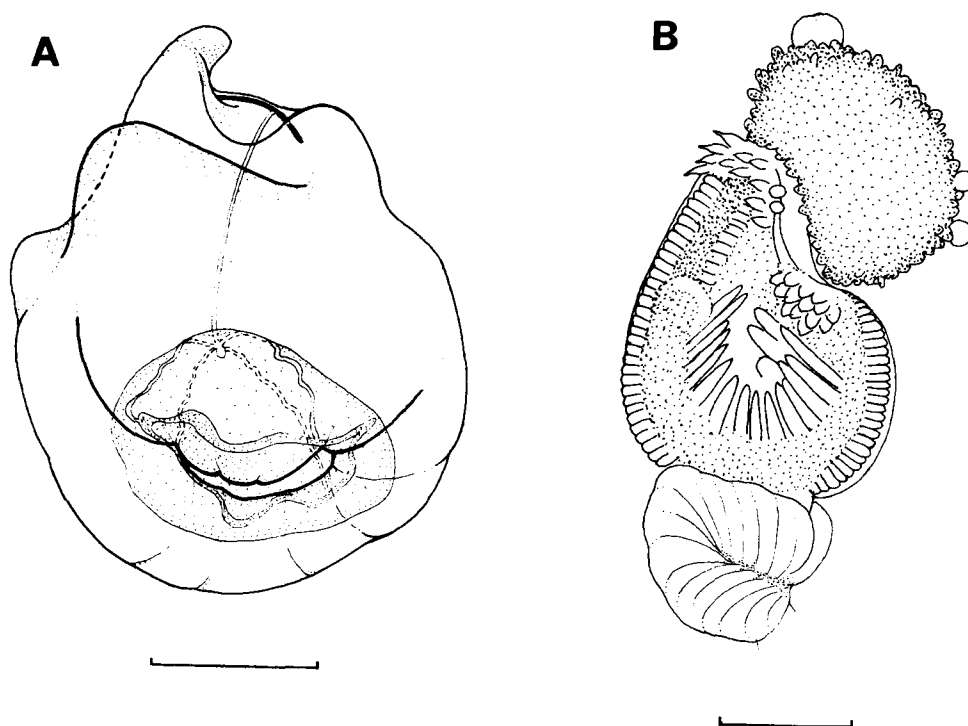


Figure 5. *Craseoa lathetica*: A. Gonophore—lateral view. Scale = 0.1 cm. B. Tentillum. Scale = 0.1 mm. Both from JSL 998 specimen.

groups. As all the existing parts were attached together on collection, it is clear that these stem groups represent the youngest, most recently developed ones, as they are attached closest to the siphosomal budding zone. In living specimens the only coloration noted was the deep-red pigmentation of the gastrozooids. The tentilla were white and opaque, while the other stem components were transparent.

Bracts (Figs. 1B, 4). The young bracts are rounded, hemispherical structures measuring 5–6 mm in height and about 5 mm in width. They are divided into two almost equal lobes by a deep incision which lies in the plane of, and through which passes, the siphosomal stem (Fig. 4A, C). The incision on the proximal side (that closest to the siphosomal budding zone) is considerably deeper than that on the distal side, and extends almost to the apex of the bract. However, the height of the distal side of the bract is greater than the proximal side, and consequently the stem runs obliquely downwards across the hydroecial cavity (Figs. 1A, 4A). In older bracts the incision between the two lobes is less pronounced, and the lobes are flattened dorso-ventrally (Fig. 4B). The whole outer surface of a bract is covered in a regular pattern of small rounded papillae, which are larger and more abundant than those on the nectophores.

The dorsal bracteal canal arises from the distal end of the right longitudinal canal (Fig. 4B). [NOTE: The terminology for the arrangement of the bracteal canals used in this paper, as in Figure 4B, is based on that used by Bigelow and Sears (1937) and, for instance, Carré (1969a; 1969b)]. The dorsal, ventral and hydroecial canals often end in small swellings, and in one case (Fig. 4A) the right hydroecial canal was forked. The left hydroecial canal is slightly longer than the right. The

longitudinal canals are well developed, and run up the sides of the bract to end at approximately the same height as the lateral incisions. The thin dorsal canal extends obliquely up to the dorsal surface of the bract and ends in a small depression, slightly distal to the midline. Narrow diverticulae of the main stem underlie the proximal parts of the ventral and hydroecial canals (Fig. 4D). The main stem, in the region where the bract and other stem group components attach, appears considerably expanded, but this may be an illusion caused by the extreme contraction of the broken parts on either side.

Gonophore (Figs. 1B, 5A). The gonophore is asymmetric in shape, being flattened, with wing-like expansions. The sub-umbrella cavity is restricted to the lower half of the gonophore (Fig. 1B) and is much less extensive than in other prayine species. Four straight radial canals are present in its lining. The pedicular canal is relatively long and at its apex gives rise to two mantle canals, which underlie the region of attachment of the gonophore to the stem (Fig. 4D). These canals are arranged asymmetrically, with one being slightly longer than the other. None of the gonophores were sexually mature.

Gastrozoid and Tentacle. The gastrozooids have a deep-red coloration in their basigaster and proboscis or buccal regions, while the stomach region is less heavily pigmented. The long tentacle bears numerous side branches or tentilla (Fig. 5B), which are similar to that of related prayine species (Carré, 1969a; 1969b). The cnidoband of the tentillum is kidney-shaped, and a single, highly coiled terminal filament stretches out from its distal end.

The arrangement of the nematocysts on the tentillum has not been examined in detail. However, in the cnidoband there are two rows of up to 20 or 30 elongated nematocysts measuring about $105 \times 10 \mu\text{m}$. These are probably microbasic mastigophores as these nematocysts are generally found in related species (Biggs et al., 1978). Other types of nematocysts were scarce in the cnidoband, but included a few (?) anisorhizas, measuring $30 \times 5 \mu\text{m}$, and desmonemes ($9 \mu\text{m}$ in diameter). Desmonemes and rhopalonemes ($18.5 \times 5 \mu\text{m}$) were found in the terminal filament, but it was not possible to determine whether they were arranged in the usual prayine pattern (Biggs et al., 1978), due to the highly contracted state of the filaments.

Distribution.—Known only from the region of the Bahamas, at depths between 607 and 715 m.

Etymology.—The name *lathetica* is derived from the Greek λαθητικωσ, meaning liable to escape notice.

Remarks.—The nectophores of *C. lathetica*, by their general shape, can be confused only with species of the genera *Rosacea* and *Desmophyes*. However, they can be distinguished easily from those of *R. plicata*, *R. cymbiformis*, and *R. flaccida* by the absence of a descending branch to the somatocyst and the S-shaped, rather than W-shaped, course of the lateral radial canals on the nectosac. Although the nectophores of *R. villafrancae* and *D. annectens* also do not have descending branches to their somatocysts, they do have ascending branches, penetrating dorsally into the mesogloea, and their lateral radial canals are straight (Table 1).

In the bracts of *C. lathetica* the origin of the dorsal canal, from the distal end of the right longitudinal one, differs markedly from most other prayine species except *R. flaccida*, *Mistoprayina fragosa* (described below), and *Praya* species. However, as discussed later, it is not certain whether this character is of more than specific importance. This may apply also to the number of mantle canals in the gonophore, although such a character clearly distinguishes *Praya* species,

which are the only ones to have three such canals. Nonetheless, the slightly asymmetrical arrangement of these canals and the relatively small size of the sub-umbrella cavity of the gonophore in *C. lathetica* are distinctive features.

Mistoprayina new genus

Diagnosis.—Prayine siphonophores with an apposed pair of conoid nectophores. The nectosac is extensive occupying the basal two-thirds of the nectophore, and has a wide dorso-basal opening. In one nectophore (N_1) the lateral radial canals are straight, while in the other (N_2) they are slightly curved. A descending branch to the somatocyst is present in both nectophores, while a simple ascending branch, penetrating dorsally into the mesogloea, occurs only in the N_2 nectophore. The young bracts are saddle-shaped, but with age become flattened, with the stem attachment region raised on a mesogloedal process. Six bracteal canals are present. The rounded gonophores possess a very extensive sub-umbrella cavity. The two mantle canals are of different lengths, the longer being distinctly recurved. No special, asexual nectophores are present.

Type Species.—*M. fragosa* new species described herein.

Etymology.—The name *Mistoprayina* is used to suggest that the specimens show morphological characters that are a mixture of those found in other prayine genera.

Remarks.—The general shape of the nectophores in *Mistoprayina fragosa*, the sole representative of this new genus, in that they are conoid and possess extensive nectosacs, suggests a close affinity with three other prayine genera, namely *Prayola*, *Lilyopsis*, and *Stephanophyes*. However, all four genera easily can be distinguished when consideration is given to the arrangement of the somatocyst and the lateral radial canals on the nectosac (Table 1). In addition, the stem groups possess features which, in combination, are of such taxonomic importance as to separate easily the other genera and to necessitate the establishment of a new genus, *Mistoprayina*, to include the species described herein. A more detailed discussion of these points is given at the end of the description of *M. fragosa*.

