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The origin of glacial relict amphipods in relation to the question of the postglacial connection between the White Sea and the Baltic.

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The question of the origin of relict species, especially marine glacial relicts, is of general biological interest both as a zoogeographical problem and from the standpoint of the production of new forms under environmental conditions which differ from their original requirements, that is, under conditions not encountered by the original ancestral forms.

The study of freshwater relicts of originally marine species makes it possible to single out a number of changes which have taken place in the species under the new environmental conditions encountered as they shifted from the sea to fresh water.

The present work is concerned with amphipods of the genera *Gammaracanthus* and *Pontoporeia*, relict species which belong to the so-called "*Yoldia* complex", which are the remains of the formerly widely extended Yoldia Sea. The view that the Yoldia Sea was a broad marine strait uniting the White Sea and the Baltic has been under discussion for a long time, and in recent years it has been thoroughly examined in the course of the work of Soviet geologists.

The distribution and the intraspecific variability of the relict species living in lakes that lie between the White Sea and the Baltic provides zoogeographical material for solving certain disputed questions concerning the postglacial connection between the Baltic and White Seas.

In addition to its theoretical importance, the study of relict crustaceans has great practical interest, for some of them, the amphipods in particular, are of considerable importance to the fishing industry. In many of the places they inhabit they are the principal component of the food of many fishes.

Pontoporeia is of especially great importance in the food of fishes, particularly whitefishes. In some lakes of Karelia *Pontoporeia* comprises up to 80-90% of the biomass (Gordeev, 1949). At the present time, *Pontoporeia* is the object of acclimatization experiments in many lakes that lie outside the boundaries of its natural range. There is a large literature dealing with the problem of relicts. Without attempting any general review, I will mention only that the problem of the origin of relicts has been approached from several points of view: *morphological* -- to establish the relationship of the relicts to a stem form; *geographical* -- to trace to its origin their range, and the /process of/ isolation from the main range; *ecological* -- to establish /p. 111/ the connection between changes in the environment and changes in the organisms; evolutionary -- considering relicts as forms characterized by a retarded rate of evolution.

However, it is only the broad ecologico-geographical formulation of the problem by Soviet scientists that has made it possible to set the relict problem out along the right path towards a solution. The basis for this approach is the definition of the "relict" concept by L. S. Berg (1916) and V. M. Rylov (1920). The concept of a "relict" applies basically to the origin of a form and it does not predetermine its further fate, which latter is entirely bound up with the conditions of life which the form encounters. We must not consider that relicts necessarily are species which have become impoverished in the processes of evolution (Birshtein, 1947), which are no longer susceptible to change. From the example of such abundant species as the relict Pontoporeia and mysids we can see that these are species which are flourishing at the present time.

Approaching the question of the formation of relicts from the point of view that their interrelation with environmental conditions, in the present work we will trace the changes that have taken place in the ecology and morphology of relicts, in comparison with the parent marine species, and connect up the data obtained with the problem of the extent of the postglacial marine transgressions.

Variability, distribution and ecology of Gammaracanthus and Pontoporeia

The marine species Gammaracanthus loricatus loricatus is characterized by being very large for an amphipod; females are up to 58 mm long (av. 44.0 mm), males somewhat less. Its carapace is thick, with strongly developed sculpture. The dorsal ridge begins at the first segment as a kind of keel and passes over into coarse projections triangular in shape, which develop extended sharp tips on the last segments of the mesosome, on the metasome and on the urosome. The segments of the body, the "koksalnye", the epimeral plates and basipodites of the legs have rib-like thickenings. The rostrum is stout and long, it extends beyond the first segment to the first antenna, and is evenly curved. The ventrolateral corner of the head is produced and is triangular in shape. The gnathopods have a strongly developed muscular 6th segment (palm). The palm of the first gnathopod is egg-shaped, noticeably shorter than the second. The third epimeral plate has a sharply produced posteroventral angle. Along its lower margin short stout spinules are inserted. The bristles by the nails of the pereiopods are in a short sparse tuft.

Distribution of marine *Gammaracanthus* is circumpolar (Fig. 1). It lives in the shoreward regions of northern seas. Interesting is the presence of the marine form in the Pechora and Amur estuaries, and in the mouths of certain rivers (North Dvina).

Outside the Soviet Union it is found near the coast of Alaska, along the arctic shores of North America, and near the coasts of Greenland, Spitzbergen and Franz Josef Land.

The distribution of marine *Gammaracanthus* is adapted to regions of somewhat reduced salinity (25-30‰); it lives in the sublittoral zone at depths of 10-25 m, /also/ in estuaries and in the mouths of rivers--not only in the sublittoral but even in the littoral zone which is subject to sharp changes in salinity and temperature: from 5-10‰ in summer to almost normal salinity in winter. In summer temperature rises to +5°, +7° and even to +15°, +18°C.

Gammaracanthus from the mouths of the White Sea rivers (Gridina, Ponoi, Mezen), and from the Pesha and Kara Rivers, differ from the typical marine species. It lives /p. 112/ in the littoral zone, under conditions of variable salinity and temperature; it is characterized by earlier attainment of sexual maturity and by greater fecundity. It has a distinctive markedly curved rostrum and the epimeral plates agree in form with those of the estuarine *Gammaracanthus* (see below). Because of the instability of some of the characters (mainly associated with size), I consider this to be a variety of the marine form, under the name of *Gammaracanthus loricatus ostiorum* var. n.

The estuaries at the mouths of the great Siberian rivers--the Ob, Yenisei, Piasina, Taimyr and Lena--are inhabited by a special form of *Gammaracanthus* which lives under conditions of prolonged and constant brackishness. The estuarine *Gammaracanthus* is absent west of the Yenisei and east of the Lena, but it occurs again at the mouth of the Anadyr River, in a region subject to the influence of marine transgressions. In the eastern portion of its distribution, in spite of considerable brackishness (in Koliuchin Bay, and along the Chukchi coast) *Gammaracanthus* is represented only by the original marine form (Fig. 1).

