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THE STATUS OF THE GENUS *PRAYOIDES* (SIPHONOPHORA: PRAYIDAE)

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The status of the prayine siphonophore genus *Prayoides*, monotypic for the species *Prayoides intermedia* Leloup, 1934, is reviewed in the light of recent collections made by the submersibles 'Johnson-Sea-Link' I and II. It is concluded that the genus is not valid, and that the species name should be reduced to that of a junior synonym of a *Praya* species. The bracts of the two *Praya* species, *P. dubia* (Quoy & Gaimard (1833) 1834) and *P. reticulata* (Bigelow, 1911) are re-described, as in the past there has been much confusion as to their true identity.

INTRODUCTION

Leloup (1934) described a new prayid siphonophore species, *Rosacea (Prayoides) intermedia*, whose nectophores (swimming bells) (Figure 1A) showed morphological features intermediate between the genera *Rosacea sensu* Bigelow, 1911, and *Praya* Quoy & Gaimard, 1834, in Blainville, 1834. (The authorities for these genera are those in recent usage, *e.g.* Totton, 1965, and differ from those quoted by Leloup, 1934.) Consequently Leloup (1934) decided to recognize only a single genus *Rosacea*, within which he erected three groups, namely *Rosacea*, *Prayoides*, and *Praya*. He noted that within these groups there was an evolutionary progression in the structure of the nectophores from the group *Rosacea*, with a simple somatocyst (gastro-vascular canal) and four simple subumbrella canals; through the group *Prayoides*, where the subumbrella canals were ramified; to the group *Praya*, with ramifications of both the somatocyst and the subumbrella canals. Totton (1965), however, considered that all three of these groups should have generic status, and so he raised *Prayoides* to generic rank.

Leloup's (1934) description of *Prayoides intermedia* was based on three nectophores, two of which remained attached to each other. One of the key features of the attached nectophores was that one had a descending branch to its simple somatocyst, while the other did not. This would suggest (see Totton, 1954) that the latter was a larval nectophore, while the former was the first definitive one. Both nectophores were also said to have short ascending branches to the somatocyst, in the region where muscular lamellae connected the two nectophores to the stem. Unfortunately it has not proved possible to verify Leloup's (1934) description, as the whereabouts of the specimens has not been traced.

Over the past 20 y more than 50 pairs of attached nectophores that show the basic features of *Prayoides intermedia*, as described by Leloup (1934), have been found in the

'Discovery' collections (Kirkpatrick & Pugh, 1984; Pugh, 1984 and unpublished data). However, none of these is well preserved and it was not until similar pairs of nectophores, with attached stem groups, were collected intact by the submersibles 'Johnson-Sea-Link' (JSL) I and II that it became possible to re-assess the status of *P. intermedia*.

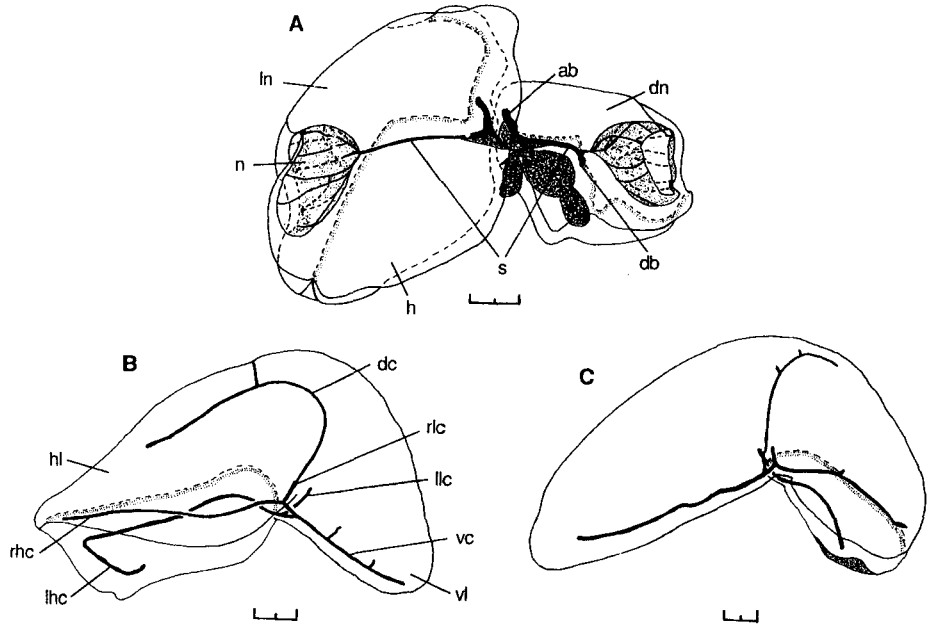

Figure 1. (A) *Prayoides intermedia* Leloup (1934). Lateral view of specimen. Redrawn from Leloup (1934, figure 4). (B) Right and (C) left lateral views of bracts of *Praya reticulata*; redrawn from Bigelow (1911, plate 3, figure 6; 1931, figure 185, respectively). Scale bars: ~2 mm. ab & db, ascending and descending branch to somatocyst, s; dn & ln, definitive and larval nectophore; h, hydroecium; hl & vl, hydroecial and ventral lobe; n, nectosac. The bracteal canals are: dc, dorsal; lhc & rhc, left and right hydroecial; llc & rlc, left and right longitudinal; and vc, ventral.

MATERIAL EXAMINED

Eleven relatively small specimens of *Praya* spp. collected in recent years by the submersibles JSL I and II in the vicinity of the Bahamas. All specimens comprise one or two nectophores, but unfortunately not all have associated bracts. Eight of the specimens belong to *P. dubia* and two to *P. reticulata*. The other specimen (JSL Dive 974) probably belongs to *P. dubia*, as is discussed below, but none of its bracts was retained. In addition, several specimens of both species housed in the 'Discovery' collections have been re-examined, and some bracts of *P. reticulata* have been loaned to me by Dr F. Pagès.