Mistoprayina fragosa new species

Figures 6–8

Material Examined.—Two specimens collected in the vicinity of the Bahamas by the submersible JOHNSON-SEA-LINK II during 1984.

Holotype.—Specimen collected using a detritus sampler during JSL Dive 990 at a depth of 416 m, where the water temperature was 16.2°C (29 October 1984; 25°22.5'N, 77°54.5'W). Preserved in 5% formalin. Presented to the British Museum (Natural History) and entered as Regd. No. 1986-6-1-2.

Paratype.—JSL Dive 993 specimen. (30 October 1984; 25°24.0'N, 78°00.8'W; Detritus sampler; Depth of collection: ca. 305 m. Housed in the biological collections of the Institute of Oceanographic Sciences, Wormley.

Diagnosis.—A monotypic genus and species of prayine siphonophore whose principal characters have been defined in the diagnosis of the genus. In the bracts of this species the dorsal canal arises from the distal end of the right longitudinal canal, and the hydroecial canals have small side branches.

Description.—The surfaces of the nectophores, bracts and gonophores are very tacky, both in life and after preservation. This stickiness makes it difficult to examine the specimens without damaging them.

Nectophores (Fig. 6). Both specimens possess two dissimilar nectophores. They are coniform with rounded apices, and the nectosacs occupy more than half

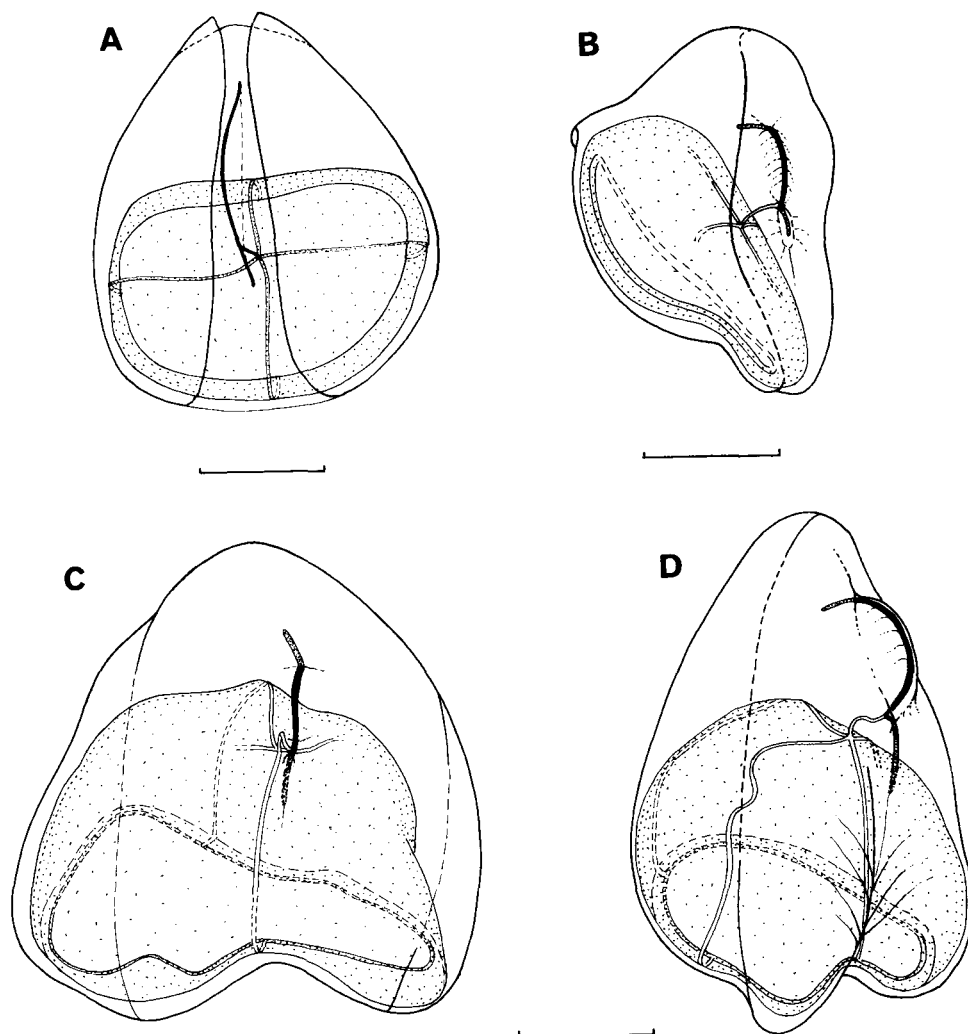


Figure 6. Nectophores of *Mistoprayina fragosa*: A. Reconstruction of N_1 nectophore from JSL 990 specimen. B. Ventro-lateral view of N_2 nectophore (JSL 993 specimen). C. Ventral and D. Ventro-lateral views of N_2 nectophore (JSL 990 specimen). Scale = 0.1 cm.

their height. The mesogloea in the basal half of the nectophores is very thin, so that after preservation the nectophores became distorted and shrivelled. One of these nectophores, which in its preserved state measures about 3.3 mm in height by 2.8 mm in width, has been designated the N_1 nectophore. Its simple somatocyst is situated within a ridge of mesogloea that projects ventrally into the very shallow hydroecium. This somatocyst has a short descending branch, but no ascending branch. A short pedicular canal runs dorsally from the somatocyst to the ventral wall of the nectosac, where the four radial canals arise directly. The courses of all of these canals are straight, such that they travel directly to the circular canal around the very large ostium, which opens dorso-basally. The narrow hydroecium extends the entire length of the ventral surface. Apically its lateral margins are produced into two small flaps.

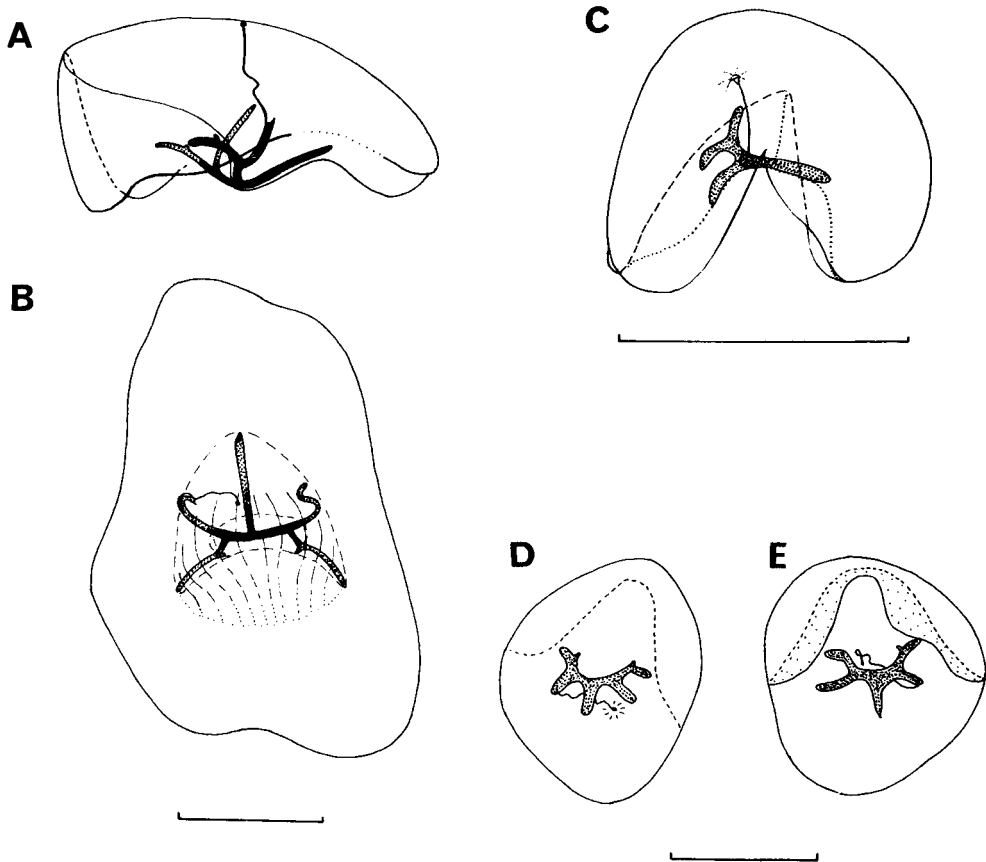


Figure 7. Bracts of *Mistoprayina fragosa*: A. Lateral and B. Ventral views of larger bract (JSL 993 specimen). C. Lateral, D. Ventral and E. Dorsal views of younger bracts (JSL 990 specimen). Scale = 0.5 mm.

