

Margulis, R.Ya. and Alekseev, D.O. 1985

On the genus *Lensia* Totton, 1932
(Siphonophora, Calyophorae)

Zoologicheski Zhurnal **64**(1), 1985

Abstract

Examination of the genus *Lensia*, which at present includes 32 species, shows that *L. roonwali* Daniel, 1970 should be considered a synonym of *L. campanella campanella* (Moser, 1925), and *L. peresi* Patrity, 1970 a junior synonym of *L. hotspur* Totton, 1941.

Genus *Lensia* (Family Diphyidae) - itself the most diverse amongst the Siphonophora. The literature contains two major accounts of the species in the genus *Lensia* (Totton, 1965; Daniel, 1974). The latter of these contains information on 29 species, including all those species mentioned in Totton's work. To these should be added *L. peresi* and *L. minuta*, described by Patrity (1970), *L. asymmetrica* and *L. canopusi* (Stepanjants 1970, 1977), *L. zenkevitchi* (Margulis, 1970), *L. lebedevi* and *L. patritii* (Alekseev, 1985). In 1967 *L. havock* Totton, 1941 was transferred to the genus *Muggiaea* Busch 1851 (Stepanjants, 1967), with which we are in full agreement. Daniel, however, retains this species in the genus *Lensia*, without discussing the work of Stepanjants. We have demonstrated that some species of this genus are invalid, of which more is said below. In consequence we recognise 32 species of the genus *Lensia*.

Taking as a basis the extensive collection of siphonophores of the genus *Lensia* collected by the Department of Zoology, Moscow University, as well as the collections of the Zoological Institute in Leningrad, and also records in the literature, we have prepared a key for the determination of the species of the genus *Lensia* and will consider the phylogenetic relationship between certain species.

Lensia Totton, 1932

Small diphyids with two nectophores - anterior and posterior. Anterior nectophore of polygastric stage with basic pentagonal shape in section, possibly bearing 3, 5, 7, 15 or more longitudinal ridges. Transverse velar ridge sometimes present. The base of the nectophore is devoid of teeth. Hydroecium usually shallow, not more than one-fifth the height of the nectophore. Dorsal wall of hydroecium consists of two small lobes ("oral" lobes), which do not have long outgrowths. Radial canals of the gastrovascular system without commissures. Somatocyst considerably variable in length and shape. Posterior nectophore cut off proximally, having rounded "oral" lobe. Base of nectophore devoid of teeth. Free-swimming cormidia - as eudoxids. Their bracts with wide, rounded posterior margin without baso-lateral teeth. Gonophores truncated proximally, with weakly defined and very narrow dorsal teeth bordering the oral lamella.

The key for the identification of *Lensia* species is constructed on the basis of the structure of the anterior nectophore, since the posterior nectophore is often lost and is not known for all species. Also when they are known they show only minor inter-specific differences in comparison with the anterior nectophores.

Key for the identification of the species of the genus *Lensia*.

* after species name indicates figure copied from original (?) source,
i.e. not found by authors (most), or material too poor (e.g. *Lensia achilles*).

1. Somatocyst absent *L. canopusi* (Fig.1,3)
- 1a. Somatocyst present 2.
2. Hydroecium completely reduced, basal facet oval, forming more or less obtuse angle with rest of surface. *L. campanella* (Fig.3, A,B,Γ,K)
 - I. Somatocyst vermiform or club-shaped, length 30-50% that of nectophore. *L. campanella elongata* (Fig.3,K)
 - Ia. Somatocyst oval, less than 30% length of nectophore. II
 - II. Apex of nectophore twisted from right to left, or ridges inclined to the right. *L. campanella campanella* (Fig.3, A)
 - Iia. Apex of nectophore not twisted from right to left, ridges not inclined to right. III
 - III. Longitudinal ridges may be reduced to varying degrees, sometimes only one right ventral ridge remaining. Length of oral lobes 20% diameter of ostium. Apex of nectophore rounded. *L. campanella cossack* (Fig.3, B)
 - IIIa. Weak, reduced longitudinal ridges, but 5 always present. Length of mouth plate considerably less than 20% diameter of ostium. Apex of nectophore pointed. *L. campanella petrovskyi* (Fig.3, Γ)
- 2a. Hydroecium not reduced, or if so, reaches to level of ostium, more or less expressing a [?] angle. 3
3. Longitudinal ridges no more than 7 in number, or entirely absent. 4
- 3a. More than 7 longitudinal ridges 25
4. 5 longitudinal ridges 5
- 4a. Other than 5 longitudinal ridges 21
5. Lateral ridges incomplete, not reaching ostium 6
- 5a. Lateral ridges complete, ending on ostial margin 11
6. Nectophore apex drawn out into peak[?]. *L. nagabhushanami* (Fig.1, H*)
- 6a. Top of nectophore not pointed or drawn out 7
7. Somatocyst long, thin, spindle-shaped not less than 50% of nectophore length. *L. panikkari* (Fig.1, H*)
- 7a. Somatocyst less than 50% length of nectophore, ovoid, spindle-shaped or vermiform 8
8. Somatocyst originates from pedicular canal at or about the level of the ostium 9
- 8a. Somatocyst originates from pedicular canal below ostial level. 10
9. Somatocyst without clear division into pedicle and distal part, which is spindle-shaped. *L. leloupi* (Fig.1, A*)
- 9a. Somatocyst with clear division into pedicle and expanded distal part, which is spherical or ovoid in shape. *L. patritii* (Fig.1, B)