MORPHOLOGY OF THE BRACTS OF *PRAYA* SPECIES

Introduction

Before describing the larval and young definitive nectophores of *Praya dubia* and *P. reticulata* it is important to establish their provenance as, for the reasons discussed below,

they may be difficult to distinguish. Their bracts, however, can be separated, although until now the structure of these bracts has not been well established, and there appears to have been some confusion in the past. Bigelow (1911) gave an illustration (see Figure 1B), but no description, of a bract that he found in association with a specimen of *Nectodroma (Praya) reticulata*. From this figure it can be seen that there is a long, recurved dorsal bracteal canal, and that the left hydroecial bracteal canal is longer than the right one, and also is recurved. Further bracts of similar design (and also collected in association with nectophores of *P. reticulata*) were described by Bigelow (1913), who stated (p. 66) that "the fact that the bracts of this type have now been taken twice with the nectophores is almost proof positive that they belong together".

Bigelow (1931) described further bracts that he also ascribed to *Praya reticulata* (see Figure 1C). He noted that the dorsal bracteal canal always arose from "the right hydroecial trunk", as it had done in his other specimens. However, it is clear from Figure 1C, and according to modern terminology (see Pugh & Harbison, 1987), that the dorsal canal actually arises from the right longitudinal canal, not the hydroecial. It appears that Bigelow did not distinguish between them. Bigelow (1931) found that the length of the dorsal canal was quite variable, such that in some bracts it merely ran to the dorsal surface, while in others it was recurved, but not to the degree previously observed, and gave off short side branches. Similarly the lengths of the other main bracteal canals were variable and, in his figure, the left hydroecial canal does not appear to be recurved (Figure 1C).

Totton (1965, p. 122) noted that the bract of *Praya dubia* had "not hitherto [been] recorded as such. I am inclined, however, to think that the bract figured by Bigelow (1931, figure 185) coming from Monterey Bay, California .... and labelled *P. reticulata* really belongs to *P. dubia*.". Totton based this assertion on the facts, as noted by Bigelow (1931), that "the right [left - according to the terminology adopted herein] hydroecial canal is not recurved at the tip as it is in *P. reticulata*, nor is the dorsal bracteal canal so long and recurved and the ventral bracteal canal ... is not branched as in the original figure of the bract of *P. reticulata*.". Totton (1965, figure 70A) reproduced Bigelow's (1931) figure, but under the name *P. dubia*, and he included another illustration of a bract (figure 70B) which was also ascribed to that species. However, the latter figure clearly shows that the dorsal and left hydroecial canals are recurved, which are the very criteria that Totton (1965) used to characterize *P. reticulata* bracts. It is concluded that Totton (1965) here was mistaken, for these characters, when present, are indeed typical of *P. reticulata*. Indeed Totton (1965) noted that both species were present in the sample from the relevant 'Discovery' station. None the less, in some of the present material of *P. reticulata* (see below) the recurving of the dorsal and left hydroecial bracteal canals is not always evident, as was also the case for Bigelow's Monterey Bay material. A re-examination of this latter material, which was kindly lent by the Museum of Comparative Zoology, Harvard, has led to the conclusion that the bracts do belong to *P. reticulata*, although they are the least typical of all those examined (see below). Thus neither of Totton's (1965, figure 70) illustrations represent *P. dubia* bracts, whose structure therefore remains to be described accurately.

Description

Figures 2 & 3 illustrate some bracts, at varying stages of development, of *Praya dubia* and *P. reticulata* respectively. The shape of the bract of both species depends greatly on how well it is preserved, and also on its age. The bract is divided into two main lobes, ventral and hydroecial (see Figure 1B), and the latter has left and right ventral extensions or flaps. In general the ventral lobe is larger than the hydroecial one in *P. dubia*, whereas in *P. reticulata* they are of approximately equal size, or the hydroecial appears larger. The right (distal) side of the bract is usually concave in shape, particularly around its outer margin, which is marked by a distinct ridge. In older, less well preserved, specimens this side tends to appear flattened. Whereas in *P. dubia* the outer margin of the right side of the bract is rounded in lateral view, in *P. reticulata*, in the younger specimens at least, it comes to a dorsal, rounded point.

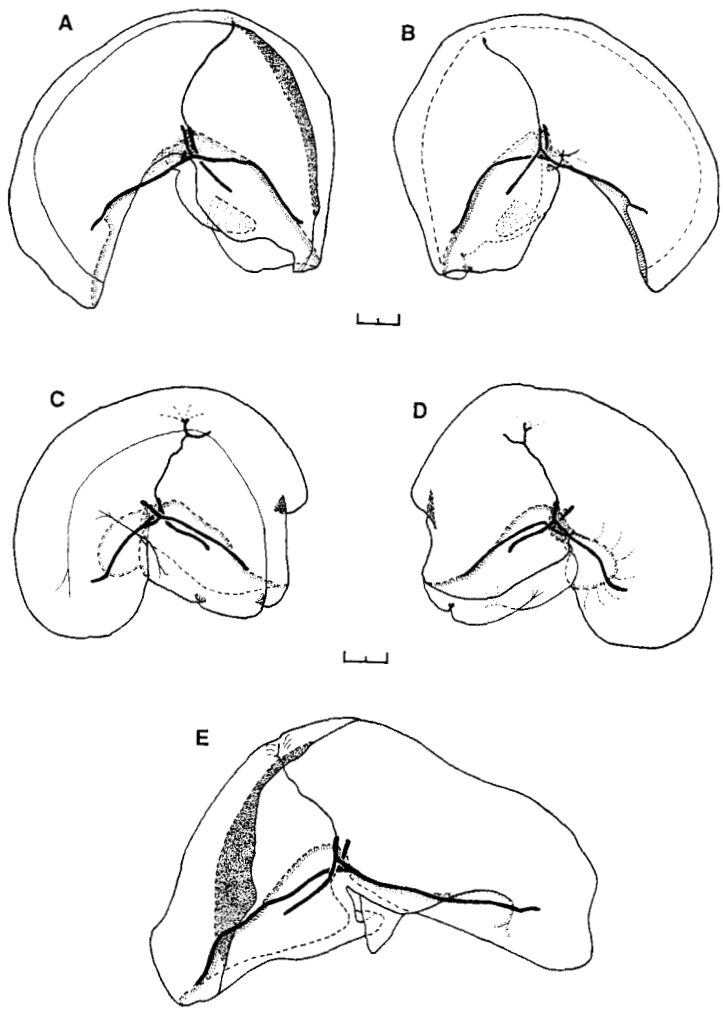

Figure 2. Bracts of *Praya dubia*. (A) & (C) Left; and (B) & (D) right lateral views of specimens from the submersible 'Johnson-Sea-Link II' Dives 962 and 1671; (E) right lateral view of larger bract from 'Discovery' Station 7709#23. Scale bars: 2 mm.

