

Is *Lensia reticulata* a diphyine species (Siphonophorae, Calyphora, Diphyidae)? A re-description*

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SUMMARY: Numerous eudoxid bracts of the calyphoran siphonophore species *Lensia reticulata* have been found in samples from recent German oceanographic expeditions and *Discovery* collections. In addition, many eudoxid gonophores and posterior nectophores, that also can be ascribed to this species, have been found in association with this material, as well as the well known anterior nectophores. With the exception of the anterior nectophores, the latter material differs markedly from that which has been previously ascribed to this species. The asexual and sexual stages, thus, are re-described. The unusual internal structure of the eudoxid bracts previously has not been described and, as it does not conform with the usual pattern for the bracts of diphyine siphonophores (Family Diphyidae), it raises questions as to the taxonomic position of this species. The five-ridged eudoxid gonophore also is unusual. It is concluded that it is necessary to remove the species *reticulata* to a new genus *Gilia* gen. nov., that is tentatively placed within a new sub-family of the family Diphyidae, the Giliinae.

Key words: Siphonophorae, taxonomy.

RESUMEN: ¿Es *LENSIA RETICULATA* (SIPHONOPHORAE, CALYPHORA, DIPHYIDAE) UNA ESPECIE DÍFINA? – Numerosas brácteas del sifonóforo calicóforo *Lensia reticulata* han sido halladas en muestras recogidas en recientes expediciones oceanográficas alemanas y en las colecciones *Discovery*. Además de los bien conocidos nectóforos anteriores, han sido encontrados en asociación con este material varios gonóforos y nectóforos posteriores que también pueden ser atribuidos a esta especie. Este material, a excepción de los nectóforos anteriores, difiere considerablemente del que había sido atribuido previamente a esta especie. Por eso, los estadios sexual y asexual son redescritos. La inusual estructura interna de las brácteas no había sido descrita previamente y como no se ajusta con la pauta habitual para las brácteas de los sifonóforos dífinos (familia Diphyidae), surgen dudas sobre la posición sistemática de esta especie. El gonóforo con cinco aristas es también inusual. Se concluye que es necesario cambiar la especie *reticulata* al nuevo género *Gilia* gen. nov. el cual es situado tentativamente dentro de una nueva subfamilia de la familia Diphyidae, la Giliinae.

Palabras clave: Sifonóforos, taxonomía.

INTRODUCTION

ALVARIÑO and WOJTAN (1984) described what they believed to be three new species of the caly-

cophoran siphonophore genus *Lensia* Totton 1932, all of which can be synonymised with known species, and included descriptions of the eudoxid stage of two other extant species. With regard to the eudoxid stage ascribed by ALVARIÑO and WOJTAN (1984) to *Lensia lelouveteau* Totton, 1941, an examination

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of their material showed that the phyllocyst of the bract, although described as globular but illustrated as having an apical horn, also has a fine basal horn running down the centre of the long neck-shield. This is a very characteristic feature of the eudoxid bract of *Dimophyes arctica* (CHUN, 1897), and so we consider that their material should be ascribed to this species. Anterior nectophores of the latter species were found in many of the samples where these eudoxids were present (ALVARIÑO *et al.*, 1990).

The specimens of the eudoxids ascribed to *Lensia reticulata* Totton, 1954 are, however, of great interest. The network of ridges on the bract most certainly does resemble that present on the anterior nectophore of that species, and it would be logical to associate the two. Unfortunately, it was not possible to discern the structure of the phyllocyst in their material. However, in the case of the gonophore, a re-examination of the material showed that the reticulate pattern as described by ALVARIÑO and WOJTAN (1984) was not really apparent. Indeed, it is not certain that these gonophores belong with the bracts, particularly as one, from *Eltanin* St. 881 (USNM 61069), clearly belongs to *Heteropyramis crystallina* (MOSER, 1925).

MARGULIS (1992), whilst reviewing the scant knowledge on the distribution of *Lensia reticulata*, commented on ALVARIÑO and WOJTAN's (1984) description of the eudoxid stage. She also had some bracts that showed a reticulate pattern of ridges on the surface, but concluded that the ascription of the eudoxid to *L. reticulata* was doubtful. This was because the structure of the phyllocyst was discernible in her material, and it was found not to conform with the normal pattern found in other *Lensia* species. MARGULIS (1992) concluded that it showed features more characteristic of bracts of the family Clausophyidae. Although no further detail was given, she did continue to consider the distribution of these bracts under the name *L. reticulata*.

Similar material now has come into our possession, from samples collected in the Southern Ocean and at high latitudes in the Northern Hemisphere by various recent German oceanographic expeditions and from recent *Discovery* collections. In addition, we have found in association with this material both posterior nectophores and gonophores, the former with a reticulated pattern of ridges, the latter without.

One of the problems in describing the various parts of a siphonophore found in net collections is that rarely do they remain attached to each other.

Thus, in the present case, none of the four basic parts, anterior and posterior nectophores, eudoxid bract and gonophore, has been found attached to any other. However, three of these parts, with the exception of the gonophore, bear a pattern of reticulated ridges on their surfaces; a characteristic otherwise unknown amongst the siphonophores. On this basis it would seem entirely reasonable to associate these three parts. In our opinion, the fact that, as MARGULIS (1992) intimated, the internal structure of the bract does not conform with the expected does not detract from this conclusion; but it does raise an interesting taxonomic question.

