

Fuseudoxid: the elusive sexual stage of the calyphoran siphonophore *Crystallophyes amygdalina* (Clausophyidae: Crystallophyinae)

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Abstract

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We have identified the sexual stage of the calyphoran siphonophore *Crystallophyes amygdalina* Moser, 1925 and it appears to be closely related to the undescribed *Eudoxia* X. In both of these sexual stages, the bract and gonophore have become fused together as a single entity. This new type of siphonophoran sexual stage warrants the creation of a particular terminology and here we name it a fuseudoxid (fused eudoxid). To demonstrate these findings, both fuseudoxids are described, and their phylogenetic relationships as well as the systematic position of the genus *Crystallophyes* are discussed. The subfamily Crystallophyinae Moser (1925) is re-established.

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Introduction

Calyphorae are considered to be the most advanced hydrozoan siphonophores (Totton 1954). This order includes about 95 of the c. 150 valid siphonophoran species and it can be subdivided between the diphyomorph families (Diphyidae, Clausophyidae, Abylidae and Sphaeronectidae) that, with very few exceptions, develop a free-swimming sexual stage or eudoxid, and the prayomorph families (Prayidae, Hippopodiidae) whose cormidial groups bear gonophores permanently attached to the stem of the asexual or polygastric stage (Mackie *et al.* 1987).

Calyphoran species traditionally have been described from the asexual stage (but not always, e.g. *Eudoxoides* Huxley, 1859) because this is morphologically more distinctive than the sexual one. About 75% of the diphyomorph eudoxids have been described, or at least are known to taxonomists. However, certain eudoxids have been described that cannot be associated with a polygastric stage. Generally these are ascribed to the catch-all genus *Eudoxia*, the most notable being *E. macra* (Totton 1954). Currently, eudoxids have been described for almost all diphyomorph genera, but with the notable exceptions of *Sulculeolaria* (Diphyidae), which is known not to release eudoxids, and the clausophyid genus *Crystallophyes* (Moser 1925).

Crystallophyes is a monotypic genus for *C. amygdalina* (Moser 1925) which was originally described from three anterior nectophores collected in the Southern Ocean. Moser (1925) placed the genus in a new subfamily, Crystallophyinae, within her Tribus Intermediae. This slender species is recognizable by the pyramidal five-ridged anterior nectophore, the carrot-shaped somatocyst, with a spindle-like apical extension, which may have irregular and short side branches, and the hydroecium that apparently is open along the entire ventral side particularly in larger specimens (Fig. 1A). *C. amygdalina* has been recorded in several studies on geographical and vertical distribution of siphonophores (Leloup 1934; Leloup and Hentschel 1935; Totton 1954; Alvarino 1967; Stepanjants 1975; Margulis 1978; Kirkpatrick and Pugh 1984; Pagès and Gili 1989; Alvarino *et al.* 1990; Pagès and Kurbjeweit 1994; Pagès *et al.* 1994; Richter 1994; Pagès and Schnack-Schiel 1996; Pugh *et al.* 1997; Pugh 1999). From these studies we know that it is most commonly found in Polar waters, although it has also been found elsewhere in the three main oceans, mainly at mesopelagic depths and in low densities.

In all the aforementioned studies, only the polygastric stage of *Crystallophyes amygdalina* was found. We have sought the eudoxid of *C. amygdalina* for a long time in the hope that it might shed more light on the systematics of the family

