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The taxonomic status of the genus *Moseria* (Siphonophora, Physonectae)

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Abstract

The status of the two species presently included within the genus *Moseria* (Siphonophora, Physonectae), *M. convoluta* (Moser, 1925) and *M. similis* Margulis, 1977, is reviewed. Based on the availability of new material, described herein, both are considered valid. They can be distinguished by the morphology of their bracts, tentilla and palpons. Whether there are differences in the nectophores remains to be resolved.

As the generic name *Moseria* is pre-occupied for a ctenophore, a new generic name is required and *Resomia*, gen. nov., is proposed. The systematic position of this genus within the physonect siphonophores is discussed in light of recent molecular phylogeny studies (Dunn *et al.* 2005b).

Key words: Siphonophora, Physonectae, *Moseria*, *Resomia*, Systematics, Molecular Phylogeny

Introduction

Moser (1925) described a new species of physonect siphonophore, *Stephanomia convoluta*, collected at three sites in the region of Posadovsky Bay, Antarctica (c. 65°S, 89°E) during the Deutsche Südpolar Expedition. She described and figured the characteristic heart-shaped nectophores, the palpons, the gastrozooids, and the bracts, which had a transverse ridge delineating a distal facet on the upper side and a patch of nematocysts at the distal end of the bracteal canal. The structures of the nectophores and bracts were particularly distinctive in comparison with other physonect species known at the time. Moser also considered that the structure of the pneumatophore, which she believed was divided into three chambers, was a clear distinguishing character.

However, it was the unique structure of the tentillum (Moser 1925, Plate XXXII, fig. 4) (see Fig. 1) that was of particular interest. Her description of the tentillum is somewhat difficult to follow as she described its cnidoband (*ibid,* p. 433) as "in der Dorsoventralebene zu einer langen, flachen Spirale mit drei Windungen aufgerollt." The

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description would be easier to understand if one considered the cnidoband as being concertinaed into three segments, all lying in the same plane. Thus, the nematocysts of the proximal third of the cnidoband lay against those of the middle third, while the inner sides of the second and third parts were juxtaposed (see Moser 1925, Plate XXXII, fig. 5). The whole cnidoband was covered in an involucrum, through which the spirally coiled terminal filament projected. Moser (1925, Plate XXXII, fig. 3) (see Fig. 2) also illustrated a gastrozooid and part of its tentacle that bore several tentilla. One of these had a loosely coiled cnidoband, which Moser interpreted as the result of the activation of the cnidoband, which had burst through the involucrum, and stretched out into a loose spiral. In this review another interpretation will be considered.

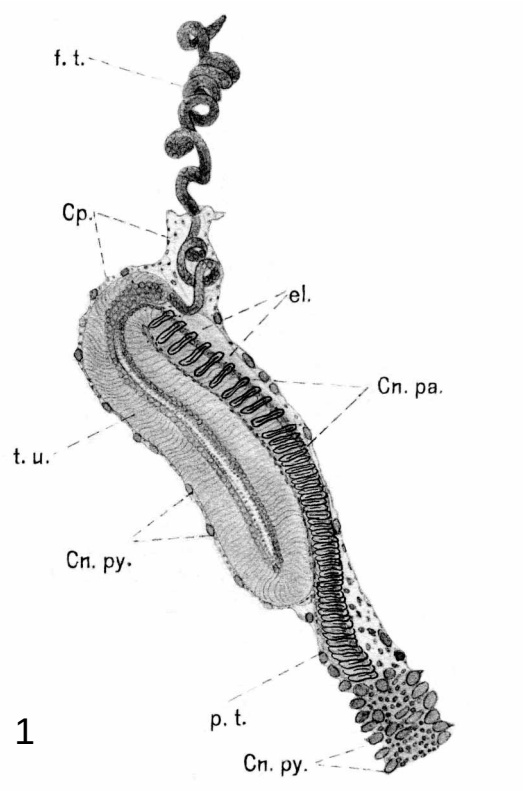

FIGURE 1. Optical section of a tentillum of *Stephanomia convoluta* from the lateral side (from Moser 1925, Plate. XXXII, fig. 4). **Cn.pa.** — Rod-shaped nematocysts; **Cn. py.** — bean-shaped nematocysts; **Cp.** — involucrum; **el.** — elastic band; **f.t.** — terminal filament; **p.t.** — pedicle; **t.u.** — cnidoband.

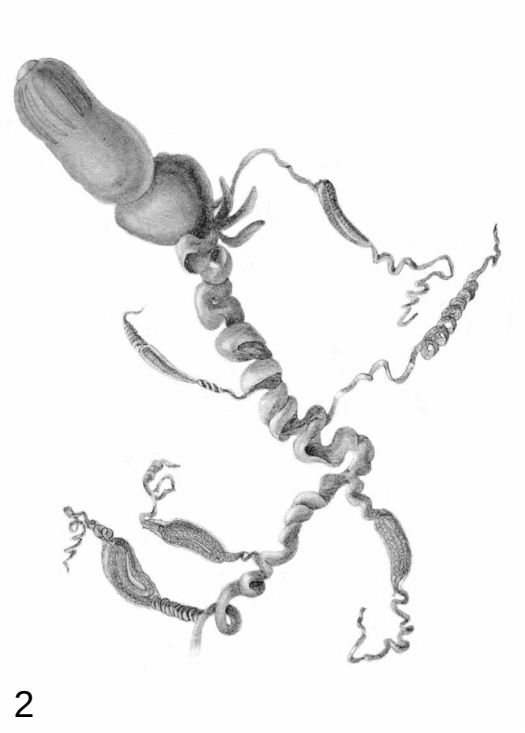

FIGURE 2. A gastrozooid and part of its tentacle, with several tentilla, of *Stephanomia convoluta*. One of the tentilla is rolled up into a spiral and has lost its involucrum. (From Moser 1925, Plate XXXII, Fig. 3).

The species *Stephanomia contorta* was not considered again in detail until Totton (1965), who had additional material, included it in his *Synopsis of the Siphonophora*. Nonetheless, it is not clear how much of Totton's description was based on that of Moser or on his own material. His nectophores and bracts were clearly in poor condition (see Totton 1965, Plate XIII, figs. 5–10), but he confirmed Moser's description, with particular regard to the transverse ridge dividing off a distal facet on the upper side of the bract. However, his description of the nematocyst batteries on the bracts appears contradictory, as discussed below. He also described both male and female gonophores as being present on a single specimen, thus indicating that the species was monoecious.

With regard to the tentilla, Totton (1965, p. 67) strongly disagreed with the original description when he stated "the tentilla described and figured by Moser (1925) did not belong to this species." He described another sort of tentillum, but unfortunately did not figure it. He noted that when this type of tentillum was fully developed, the cnidoband was spiralled into seven or eight coils, the first two or three of which were covered by an involucrum. The latter, in preserved specimens, could become turned back over the pedicle of the tentillum. There was a single terminal filament. Finally, Totton also noted that the material of *Moseria* available to him indicated the possible existence of a second species.

Moser (1925) originally placed her species in the genus *Stephanomia* Lesueur & Petit because she considered that its closest relative was *S. rubra* Vogt (= *Halistemma rubrum*), nonetheless noting that its actual systematic position was uncertain. Although Totton (1954) retained the genus *Stephanomia*, he considered that the original species *S. amphytridis* Lesueur & Petit was at that time unidentifiable, despite the fact he had earlier published records of it from the *Beebe* collections (Totton 1936). In his Synopsis, Totton (1965) abandoned the generic name *Stephanomia* and moved most of the species that he previously included within it into the genus *Halistemma* Huxley. However, he (*ibid*, p. 66) pointed out that "As Moser (1925) suspected the … species [*convoluta*] has no close link with other species for which the name *Stephanomia* has been used." Thus he proposed the new generic name *Moseria* to include the single species, *convoluta.*

Margulis (1977) described and named another species, *Moseria similis*, distinguishing it largely on the structure of the pneumatophore. In Margulis's specimen the pneumatophore was described as being typical of the family Agalmatidae in that it possessed two chambers, while Moser's (1925) was described as having three. Margulis attached much taxonomic significance to this but, presently, such differences are thought only to reflect the degree of damage to the pneumatophore when the gas inside expands during retrieval of the specimen and in reality there is only one chamber, the pneumatosaccus. Margulis thought that there might be slight differences between the younger nectophores of the two species, and believed that the palpons differed, particularly as there was a cluster of nematocysts at their distal end in *M. similis*, which had not been mentioned with regard to *M. convoluta*. She described two forms of tentilla

that were basically similar in shape in having a spiralled cnidoband, but while one possessed an involucrum the other did not. Because of the similarities of the tentilla in both her specimens and those of Totton, and the fact that they differed so markedly from those described by Moser (1925) for *M. convoluta*, Margulis concluded that Totton's specimens must also belong to *M. similis*.

Further material similar to that described by Moser (1925), Totton (1965) and Margulis (1977) is described here. Initially it was considered that there was insufficient evidence to separate *Moseria similis* from *M. convoluta*, particularly as the present material shows that both the tentilla described by Moser (1925) and those described by Totton (1965) are present on individual specimens. However, more detailed examinations, especially of the bracts and palpons, led to the conclusion that both species are valid.

Before redescribing these two species, it must be noted that the generic name *Moseria* is preoccupied for a genus of ctenophores (Ghigi 1909), and it is surprising that Totton, usually so thorough in his work, did not appreciate this. *Moseria* Totton, 1965 is thus an invalid junior homonym and must be replaced (International Code of Zoological Nomenclature, Arts. 52, 60). This is deeply regrettable as Moser wrote many papers on siphonophores in the early 20th century, although not all of her contributions were entirely accurate (see Pugh 2006). In fact, the generic name *Moseria* has also been "established" on two other occasions, for a beetle (Weise 1922) and for an acarid arachnid (Beer & Nucifora 1965). In order to retain some link to Moser, the generic name *Resomia*, gen. nov., is proposed, derived by spelling her name backwards. Although this name may sound similar to the apolemiid siphonophore genus *Ramosia* Stepanjants, it should be noted that the latter name is also preoccupied, by a clear-wing moth genus (Engelhardt 1946), and thus can no longer be used. However, the present author considers that a new generic name for *Ramosia* is unwarranted as there are at least 10 undescribed apolemiid species (Pugh, personal information) and the interrelationships between all these species has yet to be fully considered. For the time being *R. vitiazi* Stepanjants should be transferred into one of the other apolemiid genera, possibly *Tottonia* Margulis, as *T. vitiazi*.

Terminology

Recently, Haddock *et al.* (2005) redefined the terminology used to specify the axes of siphonophores, and the orientation of their various zooids, in an attempt to simplify and clarify the many previous, and often contradictory, definitions. For instance, they defined the anterior side (closer to the pneumatophore in physonect siphonophores) of a nectophore as *upper* and the posterior side as *lower*, in order to avoid the previously confusing terms such as *dorsal* and *ventral*. In consequence it seems timely to reconsider the terminology applied to the ridge patterns on these nectophores. For many physonect species Totton (1965) called the main pairs of ridges the *apico-laterals*, *infra-laterals*,

laterals and *vertical laterals*, although in the last case he variously used the terms *latero-vertical*, *lateral vertical*, *vertical lateral* and *vertical-lateral*. This terminology is generally used today. However, in other instances Totton reverted to the rather peculiar terminology suggested by Claus (1879). The equivalence of these two terminologies was discussed by Pugh and Harbison (1986) and Pugh and Youngbluth (1988). In the light of the terminology suggested by Haddock *et al.* (2005), it would seem appropriate to now refer to the apico- and infra-lateral ridges as the *upper* and *lower laterals*, respectively.

Totton (1965) also named two other types of nectophoral ridge. On very young *Resomia* (*Moseria*) nectophores he described a pair of oro-lateral ridges, which by their position can easily be equated with the upper laterals. However, he also referred, on the nectophores of *Pyrostephos vanhoeffeni* Moser, to the distal bifurcation of the upper laterals into pairs of oro-lateral and frontal ridges. The usage of this terminology seems unnecessary and, for instance, Pugh (1999a) referred to them, on the nectophores of closely related *Bargmannia* species, as the outer and inner branches, respectively, of the upper laterals (Fig. 3**B**).

We will retain the other two ridge names, *vertical lateral* and *lateral*, although the definition of both can be rather subjective, depending on the species in question. Not every physonect species has either or both of these pairs of ridges present on their nectophores. For some species (e.g. *Erenna richardi* Bedot), the term *vertical lateral* ridge is a very precise description as the ridge runs perpendicularly between the upper and lower lateral ridges, and in the majority if not all cases unites with them. In addition, the vertical lateral ridge is usually situated either at the mid-length of nectophore or proximal to it, and always proximal to the lateral ridge, if present. However, in other species the vertical lateral ridge traverses the lateral surface of the nectophore obliquely from its upper proximal junction with the upper lateral ridge to its lower distal junction with the lower lateral ridge (Fig. 3**A**, **C**). This obliquity reaches its extreme on the nectophores of species of *Bargmannia* (Fig. 3**B**). There a ridge runs almost horizontally across the lateral face of the nectophore. Because the term “vertical lateral” did not seem appropriate, Pugh (1999a) termed it the *meso-lateral* ridge. However, because the ridge arises in the proximal half of the nectophore and it unites the upper and lower lateral ridges, in the very broadest sense it can be considered as a vertical lateral ridge.

In general, a *lateral* ridge when present traverses obliquely across the lateral surface of a nectophore from its upper, more proximal part to its lower more distal one. It is usually situated in the distal half of the nectophore, and may unite with the upper lateral (Fig. 3**A**), but not the lower lateral ridge, usually ending on the lateral process that extends out from the ostium. In several species, particularly of the genera *Halistemma* (Fig. 3**A**) and *Lychnagalma*, both a lateral and a vertical lateral ridge (several in *H. striata* Totton) are present and, additionally, the upper lateral ridges bifurcate close to the ostium.

