Two new species of prayine siphonophore (Calycophorae, Prayidae) collected by the submersibles *Johnson-Sea-Link I* and *II*

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Abstract. Two new species of prayine siphonophore are described from specimens collected by the submersibles *Johnson-Sea-Link I* and *II*. Although they possess some unique morphological features, the general characters of these new species suggest that they belong to the genus, *Rosacea sensu* Bigelow. These characters are discussed in relation to the detailed comparisons of other prayine species made previously by Pugh and Harbison.

Introduction

Further studies on the siphonophore material collected, in excellent condition, by the submersibles *Johnson-Sea-Link* (JSL) *I* and *II* have revealed two more new species belonging to the calycophoran sub-family Prayinae. These are in addition to the three other new species that have been described recently by Pugh and Harbison (1987), who also discussed the distinguishing characters of all the accepted prayine species known at that time.

The two new prayine species described below are very similar to each other in general morphology. However, the course of the radial canals on the nectosac of the nectophore and the presence or absence of side branches on the left hydroecial canal of the bract clearly distinguish them. The general features of the specimens suggest that they belong to the genus *Rosacea sensu* Bigelow. These characteristics are, for the nectophores: the sinuous course of the lateral radial canals on the nectosac; and the simple somatocyst, with a descending branch but only a small apical prolongation, not a pronounced ascending branch. For the bracts, the presence of a small flap on the reduced right hydroecial lobe is a typical *Rosacea* feature, although the origin of the dorsal bracteal canal differs from some of the other species. The gonophores are asymmetric in shape and have two mantle canals of different lengths.

Special sampling devices mounted on the JSL submersibles (Youngbluth, 1984; Pugh and Harbison, 1986) allowed specimens of gelatinous zooplankton to be collected individually so that in the case of siphonophores, which often disintegrate into numerous pieces, all parts can be related to a single specimen. Two devices were used to collect the specimens described herein: a pump-driven, rotary bin sampler; and a hydraulically controlled, stationary unit. Samples were sucked gently through a funnel into one of 24 3.5-1 acrylic containers using the bin sampler, and then each container was sealed by flapper-hinged lids when the next was rotated into the sampling position. The stationary sampler is a vertically orientated, 7.5-1 acrylic cylinder which can be closed by lids which slide, horizontally, across the openings.

Rosacea repanda sp. nov. (Figures 1, 2, 3A, 4-6, 7A)

Material examined

Eight specimens collected in the vicinity of the Bahamas by the submersibles JSL I and II.

Holotype

Single specimen, comprised of two nectophores, nine bracts, four gonophores (one male, three ?female), and four gastrozooids with tentacles. Collected at a depth of 388 m during JSL II dive 777 (9 October 1983; 22°08.2′N, 74°16.5′W; water depth 805 m). Preserved in 5% formalin, and presented to the United States National Museum (Smithsonian Institution) and entered as Cat. No. 80073.

Other specimens

Components of seven specimens as listed in Table I.

The first five of the specimens shown in Table I are housed in the biological collections of the Harbor Branch Oceanographic Institution, and the last in the collections of the Institute of Oceanographic Sciences.

Diagnosis

Prayine siphonophores with a pair of large, cylindrical apposed nectophores. The hydroecium extends the full length of the nectophores, and has extensive lateral flaps, whose outer margins, where they join with the main body of the nectophore, appear to be marked by the presence of a frill. The simple somatocyst possesses a descending branch and an apical process, which extends for up to 1.5-2 mm into the mesogloea. In addition, short dorsal branches can be given off from the somatocyst of the N_2 nectophore. The lateral radial canals on the nectosac basically are S-shaped, but a cross branch also is present. The dorsal and ventral canals are straight.

The bracts are axially compressed and have two major lobes (ventral and left hydroecial) and a smaller, centrally placed right hydroecial lobe that bears a

Table I.

JSL dive no.	Date	Depth (m)	Position		Water	Components
			N	W	depth	
I 931	10-x-80	457	26°11.7′	77°38.8′	732	22b, 9g (4 ♂, 5 ♀), 19gz
I 1174	19-v-82	488	26°13.2′	77°42.3′	763	9b, 9g (7 \circlearrowleft , 1 \circlearrowleft , 1x), 7gz
II 549	16-vi-80	702	26°22.0′	7 7 °47.7 ′	702	2n, 3b, 3g(?), 1gz
II 549	16-vi-80	491	26°22.0′	77°47.7′	702	3b, $17g(10 \circlearrowleft, 5 \circlearrowleft, 2x)$, $15gz$
II 754	20-ix-83	455	26°13.9′	77°41.3′	731	23b, 16g (11 ♂, 5 ♀), 17gz
II 780	10-x-83	420	22°25.3′	74°17.4′	841	4b, 1g (\mathfrak{P}) , 5gz
II 962	18-x-84	460	26°26.6′	78°33.9′		5b, 5g $(3 \circlearrowleft, 2 \circlearrowleft)$, 4gz

b = bract; g = gonophore; gz = gastrozooid; n = nectophore. x refers to gonophores whose sex could not be determined.

small flap on its proximal surface. The hydroecial cavity usually is extensive and is enclosed within a flap of the left hydroecial lobe. The ventral canal is long and makes a ?-shaped curve up into the mesogloea. The left hydroecial canal is similarly curved, but bends down over the wall of the hydroecium. This latter canal is without side branches. The dorsal canal ends in a small dilation immediately below the superficial furrow that runs transversely across the bract. The gonophores are asymmetric in shape and have a thin lateral wing on one side, approximately at the mid-height of the gonophore. The apical diverticulum of the sub-umbrella cavity is relatively small. The arrangement of the two mantle canals is asymmetric. No special, asexual nectophores are present on the cormidia.