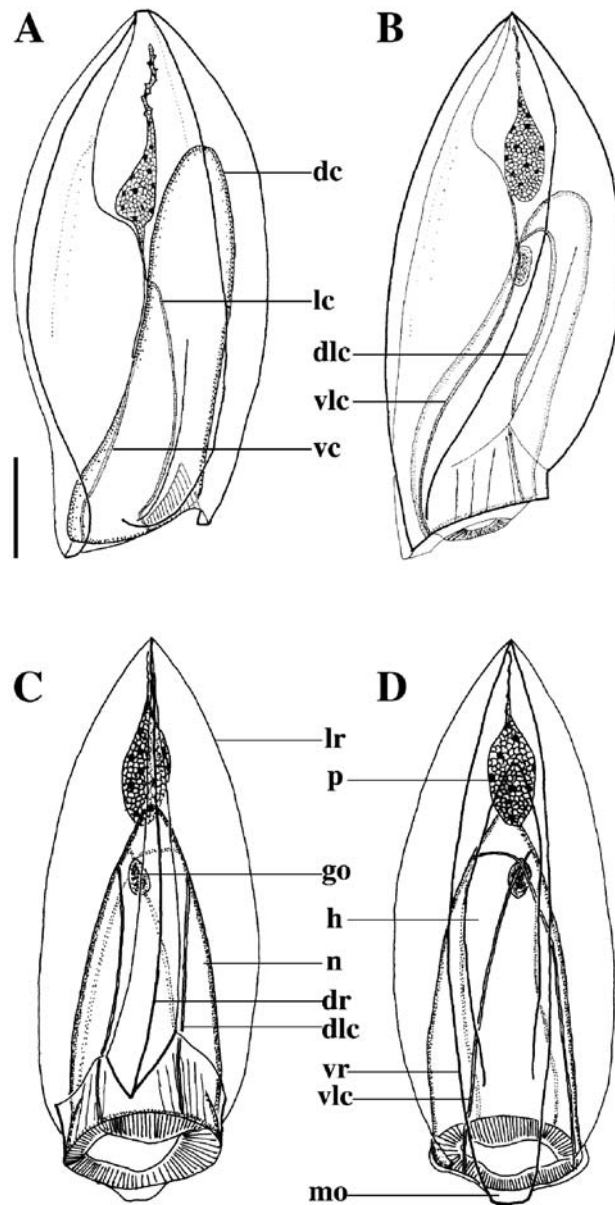


Fig. 1—*Crystallophyes amygdalina*. —**A**. Lateral view of the anterior nectophore. —**B**. Lateral, —**C**. dorsal, and —**D**. ventral views of the first fuseudoxid. Scale bar = 1 mm; dlc = dorso-lateral canal, dr = dorsal ridge, go = gonad, h = hydroecium, lc = lateral canal, lr = lateral ridge, mo = mouth-plate, n = nectosac, p = phyllocyst, vlc = ventro-lateral canal, vr = ventral ridge.

Clausophyidae and the overall phylogeny of calycophoran siphonophores. Earlier studies (Pagès and Kurbjewit 1994; Pagès and Schnack-Schiel 1996) had led us to consider the possibility that the sexual stage of this species might be an undescribed 'eudoxid' collected in the Southern Ocean and provisionally named *Eudoxia X*. However, the strange morphology of this 'eudoxid' intuitively led us to examine all the well-preserved specimens of *C. amygdalina* collected by

recent German expeditions to the Southern and Arctic Oceans. As a result of these detailed examinations, we believe that we have identified the sexual stage of *C. amygdalina*, and that it appears to be closely related to *Eudoxia X*. To demonstrate these findings, both of these sexual stages are described herein, and their phylogenetic relationships as well as the systematic position of the genus *Crystallophyes* are discussed.

Materials and methods

The specimens were sorted from zooplankton samples collected during recent *Meteor* and *Polarstern* cruises to the Southern and Arctic oceans. In total, 108 'anterior' and 20 posterior nectophores of *Crystallophyes amygdalina*, as well as 19 specimens of *Eudoxia X* have been examined. All the material was collected using a Multinet (0.25 m² mouth area, mesh size 200 µm) hauled vertically over mesopelagic depth ranges. For details, see Table 1 which shows the new terminology derived from the results.

Results

The close re-examination of the specimens of *Crystallophyes amygdalina* revealed that apparently there were two types of anterior nectophores (Fig. 1A,B). Both types were almost identical in morphology. However, only one was the true anterior nectophore (Fig. 1A); the other possessed a gonad in its subumbrella cavity, a significant dissimilarity (Fig. 1B–D). Such a difference only can be seen in well-preserved specimens in excellent condition, which probably explains why it has not been observed in the past. The observation is all the more remarkable as all calycophoran sexual stages so far described are comprised of two distinct pieces, namely a bract and one or more gonophores, together with a gastrozoid and tentacle, joined together by the original siphosomal stem. The bract is characterized by the presence of a phyllocyst (a structure homologous to the somatocyst in the anterior nectophore), and the gonophore by the possession of a gonad (Fig. 2). However, in the present case, we are led to the conclusion that the type of 'anterior nectophore' that has a gonad in its subumbrella cavity (Fig. 1B–D) is the sexual stage of *C. amygdalina*. But for this to be the case, we have to also conclude that the bract and gonophore have become fused together as a single entity. The singularity of this new type of siphonophoran sexual stage warrants the creation of a particular terminology and here we name it fuseudoxid (fused eudoxid).