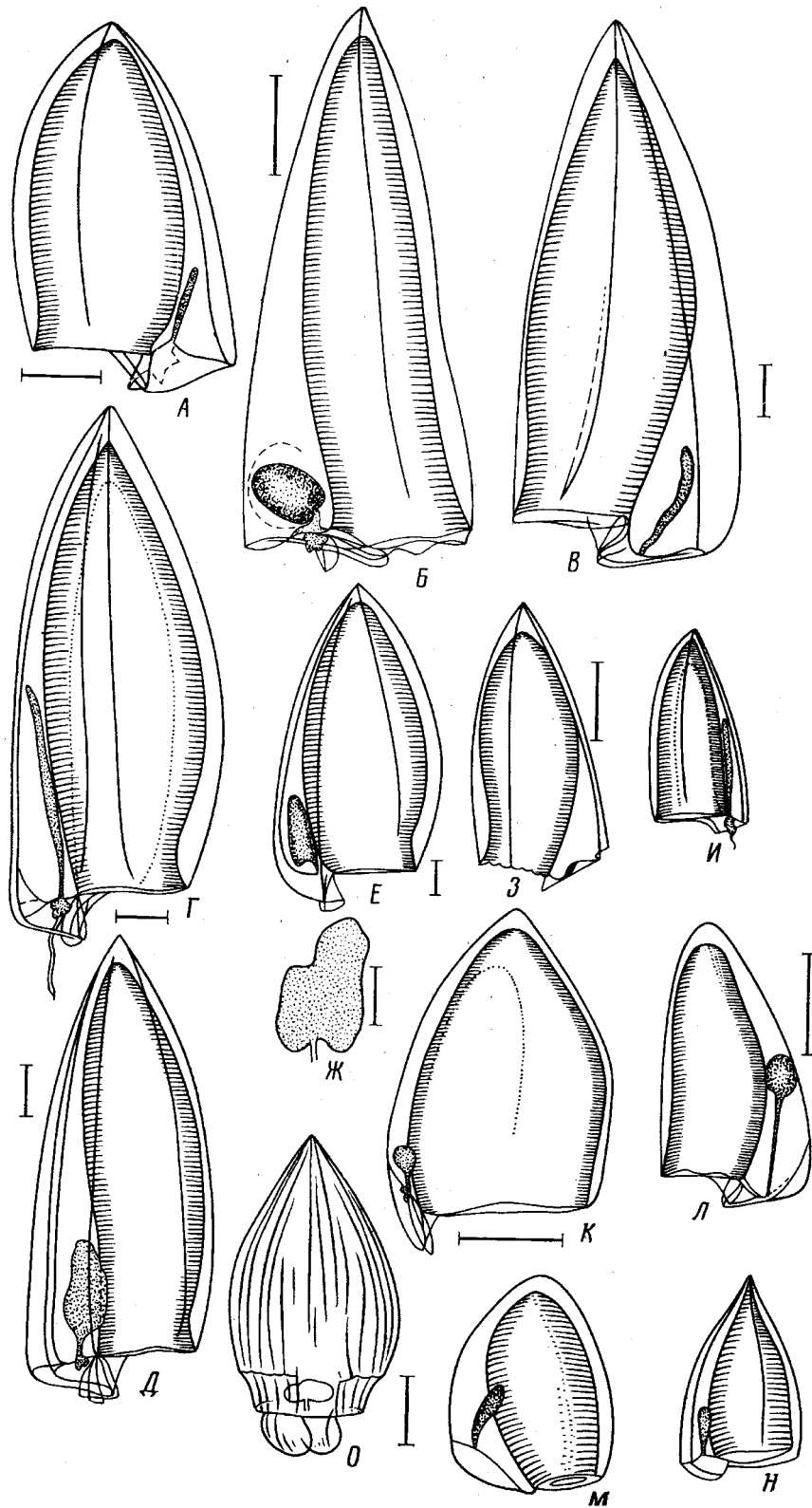


Figure 1.