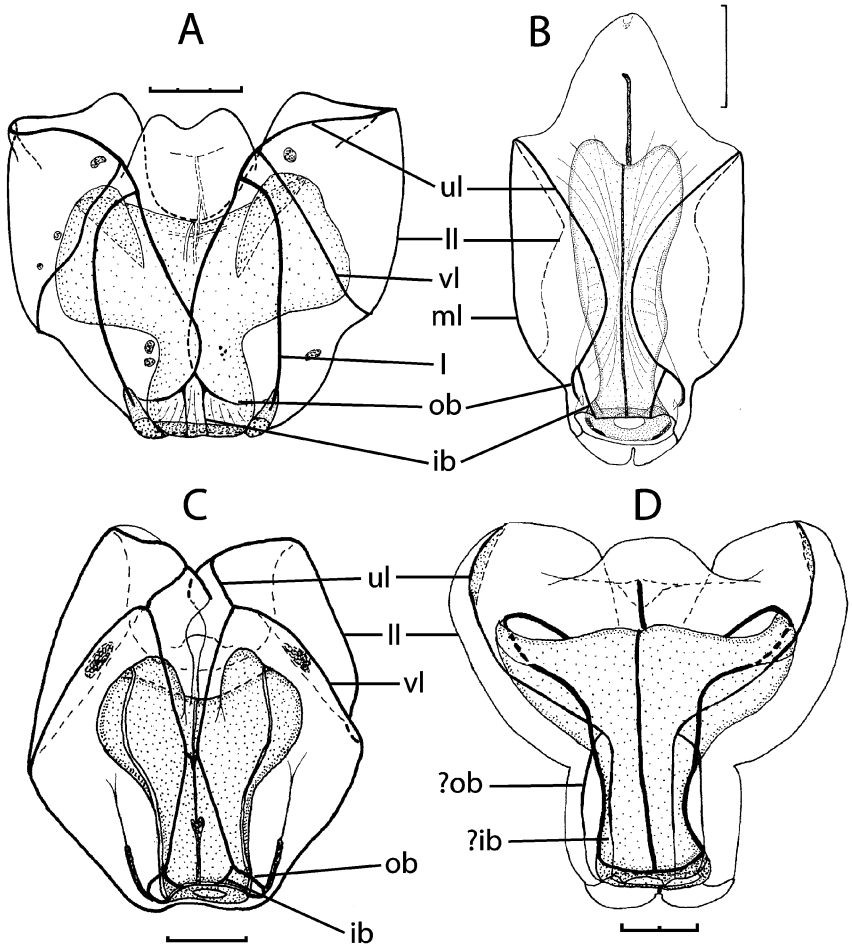

FIGURE 3. Ridge patterns on the nectophores of **A**. *Halistemma transliratum* (scale 3 mm), **B**. *Bargmannia amoena* (scale 5 mm), **C**. *Frillagalma vityazi* (scale 1 mm) and **D**. *Marrus orthocanna* (scale 2 mm). **ib.** — inner branch of upper lateral; **l.** — lateral; **ll.** — lower lateral; **ml.** — meso-lateral; **ob.** — outer branch of upper lateral; **ul.** — upper lateral.

The problem of definition arises when a lateral ridge is absent, but the upper lateral ridges still bifurcate. When this bifurcation occurs just proximal to the ostium, as in *Frillagalma vityazi* Daniel (Fig. 3**C**), there seems little reason not to consider them as inner and outer branches of the upper laterals. However, when the bifurcation occurs at some distance from the ostium, then the terminology applied to the branches becomes more subjective. In *Bargmannia elongata* Totton (Fig. 3**B**), for instance, the close association of the relatively long branches still suggests that they are best referred to as the inner and outer branches of the upper laterals, rather than calling the latter a lateral. However, in an extreme case, like *Marrus orthocanna* (Kramp) (Fig. 3**D**), the bifurcation of the upper laterals occurs just distal to the mid-length of the nectophore. For a related

species, *M. antarcticus* Totton, Totton (1965) reverted to the terminology of Claus (1879) and referred to the branches as the Vk' and Vk", the latter usually being equated with a *lateral* ridge. However, in another species of *Marrus*, *M. claudanielis* Dunn, Pugh, & Haddock, the upper lateral ridges did not divide, but a separate very weak ridge, which did not connect with the upper lateral ridge, was present that could only be referred to as a lateral one.

It is probable that there is no biologically relevant distinction to be made regarding these outer ridges that divide off from the upper laterals, although future developmental studies may clarify their homologies. For the present it seems best to not attempt imposing arbitrary distinctions but it behoves future authors to explain the terminology that they adopt.

Descriptions

Resomia, nom. nov.

Diagnosis: Physonect siphonophores with simple heart-shaped mature nectophores, bearing only upper and lower lateral ridges. Ascending and descending pallial canal present; straight radial canals on nectosac. Tentacles bearing two forms of tentilla; the more proximal ones, with spirally coiled cnidobands, transforming into the more distal ones, with a zigzagged cnidoband. Monoecious. Type species: *Stephanomia convoluta* Moser, 1925.

Resomia convoluta (Moser, 1925)

Diagnosis: Very young nectophores bearing no lateral digitate processes. Bracts with relatively small, triangular distal facet on upper surface; with bracteal canal ending at distal point below a cluster of nematocysts. Palpons without distal cluster of nematocysts.

Material examined: Two specimens kindly loaned to me by Dr Francesc Pagès collected in the Weddell Sea (see Pagès and Kurbjeweit 1994) by the RV *Polarstern* during the Antarktis IX/2 cruise at Stations 67 (2.xii.1990, 66°27.9’S, 28°43.9’W) and 94 (10.xii. 1990, 68°49.1’S, 17°55.5’W). Both specimens were collected in the 1000–500m depth range using a multiple opening/closing net system (0.25 m^2 mouth opening, 100µm mesh).

Description: The description is based mainly on the specimen captured at St. 67, as the one from St. 94 is in relatively poor condition.

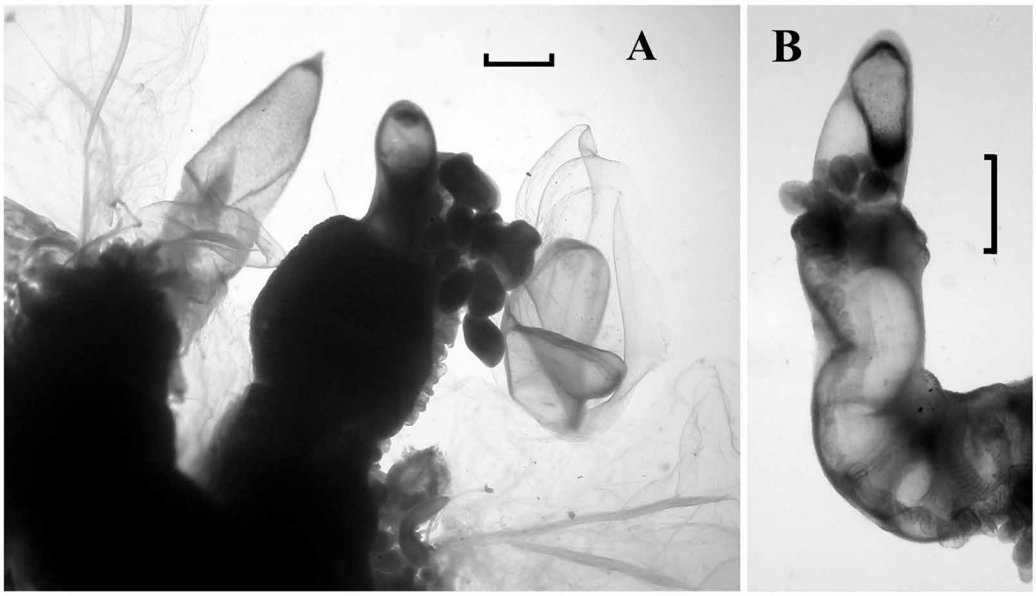

FIGURE 4. Pneumatophores of *Resomia convoluta*. **A**. from St. 67 specimen, **B**. from St. 94 specimen. Scale 1 mm.

Pneumatophore: The pneumatophore of the specimen from St. 67 (Fig. 4**A**) measured 1.88 mm in height and 0.55 mm in maximum diameter. It was quite featureless, apart from a darker patch of cells at the apex, which may have been pigmented in life. There had been some distortion as the base of the gas gland did not reach the base of the pneumatophore. The pneumatosaccus of the pneumatophore of the specimen from St. 94 (Fig. 4**B**) had clearly exploded due to gas expansion whilst being brought to the surface, as the expanded gas can be seen within the nectosome. It was greatly distorted and measured 2 mm in length and 0.95 mm in maximum diameter. The significance of this distortion is discussed below.

Nectosome: Buds of nectophores and a single young one were attached at the base of the pneumatophore on the specimen from St. 67 (Fig. 4**A**), on the ventral side of the stem.

Nectophore: Twenty six nectophores, at various stages of development, were found with the St. 67 specimen. They measured up to 15.7 mm in width and 13 mm in length. A photograph of a young one (3.1 mm wide, 2.8 mm long) is shown in Fig. 5**A**. None of these young nectophores showed any signs of lateral digitate processes, in contrast to those of *Resomia similis* (see Fig. 13). Slightly larger nectophores were found with the St. 94 specimen (Fig. 5**B**, **C**). These clearly show the upper and lower lateral ridges. The upper facet is much smaller than the lower one, and the pairs of ridges define a broad, oblique lateral facet. As the upper laterals curved in toward the mid-line they each divided off a short, weak lateral ridge that petered out on the lateral process. The upper laterals then continued to the ostium, leaving a deep median furrow between them.

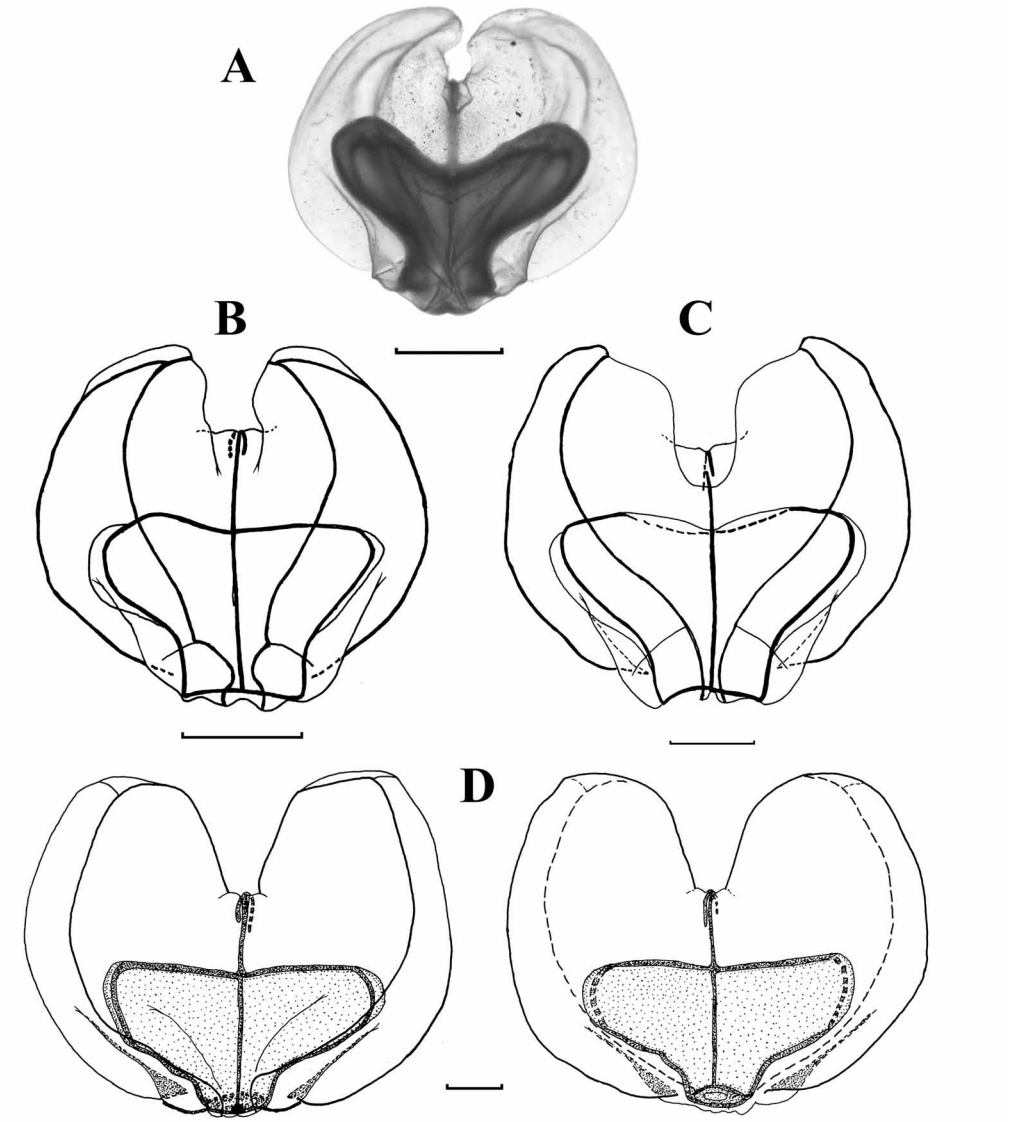

FIGURE 5. Young nectophores of *Resomia convoluta*. **A**. upper view of very young nectophore; **B**. and **C**. upper views of developing nectophores; **D**. upper (left) and lower (right) views of slightly more developed one. **A**. and **D**. from *Polarstern* St. 67, **B**. and **C**. from St. 94. Scale 1 mm.

As the nectophores develop further they gradually take on the typical heart-shaped appearance of the young nectophores described by Moser (1925). The young nectophore shown in Fig. 5**D**, which measured 5.6 mm in length and 7 mm in width, clearly showed pairs of upper and lower lateral ridges that united close to the tips of the axial wings, with a narrow, concave, oblique lateral facet between them; the upper facet still being smaller than the lower one. The upper lateral ridges remained far apart for most of their lengths before curving in to join the ostium, leaving a narrow, but quite deep, median furrow

between them. The lower lateral ridges petered out on the lower side of the nectophore marginally before reaching the ostium. Slightly swollen lateral processes extended out from the ostium, and then axially along the middle of the lateral facets for a short distance. These processes bore narrow strips of ectodermal cells on their surfaces that, in common with many other species, were probably sites of bioluminescence. As the nectophores enlarged and the upper lateral ridges moved further and further apart, the lateral branches that they gave off axial to the ostium became less and less apparent, such that at the stage shown in Fig. 5**D** no trace of them could be discerned.

In these maturing nectophores (Fig. 5**D**) the nectosac occupied only the ostial third to half of the nectophore. Its axial surface was flat, and there was no sign of any muscle-free area. The ostial opening was quite small, and slightly displaced onto the lower side of the nectophore. There was a minute thrust block over which the pallial canal ran, from the upper to the lower surface of the nectophore. Both ascending and descending pallial canals were present, and of approximately equal length. The pedicular canal arose slightly on the lower side of the nectophore and ran straight to the nectosac. There it gave rise directly to the four radial canals, all of which had straight courses to the ostial ring canal.