Estuarine *Gammaracanthus* is markedly different from the typical form: it is smaller--the average length of females is 30.6 mm, maximum 38.8 mm, and males are of the same size. The carapace is thinner, softer, and the body is little curved. The dorsal ridge is weakly developed on the first segments: it can be observed only with difficulty as a sort of keel on the first 4 segments. The projections (zubets) are less marked; they begin on the 5th or 6th segment. There is weaker development of the ribbed thickening of the carapace. The rostrum is shorter than in *G. loricatus loricatus*, usually it is equal to or less than the first segment of antenna I, and it is noticeably curved. The lateral corners of the head are rounded-triangular, and they are less produced. The second segment of antennal pair II is strongly inflated, in connection with the great development of the antennal gland (an adaptation to brackish water). The gnathopods differ somewhat from the typical form. The palm of gnathopod I is relatively larger and approximates in size to that of II. Epimeral plate III does not develop the sharp, produced posterior angle that the marine species does (the angle is about 70°, as compared with 41° in *G. loricatus loricatus*).

Along the lower margin of epimeral plate III in addition to the ordinary spinules there are sometimes found small ones, which in some cases are displaced toward the base of the large spinules. The bristles at the ends of the pereiopods are of about three-quarters of the length of the claw.

Taking into consideration the differences just outlined, the different conditions of existence of this form, and certain differences in its biology, I consider it necessary to separate the estuarine *Gammaracanthus* as a subspecies of the marine species under the name *Gammaracanthus loricatus* Sab. *aestuariorum* ssp. n.

Outside the limits of its principal range, *Gammaracanthus* has penetrated to the Caspian Sea and into certain glacial lakes.

The Caspian *Gammaracanthus* is close to the estuarine one in a number of characters, and in a few characters it is close to the marine one. As with all brackish-water forms, it is smaller than the marine one; the body length of the female is 28.3 mm, and males can scarcely be distinguished by size. The dorsal ridge is developed from the first segments, having the appearance of wavy projections with rounded tips. The form of the dorsal ridge and character of the rostrum (thin, almost straight, not reaching the end of the first segment of antenna I) show distinctive differences from the other forms. The palm of the first gnathopod is somewhat heavier than in marine *Gammaracanthus*, but it does not differ in shape. Epimeral plate III is almost square in shape (angle 84.5°). The spinules on the lower margin are the same as in the northern form. The bristles at the ends of the pereiopods are developed in a rather dense tuft, and are about ½-¾ of the length of the claw.

/p. 114/ This likeness to the estuarine subspecies supports the hypothesis that before it was introduced into the Caspian, *Gammaracanthus* had been living somewhere in brackish regions.

The development of the lake *Gammaracanthus* has taken the direction of further changes in the basic characters which distinguish the brackish forms from the marine form. The lake form is considerably smaller than the marine one, and somewhat smaller than the estuarine subspecies. The average size of females is 27.3 mm, and the maximum is 35.5 mm. Males are somewhat smaller. The body is better proportioned, more delicate, with a thin and frequently translucent covering. The dorsal ridge is more weakly exhibited than in the estuarine form. On the first 4 segments the ridge is commonly little developed. The projections begin on the 5th or 6th segment and are less apparent. The rostrum is usually shorter than the first segment of the antenna, but sometimes it reaches the end of the segment; it is fine and slightly curved. The lateral angles of the head are rounded in shape. The second segment of antennal pair II is greatly swollen, as in the estuarine form. The most constant and characteristic distinguishing feature of the lake *Gammaracanthus* is the structure of the gnathopods.

The elongation of the palms of the gnathopods (especially I), which was encountered in the estuarine subspecies, is developed in the lake species to a considerably greater degree. The palm of gnathopod I is shaped like an almond, and is narrowed in its proximal portion. In contrast to what occurs in the marine and brackish forms, the palm of gnathopod I is longer than that of II. The ratio of length to breadth of the palm is also different from the original form. The gnathopods themselves are longer. Another distinguishing character is the structure of epimeral plate III, which is almost square in shape. The posteroventral angle is blunt (equal to 107.7°). In addition to the spinules /shipiki/ along the lower margin of epimeron III there are slender bristles /tonkie iglokochki/ at the base of each of which shorter finer bristles /tonenkie iglokochki/ are situated. The bristles at the end of the pereiopods are in a thick bunch and commonly exceed the claw in length.

In the lakes of Karelia *Gammaracanthus* is a rare species, it lives in the deepest ologotrophic lakes: Ladoga, Onega, and it was found in Segozero. In Palozero and Putkozero it is absent at the present time (Gordeev, 1949). It occurs in some lakes of eastern Finland and central Sweden, and in Lake Mjøsen in Norway. In the Baltic Sea *Gammaracanthus* is not found at the present time, although it has been found at the mouth of the Neva and in Lake Loio 20 km from the Gulf of Finland (see Fig. 2).

Relict Gammaracanthus is a cold-water form with narrow range of tolerance, living at depths from 30-40 to 200 m at stable low temperatures (+4° to +6°C), and it requires a high oxygen content.

A number of adaptative changes which have developed in lake Gammaracanthus in relation to the changed hydrochemical conditions have useful properties--they permit greater buoyancy in fresh water. Among such characteristics are thinness of the carapace, reduction of the spines and ribbing, and a greater development of hairs on the extremities and epimera.

On the basis of morphological differences and changes in biology, which are a consequence of the adaptation of the relict Gammaracanthus to its new conditions of existence, I assign it to the separate species G. lacustris.

Gammaracanthus from Lakes Ladoga and Onega are not distinguishable from one another at first glance. But a more careful comparison of their characters reveals slight differences. These cannot serve /p. 115/ as a basis for separating local forms, and have no importance as absolute indices but they do illustrate degrees of divergence from the original form. The greater development of the dorsal ridge in the Ladoga Gammaracanthus, the somewhat shorter gnathopods and a less convex palm on gnathopod I, indicate less difference from the original form, as compared with the Onega Gammaracanthus. The Onega Gammaracanthus, having lost almost all trace of the ridge on the first segments, and having longer gnathopods with an elongated 6th segment, has become more divergent from the marine form.