Description

Nectophores (Figures 1 and 2). The two nectophores of the holotype are large, flaccid structures, both measuring 4 cm in length and up to 16 mm in depth (dorso-ventral direction). Those of the dive 549 specimen are considerably smaller, measuring 21 and 23 mm, although the N₁ nectophore has lost its base so that only a small part of the nectosac is present. The nectophores are very similar in construction, but the N₁, older nectophore is taken to be the one with a deeper, wider hydroecium (Figure 2A). The hydroecium extends the full length of the N₁ nectophore, and is enclosed by relatively thick lateral flaps. Apically, the hydroecium forms a deep, but narrow, gutter with a depth of about half that of the nectophore. It is deepest in the middle of the nectophore, where its dorsal wall is indented and there are two pronounced pockets in its dorsolateral walls. Basally, the hydroecium occupies about half the breadth of the nectophore and its dorsal wall ends on a level with the nectosac. The lateral hydroecial flaps, however, extend basally and ventrally below this region (Figure 1B,C). In the preserved specimens the ventral wall of the nectosac has become displaced dorsally by the hydroecium, but this is a preservation artefact as can be seen from the photographs of the living specimen (Figure 1A). On the external surface of the nectophore the lateral edges of the hydroecial flaps are demarcated by a vague ridge, which appears from the remnants to have possessed a frill in life, and apico-laterally there are a pair of small mesogloeal protuberances (Figure 1C).

The somatocyst of the N_1 nectophore is simple and possesses a descending branch, ~ 5.5 mm in length in the holotype but only 2 mm in the dive 549 specimen, and a short apical process which extends into the mesogloea for $\sim 1-1.5$ mm (Figures 1A and 2A). The descending branch ends approximately on a level with the top of the nectosac (Figure 2A).

The nectosac of the N_1 nectophore is relatively small and occupies only about a quarter of the height of the nectophore. Its ostial opening is dorso-basal. The dorsal and ventral radial canals in the walls of the nectosac are straight and run directly to the ostial ring canal (Figure 3A). The arrangement of the sinuous lateral canals is basically S-shaped, but the upper loop is united, apically, by a cross canal (Figure 3A). Distally each lateral canal runs down the nectosac,

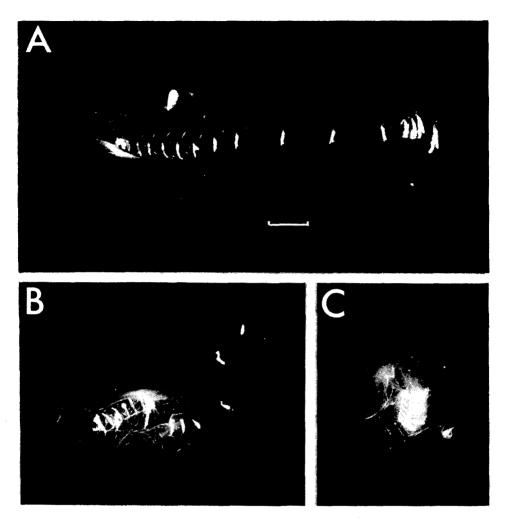


Fig. 1. Photographs of the live holotype specimen of Rosacea repanda. (A-C) Various views. Scale = 1 cm.

parallel with and very close to the ostial ring canal, before eventually joining the latter. The whole arrangement is unique amongst the known species of prayine siphonophore.

The hydroecium of the N_2 nectophore is deep, but is shallower and narrower than that of the N_1 nectophore. It extends to the apex of the nectophore only as a very shallow gutter (Figure 2B,C). At its deepest the hydroecium extends to about three-fifths the breadth of the nectophore. Basally, its arrangement is very similar to that of the N_1 nectophore with the lateral flaps extending down beyond the nectosac (Figure 1B,C). The dorsal wall of the hydroecium has a pronounced bend in its mid-region, where the stem attaches (Figures 1A and 2C) and, as in the N_1 nectophore, it also bends sharply ventrad beneath the point

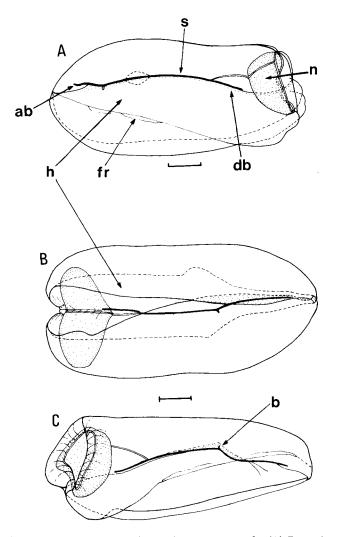


Fig. 2. Nectophores of the holotype specimen of *Rosacea repanda*. (A) Dorso-lateral view of N_1 nectophore. (B) Ventral and (C) lateral views of N_2 nectophore. Scale = 5 mm. ab and db, ascending and descending branches to the somatocyst (s), with the small dorsal branch (b) shown in (C); fr, frilled ridge; h, hydroecium; n, nectosac.

where the apical process to the somatocyst is given off. The lateral hydroecial flaps are thinner than those of the N_1 nectophore, but again their outer lateral margins are marked by the presence of a frill.