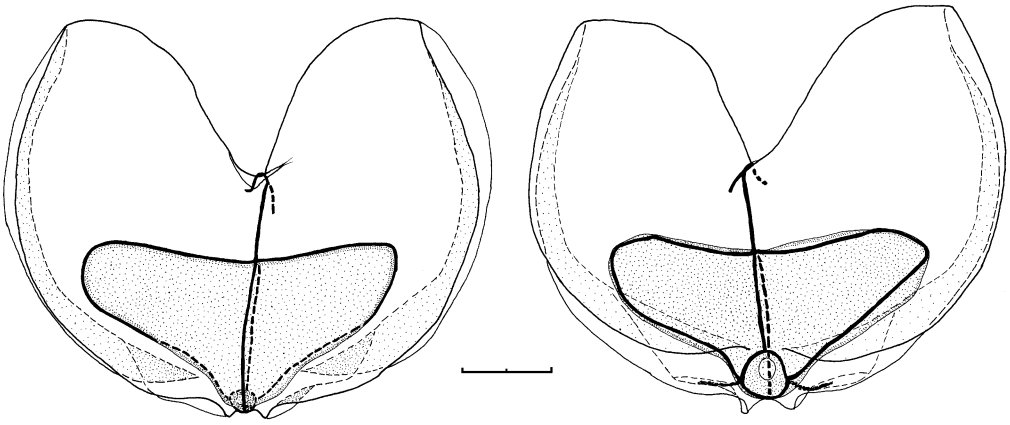

FIGURE 6. *Resomia convoluta*. Larger nectophore. Upper (left) and lower (right) views. Scale 2 mm.

An almost fully developed nectophore, 8 mm long and 10.8 mm wide, is shown in Fig. 6. The upper and lower sides were of approximately equal width, with deeply concave lateral facets between the pairs of upper and lower lateral ridges. However, it is likely that this concavity is a preservation artefact. The lower lateral ridges continued to peter out on the lower surface of the nectophore just before reaching the ostium, although in some cases they appeared to reach it. There was no trace whatsoever of the lateral branches from the upper lateral ridges as noted in the youngest nectophores. The lateral processes from the ostium were slightly less prominent than in the younger nectophores, but still very noticeable were the narrow strips of ectodermal cells passing outwards from the points

where the lateral radial canals met the ostial ring canal. The nectosac still extended to less than half the length of the nectophore, and its axial surface was flat and without any trace of a muscle-free zone.

Up to this stage the nectophores had a fairly rigid appearance, and the ridges were clearly distinguishable. However, as they enlarged further, the mesogloea, particularly in the axial wings, became more flaccid, and the ridge pattern less pronounced, although it still could be easily discerned in the well-preserved material available. These large flimsy nectophores were easily damaged. On some there was a semblance of a partial vertical lateral ridge between the upper and lower laterals. However, this was considered to be a fold caused by shrinkage or distortion during preservation.

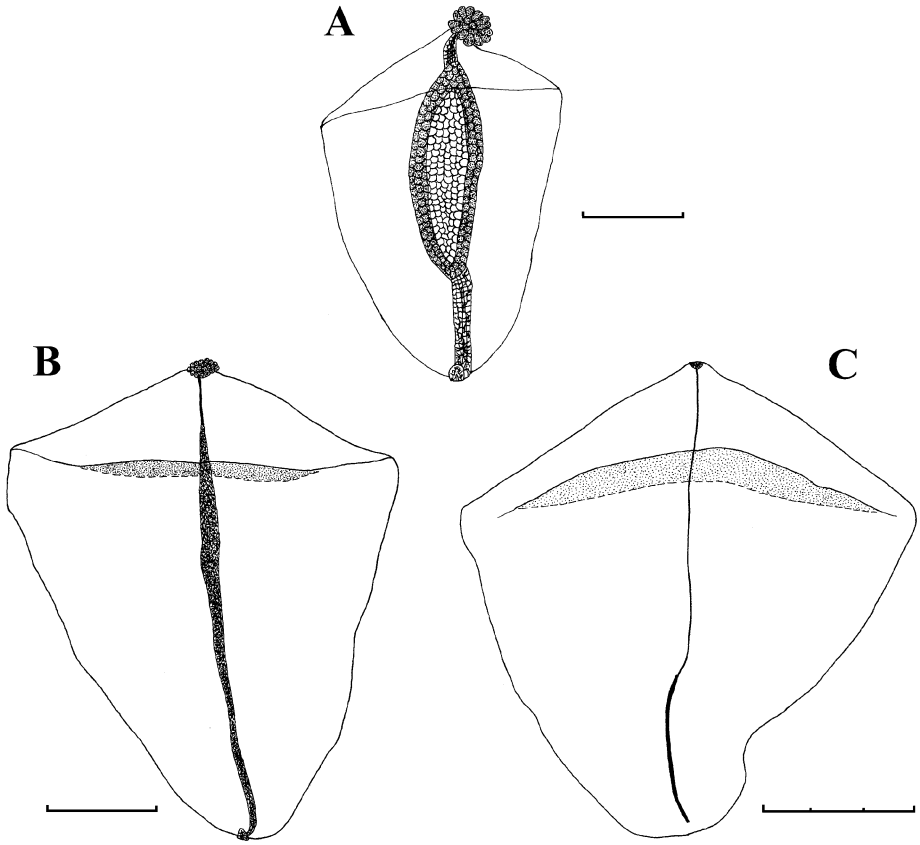

FIGURE 7. Bracts of *Resomia convoluta*. Scale – **A**. 0.5 mm, **B**. 1 mm, **C**. 3 mm.

***Siphosome*:**

Bract: (Fig. 7). The bracts were quadrangular in shape, with rounded corners, and measured up to 10 mm in length and 8 mm in greatest width. The largest bracts were very flimsy. There was a transverse ridge across the upper side of the bract close to its distal end that delineated a triangular distal facet. In the younger bracts (Fig. 7**A**), this ridge stretched

from one side of the bract to the other, but did not overhang the distal facet. On intermediate sized bracts (Fig. 7**B**) the connections to the sides of the bract were weak or totally absent, and the central part of the ridge slightly overhung the distal facet. In the largest bracts (Fig. 7(C)) the transverse ridge usually did not connect with the sides of the bract, while it overhung the distal facet more extensively. The bract was thickest in the middle region of the transverse ridge and tapered down gradually toward the proximal end. Toward the distal end the bract rapidly lost depth on its upper side, but not on its lower one.

In the youngest bracts, the proximal end of the bracteal canal extended a short distance on to the upper side of the bract, before running over on to the lower side and then directly to the distal tip. It terminated below a distinctive cluster of nematocysts. The canal had very thick walls. At its proximal and distal ends the canal was narrow, but in its middle region its cavity was extensive, and the walls had a distinctive honeycomb of large endodermal cells. In intermediate sized bracts (Fig. 7**B**) the canal still retained thickened walls except towards its distal end. Proximally it extended slightly onto the upper side of the bract, while distally it ended below a relatively less prominent cluster of nematocysts. In the oldest bracts only the proximal part of the canal, in the region of attachment to the stem, remained slightly thickened and frequently it did not extend on to the upper side of the bract.

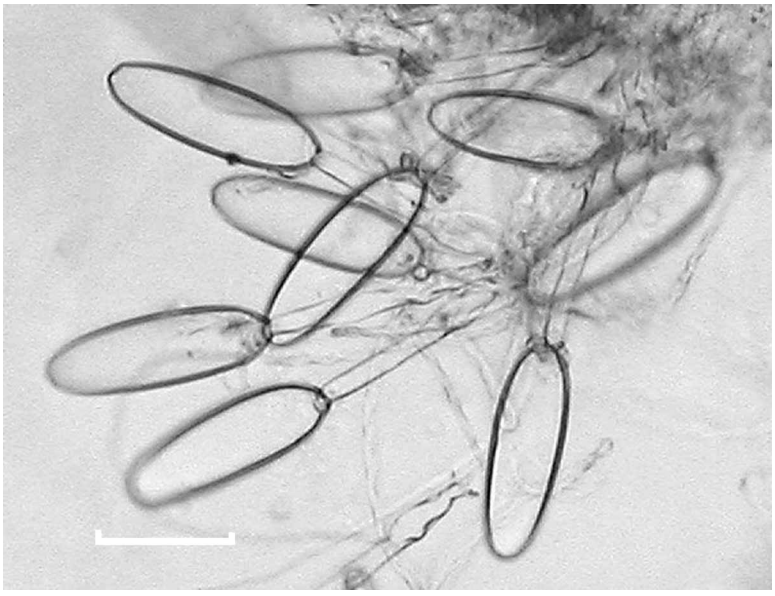

FIGURE 8. Nematocysts from bracts of *Resomia convoluta*. Scale 50 µm.

The cluster of nematocysts was always positioned at the distal tip of the bract. In the youngest bracts there were approximately 20–30 nematocysts, all of the same kind. In the material available, this number decreased as the bract increased in size, although it is not

clear whether this decrease is truly an ontogenetic pattern or whether the losses occurred through abrasion or preservation. The nematocyst capsules (Fig. 8) measured 82 µm in length and 25 µm in width. The shaft measured 78 µm in length and had a few small barbs at its distal end. They are most probably microbasic mastigophores.

Palpon: The palpons (Fig. 9) measured up to 8 mm in length and 2.7 mm in width, although the younger ones remained relatively narrow. Over 80 were found with the St. 67 specimen, together with about 12 gastrozooids, indicating that each cormidium bore at least six palpons. They were largely featureless, the younger ones often transparent, while the older ones were filled with a dense, granulose substance. The surface was covered in a dense array of patches of 6–12 ectodermal cells. There was a small proboscis at the distal end, and a constricted process at the proximal end from which the palpacle arose. The latter was long and narrow, without annulations, although at irregular intervals there were small constrictions. No nematocysts were discerned anywhere on the palpon or the palpacle.

Gastrozooid and tentacle: The gastrozooids (Fig. 10) were attached directly to the siphosomal stem, and measured up to 7.6 mm in length and 1.8 mm in diameter. Frequently each of the three main regions, the basigaster, stomach, and proboscis, occupied approximately one third of the total length of the gastrozooid, although the proboscis region could be very variable in shape. However, in one case (Fig. 10, right) the basigaster was greatly enlarged and occupied almost half the length of the gastrozooid, but still was relatively narrow. Twelve so-called longitudinal liver stripes were present in the proboscis region.

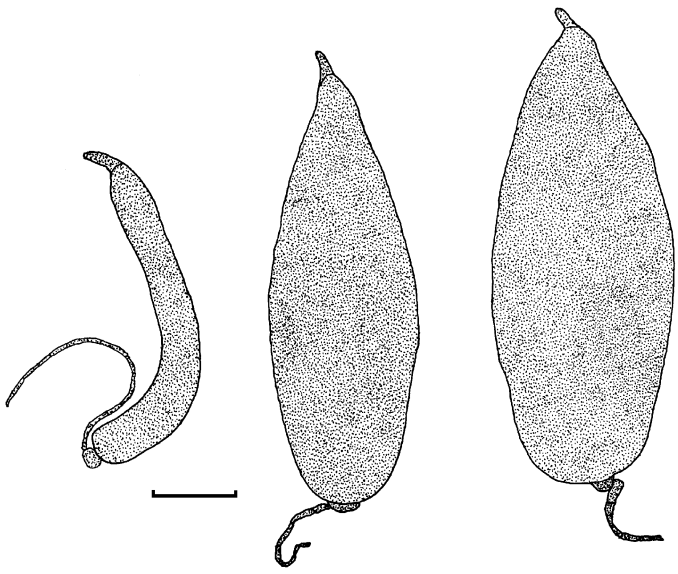

FIGURE 9. Palpons of *Resomia convoluta*. Scale 1 mm.

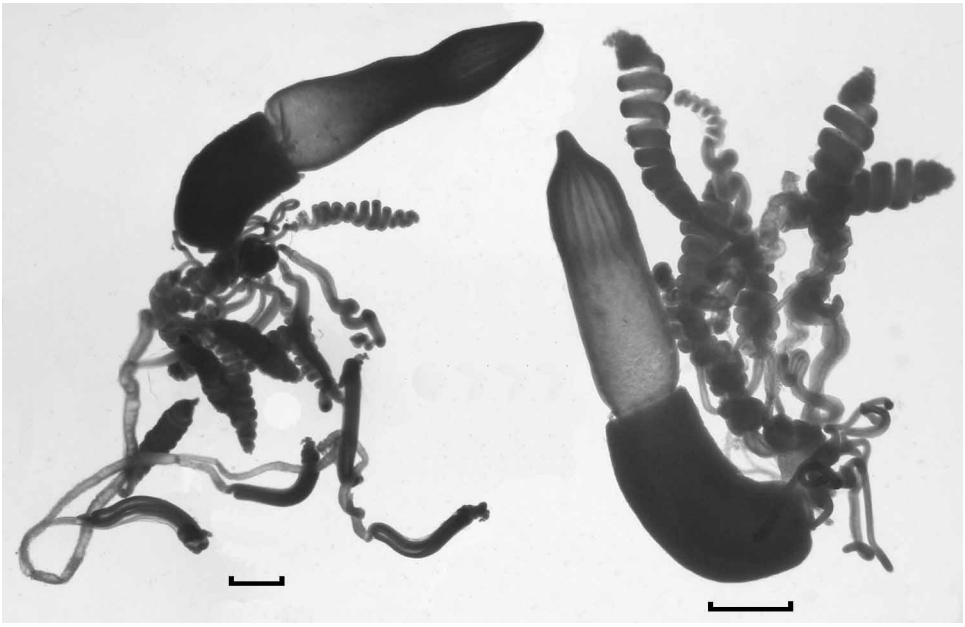

FIGURE 10. Gastrozooids of *Resomia convoluta*. Scale 1 mm.