In order to show the degree of resemblance and differences between the marine, brackish and freshwater forms, I have drawn graphs of the variation in the most typical characters which distinguish the length and shape of gnathopod I and the shape of the third epimeral plate in different forms of Gammaracanthus (Fig. 3, 4 and 5). The abscissae show the size of the corresponding indices expressed in percentages, the ordinates are the number of individuals.

From inspecting these curves it is apparent that the species which differ most from each other are Gammaracanthus loricatus loricatus and G. lacustris (the curves in the lower half of the figures).

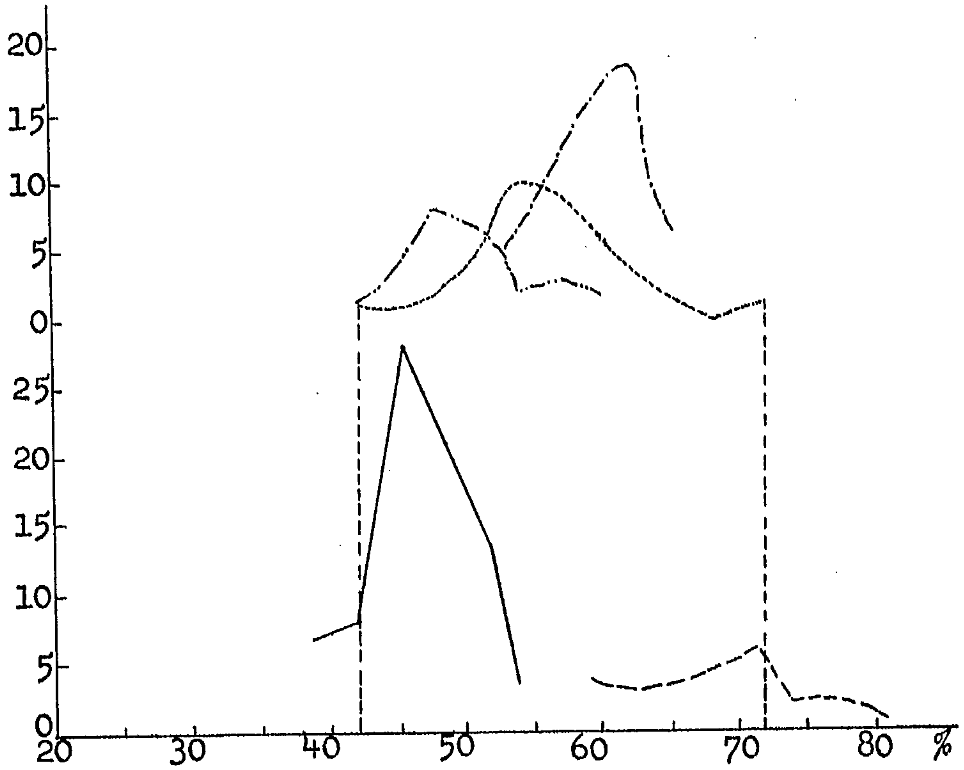


Fig. 3 Variability in length of Gnathopod I

———— G. loricatus loricatus
-··-··- G. loricatus ostiorum
········· G. loricatus aestuariorum
— — — G. loricatus caspius
- - - - - G. lacustris

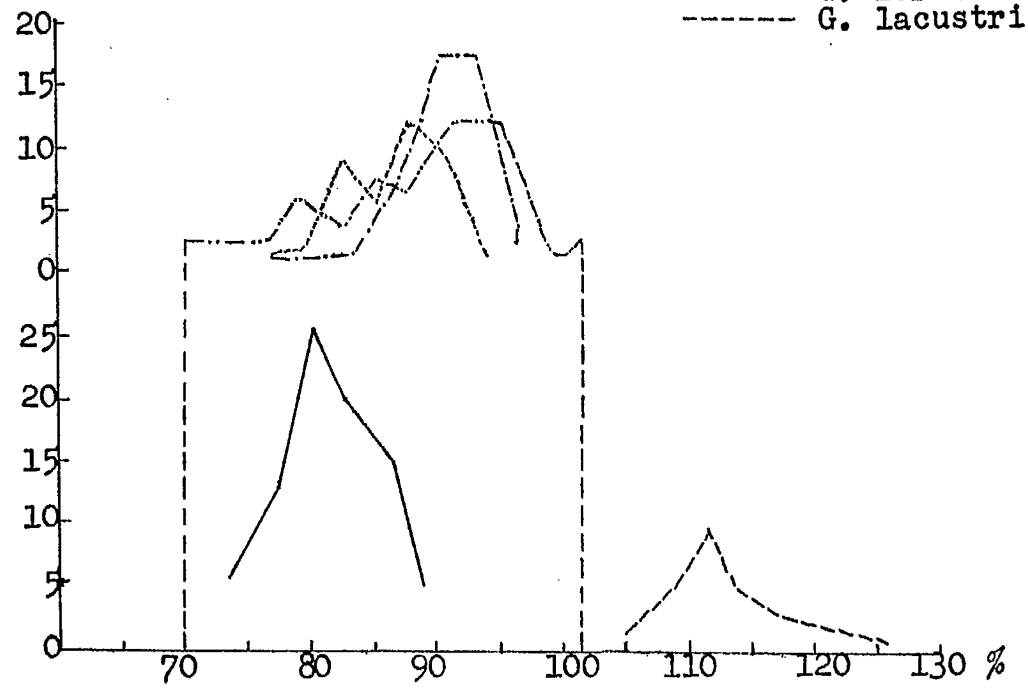


Fig. 4 Variability of measurements of 6th segment of gnathopod.

