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Reclassification of the clausophyid siphonophore *Clausophyes ovata* into the genus *Kephyes* gen. nov.

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Comparisons are made between the species currently called *Clausophyes ovata* and other *Clausophyes* species. It is concluded that *Cl. ovata* should be removed to another genus and, consequently, the genus *Kephyes* gen. nov. is established for it. The relationships of all clausophyid genera are briefly discussed.

INTRODUCTION

Keferstein & Ehlers's (1860) original description of *Diphyes ovata* was very brief and without illustration, but for its time it was more than adequate to establish the authenticity of the species, particularly with the description of heteromorphic anterior and posterior nectophores both with a somatocyst. The following year, Keferstein & Ehlers (1861) published a more detailed description, with illustrations (see Figure 1), which clearly established the species. Since then, this species has not been properly recognized for over 125 years, although the specific name, *ovata*, frequently has been used.

Chun (1897), without having seen any specimens, addressed the systematic position of the species and considered that it probably occupied an intermediate position between the two sub-families, Prayinae and Galeolarinae, of his Tribus Oppositae (Prayomorphae) but, nevertheless, he placed it within the genus *Galeolaria* Blainville, 1830 (= *Sulculeolaria* Blainville, 1834) (Figure 1), probably because he believed that the posterior nectophore of all *Galeolaria* species possessed a somatocyst.

Lens & van Riemsdijk (1908) established the genus *Clausophyes* (henceforth abbreviated as *Cl.* to avoid confusion with other clausophyid genera that begin with the same letter) for a large single nectophore, in poor condition, to which they gave the name *Cl. galeata* Lens & van Riemsdijk, 1908 (see Figure 1). They were uncertain whether it was an anterior or posterior nectophore, but it has since been established that it was a posterior one. They did, however, note the possible presence of a small somatocyst at its anterior end and the fact that the ventral mouth plate was deeply divided. They were also uncertain as to its taxonomic position but, correctly according to present systematics, associated it with another genus *Chuniphyes* Lens & van Riemsdijk, 1908.

Bigelow (1913) refuted Chun's (1897) suggestion that a somatocyst was present in the posterior nectophores of *Galeolaria* (*Sulculeolaria*) species, and thus considered that Keferstein & Ehlers's *Diphyes ovata* must belong to a different genus. He considered that there was a close relationship, particularly with regard to the presence of a somatocyst in both the anterior and posterior nectophores, between *D. ovata* and some additional specimens of *Clausophyes galeata* (see Figure 1), which he described under the *lapsus calami* name *Cl. galatea*. Nonetheless, he noted that there were clear differences between the two species, particularly with regard to the structure of the mouth plate on the posterior nectophore, and so he included *D. ovata* as a separate species within the genus *Clausophyes*.

To this point the distinctiveness of the species *Clausophyes ovata* (Keferstein & Ehlers, 1860) and *Cl. galeata* had been clearly recognized, but with Moser (1913, 1925) the situation became confused. Moser (1913) reported on the capture, in a trawl from 1000 m off Villefranche (north-west Mediterranean), of a small anterior nectophore, in poor condition, which she positively, and probably correctly, identified as belonging to *Cl. ovata*. However, subsequently Moser (1925) considered that her Mediterranean specimen was also identical to the anterior nectophore of *Cl. galeata* described by Bigelow (1913). She was, thus, convinced that there were insufficient characters to distinguish the two species and so she synonymized *Cl. galeata* with *Cl. ovata*. Not only has this conclusion proved erroneous, but the fact that the material from the *Gauss* Expedition, which Moser (1925) described and illustrated under the name *Cl. ovata*, actually belonged to a completely different species was not recognized for more than 60 years.

During those intervening years, the species *Clausophyes ovata* was referred to on many occasions, but almost exclusively with reference to the different species described by Moser (1925) under that name. The confusion was such that the species described by Keferstein & Ehlers (1860, 1861) was even redescribed under a totally different name, *Cl. massiliana* Patriti, 1969 (see Figure 1). It was Margulis (1988), in an otherwise poor and inaccurate revision of the sub-family Clausophyinae, who first recognized that Moser's *Gauss* material differed from Keferstein & Ehlers's *Cl. (Diphyes) ovata*. However, Margulis believed that Moser's material was only a sub-species of *Cl. galeata* and accordingly she ascribed the name *Cl. galeata moserae* Margulis, 1988 (see Figure 1) to them. She also redescribed *Cl. galeata galeata* (see Figure 1), but there is some doubt as to her identifications, at least with regard to the posterior nectophore, as in a subsequent correspondence she told me that the characteristic 'finger-shaped projections', as defined by Totton (1954), were absent from her specimens, thereby indicating that they probably belonged to her *Cl. galeata moserae*. Margulis also redescribed *Cl. ovata* (see Figure 1), synonymizing *Cl. massiliana* with it.