The somatocyst of the N_2 nectophore is simple and, for the most part, follows the contours of the dorsal wall of the hydroecium (Figure 2C). It has a descending branch, 5.5 mm in length in the holotype but only 2 mm in the dive 549 specimen. The apical process extends into the mesogloea for between <1 mm (dive 549) and 2 mm (holotype) (Figures 1A and 2C). In the stem attachment region of the holotype it gives off a short, 0.5-mm-long, blind-ending

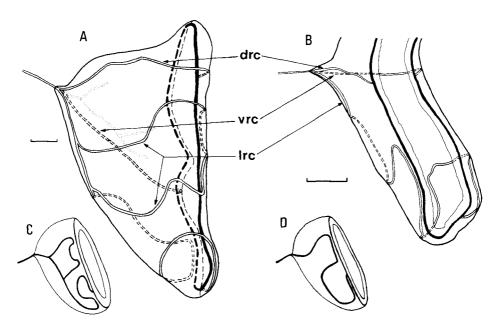


Fig. 3. The courses of the lateral radial canals on the nectosacs of the nectophores of (A) Rosacea repanda, dorso-lateral view; and (B) R.limbata, dorsal view. Scale = 1 mm. drc, lrc, vrc dorsal, lateral and ventral radial canals respectively. (C and D) Schematic lateral views illustrating the basic arrangement in R.repanda and R.limbata respectively.

dorsal branch, and there is another very short dorsal branch about half-way between there and the origin of the pedicular canal. Apart from these branches, the somatocyst of the N_2 nectophore is very similar to that of the N_1 one. The nectosac and the arrangement of its lateral radial canals again are similar to that of the N_1 nectophore, but the ostial opening is more basal (Figure 1A).

Siphosome. The maximum number of bracts found with the specimens examined was twenty three. In several specimens there was a reasonable agreement between the number of bracts and gonophores, indicating that most probably only a single gonophore was associated with each stem group.

(i) Bracts (Figures 4 and 5). The full grown bracts, measuring up to 24 mm in length, are flaccid, axially compressed, asymmetric structures. The older bracts have rounded edges, but the younger ones are more angular. The bracts are divided into three unequal lobes. A shallow incision, which is deeper on the distal side of the bract and through which the siphosomal stem passes, separates the ventral lobe from the two hydroecial ones. In the younger bracts, the ventral lobe forms a flattened plate, with the ventral bracteal canal lying on its distal side (Figure 4C). However, as the bracts enlarge the distal part of this lobe usually folds over to enclose a small ventral cavity within which, on its proximal wall, a small mesogloeal swelling appears.

The two hydroecial lobes are unequal in size. The smaller, right lobe occupies a central position on the distal side of the bract and, as in two *Rosacea* species,

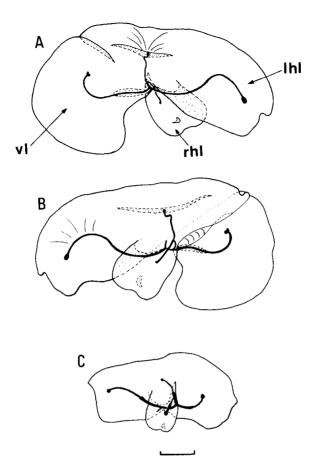


Fig. 4. Young bracts of *Rosacea repanda* from the holotype specimen. (A) Proximal view; (B and C) distal views. Scale = 1 mm. lhl, rhl, vl: left and right hydroecial, and ventral lobes respectively.

R.plicata sensu Bigelow and R.cymbiformis (Chiaje), it possesses a small flap on its inner, proximal surface. In the younger bracts, the larger left hydroecial lobe is flattened and there is no obvious hydroecial cavity. However, as the bract enlarges this lobe expands and frequently folds over to form two almost equal flaps, which enclose an extensive cavity (Figure 5B,C).

The bracteal canals have a very characteristic arrangement, the most striking feature of which is the ?-shaped course of both the ventral and left hydroecial canals (see Figure 5A for explanation of terminology). The proximal part of the ventral canal, i.e. that part lying closest to the siphosomal stem, is thickened and lies immediately below the surface of the bract. Distally, the canal thins and recurves up into the mesogloea, ending in a small dilation. The longitudinal canals, which run parallel with the siphosomal stem, are relatively short, with the right one being slightly longer than the left. The shortness of these canals is in accord with the narrowness of the bract itself and the shallowness of the incision through which the stem passes.

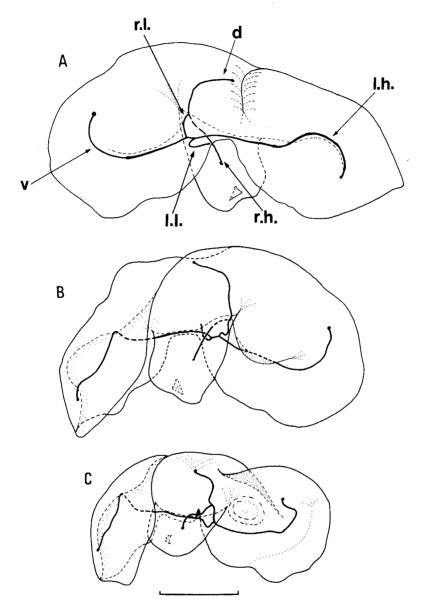


Fig. 5. Mature bracts of *Rosacea repanda*. (A) Proximal and (B) Distal views of bracts from JSL dive 1174 specimen. (C) Distal view of bract from holotype. Scale = 5 mm. Bracteal canals labelled in (A) as d., dorsal; l.h. and r.h., left and right hydroecial; l.l. and r.l., left and right longitudinal; v., ventral.

