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A re-description of *Lensia asymmetrica* Stepanjants, 1970 (Siphonophorae, Diphyidae)

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SUMMARY: Many, well-preserved anterior nectophores of *Lensia asymmetrica* Stepanjants, 1970 (Siphonophorae, Diphyidae) have been found in recent collections from the Southern Ocean. These show that there is not a superficial and incomplete reticulation present on their surfaces, as previous described. In association with this material, many eudoxid bracts, and a few posterior nectophores and gonophores have been found. These are attributed to the same species and descriptions given of all these parts.

Key words: Lensia asymetrica, Siphonophora, Southern Ocean

RESUMEN: REDESCRIPCIÓN DE *LENSIA ASYMETRICA* STEPANJANTS, 1970 (SIPHONOPHORAE, DIPHYIDAE). – Varios nectóforos anteriores de *Lensia asymmetrica* Stepanjants, 1970 (Siphonophorae, Diphyidae) han sido hallados en buen estado de preservación en recientes muestras recogidas en el océano Antártico. Estos muestran que no existe una reticulación superficial e incompleta en su superficie como fue descrita previamente. En asociación con este material, varias brácteas y unos pocos nectóforos posteriors han sido también hallados. Estos son atribuidos a la misma especie y son aportadas las descripciones de todas estas partes.

Palabras clave: Lensia asymetrica, sifonóforos. Antártida.

INTRODUCTION

Lensia asymmetrica Stepanjants, 1970 was originally described from anterior nectophores, possibly only two, found in two samples taken in the region of the Kurile-Kamchatka Trench (North Pacific Ocean). The most characteristic features were the asymmetric arrangements of the mouth plate and the somatocyst. These clearly distinguish this species from all others within the genus *Lensia*. Stepanjants (1970) also noted that, although there were no distinct longitudinal ridges on the surface of the nectophores, there was an irregular and incomplete reticulation of indistinct ridges. Thus, she likened this species to the group of *Lensia* species that are multi-ridged.

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Until recently, *Lensia asymmetrica* remained little known, but Pagès and Kurbjeweit (1994) identified many anterior nectophores in samples from the Weddell Sea, Antarctica; and in association with these they found similar numbers of eudoxid bracts. As we have stated before (Pugh and Pagès, 1995), it must remain a matter of expert opinion when associating the asexual and sexual stages of many calycophoran species. This is because of the very nature of these siphonophores where the sexual, eudoxid stage is set free from the asexual, nectophore stage and leads an independent, but perhaps short-lived life. However, the obvious similarity between the phyllocyst of the bract and the somatocyst of the anterior nectophore clearly suggests that the bracts found by Pagès and Kurbjeweit (1994) can be associated with the anterior nectophores of *L. asymmetrica*. This is all the more so as the one was found exclusively with the other in samples taken within the 1000-500 m depth range, where the volume of water filtered was relatively small, c. 125 m^3.

Many of the anterior nectophores are in excellent condition and this has enabled us to improve on the original description given by Stepanjants (1970). Additional specimens of *Lensia asymmetrica* have been identified from other samples collected during recent German Antarctic Expeditions. Amongst this material are a few posterior nectophores and eudoxid gonophores that we believe also can be associated with the same species.