Unfortunately, no photographs or drawings of the living specimen were made and, since it would be meaningless to illustrate the shrivelled, preserved nectophore, a reasoned reconstruction is presented here (Fig. 6A). This reconstruction is based on the general features of the other, better preserved nectophore and the obvious fact that the nectophore possesses an extensive nectosac. It must be emphasized, however, that all of the characters of taxonomic importance, which have been described above, can clearly be seen on the preserved specimens.

The N_2 nectophore, of both specimens, is in a better state of preservation, probably because the thicker mesogloea in the upper half of the nectophore has prevented excessive shrinkage. The N_2 nectophore from JSL Dive 990 (Fig. 6B, C) measures 4.0 mm in height and 3.5 mm in width, while the JSL 993 nectophore (Fig. 6D) is smaller (ca. 2.8 mm \times 2.5 mm respectively). As with the N_1 nectophore, the nectosac of the N_2 one is extensive, and is surrounded by a very thin layer of mesogloea. The hydroecium is virtually non-existent as almost the entire ventral surface of the nectophore forms a flattened plate. In the upper half of the nectophore there is a central mesogloea ridge projecting from the ventral surface within which runs the somatocyst (Fig. 6B). This somatocyst has both a short descending branch and an apical ascending branch, which penetrates dorsally into

the mesogloea. The descending branch is only vaguely defined, probably having become damaged when the two nectophores became separated. The relatively short pedicular canal runs to the ventral surface of the nectosac and there gives rise to the four radial canals. The course of the lateral radial canals is slightly curved such that they reach the ostial circular canal towards the base of the nectophore. Any additional meandering in these canals (Fig. 6B) probably is caused by shrinkage.

Siphosome. Judging by the number of gastrozooids present, it appears that the JSL 990 specimen possessed over 30 stem groups, while 15 remained with the JSL 993 one. No pigmentation of any parts was noted.

Bracts (Fig. 7). The younger bracts are minute (0.6–0.8 mm in length and ca. 0.6 mm in height), rounded and roughly hemispherical in shape. At this early stage, they are deeply divided, in the axial plane, into two almost equal lobes (Fig. 7C). As they enlarge they become flattened (Fig. 7D, E) and eventually take on the form shown in Figure 7A, B, with a deep hydroecial cavity dividing the hydroecial lobe. At this later stage they measure about 1.75 mm in length by 0.6 mm in height. The region of stem attachment is enclosed within the hydroecial cavity in the younger bracts, but in the older ones it lies on a central mesogloecal process protruding below the main body of the bract (cf. the ventral mesogloecal ridge on the nectophores). Six bracteal canals are present. The thin dorsal canal arises from the distal end of the right longitudinal canal, and extends to the dorsal surface of the bract where it ends at the base of a distinct depression, particularly noticeable in the younger bracts (Fig. 7C). The hydroecial canals are of approximately equal length. They bend away from the midline and as they pass over the sides of the central mesogloecal process they give rise to small side branches (Fig. 7B).

Gonophore (Fig. 8A). The almost circular gonophore bears no wing-like expansions. It is almost entirely occupied by a sub-umbrella cavity, which has four straight radial canals in its lining. The short pedicular canal gives rise, apically, to two unequal mantle canals, which underlie the stem attachment region. One of these canals, which is about twice the length of the other, is distinctly recurved. No mature gonophores were found, but asexual, special nectophores were not present.

Gastrozooid and Tentacle (Fig. 8B, C). The small gastrozooids have a very characteristic shape (Fig. 8B). The main stomach region is spherical and opaque, measuring about 0.6 mm in diameter. At its apex, the mouth is borne on a slight prominence. Proximally, the gastrozooid is reduced to a narrow tube that is sheathed by the basigaster region, from which arises the tentacle. No pedicel could be discerned, although its apparent absence may be an artifact resulting from extreme contraction.

Most of the tentacles had been lost and very few tentilla could be found. However, those still present were of the typical prayine form (Fig. 8C), with long nematocysts (?microbasic mastigophores) present in the proximal half of the cnidoband. No detailed studies have been made on the types of nematocyst present.

Distribution.—Known only from the Bahamas region at depths of 305 and 416 m.

Etymology.—The name *fragosa* refers to the extremely delicate and fragile nature of the specimens.

Remarks.—In general appearance the nectophores of *Mistoprayina fragosa* resemble those found in the species of the prayine genera *Prayola*, *Lilyopsis* and *Stephanophyes*. However, as noted above, all four genera can be distinguished

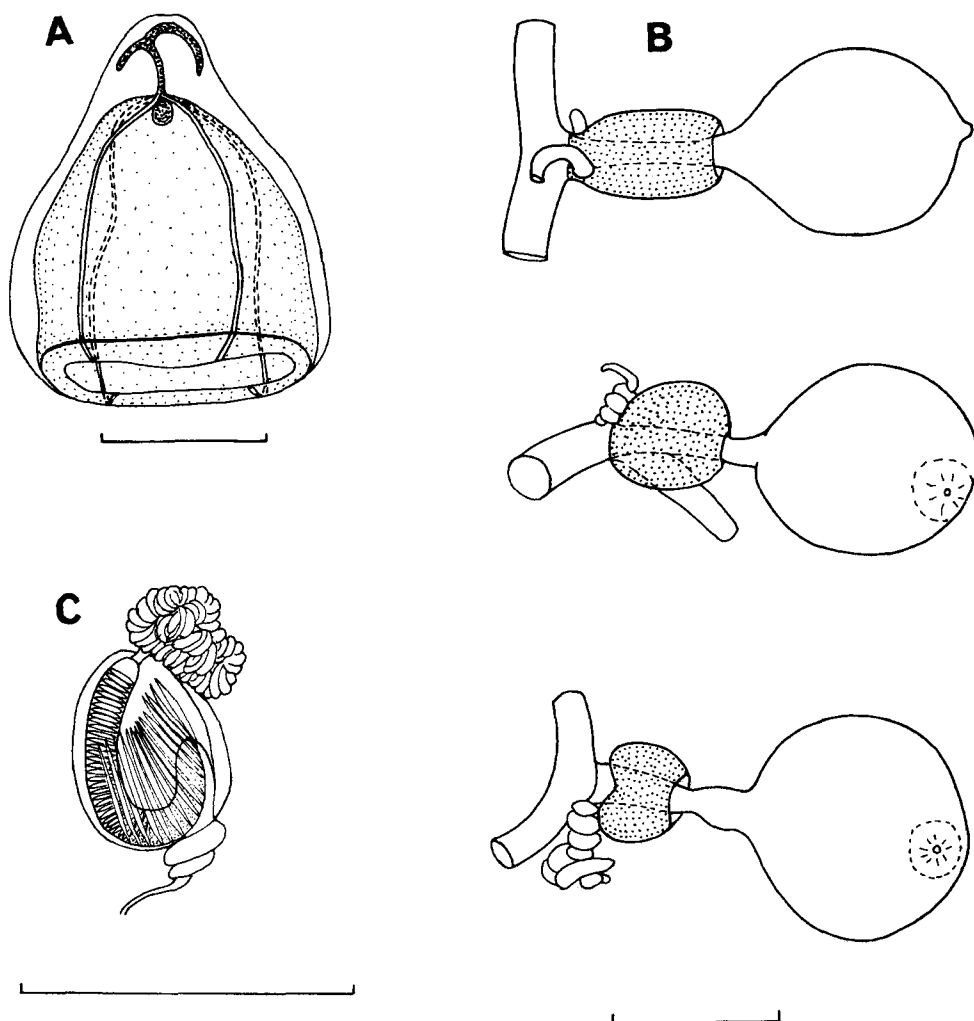


Figure 8. Stem components of *Mistoprayina fragosa* (JSL 990 specimen): A. Gonophores. B. Gastrozooids. C. Tentillum. Scale = 0.5 mm.

easily when consideration is given to the arrangement of the somatocyst and the lateral radial canals on the nectosac (Table 1). For instance, with regard to the somatocyst, in *Stephanophyes* both ascending and descending branches are present, while in *Lilyopsis* only the ascending one is to be found. *Prayola* species possess neither branch, whereas in *Mistoprayina* both branches of the somatocyst are found in the N_2 nectophore, but only the descending branch is present in the N_1 one. There are certain similarities in the arrangement of the lateral radial canals in *L. rosea* and *M. fragosa* in that in the N_1 nectophore they are straight, whereas in the N_2 one they are curved, although to a much greater extent in the former species. However, in *L. rosea*, these canals arise from the dorsal radial canal, at the apex of the nectosac, while in *M. fragosa*, in common with most other prayine species, all the canals arise together at the junction with the pedicular canal. Carré (1969b) showed that the N_1 nectophore of *L. rosea* is the larval one, retained in

the adult stage for a variable length of time. However, this is probably not the case for the N_1 nectophore of *M. fragosa* as it possesses a descending branch to the somatocyst and such a feature has not been noted in the larval nectophores of other prayine species.