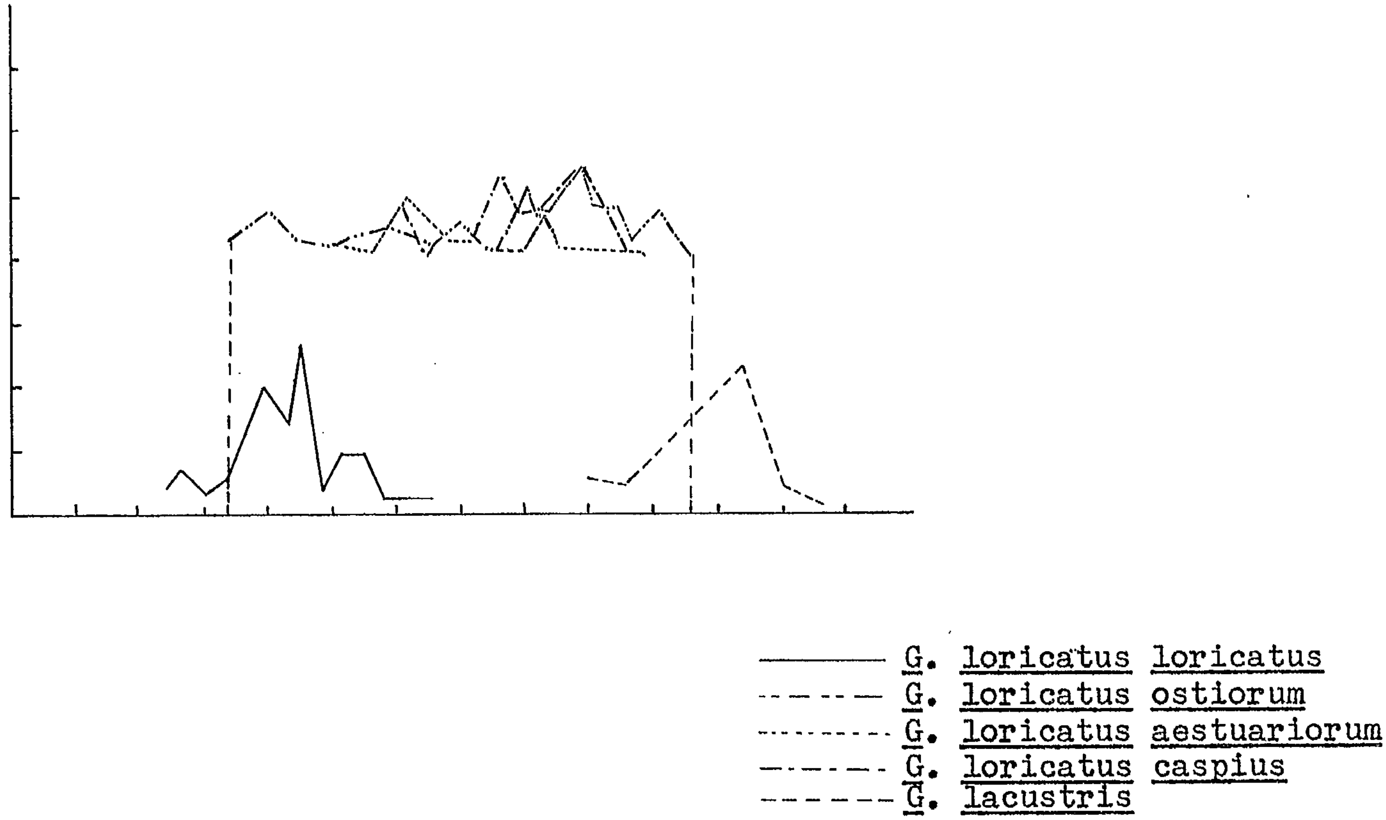


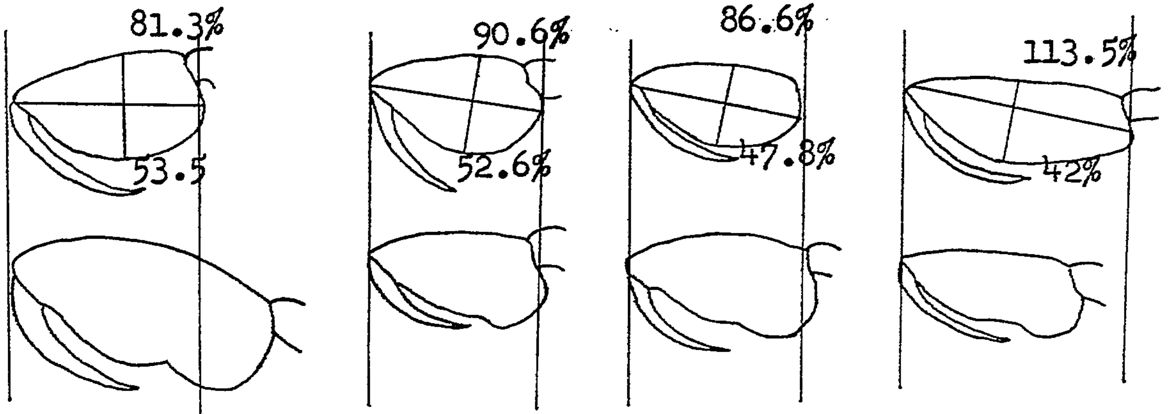
Fig. 5 Variability in size of angle of IIIrd epimeral plate.

All the brackish-water forms constitute links between these two--including estuarine, river-mouth and Caspian forms (upper half). In all the characteristics reviewed these forms occupy an intermediate position. The basic morphological changes have occurred in one /p. 116/ direction, increasing with the shift from the sea to fresh water. Obviously one of the principal factors determining the direction of change in the genus Gammaracanthus is change in salinity. The influence of this factor or, more accurately, the duration of its influence, apparently explains some morphological differences between the Ladoga and Onega Gammaracanthus. At the present time, environmental conditions in Lakes Ladoga and Onega are similar, but the length of the brackish period in the history of Lake Ladoga, which only in Littorina time became separated from the Baltic, has determined the /morphological/ appearance of the relict fauna inhabiting it, and in particular, has permitted less deviation of the Ladoga Gammaracanthus from the original marine form.

The principal morphological differences characterizing the shift from salt to fresh water can be grouped as follows: there is a decrease in body size, thinning of the carapace, smoothing of the sculpture and a decrease in the size of the rostrum associated with this. The gnathopods become lengthened, and the palms are elongated (principally on gnathopod I).

I present a figure illustrating the gnathopods of marine, Caspian, estuarine and lake forms (Fig. 6). Changes which are only suggested in estuarine Gammaracanthus become marked differences in the lake species. Changes in the epimeral plate are of this nature (Fig. 7). In the lake species there occurs a change not only /p. 119/ in the form but also in the armament of the epimeral plate: it is square in shape, and the spinules have become modified into long thin bristles /igolochki/.