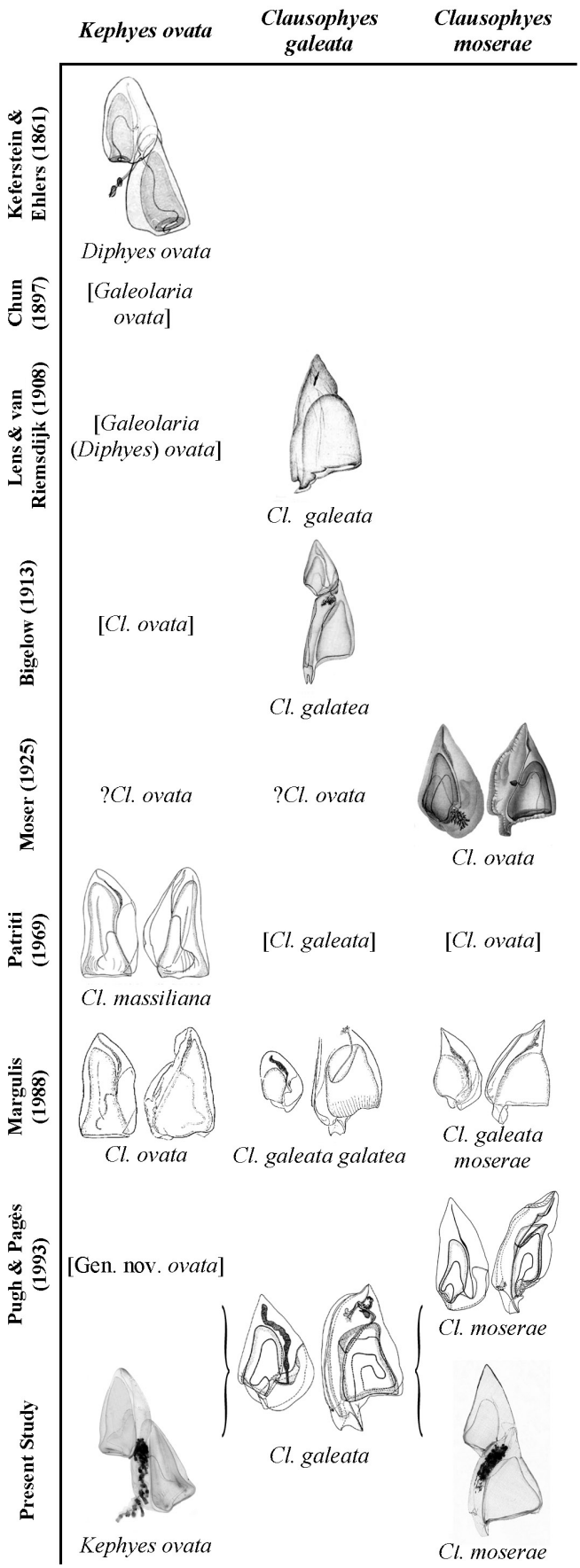

Figure 1. Time line for the descriptions of *Kephyes ovata*, *Clausophyes galeata* and *Cl. moserae*. Names in square brackets indicate a change in status for the species or its mention in the text, but without any specimens having been examined by the authors. Illustrations adapted from Keferstein & Ehlers (1861, Pl. V, figure 1), Lens & van Riemsdijk (1908, Pl. I, figure 6), Bigelow (1913, Pl. 6, figure 1), Moser (1925, Pl. XXIV, figure 4 & Pl. XXV, figure 4), Patriti (1969, figures 1A & 2A), Margulis (1988, figure 1), and Pugh & Pagès (1993, figures 3–6).

The fact that *Clausophyes galeata* and what thus became *Cl. moserae* Margulis, 1988 were two different species was later established by Pugh & Pagès (1993) (see Figure 1). These authors also described another *Clausophyes* species, *Cl. laetmata* Pugh & Pagès, 1993 and commented on their belief, based on certain distinctive morphological characters, that the species *ovata* did not in fact belong to the genus *Clausophyes*, but deferred discussion of this matter to a subsequent paper. This belief was later reiterated by Pugh (1995) who described a further *Clausophyes* species, *Cl. tropica* Pugh, 1995.