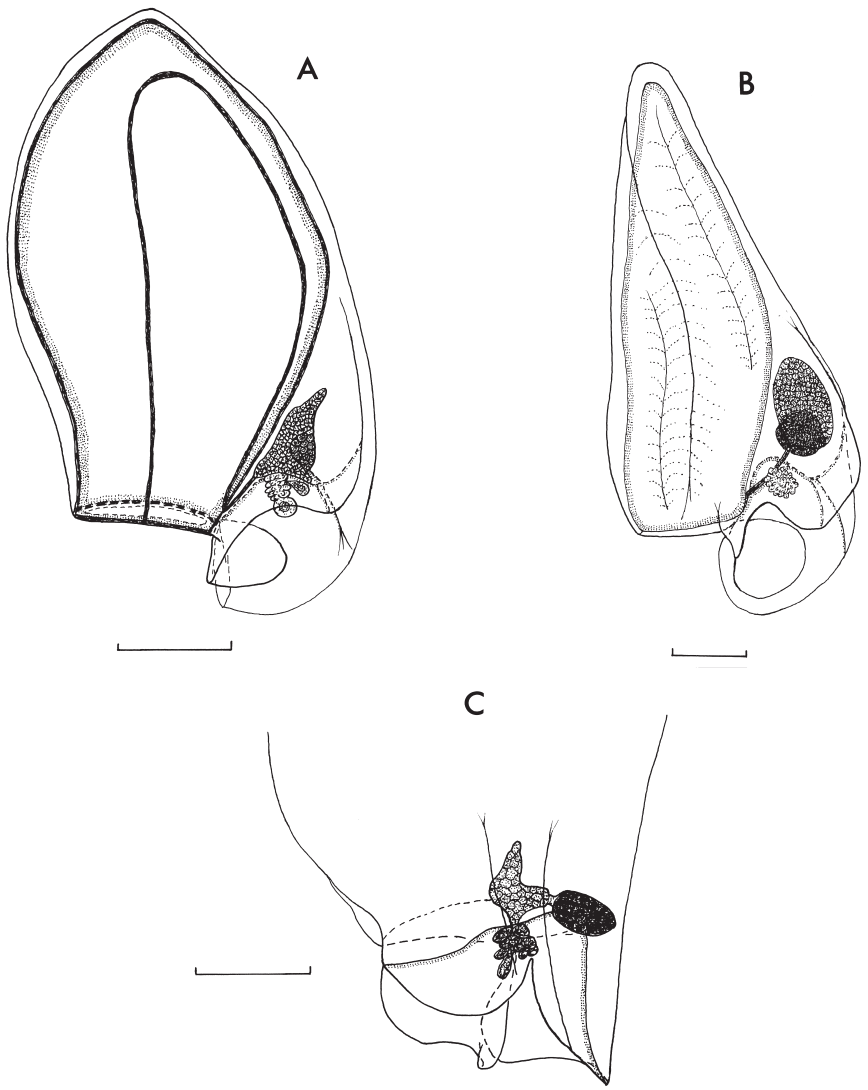

FIG. 1. – *Lensia asymmetrica*. Anterior nectophore. (A) and (B) lateral views; (C) ventral view of base, detailing hydroecium and somatocyst. Scale bar = 0.5 mm.

RESULTS

Lensia asymmetrica Stepanjants, 1970

Material examined: 86 anterior nectophores, 6 posterior nectophores, 78 eudoxid bracts, and 3 eudoxid gonophores collected during recent German Expeditions to the Southern Ocean. The approximate localities and depths of collection are given in Table 1. All specimens were collected by a vertically hauled opening/closing net system with a 0.25 m^2 mouth opening and 100 μm mesh (Weikert and John, 1981).

The material is currently housed in the collections at either the Southampton Oceanographic Centre or the Institut de Ciències del Mar, Barcelona.

Description

Anterior nectophore. (Fig. 1 and 2).

The anterior nectophores examined range in height from 2.1 to 3.9 mm, and from 1.0 to 1.8 mm in width. They are, thus, considerably smaller than the two examined by Stepanjants (1970), which measured 5-6 mm in height. The surface of the nectophore is smooth and devoid of ridges, apart from two short ventral ones. The left ventral ridge is a continuation of the ventro-basal margin of the mouth plate, while the right one stops just short of joining the opposite margin. Both ridges are indistinct and they peter out at a level just above the apex of the somatocyst, although occasionally they appear to be more extensive. The right ridge sometimes is longer than the left one.

The nectophores in the material examined appear to be of two types. Firstly (Figure 1 A), there are broad nectophores with an inflated nectosac, the subumbrella of which appears to bear little musculature. Secondly, there are narrower nectophores, with the subumbrella of the nectosac bearing obvious musculature. These latter nectophores, which make up about 80% of the material, often show an asymmetry, to a variable extent, in that the top half of the nectophore is twisted to the right (Figure 1 B). It is assumed that the latter case arises as a preservation artefact, in a similar way to that noted for *Lensia campanella* (Totton, 1965; Carré, 1968). In *L. campanella,* which has five indistinct ridges, the apical half of the anterior nectophore appears to have been subjected to a torsion of c. 30º to the right. This torsion is manifested in the spiral courses of the superficial ridges and of the radial canals on the nectosac, but in the living specimens there is no obvious twisting of the nectophore as a whole. However, after preservation this twisting usually becomes very obvious in the apical half of the nectophore.