Some changes in the biology of the species have also taken place, which apparently are associated not so much with the change in salinity as with the changes in thermal conditions which occurred as the result of their shift to lower latitudes. Populations of marine Gammaracanthus, which live for a large part of the year at temperatures below zero Centigrade, require 2.5-3 years to reach sexual maturity. The forms from the mouths of rivers, which experience considerable summer warming, begin to reproduce approximately one year earlier, that is, at the age of about 2 years, when their size is little more than half as great as the typical form. This speed-up of maturation occurs also in lakes and in the Caspian Sea, where



G.l. loricatus G.l. caspius G.l. aestuariorum G. lacustris

Fig. 6 Gnathopods I and II of Gammaracanthus.

G.l. loricatus G.l.caspius G.l.aestuariorum G.lacustris

Fig. 7 Angle of IIIrd Epimeral plate.

Gammaracanthus lives at temperatures above zero the year round. Changes have also taken place in the season of reproduction: in the northern seas Gammaracanthus reproduces mainly during the warm part of the year, whereas in the Caspian Sea and in certain lakes reproduction takes place also into the winter months. This prolongation of the reproductive period can be explained by the steady temperature and slight seasonal differences at the depths where Gammaracanthus lives.

Let us now turn to a consideration of the genus Pontoporeia. As a result of Lomakina's (1950) revision it is clear that the genus Pontoporeia is represented by only two species: Pontoporeia femorata Kr. and P. affinis Lindstr., which under different conditions of existence develop several forms. Up to recently it was considered that the genus Pontoporeia contained 7 species. However, the Caspian P. affinis microphthalma and the Japanese P. femorata ekmani agree closely with their respective type species, while species described by American authors from North American lakes and by Ekman from certain Swedish lakes and from the Baltic Sea represent not distinct species, but different stages of maturity of the males: P. filicornis Smith, P. kendalli Nort. and P. weltneri Ekm. are males of P. affinis, and P. sinuata Ekm. is a male of P. femorata.

As Segerstrale (1937) showed in the Gulf of Finland, and has been confirmed by the winter samples from our region which are available from Luga and Neva Bays, males of Pontoporeia during the autumn and winter period differ markedly from the females and also from males of earlier stages of development. They are characterized by very long and thin antennae which exceed the body in length, by large eyes, by the spur-shaped processes on the 4th segment of pereiopod VII, by more strongly developed pereiopods, by longer branches of the third pair of uropods, which bear dense feathered hairs, and by certain other characters.

These characteristics are found only in mature males; they are associated with the period of fertilization and are adaptations to the pelagic manner of life which characterizes the males at this time. Ripe males are found only in winter, and they die off toward spring. In addition to the Gulf of Finland, similar mature males were found by the Director of the Konchezero Station. O. N. Gordeev, in December 1949 in one of the Karelian lakes.

According to investigations made by E. F. Gurianova and continued by me, certain morphological changes associated with the freshwater environment have occurred in Pontoporeia, just as in Gammaracanthus and certain other crustaceans. One of the most variable characters in the genus Pontoporeia is the structure of the urosomal process (fork). In contrast to marine P. femorata, which has a well developed fork, P. femorata from brackish portions of northern /p. 120/ seas, from the Baltic Sea, and also from the freshened gulfs of the Sea of Japan, have a fork which to a greater or less degree is incompletely developed or altered. The processes of the fork in the form of spine-like outgrowths are retained in Caspian Pontoporeia. Complete reduction of the fork is observed in all of the semi-freshwater and freshwater P. affinis. We may conclude that reduction and alteration of the urosomal processes occurs in association with reduction of salinity, and its development in the genus Pontoporeia has taken place in the direction P. femorata to P. affinis.

The broad range of distribution of marine P. femorata, which inhabits all the arctic seas and the northern part of the Pacific Ocean, and the restricted distribution of the rest of the forms, also makes it correct to assume that P. femorata is the original species for the other forms of the genus, whether in brackish water or in fresh.

Without spending time on the marine representatives of the genus Pontoporeia, let us turn to the question of the origin of relict Pontoporeia in the lakes of northwestern USSR. Brackish-water Pontoporeia inhabit estuaries and the mouths of certain northern and far-eastern rivers (Fig. 1). Eastward from the Lena it is not encountered, and in the White Sea it appears to be absent. Outside the limits of the Soviet Union it is found along the coasts of Alaska.

Northern Pontoporeia live under conditions which vary from somewhat brackish to purely fresh water. The salinity in the places where they live does not exceed 4‰ in summer, though in winter it gets somewhat higher. It is subject to considerable fluctuations in temperature. It lives at a depth of 1.5-2 m to 10-15 m, mostly on muddy bottoms, which is in line with its method of feeding. Its disappearance with depth is apparently attributable to the increase in salinity. In the Baltic Sea (in its middle and western portions) there is a more typical brackish-water species, which lives at a salinity of 8-9‰. In the Gulfs of Bothnia and of Finland salinity conditions are like those in estuaries (2-3‰). In contrast to the northern form, Baltic Pontoporeia have a wide vertical distribution and occur from shallow water down to depths of more than 200 m. Apparently the principal factor determining the distribution of Pontoporeia is the presence of rich organic deposits on muddy bottoms.

The relict Pontoporeia affinis Lindstr. is a very widely distributed form throughout the whole extent of the presumed marine post-Quaternary straits /Connecting the Baltic and White Seas, presumably/. Pontoporeia occurs in more than 70 lakes of Fennoscandia and in Lake Imandra on the Kola peninsula; in postglacial time it also arrived in the lakes of North America.

Data on the distribution of Pontoporeia in Lake Ladoga (Ioffe, 1948) in certain lakes of Karelia (Gordeev, 1949) and in Lake Vattern (Ekman, 1915), show its adaptation to soft muddy bottoms; on muddy sand it occurs in smaller quantities, while on sand large assemblages of Pontoporeia are not found. Increased temperature does not restrict the distribution of Pontoporeia; it occurs in summer in shallow water at temperatures up to 20°C. In respect to oxygen its requirements are less strict than those of Gammaracanthus.