This finding stimulated the re-examination of the strange structure that had provisionally been given the name *Eudoxia X* (Pagès and Kurbjewit 1994; Pagès and Schnack-Schiel 1996). In addition to the presence of a gonad in the subumbrella cavity, it shows the same characteristics as the previous fuseudoxid (fusion of bract and gonophore) indicating that it too is a fuseudoxid (Fig. 3). However, the most evident morphological character of *Eudoxia X* is the large

Table 1 Sampling locations and specimens of *Crystallophyes amygdalina* examined for this study. ANT = Antarctic, ARK = Arctic, AN = anterior nectophore, PN = posterior nectophore, FF = first fuseudoxid, SF = second fuseudoxid

Cruise	Station	Date	Position	Depth (m)	AN	PN	FF	SF
Meteor 11/4	22	30-12-1989	60°46.0 S 55°59.5 W	1000–500	3	1		
	36	3-1-1990	62°50.2 S 60°16.1 W	800–300	2	1		
	46	4-1-1990	62°88.9 S 61°48.2 W	1000–500				1
	52	5-1-1990	62°06.2 S 61°33.6 W	2000–1000	1			1
	"	"	"	1000–500	5	1		1
	93	14-1-1990	66°08.2 S 72°45.3 W	1000–500	11	1	2	1
ANT V/1	85	23-5-1986	62°40.0 S 59°20.0 W	1480–1110	1	1		
ANT IX/2	75	5-12-1990	65°57.4 S 30°04.2 W	1000–500	1			
	94	10-12-1990	68°51.4 S 17°52.6 W	1000–500	4	2		
	108	14-12-1990	70°59.3 S 11°50.3 W	1000–500	2	1		2
ANT IX/3	141	6-2-1991	73°36.7 S 26°06.7 W	1000–500				1
	157	13-2-1991	72°15.3 S 16°58.7 W	1000–480			1	
	199	2-3-1991	68°14.0 S 00°58.7 S	1000–500	8			1
	200	4-3-1991	66°48.1 S 06°14.8 W	1000–500	1	2	1	1
	202	5-3-1991	67°58.0 S 06°15.2 W	1000–500	6	1	1	1
ANT X/3	373	13-6-1992	67°58.4 S 07°17.5 W	1000–320	7	1	1	1
ANT X/4	603	17-6-1992	69°00.3 S 00°00.5 E	1000–700	4			
	"	"	"	700–500	8			1
	"	"	"	500–200				1
ANT X/7	28	24-12-1992	68°48.8 S 17°56.0 W	500–200	1	1		
	80	15-1-1993	68°38.7 S 55°27.6 W	1000–500	1		1	
ANT XI/3	43	16-2-1994	68°59.3 S 90°32.0 W	1000–500	4		4	2
	61	1-3-1994	72°33.8 S 121°01.9 W	500–200	2	1	1	
ANT XII/4	104	12-4-1995	69°24.6 S 94°10.3 W	1000–300	6	1		1
	110	13-4-1995	69°57.7 S 91°12.5 W	1000–300	2	4	2	1
	113	13-4-1995	70°12.9 S 89°22.9 W	1000–300	2	1	1	
	134	18-4-1995	68°17.1 S 89°35.7 W	1000–300	6			1
ARK IX/4	56	14-9-1993	78°40.2 N 118°42.7 E	1500–500	1		1	
ARK XI/1	60	28-8-1995	80°17.5 N 150°17.5 E	1500–1000			2	
	51a	23-8-1995	81°07.3 N 138°47.3 E	1700–1000			1	
	"	"	"	1000–750				1

and rounded mesogloal protuberance in the apical region. In order to clearly distinguish both types of fuseudoxids, the one that is morphologically similar to the anterior nectophore of *Crystallophyes amygdalina* is called the first fuseudoxid while *Eudoxia X* is renamed as the second fuseudoxid.

