Polyphemidae of the Pontocaspian Basin

by

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I should like to attract attention to one remarkable group of Crustacea still largely unknown but worth of a more detailed study. This is the Polyphemidae group of the Pontocaspian basin.

Among the autochthonous Pontocaspian fauna they are most peculiar not only because of unusual abundance of forms but also because of the curious morphological transformation they have undergone in the Caspian Sea. In open seas, including the Black Sea, the polyphemids are known to be represented by six species of the genera Podon (P. polyphemoides, P. leuckarti, P. intermedius) and Evadne (E. spinifera, E. nordmanni, E. tergestina). In freshwaters there occur only 2 polyphemid species viz. Polyphemus pediculus (L). and Bythotrephes longimanus Leyd. (incl. B. cederstroemi Schoed.). In Caspian Sea as far back as in 1898-1902 sixteen endemic species and 12 'subspecies' of polyphemids have been found and described by G. O. Sars. Some of these or closely related species were found by Pengo (1879a, b), S. A. Zernov (1901, 1903) and V. Meisner (1908) in the Sea of Azov and in the Aral Sea. Much later A. Behning has started a reinvestigation of the Pontocaspian polyphemids but only eventual notes will be found in his papers devoted to some other topics (1938, 1940, 1941).

I had an opportunity to undertake a study of the taxonomy and biology of this group and to show that in the Caspian Sea there occur at the present not less than 23 species of polyphemids, a list of which follows:

- 1. Polyphemus exiguus G. Sars
- 2. Cercopagis socialis (Grimm)
- 3. C. pengoi Ostr. (= C. tenera G. Sars)
- 4. C gracillima G. Sars
- 5. C. neonilae G. Sars
- 6. C. robusta G. Sars
- 7. C. prolongata G. Sars
- 8. C longiventris n. sp.
- 9. C. micronyx G. Sars
- 10. C. anonyx G. Sars
- 11. Apagis cylindrata G. Sars
- 12. A. beklemischevi n. sp.

- 13. A. ossiani n. sp.
- 14. A. longicaudata G. Sars
- 15. Podon polyphemoides Leuck.
- 16. Evadne anonyx G. Sars
- 17. Podonevadne camptonyx (G. Sars)
- 18. P. angusta (G. Sars)
- 19. P. trigona (G. Sars)
- 20. Corniger auritus Behn.
- 21. C. bicornis Zern.
- 22. C maeoticus hircus (G. Sars)
- 23. Caspievadne maximowitschi (G. Sars)

All these species, with the exception of *Podon polyphemoides* which is widely distributed in open seas and has obviously penetrated into the Caspian Sea in 1957 via the Volga-Don channel (Mordukhai-Boltovskoi, 1961), are endemic for the Pontocaspian basin, and do not occur beyond it. They consist of two natural groups:

The first one is of freshwater origin: here belong *Polyphemus exiguus*, a dwarf (not exceeding 0.4 mm) relative of the freshwater *P. pediculus* (reaching 1.3 mm), and 14 species of the genera *Apagis* and *Cercopagis*, undoubtedly *Bythotrephes* descendants. These 'cercopagids' are distinguished from *Bythotrephes* by a more delicate constitution, more developed eye and first pair of legs and reduced caudal claws. *Apagis* possesses a straight fairly long caudal appendage exceeding the body not more than 3—4 times, and an elongated metasome (abdomen). In addition to the two species formerly described by G. O. Sars I have found two more species of this genus, namely *A. beklemischevi* sp. n. with a rather short metasome and *A. ossiani* sp. n. with a strongly developed point on the brood pouch and long caudal claws bent forwards (instead of backward, as in all other species).

Cercopagis is distinguished by a more elongated caudal appendage exceeding the body not less than 4—5 (up to 8—10) times and by a double loop-like curvature close to the end. A new species has also been found in this genus, namely *C. longiventris* sp. n. with an unusually long metasome, making 2/3 of the length of the body (and possibly another species not yet described). On the other hand three species with a pointed brood pouch described by G. O. Sars, namely C. pengoi Ostr. (= C. tenera G. Sars), C. neonilae, C. gracillima lacking any sharp distinctions might probably be considered as varieties of a single species. Nor is there any clear cut distinction between C. micronyx and C. prolongata. The characters of the Cercopagis species are generally variable.

Three speciation routes may be distinguished in the group of cercopagids originating and diverging from the initial *Bythotrephes*-like form (the nearest to which is *Apagis ossiani*). The first way is lengthening of the metasome and shortening of the caudal appendage leading to *Apagis cylindrata;* the second is shortening of the metasome concurrently with lengthening of the caudal appendage and reduction of caudal claws, leading via *Cercopagis socialis* - to C *micronyx;* the third is lengthening of caudal claws and emergence of a right angle between the metasome and caudal appendage and of vertical posture of the body, leading to C *pengoi- C. graciiiima* (fig. 1).