The eudoxid material found in samples from recent German expeditions usually is in excellent condition. This is because fine mesh (0.1 and 0.2 mm), vertically hauled, nets were used. The volume of water filtered, thus, was relatively small (from 12.5 to 300 m³), as was the number of siphonophore pieces collected. Yet, almost invariably, the gonophores to be described were found in association with, and in similar numbers, to the eudoxid bracts bearing the reticulated pattern of ridges. In addition, the gonophores could not be ascribed to any other siphonophore species that may have been present in the sample. We conclude, therefore, that the eudoxid bracts and gonophores both belong to the species *reticulata*. Because of the unusual organisation of the phyllocyst of the bract, this conclusion means that it is necessary to remove *reticulata* to a new genus, whose systematic position is of considerable interest. Accordingly we establish a new genus *Gilia* gen. nov. as monotypic for the species *reticulata*. In order to predicate this the species *reticulata* is redescribed.

***Gilia* gen. nov.**

Diagnosis: Calycephoran siphonophores whose exact systematic position remains to be determined. They are characterised by possessing nectophores, both anterior and posterior, that resemble those found in the sub-family Diphyinae of the family Diphyidae. However, their eudoxid bracts possess two canals that penetrate into the neck shield and, thus, are more characteristic of the family Clausophyidae. The type, and only known, species is *Gilia reticulata* (Totton, 1954).

Discussion: It should be noted that a confusion has arisen in the recent literature as to whether the clausophyid species should be included in a separate

calycophoran family or as a sub-family within the family Diphyidae. BIGELOW (1913) originally erected a new sub-family, the Clausophyinae, within the Diphyidae, to accommodate the three species that then had been described. MOSER (1925) added another three species that are now included in this group, and erected three further sub-families to encompass them, including the sub-family Chuniphyinae. Later TOTTON (1954), erroneously, re-erected the Chuniphyinae for all the known species. STEPANJANTS (1967) followed TOTTON's (1954) classification, but corrected the authority for the sub-family back to that of MOSER (1925). However, TOTTON (1965) recognised that the name Clausophyinae had precedence. None the less, he decided that there were sufficient reasons for raising its status to that of a family, the Clausophyidae. Whether STEPANJANTS (1967) knew of this change whilst she was writing her treatise is uncertain, but MARGULIS (1988) chose to follow her, and therefore TOTTON's (1954) classification, but used the sub-

family name Clausophyinae. In this paper we choose to retain TOTTON's (1965) classification, as we agree that there are sufficient reasons for the establishment of a family to accommodate the very distinctive clausophyid species.

Gilia reticulata

Material examined: Numerous bracts and gonophores collected by recent German oceanographic expeditions, mainly ANTARKTIS cruises of *Polarstern* to the Southern Ocean (see Table 1); and numerous anterior and posterior nectophores, and eudoxid bracts from recent *Discovery* collections, mainly from the North-east Atlantic (see Table 2).

The complex terminology for the anatomy of siphonophores has been explained in detail by KIRKPATRICK and PUGH (1984).

Diagnosis: Polygastric stage consisting of an anterior and posterior nectophore, both of which, in

TABLE 1. – Records for *Gilia reticulata* from recent German collections.

Cruise	No. of Samples	Range of Positions	Depth Range (m)	EB	EG	MEAN DEPTH
ANTARKTIS V/1	2	63° 51.0'S 63° 14.0'W	500-300	3		417
ANTARKTIS VII/3	5	59° 00.0'S 46° 59.6'W 61° 59.5'S 49° 00.5'W	1000-500	15	12	750
ANTARKTIS IX/2	8 1	65° 11.8'S 39° 17.6'W 71° 06.8'S 11° 22.3'W	1000-500 450-250	18 1	11 1	729
ANTARKTIS IX/3	9* 1	66° 48.1'S 00° 59.9'E 69° 42.9'S 06° 16.7'E	1000-500 500-220	61 1	30 1	744
ANTARKTIS X/3	11	66° 31.0'S 12° 14.1'W 70° 56.0'S 07° 16.8'W	1000-280	112	28	666
ANTARKTIS X/4	12 1 10	55° 00.1'S 00° 00.7'W 69° 00.3'S 00° 00.5'E	1000-500 2000-1000 500-0	82 8 33	48 6	668
ANTARKTIS X/7	11	64° 24.2'S 45° 55.0'W 70° 54.6'S 11° 57.6'W	1000-500	39	23	750
METEOR 11/4	21* 3	60° 44.5'S 55° 59.8'W 66° 16.0'S 72° 50.0'W	1500-200 100-0	55 3	37 1	584
VALDIVIA 136	5	72° 40.0'N 13° 30.5'W 77° 02.2'N 09° 03.8'W	2000-1000	15	8	1483

* Individual anterior nectophores found in 1000-500m depth range during these cruises. ANTARKTIS IX/3 - Sts. 188 & 200; METEOR 11/4 - St. 52. EB = eudoxid bract; EG = eudoxid gonophore.

TABLE 2. – Records for *Gilia reticulata* from recent *Discovery* collections.