However, these were not the first times that the systematic position of *Clausophyes ovata* has been brought into question; as Patriti (1969, p. 258) stated, in the conclusions to his description of *Cl. massiliana* 'Il semblerait que *Cl. massiliana* [=*Cl. ovata*] constitute un intermédiaire entre *Cl. ovata* [=*Cl. moserae* in this context] et *Cristallophyes* [sic] *amygdalina*. Il m'a semblé cependant plus logique d'inclure cette espèce dans le genre *Clausophyes* plutôt que de créer un genre nouveau dans une famille déjà fort embrouillée'. The purpose of this paper is to establish, particularly as new information is to hand, the differences between what is currently called *Cl. ovata* and the other species of the genus *Clausophyes*. In consequence a new generic name, *Kephyes* gen. nov., is established for *K. ovata* (Keferstein & Ehlers, 1860), and diagnoses of both genera will be given, together with further details of the morphology of *K. ovata*. It is not intended to consider the zoogeography of these species, as this is deferred to a future paper that will review the whole of the family Clausophyidae.

MATERIALS AND METHODS

Over 30,000 anterior and 48,000 posterior nectophores of *Clausophyes moserae* have been identified from recent 'Discovery' collections, mainly from the north-east Atlantic Ocean, presently housed at the National Oceanography Centre, but not a single eudoxid bract that could be associated with them has been found. With regard to *Kephyes ovata* over 700 anterior and 600 posterior nectophores have been identified from the same collections, together with about 100 eudoxids. In addition, a handful of specimens of each species have been collected in recent years by submersibles or remotely operated vehicles (ROVs). The information on other *Clausophyes* species has been reviewed in the recent papers mentioned above.

Definitions

One of the problems with describing calycophoran species, particularly those belonging to the families Prayidae and Clausophyidae, has been how to define the various parts of the gastrovascular canal system that are present in the nectophores and bracts. Haddock et al. (2005) have recently reconsidered this problem and have established strict definitions for these canals, with particular reference to prayid siphonophores. Nonetheless, they can equally be applied to the clausophyid nectophoral and bracteal canal systems and will be adopted here. To recap in reference to the nectophores, the *pedicular canal* is defined as the entire canal that runs from the gastrovascular canal of the stem to the nectosac of the nectophore, where it gives rise to some or all of the radial canals. Within the nectophore this canal either may run directly to the nectosac, or may have what was defined as a *disjunct portion*, when firstly it is directed posteriorly, running parallel to the hydroecial wall, before penetrating through the mesogloea to reach the nectosac. At the point where the disjunct portion ends and the pedicular canal turns away from the hydroecium toward the nectosac, an additional canal, defined as a *descending branch*, may arise and continue posteriorly along the hydroecial wall. The somatocyst is defined as any blind branch of the gastrovascular system that runs *anteriorly* from the point where the pedicular canal enters the nectophore. These definitions of the pedicular canal and somatocyst obviate the usage of the often confusing term *pallial canal*.

SYSTEMATICS

Order SIPHONOPHORA Eschscholtz, 1829
Suborder CALYCOPHORAE Leuckart, 1854
Family CLAUSOPHYIDAE Totton, 1965

Diagnosis

Calycophoran siphonophores with one or two definitive nectophores. Where two are present they are heteromorphic and the anterior one is partially superimposed on the posterior one. Both nectophores possess a somatocyst.

Remarks

Five genera are here recognized; *Kephyes* gen. nov., monotypic for *K. ovata*; *Clausophyes* Lens & van Riemsdijk, 1908, containing four species, *Cl. galeata*, *Cl. moserae*, *Cl. laetmata*, and *Cl. tropica*; *Chuniphyes* Lens & van Riemsdijk, 1908, with two species, *Ch. multidentata* Lens & van Riemsdijk, 1908 and *Ch. moserae* Totton, 1954; *Crystallophyes* Moser, 1925, presently monotypic for *Cr. amygdalina* Moser, 1925, although a second species is known to exist (F. Pagès, personal communication); and *Heteropyramis* Moser, 1925 with two species *H. maculata* Moser, 1925 and *H. crystallina* (Moser, 1925).

Genus Kephyes *gen. nov.*

Monotypic genus for *Kephyes ovata* (Keferstein & Ehlers, 1860).

Etymology

The genus is named for Keferstein and Ehlers, based on the initial letter of their surnames.

Kephyes ovata (Keferstein & Ehlers, 1860)

Diagnosis

Anterior and posterior nectophores smooth, ridgeless, laterally compressed, with rounded apices. Nectosac extending to ~85% height of nectophores; with slightly looped lateral radial canals; without major loop before joining ostial ring canal. Pedicular canal with long descending branch in both nectophores. Somatocyst with characteristic reticulated appearance. Hydroecium in anterior nectophore extensive, without median mesogloeal