The left (proximal) side of the bract is slightly convex, and usually smaller than the right side, allowing successive bracts, especially the younger ones, to fit snugly together. Its outer margin is also demarcated by a ridge, but in *P. dubia* bracts it is obvious only in the smallest specimens. However, for *P. reticulata*, part of the ridge usually can be found on all sizes of bracts. In this latter species there is a deep furrow (Figure 3) that runs longitudinally across the dorsal surface of the bract, which may interrupt the ridge, particularly in the younger specimens. The part of the ridge on the hydroecial lobe is more prominent than that on the ventral lobe, as it runs along a fold in the surface of the bract. This 'vertical' fold was clearly illustrated by Totton (1965, figure 70B, *f.v.*) but, as noted above, attributed to the wrong species. From the material studied it appears to be a good character to distinguish the bracts of *P. reticulata* from those of *P. dubia* as it can be discerned in bracts of all ages, and Bigelow's (1931) material shows it clearly. The 'vertical' fold (Figure 3) runs down apparently to end on the left hydroecial flap, although in the older bracts it tends to end closer to the tip of that flap. This probably reflects an age-related change in the configuration of the left side of the bract, which becomes proportionally larger in the older bracts. Totton's (1965, figure 70B, *f.h.*) 'horizontal' fold (Figure 3C) can be seen running obliquely across the left side of the furrow in some, but not all, bracts of *P. reticulata*.

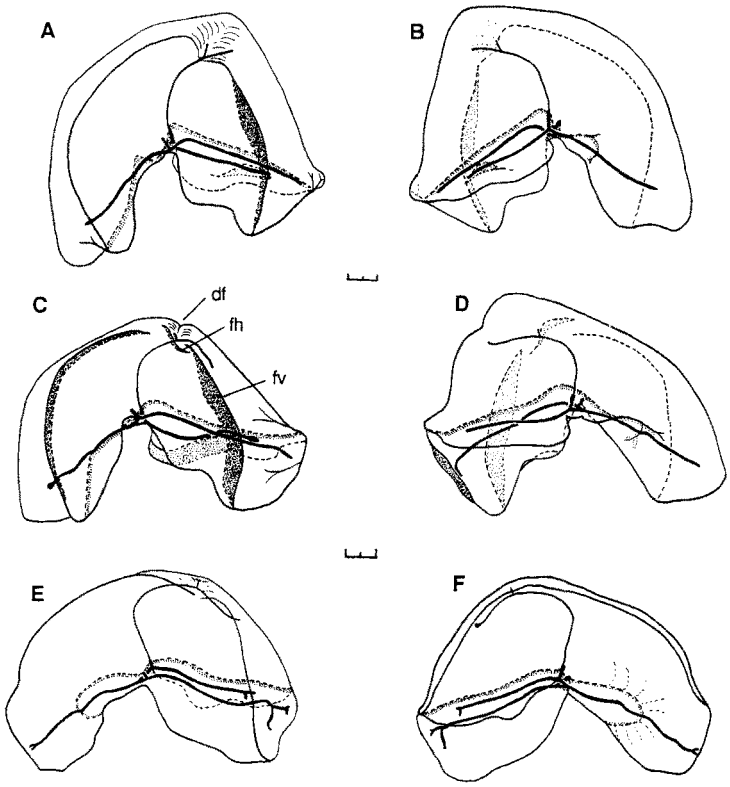

Figure 3. Bracts of *Praya reticulata*. (A), (C) & (E) Left; and (B), (D) & (F) right lateral views of specimens from the submersible 'Johnson-Sea-Link I' Dive 2655, from 'Discovery' Station 6662#10, and one kindly provided by Dr F. Pagès, respectively. Scale bars: 2 mm. df, dorsal furrow; fh & fv, horizontal and vertical fold.

In *Praya dubia* bracts, the right and left hydroecial flaps, which demarcate the hydroecium, are usually approximately the same size (Figure 2). In the younger bracts of *P. reticulata* (Figure 3A-D), the left hydroecial flap is distinctly larger than the right. However, this may not be a reliable distinguishing character, as in some older bracts, particularly from the Bigelow material, the reverse may be true. On the inner margin of the right hydroecial flap, in both species, an additional, dorsally directed, flap or thickening often can be discerned. The hydroecium itself forms only a shallow depression in the proximal part of the ventral surface of the ventral lobe. It rapidly increases in depth in the hydroecial lobe from the point where the ventral and longitudinal bracteal canals unite, and continues to the distal end of that lobe, where the two hydroecial flaps unite.

The bracteal canal system conforms to the basic prayid design. There are six recognizable canals; dorsal, ventral, and left and right hydroecials and longitudinals. However, some authors prefer to recognize only a single longitudinal canal, with proximal (left) and distal (right) branches. The latter branches are quite prominent in *Praya* species, and their distal regions are surrounded by small pockets of the hydroecium. Contact with the main siphosomal stem occurs only in the region proximal to the origins of the hydroecial canals.