The thin dorsal canal arises at the distal end of the right longitudinal canal, and runs dorsally up and proximally across the bract to end in a small dilation, below a superficial furrow that runs transversely across the bract (Figures 4 and 5). Frequently, the right hydroecial canal also appears to arise from the distal end of the right longitudinal (Figure 5), but this is an artefact, caused by a split

appearing in the bract, when the siphosomal stem is detached. As the youngest bracts show (Figure 4C), the right hydroecial canal actually branches off about half-way along the right longitudinal, and runs down over the proximal half of the right hydroecial lobe. This canal lies immediately below the surface of the lobe, except for its terminal dilation, which is inflected into the mesogloea.

The left hydroecial canal, at first, runs out along the proximal side of the hydroecial cavity, and then loops over onto the distal side and runs down to end in a small dilation. No side branches of this canal were found on any of the bracts, but the proximal part of the canal was thicker than the distal part.

The whole of the external surface of the bracts was covered in minute papillae, which were particularly noticeable in the younger ones.

(ii) Gonophores (Figure 6). The gonophores measure up to 9 mm in height and 8 mm in width. They are asymmetric, being expanded on one side to form a thin lateral wing, approximately at the mid-height of the gonophore. The attachment region, to the siphosomal stem, does not lie at the top of the gonophore as one side is expanded apically. This asymmetry is reflected in the relative lengths of the two mantle canals, one being considerably longer than the other.

In the youngest gonophores, without any distinctive gonads, the sub-umbrella cavity extends to about one-third the height of the gonophore. However, as the gonads appear, they come to lie in a small apical diverticulum of this cavity (Figure 6). With further development, this apical diverticulum expands to accommodate them and the sub-umbrella cavity, as a whole, stretches to about two-thirds the gonophoral height (Figure 6A,B). The canals in the lining of the sub-umbrella cavity are straight. Although there is a lot of variability, several specimens possess considerably more male than female gonophores. This might indicate that there is no alternation of the sexes along the siphosomal stem. In most cases the female gonophores possess five eggs.

(iii) Gastrozooids and tentacles (Figure 7A). The gastrozooid and tentacle are of the typical prayine form, as are the tentilla (Figure 7A). The cnidoband of each tentillum contains ~24 elongate ($105 \times 6.5 \,\mu\text{m}$) nematocysts, which are probably microbasic mastigophores, arranged in two rows; and numerous smaller ($45-50 \times 8 \,\mu\text{m}$), banana-shaped nematocysts (?anisorhizas) with a few desmonemes ($10.5 \times 10.5 \,\mu\text{m}$). The terminal filament contains many rhopalonemes ($24-34 \times 5 \,\mu\text{m}$) and desmonemes ($15-18 \times 10.5-12 \,\mu\text{m}$) probably arranged in an alternating sequence as found for *R. flaccida* by Biggs *et al.* (1978).

Distribution

Known only from the region of the Bahamas, at depths between 388 and 491 m.

Etymology

The specific name *repanda* is derived from the Latin *repandus*, meaning bent backwards or turned up, and refers to the arrangement of the ventral canal in the bract.

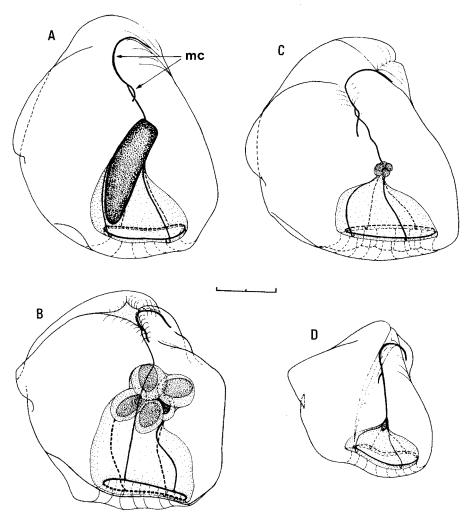


Fig. 6. Gonophores of *Rosacea repanda*. (A) Mature male and (B) mature female gonophores from JSL dive 931 specimen; mc, mantle canals. (C) Young female gonophore from JSL dive 754 specimen. (D) Very young male gonophore from holotype. Scale = 2 mm.

Ecology

Examination of some gastrozooids revealed remnants of crustacean mouth parts, but the remainder of the prey was too digested to make any detailed studies. An adult male amphipod, *Hyperoides longipes* Chevreux, was found with the dive 754 specimen, but it probably does not represent an association.

Rosacea limbata sp. nov. (Figures 3B, 7B, 8-12)

Material examined

A single specimen (holotype), comprised of three nectophores, 57 bracts, 52 gonophores (30 \circlearrowleft , 21 \circlearrowleft , plus one too young to sex), and 59 gastrozooids and

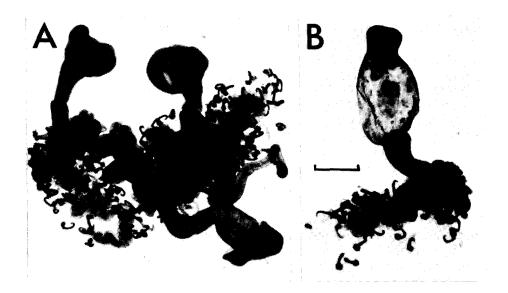


Fig. 7. Gastrozooids and tentacles of (A) Rosacea repanda and (B) R.limbata. Scale = 0.1 mm.

tentacles. It was collected during dive 575 of JSL I (20 August 1978; 26°15.5′N, 77°43.4′W; water depth 405 m) at a depth of 146 m. Preserved in 5% formalin and presented to the United States National Museum (Smithsonian Institution) and entered as Cat. No. 80072.