Siphonophores of the genus *Lensia* : **A** - *Lensia leloupi* (from Totton, 1954); **Б** - *L. patritii*; **В** - *L. lebedevi*; **Г**, **Д** *L. multicristata*; **Е**, **Ж** - *L. hunter* (from Totton, 1965); **З** - *L. canopusi*; **И** - *L. panikkari* (from Daniel, 1974); **К** - *L. meteori*; **Л** - *L. subtilis*; **М** - *L. tiwarii* (from Daniel, 1974); **Н** - *L. nagabhushanami* (from Daniel, 1974); **О** - *L. lelouveteau* (from Totton, 1965). Scale - 1mm.

10. Somatocyst without pedicle, ovoid or spindle-shaped, hydroecium reduced. *L. tottoni* (Fig.3, **B***)
- 10a. Somatocyst vermiform, hydroecium not reduced. *L. lebedevi* (Fig.1, **B**)
11. Lateral ridges basally bend dorsad. 12
- 11a. Lateral ridges do not bend dorsad. 14
12. Somatocyst inverted heart-shape, 20% or less the length of the nectophore. *L. cordata* (Fig.2, **B***)
- 12a. Somatocyst club- or spindle-shaped, not less than 20% length of nectophore. 13
13. Somatocyst club-shaped with digitate process in apical part, longitudinal ridges without teeth. *L. baryi* (Fig.2, **A***)
- 13a. Somatocyst without digitate process, spindle-shaped, longitudinal ridges toothed. *L. achilles* (Fig.2, **B***)
- I. Hydroecial arch oval, not forming protuberance. *L. achilles achilles*
- Ia. Hydroecial arch with two apical protuberances, situated at sides of base of pedicle. *L. achilles bigelowi* (Fig.2, **3**)
14. Somatocyst less than 10% height of nectophore, origin of pedicular canal below ostial level, very close to nectosac. *L. gnanamuthui* (Fig.2, **H***)
- 14a. Somatocyst greater than 10% height of nectophore, origin of pedicular canal below ostial level, but not close to nectosac. 15
15. Hydroecial arch extends from nectosac, in plane of ostium or occasionally directed upwards. 16
- 15a. Hydroecial arch stretches from border of nectosac downwards. 17
16. Somatocyst without pedicle, hoe-shaped, laterally compressed *L. minuta* (Fig.2, **K***)
- 16a. Somatocyst with pedicle, club-shaped, not laterally compressed. *L. subtiloides* (Fig.2, **M**)
17. Somatocyst expanded laterally, heart- or saddle-shaped with short pedicle. *L. hardy* (Fig.2, **D***)
- 17a. Somatocyst some other shape. 18
18. Left lobe of dorsal wall of hydroecium approx. twice as large as right; somatocyst egg-shaped, lying below ostial plane. *L. challengerii* (Fig.2, **F***)
- 18a. Dorsal lobes of hydroecial wall almost equal; at least part of somatocyst lying above ostial level. 19
19. Somatocyst globular, egg- or bean-shaped, usually enclosed by a cavity and occupying only part of it; upper limit of cavity always above ostial plane. *L. fowleri* (Fig.2, **E**, **Ж**)
- 19a. Somatocyst spindle- or club-shaped not enclosed by a cavity. 20
20. Somatocyst inclined towards ventral side, length less than 20% that of nectophore. *L. hotspur* (Fig.2, **И**)