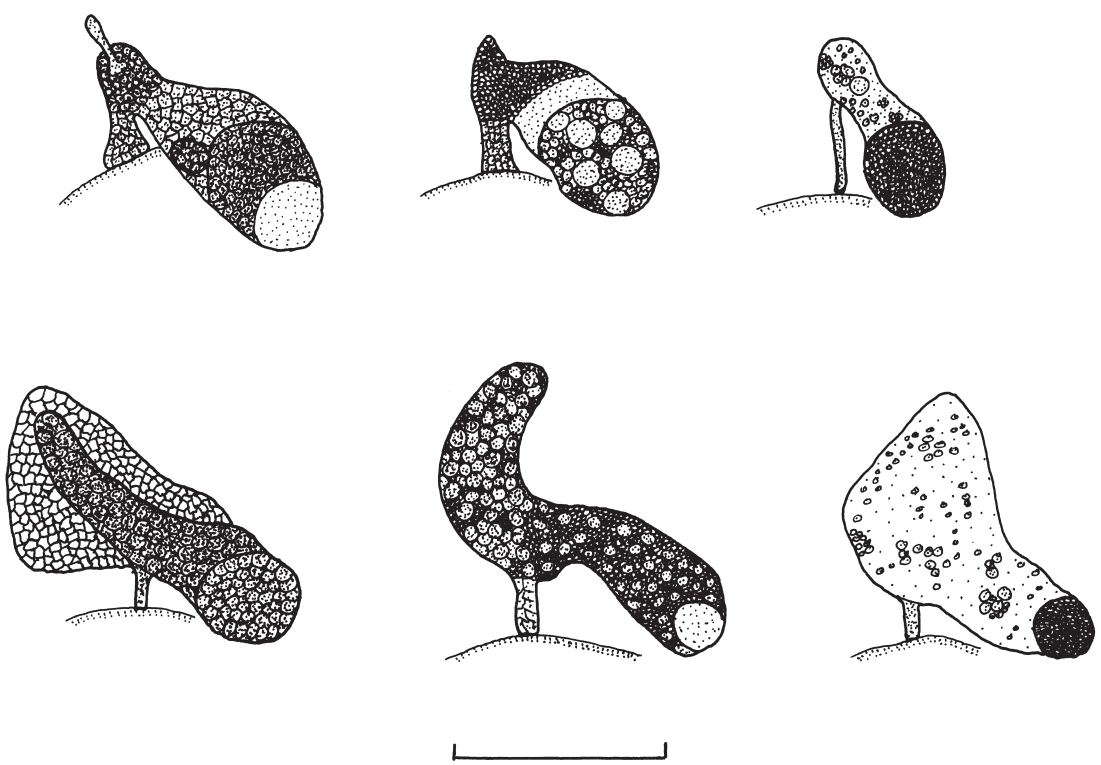

FIG. 2. – *Lensia asymmetrica*. Ventral views detailing variations in the shape of the somatocyst. Scale bar = 0.5 mm.

The most obvious, and characteristic, features of the anterior nectophores of *Lensia asymmetrica* are the asymmetric arrangements of the somatocyst and the hydroecium. The main body of the somatocyst is borne on a short stalk that arises from the point of insertion of the posterior nectophore and the main stem. There are two, asymmetric parts to the main somatocyst. Firstly there is a lateral lobe on the left hand side of the nectophore. This lobe is of a more consistent shape than the other, and usually is directed slightly baso-laterally. Oil droplets are almost invariably present in this lobe, and they vary in size from small to a single large droplet occupying almost the whole. In one, apparently previously well fed, specimen this lobe was swollen excessively, displacing almost all of the mesogloea in the vicinity.

The other lobe of the somatocyst is much more variable in size and shape, ranging from virtually absent to be considerably larger than the other (Figure 2). It can be directed apically, and may then curve back toward the left-hand side; apico-laterally toward the right-hand side; or simply laterally toward the right-hand side. Its contents also are more variable than the other lobe. Its surface may show a reticulated pattern, with no obvious contents within, or it may be filled to a variable extent with oil droplets.

The hydroecium extends to well above the level of the ostial opening of the nectosac. It is asymmetrically disposed so that it is deeper and more extensive on the left-hand side (Figure 1 C). It is open on its ventral side for most of its height, and can be said to extend up the ventral side of the nectophore, as a shallow groove between the two, short ventral ridges. The relatively large mouth plate typically consists of two lobes, that are asymmetrically arranged. The left lobe is large and rounded, while the right one is considerably smaller. The right lobe also is greatly emarginated laterally, so that most of the hydroecium is open on that side. One of the flaps usually overlaps the other on the dorsal side of the mouth plate, but there is no consistency as to whether it is the right or left one.