Diagnosis

Prayine siphonophores with a pair of large, apposed, cylindrical nectophores, which may be replaced by reserve nectophores. The hydroecium extends the full length of both nectophores and has extensive lateral flaps, whose outer margins, where they join with the main body of the nectophores, are marked by the presence of a frill. Apically, each flap has, on its external surface, a pronounced mesogloeal swelling. The somatocyst is simple and possesses a descending branch and a small apical dilation, which projects into the mesogloea. The descending branch of the somatocyst ends a short distance above the level of the nectosac. Short dorsal and, in the N_2 nectophore, lateral branches are given off from the somatocyst in the stem attachment region. The dorsal and ventral radial canals on the nectosac are straight, while the lateral canals are sinuous and have S-shaped courses.

The bracts are not so axially compressed as in *R. repanda*, but otherwise have a very similar basic construction. They differ in that the left hydroecial canal has two side branches, and that the dorsal bracteal canal extends beyond the superficial transverse furrow but is connected with it by a short, obliquely directed side branch. The asymmetric gonophores usually possess a thin apicolateral flap, and their sub-umbrella cavities have extensive diverticula. The

canals of the cavity are straight. The two mantle canals are of different lengths. No special, asexual nectophores are present.

Description

Nectophores (Figures 8–10). Three nectophores are present with the holotype, two large definitive ones and a small, developing replacement one. The two definitive nectophores are, in their preserved state, flimsy structures, whose ectodermal layer is easily damaged. The ectoderm presumably was sticky in life as hundreds of tentilla have become attached to the surface, without causing

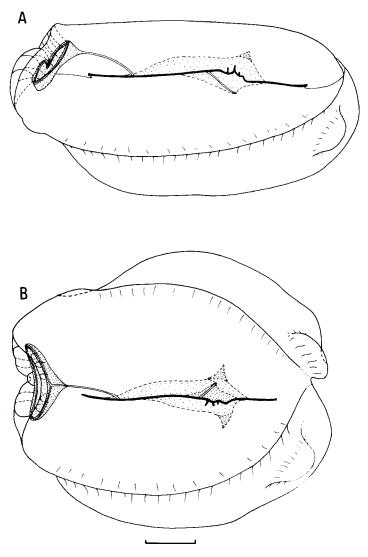


Fig. 8. (A) Lateral and (B) dorsal views of N_1 nectophore of *Rosacea limbata* (holotype). (See Figure 2B for course of radial canals.) Scale = 5 mm.

their nematocyst batteries to discharge. Despite their fragility it is evident that these definitive nectophores are not smoothly rounded, as are those in other *Rosacea* species, but that their external surfaces are structured.

The larger N_1 nectophore measures 36 mm in length and has a maximum width, with the hydroecial flaps extended, of 37 mm (Figure 8). The hydroecium is a wide, deep gutter extending the full length of the nectophore. Its lateral flaps are extensive and can cover the hydroecium completely when folded in. Basally they are relatively thin but apically they become thickened with mesogloea. In the latter region each flap possesses a mesogloeal swelling on its external surface, with a slight asymmetry in their disposition and shape (Figure 8B). The indentation at the apex of the nectophore, where the flaps unite, also is asymmetrically placed. The hydroecial flaps do not extend to the base of the nectophore but peter out approximately on a level with the top of the nectosac. The lateral junction of these flaps with the main body of the nectophore is marked by a rounded margin which, in life, appears to have possessed a frill, judging by remnants that are still attached to the preserved specimen.

The dorsal wall of the hydroecium runs parallel with that of the nectophore itself except in the region of stem attachment, where it is indented (Figure 8A). In this latter region there are also extensive dorso-lateral pockets in the wall of the hydroecium. Basally, the presence of the hydroecium causes the lower, central part of the nectosac to be displaced dorsally, but this may be a distortion caused by preservation.

The somatocyst is simple and runs just below the dorsal wall of the hydroecium (Figure 8A). It has a descending branch, which extends ~ 4.5 mm beyond the point of insertion of the pedicular canal. This branch ends ~ 1.5 mm above the top of the nectosac and there the dorsal wall of the hydroecium is inflected sharply ventrad. In the region of stem attachment the somatocyst makes several abrupt bends and gives rise to three very short (<0.5 mm), dorsal branches. Apically, the somatocyst ends in a small swelling which is slightly inflected into the mesogloea. The dorsal surface of the somatocyst is very uneven, particularly in the stem attachment region, and this might indicate that other dorsal branches can be developed.

The long pedicular canal connects the somatocyst to the radial canals on the nectosac. The dorsal and ventral of these latter canals are straight and run directly to the ostial ring canal. The lateral canals have sinuous, unbranched courses, as described below for the N_2 nectophore. The nectosac itself is small, in the preserved specimen, and extends only to about one-sixth the height of the nectophore. Its ostial opening is dorso-basal, although again there may be some distortion due to preservation.

The smaller N_2 nectophore measures 31 mm in height and, like the N_1 nectophore, its hydroecium is extensive and stretches the full length of the nectophore (Figure 9). The hydroecium has distinct lateral flaps, whose junction with the main body of the nectophore is marked by a rounded margin that bears the remnants of a frill. The flaps end just below the apex of the nectophore, such that the hydroecium continues only as a shallow gutter above them. The apex of the nectophore is rounded and not indented as in the N_1 nectophore. Apically

the lateral flaps are considerably thicker than basally, and they each bear a mesogloeal swelling, which is more pronounced than that on the N_1 nectophore (Figure 9B). The lateral flaps also do not quite reach to the base of the nectophore. In this latter region, the dorsal wall of the hydroecium curves dorsad and again causes the ventral wall of the nectosac to be indented in the mid-line. The width of the hydroecium is relatively constant in the basal half of the nectophore, but apically it narrows considerably.