The stem groups of *Mistoprayina fragosa* also can be distinguished easily from those of the other genera mentioned above. The bracteal canals of *Lilyopsis* and *Stephanophyes* are arranged asymmetrically and special, asexual nectophores are present (Table 1). The absence of the dorsal canal in the bracts of *Prayola* species distinguishes them from all other prayines.

Genus *Prayola* Carré, 1969

Diagnosis.—Prayine siphonophores with an apposed pair of conoid nectophores, whose extensive nectosacs (> half the height of the nectophore) open dorso-basally. The radial canals on the nectosac are slightly curved, suggesting an open S. The somatocyst possesses neither an ascending nor a descending branch. The bracts have only five bracteal canals, there being no dorsal one. The gonophores possess a hydroecial gutter and two mantle canals of equal length. No special, asexual nectophores are present.

Type Species.—*P. tottoni* Carré, 1969.

Remarks.—The diagnosis given by Carré (1969c) for his new genus *Prayola* obviously was based on the morphological characters of his new species, *P. tottoni*. It is necessary to amend this diagnosis slightly in order to incorporate the second species, *P. urinatrix*, described herein. Nevertheless, the characters of greatest taxonomic significance remain the same. These are the conoid shape of the nectophores; the absence of both ascending and descending branches to the somatocyst; the open S-shape of the lateral radial canals on the nectosac; the absence of a dorsal canal in the bracts; and the absence of special asexual nectophores. The other characters that Carré (1969c) mentioned, the shortness of the somatocyst and of the bracteal canals, are considered here to be only of specific importance.

Prayola urinatrix new species Figures 9–12

Material Examined.—Two specimens collected in the Bahamas region by the submersible JOHNSON-SEA-LINK II during 1984.

Holotype.—Specimen collected by a detritus sampler at a depth of 431 m during JSL Dive 1007. (4 November 1984; 25°22.4'N, 77°53.5'W). Preserved in 5% formalin. Presented to the British Museum (Natural History) and entered as Regd. No. 1986-6-1-3.

Paratype.—Specimen collected during JSL Dive 999 (1 November 1984; 25°22.9'N, 77°55.1'W; Detritus sampler; Depth of collection: 626 m). Housed in the biological collections of the Institute of Oceanographic Sciences, Wormley.

Diagnosis.—As for the diagnosis of the genus *Prayola* given above. In addition, the somatocyst of the nectophore is well-developed and situated on a mesogloecal process in the midline of the flattened ventral facet. A gutter-like indentation is present at the apex of the nectophore, the dorsal wall of which is extended into a distinct collar or frill. In the young bracts the ventral canal is approximately twice as long as the hydroecials. The mantle canals on the gonophore are longer than those in the related species, *P. tottoni*. The mature female gonophores contain three eggs.

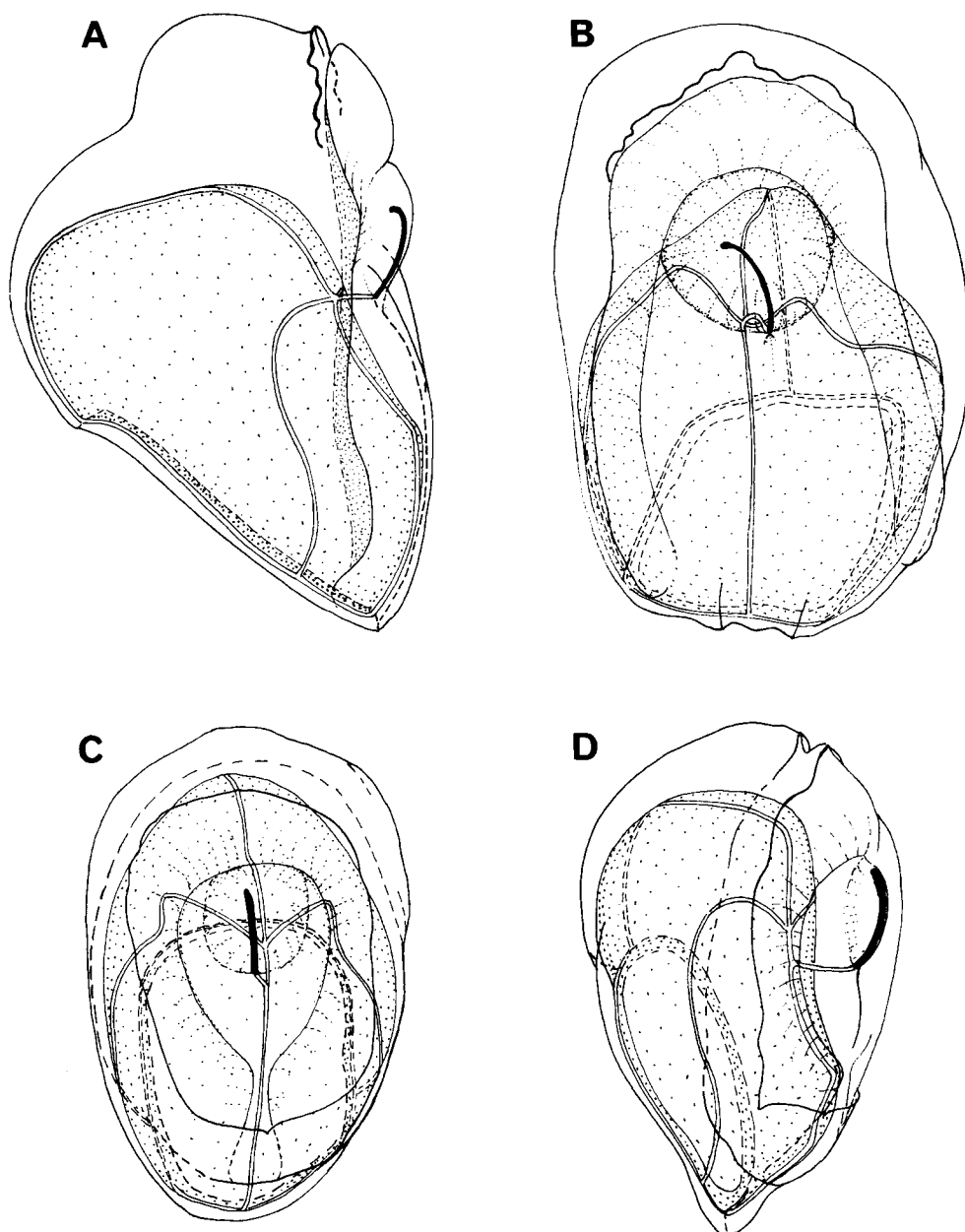


Figure 9. Nectophores of *Prayola urinatrix* (JSL 1007 specimen): A. Lateral and B. Ventral views of N_1 nectophore. C. Ventral and D. Ventro-lateral views of N_2 nectophore. Scale = 0.1 cm.

Description.—NECTOPHORES (Fig. 9). Nectophores were found only on the JSL 1007 specimen. The two nectophores, N_1 and N_2 , differ slightly in construction but, like the previous species, have a general shape reminiscent of *Prayola tottoni* and *Lilyopsis rosea*. The larger (N_1) nectophore measures about 4.1 mm in height and 2.6 mm in width (Fig. 9A, B). Its apex is not smoothly rounded, as in most other prayine siphonophores, but is interrupted by a gutter-like indentation. The dorsal edge of this gutter forms a distinct collar or frill around the apex of the nectophore and extends for a short distance down its sides before petering out (Fig. 9A). However, the lateral and ventral facets of the nectophore are still clearly demarcated by a rounded extension of the ventral edge of this gutter. A thickened bolster of mesogloea, in the shape of a horseshoe, forms the lateral and apical perimeter of the ventral facet (Fig. 9B). A central mesogloecal process also is present in the apical part of the ventral facet, within which runs the somatocyst. The somatocyst is simple, without either ascending or descending branches, but is considerably longer than that found in *P. tottoni*. Towards its apex, the somatocyst of the N_1 nectophore bends to the right (left when viewed ventrally, Fig. 9B) away from the midline, and ends in a very small swelling.

The nectosac is extensive, occupying all but the apical quarter of the N_1 nectophore, and has a large ostium that opens dorso-basally. The short pedicular canal runs to the ventral surface of the nectosac and immediately gives rise to the four radial canals (Fig. 9A). The course of both the dorsal and ventral canals is straight, the ventral one joins the ostial circular canal basally, while the dorsal one passes over the apex of the nectosac to join the circular canal at the same level as its point of origin. The lateral canals are slightly curved, running apico-dorsally away from the pedicular canal before curving round to run down the sides of the nectosac and joining the circular canal close to the base of the nectophore (Fig. 9A).