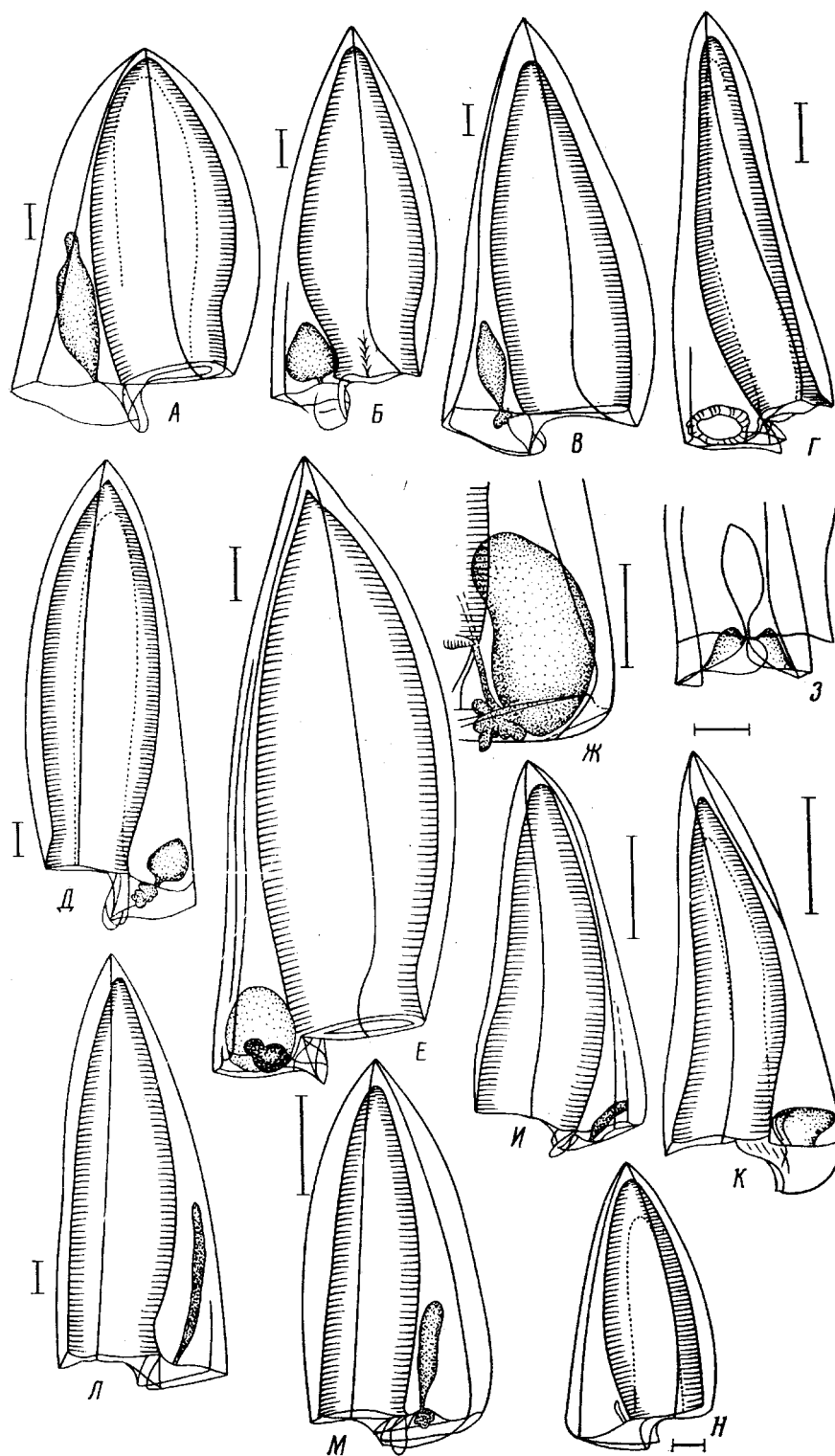


Figure 2.

Siphonophores of the genus *Lensia*. **A** – *L. baryi* (from Totton, 1965a); **Б** – *L. cordata* (from Totton, 1965a); **В** – *L. achilles* (from Totton, 1965); **Г** – *L. challenger* (from Totton, 1954); **Д** – *L. hardy* (from Totton, 1965); **Е** – *L. fowleri*; **Ж** – the same, baso-ventral part of nectophore with deep groove [?]; **З** – *L. achilles bigelowi*, baso-ventral part of nectophore; **И** – *L. hotspur*; **К** – *L. minuta* (from Patriti, 1970); **Л** – *L. conoidea pacifica*; **М** – *L. subtiloides*; **Н** – *L. gnanamuthui* (from A. Daniel and R. Daniel, 1963).

Scale – 1mm (except for **К** – 0.5mm, **Н** – 400μm).

- 20a. Somatocyst not inclined towards ventral side, length always greater than 20% that of nectophore. *L. conoidea* (Fig.2, **J**)
 I. Surface of nectophore in adult form bears numerous longitudinal furrows on ostial rim; shape of somatocyst variable from filiform to egg-shaped.
L. conoidea conoidea
 Ia. Surface of nectophore at ostial rim smooth; somatocyst slender and filiform.
L. conoidea pacifica
- 21 7 longitudinal superficial ridges. 22
 21a. Longitudinal superficial ridges absent. 23
22. Somatocyst bilobed, asymmetrical, with fine, short pedicle; ventro-lateral ridges extend onto outer border of lobes on dorsal wall of hydroecium.
L. hunter (Fig.1, **E***)
- 22a. Somatocyst spindle- or club-shaped with pedicle; ventro-lateral ridges not extending onto outer borders of lobes on dorsal wall of hydroecium.
L. multicristata (Fig.1, **Г**, **Д**)
23. Hydroecium situated so that its arch is almost parallel with wall of nectosac; only oral lobes extending below ostial level. *L. meteori* (Fig.1, **K**)
- 23a. Hydroecial arch lies at an angle of not less than 45° to wall of nectosac; at least part of lateral walls of hydroecium and oral lobes extending below ostial level. 24
24. Somatocyst clearly divided into filiform pedicle and spherical, dilated part; pedicle length 5-50% that of nectophore. *L. subtilis* (Fig.1, **J**)
 I. Length of pedicle not exceeding the width of the distal part.
L. subtilis var chuni
- 24a. Somatocyst without clear division into pedicle and distal part, spindle- or club-shaped. *L. tiwarii* (Fig.1, **M***)
25. Ridges show reticulated pattern. 26
 25a. Ridges without reticulated pattern. 27
26. Ridges forming dense reticulated pattern over whole surface of nectophore.
L. reticulata (fig.3, **И**)
- 26a. Ridges show only patchy reticulations. *L. asymmetrica* (Fig.3, **3***)
27. Velar ridge present. 28
 27a. Velar ridge absent. 30
28. Somatocyst expanded laterally, width of "head" greater than height of whole somatocyst; numerous short longitudinal ridgelets below velar ridge.
L. lelouveteau (Fig.1, **O***)
- 28a. Somatocyst spindle- or egg-shaped, height greater than width; surface of nectophore smooth below velar ridge. 29
29. Somatocyst height greater than length of lobes on dorsal wall of hydroecium.
L. exeter (Fig.3, **M***)
- 29a. Somatocyst height less than or equal to length of lobes on dorsal wall of hydroecium. *L. grimaldi* (Fig.3, **Ж***)