In both species the dorsal bracteal canal arises from the right longitudinal canal and usually at its distal end, although in some of Bigelow's (1931) material it arises subterminally (Figure 1C). It is usually narrower than the other canals (Figures 2 & 3). In *Praya dubia* the dorsal canal usually runs dorsad for a short distance, before curving towards the hydroecial lobe and then, in its simplest arrangement, recurving dorsad and running up to end just below a shallow, but marked, depression on the surface of the bract (Figure 2A). It may bifurcate sub-terminally. It may also give off a side branch, close to its distal end, which runs obliquely out, for a varying distance (up to ~1·5 mm in the material examined), towards the right side of the bract (Figure 2C-E). The arrangement of the dorsal bracteal canal in *P. reticulata* is quite similar. However, it usually runs dorsad for a longer distance before curving round towards the hydroecial lobe, and ultimately running to end below a relatively deep depression in the dorsal surface, which extends as a longitudinal furrow across the surface of the bract. A distal branch (Figure 3) to the canal, running obliquely out towards the right side of the bract, is usually present, but in several of Bigelow's (1931) bracts it is absent. This branch, when present, is usually much longer than any such branch found in *P. dubia* bracts and would then represent a characteristic feature distinguishing the bracts of the two species. However, in some of the younger bracts (Figure 3A,B) of *P. reticulata*, and in Bigelow's (1931) material, this branch can be relatively short. Many of the bracts in Bigelow's material have an additional branch, or branches, of varying length from the proximal part of the dorsal canal (Figure 1C).

The right hydroecial canal is shorter than the left in both *Praya* species, and runs down approximately in the middle of the right hydroecial flap. However, in *P. dubia* the length of this canal is always less than half, usually ~40%, that of the hydroecial lobe itself; whereas in *P. reticulata* its length is almost always greater than half, usually 65-75%, that of the lobe. In some bracts of *P. dubia* it was found that the distal end of the canal was

inflected, away from the hydroecial wall, into the mesogloea. In *P. reticulata* bracts it may end in a slight swelling, or be bifurcated (Figure 3E,F), or be inflected away from the hydroecial wall. All three of these features were particularly prevalent in the Bigelow material.

The 'characteristic' recurving of the distal end of the left hydroecial canal in *Praya reticulata* is not always apparent (Figure 3A-D), but when it is it clearly distinguishes the bracts of that species. It may also have branches or have a sub-terminal bifurcation. When it is absent, the length of the canal is similar in both species. There may be specific differences in the arrangement of the canal, but these have not been established clearly. For instance in the *P. dubia* bracts examined the canal at first runs along the left side of the hydroecium; but in its distal half it comes to lie on the dorsal wall of the hydroecium, approximately in the mid-line. In that region it may be slightly enlarged and have a short, terminal inflexion, sometimes marked by a constriction, into the mesogloea. In *P. reticulata*, for all but the Bigelow material, this canal runs along the left, lateral wall of the hydroecium, in the upper half of the left hydroecial flap. In the Bigelow material the canal appears to have a similar course to that just described for *P. dubia*. However, the distal 2-3 mm of the canal is inflected away from, but runs parallel to, the hydroecial wall. This inflected region is thickened, often markedly, and may have a subterminal bifurcation. It is much longer than the inflexions noted for *P. dubia*. In addition there are often short branches to the canal before it inflects into the mesogloea.

Although the recurvings of the dorsal and left hydroecial bracteal canals have previously been taken as characters to distinguish the bracts of *Praya reticulata* from those of *P. dubia*, it is the structure of the ventral bracteal canal that usually shows the greatest difference between the two species. In both species the ventral canal is of similar length, but in *P. dubia* it remains in contact with the surface of the shallow hydroecium for most of its length and has only a relatively short (0·5-2 mm, depending on age) sub-terminal inflexion into the mesogloea (Figure 2). In *P. reticulata*, however, a much greater proportion of the canal is inflected into the mesogloea, away from the surface wall. The actual proportion appears to vary with age: from about two-thirds in the younger bracts (Figure 3A,B), decreasing to about one-third in the oldest (Figure 3E,F). This difference in the arrangement of the ventral bracteal canal appears to be the easiest and most obvious feature that can be used to separate the bracts of *P. dubia* and *P. reticulata*. However, yet again, the Bigelow material appears to be exceptional. In some specimens the proportion of the ventral canal that is inflected may be as low as 20%, but in general it is usually longer than 2 mm. In addition, the ventral canal, as with all the major canals, may have short side branches, often where the inflexion begins.

From the above descriptions it should be possible to distinguish the bracts of the two *Praya* species. The Bigelow (1931) bracts proved to be the most difficult to speciate, but the presence of the 'vertical' fold, and the long inflexion of the left hydroecial and, usually, ventral canals leads to the conclusion that they do belong to *P. reticulata*. After an examination of the type material it is also possible to confirm that the bracts, described under the name *Nectocarmen antonioi* Alvariño, 1983, actually belong to *P. dubia*, as Pugh & Harbison (1987) asserted. The morphology of the nectophores could not be confirmed as no structures approximating their original description were found in the material sent.

Because of the presence of associated bracts it has been possible to speciate many of the 'Johnson-Sea-Link' specimens, whose young nectophores show few of the distinguishing features so characteristic of the well-developed nectophores. It has not, however, been possible to find any good characters to distinguish the gonophores of the two species (Figure 4). Both show the trifid branching at the proximal end of the pedicular canal - a characteristic of the genus *Praya*. However, it should be noted that some gonophores in the Bigelow (1931) material show short branches arising from the three main branches. In the JSL material (Figure 4) each cormidium contained only a single large gonophore, which is presumably very young as the manubrium is minute and not filled with sexual products. This differs from Bigelow's (1931) assertion that up to nine gonophores, of both sexes, were present on each cormidium. Re-examination of Bigelow's material appears to confirm the presence of several gonophores, of both sexes, on each cormidium, although the siphosomal stem is highly contracted. However, there are indications of a regularity in the arrangement of the male and female gonophores that deserves to be investigated further on fresh material.