The nectosac occupies the great majority of the nectophore, except in the region of the somatocyst. The pedicular canal arises close to the apex of the hydroecium and travels baso-dorsally to reach the nectosac close to its base. Thus, the ventral radial canal is very short. The lateral radial canals travel up the ventro-lateral sides of the nectosac, very close to the dorsal canal. Close to the apex of the nectosac, they loop over on to the lateral sides and then continue, with a fairly straight course, down to the ostial ring canal.

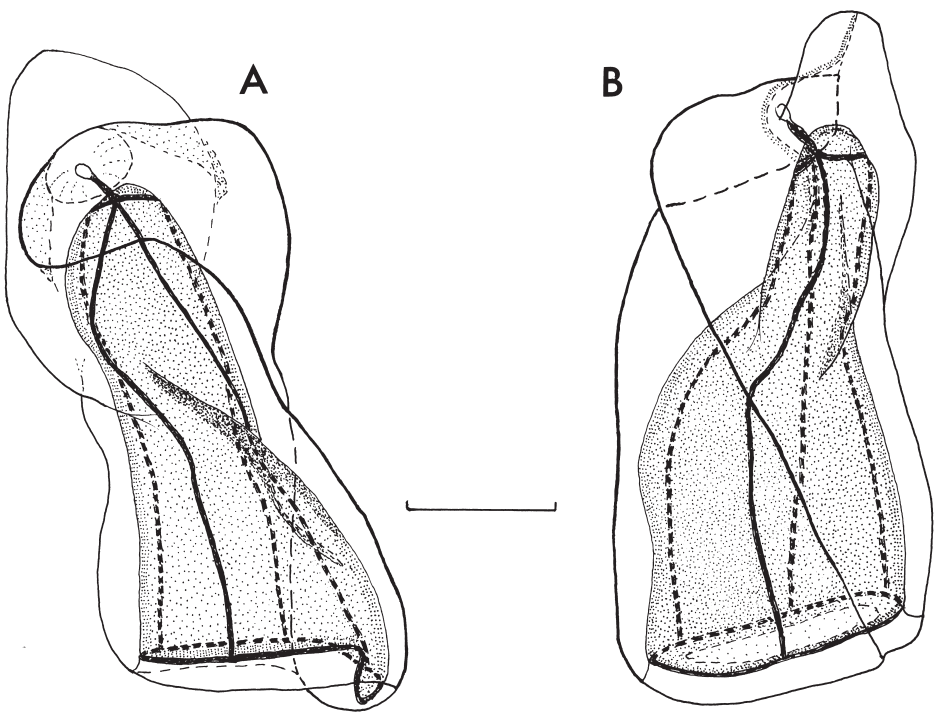

FIG. 3. – *Lensia asymmetrica*. (A) lateral and (B) ventral views of the posterior nectophore. Scale bar = 0.5 mm.

Posterior nectophore. (Fig. 3)

Six posterior nectophores have been examined in detail. Their sizes range from 2.2 to 2.5 mm in height, and 0.9 to 1.1 mm in width. The general shape of the nectophore is clearly asymmetrical with the apical half having been subjected to a torsion of almost 90º toward the right. There is a distinct apical apophysis on the dorsal side of the nectophore, but because of the torsion it appears to lie on the left side. The only ridges present are the hydroecials. They run up from each side of a very small, and ill-defined, mouth plate. In the lower half of the nectophore they enclose a broad, but very shallow hydroecium, while in the apical half the hydroecium is deeper and distinct hydroecial wings are present. These hydroecial wings are distinctly truncated, and they unite together in the midline, slightly below the apex of the nectophore. Because of the general torsion, the right hydroecial wing appears to be more extensive than the left one. Nonetheless, it is very easy to see from this arrangement, how the apex of the posterior nectophore would very neatly marry up with the hydroecial region of the anterior one. The asymmetry of the hydroecial wings of the posterior nectophore exactly matches the baso-ventral arrangement of the hydroecial ridges on the anterior one.