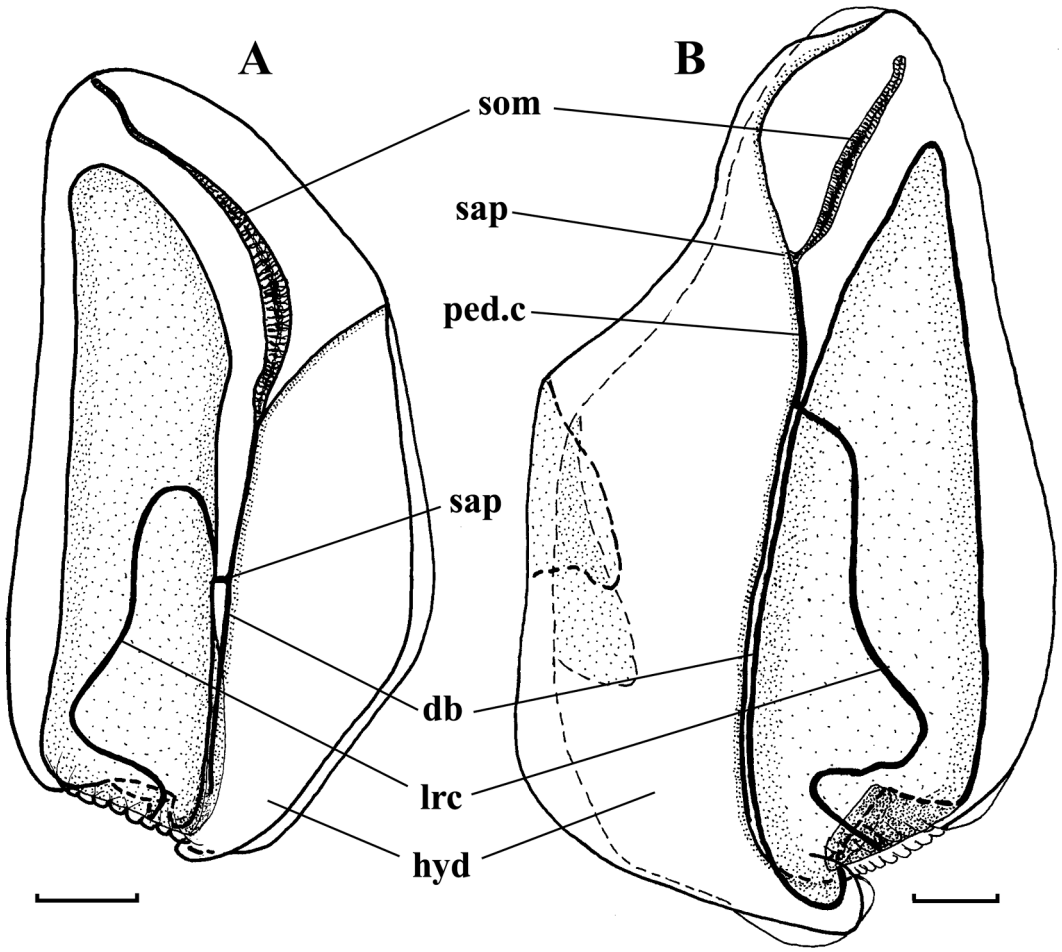

Figure 2. *Kephyes ovata* (Keferstein & Ehlers, 1860). Lateral views of (A) an anterior; and (B) a posterior nectophore. db, descending branch of pedicular canal; hyd, hydroecium; lrc, lateral radial canal; ped.c, pedicular canal; sap, stem attachment point; som, somatocyst. Scale bar: 1 mm.