Station	Gear	No. of Samples	Position	Depth Range (m)	AN	Mean Depth	EB	Mean Depth
9963	RMT1 RMT8	1 1	61° 57.2'S, 26° 14.4'E	995-2010 995-2010	1	1503	1	1503
9969	RMT1 RMT8	5 5	c. 59° 00'S, 20° 15'E	500-1000 500-2000	1 1	950 1900	24 11	696 705
9801	RMT8	1	41° 51.2'N, 17° 08.0'W	1500-1710	1	1605		
11794	RMT8	1 1	c. 47° 20'N, 19° 13'W	795-900 3010-3255	1 1	848 3133		
12096	RMT1 RMT8	2 1	c. 47° 58'N, 16° 50'W	1000-1200 1000-1100	19 1	1066 1050	5	1150
9756	RMT8	1	49° 47.0'N, 14° 04.4'W	3000-3500	1	3250		
7711	RMT8	2	c. 53° 00'N, 20° 00'W	605-800	4	678		
7709*	RMT1 RMT8	14 4	c. 60° 00'N, 20° 00'W	600-2000 810-2000	111 13	1066 939	1737	1042

*39 posterior nectophores found in the depth range 1000-1250 m.

AN = anterior nectophore; EB = eudoxid bract.

general, resemble those of diphyine species. They both bear a reticulated pattern of ridges. The anterior nectophore has lateral velar ridges, which do not unite dorsally. Its hydroecium extends to above the ostial level and is, for the most part, open ventrally. The somatocyst is small and ovoid. The posterior nectophore has lateral velar ridges that unite dorsally.

The bract of the eudoxid stage also bears a reticulated pattern of ridges, and has an extensive neck shield. The phyllocyst has a swollen central part, with a tapering process, of variable, often irregular, shape running up toward the apico-dorsal wall of the bract. In addition, from its base, arise two canals that run down into neck shield. This a feature usually characteristic of the family Clausophyidae. The gonophore is dorso-ventrally compressed and, in its lower half, it bends dorsad. There are five longitudinal ridges, of which the keel-shaped dorsal and, usually, the pair of dorso-lateral ridges are incomplete. A triangular mesogloal process, within which the pedicular canal runs, projects ventrally into the hydroecium. The point of insertion of the pedicular canal lies well below the apex of the subumbrella.

DESCRIPTION

Anterior nectophore. (Figure 1, A-C) The anterior nectophore of *Gilia reticulata*, with its irregular reticulation of superficial ridges, is so highly distinctive that it warrants little description. TOTTON (1954) provided detailed illustrations to demonstrate its complexity, and noted that, in the preserved state at least, the facets between the ridges can be deeply concave. It is implicit, from these illustrations, that the flimsy nature of these small nectophores (the *Discovery* specimens range in length from 1.6 to 4 mm) is largely due to the fact that the nectosac occupies almost the entire interior of them, except in the region of the somatocyst, and that the mesogloea is very thin. TOTTON (1954) drew attention to the short, ovate somatocyst; the well-formed hydroecium, with its ventral slit; and a horizontal velar ridge that connects the basal ends of c. six longitudinal ridges on either side of the nectophore. It is necessary only to give a few further descriptive details that may be relevant to the discussion of the taxonomic position of this species.

The somatocyst is about twice as long as it is broad. It has a flat base and taper towards its rounded

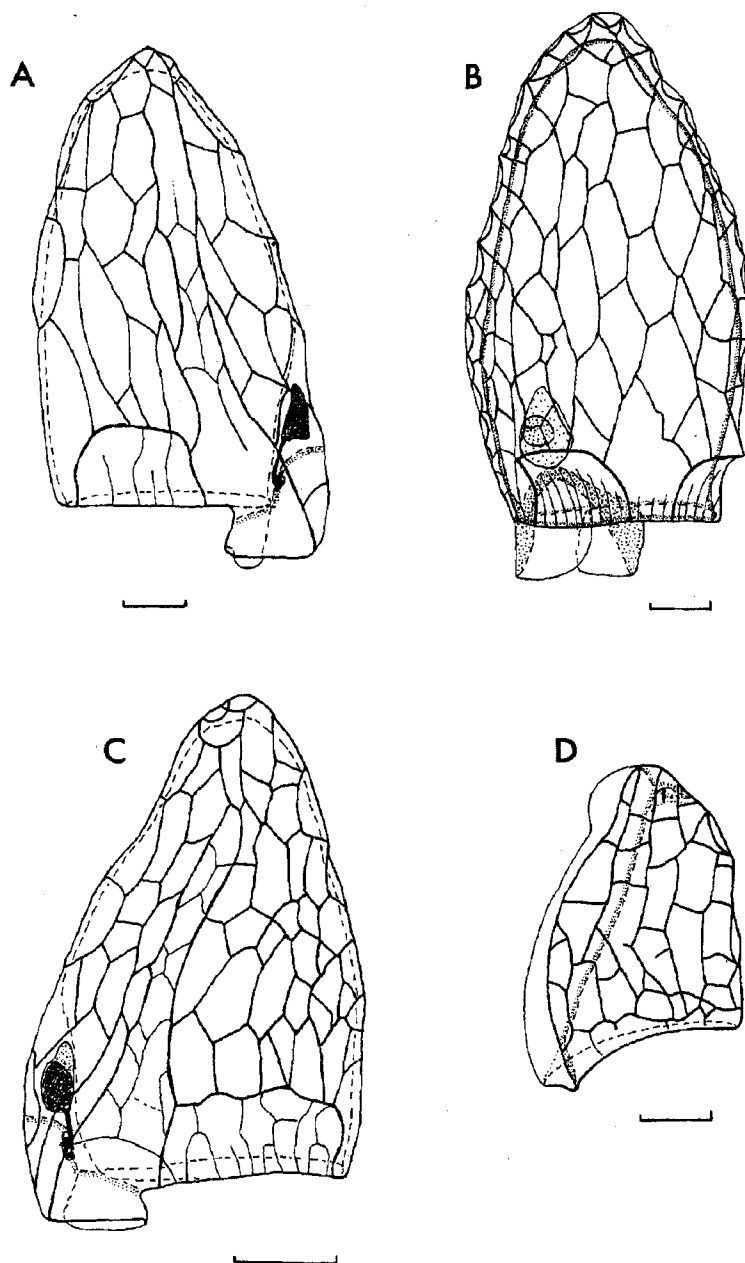


FIG. 1. — *Gilia reticulata* (Totton, 1954). Lateral (A.) and dorso-lateral (B.) views of mature, and (C.) lateral view of younger, anterior nectophore. D. Lateral view of posterior nectophore. Scale bar = 0.5 mm.