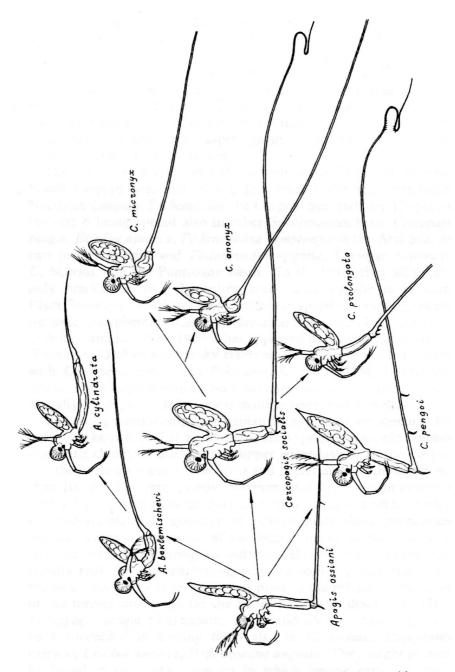
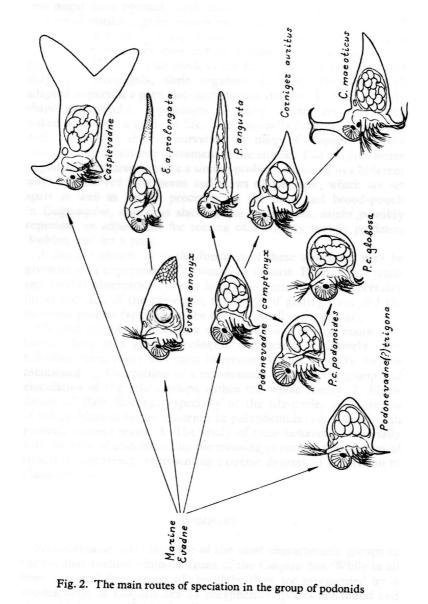


Fig. 1. The main routes of speciation in the group of cercopagids

The cercopagids and the Caspian *Polyphemus* may undoubtedly be considered as an ancient Caspian fauna constituent of freshwater origin. Another group of Caspian polyphemids, which may be named 'Podonidae' is undoubtedly of marine origin and can be considered as a descendant of some *Evadne*, which have inhabited tertiary seas -the precursors of Caspian Sea. So far, 5 species of this group have been known, but their number now increases to eight. In the Caspian Sea I have discovered *Corniger bicornis*, first found in the Sea of Azov by S. Zernov (1901), and *C. auritus*, already mentioned by A. Behning (1938) - both species have been merely mentioned but practically not described. The *Evadne* and *Podonevadne* species have numerous more or less steady forms, but with no particular distribution ranges. Especially polymorphous is *P. camptonyx*, although one of its forms should probably be considered as an independent species *P. angusta*. The whole genus Podonevadne, established by Gibitz (1922) and Behning (1940) can not apparently be accepted in its modern range. At least ft *trigona* should be excluded from this genus owing to the particular structure of its legs, viz. cxopodites setae meeting the formula 2.1.1.1 versus 2.2.2.1 in the other Caspian podonids.

Contrary to marine (oceanic) podonids with their uniform body-shape but varying structure of legs in different species, speciation in Caspian podonids manifested itself mainly in transformation of the body-shape (especially brood-pouch and head) and of the caudal claws. The major ways of speciation led here to lengthening of the incubatory part - up to an almost rod-like shape in *Evadne anonyx* f. *prolongata* and *Podonevadne angusta*, or to the development of various appendages, such as massive hollow processes on the head and brood-pouch in *Caspievadne* and long curved horns and caudal claws in Corniger (especially C maeoticus). Some few forms, however, underwent a shortening and rounding of the brood-pouch resulting in the appearance of almost sphaerical Podon-like forms (Podonevadne camptonyx podonoides, P. c. globosa) (fig. 2).



The total number of forms of polyphemids (including all lower taxons) in Caspian Sea is about 40. The abundance of intraspecific forms and variability of many species indicate that Caspian polyphemids (like some other Caspian groups, e.g. molluscs, shads) are undergoing intensive evolution.

The majority of Caspian polyphemids occur in the Middle and South Caspian Sea, and only a few inhabit also the refreshened Northern Caspian. Endemic for the Caspian Sea itself are 17 species, the rest 6 being spread also in other Southrussian seas: Cercopagis pengoi, Evadne anonyx, Podonevadne camptonyx in the Aral Sea, the two former species and Podonevadne trigona, Corniger maeoticus, C. bicornis - in the Pontoazov basin. In the latter they all inhabit only brackwater and oligohaline areas, avoiding the more saline Black Sea waters which are inhabited by six species of 'mediterranean' (oceanic) polyphemids. Corniger maeoticus is also found in freshwaters of deltas, and in 1958-1960 it has appeared in Zymljansky reservoir (Don river) and in Kachovsky reservoir (Dniepr), in the latter along with Cercopagis pengoi and Podonevadne trigona (M. Boltovskoi 1963). They have obviously been brought into these reservoirs accidentally by ships and may appear in other reservoirs as well.