Description

First fuseudoxid (Figs 1B–D and 4A–D)

Up to 5.4 mm in height, oval-pyramidal, slender, with five ridges some of which may fuse very close to the apex. Ventral ridges fully developed and forming a small basal mouth-plate (Fig. 1D). Dorsal ridge cariniform and incomplete; extending from the apex down to a very short distance above the subumbrella opening. Two lateral ridges, also incomplete, describe a broad curve down from the apex and terminate

close to the ventral side at the same level as the end of the dorsal ridge (Fig. 1C). The deep hydroecium extends to half the width of the fuseudoxid and up to nearly three-quarters of its height. The subumbrella cavity extends to about two-thirds the height of the fuseudoxid; lower half wider than upper half, ventral edge sigmoidal in lateral view, apex rounded. All four radial canals originate together from the very short pedicular canal at about the mid-height of the fuseudoxid. The dorso-lateral pair of canals, at first, arch up apically before running basad, and bending toward the dorsal surface shortly before joining the ring canal.

Gonads male or female, usually small, changing in shape from rounded to oval as size increases. They hang from the point of insertion of the pedicular canal; 3–16 eggs have been observed in female gonads (Fig. 4D). Phyllocyst extending up from the pedicular canal at first following the hydroecial wall as a narrow tube, then, on penetrating into the mesogloea,

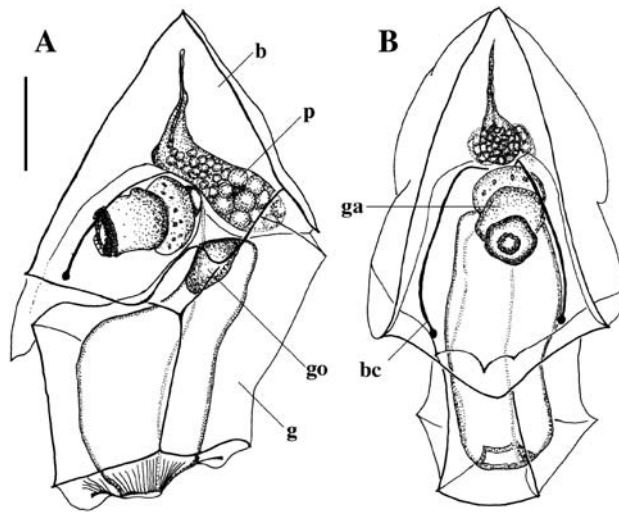


Fig. 2—Eudoxid of *Heteropyramis crystallina*. —**A.** Lateral view. —**B.** Dorso-ventral view. Scale bar = 1 mm; b = bract, bc = basal canal, g = gonophore, ga = gastrozoid, go = gonad, p = phyllocyst.

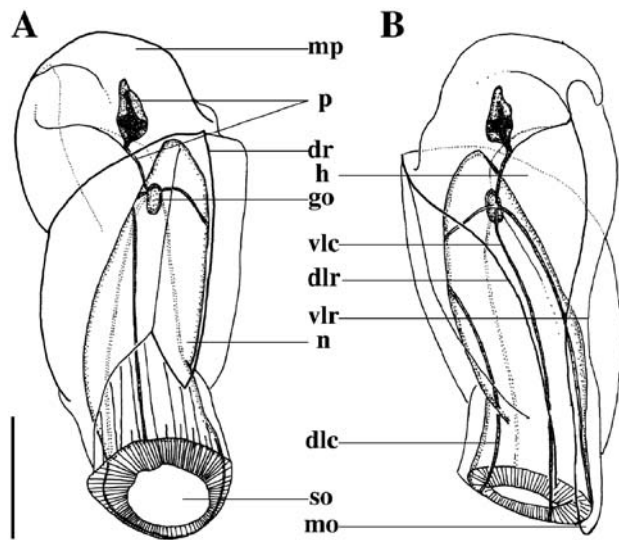


Fig. 3—Second fuseudoxid. —**A.** Lateral view. —**B.** Dorso-ventral view. Scale bar = 1 mm dlc = dorso-lateral canal, dlr = dorso-lateral ridge, dr = dorsal ridge, go = gonad, h = hydroecium, mo = mouth-plate, mp = mesogloal protuberance, n = nectosac, p = phyllocyst, so = subumbrellar opening, vlc = ventro-lateral canal, vlr = ventral ridge.

becoming inflated before narrowing to a spindle-shaped tube, sometimes with a smooth zig-zagged shape, which extends up to close to the apex of the fuseudoxid. It may have very short irregular side branches.