The nectosac has been subjected to the same torsion, such that the point of insertion of the pedicular canal appears to be almost lateral, on the right-hand side of the nectophore. The pedicular canal runs down through a median, apico-ventral, mesogloeal process that swells out at the apex of the hydroecium. The canal is inserted onto the nectosac slightly below the apex of the latter, and gives rise to four radial canals. The trajectories of these canals are also affected by the torsion of the nectosac, such that they have become twisted in the upper half of the nectophore.

Eudoxid bract. (Figs. 4 and 5)

The bracts measure up to c. 3.2 mm in height and 1.2 mm in width. As is typical for most diphyids, the bract consists of two main parts (Fig. 4). Firstly, there is the hemispherical, solid "head piece" that occupies approximately the upper third of the bract, and within which lies the phyllocyst. Secondly, there is the thin walled "neck shield" that surrounds the hydroecium. The right lateral wing of the neck shield has a distinct notch at its apex, through which the main stem of the colony originally passed. On the left side, such a notch is very indistinct or absent. The base of the neck shield is rounded, without any indentations. A gastrozooid, with its tentacle, usually remains attached to the apex of the hydroecium, and occasionally buds of gonophores are present.

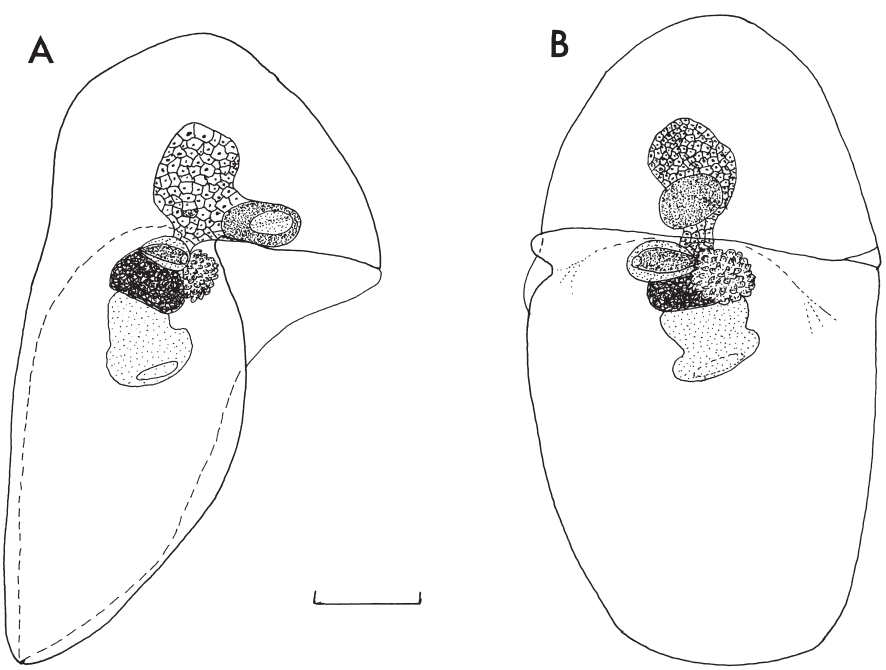

FIG. 4. – *Lensia asymmetrica*. (A) lateral and (B) ventral views of the eudoxid bract. Scale bar = 0.5 mm

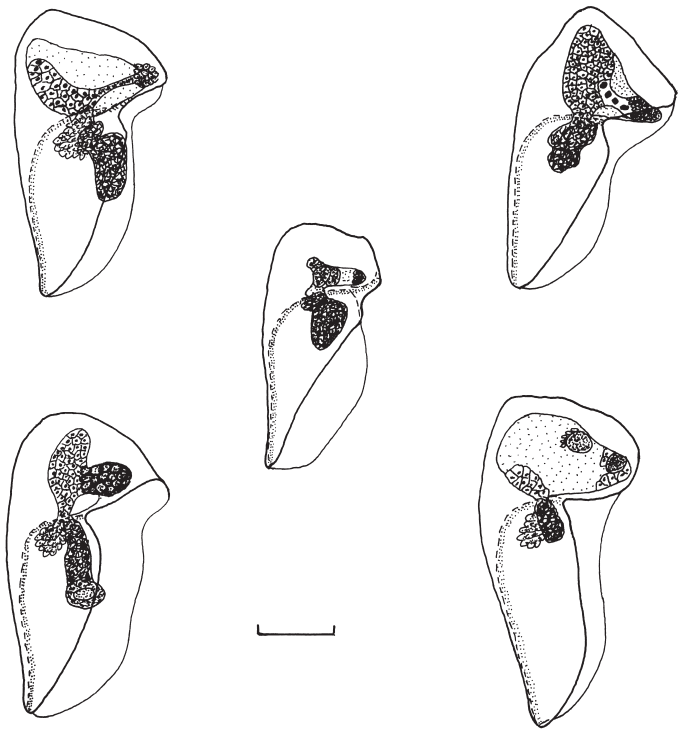

FIG. 5. – *Lensia asymmetrica*. Lateral views of bracts showing the variation in shape of the phyllocyst. Scale bar = 0.5 mm.