The ecology and biology of Caspian polyphemids are obscure. The only fact known is that all of them are typical planktonic animals, occurring chiefly in shallows and upper water-layers. In the Caspian Sea they seldom occur below 50 m and prefer areas with depths less than 100 m. The cercopagids, however, avoid also the littoral zone with a depth less than 10 m. No data at all are available on their vertical migrations. The majority of polyphemids show pronounced seasonal changes appearing at the beginning or in the middle of summer and disappearing in autumn. During the summer they rapidly reproduce by parthenogenesis; in some species the ova of the next brood appear in the pouch prior to the release of the young of the former brood. So far the males have been described only in Cercopagis pengoi (VALKANOV, 1951) and Podonevadne trigona; I have succeeded in finding them also in C. socialis, Polyphemus exiguus, Evadne anonyx, Podonevadne angusta. They might possibly be found in some other species in which resting eggs are known (Corniger maeoticus, Podonevadne camptonyx). However, in many species, including very abundant ones and of wide occurence (e.g. Apagis cylindrata, Cercopagis micronyx) the males are so far unknown and might have probably completely disappeared so that the production of resting eggs in females has been discontinued.

Feeding of Caspian polyphemids is likewise quite obscure. The structure of their legs does not fit filtration and the animals are probably predatory. This mode of life has so far been demonstrated only for cercopagids, their organisation being obviously well adapted to pursuit a prey and catch mobile animals. The quaint body shape and peculiar appendages of many species are apparently linked with such a mode of life. The unusually long caudal process with a looplike double curvature in many *Cercopagis* possibly favours quick rectilinear movement of the animal. The rod-like forms of podonids apparently solve a similar problem although in a different way. The curved long horns and claws of *Corniger*, which are set apart as well as hollow processes on the head and brood-pouch in *Caspievadne*, doubtless slacking the movements, might possibly represent an adjustment for soaring of a slightly mobile predator, 'looking-out' for a prey.

A definite answer as to the function of these structures may be given only by experiments on animals in aquaria. Rearing in aquaria and careful observations over a long time period are also necessary for elucidation of the life-cycle, the mode of getting food and the nutrition process (apparently the prey is usually sucked out).

Caspian polyphemids offer a wide field for studying many problems, those of a general biological significance inclusively. The following three major and most interesting trends of study may be mentioned: 1. Completion of a taxonomical study of the group and elucidation of the relationships within the whole family. 2. Elucidation of their biology, especially of the life-cycle, and solution of the problem as to the existence of polyphemids (i.e. Cladocera in general) without males. 3. The study of their behaviour, especially with the view of understanding the meaning of curious morphological structures apparently representing extreme degrees of adaptation to planktonic life.

SUMMARY

Polyphemidae constitute one of the most characteristic groups of the peculiar auchtochthonous fauna of the Caspian Sea. While in all open seas and freshwaters of the globe they are represented by 8 species only, in Caspian Sea 24 polyphemid species are found and about 15 intraspecific forms. Except one species, all of them are endemic for the Pontocaspian basin (and 18 species among them -for Caspian Sea).

A revision of this group (first described by G. SARS in 1897, 1902) resulted in the discovery of some new species (*Cercopagis longiventris, Apagis beklemischevi, A. ossiani*) and in a description of two practically nomina nuda species (*Corniger auritus, C. bicornis*).

The group 'cercopagids' consisting of fourteen species (not quite distinctly distinguishable) of the genera *Cercopagis* and *Apagis*, undoubtedly descendants of *Bythotrephes*, is of freshwater origin, as well as the dwarfish *Polyphemus exiguus*, which is very closely related to *P. pediculus*. Speciation in cercopagids mainly involved changes in the length of the caudal appendage and of metasome (abdomen). The group 'podonids' consisting of eight species (and numerous intraspecific forms) - descendants *of Evadne* - is of marine origin. Speciation in this case involved lengthening of the incubatory part (brood pouch) or appearance of various appendages.

The ecology of pontocaspian polyphemids is quite unknown except that they are typically planktonic and avoid areas with a lower salinity (only 5—6 species, inhabiting also the Pontoazov basin, are euryhaline). Their peculiar body shape and appendages, particularly the unusually (8—10 times longer than the body) long caudal processes with double curvature in *Cercopagis* and curved claws and horns in *Corniger* and *Caspievadne* are, probably, adjustments for life of a planktonic predator.

The polyphemids develop in great masses toward the end of summer when parthenogenesis proceeds at a very high rate but resting eggs and males have been found only in a few species and in most species are apparently lacking.

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