The somatocyst is simple, with a descending branch extending 4 mm beyond the pedicular canal (Figure 9). It ends \sim 2 mm above the top of the nectosac where, as in the N_1 nectophore, the dorsal wall of the hydroecium bends sharply ventrad. In the region of stem attachment the somatocyst is kinked in the lateral plain, and gives off a lateral branch, \sim 1.5 mm in length, on each side. Three short, <0.5 mm, dorsal branches also emerge from the somatocyst in this region. The somatocyst ends, apically, in a small swelling which projects into the mesogloea.

A long pedicular canal connects the somatocyst to the radial canals of the nectosac. As with the N_1 nectophore, the dorsal and ventral canals are straight, while the laterals have a sinuous, unbranched course (Figure 3B). The course of

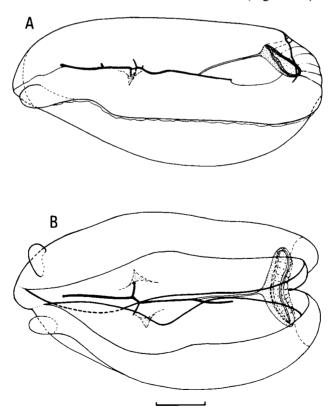


Fig. 9. (A) Lateral and (B) ventral views of N_2 nectophore of *Rosacea limbata* (holotype). Scale = 5 mm.

these laterals appears to be unique amongst the known prayine species, particularly where they run up, dorsally, parallel with the ostial ring canal, before joining it. The nectosac itself is small, reaching to only one-fifth the height of the nectophore. Its ostial opening is dorso-basal, but again shrinkage during preservation may have distorted the arrangement.

The small reserve nectophore, measuring 7 mm in length and 9 mm in width, originally was found attached to the N_1 nectophore, but was then detached for detailed examination. It has a complex structure (Figure 10). The hydroecial flaps are frilled and the hydroecium itself bends sharply dorsad in the upper half of the nectophore, so that it opens along the entire apical surface. Mesogloeal swellings are present in the vicinity of the nectosac and, more pronouncedly, in the apical region. The latter probably will form the lateral swellings seen on the definitive nectophores, but the whole structure of the reserve nectophore indicates that the definitive ones may have had a more complex external morphology than is actually apparent. The reserve nectophore also possesses numerous patches of ectodermal cells, which may once have been pigmented.

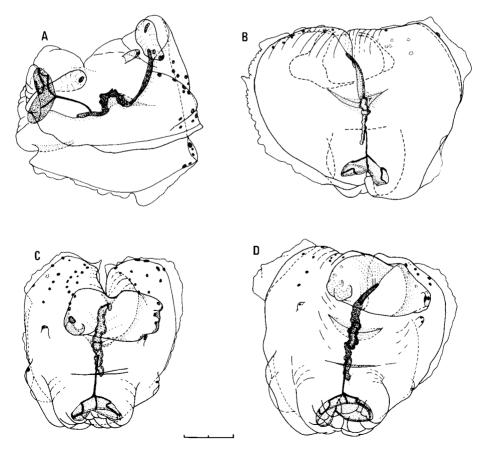


Fig. 10. Developing reserve nectophore of *Rosacea limbata* (holotype). (A) Ventro-lateral, (B) ventral, (C) apico-lateral and (D) dorsal views. Scale = 2 mm.

The course of the radial canals on the nectosac, which at this stage opens basally, is identical to that found on the definitive nectophores.

Siphosome. The siphosome of the preserved holotype specimen consisted of 57 bracts, 52 gonophores and 59 gastrozooids with tentacles.

(i) Bracts (Figure 11). Several of the bracts are at an early stage of development. However, the mature bracts average ~18 mm in length, with a maximum of 22 mm. They are rounded structures which are clearly divided into three lobes. The ventral and left hydroecial lobes are of almost equal size, while the centrally placed right hydroecial lobe is much smaller. This latter lobe typically bears a small flap on its proximal side, as in the previous species, but this flap is not always apparent as the lobe itself is very thin and easily damaged. Dorsally the bracts are relatively broad and there is a marked, deep transverse furrow. Basally, both the main bracteal lobes are thinner and there is also a depression hollowed out on the proximal side of the left hydroecial lobe (Figure 11A,D). Unlike R. repanda the distal hydroecial cavity does not usually become enclosed by a fold of the left hydroecial lobe, but occasionally a distal flap of the ventral lobe does enclose a small cavity (Figure 11C).

The course of the bracteal canals is very similar to that previously described for *R.repanda*, with both the ventral and left hydroecial canals being ?-shaped. None the less, there are some characteristic differences. All the canals end in distinct terminal dilations. The proximal part of the ?-shaped ventral canal, which lies immediately below the distal surface of the bract, is thickened while the distal part, which recurves dorsad into the mesogloea, is much thinner. At the transition point between these two regions, in about one-third of the bracts, a branch canal is given off, which runs for a short distance proximo-ventrally.

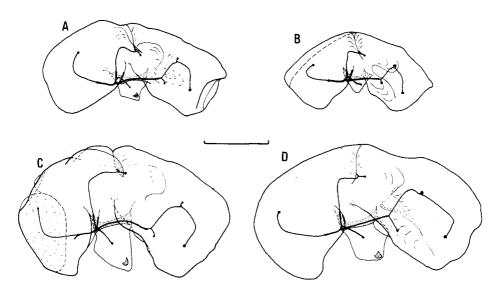


Fig. 11. Proximal view of bracts of Rosacea limbata (holotype). Scale = 5 mm.