The most characteristic feature of the bract is the phyllocyst that lies within the head piece. It is distinctly asymmetrical, and bears a striking resemblance to the somatocyst of the anterior nectophore. There is an obvious ventrad protrusion that is always present, and within which droplets of oil usually can be found. The size of this protrusion, and its contents, are, however, very variable. This is even more the case for the dorso-apical extension of the phyllocyst, which can be relatively small or be so expanded as to occupy virtually all of the head piece (Fig. 5). Again, it may be virtually empty, perhaps with a few oil droplets, or contain many droplets have a reticulated pattern on its surface.

Eudoxid gonophore. (Fig. 6)

All three of the gonophores examined in detail were sexually mature, two being female and one male. Their sizes range from 1.9 to 2.8 mm in length, and 0.9 to 1.2 mm in width. They are apically truncated. The only discernible ridges are the hydroecials that run on either side of the broad, but shallower hydroecium. Basally, they form the ventral margin of a short, but broad and thickened mouth plate. In lateral view, the basal half of the gonophore is inflected dorsad, so that the broad ostial opening of the subumbrella cavity is directed dorso-basally.

The subumbrella cavity occupies the great majority of the gonophore. It is slightly indented in the mid-ventral line, in its lower two-thirds. The pedicular canal runs down through a median mesogloeal process, similar to that seen in the posterior nectophore. This process protrudes apico-ventrally from the hydroecial wall, and dorsal to it is a shallow gutter. The canal joins the ventral side of the subumbrella cavity slightly below its truncated apex. It gives rise to four straight radial canals. The dorsolateral pair of canals arch up and over onto the dorsolateral sides of the subumbrella cavity, and then directly down to join the ostial ring canal. Si-milarly, the ventro-laterals arch out, but downwards, before running directly to the ring canal. The manubrium of the male gonophore is very swollen and occupies all of the upper two-thirds of the subumbrella cavity, while in the two female gonophores the manubrium, bearing 12-15 eggs, is restricted to its upper half.

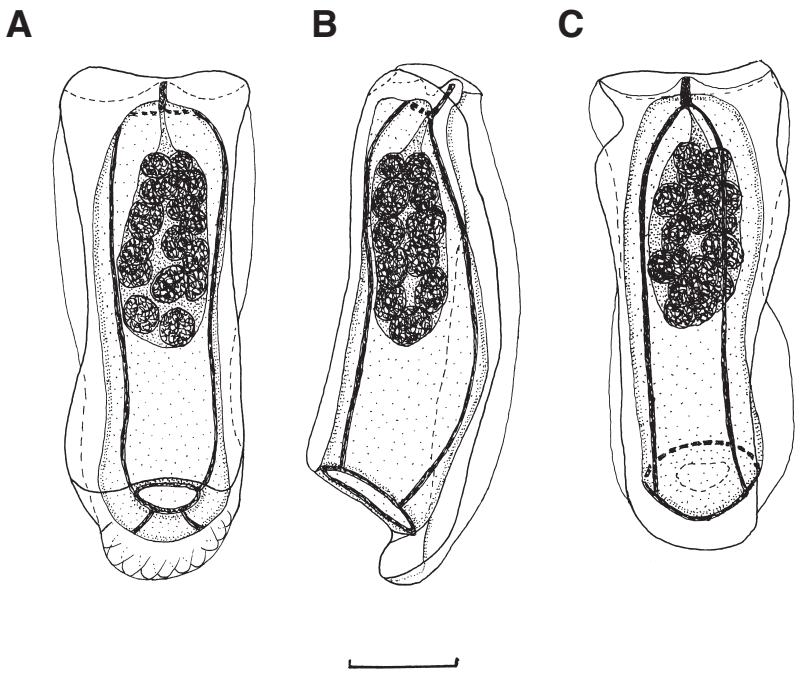

FIG. 6. – *Lensia asymmetrica*. (A) Dorsal, (B) lateral, and (C) ventral views of the eudoxid gonophore. Scale bar = 0.5 mm