Remarks

Apart from the presence of a gonad in the subumbrella cavity of the first fuseudoxid, there are other morphological

differences between it and the anterior nectophore, which became evident after careful examination under the microscope.

The somatocyst of the anterior nectophore has a descending branch extending basad for some distance from the junction with the pedicular canal. No such branch is present on the phyllocyst of the first fuseudoxid. Above the junction with the pedicular canal the tubular part of the phyllocyst is relatively longer than that of the somatocyst, and it arches up parallel to the dorsal hydroecial wall, while in the anterior nectophore the somatocyst lies almost entirely within the mesogloea.

The lateral ridges of the first fuseudoxid terminate close to the ventral side at the same level as the end of the dorsal ridge (Fig. 1B), while those of the anterior nectophore curve back on themselves (Fig. 1A). The dorsal ridge of the anterior nectophore is fully developed, that of the first fuseudoxid is incomplete. The fuseudoxid has pairs of dorso- and ventro-lateral canals, as is typical of gonophores, while the anterior nectophore typically has a dorsal, ventral, and pair of laterals. The dorso-lateral pair of canals in the first fuseudoxid, at first arch up apically before running basad, while in the anterior nectophore, the lateral canals run directly basad.

Second fuseudoxid (Figs 3A,B and 5A–D)

Flimsy appearance, up to 4.0 mm in height. Upper third formed by a large, globular, laterally compressed, mesogloal protuberance. Upper half of the ventral side rounded, lower half shaped by the hydroecium. A pair of ridges, which define the ventro-lateral margins of the deep hydroecium, originates close to the apex of the protuberance and extends down to end, basally, on either side of a small mouth plate (Fig. 3B). These ridges are prominent in the upper third of the fuseudoxid, but less distinct basally. Within the protuberance, there is a globular phyllocyst, which occasionally has a tapering process directed upwards toward the apex. Basally the phyllocyst narrows to a fine tube running down the dorsal margin of the hydroecium toward the subumbrella cavity.

Below the apical protuberance the fuseudoxid is largely filled by the subumbrella cavity which, basally, bends dorsad so that its opening lies dorso-basally. Five ridges are present. Apart from the ventro-laterals mentioned above, there are a dorsal and a pair of dorso-lateral ridges. The cariniform dorsal ridge is incomplete, extending down from its junction with the dorso-laterals approximately to the level where the subumbrella cavity bends dorsad. The two dorso-lateral ridges also are incomplete, but terminate close to the subumbrella opening.

The subumbrella cavity largely fills the region below the mesogloal protuberance. Apically, its ventral margin tapers while basally it bends dorsad so that its opening lies dorso-basally. From the subumbrella end of the extremely short, almost invisible, pedicular canal the dorso-lateral pair of