The annulated tentacle arose at the very base of the gastrozooid and bore two basic forms of tentilla (Fig. 10, 11**A**), which arose, as usual, at the tentacular nodes. The youngest, proximal tentilla (Fig. 11**B a**) were simple straight tubes that, as they enlarged, began to differentiate their three basic regions, the pedicle, cnidoband, and terminal filament. The cnidoband then began to coil up into a loose spiral (Fig. 11**B a, b**). As this spiral tightened an involucrum began to develop at the very base of the cnidoband (Fig. 11**B c**, **d** — arrowed). This involucrum gradually extended distally (Fig. 11**B e**-**g** — the distal end of the involucrum is marked by a white line) so as to almost or entirely cover the now tightly coiled cnidoband. At this point of development of the tentilla something occurred that has not been previously described for any siphonophore. The cnidoband began to unwind (Fig. 11**B h**) and completely change its topography such that it eventually arranged itself into three straight zigzagged sections (Fig. 11**B i**). On this particular tentacle this transition apparently took place when the involucrum had almost, but not entirely, covered the cnidoband. During the transition parts of the cnidoband projected distally beyond the involucrum, and once the transition was complete the involucrum still did not entirely cover the now zigzagged cnidoband. The tentillum that was the third from the distal end of the tentacle (Fig. 11**B j**) had lost its involucrum and clearly shows the overall arrangement of the three main zigzagged sections of the cnidoband, with the so-called “double elastic band” connecting its proximal and distal ends. The two distal most tentilla (Fig. 11**B k**–**l**) show that the involucrum continued to extend distally and eventually covered the whole of the cnidoband and, indeed, extended well beyond it so

that the terminal filament could be withdrawn entirely within it. The distal end of the cnidoband turned back proximally to form the beginnings of a fourth zag, and the terminal filament arose at its end.

Unfortunately, the tentacle illustrated in Fig. 11 was the only one where a tentillum was found to be in the transitional stage between the more proximal ones with a coiled cnidoband and the more distal ones with a zigzagged cnidoband. In addition, it is uncertain whether the transition begins before or after the cnidoband is completely enveloped by the involucrum. The most advanced pre-transitional tentillum was found to have the involucrum covering all of the cnidoband, together with the base of the terminal filament. However, it is clear that a transition between the two forms of tentilla does occur, rather than a succession of the zigzagged type being developed first followed by a switch over to the development of the coiled type as the gastrozooid and tentacle mature. In that case one would expect the more anterior gastrozooids to have tentacles bearing only the zigzagged form. However, all of the gastrozooids, including one still attached toward the anterior end of the siphosome, bore tentacles with coiled tentilla at their proximal ends, and half of them had zigzagged tentilla distally. In addition, broken off pieces of tentacle generally bore only zigzagged tentilla.

Four types of nematocysts were found to be present on the tentilla. Haplonemes, probably homotrichous anisorhizas, and heteronemes (microbasic mastigophores) were present on the cnidoband, while what were presumed to be desmonemes and acrophores were found in the terminal filament, although no discharged ones were found. However, these last two types of nematocysts are quite typically found on the terminal filaments of physonect siphonophores. About 300 mastigophores, measuring 80–106 x 21 µm, werefound at the proximal end of the cnidoband, flanking the haplonemes. They were present on the first two or three spirals of the coiled cnidobands and along the first zag of the zigzagged cnidobands. Their density was greatest proximally and diminished distally, becoming widely spaced apart before they disappeared entirely. Innumerable haplonemes, generally of two sizes (53–58 x 8 µm and 80–85 x 10.5 µm), were present throughout the cnidoband and arranged into several rows. Both the presumed desmonemes (25–26 x 17.5–18.5 µm) and acrophores (24–28 x 8–9.25 µm) varied in size, and the latter were far more abundant than the former but, because the terminal filaments were tightly coiled, their exact arrangement could not be elucidated.

Moser (1925) clearly illustrated the arrangement of the cnidoband in the zigzagged forms of tentilla (see Fig. 1). She showed that the nematocyst-bearing side of the first zag lay against that of the second, while that of the third lay on the outer surface of the cnidoband. She also clearly showed the strong and doubled elastic band running up the exterior side of the first zag. She believed that a much reduced elastic band was present in the second and third zags, but this may not be the case. In the spiralled cnidobands the double elastic band clearly was present throughout the length of the cnidoband, but in the zigzagged ones it directly connected the proximal and distal ends of the cnidoband (see Fig. 11 **B j**) and, thus, could not be present between the second and third zags.

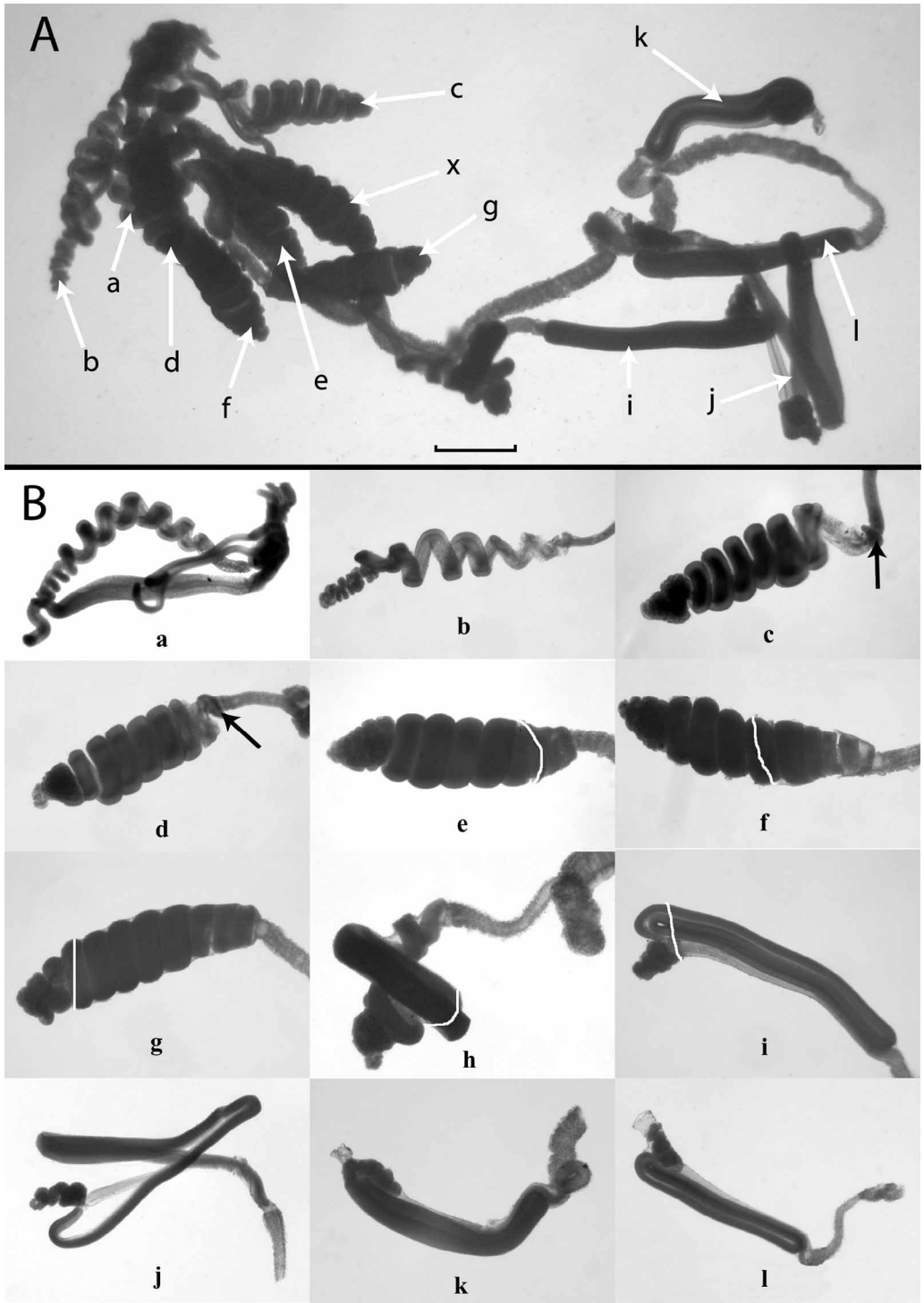

FIGURE 11. *Resomia convoluta*. **A**. A single tentacle with its various forms of tentilla (**a-l, x**). Scale 1 mm. **B**. Individual tentilla (**a-l**) removed from the tentacle shown in **A**. (**x** not illustrated). Sizes of tentilla can be gauged from **A**.

Gonophores: Unfortunately, only the anterior part of the siphosome of both *Polarstern* specimens was preserved, and no ripe gonophores could be found. Groups of small, rounded buds were present, some of which were clearly destined to become female gonophores as the nucleus of each could clearly be seen. However, no buds of male ones could be discerned, although this does not necessarily mean that they were absent. However, as noted below, some of Totton's material that has been re-examined clearly showed that both male and female gonophores were present on the same specimen.

Distribution: There are very few published records of *Resomia convoluta*, all from the Antarctic Ocean apart from an extremely unbelievable one from Baja California (Alvariño 1991). Nonetheless, it is possible that this latter record may refer to another *Resomia* species that has yet to be described (Haddock and Pugh, in preparation). The original *R. convoluta* material came from Posadovsky Bay (c. 65°S, 89°E) from depths of 400 (2 records) and 3243 m, although it is likely that open nets were used. There were no further records until Totton (1965) mentioned that the species had been collected at two or three *Discovery* stations. However, the *Resomia* material presently in the Natural History Museum, London, all of which Totton had looked at, actually comes from at least eight *Discovery* stations. In addition, Totton believed that this material represented more than one *Resomia* species. These points are considered further in the Discussion.

More recently, records for nectophores of *Resomia* (*Moseria*) sp. have been given by Margulis (1992), from two stations in the Commonwealth Sea (60+°S, 55–90°E; depth ranges 100–50 and 2000–1000 m); Pagès *et al.* (1994) and Pugh *et al.* (1997) from various stations and depths in the Atlantic sector of the Subantarctic and Antarctic. Finally, Pagès and Kurbjeweit (1994) reported the collection of 20 colonies of *R. (M.) contorta* from various stations in a transect across the Weddell Sea, in the depth ranges 1000–500 and 500–200 m.

***Resomia similis* (Margulis, 1977)**

Diagnosis: Very young nectophores usually with distinct lateral digitate processes. Bracts with relatively large rounded distal facet, often bearing a lateral cusp. Bracteal canal ends below cluster of nematocysts on slightly swollen process on upper side of bract. Palpons with cluster of nematocysts at distal tip.

Material examined: Fragments believed to represent parts of a single specimen, collected by a sediment trap; parts appeared in four out of five sequential samples, each open for ten days, over the period 5th January to 24th February 1999. The sediment trap was located at a depth of 442 m at 52°37.18'S, 174°08.75'E over a water depth of 2592 m on the Campbell Plateau, south of New Zealand. The first sample contained the posterior end of the siphosome; the second the main bulk of the specimen; while loose gastrozooids and tentacles were found in the 4th and 5th samples of the sequence. I am extremely grateful to Dr Dennis Gordon of NIWA, Wellington, New Zealand, for sending this material to me.

Description:

Pneumatophore: The pneumatophore (Fig. 12**A**) was very distinctive and measured 5.5 mm in height and 2.1 mm in diameter. There was a group of darker cells at its apex, which may indicate that it was pigmented in life, and eight external ribs that petered out toward the apex. The pneumatosaccus was restricted to a small volume in the apical half. It was not clear, however, how much distortion occurred due to the expansion of gas during retrieval.

FIGURE 12. A. Photograph of *Resomia similis* pneumatophore from the sediment trap samples. Scale 2 mm. **B**. Photograph of pneumatophore of *Resomia* specimen from *Discovery* St. 1913, labelled as *Moseria marshalli*, approximately 5 mm in length.

A pneumatophore (Fig. 12**B**), in poor condition, was found amongst Totton's material in the Natural History Museum from *Discovery* St. 1913 (See Table 1 for station details). No external ribs could be discerned, and the pneumatosaccus occupied almost three-quarters of the total length. However, the overall structure and particularly the region below the pneumatosaccus showed some similarities with the pneumatophore found in the sediment trap material. The possibility that this pneumatophore may belong to *Resomia similis* is discussed below.

Nectosome: The young nectophoral buds were attached below the pneumatophore on the ventral side of the stem (Fig. 12**A**).

Nectophore: Unfortunately no nectophores other than those at a very early growth stage were found with the material examined. Nonetheless, these very young nectophores are of interest as they clearly showed a difference from those of *Resomia convoluta* in that they usually bore digitate processes projecting laterally from the region of the axial wings (Fig. 13). These nectophores measured 2.4–2.7 mm in length, and from 2.8 to 3.7 mm in

maximum width, dependent on the presence or absence of the digitate processes. Even at this stage it can be seen that the radial canals are straight and that both ascending and descending pallial canals are present. The youngest nectophores, still attached to the stem (Fig. 12**A**, Fig. 13 – centre), bore a digitate process on both sides, but as they enlarged these processes were gradually resorbed to a point where there was only a lateral swelling on one side (Fig. 13 – left). Unfortunately this process of resorption could not be followed further because of the absence of larger nectophores in the sample.

FIGURE 13. Lower views of very young nectophores of *Resomia similis*. Scale 1 mm.

***Siphosome*:**

Bract: (Fig. 14). The bracts measured up to 10 mm in length and 6 mm in width, with the largest ones being very flimsy. There was a transverse ridge running across the upper side of the bract between two, more or less pronounced, lateral cusps. This ridge, which separated the proximal and distal parts of the bract, had a variable position, but most often it occurred at the mid-length of the bract, or slightly more distally. At all stages of growth it partially overhung the distal facet, and usually extended to the lateral margins of the bract. The ridge occasionally had a ragged appearance, particularly in the younger bracts. Proximal to the ridge the width and depth of the bract tapered gradually so that, in the oldest bracts, the proximal end formed a rounded point. The distal facet was almost hemispherical in outline, and rapidly lost depth distal to the transverse ridge. On about a third of the bracts there was a distinct lateral cusp on one side (Fig. 14**C**).

On mature bracts (Fig. 14**C**) the proximal end of the bracteal canal began on its upper side and then extended for some distance along one side before passing over onto the lower side at the proximal end of the bract. This extension was usually less marked in the younger bracts (Fig. 14**B**). In the youngest bracts (Fig. 14**A**) the walls of the canal were greatly thickened by a honeycomb of endodermal cells. The canal itself, however, was expanded only in its mid-region. As the bracts matured the walls of the canal narrowed, and in the most mature ones they were only slightly thickened in the mid-region, being relatively thin both distally, as it passed up through the mesogloea, and proximally.