In its ecology as in its biology, the lake Pontoporeia do not differ essentially from the northern one.

In 1914-1920 Ekman determined that the lake P. affinis belonged to the same species as the form inhabiting brackish regions of the northern seas. However a morphological analysis which I made has shown that Pontoporeia living in the mouths of rivers and in the Baltic are not identical with the lake ones. A number of measurements were made /p. 121/ (body length, number of antennal segments and additional bristles, number of spinules on the telson and on the third pair of uropods, and others) in populations of brackish and freshwater Pontoporeia, which showed that in spite of the considerable range of individual variation, the lake Pontoporeia differed from brackish Pontoporeia to a greater degree than did the populations of brackish forms, taken from different places, among themselves. The brackish forms on the average are larger and differ from the other forms slightly in the armament of the telson and of the third pair of uropods.

The subspecies P. affinis gurjanovae, described by Birula (1937) from the Karelian gulf, has not been compared with the other forms up to the present time and has remained unknown in the literature. Now, after revision of the genus Pontoporeia and examination of collections from a large fraction of the range it occupies, we may consider that the subspecies P. affinis gurjanovae is distributed in estuaries and river mouths of the northern and far-eastern seas, and is represented by an allied form in the Baltic.

Lake *Pontoporeia*, although it is close to the original brackish-water form, is referred to the typical species *P. affinis* Lindstr. This species is characterized by smaller size and by the cone-shaped form of the telson that characterizes the larger part of its individuals; the branches of the telson are constricted toward the tip and bear one or two spines.

Certain differences are apparent in the Ladoga *Pontoporeia*. Let us consider the variability of relict *Pontoporeia* from different lakes.

Pontoporeia from Lake Ladoga, like all freshwater *Pontoporeia*, are smaller than the brackish-water ones--length of the female is 6.7 mm (av.) but in comparison with other lakes they have a greater number of spinules on the telson (up to 4; Fig. 8; 3) and of spines on the third uropod (2-6).

Pontoporeia from Lake Onega scarcely differ in size from those of Ladoga but they usually have a less deeply split telson, and correspondingly shorter branches, bearing one or rarely two spinules (Fig. 8; 4). The number of bristles arming the branches of the third pair of uropods and the third epimeral plate is less than in brackish water or Ladoga *Pontoporeia*.

Pontoporeia from other Karelian lakes. I have had collections from the following lakes: Sandal, Urozero, Dolgaia Lamba, Utrenniaia Lamba, Oster, Segozero, Kenozero, Pochezero, Terekhovo, Saiozero, Vozhimo and Vypchozero near Umba. At our disposal were the collections of the Olnets Scientific Expedition of 1918-1920, material of the Karelian Limnological Survey of 1932, the collections of V. M. Rylov from Vypchozero in 1931 and collections made in 1947 from Lakes Dolgaia Lamba and Urozero by O. N. Gordeev, Director of the Konchezero Station, who kindly made them available to me.

In size the Karelian *Pontoporeia* do not differ from those of other lakes. In the armament of the telson there are no differences from Onega *Pontoporeia*, but in its shape and in respect to the cleft between the branches of the Telson Karelian specimens deviate less from northern *Pontoporeia* than do Onega specimens (Fig. 8; 5). The variation in these features is along similar lines.

Pontoporeia from Lake Imandra are similar to the Karelian ones. The telson has branches constricted distally, it is usually more deeply cleft than in Karelian *Pontoporeia*, and its branches are more broadly separated. There are no

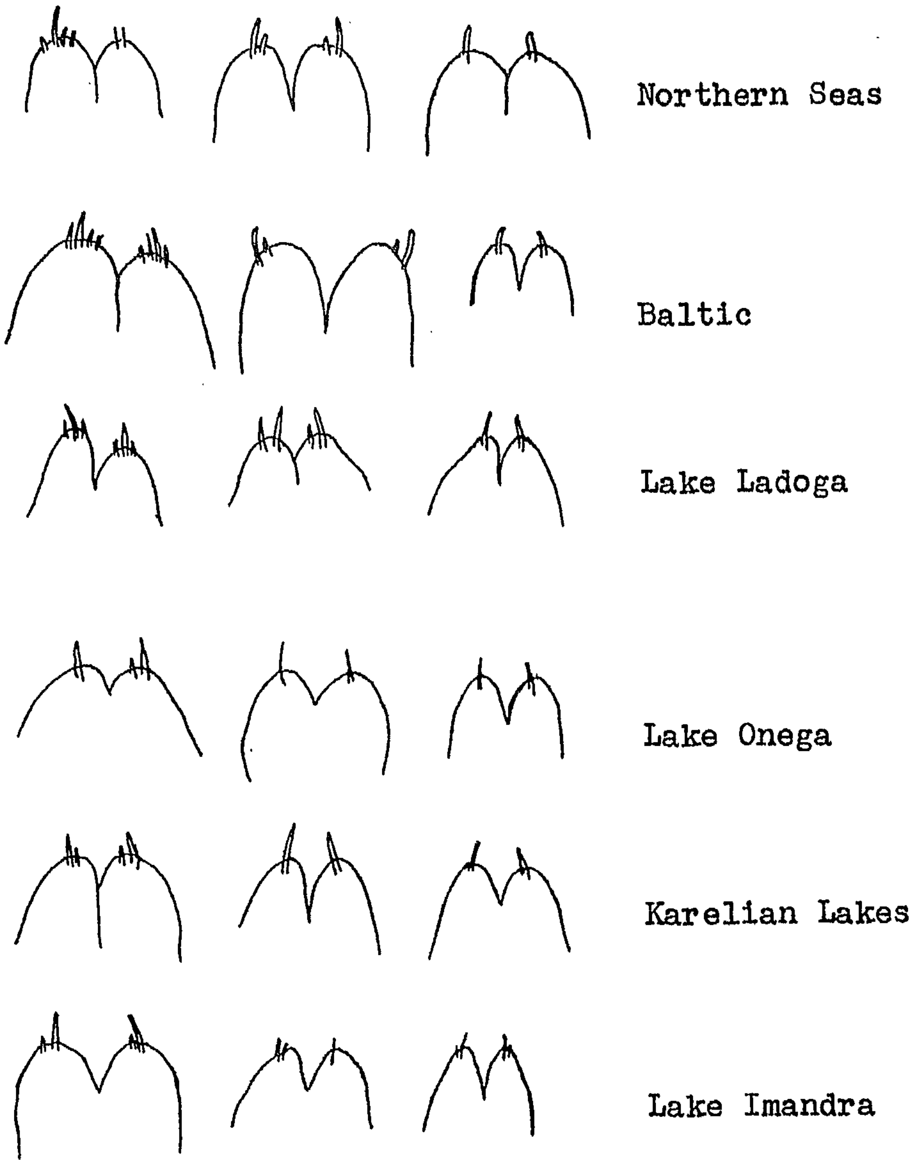


Fig. 8 Variation in armament and depth of telson cleft in *Pontoporeia affinis*.