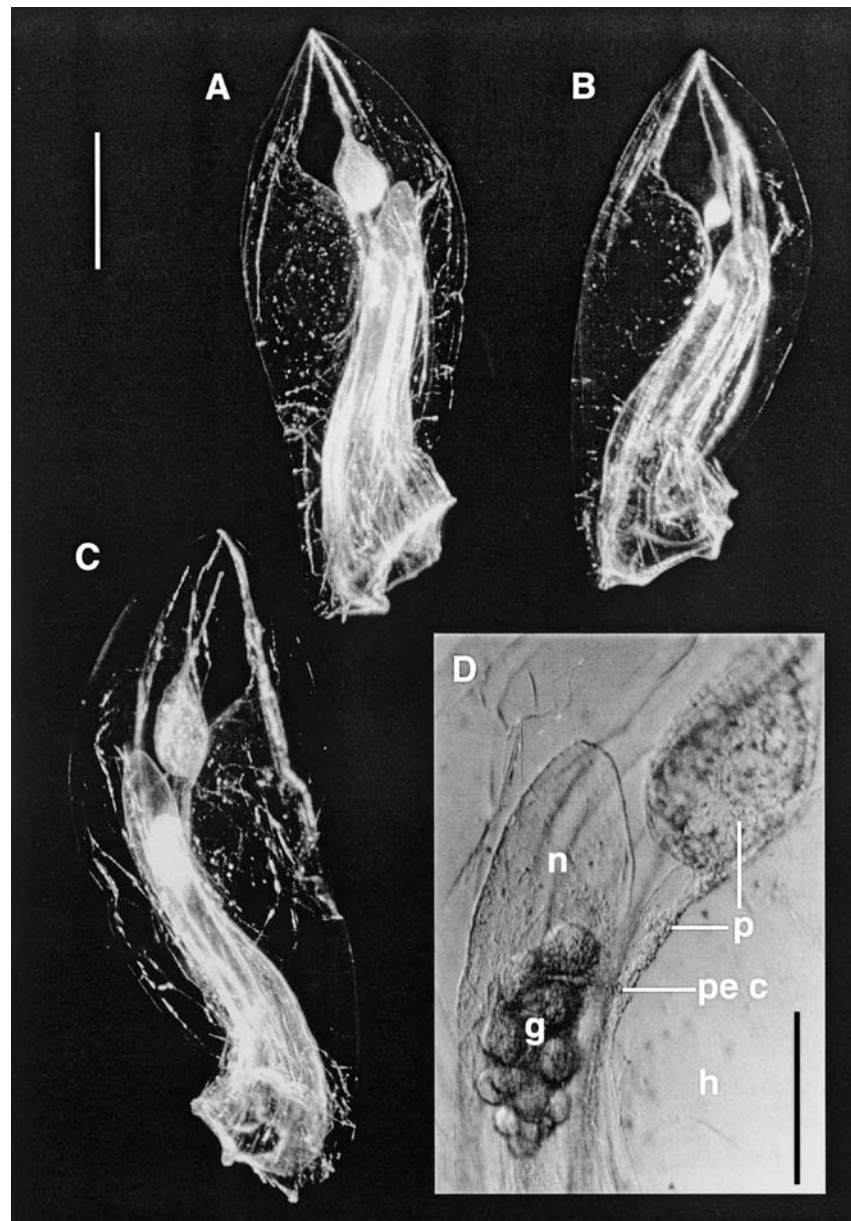


Fig. 4—**A–C.** Three different specimens of the first fuseudoxid of *Crystallophyes amygdalina*, scale: 1 mm. —**D.** Detail of the female gonad shown in (C); scale bar = 0.5 mm. g = gonad, h = hydroecium, n = nectosac, p = phyllocyst, pe c = pedicular canal.

canals arches up and out, over the sides of the subumbrella cavity and then straight down the dorso-lateral surface to the ring canal. Similarly, the ventro-lateral pair arch out, but downwards, and then run straight to the ring canal.

Gonads male or female, usually very small, from rounded to oval shape as size increases, hanging from the intersection point of the radial canals; 3–5 eggs have been observed in female gonads.

Discussion

This new type of sexual stage, with its two forms, raises some interesting questions, particularly as to whether the

fuseudoxid is an evolutionary step or an offshoot in the phylogeny of calycophorans. Studies on calycophoran development (e.g. Carré and Carré 1991) have shown that stem groups are budded off at the proximal end of the stem. After the gastrozooids, the bract arises first with the gonophore appearing very short afterwards. These stem groups are gradually moved down the stem, as more are developed, until the most developed ones usually become detached from the distal end to lead a free existence, as the sexual or eudoxid stage. The simplest explanation to the origin of fuseudoxids is that bract and gonophore in *Crystallophyes amygdalina* have fused to become a single structure, although otherwise this is completely unknown amongst calycophoran siphonophores.