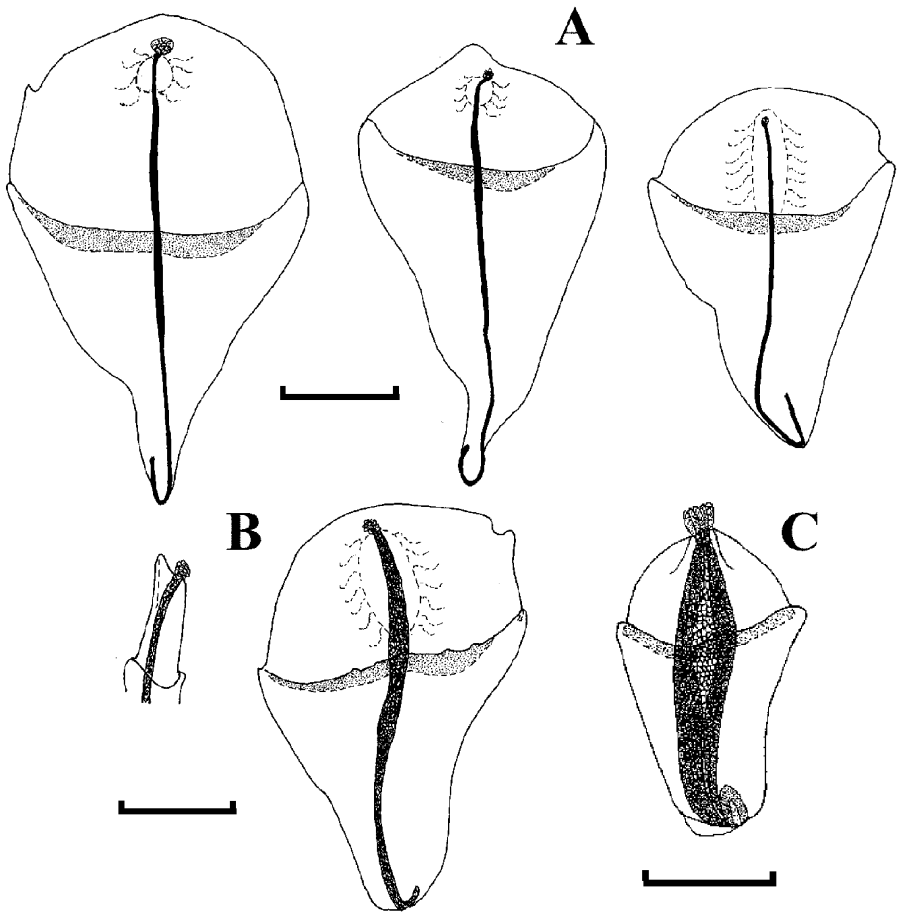

FIGURE 14. Bracts of *Resomia similis*. **A**. Upper views of mature bracts. Scale 2mm. **B**. Upper view of developing bract (right), with lateral view (left) of distal end showing patch of nematocysts lying on upper side. Scale 1mm. **C**. Upper view of very young bract. Scale 0.5mm.

The distal end of the canal terminated below a small cluster of nematocysts (Fig. 15), 10–15 in number, although in the mature bracts these often had been lost. The nematocysts were located on a pronounced mesogloeal protuberance situated on the upper side of the bract a short distance from, but not at, the distal end of the bract. This mesogloeal protuberance was more marked in the younger bracts. The nematocysts were of the same type as for *Resomia convoluta* but larger, measuring 125µm in length and 28µm in diameter. The shaft of the discharged nematocyst measured 95µm.

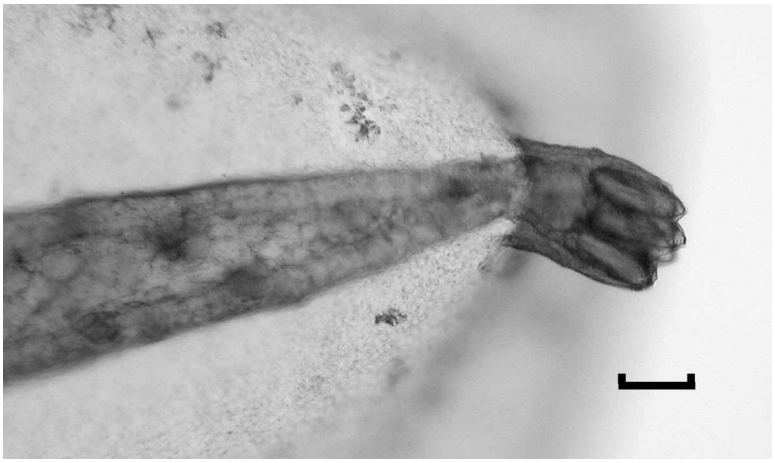

FIGURE 15. *Resomia similis* nematocyst cluster at distal end of bracteal canal of a young bract. Scale 100µm.

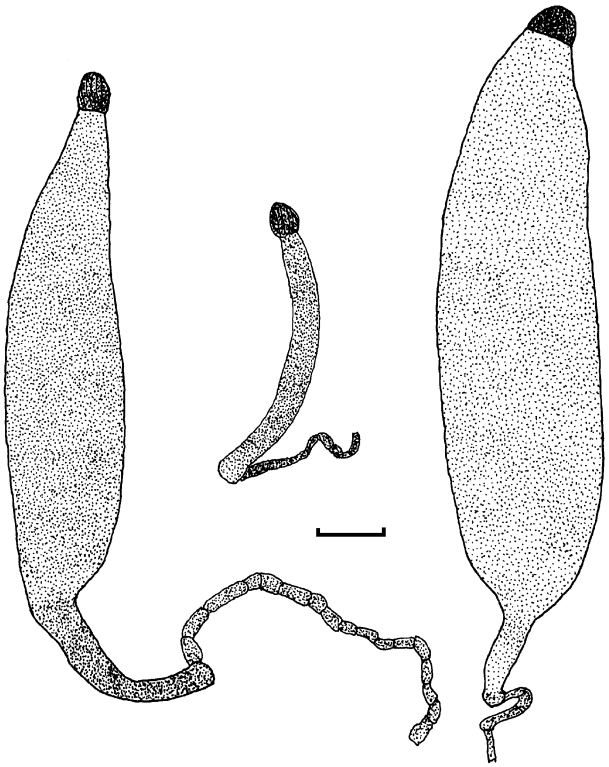

FIGURE 16. *Resomia similis* palpons. Scale 1 mm.

Palpon: The palpons (Fig. 16) were largely structureless bags, measuring up to 9 mm in length and 2.5 mm in maximum width; older ones were filled with an amorphous substance. However, there was a small but marked cluster of about 100 nematocysts at the

distal end. These nematocysts were of the same type and dimension as those found on the bract. Although the palpons narrowed towards their bases, there was no distinct button-like structure as was found on those of *Resomia convoluta*. The palpacle, arising at the very base of the palpon, had the semblance of being annulated but there were no signs of any nematocysts along its length.

More than 140 palpons were found with the specimen, alongside 23 gastrozooids. Thus, as was the case for *Resomia convoluta*, there appears to be at least six palpons present in each cormidium.

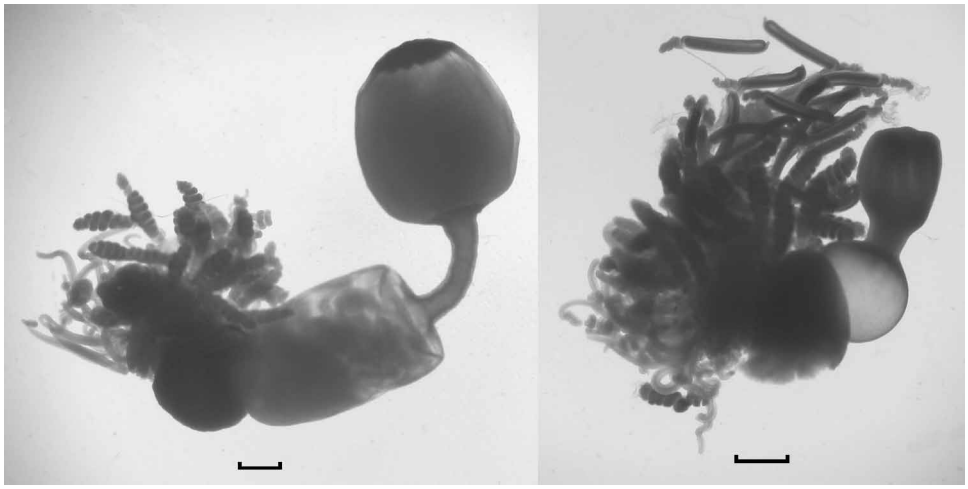

FIGURE 17. *Resomia similis*. Two gastrozooids, with tentacles. Scale 1mm.

Gastrozooid and tentacle: The gastrozooids (Fig. 17), which measured up to 11.6 mm in length and 2.8 mm in diameter, were extraordinarily variable in their shape, particularly with regard to the proboscis region. There was a distinctive basigastral region, which often occupied approximately one-third the length of the gastrozooid, and whose diameter was equal to or greater than its length. The stomach region took on a variety of shapes, varying from cylindrical to spherical. The proboscis region was usually demarcated from the stomach by a slight constriction, but in some cases (Fig. 17, left) this constriction resulted in a narrow tubular structure that separated the cylindrical stomach from the bulbous proboscis region. There were 12 longitudinal “liver stripes” arranged symmetrically around the proboscis, whose distal mouth region appeared to have been surrounded by darker pigmentation. Although the structure of this gastrozooid is very distinctive, nonetheless it is probably of no systematic value as the gastrozooids of siphonophore species are known to be extremely variable in shape, particularly with regard to the proboscis region.

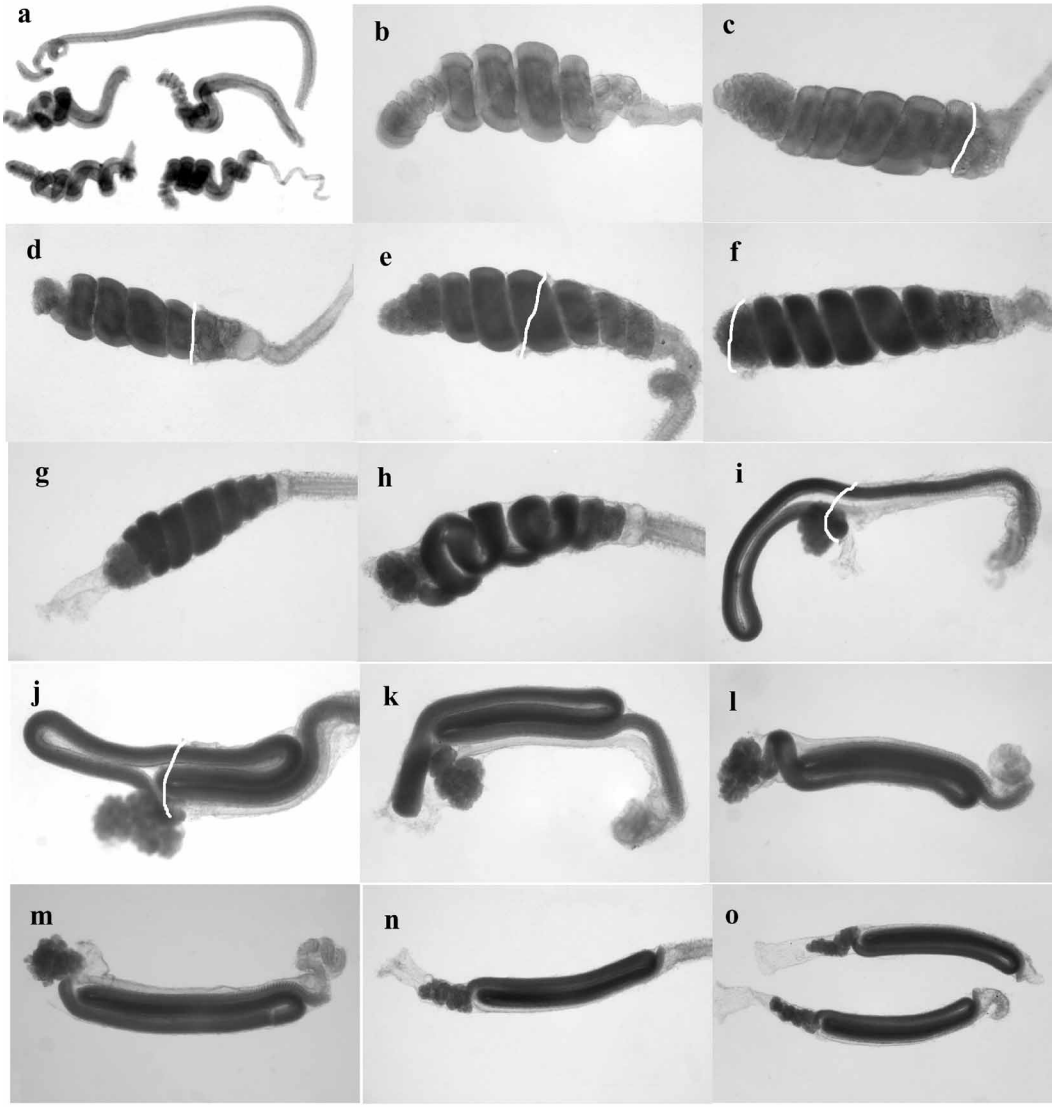

FIGURE 18. *Resomia similis*. **a-o**. Stages in the development of the tentillum. The size of the tentilla can be gauged from Fig. 17. The cnidoband in **o** is 1.5 mm in length.

The tentilla (Fig. 18) on the tentacles of *Resomia similis* followed a similar pattern of development to those described for *R. convoluta*. They first appeared as simple tubular side branches on the tentacle (Fig. 18**a**) and quickly began to differentiate the terminal filament, then the cnidoband and pedicle. The cnidoband began to coil up into a loose spiral that gradually tightened (Fig. 18**b**–**c**) and then the involucrum began to develop (Fig.18**c**). The involucrum continued to develop distally (Fig. 18**d**–**f** — the distal end of the involucrum is marked by a white line) until it entirely covered the cnidoband and the

terminal filament (Fig.18**g**). At this point the transformation of the cnidoband began and various stages of this are shown in Fig. 18**h**–**l**. In Fig. 18**h** the spiralled cnidoband was beginning to uncoil, while in Fig. 18**i**–**l** the cnidoband consisted of straight segments that were in the process of being organised into the final arrangement. At two intermediary stages (Fig. 18**i**–**j**) this reorganisation necessitated that the cnidoband project distally beyond the involucrum, but at latter stages (Fig. 18**k**–**l**) it had largely been confined within the involucrum. Finally the involucrum (Fig. 18**m**–**o**) extended further so as to cover the entire cnidoband and formed a long distal tube with the retracted terminal filament occupying only the proximal half. The terminal filament arose from the distal end of the cnidoband, which did not recurve back proximally to form the beginnings of a fourth zag as was found to be the case in *R. convoluta*.