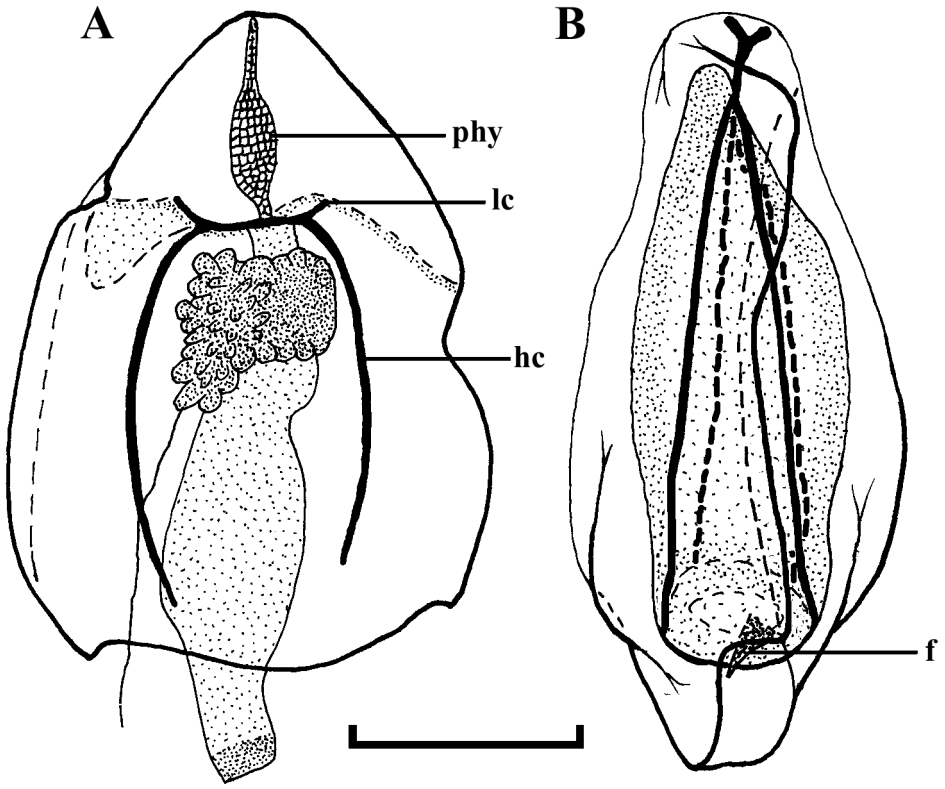

Figure 3. *Kephyes ovata* (Keferstein & Ehlers, 1860). (A) Upper view of eudoxid bract; and (B) ventro-lateral view of gonophore. f, fold; hc, hydroecial canal; lc, longitudinal canal; phy, phyllocyst. Scale bar: 1 mm.

swelling; origin of lateral radial canals variable, often arising separately from upper (dorsal) canal.

Eudoxids developed. Bracteal canal system constituted by phyllocyst, two hydroecial canals, and moderately long longitudinal canal, extending as spurs beyond the origins of the hydroecials. Gonophore with flap on posterior end of right hydroecial wing.

Description

Anterior nectophore (Figure 2A), up to 14 mm in length, with broad rounded apex. Hydroecium and nectosac extend to ~70% and 85% of its height, respectively. Hydroecium without ventro-lateral flaps or median mesogloeal process; with lateral wings barely extending basal to ostium to form ventral edges of small mouth plate. The external pedicular canal from the stem continues directly into the internal canal on penetrating into the nectophore, i.e. there is no disjunct portion.

However, there is a long descending branch extending almost to the posterior end of the nectophore. The somatocyst has a long, tubular, proximal section in contact with the hydroecial wall before it penetrates into the mesogloea as a slightly swollen caecal extension. This part of the somatocyst has a characteristic reticulated appearance and terminates very close to the apex of the nectophore.

Although Patriti (1969) did not describe the origins of the lateral radial canals on the nectosac, he illustrated them as arising separately, but it is not certain where with respect to the insertion of the pedicular canal. The present material indicates that their origins can vary greatly from both arising together at the point of insertion of the pedicular canal (Figure 2A) to their arising separately, left then right, from the upper (dorsal) canal at some distance from the pedicular canal, and with some distance between them (see Figure 5A). Their point of origin also affects the degree to which the canals initially loop anteriorly before they turn posteriorly and with smooth loops, first dorsally then ventrally and finally posteriorly, they join the ostial ring canal quite close to the point of insertion of the lower (ventral) canal.

Posterior nectophore (Figure 2B), up to 14 mm in length, with rounded apex. Hydroecium present on ventral side throughout its length, and occupying about half the width of the nectophore in its posterior two-thirds. Nectosac extends to over 85% of height of nectophore. Hydroecial wings extend to ostial level or slightly below, but do not unite to form a mouth plate. A pair of hydroecial flaps, of variable size and position, present at about half the height of the hydroecium. The point of insertion of the stem is at the posterior end of the caecal somatocyst, where it reaches the hydroecial wall. Somatocyst with an arrangement and appearance very similar to that of the anterior nectophore except that it does not extend so far anteriorly. The pedicular canal has a disjunct portion and a very short internal connection to the nectosac. There is a long descending branch that extends posteriorly and ends on a level with the ostium. Again Patriti (1969) shows the lateral radial canals to arise separately, but their position with regard to the pedicular canal is unclear. In my material these canals either arise directly from the point of insertion of the pedicular canal onto the nectosac, or the left canal arises from the lower canal just posterior to this point. The angle at which each of these canals leave the ventral line of the nectosac can vary. The courses of the lateral radial canals are very similar to those on the anterior nectophore, except that they do not have an initial anteriorly directed loop.

Eudoxid bract (Figure 3A) with central phyllocyst, of similar appearance to that of the nectophores, extending to very close to the apex. There are two hydroecial canals extending down the extensive neck-shield, and the longitudinal canal extends laterally to form two short spur canals. The base of the right hydroecial wing of the gonophore (Figure 3B) bears a distinct flap. The pedicular canal divides apically to form two mantle canals.

Genus Clausophyes *Lens & van Riemsdijk, 1908*

Type species: Clausophyes galeata Lens & van Riemsdijk, 1908.