The N_2 nectophore is smaller, measuring 3.3 mm in height and 2.1 mm in width in its preserved and clearly shrunken condition (Fig. 9C, D). The nectosac is more extensive than that of the N_1 nectophore, and occupies so much of the nectophore that thickenings of the mesogloea occur only apically and ventrally. The apical margin of the nectophore is interrupted by a gutter, which is less pronounced than that in the N_1 nectophore, as is the dorsal frill or collar (Fig. 9C). The dorsal wall of the gutter appears to extend down the sides of the nectophore, but this feature is very indistinct. The ventral wall of the gutter also forms the lateral margins of the ventral facet. However, unlike the N_1 nectophore, these margins do not reach to the base of the nectophore, but are united by a linkage running across the ventral facet at about a quarter the height of the nectophore (Fig. 9C, D). Again, there is a horseshoe-shaped bolster of mesogloea that forms the lateral and apical perimeter of the ventral facet.

The somatocyst lies on a central mesogloecal process. It is simple, without ascending or descending branches, and does not curve away from the midline, as in the N_1 nectophore. The short pedicular canal runs to the ventral wall of the nectosac. It does not immediately give rise to all four radial canals, but only to the ventral and dorsal ones. The lateral canals branch from the dorsal canal a short distance above this point. The courses of all these canals are similar to those in the N_1 nectophore, the laterals being slightly curved and joining the circular canal close to the base of the nectosac.

Siphosome. About 14 stem groups were collected with the incomplete JSL 999 specimen, while at least 24 gastrozooids were found with the more complete JSL 1007 one, which also possessed sexually mature gonophores.

Bracts (Fig. 10). All but one of the bracts were young, and most were found

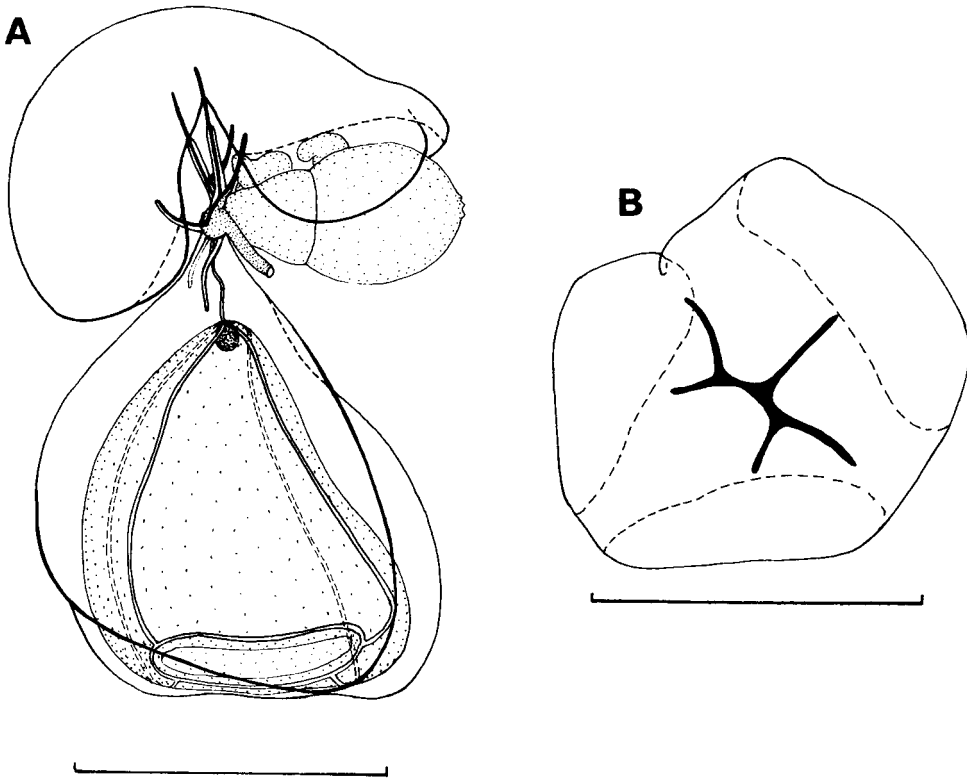


Figure 10. Bracts of *Prayola urinatrix*: A. Entire stem group (JSL 999 specimen). B. Ventral view of young bract (JSL 999 specimen). Scale = 0.1 cm.

associated with the JSL 999 specimen. These bracts have a characteristic saddle-shaped appearance (Fig. 10A) and measure about 1.4 mm in length and 1 mm in height. A deep incision, in the axial plane, divides the bract into two almost equal lobes. The incision is deepest on the lateral margins of the bract while centrally, in the stem attachment region, there is a mesogloecal swelling. In addition, the hydroecial cavity is relatively deep and subdivides the bracteal lobe above it. There are only five bracteal canals, the dorsal one being absent, as is characteristic of the genus *Prayola*. The longitudinal canals are relatively long, running up from the central mesogloecal swelling and ending slightly dorsal to the top of the lateral incisions. Diverticulae of the main stem underlie these canals for most of their length, and another underlies part of the ventral canal (Fig. 10A). The hydroecial canals are arranged symmetrically and are relatively short (Fig. 10B), being about half the length of the ventral one.

Gonophore (Fig. 11A). The young gonophores are asymmetrical, being hollowed out in the apical half on the side that is apposed to the hydroecium of the bract. This hollow provides sufficient space for the insertion of the gastrozoid onto the siphosomal stem. The extensive sub-umbrella cavity has four straight canals in its lining. The pedicular canal branches, at its apex, into two symmetrical mantle canals. These canals run along under the region of attachment of the gonophore and then turn basally and penetrate into the mesogloea for a short distance, whilst decreasing slightly in diameter (Fig. 11A).

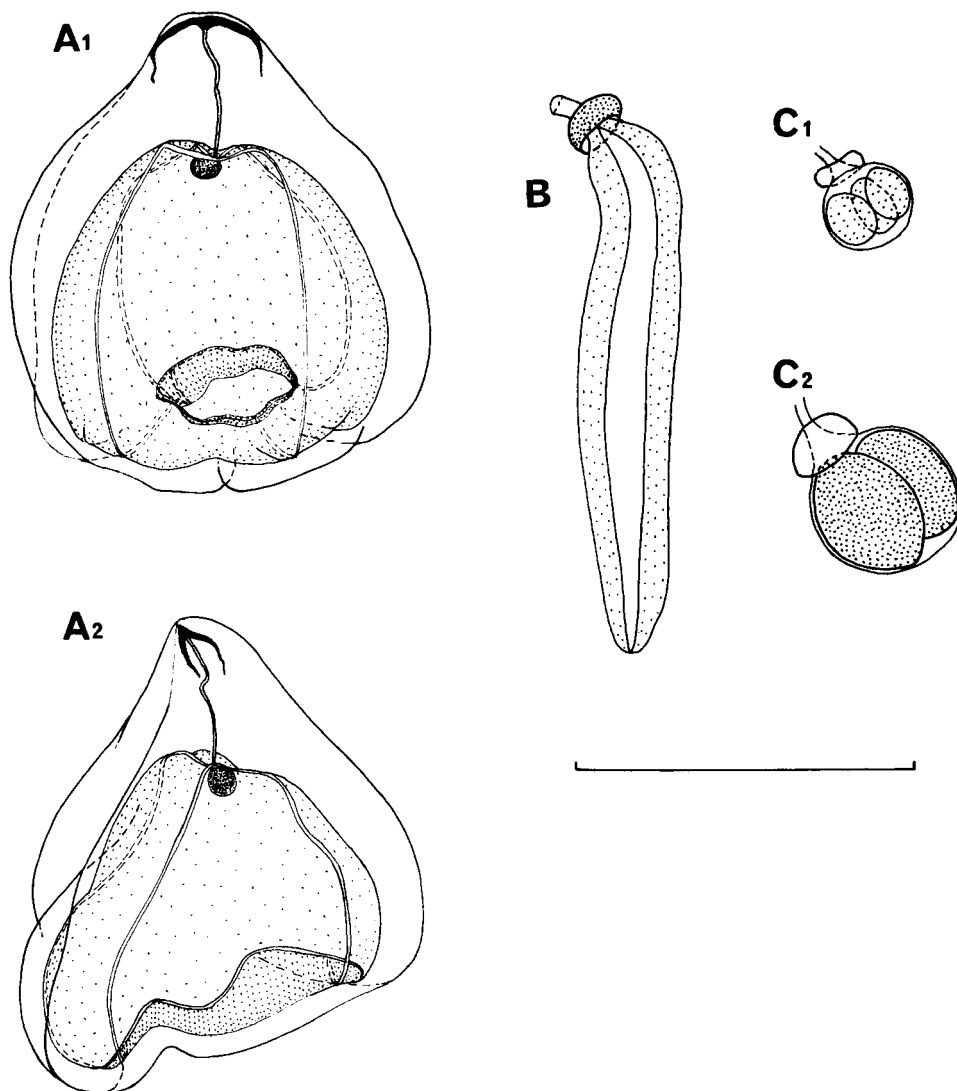


Figure 11. Gonophores of *Prayola urinatrix*: A. Young gonophore—dorsal and lateral views (JSL 999 specimen). B. Mature male gonophore (JSL 1007 specimen). C. Developing and mature female gonophores (JSL 1007 specimen). Scale = 0.1 cm.