The two longitudinal canals are thickened for most of their relatively short lengths. They run up, on either side of the bract, above the gutter through which the siphosomal stem runs. In one bract the left longitudinal canal gave off a side branch. The dorsal bracteal canal arises at the distal end of the right longitudinal one. It runs dorsally, and slightly proximally, up through the mesogloea of the bract and curves over to pass under the superficial dorsal furrow. It does not end at the base of the furrow, as in the previously described species, but extends for a short, but variable, distance beyond this into the left hydroecial lobe. The canal is, however, connected to the dorsal furrow by an obliquely inclined, subterminal, side branch (Figure 11). This side branch gives rise to two further branches at the base of the furrow which run for a short distance along the axis of the latter before petering out.

The right and left hydroecial canals branch from the respective longitudinal canals close to the junction of the latter with the ventral canal. However, because of a split which appears in the right longitudinal canal when the bract becomes detached from the siphosomal stem, often the right hydroecial canal appears to originate at the distal end of the former, where the dorsal canal arises. The right hydroecial canal runs to half way down the small, central lobe, and lies immediately below its proximal surface. The terminal dilation is inflected into the mesogloea.

The left hydroecial canal is basically ?-shaped and is thickened proximally. On entering the left hydroecial lobe the canal narrows, and almost immediately gives off a side branch which runs down into the mesogloea (Figure 10). The length of this branch varies considerably amongst the bracts examined, and in three cases a further side branch was given off. The main part of the left hydroecial canal curves dorsad, at first lying below the wall of the hydroecium but later penetrating into the mesogloea. A second short side branch is given off which often is so reduced that it appears only as a knob on the side of the main canal (Figure 11B,D). The main canal then curves ventrad to end in a dilation.

The whole external surface of the bract is covered in minute papillae, which are particularly noticeable in the younger ones.

(ii) Gonophores (Figure 12). The gonophores, none of which contained mature sexual products, measured up to 7 mm in height. They are asymmetric in shape and usually possess an apico-lateral wing, which is thinner than the rest of the gonophore. This wing is very obvious in the very young gonophores, but in some of the older ones it is not apparent. A very characteristic feature, in the preserved material, is the shape of the sub-umbrella cavity. The expanded part of this cavity occupies less than half the height of the gonophore, often only a third, but it possesses a pronounced apical diverticulum, within which the developing gonads lie. This diverticulum stretches up to almost two-thirds the height of the nectophore. The canals of the sub-umbrella cavity are straight, and the opening often is displaced onto one side, although this may be a distortion due to preservation. The two mantle canals are of very different lengths, with the longer running up towards the apex of the gonophore, before curving over to run down below an apico-lateral gutter. The shorter canal runs basally and is much thinner than the other.

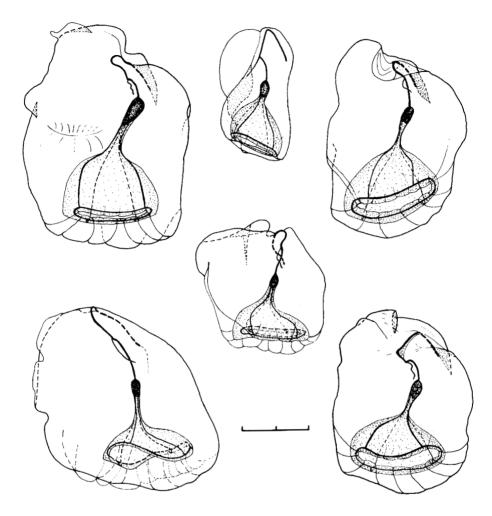


Fig. 12. Gonophores of Rosacea limbata (holotype). Scale = 2 mm.

The sex ratio appears to be more equal than in *R.repanda*, with 30 male and 21 female gonophores being present, plus one that is too young to sex. The most developed female gonophores possess three eggs, but the younger ones appear to have more, although it is not possible to make an accurate assessment. The surface of the gonophore is covered in minute papillae.

(iii) Gastrozooids and tentacles (Figure 7B). The gastrozooids and tentacles are of the typical prayine form. The cnidoband of each tentillum contains ~ 24 elongate nematocysts (110 \times 7.5 μ m), which are probably microbasic mastigophores, and a large number of smaller (40–43 \times 8–9 μ m) ?anisorhizas, plus a few desmonemes. The terminal filaments contain desmonemes (14.5 \times 10.5 or 12 \times 9 μ m) and rhopalonemes (25 \times 5 μ m), which may be arranged in an alternating sequence.

Distribution

Known only from a single specimen collected in the region of the Bahamas at a depth of 146 m.

Etymology

The specific name *limbata* is derived from the Latin *limbatus*, meaning bordered or with a fringe, and refers to the lateral fringe present on the nectophores.

Ecology

Examination of the contents of some gastrozooids revealed that the siphonophore had been feeding on an ostracod, *Conchoecia acuta* Gooday, and a copepod, *Pleuromamma abdominalis* (Lubbock). Various amphipods are found with the holotype specimen, though the occurrence of an adult male of *Eupronoe cf. armatus* is probably fortuitous. However, the presence of juveniles of *Sympronoe ?septemarticulata* definitely represents an association, as Harbison *et al.* (1977) found *S.?parva* only in association with the closely related prayine species, *Rosacea cymbiformis*. In addition, an example of *Streetsia porcella* (Claus) was found with the specimen but it may not be an association as Harbison *et al.* (1977) have found it only in association with a polycystine radiolarian colony and the ctenophore *Leucothea* sp.