differences from the Onega and Karelian specimens in respect to armament of the telson and third pair of uropods (Fig. 8; 6).

Comparing this review of the differences between brackish-water and freshwater P. affinis, we may affirm that all of the freshwater Pontoporeia are of smaller size than the brackish-water ones, and differ in the shape and armament of the telson and most of all /in the shape of/ the third pair /p. 123/ of uropods and the third epimeral plate. Some of these changes follow a well known pattern. Interesting relationships are observed in the character of the armament of the telson in populations of Pontoporeia from different environments. We are interested not so much in the taxonomic significance of the differences described, as in their degree of deviation from the original species. The variation in number of spines on the telson in Pontoporeia from different bodies of water is shown graphically in Fig. 9. The abscissa represents number of spines, and the ordinate number of individuals in percentage. Inspection of these curves shows that one group comprises the brackish-water forms (estuarine and Baltic) and another includes the Pontoporeia from Onega, the Karelian lakes and Lake Imandra. The Ladoga Pontoporeia occupy an intermediate position between the brackish and freshwater ones, but approach closer to the brackish forms in this respect. In addition to the number of spines on the telson, Ladoga Pontoporeia differ less from the original species than do the rest of the lake Pontoporeia in the shape of the telson and in the armament of the third pair of uropods. Stable differences between populations of relict Pontoporeia from the various lakes of Karelia, the Kola peninsula and Lake Onega have not been found.

Glacial relict amphipods and the question of a connection between the White and Baltic Seas

The question of a connection between the White Sea and the Baltic has been the subject of a voluminous literature. This question, which has been with us almost a century, has been answered in different ways at different times, depending on the completeness of geological and zoogeographical data. Moreover, even now it has not been finally decided, although during the past decade the existence of a connection between the White Sea and Lake Onega has been firmly demonstrated by the studies of Soviet geologists. Contemporary ideas concerning the post-Quaternary history of the Baltic and White Seas may be presented in the following manner (see Fig. 10).

Following the retreat of the glacier, the White Sea had its greatest extent at the end of the late-glacial epoch, about 12,000 years before our era. The brackish Onega-White Sea basin extended from the north into the

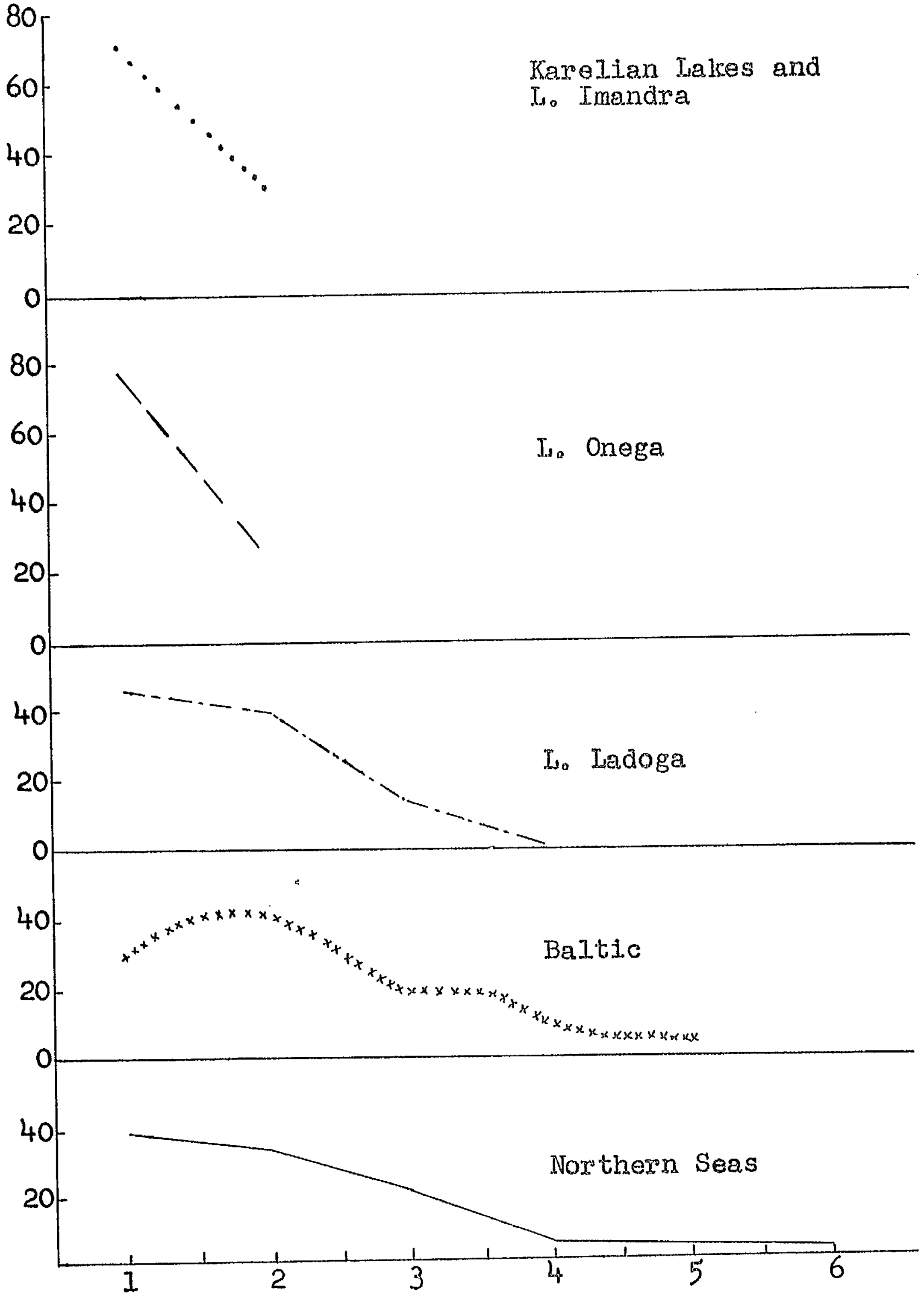


Fig. 9 The variation in number of spines on the telson of *Pontoporeia*.