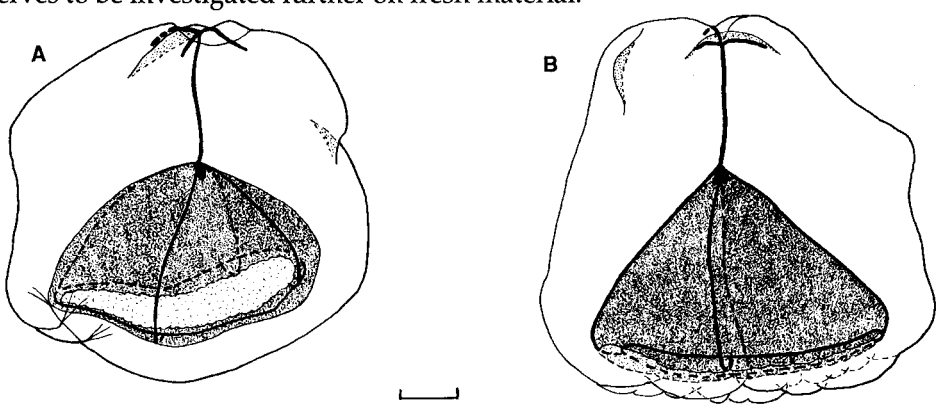

Figure 4. Lateral view of young gonophores of (A) *Praya reticulata*, and (B) *P. dubia*, from the submersible 'Johnson-Sea-Link I' Dive 2655 and from 'Johnson-Sea-Link II' Dive 717 respectively. Scale bar: 1 mm.

STRUCTURE OF THE LARVAL AND YOUNG DEFINITIVE NECTOPHORES OF *PRAYA* SPECIES

The larval and the first, young definitive nectophores of *Praya dubia* and *P. reticulata* are shown in Figures 5 & 6 respectively. The larval nectophores, which characteristically do not have a descending branch to the somatocyst, are very similar in both species. They are wide, flimsy structures, measuring up to 34 mm in length amongst the JSL specimens. They are apically truncated, but bear no signs of ridges. The hydroecium is extensive, in order to accommodate the definitive nectophore, and runs the entire length of the nectophore. However, it is very shallow basally, and relatively shallow in the region where the nectophore is attached to the stem and to the definitive nectophore (see Figure 7). The somatocyst is a simple tube, running from its basal junction with the pedicular canal along the dorsal wall of the hydroecium, in the mid-line. It is thicker in the region of attachment, where an extensive muscular lamella is apparent, which extends from the

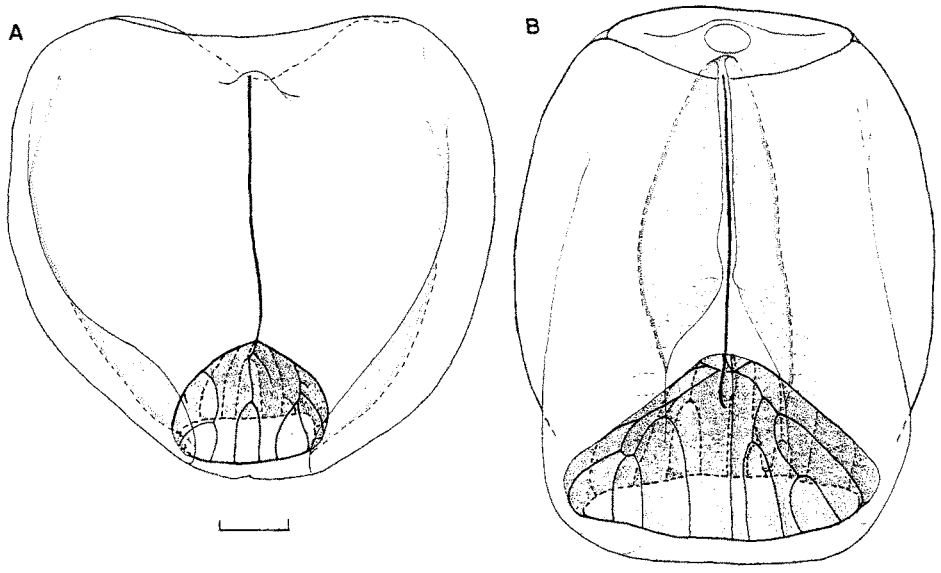

Figure 5. *Praya dubia*. Ventral views of (A) larval and (B) young definitive nectophores, from the submersible 'Johnson-Sea-Link II' Dive 1671. Scale bar: 5 mm.

apex of the somatocyst to just basal of the origin of the canal connecting the latter to the stem. There is no apical inflexion into the mesogloea. This would appear to contrast with Leloup's (1934) description of the larger (larval) nectophore of his *Prayoides intermedia*, as he described a short, thicker, simple, ascending branch to the somatocyst. However, a comparison of his figure (see Figure 1A) with Figure 7 indicates that the apical extension of the somatocyst is not a true ascending branch. In fact, in its apical region, the somatocyst continues to remain in contact with the dorsal wall of the hydroecium, which is there deep and opens extensively onto the apical surface. In accord with Leloup's (1934) description, the somatocyst is usually thickened in the region of attachment of the muscular lamellae, apical to the canal that connects the somatocyst to the stem. This interpretation also applies to the apical extension of the somatocyst of the larval nectophore of *P. intermedia* illustrated by Kirkpatrick & Pugh (1984, figure 20), although the extension is relatively thin.

The pattern of the radial canals on the nectosac of the larval nectophores of the two species is quite distinct in these specimens, and conforms to that which would be expected for each. In *Praya dubia* (Figure 5A) a simple, bifurcating arrangement of canals is discerned, with several incomplete branches being apparent. In *P. reticulata* (Figure 6C), although there are several incomplete branches, a pattern of anastomosing canals is present. The larval nectophore of the specimen from JSL II Dive 974 (Figure 7), with the definitive nectophore still attached, has a simple, bifurcating arrangement of the radial canals and so it almost certainly belongs to *P. dubia*. However, there are some peculiarities to the canal system on the nectosac of the definitive nectophore (see below). The canal system on Leloup's (1934) specimen (see Figure 1A) may show some anastomoses, but the arrangement, as drawn, appears illogical.