Diagnosis

Nectophores smooth, ridgeless, laterally compressed, more or less thickened with mesogloea. Nectosac with looped lateral radial canals arising together from pedicular canal; characteristically with a major loop before they join the ostial ring canal. Pedicular canal of both nectophores with a disjunct portion but no descending branch. Eudoxids not developed.

Generic description

Anterior nectophore (Figure 4A) tapering apically with more or less rounded apex. Hydroecium and nectosac extend to less than 2/3 and 3/4 its height, respectively. Hydroecium with (*Clausophyes laetmata*) or without ventro-lateral flaps; with hydroecial wings extending below ostial level to form an entire (*Cl. laetmata*) or deeply divided mouth plate; with more or less pronounced median dorsal mesogloeal process. Somatocyst and pedicular canal arise at or toward ventral tip of mesogloeal process (with the possible exception of *Cl. laetmata* see below), as branches of the canal that connects to the posterior nectophore. Pedicular canal with disjunct portion running along posterior border of mesogloeal process, and very short internal section connecting it with the nectosac. Somatocyst a tube-like caecal process, with regular or irregular expansions along part of its course, ascending through the mesogloea.

Posterior nectophore (Figure 4B), unknown for *Clausophyes laetmata*, with somewhat pointed apex. Hydroecium relatively shallow in region of nectosac; deep where mesogloeal process of anterior nectophore is inserted into it. Nectosac extending to less than three-quarters the height of the nectophore. Hydroecial wings truncated basally, where small flaps may be present. Distinct mouth plate. The pedicular canal has a long disjunct portion and a very short internal portion connecting to the radial canals of the nectosac. There is no descending branch. The somatocyst may have a short proximal portion running anteriorly along the hydroecial wall, before penetrating into the mesogloea as a broader, variably shaped caecal extension.

Bracts are absent on the siphosomal stem.

Remarks

Pugh & Pagès (1993) and Pugh (1995) provide illustrations of the anterior and posterior nectophores for all four

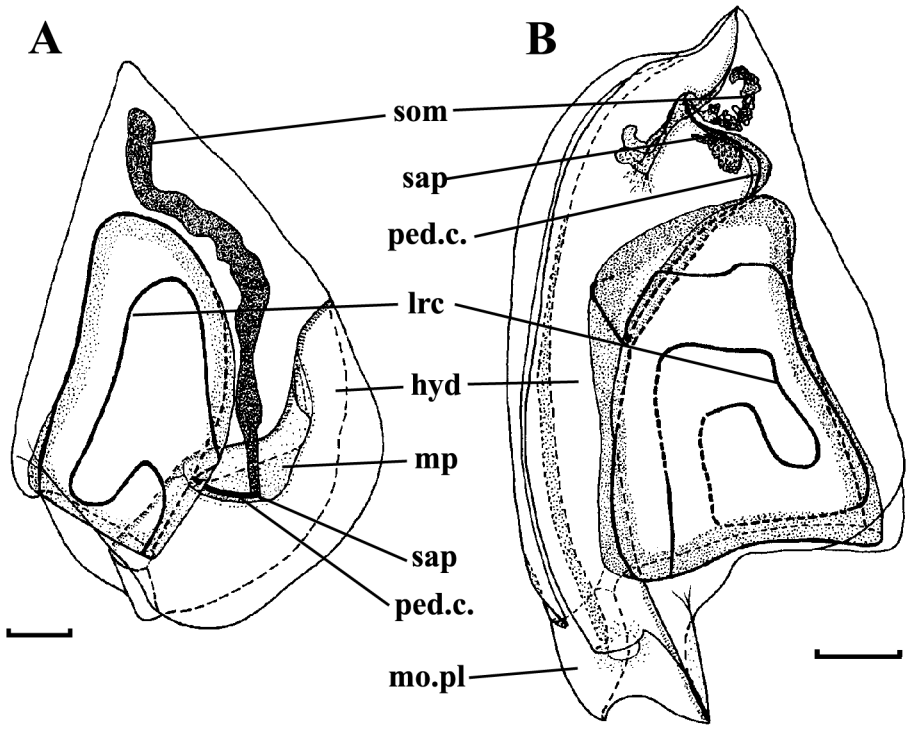

Figure 4. *Clausophyes galeata* Lens & van Riemsdijk, 1908. Lateral views of (A) anterior nectophore; and (B) posterior nectophore. After Pugh & Pagès (1993). hyd, hydroecium; lrc, lateral radial canal; mo.pl, mouth plate; mp, mesogloeal process; ped.c, pedicular canal; sap, stem attachment point; som, somatocyst. Scale bars: A, 2 mm; B, 5 mm.