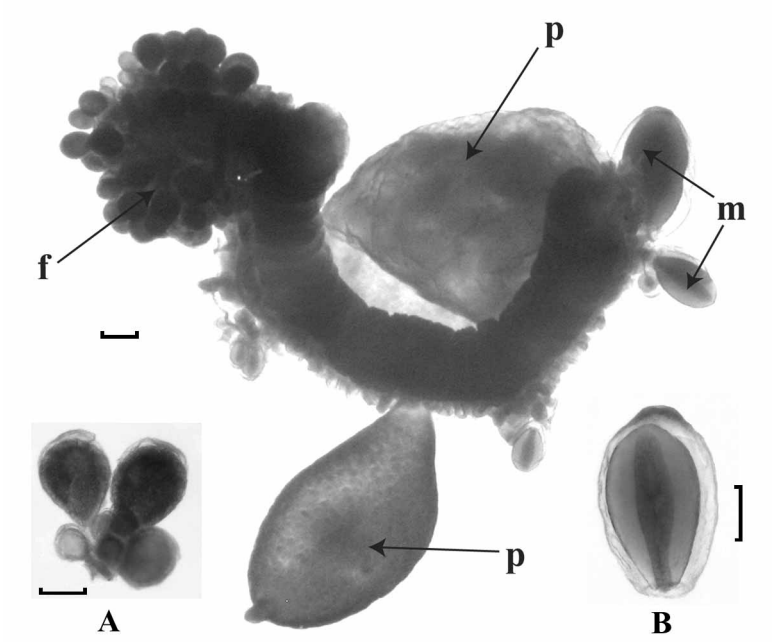

FIGURE 19. Portion of stem of *Resomia similis* showing male (**m**) and female (**f**) gonophores, and two palpons (**p**). Inset **A**: female, and **B**: male gonophores. Scale 0.2 mm.

The types of nematocysts and their arrangements on the tentilla were exactly the same as in *Resomia convoluta*. The microbasic mastigophores (heteronemes), however, were much smaller, measuring 53–66 x 16 µm, and less numerous, with only c. 100 being found on each side of the first 2½ spirals of the coiled cnidobands or about ¾ the length of the first zag on the other type. At the proximal end there were three rows on each side that, for the zigzagged form, continued up to about half the length of the first zag. The number of rows then rapidly decreased to one, and the individual nematocysts became more widely spaced. The anisorhizas (haplonemes) (53–58 x 6.5–9.25µm) were present throughout the

length of the cnidoband and, in the zigzagged form, it could be seen that there were only about four rows of these at the proximal end of the cnidoband. This number gradually increased to ca. 10 half-way along the first zag and, by the time the heteronemes had disappeared, there were about 20 rows. What were believed to be desmonemes (20–29 x 13.25–16µm) and small acrophores (13–18.5 x 5.23–8 µm) were found on the terminal filament. The doubled elastic band ran throughout the cnidoband for the spiralled type, and on the outer side of the first zag for the zigzagged type. It appeared to be much less well-developed than in *R. convoluta*.

Gonophores: Fragments of the stem bore both male and female gonophores. Both formed clusters borne on a single gonostyle (Fig. 19), with the female gonodendra forming much denser clusters than the male ones. The latter possessed gonophores at various stages of development. The largest mature male gonophore measured 1.7 x 1 mm (length/width), but all the female gonophores preserved were small, up to 0.45 mm in diameter, and immature. It was not possible to elucidate their cormidial arrangement.

Distribution

The type specimen of *Resomia similis* came from 43°02.5'S, 52°47'W, at a depth of 44–32 m. Loose nectophores also ascribed to this species were collected at four other stations in the same region (37°36' to 44°50'S, 49°48' to 52°47'W), in the Atlantic sector of the Subantarctic, at various depths from 50 to 700 m. In addition, loose nectophores were also identified from two stations in the Pacific sector, one at 56°S, 177°20'W (50 m) and the other at 53°30'S, 140°W (100 m). On what basis Margulis (1977) distinguished these nectophores from those of *R. convoluta* is not clear as Margulis (1992) subsequently commented that it was impossible to distinguish between the nectophores of the two species.

The present material, from south of New Zealand, was collected at a site very close to one of Margulis's (1977) Pacific stations, but more records are needed before any comparisons can be made between the distributions of this species and *Resomia convoluta*.

Discussion

Comparisons between *Resomia convoluta* and *R. similis*

Initially there appeared to be no reason to recognise *Resomia similis* as distinct from *R. convoluta* because Margulis's (1977) description, and particularly her illustrations, were so poor. However, from a detailed study of the sediment trap material described above, it now appears that there are sufficient criteria to separate the two species (although not necessarily for the reasons discussed by Margulis). Her primary criterion for distinguishing the two species was a difference in the structure of the pneumatophore,

although she noted that separating species based on such a character was unusual. However, considering the mode of development of the pneumatophore (see, for instance, Carré 1969), leading to the formation of a single cavity, the pneumatosaccus, then one should treat Moser's (1925) description of a three-chambered structure with caution (Fig. 20**A**). The most likely explanation is that it is an artefact caused by expansion of gas within the pneumatosaccus as the specimen was brought to the surface. This usually results in rupture of the pneumatosaccus wall such that gas escapes into the gastrovascular cavity and expands down into the nectosome. It is nonetheless striking how closely the distorted pneumatophore of *Resomia convoluta* from *Polarstern* St. 94 resembles the original illustration given by Moser (1925) (Fig. 20) but, as noted above, gas resulting from the rupture of the pneumatosaccus was clearly visible within the nectosome of the former specimen.

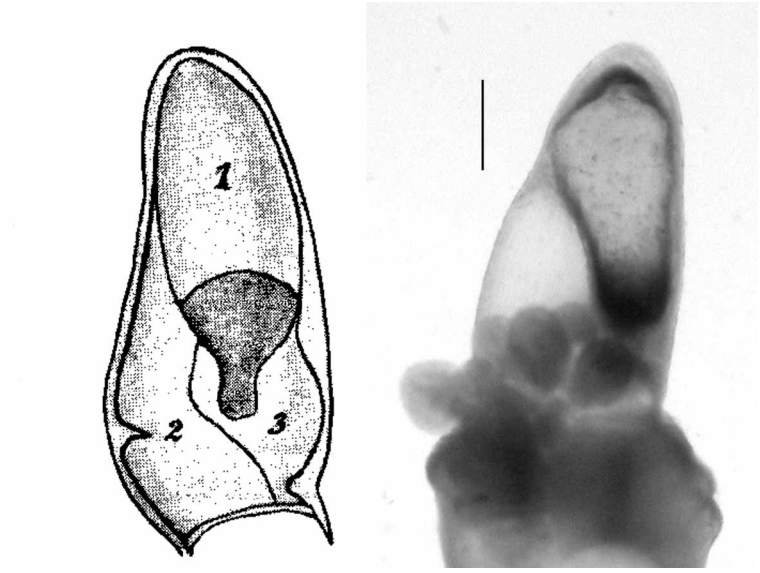

FIGURE 20. *Resomia convoluta* pneumatophores. Left: The so-called three chambered pneumatophore of Moser (1925, Fig. 56). Right: photograph of *Polarstern* St. 94 specimen. Scale 0.5 mm.

One of the few reliable morphological characters given by Margulis (1977) in her description of *Resomia similis* were the eight longitudinal stripes or ribs present on the external surface of the pneumatophore. These stripes were also found on the sediment trap specimen ascribed to *R. similis* and described above (Fig. 12**A**). They were not visible on the pneumatophore found in Totton's material (Fig. 12**B**), which otherwise bears a striking similarity to it. Such stripes were not seen on the *Polarstern* material of *R. convoluta*.

With regard to the nectophores of the two species, Margulis (1977) initially considered that the immature ones of *Resomia similis* differed from those of *R. convoluta*, as

described and illustrated by Moser (1925), by the presence in the former of upper and lower lateral ridges that made a marked bend in the lower third of the nectophore. However, Margulis (1992) later concluded that it was impossible to distinguish fully developed nectophores of the two species. Since only very young nectophores were present in *R. similis* material described above, the question whether differences exist in mature nectophores of the two species can only be resolved when further specimens of *R. similis*, in good condition, are collected. If they are identical, then this would be an unusual situation amongst physonect species, although it is known (Pugh, personal information) that the nectophores of some *Cordagalma* species are virtually indistinguishable. Nevertheless, Margulis (1977) described the presence of a light brown spot on one of the wings of the young nectophoral buds of *R. similis*. It seems probable that this can be equated with the pigmented lateral digitate processes or swellings found on the nectophoral buds of the sediment trap material. The presence of these lateral processes clearly distinguishes the very young nectophores of *R. similis* from those of *R. convoluta*, as they are absent on the latter.

Totton (1965, p. 67) was adamant that the tentilla described by Moser did not belong to *R. convoluta*, based on the fact that "Both activated and non-activated tentilla of another type have been found in abundance on a specimen from 'Discovery' Station 1283". Unfortunately, as noted below, some of this material can no longer be found. Totton described these tentilla as having a spirally coiled cnidoband, with 7–8 coils, partially covered by an involucrum, which often was turned back down the pedicle of the tentillum, and a single terminal filament. Margulis (1977) described similar tentilla, with spirally coiled cnidobands, but distinguished two types on the basis of the presence or absence of an involucrum. She was adamant that the absence of an involucrum was a true character and not a preservation artefact. Despite some very confusing remarks concerning the structure of the tentilla, Margulis finally concluded that Moser's (1925) description of the tentilla of *R. convoluta* must have been accurate and thus that her own material, and that of Totton, must belong to a separate species. However, in the light of the present observations such a distinction is not valid as it has been shown that the more proximal tentilla on the tentacle have a spirally coiled cnidoband that with age increasingly becomes enveloped by an involucrum. When the involucrum almost or completely covers the cnidoband, the latter then transforms into the zigzagged arrangement which is typical of the more distal tentilla.

No major morphological features that separate the tentillum with a spirally coiled cnidoband of *Resomia convoluta* from that of *R. similis* have been noted in the present study. However, the zigzagged tentilla of the two species can be distinguished on the basis of the point of origin of the terminal filament from the distal end of the cnidoband. In *R. convoluta* the distal end of the cnidoband curves back, proximally, to form the beginnings of a fourth zag. This arrangement also can clearly be seen in one of Moser's (1925) figures (see Fig. 1). This extra zag is not present on tentilla of *R. similis*.

The other distinguishing feature between the two species that Margulis (1977) considered was the structure of the palpons, but even she noted that the morphology of such structures can be very variable within a single specimen. However, she noted that there was a cap of nematocysts at the distal ends of those of *Resomia similis*, which was also present on the palpons from the sediment traps. Although neither Moser (1925) nor Totton (1965) made any reference to the presence or absence of nematocysts on the palpons of their specimens it does appear that this is a distinguishing character as nematocysts were absent on the palpons of the *Polarstern* specimens of *R. convoluta*.

The only feature suggested by Margulis (1977) that possibly distinguishes bracts of the two species was a light brown pigmented spot lying beneath a mesogloeal outgrowth on the very youngest bracts of *Resomia similis*. No mention of such was made in the descriptions of either Moser (1925) or Totton (1965), nor was it observed on the young bracts of either species studied herein. Thus it remains uncertain how important a character this might be.

Nonetheless, in the present material it is the structure of the bract that clearly separates the two species. In *Resomia convoluta* the distal facet of the bract was relatively small, triangular in shape, and the bracteal canal ended at its distal tip below a cluster of nematocysts. In *R. similis* the distal facet was larger, more rounded, and the bracteal canal ended in a mesogloeal bulge on the upper side of the facet, again below a cluster of nematocysts. The nematocyst capsules of *R. similis* were considerably larger than those of *R. convoluta*, but both were of the same type. A mesogloeal outgrowth was also present on the bracts described by Margulis (1977), although she placed it at the distal extremity of the bract. However, her figures of young bracts appear to indicate that this swelling in fact lies on the upper side of the bract just proximal to its distal tip. This would then be in accord with the present observations on the bracts of *R. similis*. Totton's (1965) remarks on the structure of the bracts in his possession and the arrangement of its nematocysts is discussed in the following section.

In conclusion, it appears that there are sufficient reasons to distinguish two species of *Resomia*. The differences in pneumatophores of *R. convoluta* and *R. similis* appear obvious, but further specimens are required in order to decide how good a character this is. Well-preserved specimens of *R. similis* are also needed to reliably compare the morphology of the nectophores of both species. Nonetheless, the presence of lateral digitate processes on the very young nectophores of *R. similis* and their absence on those of *R. convoluta* appears to be a good character, as will be shown further when some other closely related species are described (Haddock and Pugh, in preparation). The palpons can be distinguished by the presence or absence of a battery of nematocysts at their distal ends. The point of origin of the terminal filament on the tentilla with zigzagged cnidobands also helps to distinguish the species. Finally, there are distinct differences in the bracts, particularly in the size and arrangement of the upper distal facet and the position of the cluster of nematocysts that lies over the distal end of the bracteal canal.

Totton's specimens: All the available material relating to *Resomia* species housed in the Natural History Museum (NHM), London, has been re-examined thanks to Sheila Halsey and Andrew Cabrinovic. However, it is not entirely clear how much of Totton's (1965) description of *Moseria convoluta* is based on his own material and how much on the original description by Moser (1925). For instance, he, as did Moser, described the pneumatophore as being three-chambered, yet the one pneumatophore (Fig. 12**B**) from *Discovery* St. 1913 clearly was not.

Totton (1965) mentioned three *Discovery* stations, namely 1203, 1283 and 2023 (legend to his Plate XIII), during his description of *Resomia convoluta*. With regard to the first two it would appear that the former (St. 1203, legend to his Fig. 31) is a misprint for the second, as none of the *Moseria*-like material presently in the NHM bears that station number. The NHM material, all of which was seen by Totton, actually came from eight different samples (see Table 1), all of which were collected from south of 47°S in the Southern Ocean.