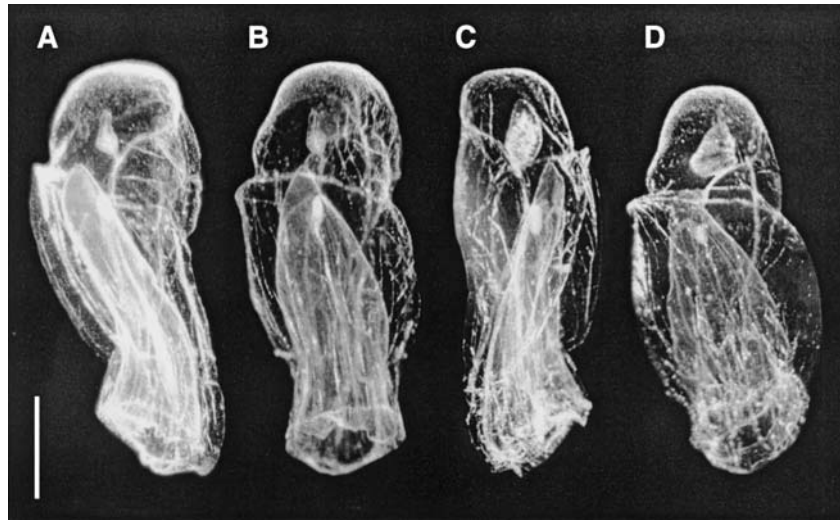


Fig. 5—Four different specimens of the second fuseudoxid. Scale bar = 1 mm.

Unfortunately, we have not been able to find a polygastric stage with sufficient stem still attached to see if it bore fuseudoxids. In the little known phylogeny of siphonophores, simplification of organs and structures appears the evolutionary pattern. Thus the fuseudoxid could be a step toward the simplification of the stem groups (bracts and gonophores), which in the extreme case of the family Hippopodiidae results in the loss of the bract entirely. In fact, one of us (PRP) believes that the true species of the genus *Clausophyes* (excluding *C. ovata*) also do not produce eudoxids, even bracts. However, why the first fuseudoxid of *C. amygdalina* is so very similar in morphology to the anterior nectophore remains a mystery. Such has never been observed in other known calycophoran siphonophores.

It is interesting to note that the globular apical protuberance of the second fuseudoxid appears to fit quite well into the concave hydroecium of the first one. This suggests that both kinds of fuseudoxids could have been attached together in live, as is intimated in Fig. 6. However, this has never been observed. But their co-occurrence in several samples (Table 1) where a relatively small volume of water (125–175 m³) was filtered, and where all other siphonophore pieces were identified to species (Pagès and Kurbjeweit 1994; Pagès and Schnack-Schiel 1996; Pagès unpublished data), cause us to believe that both structures could constitute a single organism. If this hypothetical organism does exist, then would the gonads in each fuseudoxid be of the same or different sexes? As mentioned above, both fuseudoxids can have either male or female gonads. However, in the three samples that collected a single specimen of each type, the first fuseudoxids are all clearly female and the second ones appear to be male; but this observation is not conclusive.

Apart from the obvious morphological homologies between the two fuseudoxids, the overlain arrangement shown in Fig. 6 indicates that in relation to each other they

would be mostly apposed and partially superimposed. This is a very similar arrangement, but in inverse proportion, to that of the polygastric stage of several clausophyid species (see Totton 1965; pl. XXXV: *Clausophyes ovata* from Keferstein & Ehlers 1861, *Clausophyes galeata* from Bigelow 1913, and *Chuniphyes moserae* from Bigelow, 1911b; see fig. 4C in Pugh and Pagès 1995: *Clausophyes moserae*). However, there is also some resemblance to the apposed arrangement of the definitive nectophores of several genera (e.g. *Rosacea*, *Lilyopsis*, *Praya*) of the family Prayidae (see Totton 1965).

Do fuseudoxids help to clarify the systematic position of clausophyids among the calycophorans, as various authorities disagree on this point? For instance, Leloup (1954) considered that the Clausophyinae (exclusively the genus *Clausophyes*), whose anterior and posterior nectophores are partially apposed and partially superimposed and both of which possess a somatocyst, evolved from the Prayidae. Following Moser's taxonomy, Leloup then suggested that the Clausophyinae had given rise to the Diphyidae and the latter to the subfamilies of Abylidae. However, because of the limited knowledge of the other clausophyid genera (*Chuniphyes*, *Crystallophyes*, *Heteropyramis* and, at that time, *Thalassophyes*) Leloup placed them amongst the diphyids.