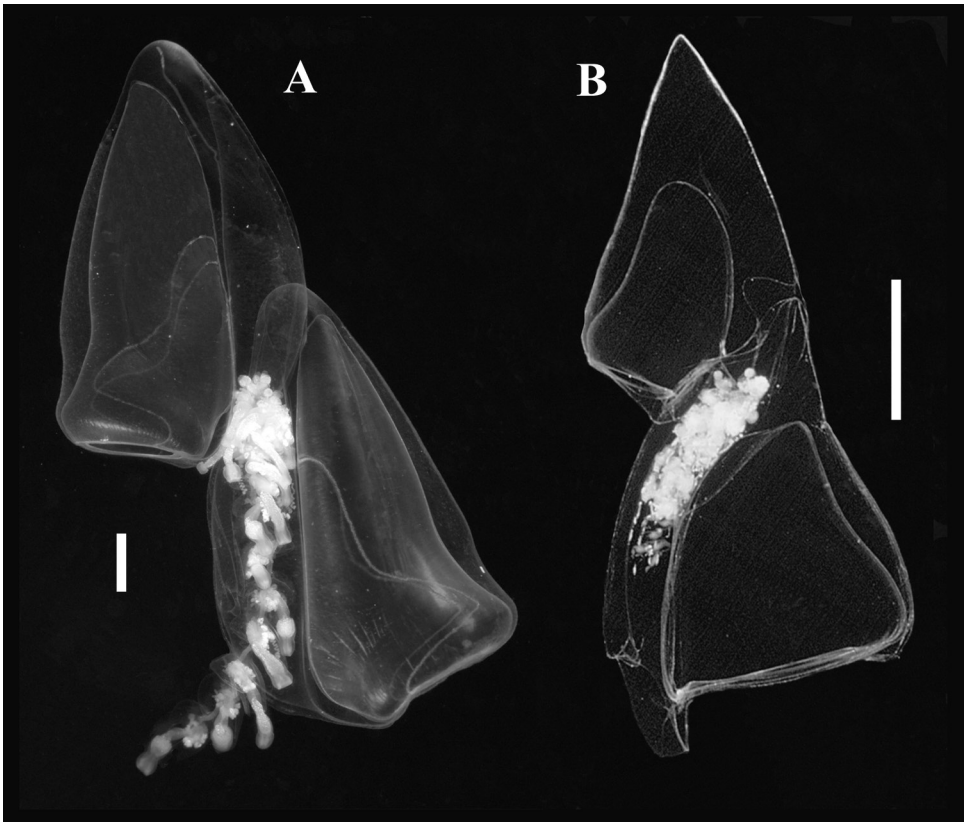

Figure 5. Photographs of lateral views of living specimens of (A) *Kephyes ovata*; and (B) *Clausophyes moserae*. Scale bar: 2 mm.

Table 1. *Comparison of morphological characters of* Kephyes ovata *and* Clausophyes *spp.*

	Kephyes ovata	*Clausophyes* spp.[1]
Anterior nectophore		
Shape	Ridgeless— with rounded apex	Ridgeless—with more pointed apex
Nectosac: total height	0.85	0.38–0.75
Radial Canals	Looped	Strongly looped
Origin	Variable	Directly from pedicular canal
Hydroecium: total height	0.7	0.5–0.67
Median mesogloeal process	Absent	Present
Pedicular canal	Disjunct portion absent	Disjunct portion present
Descending branch	Present and very long	Absent
Somatocyst	Long proximal part in contact with hydroecial wall; caecal extension into mesogloea with reticulate appearance	Caecal extension into mesogloea only—appearance variable
Posterior nectophore		
Shape	Ridgeless—with rounded apex	Ridgeless—with more pointed apex
Nectosac: total height	0.85	0.5–0.75
Radial canals	Looped	Strongly looped
Origin	Variable	Directly from pedicular canal
Hydroecium: total width[2]	0.5	0.2–0.3
Pedicular canal	Disjunct portion relatively short	Disjunct portion relatively long
Descending branch	Present and very long	Absent
Somatocyst	Caecal extension into mesogloea only, with reticulate appearance	Possible short proximal part in contact with hydroecial wall; caecal extension into mesogloea—appearance variable
Mouth plate	Absent	Present
Eudoxid stage	Present	Absent

[1], With possible exception of *Clausophyes laetmata* – see Pugh (1995) for details; [2], In posterior half of nectophore.

species currently included in the genus *Clausophyes*, and the latter paper tabulates their specific characters.