Large gonophore bells were scarce in the more developed JSL 1007 specimen, but were common in the other, although none of the latter contained well-developed sexual products. It is presumed that large bells are developed only once on each stem group and that they are lost in association with the release of their sexual products. Nevertheless, well-developed male and female gonophores were found in the JSL 1007 specimen, but the medusoid bell associated with these was reduced to a small cup-like structure around their bases (Fig. 11B, C). The mature female gonophores contained only three eggs. Each stem group possessed gonophores of one sex only, but both sexes were present on the stem. No special, asexual nectophores were found.

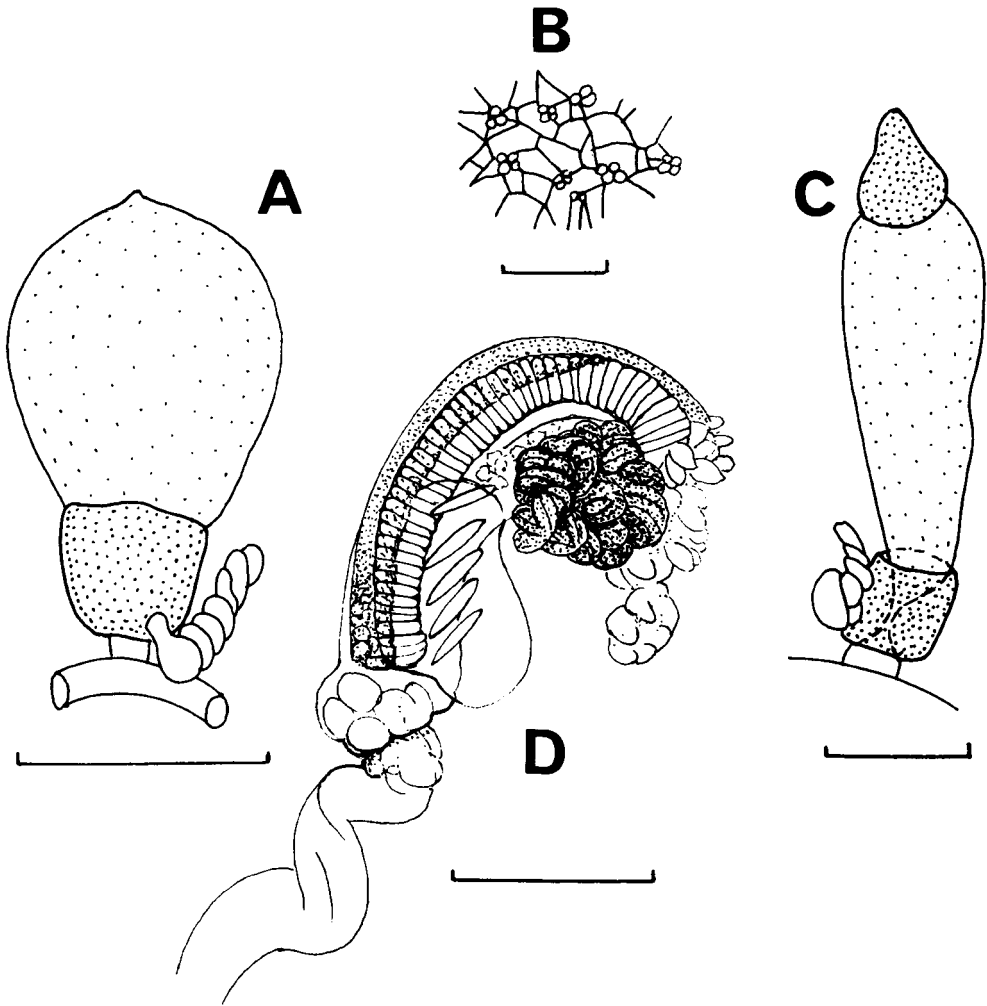


Figure 12. Gastrozooids and tentillum of *Prayola urinatrix*: A. Young gastrozoid, with B. The pattern of cells on its stomach region (JSL 999 specimen). C. Older gastrozoid, and D. Tentillum from JSL 1007 specimen. Scale: A and C = 0.5 mm, B and D = 0.1 mm.

Gastrozoid and Tentacle (Fig. 12). The gastrozooids of the JSL 999 specimen were relatively small (Fig. 12A) and possessed a characteristic pattern of cells on the surface of their stomach regions (Fig. 12B). However, the larger gastrozooids of the other specimen did not show this pattern (Fig. 12C). The younger tentilla were of the typical prayine design, with a J-shaped cnidoband, except that no large nematocysts could be found on the cnidoband. In the more developed tentilla (Fig. 12D) the cnidoband had straightened somewhat, with the pedicel inserted basally. A few large nematocysts were present in the proximal part of the cnidoband, (?)microbasic mastigophores, but no detailed studies of these have been made.

Distribution.—Known only from the Bahamas region at depths of 431 and 626 m.

Etymology.—The name *urinatrix*, meaning a female (sea) diver, is used in recognition of the invaluable role that the R.V. SEA DIVER, the tender ship for the JOHNSON-SEA-LINK II, and her crew played during the October–November 1984 cruise.

Remarks.—The species of the genus *Prayola* are immediately distinguishable from all other prayine siphonophores by the fact that a dorsal canal is absent in their bracts (Table 1). In addition, the conoid shape of the nectophores, together with the absence of both an ascending and descending branch to the somatocyst are distinctive characters. The only other prayine to show the latter character is *Craseoa lathetica*, but the general features of the nectophores and bracts set this species apart, as discussed above.

The characters that distinguish *Prayola urinatrix* from *P. tottoni* are that in the former: a) the apex of the nectophore is interrupted by a gutter and there is a characteristic mesogloal frill, particularly in the N_1 nectophore; b) the nectosac is more extensive although the course of the lateral radial canals in both species is very similar; c) the somatocyst is relatively long, whereas in *P. tottoni* it is very short; and d) the lateral radial canals of the N_2 nectophore arise from the dorsal canal slightly above the point of insertion of the pedicular canal, whereas in both nectophores of *P. tottoni* all four canals arise together.

The general structure of the stem groups is very similar in both *Prayola* species. The young bracts are deeply incised laterally and only five bracteal canals are present. The ventral and hydroecial canals in *P. tottoni* are of almost equal length, while in *P. urinatrix* the ventral is almost twice the length of the hydroecials. The young gonophores also are very similar, although the mantle canals in *P. urinatrix* are longer than those in *P. tottoni*. Carré (1969c) makes no mention of reduced gonophores in *P. tottoni*, but he did note that from four to six eggs were present in the female gonophores of his species, whereas we found only three eggs in those of *P. urinatrix*.

DISCUSSION

Biggs et al. (1978) briefly discussed how the nomenclature of the sub-family Prayinae had become very confused and complicated in the past, particularly with regard to the genus *Rosacea* and one of its species, *R. plicata*. This species was described by Quoy and Gaimard (1827), but for the remainder of the 19th century no other specimens were described under that name, although the taxonomy is very confused. However, some authors have considered that other species, particularly *Desmophyes annectens* Haeckel, 1888, might be the same as that of Quoy and Gaimard. This may be true but it is now impossible to verify as the original specimen of *R. plicata* is no longer in existence (Carré, pers. comm.). Bigelow (1911a) appears to have been the first to re-use the name *R. plicata* whilst describing some material collected in the Bay of Biscay. Later that year, he (Bigelow, 1911b) figured other specimens from the Eastern Pacific, although he did appear to have some reservations about their exact identity. Nonetheless, it is apparent, as detailed by Totton (1965), that the specimens described by Bigelow as *R. plicata* are not the same as that described originally by Quoy and Gaimard (1827).