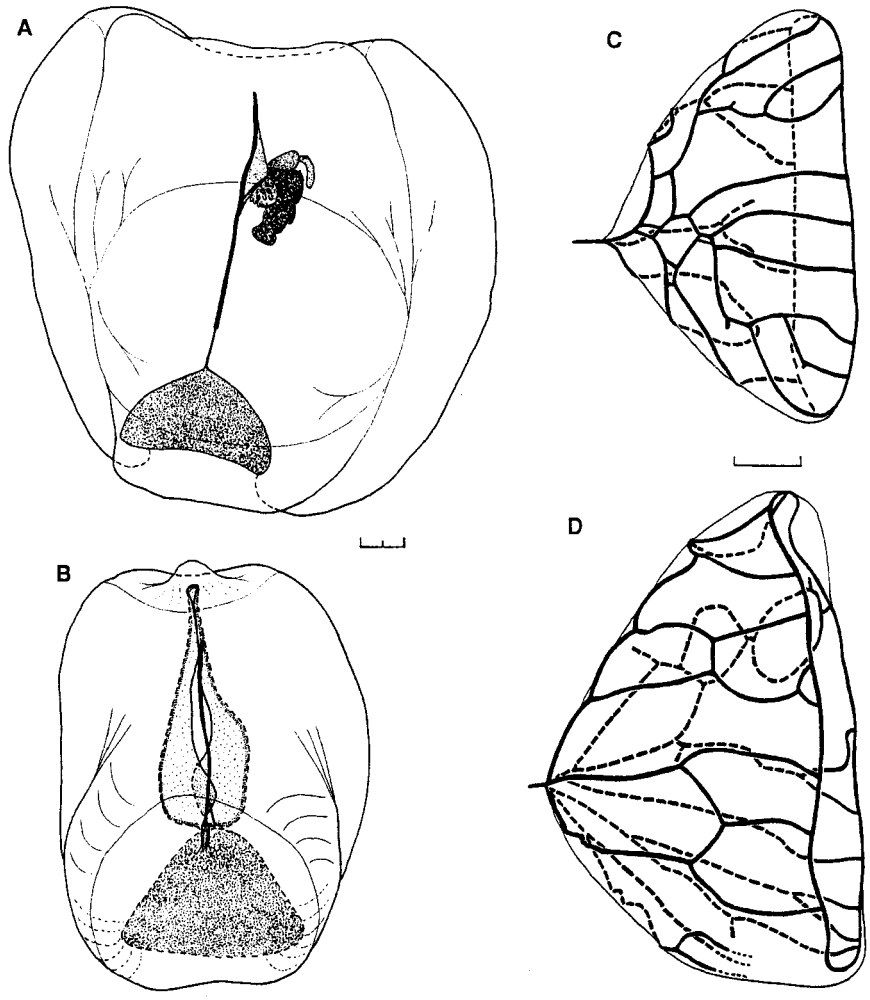

Figure 6. *Praya reticulata*. (A) & (B) Ventral views, respectively, of larval and young definitive nectophores from the submersible 'Johnson-Sea-Link II' Dive 976. Scale bar: 2 mm. (C) Dorsal and (D) ventral detail of the pattern of radial canals on the nectosac of (A) & (B) respectively. Scale bar: 1 mm.

The young definitive nectophores of *Praya dubia* and *P. reticulata* (Figures 5B, 6B, 7 & 8A) are also quite similar in basic construction. In both species the somatocyst remains simple, but apically it shows a slight inflexion into the mesogloea, away from the wall of the hydroecium, and basally it has a descending branch. The muscular lamella, in the region of attachment, is not as well-developed as in the larval nectophore, but it can be seen to extend apically, almost to the point where the somatocyst inflects into the mesogloea. This is basically in accord with Leloup's (1934) description for *Prayoides intermedia*. In the youngest specimens (Figures 6B & 7) the hydroecium is restricted in width and length. It does not reach to the base of the nectophore, and the ventral surface below the nectosac forms a round, flattened facet. In the older nectophores the hydroecium is more extensive, and reaches to and opens widely on the base of the nectophore, although it has little depth in the region beneath the nectosac. Apically the hydroecium