apex. TOTTON (1954) noted that it measured less across the dorso-ventral than across the ventro-lateral axis. Frequently it contains one or more dense globular masses. The short pedicular canal runs down from the dorso-basal margin of the somatocyst to the stem attachment point. The latter lies, not at the apex of the hydroecium, but on its dorsal wall in its upper half. The rectangular, baso-ventrally rounded, mouth plate is formed by two large lobes, with a deep ventral cleft between them, so that the hydroecium is almost entirely open ventrally.

TOTTON (1954) compared the arrangement of the velar ridges with those on the anterior nectophore of *Lensia exeter* and it is implicit, therefore, that they do not join in the mid-dorsal line, although this is not apparent in his figures. This has been confirmed (Figure 1 B). The arrangement of the ridges in the region ostial to the velar ridges, particularly in smaller specimens, can be more complex than that illustrated by TOTTON (1954) (Figure 1 C), but these ridges always are weakly defined and are difficult to see in the largest specimens. The velar ridges, them-

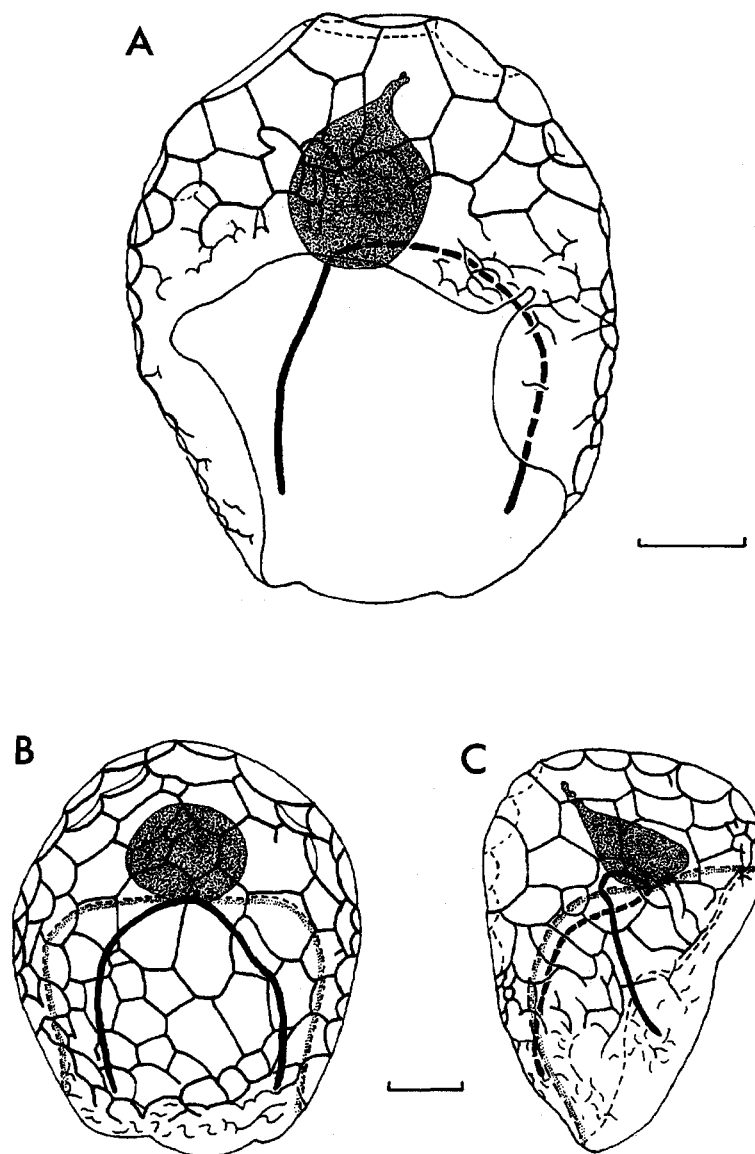


FIG. 2. – *Gilia reticulata* (Totton, 1954). Ventral (A.), dorsal (B.) and lateral (C.) views of eudoxid bract. Scale bar = 0.5 mm.

selves, may appear to have a zigzagged appearance, and occasionally may be incomplete. The ridges between the ventro-lateral longitudinal ridge, that terminates in the ventro-basal corner of the mouth plate, and the lateral ridge, that basally forms the ventro-lateral margin of the velar ridge, also are weakly defined and often cannot be discerned, even after staining. Frequently, this results in the nectophore being folded in this region.