30. Margins of lobes on dorsal wall of hydroecium toothed or wavy.

L. zenkevitchi (Fig.3, E)

30a. Margins of lobes of dorsal wall of hydroecium smooth.

31

31. Somatocyst inverted heart-shape, with well-differentiated thin pedicle; hydroecial arch above ostial level.

L. hostile (Fig.3, Д)

31a. Somatocyst spindle- or club-shaped, with poorly differentiated pedicle, or without one; hydroecial arch not reaching above ostial level.

L. ajax (Fig.3, И)

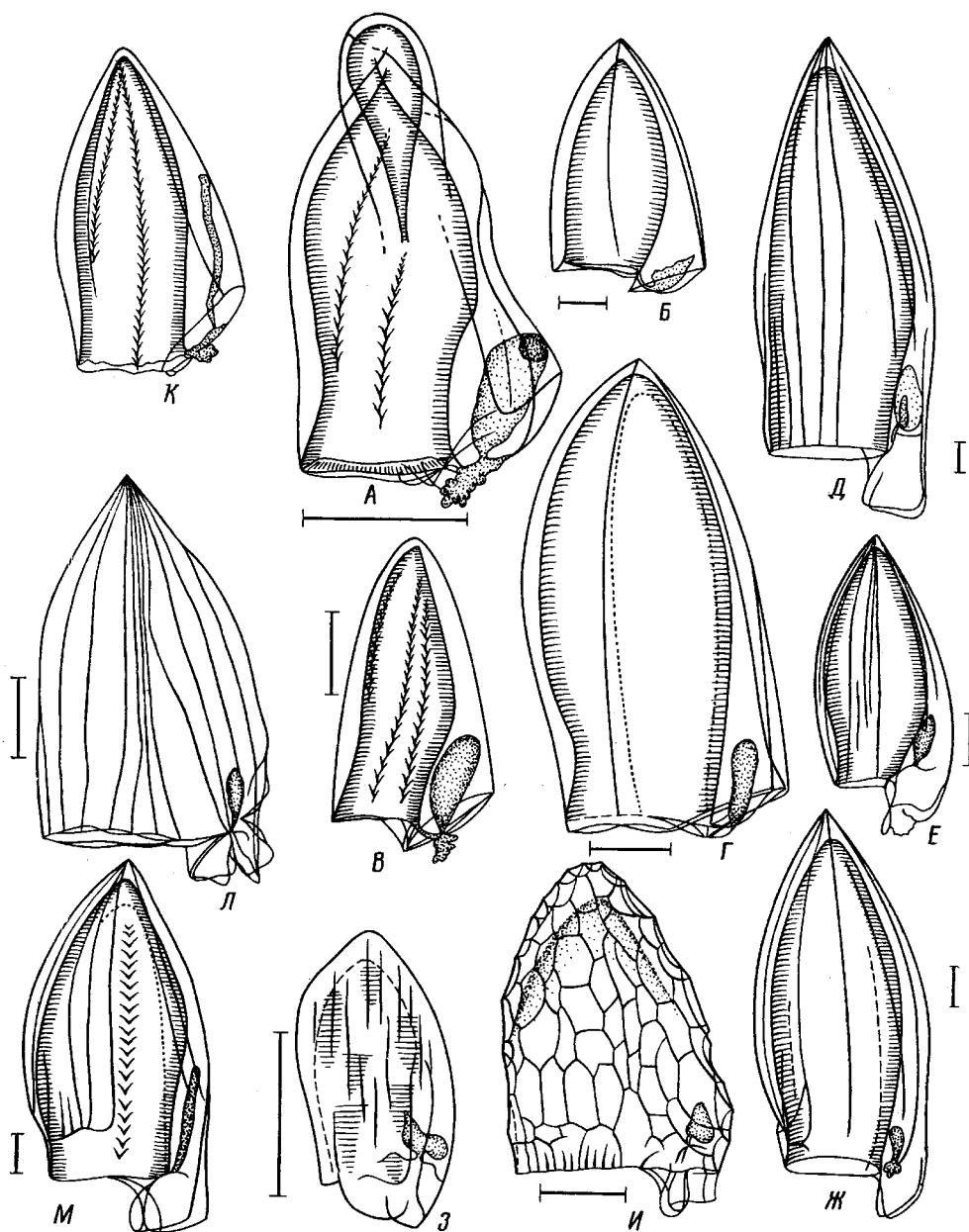


Figure 3.

Siphonophores of the genus *Lensia*. А - *Lensia campanella campanella*; Б - *L. tottoni* (from Totton, 1965); В - *L. campanella cossack*; Г - *L. campanella petrovskiyi*; Д - *L. hostile*; Е - *L. zenkevitchi*; Ж - *L. grimaldi* (from Totton, 1965); З - *L. asymmetrica* (from Stepanjants, 1970); И - *L. reticulata*; К - *L. campanella elongata*; Л - *L. ajax*; М - *L. exeter* (from Totton, 1965). Scale - 1mm (except - 2.5mm).

A study of the large number of the anterior nectophores of *L. fowleri* (Bigelow, 1911) allow us to record the characteristic structure of the somatocyst. There is a structure that we have called the "vagina" of the somatocyst. It is egg- or bean-shaped and occupies a major part of the baso-ventral region of the nectophore. It can be seen through by changing the illumination on the specimen or by staining. Usually more than half of this structure lies above ostial level; the other half below. The somatocyst seldom fills the entire lumen of the "vagina", more often only its lower part. The "vagina" is found in all larger nectophores, but in smaller and presumably younger ones it may be absent. Possibly its size varies with that of the somatocyst, which itself may be dependent on the age or the physiological state of the colony. The presence of the "vagina" shows that it is wrong to characterise the position of the somatocyst in *L. fowleri* as below the ostial level. Even if part of the somatocyst lies above ostial level, the somatocyst always departs from the pedicular canal below that level (Fig.2, E, Ж).