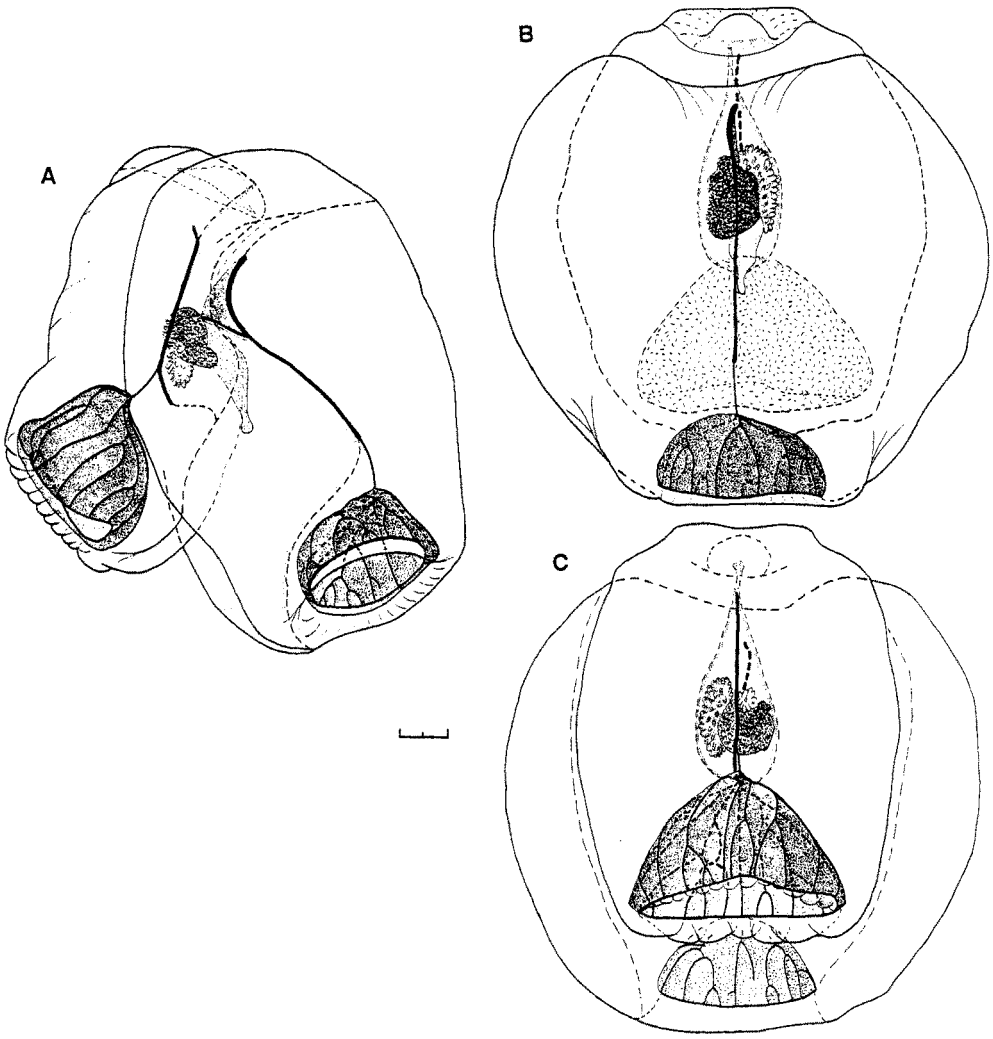

Figure 7. Post-larval specimen of *Praya dubia*. (A) Lateral view, (B) dorsal view of larval nectophore and (C) dorsal view of young definitive nectophore from submersible 'Johnson-Sea-Link II' Dive 974. Scale bar: 2 mm.

still reduces to a narrow slit that ends below the median apical protuberance. However, in the largest specimens, it is widely open apically. A distinct but rounded margin runs down the sides of the nectophores, from the truncated apex to the level of the nectosac. In the youngest *P. reticulata* specimen (Figure 6D) the radial canals on the nectosac have a haphazard distribution, with several anastomoses and blind-ending branches. However, in a larger specimen (Figure 8A) the canal system basically shows a bifurcating pattern, with relatively few anastomoses. If it were not for the presence of associated bracts, this nectophore might have been difficult to identify. This is because the radial canals on the nectosac of *P. dubia* specimens, although having a basic bifurcating pattern, also show occasional anastomoses (Figures 5B & 9B), but again the presence of the

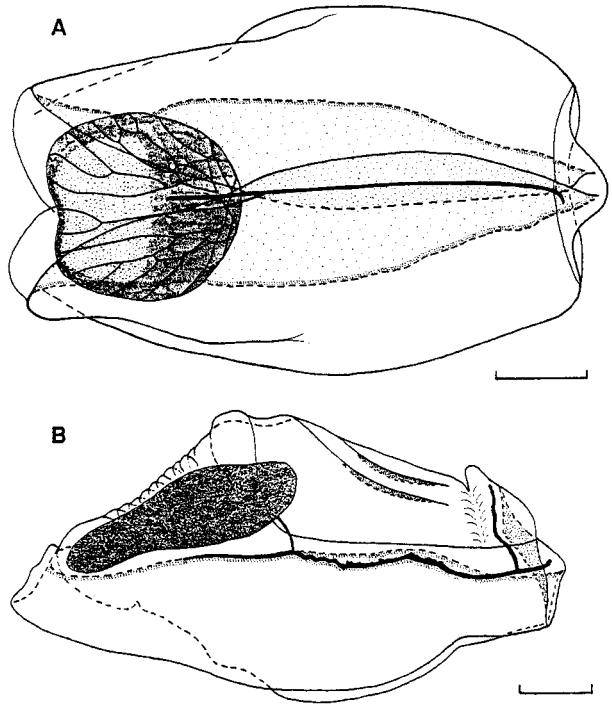

Figure 8. *Praya reticulata.* (A) Ventral view of young definitive nectophore, from the submersible 'Johnson-Sea-Link I' Dive 2655, and (B) lateral view of more mature nectophore, from 'Discovery' Station 12183#26. Scale bar: 5 mm.

characteristic bracts makes their identity certain. The young definitive nectophore of the specimen with the attached larval nectophore (Figure 7), but no associated bracts, also shows a couple of anastomoses of its radial canals. However, it is presumed that the specimen belongs to *P. dubia* because of the arrangement of the canals on the nectosac of the larval nectophore, as discussed above.

As the definitive nectophores grow, probably after the loss of the larval nectophore and the appearance of the second definitive one, the characteristic pattern of branching of the somatocyst begins to appear. In *Praya reticulata* the sub-terminal ascending branch appears (Figure 8B), which runs dorsad. Then numerous short canals begin to branch off from the main somatocyst. Also several longitudinal ridges and furrows begin to appear on the dorsal surface of the nectophore, in its apical half. These are very characteristic of the mature nectophore, although they do not seem to have been recorded previously, and serve as an easy means to distinguish the species from *P. dubia*. The nectophore now begins to take on its mature shape, with the extension of the ventro-basal region beneath the nectosac. As the definitive nectophores of *P. dubia* mature, the two lateral extensions of the somatocyst are branched off first (Figure 9A). They do not always arise together from the main canal, which itself continues to run apically with only a slight terminal inflexion into the mesogloea. At a later stage the main somatocyst comes to run dorsad from its junction with either one of the laterals, which themselves begin to branch further. This change in direction of the main somatocyst may come about in conjunction with a