Posterior nectophore. (Figure 1 D) The posterior nectophore measures up to c. 1.9 mm in height and c. 1.1 mm wide. It is an extremely flimsy structure, with very little mesogloea and with the nectosac

occupying almost the entire interior. The external surfaces, apart from within the hydroecium, are covered with an indistinct reticulation of ridges; best revealed with staining. Some of the ridges are incomplete. Basally there is a ridge, often irregular, that resembles the velar ridges of the anterior nectophore. However, unlike the latter it is a single ridge and is not interrupted dorsally. The hydroecium appears to be fairly narrow and deep, with two large lateral wings; but in life probably it is shallower, with the wings spread further apart. A very short pedicular canal is present at the apex of the nectosac, and runs through a small, central process that projects up into the hydroecium. The exact

outline of the nectosac and the course of the radial canals could not be discerned. However, it is presumed that dorsal, ventral and two lateral canals are present, as there is some indication of them originating from the pedicular canal.

Bract. (Figure 2). The largest bract from the German material measures 2.8 mm in height, 2.25 mm in maximum width, and 1.85 mm in maximum depth. Some of the *Discovery* bracts are even larger (c. 3 mm), so that, in comparison with the size of the anterior nectophore, these structures are relatively enormous. However, most of the other bracts are considerably smaller, and the smallest one found in the *Discovery* collections measures 0.7 mm. ALVARIÑO and WOJTAN's bract measured 1.6 mm in height.

Typically the bract consists of two parts; a hemispherical "head piece", that contributes approximately the upper third of the bract, and the relatively thin walled "neck shield", which surrounds the hydroecium wherein the gonophore and gastrozoid would have been attached. The dorsal and lateral surfaces of the bract are covered in a characteristic reticulation of ridges; the arrangement of which is irregular. Toward the basal and lateral edges of the neck shield, and the baso-ventral margin of the head piece, the ridge pattern becomes indistinct; except in the youngest bracts where the ridges remain distinct throughout, although the neck shield is relatively small. Most of the facets demarcated by the ridges are, in their preserved state, deeply concave, like those on the anterior nectophore.

The lateral wings of the neck shield are extensive and surround a large, dome-shaped hydroecium. Each wing is notched in the region close to the apex of the hydroecium; through which, presumably, the siphosomal stem originally passed. No ridges are present on the hydroecial walls. Basally the neck shield is truncated, but may be slightly emarginated on either side.

Within the head piece lies the large phyllocyst. This has a swollen central part, with a tapering process, of variable, often irregular, shape running up toward the apico-dorsal wall of the bract. However, the most interesting feature of the phyllocyst is that from its base arise two canals which run obliquely out and then down the sides of the neck shield. These canals arise together at the point of attachment of the other stem components. These canals, and indeed the phyllocyst itself, are only apparent in the best preserved material. The presence of such a

pair of canals is unknown amongst the siphonophores of the family Diphyidae, and the significance of this is discussed below.

Gonophore. (Figure 3). The gonophore also shows some very interesting features. The largest one measures 3.5 mm in height, and 1.9 mm in width. It is dorso-ventrally compressed and, in its lower half, it bends dorsad, so that the opening of the subumbrella lies dorso-basally. Five longitudinal ridges run down the exumbrella surface. The dorsal ridge is incomplete. It is cariniform and extends from the apex of the gonophore, where it joins with the two dorso-lateral ridges, to the region where the gonophore bends dorsad. The two dorso-lateral ridges also are usually incomplete. They run from the apex almost to the base, ventral to the sub-umbrella cavity, ending on the ventro-lateral sides of the gonophore close to the ostium. However, occasionally, the right dorso-lateral ridge does reach the ostium. The two ventro-lateral ridges, which demarcate the edges of the shallow hydroecium, are less distinct than the others. Basally, these ridges end on either side of a small mouth plate. They run up to close to the apex of the gonophore, but do not unite with the other ridges. A shallow gutter connects them. In this region there is a median, triangular, mesogloal protuberance, projecting ventrally into the hydroecium. On the ventral side of this the pedicular canal runs from its apex down to the subumbrella cavity.

The subumbrella cavity occupies about half the width of the gonophore and also is dorso-ventrally compressed. It is widest at its base, and has a large dorso-basal opening. Apically it tapers down considerably and ends, close to the apex, in a rounded point. In addition, usually it is indented along the mid-ventral line, basal to the point of insertion of the pedicular canal. The latter lies well below the apex of the subumbrella, and there the four radial canals arise. The dorso-lateral pair of canals arch up and out, over the sides of the subumbrella, and straight down the dorso-lateral surface to the ostial ring canal. Similarly the ventro-lateral pair arch out, but downwards, and then continue straight to the ring canal.

The immature male or female gonads that are all that remain attached within the sub-umbrella cavity are distinctly different. The male gonad is relatively long and pendulous, while the female one is spherical and, at this stage, contains only a single egg.