Totton decided that since the generic name *Rosacea* sensu Bigelow had been in common usage for over half a century it should be retained and, hence, he designated *R. plicata* sensu Bigelow as its type species. We follow this decision and in order to stabilize the nomenclature we designate two nectophores (N_1 and N_2), from the material that Bigelow (1911a) examined, as the neotype. These nectophores are housed in the British Museum (Natural History), and are entered

Table 1. A comparison of the morphological characters of related prayine species

	<i>Praya dubia</i>	<i>Praya reticulata</i>	<i>Prayoides intermediata</i>	<i>Rosacea plicata</i>	<i>Rosacea cymbiformis</i>	<i>Rosacea flaccida</i>	<i>Crasaea laethetica</i>	<i>Desmophyes annectens</i>	<i>Desmophyes (Rosacea) villafraancae</i>	<i>Mistopayina fragosa</i>	<i>Prayola tottoni</i>	<i>Prayola urinalix</i>	<i>Lilyopsis rosea</i>	<i>Stephanophyes superba</i>
Nectophores														
General shape	N ₁ Cyl ^A N ₂ Cyl ^A	Cyl ^A Cyl ^A	Cyl ^A Cyl ^A	Cyl ^A Cyl ^A	Cyl ^A Cyl ^A	Cyl ^A Cyl ^A	Cyl ^A Cyl ^A	Cyl ^A Cyl ^A	Cyl ^A Cyl ^A	Con Con	Con Con	Con ^B Con	Con ^B Con	Con
Nectosac: nectophore height	N ₁ 1/4 N ₂ 1/4	1/4 1/4	1/3 < 1/2	1/4 1/4	< 2/3 < 2/3	1/3 1/3	< 1/3 1/3	1/4 1/4	2/3 2/3	2/3 2/3	> 1/2 > 1/2	> 2/3 > 2/3	2/3 2/3	> 2/3 > 2/3
Ostial opening	N ₁ D-B N ₂ D-B	D-B D-B	?B ?B	B B	D-B D-B	D-B D-B	B B	B B	B B	D-B D-B	D-B D-B	D-B D-B	D-B D-B	D-B D-B
Lateral radial canals	N ₁ Br N ₂ Br	Ret Ret	Br Br	W- W-	W- W-	W- W-	S- S-	str str	str str	str str	s.c. s.c.	s.c. s.c.	str ^D sin ^D	sin sin
Hydroecium—relative depth	N ₁ Deep N ₂ Deep	Deep Deep	Deep Deep	Deep Deep	Deep Deep	Deep Deep	Medium Medium	Deep Sh.	Deep Sh.	V. Sh. V. Sh.	V. Sh. V. Sh.	V. Sh. V. Sh.	V. Sh. V. Sh.	V. Sh. V. Sh.
Somatocyst length ^E	N ₁ Long N ₂ Long	Long Long	Long Long	Long Long	Long Long	Long Long	Medium Medium	Short Short	Short Short	Short Short	V. Sh. V. Sh.	Short Short	Medium Medium	Long Long
+ ascending branch	N ₁ + N ₂ +	+ +	+ +	+ +	+ +	+ +	+ +	+ +	+ +	+ +	+ +	+ +	+ +	+ +
+ descending branch	N ₁ + N ₂ +	+ +	+ +	+ +	+ +	+ +	+ +	+ +	+ +	+ +	+ +	+ +	+ +	+ +
Bracts														
No. of canals	6	6	U	6	6	6	6	6	6	6	5 ^K	5 ^K	6 ^L	6 ^L
Origin of dorsal canal	R.L. (d.H.)	R.L. (d.H.)	N	R.H. (p.H.)	R.L. (p.H.)	R.L. (d.H.)	R.L. (d.H.)	Cent	R.H. (d.H.)	R.L. (d.H.)	—	—	Cent	L.H. or L.L. ^M
Gonophores														
No. of mantle canals	3	3	N	2	2	0?1	2	2	1	2	2	2	1 ^N	2 ^N
Mantle canal symmetry	Sym	Sym	O	Asym	Asym	—	Asym ^O	Sym	—	Asym	Sym	Sym	—	Asym
Sub-umbrella cavity ^P	> 3/4	> 3/4	W	2/3	2/3	9/10	< 1/2	2/3	2/3	3/4	2/3	2/3	3/4	2/3
Canals of sub-umbrella	str	str	N	str	str	str	str	str	str	str	str	str	str ^Q	sin

Abbreviations: Asym: Asymmetrical; B: Basal; Br: Branched; Cent: Central; Con: Conoid; Cyl: Cylindrical; D-B: Dorso-basal; L.H.: Left hydroecial; L.L.: Left longitudinal; Ret: Reticulate; R.L.: Right longitudinal; either proximal (p.H.) or distal (d.H.) to right hydroecial; S: S-shaped; sin: Sinuous; str: straight; Sym: Symmetrical; W: W-shaped; V: Sh.: Very shallow. x denotes absence, + presence.

Notes: A. With ventro-basal extension beyond nectosac. B. The N₁ nectophore is the larval one which is retained into the adult stage, but eventually is replaced. C. Probably a result of age, i.e., not fully developed and would later take on same characters as N₁ nectophore (see Carré, 1969a). D. Originate from dorsal canal, not at junction with pedicular canal. E. Relative length of somatocyst: Long = greater than half the length of the nectophore; Medium = about half; Short = less than a third; V. Sh. = Very short. F. Complexly divided. G. A very short apical extension into a pocket of mesogloea. H. The ascending branch has a terminal swelling. I. Bifurcated. J. Bifid in younger nectophores, complexly divided in older ones. K. The dorsal bractial canal is absent. L. The ventral canal is inserted asymmetrically, opposite the left hydroecial one. M. Depending on age of specimen. N. Details here refer to the special, asexual nectophore. O. Only very slightly asymmetrical. P. Expressed as the ratio of height of cavity to height of gonophore. Q. Canals do not all arise together from pedicular canal.

as Regd. No. 1939.6.10.1. They were found in a jar (Regd. No. 1939.6.10.1-5) which contained three N_1 and three N_2 nectophores of *Rosacea plicata* sensu Bigelow, plus one larval nectophore of the same species. Of course, since none of the nectophores are attached to each other, it is impossible to be certain that the two nectophores removed belonged originally to the same specimen. However, on the basis of size, the N_1 and N_2 nectophores can be paired off, and the best preserved of these pairs has been selected as the neotype. The specimens were collected during the cruise of H.M.S. RESEARCH. The label on the jar states that the depth of collection was 300-Ofm which, judging by the records for *R. plicata* given by Bigelow (1911a) would indicate that they came from haul 36k. This haul was made on 25-vii-1900 at 47°03'N, 7°55'W. However, Bigelow (1911a) stated that six superior (N_1) and two inferior (N_2) nectophores were found in this haul, which is not in accord with the extant material. Perhaps the specimens came from haul 361 (350-Ofm), in which Bigelow (1911a) found three superior and three inferior nectophores; but the museum records are insufficient to resolve this point.

Bigelow's (1911a) material of *Rosacea plicata* is of great interest as it is apparent that two of the N_1 nectophores possess a very short apical extension of the somatocyst into a pad of mesogloea that projects into the hydroecium. It was this feature that convinced Bigelow that his material could be identified with that described by Quoy and Gaimard (1827) as *R. plicata*. Nevertheless, this very short extension in no way resembles the pronounced ascending branch of the somatocyst found in other species, e.g., *Desmophyes annectens* and *R. villafrancae*, and we do not consider it to represent such a structure. However, it does bear a close resemblance to that found in the N_1 nectophore of another *Rosacea* species, *R. flaccida* (Table 1). We have examined other material of *R. plicata* sensu Bigelow, from recent R.R.S. DISCOVERY collections made in the Bay of Biscay (Pugh, 1984), and find that this short apical extension of the somatocyst is present in some, but not all, of the N_1 nectophores. Thus, we confirm that this feature is a true, but inconsistent, morphological characteristic of this species. We have examined also many specimens of *R. cymbiformis*, collected by SCUBA divers, and can find no trace of such an apical extension to the somatocyst in any of the nectophores.

In recent years four new species of prayine siphonophores have been described. Two of these were placed in the genus *Rosacea*, namely *R. villafrancae* Carré, 1969 and *R. flaccida* Biggs et al., 1978, while the third, *Prayola tottoni* Carré, 1969, formed the type species of a new genus. The fourth species, *Nectocarmen antonioi* Alvarino, 1983, we regard as an incomplete specimen of *Praya dubia*. The two minute nectophores, which Alvarino (1983) found on her specimen, are quite out of proportion with the rest of the material and would appear to be replacements, at very early stages of development, for the pair of full sized nectophores that have become detached.