Not all of the NHM material is labelled as *Stephanomia* or *Moseria convoluta*, as Totton appears to have used three additional manuscript names, namely *M. marshalli*, *M. marri*, and *Terencia* or *Terrencia scotti*. However, there is no great consistency as the specimens from a couple of stations are referred to under more than one name (Table 1). Nonetheless, Totton (1965) thought that his material indicated the existence of two *Resomia* species, although he gave no clue as to the reasoning behind this suggestion. One might infer, because of the lack of bracts and tentilla in most cases, that he believed there were differences in the structure of the nectophores but the present state of his nectophoral material is so poor that no differences could be discerned.

With regard to the tentilla Totton (1965, p. 67) clearly had some new material from *Discovery* St. 1283 that differed from that described by Moser (1925). However, the only material found from that station in the present NHM collections consists of three microscope slides and a single preserved nectophore in very poor condition. One of these slides includes two young tentilla, each with a spirally coiled cnidoband and a rudimentary involucrum at its base. The third shows an activated tentillum that appears to consist of a straightened cnidoband and the elastic band. However, there is no sign of any coiling to the cnidoband and it may well have been derived from the more developed type of tentillum, with a zigzagged cnidoband. The absence of any other stem material seems to suggest that some of Totton's original material is missing.

Totton (1965, Pl. XIII) presented photographs of the nectophores, bracts, and siphosomal stem of "?*Moseria convoluta*"; the last said to have come from *Discovery* St. 2023. It is possible that the set of 20 slides (Table 1) that show sections through the siphosomal stem also came from the St. 2023 material. These slides indicate that both male and female gonophores were present and, thus, that the specimen was monoecious.

TABLE 1. Station data for material of *Resomia* in NHM collections.

Discovery St	Net	Date	Depth (m)	Position	Notes
753	N100B	2-xii-1931	280–110	54°02.4'S 49°12.5'W	7 vials labelled *Stephanomia contorta*.
946	N100B	3-xi-1932	270–120	51°59.2'S 173°26.9'W	1 vial labelled *Terrencia scotti*
946	N70V	3-xi-1932	1000–750	51°59.2'S 173°26.9'W	1 vial labelled *Terrencia scotti*
1283	N70V	23-ii-1934	1000–750	72°01.2'S 171°25.7'W	3 slides labelled *Stephanomia convoluta*. 1 vial labelled *Stephanomia contorta*.
1913	N70B	1-xii-1936	250–160	55°55.2'S 56°45.7'W	1 vial labelled *Terrencia scotti*. 2 vials labelled *Moseria marshalli*.
2001	TYFB	16-iii-1937	1750–1300	67°04.4'S 19°41.0'W	1 vial labelled *Moseria marshalli*.
2006	TYFB	19-iii-1937	1750–1400	66°16.7'S 13°23.3'W	1 vial labelled *Terrencia scotti*
2023	N70V	29-iii-1937	1500–1000	47°46.0'S 00°20.6'E	3 slides labelled *Terencia scotti*. 1 slide labelled *Stephanomia* ?*convoluta.* 1 vial labelled ?*Stephanomia contorta*.
Unknown					20 slides labelled *Stephanomia convoluta*.

On the other hand it is apparent that neither the nectophores nor the bracts illustrated in Totton's Pl. XIII came from St. 2023 as, in the first case, no nectophores were present in the material for that station. Probably the nectophores came from St. 1913, as one of the labels states that the relevant material had been photographed. The St. 2023 material included four microscope slides, showing young bracts, a very young tentillum and some gastrozooids, palpons and female gonophores, and 13 separate bracts. Both the young and the separate bracts resembled those of *Resomia convoluta*, as described above, but were quite unlike those shown in Totton's plate. It appears that the latter came from the St. 946 (N70V) as, on re-examination, they were found to be very different from those of the *Resomia* species described above.

This may be the reason why Totton (1965) concluded that he had specimens of more than one *Resomia* species. Totton's (1965, p. 67) description of the bracts of *R. convoluta* may give a clue to this supposition as he said "The terminal part, divided by a transverse ridge on the upper side from the rest of the bract is bevelled off to a point on the under margin to form a new nematocyst battery on the end of the bracteal canal." One would presume from this that Totton was referring to the clump of nematocysts that has been found, in both *R. convoluta* and *R. similis*, at the distal end of the bracteal canal. However, in his next sentence Totton (*ibid*) stated "A longitudinal pad of nematocysts stretches from

this point to the transverse ridge." Such an arrangement is quite unlike that found on the bracts of *R. convoluta* and *R. similis*, but appears to have clear similarities with that recently described by Dunn *et al.* (2005a) on the bracts of *Marrus claudanielis*. Unfortunately it was not possible to confirm the presence of these pads of nematocysts on the bracts from *Discovery* St. 946 (N70V), which Totton labelled as *Ter(r)encia scotti*, as they were in very poor condition. Nonetheless, a species that appears to be closely related to *Resomia*, at least in the presence of two forms of tentilla, also has *Marrus*-like bracts with a longitudinal pad of nematocysts on the distal facet. This species will be described in a forthcoming paper (Haddock and Pugh, in preparation), along with a third *Resomia* species.

The systematic position of the genus *Resomia*, together with necessary changes to the systematics of the Physonectae

In order to comprehend the systematic position of the genus *Resomia*, it will first be necessary to review the systematics of all physonects, particularly in the light of recent molecular phylogenetic studies of Dunn *et al.* (2005b). The sub-order Physonectae has for many years been considered a phylogenetically distinct grouping, generally divided (see Totton 1965) into seven families, the Agalmatidae, Apolemiidae, Athorybiidae, Forskaliidae, Physophoridae, Pyrostephidae, and Rhodaliidae. Apart from the Agalmatidae, these families have usually encompassed relatively few species with very distinct morphological characters, although numerous undescribed apolemiid species are now known to exist (Pugh, personal information). However, for some time the present author has considered the Agalmatidae to be a catch-all family (see Pugh 1998) that includes several unrelated genera, some much so that Pugh (2001) decided to remove the genus *Erenna* from it and placed it in a new family, the Erennidae.

In light of a recent study of the molecular phylogeny of siphonophores, based on analyses of mitochondrial 16S and genomic 18S ribosomal RNA genes (Dunn *et al.* 2005b), this systematic arrangement must be revised considerably. The data presented by these authors showed, primarily, that the monophyletic taxon Cystonectae was a sister group to all other siphonophores (Fig. 21). The clade name Codonophora was given to the latter, and within this clade it was found that the Physonectae were paraphyletic, and gave rise to the monophyletic Calycophorae. The major difference between the Cystonectae and the ancestral codonophore was the presence, in the latter, of a nectosome, whose budding zone was situated immediately below the pneumatophore. This nectosome consisted of a series of swimming bells or nectophores, budded off in a single row, initially on the ventral side of the stem, hence "Ventral Nectosome" in Fig. 21. The ventral side of the stem has been defined (e.g. Haeckel 1888) as that side of the stem on which the siphosomal zooids are budded off. Whether such a nectosome was present in the ancestral siphonophoran form, and subsequently was lost in the Cystonectae, or whether it only appeared in the ancestral codonophore is unclear.

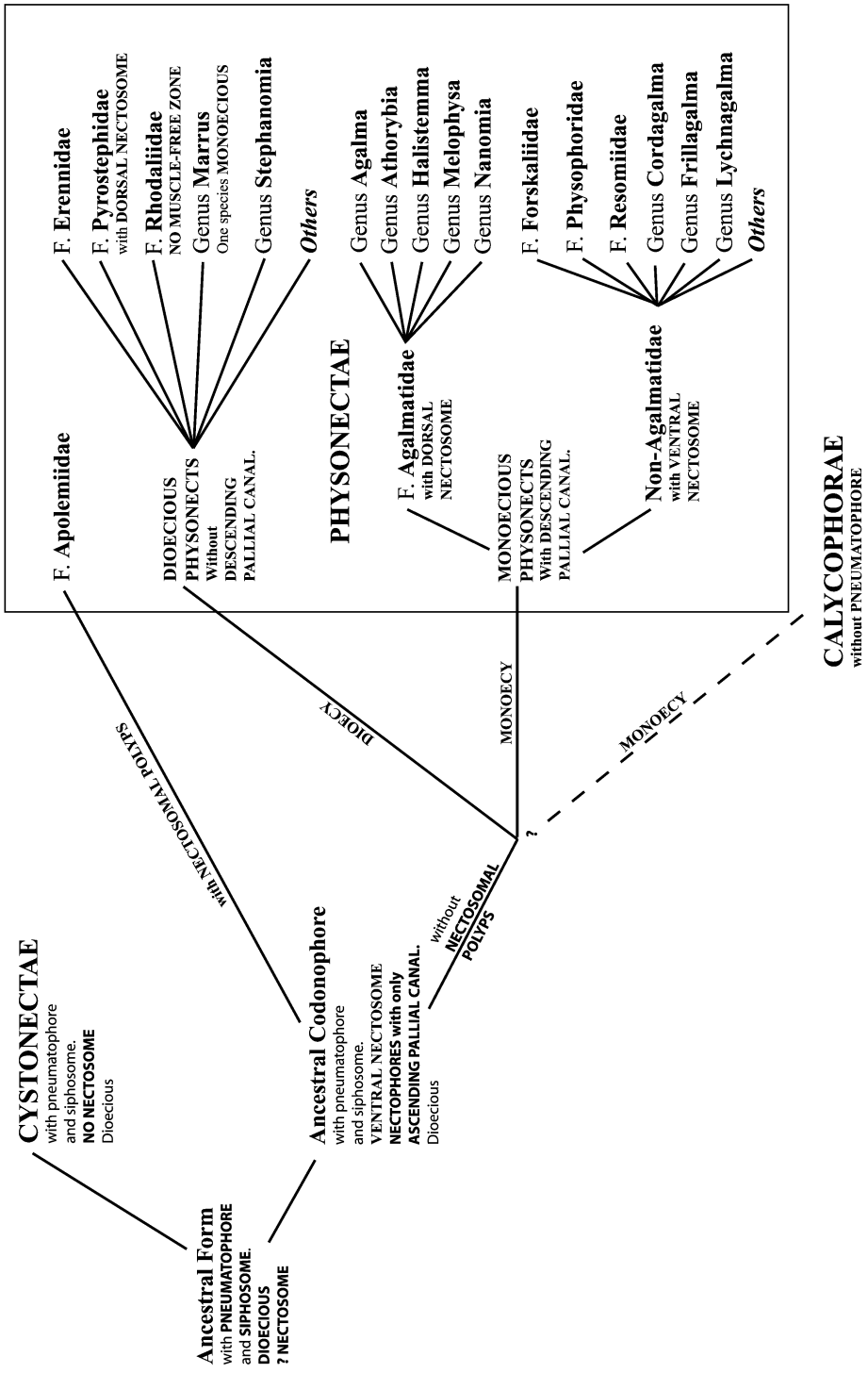

FIGURE 21. Schematic representation of a possible phylogeny for the Siphonophora, based on the molecular data of Dunn *et al.* (2005b) and general morphological characters.

According to the results of Dunn *et al.* (2005b) the family Apolemiidae branched off from all other physonects at an early stage; indeed Totton (1965) had considered it the most primitive of all physonect families. One of the distinguishing features of the apolemiids, separating it from all other physonects, is the presence of polyps, one or several, at the base of each nectophore. Again, whether or not this is an ancestral feature is uncertain. However, some suggestion that it might be ancestral comes from the detailed studies on *Bargmannia elongata* Totton (Dunn 2005b), and on *Agalma elegans* (Sars) and *Forskalia formosa* Keferstein & Ehlers (Dunn & Wagner 2006). They found that in these species there was an additional bud on the posterior side of the peduncle of each developing nectophore which gradually disappeared as the nectophore matured. They discussed the possibility that this additional bud might represent a vestigial polyp, homologous with the nectosomal polyps of apolemiids, and noted that if this was the case then it would have important implications with regard to the origin of the nectosome that may be more complex than previously thought, and possibly may have arisen as a tandem duplication of the siphosome and subsequent simplification. It would also indicate that the ancestral codonophore, and possibly the ancestral siphonophore, possessed a nectosome bearing polyps as well as nectophores.

After the loss of, or failure to gain, nectosomal polyps in all physonects apart from the Apolemiidae, the next major change in the phylogeny of the Codonophora was the transition in some physonects from the ancestral state of dioecy, as is also the situation in cystonects and apolemiids, to one of monoecy (Fig. 21). This immediately split the remaining physonect families into the dioecious Erennidae, Pyrostephidae, and Rhodaliidae, and the monoecious Agalmatidae, Athorybiidae, Forskaliidae, and Physophoridae. The position of the Calycophorae within the Codonophora has not been fully resolved by molecular data. However, the fact that they are monoecious may indicate that they are more closely related to the monoecious physonects than to dioecious ones.

At about the same time as the split into monoecious and dioecious forms occurred, two other changes in the morphology of physonect nectophores appear to have taken place. Firstly, the development of a descending pallial canal on the axial surface of the nectophore, only in monoecious physonects. Secondly, the axial part of the nectosac on its lower surface became a muscle-free zone, only in the dioecious physonects. It is uncertain as to the functionality of these changes, but they are clear-cut and distinctive characters, and neither are found in the Apolemiidae. The only known dioecious species that do not have such a muscle-free zone belong to the family Rhodaliidae, whose simple, bag-like nectophores appear to have reverted to the ancestral type.

With regard to the presence of a descending pallial canal, all the monoecious species studied by Dunn *et al.* (2005b), apart from *Athorybia rosacea* which does not develop nectophores, possessed this character and all but one, *Cordagalma ordinata* (Haeckel) (under the name *C. cordiforme* — see Appendix A), fell within a very distinct clade (Fig. 21). Within this clade, the data clearly showed that the family Agalmatidae must be

restricted to only three of the genera previously included within it, namely *Agalma*, *Halistemma* and *Nanomia*, but that it should also include at least one of the three short-stemmed species previously hived off in a separate family, the Athorybiidae. The systematic position of this latter family is considered further in Appendix B, where it is concluded that both the athorybiid genera, *Athorybia* and *Melophysa*, should be moved into the family Agalmatidae.