Clausophyes laetmata is the only one of the four species where a posterior nectophore is not known, and possibly may not be developed. The anterior nectophore of that species also shows some unusual features in comparison with the other three (see Pugh, 1995), particularly the presence of distinct flaps on the lateral walls of the hydroecium. The presence of such flaps is a character more associated with the posterior nectophores of the other species, although they are usually not quite so well developed. Thus in some ways it appears that the anterior nectophore of *Cl. laetmata* more closely resembles the posterior nectophores of the other species. Totton (1965) suggested that for clausophyid species the anterior nectophore might be the retained larval one. This would then explain the presence of a somatocyst in the posterior one as it would thus represent the first definitive nectophore, which, as in all calycophorans, always possesses a somatocyst. As pure speculation, one might then suggest that in *Cl. laetmata* the larval nectophore is not retained; such that the anterior nectophore represents the first definitive nectophore, which in the other *Clausophyes* species is represented by the posterior one. Nonetheless, the basic arrangement of the somatocyst and pedicular canal in the nectophore of *Cl. laetmata* is very similar to that found in the anterior nectophores of the other species. *Clausophyes laetmata* remains a little known species, recorded only from the Southern Ocean by Pugh & Pagès (1995) and Pugh et al. (1997), and so until further material is available it would be futile to speculate further.

COMPARISONS BETWEEN *KEPHYES OVATA* AND THE GENUS *CLAUSOPHYES*

From the above descriptions it should be obvious that there are fundamental differences between the morphological characteristics, as shown in Table 1 (see also Figure 5), of the genera *Kephyes* and *Clausophyes*. One of the key differences is the absence of bracts on the stems of *Clausophyes* species. In actuality this has only been proven for one of the known species, *Cl. moserae*, through the study of several intact specimens caught by the ROV 'Tiburon'. However, I have long suspected this as despite the identification of large numbers of anterior and posterior nectophore of *Cl. moserae* in recent 'Discovery' collections, not a single eudoxid bract could be associated with them. Additional proof also comes from the fact that no bracts were observed on the stem of a specimen of 'Clausophyid sp. 1' (S.H.D. Haddock, personal communication), which is closely related to the genus *Clausophyes*, and which was included in the molecular phylogenetics study made by Dunn et al. (2005). Totton (1965) gave a description of the eudoxid bract of what he called *Cl. ovata*, which clearly belongs to *K. ovata*.

The study on the molecular phylogenetics of the Siphonophora by Dunn et al. (2005) concentrated mainly on physonect species and, unfortunately, only three

clausophyid species, one yet to be described, were included in the analyses. Nonetheless these showed that *Kephyes ovata* (as *Clausophyes ovata*) and *Chuniphyes multidentata* were more closely related to each other than they were to a new *Clausophyes*-like species. The absence of bracts on the siphosome of probably all *Clausophyes* species sets this genus apart from the other clausophyid genera, and is strikingly similar to the situation in hippopodiid species. However, the analyses of Dunn et al. (2005) did not reveal any close relationship between these two taxa; indeed the hippopodiids were more closely related to a couple of prayine (family Prayidae) species. On the other hand the bracteal canal system in *Kephyes*, *Chuniphyes* and *Heteropyramis* is very similar to and bears a striking resemblance to that in prayine species (family Prayidae), particularly *Prayola* Carré, 1969, where the upper bracteal canal has disappeared. It is possible that the phyllocyst of these may represent a swollen version of the lateral bracteal canal of prayines, or perhaps even a fusion of both the lateral and upper canals. A similar situation also pertains in the eudoxid bracts of *Gilia reticulata* (Totton, 1954) (subfamily Giliinae, family Diphyidae), which possess a swollen phyllocyst and a pair of hydroecial canals, thereby suggesting a possible link with the clausophyids.

For *Clausophyes* species that develop both anterior and posterior nectophores, the absence of a descending branch to the pedicular canal in both nectophores again distinguishes this genus from the other clausophyid genera. *Crystallophyes amygdalina*, like *Kephyes ovata*, has a descending branch in both nectophores, while in *Chuniphyes* species it is present only in the posterior one. For *Heteropyramis* species, which apparently do not develop a posterior nectophore, a descending branch is again absent in the anterior one.

It is to be hoped that in follow up studies of the molecular phylogenetics of siphonophores more clausophyid taxa will be included, particularly *Cl. moserae* and *Crystallophyes amygdalina*. Such data will help to resolve whether or not, as the data of Dunn et al. (2005) appear to indicate, the family Clausophyidae is a natural grouping. They may also indicate how closely the other clausophyid genera are related. For instance, there appears to be a close relationship between the genera *Kephyes* and *Crystallophyes* with regard to certain characters, such as the presence of a descending branch to the pedicular canal in the anterior nectophore, but there are clearly differences not least in the absence of ridges on *K. ovata* and the different eudoxid stages (see Pagès & Pugh, 2002). Thus, without such additional molecular data, presently it is considered inappropriate to review further the systematics of the family Clausophyidae.

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