The nectophores of *L. ajax* Totton 1941 in our collections are rather worthy of description. Totton distinguished five groups of 2-4 longitudinal ridges, with the dorsal group of ridges not reaching the ostium. On our nectophores the ridges are disposed equally over the surface of the nectophore, and are not conveniently divisible into groups. Moreover, the dorsal ridges are complete, reaching the ostium, although they are only weakly expressed and difficult to discern.

We consider that *L. peresi* Patrity 1970 is a junior synonym of *L. hotspur* Totton 1941. The only distinguishing feature in Patrity's description is the presence of a ridge in the border between the outer surface wall of the hydroecium and the outer surface of the oral lobes. To us this difference is inadequate to distinguish a separate species.

L. roonwali, described by Daniel (1970), to us is a synonym of *L. campanella* (Moser, 1925) subspecies *L. campanella campanella*. The two features that characterise this species, the small somatocyst and the absence of a baso-ventral facet, vary greatly in *L. campanella*. The somatocyst length is 15-30% that of the nectophore, and the baso-ventral facet may be present or absent in different nectophores, apparently caused by fixation.

Daniel (1974) divided all known species of *Lensia* into four groups, on the basis of the number of ridges on the anterior nectophores. We are not altogether in agreement with that author and believe that the 32 species of *Lensia*, recognised in our work, may be grouped into the following way.

I. Species with 5 ridges: one dorsal, 2 ventral and 2 lateral. This group is the most numerous and can be divided into subgroups.

A. Species with 5 complete ridges, with lateral ones straight. Structure of the somatocyst and hydroecium variable: *L. conoidea* (Keferstein & Ehlers, 1861); *L. subtiloides* (Lens and van Riemsdijk, 1908); *L. gnanamuthui* Daniel & Daniel, 1963; *L. hotspur* Totton, 1941; *L. minuta* Patrity, 1970; *L. hardy* Totton, 1941; *L. challenger* Totton, 1954; *L. fowleri* (Bigelow, 1911); *L. canopusi* Stepanjants, 1977. In this group the closest relationship lies between *L. fowleri* and *L. challenger*. Both species have a reduced hydroecium, and the basal facet lies below ostial level and runs parallel with it. Somatocyst oval or egg-shaped, origin of pedicular canal below ostial plane. In *L. challenger* the entire somatocyst lies below that level plane, while in *L. fowleri* only part of it does.