The clear difference between the Agalmatidae *sensu stricto* and the two remaining monoecious physonect families, Forskaliidae and Physophoridae, together with the genera that now must be removed from the previously catch-all Agalmatidae, is that in the ancestral agalmatid there was a changeover from the nectophores being budded off on the ventral side of the nectosome to one where they were budded off on the dorsal side (Fig. 21). The functionality of this major change in morphology is uncertain, but it also occurred, quite independently, in the family Pyrostephidae, which the molecular and morphological data place within the dioecious group of physonects (Fig. 21). The fact that the nectosomal budding can occur on either the dorsal or ventral side of the stem appears not to have been noticed by earlier researchers on siphonophores. However, Totton (1965, p. 16) noted that "it has been established that in most physonects (not apparently in *Forskalia*) the budding meridian for nectophores is on the opposite side [to] that of siphosomal buds," that is dorsal. However, he later admitted that the nectosomal budding in *Marrus orthocannoides* Totton also was ventral. Totton (1954) made a similar statement, but in neither monograph was any more made of this fundamental morphological feature. Totton also does not state who had established this fact, although one must assume that he was being coy as Garstang's (1946, p. 147) thorough review of past works on the morphology and relations of siphonophores commented that "Each zone [nectosome and siphosome] has its own centre of proliferation in the ventral tract."

The genera that Totton (1965) included in the Agalmatidae but which must now be excluded are *Cordagalma*, *Erenna* (already moved into a separate family, as noted above), *Lychnagalma*, *Marrus*, and *Resomia* (*Moseria*), together with the species *Stephanomia amphytridis* (see Appendix C). In addition, many physonect species have been described or re-established since Totton (1965). Most of these can be ascribed to a recognised genus or family, but there are a few whose systematic position remains unclear. These are *Frillagalma vityazi* Daniel (see below); *Sphaeragalma rotunda* Margulis (see Appendix C); *Rudjakovia plicata* Margulis (see below); *Stepanyantsia polymorpha* Margulis, which the present author considers to be a synonym of *R. plicata*; and *Mica micula* Margulis, which appears to be a post-larval stage (see Pugh 1999b).

The enigmatic position of *Cordagalma* in the phylogenetic studies has already been discussed by Dunn *et al.* (2005b). Nonetheless, based on its morphological characters it clearly belongs within the monoecious physonects (Fig. 21), but not to the family Agalmatidae as its nectophores are developed on the ventral side of the stem. In the analyses of Dunn *et al.* (2005b) *Stephanomia amphytridis* and a species of the genus

Erenna were clearly separated off from the clade of monoecious physonects. This separation can be further verified by the fact that these species are dioecious, have no descending pallial canal on their nectophores, which are developed on the ventral side of the nectosome, and that a muscle-free zone is present on the nectosac (Fig. 21).

Representatives of two genera, *Lychnagalma* and *Marrus*, that must now be excluded from the Agalmatidae were included in a supplemental analysis of the molecular data carried out by Dunn (2005), which included species where data for only a single gene were available. He found that *L. utricularia* (Claus) clearly fell within the monoecious physonects, while *M. orthocanna* and *M. claudanielis*, which clearly were closely related, fell without (Fig. 21). From this one would expect both *Marrus* species to be dioecious, but this does not appear to be true for *M. orthocanna*. This anomaly has already been discussed by Dunn *et al.* (2005a). There are always exceptions to the rules when dealing with siphonophores, and this is one of them. There is also preliminary evidence, within the genus *Bargmannia* (family Pyrostephidae), that an undescribed species is also monoecious (Pugh, personal observation) and so the individual gain or loss of a character may not be uncommon, as Dunn *et al.* (2005b) discussed.

The morphology of the nectophores, particularly the ridge pattern and the course of the radial canals, and tentilla of *Lychnagalma utricularia* would immediately suggest a close affinity to the Agalmatidae, as Pugh (1998) noted; except that the nectosome is ventral. However, Dunn and Wagner (2006) have found that the long peduncles to the gastrozooids in this species each bore a palpon, which they called a **"**gastric palpon,**"** toward its distal end, and several bracts. The only other physonects known to have gastrozooids with long peduncles that bear other zooids are species of *Forskalia*, but in this case the zooids are only bracts. Although this suggests that there may be some affinities between the Forskaliidae and *Lychnagalma*, the supplementary analysis of Dunn (2005a) suggested that this genus was more closely allied with the Physophoridae, although the significance of this needs further assessment. Dunn and Wagner (2006) also noted that the short peduncles of the gastrozooids of *Agalma elegans* bore gastric palpons and so it is clear that further precise studies on cormidial organization in physonect species are needed in order to understand the associations between these various zooids.

Presently there are no available molecular genetic data for the genera *Frillagalma*, *Resomia*, and *Rudjakovia,* and so their systematic position can only be gauged from their morphological characters. The species *Rudjakovia plicata* Margulis is little known and, although further specimens have been collected more recently (Pagès, personal communication; Pugh, own data), it is still unclear whether the species is monoecious or dioecious. However, the nectophores appear to be budded off on the dorsal side of the stem and they have no muscle-free zone on the nectosac, but it remains to be verified whether a descending pallial canal is present or absent, as those nectophores seen by the present author are too poorly preserved. Nonetheless, the other two characters suggest that this species might belong to the family Agalmatidae *sensu stricto*, but we must await

confirmation of the other characters before the systematics of the genus *Rudjakovia* can firmly be established.

The genera *Frillagalma* and *Resomia* both share the same basic morphological characters as the non-agalmatid monoecious physonects but, as was the case for *Lychnagalma* and *Cordagalma*, neither can be associated with either of the extant families in that group. *Frillagalma vityazi* also has an agalmatid-like ridge pattern on the nectophores, but the course of the radial canals is quite different. In addition, its bracts closely resemble one of the types of bract found on the peduncles of the gastrozooids of *Forskalia* species – so much so that Totton (1965) ascribed its bracts to a species of that genus. The course of the radial canals in the nectophores of *F. vityazi* is similar to that in species of *Cordagalma*, although the characteristic heart-shaped nectophores of the latter are very distinctive. Pugh (1998) made further comparisons between *F. vityazi* and *C. ordinata*, but until further molecular data become available one can say little more about the relationships of these genera, apart from their obvious position within the non-agalmatid monoecious physonects.

But can anything be said about the systematic position of the genus *Resomia*? It shows all the basic non-agalmatid characters of the monoecious physonects, and like *Cordagalma* bears very characteristic nectophores. However, the most distinctive character is the presence of two forms of tentilla on each tentacle. The only physonect siphonophores known to possess two types of tentillum are *Athorybia rosacea* (see Appendix B) and *Erenna cornuta* Pugh, although the cystonect *Rhizophysa filiformis* (Forskål) has three. However, these tentilla are very distinctive and one type is not known to transform into another. There is, perhaps, a similarity between the tentilla of *Resomia* species and those of *Physophora gilmeri* Pugh as in the latter species (see Pugh 2005), the cnidoband, enclosed within a solid capsule much sturdier than the involucrum of *Resomia* species, appeared to be able to unravel and re-ravel itself into a variety of different shapes during its development. However, it never underwent the total transformation seen in species of *Resomia*.

More details about related species, also with two forms of tentilla, will emerge from a forthcoming paper (Haddock and Pugh, in preparation). However, even without that information, it is felt that the known characteristics of the genus *Resomia* are sufficient for it to placed in a new family, the Resomiidae (Fig. 21), whose primary diagnosis is based on the presence of two forms of tentilla on the same tentacle; the more proximal one, with a spirally coiled cnidoband, transforming into the second more distal form, with a zigzagged cnidoband.

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Appendix A. The genus *Cordagalma* Totton

The present author repeatedly forgets that, according to Mills *et al.* (1996), the species commonly called *C. cordiformis* Totton (or its corrected form *C. cordiforme*; a necessary change in order that the ending of the specific name agrees with the gender of the generic name) should really be referred to as *C. ordinata* (Haeckel). Totton's (1932) original description was based on only six loose nectophores, and it was not until Carré (1968) that a full description, including the siphosome, became available. In this re-description Carré noted that the bracts, particularly, resembled those described by Haeckel (1888) for his species *Anthemodes ordinata* Haeckel, but he considered that the two species, otherwise, could not be confused. It is true that Haeckel's description and illustrations of the nectophores of *A. ordinata* bear no resemblance whatsoever to those of *Cordagalma*, but it must be remembered that Haeckel had little interest in nectophores. However, his illustrations of the siphosomal elements cannot be ignored and, largely, they are identical to those described by Carré. Thus, following Mills *et al*. (1996), there should be no doubt that the species *A. ordinata* and *C. cordiforme* are synonymous and, as the genus *Anthemodes* is preoccupied and, thereby, cannot be used for this species, the species must be referred to as *C. ordinata* (Haeckel). It should also be noted that Carré (1968) described what he called "variabilité" in the palpons and tentilla of his specimens, but he considered that there was insufficient evidence to consider the possibility of the existence of another *Cordagalma* species. This variability will be considered in detail in a forthcoming paper (Pugh, in preparation).

Appendix B. The systematic position of the family Athorybiidae

The monoecious family Athorybiidae presently encompasses two genera, *Athorybia* and *Melophysa*, and three species, *A. rosacea* (Forskål), *A. lucida* Biggs and *Melophysa melo* (Quoy and Gaimard). The similarity between *A. rosacea* and the post-larva of *Agalma elegans* (Sars) has long been recognised (e.g. Fewkes 1880), but Dunn *et al.* (2005b) showed for the first time just how close that relationship was. Although *Athorybia* species have secondarily lost their nectosome, it has been established (Pugh, personal observation) that the nectosome in *M. melo* is dorsal, and that the nectophores possess a descending pallial canal and do not have muscle-free zone, indicating that this species should also belong within the Agalmatidae. The evidence from Dunn *et al.* (2005b) not only shows *A. rosacea* clustered amongst the agalmatid genera, but that it is deeply embedded within the genus *Agalma*, being most closely related to *A. okeni* Eschscholtz.

The key morphological feature of the genus *Agalma* is that the tentilla have an involucrum and are tricornuate, that is, at their distal ends there is a central ampulla with a lateral filament on either side. The presently included species also have linear, but rigid, siphosomes. In both *Athorybia* and *Melophysa* the siphosome has solidified into a corm around which the cormidia spiral. There are two types of tentilla in *A. rosacea*, both tricornuate, but one is not involucrate. The tentilla of *M. melo* are both tricornuate and involucrate. However, those of *A. lucida*, according to Biggs (1976), are slightly different in that they are involucrate, but distally there are only two filaments, with no central ampulla. There are thus, for the most part, great similarities between the tentilla of these three species and those of *Agalma* species. Should then all three species be moved to within the latter genus? Dunn *et al.* (2005b, p. 928) chose "not to change the name of *Athorybia* until further morphological or molecular data can clarify the implications for the other two species of Athorybiidae not included in the present analysis." This seems to be the wiser choice as if *Athorybia*, and even *Melophysa*, were considered to be synonymous with *Agalma*, then that genus would be unique amongst physonect siphonophores as encompassing both long- and short-stemmed species. Thus, presently, the generic names *Athorybia* and *Melophysa* are retained, but placed within the family Agalmatidae (Fig. 21), thereby resulting in the family Athorybiidae disappearing from siphonophoran nomenclature.

Appendix C. The species *Stephanomia amphytridis* Lesueur & Petit, 1807

The species that Dunn *et al.* (2005b) and the present author refer to as *Stephanomia amphytridis* is the same as that referred to by Totton (1936, 1965) as *S. amphitridis* and ?*Halistemma amphytridis*, respectively; the relevant specimens being still extant. This species has also been briefly described and figured by Daniel (1974, 1985) under the name *H. amphytridis*, and by Margulis (1976) under the name *Sphaeragalma rotunda* Margulis. Daniel (1985) noted that although she included the species in the genus *Halistemma*, the nectophores differed markedly from those of a "typical" *Halistemma* species indicating that the species warranted being placed in a new genus.

Several characters distinguish this species from that described by Huxley (1859), Bigelow (1911b) and Kawamura (1954) all under the name *S. amphitridis* [sic], and by Mapstone (2004) as *H. amphytridis*. All but Huxley's specimen are still in existence, and Mapstone compared her specimen with those of Bigelow, confirming that they belonged to the same species. Kawamura's specimen also belongs to the same species, as Dr. Francesc Pagès has re-examined the specimen and kindly confirmed this fact. All the authors mentioned described them as being monoecious, but the arrangement of the nectosome and the morphology of the nectophores can only be assessed from Mapstone's specimen, as all the other specimens consisted only of a siphosome. The nectophores of her specimen each have a descending pallial canal, as can be discerned from one of her figures although not mentioned in the text, and no muscle-free zone on the nectosac. In addition, my own observations of the specimen show that the nectophores are clearly budded off on the dorsal side of the nectosomal stem, although Mapstone described them as being budded on the ventral side. These characters would indicate that the species belongs to the family Agalmatidae and, based on the course of the lateral radial canals on the nectosac, can be attributed to the agalmatid genus *Halistemma*.

Nonetheless, it is the structure of the bracts that specifically characterises all these specimens. Huxley (1859, p. 72) described the bracts as being "attached by triangular, striated processes from the ectoderm, whose base was inserted on a triangular ridge, which traversed the middle of the inner face." Although Bigelow (1911) did not describe this triangular structure, it is clearly visible in his Pl. 18, fig. 8 and its presence has been confirmed (Pugh, personal observation) in both Bigelow's and Mapstone's specimens; the latter author referring to it as a "ventral keel." Francesc Pagès (personal communication) has also confirmed its presence on the bracts of Kawamura's specimen. Because of this distinctive swelling, in the region of attachment on the lower side of the bract, it is considered by the present author that the specimens described by these authors should all be synonymized with *Halistemma* (*Stephanomia*) *foliacea* (Quoy and Gaimard). Although Quoy and Gaimard's (1833, 1834) description and figures may not be up to modern day standards, nevertheless the mention of bracts "munie d'une languette triangulaire en dedans, à l'aide de laquelle ces corps se fixent sur leur axe." (*ibid*, p.75) is a very distinctive character and was, at that time, quite sufficient to establish the species, albeit incompletely known, as Bedot (1896) recognized. Indeed, Bigelow (1911) included *S. foliacea* species as a doubtful synonym of his *S. amphitridis*.

It is concluded, therefore, that it is no longer appropriate to apply the name *Stephanomia amphytridis* to this halistemmid species, but instead the name should be used for the specimens mentioned by Totton (1936, 1965) and described by Daniel (1974, 1985) and by Margulis (1976).