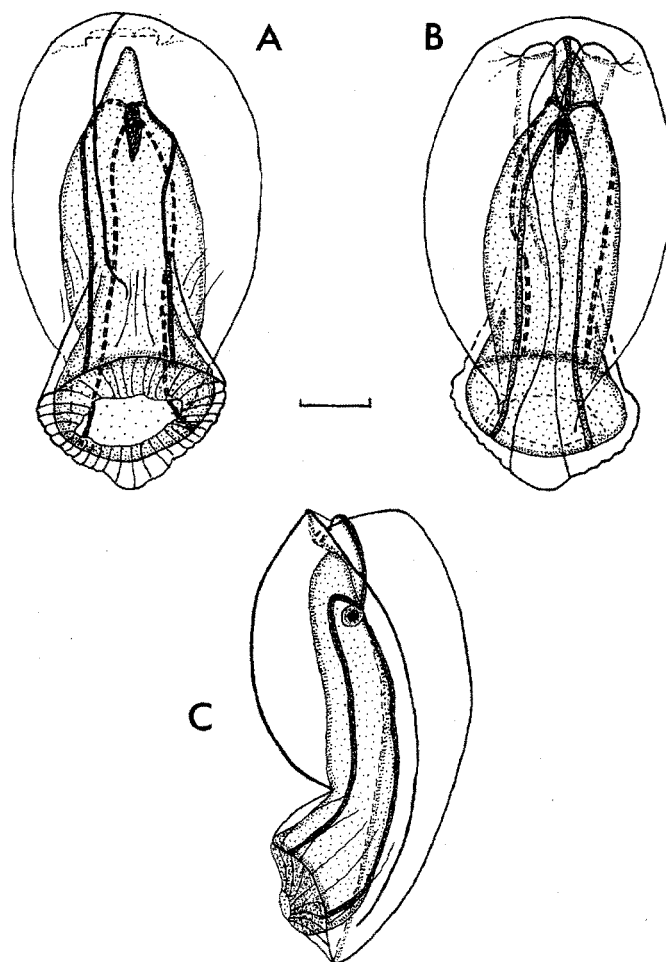


FIG. 3. – *Gilia reticulata* (Totton, 1954). Dorsal (A.), ventral (B.) and lateral (C.) views of eudoxid gonophore. Scale bar = 0.5 mm.

The gonophores that ALVARIÑO and WOJTAN (1984) ascribed to this species differ markedly from those described above. Although they described a reticulate pattern of ridges on the exumbrella, this was not apparent when the material was re-examined. Indeed, as noted above, there was a mixture of gonophores in their material, one of which clearly belonged to *Heteropyramis crystallina*. We believe that the consistent co-occurrence of both the bracts and gonophores, as described herein, in our considerable number of samples, where the volume filtered was as low as 12.5 m³, is sufficient to associate them together.

DISTRIBUTION

Before discussing the taxonomic consequences that arise from this description, particularly of the

eudoxid stage, let us consider what we know about its geographical and depth distribution. The relatively few published records for *Lensia reticulata*, very few of which give any quantitative data, have been reviewed by ALVARIÑO *et al.* (1990) and MARGULIS (1992), but neither are entirely accurate or complete, and the latter does not appear to include the data of the former. Other, and more recent, records are given by PUGH (1990), LIN and ZHANG (1991), MARGULIS and VERESHCHAKA (1994), and PAGÈS and KURBJEWIT (1994). From these records it appears that the species occurs in the Subarctic current, the Gulf of Mexico, and Subantarctic and Antarctic regions of the Atlantic Ocean; in equatorial parts of the Indian Ocean; and from the Arctic to the Antarctic in the Pacific Ocean, although the source of MARGULIS's (1992) records for the equatorial and South Pacific is unknown. That author also appears to have included some previously unpublis-

hed data for the eudoxid stage, particularly in the Southern Ocean.

Up until the inception of this paper, only 23 anterior nectophores of what we are now referring to as *Gilia reticulata* had been identified in recent *Discovery* collections. This paucity of data probably is related both to the small size and fragility of the animal, and the fact that, for the most part, only RMT8 (mesh size 4.5 mm) catches have been examined. Indeed, an examination of several RMT1 (mesh size 0.33 mm) samples exemplified this; as a further 132 anterior nectophores, and additionally over 1700 eudoxid bracts and 39 posterior nectophores, have been found (see Table 2). Eudoxid gonophores also were present in the samples, but their generally poor state of preservation makes them difficult to identify with certainty. With the exception of the stations in the Southern Ocean (see PAGÈS *et al.*, 1994; PUGH and PAGÈS, in prep.), all the *Discovery* stations lie at latitudes north of 41°N in the North Atlantic Ocean. Therefore, it would appear that this species is one of those siphonophores that is largely confined to higher latitudes in both the Northern and Southern Hemispheres.

Most of the *Discovery* specimens of *Gilia reticulata* have been collected in the 500-2000 m depth range, with a mean depth of c. 1045 m for the Northern Hemisphere population. Only a single anterior nectophore has been found at deeper depths (Table 2). Most of the eudoxid material from recent German Oceanographic expeditions came from the Atlantic Sector of the Southern Ocean, with a few specimens at high northern latitudes (Table 1). With regard to the Southern Ocean material, the vast majority was found in hauls from 1000-500 m, or in hauls that fell within, or encompassed, that depth range. However, it should be noted that depths below 1000 m were rarely sampled during these cruises. The mean depth for this eudoxid population is c. 680 m. This mean depth is somewhat shallower than the *Discovery* data from the Northern Hemisphere, but is in accord with our other data (Table 2).

DISCUSSION

TOTTON (1932) originally established the genus *Lensia* to encompass six, previously described, species of small diphyine calycophoran siphonophores that did not fit well within the extant genera of that sub-family. Basically, these species had a pentago-

nal anterior and a small, fragile posterior nectophore. The anterior nectophore had a very shallow hydroecium, a small, divided mouth plate, but no dorsal or lateral ostial teeth. TOTTON (1941, 1954) added several more species, and TOTTON (1965) recognised a total of twenty-two *Lensia* species. Since then, at least a further nineteen species, and several subspecies, have been added to the list, although it is certain that not all are valid.