Discussion

Pugh and Harbison (1987) have discussed in detail the morphological characters of the nine genera and 14 species of prayine siphonophores that they recognized as valid. They noted that these genera can be split into two groups on the basis of the shape of the nectophore, i.e. whether it is cylindrical, with a small nectosac, or conoid, with an extensive nectosac. The presence or absence of ascending and descending branches to the somatocyst then could be used to separate the individual genera. Other characteristics, such as the structure of the cormidial elements, generally were thought to be of specific importance, although the absence of a dorsal bracteal canal clearly distinguished the genus *Prayola* Carré, and the presence of three mantle canals on the gonophores separated the species of the genus *Praya* Quoy and Gaimard in Blainville.

The two new species described herein, which are very similar in structure to each other, basically have cylindrical nectophores, with small nectosacs. The somatocyst has a descending branch, but only a small apical process, quite unlike the pronounced ascending branches found in the genera *Desmophyes* Haeckel, *Praya* and *Prayoides* Leloup. These features are, however, characteristic of the genus *Rosacea*, as is the presence of sinuous lateral radial canals on the nectosac, although the arrangement in one of the new species is more complicated than that previously found.

The bracts of the new species are somewhat axially flattened and are similar to those of *Praya* species, both in general structure and in the origin of the dorsal bracteal canal, from the distal end of the right longitudinal one. However, as

discussed by Pugh and Harbison (1987), the latter feature is thought to be only of specific importance. None the less, the division of the bracts into three distinct lobes, with the right hydroecial one being smaller and bearing a small flap on its proximal surface, is reminiscent of both Rosacea plicata and R.cymbiformis. The other Rosacea species, R.flaccida, differs in both these respects, as its two small hydroecial lobes are of approximately equal size and do not bear flaps.

The gonophores of *R.repanda* and *R.limbata*, being asymmetrical, with a pronounced lateral or apico-lateral wing, and with two mantle canals of unequal length, are very similar to those of *R.cymbiformis* and *R.plicata* although the form of the sub-umbrella cavity is different. Again, the gonophores of *R.flaccida* are distinctive, as they are almost symmetrical and possess only one (?none) mantle canal. All these differences between *R.flaccida* and the other four species, which form two closely related pairs, suggest that the systematic position of *R.flaccida* is uncertain, and it may become necessary to remove it to a separate genus. However, for the sake of simplicity, the status quo is maintained for the present.

Although the basic morphological characters of R.repanda and R.limbata are very similar to those of two other Rosacea species, there are some characteristic differences that make it easy to distinguish them. Not least of these is the presence of a frill which demarcates the margin between the hydroecial flaps and the main body of the nectophore. Also, the external morphology of the nectophore of R.limbata is much more structured than in any of the other species of the genus. In addition, the course of the lateral radial canals on the nectosacs of the new species is S-shaped rather than W-shaped. The presence of a cross canal in R.repanda is also a unique characteristic and serves to distinguish that species from all other prayines siphonophores. The structure of the somatocyst is very similar in all Rosacea species, and R.cymbiformis is the only one which does not appear to have a short apical process in at least one of the nectophores. The relative length of this apical process is a feature which can be used to distinguish the two new species from each other. The presence of short lateral or dorsal branches to the somatocyst has not been noted in any of the established species.

As noted above, the bracts of the two new species appear *Praya*-like in basic construction, but there are also *Rosacea*-like characters. The ?-shaped courses of both the ventral and left hydroecial canals are, however, very distinctive features, and the presence of side branches to the latter together with a subterminal branch to the dorsal bracteal canal in *R.limbata* serve to distinguish it from *R.repanda*.

The asymmetric arrangement of the gonophores of the new species are very similar to those of *R.cymbiformis* and *R.plicata*, but the positioning of the lateral or apico-lateral wings serves to distinguish them. The structure of the sub-umbrella cavity, with its apical diverticulum, particularly well-developed in *R.limbata*, is a distinctive feature of the new species described herein.

In conclusion, it is apparent that these two new species are very closely related, although there are some clearly distinguishing features, e.g. the course of the lateral radial canals on the nectosac; the presence or absence of side branches on the left hydroecial bracteal canal; and the general structure of the

gonophores. None the less, the general features of the specimens clearly indicate that they belong to the prayine genus *Rosacea*.

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References

- Biggs, D.C., Pugh, P.R. and Carré, C. (1978) Rosacea flaccida n.sp., a new species of siphonophore (Calycophorae Prayinae) from the North Atlantic Ocean. Beaufortia, 16, 109–117.
- Harbison, G.R., Biggs, D.C. and Madin, L.P. (1977) The association of Amphipoda Hyperiidea with gelatinous zooplankton—II. Associations with Cnidaria, Ctenophora and Radiolaria. *Deep-Sea Res.*, 24, 465-488.
- Pugh, P.R. and Harbison, G.R. (1986) New observations on a rare physonect siphonophore, Lychnagalma utricularia (Claus, 1879). J. Mar. Biol. Assoc. UK, 66, 695-710.
- Pugh, P.R. and Harbison, G.R. (1987) Three new species of prayine siphonophore (Calycophorae, Prayidae) collected by submersible, with notes on related species. *Bull. Mar. Sci.*, 41, 68-91.
- Youngbluth, M.J. (1984) Manned submersibles and sophisticated instrumentation: tools for oceanographic research. In *Proceedings of SUBTECH '83 Symposium*. Society for Underwater Technology, London, pp. 335–344.

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