In the same year, however, Totton (1954) published more details on all the known species and later he (Totton 1965) moved them all into a new family, the Clausophyidae; although he did raise doubts as to the validity of the species *Thalassophyes crystallina*. More recently, Margulis (1988) reviewed what she referred to as the subfamily Clausophyinae (Family Diphyidae!!) but neglected lamentably Totton's (1965) synopsis. She mistakenly moved *Crystallophyes* into the genus *Chuniphyes* based on the naïve argument, herein translated from the original Russian, that 'the similarity in both genera of the structures described by Moser (joining of ridges below apex of the nectophore sometimes in the anterior nectophore and always in the posterior one, similarity in



Fig. 6—Photographic composition overlapping the first (Fig. 3A) and the second fuseudoxids (Fig. 4A) that gives rise to the hypothetical complete sexual stage of *Crystallophyes amygdalina*. Scale bar = 1 mm.

the structure of somatocyst structure in anterior nectophore)'. What she neglected is that the anterior and posterior nectophores of *Crystallophyes amygdalina* both have five ridges, while in *Chuniphyes* the anterior nectophore has eight and the posterior six. This is a quite sufficient to distinguish both genera even though their somatocysts are quite similar. Additionally, her conclusion was reached without knowledge of the eudoxid of *C. amygdalina* and whether there was any resemblance between it and the very characteristic ones of *Chuniphyes* species. We now know that it is most certainly not the case. However, we agree with Margulis's decision to

synonymise the genus *Thalassophyes* with *Heteropyramis*, but do not concur with her conclusion, based on Totton (1965), that the two species, *H. maculata* and *H. crystallina* are conspecific, despite the fact that their characteristic eudoxids are morphologically very similar.

Totton (1954) considered the family Clausophyidae to be a link between the Diphyidae and the, apparently more evolved, Abylidae, based on the resemblance between the ridge pattern on the anterior nectophore of *Chuniphyes multidentata* and that of the abyloid *Ceratocymba sagittata* (Quoy and Gaimard). But, he did not make any comparisons with the typical ridge pattern found in diphyids. However, a possible link between the diphyids and some of the clausophyids is *Gilia reticulata* (Totton) (Diphyidae, Giliinae). This species is characterized by having a polygastric stage of diphyid-type, but an eudoxid bract of clausophyid-type (the phyllocyst having two fine basal canals extending down into the neck shield; Pugh and Pagès 1995). This arrangement is also seen in the clausophyid genera *Chuniphyes* and *Heteropyramis* (Fig. 2), as well as in *Clausophyes ovata*. In addition some phylogenetic relationship might also exist between the gonophore of *G. reticulata* and the second fuseudoxid of *Crystallophyes amygdalina*. In particular, the morphological similarity of the lower third that bends dorsad and the dorso-basally opening of the subumbrella (Fig. 3), and the presence of five ridges with the cariniform dorsal ridge being incomplete. Five-ridged gonophores are also found in the genera *Chuniphyes* and *Heteropyramis*, while four-ridged gonophores are typical of most diphyid species.

The asexual stage of *Crystallophyes amygdalina* is clearly of the clausophyid-type as it has two dissimilar nectophores, partially apposed and partially superimposed, both of which possess a somatocyst (Fig. 7; see also Totton 1965). It appears to be most closely related to the species of the genus *Heteropyramis*, because the anterior nectophore has five ridges, with the pair of ventral ridges usually uniting very close to, but below, the apex of the nectophore, such that there are only four ridges at the apex itself. Other characters, such as the presence of a descending branch to the somatocyst in *C. amygdalina* and its absence in *Heteropyramis*, set the genera apart. Nonetheless, the sexual stage of *C. amygdalina*, consisting of fuseudoxids, neither of which have the two fine canals, descending from the phyllocyst, as seen in the bracts of some other species, sets it uniquely apart from all other calycophoran species. We believe that this fact is sufficient to warrant the re-establishment of Moser's (1925) subfamily Crystallophyinae to encompass this species. Nevertheless, we still believe that there remain more questions to be answered as to the phylogenetic position of the family Clausophyidae.

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Fig. 7—Photographic composition overlapping the anterior and the posterior nectophores of the polygastric stage of *Crystallophyes amygdalina* suggesting how a colony might be in life. Scale bar = 1 mm.

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