Distribution

Stepanjants' (1970) original specimens of *Lensia asymmetrica* were taken, in the 1000-750 m depth range, in the vicinity of the Kurile-Kamchatka Trench at 44º11'N 150º30'E (Vityaz St. 5627) and 45º06'N, 155º55'E (St. 5621). Apart from a rather doubtful record by Musayeva (1976) from the Sulu Sea (c. 8º22'S, 120º24'E), the species was not recorded again until Margulis (1992) found it in, what was stated to be, four samples, in the 500-200 m depth range, in the Commonwealth Sea, Antarctica (c. 60-65ºS 58-85ºE) in the vicinity of the Antarctic divergence. She, thus, considered *L. asymmetrica* to be a bipolar species. Margulis (1976) also figured its occurrence at four sites in the North West Pacific, citing Stepanjants (1970) as the source, although the latter only gave two. There appears to be some confusion in all these data, which Stepanjants (personal communication) has kindly clarified. In the North Pacific there is only one additional record, in the Bering Sea, of a specimen in poor condition. In the Commonwealth Sea there actually are six records, mainly collected within the 500-2000 m depth range. In addition, there is one record from the Yucatán Basin in the Caribbean. If this latter record is valid then it would suggest *L. asymmetrica* does not have a truly bipolar distribution.

Pagès and Kurbjeweit (1994) then found numerous anterior nectophores and eudoxid bracts at all oceanic stations sampled along a transect between the northern tip of the Antarctic Peninsula and Cape Norvegica in the Weddell Sea. Up to 79 anterior nectophores per 1000 m^3 (mean 34.8 ± 24.0) and 102 eudoxid bracts per 1000 m^3 (mean 46.8 ± 34.3) were found in these samples. They classified *Lensia asymmetrica* as a lower mesopelagic species (T = 0-0.6ºC), as it occurred exclusively in the 1000-500 m depth range. This is in accord with Stepanjants' (1970) data, and the corrected records of Margulis (1992).

More recently other specimens of anterior nectophores and eudoxid bracts have been found in samples from recent German expeditions to Antarctica. In addition, a few posterior nectophores and eudoxid gonophores have been found (Table 1). These records indicate that *Lensia asymmetrica* has a fairly widespread distribution in the Southern Ocean from c. 55º to 71ºS and c. 49ºW to 6ºE. With one exception only, the specimens have been collected within the 500-1000 m depth range. These records have considerably increased our knowledge of this species in the Southern Ocean, but still relatively little is known about this, apparently bipolar species, in the Northern Hemisphere.

TABLE 1. – Records for *Lensia asymmetrica* from recent German collections.

Cruise	No. of Samples	Range of Positions	Depth Range (m)	AN	PN	EB	EG
ANTARKTIS							
ANT VII/3	3	59º 00.0'S 46º 59.6'W 61º 59.5'S 49º 00.5'W	1000-500	10		12	1
ANT IX/2	10	65º 11.8'S 39º 17.6'W	1000-500	43		49	
	1	71º 06.8'S 11º 22.3'W	500-200	1			
ANT IX/3	1	66º 48.1'S 00º 59.9'E 69º 42.9'S 06º 16.7'E	1000-500	1			
ANT X/3	1	66º 31.0'S 12º 14.1'W	630-470	1			
	1	70º 56.0'S 07º 16.8'W	1000-340	2			
	1		1000-320	5		1	
ANT X/4	2	55º 00.1'S 00º 00.7'W	1000-500	7	2	5	1
	1	69º 00.3'S 00º 00.5'E	1000-750			1	1
ANT X/7	4	64º 24.2'S 45º 55.0'W 70º 54.6'S 11º 57.6'W	1000-500	15	4	10	
METEOR							
MET 11/4	1	60º 44.5'S 55º 59.8'W 66º 16.0'S 72º 50.0'W	1000-500	1			

DISCUSSION

Stepanjants (1970) noted, in her original description of *Lensia asymmetrica*, that although the surface of the anterior nectophore was devoid of any distinct ridges, there was a large number of barely visible ribs that gave the surface a striated or reticulated appearance. However, no such striations can be seen on the surfaces of our well-preserved anterior nectophores, and so we consider that those described by Stepanjants are, in fact, distortions resulting from shrinkage during preservation. Although Stepanjants' anterior nectophores were considerably larger (5-6 mm) than the present material, the characteristic arrangement of both the somatocyst and the hydroecium is the same in both, and so there is no doubt that we are dealing with the same species.