In the description of *L. challenger*, Totton (1954) linked these two species with *L. hardy* as a group of related species, which possibly might be distinguished as a separate genus. That author did not specify why he considered these species to be so closely

related. Daniel also separated this sub-group without discussion. We agree that there is a close relation between *L. fowleri* and *L. challengerii*, but the third species *L. hardy* differs significantly from them. It has a well-developed hydroecium, the somatocyst always has a pedicle, although it is short, from which the dilated part clearly is divided, and is directed vertically upwards. In the two related species the dilated part of the somatocyst always lies in the basal facet. The shape of the hydroecium and the characteristic construction of the somatocyst of *L. hardy* makes it more closely related to *L. minuta*.

Another pair of closely related species, namely *L. conoidea* and *L. subtiloides*, have high, narrow nectophores (wider in the latter), with the somatocyst of considerable length (30-50% height of nectophore) and a well-expressed, shallow hydroecium. *L. hotspur* and *L. gnanamuthui* are similar in construction having short, narrow somatocysts. However, in the former species the hydroecium is very small or completely reduced, while in the latter it is well developed and resembles that in *L. conoidea*. In this group *L. canopusi*, devoid of a somatocyst, stands alone. It is close to *L. hotspur* in the structure of the basal plate and the tiny hydroecium.

B. Basal part of lateral ridge turns toward dorsal surface. All five ridges complete. Group consists of three species: *L. achilles* Totton, 1941; *L. baryi* Totton, 1965 and *L. cordata* Totton, 1965. All species have a relatively deep hydroecial cavity, the arch of which is in the ostial plane or displaced slightly above or below. These species are distinguished by the shape of the somatocyst.

C. Lateral ridges incomplete, not reaching to ostial margin of nectophore: *L. leloupi* Totton, 1954; *L. panikkari* Daniel, 1970; *L. tottoni* Daniel, 1970; *L. nagabhushanami* Daniel, 1970; *L. patritii* Alekseev, 1984; *L. lebedevi* Alekseev, 1984. In this group the interrelationships between the species is not clear. *L. leloupi*, *L. panikkari*, *L. lebedevi* and *L. nagabhushanami* have somatocysts of similar shape, though they differ in length. In these species there are differences in the structure of the hydroecium, being deepest in the first of these. *L. leloupi*, which is closely related to *L. subtiloides*, but differs from it in having incomplete lateral ridges. *L. panikkari* also is closely related to a species of the second sub-group, *L. conoidea*; being distinguished basically by the incomplete lateral ridges on the former. *L. patritii* differs from all other species of this sub-group by the shape of its somatocyst, with a thin, short pedicle and a sharply delimited dilated part. *L. tottoni* is distinguished by the absence of a hydroecium.

D. Species with considerably reduced ridges: *L. campanella* (Moser, 1925). Daniel included this species, and *L. cossack* Totton, 1941, in a group of species without ridges. But in the case of these species ridges are more often present than not, although they are weakly expressed and partly reduced, particularly in the upper part. Comparisons of these two species (Alekseev, 1984) have shown that *L. cossack* should be considered a sub-species of *L. campanella*. Besides this, two other sub-species have been described *L. campanella petrovskii* Alekseev 1984 and *L. campanella elongata* Margulis 1984. The former of these sub-species has five ridges, which are never completely reduced. This indicates that *L. campanella* occupies an intermediate position between the group of species with five ridges and those without ridges altogether.

II. Species without ridges. Of the species placed in this group by Daniel only three remain: *L. subtilis* (Chun, 1886), *L. meteori* (Leloup, 1934) and *L. tiwarii* Daniel, 1970. They are all fairly closely related. The first two species have somatocysts of similar structure, with a thin pedicle and almost spherical dilated part. They are distinguished by the structure of the hydroecium, which in *L. meteori* lies parallel to the wall of the

nectosac. In *L. tiwarii* the somatocyst does not have a well-developed pedicle and its expanded part is cylindrical. The arrangement of its hydroecium is more similar to that in *L. meteori* than to that in *L. subtilis*.

III. Species with 7 ridges: *L. multicristata* (Moser, 1925) and *L. hunter* Totton, 1941. In this group Daniel included *Muggiaea havock* (Totton, 1941). In this group the dorso-lateral ridges reach the apex but not to the ostial opening. The ventro-lateral ridges of the first species do not reach the apex or the oral lobes, while in the second they also do not reach the summit but basally extend onto the outer border of the oral lobes. Hydroecium is deeper in *L. hunter*. The somatocyst differs in structure. Thus the feature that unites these species is the number of ridges, four of which are incomplete.

IV In this group Daniel included all multi-ridged species. The group evidently is not monophyletic and we consider it necessary to divide it into several sub-groups.