In his discussion of *P. tottoni*, Carré (1969c) produced keys for the identification of the nectophores and stem groups of all extant prayine genera. However, with the present description of three new species, it is apparent that the generic characters used by Carré (1969c) are no longer wholly satisfactory and that other characters, as detailed in Table 1, are also of taxonomic significance. We consider the following characters to be of particular importance. For the nectophores: a) the general structure of the bell; b) the structure of the somatocyst, including the presence or absence of ascending and/or descending branches; and c) the general structure of the nectosac and the courses of its canals. For the stem groups: a) the general structure of the bract and gonophore; b) the number and arrangement of the bracteal canals; and c) the number and arrangement of the mantle canals on the gonophore. Individually, some of these characters are only of specific impor-

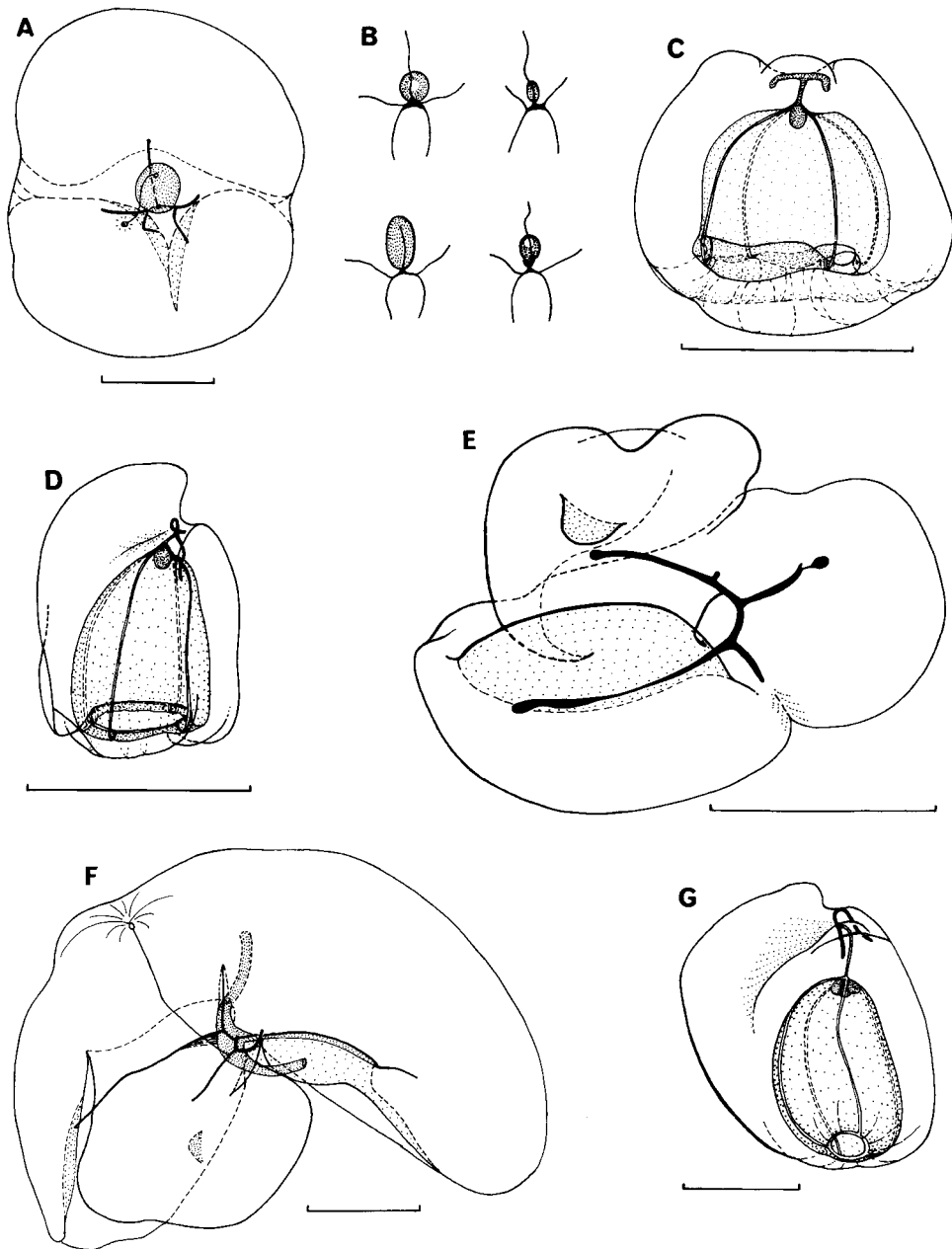


Figure 13. A. Bract (dorsal view) of *Desmophyes annectens* (JSL 969 specimen), with B the variability in the size of the central vesicle as illustrated by the pattern of canals in other bracts from the same specimen. (In these ventral views the dorsal canal is obscured.) C. Gonophore of *Desmophyes annectens* (JSL 969 specimen). D. Gonophore (lateral view) and E. Bract (ventral view) of *Rosacea cymbiformis*. F. Bract and G. Gonophore (lateral views) of *Rosacea plicata*. Scale = 0.2 cm.

tance but, when in combination with others, they can be used to establish separate genera. The presence of an asexual, special nectophore in each cormidium, as in the genera *Lilyopsis* and *Stephanophyes*, also is an important generic character. Although such a structure has been described in the stem groups of *Desmophyes annectens* we believe that it does not exist in this species, as is shown below.

It is apparent from Table 1 that the prayine genera can be split into two subgroups on the basis of the general shape of the nectophore. There are those genera that have cylindrical nectophores with nectosacs occupying less than half the height, and others which have conoid nectophores with extensive nectosacs. The presence or absence of a descending or ascending branch to the somatocyst then separates the individual genera in each subgrouping. Thus:

	Cylindrical	Conoid
Both branches present:	<i>Praya</i>	<i>Stephanophyes</i>
Ascending branch only:	<i>Desmophyes</i>	<i>Lilyopsis</i>
Descending branch only:	<i>Rosacea</i>	—
Neither branch present:	<i>Craseoa</i>	<i>Prayola</i>
Both present in N_2 , but only one in N_1 :	<i>Prayoides</i>	<i>Mistropayina</i>

As mentioned above, we do not consider the very small apical extension of the somatocyst in the N_1 nectophores of *Rosacea plicata* and *R. flaccida* to be representative of a true ascending branch, which runs dorsally into the mesogloea, and so the genus *Rosacea* remains distinct from all the other prayine genera. Nevertheless, there is one species, *R. villafrancae*, that does not fit into this general scheme as its nectophores do not have a descending branch to the somatocyst. In fact, by the presence of an ascending branch to the somatocyst and of straight radial canals on the nectosac, this species appears to be more closely allied to *Desmophyes annectens*, although there are certain differences in the stem groups, e.g., in the arrangement of the bracteal canals. In *D. annectens* the dorsal bracteal canal joins the longitudinal canal centrally, by way of a variably sized basal swelling (Fig. 13A, B), while in *R. villafrancae* this canal originates from the right hydroecial (see Carré, 1969a). However, it should be noted that in two other species, *R. plicata* and *R. cymbiformis*, which are obviously closely related to each other, there is a comparable situation. In *R. cymbiformis* the dorsal bracteal canal arises from the right longitudinal (Fig. 13E), proximal (central) to the right hydroecial, although not in the midline, while in *R. plicata* it arises from the right hydroecial (Fig. 13F). Thus it would seem that the arrangement of the bracteal canals is only of specific, not generic, importance. Nonetheless the bracts of the two latter species are very similar in basic construction, as are their gonophores (Fig. 13D, G).

We conclude that the general similarities between the nectophores and bracts of *D. annectens* and *R. villafrancae* suggest a close affinity between these two species and accordingly we transfer the latter into the genus *Desmophyes* as *D. villafrancae* (Carré, 1969). However, we are aware that this arrangement is not wholly satisfactory since there are certain differences between them, e.g., the number of mantle canals in the gonophore. Another obstacle to this transference could be the fact that *D. villafrancae* does not possess special, asexual nectophores on the siphosome while they have been described for *D. annectens*. The presence of special nectophores is certainly a valid generic character, but we believe that *D. annectens* does not possess such structures. We have examined several specimens of *D. annectens* caught by SCUBA divers and by the submersible

JOHNSON-SEA-LINK II and have been unable to find any sign of special nectophores. Large bells are present in the stem groups, but all of these possess either developing sexual products or a small manubrial rudiment. Thus they are all true gonophores (Fig. 13C). It does not seem possible that an even larger asexual nectophore also could be attached to the stem and the capture of intact specimens confirms this. History has shown that the observation of a bell without a manubrial process does not necessarily mean that it is an asexual nectophore. Bigelow (1911a) in his description of *Rosacea plicata* sensu Bigelow, suggested that asexual nectophores were present. However, Bigelow and Sears (1937) noted, for the same species, that the spadix of the gonophores could be detached without leaving any trace and concluded that the supposed asexual nectophores were old gonophores that had remained attached to the stem. We believe the same situation applies to *D. annectens* and, thus, that asexual nectophores are not developed. Nonetheless it is apparent that the gonophores of *D. annectens* possess two symmetrical mantle canals (Fig. 13C), while those of *D. villafrancae* possess only one. Although Haeckel (1888) described *D. annectens* as having up to six nectophores, arranged biserially, none of the specimens we have seen have had more than two apposed nectophores.

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