It is not known whether all extant *Lensia* species develop a posterior nectophore, as such have been described for only nine or ten species. STEPANJANTS (1970) briefly described what she thought might be the posterior nectophore of *L. reticulata*, with a small, spade-like, mouth plate, but the present material clearly contradicts that ascription. The eudoxid stages of *Lensia* species are even less well known, and to date good descriptions exist for only about five species. However, ignoring *reticulata*, there is a certain consistency in these descriptions. The bracts generally are conical in shape (Figure 4 C), with a rounded apex. The neck shield is not well developed, and occupies less than a third of the total height. The shape of the phyllocyst appears, to some extent, to reflect that of the somatocyst in the anterior nectophore. It is globular or elongate, without additional processes, or canals running down into the neck shield. The gonophore, apically, is truncated and bears a small apophysis. There are usually four longitudinal ridges on the exumbrella; pairs of dorso- and ventro-laterals. Beneath each lateral ridge runs a radial canal, on the subumbrella wall. These canals usually originate close to the apex of the subumbrella.

If this generalised *Lensia* eudoxid is compared with that of *reticulata* described above, immediately it will be seen that there are some striking differences. The bract of the latter, apart from the reticulation of ridges, has a large neck shield, occupying about two-thirds its height. In this it more closely resembles the bract of *Clausophyes ovata* (KEFERSTEIN and EHLERS, 1860) (Figure 4 D) than those of diphyid species. However, by far the most interesting feature of the bract of *reticulata* is the presence of two canals, arising at the point of junction with the gonophore and the phyllocyst, that run down on either side of the neck shield. The presence of such canals is unknown among the diphyid siphonophores, but all clausophyid species, whose eudoxids have been identified, show this feature. They also bear a resemblance to the hydroecial canals found in the bracts of species of the family

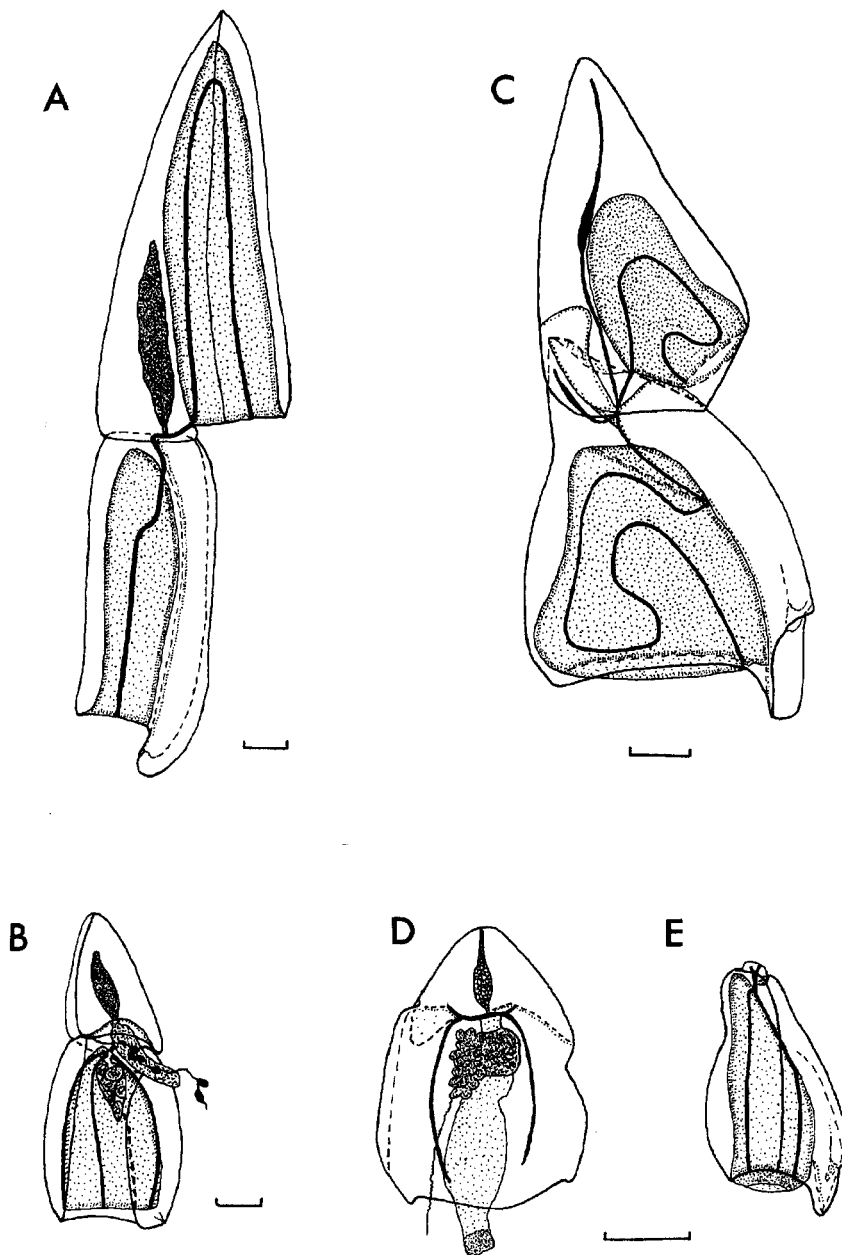


FIG. 4. – (A) and (B) Lateral views of the polygastric and eudoxid stages, respectively, of a diphyid siphonophore *Lensia conoidea* (Keferstein & Ehlers, 1860). (C) Lateral view of the polygastric stage; (D) dorsal view of the bract; (E) lateral view of the gonophore of a clausophyid siphonophore. (C) *Clausophyes moserae* Margulis, 1988; (D) *Clausophyes ovata* (Keferstein & Ehlers, 1860). Scale bar = 1 mm.