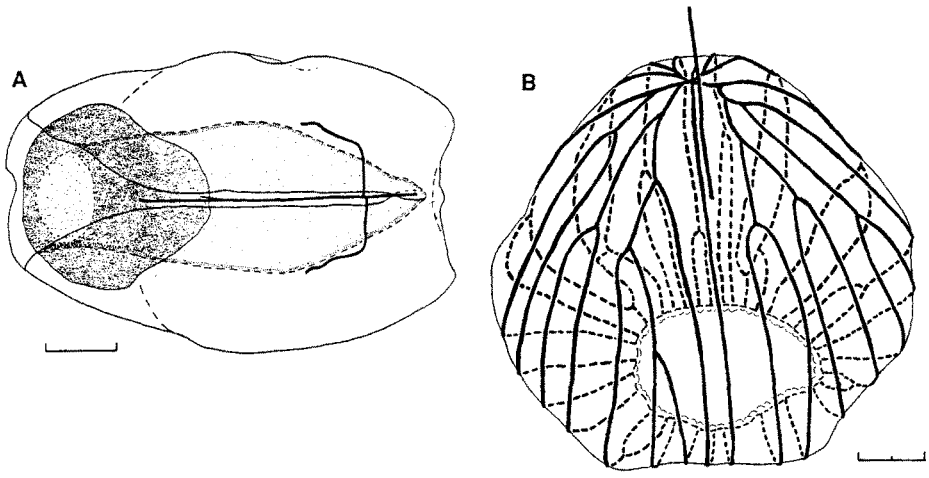

Figure 9. *Praya dubia*. (A) Ventral view of young definitive nectophore. Scale bar: 5 mm. (B) Detail of the canals on its nectosac (ventral view), from the submersible 'Johnson-Sea-Link II' Dive 717. Scale bar: 2 mm.

further truncation of the apical region of the nectophore. However, in the largest (>90 mm in length) specimens examined, another branch, running apically along the hydroecial wall, is developed, and the dorsad ascending branch becomes sub-terminal. In these fully mature nectophores an additional ascending branch usually leaves the main somatocyst, somewhere between the origins of the laterals and the pedicular canal, and runs dorsad. This branch does not appear to have been described previously. In these large specimens it is still possible to see occasional anastomoses of the radial canals on the nectosac, which possibly reflect the method of development of additional branches to the system. Although the dorsal surface of these specimens is not smooth, it does not bear the distinctive pattern of longitudinal ridges and furrows found on the *P. reticulata* nectophores.

DISCUSSION

The key criteria that led Leloup (1934) to erect a new species, *Rosacea (Prayoides) intermedia*, were that his specimens showed features intermediate between the genera *Rosacea* and *Praya*, namely the somatocyst was simple, while the radial canals on the nectosac were ramified. Although both nectophores were said to have ascending branches to the somatocyst, only one possessed a descending branch. As noted above, this could indicate that the nectophore without a descending branch was larval - although descending branches are not always present in the definitive nectophores of other prayine siphonophores (see Pugh & Harbison, 1987). The remainder of Leloup's (1934) brief description deals with the disposition of the muscular attachment lamellae, close to the top of the somatocyst of each nectophore, and the presence of a bud, possibly representing a primordial 'reserve' or replacement nectophore.

Although Leloup's (1934) description was brief, there did appear to be sufficient reason to separate his species from other prayine siphonophores. Consequently Totton

(1965) not only accepted the species as valid, but raised the name *Prayoides* to generic rank. This has been followed by subsequent authors (*e.g.* Pugh & Harbison, 1987). However, with the collection of intact specimens of young *Praya* species by the submersibles 'Johnson-Sea-Link' I and II, it has become necessary to revise this opinion. Because many of the JSL specimens comprise both nectophores and bracts, at various stages of development, it has been possible not only to establish criteria to distinguish the bracts of *P. dubia* and *P. reticulata*, regarding which there has been much confusion in the past, but also to study the various stages in the development of the nectophores, particularly with regard to the somatocyst.

It is clear, as would be expected for a prayine siphonophore, that during their development *Praya* species first of all develop a larval nectophore, which has a simple somatocyst, without ascending or descending branches. The arrangement of the radial canals on the nectosac appears to reflect that of the definitive nectophores, in that there is a bifurcating system in *P. dubia* and an anastomosing one in *P. reticulata*. The young definitive nectophores of *Praya* species also have a simple somatocyst, but both a descending branch and a short ascending one are present. The arrangement of the radial canals on the nectosac shows the characteristic features for each species, although there may be relatively few anastomoses in those of *P. reticulata*, and occasional ones in those of *P. dubia*. Even the largest specimens of *P. dubia* appear to show a few anastomoses amongst their radial canals, and this would appear to represent a stage in the development of new canals. None the less, without the presence of the characteristic bracts, it might be difficult to identify the young definitive nectophores. As development proceeds, the somatocyst of the definitive nectophore begins to branch. In *P. dubia* the characteristic lateral branches appear, while in *P. reticulata* the sub-terminal, dorsad, ascending branch is developed, as well as many small branches from the somatocyst itself.

From the above descriptions it is clear that there is a close resemblance between the larval and young definitive nectophores of *Praya* species and the nectophores described by Leloup (1934), under the name *Rosacea (Prayoides) intermedia*. It appears that a true ascending branch to the somatocyst, which penetrates into the mesogloea, is not present in the larval nectophore of any of the species. Instead the apical extension of the somatocyst remains in contact with the hydroecium, a feature that is consistent with Leloup's (1934) figure (see Figure 1A). With regard to the definitive nectophores, there are no obvious differences in the form of the somatocyst between Leloup's (1934) material and the young *Praya* specimens from the JSL collections. Leloup (1934) described the radial canals of both nectophores of *Prayoides intermedia* as being ramified, but their exact arrangement is difficult to establish from his figure. None the less, the fact that they are ramified in some way shows a close affinity with the situation in *Praya* species. Thus it is concluded that *Prayoides intermedia* is not a valid species. The specific name is hereby reduced to that of a junior synonym of a *Praya* species, most probably *P. dubia*. However, it is not possible to be absolutely sure to which species it belongs, unless the exact arrangement of the radial canals on the nectosacs of Leloup's (1934) specimens can be established.

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