Dovdozero depression, in the region of Segozero and Vygozero. The connection with Lake Onega took the form of a system of shallow narrow straits having swift currents, similar to the present-day currents in the mouth of the White Sea. The water in them was partly fresh. That time corresponded to the first stage of the Yoldia Sea in the Baltic. To the west, the Yoldia Sea connected with the ocean by way of a strait through central Sweden, and on the east it included Lake Ladoga. The connection between Lake Onega and Lake Ladoga is still in dispute at the present time. It has been suggested that it was across the northern part of the Onega-Ladoga isthmus in the depression of the Shui River, where traces of an ancient freshened strait have been found. According to another view there was no direct connection between the White Sea and the Baltic: the Onega-White Sea basin did not extend any farther than Lake Onega. The White Sea-Baltic connection that has been postulated was very short-lived (about 300 years). Then the connection between these bodies of water was destroyed, and a marine connection with Lake Onega was not subsequently restored.

The later history of Lakes Ladoga and Onega proceeded independently. Lake Ladoga has not had so long a freshwater stage as Lake Onega and the greater part of the Karelian lakes. /p. 125/ Right up to Littorina times it was connected with the Baltic Sea. As connections from the ocean into the Baltic were cut off and again reopened, stages of increased brackishness alternated with fresher stages: Yoldia SeaI--Glacial Lake II--Yoldia Sea II--Ancylus Lake--Littorina Sea. The last stage of increased salinity in Lake Ladoga lasted into Littorina time.

From work done on the origin and variability of relict amphipods, I have come to the conclusion that there are certain differences between the local forms of Gammaracanthus and Pontoporeia from Lakes Ladoga and Onega.

Ladoga Gammaracanthus deviates less than the Onega form from the original estuarine species of the northern seas, in the character of its dorsal ridge and structure of the gnathopods. The same has been shown for Pontoporeia from Lake Ladoga, which, judging by the shape and armament of the telson, occupies an intermediate position between the estuarine and Onega forms. Similar deviations were observed by L. S. Berg and V. I. Rylov in the four-spined sculpin and in Limnocalanus.

Ladoga Myoxocephalus quadricornis m. lönnbergi occupies an intermediate position along the path of change toward the freshwater form relictus.

Limnocalanus from Lake Ladoga has deviated less, morphologically, from the marine grimaldii than has the typical form <u>macrurus</u> from Segozero, Lake Onega and some other Karelian lakes.

/p. 126/ <u>Mysis</u> and <u>Mesidothea</u> also exhibit certain differences: <u>Mysis</u> of Lake Ladoga is larger than that of Onega and Segozero (Gerd, 1950). The Ladoga <u>Mesidothea</u> is almost as large as the Baltic one, being larger than the forms living in the older lakes (Gurianova, 1946; Ekman, 1919).

The closer approximation of the Ladoga relicts to the brackish-water forms, as compared with relict species from Onega and the Karelian lakes, is explained by the duration of the connection between Lake Ladoga and the Baltic Sea; it lasted more than 7,000 years. The connection of Lake Onega and the greater part of the Karelian lakes with the sea lasted a short time, and occurred more anciently.

The Ladoga relicts, being relicts of the postglacial Littorina Sea, are younger in comparison with the same forms living in Onega and certain Karelian lakes, where they are relicts of the more ancient postglacial Yoldia Sea.

As a result, the Onega and Karelian relicts, in spite of their closer geographical proximity to the original northern forms as compared with the Ladoga relicts, have freshwater characteristics more typically developed.

Differences between the local forms from Ladoga and Onega are supported by the gap in the ranges of the relict species in the region of the Ladoga-Onega isthmus (Gerd, 1950). However, in some of these lakes relict species could not live because of the prevailing hydrochemical conditions.

Thus zoogeographical information obtained during the past 10 years, and the data of the present work, tend to support the absence of direct connection between the White and the Baltic Seas during the postglacial period, rather than the existence of a direct connection between them.

The opinion, held by some geologists, that there was no strait connecting Lakes Ladoga and Onega thus finds support in the distribution of these relict species, and in the character of their intraspecific variation.

If there did exist some exchange between the fauna of lakes Ladoga and Onega in postglacial time, it was so insignificant that it did not exert appreciable influence on the formation of the relict fauna.

Within Karelia the range of the relict species (Fig. 2) mainly coincides with the limits of the postglacial Onega-White Sea basin, which had its greatest extent during the period of Yoldia Sea I. The later postglacial transgressions in the White Sea region did not have as broad an extent. Thus the glacial relicts of Karelia are indices of the highest limits of the sea level. Only a few lakes, lying eastward from Lake Onega, in which Mysis and Pontoporeia are found, and Lake Niukozero (west Karelia) where Mysis is found (Gerd, 1950) were outside the limits of this transgression. In these lakes relict crustaceans do not have true representative forms /or "distinctive forms at the present time"/.

Thus the absence of relicts in lakes of the Onega-Ladoga isthmus, together with the morphological differences between the relicts from these lakes force us to conclude that there was no connection between lakes Ladoga and Onega.

The faunas of these lakes must have arrived in them directly from two sides. In Lake Ladoga and the Finnish lakes nearby the northern marine form came apparently, mainly /p. 12/ from the west, through the Atlantic Ocean and Baltic Sea. In the lakes of Karelia and Lake Onega the few /edinichnye/ forms of marine origin must have come in from brackish estuarine portions of the Arctic Ocean.

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