As Pugh and Pagès (1995) noted, the identification and association of the separated parts of a calycophoran species is a matter of expert opinion. Unfortunately, unless the specimen is collected *in situ,* it is rare to find the parts of the polygastric or eudoxid stages still attached to each other. In the case of the present material that we have identified as belonging to *Lensia asymmetrica*, it should be noted that the posterior nectophores, eudoxid bracts and gonophores have almost invariably been found in the same hauls as the anterior nectophore. In addition, as the volume of water filtered in the 1000-500 m depth range was very small (c. 125 m^3), the anterior nectophores of *L. asymmetrica* frequently were the only ones present in the samples.

Further evidence for the association of the material with *Lensia asymmetrica* comes from their morphological characteristics. As noted above, the asymmetric shape of the posterior nectophore means that it fits perfectly into the asymmetric hydroecium of the anterior one. Thus, there seems little doubt that the two parts belong together. For many *Lensia* species, there is a close resemblance between the shape of the phyllocyst in the eudoxid bract and the somatocyst in the anterior nectophore. That is certainly the present case, and is good evidence to suggest that they belong to the same species. Eudoxid gonophores are more difficult to attribute, and none of the present material has been found attached to a bract. However, their presence in hauls that otherwise contained only *L. asymmetrica* bracts, is indicative of an association. Further, the absence of ridges, apart from the hydroecials, and the swollen mesogloeal process, through which the pedicular canal runs, are very reminiscent of the posterior nectophore. Thus there seems to be good reasons to associate all these pieces with the species *L. asymmetrica*.

Stepanjants (1970) considered that *Lensia asymmetrica* was related to a group of *Lensia species* (*L. ajax, L. grimaldi, L. hostile, L. exeter, L. lelouveteau,* and *L. reticulata*) because they all possess a large number of superficial ridges on their anterior nectophores. In addition, the anterior nectophores have a relatively large, ventrally open hydroecium and, except for *L. exeter,* a comparatively small somatocyst. Since our *L. asymmetrica* material shows that such ridges are absent, it appears that the relationship is not as close. However, the ventrally open hydroecium still suggests some affinity with that group. On the other hand, because of the absence of ridges, it is possible that this species is more closely related to another group of *Lensia* species whose anterior nectophores are either devoid of, or bear very indistinct, longitudinal ridges. This group includes *L. cossack, L. meteori* and *L. campanella*. However, none of these species possesses a distinct hydroecium, although they do have an oblique ventro-basal facet. Nonetheless, it is interesting to note that the preserved anterior nectophore of *L. campanella,* like that of *L. asymmetrica* often are subjected to a right-hand torsion in their apical halves. The fact that the posterior nectophore of *L. asymmetrica* also shows such an even greater torsion, is of interest, because that of *L. campanella* does not (Carré, 1968). This is probably a reflection of the differences in the structure of the hydroecium of the anterior nectophore, as it is not distorted in the latter species.

Diagnosis:

Anterior nectophore up to 6 mm in height, smooth walled, and devoid of ridges apart from two short, weak ventrals. Apical half often twisted to the right. Hydroecium extends to well above ostial level. It is asymmetric in shape, and mostly open on the ventral and right lateral sides. Large bilobed, asymmetric mouth plate. Asymmetric somatocyst with a short stalk and two main lobes. Left lobe, usually directed baso-laterally, is of fairly consistent shape. Right lobe of very variable shape, size, and disposition.

Posterior nectophore up to 2.5 mm in height, with distinct, almost 90º twist to the right in its apical half. Only hydroecial ridges present. Pedicular canal runs through a median, apico-ventral mesogloeal process.

Smooth walled eudoxid bract up to 3.2 mm in height. Rounded neck shield occupies lower two-thirds. Head piece contains large, asymmetric phyllocyst, very similar in size and shape variations, and disposition to that of the somatocyst in the anterior nectophore.

Apically truncated eudoxid gonophores up to 2.8 mm in height, with only hydroecial ridges present. Basal half inflected dorsad, so ostium opens dorso-basally. Short, broad and thickened mouth plate. Pedicular canal runs through a median, apico-ventral mesogloeal process.

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