A. Species with large number (more than 7) of longitudinal ridges, some of which are incomplete: *L. ajax* Totton, 1941; *L. hostile* Totton, 1941; and *L. zenkevitchi* Margulis, 1970. All the species of this group are closely related by the structure of the somatocyst and hydroecium. The latter is comparatively deep. The number of ridges is variable, within limits, for each species.

B. Species with a velar ridge and a large number of longitudinal ridges: *L. lelouveteau* Totton, 1941; *L. exeter* Totton, 1941, *L. grimaldi* Leloup, 1933. The last two species are more closely related to each other than to *L. lelouveteau*, the nectophore of which is considerably smaller in size, squat, and with the velar ridge greatly extended. The somatocyst of *L. lelouveteau* has a thin stalk and a dilated part, expanded laterally, while in the other two species a stalk is absent, and the dilated part is expanded vertically.

C. Species with a large number of transverse ridges, in addition to longitudinal ones: *L. reticulata* Totton, 1954; *L. asymmetrica* Stepanjants, 1970. In the latter species both types of ridge are short, not covering the whole of the nectophore, but forming a network in parts. One cannot say that *L. reticulata* only has longitudinal and transverse ridges, as not all ridges have a clear direction, some uniting at different angles, but overall forming a network over the whole surface of the nectophore. Totton (1954) described a velar ridge. But familiarity with a large number of nectophores shows that only occasionally do those ridges neighbouring the ostial border unite to form a velar ridge. Usually such a clear picture is not seen. In the basal part of the nectophore, above ostial level, is seen a row of short vertical ridgelets. The structure of the somatocyst and the hydroecium in both species is similar.

The above investigations show that the majority of the species of the genus *Lensia* have five longitudinal ridges. The greatest variability lies in the arrangement of the lateral ridges, the basal part of which may be reduced or of variable form. The specific differences in this group lie in the structure of the hydroecium and the shape of the somatocyst. Sub-species of certain species show a sequence of ridge reduction through to ridgeless forms. It is possible to see this process in the sub-species of *L. campanella*. Another line of evolution in the *Lensia* species produces multiridged forms. Within each group (ridgeless and multiridged), as well as the basic five ridged group, there are variations in the structure of the hydroecium and somatocyst independent of the structure of the nectophore. The variations in the form of the somatocyst and hydroecium are not influenced by each other.

Literature.

- Alekseev, D.O. 1984. New species and subspecies of siphonophores of the genus *Lensia* (Calycophorae). Zool. Zh., 63(7), 965-970.
- Daniel, R. 1970. Some new species of Siphonophora (Coelenterata) from the Indian Ocean. *Journal of the Zoological Society of India*, **22**, 147-156.
- Daniel, A. & Daniel, R. 1963. *Lensia gnanamuthui*: a new siphonophore from the Madras plankton. *Journal of the Bombay Natural History Society*, **60**, 751-753.
- Margulis, R.Ya., 1970. New species of siphonophore, *Lensia zenkevitchi* sp.n. (Siphonanthae, Calycophorae) from the Atlantic Ocean. Zool. Zh., 49(1), 148-9
- Margulis, R.Ya., 1984. New subspecies of siphonophore *Lensia campanella elongata* subsp.n. (Hydrozoa, Siphonophora). Vestn. Mosk. oon-ta, Ser. Biol. No.4.
- Patriti, G. 1970. Note sur deux nouvelles espèces du genre *Lensia*, recueillies dans les eaux du large de Tulear (S.W. de l'Océan Indien, Madagascar). *Recueil des Travaux de la Station Marine d'Endoume* Fasc. ? Suppl. 10, 103-106.
- Stepanjants, S.D. 1967 Siphonophores of Russian Seas and northern part of Pacific Ocean. L: Nauka 1-210.
- Stepanjants, S.D., 1970 Siphonophores collected from southern part of Kurile-Kamchatka trench and equatorial region. Trudy Inst. Okeanol. AN, SSSR, 96, 222-235.
- Stepanjants, S.D., 1977. Siphonophores from central part of Pacific Ocean. V. KN. Mosc. Plankton L. ZVH, An, SSSR, 54-81.
- Totton, A.K. 1954. Siphonophora of the Indian Ocean together with systematic and biological notes on related specimens from other oceans. *Discovery Reports* **27**, 1-162.
- Totton, A.K. 1965. *A Synopsis of the Siphonophora*. London: British Museum (Natural History).
- Totton, A.K. 1965a. A new species of *Lensia* (Siphonophora: Diphyidae) from the coastal waters of Vancouver, B.C.; and its comparison with *Lensia achilles* Totton and another new species *Lensia cordata*. *Annals and Magazine of Natural History*, **Ser. 13, Vol. 8**, 71-76.