Prayidae. One diphyid species, *Dimophyes arctica*, is exceptional, not only in having a long neck shield, but by the presence of a single canal, or horn, running down the middle of it. This canal, however, is actually an extension of the phyllocyst itself, and does not arise at the junction point with the gonophore.

The gonophore here ascribed to *reticulata* also is of interest in that it has five ridges, although three are usually incomplete. The presence of five ridges

is a feature of the gonophores of some clausophyid species where, as in the sub-family Abylinae (family Abylidae), a dorsal ridge is added to the pairs of dorso- and ventro-laterals that usually typify diphyid gonophores. However, this is not the case for *Clausophyes ovata*, where the dorsal ridge is absent.

It now becomes clear why MARGULIS (1992) doubted the ascription of the eudoxid bract, described by ALVARIÑO and WOJTAN (1984), to *Lensia*

reticulata. As TOTTON (1965, p. 192) noted, one of the characteristic features of the family Clausophyidae is that "in species, whose eudoxid phase is known, there are two longitudinal horns or branches of the phyllocyst lying in the neck shield of the bract." None the less, on the basis of the similarity in the ridge reticulation patterns on both the nectophores (anterior and posterior) and bracts, there seems every reason to believe that we are dealing with the asexual and sexual stages of the same species, namely *reticulata*. The question then remains as to whether the species *reticulata* is a diphyid or a clausophyid siphonophore?

On the basis of the characteristics of the eudoxid stage, as discussed above, the species *reticulata* could be considered a clausophyid. However, the asexual stage of *reticulata* appears to be more typical of a diphyid siphonophore. In order to establish this, it is necessary to give a brief and generalised description of the organisation of the asexual stage in each family. Most species, in both families, develop two nectophores (anterior and posterior) that differ in structure. In the Diphyidae it is generally thought that most species develop a caducous larval nectophore, which possesses a somatocyst. The anterior and posterior nectophores, then, are definitive nectophores of neof ormation, of which only the anterior one has a somatocyst. The anterior nectophore is superimposed upon the posterior one (Figure 4 A). The hydroecium of the former usually is small, but of course there are always exceptions to the rule, and the junction point between the canal systems of the nectophores and stem lies at, or close to, its apex. The apical end of the posterior nectophore, where its canal system originates, usually is truncated to abut against the base of the anterior one.

In clausophyid species the nectophores are partially superimposed, and partially apposed (Figure 4 B). To accomplish this, the hydroecium of the anterior nectophore is extensive, extending up to at least a third the height of the nectophore. It is completely open ventrally, so that its lateral flaps can surround the upper part of the posterior nectophore. The attachment point, for the stem and the posterior nectophore, is positioned well below the apex of the hydroecium, often on a pronounced mesogloeal protuberance (PUGH and PAGÈS, 1993). The somatocyst is well developed, and often has a relatively complex structure, with a terminal prolongation running up toward the apex of the nectophore.

The attachment point on the posterior nectophore also lies well below its apex. However, of great

interest is the presence of a somatocyst, which runs apically up from the attachment point. The presence of a somatocyst in both the anterior and posterior nectophores is a feature characteristic of the family Clausophyidae. It is thought (TOTTON, 1965) that the anterior nectophore is the larval one retained, and thus that the posterior one represents the first definitive nectophore that, as in the diphyids, possesses a somatocyst. TOTTON (1965) considered the Clausophyidae to be a link between the Diphyidae and another calyophoran family, the Abylidae. Certainly, in the latter, the larval nectophore is retained as the anterior one (CARRÉ, 1967); but the first definitive nectophore, the posterior one, does not possess a somatocyst. However, on the basis of the limited evidence available, the abyliids appear to be unique amongst the calyophoran siphonophores in that they develop a larval bract (CARRÉ, 1967), although we know nothing about the development of clausophyid species.

Returning to the asexual stage of *reticulata* it is apparent that the general shape of the anterior nectophore more closely resembles a diphyid than a clausophyid siphonophore. In addition, the somatocyst is small and has no apical prolongation. However, it is interesting to note that its hydroecium is open ventrally for most of its height, and that the stem attachment point is displaced slightly below its apex, onto its dorsal wall. These features could indicate an intermediate stage in the transformation toward (or from) the clausophyid condition, where both are much more pronounced. None the less, these features also are present in several, mainly multistriate, *Lensia* species.

Together, the structure of both the asexual and sexual stages of *reticulata* show sufficient differences from that of the typical *Lensia*, or even diphyid, to warrant the removal of the species into a new genus. Thus we erect the genus *Gilia* gen. nov., in honour of Dr. Josep-Maria Gili and his work on gelatinous plankton. The question still remains as to the exact systematic status of this genus. Should it be considered as a clausophyid; retained within the diphyid sub-family Diphyinae; or should it be placed in a new sub-family of the Diphyidae, the Giliinae? For the present, we will adopt the last of these alternatives because of the resemblance of the nectophore to other diphyids and because of the distinctiveness of the eudoxids. However, we will have to await further evidence, that might come from the identification of the eudoxids of some multistriate *Lensia* species, to finally resolve this question.

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